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University of Kansas

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Part R
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EDITORIAL PREFACE

The aim of the *Treatise on Invertebrate Paleontology,* as originally conceived and consistently pursued, is to present the most comprehensive and authoritative, yet compact statement of knowledge concerning invertebrate fossil groups that can be formulated by collaboration of competent specialists in seeking to organize what has been learned of this subject up to the mid-point of the present century. Such work has value in providing a most useful summary of the collective results of multitudinous investigations and thus should constitute an indispensable text and reference book for all persons who wish to know about remains of invertebrate organisms preserved in rocks of the earth's crust. This applies to neozoologists as well as paleozoologists and to beginners in study of fossils as well as to thoroughly trained, long-experienced professional workers, including teachers, stratigraphical geologists, and individuals engaged in research on fossil invertebrates. The making of a reasonably complete inventory of present knowledge of invertebrate paleontology may be expected to yield needed foundation for future research and it is hoped that the *Treatise* will serve this end.

The *Treatise* is divided into parts which bear index letters, each except the initial and concluding ones being defined to include designated groups of invertebrates. The chief purpose of this arrangement is to provide for independence of the several parts as regards date of publication, because it is judged desirable to print and distribute each segment as soon as possible after it is ready for press. Pages in each part bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part.

The outline of subjects to be treated in connection with each large group of invertebrates includes (1) description of morphological features, with special reference to hard parts, (2) ontogeny, (3) classification, (4) geological distribution, (5) evolutionary trends and phylogeny, and (6) systematic description of genera, subgenera, and higher taxonomic units. In general, paleoecological aspects of study are omitted or little emphasized because comprehensive treatment of this subject is given in the *Treatise on Marine Ecology and Paleoecology* (H. S. LADD, Editor, Geological Society of America, Memoir 67, 1957), prepared under auspices of a committee of the United States National Research Council. A selected list of references is furnished in each part of the *Treatise*.

Features of style in the taxonomic portions of this work have been fixed by the Editor with aid furnished by advice from representatives of the societies which have undertaken to sponsor the *Treatise*. It is the Editor's responsibility to consult with authors and co-ordinate their work, seeing that manuscript properly incorporates features of adopted style. Especially he has been called on to formulate policies in respect to many questions of nomenclature and procedure. The subject of family and subfamily names is reviewed briefly in a following section of this preface, and features of *Treatise* style in generic descriptions are explained.

A generous grant of $35,000 has been made by the Geological Society of America for the purpose of preparing *Treatise* illustrations. Administration of expenditures has been in charge of the Editor and most of the work by photographers and artists has been done under his direction at the University of Kansas, but sizable parts of this program have also been carried forward in Washington and London.

In December, 1959, the National Science Foundation of the United States, through its Division of Biological and Medical Sciences and the Program Director for Systematic Biology, made a grant in the amount of $210,000 for the purpose of aiding the completion of yet-unpublished volumes of the *Treatise*. Payment of this sum was provided to be made in installments distributed over a five-year period, with administration of disbursements handled by the University of Kansas. An additional grant (No. GB 4544) of $102,800 was made by the National Science Foundation in January, 1966, for the two-year period 1966-67, and this was extended for the calendar year 1968 by payment of $25,700 in October, 1967. Expenditures planned are primarily for needed assistance to authors and may be arranged through approved institutions located anywhere. Important help for the Director-Editor of the *Treatise* has been made available from the grant, but no part of his stipend has come from it. Grateful acknowledgment to the Foundation is expressed on behalf of the societies sponsoring the *Treatise*, the University of Kansas, and innumerable individuals benefited by the *Treatise* project.

ZOOLOGICAL NAMES

Many questions arise in connection with zoological names, especially including those that relate to their acceptability and to alterations of some which may be allowed or demanded. Procedure in obtaining answers to these questions is guided and to a large extent governed by regulations published (1961) in the *International Code of Zoological Nomenclature* (hereinafter cited simply as the *Code*). The prime object of the *Code* is to promote stability and universality in the scientific names of animals, ensuring also that each name is distinct and unique while avoiding restrictions on freedom of taxonomic thought or action. Priority is a basic principle, but under specified conditions its application can be modified. This is all well and good, yet nomenclatural tasks confronting the zoological taxonomist are formidable. They warrant the complaint of some that zoology, including paleozoology, is the study of animals rather than of names applied to them.

Several ensuing pages are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the *Treatise*. Terminology is explained, and examples of style employed in the nomenclatural parts of systematic descriptions are given.

TAXA GROUPS

Each taxonomic unit (taxon, pl., taxa) of the animal and protistan kingdoms belongs to some one or another rank in the adopted hierarchy of classificatory divisions. In part, this hierarchy is defined by the *Code* to include a species-group of taxa, a genus-group, and a family-group. Units of lower rank than subspecies are excluded from zoological nomenclature and those higher than superfamily of the family-group are not regulated by the *Code*. It is natural and convenient to discuss nomenclatural matters in general terms first and then to consider each of the taxa groups separately. Especially important is provision that within each taxa group classificatory units are coordinate (equal in rank), whereas units of different taxa groups are not coordinate.

FORMS OF NAMES

All zoological names are divisible into groups based on their form (spelling). The first-published form (or forms) of a name is defined as original spelling (*Code*, Art. 32) and any later-published form (or forms) of the same name is designated as subsequent spelling (Art. 33). Obviously, original and subsequent spellings of a given name may or may not be identical and this affects consideration of their correctness. Further, examination of original spellings of names shows that by no means all can be distinguished as correct. Some are incorrect, and the same is true of subsequent spellings.

Original Spellings

If the first-published form of a name is consistent and unambiguous, being identical wherever it appears, the original spelling is defined as correct unless it contravenes some stipulation of the *Code* (Arts. 26-31), unless the original publication contains clear evidence of an inadvertent error, in the sense of the *Code*, or among names belonging to the family-group, unless correction of the termination or the stem of the type-genus is required. An unambiguous original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Arts. 26-31), including its provision for automatic emendations of minor sort.

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, or that represent an inadvertent error, or that are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and therefore cannot enter into homonymy or be used as replacement names. They call for correction wherever found. For example, a name originally published with a diacritic mark, apostrophe, diaeresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel is accompanied by inserting "e" after the vowel.

Subsequent Spellings

If a name classed as a subsequent spelling is identical with an original spelling, it is distinguishable as correct or incorrect on the same criteria that apply to the original spelling. This means that a subsequent spelling identical with a correct original spelling is also correct, and one identical with an incorrect original spelling is also incorrect. In the latter case, both original and subsequent spellings require correction wherever found (authorship and date of the original incorrect spelling being retained).

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name (except that such changes as altered terminations of adjectival specific names to obtain agreement in

gender with associated generic names, of family-group names to denote assigned taxonomic rank, and corrections for originally used diacritic marks, hyphens, and the like are excluded from spelling changes conceived to produce a different name).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If demonstrably intentional, the change is designated as an emendation. Emendations are divisible into those classed as justifiable and those comprising all others classed as unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication; they are junior objective synonyms of the name in its original form.

Subsequent spellings that differ in any way from original spellings, other than previously noted exceptions, and that are not classifiable as emendations are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

AVAILABLE AND UNAVAILABLE NAMES

Available Names

An available zoological name is any that conforms to all mandatory provisions of the *Code.* Such names are classifiable in groups which are usefully recognized in the *Treatise,* though not explicitly differentiated in the *Code.* They are as follows:

1) So-called *"inviolate names"* include all available names that are not subject to any sort of alteration from their originally published form. They comprise correct original spellings and commonly include correct subsequent spellings, but include no names classed as emendations. Here belong most genus-group names (including those for collective groups), some of which differ in spelling from others by only a single letter.

2) Names may be termed *"perfect names"* if, as originally published (with or without duplication by subsequent authors), they meet all mandatory requirements, needing no correction of any kind, but nevertheless are legally alterable in such ways as changing the termination (e.g., many species-group names, family-group names, suprafamilial names). This group does not include emended incorrect original spellings (e.g., *Oepikina,* replacement of *Öpikina*).

3) *"Imperfect names"* are available names that as originally published (with or without duplication by subsequent authors) contain mandatorily emendable defects. Incorrect original spellings are imperfect names. Examples of emended imperfect names are: among species-group names, *guerini* (not *Guérini*), *obrienae* (not *O'Brienae*), *terranovae* (not *terra-novae*), *nunezi* (not *Nuñezi*), *Spironema rectum* (not *Spironema recta,* because generic name is neuter, not feminine); among genus-group names, *Broeggeria* (not *Bröggeria*), *Obrienia* (not *O'Brienia*), *Maccookites* (not *McCookites*; among family-group names, Oepikidae (not Öpikidae), Spironematidae (not Spironemidae, incorrect stem), Athyrididae (not Athyridae, incorrect stem). The use of "variety" for named divisions of fossil species, according to common practice of some paleontologists, gives rise to imperfect names, which generally are emendable (*Code,* Art. 45e) by omitting this term so as to indicate the status of this taxon as a subspecies.

4) *"Vain names"* are available names consisting of unjustified intentional emendations of previously published names. The emendations are unjustified because they are not demonstrable as corrections of incorrect original spellings as defined by the *Code* (Art. 32,c). Vain names have status in nomenclature under their own authorship and date. They constitute junior objective synonyms of names in their original form. Examples are: among species-group names, *geneae* (published as replacement of original unexplained masculine, *geni,* which now is not alterable), *ohioae* (invalid change from original *ohioensis*); among genus-group names, *Graphiodactylus* (invalid change from original *Graphiadactyllis*); among family-group names, Graphiodactylidae (based on junior objective synonym having invalid vain name).

5) An important group of available zoological names can be distinguished as *"transferred names."* These comprise au-

thorized sorts of altered names in which the change depends on transfer from one taxonomic rank to another, or possibly on transfers in taxonomic assignment of subgenera, species, or subspecies. Most commonly the transfer calls for a change in termination of the name so as to comply with stipulations of the *Code* on endings of family-group taxa and agreement in gender of specific names with associated generic names. Transferred names may be derived from any of the preceding groups except the first. Examples are: among species-group names, *Spirifer ambiguus* (masc.) to *Composita ambigua* (fem.), *Neochonetes transversalis* to *N. granulifer transversalis* or vice versa; among genus-group names, *Schizoculina* to *Oculina (Schizoculina)* or vice versa; among family-group names, Orthidae to Orthinae or vice versa, or superfamily Orthacea derived from Orthidae or Orthinae; among suprafamilial taxa (not governed by the *Code*), order Orthida to suborder Orthina or vice versa. The authorship and date of transferred names are not affected by the transfers, but the author responsible for the transfer and the date of his action may appropriately be recorded in such works as the *Treatise*.

6) Improved or *"corrected names"* include both mandatory and allowable emendations of imperfect names and of suprafamilial names, which are not subject to regulation as to name form. Examples of corrected imperfect names are given with the discussion of group 3. Change from the originally published ordinal name Endoceroidea (TEICHERT, 1933) to the presently recognized Endocerida illustrates a "corrected" suprafamilial name. Group 6 names differ from those in group 5 in not being dependent on transfers in taxonomic rank or assignment, but some names are classifiable in both groups.

7) *"Substitute names"* are available names expressly proposed as replacements for invalid zoological names, such as junior homonyms. These may be classifiable also as belonging in groups 1, 2, or 3. The glossary appended to the *Code* refers to these as "new names" *(nomina nova)* but they are better designated as substitute names, since their newness is temporarv and relative. The first-published substitute name that complies with the definition here given takes precedence over any other. An example is *Marieita* LOEBLICH & TAPPAN, 1964, as substitute for *Reichelina* MARIE, 1955 (*non* ERK, 1942).

8) *"Conserved names"* include a relatively small number of species-group, genus-group, and family-group names which have come to be classed as available and valid by action of the International Commission on Zoological Nomenclature exercising its plenary powers to this end or ruling to conserve a junior synonym in place of a rejected "forgotten" name *(nomen oblitum)* (Art. 23,b). Currently, such names are entered on appropriate "Official Lists," which are published from time to time.

It is useful for convenience and brevity of distinction in recording these groups of available zoological names to employ Latin designations in the pattern of *nomen nudum* (abbr., *nom. nud.*) and others. Thus we may recognize the preceding numbered groups as follows: 1)*nomina inviolata* (sing., *nomen inviolatum*, abbr., *nom. inviol.*), 2) *nomina perfecta (nomen perfectum, nom. perf.)*, 3) *nomina imperfecta (nomen imperfectum, nom. imperf.)*, 4) *nomina vana (nomen vanum, nom. van.)*, 5) *nomina translata (nomen translatum, nom. transl.)*, 6) *nomina correcta (nomen correctum, nom. correct.)*, 7) *nomina substituta (nomen substitutum, nom. subst.)*, 8) *nomina conservata (nomen conservatum, nom. conserv.)*.

Additional to the groups differentiated above, the *Code* (Art. 17) specifies that a zoological name is not prevented from availability a) by becoming a junior synonym, for under various conditions this may be re-employed, b) for a species-group name by finding that original description of the taxon relates to more than a single taxonomic entity or to parts of animals belonging to two or more such entities, c) for species-group names by determining that it first was combined with an invalid or unavailable genus-group name, d) by being based only on part of an animal, sex of a species, ontogenetic stage, or one form of a polymorphic species, e) by being originally proposed for an organism not considered to be an animal but now so regarded, f) by incorrect original spelling which is correctable under the *Code*, g) by anonymous publication before 1951, h) by conditional proposal before 1961, i) by designation as a variety or form before 1961, j) by concluding that a name is inappropriate (Art. 18), or k) for a specific name by observing that it is tautonymous (Art. 18).

It is worthy of mention that names published for collective groups (see later discussion under "Genus-Group Names") are authorized by the *Code* (Art. 42c) for use in zoological nomenclature and therefore may be construed to be available names which are treated for convenience exactly as if they were generic names.

Unavailable Names

All zoological names which fail to comply with mandatory provisions of the *Code* are unavailable names and have no status in zoological nomenclature. None can be used under authorship and date of their original publication as a replacement name *(nom. subst.)* and none preoccupies for purposes of the Law of Homonymy. Names identical in spelling with some, but not all, unavailable names can be classed as available if and when they are published in conformance to stipulations of the *Code* and they are then assigned authorship and take date of the accepted publication. Different groups of unavailable names can be discriminated, as follows.

9) *"Naked names"* include all those that fail to satisfy provisions stipulated in Article 11 of the *Code,* which states general requirements of availability, and in addition, if published before 1931, that were unaccompanied by a description, definition, or indication (Arts. 12, 16), and if published after 1930, that lacked accompanying statement of characters purporting to serve for differentiation of the taxon, or definite bibliographic reference to such a statement, or that were not proposed expressly as replacement *(nom. subst.)* of a pre-existing available name (Art. 13,a). Examples of "naked names" are: among species-group taxa, *Valvulina mixta* Parker & Jones, 1865 (=*Cribrobulimina mixta* Cushman, 1927, available and valid); among genus-group taxa, *Orbitolinopsis* Silvestri, 1932 (=*Orbitolinopsis* Henson, 1948, available but classed as invalid junior synonym of *Orbitolina* d'Orbigny, 1850); among family-group taxa, Aequilateralidae d'Orbigny, 1846 (lacking type-genus), Hélicostègues d'Orbigny, 1826 (vernacular not latinized by later authors, Art. 11,e,iii), Poteriocrinidae Austin & Austin, 1843 (=fam. Poteriocrinoidea Austin & Austin, 1842) (neither 1843 or 1842 names complying with Art. 11,e, which states that "a family-group name must, when first published, be based on the name then valid for a contained genus," such valid name in the case of this family being *Poteriocrinites* Miller, 1821).

10) *"Denied names"* include all those that are defined by the *Code* (Art. 32,c) as incorrect original spellings. Examples are: Specific names, *nova-zelandica, mülleri, 10-brachiatus;* generic names, *M'Coyia, Størmerella, Römerina, Westgårdia;* family name, Růžičkinidae. Uncorrected "imperfect names" are "denied names" and unavailable, whereas corrected "imperfect names" are available.

11) *"Impermissible names"* include all those employed for alleged genus-group taxa other than genus and subgenus (Art. 42,a) (e.g., supraspecific divisions of subgenera), and all those published after 1930 that are unaccompanied by definite fixation of a type species (Art. 13,b). Examples of impermissible names are: *Martellispirifer* Gatinaud, 1949, and *Mirtellispirifer* Gatinaud, 1949, indicated respectively as a section and subsection of the subgenus *Cyrtospirifer; Fusarchaias* Reichel, 1949, without definitely fixed type species (=*Fusarchaias* Reichel, 1952, with *F. bermudezi* designated as type species).

12) *"Null names"* include all those that are defined by the *Code* (Art. 33,b) as incorrect subsequent spellings, which are any changes of original spelling not demonstrably intentional. Such names are found in all ranks of taxa.

13) *"Forgotten names"* are defined (Art. 23,b) as senior synonyms that have remained unused in primary zoological literature for more than 50 years. Such names are not to be used unless so directed by ICZN.

Latin designations for the discussed groups of unavailable zoological names are as follows: 9) *nomina nuda* (sing., *nomen nudum,* abbr., *nom. nud.*), 10) *nomina negata (nomen negatum, nom. neg.),* 11) *nomina vetita (nomen vetitum, nom. vet.),* 12) *nomina nulla (nomen nullum, nom.*

null.), 13) *nomina oblita (nomen oblitum, nom. oblit.).*

VALID AND INVALID NAMES

Important distinctions relate to valid and available names, on one hand, and to invalid and unavailable names, on the other. Whereas determination of availability is based entirely on objective considerations guided by Articles of the *Code,* conclusions as to validity of zoological names partly may be subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct name, generally the oldest. Obviously, no valid name can also be an unavailable name, but invalid names may include both available and unavailable names. Any name for a given taxon other than the valid name is an invalid name.

A sort of nomenclatorial no-man's-land is encountered in considering the status of some zoological names, such as *"doubtful names," "names under inquiry,"* and *"forgotten names."* Latin designations of these are *nomina dubia, nomina inquirenda,* and *nomina oblita,* respectively. Each of these groups may include both available and unavailable names, but the latter can well be ignored. Names considered to possess availability conduce to uncertainty and instability, which ordinarily can be removed only by appealed action of ICZN. Because few zoologists care to bother in seeking such remedy, the "wastebasket" names persist.

SUMMARY OF NAME GROUPS

Partly because only in such publications as the *Treatise* is special attention to groups of zoological names called for and partly because new designations are now introduced as means of recording distinctions explicitly as well as compactly, a summary may be useful. In the following tabulation valid groups of names are indicated in boldface type, whereas invalid ones are printed in italics.

DEFINITIONS OF NAME GROUPS

nomen conservatum (nom. conserv.). Name unacceptable under regulations of the *Code* which is made valid, either with original or altered spelling, through procedures specified by the *Code* or by action of ICZN exercising its plenary powers.

nomen correctum (nom. correct.). Name with intentionally altered spelling of sort required or allowable by the *Code* but not dependent on transfer from one taxonomic rank to another ("improved name"). (*See Code,* Arts. 26-b, 27, 29, 30-a-3, 31, 32-c-i, 33-a; in addition change of endings for suprafamilial taxa not regulated by the *Code.*)

nomen imperfectum (nom. imperf.). Name that as originally published (with or without subsequent identical spelling) meets all mandatory requirements of the *Code* but contains defect needing correction ("imperfect name"). (*See Code,* Arts. 26-b, 27, 29, 32-c, 33-a.)

nomen inviolatum (nom. inviol.). Name that as originally published meets all mandatory requirements of the *Code* and also is not correctable or alterable in any way ("inviolate name").

nomen negatum (nom. neg.). Name that as originally published (with or without subsequent identical spelling) constitutes invalid original spelling, and although possibly meeting all other mandatory requirements of the *Code,* cannot be used and has no separate status in nomenclature ("denied name"). It is to be corrected wherever found.

nomen nudum (nom. nud.). Name that as originally published (with or without subsequent identical spelling) fails to meet mandatory requirements of the *Code* and having no status in nomenclature, is not correctable to establish original authorship and date ("naked name").

nomen nullum (nom. null.). Name consisting of an unintentional alteration in form (spelling) of a previously published name (either available name, as *nom. inviol., nom. perf., nom. imperf., nom. transl.*; or unavailable name, as *nom. neg., nom. nud., nom. van.,* or another *nom. null.*) ("null name").

nomen oblitum (nom. oblit.). Name of senior synonym unused in primary zoological literature in more than 50 years, not to be used unless so directed by ICZN ("forgotten name").

nomen perfectum (nom. perf.). Name that as originally published meets all mandatory requirements of the *Code* and needs no correction of any kind but which nevertheless is validly alterable by change of ending ("perfect name").

nomen substitutum (nom. subst.). Replacement name published as substitute for an invalid name, such as a junior homonym (equivalent to "new name").

nomen translatum (nom. transl.). Name that is derived by valid emendation of a previously published name as result of transfer from one taxonomic rank to another within the group to which it belongs ("transferred name").

nomen vanum (nom. van.). Name consisting of an invalid intentional change in form (spelling) from a previously published name, such invalid emendation having status in nomenclature as a junior objective synonym ("vain name").

nomen vetitum (nom. vet.). Name of genus-group taxon not authorized by the *Code* or, if first published after 1930, without definitely fixed type species ("impermissible name").

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nom-*

ina inviolata or *nomina perfecta* (omitting from notice *nomina correcta* among specific names) and these are not discriminated. Names which are not accepted for one reason or another include junior homonyms, senior synonyms classifiable as *nomina negata* or *nomina nuda,* and numerous junior synonyms which include both objective *(nomina vana)* and subjective types; rejected names are classified as completely as possible.

NAME CHANGES IN RELATION TO TAXA GROUPS

SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here because it is well understood and relatively inconsequential. When the form of adjectival specific names is changed to obtain agreement with the gender of a generic name in transferring a species from one genus to another, it is never needful to label the changed name as a *nom. transl.* Likewise, transliteration of a letter accompanied by a diacritical mark in manner now called for by the *Code* (as in changing originally published *bröggeri* to *broeggeri*) or elimination of a hyphen (as in changing originally published *cornu-oryx* to *cornuoryx*) does not require *"nom. correct."* with it.

GENUS-GROUP NAMES

So rare are conditions warranting change of the originally published valid form of generic and subgeneric names that lengthy discussion may be omitted. Only elimination of diacritical marks of some names in this category seems to furnish basis for valid emendation. It is true that many changes of generic and subgeneric names have been published, but virtually all of these are either *nomina vana* or *nomina nulla.* Various names which formerly were classed as homonyms are not now, for two names that differ only by a single letter (or in original publication by presence or absence of a diacritical mark) are construed to be entirely distinct.

A category of genus-group taxa and names for them calls for special notice. This comprises assemblages of identifiable species which cannot with any certainty be placed in a known genus. Such assemblages are recognized by the *Code* as valid zoological entities called **collective groups,** with names for them "treated as generic names in the meaning of the *Code*" (Art. 42c). They differ from genera in that collective groups require no type species. Particularly for dealing with fossil assemblages of dissociated skeletal remains of echinoderms (chiefly crinoids) procedures based on definition of collective groups must find place in the *Treatise.* Names for these will uniformly be labeled as applied to collective groups with accompanying abbreviation *"coll. coll."* (for Latin *collectio collectiva,* collective group or assemblage), thus distinguishing them from names for genera. An example is *Pentagonopentagonalis* Yeltysheva, 1955 *(coll. coll.),* no type species. The species *P. bilobatus* Yeltysheva, 1960, is available as the type species of *Obuticrinus* Yeltysheva in Yeltysheva & Stukalina, 1963, in accordance with its original designation as such by these authors.

Examples in use of classificatory designations for genus-group names as previously given are the following, which also illustrate designation of type species as explained later.

Kurnatiophyllum Thompson, 1875 [**K. concentricum;* SD Gregory, 1917] [=*Kumatiophyllum* Thompson, 1876 *(nom. null.); Cymatophyllum* Thompson, 1901 *(nom. van.); Cymatiophyllum* Lang, Smith & Thomas, 1940 *(nom. van.)*].

Stichophyma Pomel, 1872 [**Manon turbinatum* Römer, 1841; SD Rauff, 1893] [=*Stychophyma* Vosmaer, 1885 *(nom. null.); Sticophyma* Moret, 1924 *(nom. null.)*].

Stratophyllum Smyth, 1933 [**S. tenue*] [=*Ethmoplax* Smyth, 1939 *(nom. van. pro Stratophyllum); Stratiphyllum* Lang, Smith & Thomas, 1940 (*nom. van. pro Stratophyllum* Smyth) (non *Stratiphyllum* Scheffen, 1933)].

Placotelia Oppliger, 1907 [**Porostoma marconi* Fromentel, 1859; SD deLaubenfels, herein] [=*Plakotelia* Oppliger, 1907 *(nom. neg.)*].

Walcottella deLaubenfels, 1955 [*nom. subst., pro Rhopalicus* Schramm, 1936 (*non* Förster, 1856)].

Cyrtograptus Carruthers, 1867 [*nom. correct.* Lapworth, 1873 (*pro Cyrtograpsus* Carruthers, (1867), *nom. conserv.* proposed Bulman, 1955 (ICZN pend.)].

Pentagonopentagonalis Yeltysheva, 1955 *(coll. coll.),* for species based on crinoid-stem parts [no type species] (ICZN pend.).

FAMILY-GROUP NAMES; USE OF *"NOM. TRANSL."*

The *Code* specifies the endings only for subfamily (-inae) and family (-idae) but all family-group taxa are defined as coordinate, signifying that for purposes of priority a name published for a taxon in any category and based on a particular type genus shall date from its original publication for a taxon in any category, retaining this priority (and authorship) when the taxon is treated as belonging to a lower or higher category. By exclusion of -inae and -idae, respectively reserved for subfamily and family, the endings of names used for tribes and superfamilies must be unspecified different letter combinations. These, if introduced subsequent to designation of a subfamily or family based on the same nominate genus, are *nomina translata,* as is also a subfamily that is elevated to family rank or a family reduced to subfamily rank. In the *Treatise* it is desirable to distinguish the valid alteration comprised in the changed ending of each transferred family-group name by the abbreviation *"nom. transl."* and record of the author and date belonging to this alteration. This is particularly important in the case of superfamilies, for it is the author who introduced this taxon that one wishes to know about rather than the author of the superfamily as defined by the *Code,* for the latter is merely the individual who first defined some lower-rank family-group taxon that contains the nominate genus of the superfamily. The publication of the author containing introduction of the superfamily *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the unit.

Examples of the use of *"nom. transl."* are the following.

Subfamily STYLININAE d'Orbigny, 1851

[*nom. transl.* EDWARDS & HAIME, 1857 (*ex* Stylinidae D'ORBIGNY, 1851)]

Superfamily ARCHAEOCTONOIDEA Petrunkevitch, 1949

[*nom. transl.* PETRUNKEVITCH, 1955 (*ex* Archaeoctonidae PETRUNKEVITCH, 1949)]

Superfamily CRIOCERATITACEAE Hyatt, 1900

[*nom. transl.* WRIGHT, 1952 (*ex* Crioceratitidae HYATT, 1900)]

FAMILY-GROUP NAMES; USE OF *"NOM. CORRECT."*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of family-group units to another but most commonly involve correction of the stem of the nominate genus; in addition, they include somewhat arbitrarily chosen modification of ending for names of tribe or superfamily. Examples of the use of *"nom. correct."* are the following.

Family STREPTELASMATIDAE Nicholson, 1889

[*nom. correct.* WEDEKIND, 1927 (*pro* Streptelasmidae NICHOLSON, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944

[*nom. correct.* PETRUNKEVITCH, 1955 (*pro* Palaeoscorpionidae LEHMANN, 1944, *nom. imperf.*)]

Family AGLASPIDIDAE Miller, 1877

[*nom. correct.* STØRMER, 1959 (*pro* Aglaspidae MILLER, 1877, *nom. imperf.*)]

Superfamily AGARICIICAE Gray, 1847

[*nom. correct.* WELLS, 1956 (*pro* Agaricioidae VAUGHAN & WELLS, 1943, *nom. transl. ex* Agariciidae GRAY, 1847)]

FAMILY-GROUP NAMES; USE OF *"NOM. CONSERV."*

It may happen that long-used family-group names are invalid under strict application of the *Code.* In order to retain the otherwise invalid name, appeal to ICZN is needful. Examples of use of *nom. conserv.* in this connection, as cited in the *Treatise,* are the following.

Family ARIETITIDAE Hyatt, 1874

[*nom. correct.* HAUG, 1885 (*pro* Arietidae HYATT, 1875) *nom. conserv.* proposed ARKELL, 1955 (ICZN pend.)]

Family STEPHANOCERATIDAE Neumayr, 1875

[*nom. correct.* FISCHER, 1882 (*pro* Stephanoceratinen NEUMAYR, 1875, invalid vernacular name), *nom. conserv.* proposed ARKELL, 1955 (ICZN pend.)]

FAMILY-GROUP NAMES; REPLACEMENTS

Family-group names are formed by adding letter combinations (prescribed for family and subfamily but not now for others) to the stem of the name belonging to genus (nominate genus) first chosen as type of the assemblage. The type genus need not be the oldest in terms of receiving its name and definition, but it must be the first-published as name-giver to a family-group taxon among all those included. Once fixed, the family-group name remains tied to the nominate genus even if its name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the *Code* (Art. 39) requires replacement of a family-group name only in the event that the nominate genus is found to be a junior homonym, and then a substitute family-group name is accepted if it is formed from the oldest available substitute name for the nominate genus. Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family group-name, but for purposes of the Law of Priority, they take the date of the replaced name. Numerous long-used family-group names are incorrect in being *nomina nuda,* since they fail to satisfy criteria of availability (Art. 11,e). These also demand replacement by valid names.

The aim of family-group nomenclature is greatest possible stability and uniformity, just as in case of other zoological names. Experience indicates the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of different workers as to the synonymy of generic names founded on different type species may not agree and opinions of the same worker may alter from time to time. The retention similarly of first-published family-group names which are found to be based on junior objective synonyms is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. To displace a much-used family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

Replacement of a family-group name may be needed if the former nominate genus is transferred to another family-group. Then the first-published name-giver of a family-group assemblage in the remnant taxon is to be recognized in forming a replacement name.

FAMILY-GROUP NAMES; AUTHORSHIP AND DATE

All family-group taxa having names based on the same type genus are attributed to the author who first published the name for any of these assemblages, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Also, every family containing differentiated subfamilies must have a nominate *(sensu stricto)* subfamily, which is based on the same type genus as that for the family, and the author and date set down for the nominate subfamily invariably are identical with those of the family, without reference to whether the author of the family or some subsequent author introduced subdivisions.

Changes in the form of family-group names of the sort constituting *nomina correcta,* as previously discussed, do not affect authorship and date of the taxon concerned, but in publications such as the *Treatise* it is desirable to record the authorship and date of the correction.

SUPRAFAMILIAL TAXA

International rules of zoological nomenclature as given in the *Code* (1961) are limited to stipulations affecting lower-rank categories (infrasubspecies to superfamily). Suprafamilial categories (suborder to phylum) are either unmentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoological Nomenclature* (1953, Arts. 59-69) proposed to adopt rules for naming suborders and higher taxonomic divisions up to and including phylum, with provision for designating a type genus for each, hopefully in such manner as not to interfere with the taxonomic freedom of workers. Procedures for applying the Law of Priority and Law of Homonymy to suprafamilial taxa were outlined and for dealing with the names for such units and their authorship, with assigned dates, when they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on zoological nomenclature which met in London during the week just before the XVth International Congress of Zoology convened in 1958 thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision which was supported by a wide majority of the participants in the Colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, if a class or order was defined by some author at a given date, using chosen morphologic characters (e.g., gills of pelecypods), this should not be allowed to freeze nomenclature, taking precedence over another later-proposed class or order distinguished by different characters (e.g., hinge-teeth of pelecypods). Even the fixing of type genera for suprafamilial taxa might have small value, if any, hindering taxonomic work rather than aiding it. At all events, no legal basis for establishing such types and for naming these taxa has yet been provided.

The considerations just stated do not prevent the Editor of the *Treatise* from making "rules" for dealing with suprafamilial groups of animals described and illustrated in this publication. At least a degree of uniform policy is thought to be needed, especially for the guidance of *Treatise*-contributing authors. This policy should accord with recognized general practice among zoologists, but where general practice is indeterminate or nonexistent our own procedure in suprafamilial nomenclature needs to be specified as clearly as possible. This pertains especially to decisions about names themselves, about citation of authors and dates, and about treatment of suprafamilial taxa which on taxonomic grounds are changed from their originally assigned rank. Accordingly, a few "rules" expressing *Treatise* policy are given here, some with examples of their application.

1) The name of any suprafamilial taxon must be a Latin or latinized uninominal noun of plural form, or treated as such, a) with a capital initial letter, b) without diacritical mark, apostrophe, diaeresis, or hyphen, and c) if component consisting of a numeral, numerical adjective, or adverb is used, this must be written in full (e.g., Stethostomata, Trionychi, Septemchitonina, Scorpiones, Subselliflorae). No uniformity in choice of ending for taxa of a given rank is demanded (e.g., orders named Gorgon*acea,* Millepor*ina,* Rugos*a,* Scleractin*ia,* Stromatopor*oidea,* Phalang*ida*).

2) Names of suprafamilial taxa may be constructed in almost any way, a) intended to indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa), b) based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina), or c) arbitrary combinations of letters, (e.g., Yuania), but none of these can be allowed to end in -idae or -inae, reserved for family-group taxa. A class or subclass (e.g., Nautiloidea), order (e.g., Nautilida), or suborder (e.g., Nautilina) named from the stem of an included genus may be presumed to have that genus (e.g., *Nautilus*) as its objective type. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda Latreille, 1803, crustaceans, and order Decapoda Leach, 1818, cephalopods; suborder Chonetoidea Muir-Wood, 1955, and genus *Chonetoidea* Jones, 1928). Worthy of notice is the classificatory and nomenclatural distinction between suprafamilial and family-group taxa which respectively are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina Ulrich & Scofield, 1897; superfamily Bellerophontacea M'Coy, 1851; family Bellerophontidae M'Coy, 1851). Family-group names and suprafamilial names are not coordinate.

3) The Laws of Priority and Homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatural stability and the avoidance of confusion these laws are widely accepted by zoologists above the family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4) Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such change(s) cannot rationally be judged to alter the authorship and date of the taxon as published originally. a) A name revised from its previously published rank is a "transferred name" *(nom. transl.),* as illustrated in the following.

Order CORYNEXOCHIDA Kobayashi, 1935

[*nom. transl.* MOORE, 1955 (*ex* suborder Corynexochida KOBAYASHI, 1935)]

b) A name revised from its previously published form merely by adoption of a different termination, without changing taxonomic rank, is an "altered name" *(nom. correct.).* Examples follow.

Order DISPARIDA Moore & Laudon, 1943

[*nom. correct.* MOORE, 1952 (*pro* order Disparata MOORE & LAUDON, 1943)]

Suborder AGNOSTINA Salter, 1864

[*nom. correct.* HARRINGTON & LEANZA, 1957 (*pro* suborder Agnostini SALTER, 1864)]

c) A suprafamilial name revised from its previously published rank with accompanying change of termination (which may or may not be intended to signalize the change of rank) is construed to be primarily a *nom. transl.* (compare change of ending for family-group taxa -idae to -inae, or vice versa, and to superfamily) but if desired it could be recorded as *nom. transl. et correct.*

Order ORTHIDA Schuchert & Cooper, 1931

[*nom. transl.* MOORE, 1952 (*ex* suborder Orthoidea SCHUCHERT & COOPER, 1931)]

5) The authorship and date of nominate subordinate and superordinate taxa among suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* TEICHERT, 1964 (*ex* superorder Endoceratoidea SHIMANSKIY & ZHURAVLEVA, 1961, *nom. transl. ex* order Endoceroidea TEICHERT, 1933)]

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* order Endoceroidea TEICHERT, 1933)]

Suborder ENDOCERINA Teichert, 1933

[*nom. correct.* TEICHERT, 1964 (*pro* suborder Endoceracea SCHINDEWOLF, 1935, *nom. transl. ex* order Endoceroidea TEICHERT, 1933)]

6) A suprafamilial taxon may or may not contain a family-group taxon or taxa having the same type genus, and if it does, the respective suprafamilial and family-group taxa may or may not be nominate (having names with the same stem). The zoological *Code* (Art. 61) affirms that "each taxon [of any rank] has, actually or potentially, its type." Taxa above the family-group level which may be designated as having the same type genus (such designations not being stipulated or recognized by any articles of the zoological *Code*) are considered to have identical authorship and date if the stem of names employed is the same (illustrated in preceding paragraph), but otherwise their authorship and date are accepted as various. Examples showing both suprafamilial and familial taxa in a group of spiders follow.

Class ARACHNIDA Lamarck, 1801

[*nom. correct.* NEWPORT, 1830 (*pro* class—not family—Arachnidae LAMARCK, 1801) (type, *Araneus* CLERCK, 1757, validated ICZN, 1948)]

Subclass CAULOGASTRA Pocock, 1893

[type, *Araneus* CLERCK, 1757]

Superorder LABELLATA Petrunkevitch, 1949

[type, *Araneus* CLERCK, 1757]

Order ARANEIDA Clerck, 1757

[*nom. correct.* DALLAS, 1864 (*pro* Araneidea BLACKWALL, 1861, *pro* Araneides LATREILLE, 1801, *pro* Aranei CLERCK, 1757, validated ICZN, 1948) (type, *Araneus* CLERCK, 1757)]

Suborder DIPNEUMONINA Latreille, 1817

[*nom. correct.* PETRUNKEVITCH, 1955 (*pro* Dipneumones LATREILLE, 1817) (type, *Araneus* CLERCK, 1757)]

Division TRIONYCHI Petrunkevitch, 1933

[type, *Araneus* CLERCK, 1757]

Superfamily ARANEOIDEA Leach, 1815

[*nom. transl.* PETRUNKEVITCH, 1955 (*ex* Araneides LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

Family ARANEIDAE Leach, 1815

[*nom. correct.* PETRUNKEVITCH, 1955 (*pro* Araneadae LEACH, 1819, *pro* Araneides LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

Subfamily ARANEINAE Leach, 1815

[*nom. transl.* SIMON, 1892 (*ex* Araneidae LEACH, 1815) (type, *Araneus* CLERCK, 1757)]

TAXONOMIC EMENDATION

Emendation has two measurably distinct aspects as regards zoological nomenclature. These embrace 1) alteration of a name itself in various ways for various reasons, as has been reviewed, and 2) alteration or taxonomic scope or concept in application of a given zoological name, whatever its hierarchical rank. The latter type of emendation primarily concerns classification and inherently is not associated with change of name, whereas the other type introduces change of name without necessary expansion, restriction, or other modification in applying the name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleozoologists, who have signified emendation of zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation *"emend."* then may accompany the name, with statement of the author and date of the emendation. On the other hand, a multitude of workers concerned with systematic zoology think that publication of *"emend."* with a zoological name is valueless, because more or less alteration of taxonomic sort is introduced whenever a subspecies, species, genus, or other assemblage of animals is incorporated under or removed from the coverage of a given zoological name. Inevitably associated with such classificatory expansions and restrictions is some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat radical revisions are put forward, generally with published statement of reasons for changing the application of a name. To erect a signpost at such points of most-significant change is worthwhile, both as aid to subsequent workers in taking account of the altered nomenclatural usage and as indication that not-to-be-overlooked discussion may be found at a particular place in the literature. Authors of contributions to the *Treatise* are encouraged to include records of all specially noteworthy emendations of this nature, using the abbreviation *"emend."* with the name to which it refers and citing the author and date of the emendation.

In Part G (Bryozoa) and Part D (Protista 3) of the *Treatise,* the abbreviation *"emend."* is employed to record various sorts of name emendations, thus conflicting with usage of *"emend."* for change in taxonomic application of a name without alteration of the name itself. This is objectionable. In Part E (Archaeocyatha, Porifera) and later-issued divisions of the *Treatise,* use of *"emend."* is restricted to its customary sense, that is, significant alteration in taxonomic scope of a name such as calls for noteworthy modifications of a diagnosis. Other means of designating emendations that relate to form of a name are introduced.

STYLE IN GENERIC DESCRIPTIONS

CITATION OF TYPE SPECIES

The name of the type species of each genus and subgenus is given next following the generic name with its accompanying author and date, or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names for this species is cited, accompanied by an asterisk (*), with notation of the author and date of original publication. An exception in this procedure is made, however, if the species was first published in the same paper and by the same author as that con- of the generic name followed by the trivial taining definition of the genus which it serves as type; in such case, the initial letter name is given without repeating the name of the author and date, for this saves needed space. Examples of these two sorts of citations are as follows:

Diplotrypa Nicholson, 1879 [**Favosites petropolitanus* Pander, 1830].

Chainodictyon Foerste, 1887 [**C. laxum*].

If the cited type species is a junior synonym of some other species, the name of this latter also is given, as follows:

Acervularia Schweigger, 1819 [**A. baltica* (=**Madrepora ananas* Linné, 1758)].

It is judged desirable to record the manner of establishing the type species, whether by original designation or by subsequent designation.

Fixation of type species originally. The type species of a genus or subgenus, according to provisions of the *Code,* may be fixed in various ways originally (that is, in the publication containing first proposal of the generic name) or it may be fixed in specified ways subsequent to the original publication. Fixation of the type species of a genus or subgenus in an original publication is stipulated by the *Code* (Art. 68) in order of precedence as 1) *original designation* (in the *Treatise* indicated as OD) when the type species is explicitly stated or (before 1931) indicated by "n. gen., n. sp." (or its equivalent) applied to a single species included in a new genus, 2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the *Treatise* by the specific name), 3) established by *monotypy* if a new genus or subgenus includes only one originally included species which is neither OD nor TYP (in the *Treatise* indicated as M), and 4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as type belonging to one of the three preceding categories (indicated in the *Treatise* as T).

Fixation of type species subsequently. The type species of many genera are not determinable from the publication in which the generic name was introduced and therefore such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus, and in the *Treatise* fixation of the type species in this manner is indicated by the letters "SD" accompanied by the name of the subsequent author (who may be the same person as the original author) and the date of publishing the subsequent designation. Some genera, as first described and named, included no mentioned species and these necessarily lack a type species until a date subsequent to that of the original publication when one or more species are assigned to such a genus. If only a single species is thus assigned, it automatically becomes the type species and in the *Treatise* this subsequent monotypy is indicated by the letters "SM." Of course, the first publication containing assignment of species to the genus which originally lacked any included species is the one concerned in fixation of the type species, and if this named two or more species as belonging to the genus but did not designate a type species, then a later "SD" designation is necessary. Examples of the use of "SD" and "SM" as employed in the *Treatise* follow.

Hexagonaria GÜRICH, 1896 [**Cyathophyllum hexagonum* GOLDFUSS, 1826; SD LANG, SMITH & THOMAS, 1940].

Muriceides STUDER, 1887 [**M. fragilis* WRIGHT & STUDER, 1889; SM WRIGHT & STUDER, 1889].

Another mode of fixing the type species of a genus that may be construed as a special sort of subsequent designation is action of the International Commission on Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters "ICZN," accompanied by the date of announced decision and (generally) reference to the appropriate numbered Opinion.

Worthy of repetition is the lack of requirement of a type species for definition of collective groups *(coll. coll.),* but when differentiated and named these are treated for convenience as genera in the meaning of the *Code* (Art. 42c).

HOMONYMS

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to 2 or more distinct taxonomic units, however, it is necessary to differentiate such homonyms, and this calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, *Callopora* HALL, 1851, introduced for Paleozoic trepostome bryozoans, is invalid because GRAY in 1848 published the same name for Cretaceous-to-Recent cheilostome bryozoans, and BASSLER in 1911 introduced the new name *Hallopora* to replace HALL's homonym. The *Treatise* style of entry is:

Hallopora BASSLER, 1911, *nom. subst.* [*pro Callopora* HALL, 1851 (*non* GRAY, 1848)].

In like manner, a needed replacement generic name may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is avoided). The requirement that an exact bibliographic reference must be given for the replaced name commonly can be met in the *Treatise* by citing a publication recorded in the list of references, using its assigned index number, as shown in the following example.

Mysterium DE LAUBENFELS, *nom. subst.* [*pro Mystrium* SCHRAMMEN, 1936 (ref. 40, p. 60) (*non* ROGER, 1862)] [**Mystrium porosum* SCHRAMMEN, 1936].

For some replaced homonyms, a footnote reference to the literature is necessary. A senior homonym is valid, and in so far as the *Treatise* is concerned, such names are handled according to whether the junior homonym belongs to the same major taxonomic division (class or phylum) as the senior homonym or to some other; in the former instance, the author and date of the junior homonym are cited as:

Diplophyllum HALL, 1851 [*non* SOSHKINA, 1939] [**D. caespitosum*].

Otherwise, no mention of the existence of a junior homonym generally is made.

Synonymic homonyms. An author sometimes publishes a generic name in two or more papers of different date, each of which indicates that the name is new. This is a bothersome source of errors for later workers who are unaware that a supposed first publication which they have in hand is not actually the original one. Although the names were separately published, they are identical and therefore definable as homonyms; at the same time they are absolute synonyms. For the guidance of all concerned, it seems desirable to record such names as synonymic homonyms and in the *Treatise* the junior one of these is indicated by the abbreviation "jr. syn. hom."

Identical family-group names not infrequently are published as new names by different authors, the author of the later-introduced name being ignorant of previous publication(s) by one or more other workers. In spite of differences in taxonomic concepts as indicated by diagnoses and grouping of genera and possibly in assigned rank, these family-group taxa are nomenclatural homonyms, based on the same type genus, and they are also synonyms. Wherever encountered, such synonymic homonyms are distinguished in the *Treatise* as in dealing with generic names.

SYNONYMS

Citation of synonyms is given next following record of the type species and if two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation "(obj.)," others being understood to constitute subjective synonyms. Examples showing *Treatise* style in listing synonyms follow.

Calapoecia Billings, 1865 [**C. anticostiensis;* SD Lindström, 1883] [=*Columnopora* Nicholson, 1874; *Houghtonia* Rominger, 1876].

Staurocyclia Haeckel, 1882 [**S. cruciata* Haeckel, 1887] [=*Coccostaurus* Haeckel, 1882 (obj.); *Phacostaurus* Haeckel, 1887 (obj.)].

A synonym which also constitutes a homonym is recorded as follows:

Lyopora Nicholson & Etheridge, 1878 [**Palaeopora? favosa* M'Coy, 1850] [=*Liopora* Lang, Smith & Thomas, 1940 (*non* Girty, 1915)].

Some junior synonyms of either objective or subjective sort may take precedence desirably over senior synonyms wherever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a generic assemblage. This requires action of ICZN using its plenary powers to set aside the unwanted name and validate the wanted one, with placement of the concerned names on appropriate official lists. In the *Treatise* citation of such a conserved generic name is given in the manner shown by the following example.

Tetragraptus Salter, 1863 [*nom. correct.* Hall, 1865 (*pro Tetragrapsus* Salter, 1863), *nom. conserv.* proposed Bulman, 1955, ICZN pend.] [**Fucoides serra* Brongniart, 1828 (=*Graptolithus bryonoides* Hall, 1858)].

ABBREVIATIONS

Abbreviations used in this division of the *Treatise* are explained in the following alphabetically arranged list.

Abbreviations

Abhandl., *Abhandlung(en)*
Abt., *Abteilung*
aff., *affinis* (related to)
Afr., Africa, -an
Ala., Alabama
Alb., Albian
Alg., Algeria
Alleghen., Alleghenian
Am., America, -n
Anis., Anisian
Ann., *Añnaes, Annales,* Annual
ant., anterior
Antarct., Antarctic
append., appendix
approx., approximately
Apt., Aptian
Aquitan., Aquitanian
Arbeit., *Arbeiten*
Arch., Archipelago, Archives, *Archivos*
Ark., Arkansas
Arg., Argentina
art., article
AsiaM., Asia Minor
Atl., Atlantic
auctt., *auctorum* (of authors)
Aus., Austria
Auvers., Auversian
Bajoc., Bajocian
Barton., Bartonian
B.C., British Columbia
Bd., *Band*
Beil., *Beilage*
Belg., *Belgique,* Belgium
Bk., Book
Boh., Bohemia
Bol., *Boletim, Boletin*
Boll., *Bolletino*
Br.I., British Isles
Brit., Britain, British
Bull., Bulletin
Burdigal., Burdigalian

C., Centigrade, Central
ca., *circa*
Calif., California
Cam., Cambrian
Can., Canada
Canad., Canadian
Carb., Carboniferous
Carib., Caribbean
Cenoman., Cenomanian
cf., *confer* (compare)
Chester., Chesteran
circ., circular
cm., centimeter
Co., County
Coblenz., Coblenzian
Coll., Collections(s)
coll. coll., *collectio collectiva* (collective group)
Colo., Colorado
commun., communication
Comun., *Comunicaciones*
Coniac., Coniacian
Conn., Connecticut
cont'd., continued
Contrib., Contribution(s)
cosmop., cosmopolitan
Couvin., Couvinian
Cret., Cretaceous
Czech., Czechoslovakia

Dan., Danian
D.C., District of Columbia
Del., Delaware
Denkschr., *Denkschrift(en)*
Denm., Denmark
Dev., Devonian
Dinant., Dinantian
Distr., District
Ditton., Dittonian
div., division
dors., dorsal

E., East
ed., editor
edit., edition
e.g., *exempli gratia* (for example)
emend., *emendatus(-a)*
Eng., England
enl., enlarged
Eoc., Eocene
Equat., Equatorial
err., *errore* (by error)
est., estimated
Est., Estonia
et al., *et alii* (and others, persons)
etc., *et cetera* (and others, objects)
Eu., Europe
ext., exterior
Extr., Extract, *Extrait*

F., Formation
fam., family
Famenn., Famennian
fasc., fascicle, *fascicule*
fig., figure(s)
Fla., Florida
Förhandl., Förhandlinger
Forhandl., Forhandlinger
Fr., *Français, -e,* France, French
Frasn., Frasnian

G.Brit., Great Britain
Gedinn., Gedinnian
gen., genus
Geol., Geological, *Geologische,* Geology, etc.
Ger., German, Germany
Givet., Givetian
Gr., Great, Group
Greenl., Greenland

Handl., *Handlingar*
Hauteriv., Hauterivian
Helvet., Helvetian
hom., homonym
Hung., *Hungarica,* Hungary

I., Isle(s)
ICZN, International Commission of Zoological Nomenclature
i.e., *id est* (that it)
Ill., Illinois
illus., illustrated, -ions
incl., inclined, including
Ind.O., Indian Ocean
int., interior
Ire., Ireland
Is., Island(s)

Jahrb., *Jahrbuch*
Jahrg., *Jahrgang*
Jan., January
Jour., Journal
jr., junior
Jur., Jurassic

Kans., Kansas
Kazakh., Kazakhstan
Kazan., Kazanian
Kimmeridg., Kimmeridgian
Ky., Kentucky

L., Lower
La., Louisiana
lat., lateral
Lattorf., Lattorfiian
Lias., Liassic
Lief., *Lieferung*
litt., letters
long., longitudinal
Ls., Limestone
Ltd., Limited
Lutet., Lutetian
LV, left valve

m., meter
M., Middle
M, monotypy
Maastricht., Maastrichtian
Madag., Madagascar
mag., magnification
Mass., Massachusetts
Medd., *Meddelanden, Meddelelser*
Meded., *Mededeelingen*
Medit., Mediterranean
Mem., Memoir(s), *Memoria, Memorie*
Mém., *Mémoire(s)*
Mex., Mexico
Mio., Miocene
Miss., Mississippi, Mississippian
mm., millimeter(s)
mod., modified
Mon., Monograph, *Monographia, Monographie*
Monatsber., *Monatsberichte*
Monatsh., *Monatshefte*
Mont., Montana
Mt., Mount, Mountain
Mts., **Mtns.**, Mountains

n., new
N., North
N.Am., North America(n)
Namur., Namurian
Nat., Natural
N.Car., North Carolina
N.Dak., North Dakota
NE., Northeast
Neocom., Neocomian
Neth., Netherlands
Nev., Nevada
N.J., New Jersey
no., number
nom. conserv., *nomen conservatum* (conserved name)
nom. correct., *nomen correctum* (corrected or intentionally altered name)
nom. dub., *nomen dubium* (doubtful name)
nom. imperf., *nomen imperfectum* (imperfect name)
nom. neg., *nomen negatum* (denied name)
nom. nov., *nomen novum* (new name)
nom. nud., *nomen nudum* (naked name)
nom. null., *nomen nullum* (null, void name)
nom. oblit., *nomen oblitum* (forgotten name)
nom. subst., *nomen substitutum* (substitute name)

nom. transl., *nomen translatum* (transferred name)
nom. van., *nomen vanum* (vain, void name)
nom. vet., *nomen vetitum* (impermissible name)
Nomencl., Nomenclature
Notizbl., Notizblatt
Nouv., *Nouvelle*
Nov., November
NW., Northwest
N.Y., New York
N.Z., New Zealand

O., Ocean
obj., objective
OD, original designation
Okla., Oklahoma
Oligo., Oligocene
Op., Opinion
Ord., Ordovician
orig., original
Ore., Oregon

p., page(s)
Pa., Pennsylvania
Pac., Pacific
Paleoc., Paleocene
Palest., Palestine
pend., pending
Penn., Pennsylvanian
Perm., Permian
Permocarb., Permocarboniferous
Permotrias., Permotriassic
pers., personal
Philip., Philippines
Philos., Philosophical
Piacenz., Piacenzian
pl., plate(s), plural
Pleist., Pleistocene
Plio., Pliocene
Pol., Poland
Port., Portugal
post., posterior
Precam., Precambrian
Proc., Proceedings
Prof., Professional
pt., part(s)
pubbl., *pubblicato*
publ., publication, published

Quart., Quarterly
Que., Quebec
Qzt., Quartzite

Rec., Recent, Record(s)
reconstr., reconstructed, -ion
Rept., Report
rev., revised
Rev., Review, *Revista, Revue*
Rhaet., Rhaetian
RV, right valve

S., Sea, South
S.Am., South America
Santon., Santonian
Scot., Scotland
SD, subsequent designation
S.Dak., South Dakota
SE., Southeast
sec., section(s)
Senon., Senonian
ser., serial, series, etc.
Sh., Shale
Sib., Siberia
Siegen., Siegenian
Sil., Silurian
sing., singular
Sitzungsber., *Sitzungsberichte*
Skrift., *Skrift(er)*
s.l., *sensu lato* (in the wide sense, broadly defined)
SM, subsequent monotypy
sp., species (spp., plural)
spec., special, specimen
Spitz., Spitzbergen
sq., square
sr., senior
s.s., *sensu stricto* (in the strict sense, narrowly defined)
Staffs., Staffordshire
Stephan., Stephanian
subfam., subfamily
subj., subjective
Subrec., Subrecent
superfam., superfamily
suppl., supplement
SW., Southwest
Swed., Sweden
Switz., Switzerland
syn., synonym

t., *tome*
T, tautonymy
Tartar., Tartarian
Tasm., Tasmania
temp., temperate
Tenn., Tennessee
Terr., Territory, -ies
Tert., Tertiary
Tex., Texas
Tithon., Tithonian
Trans., Transactions
transl., translated, -ion
transv., transverse
Trias., Triassic
trop., tropical
Turon., Turonian

U., Upper
undet., undetermined
Univ., *Universidad, Università, Universität, Université, Universitets*, University
U.S., United States
USA, United States of America
USSR, Union of Soviet Socialist Republics

v., volume(s)
var., variety
Verhandl., *Verhandlungen*
viz., *videlicet*, namely

W., West
Wash., Washington
Weald., Wealdian
Westphal., Westphalian
Wis., Wisconsin

Ypres., Ypresian
Yugosl., Yugoslavia

Z., Zone
Zeitschr., *Zeitschrift*
Zool., Zoological, *Zoologie, Zoologisch*, Zoology

REFERENCES TO LITERATURE

Each part of the *Treatise* is accompanied by a selected list of references to paleontological literature consisting primarily of recent and comprehensive monographs available but also including some older works recognized as outstanding in importance. The purpose of giving these references is to aid users of the *Treatise* in finding detailed descriptions and illustrations of morphological features of fossil groups, discussions of classifications and distribution, and especially citations of more or less voluminous literature. Generally speaking, publications listed in the *Treatise* are not original sources of information concerning taxonomic units of various rank but they tell the student where he may find them; otherwise it is necessary to turn to such aids as the *Zoological Record* or NEAVE's *Nomenclator Zoologicus.* References given in the *Treatise* are arranged alphabetically by authors and accompanied by index numbers which serve the purpose of permitting citation most concisely in various parts of the text; these citations of listed papers are enclosed invariably in parentheses and, except in Part C, are distinguishable from dates because the index numbers comprise no more than 3 digits. The systematic descriptions given in Part C are accompanied by a reference list containing more than 2,000 entries; the index numbers for them are marked by an asterisk.

The following is a statement of the full names of serial publications which are cited in abbreviated form in the *Treatise* lists of references. The information thus provided should be useful in library research work. The list is alphabetized according to the serial titles which were employed at the time of original publication. Those following it in brackets are those under which the publication may be found currently in the *Union List of Serials,* the United States Library of Congress listing, and most library card catalogues. The names of serials published in Cyrillic are transliterated; in the reference lists these titles, which may be abbreviated, are accompanied by transliterated authors' names and titles, with English translation of the title. The place of publication is added (if not included in the serial title).

The method of transliterating Cyrillic letters that is adopted as "official" in the *Treatise* is the so-called Anglo-American method given by the Geographical Society of London. It follows that names of some Russian authors in transliterated form derived in this way differ from other forms, possibly including one used by the author himself. In *Treatise* reference lists the alternative (unaccepted) form is given enclosed by square brackets (e.g., Chernyshev [Tschernyschew], T.N.).

List of Serial Publications

Academia Brasileira de Ciências, Anñaes. Rio de Janeiro.

Académie Roumaine, Bulletin de la Section Scientifique. Bucharest.

Académie Royale de Belgique, Classe des Sciences, Bulletins, Mémoires. Bruxelles.

Académie des Sciences de Paris, Comptes Rendus, Mémoires. Paris.

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Academy of Natural Sciences of Philadelphia, Journals; Proceedings.

[R.] Accademia Pontaniana, Atti. Napoli.

Acta Adriatica Instituti Biologico-oceanographici. Split, Yugoslavia.

Acta Geologica Hispanica. Barcelona.

Acta Litterarum ac Scientiarum R. Universitatis Hungarica Francisco-Josephina, Sectio Scientiarum Naturalium. Szeged.

Acta Zoologica. Stockholm.

Akademie der Wissenschaften und der Literatur zu Mainz, mathematisch - naturwissenschaftlichen Klasse, Abhandlungen. Wiesbaden.

Akademie der Wissenschaften zu München, mathematische-physikalische Klasse, Sitzungsberichte; Denkschriften.

[K.] Akademie der Wissenschaften St. Petersburg [Akademiya Nauk SSSR, Leningrad.]

[K.] Akademie der Wissenschaften zu Wien, mathematische-naturwissenschaftliche Klasse, Denkschriften; Sitzungberichte.

Akademiya Nauk SSSR, Doklady. Moskva.

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Annales des Mines (Bureau de Recherches Géologiques, Géophysiques et Minières). Paris.

Annales de Paléontologie. Paris.
Annals of Philosophy. London.
Annales des Sciences Géologiques. Paris.
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Annals and Magazine of Natural History. London.
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Arbeiten der Nord-Kaukasischen Assoziation Wissenschaftlicher Institute. Rostov.
Arbeiten aus den Zoologischen Instituten Zootomischen Würzburg.
Arbeiten aus den Zoologischen Instituten der Universität Wien und der Zoologische Station in Triest. Wien.
Archiv für Hydrobiologie (und Planktonkunde). Stuttgart.
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Archiv für Naturgeschichte. Berlin, Leipzig.
Archiv Naturwissenschaftliche Landesdurchforschung von Böhmen. Praha.
Archives de Zoologie, Expérimentale at Générale, Paris.
Arkiv för Zoologi. Uppsala.
Australian Museum, Memoirs; Records. Sydney.
[K.] Bayerische Akademie der Wissenschaften, mathematisch-physikalische Klasse, Abhandlungen; Sitzungsberichte. München.
Bayerische Staatssammlung für Paläontologie und Historische, Geologie, Mitteilungen. München.
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Biological Reviews (see Cambridge Philosophical Society). Cambridge, Eng.
Bollettino di Zoologia, pubblicato dall' Unione Zoologica Italiana. Napoli.
Boston Society of Natural History, Memoirs; Occasional Papers; Proceedings.
Brazil, Divisão de Geologia e Mineralogia, Notas Preliminares e Estudos (Departamento Nacional da Produção Mineral). Rio de Janeiro.
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Bulletin of Zoological Nomenclature. London.
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California, University of, Publications in Zoology. Berkeley.
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Cambridge Philosophical Society, Biological Reviews and Biological Proceedings. Cambridge, Eng.
Canada, Geological Survey of, Department of Mines and Resources, Mines and Geology Branch, Bulletins; Memoirs; Museum Bulletins; Victoria Memorial Museum Bulletins. Ottawa.
Canadian Journal of Research. Ottawa.
Canadian Naturalist and Geologist. Montreal, Canada.
Carnegie Institution of Washington, Papers; Publications. Washington, D.C.
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[K.K.] Geologische Bundesanstalt Wien, Abhandlungen; Jahrbuch; Verhandlungen.
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Journal of Morphology. Philadelphia.
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Museo Libico Storia Naturale, Annali. Tripoli.

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[K.] Norske Videnskabernes Selskabs Matematisk-naturvidenskapelig Klasse, Forhandlinger; Skrifter. Trondheim, Oslo.

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SOURCES OF ILLUSTRATIONS

At the end of figure captions an index number is given to supply record of the author of illustrations used in the *Treatise,* reference being made either (1) to publications cited in reference lists or (2) to the names of authors with or without indication of individual publications concerned. Previously unpublished illustrations are marked by the letter "n" (signifying "new") with the name of the author.

STRATIGRAPHIC DIVISIONS

Classification of rocks forming the geologic column as commonly cited in the *Treatise* in terms of units defined by concepts of time is reasonably uniform and firm throughout most of the world as regards major divisions (e.g., series, systems, and rocks representing eras) but it is variable and unfirm as regards smaller divisions (e.g., substages, stages, and subseries), which are provincial in application. Users of the *Treatise* have suggested the desirability of publishing reference lists showing the stratigraphic arrangement of at least the most commonly cited divisions. Accordingly, a tabulation of European and North American units, which broadly is applicable also to other continents, is given here.

Generally Recognized Divisions of Geologic Column

EUROPE

ROCKS OF CENOZOIC ERA
  NEOGENE SYSTEM[1]
    Pleistocene Series (including Recent)
    Pliocene Series
    Miocene Series
  PALEOGENE SYSTEM
    Oligocene Series
    Eocene Series
    Paleocene Series

ROCKS OF MESOZOIC ERA
  CRETACEOUS SYSTEM
    Upper Cretaceous Series
      Maastrichtian Stage[2]
      Campanian Stage[2]
      Santonian Stage[2]
      Coniacian Stage[2]

NORTH AMERICA

ROCKS OF CENOZOIC ERA
  NEOGENE SYSTEM[1]
    Pleistocene Series (including Recent)
    Pliocene Series
    Miocene Series
  PALEOGENE SYSTEM
    Oligocene Series
    Eocene Series
    Paleocene Series

ROCKS OF MESOZOIC ERA
  CRETACEOUS SYSTEM
    Gulfian Series (Upper Cretaceous)
      Navarroan Stage
      Tayloran Stage
      Austinian Stage

Turonian Stage	
Cenomanian Stage	Woodbinian (Tuscaloosan) Stage
	Comanchean Series (Lower Cretaceous)
	Washitan Stage
Lower Cretaceous Series	
Albian Stage	Fredericksburgian Stage
	Trinitian Stage
Aptian Stage	
	Coahuilan Series (Lower Cretaceous)
Barremian Stage[3]	Nuevoleonian Stage
Hauterivian Stage[3]	
Valanginian Stage[3]	Durangoan Stage
Berriasian Stage[3]	
JURASSIC SYSTEM	**JURASSIC SYSTEM**
Upper Jurassic Series	**Upper Jurassic Series**
Portlandian Stage[4]	Portlandian Stage
Kimmeridgian Stage	Kimmeridgian Stage
Oxfordian Stage	Oxfordian Stage
Middle Jurassic Series	**Middle Jurassic Series**
Callovian Stage (or Upper Jurassic)	Callovian Stage (or Upper Jurassic)
Bajocian Stage	Bathonian Stage
Bathonian Stage	Bajocian Stage
Lower Jurassic Series (Liassic)	**Lower Jurassic Series (Liassic)**
Toarcian Stage	Toarcian Stage
Pliensbachian Stage	Pliensbachian Stage
Sinemurian Stage	Sinemurian Stage
Hettangian Stage	Hettangian Stage
TRIASSIC SYSTEM	**TRIASSIC SYSTEM**
Upper Triassic Series	**Upper Triassic Series**
Rhaetian Stage[5]	(Not recognized)
Norian Stage	Norian Stage
Carnian Stage	Carnian Stage
Middle Triassic Series	**Middle Triassic Series**
Ladinian Stage	Ladinian Stage
Anisian Stage (Virglorian)	Anisian Stage
Lower Triassic Series	**Lower Triassic Series**
Scythian Stage (Werfenian)	Scythian Stage
ROCKS OF PALEOZOIC ERA	**ROCKS OF PALEOZOIC ERA**
PERMIAN SYSTEM	**PERMIAN SYSTEM**
Upper Permian Series	**Upper Permian Series**
Tartarian Stage[6]	Ochoan Stage
Kazanian Stage [7]	Guadalupian Stage
Kungurian Stage	
Lower Permian Series	**Lower Permian Series**
Artinskian Stage[8]	Leonardian Stage
Sakmarian Stage	Wolfcampian Stage
Asselian Stage	
CARBONIFEROUS SYSTEM	**PENNSYLVANIAN SYSTEM**
Upper Carboniferous Series	**Kawvian Series (Upper Pennsylvanian)**
Stephanian Stage	Virgilian Stage
	Missourian Stage

Westphalian Stage	**Oklan Series (Middle Pennsylvanian)**
	Desmoinesian Stage
	Bendian Stage
	Ardian Series (Lower Pennsylvanian)
	Morrowan Stage
	MISSISSIPPIAN SYSTEM
Namurian Stage	**Tennesseean Series (Upper Mississippian)**
	Chesteran Stage
Lower Carboniferous Series	
Visean Stage	Meramecian Stage
	Waverlyan Series (Lower Mississippian)
Tournaisian Stage	Osagian Stage
Strunian Stage	Kinderhookian Stage
DEVONIAN SYSTEM	DEVONIAN SYSTEM
Upper Devonian Series	**Chautauquan Series (Upper Devonian)**
Famennian Stage	Conewangoan Stage
	Cassadagan Stage
Frasnian Stage	**Senecan Series (Upper Devonian)**
	Chemungian Stage
	Fingerlakesian Stage
Middle Devonian Series	**Erian Series (Middle Devonian)**
Givetian Stage	Taghanican Stage
	Tioughniogan Stage
Couvinian Stage	Cazenovian Stage
Lower Devonian Series	**Ulsterian Series (Lower Devonian)**
Emsian Stage	Onesquethawan Stage
Siegenian Stage	Deerparkian Stage
Gedinnian Stage	Helderbergian Stage
SILURIAN SYSTEM	SILURIAN SYSTEM
Ludlow Stage	**Cayugan Series** Includes age equivalents of middle and upper Ludlow (in New York)
Wenlock Stage	**Niagaran Series** Includes age equivalents of upper Llandovery, Wenlock, and lower Ludlow (in New York)
Landovery Stage	**Medinan Series** Includes age equivalents of lower and middle Llandovery (in New York)
ORDOVICIAN SYSTEM	ORDOVICIAN SYSTEM
	Cincinnatian Series (Upper Ordovician)
	Richmondian Stage
Ashgill Stage	Maysvillian Stage
	Edenian Stage
Caradoc Stage	**Champlainian Series (Middle Ordovician)**
	Mohawkian Stage

	Trentonian Substage
	Blackriveran Substage
Llandeilo Stage	Chazyan Stage
Llanvirn Stage	
Arenig Stage	**Canadian Series (Lower Ordovician)**
Tremadoc Stage[9]	
CAMBRIAN SYSTEM	**CAMBRIAN SYSTEM**
Upper Cambrian Series	**Croixian Series (Upper Cambrian)**
	Trempealeauan Stage
	Franconian Stage
	Dresbachian Stage
Middle Cambrian Series	**Albertan Series (Middle Cambrian)**
Lower Cambrian Series	**Waucoban Series (Lower Cambrian)**
EOCAMBRIAN SYSTEM	**EOCAMBRIAN SYSTEM**
ROCKS OF PRECAMBRIAN AGE	**ROCKS OF PRECAMBRIAN AGE**

RAYMOND C. MOORE

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[1] Considered by some to exclude post-Pliocene deposits.

[2] Classed as division of Senonian Subseries.

[3] Classed as division of Neocomian Subseries.

[4] Includes Purbeckian deposits.

[5] Interpreted as lowermost Jurassic in some areas.

[6] Includes some Lower Triassic and equivalent to upper Thuringian (Zechstein) deposits.

[7] Equivalent to lower Thuringian (Zechstein) deposits.

[8] Equivalent to upper Autunian and part of Rotliegend deposits.

[9] Classed as uppermost Cambrian by some geologists.

PART R

ARTHROPODA 4

CRUSTACEA (EXCEPT OSTRACODA)

MYRIAPODA—HEXAPODA

By H. K. Brooks, F. M. Carpenter, M. F. Glaessner, Gerhard Hahn, R. R. Hessler, R. L. Hoffman, L. B. Holthuis, R. B. Manning, S. M. Manton, Lavon McCormick, R. C. Moore, W. A. Newman, A. R. Palmer, W. D. I. Rolfe, Paul Tasch, †T. H. Withers, and V. A. Zullo

VOLUME 1

CONTENTS

[Volume 1, p. i-xxxvi, *R*1-*R*398; Volume 2, p. *R*399-*R*651; Volume 3 (to follow)]

INTRODUCTION

By Raymond C. Moore
[The University of Kansas]

This unit of the *Treatise* to which the letter R was assigned in original plans has been exceptionally slow in taking form and more difficult that any other yet published to organize. For example, the first major sections of systematic descriptions and illustrations were received from O. W. Tiegs and T. H. Withers in 1954. After editorial work had been approved by the authors, the materials were placed in files as Part R "nest eggs." Prior to 1960, F. M. Carpenter, M. F. Glaessner, and Paul Tasch had accepted Part R assignments, and in the period 1961-65 the list of contributing authors was enlarged to include H. K. Brooks, Isabella Gordon, Gerhard Hahn, R. R. Hessler, R. L. Hoffman, L. B. Holthuis, R. B. Manning, S. M. Manton, W. A. Newman, A. R. Palmer, W. D. I. Rolfe, and V. A. Zullo.

Completed first drafts of sections, varying considerably in length, or revisions of previously submitted typescripts and figures were received by me as follows: 1956—Tasch; 1960—Tasch; 1961—Hessler, Rolfe, Tasch; 1962—Carpenter, Hessler, Manton, Palmer, Rolfe, Tasch; 1963—Carpenter, Glaessner, Hessler, Holthuis & Manning, Manton, Rolfe, Tasch; 1964—Brooks, Carpenter, Glaessner, Hessler, Rolfe; 1965 — Carpenter, Glaessner, Hahn, Hoffman, Holthuis & Manning, Palmer, Rolfe; 1966—Carpenter, Glaessner, Manton, Newman & Zullo, Rolfe; 1967 — Carpenter, Hahn, Newman & Zullo.

With expectation that unfinished portions of Part R would be ready for the press within a few months at most, type-setting was begun in June, 1965, and continued steadily through November of that year. Then, owing to the unavailability of awaited typescripts, it was necessary to halt press work until June, 1967, only to shut down again in less than three weeks' time. The final stage of type-setting was delayed until February, 1968. This record amply demonstrates the arduousness of coordinating the labors of numerous specialists, each of whom is needed to round out a taxonomic "package" in manner aimed at maximum comprehensiveness and authoritativeness. I am very grateful to all of the *Treatise* contributors who have conscientiously worked to meet our objectives by able completion of their accepted assignments, but from the viewpoint of all concerned—participating authors and an anticipated host of persons who will be benefitted by use of this and other *Treatise* units—I deprecate the slowness in accomplishing publication.

I call special attention to the two chapters of general scope next following this short introduction. They have been contributed by Sidnie M. Manton in response to invitations extended by me, that on classification of Arthropoda after she and other *Treatise* authors concerned with arthropodan groups had criticized (1965, *in litt.*) the so-called subphylum assemblage named Mandibulata or Antennata as quite outmoded and therefore unacceptable in classification. The breadth and thoroughness of Dr. Manton's many years of investigations on most important morphological features of virtually all main divisions of living arthropods, coupled with studies of their anatomy, physiology, interrelationships, and evidence bearing on their evolutionary changes and phylogeny, especially qualify her for a comprehensive, appraisal of the phylum—granting that groups known only as fossils have received little first-hand attention from her. For these, judicious dependence on the work of paleontologists has been requisite.

Manton's discussion of the problems of arthropodan major classification in the light of multitudinous factual observations which have been accumulated points to the need for emending the outline of main divisions of the Arthropoda given in *Treatise* Part O (1959, p. *O*15-*O*16). This is now given in her chapter (p. *R*13) and adopted as a guide for arranging most of the sections of systematic descriptions.

Comparison of the chapter on *Introduction to Classification of Arthropoda* with the next one on *Evolution and Affinities of Onychophora, Myriapoda, Hexapoda, and Crustacea,* written earlier, shows how one complements the other in stressing important common features of main groups as contrasted with equally important differences.

The chapter on *General Feaures of Crustacea* by MOORE & MCCORMICK is substitute for one which ISABELLA GORDON had agreed and expected to prepare, but which cirsumstances prevented her from submitting. Invitations to other crustacean specialists were declined. Such a chapter by GORDON may yet be offered for later *Treatise* publication in a supplement or revision of Part R.

Authorship of systematic descriptions of crustaceans, myriapods, and insects is indicated with each division. Mostly it was arranged several years ago. On the basis of counsel received from *Treatise* advisers and on my own responsibility, the contributions received in 1954 from WITHERS on Cirripedia and from TIEGS on Myriapoda have been considerably revised by others, including changes of illustrations. Late submissions (June, 1966) were valuable self-originated sections by ROLFE on Arthropleurida and Arthropoda Incertae Sedis and by HAHN on Bostrichopodida.

A departure from previous practice in publication of *Treatise* units is made in issuing two volumes of Part R, here given, in advance of a third one containing text and illustrations for fossil insects. This is a comparatively large section which is not yet ready for the press. The index for Part R is divided accordingly.

INTRODUCTION TO CLASSIFICATION OF ARTHROPODA

By S. M. MANTON

[British Museum (Natural History), London]

[Chapter submitted January, 1966]

Different parts of this *Treatise* refer to a variety of classifications, either of the Arthropoda as a whole, or of parts of this vast assemblage of animals. Fossil remains do not demonstrate either the origin of the Arthropoda or of its classes. When the fossil record provides no decisive evidence of interrelationships, classifications can be, at best, only working hypotheses. But such hypotheses must conform to the ever-growing body of evidence relating to past history of living animals which stems from all available sources. Classifications should be based upon facts and not upon speculations. The practical necessities of taxonomic and other work makes subdivision or classification of arthropods an imperative requirement. It is not surprising that some of the imperfectly known fossil arthropodan remains cannot be referred with certainty to any modern group and others appear to be decidedly unlike animals in any extant class.

A classification of arthropods should be based upon phylogeny, but in the absence of sufficient fossil evidence, taxonomic groupings must rest largely upon the comparative anatomy of living species, on embryology, and life histories, and probably to some extent also on biochemistry and biophysics. The available evidence concerning the extinct arthropods is more limited and much less detailed. A very large measure of convergence is shown by the morphology and physiology of living arthropods whose past histories, it is inferred, must have been fundamentally different. An appreciation of such convergences is of immense importance in the elucidation of arthropodan relationships. No simple scheme of classification which ignores convergence can provide a basis for the reconstruction of past history and relationships of arthropods. A review was given by Tiegs & Manton (25) of theories of arthropod phylogeny and classification which had been advanced prior to 1958. In recent years important new factual evidence concerning these matters has been obtained. This introduction for *Treatise* Part R is intended to be a brief summary of the present position of arthropod classification based upon older considerations and newer factual evidence.

Abundant evidence concerning the evolution and relationships of living arthropods, at first unexpected, has been provided by an increasing body of studies of functional anatomy and of the habits of life with which the morphology is intimately associated, a line of work not easy to apply to fossil materials. Vast arrays of complex anatomy, such as those shown by crustacean limbs or the trunk skeletomusculature of myriapods, takes on a new and ordered meaning. An understanding of the manner of working of different morphological systems, together with the circumstances under which they work, lead to two advances in our appreciation of arthropodan evolution. Firstly, the different morphologies which characterize many of the larger groups of living arthropods have been shown to be related to habits of life which are not adaptations to particular environmental niches. Evolutionary advances in morphology and physiology can enable an animal to live better both in the same and in a variety of environmental circumstances. The end terms of evolution within a particular order or other category, on the contrary, often form adaptive radiations to particular niches, and these adaptations, superimposed upon the more basic characters of each group, have less far-reaching evolutionary significance in that they do not give rise to new forms of evolutionary significance (p. *R*21). Secondly, when the functional advantages, or the mode of action, of various morphological set-ups are known, any postulated evolution from one to another which entails a functionally impossible intermediate or one which negates the functional advantages already achieved, at once becomes apparent. The factual matters brought forward by this type of work are of basic and essential importance in any attempt to arrive at a natural classification of the Arthropoda. These lines of work are as yet in their infancy, and for their successful development the comparative approach is essential. Detailed study of one animal alone gives few clues, but a knowledge of the functional assets of animals showing very different and closely similar habits at once becomes revealing as to the possible manners in which their evolution can have proceeded.

The Arthropoda have in common a metamerically segmented body with a differentiated anterior end which forms either a localized head or the anterior part of a cephalothorax or prosoma, according to the class. They possess serially repeated limbs along a trunk; an ostiate heart and a hemocoelic body cavity; and a cuticle, which even when thin and flexible, is constructed in a definite arthropod manner. Growth is intermittent, owing to periodic ecdysis of the cuticle. The features which link the arthropods together are thus few in number. The conspicuous sclerites on the body and limbs of most arthropods are not necessarily basic arthropodan features (see below). Many arthropods have a cuticle which is little sclerotized and bends easily. Many sclerites are not associated in any way with muscles and perform protective and other functions (1, 15). Muscles insert upon subcutaneous sheets of connective tissue, on basement membranes and on internal tendon systems far removed from the body surface. Muscles frequently pull on arthropodial membranes (13, 14, 15). Muscles are attached to sclerites only indirectly by tonofibrils traversing ectodermal cells from the subectodermal connective tissues. Extreme sclerotization, coupled with the formation of elaborate joints, lever-like apodemes, etc., represent arthropodan advances which are far less basic than the hemocoel, although found among the earliest recognizable arthropodan remains.

The head end is formed ontogenetically in a manner unlike that in other phyla. Ventrolaterally the anterior segmental mesodermal somites (which form most of the internal tissues of the adult) and the corresponding ectodermal areas, many of which bear limb rudiments, grow forward relative to the mouth. The oral aperture with the unsegmented rudiment forming the upper lip (labrum), shifts backwards, as shown diagrammatically in Figure A. Some of the anterior limb rudiments are thereby carried to a preoral level, while the mouth becomes subterminal and ventrally directed, unless other specializations ensue. A preoral cavity is frequently formed by these shifts, and into it the mouth parts crush, grind, or bite the food. The mouth does not shift out of one segment and into another (23; 25, p. 269). It is the lateral parts of the segments which bend forward around the mouth. The anterior segments are not even roughly cylindrical in shape, as are those of the trunk. The dorsal tissue of much of the head is formed by unsegmented acron, tissue which has persisted from the embryonic or developmental stage previous to that in which segmentation is initiated (Fig. A). The figure by WEBER, reproduced in the *Treatise* Part O (Fig. 6) is a purely theoretical concept. The varying amounts of yolk in arthropodan eggs determines the early distance (large in Fig. A) between the unsegmented dorsal blastoderm and the ventral segment rudiments at the future anterior end of the body. Comparative embryology of the more primitive members of the larger arthropod groups does not substantiate WEBER's theoretical concept, accepted by STØRMER in the *Treatise*.

The limbs which become preoral in position tend to become sensory or trophic, in whole or in part, and perform other functions according to the group. Limbs just behind the mouth are usually specialized for feeding to some extent, and the unsegmented acron provides eyes of various kinds.[1]

The major classes of arthropods each have characteristic head structure which alone is sufficient to separate one class from another. The differentiating characters comprise: 1) number of segments which have shifted to a preoral position, one in the Onychophora, two in the Chelicerata, and three in Crustacea, Myriapoda, and Hexapoda; 2) number and nature of preoral limbs—prehensile chelicerae characterize the Chelicerata (Merostomata, Arachnida), two pairs of antennae occur in Crustacea, and one pair in the Onychophora, Myriapoda and Hexapoda; 3) presence or absence of mandibular appendages just behind the mouth and nature of these limbs—the mandibles in Crustacea are formed by the leg base and those of the Onychophora, Myriapoda, and Hexapoda by a whole limb which bites with the tip and not with the base; 4) number of paired postoral limbs used in feeding; the Chelicerata usually employ one or more pairs of gnathobases for chewing or cutting and use a movement (and associated morphology) quite unlike that operating the crustacean gnathobases. The Crustacea, Myriapoda, and Hexapoda show two pairs of limbs largely or entirely devoted to feeding (maxillules, maxillae) and further limbs may be used in part, or entirely, for such purposes in Crustacea and certain Myriapoda. Cephalic segmentation and limb equipment in fossil arthropods is seldom known with certainty. We do not know whether trilobite antennules correspond with the antennules or antennae of Crustacea, and the four following biramous limbs of some trilobites may be common to the class and may correspond with the post-antennulary head appendages of Crustacea. The many middle Cambrian merostome-like arthropods cannot be assigned with certainty to Crustacea, Trilobita, or Merostomata on their imperfectly known cephalic features (17, 19, 21). There is every probability that many extinct Arthropoda, such as *Sidneya* (19), do not belong to any of the well-known classes.

The arthropodan trunk region may or may not be divisible into definite tagmata, but these regions when clearly defined are characteristic of only certain classes and orders. The tagmata shown by the Arthropoda are well known and need not be enumerated here.

In some arthropods all trunk segments are laid down embryologically before hatching, and in others only a few segments are so formed, additional segments being added progressively during early life. The details

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[1] The table in *Treatise* Part O (p. O11) suggesting homologies of anterior segments in arthropods is not in accord with factual knowledge (*see* footnote, Part R, p. R42).

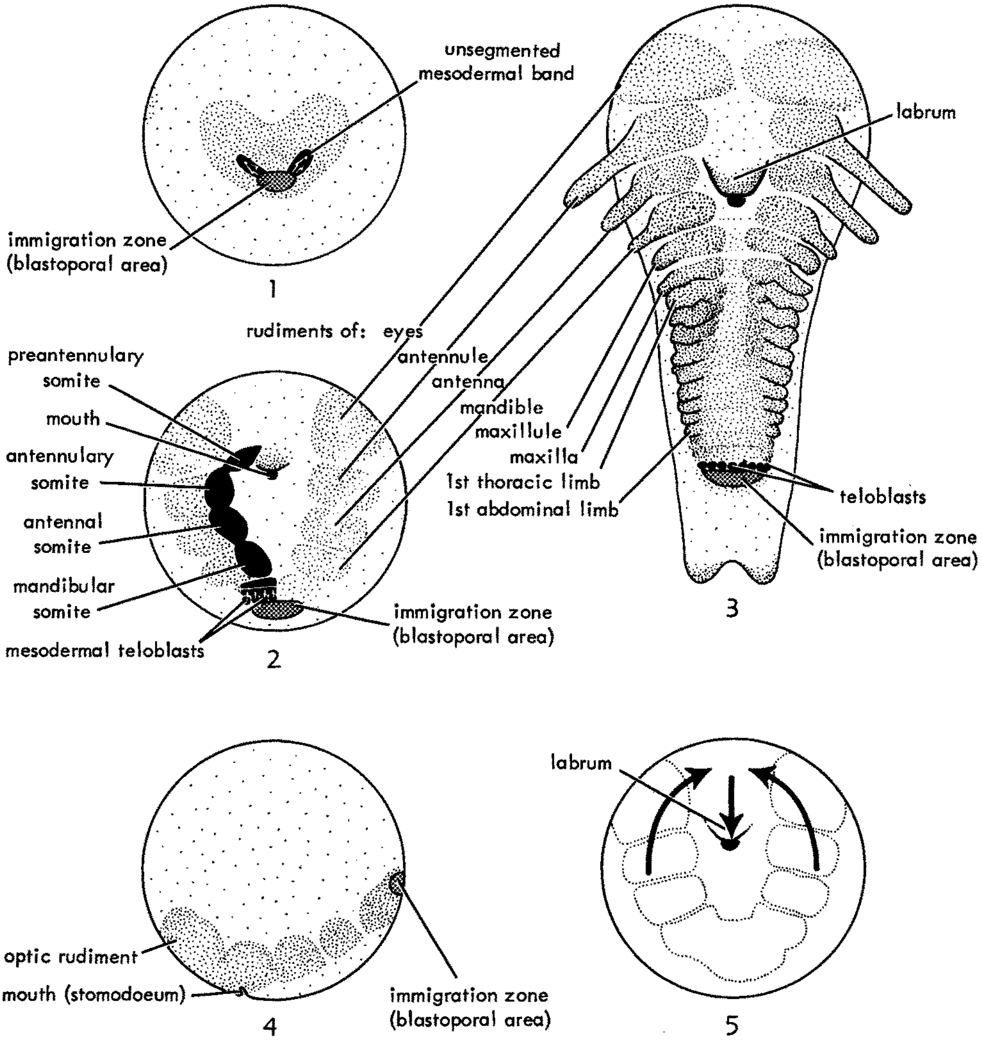


Fig. A. Diagrams illustrating manner in which a head is formed during development in an arthropod, the example being a mysid crustacean.

1-5. Progressive stages shown in *(1-3)* in ventral view, *(4)* in side view and *(5)* diagram of *(2)* showing directions in which tissues shift as they grow.

The unsegmented embryo becomes segmented only ventrally at the head end *(4)*, the dorsal surface being unsegmented. The head is formed by elaborations from this unsegmented anterodorsal tissue (acron), forming eyes, etc., and the preantennulary, antennulary, and antennal segments bend forward relative to the backgrowth of the labrum and oral aperture *(2,3)*. Stippling shows concentrations of outer ectoderm to form the optic rudiment, segmental rudiments, and upper lip (labrum). White stipple on black shows forward migration of mesoderm from its site of origin in *(1)* to form the mesodermal somites in *(2)*. The immigration zone, or blastoporal area, forms mesoderm and endoderm.

whereby segments are formed differs from class to class (4, 4a, 7, 22, 23, 24).

A characteristic of great evolutionary and classificatory significance concerns the limbs. Simple uniramous limbs characterize the Onychophora-Myriapoda-Hexapoda assemblage. Biramous limbs of two contrasting types occur in the primarily

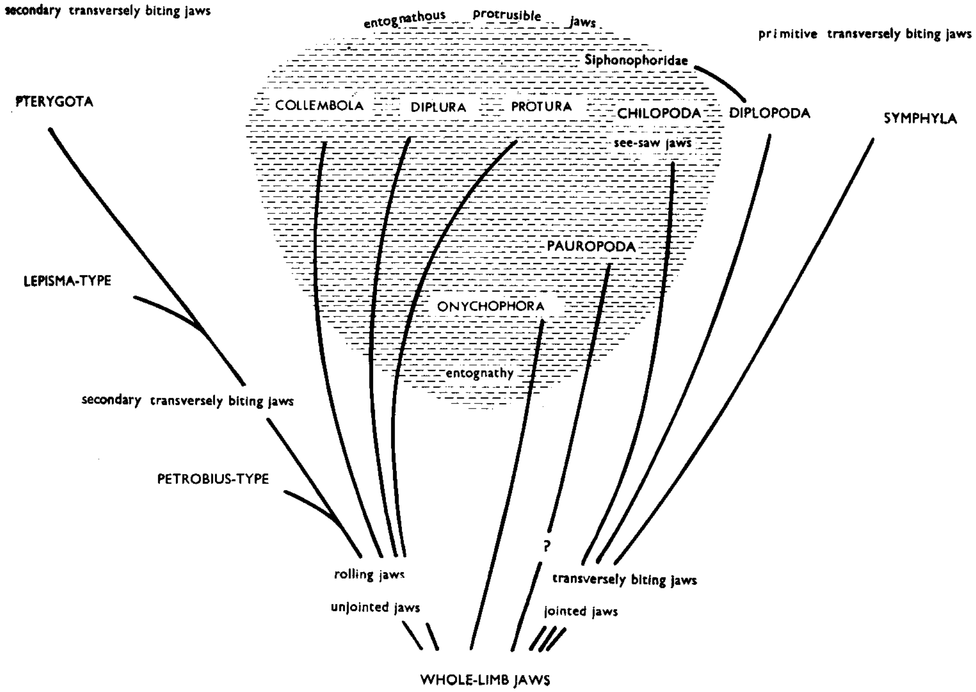
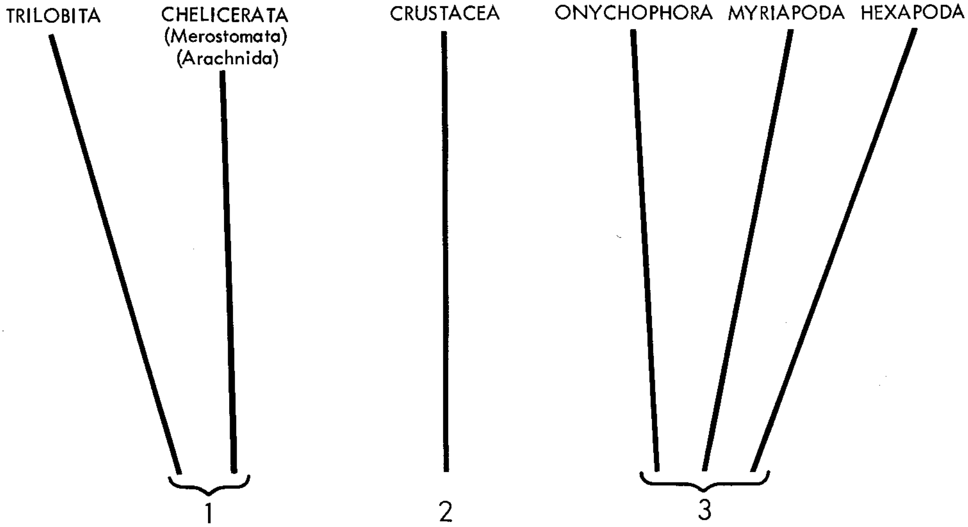


FIG. B. Diagram showing conclusions reached concerning interrelationships and evolution of jaw mechanisms in classes Onychophora, Myriapoda, and Hexapoda, based upon detailed study of structure and mode of action of mandibles throughout the Arthropoda (14).

Two independent lines of evolution are shown, utilizing an unjointed (left side) and jointed (right side) whole-limb mandible. The shaded area indicates independent evolution of entognathy and protrusible mandibles in seven groups. The left-hand branching line is not intended to mean more than the derivation of the mandible of the Pterygota whose ancestors may have passed through stages in which the mandible resembled those of *Lepisma* and *Petrobius* in certain essentials. The lower convergence of the lines denoting the several Apterygota is not meant to imply a common ancestry, but only a closer affinity between the hexapods than between them and any myriapod.

aquatic groups (Fig. B); a limb with the exopod arising distally on the protopod occurs in Crustacea, but in the Trilobita the outer ramus arises proximally on the protopod, so corresponding with the exites on the protopod of Crustacea which are situated proximal to the exopod. Reconstructions from sections of the trilobite *Olenoides* (20) show flattened respiratory filaments on the outer ramus, quite unlike the exopod setae of Crustacea so often used in swimming (25). A uniramous trunk limb in many Crustacea results from the progressive reduction of the exopod and is used for walking and not swimming. A corresponding reduction of the outer ramus is presumed to have occurred also in the Chelicerata, only a few biramous limbs remaining, such as the branchial and sixth prosomal limbs of *Limulus*. There is no indication of a biramous limb in the Onychophora, Myriapoda, or Hexapoda. The fossil record does not in any way bridge the gap between these three limb types; they all may have evolved independently from the limbs of soft-bodied ancestors. Regrettably little information of a precise nature is available concerning limb structure in fossil arthropods, and great care is needed before a limb can be assigned either to the crustacean or to the trilobite type or to something different.

The outstanding convergences among arthropods, which should be faced in any attempt at a natural classification, concern: 1) **biramous limbs,** which differ basically in structure, at least in Crustacea and Trilobita, and which are insufficiently known in most fossil Arthropoda; 2) **mandibles,** which are entirely different in derivation in Crustacea and in the Onychophora-Myriapoda-Hexapoda assemblage (14)—even in the latter group the myriapod whole limb segmented mandible, utilizing a basic adductor-abductor movement, contrasts fundamentally with the hexapod whole-limb unsegmented mandible; the basic movement of this latter mandible is a promotor-remotor roll giving a good grinding action and some cutting, and a transition from this, to mandibles which cut much more strongly in the transverse plane, takes place by morphological changes which are parallel to those Crustacea which also acquire transverse biting from a primitive rolling mandible (p. *R*25, 14); 3) **entognathy,** or boxing in of the mandibles, and in some forms of other mouth parts also, confers proximal freedom on the mandible which permits protractor and retractor movements, additional to the basic promotor-remotor roll giving grinding and cutting—entognathy has been evolved independently many times (Fig. B) and the possession of this general feature, with details differing in the several groups (15), is not indicative of close affinity, as has at times been suggested; 4) **compound eyes** do not appear to be basic in all classes—trilobite compound eyes lacked the refinements present in Hexapoda and in Crustacea which possess compound eyes, for such eyes appear to have



(1) The form of limbs and tagmata of the body perhaps suggests distant affinity between the Chelicerata and Trilobita and a lack of affinity between these classes and the other Arthropoda.

(2) The basic form of the biramous limbs and gnathobasic mandibles of Crustacea are so unlike the corresponding limbs of other Arthropoda as to preclude close affinity between them.

(3) The Onychophora, Myriapoda, and Hexapoda have similar uniramous limbs and all bite with the tips, not bases, of the mandibles. Also, similarities in the embryonic development of these groups contrast with chelicerate and crustacean developments. The three groups probably have had a roughly common origin, but the construction and mode of action of the segmented mandibles of the Myriapoda are so unlike those of the unsegmented hexapod mandibles as to indicate that the Hexapoda have not descended from any one class of the Myriapoda.

FIG. C. Diagram illustrating three major subdivisions of the Arthropoda between which there are no known connecting links.

been evolved independently in the latter classes; the eye structure in some crustacean orders and in Hexapoda, although closely similar, is not identical. Physiological requirements for this type of vision do not permit wide deviation from the most suitable mechanism, which consequently appears to have been a parallel evolution in the two groups; 5) **tracheal systems** used in air-breathing have evolved independently in Onychophora, Myriapoda, and Hexapoda, in Arachnida and certain Crustacea—the fine, almost unbranched tracheae of the Onychophora are not unique, as has often been supposed; similar tracheae are found in certain Chilopoda *(Craterostigmus)* where extensive changes in hydrostatic pressure occur in the hemocoel in association with various specialized abilities as in Onychophora (15); 6) **uric acid excretion** and the conservation of water in the excretory processes in land forms is achieved by Malpighian tubules in Arachnida and in Myriapoda and Hexapoda; uric acid secretion is done very simply by the mid-gut in Onychophora, but the presence of Malpighian tubules is not necessarily indicative of a uricotelic metabolism such as occurs in pterygote insects (BENNETT & MANTON, 1962); 7) **progoneate condition** of the Symphyla and Pauropoda has been shown by TIEGS (23, 24) to be secondary and probably related to anamorphosis. Further convergences could be noted, and see below for cuticular sclerotization.

No simple monophyletic scheme of arthropod classification can account for the distribution and morphology of the above features. Some measure of polyphyletic evolution within the group seems inescapable. At least three major groupings can be made, as shown diagrammatically in Figure C and distinguishable on tagmata and on the basic structure of the jaws and trunk limbs. This grouping is endorsed by STØRMER (21) who can find no bridging of the gaps between them.

The Onychophora are not separable from the other classes of Arthropoda by any characteristics of fundamental importance. There is no sound evidence to justify the view that this class should be excluded from the Arthropoda. Onychophoran structure and embryology are basically arthropodan in great detail, and onychophoran peculiarities of structure and development are related to habits of life which are of survival value (5, 6, 7, 10a; Manton, 1959). Moreover, the Onychophora share many important features with the myriapod classes in contrast to all other Arthropoda (Manton, 1964; 15, 23, 24). The views to the contrary concerning the Onychophora and classification and phylogeny of the Arthropoda in general, recently put forward by SHAROV (18), are not considered to be valid. They do not accord with the known evidence, they conflict with easily ascertainable new facts and rest on speculative bases. The principle advocated by SHAROV that anthropod structure can only be understood by reference to the origin of the Articulata is hardly commendable since this province is unknown. A classification of the Arthropoda is not advanced by assertions that the group arose from the Ctenophora via annelids akin to the highly specialized Spintheridae. Such statements are unprovable. A reply to many of the points by SHAROV is given by MANTON (16 and 1967) and ANDERSON, 1966, together with the presentation of new data.

The factual evidence provided by the jaws is summarized in Figure D, and it divides the Arthropoda into the same three groups, separated by the heavy vertical lines, as in Figure C. The gnathobases, used for cutting and squeezing, in the Chelicerata are fundamentally different in skeletomuscular action from those of Crustacea, and the one could not have given rise to the other. The primitive rolling movement of the jaws of Crustacea and Hexapoda, described in another chapter (p. *R*49), must have arisen from the promotor-remotor swing of a walking or swimming limb, the actual mandibles in the two groups being quite different in derivation. Biting in the transverse plane is a secondary acquisition in many Crustacea and Hexapoda (shaded area), but is a primitive movement for the gnathobasic limbs of the Chelicerata and mandibles of Myriapoda. However, the limb structure in Chelicerata and Myriapoda is quite different.

The similarity in the structure and movement of the mandibles in the myria-

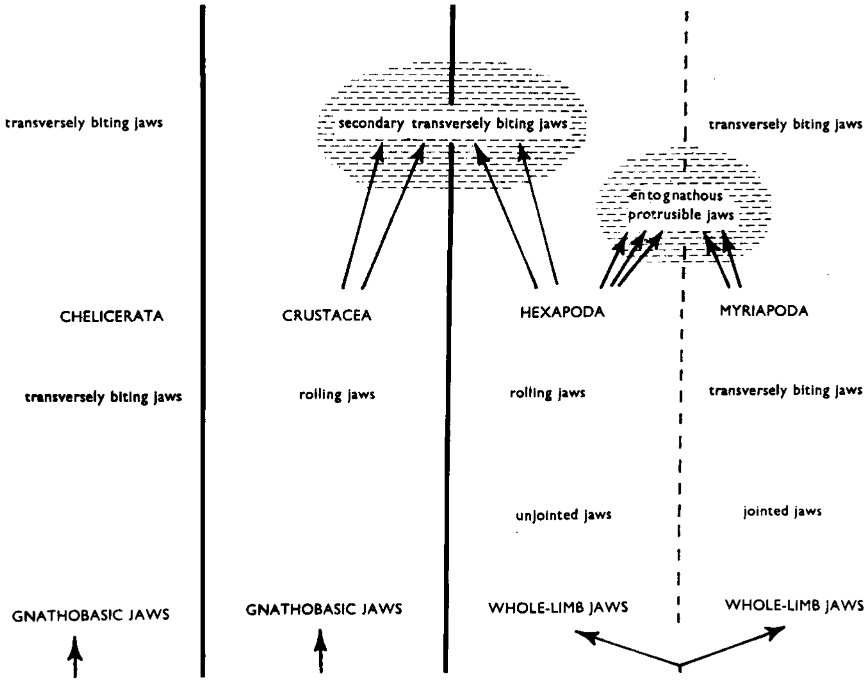


FIG. D. Diagram showing distribution of jaw types among Chelicerata, Crustacea, Hexapoda, and Myriapoda.

The heavy vertical lines indicate an entire absence of common ancestry of the jaw types, and the interrupted vertical line indicates the separate evolutions of jaw mechanisms in the classes Myriapoda and Hexapoda, although both are based on a whole-limb mandible. The shaded areas indicate convergently acquired biting in the transverse plane and convergently acquired entognathy (as in Fig. B).

pod classes, irrespective of the presence (Chilopoda, Pauropoda) or absence (Diplopoda, Symphyla) of enthognathy is of great importance (Fig. D, right side). In all, the abductor mechanism of the mandible is provided in whole or in part by the mechanical action of a swinging anterior tentorial apodeme (3, 14). No hexapod has a jointed mandible working in the myriapod manner. The hexapod anterior tentorial apodeme is rigid and is never concerned directly with causing mandibular movements. No myriapod either possesses or requires a posterior tentorial apodeme such as is present in all hexapods. Even the superficially similar maxilla *1* and maxilla *2* of Symphyla and hexapods contrast in their skeletomusculature and modes of action (14). TIEGS (23, 24) showed that the progoneate condition of Symphyla and Pauropoda is secondary and probably related to anamorphosis. There is a community in structure of the leg and of the coxa-body joint in all myriapods, which contrasts decisively with those of hexapods and the one could not have given rise to the other (16). Further, the myriapod type of coxa-body joint and its obligatory movements are not at all suitable for transition to a hexapodous state. The evolution of the myriapod type of leg base commits these animals to a multilegged condition. An opposite type of leg base in an early multilegged animal would have the potentiality of supplying the mechanical features necessary for the evolution of pterygote limbs. And it is only this type of leg base that is suitable for the further evolution of flight. The swinging pleurite, so essential to the classes of fleeter myriapods, and the associated leg base musculature, is not in the least appropriate for a further evolution of flight muscles. These are the principal reasons for the reinstatement of the once discredited Myriapoda as a natural group (14, 16). And they are the reasons for the destruction of the dream, so dear to entomologists, concerning a supposed close affinity between Symphyla and certain hexapoda. The marked differences in head and trunk anatomy between the several classes of myriapods has been shown to be associated in considerable detail with divergent habits of life (9, 10, 13, 14, 15, 16), and all could have evolved in parallel from a similar basic stock, although no one class could have given rise to any other.

The possession of only three pairs of legs borne on a thorax is functionally advantageous in that it permits the use of long legs, capable of taking a long stride, with a wide range of gait patterns, as is impossible to myriapods which possess long and many legs (MANTON, 1952b; 8, 16). The advantages of walking or running on only three pairs of legs have been acquired independently by many classes, notably certain Arachnida and Crustacea (8). It would therefore be conceivable that the six-legged state of the hexapod classes might also have been independent and parallel evolutions. Certain it is that the gulfs between the various hexapod groups are deep. But the discovery of the decisive differences between the morphology and modes of action of the head endoskeleton, the jaws and the trunk limbs of all Myriapoda, on the one hand, and of the several groups of pterygote and apterygote Hexapoda, on the other, indicates that the hexapods are indeed more akin to one another than to any other classes of arthropods. This does not mean that the hexapods had a common origin, or that the hexapodous state was acquired only once in their past history. All it suggests is that the hexapods may have had several origins from an ancestral stock of animals which was quite distinct from the ancestral myriapods. The same conclusion is indicated by a modern assessment of entognathy based upon accurate facts of morphology and function. These facts clearly demonstrate the fundamental differences between the several classs of entognathous Apterygota and the probability that their entognathy has been convergently acquired from a known basic condition, just as the entognathy of certain Crustacea and Myriapoda has been independently acquired (14).

Thus the evidence available to date suggests that the component classes of the Myriapoda and of the Hexapoda are more closely related to one another, within each of the two assemblages, than to any other Arthropoda, and that none of the hexapod classes has a claim to close relationship with any myriapod class. The common segment number shown by some hexapods and Symphyla and the possession of a labiate maxilla *2* in both are convergent similarities which do not outweigh the fundamental differences between the two groups.

The Merostomata clearly comprise the Xiphosura and the Eurypterida as major groups, and other probable merostome taxa have become extinct and are insufficiently known (19). There is evidence suggesting the derivation of the Arachnida from aquatic chelicerates, but whether the transition to land occurred once or several times is unknown (25, p. 304-307). There is no decisive evidence concerning the interrelationships of the several orders of either the Arachnida or Crustacea. The distinctions between the component orders of the Crustacea and of the Arachnida are just as profound as are those between the four myriapod classes and the several hexapod classes. But the reality of the Crustacea, Arachnida, Myriapoda, and Hexapoda as major groups seems clear.

Finally, reference must be made to the concept of grades in arthropod evolution. Such terms were first applied by TIEGS (24) to the Onychophora-Myriapoda-Hexapoda assemblage. The Monognatha (Onychophora) use one pair of postoral gnathal limbs, the Dignatha (Pauropoda and probably Diplopoda) use two pairs, the diplopod gnathochilarium probably representing but one pair of limbs, and the Trignatha (Symphyla and Hexapoda) use three pairs. These terms do not now indicate taxonomic groupings of affinity.[1] They show, on the contrary, levels of organization reached independently by various classes (Fig. E). The

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[1] The up-to-date use of the terms denoting grades in Myriapoda and Hexapoda is not appreciated in the article on the Myriapoda, where it is implied that the grades have a taxonomic sense (*Treatise*, p. R575).

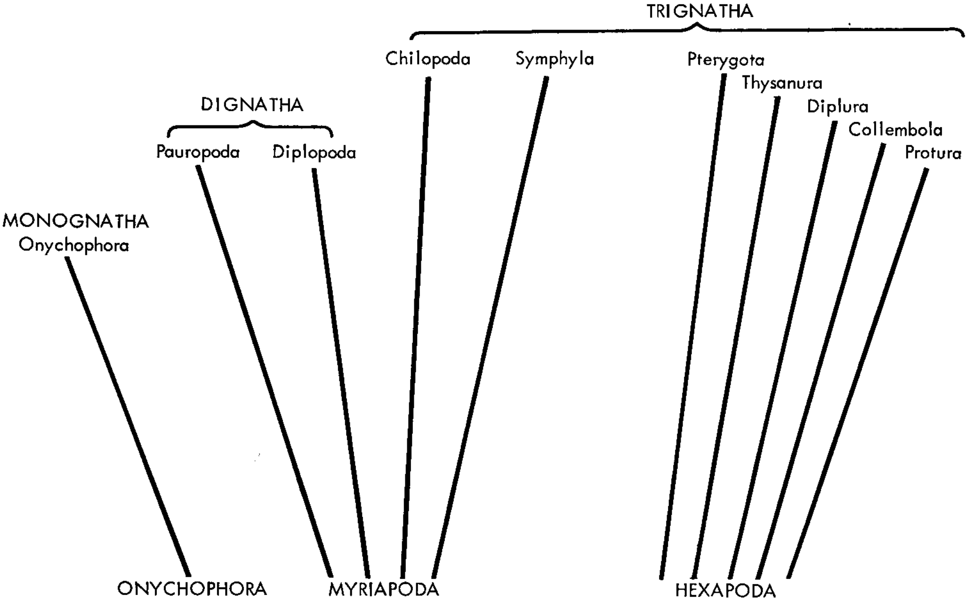

FIG. E. Diagram illustrating significance of grades in relation to taxonomy of Onychophora, Myriapoda, and Hexapoda.

The grades Monognatha, Dignatha, and Trignatha represent stages of advancement reached independently by various classes and do not represent taxa denoting close affinity. Positions of the two groups of converging lines show the related myriapod and related hexapod classes which have each evolved in parallel. For further description see text.

trignathy of the Symphyla does not separate this class from the other Myriapoda with which they have fundamental resemblances in the mandible, head endoskeleton, and structure of limbs and joints. Further, there is no reason to suppose that these grades have been acquired progressively. In any one phylogeny a monognathous state need not have preceded dignathy and the latter need not have come before a trignathous condition. These three states probably evolved directly from animals with undiversified limbs, as have the three or the one pair of maxillipeds in the eucaridan and pericaridan Crustacea. The absence of a dignathous hexapod or a monognathous myriapod probably means that no such animals ever existed. Similarly the term "Mandibulata" represents a grade of organization, of great functional importance, reached independently and by different means in Crustacea and terrestrial myriapods and hexapods.

The above outline of arthropodan classification is based rigidly upon factual evidence available in 1966, and no speculations are offered concerning the ultimate origins of the groups of arthropods set out in the figures. But one further point may be made. The Arthropoda as a whole appear to be polyphyletic at least to the extent of the three main groups shown in Figure C, but there were probably more independent taxa which are now extinct. The basic unity of the Onychophora-Myriapoda-Hexapoda assemblage has been demonstrated by TIEGS (23, 24, etc.) but this does not imply just one ancestor for all. The probability that the Onchophora are primitively soft-bodied, lacking surface sclerites, but not the ability for high levels of sclerotization, follows from the demonstration of the functional assets of onychophoran anatomy (MANTON, 1950; 10a). It is thus possible that the evolution or an armor of surface sclerities may have occurred more than once during the evolution of arthropods, taking place independently in the sea and on land, and that this most conspicuous characteristic of the phylum should be added to the list given above of major features which have arisen by convergence.

The popular mode of classification of the Arthropoda into graded hierarchies which correspond from one major group to another probably has little reality. CALMAN (2a) drew attention to the much larger series of units needed in the classification of some groups than of others. Within one major assemblage it matters little whether the hierarchies run from superclass to class and subclass or from class to subclass and order, or some other series of labels. It is a meaningless task to force one system of labeling onto all groups.

The main groups of the Arthropoda, on the evidence available to date, can be listed as shown below. Some doubt may be expressed as to the validity of the rank of class indicated for the Cephalocarida, Mystacocarida, and Branchiura among the Crustacea; these three groups may not be as separate from the Branchiopoda and Copepoda as the title of class suggests. Very little is known concerning the status of the Pentastomida and Tardigrada. Further subdivision of the listed classes is often long. For example, there is no general agreement concerning the existence of a few major groupings within the Arachnida and it is necessary to give 16 subclasses of the Arachnida if division is undertaken.

Main Divisions of Arthropoda

- ARTHROPODA *(phylum)*. *?Precam., Cam.-Rec.*
  - Trilobitomorpha *(superclass)* . *Cam.-Perm.*
    - Trilobitoidea *(class)* . *Cam.-Dev.*
    - Trilobita *(class)* . *Cam.-Perm.*
  - Chelicerata *(superclass)* . *Cam.-Rec.*
    - Merostomata *(class)* . *Cam.-Rec.*
    - Arachnida *(class)* . *Sil.-Rec.*
  - Pycnogonida *(superclass)* . *Dev.-Rec.*
  - Crustacea *(superclass)* . *Cam.-Rec.*
    - Cephalocarida *(class)* . *Rec.*
    - Branchiopoda *(class)* . *L.Dev.-Rec.*
    - Mystacocarida *(class)* . *Rec.*
    - Ostracoda *(class)* . *L.Cam.-Rec.*
    - Euthycarcinoidea *(class)* . *Trias.*
    - Copepoda *(class)* . *Mio.-Rec.*
    - Branchiura *(class)* . *Rec.*
    - Cirripedia *(class)*. *U.Sil.-Rec.*
    - Malacostraca *(class)* . *L.Cam.-Rec.*
  - Onychophora *(superclass)* . *?Precam., Cam.-Rec.*
  - Myriapoda *(superclass)* . *U.Sil.-Rec.*
    - Archipolypoda *(class)* . *U.Sil.-U.Carb.(Penn.).*
    - Diplopoda *(class)* . *U.Carb.(Penn.)-Rec.*
    - Pauropoda *(class)* . *Rec.*
    - Chilopoda *(class)* . *Cret.-Rec.*
    - Symphyla *(class)* . *Oligo.-Rec.*
  - Hexapoda *(superclass)* . *U.Carb.(Penn.)-Rec.*
    - Protura *(class)* . *Rec.*
    - Collembola *(class)* . *Rec.*
    - Diplura *(class)* . *Rec.*
    - Thysanura *(class)* . *Oligo.-Rec.*
    - Insecta *(class)* . *U.Carb.(Penn.)-Rec.*
  - Pentastomida *(superclass)* . *Rec.*
  - Tardigrada *(superclass)* . *Rec.*

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EVOLUTION AND AFFINITIES OF ONYCHOPHORA, MYRIAPODA, HEXAPODA, AND CRUSTACEA

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[Chapter submitted December, 1962; revised January, 1963]

CONTENTS

INTRODUCTION

The elucidation of phylogenetic relationships within the Arthropoda is essentially speculative, since the fossil record is noncommittal. Apart from the general thesis that the arthropod phylum has sprung from metamerically segmented coelomates, there are few points relating to its ancestry on which general agreement has been reached; indeed, it is uncertain whether the great arthropod assemblage is a "natural" group or whether it comprises more than one line of descent derived independently from segmented coelomates. Theories of arthropod evolution have been many and have formed the basis of various classifications which have been put forward since the time of Cuvier. A survey of these theories, associated with the names of von Siebold, Haeckel, Moseley, Kennel, Balfour, Sedgwick, Lankester, Woodward, Packard, Handlirsch, Snodgrass, Tiegs, and others, has been given by Tiegs & Manton (67) and will not be repeated here. It is pertinent now to consider the present position of our understanding of this subject, furthered by recent work in the fields of comparative embryology and of comparative functional morphology. The latter studies, in particular, have thrown a wealth of light upon the functional significance of conspicuous characters which are diagnostic of classes and of orders. Such knowledge shows the detailed relationships between habits of life and body design, and gives sure guides as to the modes of evolution of many of these characteristics. The appli-

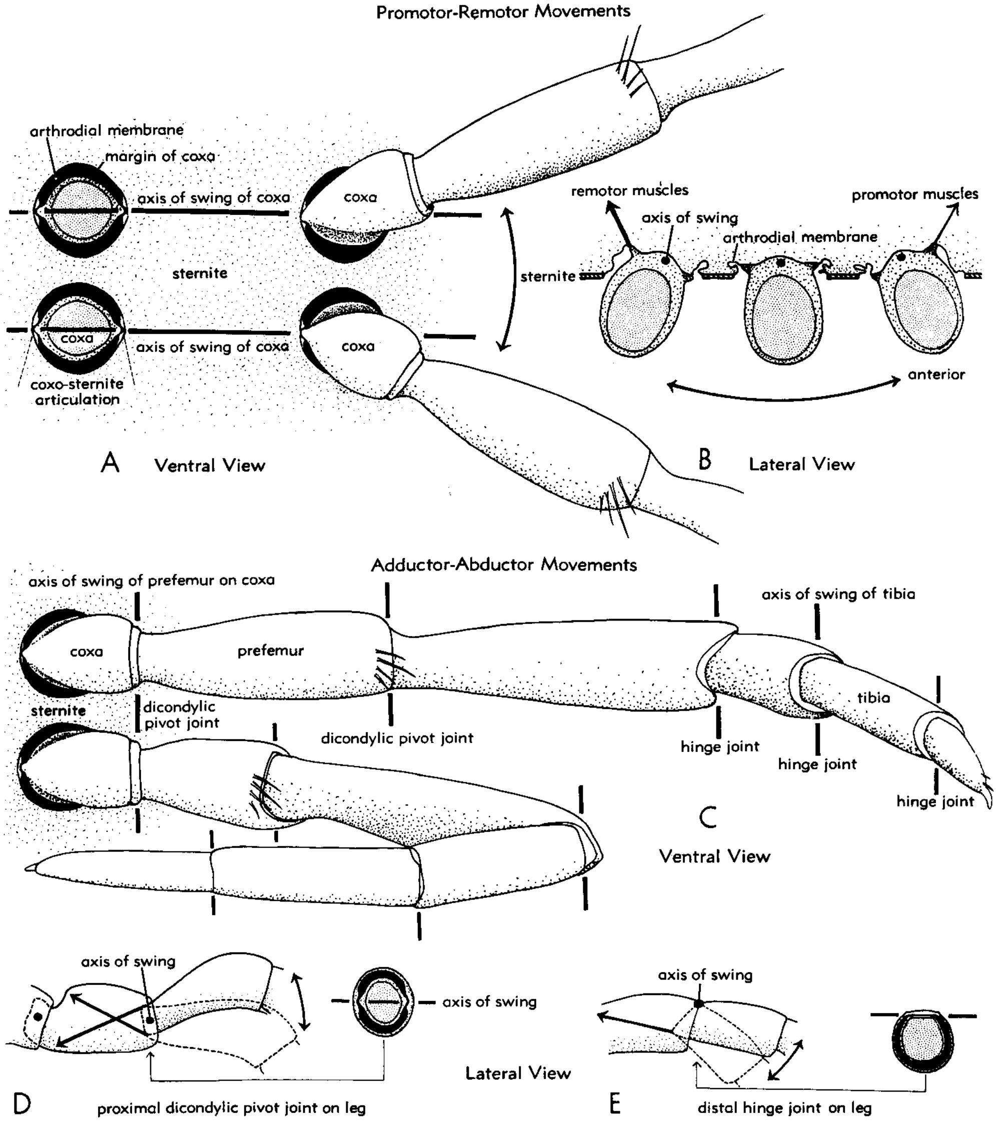

FIG. 1. Diagrams showing the two basic movements employed by many arthropodan limbs, exemplified by *Polydesmus* (Diplopoda). One or other of these movements are also used by the several types of mandibles. [Arthrodial membrane at the coxa-body joint is indicated in black.]

A. Ventral view of two successive pairs of legs, those on one side of the body being cut short close to the coxo-sternite articulation. The axis of swing, passing through the dicondylic coxo-sternite articulation, is shown by a heavy line. The legs on the right show the forward and backward positions resulting from the promotor-remoter swing of the coxa about its axis of movement on the body.

B. Lateral view of three successive coxae cut short near the coxo-sternite articulation to show the promotor-remotor swing about the axis (indicated by a black dot).

C. Ventral view of two successive legs in positions of abduction (away from) and adduction (toward) their fellows, which are not drawn. The coxae cannot participate in this movement. The

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cation of this approach to the vast assemblage of arthropods is in its infancy, but a rewarding start has been made.

Extant arthropods fall readily into at least the following distinct groups: Chelicerata, Crustacea, Onychophora, Pauropoda, Diplopoda, Chilopoda, Symphyla, Apterygota, Pterygota, Pycnogonida, and Tardigrada. The fossil record displays the long history of the Trilobita, which were the dominant arthropods of the early Paleozoic seas, becoming extinct in the Permian. Many bewildering aquatic arthropods from the Cambrian to Devonian do not fall clearly into any of the above categories. Regrettably, as yet the structure of these animals is insufficiently known for a full assessment. The name of TIEGS will be remembered for his major contribution in establishing the unity of the Onychophora, Myriapoda (Pauropoda, Diplopoda, Chilopoda, Symphyla), and Insecta, based primarily upon embryology (28, 30, 32, 61, 62, 66) and on adult form. The Chelicerata and Crustacea stand in marked contrast both to the land stem and to each other.

The differences between the structure of the head or anterior end of the body in the major groups of arthropods are alone sufficient to separate the classes. A functional consideration of the requirements at the anterior end of the body, and of the ways of meeting these needs, is particularly revealing as to the modes of head evolution. The primary anterior requirements of a bilaterally symmetrical forwardly moving animal concern the sensory equipment and the feeding organs, particularly the mandibles in the classes that possess them. Differing habits of life are associated with the evolution of the very different trunk morphologies which are diagnostic of classes and of orders.

EARLY ARTHROPOD EVOLUTION AND CONVERGENCE

The Arthropoda are bound together by very few essential characteristics: (1) metameric segmentation, coupled with modifications at the anterior end which are different from those of annelids;[1] (2) usually many paired limbs (Fig. 1, 2), which are different from those of annelids; (3) an ostiate heart and hemocoelic body cavity; and (4) a surface cuticle usually sclerotized into more or less rigid sclerites separated by flexible intersegmental arthrodial membranes at the joints on the body and limbs. Sometimes functional advantages associated with particular habits of life result from sclerotization remaining thin, giving an absence of sclerites or scutes, as in Onychophora, some insects, and the thorax and abdomen of barnacles, etc. In others, a fusion together of the sclerites of one or of several segments provides strength and rigidity.

Metamerically segmented muscles in arthropods with or without sclerites facilitate precise local actions in controlling body shape or limb movements, or both. Many

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[1] The work of ANDERSON (1) has shown that the composition of the externally simple head end of the polychaete *Scoloplos* is far from simple and its embryonic development does not follow the lines shown by simple arthropods.

FIG. 1. *(Continued from facing page.)*

axes of swing of the leg joints distal to the coxa are shown by heavy lines, the two proximal joints being dicondylic pivot joints and the three distal joints being hinge joints. The tarsal claw is hinged to the tarsus in the same plane as the other hinge joints.

D. Proximal dicondylic pivot joint on a leg showing two positions of the distal segment; the antagonistic muscles are indicated by arrows within the leg segment. A diagrammatic transverse section through the joint at the level indicated shows the lateral points of locally strengthened cuticle on the two leg segments united by very short arthrodial membrane.

E. Distal hinge joint on the leg showing two positions of the distal segment, the single flexor muscle (adductor, or depressor) being indicated by an arrow within the leg segment. A diagrammatic transverse section through the joint at the level indicated shows the dorsal point of close union between strengthened cuticle of the two leg segments which forms the hinge.

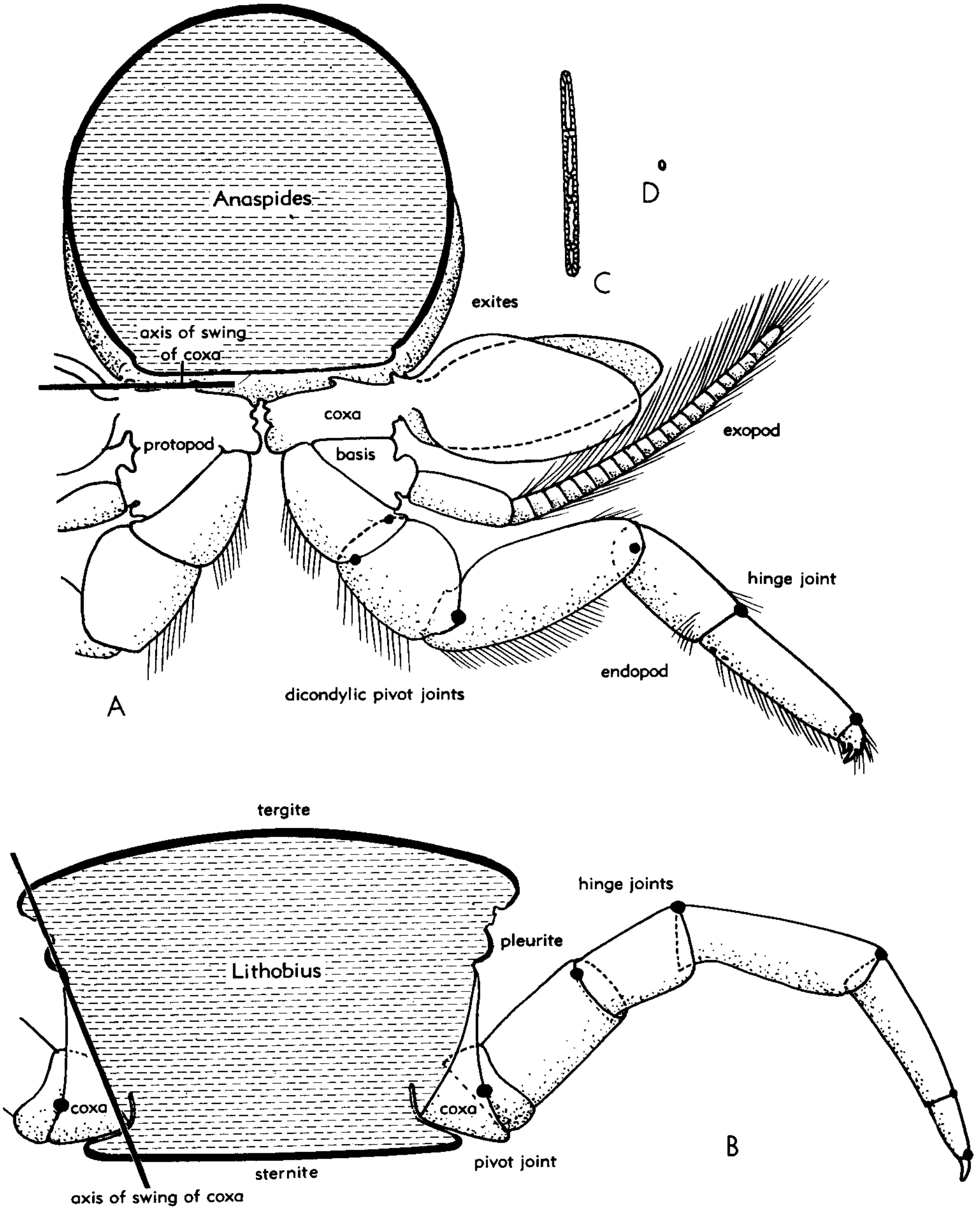

FIG. 2. Typical biramous and uniramous limbs and two types of coxa-body articulation.

A. Posterior transverse view of 6th thoracic leg of *Anaspides tasmaniae.*

B. Anterior transverse view of middle thoracic leg of *Lithobius forficatus.* A heavy line, horizontal in the crustacean and dorsoventral in the centipede, indicates the axis of swing of the coxa on the body; intermediate positions of the coxa-body axis of swing can be found among other arthropods. The crustacean coxa bears exites (also termed epipods and epipodites) laterally, and endites are present on the mesial side of certain mouth parts and on the more anterior thoracic limbs (see Fig. 13). The centipede coxa is simple. The crustacean protopod consists of two segments, the coxa and the basis, and bears two rami, the

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segmentally placed limbs make possible strong or speedy movements and give the potentiality of structural and functional differentiation along the series which is so characteristic of the more specialized Arthropoda.

The possession of a thick laminated sclerotized cuticle is not restricted to the Arthropoda. Nematodes also have such a cuticle, which is differentiated internally to a greater extent than in most Arthropoda (6, 24), and molting also takes place. The high degree of internal cuticular differentiation in nematodes is probably correlated with the maintenance of body shape and suitable flexibility under conditions of high hydrostatic pressure in the body cavity. But the absence of metameric segmentation in nematodes is coupled with the absence of joints. All arthropodan cuticles show regions where the sclerotization or calcification, or both, is minimal, so forming the flexible arthrodial membranes.

Surface sclerites do not necessarily carry muscles (see the pleural sclerites of epimorphic centipedes). The primary function of sclerites appears to be protective, and in burrowing forms they provide an armor used in pushing against the substratum (*Limulus*, Diplopoda, and geophilomorph centipedes). The possession of striated muscles inserted onto subectodermal connective tissue or basement membrane below the inner face or near to the edges of sclerites (the latter position, used by many muscles of Diplopoda, is not necessarily the more primitive) permits rapid or strong movements used in walking or swimming. Joint formation between sclerites may be elaborate and can lead to economy in certain muscles by the use of hard parts to direct movements, so permitting more musculature to be available for other purposes (38); and the sclerites themselves may be heavy, extensive, and strongly protective. On land a high degree of surface sclerotization and surface lipoids render the sclerites very hydrofuge. Thereby, internal moisture is conserved and, much more important, osmotic uptake of fresh water, rain, and dew is hindered, the latter being the greater hazard in a terrestrial habitat. PANTIN (46) has shown how the great danger to land planarians and land nemertines is osmotic uptake of water, and in consequence, these animals are found in damp niches in comparatively dry country, not in wet habitats where at first sight easier living might be anticipated.

The functional advantage of hemocoel evolution is little understood and seldom considered, apart from its physiological aspects, although the presence of the hemocoel is always regarded as an important arthropodan attribute. LANKESTER (27) suggested that a swelling of vascular spaces, or "phloebedesis," may have promoted local changes in shape in a soft-bodied arthropodan ancestor in a more advantageous manner than can be accomplished by an animal with a coelomic body cavity. The probable truth of this idea is supported by the discovery that a burrowing geophilomorph centipede can exert some four times as much force aaginst the substratum from its armored body surface as can an annelid worm of similar size (41 and MANTON, 43a). Striated muscles far from the site of application of the thrust, as well as

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FIG. 2. *(Continued from facing page.)*

endopod and exopod. In the centipede the limb distal to the coxa forms a single ramus, the telopod, as in all other myriapods and in hexapods. The positions of the close articulations between the leg segments are shown by heavy dots; pivot joints allow movement in two directions about the articulation and are served by antagonistic pairs of muscles (Fig. 1,*D*); hinge joints allow movement in one direction about the articulation and are usually served by flexor muscles only (Fig. 1,*E*), hydrostatic pressure and proximal depressor muscles supplying the antagonistic force producing leg extension (Fig. 1,*A;* 1,*E*). Both types of articulation may be dicondylic or may be formed by one principal articulation. In life, the exites of *Anaspides* are forwardly directed. Only in fast-running centipedes is the tarsus divided into two segments as shown here; the distal tarsal segment possesses no muscles of its own.

C. Transverse section through an exite showing its flat shape and internal vascular spaces.

D. Transverse section through a seta from the exopod.

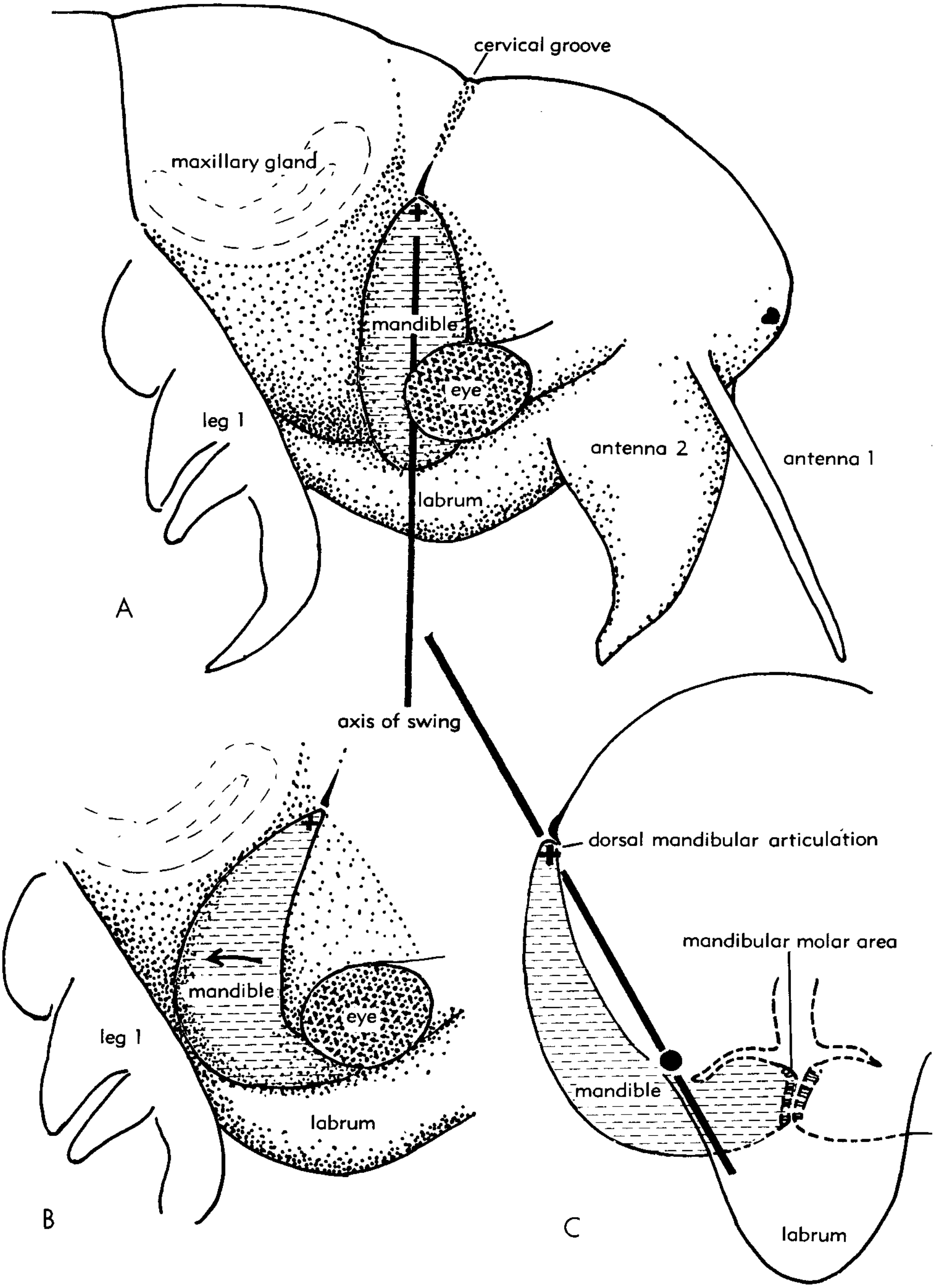

FIG. 3. A gnathobasic mandible.

A,B. Lateral views of the head of the crustacean *Chirocephalus diaphanus* showing the mandibular movements and their relationship to those of the coxa of a walking leg (Fig. 2,*B*). The movements provide a crushing or grinding mechanism, but no strong cutting in the transverse plane, and are characteristic of the less specialized mod-

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local musculature, maintain high hydrostatic pressure in the hemocoel, and assist in providing a strong local heave, which moreover can be repeated again and again. An annelid, such as *Arenicola*, cannot repeat its maximum effort without a bursting of capillaries and leakage of coelomic fluid. It is possible that the evolution of this basic attribute of all arthropods, the hemocoel, occurred along with a habit of shallow grubbing into the pre-Cambrian sea floor. Such a habit represents the simplest of escape reactions, and the evolution of a better or easier way of burrowing may have had great survival value at the dawn of arthropod evolution. It may be significant that a similar habit is envisaged for the primitive Mollusca, the hemocoel of which may have arisen in association with similar functional advantages. Later, with the acquisition of arthropodan protective armor, facilitating both shallow burrowing and surface living, the original advantage of a hemocoel largely seems to have disappeared. However, it persists in part in the frequent use of blood pressure for the extension of legs where all the musculature of the distal segments is flexor in function (14, 38, 39). Sometimes blood pressure causes leg extension in jumping, when both legs of a pair push in the same phase, as in jumping spiders (47).

Thus, evolution of the arthropodan hemocoel may have preceded the evolution of surface sclerites. It is also possible that the acquisition of surface sclerites on the trunk may have preceded those on the legs, since the force exerted by the surface of the trunk of an annelid or arthropod when burrowing is usually not generated by segmental limbs. Whether the wormlike *Anomalocaris* from the Cambrian, which has so intrigued SNODGRASS (personal communication) and which perhaps shows segmental sclerites but no leg segmentation, represents or is derived from such a stage of arthropodan evolution is uncertain. Regrettably, the fossil remains, although numerous, all lack the head end.

The Arthropoda exhibit a wealth of structural specialization suiting particular ways of life and favoring survival in particular niches. The hermit crabs inhabiting gastropod shells and the gall-forming crab *Hapalocarcinus,* living on the coral *Seriatopora,* are typical examples. The most important of the evolutionary advances of the Arthropoda, however, did not result in adaptation to particular niches, but, on the contrary, adaptation of an animal to better living in the same or in a variety of habitats. A large decaying log in South Africa or South America may harbor Onychophora, Diplopoda, Chilopoda, Symphyla, insects, arachnids, etc. The environment is roughly the same for all but the basic habits of the animals differ, and it is these habits which are associated with the trunk characters of the several groups (see below).

Where specialization of all kinds is abundant and varied, as it is within the Arthropoda, there is possibility of unlimited convergence. And, when the distinctive arthropodan characters are so few, the possibility must be faced that even these may have arisen more than once. There has been a reluctance to recognize some of the outstanding cases of convergence, although others have been readily accepted as such. There is no denying the parallel evolution of tracheae serving aerial respiration which has taken place at least four or five times. The histology or mode of embryonic origin of tracheae or both of these are not the same in land isopods, arachnids, Onychophora, and myriapods. Similarly, malpighian tubules have arisen independently and by different means in certain Arachnida and

FIG. 3. *(Continued from facing page.)*

ern Crustacea. A cross marks the dorsal articulation of the mandible with a small sclerite in the cervical groove.

C. Transverse view of head of the same showing the manner in which the mandible swings about a dorsoventral axis (cf. Fig. 2,*B*), the ventral end of the axis (black spot) not being firm. At the end of the promotor swing *(A)* the mandibles are set transversely to the body (see also Fig. 5,*C*, left-hand diagrams). At the end of the remotor swing *(B)* the lateral parts of the mandible, moving in the direction of the arrow, are backwardly directed while the molar areas are forwardly directed. The eye and trunk limb 1 are in the same position in both diagrams.

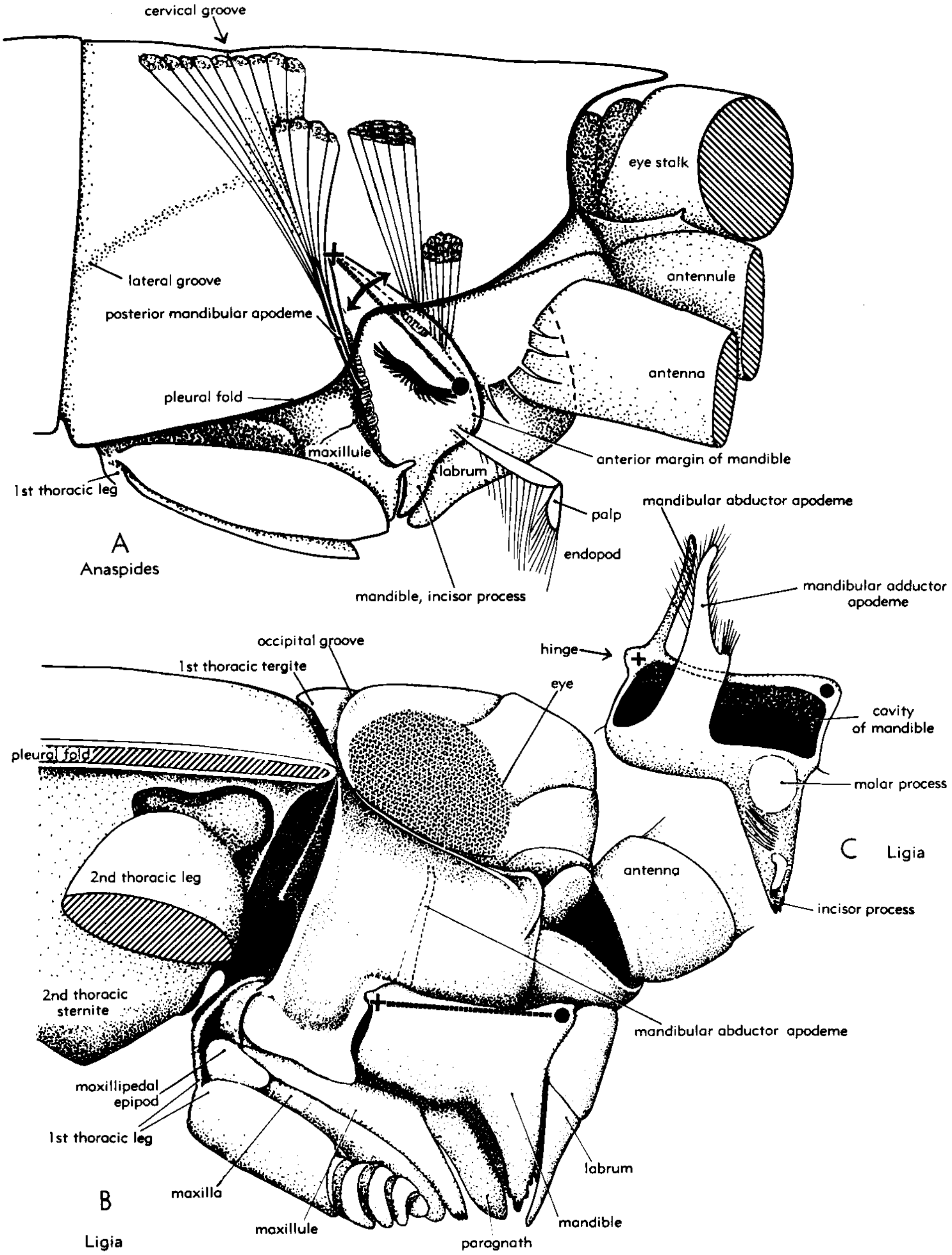

FIG. 4. Gnathobasic mandibles.

A,B. Lateral views of the heads of *Anaspides* and *Ligia* showing one mode of obtaining strong transverse biting from the simple promotor-remotor swing of a grinding mandible such as that of *Chirocephalus* (Fig. 3). Other and quite different methods of achieving transverse biting occur among some of the more specialized Crustacea. The mandibles in *A* and *B* consist of a massive gnathobasic portion with a distal palp (endopod) in *Anaspides*. The axis of mandibular movement is marked by a dotted line be-

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in Myriapoda-Insecta. These tubules often serve to eliminate dry or semidry urate excretion in place of the ammonotelic excretion by segmental organs existing in aquatic Crustacea, but the recent discovery that malpighian tubules of the centipede *Lithobius* excrete some 70 per cent of the total nitrogen as ammonia and only 8 per cent as uric acid (5) indicates how little we know of the full significance of the parallel evolution of these tubules.

That the compound eye of arthropods represents a "unique mechanism," the only practicable manner of meeting a common need, seems now inescapable. The compound eye appears to have evolved independently within the Crustacea and Insecta. Only some Crustacea possess a compound eye (Branchiopoda, Branchiura, Malacostraca) and their eyes are not exactly similar. Crustacea which lack the compound eye (Copepoda) do not appear to have secondarily lost these organs. A compound eye would not be expected to occur in the earliest ancestral Crustacea, although such eyes were possessed by the Trilobita and probably the Merostomata. Only the more advanced members of the Myriapoda (Scutigeromorpha) possess, with the hexapods, a compound eye, and again it is improbable that Onychophora and Myriapoda equipped with simpler eyes are anything but primitively so, although species living in darkness may be blind by secondary loss of eyes.

Until recently, the possession of a mandible has sometimes been regarded as a common feature linking the Myriapoda, Crustacea, and Insecta. Indeed, the conviction that all mandibles situated on the third head segment are directly homologous and indicate common inheritance has been strong enough for the erection of a taxonomic category, the Mandibulata. However, a functional, anatomical and developmental study of jaw mechanisms throughout the major groups of living arthropods shows that mandibles also have been independently acquired (43). A proximal endite or gnathobase is present on one or on many pairs of legs in Crustacea and Chelicerata and serves for manipulation or direction of food. The crustacean mandibular segment usually carries a very large pair of gnathobases, which, with the proximal part of the leg, forms a massive pair of mandibles; the distal part of the leg is reduced to a biramous or uniramous palp and may be entirely absent (Fig. 3-6). The jaws of the Onychophora, Myriapoda, and Insecta, on the contrary, develop from a whole limb, the distal part of the biting edge representing the limb tip (Fig. 8-11). The onychophoran jaw is very short, bearing a larger pair of terminal claws than do the walking legs (Fig. 9,*B*). The jaws of myriapods and hexapods are often longer than those of Onychophora, and, as in Crustacea, may extend up the "cheeks."

The onychophoran jaws slice anteroposteriorly, the pair moving in opposite phase essentially like the walking legs (Fig. 9,*B*). The movements of gnathobases or jaws of other arthropods are derivatives of one or other of two types of movement characteristic of ambulatory limbs, (1) the promotor-remotor swing of the coxa on the body about a more or less transversely placed axis, and (2) direct adductor-abductor movements in the transverse plane such as shown by a pair of telopods (Fig. 1, 2). Direct biting in the transverse plane is usually not a primitive arthropodan attribute owing to the difficulty of providing an abductor mechanism which will part mandibles so large that they form the most

FIG. 4. *(Continued from facing page.)*

tween the cross and spot, corresponding with the points similarly marked on Fig. 3. The pre-axial part of the mandible is progressively reduced as the dorsal articulation (cross) becomes more posterior in position (Fig. 5, right-hand side). An incisor process, situated far from the axis, gives effective transverse biting in *Anaspides* (Fig. 6), combined with some grinding by the molar areas, as a result of the promotor-remotor swing. In *Ligia* the promotor-remotor swing becomes a strong direct biting movement in the transverse plane and only a little grinding by the edges of the molar process is possible. A firm anteroposterior hinge forms the axis of movement in *Ligia*.

C. Mandible of *Ligia* (devoid of muscles) viewed from the sagittal plane, the esophagus passing directly upward above the molar process.

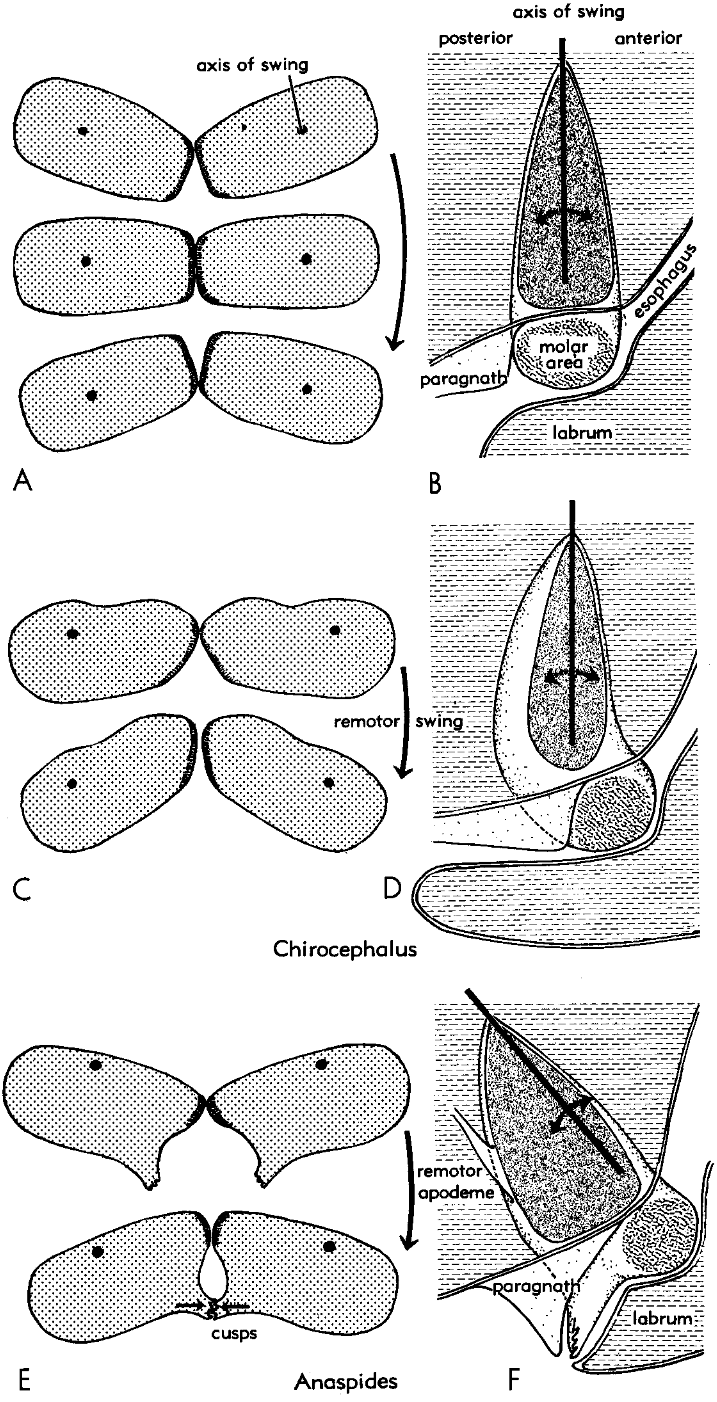

FIG. 5. Gnathobasic mandibles.

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lateral parts of the head. In Crustacea (gnathobasic mandible) and in the hexapods (whole-limb mandible) the more primitive living forms show a promotor-remotor swing of the mandible about an axis on which the lateral end slopes upward toward the dorsal head extremity (Fig. 3, 4,*A*, 5,*A*). Frequently a firm dorsal articulation is seen, but the mandible does not swing toward the middle line from this point to any great extent.

When the axis of the promotor-remotor swing slopes neither forward nor backward, the molar faces of the mandibles roll across one another on the promotor, as well as the remotor swing of the mandible, and there is very little direct abduction (many Branchiopoda and the thysanuran *Petrobius*) (Fig. 3, 5,*A*,*B*). The strong remotor movements roll the molar processes forward and together at the same time as the lateral bulge of the mandibles rolls backward. Adduction of incisor processes and grinding by molar processes both take place on the remotor roll as a consequence of the shape of the mandible and a backward-upward slope of the axis of swing (e.g., *Anaspides, Mysis,* etc.); abduction of the incisor processes and a parting of the molar processes occur on the promotor swing of the mandible as a whole (Fig. 4,*A*, 5, 6). Biting by incisor processes and grinding by molar processes are implemented by massive remotor musculature, inserted on to the head wall and on to a transverse mandibular tendon; the promotor muscles insert on the same sites but are much weaker.

The farther back the dorsal end of the axis of swing is situated, the greater is the adductor-abductor movement of the incisor processes and the less is the grinding movement of the molar areas. When the position of the axis approaches the horizontal, as in isopods, some Thysanura, and pterygote insects, the preaxial part of the mandible becomes much reduced and the axis forms a strong hinge line (Fig. 4,*B*, 8,*B*-*D*). Variety in mandibular movements is lost, grinding is impossible, but very much stronger adductor movements through a wide angle take place. The disappearance of the transverse mandibular tendon permits the wide gape, and direct adductor and abductor muscles, often pulling on very well-formed tendons and apodemes set at advantageous angles, result in a large mandible which can cut very strongly in the transverse plane. This end term in the evolution of mandibles has been reached independently many times from different initial conditions and by different means. For example, the nature of the mandible and the principles of its movement in the woodlouse and the crab are the same, but the details are entirely different and transverse biting has been convergently acquired. Also, it happens that mandibles of unlike nature in Crustacea and in Thysanura-

FIG. 5. (*Continued from facing page.*)

Diagrams showing the movements of simple crustacean mandibles that provide grinding only or grinding combined with some biting. Figures on the right show the median aspect of each mandible as seen in the left half of the body (muscles omitted and mandible drawn as if body is transparent, mechanical tint indicating the open concavity of the mandible that in life is filled by muscles). Figures on the left show frontal sections across the mandibles at successive moments during the remotor roll (axis of movement shown by black spots corresponding to heavy lines in right-hand figures, with arrows indicating direction of movements about the axis).

A,B. An ideally simple crustacean mandible which serves only for grinding. The axis is vertical (as in *Chirocephalus,* Fig. 3) and the symmetrical promotor-remotor swing about this axis rolls the molar areas across each other. The mandibles of *Daphnia* and of many other Cladocera closely approach this type.

C,D. Mandible of *Chirocephalus diaphanus* showing a forwardly bent molar lobe with range of the promotor-remotor swing enabling the mandibles not only to grind food but to push it forward toward the esophagus.

E,F. Mandible of *Anaspides tasmaniae* showing an oblique axis of swing placed near the anterior border of the mandible and a cusped incisor process lying far from this axis of swing. The promotor-remotor movement causes grinding by the molar areas and also biting by the incisor processes in approximately the transverse plane (see also Fig. 6). The above are the principal movements of these mandibles, but the looseness of the ventral end of the axis of movement permits other small movements to occur at times.

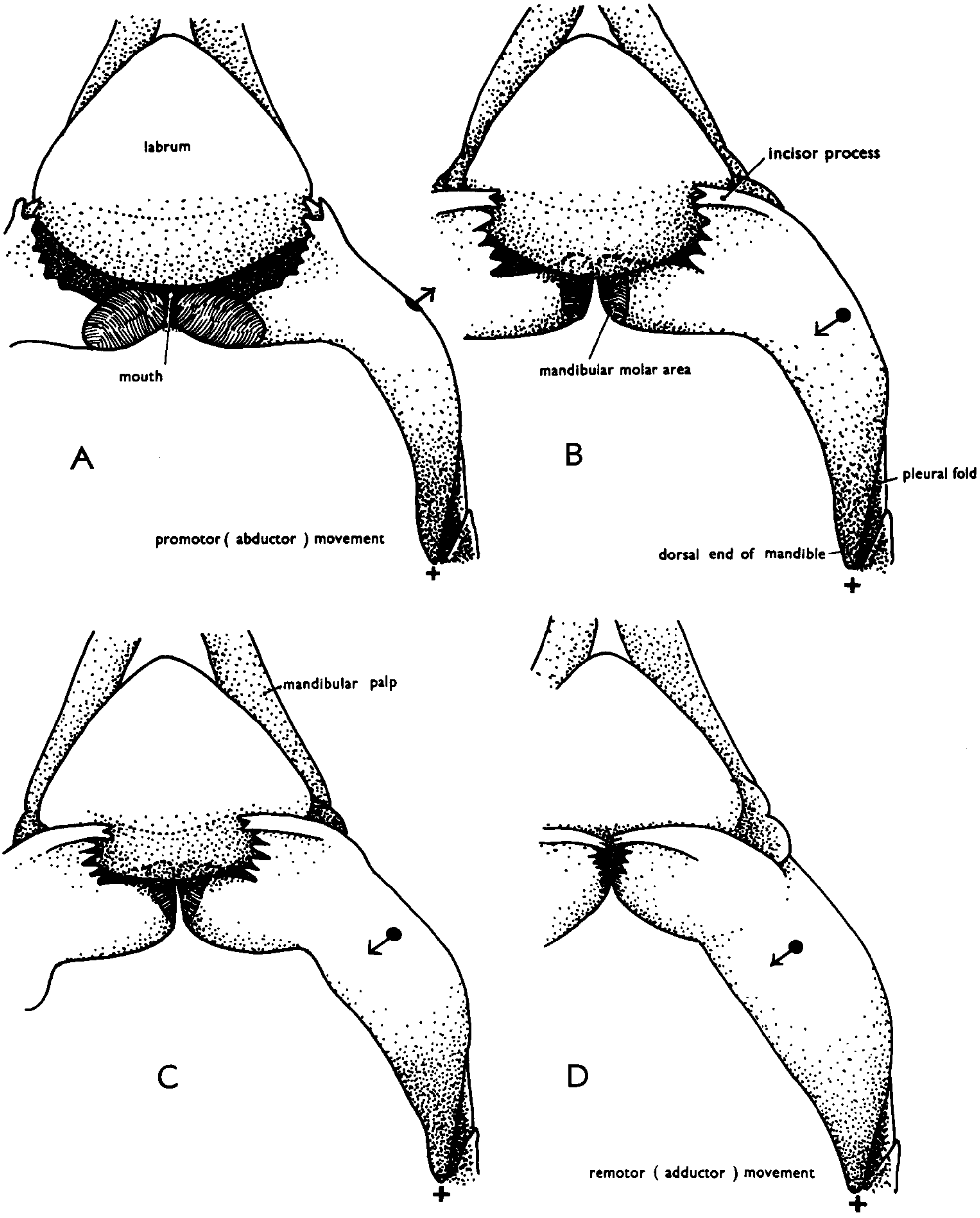


FIG. 6. Gnathobasic mandible.

Ventral views of the mandibles of *Anaspides tasmaniae* to show grinding by the molar processes and biting in the transverse plane by the incisor processes, both due to the shape of the mandible and the oblique position of the axis of movement. ——*A* shows the extreme end of a promotor swing (a little more extreme than in life), which opens a space between the molar lobes and parts the incisor processes as far as the labral margins.——*B,C,D* show the remotor (backward) roll of the lateral part of the mandibles, the black spot moving in the direction of the arrow, which brings the incisor processes together, moving along a hollow in the labrum. A further displacement of the axis of movement results in a predominantly biting mandible such as that of *Ligia* (Fig. 4,*B*). Other small movements occur at times.

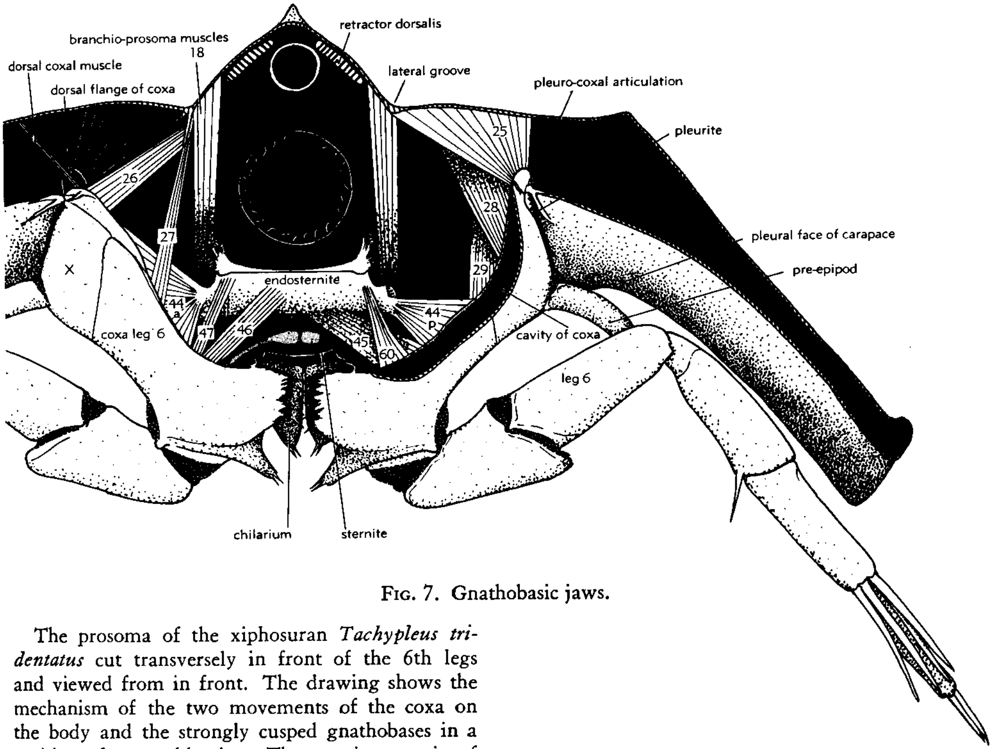


FIG. 7. Gnathobasic jaws.

The prosoma of the xiphosuran *Tachypleus tridentatus* cut transversely in front of the 6th legs and viewed from in front. The drawing shows the mechanism of the two movements of the coxa on the body and the strongly cusped gnathobases in a position of near adduction. The anterior margin of the 6th coxa is cut away on the right in order to display the posterior margin. The tight pleurocoxal articulation is marked. Elsewhere there is ample arthrodial membrane between coxa and body. Adductor-abductor movements in the transverse plane about the pleuro-coxal articulation cause direct biting by the gnathobasic cusps. Adductor muscles 44a, 46, 44p, and 45 are opposed by abductors 25 and 26 pulling on short levers dorsal to the pleurocoxal articulation. The walking movement takes place at right angles to the biting movement and is a promotor-remotor swing about a dorsoventral axis (cf. Fig. 2,*B*). Promotor muscles 27 and remotors 28 and 29 are probably aided by the dorsal parts of muscles 44a and 44p (muscles 28, 47, and 60 have other functions). The area X has been claimed to represent part of a precoxal segment but the evidence is considered to have doubtful validity, since the structures in question are directly related to the adductor-abductor mechanism and may not have a segmental significance (43a). The pre-epipod arises from this region and serves to keep sand away from the branchial filaments during the digging movements of the 6th telopods. The pre-epipod corresponds in position of origin with the outer ramus of the trilobite limb (see Fig. 12) and with the proximal exite of the crustacean *Anaspides* (Fig.2,*A*) and of *Chirocephalus* (see Fig. 13,*C*).

Pterygota have independently evolved very similar solutions to the problem of obtaining strongly cutting mandibles (Fig. 4,*B*, 8,*D*).

Two groups of arthropods (Myriapoda, Xiphosura), have achieved transverse biting without a preliminary promotor-remotor swing, and they have done so quite independently. The segmented mandibles of the Myriapoda essentially adduct like a pair of gripping telopods (Fig. 1,*C*). Their musculature is entirely or largely adductor in effect and there is little or no abductor mechanism appertaining to the mandibles themselves. In Chilopoda, Diplopoda, and Symphyla the tentorium is not a rigid endoskeletal system, as in the Pterygota, but has the form of internal bars which swing from the cranium. A downward-forward movement of the tentorium presses on the mandibles and causes abduction of the gnathal lobes. This mechanism is seen in its sim-

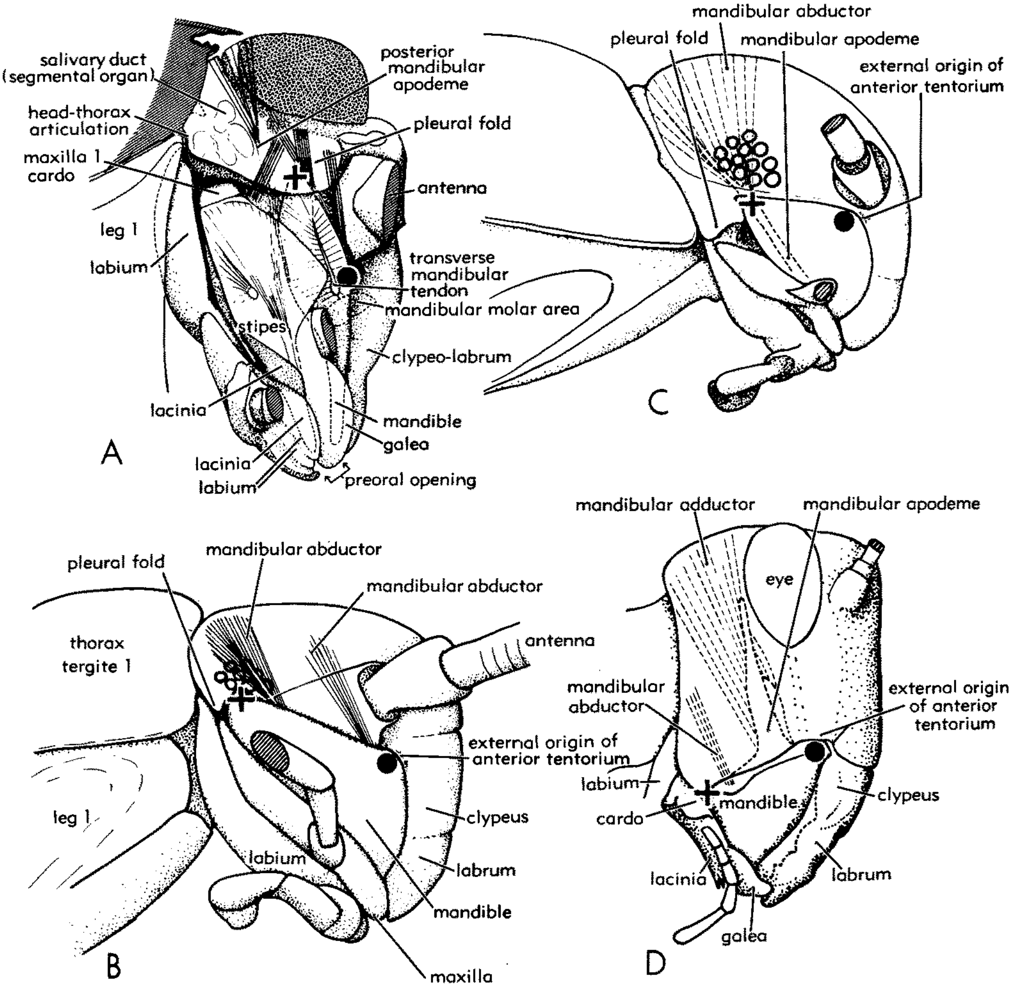


FIG. 8. Unsegmented whole-limb mandibles.

Side views of the heads of the thysanurans *(A) Petrobius brevistylis, (B) Ctenolepisma longicaudata,* and *(C) Thermobia domestica* and *(D)* of the migratory locust. The series shows a mode of obtaining strong transverse biting similar to that seen in the crustaceans *Anaspides* and *Ligia* (Fig. 3-6), but the mandible is formed from a whole limb and not from a gnathobase. The axis of movement passes through the cross and black spot of the diagrams.

In *Petrobius (A)* a tight articulation lies at the cross, and promotor-remotor movements cause grinding by the molar areas as in the branchiopod Crustacea (Fig. 3, 5). Scraping of the food surface by the distal points of the mandibles loosens particles which are then sucked up a food channel, owing to the boxing in of the mandible by the other mouth parts and superlinguae. No biting is possible.

In *Ctenolepisma (B),* as in *Anaspides,* the dorsal articulation of the mandible is displaced posteriorly, the pre-axial part of the mandible is reduced, and a firm hinge (between the cross and black spot) forms the axis of movement. There are no molar areas and strong transverse cutting and scraping by the distal mandibular cusps are now possible. The gape is small because many of the mandibular muscles still arise from the internal face of the mandible.

In *Thermobia (C)* the axis of movement is more horizontal and approaches the condition of *Ligia* (Fig. 4,*B*), but for the same reason the gape is small.

In the locust *(D)* the dorsal articulation of the mandible (cross) lies a little below the black spot. Strong articulations lie at these points and the pre-axial part of the mandible is small. The absence

(Continued on facing page.)

plest form in the Diplopoda (Fig. 11). The base of the mandible is strongly articulated with the head by an anteroposterior hinge line permitting adductor-abductor movements only. Very strong biting in the transverse plane is used by the diplopods in eating the large quantities of humus, leaf mold, decaying timber, etc., of low food value on which they feed. The symphylan mandible is more complex, being linked to the head by a single point of close union. This articulation allows a little promotor-remotor swing of the mandible to be combined with greater direct adductor-abductor movements, and some remotor mandibular muscles contribute to the biting effect. An additional extraneous abductor mechanism is provided by maxilla 1 which assists the tentorium in pushing the mandibles apart. The Chilopoda possess an even more elaborate mandibular mechanism in which, in contrast to the Diplopoda, proximal freedom and mobility in many directions of the mandible on the head is a conspicuous feature. This freedom is associated with the development of entognathy (see below) and is not primitive. The tentorial muscles again provide an abductor mechanism.

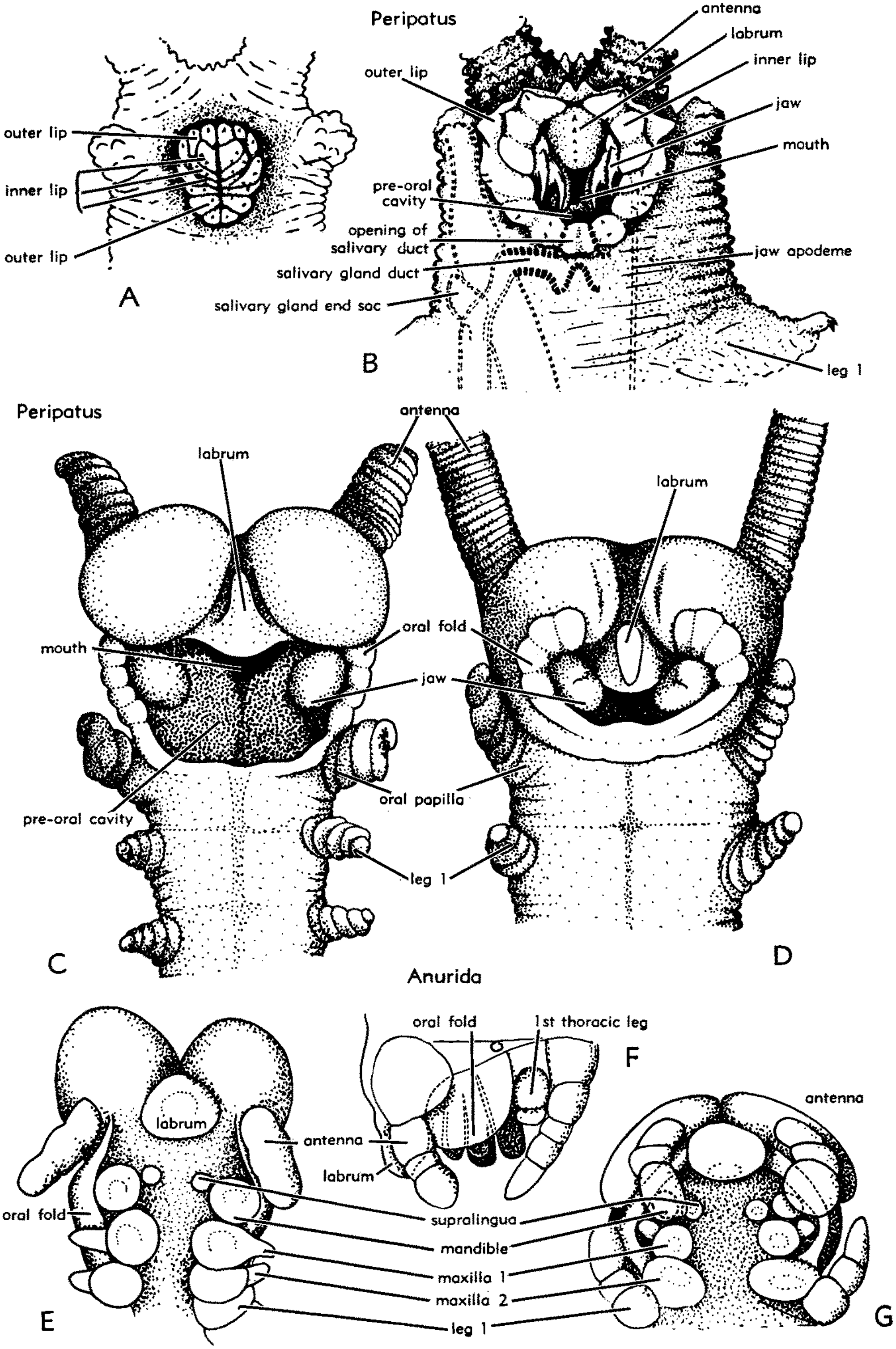
The segmented mandible of the myriapod classes represents an entire limb, as does the unsegmented mandible of the hexapods, but the principles and detail of the mechanisms of movement are entirely different in the two groups, and the one could not have given rise to the other. These groups show quite independent lines of jaw evolution, although based upon the use of a whole limb. An understanding of these jaw mechanisms makes the symphylan theory of insect origin untenable. The jaw and head evolution of the myriapod classes, although sharing a common basis, must have evolved independently. The mandibles of each class are much too specialized along their own lines to have been able to give rise to the types shown by the other myriapod classes.

Limulus also bites in the transverse plane, the gnathobases of prosomal limbs 3 to 5 chewing food by direct transverse biting, the phase difference between each pair being about half a cycle. The massive cusped gnathobases of legs 6 are used as "nutcrackers" to break the shells of lamellibranchs and cut up tough molluscan tissue (Fig. 7). The endopodites of these legs are used for walking and digging. The coxae are very wide at their attachment to the body, flattened anteroposteriorly and spread far up the flanks of the animal.

The basic walking movement in *Limulus* is the usual arthropodan promotor-remotor swing of the coxa on the body, implemented by extrinsic muscles pulling on the anterior and posterior margins of the coxa (Fig. 7, muscles 27, 28, 29). The biting movement takes place at right angles to this and is alternative to it. The dorsolateral coxal extremity forms a ball-and-socket joint with the pleurite. In front and behind this joint, two short cuticular expansions extend dorsally from the coxa and bear very stout but short abductor muscles (Fig. 7, muscles 25, 26). These levers, working at poor mechanical advantage, can pull the extreme dorsal part of the coxa inward a little and this results in much greater outward movement of the gnathobases. Massive adductor muscles pass from the coxa to the endosternite (Fig. 7, muscles 44a, 44p, 45, 46), a structure comparable with the partially fused transverse segmental tendons of postoral segments in Crustacea (30, 43a). No crustacean mandible or gnathobase has been found to possess a dorsal lever system causing direct abduction. Since the gnathobases of *Limulus* and crustaceans bite in such fundamentally different ways it seems unlikely that their limb evolution can have followed a common path.

FIG. 8. *(Continued from facing page.)*

of muscles arising from the internal face of the mandible and the mechanically advantageous disposition of the mandibular adductor and abductor muscles permit the use both of a wide gape and of a very large cutting edge which bites strongly in the transverse plane. This end term in jaw evolution parallels that of the crustacean *Ligia,* in general principles, but all the details are different, as is the nature of the jaw itself. [For further details see MANTON (43a).]


Peripatus
outer lip
inner lip
outer lip
A
antenna
labrum
inner lip
jaw
mouth
outer lip
pre-oral cavity
opening of salivary duct
salivary gland duct
salivary gland end sac
jaw apodeme
leg 1
B
Peripatus
labrum
antenna
labrum
mouth
oral fold
jaw
pre-oral cavity
oral papilla
leg 1
C
D
Anurida
oral fold
1st thoracic leg
F
labrum
antenna
labrum
antenna
oral fold
supralingua
mandible
maxilla 1
maxilla 2
leg 1
E
G

The survey which has recently been made of arthropodan jaw mechanisms (43) has disclosed yet another parallel evolution, that of entognathy or the formation of a pouch around the mandible so that only the tip can be protruded. Maxilla 1 sometimes is found to be lodged in the same pouch (Fig. 10). This character, in the absence of full morphological and functional details, has been put forward as one of taxonomic value (68) indicating close affinity between animals possessing it (Diplura, Collembola, Protura). But the jaws of Onychophora (Fig. 9) and the mandibles of Chilopoda are essentially entognathous and the mandibles of the Pauropoda also are functionally so, the boxing in being differently accomplished. Many parasitic Crustacea with stylet-like mandibles are entognathous, but no information is available as to how their stylets move. The principal advantage of the entognathous condition resides in the great freedom which is permissible at the mandibular union with the head, so that the mandible can become protrusible and very mobile; in many it shows rapid rotator and counter-rotator movements. The different ways in which mandibular protraction is achieved in Diplura and Collembola (and other differences) suggest that entognathy in these two groups has been independently acquired. Both could readily have been derived from an archi-*Petrobius*-like thysanuran state by enlargement of the small pleural fold, seen in *Petrobius* (Fig. 8,*A*), to form the side walls of the gnathal pouch. The preoral gnathal space of the Onychophora is developed embryologically in a very similar manner by the enlargement of lateral "oral" folds (Fig. 9,*C-G*).

The last important case of probable convergence which should be considered in any discussion of arthropodan interrelationships concerns the trunk limbs themselves. A biramous limb occurs in Trilobita, Merostomata, Chelicerata, and Crustacea (Fig. 2,*A*, 12, 13). No onychophoran, myriapod, or hexapod shows a trace of a true biramous condition in the leg; the walking legs of these animals represent the whole limb (Fig. 1, 2,*B*, 9,*B*; see Fig. 15, 16). The walking legs of Crustacea, trilobites, and *Limulus* (Fig. 2,*A*, 7, 12) are formed by the endopodite only, an exopodite being present or absent. This limb difference, combined with the jaw difference between the Crustacea and the myriapod-insect stem, is important and an indication of a fundamental lack of affinity between these groups.

Størmer (59, 60) and others have stressed the differences between the proximal exite or pre-epipod of the trilobite limb and the more distal single exopod of the crustacean limb. The Crustacea protopod may possess one or two proximal exites as well as the distal exopod, as in *Anaspides* (Fig. 2,*A*), but among the vast and varied assemblage of crustacean limbs none show a proximal exite or pre-epipod possessing a comb of respiratory plates as on the trilobite pre-epipod or the outer part of the branchial limbs of *Limulus*. The 6th prosomal limb of *Limulus* possesses a nonbranchial pre-epipod or exite (Fig. 7) resembling the pre-epipod of the trilobites and the proximal exite of *Anaspides* (Fig. 2,*A*), but not the crustacean exopod. These fundamentally different leg patterns suggest independence in their evolution.

Fig. 9. Form and development of gnathal pouch in arthropods *(on facing page)*.

A,B. Ventral views of the oral region of *Peripatopsis sedgwicki* showing (in *A*) the round lip (outer and inner lips) closed over the jaws and pre-oral cavity, and (in *B*) the position of the mouth behind the labrum with jaw blades (two to each jaw) slicing widely from front to back at sides of the mouth (jaw apodemes indicated by dotted lines). The circular lip is composed of inner-lip and outer-lip folds.

C,D. Oral views of embryos of *Peripatus edwardsii* (younger one in *C*, and older one in *D*, redrawn from Kennel, 1886). Paired oral folds at sides of the jaws in young embryos *(C)* unite with each other behind the jaws in older embryos *(D)* so as to enclose the pre-oral cavity, later joining also in front of the labrum.

E-G. Oral views of embryos of the collembolan *Anurida maritima* showing oral folds in early stage (*E*, redrawn from Folsom, 1900) lateral to both mandibles and maxillules but at later stage (*F*, lateral, *G*, ventral) with labrum and labium (maxillae) united to form walls of the gnathal pouch.

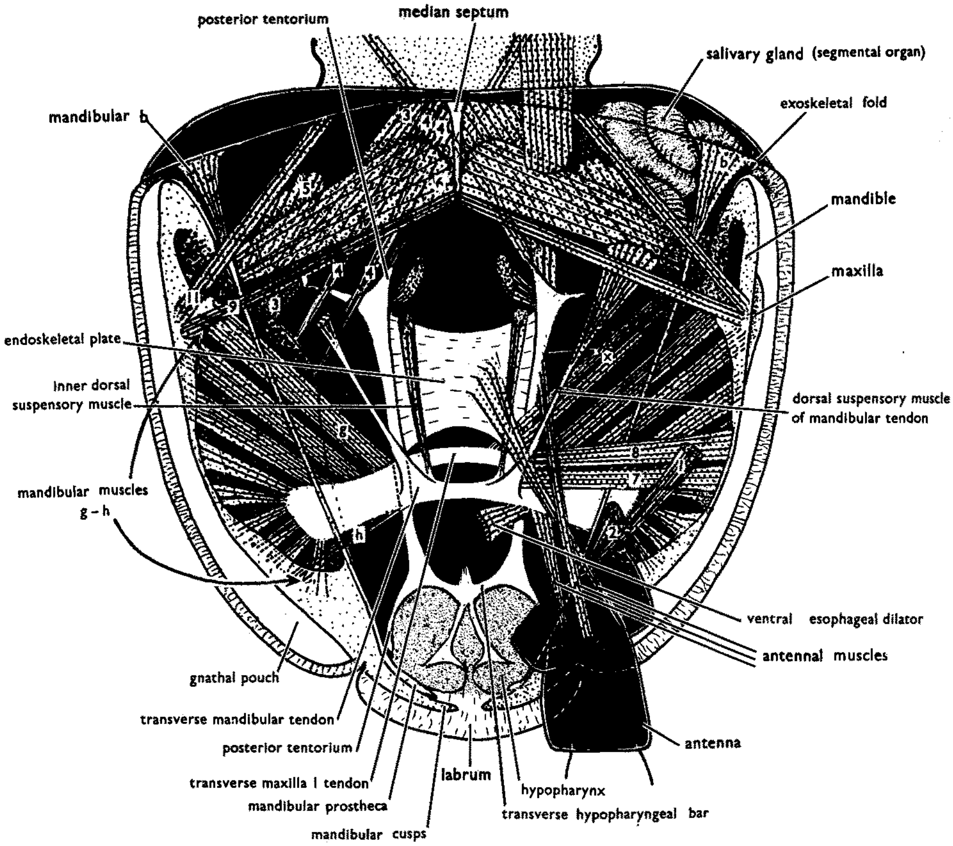


Fig. 10. Unsegmented whole-limb entognathous mandible.

Anterodorsal reconstruction of the head of the dipluran *Campodea staphylinus,* drawn as a transparent object, to show the entognathous mandible enclosed in a gnathal pouch. The antenna is omitted on the left. The mandible is not articulated with the head but is attached by loose arthrodial membrane and moves against cuticular bearings which permit a great variety of movements, including protraction and retraction. A promotor-remotor rolling movement about the long axis of the mandible essentially resembles that of *Petrobius.*

The positions of origin (Fig. 2) and the movements of arthropodan coxae are various, both being bound up with the leg mechanisms. Evolution along one path of coxal advancement may be just as effective a one-way street as are some of the types of mandibles or the basic forms of the trunk. There does not appear to be adequate support for the view (56, 58) that arthropod limbs are primitively pleural in position and basically associated with or articulated with pleural sclerites, as in insects. A ventral or ventrolateral origin of the legs exists in Onychophora, Diplopoda, and Crustacea, the legs arising on or against the sternite unless the leg base is so wide, as in some Branchiopoda, as to need no particular articulation and to leave no space for a sternite. The flanks of Diplopoda and Crustacea are well armored in contrast to those of *Limulus,* Arachnida, Chilopoda, and Symphyla. In the latter classes the legs are set in flexible pleuron, except at one point, and the coxae perform multiple movements. Here there is a ventral point of close union between the coxa and some major sclerite, usually the sternite, but with a pleurite in insects. There is no justification for explaining away these differences in leg insertion by feats of terminology, such as calling the diplopod sternite a pleurite (58).

The reconstruction in the transverse plane of trilobite limbs (59) shows a wide base to the coxa, as in *Limulus* (Fig. 7, 12), and there must have been ample flexible cuticle around most of the coxa-body union. One would like to know whether the trilobite coxal insertions were really as ventrally directed as suggested by the reconstructions. Enrolment was possible at least to some trilobites, and this implies considerable ventral flexibility in association with the stiff dorsal cuticle. Possibly ventrally directed coxae and an approximation of the body proper to a half cylindrical shape facilitated enrolment, as in modern arthropods (36, 41). But it is also possible that dorsoventral flattening of a trilobite occurred after death, producing the apparently ventrally directed fossil coxae which in life mav not have been unlike those of the prosomal limbs of *Limulus*. Thus it is clear that the Crustacea contrast with the Xiphosura and Trilobita in the pattern of their biramous limbs; and that the Crustacea contrast with the Xiphosura, and perhaps with the Trilobita also in the absence of the flexible pleuron which allows the various types of coxal movements seen in *Limulus*.

In view of basic differences in the types of coxal insertions and of outer ramus, and the complete absence of this ramus in the Onychophora-Myriapoda-Insecta group, the general similarities in some details of a leg and of a walking endopod are likely to be explicable on a basis of similar functional needs (Fig. 2). No evidence supports the suggestion (58) that a particular number of leg segments existed in an archiarthropodan leg, and that present numbers in the various groups have arisen by reduction or multiplication of leg segments from this archetype.[1] It is more probable that a single ancestral type of leg never existed. The more we are able to comprehend the mechanics of leg movement and the variety of ways in which legs are used, the clearer it becomes that segment number, type of jointing, position of a "knee," etc., are intimately bound up with function (38). But there are differences, such as the coxa-body articulations of myriapods and insects, which indicate a fundamental and early divergence of two groups along independent and mutually exclusive evolutionary lines.

In myriapods the principal proximal coxal articulation is ventral and with the sternite, but in insects it is lateral and with a pleurite, the latter being firmly fixed to both tergite and sternite. In all myriapods a promotor-remotor swing of the coxa on the body takes place, as in Crustacea, but in Symphyla, Chilopoda, and Pauropoda mechanical usefulness results from a simultaneous rock of the coxa about its sternal articulation, so that the dorsal surface of the leg becomes a little anterior during the propulsive backstroke, rocking in the opposite direction on the recovery forward swing. Mobile pleurites and special musculature causes this movement. In insects such a rocking movement is impossible because of the rigidity of the pleurite to which the coxa is articulated. The myriapod type of coxal movement carries with it the suitability and usefulness of a series of hinge joints between the more distal leg segments, each joint lacking extensor muscles. The insect type of coxal articulation permits far more varied movements of the coxa on the body than in myriapods, promotor-remotor, adductor-abductor and twisting about the pleurite, but a series of pivot joints worked by antagonistic pairs of muscles is needed all along the leg. No myriapod leg could be considered as a mechanically suitable forerunner of insect legs. In the pursuit of speedy running in myriapods many specializations have occurred in leg and joint construction: long intrinsic and extrinsic muscles give large displacements of the segments they move; leg joints are weak but allow wide angles of flexure; and mobile pleurites support the leg base in progressive measure as leg length and speed of running increases, culminating in *Scutigera*. In strongly burrowing centipedes four pleurites encircle the coxa and support the strong slow leg move-

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[1] There are, however, examples of arthropods in which certain leg segments have divided and others which have fused in association well-known functional needs. The tarsus of fast-running Diplopoda (Lysiopetaloidea) and Chilopoda (some Scolopendromorpha and Anamorpha) has divided into two or more segments, and the trochanter in certain myriapods has fused with the next distal or proximal segment (38).

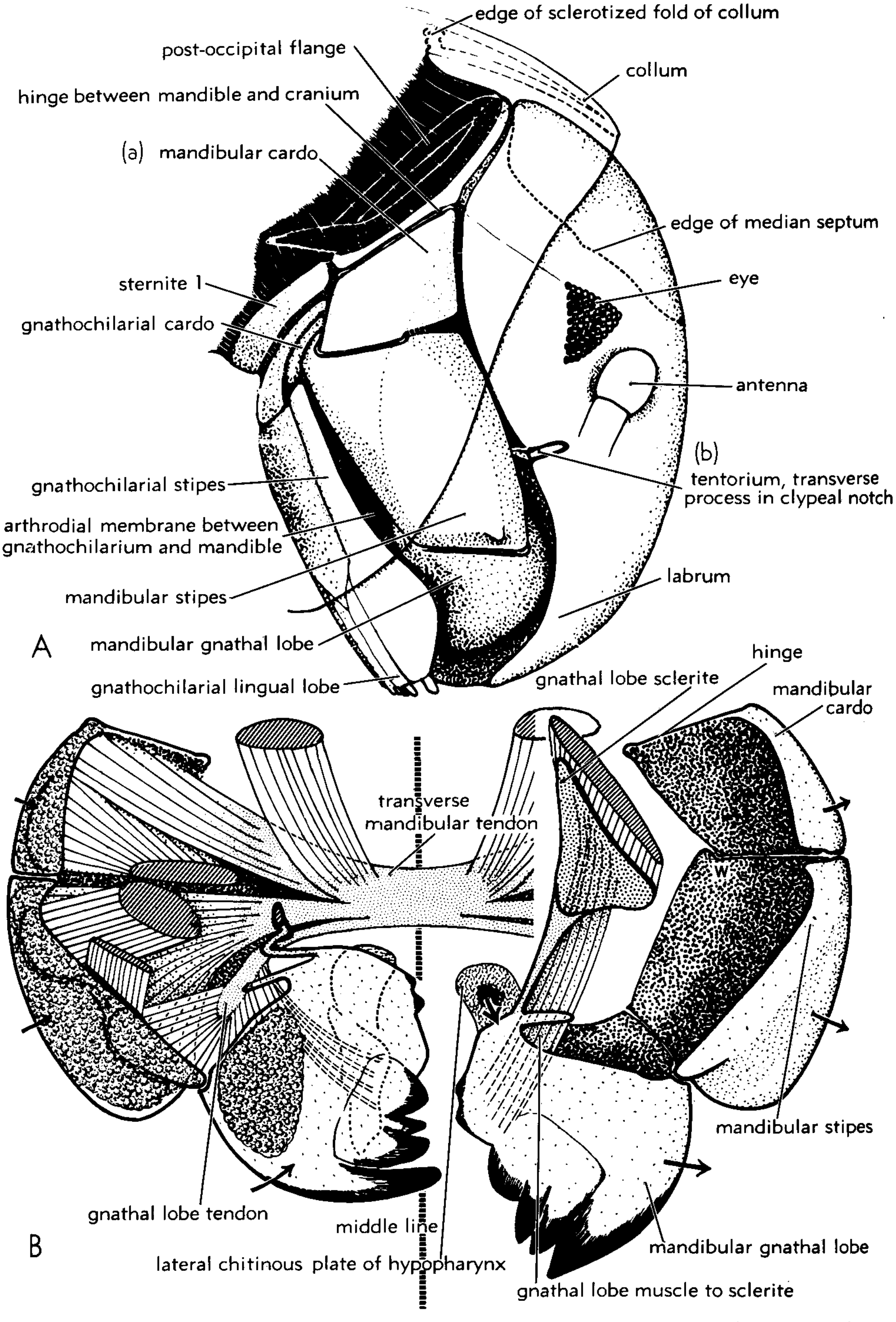

FIG. 11. Three-segmented whole-limb mandible of a iuliform diplopod *(Poratophilus punctatus)*.

ments, another advancement of pleurite evolution. The myriapod type of leg is suitable for a many-legged animal, and an end term in respect of speedy running appears already to have been reached. This type of leg does not have the potentiality of leading to few pairs of relatively larger, stronger, longer legs as in insects. And myriapod extrinsic and leg-base muscles are not suitable for evolution into flight muscles, as are the comparably placed muscles in insects (44).

The brief references made here to mandibular mechanisms and to limb movements in living arthropods need amplification for their full comprehension (38, 43, 43a, 44, and future publications). It is clear that all available data concerning details of joints, possible axes of movement, etc., in fossil forms, besides the morphology of leg rami, respiratory filaments, etc., will be most valuable in building up a fuller picture of arthropod evolution and interrelationships.

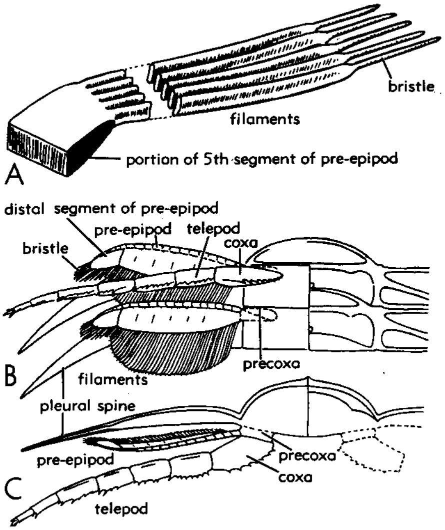

FIG. 12. Limbs of trilobites.

A. Diagrammatic reconstruction of the filaments of the outer branch of a limb of *Ceraurus pleurexanthemus* (Ordovician).

B,C. Reconstruction of limbs of *Olenoides* [*Neolenus*] *serratus* (Middle Cambrian) (after 59).

In view of the strong probability of a parallel evolution of uniramous legs and of more than one type of biramous leg, as well as several types of jaws and compound eyes, and a variety of respiratory and excretory organs, we may ask, what surety have we that surface sclerites and a hemocoel have been evolved once only in metamerically segmented animals? It must be remembered that Mollusca also have a hemocoel, that the Annelida comprise animals (e.g., *Hermione*) which can stand up on very leglike parapodia and walk without any ventral contact with the ground; the mechanism of movement, however, is annelidan and not arthropodan in that to a considerable extent the annelids use the motive force of trunk muscles in walking, and an acicular mechanism provides essential parapodial length changes during stepping. The Annelida, as well as Arthropoda, possess a surface cuticle, and the arthropodan cuticles do not fall into a simple unified scheme in their fine structure and chemical composition. It will be shown below how the absence of surface sclerites in the Onychophora is bound up with the manner of survival of these animals and does not constitute a reason for regarding the group as subarthropodan in status. It should also be

FIG. 11. *(Continued from facing page.)*

This mandible, which bites directly in the transverse plane, cannot have been derived from one that utilizes a promotor-remotor swing such as is seen in hexapods (cf. Fig. 8, 10).

A. Lateral view of head with the antenna cut short and the collum drawn as if it were transparent. The mandibular cardo *(a)* articulates with the head along the marked hinge line. The tentorium *(b)*, which provides the abductor force used to part the mandibles, swings from the clypeal notch.

B. Anterior view of isolated mandibles showing musculature and articulations. All mandibular muscles are adductor in function. On the left the mandible is in a position of maximum adduction. On the right most of the muscles have been removed to display the three mandibular segments, and the gnathal lobe is in a position of extreme abduction. The contrasting positions of the lateral hypopharyngeal scutes on either side are shown. The heavy arrow on the right indicates the direction of thrust by the anterior tentorial apodeme aaginst the gnathal lobe which abducts the mandibles.

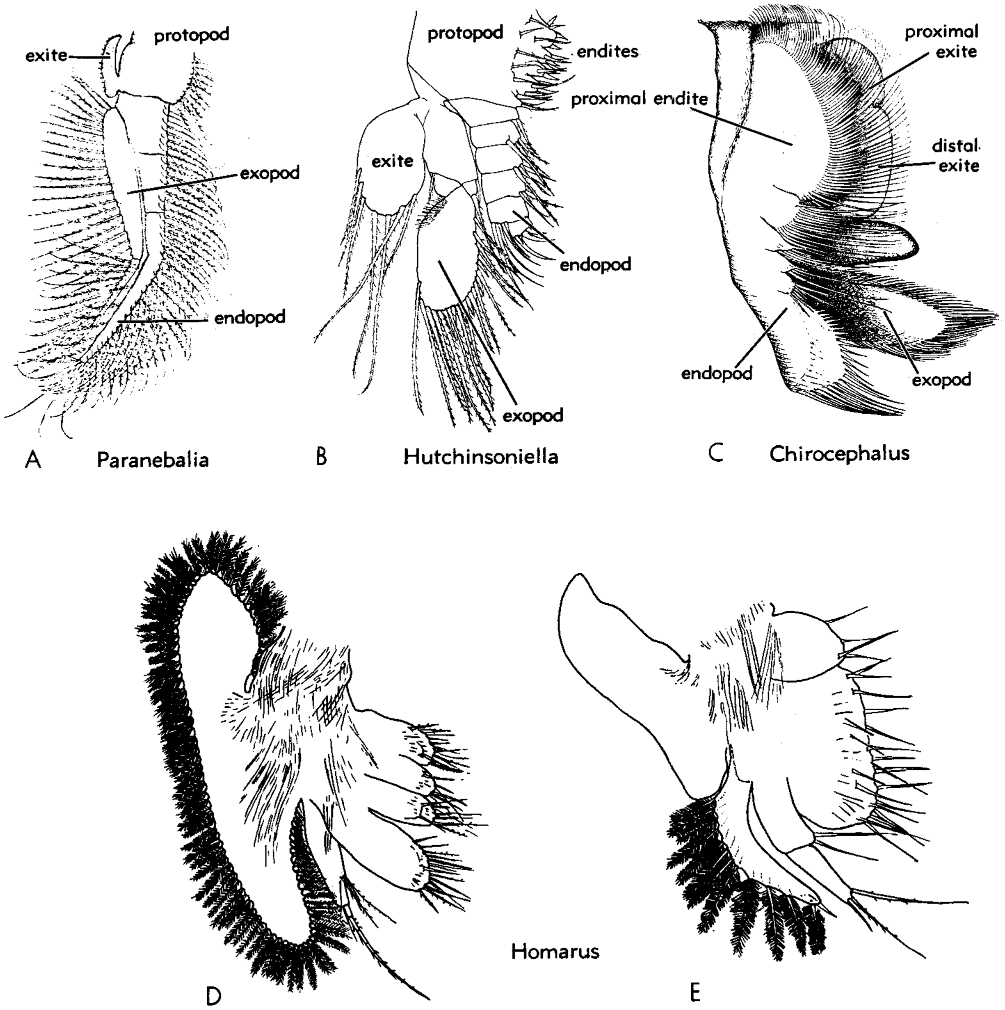

FIG. 13. Crustacean limbs which possess most of the basic parts—protopod, endopod, exopod, endites, and exites.

A. Fifth thoracic leg of *Paranebalia longipes* (after Calman, 1909).

B. Fifth thoracic leg of *Hutchinsoniella macracantha* (after 50).

C. Median view of trunk limb of *Chirocephalus diaphanus* in its natural position with backwardly directed exites and endites (after 8).

D. Second maxilla of first larva of *Homarus americanus* (after Herrick, 1895).

E. First maxilliped of first larva of *Homarus americanus* (after Herrick, 1895).

The limbs shown in *C-E* are markedly flattened (phyllopodia).

The limb of *Anaspides tasmaniae* (Fig. 2,*A*) is a typical stenopodium and also possesses most of the basic parts. Many stenopodia are reduced to the protopod and a walking endopod, thus superficially resembling the uniramous limbs of myriapods and hexapods (Fig. 2,*B*).

noted how clearly the polyphyletic origin of mammals (26) and of reptiles has been demonstrated by the fossil record. Quite independently, a number of separate lines of vertebrates have reached these grades of organization. The threshhold of a new grade depends on definitions and is essentially arbitrary. It would be surprising indeed to find no polyphyly in the origin of so vast and varied a group as the Arthropoda.

Many questions remain to be answered. As yet, we can give no precise functional interpretation of the formation of the arthropodan procephalon. A preoral cavity is more marked in most myriapods and hexapods than in Crustacea, and is formed by ventrolateral bending of anterior segmental components relative to the mouth, so that three segments become apparently preoral. The preoral cavity surrounding the mouth usually opens subterminally. At first sight, this similarity in head composition, in spite of the disparity in number of sensory limbs (antennules and antennae), appears so striking as to preclude explanation by convergence. But with the evidence concerning eyes, limbs, jaws, etc., before us, together with present ignorance of the factors which have led to head formation, the matter of segmentation of the procephalon must await further functional study. Meanwhile, the possession of three preoral segments cannot be taken as sound evidence of affinity between Crustacea and the land types.

HABITS CORRELATED WITH EVOLUTION OF LARGE TAXONOMIC UNITS

Specializations which fit animals to live in particular ecological niches are easily recognized, but this type of structural modification has usually not led to the evolution of classes or orders. Structural features which facilitate habits of life, such as running, pushing or squeezing through cracks, have hitherto been little appreciated and are of great importance. Recent work (34, 36, 37, 38, 41, 42, 43a, 44 and future publications) on the locomotory mechanisms and other habits of terrestrial arthropods has shown how conspicuous characters, which are diagnostic of classes and of orders, are correlated with some all-important habit or habits. These may be one or two of many habits exhibited by the animal, and if exercised frequently are easily recognized (e.g., diplopod bulldozer-like burrowing and characteristic feeding), but if the habit becomes of selective value only occasionally it may be less easy to apprehend. For example, the amazing structure of the Pselaphognatha is bound up with the ability to live, molt, and reproduce on the ceilings of small crevices, even on glass-smooth rock, together with an ability to run fast, which takes these tiny creatures out to alga-covered surfaces for feeding and back again to the same hiding place. These animals can survive in this manner under adverse conditions which would exterminate them from the many less favorable habitats they adopt when survival pressure permits.

Characters such as overall shape of the animal, number of segments, details of the skeleton and joints on the body and legs, form of the sclerites, together with their reduction or multiplication in number, detail of the musculature, formation of a thorax, etc., are correlated with habits such as (1) the diplopod ability to burrow by bulldozer-like pushing, the motive force being supplied by the legs; (2) the geophilomorph centipede habit of burrowing by an earthworm-like technique, the body surface applying the thrust; (3) the fast running and carnivorous habits of Chilopoda; the Scolopendromorpha and Lithobiomorpha strongly adapted for crevice living and catching and eating prey in confined places no deeper than the tergite-sternite span, while the Scutigeromorpha show end terms in structural modifications of trunk and legs which permit these fleetest of all centipedes to lead a more open life, catching flies, etc.; (4) the symphylan habit of seeking shelter deeply in soil, litter, or logs, but without pushing, the great flexibility of the body permitting sufficient twisting and turning for these little creatures to pass through small channels without extreme deformation; (5) the onychophoran habit of seeking refuge by extreme body deformation, again without pushing, so passing through narrow crevices which give access to larger cavities in decaying logs, under stones, etc., into which sizable

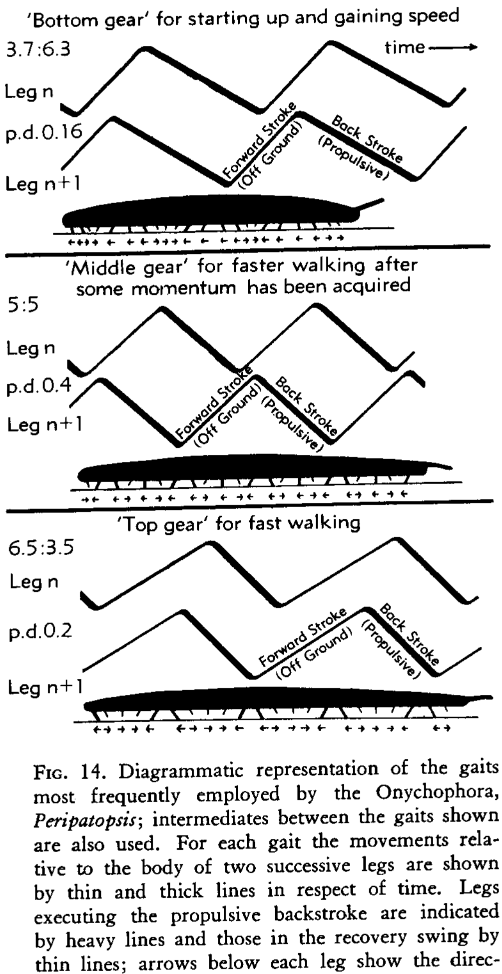

FIG. 14. Diagrammatic representation of the gaits most frequently employed by the Onychophora, *Peripatopsis*; intermediates between the gaits shown are also used. For each gait the movements relative to the body of two successive legs are shown by thin and thick lines in respect of time. Legs executing the propulsive backstroke are indicated by heavy lines and those in the recovery swing by thin lines; arrows below each leg show the direction of movement. The durations of the forward and backward strokes are as (3.7:6.3), (5:5), and (6.5:3.5) in *A, B,* and *C,* respectively, *p.d.* indicating the phase difference between successive legs (see legend to Fig. 15). A further advancement of the type of gait shown in *A* has led to the gaits and diagnostic trunk features of the Diplopoda (Fig. 15,*A-C*); an exploitation of the type of gait shown in *B* has led to the gaits of the epimorphic Chilopoda and the associated trunk characters (Fig. 15,*D-F*); the type of gait shown in *C* has been elaborated by the anamorphic Chilopoda again in association with the evolution of conspicuous trunk morphology. The type of gait shown in *B* is seen also in the slower gaits of the Pauropoda and in the faster gaits of Symphyla, but with an improvement in the stepping made possible by the presence of pointed sclerotized limb tips. The utilization of the latter type of gait by the ancestors of hexapods has avoided the morphological specializations referred to above and paved the way for hexapod evolution.

predators cannot follow; (6) the habit of hexapods in running on three pairs of legs and of arachnids in running on three or four pairs represents a way of achieving speedy movement which does not limit the choice and variety of practicable gaits, as is imposed on some centipedes and isopods by the evolution of many pairs of long legs. [This list could be lengthened but it suffices to indicate the type of habits that are important in the evolution of the structural features which are diagnostic of large terrestrial taxonomic groups, features which facilitate the attainment of the various proficiencies.] There are also interesting secondary habit reversals, such as lysiopetaloidean diplopods which have given up the ability to push strongly and have achieved a measure of fleetness and carnivorous feeding. Here, chilopod-like modifications of structure are superimposed upon the basic diplopodan anatomy of these animals, but they are neither primitive diplopods nor related to centipedes.

When the relationship between structure and habits is understood it is possible to assess the significance of much hitherto meaningless body structure. Real affinity can be distinguished from convergence, and one can decide with surety which end of a morphological series is the less advanced. There has been much doubt and controversy about such matters in the Myriapoda. The Scutigeromorpha, for example, in the absence of any functional understanding of the conspicuous characteristics of their trunk and limbs, have been considered to be the most primitive and not the most advanced of all centipedes. No doubt now arises as to the trunk and limbs of *Scutigera* being end terms in centipede advancement correlated with speedy running. Only the heads lacks the extreme flattening seen in burrowing and crevice-living centipedes, and these specializations are not needed by the Scutigeromorpha. The eyes of these animals are fittingly the most advanced of all Myriapoda, as are the mandibles (43a).

Similarly, opinions have been divided as to the probable primitive length of body in myriapods. In the absence of a functional appraisal of these features, some persons have suggested that short bodies, and others that long bodies, are the more primitive. An analysis of locomotory mechanisms (5, 34, 36) shows that a moderate or small number of trunk segments favors speedy running; many segments, forceful burrowing. As with a machine, even loading contributes to smooth running, and an even load on each leg of *Lithobius* during its propulsive backstroke can be achieved during the fastest gaits if 13 pairs of legs are employed; a smaller or a larger number leads to uneven loading. The early instar with 8 pairs of legs cannot employ so speedy a pattern of gait as can the adult if the mechanical advantage of even loading is maintained. Mechanical advantages are associated with the presence of 14 pairs of ambulatory limbs in *Lithobius*, the 14th pair being ambulatory only during slow running, and on occasion provide a gripping posterior holdfast. The functionally optimum number of trunk segments is bound up with other matters also, such as the potentialities of muscle physiology.

This brief outline roughly indicates the scope of morphological interpretation of trunk characters which has so far been reached, and, as with the jaw mechanisms, reference must be made to the full accounts for details. The bearing of this type of investigation on elucidation of the evolution and affinities of some of the major classes of arthropods may now be considered.

EVOLUTION AND RELATIONSHIPS OF ONYCHOPHORA

The Onychophora, which frequent damp environments in logs, crevices, under stones, etc., mainly in the southern hemisphere, have variously been interpreted as primitive, intermediate between annelids and arthropods, and even nonarthropodan. A reasoned argument for alignment of the Onychophora with the progenitors of myriapods has been given by Tiegs (66). An arthropodan heart, hemocoel, and cuticle are present, confirming their arthropodan status. A simple head, comprising three segments, is followed by a trunk not demarcated into regions and bearing many pairs of uniramous limbs. A simple alimentary canal performs excretory functions, as well as digestion and storage, and segmental organs are well developed, those on the third segment forming the enormous salivary glands which correspond with the premandibular salivary glands of Pauropoda and Symphyla.

Onychophoran embryonic development is of myriapodan type, not of crustacean or chelicerate type. Coelomic sacs are strongly developed, with large initial cavities, and the long series of coelomoducts even includes those of the antennal somites. The penultimate coelomoduct forms a genital duct directly comparable to the primitive opisthogoneate ducts of myriapods. The progoneate myriapods appear to be secondarily so (62, 65, 66). The teloblastic manner of laying down the embryonic trunk, which characterizes the Malacostraca with long embryonic developments (Manton, 28, 30, and the many subsequent workers on other species), is entirely absent in Onychophora, Myriapoda, and Insecta.

In *Peripatopsis capensis*, among the Onychophora, and in *Pauropus silvaticus*, among the Myriapoda, a recognizable gastrula is present. In *P. balfouri* the blastopore is virtual and the primitive endodermal cells degenerate, never forming an epithelium. In *P. sedgwicki* and in *P. moseleyi* these cells are never formed, the apparent blastula being really a gastrula devoid of endoderm, the definitive adult endoderm arising later and in another manner (32). Tiegs (62, 66) has pointed out essentially the same sort of series in the Myriapoda-Hexapoda. In *Pauropus* only one, or at most two, primitive endodermal cells lie within the gastrula epithelium, and give rise to the endoderm. The symphylan gastrula is composed of a superficial blastoderm covering a mass of yolk cells, a large proportion of which degenerate but some form the mid-gut. In most myriapods and insects the primitive endoderm disappears and the "blastoderm stage" is a postgastrula, not a blastula stage as had commonly been believed. It is remarkable to find such close correspondence in gastrula modifications

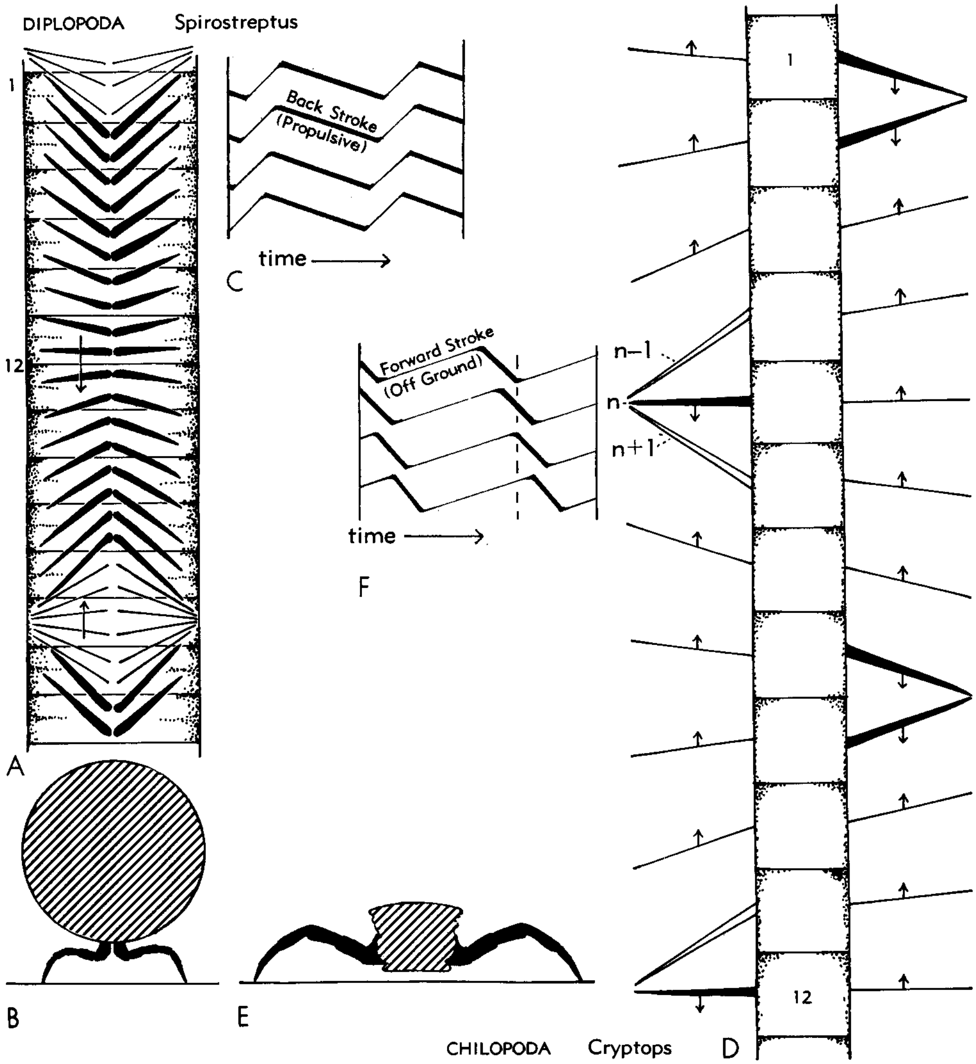

Fig. 15. Diagrams representing types of gait used in pursuance of the contrasting habits of Diplopoda and Chilopoda, together with some of the characteristic trunk morphology of these two classes which is correlated with the execution of these gaits.

The segment volumes of the diplopod *(A, B)* and of the chilopod *(D, E)* are similar and the figures show the very different shapes of the segments and the position of origin of the legs. The 12 trunk segments of the chilopod *(D)* correspond with the 6 marked diplosegments, each with two pairs of legs of the diplopod *(A)*.

In *C* the movements of four successive legs illustrate one of the slow strong gaits of a diplopod which are used in burrowing, and *F* shows a fast gait of an epimorphic chilopod used in running. The forward swing of a leg is indicated by a thin line and the propulsive backstroke by a thick line, as in Fig. 14. The relative durations of the forward and backward strokes are (2.5:7.5) in *C* and (7.5:2.5) in *F*. The phase difference between successive legs, expressed as that proportion of a pace by which leg n+1 is in advance of leg n, is 0.042 in *C* and 0.857 in *F*. Thus many legs are in the propulsive phase at one moment in the diplopod *(A)*, resulting in strong pushing, and few legs are in contact with the ground at one moment in the chilopod *(D)*, resulting in speed. Limb tips n—1

(Continued on facing page.)

proceeding in parallel manner within the Onychophora and the Myriapoda-Insecta, in contrast to the Crustacea.

Lastly, the nerve ganglia of Onychophora develop in association with "ventral organs," as they do in myriapods but in no other arthropod. These embryonic features provide very strong evidence of onychophoran-myriapodan affinity, which, although outside the scope of paleontology, should be generally recognized.

The superficial similarity between the mid-Cambrian *Aysheaia* and extant Onychophora is very great and appears to indicate antiquity of the onychophoran stem. Whether *Aysheaia* was sea-living or littoral is uncertain. If this type of animal "has set in train the evolution of the great terrestrial groups of myriapods and insects . . . it will have been one of the most momentous events in the whole Palaeozoic age" (66).[1] Further data concerning this important matter emerge from a study of habits.

Peripatopsis can pass through a hole in a card which is but one-ninth of the transverse sectional area of the resting animal. Slowly, by locally deforming the body and one leg at a time, the animal voluntarily traverses such a space, and Onychophora habitually squeeze through narrow passages before coming to rest (39a, 43a). The advantages of gaining protection from predators in this manner appears to have been over-riding, and the whole morphology, slow movements, and primitive undifferentiated gaits (Fig. 14) are associated with it. Correlated features are (1) the furrowed cuticle, which consequently can expand in all directions, though the surface layer of sclerotization is unstretchable; (2) the velvety appearance, due to the presence of papillae bearing sensory spines; (3) the fibrous subcutaneous connective tissue "skeleton" on to which the muscles are inserted, expandable in all directions though its fibers are probably unstretchable (cf. coelenterate mesogloea); (4) the lack of surface sclerites, although the capacity to form sclerotized plates is present (see jaw blades, claws, and long jaw apodeme extending through several segments figured by MANTON, 31); (5) the primitive jaws, made very effective by entognathy, with ability to cut a hole in a sizable arthropod, so that the contents can be sucked out or portions cut up and swallowed (31); (6) unstriated muscle fibers capable of great length changes, such as are impossible to striated but more quickly moving fibers, and the slow movements which keep changes in hydrostatic pressure minimal, as in Actiniaria (2, 3); (7) the defensive weapons in the form of slime ejection from oral papillae, the slime setting at once and entangling a predator at a distance of some inches; (8) the gaits employed in walking are amazingly primitive (33, 34, 42, and a future publication), but an animal depending for its survival on the habits already described has no need of speedy running or strong pushing, etc.; (9) Onychophora do not need acute vision for their crevice-living and walking abroad at night, or (10) an ability to hinder water loss from their innumerable spiracles supplying unbranched tracheae, a ureotetic metabolism effecting considerable conservation of water (31). Dry places do not easily provide food and are no attraction. (11) The extremely hydrofuge cuticular surface serves to keep water out. (12) Internal fertilization, with oviparity in some species and a variety of very efficient modes of viviparous development, constitute reproductive advances which are second to none among the Arthropoda.

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[1] TIEGS' (66) admirable discussion of this subject contains erroneous references to and deductions from the embryology of Onychophora because a modern account (32) was not then available to him and he based his remarks upon the work of the last century.

FIG. 15. *(Continued from facing page.)*

and n+1 in *D* are stationary; these legs are being lifted up and put down respectively at the moment shown by the vertical dotted line in *F*. Legs of a pair are in similar phase in *A* and in opposite phase in *D*. The pace duration of the chilopod can be very much less than that of the diplopod. The diplopod gait is a derivative of the type shown in Fig. 14,*A*, and the epimorphic chilopod gait is a derivative of the type shown in Fig. 14,*B*. For further description see text and the original accounts (33, 34, 35, 36, 43a, etc.).

A functional account can thus be given of all the major features of the Onychophora. The head segmentation stands at a lower level of advancement than that of all myriapods, hexapods, and crustaceans, and possibly indicates a very early adoption of the over-riding habit of life. Archiarthropods of this general type, but with less specialized heads (appendages and preoral cavity), could have become pauropods, diplopods, chilopods, symphylans, and hexapods by progressive evolution of the head and the pursuit of other habits of life, but no community exists with arthropods possessing biramous legs and gnathobasic jaws. An independence of early arthropods with uniramous limbs from other lines with biramous limbs is probable, and the acquisition of such limbs probably preceded the development of sclerites in the onychophoran-like line or lines which led to the dominant land types.

EVOLUTION AND RELATIONSHIPS OF MYRIAPODA AND HEXAPODA

These groups have in common a three-segmented procephalon with antennae borne on the second segment and in some species evanescent limb rudiments on the third or premandibular segment. This entails the formation of an antenna on the second segment, instead of a jaw, as seen in the Onychophora. Many examples of a shift of the segmental origin of jawlike or grasping organs in Arthropoda can be cited, and an early separation of the onychophoran and myriapodan types of procephalon might not be extraordinary in a related stock of terrestrial arthropods. Some crustaceans bite with a mandible-like antennal gnathobase and not with the mandible (e.g., nauplius of *Thalestris rodameniae*); male claspers arise on the antennal or on the first and second thoracic segment in Branchiopoda. A two-jointed gripping claw is present on the antenna in the naupliar stages and on the maxilliped in the copepodites and adult of the harpacticid *Thisbe,* both claws being exactly similar in shape and size.

The sclerotized head capsule presumably arose by the incorporation of the three-segmented procephalon with two (*Dignatha,* comprising Pauropoda and perhaps Diplopoda) or three (*Trignatha,* comprising Chilopoda, Symphyla, and hexapods) trunk segments, the limbs of these segments serving feeding purposes.[1] A preoral cavity is formed by a bending of segments and not by a progressive backward shift of the mouth out of one segment into the next. This cavity primarily conserves fluid and digestive juices around the mandible, and around other mouth parts in some arthropods.

All myriapod and hexapod classes typically possess a partial or complete armor of sclerites. The evolution of sclerites has permitted the formation of more quickly moving striated muscle fibers, and an abundance of joints is needed for speedier ways of life and a differentiation of habits. The initial function of sclerites was probably protective and useful in pushing against the substratum, but, as in present-day Geophilomorpha and some Scolopendromorpha, the sclerites probably did not form an inflexible armor. The presence of tiny cones of sclerotization set in the flexible unsclerotized endocuticle of the margins of certain sclerites (6) enables these sclerites to change shape considerably by rolling the margins inward to various extents. This capacity is much specialized in present-day epimorphic centipedes, but a less perfect version may have been a first step in habit divergence from seeking shelter by body deformability without pushing (as in Onychophora) to shallow burrowing by actively pressing on the

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[1] The table showing arthropod segmentation given in *Treatise Part O,* Arthropoda 1, p. O11, and the accompanying account of arthropod segmentation needs emendation. The embryology of no chelicerate shows more than one precheliceral segment (see Dawydoff, 15, and the original accounts). The fallacy of interpreting an arthropod head as composed of a series of modified cylindrical segmental components has been considered (40). Much of the dorsal part of the head has no primary segmental origin because it is derived from unsegmented blastoderm taken over from an unsegmented ontogenetic stage. The diagrams in text-fig. 7*A-C* of *Treatise* Part O, have no reality in living arthropods. The reference to the concept of primary and secondary segmentation (put forward originally by Ivanov, 25), does not represent the views of embryologists in general on this subject (32).

soil. Once sclerites were present, unlimited possibilities in habit divergence were opened up, culminating in the ability to lead an exposed life in dry places and to fly.

PAUROPODA

Tiegs' (66) studies of *Pauropus* led him to regard it as "a dwarfed, simplified, but also in some respects very specialized, survivor of a primitive stock of myriapods, in which only two segments have been added to the procephalon; and it is probable that when their development is better known, the diplopods also will be found to be members of this group. . . . The presence of a limbless collum segment in Diplopoda and Pauropoda even suggests a community of origin for these two groups."

Both the feeding arrangements and the locomotory mechanism of *Pauropus* are specialized. The elimination of alternate tergites gives stability to the body and limbs in executing fast gaits. A similar tendency is seen progressively in the Chilopoda (35, 43a). The limbless collum segment with its great dorsal shield in the Diplopoda is correlated both with bulldozer-like burrowing and with the ability to enroll in a spiral. *Pauropus* is much too wide to roll up and too small to push effectively. If its ancestors had been larger, less fleet, and less specialized, it might be possible to guess from the general morphology of fossil finds the original usefulness of the collum in this class. The mobile, protrusible entognathous jaws and the tentorium (hypopharyngeal apophysis) are clearly specialized along lines of their own, although giving the same general advantages of entognathy seen in other groups (43, 43a).

DIPLOPODA

The longitudinally incompressible strongly calcified armor and the formation of diplosegments are the most conspicuous features of this group, together with the usual smooth strong outlines of the head and the manner in which the antennae can be tucked away. Both these and a host of other details are correlated with the ability to burrow by strong head-on pushing using the motive force of the legs (36, 37, 39, 42). Many legs provide a strong anterior thrust on the soil (See Fig. 15,*A*,*C*), but a very long body must be firmly held by intersegmental musculature and in any curvature dictated by the soil contents, in order that the force exerted by the legs may be transmitted to the head end. A shortening and deepening of segments will mitigate the evil, but much greater shortening and deepening can be effected if segments are fused together in pairs because the space needed by every other joint is eliminated. Propulsive legs cannot project far without causing interference in soil burrowing, and their mid-ventral origin gives maximum protection by the flanks, in contrast to chilopod legs which arise laterally and are fully exposed (see Fig. 15,*B*,*E*). The parallel-sided Iuliformia probably show the closest approach to an ancestral diplopodan method of burrowing, but there are many divergencies. An anteriorly tapered body and the long laterally projecting legs of the Polydesmoidea favor the splitting open of layers of decaying leaves. The thrust is exerted by the whole dorsal surface and a progressive forward movement of the wedge-shaped front end widens the crevice. Such animals cannot burrow into compact material.

It seems probable that diplosegments and a burrowing habit may have evolved before the perfection of an ability to enroll. The manner of formation of diplosegments is uniform, but the modifications facilitating enrollment at the anterior end are very different in the various orders (36, 42) suggesting independent acquisition. The modifications include the limblessness of the collum segment, its large tergite extending no more than halfway down the flanks. The three following segments carry only one pair of legs and commonly possess free sternites; these segments are less deep than the main part of the body and have a variety of muscular specializations, and permit space being found for the intucked head on enrolment and a spreading out of the legs on walking. The exactly cylindrical shape of the body or joints is associated with spiraling, for the segments need to twist on one another as the animal walks away from the spiral position (a total rotation of 90 degrees may be needed). Further specializations for enrolment into a sphere and not a spiral are shown by the short-bodied Oniscomorpha; their capacity for burrowing is poor, since they possess fewer limbs. As yet, the diplopod fossil material does not show clearly whether the anterior segments had only one pair of legs, but the general form of the anterior segments in fresh finds of early diplopodan fossils may indicate whether enrolment was practiced or not. There is nothing in common functionally between the three single-legged segments of a diplopod and the thorax of a hexapod; the two are in no way comparable, as has sometimes been supposed.

The Colobognatha have, on quite inadequate grounds, been regarded as the most primitive of living diplopods. In fact, they show a perfection of "wedge"-burrowing carried further than by the Nematophora (42). A propulsive thrust for burrowing is enhanced by the utilization of trunk as well as limb musculature. *Dolistenus savii* can exert a pushing force some three times greater than that of any other diplopod of comparable size which has so far been recorded. The segmental sclerites can telescope into one another, unlike the longitudinally incompressible Iuliformia and Polydesmoidea. Segments of progressively larger diameter at the anterior end are dragged forward by the trunk muscles, so widening a crevice. That this represents a secondary and not a primitive condition is shown by the very great muscular changes which make this habit possible. The progressive development of suctorial feeding within the Colobognatha entails profound modifications of mandible and tentorium and represents a major divergence from the feeding apparatus of typical diplopods.

It is probable that in myriapods several sclerites per segment preceded a welding of the sclerites into a rigid whole (cf. Crustacea; see below). The latter condition facilitates strong burrowing. But the usual presence of free sternites and frequently free pleurites also in the Colobognatha cannot, in their present form, be regarded as primitive. These sclerites are invisible or hardly visible in side view, and they contribute to the reduction of the body to a dorsal half cylinder with a flat ventral surface. This shape facilitates enrolment; the transverse axis of movement between the tergal arches is maintained at the ventral diameter of the cylinder, so eliminating a need for considerable ventral compression on enrollment. The axis of movement is sometimes maintained in this position by sternites which overlap from behind forward and pleurites which overlap in the reverse direction (36, 42). These features suggest specialization and are not at all like the probably primitively free pleurites of the Permian *Pleuroiulus* (17). Some Colobognatha (e.g., *Siphonophora hartii*) are even capable of enrolment in the lateral plane upon the ceilings of hides, an ability not found in other orders, and certainly not primitive.

The strong slow movements of diplopod legs when moving against a resistance show, at any one moment, very many legs in the slow propulsive backstroke and few legs performing a rapid recovery forward swing. This type of gait is a direct derivative of the onychophoran "bottom gear" gaits, and the greater the number of simultaneously pushing legs, the greater will be the total momentary output of force (Fig. 14, 15).

Reference has already been made to the diplopod mandibular mechanism composed of a very strong three-segmented mandible biting in the transverse plane (Fig. 11), and a mobile tentorium providing the abductor force. Such a mandible could have been derived from a simple whole-limb mandible, presumably characteristic of early unknown terrestrial arthropods.

Thus the primary habits of life which have acted as determinants of the evolution of diplopod characteristics relate to strong pushing, protective enrolment, and the eating of large quantities of vegetable matter of low food value.

CHILOPODA

Centipedes possess a trignathan grade of head development and the evolution of their outstanding features is associated with carnivorous feeding and more speedy running than practiced by Diplopoda and Onychophora. Primitive fossil chilopods, should they be discovered showing more detail than those recorded by Scudder (53), would be expected to possess a moderate number of segments (perhaps 25-35), each segment armored by a principal and an intercalary tergite and sternite and a few pleural sclerites set in ample flexible lateral body cuticle. No further tergite heteronomy would be expected. Moderate powers of burrowing would have been exercised by the body, locally becoming alternately thicker and thinner, the dorsal and ventral surfaces pressing on the soil. The legs would be short and freely projecting from a lateral origin; the coxae would be wide and short.

Among living centipedes well-formed intercalary sclerites are present in Geophilomorpha and the less advanced of the Scolopendromorpha. Here the intercalary and principal sclerites slide over one another dorsally and also become convex on body, shortening under the influence of the stout longitudinal trunk musculature. A thickening of a few segments travels tailward, the segments in front of the thickened zone, which is stationary to the ground, becoming thin and advancing forward. Speedy running is accomplished by swinging of the legs through a wide angle and the utilization of fast patterns of gait in which the duration of the propulsive backstroke may be only one hundredth of a second (*Cryptops*) and few legs (1 in 10 to 1 in 20) are in the propulsive phase at any one moment.

An early parting of the ways of centipedes in two directions has led to (1) the perfection of an earthworm-like burrowing technique (Geophilomorpha), and (2) speedy running, and at night a more surface-living habit (Scolopendromorpha and Lithobiomorpha), culminating in the very fleet Scutigeromorpha, which hunt flies by day. Worm burrows, soil cracks, and stones, particularly in warm countries, provide deep shelter for inexpert burrowers that can run. The requirements for these two habits are in many ways opposed. For burrowing, short wide segments and many of them, a pavement of pleural armor, and short legs are required, the legs on the anterior third of the body being stouter than the rest. Extrinsic leg muscles are not bulky, but the dorsal, lateral, and ventral longitudinal muscles need and use all the space they can obtain. For speedy running a flexible pleuron with isolated sclerites is required so that the coxa can swing tangentially to the surface about a ventral fulcrum. The coxae need to be short but dorsoventrally deep and well emarginated posteriorly. These coxal modifications, found also in Pauropoda and Symphyla, are bound up with fast movements.

Acceleration is obtained in Scolopendromorpha by the use of gaits with progressively fewer legs in contact with the ground at any one moment, until a minimum of two to three points of support on each side of the body is reached, legs of a pair being used in opposite phase (Fig. 16,*D*). During slow running, when the points of support along each side are close together and more numerous, the body can be held straight, but as the points of support become farther apart, the body tends to undulate in a horizontal plane. Such undulations are undesirable for mechanical reasons, and devices providing a progressive measure of control are found in the fleeter members of the Scolopendromorpha and in the Anamorpha. Intercalary tergites become smaller, less mobile and disappear, tergites become alternately long and short, the short ones finally being so small as to be invisible in dorsal view (Scutigeromorpha); extrinsic leg muscles and dorsoventral and oblique trunk muscles shift their insertions from the short to the long tergites, and the dorsal musculature becomes heteronomous. Each long tergite becomes strongly tied by muscles, directly and indirectly to five successive sternites. These features progressively reduce the mobility of the joint between the anterior end of each long tergite and the posterior end of the short tergite in front during fast running. The most stable part of the body lies at the seventh and eighth tergites, both of which are long, and fused together in Scutigeromorpha. The head and antennae of *Peripatus*, centipedes and some diplopods are alternately turned from side to side as the animal walks, the antennae touching the ground and sensing a path wide enough to take the leg track. In fast-running centipedes these movements start the anterior body undulations which are damped out or reduced at the seventh or eighth tergite region. *Scutigera* possesses

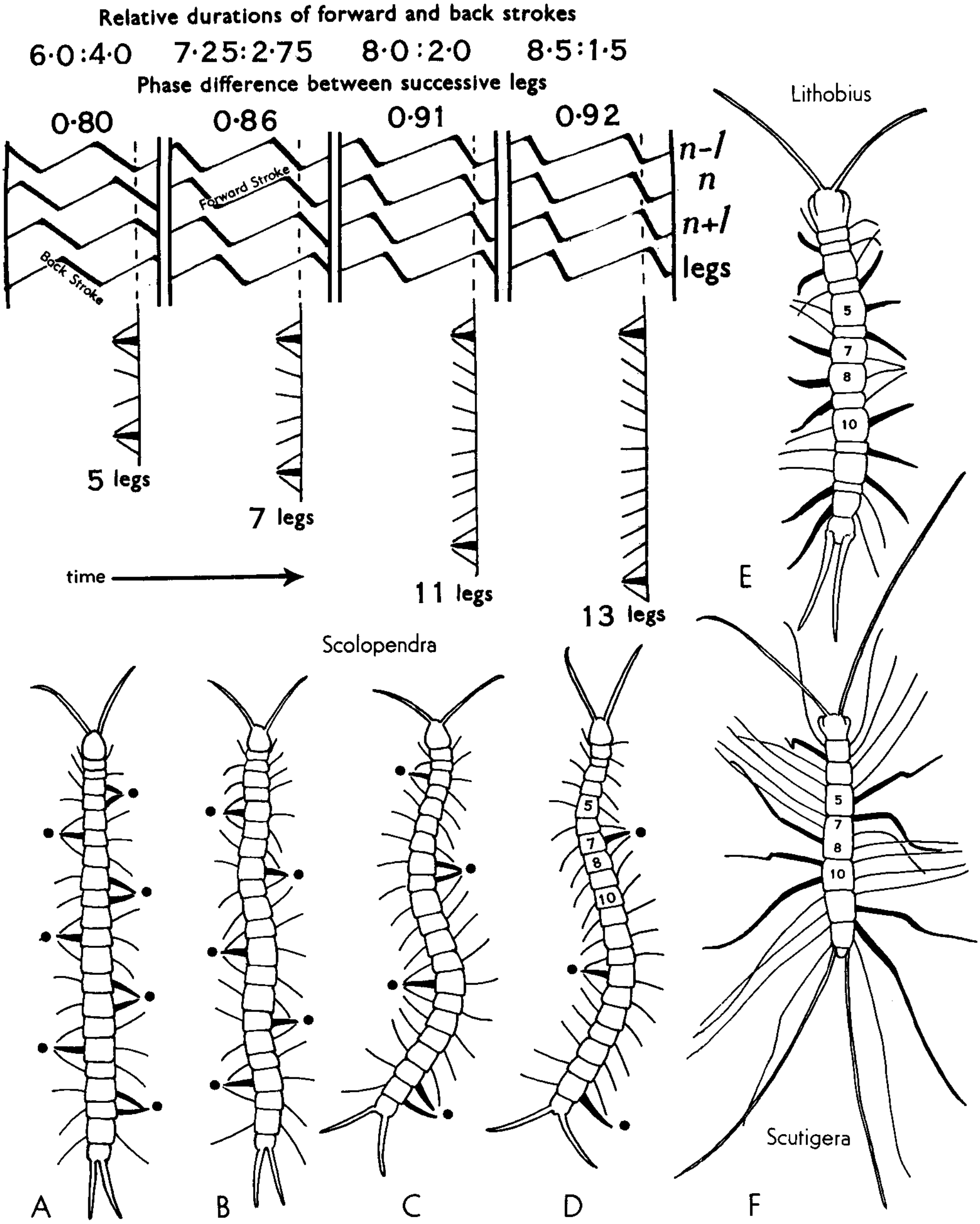

FIG. 16. Data illustrating some of the correlations between the habit of fast running of centipedes and their trunk morphology.

The lower diagrams *(A-D)* are tracings of photographs of *Scolopendra cingulata* running progressively faster. Legs with their tips in contact with the ground and performing the propulsive backstroke are shown in heavy lines; legs off the ground performing the recovery forward swing are shown by thin lines. The points of support of the body against the ground are indicated by black spots. The distances between the black spots show the stride lengths. Legs 1 and 21 are not used in fast running.

(Continued on facing page.)

the longest and most elaborate of centipede legs, each operated by 33 extrinsic muscles as compared with 13 pairs in a geophilomorph and two in a iulid. If the antiundulation mechanism here were less perfect, undulations would make the use of a large angle of swing by so many long legs set close together quite impossible and slower speeds would result. Sclerite perfection has, in fact, led to an economy in longitudinal trunk musculature, so making space for the abundance of extrinsic leg muscles. These locomotory perfections, together with the greater control of water loss by the formation of only eight median respiratory openings, the utilization of the blood for the transport of respiratory gases, and the compound eyes have made possible the more open habits of Scutigeromorpha. Centipedes do not run fast all the time, they run their fastest with reluctance, but it is the ability to make a supremely speedy effort occasionally which secures a meal or escape from a predator and is of selective value.

The specialized poison claws, the entognathous whole limb, but segmented, mandibles and the first and second maxillae suit flesh-eating but not the cutting up and swallowing of hard parts. The extreme head-flattening in all but the Scutigeromorpha is related to hunting and manipulating food in narrow places. This type of head evolution is entirely opposed to that of the Diplopoda, although both could have come from a common archimyriapodan type, and both use the mobility of the tentorium to obtain mandibular abduction.

Thus, the Chilopoda clearly represent an evolutionary line parallel to that of the Diplopoda, neither being the more primitive nor specialized in similar ways. Chilopodan evolution shows a dichotomy in life cycle, the Epimorpha hatching with many segments and the Anamorpha with few; but these groups differ also in their basic manner of hunting and in the use and structure of their poison claws and mandibles. Both have gone in for speed but in rather different manners, and they have solved their common antiundulation

Fig. 16. *(Continued from facing page.)*

Above are shown the gaits employed by the animals drawn below. The movements of four successive legs are given from left to right (arrow), the forward swing being indicated by a thin line and the propulsive backstroke by a thick line. The vertical dotted lines show the moment in time when leg n is halfway through the backstroke legs n—1 and n+1 converging on to the same footprint as they are picked up and put down respectively. The phase difference between successive legs is defined in the legend to Fig. 15.

As the faster patterns of gait are employed *(A-D)* so the relative duration of the backstroke decreases, and it is obligatory for the phase difference between successive legs to increase simultaneously (in order that the body always be supported over the common footprint and very long stretches of unsupported body be avoided). The points of support of the body on each side become farther apart in *A-D,* the metachronal waves comprising 5, 7, 11, and 13 legs respectively. Body undulations are absent in *A,* and are present in progressive measure in *B-D*; in *D* the animal is supported by three points in all.

The body length and segment number allow slight, but advantageous, anterior and posterior fanning out of the fields of movement of the legs; a shorter body could not accommodate the fastest gaits of *F*; the lateral origin of the legs and their length ensure a wide angle of swing and a long stride; the alternate-sized tergites, and the successive long tergites corresponding with legs 7 and 8, by their morphology and muscular connections, provide a measure of control of the deleterious body undulations.

Figures *E* and *F* are tracings of photographs of *Lithobius forficatus* and *Scutigera coleoptrata,* respectively, running fast (conventions as in *A-D*). Compared with *Scolopendra (D),* the legs of *Lithobius* and *Scutigera* are progressively longer, yet the undulations of the body are progressively smaller, owing to the increase in heteronomy of tergite lengths. The short tergites 2, 4, 6, 9, 11, and 13 are minute and covered by the long tergites in *Scutigera,* where 7 and 8 are fused at the zone of maximum stability. *Scutigera* is the fleetest of all centipedes and a lack of control of body undulations would make speedy running by long legs an impossibility. The exact number of trunk segments, tergite shapes, and leg lengths in these anamorphic centipedes are correlated with fast-running habits, but the gaits employed differ from those of *Scolopendra* (for further details see MANTON, 35, 43a).

needs in the same way but to different degrees. The Epimorpha alone have perfected the primitive method of burrowing (Geophilomorpha), and without doubt the Scutigeromorpha represent the most advanced of all Chilopoda (43a).

SYMPHYLA

This small class of myriapods is of great interest because it appears to resemble the hexapods more closely than does any other myriapodan class. The Symphyla possess 14 trunk segments as in some insects (62, 65), with cerci on the 13th (62) as in Campodea (69). The trignathan head bears a labiate second maxilla, the progoneate condition secondarily superseding the primitive opisthogoneate state, probably as a consequence of anamorphic development. Many curious resemblances exist, such as the presence of a similar embryonic dorsal organ in Symphyla, Collembola, and *Campodea.* A range of gaits such as seen in Symphyla could have given rise to those of hexapods simply by reduction of leg number. The gaits of diplopods, chilopods, and pauropods are much too specialized along their own lines to form a basis for hexapod movements. The easy conclusion that Symphyla stand nearer to the insects than any other group of myriapods is not, however, substantiated by a further understanding of the head and trunk.

The mobile anterior tentorium of Symphyla resembles that of the myriapods and does not resemble that of insects where a posterior as well as an anterior tentorial apodeme is present (43). The two-segmented mandible, performing direct adductor-abductor movements, contrasts with that of the hexapods and could not have been a forerunner of the latter. As in other myriapods, an abductor mechanism extraneous to the mandible is present. This is partly provided by the swinging tentorium, in principle, but not in details resembling other myriapods, and in part by maxilla 1 in a unique manner. The adult head segmental organ lies on the maxilla 1 segment in Symphyla, whereas it is labial in Thysanura. The coxa is of the myriapod type and unlike that of insects. These facts are not reconcilable with a supposed symphylan origin of insects.

The outstanding habits of the Symphyla are an ability to penetrate deeply into soil, decaying logs, etc., and to dart about on an exposed surface, changing direction repeatedly and sharply. Symphyla cannot push their way into soil, neither can they deform their bodies in the manner of the Onychophora, but they are adept at twisting and turning, so utilizing minute spaces. This habit is made possible by: the presence of intercalary tergites all along the body, as well as divided ones on segments 4, 6 and 8, giving added flexibility to the middle part of the body; by the flexible chilopod-like pleura; and by the ventral surface being capable of longitudinal folding like a concertina. The gaits employed are of the chilopod type, but form the slower end of this series, and speed is obtained by very short pace durations. The ability to change direction, and suddenly run in the opposite or another direction, may be of survival value against small arachnid predators which cannot turn so easily. The trunk anatomy, including musculature, and antennal movements are bound up with these habits (44).

One can but conclude that the hexapods and Symphyla cannot have shared an immediate common ancestor,[1] even an archisymphylan (21), perhaps lacking the progoneate condition and possessing eyes, would be clearly a myriapodan line parallel to those of Diplopoda and Chilopoda, with the same basic type of myriapodan anatomy but modified for different habits. A similarity in sensory organs of Tomosvary in Diplopoda, Symphyla, and Collembola is probably related to needs, but the function of these organs is not yet clearly known.

HEXAPODA

Six-legged arthropods with a thorax more or less demarcated from the abdomen, and often with a much more elaborate exoskeleton, possess some functional advantages for certain habits over most myriapods. A re-

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[1] This view is contrary to that expressed by TIEGS & MANTON (67) when the relevant data concerning mandibles, tentorium, and trunk (43, 43a) were not available.

duction in leg number permits longer legs, these can give longer strides which contribute to faster running, suitable for more open habits; the three pairs of legs are always fanned out so that their fields of movement overlap little or not at all (34). Changes in speed can be effected by wide changes in pattern of gait, besides changes in pace duration. Walking or running on six legs has been evolved many times in unrelated classes. It is seen in some prawns and spider crabs, *Galeodes* and sometimes in spiders. Thus, the possibility of a hexapodous state having arisen more than once in the radiation of terrestrial groups persisting today as the myriapods and hexapods cannot be set aside, and the mere possession of three pairs of legs is not in itself sufficient justification for a supposed unity of pterygote and apterygote insects.

Insect ancestry has often been discussed (CALMAN, 1936; IMMS, 21, 22, 23; TIEGS & MANTON, 67). WILLE (70) has listed the resemblances and differences between the various hexapods and considered the implications. But adequate knowledge of existing jaw and tentorial systems in hexapods and myriapods has only just become available, and these data, together with an appreciation of the functional significance of entognathy and its probable parallel evolution, give clear pointers to affinities (43).

In considering the tentorium and mandibles it is necessary to make reference to the more generalized types found in the larger hexapod groups, since the extreme and varied specializations existing among some insects are not primitive and not relevant to the general question. The remarks which follow without further qualification apply to the more generalized known examples. The hexapod mandible is primitively a whole limb and unsegmented (as in Thysanura, e.g., *Petrobius*). Its movement is a basic promotor-remotor swing about a more or less dorsoventral axis, as in Crustacea, but presumably independently acquired. Dorsal close articulation exists, and some freedom about the axis of swing is conferred by the absence of a ventral or anterior articulation. This is useful as it is in the more primitive Crustacea performing the same basic movement. A primary effect of this movement is grinding by molar areas, as in *Petrobius*. The Thysanura and Pterygota show a series of mandibles (not phylogenetically connected) indicating the course of evolution which has led to strong biting in the transverse plane as seen in a cockroach or locust. The course is similar to that employed by the Peracarida culminating in the Isopoda. A backward shift of the dorsal end of the axis of swing, and a reduction in the preaxial part of the mandible leads to a more or less horizontal hinge between two principal condyles. Molar grinding becomes impossible, strong cutting by the distal edge increases, and a wide angle of swing is obtained by dissolution of the transverse mandibular tendon. Muscle modifications lead ultimately to a very simple but strong system of adductor and abductor muscles, tendons, and apodemes which work a very large mandible with relatively enormous cutting surfaces. These are parallel evolutions to certain Crustacea, and the details are different.

The mandible of *Petrobius*, although in some ways strongly suggestive of what the archihexapodan mandible may have been like, is itself specialized for a particular mode of feeding. The mandible is not exposed, as drawn in the textbooks. It is shut in, working in an enclosed space formed by the overlapping lateral parts of the labium, galea, labrum, and superlingua. The scratching activities of the tips of the mandibles and laciniae within enclosed spaces allow particles and salivary juice to be sucked up. There is no biting by the pair of mandibles. The hydraulic efficiency round the oral cone of *Petrobius* may not have been present in the thysanuran anestors where the mandible may have been less long and thin.

The mandibles of the other apterygote classes may have had a common or similar origin with that of the Thysanura, but thereafter their evolution has been totally opposed, precluding any supposed origin of the Pterygota from an apterygote group other than the Thysanura. An enlargement of the small pleural fold of *Petrobius* could have led to the entognathous condition of the Collembola and Diplura. The development of entognathy permits of the evolution of proximal freedom and protrusibility of the mandible, and is an entirely opposite trend to that seen in the Thysanura (Machilidae)-Pterygota group. The rotator-counter-rotator movements of the mandible in Collembola and Diplura has resulted in certain general similarities in musculature, but the many differences in detail suggest that entognathy has been independently acquired in these two classes. Anterior and posterior tentorial apodemes are present in Collembola, but they possess some mobility and are modified to suit mandibular protrusibility and entognathy. Posterior tentorial apodemes are present alone in Diplura (for functional and spacial reasons), while the Myriapoda all possess an anterior pair of tentorial apodemes only. The trend in tentorial evolution in the Thysanura-Pterygota line is one of progressive fusion, rigidity and massiveness. This is associated with transversely biting mandibles moving from a rigid hinge line and with strongly moving maxillae, an entirely opposite trend to that of the entognathous classes.

A functional and anatomical study of the head region does not support a phylogenetic unity of entognathous apterygotes[1] (68). It is more probable that entognathy, and all that goes with it, the details far exceeding those mentioned above (43), have been evolved several times within the Hexapoda. The Collembola and Diplura may have had a common origin in an archithysanuran stem, but thereafter their evolution has been independent and convergent in some ways. The Protura are clearly specialized minute crawlers into soil, litter, and crevices. The antennae presumably are secondarily absent, and the entognathous stylet-like mandibles and the tentorium are highly specialized. The prothoracic legs are used for intermittent hauling by movements requiring no lateral "elbow room." The meso- and metathoracic legs are together ambulatory, performing cart horselike walking gaits. These characters cannot be primitive in spite of the presence of an apparently primitive number of 14 abdominal trunk segments.

That the apterygote and pterygote groups all share the same type of mandible with the same movements and also show basically similar anterior and posterior tentorial apodemes (43) and a similar type of coxa-body articulation suggests that the pterygotes and apterygotes may have had a common origin. Their many-legged ancestors probably used the simple range of gaits found also in the Symphyla. These gaits are directly related to those of the Onychophora and avoid the specializations displayed by the Diplopoda and Chilopoda and the faster gaits of the Pauropoda. Whether the number of 14 trunk segments of Symphyla, the Permian Monura (55), and Protura, a number also recognizable in the Pterygota, is related to locomotion has not yet been ascertained. Since chilopod segment numbers, particularly in the Anamorpha, are so closely related to locomotory needs, possibly a similar number of trunk segments in some hexapods and in Symphyla may be the result of convergence, but the details are not yet ascertained. Such a number does not suit the jumping mechanism of the Collembola, in which a smaller number of segments is more favorable; this small number was already established in the Middle Devonian (52).

At what stage the hexapodous state appeared is uncertain. There are not many ways of using only three pairs of legs (MANTON, future publication), so that the same usage may have been independently acquired. The less specialized Pterygota, and *Petrobius* under some circumstances, exhibit the same type of leg movements, but different methods are employed by some other apterygotes. Thus, there seems to be as strong an indication of distant unity between the hexapod groups as there is between the several myriapod groups, but the former cannot have arisen from the primitive members of any extant class of myriapods. Such a conclusion is not surprising. Had a modern group possessed the genetic potentiality of giving rise to the most dominant of present-day land arthropods, some of its members would not be expected to remain arrested at imperfect stages of such a momentous evolutionary advance. Rather must we endorse the view of SEDGWICK (1909), who considered the present myria-

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[1] As suggested by TUXEN.

pod and insect fauna to represent the isolated descendants of a once widespread early radiation of terrestrial arthropods.

The recent work by SHAROV (54, 55) on the Lower Permian Monura shows animals which are close to the Thysanura, but more primitive in some respects. In *Dasyleptus* we have the 14 thoracic and abdominal segments but forming an even series with a large 14th segment, and nine pairs of short abdominal limbs following the three thoracic legs. The head capsule of *Dasyleptus* shows separate tergite rudiments of the mandibular to labial segments, and large maxillary palps are present much as in *Petrobius*. SHAROV (54) has shown that the nymphs and life cycle of various Lower Permian insects were more primitive than those of modern Hemimetabola. On all counts we can agree with SHAROV in looking to this type of animal as the forerunner of the winged insects.

EVOLUTION AND RELATIONSHIPS OF CRUSTACEA

Little can be added with certainty to the many previous considerations of phylogeny of the crustacean subclasses. We have no direct or indirect conclusive evidence concerning interrelationships of the Branchiopoda, Copepoda, Cirripedia, Ostracoda, and Malacostraca. The Leptostraca, although possessing a caudal furca in the adult, are clearly malacostracan in limb construction, feeding mechanism (7, 10), abdominal segmentation, and embryonic development (28, 30). Leptostraca retain the seventh abdominal segment in the adult, seven being the apparently primitive number for the Malacostraca (28, 29, 30). Leptostraca can no longer be regarded as a possible link between the Malacostraca and the "lower" Crustacea. A modern tendency to add taxonomic units to the existing system, in order to accommodate the newer finds as Mystacocarida, Cephalocarida, and additional taxa within the Malacostraca, has not given trustworthy indications of the relationships of the larger crustacean groups. The Cephalocarida show certain primitive features, such as the leglike second maxilla in series with undifferentiated trunk limbs each showing a generalized form (49, 50). Food collection of suspended material by many limbs without true filtration is probably another primitive attribute. The common pattern of maxilla 2 and the trunk limbs of *Hutchinsoniella* is as generalized as can be found among living Crustacea, but there are other examples (Fig. 13*A,B*). Limbs roughly of this form could have given rise to the various types of phyllopodium and stenopodium (Fig. 2, 13*C,D*); but a consideration of the modes of evolution of crustacean limbs put forward by CANNON (7, 8, 10, 11, 13, etc.) based on observation and detailed functional analysis are far more plausible than the theoretical suggestions of SANDERS (50).

Almost every class of Crustacea contains members which swim and others which crawl over the substratum. But we cannot as yet associate the more obvious of the diagnostic features of each class (apart from Cirripedia and Ostracoda) with particular habits or functions, and therefore we cannot appreciate the needs for these characters or the circumstances of their evolution. The ever-growing body of information concerning suspension and other feeding (summarized by TIEGS & MANTON, 67) serves to emphasize how different are the mechanisms in the several classes. Similar principles may be used, but the details are so unlike as to preclude the filter- and suspension-feeding mechanisms of any one class from having had the capacity to give rise to that of any other (see in particular the work of CANNON, 7, 8, 9, 10, 11, 12, etc.). Similarly the ability to tackle large food is correlated with the same general changes and specializations in mouth parts and anterior trunk limbs, but the details differ from group to group. Further comparative anatomical studies have produced no clear picture, although there are certain discoveries, such as the life cycle of *Hutchinsoniella,* which may help to bridge the gaps between Malacostraca and other classes. Since we have no primitive Ostracoda, Cirripedia, or Branchiura alive today, we are left with a consideration of Branchiopoda, Copepoda, Malacostraca, and the small new groups.

With no clear evidence concerning the interrelationships of the main crustacean classes, a consideration of the possible morphology of ancestral types of Crustacea becomes very speculative. It appears necessary at the present time to reaffirm the fallacy of considering a nauplius larva to represent a modified adult crustacean ancestor, as has recently been claimed (50, 51). GARSTANG (18), DE BEER (4) and others have given ample reasons for regarding the nauplius as representing only the larva of ancestral Crustacea. Metamerically segmented wormlike coelomates with short-bodied larvae may have given rise to arthropods, but it is unjustifiable to suppose that such an ancestor shortened its adult body to naupliar dimensions, elongated the adult again to the lengths found in the less advanced of modern Crustacea, and then embarked upon the shortening and posterior modifications seen in the most advanced of living species.

Presumably Crustacea arose from coelomate ancestors, at first as more open living bottom-dwellers whose exoskeleton gave better protection. Little differentiation into separate sclerites would be expected on each segment. A walking habit may have preceded a swimming one, although the possession of a biramous leg may have favored swimming as an alternative method of progression at an early stage. There have doubtless been many habit reversals and changes in the ways of life of Crustacea, and often it is not clear which habits are the secondary ones within a class. On functional grounds it is difficult to see how the differentiation of the malacostracan thorax and abdomen could have taken place in other than predominantly bottom-living animals. A reduction in leg number and an increase in length of endopodite would give the locomotory advantage of a walking thorax. A persistence of abdominal limbs may initially have been of service in swimming, and might have disappeared had the Malacostraca remained entirely bottom-living, as have the posterior limbs of arachnids and hexapods. Thereafter, there may have been several parallel evolutions of the shrimplike form and pelagic habit, each with a perfection of filtratory feeding. The latter cannot be an absolutely primitive method of food collection. Something less localized than a single pair of maxillary filters probably preceded it and may have been practiced on the bottom. CANNON (7, 8, 10) has suggested how a maxillary filtering mechanism may have arisen initially to assist a primitive trunk-limb-feeding mechanism. Perfection of the former in the Leptostraca and other Malacostraca would then allow many changes to take place in the form and usage of the carapace and trunk limbs. If the caridoid facies is a parallel evolution in Peracarida, Syncarida, and Eucarida, although comprising in many ways the more primitive living types in these divisions, the more specialized adaptive radiations within each division need not be regarded as having been derived from pelagic filter-feeding ancestors. The benthic forms may have come directly from the bottom-living stocks which also gave rise to the pelagic mysids, syncarids, euphausiids, and penaeids within the several divisions. The benthic adaptive radiations have also led to secondary pelagic types such as swimming crabs and secondary filter-feeders such as *Porcellana* (45), *Haustorius* (16), and *Nebaliopsis* (10). The Branchiopoda and Copepoda also show habit reversals, but the direction of interpreting the series is not always clear. A further functional study of pelagic and bottom-living members of these groups would be most welcome.

Some apparently simple conditions, when properly investigated, are seen to be anything but simple or primitive. The coupler of *Calanus,* one of the most primitive copepods, linking each pair of thoracic swimming legs, is characteristic of the subclass. The structure of the coupler is highly complex and related to an elaborate sternal system of sclerites. The coupler enables these legs to swing through a large angle—some 105 degrees (48)—thus facilitating the (almost synchronous) backstroke of these legs which gives the sudden copepod dart through the water. A complex system such as the coupler ranks as a very great and unique specialization which could not have been present in primitive types.

What has already been said about the fundamental difference between the mandibles of crustaceans and hexapods, the differences in head endoskeleton, sense organs, and sensory limbs, the differences in embryonic development and the persistence of segmental organs on different segments, suggests that there can be no close relationship between Crustacea and the Onychophora-Myriapoda-Insecta stem, and that there is no such taxon as the "Mandibulata." This conclusion implies a parallel evolution here of two types of limbs and mandibles, and a parallel development of exoskeleton, if, as seems probable, the early onychophoran line lacked surface sclerites.

The structure of the biramous crustacean limb and the contrasting manner in which the gnathobases of Crustacea and of *Limulus* are formed and used, the pleural origin of the limbs in chelicerates and their basically ventral origin in Crustacea (Fig. 2-4, 7, 12, 13) suggests a wide gap between Crustacea, Merostomata, and Trilobita. The head shields and limbs of the Merostomata and Trilobita have more in common than either has with the heads and limbs of Crustacea.

In considering the possible mode of evolution of the arthropodan armor, the chilopodan disposition of sclerites has sometimes been taken as representing a common primitive stage (SNODGRASS, 56, 58; STØRMER, p. O11, Vol. O, Arthropoda 1, and various modern textbooks). The probability of this is far from clear. Chilopoda need a flexible lateral body wall both for their technique in burrowing and for their coxal movements. A diplopod and a crustacean, by contrast, need a rigid lateral body wall, no matter whether this is provided by fused pleurites or by a pleural extension of the tergal arch. The diplopod and crustacean types of skeleton need not have passed through a chilopod-like evolutionary stage.

The more we appreciate the functional significance of structure, the clearer can we see how evolution can have proceeded, and the better will we be able to interpret structure in fossil arthropods where no direct study of function can be made. Even the details whereby tight enrolment is achieved by living animals, together with an appreciation of the mechanical difficulties which have had to be faced, is one of many examples of data derived from living animals which may be very useful to paleontologists.

Thus, as far as the evidence at present available goes, a supposed polyphyletic evolution of Arthropoda seems inescapable in the sense that the Onychophora-Myriapoda-Insecta and the Crustacea have evolved independently from each other and from the Merostomata and Trilobita. But the evidence does not indicate the state of advancement reached at the dawn of differentiation of these great groups. We should, however, be less dogmatic in upholding a supposed annelidan origin of the Arthropoda, if the term Annelida implies the Polychaeta, Oligochaeta, Hirudinea, and Archiannelida.

A metamerically segmented coelomate is as far as can justifiably be envisaged, a grade of animal perhaps very different from any modern annelid. Spiral cleavage characterizes the less yolky embryos of both annelids and molluscs, the cell lineages being extraordinarily similar in the two phyla, but arthropods show little of these features. As yet we know too little about the Tardigrada to decide whether they are more closely related to the Onychophora than to any other class, and the affinities of the Pycnogonida are also debatable (19, 20).

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GENERAL FEATURES OF CRUSTACEA

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CONTENTS

INTRODUCTION

The purpose of this chapter is to scan the general nature of crustaceans, mainly based on extant forms. Such a survey is desirable as an approach to detailed descriptions of the numerous major and minor crustacean groups, with emphasis on their fossil records, which follow. Though intended to be generalized and comprehensive, the initial review must be confined to relatively small space and cannot be allowed to duplicate discussions given at greater length by authors of systematic chapters included in this volume. Various generalizations may be expressed at known risk of ignoring exceptions (though hopefully none very important). Examples of morphological and other features are chosen on the basis of judgment that they are representative and illustrative, thus lending some degree of specificity to general statements.

The Crustacea are prevailingly aquatic arthropods distinguished basically from others by the presence of two pairs of antennary appendages on the **head,** for in other groups only a single pair of these structures is found or none at all. Behind the region of the antennae are three head somites which bear appendages functioning as jaws (mandibles) and for handling food (maxillules, maxillae). These components

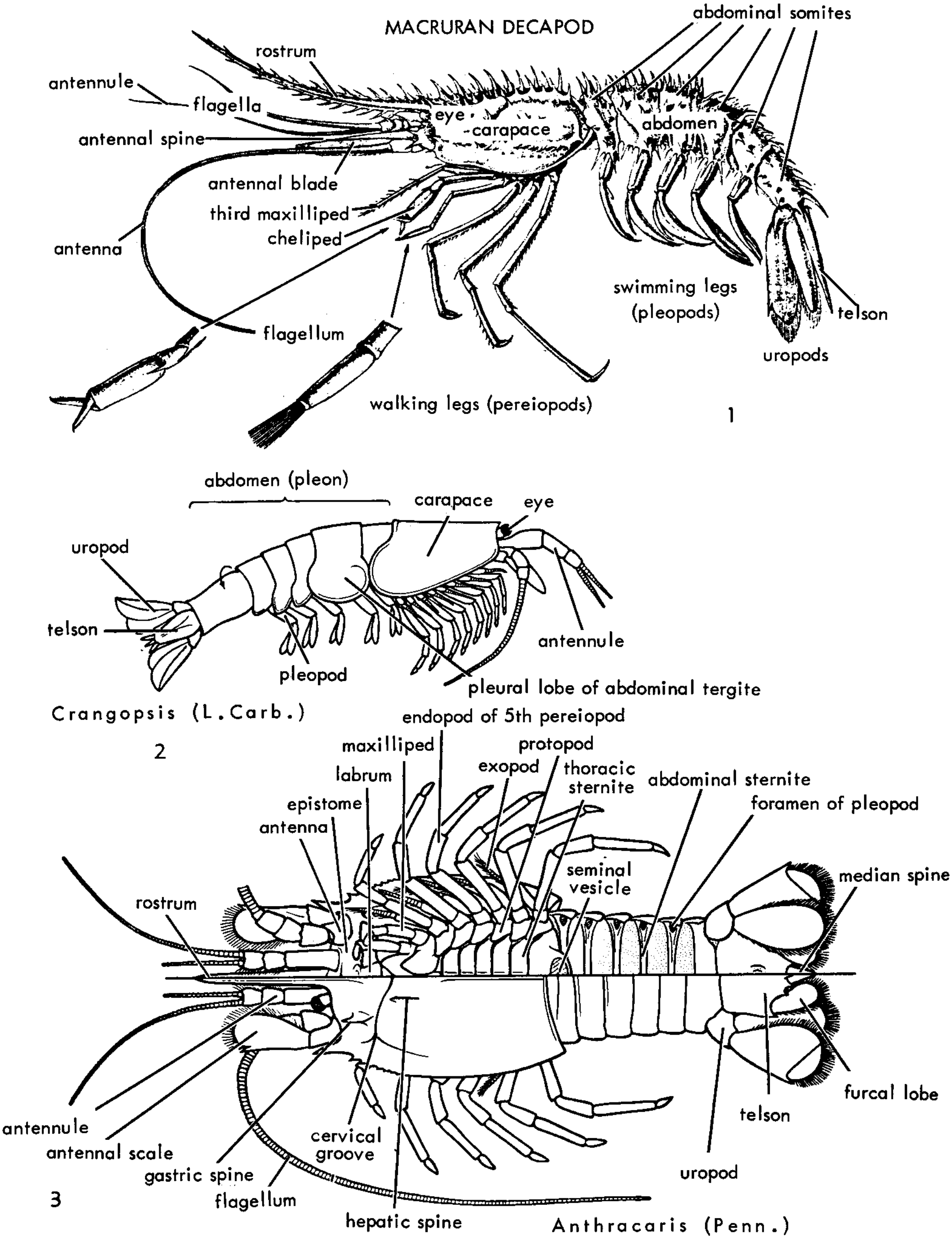

FIG. 17. Malacostracan crustaceans showing features of exoskeleton enclosing body and variously differentiated appendages.

1. Spinose living caridean, *Psalidopus spiniventris,* from Indian Ocean with unusually elongate rostrum projecting forward from carapace which covers head and thorax, with six abdominal somites. Appendages of the cephalothoracic region include antennules, antennae, a visible maxilliped, and dissimilar sorts of pereiopods, among which the frontmost pair is unusual in of the head region are reasonably consistent and diagnostic, whereas other parts of the body may vary considerably. Generally, parts of the crustacean body behind the head are differentiated in two major groups or tagmata of somites, anterior ones forming a **thorax** and posterior ones an **abdomen** (Fig. 17).

An **exoskeleton** consisting of hardened cuticle (L., *crusta,* hard shell) covers the soft parts of most crustaceans, including their appendages, and it even lines front and rear parts of the alimentary canal. This external integument is generally chitinoid but may be chitinous (Branchiopoda). Almost universally it is strengthened by calcareous deposits, sufficiently in some to develop extreme rigidity. Commonly, parts of the exoskeleton covering the body include in the anterior region a unified dorsal shield **(carapace)** with lateral extensions over the sides or developed as a hinged bivalve structure, and jointed segments covering rear parts of the body. The jointed appendages are encased in exoskeletal covers.

The vast majority of crustaceans are marine, ranging from near-shore shallow waters to the open ocean, where their distribution ranges from the surface to abyssal depths. Many are free-swimmers but some are planktonic floaters; others crawl about on the bottom or burrow in sediment, and a few (barnacles) live in fixed locations after attaining the adult stage. These sessile forms may be attached to almost any foreign object, including the shells of other marine invertebrates. Crustaceans also have invaded fresh waters of the land where they are found in streams, lakes, ponds, swamps, and even hot springs. A few have become air-breathers and thus adapted to terrestrial habitats (generally moist) far inland.

Only insects exceed crustaceans in numbers of individuals—at least this is generally considered to be so. Actually, crustaceans may considerably surpass insects in aggregate numbers, in view of the incredibly large populations of tiny marine copepods ("insects of the sea") and ostracodes with ocean habitat, for the oceans are vastly greater in spatial extent than all land areas combined. Additional are similarly stupendous hordes of branchiopods and other crustaceans of continental waters and less abundant air-breathing terrestrial forms. Crustaceans do not remotely compete with insects in variety, however, since the estimated number of known species of crustaceans (40,000) (GRUNER & HOLTHUIS, 1967, p. iii, iv) is only 1/25 (0.04) of the approximate total of described species of insects (900,000) (Ross, 1965, p. 45) (nearly 1,000,000) (Wigglesworth, 1964, p. 1).

In comparing crustaceans with other main divisions (superclasses) of the Arthropoda some far-reaching resemblances are easily discernible, foremost of which are the jointed nature of nearly all body appendages, encasement of soft parts prevailingly by an exoskeleton, division of the body into a series of more or less similar parts (somites) following one another in succession longitudinally but highly variable in number and distinctness (Table 1), and generally by well-developed articulations between segments of appendages and exoskeletal coverings of contiguous somites. As known to almost everyone, the name of the whole arthropod assemblage, signifying jointed foot, indicates a common denominator, though it must be admitted that some representatives hardly seem to qualify for membership.

FIG. 17. *(Continued from facing page.)*

having chelae with two movable fingers, and the second in bearing terminal brushes for work as cleaners of skeletal parts. The abdomen carries five pairs of biramous swimming appendages and a tail fan composed of uropods and telson. (Mod. from W. T. Calman in E. R. Lankester, *Treatise on Zoology,* by permission A. & C. Black, publ.)

2. Side view (reconstr.) of eocaridacean eocarid, *Crangopsis socialis* (SALTER), from Lower Carboniferous of Scotland, ×3. The head and thorax are concealed by a carapace unmarked by projections or grooves. Beneath the stalked eyes are robust antennules and antennae. The pereiopods and pleopods are all biramous and very similar to one another within each group. Tail fan well developed (Brooks, 1962).
3. Ventral (upper part of figure) and dorsal (lower part) views of exoskeleton of pygocephalomorph eocarid, *Anthracaris gracilis* (MEEK & WORTHEN), from Pennsylvanian of Illinois, ×1.7. The abdominal somites lack pleopods (Brooks, 1962).

Only a few distinguishing differences in arthropodan superclasses can be enumerated here. 1) Whereas crustaceans are characterized by biramous limbs and possession of two pairs of antennary appendages in front of the mouth, only trilobitomorphs also have biramous limbs and no noncrustacean arthropods are known to have more than a single pair of antennae. 2) Chelicerates are distinguished by the presence of one or more pairs of preoral pincer-bearing appendages (chelicerae). Many crustaceans also possess chelate limbs, but invariably these are located postorally. Chelicerates lack antennae. 3) Onychophores and myriapods are elongate wormlike arthropods characterized by very numerous almost identical somites. Both have a single pair of antennae, and both lack biramous limbs, thus differing from crustaceans. 4) Hexapods possess one pair of antennae and six pairs of uniramous limbs. Many of them differ from all other arthropods in having wings and thus in being able to fly. 5) Pycnogonids (sea spiders) and the primitive aberrant ill-known Tardigrada and Pentastomida are so unlike Crustacea as to need no statement of distinctions.

As recorded by Manton (p. *R*5), diagnostic distinctions among the main groups of arthropods relate to the number of paired postoral limbs used in feeding and the manner in which these operate. Crustaceans correspond to myriapods and hexapods in having the first three pairs of these limbs (mandibles, maxillules, maxillae) largely or entirely employed for feeding, and additional limbs may be used similarly in Crustacea and certain Myriapoda. Crustaceans have gnathobasic jaws, biting with bases of the mandibles, whereas all myriapods and hexapods bite with the tips of the mandibles. In Trilobitomorpha homologous limbs are biramous appendages which appear to have served no function for aid in feeding. Chelicerates generally utilize the gnathobases of one or more pairs of postoral limbs for cutting and chewing food, but in manner quite unlike that of operating the crustacean gnathobases.

Observations of the habitats of arthropodan groups are worthy of mention in comparing crustaceans with other superclasses. Trilobitomorpha and Pycnogonida are exclusively marine. Crustacea are prevailingly marine but include a minority of fresh-, brackish-, and hypersaline-water forms, as well as a few air-breathing terrestrial species. Hexapoda are overwhelmingly terrestrial arthropods, including fliers and burrowers, but some are fresh-water aquatic and a small number are adapted for life in the sea. Chelicerates are found in all environments, except the air. Myriapods and onychophores are mainly terrestrial, but taking account of the fossil record, some kinds appear to have been aquatic. Pentastomids and tardigrades, of insignificant importance, may not belong to Arthropoda.

DIVERSITY OF GROUPS

GENERAL STATEMENT

Antecedent to consideration of appropriate subjects of general scope relating to the Crustacea—comparative morphology of the body, nature and function of appendages, features of internal anatomy, various physiological systems, modes of reproduction, ontogenetic development, life habits, ecologic adaptations, distribution in time and space, and classification—it is desirable to survey briefly main attributes of the several distinct groups that are recognized. These are enumerated in a preceding chapter by Manton in her tabulation of main divisions of Arthropoda (p. *R*13). The groups are considered in the order there given, which is followed also in the arrangement of systematic descriptions in subsequent pages of this volume.

Nineteenth-century students of the Crustacea prevailingly divided them into two major assemblages, respectively named Entomostraca (insect-shelled) and Malacostraca (soft-shelled). From several viewpoints both are misnomers.

In the first group little more than average diminutive size and considerable range

TABLE 1. *Somites of Some Crustacean Groups and Appendages Borne by Them.*
[Somites are serially numbered from front to back (limbless eye-bearing anterior one of head region omitted). Data from Borradaile, *The Invertebrata* (4th edit.), 1963, and other sources.]

somite	CEPHALOCARIDA - Hutchinsoniella	NOTOSTRACA - Triops	MYSTACOCARIDA - Derocheilocaris	OSTRACODA - Cythere	COPEPODA - Cyclops	CIRRIPEDIA - Lepas	PHYLLOCARIDA - Nebalia	EOCARIDA - Eocaris	SYNCARIDA - Palaeocaris	MYSIDACEA - Mysis	CUMACEA - Diastylis	TANAIDACEA - Apseudes	ISOPODA - Ligidium	AMPHIPODA - Gammarus	DECAPODA - Astacus
2	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a
3	A	A	A	A	A	A	A	A	A	A	A	A	A	A	A
4	m	m	m	m	m	m	m	m	m	m	m	m	m	m	m
5	mx	mx	mx	mx	mx	mx	mx	?	mx	mx	mx	mx	mx	mx	mx
6	Mx	Mx	Mx	Mx	Mx	Mx	Mx	?	Mx	Mx	Mx	Mx	Mx	Mx	Mx
7	th	th	Mxp	th	Mxp	c ♀	th	Mxp	th	Mxp	Mxp	Mxp	Mxp	Mxp	Mxp
8	th	th	th	th	th	c	th	Mxp	th	th	Mxp	th*	th	th*	Mxp
9	th	th	th	g ♂♀	th	c	th	th	th	th	Mxp	th	th	th*	Mxp
10	th	th	th♂♀	0	th	c	th	th	th	th	th	th	th	th	th*
11	th	th	th	f f	th	c	th	th	th	th	th	th	th	th	th
12	th♂♀	th	0		th(g)	c ♂	th♀	th♀	th♀	th♀	th♀	th♀	th♀	th♀	th♀
13	th	th	0		g♂♀		th	th	th	th	th	th	th	th	th
14	th	th	0		0		th♂	th♂	th♂	th♂	th♂	th♂	th♂	th♂	th♂
15	g	th	0		0		p	p	p	p	0	p	p	p	p
16	0	th	0		0		p	p	p	p	0	p	p	p	p
17	0	th♂♀	T		0		p	p	p	p	0	p	p	p	p
18	0	p	f f		f f		p	p	p	p	0	p	p	u	p
19	0	p					p	p	p	p	p	p	p	u	p
20	0	p					p	u	u	u	u	u	u	u	u
21	0	p					0	T	T	T	T	(1)	T	T	T
22	0	p					T	f f	f f		(1)				
23	0	p					f f		?						
24	0	p													
25	0	p													
26	T	p													
27	f f	p													
28		p													
29		p													
30		p													
31		p													
32		p													
33		p													
34		p													
35 to 39 (variable)		0													
		T													
		f f													

EXPLANATION

a = antennules
A = antennae
m = mandibles
mx = maxillules
Mx = maxillae
Mxp = maxillipeds (thoracopods)
th = thoracopods
p = pleopods (or natatory limbs)
u = uropods

c = cirri (thoracopods of Cirripedia)
0 = limbless somite
g = genital appendage
T = telson (not true somite)
f f = caudal furca
♂ = male genital aperture
♀ = female genital aperture
* = chelate or subchelate

(1) Note. Abdominal somites of female commonly lacking pleopods, those of male having variable number.

in form, besides the segmented body and generally similar appendages, remotely suggest the insects. The entomostracans, which include the branchiopods, ostracodes, copepods, and a few other kinds of crustaceans, collectively display characteristics less specialized or highly developed than those observed in the malacostracans and hence they have been considered to be low-rank divisions of Crustacea. Including extinct forms, their diversity furnishes basis for present-day differentiation of them into eight independent classes (or subclasses as ranked by many zoologists).

Oppositely, the Malacostraca remain as a morphologically somewhat closely related assemblage having more complex structures and more advanced specializations than in other crustaceans, but except at times of molting they cannot qualify for designation

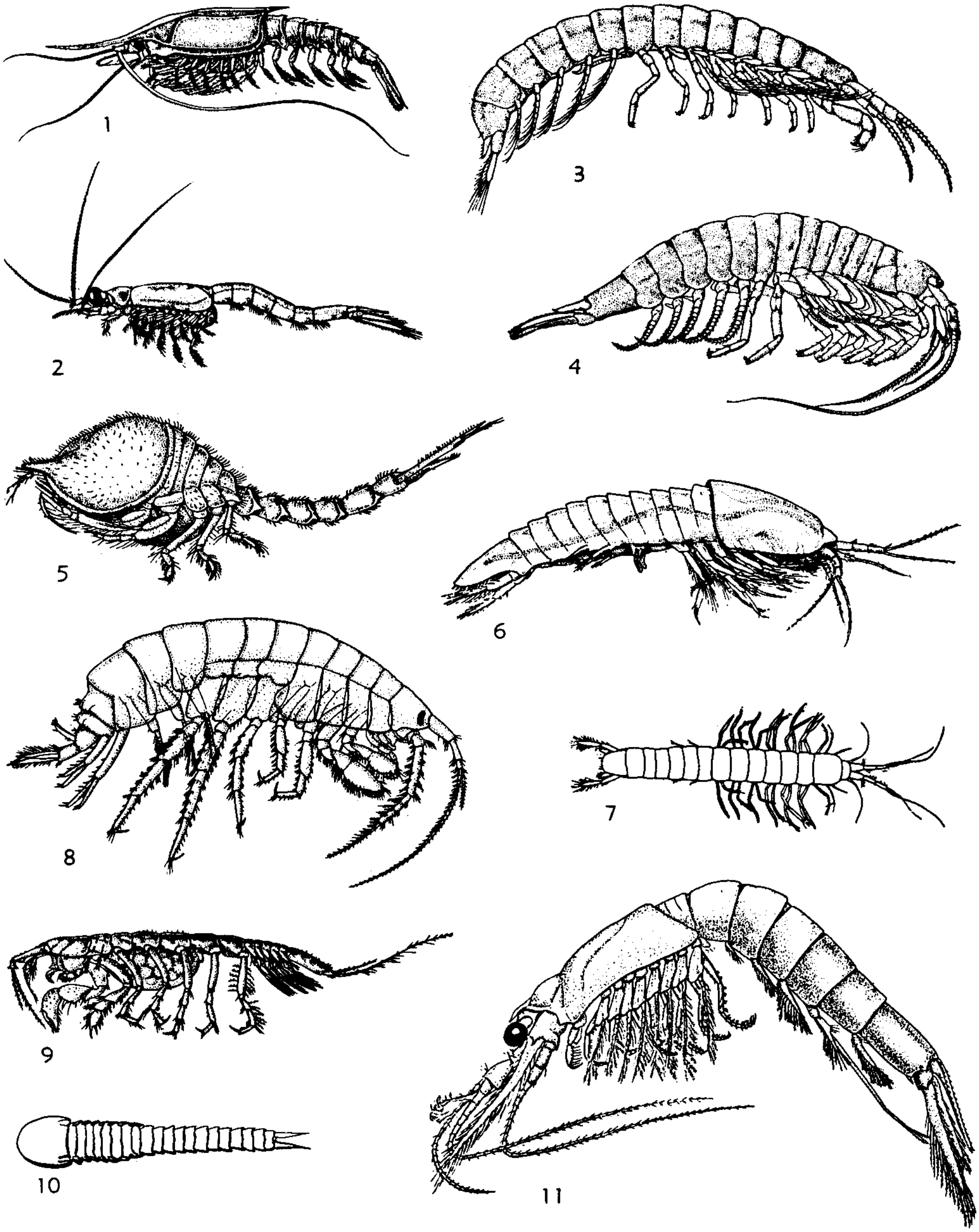

Fig. 18. Types of crustaceans illustrating diversity of groups, all extant.

1-2, 11. Mysidacean peracarids (Malacostraca).——*1. Gnathophausia zoea,* marine form from Atlantic off east coast of North America, characterized by possession of branched gills on some thoracopods, ×0.3.——*2. Mysis relicta,* fresh-water form lacking gills, from North American Great Lakes, ×2.——*11. Neomysis integer,* marine form with smooth somites behind carapace, male from English Channel, ×3.7.

3-4. Syncarids (Malacostraca), fresh-water.——*3. Koonunga cursor,* female from small stream near Melbourne, Australia, ×7.——*4. Anaspides tasmaniae,* mountain shrimp from pool 3,500 feet above sea level in Tasmania, male, ×2.

as soft-shelled. Many develop rock-hard exoskeletons or at least have a tough cuticle covering the body somites and appendages. The host of decapods, including lobsters, crabs, shrimps, and the like, together with less well-known groups (amphipods, isopods, mysidaceans, and others) belong to the Malacostraca.

SIZE AND MODE OF LIFE

Adult crustaceans range in size from less than 0.25 mm. (0.01 inch), measured as miximum length or width, to a "wing spread" of outstretched appendages amounting to 12 feet (3.6 m.) in the giant spider crab *(Macrocheira kaempferi)* of Japan. If account is taken of the hugely preponderant number of diminutive crustaceans, as compared with species having maximum dimensions of 25 mm. (1 inch) or more, a conservative estimate indicates that the average size of all crustaceans cannot exceed 1 mm. Further, if weight is given to the uncountable trillions of tiny copepods, ostracodes, and branchiopods having adult sizes of 0.5 mm. or less to 1 mm. the grand average must be in the neighborhood of 0.7 mm. This is a relevant guess for the crustacean world as a whole, emphasizing the quantitative importance of diminutive forms which are unrivaled as direct or indirect food sources for most aquatic animal life, but otherwise it is unrealistic to compute averages of the many different kinds of crustaceans in terms of size.

Consideration of the mode of life and ecologic adaptations of different groups of crustaceans is reserved for a subsequent section of this chapter. Here it is sufficient to note that the vast majority of these arthropods live in the sea, that they are most abundant in shallow waters of neritic belts and surface or near-surface waters of open oceans, that a few range to abyssal depths, and that crustaceans of land areas are predominantly aquatic forms found in fresh-water bodies or in saline lakes and ponds, as well as coastal lagoons. The temperature of crustacean-inhabited waters on land ranges from hot springs and spring-fed pools to icy cold, and levels at which crustaceans have been collected reach from more than 30,000 feet below sea level to at least 12,000 feet above sea level. A modest number of crustaceans are air-breathers which have acquired ability to travel about on land (e.g., numerous isopods, some amphipods), generally seeking out moist environments.

CEPHALOCARIDS

Cephalocarids are diminutive crustaceans (length of adults 2 to 3.7 mm.) which live as burrowers in fine sediment distributed from slightly below low-tide level to 1,000 feet or more below sea level (SCHMITT, 1965, p. 42). They are blind and colorless. Since only four species are known, differentiation of them as a separate class may seem surprising. This is based on their extremely primitive nature, which precludes placement of them in any already-recognized crustacean group. Behind a horseshoe-shaped cephalon formed by five fused somites (in addition to an embryonic, partly hypothetical preantennary first somite with

FIG. 18. *(Continued from facing page.)*

5. Cumacean peracarid (Malacostraca); *Diastylis goodsiri,* female from Arctic Ocean showing head and thorax sharply marked off from abdomen, ×3.

6-7. Thermosbaenacean peracarids (Malacostraca). ——*6. Thermosbaena mirabilis,* male from hot-water pool in Tunisia, ×20.——*7. Monodella halophila,* male from subterranean pool in Yugoslavia, ×13.

8 Amphipod peracarid (Malacostraca); *Gammarus locusta,* fresh-water form from northern Europe, male, ×3.

9. Tanaidacean peracarid (Malacostraca); *Apseudes spinosus,* female from North Atlantic, ×7.5.

10. Cephalocarid; *Hutchinsoniella macracantha,* primitive shallow-water marine crustacean from Long Island Sound, showing rounded cephalon and subequal body somites, ×11.

[*1-5, 8-9,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission A. & C. Black, publ.; *6,* from T. Monod in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission Akademische Verlagsgesellschaft, publ.; *7, 10 11,* from T. Monod, H. L. Sanders, and K. Lang in Encyclopedia of Science and Technology, by permission, McGraw-Hill, publ., copyright 1960.]

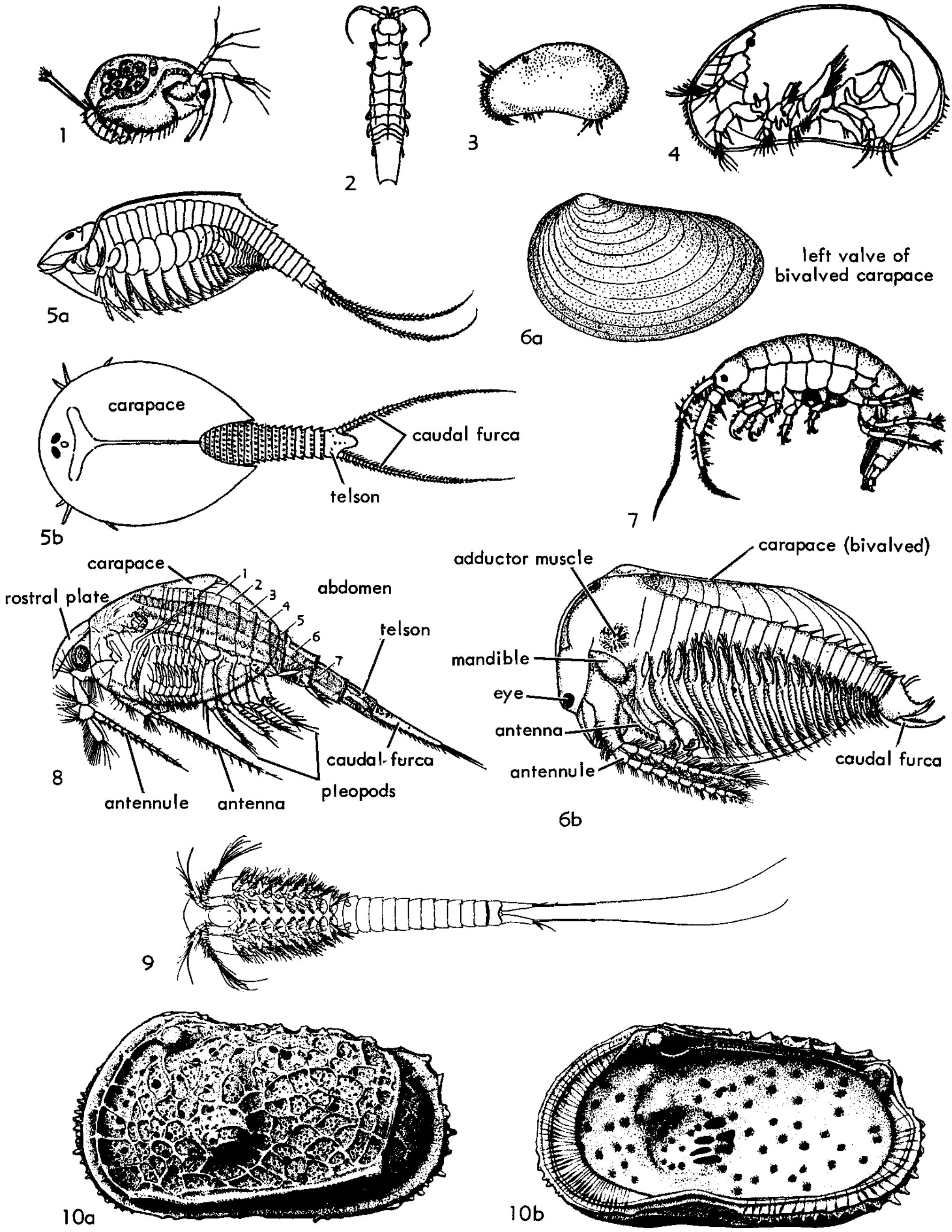

Fig. 19. Types of crustaceans illustrating diversity of groups, all extant.

1, 5-6. Branchiopoda.——*1.* Cladoceran, *Maerothrix rosea,* fresh-water, USA, enl.——*5.* Notostracan, *Lepidurus glacialis,* fresh-water, northern Europe; *5a,b,* lateral with left part of carapace removed, and dorsal views, ×1.7.——*6.* Conchostracan, *Cyzicus obliquus,* fresh-water, northern eye rudiments—Fig. A of Manton) are eight thoracic somites and 12 abdominal ones, each identical in all essential features to others (Fig. 18,*10;* 19,*9*) (Table 1). The maxillules and maxillae are nearly the same in structural pattern as the thoracic limbs (thoracopods), which display nearly complete lack of serial specialization. Simplicity of the digestive tube, ladder-like ventral nerve cord, and homology of musculature from somite to somite mark the cephalocarids as uniquely generalized crustaceans, interpretable as approaching morphological attributes of ancestors of the Crustacea.

BRANCHIOPODS

Next to the cephalocarids, branchiopods are considered to be the most primitive living crustaceans, marked by morphological similarities of their numerous somites and multifilamentous limbs, and (commonly but not exclusively) by their filter-feeding mode of obtaining nourishment (Fig. 19,*1,5-6*). They swim about freely, mainly in continental waters ranging from fresh to hypersaline. Branchiopods (gill-feet), also known as phyllopods (leaf-feet), use their limbs for locomotion in swimming, for respiration, and for sieving water to extract food particles. They are mostly tiny, with length of adults 3 mm. or less, but in some groups (e.g., Notostraca) 15 to 30 mm. and exceptionally up to 90 mm. (Linder, 1952). The head bears compound eyes, generally reduced and unsegmented antennules, biramous antennae, which may be relatively large or reduced to rudiments, mandibles usually lacking palps, maxillules and maxillae varyingly reduced in most. Thoracic and abdominal somites are highly variable in number but commonly are numerous. The front part of the body usually is protected by a carapace (Fig. 19,*5b-6a*), but anostracan branchiopods lack this covering. Paired limbs range from as few as four pairs (Cladocera) to 70 (Notostraca) (Table 1). In all branchiopods the posterior part of the abdomen is limbless, and posterior somites of the thorax also may lack limbs. A caudal furca is present in nearly all forms, and the multiarticulate rami of this may be very long (Fig. 19,*5a,b*).

MYSTACOCARIDS

Mystacocarids resemble cephalocarids in small size (length of adult 0.5 mm.), colorless subcylindrical slender body composed of similar somites, mode of life interstitial in near-shore sediment, and in being represented by only three known species. They also are primitive but have fewer and more specialized cephalic and thoracic appendages than the cephalocarids, in some respects suggesting those of copepods. The three known species all live in the interstitial environment of sand beaches.

OSTRACODES

Ostracodes are ubiquitous, mainly marine crustaceans which are characterized mainly by their few somites (distinctly less numerous than in other classes, Table 1) and by

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Fig. 19. *(Continued from facing page.)*

Europe; *6a,* left valve of female, enl.; *6b,* side view of male with left valve removed, enl.

2. Isopod peracarid (Malacostraca); *Pentidotea resecata,* intertidal marine, off California, dorsal view, ×0.6.

3-4, 10. Ostracoda.——*3-4. Cylindroleberis* sp., fresh-water, northern Europe; *3,* left valve exterior, enl.; *4,* left side of animal with left valve removed, female, enl.——*10. Australicythere polylyca,* shallow-water marine form of southwestern Pacific, hemicytherid podocopid; *10a,b,* left valve exterior and right valve interior, latter showing subcentral adductor muscle scars (clustered elongate black areas), ×53.

7. Amphipod peracarid (Malacostraca); *Ampithoe* sp., intertidal marine form, Pacific off California coast, ×0.7.

8. Leptostracan phyllocarid (Malacostraca); *Nebalia bipes,* marine, left side of female from north Atlantic, with carapace shown as though transparent, ×6.

9. Cephalocarid, *Hutchinsoniella macracantha,* from Long Island Sound, ventral side showing thoracic appendages and caudal furca with very elongate rami, ×14.

[*1-4, 7,* from S. F. Light *et al., Intertidal invertebrates of the central California coast,* by permission, University of California Press; *5-6, 8,* from W.T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *9,* from H. L. Sanders, 1963; *10,* from R. H. Benson, 1966.]

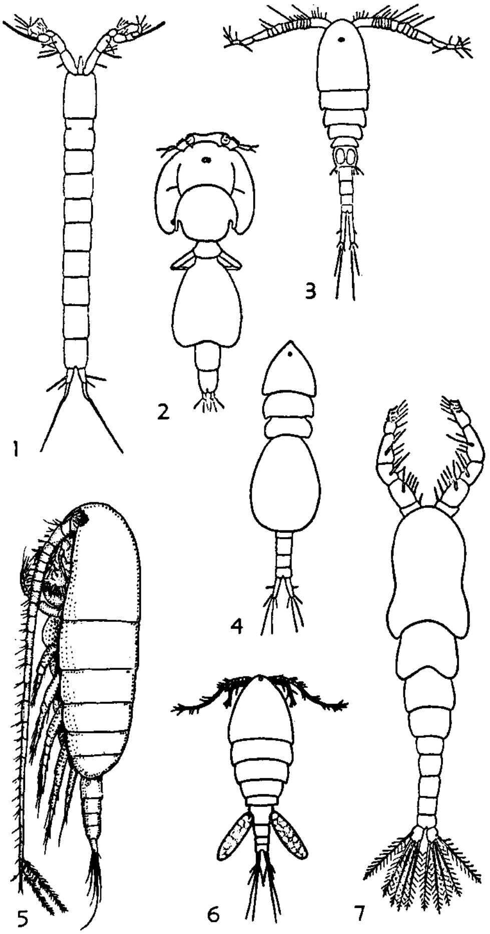

FIG. 20. Types of copepod crustaceans, all extant and chiefly marine.

1. Harpacticoid, *Evansula incerta,* characterized by elongate slender body, male, ×53.
2. Caligoid, *Caligus mirabilis,* widely distributed external parasite on fishes, ×33.
3, 6. Cyclopoids, *Cyclops bicuspidatus* and *Cyclops* sp., representing diminutive one-eyed fresh-water and marine group important as food source for fishes and other animals, ×33, ×20.
4. Notodelphyoid, *Notodelphys agilis,* belonging to estuarine and marine environments, generally found in body cavity of sedentary tunicates, ×10.
5. Calanoid, *Calanus finmarchicus,* among largest and most abundant pelagic copepods, this form characteristic of boreal waters, side view of female, ×11.
7. Monstrilloid, *Monstrilla dudica,* diminutive planktonic copepod, free-swimming as adult but with immature form parasitic on marine invertebrates, ×10.

enclosure of the head, entire body, and most of the appendages within a bivalved carapace (Fig. 19,*3,4,10*). Their extremely long geologic record (L.Cam.-Rec.) is rivaled only by the bivalved primitive malacostracans known as Phyllocarida. Ostracodes are much smaller than phyllocarids, having average length of adults barely more than 1 mm. (maximum 34 mm.) as compared with an average of approximately 10 mm. in modern phyllocarids (maximum 40 mm.) and nearly 200 mm. in some fossil forms. Both in ostracodes and most phyllocarids the carapace is hinged along the dorsal margin of the valves (Fig. 19,*10*). More than 1,000 genera of ostracodes have been described, among which extant ones only slightly exceed 10 percent.

The head region of ostracodes bears well-developed eyes, antennules, antennae, mandibles, maxillules, and maxillae. Two or three pairs of thoracic limbs are present and the posterior extremity of the abdomen is modified as a bilobed furca. The arrangement of antennary, mandibular, and adductor muscle scars on valve interiors and nature of the dorsal hingement are important for classification (Fig. 19,*10b*), as in different groups are other morphological features of the carapace (radial and pore canals, duplicature, surface ornament).

Ostracodes are mostly swimmers and they thrive on almost any kind of food. Some subsist by sucking juices of marine plants, some by feeding largely on diatoms. Copepods and other small organisms may be consumed in considerable quantities, and many ostracodes are scavengers which feed on any available dead tissue.

EUTHYCARCINOIDS

Interesting but numerically insignificant crustaceans known only as fossils (Trias.) from central Europe and Australia are named euthycarcinoids. In peculiar manner

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[*1-4, 7,* from Wilson, 1932; *5,* from W. T. Calman in E. R. Lankester, *Treatise on zoology;* by permission, A. & C. Black, publ.; *6,* from S. F. Light *et al., Intertidal invertebrates of the central California coast,* by permission, University of California Press.]

they appear to combine some characteristics of merostome chelicerates and diplopod myriapods, both of which are distantly related at best to crustaceans. Even so, the euthycarcinoids are thought to have closest affinities with the Crustacea.

Moderately large arthropods (average length of adults 40 mm., maximum 65 mm.), somites of the head region are fused together. Preoral appendages identified as antennules and antennae are crustacean attributes. The first thoracic somite, attached to the head, bears appendages considered to have functioned as maxillipeds. Pairs of thoracopods borne by 11 somites of the thorax behind the first one are uniramous, multijointed, and equipped with long setae adapted for swimming. The five abdominal somites are limbless, the posterior one being followed by a long *Limulus*-like telson.

COPEPODS

Much the most abundant of all marine animals are crustaceans belonging to the class Copepoda (Table 1, Fig. 20). A majority are benthonic free-swimmers, or planktonic floaters, but very numerous kinds are parasites as adults which infest fishes, such mammals as whales, and many invertebrates, including other crustaceans. Free-living copepods usually range in size from less than 0.5 mm. to about 10 mm. in length. One of the largest parasitic forms *(Penella)* may be more than 300 mm. long, with trailing egg sacs approximately equal in length (overall some 2 feet).

Copepods lack compound eyes and have no carapace. Typically, they possess long antennules and short antennae, six pairs of thoracic limbs, and a limbless abdomen. The thoracopods are biramous, except for the first pair which invariably is uniramous and the last pair which also may be uniramous.

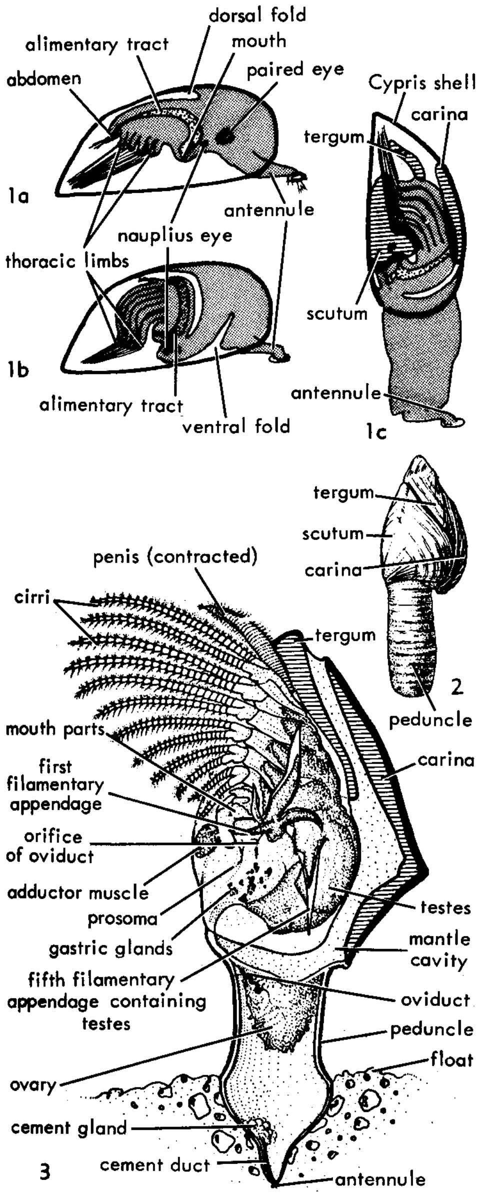

FIG. 21. Types of extant crustaceans—cirripeds.

1. *Lepas* sp., immature stages proving crustacean nature of cirripeds; *1a,b,* free-swimming cypris larvae, much enl.; *1c,* initial attached stage, much enl.
2. *Lepas anatifera,* goose-neck barnacle from North Sea showing stout, moderately flexible stalk, ×1.
3. *Lepas fascicularis,* lepadomorph thoracican barnacle from north Atlantic, with calcareous plates on right side of body removed to show enclosed body and thoracic appendages (cirri), ×1.8.

[*1-2,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *3,* from D. P. Henry in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960.]

Many copepods inhabit fresh waters, and it happens that the only known fossils occur in Miocene lake deposits. Despite what must have been vast numbers of marine Cenozoic forms, probable Mesozoic, and possible Paleozoic copepods, such representatives of the class are lacking in the paleontological record.

BRANCHIURANS

Branchiurans, unknown as fossils, are ectoparasites on marine and fresh-water fishes—hence are called fish lice. They have a disc-shaped cephalothorax 5 to 25 mm. in diameter with dorsal compound eyes and ventral suctorial cups for attachment to the host in some. The limbless abdomen lacks somite divisions.

CIRRIPEDS

The cirripeds are a varied group of highly modified crustaceans characterized by permanent fixation of adults, lacking compound eyes except in larval stages. In the order named Thoracica, which includes the barnacles and which alone is represented by fossils, the body, with head end downward, is enclosed by movable or somewhat firmly united calcareous plates (Fig. 21, 22). Six pairs of upwardly directed biramous thoracic limbs (called cirri) function in producing water currents by back-and-forth and inward-drawing movements which serve for gathering food particles carried to the mouth (Table 1). Abdominal somites are lacking.

Some barnacles attach themselves to the shells of sea turtles or to flippers, flukes, and jaws of whales (Fig. 22,2), as well as to

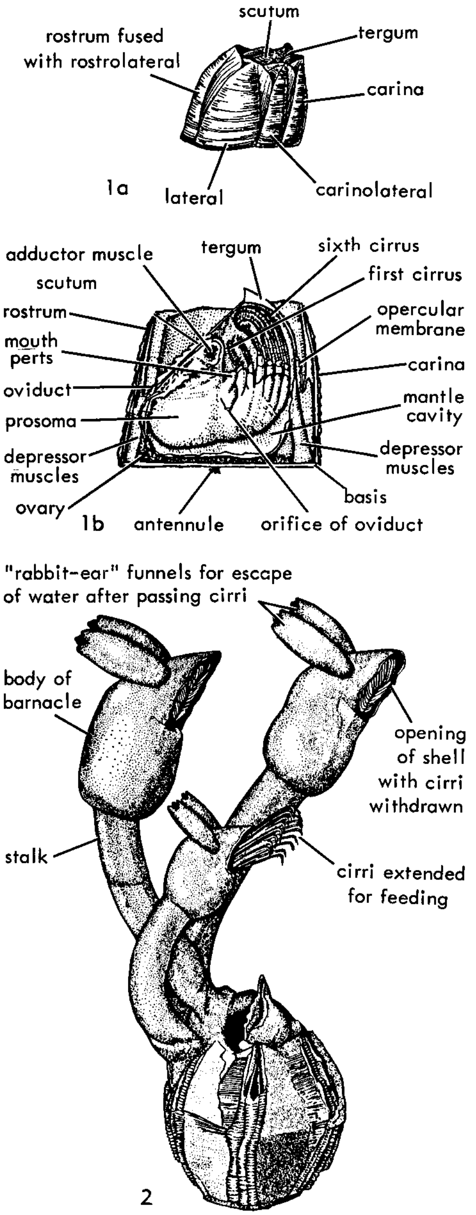

FIG. 22. Types of extant crustaceans—cirripeds.

1. *Balanus hameri,* balanomorph thoracican barnacle from north Atlantic; *1a,* side view of calcareous shell showing component valves, ×1; *1b,* same with part of shell removed to show body of cirriped within it, ×2.
2. Whale barnacles, which live attached to whales and are carried about by these hosts, illustrating a commensal rather than parasitic association; subglobular acorn barnacle *(Coronula diadema)* below and three rabbit-eared goose-neck barnacles *(Conchoderma auritum)* fastened to the acorn barnacle, ears oriented toward tail of swimming whale, ×0.7.

[*1a,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *1b,* from D. P. Henry in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *2,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill, publ., copyright 1949.]

some other marine animals, different kinds of barnacles showing high specificity not only in choosing particular hosts but in their location on the host. Because the uninvited crustacean travelers which are carried about in this manner do not derive nourishment from their host or seem to harm it in any way, these barnacles are not true external parasites but simply are benefitted by their life-long free ride in presumably food-rich waters.

Other groups of cirripeds are distinguished by lack of skeletal covers, some by less than six pairs of thoracopods, or none at all, and some by extreme adaptation for parasitic mode of life (e.g., *Sacculina,* which lacks an alimentary tract and has no appendages).

MALACOSTRACANS

Most highly developed, greatly varied, and generally considered most representative of the Crustacea are groups brought together in the class Malacostraca. Collectively, these are distinguished by the possession of compound eyes which in many are borne on stalks near front of the head, by a thorax composed of eight somites which typically is covered by a carapace (Fig. 17) (Table 1), and by an abdomen of six or seven somites, most of which generally bear pairs of appendages. Malacostracans vary widely in shape and size, ranging from diminutive forms only 2 or 3 mm. in length to the giant Japanese crab with 3.6 m. spread of its front limbs. They live in all sorts of environments, but chiefly in shallow seas not far from coasts. Relatively numerous as fossils, although much less so than ostracodes, their paleontologic record equals that of the ostracodes in extending probably from Lower Cambrian to Recent.

PHYLLOCARIDS

The phyllocarid malacostracans are characterized by the presence of a proportionally large bivalved carapace which may be hinged along the dorsal margin as in ostracodes or may lack such hingement. The carapace is not fused to any of the thoracic somites. Eyes are stalked. The thoracic limbs are all alike, consisting of biramous, usually foliaceous ventral appendages of the somites. The abdomen, which is relatively slender, has seven somites, with pleopods borne by all except the hindmost one. A telson with caudal furca is present (Table 1, Fig. 19,*8*). Leptostracans, which are the only extant phyllocarids, mostly do not exceed a length of 12 mm. in adults but some more than three times as large are known. Archaeostracans (L.Ord.-U. Trias.) may attain a length of 75 cm. Modern phyllocarids are chiefly inhabitants of shallow seas, but they range to a depth of at least 2,500 m.

EOCARIDS

Exclusive of the phyllocarids, all malacostracans are grouped together in the subclass Eumalacostraca, and of these the oldest and only division not represented by living forms comprises the Eocarida. Eocarids are caridoid (shrimplike) crustaceans with a moderately large carapace which is not fused to the thoracic somites (Fig. 17,*2,3*). It bears a single transverse groove. The thoracic limbs are biramous and closely similar to one another, with protopod consisting of a single segment. Diagnostic features are furcal lobes and a median articulated spine on the telson attached to the sixth abdominal somite (Table 1).

SYNCARIDS

The syncarids are mainly characterized by entire lack of a carapace, evidence from fossils, which include moderately common late Paleozoic and some Mesozoic forms, indicating that absence of this body cover is a primary feature, rather than secondary, as in certain isopods, amphipods, and cumaceans (Fig. 18,*3,4*). In different genera the eyes are stalked, sessile, or absent. The pereiopods are biramous and none are chelate or subchelate. A seminal receptacle may be present but no egg-carrying structures (oostegites) on appendages. Although modern syncarids are fresh-water crustaceans (excepting a single brackish-water species at mouth of the Amazon), Brooks (*Treatise,*

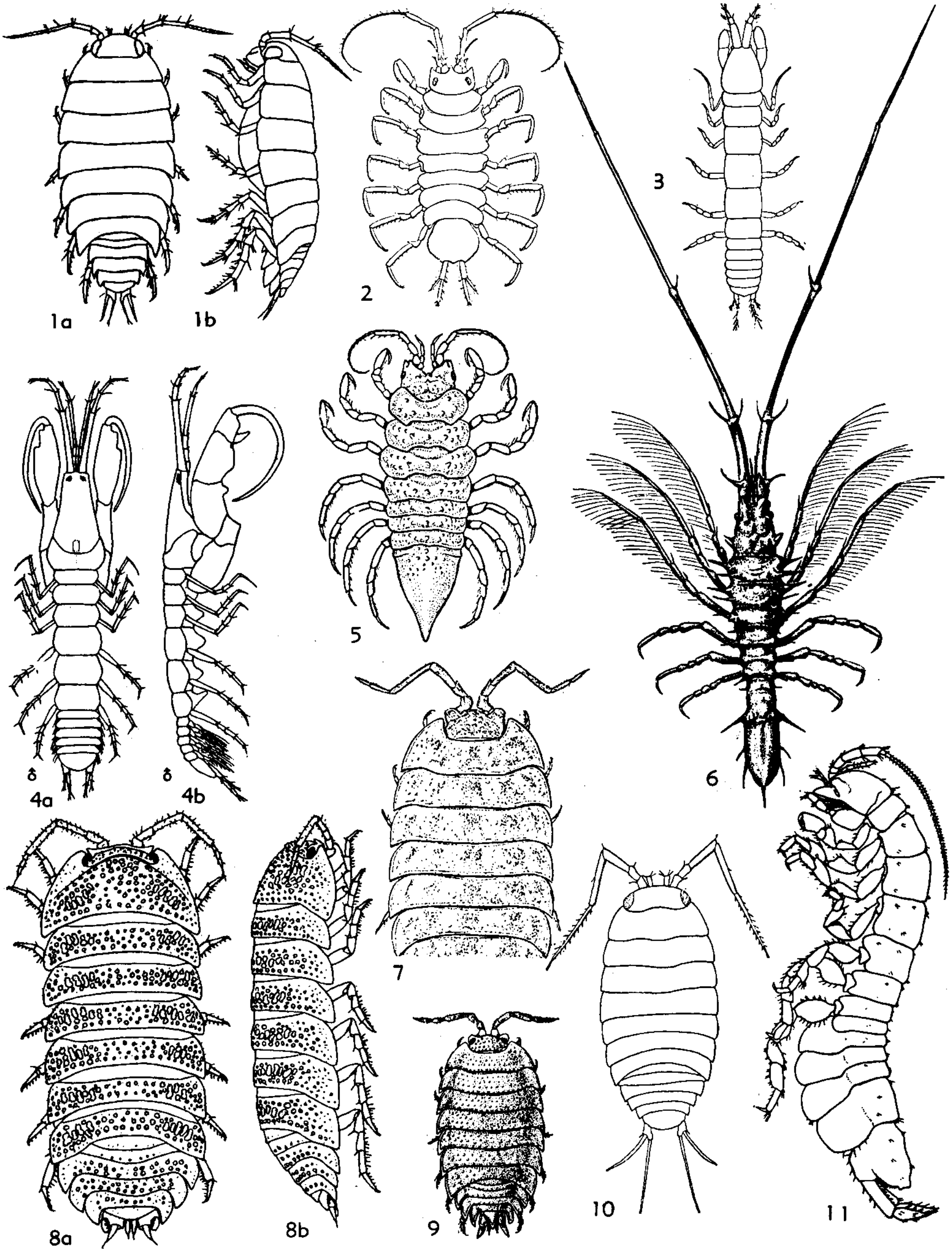

FIG. 23. Types of crustaceans illustrating diversity of groups, all extant—isopod and tanaidacean peracarids (Malacostraca).

1, 7-10. Oniscoid terrestrial isopods.——*1. Ligidium hypnorum,* inhabiting damp forests, northwestern Europe; *1a,b,* dorsal and side views of female, ×4.——*7. Porcellio spinicornis,* female from New York, ×3.——*8. Scleropactes zeteki,* female from Panama; *8a,b,* dorsal and side views, ×3.5.——*9. Porcellio scaber,* female from northern Europe, ×2.——*10. Ligidium*

p. *R*352) judges that nearly all Paleozoic forms undoubtedly were marine. The relatively indistinct differentiation of thorax and abdomen found in this group is a primitive character possessed by no other malacostracan.

PERACARIDS

A very large assemblage of malacostracans which includes most kinds not classed as decapods or stomatopods is placed in the superorder Peracarida. The most important peracarid groups are amphipods (nearly 4,000 extant species), isopods (approximately 3,000 Recent species) cumaceans (700 modern forms), mysidaceans (more than 500 extant species), and tanaidaceans (at least 350 living species). In addition, each of the mentioned divisions is represented by fossils, oldest of which are Permian isopods, cumaceans, and tanaidaceans (ignoring the order Anthracocaridacea, two Mississippian genera, tentatively classed as peracarids).

The chief common characteristics of the Peracarida are invariable fusion of the first thoracic somite to the cephalon, carapace (when present) never fused to more than four thoracic somites, peduncles of antennae typically three-segmented, mandibles with movable structure termed the lacinia mobilis in all but parasitic and highly specialized forms, first pair of thoracopods modified as maxillipeds, eggs and young nearly always carried in a marsupium formed by oostegites (Fig. 18,*1*,*2*). Comparative information on somites of peracarids and their appendages is given in Table 1. Peracarid eyes may be stalked or sessile, but at least two small subterranean species of minor groups (Spelaeogriphacea, Thermosbaenacea, Fig. 6-7) are blind, as are several burrowing or cave-dwelling isopods and amphipods.

A majority of peracarid species are marine shallow-water crustaceans, but many descend to abyssal depths. Isopods, amphipods, and tanaidaceans are both marine and nonmarine, mysidaceans and cumaceans predominantly marine, and remaining minor peracarid groups restricted to continental waters.

MYSIDACEANS

Mysidaceans, because of their shrimplike form and possession of a well-developed carapace for protection of the head and thorax, are interpreted to be more generalized, and hence more primitive than other peracarid crustaceans. Commonly, adults range in length from 12 to 20 mm. (maximum 200 mm.). They have movable stalked eyes, biramous antennules, and antennae with scalelike exopods. The first one, two, or three (rarely four) thoracic somites are fused to the cephalon and appendages of the first one or two are modified to function as maxillipeds (Table 1, Fig. 18,*1*,*2*,*11*). Ramified gills occur at the base of thoracopods in some and abdominal limbs may function as swimming organs (pleopods). A well-defined tail fan is formed by a pair of uropods and median telson. The mysidaceans are widely distributed, essentially pelagic animals which commonly migrate vertically during day and night, but they also live on the sea bottom and even burrow into it temporarily. A very few are found in fresh waters. They

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FIG. 23. *(Continued from facing page.)*

longicaudatum, female from eastern USA, ×3.

2. Asellote marine isopod, *Janira alta,* from east coast of USA, dorsal view, ×3.3.

3. Marine tanaidacean, *Heterotanais limicola,* dorsal view of female from Massachusetts Bay, ×14.

4. Fresh-water tanaidacean, *Nototanais beebei,* taken from stomach of catfish in British Guiana; *4a,b,* dorsal and side views, ×25.

5-6. Valviferan marine isopods.——*5. Synidotea muricata,* from near-shore off Arctic coast of Alaska, ×11.7.——*6. Arcturus purpureous,* female from north Atlantic at depth of 900 m., ×2.5.

11. Phreatoicid fresh-water isopod, *Phreatoicus assimilis,* amphipod-like female from northern Europe, ×5.

[*1, 4, 8* from Van Name, 1936; *2-3, 5-7, 10* from Richardson, 1905; *9, 11* from W. T. Calman in Lankester, *Treatise on Zoology,* by permission, A. & C. Black, publ.]

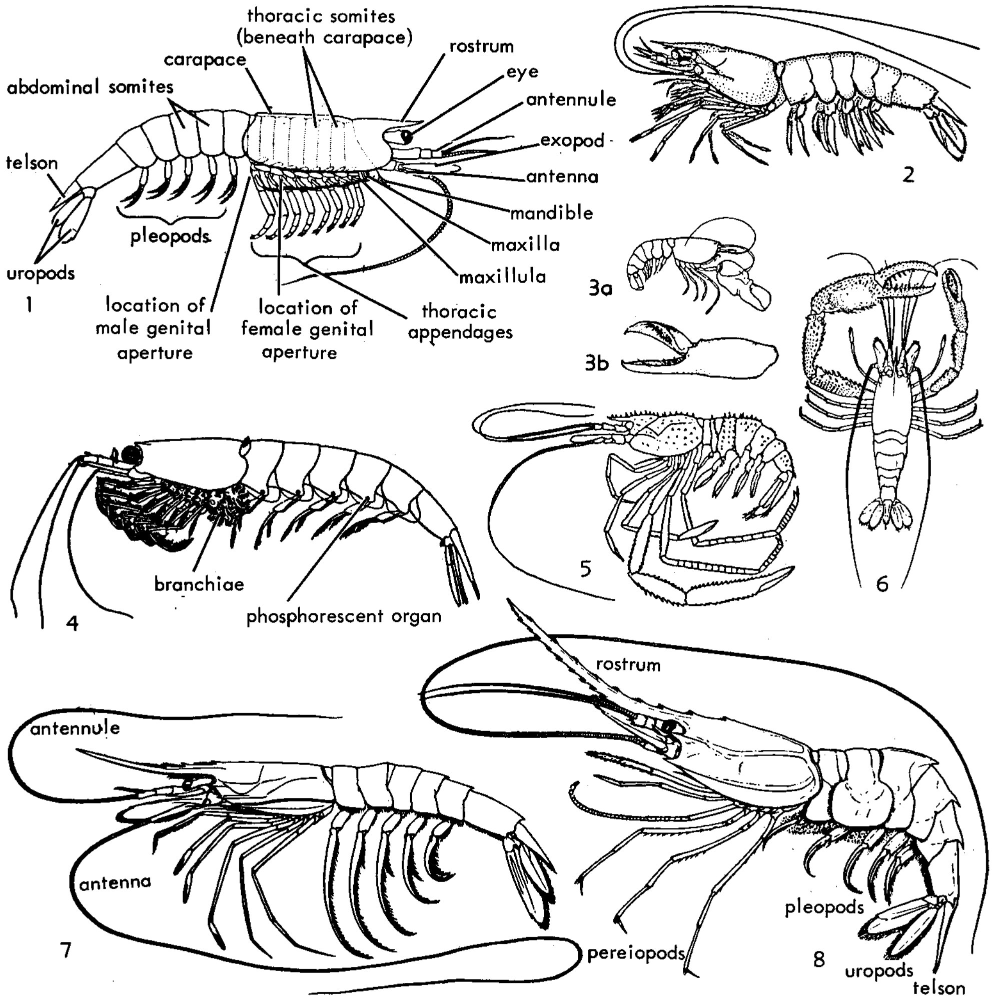

FIG. 24. Types of crustaceans illustrating diversity of groups, all extant eucarid Malacostraca.

1. Generalized macruran decapod showing morphological elements of exoskeleton, and "caridoid facies."

2. Penaeid prawn, *Penaeus setiferus,* jumbo shrimp abundant in warm-waters of Gulf of Mexico, X0.25.

3. Snapping shrimp, *Alpheus heterochelis,* provided with over-developed first pair of pereiopods capable of making loud popping noises; *3a,* side view, X0.5; *3b,* distal part of cheliped, X1.3.

4. Euphausiid, *Meganyctiphanes norvegica,* wide-ranging pelagic crustacean characterized by phosphorescent organs on abdominal pleura and large light-sensitive eyes, X0.8. Euphausiids are a main food source for whales.

5. Stenopodid shrimp, *Stenopus hispidus,* distinguished by prominence of third pair of chelate pereiopods, X0.6.

6. Tropical fresh-water prawn, *Macrobrachium faustinum,* characterized by exceptionally long chelate second pereiopods and in some species large size (to length of 30 cm. or more), X0.3.

7. Deep-sea penaeid prawn, *Aristeus coruscans,* with very elongate antennules and antennae, glands at base of latter emitting phosphorescence, X0.3.

8. Caridean prawn, *Heterocarpus alphonsi,* marked by prominent spinose rostrum, first pereiopods developed as prominent maxillipeds, third pair with multiarticulate distal parts, and humped abdomen, X0.7.

[*1, 7-8,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *2-3; 5-6,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *4,* from Watase in Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University, publ.]

are mostly carnivorous predators and scavengers, but also are filter-feeders and plant-eaters. Chiefly Recent, a few fossil forms are known from Triassic and Jurassic formations.

CUMACEANS

A well-developed carapace covers the anterior part of the thorax and projects in front of the head of cumaceans. It is fused to at least the first three thoracomeres, in some also to the fourth, and rarely to fifth and sixth somites. Laterally expanded parts of the carapace provide gill chambers. Eyes are sessile (when present) and usually joined together as a single median sight organ. The antennules may be biramous, the antennae without exopods, and the first three thoracopods are modified as maxillipeds (Table 1, Fig. 18,*5*). The slender abdomen is sharply set off from the thorax, its somites limbless in females but some of them bearing pleopods in males. A pair of slender spikelike uropods and telson, which may be absent, do not form a tail fan.

Cumaceans mostly range in length of adults from 1 to 12 mm., but a few of them reach a length of 35 mm. They are marine, near-coast to abyssal bottom-dwellers which burrow in mud or sand with the front of the carapace protruding. A few brackish- and fresh-water species are known. Their stratigraphic range is Upper Permian to Recent.

TANAIDACEANS

The body of tanaidaceans is cylindrical or somewhat depressed and nearly uniform in width throughout. It is diminutive, for very few adults are more than 10 mm. long, not counting forward and backward projecting appendages. As a group, these peracarids are distinguished by shortness of their carapace, which extends from the head over only two thoracic somites (Fig. 18,*9*). It is fused to these somites and lacks lateral expansions such as those of cumaceans but provides very small gill chambers. If eyes are present, they are located on short immovable stalks. The first pair of thoracopods are developed as maxillipeds; the second ones are chelate, generally with large chelipeds. Although the abdomen is abbreviated, its somites are distinct;[1] pleopods may be present or absent and the pair of terminal filiform uropods does not form a tail fan (Table 1).

Tanaidaceans are almost exclusively sea-bottom-dwellers inhabiting burrows. They are distributed from strand lines to depths of 6,000 m. A few forms are found in brackish waters. The group ranges from Permian to Recent.

ISOPODS

In isopods a carapace has disappeared, so that the head with its sessile eyes and all somites are exposed. Body shapes are many, but nearly all are depressed. Limbs of the first thoracic somite (or rarely first two) function as maxillipeds and those of the remaining seven are nonchelate uniramose pereiopods (Table 1, Fig. 19,*2*). Most isopods do not have the equal legs called for by their name. Commonly the pereiopods are divided into groups, the first three being directed forward, the fourth one sideward, and the fifth to seventh backward (Fig. 23,*1*,*9*) or they may display a different arrangement (Fig. 23,*2*-*6*,*8*,*11*). Also, these groups tend to be specialized in different ways. The coxopodites of the thoracic limbs may be fused with the pleura so that in females the plates (oostegites) which form a brood pouch appear to arise from the sterna. Appendages of the abdominal somites of isopods are pleopods with broad platelike endopodites and exopodites adapted both for swimming and respiration. Pleopods may develop air-breathing pseudotracheae in terrestrial forms. A feature of some isopods is ability to roll up their body into a ball with only the dorsal side of the somites exposed, the ventral side and appendages being tucked neatly inside.

Isopods are both predatory and scavengers with biting mouth parts. Some feed on wood and sea weeds. A few kinds infest fishes and other crustaceans as parasites.

Typical isopods range in length from 1 to 20 mm. Greatest size is attained by

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[1] Last somite (6th) is fused with telson, as in isopods.

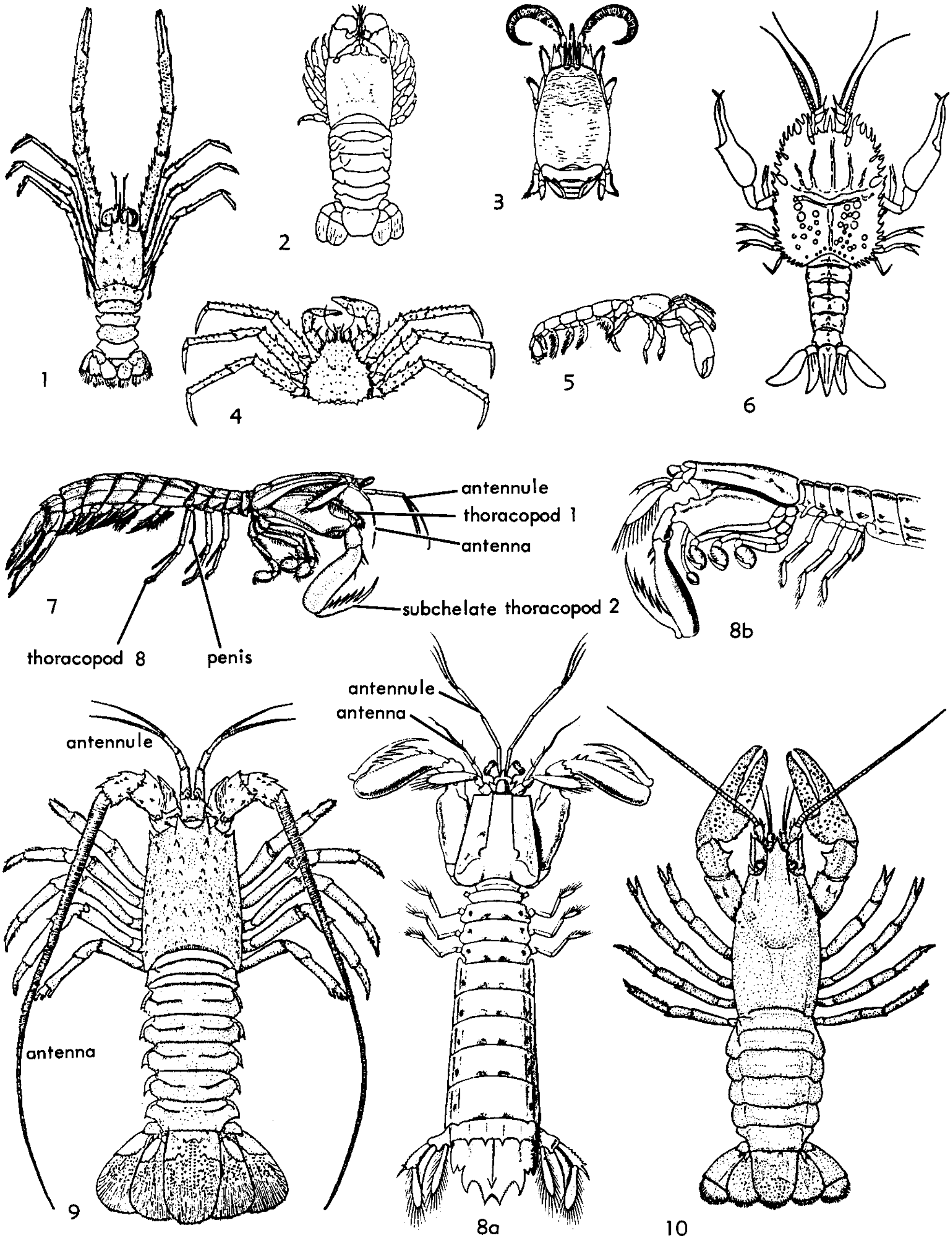

FIG. 25. Types of crustaceans illustrating diversity of groups, all extant Malacostraca.

1-2, 5-6, 9-10. Lobster-like decapods.——*1.* Galatheid anomuran, ***Munida evermanni,*** marine form with long slender chelipeds, symmetrical abdomen with broad tail fan used for swift backward swimming, ×0.7.——*2.* Shovel-nosed Spanish lobster, ***Scyllaridia aequinoctialis,*** marked by absence of rostrum and chelae, stoutly armored, ×0.15.——*5.* Mud shrimp, ***Cal-***

an abyssal isopod *(Bathynomus)*, some individuals of which range from 200 to 300 mm. in length.

The recorded geologic range of isopod peracarids is Triassic to Recent.

AMPHIPODS

The amphipods, commonly called sandhoppers on beaches and scuds in aquatic environments, correspond to isopods in lacking a carapace and in having unstalked sessile eyes. They are medium-sized crustaceans (adult length 3 to 12 mm., maximum 140 mm.) which prevailingly differ from isopods in the laterally compressed form of their body, rather than dorsoventral flattening. The first and second thoracic somites are fused to the cephalon[1] (Fig. 18,*3*; 19,*7*). The thoracic limbs lack exopodites, the first pair being modified as maxillipeds, the second and third pairs usually chelate or subchelate and prehensile, and others having more than one form (Table 1). In general, amphipods are poor walkers. The abdominal appendages generally consist of three pairs of multiarticulate pleopods next behind the thorax and others resembling uropods not developed as a fan tail.[2] The last three pairs of abdominal limbs are used by sandhoppers to kick the ground in jumping.

Amphipods are most abundant in marine environments, ranging from the shore line to abyssal depths. Approximately 15 percent of described species inhabit fresh waters of continents and islands distributed from virtual sea level to an altitude of at least 4,000 m. Some 80 species are air-breathing forms. Excluding some Devonian tracks and trails doubtfully attributed to amphipods, the geologic distribution of amphipods is recorded from Eocene to Recent.

EUCARIDS

Malacostracans with the carapace fused dorsally to all somites of the thorax are classified as eucarids, chief kinds of which are the familiar shrimps, prawns, crayfishes, lobsters, and crabs belonging to the Decapoda (Fig. 17,*1*; 24,*1-8*; 25,*1-6*,*9-10*; 26,*1-12*; 27,*1*). Eucarids differ from the peracarids in lacking brood pouches formed by oostegites in females and absence of the movable structure called lacinia mobilis on the mandible, as well as in more obvious morphological distinctions. All eucarids have stalked eyes. Besides the decapods, crustaceans designated as euphausiaceans are included in this assemblage.

EUPHAUSIACEANS

Euphausiaceans are medium-sized (adult length 20 to 30 mm., maximum 90 mm.) shrimplike forms (Fig. 24,*4*), not very numerous as to species (about 85 in two families) but abundant enough in all oceans to furnish the major food of whales, one of which may gulp down two or three tons

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[1] In Caprellidea, but only first thoracic somite in Gammaridea.

[2] Except in Hyperiidea, for example.

FIG. 25. *(Continued from facing page.)*

lianidea laevicauda, thin-shelled burrower with large chelate first pereiopods, ×0.3.——*6*. Blind, deep-sea eryonid decapod, *Polycheles crucifer*, with relatively thin shell, carapace laterally widened and dorsally flattened, ×1.1.——*9*. Commercially important spiny lobster or langouste, *Panulirus interruptus*, heavily armored decapods lacking rostrum and chelae, ×0.12. ——*10*. Fresh-water crayfish, *Orconectes limosus*, with firm shell, large chelipeds, and short rostrum, ×0.8.

3-4. Anomura.——*3*. Mole crab, *Emerita talpoida*, shallow-sea mud-burrower marked by elongate oval carapace and short nonchelate limbs, ×0.9. ——*4*. Free-moving king crab, *Lithodes maja*, relative of hermit crabs with asymmetrically arranged abdominal plates in females, living on well off-shore sea bottoms, ×0.6.

7-8. Stomatopods, characterized by powerful raptorial subschelae of second pereiopods, posterior thoracic somites resembling those of elongate abdomen.——*7*. *Squilla mantis*, side view of male, ×0.7.——*8*. *Squilla desmaresti*; *8a,b*, dorsal and side views of male, ×0.8.

[*1-6, 9-10*, from F. A. Chace in *Encyclopedia of science and technology*, by permission, McGraw-Hill, publ., copyright 1960; *7*, from W. T. Calman in E. R. Lankester, *Treatise on zoology*, by permission, A. & C. Black, publ.; *8*, from A. Gerstaecker in H. G. Bronn, *Klassen und Ordnungen des Tierreichs*, by permission, Akademische Verlagsgesellschaft, publ.]

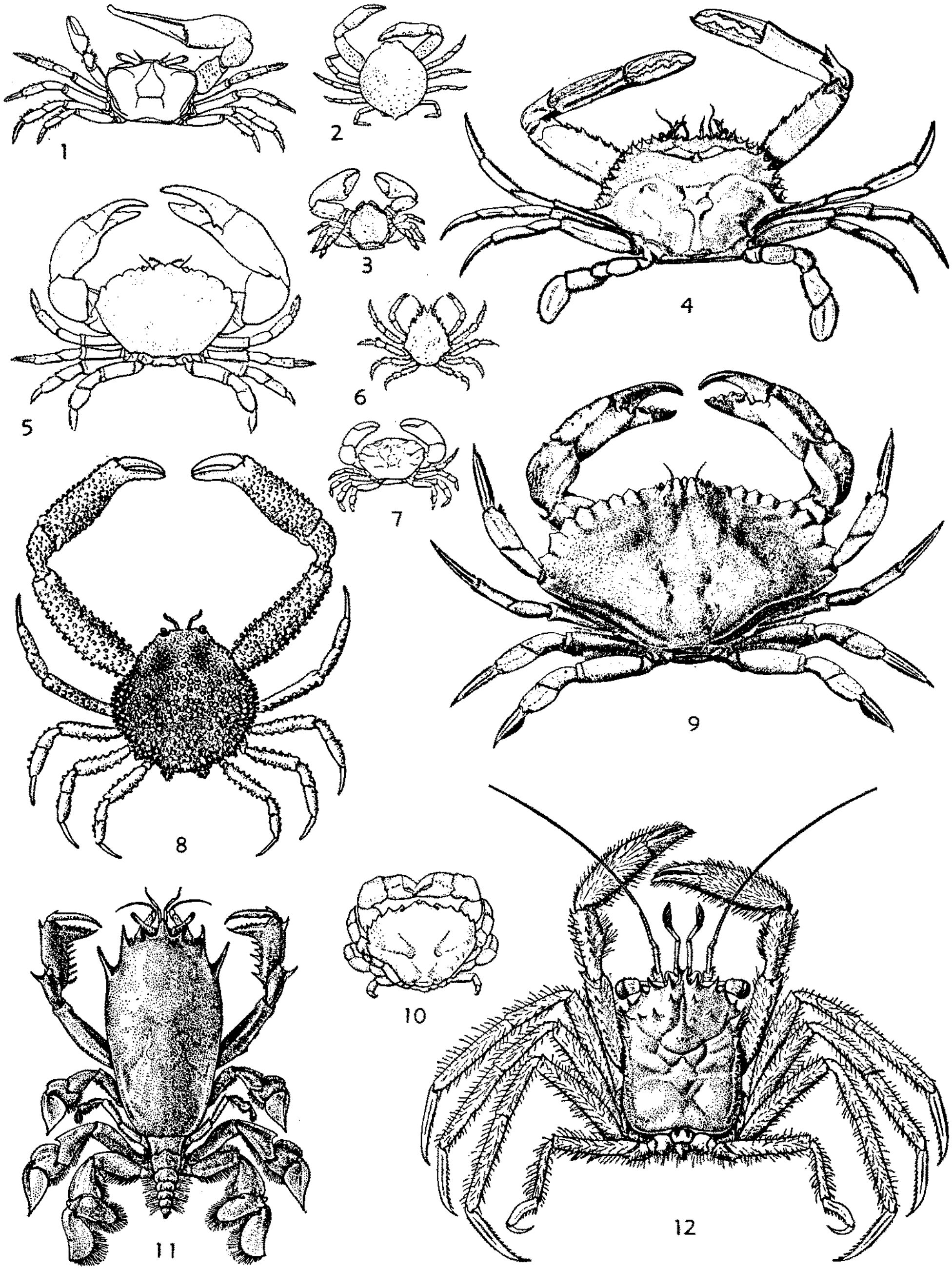

FIG. 26. Types of crustaceans illustrating diversity of groups, all extant eucarid Malacostraca (decapods—crabs).

1. Fiddler crab, *Uca pugilator*, inhabitant of sandy sea shores distinguished by strongly disparate chelipeds, ×0.6.

2. Purse crab, *Persephona punctata*, oxystomate form characterized by ovoid carapace, ×0.2.

3. Porcellanid crab, *Petrolisthes tridentatus*, so-of them for a meal. They also furnish food for seals, penguins, petrels and other creatures of the sea far from land. Euphausiaceans are found in neritic belts but most of them are pelagic, living at depths to more than 2,000 m. in daytime and near the ocean surface at night. This pronounced diurnal migration and the possession of phosphorescent organs are distinctive attributes of this and some other groups.

The carapace of euphausiaceans usually bears a transverse cervical furrow and extends forward in a short rostrum. Laterally it does not form branchial chambers, and thus the feather-like gills of the biramous swimming thoracopods are plainly visible from the side. Anatomical features that differentiate euphausiaceans from decapods are small size of the maxillary exopodite (scaphognathite) and lack of maxilliped adaptation of any anterior thoracopods, Pleopods of the moderately elongate abdomen are biramous; the terminal somite bears a small tail fan.

The euphausiaceans are filter-feeders, living on planktonic diatoms and other microorganisms or they are raptorial carnivores. Before reaching adult size, they pass through numerous larval stages, one or two years being required for this development.

No undoubted fossil euphausiacean has been discovered.

DECAPODS

The decapod eucarids are so named because limbs of the thorax behind anterior ones modified to form maxillipeds consist of five pairs. The maxillipeds comprise three limb-pairs (Table 1) and in front of them the large exopod (scaphognathite) borne by the maxilla is a distinguishing decapod character. The ten legs behind the maxillipeds are uniramous appendages adapted for locomotion, either crawling or swimming, except that in many decapods (e.g., lobsters, crayfishes, crabs) the first pair of limbs bear chelae which are incapable of aiding locomotion (Fig. 17,*1;* 24,*2-8;* 25,*1-6, 9-10;* 26,*1-12*). Uncommonly, other limbs may be similarly modified (e.g., rearmost two pairs in hermit crabs) (see Fig. 37,*1*). In relatively elongate (macrurous) decapods (Fig. 17,*1*), any of the five rear pairs of thoracopods may be chelate (Fig. 24,*2-3, 5-8;* 25,*5-6,10;* 28,*13*); the anterior five somites of their extended abdomen bear pairs of biramous pleopods and the sixth (terminal) one supports laterally widened uropods and a telson which together make a tail fan (Fig. 17,*1;* 28,*13*). So-called brachyurous (short-tailed) types, represented by a host of crabs and some other forms, commonly have a cephalothorax which is dorsoventrally flattened, longitudinally shortened, and laterally widened. Their abdomen is much reduced, typically lacking a fan tail (Fig. 26).

Decapods include marine forms, many of them pelagic (not only shrimplike macrurous types but swimming crabs), species most commonly found in brackish waters, abundant inhabitants of fresh-waters, and not a few terrestrial air-breathers. Some are

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FIG. 26. *(Continued from facing page.)*

called rock-slider distinguished from true crabs by much-reduced and chelate fifth pereiopods and well-developed tail fan, ×0.7.

4. Marine swimming crab, *Portunus xantusii,* with hind pair of pereiopods paddle-like, ×0.5.

5. Stone crab, *Menippe mercenaria,* edible form with stout chelae, found along sea shores, ×0.13.

6, Spider crab, *Mithrax acuticornis,* slow-moving shallow-water marine form, known also as decorator crab because of habit of attaching seaweeds and sessile invertebrates to dorsal side of its carapace for concealment, ×0.3.

7. Mud crab, *Eurypanopeus abbreviatus,* small shore crab resembling stone crabs, ×0.5.

8. Oxystomatous crab, *Randallia agaricias,* with triangular mouth frame extended forward over epistome, ×1.3.

9. Cancroid crab, *Cancer productus,* relatively large commercially important marine form, ×0.3.

10. Dromiid crab, *Dromia erythropus,* with hindmost pereiopods modified for holding sponges, tunicates, or bivalves over carapace for concealment, ×0.13.

11. Raninoid crab, *Raninoides louisianensis,* primitive burrower with narrow extended abdomen and most limbs modified for digging, ×0.7.

12. Homolid crab, *Homola barbata,* with subrectangular carapace, ×0.7.

[*1-3, 5-7, 10,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill, publ., copyright 1960; *4,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill, publ., copyright 1949; *8-9, 11-12,* from Rathbun, 1925, 1930, 1937.]

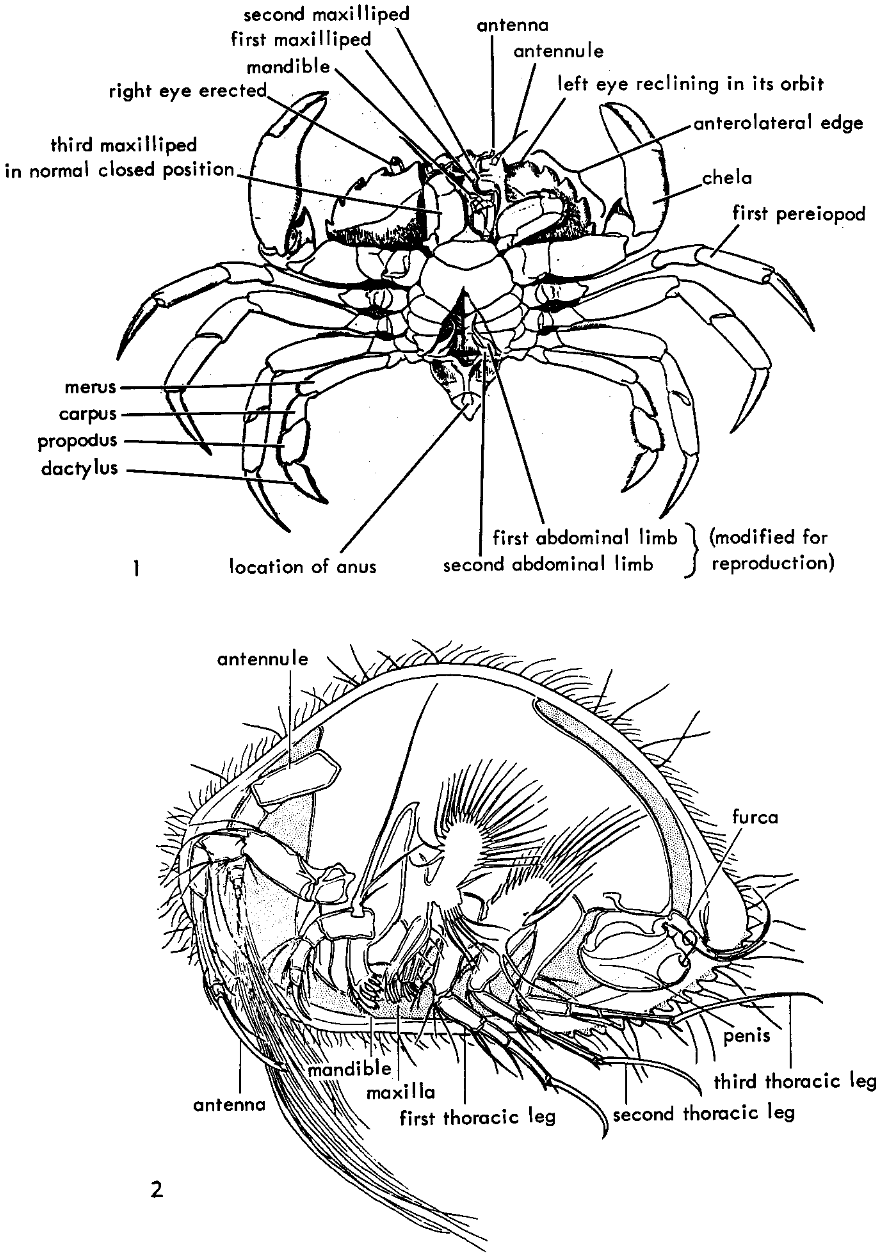

FIG. 27. Morphology of Crustacea—appendages.

1. Ventral view of shore crab, *Carcinus maenas*, showing diversely formed limbs, including abdominal ones modified for reproduction, visible only by turning abdomen backward from normal tucked in position, ×1.

2. Side view of marine podocopid ostracode, *Bairdia frequens*, with left valve removed to show appendages of male, mostly concealed within carapace, ×65.

[*1*, from Shipley & MacBride in Borradaile & Potts, *The Invertebrata* (4th edit., 1961), by permission, Cambridge University Press, publ.; *2*, from Kesling, 1961, *Treatise on invertebrate paleontology*, Part Q.]

burrowers and some can climb trees. True crabs (about 4,500 Recent species) slightly outnumber all other decapods combined. The known geologic distribution of decapods ranges from Permotriassic to Recent.

Morphological features of this very important group of crustaceans are described and illustrated in detail in the chapter on decapods by GLAESSNER (p. *R*401). For comparison with other assemblages which are surveyed briefly here as introduction to systematic treatment of the various divisions of Crustacea, it is sufficient to provide selected illustrations, including some with labeled parts of the exoskeleton (Fig. 27,*1*).

HOPLOCARIDS

The Hoplocarida are comparable to the Eucarida in containing crustaceans of larger than average size and in being highly developed in morphological features. Extant hoplocarids, all of which are known as stomatopods, range in length of adults from approximately 20 mm. to more than 300 mm. (1 foot); two kinds of late Paleozoic hoplocarids, called palaeostomatopods, have lengths of 3 and 13 mm. Stomatopods include fewer than 200 described species, as against more than 8,600 species of modern eucarids.

Stomatopods have an elongate, narrow body like that of a flattened caterpillar. Their shallow carapace is formed by fusion of the cephalic cover with that of the anterior three thoracic somites. Head somites bearing the large stalked and movable eyes and the antennulae are free, being visible in front of the carapace. Four thoracic somites behind the carapace also are exposed, as are the six abdominal ones, last of which bears a tail fan composed of uropods and a telson (Fig. 25,*7-8*).

Mouth parts consist of strongly calcified mandibles, small flattened maxillules, and much larger maxillae which are also flattened plates. Anterior thoracopods are not modified as maxillipeds. Instead, the first pair are slender hairy appendages, probably used for cleaning. The second thoracic legs are very strong and heavy raptorial weapons with distal claws turned back like blades of a penknife (subchelae) (Fig. 25,*7-8*; 29,*1*). This claw and limb closely resemble the distinctive corresponding structures of a praying mantis, and accordingly, the stomatopods commonly are called mantis shrimps. In several species the claws and apposed penultimate limb segment are provided with fixed and movable sharp spines, on which prey caught by the claws is impaled and easily held. The next three pairs of thoracopods are shorter and more slender than the second pair; they also are tipped with raptorial claws used for cutting up food and carrying it to the mouth. The last three thoracic limbs are walking legs which lack subchelae. The first five abdominal somites bear pairs of pleopods (Fig. 25,*7*).

All known kinds of stomatopods, except for representatives of four genera found in Jurassic and Cretaceous rocks, live in present-day seas.

GENERAL MORPHOLOGY

The body of crustaceans is composed of a linear succession of divisions termed **somites** (or metameres), each of which generally is somewhat depressed or compressed, rather than circular in transverse section (Fig. 17). Their number varies widely (Table 1), as does also fusion together of different groups. The dorsal part of the exoskeleton surrounding a somite is called **tergum** (or tergite), the ventral part **sternum** (or sternite), and the part on either side **pleuron** (or epimere). The pleura may be extended downward to protect appendages borne by the somites. More or less distinctive groups of somites having characters that differ from one another commonly are defined as separate **tagmata** (or regions). These comprise the **head** (or

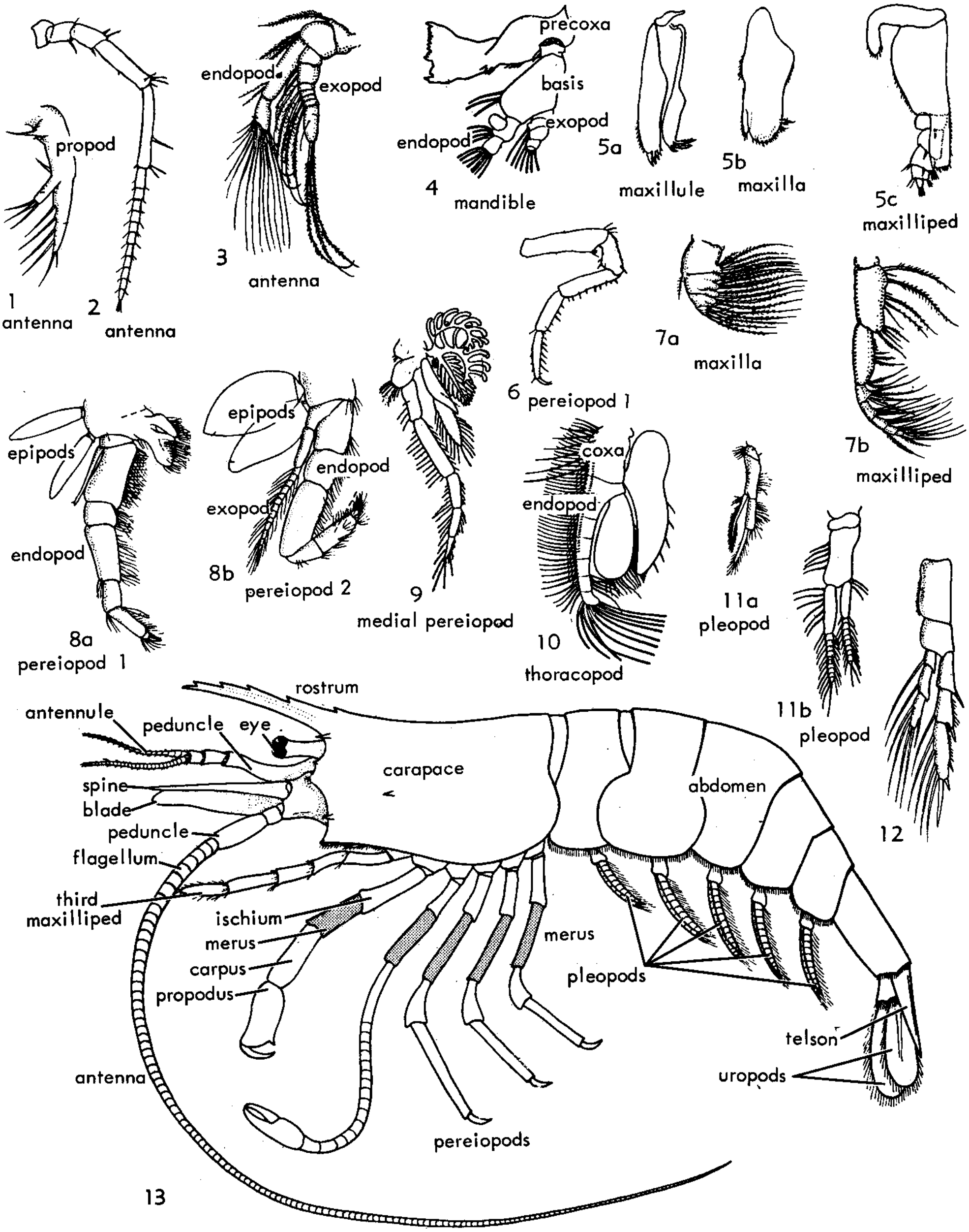

FIG. 28. Morphology of Crustacea—appendages.

1. Limb (antenna) of second pair of naupliar appendages of branchiopod *Triops* (notostracan), enl.

2,5-6. Appendages of terrestrial isopod, *Ligidium hypnorum,* enl.——*2,5.* Tactile (antenna) and food-working (maxillule, maxilla, maxilliped) appendages of head region.——*6.* Walking limb (pereiopod).

3-4,7,12. Head and thoracic appendages of copepod, *Calanus* sp., enl.——*3.* Sensory biramous head appendage (antenna).——*4,7.* Food-working head appendages (mandible, cephalon), **thorax** (or pereion), and **abdomen** (or pleon), or the first two may be united as a **cephalothorax.** Tergites fused together may form a **carapace** of variable size and shape, in some crustaceans (e.g., ostracodes, phyllocarids) having the form of a hinged or hingeless bivalve shell.

HEAD REGION

The simplest sort of head region in crustaceans is seen in the characteristic larva of the group, known as the **nauplius** (see Fig. 35,*1a*). It consists of fused somites which bear three pairs of appendages, two (antennules, antennae) in front of the mouth and one (mandibles) behind it. A single compound median eye is located anteriorly. In more advanced stages two additional somites with appendages termed maxillules and maxillae become coalesced with the one carrying the pair of mandibles. Thus, counting the embryonic frontmost somite **(acron)** with eye or eye lobes but no appendages, the crustacean head region comprises basically three preoral and three postoral somites, the one with maxillae being rearmost. In several crustacean groups (e.g., copepods, isopods, amphipods, decapods), however, anterior trunk somites become joined to the head and their appendages, differentiated as maxillipeds, aid in feeding (Fig. 28,*5c,7b*) (Table 1). The separation of head from thorax is then indistinct, or at least quite arbitrary. Because the maxilliped-bearing somites usually show features of transition to those behind them and because the skin fold forming the carapace first arises from the maxillary somite, the true head of crustaceans is held to exclude somites behind the maxillae-bearing one.

A furrow (mandibular groove) immediately behind the mandibles persists in some crustaceans (e.g., *Chirocephalus, Triops*—branchiopods, *Mysis*—malacostracan), setting off the three somites with appendages of the nauplius head from those bearing maxillules and maxillae. Another furrow delimits the head and thorax in some forms. A median forward-projecting part of the carapace in many crustaceans is termed the **rostrum** (Fig. 17,*1*).

THORAX AND ABDOMEN

Unlike somites of the head region which generally are similar in nature, containing the principal sense organs and structures used in feeding, somites of the thorax and abdomen are dissimilar in various ways and degrees (Fig. 17-20, 23-27). Commonly those of the thorax bear limbs, whereas abdominal somites carry a different sort of limbs or are limbless. The boundary between thoracic and abdominal regions may be sharply marked by changes in shape of the somites and their appendages, or it may be difficult to define consistently and clearly. Generally, the thorax is considered to extend backward to include the somite bearing the male genital aperture (Table 1). The number of combined postcephalic somites ranges from one or two in the limbless stump of some ostracodes to more than 60 in some branchiopods. The terminal somite of the abdomen very commonly bears a spikelike telson and associated with this may be a pair of caudal rami forming the so-called **caudal furca.** Also, in eumalacostracans appendages (uropods) expanded in leaf-shaped manner constitute part of a tail fan, useful as rudder and as propelling organ for backward swimming.

FIG. 28. *(Continued from facing page.)*

maxilla, maxilliped).——*12*. Swimming appendage of thorax (thoracopod).

8. Thoracic appendages (pereiopods) of fresh-water syncarid malacostracan, *Anaspides tasmaniae,* enl.

9. Pereiopod of marine euphausiacean (Malacostraca), enl.

10. Thoracic limb of marine leptostracan, *Nebalia bipes* (Malacostraca), enl.

11. Swimming appendages of crayfish, *Astacus,* enl.

13. Side view of caridean prawn, *Pandalus* (marine malacostracan) showing skeletal morphology, especially varied nature of appendages borne by head region, thorax, and abdomen, approx. ×1.

[*1,3,7-8,12,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *4, 9-11,* from Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University Press, publ.; *2,5-6,* from Van Name, 1936; *13,* from Schmitt, 1921.]

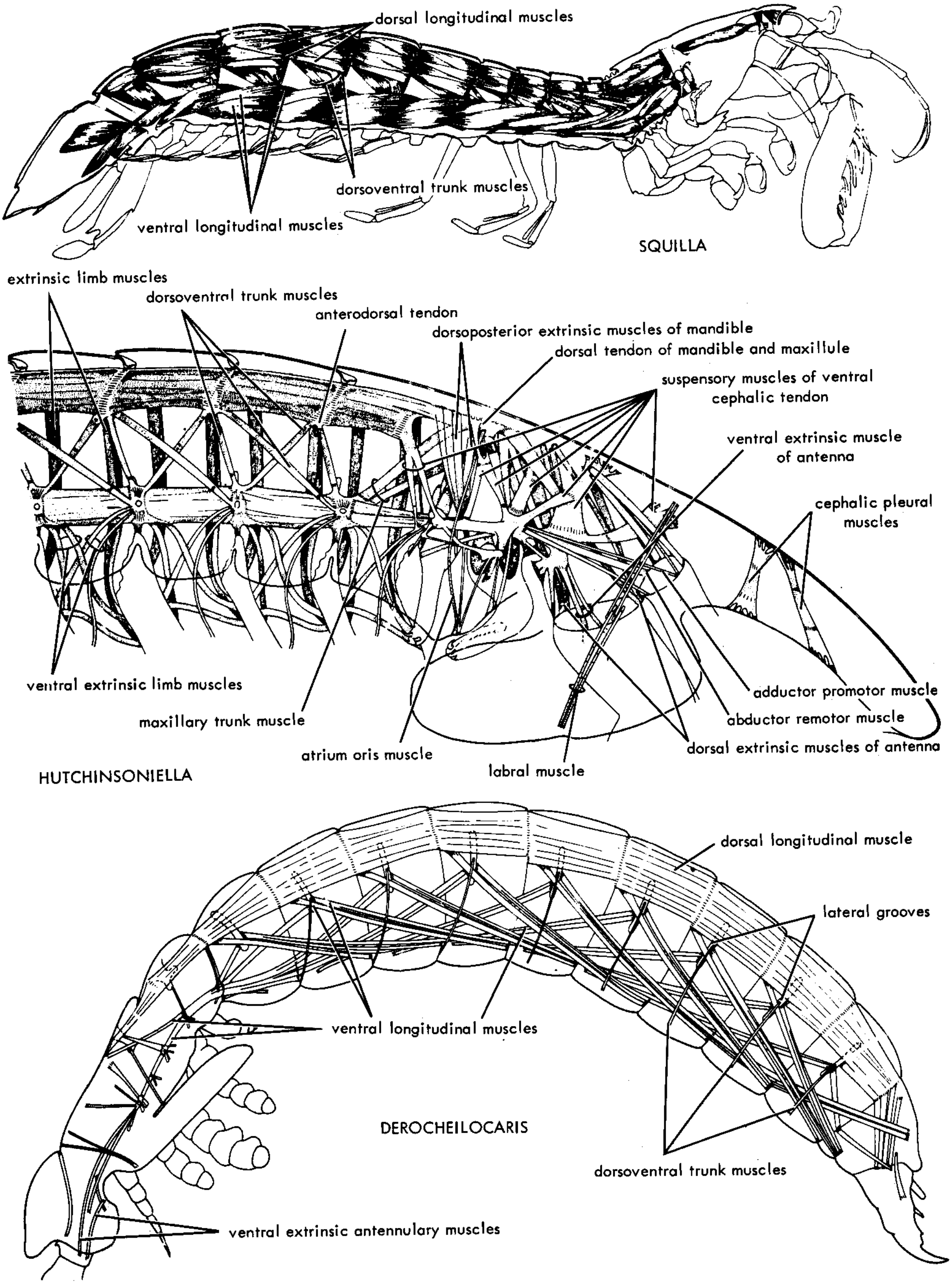

FIG. 29. Morphology of Crustacea—muscle systems in advanced and relatively simple, primitive examples (from Hessler, 1964).

1. Stomatopod malacostracan, *Squilla empusa,* medial view of left side showing trunk musculature, approx. ×1.

2. Cephalocarid, *Hutchinsoniella macracantha,* left half of cephalon and anterior part of thorax viewed from mid-line showing trunk muscula-

APPENDAGES

The paired appendages of crustaceans typically are biramous, with outer **(exopod)** and inner **(endopod)** branches joined to a common stem **(protopod)**, but some (e.g., antennules of many but not all forms) may be uniramous (Fig. 17, 28). Prevailingly, the appendages are relatively slender and these represent the type named **stenopodium,** which commonly is well jointed, with few or numerous segments. Broader and flatter limbs, such as characterize the thorax and abdomen of many branchiopods, have a thin cuticle which allows movement without need for joints; this type is called **phyllopodium.** Outward from the body the segments of well-jointed appendages are differentiated as **coxa, basis, ischium, merus, carpus, propodus,** and **dactylus,** or where very numerous and similar to one another (e.g., antennules, antennae, exopods of swimming appendages) they are not separately indicated (Fig. 27,*1*; 28,*13*). The endopods of crustacean limbs may be generalized in form, but mostly they are modified to serve a wide variety of functions. Among these are sensory perception, locomotion, respiration, prehension and comminution of food, sex recognition and attraction, reproduction, incubation of eggs and larvae, self-protection, and nearly all others that pertain to successful existence. Thus, the possession and use of appendages are prime requisites of crustaceans.

Names given to crustacean appendages depend to some extent on their form and function, but mostly take account also of their location. In the head region, from the front backward, the paired appendages are the sensory antennules and antennae (Fig. 17; 28,*1-3,13*), followed behind the mouth by the food-working mandibles, maxillules, and maxillae (Fig. 17; 28,*4-5,7a*). The food-handling work of the three last-mentioned pairs is done by their proximal segments **(gnathobases)**. Appendages of the thoracic region are collectively designated as **pereiopods** and **thoracopods** (Fig. 17; 27,*1*; 28, *6,8-10,13*). The anterior thoracopods in some crustaceans (termed **maxillipeds**) aid in feeding (Fig. 28,*5c,7b,13*). Abdominal appendages are called **pleopods** or rearmost ones **uropods.** The abdominal limbs chiefly serve functions of locomotion, especially in swimming. In many crustaceans pleopods are lacking. Also a **telson** may form a spike-like rear extremity.

Pereiopods are adapted for walking, crawling, or swimming and may be variously modified for digging, grasping or shearing prey, and for brood-carrying. Those bearing pincer-like claws **(chelae)** are **chelipeds** or **gnathopods;** their chelae range from small to very large and powerful (e.g., numerous lobsters, crabs, other decapods) (Fig. 26; 27,*1*). In stomatopods, the most distal segment of front thoracopods is reflexed so as to bear against the one preceding it and this type of limb is called subchelate; the **subchelae** of the second thoracopods are enlarged spinose structures which resemble the stout raptorial limbs of a praying mantis and serve the same function (Fig. 25,*7-8*). Among peracarid malacostracans, leaflike pereiopod elements **(oostegites)** of females are used for protection of eggs and larvae. Exceptionally modified thoracopods are the biramous **cirri** of thoracican cirripeds (Fig. 21,*3*; 22,*1b*).

Typical pleopods of most malacostracans are biramous swimming appendages formed by subequal exopod and endopod extending from the protopod extremity. The two branches of each pleopod may be coupled together by tiny hooks (retinacula) to form a more efficient oarlike structure. In some groups of crustaceans (e.g., isopods, stomatopods) the pleopods are altered to function as gills. Terminal ones (uropods) of many crustaceans are shaped and arranged

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FIG. 29. *(Continued from facing page.)*

ture and proximal part of extrinsic limb musculature, much enl.

3. Mystacocarid, *Derocheilocaris typicus,* medial view of right half of body showing trunk musculature and origins of few cephalic extrinsic limb muscles, much enl.

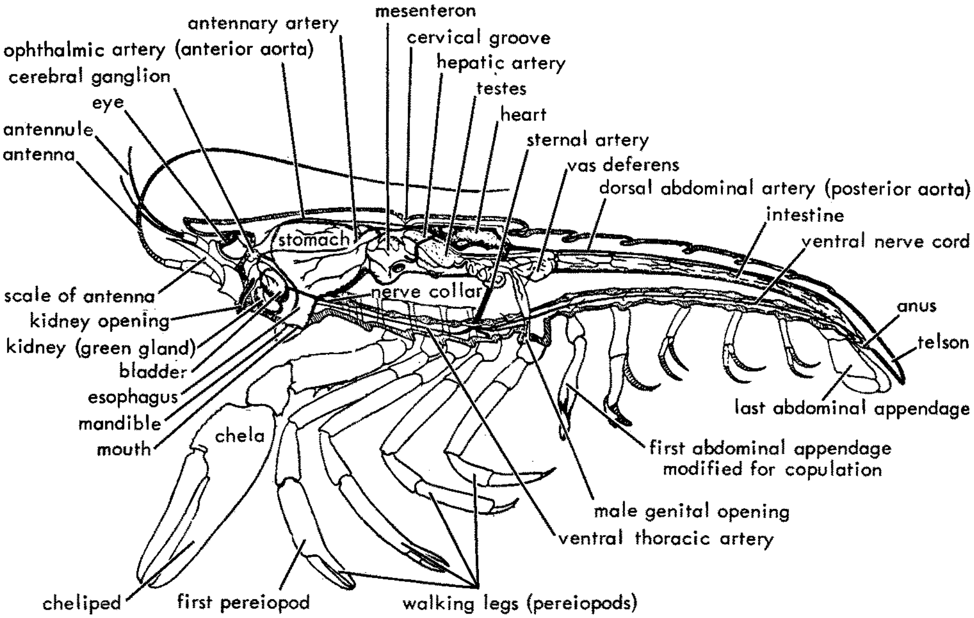


Fig. 30. Morphology of Crustacea. Median longitudinal section of crayfish, *Astacus astacus,* with appendages attached to right side of head and body. Internally, placement and some divisions of digestive and nervous systems are shown. [From Shipley & MacBride in Borradaile & Potts, *The Invertebrata* (4th edit., 1963), by permission, Cambridge University Press, publ.]

as parts of a powerful tail fan for steering and backward swimming. Also a very common structure at end of the abdomen is a caudal furca.

INTERNAL FEATURES

Internal features of crustaceans which call for notice include some aspects of the inner side of their exoskeleton, but chiefly concern soft parts such as their musculature and digestive, circulatory, respiratory, nervous, glandular, and reproductive systems. These vary widely in nature and complexity, functioning in ways dictated by organization of the body, diversity of habit, and adaptations to environment developed in each group.

MUSCULATURE

Movements of the body for walking, crawling, burrowing, and swimming, for feeding, for breathing, and for copulating are controlled by many sorts of muscles, some oriented longitudinally and others transversely or obliquely in relation to somites and to segments of appendages. Individual muscles may be relatively long or short and weak or powerful. Commonly they are attached to ingrowths of cuticle termed **apodemes** or directly to the inner surface of the hardened integument of the body. Even in primitive forms such as cephalocarids, mystacocarids (Fig. 29) and branchiopods their number and complexity are great. In ostracodes, the pattern of muscle scars on the valve interiors (Fig. 19,*10b*) is found to be helpful in classification. Commonly, crustacean muscles are supplied with only a few nerve fibers, some of which serve to stimulate and others to inhibit contraction.

DIGESTIVE SYSTEM

The digestive system of crustaceans varies considerably in different groups, ranging from a simple, straight alimentary canal extending from mouth to anus without perceptible differentiation into regions, to complex types in which parts of the tract are distended into a foregut, a midgut, and a hindgut (Fig. 30; 31,*1*).

The front part of the **foregut,** or **stomodeum,** is esophageal in nature, whereas the strongly muscled and generally enlarged rear part comprises a **stomach** or gizzard. This may be lined with small teeth to form a gastric mill that serves for mastication of food. Bristles may be present to strain particles of food.

The **midgut** or mesenteron is a digestive and absorptive region, lined with tubules of cells which secrete digestive enzymes or serve for absorption of digestive products. At its anterior end are paired digestive glands, which may branch to form a "liver."

At its posterior extremity the midgut opens into an intestine or **hindgut** (also called **proctodeum**). The hindgut, which may be absent, passes waste material along for ejection at the anus. With few exceptions, the anal opening is located on the rearmost somite of the abdomen, on the underside of the telson.

The alimentary canal is absent throughout the life of the cirriped group known as Rhizocephala and it may be undeveloped in other parasitic forms. The food of these parasites is absorbed through the skin.

CIRCULATORY SYSTEM

The circulatory system of crustaceans generally consists of one or more branching arteries that conduct blood from the heart, which lies in a pericardial blood sinus, to the various organs (Fig. 30; 31,*1*,*3*; 32). The blood, a pale fluid bearing leucocytes in most forms but containing hemoglobin in some branchiopods, percolates from arteries through the tissues and collects in hemocoelic sinuses. Primitive branchiopods (Anostraca) and also peracarid malacostracans have an elongate heart and blood flows through a single, short artery. The heart is absent in Cirripedia and many copepods and ostracodes and the blood circulates by movements of the body and the alimentary canal. In higher Crustacea (decapods) the blood flows from the general hemocoel of the body ventrally into sternal and lateral sinuses and vents to the gills for oxygenation (Fig. 30; 31,*3*; 32). Carbon dioxide is exchanged for oxygen in the gills and nitrogenous wastes are removed in excretory organs. The blood returns through venous channels to reenter the polygonal heart through openings termed ostia.

RESPIRATORY SYSTEM

Respiration in smaller crustaceans is effected through the general surface of the body. The process may be supplemented in forms with stronger cuticle by differentiation of appendages or lining of the carapace to form **gills** or **branchiae** (Fig. 32). Limbs of branchiopods serve in respiration as well as for other functions. Epipods are branched and folded in Malacostraca to form gills. The euphausiaceans have branchiae on all thoracopods, which are progressively larger and more complex from front to rear. The inflated carapace of some peracarids (Cumacea) is due to large lateral **branchial chambers,** each containing a large epipod composed of a complex gill and an exhalant siphon. Branchial chambers are also seen in decapods, in the thoracic region and protected by extension of the carapace (Fig. 31,*3*; 32). The gills may be differentiated by their points of origin as podobranchs, arthrobranchs, and pleurobranchs.

Isopods respire through rami of the abdominal limbs, but when they become terrestrial the integument takes the form of branching tubules resembling tracheae. Some land crabs also have special adaptations for air breathing in the form of vascular papillae on the lining of the gill chamber.

NERVOUS SYSTEM

The nervous system in primitive crustaceans consists of a mass of antennal ganglia behind the mouth united by nerve cords passing around the esophagus. These connect with a widely separated ladder-like chain of nerve cords extending longitudinally, passing through all of the somites, and connected crosswise by short commissures (Fig. 31,*5*). In other groups varying degrees of complexity are seen. The two halves of the ladder coalesce into a ventral chain, with a ganglionic mass above the esophagus comprising a "brain" from which nerves extend to the eyes and antennae (Fig. 31, *1,4*). In the decapods additional centers are developed in the brain and a subesophageal ganglion at the front end of the ventral

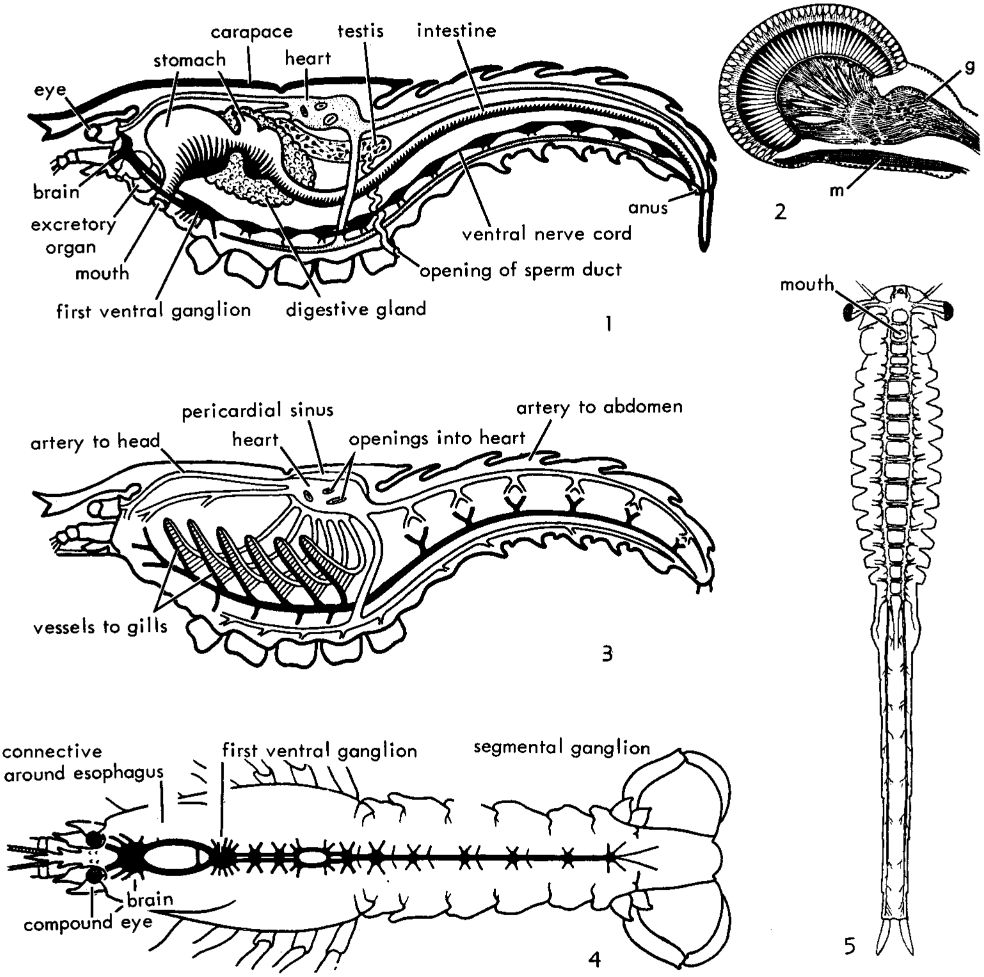


FIG. 31. Morphology of Crustacea—digestive, nervous, and circulatory systems.

1. Internal anatomy of lobster, *Homarus,* shown in diagrammatic median longitudinal section. Digestive system not segmented but divided into anterior esophageal region, stomach surrounded by digestive glands, and intestine. Nervous system clearly segmental, located on ventral side of alimentary canal.

2. Horizontal medial section of eye and ocular stalk of anostracan branchiopod, *Branchipus,* showing visual cells (ommatidia) joined to optic ganglia *(g)* of eyestalk, muscle *(m)* controlling movement of stalk, below, much enl.

3. Diagram of circulatory system of lobster showing main blood channels. Blood returning from tissues passes through gills before returning to heart.

4. Nervous system of lobster diagrammatically represented from dorsal side, with nerve ring around esophagus and gangliated double nerve cord running near ventral mid-line of body.

5. Ladder-like nervous system of anostracan branchiopod, *Branchinecta paludosa,* transverse commissures in thoracic region but lacking in abdominal part of body.

[*1, 3-4,* from Ralph Buchsbaum, *Animals without backbones,* by permission, The University of Chicago Press, publ., copyright 1948; *2, 5,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.]

nerve cord innervates the oral appendages, green glands, esophagus, and muscles of the front part of the thorax.

Sense organs are of several kinds and may be well developed. Many crustaceans possess an unpaired median eye comparable to that of the nauplius larva, or they have a pair of compound eyes. The median eye functions as the only organ of vision in copepods (Fig. 20), but is vestigial in various primitive crustaceans or may persist in advanced types accompanying the compound eyes. The median eye is divided into three pigmented masses filled with retinal cells meeting nerve fibers at their outer ends. Compound eyes are sessile or set on movable peduncles and consist of a number of visual units (ommatidia) each surrounded by pigment and all covered by a cornea, which is a transparent region of the cuticle usually divided into lenslike facets (Fig. 31,*2*). Eyes are reduced or not developed in some deep-sea decapods, some syncarids, and other blind crustaceans.

In addition to the sense of sight, the sense of touch and perhaps of taste and other sensations are transmitted by hairlike setae on the antennae and antennules and other parts of the body. The setae are hollow chitinous shafts containing nerves which transmit sensations to the nervous system. Olfactory setae sensitive to chemical stimuli perform a function similar to smelling and are responsible for leading lobsters into the bait traps. For the sense of balance there is an organ, the **statocyst,** located at the base of each antennule of many crustaceans to enable them to orient themselves with respect to the force of gravity. It consists of a pit with hair-lined walls which usually contains sand grains and other minute foreign bodies that enable the statocyst to function for equilibration. Also, statocysts occur in the uropods of various mysids.

GLANDULAR SYSTEMS

Excretory organs of Crustacea include two pairs of glands at the bases of the antennae and maxillae, opening forward (Fig. 31,*1*). The two usually are not functional at the same time, the **antennal glands** commonly functioning in the larval stage, whereas the **maxillary glands** operate in the adult. Each type has an end sac and ectodermal ducts leading to the exterior. In adult ostracodes, however, they lack openings. The antennal gland is known as the green gland in the Malacostraca and is well developed, being commonly dilated into a bladder or extended into diverticula. In other crustacean groups various additional glands may be excretory, for example, the caeca of the midgut in barnacles and ectodermal glands at bases of thoracic limbs in leptostracans (e.g., *Nebalia,* Fig. 19,*8*).

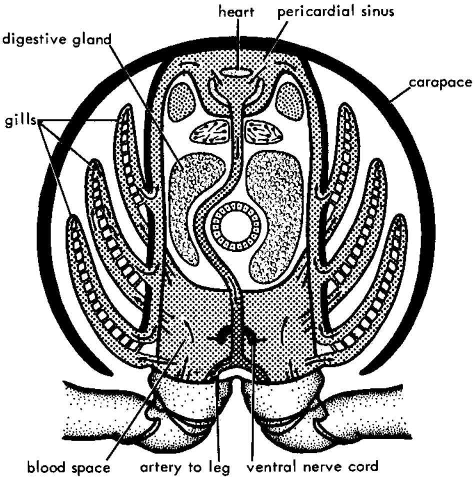


FIG. 32. Morphology of Crustacea. Transverse section through thorax of lobster, *Homarus,* showing relations of gill chambers to other organs and path of blood circulating through some main channels. [From Ralph Buchsbaum, *Animals without backbones,* by permission, The University of Chicago Press, publ., copyright 1948.]

In addition to these and the digestive glands already mentioned, are various types of **dermal glands.** Some of these in the vicinity of the mouth secrete a mucous substance which binds together small food particles to aid in swallowing them. Others on the surface of the body and limbs of amphipods secrete a protective covering. A gelatinous secretion produced by some freshwater copepods is resistant to desiccation.

Cement glands secrete substances serving in Cirripedia for attachment of the animals to supporting surfaces or, in some other crustaceans, for agglutination of sediment in building tubular burrows. The cypris larvae of cirripeds have cement glands

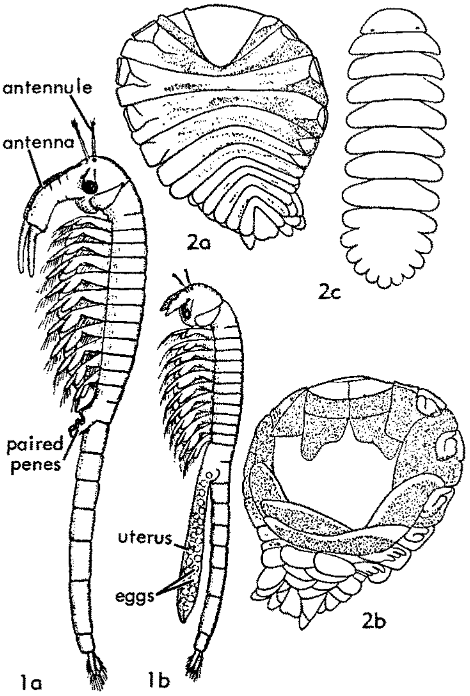


Fig. 33. Morphology of Crustacea—sexual dimorphism.

1. Anostracan branchiopod, *Branchinecta paludosa;* side views of male *(1a)* and female *(1b)* showing differences both in form and size. Ordinarily dimorphic males are smaller than females, but here the reverse is true, ×2.7.
2. Epicaridean fresh-water isopod, *Probopyrus floridensis,* which lives parasitically on gills of other crustaceans; *2a,b,* dorsal and ventral sides of female, showing asymmetry and width subequal to length, ×8; *2c,* dorsal side of male, which is much smaller than female, long-bodied, and symmetrical, ×27.

[*1,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *2,* from Richardson, 1905.]

located at ends of antennules opening through discs, by which they become attached to fixed objects. In the Lepadomorpha secretions of cement glands form vesicular balls which serve to keep the barnacles afloat.

Many pelagic crustaceans, such as the euphausiaceans (Malacostraca) have dermal glands **(photophores)** that secrete a phosphorescent or luminous substance (Fig. 24, *4*). In Decapoda and Mysidacea the secretion may come from the excretory organs or from other locations on the body and limbs. The light emitted in this way, which is brilliant blue-green in euphausiaceans, may be used to attract prey, for illumination of surroundings, or for protection of a group.

Another gland is the **sinus gland** located in the eyestalks, which has been found to store hormones controlling the molting cycle, formation and development of eggs within the ovary, and color changes.

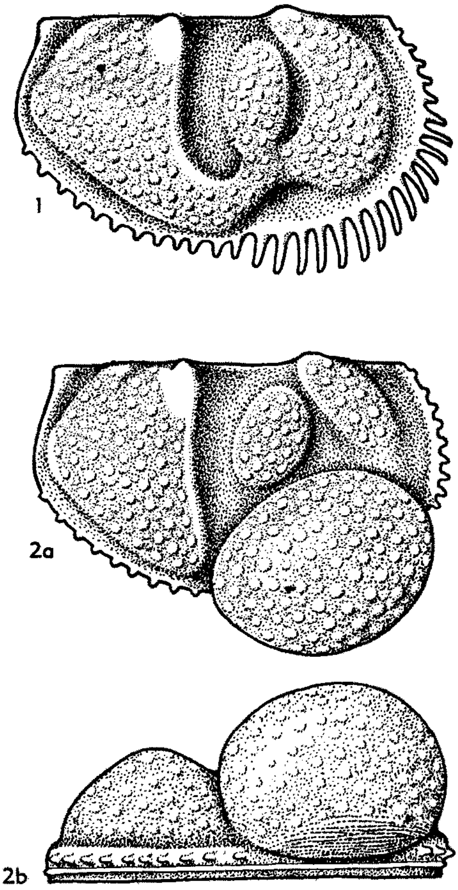


Fig. 34. Sexual dimorphism in Crustacea exhibited by carapaces of male ostracode *(1)* and female *(2a,b)* specimens of *Beyrichia kiaeri* Henningsmoen, from Upper Silurian of Norway; *1, 2a,* side views of right valves; *2b,* ventral view of right valve; ×22 (Kesling, 1957). The female valves are chiefly distinguished by the expanded brood pouch developed in the anteroventral region.

REPRODUCTIVE SYSTEM

The sexes of most crustaceans are separate, although some cirripeds, parasitic isopods, and certain other forms are hermaphroditic. Parthenogenesis occurs in various lower crustaceans. The reproductive system generally consists of internal tubular gonads, ovaries or testes, placed in the thorax dorsally and laterally from the digestive canal. Paired reproductive ducts of both sexes commonly pass laterally and ventrally to separate openings on specific thoracic appendages (Table 1). In most groups the male tends to be smaller than the female, even extremely minute in some parasitic forms. During copulation of various decapods and other crustaceans **spermatophores** (packets of sperm bound together by mucous secretion) are emitted from the male genitalia and transferred to a pouch-like cavity of the female termed the **seminal receptacle** or **vesicle** (Fig. 17,*3*). This is connected internally to the oviducts with a median aperture opening to the exterior of the thorax, although in some forms it may be external and temporary. Its function is merely to hold the immobile sperm until time of fertilization, when eggs are emitted by the female. After extrusion, the eggs are carried in some manner for a time by many crustaceans in a brood pouch, adhering to the body, or attached to appendages under the abdomen.

DIMORPHISM

Sexual dimorphism is a common attribute of crustaceans but by no means universal. It is prevalent in such branchiopod groups as conchostracans, cladocerans, and anostracans (Fig. 33,*1*), marked by differences in size and shape of males and females, as well as in the nature of some appendages. Commonly males are smaller than females, but the reverse may be true (e.g., anostracan *Branchinecta,* which also has antennae much larger than those of females, Fig. 33,*1*). In epicaridean isopods, as illustrative of strong dimorphism in another group, the females are greatly modified in shape and symmetry from the smaller males (Fig. 33,*2a-c*); in some of these crustaceans the females are so specialized as to be little more than formless sacs containing eggs.

Well-developed sexual dimorphism characterizes the bivalved carapace of numerous genera of ostracodes, especially in such marine fossil groups as Ordovician-to-Permian palaeocopids (Fig. 34). In a host of copepods dimorphism is marked by differences in body shape and nature of the appendages, very evident in some but less so in others. As a rule, advanced types of crustaceans, as represented by the highly diverse malacostracans, display modest distinctions between males and females, rather than accentuated ones, and these relate more to the nature of appendages than to body size and shape.

Extreme dimorphism is found in some parasitic crustaceans, for example, rhizocephalan cirripeds with relatively huge saclike females which carry hyperparasitic larval males (e.g., *Peltogaster,* see Fig. 39,*1*). A curious effect of parasitism is seen in crabs infested by rhizocephalans, for the male crabs "degenerate" into female-like forms and females revert to juvenile types with loss of their gonads.

GLOSSARY OF MORPHOLOGICAL TERMS

The exceptional variety and complexity of morphological features displayed by crustaceans have led to an unusually large number of morphological terms. The following list does not undertake to be exhaustive, but it brings together for convenient reference essentially all terms used in the *Treatise* for exoskeletal features and provides also numerous synonyms. In general, the usage preferred by *Treatise* authors is indicated by terms which are accompanied by definitions, alternative designations lacking such definitions but providing a cross reference (e.g, abdominal limb. *See* pleopod, uropod.).

Acknowledgment is made to *Treatise* authors who have given special help in preparation of the glossary: M. F. Glaessner, R. R. Hessler, L. B. Holthuis, W. A. Newman, W. D. I. Rolfe, and Paul Tasch.

abdomen. Trunk tagma following thorax and including telson; somites either without limbs or (in Malacostraca) bearing pleopods or uropods or both; in crabs bent sharply forward under thorax and much wider in females than in males; *syn.,* pleon. *See* also metasome, urosome.

abdominal limb. *See* pleopod, uropod.

abdominal process. Finger-like projection (one to several) on dorsal surface of cladoceran abdomen; may help to retain eggs in brood chamber.

abdominal somite. Any single division of body behind thorax; *syn.,* pleomere, pleonite.

abreptor. Postabdomen of cladocerans, bent forward from junction with body and terminating in 2 claws with spines and teeth on their concave sides.

acanthopod. In Cirripedia (Thoracica), appendage where rami of cirrus have setae along lesser curvature much reduced; setae of greater curvature arranged in transverse row, as strong sharp spines at each articulation (cf., ctenopod, lasiopod).

acron. Anteriormost part of body carrying eyes, not considered to be true cephalic somite; *syn.,* ophthalmic somite, presegmental region. [Some authors recognize as protocephalon anterior part of head bearing eyes and antennules, thus interpreting cephalon as composed of only 4 somites.]

adductor muscle (of carapace). Muscle attached to carapace for pulling it to body (thorax) or connecting halves of bivalve shell (e.g., Conchostraca, Ostracoda, Leptostraca) or valves of cirriped capitulum for closure of them. In Cirripedia, any transverse muscles, particularly that of maxillary segment, for closure of aperture; in Thoracica, adductor (adductor scutorum) acts upon scutal plates or valves.

adductor pit. In cirripeds, depression on interior of scutum for attachment of adductor muscle, located between adductor ridge and occludent margin.

adductor ridge. In cirripeds (Balanomorpha), linear elevation on interior of scutum between adductor pit and tergal margin.

aesthetasc. *See* esthetasc.

aesthete. *See* esthetasc.

afferent channels. Openings through which water passes to gills, in brachyuran crabs generally located in front of bases of chelipeds.

ala (pl., **alae**). One of pair of posteriorly directed cephalic-shield extensions; in cirripeds (Balanomorpha), triangular lateral part of compartment plate delimited from paries, which is overlapped by adjacent compartment plate with or without radius.

aliform apophyses. Incurved anterior and posterior extremities of growth lines (e.g., Conchostraca, characteristic of *Ipsilonia*).

ambulatory leg. *See* pereiopod.

anal spines. Single row of spines on either side of cladoceran postabdomen (e.g., Sididae, Holopedidae, Daphniidae). [In addition, some cladocerans possess lateral spines (e.g., Macrothricidae, Chydoridae).]

antenna (pl., **antennae**). One of pair of anterior appendages of head region placed morphologically next behind antennule, uniramous in some crustaceans but biramous in all nauplii and in adults of most classes; may be extremely long and composed of multitudinous small segments or reduced to mere rudiment or lacking; *syn.,* second antenna.

antennal carina. *See* carapace carina, a.

antennal gland. *See* green gland.

antennal groove. *See* carapace groove, a.

antennal region. *See* carapace region, a.

antennal scale. *See* scaphocerite.

antennal spine. *See* carapace spine, a.

antennula. *See* antennule.

antennular scale. *See* stylocerite.

antennule. One pair of morphologically frontmost appendages of head region, usually filiform and multiarticulate, uniramous except in Malacostraca where it is generally biramous or even triramous; may be larger or smaller than morphologically next following appendages named antennae; *syn.,* antennula, first antenna.

anterior tubercle. Swelling or small protuberance in anterior region of carapace of Archaeostraca; polygenetic, includes the "optic tubercle" of some authors.

anterolateral region. *See* carapace region, b.

aperture. Posteroventral opening into cirriped mantle cavity.

apex. Upper angle of scutum or tergum of cirripeds.

apicobasal ridge or furrow. In cirripeds longitudinal feature which divides tergal slip (tergum) from rest of valve.

apodeme. Infold of exoskeleton serving for attachment of muscles.

appendix interna. Medial projection stemming from pleopodal endopods, serving to unite members of each pair of pleopods; *syn.,* stylamblys.

appendix masculina. Complex median process of endopod of second pleopods of male Caridea and some isopods; serves in copulation.

arm. Merus of cheliped (obsolete term).

arthrobranch. Gill of decapods attached to articular membrane between limb and body; *syn.,* arthrobranchia.

arthrobranchia (pl., **arthrobranchiae**). *See* arthrobranch.

arthrophragm. *See* endophragm.

article. Individual element of crustacean appendage; *syn.,* joint, segment.

articular furrow. In cirripeds, groove on tergal margin of scutum or scutal margin of tergum forming part of articulation between these plates.

articular ridge. In cirripeds (Balanomorpha), linear elevation on tergal margin of scutum or scutal margin of tergum close to articular furrow and with it forming articulation between these plates.

atrium oris. Preoral cavity, bounded ventrally by posteriorly directed labrum, dorsally by ventral surface of cephalon just behind mouth, and laterally by paragnaths and mandibles.

attractor epimeralis muscle. Important muscle in many decapods, inserted along line of branchiocardiac groove in carapace.

basal margin. In cirripeds, lower edge of scutum or tergum or other plate.

basicarinal angle. Intersection of basal and carinal margins of cirriped tergum.

basicerite. Second segment of antennal peduncle (in Caridea bearing scaphocerite).

basilateral angle. In cirripeds, intersection of lateral and tergal margins of scutum; *syn.,* basitergal angle.

basiocclудent angle. Intersection of basal and occludent margins of cirriped scutum.

basiophthalmite. Proximal segment of eyestalk, articulating with distal segment (podophthalmite) which bears corneal surface of eye.

basipod(ite). *See* basis.

basis (pl., **bases**). Limb segment adjoining coxa on its distal side and commonly bearing endopod and exopod; *syn.,* basipod(ite); in nonpedunculate cirripeds comprises basal calcareous or membranous plate which furnishes anchorage to foreign body or substrate.

basiscutal angle. Intersection of basal and scutal margins of cirriped tergum.

basitergal angle. Intersection of basal and tergal margins of cirriped scutum.

beaked apex. In cirripeds (Balanomorpha), upper angle of tergum produced into long narrow point.

biformes. Carapaces reflecting sexual dimorphism (e.g., Conchostraca), marked by differing valve proportions for each sex of same species (DADAY); a given species may have carapaces that are "biformes."

biramous. Two-branched; crustacean limb in which basis bears both exopod and endopod.

blood rooms. Network of anastomosing cavities in body of conchostracans which provide for circulation of blood (SARS).

body chamber. In cirripeds, interior of shell containing soft parts of animal.

body of mandible. *See* mandible body.

body ring. Combined tergite and sternite of single somite, bearing legs or legless (as used by some specialists on Notostraca, not equivalent to somite).

body somite. Generally refers to unit division of thorax + abdomen in contrast to cephalic somite.

branchia (pl., **branchiae**). Thin-walled finger-like or leaflike structure extending outward from limb or secondarily from side of body, functioning for respiration; *syn.,* gill. [Special types are termed arthrobranchs, pleurobranchs, and podobranchs, depending on their place of attachment, and dendrobranchs, phyllobranchs, mastigobranchs, and trichobranchs, depending on their shape. In Cirripedia (Balanomorpha) pair of leaflike fleshy extensions of mantle lining, within mantle cavity, presumed to be respiratory in function.]

branchial carina. *See* carapace carina, b.

branchial cavity. *See* branchial chamber.

branchial chamber. Space between body and wall of carapace enclosing branchiae; *syn.,* gill chamber.

branchial glands. Masses of connective-tissue cells surrounding venous channels in branchiae and devoid of ducts.

branchial region. *See* carapace region, c.

branchiocardiac carina. *See* carapace carina, c.

branchiocardiac groove. *See* carapace groove, b.

branchiostegal area. Part of carapace extending laterally and downward over branchiae.

branchiostegal spine. *See* carapace spine, b.

branchiostegite. Part of carapace extending over top and side of branchial chamber.

buccal cavity. Hollow space on ventral side of body containing mouth parts, in Malacostraca bounded by epistome in front and free edges of carapace on sides.

buccal frame. Structure of brachyuran decapods enclosing mouth parts, its sides formed by free anterolateral edges of carapace, its front delimited by epistome, and commonly closed by operculiform third maxillipeds.

calceolus (pl., **calceoli**). Complex sensory filaments on antennules of some amphipods.

calyptopis stage. Third larval stage in euphausiaceans, characterized by differentiation of abdomen and appearance of compound eyes.

capitulum. In pedunculate cirripeds portion of carapace enclosing trophic structures, commonly armored by calcareous plates.

carapace. Cuticular, varyingly calcified structure comprising cephalic shield and fold of integument arising from posterior border of maxillary somite extending over trunk, usually covering it laterally as well as dorsally; commonly fused to one or more thoracic somites and in many forms having mid-dorsal hinge.

carapace adductor muscle. *See* adductor muscle.

carapace angles. In Leaiidae (Conchostraca), angle made by straight dorsal margin with anterior rib (α) and with posterior rib (β); these angles may have utility in tracing evolutionary development and in stratigraphic zonation.

carapace carina. Narrow ridge variously located on surface of decapod carapace——named types:

a) **antennal.** Narrow ridge extending backward from antennal spine.

b) **branchial.** Narrow ridge extending backward from orbit over branchial region.

c) **branchiocardiac.** Narrow ridge marking off branchial from cardiac regions of carapace.

d) **gastroorbital.** Narrow ridge extending backward from supraorbital spine.

e) **lateral.** Narrow ridge on side margin of carapace.

f) **orbital.** Narrow ridge on margin of orbit.

g) **posterior.** Transverse narrow ridge in front of carapace marginal groove.

h) **postorbital.** Narrow ridge slightly behind orbital margin and parallel to it.

i) **postrostral.** Narrow ridge behind rostrum extending along dorsal mid-line of carapace.

j) **rostral.** Longitudinal narrow ridge continuous with lateral margin of rostrum.

k) **subhepatic.** Narrow ridge extending backward from branchiostegal spine.

l) **submedian.** Narrow ridge on either side of postrostral carina and parallel to it; may join rostral carina.

m) **supraorbital.** *See* gastroorbital carina.

carapace costae. Closely spaced radial ridges, grading from fine to coarse, that become obsolete near umbo and do not cross it (=radial lirae, radial riblets, accessory ribs) (e.g., Conchostraca, especially Estheriellidae, in which valves generally have more than 5 costae).

carapace costellae. Fine radial ridges that run from ventral margin to and across umbo, and are usually numerous on any given valve (e.g., Conchostraca).

carapace groove. Furrow on surface of decapod, generally dorsal——named types:

a) **antennal.** Furrow on carapace extending backward from vicinity of antennal spine.

b) **branchiocardiac.** Oblique furrow approximately in middle of posterior half of each side of carapace, separating branchial and cardiac regions and reaching dorsomedian part of carapace well behind cervical or postcervical grooves; may be longitudinal, connecting cervical and postcervical grooves, or extending backward from submedian point on postcervical groove.

c) **cervical.** Transverse furrow in median part of carapace between gastric and cardiac regions, curving forward toward antennal spine.

d) **gastroorbital.** Short longitudinal furrow branching from cervical groove at level of orbit and running toward it.

e) **hepatic.** Short longitudinal furrow connecting cervical with postcervical and branchiocardiac grooves, more or less continuing antennal groove.

f) **inferior.** Transverse furrow extending from junction or hepatic and cervical grooves toward side margin of carapace, more or less continuous with cervical groove.

g) **marginal.** Furrow close to posterior edge of carapace and parallel to it.

h) **postcephalic.** One of three transverse furrows on carapace of many fossil decapods.

i) **postcervical.** Furrow located behind cervical groove and parallel to it, dividing cardiac region into two parts.

j) **submedian.** Longitudinal furrow in submedian dorsal part of carapace closely adjacent to postrostral carina.

carapace growth line. Peripheral margin of successive membranes added to shell during each molt (e.g., Conchostraca).

carapace horn. Anterodorsal termination of carapace valves in some Archaeostraca; may be indurated (e.g., *Ceratiocaris*) or produced into long processes (e.g., *Caryocaris*).

carapace lirae. Raised, linear, fine concentric ridges parallel to growth lines and occupying an interspace e.g., Conchostraca).

carapace region or area. Differentiated portion of decapod carapace surface distinguished in descriptions and used in classification——named types:

a) **antennal.** Anterior marginal part of carapace bordering orbital region laterally and also touching hepatic, pterygostomial, and, in some forms, frontal region.

b) **anterolateral.** Lateral part of carapace bordering subhepatic or hepatic regions.

c) **branchial.** Lateral part of carapace behind pterygostomial region and overlying branchiae, divided by some authors into epibranchial, mesobranchial, and metabranchial subregions.

d) **cardiac.** Median part of carapace behind cervical groove or suture, between urogastric and intestinal areas.

e) **frontal.** Anteromedian part of carapace including rostrum and area behind it.

f) **gastric.** Median part of carapace in front of cervical groove and behind frontal region; divided by some authors into epigastric, mesogastric, metagastric, protogastric, and urogastric subregions.

g) **hepatic.** Part of carapace which may touch antennal, cardiac, and pterygostomial regions.

h) **intestinal.** Short transverse part of carapace behind cardiac region, designated by some as posterior cardiac lobe.

i) **jugal.** *See* pterygostomial region.

j) **orbital.** Part of carapace behind eyes, bordered by frontal and antennal regions.

k) **pterygostomial.** Anterolateral part of carapace on ventral surface located on opposite sides of buccal cavity.

l) **subhepatic.** Part of carapace below hepatic region and extending below lateral edge of latter.

carapace spine. Sharp projection of carapace important for classification——chief types:

a) **antennal.** Spine on front margin of carapace slightly below orbit.

b) **branchiostegal.** Spine on front margin of carapace or slightly behind it about halfway between antennal and pterygostomial spines.

c) **hepatic.** Spine in hepatic region of carapace below lower branch of cervical groove and behind it.

d) **infraorbital.** Spine on lower angle of orbit.

e) **postorbital.** Spine at moderate distance behind middle of orbit.

f) **postrostral.** Dorsomedian spine immediately behind rostrum.

g) **pterygostomial.** Spine on anterolateral angle of carapace.

h) **suborbital.** Spine at moderate distance below middle of orbit and slightly beneath it.

i) **supraorbital.** Spine at moderate distance obliquely behind and above orbit (may be placed on postorbital carina).

carapace tooth. Small sharp spinous projection in varied locations——named types:

a) **cardiac.** Tooth on mid-line of carapace just behind cervical groove.

b) **gastric.** Tooth on mid-line of carapace just in front of cervical groove.

c) **lateral.** Tooth placed on lateral margin of carapace (includes anterolateral, mediolateral, posterolateral teeth).

d) **orbital.** Tooth on orbital margin.

e) **posterior.** Tooth on mid-line of carapace just in front of posterior margin between it and marginal groove.

f) **pregastric.** Tooth on mid-line of carapace between gastric tooth and rostrum.

g) **rostral.** Tooth on rostrum; may be single (e.g., scyllarid palinurans) or multiple and classified as upper, lower, or lateral (e.g., nephropid astacideans and natantian crabs).

cardiac notch or incision. Indentation on posterior margin of carapace (e.g., some Alpheidae).

cardiac region. *See* carapace region, d.

cardiac tooth. *See* carapace tooth, a.

cardo. Basal segment of maxillula articulating with head.

caridean lobe. External rounded projection on basal part of exopod of first maxilliped (e.g., Caridea).

caridoid facies. Aspect of primitive Eumalacostraca distinguished by enclosure of thorax by carapace, movably stalked eyes, biramous antennules, scaphocerite-bearing antennae, thoracopods with natatory exopods, elongate abdomen ventrally flexed and powerfully muscled, and caudal fan.

carina. Any keel-like structure, as on dorsum of pleon of some amphipods; in cirripeds, single compartment plate at end of shell where cirri are protruded, or adjacent to tergum, possessing alae only. *See* carapace carina.

carinal. In cirripeds (Thoracica), toward or adjacent to compartment plate termed carina.

carinal latus. *See* latus (carinal), a.

carinal margin. In cirripeds (Thoracica), edge of tergum adjacent to carina, occluding with carinal margin of opposed tergum.

carinate. Conchostracan valve bearing rib(s), chiefly applicable to Leaiidae.

carinolateral. Compartment plate of cirripeds located on either side of carina, with radii on cardinal side and alae on rostral side; *syn.*, latus (cardinal).

carpocerite. Distal (5th) segment of antennal peduncle.

carpopod(ite). *See* carpus.

carpus. Segment of limb located next distally from merus and joined to propodus proximally; *syn.*, carpopod(ite), wrist.

caudal appendage. In cirripeds, one of terminal, multiarticulate or uniarticulate, uniramous paired appendages, homologous with caudal furca of other crustaceans.

caudal fan. Combination of laterally expanded uropods and telson turned backward to form powerful swimming structure or means of steering and balancing; *syn.*, tail fan, rhipidura.

caudal filament. *See* caudal ramus.

caudal furca. Pair of caudal rami.

caudal ramus. Single appendage of terminal abdominal somite paired with another to form caudal furca, both articulated with telson; usually rodlike or bladelike but may be filamentous and multiarticular (caudal filament); *syn.*, cercus, cercopod, caudal style, stylet.

caudal style. *See* caudal ramus.

cement gland. Special concentrations of cells in dermal cover of cirripeds which function for secreting calcareous substance of valves; possibly equivalent to dermal glands of other crustaceans.

cephalic flexure. Forward or even upward deflection of anterior sterna of some decapods.

cephalic shield. Chitinous, more or less calcified covering structure of head region formed of fused tergites of cephalic somites commonly having pleura.

cephalic somite. Unit division of head region, generally recognized as one of five such parts which bear distinctive paired appendages (antennules, antennae, mandibles, maxillules, maxillae) in addition to "precephalic" acron bearing eyes.

cephalomere. Cephalic somite.

cephalon. Most anterior tagma, bearing eyes, mouth, 2 pairs of antennae, and 3 pairs of mouth-part appendages (e.g., Branchiopoda, Ostracoda, Leptostraca, *Bathynella*); *syn.*, head.

cephalosome. Head region when this includes only somites bearing maxillipeds or gnathopods, or both.

cephalothorax. Anterior part of body composed of united cephalic and thoracic somites, latter comprising not only those with appendages modified as mouth parts or for food capture but others with relatively unmodified appendages, all forming a fused complex.

[Note. The most common definition of cephalothorax seems to be "unit resulting from fusion of one or more thoracic segments to cephalon." This seems too all-inclusive, for it can be applied to the very common situation in which only the first thoracic segment (because its limb is a maxilliped) is fused to the cephalon. A unit of this sort is not well fitted to the concept of cephalothorax. Fusion of thoracic segments to the cephalon seems to follow 2 patterns: (1) not all thoracic segments become fused, and the limbs of those that do become modified as mouth parts or for food capture (copepods, peracarids, stomatopods); (2) all thoracic segments become fused, including those which bear relatively unmodified locomotory appendages (eucarids). Gnathothorax is proposed as a term applicable to case 1 and cephalothorax is appropriate for designation of case 2. HESSLER & ROLFE]

cercopod. *See* caudal ramus.

cercus (pl., **cerci**). *See* caudal ramus.

cervical furrow. *See* cervical groove.

cervical groove. *See* carapace groove, c.

cervical notch or incision. Strong indentation of carapace at level of cervical groove (e.g., scyllarid palinurans).

cervical sinus. Rounded to angular indentation at front of cladoceran carapace along dorsal edge, exposing rear part of head.

cervical suture. *See* cervical groove.

chela. Pincer-like distal part of limb consisting of opposed movable, and immovable fingers.

chelate. Bearing chela (chelae).

cheliped. Any thoracopod bearing chelae.

cincinnulus (pl., **cincinnuli**). *See* retinaculum.

cirrus (pl., **cirri**). Multiarticulate food-gathering appendage of "thoracic" region of cirriped, normally one of six pairs, each with 2 long hairy rami curled toward mouth.

clasper. Appendage, including antenna, that serves for attachment in copulation or as organ for fixation in parasites.

clypeus. Part of head carrying labrum; plate on anterior medial part of head formed by fusion of basal segments of antennae (e.g., *Branchipus*, also Hexapoda).

colleteric gland. In Cirripedia (Rhizocephala), a single or paired saclike gland in female or hermaphrodite, producing viscid material binding eggs together.

comb collar. In Cirripedia (Acrothoracica), retractable membranous collar supporting row of numerous uniform setae at superior angle of aperture.

compartment. *See* compartment plate.

compartment plate. In sessile cirripeds (Verrucomorpha, Balanomorpha), rigid articulated skeletal element (valve) forming part of shell wall; *syn.*, mural plate.

compound eye. Array of contiguous ommatidia having common optic nerve trunk; paired.

compound rostrum. In cirripeds (Balanomorpha), projection formed by fusion of rostrolateral plates, forming compound compartment overlapping latera, and on which radii may develop (cf. rostrum).

conchostracan carapace interspace. Area between any 2 growth lines of conchostracan carapace; synonyms used interchangeably include intervales, growth zone, growth band.

conchostracan carapace interval. Space between any 2 ribs, costae, or costellae on conchostracan carapace.

conchostracan carapace ribs. Strong radial ridges radiating from and across umbo of conchostracan carapace, with intervals of variable width between any pair and commonly nodose at intersections of growth lines; may be partial or embryonic in expression; synonyms include longitudinal striae, carinae, radials, diagonal ridges, radial costae, and keels. [Characterize Leaiidae, never exceeding 5 in number on any given leaian valve; ribs also occur in *Protomonocarina* and *Limnadiopsileaia*.]

copepodid. Postnaupliar developmental stages of copepods.

cormopod(ite). *See* thoracopod(ite).

cormus. *See* thorax.

cornea. Transparent cuticle covering ommatidia of compound eye.

corpus mandibulae. *See* mandible body.

coxa. Segment of limb directly attached to sternite of body (except rarely in forms having distinguishable precoxal segment); *syn.*, coxopod(ite).

coxal plate. Lateral expansion of pereiopod coxa joined broadly to lateral margins of tergites.

coxepipod(ite). Coxal exite.

coxite. *See* protopod(ite).

coxopod(ite). *See* coxa.

ctenopod. In cirripeds, appendage where rami of cirrus have setae arranged in linear series along lesser curvature, like a comb (cf. acanthopod; lasiopod).

cycladiformes. Conchostracan carapaces having dorsal margin of valves forming obtuse angle with posterior margin (DADAY).

cyclops stage. Post-metanaupliar stage in ontogeny of some copepods.

cypris stage. Ostracode-like larval stage (e.g., Cirripedia).

cyrtopia stage. Fifth larval stage in euphausiaceans in which antennae no longer serve for locomotion.

dactyl. *See* dactylus.

dactylopod(ite). *See* dactylus.

dactylus. Distalmost segment of limb; *syn.*, dactylopod(ite).

deflexed front. Broadly downturned front marginal part of carapace in some decapods.

dendrobranch. Type of gill having tubes divided into arborescent bundles.

denticle. In cirripeds (Balanomorpha), primary or secondary toothlet on sutural edge of radius of compartment plate or opposed buttress of adjoining plate, serving to strengthen articulation of plates.

depressor muscle. In Cirripedia (Balanomorpha), muscle inserted at basicarinal angle of tergum, for which depressor muscle crests are usually developed.

depressor muscle crests. In cirripeds (Balanomorpha), elevated denticles on interior of tergum near basicarinal angle for attachment of depressor muscles (crests may extend apically).

depressor muscle, lateral. In Cirripedia (Balanomorpha), muscle inserted on basitergal angle of scutum, for which lateral depressor muscle pit, depression or crests may develop.

dermal gland. Single cell or concentration of cells in epidermis of body and limbs, traversed by canals and communicating with surface by fine ducts, their functions various and possibly corresponding to cement glands of cirripeds.

deuterocerebrum. *See* mesocerebrum.

diaeresis. Transverse groove on posterior part of exopod (rarely also endopod) of uropod appendage, in some forms dividing exopod into 2 movably connected parts.

distal. Direction away from central part of body; opposite of proximal.

dorsal organ. Thickened glandular area of hypoderm of dorsal surface just behind head in various branchiopods, isopods, amphipods, mysidaceans, tanaidaceans, and syncarids, its function obscure.

dorsal plate. Spindle-shaped division of carapace in some astacidean decapods (Erymidae) intercalated in median suture; may be related to dorsal organ.

dorsoventralis posterior. Important muscle in crayfish and other decapods connecting head apodemes with internal surface of carapace just behind cervical groove.

doublure. Reflexed ventral continuation of carapace integument.

efferent channels. Passageways through which water moves away from gills and out of branchial region.

endite. Inwardly (medially) directed lobe of precoxa, coxa, basis, or ischium.

endognath. Endopod (inner and principal branch) of maxilliped.

endophragm. Wall formed by union of apposed apodemes forming part of endoskeleton of some decapods; *syn.*, arthrophragm.

endophragmal skeleton. Complex internal skeletal structure formed by fusion of apodemes in decapods providing framework for muscle attachment, generally not strongly calcified.

endopleurite. Lateral apodeme of endoskeleton in decapods.

endopod(ite). Innermost ramus of limb arising from protopod basis; in the Eumalacostraca typically composed of 5 segments (ischium, merus, carpus, propodus, dactylus).

endoskeleton. Internal hard parts of some decapods consisting mainly of endophragms.

endosternite. Mesodermal tendonous plate below anterior part of alimentary canal (e.g., Notostraca); also firm calcareous plate between nerve cord and alimentary canal in anterior part of thorax in some crabs.

endostome. Palate-like part of buccal frame in some brachyuran decapods; *syn.*, palate.

ephippium (pl., **ephippia**). Semielliptical part of dorsal region in each valve of cladoceran branchiopods altered to form encasement for eggs, shed as unit and constructed in manner that facilitates ultimate hatching after desiccation (especially characteristic of Daphniidae).

epibranchial lobe or area. Anterior part of branchial region of decapod (brachyuran) carapace.

epibranchial space. Part of gill chamber above (external to) gills.

epigastric lobe or area. Anterior extension of gastric region of decapod (brachyuran) carapace.

epimeral fold. Steep fold of endopleurites in some decapods connected with branchiostegite to form branchial chamber.

epimere. Lateral downfold of tergite; *syn.*, epimeron, pleurepimere, pleurite, pleuron (pl., pleura), pleura (pl., pleurae), tergal fold.

epimeron (pl., **epimera**). *See* epimere.

epipod(ite). Laterally directed ramus (exite) of coxa; may be present or absent.

episternum. Posterolateral projection of various sterna of decapods.

epistome. Plate of varying shape between labrum and bases of antennae in brachyuran decapods, also defined as sternum of antennal somite.

esophagus. Anterior part of alimentary canal between pharynx or mouth and stomach or stomodeum; *syn.*, oesophagus.

esthetasc. Sensory seta covered by delicate cuticle projecting from most antennules and antennae; *syn.*, olfactory hair, esthete.

esthete. *See* esthetasc.

exhalant passage. Canal in front of gill chamber containing scaphognathite which functions for driving water outward, leads to large anterior opening.

exite. Laterally directed ramus of protopodal segment of limb (e.g., Notostraca).

exognath. Exopod (outer and secondary branch) of maxilliped.

exopod(ite). Outer ramus of limb arising from protopod basis; may contain variable number of segments or be much reduced or lacking.

exoskeleton. Entire horny (in part chitinous) more or less calcified outer covering of crustacean body and its appendages.

eye. Visual organ, in Crustacea either compound or naupliar (simple).

eyestalk. Peduncle movably articulated with head, carrying eye at its distal extremity, may be divided into 2 or 3 segments and may be retractable; *syn.*, ocular peduncle.

filamentary appendage. Membranous process developed on body in many cirripeds (Ascothoracica, Lepadomorpha) commonly on bases of cirri; may contain branches of testes; presumed to be respiratory in function.

filter chamber. Space beneath thorax (e.g., phyllocarids) enclosed by ventral body wall and rhythmically moved thoracopods which functions for food-gathering from currents sucked into it.

fingers. Scissor-like blades of claw end of cheliped, one finger movable and other immovable (fixed); very exceptionally *(Psalidopus)* both fingers are movable.

first antenna. *See* antennule.

first maxilla. *See* maxillule.

fixed finger. Immovable distal part of propodus of chela; *syn.*, pollex, thumb.

flabellum. Thin distal exite of branchiopod gnathobase with setose margin.

flagellum (pl., **flagella**). Slender, multiarticulate distal part of antennule, antenna or exopod.

foregut. *See* stomodaeum.

frena. Tegumentary folds holding eggs (Cirripedia).

front. Part of crab carapace between orbits.

frontal appendage. One pair of filaments arising in many Anostraca from bases of antennae but independent of them; may be ramified.

frontal band. Glandular organ of adhesion in frontal region of various parasitic copepods serving for attachment to host fishes.

frontal organs. Sensory cells or setae on front surface of heads of some branchiopods, copepods, and decapods.

frontal plate. Modified rostrum of brachyuran decapods which bears downward projecting process between antennules that unites with epistome.

frontal region. *See* carapace region, e.

frontolateral horn. One of pair of tubular frontolateral extensions of cuticle of cirriped nauplii (except Ascothoracica), apparently perforate at tips and provided with mass of gland cells at bases.

furca. *See* caudal furca.

furcal ramus. Branch of caudal furca.

furcilia stage. Fourth larval stage in euphausiaceans, marked by movable compound eyes that project beyond edge of carapace.

galea. Outer distal hoodlike lobe of 2nd segment of maxillule; adjacent to inner spiny lobe (lacinia).

gastric groove. Longitudinal furrow on either side of median carina on stomatopod carapace.

gastric mill. Apparatus of varying complexity in stomodeum which serves to break up food; consists of framework of movably articulated ossicles developed as thickened and calcified part of stomodeal lining, most highly specialized in decapods.

gastric region. *See* carapace region, f.

gastric tooth. *See* carapace tooth, b.

gastrolith. Discoid calcareous nodule common in stomodeum of some decapods

gastroorbital carina. *See* carapace carina, d.

gastroorbital groove. *See* carapace groove, d.

genital region. *See* urogastric lobe or area.

gill. *See* branchia.

gill chamber. *See* branchial chamber.

glaucothoe stage. Ontogenetic stage in larval development of pagurid decapods.

gnathal lobe. Masticatory endite of mandible; *syn.*, masticatory process.

gnathobase. Endite which through medial contact with opposite member of its pair serves for comminution of food; may also serve in food transport.

gnathopod. Chelate or subchelate, prehensile maxilliped (e.g., Amphipoda); also used for first two prehensile pereiopods of amphipods whether chelate or subchelate.

gnathothorax. Tagma resulting from fusion of gnathal somites (mandibular, two maxillary) with one or more thoracic somites, limbs of which are modified to act as mouth parts. *See* cephalothorax.

gonad. Hollow reproductive organ in either sex, cavity communicating with pair of efferent ducts (pair in some parasitic isopods).

gonapophysis. Median process arising from base of first or second pleopods of male syncarids.

gonopod. Modified male pleopod serving for transmittal of spermatophores to female.

gonopore. Outlet for genital products, generally placed constantly in different crustaceans; *syn.*, sexual pore.

green gland. One of pair of complex excretory glands located in antenna on front of head of decapod (e.g., crayfish); *syn.*, antennal gland.

groove. *See* carapace groove.

haft organ. Pear- to wedge-shaped appendage of some branchiopods (e.g., *Limnadopsis*) attached to mid-dorsal surface of head at narrower end; *syn.*, frontal organ, affixing organ.

head. *See* cephalon.

head apodeme. Fused endopleurite and endosternite forming place for muscle attachment at anterior end of skeleton in Astacidea.

hemocoel. Lacunar system extending throughout much of body, filled by blood.

hemocyanin. Copper-containing respiratory pigment in blood of malacostracans.

hemoglobin. Oxygen-carrying protein coloring substance of red plasma in blood, found in some crustaceans (e.g., Ostracoda), may be colored or colorless in conchostracans, present also in blood of anostracans, cladocerans, notostracans, some harpacticid and parasitic copepods, branchiurans, and some parasite cirripeds.

hepatic caeca. Pouchlike diverticula generally connected with mesenteron, serving functions of liver; *see* hepatopancreas.

hepatic groove. *See* carapace groove, e.

hepatic region. *See* carapace region, g.

hepatic spine. *See* carapace spine, c.

hepatopancreas. Digestive gland consisting of ramified tubules spread through cephalothorax performing functions of both liver and pancreas.

heterochelate. Chelae of left and right chelipeds differing in shape and size.

hindgut. *See* proctodeum.

hinge line. Mid-dorsal line of junction of two valves composing carapace, permitting movement between them (e.g., Conchostraca, Ostracoda, Phyllocarida).

hinge nodes. Localized thickened parts of right-valve hinge of phyllocarids, somewhat elongate in line of hinge and serving to strengthen it.

hypobranchial space. Part of gill chamber below gills.

hypopharynx. *See* metastoma.

hypostoma. *See* metastoma.

hypostome. *See* metastoma.

imbricate plates. *See* lower latera.

incisor process. Biting portion of gnathal lobe of mandible; *syn.*, pars incisiva.

inferior groove. *See* carapace groove, f.

inframedian lateral. *See* latus (inframedian), b.

inframedian latus. Valve of some cirriped shells located below upper latus.

infraorbital spine. *See* carapace spine, d.

inner lamina. In cirripeds, innershell layer of compartmental plate separated from outer lamina by parietal tubes.

interantennular septum. Plate in some malacostracans that separates one antennular cavity from other; *syn.*, proepistome.

interlaminate figure. In Cirripedia (Balanomorpha), simple or arborescent lines seen running between epicuticle of outer lamina through longitudinal septa into inner lamina, when paries is sectioned parallel to base.

intestinal region. *See* carapace region, h.

intestine. Elongate slender posterior part of alimentary canal, in some crustaceans partly corresponding to mesenteron and invariably to part of proctodeum.

intraparies (pl., **intraparietes**). Secondary lateral margin of carina in some cirripeds (Lepadomorpha).

ischiocerite. Third segment of antennal peduncle.

ischiopod(ite). *See* ischium.

ischium. Third limb segment distal from body articulating with basis and comprising first segment of endopod; *syn.*, ischiopod(ite).

joint. Articulation (most commonly applicable to movable connection of individual segment of appendage with neighbors or body but relates also to movable connection of body parts); loosely and undesirably employed as synonym of segment.

jugal region. *See* carapace region, i.

kentrogon. In Cirripedia (Rhizocephala), dedifferentiated cells of female or hermaphrodite cyprid larva, at time they are being extruded through cyprid first antenna into host crustacean; or of male cyprid, being extruded into mantle cavity of female.

knee. Point of most pronounced flexure of endopod.

labium. *See* metastoma.

labrum. Unpaired outgrowth arising just in front of mouth and more or less covering it; *syn.*, upper lip.

lacinia. Inner distal spiny lobe of 2nd segment of maxillule, adjacent to outer hoodlike lobe (galea).

lacinia mobilis. Small, generally toothed process articulated with incisor process of mandible.

lappet. Downhanging lateral part of carapace.

lasiopod. In Cirripedia (Lepadomorpha), appendage where rami of cirrus have setae arranged in groups along lesser curvature; like brushes (cf. ctenopod; acanthopod).

latera. *See* latus.

lateral. Plate of cirriped shell between carinolateral and rostrum; *syn.*, latus.

lateral bar. In Cirripedia (Acrothoracica), pair of chitinous thickenings (best developed in Cryptophialidae) running from chitinous apertural thickenings medially down each side of mantle sac.

lateral carina. *See* carapace carina, e.

lateral depressor pit. In cirripeds, small hollow near basitergal angle of scutum for attachment of lateral depressor muscle.

lateral gastrocardiac markings. Insertions of attractor epimeralis muscle in most Brachyura, in which the branchiocardiac groove has disappeared.

lateral margin. Differentiated edge of carapace in some advanced macrurans and many brachyurans.

lateral tooth. *See* carapace tooth, c.

latus (pl., **latera**). In cirripeds (Lepadomorpha), any of paired plates forming part of shell, not including carina and rostrum or opercular plates (scutum, tergum); *syn.*, lateral. Includes following different types:

a) **carinal.** Plate located on either side of carina, with radii on carinal side and alae on rostral side; corresponds to carinolateral in Balanomorpha.

b) **inframedian.** Plate beneath median latera in some cirripeds (e.g., *Arcoscalpellum*).

c) **lower.** Plate in some cirripeds (e.g., *Zeugmatolepas*) near basis; *syn.*, imbricate plate(s).

d) **median.** One of series of plates between carina and rostrum which may be disposed in whorls (e.g., *Scillaelepas*).

e) **rostral.** Plate located on either side of rostrum, with radii on both rostral and carinal sides; corresponds to rostrolateral in Balanomorpha.

f) **upper.** Plate between carinal and rostral latera just below opercular valves (e.g., scalpellids).

limnadiiformes. Conchostracan carapaces exhibiting recurvature of posterior margin near dorsal line, characteristic of several of the Limnadioidea; pseudorecurvature observed in some leaiids.

linea (pl., **lineae**). Linear marking on carapace.

linea anomurica. Longitudinal groove or uncalcified line on carapace of many anomuran decapods.

linea branchiostegalis. Longitudinal groove or uncalcified line extending backward from front margin of carapace slightly above branchiostegal spine and reaching to or beyond hepatic spine (e.g., palaemonid carideans).

linea dromica. Feature on carapace of dromiid crabs comparable to linea thalassinica; *syn.*, linea dromiidica.

linea dromiidica. *See* linea dromica.

linea homolica. Feature similar to linea thalassinica and possibly equivalent to it.

linea lateralis. Longitudinal groove or uncalcified line extending backward from front margin of carapace below orbit, in some forms to rear extremity of carapace (e.g., some penaeids).

linea thalassinica. Longitudinal groove or uncalcified line on dorsal part of carapace extending from anterior margin below antennal spine across entire length of carapace to its posterior edge (most thalassinoid decapods).

longitudinal septum. In cirripeds (Balanomorpha), wall of tubes disposed normal to inner and outer laminae of compartment plate and separating them; *syn.*, parietal septum.

lower lateral. Valve in shell of some cirripeds; *see* latus (lower), c.

lower lip. *See* metastoma.

male-cell receptacle. In Cirripedia (Rhizocephala), pocket or pair of pockets within mantle cavity of female into which dedifferentiated cells of male cyprid migrate and differentiate into "testes."

manca. Young of some Peracarida (e.g., Isopoda, Tanaidacea, Cumacea) in which last thoracopod is lacking.

mancoid stage. Postlarval leptostracan that differs from adult in having rudimentary 4th pleopod.

mandible. One of third pair of cephalic appendages used to masticate food.

mandible body. Inflated base (coxa) of mandible providing for attachment of mandibular muscles; *syn.*, body of mandible, corpus mandibulae.

mandibular foramen. Relatively large opening in body of mandible for passage of transverse adductor muscle.

mandibular palp. Distal articulated part of mandible that functions as aid in feeding or cleaning.

mantle. Fleshy structure of cirripeds strengthened by five calcified plates (carina, terga, scuta).

mantle cavity. Space in cirripeds occupied by body, opening by posteroventral aperture.

manus. Broad proximal part of cheliped propodus (i.e., this propodus minus fixed finger); *syn.*, palm.

marginal groove. *See* carapace groove, g.

marsupium. Brood pouch.

masticatory process. *See* gnathal lobe.

mastigobranch. Slender respiratory process at base of epipod(ite); *syn.*, mastigobranchia (pl., mastigobranchiae).

mastigopus stage. Larval stage in ontogeny of some decapods equivalent to permanent adult form of *Leucifer* (penaeid).

maxilla (pl., **maxillae**). Appendage next behind maxillule serving functions in feeding and respiration; *syn.*, second maxilla.

maxillary gland. Excretory organ located in maxillary segment, having its duct opening on maxilla; *syn.*, shell gland.

maxilliped. Anterior thoracic limb (one, two, or three) modified to act as mouth part, its body segment usually fused to cephalon.

maxillipede. See maxilliped.

maxillipes (pl., *maxillipedes*). *See* maxilliped.

maxillule. Cephalic appendages next behind mandible, serving as mouth part; *syn.*, first maxilla, maxillula. In cirripeds, also termed inner maxilla.

median articulated spine. Projection of telson in eocarids, seemingly not homologous with skeletal structure of any extant crustacean.

median dorsal plate. Elongate plate separating carapace valves posterodorsally (Phyllocarida Rhinocarina).

median eye. Sessile unpaired eye of nauplius larva which persists in some adults; *syn.*, naupliar eye.

median lateral. *See* latus (median), d.

megalopa stage. First postlarval stage in ontogeny of crabs, not developed in macruran decapods or other crustaceans; *syn.*, megalops stage.

megalops stage. *See* megalopa stage.

meropod(ite). *See* merus.

merus. Fourth limb segment distally from body, its proximal extremity articulating with ischium; usually forms first long segment of cheliped and pereiopod; *syn.*, meropod(ite).

mesenteron. Mid-portion of alimentary tract of endodermal origin with surface commonly increased by pouchlike extensions which serve as digestive glands and aid absorption of partly digested food; *syn.*, midgut.

mesobranchial lobe or area. Intermediate part of branchial region of decapod (brachyuran) carapace.

mesocerebrum. Ganglion of antennular somite; *syn.*, deuterocerebrum.

mesogastric lobe or area. Medial division of gastric region of decapod (brachyuran) carapace, generally pentagonal in outline with long narrow forward prolongation.

mesosome. Collective term for all free thoracic somites behind head.

mesosternum. Median plate arising from sternum in many brachyurans.

metabranchial lobe or area. Posterior part of branchial region of decapod (brachyuran) carapace.

metacerebrum. Ganglion of antennal somite; *syn.*, tritocerebrum.

metagastric lobe or area. Posterior division of gastric region of decapod (brachyuran) carapace; may be ill-defined or undifferentiated.

metanauplius. Postnaupliar larva with same general body and limb morphology as nauplius, but having additional limbs.

metasoma. *See* metasome.

metasome. In copepods, part of prosome consisting of free thoracic somites in front of major articulation; in amphipods first three abdominal somites bearing unmodified pleopods.

metastoma. Lower lip behind mandibles, usually cleft into pair of lobes termed paragnatha; *syn.*, hypostoma, hypostome, hypopharynx, labium, lower lip, paragnath.

metazoea. Last stage of zoea larva in Brachyura.

metopon. Entire preoral area in decapods, including parts of mandibular somite.

midgut. *See* mesenteron.

molar process. Grinding portion of gnathal lobe of mandible; *syn.*, pars molaris.

movable finger. Dactylus of chela.

mucro (pl., **mucrones**). Spine on inferoposteal angle of carapace in some Cladocera.

mysis stage. Post-cypris larval stage in ontogeny of most crustaceans, characterized by presence of biramous limbs on all thoracic somites; *syn.*, schizopod larva.

naupliar eye. Unpaired median eye found in naupliar larval stages and commonly in more mature stages as well; *syn.*, median eye.

nauplius (pl., **nauplii**). Early larval stage having only antennules, antennae, and mandibles.

neck organ. *See* nuchal organ.

nephropore. Elevated outlet of antennal gland, located on coxa of antenna.

notum. Posterior part of dorsal region of macruran decapod carapace.

nuchal organ. Sense organ on upper side of head in many branchiopods; *syn.,* neck organ.

occipital notch. Angulated indentation at rear of head in some conchostracans.

occludent margin. In cirripeds, margin of scutum and tergum forming aperture and occluding with comparable margins of opposed scutum.

occludent teeth. In cirripeds, small projections on occludent scutal margin formed by extensions of external growth ridges that interdigitate with similar teeth on margin of opposed scutum.

ocellus (pl., **ocelli**). Unpaired median eye, common in some branchiopods (e.g., Notostraca) and copepods (e.g., Cyclopoida) but otherwise uncommon.

ocular bulla. Knob on inner surface of carapace connecting lower and upper orbital margins with basal segment of antenna, serving for protection of eye.

ocular papilla. Anterior projection on eyestalk of some mysidaceans.

ocular penduncle. *See* eyestalk.

oesophagus. See esophagus.

olfactory hair. Sensory seta covered by delicate cuticle projecting from most antennules and antennae; *syn.,* aesthetasc, esthetasc, aesthete, esthete.

ommatidium (pl., **ommatidia**). Cylindrical or prismoidal visual constituent of compound eye covered by transparent cuticle (cornea).

oostegite. Inner medially directed lamella arising from coxa of pereiopod in females participating in formation of mid-ventral marsupium.

oostegopod. Appendage of genital somite in some branchiopods modified as brood pouch.

opercular valve. Movable plate in orifice of cirriped shell, one of pairs of scuta and terga joined to sheath by opercular membrane.

operculum. In cirripeds, terga, scuta and associated membranes (Balanomorpha), or tergum and scutum of one side (Verrucomorpha), forming apparatus guarding aperture.

ophthalmic somite. *See* acron.

optic lobe. Ganglion of brain for nervation of eye.

orbit. Circular opening in front part of some decapod carapaces enclosing eyestalk.

orbital carina. *See* carapace carina, f.

orbital hiatus. Gap in orbital margin of carapace at its lower (inner) angle.

orbital region. *See* carapace region, j.

orbital tooth. *See* carapace tooth, d.

orifice. Opening in upper part of cirriped shell containing opercular valves.

ostium (pl., **ostia**). Valve of heart.

oviduct. In females passageway from ovary to uterus and leading to genital aperture.

ovigerous frena (pl., **frenae**). In Cirripedia (certain Lepadomorpha), fleshy ridge or flap on interior mantle surface, adhering to and holding egg masses (ovigerous lamellae) in place.

ovigerous lamella. In Cirripedia, eggs adhering in one or more lamellae, within mantle cavity and in certain Lepadomorpha, held in position by ovigerous frenae.

palate. *See* endostome.

palm. *See* manus.

palp. Reduced distal portion of limb, usually only one of its rami, but may comprise both rami plus basis; usually consists of distal 2 or 3 segments following merus.

palp foramen. Small circular opening in body of mandible communicating with mandibular palp.

palpus (pl., **palpi**). Oval setose mandibular endopod of cirripeds, attached directly to mandible (Acrothoracica) or to lateral margin of labrum (Thoracica).

paracopulatory organ. Specialized endopod of pleopod in some Isopoda serving accessory function in copulation.

paragnath. *See* metastoma.

paries (pl., **parietes**). Median triangular part of cirriped compartment plate, with lower edge attached to basis and adjoined laterally by margins of carinal tectum.

parietal plate. One of different kinds of shell elements forming calcareous wall surrounding body of cirripeds.

parietal septum. In cirripeds, same as longitudinal septum.

parietal tube. One of myriad porelike canals in longitudinal septum of balanomorph cirripeds, disposed normal to inner and outer laminae of compartment plate and separating them; *syn.,* parietal pore, longitudinal pore, longitudinal tube.

pars ampullaris. Bottle-shaped diverticulum on entrance of caeca into pyloric chamber of stomach in syncarids.

pars incisiva. *See* incisor process.

pars molaris. *See* molar process.

parva stage. First postlarval stage in ontogeny of Caridea.

peduncle. Basal portion of certain appendages; also fleshy part of body in some cirripeds (Lepadomorpha), between capitulum and attachment to substrate with or without armor of chitinous or calcareous beads, scales, or filaments.

penicillus (pl., **penicilli**). Tuft of fine hairs resembling small brush.

penis (pl., **penes**). Male copulatory organ. [May be exceptionally long in some cirripeds.]

peraeopod. *See* pereiopod.

pereion. Anterior portion of trunk, usually provided with locomotory appendages; differs from thorax in excluding somite of maxillipeds; *syn.,* pereon.

pereionite. Thoracic somite; *syn.,* pereonite.

pereiopod. Locomotory thoracopod; *syn.*, peraeopod, pereopod, ambulatory leg, walking leg.

pereon. *See* pereion.

pereopod. *See* pereiopod.

pericardium. Blood sinus surrounding heart and communicating with it by pair of ostia in each somite except terminal one, may run entire length of trunk above gut.

peritrophic membrane. Chitinous sheath secreted around feces (e.g., some Ostracoda).

petasma. Abdominal appendage modified as gonapophysis in males of some eucarids, syncarids, and stomatopods.

pharynx. Part of alimentary tract next to mouth and adjoining esophagus.

photophore. Luminous organ generally located on eyestalk, limbs or abdomen of various crustaceans.

phyllobranch. Gill with leaflike filaments; *syn.*, phyllobranchia.

phyllobranchia (pl., **phyllobranchiae**). See phyllobranch.

phyllopodium (pl., **phyllopodia**). Leaflike thoracic appendage of some crustaceans (e.g., Branchiopoda) including maxillulae and maxillae of Decapoda.

phyllosoma stage. Early schizopod larval stage in ontogeny of palinurid and scyllarid lobsters.

pleomere. *See* abdominal somite.

pleon. Abdomen of crustacean.

pleonite. *See* abdominal somite.

pleopod. Limb of any of first five abdominal somites in Eumalacostrica (six in Phyllocarida), in many crustaceans adapted for swimming; *syn.*, swimmeret.

pleotelson. Structure formed by fusion of one or more abdominal somites with telson, as in most isopods.

pleura (pl., **pleurae**). *See* epimere.

pleural lobe. *See* epimere.

pleural suture. Line of splitting apart of carapace in molting, corresponding to linea dromica, and present in all brachyurans.

pleurepimere. *See* epimere.

pleurite. *See* epimere.

pleurobranch. Gill of decapods attached directly to body wall; *syn.*, pleurobranchia.

pleurobranchia (pl., **pleurobranchiae**). *See* pleurobranch.

pleuron (pl., **pleura**). *See* epimere.

pleuropod. *See* precoxa.

podobranch. Gill placed on epipods of thoracopods; *syn.*, podobranchia.

podobranchia (pl., **podobranchiae**). *See* podobranch.

podomere. Individual segment of limb; *not* syn. joint.

podophthalmite. One of 2 segments of eyestalk, articulating with basophthalmite proximally and bearing corneal surface of eye distally.

pollex. *See* fixed finger.

postabdomen. *See* telson.

postcephalic groove. *See* carapace groove, h.

postcervical groove. *See* carapace groove, i.

postcervical notch or incision. Strong indentation of carapace at level of postcervical groove (e.g., scyllarid palinurans).

posterior cardiac lobe. *See* intestinal carapace region.

posterior carina. *See* carapace carina, g.

posterior gastric pit. One of 2 small depressions near mid-line of dorsal exterior of decapod carapace marking insertion point of stomach muscle.

posterior tooth. *See* carapace tooth, e.

postlarval stage. Ontogenetic stage reached after completion of all nauplius-to-zoea or megalopa metamorphoses, marked by initial appearance of adult characters.

postorbital carina. *See* carapace carina, h.

postorbital spine. *See* carapace spine, e.

postrostral carina. *See* carapace carina, i.

postrostral spine. *See* carapace spine, f.

postsegmental region. Telson.

precoxa. Limb segment proximal to coxa, present only in certain subclasses; *syn.*, pleuropod.

pregastric tooth. *See* carapace tooth, f.

pre-epipod(ite). Secondary ramus of coxa directed outward (e.g., *Chirocephalus*).

presegmental region. *See* acron.

prezoea stage. Just-hatched larva still covered by embryonic cuticle.

primary denticle. *See* denticle; primary denticle disposed normal to suture edges of compartment plate.

primordial valve. Chitinous plate in Cirripedia (Lepadomorpha and Verrucomorpha) having a distinctive honeycomb appearance, developing at incipient umbones of terga, scuta and carina, during metamorphosis.

proctodaeum. *See* proctodeum.

proctodeum. Posterior part of alimentary canal lined with cuticle of ectodermal origin that is continuous with anus; *syn.*, hindgut, proctodaeum.

proepistome. *See* interantennular septum.

prosarthema. Scale implanted on inner margin of basal segment of antennular peduncle in Penaeidae.

prosoma. *See* prosome.

prosome. Anterior region of body, commonly limited behind by major articulation. In cirripeds, large saclike body in position of "head" in front of (and rostral from) thoracic limbs, supporting trophi and commonly first cirri.

protocephalon. *See* acron.

protocerebrum. Ganglion of first (preantennulary) somite.

protogastric lobe or area. Anterolateral division of gastric region of decapod (brachyuran) carapace.

protopod(ite). Proximal portion of limb, consisting of precoxa, coxa, and basis, fused together in some forms; its distal edge generally bearing endopod(ite) and exopod(ite); *syn.*, coxite, sympod(ite).

protozoea stage. Larval stage in ontogeny of some decapods preceding zoea stage.

proventriculus. Elaborated anterior part of alimentary canal in some crustaceans (e.g., Isopoda) adapted for pressing juices from food and straining out solid particles.

proximal. Direction toward center of body; opposite of distal.

pseudepipod(ite). Lateral ramus arising from proximal portion of exopod or from basis just proximal to exopod.

pseudorostrum. Anterior portion of gnathothorax in Cumacea, formed by pair of anterolateral parts of cephalic shield grown forward so as to meet medially in front of true rostrum.

pseudotrachea. Respiratory structure developed in pleopods of some Isopoda for air-breathing; they consist of small ramified tubules inside limb opening outward in slitlike apertures and filled with air.

pterygostome. *See* pterygostomial region.

pterygostomial region. *See* carapace region, k.

pterygostomial spine. *See* carapace spine, g.

radius (pl., **radii**). In cirripeds (Balanomorpha), lateral part of compartment plate adjoining paries, marked off from it by change in direction of growth lines and by depressed exterior surface; overlaps ala of adjoining compartment plate.

ramus. Branch of limb or other appendage (e.g., caudal furca).

raptorial claw. Generally strong, curved and toothed dactylus suited for catching prey (e.g., *Squilla*).

receptaculum seminalis. *See* seminal receptacle.

retinaculum (pl., **retinacula**). Small hook at tip of appendices internae (e.g., Caridea), one of many serving to join left and right pleopods together; *syn.*, cincinnulus.

rostral angle. In cirripeds angle of plate directed toward rostrum.

rostral carina. *See* carapace carina, j.

rostral plate. Anteriorly projecting, unpaired, movably articulated, median extension of carapace (e.g., Phyllocarida); *see* rostrum, compound rostrum.

rostral tooth. *See* carapace tooth, g.

rostrolateral. In cirripeds, one of pair of compartment plates lying between and overlapping rostrum and laterals, having radii on both rostral and cardinal sides and tending to fuse with rostrum; *see* latus (rostral), e.

rostrum. Anteriorly projecting, unpaired, usually rigid median extension of carapace between eyes or eyestalks; in cirripeds (Thoracica) unpaired valve between laterals and opposite carinal at basiscutal end of capitulum, simple and provided with alae in lower balanomorphs but compound and overlapping laterals in higher balanomorphs; *see* compound rostrum.

saw bristles. Row of heavy setae on gnathal lobe of mandible between molar and incisor processes in many Eumalacostraca, especially Peracarida.

scale. In cirripeds (Lepadomorpha), platelet on side of peduncle. *See* scaphocerite.

scaphocerite. Exopod(ite) of antenna in Eumalacostraca; *syn.*, scale. [Similar structure occurs on antennules of Leptostraca.]

scaphognath(ite). Exopod comprising boat-shaped extension of maxilla opposite endopod.

schizopod larva. Ontogenetic stage characterized by presence of biramous limbs on all thoracic somites; *syn.*, mysis stage.

scutal margin. In cirripeds, articular edge of tergum adjoining scutum, or edge of any other plate abutting scutum.

scutum (pl., **scuta**). Valve of cirriped shell opposite carina and adjacent to peduncle in some forms (Lepadomorpha) or opercular in others (Balanomorpha).

second antenna. *See* antenna.

second maxilla. *See* maxilla.

secondary denticle. *See* denticle; secondary denticle located on primary one and disposed normal to it.

segment. Individual component of crustacean limb connected by movable articulation with adjoining segments; *syn.*, podomere (not equivalent to somite, though used by some authors in this sense). (*not* joint.)

seminal receptacle. Diverticulum of oviduct or external pouch (some pygocephalomorph eocarids, isopod peracarids, and decapods) for storing spermatozoa delivered by male; *syn.*, receptaculum seminalis.

seminal vesicle. Sac in male independent of testes for storage of spermatozoa (e.g., some anostracans, Chirocephalidae); *syn.*, vesicula seminalis.

serration. Irregular saw-toothed outline on dorsal edges of some conchostracan valves where growth bands do not end on same hinge line; may have various expression from strongly serrate (e.g., Paleolimnadiopsidae) to subdued serrate (e.g., extant Caenestheriellia) and pseudoserrate (e.g., some extant *Cyzicus*).

seta (pl., **setae**). Hairlike process of cuticle with which it is articulated; in cirripeds, bristle or spine on trophi and cirri.

sexual pore. *See* gonopore.

sheath. In cirripeds (Balanomorpha), thickened upper part of internal shell wall and alae forming cylindrical collar to which opercular membrane is attached.

shell. In cirripeds, general term for hard parts of balanomorphs including compartment plates, basis (if calcareous), and opercular valves.

shell fold. Portion of carapace behind cephalic shield.

shell gland. *See* maxillary gland.

skeletal duplicature. Outer chitinous body cover of conchostracans shed during ecdysis, individual duplicatures being very thin whitish translucent layer resembling entire animal when floating in water; may occur also in notostracans and cladocerans.

somite. Division of body (head, thorax, abdomen) with exoskeleton comprising body-ring that is generally divisible into dorsal (tergite) and ventral (sternite) portions.

spermatheca. Pouch in oviduct of females for reception and retention of spermatozoa.

spermatophore. Packet of spermatozoa for transfer from male to female.

spur. In cirripeds (Balanomorpha), dependent projection on basal margin of tergum.

spur fasciole. See spur furrow.

spur furrow. In cirripeds (Balanomorpha), groove on outer surface of tergum extending to apex in line with spur; *syn.,* spur fasciole.

squama. *See* scaphocerite.

statocyst. Diminutive organ providing sense of balance, present in most crustaceans.

stenopodium. Slender, elongate limb composed of rodlike segments.

sternal canal. Internal skeletal structure of some crabs formed by meeting of sternal apodemes of opposite sides above nerve cord; may be developed as firm plate (endosternite) in anterior part of thorax.

sternal plastron. *See* sternum.

sternal process. Projection from mid-section of sternite of mysidaceans and pygocephalomorph eocarids, unknown as to function.

sternite. Sclerotized ventral surface of single body somite.

sternum (pl., **sterna**). Sternites of all body somites taken together, and abdomen; ventral segmented floor of thorax; *syn.,* sternal plastron.

stipe. Stemlike part of limb bearing squamate or other-shaped exopod (e.g., various eocarids).

stomodaeum. *See* stomodeum.

stomodeum. Anterior part of alimentary tract, ectodermal in origin and lined with cuticle continuous with mouth; includes esophagus and dilated part corresponding to stomach, and may contain so-called gastric mill of varying complexity for trituration of food; *syn.,* foregut; stomodaeum.

stridulating organ. Structure in which two parts of exoskeleton are rubbed together in order to produce sound, one part consisting of ridge or tuberculate or cross-ridged surface which is apposed to another part usually having single transverse ridge or tubercle.

stylamblys. *See* appendix interna.

style. *See* telson.

stylet. *See* caudal ramus.

stylocerite. Rounded or spiniform process on outer part of proximal segment of antennular peduncle in some decapods (e.g., natantian decapods); *syn.,* antennular scale.

subbranchial region. Ventrally placed part of brachyuran carapace corresponding in position to branchial region of dorsal part of carapace.

subcarina. In cirripeds (e.g., scalpellids), small unpaired plate below carina.

subchela. Distal extremity of limb developed as prehensile structure by folding back of dactylus against propodus or broadened part of it (e.g., Stomatopoda); may comprise propodus folded back against carpus; *syn.,* gnathopod.

subchelate. Provided with subchelae.

subesophageal ganglion. Nerve plexus below esophagus in head of malacostracans.

subhepatic carina. *See* carapace carina, k.

subhepatic region. *See* carapace region, l.

submedian carina. *See* carapace carina, l.

submedian groove. *See* carapace groove, j.

suborbital region. Narrow area bordering lower margin or orbit; may be ill-defined or indistinguishable.

suborbital spine. *See* carapace spine, h.

subrostrum. In cirripeds (e.g., scalpellids), small unpaired plate below rostrum.

suctorial structures. Mouth parts of ectoparasites modified for piercing body wall of host and for sucking out body fluids.

supra-anal plate. Portion of notostracan telson, usually tongue-shaped but may be spatulate to round; produced backward on dorsal side as a plate.

supra-esophageal ganglion. Nerve plexus above esophagus in head of malacostracans.

supraorbital carina. *See* carapace carina, m.

supraorbital spine. *See* carapace spine, i.

sutural edge. In cirripeds, margin of compartment plate along suture.

suture. In cirripeds (Balanomorpha, Verrucomorpha), line or seam at juncture of two compartment plates; also articulation line between joints.

swimmeret. *See* pleopod.

sympod(ite). *See* protopod(ite).

syncerebrum. *See* supra-esophageal ganglion.

tagma (pl., **tagmata**). Major division of body (e.g., head, thorax, abdomen), each composed of varying number of somites.

tail fan. *See* caudal fan.

tectum. Central part of carina in cirripeds (Lepadomorpha).

telopod. Part of limb distal to coxa.

telson. Last somite of body, bearing anus and commonly caudal furca or pair of cerci, growth zone for postcephalic somites located at its anterior edge; *syn.,* postabdomen, style (Archaeostraca).

telson head. Enlarged part of telson in Archaeostraca, with which furcal rami articulate.

tergal fold. *See* epimere.

tergal margin. In cirripeds (Thoracica), edge of scutum adjacent to tergum or edge of any plate abutting tergum.

tergite. Sclerotized dorsal surface of single body somite.

tergolateral margin. Angular inner edge of scutum in cirriped shells having upper laterals.

tergum (pl., **terga**). Dorsal part of exoskeleton comprising tergites of all body somites taken together; also valve of cirriped shell adjacent to carina and generally opercular.

terminal claw spines. Toothlike projections of varying size at concave end of postabdomen in cladocerans, having taxonomic value; few large *basal* spines near base of claw, minute *denticles* along greater part of claw, and spines of intermediate size grouped as *comb,* all serving for riddance of foreign particles and parasites.

thelycum. External pocket on ventral side of thorax in penaeid females which functions as seminal receptacle (receptaculum seminalis).

thoracic limb. Any limb attached to somite of thorax; *syn.,* thoracopod.

thoracomere. Somite of thorax.

thoracopod(ite). Limb attached to any thoracic somite; *syn.,* thoracic limb. [Maxillipeds and pereiopods are thoracopods.]

thorax. Tagma between cephalon and abdomen comprising anterior portion of trunk, last somite bearing most posterior genital pore or just anterior to this pore-bearing somite and nearly always limb-bearing; *syn.,* cormus (not precise equivalent of pereion).

thumb. *See* fixed finger.

transverse septum. Thin wall of cirripeds normal to longitudinal septum and parallel to basis, dividing parietal tubes into series of cells.

trichobranch. Gill of filamentous structure with hairlike projections from axis (e.g., crayfish); *syn.,* trichobranchia.

trichobranchia (pl., **trichobranchiae**). *See* trichobranch.

tritocerebrum. *See* metacerebrum.

trophi. Mouth parts of cirripeds, including labrum, mandibles, maxillules, maxillae, palpi, and in some, first pair of cirri.

trunk. Postcephalic portion of body; *syn.,* thorax.

umbo. Apical portion of either valve of bivalved crustaceans (e.g., Conchostraca, Phyllocarida); in cirripeds, central point on plate from which successive growth increments extend.

umbonal spine. Hollow, minute to large spinose projection of conchostracan carapace that may involve entire umbo; may be curved, looped, or represented as node or nipple. [Larval condition characteristic in Vertexiidae.]

upcurved growth lines. Upwardly bent growth lines covering tear in conchostracan shell-margin at site of injury.

upper lateral. Plate of some cirriped shells; *see* latus (upper), f.

upper lip. *See* labrum.

urogastric lobe or area. Posterior division of gastric region of decapod (brachyuran) carapace; sometimes called genital region.

uropod(ite). Limb of sixth abdominal segment of Eumalacostraca, generally fanlike but may be reduced or modified.

urosoma. See urosome.

urosome. In copepods, part of body behind major articulation marking posterior boundary of prosome; in amphipods, last three abdominal somites bearing modified appendages.

valve. Lateral part of divided carapace commonly joined to opposite part by hingement along dorsal mid-line (e.g., Ostracoda, Conchostraca, Leptostraca).

vas deferens. Duct in males for passage of spermatozoa from testis to penis.

ventral nerve chain. Ganglia or connectives on somites joined by single or double nerve cord running longitudinally beneath alimentary canal.

ventral platform. Part of archaeostracan telson head embracing proximal extremities of furcal rami.

vertex. Top part of head (cephalon).

vesicula seminalis. *See* seminal vesicle.

walking leg. *See* pereiopod.

wrist. *See* carpus.

zoea stage. Larval stage in ontogeny of various malacostracans but unknown in some.

ONTOGENY

EGGS AND LARVAL STAGES

Crustaceans hatch from eggs which in some groups (e.g., commonly in various branchiopods, ostracodes, cirripeds, isopods) are produced parthogenetically but generally by sexual fertilization. These may be released in extraordinary numbers directly into water surrounding females or carried in brood pouches until ready for hatching, but (except in very few) without releasing viviparous young. In some branchiopods (e.g., Cladocera) the brood pouch is located dorsally between the carapace valves. Among malacostracans, the Peracarida carry eggs in a brood pouch formed by overlapping plates (oostegites) borne by the bases of some of the thoracic limbs, and in Decapoda the eggs are attached to abdominal appendages of females.

A common denominator in the ontogeny of crustaceans is the larval stage of development known as the **nauplius** (Fig.

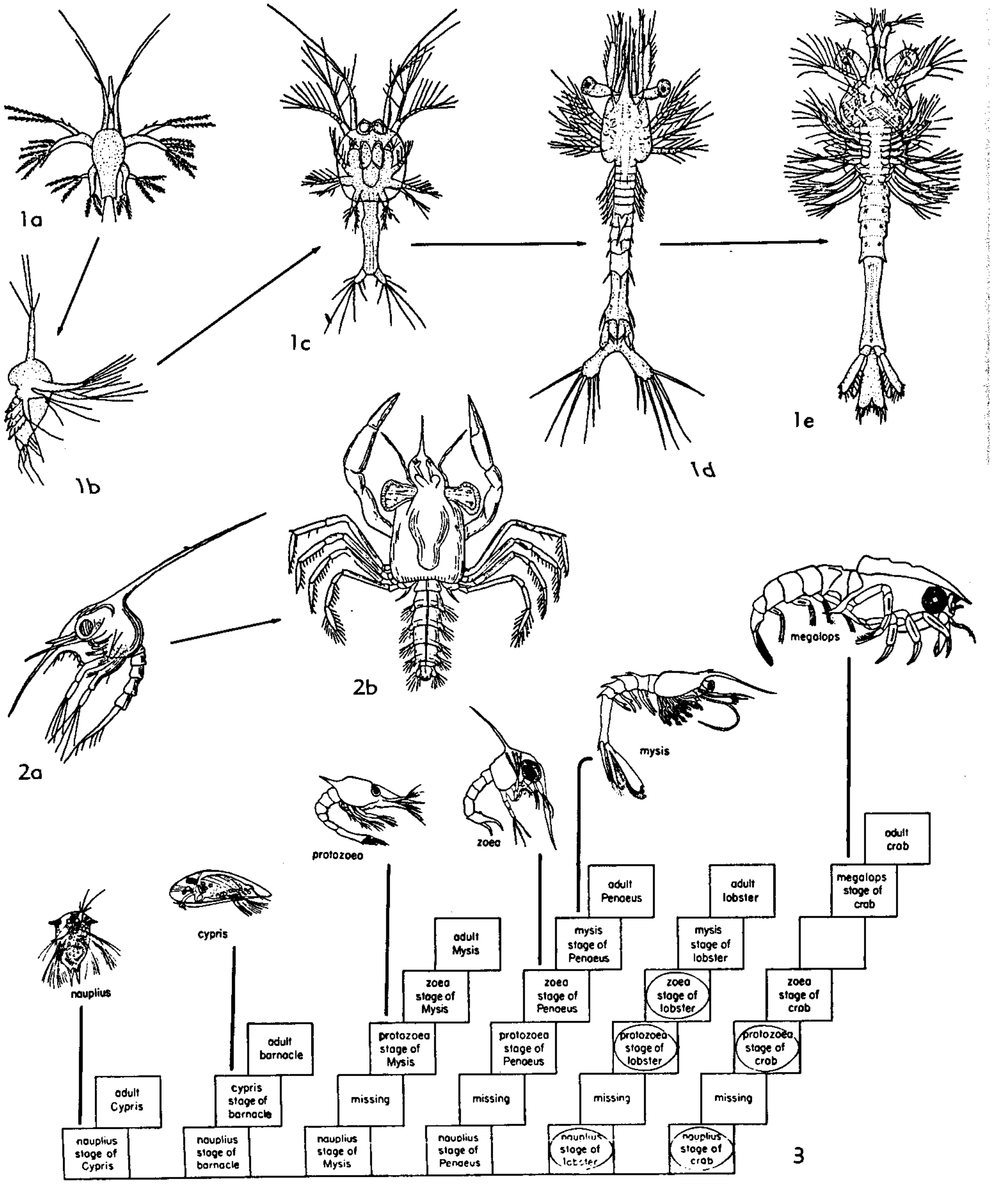


FIG. 35. Ontogeny of Crustacea (stages in ovals confined to eggs, others free-living). [For megalops, read megalopa.]

1. Larval stages of penaeid prawns (eucarid Malacostraca); *1a,* nauplius, ×53; *1b,* metanauplius, ×47; *1c,* zoea, ×25; *1d,* metazoea, ×23; *1e,* mysis, ×14.

2. Larval stages of crabs (decapod Malacostraca); *2a,* zoea, characterized by elongate cephalic spines, ×23; *2b,* megalopa stage of swimming crab, *Ovalipes,* ×11.7.

3. Recapitulation of larval stages in several crustacean groups (not to scale).

[*1-2,* from F. A. Chace in *Encyclopedia of science and technology,* by permission, McGraw-Hill Book Company, copyright, 1960; *3,* mod. from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, copyright 1949.]

35,*1a*), which prevails widely as the first larval stage after hatching, or if not so, is suppressed within the egg (SCHMITT, 1965, p. 35). The nauplius is a very minute, unsegmented, egg-shaped fore-runner of one or more successive larval stages or of next-following adult forms (e.g., cypris stage, Fig. 35). It is broadest in front, where a median eye provides vision. Behind this are three pairs of appendages—uniramous antennules, biramous antennae, and biramous mandibles. The mouth, covered by a large labrum, leads directly to a slender alimentary canal in which foregut, midgut, and hindgut are recognizable. In branchiopods and ostracodes transformation of the nauplius into juveniles and adults is gradual, with addition of somite after somite in successive molts by intercalation in front of the terminal somite (telson) of the abdomen. Immature instars may be numerous. Early stages in this process which differ perceptibly from the initial nauplius but which have not yet attained adult form are called metanauplii (Fig. 35,*1b*).

Recognition of the cirripeds as crustaceans is affirmed by their ontogeny, in which a free-swimming cyprid larval stage is particularly significant (Fig. 21,*1a-c;* 35,*3;* see Fig. 39,*2a,b*).

In the various crustacean classes post-nauplial larval stages named cypris, protozoea, zoea, mysis, and megalopa are recognized (Fig. 35), as well as several additional special ones. These differ vastly from one another in appearance and correspondingly in their morphological features, but tend generally to approach adults of their group. Most of the larval forms swim freely at or near the water surface. The commonly setose nature of their appendages and development of spinous processes, which in some are remarkably extended, undoubtedly serve as aids in flotation. Literally dozens of molts may occur during larval life, and still others after maturity is attained. Larval metamorphoses are entirely suppressed in crayfishes and river crabs, but this is not true of most other fresh-water crustaceans. A few marine crabs are known to be hatched with near-adult form, being thus decided exceptions to the rule.

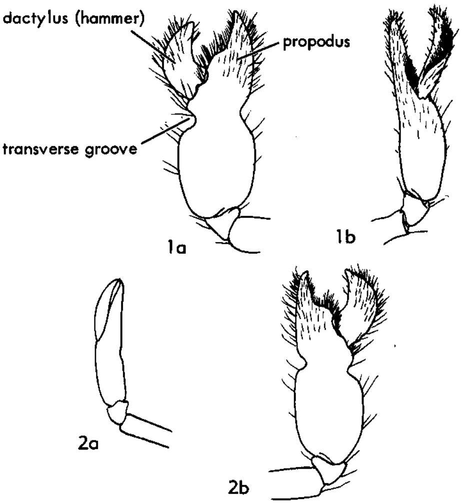


FIG. 36. Regeneration of appendages in Crustacea, illustrated by snapping shrimp, *Alpheus heterochelis,* in this instance accompanied by reversal in placement of larger and smaller front chelipeds, X2.3 (mod. from Wilson, 1903).——*1a,b.* Chelipeds of left-handed male from North Carolina coast.——*2a,b.* Left and right chelipeds immediately after molting, small left one regenerated on stump of original larger cheliped with hammer-like dactylus and grooved propodus.

MOLTING AND GROWTH

A characteristic feature of crustaceans is molting of the exoskeleton effected by periodic resorption of some of the materials of the old skeleton and secretion of a thin new integument beneath it. The old skeleton, with lining of the front and rear ends of the alimentary canal is then (usually but not invariably) shed or molted. At the same time, by addition of water, the soft parts swell to a distinctly larger size beneath the thin elastic flexible new skeleton which later quickly hardens to form a relatively rigid cover. The molting process is termed **ecdysis.**

ADULTS AND LIFE DURATION

Adulthood is distinguished by qualitative stability of morphological features, for changes at times of molting become re-

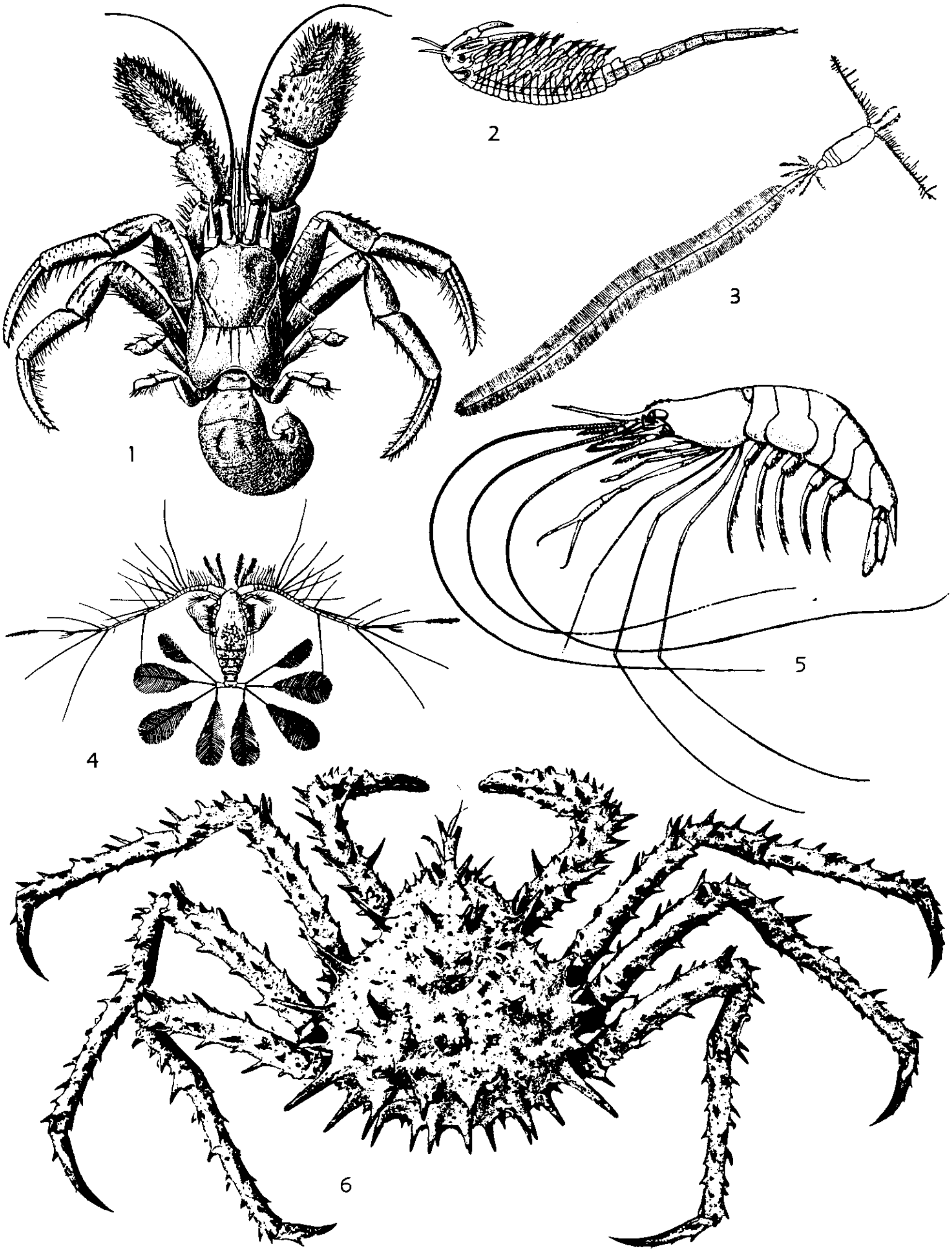


Fig. 37. Adaptation of Crustacea to diverse habitats and modes of life.

1. Dorsal view of hermit crab, *Pagurus setosus,* removed from snail shell which protects soft, asymmetrically twisted abdomen and into which most of crab's body can be withdrawn, ×0.7. This species lives along the Pacific coast of North America from Alaska to California at depths of 100 to 500 m. Other hermit crabs inhabit beaches above tidewater and range considerably in size.

2. Brine shrimp, *Artemia,* an anostracan branchio-

stricted to mere growth in size. No longer are external and internal structures modified significantly and no additions of somites or their appendages appear. Many species seem not to grow beyond an approximate limit in size, whereas others continue to increase in dimensions and bulk throughout life.

The duration of adult existence of most crustaceans is quite unknown. It may be measured in days or weeks in the case of some branchiopods but certainly in years for many balanomorph cirripeds and malacostracans. SCHMITT (1965, p. 110-111) has reported that the average life span of some crabs is three years and of others approximately 12 years. He estimated that probably the longest-lived among modern crustaceans are giant American lobsters *(Homarus americanus)* off the New England coast, for which a 35-pound individual was judged to be about 50 years old. The largest yet-caught specimen, with body length of two feet and weight of 44.5 pounds, on similar basis would be approximately 65 years old, an ancient patriarch.

AUTOTOMY AND REGENERATION

Appendages which are lost are regenerated during subsequent molting stages. Anostracan branchiopods such as *Artemia* have this ability to a marked degree, and it has been shown that regeneration is more rapid in salt water than in fresh water. Injured valves of conchostracans may show deformation in growth lines at points of repair.

Autotomy, or breaking-off of injured limbs, is demonstrated by decapods and various other crustaceans. The injured appendage is dropped at a preformed breaking plane by means of a reflex muscle action. A blood clot forms at the breaking plane, then a bud, which grows into a new limb, appears beneath the scar. The resulting regenerated limb may differ from the original; asymmetry of chelae may be reversed when the larger chela is lost, the regenerated one becoming a small cutting chela and the uninjured one assuming the crushing abilities (Fig. 36). When the eye stalk of a living lobster or prawn is removed, it may be replaced by an antenna. This is heteromorphic regeneration.

ADAPTATION

MODES OF LIFE

Crustaceans are generally aquatic animals, both marine and fresh-water, although they inhabit many diverse environments. Some live on land, in rock crevices, earth burrows or in trees, and some are parasites living on or within nearly every kind of animal, including other crustaceans. Body structures and appendages are adapted according to requirements of their habits and habitats.

FIG. 37. *(Continued from facing page.)*

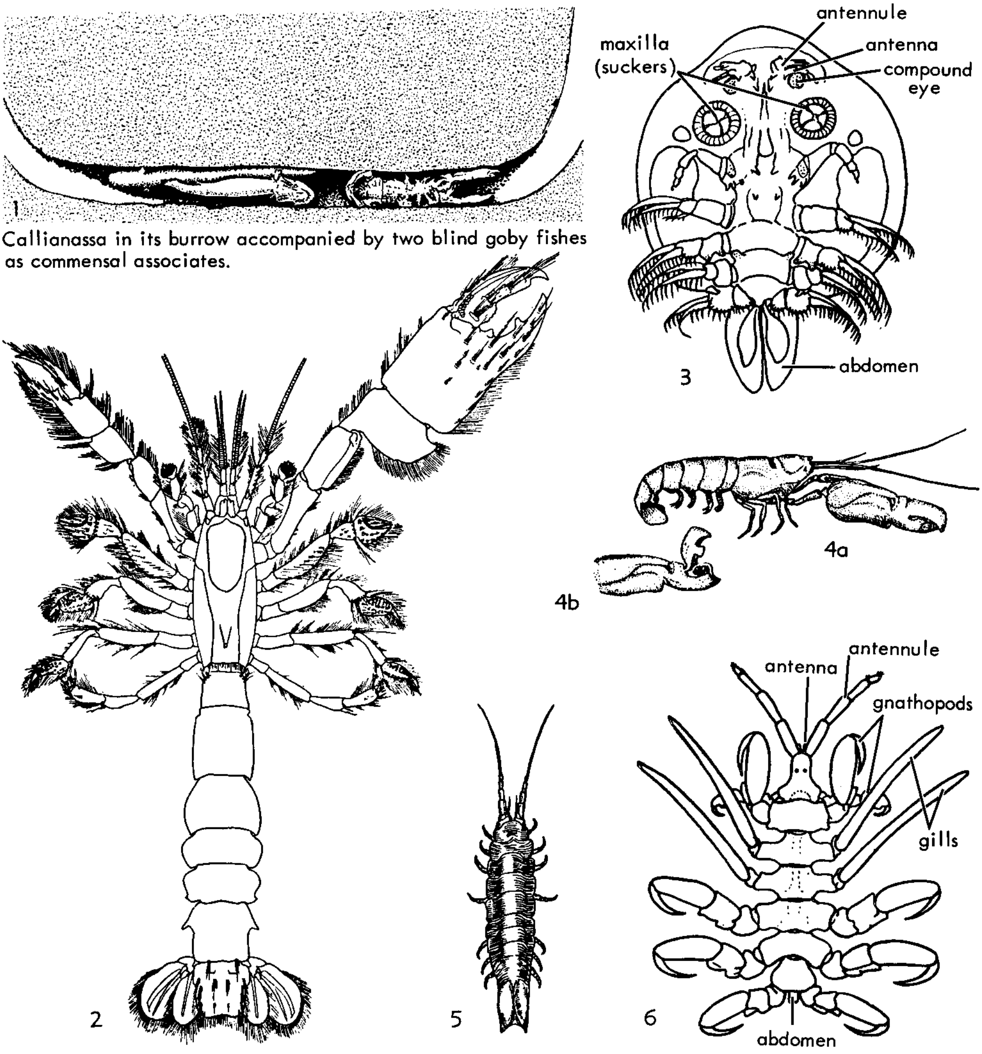
pod adapted to existence in hypersaline lakes and lagoons, where populations may be extremely large, ×3.3.

3-4. Open-ocean planktonic copepods with setose appendages which aid in flotation.——*3. Calocalanus* sp., ×10.——*4. C. pavo,* ×11.

5. Caridean prawn, *Palaemon tenuipes,* a decapod malacostracan adapted for living in brackish-water lagoons and estuaries, with very elongate and slender pereiopods supplementing antennules and antennae as feelers, ×0.7.

6. Female pagurid crab, *Paralithodes rathbuni,* from sea bottom off California coast at depth of 400 m. These crabs, relatives of hermit crabs, have abandoned use of mollusk shells for housing and with stout carapace of their own move about freely, females retaining asymmetry of ventral abdominal plates, ×0.5.

[*1,6,* from Schmitt, 1921; *2-3,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, copyright 1949; *4,* from W. T. Calman in E. R. Lankester, *Treatise on zoology,* by permission, A. & C. Black, publ.; *5,* from W. Buddenbrock in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission, Akademische Verlagsgesellschaft, publ.]



Callianassa in its burrow accompanied by two blind goby fishes as commensal associates.

Fig. 38. Adaptation of Crustacea, including commensalism and parasitism.

1-2. Burrow-building shrimplike decapod, *Callianassa,* which is adapted to existence in shallow-sea mud bottoms and in gravelly beaches.——*1.* Longitudinal section of *Callianassa*-made permanent burrow in southern California beach sand, occupied by male *(C. affinis)* in feeding position and accompanied by pair of small commensal fishes. In this association a pair of shrimps invariably are hosts to a pair of fishes, each pair proportional to the other in size (small shrimps with small fishes and larger shrimps with larger fishes).——*2.* Dorsal view of female *C. goniophthalmus* from sea bottom off California coast at depth of 500 m., ×0.7.

3. Branchiuran fish louse, *Argulus japonicus,* common ectoparasite on goldfishes; ventral view of female, enl.

4. Pistol shrimp, *Alpheus californiensis,* a beach dweller; *4a,* side view of entire shrimp, ×0.7; *4b,* cocked claw of cheliped, ×0.7.

5. Marine isopod, *Pentidotea resecata,* which lives on stems of seaweeds, orienting its slender body along the stem and closely resembling the weed in color, thus gaining protection by inconspicuousness, ×0.7.

6. Caprellidean amphipod, *Paracyamus boopis,* so-called whale louse, because ectoparasitic on whales; dorsal view of male, ×4.

[*1, 4-5,* from MacGinitie & MacGinitie, *Natural history of marine animals,* by permission, McGraw-Hill Book Company, publ., copyright 1949; *2,* from Schmitt, 1921; *3, 6,* from S. F. Light *et al., Intertidal invertebrates of central California coast,* by permission, University of California Press, publ.]

The endopods of thoracic and abdominal limbs are modified to perform various functions: locomotion, respiration, food-gathering, cleansing, defense, reproduction, and sensory perception. The planktonic types of crustaceans have long feathered setae and antennae enabling them to float (Fig. 37, *3-4*). If an animal is predatory, the chelae (or subchelae in stomatopods) of one or more thoracic limb pairs are specialized and enlarged for capturing and tearing food (Fig. 25, 26, 30). Burrowers have slender bodies to aid in burrowing and slipping into crevices (Fig. 38,*1-2*).

Deep-sea forms usually are blind or nearly so, but free-swimmers living near the surface have well-developed eyes and other sense organs. Certain types have phosphorescent or luminous organs called photophores which emit light and may be used for illumination in searching for food and detecting enemies. Those that have become terrestrial have special organs for respiration; the vascular lining of the carapace performs this function in land crabs, whereas in wood lice (Isopoda) breathing is accomplished through invaginations of the abdominal limb integuments.

Parasitic and commensal forms have prehensile devices for attachment, structures modified for piercing skin of the host, and sucking organs, and may lose appendages for locomotion (Fig. 38,*3*).

Cephalocarida and Mystacocarida are exclusively benthonic marine crustaceans living from the intertidal zone to depths of 300 meters. They are diminutive deposit-feeders, living in the loose, organic-rich sediment of the subtidal zone and are unable to swim.

Most Branchiopoda inhabit fresh to brackish and slightly alkaline water in lakes and temporary ponds among weedy vegetation, although *Artemia* is found in salt lakes and briny pools (Fig. 37,*2*). *Triops* survives periods of desiccation; in fact, the eggs normally require a drying-out period prior to hatching. Branchiopods swim, crawl, or burrow in muddy substrates, feeding on algae and diatoms. Notostracan branchiopods occur commonly in temporary lakes and ponds and even alkaline pools, crawling on bottom and feeding on detritus including parts of larger organisms. Eggs in mud distributed by birds and in dried mud may be viable even after 15 years. Transported hermaphroditic populations possibly explain geographic distribution of species.

Copepoda are prevalent in all open-ocean areas, as well as fresh-water environments (Fig. 20); many forms are pelagic, but most are benthonic (Fig. 37,*3*,*4*). Cyclopoid and harpacticoid species may construct cysts for survival during anaerobic periods. Ostracoda thrive in virtually all kinds of aquatic environments, ranging from streams, lakes, temporary ponds, and brackish estuaries or lagoons to shallow seas and intermediate and abyssal depths in oceans. In the fossil record a preponderant majority of ostracode species consist of shallow marine bottom-dwellers.

Cirripedia are marine animals except for a few which live in brackish water. They attach themselves to rocks, seaweed, hulls of ships and floating objects, some forms exhibiting parasitism on larger animals, and some are commensal with fishes and whales (Fig. 21, 22).

Among Malacostraca the numerous varied groups exhibit adaptations to many different environments and modes of life. The Phyllocarida are predominantly marine, Leptostraca being strong swimmers but also adapted for burrowing in the mud in shallow coastal waters (Fig. 19,*8*). Phyllocarids are found in depths ranging to 6,000 meters, although some (e.g., *Caryocaris*) are planktonic; most are bottom-dwellers. Eocarids (Fig. 17,*2-3*) were marine scavengers probably living in coastal lagoons and swamps. Extant Syncarida inhabit fresh water (Fig. 18,*3-4*), although many fossil species were marine. They are nektonic to benthonic, microphagous to carnivorous, as shown by variations in development of eyes and maxillipeds. Most groups of Peracarida are predominantly marine, occurring at all depths; many are benthonic detritus-feeders burrowing and building tubes in the substrate.

Dominantly pelagic malacostracans include the carnivorous or detritus-feeding Mysidacea (Fig. 18,*1-2*,*11*) and Euphausiacea (Fig. 24,*4*), which are main food sources of many marine fishes and whales. The Cumacea (Fig. 18,*5*) and Tanaidacea (Fig.

18,*9*) are mainly crawlers and burrowers in shallow sea-bottom mud, but many range to abyssal depths. A majority of the Isopoda (Fig. 19,*2;* 23,*1-11*) and Amphipoda (Fig. 19,*7*) also are marine (e.g., *Limnoria,* a ubiquitous isopod wood-borer) and found at most depths. Both of these groups include fresh-water and terrestrial members, however. Some degenerate isopods infest other crustaceans as parasites (Fig. 33, *2*) and are vicious enemies of fishes; likewise, amphipods include such ectoparasites as the whale louse *Paracyamus* (Fig. 38,*6*). Ability to live in the water of hot springs and in underground waters is a feature of the Thermosbaenacea. Mimicry and concealment are illustrated by such isopods as the slender-bodied *Idotea* (Fig. 38,*5*), which orient themselves parallel to seaweed stems and assume coloration identical with them.

Only the Isopoda rival the Decapoda in variety of effective adaptation to living habits and habitats. Decapods may be strong swimmers (Fig. 17,*1;* 24,*2,5-8;* 25,*1-2,6;* 26,*4*) and many are able to burrow swiftly to moderate depths in sea-bottom or fresh-water sediment (Fig. 25,*3-5;* 26,*1,5,7,11*) or on land, along streams, or on shores (e.g., *Callianassa,* Fig. 38,*1-2*). Numerous crabs can scuttle over the earth surface and robber crabs are adept at climbing trees. The hermit crabs (Fig. 37,*1*) are peculiarly specialized for using empty snail shells for protection, with the naked abdomen twisted into coils of the shell interior. Fiddler crabs (Fig. 36,*1-2*) and pistol shrimps (Fig. 38,*4*) are examples of unusual adaptations, the first for effective burrowing and the second seemingly for offensive-defensive protection. Long persistence of acquired adaptive characters is illustrated by the stout-shelled lithodid crabs (Fig. 37,*6*), which have abandoned an ancestral mode of life like that of hermit crabs and become suited to a free existence, while retaining asymmetry of the abdomen inherited from shell-inhabiting predecessors.

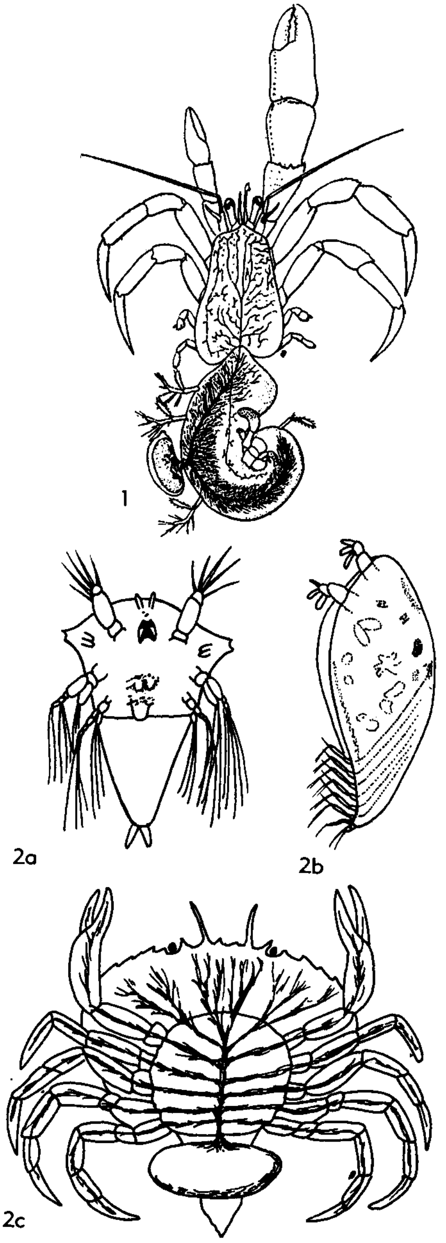


FIG. 39. Crustacean parasites illustrated by rhizocephalan cirripeds preying on crabs.——*1. Peltogaster pagurus* (rhizocephalan) on hermit crab, *Pagurus bernhardus,* saclike body of parasite containing viscera and eggs visible on left side of crab's twisted naked abdomen, with food-gathering roots permeating its host's abdomen and thorax, ×0.7 (from Paul Krüger in H. G. Bronn, *Klassen und Ordnungen des Tierreichs,* by permission, Akademische Verlagsgesellschaft, publ.).——*2. Sacculina carcini; 2a,b,* nauplius stage (dorsal) and cypris stage (lateral) larvae, much enl; *2c,* ventral view of crab with attached adult female rhizocephalan distinguished by saclike body and roots penetrating interior and appendages of crab, ×0.7 (from Stempell).

COMMENSALISM AND PARASITISM

Only one genus of Branchiopoda, the cladoceran *Anchistropus,* is known to be parasitic (on *Hydra*). Certain ostracodes are parasitic on fishes and other crustaceans. Caligoid copepods are parasitic or commensal on fish, attached by the head, the mouth being modified for sucking and hooklike mandibles adapted to pierce the skin of the host. Lernaeopodoid copepods, the so-called fish maggots, are ectoparasites, which as larvae bury themselves in the walls of the mouth cavity or gill chamber of salmon and other fishes to feed on body fluids. Some copepods embed themselves in the eyes or other organs of fishes, hard-shelled mollusks, nudibranchs, and in other crustaceans, and may live their entire life cycle on or within the host. Those that live on marine annelid worms have degenerated to become limbless, being attached by a tubular branched structure within the host. Branchiuran argulids are external parasites which fasten themselves by means of powerful discs; their antennae are equipped with hooks and spines to further grip the surface of fishes (Fig. 38,*3*).

Cirripedia contain several parasitic orders, the Acrothoracica being content to occupy shells of other barnacles, corals, snails, clams and other animals after boring into them. The Ascothoracica are external or internal parasites of echinoderms or coelenterates obtaining sustenance from the body of the host. The highly parasitic Rhizocephala are world-wide in distribution (Fig. 39). They infest other crustaceans, principally Decapoda, and have no appendages or typical crustacean features, but consist of a thin-walled sac enclosing a visceral mass containing reproductive organs. They penetrate the abdomen of the host by means of a threadlike root which branches in all directions to absorb nourishment (Fig. 39, *1,2c*). The crustacean nature of these parasites is affirmed by their larval development which passes through nauplius and cypris stages (Fig. 39,*2a,b*). The larvae hatch out and settle on another decapod host, where the life cycle is repeated.

Epicaridean isopods (Fig. 33,*2*) are ectoparasitic on other crustaceans (copepods, ostracodes, mysidaceans, euphausiaceans, isopods, amphipods, parasitic cirripeds, and decapods). Caprellidean amphipods (Cyamidae) are ectoparasites on whales (Fig. 38,*6*). Decapods are commensal with mollusks, sponges, echinoderms, and ascidians.

CLASSIFICATION

In older classification, as previously noted, all crustaceans were divided into groups termed Entomostraca and Malacostraca. The first included a heterogeneous assemblage of mostly small forms now included in classes (or subclasses) named Cephalocarida, Branchiopoda, Ostracoda, Copepoda, Branchiura, Euthycarcinoida, Mystacocarida, and Cirripedia. The category of crustaceans consisting of so-called entomostracans has long been abandoned. The Malacostraca, on the other hand, persist in classification. They contain most of the larger crustaceans with a thorax of eight somites and an abdomen containing seven or eight somites. A majority of the higher crustaceans grouped in the Malacostraca are medium-sized to large marine forms.

The development of crustacean classification, with notice of the numerous divergent arrangements advocated by authors, is not outlined in this chapter. Instead, it is judged sufficient to summarize here the classification adopted in the *Treatise* with statement of the stratigraphic occurrence of suprageneric taxa and record of numbers of genera and subgenera contained in them as given by *Treatise* authors.

It should be explained that a very large number of extant genus-group taxa unknown as fossils are not included in systematic descriptions of *Treatise* chapters on crustacean groups and these necessarily are omitted from tabulation. The magnitude of such omissions can be indicated by very incomplete information on numbers of extant genera of the Mysidacea and Isopoda.

Tattersall & Tattersall (1951) have described 40 genera of British mysidaceans and Tattersall (1951) has recorded genera of the same group known from North America, the latter including numerous forms found also in Britain, as well as 24 additional genera. The total of 64 genera is only part of the mysidacean fauna of the world. The *Treatise* contains no description and illustration of an extant mysidacean. Including fossil forms, the *Treatise* lists 29 genera of isopods (Trias.-Rec.), only a few of which are represented by living species from any part of the world. By way of contrast, Richardson (1905) described 128 genera of North American isopods and Van Name (1936) added 72 genera to the isopod fauna of the same continent. Many of these 190 forms are fresh-water and terrestrial.

OUTLINE OF TREATISE CLASSIFICATION OF CRUSTACEA

An outline of classification of crustaceans adopted in the *Treatise* is given in the following tabulation, which shows suprageneric taxa down to subfamily rank, accompanied by records of geologic occurrence and numbers of included genera. The last-mentioned data provide information on numbers of subgenera additional to nominotypical ones which are differentiated in some family groups, as well as numbers of doubtfully recognized genera. For example, the notation "(41+?20;3)" indicates recognition of 41 genera, 20 doubtfully recognized genera, and 3 subgenera other than nominotypical ones.

Totals include only genus-group taxa for which systematic descriptions are given in the *Treatise*. Suprageneric taxa recorded as ranging to the Recent contain an unspecified number (generally large) of additional Recent genera not listed in the *Treatise*.

Treatment of the Crustacea as a superclass and its main divisions as classes has been discussed adequately by Manton in a preceding chapter (p. *R*3). Here it is desirable merely to add that complexity of the taxonomic hierarchy above the genus-group rank in the Malacostraca, for example, furnishes intrinsic justification for recognizing categories designated as superorders within a subclass, infraorders within a suborder, and sections within an infraorder. Either family or superfamily may be the next lower-rank assemblage within an order, suborder, infraorder, or section.

Main Divisions of Crustacea Exclusive of Ostracoda

- Crustacea *(superclass)* (833+?20;46). *Cam.-Rec.*
- Cephalocarida *(class)* (2). *Rec.*
  - Brachypoda *(order)* (2). *Rec.*
    - Hutchinsoniellidae (1). *Rec.*
    - Lightiellidae (1). *Rec.*
- Branchiopoda *(class)* (99+?20;3). *L.Dev.-Rec.*
  - Calmanostraca *(subclass)* (10). *L.Dev.-Rec.*
    - Notostraca *(order)* (2). *U.Carb.-Rec.*
      - Triopsidae (2). *U.Carb.-Rec.*
    - Kazacharthra *(order)* (7). *L.Jur.*
      - Ketmeniidae (7). *L.Jur.*
    - Acercostraca *(order)* (1). *L.Dev.*
      - Vachonisiidae (1). *L.Dev.*
  - Diplostraca *(subclass)* (75+?20:3). *L.Dev.-Rec.*
    - Conchostraca *(order)* (56+?20;3). *L.Dev.-Rec.*
      - Laeviscaudata *(suborder)* (1). *L.Cret.-Rec.*
        - Lynceidae (1). *L.Cret.-Rec.*
      - Spinicaudata *(suborder)* (55+?20;3). *L.Dev.-Rec.*
        - Limnadioidea *(superfamily)* (7+?5). *Carb.-Rec.*
          - Limnadiidae (5+?5). *Carb.-Rec.*
            - Limnadiinae (2). *Rec.*
            - Estheriininae (3+?5). *Carb.-L.Cret.*
          - Cyclestheriidae (1). *Rec.*
          - Leptestheriidae (1). *Rec.*
        - Cyzicoidea *(superfamily)* (18+?11;2). *L.Dev.-Rec.*
          - Cyzicidae (6+?9;2). *L.Dev.-Rec.*
          - Asmussiidae (12+?2). *L.Dev.-U.Cret.*
            - Asmussiinae (9). *L.Dev.-U.Cret.*
            - Torgalykiinae (3+?2). *Dev.-U.Jur.*
        - Estherielloidea *(superfamily)* (4+?1;1). *U.Carb.-L.Cret.*
          - Estheriellidae (4+?1;1). *U.Carb.-L.Cret.*
            - Estheriellinae (3;1). *U.Carb.-L.Cret.*
            - Monoleiolophinae (1+?1). *Penn.-L.Cret.*
        - Leaioidea *(superfamily)* (13). *M.Dev.-L.Cret.*
          - Leaiidae (13). *M.Dev.-L.Cret.*
        - Vertexioidea *(superfamily)* (13+?3). *L.Carb.-Rec.*
          - Vertexiidae (6). *L.Carb.-U.Trias.*
          - Limnadopsidae (3+?2). *L.Carb.-Rec.*
          - Pemphilimnadiopsidae (1). *Penn.*
          - Ipsiloniidae (3+?1). *Dev.-L.Cret.*
    - Cladocera *(order)* (19). *Oligo.-Rec.*
      - Eucladocera *(suborder)* (18). *Oligo.-Rec.*

        - Sidoidea *(superfamily)* (1). *Rec.*
          - Sididae (1). *Rec.*
        - Daphnioidea *(superfamily)* (15). *Oligo.-Rec.*
          - Daphniidae (1). *Oligo.-Rec.*
          - Chydoridae (13). *Rec.*
            - Chydorinae (12). *Rec.*
            - Eurycercinae (1). *Rec.*
          - Bosminidae (1). *Rec.*
        - Polyphemoidea *(superfamily)* (2). *Rec.*
          - Polyphemidae (2). *Rec.*
      - Haplopoda *(suborder)* (1). *Rec.*
          - Leptodoridae (1). *Rec.*
  - Sarsostraca *(subclass)* (14). *L.Dev.-Rec.*
    - Anostraca *(order)* (13). *L.Dev.-Rec.*
          - Artemiidae (1). *Pleist.-Rec.*
          - Branchipodidae (4). *?U.Carb., ?Eoc., Rec.*
          - Branchinectidae (1). *Rec.*
          - Chirocephalidae (2). *Rec.*
          - Polyartemiidae (1). *Rec.*
          - Streptocephalidae (1). *Rec.*
          - Thamnocephalidae (1). *Rec.*
          - Gilsonicarididae (1). *L.Dev.*
          - Uncertain family (1). *U.Carb.*
    - Lipostraca *(order)* (1). *M.Dev.*
          - Lepidocarididae (1). *M.Dev.*
- Mystacocarida *(class)* (1). *Rec.*
    - Mystacocaridida *(order)* (1). *Rec.*
          - Derocheilocarididae (1). *Rec.*
- Euthycarcinoidea *(class)* (2). *L.Trias.-M.Trias.*
    - Euthycarcinida *(order)* (2). *L.Trias.-M.Trias.*
          - Euthycarcinidae (2). *L.Trias.-M.Trias.*
- Copepoda *(class)* (2). *Mio.-Rec.*
    - Calanoida *(order)*. *Rec.*
    - Cyclopoida *(order)* (1) *Mio.-Rec.*
          - Genus undetermined (1). *Mio.*
    - Harpacticoida *(order)* (1). *Mio.-Rec.*
          - Cletodidae (1). *Mio.-Rec.*
    - Caligoida *(order)*. *Rec.*
    - Notodelphyoida *(order)*. *Rec.*
    - Lernaeopodoida *(order)*. *Rec.*
    - Monstrilloida *(order)*. *Rec.*
- Branchiura *(class)* (4). *Rec.*
    - Arguloida *(order)* (4). *Rec.*
          - Argulidae (4). *Rec.*
- Cirripedia *(class)* (107;29). *U.Sil.-Rec.*
    - Acrothoracica *(order)* (12). *Carb.-Rec.*
      - Pygophora *(suborder)* (7). *Rec.*
          - Lithoglyptidae (6). *Rec.*
          - Cryptophialidae (1). *Rec.*
      - Apygophora *(suborder)* (1). *Carb.-Rec.*
          - Trypetesidae (1). *Carb.-Rec.*
      - Suborder uncertain (4). *Trias.-Plio.*
          - Rodgerellidae (1). *M.Jur.-L.Plio.*
          - Zapfellidae (3). *Trias.-Plio.*
    - Rhizocephala *(order)* (11). *Rec.*
      - Kentrogonida *(suborder)* (5). *Rec.*
          - Peltogastridae (1). *Rec.*
          - Sacculinidae (1). *Rec.*
          - Lernaeodiscidae (1). *Rec.*
          - Clistosaccidae (1). *Rec.*
          - Sylonidae (1). *Rec.*
      - Akentrogonida *(suborder)* (5). *Rec.*
      - Uncertain affinities (1). *Rec.*
    - Ascothoracica *(order)* (12). *Cret.-Rec.*
          - Synagogidae (3). *Rec.*
          - Lauridae (3). *Rec.*
          - Petrarcidae (1). *Rec.*
          - Dendrogastridae (3). *Rec.*
          - Uncertain family (2). *U.Cret.*
    - Thoracica *(order)* (72;29). *U.Sil.-Rec.*
      - Lepadomorpha *(suborder)* (38;9). *U.Sil.-Rec.*
          - Cyprilepadidae (1). *U.Sil.*
          - Praelepadidae (1). *M.Carb.*
          - Scalpellidae (17;3). *U.Trias.(Rhaet.)-Rec.*
          - Heteralepadidae (2). *Rec.*
          - Iblidae (1). *Rec.*
          - Koleolepadidae (1). *Rec.*
          - Lepadidae (4;2). *?U.Trias., M.Eoc.-Rec.*
          - Malacolepadidae (1). *Rec.*
          - Oxynaspididae (1). *M.Eoc.-Rec.*
          - Poecilasmatidae (3;4). *U.Eoc.(Barton.)-Rec.*
          - Stramentidae (3). *Cret.(Alb.-Senon.).*
          - Uncertain family (3). *Rec.*
      - Verrucomorpha *(suborder)* (3;4). *U.Cret. (?Cenoman.-U.Senon.)-Rec.*
          - Verrucidae (3;4). *U.Cret.(?Cenoman.-U.Senon.)-Rec.*
      - Brachylepadomorpha *(suborder)* (2). *U.Jur. (Tithon.)-U.Mio.(Helvet.).*
          - Brachylepadidae (2). *U.Jur.(Tithon.)-U.Mio. (Helvet.).*
      - Balanomorpha *(suborder)* (29;16). *U.Cret. (U.Senon.)-Rec.*
          - Chthamalidae (9;2). *U.Cret.(U.Senon.)-Rec.*
          - Balanidae (20;14). *M.Eoc.-Rec.*
            - Balaninae (9;11). *M.Eoc.(Auvers.)-Rec.*
            - Tetraclitinae (1;2). *Oligo.-Rec.*
            - Chelonibiinae (1). *L.Mio.-Rec.*
            - Coronulinae (8;1). *U.Mio.-Rec.*
            - Emersoniinae (1). *U.Eoc.*
- Malacostraca *(class)* (586;14). *L.Cam.-Rec.*
- Phyllocarida *(subclass)* (52). *L.Cam.-Rec.*
    - Leptostraca *(order)* (4). *U.Perm.-Rec.*
          - Nebaliidae (4). *U.Perm.-Rec.*
    - Hymenostraca *(order)* (1). *?L.Cam., M.Cam.-L.Ord.*
          - Hymenocarididae (1). *?L.Cam., M.Cam.-L.Ord.*
    - Archaeostraca *(order)* (22). *L.Ord.-U.Trias.*
      - Ceratiocarina *(suborder)* (15). *L.Ord.-U.Trias.*
          - Ceratiocarididae (4). *L.Ord.-L.Dev., ?Carb., ?U.Perm.*
          - Austriocarididae (2). *M.Dev.-U.Trias.*
          - Echinocarididae (5). *L.Dev.-L.Miss.*
            - Echinocaridinae (3). *L.Dev.-L.Miss.*
            - Montecaridinae (2). *?L.Dev., M.Dev.-U.Dev.*
          - Pephricarididae (1). *U.Dev.*
          - Aristozoidae (3). *?M.Ord., U.Sil.-M.Dev.*
      - Rhinocarina *(suborder)* (7). *?Sil., L.Dev.-M.Penn., ?U.Perm.*
          - Rhinocarididae (6). *?Sil., L.Dev.-M.Penn., ?U.Perm.*

Ohiocarididae (1). *U.Dev.*
Uncertain order and family (25). *L.Cam.-L.Carb., L.Perm.*
Nonphyllocarid and uncertain genera formerly attributed to Phyllocarida
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Peltocarididae (2). *?L.Cam.-?M.Cam., ?L.Ord., U.Ord.-U.Sil., ?U.Perm.*
Uncertain genera (19). *M.Cam.-U.Trias.*
Eumalacostraca *(subclass)* (534;14). *M.Dev.-Rec.*
Eocarida *(superorder)* (14). *M.Dev.-Perm.*
Eocaridacea *(order)* (6). *M.Dev.-Penn.*
Eocarididae (2). *M.Dev.*
Palaeopalaemonidae (1). *U.Dev.-L.Miss.*
Anthracophausiidae (3). *Miss.-Penn.*
Pygocephalomorpha *(order).* (8). *Miss.-Perm.*
Tealliocarididae (2). *L.Carb.*
Pygocephalidae (4). *Miss-Penn.*
Notocarididae (2). *Perm.*
Syncarida *(superorder)* (20). *U.Miss.-Rec.*
Palaeocaridacea *(order)* (6). *U.Miss.-Perm.*
Palaeocarididae (3). *U.Miss.-Perm.*
Uronectidae (1). *L.Perm.*
Acanthotelsonidae (1). *Penn.*
Pleurocarididae (1). *Penn.*
Anaspidacea *(order)* (5). *Trias.-Rec.*
Anaspididae (3). *Trias.-Rec.*
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      - Eryminae (5;1). *L.Jur.-U.Cret., ?Paleoc.*
      - Clytiopsinae (6). *?Permotrias., L.Trias.-U.Trias.*
    - Platychelidae (2). *U.Trias.*
    - Nephropidae (13;1). *M.Jur.-Rec.*
      - Nephropinae (4). *U.Cret.-Rec.*
      - Homarinae (3;1). *Cret.-Rec.*
      - Neophoberinae (3). *M.Jur.-Rec.*
      - Uncertain subfamily (3). *?M.Jur., U.Jur.-U.Cret.*
    - Astacidae (2). *U.Jur. or L.Cret.-Rec.*
    - Parastacidae (2). *Pleist.-Rec.*
    - Austroastacidae (1). *Rec.*
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  - Glypheoidea *(superfamily)* (11;1). *?L.Trias., M.Trias.-L.Tert.*
    - Glypheidae (4;1). *?L.Trias., M.Trias.-L.Tert.*
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    - Pemphicidae (2). *M.Trias.*
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    - Tetrachelidae (1). *U.Trias.*
    - Coleiidae (2). *L.Jur.-L.Cret.*
    - Eryonidae (4). *L.Jur.-L.Cret.*
    - Polychelidae (4). *M.Jur.-Rec.*
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    - Palinuridae (9;1). *L.Jur.-Rec.*
    - Cancrinidae (1). *U.Jur.*
    - Scyllaridae (5). *L.Cret.-Rec.*
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    - Thalassinidae (1). *?Pleist., Rec.*
    - Axiidae (5). *L.Jur.-Rec.*
    - Laomediidae (2). *Mio.-Rec.*
    - Callianassidae (4). *U.Jur.-Rec.*
      - Callianassinae (2). *U.Cret.-Rec.*
      - Protocallianassinae (1). *?L.Cret., U.Cret.-Paleoc.*
      - Upogebiinae (1). *U.Jur.-Rec.*
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    - Pylochelidae (1). *Rec.*
    - Paguridae (12). *Jur.-Rec.*
      - Pagurinae (2). *L.Cret.-Rec.*
      - Diogeninae (6). *U.Cret.-Rec.*
      - Uncertain subfamily (4). *Jur., ?L.Cret.-?U.Cret.*
    - Coenobitidae (1). *?L.Mio., Rec.*
    - Lithodidae (1). *Rec.*
    - Lomidae (1). *Rec.*
  - Galatheoidea *(superfamily)* (12). *M.Jur.-Rec.*
    - Galatheidae (9). *M.Jur.-Rec.*
      - Galatheinae (4). *L.Cret.-Rec.*
      - Munidopsinae (1). *Rec.*
      - Uncertain subfamily (4). *M.Jur.-U.Cret.*
    - Aeglidae (1). *Rec.*
    - Porcellanidae (2). *U.Cret.-Rec.*
  - Hippoidea *(superfamily)* (3). *Tert.-Rec.*
    - Albuneidae (2). *Tert.-Rec.*
    - Hippidae (1). *Rec.*
- Brachyura *(infraorder)* (269;10). *L.Jur.-Rec.*
  - Dromiacea *(section)* (41;2). *L.Jur.-Rec.*
    - Dromioidea *(superfamily)* (33;2). *L.Jur.-Rec.*
      - Eocarcinidae (1). *L.Jur.*
      - Prosopidae (13;2). *M.Jur.-Cret., Rec.*
        - Prosopinae (4). *M.Jur.-L.Cret.*
        - Pithonotinae (7;2). *M.Jur.-U.Cret.*
        - Homolodromiinae (2). *Rec.*
      - Dromiidae (3). *Paleoc.-Rec.*
      - Dynomenidae (10). *U. Jur.-Rec.*
      - Uncertain family (6). *U.Jur.-U.Cret., ?Paleoc.*
    - Homoloidea *(superfamily)* (5). *U.Jur.-Rec.*
      - Homolidae (5). *U.Jur.-Rec.*
    - Dakoticancroidea *(superfamily)* (3). *U.Cret.*
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  - Oxystomata *(section)* (59;2). *L.Cret.(Alb.)-Rec.*
    - Dorippoidea *(superfamily)* (8). *L.Cret.(Alb.)-Rec.*
      - Dorippidae (8). *L.Cret.(Alb.)-Rec.*
        - Dorippinae (3). *L.Cret.(Alb.)-Rec.*
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      - Calappidae (19). *L.Cret.-Rec.*
        - Calappinae (15). *L.Cret.-Rec.*
        - Matutinae (4). *?L.Cret., M.Tert.-Rec.*
      - Leucosiidae (15). *?L.Eoc., M.Eoc.-Rec.*
    - Raninoidea *(superfamily)* (17;2). *L.Cret. (Alb.)-Rec.*
      - Raninidae (17;2). *L.Cret.(Alb.)-Rec.*
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    - Majidae (24). *?U.Cret., Eoc.-Rec.*
      - Majinae (6). *?U.Cret., Eoc.-Rec.*
      - Micromaiinae (3). *Eoc.-Oligo.*
      - Inachinae (6). *U.Eoc.-Rec.*
      - Pisinae (6). *Mio-Rec.*
      - Acanthonychinae (3). *Plio-Rec.*
    - Parthenopidae (5;2). *Eoc.-Rec.*
      - Parthenopinae (4;2). *M.Eoc.-Rec.*
      - Eumedoninae (1). *Rec.*
    - Uncertain family (1). *Mio.*
  - Cancridea *(section)* (9). *Eoc.-Rec.*
    - Corystidae (1). *Rec.*
    - Atelecyclidae (4). *Eoc.-Rec.*
    - Cancridae (4). *M.Eoc.-Rec.*
      - Cancrinae (3). *Mio.-Rec.*
      - Lobocarcininae (1). *M.Eoc.-U.Eoc.*
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      - Portunidae (17;2). *Eoc.-Rec.*
        - Portuninae (6;2). *Eoc.-Rec.*
        - Macropipinae (2). *Oligo.-Rec.*
        - Carcininae (4). *L.Eoc.-Rec.*
        - Psammocarcininae (3). *L.Eoc.-L.Oligo.*
        - Podophthalminae (2). *Oligo.-Rec.*
      - Carcineretidae (5). *U.Cret.*
    - Xanthoidea *(superfamily)* (85;2). *U.Cret.-Rec.*
      - Xanthidae (46). *U.Cret.-Rec.*
      - Potamidae (1). *U.Tert.-Rec.*
      - Geryonidae (4;2). *Eoc.-Rec.*
      - Goneplacidae (21). *?U.Cret., Paleoc.-Rec.*
        - Goneplacinae (3). *Eoc.-Rec.*
        - Carcinoplacinae (11). *Paleoc.-Rec.*

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Uncertain subfamily (2). *M.Eoc.-U.Eoc., ?Oligo.*
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Ocypodidae (6). *M.Eoc., Mio.-Rec.*
Ocypodinae (2). *Plio.-Rec.*
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Uncertain subfamily (2). *M.Eoc., L.Mio.*
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Uncertain superfamily (4). *?L.Cret.-U.Cret., ?M.Eoc., Rec.*
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Cyclidae (3). *L.Carb.-U.Trias.*
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CEPHALOCARIDA

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[Chapter submitted January, 1962]

CONTENTS

MORPHOLOGY

GENERAL FEATURES

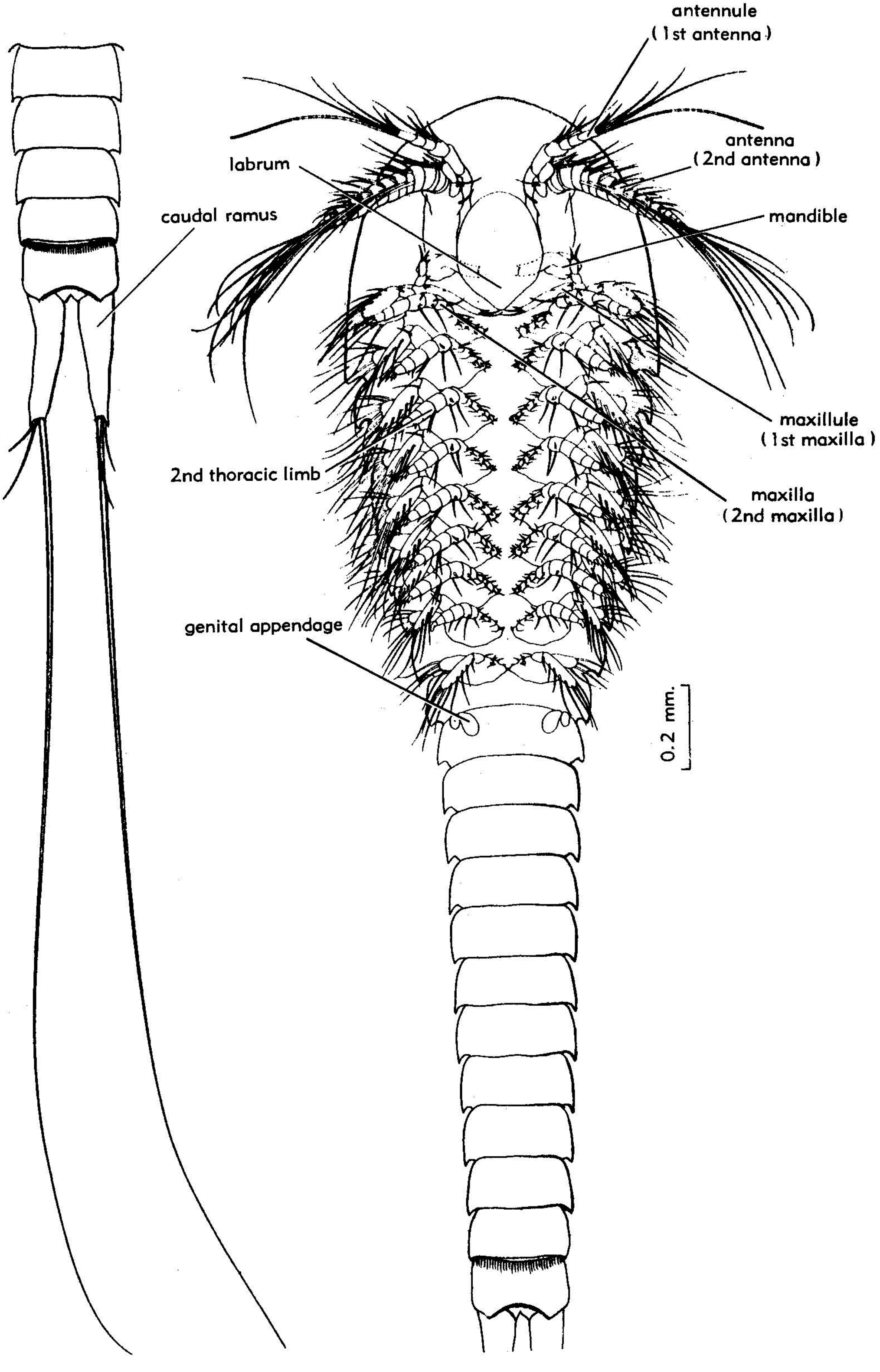
The body (Fig. 40) consists of a horseshoe-shaped cephalon, an eight-somite thorax, and a 12-somite abdomen (including the telson). Both the cephalon and thorax bear flat pleura, which are directed somewhat backward on the thoracic somites. On the cephalon the pleural lobes are continuous with each other anteriorly. Pleural lobes are reduced to posteriorly directed spines on the abdominal somites.

On the middle of the ventral surface of the cephalon is a conspicuous **labrum** which projects distinctly ventrally and posteriorly past the mouth, forming the floor of the **atrium oris.** There are five pairs of cephalic appendages: two pairs of antennae, a pair of mandibles, and two pairs of maxillae (Fig. 40).

Each thoracic somite bears a limb, except in *Lightiella,* where they are absent on the eighth. The first abdominal somite has a pair of reduced limbs which form genital appendages. The telson bears a well-developed caudal furca. The other abdominal somites lack appendages.

(On facing page.)

Fig. 40. Morphology of adult cephalocarid, *Hutchinsoniella macracantha* Sanders, ventral view, showing striking similarity of maxillae and all thoracic limbs, ×64 (9).


antennule
(1st antenna)
antenna
(2nd antenna)
labrum
caudal ramus
mandible
maxillule
(1st maxilla)
2nd thoracic limb
maxilla
(2nd maxilla)
genital appendage
0.2 mm.

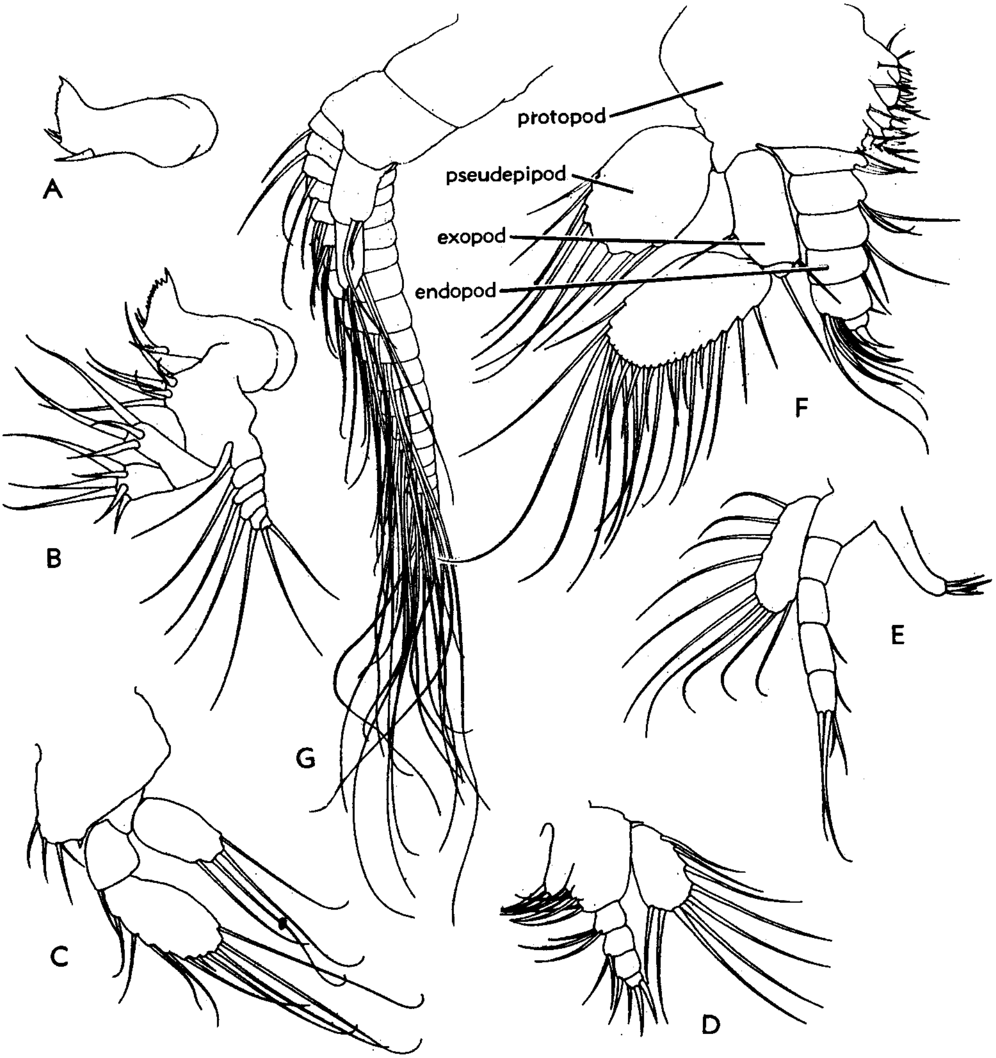


FIG. 41. Limbs of *Hutchinsoniella macracantha.*——*A.* Adult left mandible, ventral view.——*B.* Left mandible of stage 4 larva, ventral view.——*C.* Left 8th thoracic limb of adult, anterior view.——*D.* Left maxillule of stage 4 larva, anterior view.——*E.* Adult right maxillule, anterior view.——*F.* Adult right 4th thoracic limb, anterior view.——*G.* Adult right antenna, medial view. All figures of adults *(A, C, E-G)* ×150; those of larvae *(B, D)* ×170 *(A, B, D,* 9; *C, E-G,* Hessler, n).

APPENDAGES

The maxillae (2nd maxillae) and first seven thoracopods are alike except for details (Fig. 41,*F*). A foliaceous protopod bears three rami distally—a slightly flattened ambulatory endopod with five or six segments, and a three-segmented exopod, which gives rise to a single-segmented pseudepipod from its basal segment. SANDERS (9) considers the exopod to have four segments. However, the penultimate one is poorly developed and is more probably part of the segment proximal to it. The protopod bears six movable, medial endites (five on the maxilla) and an ill-defined transverse furrow by which the distal half of the protopod may bend somewhat with relation to the proximal half. The medial edge of the endopod is continuous with the median endites of the protopod. Both bear rows of setae, the orientation and morphology of which vary depending on their task in the capture and transport of food particles toward the mouth. Terminally the endopod bears three claws, except on the 7th thoracopod. Sanders (8) considered the medial claw to be the terminal segment and called it a dactylus. However, no muscles extend to this claw and therefore it cannot properly be considered a limb segment. The basal segment of the exopod is broadly joined to the protopod. The 2nd segment of the exopod is rodlike, with a few distal setae. Both the distal exopodal segment and the pseudepipod are paddlelike and have a distal fringe of setae.

The 8th thoracic limb (Fig. 41,*C*), when present, is basically like the preceding except that the endopod is missing.

The adult maxillule (Fig. 41,*E*) differs from the basic pattern of the thoracic limbs in that the pseudepipod is missing, the exopod is unjointed, the anteriorly oriented endopod is four-segmented, and the much-reduced protopod bears only a single endite, which forms a long, anteriorly curved finger. The larval maxillule (Fig. 41,*D*) is much more similar to the basic thoracic plan. The endopod curves posteriorly, and four normally developed endites occur on the proportionately larger protopod.

The adult mandible (Fig. 41,*A*) is a palpless, masticatory process. However, the morphology of the palp-bearing larval mandible (Fig. 41,*B*) is clearly based on the pattern of the thoracic limbs. Here the masticatory process is seen to be an endite of the coxa. The palp consists of the basis bearing a single endite, a two-segmented endopod, and a six-segmented exopod. The basic difference from the thoracic limbs is that the exopod is multisegmented.

The antennae (Fig. 41,*G*) are also interpretable in terms of the basic limb pattern. The protopod consists of coxa and basis. A two-segmented endopod and 19-segmented exopod are observed, the ventral surface of the latter being richly supplied with long setae. On the larval antenna the basis has a single endite, and a long naupliar process arises from the coxa. The naupliar process is homologous to the masticatory process of the mandible, the single endite of the maxillule, and the basal endite of the subsequent limbs.

The antennules have six segments and are uniramous. Each bears a long, multiarticular, sensory flagellum on its distal end.

INTERNAL ANATOMY

The digestive tract is a simple tube which ascends anteriorly from the mouth and then bends posteriorly to traverse the entire trunk. A pair of simple, glandular diverticula located in the cephalon open posteriorly into the anterior end of the mesenteron.

The excretory organ of the later larval stages and adult is a noncoiled maxillary gland with an external pore located on the posterior surface of the base of the maxilla. Antennary glands are present in the larva, and possibly in the adult as well.

The paired tracts of the ventral nerve cord form a simple ladder, as in the Branchiopoda, but with much shorter commissures. In each somite are large ganglia. The ganglia of the mandibular and two maxillary somites are somewhat coalesced.

Movement of the trunk is effected by paired dorsal and ventral longitudinal muscles, which run the length of the body, attaching at each intersomitic boundary, and by paired intrasomitic dorsoventral muscles. Each limb, except for the antennules and antennae, is moved by body-limb muscles having four origins; anterior and posterior dorsolateral origins, and anterior and posterior ventromedial origins. Intrinsic limb muscles move the rami and endites.

The heart extends the length of the thorax, with paired ostia in each somite.

Hutchinsoniella is hermaphroditic. Both the testes and ovaries are paired, finger-like organs located in the abdomen. The vas deferens opens on the protopod of the 6th thoracic limb; the oviduct opens on the genital appendages of the 1st abdominal somite. Only two large yolky eggs can be carried at a time, one on each genital appendage.

DEVELOPMENT

Development is gradual. The first free-living stage is a benthonic metanauplius

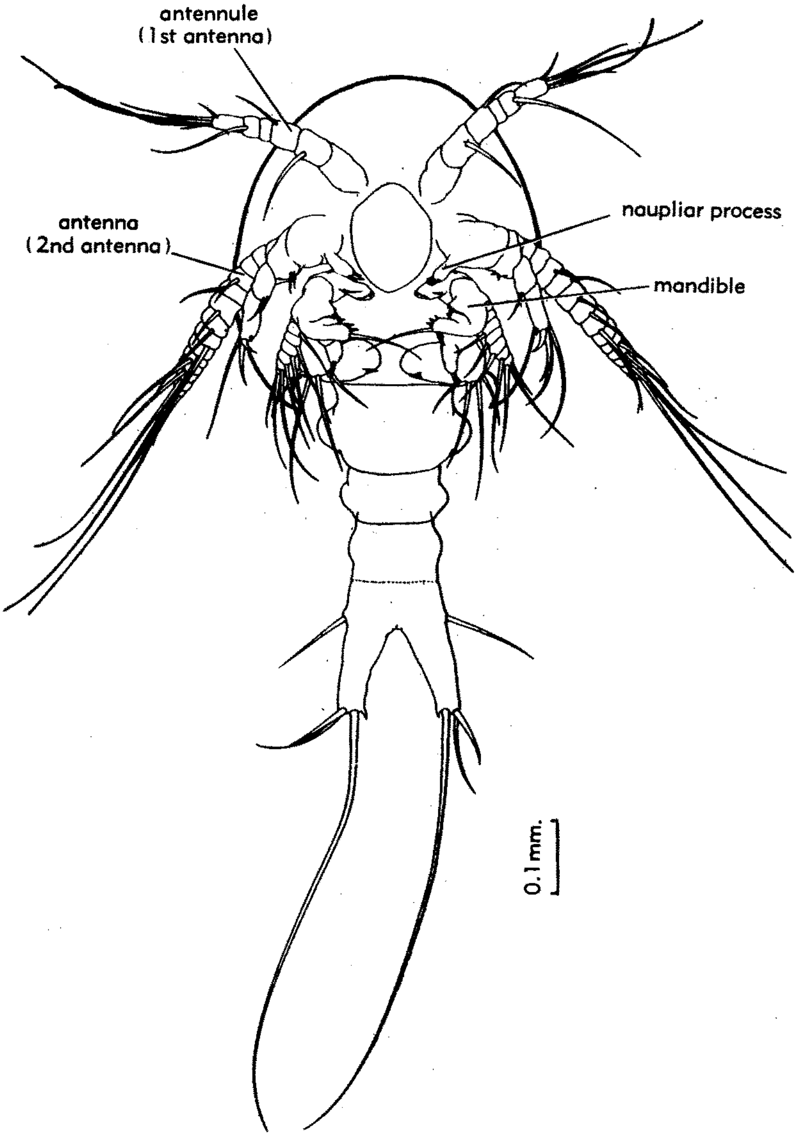


FIG. 42. Stage-1 larva (metanauplius) of *Hutchinsoniella macracantha,* ventral view, ×95 (9).

(Fig. 42) having well-developed antennules and antennae and mandibles, and rudimentary maxillules and maxillae. Three postcephalic somites are seen in *Hutchinsoniella* but eight in *Lightiella incisa.* The dorsal carapace is of the same form as that of the adult. From this stage on, both somites and limbs are added gradually. The limbs first appear in a rudimentary form, and require about three instars to attain functional maturity.

The antennae, mandibles, and maxillules undergo correlated metamorphic change from larval to adult morphology. This change occurs after the 13th stage in *Hutchinsoniella* and marks the end of the larval period and the naupliar mode of feeding. At this time the naupliar process of the antennae disappears. The palp disappears from the mandible, having undergone some previous reduction. The maxillules rotate anteriorly so that their endopods become directed forward. All protopodial endites of the maxillules disappear except for the basal endite, which appeared in the eighth larval stage and gradually became longer throughout the rest of the larval period. The antennules and limbs behind the maxillules undergo no change once they have developed.

The pleura of limbless larval thoracic somites are like those of the adult abdomen. Each thoracic somite develops adult thoracic pleura only as its limbs develop.

MODE OF LIFE

ENVIRONMENT

The known Cephalocarida are wholly benthonic marine crustaceans occurring from the intertidal zone to depths of 300 m. *Hutchinsoniella macracantha* SANDERS (7) is a nonselective deposit-feeder living in the loose, organic-rich zone on the surface of subtidal silt-clay sediments. *Lightiella serendipita* JONES (6) has been found subtidally on silty sands. *Lightiella incisa* GOODING (4) was found associated with the fine sediments trapped by the roots of *Thalassia* (turtle grass).

FEEDING

The method of feeding is known only for *Hutchinsoniella* (8). Feeding results from a metachronal anteroposterior beating of its limbs. The motion is initiated posteriorly and passes forward from limb to limb in a smooth wave.

The two pairs of antennae sweep backward with an oarlike motion. Their setae, particularly the numerous large setae on the ventral surface of the antennae, sweep food and detritus posteriorly and medially into the region of the thoracic limbs.

In the cycle of movement of the thoracic limbs and maxillae, the volume of the space between the limb and one behind it increases and decreases. The three rami of the limb alternately fold backward against the following limb and extend forward again. This action acts as a valve, rhythmically closing off the interlimb space laterally and ventrally, and then opening again. The thoracic pleura serve to block flow of water dorsolaterally. As the volume of the interlimb space increases on the forestroke, the valves are closed, resulting in a current of water that enters the median space between the paired rows of limbs from below, and proceeds into the interlimb space. The valves are open as the interlimb space decreases on the backstroke, allowing the water to flow out laterally and ventrolaterally. Food and detritus carried by the inflowing current is trapped by the spines and setae on the median surface of the endopods and endites of the protopods. Interdigitation of these setae with other setae on the median edge of the following limb brushes this material loose and concentrates it dorsally along the ventral surface of the thorax between the two rows of limbs (i.e., in the food groove). The endites of the protopods move this food forward toward the posterior end of the labrum. Here the long endites of the maxillules push the food into the atrium oris, where it is broken down by the mandibles and swallowed. All these actions occur simultaneously within the metachronal cycle, so that the feeding process is continuous.

During early larval life, thoracic limbs are insufficient to sustain the kind of feeding employed by the adult. Instead, food is swept toward the body by the antennules and antennae and exopods of the mandibles. It is concentrated at the posterior end of the labrum by means of setae on the antennae and endopods of the mandibles. From here it is passed to the molar processes of the mandibles by endites of the maxillules and naupliar processes of the antennae.

As thoracic limbs are added, the adult mode of feeding becomes increasingly effective, until finally at the 14th stage it becomes the sole method of food collection. Up until that time both methods of feeding function simultaneously.

LOCOMOTION

Hutchinsoniella cannot swim. It moves along the bottom by means of the same metachronal movement by which feeding takes place. Forward movement results from the backward thrust of the distal claws of the thoracic endopods on the substrate, the paddle-like action of the thoracic exopods and pseudepipods, and the oarlike action of the two pairs of antennae.

EVOLUTIONARY SIGNIFICANCE

Although the Cephalocarida are represented by few species and are unknown in the fossil record, they are of extreme interest because of their central position in the evolution of the Crustacea. Cephalocarids are the most primitive known crustaceans, as judged by their high degree of serial homology and the generalized nature of their morphology. Furthermore, where the cephalocarids show similarities to members of other classes, it is to the most primitive members that the resemblance is closest (SANDERS, 8, 9; HESSLER, 5).

In no other known crustacean is there less serial specialization of the limbs. Except for reduction or loss of the last thoracic limb, all thoracopods are alike. Whereas in the Copepoda, Mystacocarida, and most of the Malacostraca, the first thoracopods are modified as mouth parts, here they are totally unmodified, and even the maxillae conform precisely to the thoracic-limb pattern, a condition unique to the Cephalocarida. In addition, the pattern expressed by the thoracic limbs is easily seen in all of the more anterior adult or larval cephalic appendages except the antennules. In contrast to the Branchiopoda, often considered quite primitive, there is little reduction of the two pairs of maxillae and the antennules. The cephalocarid antennae stand in contrast to those of the Notostraca, where they are reduced, and to those of the Anostraca, which are modified as a copulatory structure.

With exception of the adult mandibles and maxillules, all limbs share equally in trophic and locomotory functions. There is no modification for copulation other than slight alteration of the distal setae of the endopod of the seventh thoracic limb for clasping.

The skeletomuscular system displays the same high degree of serial homology seen in the external morphology. The muscles of the maxillae and thoracic limbs are alike, and the pattern found in the maxillules and mandibles are easily derived from that of more posterior appendages. The extrinsic limb muscles and the serially repetitious ventral longitudinal muscles of the trunk take origin from transverse, endoskeletal bars which are the same in all thoracic somites. The complex ventral cephalic tendon which gives rise to all the ventral extrinsic limb muscles of the head is clearly derived from the fusion of three transverse bars.

The heart and the ventral nerve cord also repeat the same form from somite to somite.

The simple cephalocarid development, in which both limbs and somites are added gradually, stands in contrast to that of other Crustacea, wherein limbs and somites are added in blocks.

The Cephalocarida are not only primitive, but probably stand near to the protocrustacean stock; it is possible to derive the limbs of all classes of crustaceans from a cephalocarid type of limb. With *Lepidocaris* as an intermediate, the thoracic limbs of living branchiopods result from the loss of the endopod and shifting of the exopod and pseudepipod. (This conclusion is in great contrast to the classically held notion of the composition of the branchiopod limb.) The thoracic limbs of copepods may have a similar origin. The head appendages of calanoid Copepoda, Mystacocarida, cladocopan Ostracoda, and larval Cirripedia bear strong similarity to those of larval Cephalocarida. The appendages of adult Eumalacostraca bear little resemblance to those of the Entomostraca. However, during early larval stages of euphausiids and pennaeids the appendages show close similarity to those of the cephalocarids. During later development of these groups, the cephalocarid-like larval limbs are altered through secondary replacement of parts or profound modification, to form the typical, adult, malacostracan appendages. Thus the adult morphology of these forms is clearly secondary. The form of the leptostracan thoracic limb is quite similar to that of the cephalocarid.

Many parts of the cephalocarid musculature and its skeletal support are generalized in form. For example, the pattern of trunk muscles in the various crustacean classes is diverse, yet in all they can be derived easily from the generalized condition found in the Cephalocarida. The basic processes involved in these changes are loss of connection of muscles with the body wall and endoskeleton, or shifting of the position of these origins, commonly to form spiraled muscular bundles. Even the complex caridoid musculature in the abdomen of the Eumalacostraca can be derived from a cephalocarid-like condition. The caridoid musculature is found in the basic members of the Syncarida, Eucarida, and Peracarida, that is, in all Eumalacostraca except the Hoplocarida. The latter group, which is thought to have branched off early in eumalacostracan evolution, has an abdominal musculature like that of the caridoid facies, but simpler in form and reflecting an earlier grade of evolutionary development. The hoplocarid condition can in turn be derived from a cephalocarid-like musculature, such as is found in the most primitive malacostracans, the Leptostraca.

CANNON (3), in a detailed study of the feeding mechanisms of the Branchiopoda, postulated the ancestral type from which the various branchiopod feeding types could be derived. This theoretical ancestor corresponds closely to the actual condition in the Cephalocarida. In the cephalocarids the food groove is not invaginated into the trunk as in the Anostraca and Diplostraca. There is no specialization among the protopodial endites such as occurs in all Branchiopoda. The enditic setae are relatively unspecialized, suited only for the retention of coarse particles, not a highly developed filter bed, as in the Diplostraca and Anostraca.

SYSTEMATIC DESCRIPTIONS

Class CEPHALOCARIDA Sanders, 1955

Body consisting of cephalon, thorax with eight somites, and abdomen with 12 somites; cephalon and thorax with well-developed pleura. Labrum projecting strongly backward to form atrium oris. Telson bearing caudal furca. Thoracic limbs and maxillae all similar, mixopodial; foliaceous protopods bearing several endites; multisegmented, ambulatory endopods; jointed paddle-like exopods; unjointed, paddle-like pseudepipods. Eighth thoracic limb reduced or absent. Maxillules reduced but of thoracic limb type. Mandibles palpless in adults, but with biramous palp in larvae. Antennae biramous, with large, multisegmented exopods. Antennules uniramous. Total size of adult about three to four mm. *Rec.*

Extant representatives of the Cephalocarida are found on the northeastern and western coasts of North America, in the Caribbean, in the Pacific off Japan, and in the South Pacific (N. Caledonia) (Delamare Deboutteville, personal communication).

Tesnusocaris goldrichi BROOKS is the only known fossil crustacean included in the Cephalocarida (2). Later BIRSHTEYN (1) made this species the basis for a new cephalocarid order, named Enantiopoda. This species should be rejected from the Cephalocarida. The two pairs of maxillae are too greatly reduced, being reminiscent of the Branchiopoda in this respect. The entire structure of the thoracic limbs is so different as hardly to allow comparison with the cephalocarid condition.

Order BRACHYPODA Birshteyn, 1960

Characters of subclass. *Rec.*

BIRSHTEYN mistakenly included the maxillae with the thoracic limbs. That they are truly maxillae is shown by the presence of openings for the maxillary glands.

Family HUTCHINSONIELLIDAE Sanders, 1955

Characters of type genus. *Rec.*

Hutchinsoniella SANDERS, 1955, p. 61 [**H. macracantha*; OD]. Eighth thoracic somite with limb and well-developed pleura. Basal segment of endopods of thoracic limbs clearly defined from protopods. Ventral comb on abdominal somite preceding telson. *Rec.*, NE.N.Am.——FIG. 40-42. **H. macracantha*; 40, ventral view of adult showing morphological features, ×64 (9); 41, *A, C,* *E-G,* limbs of adult, ×150 (*A,9; C, E-G,* Hessler, n); 41,*B,D,* limbs of larva, ×170 (8); 42, stage-1 metanauplius, ×95 (9).

Family LIGHTIELLIDAE Jones, 1961

Characters of type genus. *Rec.*

Lightiella Jones, 1961, p. 32 [**L. serendipita*; OD]. Eighth thoracic somite without limb, and with pleura weakly developed or absent. Basal segment of endopods of thoracic limbs not defined from protopods or defined only posteriorly. No ventral comb on abdominal somite preceding telson. *Rec.,* W.N.Am.-Carib.

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BRANCHIOPODA

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[Chapter submitted June, 1956; revised 1961, 1963]

CONTENTS

INTRODUCTION

The phyllopod crustaceans (exclusive of the malacostracan phyllocarids) have been classified until recently in five orders; Notostraca, or tadpole shrimps; Conchostraca, or clam shrimps; Cladocera, or water fleas; Anostraca, or fairy shrimps; and Lipostraca, known only as fossils. In general, all are characterized by the nature of their swimming appendages, which are flattened, leaf-like, and lobate (83). Two additional orders —Kazacharthra and Acercostraca—now are known from the fossil record, both with affinities to the Notostraca.

Besides presence of a head and trunk, gross morphological features of the better-known branchiopod orders can be summed up briefly as follows (83, p. 4; 107, p. 324). Anostraca are characterized by a cylindrical body. Notostraca typically have a dorsoventrally depressed shieldlike carapace that covers most of the body. Conchostraca have a body enclosed by a bivalved carapace that is laterally compressed. Cladocera have an obscurely segmented laterally compressed body, covered by a folded carapace, and possess a postabdomen. All mentioned orders have a telson and caudal rami except the Cladocera, which have a postabdomen and claws. Like the Anostraca, the Lipostraca lack a carapace. A considerable range in size, as indicated by length, is seen within the orders: Anostraca, 7 to 100 mm.; Notostraca, 10 to 58 mm.; Conchostraca, 2 to 16 mm.; Cladocera, 0.2 to 18 mm.; Lipostraca, adults about 3 mm. (107).

Examination of the five branchiopod orders having a carapace calls attention to certain similarities. Equivalents of the shieldlike carapace of notostracans, kazacharthrans, and acercostracans occur in conchostracans and cladocerans at one stage or another. Thus, Sars (122) showed that in the later larval stage of *Limnadia lenticularis* (conchostracan) a hood-shaped carapace occurs. It consists of two symmetrical halves without any distinct division and bears a notostracan-like posterior emargination. A line of weakness is thus marked off on the carapace and a dorsal break occurs in postlarval development that separates the carapace into two distinct valves. In the Cladocera, too, the carapace is a single folded piece (107, p. 350). Although it presents a bivalved appearance, separation into two distinct valves does not occur.

Close relationships between cladocerans and conchostracans, as noted subsequently, is indicated by the presence on cladoceran shells of the kind of surface markings (ornamentation) that is so characteristic of conchostracans. These consist of reticulations, striations, and other types of ornament (19). The morphology, anatomy, and other aspects of each order will be discussed separately, and therefore elaboration of these topics is deferred.

BRANCHIOPOD TAXONOMY

Linder (70) has presented convincing evidence and argument in support of a regrouping of the Branchiopoda according to affinities found to exist between the orders. His proposed arrangement, which divides the Conchostraca into two "tribes" named Laeviscaudata and Spinicaudata, here designated as suborders, and which isolates the Anostraca and Lipostraca in a separate series equivalent to a superorder, is followed in the *Treatise*. Modifications introduced here include placing cyzicid-like fossil forms in the Spinicaudata and adding two fossil orders.

An alternate grouping used by Pennak (107), which is stated to be accepted by the majority of carcinologists, recognizes two "divisions" ("superorders" of F. Linder) of the subclass Branchiopoda; these are named the Eubranchiopoda and the Oligobranchiopoda. The Cladocera are placed in the latter division, whereas the Anostraca, Notostraca, and Conchostraca are assigned to the former. This grouping fails to take account of the fossil orders and, further, it is insensitive to sharp distinctions that separate the Anostraca from all other branchiopod orders.

A superior arrangement in three superorders which expand Linder's grouping has been proposed by Brooks (17, 19). The superorder Diplostraca Gerstaecker, 1866 (=*Onchyura* Eriksson, 1934) was erected to embrace the orders Conchostraca and Cladocera. Brooks pointed out that the "close similarity between the structure of adult Cladocera and the larvae of certain conchostracans strongly suggests that the Cladocera are neotenic (paedomorphic) derivatives of some early conchostracan." He also noted that "the fossil Lipostraca are very much more like the Anostraca than they are like the other orders." Accordingly, he proposed that a superorder (unnamed by him) should be defined to embrace the last two-mentioned orders (equal to Linder's Series B) and that the Notostraca alone should constitute a third superorder. The two recently discovered fossil orders, Kazacharthra and Acercostraca, would have to be associated with the Notostraca in such a superorder. In my opinion this indicates the basic soundness of Linder's grouping and does not accord with the classification used by Pennak.

An outline of classification of the branchiopod crustaceans adopted in the *Treatise* is given in the tabulation on pages *R*112-113, which shows suprageneric taxa down to subfamily rank, accompanied by records of geologic occurrence and numbers of included genera. The last-mentioned data provide information on numbers of subgenera additional to nominotypical ones which are differentiated in some family groups, as well as numbers of doubtfully recognized genera.

SYSTEMATIC DESCRIPTIONS

Class BRANCHIOPODA Latreille, 1817

[=order Branchiopoda Latreille, 1817, p. 59; 1829, p. 149; order Phyllopoda Latreille, 1825, p. 301] [*emend.* G. O. Sars, 1867; raised to subclass, Calman, 1909] [Assignment of taxonomic rank in this section is a responsibility of the editor and is based on consistency with other major divisions of the Crustacea]

Crustacea in which carapace may form dorsal shield or bivalve shell, or may be entirely absent; number of trunk somites varying greatly; posterior part of trunk without limbs and usually ending in caudal furca; antennules generally reduced and unsegmented; mandibles lacking palp or with only vestige of one; maxillae reduced or absent; trunk limbs, which vary greatly in number, generally of uniform structure, rarely pediform, generally foliaceous and lobed; position of genital apertures varies greatly; paired eyes rarely absent; development usually with metamorphosis; young hatched in nauplius or metanauplius stage (21). *L.Dev.-Rec.*

Subclass CALMANOSTRACA Tasch, new subclass

Carapace broad shieldlike, with or without telson-furca development. *L.Dev.-Rec.*

Order NOTOSTRACA Sars, 1867

[*nom. transl.* Calman, 1909 (*ex* suborder Notostraca Sars, 1867)] [=tribe Monostraca Gerstaecker, 1866; tribe Notophylla Stebbing, 1902]

[For specific technical advice on notostracans I am indebted to Dr. James E. Lynch, of the University of Washington, and to Dr. Alan Longhurst, of Bedford College, University of London. Mr. Wilhelm Bock, of the Philadelphia Academy of Natural Sciences, and Prof. B. F. Howell, Princeton University, provided some needed literature.]

Body elongate, more or less covered dorsally by broad, shieldlike (univalve) carapace, attached anteriorly to head, tapering backward and ending in long, caudal furca; posterior somites varying in number lack legs (apodous). Two sessile compound eyes occur close together on dorsal surface of head, with minute obscure ocellus in front of them. Antennae greatly reduced or absent. Body appendages (legs), 35 to 71 pairs, of which 29 to 52 are postgenital; first pair with endites filiform, commonly very long. Rami of caudal furca very long, multiarticulate. Genital ducts open on 11th somite. Ova retained in capsular ovisac formed by 11th pair of trunk limbs. No special prehensile organs occur in males. Young hatched in the metanauplius stage (7, 71, 74). *U.Carb.-Rec.*

ANATOMY

The appendages of notostracans, like those of other branchiopods, appear to be leaflike. Due to this feature, the name Phyllopoda (leaf feet) was originally given to the entire group (Latreille, 1803).

Tadpole shrimps have a shieldlike, arched carapace (Fig. 43,*1*; 44,*2*). This "univalve" ends in a posterior emargination (notch or sinus) that may or may not be denticulate. On its outer surface, the carapace bears sessile **compound eyes,** a **median eye,** and a dorsal, **nuchal organ** (71, pl. 7, figs. 3-6; 74, fig. 4) (Fig. 43,*1b*). Also visible on the surface is a cervical groove. Behind the groove, a carina extends along the mid-dorsal line to the posterior emargination. The arched carina may bear short spines along its length. In flattened specimens these appear as a ladder-like series of flattened spines. Behind the cervical groove, coiled tubes of the shell gland extend diagonally on either side of the carina. These glands serve as excretory organs and empty at the base of the maxillae. They can be seen through the dorsal surface of the carapace and may be preserved as internal casts (e.g., *Triops beedei,* Fig. 43,*2*).

Exclusive of the terminal telson, notostracans have 25 to 44 body somites (or body rings) (71). These rings may bear more than two pairs of legs each and toward the rear some bear ten or more pairs. All body rings are of comparable length. The **thorax** consists of the first 11 rings, the remainder constituting the abdomen.

In all species of the genus *Triops* the supra-anal plate is absent, excepting *T. cancriformis,* in which it is rudimentary (74). In species of *Lepidurus* it is invariably present and prominent.

The notostracan **telson** is heavily chitinized.[1] This can account for its occurrence as a fossil in the sparse record of the order.

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[1] A. G. Richards (1951, Table 2) indicates that *Triops* gives a positive test for chitin in its body wall (see footnote, p. *R*168).

It is difficult to determine a "normal" adult size in notostracans because of the wide range of variations within species. The usual adult size for all species of *Triops* is between 15 and 30 mm. for carapace length. A "giant" species has been reported from Siberia. Large individuals up to 40 mm. in carapace length are also known elsewhere. In general, species of *Lepidurus* tend to be smaller than those of *Triops*. The growth of the carapace is isometric in *Triops,* that is, the ratio of carapace length to total body length remains constant during growth (74, p. 6, fig. 1).

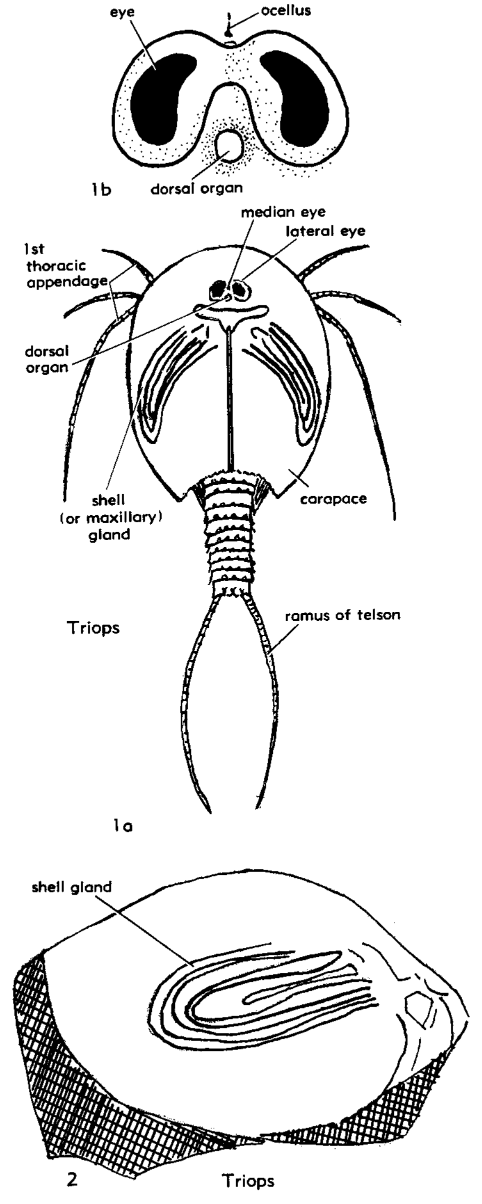

FIG. 43. Morphological features of living and fossil notostracans.——*1.* **Triops cancriformis* (SCHAEFFER); *1a,* complete individual seen through carapace, enlarged (15); *1b,* detail of eye region, enlarged (74).——*2. T. beedei* (RUEDEMANN), shell gland and cervical fold on half of carapace, ×3.5 (170a).

REPRODUCTION

Notostracan populations in which males are absent have generally been referred to as parthenogenetic (72). Recent cytological work, however, raises questions as to the validity of this assumption. LONGHURST (72, 74) confirmed earlier findings of H. M. BERNARD, that in *Triops cancriformis* and some species of *Lepidurus,* the gonads are ovotestes. Thus, the assumed parthenogenetic females are actually hermaphrodites, self-fertilizing, and hence capable of laying viable eggs in the absence of males (74, fig. 12). This finding is confirmed by chromosome number counts (74, table 2, fig. 14).

The role of hermaphroditism in the distribution of notostracans is discussed below. Note may be made that this reproductive mechanism is rare in Crustacea (72). Other notostracan species appear to be characterized by an invariable bisexuality.

In the female, the limbs of the genital somite (11th thoracic ring) are modified to form brood pouches for carrying eggs ("oostegopods" of PEARSE). Notostracans, like other phyllopods, after leaving the eggs, pass through a free-swimming larval stage. As a newly hatched metanauplius, *Triops cancriformis* has an oval body in which one can discern the beginnings of five trunk somites.

SPECIES VARIATION

Many notostracan species are cosmopolitan and exhibit a wide range of variation. For example, all North American and some South American forms of the living *Triops* have recently been assigned to a single species (71). A similar tendency lumps together different species of *Lepidurus.* Study of LINDER's monograph (71) of North American notostracans indicates that considerable variation will be encountered in the following characteristics (both in fossil and living forms): number of body rings, total number of legs on a particular ring, number of leg-bearing abdominal rings, number of legless abdominal rings, form of the supra-anal plate, and spines on dorsal side of the supra-anal plate.

Longhurst systematically considered every character previously employed to separate species of *Triops* and found that the most important diagnostic character of this genus is armature of the telson (74, p. 18-23, fig. 5). The only other valid characters recognized by him were: presence or absence of the maxillae, arrangement of the eyes, and nature of the dorsal organ. He ruled out as invalid characters that can be correlated with number of body somites or sex of an individual.

Lepidurus apus has a larger geographic range than any other known notostracan, for it is found in Europe, exclusive of Britain, North Africa, Palestine, Asia Minor, Russia, North and South America, New Zealand, and Australia (74, p. 50). Despite this cosmopolitan distribution, very little morphological variation has been observed in its entire range. Longhurst recognized five geographic races of this species.

A remarkable homogeneity in almost all characters seems to mark species of *Triops* regardless of geographic distribution. Even in a character like protein specificity, determined by spectrographic study of the blood, little individual variation has been found to exist between apparently different populations (74, p. 29-30, table 1).

ECOLOGY

Much confusion in the literature relates to the ecology of notostracans. Most recent work indicates that the ecological differences beween *Triops* and *Lepidurus* are "slight" (74). Between species of *Triops* almost no difference is found, although in some places (e.g., western Australia) this does not hold. Only *L. arcticus,* from the circumpolar Arctic region, differs from all other notostracans.

HABITAT

Species of *Triops* are known from temporary and brackish waters all over the world. *T. cancriformis* does not extend beyond 60°N (74, p. 42). The annual precipitation appears to affect the distribution of two species of *Triops* in North Africa, *T. cancriformis* being found in steppe and substeppe areas where the annual rainfall is 300 mm. (steppe) or 300 to 500 mm. (substeppe), whereas *T. granarius* is found only in substeppe regions. Species of *Triops* (e.g., *T. longicaudatus*) are also known from rice fields in California and Japan, where they uproot rice seedlings.

A recent collaborator of mine, Dr. J. R. Zimmerman (formerly of Wichita State University), conducted a survey of Kansas-Oklahoma ponds in the general area of the Leonardian clam-shrimp-bearing beds. During the summers of 1958 through 1960 he sampled some 500 ponds and in only two found living *Triops cancriformis*—one observed in the summer of 1958 (Seward County, Kansas), and the other in the summer of 1960 (Sumner County, Kansas). In both occurrences he reported that notostracan ponds—some 180 miles apart—were clear, with soft mud bottoms, and not more than one foot deep. Only in Seward County were conchostracans co-inhabitants with *Triops.*

Triops has been found in large temporary lakes, as well as in persistent saline lakes of the Tibetan Plateau (74, p. 35). In general, species prefer temporary waters that dry out with some regularity. The eggs normally require a period of desiccation to hatch out, although exceptionally *Triops* eggs hatch without prior desiccation.

The clearest picture of the "slight" ecological difference between *Triops* and *Lepidurus* derives from study of their distribution in western Australia (74). Here, *Lepidurus* is restricted to the southwestern coastal belt, which enjoys a regular winter rain. On the contrary, *Triops* is confined to the arid interior, where rainfall is slight or absent.

In North America, *Lepidurus* is known from temporary alkaline pools. *L. lynchi* occurs in muddy lake water 2 feet deep. *L. arcticus* predominates in shallow lakes of melted snow and ice and is reported to show remarkable growth in a few weeks. Eggs of this species from Iceland were observed to hatch after desiccation. This contradicts earlier reports by Brauer and others that *Lepidurus* eggs cannot withstand desiccation. In Europe, *Lepidurus* species are often found in peat bogs and moors that are always under a cover of clear water (7). Humic acids and noxious gases are apparently so diluted or dispersed that they do not interfere with normal egg development.

TEMPERATURE AND pH

In Algeria it was observed that *Triops cancriformis* tolerates a pH range of 7.4 to 7.6 and a temperature range of 14° to 19°C. *Lepidurus lubbocki* (=*L. apus*) had a pH range of 6.4 to 6.6 and a temperature range of 10.5° to 18°C. (Gauthier, in 83). While the temperature ranges overlap, it is apparent that in Algerian pools, *L. apus* is more readily able to survive under lower pH conditions.

Mathias subjected *Triops cancriformis* to a temperature of 80°C. while dry and to 42°C. while in contact with water, without observable adverse effects (83). This bears out Longhurst's report (72) that the Notostraca grown by him in the laboratory under variable conditions of temperature, food, and vessel size, all remained "remarkably uniform" morphologically (74).

FOOD

Members of both genera are detritus-feeders and stir up the bottom detritus with the tips of their thoracic limbs prior to filtering it. Besides consuming microscopic organisms, they have been known to gnaw on the living and dead bodies of larger organisms, such as earthworms, mollusks, and even dead tadpoles. They will also tackle frogs' eggs. Trusheim has reported evidence of cannibalism in fossil forms of *Triops* (149).

LOCOMOTION, HABIT, AND POPULATION DENSITY

Individuals of both genera have a choice of varying modes of locomotion. They can crawl, swim, or clamber. A good deal of the time tadpole shrimps creep or burrow superficially in the soft substrate of their respective habitats. This comes about because they inhabit temporary water basins. During drought periods they can burrow or bury themselves in the bottom mud. In such muds their numbers may be very great. In a shallow, dried depression about 20 feet in diameter in Nebraska, Pearse estimated that almost a half-bushel of dead *Triops* bodies were spread over the bottom. Considering their average size of 15 to 30 mm., this denotes a high population density. Equivalent populations are known from the fossil record. Trusheim found literally thousands of *Triops* fragments in thin beds of Middle Keuper (Triassic) age (148).

These dried Recent muds often contain a varied fauna capable of being awakened to life by the addition of water. The material Longhurst studied came from dried muds from phyllopod pools all over the world. While many of the samples received by him contained no viable eggs, quite a number did (74). An example is on record of one sample of dry mud from East Africa that yielded active larvae when wetted, although it had been kept dry for 15 years.

DISTRIBUTION

Still another effect arises from the drought-resistant habit. Muds of desiccated narrow, shallow temporary basins can adhere to the feet of birds that visit them to feed on notostracans and other fauna (e.g., starlings, gulls, Arctic terns, 74, p. 39), or they can be blown great distances by winds or carried by other means. Longhurst has referred to this as "passive distribution." In this way one can easily account for the cosmopolitan distribution of many notostracan species.

Coupled with "passive distribution" is another notostracan attribute, namely, the occurrence of hermaphroditic populations. Thus, hermaphrodites that were probably passively transported are credited with the postglacial extension of the range of *Triops cancriformis.* This reproductive mechanism may also explain the westward extension of *T. longicaudatus* across the Pacific (74, p. 40). This seems to be indicated since no males have been reported from Pacific notostracan populations.

GEOLOGIC OCCURRENCE

Fossil notostracans are closely similar to living forms and represent a stagnant group, in an evolutionary sense (73). Thus, *Lepidurus stormbergensis,* from the Triassic of South Africa, is very close to the Pleistocene *L. arcticus* and living representatives of this species (8, 50). Chernyshev's Lower Cretaceous notostracans from Turkestan are slight variants of *Lepidurus* species (25).

Although the fossil record of *Triops* (=*Apus*) is more extensive than that of *Lepidurus,* most fossil material parallels living forms. Trusheim's remarkable collection from a thin green shale and sandstone zone (Middle Keuper) astonished him by the near-identity of fossils when compared with the living *T. cancriformis* (149). He was so intrigued by notostracans that he raised living forms in an aquarium for a year to study their life cycle and habits and his study provides the most complete information available on the fossil record of *Triops* (148, 149). By the nature of preservation and the condition of detachment of carapace and body parts, Trusheim inferred that fossil *Triops* had a predilection for cannibalism (148, p. 200).

Schimper's species *Triops antiquus,* from the Bunter Sandstone (L.Trias.) is identical with living *Triops,* as Soergel's species from Keuper (U.Trias.) beds appears to be. Soergel originally assigned his material to Schimper's *Apudites,* suggesting that, like Schimper's species, it too belongs to *T. cancriformis.* Ruedemann's *T. beedei,* from Permian rocks of Oklahoma, is also most likely assignable to living *Triops,* although this cannot be proved from a mere shell gland. This leaves only one fossil species at present that eludes definite assignment to living *Triops*; it is GOLDENBERG'S *T. ornatus*, from the Stephanian (U.Carb.) of Germany. GUTHÖRL removed this species, which had been placed with cladocerans, to the notostracans. LONGHURST (personal communication, June 1, 1955) could not place GUTHÖRL'S specimens of *T. ornatus* in a modern species because available illustrations were inadequate. In view of the known identity to living forms of other *Triops* fossils, it is quite likely that *T. ornatus* will be found to be a synonym for *T. cancriformis.*

Family TRIOPSIDAE Keilhack, 1910

[=Apodidae BURMEISTER, 1834; Lynceitidae COPELAND, 1957]

Shell shieldlike; abdomen formed of more than 15 rings; terminal spine of last ring long, movable, and articulated. *U. Carb.-Rec.*

Triops SHRANK, 1803 [**Apus cancriformis* SCHAEFFER, 1756, p. 131; OD] [=*Apus* SCHAEFFER, 1756 (pre-Linnaean) (*non Apus* CUVIER, 1798, *pro Apos* SCOPOLI, 1777; *nec Apus* SCHOCH, 1868); *Thriops* GHIGI, 1921; *Lynceites* GOLDENBERG, 1870]. Carapace smaller than that of *Lepidurus,* leaving more somites exposed; no telsonic supra-anal plate; first pair of legs with very long endites; commonly more than 8 apodal somites. *U.Carb.-Rec.,* cosmop. [Fossil species include the following forms: (1) *T. ornatus* (GOLDENBERG), represented by impressions of broadly oval dorsal shield (4 by 4.5 mm.), weakly arched, with elevated keel (49), U.Carb.(Stephan.), Ger.; (2) *T. beedei* (RUEDEMANN), with shell gland visible on interior of carapace, 6 urinary tubes represented by pair of concentric furrows (median and outer longitudinal), and cervical fold (115), Perm., USA(Okla.); (3) **T. cancriformis,* =*Triops cancriformis minor* (TRUSHEIM), represented by some 400 carapace fragments, without marks of body parts, 70 carapace-and-body fragments, 30 fragments of abdomen with impressions of furcal setae, eggs, carapace margins, not distinguishable from Recent *T. cancriformis,* U.Trias.(M.Keuper), Ger.; (4) **T. cancriformis,* =*Apudites* sp. SOERGEL, L.Trias.(Bunter), Ger.; (5) **T. cancriformis,* =*Apudites antiquus* SCHIMPER, with compound and median eyes visible on carapace and paired caudal filaments; L.Trias.(Bunter), Ger. (Vogesian Mts.)].——FIG. 43,*1*. **T. cancriformis,* Rec., Eng.; *1a,* dorsal view, ×1.3 (15); *1b,* detail of eyes, dorsal organ, and ocellus, enlarged (74). ——FIG. 43,*2*. *T. beedei* (RUEDEMANN), Perm., USA(Okla.); shell gland and cervical fold on half of carapace, ×3.5 (170a).

Lepidurus LEACH, 1819 (p. 539) [**Apus productus* BOSC, 1802; OD] [=*Bilobus* SIDOROV, 1924; *Prolepidurus* CHERNYSHEV, 1940]. Carapace very large, leaving only few somites exposed; last somite (telson) produced as thin, flat, supra-anal plate between caudal filaments. First pair of legs with comparatively short endites; never more than 8 apodal somites. *Trias.-Rec.,* cosmop.——FIG. 44,*7*. *L. lynchi* LINDER, Rec., USA; telson, body rings and supra-anal plate, ×8.5 (71).——FIG. 44,*2*. *L. apus* (LINNÉ), Rec., cosmop.; dorsal view, ×1.5 (74). [Fossil species include the following forms.] ——FIG. 44,*8*. *L. stormbergensis* HAUGHTON, distinguished by pointed or well-rounded supra-anal plate with well-marked mediodorsal keel (50), Trias.(Stormberg Series), S.Afr.; supra-anal plate and caudal filaments, ×4 (50).——FIG. 44,*5,6*. *L. arcticus* (PALLAS), characterized by very small supra-anal plate (74); *5,* Pleist.; ? ♀ telson and supra-anal plate from Isle of Man, ×50 (162); *6a,b,* Pleist.-Rec., Eng., and circumpolar, Rec. ♀ and ♂ telson and supra-anal plate, ×50 (74). ——FIG. 44,*1*. *L. daja* CHERNYSHEV, with wide, tongue-shaped supra-anal plate (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and caudal filaments, ×2 (25).——FIG. 44,*3*. *L. schewija* CHERNYSHEV, with supra-anal plate larger than telson and constricted in anterior part while enlarged near middle (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and caudal filaments, ×1.5 (25).——FIG. 44,*4*. *L. kuenga* CHERNYSHEV, with very small telson and acutely triangular supra-anal plate equal in length to telson (25), L.Cret., Turkestan (Kelmensk Mts.); supra-anal plate and telson, ×6 (25).

Order KAZACHARTHRA Novozhilov, 1957

Six pairs of crustacean-type appendages. Cephalothorax more or less semicircular, incurved at front and rear, or with elongated leaf form, with or without spines on margins; two ocular tubercles bear paired contiguous eyes. Abdomen with two longitudinal rows of spines on dorsal and ventral surfaces; lateral margins of somites with pleura or spines; segmentation visible also on ventral anterior portion of abdomen; number of abdominal somites variable, ranging from 32 to 40. Telson oval or more or less round, with spines on lateral margins and dorsal and ventral surfaces, with or without cerci. Antennae unknown (97). *L.Jur.(Lias.).*

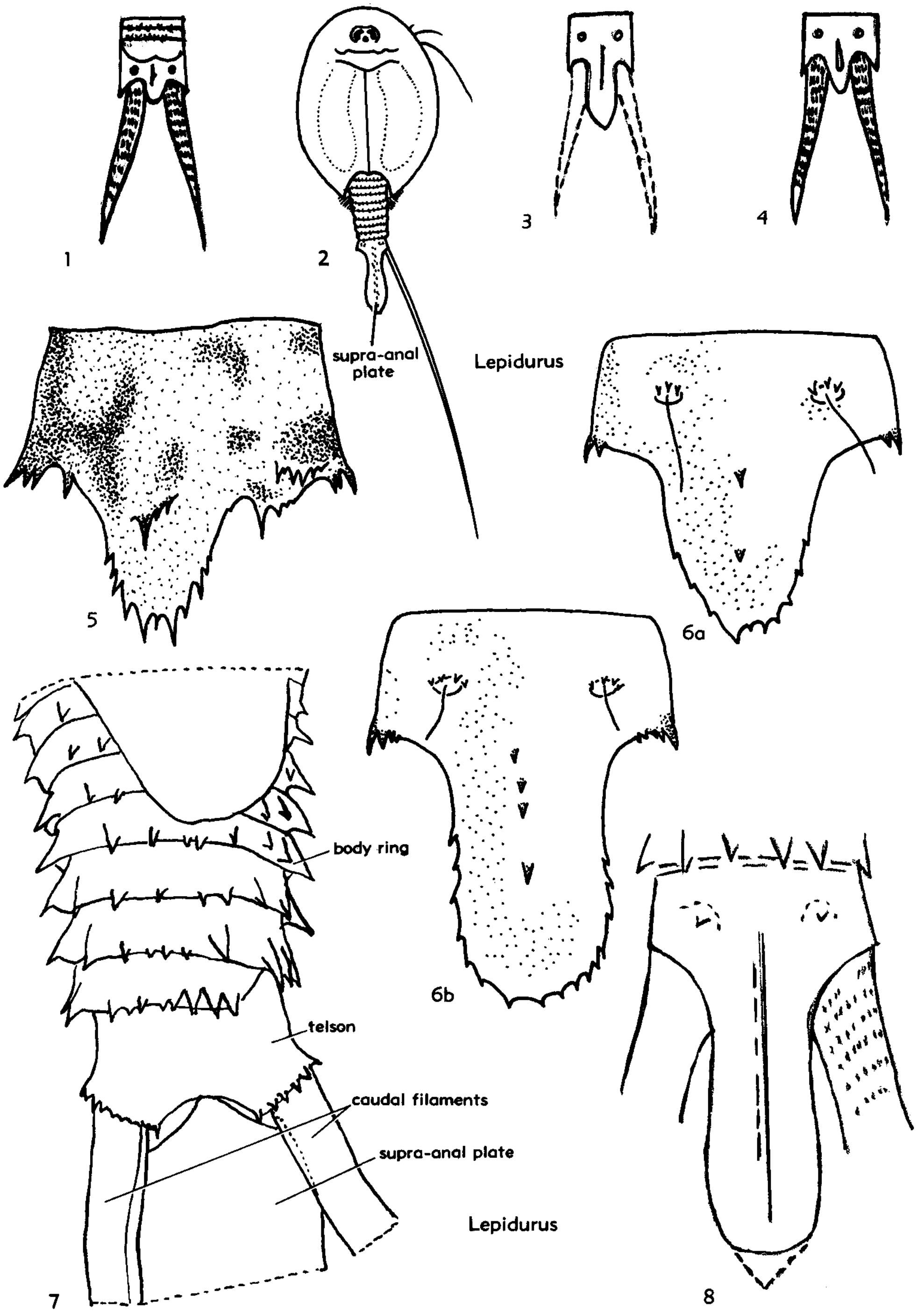

FIG. 44. *(Continued on facing page.)*

ANATOMY

NOVOZHILOV (100, p. 266) has observed that in ventral view, the mouth parts of *Almatium,* a genus classed by him in the order Kazacharthra, are of the same type as in true notostracans—that is, they have the general form of a horseshoe that reaches the posterior margin of the cephalothorax. Study of published photographs shows (100, pl. 7, fig. 4) the presence on one specimen of a labrum, antennule, and three somites apparently displaced anteriorly, somites which could correspond to the paragnathum, maxillule, and maxilla of notostracans; another figure (100, pl. 7, fig. 5) shows a labrum, antennule, and ?mandible, which are notostracan-type mouth parts.

For the appendages, NOVOZHILOV (100, fig. 2) provided a line drawing, which indicates that these possess three branches (proepipodite, epipodite, exopodite) in addition to several endites. The number of short appendages attached to the anterior portion on the ventral face of the abdomen is fewer than found in notostracans. In the Kazacharthra NOVOZHILOV has noted that the segmentation of the anterior part of the abdomen is complete on two sides—dorsal and ventral. Genera of the Kazacharthra are also distinguished by structure of the telson, which, though possessing cerci, lacks a terminal segment. In certain genera *(Panacanthocaris)* the telson has a complex structure.

D. G. SHAROV (cited 100, p. 266), who helped in collecting materials from the Sajkan Mountains, is of the opinion that two features—cerci on the telson and similarity of appendages—warrants assignment of the kazacharthrans with notostracans. NOVOZHILOV explained that he rejected the "presence of cerci" as a character having taxonomic importance, since they occur in many arthropod orders, as well as in the Trilobitomorpha. As for swimming appendages, notostracan resemblances lose taxonomic importance in NOVOZHILOV's view because the Kazacharthra lack the greater number of short appendages found in notostracans.

It is certainly clear that in shield characteristics, mouth parts, appendage structure, and some abdominal features, the Kazacharthra rather closely resemble notostracans. Only additional material and further study can determine if the smaller number of short appendages and variable characteristics of the telson merit assignment of ordinal rank.

As yet, evidence on which the order is based has not been adequately analyzed by specialists in the study of crustacean evolution. Hence, the order is simply reported here for completeness.

GEOLOGIC OCCURRENCE

Specimens of the Kazacharthra are so far known only from the Ketmen and Sajkan Mountains of southeastern and northeastern Kazakhstan. *Ketmenia gusevi* CHERNYSHEV (1940) was originally based on poorly preserved fossils, but a fortunate discovery in 1957 by L. F. BELZHANKIN yielded abundant new and better-preserved specimens which permitted NOVOZHILOV (100) to distinguish a new genus *(Almatium),* with the above-named species as type. According to NOVOZHILOV, *Almatium* is based on more than 200 cephalothoraxes, dozens of abdomens (some with telson attached), as well as isolated body parts (e.g., labra, mandibles, appendages). In addition, parts of several new genera were more

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(Continued from facing page.)

FIG. 44. Morphological features of living and fossil notostracans.——*1. Lepidurus daja* CHERNYSHEV, showing wide, tongue-shaped supra-anal plate and caudal filaments, ×2 (25).——*2. L. apus* (LINNÉ), showing eye region, dorsal shield with shell glands outlined, body rings, supra-anal plate and caudal filament, ×1.5 (74).——*3. L. schewija* CHERNYSHEV, with supra-anal plate larger than telson and constricted in anterior part while enlarged near middle, ×1.5 (25).——*4. L. kuenga* CHERNYSHEV, with very small telson and acutely triangular supra-anal plate equal in length to telson, ×6 (25).——*5. L. arcticus* (PALLAS), characterized by very small supra-anal plate, ×50 (74).——*6. L. arcticus* (PALLAS), *6a,b,* ♀ and ♂ telson and supra-anal plate, ×50 (74).——*7. L. lynchi* LINDER, showing telson, body rings and supra-anal plate (spines omitted on caudal filament), ×8.5 (71).——*8. L. stormbergensis* HAUGHTON, characterized by pointed or well-rounded supra-anal plate with well-marked mediodorsal keel, ×4 (50).

recently made available. The finding of abundant fossil remains of any branchiopod is always of great interest and where a new order seems to be indicated, such discoveries are noteworthy for the light they may shed on branchiopod evolution and ultimately on crustacean evolution also.

The lithology of the Jurassic beds yielding specimens of the Kazacharthra is sketchily given by Schultz (cited 97, 1957) for the Kyzyl-Tam ravine section, in which Bed 3, bearing the crustacean fauna, occurs 120 m. above the base. It overlies a bed of alternating red and gray-yellow shale with beds of sandstone, conglomerates, and disseminated and bedded carbon containing a Lower Jurassic flora associated with coleopteran elytra, a deformed conchostracan valve, and a new species of cockroach. Bed 3 itself is a gray to yellow-gray slaty clay containing gypsum. Whether the crustacean fauna is found in large wheel-shaped concretions or in the slaty clay is not clearly stated.

No branchiopod occurrences have been reported from the American Jurassic, although an interesting specimen from the Sundance beds (L.Jur.) of southwestern Wyoming was recently sent to me. It is poorly preserved, but seems to be closer to conchostracans in shell morphology and surface features than to any other group.

The Kazakhstan section mentioned above includes (in argillites) an insect-bearing bed below a crustacean horizon, together with carbonized material, plant fossils, and other organic remains. This lithic-biotic evidence may be taken, together with the Sundance material, as a provocative indication. American Jurassic deposits probably contain and would yield branchiopod faunas if workers undertook to search for them. In and above carbonized beds seem to be promising places in the light of the evidence from Kazakhstan.[1]

Family KETMENIIDAE Novozhilov, 1957

[=Paratriopsidae Chernyshev, 1940, invalid name (25)]

Large flat shield, rounded, rectilinear or concave in front, with or without spines on margins. Elongated abdomen composed of three longitudinal divisions of movable somites, which have equal or nearly equal length; dorsal median part of somites separated from lateral parts by pairs of spines forming two longitudinal series; somites approximately 42, of which six are covered by shield and remainder project beyond shield. Telson of single angular, rounded or nearly rectangular somite, notched at its posterior margin, or with lateral margins curved in truncated ellipse (97). *L.Jur.(Lias.).*

Ketmenia Chernyshev, 1940 [**K. schultzi*; OD]. Anterior margin of shield rectilinear or slightly recurved; posterior margin largely concave; spines developed on posterior lateral margins. Flattened, subtriangular bulge with equal sides on median portion of shield. Large, flat telson shaped like truncated ellipse, with spines on lateral margin and on posterior margins of dorsal and ventral surfaces (25). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——Fig. 45,*5*. **K. schultzi,* Ketmen Mts.; *5a,* elongated abdomen and telson, ×2 (25, 97); *5b,* shield, ×1.25 (25, 97).

Almatium Novozhilov, 1957 [**Ketmenia gusevi* Chernyshev, 1940; OD]. Cephalothoracic shield more or less rounded, with concave posterior margin, all sides without spines; projecting ocular, rounded, anterior, with paired eyes adjoining. Appendages short, not projecting beyond limits of shield. Abdomen composed of 32 to 40 somites, with more or less long cerci (97). *L.Jur.(Lias.),* SE. Kazakh. (Ketmen Mts.)-NE. Kazakh. (Sajkan Mts.).——Fig. 45,*1*. **A. gusevi* (Chernyshev), Ketmen Mts.; shield, ×0.8 (97).

Iliella Chernyshev, 1940 [**I. spinosa*; OD]. Shield concave in front and rear, with spines along entire circumference; contour of shield in form of figure 8; raised mandibulars located in rear portion of shield; ocular tubercles, even and odd, in upper sector of shield (25). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——Fig. 46,*2*. **I. spinosa,* Ketmen Mts.; shield, ×2 (25, 97).

Jeanrogerium Novozhilov, 1959 [**J. sornayi*; OD]. Cephalothoracic shield oval, flattened, without spines on margins, or with short, small spines on posterior margin; appendages longer than cephalothoracic shield; 2 branches of somites projecting from cephalothorax. Somites of abdomen without spines on margin, at least in young individuals; number of somites 18+?15+8. Telson more or less rectangular, with long cerci (100). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——Fig. 45,*3*. **J. sornayi,* Ketmen Mts.; complete individual (reconstr.), ×2 (100).

Kungeja Novozhilov, 1957 [**K. tchakabaevi*; OD]. Shield helmet-shaped, with posterolateral growth diverging from sides; anterior margin rectilinear,

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[1] Since this was written *Cyzicus (Lioestheria)* sp. have been reported from the American Jurassic and Cretaceous.

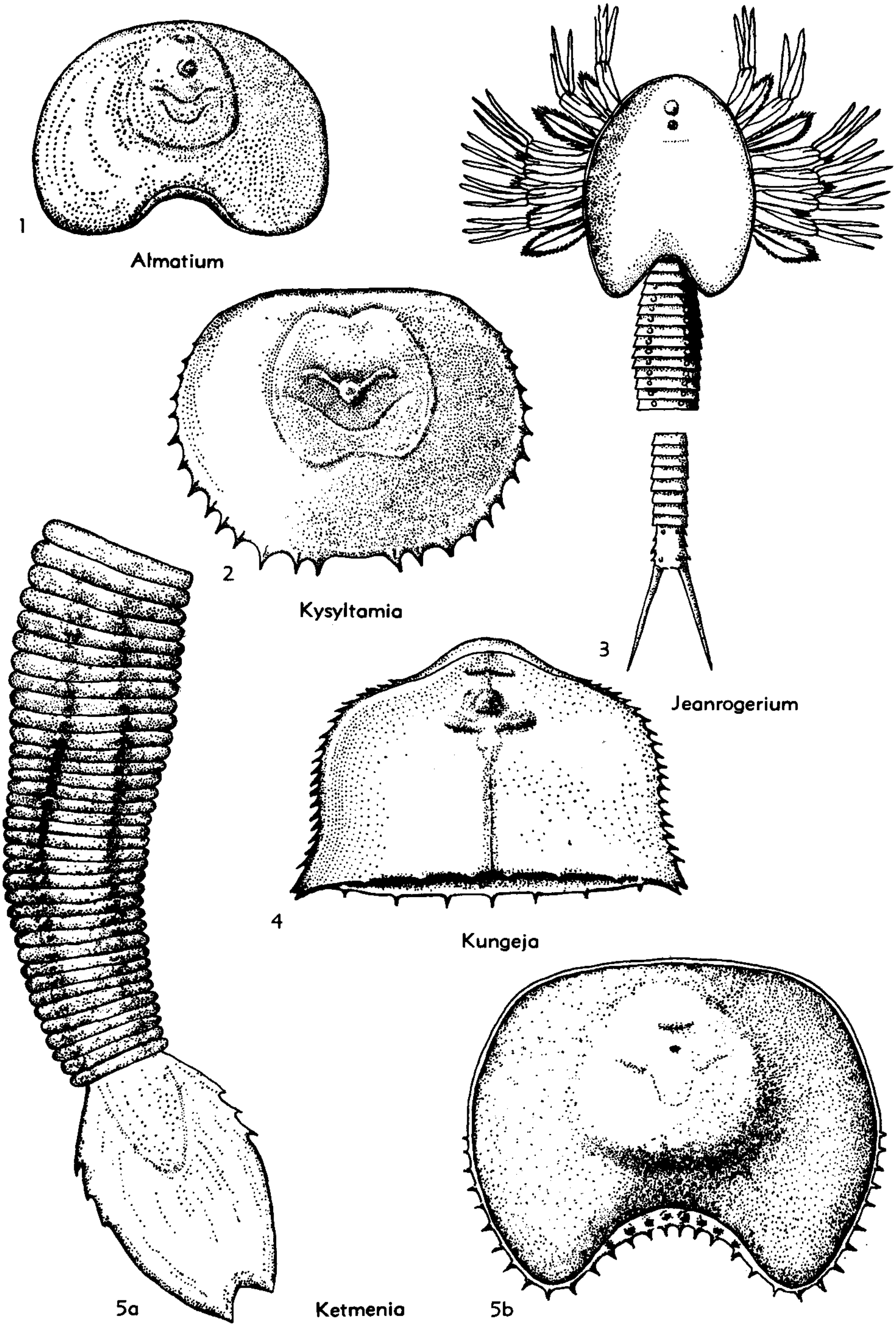

FIG. 45. Ketmeniidae (p. *R*138, *R*140).

limited by furrow or groove; spines on lateral and posterior margins; transverse equal ocular tubercles and rounded odd tubercle on rise of carapace; no flattened bulge in middle of shield (97). *L.Jur.(Lias.),* USSR(SE.Kazakh.).——Fig. 45,*4*. **K. tchakabaevi,* Ketmen Mts.; shield, ×1.1 (97).

Kysyltamia Novozhilov, 1957 [**K. tchiiliensis;* OD]. Shield irregularly oval, without concavity of posterior margin; lateral margin and posterior margins with spines. Unique ocular tubercle between mandibular rise (97). *L.Jur.(Lias.),* USSR (SE.Kazakh.).——Fig. 45,*2*. **K. tchiiliensis,* Ketmen Mts.; shield, ×1.1 (97).

Panacanthocaris Novozhilov, 1957 [**P. ketmenia;* OD]. Shield oval, with large shallow concavity on front margin, narrow on back margin, spines of different lengths on all perimeters but absent in posterior concavity; much of middle part of shield near anterior margin occupied by an ovate flattened bulge; odd ocular tubercles and raised mandibulars located in upper middle part of shield. Abdomen incompletely known. Telson large, divided into large winglike portions and bearing spines (97). *L.Jur.(Lias.),* USSR(SE.Kazakh.). ——Fig. 46,*1*. **P. ketmenia,* Ketmen Mts.; complete individual (reconstr.), ×1.1 (97).

Order ACERCOSTRACA
Lehmann, 1955

Dorsal carapace present; pair of sessile eyes; small antennae; 5 pairs of articulated thoracic appendages and numerous postgenital abdominal appendages. Like *Triops* but lacking postabdominal telson-furca development (66). *L.Dev.*

ANATOMY

Lehmann's (1955) order Acercostraca closely resembles the notostracans, in general, and *Triops* in particular, in having a dorsal carapace, a pair of sessile eyes, small antennae, and about 50 pairs of appendages. Members of this assemblage lack the characteristic notostracan telson and furca, however (55).

X rays of fossil acercostracans have revealed the intestinal tract and anus, as well as some dorsal features of the carapace, such as the sessile eyes.

The Acercostraca, lacking telson and furca, have soft-part anatomy totally confined to the carapace. It is of interest that Novozhilov's Kazacharthra also closely resemble the notostracans, differing from them in having fewer appendages and variable telson features. The Acercostraca apparently first appeared in Early Devonian time, whereas the oldest known representatives of the Kazacharthra occur in Lower Jurassic deposits.

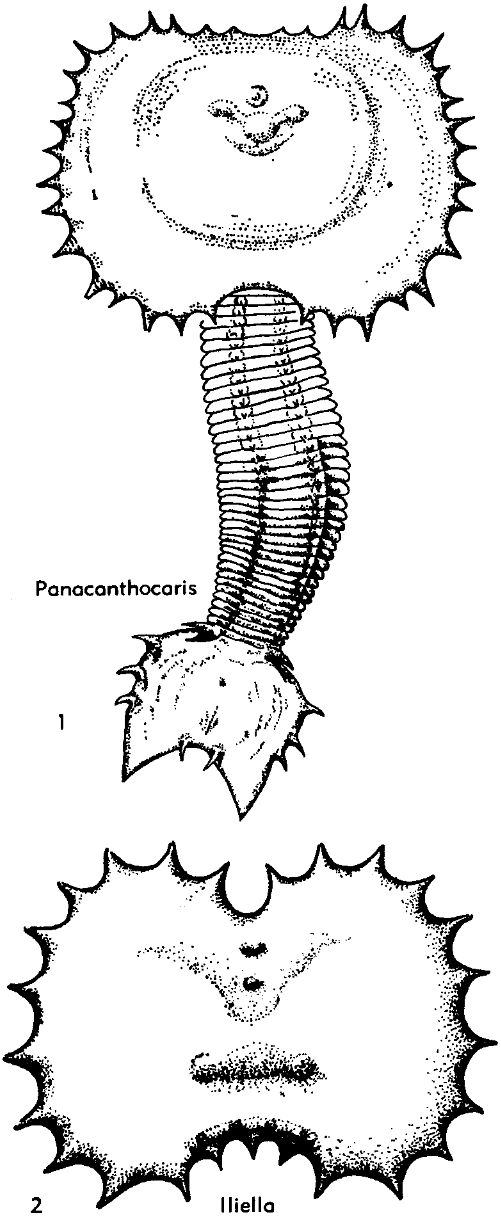

Fig. 46. Ketmeniidae (p. *R*138, *R*140).

INFERRED EVOLUTIONARY RELATIONSHIPS

Fossil notostracans are distributed from the Carboniferous to Permian and Triassic, in each of which systems *Triops* species are recorded. It thus appears that LEHMANN'S order, derived from a still older type, may have given rise to the *Triops* line in Carboniferous time. An alternative possibility is that *Triops* descended from a pre-Carboniferous ancestral type and from this same ancestor, a side line branched off leading to the Acercostraca. The Kazacharthra then might be a Mesozoic offshoot of the *Triops* line.

The relative stability of living notostracan forms, classifiable in only two genera *(Triops, Lepidurus),* indicates that one branch of the *Triops* stock has been conservative in speciation from at least Carboniferous times onward.

Family VACHONISIIDAE Tasch, new family

Characters of order. *L.Dev.*

Vachonisia LEHMANN,[1] 1956, *nom. subst.* [*pro Vachonia* LEHMANN, August, 1955 (*non Vachonia* ABALOS, March, 1955)] [**Vachonia rogeri*; OD]. Shield broadly expanded, *Triops*-like, with median anterior notch and gently convex posterior margin, apparently covering entire body. Single pair of very small antennae; 5 pairs of thoracic appendages; about 50 pairs of postgenital abdominal appendages (66). *L.Dev.(U.Coblenz.),* Ger.——FIG. 47,*1*. **V. rogeri,* Hunsrück Shale; *1a,b,* ventral side, dorsal side shown by X-ray, X9.4 (66).

Subclass DIPLOSTRACA Gerstaecker, 1866

[*nom. transl.* TASCH, herein (*ex* superorder Diplostraca BROOKS, 1959, *nom. transl. ex* subsection Diplostraca—of suborder Branchiopoda—GERSTAECKER, 1866, p. 1029)] [=Onchyura ERIKSSON, 1934] [*emend.* BROOKS, 1959, and TASCH, herein]

Bivalve carapace (single piece in cladocerans), laterally compressed, enclosing body and appendages, abdomen with end (together with postabdomen in cladocerans) bent ventrally forward. Antennules uniramous, small, tactile; antennae powerful swimming appendages. *L.Dev.-Rec.*

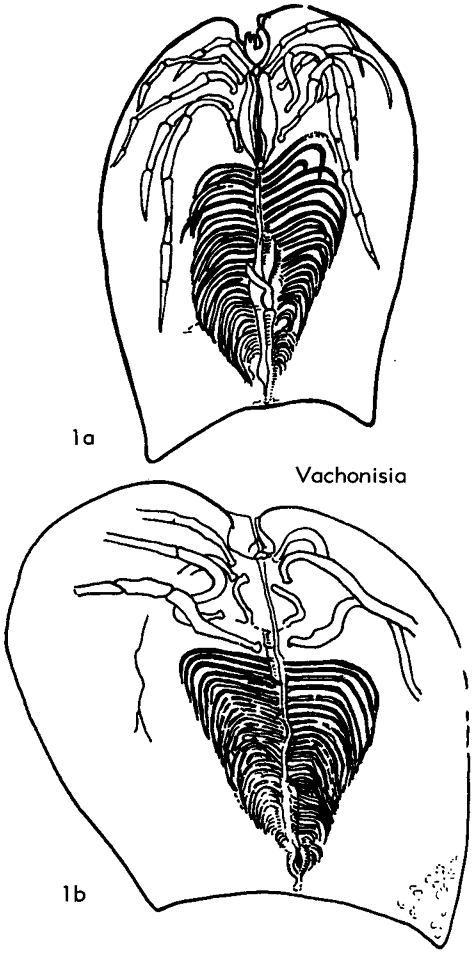

FIG. 47. Vachonisiidae (p. *R*141).

Order CONCHOSTRACA Sars, 1867[2]

[*nom. transl.* CALMAN, 1909 (*ex* suborder Conchostraca SARS, 1867)] [=tribe Holostraca GERSTAECKER, 1866; Phyllopoda conchiformia SIMON, 1866; Conchophylla STEBBING, 1902]

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[1] Paläont. Zeitschr., v. 30, p. 225, 1956.

[2] Completion of the conchostracan section of the Branchiopoda chapter was greatly expedited by two Sigma Xi research grants-in-aid. A Wichita State University research grant facilitated preparation of the plates.

RAYMOND'S type material was studied at the Museum of Comparative Zoology at Harvard College. Types on deposit at the New York State Museum and the Geological Survey of Canada were loaned for study.

Messrs. E. S. BELT and W. BOCK and Drs. ADA SWINEFORD and E. G. WILLIAMS contributed material from the Upper Mississippian of Nova Scotia, Triassic of Pennsylvania, Permian of Kansas, and Pennsylvanian of Pennsylvania. Prof. Dr. ZDANEK SPINAR kindly sent representative specimens from the Carboniferous of Czechoslovakia. Data on South American conchostracans were graciously supplied by Prof. Dr. JOSUÉ CARMARGO MENDES.

Dr. M. T. COPELAND provided data on Canadian conchostracans and supplied excellent photographs and descriptions

Body enclosed within translucent bivalve shell, ending posteriorly in clawlike furca (with single exception); front of head produced downward, forming frontal process or rostrum; paired compound eyes sessile, more or less confluent; ocellus placed below compound eyes. Antennules short or long, variable from unjointed to multijointed; antennae natatory, biramous, much larger than antennules; trunk limbs (legs) variable, 10 to 32 pairs, of which 1 to 16 are postgenital; rami of caudal furca short, clawlike. Genital ducts opening on 11th segment; ova retained within shell, attached to 9th to 15th pair of legs. Young usually hatched in nauplius stage (120). *L.Dev.-Rec.*

ANATOMY

Conchostracans, or clam shrimps, have a short, laterally compressed body enclosed between two lateral valves that constitute the carapace. The head is located anteriorly, somewhat beyond the umbonal region, and bears sessile paired compound eyes and a well-developed ocellus. The front of the head is produced downward so as to form a rostral process or beak. Posteriorly, the telson is distinguished by two flattened, upwardly curved processes or claws. Two pairs of antennae are present, the antennules being small and simple, whereas the antennae are modified into powerful biramous swimming organs. During mating, males of *Cyzicus* (=*Isaura*) *cycladoides* have been observed (83) to use the antennae as aid in seizing the female carapace. I have noted multiple uses of these antennae in aquarium-reared conchostracans in my laboratory.

The antennae are employed as an aid in burrowing, as well as in escaping from bottom muds in which the clam shrimp has burrowed. They are also used to clamber up aquarium walls. When individuals rise nearly to water surface, anterior side up, the antennae are looped and act as a propellant. Sometimes they serve to aid in floating, when, in particular, clam shrimps graze on surface microplankton.

Trunk legs (swimming legs) vary from 10 to 32 pairs, of which from 1 to 16 are postgenital. Although phyllopod trunk appendages display a basic plan—that is, biramous, flat, translucent, lobed, and setose legs with a series of small lobes (endites) along the median margin—modifications of the plan occur in both male and female conchostracans. In males the initial one or two pairs of legs are hooked and prehensile. Gravier & Mathias (83) observed that during mating the male appears to use these robust hooks in maintaining steady attachment to the female (see Fig. 50,*1a,b*).

Repeated observations and experiments on aquarium populations during mating have convinced me that the mating attachment is not readily disturbed. The mating pair, with the male shell in a position perpendicular to the female shell, moved as a single unit when touched by a brush or when a passing individual clam shrimp collided with them. There also appears to be some competition for females. Individual males were seen on several occasions unsuccessfully attempting to seize copulating females with their prehensile legs. Such incidents cause the mating pair to migrate from the area.

In females, the elongated flabella, consisting of as many as three pairs of posterior legs, appears to serve the function of retaining eggs in position (85, 107).

CARAPACE

COMPOSITION

The composition of the carapace of *Limnadia lenticularis* may be taken as indicative of other conchostracan carapaces. Sars (122) found that it is composed of two distinct parts, an exterior chitinous coating that seems to consist of several layers, and an interior membranous lining that is continuous with the integument of the body. A similar composition has been reported for *Caenestheriella davidi* (58, p. 9). More recent researches on living clam shrimps have added further details (35).

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of recently collected specimens from Devonian rocks of the Canadian Arctic.

Other individuals who assisted with references, literature, specimens, or discussion and advice on pertinent problems include: Mme. Simone Defretin, Mr. H. W. Dresser, Dr. M. K. Elias, Mr. C. F. Kilfoyle, Prof. Teiichi Kobayashi, Dr. S. A. Levinson, Dr. N. Novozhilov, Dr. Jean Roger, Dr. C. J. Stubblefield, Dr. H. B. Whittington, and Dr. J. L. Wilson. Dr. K. E. Caster communicated personal observations on conchostracan-xiphosuran associations on Brazilian coastal salt flats. Dr. G. Fryer generously supplied requested information on the habitat of living central African conchostracans. The late Dr. N. T. Mattox helped me to decipher the taxonomy of *Cyzicus* and provided other valuable data on the ornamentation of living forms. Others who supplied data on and specimens of living conchostracans include Dr. Louis Kornicker, Mr. Bernard L. Shaffer, and Dr. J. R. Zimmerman.

A diverticule which separates the two cuticular layers of the valve is bounded by two epidermal layers, one above, and one below it. The surface ornament of conchostracan valves originates in the epidermal cells of the uppermost of these layers. Thus, certain adjacent epidermal cells give rise to fibers (cuticular prisms?) which either radiate in the corresponding cuticle or are sunk in the tissue itself. The latter fibers (prisms?) may unite and form a series of resistant pillars rooted in the external cuticle. Thus, a moderate relief is determined and its reflection on the exterior of the valve constitutes the valve ornamentation. Such pillars may be isolated, associated in a polygonal network, or appear as radial rows. In turn, they appear on the exterior of the valve as polygonal, reticulate, or radial. Punctate ornamentation may be accounted for by pore-canals penetrating cuticular fibers (prisms?).[1]

Sars (122) further noted that in *Limnadia* the two distinct carapace parts are connected by numerous cross bars. These, he found, were partially visible externally as small irregular opaque spots.

There can be little doubt, then, that surface ornamentation reflects epidermal-cell-generated fibers (prisms?) and their condition of merger or isolation, and the further condition of creation of relief on the inner side of the external cuticle. One wonders, since the same kind of fiber (prism?) enters into so many different types of ornamentation, whether the vagaries entering into determination of thickness of fiber bundles (prisms?) merits generic or familial taxonomic status. Insight leading to a plausible answer to this question is considered in discussion of "Ornamentation." Here it suffices to indicate that the epidermal cells can generate pore-penetrated fibers (prisms?) that yield punctate ornamentation and later in the same individual, fibers (prisms?) of radial type. This capacity for variable expression precludes fiber (prism?) arrangements themselves as more than secondarily useful taxonomic indicators.

I have studied six specimens of *Caenestheriella belfragei* from a large sample taken by a colleague from a pond near Liberal, Kansas. Thickness of valves in this sample measured along freshly broken edges varied from 0.06 to 0.08 mm. Individual layers, of which the exterior coating was composed, numbered six or seven, which indicates an average thickness of each layer ranging from 0.008 to 0.013 mm. While some variation may be expected in these figures for other genera and species, they are likely to be of the right magnitude.

In life, the corneous conchostracan carapace is never strongly calcified (83, p. 4).

The shells of living conchostracans are semitransparent to translucent and colored light amber, brown to brownish-red, or yellow. I have observed valves change to a deeper red-brown color prior to the animals' demise. This is due to changes in the color of the unoxygenated blood in the valve which in life serves a respiratory function.

GROWTH LINES

All above-mentioned species have carapaces with lines that reflect successive moltings. That is to say, during ecdysis, in addition to the casting off of a chitinous inner skeletal duplicature, a line of growth is added peripherally to each valve. Only the Lynceidae lack growth lines. In mature individuals of *Caenestheriella gynecia,* lines of growth are variable (15 to 26), with an average of about 20. In *Limnadia lenticularis* adults, growth lines are also variable (11 to 15, according to Sars; 5 to 16, according to Daday); in mature individuals of *Eulimnadia stoningtonensis,* 10 growth lines are reported. Because number of growth lines is important in studies of fossil conchostracans, variation found in living species of *Limnadia* is of interest (30, t. 8, p. 151-175). Growth lines vary from three in *L. nipponica* females, to 45 in *L. grobbeni* females. In the latter species males have ten fewer growth lines. Sexual difference in number of growth lines is well shown by *L. stanleyani,* in which males have ten growth lines and females 13 to as many as three times the maximum male number, even though the carapaces of both sexes are very similar in size.

It has been suggested (58, p. 42, 141) that for estherian conchostracans, low temperature retards carapace growth and is reflected in a smaller number of growth lines. Species reported from tundra regions are all small. In a temperate region, Mattox (86) found that living individuals of *Caenestheriella gynecia* collected during June of one year showed an average length of 10.6 mm. and 18 growth lines, whereas in July five years later similar individuals averaged 7.3 mm. in length and had 16 growth lines. This difference in growth rate was attributed to a greater precipitation in the earlier year, since more rainfall is reflected in larger or more permanent pools and increased food supply. It is helpful to keep factors of this sort in mind when studying fossil populations that show wide ranges in size and number of growth lines for the same overall shell size.

ORNAMENTATION

Living conchostracans, with few exceptions, display a variety of types of carapace sculpture. Kobayashi (58, fig. 1, table 1), based on data of Daday (30), classified these into some 20 types and noted that in a few forms female sculpture differs from that of males. He deduced a morphological series that may or may not correspond to any actual evolutionary or ontogenetic sequence but which is given here since it sums up the main

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[1] Cf. M. Novikoff, 1905, Zeitschr. wissensch. Zoöl., v. 78, p. 569-571, pl. 21, fig. 19, 26, 27, 31.

kinds of sculpture: (1) appearance of spots or striae, (2) enlargement of spots, (3) appearance and disappearance of grooves, (4) change of grooves from radial to dendritic, and (5) change of pattern from polygonal to reticulate.

As already noted for *Eulimnadia stoningtonensis,* the larval carapace is minutely punctate and this is retained in the adult. Various estherians studied by BAIRD (5) are reported to show minute raised clots or punctation on carapace interspaces. SARS (122, p. 119) noted that even in smooth and unornamented *Lynceus brachyurus,* under high magnification, the external lamella of the shells displays regularly rounded meshes or hollows.

NOVOZHILOV has founded his entire system of classification of fossil conchostracan valves (95, 98, 99) on fine shell sculpture of the type mentioned above. In so doing, he follows the lead of BAIRD, who originally tried to classify living clam shrimps on whether their valves were "dotted or punctate on the surface" or "longitudinally striated on their surface" (5). These efforts, based on living forms, have been rejected by all workers. No presently acceptable biological classification is based on valve sculpture. In fact, MATTOX (87) has eloquently spoken out against use of this feature for fossil clam-shrimp valves as well. He simply demonstrated that the same valve in numerous instances has both of BAIRD's types of sculpture. JONES (53) and others have shown—without addressing themselves to this particular debate but rather in the course of describing new material—that numerous species of the same genus may have as many as three different types of ornamentation. DEFRETIN (35) more recently has indicated that, while some species may be separable on the basis of shell sculpture, many are not, and thus classifications so predicated lead to blind alleys.

We may conclude that a wide spectrum of variation occurs in the above-noted valve-sculpture patterns within the same individual valve belonging to a given species, as well as within different species of the same genus. In brief, this characteristic cuts across specific, generic, and sexual lines. For conchostracan fossils, ornamentation can at best provide secondary evidence for distinguishing species and possibly subgenera. More rarely it may also serve in the same population to distinguish male and female shells. All evidence available is opposed to use of shell ornamentation for discriminating genera and families of fossil or living conchostracans.

ATTACHMENT OF CARAPACE TO BODY AND ORIENTATION

The mode of attachment of conchostracan shells to the body can be exemplified by living *Limnadia lenticularis.* SARS (122, p. 86, pl. 14) reported that the shell is attached to the body above by a narrow ligament, and a little below this, to each side by a strong adductor muscle, the insertion of which on the interior surface of each valve appears as a well-defined circular area in the foremost part of the valve. The ligamental attachment is anterodorsal and within the upper umbonal area. *Cyzicus morsei* shows a similar mode and location of shell attachment.

Fossil carapaces with subcentral beaks indicate that ligamental attachment of these forms was mediodorsal.

Dorsal and ventral sides, right and left valves, anterior and posterior locations on fossil conchostracan carapaces can readily be determined. Most often fossils cannot be removed from the bedding plane and orientation of the several valves must be achieved by inspection.

In exterior view, the umbo or umbonal beak occurs on the dorsal side. Since the conchostracan body is attached to the umbonal area on the interior, and behind the head region, the anterior location is always headward. If the umbonal region on a given valve is to the right, it is a right valve; if to the left, it is a left valve.

Both valves of fossil estherians in some occurrences are preserved on the same bedding plane. In such cases, direction and strength of bottom currents may be estimated by measuring the displacement and direction of displacement of the two valves along the dorsal margin (61, p. 5-6, fig. 2). Such displacement is generally negligible, owing to weakness of currents which might be expected from the nature of water bodies in which conchostracans are found.

Where fossil valves are found only with umbones and dorsal margins visible on a bedding plane, the individuals represented by such valves evidently died while burrowing in the bottom mud. Most conchostracan valves settle to the bottom and come to rest on their right or left sides, with the convex portion outward.

DIMORPHISM

The male and female shells of many conchostracans differ in shape. Thus, SPENCER & HALL (132) reported that female shells are narrower than those of males in species of *Limnadopsis.* KOBAYASHI & KUSUMI (61) measured carapaces of six genera *(Eulimnadia, Caenestheriella, Caenestheria, Leptestheria, Lynceus, Eocyzicus)* of living estherians on deposit at a hydrobiological station at Otsa, Japan, finding that the carapace outline commonly is different in male and female shells of the same species. In a sample of 15 male and 15 female carapaces of *Eocyzicus mongolianus* UENO plotted on a curve (61, fig. 9), I observed that a zone of overlap on the graph for length ranges from 10.7 mm. to 11.2 mm. In this zone, male and female carapaces were the same in size, whereas on either side of this zone only larger male shells are recorded, or in the opposite direction, only smaller female shells. As for height, the range in height of the male carapace falls within the broader range for females.

The interpretation given above differs from that of the cited authors who concluded that "the female is shorter than the male in *E. mongolianus.*" Yet study of their graph suggests that dimorphism is expressed gradationally. This becomes an important consideration in dealing with fossil material, since dimorphism has been reported frequently (13, 58).

When considering dimorphism, it is useful to bear in mind the proportion of males to females found in natural populations of living conchostracans. SPANDL (131, fig. 10) indicated that for *Leptestheria dahalacensis* (RÜPPEL) males predominate in warm countries and constitute as much as 75 per cent of the population, whereas elsewhere males may constitute as little as 10 per cent of the population. JOLY (52) found 24 males in a population containing 30 individuals of *Isaura* (=*Cyzicus*) *cycladoides* in Toulouse, France, while other workers reported (83) three males for every female of this same species. In Breslau, Germany, SIEBORD (83) found in a population of 1,364 individuals almost 2.5 times the number of females compared with males of *Cyzicus tetracerus* (KRYNICKI) and SIMON (83) reported a marked predominance of males in populations of *Caenestheriella gubernatur* KLUNZINGER in Egypt.

MATTOX (86) has noted that in the genus *Caenestheriella* all American species are described on the basis of male and female specimens, though his new species from Ohio, *C. gynecia,* consisted only of female individuals.

INJURY AND REPAIR

Injury to the growing edge of conchostracan valves has been observed in living and fossil specimens (144). Successive growth lines posterior to the injured site curve upward to fill the gap in the valve created by the injury. New morphological structures may thus be formed in the process of healing the injury. Such structures have been observed and include a sinus or downwarp in the upcurve growth-line zone and one or more scallops on the peripheral margin between any two repaired zones on the same valve. This capacity for shell repair has continued unchanged from at least Permian (probably from Devonian) time to the present.

Individual valves with unique structures must be examined for injury-repair zones. Only when this kind of explanation of the unique feature has been excluded, can taxonomic recognition be made.

SOFT PARTS PRESERVED WITH FOSSIL VALVES

Very few instances of partial soft-part preservation of conchostracans have been recorded. Of these, only two (33, 158) have provided excellent anatomical data. The rarity of such finds is confirmed by my own experience in tracing conchostracan-bearing beds of the Wellington and Ninnescah Formations (Lower Permian) in the Kansas region. Although literally thousands of fossil clam shrimps have been collected from almost 1,000 feet of these deposits and from numerous zones, not one example was found where partial soft-part preservation could be seen.

WRIGHT's genus *Limnestheria* (158) was erected on soft-part anatomy found associated with valves. Her material included second antennae, mandible, trunk, telson, and appendages, from which she was able to show that the first pair of trunk limbs in males were modified as claspers. MATTOX (87), in reviewing her evidence, concluded that her interpretation of the appendages was erroneous in that two pairs of trunk limbs had been modified as claspers. This last factor affected classification of *Limnestheria,* and MATTOX proposed that it be placed in the Cyzicidae instead of Lynceidae. However, no cyzicids are known with valves bearing a large umbo surrounded by few growth lines, a condition that characterizes the valves of *Limnestheria.* The genus should be assigned to the Limnadiidae, in which family valves of this type are common. The fact that specialists such as WRIGHT and MATTOX differ in interpreting the appendages of *Limnestheria* indicates to me that any such interpretation in itself is inconclusive. MATTOX also noted that the antennae and telson are very similar to those of modern estheriids, denoting in his opinion a close relationship of the Carboniferous forms with living species.

DECHASEAUX (33) studied the soft-parts preserved in valves of *"Estheria"* (=*Cornia*) *cebennsis,* observing mandibles, fragments of the biramous antenna, impression of the ocellus and interior of the digestive tube, and the caudal furca. Some strings of eggs were also found fossilized with the valves. As compared with modern estheriids, she concluded that the Carboniferous specimen had larger and fewer eggs, a characteristic head profile, more or less elongate appendages, shorter antennae, and a longer caudal furca. She further observed that the eggs of Triassic clam shrimps are smaller and more numerous in given individuals, attributing this change to natural selection.

The examples cited make it obvious that those rarely fossilized soft parts of clam shrimps provide an insight into anatomical similarities with living forms and show significant differences too. Unfortunately, the rarity itself prevents paleontologists working with fossil clam shrimps from relating their material directly to living forms described on the basis of soft-part anatomy.

Modification and specialization of appendages appears to have been achieved in the conchostracans by Carboniferous time. Since the fossil record of this group at present extends back to the Devonian, we can surmise that many of the evolutionary trends inferred from fossil valves in younger beds date back at least to Devonian time.[1]

ONTOGENY

GENERAL FEATURES

Several studies on the life cycles of living conchostracans are available (Sars, 122; Berry, 9; Mattox, 86; and others). The reported investigations deal with three distinct genera, *Limnadia, Eulimnadia,* and *Caenestheriella.* A resumé of essential findings is helpful to paleontologists in understanding the probable rate and mode of growth of the animals represented by fossil conchostracan carapaces.

The body length at time of hatching of the nauplii is 0.25 mm. for *Limnadia lenticularis* and 0.37 mm. for *Caenestheriella gynecia.* Comparative figures are lacking for *Eulimnadia stoningtonensis,* although we know that the end of the first 24 hours it attains a body length of 0.75 mm. At hatching, no shell is discernible in any of these species.

In *Limnadia,* the earliest rudiments of a shell and the first appearance of the six foremost legs—all encased in larval skin—occur at a body length of 0.65 mm. At 96 hours after hatching, *Caenestheriella gynecia* has a body length of 1.1 mm. and a shell of 1.5 mm. in length. *Eulimnadia stoningtonensis* starts to develop its carapace on the third day. The carapace is minutely punctate, suggesting that punctation of the adult carapace, at least in some genera, is a larval characteristic.

CONCHOSTRACAN EGGS

An excellent literature is now available on experimental studies of conchostracan eggs. Studies make clear that conchostracan eggs when kept dry, moist, or frozen, can hatch and all at approximately the same time (85). Kelley (57) noted a variation in number of eggs produced by females according to age of individuals. He also observed that once egg production begins, as few as 15 to 20 eggs may be shed at each ecdysis. Mattox & Velardo (1950) reported that for *Caenestheriella gynecia,* the egg masses were attached to the exopodite of the tenth swimming appendage in groups of 35 to 120. During ecdysis, the cuticle (or skeleton) is cast off and with it the attached egg masses. Kelley found that if feeding conditions are satisfactory, ecdysis occurs every second or third day but diminishes toward the end of life.

These experimental data are of interest to paleontologists since fossil clam shrimp eggs have been reported (33, 53, 58). It also has important bearing on such items as population density, number of generations per season, temperature of the water, and other related factors pertaining to clam-shrimp-bearing beds in the rock column. In turn, these sorts of data can help in elucidating paleoecology.

My study of the eggs of *Cyzicus mexicanus* was directed toward obtaining details of special interest to a paleontologist. Since conchostracan eggs, when fossilized, are found in association with clam-shrimp valves, it is useful to know how, in the living condition, these eggs are placed in the valves. Egg masses were found to lie below the dorsal margin behind the umbo in a tilelike pavement of white-brownish spheres about 0.1 mm. in diameter. They were separated by a darker mucoid-type matrix so that no two eggs were in contact.

A count of four layers of eggs in a rectangle 3.3 mm. long by 3 mm. wide was recorded for each valve. A few eggs were observed that stretched in a stringlike arrangement beyond the roughly rectangular or ovate egg mass. Under high power, the eggs were found to have a thin, fibrous, translucent pellicle or outer sheath and an inner dense yolk. Measurements of several eggs yielded an average diameter of 0.13 mm.

ECOLOGY AND PALEOECOLOGY

A chief habitat of living conchostracans is small, temporary, alkaline, inland ponds. These are generally no larger than an acre

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[1] Cf. P. Tasch, 1963, *Evolution of the Branchiopoda:* Harvard Univ., Museum Comp. Zoology, Spec. Publ. 1963, Chapter XI.

in extent (107) and mostly much smaller. Flood-plain pools (Missouri River, for example), roadside ditches, puddles in cultivated fields, and almost any shallow depression filled with water are more often than not likely to have a brood of conchostracans (144, 146, 147). They have also been reported from spring water (102), along margins of certain large lakes (e.g., Africa) and on coastal salt flats (e.g., Brazil).

The pH of waters inhabited by clam shrimps ranges from 7 to 9.

Some living species are known from both fresh and brackish water *(les eaux saumâtres)* environments. These include *Cyzicus (=Isaura) cycladoides* JOLY, *Cyzicus (=Isaura) jonesi* (BAIRD), *Lynceus rotundus* THIELE, and *Leptestheria vieligera* THIELE (83, p. 8).

Conchostracans are found in temporary pools at all altitudes and are cosmopolitan in distribution. The latter fact can be explained by the properties of the resting egg, which can withstand long desiccation of the pools so as subsequently to become dispersed by wind or water. This, in turn, can explain the world-wide distribution of fossil estheriid conchostracans.

According to PENNAK (107, p. 338), with rare exceptions, a pond never contains more than one species of a particular genus at a time. Collections from some 500 ponds in Kansas and Oklahoma by one of my colleagues revealed the presence of only a single conchostracan species *(Cyzicus mexicanus)*. This contrasts with fossil occurrences of distinct species of the same genus obtained from the same horizon (and hence presumably in life, occupants of the same water body or closely adjacent water bodies). A possible explanation, if we grant that lumping might reduce the number of distinguished fossil species, could be that in succeeding years a given pond of the geologic past was inhabited by different species. The increment of sediment during a geologically negligible period of time would be undetectable in the rock record, so that different species would occur apparently on the same time plane though actually having existed in different years.

In this regard, it should be stressed that several living conchostracan genera commonly occur side by side in the same pool, as in Australia (132, p. 458), in which species of *Limnadopsis, Lynceus,* and *Cyzicus* occur together. Fossil leaiid and estheriid valves are not uncommon on the same bedding plane in both Pennsylvanian and Permian beds sampled by me and others. Several distinct genera bearing spines on the initial (or larval) valve were found together on the same bedding planes in the Wellington Formation of Kansas (142). Also, different phyllopod orders are not uncommon in the same body of water. GAUTHIER (83, p. 11), for example, has reported the notostracan *Triops (=Apus)*, the anostracan *Streptocephalus,* and the conchostracan *Leptestheria,* in the same Algerian pond.

A variety of nonmarine and marine forms are found in association with conchostracan fossils. These include *Unio, Anodonta, Trigonia, Gervillia, Spirorbis, Anthracomya, Lingula,* and *Limulus*. An association with ammonoids has also been reported (98, p. 57). Estheriid valves have been found in coelocanth coprolites or in beds containing coelocanth remains. They have been reported in typical marine strata bearing trilobites and in association with insects and plants. The fossil notostracan *Triops* has been found in the same beds as *Cyzicus* and *Leaia.*

My study of Wellington deposits (Lower Permian) in Kansas and Oklahoma has revealed that faunal and floral associates included xiphosurans, ostracodes, eurypterids (143, 146, 147), numerous insect orders (including many extinct orders) (147), fresh- and brackish-water mollusks (clams and snails), fish, and a considerable number of plant fossils in some places, largely consisting of carbonized wood, seed coats, leaves, and charophytes. Fishes are represented in some deposits by teeth attached to jaws, scales, and fragments of other parts. Segmented worms are represented by burrows. A microflora of pollen and spores has also been found (147).[1]

It may be observed that test tubes placed in some modern ponds bearing clam shrimps have yielded samples of copepods, cladocerans, numerous protozoans, and algae, as well as numerous water beetles and insect larvae. Some or all of these are present before, during, or after the occupancy of clam shrimps. The most abundant large crustacean in most modern ponds sampled by the writer and colleagues is the crayfish. Snails and more infrequently clams are prominent faunal associates of living clam shrimps.

Association with marine forms has led one investigator (58, p. 52) to speculate as to whether estherians did not originally

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[1] Other palynomorphs and protists have since been reported and include hystrichosphaerids and dinoflagellates (Tasch, P., 1962, Internatl. Palynology Conf., Tucson, Ariz., abstracts).

live in a shallow sea. Several other explanations that eliminate need to postulate a unique event might explain such occurrences: (1) existence of temporary pools close to ancient fluctuating shore lines or lagoons and invasion of the sea over such

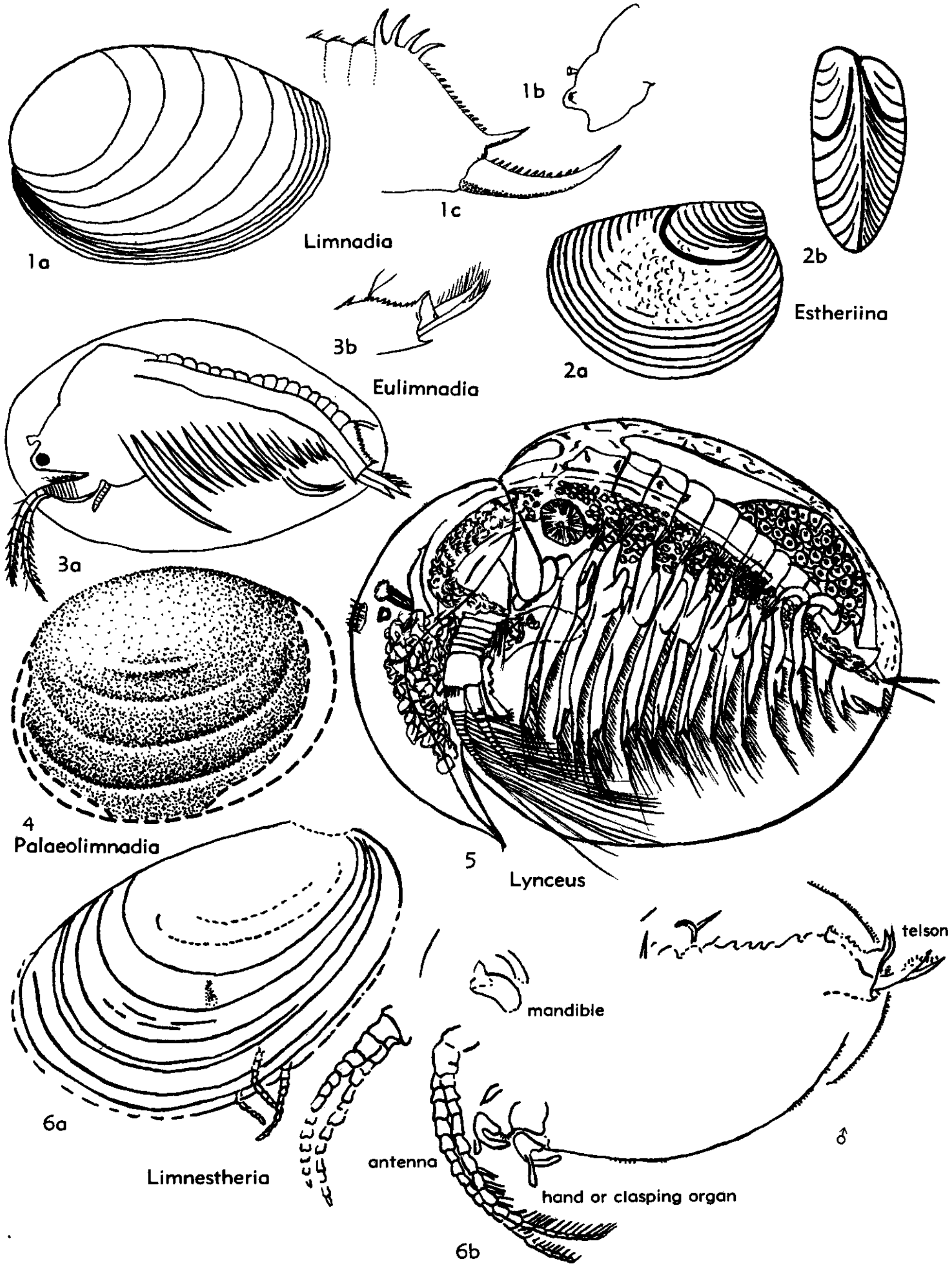

FIG. 48. Lynceidae *(5)*; Limnadiidae (Limnadiinae) *(1,3)*, (Estheriininae) *(2,4,6)* (p. *R*149-*R*150).

an area, mixing the faunas, and (2) dispersal of estheriid eggs to near-shore marine or estuarine area.

The close proximity of shales and marls containing fossil estheriids to fossiliferous marine beds or beds bearing casts of salt crystals favors the first explanation, whereas the second is supported by extensive distribution of estheriids. A third possibility could be torrential flooding that covered pools so as to form a widespread sheet of water which then ran off to the sea, mingling the faunas. Flooding of modern rivers definitely accounts for the distribution of some living clam-shrimp species (57).

As noted above, living conchostracans can withstand brackish water and it is in zones of brackish-water deposits that the mixture of the fresh-water and marine forms in question probably occurred. A good fossil example is the genus *Limnestheria* of the Kilkenny Coal Measures of Ireland. Here, the almost black carbonaceous shales containing the conchostracan fauna grade downward into the so-called "fleck-rock" which grades laterally eastward into marine (goniatite) shales. An ancient delta is suggested by these relationships and the conchostracan fauna is thought to have lived in an estuarine environment (158).[1]

Suborder LAEVISCAUDATA Linder, 1945

[=*nom. transl.* Tasch, herein (*ex* "tribe" Laeviscaudata Linder, 1945)]

Shell more or less globular, without umbones, with very few lines of growth or lacking them; connection between 2 halves in groove; terminal claws rudimentary without dorsolateral spines (70). *L.Cret.-Rec.*

Family LYNCEIDAE Stebbing, 1902 (1896)

[Lynceidae Stebbing, 1902 (March), based on *Lynceus* Linné, 1785, having "won general acceptance, is to be maintained in the interests of stability" (Zool. Code, 1961, Art. 40,a), cited with its own author and date, but it "takes the date of the rejected name of which it is to be considered the senior synonym" (Art. 40,b), thus replacing Limnetidae Sars, 1896, based on *Limnetis* Lovén, 1846] [=superfamily Lynceoidea Stebbing, 1902 (*nom. transl.* Novozhilov, 1960); Lynceidae Sayce, 1902 (August), p. 257; Paleolynceinae Tasch, 1956 (*nom. nud.*)].

Valves lacking growth lines; head not entirely covered by carapace. Antennules 2-segmented; only the first pair of postcephalic limbs prehensile in males. *L.Cret.-Rec.*

Lynceus O. F. Müller, 1785 [*L. brachyurus; OD] [=*Limnetis* Lovén, 1846 (75)]. Head beak-shaped in profile; rostrum broad in male, pointed in female; flagella of antennae 16-segmented; claw of claspers regularly and smoothly curved, sickle-shaped. *L.Cret.-Rec.*, N.Am.(Can.-USA)-Eu.-Asia.——Fig. 48,*5*. *L. brachyurus, USA(Ill.); ♀ left valve cut away to show head, trunk, appendages, egg masses, ×25 (107). [Fossil species: *L. stschukini* Chernyshev, 1940, =*Paleolynceus* Tasch, 1956 (*nom. nud.*), *L.Cret.*, USSR(Transbaikal) (25).]

Suborder SPINICAUDATA Linder, 1945

[*nom. transl.* Tasch, herein (*ex* "tribe" Spinicaudata Linder, 1945)]

Laterally compressed, with or without umbones and with many lines of growth; connection between halves elevated; telson with dorsolateral spines and with large terminal claws (70). *L.Dev.-Rec.*

Superfamily LIMNADIOIDEA Baird, 1849

[*nom. transl.* Tasch, herein (*ex* Limnadiadae Baird, 1849)]

Valves characterized by prominent umbo. *Carb.-Rec.*

The carapaces of several genera of the Limnadioidea exhibit well-marked curvature of the posterior margin near the dorsal line, thus producing a distinctive outline. Branchiopod bivalves of this type are designated as **limnadiiformes.** Such recurvature is observed in some other superfamilies (e.g., Leaioidea, Vertexioidea) of the Spinicaudata and may result in a spinous projection above the dorsal margin of the carapace (e.g., *Keratestheria,* Ipsiloniidae).

Family LIMNADIIDAE Baird, 1849

[*nom. correct.* Tasch, herein (*pro* Limnadiadae Baird, 1849, p. 86, *nom. imperf.*, Zool. Code, 1961, Art. 29)] [=Limniadiidae Burmeister, 1843, (*nom. null.*)]

Carapace broadly oval, compressed, with variable number of concentric growth lines around prominent umbo, mid-dorsal surface of head bearing pedunculate, pyriform frontal organ. *Carb.-Rec.*

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[1] Present evidence suggests transition from an original marine to a fresh water environment during the Carboniferous. With regard to conchostracans several such events, occurring in pulses, may have taken place at different times (cf. P. Tasch, 1963 (Harvard Univ., Museum Comp. Zoology, Spec. Publ. chapter XI).

Subfamily LIMNADIINAE Baird, 1849

[*nom. transl.* Tasch, herein (*ex* Limnadiadae Baird, 1849, *nom. imperf.*)]

Characterized by distinctive frontal organ. *Rec.*

Limnadia Brongniart, 1820 [**Monoculus lenticularis* Linné, 1761; OD]. Shell broad, ovate; antennules shorter than scape of antennae, flagella of antennae with 12 to 14 segments; 22 pairs of legs. *Rec.,* cosmop.——Fig. 48,*1*. **L. lenticularis* (Linné); Mass. (Woods Hole); *1a,* left valve, enlarged; *1b,* pyriform frontal organ on dorsal surface of head, ×4 (87); *1c,* telson and cercopods, enlarged (129).

Eulimnadia Packard, 1874 [**E. agassizii*; OD]. Carapace narrow, ovate; growth lines ranging from 1 to 12; conspicuous ventral spine on telson at base of terminal spines (cercopods); 18 pairs of legs; antennules variable in length, flagella of antennae with 9 segments. *Rec.,* USA-W.Indies-Mexico.——Fig. 48,*3*. **E. agassizii,* USA (Mass.); *3a,* left valve cut away to show soft-part anatomy, ×6; *3b,* telson, enlarged (102).

Subfamily ESTHERIININAE Kobayashi, 1954

[=Estheriinidae Kobayashi, 1954 (*nom. transl.* Novozhilov, 1957, *ex* Estheriininae Kobayashi, 1954); Paleolimnadiinae Tasch, 1956]

Valves with large prominent umbo resembling living *Limnadia.* Presence and morphology of frontal organ unknown. *Carb.-L.Cret.*

Estheriina Jones, 1897 [**E. bresiliensis*; OD] [=*Sinoestheria* Chang, 1957]. Valves more convex for limited area in umbonal region (neanic stages) than lower down in ventral region; growth lines sharp and widely spaced on convex portion but more numerous and closer together on flat marginal area. *L.Cret.(Bahian),* Brazil.——Fig. 48,*2*. **E. bresiliensis*; *2a,* right valve, ×6; *2b,* ventral view, ×5 (54).

Bilimnadia Novozhilov, 1957 [**Estheria anabarensis* (Novozhilov), 1946; OD] [Inadequately documented; doubtful]. *M.Trias.,* SW.Asia.

Leptolimnadia Novozhilov, 1954 [**L. rhombiformis*; OD]. [Inadequately documented; doubtful.] *L.Cret.,* NE.Asia(Sib.-Mongolia).

?Limnestheria Wright, 1920 [**L. ardra*; OD]. Carapace oval, punctate, about 10 growth lines surrounding large, smooth, umbonal area. Antennae, trunk limbs, telson of estherian type; first one (158) or two (87) pairs of trunk limbs modified as claspers in males. *Carb.(Kilkenny Coal Measures),* Eire.——Fig. 48,*6*. **L. ardra,* Ardra; *6a,* right valve, ×7; *6b,* male with modified hooked appendages, ×10 (158).

Notocrypta Novozhilov, 1954 [**N. altissima*; OD] [Inadequately documented; doubtful]. *U.Cret.,* NE.Asia(Mongolia).

Palaeolimnadia Raymond, 1946 [**Estheria wianamattensis* Mitchell, 1927; OD] [=*Paleolimnadia* Tasch, 1956]. Relatively long oval carapace, large smooth umbonal region, and few growth lines. *Trias.(Wianamatta Series),* Australia (New S. Wales).——Fig. 48,*4* **P. wianamattensis* (Mitchell); left valve, ×21 (111).

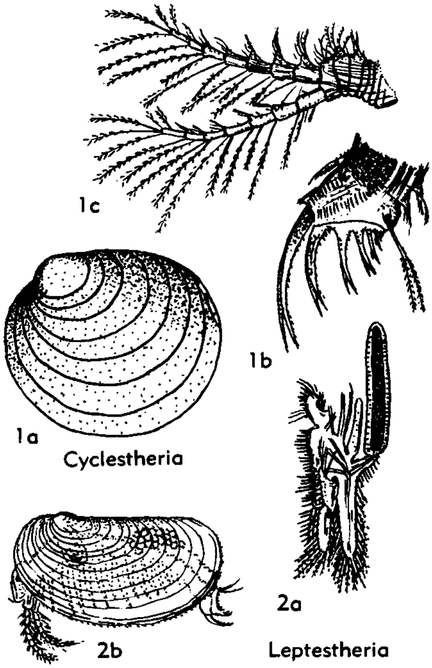


Fig. 49. Cyclestheriidae *(1);* Leptestheriidae *(2)* (p. *R*150-*R*151).

Pseudolimnadia Novozhilov, 1954 [**P. remota*; OD]. [Inadequately documented; doubtful]. *L. Cret.,* NE.Asia(Sib.-Mongolia).

Trigonlimnadia Novozhilov, 1954 [**T. trigonoides*; OD]. [Inadequately documented; doubtful.] *L.Cret.,* NE.Asia(Mongolia).

Family CYCLESTHERIIDAE Sars, 1899

Shell subspherical, with distinct umbonal region. Head strongly compressed anteriorly; surrounded by thin crest, rounded in front. Eyes united in single organ removed from anterior edge of head. Antennules simple cylindrical, neither articulate nor lobular; antennae stout with upper branch and part of scape bearing strong recurved spines; 16 pairs of legs with only first pair prehensile in males. *Rec.*

Cyclestheria Sars, 1887 [**Estheria hislopi* Baird, 1859; OD]. Characters of family. Caudal plate with dorsal spines strongly developed (121). *Rec.,* Australia-India-E.Afr.-Brazil?.——Fig. 49,*1*. **C.*

hislopi (BAIRD), India; *1a,* left valve, enl.; *1b,* caudal plate from right side, enl.; *1c,* right antenna from inner side, enl. (121).

Family LEPTESTHERIIDAE Daday, 1923

Rostrum at anteroventral extremity armed with conspicuous spine. *Rec.*

Leptestheria SARS, 1898 [**L. siliqua*; OD]. Shell much compressed, oblong, umbones very small. Upper lappets of exopodites on 10th and 11th pairs of branchial legs in female transformed to thick, sausage-shaped appendages for support of egg-mass (124). *Rec.,* Eu.-N.Am.-S.Am.-Afr.——FIG. 49,*2*. **L. siliqua,* S.Afr.(Capetown); *2a,* legs of 10th pair showing peculiarly transformed upper lappet of expodite, enlarged; *2b,* egg-bearing female, ×12 (124).

Superfamily CYZICOIDEA Stebbing, 1910

[*nom. transl.* NOVOZHILOV, 1958 (*ex* Cyzicidae STEBBING, 1910)]

Lacking serrate dorsal margin or radial ribs on valves, or large umbonal area. *L. Dev.-Rec.*

Family CYZICIDAE Stebbing, 1910

[=*emend.* BARNARD, 1929] [=Estheriidae SARS, 1900; Caenestheriellidae DADAY, 1913; Lioestheriidae RAYMOND, 1946; Isauridae BOCK, 1953; Bairdestheriidae NOVOZHILOV, 1954; Eocyzicinae (subfamily) *nom. transl.* NOVOZHILOV, 1954 (*ex Eocyzicus* DADAY, 1915); Aquilonoglyptidae NOVOZHILOV, 1958; Kontikiidae NOVOZHILOV, 1958]

Rostrum apex without spine. Shell thin, pellucid, laterally compressed, outline variable from ovate and elliptical to subrectangular, with numerous growth lines. Ornamentation distinct and variable, ranging from polygonal pattern in interspaces to longitudinal striae that may anastomose. *L.Dev.-Rec.*

Cyzicus AUDOUIN, 1837 [**Limnadia tetracera* KRYNICKI, 1830, p. 176; OD]. Rostrum of male broadly spatulate in profile; rostrum of female terminating acutely; flagella of antennae with 16 to 22 segments (2). *L.Dev.-Rec.,* cosmop.

C. (Cyzicus) [=*Estheria* RUEPPELL, 1837 (*non* ROBINEAU-DESVOIDY, 1930); *Isaura* JOLY, 1841, (p. 1068).] Rostrum and segmentation of flagella of antennae as in genus. *Rec.,* cosmop.——FIG. 50,*1a,b*. *C. (C.) cycladoides* (JOLY), Eu.(Fr.); *1a,* mating pair, ×4 (83); *1b,* right valve with appendages, ×3 (52).——FIG. 50,*1c*. **C. (C.) tetracera* (KRYNICKI), USSR; telson and cercopods, enl. (129).——FIG. 50,*1d*. *C. (C.) mexicanus* (CLAUS), USA; section through entire animal (front part of thorax), enl. (102).

C. (Euestheria) DEPÉRET & MAZERAN, 1912 [**Posidonia minuta* VON ZEITEN, 1833, p. 453; SD RAYMOND, 1946, p. 238] [=*Estheria (Euestheria)* DEPÉRET & MAZERAN, 1912; *Palaeestheria* DADAY, 1915; *Estherites* KOBAYASHI & HUZITA, 1941; *Bairdestheria* RAYMOND, 1946; *Estheriellites, Howellisaura* BOCK, 1953; *Indoestheria, Palaeoorthothemos, Paleoleptestheria, Pseudoasmussia, Rossoestheria, Trigonestheria, Trigononorassaia* NOVOZHILOV, 1954; *Concherisma* NOVOZHILOV, 1956; *Aquilonoglypta* NOVOZHILOV, 1958; *Sphaerorthothemos* NOVOZHILOV, 1960]. Carapace generally ovate but with wide variation in shape, size, and ornamentation. Characterized by pattern of minute polygons in spaces between growth lines. *L.Dev.-U.Cret.,* cosmop. (36).——FIG. 50,*4*. **C. (E.) minuta* (VON ZEITEN), U.Trias., G.Brit.; *4a,* left valve, ×5; *4b,* detail of polygonal ornamentation, ×45 (111).

C. (Lioestheria) DEPÉRET & MAZERAN, 1912 [**Estheria (Lioestheria) lallyensis* DEPÉRET & MAZERAN, 1912, p. 167; OD] [=*Estheria (Lioestheria)* DEPÉRET & MAZERAN, 1912; *Estheria (Diaplexa), Estheria (Diaphora), Estheria (Polygrapta)* NOVOZHILOV, 1946; *Pseudestheria, Lioestheria* (DEPÉRET & MAZERAN), 1912; *Bairdestheria* RAYMOND, 1946; *Liograpta, Brachygrapta, Rhombograpta, Pseudopolygrapta* NOVOZHILOV, 1954; *Sphaerograpta* NOVOZHILOV, 1958]. Carapace variable in size and shape, though generally ovate; numerous extremely close-set, irregular, and fine concentric growth lines; intervales with fine sculpture, dominantly punctate and granulate—latter commonly expressed as hachure-type markings (longitudinal striae); polygonal mosaic sculpture of *C. (Euestheria)* completely absent, irregular, or feebly expressed. *L.Dev.-L.Cret.,* cosmop. (36).——FIG. 50,*6a*. *C. (L.) raaschi* (RAYMOND), Perm.(Leonard.), USA(Okla.); numerous costellae with narrow, minutely punctate, intervales between them, ×12 (111).——FIG. 50,*6b,c*. *C. (L.) sibirica* (NOVOZHILOV), Perm.(Tartar.), USSR(Lower Toungouska River); *6b,* right valve, ×8; *6c,* detail, long. striae, ×64 (98).

Caenestheria DADAY, 1913 [**Estheria sarsii* SAYCE, 1902; SD TASCH, herein (based on first named nominal species in Hungarian edition, 1913)]. Occipital angle (notch) of head is brief in both sexes, more or less broadly rounded. *Rec.,* cosmop.——FIG. 50,*2*. **C. sarsii* (SAYCE), Australia; *2a,* right valve, male; *2b,* male, head, enl. (30).

Caenestheriella DADAY, 1913 [**C. variabilis*; SD RAYMOND, 1946, p. 225] [=*Opsipolygrapta* NOVOZHILOV, 1954]. Rostrum extended, compressed, and acutely terminated in both sexes, and with conspicuous, deeply cleft occipital notch. *Rec.,*

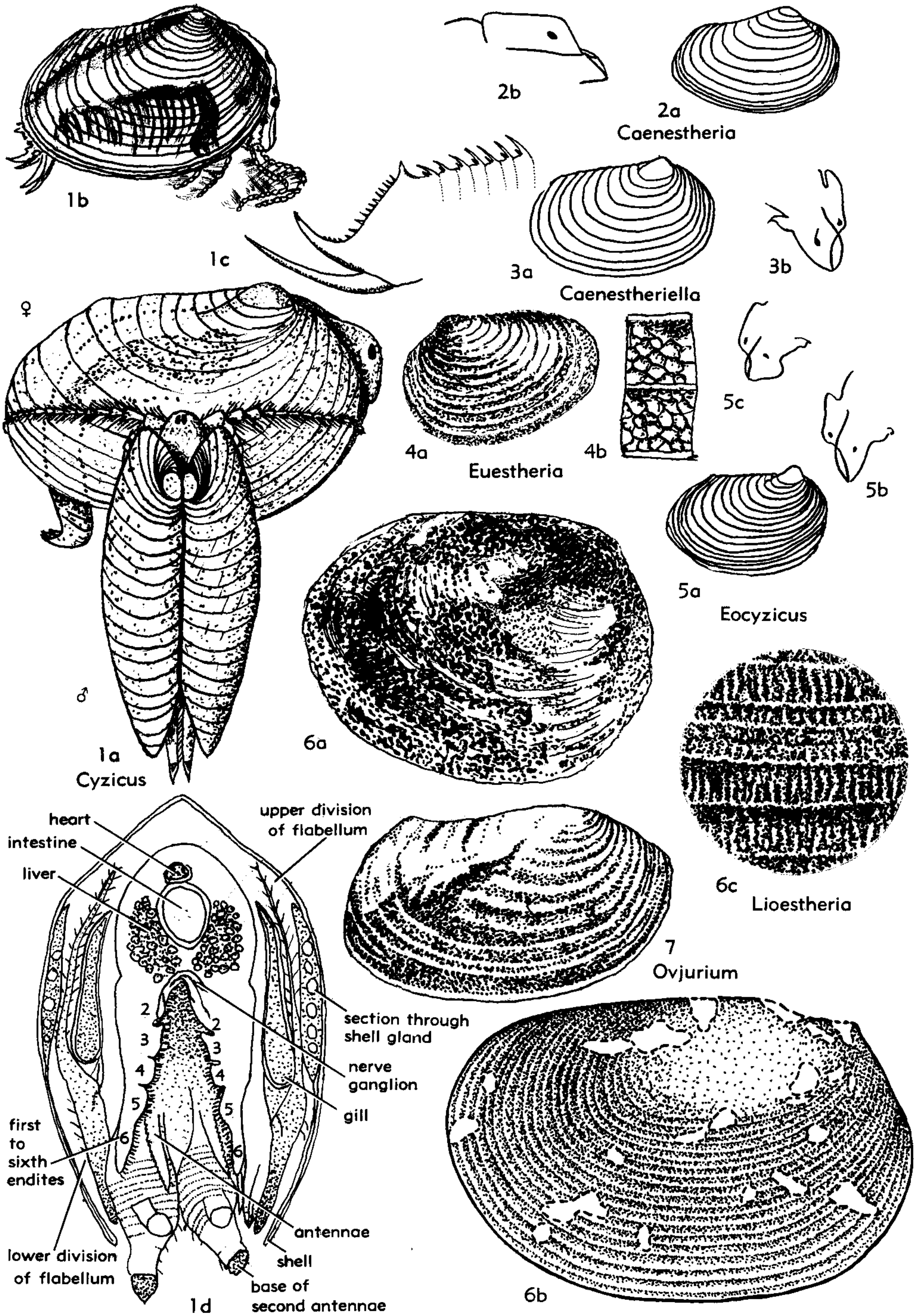


Fig. 50. Cyzicidae (p. R151, R153).

cosmop.——FIG. 50,*3*. **C. variabilis,* Hung.; *3a,* male, right valve; *3b,* female, head showing rostrum and occipital notch, enl. (30, 31).

Eocyzicus DADAY, 1913 [**Estheria digueti* JULES RICHARD, 1895, p. 103; SD TASCH, herein (based on first-named nominal species in Hungarian edition, 1913)]. Rostrum of female terminating acutely but male rostrum spatuliform in side view; occipital notch shallow and rounded. *Rec.,* N.Am.-Australia - India - E. Afr. - ?Brazil.——FIG. 50,*5*. **Eocyzicus digueti* (RICHARD), USA(Calif.); *5a,* male or female valve; enlarged; *5b,* female rostrum; *5c,* male rostrum, enl. (30).

Kontikia NOVOZHILOV, 1958 [**Estheria wianamattensis* MITCHELL, 1926; OD]. [Inadequately documented; doubtful.] *U.Trias.,* Australia.

Ovjurium NOVOZHILOV & VARENTSOV, 1956 (p. 672) [**O. ubsanuri*; OD]. Characterized by elongate valves with parallel anterior and posterior margins; length of valves equal to height; irregular alveolar ornamentation. *M.Dev.(Givet.),* DANSSR(Tuva).——FIG. 50,*7*. **O. ubsanuri,* Touva; right valve, ×9 (165).

Ragozinia NOVOZHILOV, 1958 [**Estheria evenkensis* LYUTKEVICH, 1938 (=*R. leonidi* NOVOZHILOV, 1958; OD]. [Inadequately documented; doubtful.]

Rossokontikia NOVOZHILOV, 1958 [**R. tikhomirovi*; OD]. [Inadequately documented; doubtful.] *U. Dev.(Frasn.),* USSR(Povolzhya).

Sedovia NOVOZHILOV, 1958 [**S. fecunda*; OD]. [*Inadequately documented; doubtful.] *M.Trias. (Anis.),* ArcticO.(Laptevykh Sea).

Sinokontikia NOVOZHILOV, 1958 [**S. youngi*; OD]. [Inadequately documented; doubtful.] *M.Trias. (Anis.),* S. China.

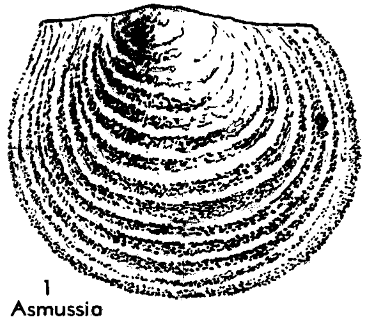
Tigjanium NOVOZHILOV, 1958 [**T. dorofeevi*; OD]. [Inadequately documented; doubtful.] *M.Trias. (Anis.),* ArcticO.(Laptevykh Sea).

Turfanograpta NOVOZHILOV, 1958 [**T. chowmincheni*; OD]. Longitudinal striae in intervals and short, curved spines about 0.05 mm. apart on ventral margin of each interval. [Similar spines in some living conchostracans are more closely spaced.] *L.Cret.(Tougoulouk Ser.),* W.China(Sin-Kiang, Tourfan Basin).——FIG. 51,*3*. **T. chowmincheni*; *3a,* left valve, ×10; *3b,* detail showing curved spines, ×120 (99).

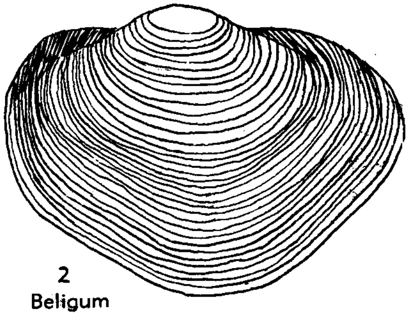
Ubsanuria NOVOZHILOV & VARENTSOV, 1956 [**Trigonestheria kyzylensis* NOVOZHILOV, 1954; OD]. [Inadequately documented; doubtful.] *M.Dev. (Givet.),* USSR(Tuvinsk).

Ujgurokontikia NOVOZHILOV, 1958 [**U. chaoi;* OD]. [Inadequately documented; doubtful.] *U.Jur.,* S. China.

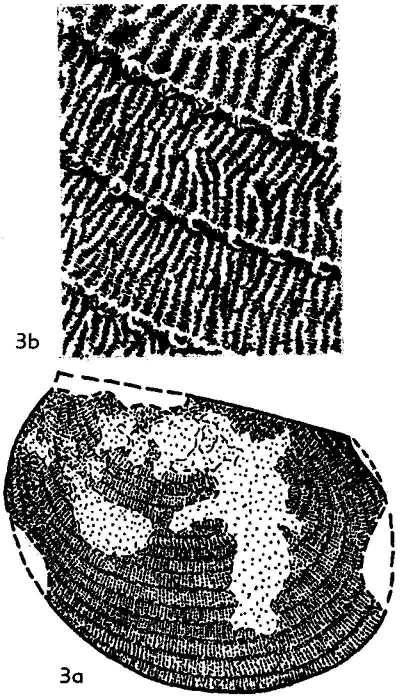
Vilegenia NOVOZHILOV, 1953 [**D. tuberculata* NOVOZHILOV, 1946; OD]. [Inadequately documented; doubtful.] *M.Trias.(Anis.),* ArcticO. (Laptevykh Sea).



Asmussia



Beligum



Turfanograpta

FIG. 51. Cyzicidae *(3);* Asmussiidae (Asmussiinae) *(1,2)* (p. *R*153-*R*154).

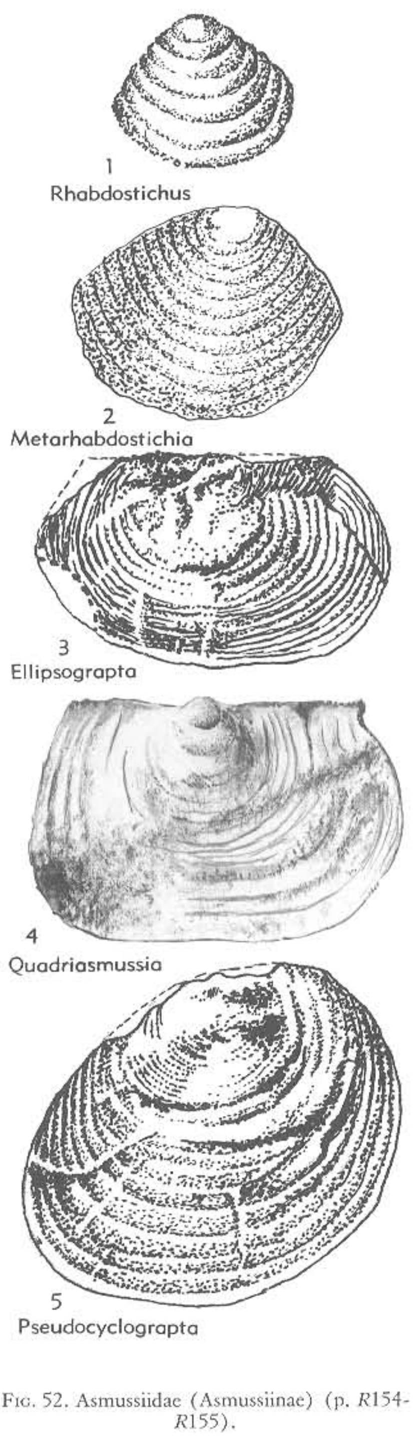


FIG. 52. Asmussiidae (Asmussiinae) (p. R154-R155).

Family ASMUSSIIDAE Kobayashi, 1954

[*nom. transl.* NOVOZHILOV, 1958 (*ex* Asmussiinae KOBAYASHI, 1954] [Rhabdostichidae RUSCONI, 1946; Cyclestherioidinae KOBAYASHI, 1954; Asmussidae TASCH, 1956 (syn. homonym); Glyptoasmussiidae NOVOZHILOV, 1957]

All members of family characterized by generally straight hinge line; carapace shape and beak position variable; ornamentation ranging from hachure-type to alveolar. *L. Dev.-U.Cret.*

Subfamily ASMUSSIINAE Kobayashi, 1954

[=*emend.* TASCH, herein] [=Asmussiinae NOVOZHILOV, 1954 (synhomonym); Loxomegaglyptinae NOVOZHILOV, 1958]

Subcentral beaks generally rising slightly above dorsal margin; carapace outline varying from subovate to subcircular or subquadrate. *L.Dev.-U.Cret.*

Asmussia PACHT, 1849 [**A. membranacea*; OD] [=*Posidonomya* PACHT, 1852 (*non* BRONN, 1834); *Estheria* JONES, 1856 (*non* ROBINEAU-DESVOIDY, 1830; *nec* RUEPPEL, 1837); *Erisopsis, Orthothemos* RAYMOND, 1946; *Loxomicroglypta* NOVOZHILOV & VARENTSOV, 1946; *Cyclograpta* NOVOZHILOV, 1954; *Levenkia* NOVOZHILOV, 1955; *Glyptoasmussia* NOVOZHILOV & VARENTSOV, 1956; *Loxopolygrapta, Loxomegaglypta* NOVOZHILOV, 1958]. Carapace subovate, hinge line straight, beak subcentral, number of concentric growth lines variable, ranging from 13 to 30 or more; interspaces bearing reticulate pattern. *L.Dev.-U.Cret.,* Eu. (G. Brit.-USSR)-Asia(China)-N. Am.(USA). ——FIG. 51,*1*. **A. membranacea,* Dev., Livonia; left valve, ×12 (53).

Beligum NOVOZHILOV, 1958 [**B. doroshkoi*; OD]. Irregularly subovate valves showing dual curvature, that is, of both anterior and posterior ventral portions; beak median, umbo rising above dorsal margin. *U.Dev.(Frasn.),* USSR(Khakassie, Bereck River).——FIG. 51,*2*. **B. doroshkoi*; left valve, ×7 (98).

Ellipsograpta CHANG, 1957 [**E. elliptica*; OD]. Carapace elliptical, dorsal margin straight; both anterior and posterior margins well rounded; umbo subcentral; ornament of hachure-type or of small radially aligned tubercles. *M.Cret.* or *U.Cret.,* China(NW.Heilungkiang).——FIG. 52,*3*. **E. elliptica*, Nenkiang Sh.; left valve, ×10 (23).

Metarhabdostichia NOVOZHILOV, 1958 [**M. tverdoklebovi* (=*Estheria meta* NOVOZHILOV, 1946); OD]. Like *Rhabdostichus* but with valves 10 to 15 times larger. *L.Trias.,* USSR(Tigrian River, Sea of Laptev).——FIG. 52,*2*. **M. tverdoklebovi*; right valve, ×10 (98).

Pseudocyclograpta CHANG, 1957 [**P. convexa*; OD]. Carapace subcircular, with straight or slightly arched dorsal margin and central or subcentral umbo, chiefly characterized by swollen umbonal region, bearing more numerous growth lines than rest of valve; ornament of hachure type. *M.Cret.*

or *U.Cret.,* China(Nengkiang).——Fig. 52,*5*. **P. convexa,* Nenkiang Sh.; right valve, ×9 (23).

Quadriasmussia Kobayashi, 1954 (*emend.* Tasch, 1955) [**Estheria hercynica* Kummerow, 1939; OD]. Carapace subquadrate, expanded ventrally, hinge line straight; prominent convex umbonal area (neanic stage) tapering to subrounded beak, whole area resembling complete valve of *Rhabdostichus pulex* in number of growth lines, shape and size; adult portion of valve gently undulating to flat. *L.Carb.(Culm),* Eu.(Ger.).——Fig. 52,*4*. **Q. hercynica* (Kummerow), Harz Mtns.; left valve, ×12 (62).

Rhabdostichus Raymond, 1946 (*emend.* Tasch, 1955) [**Estheria pulex* Clarke, 1882; OD] [=*Estheria* Clarke, 1882 (*non* Robineau-Desvoidy, 1830; *nec* Rueppell, 1837; *nec* Jones, 1856); *Cyclestherioides* Raymond, 1946; *Brachysteria* Novozhilov, 1954; *Ausmussiella* Novozhilov, 1955; *Cyclotunguzites* Novozhilov, 1958]. Carapace subovate to subcircular, with rounded subcentral umbonal beak and few, relatively widely spaced concentric growth lines. [One or more species of this genus (e.g., *R. pulex*) may represent the neanic stage of other members of the family, as suggested by unusually small size and general characteristics.] *L.Dev.-M.Cret.,* N.Am.(USA)-S.Am.-USSR.——Fig. 52,*1*. **R. pulex* (Clarke), M.Dev.(Hamilton), USA(N.Y.); left valve, ×48 (26).

Ulugkemia Novozhilov, 1955 [**Estheria(?) sinuata* Lyutkevich, 1929; OD] [=*Rhodendorfium* Novozhilov, 1955; *Tshuvashium* Novozhilov, 1958]. Carapace with concavity at anterior, posterior or ventral margins of valves; ornamentation finely alveolar. *M.Dev.(U.Givet.),* N.Asia(USSR).——Fig. 53,*3*. *U. sinuata* (Lyutkevich), Sib.; left valve, ×6 (78).

Wetlugites Novozhilov, 1958 [**W. pronus*; OD]. Lower portion of valve semiovate, upper portion trapezoidal; dorsal margin straight; initial valve with berry-shaped projection above dorsal margin which is anteroterminal in position; ornament alveolar. *L.Trias.,* USSR(Viatka Valley).——Fig. 53,*5*. **W. pronus,* right valve, ×15 (98).

Subfamily TORGALYKIINAE Tasch, 1961

Beaks terminal or nearly terminal, not rising above dorsal margin; valve shape variable. *Dev.-U.Jur.*

Torgalykia Novozhilov, 1955 [**T. ovjurensis*; OD]. Valves rounded, irregular; beak terminal. *Dev.,* USSR(Touva Region).——Fig. 53,*4*. **T. ovjurensis,* Torgalyk River; left valve, ×6 (164).

Eremograpta Novozhilov, 1958 [**Cyclograpta (s.s.) insperata* Novozhilov, 1954; OD]. Shape of valves in form of pouch or almost rounded. *U.Jur.,* E.Asia(Mongolia).——Fig. 53,*1*. **E. insperata* (Novozhilov); left valve, ×2 (95).

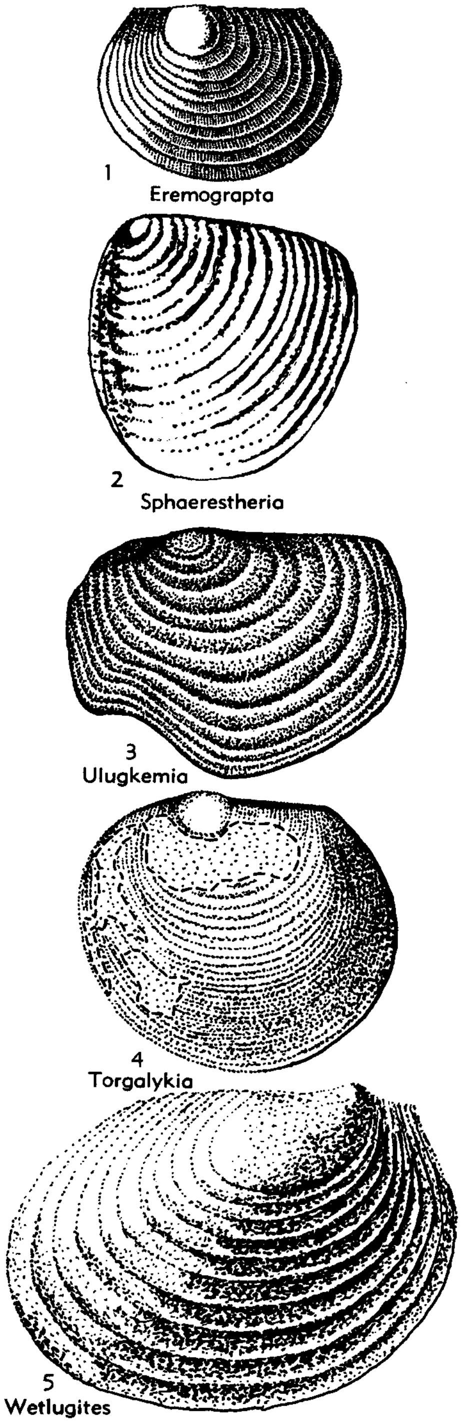


Fig. 53. Asmussiidae (Asmussiinae) (*3,5*), (Torgalykiinae) (*1,2,4*) (p. *R*155-*R*156).

Estheridium Novozhilov, 1958 [**E. parvum*; OD]. [Inadequately documented; doubtful.] *U.Perm.(Tatar.),* Sib.(Lower Tunguska).

Sphaerestheria Novozhilov, 1954 [**Estheria koreana* Ozawa & Watanabe, 1923; OD]. Distinguished by roundly trigonal configuration of valves; ornament unknown. *U.Trias.(Rhaet.)-L.Jur.(Lias.),* Korea (Kyonguito).——Fig. 53,2. **S. koreana* (Ozawa & Watanabe); left valve, ×6 (166).

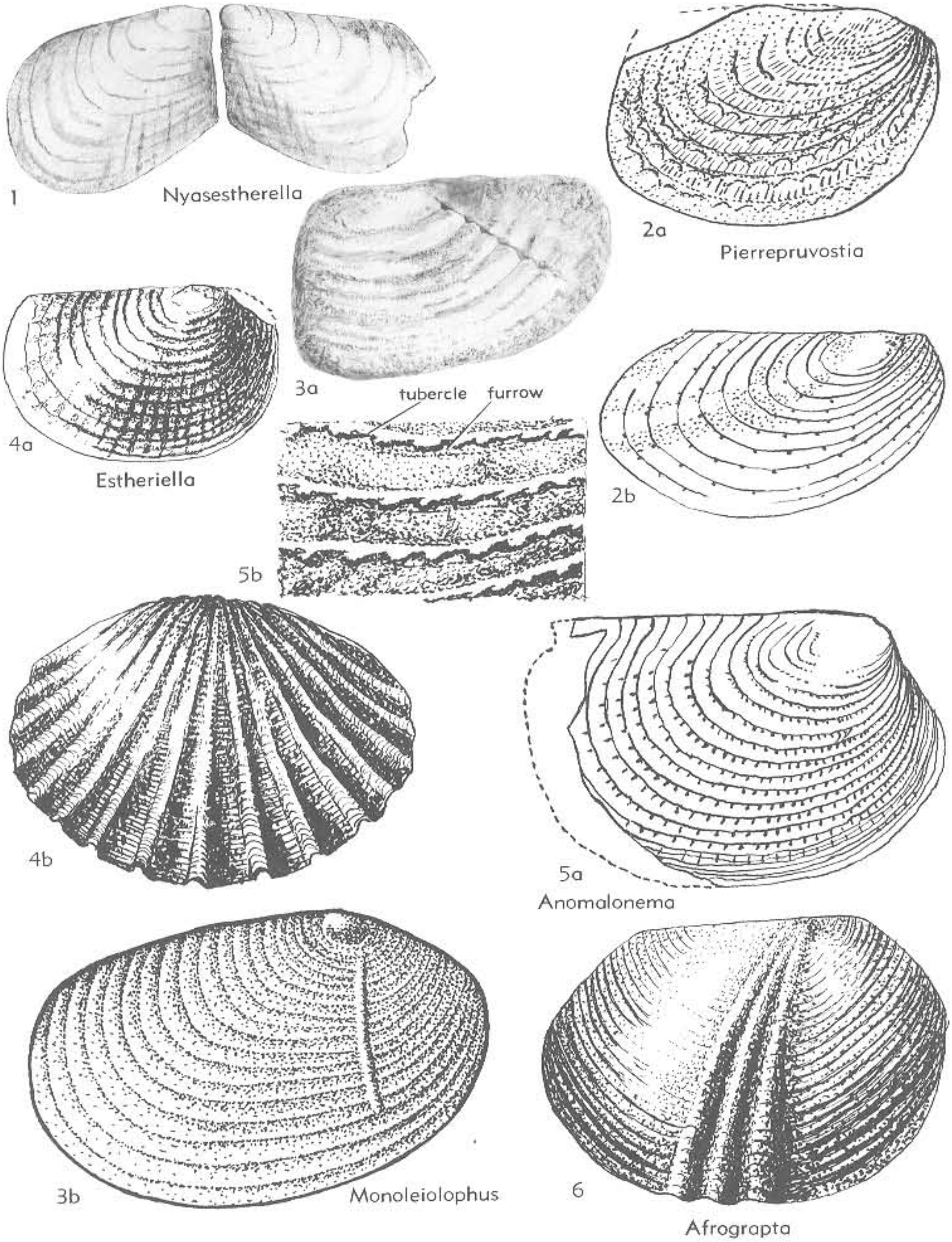


Fig. 54. Estheriellidae (Estheriellinae) *(1,2,4,5)*, (Monoleiolophinae) *(3,6)* (p. R157).

Taimyrites Novozhilov, 1958 [**T. strachovi*; OD]. [Inadequately documented; doubtful.] *L.Trias.*, Sib.(Taimyr).

Superfamily ESTHERIELLOIDEA Kobayashi, 1954

[=*nom. transl.* Tasch, herein (*ex* Estheriellidae Kobayashi, 1954)]

Valves bearing variable number of interrupted or continuous radial costae that do not cross umbo. *U.Carb.-L.Cret.*

Family ESTHERIELLIDAE Kobayashi, 1954

[*non* Estheriellidae Kobayashi, 1953, 58, p. 138, *lapsus calami?*] [=Afrograptidae Novozhilov, 1958 (99); Teixeiriinae Novozhilov, 1958]

Carapace bearing variable number of radial costae which, in general, become obsolete near umbo. *U.Carb.-L.Cret.*

Subfamily ESTHERIELLINAE Kobayashi, 1954

[*nom. transl.* Tasch, herein (*ex* Estheriellidae Kobayashi, 1954] [=Anomalonematinae Novozhilov, 1958]

Carapace bearing five or more costae. *U. Carb.-L.Cret.*

Estheriella Weiss, 1875 [**Posidonomya nodocostata* Giebel, 1857 (=*Estheriella costata* Weiss, 1875; OD] [=*Congestheriella, Mesoleaia* Kobayashi, 1954: *Pteriograpta* Novozhilov, 1954: *Tancrediella, Pseudoestheriella* Novozhilov, 1956; *Angolestheriella, Camerunograpta* Novozhilov, 1958]. Carapace suboval to subelliptical, with several (usually 7 to 12) nodose radiating costae, weak on anterior and posterior sides. *L.Trias.(Bunter)*, Ger. (Sachsen); *L.Cret.(Weald.)*, W.Afr.——Fig. 54, *4a*. **E. nodocostata* (Giebel), Durrenberg; right valve, ×10 (53).——Fig. 54,*4b*. *E. camerouni* Defretin, L.Cret., N.Cameroun; valve showing details of radiating costae, ×75 (35).

Anomalonema Raymond, 1946 [**Estheriella reumauxi* Pruvost, 1911; OD]. Valves with or without posterodorsal recurvature but always characterized by interrupted radial costae. *U.Carb. (Penn.)*, Eu.-N.Am.

A. (Anomalonema). Valves with posterodorsal recurvature, beak terminal; individual growth lines presenting scalloped appearance of low relief on ventral side owing to numerous small tubercles that represent interrupted very fine costae; in anteroventral region crowding of growth lines leads to visual illusion of continuous costae (109). *U.Carb.(Westphal.)*, Eu.(NE. Fr.)-G.Brit.(Kent-Lancashire coal fields, *Anthraconauta phillipsi-tenuis* Zone).——Fig. 54,*5*. **A. (A.) reumauxi* (Pruvost), Fr.; *5a*, right valve, ×9 (109); *5b*, detail of ornament, ×35 (110).

A. (Pierrepruvostia). [**Pierrepruvostia defretinae* Novozhilov, 1958; OD] [=*Estheriella reumauxi* Pruvost, 1919, fig. 34, *non* 35; *Anomalonema (Pierrepruvostia) defretinae* Tasch, 1960]. Lacking posterodorsal recurvature; beak not terminal; subovate; otherwise like *A. (A.) reumauxi* (109). *U.Carb.(Penn.)*, Eu.(NE.Fr.)-N.Am.(NE.USA).——Fig. 54,*2a*. **A. (P.) defretinae* (Novozhilov); right valve, ×10 (110).——Fig. 54,*2b*. *A. (P.) williamsi* Tasch, Alleghen., USA(Pa.); right valve, ×7 (140).

Nyasestheriella Kobayashi, 1954 (*emend.* Tasch, 1955) [**Estheriella nyasana* Newton, 1910; OD]. Carapace extremely small, obliquely subquadrate, with anterior margin straight, truncated, umbones anteroterminal, 12 equidistant concentric lines crossed by numerous obscure radial riblets (costae); fine pits and granules covering thin test. *Permo-Carb.(Karoo)*, Nyasaland.——Fig. 54,*1*. **N. nyasana* (Newton), Nrana; paired valves, ×30 (93).

Subfamily MONOLEIOLOPHINAE Novozhilov, 1954

[=Karagandiinae Tasch, 1961] [=*emend.* Tasch, 1961]

Carapace with one to four radial costae. *Penn.-L.Cret.*

Monoleiolophus Raymond, 1946 (*emend.* Tasch, 1955) [**Monoleiolophus unicostatus* Raymond, 1946 (*non* Reed, 1929) (=*M. conemaughensis* Kobayashi, 1954); OD] [=*Monoleaia* Miroschnichenko, 1956; *Monoleiopholus* Tasch, 1956 (*nom. null.*)]. Carapace with single posterior nodose costa which reaches posterior ventral margin but fades anteriorly and does not reach beak. *Penn.(Conemaugh)*, USA(Pa.).——Fig. 54,*3a*. **M. unicostatus*; left valve, ×7.5 (111).——Fig. 54,*3b*. *M. karagandica* (Miroschnichenko), U. Carb.(U.Namur.), USSR(Karaganda Basin); left valve, ×14 (91).

Afrograpta Novozhilov, 1958 (99) [**Estheriella (Dadaydedeesia) tricostata* Defretin, 1953; OD]. Carapace with 3 radial ribs in medial sector. *L. Cret.(Wealden)*, Afr.——Fig. 54,*6*. **A. tricostata* (Defretin), N.Cameroun, right valve, ×7.5 (35).

Superfamily LEAIOIDEA Raymond, 1946

[*nom. transl.* Novozhilov, 1958 (*ex* Leaiadidae Raymond, 1946)]

Valves bearing up to five radial ribs that cross umbo. *M.Dev.-L.Cret.*

Family LEAIIDAE Raymond, 1946

[*nom. correct.* Novozhilov, 1958 (*pro* Leaiadidae Raymond, 1946, p. 280)] [=Hemicycloleaiinae, Cycloleaiidae, Lioleaiinae Novozhilov, 1952; Amphikoilidae Novozhilov, 1953; Praeleaiinae, Igorvarentsoviinae, Rostroleaiinae Novozhilov, 1956]

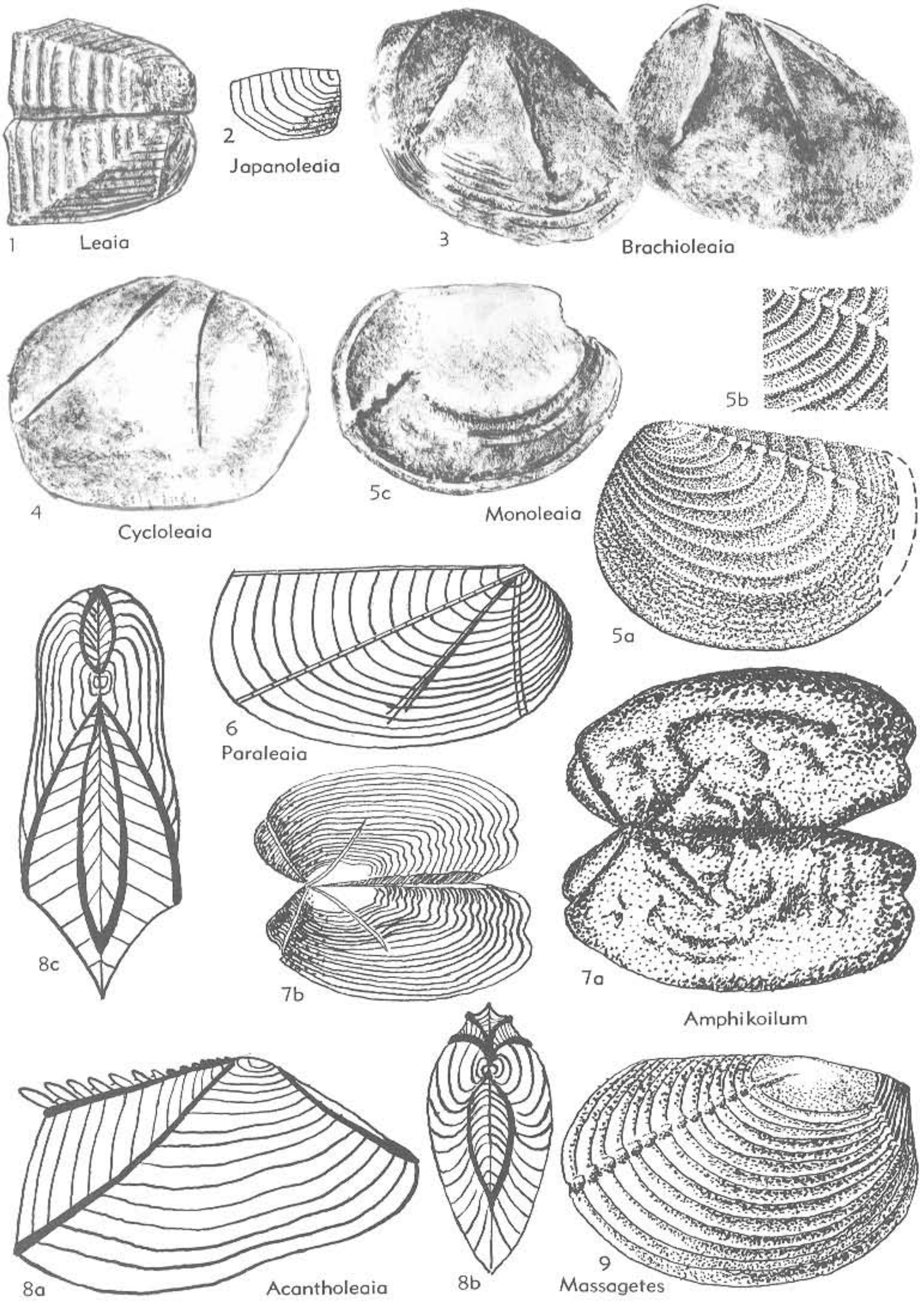


FIG. 55. Leaiidae (p. *R*159).

Carapace with one or more (up to 5) radial ribs, carinae or flat, diagonal edges which diverge from umbo and have concave areas between them; carina may be nodose. *M.Dev.-L.Cret.*

Leaia Jones, 1862 [**Cypricardia leidyi* Lea, 1855, p. 341; OD] [=*Hemicycloleaia* Raymond, 1946; *Dolicholeaia, Leaianella, Kaltanleaia, Gonioleaia, Lioleaia* Novozhilov, 1952; *Mimoleaia, Australoleaia, Siberoleaia* Novozhilov, 1954; *Eoleaia* Kobayashi, 1954; *Igorvarentsovia, Falsirostria, Granirostria, Brachiorrhynchia, Tataroleaia* Novozhilov, 1956]. Carapace outline variable from quadrate to semicircular; valves bearing 2 radial hollow ribs, indistinct in some species, and 3rd rib may be present where dorsal margin thickens, *Miss.(L.Carb.)-U.Perm.*, cosmop.——Fig. 55,*1*. **L. leidyi* (Lea), Miss.(Chester.), USA(Pa.); paired valves, ×5 (53).

Acantholeaia Almeida, 1950 [**A. regoi*; OD]. Carapace suboval; valves tricarinate, with series of spines which issue obliquely from subdorsal carina at points where growth lines intersect carina and diminish in size toward umbonal region; median sector very wide. *U.Perm.*, S.Am.(Brazil).——Fig. 55,*8*. **A. regoi*, Estrada Nova Gr., São Paulo; *8a*, right valve, lateral view; *8b,c*, both valves, anterior and dorsal views, all ×15 (1).

Amphikoilum Novozhilov, 1953 [**A. ermakorum*; OD]. Bicarinate, undulant valves with elevated anterior carina that proceeds from just below or at dorsal margin, crosses umbo, and reaches anterior sector of ventral margin; another thinner, posterior carina in groove proceeds at acute angle from anterior carina, ending high above ventral margin at about 9th growth line; anterior cavity in front of anterior carina, posterior cavity also present, both carinae confined to anterior third of valves. *L.Carb.(Dinant.)*, USSR(Kemerovovskaya Oblast, E. of Novosibirsk).——Fig. 55,*7*. **A. ermakorum*, Ostrog Series, Barzasski Region; *7a*, both valves, ×14; *7b*, carapace (reconstr.), ×11 (96).

Brachioleaia Novozhilov, 1952 [**Leaia quadriradiata* Mitchell, 1925; OD] [=*Quadrileaia* Kobayashi, 1954]. Carapace outline suboval to subsemicircular; valves with 2 typical leaian radials and 2 additional, unequal, weak, short marginal radials located anteriorly and posteriorly near margin. *U.Perm.*, Australia(NewS.Wales).——Fig. 55, *3*. **B. quadriradiata* (Mitchell); two right valves, ×10 (92).

Cycloleaia Novozhilov, 1952 [**Leaia discoidea* Mitchell, 1925; OD] [=*Symmetroleaia* Novozhilov, 1952; *Discoleaia* Kobayashi, 1954 (obj.); *Kargalia* Novozhilov, 1956]. Shape discoidal; valves with two unequal radial ribs originating from blunt umbo, far apart distally. *L.Perm.-U.Perm.*, Australia (New S. Wales)-Eurasia (Urals).——Fig. 55,*4*. **C. discoidea* (Mitchell), New S. Wales; right valve, ×6 (92).

Japanoleaia Novozhilov, 1952 [**Estheria rectangula* Yokahama, 1894; OD] [=*Pseudoleaia* Kobayashi, 1953]. Carapace subquadrate; valves with two flat diagonal edges that (expressed as carinae or radial ribs in other members of family) proceed from umbo, one to posteroventral angle and other to middle part of ventral margin. *L.Cret.(Neocom.)*, Japan.——Fig. 55,*2*. **J. rectangula* (Yokahama), Yuasa; right valve, ×5 (159).

Massagetes Novozhilov, 1954 [**M. karagandensis*; OD]. Valves subovate, characterized by thin anterior carina that proceeds from lower portion of umbo and terminates at about 9th growth line and by thickened posterior carina that proceeds higher up on umbo and forms acute angle with anterior carina, posterior carina extending to ventral margin. *U.Carb.(Stephan., Tentek Series)*, SW.Asia(Kazakhstan).——Fig. 55,*9*. **M. karagandensis*, Karagand Dist.; right valve, ×13 (96).

Monoleaia Tasch, 1956 [**Leaia unicostata* Reed, 1929; OD] [=*Jaxartus* Novozhilov, 1954; *Inkus* Novozhilov, 1956; *Monoleaia* Miroschnichenko, 1956 (jr. homonym?, month of publication uncertain)]. Carapace subovate, valves with single imbricate or nodose radial extending from umbo to rounded posterior ventral margin. *U.Carb.-U. Perm.*, SW. Asia (Kazakhstan)-S. Am. (Brazil).——Fig. 55,*5a,b*. **M. unicostata* (Reed), U.Perm., Brazil; *5a*, left valve, ×9; *5b*, detail of ornamentation, ×9 (112).——Fig. 55,*5c*. *M. monocarinata* (Lyutkevich), 1956 [=*Leaia monocarinata* Lyutkevich, 1941], U.Perm.(Tartarian), USSR; right valve, ×20 (80).

Paraleaia Raymond, 1946 [**P. klieveri* (=*Leaia leidyi* var. *klieveri* Goldenberg, 1873); OD] [=*Troisleaia* Miroschnichenko, 1956; *Teiichium* Novozhilov, 1956]. Narrow and short radial groove, furrow *(Furche)* or accessory radial in wide median section between 2 typical leaian radials. *U.Carb.(Stephan.)*, Eu.(W.Ger.).——Fig. 55,*6*. **P. klieveri*, right valve, ×10 (49).

Praeleaia Lyutkevich, 1929 [**P. quadricarinata*; OD] [=*Lioleaiina* Novozhilov, 1952; *Metaleaia* Kobayashi, 1953]. Carapace elongate-oval; valves bearing four or five radials that fan out from umbo; no radial or dorsal margin. *M.Dev.*, Eu. (Est.); *L.Trias.*, USSR(Sib.).——Fig. 56,*1a*. **P. quadricarinata*, M.Dev., confluence of Ruia and Pliusa Rivers; left valve, ×4 (78).——Fig. 56, *1b*. *P. triasiana* Chernyshev, L.Trias., Kuznetsk Basin; right valve, ×8 (24).

Pteroleaia Copeland, 1962 [**P. canadensis*; OD]. Multiribbed, rostrate carapace with dorsal marginal rib or keel around which growth lines are recurved sinuously. *M.Dev.-U.Dev.*, Canad. Arctic.——Fig. 56,*2*. **P. canadensis*, Can.(Melville Is.); left valve, 4-ribbed specimen, ×4 (29).

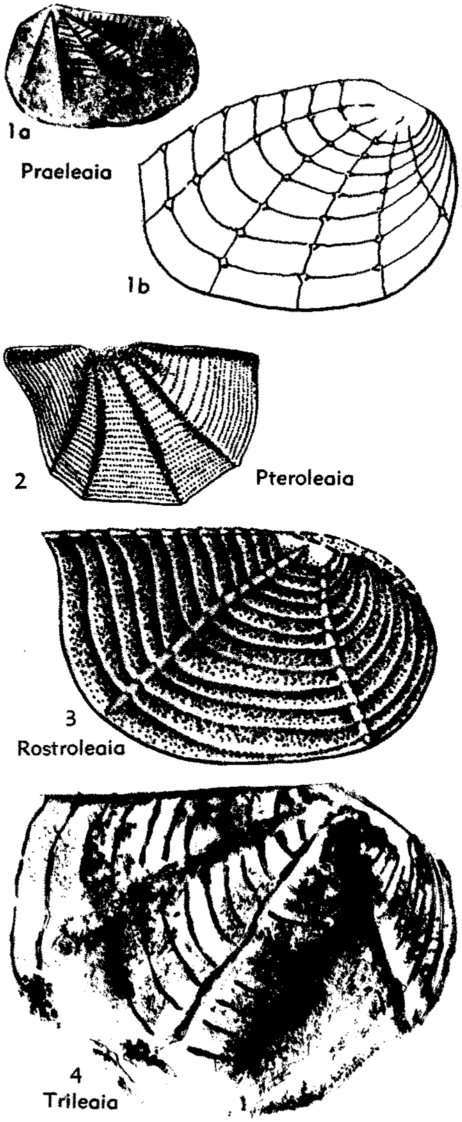


FIG. 56. Leaiidae (p. *R*159-*R*160).

Rostroleaia Novozhilov, 1952 [**R. martynovae*; OD]. Elongated pod-shaped valves bearing 2 carinae; posterodorsal sector limnadiiform, this feature being expressed in some species by sharply pointed termination of dorsal margin. *U.Perm. (Kazan.)*, USSR(Urals).——FIG. 56,*3*. **R. martynovae*, Nikolaevsk Gorge; right valve, ×8 (96).

Trileaia Kobayashi, 1954 [**Leaia belmontensis* Mitchell, 1925; OD]. Carapace outline semicircular to subelliptical; valves with three distinct carinae in addition to thickened straight dorsal margin. *U.Perm.*, Australia(NewS.Wales).——FIG. 56,*4*. **T. belmontensis* (Mitchell); right valve, ×11 (92).

Superfamily VERTEXIOIDEA Kobayashi, 1954

[*nom. transl.* Tasch, herein (*ex* Vertexiinae Kobayashi, 1954] [=Limnadiopseoidea Novozhilov, 1958 (superfam.) (name not based on first-published family-group taxon included in superfamily)]

Carapace with posterior or anteroposterior recurvature of growth lines, or growth lines ending in one or several spinous apophyses, with or without spine or tubercle on initial valve or may bear single rib; also, may be characterized only by single rib and posterodorsal recurvature of growth lines. *L. Carb.-Rec.*

Family VERTEXIIDAE Kobayashi, 1954

[*nom. transl.* Novozhilov, 1958 (*ex* Vertexiinae Kobayashi, 1954)]

Carapace bearing spine or tubercle on each larval valve; serrated margin also occurs where extremities of zones of growth do not all terminate at dorsal margin, and extremities then may be expressed as spinous apophyses. Ornament variable, from irregular alveoli to punctate. *L.Carb.-U. Trias.*

Vertexia Lyutkevich, 1941 [**V. tauricornis*; OD]. Carapace subovate, beak (of larval valve) developed as hollow spine with broad base; spinous apophyses terminate extremities of growth bands; last apophysis a broad-based spine. Sculpture punctate. *U.Perm.(Tatar.)*, Eu.(USSR).——FIG. 57,*1*. **V. tauricornis*, Fileyskoe beds, N.Dvina Valley; *1a*, lat. view, ×21; *1b*, lat. view with two spines, ×10; *1c*, umbonal view, ×11 (80).

Cornia Lyutkevich, 1937 [**C. papillaria* Lyutkevich, 1937, p. 63; OD, *non C. melliculum* Lyutkevich, 1937, p. 64 (*nom. nud.*, incorrectly designated as genotype); *non C. melliculum* Lyutkevich, 1941, p. 36, not "one of the originally included nominal species"—ICZN Code (1961) Art. 69,a] [=*Pemphicyclus* Raymond, 1946]. Valve shape varying from subovate to subrectangular, beak position subcentral to anterior; small spine or tubercle rising from center of initial valve; sculpture punctate. *U.Carb.(Westphal.)-U. Perm. (Tatar.)*, USSR (Sib.)-N. Am. (USA).——FIG. 58,*1a*. *C. papillaria*, U.Perm.(Tatar.), Kuznetsk Basin; two valves, ×17 (79).——FIG. 58, *1b*. *C. laminata* (Raymond), L.Perm.(Leonard.), USA(Kans.-Okla.); right valve, ×24 (142).

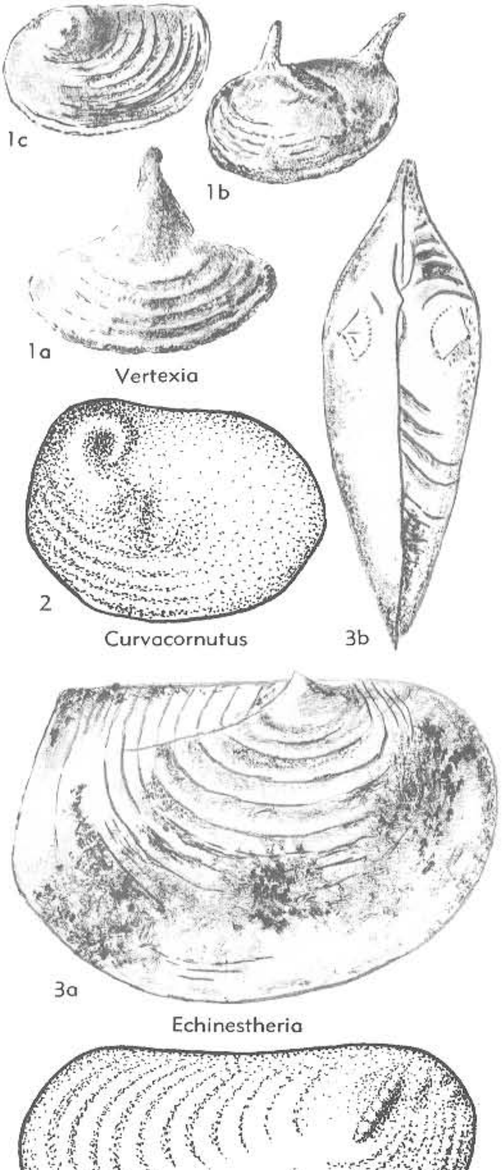


FIG. 57. Vertexiidae (p. *R*160-*R*161).

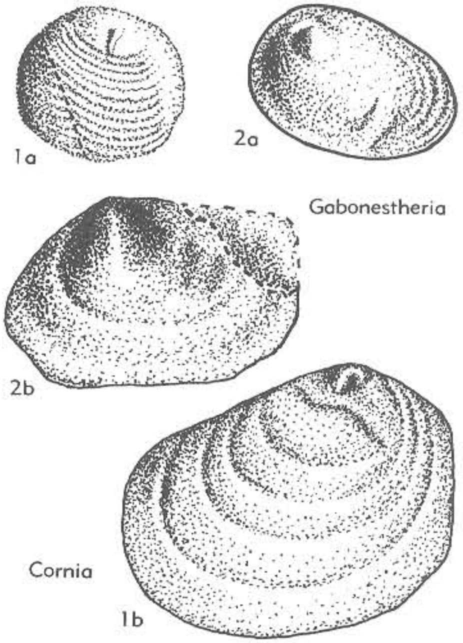


FIG. 58. Vertexiidae (p. *R*160-*R*161).

Curvacornutus TASCH, 1961 [**C. prima;* OD]. Subovate valves bearing looped or markedly curved spine on each initial valve; umbo situated in anterodorsal sector of valve. *L.Perm.,* N.Am. (USA).——FIG. 57,*2*. **C. prima,* Leonard, USA (Kans.); left valve, ×15 (142).

Echinestheria MARLIÈRE, 1950 [**Estheria (Echinestheria) marimbensis*; OD]. Carapace cycladiform, with straight dorsal margin; submedian beak (in larval shell) expressed as large conical spine with broad base. Ornament of interspaces finely reticulate. *U.Trias.,* Port.-W.Afr.——FIG. 57,*3*. **E. marimbensis* (MARLIÈRE), Cassanje F., Angola; *3a,b,* right valve, dorsal view, ×15 (82).

Gabonestheria NOVOZHILOV, 1958 [**Estheria (Pemphicyclus) gabonensis* MARLIÈRE, 1950; OD] [=*Estheria (Pemphicyclus)* MARLIÈRE, 1950]. Large, robust spine on initial shell situated in anterodorsal sector of valve; sculpture finely reticulate. *L.Perm.,* W.Afr.-N.Am.(USA).——FIG. 58, *2a*. **G. gabonensis* (MARLIÈRE), Fr.Equat.Afr. (Gabon); left valve, ×16 (82).——FIG. 58,*2b*. *G. dickinsoni* TASCH, 1960, Leonard, USA(Kans.); left valve, ×19 (142).

Protomonocarina TASCH, 1962 [**P. kechii;* OD]. Subovate valve bearing embryonic rib of five beadlike segments. *L.Perm.,* N.Am.(USA).——FIG. 57,*4*. **P. kechii,* Leonard, USA(Kans.); right valve, ×18 (145).

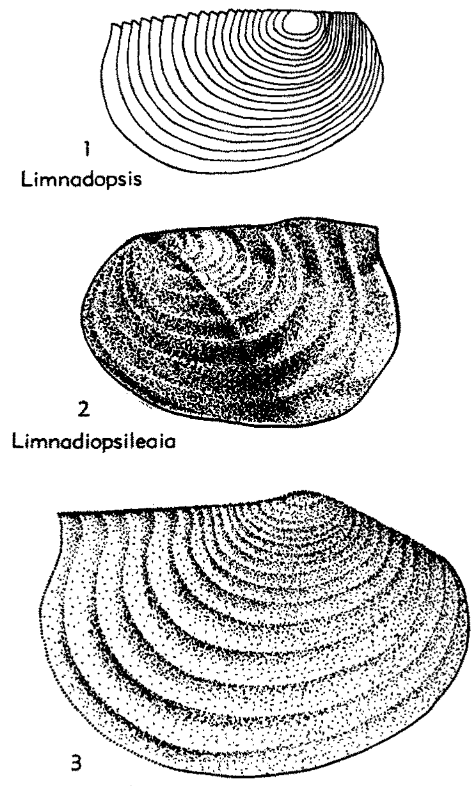


FIG. 59. Limnadopsidae (p. R162).

Family LIMNADOPSIDAE[1] Tasch, new family

[=Limnadiopseidae NOVOZHILOV, 1958 (*recte* Limnadiopsidae) (name based on *Limnadiopsis* DADAY, 1925, *nom. neg.*)]

Posterodorsal margin recurved, dorsal margin varying from subdued serrate (hence, almost straight) to markedly serrate, with spinous apophyses at end of growth bands. Soft parts unknown in fossilized state. *L.Carb.-Rec.*

Limnadopsis SPENCER & HALL, 1896 [**L. brunneus*; SD RAYMOND, 1946 (p. 269)] [=*Limnadiopsis* DADAY, 1925, p. 177 *(nom. null.)*; *Limnadiopsium, Limnadiopseites* NOVOZHILOV, 1958]. Carapace ovate to subovate, compressed, narrower in male than female; union between halves of carapace extending along whole length of dorsal line and rising into much-compressed spined keel (strongly to moderately serrate condition); lines of growth continued on dorsal keel into backwardly directed spines, posterior edges of which are formed by lines of growth, spines decreasing in size from behind forward; beaks well marked. Antennules much smaller than antennae, 26 to 32 pairs of feet. Haft organ present. *Rec., C.Australia* (N.W.Terr.).——FIG. 59,*1*. **L. brunneus*, Port Darwin; right valve, ×4.9 (132).

Belgolimnadiopsis NOVOZHILOV, 1958 [**Estheria (Euestheria) stockmansi* MALLIEUX, 1939]. [Inadequately documented; doubtful.] *L.Dev.*, Eu. (Belg.).

Limnadiopsileaia TASCH, 1962 [**L. noblensis*; OD]. Valves resembling *Palaeolimnadiopis* but bearing single anterior rib. *L.Perm.(Leonard.)*, N.Am. (USA).——FIG. 59,*2*. **L. noblensis*, Wellington F., USA(Okla.); left valve, ×3.2 (145).

Palaeolimnadiopsis RAYMOND, 1946 (*emend.* TASCH, 1960) [**P. carpenteri*; OD] [=*Macrolimnadiopsis* BEURLEN, 1954; *Paleolimnadiopsis* TASCH, 1956 *(nom. null.)*]. Well-defined terminal beak rising above straight dorsal margin (subdued serrate); growth lines closely spaced and numerous on beak, fewer and more widely spaced on rest of valve. *L.Carb.-Cret.*, N.Am.(USA)-S.Am.-Eu.-(USSR).——FIG. 59,*3*. **P. carpenteri*, L.Perm. (Leonard.), USA(Okla.); right valve, ×2.4 (111).

Rossolimnadiopsis NOVOZHILOV, 1958 [**Rossolimnadiopsis marlieri*; OD]. [Inadequately documented; doubtful.] *U.Perm.(Kazan.)*, USSR (Vladimirskaya Oblast).

Family PEMPHILIMNADIOPSIDAE Tasch, 1961

Carapace bearing a tubercle-type spine on initial valve and posterior recurvature of growth lines in adult portions of valves. *Penn.*

Pemphilimnadiopsis TASCH, 1961 [**Estheria ortoni* CLARKE, 1900; OD]. Initial valve with node-like hollow spine, last few growth lines recurved near dorsal margin; relatively large umbo on generally small valve. Resembles *Cornia* but differs in having posterior recurvature. *Penn.*, USA (Ohio).——FIG. 60,*1*. **P. ortoni* (CLARKE), Conemaugh, Carollton; left valve, ×11.3 (141).

Family IPSILONIIDAE Novozhilov, 1958

[*emend.* TASCH, herein] [=Keratestheridae NOVOZHILOV, 1958]

Carapace variable in shape, dorsal margin terminating in aliform apophyses formed by

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[1] Note to R. C. MOORE from Professor L. W. GRENSTED at request of W. E. CHINA, ICZN: "The generic ending *-opsis* makes it genitive ὄχεως, *opseos*, and this (as the accent shows) is treated as a dissyllable. The stem therefore is not *-opse* (or Ionic, *-opsi*) but *-ops*. Poeciliopsinae and Macropsidae are therefore quite correct."

incurvature of anterior or posterior extremities of growth lines, or both of these. Ornament alveolar. *Dev.-L.Cret.*

Ipsilonia Novozhilov, 1953 [**I. auriculata*; OD]. Both ends of dorsal margin winged, valves having form of Greek small letter epsilon. *Dev.*, Eu. (USSR).——Fig. 60,*3*. **I. auriculata*, Koura Region (N. of Caucasus Mtns.); right valve, ×8.1 (98).

Aculestheria Cardosa, 1963 [**A. novojilovi* Cardosa, 1963; OD]. Like *Ipsilonia* but valves broader from anterior to posterior and less elongate dorsal to ventral; apophyses subequal, posterior one being more pronounced. *L.Cret.(Wealden)*, Bahia Series, Brazil.

Keratestheria Chernyshev, 1948 [**K. rugosa*; OD]. Slight incurvature anteriorly below dorsal margin; incurvature of last few growth lines posteriorly forming spine-type projections above dorsal margin with apex directed away from umbonal area. *M.Jur.*, USSR(Sib.).——Fig. 60,*2*. **K. rugosa*, Chitinskaya Oblast (E. of Lake Baikal); right valve, ×4 (161).

Sajania Novozhilov, 1958 [**Ipsilonia kashtagensis* Novozhilov & Varentsov, ?unpubl.); *Sajania kashtagensis* Novozhilov, 1958, p. 110, fig. 17 (98)]. [Inadequately documented; doubtful.] *M.Dev.*, USSR(Sib.), Tuvinskaya Aut. Oblast (SW. of Lake Baikal).

REJECTED GENERIC NAMES

Bileaia Kobayashi, 1954 (127), *nom. dub.*

Palermisca Novozhilov, 1956 (128), jr. subj. syn. of *Dadaydeesia.*

Dadaydeesia Raymond, 1946 (104), pelecypod.

Estheriopsis Rusconi, 1947, probably pelecypod.

Teixeirium Novozhilov, 1958, probably pelecypod.

Fernandoalmeidium Novozhilov, 1958, *nom. dub.*

Innocentium Novozhilov, 1957, inadequately documented.

Eoasmussia Soot-Ryen, 1960, probably pelecypod.[1]

REJECTED SUBFAMILY NAMES

Fernandoalmeidiinae Novozhilov, 1958 (see *Fernandoalmeidium*).

Teixeiriinae Novozhilov, 1958 (see *Teixeirium*).

Order CLADOCERA Latreille, 1829

[=suborder Cladocera Sars, 1865] [*nom. transl.* Calman, 1909 (*ex* Cladocera Latreille, 1829)]

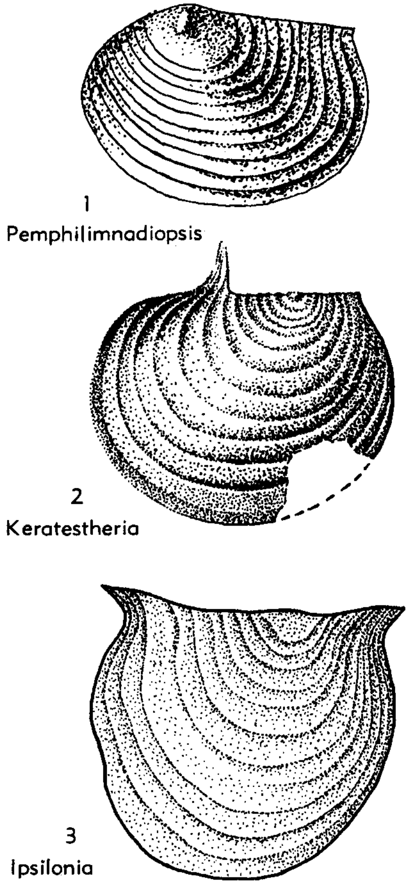

Fig. 60. Pemphilimnadiopsidae *(1)*; Ipsiloniidae *(2,3)* (p. *R*162-*R*163).

[Dr. J. L. Brooks of the Osborn Zoological Laboratory, Yale University, kindly provided, in advance of publication, the first few pages of his chapter on taxonomy of the Cladocera for a revised edition of Ward & Whipple's "Fresh Water Biology." In addition, he provided some valuable references to the literature and technical advice on specific questions. Dr. J. G. Mackin, of the Department of Oceanography, Texas Agricultural and Mechanical College, kindly aided with references to the literature. Dr. F. M. Swain, of the University of Minnesota, confirmed his find of calcified cladoceran fossils. Dr. D. G. Frey, of Indiana University, generously provided some of his publications on cladocerans and discussed with me various aspects of known cladoceran subfossils. Illustrations for this chapter were financed by a Wichita State University Research Grant.]

Carapace univalved, generally enclosing body but leaving head free, reduced in some forms and serving only as a brood sac; paired eyes sessile, coalesced. Antennae biramous (with single exception), natatory; trunk limbs four to six pairs, none of which are postgenital; furcal rami clawlike. De-

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[1] If any conchostracans are found in Ord.-Sil. strata, they are likely to be marine. Soot-Ryen's figured material (Norsk Geol. Tidss., 1960, Bd. 40, pl. 1, fig. 4), however, is closer to a pelecypod-type of organization and lacks definitive conchostracan characters. Homeomorphy between pelecypods and conchostracans is not uncommon. An alleged, but unnamed, Silurian conchostracan genus (Adamazak, 1961, Acta Paleont. Polonica, VI(1): 29-104, pl. 7) is a likely homeomorph of ostracodes in the suborder Eridoconcha.

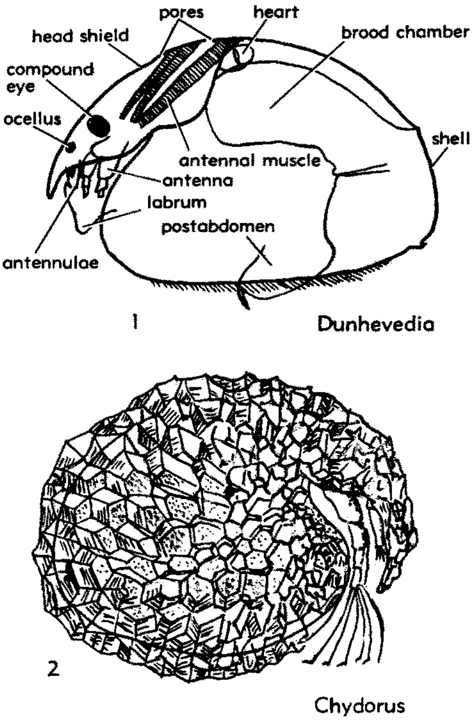

FIG. 61. Anatomical features of cladocerans.——*1. Dunhevedia crassa,* lateral view showing head pores and other anatomy, enlarged (42).——*2. Chydorus faviformis,* male, shell covered with deep polygonal cells, enlarged (42).

velopment embryonic, rarely with metamorphosis. *Oligo.-Rec.*

ANATOMY

The Cladocera, or water fleas, have a body composed of a few somites, exhibiting only obscure segmentation. The head is free of the apparently bivalved shell that covers the body and limbs. Actually, the carapace is a single piece, its point of juncture with the body being marked by a cervical sinus or notch (21, 107). The front of the head is produced downward to form a beaklike rostral process, as in conchostracans. Adult cladocerans possess only four head appendages (antennules, antennae, mandibles, maxillules), but embryos have distinct rudimentary maxillae also. In adults of most other fresh-water crustaceans, however, maxillae are well developed (107).

FREY (42) observed that head pores apparently occur in all Cladocera, at least during embryonic growth or in early instars. He described two series of minute head pores on or near the mid-line of species belonging to genera of the Chydoridae. The number and symmetry of such pores, he noted, were indicators of relationships at generic and suprageneric levels, and thus he was able to employ this known but little used structural feature of the shield to distinguish subfossils from the Schleinsee and Wallensen (41, Table 1) in Germany, as well as exuvia of Recent forms (Fig. 61,*1*).

The antennules perform a sensory function, although in males of some species they serve as clasping organs for holding the female. They are usually very small, unsegmented, and attached to the rear of the rostral process. In contrast, the antennae are large biramous swimming appendages, as in conchostracans. Like the head from which they rise, they are free of the shell and are the chief organs of locomotion.

The mouth parts of the head consist of mandibles and maxillules. The mandibles are formed of single sclerotized pieces, the opposite faces of which are toothed and ridged to form a grinding surface for food. The maxillules, located just behind the mandibles, are small pointed appendages that bear curved setae. These structures serve as a pair of "hands" to pass food to the grinding surface of the mandibles (21). The head also bears large compound-lensed eyes that operate by three muscles on each side. They are capable of rotation.

Trunk appendages are usually five in number. They are leaflike in form, bearing numerous hairs and long setae. The structure of the feet differs in different families but serves the general function of creating water currents through the valves for respiratory and nutritional ends. Modifications for other functions can be seen in the Daphniidae and other families. Here the first pair of feet are prehensile. The hooks and spines serve to anchor the cladocerans to weeds, among which they live, or are used for prehension of food, such as algae. In the genus *Leptodora* the foliaceous character of the limbs is lost, for they are modified to serve in seizing and holding prey (21).

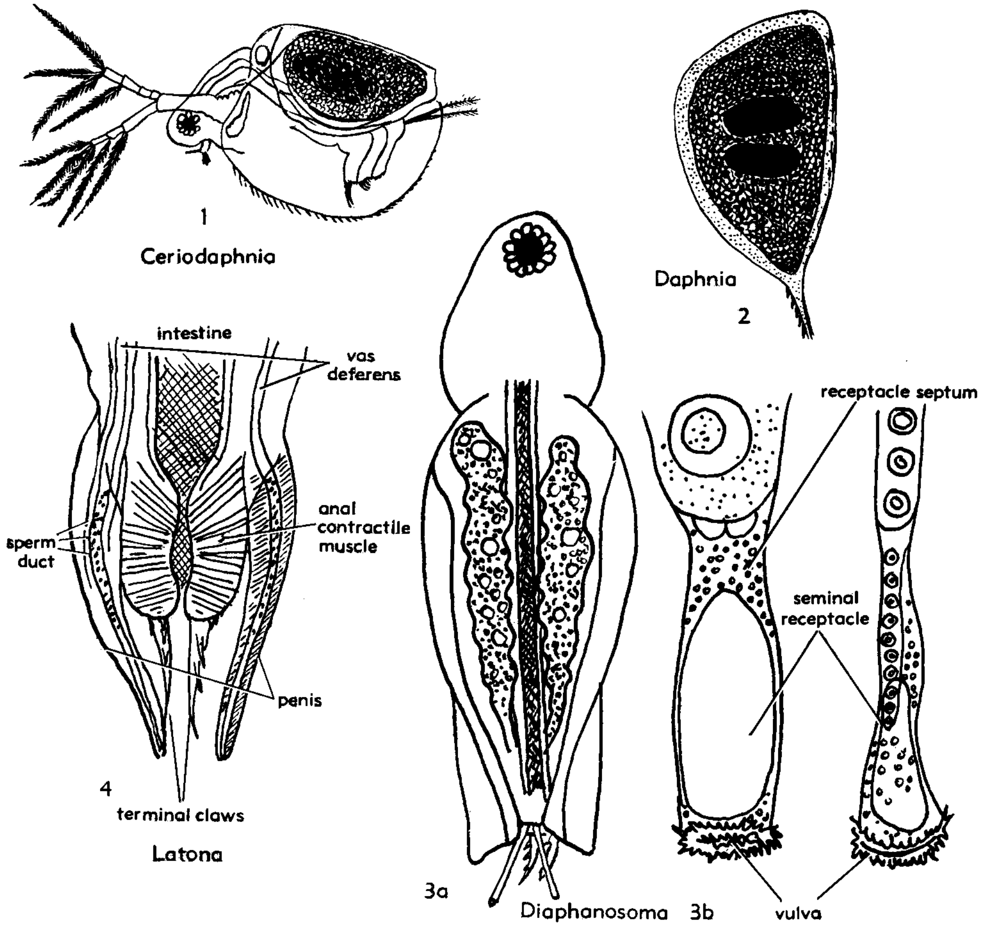

FIG. 62. Anatomical features of cladocerans.——*1. Ceriodaphnia megops,* adult female with ephippial eggs, ×42 (150).——*2. Daphnia pulex,* a separated ephippium containing eggs, enlarged (12).——*3. Diaphanosoma brachyurus*; *3a,* showing disposition of ovaries; *3b,* two views of the posterior part of the ovary, enl. (105).——*4. Latona setifera,* male genitalia, enl. (105).

CARAPACE

FORM AND STRUCTURE

For paleontologists the shell of cladocerans holds chief interest because it is commonly preserved wholly or partially in postglacial deposits. Furthermore, it bears close analogies to the conchostracan carapace, particularly in ornament. Although the cladoceran shell comprises a single piece, as previously noted, it is bent along the back in a manner that gives a bivalved appearance. In side view, different cladoceran shells are variable in shape, ranging from nearly square to oval and subcircular.

Forms like *Daphnia* have a single posterior dorsal spine that prolongs the junction of the carapace halves (12, fig. 1064, p. 695). In *Scapholeberis* a spine projects from the junction of straight posterior and ventral margins (12, fig. 1076, p. 699). The shell is actually a duplicature of the skin and has a very delicate inner layer and a tougher outer wall.

A remarkable adaptation of the shell is seen in the Chydoridae and Daphniidae (12, p. 357, 684) (Fig. 62,*1,2*). After the fertilized egg enters the brood chamber, the walls thicken and darken to form an ephippium. During molting in species of

Daphniidae, the semielliptical portion of the dorsal region of each half of the carapace (ephippium) separates from the rest, whereas in the Chydoridae this part does not separate and the eggs remain enclosed in the carapace.

Pennak (107, p. 357) has observed that the separated ephippia (Fig.62,2) may sink to the bottom or float on the surface. Where they do not sink, the ephippia may be blown ashore and accumulate in diminutive windrows. One might anticipate future finds of such windrows in the fossil record.

The ephippial development is apparently an adaptation to withstand drying and freezing conditions. Especially in small ponds, drying up during summer months is common. The ephippia and their contained eggs can withstand such adverse conditions. When the basins fill again in early autumn, ephippial eggs give rise to parthenogenetic females.

Groschopf (47, p. 32) has reported fossil ephippia of *Daphnia* in addition to other cladoceran remains, in samples from borings through postglacial lake deposits. Scourfield (128) also found fossil ephippia belonging to *Bosmina* and several species of *Alona* in postglacial sediments. Frey (41) found numerous ephippia in lake deposits (Wallensen) of Germany.

ORNAMENTATION

Shell markings, or ornament, in cladocerans are quite varied. In *Ceriodaphnia acanthina* the carapace is strongly reticulated (12, fig. 1080, 1081) and reveal, under high power, a series of irregular polygons with short spinules emerging at points of contact of any two polygon sides (see Fig. 62, *1*). *Streblocerus pygmaeus* also has a reticulated carapace. The reticulations of this form, however, make scalelike ridges, which give the dorsal margin a serrate appearance. Many other genera exhibit reticulation, but the most remarkable development of this condition is to be found in the carapace of certain species of *Chydorus,* in which the shell is covered by very distinctive deep polygonal cells (Fig. 61,*2*) (see Fig. 64,*6c*).

Numerous genera have carapaces bearing longitudinal striations. These generally run from front to back in an almost parallel series of straight or arcuate lines (12, figs. 1119, 1127, 1130). Some species, like *Chydorus piger,* have oblique striae on the lower portion of the shell, whereas the dorsal anterior part lacks striae and is smooth. Many reticulated shells may also bear fine striae (12, figs. 1143, 1165), as in *Alonella excisa.* Still others may have both longitudinal and oblique striae, as in *Pleuroxus truncatus.* Forms like *Euryalona occidentalis* (12, fig. 1124) bear a series of obscure concentric lines that parallel the ventral margin.

ONTOGENY

During growth, cladocerans undergo molting, although this is variously expressed in different genera and species. *Moina macrocopa* has two juvenile instars, whereas species of *Daphnia* vary from three *(D. longispina)* to as many as five *(D. pulex).* The next later instar represents the adolescent stage, occurring between the last juvenile and first adult stages. Adult cladocerans shed successive instars. These are more variable in number than the juvenile instars, so that *D. pulex* has 18 to 25 and *D. longispina* 10 to 19.

Accompanying final development of each adult instar, the young are released from the brood chamber to the outside (107). Birge (12, p. 681) observed that no free-swimming larval forms are known among cladocerans. It should be noted, however, that *Leptodora* is an exception to the general rule. Upon release from the brood chamber, the young are well grown, hatching out in a form closely resembling that of their parents. This event is followed by molting in most genera, i.e., casting off the old skin. Exceptions are found in *Ilyocryptus* and *Monospilus* (12, figs. 1110, 1168). In these genera a new and larger shell appears beneath the old one, which is not cast off. Next follows an observable increase in size and release of a new clutch of eggs to the brood chamber. In still other cladocerans, such as *Polyphemus* and *Leptodora,* the shell is reduced to an egg case.

REPRODUCTION

Reproduction may be sexual or asexual (parthenogenetic). According to Birge (12), species that live in open waters of lakes reproduce chiefly by asexual means. Males of any species are rarely seen and are invariably outnumbered by females.

DIMORPHISM

Dimorphism is expressed in the smaller size of males, which, however, have larger antennules and modified abdomens. Their first feet commonly bear a stout hook for clasping females during copulation (21, 107).

CYCLOMORPHOSIS

A problem such as occurs in study of species of the genus *Daphnia* might well confuse paleontologists. Finding fossil forms of radically variant morphology, one would generally conclude that distinct species should be erected to embrace each morphological type. Yet, cyclomorphosis, or seasonal changes in morphology, is found to alter drastically the appearance of individuals belonging to a single given species of *Daphnia*. Thus, the normal round head of the species in winter becomes a bizarre helmet by midsummer, and reversion to the "normal" head type begins in early autumn (107, fig. 226, p. 360; 118, pl. 21, fig. 223). Cyclomorphic changes also involve variations in size of the eye and posterior spine length (107). The cause or causes of this phenomenon are still baffling. Coker and others suggest that the more prominent helmet-type heads are produced by high temperatures. Genetic factors and turbulent conditions are also credited with a causative role (107).

Specialists on living cladocerans generally recognize that *Daphnia pulex* and *D. longispina* are two highly variable species. The endless numbers of intergrades representing these two species can be accounted for by cyclomorphosis and are not regarded as meriting separate nomenclatural designations.

ECOLOGY

HABITAT

Cladocerans live in fresh to brackish and slightly alkaline waters of all types (12, 107). They are found associated with the marginal vegetation of rivers, in the weedy margins of lakes and swamps, in shallow, silty, and muddy ponds, in both permanent pools and temporary rain-water pools. Some species are common in the shallow ditches of rice paddies (150).

A few marine genera are known; for example, Uéno has reported the genus *Penilia* from the Pacific Coast of Japan. American and South American marine genera include *Evadne* and *Podon* (14, 107). In addition, a few species are restricted to or frequently found in acid or bog waters. *Acantholeberis curvirostris* is abundant in sphagnum bogs of Maine, Wisconsin, and Louisiana. *Streblocerus serricaudatus,* found in weedy pools and lake margins in North America, occurs in weedy bog ponds in the Kyoto region of Japan.

Although various species most frequently live among weeds and feed on algae, bottom-dwellers are known. The latter include *Ilyocryptus* and *Monospilus*. The former lives in mud (12).

SALINITY, pH, TEMPERATURE

Most cladocerans are found in waters with a pH range of 6.5 to 8.5. Very few species are limited in distribution by temperature (105). Most species are eurythermal (107).

The amount of calcium and magnesium in solution plays an important role in the life of some cladocerans. *Holopedium* is apparently confined to calcium-poor waters. Magnesium appears to inhibit reproduction in various species of *Daphnia* (107).

PREDATORS AND FOOD

Cladocerans, together with copepods, play an important role in the food chain of waters which they inhabit. Insect larvae consume cladocerans and in turn are eaten by larger fishes. Certain fish feed directly on cladocerans. In Japan some species of *Moina, Daphnia,* and other genera are known as "mijinko," used by pisciculturists as food for goldfish fry (150).

Birge has pointed out that cladocerans have definite food preferences (12). Diatoms, for example, are preferred to blue-green algae. Some forms of algae are favored over others. Both of these are generally plentiful in the ecological niches that cladocerans fill.

FAUNAL AND FLORAL ASSOCIATES

Frey (41) lists the following microfossil associates found with fossil cladocerans in a German glacial lake: Protozoa rhizopods *(Assulina, Nebella)*; Porifera *(Spongilla,* spicules, gemmules); Turbellaria *(Gyratrix, Otomesostoma, Dendrocoelum, Polycelis, Planaria)*; Bryozoa *(Plumatella, Cristatella,* statoblasts); Oligochaeta (cocoons); Ostracoda; Tendipedidae (midges); Hydrocarina *(Notaspis)*; water mites.

In test tubes planted in a Sedgwick County (Kansas) pond, I have found cladocerans, copepods, insect larvae, and varied protozoans. Blue-green algae, diatoms and other flora, as well as various fishes, have been reported in modern cladoceran-stocked ponds.

STRATIGRAPHICAL AND BIOLOGICAL VALUE

SUBFOSSIL GROUPS

Published references to subfossil (Recent) cladocerans are few. Investigations generally have not been directed primarily to search for cladocerans but rather to determining the nature of animal and plant remains contained in successive layers of lake deposits. Essentially, work has been restricted to that done by limnologists. Recently, SWAIN, a geologist, made an extensive limnological study, giving emphasis to types of data which have greatest interest to geology (135). MESSIATZEV and associates have studied the bottom sediments of three very large lakes near Moscow (90) and have figured species of cladocerans found buried in them (e.g., *Bosmina, Alona, Pleuroxus, Chydorus, Graptoleberis, Acroperus, Alonella, Peracantha, Eurycercus, Sida, ?Daphnia*).

LUNDQUIST (76) has reported *Lynceus* (= *Alona*) and other *Cladocerenschale* from postglacial bottom deposits. In similar deposits of the Grossen Plöner Sees, Ostholstein, GROSCHOPF (47), whose primary concern was a pollen analysis of the bottom sediments, found ephippia of *Daphnia* sp. Shells, antennae, mandibles, and other remains of *Daphnia, Bosmina,* and other cladocerans have been found in deep cores of pelagic "gyttja." CONGER (28), primarily interested in diatoms occurring in sediments of Crystal Lake, Wisconsin, merely mentioned crustacean remains also obtained, presumably cladocerans.

An excellent description of "fossil species" of cladocerans was published by AUSTIN in a study of Connecticut lake sediments (3). This reports the occurrence of *Bosmina* remains, postabdomens of *Leydigia,* carapaces of *Chydorus,* and abdomens of *Eurycercus.*

SCOURFIELD (128) has studied cores of bottom deposits of Lake Windermere, England. The cores consisted mainly of dark brown organic deposits resting on pink laminated glacial clay. Overlying the organic deposit was a semiliquid ooze that was not considered to be part of the core. Cladoceran remains were generally empty valves and head shields, detached abdomens, mandibles, claws, setae, etc. Most common were remains of the planktonic genus *Bosmina.* Three other planktonic genera included *Daphnia, Bythotrephes,* and *Leptodora.* All other forms belonged to the littoral Chydoridae, including *Eurycercus, Camptocercus, Alonopsis, Graptoleberis, Alona, Rhynchotalona, Alonella, Paracantha, Chydorus,* and *Anchistrophus.*

FREY (41, table 4) has listed species and subspecies of Chydoridae in seven major studies of European lake sediments. In addition to work by MESSIATZEV (90) and SCOURFIELD (128), already mentioned, papers by ROSSOLIMO (114), ZEMP (160), and FREY (40, 41) are cited. Still other reports on subfossil cladocerans include publications by POULSEN (Denmark) (108), BREHM, KRASSKE, and KREGER (Austria) (16). FREY (41) has culled data from the works of five other investigators: TIDELSKI (Germany), NIPKOW (Switzerland), GAMS (Austria), SCOURFIELD (Ponder's End, England), and DEEVEY (New Zealand). Noticeably absent from the literature are reports on subfossil cladocerans from Canada, Central and South America, Africa, Australia, and Asia.

A recent study of lake deposits in Minnesota has indicated that cores from Burnside Lake, at a depth up to 5 inches below the bottom, consist of "silty clay, abundant pollen, diatoms, cladocerans" (135, p. 621). In the coarse fractions of copropel from Prior and Minnetonka Lakes, some 18 percent of the fraction consist of sclerotized exoskeletons of arthropods, mainly cladocerans. Also it was noted that cladocerans, along with planktonic diatoms and testate protozoans, are abundant in the upper parts of the cores. Cladocerans are not very common in the lower parts of the cores. It will be valuable to have all cladoceran fragments from such samples identified, as in various studies mentioned above.

All cladocerans reported in the above-mentioned studies are subfossils, being found preserved but not fossilized, sclerotized[1] but not calcified. Faunas preserved

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[1] A. G. RICHARDS (1951, *The integument of arthropods,* Univ. Minnesota Press, p. 48) indicates that the body wall of *Daphnia* and *Leptodora* gives a positive test for chitin. Where such evidence exists, we may speak of "chitinous" rather than "sclerotized."

in postglacial deposits make it obvious that the depositional and faunal history of such lakes can be unraveled by coring at several stations along a traverse (41, figs. 1, 2). Since all subfossil genera and species have living representatives in the waters of present-day lakes, important biological data can be derived. Thus, Scourfield (128) has indicated that morphologically the species of *Bosmina* in cores studied by him, when compared to species now living in lake waters, "probably does point to a less evolved condition." More systematic work in such directions can provide valuable data on cladoceran, and hence on branchiopod, evolution.

From the point of view of geology and paleontology, students of the Pleistocene, especially, may derive new data relating to glacial lakes and postglacial sedimentation, climatic changes, and the like through systematic study of cladocerans and related forms found in cores. Cladocerans can be of value as stratigraphic markers for correlating equivalent horizons of lake deposits both within a region and in neighboring or distantly separated regions. This will probably be found true when, instead of generalized reports that merely record the presence of remains found in cores, generic and specific identifications of the material are given.

Some genera of cladocerans have been reported from marine environments (14, 107, 150) and it is altogether possible that certain Recent and older lagoonal or other sediments may contain remains of these or related genera.

Frey (41) has pointed out two assumptions used by him in identifying fossil cladocerans from a late glacial lake (Wallensen, northern Germany). First, he assumed "no major shift in the zoogeography of the Cladocera, aside from a northward readjustment with the retreat of the glaciers and the amelioration of climate." Second, he assumed that no extensive morphological changes had occurred in cladoceran species during the last 11,000 years or so. On this basis, he found it possible to make seemingly useful comparisons of subfossil cladocerans with species occurring in Europe at the present time.

POPULATION STUDIES

Brooks (18) has discussed an interesting difference in the reproductive biology of *Daphnia middendorfiana,* pointing out that high-latitude populations produce viable resting eggs in the absence of males, whereas low-latitude populations produce males and require that resting eggs be fertilized. This last is thought to be the "more primitive" condition. Brooks surmised that the expansion of this species from low latitudes to the Arctic of North America, Greenland, and Siberia probably occurred in relatively recent times. He further commented on the "nearly identical appearance" of *D. middendorfiana* populations wherever they occur. Thus, the difference in reproductive biology lacks morphological analogues and since it is a "secondary condition" may be regarded as a "temporary clone" not justifying nomenclatural recognition (88).

The chief differences discernible in cladoceran populations may be regarded as minor variations (geographic clines). On the other hand, present evidence indicates that major variation in cladoceran populations probably dates back to the older Tertiary. It is hoped that future fossil finds will document this speculation.

GEOLOGIC OCCURRENCE AND ORIGIN

Brooks (18) has suggested that forms such as *Daphnia retrocurva* and *D. dubis,* inhabitants of large deep glacial lakes, originated "sometime during the Pleistocene." His suggestion is based on present geographical and ecological distribution, coupled with morphological distinctness of observed forms. On the other hand, *D. laevis,* a southern species inhabiting shallow pools, and *D. parvula,* inhabiting small lakes, denote a "relatively old" origination. This thesis is sustained, according to Brooks, by the fact that *D. laevis* is morphologically similar to species restricted to Africa south of the Sahara, whereas *D. parvula,* widely distributed in South America and North America, is judged to be older than *D. retrocurva.*

Frey (41) has observed that the mentioned seven major studies of cladocerans collected from European glacial lake sediments include, among other families, 43 species and subspecies of central European chydorids listed by Wagler. Brooks (18) thought that *Daphnia thorata* may have lived in extinct glacial lakes such as Lakes Lahontan and Bonneville, as well as in contemporary lakes of the time, judging from their present distribution.

Noting the "close similarity between the structures of adult Cladocera and larvae of certain conchostracans" [*Cyclestheria* (121)], Brooks (17, 19) was persuaded that "the Cladocera are (or may be) neotenic (paedomorphic) derivatives of some early conchostracan." As already discussed, Permian collections from the Kansas-Oklahoma region or other parts of the world have not yet yielded any cladoceran remains. My experiments with living cladocerans allowed freshly caught specimens to dry on pond muds. Even after thorough desiccation, the general morphology of the carapace could be deciphered. Hence, in ancient lacustrine sediments also, one could expect that, in some instances in Permian fresh-water sediments, cladocerans would have been found by now, if present. While tracing Leonardian conchostracan-bearing beds in Kansas and Oklahoma, I have hunted thoroughly for cladoceran remains in the sediments. None were found. We may thus, at present, place cladoceran origination in the Mesozoic or possibly early Cenozoic time. [As noted subsequently, Miocene cladocerans have been discovered.]

Evidence for the missing link at the point of conchostracan-cladoceran separation should be sought in fluvatile and lacustrine sediments of Upper Cretaceous-pre-Oligocene age. Association with post-Cretaceous or younger fossil clam shrimps is one possibility. Another may be found in organic shales of Mesozoic-Tertiary age. Living *Cyclestheria hislopi* (Baird) is the most likely candidate for the type transitional conchostracan. Postulates such as this have been made for various ancestral and transitional types among fossil vertebrates. These types were sought for and occasionally field search has been rewarded. It is time for invertebrate paleontologists to pursue such germinal suppositions. The possibility is very real that fossilized cladoceran remains, impressions, and the like, may be found in Tertiary lacustrine or near-shore marine sediments.[1]

Suborder EUCLADOCERA Eriksson, 1934

Body and legs enclosed in small univalved carapace (less than 6 mm. in length) bent along back and appearing bivalved, legs usually flattened branchial appendages (17, 19). *Oligo.-Rec.*

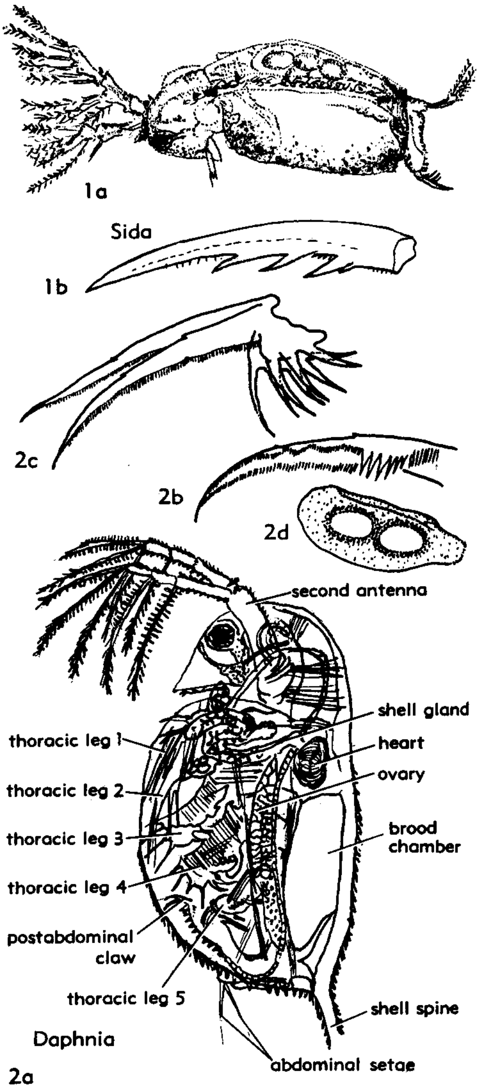

Fig. 63. Sididae *(1)*; Daphniidae *(2)* (p. R171).

Superfamily SIDOIDEA G. O. Sars, 1888

[*nom. transl.* Brooks, 1959 (*ex* Sididae G. O. Sars, 1888)]
[="tribe" Ctenopoda Sars, 1865]

Six pairs of legs, all foliaceous and all similar except last (19). *Rec.*

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[1] After this had been written, it was gratifying to learn that Dr. F. M. Swain (oral communication) has collected calcified cladoceran ephippia from Miocene lacustrine sediments in Nevada. Subsequently two important preliminary reports have become available: (1) D. G. Frey, 1960, "Cladocera from the Eemian Interglacial of Denmark," Paleont. Soc. program (Denver), abstract, p. 100, recording 25 species of chydorids; and (2) K. A. Dickinson & F. M. Swain, 1961, "Ostracoda and Cladocera of the Late Tertiary Humboldt Formation, Northeastern Nevada," Soc. Econ. Paleont. Mineral. program (Denver) abstract, p. 91, recording three calcified ephippia assigned to a new genus, *Daphnia,* n.sp., and *D.* sp., which were illustrated and described in the oral presentation of the paper.

Family SIDIDAE G. O. Sars, 1888

Carapace of usual eucladoceran type, without gelatinous mantle; feet entirely covered by shell. Antennae biramous in female, rami flattened, dorsal ones with numerous setae, both lateral and terminal. *Rec.*

Sida Strauss, 1820 [**Daphnia crystallina* O. F. Müller, 1785; OD]. Dorsal ramus of antennae 3-jointed; rostrum pointed; shell elongate with rounded ends. *Rec.,* Eu.(Eng.-USSR)-N.Am.——Fig. 63,*1*. **S. crystallina* (Müller); *1a,* entire individual (USA), lat. view, ×12 (12); *1b,* subfossil (USSR, Moscow, postabdominal claw, enl. (90). [Other subfossils are known from USA (Conn.) (3).]

Superfamily DAPHNIOIDEA Strauss, 1820

[*nom. transl.* Tasch, herein (*ex* Daphnides Strauss, 1820, *nom. imperf.*)] [="tribe" Anomopoda Sars, 1865; superfamily Chydoroidea Stebbing, 1902 (*nom. transl.* Brooks, 1959 (*ex* Chydoridae Stebbing, 1902)]

Legs five or six pairs, first and second pairs more or less prehensile, with cylindrical joints, others foliaceous (19). *Oligo.-Rec.*

Family DAPHNIIDAE Strauss, 1820

[*nom. correct.* Tasch, herein (*pro* Daphnides Strauss, 1820, *nom. imperf.*) Zool. Code (1961), Art. II,e,iii] [=Daphniades Baird, 1850; Daphnidae F. Leydig, 1860 (*nom. imperf.*)]

Body oval, head rounded, dorsal ramus of antenna three-segmented; ventral ramus four-segmented; postabdomen distinctly set off from body, usually compressed and bearing anal spines; claws invariably denticulate; may be pectinate; typical ephippium formed. *Oligo.-Rec.*

Daphnia O. F. Müller, 1785 [**Monoculus pulex* De Geer, 1778; OD]. Carapace with sharp caudal spine extending from upper posterior angle, no cervical sinus; surface with polygonal usually rhomboid markings (12). *Oligo.-Rec.,* cosmop.——Fig. 63,*2a,b*. **D. pulex* (De Geer), *Rec.,* USA; *2a,* ♀, configuration of valve and gross anatomy, enl. (12); *2b,* subfossil (Conn.), *D. pulex*-type claw, enl. (41). [Other subfossils are known from Ger.(Schleinsee, Grossen Plöner Sees, 41, 47) and USSR(Moscow, 90).]——Fig. 63,*2c*. *D. longispina* (Müller); subfossil from Aus.(Längsee), *D. longispina*-type claw and postabdominal teeth, enl. (41). [Other subfossils are known from Switz.(Zürichsee, 41), USSR(lakes near Moscow), Eng.(Lake Windermere), fossils from Mio. lake deposits (Humboldt F.) of NE. Nevada.].——Fig. 63,*2d*. *D. fossilis* Heyden, Oligo.(Braunkohle), W.Ger.; fossil ephippia bearing two ephippial eggs (0.2-0.4 mm. diameter), enl. (170b). [*See* also Fig. 62,*2*.]

Family CHYDORIDAE Stebbing, 1902

Fornices extended and covering antennules in whole or part, and uniting with rostrum to form beak that projects in front of antennules (19). *Rec.*

Subfamily CHYDORINAE Stebbing, 1902

Anus on dorsal side of postabdomen with postanal portion bearing denticles; no hepatic caeca. Two summer eggs and ephippial egg. Male with strong hook on first legs (19). *Rec.*

Chydorus Leach, 1843 [**Lynceus sphaericus* O. F. Müller; OD]. Postabdomen ordinarily short, with prominent preanal angle; shape spherical or ovate; rostrum long and acute (19). *Rec.,* cosmop. ——Fig. 64,*6a,b*. **C. sphaericus* (Müller), cosmop.; *6a,* entire individual, lat. view, ×120 (12); *6b,* subfossil from Ger.(Wallensen); shell fragment, enl. (41). [Other subfossils are known from Eng. (Arctic bed at Ponder's End, Lake Windermere, 41, 128), USSR (small lakes and bogs near Moscow, 90, 114), Switz. (Wauwiler See, 160), Denm. (Naestved, 108), Aus. (Schwarzsee, Langsee, 16, 40).]——Fig. 64,*6c*. *C. faviformis* Birge, subfossil from USA(Conn.); carapace, ×90 (3).——Fig. 64,*6d*. *C. piger* Sars, USA (Maine); carapace, ×100 (12). [Subfossils are known from Eng. (Lake Windermere, 128), USSR (lakes and bogs near Moscow, 90), Switz. (Wauwiler See, 160), Ger. (Wallensen, 41).]——Fig. 64,*6e*. *C. globosus* Baird, USA; carapace, enl. (12). [Subfossils are known from USSR (Moscow, 90).] [*See* also Fig. 61,*2*.]

Acroperus Baird, 1843 [**A. harpae*; OD]. Crest on head and back, carapace subquadrate, obliquely striated, inferoposteal angle rounded or acute, usually with teeth, postabdomen broad, without marginal denticules (19). *Rec.,* Eu.(Eng.-USSR)-N.Am.——Fig. 64,*3*. **A. harpae,* USA; *3a,* entire individual, lat. view, ×20 (12); *3b,c,* subfossil from Ger.(Wallensen), showing shell and posterior ventral angle, both enl. (41). [Other subfossils are known from Eng. (Arctic bed at Ponder's End, 41), USSR (small lakes and bogs near Moscow, 90), Switz. (Wauwiler See, 160), Aus. (Schwarzsee, Längsee, 16, 40).]

Alona Baird, 1843 [**Lynceus quadrangularis* O. F. Müller, 1785; OD]. Shell subquadrate, surface with longitudinal striae (19). *Rec.,* cosmop.——Fig. 64,*1a,b*. **A. quadrangularis* (Müller); *1a,* postabdomen from USA, enlarged (12); *1b,* subfossil from USSR(Moscow), postabdomen, enl. (90). [Other subfossils are known from USSR (lakes and bogs near Moscow, 114), N.Ger. (small morainal basins and Wallensen brown coal pit, 41), USA(Conn., Linsley Pond, 3), Switz. (Wauwiler See, 160), Aus. (Längsee, 40).].——Fig. 64,*1c*. *A. guttata* Sars; postabdomen from USA, enl. (12). [Subfossils are known from Eng. (Lake Windermere, 128), USSR (lakes and bogs near Moscow, 114), Switz. (Wauwiler See, 160), Aus. (Schwarzsee, Längsee, 16, 40), Ger. (Wallensen, 41).]——Fig. 64,*1d*. *A. affinis* (Leydig); subfossil, from USA(Conn.), postabdomen and claw, ×100 (3). [Other subfossils are known from Eng. (Lake Windermere, 127), Denm. (Naestved,

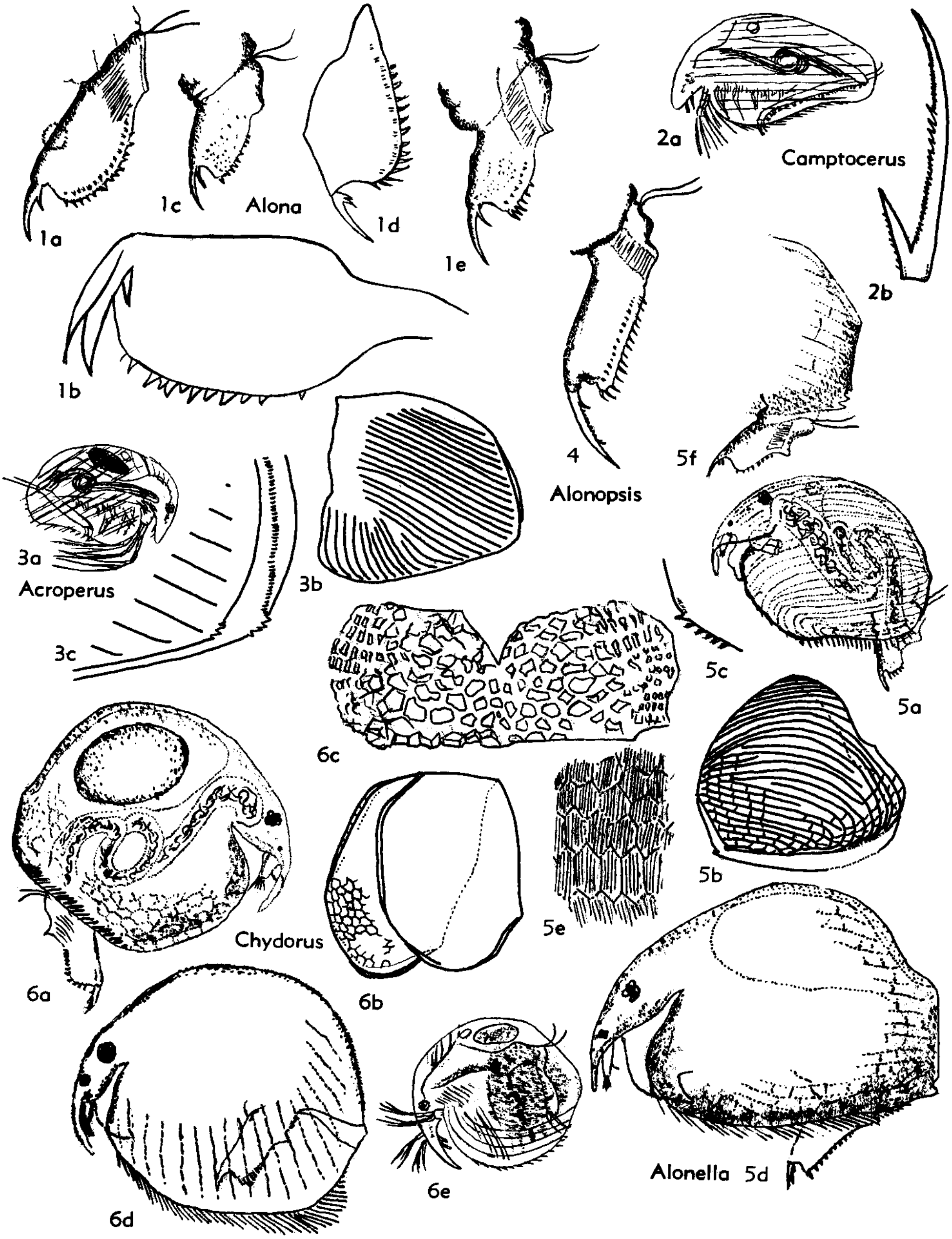

Fig. 64. Chydoridae (Chydorinae) (p. R171-R173).

108), Aus. (Schwarzsee, Längsee, 16, 40), Ger. (Wallensen, 41).]——FIG. 64,*1e*. *A. costata* SARS; postabdomen from USA, enl. (12). [Subfossils are known from Eng. (Lake Windermere, 128.]

Alonella SARS, 1862 [**A. pygmaea*; OD]. Postabdomen large, preanal angle ordinarily prominent (12). *Rec.*, cosmop.——FIG. 64,*5a-c*. *A. nana* (BAIRD); *5a*, subfossil from Eng. (Lake Windermere) entire individual, lat. view, ×150 (128); *5b,c*, subfossil from Ger. (Wallensen); shell and posteroventral angle, both enl. (41). [Other subfossils are known from Aus. (Längsee, 40), USSR (small lakes and bogs near Moscow, 90, 114).] ——FIG. 64,*5d,e*. *A. excisa* (FISCHER); *5d*, entire individual from USA, lat. view, ×150; *5e*, detail of valve markings, enl. (12). [Subfossils are known from USSR (small lakes near Moscow, 90), Eng. (Lake Windermere, 128), Aus. (Schwarzsee, Längsee, 16, 40), N.Z. (Pyramid Lake, 41).]——FIG. 64,*5f*. *A. exigua* (LILLJEBORG); specimen from USA, post. part of shell and postabdomen, ×50 (12). [Subfossils are known from Eng. (Lake Windermere, 128), Aus. (Längsee, 40), Ger. (Wallensen, 41).]

Alonopsis SARS, 1862 [**Alona elongata* SARS, 1861; OD]. Carapace not tumid, postabdomen broad (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.——FIG. 64, *4*. **A. elongata* (SARS); specimen from USA, postabdomen, ×120 (12). [Subfossils are known from USSR (lakes and bogs near Moscow, 106), Switz. (Wauwiler See, 160), Eng. (Lake Windermere, 128), Ger. (Wallensen, Up. Alleröd, 41), Aus. (Längsee, 40).]

Anchistrophus SARS, 1862 [**A. emarginatus*; OD]. Carapace with conspicuous projection on anterventral margin (12). *Rec.*, Eu.-N.Am. Subfossils are known from Eng. (Lake Windermere, 128).

Camptocerus BAIRD, 1843 [**Lynceus macrourus* O. F. MÜLLER, 1785; OD]. Ovoid shape; crest on head or back; carapace with angles rounded and small teeth at inferoposteal angle; surface longitudinally striated (12). *Rec.*, Eu.-N.Am.-Australia. ——FIG. 64,*2a*. **C. macrourus* (MÜLLER); entire individual from USA, lat. view, ×50 (12). ——FIG. 64,*2b*. *C. rectirostris* SCHOEDLER; subfossil from Ger. (Wallensen), female claw, enl. (41). [Other subfossils are known from Eng. (Lake Windermere, 128), USSR (small lakes near Moscow, 90), Switz. (Wauwiler See, 160), Denm. (Naestved, 108), Aus. (Längsee, 40).]

Graptoleberis SARS, 1863 [**Lynceus testudinaria* FISCHER, 1848; OD]. Rostrum broad, semicircular, posterior margin of carapace with 2 strong teeth at inferoposteal angle; shell and head with conspicuous reticulation (12). *Rec.*, Eu.-N.Am.-S. Am.——FIG. 65,*5*. **G. testudinaria* (FISCHER); *5a*, entire individual from USA, lat. view, ×100 (12); *5b*, subfossil from USSR (Moscow); portion of carapace, enl. (90). [Other subfossils are known from Switz. (Wauwiler See, 160), Eng. (Lake Windermere, 128); Aust. (Längsee, 40), Ger. (Wallensen, 41).]

Leydigia KURZ, 1874 [**Lynceus quadrangularis* LEYDIG, 1860; OD]. Postabdomen with numerous clusters of large spines; carapace without markings. *Rec.*, Eu.-N.Am.——FIG. 65,*4a*. **L. quadrangularis* (LEYDIG); postabdomen of specimen from USA, ×100 (12).——FIG. 65,*4b*. *L. acantheroides* (FISCHER); entire individual from USA (La.) showing longitudinally striated carapace, ×80 (12).

Percantha BAIRD, 1843 [**Lynceus truncata* O. F. MÜLLER, 1785; OD]. Oval carapace with lower extremity slightly curved backward and like upper extremity of anterior margin beset with strong hooked spines (12). *Rec.*, Eu.(Eng.-USSR)-N.Am. (Can.)-C.Asia.——FIG. 65,*1*. **P. truncata* (MÜLLER); *1a*, entire individual from Eng., lat. view, enl. (4); *1b*, subfossil from Ger. (Wallensen), caudal margin of shell, enlarged (41). [Other subfossils are known from USSR (Moscow, near small lakes and bogs, 90, 114), Switz. (Wauwiler See, 160), Aus. (Längsee, 40).]

Pleuroxus BAIRD, 1843 [**Lynceus trigonellus* O. F. MÜLLER, 1785; OD]. Inferoposteal angle with 2 or 3. small teeth, commonly minute or may be absent; dorsal margin of postabdomen slightly convex, broader behind anus, apex rounded; 14 to 16 marginal denticles (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.-S.Am.-C.Asia.——FIG. 65,*2*. **P. trigonellus* (MÜLLER); *2a*, entire individual from USA, lat. view enl. (12); *2b,c*, subfossil from Ger. (Wallensen), postabdomen, shell, enl. (41).

Rhynchotalona NORMAN, 1903 [**Alona falcata* SARS, 1861; OD]. Postabdomen stout, thick, bent at anus, truncate at apex, with two to four stout marginal denticles near apex and lateral series of very fine spinules in continuous row almost to anus (12). *Rec.*, Eu.(Eng.-USSR)-Afr.-N.Am.——FIG. 65,*3*. **R. falcata* (SARS); entire individual from USA, lat. view, ×100 (12). [Subfossils are known from Eng. (Lake Windermere, 128).]

Subfamily EURYCERCINAE Kurz, 1874

Anus terminal; two hepatic caeca (63). *Rec.*

Eurycercus BAIRD, 1843 [**Lynceus lamellatus* O. F. MÜLLER, 1785; OD]. [*non Eurycercus* BLYTH, 1844; *nec* BUSCH, 1851]. Postabdomen very large, flattened, quadrangular, dorsal margin with more than 100 sawlike teeth; claws on spiniferous projection with 2 basal spines, and denticulate (12). *Rec.*, Eu.(Eng.-USSR)-N.Am.——FIG. 65,*6*. **E. lamellatus* (MÜLLER); *6a*, entire individual from USA, lat. view, ×17; *6b*, postabdomen, ×50 (12). [Subfossils are known from USSR (lakes and bogs near Moscow, 90, 114), N.Ger. (small ground moraine basins, 41), USA(Conn., 3); Switz. (Wauwiler See, 160), Denm. (Naestved, 108); Ger. (Wallensen, 41), Aus. (Längsee, 40).]

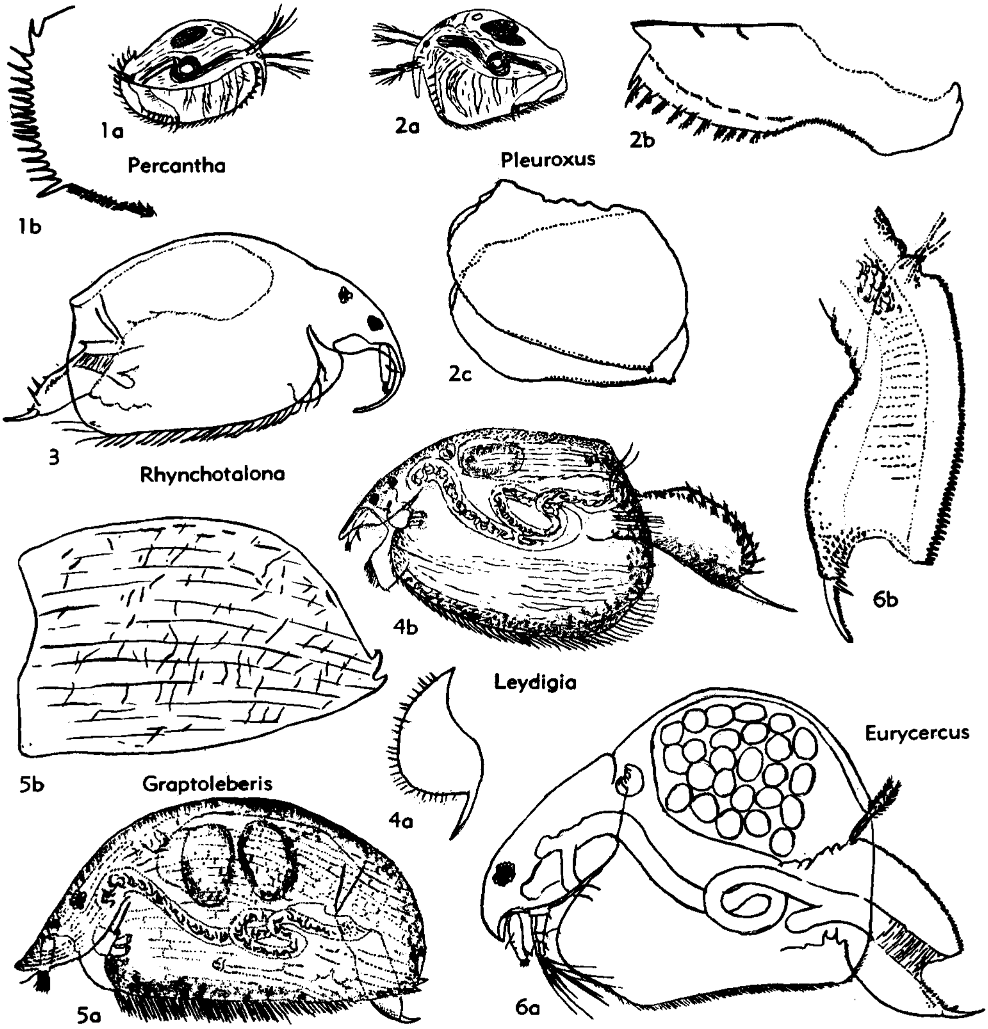

Fig. 65. Chydoridae (Chydorinae) *(1-5)*, (Eurycercinae) *(6)* (p. *R*173).

Family BOSMINIDAE Sars, 1863

Carapace small, rarely greater than 0.5 mm.; six pairs of legs; body short, high, commonly oval or round; carapace covering entire body. *Rec.*

Bosmina Baird, 1845 [**Lynceus longirostris* O. F. Müller, 1785; OD]. Antennules of female approximately parallel to each other, curving backward, fixed to head; carapace thin, inferoposteal angle with spine (=*mucro*); postabdomen subquadrate; claws set in cylindrical process; female with short, blunt rostrum, smaller than male (12). *Rec.*, Eu.-Asia M.-Afr.-N. Am.-S. Am.——Fig. 66, *4a,b*. **B. longirostris* (Müller); *4a*, entire individual, lat. view, ×100; *4b*, postabdomen, enl. (12). [Subfossils are known from USSR (small lakes and bogs near Moscow, 90, 114), Ger. (Wallensen, 41), Switz. (Wauwiler See, 160), Aus. (Schwarzee, Längsee, 16, 40).]——Fig. 66,*4c*. *B. longirostris cornuta* Jurine; subfossil from USSR (Moscow), mucrones of shell, enl. (90). [Other subfossils are known from Switz. (Wauwiler See, 160).]——Fig. 66,*4d,e*. *B. longispina* Leydig; *4d*, subfossil from USA (Conn.), claws, enl.; *4e*, claws of living form, USA, enl. (12).——Fig. 66,*4f,g*. *B. coregoni* Baird; *4f*, subfossil from Aus. (Längsee), claws, enl. (40); *4g*, subfossil from USA (Conn.),

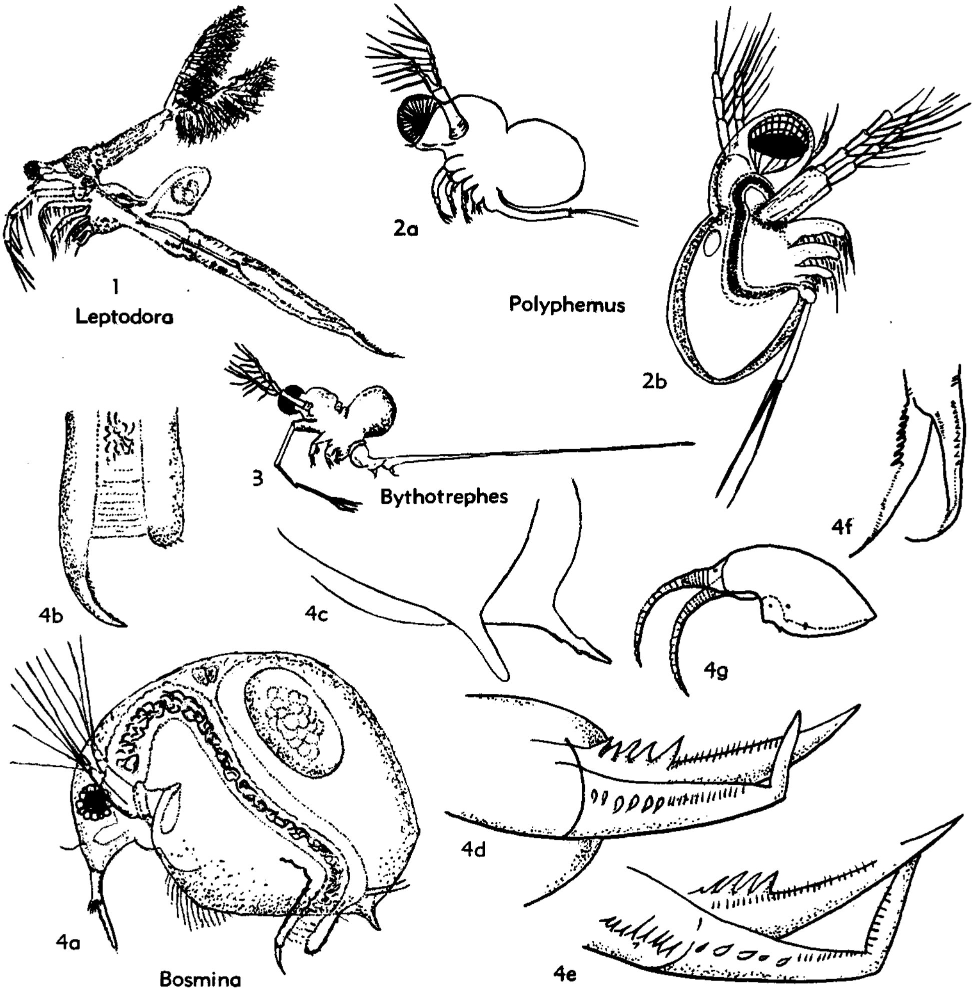

FIG. 66. Bosminidae *(4);* Polyphemidae *(2,3);* Leptodoridae *(1)* (p. *R*174-*R*176).

head shield and rostrum, enl. (3). [Other subfossils are known from USSR (small lakes and bogs near Moscow, 90, 114), Aus. (Lunzer Untersee, Lünnersee, 41). In addition, subfossils from Eng. (Lake Windermere) and USSR (Moscow) are assigned to *B. obtusirostris* SARS.]

Superfamily POLYPHEMOIDEA Baird, 1845

[*nom. transl.* BROOKS, 1959 (*ex* Polyphemidae BAIRD, 1845)] [=tribe Onchyopoda SARS, 1865]

Four pairs of jointed appendages with subcylindrical joints (19). *Rec.*

Family POLYPHEMIDAE Baird, 1845

Carapace not enclosing legs and abdomen, being converted into large globular brood sac (12). *Rec.*

Polyphemus O. F. MÜLLER, 1785 [**Monoculus pediculus* LINNÉ, 1761; SD]. Four pairs of legs not covered by shell; shell only extends to brood pouch. Head separated from thorax through a long notch. Setae of the root (base) of swimming antennae, pinnate. Postabdomen drawn out backward in cylindrical process. *Rec.*, cosmop.——FIG. 66,*2a*. *P.* sp., showing carapace (dorsal posterior bulge) modified to serve as brood sac, enl.

(12).——FIG. 66,*2b*. **P. pediculus* (LINNÉ), Eng.; entire individual, enl. (4).

Bythotrephes LEYDIG, 1860 [**B. longimanus*; OD]. Body resembling that of *Polyphemus*; huge eye in front of head; brood sac not overhanging caudal process as in *Polyphemus*, hence better defined; extreme elongation of slender caudal process is a distinctive character (12). *Rec.*, Eu. ——FIG. 66,*3*. **B. longimanus*; entire individual, lat. view, enl. (167). [Subfossils are known from Eng. (Lake Windermere), mandibles, detached terminal seta of first pair of legs (128) (cf. *Polyphemus*, Fig. 66,*2a*).]

Suborder HAPLOPODA Sars, 1865

Largest of cladocerans (to 18 mm.) with carapace reduced to small brood sac. Legs not flattened but with cylindrical joints; without branchial appendages (19). *Rec.*

Family LEPTODORIDAE Lilljeborg, 1900

Head elongated, slender, eye filling its anterior end; body with four somites, first part bearing six legs and dorsal brood sac (i.e., shell reduced to an egg case); abdomen with three somites, ending in two short claws; mandibles long, slender, pointed, with three spines near apex (19, 67). *Rec.*

Leptodora LILLJEBORG, 1900 [**Polyphemus kindtii* FOCKE, 1844; OD]. Characters of family. [BROOKS (17) has observed that "in some ways *Leptodora* is more like an aberrant conchostracan than a derivative of the Eucladocera."]. *Rec.*, Eu.-N.Am.-C.Asia.——FIG. 66,*1*. **L. kindtii* (FOCKE); entire individual from USA showing appendages and carapace reduced to egg case, X3 (12). [Subfossils are known from Eng. (Lake Windermere), consisting of characteristic mandibles (128).]

Subclass SARSOSTRACA Tasch, new subclass

Body elongate, lacking carapace, with 11 to 19 pairs of trunk limbs which are either typically branchiopod or modified, and ending posteriorly in single or double furcae; furcal rami unsegmented. *L.Dev.-Rec.*

Order ANOSTRACA Sars, 1867[1]

[*nom. transl.* CALMAN, 1909 (*ex* suborder Anostraca SARS, 1867)] [=Phyllopoda LATREILLE, 1802; tribe Gymnota GERSTAECKER, 1866; Phyllopoda pisciformis E. SIMON, 1886; suborder Phyllopoda anostraca SARS, 1867; tribe Gymnophylla STEBBING, 1902]

Body elongate, without carapace, ending posteriorly in caudal furca; posterior somites without legs (apodous); paired compound eyes pedunculate, small median sessile ocellus in front. Antennules short and slender; antennae large and prehensile in males, reduced in females; trunk limbs (swimming legs) 11 to 19 pairs, none postgenital; rami of caudal furca unsegmented. Genital ducts opening on first two apodous segments which are more or less fused; paired eversible penes in male; ova retained in ovisac formed of united oviducts; young hatched in metanauplius state (21). *L.Dev.-Rec.*

ANATOMY

The Anostraca, or fairy shrimps, lack a shell, as indicated by the name of the order, and have an elongate body composed of distinct somites. The head bears stalked compound eyes, antennules, and antennae. The antennae of males are greatly enlarged and specialized for clasping females during copulation (Fig. 67,*1a,b*).

The thoracic somites bear 11 to 19 pairs of swimming legs. The four to nine abdominal somites are limbless (Fig. 67,*2*), the anterior two being coalesced to form the genital somite. The most posterior somite is the telson, which bears two terminal, platelike, plumose cercopods (caudal rami, furcal rami) (21, 69).

Some interesting variations from the general pattern are observed within the anostracans. The American genus *Thamnocephalus*, for example, is reminiscent of the notostracan *Lepidurus* in that the telson is produced as a thin plate above the anal opening (supra-anal plate in *Lepidurus*) (102).

Each thoracic somite bears a pair of very similar foliaceous appendages (exclusive of the less-developed last pair). These are biramous, lobed, and setose. The functions of food-gathering, movement, and respiration are served by these versatile appendages. The components of each appendage include (1) one or two pre-epipodites which

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[1] Technical advice and literature were provided by Prof. R. W. DEXTER, of Kent State University (Ohio), and Prof. J. E. LYNCH, College of Fisheries, University of Washington. Dr. A. R. PALMER, of the U. S. Geological Survey, kindly provided photographs of his Mojave Desert anostracans and literature concerning them. Illustrations for this chapter were financed by a Wichita State University Research Award.

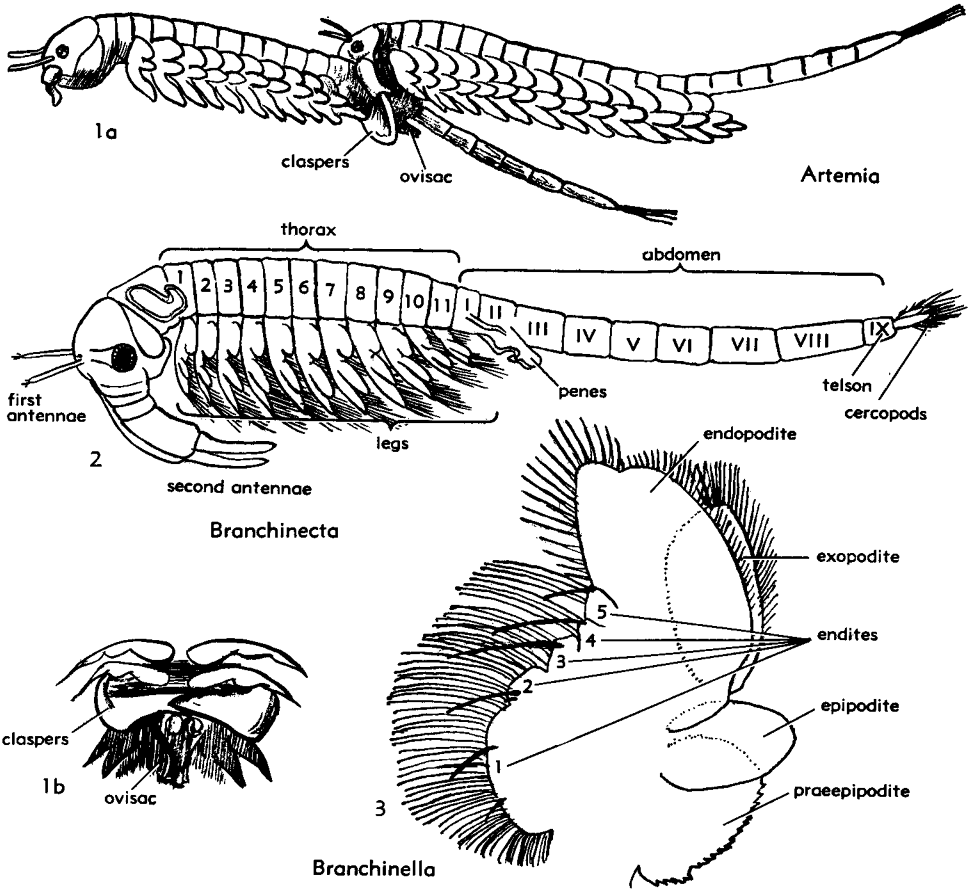

FIG. 67. Morphological characteristics of anostracans.——*1. Artemia salina,* Great Salt Lake; *1a,* a pair of swimming individuals, male clasping mate with claspers in front of ovisac, ×6 (102); *1b,* detail of *1a,* view from beneath of male claspers and ovisac, ×30 (102).——*2. Branchinecta paludosa,* male, terminology after LINDER (69).——*3. Branchinella compacta,* male, eighth leg from the front, anterior setae sharply marked; terminology after LINDER, ×15 (69).

exhibit variable fusion (lateral view); (2) a spineless epipodite at the base, and an exopodite and an endopodite distally; and (3) along the medial margin, five setae and filament-bearing endites (37) (Fig. 67,*3*).

The sexes are separate (Fig. 67,*1a*; 68,*3a*). Eggs are retained in the uterine portion of the oviduct of females (21), the young being hatched in the metanauplius stage. Parthenogenesis is also known (e.g., *Artemia*) (83). Where both sexes are represented, females outnumber males as much as two to one. Males of *Artemia,* for example, are commonly completely absent from communities of parthenogenetic females (83, p. 37-39). DEXTER (37) has observed that males are "not as uncommon as is generally believed" and may outnumber females in a given population.

Although anostracans lack a carapace, they possess a tissue system that CALMAN (21) considered almost equivalent to an endoskeleton. A marked development of structures to which muscles can be attached includes trabeculae and plates of connective tissue. The external cuticle, by contrast, is almost membranous.[1]

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[1] A. G. RICHARDS (1951, p. 48) indicates that the body wall of *Artemia* gives a positive test for chitin. *See* footnote 1, p. *R*000).

Among living anostracans, anatomical features of taxonomic value are (1) unique characteristics of the antennae at the species level; (2) frontal appendage between the antennae; (3) position and structure of the two penes of males at the familial level (37).

ECOLOGY

SALINITY AND pH

Anostracans generally live in small, temporary, alkaline water pools (83). Dexter (37) has noted that the most usual habitat is in rain pools and temporary ponds formed from melting snow and ice.

One anostracan species (*Branchinecta shantzi*) is known from Alpine lakes (37). The brine shrimp (*Artemia salina*, Fig. 67,*1a*), is an exception to the general rule, since it inhabits inland saline water bodies such as the Great Salt Lake (102). Recently, Lynch (77) described a new anostracan species (*Branchinecta campestris*) found associated with *Artemia salina* in several ponds in Grant County, Washington. He noted that the new species was adapted to life in water "of so high a content of dissolved salts that only *Artemia salina* can develop abundantly in the same habitat." Other anostracans display this salinity tolerance also. For example, laboratory experiments indicate that although adults of *Branchipus stagnalis* rapidly succumb in sea water, they can survive a half month in water containing 1 to 5 grams of NaCl per liter (83, p. 9). Thus, we may conclude that certain anostracans can become adapted to an inland or a marine coastal, brackish-water environment. No marine species of Anostraca are presently known, however.

Small quantities of ammonium salts were found necessary for normal growth of *Branchipus stagnalis*, and this species, as well as *Chirocephalus diaphanus*, were able to live in waters containing up to 0.5 gram per liter of gypsum. This indicates that organic decay in bottom sediments or small amounts of evaporites in solution are not inimical to anostracan survival.

Experiments with *Artemia* eggs (Tasch, 1954, unpublished) have shown that small quantities of phosphates, ferric oxides, and ferrous oxides added to brine solutions inhibited normal hatching. The egg cases were observed to break and the yolk to extrude but no hatching occurred as in normal brine solutions.

Different anostracan species can withstand differing ranges of pH: *Chirocephalus* (6.4 to 7.8), *Branchipus* (7.2 to 7.6), *Streptocephalus* (7.4 to 7.6), although the usual range reported is between 7 and 7.5.

TEMPERATURE

Anostracan genera and species vary in their temperature tolerance. A species of *Branchinecta* from the Antarctic was collected under a layer of ice. Laboratory experiments show that *Branchipus stagnalis* can withstand a range of 17° to 41° C. even when the temperature varies rapidly (83). The most favorable temperature reported is between 15° and 20° C. *Branchipus* becomes inert at 0° C.

FAUNAL ASSOCIATES AND PREDATORS

Three of the branchiopod orders may occur together in the same pool. The anostracan genus *Thamnocephalus* was reported to have occurred in the same Ellis County (Kansas) pool in which the notostracan *Triops longicaudatus* and the conchostracans *Leptestheria compleximanus* and *Cyzicus mexicanus* were also found (102). Species of *Triops* are almost always found with the anostracan *Branchipus stagnalis* in certain localities, and *Lepidurus* species almost always occur with *Chirocephalus diaphanus* and conchostracan young.

Since natural predators of anostracans include frog tadpoles, salamanders, ostracodes (*Cypris, Cyclocypris*), and various insect larvae, one might anticipate that future finds will be made in the fossil record of such predator-prey assemblages. A recent fossil discovery discussed below is an augury of others to come. Mathias observed an egg of *Chirocephalus* that had passed through the digestive tube of a frog and voided in its feces, yet developed into a normal nauplius (83, p. 78).

FOOD

The food of anostracans is mainly plankton. Included in their diet, as reported by several observers, are: infusoria, rotifers, diatoms, and algae (83).

REGENERATION

A remarkable crustacean attribute is the capacity to regenerate torn or lost appendages and body parts. Anostracans such as *Artemia salina* show this capacity to a marked degree, although it should be noted that only 1 or 2 per cent of injured individuals show partial or total regeneration (83, p. 70). Experiments indicate that *Artemia* will show more rapid regeneration in saline water than in fresh water. Other anostracans have demonstrated this regenerative capacity. *Chirocephalus diaphanus*, for example, regenerated severed furca in three or four days.

GEOLOGIC OCCURRENCE

Although the fossil record of anostracans seems to be sparse, published discoveries are of great interest. The Eocene

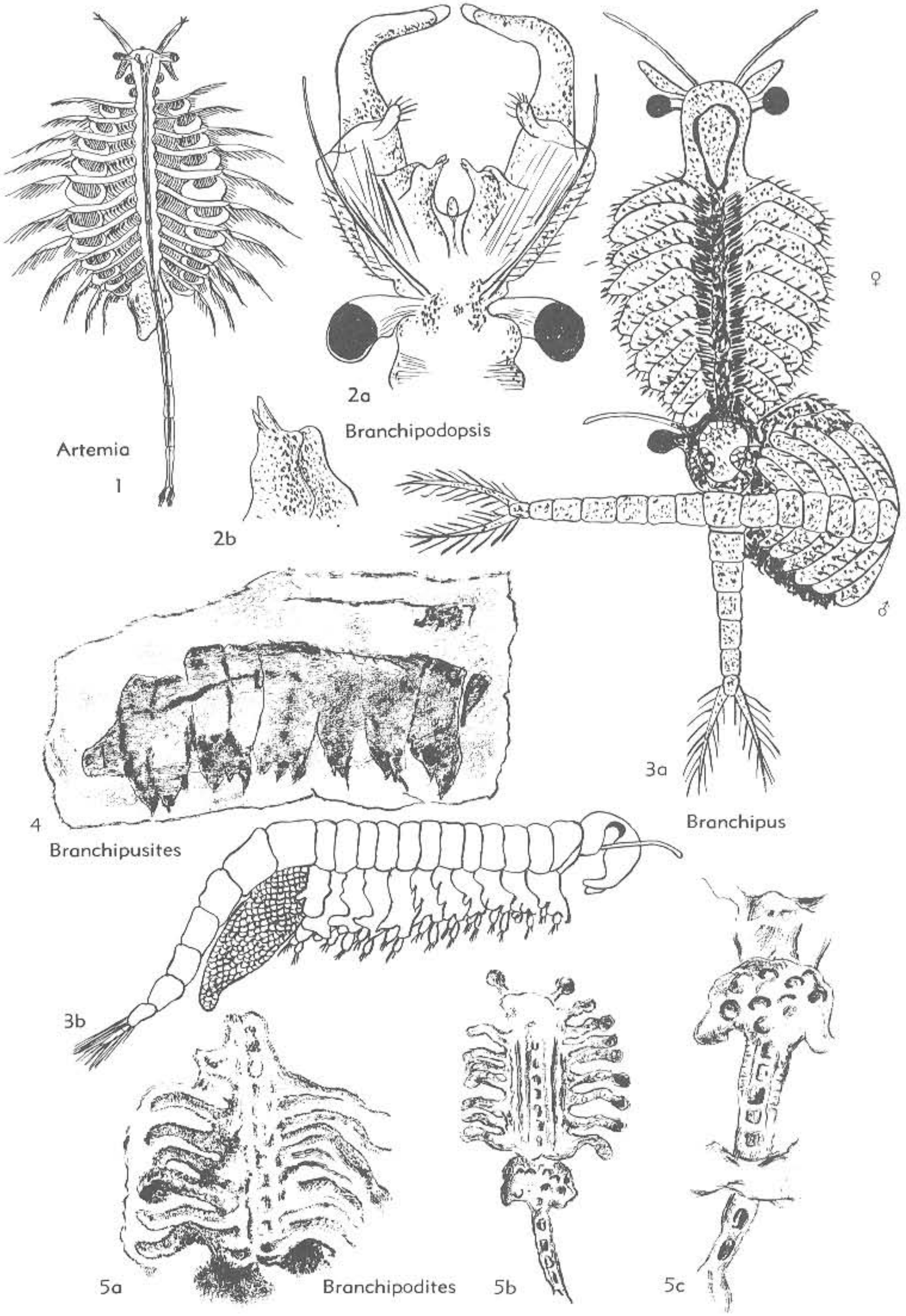

FIG. 68. Artemiidae *(1);* Branchipodidae *(2-5)* (p. *R*181).

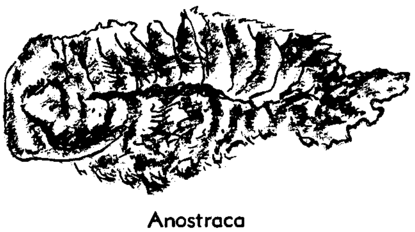

Fig. 69. Fossil anostracan from ?middle Miocene lake deposits in Mojave Desert, California, ×? (170c).

fresh-water argillaceous limestone from the Isle of Wight has yielded, in association with plant remains and an insect fauna, an undoubted *Branchipus*-like anostracan (*Branchipodites,* Fig. 68,5). The plant remains included palm leaves *(Flabellaria),* seeds of a water lily *(Nelumbium),* leaves of rushes, and remains of other aquatic plants. The insect fauna included representatives of the orders Coleoptera, Hymenoptera, Lepidoptera, Diptera, Neuroptera, Orthoptera, and Hemiptera, and the class Arachnida. Of the neuropterids, caddis flies were represented by the well-known genus, *Phryganea* (156). Experiments performed by Mathias showed definitely that larval *Phryganea* preys on anostracans (83). It is not surprising, then, to find such a predator-prey association in the fossil record.

In 1954 another remarkable arthropod fauna represented by silicified fossils has been reported in calcareous nodules of lacustrine deposits of ?middle Miocene age in the Mojave Desert, California (103, 104). The nodules were associated with borate beds (cf. discussion on evaporites above) and occurred in brown, paper-thin shales, laminated siltstones, and thin limestone beds. A large part (35 percent) of the fauna consisted of fairy shrimps (Fig. 69). The insect fauna was represented by the orders Ephemerida (mayfly nymphs), Odonata (dragonfly nymphs), Thysanoptera (thrips), Hemiptera (true bugs), Coleoptera (beetle larvae), Diptera (midge larvae, pupae, and adults), and the class Arachnida (cf. Isle of Wight Eocene insect fauna).

Since genital organs were not found to be preserved in the Mojave Desert silicified fossil anostracans (released from the nodules by formic acid treatment), no assignment of the 150 specimens has been made. The best specimen in the collection was preserved in an undetermined organic material—all the rest were silicified (A. R. Palmer, 1956, personal communication). One may observe that the insect fauna here too, may include anostracan predators. Among the 150 specimens of the Mojave Desert anostracans, the overall body length was found to be 4 to 5 mm. Parts preserved and recognizable in the head region included antennae, mandibles, maxillules, and maxillae. Typical anostracan legs were also observed (Fig. 69) (104).

The oldest yet-discovered fossil anostracan is *Gilsonicaris,* from the Lower Devonian of Germany (151). Its elongate segmented body and the cephalon bear closest affinities to the anostracans. Van Straelen concluded that it is very close to *Branchipodites vectensis* in all characters except the larger number of trunk segments in *Gilsonicaris.* Van Straelen assigned the genus to a new family, Gilsonicaridae (*recte* Gilsonicarididae). This family is here included in systematic descriptions for completeness, but it should be realized that anostracan assignments at the familial level have little meaning in the absence of preserved genitalia.

Other fossils considered to represent anostracans are doubtful. Goldenberg found a *Branchipus*-like impression with only swimming legs and portions of the trunk preserved in Stephanian deposits of West Germany (45). The same deposits yielded a variety of arthropod crustaceans and estheriid conchostracans. Woodward found an anostracan-like fossil *(Rochdalia)* in the middle Coal Measures of England (157).

The recent discovery of Miocene cladocerans, noted previously, indicates the probable existence of branchiopod faunas yet to be found in Tertiary nonmarine beds. Anostracan fossils should be sought in any Tertiary formation yielding insect fossils, since likelihood of an insect predator-anostracan prey association exists.

The presence of the brine shrimp *Artemia salina* in Aftonian interglacial deposits (Pleistocene) of the Great Salt Lake is indicated by fecal pellets found in a recently obtained core (at Saltair). The oldest initial occurrence of these shrimps in the Salt Lake area is about 600,000 years before the present, as estimated by me from published core-log data (39). One may anticipate future discovery of fossil brine shrimps in interglacial sediments at different localities. It is likely that they would be preserved as impressions.

Family ARTEMIIDAE Grochowski, 1896

Thoracic somites 11; penes proceeding ventrally close to each other, rigid and apical parts without spines, no sharply defined vesiculae seminales. Single pre-epipodite on each leg; rami of caudal furca variably fused with last abdominal somite or freely movable; ovisac subglobular or cylindrical. Head of males without frontal process; antennae of males biarticulate, not fused or only slightly so at base (46, 69). *Pleist.-Rec.*

Artemia LEACH, 1819 [**Cancer salina* LINNÉ, 1758; OD]. Postgenital region with eight somites; distal segment of male clasping antennae compressed and blade-shaped. *Rec.*, cosmop.——FIG. 68,*1*. **A. salina* (LINNÉ), USA(Conn.); ventral view, ×6.5 (102). [*See* also Fig. 67,*1*.]

Family BRANCHIPODIDAE Simon, 1886

[=restricted DADAY, 1910 (30); *emend.* LINDER, 1941 (69)]

Like *Artemiidae* in number of somites and genital organs except that apical parts of penes bear several spines. Basal segments of antennae in males coalescing medially in so-called clypeus (Fig. 68,*2b*) (69, 129). *?U.Carb., ?Eoc., Rec.*

Branchipus SHÄFFER, 1776 [**Cancer stagnalis* LINNÉ, 1758; OD]. Penis without basal process; apical segment or copulatory part of penis elongate, cylindrical, and on both lateral sides serrate-denticulate; ovisac short, oval-shaped, sharply rounded at posterior apex, forming prominent tubercle above in middle. *Rec.*, Eu.-Asia-Afr.——FIG. 68,*3*. **B. stagnalis* (LINNÉ); *3a*, copulating pair (Fr.), enl. (83); *3b*, female (Ger.), lat. view showing ovisac, ×16 (45).

Branchipodopsis G. O. SARS, 1898 [**B. hodgsoni*; OD]. Digitiform, short, plainly sensory outgrowth from distal parts of clypeus (69, 123). *Rec.*, Asia-Afr. (arid regions).——FIG. 68,*2*. **B. hodgsoni*, S.Afr.; *2a*, head of male, dorsal view, enl.; *2b*, lat. dorsal view of clypeus, enl. (30).

?**Branchipodites** WOODWARD, 1877 [**B. vectensis*; OD]. Males with large clasping antennae, females with small antennae and egg pouches; female trunk with 8 pairs of legs; abdominal somites narrow, elongated. Eyes stalked. *Eoc.*, Eng.——FIG. 68,*5*. **B. vectensis*, Bemdridge Ls. (freshwater), Isle of Wight; *5a*, thorax and paired legs, ×11; *5b*, female with egg pouch, eight pairs of legs, and stalked eyes, ×14; *5c*, ventral view of egg-pouch containing eggs, and abdominal somites, ×19 (156).

?**Branchipusites** GOLDENBERG, 1873 [**B. anthracinus*; OD]. Preserved eight trunk somites with lateral appendages that resemble lamellar branchial feet of *Branchipus*. *U.Carb.(Stephan.)*, W.Ger. ——FIG. 68,*4*. **B. anthracinus*, Saarbrücken; lat. view showing *Branchipus*-type lamellar branchial feet and eight thoracic somites, ×15 (45). [*See Arthropleura*, p. *R*617.]

Family BRANCHINECTIDAE Daday, 1910

Thoracic somites 11; penes proceeding ventrolaterally to laterally, widely separated from each other; male antennae not fused basally and terminal segment not laminate (30, 69). *Rec.*, Eu.-Asia-N.Am.-S.Am.

Branchinecta VERRILL, 1869 [**Branchipus paludosus* O. F. MÜLLER, 1788 (=*B. arctica, B. groenlandica* VERRILL, 1869); OD]. Basal segment of male clasping antennae serrate on inner margin (30, 152). *Rec.*, N.Am.(Alaska-Can.-Greenl.)-N. Eu.——FIG. 70,*1*. **B. paludosa* (MÜLLER), N. Greenl.; *1a,b*, ♂ and ♀, lat. views, ×5 (102). [*See* also Fig. 67,*2*.]

Family CHIROCEPHALIDAE Daday, 1910

Thoracic somites 11; penes proceeding ventrally close to each other, sharply defined and mostly with large seminal vesicles. Each leg with two pre-epipodites or only one with deep incision on its edges; male antennae two-segmented, quite separate from each other; basal segment seldom without all outgrowths; frontal appendages missing (30, 69). *Rec*

Chirocephalus PRÉVOST, 1803 [**C. diaphanus* (=*Cancer stagnalis* SHAW, 1791; *Branchipus diaphanus* MILNE-EDWARDS, 1840; *Chirocephalus stagnalis* (SHAW) DADAY, 1910); OD]. Characters of family (30). *Rec.*, Eu.-Afr.-Asia.——FIG. 70,*2*. **C. diaphanus*, Eng.; female, ovisac containing eggs, enl. (15).

Eubranchipus Verrill, 1870 [**Branchipus vernalis* Verrill, 1869; OD]. Antennal appendages nearly bilaterally symmetrical with slightly obtuse apex (37, 153). *Rec.*, N.Am.——Fig. 70,*3*. **E. vernalis* (Verrill), USA(New England); ♂, lat. view, ×3.5 (102).

Family POLYARTEMIIDAE Simon, 1886

Thoracic somites 17 to 19; sharply marked off seminal vesicles absent and penes proceeding ventrally close to one another with

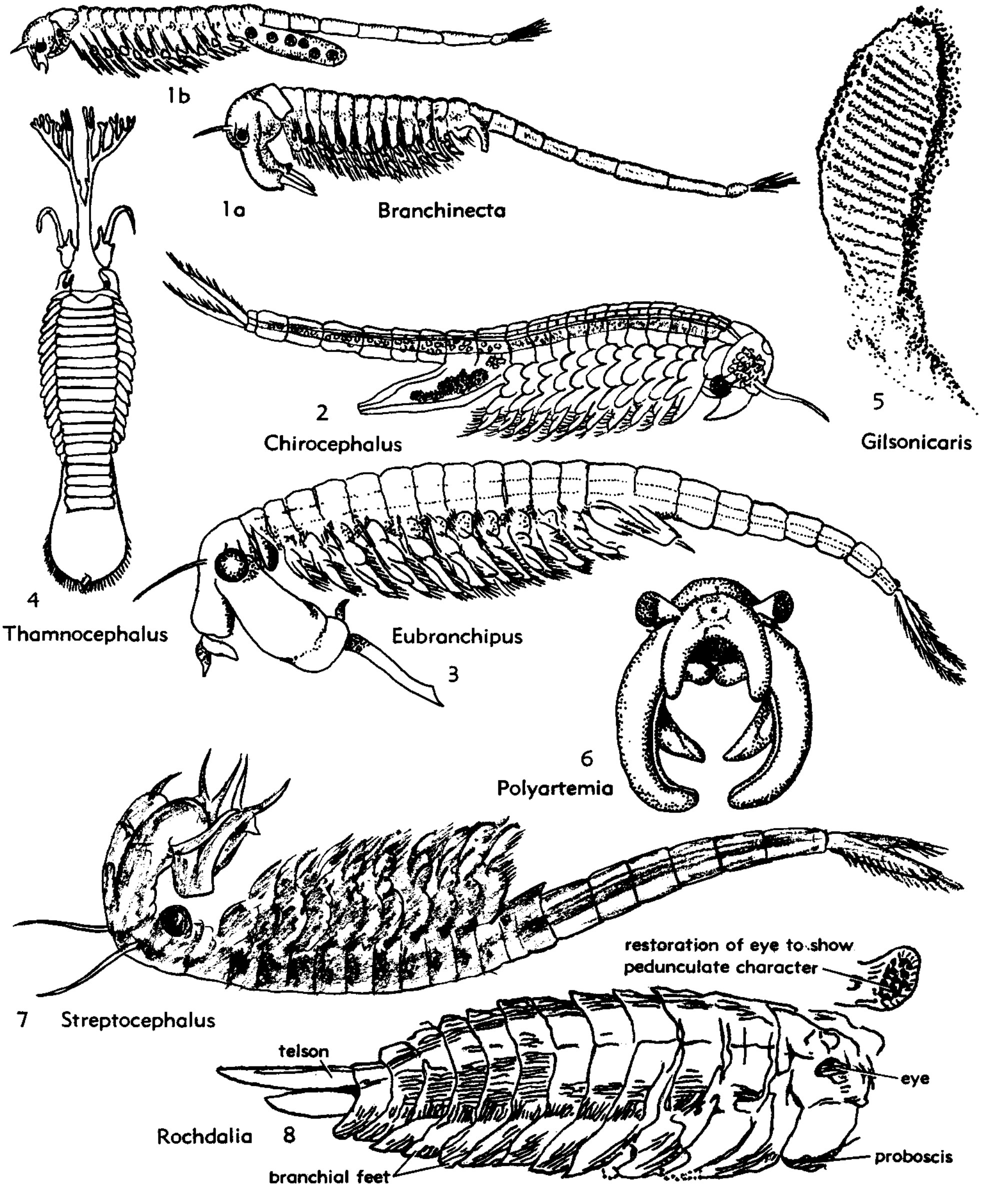

Fig. 70. Branchinectidae *(1)*; Chirocephalidae *(2,3)*; Polyartemiidae *(6)*; Streptocephalidae *(7)*; Thamnocephalidae *(4)*; Gilsonicarididae *(5)*; Family Uncertain *(8)* (p. *R*181-*R*183).

rigid basal parts, which bear two faint median warts (69, 129). *Rec.*

Polyartemia Fischer, 1851 [**P. forcipata*; OD]. Thoracic segments 19. *Rec.,* Eu.-Asia.——Fig. 70,*6*. **P. forcipata,* Arctic; head, enl. (168).

Family STREPTOCEPHALIDAE
Daday, 1910

Thoracic somites 11; penes proceeding ventrally close to each other, lacking sharply defined seminal vesicles; one pre-epipodite on each leg; basal parts of penes soft and flexible; antennae of males with "hand" (Fig. 71) (30). *Rec.*

Streptocephalus Baird, 1852 [**S. similis*; OD]. Characters of family (6). *Rec.,* cosmop.——Fig. 70,*7*. **S. similis,* Santo Domingo, W.Indies; ♂, lat. view, ×8 (6).

Family THAMNOCEPHALIDAE
Simon, 1886

[=*emend.* Linder, 1941]

Like Streptocephalidae in number of thoracic somites and nature of male genital organs (except for upward loop of vas deferens in first genital somite and retractibility of whole penes); differs in that antennae of males lack "hand"; cercopods densely and uniformly setose along margin, generally thin and slender, rarely broadly leaflike and partly running along sides of abdomen (69, 129). *Rec.*

Thamnocephalus Packard, 1879 [**T. platyurus*; OD]. *Rec.,* N.Am.——Fig. 70,*4*. **T. platyurus,* USA(Kans.); ♂, dorsal view, ×1 (102).

Family GILSONICARIDIDAE
Van Straelen, 1943

[*nom. correct.* Tasch, herein (*pro* Gilsonicaridae Van Straelen, 1943)]

Trunk segments 18. *L.Dev.*

Gilsonicaris Van Straelen, 1943 [**G. rhenanus*; OD]. Elongate, regularly segmented body without carapace; 18 trunk somites, of which 11 bear appendages; somites subequal in length, diminishing in size posteriorly; cephalon wider than long and equal in length to first three thoracic somites, divided by longitudinal groove. [Very close to *Branchipodites vectensis* but with many more segments.] *L.Dev.(Hunsrück.),* Ger.——Fig. 70, *5*. **G. rhenana,* Bundenbach; ventral view of thorax and abdomen, ×3 (151).

Family UNCERTAIN

Rochdalia Woodward, 1913 [**R. parkeri*; OD]. Head rounded, expanded downward in beaklike proboscis; eyes pedunculate; 11 thoracic somites ending in pointed telson; four somites behind head largest, all somites with recurved lobelike swimming feet. *U.Carb.(M.Coal Measures),* Eng.——Fig. 70,*8*. **R. parkeri* Rochdale; carapace, oblique dorsal view, ×3 (157).

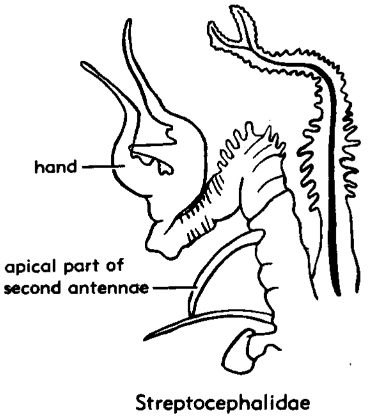

Fig. 71. *Streptocephalus proboscideus,* male, enl. (69).

Rolfe (1967, Palaeontology, v. 10, no. 2, p. 307-313) has presented evidence indicating that *Rochdalia,* heretofore thought to be an anostracan, is indistinguishable from a Carboniferous insect nymph of the family Breyeriidae, order Palaeodictyoptera. It is also possible, as has been suggested previously by authors and reiterated by Rolfe, that such presumed anostracan fossils as *Gilsonicaris* and *Branchipusites* may prove to be a myriapod and a trilobitomorph *Arthropleura,* respectively.

Order LIPOSTRACA Scourfield, 1926

Carapace lacking. Antennae biramous, natatory; trunk limbs about 11 pairs in two series, first three pairs foliaceous and lobed, posterior eight pairs biramous; furcal rami unsegmented, styliform, preceded by another smaller pair of styliform appendages in terminal somite (127). *M.Dev.*

ANATOMY

The Lipostraca, known only from fossils, are elongated branchiopods. Even so, a fully grown adult reaches a maximum of 3 mm. in length. A bivalved shell or dorsal shield is absent. While the head lacks stalked eyes, it has mouth parts, antennules, and antennae. The antennules are very distinctive, being three-jointed. The essential features, found in the larval forms of other branchiopods, are retained in the antennae.

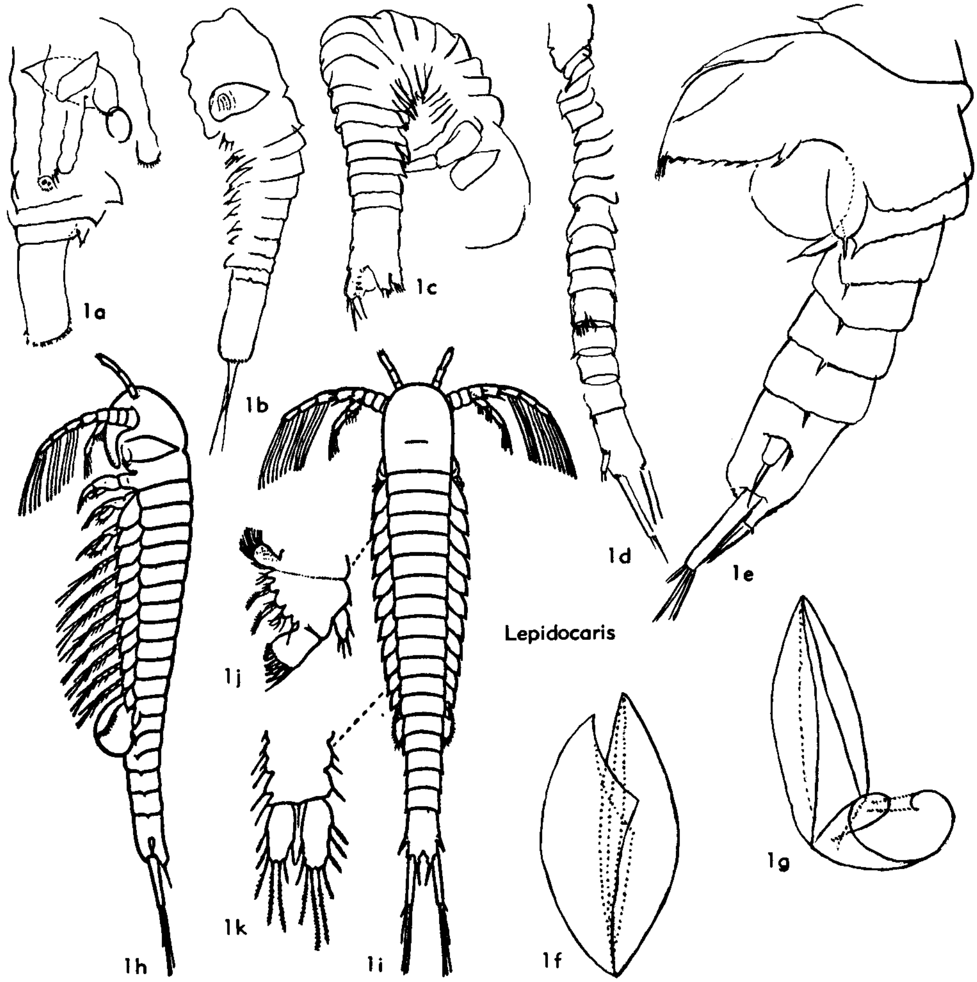

FIG. 72. Lepidocarididae (p. *R*185).

In adults of both sexes, these are large, biramous, swimming organs. In adult males, the pair of powerful clasping organs arise just behind the mandibles and are developed from the maxillules. In this feature they differ importantly from the anostracans, in which the antennae have been modified to give rise to this organ.

It is especially the 11 pairs of trunk limbs that make lipostracans "somewhat peculiar" branchiopods. Two sharply separate series can be distinguished, the first including the front three pairs. Even these, though of usual branchiopod type (i.e., foliaceous), are modified, for their terminal parts are modified quite uniquely to serve as scraping and rasping organs. The second series of trunk appendages includes the 4th to 11th pairs of limbs, which differ from equivalent pairs in all other branchiopods in having the form of biramous copepod-like swimming feet.

Adult females bear an egg pouch and its cover, which may have developed from modified trunk limbs. In adult males the last two pairs of appendages are modified somewhat from the preceding copepod-type swimming feet.

Finally, the distinctive character of the caudal segment should be noted. It terminates in two short knobs (primary furcae), from the center of which two long articulated processes project backward (secondary furcae). These double furcae are one of several unique lipostracan features.

GEOLOGIC OCCURRENCE

Lipostracans have so far been found only in the Rhynie Chert, Devonian Old Red, of Scotland. The chert is semitransparent rock, so that a drop of oil on the surface of flakes or thin sections brings out astonishingly minute structural details of lipostracans contained in the chert.

Although microscopic in size, the Lipostraca are abundantly represented by both sexes in various stages of growth from minute larvae with only four somites to fully grown adults (Fig. 72,*1*). There has never been any doubt that SCOURFIELD's evidence was adequate to establish a new order. No other trace of pondlife was found with the lipostracans. However, from the same chert beds, arachnids and plant fossils have been described. SCOURFIELD was impressed by the primitive characters seen in lipostracans (such as the biramous II antennae) combined with greater specialization than is found in living anostracans (127). He also noted the absence of associated pondlife. Making these two observations led him to infer that the environment into which lipostracans fitted must have been "very peculiar." As a result, he favored the postulate that the water in which the Rhynie Chert was deposited may have been hot and highly charged with silica.

TASCH (137), from a review of all published evidence concerning the Rhynie Chert biota concluded that "the fifteen points of difference which SCOURFIELD found between lipostracans and anostracans cannot be attributed to the Rhynie thermal environment." Further, "all mutational effects leading to the appearance of the new crustacean order Lipostraca should be referred to specific variations that occurred outside the Rhynie area."

Family LEPIDOCARIDIDAE Scourfield, 1926

Characters of order. *M.Dev.*

Lepidocaris SCOURFIELD, 1926 [**L. rhyniensis*; OD]. Characters of order. *M.Dev.(Rhynie Chert, Middle Old Red Sandstone),* Scot.——FIG. 72,*1*. **L. rhyniensis*; *1a*, young with four somites, ×2.40; *1b*, young with 10 somites, ×150; *1c*, half-grown individual, ×130; *1d*, adult, with 19 somites, ×150; *1e*, female adult (note egg pouch marked by dotted arc), ×130; *1f,g*, ?egg cases, ×210 (127); *1h,i*, lat. and dorsal views of adult female (reconstr. by Scourfield, 127), ×25; *1j,k*, appendages of trunk, enl. (169).

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MYSTACOCARIDA

By Robert R. Hessler
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[Submitted December, 1961]

GENERAL FEATURES

The mystococarids are very minute crustaceans, fully developed adults having a length of only 0.5 mm. Their elongate body (Fig. 73,*A*) is divided into cephalon, maxilliped segment, and thoraco-abdomen. The cephalon is about one-third the length of the body and bears antennules (first antennae), antennae (second antennae), mandibles, maxillules (first maxillae), and maxillae (second maxillae) (Fig. 73). The anterior end of the cephalon is marked off from the remainder by a deep constriction and is characterized by a pair of anterolateral indentations and a single anteromedial indentation. This anterior division of the head carries the antennules and, dorsally, paired simple eyes (ocelli) (Fig. 73,*B*). Ventrally, a very long labrum extends posteriorly past the end of the cephalon to the region of the maxilliped somite (Fig. 73,*A*).

Functionally the maxilliped is a cephalic limb (Fig. 73,*G*), although the maxilliped somite is not fused to the cephalic complex. However, because of the nature of the musculature, movement of the maxilliped somite with the first thoracic somite is freer than with the cephalon.

Following the maxilliped somite are four thoracomeres bearing reduced limbs. In all other respects these thoracic somites do not differ from the five which follow them, and functionally the two groups of somites cannot be considered as separate tagma. Dahl (1) has labeled the nine somites, plus the telson, as the thoraco-abdomen. A caudal furca occurs at the end of the telson (Fig. 73,*A*).

Pairs of toothed irregular furrows (Fig. 73,*B*) are found dorsolaterally on the posterior end of the cephalon and on the maxilliped somite. Homologous to these are a pair of regular dorsoventral furrows, also toothed, located laterally on each of the thoracoabdominal somites except the telson. The function of these furrows is not known.

APPENDAGES

The antennules are uniramous and consist of eight segments. Each segment carries setae, usually distributed in an irregular, distal crown. This rather inflexible appendage is directed strongly forward and is probably primarily sensory in function.

The antennae (Fig. 73,*C*) are biramous. A fringe of conspicuous setae runs down the ventral edge of the nine-segmented exopod, with setal length increasing distally. The endopod has four segments which bear a few stiff medioventral setae. Subdivision of the protopod is unclear.

The mandibles (Fig. 73,*D*) are strikingly like the antennae. The exopod has seven or eight segments, of which the basal ones never bear setae. The three- or four-segmented endopod carries setae on the medial edge of all its segments. A masticatory process projects from the protopod medially under the labrum. Both the mandibles and antennae function in feeding, as well as locomotion.

The uniramous maxillule (Fig. 73,*E*) consists of a four-segmented endopod and a protopod of uncertain subdivision. It bears large, stout setae which are particularly concentrated on the distal segment, where they aid locomotion, and on the basal two segments, where they are used in feeding.

The maxillae (Fig. 73,*F*) are like the maxillules in form, segmentation, and general setation, but their protopodial segments are even more richly supplied with trophic setae.

In *Derocheilocaris typicus* Pennak & Zinn, and *D. remanei* Delamare Deboutteville & Chappuis, the maxilliped is a biram-

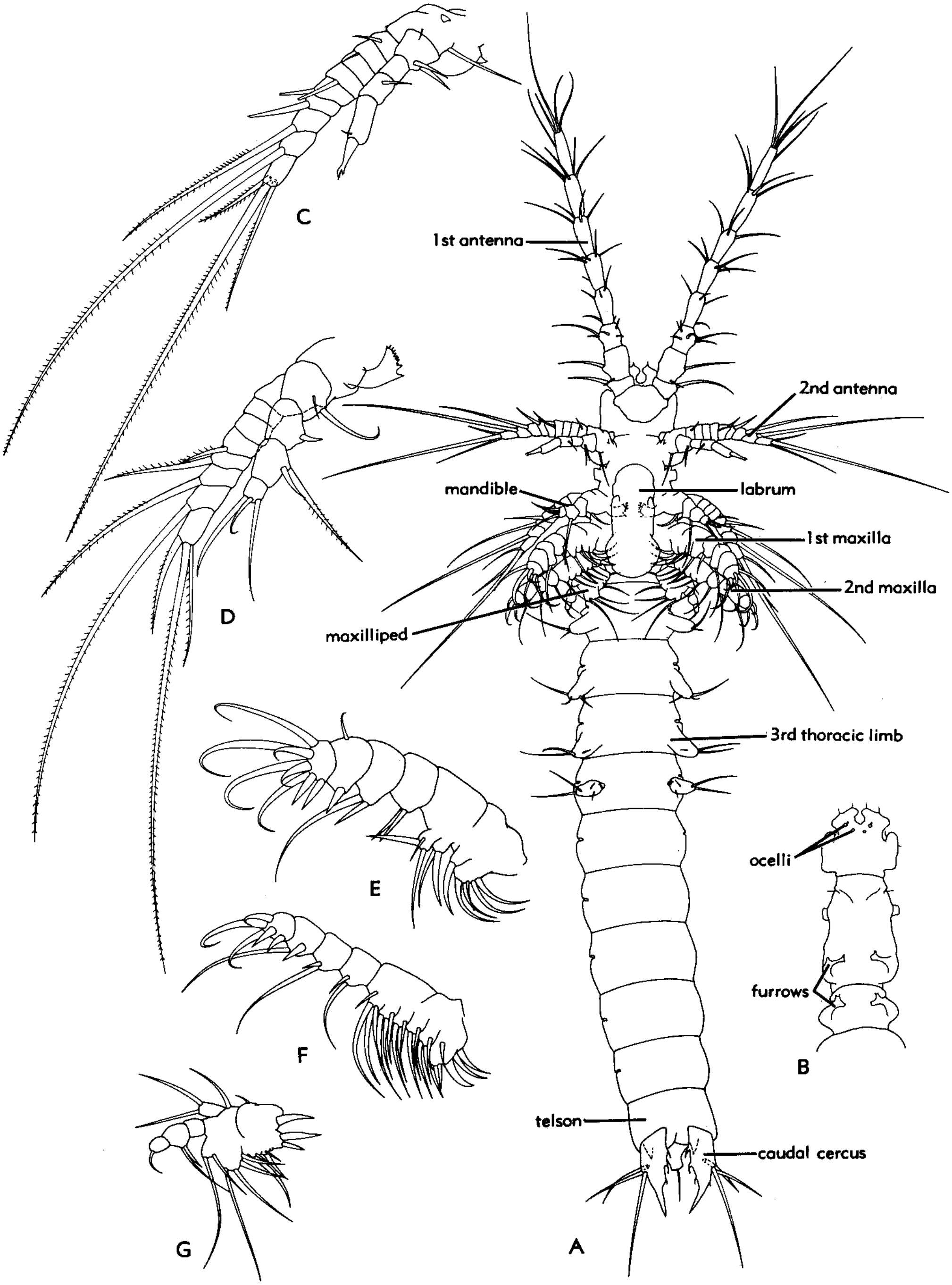

Fig. 73. Morphology of typical adult mystacocarid, *Derocheilocaris typicus* Pennak & Zinn.——*A*. Complete specimen, ventral view.——*B*. Cephalon and maxilliped somite, dorsal view.——*C*. Antenna.——*D*. Mandible.——*E*. Maxillule.——*F*. Maxilla.——*G*. Maxilliped (*A,B*, ×250; *C-G*, ×500) (Hessler, n).

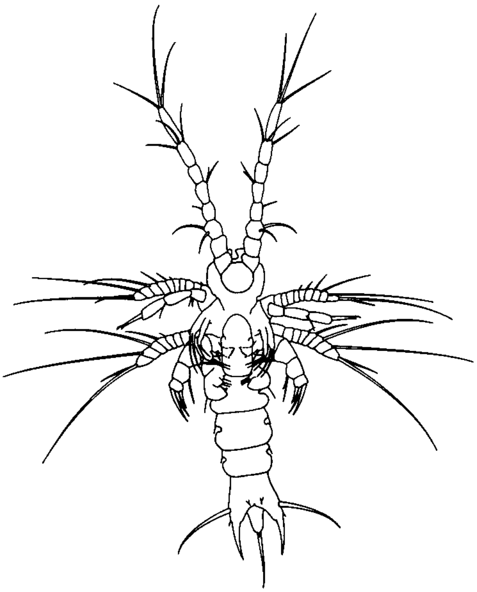

FIG. 74. Stage one metanaupliar larva of *Derocheilocaris typicus* PENNAK & ZINN, ventral view, ×250. At this stage, only antennules, antennae, mandibles, and rudimentary maxillules are present (Hessler, n).

ous limb with a foliaceous protopod (Fig. 73,*G*) (2-4, 6). The endopod has three segments, whereas the exopod is unjointed. In *D. galvarini* DAHL, both endopod and exopod are absent. This limb probably functions only in feeding.

The much-reduced, unjointed limbs of the first four thoracoabdominal somites are nearly immobile. The third pair of limbs bears the genital pore in both sexes and the fourth limb of the male is modified for copulation.

Stout, claw-like caudal rami are used for grooming and to give purchase as the animal moves forward.

DEVELOPMENT

The development of the Mystacocarida is gradual, beginning with a nauplius (Fig. 74) or metanauplius having four postcephalic somites. Limbs and somites appear gradually. There are no metamorphic changes in limb morphology except the eventual loss of the naupliar process of the antennae and mandibles.

MODE OF LIFE

Both larva and adult are totally benthonic, living in the interstitial spaces between sand grains. Their elongate body form is typical of arthropods living in this habitat. Mystacocarids are best known from intertidal beaches, but they occur in subtidal sand as well.

AFFINITIES

The Mystacocarida are thought to be related to the Copepoda, as suggested by the similar tagmosis of the two classes, and by the similarity of the cephalic limbs. Yet it is clear that mystacocarids are more primitive than copepods, for they possess features which unite them to other classes as well. The musculature of the antennules is like that of the cephalocarids and larval branchiopods. The nerve cord is a simple ladder resembling that of the branchiopods, but is even similar to that of the cephalocarids. The cephalic limbs, although like those of the copepods, are most easily related to the cephalocarid condition. Indeed, the mystacocarid mandible, because of its unreduced condition in adults and close similarity to the antenna, is even more primitive than that of cephalocarids. Finally, although the maxillipeds functionally are cephalic appendages, the somite bearing them is free and appears to be only now in the process of cephalization.

DISTRIBUTION

The Mystacocarida are an unusually conservative group. Not only do all the species closely resemble each other, but individual species have extremely wide geographic ranges (4, 6). *Derocheilocaris typicus* extends from Massachusetts to Florida and lives in microenvironments varying from subarctic at one end of this range to tropical at the other. *D. remanei* extends from the Atlantic coast of France, into the Mediterranean, down the coast of Africa, and around the Cape of Good Hope into the Indian Ocean as far as Durban. These extensive ranges exist in spite of the fact that both adults and larvae are entirely infaunal, with the result that gene flow must be very limited.

Class MYSTACOCARIDA Pennak & Zinn, 1943

Body divided into cephalon, maxilliped somite, and thoracoabdomen of ten somites (including telson). Antennules uniramous. Antennae and mandibles similar, biramous; fewer segments on endopods than on multiarticulate exopods. Maxillules and maxillae similar, uniramous, multisegmented; maxillipeds either lacking rami or bearing reduced exopods and endopods. Thoracic limbs reduced. Caudal cerci present. Nerve cord ladder-like, with short commissures. Labrum large. Total size of adult about 0.5 mm. *Rec.*

Since the class is monogeneric, it is not possible to characterize separately the class, order, family, and genus.

Order MYSTACOCARIDIDA Pennak & Zinn, 1943

[*nom. correct.* HESSLER, herein (*pro* order Mystacocarida PENNAK & ZINN, 1943)]

Characters of class. *Rec.*

Family DEROCHEILOCARIDIDAE Pennak & Zinn, 1943

[*nom. correct.* HESSLER, herein (*pro* Derocheilocaridae PENNAK & ZINN, 1943)]

Characters of order. *Rec.*

Derocheilocaris PENNAK & ZINN, 1943, p. 4 [**D. typicus*; OD]. Characters of family. *Rec.*, N.Am.-S.Am.-SW.Eu.-Medit.-Afr.——FIG. 73, 74. **D. typicus*, N.Am.(Atl. Coast); 73,*A-G*, adult, showing morphological features, 73,*A,B*, ×250, 73, *C-G*, ×500; 74, early naupliar larva, ×250 (Hessler, n).

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OSTRACODA

By RAYMOND C. MOORE

The bivalved crustaceans termed ostracodes are represented by nearly 1,000 described genera which range in age distribution from Cambrian to Recent. They include innumerable species known only as fossils and countless collected individual specimens are referred to them. As a group their paleontological importance merits special attention. Accordingly, they have been assigned a *Treatise* volume (Part Q, 442 p., 1961) that removes them from a place in taxonomic sequence of the divisions of Crustacea described and illustrated in the present volume.

The following outline of main divisions of the Ostracoda is given, changed from that published in Part Q by elevating the rank of the assemblage to class, matching others such as Branchiopoda, Cirripedia, Malacostraca, and by omission of superfamilies.

Main Divisions of Ostracoda

- Class OSTRACODA Latreille, 1806
  - Order ARCHAEOCOPIDA Sylvester-Bradley, 1961
  - Order LEPERDITICOPIDA Scott, 1961
  - Order PALAEOCOPIDA Henningsmoen, 1953
    - Suborder BEYRICHICOPINA Scott, 1961
    - Suborder KLOEDENELLOCOPINA Scott, 1961
  - Order PODOCOPIDA Sars, 1866
    - Suborder PODOCOPINA Sars, 1866
    - Suborder METACOPINA Sylvester-Bradley, 1961
    - Suborder PLATYCOPINA Sars, 1866
  - Order MYODOCOPIDA Sars, 1866
    - Suborder MYODOCOPINA Sars, 1866
    - Suborder CLADOCOPINA Sars, 1866

EUTHYCARCINOIDEA

By Raymond C. Moore
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INTRODUCTION

Euthycarcinoids are a distinctive group of arthropods which combine some characteristics of merostomes and diplopods with features that are judged to indicate proper placement of them among the Crustacea. They are known only as Lower Triassic fossils from northern Alsace and Moselle in the Saar region and from the Middle Triassic of Australia. The first ones discovered were three rather poorly preserved specimens which Handlirsch (1914) described. He made reconstructions that prove to be erroneous in various ways and interpreted the fossils to be archaic copepods. He named the species *Euthycarcinus kessleri* and because it fitted no recognized group of copepods, erected for it a new order termed Archicopepoda. Not until a half century later has significant information been obtained, so that meanwhile archicopepods have remained as a puzzling, little-understood group, supposedly related to the copepods. An exceptionally fine contribution to knowledge of these fossils recently has been published by Gall & Grauvogel (1964), based on more than 100 specimens, most of which are beautifully preserved. Plates accompanying the descriptions given by these authors adequately document important revisions of Handlirsch's work both in respect to morphology and to interpretation of relationships. They reject the order Archicopepoda as a misnomer and introduce in its place the new name Euthycarcinoidea, with proposal that it should be applied to an independent subclass of the Crustacea.

MORPHOLOGY

Euthycarcinoids have a moderately slender elongate body which is divisible into three tagmata defined as head, thorax, and abdomen (Fig. 75). The length of observed specimens ranges from 5 to 65 mm., with an average of approximately 40 mm.; maximum width of the body is 12 mm. The head is not divided into somites, though attached appendages indicate its derivation by fusion of antecedent anterior somites. Annexed to the head is the first thoracic somite, with appendages functioning as maxillipeds inferred to belong with the buccal complex. The thorax contains 11 somites in addition to the first one, each provided with pairs of uniramous appendages. The abdomen includes five somites and an elongate telson.

The head is semicircular in outline, with evenly rounded front and sides and rectilinear posterior edge, except for small genal spines at the posterolateral angles. The dorsal side, which is gently convex, bears medium-sized sessile eyes, elliptical in outline, close to the lateral margins slightly in front of mid-length. The ventral side, presumably nearly flat, shows a small rostral plate medially in front. Behind this plate is a pair of mandibles and the buccal complex; antennules and a pair of antennae are attached in anterolateral locations. The exoskeletal covering is chitinous, somewhat thickened along the dorsal posterior edge and at the genal angles.

The thoracic somites are protected dorsally and to some extent laterally by five chitinous tergites, each of which is strengthened by a median crest that forms part of a longitudinal ridge running from the head to the telson. The tergites are weakly convex and trapezoidal in outline, with anterior portions projecting beneath neighbors and posterior borders thickened and provided with small spines. The second thoracic somite, bearing one pair of thoracopods, corresponds to the first tergite; the third to fifth somites with three pairs of thoracopods are covered by the second tergite; two additional groups of three somites and six pairs

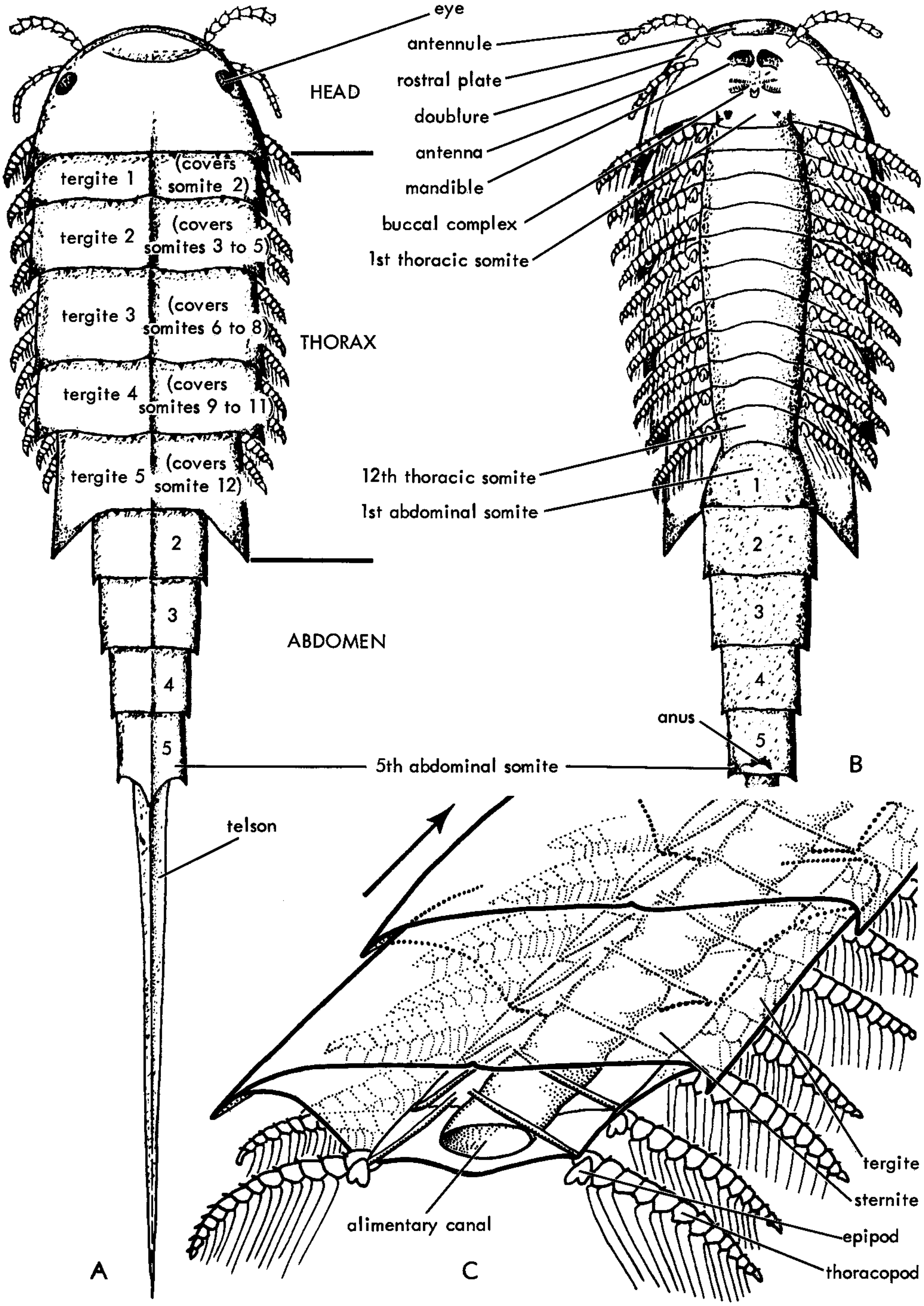

FIG. 75. Morphological features of *Euthycarcinus kessleri* (HANDLIRSCH), L.Trias., France.——A,B. Dorsal and ventral views (reconstr.), ×3.——*C*. Oblique view of mid-portion of thorax with exoskeleton treated as though transparent (arrow points to front of animal), *ca.* ×6 (all mod. from Gall & Grauvogel, 1964).

of thoracopods match the third and fourth tergites; and the last thoracic somite (12th) with one pair of appendages underlies the fifth tergite. Thus, 11 limbs are present on each side of the thorax (Fig. 75,*1*,*2*). The anterior thoracopods are largest and the posterior ones smallest. Each contains 12 or 13 similar segments, the proximal one being identified as a coxa and bearing a small epipod. Posterior sides of the limbs are lined by rows of long setae, providing adaptation for swimming.

In the Middle Triassic euthycarcinoids named *Synaustrus* (3) multiple thoracic somites correspond to tergites *2*, *3*, and *4*, as in *Euthycarcinus*, but only two somites (instead of three) belong with tergite *2* (Fig. 75A). Riek reported two somites associated with tergite *5*, but one of these is abdominal and therefore structure of this region is exactly similar to that of *Euthycarcinus*.

The abdominal somites have subcylindrical sheaths of chitin and are limbless. Four of these skeletal units are visible on the dorsal side but five are seen on the ventral side, for the anterior abdominal somite is concealed by the fifth thoracic tergite. The anus is located on the ventral side of the fifth abdominal somite just in front of the base of the telson. The telson of *Euthycarcinus* resembles the large caudal spike of *Limulus;* it is an elongate rigid structure strengthened by its dorsal keel.

The chief endoskeletal structures of the euthycarcinoids are slender arched struts with outer extremities adjoining bases of the limbs but inner positions somewhat variable (Fig. 75,*3*). They extend above the digestive canal and probably furnished support for it. This canal, identified in fossils by a filling of fine sediment, extends from the head to the terminal somite of the abdomen. Except for minor swellings in each somite, it is featureless.

Several pairs of brownish spots in the cephalic region are inferred to mark attachment places for muscles, chiefly for buccal appendages. Paired elliptical imprints along the axis of the body are interpretable as insertion spots for longitudinal ventral muscles; in the abdominal region the spots are accented by small ferruginous deposits.

ONTOGENY

Some specimens of *Euthycarcinus* have been found with almost perfectly preserved brood sacs, adjacent to which indeterminable remains of small arthropods may occur, seemingly just emerged from eggs. The most diminutive yet-observed individual belonging to the species is a specimen 5 mm. in length. At this stage of growth the head, thorax, and abdomen with telson are already well developed and multi-articulated appendages have appeared.

Comparative examination of specimens of *Euthycarcinus* ranging in length from 5 to 35 mm. indicates that in the course of growth size increase of the thorax is much more rapid than enlargement of the head and that the thorax progressively becomes more slender. No changes in the number of thoracic somites during ontogeny are reported. Abdominal somites become elongated during growth.

The eyes of juvenile individuals are centrally located on the head and during growth of the animal migrate laterally to their near-marginal position in adults.

Molting was facilitated by a splitting apart of the exoskeleton along a line of dehiscence near the front and side margins of the head. Numerous fossils, distinguished by delicacy of cuticle and lack of coloration, are interpreted to represent exuviae—the cast-off exoskeletons of molted individuals.

ECOLOGY

Euthycarcinoids are judged to have been adapted to burrowing in the soft bottom sediments of shallow fresh-water ponds and swampy areas, although undoubtedly they could swim. Evidently they were mud-eaters, as indicated by the fine-sediment filling of alimentary tracts in fossils and by the nature of the buccal apparatus, ill-suited for tearing and chewing large food chunks.

Class EUTHYCARCINOIDEA Gall & Grauvogel, 1964

[*nom. transl.* Moore, herein (*ex* subclass Euthycarcinoidea Gall & Grauvogel, 1964, p. 17)]

Moderately slender elongate body divisible into head, thorax, and abdomen; head bearing pair of sessile eyes near lateral margins and incorporating anterior thoracic somite, antennules and antennae attached to underside of head, which also contains mouth parts; thoracic somites (11 in addition to that joined with head) covered by articulated exoskeleton consisting of five tergites and bearing 11 pairs of multisegmented uniramous thoracopods, each provided with long setae along posterior margins; abdomen with five subcylindrical somites, limbless, but with long styliform telson. *L.Trias.-M.Trias.*

Order EUTHYCARCINIDA Gall & Grauvogel, 1964

[*nom. transl. et correct.* MOORE, herein (*ex* subclass Euthycarcinoidea GALL & GRAUVOGEL, 1964, p. 17)]

Characters of class. *L.Trias.-M.Trias.*

Family EUTHYCARCINIDAE Moore, new family

Characters of order and class. *L.Trias.-M. Trias.*

Euthycarcinus HANDLIRSCH, 1914, p. 5 [**E. kessleri*; OD, M]. Characters of family. *L.Trias.(Upper Bundsandstein),* France(Alsace-Moselle).——FIG. 75,*1-3*. **E. kessleri*; *1,2,* dorsal and ventral aspects of entire specimen (reconstr.), ×3 (Gall & Grauvogel, 1964); *3,* oblique schematic view of mid-thoracic region, exoskeleton treated as though transparent, anterior direction indicated by arrow, *ca.* ×70 (mod. from Gall & Grauvogel, 1964).

Synaustrus RIEK, 1964 [**S. brookvalensis;* OD]. Closely similar to *Euthycarcinus* in morphological features and size, differing only in having one less thoracic somite corresponding to the 2nd tergite. *M.Trias.,* Australia.——FIG. 75A. **S. brookvalensis,* Hawkesbury Series, New South Wales; dorsal view of holotype (reconstr.), ×2 (Riek, 1964).

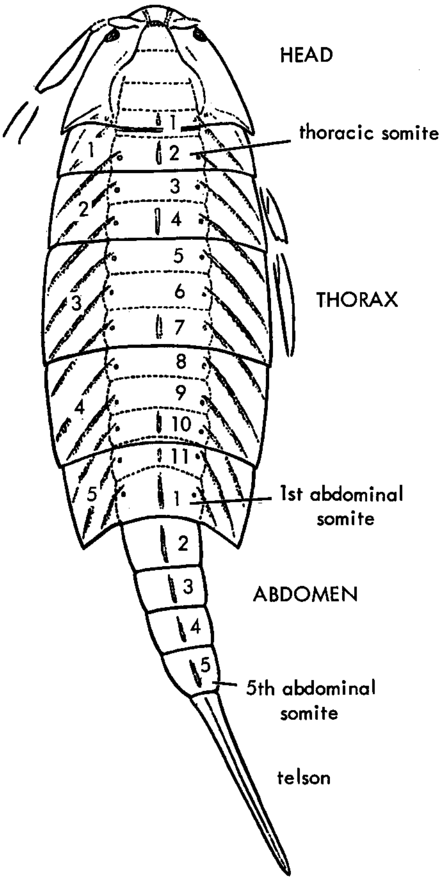

FIG. 75A. Euthycarcinidae (p. R199).

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COPEPODA

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[Chapter submitted January, 1962; revised July, 1965]

INTRODUCTION

Copepods are small crustaceans, rarely exceeding 5 mm. in length, that are found in nearly all aquatic environments. Both free-living and parasitic forms exist within the group. Only free-living forms have been found as fossils.

The bodies of free-living copepods are typically elongate, distinctly segmented, and commonly subcylindrical in shape. A prominent movable articulation at about the mid-length of the body furnishes a natural basis for differentiating fore and rear divisions (**prosome, urosome**) (Fig. 76,*A*). The prosome includes the head region with its paired appendages, covered dorsally and laterally by a cephalic carapace, and four or five thoracic segments that bear biramous jointed legs with setae that aid in swimming. The urosome includes one or two thoracic somites with appendages, four to six abdominal somites without appendages, and a terminal pair of setose caudal rami.

CLASSIFICATION

The conventional classification of copepods is that of Sars (1901-03) (3) in which three orders of free-living forms and four orders of mainly parasitic or commensal forms were recognized, as follows:

Main Divisions of Copepoda Recognized by Sars (1901-03)

Free-living orders	Commensal or parasitic orders
Calanoida	Caligoida
Harpacticoida	Monstrilloida
Cyclopoida	Notodelphyoida
	Lernaeopoida

Lang (1948) (1) has proposed an alternative classification based on his arguments that Sars' classification places in widely separated orders more or less closely related free-living and parasitic forms. This classification, which stresses morphologic relationships rather than adaptive characteristics, reduces the copepods to four groups that he calls suborders, as follows:

Main Divisions of Copepoda Recognized by Lang (1948)

Progymnoplea (equivalent to part of Calanoida)
Gymnoplea (equivalent to part of Calanoida)
Propodoplea (for one family of Sars' Harpacticoida)
Podoplea (includes all copepods not assigned to other suborders, these being divided among revised groups named Harpacticoida and Cyclopoida)

All known fossil copepods are harpacticoids or cyclopoids in either classification. They are assigned here to the orders Cyclopoida and Harpacticoida following the conventional classification of Sars.

Although body form is sufficient for differentiation of the Cyclopoida and Harpacticoida, precise identification of specimens below the ordinal level requires knowledge of morphologic details of the appendages that are rarely well preserved in fossils. Therefore, meaningful determination of species may be difficult or impossible.

ECOLOGY AND PALEOECOLOGY

Recent copepods are found in nearly all aquatic environments. The majority of the calanoid and cyclopoid species comprise a significant part of the plankton assemblages in marine and fresh standing waters and are a major food for fish. The harpacticoid species are mostly benthonic and have been reported from unusual environments, including interstitial waters of beach sands and damp forest moss. Some cyyclopoid and harpacticoid species may form cysts or cocoons for survival during anaerobic periods

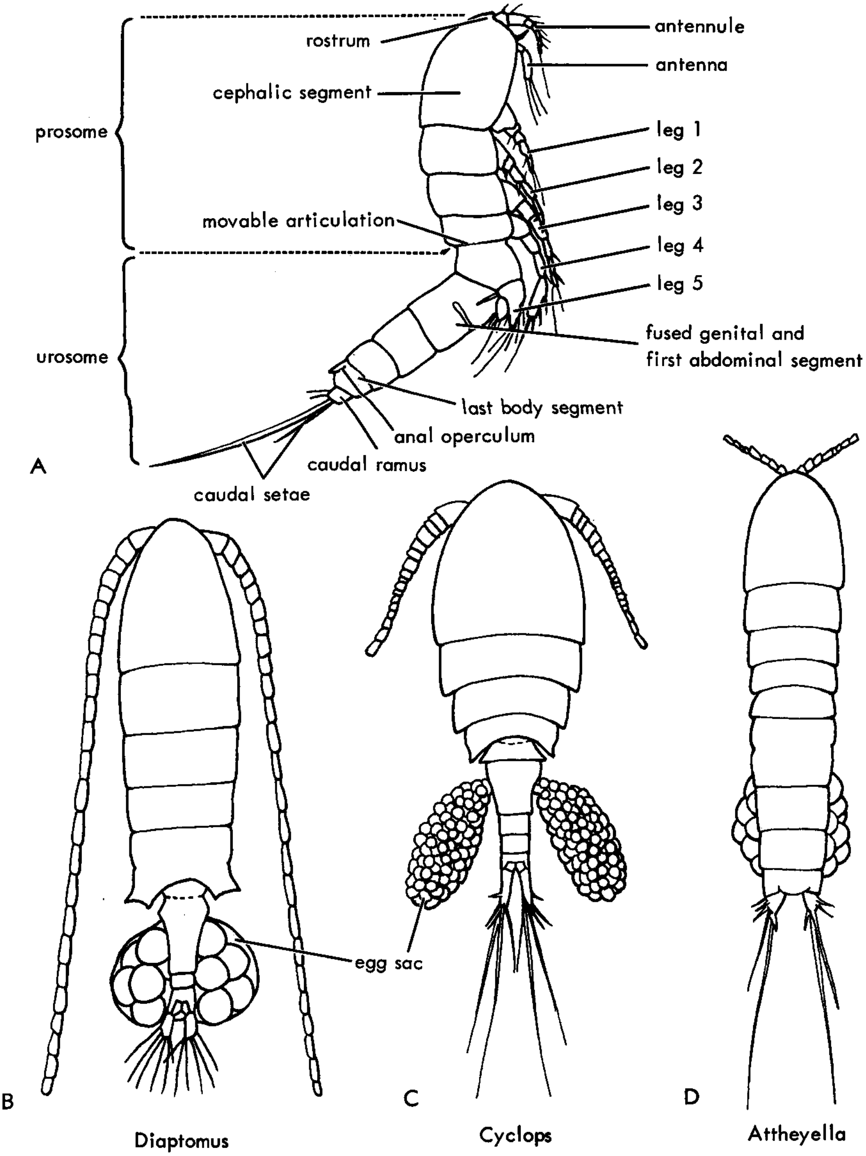

FIG. 76. General morphology of free-living copepods.——*A*. Descriptive terminology for a harpacticoid copepod.——*B-D*. Typical habitus of female of free-living fresh-water copepods, dorsal views: *B*, calanoid; *C*, cyclopoid; *D*, harpacticoid. (From Ward and Whipple, Fresh-water Biology; Fig. *A* slightly modified.)

in lacustrine environments. Cyclopoid cysts are also resistant to desiccation.

Fossil copepods have been found both in North and South America only in lake deposits associated with boron minerals.

Class COPEPODA
H. Milne-Edwards, 1840

Elongate body composed of more or less fused cylindrical chitinous segments which

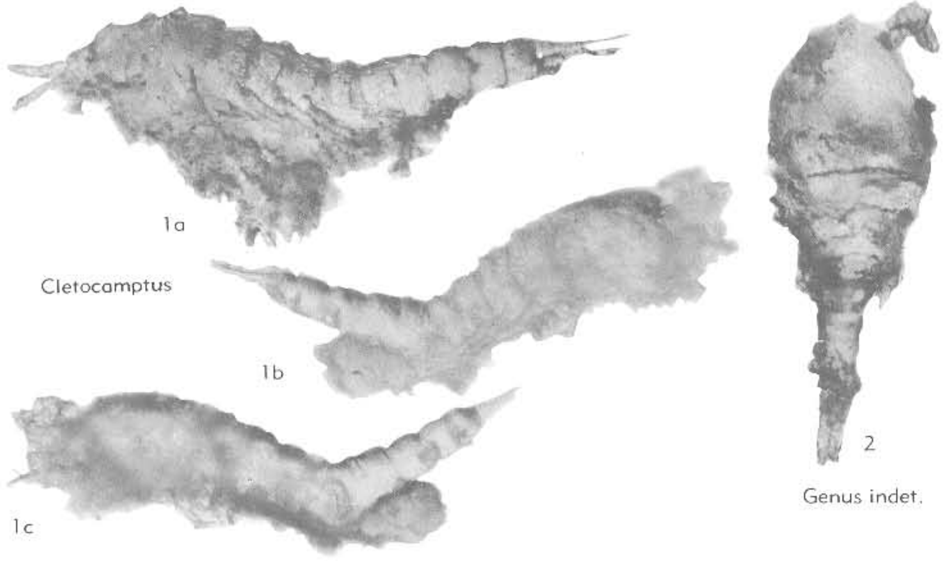

FIG. 77. Cyclopoida *(2)*; Harpacticoida (Cletodidae) *(1)* (p. *R*202).

are divided at prominent movable articulation into prosome (in front) and urosome (in rear); prosome including four or five thoracic somites which bear biramous swimming legs and cephalic somite which bears pairs of antennules, antennae, mandibles, maxillules, maxillae, and maxillipeds; urosome including one or two thoracic somites and five to seven limbless abdominal somites, terminal one bearing pair of caudal rami. Body form substantially modified in parasitic groups. *Mio.-Rec.*

Order CALANOIDA Sars, 1903

Prosome distinctly broader than urosome, movable articulation separating them placed between thoracic somites 6 and 7; antennules long (Fig. 76,*B*). *Rec.*

Order CYCLOPOIDA Sars, 1903

Prosome distinctly broader than urosome, movable articulation located between thoracic somites 5 and 6; antennules short (Fig. 76,*C*). *Mio.-Rec.*

Genus undet., Mio., USA(Calif.).——FIG.77,2. Genus and species undet., Mojave Desert; dorsal view of body, ×90 (2).

Order HARPACTICOIDA Sars, 1903

Prosome only slightly broader than urosome, movable articulation located between thoracic somites 5 and 6; antennules short (Fig. 76,*A,D*). *Mio.*, N.Am.; *Pleist.*, S.Am. (Arg.); *Rec.*

Family CLETODIDAE T. Scott, 1904

Maxillipeds composed of two, less frequently three segments, ultimate one terminating in movable claw. First leg of swimming type, without claws or clawlike setae on ultimate segment of exopod. Body normal, not markedly elongate; body somites distinct, wider distally than proximally. Antennules reduced; antennal appendage with single segment. Endopods of second to fourth legs usually with reduced number of segments; endopods of male as in female, or endopods of third leg modified. *Mio.-Rec.*

Cletocamptus SCHMANKEVITSCH, 1875 [**C. retrogressus*; ?OD]. Antennules 6-segmented; 5th leg single-segmented in both sexes. *Mio.-Rec.*, N.Am. ——FIG. 77,*1*. *C.* sp., Mio., Mojave Desert lake beds, USA(Calif.); *1a*, left lat. view of female, ×90; *1b,c*, right and left lat. views of female, showing eggs below thorax, ×90 (2).

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BRANCHIURA

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[Chapter submitted June, 1962]

INTRODUCTION

The Branchiura comprise one of the most highly specialized and closely circumscribed of all classes of Crustacea. The members of this group are ectoparasites of fishes (although some have been found occasionally on amphibians as well) both in fresh and salt water. Unlike most parasites, they swim quite well and are completely capable of leaving their host. Many of the characteristics of the class obviously are adaptations for this ectoparasitic mode of life.

MORPHOLOGY

The strongly dorsoventrally flattened body is divided into cephalon, thorax, and abdomen (Fig. 78). The lateral portions of the cephalic shield project a variable distance posteriorly as a pair of rounded lobes or alae. A single naupliar eye is located dorsally, while paired compound eyes occur ventrally.

The cephalon carries the usual five pairs of cephalic limbs. The proximal two segments of the uniramous, four-segmented antennules are heavily developed, the second segment bearing a large, posteriorly directed hook. The basal segments of the uniramous, four-segmented antennae are also strongly developed and likewise fitted with a hook. The mouth is located at the tip of a piercing proboscis, while the mandibles are tiny, bladelike jaws at sides of the mouth. When not in use the proboscis folds back into a mid-ventral groove. Anterior to the proboscis is a delicate preoral spine, with which a poison gland is associated.

The maxillules are uniramous. In *Dolops* Audouin, 1837, they are normally developed and bear distal claws, but in the other three described genera they are modified to form paired, stalked sucking discs. The six-segmented uniramous maxillae are characterized by generally having numerous large and small, posteriorly directed spines on their ventral surface. The ventral surface of the cephalon may also be studded with small spines of the same sort. All of these spines serve to prevent the animal from slipping backward on its host.

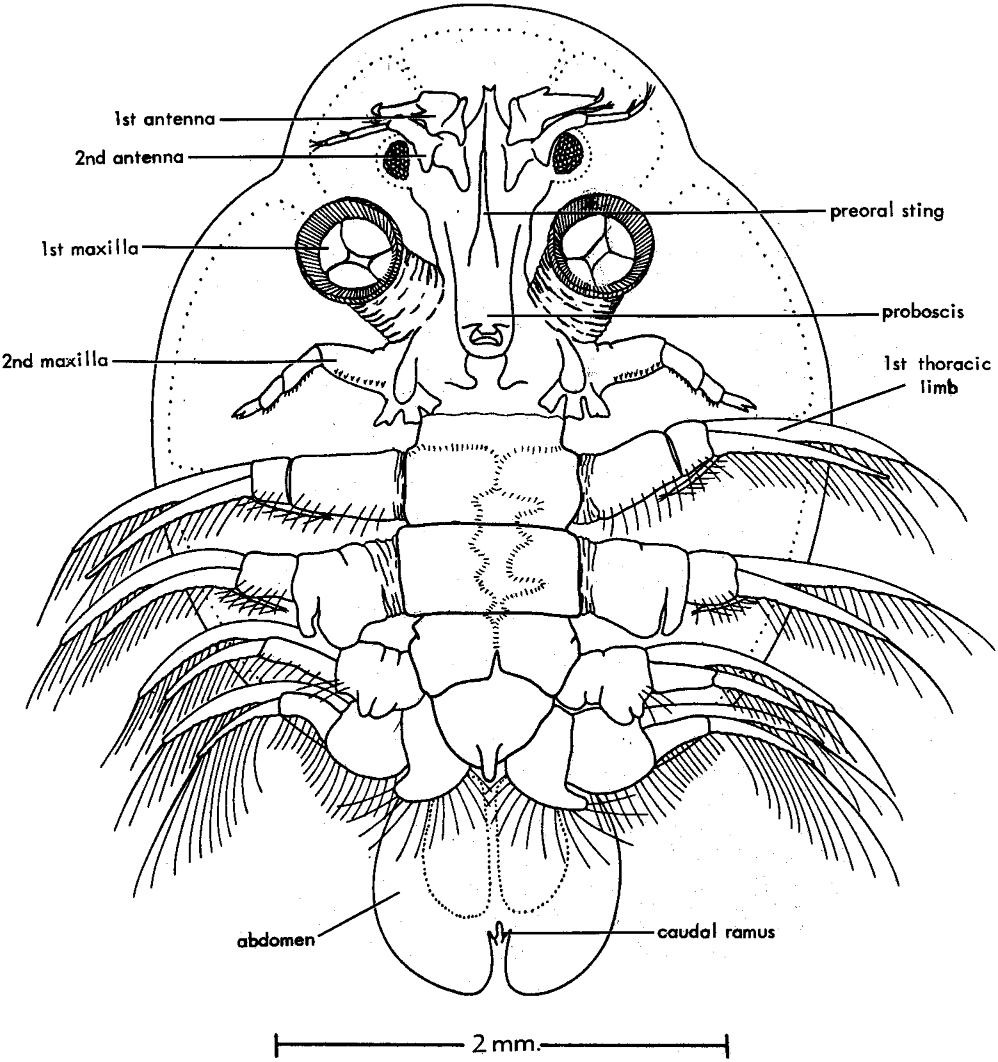

FIG. 78. *Argulus laticauda* SMITH, ventral view of adult male, ×58 (6).

Four thoracic somites occur, of which the first is partially fused to the cephalon. Each thoracic limb extends strongly laterally and serves as a swimming appendage. It has a three-segmented protopod and two rami which are fringed with natatory setae. The unjointed exopod is larger than the endopod and on the first two thoracic limbs has a flabellum which is reflected medially. The endopod may consist of one to three segments. In the male the basal segments of the last three thoracic limbs are modified for copulation.

The abdomen is undivided (although the nervous system indicates that it may consist of two fused somites) and bifurcates posteriorly. A pair of minute caudal rami are present.

DEVELOPMENT

In many species the first free-living stage is a metanauplius (FIG. 79) (5). The mandibles and antennules, in contrast to those of adults, are natatory, much as nauplii of other classes, and no sucker is present on the maxillules.

With later development the antennae are reduced to their adult form. The distal segments of the mandibles are lost, while the basal portion develops into the sides of the proboscis. In *Argulus, Chonopeltis,* and *Dipteropeltis,* the basal portion of the maxillules develops into a sucker. At the same time, thoracic limbs develop.

In other species, the young hatch at a far more mature stage of development.

AFFINITIES

The Branchiura have long been classed under the Copepoda, particularly because of their similarity to the Siphonostoma (6). In conjunction with this determination it was thought that the maxillules were minute processes on the tip of the proboscis, and that the two pairs of subsequent limbs were maxillae and maxillipeds. However, Martin (2) has shown that the proboscis is primarily a derivative of the basal portion of the larval mandible and that it does not bear minute maxillules. The last two pairs of cephalic limbs are, then, maxillules and maxillae. Thus, the tagmosis of the Branchiura is basically different from that of the Copepoda and warrants independent status of the group.

Class BRANCHIURA Thorell, 1864

Body dorsoventrally flattened with five pairs of cephalic appendages; mouth on suctorial proboscis which is formed largely from mandibular components; thoracic somites four, first being partially fused to cephalon; thoracic limbs biramous, natatory; abdomen undivided, with caudal rami. [Ectoparasites on fishes.] *Rec.*

The Carboniferous family Cyclidae Packard, 1885, containing the genera *Cyclus* de Koninck, 1842, and *Halicyne* von Mayer, 1844, were included by Hopwood (1925) in the Branchiura. The resemblance of members of this family to living branchiurans is superficial, however. The cyclids differ from the branchiurans in several basic ways. The mouth is not modified for piercing and the antennae are normally developed, not modified for hooking into the host. The presence of a pair of maxillules modified as suckers is highly conjectural. Finally, the cyclids have too many thoracic limbs and therefore are considered to be unrelated to the Branchiura.

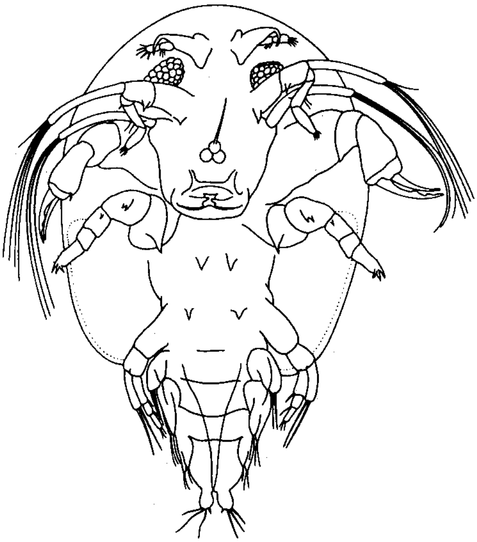

Fig. 79. *Argulus japonicus* Thiele, ventral view of stage-one metanaupliar larva, ×80 (5).

Order ARGULOIDA Wilson, 1932

Characters of class. *Rec.*

Family ARGULIDAE Leach, 1819

Characters of class. *Rec.*

Argulus Müller, 1785, p. 121 [**Monoculus foliaceus* Linné, 1758; SD Jurine, 1806, p. 433] [=*Binoculus* Geoffroy-St. Hilaire, 1732; *Ozolus* Latreille, 1802; *Agenor* Risso, 1826; *Huargulus* Yü, 1939]. Antennules present; maxillules developed as suckers. Rec., cosmop.——Fig. 78. *A. laticauda* Smith, N.Am.; adult, showing morphological features, ×25 (6).——Fig. 79. *A. japonicus* Thiele, Japan; nauplius, ×80 (5).

Dolops Audouin, 1837, p. 13 [**D. lacordarei*; OD] [=*Gyropeltis* Heller, 1857]. Maxillules normally developed, not modified as suckers; preoral sting absent. *Rec.*, S.Am.-C.Am.-Afr.

Chonopeltis Thiele, 1901, p. 46 [**C. inermis*; OD]. Antennules and preoral sting absent; maxillules developed as suckers. *Rec.*, Afr.

Dipteropeltis Calman, 1912, p. 766 [*D. hirundo*; OD] [=*Talaus* Moreira, 1913; *Moreiriella* Mella Leitão, 1914]. Antennules and antennae minute, imperfectly segmented, maxillules developed as suckers; preoral sting reduced; alae greatly elongate. *Rec.,* S.Am.

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CIRRIPEDIA

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CONTENTS

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[4] A *Treatise* chapter on the Cirripedia Thoracica was prepared (1953) by T. H. Withers. Following his death, this manuscript was revised and enlarged by Newman and Zullo. They also added sections on methods, anatomy of soft parts, life histories and evolution of the Thoracica, and sections on systematics of the remaining orders (Apoda, Ascothoracica, Acrothoracica and Rhizocephala), thus forming an integrated treatment of the entire class. The completed typescript and illustrations were received in December, 1967.—Editor.

ACKNOWLEDGMENTS

We have expressed our personal thanks and appreciation to many persons, and wish it were possible to do so again here. Regardless of limitation on space, we must mention our gratitude to our editor, Professor R. C. Moore, for his relentless and high spirited encouragement, critical supervision and advice, and to his staff for careful attention to virtually all figures and other aspects of assembling the manuscript. We would also like to thank Mr. Arnold Ross for his critical and helpful reading of the entire galley proof, Dr. J. T. Tomlinson for allowing us to use his manuscript classification of the Acrothoracica and Drs. P. Reishman and J. Bocquet-Védrine for critically reviewing the classification of the Rhizocephala. We much appreciate the help of Drs. T. E. Bowman and A. G. Humes in making decisions on certain quasi-rhizocephalans, and Drs. R. Yanagimachi and P. Reishman on the systematic position of *Thompsonia*. Many thanks are due Mrs. C. Platt Kourtz (SIO) for extensive and critical reference work, and for careful attention to countless details during the preparation of the manuscript. Support from the National Science Foundation is most gratefully acknowledged, W. A. N., GB-4937X; V. A. Z., GB-4507.

INTRODUCTION

HISTORICAL ACCOUNT

Linné placed the Cirripedia in the class Testacea, along with most of the Mollusca. Cirripeds were not generally accepted as crustaceans until the discovery of the larvae and larval metamorphoses by J. Vaughan Thompson in 1829, even though their internal morphology was known to Cuvier, and though Straus had stressed their crustacean affinities as early as 1819.

It was Charles Darwin who established the morphological nomenclature and systematic concepts upon which subsequent work was based. His two volumes on Recent cirripeds (1851,*38*; 1854,*39*) are among the finest morphological and systematic publications in zoological literature. Even after a lapse of more than a century, these works are still among the chief sources of reference.

Upon this basis, and the collections amassed by numerous biological expeditions of the turn of the century and early 1900's, a number of significant works appeared which refined and expanded our knowledge. Principal contributors include: Annandale, Aurivillius, Broch, Gruvel, Krüger, Nilsson-Cantell, Pilsbry, Weltner, and Utinomi (=Hiro prior to 1939).

Darwin also monographed the British fossil cirripeds *(37, 40)* but fossil representatives have not received nearly the attention given the extant fauna. Prior to 1928, the only other comprehensive works on fossil cirripeds were those of Bosquet on Cretaceous fossils from Holland; Seguenza on Tertiary forms from Sicily and Italy; de Alessandri on Tertiary cirripeds from Italy; and Withers on Tertiary fossils from New Zealand.

Between 1928 and 1953 Withers published three monographs on fossil Cirripedia, including those of the Triassic and Jurassic (1928), the Cretaceous (1935) and the Tertiary (1953, exclusive of Balanomorpha and Verrucomorpha). Much of the data accumulated during the last twenty years on fossil Balanomorpha has come from the works of DAVADIE and KOLOSVARY. Significant papers on early cirripeds are those of CHERNYSHEV (1930) on *Praelepas* (M.Carb., USSR), WILLS (1963) on *Cyprilepas* (U.Sil., Estonia), and TOMLINSON (1963) on *Trypetesa* (Penn., N.Am.).

WITHERS (1926) demonstrated the echinoderm affinities of the early Paleozoic Machaeridia, and thus removed these puzzling fossils from consideration as primitive cirripeds. Recently, POPE (1961) has shown the machaeridian family Lepidocoleidae to be cover plates of the brachial spines of carpoid echinoderms. Various Paleozoic fossils from the Silurian and Devonian of New York State have been attributed to the Cirripedia and proposed as ancestral stocks. These fossils, which include *Eobalanus* RUEDEMANN, *Eopollicipes* RUEDEMANN, *Palaeocreusia* CLARKE, *Palaeopseudobalanus* FISHER, *Protobalanus* WHITFIELD, and *Strobilepas* CLARKE, superficially resemble cirripeds, but on detailed examination exhibit no affinities with the group. For example, LADD (1959) has shown that *Palaeocreusia* is not a cirriped, but more likely the shell of a fissurellid gastropod. Likewise, detailed examination of the shell of *Palaeopseudobalanus* reveals the stereome mesh structure characteristic of echinoderm plates. This structure, together with the arrangement of the imbricating whorls of plates suggests affinities with the machaeridians.

The present day has been described as the "Age of Barnacles," for these animals inhabit the shore line of every coast and are found from the surface to the greatest depths of the oceans. Explanation of the origins and development of this extant fauna requires detailed information on the fossil history of Cirripedia, and, conversely, an understanding of fossil cirripeds is best arrived at through knowledge of the living fauna. It is within this framework that the following synthesis is based. Additional references basic to cirriped systematics include the four monographs of DARWIN *(37-40)* previously mentioned, the monographs by GRUVEL (1905) and by PILSBRY (1907, 1916), and the synthesis of KRÜGER (1940) which includes a comprehensive bibliography to be consulted for many of the references cited herein.

TABLE 1. *Comparative segmentation of Malacostraca, Cephalocarida, Maxillopoda, and Ostracoda.*

			Maxillopoda				
	Malacostraca	Cephalocarida	Copepoda	Cirripedia	Mystacocarida	Ostracoda	
1	A′	A′	A′	A′	A′	A′	HEAD
2	A″	A″	A″	A″	A″	A″	
3	M	M	M	M	M	M	
4	M′	M′	M′	M′	M′	M′	
5	M″	M″	M″	M″	M″	?M″	
6	1P	1P	1P	1P♀	1P	1P	THORAX
7	2P	2P	2P	2P	2P	2P	
8	3P	3P	3P	3P	3P	3P	
9	4P	4P	4P	4P	4P⚥	4⚥	
10	5P	5P	5P	5P	5P	T+F	
11	6P♀	6P♂	6P	6P	6		
12	7P	7P	1⚥	1♂	1		
13	8P♂	8P	2	2	2		
14	1P	1P♀	3	3	3		ABDOMEN
15	2P	2	4	4	4		
16	3P	3	5T+F	5T+F	5T+F		
17	4P	4					
18	5P	5					
19	6P	6					
20	7	7					
21	8T+F	8					
22		9					
23		10					
24		11					
25		12T+F					

[Explanation: A′, first antenna; A″, second antenna; M, mandible; M′, first maxilla; M″, second maxilla; P, pod; T, telson; F, furca.]

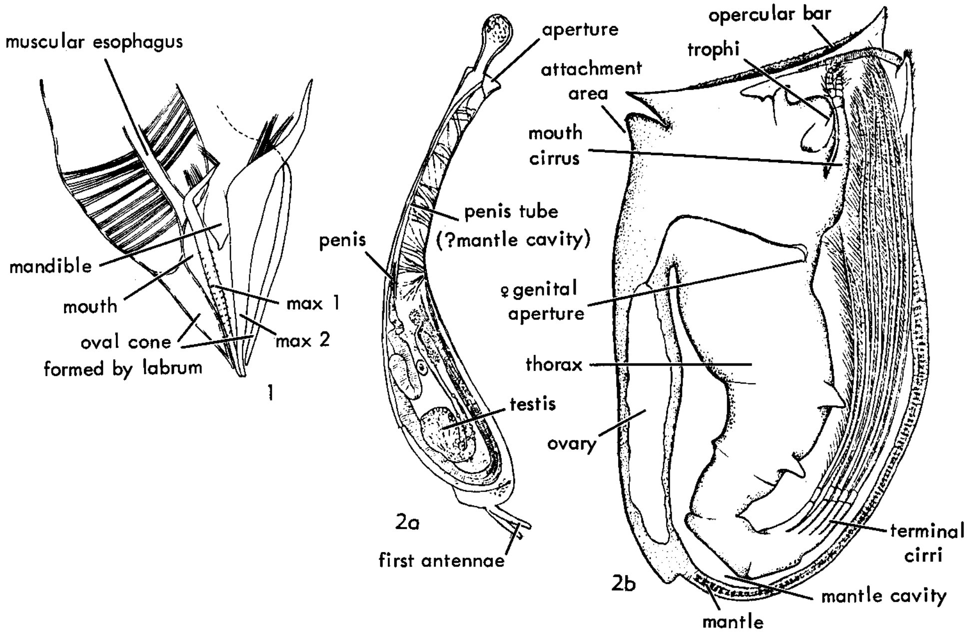

FIG. 80. Morphology of cirripeds.

1. Arrangement of biting mouth parts in female ascothoracican, *Synagoga metacrinicola* OKADA, ×50 (after Okada, 1939).

2. General anatomy of acrothoracican, *Berndtia purpurea*.——*2a*. Male, ×47 (after *103a*).——*2b*. Female, ×20 (*105*, mod.).

DEFINITION OF CIRRIPEDIA

The Cirripedia comprise a diverse and conspicuous group of sedentary marine Crustacea. The fundamental body plan is that of the Maxillopoda[1] (DAHL, 1956): five head and six thoracic appendage-bearing somites; and five abdominal somites, the last bearing a furca (Table 1). Parasitism has evolved in four of the five orders, and in one has resulted in appendageless forms unrecognizable as cirripeds except for their characteristic naupliar and cyprid larval stages.

Attachment in cirripeds occurs during the cyprid stage and is effected initially by the first antennae. The bivalved cyprid carapace is homologous with the so-called mantle of the adult, and it forms the mantle cavity enclosing the appendage-bearing portions of the body of the adult. The mantle itself is either membranous, armed with chitinous spines, or more or less covered with calcareous plates. Food is obtained by setose feeding with the thoracic appendages in nonparasitic forms. Parasitic forms feed by piercing mouth parts; by absorption through cephalic or derived root systems; or through the surface of the carapace.

Sexes are separate or combined. The male genital apertures open on the first abdominal somite, or the last thoracic somite when the abdomen is reduced. The female genital apertures open on the first thoracic somite, near the basis of the first cirri, and this is the most anterior position occupied by genital apertures in any known crustacean. Eggs are laid and retained in the mantle cavity of the female or hermaphrodite, where they develop before being released, usually as planktonic nauplius larvae.

Five orders are generally recognized as Cirripedia: 1) Acrothoracica, 2) Rhizocephala, 3) Ascothoracica, 4) Thoracica, 5) Apoda. The placing of the last among the cirripeds appears to be questionable, however.

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[1] Not recognized in *Treatise* classification. According to DAHL (1963, p. 1) includes Mystacocarida, Copepoda, Branchiura, and Cirripedia, but branchiurans are omitted in Table 1 of this chapter.—Ed.

GENERAL FEATURES OF ORDERS

1) The Acrothoracica are free-living, burrowing cirripeds. Extant species are found in shells of bivalve and gastropod mollusks, living and dead corals, and limestone. Fossils are known only by their burrows that occur in a variety of invertebrate skeletons (see "Fossil Traces"), the earliest having been found in Pennsylvanian pelecypod shells. The anatomically most primitive or unmodified living genus is *Weltneria* Berndt.

Sexes are separate in all known Acrothoracica. Females excavate individual burrows where they are usually accompanied by one or more minute males (Fig. 80,*2a,b*).

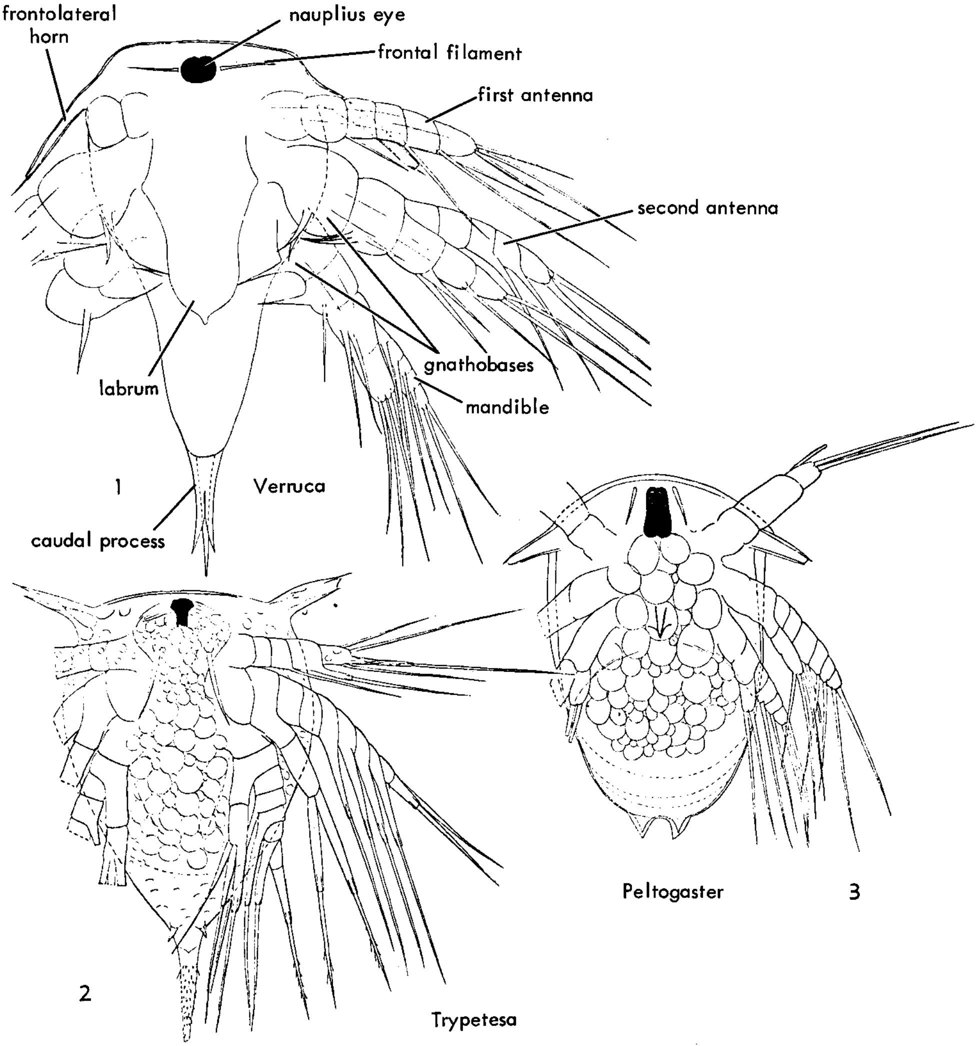


Fig. 81. Morphology of cirripeds; nauplius larvae (mod. from *61*).

1. Thoracican, *Verruca (Verruca) stroemia* (Müller), stage 1 nauplius, ×267.
2. Acrothoracican, *Trypetesa lampas* (Hancock), ×107.
3. Rhizocephalan, *Peltogaster sulcatus* Lilljeborg, ×189.

The male consists of little more than a sac of gametogenic material, sometimes provided with a visible copulatory apparatus. The life cycle includes nauplius and cyprid stages, although the former may be passed through in the egg. The female cyprid settles and initially becomes attached by its first antennae. In general, while in the process of metamorphosis, the cyprid begins to burrow mechanically into the substratum. The first antennae are left at the exterior attachment point, as the burrow becomes occupied.

In the adult, the mantle sac lines the burrow and opens to the exterior through an aperture at the entrance. The sac commonly is cemented to the wall of the burrow by the anterior end (attachment disc). The animal resides within the cavity formed by the mantle. The mouth field is made up of the labrum, the usual three pairs of mouth parts, and the first pair of cirri (mouth cirri) which are reduced in size and situated along the posterolateral margins of the oral cone. A maximum of five pairs of cirri are situated in a group at the posterior end of the thorax, and a pair of anal or caudal appendages may be present. The abdomen, present in the cyprid, is completely wanting. The most complete recent anatomical studies have been made on *Berndtia* by UTINOMI (1957, 1960, 1961).

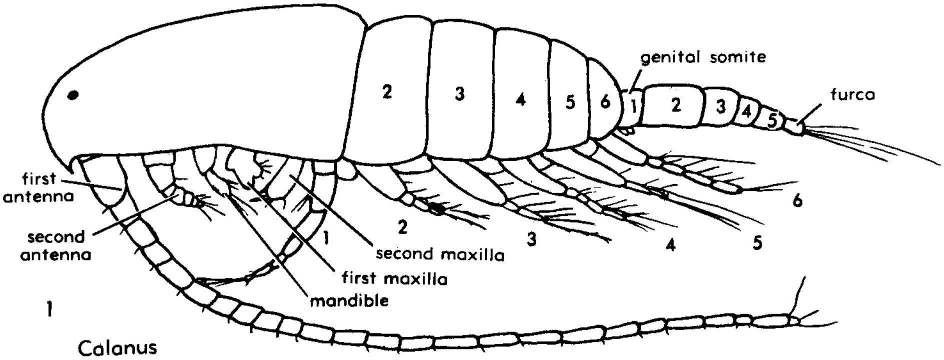
2) The Rhizocephala are parasites primarily of decapod crustaceans. In general, the cyprid seeks out and attaches itself to the host. Metamorphosis proceeds and a larval form known as kentrogon is developed that invades and ramifies through the tissues, usually resulting in parasitic castration of the host. Reproductive structures appear on the surface of the host after the nutritive structures have become well developed. The mantle, mantle cavity or brood chamber, ovaries and nervous elements of the reproductive body of the rhizocephalan are considered homologous with these structures in other cirripeds. However, the Rhizocephala are so modified that virtually no characteristics identify them as arthropods, much less crustaceans, other than their larval forms which are comparable to those of the acrothoracican and thoracican Cirripedia (Fig. 81,*3*).

Recent work has demonstrated that some species previously thought to be hermaphroditic have separate sexes. The female parasitizes the host while the male exists as a mass of spermatogenic material delivered to the female by the male cyprid larva (YANAGIMACHI, 1961). Another recently investigated rhizocephalan has been found to lack kentrogon and consequently to be externally parasitic (BOCQUET-VÉDRINE, 1961). BOSCHMA (1925 to date) can be consulted for taxonomic details of the group. A comprehensive bibliography is given in Zool. Meded. *39:* xli-xlvi, 1964.

3) The Ascothoracica are parasitic on hexacorals and echinoderms. The order is ranked by some workers among the Cirripedia, and by others as a separate subclass of crustaceans, the Ascothoracida WAGIN. The least specialized forms have separate sexes, a life cycle including nauplius and cyprid larvae, a head reduced in the same manner as in ordinary cirripeds, an initial attachment by prehensile first antennae, and the same unique position of the female genital aperture as in other cirripeds (Fig. 82). Differences that have been utilized to separate them from the cirripeds are for the most part secondary and therefore of no great weight in a diagnosis of a separate subclass. We therefore have retained the Ascothoracica as an order of the Cirripedia.

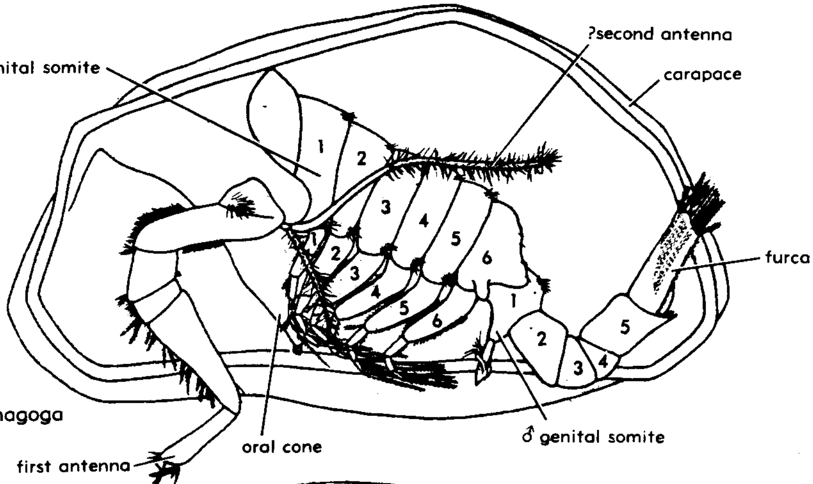
The adult consists of a bivalved carapace gaping ventrally, permeated by gastric ceca, and provided with a postoral adductor muscle. The prosoma supports the prehensive first antennae, succeeded by a pair of filamentary appendages which have been interpreted as rudiments of the second antennae. The second antennae are usually lost in ordinary barnacles, appearing only in the nauplius and as rudiments in certain cyprids.

The mouth field is produced into an oral cone formed by the labrum, mandibles and two pairs of maxillae, and is apparently adapted to piercing and sucking (Fig. 80, *1*). The thorax supports six biramous, natatory appendages. The abdomen of five somites is well developed in many species; the first somite supporting a penis or rudiment thereof, the last the furca. This is



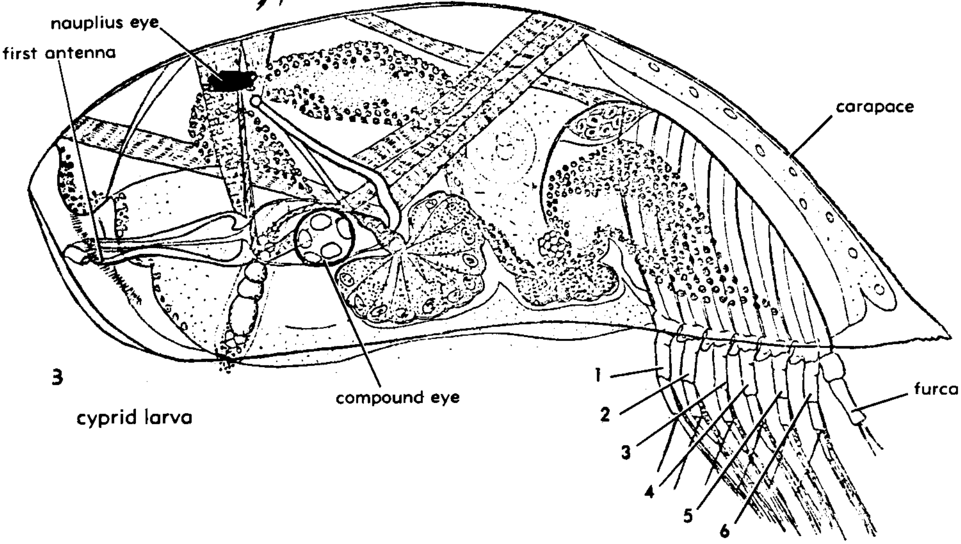
1

Calanus



2

Synagoga



3

cyprid larva

the most generalized somite pattern found in the cirripeds and corresponds to that of the unspecialized Copepoda (cf. Fig. 82, *1-3*). Hermaphroditism is apparently secondarily acquired. There are no fossils, although VOIGHT (1959) has described cysts in a Cretaceous octocoral; and MADSEN & WOLFF (1965) describe scars in an Upper Cretaceous echinoid they suggest were caused by ascothoracicans. WAGIN (1946) and BRATTSTRÖM (1947, 1948) can be consulted for systematic and biological aspects of the order.

4) Most Thoracica are free-living or commensal cirripeds found attached to a variety of living and inanimate substrata. They gain their greatest diversity in shallow waters but representatives are found at all depths. The earliest undoubted fossils *(Cyprilepas)* are found in the Silurian, but it is not until the Mesozoic that fossils become numerous. These are stalked forms belonging to the suborder Lepadomorpha (Fig. 83,*1,3a,b*). The Cenozoic marks the advancement of the sessile barnacles of the suborder Balanomorpha, an expansion that has continued through to the present time (Fig. 83,*2*).

Most of the Thoracica are hermaphroditic, with internal fertilization. There is evidence for self-fertilization, but cross fertilization is generally the rule. The Scalpellidae and Iblidae, among the Lepadomorpha, have species in which sexes are separate or combined; reduced attached males occurring with females; or complemental males with hermaphrodites; or all individuals are hermaphrodites. The Balanomorpha were thought to be exclusively hermaphroditic. Recently, however, complemental males were discovered in a species of *Balanus* (HENRY & MCLAUGHLIN, 1965).

The life cycle of the Thoracica is comparable to that of the Acrothoracica, including nauplius and cyprid stages. Anatomically the adult differs primarily in having the cirri nearly evenly distributed along the thorax, the mandibular palp associated more closely with the lateral margin of the labrum than with the mandible, and in not molting the exterior of the mantle along with the exoskeleton lining the mantle cavity and covering the appendages. This last feature is correlated with the ability to build up a permanent calcareous armament. Further details of structure will be taken up in the following section.

5) The Apoda was established by DARWIN to accommodate a curious parasite, *Proteolepas bivincta* DARWIN, found in the mantle cavity of the pedunculate barnacle *Heteralepas cornuta* (DARWIN) from the West Indies (Fig. 84). *Proteolepas* has not been seen since DARWIN described it. Because its segmentation can be interpreted as that of a copepod, or possibly a malacostracan (epicaridean), rather than that of a cirriped, it is presently considered to be an organism of unknown affinities. Therefore, the Apoda, and the larval forms attributed to it by HANSEN, STEUER, and MCMURRICH, are retained *incertae sedis* in the Cirripedia only as a matter of convenience.

MORPHOLOGY OF THORACICA

GENERAL FEATURES

Thoracican cirripeds are sedentary animals. When at rest, the body and appendages are enclosed within a "mantle" formed by bilateral folds of the carapace. The mantle is usually protected externally by a number of calcified plates (Fig. 83, 85). In the adult stage, the animal is attached to the substratum by the anterior part of the cephalic region. The first antennae and their associated cement glands form the

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(See facing page.)

FIG. 82. Comparison of maxillopodan body plan of copepod with that of ascothoracan and thoracican cyprid larva.

1. Male *Calanus,* ×32 *(23).*

2. Male *Synagoga metacrinicola* OKADA, ×25 (after Okada, 1939).

3. Cyprid larva, *Trypetesa lampas* (HANCOCK), ×233 (after Kühnert, 1935, in *61*).

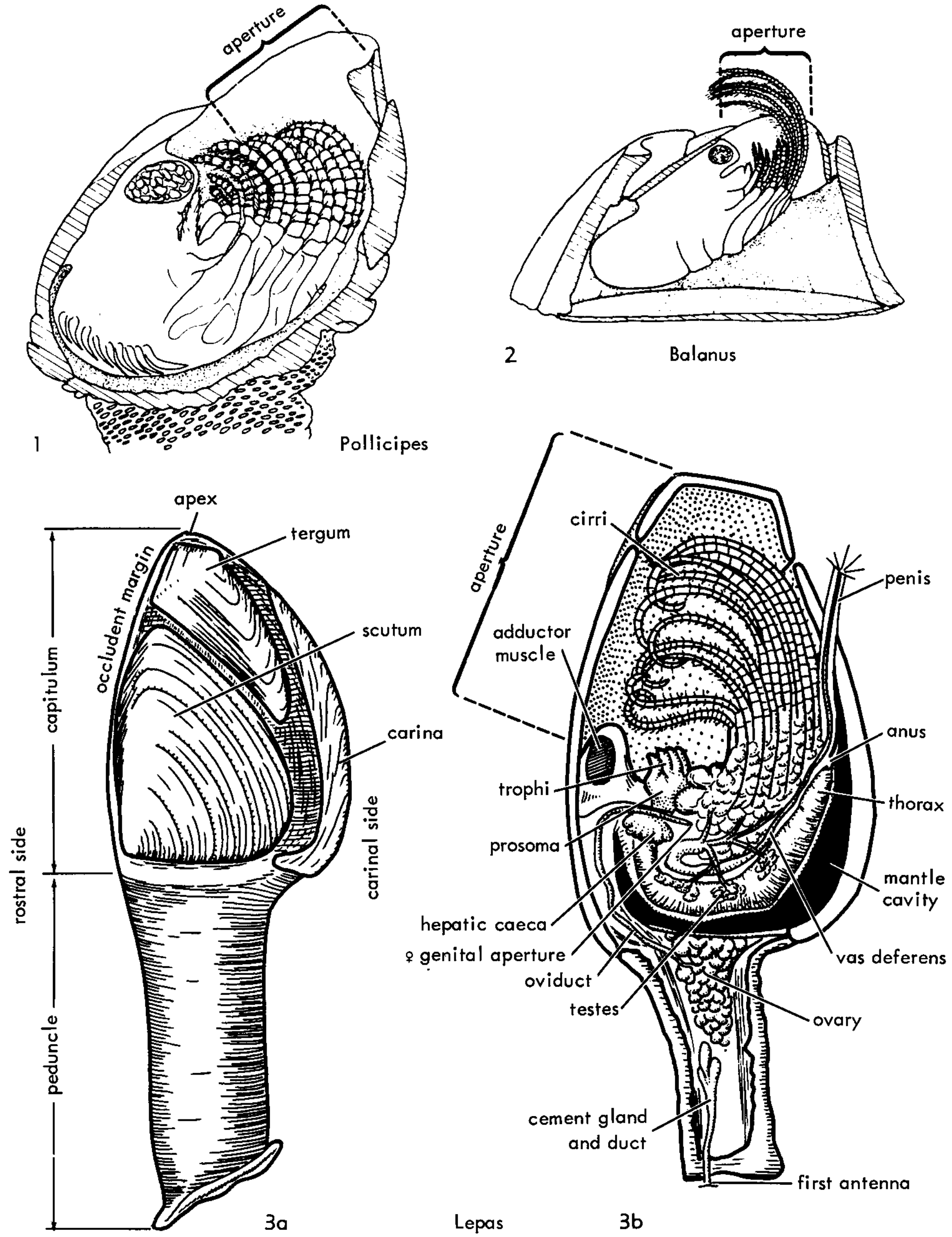


FIG. 83. Morphology of cirripeds; body plan of lepadomorphs compared with that of balanomorph.

1. Lepadomorph (Scalpellidae), *Pollicipes polymerus* SOWERBY, with right side of capitulum removed, ×2.4 (Newman, n).
2. Balanomorph (Balanidae), ***Balanus (Balanus) amphitrite*** DARWIN, with right side of wall and lining of mantle cavity removed, ×2.4 (Newman, n).
3. Lepadomorph (Lepadidae), *Lepas*.——*3a. L. (L.) hillii* LEACH, outer view of individual from right side, ×2 (after Darwin).——*3b. L. (L.)* sp., dissection from right side, ×2.5 (after Claus).

initial attachment of the free-living cyprid larva. After metamorphosis, the base of the peduncle in the Lepadomorpha, or where the margin of the wall meets the basis in Verrucomorpha and Balanomorpha, take over the function of attachment and cement the animal in place.

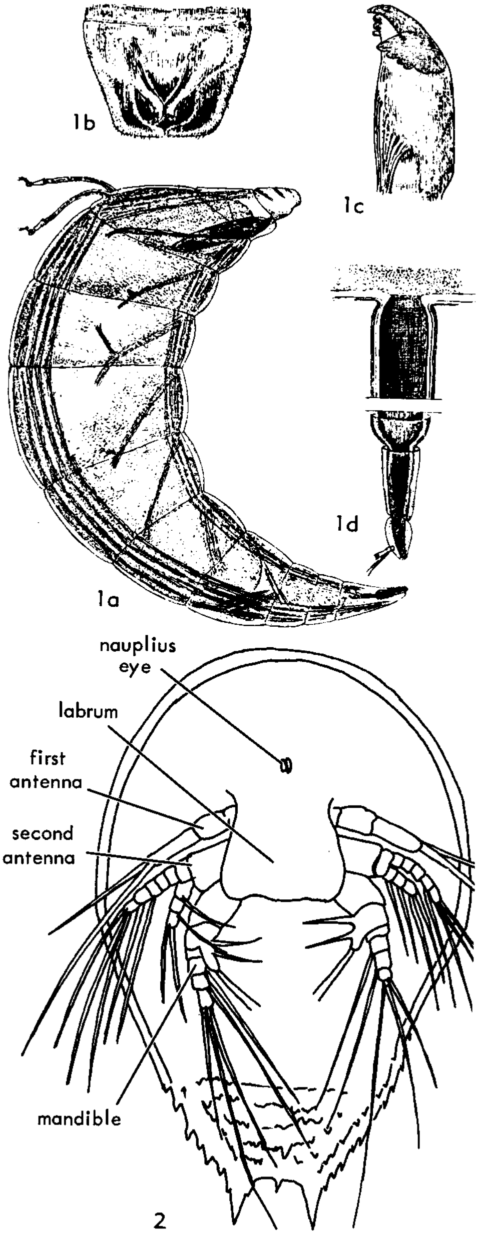


FIG. 84. Morphology of Apoda.——*1. Proteolepas bivincta* DARWIN; *1a,* hermaphrodite, ×17; *1b,* mouthfield, enl.; *1c,* "compound mandibular organ," greatly enl.; *1d,* "first antenna," greatly enl. (after Darwin).——*2.* HANSEN'S "Y" larva, supposed larva of the Apoda, ×240 (after *51*).

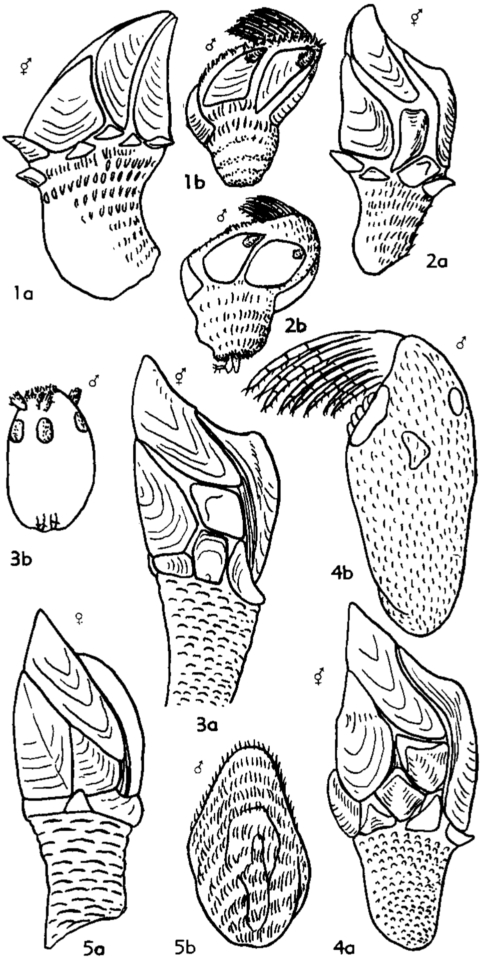


FIG. 85. Morphology of cirripeds. Sexuality in scalpellid genera, individuals viewed from right side, hermaphrodites *(1a-4a)* and their complemental males *(1b-4b)* and a female *(5a)* with dwarf male *(5b)* (males greatly enl.) (from Pilsbry, after Withers).——*1a,b. Calantica (Calantica) villosa* (LEACH).——*2a,b. Smilium peroni* GRAY. ——*3a,b. Scalpellum scalpellum* (LINNÉ).——*4a,b. Euscalpellum rostratum* (DARWIN).——*5a,b. Acroscalpellum velutinum* (HOEK).

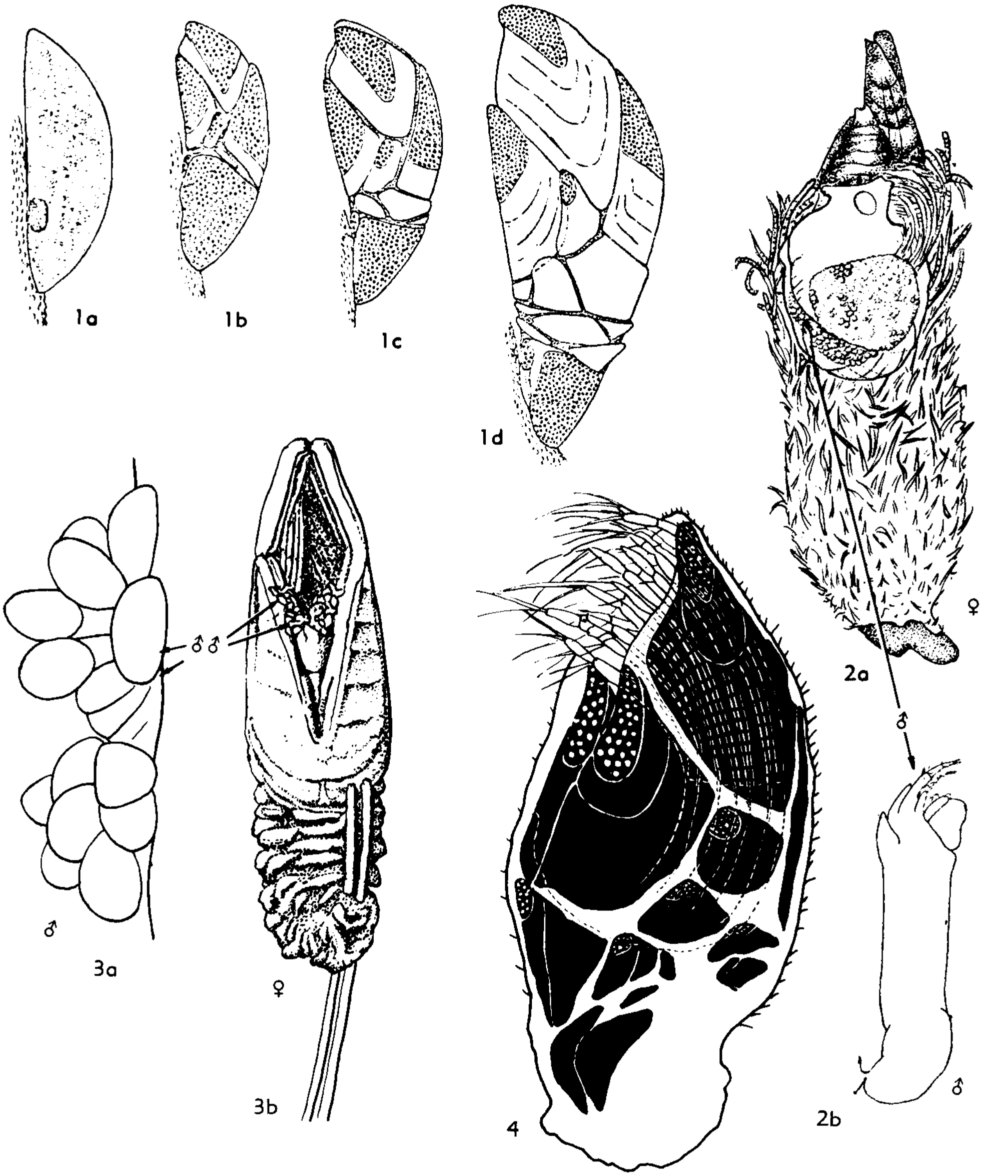


FIG. 86. Morphology of cirripeds. Ontogeny and sexuality.

1. Ontogeny of *Arcoscalpellum balanoides* (HOEK), illustrating appearance of additional primordia over basic number of five, ×50 (after *22*).——*1a*. Newly settled cyprid larva.——*1b*. Cyprid shell cast, six primordia visible including that for upper latus and one each for dorsal and ventral peduncular scales, inframedian latus and carinal latus appearing as calcified plates without primordial precursor.——*1c*. Later stage, rostral latus appearing without primordial precursor.——*1d*. Still later stage showing appearance of additional peduncular plates and continuing calcification of capitular plates, carrying primordia apically at their umbones.
2. *Ibla cumingi* DARWIN.——*2a*. Female, ×4.5 (right side of capitulum cut away, male and ovigerous lamellae seen *in situ*).——*2b*. Dwarf male, viewed from left side, ×18 (Newman, 1960).

The cephalic region in Lepadomorpha is developed into a more or less flexible stalk or **peduncle**. In the sessile forms Balanomorpha and Verrucomorpha, the anterior region is represented by a flattened disc or **basis**. The homology of these two regions in pedunculate and sessile forms was demonstrated by DARWIN (1851-54), who observed in both groups that initial attachment was made by the first antennae of the cyprid larva, and that traces of these appendages were located centrally, embedded in the cement of the attachment disc.

In the pedunculate cirripeds, the mantle, with or without its protective plates, is termed the **capitulum** (Fig. 83,*3a*). The body occupies the cavity formed by the capitulum, where it lies attached at the scutal margin in a curved position. The long axis of the body is curved, but for the most part, it is oriented at right angles to the long axis of the animal when at rest. Because of this distortion in the relationship of one part of the animal to the other, confusion arises if ordinary terms of orientation are followed. It therefore has been customary in describing cirripeds to use the arbitrary terminology established by DARWIN. By convention, pedunculate cirripeds are illustrated in an upright position, with the capitulum above and the peduncle below, so that the animal is effectively "standing on its head." In this position, what would be anatomically equivalent to the ventral surface, including the occludent margin, is termed **rostral**, and what would be dorsal is termed **carinal**, names being derived from the unpaired calcified plates that occur on these margins in many species. The body lying within the capitulum is reflexed toward the carinal margin from the prosoma. When extended during feeding, it assumes a position more parallel to the long axis of the entire animal, so that its ventral and dorsal surfaces more closely correspond to the dorsal (carinal) and ventral (rostral) surfaces of the capitulum.

The relationship of the body to the mantle wall is basically the same in the pedunculate and sessile cirripeds (cf. Fig. 83,*1-3*). However, the body is reflexed even more in the latter, so that when the animal is at rest, the body tends to lie almost parallel to the substratum. When feeding, however, the body is rotated and extended posteriorly, so that the same general relationships hold for sessile forms as for the lepadomorphs. Further similarities and homologies between these two basic forms will be taken up under the section on evolution.

The majority of the extant thoracican cirripeds are hermaphroditic. However, some species produce relatively small males (Fig. 85, 86,*2-3*). Following DARWIN, the male is referred to as a **complemental male** when it occurs with a hermaphrodite, and as a **dwarf male** when it occurs with a female. In Recent forms, the males are considerably smaller than the female or hermaphrodite and are always attached either externally or within the mantle cavity. Usually the armature, trophic structures and digestive system of such males are degenerate or nonexistent.

Among Recent scalpellids (e.g., *Scalpellum ornatum, Mesoscalpellum gruvelii*, Fig. 86,*3*) a depression or pocket occurs internally in the scuta, above the attachment for the adductor muscle closing these plates, and accommodates one or more minute males. A similar depression is seen in the scutal plates of *Arcoscalpellum* from the Upper Cretaceous, suggesting the presence of dwarf or complemental males in Mesozoic times. (See Addendum to Cirripedia, p. *R*628.)

It is assumed that fossil lepadomorphs are large females or hermaphrodites. Presently, however, there is no way of knowing that free-living separate sexes did not occur. The trend seen in Recent forms suggests that they did, and if such were the

FIG. 86. *(Continued from facing page.)*

3. Mesoscalpellum gruvelii (ANNANDALE).——*3a*. Dwarf males, enl.——*3b*. Female with males *in situ*, viewed from rostral end, ×2 (Annandale, 1907-1908).

4. Primordial plates (possibly more than basic number of five) in *Euscalpellum bengalense* (ANNANDALE), ×48 (after Stubbings, 1936).

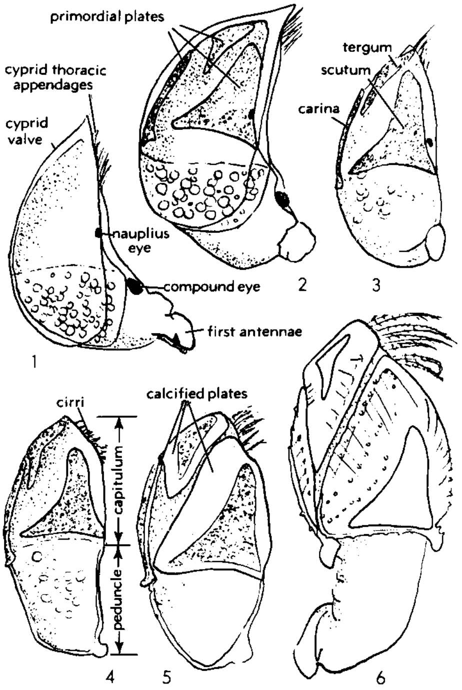


Fig. 87. Morphology of cirripeds. Metamorphosis of *Lepas (Lepas) anatifera* Linné, ×16 (Newman, n).——*1.* Recently settled cyprid larva beginning metamorphosis.——*2.* Primordial plates appearing beneath cyprid shell, compound eyes being shed.——*3.* Cyprid shell shed, nauplius eye still visible near middle of occludent margin of scutal primordium.——*4.* Further differentiation of capitulum and peduncle, cirri but not calcareous plates having appeared.——*5.* Calcification beginning beneath and progressing away from primordial plates.——*6.* Juvenile stage having much the same proportions as adult.

case, it seems likely that the males would have been smaller than the females of the same species.

HARD PARTS

A fundamental characteristic of the Arthropoda is molting of the exoskeleton during growth and development. Among the Crustacea, only the Conchostraca, certain fossil supposed Ostracoda and the thoracican Cirripedia, all forms with a basically bivalved carapace, have developed the ability to retain and build up portions of the exoskeleton of the carapace with calcium carbonate, while frequently molting the chitinous exoskeleton of the rest of the body. Among Cirripedia, the Thoracica, but not the Ascothoracica, Acrothoracica, or Rhizocephala, produce a shell of calcium carbonate.

According to Clarke & Wheeler (1917), the barnacle shell differs from that of other crustaceans in containing very little phosphate or organic material. Chave (1954) reported the shell of various forms to be predominantly calcite, to contain no aragonite and to have a magnesium carbonate fraction ranging between 1.35 and 4.60 percent, varying proportionally to the temperature at which it was laid down.

The calcareous portion of the thoracican shell appears during the metamorphosis of the cyprid larva into a young barnacle. In the Lepadomorpha and Verrucomorpha the appearance of certain of the calcified plates or valves is preceded by the appearance of so-called **primordial valves** or **plates,** which are presumably chitinous and for which the function is unknown. The primordial valves appear attached to the hypodermis, beneath the cyprid shell (Fig. 87-89). In the Lepadidae *s.l.* there are five primordia, corresponding to the five calcified plates that will develop beneath them as metamorphosis progresses. In the Scalpellidae there are also usually five primordia, associated with the same centers of calcification as in the Lepadidae, but in certain species additional primordia may be present as well (Fig. 86,*1c,d*).

The shape and size of a primordial plate is apparently determined when it is formed and it appears that it becomes physiologically isolated from the hypodermis after calcification sets in. In the adult barnacle, it resides at the umbo of the calcified plate with which it is associated, and although small, it can be found, unless eroded away. Primordial plates have been found on the umbones of certain fossil scalpellids from the Middle Carboniferous and Jurassic (Kimmeridgian).

Interpretations of the phylogenetic significance of the primordial plates will be taken up in the section on phylogeny. Suffice it to say at this point that primordial

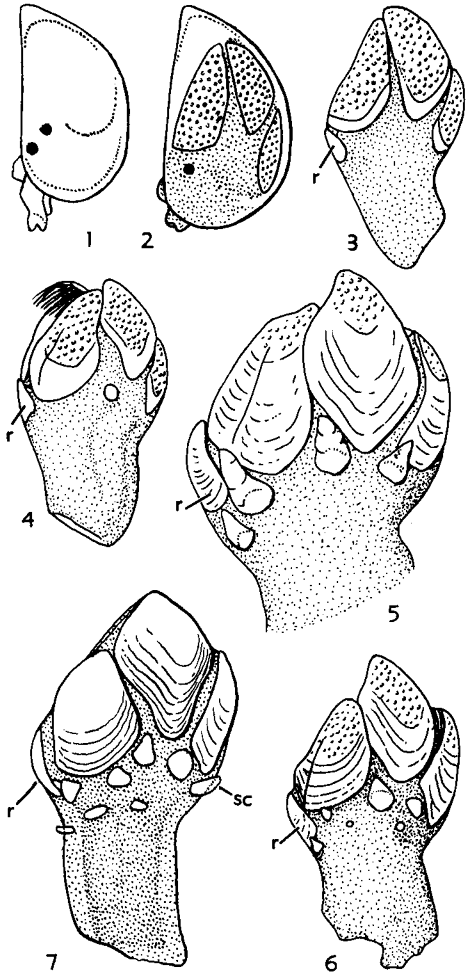


FIG. 88. Morphology of cirripeds. Ontogenetic development of *Pollicipes polymerus typica* BROCH, Rec. (not to scale) (Broch, mod.).——*1*. Cyprid just attached.——*2*. Cyprid with primordial plates.——*3*. Cyprid shell shed, calcification around primordia and rostrum developing.——*4*. Specimen with upper latus.——*5*. Somewhat aberrant specimen with three latera and subrostral latus.——*6*. Normal specimen with two lower latera developed.——*7*. Specimen with subcarina well developed, and first peduncle scale appearing below rostrum. [Explanation; *r*, rostrum; *sc*, subcarina.]

plates, while found in Lepadomorpha and Verrucomorpha, are unknown in the Balanomorpha.

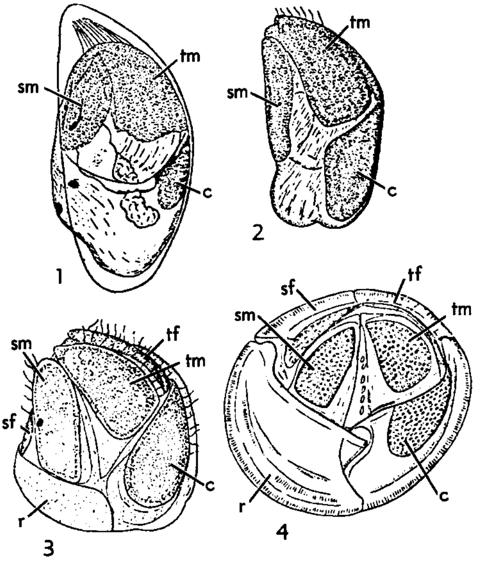


FIG. 89. Morphology of cirripeds. Metamorphosis in *Verruca (Verruca) stroemia* (O. F. MÜLLER), all enl. (after Runnström, 1926, from *61*).——*1*. Attached cyprid with primordial plates of movable scutum, movable tergum and carina visible.——*2*. Cyprid shell cast, carina rotated somewhat to right side.——*3*. Calcification beginning—movable scutum, movable tergum, fixed scutum, fixed tergum and rostral plate visible.——*4*. Juvenile resembling adult. [Explanation: *c*, carina; *r*, rostrum; *sf*, scutum (fixed); *sm*, scutum (movable); *tf*, tergum (fixed); *tm*, tergum (movable).]

LEPADOMORPHA

The armature of the capitulum consists of a distinct number of principal calcareous plates formed and arranged in a definite manner, depending on the species, genus, and generally the family. Therefore, the number of relative positions of the plates are of systematic, ontogenetic, and phylogenetic significance. For descriptive purposes, it has been found necessary to name not only each principal capitular plate, but also various conspicuous features of most of them.

The principal plates seem to be fundamentally six in number, in the Scalpellidae, namely the paired **scuta** and **terga**, **a carina** and a **rostrum** (Fig. 90,*1a*). During meta-

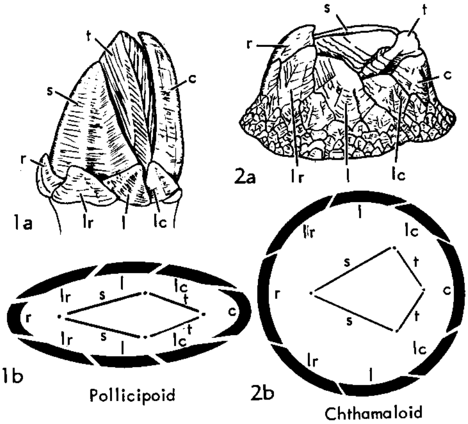


FIG. 90. Morphology of cirripeds. Comparison of *(1)* pollicipoid form comparable to *Calantica (Scillaelepas) dorsata* (STEENSTRUP), U.Cret.(Dan.), Denmark, but with relationship of latus to other latera altered and *(2)* the chthamaloid *Catophragmus (Catomerus) polymerus* DARWIN, Rec., Tasm.; *1a, 2a,* ×2.2 *(1a,* after *118, 120)*; *1b, 2b,* plan views of principal plates (Newman, n). [Explanation: *c,* carina; *l,* latus; *lc,* latus (carinal); *lr,* latus (rostral); *r,* rostrum; *s,* scutum; *t,* tergum.]

morphosis from the cyprid larva to the adult, in the Verrucomorpha, as well as the scalpellid Lepadomorpha, all but the last, or rostral plate, is preceded by a primordial plate (Fig. 88, 89). In the Lepadidae, there are basically only five capitular plates, the rostrum being completely absent (Fig. 87). The carina forms the dorsal margin of the capitulum. In *Praelepas,* one of the oldest known thoracicans, and in the Lepadomorpha *s.l.,* the carina extends between both the terga and the scuta (cf. Fig. 83,*3,* see Fig. 114,*10*). However, in the scapellids, it borders on the terga alone, and this is another fundamental difference between the two groups. The scuta, usually larger than the terga in lepadids and equal or smaller in the scalpellids, serve to protect the ventrolateral part of the animal while the terga form the ventral or posteroventral aperture through which the cirri are protruded during feeding. A free scutum can often be recognized by the presence of an adductor muscle pit or scar on the interior.

The terga are usually large and flat, adjoin the scuta, and serve to protect the posterior part of the animal. These plates are not provided with muscles, but are affected by opening and closing movements of the scuta. The rostrum, present in the scalpellids, commonly resembles the carina in shape, but is usually much smaller and adjoins the rostral angles of the scuta. This plate can usually be distinguished by the greater development of growth ridges on the apical part of the inner surface.

Only the principal six plates are present in the Carboniferous *Eolepas,* and they form a single whorl (see Fig. 115,*1*). *Archaeolepas* has the same basic arrangement of plates, but the peduncle has become armed with successive whorls of uniform additional plates (see Fig. 115,*6*). In *Calantica (Scillaelepas),* the scuta, terga and carina form an upper whorl, whereas the rostrum and basal portion of the carina, in conjunction with a number of secondary plates, form a secondary basal whorl, the margins of which overlap one another (Fig. 91,*6*). This secondary whorl has nine parts—the **rostrum,** three pairs of **latera** (sing., **latus**) known as the **rostral, median** and **carinal latera,** the **carina** and a **subcarina.** Eight of the nine can be compared with the wall plates of *Catophragmus* spp., forms intermediate between pedunculate and sessile barnacles to be taken up later (Fig. 90).

In genera such as *Arcoscalpellum* (see Fig. 115,*8*), the median latus, rather than forming part of the basal whorl, is located up between basal portions of the scutum and tergum, where it is known as the **upper latus,** the plate below it being termed the **inframedian latus.** The subcarina is highly developed in the Cretaceous *Cretiscalpellum* (see Fig. 115,*4*) and the Cretaceous to Recent *Calantica (Scillaelepas)* (see Fig. 115,*9*).

The margins of the plates are named according to the plates which they adjoin. Details of the scutum and tergum are given in Figure 92,*1a-e, 2a,b,* and of the carina in Figure 92,*3.* A number of smaller plates arranged in whorls below the latera are seen in *Zeugmatolepas* (see Fig. 115,*5*), and *Pollicipes (=Mitella)* (see Fig. 115,*7*). These plates are collectively termed **lower latera.**

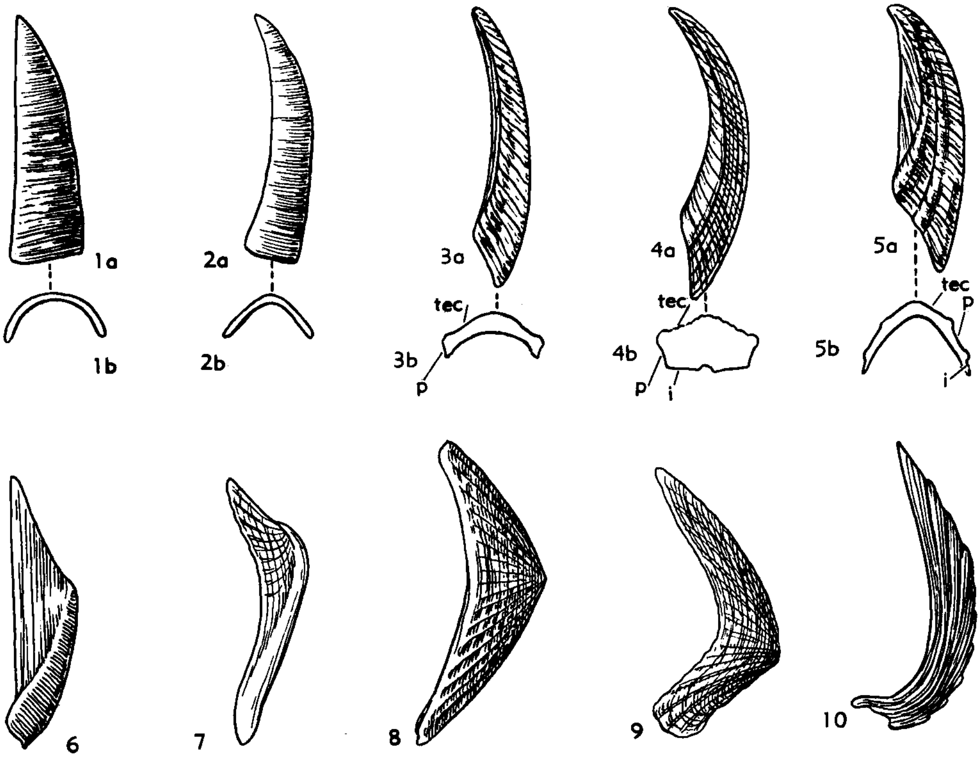


FIG. 91. Morphology of cirriped plates: carinae (not to scale) (after Withers).

1. *Eolepas quenstedti* (VON AMMON); *1a,b,* lat., transv. sec.
2. *Archaeolepas suprajurensis* (DE LORIOL); *2a,b,* lat., transv. sec.
3. *Arcoscalpellum simplex* (DARWIN); *3a,b,* lat., transv. sec.
4. *Arcoscalpellum arcuatum* (DARWIN); *4a,b,* lat., transv. sec.
5. *Arcoscalpellum maximum sulcatum* (J. DE C. SOWERBY); *5a,b,* lat., transv. sec.
6. *?Smilium parvulum* (WITHERS); lat. view.
7. *Virgiscalpellum hagenowianum* (BOSQUET); lat. view.
8. *V. darwinianum* (BOSQUET); lat. view.
9. *Oxynaspis celata* DARWIN; lat. view.
10. *Lepas (Lepas) anatifera* LINNÉ; lat. view.

[Explanation: *i,* intraparietes; *p,* parietes; *tec,* tectum.]

In some forms the inner surface of the carina, rostrum, and tergum is marked by ridges or lines of growth at the apical end. This feature is best developed in forms with massive plates. These growth ridges are caused by the recession of the hypodermis during periodic growth of the plates. In forms where this occurs, the ends of the plates come to project freely beyond the capitulum. This is a feature of great phylogenetic significance, as will be discussed shortly.

The carina in the Triassic (Rhaetic) and Jurassic Scalpellidae and the Middle Carboniferous Praelepadidae has an apical (posterior) umbo and is simple in structure (Fig. 91,*1-5*). The carina of *Eolepas* (Fig. 91,*1*) is almost straight, transversely convex, with a straight or concave basal margin, and not inwardly bowed. *Archaeolepas* (Fig. 91,*2*) shows further development, the carina being somewhat bowed inwardly, and the basal margin is rounded. The carina of other Jurassic genera such as *Calantica,* has a rounded or angular basal margin, which reflects the development of basal latera. In Cretaceous species of *Arcoscalpellum* (e.g., *A. simplex,* Aptian, Fig. 91,*3*), a roof or

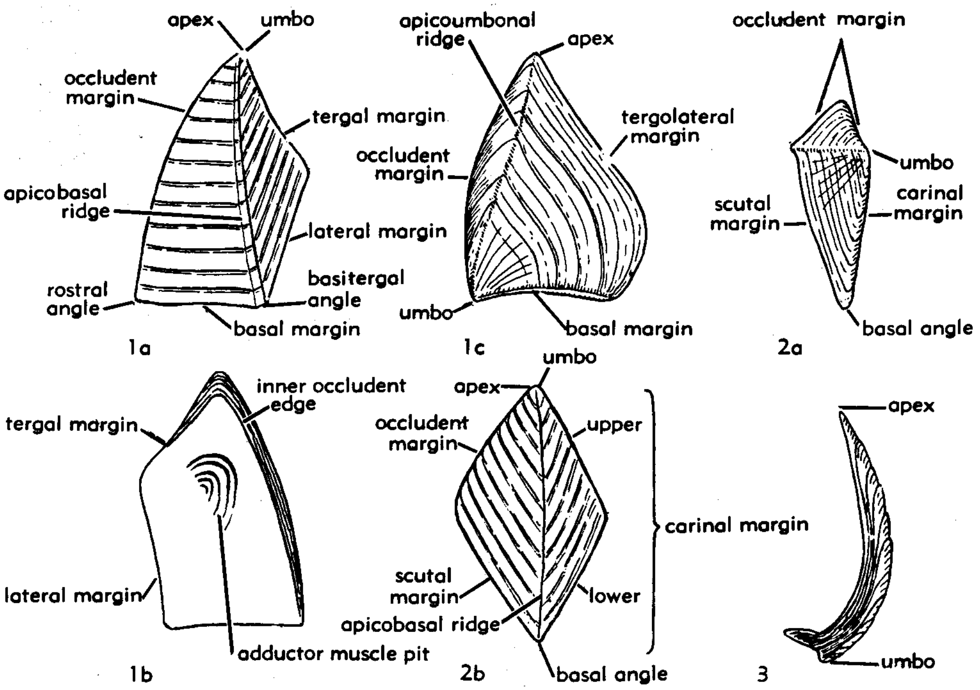


FIG. 92. Morphology of cirripeds, showing lepadomorph plates (not to scale) (after Withers).

1. Scutum.——*1a,b.* Scalpellid, exterior and interior.——*1c.* Lepadid, outer side.

2. Tergum.——*2a.* Lepadid, exterior.——*2b.* Scalpellid, exterior.

3. Carina; lepadid, lat. view.

tectum of the carina becomes demarcated from the sides, by an angle or ridge. The sides in such a carina are termed **parietes.** This term is unfortunate because of the confusion it may cause. It does not apply to the same part of the plate in the Lepadomorpha as in the Balanomorpha.

On the inner edge of the parietes in species such as the Aptian *A. accumulatum* and the Albian *A. arcuatum* (Fig. 91,*4*), a further development has taken place. The interior of the upper part of the carina is thickened by successive laminae, and the portions formed by the edges of these laminae are termed **intraparietes.** The intraparietes are marked off from the parietes by an angle or ridge. In later forms (e.g., *Arcoscalpellum maximum sulcatum,* Senonian, Fig. 91,*5*) the intraparietes are not rectangularly bent inward as in *A. arcuatum,* but form a thin wall on each side of the plate. The intraparietes always have growth lines turned obliquely upward, and these parts bridge the interval between the carina and tergum. The intraparietes extend a little beyond the umbo in the Cenomanian *A. lineatum,* and in the upper Senonian *Virgiscalpellum darwinianum* (Fig. 91,*8*) the umbo of the carina is almost equal above and below the umbo. In the Recent *Oxynaspis* (Oxynaspididae) (Fig. 91,*9*) the umbo is well below center, and in *Lepas* (Lepadidae) (Fig. 91,*10*) the umbo is basal. What is called the carina in *Stramentum* (Stramentidae) (see Fig. 116, *6*) is split longitudinally into two parts.

The scutum (Fig. 92,*1a-c*) is triangular or rhomboidal with the ventral border being termed the **occludent margin,** and the basal border simply termed the basal margin. In forms with a straight lateral border such as *Eolepas* (Fig. 93,*1*) this border is

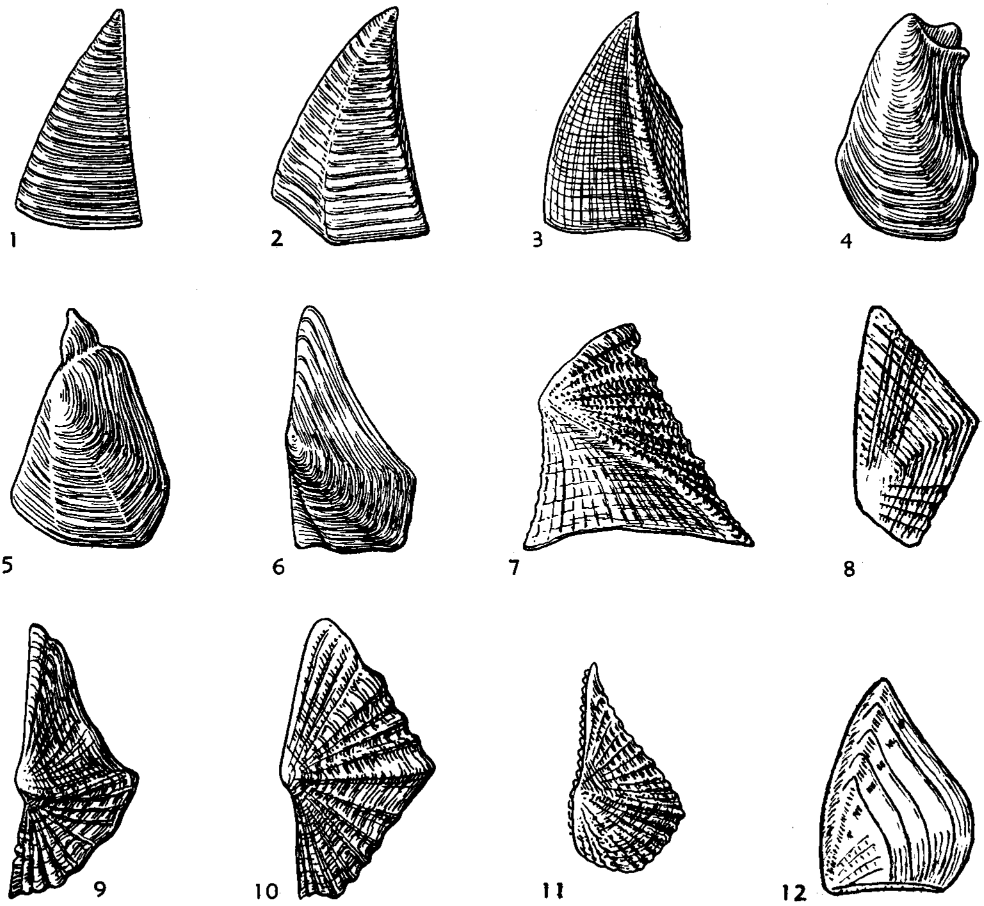


FIG. 93. Morphology of cirriped plates; scuta (all lat. views, not to scale) (after Withers).

1. *Eolepas quenstedti* (VON AMMON).
2. *Archaeolepas suprajurensis* (DE LORIOL).
3. *Arcoscalpellum arcuatum* (DARWIN).
4, 5. *Zeugmatolepas mockleri* WITHERS.
6. *Z. cretae* (STEENSTRUP).
7. *Calantica (Titanolepas) tuberculata* (DARWIN).
8. *Virgiscalpellum darwinianum* (BOSQUET).
9. *V. hagenowianum* (BOSQUET).
10. *V. beisseli* (BOSQUET).
11. *Oxynaspis celata* DARWIN.
12. *Lepas (Lepas) anatifera* LINNÉ.

termed the **tergal margin**. In forms with an angulate lateral border, such as *Cretiscalpellum* (see Fig. 115,*4*) and *Arcoscalpellum* (Fig. 93,*3*), the posterior part is termed the tergal margin, and the anterior part is termed the **lateral margin**. Along the tergal margin the growth lines of the scutum may turn abruptly, forming an area known as the **tergal slip** which may be demarcated from the bulk of the scutum by a longitudinal ridge. The basal angle adjacent to the rostrum is termed the **rostral angle**, and the opposite angle the **basitergal angle**. The angle between the tergal and lateral margins, when present, is termed the **tergolateral** angle. That formed by the occludent and scutal margins is termed the **apical angle**. In the earliest Jurassic form *Eolepas* (Fig. 93,*1*) the scutum is triangular, without a tergal slip, and the tergal and basal margins are straight. *Archaeloepas* (Fig. 93,*2*) has a narrow tergal slip, and this fea-

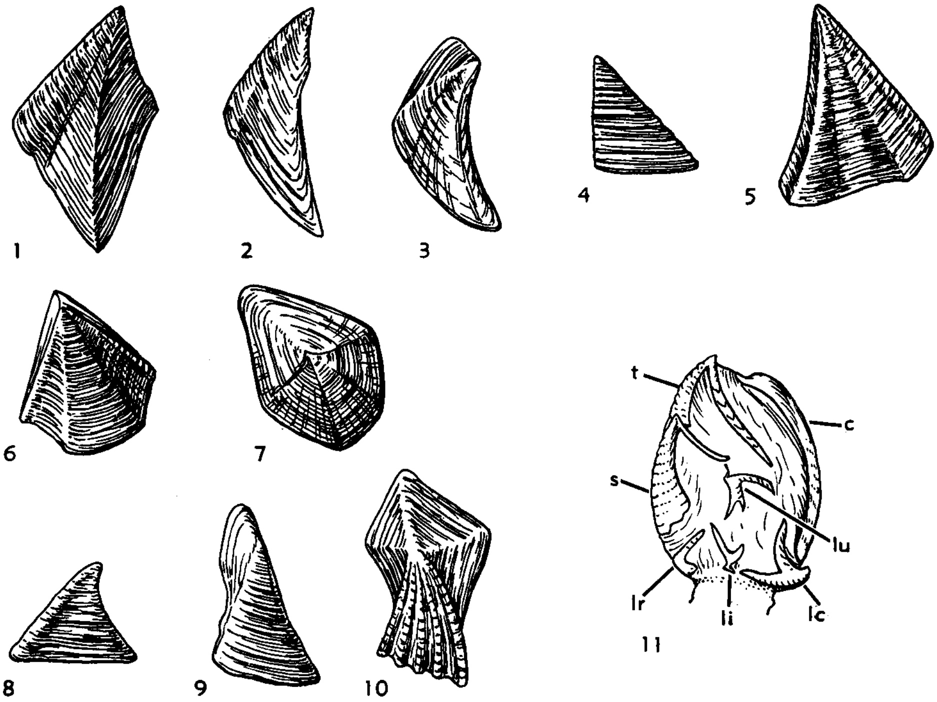


FIG. 94. Morphology of cirriped plates (all lat. views, not to scale) (*1-10*, after Withers; *11*, after Pilsbry).

1-3. Terga.——*1. Cretiscalpellum glabrum* (F. A. Roemer).——*2. Scalpellum magnum* Darwin. *3. S. burdigalense* des Moulins.
4-7. Upper latera.——*4. Cretiscalpellum glabrum* (F. A. Roemer).——*5. Arcoscalpellum fossula* (Darwin).——*6. A. quadratum* (Dixon).——*7. Scalpellum magnum* Darwin.
8-10. Inframedian latera.——*8. Arcoscalpellum fossula* (Darwin).——*9. A. maximum* (J. de C. Sowerby).——*10. Virgiscalpellum darwinianum* (Bosquet).
11. Capitulum of *Mesoscalpellum dicheloplax* (Pilsbry).
[Explanation: *c*, carina; *lc*, latus (carinal); *li*, latus (inframedian); *lr*, latus (rostral); *lu*, latus (upper); *s*, scutum; *t*, tergum.]

ture is further developed in forms such as the Albian *Arcoscalpellum arcuatum* (Fig. 93,*3*).

The scutal umbo in early Scalpellidae is apical. Young individuals of the Cenomanian *Zeugmatolepas mockleri* (Figs. 93,*4-5*) have an apical umbo, but in older individuals the upper tergal part of the plate extends beyond the umbo. Development of the upper tergal part in the higher upper Senonian species *Z. cretae* (Fig. 93,*6*) is more pronounced, bringing the umbo to a more central position. In Scalpellidae such as the Cenomanian *Calantica (Titanolepas) tuberculata* (Fig. 93,*7*), the Maastrichtian *Virgiscalpellum darwinianum* (Fig. 93,*8*), and *V. hagenowianum,* and the Senonian *V. beisseli* (Fig. 93,*10*) the umbo is subcentral. The umbo is also subcentral in the Recent *Oxynaspis* (Oxynaspididae) (Fig. 93,*11*), but is basal in the unmodified Lepadidae (*Lepas,* Fig. 93,*12*) and most Poecilasmatidae.

The tergum (Fig. 92,*2a-b*) is commonly diamond-shaped. The ventral border is termed the **occludent margin**; that adjoining the scutum, the **scutal margin**; and that adjoining the carina, the **carinal margin,** the last usually being divided into upper and lower parts. A submedial ridge or furrow usually divides this plate. The tergum of Mesozoic forms varies little, but in the Tertiary upward-directed growth from the occludent margin is observed (e.g., *Scalpellum burdigalense,* Mio., Fig. 94,*3*; *S. magnum,* Plio., Fig. 94,*2*).

The rostrum is a single plate situated at the rostral angles of the scuta. In forms where it approaches the carina in size, such as *Eolepas* (see Fig. 115,*1*) and the Recent *Pollicipes mitella,* the extent of the rostrum that projects freely is greater than in the carina. The rostral latera, when present, adjoin or may overlap the rostrum, as in *Calantica (Scillaelepas), Arcoscalpellum,* and *Scalpellum.*

The simplest form of the upper latus, as seen in *Cretiscalpellum* (Aptian-U.Senon., Fig. 94,*4*), is triangular, with a straight basal margin and an apical umbo. In certain species of *Arcoscalpellum,* such as *A. fossula* (Fig. 94,*5*), the growth lines are upturned at the sides and the basal angles consequently truncate. In other species (e.g., *A. quadratum,* Eoc., Fig. 94,*6*) the edges of the laminae forming the plate extend slightly beyond the umbo, a condition much emphasized in the Pliocene *Scalpellum magnum* (Fig. 94,*7*). Similar changes in the position of the umbo are found in the inframedian latus of some Cretaceous species of *Arcoscalpellum* (Fig. 85,*5*), and in one *Virgiscalpellum* (Fig. 85,91). The rostral and carinal latera exhibit comparable changes in umbonal position.

In certain stocks, the plates have unusual shapes which are the result of incomplete calcification, a condition usually associated with a special mode of life. This condition, for example, is seen in Recent species of *Mesoscalpellum* (Fig. 85,94) (Scalpellidae), *Octolasmis* (Poecilasmatidae), *Conchoderma* (Lepadidae), and *Oxynaspis* (Oxynaspididae).

VERRUCOMORPHA

These are sessile thoracicans with pronounced asymmetry of the shell. Of the three genera, *Proverruca, Eoverruca* and *Verruca* appearing in the Upper Cretaceous, only *Verruca* is surviving today.

The entire shell of the adult *Verruca* consists of but six plates; the paired terga and scuta, the carina and rostrum. The carina and rostrum, and the tergum and scutum of either the right or left side, form the box-like wall. The remaining tergum and scutum are movable and form a lid or operculum to the box. The basis is membranous except in one modern species (Withers, 1935).

The ontogeny of these peculiar forms was analyzed by Darwin (1854) and the gross features are briefly illustrated here (Fig. 89,*1-4*). Some asymmetry is seen in the arrangement of the primordial plates when they first appear beneath the cyprid shell, and it becomes more pronounced with development. This is particularly true of the terga and scuta, fixed and movable members of which bear little resemblance to each other in the adult. Once metamorphosis has been completed, the carina, rostrum, and fixed tergum and scutum rest directly on the substratum. The movable tergum and scutum are articulated with one another and form a rigid lid or operculum having an essentially straight hinge line along the upper margins of the carina and rostrum (see Fig. 117,*4a,b*).

The six-plated condition and asymmetry no doubt has been derived from a symmetrical ancestral stock as pointed out by Darwin (1854). Both he and Withers (1935) called attention to similarity of the unmodified tergum and scutum with the same plates in forms presently assigned to the Brachylepadomorpha. The asymmetry found in fossil verrucomorphs is somewhat less pronounced, and two lateral plates not found in modern forms, contributed to the structure of the wall. These, the rostrolateral and carinolateral plates, lie between the carina and rostrum on the side opposite the fixed tregum and scutum, as seen in *Proverruca* and *Eoverruca* (see Fig. 117,*1b, 3b*).

In *Eoverruca,* the fixed tergum and scutum stand in a relatively vertical position and resemble their movable counterparts in having surfaces divided into two regions by a central ridge or rib, and in the manner in which they articulate with one another. The central ribs have been interpreted by Pilsbry (1916) and Withers (1935) as forming a primitive articulation between the two plates in Brachylepadomorpha. Their persistence on the fixed plates in *Eoverruca* would therefore be as vestigial structures. The rostrum and carina, on the other hand, are also more normal in not extending laterally any more on one side than on the other, the lateral space on the side opposite the fixed tergum and scutum being filled by two lateral plates not found in *Verruca*. Thus the general form is higher and more laterally flattened, and as pointed out by WITHERS (1935), when viewed from the side of the movable opercular parts, there is a marked resemblance to the Brachylepadomorpha.

BRACHYLEPADOMORPHA

These are extinct symmetrical sessile thoracicans that have eight primary plates forming the shell, the basal margin of which was surrounded by several whorls of small imbricate plates. In most cases, the basis was membranous. Although sessile, the general form of these barnacles resembles the capitulum of a pedunculate barnacle, in that it is not divided functionally into wall and operculum as in the Verrucomorpha and Balanomorpha. In fact, some of the first described species were placed in the scalpellid genus *Pollicipes,* and the resemblance between *Pycnolepas* and the capitulum of *Pollicipes mitella* is remarkable (cf. Fig. 115,*7* and 117,*5*). The more primitive of the two recognized genera, *Pycnolepas,* is known probably as early as the Upper Jurassic. *Brachylepas* appears in the Upper Cretaceous.

The principal components of the shell, as in the Verrucomorpha, are the paired terga and scuta, and the carina and rostrum. The tergum and scutum of each side appear to be loosely articulated with each other, perhaps showing some advance over the condition seen in the Lepadomorpha. However, the articulation is overlain by a narrow upper latus which indicates that the articulation was no better developed than in *Pollicipes*. These six plates form the bulk of the shell and are contained between the large rostrum and the carina. Around the base small imbricate plates are arranged in several whorls.

Although these were sessile barnacles, they differed from other sessile forms in not having developed a functional separation between the plates forming the aperture and those primarily involved in forming the wall. The development of such a functional separation took two courses in other sessile forms; one seen in the Verrucomorpha, the other in the Balanomorpha, and until the separation was achieved, a truly rigid wall could not be formed.

BALANOMORPHA

The shell (Fig. 95,*1*) in balanomorph barnacles consists of a circular wall composed of a number of more or less rigidly articulated compartmental plates (Fig. 95, *4-6*) with or without a calcareous basal disc (**basis,** Fig. 95,*1*). An uncalcified basis is simply membranous. The **orifice** (Fig. 95,*1*) is occupied by four **opercular valves (or plates)**: the paired **terga** (Fig. 95,*2a-b*) and **scuta** (Fig. 95,*3*), which together form an **operculum.** The tergum and scutum of each side are more or less intricately articulated, an aperture to the exterior being retained between the opposing pairs, through which the animal can protrude the feeding appendages or cirri.

The opercular valves and compartmental plates of Balanomorpha are considered homologous to specific plates in Lepadomorpha. The accepted homologies are depicted in Fig. 90. It will be noted that whereas in the Lepadomorpha *all* hard parts are termed plates, in the Balanomorpha the opercular parts, although they are homologous with certain lepadomorph plates, are termed valves.

Each compartmental plate is usually divided into three parts (Fig. 95,*4-6*): a large, central, triangular area (**paries,** pl. **parietes**) and narrower, linear areas on either side of the paries, overlapping or being overlapped by corresponding parts of adjacent compartmental plates. When the overlapping portions differ in structure from the paries, they are termed **radii** (sing., **radius**); those which are overlapped are termed **alae** (sing., **ala**). In Chthamalidae and most Balanidae, the parieties and radii are solid. In some balanids the parietes and radii are composed of an **outer** and an **inner lamina** or lamella. The lamellae are separated by **longitudinal septa** forming **longitudinal tubes** (pores) and in some species these ~~are~~ crossed by secondary **transverse septa,** or are secondarily filled with calcium carbonate (see Fig. 105,106). In a few balanids, more than one row of tubes are formed (see Fig. 119,*2b,4b,9a,c,e*).

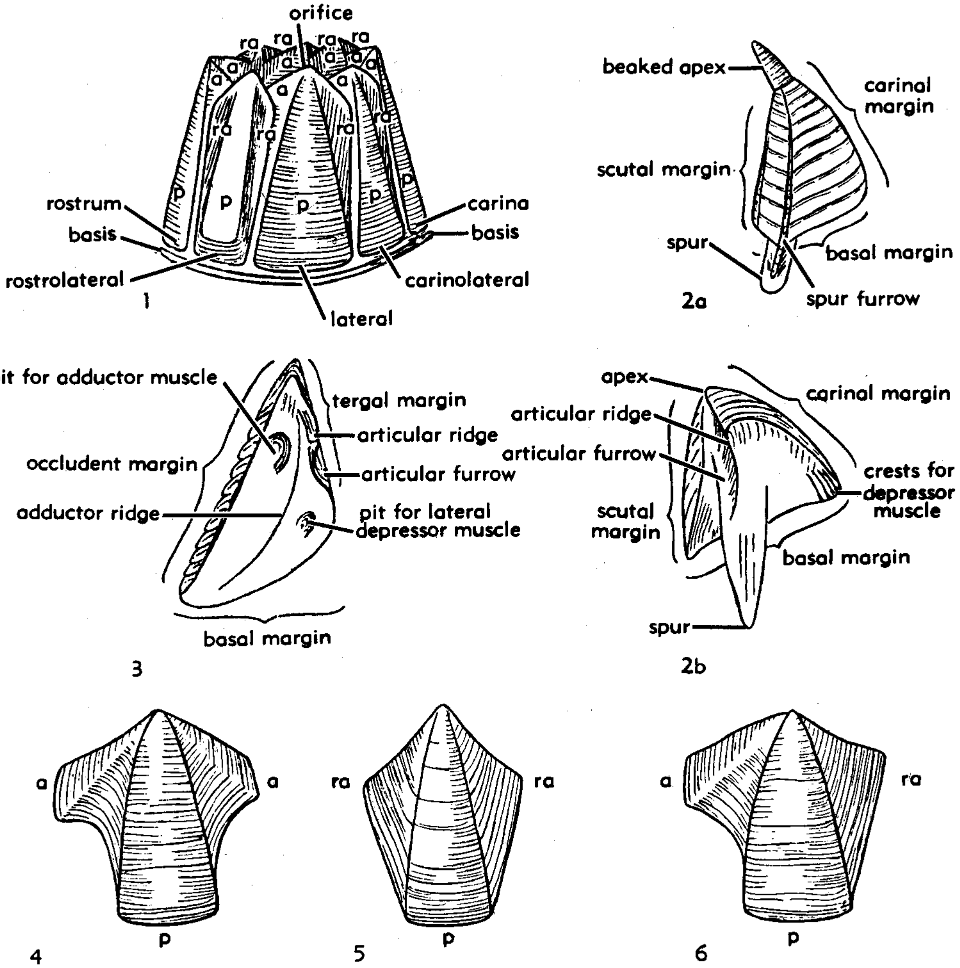


Fig. 95. Morphology of balanomorph plates and valves (not to scale) (*1, 4-6,* after Darwin; *2, 3,* after Withers).

1. Entire shell of eight plates, showing part of sheath in orifice; rostrum and rostrolateral compartment, usually unfused in chthamalids and fused in all balanids.
2. Tergum.——*2a,b.* Exterior and interior.
3. Scutum, interior.
4. Compartment with alae on sides as in carina or true rostrum.
5. Compartment with radii on sides, as in rostrolateral or compound rostrum.
6. Compartment with ala on one side and radius on other, as in lateral or carinolateral.

[Explanation: *a,* ala; *ra,* radius; *p,* paries.]

The balanomorph shell wall includes, at most, eight primary plates: a rostrum, paired rostrolaterals, paired laterals, paired carinolaterals, and a carina (Fig. 96,*1-2*). Some species possess one or more whorls of small supplementary plates at the base of the shell wall (Figs. 96,*1*).

A true rostrum has alae on both sides (Fig. 95,*4*). In some genera, the rostrum may be fused with the adjacent rostrolaterals to form a compound **rostral plate** in which case it overlaps rather than underlaps the adjacent lateral plates (Fig. 96,*5-7*).

The laterals and carinolaterals have alae on their carinal margins (Fig. 95,*6*). The carina has alae on both margins (Fig. 95,*4*), as does the true rostrum.

Catophragmus (Fig. 96,*1*) and *Octomeris*

(Fig. 96,*2*) have the full complement of eight plates. *Catophragmus* has several basal whorls of supplementary plates, in addition. *Chionelasmus* has a single whorl of supplementary plates. The wall is made up of six plates rather than eight, and the rostrum, having alae, is simple. In this case, the reduction to six plates has been through the loss of carinolaterals rather than by fusion of rostrolaterals to the rostrum. In *Chamaesipho* (Fig. 96,*4*), a simple rostrum is present, the carinolaterals are lacking, the laterals are apparently fused with the rostrolaterals and the carina is present. This arrangement results in a wall of four plates.

The chthamalid genera *Pachylasma, Hexelasma* (Fig. 96,*5*), and *Tessarelasma,* and all Balanidae superficially appear to have walls of six plates. In the chthamalid *Pachylasma* and the balanid *Chelonibia* (Fig. 96,*7*), eight plates can be discerned, for the rostrum is incompletely fused with the rostrolaterals. That the middle element is the rostrum in *Chelonibia* is demonstrated in a Miocene specimen of *C. caretta* (see Fig. 119,*8*) in which the middle element is not only separated from the lateral elements by deep sutures toward the apex (much deeper than in Recent specimens), but it has slightly developed alae over which the adjacent rostrolaterals distinctly overlap. In *Balanus,* on the other hand (Fig. 96,*8*), the rostral plate is considered to be formed of the fused rostrolaterals only, the true rostrum having been eliminated, and retention of the carinolaterals provides six compartmental plates. Thus, certain of the wall elements, although six in each genus, differ between *Balanus* and *Chthamalus.* In the latter, the arrangement is the same as in *Chionelasmus* excepting that the supplementary whorl is lacking. The balanids *Tetraclita* (Fig. 96, *9*) and *Creusia* (see Fig. 118A, *15a*) have lost the carinolaterals, leaving four plates, and in *Pyrgoma* (Fig. 96,*10*), these four plates are fused into a single shell, although traces of a pair of sutures in the sheath can sometimes be seen at the carinal end on the interior in some species (see Fig. 118A, *16*).

GROWTH

Both determinate and indeterminate growth occurs in the Balanomorpha. In many species of *Balanus,* full size may be attained within the first year after settlement with only small growth increments occurring during the next year or so of life. Some species (e.g., *B. (B.) nubilis*) presumably have a much longer life span, apparently within the neighborhood of 15 years. Growth of the shell wall and basis of this species appears to continue through much of the life of the individual. The remarkable growth form of the basis in the California Miocene and Pliocene species *B. (B.) gregarius* (the so-called *"Tamiosoma"*) has often been cited. Elongation of the basis into a cup-shaped or tubular form is not unusual in balanids, and is characteristic of such taxa as *Creusia, Pyrgoma, B. (B.) laevis,* and *B. (Megabalanus) tintinnabulum.* However, the filling of this cavity in *B. (B.) gregarius* with numerous thin irregular horizontal partitions results in a peculiar cellular structure which resembles that of rudistid pelecypods. In *Chthamalus hembeli* and *C. intertextus,* growth is determinate, ceasing with the advent of secondary calcification within the interior of the shell.

Growth of the shell occurs along the basal and lateral margins of the compartmental plates, and around the circumference of the basis. As the general form of the balanomorph shell is conic, increase in height and diameter, and, therefore, volume, can be attained entirely through growth at the basal margins of the shell. However, without marginal growth, the diameter of the orifice at the top (or oldest part) of the cone would remain constant and communication with the external environment as growth progressed would become proportionately reduced. In most balanomorphs, the orificial opening is enlarged by lateral growth at the sutural edges of the plates. In some taxa (e.g., *Tetraclita, Pyrgoma*) in which partial or complete concrescence of the compartmental plates has occurred, expansion of the orifice is apparently achieved by the wearing away of the upper portions of the wall by external erosion and activities of the animal.

Color and, more specifically, color pattern has proven useful in the classification of species-group taxa in the Balanidae. Various shades of red and red-brown are the prevalent colors exhibited, although blues and purples are also found (e.g., *Balanus (Austrobalanus) imperator*). Coloration appears to be confined mainly to the exterior of the parieties and to the surface of the opercular valves. In some cases, the entire surface of the parieties is of a uniform shade, but in most taxa, the coloration consists of radial color stripes on a background of a different color or shade (e.g., *B. (Megabalanus) tintinnabulum, B. (Balanus) venustus niveus, B. (B.) amphitrite amphitrite*). The pattern of these stripes has proved useful in distinguishing between various so-called subspecies of the *B. (M.) tintinnabulum* and *B. (B.) amphitrite* complexes. Radial bands are also common in such taxa as *B. (M.) tintinnabulum,* and have been employed as diagnostic characters. The origin and purpose of these colors and color markings, however, are not understood.

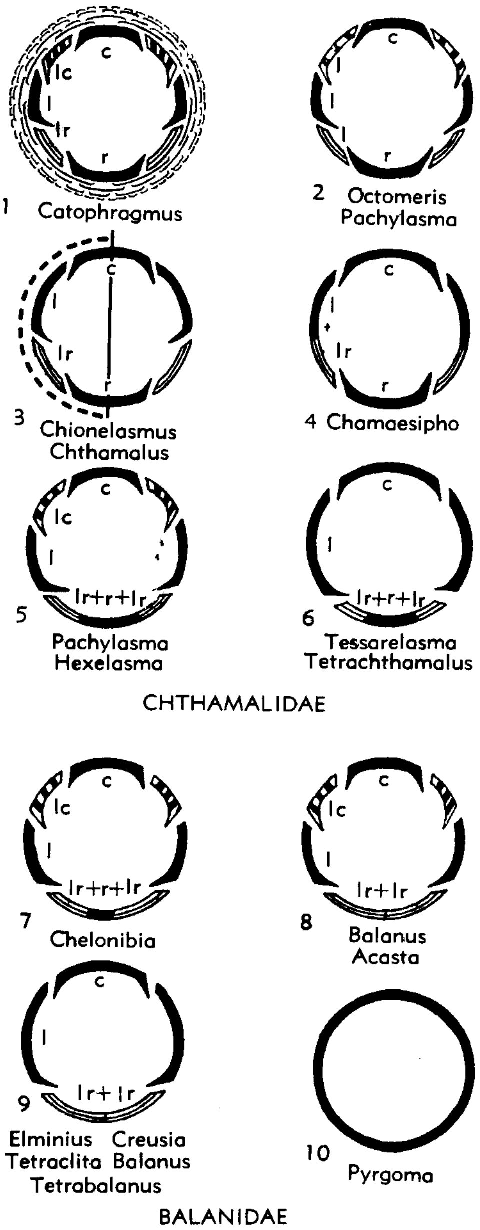


FIG. 96. Cirriped morphology. Diagrams showing modes of imbrication and homologies of compartments in the Chthamalidae *(1-6)* and Balanidae *(7-10)* (after Darwin and Pilsbry). [Explanation: *c,* carina; *lc,* latus (carinal); *l,* lateral; *lr,* latus (rostral); *r,* rostrum.]

ARTHROPODAL STRUCTURES

The Cirripedia have the fundamental body plan of the Maxillopoda (DAHL, 1956), that is, five appendage-bearing head somites, six appendage-bearing thoracic somites and five abdominal somites. Basically the abdomen is appendageless, except for the first and the last somites which bear male reproductive structures and a furca respectively (Table 1). Only a few of the least specialized Ascothoracica have an entire complement of somites and appendages in the adult stage, although it is not certain that the so-called second antenna of *Baccalaureus* (PYFINCH, 1939) is actually the homologue of this structure. In adults of all other orders, the second antennae and abdomen are lost, although a vestige of the latter may be represented by the so-called **basidorsal point** seen in certain Balanomorpha. Most of the Acrothoracica, the Verrucomorpha, most of the Lepadomorpha, and a few of the primitive Chthamalidae among

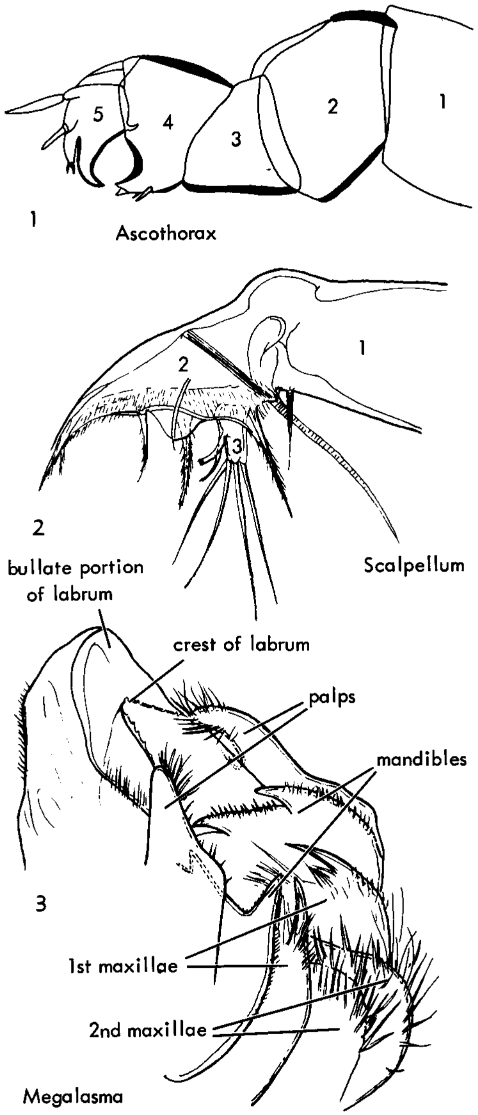


Fig. 97. Cirriped morphology. Antennae and trophi. ——*1*. First antenna, male *Ascothorax ophioctenis* Djakonov, ×35 (after *111*).——*2*. First antenna, cyprid stage, of *Scalpellum gibberum* Aurivillius, ×290 (after *77*).——*3*. Trophi, *Megalasma striatum* Hoek, ×63 (after *53*).

the Balanomorpha have terminal or caudal appendages, probably representing the caudal furca (Calman, 1909) (see Fig. 104, *1c,2a,3,4*).

In the Cirripedia, the antennules or first antennae are uniramous, and always prehensile at some stage of development. In the cyprid and adult of the Ascothoracica, they are four- or five-jointed, subchelate, and serve as devices for temporary attachment in most species. In the other orders, they are four-segmented, provided with a suction disc on the second segment used for temporary attachment in the cyprid, and with cement-producing glands, opening on the second segment used for permanent attachment prior to metamorphosis into the adult (Fig. 82; 97,*2*).

The next pair of head appendages, the second antennae, are biramous during the naupliar stages, but are lost in the cyprid and adult (Fig. 81; 82,*3*). A vestige may be found in some cyprids (Batham, 1945) or may be represented as a much modified filament-like process extending into the dorsal brood chamber of the female or hermaphroditic Ascothoracica where they probably function in care of eggs (Utinomi, 1962).

The third head appendages are also basically biramous, as in all Crustacea, and where present in the adult, the gnathobases of the protopods form the mandibles. In the Ascothoracica, the mandibles and other mouth parts are modified for piercing and sucking, but in the Acrothoracica and Thoracica, they function in grasping, manipulating, and in some forms triturating the food before delivering it to the mouth. In the Acrothoracica, the mandibles are each provided with a one-segmented palp, also present in the Thoracica. In the latter, however, the position has shifted from the outer margin of the mandibles to the outer margins of the labrum or upper lip. In either position, the palps serve to control food particles in the area over the exposed margins of the labrum, mandibles, and following mouth appendages (cf. Fig. 80, 97, 98).

Although the general form of the mandible in Acrothoracica and Thoracica is quite similar, the number, arrangement, and development of teeth, spines, and setae differs considerably among genera, particularly in the Lepadomorpha, suggesting differences in food habits (Fig. 98). These differences in structure are of considerable systematic value.

Immediately behind the mandibles, and acting in essentially the same plane, are the

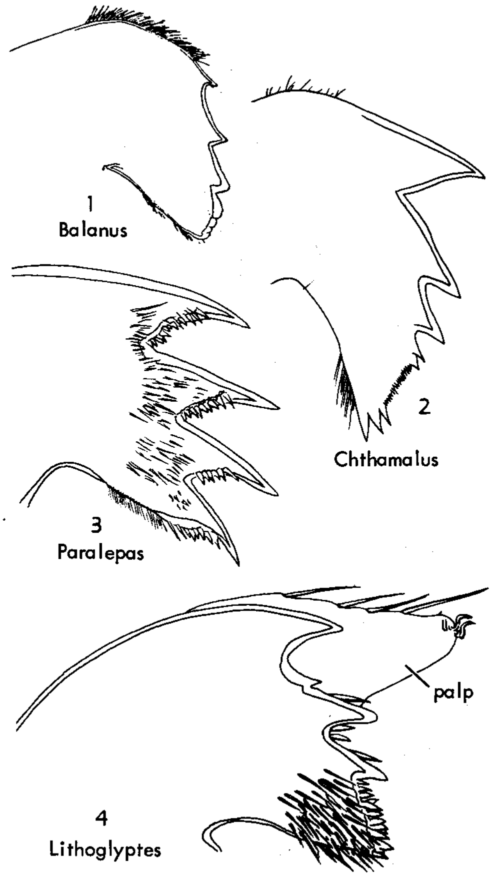


Fig. 98. Mandibles of cirripeds.——*1. Balanus (Balanus) hystrix* Hoek, ×96 (after *55*).——*2. Chthamalus challengeri* Hoek, ×147 (est.) (after *83*).——*3. Paralepas palinuri* Barnard, ×33 (after Newman, 1960).——*4. Lithoglyptes spinatus* Tomlinson & Newman, mandible and palp, ×267 (after *103*).

first maxillae. They are somewhat similar in form to the mandibles, and, on theoretical grounds, were inferred to represent modified gnathobases of a biramous limb. Evidence that this is the case was only recently forthcoming, where the biramous rudiment was observed in a late nauplius stage (Crisp, 1962). The first maxillae are as diverse in form and armament as the mandibles, and some features, such as the presence or absence of a notch or a stepwise or protuberant portion of the cutting edge, appear to be of systematic value (Fig. 99,*1-4*).

The fifth pair of head appendages, the second maxillae, are comparable in general form to the preceding two pairs, but are more delicate and less jawlike, being provided with relatively soft setae and thin cuticle (Fig. 99,*1b,4*). They appear to act in the manner of a lower lip or labium and indeed, as in the labiate arthropods, they may be fused together, basically serving to close the back of the mouth field. Openings at or near their bases are the apertures of the maxillary glands.

In the Ascothoracica, the trophi or mouth parts are cutting, piercing, and sucking, and are surrounded by the labrum, forming a protuberant oval cone apparently adapted to dealing directly with the matter of obtaining food (Fig. 80,*1*). The trophi of the Acrothoracica and Thoracica on the other hand, are manipulating and triturating structures, having the food passed to them by the following appendages, rather than being applied directly to the matter of gathering food. The trophi nontheless are surrounded anteriorly and laterally by the labrum which extends nearly vertical from the body. This entire complex surrounds the mouth and protrudes as a unit below the ventral surface of the body. According to Darwin, the entire trophic complex can be moved about to a considerable extent (Fig. 97,*3*).

Primitively, the labrum is bullate, with a broad, straight, or somewhat concave ventral margin or cutting edge, with or without soft setae or small sharp toothlike spines (Fig. 97,*3;* Fig. 100,*2*). This condition is seen in the Acrothoracica, Verrucomorpha, and Lepadomorpha, and in the Chthamalidae among the Balanomorpha. In the Balanidae, however, a median notch has developed as a specialization along with the loss of the bullate appearance of the labrum as a whole.

The six pairs of appendages following the second maxillae are thoracic and basically biramous. Except in the Ascothoracica, where they are straight and natatory as they are in the cyprid, they have a characteristic curled form and are called cirri. A cirrus consists of a two-segment protopod or pedicle, supporting a multiarticulate exopod and endopod. The rami are usually designated as outer and inner, but in many

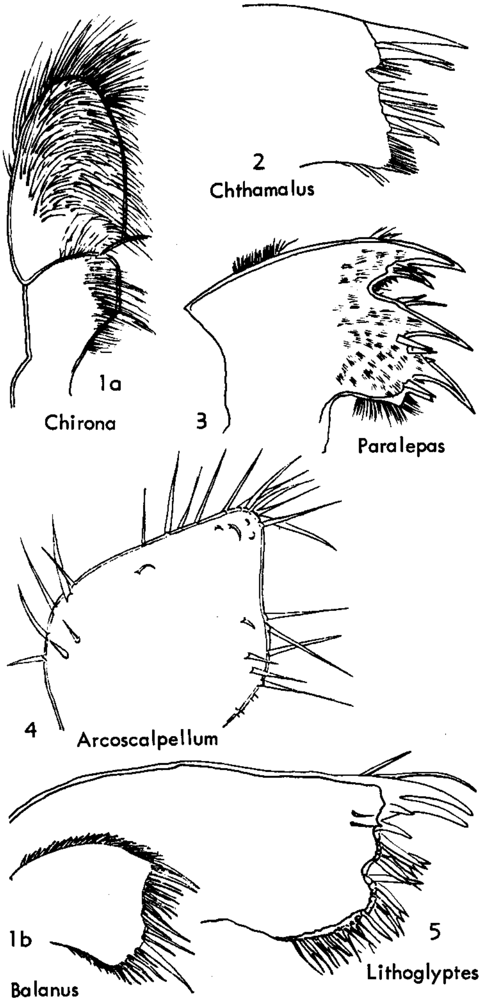


Fig. 99. Maxillae of cirripeds.——*1. Balanus; 1a, B. (Chirona) amaryllis* Darwin, second maxilla, ×20; *1b, B. (Balanus) hystrix* Hoek, first maxilla, ×96 (after *55*).——*2. Chthamalus challengeri* Hoek, first maxilla, ×147 (est.) (after *83*).——*3. Paralepas palinuri* Barnard, first maxilla, ×33 (Newman, 1960).——*4. Arcoscalpellum ventricosum* (Hoek), second maxilla, ×110 (after *77*).——*5. Lithoglyptes spinatus* Tomlinson & Newman, first maxilla, ×267 (*103*).

forms, it is necessary to refer to them as anterior and posterior, when they appear so arranged. In the Ascothoracica, the homologues of the cirri are natatory (Wagin, 1946) (Fig. 101,*1*), while in the Acrothoracica and Thoracica the cirri serve to capture food (Fig. 101; 102,*1-3*).

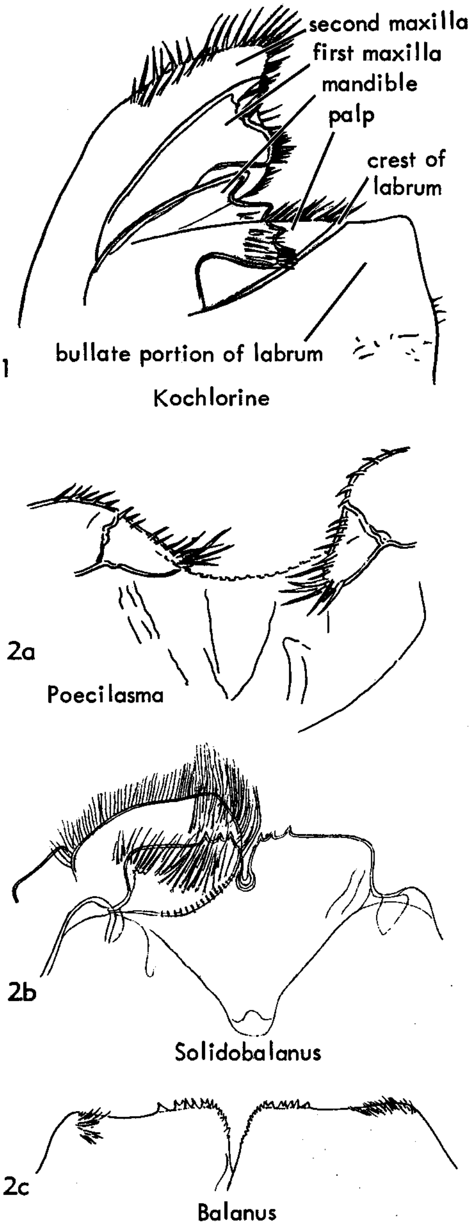


Fig. 100. Trophi and labra of cirripeds.——*1.* Trophi, *Kochlorine floridana* (Wells & Tomlinson), ×230 (Tomlinson, n).——*2.* Labrum and palps, *2a, Trilasmis (Poecilasma) gracile* (Hoek), ×72 (after *53*); *2b, Balanus (Solidobalanus) ciliatus* (Hoek), right palp removed, ×34 (after *55*); *2c, Balanus (Balanus) eburneus* Gould, both palps removed, ×16 (after *83*).

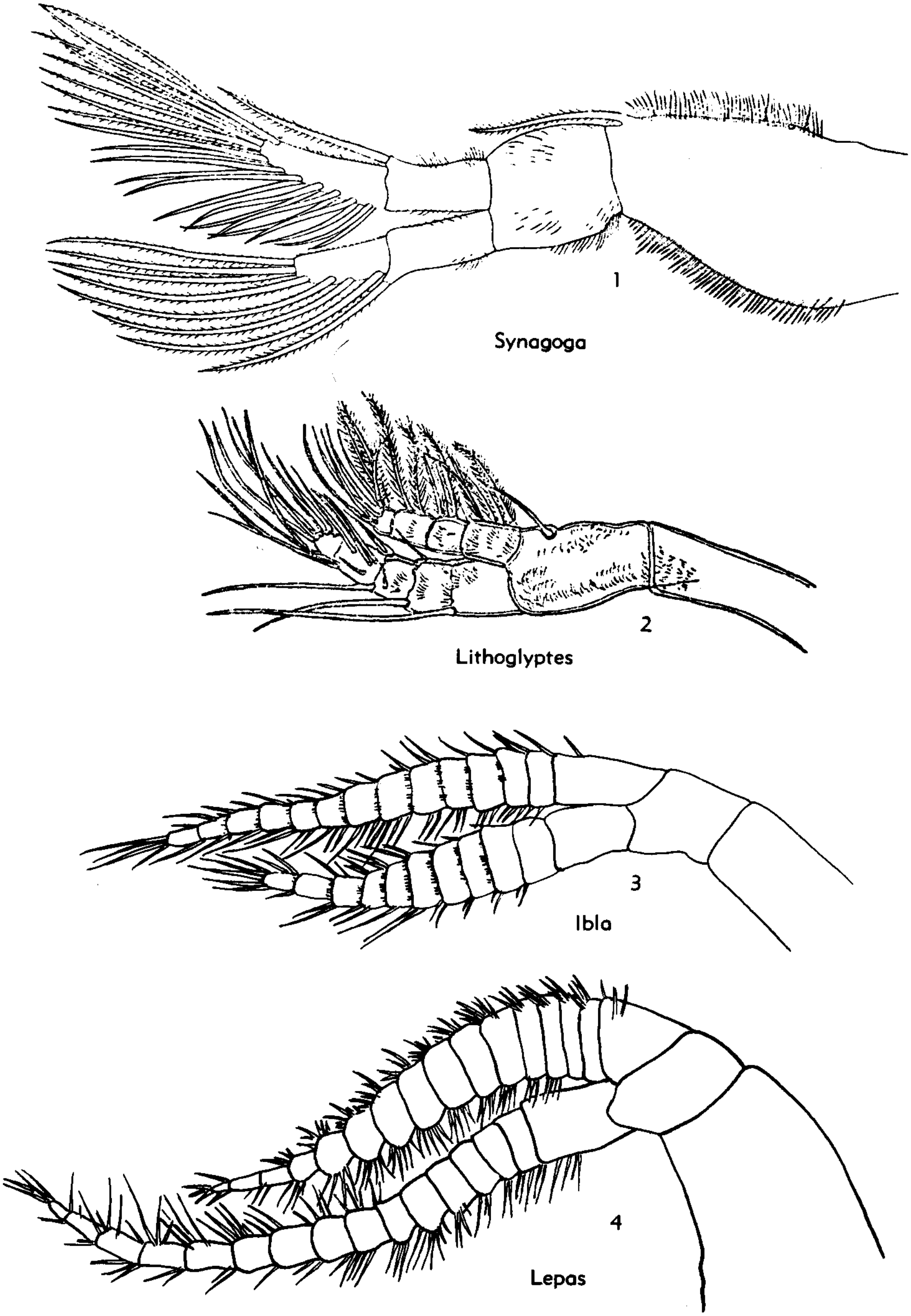


FIG. 101. First cirri of cirripeds.

1. *Synagoga metacrinicola* OKADA, ×100 (est.) (after Okada, 1939).
2. *Lithoglyptes spinatus* TOMLINSON & NEWMAN, ×150 (after *103*).
3. *Ibla cumingi* DARWIN, ×44 (Newman, n).
4. *Lepas (L.) hillii* LEACH, ×44 (Newman, n).

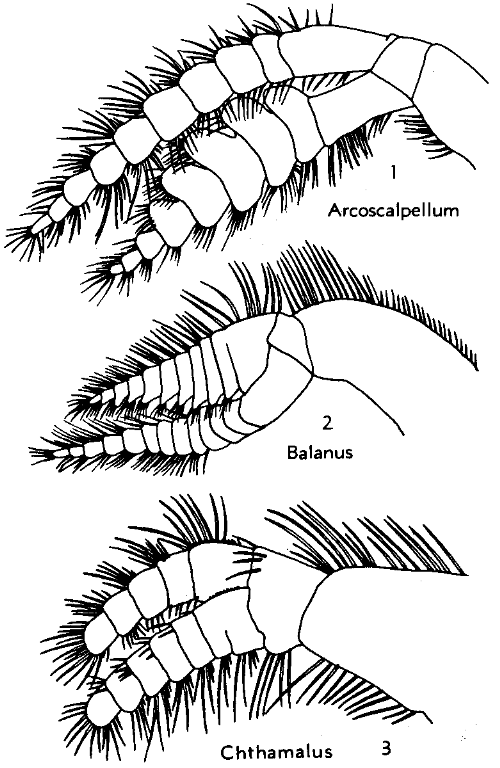


FIG. 102. First cirri of cirripeds (Newman, n).——*1. Arcoscalpellum osseum* (PILSBRY), ×16.——*2. Balanus (Balanus) amphitrite* DARWIN, ×18.——*3. Chthamalus panamensis* PILSBRY, ×40.

The first pair of cirri usually differ somewhat in structure from the others, functioning as accessory mouth parts, and they can legitimately be called maxillipeds in all but the most primitive forms. Additional cirri may also be modified as maxillipeds in higher forms. Clearly they have become so modified independently of the development of this condition in other Maxillopoda and in the Malacostraca.

The first pair of cirri, when modified to form maxillipeds, have been drawn into close association with the trophi in transferring food from the cirri to the mouth. This separation from the following cirri is especially marked in the Acrothoracica, where all cirri behind the single pair of maxillipeds (formerly mouth cirri) are separated by the entire length of the thorax (Fig. 80,2). The Thoracica have up

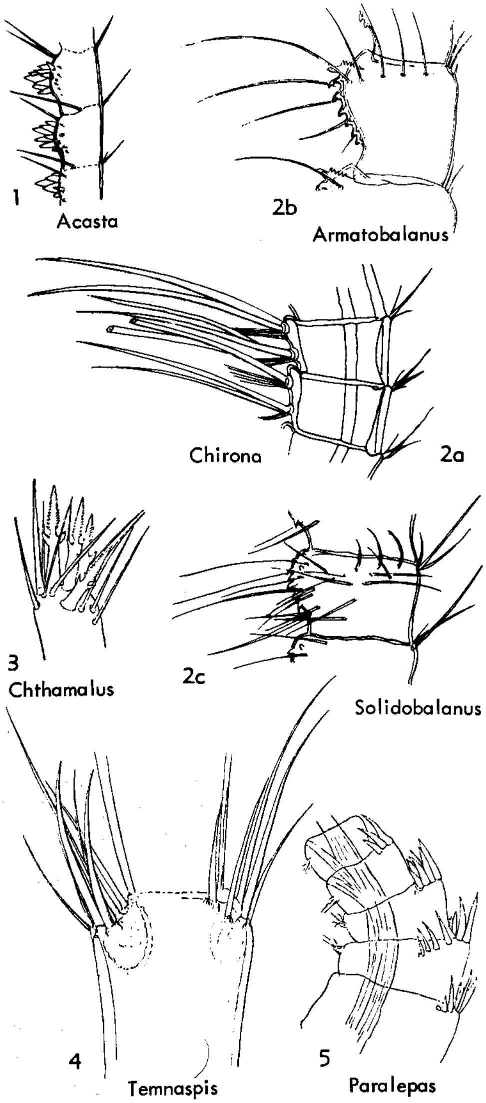


FIG. 103. Cirral armament of cirripeds.——*1. Acasta conica* HOEK, intermediate segments, fourth cirrus, ×96 (after *55*).——*2. Balanus; 2a, B. (Chirona) amaryllis* DARWIN, intermediate segments of sixth cirrus, ×30; *2b, B. (Armatobalanus) arcuatus* HOEK, intermediate segments, third cirrus, ×137 (ctenopod type); *2c, B. (Solidobalanus) ciliatus* HOEK, intermediate segments, third cirrus, ×96 (after *55*).——*3. Chthamalus fragilis* DARWIN, terminal spines, second cirrus, enl. (after *83*).——*4. Trilasmis (Temnaspis) fissus* DARWIN, intermediate segments, sixth cirrus (lasiopod type), ×169 (after *54*).——*5. Paralepas palinuri* BARNARD, intermediate segments, fifth cirrus (acanthopod type), ×33 (Newman, 1960).

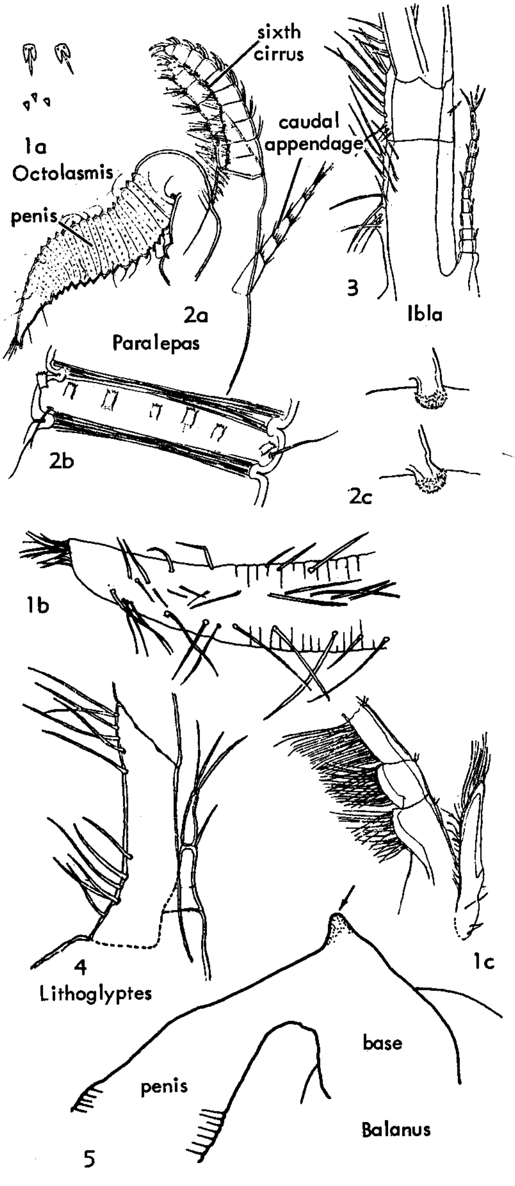


FIG. 104. Terminal appendages and penes of cirripeds.——*1. Octolasmis; 1a, O. (O.) cor* (AURIVILLIUS), two types of barbs clothing the penis, ×147; *1b, O. (O.) californiana* NEWMAN, terminal portion of penis, ×134; *1c, O. (O.) cor,* caudal appendage and pedicle of sixth cirrus, ×40 (Newman, 1960).——*2. Paralepas; 2a, P. lithotryae* HOEK, penis, sixth cirrus and caudal appendage, ×35 (after *54*); *2b, P. lithotryae* HOEK, rivet-like barbed structures clothing penis, ×169 (after *54*); *2c, P. palinuri* BARNARD, rivet-like barbed structures clothing penis, ×334 (Newman, 1960).——*3. Ibla cumingi* DARWIN, caudal appendage and pedicle of sixth cirrus, ×14 (Newman, 1960).——*4. Lithoglyptes spinatus* TOMLINSON & NEWMAN, caudal appendage and pedicle of terminal cirrus, ×100 *(103)*.——*5. Balanus (Balanus) amphitrite* DARWIN, basal portion of penis, arrow indicating basidorsal point, ×22 (Newman, n).

to three pairs of maxillipeds assisting in the transfer of food, and, in general, their addition, pair by pair, follows phylogenetic lines. In the primitive Lepadomorpha (i.e., *Lepas*), only the first pair differs from the following, and then only slightly. In more advanced forms, the first pair differs considerably from the following, while the second pair has been modified slightly. In the Balanomorpha, the Chthamalidae have the first and second cirri serving as maxillipeds, while in the Balanidae, the first, second, and third pairs form a graded series on their degree of modification, differing conspicuously from the posterior three cirriform pairs.

The cirri are generally flattened laterally and curled anteriorly. The anterior margin of each ramus can be designated as the lesser curvature; the posterior margin as the greater curvature. The lesser curvature of the articles usually supports long setae arranged in a number of pairs along the length of each article, and it was suggested by PILSBRY (1911) that cirri with this arrangement be designated as **ctenopod cirri** (Fig. 103,*2a*). In ctenopod cirri, the setae of each pair spread laterally away from each other, crossing the spaces between rami, forming the cirral net when the cirri are extended. These setae can be simple or slightly plumose. Ctenopod cirri usually have a few setae at the distal edge of each article, along the greater curvature. Another type of cirrus was noticed by DARWIN (1851) in a small pedunculate barnacle, where the setae at each articulation tended to be arranged in a transverse row, and PILSBRY suggested this type be designated as **lasiopod cirri** (Fig. 103,*4*). In some species, the row of the greater curvature is composed of stout, sharp spines while there were few or no setae along the lesser curvature. This arrangement is quite distinct from the previous two types and has been designated as **acanthopod cirri** (Fig. 103,*5*).

In certain species of *Chthamalus,* a few of the terminal setae of the second cirrus are

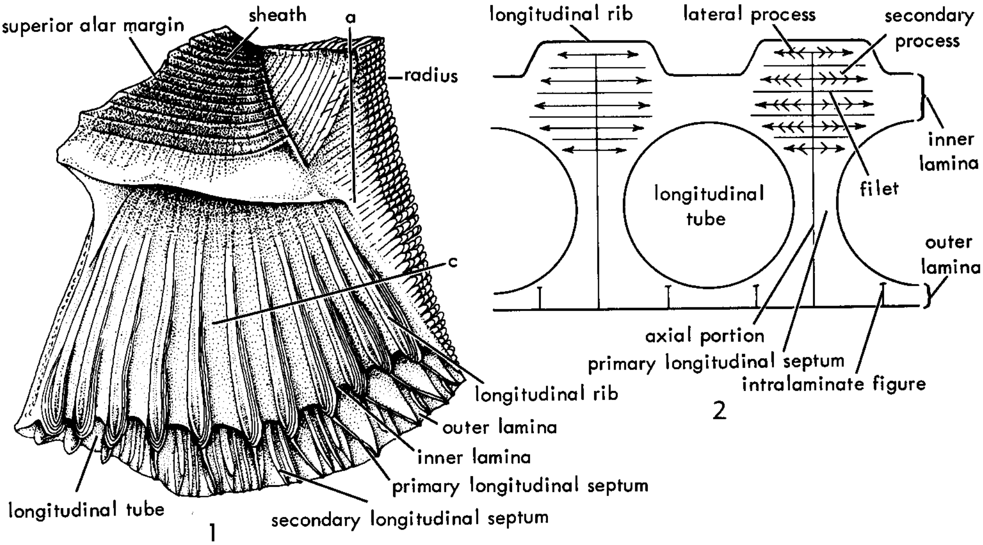


FIG. 105. Morphology of cirripeds; interlaminate figures in balanomorph shell wall (after *76*, mod.).

1. *Balanus (Balanus) amphitrite* DARWIN, left lateral plate viewed from interior, enl.
2. Schematic cross section of *Balanus (Balanus)* shell wall at level *c* indicated in *1*, illustrating parts of wall and characteristics of figures; axial portion+filet+lateral process+secondary process (all or in part) belong to interlaminate figure.

[Explanation: *a*, area of transverse section in radius (see Fig. 106,*2*); *c*, area of transverse section in parietes (see Fig. 106,*3*).]

lanceolate, with serrate and barbed edges (Fig. 103,*3*). In the balanids, in addition to supporting setae, the articles are frequently armed with denticles and true spines (Fig. 103,*1,2b,2c*), especially those of the third and fourth cirri.

The number of articles of the cirri, their relative lengths, the relative lengths of the rami, and the arrangement of setae, spines, and hooks, differ considerably between many genera and species of Thoracica, indicating differences in feeding, and these characteristics are of obvious systematic value.

All female or hermaphroditic Thoracica have six pairs of cirri, but in males of this order and in female Acrothoracica the number is usually reduced. In the Acrothoracica, the full complement seen in the primitive genus *Weltneria* is present, but there are as few as two uniramous pairs in *Trypetesa.* The rami of cirri have retractor muscles but no protractors. Their extension is accomplished by hydrostatic pressure of the hemolymph (CANNON, 1947). They are therefore well provided with blood channels and under certain conditions of activity probably function as respiratory, as well as feeding organs.

On the pedicles of the cirri, particularly the first, in genera of Lepadomorpha (e.g., *Pollicipes, Heteralepas s.l., Lepas, Conchoderma, Megalasma*) filament-like extensions of the body wall are found (Fig. 83,*1*). These have been thought to be respiratory structures, but it seems likely that they are at least also concerned with the incubation of eggs within the mantle cavity. In this regard, the present authors suggest that they are analogous with the so-called branchiae or much elaborated extensions of the mantle lining found in most Balanomorpha (e.g., *Balanus, Chelonibia, Chthamalus*). It has been noted that the female genital apertures open at the bases of the first cirri, and this is the most anterior position known among the Crustacea. When cirral filamentary appendages occur in reduced numbers, they are usually found on the first cirrus or near its base and not uncommonly in close association with the genital aperture.

Sexes are separate in many of the Ascothoracica, some Thoracica, and all of the Acrothoracica, but the method of fertilization is unknown. Ascothoracica and some of the reduced males among the Acrothoracica and Thoracica have a so-called penis or intromittent organ. In the former (Fig. 82,*2*), this is located on the first abdominal somite, and in the latter, within the sac constituting the reduced male (Fig. 80,*2a*). In the Thoracica, the abdomen has been lost and in hermaphroditic species, that is, the majority of Lepadomorpha, all known Verrucomorpha, and the Balanomorpha, the intromittent organ arises from between the base of the last or sixth pair of cirri (Fig. 104,*2a*). It is prosbosciform, greatly distensible, and in many species capable of transferring sperm to neighboring individuals some distance away. In hermaphrodites, fertilization at a given mating is not known to be reciprocal, but rather one individual acts as the female and the other as the male. Presumably the roles are reversed at another time. Although sperm is actually transferred from one individual to another, where well investigated the act is not strictly copulation, for the sperm are deposited in the mantle cavity, outside the body, where fertilization occurs. The intromittent organ is generally annulated, in some cases strongly so, and Darwin (1851-54) was inclined to consider the annulations as somites of the reduced abdomen, an interpretation accepted by Krüger (1940). However, the fact that no other metameric structures are associated with the annulations, that the presumably homologous intromittent organ of the Ascothoracica arises on the first abdominal somite, and that no other crustacean is known to be opisthogoneate, precludes this interpretation.

The intromittent organ is usually provided with soft setae, particularly at the apex (Fig. 104,*1b*). Setae in some forms are arranged in particular patterns, and bristles, knobs or complex spiny knobs directed basally (e.g., *Heteralepas, Octolasmis*) may be present (Fig. 104,*1a,b;2a,b*). Where such specially developed and arranged structures occur, they are regarded to be of considerable systematic value.

STUDY TECHNIQUES

PALEONTOLOGICAL METHODS

COLLECTION

Fossil taxa of lepadomorphs, brachylepadomorphs, and verrucomorphs are often based on isolated plates, as the shell of the animal usually becomes disarticulated soon after death. The shell of most balanomorph barnacles is more rigidly articulated, and complete specimens are often recovered. However, the opercular valves, which are important in identification, rarely remain fixed in their position in the orifice after death, and they may be lost.

In collecting from rocks where fossil barnacles are known to occur, a bulk sample should be taken from each barnacle-bearing stratum, washed, and screened (if possible), and sorted for all barnacle plates or fragments. In the case of loosely articulated forms such as the lepadomorphs, the complete individual can often be reconstructed. Opercular valves can usually be recovered in this manner also, although examination of the interior of shells will often reveal the full complement of valves preserved where they have fallen to the bottom of the body chamber.

INTERLAMINATE FIGURES AND THIN SECTIONS

Interlaminate figures, discovered by de Alessandri (1895) are found in balanomorphs having a wall permeated by longitudinal tubes. Cornwall (1962 and earlier) and Davadie (1963) have used interlaminate figures in the shell for determination of balanomorph species from fragmentary remains. Interlaminate (and shorter intralaminate) figures are observed in the transverse section of the parietes and represent crystalline organization about an organic matrix developed during the formation of the complex articulation between the parie-

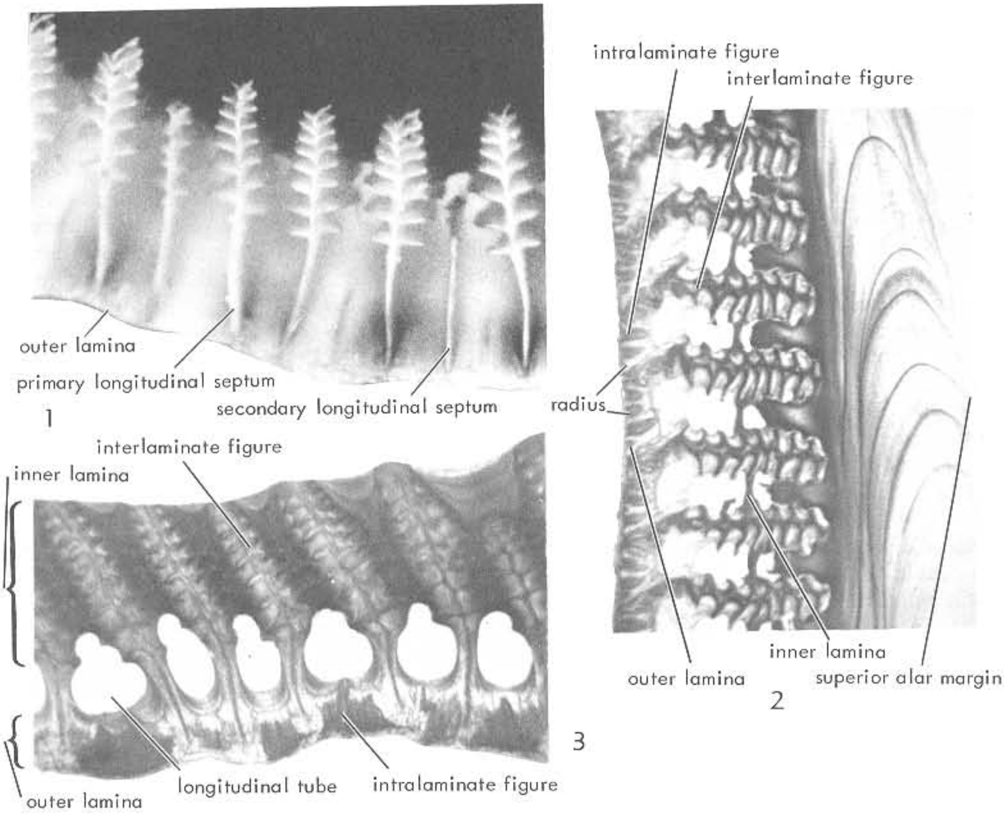


FIG. 106. Morphology of cirripeds; interlaminate figures in balanomorph shell wall *(Balanus (Megabalanus) tintinnabulum californicus* (PILSBRY), enl.

1. Basal margin of wall viewed from below, showing septa and teeth which lock between radial septa of basis (from *76*).
2. Interlaminate figures seen in radius where radial teeth interlock with ala of adjacent plate; section cut at level *a* shown in Fig. 105,*1* (Newman, n).
3. Interlaminate figures seen in transverse section of wall plate cut at level *c* in Fig. 105,*1* (Newman, n).

tes and the basis (Fig. 105,*1-2;* Fig. 106,*2*) (NEWMAN, ZULLO, & WAINWRIGHT, 1967). A similar pattern may be seen in a longitudinal section of the radii, reflecting the development of articulating sutural edges. The pattern related to these articular structures is observed as darker "figures" against the light background of the shell (Fig. 106,*1*).

Interlaminate figures appear to be characteristic of some species and are potentially of value in the determination of taxa from fragmentary material. Studies of the interlaminate figures of some Recent and Tertiary Californian barnacles indicate that some species may display more than one type of figure, and that several species may share a particular figure type. A thorough study of extant and fossil species from various localities throughout their geographic range will be required before the taxonomic value of this method can be established.

A variety of techniques and equipment are available for cutting thin sections of cirriped hard parts. The simplest procedure is to mount a piece of shell to be sectioned on a glass microscope slide and hand grind the exposed surface with a circular motion flat to about 1 mm. thickness. The specimen is then removed, turned over and reaffixed, with the freshly ground flat side toward the slide. The newly exposed surface is then ground in the same manner until, ideally, it is flat and 20-30μ thick.

The piece being sectioned can be affixed to the slide with any petrographic thermoplastic cement. The cement is melted on the slide, over an alcohol lamp, hot plate, or other heat source, with the specimen in place. Pressure is applied to the specimen before cooling, so that it comes into even contact with the slide surface. The melted cement is hot (145°F. or more) so that a piece of sponge is useful in applying the needed pressure. A piece of thin aluminum foil, foil-coated wrapping paper being ideal, is placed between the sponge and the specimen to prevent sticking.

Rough cutting and rapid removal of material requires abrasives of 100- to 200-grit, while finishing cuts and polishing utilize 400- to 600-grit. A few intermediate grades between these two extremes are useful during the grinding process. Grinding can be done by sprinkling an appropriate abrasive, or by using so-called wet and dry sand papers, on a sheet of plate glass flooded with water. Surfaces should be carefully cleaned when changing from one grit to another.

This method will yield satisfactory sections if the operator is particularly skilled, but it is difficult to get hand-held sections perfectly flat and uniformly thick. Performance can readily be improved by using guides or shims of various thicknesses. Two strips of steel shim stock placed on the glass or paper form tracks on either side of the specimen, separating the slide an appropriate distance from the cutting surface. Shims 0.001 inch thick will allow the specimen to come to within approximately 25μ of the cutting surface, and would be used for the final cut. When the section is finished, optical interference from scratches and other surface irregularities can be minimized by applying a drop of balsam and a cover slip.

For the worker cutting a section or two at infrequent intervals, the procedure outlined above is probably sufficient. If large quantities and sustained production are anticipated, one had best consult petrographic hand books on the subject, or professionals in the field, for a considerable amount of mechanization would be required. In between these two requirements are those who wish to carry out repetitive sectioning of perhaps ten samples ten times a year, and here a few accessories to the bare essentials outlined above would be reasonable. We have found the following improvements useful and they require only a modest outlay in funds.

Aside from the difficulties of getting good sections, one of the problems in hand-sectioning is holding the slide without acquiring numerous small cuts and abrading away significant amounts of skin. Also, the shim stock, although it can be held in line with tape, tends to skid about and get abrasive between it and the grinding surface and the slide, or both. To overcome these difficulties, increase the rate of production and improve the quality of the sections, a slide holder is desirable and some are commercially available. A slide holder consists of two accurately ground metal blocks, held in alignment by rods running through them, and grooved to hold a standard slide by tightening a thumb screw, which draws the blocks together. The outer surface of the slide is held slightly below the surface of the blocks so that a specimen on the slide will be ground to a thickness equaling this distance, when the surface of the block comes into complete contact with the grinding plate at the end of the cut. A specimen so ground can be dead flat and of uniform thickness. To prevent the block itself from being slowly ground away with each operation, and thus gradually decreasing the distance between the surface of the slide and the surface of the block, surfaces of the block coming in contact with the grinding surface are faced with precision ground boron carbide runners. This material is much harder than abrasives such as silicon carbide, and therefore undergoes little wear and loss of accuracy.

Slide holders presently cost less than one hundred dollars. They are designed to hold petrographic slides, which, after having been ground to a standard thickness in another specially designed holder, will clear the grinding surface of approximately 50μ, thereby yielding sections too thick for our purposes. This can be overcome by placing a piece of shim stock 0.001 inch thick between the slide and the holder, which advances the slide approximately 25μ and yields a section of comparable thickness.

We have found it convenient to use ordinary microscope, rather than petrographic slides. However, slides from any given lot, although parallel-sided, usually vary in thickness from one end to another and from side to side, some to a marked degree. A box can be checked over quickly by measuring the thickness of individual slides at each end, and at each side near the middle. Those varying only a few microns, especially from side to side, can be used for grinding thin sections. A micrometer, calibrated in 100ths of a millimeter (10μ) and readable to within a few microns by interpolation, is satisfactory for this purpose, and for estimating the thickness of the section.

Ordinary microscope slides are considerably thinner than petrographic slides, so that when used without backing shims, the first surface grinding results in a section more than 100μ thick. Such a section is strong enough to be turned over and pressed flat against the slide, in order to cut the second surface. The thickness of the section can be estimated by subtracting the thickness of the slide adjacent to the specimen from thickness of the slide and the specimen, as measured with a micrometer before beginning the second cut. The amount of material to be removed is then estimated and an appropriate number of shims placed between the slide and backing face of the holder. When the last polishing cut is to be made, it is a good policy not to rely on estimates made with the micrometer of the number of shims necessary to bring the section to final thinness, but rather to use a 0.001-inch shim as a feeler gauge inserted between the surface of the slide and a straight edge (the long edge of another slide), held across the two boron carbide runners. Sections will occasionally be lost without taking this precaution.

A sheet of plate glass, about 9x12 in. or larger, is a convenient grinding surface. The surface should be wet and, when using sand paper, running water is desirable. If a sink is available, a simple way to achieve this is to mount the glass on a pair of wooden supports arranged so as to bridge the sink. The relatively new silicon rubber cements for glass and ceramics are excellent for bonding the glass to the supports. A rubber tube from the cold water faucet can then be used to provide a slow stream of water, the runoff spilling into the sink.

Ordinary water-proof sand paper, especially in the coarser grits, has proved satisfactory. The relatively new abrasive coated *Mylar* films sold under the trade name *Flex-i-grit,* are more durable, especially in the finer grits, but are not generally available locally.

Preparation of blanks of the material to be sectioned can be accomplished by breaking, filing, sawing, and power grinding. Small, relatively inexpensive, diamond-impregnated discs or wheels available through dental supply houses, driven and manipulated by hand-held motors such as those available under the trade name *Mototool,* are highly recommended. With them, relatively thin, flat-sided portions of a specimen can be removed, often leaving the bulk of the specimen intact. Although manufacturers recommend that these wheels be run wet, satisfactory cutting or microslabbing can be accomplished dry.

NEONTOLOGICAL METHODS

The diversity of habitats in which cirripeds occur may even be surprising to the marine biologist with considerable field experience. This would be especially true in the tropics where, although not usually occurring in great numbers in any one place, the variety of niches occupied is remarkable.

The Acrothoracica are burrowing forms, able to penetrate any calcareous substratum, particularly mollusk shells and skeletons of living and dead scleractinian corals. They are less often found in echinoid and balanoid shells, but are frequently encountered in limestone. All described species are from shallow water, although an undescribed species is known from approximately 1,000 meters of depth on the Bermuda slope in the western Atlantic.

Usually the only visible sign of an acrothoracican's presence in a piece of calcareous substratum is the small slitlike opening to the burrow, generally a millimeter or so in length and shaped like a straight or slightly curved apostrophe. This small aperture opens into a commodious oval chamber excavated and inhabited by the female which usually is accompanied by one or more dwarf males. The chamber may extend straight or somewhat obliquely down from the surface and can be studied by making casts with materials not attacked by acid and then dissolving away the substratum, or by successively grinding the substratum, gradually exposing the outline of the burrow. X rays are useful in exploring certain kinds of materials, especially gastropod shells inhabited by hermit crabs, where the burrows open on the interior surface.

The aperture of the burrow is guarded by the chitinous lips formed at the mantle opening of the barnacle. Shortly after placing an object bearing living acrothoracicans back in sea water, the operculum formed by these lips will be drawn back and the cirri thrust forth forming the cirral net. The appearance of cirri is useful in confirming the presence of living specimens and is especially useful in locating them in materials encrusted with sponges, bryozoans, and algae. Females can be removed by chipping the substratum away, but usually not without some obvious damage, especially if cemented to the burrow. Another method involves treatment with acid after the material has been properly fixed in Bouin's fluid, 70 percent alcohol, or another appropriate fixative. A specimen can be studied externally and dissected in much the same manner as the relatively unarmored Lepadomorpha described below. Or it can be treated with dilute sodium hydroxide in the manner described by Tomlinson (1960), until most of the soft tissues have been digested away, but care must be taken in making observations on specimens so treated, because frequently the new cuticle developing beneath the old will have separated, giving a multiple or otherwise inaccurate appearance of structures. After this treatment and a thorough washing, the specimens may be stained or simply mounted directly in an appropriate medium on a microscope slide. Glycerin as a mounting medium is useful in allowing specimens to be manipulated, although, to avoid distortion of delicate structures, it is best to infiltrate the specimen gradually by placing it in a glycerin and alcohol solution and allowing the latter to evaporate. This procedure is equally desirable before mounting a specimen in glycerin jelly. Whole mounts need the support of a glass or plastic ring. The whole preparation should be sealed with an appropriate ringing medium, and clear "finger-nail polish" is convenient.

The acrothoracicans occur in calcareous substrates and therefore are relatively limited in the diversity of habitats they can occupy. The thoracicans on the other hand, are rarely obligated to any one particular substratum or association, are basically not dependent on support or armament provided by the environment, and consequently, exploit a great diversity of habitats. Some members of each of the suborders are found intertidally, on rocks and other intertidal organisms, and most are in a size range readily detected with the unaided eye. Of the Lepadomorpha, only a few genera occur intertidally. In particular, there are *Pollicipes* and *Lithotrya* among the Scalpellidae and *Ibla* of the Iblidae. The Verrucomorpha are primarily subtidal, but there are a few intertidal species, some being very small. The Balanomorpha contain a large number of species in both subtidal and intertidal situations. Although there are probably no rules for general collecting, it is desirable to obtain all of a particular specimen. The ease with which this can be accomplished will depend on where and how the animal is attached and, it is probably best to bring materials to the laboratory where they can be observed alive and carefully removed from their attachment place. As far as collecting is concerned, every conceivable habitat washed by sea water should be explored, specifically the surfaces of rocks to the highest reaches of the tides, the surfaces of living animals including mollusks, crustaceans, large jellyfish, sea urchins, other barnacles, sea snakes, turtles, cetaceans and so forth. The interiors of other animals should also be explored, especially the gill chambers of large decapod crustaceans, sponges, turtle gullets, and corals, and alcyonarians. At least one genus is known from within living clams and another between the pedal disc of sea anemones growing on gastropod shells inhabited by hermit crabs. Some species are also found on plant materials, including mangrove roots and leaves, seaweeds and flotsam in the sea.

Observations on living barnacles are interesting and instructive. Adult shore barnacles, especially estuarine or harbor forms, can often be maintained on young brine shrimp *(Artemia)* for extended periods of time, and frequently individuals will reattach to the walls of the container in which they are kept. Growth, molting, feeding, reactions to currents and shadowing, and mating can be observed. The mantle forms lips around the aperture that can adequately be observed only in living material. These are expanded when the animal is relaxed or feeding and have more or less striking color patterns. The function of these colors has not been determined, but they are of some systematic value (SOUTHWARD & CRISP, 1963).

Larvae can also be obtained in the laboratory, either spawned directly from the adults or from ovigerous lamellae removed from sacrificed animals and suspended in sea water (COSTLOW & BOOKHOUT, 1957). Culture techniques have become considerably refined, and differences in dietary requirements are being analyzed (MOYSE, 1963). Through the rearing of larvae, much has been learned of the morphology of different species, and methods of description are still in the process of development. Setation formulae have been used for descriptive purposes and appear to be an important aspect in comparative studies. However, considerably more work is needed before an understanding of larval relationships and affinities contribute to our knowledge of the systematics of the cirripeds *(75)*.

The larvae or their molts are readily prepared for microscopical study. Molts are usually obtained from individuals reared singly. Living nauplii, on the other hand, are generally handled in relatively large numbers. They are usually photo-positive and can be pipetted from a container illuminated on one side. These can be concentrated in a small glass tube opened at one end, and with a fine mesh of silk bolting cloth stretched and secured over one end. In this, the larvae are washed, fixed, and stained if desired, before transferring to a drop of glycerin on a microscopic slide. In glycerin, individuals can be manipulated or dissected so that the appendages can be observed, drawn, and setation counts made. If dissection proves difficult, preparations can be lightly squashed under a coverslip.

Preparation of adult barnacles for examination is relatively simple once the anatomical relationships are understood. Removing the body from the mantle or shell requires certain tools, the sizes of which will depend on the size and type of barnacle. In general, ordinary dissecting needles and forceps are useful. For small specimens, finer instruments are necessary. Small dissecting needles can be constructed from small sewing needles or insect pins mounted in appropriate holders. Fine jeweler's forceps are indispensible and not infrequently the finest available can be ground a little finer.

Acrothoracicans and small unarmored lepadomorphs can be removed from the mantle by plucking a hole in the side, withdrawing the body and then freeing it completely by teasing away the attachments of the adductor muscles. The body of armored lepadomorphs usually can be removed through the aperture by grasping the attachment area at the adductor muscle lying between the scuta, and gently withdrawing the body. Some teasing of the membranes between the scuta may be necessary in order to enlarge the aperture sufficiently, but this is usually unnecessary. In the Balanomorpha, the body is too large, relative to size of the aperture, to be removed in this manner, but it can be removed through the base, leaving the shell wall intact. The body is attached almost entirely to the scutal valves, which are in turn articulated with the terga. Therefore, in removing the opercular parts, the body is removed at the same time. The ease with which these parts are removed will depend on the structure and condition of the barnacle. Usually, inward pressure applied to the operculum, and teasing or cutting of the arthrodial membrane connecting it to the sheath of the wall, will allow the entire mass to be forced out through the base. Once removed, the body is easily dissected free of the opercular parts, under water in a small dish such as a Syracuse dish. The mantle cavity may contain ovigerous lamellae of eggs, developing embryos or larvae, and these should be saved for study. Frequently, the first larval stage can be obtained in this way. It can be either the first naupliar stage or the cyprid larva, depending on the life history of the species.

The opercular parts, as well as the wall plates, can be cleaned and disarticulated by soaking in sodium hypochlorite (commercial bleach such as Clorox). Methods of handling these parts will vary with the nature of the material and the interests of the investigator. Small vials, gelatin capsules, boxes, Curtin and Riker mounts are useful.

Once the body is removed, it can be studied under water, note being taken of the attachment and arrangement of cirri, the presence or absence of filamentary appendages (Lepadomorpha) or branchiae (Balanomorpha), and so forth. After these observations, the specimen can be dissected. The appendages and parts will usually mount satisfactorily on one or two slides, although large specimens may require special handling. Before dissection begins, some estimate of these requirements should be made. The actual dissection will vary with the worker, as will the selection of the mounting medium. Permanent synthetic resins and media such as Turtox CMC and Euparal, have certain advantages, but glycerin jelly has been satisfactory for us.

A clean microscope slide is warmed over an alcohol lamp and a few square millimeters of glycerin jelly are placed on it. The jelly should be spread so as to form a film covering the area to be occupied by the cover slip. Spreading can be aided with a warm dissecting needle and bubbles can be removed by pricking with the tip of a hot needle. The slide is then placed conveniently near the microscope and allowed to cool. The body of the barnacle in a dish of water will usually lie on one side or the other. For right-handed workers, it is usually convenient to place the animal on its left side and to dissect away the right cirri one by one, starting with the first. Special care must be taken if caudal appendages are present, as it is preferable that each remain attached to the base of the pedicle of each sixth cirrus. Then usually the cirri of the left side are removed, working from posterior to anterior.

As each cirrus of the right side is removed, it is generally placed in glycerin jelly on the slide outside surface up, in order from left to right. A little water is carried with the appendage and the tips of the forceps, and this aids in slowing the infiltration of jelly and rapid osmotic removal of water. The cirri of the left side are placed in a like manner so that their inner surfaces are up. Due to the osmotic situation, the penis with its delicate cuticle will generally shrivel if placed directly in the glycerin jelly and should be first infiltrated with glycerin.

At this point one is left with the appendageless thorax, and the prosoma supporting the buccal mass. These can be separated, and the former discarded, provided it does not support filamentary appendages. Some experience is helpful in dissecting out the mouth parts. Generally the first maxillae and mandibles are removed before attempting to remove the second maxillae. This is because the second maxillae are rather delicate and are fused together basally. They are best taken off as a pair and then teased apart, before mounting. The numerous muscles and adhering shreds of cuticle are removed from the labrum. It may be desirable to detach one of the palps and mount it separately, so that the crest of the labrum can be viewed. Although the mouth parts are readily distinguishable and there is little likelihood of getting them confused, it is best to mount them in a meaningful way, as was done with the cirri. This completes the dissection and the mount should be inspected and adjustments in the positions of parts made with the tip of a warm needle. The slide is then warmed gently to soften but not completely liquify the jelly, and a warmed coverslip is lowered into place, allowing one edge to touch first so that air can escape without forming bubbles. The finished slide should be cleaned and sealed and given an identifying mark or label.

A certain amount of flattening is unavoidable in a preparation of this sort, and structures such as the penis and labrum may best be studied in glycerin alone, without a coverslip, before being transferred to glycerin jelly.

It has long been customary to store barnacles dry and many collections are presently so maintained. Dried materials that have not been damaged by insects can be "reconstituted" to a considerable extent by soaking for several days in alcohol and glycerin. If the preparation does not soften sufficiently for dissection, it should be treated with a dilute solution (0.5 to 1 percent) of trisodium phosphate for one to several days. Specimens that have been dried for more than one hundred years have been successfully dissected after having been treated in this way.

ONTOGENY

EMBRYONIC AND LARVAL LIFE

Eggs are laid in the mantle cavity of the female or hermaphrodite where they are fertilized (Fig. 107). A substance secreted during laying forms a matrix holding the eggs in a mass of a more or less definite form. When formed in sheets, the masses are termed **ovigerous lamellae** (Darwin, 1851). In many species, the egg masses lie free within the mantle cavity, conforming closely to the space occupied, or, in *Lepas*

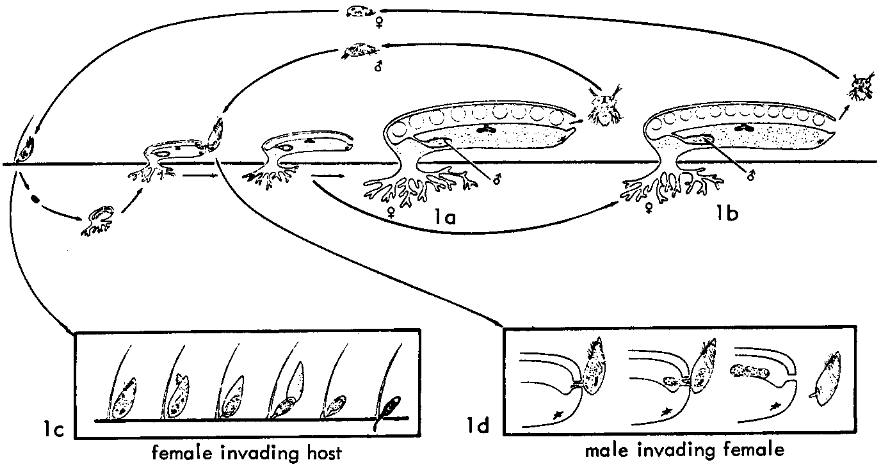


FIG. 107. Life cycle of *Peltogasterella gracilis* (BOSCHMA) (Rhizocephala); *1a,* female producing large eggs, nauplii and male cyprid larvae; *1b,* female producing small eggs, nauplii and female cyprid larvae; *1c,* female cyprid kentrogon invading hermit crab host; *1d,* male cyprid cells being injected into mantle cavity of young female and migrating toward male cell receptacles (Newman, simplified, after Yanagimachi, 1961).

and its allies, a pair of ovigerous lamellae are held in position by special structures called **ovigerous frenae.** Although the eggs are relatively yolky, cleavage is characteristic of the Spiralia, being total, unequal and presumably determinant in genera such as *Lepas* (BIGELOW, 1902). After a period of incubation, the eggs usually hatch as **nauplii** which are subsequently released by the adult (GROOM, 1894). The free-swimming nauplius generally molts five times, thus passing through six stages, each of increasing complexity (BASSINDALE, 1936). The nauplius has a pair of **frontolateral horns**—distinguishing the nauplii of Thoracica, Acrothoracica, and Rhizocephala from all other Crustacea; a nauplius eye, uniramous first antennae and natatory biramous second antennae and mandibles (Fig. 81). Gnathobases on the last two pairs of appendages serve to capture food and tuck it beneath a large labrum covering the mouth. By the last naupliar stage, compound eyes, first maxillae, the incipient six thoracic somites have appeared beneath the cuticle, and the setation of the naupliar appendages has gained considerable complexity. The sixth naupliar molt involves a complicated metamorphosis into a **cyprid larva** (GROOM, 1895; BATHAM, 1945) (Fig. 81, 84). The broad dorsal shield of the nauplius becomes the bivalved carapace of the cyprid, the first antennae become prehensile (Fig. 91, 2), the second antennae disappear, the mouth parts persist as rudiments, and the six thoracic limbs appear as natatory appendages.

The cyprid larva is not known to feed. It settles out of the plankton and selects the site where it will attach. Attachment is effected initially by the first antennae and once cemented in place, the cyprid undergoes a complex metamorphosis and reorganizaton in attaining a juvenile form (RUNNSTRÖM, 1925; BERNARD & LANE, 1962) (Fig. 108).

The nauplius stage is passed through in the egg in a number of thoracic cirriped species (Fig. 109,*A*), the larvae being liberated as fully developed cyprids (BARNARD, 1924; BROCH, 1924; HOEK, 1883; NILSSON-CANTELL, 1921) (Fig. 109,*B*). The deletion of the nauplius as a free-swimming stage is seen in the other orders of cirripeds: Ascothoracica (WAGIN, 1946; BRATTSTRÖM, 1948), Acrothoracica (NILSSON-CANTELL, 1921; TOMLINSON & NEWMAN, 1960; BATHAM & TOMLINSON, 1965), and Rhizocephala (NILSSON-CANTELL, 1921; BOCQUET-VÉDRINE, 1961). Yet the nauplius is a fundamental part of the basic cirriped life cycle, its elimination being a secondary development that appeared independently in the various orders.

EARLY DEVELOPMENT OF LEPADOMORPHA

Lepas has a nauplius larva which passes through six stages (MOYSE, 1963). The last stage metamorphoses into a cyprid, which is weakly free-swimming. The cyprid swims about for an unknown, but presumably short, period of time, and then settles on virtually any floating or suspended object. Shortly after settling, five uncalcified primordial plates (carina and paired scuta and terga) appear beneath the bivalved cyprid shell. Then the cyprid shell becomes loosened, opens along the ventral margin, and is worked off, usually before the calcified plates appear (Fig. 87,*2-3*). The calcified plates are formed under, and extend beyond, the primordial plates and in later stages may be seen on the umbo of the calcified plates unless worn away (Fig. 87,*5-6*).

Development of plates in the Scapellidae is well shown in a series of *Pollicipes polymerus typica* described by BROCH (1922), whose figures are reproduced here (Fig. 88,*1-7*). This barnacle exhibits a similar ontogeny to that of *Lepas,* including the appearance of five primordial plates as primary centers of calcification. At this point, a number of additional calcified plates appear which are not associated with primordial plates. Thus, although the basic number of primordia seems to be five, primordia are not required for a calcified plate to develop. In fact, the functional relationship between the primordial plates and calcification is unknown.

In the ontogenetic development of *Pollicipes* and *Lepas*, it was seen that a stage occurs where the animal is enclosed by the primordial plates and connecting membrane. It is only later that the calcareous plates are formed, and as they develop, the primordial plates are displaced farther and farther from each other, remaining on the umbo of the calcified plates. In Lepadomorpha, the five primordial plates are present, as they also are in the sessile asymmetrical forms included in the Verrucomorpha (Fig. 89,*1-4*).

Primordial plates, however, have not been found in Balanomorpha.

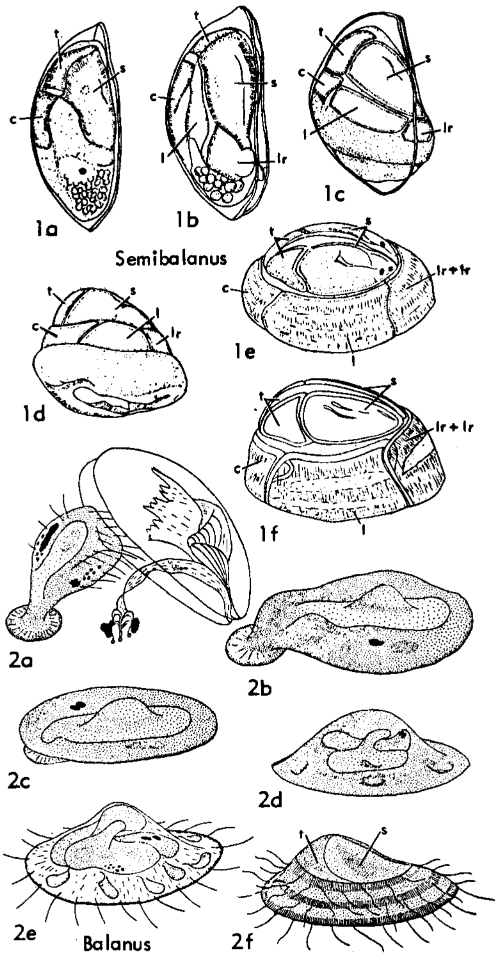


FIG. 108. Morphology of cirripeds. Metamorphosis in *Balanus*.——*1. Balanus (Semibalanus) balanoides* (LINNÉ), enl.; *1a,* freshly settled cyprid larva with presumptive tergum, scutum and carina beginning to appear; *1b,* further differentiation of presumptive plates and appearance of two pairs of lateral plates; *1c,* cyprid shell about to be cast, terga and scuta becoming organized to form the opercular valves; carina, lateral and rostrolateral plates becoming organized into wall; *1d,* further differentiation and development of opercular and wall parts, rostrolaterals still separate; *1e,* rostrolaterals fusing, forming compound rostrum; *1f,* four-plated stage of *Semibalanus* (after Runnström, 1925, from *61*).——*2. Balanus (Balanus) amphitrite* DARWIN; *2a,* settled larva shedding cyprid shell and compound eyes, devoid of presumptive plates, ×53; *2b-e,* successive metamorphic stages with changes in external morphology toward the juvenile form, ×93; *2f,* differentiation of opercular valves (terga and scuta) and wall, ×93 (after *10*). [Explanation: *c,* carina; *l,* latus; *lr,* latus (rostral); *r,* rostrum; *s,* scutum; *t,* tergum.]

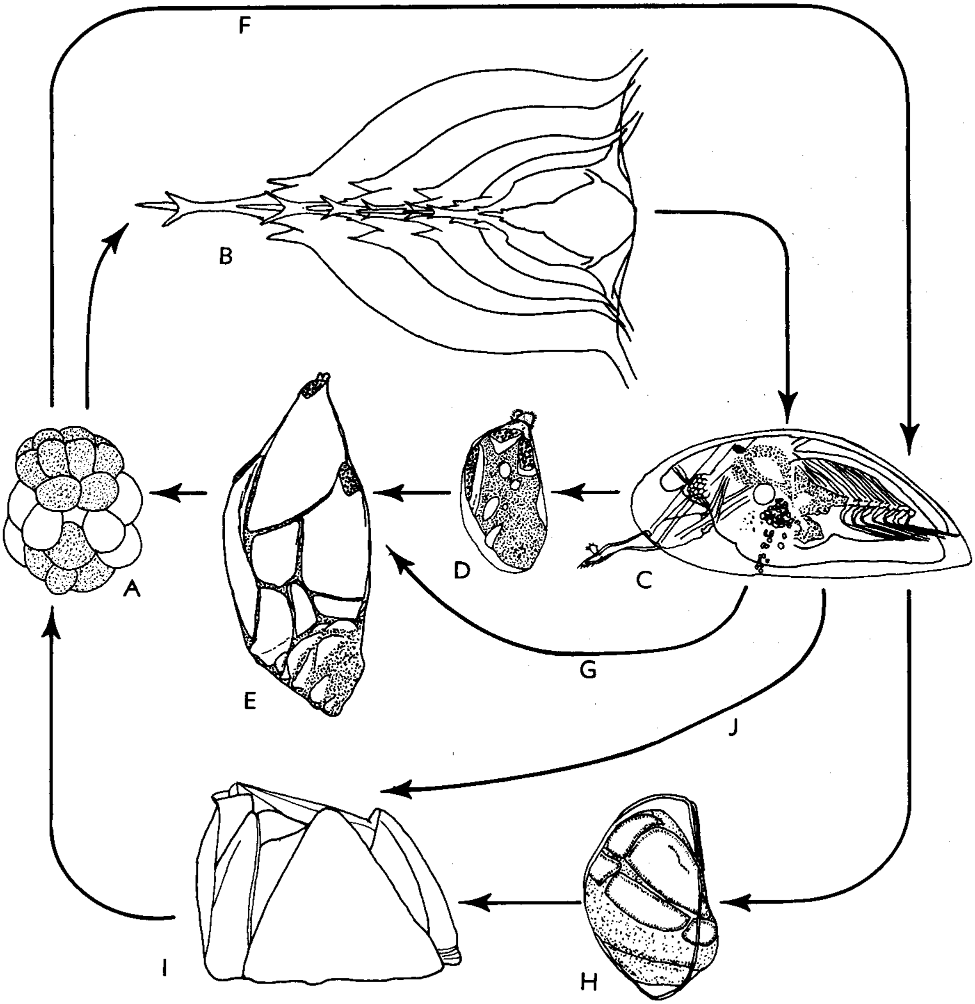


Fig. 109. Life cycles of thoracican cirripeds (Newman, n).

The generalized life cycle includes spirally cleaving egg brooded in mantle cavity *(A)*, naupliar stages, usually six *(B)*, nonfeeding cyprid larva *(C)*, pupal or metamorphic stage *(D* or *H)*, and adult, usually pure hermaphrodite, less commonly hermaphrodite accompanied by complemental males or female accompanied by dwarf males *(E* or *I)*. In some species, naupliar stages are passed through in egg, and cyprid emerges as first larval stage *(A,* through *F,* to *C)*. In some species with males, certain cyprids metamorphose into minute degenerate male attached to hermaphrodite or female *(C,* through *G* or *J,* to *E* or *I)*, within mantle cavity (Iblidae, Fig. 86,*2a*); along scutal margin of aperture (Scalpellidae, Fig. 86,*3b*); at rostral end of aperture (Koleolepadidae, Fig. 114,9), or on inner surface of rostrum and rostral ends of scuta (Balanidae, Fig. 118,*3a-b*) *(A,* after *12; B,* after *7; C,* mod. from Kühnert, 1935; *D, E,* after *20; H,* after *91; I,* after *55)*.

EARLY DEVELOPMENT OF BALANOMORPHA

The balanomorph larva also passes through six naupliar stages and one cyprid stage (Bassindale, 1936; Costlow & Bookhout, 1957; Barnes & Costlow, 1961). Upon settlement, the cyprid body has been observed to undergo a metamorphosis similar to that seen in the Lepadomorpha (Runnström, 1925), or to enter a stage in which no structure can be discerned

(Doochin, 1951; Bernard & Lane, 1962). These two types of metamorphosis have been described for species belonging to different subgenera of *Balanus* so that it is possible the apparent differences are real rather than mistaken observations. The two processes are illustrated here (Fig. 108,*1a-f, 2a-f*). In the latter, the cyprid carapace is discarded and the barnacle appears as a small, dome-shaped, amorphous lump attached to the substrate. The compartmental plates and the opercular valves begin to take form after the carapace is discarded, and presumably at this time the adult body also forms.

Runnström (1925) and Broch (1927) have described the ontogeny of the shell wall in *Balanus (Semibalanus) balanoides* in which five wall plates (two rostrolaterals, two laterals, and carina; rostrum being absent), are first discernible. The rostrolaterals fuse to form a single plate, leaving four in the shell wall. This is followed by the appearance of the carinolaterals, on either side of the carina, to form the full complement of six compartmental plates. The observations on the formation of the rostral plate are, for a good part, the basis for concluding that it is made up of the fused rostrolaterals and that actually the true rostrum is lacking in *Balanus* and derived genera (Fig. 96,*8*). However, Costlow's (1956) observations on *B. (B.) improvisus* do not confirm this finding. Two plates first appear, one of which is the rostrum. The other subsequently divides to form the carina and paired laterals, yielding the four-plated stage. The carinolaterals then appear between the carina and the laterals, in the same manner as described for *B. (S.) balanoides.* From this description, the rostral plate would be homologous with the rostrum of other Thoracica. Whether one or the other, or both, of these methods of formation of the rostral plate is actually the case is not known.

Costlow (1956) has also described the early ontogeny of the wall in *Balanus (Balanus) improvisus,* and identifying certain cells in the basal margin of the mantle responsible for the secretion of the cuticle and the organic matrix that subsequently becomes calcified. His description includes details of the inception of complex wall elements such as parietal tubes, septa, and the inner lamina composing the wall of higher balanomorphs.

CLASSIFICATION

An outline of the taxonomic divisions of the Cirripedia, which seems most acceptable in light of published knowledge of these crustaceans accumulated to the present, follows.

Order ACROTHORACICA Gruvel, 1905

In his first volume on the living cirripeds, Darwin (1851), considered *Alcippe* Hancock (=*Trypetesa*), and an undescribed form *(Cryptophialus),* were sufficiently distinct from the ordinary cirripeds (Thoracica) to constitute a distinct order. However, when the time came to erect the order (Abdominalia), he described and placed *Cryptophialus* but not *Alcippe* in it (1854). This decision was in good part due to difficulties in the homologies of segmentation in the cirripeds that had grown out of the prevalent tendency to compare entomostracan segmentation patterns to that of the Malacostraca, to difficulties in reconciling the apparently aberrant segmentation of *Alcippe* with that of *Cryptophialus,* and in the similarities he noted between the plan of *Alcippe* and that found in other lepadomorphs, especially the reduced males of some species. Noll (1872) recognized the underlying bases for certain of these difficulties and placed *Alcippe* in the Abdominalia, and Gruvel (1905) cognizant of the thoracic rather than abdominal situation of the posterior cirri, changed the name of the order to Acrothoracica.

Since Darwin, more than 30 Recent and fossil species have been described. The classification of living species generally reflects the degree of reduction of the appendages. The most generalized genus, *Weltneria,* has a complete complement of cirri, and caudal appendages are present. Other genera are primarily characterized by the loss of one or more pairs of cirri, the presence or absence of caudal appendages, the condition of the mouth parts and to some degree, the musculature. All those having a well-developed posterior end and complete gut, BERNDT (1907) considered to form a suborder, the Pygophora. In contrast, *Trypetesa,* with the posterior end quite rudimentary and hind gut closed, he set aside as a separate suborder, the Apygophora. Classification in the *Treatise* follows that of BERNDT (1907) as suggested by TOMLINSON (1967, personal communication) (p. *R*251).

Order RHIZOCEPHALA F. Müller, 1862

The Rhizocephala were first recognized as crustaceous organisms by CAVOLINI (1787), through the discovery of nauplius larvae in *Sacculina.* It was 50 years later, without knowledge of CAVOLINI's work, that J. V. THOMPSON (1836) correctly referred these highly modified parasites of crustaceans to the Cirripedia. MÜLLER (1862-63) advanced knowledge of their life history and adult anatomy, and confirmed LILLJEBORG's (1861) observations and interpretations on the existence of males, found as cyprids attached to the parasite. The males were considered complemental in function because the parasites were presumed to be hermaphroditic, a sexual relationship comparable to that discovered by DARWIN (1851-54) in certain thoracican cirripeds. DELAGE (1884) made important studies on anatomy, further confirmed the presence of males, and discovered the manner in which the cyprid stage of the parasite infects and establishes the internal parasitic phase, by way of the so-called kentrogon stage. GIARD (1891) recognized that infection resulted in parasitic castration of the host.

Much controversy has surrounded sexuality in the rhizocephalans. The consensus primarily fostered by SMITH (1906) and POTTS (1912) was that when so-called testes were found along with ovaries in the same parasite, the individual was a hermaphrodite. In such cases, the males would be complemental and were construed as functionless. This concept persisted until REINHARD (1942) demonstrated in *Peltogaster* that the so-called complemental male was functional. That the so-called testes were in fact males that had left their cyprid integument attached outside the mantle opening, and had migrated into special pockets formed for them within the mantle cavity of the female and many other important details in the life cycle were uncovered by ICHIKAWA & YANAGIMACHI (1958) in *Peltogasterella.* Comparable processes have been recently described in other rhizocephalans (VEILLET, 1962; YANAGIMACHI & FUJIMAKI, 1967).

Whereas the Rhizocephala were generally considered more closely related to ordinary cirripeds than to other crustaceans, DELAGE (1884) inferred that they were sufficiently distinct to form a coordinate group, and proposed the name Kentrogonida for them. Such separation was not generally accepted, however. KOSSMANN (1872) considered them best regarded as a subfamily of the Lepadidae. Morphological intergradations between pedunculate barnacles and rhizocephalans have been observed and the nauplii of Rhizocephala, Acrothoracica, and Thoracica have frontolateral horns, structures found in no other Crustacea. The Rhizocephala are simply cirripeds highly modified for parasitism. Furthermore, it is likely that the Rhizocephala are polyphyletic, lines having arisen from different thoracican stocks.

The studies of COUTIÈRE (1902) suggested that, unlike *Sacculina, Thylacoplethus* (=*Thompsonia*) probably did not pass through an internal phase, and therefore lacked a kentrogon stage. On this basis, HÄFELE (1911) divided the Rhizocephala into two groups, the Kentrogonida and Akentrogonida. This division was not adopted by CALMAN (1909) or KRÜGER (1940).

It had been thought that each reproductive sac of *Thompsonia* was supported by an individual set of nutritive processes that had become established in the host without loss of communication with the exterior. This level of organization, on theoretical grounds, would have to have preceded the evolution of the kentrogon. However, POTTS (1915) demonstrated that the individual reproductive bodies in *Thompsonia* were actually interconnected by nutritive processes and were undoubtedly developed from a single individual, rather than by multiple infection. Yet it has not been determined whether *Thompsonia* passes through a kentrogon stage. Consequently, the retention of the genus in the Akentrogonida is tentative. *Duplorbis* and *Mycetomorpha,* especially the former, are suspected of being at the akentrogonid level of organization, but their life histories, too, are incompletely known. *Chthamalophilus,* on the other hand, has been critically examined and is defintiely assignable to the Akentrogonida (Bocquet-Védrine, 1961), so that the suborder, provisionally including *Thompsonia, Duplorbis, Microgaster,* and *Mycetomorpha,* is adopted here, outlined on p. *R*251.

Order ASCOTHORACICA Lacaze-Duthiers, 1880

When Lacaze-Duthiers (1880) described *Laura,* he recognized its affinities with the Cirripedia. The prehensile first antennae, bivalved carapace and natatory thoracic limbs provide a strong facies similarity with cyprid larvae, and the female genital ducts opening on the first thoracic somite, as in the ordinary cirripeds but in no other crustaceans, further indicated this. In consideration of the uniqueness of organization, and adaptations made to parasitism, he proposed a separate category for *Laura,* the Ascothoracida or Rhizothoracida, to be included as the fourth suborder of otherwise peculiar or parasitic forms, or both, the *Cirripedia abortiva* of Gerstaecker (1866). Thus he recognized suborders designated as 1) Suctoria or Rhizocephala, 2) Apoda, 3) Abdominalia, and 4) Ascothoracida or Rhizothoracida.

The inclusion of these suborders under an order distinguishing them from the Cirripedia genuina (Thoracica), proved highly artificial in terms of natural affinities, and in his revisionary work, Gruvel (1905) arranged them simply as separate orders under the subclass Cirripedia: 1) Thoracica, 2) Acrothoracica (=Abdominalia), 3) Ascothoracica (=Ascothoracida or Rhizothoracida), 4) Apoda, and 5) Rhizocephala.

In subsequent studies, Wagin (1937, 1946) concluded that the Ascothoracica were sufficiently distinct from the cirripeds to be considered as separate and of equal rank. This view was accepted by Krüger (1940). Yet, the comparative analyses were made with respect to the thoracican barnacles rather than with the cirripeds in general, and as Wagin (1946) pointed out, there were difficulties in separating specialized from fundamental features. Upon reexamination, the only fundamental difference between the two groups seems to be the absence of frontolateral horns in ascothoracican naupliar stages. Otherwise the closer affinities of the ascothoracicans with the cirripeds than with any other group of crustaceans is admitted by all. There is no compelling reason, then, to place the Ascothoracica equal in rank with other maxillopodan subclasses, and the category is retained here as the most generalized order of Cirripedia (p. *R*251).

Order THORACICA Darwin, 1854

Linné (1758) did not distinguish genera among the cirripeds, but included all known species in *Lepas.* Da Costa (1778) was the first binomial author to distinguish between the "sessile" barnacles, which he placed in the genus *Balanus,* and the stalked or pedunculate barnacles for which he retained the name *Lepas.*

Leach (1817, 1818, 1825) and Gray (1825) were among the first to classify barnacles in a more modern manner. Leach (1825, p. 208-209) proposed orders designated as 1) Campylosomata (="Pedunculata" of later authors), including families Clytiadae, Pollicipedidae, Iblidae, and 2) Acamptosomata (="Operculata" of later authors), including families Coronuladae, Balanidae, Clisiadae.

In the same year Gray (1825) proposed division of the Thoracica into families named Anatiferidae, Pollicipedidae, Pyrgomatidae, Balanidae, and Coronulidae.

Darwin (1851, 1854) not only revised the classifications of Leach and Gray, but established the genera on firm morphological bases, defined species which at that time were in a chaotic state, and established a definite terminology. He demonstrated relationships between supraspecific taxa, his more important contributions being definition of the families Lepadidae, Verrucidae, and Balanidae as groups of equal rank, separation of the Chthamalinae and Balaninae as subfamilies of the Balanidae, and determination of important differences in the morphology of the "turtle" *(Chelonibia)* and "whale" *(Coronula)* barnacles.

GRUVEL's (1905) classification represents a radical departure from that proposed by DARWIN, being based, especially in the Balanomorpha, on number of plates in the shell wall. The inadequacies of this classification, discussed by PILSBRY (1916, p. 13), WITHERS (1928, p. 62) and KRÜGER (1940, p. 26-27), result from the fact that the compartmental plates are not always homologous in taxa having a like number of plates in the shell wall. Continued usage of this classification is not recommended.

PILSBRY (1907) divided the Lepadidae into five subfamilies: Lepadinae, Scalpellinae, Oxynaspidinae, Alepadinae, Iblinae.

HOEK (October, 1907) and PILSBRY (November, 1907) independently proposed to group members of *Scalpellum* into a number of subgenera. These studies later led PILSBRY (1908) to divide *Scalpellum* into four genera: *Calantica* (with subgenera *Calantica s.s.*, and *Scillaelepas*), *Smilium, Euscalpellum,* and *Scalpellum* (with subgenera *Scalpellum s.s.* and *Arcoscalpellum* (=*Holoscalpellum*), the latter including the "sections" *Mesoscalpellum* and *Neoscalpellum*). *Arcoscalpellum* and *Mesoscalpellum* (=*Neoscalpellum*) have subsequently been recognized as genera. These six genera are based on the armature of the females or hermaphrodites and to some extent that of the males.

PILSBRY (1916) confirmed revision of the Thoracica, and expanded and modernized the classification of DARWIN's Balanidae. His major contributions include separation of the Chelonibiinae ("turtle" barnacles) and the Coronulinae ("whale" barnacles) as distinct subfamilies apart from the Balaninae; the creation of a number of subgenera in the genus *Balanus* following the basic work of HOEK (1913); the designation of type species for genera and subgenera; and the recognition of two distinct morphological groups in the genus *Chthamalus*. PILSBRY's (1916) classification of the Thoracica recognized 1) suborder Turrilepadomorpha (=Machaeridia, WITHERS, 1926), Lepidocoleidae, Turrilepadidae; 2) suborder Lepadomorpha, Loriculidae (=Stramentidae), Brachylepadidae, Scalpellidae, Lepadidae; 3) suborder Verrucomorpha, Verrucidae; 4) suborder Balanomorpha, Balanidae, (Balaninae, Chelonibiinae, Coronulinae), Chthamalidae.

The suborder Turrilepadomorpha was renamed Machaeridia by WITHERS (1926) and removed by him from the Cirripedia. WITHERS concluded from crystal structure of the plates that the machaeridians were probably allied to the echinoderms. This conclusion was in part substantiated by POPE (1962) who recognized that the Lepidocoleidae represent cover plates of the brachial spines in echinoderm "Carpoidea." It can be assumed reasonably that the Turrilepadidae are of similar origin. WITHERS (1923) also removed the family Brachylepadidae from the Lepadomorpha and created a separate suborder Brachylepadomorpha for this group.

The diversity of opinion regarding classification of the Lepadomorpha is exhibited in the following two examples. In 1909 ANNANDALE divided what is now recognized as the Lepadomorpha into three families: Pollicipedidae, including *Pollicipes, Scalpellum,* and *Lithotrya;* Iblidae, with the genus *Ibla;* and Lepadidae. The Lepadidae were divided into four subfamilies: Oxynaspidinae, with *Oxynaspis;* Lepadinae, including *Lepas, Conchoderma,* and *Heteralepas;* Poecilasmatinae including *Poecilasma, Dichelaspis* (=*Octolasmis*), and *Megalasma;* and Alepadinae, including *Alepas s.s., Chaetolepas* (=*Ibla*), *Microlepas, Anelasma,* and *Koleolepas.* Later ANNANDALE (1910, 1916) distinguished two subgenera in *Scalpellum: Smilium* and *Scalpellum s.s.*

NILSSON-CANTELL (1921) divided the Lepadomorpha into the families Scalpellidae, including *Pollicipes, Scalpellum* (with groups *Calantica, Smilium, Euscalpellum, Scalpellum*), and *Lithotrya;* Iblidae containing only *Ibla;* Oxynaspididae with *Oxynaspis;* Lepadidae, including *Lepas, Conchoderma,* and *Alepas;* Heteralepadidae, containing *Heteralepas* (with the subgenera *Heteralepas s.s.,* and *Paralepas*); and Poecilasmatidae, including *Poecilasma* (with the subgenera *Poecilasma s.s., Glyptelasma,* and *Temnaspis*), and *Octolasmis.*

The generally acceptable features of this classification were incorporated by Withers (1953), and with some additions and emendations, his classification has been adopted for the *Treatise,* as given in the following outline.

Order APODA Darwin, 1854

Proteolepas bivincta, a curious parasitic crustacean, was found in the mantle cavity of a pedunculate barnacle, *Heteralepas cornuta* (Darwin) from the West Indies. On the basis of a single specimen, Darwin (1854) developed an analysis that led him to believe the form was a member of the Cirripedia, for which he established the order Apoda. No specimens attributed to *Proteolepas* have been found subsequently.

The interpretation, that *Proteolepas* is a cirriped, was based primarily on the marked similarity between the pair of appendages by which it attached to the host and the first antennae of ordinary cirripeds. However, in order to consider these appendages homologous with the first antennae of cirripeds requires that they should have migrated backward on the body as many as five segments. Peculiarities in the pair of biting mouth parts, as compared to the cirriped mandible, led Darwin to speculate on their formation. He concluded that the relatively complex structure had resulted from fusion of the mandibles with the first and possibly the second maxillae, and had rotated through 180°. At the present level of our knowledge, both of these interpretations seem highly unlikely. The appendages of attachment could be first or second maxillae, rather than first antennae, and thus the parasite could be interpreted as a copepod. On the other hand, if the mouth parts were interpreted as malacostracan mandibles, as they appear, then the parasite might be an epicaridean. Therefore, until new material is discovered, the affinities of *Proteolepas* remain conjectural.

Certain larvae were attributed to the Apoda by Hansen (1899). Termed Y-larvae by him, they were subsequently found by other workers (Steuer, 1904; McMurrich, 1917). The assignment of Y-larvae to the Apoda was by process of elimination, since they resembled the larvae of no cirriped known at the time. On the basis of present knowledge, it seems equally possible that Y-larvae, provided they are cirripeds, belong to ascothoracicans, because of the absence of frontolateral horns. However, some of them have compound eyes, which, while found in late naupliar and cyprid stages of other cirripeds and in the Branchiura, are unknown in larvae of Ascothoracica. Therefore the affinities of the Y-larvae with the Apoda, with other cirriped groups, or with other crustaceans remain doubtful.

Classification of Class Cirripedia

Order Acrothoracica
Suborder Pygophora: Lithoglyptidae, Cryptophialidae (Rodgerellidae, Zapfellidae provisional).
Suborder Apygophora: Trypetesidae
Order Rhizocephala
Suborder Kentrogonida: Peltogastridae, Sacculinidae, Lernaeodiscidae, Clistosaccidae, Sylonidae.
Suborder Akentrogonida
Order Ascothoracica: Synagogidae, Lauridae, Petrarcidae, Dendrogastridae
Order Thoracica
Suborder Lepadomorpha: Cyprilepadidae, Praelepadidae, Scalpellidae, Heteralepadidae, Iblidae, Koleolepadidae, Lepadidae, Malacolepadidae, Oxynaspididae, Poecilasmatidae, Stramentidae, Family uncertain
Suborder Verrucomorpha: Verrucidae
Suborder Brachylepadomorpha: Brachylepadidae
Suborder Balanomorpha: Chthamalidae, Balanidae (Balaninae, Tetraclitinae, Chelonibiinae, Coronulinae, Emersoniinae)
Order Apoda

FOSSIL TRACES

Of the four orders of Cirripedia, only the Thoracica is represented by actual fossil remains. No fossil evidence has been found for the purely parasitic Rhizocephala. The remaining two orders (Acrothoracica, Ascothoracica) have been identified by the traces left in the substrates they inhabited.

The characteristics of fossil acrothoracican burrows were summarized by TOMLINSON (1963) from whose table the following list of species was obtained.

Acrothoracican Fossil Burrows

Family ZAPFELLIDAE

Zapfella pattei SAINT-SEINE, 1954, Mio.-Plio., in large gastropods, few pelecypods, calcareous marls.

Simonizapfes elongata CODEZ, 1957, Trias.-Jur., in belemnites, pelecypods, crinoids, gastropods, etc.

Brachyzapfes elliptica CODEZ, in belemnites, pelecypods. TAYLOR (1965) has described burrows identified as *B. elliptica gigantea* (new), from Antarctic (Aptian) belemnite rostra.

Family RODGERELLIDAE

Rodgerella lecointrei SAINT-SEINE, 1951, Cret., in echinoids.

Rodgerella mathieui SAINT-SEINE, 1955, M.Jur.-Cret., L.Mio.-Plio., in echinoids, pelecypods, belemnites, corals.

Rodgerella cragini SCHLAUDT & YOUNG, 1960, Cret.(Alb.), in *Ceritella proctori* (gastropod).

Family TRYPETESIDAE

Trypetesa caveata TOMLINSON, 1963, Penn.-L. Perm., in myalinid pelecypods. Unnamed species, in JOYSEY, 1959, Cret., in *Echinocorys* (echinoid).

Unidentified acrothoracican burrows were also described by SCHLAUDT and YOUNG (1960) and later by RODDA and FISHER (1962) from the Pennsylvanian and Permian of Texas in myalinid pelecypods, brachiopods, crinoids, rugose corals, and bryozoans, and by ROSS (1965) from the Miocene of Florida in the bryozoan *Holoporella*.

The Ascothoracica were apparently represented in the Cretaceous. Fossil traces, in the form of cysts in the octocoral *Moltkia minuta,* from the Maastrichtian, have been identified and named *Endosacculus moltkiae,* by VOIGT (1959). Furthermore, holes comparable to those made by the ascothoracican *Ulophysema* in the test of certain extant sea urchins, have been discovered in the Upper Cretaceous (Turon.-Maastricht.) in an extinct irregular urchin, *Echinocorys* by MADSEN & WOLFF (1965). Therefore, not only does it appear that Ascothoracica were present in the Cretaceous, but some members were already highly specialized endoparasites before the close of the Mesozoic.

STRATIGRAPHIC DISTRIBUTION

Fossil cirripeds have a total known range from Upper Silurian to Recent, Paleozoic forms being represented by thoracicans, except for a genus of acrothoracicans *(Trypetesa)* identified from borings in bivalve shells (Penn.-Perm. myalinids). Also, discovered Mesozoic and Cenozoic cirripeds belong almost entirely to the Thoracica.

The stratigraphic distribution of Cirripedia found preserved as fossils is indicated graphically in the accompanying Tables 2 and 3.

PHYLOGENY

ORIGIN OF CIRRIPEDS

Within the Crustacea, the Cirripedia have their closest affinities with the Maxillopoda. The Maxillopoda are typified by a fundamental five-six-five body plan, in contrast, for example, to the Malacostraca with a fundamental five-eight-seven plan. The divisions include a head with five pairs of appendages, a thorax of six appendage bearing segments, and a five-segmented abdomen which includes a telson with furca (Table 1). The abdominal somites are without appendages, except for the furca and the male reproductive structure on the first somite which may represent modified limbs. The Maxillopoda include, either by definition or by inference, the Copepoda, Branchiura, and Mystacocarida, as well as the Cirripedia. The Ostracoda, although highly reduced segmentally, could have been derived from a basic five-six-five plan, and are generally considered closer to the Maxillopoda than to other groups.

Among the Cirripedia, only the Ascothoracica have a complete five-six-five plan (Fig. 82,2). The abdomen is absent in adult Acrothoracica and Thoracica, but is represented by at least three segments in the cyprid larvae of these orders (Fig. 82,*3*). The Cirripedia seem to have their closest affinities with the Copepoda and Branchiura. Before the life cycle of the harpacticoid copepod *Longipedia* was known, its nauplius larvae were thought to be those of a cirriped. The carapace and cirrus-like thoracic appendages of Branchiura are comparable to those of cirripeds, and detailed similarities between larval cirriped and branchiuran compound eyes further indicate a relationship between the two groups. Thus it can be inferred that the stemline of the Cirripedia is closer to the copepod-branchiuran line of the Maxillopoda than to any other crustacean group (Tables 1, 3).

The ascothoracican grade of construction is the most generalized body plan found in cirripeds, despite the secondary parasitic nature of the group. This body plan is not readily detected in other cirriped groups, but is clearly defined in their cyprid larvae. Therefore, it appears that cirripeds stem from free-living Maxillipoda that had a bivalved carapace, compound eyes, prehensile first antennae, generalized copepod-like mouth parts, natatory thoracic appendages, and an abdomen with telson and furca. Such a form would differ from other Maxillopoda in having female genital apertures on the first thoracic somite, and male genital apertures on the first abdominal somite. The majority of cirripeds are hermaphroditic. However, it may be possible that some species among the Thoracica, having either separate sexes or hermaphrodites accompanied by complemental males, have arrived at this condition through reversion from a purely hermaphroditic condition. It can be inferred that fundamentally the sexes were separate, as separate sexes are found in all cirriped orders, as in the Maxillopoda in general.

The hypothetical ancestral cirriped stock would have resembled extant Ascothoracica in many details, including a basic nonsetose omnivorous feeding mechanism in which only the mouth parts were involved. Such an organism would be suited to an epibenthic existence, but the prehensile first antennae, so fundamental to cirripeds, suggest an epizootic habit, probably on arborescent forms of life (Fig. 110,*A*).

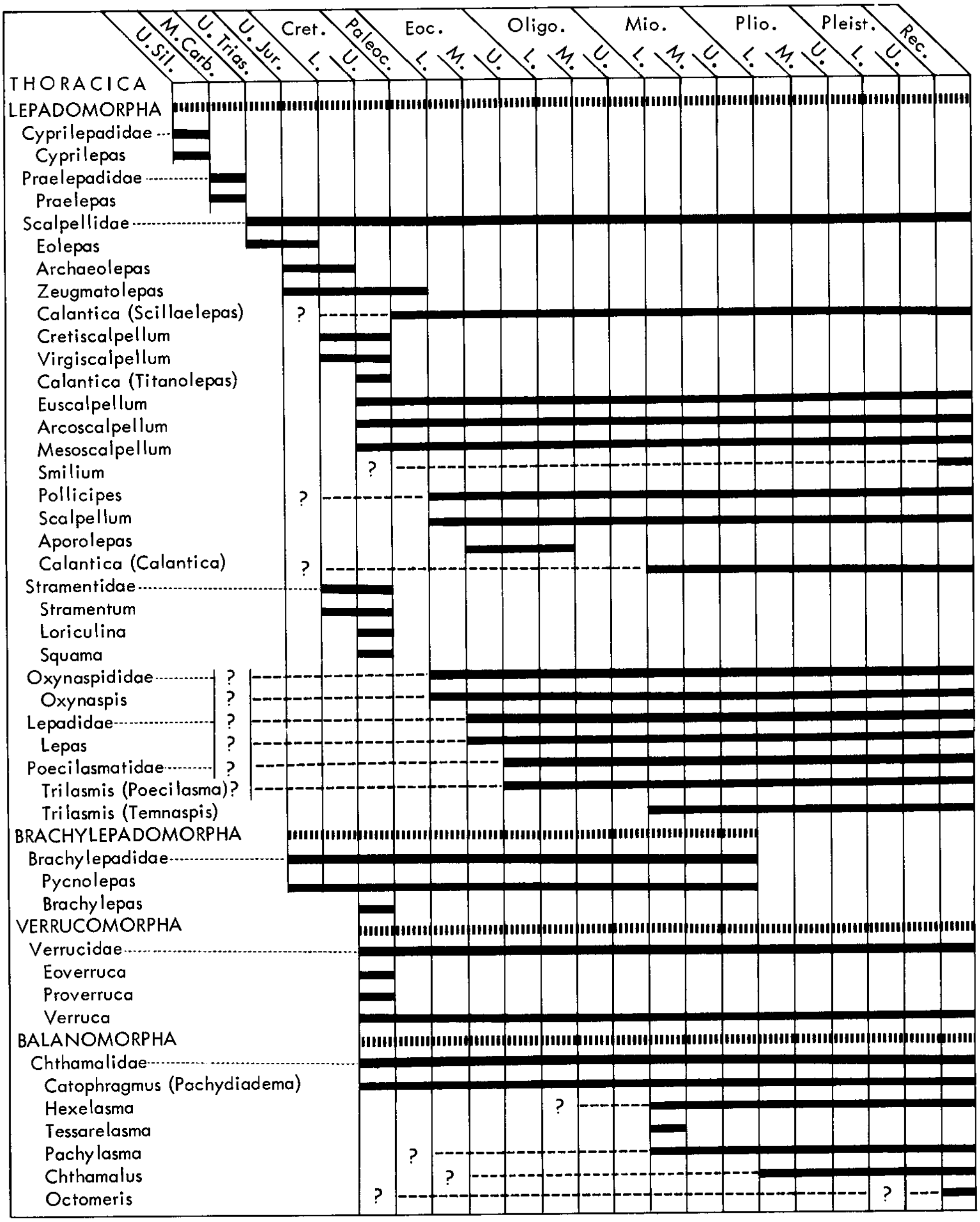
ORIGIN OF CIRRIPED ORDERS

The ancestral cirriped would have given rise directly to the Ascothoracica with little modification. The early separation of Ascothoracica from other Cirripedia is exemplified by the generalized form, lack of setose feeding mechanism, complete loss of compound eyes in all stages of the life cycle, and the absence of frontolateral horns in the nauplii.

Two fundamental developments are necessary for transition from the hypothetical cirriped to the level of organization seen in Thoracica and Acrothoracica. The first is acquisition of a setose feeding mechanism, and the second is development of cement glands in connection with the prehensile first antennae. Beyond these basic advances relatively few and simple modifications are necessary to arrive at the highest forms among the cirripeds. Acquisition of a setose feeding mechanism by a generalized omnivore probably developed through modification of a grooming or cleaning behavior, in which the natatory appendages were drawn over the mouth parts to remove particles of detritus adhering to the setae. Sufficient nutrients must have been obtained in this way to place a selective advantage on forms having thoracic appendages with setae that required frequent cleaning. The more food was collected in this manner, the less the necessity of foraging, thus allowing for a more sedentary existence. Once freed of foraging, it is possible for an organism to become cemented in place, if ecological factors such as substratum and predation permit.

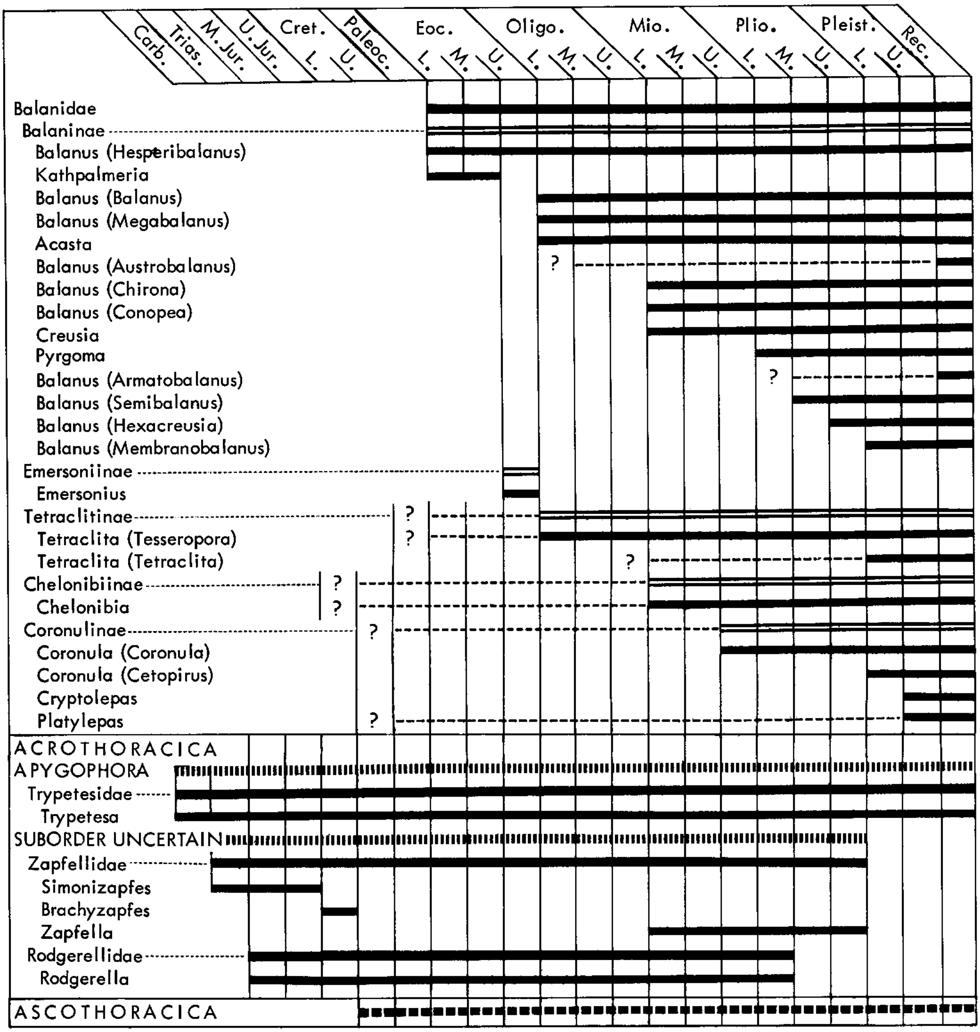
It follows, therefore, that the Thoracica and Acrothoracica could have evolved from a stock at the ascothoracican grade of construction (Fig. 110, Table 3). The inferences utilized, however, rest entirely on knowledge of extant cirripeds. Nothing has been recognized in the fossil record that sheds light on the subject. This is not surprising, because most Maxillopoda are small and lack a heavily calcified exoskeleton. Therefore, the probability of being preserved is low, and of being detected, even lower. It is not until the cirripeds gained a well-calcified exoskeleton that their fossil history becomes well documented.

TABLE 2. *Stratigraphic Distribution of Genus-group Taxa with Fossil Records.*



The earliest and perhaps most remarkable fossil attributed to the Cirripedia is *Cyprilepas* WILLS, found attached to the appendages of Upper Silurian eurypterids (Fig. 111,*1*). *Cyprilepas* is clearly divided into peduncle and capitulum, and, therefore, is already a thoracican at the lepadomorph grade of construction. With one exception it differs from all known Lepadomorpha in having a bivalved carapace. The extant *Trilasmis eburneum* HINDS also has a bivalved shell, but as shown by DARWIN

Table 2. *(Continued).*



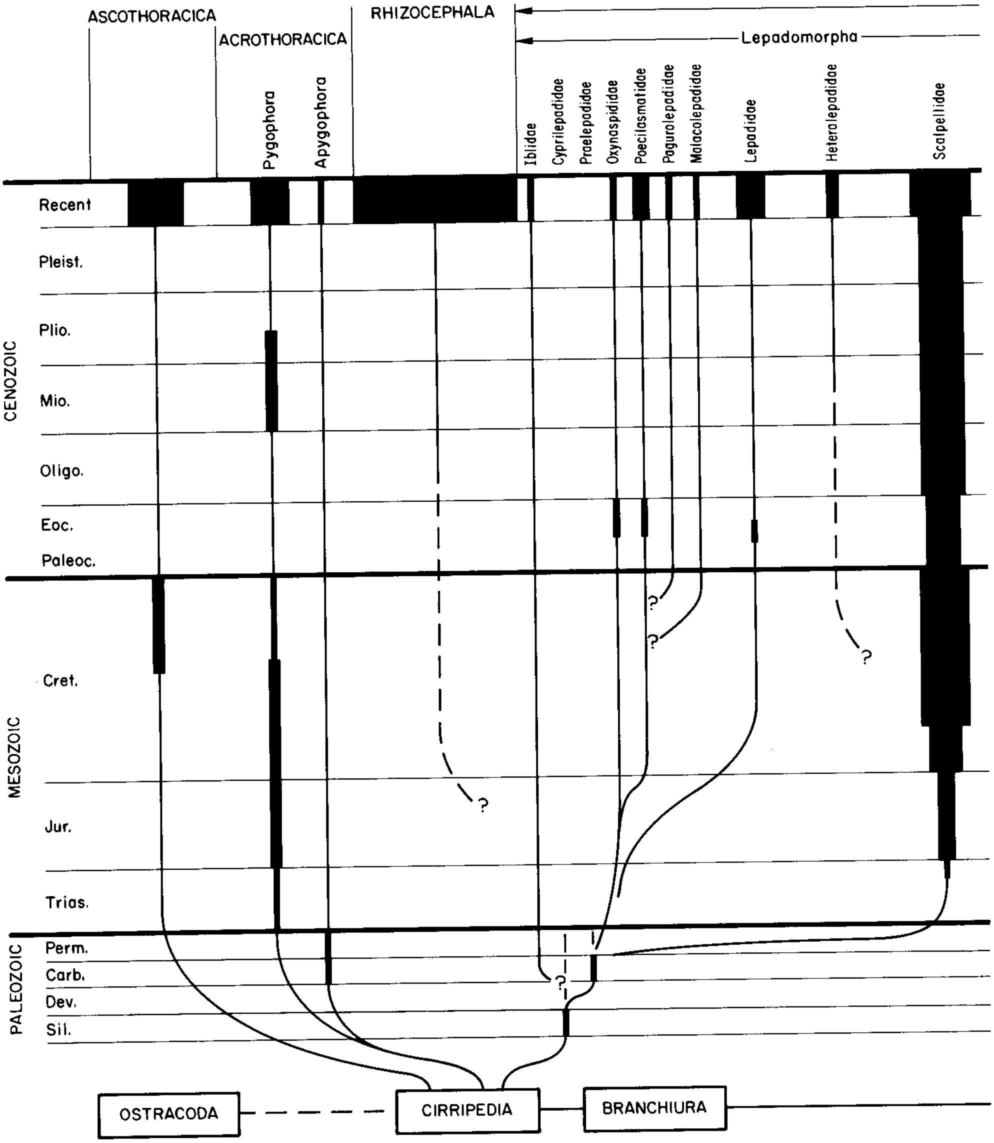
Explanation: Known ranges, solid bar; inferred ranges, broken bar (Zullo, n).

(1851), this condition is the result of secondary reduction (see Fig. 116,9). On the other hand, the bivalved condition seen in *Cyprilepas* probably represents the level of organization attained by cirripeds in the early Paleozoic, and is homologous with the bivalved carapace of Ascothoracica and cyprid larvae of other orders.

Cyprilepas may differ from known Lepadomorpha in an even more fundamental way. The absence of growth lines on the carapace suggests that the entire exoskeleton was shed at each molt, rather than only the exoskeleton lining the mantle cavity and clothing the body and appendages. This is the manner of growth in Acrothoracica, Ascothoracica, and most crustaceans, and could be expected in the stock leading to Thoracica.

In size and grosser form, *Cyprilepas* fits the concept of the ancestral thoracican. However, nothing is known of the body

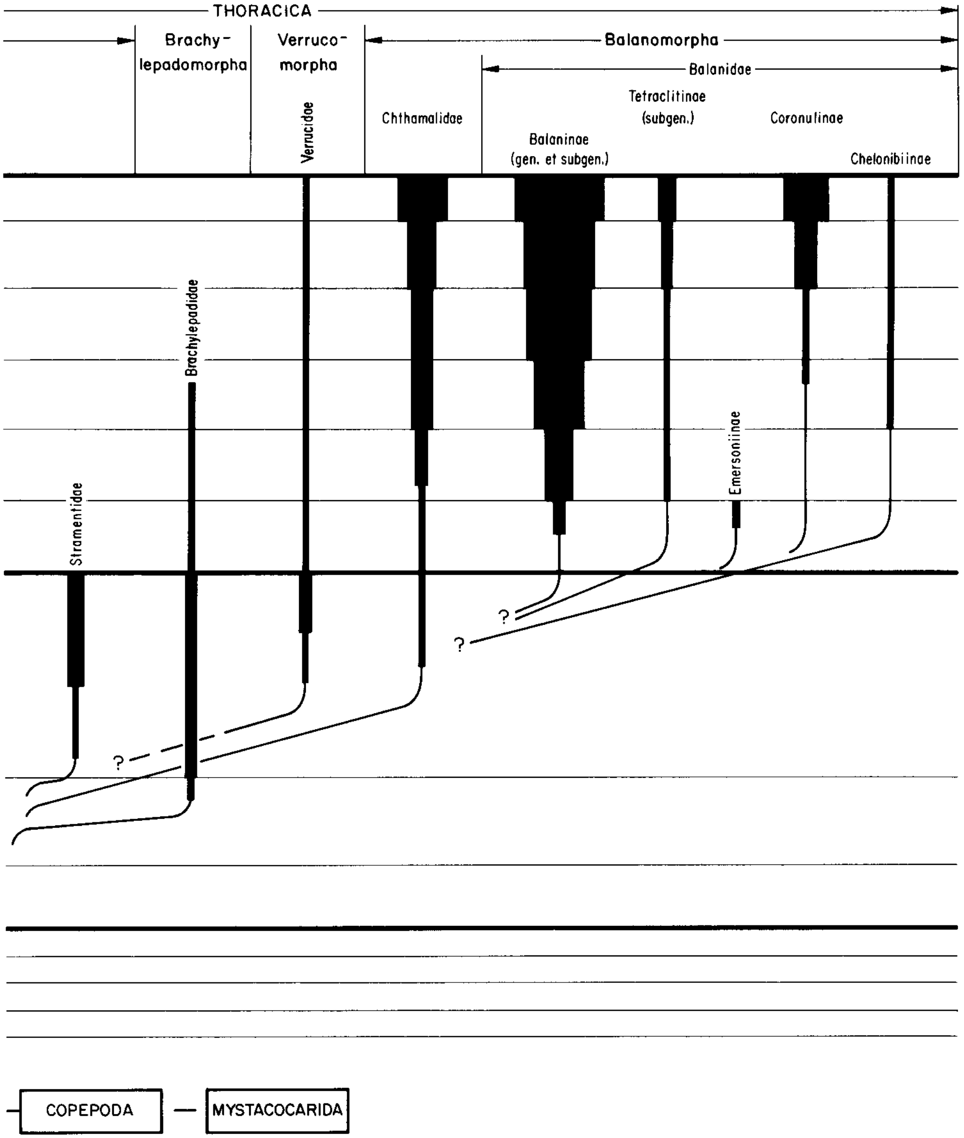
TABLE 3. *Stratigraphic Distribution and Inferred Phylogeny of Cirriped Orders and Families (Newman, n).*



and appendages, and such information would be desirable in assessing its significance in cirriped evolution. From present knowledge, the *Cyprilepas* grade of construction can be considered the basis from which the array of forms seen in the Lepadomorpha, Verrucomorpha, Brachylepadomorpha, and Balanomorpha have evolved.

It has not been resolved whether the Acrothoracica are descended from the ancestral stock of the Thoracica, or from Thoracica themselves. No fossil acrothoracicans are known, although their characteristic burrows have been recognized in carbonate substrata from as early as Late Carboniferous. The ability to burrow is a specialization acquired after the develop-

TABLE 3. *(Continued).*



ment of a setose feeding mechanism and attached mode of life. Unlike Thoracica, with the possible exception of *Cyprilepas,* Acrothoracica molt the exterior as well as the interior lining of the carapace, along with the lining of the body and appendages. Burrowing is accomplished, at least initially, by chitinous hooks and spines covering the exterior of the carapace, and these, too, are replaced at each molt. The cyprid larva attaches itself by the first antennae, with the ventral surface of the shell applied to the substratum. The metamorphosing barnacle, covered by the cyprid shell, begins

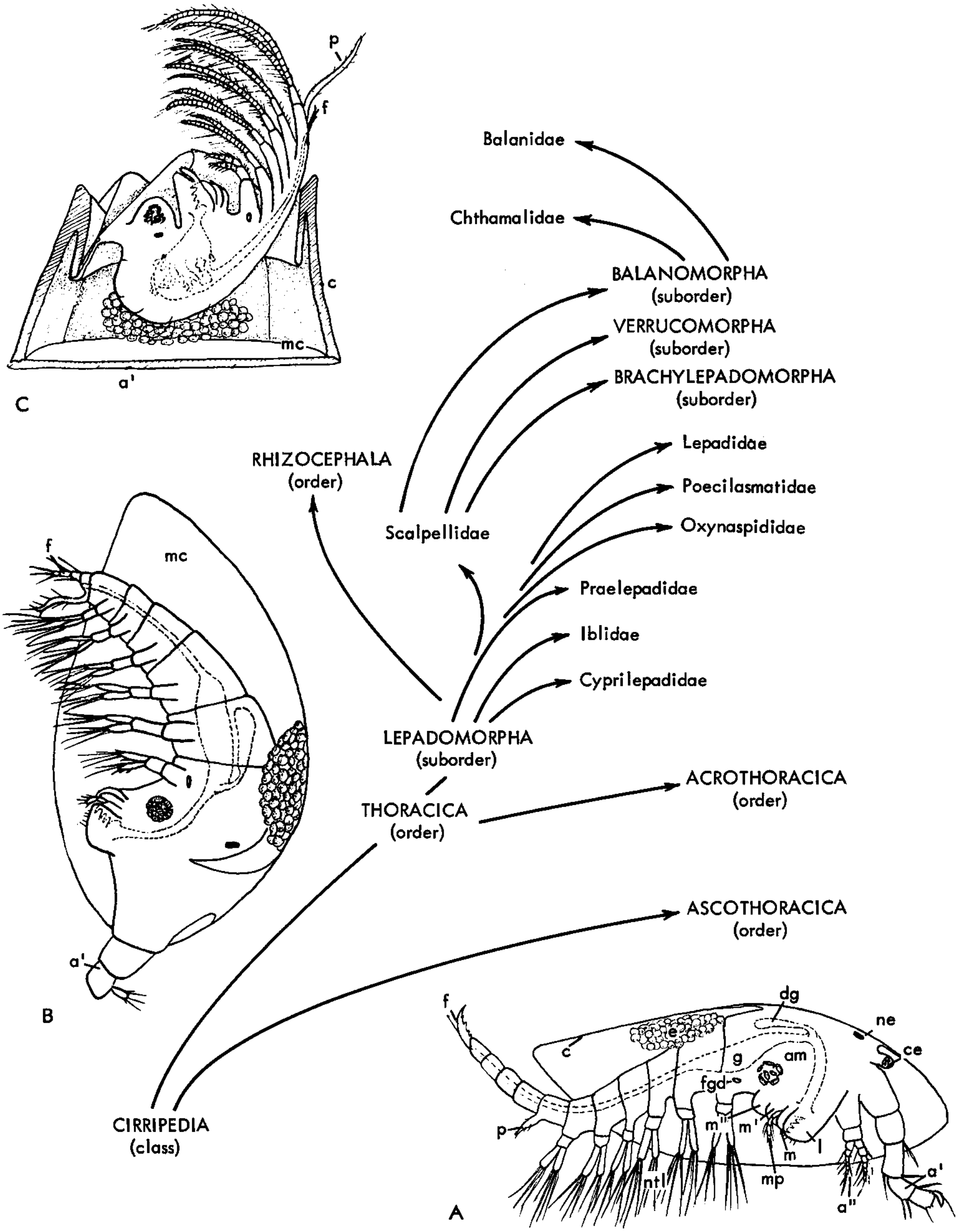


FIG. 110. Evolution of Cirripedia (Newman, n).

A. The ascothoracicans share a 5-6-5 body plan with the Maxillopoda. A generalized ancestral stock having prehensile first antennae and bivalved carapace and differing from Acosthoracica only in having compound eyes and generalized rather than piercing mouth parts, is hypothesized. Such a stock, sharing characters of the Copepoda, Branchiura and Ascothoracica, woud be typified by the form illustrated at the lower right.

B. Transition from the ascothoracican to thoracican level of organization would include acquisition of setose feeding, concomitant with more or less permanent attachment by means of first antennae.

C. From this level remaining cirripeds evolved, the to burrow mechanically into the substratum by chipping away flakes of carbonate with the carapace spines (BATHAM & TOMLINSON, 1965). If these barnacles did not burrow, but merely remained attached to the substratum, they probably would be included in Thoracica, rather than in a separate order. Since burrowing is a secondary adaptation in the cirriped facies, and in consideration of the geological record of the order, it seems likely that the Acrothoracica descended from lepadomorphan ancestors at a level of organization comparable to that found in *Cyprilepas*. Whereas most Lepadomorpha have developed an external calcareous armament, the Acrothoracica rely on the substratum for protection.

The origin of the Rhizocephala is presently unknown. Members of the order are exclusively parasitic. It might seem that the Rhizocephala are most closely allied to the parasitic Ascothoracica in which the feeding mechanism involves only the mouth parts. However, the rhizocephalan nauplius larva bears frontolateral horns, and although the functional significance of these horns is unknown, their presence demonstrates a closer affinity of the Rhizocephala with Thoracica and Acrothoracica than with Ascothoracica. Furthermore, while the cyprid larva of these three orders cement themselves in place, the cyprid of the Ascothoracica does not.

While Acrothoracica show no tendency towards parasitism, grades of parasitic development are found in Thoracica that suggest the direction evolution must have taken in development of rhizocephalan organization. *Rhizolepas* DAY, parasitic on a polychaete annelid, and *Anelasma* DARWIN, parasitic on sharks, are lepadomorphs, which, although retaining vestigial limbs, have given up setose feeding in favor of development of a system of processes which invade and draw nutrients from the host tissues. The gut is complete in *Anelasma*, but mouth parts are vestigial (Fig. 112,*2-3*). The gut in *Rhizolepas* closes blindly at both ends and mouth parts are apparently lacking. Forms such as these give us definite clues to rhizocephalan evolution.

FIG. 111. Silurian cirriped, interpreted as possible and most generalized ancestral thoracican, *Cyprilepas holmi* WILLS; *1a*, large specimen, viewed from left side, peduncle somewhat wrinkled and bilateral valves of carapace forming capitulum displaced, thickening along carinal and basal margin of carapace evident; occludent margins forming aperture of carapace visible; *1b*, small, less distorted specimen, viewed from same side, revealing same characteristics, ×11 *(112)*.

Rhizocephala are generally considered to pass through an endoparasitic phase before the appearance of the external reproductive structures. However, the recently discovered *Chthamalophilus* BOCQUET-VÉDRINE (1961), although a rhizocephalan by most criteria, does not develop a kentrogen, and has an entirely ectoparasitic life cycle (Fig. 112,*1*). Thus it would

FIG. 110. *(Continued from facing page.)*

highest level of organization being attained in the Balanomorpha, as discussed in text.

[Explanation: *a'*, first antennae; *a''*, second antennae; *am*, adductor muscle; *c*, carapace; *ce*, compound eye; *dg*, digestive gland; *e*, egg mass; *f*, furca; *fgd*, female genital duct; *g*, gut; *l*, labrum; *m*, mandible; *m'*, first maxilla; *m''*, second maxilla; *mc*, mantle cavity; *mp*, mandibular palp; *ne*, naupliar eye; *ntl*, natatory thoracic limbs; *p*, penis.]

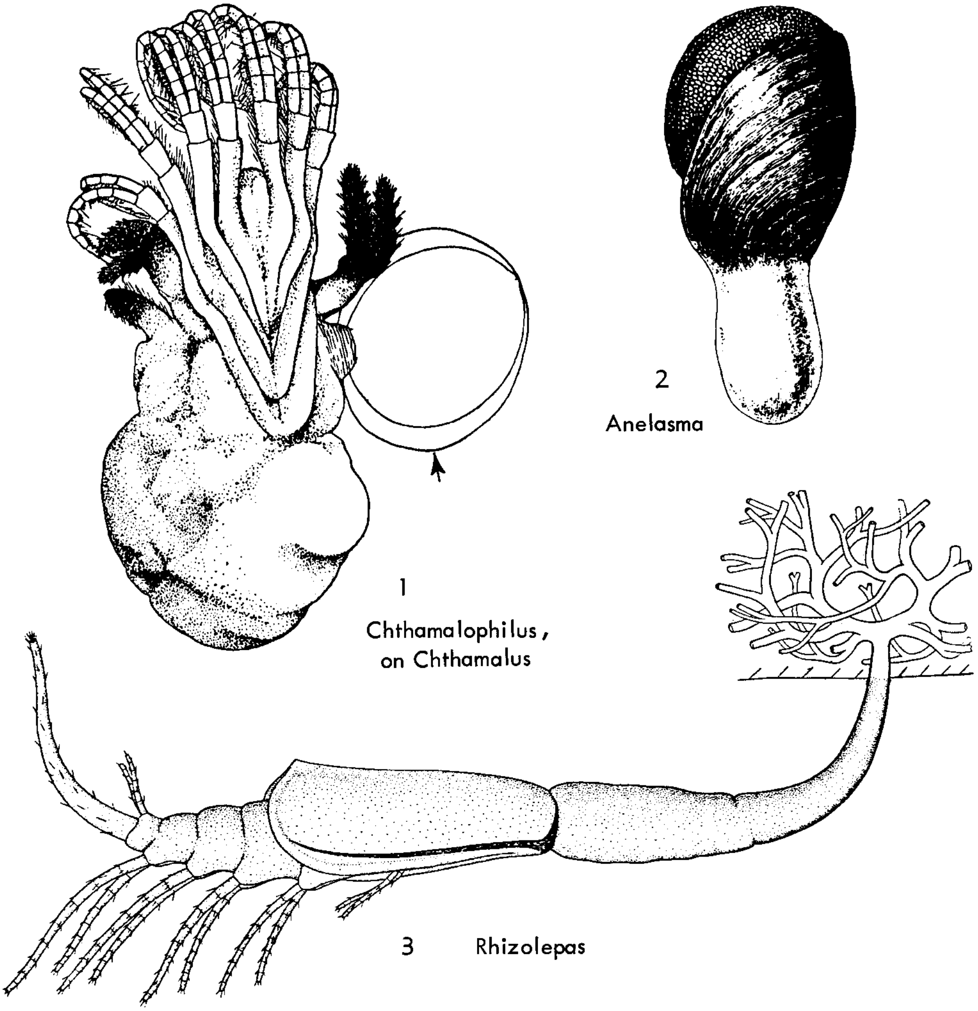


FIG. 112. Parasitic adaptations of cirripeds:——*1*. Akentrogonid rhizocephalan on a barnacle (after *13*). ——*2*. Lepadid parasitic on certain sharks (peduncular nutritive processes not illustrated) (after Darwin, 1851, 37).——*3*. Lepadomorph parasitic on a polychaetous annelid (after Day, 1939).

appear that *Chthamalophilus* represents a level of organization intermediate between the rhizocephaloid lepadomorph parasite and the endoparasitic Rhizocephala.

In summary, it appears that the Cirripedia evolved along two major lines, one giving rise to the basically free-living Ascothoracica and the other to the permanently attached Acrothoracica, Thoracica, and Rhizocephala. These two lineages stemmed from a common maxillopodan ancestral stock related to the progenitors of the Copepoda and Branchiura. This stock was similar in general organization to the Ascothoracica, but differed mainly in possessing compound eyes of branchiuran type. Setose feeding and the development of cement glands in conjunction with the prehensile first antennae led to a lepadomorphan level of organization, probably comparable to that seen in the fossil *Cyprilepas*. This level of organization differs from that seen in other fossil and living Lepadomorpha in the periodic molting, rather than retention of the carapace exterior. At this point, one group, leading to Acrothoracica, gained the ability to burrow mechanically into calcareous substrata, whereas another, leading to Thoracica, developed the ability to retain exterior portions of the carapace while molting the remaining exoskeleton, thus forming a tough exterior shell that provided protection during all periods of the molt cycle. This step apparently preceded the development of the typical thoracican shell laid down in successive layers. Subsequent lines of Lepadomorpha developed sessile forms, such as the extinct Brachylepadomorpha, the Verrucomorpha, and the Balanomorpha. It appears further that the trend towards parasitism seen in certain Lepadomorpha led to the evolution of the Rhizocephala.

THORACICA

LEPADOMORPHA

The Lepadomorpha can be distinguished from other suborders by the presence of a peduncle representing a prolongation of the anterior part of the cephalic region, and a capitulum supporting two or more plates derived from the carapace. The suborder includes ten families, three of which are extinct. The oldest, Cyprilepadidae, appears only in the Silurian. There are 38 recognized lepadomorph genera, of which only two occur in the Paleozoic. One Recent genus, *Arcoscalpellum,* ranges back to the Lower Cretaceous. The two principal families are named Scalpellidae and Lepadidae and it is with these and their relationship to less well known groups that the following discussion is mostly concerned.

The origin of the Lepadomorpha has been considered in the preceding section. Within the suborder, the Scalpellidae are generally interpreted to be more primitive than the Lepadidae (Darwin, 1851; Hoek, 1883; Gruvel, 1905; Pilsbry, 1907; Annandale, 1910; Krüger, 1920; Nilsson-Cantell, 1921; Withers, 1928-53). In fact, the original scheme proposed by Darwin in 1851 has been little modified in its essentials since it was proposed. He envisaged a *Pollicipes*-like stem form giving rise to *Pollicipes, Lithotrya,* and the Balanomorpha, on one hand, and to the Lepadidae, through *Scalpellum* and *Oxynaspis,* on the other. Following this view, the ancestral stock would have been already highly derived, having a capitulum and peduncle well armored with numerous calcareous plates. For the capitulum there would have been six plates—paired terga and scuta associated with carina and rostrum—all with apical umbones, and for the peduncle, numerous unspecialized calcareous plates or scales. Subsequent evolution would then involve the addition of peduncular plates to the basal area of the capitulum. In one line these would form basal whorls of imbricate plates, some of which would become latera, as seen in *Pollicipes,* and these would ultimately be utilized in the formation of the balanomorph wall. In another, some of the latera become incorporated into the capitulum in the manner seen in *Scalpellum.* Concomitant with this, umbones of certain plates, in particular the carina and scuta, shift from apical to subcentral, because, while previously the body had been contained within a mantle cavity formed by both the peduncle and the capitulum, the body has come to lie more within the capitulum alone. With this change, the armament of the peduncle and the basal portion of the capitulum becomes reduced, and this eventually results in a five-plated *Oxynaspis*-like form, which in turn leads to the other five-plated Lepadomorpha. In this conception, the six-plated scalpellids are primitive.

Fossil Mesozoic scalpellids, particularly *Eolepas* and *Archaeolepas,* discovered after the time of Darwin, support the view that the six-plated facies was basic to the archetype thoracican, as Withers (1928-53) further advocated. However, Broch (1922), while admitting the great age of the six-plated Scalpellidae, did not concede that this meant they were necessarily archetypes. He pointed out that the really primitive thoracicans probably lacked plates impregnated with carbonate, and therefore would be unlikely subjects for fossilization. Furthermore, Broch looked to ontogenetic evidence suggesting that a five-plated condition is actually as fundamental to the Scalpellidae as to the Lepadidae, and accordingly judged that both groups must have descended from a common five-plated stock. This would place the Lepadidae as primitive as the Scalpellidae, if not more so, quite the reverse of what other authors had thought. These two fundamentally different points of view have not been reconciled, but we offer an argument here which is more in keeping with that of Broch.

Withers (1928-53) assumed the primitive capitular valve complement to be six, paired terga and scuta plus carina and rostrum, as exhibited by the oldest known Triassic and Jurassic scalpellids, *Eolepas* and *Archaeolepas*. Broch (1922), on the other hand, considered the complement of primitive capitular plates to be five, the same as in scalpellids minus the rostrum, as seen in the ontogeny of extant members of both families where five chitinous primordial plates appear before calcification begins. The development of the rostral plate has never been observed to be anticipated by a chitinous primordium. At the time, Broch's arguments were weakened by the relative scarcity of paleontological evidence, and Withers' argument by giving little weight to the ontogenetic evidence. Withers also minimized the importance of the only Paleozoic thoracican known at the time, *Praelepas,* described by Chernyshev in 1930, from the Upper Carboniferous. This genus not only had chitinous rather than calcareous capitular plates, a condition thought probable by both authors on theoretical grounds, but it also had only five plates (rostrum lacking), a fact that adds much support to Broch's hypothesis.

Withers rejected *Praelepas* as an important form in thoracican evolution not only because it lacked the sixth capitular plate, but because the umbo of the scutum was central rather than apical. Since Mesozoic forms, *Eolepas* and others had apical umbones on all plates, this condition was taken as primitive and the idea rigorously adhered to. Thus he was compelled to regard the Carboniferous *Praelepas* as an early specialization ancestral to neither the Mesozoic scalpellids nor the Cenozoic lepadids.

We think, however, that *Praelepas* should not be so readily dismissed as an early specialization. Broch (1922) has stressed the generality and uniformity of five rather than six principal primordial plates in the development of both the Scalpellidae and Lepadidae, and this cannot be lightly put aside. Even where as many as 11 primordia are known during development (*Scalpellum balanoides* Hoek, cf. Broch, 1931), the rostrum appears without one. At the present level of our knowledge it seems inescapable that there are five fundamental capitular plates in both the Scalpellidae and Lepadidae, and that any larger number is secondarily derived. The rostrum, so fundamental to the Scalpellidae, never has a primordial plate and is therefore very much secondary. These facts must be considered as such in our thinking on the evolution of the Lepadomorpha, even though at present they do not clarify the phylogenetic history of the group.

The next problem relates to position of the umbo. In the Scalpellidae all the umbones appear to be fundamentally apical, whereas those of the carina and scuta in the Lepadidae seem to be fundamentally basal. Following Withers, the apical position would be primitive, whereas other conditions were derived. The apical condition seen in the earliest known scalpellid, *Eolepas* of the Triassic and Jurassic, carries through in Recent *Pollicipes* and its allies, but this line, while old as far as fossil evidence is concerned, appears well advanced. In particular, the rostrum is very large, the apical portion having grown free of the capitulum, and the plates in general overlap, a specialized condition in itself. *Eolepas* and its allies, including *Archaeolepas, Zeugmatolepas, Pycnolepas,* and others, are clearly already well separated from the stem line of the Lepadomorpha.

Apical umbones and more or less overlapping plates seem to be general features in other Mesozoic scalpellids. A notable exception, however, is seen in *Virgiscalpellum,* from the Lower and Upper Cretaceous. Not only do the plates lack overlap, but the umbones of the scuta and carina are central rather than apical, and the rostrum is minute. This is a very different facies from that presented by *Eolepas* and its allies, and one that, according to Withers' suggestion, anticipated the five-plated Eocene lepadid *Oxynaspis,* a form considered primitive to the Lepadidae. Although the primordium of the carina is generally subcentral or basal in adults of most oxynaspidid species, it was shown by TOTTON (1940) to move considerably during ontogeny from an apical position. This suggests that *Oxynaspis* is more primitive than the adult form had previously indicated. It should be mentioned also, that BROCH (1922) tended to dismiss the so-called primitive features seen in *Oxynaspis* because of its special way of life in association with antipatharians, and in one case a sponge. However, it seems just as reasonable that *Oxynaspis* has retained rather than evolved these features, just as *Chelonibia,* although specialized to life on turtles and large decapod crustaceans, has retained a very primitive feature (separate rostrum) seen in no other balanid. It happens that these characters, specifically the central scutal umbo and apical carinal umbo, as well as simply five plates, the characters that lead us to believe *Oxynaspis* is primitive, are the characters it shares with the oldest known five-plated thoracican, *Praelepas* from the Carboniferous. In fact, if *Praelepas* existed today, and nothing of its internal anatomy indicated otherwise, it would be classified as an oxynaspidid.

Thus it seems that evidence based on the position of umbones is not alone valid in establishing primitiveness. Comparisons that have been made assume the lineage from Scalpellidae to Lepadidae (or "migration" of the umbo from an apical to basal position) to be established, whereas this is not the case. The definitive position of the umbo is related to allometric growth of the plate and therefore is interrelated with the overall form of the capitulum and the distribution and number of plates. The great antiquity of the five-plated *Praelepas,* and its possession of chitinous rather than calcareous plates, are strong points in favor of its consideration as a primitive, unmodified lepadomorph at the level of organization of the extant Oxynaspididae. *Praelepas* and the general lack of Paleozoic thoracicans suggests that calcareous plates did not evolve until the Mesozoic.

This general hypothesis is supported by the recent discovery of *Cyprilepas* in the Silurian, found living on eurypterids (WILLS, 1963). These minute (2.2 to 4.8 mm.) lepadomorphs consist of a chitinous bivalved capitulum and cylindrical peduncle, and somewhat resemble recently settled lepadomorph cyprid larvae. Although there is no indication that the capitulum bore calcareous plates, the microstructural patterns found on the plates of some specimens are suggestive of the hexagonal pattern apparently occurring in the cyprid shell of *Lepas* and in the primordial plates of the lepadomorphs in general. The presence of a peduncle with attachment disc, and the relatively large size of the biggest individuals, rule out the possibility that *Cyprilepas* is only a cyprid stage. It appears that there are actually two size classes and these could be interpreted either as growth stages or separate male and female individuals. *Cyprilepas* is very similar in size and form to certain of the Poecilasmatidae living on large decapod crustaceans.

Cyprilepas and *Praelepas* suggest a primitive lepadid facies. The relative primitiveness of extant Lepadidae is further demonstrated by the nervous system (CORNWALL, 1953). The nerve cord of *Lepas* is the most ladder-like of the known Thoracica, with greatest separation of the ganglia. In contrast, the Scalpellidae show progressive fusion of the cords and condensation of ganglia. In the Balanomorpha, which are without question phylogenetically most highly advanced, all cirral nerves stem from one large subesophageal ganglionic mass.

The cirral arrangement is no more specialized or generalized in the Scalpellidae than in the Lepadidae. In *Lepas, Alepas,* and *Scalpellum* only cirrus *I* is modified as a maxilliped, with the anterior ramus rotated posteriorly and attenuated, the articles of both rami somewhat protuberant. In *Conchoderma,* a close relative of *Lepas,* cirrus *I* is hardly modified, with nonrotated anterior ramus, and the cirri form a simple graded series. The simplest and perhaps most primitive arrangement is found in the Iblidae, where all cirri are structurally similar (cf. Fig. 101,*3-4;* 102,*1*).

In summary, available paleontological and neontological evidence indicates that the Lepadidae are more closely related to *Cyprilepas* and *Praelepas* stocks than are the Scalpellidae. It had been assumed by DARWIN and WITHERS that shell development exhibited by Scalpellidae is the more primitive method. However, the situation seen in *Cyprilepas* and *Praelepas* suggests that the lepadid type of shell development is probably the more primitive mode. Here the scutum or its equivalent is the principal capitular plate, covering most of the animal's body, as does the single bivalved shell of the Ascothoracica and the cyprid larva of cirripeds in general.

Withers (1928, 1935, 1953) has described in some detail the phylogeny of Mesozoic Scalpellidae for which there is a relatively continuous although fragmentary fossil record. Much less, however, is known of other lepadomorph families. The Lepadidae (Lepadinae) are known only from the Cenozoic by a few fossil representatives included in the genus *Lepas*. Withers (1953) proposed *L. (Dosima) fascicularis* as the most primitive of extant species, based on the more central position of the carinal umbo. However, he pointed out that this species is highly specialized for a pelagic existence. It is very thin-shelled, the peduncle produces a gas-filled float, and the entire animal is globular in form. Of other five-plated families, the Oxynaspididae are represented in the fossil record by one species from the middle Eocene of England, and the Poecilasmatidae are known by two scuta and a tergum from the English upper Eocene.

EVOLUTION OF SCALPELLIDAE

Withers postulated three trends in the evolution of the Scalpellidae, in regard to the capitular plates: 1) changes in number, 2) change in position of umbones as a result of differential growth, and 3) reduction in the extent of calcification.

1) Many-plated scalpellids of the genera *Calantica* and *Zeugmatolepas* occur with six-plated *Archaeolepas* and *Eolepas* in the late Middle and Upper Jurassic, suggesting an initial trend toward multiplication of the number of capitular plates. In the Cretaceous, *Scalpellum*-like forms are first found, suggesting a reversal in trend toward fewer plates, from 17 in *Cretiscalpellum* to 15 in extinct, or 14 or ?13 in extant species of *Arcoscalpellum*, and 14 in *Virgiscalpellum*. The reduction to 13, through loss of the rostrum in many species of *Arcoscalpellum*, is in need of confirmation. Among extant scalpellids, the 11-plated *Scalpellopsis* exhibits yet further reduction from the condition seen in *Arcoscalpellum*, through the loss of the rostral latera.

On the other hand, a trend toward an increased number of capitular plates is seen in *Zeugmatolepas* and Jurassic *Calantica*, and this is apparently continued in extant *Calantica* and the related *Pollicipes*. Thus it appears that both multiplication and reduction has occurred in various scalpellid lineages.

2) The position of the umbo, which was discarded above as the definitive guide to major evolutionary trends in the Lepadomorpha, is apparently of real value in the interpretation of lineages within genera or closely related groups, as illustrated by the following examples.

Euscalpellum. This genus ranges from Upper Cretaceous to Recent, but is known in the Cretaceous only by large peduncles. *E. minutum* (Brown) from the lower Eocene (Ypresian) of England has the umbo of each plate in an apical position, and also has an extra plate, the subrostrum, unknown in later species. The umbo is removed from the apex of the carina, scutum, and upper latus of *E. vomer* (Bertrand) from the middle Eocene (Lutetian) of France and England. The umbones of the carina and scutum are subapical in *E. eocenense* (Meyer) from the middle Eocene (Claiborne, Lutetian) of the USA, but the upper latus still possesses an apical umbo. The greatest change in position of the umbones is found in the extant *E. rostratum* (Darwin) from the Philippines, in which on the carina, scutum, upper latus, and all latera they are subapical. However, some Miocene and Recent species still have the umbones of all plates apical in position.

Arcoscalpellum. In *Cretiscalpellum* and the earlier Cretaceous species of *Arcoscalpellum*, the umbo of every valve is apically situated. However, the later upper Senonian species *A. fossula* (Darwin), which is apparently derived from the Cenomanian-Turonian *A. angustatum* (Geinitz), exhibits definite upward growth of the inframedian and upper latera, leaving the umbones slightly removed from the apex. The Eocene *A. quadratum* (Dixon) shows this development more clearly, especially in the inframedian latus.

Scalpellum. The earliest known species of *Scalpellum* is *S. fischeri* BERTRAND from the lower Eocene of France and England. It exhibits an upward growth in all the plates except the rostral latus, and this growth is greatest in the upper and inframedian latera. It is in these latter plates that upward growth is first seen in *Arcoscalpellum.* Some Eocene, Miocene, and Recent species (e.g., *S. stearnsi* PILSBRY) show progressive migration of the umbones away from the apices of the plates. In fact, *S. stearnsi* differs from *S. fischeri* only in the progressive development of the plates, for the umbones, especially of the carina and scutum, are still farther removed from the apices, and the rostral and carinal latera have become lower and wider. Instructively, the *S. fischeri* stage is ontogenetically recapitulated during development of *S. stearnsi.*

From examination of the fossil species of *Arcoscalpellum* and *Scalpellum,* and from studying the ontogeny of *S. stearnsi,* it appears that *Scalpellum* was derived from an *Arcoscalpellum* stock.

Virgiscalpellum. This genus is first found in the Lower Cretaceous (Aptian) together with *Arcoscalpellum* and *Cretiscalpellum.* The capitulum has 14 plates, including a long, thick and narrow rostrum; no subcarina has been found. *Virgiscalpellum* represents the earliest known scalpellid in which both the carinal and scutal umbones are subapical. It is peculiar among *Scalpellum*-like barnacles in that the scutum possesses a nearly central umbo, except in the Maastrichtian *V. darwinianum,* in which the umbo is in the basal third of the scutum. The placement of the carinal umbo varies widely in the several species, and in fact is nearest the base of the carina in the earliest (Aptian) species, *V. wrighti.* In other species (e.g., *V. ryckholti, V. hagenowianum*) the carinal umbo is subapical. In *V. darwinianum* the umbo is nearly central, although in some older specimens it is nearer the base. The scutal umbo varies little in position from species to species. The form of the upper, rostral, inframedian, and carinal latera suggests either that *Virgiscalpellum* represents a side lineage from *Arcoscalpellum,* or that both genera had a common ancestor. *Virgiscalpellum* reached a more advanced stage of capitular development than any other scalpellid genus, and has little in common with the *Scalpellum* stock.

3) WITHERS (1928), in concurrence with interpretations of other students of the cirripeds, in particular DARWIN (1851), has pointed out that certain species of the Lepadomorpha, having plates that do not fully cover the capitulum, are forms that have descended from fully armored stocks. Trends in reduced armament occur in very distantly related lines, as can be amply documented in the families Lepadidae, Poecilasmatidae, Oxynaspididae and Scalpellidae. Such trends were categorized by WITHERS under the heading "Decalcification" but this term is somewhat misleading because the plates are not first formed ontogenetically and then subsequently reduced by a decalcification process as it would imply. Rather, the situation is a case of allometry where calcification of the plates has lagged behind general growth, so that the plates come to occupy proportionately less and less of the area of the capitulum, during development of an individual. HOEK (1883) considered such forms among the Scalpellidae as "imperfectly calcified" and PILSBRY (1907) pointed out that ontogenetic development progressed from fully armored juveniles to adults with reduced plates.

The failure of a particular calcified plate to develop at a rate sufficient to maintain its margins approximate to those of its neighbors may occur uniformly around its perimeter, so that its fundamental shape is retained, or it may occur in specific areas while the remainder continues to grow. This type of development is clearly illustrated in *Mesoscalpellum convexum* (NILSSON-CANTELL), in which the juvenile stages are initially completely armored, but become progressively less so as maximum size is reached. In the adult of this species, the latera have come to occupy as little as a sixth of the space available to them, yet their original shape has for the most part been maintained. However, only portions of the terga have been affected, so that while the distal portions appear normal, development of the proximal portions have lagged behind, thus altering the form of the plate from simply triangular to quadrangular, with a basal spur (NILSSON-CANTELL, 1930,

p. 2445, fig. 9). A more extreme example is seen in the Recent *M. dicheloplax* (PILSBRY) where the basic form of all plates, except the carina, is modified in this manner (Fig. 94,*11*).

In the Lepadidae and Poecilasmatidae with reduced armor, an ontogenetic recapitulation of the fully armored form is not seen, and the juvenile begins virtually as fully armored as the adults. In the Poecilasmatidae, a curious reversal has come about. A typical case of reduction in calcified portions of the plates is seen in *Octolasmis (Octolasmis) neptuni* (MACDONALD) where, while the full extent of the plates can be seen in the chitin of the capitulum, the calcified portions are much reduced at their inception and they retain relatively the same proportions during subsequent growth. However, certain other species of the genus, *O. (O.) cor* (AURIVILLIUS), *O. (Dichelaspis) orthogonia* (DARWIN), and *O. (O.) tridens* (AURIVILLIUS) for example, begin their ontogenetic development in the same ways as *O. (O.) neptuni,* but as growth progresses the plates become proportionately more extensive and appreciably altered in form. This is effectively a rearmament process where adults come to have more complete plates than juveniles. In fact, the trend towards rearmament is completed in such species as *Trilasmis (Trilasmis) eburneum* HINDS and *T. (Temnaspis) fissus* (DARWIN), where, although the plates cover the entire capitulum, it is evident that the scutum was once very much reduced, having been formed of two principal arms as in *O. (Octolasmis).* However, the terga are missing in *T. (T.) eburneum,* indicating that this plate was completely lost during an earlier phylogenetic period when the plates in general were much reduced, as in present day *O. (O.) cor.* This

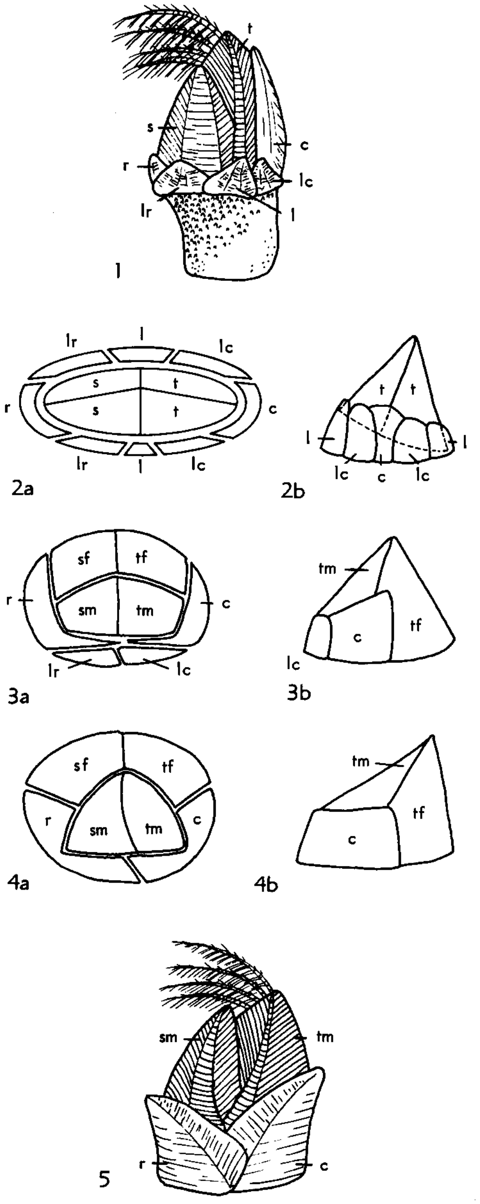


FIG. 113. Inferred origin of plate arrangement in Verrucomorpha (Newman, n).

1. Bilaterally symmetrical pedunculate ancestor comparable to living species of *Calantica,* viewed from right side.
2. Hypothetical intermediate sessile form in which tergum and scutum of one side contact the substratum basally, to become incorporated into structure of the wall, while tergum and scutum of other side act as the operculum.
3. Arrangement of plates in extinct genera *Eoverruca* and *Proverruca,* in which rostrolateral and carinolateral plates of one side are still present.
4. Arrangement of plates, as in *Altiverruca.*
5. Generalized *Verruca,* viewed from right side.

[Explanation: *2a, 3a, 4a,* plan views; *2b, 3b, 4b,* carinal or dorsal views; *c,* carina; *l,* lateral plate; *lc,* carinolateral plate; *lr,* rostrolateral plate; *r,* rostrum; *s,* scutum; *sf,* scutum (fixed); *sm,* scutum (movable); *t,* tergum; *tf,* tergum (fixed); *tm,* tergum (movable).]

indicates that once a plate is lost, a homologue is not likely to be regained.

In the Scalpellidae, then, since the Mesozoic two trends can be discerned, one in reduced number and the other in reduced area occupied by plates of the capitulum. These do not necessarily go hand in hand, for many species with plates much reduced in number have remained fully armored. However, reduction in extent has led to loss in number in such forms as *Scalpellopsis.*

The lepadids have undergone similar trends, but the trend in reduction of area covered by the capitular plates has been reversed in some species. Some of these through a rearmament process, in particular in *Trilasmis (Temnaspis) fissus,* have come to appear structurally as armored as species that cannot be demonstrated to have passed through a reductional phase. Both the Lepadidae and Scalpellidae have given rise to forms in which only a trace of the scutum remains: *Alepas,* showing affinities with *Lepas* on one hand, and Heteralepadidae showing affinities with the scalpellids on the other.

VERRUCOMORPHA

The Verrucomorpha contain a single family, the Verrucidae. Three genera are known: *Proverruca* ranging from the upper Senonian (Cretaceous) to the Miocene; *Eoverruca* known only from the middle Senonian; and *Verruca* ranging from upper Senonian to Recent.

The Verrucomorpha are sessile cirripeds, differing from the Balanomorpha in the highly asymmetrical development of the shell wall and the operculum (Fig. 113). In the Lepadomorpha, two pairs of plates, the terga and scuta, border along the occludent margin of the aperture. In the scalpellids, these plates never form the operculum-like arrangement as that seen in the Balanomorpha, but they do become somewhat specialized in their role of guarding the aperture. The separation of these plates from those forming the wall develops during the transition from a pedunculate to a sessile mode of life. In the transition from pedunculate to balanomorph, a clear separation is made between the opercular and wall plates, and the basic bilateral symmetry of the plates is maintained. However, in the transition from pedunculate to verrucomorph, one of each pair of potential opercular plates becomes incorporated into the wall, rather than separating off to form one side of the operculum, so that the basic bilateral symmetry both of the shell wall and the operculum is lost (Fig. 90).

The earliest known verrucomorphs, *Proverruca* and *Eoverruca,* have a six-plated wall closed by two plates forming the opercular valves. The carina and rostrum form the ends of the boxlike shell, a carinolateral and rostrolateral form one side, and a fixed tergum and fixed scutum form the other. It is quite evident that this asymmetrical arrangement has come about through the loss of at least two latera, in conjunction with the incorporation of the tergum and scutum into that side of the wall. Thus the protoverrucomorph, before the separation of the operculum from the wall, must have had a bilaterally symmetrical wall composed of carina, rostrum, and at least two pairs of latera; effectively the same grade of construction is seen in *Calantica (Paracalantica),* although without phylogenetic implications. Like *C. (Paracalantica),* the verrucomorph presumably descended from a form with three pairs of latera, such as *Calantica (Scillaelepas)* or *C. (Titanolepas)* (Fig. 115,*9*,*12*).

The grade of construction seen in *Proverruca* and *Eoverruca* leads to that seen in *Verruca,* through the loss of the remaining latera, and the joining of the carina and rostrum on the carinorostral side (Fig. 113). As will be seen, this trend toward simplification and rigidity by reduction in number of parts in the verrucomorphs is paralleled in several distinct lines of balanomorphs, although the latter maintain their bilateral symmetry.

Except for the carina and rostrum, the plates of *Proverruca* (see Fig. 117,*1*) have not departed far in structure from those of the Lepadomorpha. The suppression of the two latera of *Proverruca,* and the joining of the carina and rostrum on what becomes the carinorostral side, are all the changes required to arrive at the plate arrangement seen in *Verruca.* This trend is indicated in *Proverruca,* as one of the two latera is already nearly excluded from the wall by the underlying carinal latus and the rostrum.

Eoverruca (see Fig. 117,*3*), like *Proverruca,* had at least two latera opposite the side of the fixed tergum and scutum, but the carina and rostrum are only slightly asymmetrical. In this respect *Eoverruca* is closer to the pedunculate ancestor than *Proverruca,* but on the other hand, the fixed scutum and tergum possess interlocking ribs which indicate an advanced condition. The plates of *Eoverruca* bear a marked resemblance to those of the brachylepadomorph *Pycnolepas,* and differ considerably from those of *Proverruca,* suggesting that these two verrucomorph genera are not closely related.

The shell of *Verruca* exhibits the greatest degree of asymmetry seen in the suborder, and even in Cretaceous representatives, the carina and rostrum form one side of the wall and are articulated by means of several interlocking ribs. An asymmetrical shell wall is not confined to the Verrucomorpha. In the lepadomorph *Calantica,* the rostrum and subcarina are often asymmetrical. Also, the carina and rostrum in the balanid *Chelonibia* and the chthamalid *Chthamalus* are not precisely opposing, although the animals remain effectively bilaterally symmetrical. However, a curious parallel has occurred in *Chthamalus anisopoma* PILSBRY that verges on the type of asymmetry seen in verrucomorphs. The opercular valves, although fundamentally bilateral in the genus, have been displaced on one side so that the set formed by one tergum and scutum lies horizontally across the aperture and acts as the principal part of the operculum. The other set is very much reduced in size and serves more as a rim on which the opercular set rests, than as a movable part of the opercular apparatus. The body of the animal also lies somewhat on its side, and like *Verruca,* the cirri tend to be projected laterally rather than vertically, but the functional significance of this is unknown.

BRACHYLEPADOMORPHA

The suborder Brachylepadomorpha includes a single family, the Brachylepadidae, and the two genera, *Pycnolepas* and *Brachylepas.* The shell is formed by the carina and rostrum, surrounded at the base by three or four whorls of small imbricating plates. A feature that distinguishes this suborder from all sessile cirripeds but is shared with *Pollicipes mitella* among the scalpellid Lepadomorpha is the presence of a long, narrow upper latus between the scuta and terga of each side.

Pycnolepas (see Fig. 117,*5*) is possibly represented in the Upper Jurassic (Tithon.) by certain carinae, but it is definitely represented in the Albian by *P. rigida* (SOWERBY); which ranges into the Cenomanian. Another species, *P. brünnichi* WITHERS, which is related to *P. rigida,* occurs in the Danian, but the evolution of this lineage in the intervening time is not known. *Pycnolepas* has a cylindrical carina and a laterally flattened shell, the plates being similar to those of lepadomorphs. Imbricating plates form whorls at the base of the carina and rostrum, and at least the two outer whorls have deep "muscle-pits" on the inner extremity of the inwardly projecting basal ledge.

Brachylepas fallax (DARWIN) (Turon.-L. Maastricht.) once assigned to *Pycnolepas,* was transferred to the genus *Brachylepas,* on the basis of the structure of the basal imbricating plates. Since it occurs in the time interval between the two above-mentioned species, the reassignment alleviated the problem of attempting to include *B. fallax* in the *Pycnolepas* lineage. *B. fallax* is like *Pycnolepas* in having a cylindrical carina and laterally flattened shell, and was probably a derivative of the *Pycnolepas* stock. *B. naissanti* (HEBERT) (see Fig. 117, 2) which is widespread in comparatively deep-water deposits of the upper Senonian (*Belemnitella mucronata* Zone), has a radially symmetrical shell, but the basis was probably membranous. The remaining species, *Brachylepas guascoi* (BOSQUET) (Maastricht.) from shallow-water deposits, also has a radially symmetrical shell, but the basis is calcareous and the scuta and terga resemble somewhat those of primitive Balanomorpha.

In the Brachylepadomorpha, the geologically earliest representative *(Pycnolepas)* is closely similar in structure to the Lepadomorpha. *Brachylepas,* which was probably derived from *Pycnolepas,* appears to be transitional between a form with laterally flattened shell and membranous basis to one with a radially symmetrical shell and a calcareous basis. The Brachylepadomorpha, in view of the reduced number of elements in the shell wall, are apparently not ancestral to the Balanomorpha, but represent an early and independently developed group which became widespread in the late Senonian and Maastrichtian. Except for the reduced number of shell plates and the retention of the upper lateral, brachylepadomorphs bear a closer resemblance to the chthamalid *Catophragmus* and to the scalpellid *Pollicipes mitella* than to other extant thoracicans. In fact, species of *Pycnolepas* and *Brachylepas* were assigned to *Pollicipes* by early workers, including both DARWIN and WITHERS. Although it seems inescapable that they represent a specialization in themselves and are not in the stem line of the balanomorphs, the evidence is equally convincing that they are closely related to the pedunculate stock that did give rise to the Balanomorpha.

Even though the Brachylepadomorpha appear to have no direct relationship to Balanomorpha, such fossils as *Brachylepas guascoi* help to elucidate the homologies of the opercular valves in balanomorphs. In *Pycnolepas* and *B. fallax* the scutum has an almost median apicobasal ridge, in *B. naissanti* the tergal side is narrower and more steeply sloping, and in *B. guascoi* the tergal side of the scutum is very narrow and reflexed at right angles to the outer surface so that the apicobasal ridge forms the tergal margin. The scutum of *B. guascoi* is similar in shape to that of *Balanus,* but lacks the articular ridge and lateral depressor muscle pit on the inner surface. The narrow basal part of the tergum of *B. guascoi* needs little modification to form the characteristic balanid spur, but lateral depressor muscle crests are absent. The upper latus of *B. guascoi* has not yet been identified, and there is some indication from the form of the scutum that it was reduced or even absent.

BALANOMORPHA

The suborder Balanomorpha includes two families, Chthamalidae and Balanidae. It is distinguished from other sessile thoracican groups by the presence of a symmetrical, basically eight-plated shell wall, with paired scuta and terga forming an operculum. The Chthamalidae are considered phylogenetically more primitive and to have been derived from a lepadomorph stock. *Catophragmus* most closely resembles the present concept of the early balanomorph. The presence of eight compartmental plates, additional whorls of smaller plates about the base of the shell wall, opercular valves which lack well-defined internal structures, caudal appendages, and an unmodified cirrus *III* are all features which link *Catophragmus* with such scalpellid lepadomorphs as *Pollicipes* (as noted by DARWIN, 1854) and *Calantica (Scillaelepas)* (as indicated by PILSBRY, 1916). It is probable that *Catophragmus* and the above mentioned scalpellids shared a common ancestry. Also, it is significant (and fortuitous) that the oldest known balanomorph, the only undoubted balanomorph from Mesozoic deposits, belongs to the genus *Catophragmus* (i.e., *C. (Pachydiadema) cretaceum*).

Chthamalids are not well represented in the fossil record. *Hexelasma* has been identified tentatively from early Oligocene rocks and is definitely recorded from Miocene deposits of New Zealand *(114)*. *Pachylasma* is known from the Miocene of Italy *(2)*. *Tessarelasma* is known only from the early Miocene of India (WITHERS, 1936), and *Chthamalus* has been recorded from Pliocene (Piacenz.) deposits in Italy (ALESSANDRI, 1906). *Chthamalus* is found rarely in late Pleistocene deposits in southern and Baja California (ZULLO, herein), and WITHERS (1932) has reported *Octomeris* from a supposed Pleistocene limestone in Australia. Therefore, many of the inferences made at the present time concerning the phylogeny of the Chthamalidae must be based on comparisons of extant taxa.

The evolutionary history of the Chthamalidae has been one of reduction in the number of elements in the shell wall and modifications in the feeding apparatus (ZULLO, 1963). Two lineages can be distinguished. In the first, leading from *Catophragmus* to *Octomeris, Chionelasmus, Chthamalus,* and *Chamaesipho,* shell wall reduction was achieved primarily through exclusion of elements, and feeding modifications were confined to changes in mandibular structure. *Octomeris* differs from *Catophragmus* principally in the absence of whorls of smaller plates about the base of the shell wall. *Chionelasmus* retains one of the basal whorls, but the carinolaterals have been lost. *Chthamalus* is closely related to *Chionelasmus,* but differs in having lost all traces of the basal whorls, and in possessing (in some species) a mandible modified from the basic lepadomorph type. *Chamaesipho* represents a further step beyond *Chthamalus* in the reduction of the number of elements in the shell wall. In this genus, the laterals and rostrolaterals have apparently fused to form a four-plate shell wall (Fig. 96).

In the second lineage, leading from *Octomeris* to *Pachylasma* to *Hexelasma,* and *Tessarelasma,* shell wall reduction was accomplished primarily through fusion of elements, and feeding adaptations involved the modification of cirrus *III* for use as a mouth appendage. Fusion of the rostrum with the adjacent rostrolaterals is exhibited in species of *Pachylasma,* and from this, the tripartite rostral plate is inferred in *Hexelasma,* and *Tessarelasma.* These last two genera also differ from *Pachylasma* in the form of the opercular valves which are more like those of the balanid barnacles than of other chthamalids. Also, in *Hexelasma,* in which the body is known, cirrus *III* has been modified somewhat for use as a mouth appendage. *Tessarelasma,* as *Chamaesipho,* has attained a four-plate shell wall, but in this case the reduction was apparently achieved through loss of the carinolaterals as in *Tetrachthamalus* (Newman, 1967).

The development of a compound rostral plate, the modification of cirrus *III,* and the change in form of the opercular valves in the *Pachylasma-Hexelasma* lineage indicates that the Balanidae were derived from a *Pachylasma*-like ancestor. The compound nature of the balanid rostral plate is demonstrated by *Chelonibia,* in which the sutures between the rostrum and rostrolaterals are still visible. It is no doubt through the highly specialized habitat of this genus that this primitive character has been retained. All other balanids bear no trace of the sutures uniting the elements of the rostral plate. RUNNSTRÖM (1925) and BROCH (1927) have concluded from a study of ontogenetic development of the shell in *Balanus (Semibalanus) balanoides,* that the rostrum is not present in the balanid rostral plate, which therefore would be formed only of the two rostrolaterals.

The ancestral balanid was probably a form similar to *Balanus (Solidobalanus)* [includes *Hesperibalanus*] in possessing a shell wall with solid parietes and moderately developed radii, a solid calcareous basis, and heavy opercular valves which lacked prominent internal structures. Some of the geologically earliest balanids from the middle and late Eocene of Europe, and southeastern and northwestern United States can be included in the subgenus *B. (Solidobalanus)* (ZULLO, 1960). More recently Ross (1965) has established a new genus *Kathpalmeria* to include other Eocene balanids. Rapid diversification apparently took place during the Oligocene. Forms with parietal tubes and tubes in the radii (e.g., *B. (Balanus), B. (Megabalanus), Tetraclita*) have been reported from Oligocene strata, as well as the solid-walled subgenus *B. (Austrobalanus). B. (Balanus)* was probably derived from a solidobalanid-like stock through a form similar to *B. (Balanus) crenatus. B. (Balanus)* gave rise to *B. (Semibalanus)* through the multiplication of rows of parietal tubes and the loss of the calcareous basis, and subsequently to *Tetraclita* (?and *Elminius*) through loss of the carinolaterals. *Tetrabalanus* also appears to be a derivative of *Balanus s.s.,* perhaps through such a species as *B. (B.) amphitrite. B. (Chirona)* was probably derived independently from a solidobalanid-like stock, with *B. (Metabalanus)* representing a relatively recent offshoot of *B. (Chirona).*

The complex *Balanus (Armatobalanus), B. (Conopea), B. (Membranobalanus),* and *Acasta* represents another independent offshoot of the hesperibalanid stock, and the differences between these taxa primarily reflect differences in habitat. The lineage *Hexacreusia - Creusia - Pyrgoma-Pyrgopsella* was derived in the Miocene from this *Armatobalanus* complex which may also have given rise to the coronuline barnacles. The proposed derivation of *Cryptolepas* from *Coronula,* and *Tubicinella* from *Cryptolepas* appears valid, but the relations between the other coronuline taxa are at present difficult to interpret.

SYSTEMATIC DESCRIPTIONS

Class CIRRIPEDIA Burmeister, 1834

Sedentary marine Crustacea having fundamental affinities with the Maxillopoda;[1] forming initial attachment by first antennae; following appendages (when present) and body contained within carapace (mantle); mantle in principal order (Thoracica) typically supporting calcareous plates persisting through molt cycles during adult life. Development usually includes six naupliar stages, and bivalved cyprid stage. Sexes separate or combined; males, when present, always reduced, occurring with females or hermaphrodites. *U.Sil.-Rec.*

Order ACROTHORACICA Gruvel, 1905

[=Abdominalia DARWIN, 1854]

Cirripedia with separate sexes; females always found burrowing in calcareous substrate, accompanied by reduced males which lack feeding appendages. Females differ from thoracican cirripeds in having the cirri (except first pair) terminal rather than evenly distributed along thorax, in not developing calcareous plates, and in molting the entire exoskeleton, including exterior of carapace, rather than just the interior lining and appendages. *Carb.-Rec.*

Suborder PYGOPHORA Berndt, 1907

Gut complete, and three or more pairs of biramous terminal cirri present. *Rec.*

The following classification parallels that of BERNDT (1907), as suggested by TOMLINSON (1967, personal communication).

Family LITHOGLYPTIDAE Aurivillius, 1892

[=Kochlorinidae GRUVEL, 1905; BERNDT, 1907; Balanodytidae UTINOMI, 1950 *(103a)*; Berndtiidae UTINOMI, 1950 *(103b)*; Chytraeidae UTINOMI, 1950 *(103b)*; Utinomiidae TOMLINSON, 1963]

Pygophora without lateral bar, gastric mill or elongate labrum. *Rec.*

Lithoglyptes AURIVILLIUS, 1892 (p. 133) [**L. indicus;* OD]. Five pairs of cirri (1 mouth, 4 terminal), and caudal appendages. *Rec.,* IndoPac.-Carib.

Balanodytes UTINOMI, 1950 (p. 1) [**B. taiwanus;* OD]. Five pairs of cirri (1 mouth, 4 terminal), without caudal appendages. *Rec.,* Taiwan.

Berndtia UTINOMI, 1950 (p. 7) [**B. purpurea;* OD]. Six pairs of cirri (1 mouth, 5 terminal), without caudal appendages. *Rec.,* Japan.

Kochlorine NOLL, 1875 (p. 114) [**K. hamata;* OD]. Four pairs of cirri (1 mouth, 3 terminal) and caudal appendages. *Rec.,* Spain.-S.Afr.-W.Atl.

Kochlorinopsis STUBBINGS, 1967 (p. 306) [**K. discoporellae;* OD]. Like *Kochlorine* but lacking longitudinal retractor muscles along rostral sides of mantle. *Rec.,* W.Afr.

Weltneria BERNDT, 1907 (p. 289) [**W. spinosa;* OD] [=*Utinomia* TOMLINSON, 1963 (p. 264)]. Six pairs of cirri (1 mouth, 5 terminal), and caudal appendages. *Rec.,* S.Afr.-Japan-Hawaii-Bermuda.

Family CRYPTOPHIALIDAE Gerstaecker, 1866

Pygophora with lateral bar, gastric mill, and much elongated labrum. *Rec.*

Cryptophialus DARWIN, 1854 (p. 566) [**C. minutus;* OD]. Five or four pairs of cirri (1 mouth, 4 or 3 terminal), no caudal appendages. *Rec.,* S. Am.-S.Afr.-W.Afr.-Antarctic-N.Z.

Suborder APYGOPHORA Berndt, 1907

Acrothoracica with incomplete gut, three pairs of uniramous terminal cirri. *Carb.-Rec.*

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[1] As previously noted, not recognized in *Treatise* classification. DAHL (1963, p. 1) grouped cirripeds with mystacocarids, copepods, and branchiurans in so-called maxillopods.—Ed.

Family TRYPETESIDAE Stebbing, 1910

[=Alcippidae Hancock, 1849]

Trypetesa Norman, 1903 (p. 369) [**Alcippe lampas* Hancock, 1849; SD Stebbing, 1910]. Characteristics of family. *Carb.-Perm.* (burrows in exterior of mollusk shells); *Rec.* (burrows in interior of gastropod shells inhabited by hermit crabs), cosmop., N.Hemis.

Suborder UNCERTAIN

Burrows in a variety of calcareous substrates have been identified as those of Acrothoracica. The appropriateness of applying Linnean nomenclature has been questioned by Rodda & Fisher (1962), and there is in fact good reason to voice concern when it is recognized that only *Cryptophialus* and *Trypetesa,* among extant Acrothoracica, can be recognized presently by the form of their burrows alone. *Trias.-Plio.*

Family RODGERELLIDAE Saint-Seine, 1951

Burrow depth exceeding length, with peduncular slit and marginal flange; in echinoid tests, mollusk shells, and corals. *M.Jur.-L.Plio.*

Rodgerella Saint-Seine, 1951 (p. 1053) [**R. lecointrei;* OD]. Characteristics of family. *M.Jur.-L.Plio.,* Eu.-N.Am.

Family ZAPFELLIDAE Saint-Seine, 1954

Burrow depth at least half length, without peduncular slit or marginal flange. *Trias.-Plio.*

Zapfella Saint-Seine, 1954 (p. 449) [**Z. patei;* OD]. One end of aperture greatly enlarged. [Burrows in gastropods, pelecypods, and marl.] *Mio.-Plio.,* Eu.

Brachyzapfes Codez, 1957 (p. 706) [**B. elliptica;* OD]. Form of aperture elliptical. [Burrows in belemnites and pelecypods.] *L.Cret.,* Eu.-Antarctica.

Simonizapfes Codez, 1957 (p. 704) [**S. elongata;* OD]. One end of aperture slightly enlarged. [Burrows in belemnites and other mollusk shells.] *Trias.-Jur.,* Eu.

Order RHIZOCEPHALA F. Müller, 1862

[=Suctoria Lilljeborg, 1861; Kentrogonida Delage, 1884]

Parasitic crustaceans without appendages or digestive tract in adult stage; recognized as Cirripedia by characteristic nauplius larvae or cyprid stage, or both. Parasitic on crustaceans, primarily Decapoda. *Rec.*

Suborder KENTROGONIDA Delage, 1884

[Kentrogonidae Häfele, 1911; Kentrogonidea Guerin-Ganivet, 1911; Bocquet-Védrine, 1961]

Rhizocephala with kentrogon stage establishing endoparasitic phase; development generally including naupliar stages. *Rec.*

Family PELTOGASTRIDAE Lilljeborg, 1861[1]

[Peltogastridae Lilljeborg, 1861, p. 96; Boschma, 1928, p. 3 *emend.*]

Peltogaster Rathke, 1843, p. 244 [**P. paguri;* SD Lilljeborg, 1861, p. 25]. Body elongate or ovoid, long axis parallel to long axis of host; colleteric glands and male-cell receptacles ("testes") paired; latter opening backward into mantle cavity. [Family divisible into gregarious (colonial) and nongregarious genera. Parasitic on pagurids and galatheids.] *Rec.*

Family SACCULINIDAE Lilljeborg, 1861[1]

[Sacculinidae Lilljeborg, 1861, p. 96; Boschma, 1928, p. 13 *emend.*]

Sacculina Thompson, 1836, p. 452 [**S. carcini;* SD Boschma, 1955, p. 3]. Body laterally compressed; colleteric glands and male-cell receptacles paired; latter opening ventrally into mantle cavity. [Parasitic on anomurans (Hippidea and Galatheidea); brachyurans (Gymnopleura, Dromiacea, Brachygnatha and Oxyrhyncha).] *Rec.*

Family LERNAEODISCIDAE Boschma, 1928[1]

[Lernaeodiscidae Boschma, 1928, p. 17]

Lernaeodiscus F. Müller, 1862, p. 2 [**L. porcellanae;* SD Van Baal, 1935, p. 51]. Body dorsoventrally compressed; colleteric glands and male-cell receptacles ("testes") paired; latter opening into posterior part of mantle cavity. [Parasitic on galatheids and thalassinideans.] *Rec.*

Family CLISTOSACCIDAE Boschma, 1928

[Clistosaccidae Boschma, 1928, p. 26]

Clistosaccus Lilljeborg, 1861, p. 81 [**C. paguri* (=*Apeltes paguri* Lilljeborg, 1861, p. 95); SD Boschma, 1928, p. 26]. Body elongate or ovoid, long axis parallel to long axis of host; colleteric

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[1] Additional genera listed in Addendum to Cirripedia, p. R628.

gland and "testis" unpaired; the latter opening into anterior part of mantle cavity. [Parasitic on Paguridea.] *Rec.*, N.Atl.-N.Pac.

Family SYLONIDAE Boschma, 1928

[Sylonidae BOSCHMA, 1928, p. 33]

Sylon KRÖYER, 1855, p. 128 [**S. hippolytes* M. SARS, 1870; SD BOSCHMA, 1928, p. 35]. Body ovoid, long axis parallel to long axis of host; colleteric glands unpaired, ?forming male-cell receptacle; mantle cavity with paired opening to exterior; development without free naupliar stages. Rec., N.Pac.-N.Atl. Inclusion of *Thompsonia, Duplorbis* and *Mycetomorpha* (YANAGIMACHI & FUJIMAKI, 1967) by *lapsus calami* (YANAGIMACHI, pers. comm.; REISCHMAN, pers. comm.).

Suborder AKENTROGONIDA Häfele, 1911

[Akentrogonidae HÄFELE, 1911; Akentrogonidea GUERIN-GANIVET, 1911; BOCQUET-VÉDRINE, 1961]

Rhizocephala without kentrogon stage; ectoparasitic penetration superficial or with moderate to extensively developed nutritive processes; development without free naupliar stage; no male-cell receptacles. [Genera other than *Chthamalophilus* included provisionally.] *Rec.*

Chthamalophilus BOCQUET-VÉDRINE, 1957, p. 1545 [**C. delagei;* OD]. Solitary rhizocephalan, with bulbous localized nutritive process; "testes" residing in mantle cavity. [Ectoparasite on cirriped *Chthamalus*]. *Rec.*, E.Atl. (vicinity of Roscoff).

Duplorbis SMITH, 1906, p. 118 [**D. calathurae;* OD]. Solitary rhizocephalan; apparently without extensive nutritive processes, attached to host by tube opening into mantle cavity; ?male-cells residing in mantle cavity. [Parasitic on Isopoda.] *Rec.*, N.Atl.

Microgaster BOCQUET-VÉDRINE, 1967, p. 1630 [**M. balani;* OD]. Solitary, much like *Chthamalophilus* except for rootlike nutritive processes, invading tissue of host. [Parasitic on *Balanus.*] *Rec.*, E.Atl.

Mycetomorpha POTTS, 1912, p. 591 [**M. vancouverensis;* OD]. Multilobed solitary rhizocephalan; nutritive processes not widely distributed; situated under abdominal nerve cord of host; male-cells residing in mantle. [Parasitic on Caridea.] *Rec.*, N.Pac.

Thompsonia KOSSMANN, 1873, p. 132 [**T. globosa;* OD] [=*Thylacoplethus* COUTIÉRE, 1902; POTTS, 1915, p. 28, *emend.*]. Colonial rhizocephalan without mantle cavity; internal nutritive processes giving off numerous external reproductive sacs, male-cells residing in mantle. [Parasitic on Caridea, Galatheidea, Paguridea, Thalassinidea, Brachygnatha.] *Rec.*, N.Pac.-Carib.-Medit.

UNCERTAIN AFFINITIES

Sphaerothylacus SLUITER, 1884, p. 205 [**S. polycarpae;* OD]. Body containing reproductive organs and alimentary canal, covered by mantle. Attached to pharynx of tunicate by branching nutritive processes; ovaries opening near mouth suggesting cirriped affinities; nauplii without frontolateral horns suggesting ascothoracican or copepod; host selection suggests copepod. [Parasitic on *Polycarpa.*] *Rec.*, E.Indies.

Order ASCOTHORACICA Lacaze-Duthiers, 1880

[=Ascothoracida or Rhizothoracida LACAZE-DUTHIERS, 1880 (p. 580); Ascothoracica GRUVEL, 1905 (p. 336)]

Cirripedia with prehensile first antennae; body enclosed in bivalved carapace; sexes separate or combined; mouth parts forming oral cone modified for biting and piercing; thoracic appendages basically natatory, first pair not conspicuously modified to form accessory mouth parts; fifth abdominal segment bearing furca. [Ectoparasitic and endoparasitic on coelenterates and echinoderms; generic definitions based on degree of reduction related to parasitic mode of existence.] *Cret.-Rec.*

Family SYNAGOGIDAE Gruvel, 1905

Six pairs of thoracic appendages; abdomen of four or five distinct somites and furca; carapace distinctly bivalved. [Ectoparasitic on antipatharians, crinoids, and ophiuroids.] *Rec.*

Synagoga NORMAN, 1887 (p. 87) [**S. mira;* OD]. Thorax of 6 distinct somites, each bearing pair of biramous natatory appendages. [Ectoparasitic on crinoids and Antipatharia.] *Rec.*, Medit.-Japan. [See Fig. 82,*2*.]

Ascothorax DJAKONOV, 1914 (p. 158) [**A. ophioctenis;* OD]. First thoracic somite fused with head; thoracic limbs somewhat reduced; 1st and 6th pairs biramous or uniramous; abdomen of 4 or 5 somites. [On ophiuroids.] *Rec.*, Arctic-Antarctic.

Parasothorax WAGIN, 1964 (p. 271) [**P. synagogoides;* OD]. First thoracic somite fused with head, 1st thoracic limbs uniramous; abdomen of 5 somites, furca multiarticulate. [On ophiuroid.] *Rec.*, Okhotsk Sea-NW.Pac.

Family LAURIDAE Gruvel, 1905

Three to six pairs of uniramous unsegmented thoracic limbs; abdomen with four distinct somites (except *Gorgonolaureus*); carapace a sac (bivalved in *Baccalaureus maldivensis*). [On Octocorallia and Hexacorallia.] *Rec.*

Laura Lacaze-Duthiers, 1866 (p. 5) [**L. gerardiae;* OD]. Five pairs of thoracic limbs (5th one reduced) [On Antipatharia.] *Rec.*, Medit.

Baccalaureus Broch, 1929 (p. 242) [**B. japonicus;* OD]. Thorax of 4 or 5 somites which bear 3 to 5 pairs of uniramous limbs, with lateral chitinous ridge. [On Zoantharia.] *Rec.*, IndoPac.

Gorgonolaureus Utinomi, 1962 (p. 458) [**G. bikiniensis;* OD]. Thorax apparently unsegmented, bearing 6 pairs of uniramous limbs; abdomen unsegmented yet bearing furca. [Only member of order known from Octocorallia (on gorgonian).] *Rec.*, C.Pac.

Family PETRARCIDAE Gruvel, 1905

Unsegmented thorax bearing six pairs of unsegmented uniramous appendages; abdomen three-segmented; furca minute. *Rec.*

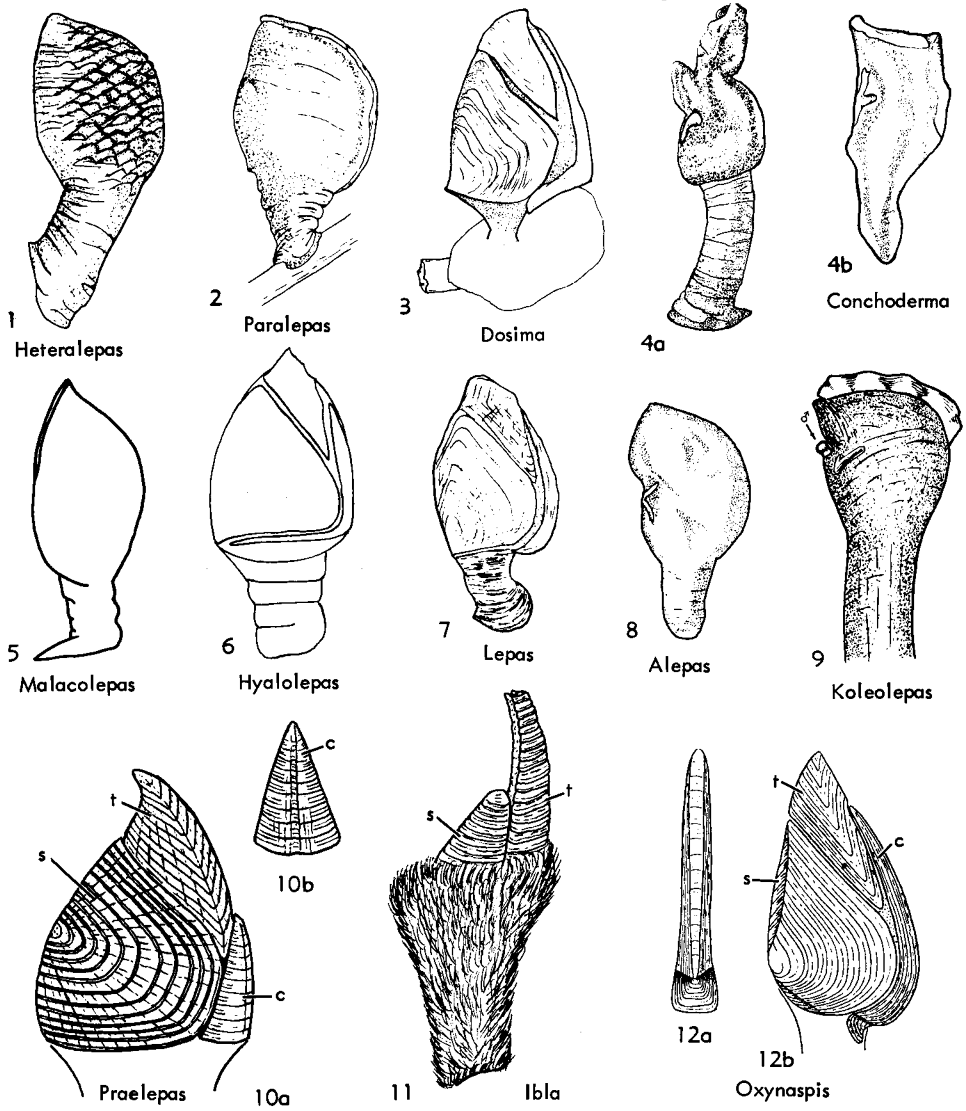

Fig. 114. Praelepadidae *(10)*, Heteralepadidae *(1-2)*, Iblidae *(11)*, Koleolepadidae *(9)*, Lepadidae *(3-4, 6-8)*, Malacolepadidae *(5)*, Oxynaspididae *(12)*, (p. *R*275-*R*279).

Petrarca FOWLER, 1889 (p. 107) [**P. bathyactidis;* OD]. Characteristics of family. [On madreporarian, 4,200 m.] *Rec.,* Japan.

Family DENDROGASTRIDAE Gruvel, 1905

[*nom. correct.* NEWMAN & ZULLO, herein (*pro* Dendrogasteridae GRUVEL, 1905)]

Thoracic somites more or less evident, limbs rudimentary stubs or absent; furca partially fused rudimentary stubs, or absent. [On asteroids and echinoids.] *Rec.*

Dendrogaster KNIPOWITSCH, 1891 (p. 1) [**D. astericola;* OD]. Thorax of indistinct somites, without limbs; abdomen of ?4 somites, without furca. [On asteroids.] *Rec.,* White Sea-?NW.Atl.

Myriocladus OKADA, 1925 (p. 370) [**Dendrogaster arborescens* LEROI, 1905 (p. 400) (*non M. arborescens* OKADA, 1925, p. 365, =*M. okadai* YOSII, 1931, p. 337); SD]. Like *Dendrogaster,* but abdomen coalesced with thorax. [On asteroids.] *Rec.,* IndoPac.-Calif.

Ulophysema BRATTSTRÖM, 1936 [**U. öresundense;* OD]. Thorax of ?6 more or less distinct somites bearing 4 or 5 limb stubs; ?3-segmented abdomen bearing rudimentary furca. [On irregular echinoids.] *Rec.,* NE.Atl.

Family UNCERTAIN

Endosacculus VOIGHT, 1959 [**E. moltkiae;* M]. *U.Cret.(Maastricht.),* W.Ger.

Genus cf. Ulophysema MADSEN & WOLFF, 1965. *U. Cret.(Turon.-Maastricht.),* W.Ger.

Order THORACICA Darwin, 1854

Permanently attached cirripeds as adults; mantle usually strengthened by calcareous plates; with six pairs of biramous thoracic appendages or cirri (?except *Rhizolepas*), first usually associated closely with mouth parts, second through sixth evenly distributed along thorax; nauplii usually, cyprid larva always present, latter undergoing complex metamorphosis into adult form. *U.Sil.-Rec.*

Suborder LEPADOMORPHA Pilsbry, 1916

Usually differentiated into capitulum containing body with mouth parts and thoracic appendages and peduncle containing testes in males or ovaries in females or hermaphrodites; capitulum usually protected by calcareous plates of specific form; peduncle protected in some by calcareous plates, usually muscular, allowing changes in orientation. *U.Sil.-Rec.*

Family CYPRILEPADIDAE Newman & Zullo, new family

Capitulum distinct from peduncle, possibly weakly calcified, although lack of growth lines in cuticle indicates complete molting as in Acrothoracica; thickening along carinal and basal margins separates capitulum into single lateral plate on each side; appendages unknown. *U.Sil.*

Cyprilepas WILLS, 1962, p. 567 [**C. holmi;* OD]. Characters of family. [Occurring on appendages of *Eurypterus fischeri* EICHWALD.] *U.Sil.,* Estonia. ——FIG. 111,*1.* **C. holmi; 1a,b,* large and small individuals from left side, ×17 (Wills).

Family PRAELEPADIDAE Chernyshev, 1930

[=Cirravidae CHERNYSHEV, 1935]

Plates probably five, chitinous; scutal umbones subcentral; tergal umbones apical; carina short, semiconical, umbo apical. *M. Carb.*

Praelepas CHERNYSHEV, 1930, p. 28 [**P. jaworskii;* SD WITHERS, 1953, p. 11] [=*Cirravus* CHERNYSHEV, 1935, p. 36]. Characters of family. *M.Carb.;* USSR.——FIG. 114,*10.* **P. jaworskii; 10a,* reconstr., *10b,* carina, ×8 *(118).*

Family SCALPELLIDAE Pilsbry, 1916

Capitulum protected by more than five plates; peduncle armed with plates. *U.Trias. (Rhaet.)-Rec.*

Scalpellum LEACH, 1817, p. 68 [**Lepas scalpellum* LINNÉ, 1767, p. 1109 (=*Scalpellum vulgare* LEACH, 1824, p. 170); SD LEACH, 1824]. Carina bent, forming angle at position of umbo; scutal umbo usually subapical; inframedian latus usually large, umbo varying in position from middle to basal. *L.Eoc.-Rec.,* N.Atl.-Medit.——FIG. 115,*3. S. fischeri* BERTRAND, M.Eoc.(Lutet.), France.; reconstr., ×3 *(120).*

Aporolepas WITHERS, 1953, p. 116 [**Scalpellum recurvatum* BERTRAND, 1891, p. 694; OD]. Capitular plates 21 or more, umbones all apical, with at least 8 pairs of comparatively large modified lower latera; rostrum and subcarina present; upper latus long and narrow, extending well up between scutum and tergum. *M.Eoc.(Lutet.)-L.Oligo. (Lattorf.);* Eu.(France-Eng.)-USA.

Archaeolepas Zittel, 1884, p. 581 [**Pollicipes redtenbacheri* Oppel, 1862, p. 116; SD Withers, 1928, p. 83]. Capitular plates 6; scutum triangular, with tergal slip; tergum with base widely truncated; carina comparatively small; rostrum much smaller than carina. *U.Jur.-L.Cret.*, Eu. (Eng.-France-Ger.)-S.Am.——Fig. 115,6. **A. redtenbacheri* (Oppel), U.Jur.(Kimmridg.), Ger.; reconstr., ×2 *(116)*.

Arcoscalpellum Hoek, 1907, p. 59, 85 [**Scalpellum*

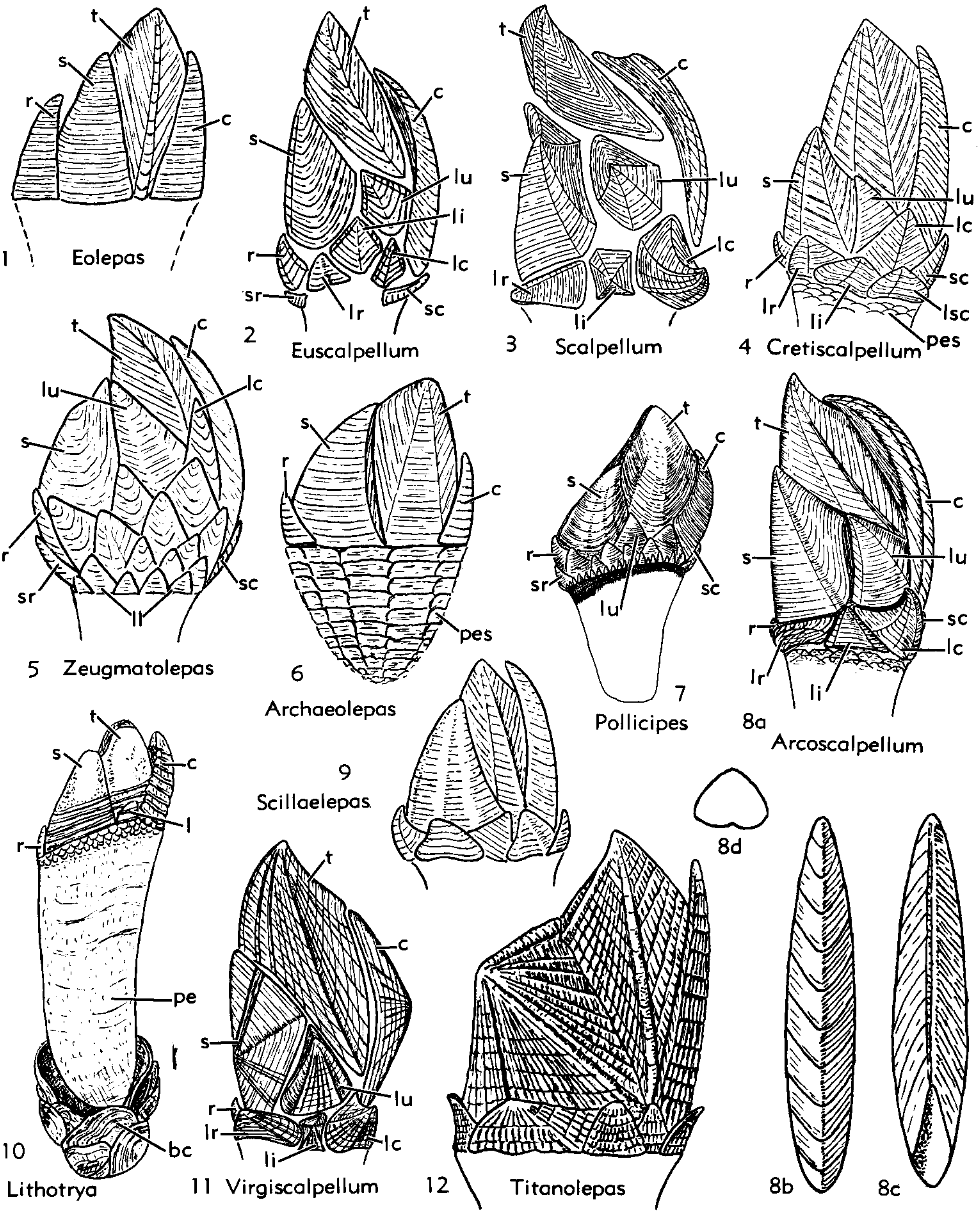

Fig. 115. Scalpellidae (p. R275-R278).

[Explanation: *bc*, basal cup (calcareous); *c*, carina; *l*, latus; *lc*, latus (carinal); *li*, latus (inframedian); *ll*, latus (lower); *lm*, latus (median); *lr*, latus (rostral); *lsc*, latus (subcarinal); *lu*, latus (upper); *pe*, peduncle; *pes*, peduncle scale; *r*, rostrum; *s*, scutum; *sc*, subcarina; *sr*, subrostrum; *t*, tergum.]

michelottianum Seguenza, 1876, p. 381, 464 (=*S. velutinum* Hoek, 1883, p. 96); OD] [=*Holoscalpellum* Pilsbry, 1907, p. 25]. Capitular plates 15 in fossil and ?13-14 in Recent forms; rostral latus low and wide, larger than inframedian latus; carina with umbo apical. *U.Cret. (Senon.)-Rec.*, cosmop.——Fig. 115,*8a. A. fossula* (Darwin), U.Senon.; reconstr., X2 *(116)*.——Fig. 115,*8b-d. A. maximum solidulum* (Steenstrup), U.Cret.(Senon.), *B. mucronata* Zone, E. Ger. (I. of Rügen); *8b-d,* carina (reconstr.), outer side, inner side, cross sec., X2 *(116)*.

Calantica Gray, 1825, p. 100 [**Pollicipes villosus* Leach, 1824, pl. lvii; OD]. Capitulum with 2 whorls of plates; upper whorl comprising paired scuta, terga, and carina; tergum occupying entire space between scutum and carina; lower whorl comprising rosrtum, subcarina, subrostrum in some species, and 3 pairs of latera (2 pairs in subgenus *Paracalantica;* umbones all apical (scutal umbo subcentral in subgenus *Paracalantica,* central in subgenus *Titanolepas*). *U.Jur.-Rec.*, Eu.-S.Am.-N. Z.-Australia-N.Am.-?E.Indies.

C. (Calantica). Plates of lower whorl low and wide, small, barely concealing bases of upper whorl, scales of peduncle minute. *?U.Jur., Mio.-Rec.*, Eu.-N.Z.——Fig. 85,*1*. **C. (C.) villosa* (Leach), Rec., N.Z.; *1a,b,* X1 (Withers).

C. (Paracalantica) Utinomi, 1949, p. 93 [**C. (P.) ikedai,* p. 93; OD]. Only 2 pairs of latera, scutum with subcentral umbo. *Rec.*, Japan.

C. (Scillaelepas) Seguenza, 1876, p. 390 [**Pollicipes carinatus* Phillipi, 1835, p. 512; OD]. Plates of lower whorl large, high, concealing bases of upper whorl; scales of peduncle large. *?U.Jur., Paleoc.-Rec.*, N.Atl.-Eu.-Australia.——Fig. 115,*9. C. (S.) dorsata* (Steenstrup), Paleoc., Denm.; reconstr., X2 *(120)*.

C. (Titanolepas) Withers, 1913, p. 943 [**Scalpellum tuberculatum* Darwin, 1851, p. 43; OD]. Like *C. (Scillaelepas),* but with scutal umbo subcentral. *U.Cret.(Cenoman.-U.Senon.),* Eu.-N. Am.——Fig. 115,*12*. **C. (T.) tuberculata* (Darwin), Cenoman, Eng.; reconstr., X10 (Withers, 1913).

Cretiscalpellum Withers, 1922, p. 374 [**Pollicipes unguis* J. de C. Sowerby, 1836, p. 335; OD]. Capitular plates 17, including 4 pairs of large, overlapping and little-modified lower latera; subcarina much larger than rostrum; all umbones apical. *L.Cret.-U.Cret.(Apt.-Maastricht.),* Eu.——Fig. 115,*4*. **C. unguis* (J. de C. Sowerby), Alb., Eng.; reconstr., X1.5 *(118)*.

Eolepas Withers, 1928, p. 65 [**Pollicipes rhaeticus* Moore, 1861, p. 512, 497; OD]. Capitular plates 6, scutum without tergal slip and apicobasal ridge; tergum not truncated at base; rostrum large, almost equaling carina in size. *U.Trias.(Rhaet.)-U. Jur.(Kimmeridg.),* Eu.(Eng.-France-Ger.).——Fig. 115,*1*. *E. quenstedti* (Von Ammon), U.Jur. (Kimmeridg.), Ger.; reconstr., X1.5 *(116)*.

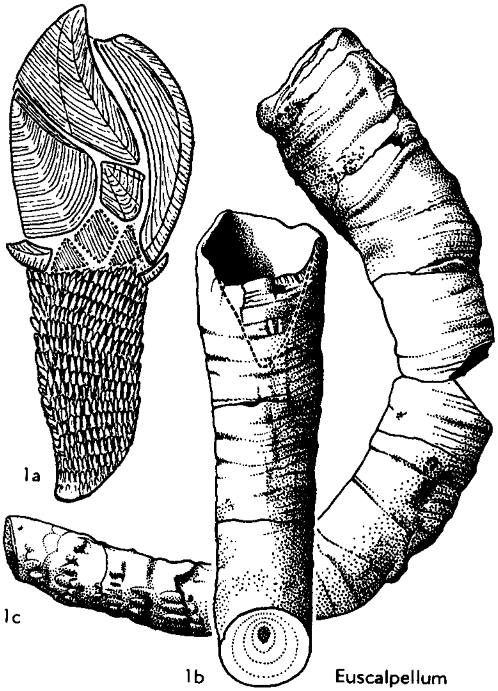

Fig. 115A. Scalpellidae, shells showing secretion of calcium carbonate; *1a, Euscalpellum eocenense* (Meyer); *1b,c, E. zelandicum* Withers (p. *R277*).

Euscalpellum Hoek, 1907, p. 59, 65 [**Scalpellum rostratum* Darwin, 1851, p. 259; SD Pilsbry, 1908, p. 107]. Capitular plates 15; rostrum large and prominent; subcarina well developed; inframedian latus diamond-shaped. *U.Cret.-Rec.*, Eu.-USA-S. Am.-N. Z.-Antarctica-Malay Arch.——Fig. 115,*2. E. minutum* (T. Brown), L.Eoc.(Ypres.; London Clay), Eng.; reconstr., X3.5 *(120)*.——Fig. 115A,*1a. E. eocenense* (Meyer), M.Eoc. (Claiborne), USA; side view of shell, reconstr., X1.5 *(120)*.——Fig. 115A,*1b,c. E. zelandicum* Withers, U.Cret.(Senon.), N.Z.; *1b,* whole peduncle, X1.4; *1c,* upper half of peduncle showing cavity above and cross section below, X1.4 (Withers, 1951).

Lithotrya G. B. Sowerby, 1822, no. 8 [**Lepas dorsalis* Ellis & Solander, 1786, p. 197; OD]. Capitulum of 8 plates, umbones apical; scuta, terga and carina large; rostrum and pair of latera small; peduncle with small scales, those of upper row crenated; base terminating in calcareous cup; inhabits cavities bored in calcareous substrata. *Rec.*, E.Atl.-IndoPac.——Fig. 115,*10*. **L. dorsalis* (Ellis & Solander), Rec., W.Indies; X2 *(37)*.

Mesoscalpellum Hoek, 1907, p. 39, 73 [**Scalpellum javanicum* Hoek, 1907, p. 78; SD Pilsbry, 1908, p. 110] [Includes *Neoscalpellum* Pilsbry, 1907, p. 69, 1908, p. 110]. Juveniles typically arcoscalpelloid, adults with capitular plates variously reduced; tergum V-shaped, carinal umbo apical. [Deep sea.] *U.Cret.(M.Senon.)-Rec.,* cosmop.——Fig. 94,*11*. *M. dicheloplax* (Pilsbry), Rec., W. Atl., ×1 (Pilsbry).

Pisiscalpellum Utinomi, 1958, p. 113 [**P. withersi;* OD]. Similar to *Calantica (Scillaelepas)* but lacking subcarina and males attached in different position. *Rec.,* Japan.

Pollicipes Leach, 1817, p. 68 [**Lepas pollicipes* Gmelin, 1790, p. 3213; OD]. Capitular plates 18 or more, all umbones apical; lower latera numerous, arranged in one or more whorls. *?U.Jur., L. Eoc. - Rec.,* Eu.-Greenl.-Medit.-Indo Pac.-E. Pac. ——Fig. 115,*7*. **P. pollicipes* (Gmelin), Rec., N. Atl.-Medit.; ×1 *(120)*.

Protomitella Broch, 1922, p. 246 [**P. paradoxa,* p. 247; OD]. Similar to *Pollicipes,* capitular plates nearly identical to some variants of *P. spinosus,* except lower latera digitiform rather than pointed and complemental males present. *Rec.,* N.Z.

Scalpellopsis Broch, 1922, p. 243 [**S. striatociliata,* p. 243; OD]. Like *Arcoscalpellum* but with inframedian latera highly reduced and rostral latera wanting. *Rec.,* Philip.Is.

Smilium Leach, 1825, p. 209 [**S. peronii* Gray, 1825, p. 100; SD Pilsbry, 1907, p. 13]. Similar to *Calantica* but with pair of upper latera interposed between carina and scuta. *?U.Cret. (Cenoman.-Turon.), Rec.,* cosmop.

Virgiscalpellum Withers, 1935, p. 283 [**Scalpellum beisseli* Bosquet & Miller, 1857, p. 7; OD]. Capitulum as in *Arcoscalpellum,* but with carinal umbo subapical to subcentral and scutal umbo subcentral or lower; rostrum long and narrow; 14 plates known. *L. Cret.-U. Cret. (Apt.-Maastricht.),* Eu.-N.Am.-S.Am.——Fig. 115,*11*. *V. darwinianum* (Bosquet), Maastricht., Neth.; reconstr., ×2 *(118)*.

Zeugmatolepas Withers, 1913, p. 938 [**Z. mockleri,* p. 939; OD] [=*Cretaspis* Joleaud, 1916, p. 43]. Capitulum like that of *Scalpellum,* but with at least 34 plates, including 3 or more whorls of lower latera; scutal umbo apical in Jurassic forms, subcentral in Cretaceous forms. *U.Jur.-Paleoc.,* Eu.-S. Am.-W. Australia.——Fig. 115,*5*. **Z. mockleri,* U.Cret.(Cenoman.), Eng.; reconstr., ×10 *(118)*.

Family HETERALEPADIDAE Nilsson-Cantell, 1921

Capitulum without calcareous plates; position of scuta (attachment of scutal adductor muscle) marked by small chitinous thickening on each side and below aperture; multiarticulate caudal appendages present; one or more filamentary appendages at base of first cirrus; no ovigerous frena. *Rec.*

Heteralepas Pilsbry, 1907, p. 100 [**Alepas rex* Pilsbry, 1907, p. 186, 1911, p. 171; OD]. Cirri ctenopod or lasiopod; outer rami of 2nd through 6th pairs normal; inner rami of 5th and 6th moderately to very much reduced. *Rec.,* cosmop. ——Fig. 114,*1*. **H. rex* (Pilsbry), Hawaii; ×1.5 *(80,* mod.).

Paralepas Pilsbry, 1907, p. 100 [**Alepas percarinata* Pilsbry, 1907, p. 185; 1911, p. 171; OD]. Cirri acanthopod; outer rami of 2nd through 6th stout; inner rami somewhat more slender but not reduced. *Rec.,* cosmop.——Fig. 114,2. **P. percarinata* (Pilsbry), Hawaii; ×2 *(80,* mod.).

Family IBLIDAE Leach, 1825

Capitulum of female or hermaphrodite supporting two pairs of weakly calcified plates; scuta and terga, with apical umbones. Peduncle not separated from capitulum, clothed with blunt chitinous spines. *Rec.*

Ibla Leach, 1825, p. 209 [**I. cumingi* Darwin, 1851, p. 183; SD]. Diagnosis as for family. *Rec.,* W.Afr.-IndoPac.——Fig. 114,*11*. **I. cumingi* Darwin, IndoPac.; ×4 *(37)*. [Also see Fig. 86,2.]

Family KOLEOLEPADIDAE Hiro, 1937

Capitulum of female or hermaphrodite without calcareous plates; scuta chitinous, small, left usually better developed than right; mouth parts well developed, mandible atypical; cirri biramous, short, posterior pairs acanthopod, filamentary appendage at base of first cirrus; caudal appendage uniarticulate. Male much reduced, attached at base of aperture. [Living attached between pedal disc of anemone on gastropod shell inhabited by hermit crab.] *Rec.*

Koleolepas Stebbing, 1900, p. 677 [**K. willeyi;* OD]. Characters of family. *Rec.,* IndoPac.(Loyalty Is.-Japan-Hawaii).——Fig. 114,9. *K. tinkeri* Edmondson, Hawaii; ×2 (Newman, n).

Family LEPADIDAE Darwin, 1851

Capitulum with five approximate plates *(Lepas),* five or two reduced plates *(Conchoderma),* two reduced plates *(Alepas),* or naked *(Anelasma);* scutal and carinal umbones fundamentally basal; caudal appendages continuous with thorax, simple points without long setae; first maxillae with steplike cutting edge; ovigerous frena present; peduncle naked. *?U.Trias., M.Eoc.-Rec.*

Lepas Linné, 1758, p. 667 [**L. anatifera* Linné, 1785, p. 668; SD Pilsbry, 1907]. Capitular plates

5, approximate. [Pelagic.] *?U.Trias., M.Eoc.-Rec.,* Eng.-France-Italy-Australia-all seas.

L. (Lepas). Plates well calcified; basal portion of carina forming small fork or knob. [On floating objects.] *M.Eoc.-Rec.,* Eng.-France-Italy-Australia-N.Z.——FIG. 114,*7*. **L.* (*L.*) *anatifera* LINNÉ, L.Mio. (Southland Series), N.Z.; ×0.5 *(80)*.

L. (Dosima) GRAY, 1825, p. 100 [**Lepas fascicularis* ELLIS & SOLANDER, 1786, p. 197; SD ANNANDALE, 1909, p. 72]. Plates weakly calcified; basal portion of carina forming large disc. [Pelagic; larvae attached to floating objects, subsequently forming floats of their own.] *Rec.,* all seas.——FIG. 114,*3*. **L.* (*D.*) *fascicularis* (ELLIS & SOLANDER), W.Atl.; ×1 (after *80*).

L. (Hyalolepas) ANNANDALE, 1909, p. 72 [**Dichelaspis tenuivalvata* ANNANDALE, 1906, p. 193; OD]. Plates weakly calcified; arms of basal fork of carina long, slender, running about parallel to each other along basal margins of scuta. [On sea snakes, feathers.] *Rec.,* Ind.O.——FIG. 114, *6*. *L.* (*H.*) *begalensis* DANIEL, Ind.O.; ×14 (Daniel, 1952, mod.).

Conchoderma OLFERS, 1814, p. 177 [**Lepas virgata* SPENGLER, 1790, pl. 6, fig. 9; OD]. Capitulum generally striped, typically with 5 vestigial plates or two pair of scuta in some species. [Attached to floating objects and organisms.] *Rec.,* all seas.——FIG. 114,*4a*. *C. auritum* (LINNÉ), Cape Hatteras; ×0.5 (after *80*).——FIG. 114,*4b*. **C. virgatum* (SPENGLER), Woods Hole; ×1 (after *80*).

Alepas RANG, 1829, p. 364 [**Anatifa univalvis* QUOY & GAIMARD, 1827, p. 234; (=*Alepas parasita* RANG, 1829, p. 364); SD PILSBRY, 1907]. Capitulum thin, translucent, typically with small, lobed, weakly calcified scuta. [On large medusae.] *Rec.,* cosmop.——FIG. 114,*8*. *A. pacifica* PILSBRY, Calif.; ×0.7 (after *80*).

Anelasma DARWIN, 1851, p. 169 [**Alepas squalicola* LOVÉN, 1844, p. 192; OD]. Capitulum without valves; trophi and cirri apparently functionless; peduncle with root system invading host tissues. [Parasitic on dogfish, *Etmopterus,* and *Squalus.*] *Rec.,* N.Sea.——FIG. 112,*2*. **A. squalicola* (LOVÉN); ×2 (est.) (after Darwin).

Family MALACOLEPADIDAE Hiro, 1937

Capitulum thin, membranous, without plates; mouth parts and ctenopod cirri well developed, mandible with six or seven teeth; filamentary and caudal appendages absent. [Inhabiting calcareous tubes between mantle and shell of living bivalve mollusks.] *Rec.*

Malacolepas HIRO, 1933, p. 233 [**M. conchicola;* OD]. Characters of family. *Rec.,* Japan.——FIG. 114,*5*. **M. conchicola;* ×4 (Hiro, 1933, mod.).

Family OXYNASPIDIDAE Pilsbry, 1907

Capitulum with five plates; scutal umbo subcentral; tergal umbo usually apical; carina extending upward between terga, umbo subapical to subbasal, basal portion sometimes formed into broad plate or fork. Caudal appendages minute, uniarticulate; ovigerous frena absent. [Extant forms (except *O. connectens* BROCH) on antipatharians.] *M.Eoc.-Rec.*

Oxynaspis DARWIN, 1851, p. 133 [**O. celata;* OD]. Characters of family. *Eoc.-Rec.,* Atl.O.-Ind.O.-W. Pac.-E.Pac.——FIG. 114,*12*. *O. eocenica* (WITHERS), M.Eoc., Eng.; *12a,b,* reconstr. ×8 *(120)*.

Family POECILASMATIDAE Nilsson-Cantell, 1921

[=Trilasmatidae NILSSON-CANTELL, 1934]

Capitulum typically with five calcified, approximate plates or plates five, three, or two, in varying degrees of reduction; scutum may be divided into two calcified portions, but parts always connected by chitinous ligament, having developed from common primordial plate; scutal and carinal umbones fundamentally basal; caudal appendages well developed, uniarticulate, provided with long setae; cutting edge of first maxilla not steplike; peduncle naked or with chitinous thickenings. *U. Eoc. (Barton.)-Rec.*

Trilasmis HINDS, 1844, p. 71 [**T. eburneum;* SD PILSBRY, 1928, p. 308]. Capitulum typically with 5, in one case 3, well-calcified plates; scutum entire or divided into 2 parts, umbo at rostral or basal angle. *U.Eoc.-Rec.,* Atl.-IndoPac.-Medit.

T. (Trilasmis). Capitulum with 3 well-calcified plates; terga wanting; scuta with internally visible, fused suture; carina with base expanded into large disc. *Rec.,* IndoPac.——FIG. 116,*9*. **T.* (*T.*) *eburneum* HINDS, New Guinea; ×8 *(37)*.

T. (Poecilasma) DARWIN, 1851, p. 99 [**Poecilasma kaempferi* DARWIN, 1851, p. 102; SD PILSBRY, 1907]. Capitulum with 5 approximate plates; scutum not split into 2 parts; carina not expanded laterally at base. *U.Eoc.(Barton.)-Rec.,* Atl.-IndoPac.——FIG. 116,*5*. **T.* (*P.*) *kaempferi* (DARWIN), Rec., Japan; ×5 *(37)*.

T. (Temnaspis) FISCHER, 1884, p. 357 [**Poecilasma fissa* DARWIN, 1851, p. 109; OD]. Capitulum with 5 approximate plates; scutum split into 2 parts. *L.Mio.-Rec.,* IndoPac.-Medit. (Malta I.).——FIG. 116,*8*. **T.* (*T.*) *fissus* (DARWIN), Rec., Philip. Is.; ×5 (after Darwin).

Megalasma HOEK, 1883, p. 50 [**M. striatum;* OD]. Capitulum with 5, approximate, heavily calcified plates; carina progressively larger towards base, with internal transverse shelf; scutal umbo subcentral; peduncle very short. *Rec.*, Atl.-IndoPac.-E. Pac.

M. (Megalasma). Basal margin of scutum nearly continuous with occludent margin. *Rec.*, Indo-Pac.-E.Pac.——Fig. 116,*12*. *M. (M.) bellum* (Pilsbry), ×5 *(80)*.

M. (Glyptelasma) Pilsbry, 1907, p. 87 [**Megalasma subcarinatum* Pilsbry, 1907, p. 91; OD].

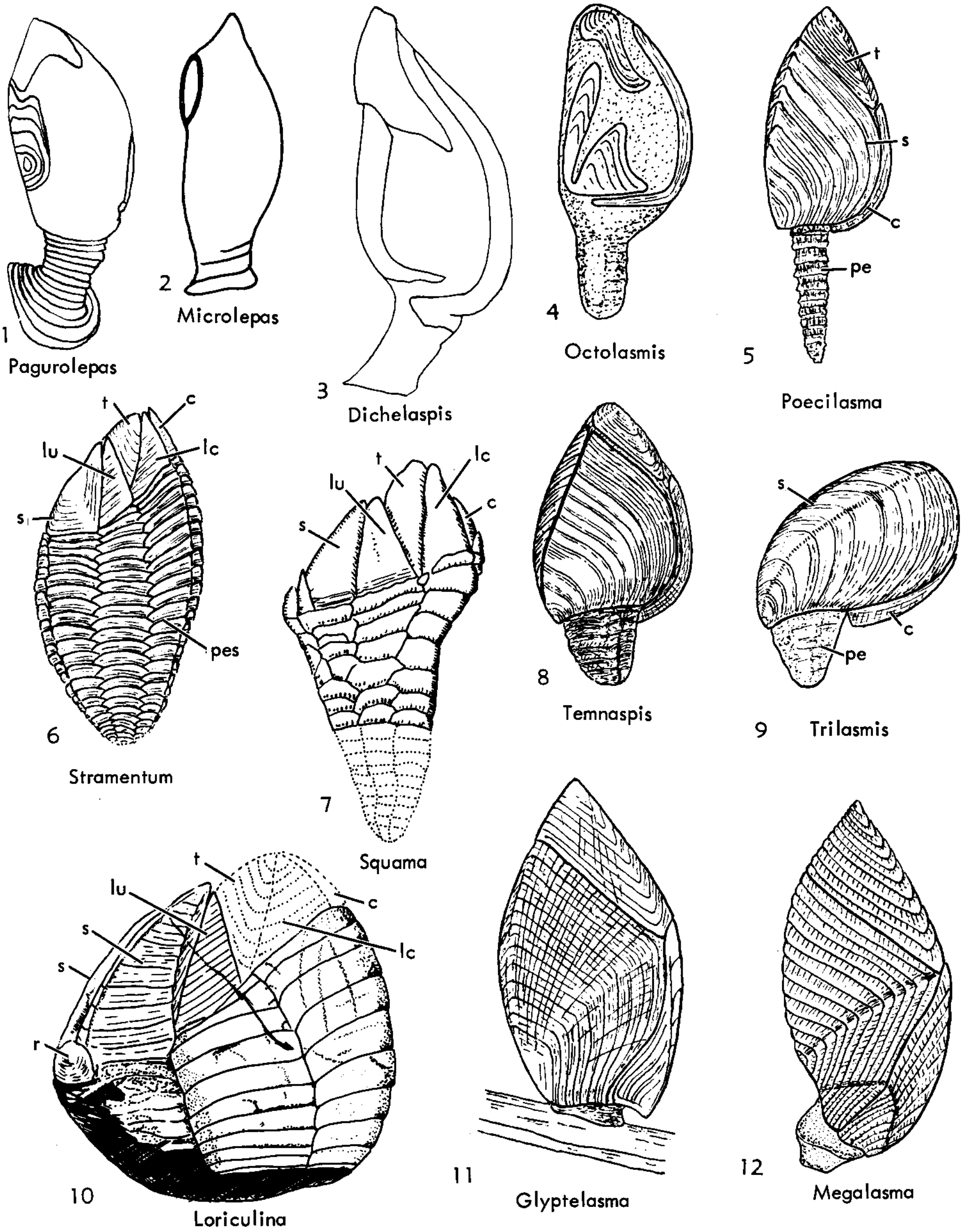

Fig. 116. Poecilasmatidae *(3-5, 9, 11-12)*, Stramentidae *(6-7, 10)*, Family Uncertain *(1-2)* (p. *R*279-*R*281). [Explanation: *c*, carina; *lc*, latus (carinal); *lu*, latus (upper); *pe*, peduncle; *pes*, peduncle scale; *r*, rostrum; *s*, scutum; *t*, tergum.]

Basal margin of scutum nearly at right angles with occludent margin. *Rec.*, Atl.-IndoPac.——Fig. 116,*11*. **M. (G.) subcarinatum* Pilsbry, USA(N.J.); ×5 *(80)*.

Octolasmis Gray, 1825, p. 100 [**O. warwickii;* OD]. Capitulum with 5, 3 or 2 incompletely calcified plates; carina extending up between terga when present. *Rec.*, cosmop., all warm seas.

O. (Octolasmis). Plates very incompletely calcified; scutum usually with 2 principal arms, connected by chitinous ligament; carina, when present, usually with slender basal fork; tergum, when present, usually with 2 or more diverging points. *Rec.*, cosmop., all warm seas and in deep water.——Fig. 116,*4*. **O. (O.) warwickii* Gray, Borneo; ×10 *(37)*.

O. (Dichelaspis) Darwin, 1851, p. 115 [**D. orthogonia;* SD Pilsbry, 1907, p. 94]. Plates 5, incompletely calcified; scutum usually with 2 principal arms calcified together at their junction; carina terminating in basal disc; tergum usually triangular, commonly with projecting points. *Rec.*, Atl.-IndoPac.——Fig. 116,*3*. *O. (D.) hawaiiense* (Pilsbry), Hawaii; ×10 (after *80*).

Family STRAMENTIDAE Withers, 1920

[=Loriculidae Pilsbry, 1916]

Capitulum short, composed of single whorl of nine to 12 plates; upper latus interposed for its whole length between scutum and tergum; carinal latus placed between carina and tergum. Peduncle composed on each side of five vertical rows of closely imbricating plates, two outer rows in free apposition. *Cret.(Alb.-Senon.)*.

Stramentum Logan, 1897, p. 188 [**Pollicipes haworthi* Williston, 1896, p. 243; SD Withers, 1920, p. 68] [=*Loricula* G. B. Sowerby, Jr., 1851, p. 81]. Capitulum of 9 plates; no rostrum; carina split longitudinally into 2 halves; scutal umbo subcentral. *Cret.(?Alb.-U.Senon.)*, Eu.-Syria-N.Am.——Fig. 116,*6*. *S. pulchellum* (Sowerby), Turon., Eng.(Kent); ×6 *(116)*.

Loriculina Dames, 1885, p. 155 [**Loricula noetlingi* Dames, 1885, p. 152; SD Withers, 1935, p. 303]. Capitular plates 10; paired scuta, upper latera, carinal latera, carina and entire rostrum; scutum elongate, umbo apical. *U.Cret.(Cenoman.-U.Senon.)*, Eu.-Syria-USA.——Fig. 116,*10*. **L. noetlingi* (Dames), U.Senon., Syria; ×6 *(118)*.

Squama Logan, 1897, p. 187 [**S. spissa;* SD Withers, 1935, p. 309]. Capitular plates probably 12, subcarina, rostrum and subrostrum in addition to plates in *Stramentum;* carina probably entire. *U.Cret.(Senon.)*, N.Am.——Fig. 116,*7*. **S. spissa,* U.Niobrara, USA(Kans.); ×1.5 *(118)*.

Family UNCERTAIN

Microlepas Hoek, 1907, p. 43 [**M. diademae;* OD]. Capitulum continuous with short peduncle, without calcareous plates; mouth parts and cirri peculiar; 1st cirrus single article, 2nd through 6th biramous, rami uniarticulate, unequal in length; no caudal appendages. [On sea urchin spines.] *Rec.*, Ind.O.(Savu Sea).——Fig. 116,*2*. **M. diadema,* Savu Sea; ×10.5 (*54*, mod.).

Pagurolepas Stubbings, 1940, p. 383 [**P. conchicola;* OD]. Capitulum with 5 calcified, reduced plates; carinal umbo basal; scutal umbo subcentral; mandible normal, 1st maxilla atypical; cirri biramous, rami each of 3 articles; caudal appendage well developed, uniarticulate. [In gastropod shells inhabited by hermit crab.] *Rec.*, Ind.O.(Zanzibar)-W.Atl.(Fla.).——Fig. 116,*1*. **P. conchicola,* Zanzibar; ×8 (Stubbings, 1936, mod.).

Rhizolepas Day, 1939, p. 64 [**R. annelidicola;* OD]. Capitulum without plates; not completely covering thorax; with chitinous ribs supporting occludent margins; peduncle long, forming root system in host; cirri uniramous, weakly developed, rami multiarticulate; ?caudal appendages multiarticulate. [Parasitic on polychaete annelid.] *Rec.*, S.Afr.——Fig. 112,*3*. **R. annelidicola,* S. Afr.; ×8.5 (after Day).

Suborder VERRUCOMORPHA Pilsbry, 1916

Cirripeds lacking peduncle; with asymmetrical shell composed of rostrum, carina, scutum, tergum, and in some forms carinal and rostral latera; remaining scutum and tergum reduced in size, forming movable lidlike top to shell; basis membranous or calcareous. *U. Cret.(?Cenoman.-U.Senon.)-Rec.*

Family VERRUCIDAE Darwin, 1854

Characters of suborder. *U.Cret.(?Cenoman.-U.Senon.)-Rec.*

Verruca Schumacher, 1817, p. 35 [**Lepas stroemia* Müller, 1776, p. 251; OD]. Wall composed of 4 compartmental plates. [Pilsbry (1916) divided *Verruca* into four sections. Broch (1922) elevated a subgroup of one of these, forming a fifth. He and other authors have used the sections as subgenera.] [Littoral-bathyal.] *U.Cret. (Senon.)-Rec.*, temp. and tropic seas (except *Rec.* in N.Pac.).

V. (Verruca) [=*Euverruca* Broch, 1924, p. 63]. Top of movable plates flat, plane nearly parallel to that of base; radioalar area between parietes of fixed scutum and tergum narrow and linear.

U.Cret.(Senon.)-Rec., cosmop.——Fig. 117,*4*. *V. (V.) prisca* Bosquet, U.Senon., Eng.; *4a,b*, ×20 *(118)*.

V. (Altiverruca) Pilsbry, 1916, p. 40 [**V. hoeki* Pilsbry, 1907, p. 113; OD]. Top nearly vertical; fixed scutum without adducor ridge; no internal recesses of general cavity. *Rec.*, cosmop.

V. (Cameraverruca) Pilsbry, 1916, p. 39 [**V.*

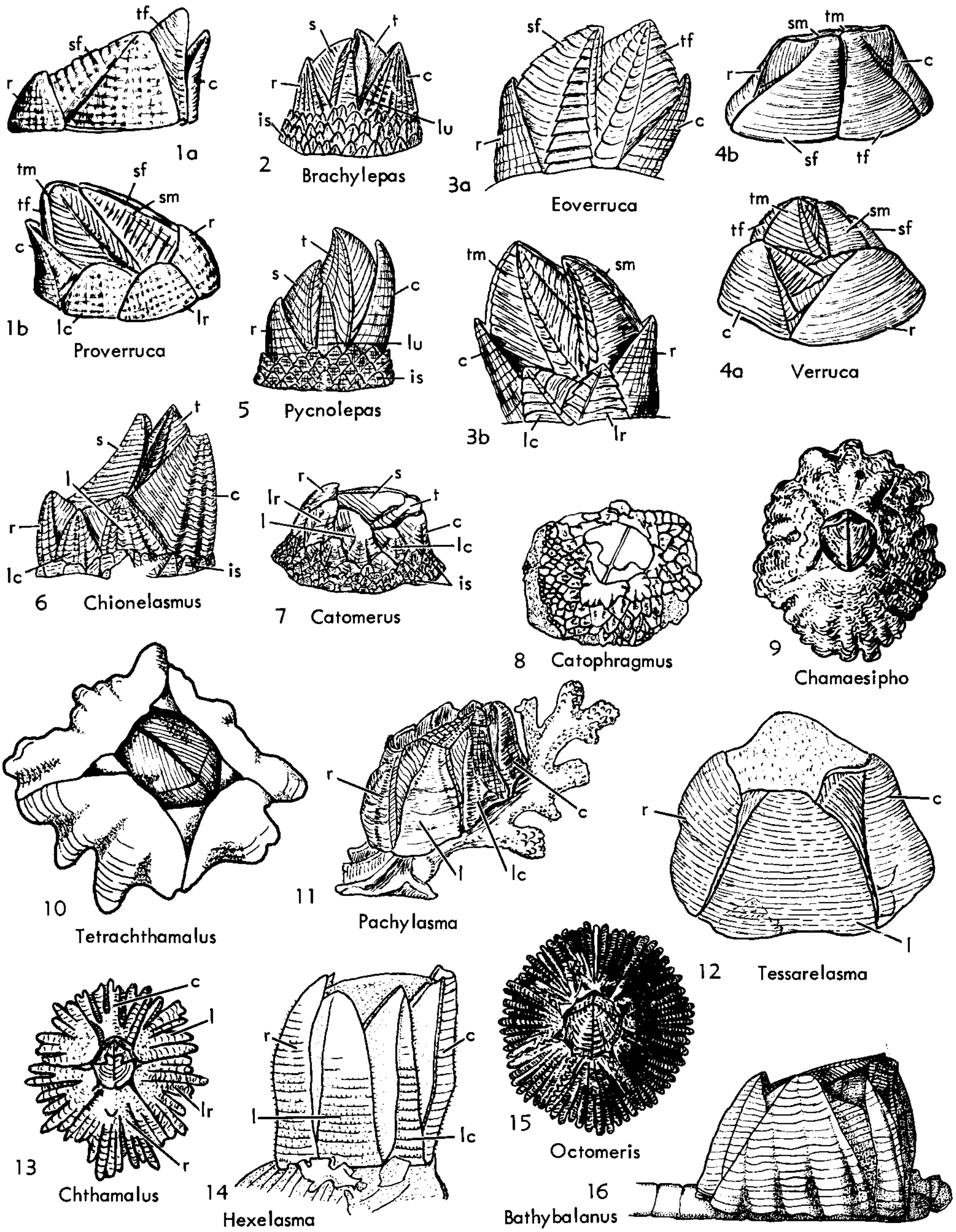

Fig. 117. Verrucidae *(1,3-4)*; Brachylepadidae *(2,5)*; Chthamalidae *(6-15)*; Balanidae *(16)* (p. *R*281-*R*285). [Explanation: *c*, carina; *is*, imbricating scales; *lc*, latus (carinal); *lr*, latus (rostral); *lu*, latus (upper); *r*, rostrum; *s*, scutum; *sf*, scutum (fixed); *sm*, scutum (movable); *t*, tergum; *tf*, tergum (fixed); *tm*, tergum (movable).]

euglypta Pilsbry, 1907, p. 108; OD]. Top steeply sloping; adductor ridge of fixed scutum forming vertical partition-like myophore; partitioned off apical cavities in fixed tergum and rostrum forming recesses of general cavity. *Rec.*, USA(Fla.).

V. (Metaverruca) Pilsbry, 1916, p. 21 [**V. coraliophila* Pilsbry, 1916, p. 21; OD]. Top flattened; basal border of wall plates inflected; adductor ridge of fixed scutum forming tongue-shaped myophore. *Rec.*, cosmop.

V. (Rostratoverruca) Broch, 1922, p. 297 [**V. nexa* Darwin, 1854, p. 522; OD]. As *V. (Verruca)*, but with apex of rostrum removed from upper edge of the plate. *Rec.*, IndoPac.

Eoverruca Withers, 1935, p. 388 [**E. hewitti;* OD]. Two lateral plates on rostrocarinal side; rostrum and carina nearly symmetrical; interlocking ribs present on fixed and movable scuta and terga. *U.Cret.(M.Senon.)*, Eng.——Fig. 117,*3*. **E. hewitti: 3a,b,* reconstr., ×20 *(118)*.

Proverruca Withers, 1914, p. 946 [**P. vinculum;* OD]. Two lateral plates on rostrocarinal side; rostrum and carina asymmetrical; plates without interlocking ribs. *U.Cret.(Turon.-U.Senon.)*, Eu. ——Fig. 117,*1*. **P. vinculum,* L.Senon., Eng.; *1a,b,* reconstr., ×15 *(118)*.

Suborder BRACHYLEPADOMORPHA Withers, 1923

Cirripeds lacking peduncle; with laterally flattened or circular, bilaterally symmetrical shell composed of rostrum and carina; with up to four whorls of smaller imbricating plates at base of wall; operculum formed of paired scuta and terga separated by long, narrow upper latus; basis membranous or calcareous. *U. Jur. (Tithon.) U. Mio. (Helvet.)*.

Family BRACHYLEPADIDAE Woodward, 1901

Character of suborder. *U.Jur.(Tithon.)-U.Mio.(Helvet.)*.

Brachylepas Woodward, 1901, p. 150 [**Emarginula(?) naissanti* Hebert, 1855, p. 374; OD]. Shell laterally flattened or circular; carina cylindrical or semiconical; outer whorls of imbricating plates with inwardly projecting ledge which fits into median basal notch on plates of inner whorl; basis membranous, except in *B. quascoi*. *U.Cret.(Turon.-Maastricht.)*, Eu.——Fig. 117,*2*. **B. naissanti* (Hebert), U.Senon., Eu.; reconstr., ×1.3 (Withers).

Pycnolepas Withers, 1914, p. 170 [**Pollicipes rigidus* Sowerby, 1836, p. 335; OD]. Shell laterally flattened; carina cylindrical; outer whorls of imbricating plates with inwardly projecting ledge bearing median basal socket (?muscle pit); basis probably membranous. *U.Jur.(Tithon.)-U.Mio.(Helvet.)*, Eu.——Fig. 117,*5*. **P. rigida* (Sowerby), L.Cret.(Alb.), Eng.; reconstr., ×3 (Withers).

Suborder BALANOMORPHA Pilsbry, 1916

Cirripeds lacking peduncle; with bilaterally symmetrical shell composed of carina, rostrum, and one to three pairs of lateral compartmental plates variously fused or totally concrescent; opercular valves when present paired, members of each pair separate, articulated or concrescent; with but one or two exceptions in the Balaninae, purely hermaphroditic. *U.Cret.(U.Senon.)-Rec.*

Family CHTHAMALIDAE Darwin, 1854

[*nom. transl.* Pilsbry, 1916 (*ex* Chthamalinae Darwin, 1854)]

Wall of eight, six, or four distinct, solid compartmental plates; some forms with one or more whorls of smaller accessory plates encircling base of wall; rostrum free or fused with rostrolaterals; carinolaterals absent in six- and four-plated groups with free rostra; inner surface of parieties without regular longitudinal ribs; cirrus *III* usually more similar in structure to cirrus *IV* than to cirrus *II*, or intermediate in structure between cirri *II* and *IV;* labral crest straight or concave, not notched, labrum usually swollen externally. *U.Cret. (U.Senon.)-Rec.*

Chthamalus Ranzani, 1817, p. 276 [**Lepas stellata* Poli, 1791, p. 29; OD]. Six compartmental plates in wall; rostrum free; carinolaterals absent; basis membranous or calcareous. [The genus falls into two natural divisions *(C. stellatus, C. hembeli)*, primarily on the form of the mandible and opercular parts (Nilsson-Cantell, 1921, p. 279, 290). These will no doubt eventually receive at least subgeneric status.] *Plio.(Piacenz.)-Rec.*, warm temp.-tropic seas.——Fig. 117,*13*. **C. stellatus* (Poli), Rec., Madeira Is.; ×4 *(39)*.

Catophragmus Sowerby, 1826, no. 28 (June 28) [**C. imbricatus* Sowerby, 1827, plate; OD]. Eight compartmental plates in wall, including rostrum, carina, 2 laterals, 2 rostrolaterals, and 2 carinolaterals; 2 or more basal whorls of accessory plates present; basis membranous or calcareous; scutum without adductor ridge. *U.Cret.(U.Senon.),* Sweden; *Rec.,* Australia-E.Pac.(Panama)-Carib.-Bermuda.

C. (Catophragmus). Plates of basal whorls few, not keeled, imbricating over sutures of inner whorls; basis calcareous, small caudal appendages present. *Rec.,* E.Pac.(Panama)-Carib.-Bermuda.——Fig. 117,*8*. *C. (C.) pilsbryi* Broch, Panama; ×1.3 (after *18*).

C. (Catomerus) Pilsbry, 1916, p. 335 [**Catophragmus polymerus* Darwin, 1854, p. 487; OD]. Plates of basal whorls numerous, carinate, imbricating over sutures of each preceding whorl, basis membranous; caudal appendages absent. *Rec.,* SE.Australia.——Fig. 117,*7*. **C. (C.) polymerus* Darwin; ×1.2 *(118)*.

C. (Pachydiadema) Withers, 1935, p. 389 [**Catophragmus cretaceus* Withers, 1935, p. 390; OD]. Basal plates arranged in more than 2 whorls, not keeled or toothed; articular ridge and furrow of both scutum and tergum weakly developed. *U.Cret.(U.Senon.),* Sweden.

Chamaesipho Darwin, 1854, p. 470 [**Lepas columna* Spengler, 1790, p. 192; SD Pope, 1965, p. 63]. Four compartmental plates in wall, including rostrum, carina, and composite lateral-rostrolaterals; basis membranous. *Rec.,* SE.Australia-N.Z.-?China seas.——Fig. 117,*9*. **C. columna* (Spengler), Australia; ×2.2 *(39)*.

Chionelasmus Pilsbry, 1911, p. 82 [**Catophragmus darwini* Pilsbry, 1907, p. 188; OD]. Six compartmental plates in shell wall, including free rostrum, carina, 2 laterals, and 2 rostrolaterals; single basal whorl of accessory plates present; basis calcareous; caudal appendages present. *Rec.,* Hawaiian Is.-Ind.O.——Fig. 117,*6*. **C. darwini* (Pilsbry), Ind.O.; ×3 *(118)*.

Hexelasma Hoek, 1913, p. 157, 244 [**H. velutinum;* SD Utinomi, 1965, p. 13]. Six compartmental plates in shell wall as in *Pachylasma,* but compound rostral plate showing no sign of fusion; radii absent; basis membranous or thinly calcareous; cirrus *III* intermediate in structure between cirri *II* and *IV;* caudal appendages absent. *?L.Oligo., L.Mio.-Rec.,* W.Pac.-SW.Pac.-Anarctic-N.Atl.——Fig. 117,*14*. **H. velutinum,* Rec., Malay Arch.; ×3.2 *(54)*.

Octomeris Sowerby, 1825, no. 26 (Nov. 8) [**O. angulosa;* OD]. Eight compartmental plates in shell wall as in *Catophragmus;* without basal whorls of accessory plates; basis membranous; caudal appendages absent. *?Pleist., Rec.,* S.Afr.-IndoPac.-Japan.——Fig. 117,*15*. *O. brunnea* Darwin), Rec., Philip. Is.; ×3 *(39)*.

Pachylasma Darwin, 1854, p. 475 [**Chthamalus giganteus* Philippi, 1836, p. 250; SD Pilsbry, 1916]. Six compartmental plates in shell wall, including tripartite rostral plate formed by partial or complete fusion of rostrum with adjoining rostrolaterals, 2 laterals, 2 carinolaterals, and carina; radii rudimentary or absent; basis calcareous; cirrus *III* similar to cirri *IV-VI;* caudal appendages present. *Mio.(Helvet.)-Rec.,* Medit.-W. Pac.-IndoPac.——Fig. 117,*11*. **P. giganteum* (Philippi), Rec., Medit.; ×2 *(39)*.

Tessarelasma Withers, 1936, p. 591 [**T. pilsbryi;* OD]. Four compartmental plates in shell wall, including compound rostral plate, 2 laterals, and carina; radii absent; basis possibly calcareous; indistinct longitudinal ribs on inner surface of parietes; opercular valves as in balanids. *L.Mio. (?Burdigal.),* India.——Fig. 117,*12*. **T. pilsbryi,* E.Bengal; ×2 *(39)*.

Tetrachthamalus Newman, 1967, p. 425 [**T. oblitteratus;* OD]. Wall composed of 4 compartments (rostrum compound, carinolaterals lacking); basis membranous; opercular parts, trophi and cirri similar to species of the *Chthamalus stellatus* group. *Rec.,* Red Sea (Gulf of Aqaba)-W.Ind.O.——Fig. 117,*10*. **T. oblitteratus;* ×10 (Newman, n).

Family BALANIDAE Leach, 1817

Wall of four or six distinct compartmental plates, or single fused plate; rostrum apparently fused with rostrolaterals, (?) or absent, forming compound rostral plate; carinolaterals usually present. Radii usually developed; parietes either solid or with parietal tubes; inner surface of parietes usually longitudinally ribbed; cirrus *III* similar in structure to cirri *I* and *II;* labrum not swollen externally; labral crest usually notched centrally, penis usually with basidorsal point. *L.Eoc.-Rec.*

Subfamily BALANINAE Leach, 1817

[*nom. transl.* Darwin, 1854 (*ex* Balanidae Leach, 1825)]

Wall of hermaphrodites composed of six, four, or single compartmental plates; parietes solid or with parietal tubes; basis membranous or calcareous; labral crest with deep, V-shaped notch; paired scuta and terga present, articulated, and filling orifice. Males, when present, variously reduced, located on interior of rostral plate. *L.Eoc. (Auvers.)-Rec.*

Balanus da Costa, 1778, p. 248 [**Lepas balanus* Linné, 1758, p. 667 (=*B. porcatus* da Costa, 1778, p. 249); SD Pilsbry, 1916, p. 49]. Wall of 6 usually rigidly articulated compartmental plates. *M.Eoc.(Auvers.)-Rec.,* all seas.

B. (Balanus). Parietes with parietal tubes; radii solid; basis calcareous. *Oligo.-Rec.,* all seas.——Fig. 118,*1*. **B. (B.) balanus* (Linné), Plio., Eng.; *1a,* shell, ×0.75; *1b,* part of basal margin, *1c,* part of basis, enl. *(39)*.——Fig. 118,*2*. *B. (B.) laevis* Bruguière, Pleist., Coquimbo, Chile; lower part of basal cup filled with bubble-like septa, ×2.5 *(40)*.

B. (Armatobalanus) Hoek, 1913, p. 159 [**B. quadrivittatus* Darwin, 1854, p. 284; SD Pilsbry, 1916]. Parietes and radii solid; radii well developed with denticulate sutural edges; basis calcareous; interior of parietes with sharp, longitudinal ribs; tergal spur wide, one third to more than one-half width of basal margin, teeth on anterior margins of some cirri. *Mio.,* USA(Md.); *Rec.,* Japan-Australia-W. Indies-USA(Calif.)-Eng. ——Fig. 118A,*6*. **B. (A.) quadrivittatus* Darwin, Rec., ×3.5 *(39)*.

B. (Austrobalanus) Pilsbry, 1916, p. 218 [**B. imperator* Darwin, 1854, p. 288; OD]. Parietes and radii (when present) solid; radii without denticles on sutural edges; internal basal edge of parietes with irregular points, ridges, or strong, irregular ribs; basis calcareous; scutum with adductor ridge and crest for lateral depressor muscle. *?Oligo.,* Chatham I.; *Rec.,* W.S.Am.-N.Z.-SE.Australia.——Fig. 118A,*7*. *B. (A.) flosculus* Darwin, Rec, S.Am.; ×1.5 *(39)*.

B. (Chirona) Gray, 1835, p. 37 [**Lepas hameri* Ascanius, 1767, p. 8; OD]. Characterized by thin, solid parietes and radii; basis calcareous; sutural edges of radii smooth or weakly crenulate; tergal spur narrow, moderately long. *Mio.-Rec.,* N. Pac.-Bering Sea-N. Atl.-Ind. O.-W. Pac.-Medit.——Fig. 118A,*9*. **B. (C.) hameri* (Ascanius), Rec., Sweden; ×1 *(39)*.

B. (Conopea) Say, 1822, p. 323 [**Lepas galeata* Linné, 1771, p. 544; OD]. Parietes of hermaphrodites(?) with or without parietal tubes; radii solid, well developed; basis calcareous, elongate along carinorostral axis, boat-shaped; shell attached to gorgonians. Males, when present, occurring on inner surface of rostral plate. *Mio.-Rec.,* Ind.O.-W.Pac.-S.Calif.-Gulf Calif.-E.C.Am.-SE. USA-W. Afr.-Medit.-N.S. Am.——Fig. 118A, *12*. *B. (C.) cymbiformis* Darwin, Rec., E.Indies; ×7 *(22)*.

B. (Hesperibalanus) Pilsbry, 1916, p. 192 [**B. hesperius;* OD]. Parieties and radii solid; basis calcareous; radii narrow with denticulate sutural edges; scutum ridged between adductor muscle scar and articular ridge; juncture between tergal spur and basal margin angulate. [*See B.(Solidobalanus).*] *Eoc.-Oligo.,* G.Brit.-France-USA; *Rec.,* N.Pac.——Fig. 118A,*8*. **B. (H.) hesperius* Pilsbry, Rec., Alaska (Bering Sea); ×2.7 *(83)*.

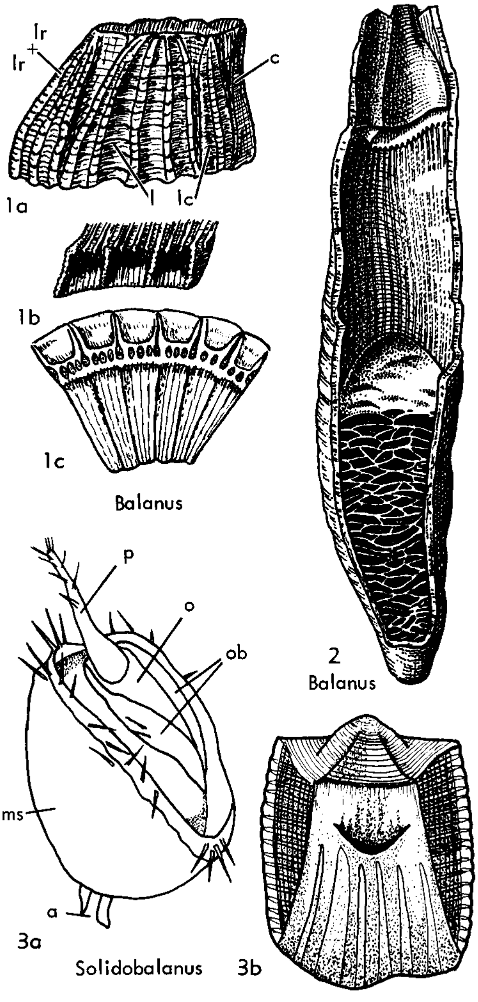

Fig. 118. Balanidae (Balaninae) (p. *R*285-*R*287). [Explanation: *a,* first antennae; *c,* carina; *l,* latus; *lc,* latus (carinal); *lr,* latus (rostral); *ms,* mantle sac; *o,* orifice; *ob,* opercular bars; *p,* penis.]

B. (Hexacreusia) Zullo, 1961, p. 72 [**B. durhami;* OD]. Parietes and radii solid; radii broad, with thick, denticulate sutural edges; sheath extending nearly to basal margin; lower edge of sheath free, continuous; basis calcareous, cup-shaped to subcylindrical; opercular valves as in *Creusia;* embedded in corals. *U.Plio.-Rec.,* Gulf Calif.-Tres Marias Is.——Fig. 118A,*5*. **B. (H.) durhami* Zullo, Rec., Gulf Calif.; ×10 (after Ross).

B. (Megabalanus) Hoek, 1913, p. 158 [**Lepas tintinnabulum* Linné, 1758, p. 668; OD]. Both parietes and radii with tubes; basis calcareous. *Oligo.-Rec.,* temp. and tropic seas.——Fig. 118A, *2*. **B. (M.) tintinnabulum* (Linné), Plio., Eng.; *2a,* shell, ×1.5; *2b,* basal margin of wall, enl. *(40)*.

B. (Membranobalanus) Hoek, 1913, p. 159 [**B. declivus* Darwin, 1854, p. 275; SD Pilsbry, 1916]. Parietes and radii thin, solid; sutural edges of radii not crenulate; basis membranous; rostrum extending below and nearly twice as long as other compartmental plates; tergal spur short, broad. *Pleist.-Rec.,* E.Indies-S.Japan-W.Indies-S.Calif.-Gulf Calif.——Fig. 118A,*10*. **B. (M.) declivus* Darwin, Rec., W.Indies; ×4.5 *(39)*.

B. (Metabalanus) Pilsbry, 1916, p. 200 [**B. hoekianus* Pilsbry, 1911, p. 77; OD]. Parieties solid; radii absent; adductor ridge of scutum absent; tergal spur well differentiated from tergal

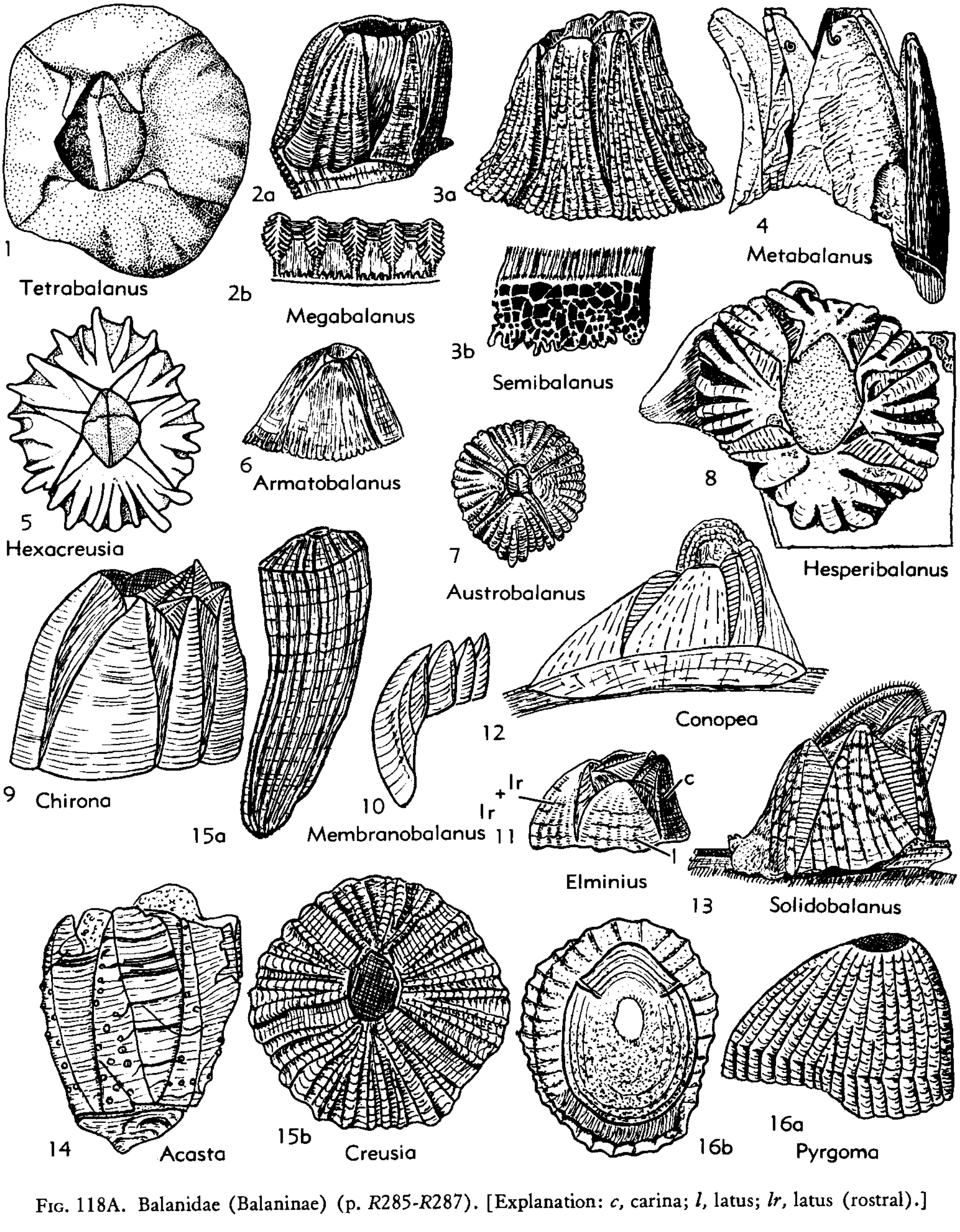

Fig. 118A. Balanidae (Balaninae) (p. R285-R287). [Explanation: *c*, carina; *l*, latus; *lr*, latus (rostral).]

margin. _Rec.,_ Bering Sea.——Fig. 118A,_4._ *_B. (M.) hoekianus_ Pilsbry; ×4 _(83)._

B. (Semibalanus) Pilsbry, 1916, p. 182 [*_Lepas cariosa_ Pallas, 1788, p. 234; OD]. Parietes with one or more rows of parietal tubes; radii solid; basis membranous; rostrum not extending downward below other compartmental plates. _M.Plio.-Rec.,_ N.Pac.-N.Atl.——Fig. 118A,_3._ *_B. (S.) cariosus_ (Pallas), Rec., NE.Pac.; _3a,_ shell, ×1.5; _3b,_ basal view of wall, enl. _(39)._

B. (Solidobalanus) Hoek, 1913, p. 159 [*_B. auricoma;_ SD Pilsbry, 1916]. Hermaphrodite with parietes and radii solid; radii well developed, with denticulate sutural edges; basis calcareous; adductor ridge of scutum reduced or absent; sides of tergal spur curving into basal margin. Complemental male, when present, may be found in pit inside rostral plate of hermaphrodite. [Includes _Hesperibalanus, fide_ Henry & McLaughlin, 1967.] _Rec.,_ RedSea-Ind.O.-W.Pac.-Hawaiian Is.-SE.Pac.-SE.Atl.——Fig. 118A,_13._ *_B. (S.) auricoma_ Hoek, N.Z.; ×3.3 _(18)._——Fig. 118, _3. B. (S.) masignotus_ Henry & McLaughlin, Rec.; _3a,_ complemental male, ×135; _3b,_ int. view of rostrum, ×1.7 (from Henry & McLaughlin, 1967).

Acasta Leach, 1817, p. 69 [*_Lepas spongites_ Poli, 1795, p. 25 (=_A. montagui_ Leach, 1817); OD] [=_Pseudacasta_ Nilsson-Cantell, 1930]. Six solid compartmental plates arranged as in _Balanus;_ radii well developed; compartmental plates weakly articulated; form of shell globose; basis solid, rounded or cup-shaped; shell not elongate along carinorostral axis; cirrus _IV_ with or without recurved teeth or hooks; commonly embedded in sponges. _L. Oligo.-Rec.,_ Ind. O.-W. Pac.-Red Sea-Medit.-W.Afr.-Eng.-SE.USA-Cuba.——Fig. 118A, _14. A._ sp. _cf. cyathus_ Darwin, Rec., Cuba; ×2 (Withers, ?n).

Bathybalanus Hoek, 1913, p. 230 [*_Balanus pentacrini_ Hoek, 1913, p. 230; OD]. Six compartmental plates solid, ribbed internally; radii well developed; basis calcareous, solid; labrum with notch; cirrus _III_ more like cirri _I_ and _II_ than cirri _IV-VI;_ caudal appendages absent. Penis with basidorsal point. _Rec.,_ Moluccas.——Fig. 117,_16._ *_B. pentacrini_ (Hoek); ×4.4 _(54)._

Creusia Leach, 1817, p. 68 [*_C. spinulosa_ Leach, 1818, p. 171; OD]. Four solid compartmental plates in shell wall, including rostral plate, carina, and 2 laterals; radii present or absent; sutural edges distinct or interlocked so as to appear to have become concrescent; basis cup-shaped to cylindrical, solid; embedded in corals. _L.Mio.-Rec.,_ Medit.-Ind.O.-W.Pac.-W.Indies.——Fig. 118A,_15a._ *_C. spinulosa,_ Rec.; ×7 (Withers, after Darwin).——Fig. 118A,_15b. C. barbadensis_ Withers, Pleist., Barbados; top view, ×6 _(115)._

Elminius Leach, 1825, p. 210 [*_E. kingii_ Gray, 1831, p. 13; SD Pilsbry, 1916, p. 260]. Wall composed of 4 solid compartmental plates, including rostral plate, carina, and 2 laterals; basis membranous. _Rec.,_ W. S. Am.-N. Z.-Australia-Azores-(introduced by ships into NE.Atl.).——Fig. 118A,_11._ *_E. kingii_ Gray, Rec., S.Am.; ×1.5 _(39)._

Kathpalmeria Ross, 1965, p. 61 [*_K. georgiana;_ OD]. Wall form of 6 solid compartmental plates; basis calcareous, solid; reentrant buttresses forming ribs on inner surface of parietes; radii narrow or wanting; scutum without adductor ridge. _L. Eoc.,_ SE.USA; _M.Eoc.,_ Eu.(Hung.).

Pyrgoma Leach, 1817, p. 68 [*_P. cancellata_ Leach, 1818, p. 161; OD]. Shell wall composed of single plate; although carinolateral sutures may be seen in sheath in some species; basis calcareous, cup-shaped or cylindrical. _Plio.-Rec.,_ Medit.-Ind.O.-W. Pac.-Carib.——Fig. 118A,_16._ *_P. anglicum_ G. B. Sowerby, Rec., W.Indies; _16a,_ shell, side view, ×7; _16b,_ shell, top view, ×7 _(115)._

Pyrgopsella Zullo, 1967 [_nom. subst. pro Pyrgopsis_ Gruvel, 1907 (_non_ Rochebrune, 1884)] [*_Pyrgopsis annandalei_ Gruvel, 1907, p. 8; OD]. Shell wall composed of single plate; basis membranous, in form of short peduncle. _Rec.,_ Andaman Is.

Tetrabalanus Cornwall, 1941, p. 227 [*_T. polygenus;_ OD]. Shell wall of 4 plates including rostral plate, carina, and 2 laterals; parietes with single row of parietal tubes; radii solid, well developed; basis calcareous with radial tubes; inner surface of parietes ribbed. _Rec.,_ Ecuador.——Fig. 118A,_1._ *_T. polygenus,_ Puna I.; ×5.5 (after Cornwall, 1941).

Subfamily TETRACLITINAE Gruvel, 1903

[_nom. transl._ Nilsson-Cantell, 1921 (_ex_ Tetraclitinae Gruvel, 1903)]

Wall composed of four compartmental plates, including rostral plate, carina, and two laterals; parietes with one row, or more commonly with many irregular rows of parietal tubes; basis usually membranous; labrum with or without moderately developed notch. _Oligo.-Rec._

Tetraclita Schumacher, 1817, p. 91 [*_Balanus squamosus_ Bruguière, 1789, p. 170 [=_Tetraclita squamulosa_ Schumacher, 1817); OD] [=_Conia_ Leach, 1817; _Asemus_ Ranzani, 1817; _Polytrema_ Férussac, 1822]. Characters of subfamily. _Oligo.-Rec.,_ all seas.

T. (Tetraclita). Two or more irregularly arranged rows of parietal tubes; radii inconspicuous; adult shell externally concrescent in some specimens; scutum with prominent adductor ridge, and crests for lateral depressor muscle; tergum narrow, elongate. _?Mio.-?Plio., Pleist.-Rec.,_ W. Ind.O.-W. Pac.-E. Pac.-SW. Atl.-S. Afr. —— Fig.

119,*2*. *T.* (*T.*) *squamosa rubescens* Darwin, 1854, Rec., USA(Calif.); *2a*, shell, ×1.5; *2b*, basal edge of wall, enl. *(39)*.

T. (Tesseropora) Pilsbry, 1916, p. 259 [**Conia rosea* Krauss, 1848, p. 136; OD]. Parietes of adult usually with single row of large parietal tubes; some with 1 or 2 secondary rows of small tubes; radii solid. *Oligo.(Lattorf.)-Rec.*, W.Pac.-Carib.-Medit.-E.Afr.——Fig. 119,*1*. **T.* (*T.*) *rosea* (Krauss), Rec., ?S.Afr.; *1a*, shell, ×1; *1b*, basal edge of wall, enl. *(39)*.

T. (Tetraclitella) Hiro, 1939, p. 273 [**Lepas purpurascens* Wood, 1815, p. 55; OD]. Parietes with more than one row of irregularly arranged parietal tubes; radii broad, with nearly horizontal summits and interseptal tubes; scutum broad with poorly developed adductor ridge and without crests for lateral depressor muscles; tergum short, broad. *Rec.*, W.Pac.-Hawaiian Is.-W. Indies-Madras.——Fig. 119,*4*. *T.* (*T.*) *divisa* Nilsson-Cantell, Hawaii; *4a*, shell from above, ×12; *4b*, view from below of basal margin on interior, enl. (Newman, n).

Subfamily CHELONIBIINAE Pilsbry, 1916

Six compartmental plates in shell wall, including tripartite rostral plate, two laterals, two carinolaterals, and carina; sheath extending to base of shell, forming inner wall of body chamber; sutures uniting rostrum and rostral plate; compartmental plates

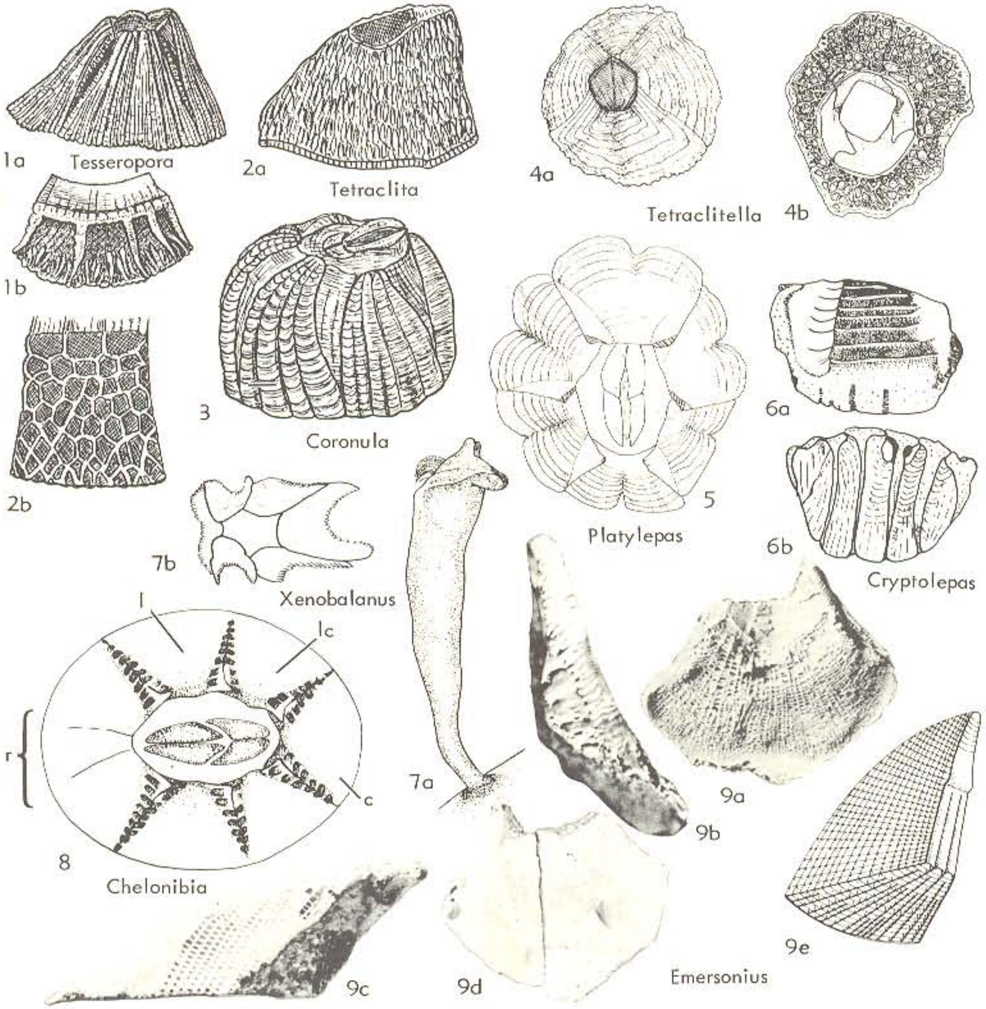

Fig. 119. Balanidae (Tetraclitinae) *(1-2, 4)*, (Chelonibiinae) *(8)*, (Coronulinae) *(3, 5-7)*, (Emersoniinae) *(9)* (p. *R*287-*R*290). [Explanation: *c*, carina; *l*, latus; *lc*, latus (carinal); *r*, rostrum.]

with cavity between outer lamina and sheath partially filled by lamellar plates normal to shell wall; basis membranous; opercular valves smaller than orifice; articular ridge of scutum chitinous. *L.Mio.-Rec.*

Chelonibia Leach, 1817, p. 68 [**Lepas testudinaria* Linné, 1757, p. 668; SD Pilsbry, 1916]. Diagnosis as for subfamily. [On turtles, sea snakes, manatees, and crabs.] *L.Mio.(Aquitan.)-Rec.*, temp. and tropic seas.——Fig. 119,*8*. **C. testudinaria* (Linné), Rec., Baja Calif.; ×1 (Newman, n).

Subfamily CORONULINAE Leach, 1825

[*nom. transl.* Pilsbry, 1916 (*ex* Coronuladae Leach, 1825)]

Six compartmental plates in shell wall, including rostral plate, two laterals, two carinolaterals, and carina; opercular valves, when present, smaller than orifice, not articulating; sheath extending nearly to base, but with inner lamina present below; basis membranous; shell attached to marine animals. *U.Mio.-Rec.*

Coronula Lamarck, 1802, p. 464 [**Lepas diadema* Linné, 1767, p. 1108; SD Pilsbry, 1916] [=*Diadema* Schumacher, 1817; *Diadema* Ranzani, 1817; *Cetopirus* Ranzani, 1817; *Polylepas* Klein, 1825; *Coronulities* Parkinson, 1833; *Polylopas* Mörch, 1852; *Ceteopirus* Mörch, 1852; *Flabelcorona* de Gregorio, 1895]. Body contained in shell wall composed of 6 equal-sized compartmental plates; opercular valves present; parieties with similar structure throughout, without internal midribs; radiating accordion-like folds of parietes (ribs) ending in T-shaped flanges forming exterior of wall; radii well developed; sheath smooth. [On cetaceans.] *U.Mio.-Rec.*, cosmop.

C. (Coronula). Orifice of body chamber larger than basal openings; sheath as long as inner wall; radiating ribs on either side of sutures unbranched or asymmetrically branched; opposed sides of terminal flanges crenulate; radii less than half thickness of compartmenal plates, leaving cavity between radii and adjacent alae. *U.Mio.-Rec.*, N. Am.-S.Am.-Eu.-Australasia-Japan.——Fig. 119,*3*. **C. (C.) diadema* (Linné), Rec., Arctic; ×1 *(39)*.

C. (Cetopirus) Ranzani, 1817, p. 276 [**Ceteopirus complanatus* Mörch, 1852, p. 67 (=*Cetopirus balaenaris* Ranzani, 1817); OD]. Orifice of body chamber equal to or smaller than basal opening; sheath shorter than inner wall; branches of sutural ribs symmetrical; opposed sides of terminal flanges not crenulate; radii almost as thick as compartments, filling cavity between adjacent plates. *Pleist.*, USA(Ore.); *Rec.*, S. Hemis.-Norway-?USA(Calif.).

Cryptolepas Dall, 1872, p. 300 [**C. rachianecti;* OD]. Body contained in shell wall; opercular valves present; parietes with similar sculpture throughout, without internal mid-ribs; radiating ribs of parietes with or without terminal T-shaped flanges; radii well developed; sheath transversely grooved. *U.Pleist.-Rec.*, N.Pac.——Fig. 119,*6*. *C. murata* Zullo, U.Pleist., Baja Calif.; *6a,* inner view of compartmental plate showing grooved sheath, ×3; *6b,* bottom view of same showing T-shaped terminal flanges, ×3 (Zullo, 1961).

Cylindrolepas Pilsbry, 1916, p. 287 [**C. darwiniana;* OD]. Cylindrical shell with orifice and basal opening of same size; bases of compartmental plates obtusely dentate, with median tooth in each compartmental plate largest, slightly inflected; sheath long; basis and opercular valves as in *Platylepas*. *Rec.*, ?W.Indies-USA(Hawaii)-E.Pac.

Platylepas Gray, 1825, p. 105 [**Lepas hexastylos* Fabricius, 1798, p. 35; OD] [=*Columellina* Bivona, 1832]. Conic shell wall composed of 6 compartmental plates, each with internal, downward projecting median rib; basis membranous, supported by median ribs; sheath short; opercular valves occupying entire orifice. *U.Pleist.*, USA (Fla.-Calif.); *Rec.*, warm temp. and tropic seas. ——Fig. 119,*5*. **P. hexastylos* (Fabricius), Rec., Baja Calif.; ×17 (Newman, n).

Stephanolepas Fischer, 1886, p. 193 [**S. muricata;* OD]. Body contained in globoconic (young) or tubular (adult) shell wall composed of 6 compartmental plates; opercular valves not distinctly articulated; parietes with median, longitudinally ridged area flanked by spinose areas bearing horizontally flattened projections irregularly arranged in transverse rings; basal opening smaller than orifice; sheath 0.7 length of inner wall. *Rec.*, Indochina-Ceylon-USA(Calif.).

Stomatolepas Pilsbry, 1910, p. 304 [**S. praegustator;* OD]. Wall bowl-shaped, with orifice larger than basal opening; composed of 6 compartmental plates, each with external median sulcus; sheath long, transversely grooved, without distinct lower edge; opercular valves thin, long, narrow; basis membranous. *Rec.*, Medit.-W.Indies-Japan.

Tubicinella Lamarck, 1802, p. 461 [**T. major;* OD]. Body contained in elongate, tubular shell wall composed of 6 equal compartmental plates; parietes similar in structure throughout, without internal mid-ribs or radial ribs or parietal folds on exterior of parietes; radii narrow; sheath transvesely grooved. [On whales.] *Rec.*, S.Hemis.-Faroe Is.

Xenobalanus Steenstrup, 1851, pl. 3, fig. 11-15 [**X. globicipitis;* OD] [=*Siphonicella* Darwin, 1852]. Lengthened body not contained in shell wall; shell star-shaped, small, composed of 6 compartmental plates embedded in skin of host; opercular valves absent. *Rec.*, Atl.-NE.Pac.——Fig. 119,*7*. **X. globicipitis,* Calif.; *7a,* shell, ×2 (Newman, n); *7b,* wall plates embedded in skin of cetacean seen from above, enl. (Newman, n).

Subfamily EMERSONIINAE Ross, 1967

[*nom. correct.* NEWMAN & ZULLO, herein (*pro* Emersoninae Ross, 1967)]

Known from single rostral plate, paries and radii of which are permeated by tubes divided into cubes by uniformly spaced transverse septa. Unique, regularly spaced, intercalated laminae occurring between inner and outer laminae, distinguish this from other known Balanomorpha. *U.Eoc.*

Emersonius Ross, 1967, p. 7 [**E. cybosyrinx;* OD; in Ross & NEWMAN, 1967]. Characteristics of subfamily. *U.Eoc.*, USA(Fla.).——FIG. 119,*9*. **E. cybosyrinx; 9a,* internal surface of rostrum, ×1.6; *9b,* lateral view of articulating surface of left radius, showing arborescent teeth, ×3; *9c,* cross section taken at primary septum showing transverse septa, intercalated laminae, inner and outer laminae, ×2; *9d,* external surface of rostral plate showing radii slightly below surface of parietes and the exposed transverse septa in tubes of right radius, ×1.5; *9e,* schematic projection of wall portion depicting relationships of transverse and longitudinal septa *(90a)*.

Order APODA Darwin, 1854

Single specimen of a parasitic crustacean described by DARWIN (1851-54), not encountered since. Body markedly segmented, but bearing only two pairs of appendages; mandibles, with fused first and possible ?second maxillae; and ?first antennae. Presumed hermaphroditic. Attached by mouth parts within the mantle cavity to prosoma of a barnacle. [Assignment to Cirripedia questioned by KRÜGER (1940); interpreted as a copepod, or more likely an epicaridean isopod *(74)*.] *Rec.*

Proteolepas DARWIN, 1854; p. 589 [**P. bivincta;* OD]. Parasitic within mantle cavity of *Heteralepas cornuta* (DARWIN), *Rec.*, W.Indies [Fig. 84, *1a-d*].

Y-larvae. Metanauplii inferred to be those of Apoda. If Cirripedia, equally and likely of Ascothoracica; if not, possibly of Branchiura.

Y-larvae HANSEN, 1899, p. 41. Metanauplii lacking frontolateral horns but otherwise resembling those of cirripeds. [Not assignable to any group in which larval forms are well known, and therefore, relegated to Apoda by HANSEN.] *Rec.*, North Sea-W.Indies-S.Atl. [Fig. 85,*2*].

Y-larvae STEUER, 1904, p. 3. Metanauplii comparable to HANSEN's *Y-larvae,* considered to be those of Apoda and named *Proteolepas hanseni* by STEUER. *Rec.*, Medit.

Y-larvae MCMURRICH, 1917, p. 50. Metanauplii apparently identical to certain of those of HANSEN. Recognized as probably of cirripeds, but assignment to Apoda considered highly speculative. *Rec.*, E.Atl.

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MALACOSTRACA

By H. K. Brooks, M. F. Glaessner, Gerhard Hahn, R. R. Hessler,
L. B. Holthuis, R. B. Manning, R. C. Moore, and W. D. I. Rolfe

CONTENTS

Class MALACOSTRACA Latreille, 1806

[Diagnosis prepared by R. C. Moore]

Crustaceans with carapace of widely varied form covering all or most of head and trunk regions, but vestigial in some. Head typically bearing paired compound eyes, commonly located at tips of movable stalks, rarely much reduced or lacking, with five pairs of appendages behind eyes, termed antennules (or first antennae), antennae (or second antennae), mandibles, maxillules, and maxillae. Trunk composed of well-differentiated thoracic and abdominal tagmata, former having eight somites and latter six (or uncommonly seven), all equipped with paired appendages except seventh abdominal somite, if present. Male genital apertures located on eighth thoracic somite (rarely on seventh) and female genital openings invariably on sixth thoracic somite. Development usually with metamorphosis, although young seldom are hatched as nauplii. *L.Cam.-Rec.*

Despite exceptional diversity in form and size, malacostracans are joined together by more numerous morphological features in common than can be found in almost any other class of Crustacea. These include 1) the carapace enveloping the thoracic region, 2) movable paired stalked eyes, 3) biramous antennules, possessed by no other crustacean group, 4) flattened scalelike exopod on the antennae, 5) pairs of pereipods adapted for swimming, 6) generally elongate, ventrally flexed abdomen, and 7) commonly developed tail fan composed of uropods and the telson. These characters suggest that the Malacostraca are descendants of crustaceans of so-called caridoid facies, resembling the shrimps.

PHYLLOCARIDA

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[Chapter submitted April, 1961; revised 1962, 1963, 1964, 1965, 1966]

CONTENTS

INTRODUCTION

Phyllocarids are an important group of malacostracans distinguished by the bivalved nature of their carapace, in this respect being reminiscent of less advanced crustacean assemblages such as the conchostracan branchiopods and the ostracodes. Unlike conchostracans and ostracodes, in which the entire body is enclosed by the two

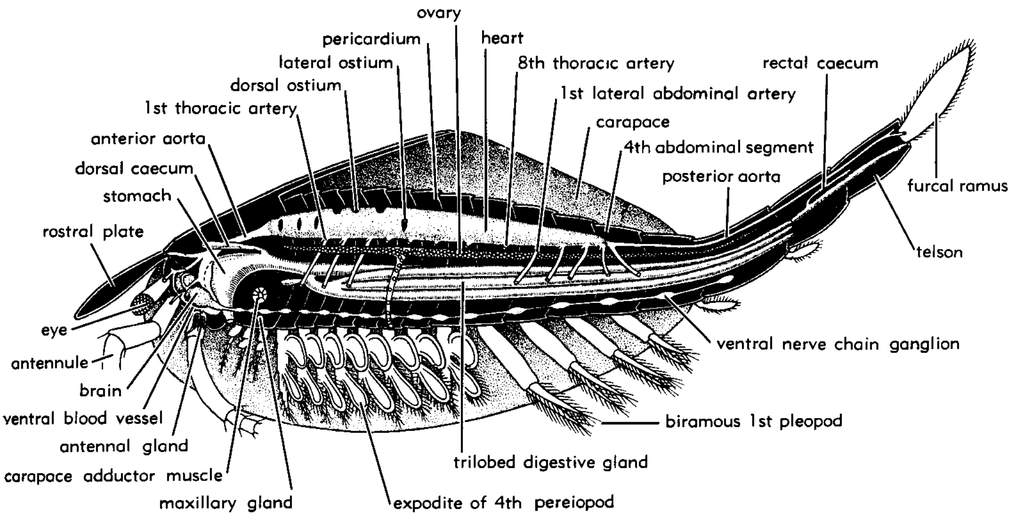


FIG. 120. Idealized figure of female *Nebalia bipes* (Fabricius), Rec., showing leptostracan morphology, ×12 (68, after 271). (From H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1.)

valves, the carapace of phyllocarids covers only the anterior parts of the body, however, and phyllocarids are relatively much larger than the other groups mentioned. Also, at the front of the phyllocarid carapace is a movably articulated lanceolate rostral plate, which is a distinctive feature.

Appendages of the head, as observed in various genera of Phyllocarida, may project well in front of the carapace margin. In addition to pairs of antennules and antennae, stalked eyes are present and may be seen in side view of individuals. The thorax, which is mainly or entirely concealed by the covering valves, consists of eight short free segments. Commonly, their appendages (thoracopods) are well-developed limbs, long enough to reach beyond the lower margins of the carapace. The abdomen is exposed partly or entirely behind the carapace and consists of seven segments and a telson. In the living phyllocarids (Leptostraca) all except the pretelson segment bear appendages, but in only a few genera of fossil phyllocarids (Archaeostraca) are abdominal appendages known with certainty. The abdominal limbs are moderately short pleopods, adapted for swimming. Appendages of the telson are the two branches of a caudal furca, which are movably articulated with the telson but unsegmented.

Phyllocarids are distributed from the Lower Cambrian to the Recent and they have wide occurrence geographically. They include the stock from which the higher Malacostraca arose, presumably during the Early Devonian.

MORPHOLOGY

The chief morphological features of Phyllocarida are shown in Figures 120 and 121 (see also Fig. 124).

SIZE

The largest leptostracan is *Nebaliopsis,* which reaches a length of about 4 cm.; the other Leptostraca are rarely longer than 12 mm. Many of the Archaeostraca, however, are very large; *Ceratiocaris ludensis* Woodward (U.Sil., Eng.) and *Schugurocaris? cornwallisensis damesi* (Chlupáč) (U.Sil., Czech.) reach a length of 75 cm., other Silurian species of *Ceratiocaris* and *Heroldina rhenana* (Broili) (L.Dev., Ger.) attaining a length of 60 cm. *C. pyriformis* Ryabinin (U.Perm., Perm. region of USSR) and Rothpletz's (1913) phyllocarid (U.Sil., Gotland) have carapace lengths of only 0.8

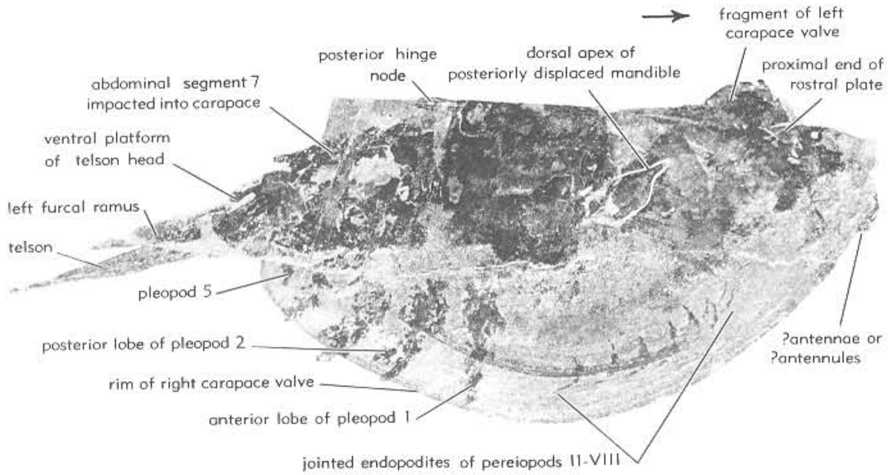


FIG. 121. *Ceratiocaris papilio* SALTER in MURCHISON, M.Sil., Scot.; showing limbs and morphological features of Archaeostraca Ceratiocarina, ×1.5 (258).

mm. and 0.7 mm. respectively, but neither of these is an undoubted phyllocarid. Possibly the smallest genuine archaeostracan is *C. oklahomensis* (RUEDEMANN) (U.Sil., Okla.), which has a total length of only 8 mm.

INTEGUMENT AND PRESERVATION

In the Leptostraca the integument is thin and flexible, whitish, and transparent or semiopaque. Typical arthropod cuticular prisms, pore canals and gland-duct openings have been described from the cuticle of *Nebalia* by CLAUS (1888).

Many Paleozoic phyllocarids occur in concretions preserved as a substance that superficially appears to be collophane. This mineraloid has only been proved by analysis in the Middle Silurian *Ceratiocaris papilio,* however, where the dark brown collophane has been partially replaced within the thickness of the cuticle by calcite and dolomite (257). The cuticle of *ca.* 50 cm.-long specimens of *C. papilio* does not normally exceed 0.6 mm. in thickness, although it is locally thickened in such regions as the tips of the mandibular teeth. Microstructures recognized in the cuticle include moniliform and spiral ?pore canals up to 17μ in external diameter and up to 4,700 per sq. mm., laminae up to 7μ thick, "Balkenlagen," and prisms up to 270μ in diameter. In many phyllocarids, the cuticle is penetrated by tubules attributable to aquatic thallophyte perforants.

Microstructure is probably detectable in many phyllocarids, and further study might enable the recognition of major stratifications needed to establish stages reached in the intermolt cycle. Prismatic structure has been detected in *Aristozoe, Caryocaris, Concavicaris, Dictyocaris, Echinocaris,* and *Montecaris.* Fossil phyllocarids, such as *Ceratiocaris,* probably had a flexible cuticle in life, although it is impossible to be certain of this in view of the ravages wrought by selective diagenesis. Others, such as *Aristozoe* and *Dithyrocaris paradoxides* (DE KONINCK), probably had a less flexible, possibly calcified cuticle. Phyllocarid cuticles show a great variety of surface sculpture, raised thick or thin anastomosing ridges or striae forming various patterns, scalelike elevated cusps, tubercles, and pits.

Phyllocarids probably formed part of the diet of contemporary predators, and GÜRICH has suggested that the fragmentary and crumpled nature of *Silesicaris* specimens indicates that they had passed through the gut of some predator (128).

CARAPACE

The carapace loosely envelops the thorax and part of the abdomen, except in *Sairo-*

GENUS	Rostral plate present	Carapace with hinge line	Carapace without hinge line	Median dorsal plate present	Anterior tubercle present	Number of thoracic segments	Number of abdominal segments	Telson present	Furca present	Cephalic appendages present	Mandible present	Thoracic appendages	Abdominal appendages	Intestinal infilling present	
Aristozoe	-	●	-	-	-	-	+3	●	-	-	-	-	-	-	?Ord.,Sil.-Dev.
Austriocaris	●	●	-	-	-	-	-	-	-	-	-	-	-	-	U.Trias.
Baituganocaris	?	●	-	-	-	-	?4	●	●	-	-	-	-	-	U.Dev.
Callizoe	-	●	-	-	●	-	-	-	-	-	-	-	-	-	L.Dev.
Canadaspis	●	●	-	-	-	?8	?7	?	?	●	-	●	-	●	M.Cam.
Caryocaris	?	●	-	-	-	-	?7	●	●	-	-	-	-	-	Ord.
Ceratiocaris	●	●	-	-	?	8	7	●	●	●	●	●	5	●	?Ord.,?Perm.
Concavicaris	●	●	-	-	-	-	-	●	●	-	-	-	-	-	Dev.-Penn.
Coreocaris	-	-	?	-	-	-	?4	●	?	?	-	-	-	-	L.Perm.
Dictyocaris	-	-	●	-	-	?8		-	-	-	-	-	-	-	Sil.-Dev.
Dithyrocaris	-	●	-	●	●	+7	7	●	●	-	●	-	-	-	Dev.-Penn.
Echinocaris	-	●	-	-	?	-	+6	●	●	-	●	-	-	?	Dev.-Miss.
Eleutherocaris	-	●	-	-	-	-	-	●	●	-	-	-	-	-	U.Dev.
Elymocaris	●	●	-	●	●	-	+6	●	●	-	●	-	-	-	Dev.
Gonatocaris	?	●	-	-	●	-	+5	?	-	-	-	-	-	-	U.Sil.
Heroldina	●	●	-	-	-	-	+5	●	●	-	-	-	-	-	L.Dev.
Hymenocaris	-	-	●	-	-	?11		●	●	?	-	-	-	-	Cam.-Ord.
Montecaris	-	●	-	-	-	+4	7	●	●	-	●	-	-	-	Dev.
Nahecaris	●	-	●	●	?	?8	7	●	●	●	●	●	5	●	L.Dev.
Odaraia	-	?	-	-	-	-	+2	-	●	-	-	-	-	-	M.Cam.
Ohiocaris	-	●	-	●	-	-	+3	●	●	-	●	●	-	-	U.Dev.
Orozoe	-	●	-	-	-	-	-	-	-	-	-	-	-	-	Dev.
Pephricaris	-	●	-	-	-	+3	?6	●	●	-	●	-	-	-	U.Dev.
Ptychocaris	-	●	-	-	-	-	-	-	-	-	-	-	-	-	Dev.
Pygocaris	●	●	-	-	-	-	+3	●	-	-	-	-	-	-	?L.Dev.
Rhinocaris	●	●	-	●	●	-	+4	●	●	-	●	●	-	-	Dev.
Saccocaris	-	-	-	-	-	-	?3	?	?	-	-	-	-	-	Cam.-Ord.
Sairocaris	-	-	●	-	-	+3	7	●	●	-	●	-	-	●	L.Carb.
Silesicaris	-	●	-	-	-	-	-	●	-	-	-	-	-	-	L.Dev.
Tropidocaris	●	●	-	●	●	-	+3	●	●	-	-	-	-	-	Dev.

FIG. 122. Morphological features observed in 30 phyllocarid genera (Rolfe, n).

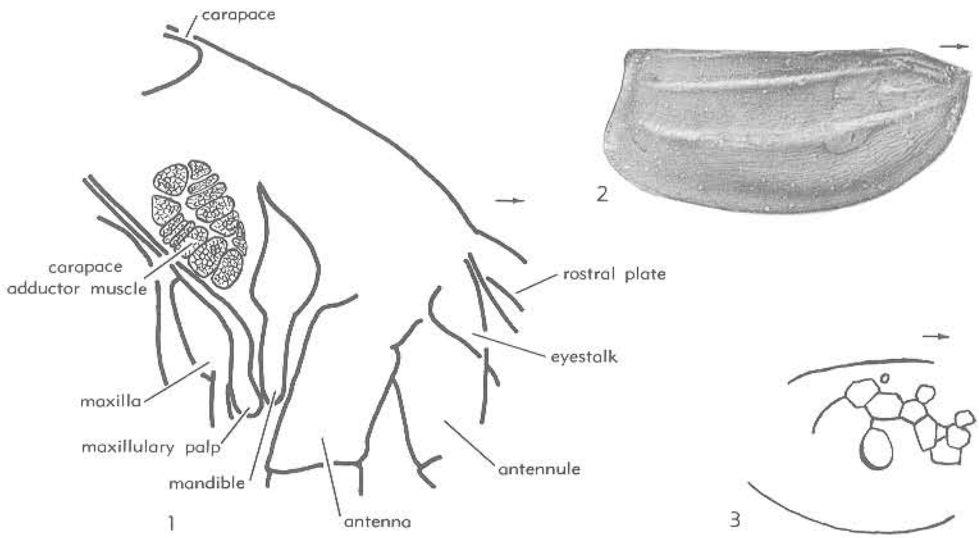


FIG. 123. Carapace muscle attachments in Phyllocarida; right lateral views.——*1.* Leptostracan *Nebalia bipes* (FABRICIUS), Rec., showing attachment of carapace adductor muscle, *ca.* ×50 (366).——*2. Tropidocaris bicarinata* BEECHER, U.Dev., USA, showing anteromedian carapace adductor and cephalic limb muscle impressions between carinae, ×6 (Rolfe, n).——*3. Ceratiocaris praecedens* CLARKE, U.Sil., USA; muscle scar on anterior tubercle, ×10 (Rolfe, n).

caris where the posterior thoracic somites are exposed, as in many mysids. It may possess or lack a **hinge line** (Fig. 122), and in species of *Ceratiocaris* the hinge line is strengthened by three simple **hinge nodes** borne on the right valve (see Fig. 136). A large carapace must be more heavily sclerotized in order to maintain its shape and a zone must be left unsclerotized to permit hingement of the valves. In smaller, weakly sclerotized carapaces there is sufficient rigidity to maintain the shape and yet enough flexibility for movement without such a hinge line. In the Rhinocarina the valves are separated by a **median dorsal plate** extending back from the anterodorsal region. A double hinge structure is thus produced which may have permitted the valves to open out laterally.

In the Leptostraca the two valves of the carapace can be approximated by the **carapace adductor muscle,** derived from the maxillary somite. It is composed of a pair of lateral bundles of muscles united medially by a horizontal ligament, and is attached to the carapace anterolaterally (Fig. 123,*1*). Well-defined scars occur in *Canadaspis* and *Tropidocaris* (Fig. 123,*2*). The muscle scar seen above the carapace adductor scar presumably indicates the attachment of a cephalic limb dorsal muscle. Although carapace adductor muscle scars have been reported from many archaeostracans, few have been adequately demonstrated.

Pits left by individual muscle bundles have been observed on what CLARKE regarded as the "distinct eye node" of *Ceratiocaris praecedens* CLARKE (Fig. 123,*3*). This raises the question of whether such nodes may not be apodemes for the attachment of cephalic muscles to an otherwise probably flimsy carapace. BEECHER (1902) observed the apical invagination of these nodes in the Rhinocarididae and suggested that they might be attachment points for mandibular muscles. Other "optic nodes" described from fossil Phyllocarida are impressions through the carapace of the thickened dorsal apex of the mandible, or scars left by epiphytic organisms, such as discinid or craniid brachiopods. Others might be genuine eye tubercles, and would have value in generic or familial classification.

However, the tubercle may or may not be discernible in individuals of the same species of *Silesicaris* (128) and *Rhinocaris,* and is a variable character within these

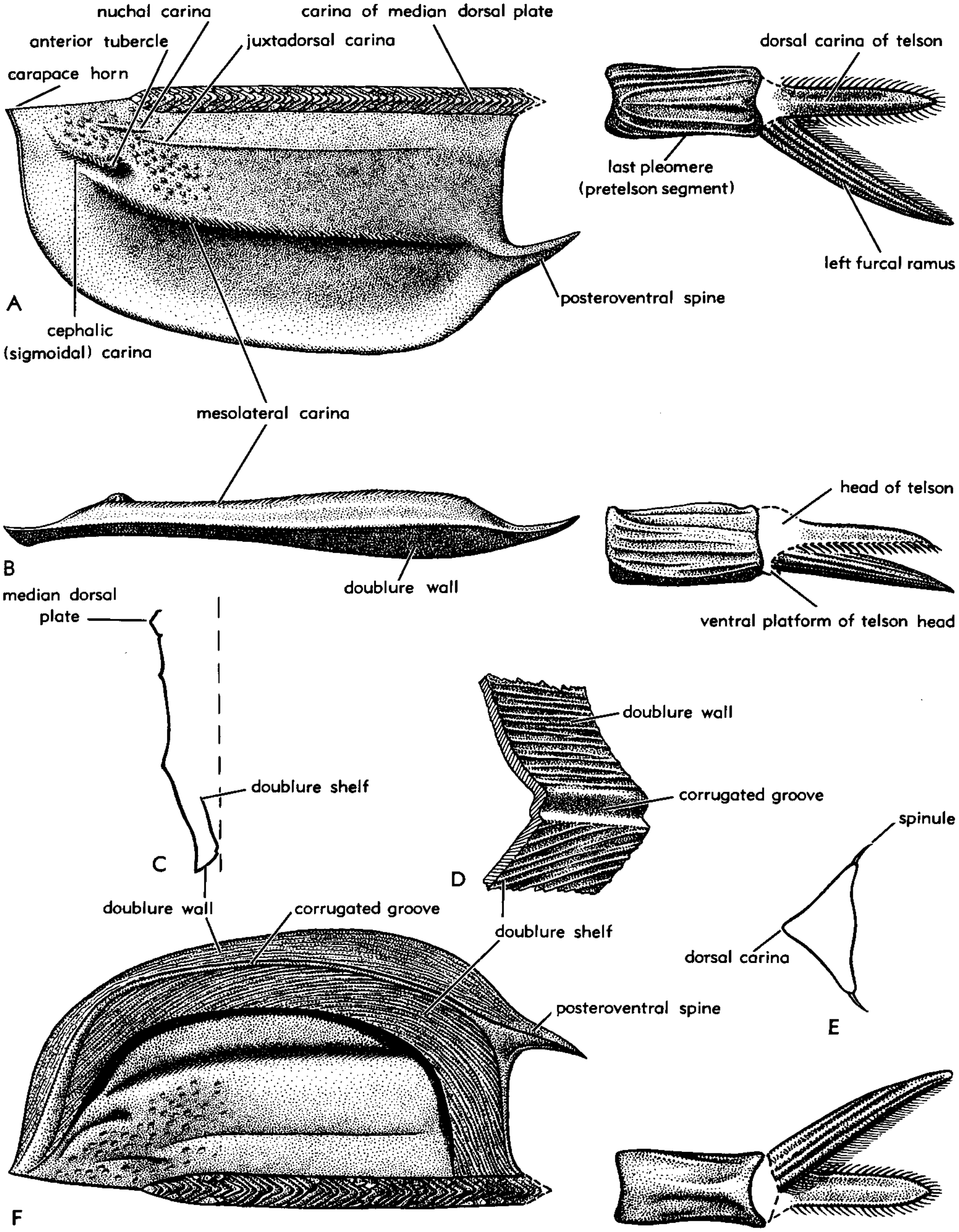


FIG. 124. *Dithyrocaris paradoxides* (DEKONINCK), L. Carb., Belg., showing morphological features of Archaeostraca Rhinocarina; only left side shown. The median dorsal plate is unknown in this species but one of *D. granulata* type has been interpolated. *A.B.* Dorsal and left lateral views, ×1. *C.* Transverse section through middle of carapace, the broken line suggesting position of horizontal plane in relation to attitude of the valve during life, ×1. *D.* Oblique view of slice of ventral doublure showing longitudinal striae of the wall and asymptotic striae of the shelf separated by corrugated groove, ×7. *E.* Transverse section through middle of telson, ×4. *F.* Ventral view, ×1 (Rolfe, n).

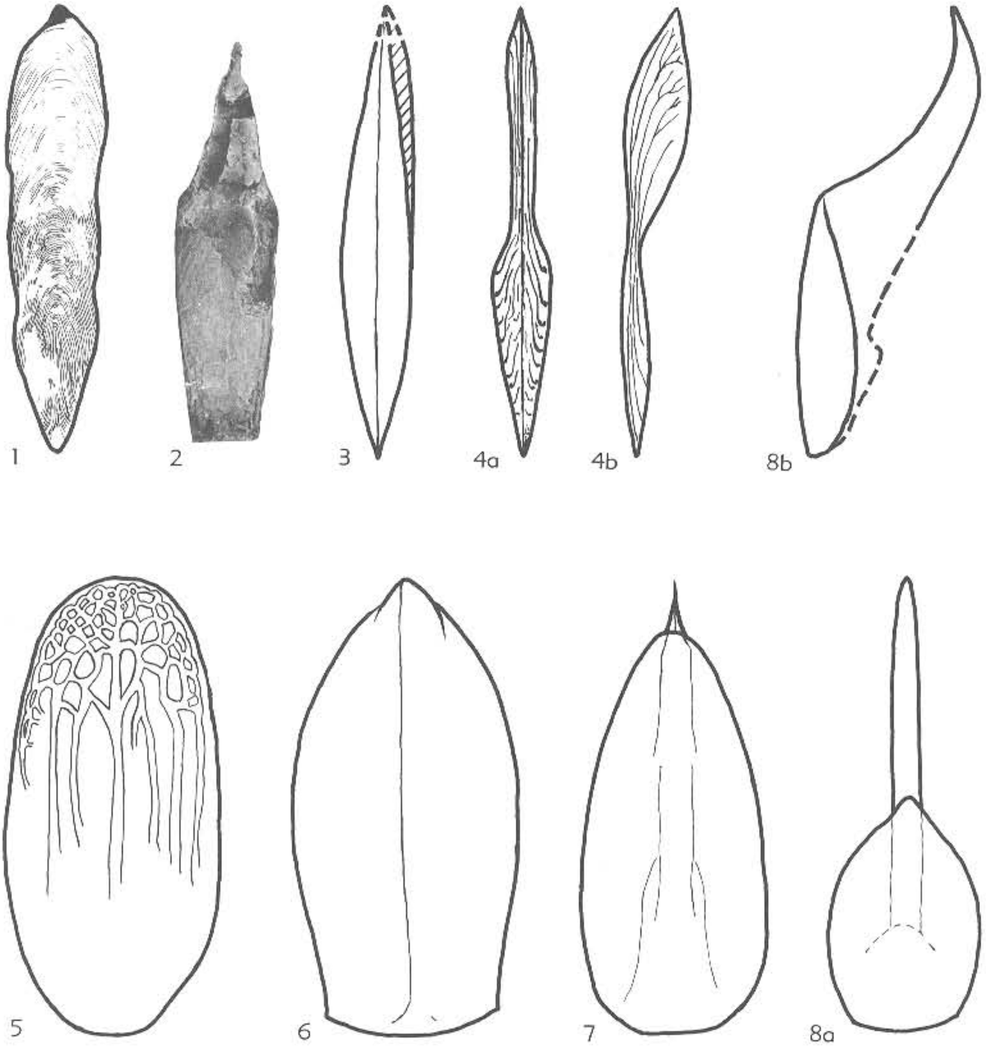


FIG. 125. Rostral plates of Phyllocarida; dorsal views, except where indicated, and oriented with anterior tip uppermost.——*1. Ceratiocaris papilio* SALTER in MURCHISON, M.Sil., Scot., ×3 (258).——*2. Pygocaris schuberti* PERNER, ?L.Dev., Czech., ×5 (Rolfe, n).——*3. Elymocaris siliqua* BEECHER, U.Dev., USA, right dors. lat., ×7.5 (Rolfe, n).——*4. Rhinocaris columbina* CLARKE in HALL & CLARKE, M.Dev.-U.Dev., USA; *4a,b,* dors., right lat., ×3.3 (351, mod.).——*5. Nebalia geoffroyi* H. MILNE-EDWARDS, Rec., Medit.-E.Atl., showing median blood vessel and afferent network, ×60 (352).——*6. Nebaliopsis typica* SARS, Rec., Atl.-Pac.-SW.Ind.O., ×20 (382a, mod.).——*7. Paranebalia longipes* (WILLEMOES-SUHM), Rec., NW. Atl.-NW.Pac., ×75 (377b).——*8. Nebaliella extrema* THIELE, Rec., Antarct.O.; *8a,b,* dors., right lat., ×46 (349, 382b).

genera. For this reason the significance previously accorded this polygenetic character is here minimized by synonymizing genera (e.g., *Emmelezoe, Limnocaris*) that are differentiated solely by the possession of such a structure (here termed **anterior tubercle**).

The carapace valves of Leptostraca are pervaded by a dense network of blood vessels and lacunae and, like the thoracopodal epipods and exopods, function as respiratory organs. Blood leaves the tubular heart anteriorly, flows through the network of each carapace valve and returns to the pericardium opposite the last lateral ostium by a large posterodorsal afferent vessel. The well-marked branching ridges on the valves of *Carnarvonia* (see Fig. 149), *Rhinocaris,* and *Tropidocaris* (see Fig. 146) mark the position of internal grooves which possibly accommodated afferent blood vessels. These genera show a similar pattern of a posterior group of vessels converging into one main vessel which terminates anteriorly just dorsal from the carapace adductor muscle. This contrasts with the subvertical direction of the main blood vessel in the Ostracoda (HENNINGSMOEN, 1954, p. 55).

In the Aristozoidae and Echinocarididae the anterodorsal region of the carapace is inflated into lobes, which BEECHER attempted to correlate with subjacent cephalic appendages. Most of the lobes are situated too far dorsally to mark the position of such appendages, however.

A thickened rim is present along the free margin of most archaeostracan carapaces, in some forms separated from the main area of the valves by a marginal groove. This rim is distally reflected to form a **doublure,** in life connected with the cephalon by thin unsclerotized integument. The doublure is usually simple, but it may be elaborated into a proximal wall and a distal shelf in species of *Dithyrocaris* (Fig. 124). These marginal structures are commonly impressed through the outer integument of the carapace during diagenesis.

Anterodorsally, the carapace valve may terminate in a thickened **carapace horn,** which abuts against the thickened tip of the rostral plate in *Ceratiocaris.* In *Caryocaris maccoyi* (ETHERIDGE), the right and left carapace horns are produced into long slender processes, but they do not fuse together to form the eumalacostracan type of rostrum.

ROSTRAL PLATE

The carapace is produced anteriorly into a movable **rostral plate.** In the Archaeostraca the few rostral plates known (Fig. 122) are situated more dorsally than in Recent Leptostraca, where the rostral complex (68) is specialized for feeding. Figure 125 shows the variation in shape of phyllocarid rostral plates, which suggests that this structure may be of use for future classification of the Archaeostraca.

EYES

Pedunculate compound eyes are present in Leptostraca, although the ommatidia have been lost in *Nebaliella* and *Nebalia typhlops.* Stalked eyes are known only from *Canadaspis* (see Fig. 149) and *Nahecaris,* but presumably most Archaeostraca had such eyes. The supposedly sessile eyes have been discussed above.

TRUNK

Two tagma can be distinguished in the trunk of Leptostraca and in several Archaeostraca (Fig. 122). These comprise a thorax of eight short segments, and an abdomen of eight longer segments, including the telson. Short pleurae may be present on the pleomeres of Leptostraca and Archaeostraca; large pleural spines are found in *Montecaris lehmanni* and *Pephricaris.*

In the Leptostraca, and also probably in the Hymenostraca, the telson resembles the preceding pleomeres except that it bears a pair of posteroventral spines and the **furcal rami** at its distal end. In the Archaeostraca, however, the telson is produced dorsally between the furcal rami, which articulate proximally with the enlarged **telson head.** The furcal rami are commonly rodlike, but in *Nebaliopsis* and many Archaeostraca they are dorsoventrally flattened. In many Archaeostraca these expanded and densely setiferous rami formed with the flattened telson an efficient swimming structure analogous to the eumalacostracan tail fan (27). The archaeostracan telson head usually bears a **ventral platform** embracing the proximal part of the furca. In one species of *Schugurocaris?* (Fig. 126) the ventral surface of the telson head has a large area without cuticle, which probably was originally filled by the unsclerotized integument around the anus. The small median process just in front of this area (Fig. 126) is homologous with that in *Aristozoe regina* BARRANDE, which NOVÁK suggested controlled ventral flexure of the telson.

The spiniferous telson of the small *Ceratiocaris pusilla* MATTHEW is unusual in having been whiplike and flexible during life.

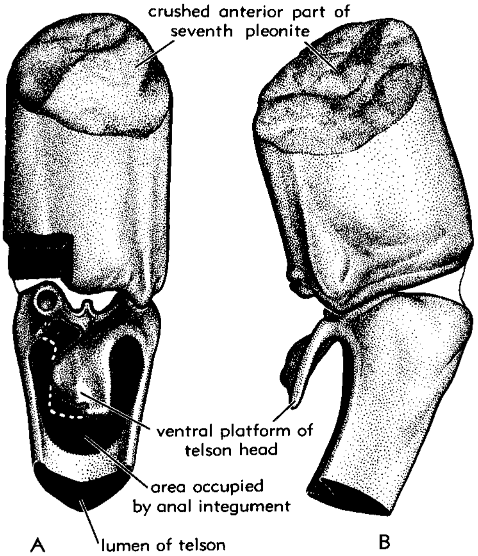


FIG. 126. Seventh pleonite (crushed anteriorly) and telson head of *Schugurocaris? cornwallisensis damesi* (Chlupáč), U.Sil., Czech., showing articulation, ventral platform of telson head and space originally occupied by thin anal integument.——*A*. Ventral view, with right posteroventral process of pleonite cut away to show telson socket, ×1.——*B*. Left lateral view, ×1 (376b, mod.).

Dorsal spinules on the telson of *C. papilio* are set in thin-walled sockets (see Fig. 136), and were probably sensory.

APPENDAGES

The limbs of fossil Phyllocarida are poorly known, with the exception of the mandible, which has been recorded from numerous genera (Fig. 122). The following list tabulates the major records of such limbs with a brief description of each.

Fossil Phyllocarida Appendages

Canadaspis perfecta (Walcott), *M.Cam.*, B.C.; uniramous antenna, ?cephalic limbs, eight thoracopods composed of eight short segments with basal nonfilamentous ?epipod (Walcott, 1912; Størmer, 1944).

Ceratiocaris telleri (Whitfield) and *C. monroei* Whitfield, *U.Sil.*, USA(Wis.); limb fragments (Whitfield, 1896).

Ceratiocaris papilio Salter in Murchison, *M.Sil.*, Scot.; ?antennae, ?maxillipeds, seven slender thoracic endopods of at least four segments, five stouter pleopods (Jones & Woodward, 1888; Rolfe, 1962).

Coreocaris eishunensis Kobayashi, *L.Perm.*, S.Korea; ?antennae (Kobayashi, 1937).

Dithyrocaris sp., *L.Carb.*, N.Fr.; cephalic limb fragments (Carpentier, 1913).

Dithyrocaris? sp., *L.Carb.*, S.Fr.; thoracic branchiae (Böhm, 1935).

Hymenocaris ornata Sherrard, *L.Ord.*, S.E.Australia; ?antennae (Sherrard, 1930).

Nahecaris stuertzi Jaekel, *L.Dev.*, Ger.; antennae, eight thoracopods, five pleopods (Broili, 1928, 1929).

Nahecaris balssi Broili, *L.Dev.*, Ger.; antennae (Broili, 1930).

Ohiocaris wycoffi Rolfe, *U.Dev.*, USA(Ohio); four thoracic ?endopods (Rolfe, 1962).

Rhinocaris? bipennis Clarke, *U.Dev.*, USA(N.Y.); cephalic or thoracic limb fragments (Clarke, 1898).

The archaeostracan mandible is well known only from *Ceratiocaris*, but that of other genera seems to have been identical. As can be seen in Fig. 127,*2* the mandible is of generalized type, with a large inflated **mandible body** (corpus mandibulae) and a **gnathal lobe** set with paired incisor teeth and a simple molar process. In two species of *Ceratiocaris* the molar process is known to have a broad, laterally ridged surface for grinding (Fig. 127,*1*). The large **mandi-**

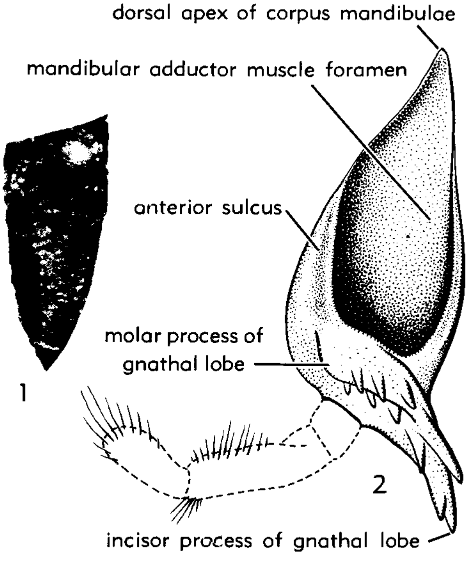


FIG. 127. Mandible of *Ceratiocaris*.——*1*. *C. monroei* Whitfield, U.Sil., USA(Wis.), tooth base and ridged molar process of left mandible, ×6 (258). ——*2*. *C. papilio* Salter in Murchison, M.Sil., Scot., right mandible, mesial view, with palp of *Anaspides* type reconstr., ×6 (Rolfe, n).

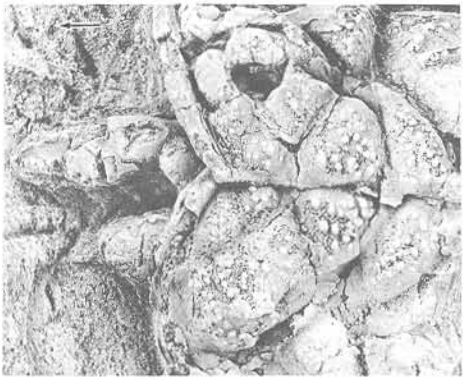


FIG. 128. *Echinocaris randallii?* BEECHER, L.Miss., USA(Pa.), three segmented ?mandibular palps at left, protruding from anterior of carapace valves, ×2.4 (Rolfe, n). [According to K. E. CASTER, the right appendage was chelate when the specimen was originally collected by him.]

bular adductor muscle foramen for the transverse adductor muscle is rimmed by shallow anterior and posterior sulci marking internal ridges for attachment of dorsal muscles. BEECHER's "manubrium" was simply a part of the corpus mandibulae preserved adjacent to this foramen. A palp has not been found in *Ceratiocaris*, although a small circular **palp foramen** is always present. A **palp** of at least three segments is present in *Echinocaris punctata* (HALL) and this was figured, although not recognized as such, by HALL & CLARKE (140, pl. 29, fig. 7). The stout, three-segmented appendages occasionally found protruding from the carapace of *Echinocaris* may be mandibular palps (Fig. 128).

No proof has been found that gastric teeth or ossicles are present in the Archaeostraca, although such teeth might be expected to occur. The structures referred to as such by previous authors are the heavily sclerotized, commonly abraded, gnathal lobes of the mandible, which are commonly all that remains after the thinner corpus mandibulae has been broken off or crushed. The broader teeth illustrated by JONES & WOODWARD (160, pl. 26) are internal molds of the paired, thick-walled teeth, and not the surface of the cuticle.

The significance of the cephalic limbs of *Nahecaris* and the thoracopods of *Canadaspis* will be discussed under phylogeny, but it may be emphasized here that knowledge of the limb structure of these genera is inadequate for phylogenetic speculation.

Filamentous thoracic branchiae have been figured from *Dithyrocaris*; they are unknown in other Phyllocarida, however, and detailed study is required.

The least specialized leptostracan thoracopods are found in *Paranebalia*, and these contrast with the specialized thoracopods of *Nebalia*, which have large epipods and exopods (Fig. 129). The thoracopods are all similar, except in *Nebaliopsis*, where the first limb is modified to act as an interlimb space valve. In all Leptostraca except *Nebaliopsis*, the tip of each thoracic endopod of the breeding female carries long setae which curve inward to form the floor of a brood chamber in which the embryos develop.

Five pairs of lamellar pleopods occur in *Nahecaris* and probably also in *Ceratiocaris papilio*. In the Leptostraca six pairs of pleopods are present but only the first four are large and biramous, the posterior two being small and uniramous. The right and left limbs of the anterior four pairs are linked together by a small spined appendix interna at the base of the endopod to form powerful swimmerets.

SEXUAL DIMORPHISM

All Recent Leptostraca, except *Nebaliopsis,* show pronounced sexual dimorphism. Males also occur much more rarely than females. The carapace of the male is less deep than that of the female and the antennae are much longer (Fig. 130). In the male *Nebalia* the antennae may reach to the tips of the furca, whereas in the female they are shorter than the carapace. The furca of the male *Nebalia* is also longer than that of the female, the pleopods are larger and the antennules bear a greater number of sensory bristles.

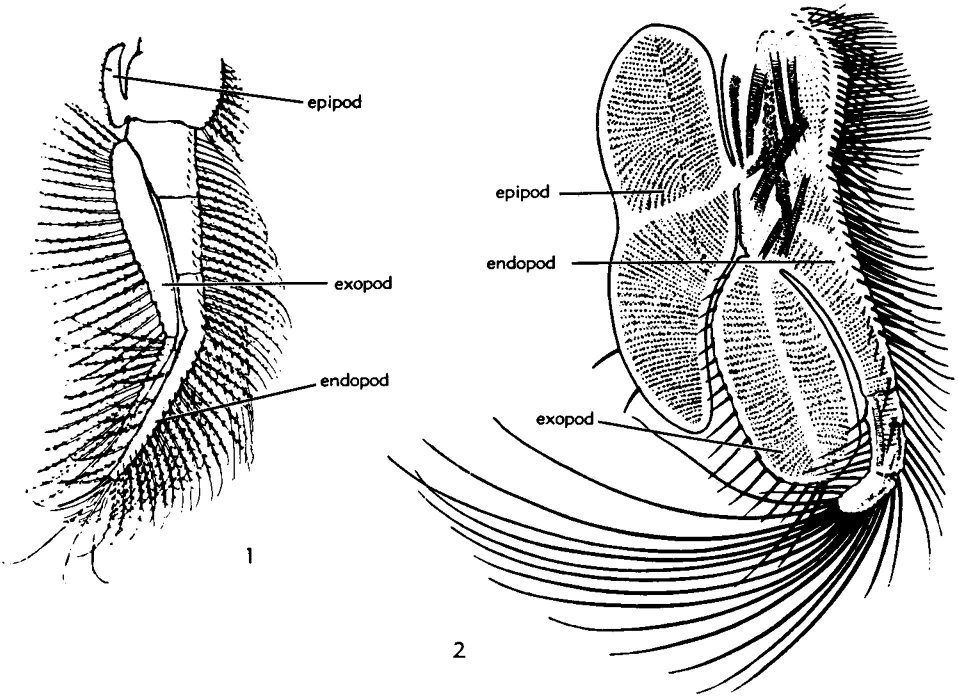


Fig. 129. Thoracopods of Recent Leptostraca showing little specialized and highly specialized conditions. ——*1. Paranebalia longipes* (Willemoes-Suhm), fifth thoracopod of adult female, ×40 (65, after 377b). ——*2. Nebalia geoffroyi* H. Milne-Edwards, first thoracopod of adult female, *ca.* ×25 (68, after 352). (Fig. 129,*1* from W. T. Calman in Lankester Treatise on Zoology, Pt. 7, Appendiculata, fasc. 3, A. & C. Black, Ltd., publishers, London; Fig. 129,*2*, from H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1.)

The antennules or antennae of the male may be modified in different genera, presumably to function as clasping organs. *Nebalia pugetensis* (Clark) has an anteriorly curved, sickle-shaped region of the antenna consisting of about 30 segments, each segment bearing in front a spoon-shaped seta. In *Paranebalia* the antennular flagellum is transformed into a papillate cushion, and in *Nebaliopsis* the two terminal segments of the antenna are bent back to form a hook.

The ratio of carapace length to height has been used to differentiate species of *Ceratiocaris* and *Caryocaris*, although paleontologists since Salter have been aware of the problem of sexual dimorphism. Scottish Silurian species of *Ceratiocaris* have been examined statistically but no significant difference in carapace shape was found between forms previously regarded as sexual dimorphs and distinct species. Variation within one species of *Austriocaris* was attributed by Glaessner to sexual dimorphism.

PATHOLOGY

Fig. 131 shows a specimen of *Dithyrocaris* in which the mesolateral carina has been bowed out, presumably owing to a wound received during the soft-shell period of the molt cycle.

MISIDENTIFICATION

Fossil phyllocarids have commonly been misidentified, perhaps for the first time by Louis Agassiz, who in 1837 referred a species to his fish-spine genus *Onchus*. Barrande (1853) showed that this was neither *Onchus*, nor a eurypterid claw, as M'Coy had suggested in 1849, but the telson and furcal ramus of a species of M'Coy's own crustacean genus *Ceratiocaris*, previously known only from carapaces. Other instances

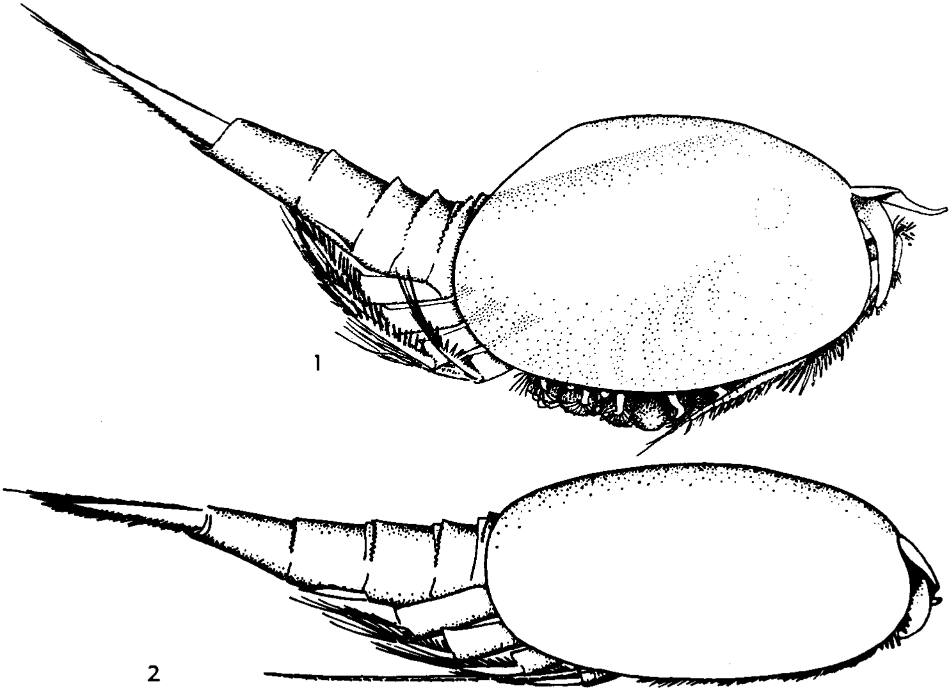


FIG. 130. Sexual dimorphism in *Nebaliella extrema* THIELE, Rec., right lateral view.——*1.* Female, ×10 (349).——*2.* Male, *ca.* ×20 (68) (Fig. 129,*2*, from H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1).

of archaeostracan telsons and furcal rami being mistaken for fish spines are known, although they are quite distinct in general morphology and especially in microstructure.

Isolated archaeostracan carapaces may be difficult to distinguish from Bivalvia, and numerous carapaces now regarded as Ostracoda Archaeocopida are indistinguishable, except by their smaller size, from carapaces referred to the Phyllocarida. Whether such resemblances as that of the large *Pseudoarctolepis sharpi* to the ostracode *Pteroleperditia* are only due to convergence it is impossible to say. Convergent resemblances among crustacean carapaces are well known, as ROGER (1946) has pointed out, and carapaces should therefore not be referred to the Archaeostraca until the trunk tagma and furca are known. It is worth recalling that the Recent phyllocarid *Nebaliopsis* was first described as a gigantic ostracode, since only the carapace was brought up in the dredge.

Carapaces, telsons, and furcal rami of *Caryocaris* have been interpreted as graptolite rhabdosomes, floats, and "ovarian capsules," primarily on account of their occurrence in graptolite-rich shales.

Isolated archaeostracan mandibles are sometimes regarded as problematica, and CHLUPÁČ (73) has pointed out such an instance where gnathal lobes were described in a 1958 work on conodonts.

ONTOGENY

The eggs of all Leptostraca, except possibly in *Nebaliopsis,* are carried in the thoracopod brood chamber beneath the carapace. Development is embryonic and the young hatch as postlarvae. These postlarval or **mancoid stages,** as LINDER has termed them, differ from the adults in having a rudimentary 4th pleopod. CANNON has recently attributed a free-swimming, pelagic larva to *Nebaliopsis* (68), and suggested that the eggs of *Nebaliopsis* were laid

Fig. 131. Pathological right valve of *Dithyrocaris paradoxides* (deKoninck), L.Carb., Belg., rubber mold of fragment showing mesolateral carina bowed out in median region; (compare with normal valve shown in Fig. 124,A), ×3 (Rolfe, n).

directly in the water. The presence of large antennae and yolk mass in the larva are, Cannon has suggested, adaptations for this planktonic existence.

HABITAT, DISTRIBUTION, AND HABITS

The only nonmarine form attributed to the Phyllocarida is the problematical *Coreocaris*. Other fossil genera are associated with undoubtedly marine faunas, or with primitive vertebrates and eurypterids. The second association is almost always enhanced by selective diagenesis of calcareous shells, with consequent enrichment of the preserved fauna in the noncalcified elements. No convincing evidence is found to indicate that the Archaeostraca were either fluviatile (O'Connell) or "continental" (Jux, 162).

Fossil phyllocarids are generally rare, although they are locally abundant in the Middle Silurian laminated siltstones of Lesmahagow, South Scotland, the Upper Devonian of Cologne, Germany, and of Western Australia, the Visean limestones of Visé, Belgium, and the Middle Pennsylvanian Mecca Shale of Indiana.

The wide distribution of the fossil *Caryocaris* and Recent *Nebaliopsis* is doubtless correlated with their large expanded furcal rami, which made sustained swimming possible. *Nebaliopsis* is bathypelagic and lives at depths down to 2,500 m., whereas *Caryocaris* occurs in graptolitic shales and has been suggested to be planktonic. The remaining Leptostraca are bottom-dwellers and commonly live buried in the mud or under stones in shallow coastal waters, although species occur down to depths of 2,200 m. *Nebalia bipes* is extremely widespread, very resistant to unfavorable conditions, and thrives in water foul with decaying organic matter (65).

From studies of facies in Czechoslovakia and Eastern Europe, Chlupáč (73) and Krestovnikov (168) have independently concluded that the thick-shelled forms *Aristozoe, Callizoe,* and *Orozoe* were benthonic and confined to shallow reef environments. Genera with a thinner cuticle, such as *Ceratiocaris,* they suggested were nektonic and planktonic and favored calmer, coastal lagoonal or neritic habitats. The Upper Permian *Nebalia? bentzi* inhabited shallow, coastal marine conditions, according to Malzahn (186).

Although all Leptostraca are strong swimmers, only *Nebaliopsis* is adapted for a nektonic life. The other genera are highly adapted for burrowing in the mud, and such features as the plowshare-like rostral plate, the blind, curved eyestalks, and the extra segment in the antenna of *Nebaliella* have all been explained by Cannon as modifications to that end. *Nebalia* has an extremely efficient feeding mechanism for collecting the fine edible detritus from the mud, and this has been described in great detail by Cannon (1927). A feeding-respiratory current is sucked into a **filter chamber,** formed by the thoracopods and ventral body wall, by metachronal movements of the thoracopods. The current enters anteriorly, since the lamellar epipods and exopods act as valves preventing the lateral entry of water, while the amount entering is controlled by elevating or depressing the rostral plate. Food particles are filtered off by rows of setae on the endopodites and then combed from the filter setae and passed anteriorly to the mouth parts by other setae. The filtered current of water is then pumped laterally out of the chamber by the eighth thoracopods via the seventh interlimb space. When the filter chamber is blocked with eggs, the female utilizes food reserves stored in the fat-body.

FIG. 132. X-ray photograph of *Nahecaris stuertzi* JAEKEL, L.Dev., Ger., dors., showing mud-filling of intestine (light) through pyritized (dark) abdomen, ×0.75 (Rolfe, n).

Nebaliopsis is specialized for feeding in quite a different way, as ROWETT has shown (1943, 1946). Although it possesses a filter chamber formed by the maxilla and first thoracopod, its main sustenance is probably derived from eggs floating in the water. These are sucked in and stored in the large midgut diverticulum and assimilated as required.

The alimentary canal of many fossil phyllocarids may be traced by the sediment originally filling the gut (Fig. 132). This suggests that these genera were deposit-feeders, which probably, like CANNON's "ancestral *Nebalia,* would have fed simply on large pieces of detritus picked up directly by the mouth parts." The powerful archaeostracan mandible would be very suitable for dealing with large fragments.

BROILI (1928) has interpreted the antennae of *Nahecaris* as locomotory organs and suggested that the body limbs formed good swimmerets. The telson and furca were doubtless moved by powerful muscles situated in the elongated seventh abdominal segment, and BROILI has pointed out that the tail was probably used in swimming and steering. BEURLEN (1930) has suggested that most Archaeostraca were benthonic and that the furcal spines were used in leaping forward.

Rhinocarididae, such as *Dithyrocaris,* may have had their carapace valves spread out laterally during life, suggesting a benthonic habit. This would imply considerable modification of the limbs and internal structures such as the carapace adductor muscle.

PHYLOGENY

The lack of detailed morphological data for most fossil phyllocarids, rightly emphasized by neontologists since CLAUS, has led to much speculation about their affinities. They have been compared with Notostraca, Conchostraca, Ostracoda, and free-living Cirripedia by FEDOTOV and others, and with Eumalacostraca Euphausiacea by ROGER (256). Although some specimens may belong to some of these groups, no basis is seen for JUX's assertion (162) that all Archaeostraca should be referred to the Branchiopoda. The number and tagmosis of body segments and limbs, and the differentiation of the gnathal lobe of the mandible into incisor and molar processes, known from some of the Archaeostraca, leave no doubt that these are genuine Malacostraca. The large carapace, adductor muscle scar, rostral plate, and furca indicate their close relation to the Leptostraca.

Despite these complications, the Phyllocarida have long been recognized as the most primitive of malacostracans, the Paleozoic forms occupying various ecological niches from which the later, higher Malacostraca were to displace them. Primitive features present in the Leptostraca according to SIEWING (271) are the rostral plate, eight free thoracomeres covered by a carapace but not fused with it, seven pleomeres, furca, both antennal and maxillary glands, heart extending from head into abdomen, lateral arteries segmentally arranged and consisting of visceral and limb components, gonads extending through whole body, and simple stomach and brain.

The presence of foliaceous thoracopods in *Nebalia* has classically been taken to indicate that the Leptostraca form a connecting link between the Branchiopoda and the Malacostraca. The absence of true endites from the thoracopods of *Nebalia,* together with the presence of more stenopodous thoracopods in *Paranebalia,* led CALMAN (65) to suggest that the phyllopodous form of the thoracopods might be secondary. CANNON has attacked the theory that the phyllopodium represents the archetypal crustacean limb and from a study of the feeding mechanism of *Nebalia* concluded that its foliaceous limbs are secondary adaptations for filter-feeding. Furthermore, the embryology of *Nebalia* was shown by MANTON (1934) to be eumalacostracan and not at all entomostracan.

Leptostracan specializations other than the lamellar thoracopods, according to SIEWING, are the carapace with adductor muscle, absence of posterior pleopods, presence of a scale on the antennule instead of a second flagellum, and absence of antennal exopod. The first two characters are present in Middle Cambrian forms and suggest that the Phyllocarida were already well differentiated from the ancestral malacostracan by that time.

The Middle Cambrian *Canadaspis* is poorly known and the supposedly trilobitan nature of the thoracopods has never been adequately demonstrated. The limbs can also be interpreted as endopods with a lamellar epipod but lacking an exopod. In the Upper Silurian-Lower Devonian, a great radiation from the Ordovician-Silurian ceratiocaridid stock gave rise to the Aristozoidae and Echinocarididae via *Callizoe* and *Ptychocaris.* It is possible that the Aristozoidae have reduced or lost the furca completely, thereby indicating a major departure from the Ceratiocarina condition, as CHLUPÁČ has pointed out. If this can be verified it would be of great interest as a reverse trend from that in the Leptostraca where the telson has been reduced. In the Middle Devonian the Rhinocarina were established from some line presumably within the Ceratiocarina. In terms of the number of genera, however, the Rhinocarina were less successful than the Ceratiocarina. The diminution in number of genera through the upper Paleozoic to only one genus in the Triassic suggests that the Archaeostraca were extinguished by the increase in number and diversity of the better adapted Eumalacostraca. Part of the post-Triassic lack of fossil Phyllocarida may be due to oversight. Little-known carapaces from the Mesozoic such as *Clausia* and *Protozoea* are regarded as stomatopod larvae, but if found in Paleozoic strata they would be referred to the Phyllocarida.

The origin of the Leptostraca in or before the Late Permian is obscure; they were possibly derived from some basal stock within the Ceratiocarina or even the Hymenostraca. More probably, however, they diverged from the hypothetical cephalocarid-like ancestor (SANDERS, 1955, 1957, 1959) earlier than the other Phyllocarida. The long preperacarid geological history of the Phyllocarida does not support CANNON's suggestion(1927) that *Nebalia* "evolved from some primitive mysid-like malacostracan." It is likely that the reverse derivation occurred, the Phyllocarida representing the stock from which the eumalacostracan or caridoid type was eventually derived.

Following BROILI and BEURLEN, SIEWING (271, p. 153) has emphasized that the lack of a hinge line in the carapace, the biramous nature of the antennules, and the antennal exopod of *Nahecaris* are eumalacostracan features, and that *Nahecaris* can thus be regarded as a link between the Leptostraca and Eumalacostraca. However, BROILI's interpretation of the carapace structure is probably erroneous and *Nahecaris* is here reassigned to the Rhinocarina. The specialized rhinocaridid carapace structure prevents *Nahecaris* from being a simple "missing link" between the two groups. Furthermore, BROILI was not able to prove that the supposed exopod of the antenna did, in fact, spring from the antennal protopod. Although this may be the case, the supposed exopod might belong to a more posterior cephalic appendage, and restudy is required. The biramous antennules do suggest an affinity with the Eumalacostraca and they contrast with the small antennular exopods of the Leptostraca, which may be secondary and due to relatively recent reduction, rather than being a primitive feature.

Several attempts have been made to relate other crustacean subclasses to the Phyllocarida. RUEDEMANN (1918) suggested that the sessile Cirripedia were derived from one of the Rhinocarina by a modification of the carapace to form compartments. This speculation, which recalls THOMPSON's (1830) idea that *Nebalia* was the active larva of the sessile whale-barnacle *Coronula,* was shown by CALMAN (1919) to be based on superficial resemblances. BERNARD (1892), a proponent of the phyllopodan nature of the Phyllocarida, argued that "the extraordinary likeness of the shells of some of the early Ostracoda *(e.g., Leperditia)* to the shells of such phyllopods as *Ceratiocaris salteriana* makes a phyllopodan origin for at least some of the Ostracoda very probable." Similarly, the genera now grouped under Ostracoda Archaeocopida were suggested by KUMMEROW in 1931 to bear the same relation to the Phyllocarida as the Decapoda Brachyura do to the Macrura. This suggestion was effectively formalized in RAYMOND's 1935 classification of the Archaeostraca. Again, the similarity of the carapaces in these is probably only superficial and due to convergence. GLAESSNER (1928) suggested that the Cycloidea could be considered as benthonic Phyllocarida, the lack of a free abdomen perhaps paralleling the brachyuran trend of the Decapoda. Despite the work of HOPWOOD (1925) and others, the ventral morphology of the Cycloidea is still inadequately known and thus, as VAN STRAELEN & SCHMITZ (312) have pointed out, the systematic position of the group must remain uncertain.

CLASSIFICATION

The first phyllocarid found was described as *Cancer bipes* by FABRICIUS in 1780 and initially regarded as a malacostracan. From the foliaceous nature of the thoracopods, MILNE-EDWARDS (1828) was led to suggest that this species was a branchiopod, and it was not until 1868 that *Nebalia* was shown to be a malacostracan (a "phyllopodiform decapod") by METCHNIKOV from its embryology and gastric mill. Meanwhile, several fossil phyllocarids had been described. SCOULER (1835) had described two Carboniferous phyllocarids and referred them to the Entomostraca Branchiopodes, the group to which LATREILLE had already in 1829 referred *Nebalia.*

The first direct comparison of a fossil form with *Nebalia* was not made until 1853, when SALTER described *Hymenocaris.* In 1879 PACKARD proposed that the fossil forms be united with the Nebaliidae to form a separate order of Crustacea, named Phyllocarida. CLAUS had already stressed (1872) that little was known of the fossil forms and their relationships, and in 1880 he reiterated this and, apparently unaware of PACKARD's order, proposed the term Leptostraca for the Recent forms. In 1888 CLAUS firmly established the malacostracan nature of *Nebalia* and, emphasizing the supposed variability in number of body somites, separated the fossils as Archaeostraca. Subsequent use of the three names has been confused, despite BEURLEN's clear summaries (29) of the history outlined above.

In the present treatment the old division of the Phyllocarida into Archaeostraca and Leptostraca is accepted with the addition of a new order, Hymenostraca. The GROBBEN (1892) and CALMAN (1904) position of the Leptostraca is thus slightly emended, but the term will still be available to neontologists in its most usual connotation, namely for the Nebaliidae.

Ordinal classification is based essentially on the nature of the telson and furca. Such single-character classification is obviously unsatisfactory, but few other morphological features observable in fossil material are as conservative or reliable. Since 1880, when WHITFIELD published a table showing the "maximum number of naked segments known" in 13 fossil forms, undue emphasis has been laid on the supposed variation in number of body segments. As CALMAN (1913) pointed out, if this variation did exist new orders would be required, and it would be difficult to regard them even as Malacostraca (271, p. 143). In fact, as Figure 122 shows, of 30 fossil phyllocarid genera tabulated, the number of abdominal somites (telson not included) is known with certainty in only five genera and the number of thoracic somites in only one, or possibly three. Significantly, the numbers of somites in these tagmata are respectively seven and eight, as in the Leptostraca. *Dithyrocaris,* for example, was reported by Whitfield to have one somite and by Jones & Woodard (1898) to have three; but it was not until 1916 that Carpentier was able to prove the presence of seven abdominal somites and at least seven thoracic somites. The number of somites in other genera may be different but it has never been shown to be so.

Another character used in classification has been the nature of the carapace, whether with or without a hinge line. Jones & Woodward (1883-1899) and others, in reports on British Paleozoic Phyllocarida, divided the fossil forms into two major groups on this single character, although they proposed no formal names for divisions thus recognized. This character is often difficult to ascertain, and such a classification minimizes the significance of the median dorsal plate first recognized by Hall & Clarke (140). The presence or absence of a simple hinge line is probably phylogenetically insignificant and functionally dependent on the size and degree of induration of the valves to be articulated.

The characters most used in generic and familial classification have been carapace shape and the nature of surface ornament. By analogy with other crustacean groups, however, these might be expected to be the most variable of characters. Recent Leptostraca are differentiated mainly by their limb structure, and if found fossil they would be separated into only two genera on the basis of carapace form, one comprising *Paranebalia-Nebalia-Nebaliella* and the other *Nebaliopsis.* Thus, *Montecaris* has convergently acquired the peculiar doublure structure, mesolateral ridge, and posteroventral spine of *Dithyrocaris paradoxides,* but, as known at present, it lacks the median dorsal plate, thereby excluding it from the Rhinocarina. Further convergences are undoubtedly hidden by the present classification, but the lack of more conservative characters suggests that this problem will not be solved easily.

In the present systematic descriptions only genera which are known from several tagmata are classified, with the exception of genera such as *Austriocaris* where relationships seem clear. The others are listed and described subsequently. A tabulation of suprageneric divisions of the Phyllocarida with numbers of genera contained in each is given on page *R*113.

SYSTEMATIC DESCRIPTIONS

Subclass PHYLLOCARIDA Packard, 1879

[=Phyllocardia Etheridge, 1892; Phyllostraca Hennig, 1922; Phyllodarida Richter & Richter, 1927; Phillocarida Rein, 1936; Plyllocarida Krestovnikov, 1961; Phyllocardida Howe, 1962, p. 162]

Malacostraca with large carapace of two valves, with or without hinge line along dorsal margin, connected by adductor muscle, produced anteriorly into movably articulated lanceolate rostral plate. Thorax of eight short, free somites; abdomen of seven somites and telson, seventh abdominal somite without appendages, telson bearing unsegmented, movably articulated furca. *L. Cam.-Rec.*

Order LEPTOSTRACA Claus, 1880

[=Leptocarida Haeckel, 1889; Nebaliadae Grobben, 1892; includes Nebaliina Clarke in Zittel, 1900; Nebaliacea Calman, 1904]

Small to medium-sized, carapace without hinge line, telson not produced dorsally between furcal rami; outer ramus of antennule reduced to a scale; antenna without exopod. Gnathal lobe of mandible reduced or with only single row of teeth; six pairs of pleopods, anterior four pairs comprising biramous swimmerets with large protopod, posterior two pairs small and uniramous. *U.Perm.-Rec.*

Family NEBALIIDAE Baird, 1850

[*nom. correct.* Sars, 1887 (*pro* Nebaliadae Baird, 1850)] [=Nebalidae Claus, 1880; Nebalida Haeckel, 1896]

Characters of order. *U.Perm.-Rec.*

Malzahn has described an eight-somite, 8 mm. long, furca-bearing abdomen from

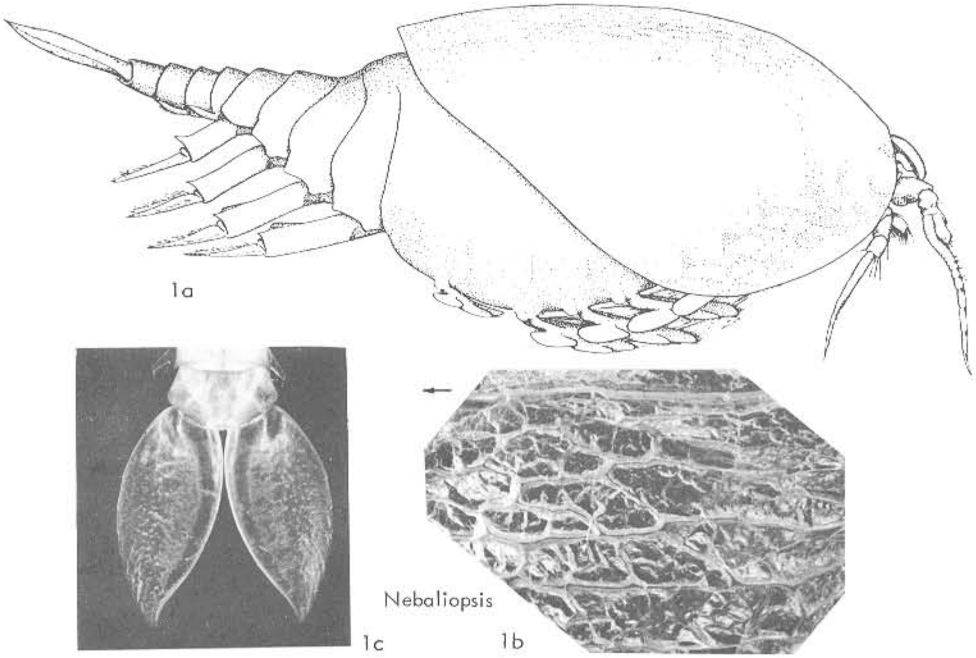


FIG. 133. Nebaliidae (p. *R*314).

the Upper Permian (Zechstein 1) of Germany as *Nebalia bentzi* (the carapace doubtfully referred to this species by MALZAHN, 186, is that of a young cumacean). The four most anterior somites bear large, two-segmented limbs, although they are not described as biramous. This specimen is probably a leptostracan, but it is impossible to refer it with certainty to any of the Recent genera, *Nebalia, Nebaliella,* or *Paranebalia.* Two generic names not listed below are *Pseudonebalia* and *Neonebalia,* quoted by KRESTOVNIKOV (1961). I have been able to find no other reference to these genera and it is presumed that they are *nomina nulla.*

Nebalia LEACH, 1814 [**N. herbstii* LEACH, 1814 (=**Cancer bipes* FABRICIUS, 1780; *Monoculus rostratus* MONTAGU, 1813; *Nebalia glabra, N. ciliata* LAMARCK, 1818; *N. montagui* THOMPSON, 1830); OD, M] [Although *N. herbstii* is type species of *Nebalia,* it is usually classed as a junior synonym of *Cancer bipes.* This misidentification of the type species needs to be referred to ICZN for decision by neontologists (Code, 1961, Art. 67, j, 70a)] [=?*Epinebalia* CLARK, 1932]. Carapace laterally compressed, valves elliptical, posterodorsally truncate, smooth and translucent. Furcal rami rodlike, with rows of setae and spines. Eyestalk with basal scale; 4th segment of antennule without process; antennal peduncle of 3 segments; incisor process of mandible small and simple; maxillule with 2 endites and long setiferous palp; maxilla small, with 4 endites; 8 pairs of undifferentiated thoracopods concealed beneath carapace, each limb bearing large lamellar exopod and epipod. *Rec.,* cosmop.——FIG. 120. **N. bipes* (FABRICIUS), Atl.; ♀ idealized, ×12 (68, after 271).——FIG. 129,2. *N. geoffroyi* H. MILNE-EDWARDS, Atl.; ♀ 1st thoracopod, *ca.* ×25 (68, after 352). [=*Epinebalia* CLARKE, 1932 (type, *E. pugettensis;* OD).]

Nebaliella THIELE, 1904 [**N. antarctica*; OD]. Like *Nebalia* but with short row of setae inside posterior carapace margin; rostral plate with prominent ventral keel produced anteriorly into spine; eyestalk elongate, flat and crescentic, without ommatidia and lacking basal scale; 4th segment of antennule with tuft of bristles; antennar peduncle of 4 segments; incisor process of mandible large and with several teeth; thoracic limbs without epipods. *Rec.,* N. Atl.-S. Pac.-S. Ind. O.-Antarct.O.——FIG. 130,*1*,*2*. *N. extrema* THIELE, Antarctic O.; *1,* ♀, ×10 (349); *2,* ♂, ×20 (68).

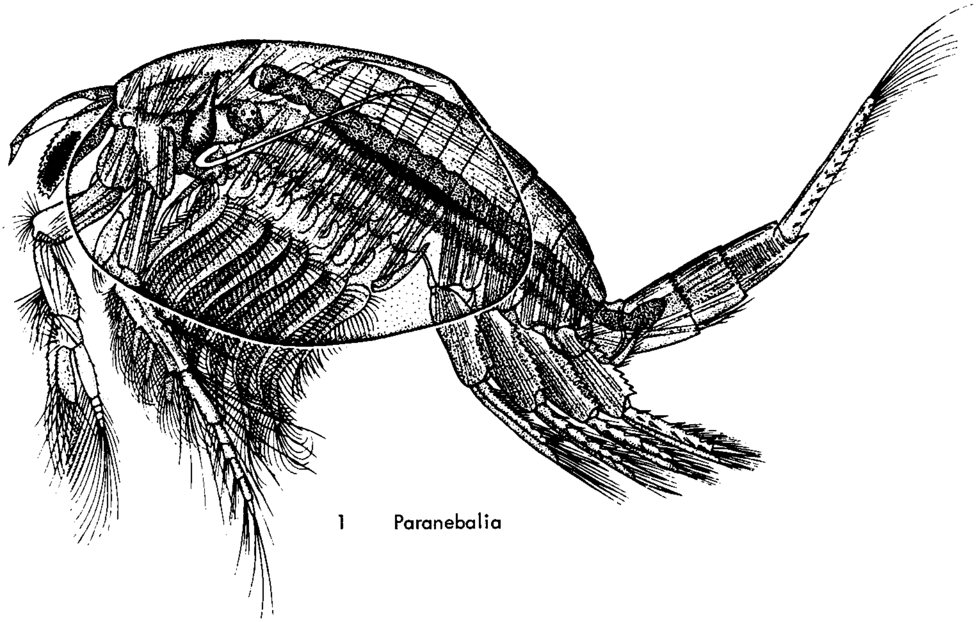


FIG. 134. Nebaliidae (p. *R*314). (From H. G. Cannon, 1960, in Bronn's Klassen und Ordnungen des Tierreichs, v. 5, Abt. 1, Buch 4, Teil 1, Akad. Verlag. publ., by permission).

Nebaliopsis SARS, 1887 [**N. typica;* OD] [=*Nebaliopis* KRESTOVNIKOV, 1961 *(nom. null.)*]. Carapace subtriangular, posteriorly acuminate, with median dorsal keel, transparent, and with large polygonal ornament of ridges; rostral plate short, triangular in cross section; thorax large, distensible; furcal rami flattened, leaflike, with serrate outer margins; eyes small, with few ommatidia, without basal scale; 4th segment of antennule produced distally into anteriorly denticulate, curved and pointed process; antennar peduncle of 4 segments; gnathal lobe of mandible reduced to simple knob; maxillule with vestigial palp; maxilla with greatly enlarged 1st endite; thoracopods reduced to lanceolate lobes; 1st limb with shorter protopod, longer endopod, and more setiferous epipod than succeeding limbs; 2nd to 4th pleopods with broad exopods. *Rec.,* Atl.-Pac.-SW. Ind.O.——FIG. 133,*1*. **N. typica,* W.Atl.; *1a,* ♀, adult, right lat. view showing thorax distended by food in digestive sac, ×4.8 (349); *1b,* anterodorsal region of carapace showing median dorsal keel at top and network of ridges, ×4 (Rolfe, n); *1c,* dorsal view of posterior part of 7th abdominal somite showing tips of 6th pleopods, telson, and furca, ×3.8 (Rolfe, n).

Paranebalia CLAUS, 1880 [**Nebalia longipes* WILLEMOES-SUHM, 1875; OD, M]. Like *Nebalia* but eyestalks elongate and denticulate, without basal scale; 4th segment of antennule produced distally into anteriorly serrate, pointed process; tips of thoracopods projecting well beyond ventral margin of carapace, their endopods and exopods elongate, slender, with long setae on outer edge, epipods small, subtriangular. *Rec.,* NW.Atl.-NW.Pac. ——FIG. 134,*1*. **P. longipes* (WILLEMOES-SUHM), W.Atl.; ♀, adult, left lat. view, ×22 (68, after 377b).

Order HYMENOSTRACA Rolfe, new order

[=order *Hymenocarina* CLARKE in ZITTEL, 1900 (*nom. transl.* WALCOTT, 1912, p. 182, *ex* suborder Hymenocarina CLARKE in ZITTEL, 1900)]

Carapace without hinge line, last somite not elongate, telson ?not posteriorly produced, three pairs of caudal spines (?furcae) of unequal length. *?L.Cam., M.Cam.-L.Ord.*

The tentative erection of this new order is demanded by the peculiar character of the telson and furca. Such a single-character classification is unsatisfactory, but little better can be done in view of the present lack of information on more significant features.

Family HYMENOCARIDIDAE Haeckel, 1896

[*nom. correct.* ROLFE, herein (*pro* family Hymenocarida HAECKEL, 1896, *nom. imperf.*)] [=Hymenocaridae CLARKE in ZITTEL, 1900 *(nom. imperf.)*]

Characters of order. *?L.Cam., M.Cam.-L. Ord.*

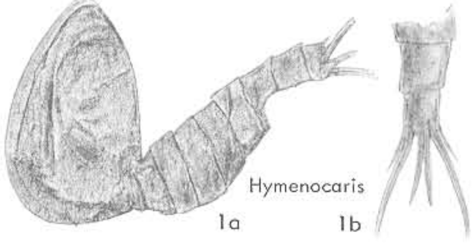


FIG. 135. Hymenocarididae (p. *R*315).

Hymenocaris Salter, 1853 [**H. vermicauda;* OD, M] [=*Hymenocarys* Brinkmann, 1954 *(nom. null.)*]. Carapace subovate, with posterior rim; surface smooth; telson similar to preceding somites; outer pair of caudal spines divergent, shortest; inner pair subparallel, of medium length; intermediate pair longest. [Middle Cambrian (Burgess Shale) species from Canada previously assigned to this genus now are assigned to *Canadaspis*.] *?L.Cam., M.Cam.-L.Ord.,* NW.Eu.(G.Brit.-?Swed.)-?N.Am.(Can.)-Australia-N.Z.——FIG. 135,*1*. **H. vermicauda,* L.Ord., G.Brit.(Wales); *1a,* left lat. view of distorted specimen, ×1; *1b,* ?dorsal view of somites, telson, and caudal spines, ×2 (160).

Order ARCHAEOSTRACA Claus, 1888

[*nom. correct.* Stromer, 1909 (*pro* Archaeostraken Claus, 1888)] [=Palaeocarida Haeckel, 1889; Palacarides Haeckel, 1896; Archaeocarida Hennig, 1921; Archaeostraka Richter & Richter, 1927; Nahecarida Broili, 1928; Paléostracés Lameere, 1933; Archeostrata Størmer, 1935]

May be large, carapace with hinge line, seventh abdominal somite usually much longer than preceding ones, telson produced dorsally as median process between furcal rami; antennule biramous (known only in *Nahecaris*); antenna ?with flagellar exopod (supposedly in *Nahecaris*); gnathal lobe of mandible with large, paired teeth; ?five pairs of pleopods only. *L.Ord.-U.Trias.*

Suborder CERATIOCARINA Clarke in Zittel, 1900

[=Ceratocarina Raymond, 1935; Ceartiocarina Ivanova, 1960; Ceratiocarinae Jux, 1960; Ceratiocarida Krestovnikov, 1961]

Carapace with hinge line; rostral plate without longitudinal ridge, no median dorsal plate; eight short thoracic somites and seven longer abdominal somites where known (Fig. 122), pretelson somite usually elongated. *L.Ord.-U.Trias.*

Family CERATIOCARIDIDAE Salter, 1860

[*nom. correct.* Rolfe, 1961 (*pro* Ceratiocaridae Salter, 1860)] [=Ceratiocaridiae Beecher, 1884; Ceratocarida Haeckel, 1896; Caryocaridae (*recte* Caryocarididae) Chapman, 1903]

Carapace large, covering thoracic and anterior abdominal somites, lacking prominent nodes and ridges; furca long. *L. Ord.-L. Dev., ?Carb., ?U.Perm.*

Ceratiocaris M'Coy, 1849 [ICZN, March, 1964, Op. 690] [**C. solenoides;* SD Miller, 1889 (=*Cultellus rectus* M'Coy, 1851, obj., *nom. nud.*)] [=*Leptocheles* M'Coy, 1849 (type, *Pterygotus (Leptocheles) leptodactylus* M'Coy, 1849; OD, M); *Leptonotus* Barrande, 1856 *(nom. nud.); Physocaris* Salter, 1860 (type, *Ceratiocaris (Physocaris) vesica;* OD =*C. cassia* Salter, 1860); *Phytocaris* Etheridge, 1888 *(nom. null.); Astacoderma* Harley, 1861 (type, *A. subundulatum var. compositum*; SD Rolfe, herein); *Ceriatocaris* Claus, 1880 *(nom. null.)*; *Caratiocaris* Packard, 1889 *(nom. null.)*; *Ceratocaris* Haeckel, 1889 *(nom. null.)*; *Cerathiocaris* Scalia, 1922 *(nom. null.)*; *Cerotiocaris* Péneau, 1935 *(nom. null.)*; *Ceratiocaries, Leratiocaris* Péneau, 1946 *(nom. null.)*; *Ceratioceras* Krestovnikov in Orlov, 1960 *(nom. null.)*; *Emmelezoe* Etheridge, Jones & Woodward, 1886 (type, *Ceratiocaris elliptica* M'Coy, 1849; SD Gürich, 1929); *Emmelozoe* Lindström, 1895 *(nom. null.)*; *Emmelzoe* Clarke, 1902 *(nom. null.); Entomocaris* Whitfield, 1896 (*non* Gürich, 1929) (type, *E. telleri;* OD); *?Calyptocaris* Jones & Woodward, 1898 (type, *Dithyrocaris? striata* Woodward & Etheridge in Geikie, Geikie, Peach, & Etheridge, 1873; OD, M); *Limnocaris* Clarke, 1902 (type, *Ceratiocaris (L.) praecedens;* OD, M); *?Polystomurum* Novozhilov, 1958 (type, *P. stoermeri*)]. Carapace elongate to subovate, with prominent anterior horn, posterior margin usually sinuous; right valve with or ?without 3 dorsal hinge nodes; rostral plate of medium length, only anterior indurated tip projecting free of valves; rostral plate and carapace with anastomosing, longitudinal striae. Body somites commonly encircled by posteroventrally inclined striae and anteriorly imbricating scale ornament; telson and furca rodlike, usually longitudinally grooved and bearing spinules, telson longer than furca; 8 thoracic appendages differentiated from ?5 abdominal appendages, poorly known. [*Emmelezoe* and *Limnocaris* are here synonymized since the presence or absence of the anterior tubercle or "eye spot" is at present unreliable for generic differentiation.] *?L.Ord., U.Ord.-L.Dev., ?L.Carb., ?U.Perm.,* cosmop.——FIG. 136,*1*. *C. papilio* Salter in Murchison, M.Sil., Scot.; right dorsolat. view (reconstr.), pleopods known to be present, but their structure unknown,

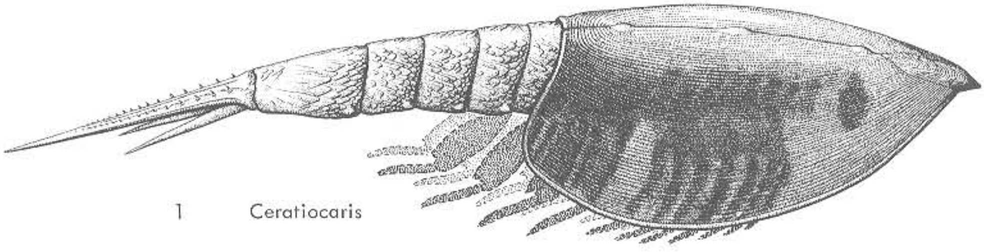


FIG. 136. Ceratiocarididae (p. *R*315).

hence pleopods of *Paranebalia* type are shown, ×1 (258).

Caryocaris SALTER, 1863 [**C. wrightii*; OD] [=*?Dawsonia* NICHOLSON, 1873 (type, *D. campanulata*; SD S. A. MILLER, 1889) (*non Dawsonia* HARTT in DAWSON, 1868; *nec* FRITSCH, 1879; *nec* CARPENTER in DALL, 1882); *Caryocarus* GURLEY, 1896 *(nom. null.)*; *?Rhinopterocaris* CHAPMAN, 1903 (type, *Lingulocaris mcoyi* ETHERIDGE, 1892; OD, M); *Rhinopteriocaris* KRESTOVNIKOV, 1961 *(nom. null.)*; *Lamprocaris* NOVÁK *in* ŽELÍZKO, 1907 *(nom. nud.)*; *Lamprocaris* ŽELÍZKO, 1919 (*fide* CHLUPÁČ) (type, *L. micans;* SD VAN STRAELEN & SCHMITZ, 1934)]. Carapace elongate-subovate, posterior margin with (or ?without) fringe of spines and spinules, anterodorsal carapace horn of each valve may be anteriorly produced; midventral ridge may be present, subparallel to ventral margin but confluent with it antero- and posteroventrally; surface smooth, striate, or reticulate; telson and furca laterally expanded, leaflike; telson shorter than furca; external margins of furcal rami ?notched or serrate. [*Rhinopterocaris* may prove to be generically distinct, but the absence of posterior spinules and produced carapace horn from the type species and other species of *Caryocaris* may only be due to preservation. These structures are commonly not preserved in specimens of *"Rhinopterocaris"* and indeed were not noticed or figured by ETHERIDGE in his original description of the syntypes of the type species of *Rhinopterocaris*. Furthermore the significance of these characters at the generic level seems doubtful.] *L.Ord.-U.Ord.*, cosmop. [*U.Cam.* and *Sil.* records of this genus are based on generically indeterminable specimens.]——FIG. 137,*1*. **C. wrightii*, L. Ord., Eng.(Skiddaw, Cumberland), left lat., ×1.5 (160).——FIG. 137,*2*. *C. maccoyi* (ETHERIDGE) [=*C. curvilata* GURLEY], L.Ord., USA(N.Y., N. Granville); LV lat., ×1.5 (Rolfe, n).——FIG. 137,*3*. *C. monodon* (GURLEY), L.Ord., Can. (Que.); telson and furca, dors. (reconstr.), ×3 (Rolfe, n).

Gonatocaris GÜRICH, 1929 [**Emmelezoe decora* CLARKE, 1902; OD]. Like *Ceratiocaris* but with carapace valves truncate anteriorly, coarsely ribbed

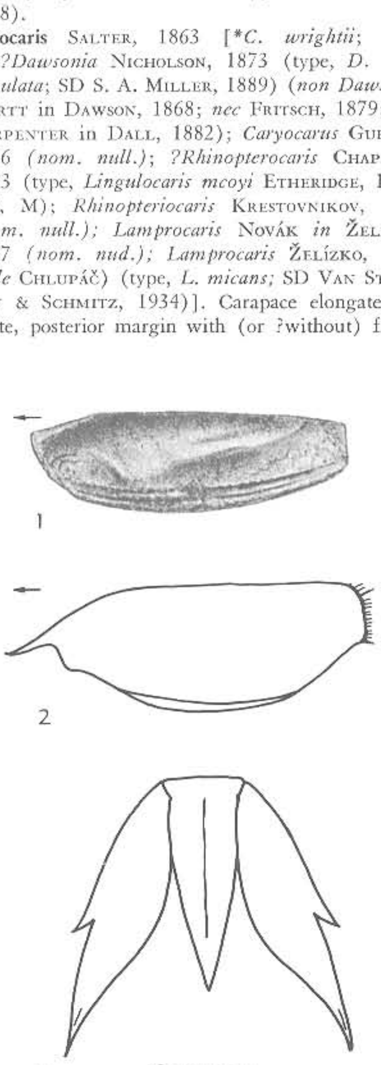


FIG. 137. Ceratiocarididae (p. *R*316).

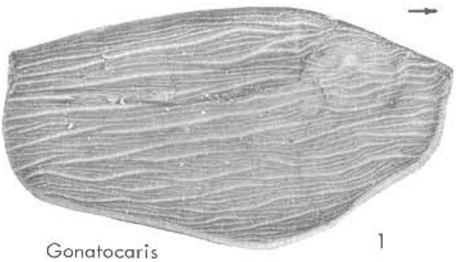


FIG. 138. Ceratiocarididae (p. *R*316).

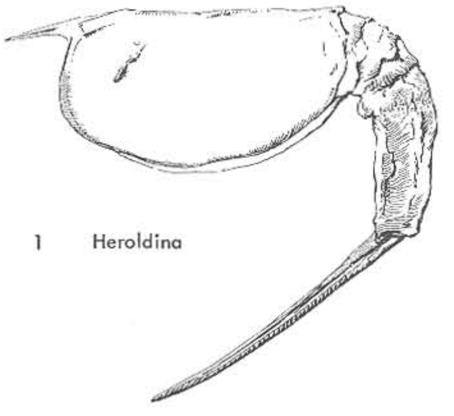


FIG. 139. Ceratiocarididae (p. *R*317).

and with anterior tubercle. *U.Sil.*, N.Am.——FIG. 138,*1*. **G. decora* (Clarke), Salina Gr.(Vernon Sh.), USA(N.Y.); RV (syntype) lat., ×4 (Rolfe, n).

Heroldina Broili, 1931 [*pro Heroldia* Broili, 1929 (*non* Verhoeff, 1926)] [**Mesothyra rhenana* Broili, 1928; OD] [=*Allolepichthys* Whitley, 1940 (*pro Allolepis* Heintz, 1932, *non* Jordan & Hubbs, 1925) (type, *A. longicornis;* OD)]. Like *Ceratiocaris* but carapace valves less acuminate anteriorly, larger rostral plate (length almost half that of carapace), projecting free from carapace anteriorly as triangular spine, and last abdominal somite very elongate. [Chlupáč (1963) has suggested that this genus belongs to the Aristozoidae; although the last abdominal somite and telson indicate such an affinity, the carapace is unlike that of any aristozoid.] *L.Dev.*, W.Ger.——FIG. 139,*1*. **H. rhenana* (Broili), Hunsrück Sh., Gemünden; left lat. view, ×0.25 (346b).

Family AUSTRIOCARIDIDAE
Glaessner, 1931

[*nom. correct.* Rolfe, herein (*pro* Austriocaridae Glaessner, 1931)] [=Austricaridae Brooks & Caster, 1956 (*nom. null.)*]

Carapace with excavate posterior margin and commonly a mesolateral or juxtadorsal ridge; rostral plate relatively short; posteroventral or posteromedian protuberances or internal impressions may represent carapace adductor muscle scars, suggesting that thorax projected free from carapace. *M.Dev.-U.Trias.*

Austriocaris Glaessner, 1931 [**A. carinata*; OD]. Carapace only known, posterior excavation arcuate or irregular, anterior margin concave or produced into small beak; posteroventral or ventromedian V-shaped furrow; surface smooth with mid-dorsal granulations or posteroventral pits, or dorsoventrally striate. *U.Trias.*, W.Eu.(Austria).——FIG. 140,*2*. **A. carinata*; RV with rostral plate, lat., ×0.6 (111).

Concavicaris Rolfe, 1961 [*pro Colpocaris* Meek, 1872 (*non* von Meyer, 1862)] [**Ceratiocaris (Colpocaris) bradleyi* Meek, 1872; SD S. A. Miller, 1889]. Posterior excavation of carapace valves semicircular, anterior margin truncate or acuminate; may bear mesolateral ridge or bluntly serrate juxtadorsal ridge; surface ?smooth, reticulate or striate; doublure may be broad; telson shorter than furca, all smooth or longitudinally striate. *M.Dev.-M.Penn.*, Czech.-USA.-?E.Can.-Australia.——FIG. 140,*1a*. *C. sinuata* (Meek & Worthen), M.Penn., USA(Ill.); LV (holotype) lat., ×0.6 (Rolfe, n).——FIG. 140,*1b*. *C. rostellata* Rolfe, M.Penn., USA(Ill.); LV (holotype) lat., with anastomosing striae ornament shown diagrammatically, ×0.9 (Rolfe, n).

Family ECHINOCARIDIDAE
Clarke in Zittel, 1900

[*nom. correct.* Chlupáč, 1963 (*pro* Echinocaridae Clarke in Zittel, 1900)] [=Echinocharidae Bock, 1946]

Carapace with hinge line, without anterior horn, with anterior swellings and lateral ridge. *L.Dev.-L.Miss.*

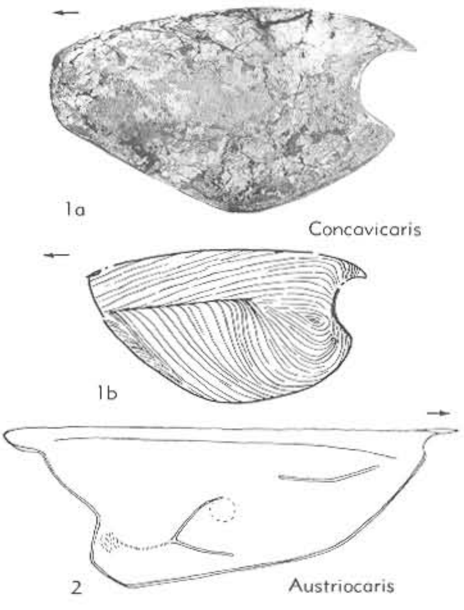


FIG. 140. Austriocarididae (p. *R*317).

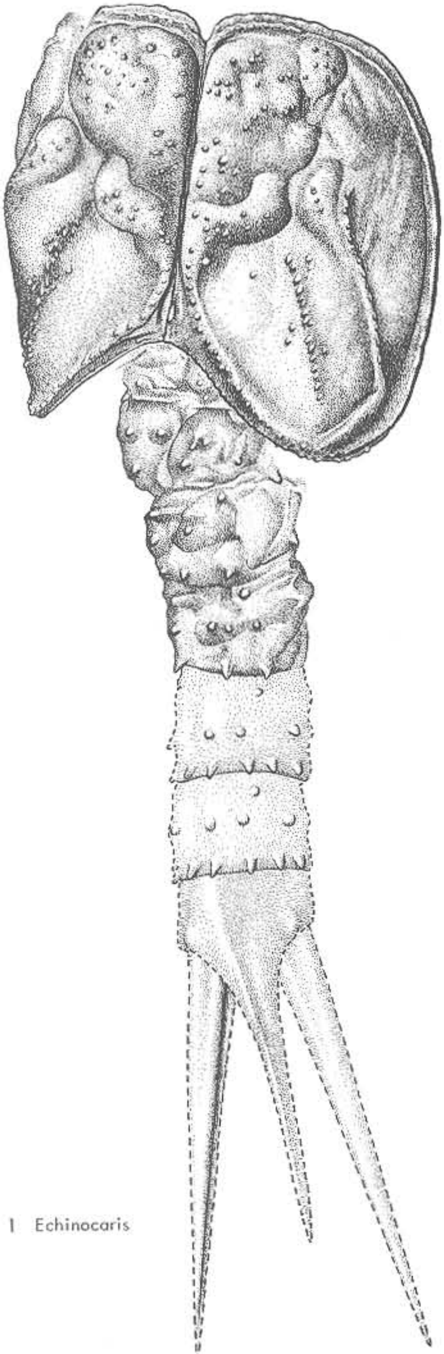


FIG. 141. Echinocarididae (Echinocaridinae) (p. *R*318).

Subfamily ECHINOCARIDINAE
Clarke in Zittel, 1900

[*nom. transl.* ROLFE, herein (*ex* Echinocaridae CLARKE in ZITTEL, 1900)]

Carapace subovate-subquadrate, anterodorsally rounded and without posteroventral spine; telson and furca thin, rodlike. *L. Dev.-L.Miss.*

Echinocaris WHITFIELD, 1880 [**E. sublevis*; OD] [=*Echinocarys* BARROIS, 1891 *(nom. van.)*]. Carapace subovate-subelliptic, posterodorsally truncated, with prominent anterodorsal and mid-dorsal lobes; lateral ridge carinate, sigmoidal or sinuous; carapace and somites characteristically tuberculate or spinose; furca longer than telson, all slender, each furcal ramus grooved along inner side. *M.Dev.-L.Miss.,* cosmop.——FIG. 141,*1*. *E. socialis* BEECHER, U.Dev. (Chemung), USA(Pa.); right dors. lat. (part reconstr.), ×4 (Rolfe, n).——FIG. 142,*3*. *E. punctata* (HALL), M.Dev. (Hamilton Gr.), USA(N.Y.); last 2 somites of abdomen, telson and furca; *3a,* dors., showing clasping posterior spines, ×0.5; *3b,* vent., ×0.5 (140).

Callizoe BARRANDE, 1872 [**C. bohemica;* OD, M] [=*Callizoe* BARRANDE in BIGSBY, 1868 *(nom. nud.)*; *Callozoe* NICHOLSON & LYDEKKER, 1889 *(nom. null.)*; *Calizoe* KRESTOVNIKOV, 1961 *(nom. null.)*]. Carapace like *Ptychocaris* but margin concave anteroventrally, anterior tubercle anteroventrally situated, lacks anteromedian pair of nodes and furrow, lateral ridge faint, not carinate; doublure wall concave; pitted ?hinge node developed at posterior end of hinge line. *L.Dev.,* Czech.——FIG. 142,*2*. **C. bohemica,* U.Koněprusy Ls.; lat. view of LV (int. mold), ×3 (Rolfe, n).

Ptychocaris NOVÁK, 1885 [**P. parvula*; SD VAN STRAELEN & SCHMITZ, 1934] [=*Pthychocaris* KRESTOVNIKOV, 1961 *(nom. null.)*]. Carapace elongate-subquadrate, with mid-anterior group of ?3 low nodes, anterodorsally situated prominent anterior tubercle, and posterior pair of large nodes (?carapace adductor and mandibular muscle attachments) bordered posteriorly and separated by furrows; lateral ridge prominent, carinate. *L.Dev.-M. Dev.,* Czech.-N.Can.——FIG. 142,*5*. *P. simplex* NOVÁK, L.Dev. (Koněprusy Ls.), Czech.; lat. view of RV, ×1 (77, after 370b).

Subfamily MONTECARIDINAE Rolfe, 1966

Carapace valves elongate-subquadrate, anterodorsally truncate, with anterodorsal grooves perpendicular to hinge line separating tuberculate areas; with carinate lateral ridge and posteroventral spine; telson and furca laterally expanded; telson with prominent, movable, lateral spines. *?L. Dev., M. Dev.-U.Dev.*

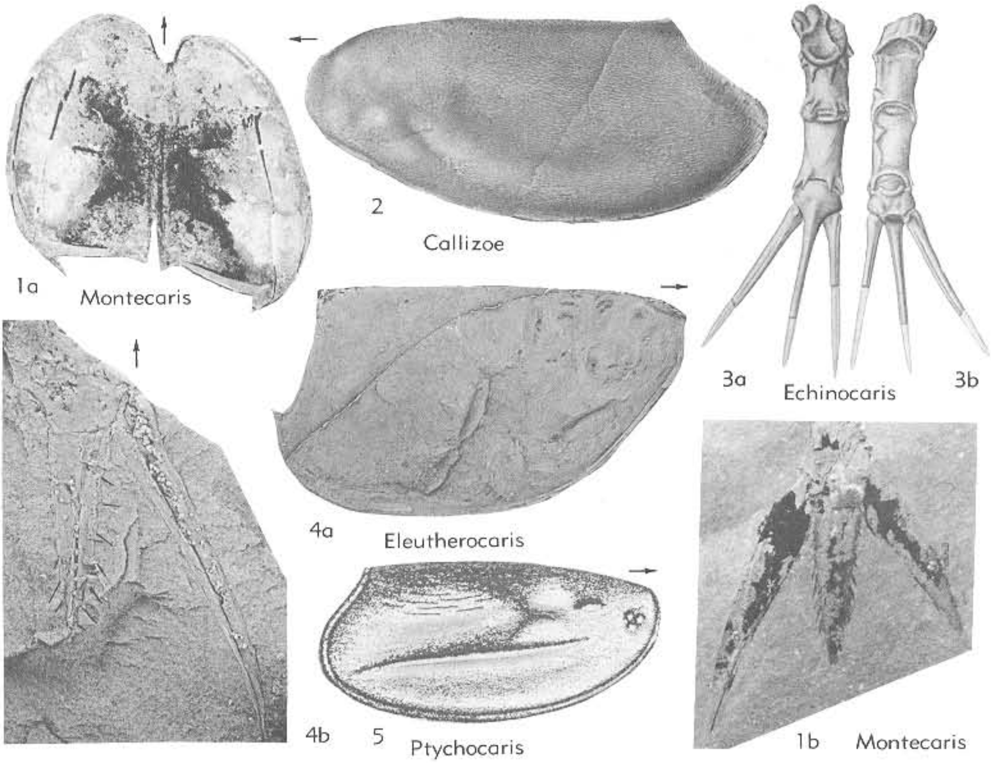


FIG. 142. Echinocarididae (Echinocaridinae) *(2-3, 5)*, (Montecaridinae) *(1, 4)* (p. *R*318-*R*319).

Montecaris Jux, 1959 [**M. strunensis*; OD]. Anterodorsal grooves deep, 4 in number, 1st and 4th uniting ventrally; doublure broad; lateral ridge long, extending to posteroventral spine; small posterodorsal spine present; posterior margin of abdominal somites produced into spines; telson broad, equal in length to furca or shorter than it. *?L.Dev., M.Dev.-U.Dev.*, C.Eu.-?W.Can.-Australia.——FIG. 142,*1*. **M. strunensis* Jux, U.Dev. (Frasn.), Ger.; *1a*, dorsal view of holotype, carapace valves spread out, ×0.5; *1b*, incomplete telson and furca, ×1 (Rolfe, n).

Eleutherocaris Clarke in Zittel, 1900 [**Echinocaris whitfieldi* Clarke, 1885; SM Clarke, 1902]. Like *Montecaris* but anterodorsal grooves of carapace shallow, lateral ridge short and restricted to anteroventral region, telson narrower; carapace with dorsal-ventral rows of anteriorly convex crescentic ridges or scales. *U.Dev.*, USA(N.Y.).——FIG. 142,*4*. **E. whitfieldi*, Naples Gr. (Hatch Hill), Naples; rubber molds of holotype; *4a*, lat. view of LV, ×1.7; *4b*, telson and right furcal ramus, dorsal, ventral platform of telson head impressed through tergum, telson spines retouched, ×1.7 (Rolfe, n).

Family PEPHRICARIDIDAE Van Straelen, 1933

[*nom. correct.* Rolfe, herein (*pro* Pephricaridae Van Straelen, 1933)]

Carapace valves semicircular, with prominent, posteriorly tapering, mid-dorsal-posteromedian fold; rim with long spines; last two abdominal somites with long spine on each side; telson shorter than curved furcal rami. *U.Dev.*

Pephricaris Clarke, 1898 [**P. horripilata;* OD, M] [=*Pephrycaris* Rusconi, 1950 *(nom. null.)*]. Characters of family. *U.Dev.*, USA(N.Y.).——FIG. 143,*1*. **P. horripilata*, Chemung, Alfred, Allegany Co.; dorsal view of lectotype showing anterodorsal "pits" due to erosion of mandible bodies, ×1.5 (351b, mod.).

Family ARISTOZOIDAE Gürich, 1929

Carapace strongly convex, with dorsal-median nodes and large anterior horn but without lateral ridge; deep marginal groove

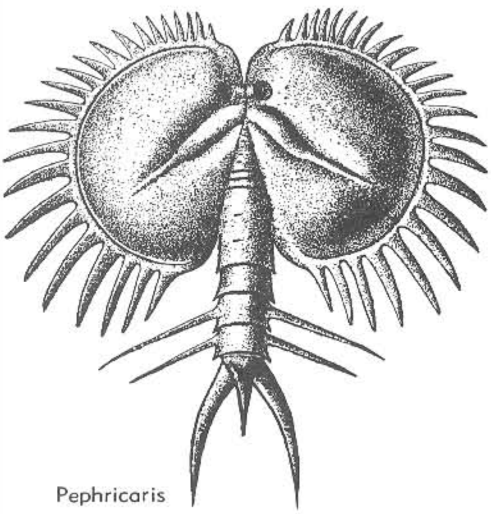


FIG. 143. Pephricarididae (p. *R*319).

demarcating broad rounded rim; last abdominal somite very elongate. [Furca unknown and possibly lacking. If this can be substantiated a new order would be indicated as CHLUPÁČ has suggested.] *?M.Ord., U.Sil.-M.Dev.*

Aristozoe BARRANDE, 1872 [**A. bisulcata*; SD S. A. MILLER, 1889] [=*Aristozoe* BARRANDE in BIGSBY, 1868 *(nom. nud.)*; *Ariztozoe* BARRANDE, 1872 *(nom. null.)*; *Bactropus* BARRANDE, 1872 (type, **B. longipes*; SD ROLFE, herein); *Bractropus* CANU, 1886 *(nom. null.)*; *?Phasganocaris* NOVÁK, 1886 (type, *Eurypterus pugio* BARRANDE, 1872; OD, M); *Phasgonocaris* ROGER in PIVETEAU, 1953 *(nom. null.)*]. Carapace with relatively thick cuticle, subcircular-subelliptical, with rounded anterior horn, anterodorsal nodes separated by grooves, posterodorsal angle rounded; telson as in *Ceratiocaris*. [The two synonymized genera were described from last abdominal somites and a telson only, and were subsequently suggested by NOVÁK and GÜRICH to correspond with carapaces of *Aristozoe* spp.]. *?M.Ord., U.Sil.-M.Dev.,* Eu.-Novaya Zemlya-?SE.Can.——FIG. 144,*1*. *A. regina* BARRANDE, L.Dev.(U.Koněprusy Ls.), Czech.; *1a,* left lat. view of carapace, ×0.8; *1b,* 7th abdominal somite and telson, ×0.8 (370a). [=*Bactropus* BARRANDE in BIGSBY, 1868 *(nom. nud.)*.]

Orozoe BARRANDE, 1872 [**O. mira;* OD, M]. Like *Aristozoe* but carapace subquadrate, rim anteroventrally and posteroventrally flattened and produced, with large, dorsoventrally flattened, posteriorly directed blunt spine on posteromedian area. *L.Dev., ?M.Dev.,* Czech.-?Ger.——FIG. 145, *1*. **O. mira,* L.Dev.(U.Koněprusy Ls.), Czech.; *1a,b,* lat. and dorsal views of LV with spine restored, ×4 (Rolfe, n).

Pygocaris PERNER, 1916 [**P. schuberti*; OD]. Like *Aristozoe* but with (?secondarily) thin cuticle, anterior horn acuminate, anterodorsal nodes not separated by grooves and may be only poorly developed, posterodorsal corner produced; rostral plate lanceolate, with 2 anterior constrictions. *?L. Dev.,* Czech.——FIG. 145,*2*. **P. schuberti,* Lochkov Ls., Kosoř; lat. view of LV (paralectotype), ×0.75 (372).

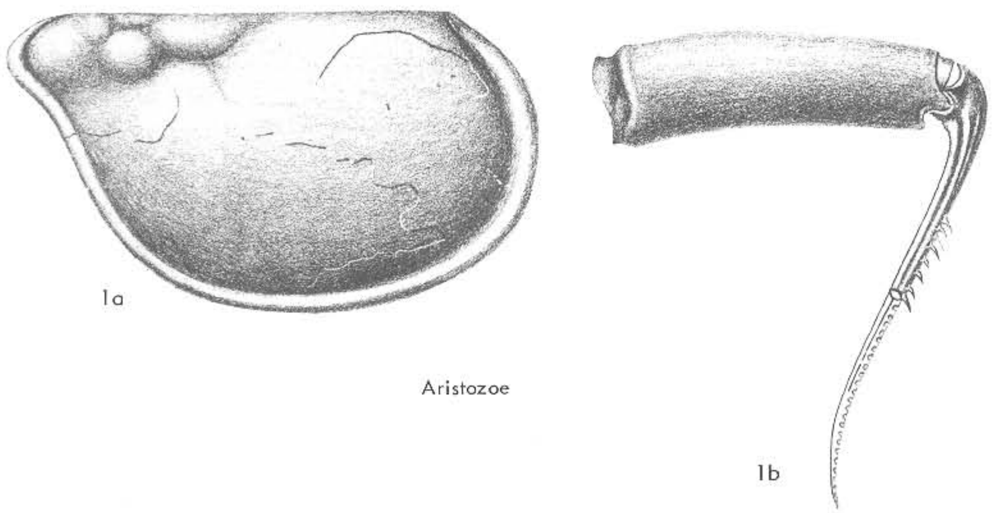


FIG. 144. Aristozoidae (p. *R*320).

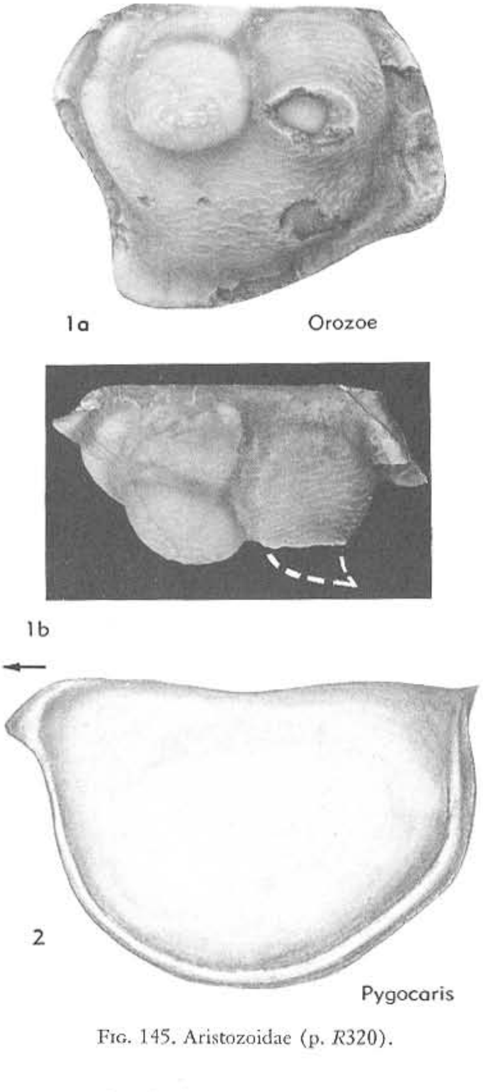


FIG. 145. Aristozoidae (p. *R*320).

Suborder RHINOCARINA Clarke in Zittel, 1900

[=Nahecarina Richter, 1933; Rchinocarina Ivanova, 1960]

Carapace with median dorsal plate separating valves behind rostral plate; last abdominal somite elongated. *?Sil., L.Dev.-M.Penn., ?U.Perm.*

Family RHINOCARIDIDAE Hall & Clarke, 1888

[*nom. correct.* Rolfe, 1962 (*pro* Rhinocaridae Hall & Clarke, 1888)] [=Pinacaridae Hall & Clarke, 1888; Pinnicaridae Clarke, 1893; Rhinocardidae Cleland, 1903; Nahecaridae (*recte* Nahecarididae) Broili, 1928; Reinocaridae Brooks & Caster, 1956; Pseudodontichthyidae Obruchev in Orlov, 1964; includes Rhinocarinae (*recte* Rhinocaridinae) Hall & Clarke, 1888 (*nom. transl.* Krestovnikov in Orlov, 1960, *ex* Rhinocaridae Hall & Clarke, 1888); Dithyrocarinae (*recte* Dithyrocaridinae) Jones & Woodward, 1899 (*nom. transl.* Krestovnikov in Orlov, 1960, *ex* Dithyrocaridae Jones & Woodward, 1899); Rachuridae Miller, 1889 (*nom. neg.*)]

Carapace valves elongate, subovate; median dorsal plate narrow and with chevron ornament; rostral plate and median dorsal plate slightly bent along median carina. *?Sil., L.Dev.-M.Penn., ?U.Perm.*

Rhinocaris Clarke in Hall & Clarke, 1888 [**R. columbina;* SD S. A. Miller, 1889] [=*Phinocaris* Matthew, 1888 (*nom. null.*); *Rhynocaris* Chernyshev, 1938 (*nom. null.*)]. Posterior margin of carapace valves concave, with small to medium posteroventral and rarely posterodorsal spine; mesolateral carina faint or absent; anterior node may be present and from it branching furrows may radiate posteriorly; rostral plate projecting anteriorly from carapace, anterior half laterally compressed; somites encircled by posteroventrally inclined striae; telson subcircular in cross section, equal in length to furca or shorter than it. *M.Dev.-U.Dev.,* N.Am.——FIG. 146,*4*. **R. columbina,* USA(N.Y.); *4a,b,* left lat. and dorsal views (reconstr.), ×0.7 (351). [=*Pseudodontichthys* Skeels, 1962 (type, *P. whitei;* OD)].

Dithyrocaris Scouler in Portlock, 1843 [*pro Argas* Scouler, 1835 (*non* Latreille, 1795; *nec* Oken, 1815)] [**Argas testudineus* Scouler, 1835; SD Roemer in Bronn & Roemer, 1854] [=*Argus* Geinitz, 1853 (*nom. null.*); *Arges* Claus, 1876 (*nom. null.*); *Anthropodontoides* Barkas, 1871 (type, *A. bailesii;* OD, M); *Dithyrocarus* M'Coy in Griffith, 1842 (*nom. nud.*); *Ditryocharis* Roemer, 1866 (*nom. null.*); *Dithyrocraris* Meek & Worthen, 1873 (*nom. null.*); *Dythyrocaris* Kayser, 1878 (*nom. null.*); *Dithyocaris* Bigsby, 1878 (*nom. null.*); *Dithyriocaris* Hind *et al.,* 1903 (*nom. null.*); *Dithyrocarys* Barrois, 1891 (*nom. van.*); *Rhachura* Scudder, 1878 (type, *R. venosa;* OD, M); *Rachura* Zittel, 1885 (*nom. null.*); *Rhaehura* Jones & Woodward, 1899 (*nom. null.*); *Mesothyra* Hall in Hall & Clarke, 1888, (type, *Dithyrocaris oceani;* OD); *Mesothyris* Ruedemann, 1918 (*nom. null.*); *Chaenocaris* Jones & Woodward, 1898 (type, *Dithyrocaris tenuistriata* M'Coy, 1844; SD Rolfe, herein)]. Like *Rhinocaris* but posterior margin of carapace valves straight or convex, with large posteroventral spine and usually with prominent mesolateral carina and anterodorsal granules; may bear up to 4 lateral carinae; doublure usually broad, rim may have oblique, posteriorly imbricating ridges; somites ornamented as in *Rhinocaris* or with longitudinal carinae; telson subtriangular in cross section, shorter, equal in length to furca or longer than it; furcal rami flattened, commonly with deep longitudinal grooves. *?Sil.,*

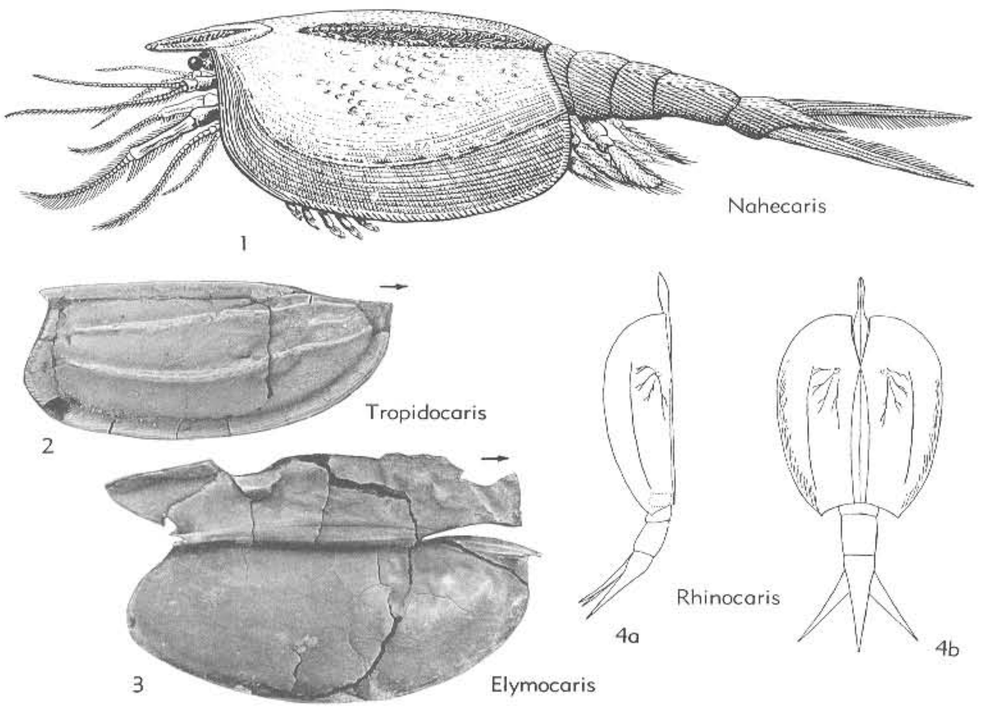


FIG. 146. Rhinocarididae (p. *R*321-*R*322).

?L.Dev., M.Dev.-M.Penn., ?U.Perm., Eu.-N.Am.-USSR-?Australia.——FIG. 147,*1*. **D. testudinea* (Scouler), L.Carb., Scot.; dorsal view of holotype, ×2 (Rolfe, n). [=*Chaenocartis* Yanishevskii, 1910 *(nom. null.)*.]

Elymocaris Beecher, 1884 [**E. siliqua*; OD] [=*Elimocaris* Krestovnikov, 1961 *(nom. null.)*]. Like *Rhinocaris* but carapace valves without posteroventral spine; no mesolateral carina, anterior tubercle present; rim with oblique, posteriorly imbricating ridges; rostral plate folded ventrally along 2 lateral, anteriorly converging carinae; telson with broad median ridge. *M.Dev.-U.Dev.*, USA-?Can.——FIG. 146,*3*. **E. siliqua*, U.Dev. (Chemung), USA(Pa.); dorsal view of carapace showing median dorsal plate, rostral plate, and crushed LV, ×1.6 (Rolfe, n).

Macrocaris S. A. Miller, 1894 [**M. gorbyi;* OD]. Like *Rhinocaris* but carapace with short longitudinal ridges; no mesolateral carina. [Poorly known; ventral region of carapace and tailpiece unknown. Supposed body segments of Miller's syntypes lack ornament of lectotype (Miller, 1894, fig. 43; Chicago Field Museum) and probably not crustacean; supposed "masticatory apparatus" is scolecodont.] *L.Miss.*, USA(Ind.).

Nahecaris Jaekel, 1921 [**N. stuertzi*; OD] [=*Nehecaris* Gürich, 1929 *(nom. null.)*]. Like *Tropidocaris* but with single lateral carina on each carapace valve. *L.Dev.*, Ger.——FIG. 146,*1*. **N. stuertzi*; left dorsolat. view (reconstr.), ×0.7 (Rolfe, n).

[Broili maintained that the rostral plate of *Nahecaris* was completely fused with the carapace, but Hennig and Gürich showed that it was free, at least in some specimens (which Broili therefore asserted belonged to a different genus). Specimens in the Harvard Museum of Comparative Zoology show the rostral plate separated from the carapace laterally and probably posteriorly, though obscured by pyritization. A median dorsal plate is present, so that *Nahecaris* is certainly one of the Rhinocarina, as Hennig and Gürich affirmed, but Broili and Raymond denied. Thus no basis exists for Broili's order Nahecarina, although, should the rostral plate definitely prove to be fused, the separate family might be resurrected.]

Tropidocaris Beecher, 1884 [**T. bicarinata*; SD S. A. Miller, 1889] [=*Tropocaris* Jones & Woodward, 1888 *(nom. null.)*; *Tropicodaris* Clarke, 1892 *(nom. null.)*; *Tropodocaris, Tropodicaris, Trapidocaris* Chernyshev, 1938 *(nom. null.)*; *Tropidocarinatus* Sturgeon, Hlavin, & Kesling, 1964 *(nom. null.)*]. Like *Dithyrocaris* but with mesolateral carina extending to anterior border of carapace; rim broader and more convex; commonly lacks posteroventral spine. [The characters by which present genera of Rhinocarididae are differentiated are probably only of specific value and considerable revision is required.] *?M.Dev., U.Dev.*, Eu.-N.Am.——FIG. 146,*2*. **T. bicarinata*,

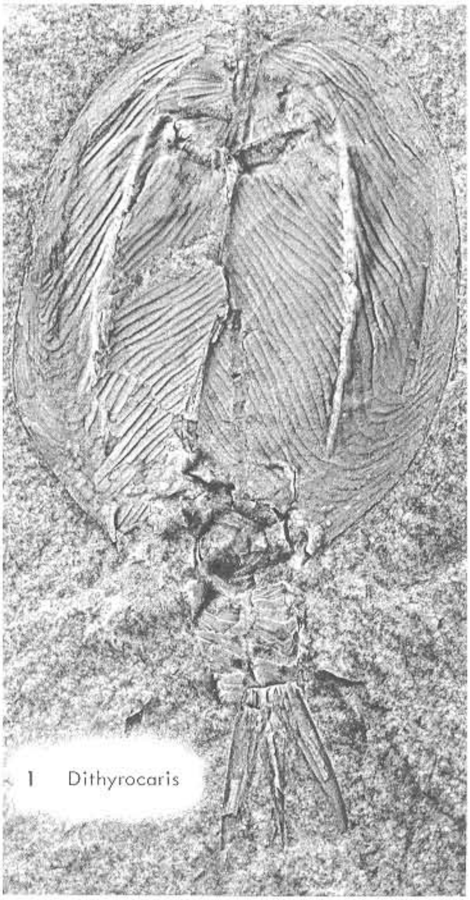


FIG. 147. Rhinocarididae (p. *R*321-*R*322).

U.Dev., USA(Pa.); lat. view of RV (lectotype), right half of median dorsal plate only preserved, showing adductor muscle impression and vascular ridges between lateral carinae, ×2 (Rolfe, n).

Family OHIOCARIDIDAE Rolfe, 1962

Carapace valves subcircular, with anterodorsal-medioventral fold and marginal ridge dorsal from ventral margin; median dorsal plate broad, without median carina. *U.Dev.*

Ohiocaris ROLFE, 1962 [**O. wycoffi*; OD]. Characters of family. *U.Dev.*, USA(Ohio).——FIG. 148, *1*. **O. wycoffi*, Chagrin Sh., Porter Creek (Cuyahoga Co.); dorsal view of holotype showing mandibles impressed through anterodorsal region of carapace valves; abdomen inverted relative to carapace, ×1 (376a, mod.).

Phyllocarida Order and Family UNCERTAIN

Genera and families founded on isolated carapaces or tail pieces, or of family or order incertae sedis are described below. Some genera may not even be Phyllocarida, but they are too poorly known to be assigned with certainty to other groups.

Anomalocaris WHITEAVES, 1892 [*non* ORTMANN, 1893] [**A. canadensis;* OD] [=*Anomolocaris* WALCOTT, 1908 *(nom. null.)*; *Anormalocaris* KRESTOVNIKOV, 1961 *(nom. null.)*]. Curved body of at least 14 subquadrate segments including telson, each segment with pair of ?ventral, elongate pointed, unsegmented appendages; dorsal and ventral processes on telson may represent ?furcae of *Hymenocaris* type. [Possibly the body of *Tuzoia*. Type of Anomalocaridae (*recte* Anomalocarididae) RAYMOND, 1935]. *L.Cam.-M.Cam., ?U. Sil.*, N.Am.——FIG. 149,*2*. **A. canadensis*, M. Cam., Can.(B.C.); part of body, lat., ×0.5 (Rolfe, n).

Baituganocaris KRESTOVNIKOV, 1961 [**B. tatarica*; OD]. Like *Montecaris,* but carapace without posteroventral spines and anterodorsal grooves. [Type of Baituganocarinae (*recte* Baituganocaridinae) KRESTOVNIKOV, 1961. Should this genus prove synonymous with *Montecaris,* as CHLUPÁČ has suggested, the subfamily Baituganocaridinae would have priority over Montecaridinae.] *U.Dev.*, E.Eu.-?Czech.——FIG. 149,*3*. **B. tatarica,* Shugurov Beds (Frasn.), Orenburg distr., E.Eu.; carapace displaced from abdomen (holotype), ×1.5 (168).

Canadaspis NOVOZHILOV in ORLOV, 1960 [**Hymenocaris perfecta* WALCOTT, 1912; OD]. Carapace

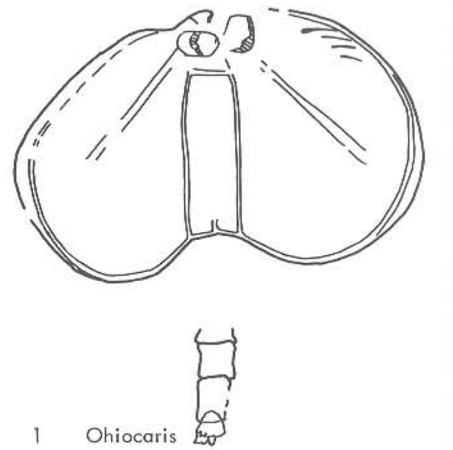


FIG. 148. Ohiocarididae (p. *R*323).

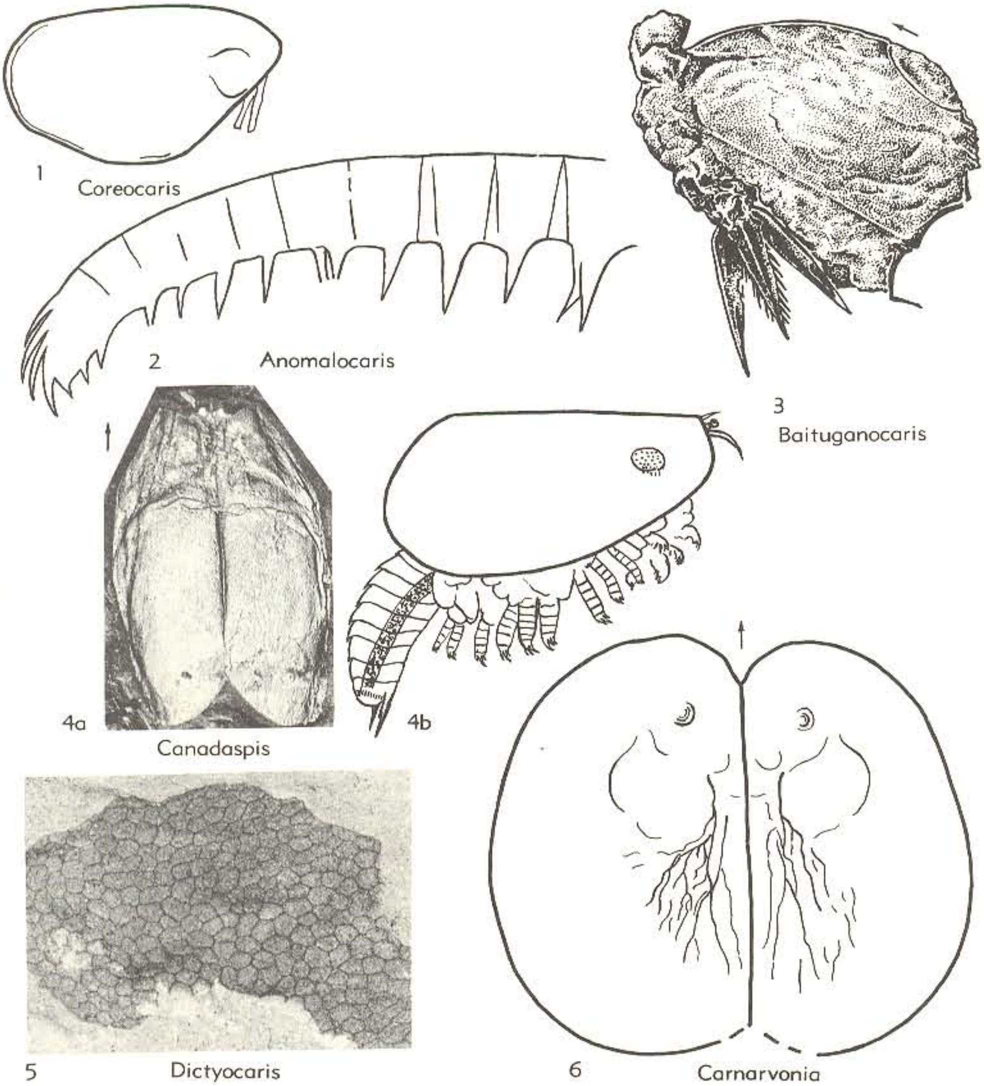


FIG. 149. Phyllocarida, Order and Family Uncertain (p. R323-R325).

with hinge line, valves subovate, each with large anteromedian adductor muscle scar; rostral plate small, eyes pedunculate; pleomeres of same length as thoracomeres, without pleopods; with posteroventral spines, especially well developed on ?pretelson somite and simulating furca; telson small, rounded, ?without furca; ?amandibulate; thoracopods of at least 8, short segments wtih 4 distal, anteriorly curved claws and large proximally attached lamella. [Type of order Canadaspidida and family Canadaspididae NOVOZHILOV in ORLOV, 1960.] *M.Cam.*, W.Can.——FIG. 149,*4*. **C. perfecta* (WALCOTT), Burgess Sh., B.C.; *4a*, dorsal view of carapace showing left ?antenna, eyes, and rostral plate, ×1.6 (Rolfe, n); *4b*, right lat. view of holotype (reconstr.) showing intestinal filling, ×1.7 (Rolfe, n, after 384c).

Carnarvonia WALCOTT, 1912 [**C. venosa*; OD] [=*Caanarvonia* KRESTOVNIKOV, 1961 *(nom. null.)*]. Carapace with hinge line, valves subelliptical, with anterior tubercle; prominent ?vascular markings diverge posteriorly from main mid-dorsal, longitudinal trunk on each valve. *M.Cam.*, Can.——FIG. 149,*6*. **C. venosa*, Burgess Sh.,

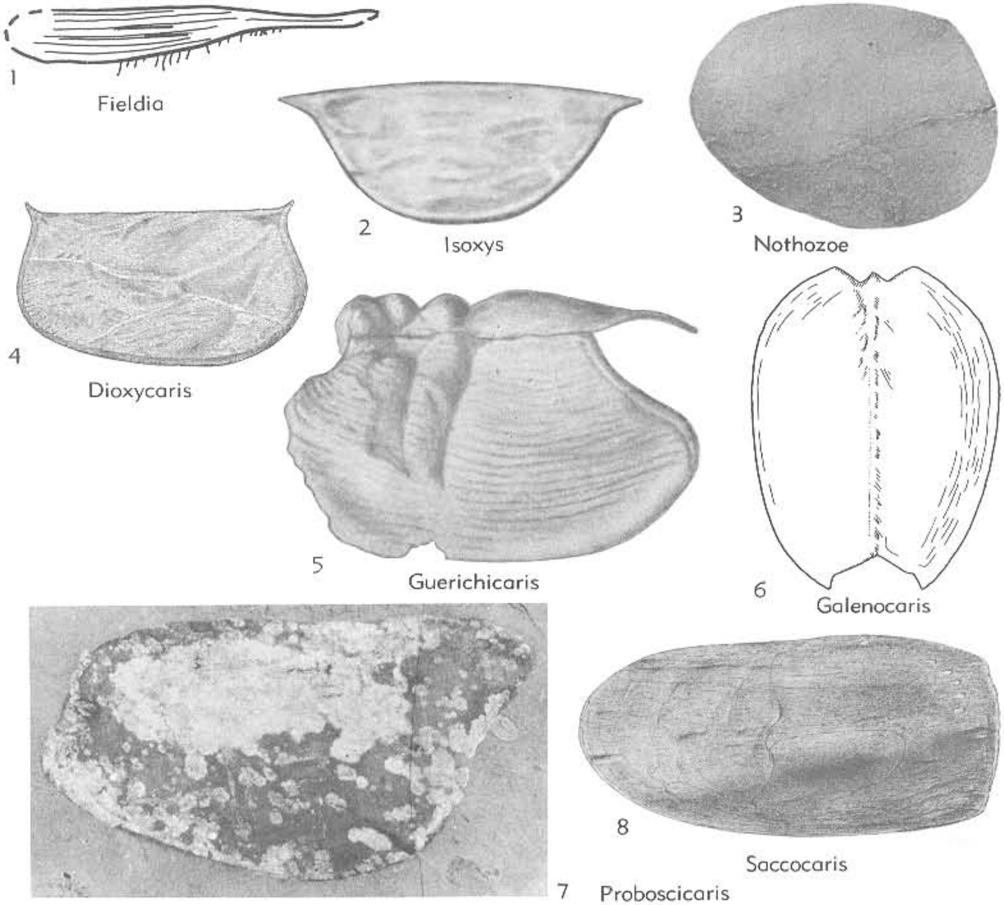


FIG. 150. Phyllocarida, Order and Family Uncertain (p. *R*325-*R*327).

B.C.; dorsal view of carapace (holotype) with valves spread out, ×0.6 (Rolfe, n).

Coreocaris Kobayashi, 1937 [**C. eishunensis*; OD]. Carapace valves subovate, ?without hinge line. *L.Perm.*, S.Korea.——Fig. 149,*1*. **C. eishunensis*, Jido Ser.; right lat. view of carapace (holotype) showing ?cephalic appendages, ×4 (Rolfe, n).

Dictyocaris Salter, 1860 [**D. slimoni*; OD] [=*Dictyacris* Henderson, 1880 *(nom. null.)*; *Didyocaris* Vogdes, 1889 *(nom. null.)*; *Eohepatica* Heard & Jones, 1931 (type, *E. dyfriensis;* OD, M); *Thallomia* Heard & Jones, 1931 *(nom. van.)*]. Carapace without hinge line, valves subtriangular, with reticulation of grooves or ridges (probably indicating outlines of cuticular prisms). *M.Sil.-L.Dev.*, NW.Eu.-USA.——Fig. 149,*5*. **D. slimoni*, ?M.Sil., Scot.; carapace fragment showing reticulation, ×3 (Rolfe, n).

Dioxycaris Gürich, 1929 [**Leperditia? argenta* Walcott, 1886; OD] [=*Dyoxycaris* Krestovnikov, 1961 *(nom. null.)*]. Carapace ?with hinge line, valves subrectangular, anterodorsal and posterodorsal extremities produced obliquely into processes. *L.Cam.*, N.Am.——Fig. 150,*4*. **D. argenta* (Walcott), USA(Utah); lat. view of ?LV (holotype), ×0.7 (384a).

Fieldia Walcott, 1912 [**F. lanceolata*; OD]. ?Carapace lanceolate, with at least 5 longitudinal furrows. *M.Cam.*, N.Am.——Fig. 150,*1*. **F. lanceolata*, Burgess Sh., Can.(B.C.); ?carapace lat., holotype, ×1.3 (384c).

Galenocaris Wells, 1944 [**G. campbelli;* OD, M]. Carapace ?without hinge line, valves elongate, with short posteroventral spine; anterodorsally and posteriorly truncate; short process between valves anteriorly. *U.Ord.*, N.Am.——Fig. 150,*6*. **G. campbelli*, Maquoketa Sh., USA(Ill.); dorsal view of carapace (holotype), ×2 (385).

Guerichicaris Van Straelen, 1933 [*pro Entomo-*

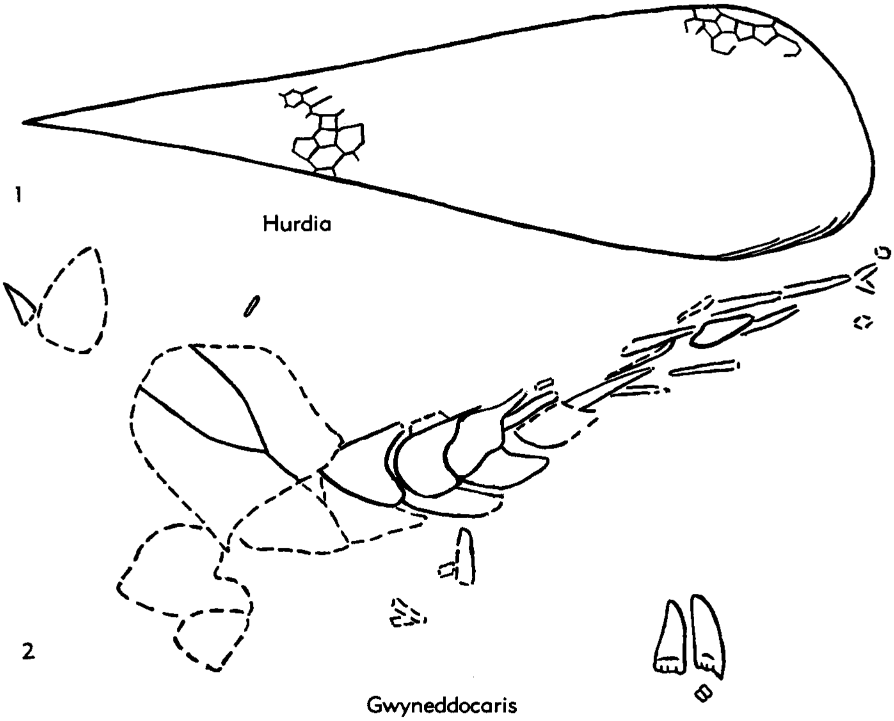


Fig. 151. Phyllocarida, Order and Family Uncertain *(1)*; Discinocarina, Family Uncertain *(2)* (p. *R*325-*R*326).

caris Gürich, 1929 (*non* Whitfield, 1896)] [**Entomocaris dohmi* Gürich, 1929 (=*Entomocaris dohmi* Richter & Richter, 1918, *nom. nud.)*; OD] [=*Guerichocaris* Krestovnikov, 1961 *(nom. null.)*]. Carapace with hinge line, valves subovate, anteriorly rounded, posterodorsally truncate; marginal rim narrow anteroventrally, broadening posteriorly; anterodorsal region of carapace with 3 deeply incised, oblique furrows separating 3 swellings; valves with coarse longitudinal striation. [Type of Guerichicaridae (*recte* Guerichicarididae) Van Straelen, 1933, of Ceratiocarina.] *M.Dev.*, Ger.——Fig. 150,*5*. **G. dohmi* (Gürich), Couvin., Eifel; left posterodorsal view of carapace (paratype), ×3 (128).

Hurdia Walcott, 1912 [**H. victoria*; OD]. ?Carapace triangular, commonly reticulate. *M.Cam.*, N. Am.——Fig. 151,*1*. **H. victoria*, Burgess Sh., Can.(B.C.); lat. view of small specimen showing reticulation, ×0.6 (Rolfe, n).

Isoxys Walcott, 1890 [**I. chilhoweanus*; OD] [=*Isoxis, Isoxis*, Krestovnikov, 1961 *(nom. null.)*]. Carapace with convex hinge line, valves subelliptical; anterodorsal or mid-anterior and posterodorsal extremities of valves produced into sharp processes. [Type of Isoxyidae Brooks & Caster, 1956 (*nom. correct.* Rolfe, 1962, *pro* Isoxysidae Brooks & Caster, 1956) including *Isoxys, Dioxycaris,* and *Tuzoia,* and thus junior synonym of Tuzoiidae Raymond, 1935.] *L.Cam.-M.Cam.*, N.Am.-Spain.——Fig. 150,*2*. **I. chilhoweanus,* L.Cam., USA(Tenn.); lat. view of carapace (syntype), ×1.5 (384b).

Lebesconteia Jones & Woodward, 1899 [*nom. correct.* Rolfe, herein (*ex Lebescontia* Jones & Woodward, 1899)] [**L. aenigmatica;* OD]. Carapace of *?Dithyrocaris,* indeterminable. Other species may be Bivalvia. *U.Ord., L.Carb.,* NW.Eu.

Mendocaris Rusconi, 1950 [**M. australis;* OD, M]. Carapace with marginal excavation and anterior depression; poorly described and unfigured. *U. Cam.,* Argentina.

Nothozoe Barrande, 1872 [**N. pollens;* OD, M] [=*Nothozoe* Barrande in Bigsby, 1868 *(nom. nud.); Notozoe* Zittel, 1885 *(nom. null.)*]. Elliptical, subovate, or subcircular, smooth and gently arched molds of carapace valves. *L. Cam.-M.Ord., ?L.Dev.,* W.Eu.-USA-?SW.China.——Fig. 150,*3*. **N. pollens,* M.Ord., Drabov Qtzt., Czech.; convex mold of ?LV of large specimen, ×0.6 (Rolfe, n).

Odaraia Walcott, 1912 [**O. alata*; OD] [=*Odaria* Fedotov, 1925 *(nom. null.)*; *Odoraia* Roger in Piveteau, 1953 *(nom. null.)*; *Odria*

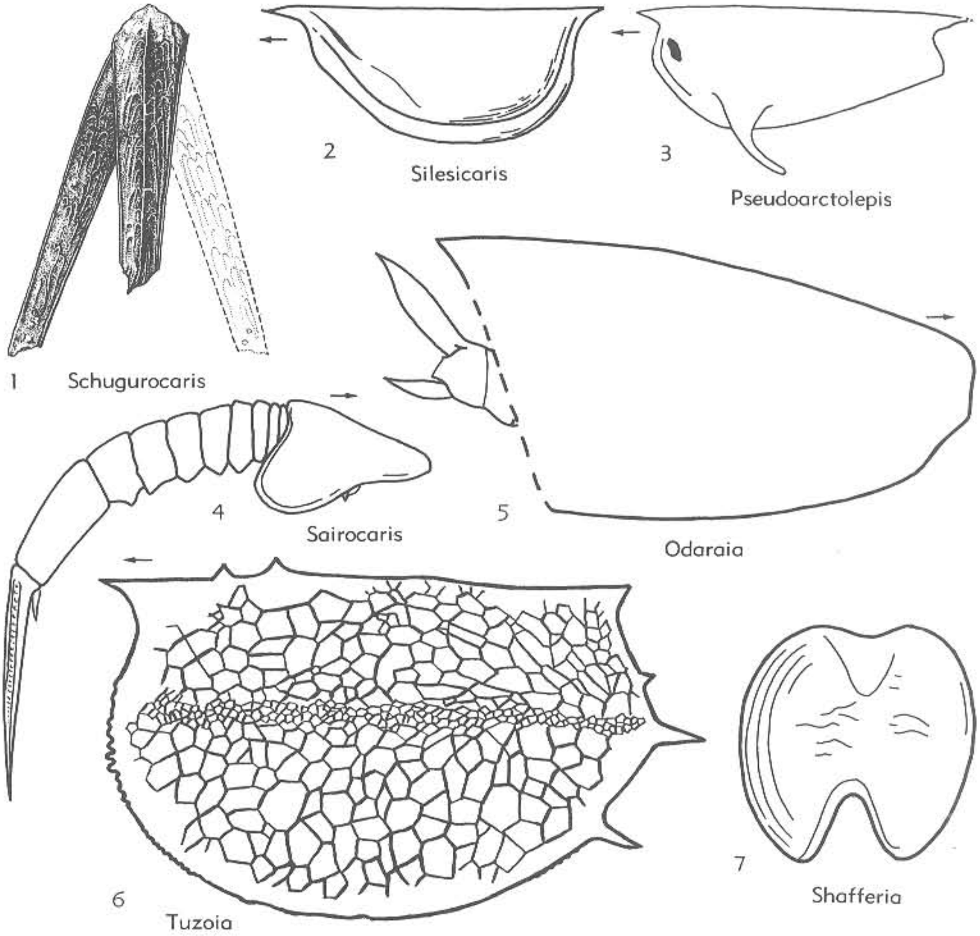


FIG. 152. Phyllocarida, Order and Family Uncertain (p. *R326-R328*).

KRESTOVNIKOV, 1961 *(nom. null.)*]. Carapace subtriangular, with oblique posterior truncation, furcal rami laterally expanded, lanceolate. *M.Cam.*, N.Am.——FIG. 152,*5*. *O. alata, Burgess Sh., Can.(B.C.); lat. view of lectotype, ×0.5 (Rolfe, n).

Proboscicaris ROLFE, 1962 [*P. agnosta; OD]. Carapace valves subovate to subrectangular, with carapace horn anteriorly produced into spatulate beak. *M.Cam.*, N.Am.——FIG. 150,*7*. *P. agnosta, Burgess Sh., Can.(B.C.); lat. view of RV (holotype), blotched with ?alga *Morania parasitica* WALCOTT, ×0.5 (376a).

Pseudoarctolepis BROOKS & CASTER, 1956 [*P. sharpi; OD]. Carapace elongate, with hinge line; anterodorsal and posterodorsal extremities of valves produced into processes, posterior margin concave; large, posteriorly curved, anteroventrally situated hollow spine and eroded area marking site of anterior tubercle on each valve. [Type of Pseudoarctolepididae BROOKS & CASTER, 1956 (*nom. correct.* ROLFE, 1962, *pro* Pseudoarctolepidae BROOKS & CASTER, 1956). This large form shows remarkable convergent resemblance to the ostracode *Pteroleperditia armata* (WALCOTT).] *M.Cam.*, N.Am.——FIG. 152,*3*. *P. sharpi, Wheeler Sh., USA(Utah); lat. view of LV (reconstr.), ×0.7 (58).

Saccocaris SALTER, 1873 [*Hymenocaris (Saccocaris) major; M] [=*Sacocaris* SALTER, 1868 *(nom. oblit.)*]. Carapace ?without hinge line, valves subrectangular. *U.Cam.-L.Ord.*, G.Brit.-?Australia.——FIG. 150,*8*. *S. major (SALTER), Wales; lat. view of LV (holotype), ×0.5 (160).

Sairocaris ROLFE, 1963 [*pro Acanthocaris* PEACH, 1883 (*non* SIM, 1872)] [*Acanthocaris attenuata

Peach, 1883; SD Van Straelen & Schmitz, 1934] [=*Acantocaris* Krestovnikov, 1961 *(nom. null.)*]. Carapace reduced, triangular, without hinge line, with or without mid-ventral excavation which may have allowed ventral exposure of gnathal lobes of mandibles; carapace smooth or ?longitudinally striate; abdomen and ?posterior thoracic somites not covered by carapace; telson as in *Ceratiocaris,* dorsal ridge may be tuberculate; furca reduced to short spines. [Emendation of the Ceratiocarina may be needed to include a family based on this genus without a hinge line. At present *Sairocaris* is too poorly known to warrant such a major change.] *L.Carb.,* W.Eu.——Fig. 152,*4*. *S. elongata* (Peach), Visean, Scot.; right lat. view (reconstr.), ×1 (Rolfe, n, after 371).

Schugurocaris Krestovnikov, 1961 [**S. magnifica*; OD] [=*?Neurocaris* Krestovnikov, 1961 (type, *N. libelluliformis;* OD)]. Telson triangular in cross-section, longer than furca, both with ornament of cusps or oblique striae. *U.Dev.,* E.Eu.-Australia-?N.Can.——Fig. 152,*1*. **S. magnifica,* Shugurov Beds (Frasn.), Orenburg distr., E.Eu.; dorsal view of telson and furca (holotype) (part reconstr.), ×1 (168).

Shafferia Walcott, 1917 [**S. cisina*; OD] [=*Schafferia* Sharp, 1901 *(nom. null.)* (Walcott's original spelling should be conserved and not treated as a *lapsus* since Mount Schaffer, after which the fossil was named, is also (and more correctly) written Schaeffer. Confusion will then be avoided with *Schaefferia* Absolon, 1900 (*non* Houlbert in Oberthür, 1918)]. Like *Discinocaris* but shell thicker, bent along mid-line and with shallow indentation at end farthest from notch. *M.Cam.,* N.Am.——Fig. 152,*7*. **S. cisina,* Mt. Whyte F., Can.(B.C.); dorsal view of holotype, ×6 (Rolfe, n).

Silesicaris Gürich, 1926 [**S. nasuta;* OD, M] [=*Silesiocaris* Kobayashi, 1937 *(nom. null.)*]. Outline of carapace valves like that of *Isoxys* but with well-defined marginal groove demarcating broad rounded rim and with deep, oblique antero-dorsal-mid-anterior furrow continued as fold which joins margin mid-ventrally; anterior tubercle sometimes detectable. *L.Cam.* (not L.Dev. as originally described), SW.Pol.——Fig. 152,*2*. **S. nasuta,* Bolków; lat. view of LV, ×2 (128).

Trigonocarys Barrois, 1891 [**T. lebescontei;* OD, M] [=*Trigonocaris* Wiltshire, Woodward & Jones, 1892 *(nom. van.)*]. Telson triangular, with 4 longitudinal, ventral ribs separated by furrows; furca shorter than telson, furcal rami laterally compressed, hourglass-shaped in cross section. *U. Ord.,* NW.Fr.

Tuzoia Walcott, 1912 [**T. retifera*; OD] [=*Puzoia* Gürich, 1929 *(nom. null.)*; *Tusoia* Brooks & Caster, 1956 *(nom. null.)*]. Carapace with hinge line, valves subelliptical, carapace horn slightly produced; usually reticulate; prominent lateral ridge carinate, with smaller reticulae than on main area of valves; spines and spinules projecting from entire margin except anterior, and may occur on lateral ridge. [Type of Tuzoiidae Raymond, 1935 (=Isoxyidae Brooks & Caster, 1956).] *L.Cam.-M.Cam.,* W.Can.-China.——Fig. 152,*6*. *T. burgessensis* Resser, M.Cam. (Burgess Sh.), B.C.; lat. view of LV (paratype) (reconstr.), ×0.5 (Rolfe, n).

NONPHYLLOCARID AND UNCERTAIN GENERA

In this section consideration is given to various nominal genera which have been improperly classed by authors as belonging to the Phyllocarida and to some which now are regarded as *incertae sedis.*

FORMS REFERRED TO DISCINOCARINA

The genera grouped by Clarke (1900) in his suborder Discinocarina and referred to the Phyllocarida are of uncertain affinity. They have been compared and confused with graptolite "swim-bladders" and "gonangia," eurypterid metastomata, hyolithid opercula, polyplacophoran plates, bivalves, arthrodire dermal plates, and branchiopod carapaces. *Discinocaris gigantea,* which may be up to 18 cm. in diameter, has been suggested by analogy with *Oxlosia* to be a genuine acrotretid brachiopod. Some of these genera are known to be ammonoid anaptychi and have been synonymized with *Sidetes* (*Treatise,* p. *L*467-*L*468). Other genera are pre-Devonian and hence cannot be ammonoid aptychi, but Ruedemann's (1916) suggestion that aptychi "would naturally also have existed in the Ordovician and Silurian cephalopods" has been largely overlooked. The sole crustacean feature of the remaining Discinocarina is the supposed "rostral plate," which shows little similarity to rostral plates of other fossil phyllocarids. Two cases of body segments associated with Discinocarina have been described, but these are both doubtful. It is tempting to suggest an analogy between the bivalved Peltocarididae and ammonoid diaptychi, and between the Discinocarididae and ammonoid anaptychi. Significantly, their stratigraphic range coincides with that of the michelinoceratid nautiloids. The isolated occurrence

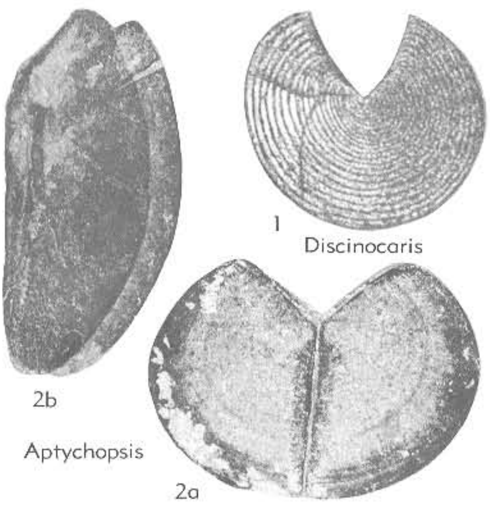


FIG. 153. Subclass Uncertain (Discinocarididae) *(1)*; (Peltocarididae) *(2)* (p. *R*329).

of these shields may result from current sorting and selective diagenesis (KEYSERLING, 1846; CLARKE, 1902) in the same way as aptychi occur in aptychus beds.

No pre-Devonian Discinocarina have been found in nautiloid apertures, however, which makes difficult a ready acceptance of RUEDEMANN's hypothesis. On the other hand, it seems worth recalling that, as DAMES (1884) and MATERN (1931) stressed, "only in exceptional cases do anaptychi and shells occur together."

Two groups of nominal genera previously classed as belonging to CLARKE's order Discinocarina are included under this heading. One consists of forms which now are regarded as synonyms of *Sidetes*. The other contains genera *incertae sedis* which are not synonymized with *Sidetes*. Fossils included in this latter group are represented by circular to subcircular, ?originally conical, concentrically ridged, thin organic or carbonized films, with subtriangular plate filling a prominent notch. For reference purposes it is useful to retain the familial classification employed for them.

The genera here cited as synonyms of *Sidetes* are additional to those given in *Treatise* Part L (1957, p. *L*467-*L*468).

Sidetes GIEBEL, 1847, p. 821 [**S. striatus* GIEBEL, 1851; SM] [?=*Ellipsocaris* WOODWARD in DEWALQUE, 1880 (type, *E. dewalquei;* OD, M); *Spathiocaris* CLARKE, 1882 (type, *S. emersonii*; OD); *Spathocaris* ETHERIDGE, WOODWARD & JONES, 1883 *(nom. null.)*; *Spathiogaris* CAMPBELL, 1946 *(nom. null.)*; *Ellipsiocaris* BROOKS & CASTER, 1956 *(nom. null.)*; *Spathyocaris, Spatiocaris, Spatchiocaris* KRESTOVNIKOV, 1961 *(nom. null.)*; *Dipterocaris* CLARKE, 1883 (type, *D. pennaedaedali*; SD S. A. MILLER, 1889) (holotype of the type species is a *Spathiocaris* torn along its mid-line, as surmised by ETHERIDGE, WOODWARD & JONES, 1885)].

Family DISCINOCARIDIDAE
Etheridge, Woodward & Jones, 1885

[*nom. correct.* ROLFE, herein (*pro* family Discinocarida ETHERIDGE, WOODWARD & JONES, 1885, *nom. imperf.*)] [=Discinocaridae HALL & CLARKE, 1888]

Without median suture line. *M.Ord.-U. Trias., ?L.Jur.*

Discinocaris WOODWARD, 1866 [**D. browniana*; OD, M] [=*Aspidocaris* REUSS, 1867 (type, *A. triasica;* OD)]. Sides of notch straight. *M.Ord.-U. Trias., ?L.Jur.,* W.Eu.-USA.——FIG. 153,*1*. **D. browniana,* L.Sil. (Birkhill Sh.), Scot.; syntype, lacking triangular plate, ×2 (386a).

Family PELTOCARIDIDAE
Clarke in Zittel, 1900

[*nom. correct.* ROLFE, herein (*pro Peltocaridae* CLARKE in ZITTEL, 1900)] [=*Peltocariden* HAECKEL, 1896 (vernacular)]

With median suture line. *?L.Cam.-?M. Cam., ?L.Ord., U.Ord.-U.Sil., ?U.Perm.*

Peltocaris SALTER, 1863 [**Dithyrocaris? aptychoides* SALTER, 1852; SD ETHERIDGE, WOODWARD & JONES, 1884] [=*Peltocharis* ETHERIDGE in GEIKIE, A., HORNE, SKAE, & ETHERIDGE, 1877 *(nom. null.)*; =?*Culampaia* RUSCONI, 1949 (type, *C. ornata;* OD, M); *Culampia* ROGER in PIVETEAU, 1949 *(nom null.)*; *Peltoceras* KRESTOVNIKOV, 1961 *(nom. null.)*]. Notch semicircular, ?with nodes on valves at base of notch. *?M.Cam., ?L.Ord., M. Sil.,* Eu.-?S.Am.

Aptychopsis BARRANDE, 1872 [**A. prima;* OD, M] [=*Aptychopsis* BARRANDE, 1870 *(nom. nud.)*; *Aptychoides* BARRANDE, 1872 (obj.); *Aptichopsis* DUNCAN, WOODWARD & ETHERIDGE, 1872 *(nom. null.)*; *Apthycopsis* WOODWARD, 1882 *(nom. null.)*; *Aptychosis* RUSCONI, 1949 *(nom. null.)*]. Like *Peltocaris* but sides of notch straight; valves without nodes. *?L.Cam., ?L.Ord., U.Ord.-U.Sil., ?U.Perm.,* Eu.-?E.Can.-?Australia.——FIG. 153,*2*. **A. prima,* L.Sil.-M.Sil.(Liten Beds), Czech.; *2a,* dors., ×3; *2b,* lat. with valves displaced, ×4 (Rolfe, n).

GENERA UNCERTAIN

Anatifopsis BARRANDE, 1872 [**A. bohemica;* OD, p. 578] [=*Anatifopsis* BARRANDE in BIGSBY, 1868

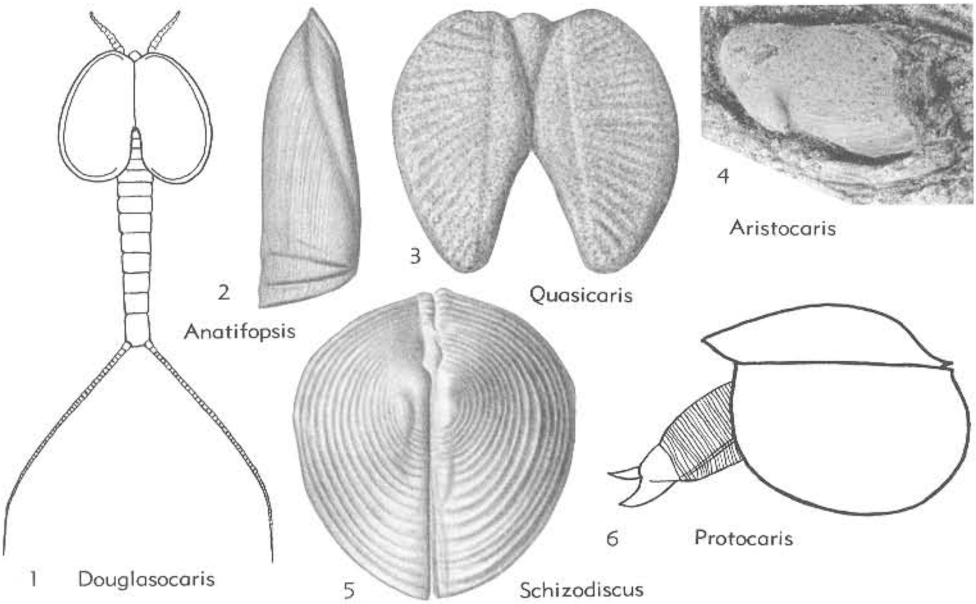


FIG. 154. Subclass Uncertain (Genera Uncertain) (p. *R*329-*R*331).

(nom. nud.)]. Thin-shelled ?Bivalvia; valves elongate, strongly convex, one end truncate, ?open in life; concentrically striate and with 2 vertical internal septa, diverging ventrally away from hinge line; may have platform developed along hinge line perpendicular to surface of valves. [Other species referred to this genus are polyplacophorans and dermal plates of *Cyathaspis*.] *L.Ord.-U.Ord.*, Eu.——FIG. 154,2. *A. prima*, L.Ord., Czech., single valve, lat., ×2 (343).

Aristocaris TOLMACHOV, 1926 [**A. incerta*] [=*Aristoscaris* NEAVE, 1950 *(nom. null.)*]. ?Ostracode. *M.Dev.*, N.Can.——FIG. 154,4. **A. incerta*, Givet., Ellesmere I.; lat. (holotype), ×9 (Rolfe, n).

Caridolites ETHERIDGE, WOODWARD & JONES, 1890 [**C. wilsoni;* OD, M] [=*Caridolites* NICHOLSON, 1873 *(nom. nud.)*; *Cardiolites* CLARKE in ZITTEL, 1900 *(nom. null.)*; *Cardiolies* KRESTOVNIKOV, 1961 *(nom. null.)*]. Based on supposed tracks of *?Ceratiocaris*, possibly groove casts. *M.Sil.*, Scot.

Cryptozoe PACKARD, 1886 [**C. problematica*; OD] [=*Cryptozoa* POMPECKJ, 1912 *(nom. null.)*; *Schopfia* JANSSEN, 1940]. [Dr. J. M. SCHOPF has isolated plant epidermis from the holotype (U.S. Natl. Mus. 38865) and suggests that this is a lycopod sporangium.] *M.Penn.*, USA(Ill., Mazon Creek).

Douglasocaris CASTER & BROOKS, 1956 [**D. collinsi*; OD]. Carapace with hinge line, valves subelliptical, smooth; ?9 abdominal somites, telson elongated but not produced and bearing pair of annulated cerci; thoracic limbs biramous, nonfoliaceous, with 2- or 3-segmented protopod. ?Notostracan branchiopod. [Type of Douglasocaridae *(recte* Douglasocarididae) CASTER & BROOKS, 1956.] *L.Ord.*, N.Am.——FIG. 154,*1*. **D. collinsi*, "33 Formation," Douglas Dam, USA(Tenn.); dors. holotype (reconstr.), ×2 (350, mod.).

Gwyneddocaris BOCK, 1946 [**G. parabolica*; OD]. *U.Trias.*, N.Am.——FIG. 151,2. **G. parabolica*, Lockatong F., USA(Pa.); dorsal view of holotype, ×4.8 (Rolfe, n).

Dr. DONALD BAIRD recognized that the unique specimen of *Gwyneddocaris* comprises the mid-line scales and fin fulcra of a ganoid fish. He therefore obtained the independent opinion of Dr. HAROLD F. ROELLIG who agreed that "The specimen does represent the midline region of a fish. . . . The 'univalved carapace' is probably scalation associated with the vent. I know of nothing quite like it along the dorsal midline. The 'thoracic somites' [Bock's numbers] 2,3,4,5,6 are midline scales. The 'spines' 20 and 21 are fulcra. The small size of these fulcra indicates that the fish is not *Semionotus* but probably *Catopterus*; fulcra of *Semionotus* are more robust. The tubercles illustrated in Bock's Fig. 5 as on the 'spines' are to be seen on the fulcra of both *Semionotus* and *Catopterus*."

Lingulocaris SALTER in RAMSAY, 1866 [**L. lingulaecomes;* OD, M] [=*Mytilocaris* ETHERIDGE, 1888 *(nom. nud.)*; *Lingulocarys* BARROIS, 1891 *(nom. van.)*; *Lingulocasis* MARR, 1892 *(nom. null.)*; *Modiolocaris* PEACH in JEHU & CAMPBELL, 1917 (type, *M. dakynsi;* OD, M]. Thin bivalve shell with slight umbo, concentrically striate; ?ribeiroiid or Bivalvia. [Refers to type-species and *Modiolocaris* only. Other Lower Ordovician species referred to this genus are based on elongate carapaces resembling *Hymenocaris*. Further knowledge of these is needed before establishing a separate genus. The body segments shown on Peach's restoration of *Modiolocaris* are imaginary; the holotype shows only a fracture plane.] *U.Cam.-L.Ord.*, G.Brit.

Myocaris Salter, 1864 [**M. lutraria*; OD]. Ribeiroiid. *L.Ord.-U.Ord.*, W.Eu.

Pinnocaris Etheridge, 1878 [**P. lapworthi*; OD]. ?Ribeiroiid or Bivalvia. *U.Ord.-U.Sil.*, Brit.

Portalia Walcott, 1918 [**P. mira*; OD]. The holotype of the type species is a ?sponge (Madsen, 1957) and is overlain by a specimen of the ?actiniarian *Mackenzia costalis* Walcott (according to Walcott, 1918; later identified as the worm *Miskoia* by Resser, 1931). Størmer (1944, p. 101) has compared the specimens with *Protocaris*, interpreting the *Mackenzia* as a carapace, and has referred to the "papillae" of *Portalia* as arthropod appendages with "indications of gill-blades."

Proricaris Baily, 1870 [**P. machenrici;* OD, M] [=*Protacaris* Etheridge, Woodward & Jones, 1883 *(nom. null.); Proracaris* Baily, 1875 *(nom. null.)*; *Protocaris* Jones & Woodward, 1888 *(nom. null.)*]. Fragments of eurypterid according to Etheridge, Woodward & Jones, 1890. *U.Dev.*, SE.Eire.

Protocaris Walcott, 1884 [*non* Jones & Woodward, 1888 *(nom. null.)*] [**P. marshi*; OD] [=*Procaris* Woodward, 1895 *(nom. null.)*]. Carapace with hinge line, valves subelliptical. Large number (may exceed 45) of short body somites bearing lamellate appendages anteriorly. Telson not produced, furcal rami curved. ?Branchiopod. [Type of Protocaridae(*recte* Protocarididae) Miller, 1889.] *L.Cam.-M.Cam.*, N. Am.——Fig. 154,*6*. *P. pretiosa* Resser, M.Cam. (Burgess Sh.), Can.(B.C.); right lat. (holotype), ×0.7 (Rolfe, n).

Quasicaris Rolfe, 1961 [*pro Pterocaris* Barrande, 1872 (*non* Heller, 1862; *nec* Claus, 1876)] [**Pterocaris bohemica* Barrande, 1872; OD, M]. Like *Aptychopsis* but with posterior notch, thin radial striae and single longitudinal line on each ?valve. *M.Ord.*, Czech.——Fig. 154,*3*. **Q. bohemica* (Barrande), Drabov Qtzt., Mt. Drabov; internal mold, dors. (holotype), ×3 (343).

Salterina Jones & Woodward, 1888 [**S. pholadiformis;* OD, M (=*Dithyrocaris pholadomya* Salter, 1863, *nom. nud.; D. pholadiformis* Huxley & Etheridge, 1865, *nom. nud.*)] [=*Salterella* Jones & Woodward, 1888 (*non* Billings, 1861) (obj.), an offprint of the 1888 paper signed by T. R. Jones in the Harvard Museum of Comparative Zoology has the spelling corrected in Jones' handwriting.)]. Fragment of large bivalve mollusk. *L.Carb.*, Eng.

Schizodiscus Clarke in Hall & Clarke, 1888 [*non* Kittl, 1891; *nec* Kishinouye, 1902] [**S. capsa;* OD, M]. Carapace with hinge line, valves semicircular, with ridges concentric about mid-dorsal umbo. ?Conchostracan branchiopod. *M.Dev.*, N.Am.——Fig. 154,*5*. **S. capsa,* Hamilton Gr., USA(N.Y.); carapace valves spread out, dorsal (lectotype), ×3 (140).

Sinocaris Mansuy, 1912 [**S. asiatica*; SD van Straelen & Schmitz, 1934]. Elongate valves with slight ventral excavation, posterior attenuation and prominent, longitudinal folds. ?Bivalvia. *Sil.*, SW. China.

Strigocaris Vogdes, 1889 [*pro Solenocaris* Meek, 1872 (*non* Young & Young, 1868)] [**Ceratiocaris (Solenocaris) strigata* Meek, 1872; OD, M] [=*Stringocaris* Kobayashi, 1937 *(nom. null.)*]. Two of the syntypes of the type species are Bivalvia, and the third is a fish bone, probably a coelacanth jugular plate. [*Strigocaris sanctiludovici* (Worthen) is possibly a phyllocarid carapace, but poorly preserved.] *L.Miss.*, USA.

Trilobocaris Přibyl, 1953 [**T. bohemica;* OD]. ?Carapace small, elongate, one valve convex, trilobed, the other flat, weakly bilobed. ?Ostracode or crinoid calyx plate (*fide* J. Bouška and I. Chlupáč). *M.Dev.*, Czech.

Xiphidiocaris Clarke in Zittel, 1900 [*pro Xiphocaris* Etheridge, Woodward & Jones, 1886 (*non* Martens, 1872)] [**Ceratiocaris? ensis* Salter, 1860; OD, M] [=*Xyphocaris* Gürich, 1929 *(nom. null.)*]. Telson of eurypterid *Carcinosoma,* according to Ruedemann. *M.Sil.-U.Sil.*, Eng., Australia.

EUMALACOSTRACA

By R. C. Moore

Subclass EUMALACOSTRACA Grobben, 1892

Malacostraca generally of shrimplike form distinguished from Phyllocarida by nonbivalve nature of carapace and lack of seventh abdominal somite, telson without unsegmented, movably articulated caudal furca. *M.Dev.-Rec.*

The Eumalacostraca include all malacostracans considered to be relatively advanced in divergent lines of evolution. They are divided into superorders designated as Eocarida, contained archaic forms, Syncarida, Peracarida, Eucarida, and Hoplocarida, of which the last four include most post-Paleozoic malacostracans.

EOCARIDA

By H. K. Brooks
[University of Florida]

[Chapter submitted August, 1964]

CONTENTS

INTRODUCTION

Most of the Paleozoic eumalacostracan fossils with a carapace have a puzzling combination of morphological characteristics not consistent with the definition of any one of the Recent superorders. They are unique in that all have biramous thoracic appendages with a single joint in the protopod and there are furcal lobes and a median spine on the telson. However, structural trends toward the Mysidacea, Euphausiacea, and Decapoda are displayed. The superorder Eocarida was established (Brooks, 1962) for this archaic caridoid stock.

In older papers on eumalacostracan fossils from the Paleozoic, most authors classified shrimplike specimens as decapods. The single exception was Huxley (1857), who recognized some homologies between *Pygocephalus* and the Mysidacea. Woodward (1907) figured and described a peracarid marsupium on *Pygocephalus*. In the following year Peach (226) published a monographic study on the Upper Paleozoic Eumalacostraca from Scotland in which oöstegites were proved to exist also on *Tealliocaris*. He envisioned that a marsupium was present on all other contemporaneous caridoid genera. Peach repeatedly compared morphological features of the fossils with those of the Recent Lophogastridae.

Brooks (55) has demonstrated that a vertical classification of these caridoid Malacostraca consistent with established taxa for Recent Eumalacostraca is impossible. Their primitiveness and phylogenetic significance are best emphasized by recognition of the superorder Eocarida, fossils of which occur sporadically from Middle Devonian through the Permian.

MORPHOLOGY

Furcal lobes and a large median telson spine have been frequently figured on specimens of Paleozoic caridoid fossils. It was not until detailed morphological studies by Brooks (55) that the significance of these and other archaic crustacean features were realized. It is possible that none of the known fossil eocarids are the direct ancestors of the extant Mysidacea, Euphausiacea, and Decapoda, but as a group they provide valuable morphological evidence bearing on malacostracan phylogeny.

Tagmosis of the body is into a **head, thorax, abdomen,** and a terminal **telson.** In the shrimplike members of the order Eocaridacea the abdomen is longer than the **cephalothorax** (Fig. 155,*A*), whereas in the prostrate eryonid and crablike Pygocephalomorpha (Fig. 155,*B*) they are subequal or the telson is reduced.

The **carapace** completely covers the head and thorax, but it is not fused with any of the postcephalic somites. The pygocephalomorphs all have the ventral margin of the carapace folded under and the **branchiostegal area** produced laterally, the lateral margins thus formed being keeled and usually serrate. The **lappets** of the carapace of the Eocaridacea fit closely against the pleura of the thoracic somites. However, in *Palaeopalaemon* an incipient doublure occurs near the ventral margins of the carapace.

Only one transverse sulcus is conspicuously developed on the carapace and this appears to be homologous with the **cervical groove** of decapods. In that the furrow bifurcates dorsally in *Palaeopalaemon*, it is possible that the posterior branch reaching the dorsum is equivalent to the "postcervical furrow" of Glaessner (118). There is no basis for derivation of a quadruple system of dorsal carapace sulci from a *Palaeopalaemon*-like animal, as Burkenroad (62) has postulated.

Structure of the five pairs of cephalic appendages is believed to be comparable to that of the syncarids and mysidaceans. The **antennules** each consist of two multiarticulate **flagella** arising from a three-jointed **peduncle.** The **antennae** have a two-jointed protopod, the second of which extends as a **stipe** for the squamate exopod, the caridoid **scaphocerite.** The endopod consists of three joints and a long flagellum.

Little is known of the **mandible** except that in *Anthracaris* secondary articulation with the epistome is observed (Fig. 156,*B*), a feature found in Recent decapods and some stomatopods and mysidaceans. The two pairs of **maxillae** are unknown. The structures of *Tealliocaris* designated by Peach (226) as mandibular palps and maxillae are incorrectly interpreted portions of thoracic appendages.

Each of the eight thoracic somites bears a pair of **pereiopods,** which are biramous appendages. In all known fossils the appendages are distinct in possessing only one segment in the **protopod** (Fig. 156,*C*), as does the most primitive extant crustacean known, *Hutchinsoniella.* In all other eumalacostracans two or three segments occur in the protopod. The **endopods** have five segments, as do those of euphausiids and decapods. The **exopods** that have been observed have an unjointed stipe and a short flagellum (Fig. 156,*D*).

Nothing is known of the **branchiae** of eocarids; however, the branchiostegal development of the carapace of the pygocephalomorphs is suggestive of a **branchial chamber.** Peach (226) reported podobranchiae on *Tealliocaris,* but re-examination of the specimens failed to confirm his interpretation.

Thoracic sexual features found on some eocarids are sternal processes, oöstegites forming a brood pouch, and a seminal receptacle. **Gonopores** have not been observed, but it must be assumed they were associated with the base of the appendages of the sixth thoracic somite in females and the eighth thoracic somite in males. The function of **sternal processes** is unknown, but they are characteristic of mysidaceans and occur mid-ventrally on the sternites. It is only on *Tealliocaris* that low conical projections (Fig. 156,*E*), which may be homologous, are known to occur. Peach (226) reported seeing **oöstegites** on a variety of Paleozoic caridoid fossils, including the Palaeostomatopoda, but close scrutiny has proved their existence only on *Tealliocaris* and *Pygocephalus* (Fig. 156,*F,G*). In

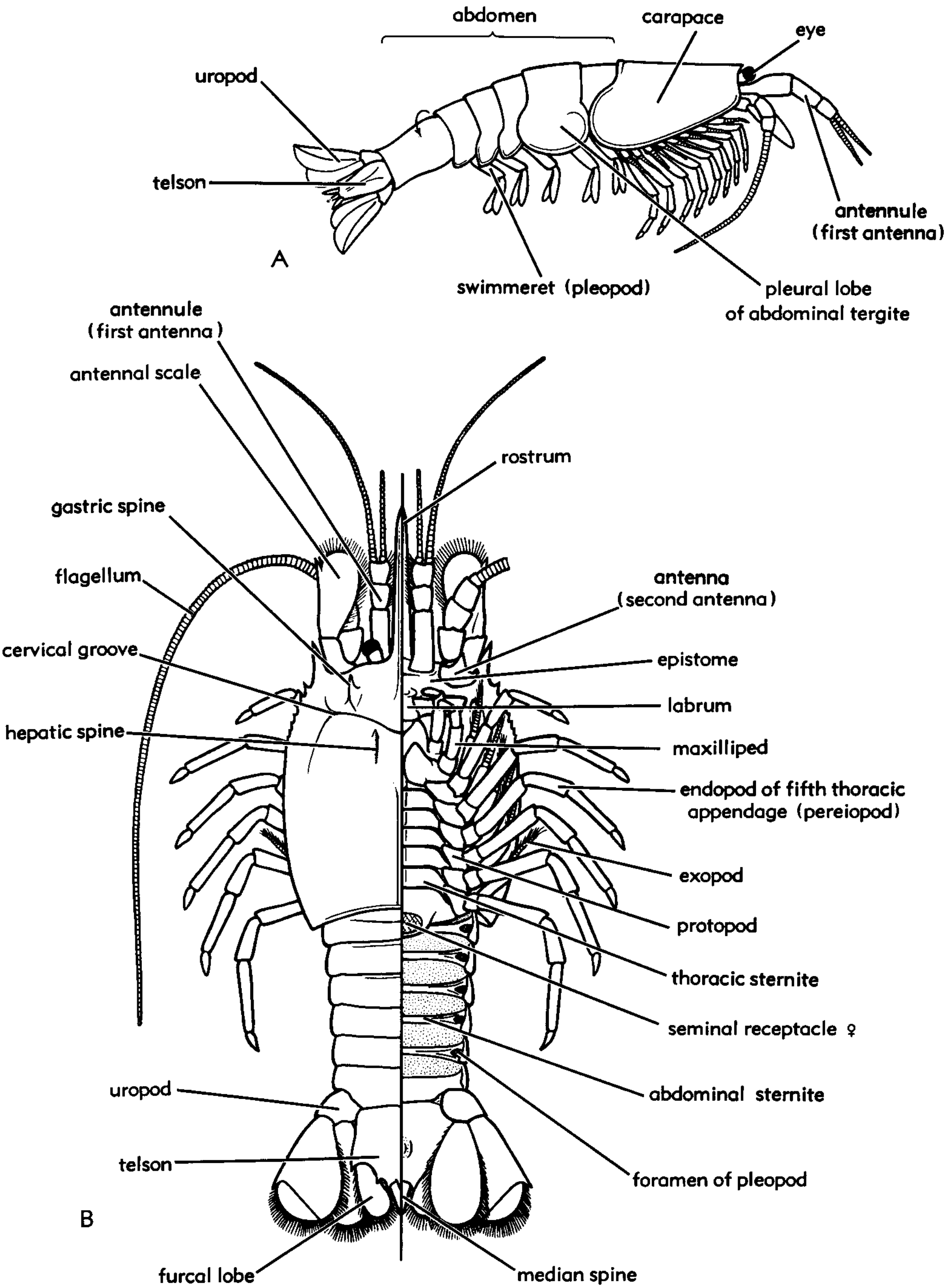


FIG. 155. Morphology of Eocarida.——*A. Crangopsis socialis* (SALTER), Eocaridacea, L.Carb., Scot.; ×4. ——*B. Anthracaris gracilis* (MEEK & WORTHEN), Pygocephalomorpha, Penn., USA(Ill.); ×2 (55).

these fossils the **marsupium** occurs only on a few mature specimens, presumably the females, and is composed of large imbricating endites of the thoracic appendages. The **seminal receptacle** occurs as a large medial pouch on the eighth thoracic sternite of *Pygocephalus* and *Anthracaris* (Fig. 156, *C*). Comparable but not homologous struc-

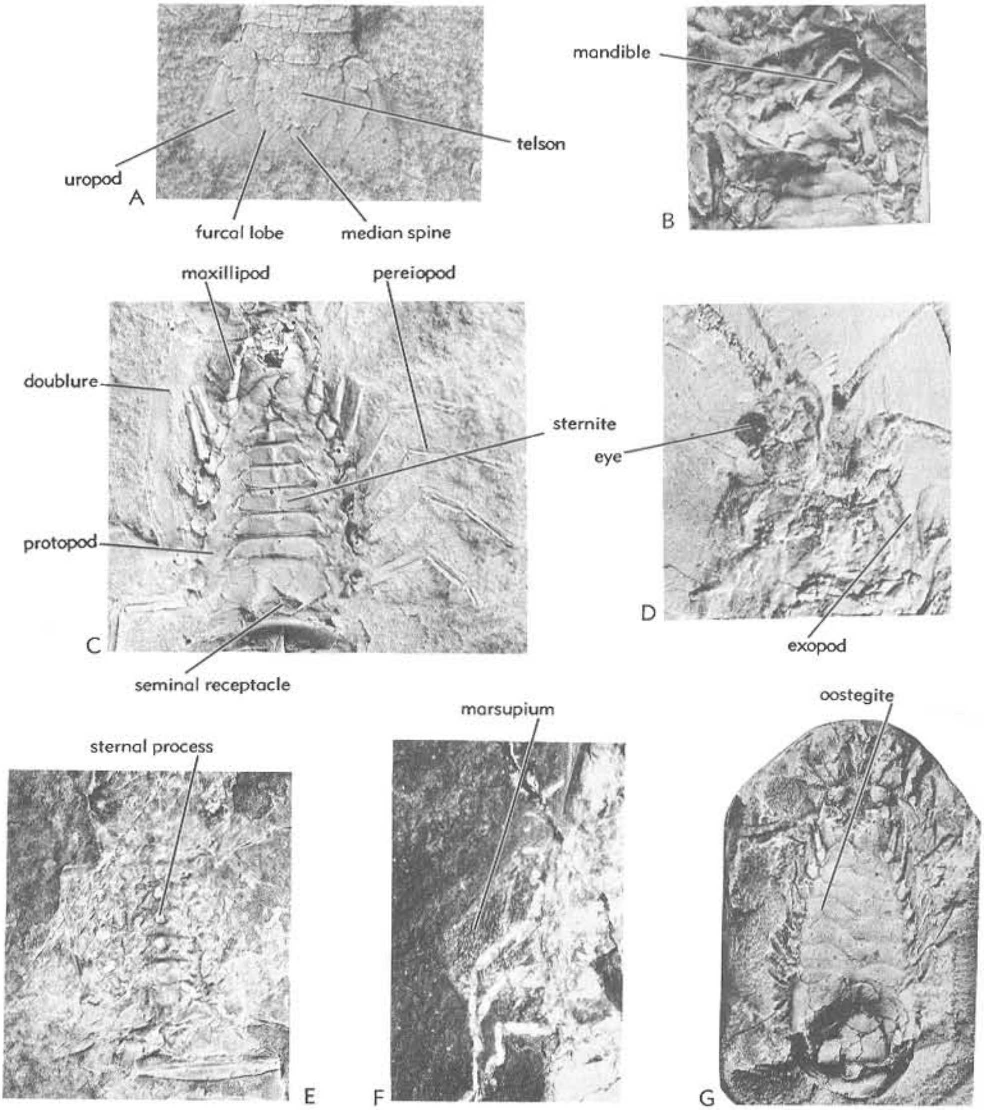


FIG. 156. Morphological features of Eocarida exemplified by photographs (all 55).——*A*. Caudal fan of *A. gracilis* showing uropods and telson with furcal lobes and median spine, ×3.——*B*. *Anthracaris gracilis* (MEEK & WORTHEN), Penn., USA(Ill.), showing mandible with secondary epistome articulation, ×4.——*C*. *A. gracilis,* showing sternal features of thorax and 1st 2 thoracic appendages modified as maxillipeds, also single joint of protopod of pereiopods, ×4.——*D*. *Mamayocaris jepseni* BROOKS, L.Perm., USA(Tex.), showing stalked compound eye and flagellate exopod of thoracic appendage, ×4.——*E*. *Tealliocaris loudonensis* PEACH, L.Carb., Scot., showing sternal processes, ×2.——*F*. Marsupium of *T. loudonensis,* female, ×3.——*G*. *Pygocephalus dubius* (MILNE-EDWARDS), U.Carb., Eng., showing marsupium composed of individual oostegites, ×3.

tures are seen in some isopods, syncarids, and decapods. It is remarkable to find both a marsupium and a seminal receptacle on *Pygocephalus*.

The **abdomen** of the eocarids is variously modified for nektonic and benthonic modes of life. The six somites are shrimplike, with large **pleural lobes** in the order Eocaridacea, but in the Pygocephalomorpha they are of moderate development. In some Permian forms (e.g., *Notocaris*), the abdomen is reduced and flexed under the thorax.

Biramous **pleopods** (swimmerets) have been observed on *Anthracaris, Crangopsis,* and *Tealliocaris*. It must be presumed that an appendix interna was present, at least on the more primitive forms, as this process of the endopod occurs on phyllocarids, stomatopods, euphausiids, and decapods. Sexual modification of the pleopods has not been observed.

Uropods are the most significant caridoid feature of these primitive eumalacostracans. The large, biramous spatulate appendages of the sixth abdominal somite combine with the platelike telson to form the **caudal fan.**

The **telson** of the eocarids has retained the crustacean **furca** (Fig. 156,*A*). In most Crustacea, including the phyllocarid malacostracans, this structure consists of two spinelike processes, whereas in eocarids the processes are lobate and contribute to formation of the caudal fan. A furca has been reported in larval stages of the Mysidacea, Euphausiacea, and Decapoda. However, ontogenetic evidence has been interpreted to indicate that the paired spines of adults are not homologous but are secondarily formed bristles. This may be correct, but true furca are retained on some extant syncarids.

The **median articulated spine** on the telson of the eocarids may not have a homologue in any extant Crustacea. Such a spine does occur on many Cambrian Pseudocrustacea. The Paleozoic phyllocarids and paleostomatopods have a median spine, but it is not articulated.

Internal anatomy of the eocarids can be inferred from the study of extant Crustacea. In the discussion of the phylogenetic relationships, some features will be discussed.

Small slitlike openings are present on the abdominal pleura of *Pygocephalus* and *Anthracophausia*. The slits also occur on the telson. If they are openings of serial homologous glands of the archaic arthropod, then their presence on the telson is significant in indicating this to be a true somite. Peach (226) has interpreted the opening on *Anthracophausia* as luminous organs. This is unlikely, considering the shallow coastal and estuarine water in which these animals lived.

ONTOGENY

No early ontogenetic stages have been recognized among Paleozoic eocarid fossils. The size frequency of the individuals in a normal sample is skewed toward the largest size.

The embryological development of this ancestral stock of the mysidaceans, euphausiids, and decapods can be inferred. The fact that all euphausiids and some penaeid decapods hatch as free-swimming nauplii prove that the Paleozoic eumalacostracans had retained their original crustacean larval stages. Secondary abbreviated development of the peracarids is correlated with incubation; thus only such Paleozoic pygocephalomorphs as possessed a similar brood pouch must have lacked free-swimming larval stages. Zoeal eclosion and extensive metamorphism are relatively modern contrivances for greater adaptation to the benthonic mode of life by the more advanced decapods.

PALEOECOLOGY AND STRATIGRAPHIC OCCURRENCE

Form and function as interpreted by analogy with extant Crustacea and the stratigraphic occurrence of the fossils provides a basis for paleoecological conclusions and inferences.

The earliest eumalacostracan fossils known (*Eocaris, Devonocaris, Palaeopalaemon*) all have shrimplike bodies. This supports the hypothesis that eumalacostracans arose from nekto-benthonic crustaceans. In fact, the antennal scale and the caudal fan are caridoid nektonic adaptations that distinguish this taxon. Suppression of the styliform furca and median spine correlates with the development of the enlarged uropods and telson into a swimming structure. That the eocarids had not fully developed the retrograde evasion propulsion of the eucarids was suggested by BURKENROAD (62). He has correlated fusion of the carapace to the thoracic somites in eucarids with this habitus. The position of the intestine relatively low in the abdomen of *Anthracophausia* also was cited as evidence that the abdominal flexor muscles were not enlarged relative to the extensors.

The reduction of the relative size of the abdomen, widening of the cephalothorax, and modification of the anterior pereiopods into maxillipeds in the pygocephalomorphs correlate with adaptation to a predominantly benthonic mode of life. The crablike *Notocaris,* from the Permian of Africa, is the culmination of this adaptive trend.

Evidence relative to feeding habits of the Paleozoic Eumalacostraca is inconclusive. It should be noted that the typical crustacean jaw is a biting, triturating structure—in fact, Malacostraca are distinguished by possessing both molar and incisor mandibular processes. The presence of detrital casts of the intestine of some eocarid fossils (e.g., *Anthracophausia, Anthracaris*) suggests ingestion of clastic sediment in feeding on organic bottom detritus. None of the eocarids had chelate appendages. These facts are suggestive of scavenging to low-grade carnivorous modes of life.

Fossil eocarids occur sporadically in Paleozoic deposits, the conclusion being not that these Crustacea failed to thrive in the Paleozoic seas, but rather that their chitinous exoskeletons were destroyed under normal conditions of marine deposition (55, p. 261-262). Only *Palaeopalaemon*, with a calcareous reinforced exoskeleton, is found associated with a typical marine fauna. Most of the eocarid fossils occur in deposits indicative of coastal lagoons, estuaries, and swamps. As is true today, many of the coastal crustaceans probably were euryhaline and wandered into environments where catastrophic silting, hypersalinity, and stagnation enhanced the preservation of uncalcified chitinous remains. There is no positive evidence that any of the eocarids actually inhabited fresh water.

The known biostratigraphic range of the Eocarida is upper Middle Devonian to Permian. The Eocaridacea appear in the Devonian, reach their maximum development in the Mississippian, and are not known in deposits younger than Middle Pennsylvanian. Pygocephalomorphs originate in the Mississippian, occur with great frequency and diversity in Pennsylvanian dark shales and ironstone concretions, and last occur as highly specialized crablike forms in Permian strata.

PHYLOGENY

The rigid plan of tagmosis of the body and the consistency of position of the genital openings are indicative of a monophyletic origin of the subclass Malacostraca. The phyllocarids are the most primitive representatives of this natural group. Their remains occur in Cambrian to Recent deposits, whereas the caridoid Eumalacostraca first appear in the Devonian.

Ontogenetic, morphological, and stratigraphic evidence supports the theory of a phyllocarid ancestry for the Malacostraca, not the caridoid theory of CALMAN (65, p. 144). The presence of a seventh abdominal somite, a furca on the telson, occurrence of both antennal and maxillary glands, heart and gonads extending the length of the body, segmented arrangement of the lateral arteries, and the simple structure of the brain and stomach of the Recent *Nebalia* attest to their primitiveness (275, p. 88). That they are not on the direct line of descent for the Eumalacostraca is indicated by the possession of a rostral plate, carapace adductor muscle, and absence of the posterior abdominal appendages. Phyllocarids from the Cambrian already possessed these unique characteristics.

SIEWING (275, p. 90) has proposed that *Nahecaris*, from the Devonian of Germany, is ancestral to the Eumalacostraca. The antennules of this phyllocarid does have two flagella, but the other eumalacostracan features reported by BROILI (54) do not exist. Thus, we must conclude that the archetype of the Malacostraca has not been discovered.

The first eumalacostracan fossils are also the most primitive caridoid Crustacea known, members of the order Eocaridacea.

These nekto-benthonic crustaceans have a relatively large abdomen, a caudal fan, scaphocerites, and undifferentiated biramous thoracopods. PEACH's (226) report of oöstegites on *Crangopsis* has not been substantiated by critical restudy. The only morphological criteria that can be determined which prevent their being classified as Euphausiacea are the single joint of the thoracic protopod and absence of fusion of the thoracic somites with the carapace. Ontogenetic evidence bearing on the homology of the "furca" and median spine on the telson of Recent adult euphausiids is inconclusive.

Except for the single segment in the protopod of the thoracopods, furcal lobes, and median articulated spines on the telson of adults, and especially the absence of oöstegites, the eocarids are comparable to lophogastrid mysidaceans. The peracarid marsupium of the mysidaceans correlates with abbreviated ontogenetic development. Free nauplius stages are the original eumalacostracan mode of development, not incubation.

Syncarids have retained a remarkable number of primitive eumalacostracan characteristics; even furcal lobes are present on members of the Bathynellacea and Stygocarididae. Absence of a carapace, presence of two segments in the thoracic protopod, and absence of a median articulated spine on the telson distinguish them from the Eocaridacea. The presence of a sperm receptacle on some extant syncarids is of no phylogenetic significance, as this structure is known to have evolved independently on different somites of various races of Malacostraca.

Comparison of the eocarids with the most primitive extant eumalacostracans, the euphausiaceans, lophogastrid mysidaceans, and syncarids, has emphasized the significance of the single segment in the thoracic protopod and the presence of furcal lobes and median spine on the telson. These are primitive crustacean features that have been lost or suppressed on extant forms. Loss of carapace, fusion of carapace with thorax, development of brood pouch, and other features mentioned above that are not present on the eocarids have been secondarily acquired by the different descendent races. The Eocaridacea must be the ancestors of the modern Eumalacostraca, hoplocarids excepted.

The primitive skeletal morphology and internal anatomy of the Syncarida suggest that they were differentiated early in evolutionary history of the Eocaridacea. They first occur in Mississippian rocks. The taxonomic affinities of *Anthracocaris* (CALMAN, 1932) and *Acadiocaris* (BROOKS, 1962), of Mississippian age, which have a short carapace, are dependent on morphological details still unknown. We must accept the suggestion of CALMAN (66) that they are related to the Peracarida. They could be ancestral tanaidaceans, spelaeogriphaceans, or if they lack oöstegites, a stage in the evolution of the carapaceless syncarids.

Hoplocarid fossils first occur in the Mississippian. Their internal anatomy is indicative of early derivation from the malacostracan stock. Though they are caridoid, they are distinguished from the very beginning by possessing an articulated rostrum, subchelate thoracopods, and triramous antennules.

Admittedly, the superorder Eocarida represents several divergent stocks, the order Eocaridacea being the most primitive. *Palaeopalaemon* (U.Dev.-L.Miss.) is distinguished by a thorax that is only slightly shorter than the abdomen and by the presence of incipient branchiostegal development of the pleura of the carapace. It may have been from such a morphological type that the late Paleozoic Pygocephalomorpha evolved.

The pygocephalomorphs retained the primitive telson and unjointed thoracic protopod but show homeomorphic structural trends toward the decapods and mysidaceans. *Tealliocaris* has a brood pouch, sternal processes, and no seminal receptacle. These are mysidacean characteristics. On the other hand, *Anthracaris* lacks oöstegites, has a seminal receptacle, displays a secondary articulation between the mandible and epistome, and has endopods on the first three thoracopods that are incipiently adapted as decapod maxillipeds. The problems in classification are best exemplified by *Pygocephalus,* which not only has a peracarid marsupium but also the seminal receptacle of syncarids and decapods. All of these Paleozoic genera have a laterally extended carapace and abdomen and cephalothorax of subequal length or a reduced abdomen. It is apparent that the pygocephalomorphs are the Paleozoic benthonic eumalacostracans. It is probable that the mysidacean and decapod characteristics cited are analogues and that the pygocephalomorphs are not ancestral to any extant Crustacea.

BURKENROAD (62) has presented a hypothetical argument that the Eucarida arose monophyletically from some unknown Paleozoic Malacostraca. The oldest decapod-like crustaceans are *Palaeopemphix* (GEMMELLARO, 1892), from the Permian of Sicily, *Antrimpos* (VAN STRAELEN, 1933), from the Permotriassic of Madagascar, and *Protoclytiopsis* (BIRSHTEYN, 1958), from the Permotriassic of Siberia. Probably these are not directly ancestral to the decapods. Morphological considerations that must be taken into account in deriving the eucarids from the eocarids are: (1) triple system of transverse carapace grooves on the older fossil decapods, (2) body gills of decapods, (3) carapace fused to thorax and enlarged abdominal flexor muscles of all eucarids, (4) development of an accessory process of the endopod of the second male pleopod to form the appendix masculina in euphausiaceans and decapods, (5) furca and median spine of the eocarids, and (6) the single segment in the protopod of the eocarids.

The triple system of transverse carapace grooves may be strictly a decapod feature that has independently evolved and need not be expected in the ancestral malocostracan stock. It is true that most of the earliest fossil decapods, including some species of *Palaeopemphix,* display this characteristic (118). Comparative morphology and embryology of extant decapods prove the primitiveness of the penaeids and carids, neither of which have the triple system. The nektonic euphausiaceans have retained the greatest number of eocarid characteristics and have only one transverse carapace groove.

The gills of the eocarids are unknown. Euphausiaceans have branchiae (podobranchiae) attached to the coxae of their appendages, whereas decapods have arthrobranchiae, and pleurobranchiae in addition to podobranchiae. Arthrobranchiae originate ontogenetically on the proximal portion of the appendages and later change position to the basal articular membrane. The pleurobranchiae appear later and their place of origin is close to, if not actually on, the basal part of the embryonic appendages that have coalesced with the thorax. Thus, the development of the "body gills" of decapods can be correlated with increased body size, development of the branchial chamber, and especially the evolution of the efficient maxillary pump.

Fusion of the carapace with the thorax and the enlarged abdominal flexor muscles of both euphausiaceans and decapods has been attributed to the development of retrograde evasive propulsion (62). The caridoid caudal fan of all eumalacostracans is a swimming structure. Though it may have originally functioned principally for planing and steering, it is sometimes used by all nektonic forms, including the syncarid *Paranaspides,* for backward darting. Therefore, BURKENROAD's first criterion for monophyletic origin of the eucarids is of questionable significance.

The second and most relevant criterion suggested by BURKENROAD is the presence of an appendix masculina in both euphausiaceans and decapods. The development of copulatory structures from pleopods has evolved independently in male syncarids, stomatopods, eucarids, and even isopods. It is not altogether improbable that this copulatory structure of the euphausiaceans and decapods is a true analogy. Even BURKENROAD (62, p. 15) admits the modification of the first pleopod of the decapod as a spermatophore-handling organ is "not homologous with the Euphausid [euphausiid] organ derived from a branch of the *appendix interna,* nor with the also independently-modified first endopods in various Reptant Decapods. . . ."

A furca and median spine on the telson are primitive crustacean characteristics. The furca is retained in the adults of eocarids, some extant adult syncarids and possibly the euphausiaceans. Embryologically these features are present throughout the Malacostraca. It is to be expected that these

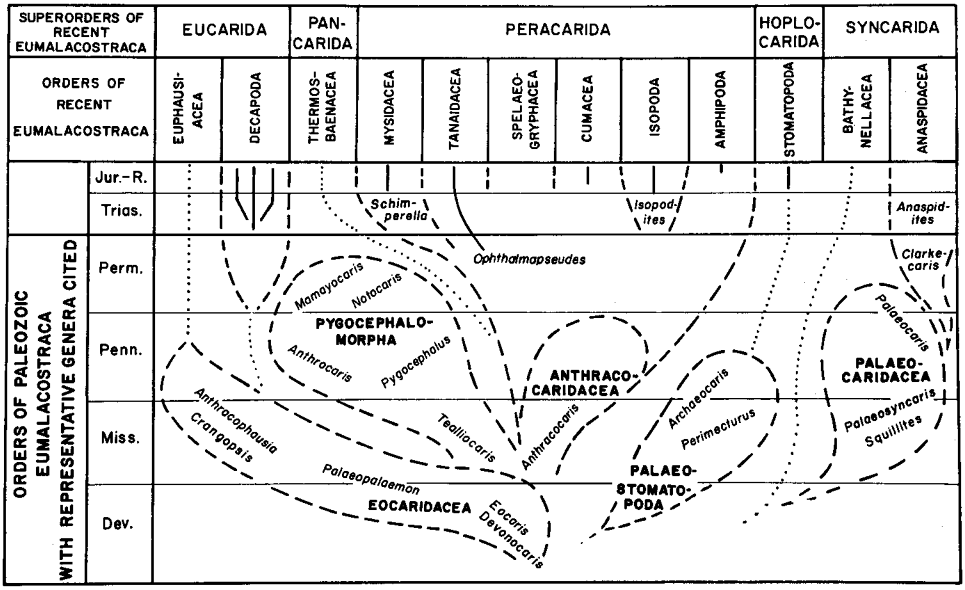


FIG. 157. Diagram showing inferred phylogenetic relationships of Paleozoic Eumalacostraca.

crustacean structures would be present on the Paleozoic ancestral eumalacostracan stock, the Eocarida.

Traditionally it has been assumed that the original crustaceans had three segments in the protopod of their appendages. The discovery of *Hutchinsoniella* (SANDERS, 1957) has cast doubt upon this theory. Again, the single segment of the eocarid protopod may be an archaic characteristic.

In summary, no valid objections are seen for considering the Paleozoic eocarids as ancestral to the Peracarida and Eucarida and for postulating that the euphausiaceans and decapods evolved their two common eucarid characteristics independently. The Syncarida and Hoplocarida are earlier derivatives (Fig. 157).

CLASSIFICATION

As indicated in foregoing discussion, a phylogenetic (vertical) classification consistent with the taxa established for Recent Eumalacostraca is impossible. Divergent evolution toward extant morphological types can be distinguished, but in the pygocephalomorphs they are homeomorphic. Accordingly, the superorder Eocarida was established (55) for caridoid fossils which have a carapace not fused with the thorax, biramous thoracic appendages, a single segment in the protopod, and furcal lobes and a median articulated spine on the telson. Two orders, Eocaridacea and Pygocephalomorpha, are recognized.

Anthracomysis and *Palaemysis*, previously assigned to the Eocaridacea (55) on the basis of published descriptions, have been restudied. *Palaemysis* lacks statocysts in the uropods as portrayed by PEACH (226), and most fossils assigned here are abdomens and telsons of *Anthracophausia*. *Anthracomysis* (VAN STRAELEN, 1922) is the caudal fan of *Perimecturus fraiponti* VAN STRAELEN, a palaeostomatopod. *Gitocrangon granulata* RICHTER (1848) is a pseudofossil.

A revision of the European genera and species of eocarids is in progress. Many described species are synonyms and some have incorrect generic assignment. As previously suggested by BEURLEN (27, p. 126)

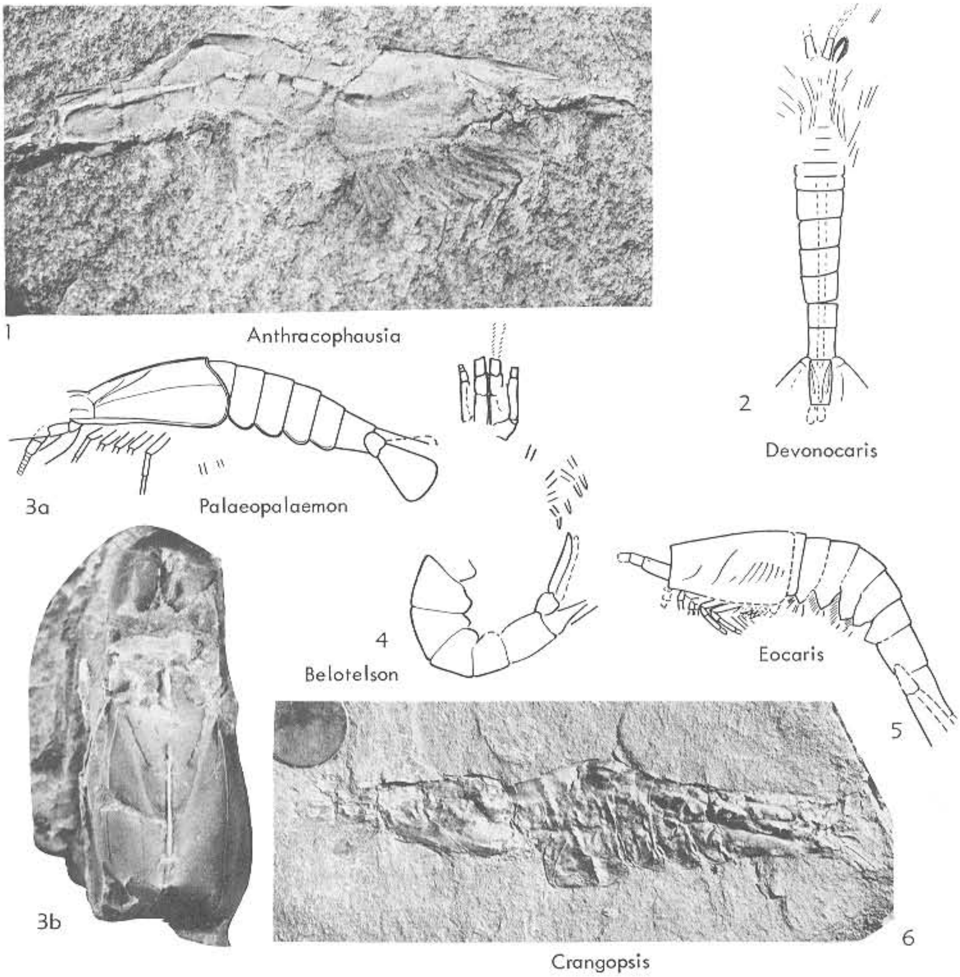


FIG. 158. Eocaridacea—Eocarididae *(2,5)*; Palaeopalaemonidae *(3)*; Anthracophausiidae *(1,4,6)* (p. *R*342-*R*343).

and GLAESSNER (117, p. 178), *Anthrapalaemon* is believed to be a synonym of *Pygocephalus*. Two or three new genera need to be proposed.

The Palaeostomatopoda (BROOKS, 1962), assigned tentatively to the superorder Eocarida, have now proved to be true hoplocarids. In addition to possession of subchelate thoracopods by *Perimecturus* and *Archaeocaris*, these genera have the distinctive triramous antennules of Recent Stomatopoda. PEACH (226) was mistaken in portraying a marsupium on these fossils.

A tabulation of suprageneric divisions of the Eocarida with numbers of genera contained in each is given on page *R*114.

SYSTEMATIC DESCRIPTIONS

Superorder EOCARIDA Brooks, 1962

Carapace with single transverse groove and not fused with thoracic tagmata; biramous thoracopods with single segment in

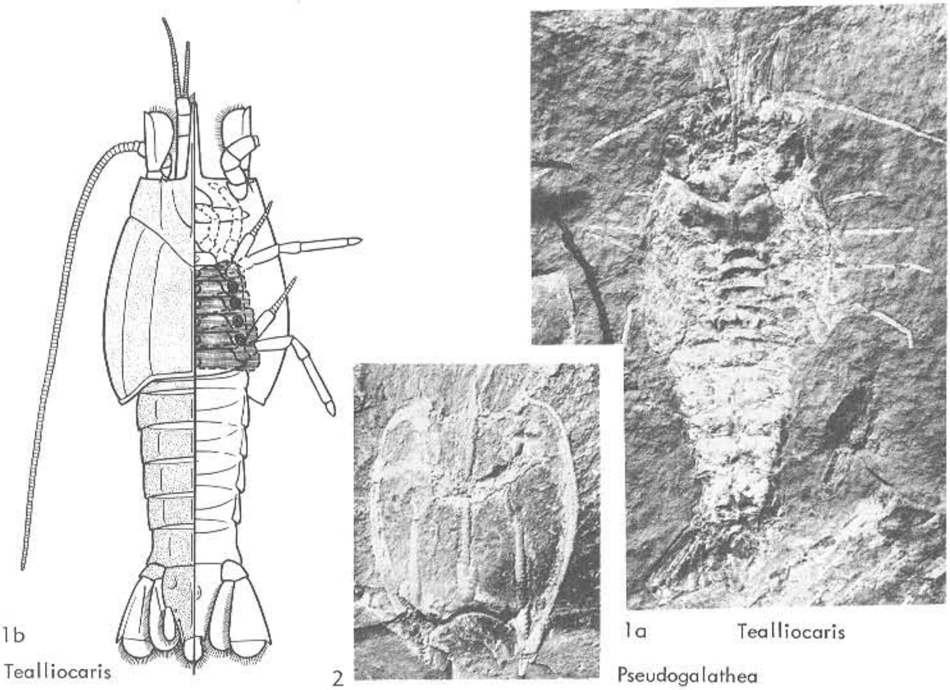


FIG. 159. Pygocephalomorpha (Mississippian)—Tealliocarididae (p. R344).

protopod. Chief diagnostic characters are furcal lobes and median articulated spine on telson. *M.Dev.-Perm.*

Order EOCARIDACEA Brooks, 1962

Carapace relatively shorter than abdomen; pleura of carapace not produced laterally. *M.Dev.-Penn.*

Family EOCARIDIDAE Brooks, 1962

Transverse carapace grooves indistinct, not reaching dorsum; pleura of abdominal tergites large and pointed. *M.Dev.*

Eocaris BROOKS, 1962, p. 312 [**E. oervigi*; OD]. Presence of rostrum doubtful and ventral margin of carapace forming nearly right angle with straight anterior margin; carapace with 2 transverse grooves, neither reaching dorsum. *M.Dev.*, Eu. (Ger.).——FIG. 158,*5*. **E. oervigi*; ×1 (55).

Devonocaris BROOKS, 1962, p. 308 [**Palaeocaris? cuylerensis* WELLS, 1957, p. 983; OD]. Thoracic somites relatively large, body of telson spade-shaped. *M.Dev.-U.Dev.*, N.Am.(N.Y.)-Eu.(Belg.).——FIG. 158,*2*. **D. cuylerensis* (WELLS), M.Dev., N.Y.; ×3 (55).

Family PALAEOPALAEMONIDAE Brooks, 1962

Peduncle of antennules hypertrophied; carapace with well-developed cervical groove and incipient branchiostegal keel near ventral margin. *U.Dev.-L.Miss.*

Palaeopalaemon WHITFIELD, 1880, p. 41 [**P. newberryi*; OD]. Carapace with pair of longitudinal lateral carinae which become spines anterior to cephalic sulcus, rostrum probably present; pleural lobes of abdominal tergites rounded. *U. Dev.-L. Miss.*, N.Am.(Ohio-Ky.-Iowa).——FIG. 158,*3*. **P. newberryi*, U.Dev., Ohio; *3a,b*, ×1, ×4 (55).

Family ANTHRACOPHAUSIIDAE Brooks, 1962

Proximal segment of peduncle of antennules with recessed "eye socket"; rostrum prominent; carapace lacking ridges and spines but having large lappets. *Miss.-Penn.*

Anthracophausia PEACH, 1908, p. 61 [**A. dunsiana*; OD] [=*Palaemysis* PEACH, 1908 (type, *P. dunlopi*; OD)]. Rostrum keeled and falciform; pleural lobes of all abdominal tergites similar and pointed.

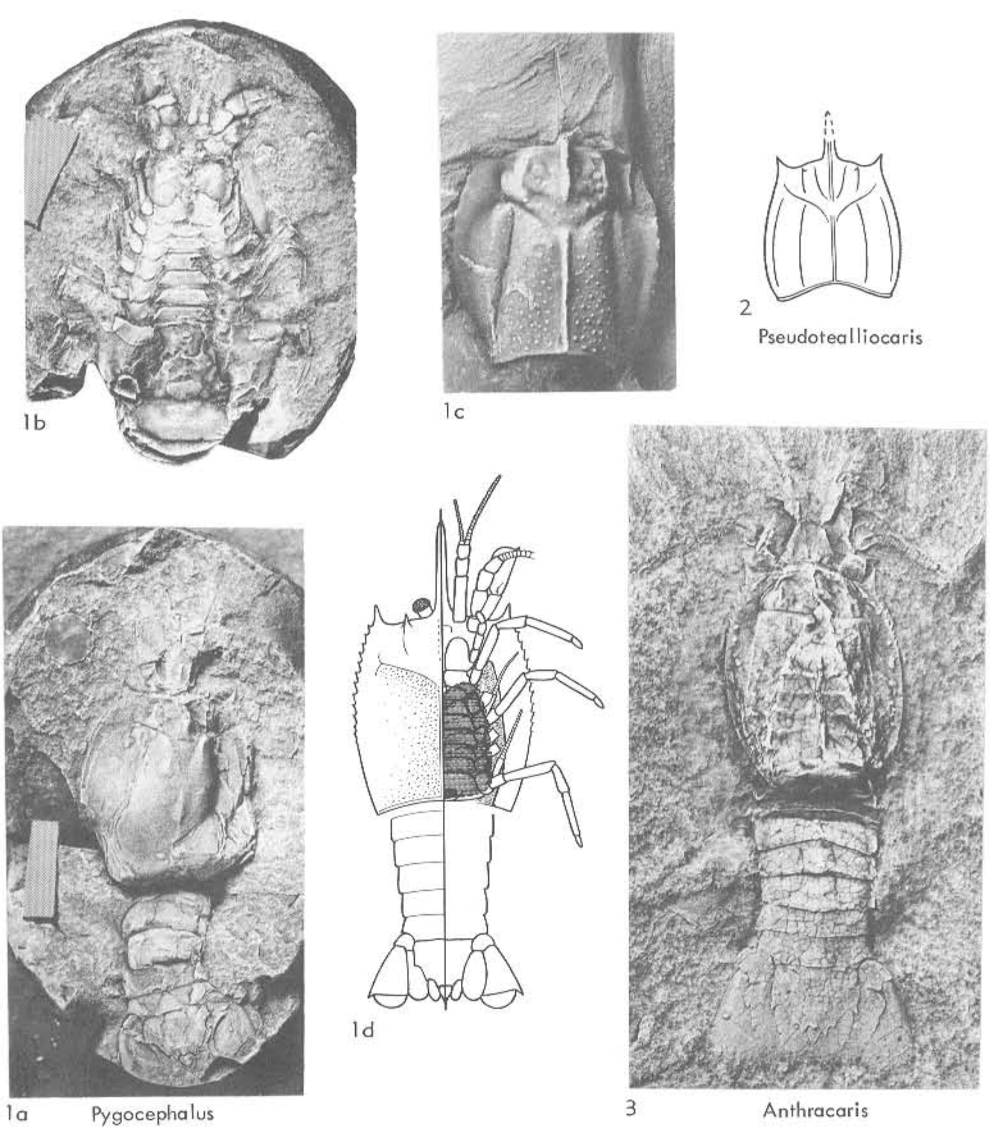
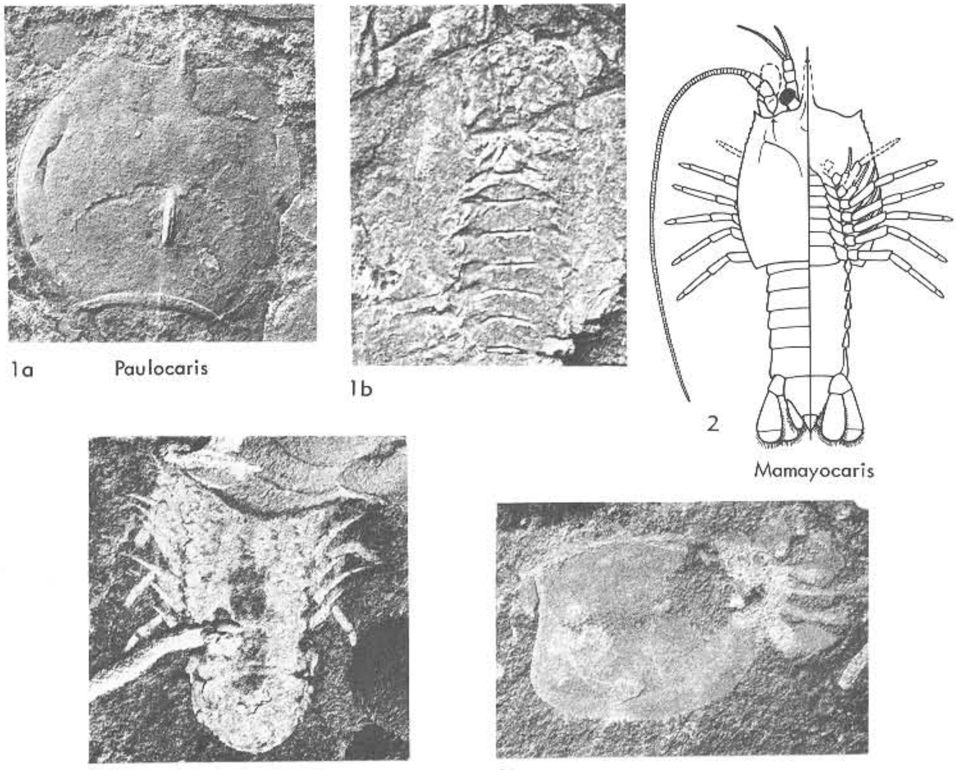


FIG. 160. Pygocephalomorpha (Pennsylvanian)—Pygocephalidae (p. *R344-R345*).

[Several species assigned to *Crangopsis* by PEACH (1908) belong to *Anthracophausia*. These include *C. couttsi, C. rhodesi, C. magna, C. robusta, C. minuta,* and *C. hastata*.] *Miss.-Penn.,* Eu.(Scot.-Eng.-?Fr.)-N.Am.(Ill.).——FIG. 158,*1*. *A. strongi* BROOKS, Penn., Ill.; ×3 (55).

Belotelson PACKARD, 1886, p. 128 [**Acanthotelson? magister* PACKARD, 1886, p. 127; OD]. Spinelike telson and heavily chitinized bladelike outer margin of exopods of uropods characterize this inadequately known caridoid. *Penn.,* N.Am.(Ill.).——FIG. 158,*4*. **B. magister* (PACKARD); ×0.7 (55).

Crangopsis SALTER, 1863, p. 531 [**Uronectes socialis* SALTER, 1861, p. 394; OD]. Carapace thin, with faint suggestion of cervical groove; rostrum short, blunt; pleura of 2nd abdominal tergite large and rounded, overlapping those of both adjacent somites. *L.Carb.-U.Carb.,* Eu.(Scot.).——FIG. 158, *6*. *C. eskdalensis* (PEACH), L.Carb.; ×2 (55).


1a Paulocaris 1b

2 Mamayocaris

3a Notocaris 3b

FIG. 161. Pygocephalomorpha (Permian)—Pygocephalidae *(2)*; Notocarididae *(1,3)* (p. *R*345).

Order PYGOCEPHALOMORPHA Beurlen, 1930

[*emend.* BROOKS, 1962]

Branchiostegal development in pleura of carapace; cephalothorax and abdomen subequal in length or abdomen reduced. *Miss.-Perm.*

Family TEALLIOCARIDIDAE Brooks, 1962

Carapace with prominent longitudinal carinae; anterolateral spines, if present, small; median process of telson lobate. *L. Carb.*

Tealliocaris PEACH, 1908, p. 9 [**T. loudonensis*; OD]. Carapace lacking anterolateral spines but bearing sternal processes and oöstegites. *L.Carb.*, Eu.(Scot.-Fr.).——FIG. 159,*1*. **T. loudonensis*, Scot.; *1a,b*, dorsal view and reconstr., ×2 (55).

Pseudogalathea PEACH, 1882, p. 514 [**P. rotunda*; OD]. Anterior and posterolateral angles of carapace produced, latter very prominent; carapace with median and 2 lateral longitudinal ridges and with heavy lateral thickening; abdomen and caudal fan relatively small. *L.Carb.*, Eu.(Scot.).——FIG. 159,*2*. *P. macconochiei* (PEACH); ×3 (55).

Family PYGOCEPHALIDAE Brooks, 1962

Carapace produced laterally with doublure, longitudinal carinae absent, but with prominent anterolateral spines; sternal processes lacking. *Miss.-Penn.*

Pygocephalus HUXLEY, 1857, p. 363 [**P. cooperi*; OD] [=*Anthrapalaemon* SALTER, 1861, p. 530 (type, *A. grossarti*; OD); *Palaeocarabus* SALTER, 1861, p. 530 (type, *Apus dubius* PRESTWICH, 1840); *Necroscilla* WOODWARD, 1879, p. 551 (type, *N. wilsoni*; OD); *Diplostylus* SALTER, 1863, p. 76 (type, *D. dawsoni*; OD)]. Hepatic spines absent from carapace; some female specimens bearing oöstegites and seminal receptacle; telson narrowing backward in 2 abrupt steps, furcal lobes originating at last. *Penn.(U.Carb.),* N.Am.(N. Scotia-Ohio).——Fig. 160,*1*. *P. dubius* (Milne-Edwards), Eng.; *1a,b,* dorsal and ventral views of specimens; *1c,* dorsal view of carapace; *1d,* reconstr.; all ×1.5 (55). [=*Amphipeltis* Salter, 1863.]

Anthracaris Brooks, 1962, p. 173 [**Anthrapalaemon gracilis* Meek & Worthen, p. 50; OD]. Hepatic and gastric spines present on carapace, oöstegites never present, but large seminal receptacle on last thoracic sternite of mature females; base of telson broad; its width constricting abruptly at position of origin of furcal lobes. *Penn.,* N.Am.(Ill.).——Fig. 160,*3*. **A. gracilis* (Meek & Worthen); dorsal view of complete specimen, ×3 (55).

Pseudotealliocaris Brooks, 1962, p. 199 [**Tealliocaris caudafimbriata* Copeland, p. 44, 1957; OD1]. Carapace as wide as long, with large anterolateral spines, median keel, and 2 pairs of lateral carinae. *Penn.,* N.Am.(N.Scotia).——Fig. 160,*2*. **P. caudafimbriata* (Copeland); dorsal view of carapace, ×1.3 (55).

Mamayocaris Brooks, 1962, p. 188 [**M. jepseni*; OD]. Carapace lacking hepatic spines, dorsal carinae indistinct; body of telson subtriangular. *L.Perm.,* N.Am.(Tex.-S.Dak.).——Fig. 161,*2*. *M. jepseni* Brooks; dorsal view (reconstr.), ×2 (55).

Family NOTOCARIDIDAE Brooks, 1962

Abdomen reduced and reflexed under thorax. *Perm.*

Notocaris Broom, 1931, p. 572 [**Pygocephalus tapscotti* Woods, p. 41, 1923; OD]. Carapace relatively long and narrow, without spines and dorsal keel. *Perm.,* S.Afr.——Fig. 161,*3*. **N. tapscotti* (Woods); *3a,* thorax with appendages and abdomen reflexed; *3b,* lateral compression of cephalothorax, ×2 (55).

Paulocaris Clarke, 1920, p. 219 [**P. pachoecoi*; OD] [=*Pygaspis* Beurlen, 1934, p. 126 (type, *P. brasiliensis;* OD); *Liocaris* Beurlen, 1931, p. 40 (type, *L. huenei*; OD)]. Carapace as wide as long, with prominent dorsal keel. *Perm.,* S.Am. (Brazil).——Fig. 161,*1*. **P. pachoecoi*; *1a,b,* dorsal views of carapace and abdomen, ×2 (55).

SYNCARIDA

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[Chapter submitted February, 1964]

CONTENTS

INTRODUCTION

Syncarids possess a unique combination of characteristics that impart to them a decisive position in any phylogenetic discussion of the Eumalacostraca. This is not because they were ancestral to any other crustacean main groups, but rather because they are a relatively unmodified lineage that differentiated early in the history of crustacean evolution.

The feature that most distinguishes the Syncarida is absence of a carapace. Some other Eumalacostraca (e.g., isopods, amphipods, cumaceans) have the carapace aborted or greatly reduced, but in these the absence or reduction can be proved to be secondary.

In the Syncarida no evidence indicates that a cephalothoracic shield ever was present.

Only a few syncarid species have survived to the present. The fossil record, however, indicates that they flourished during the late Paleozoic; indeed, representatives of the Paleozoic fauna were discovered approximately 50 years before any extant species belonging to the assemblage was known. At first the fossils were interpreted as amphipods or isopods, but in 1885 Packard recognized their singularity and pro-

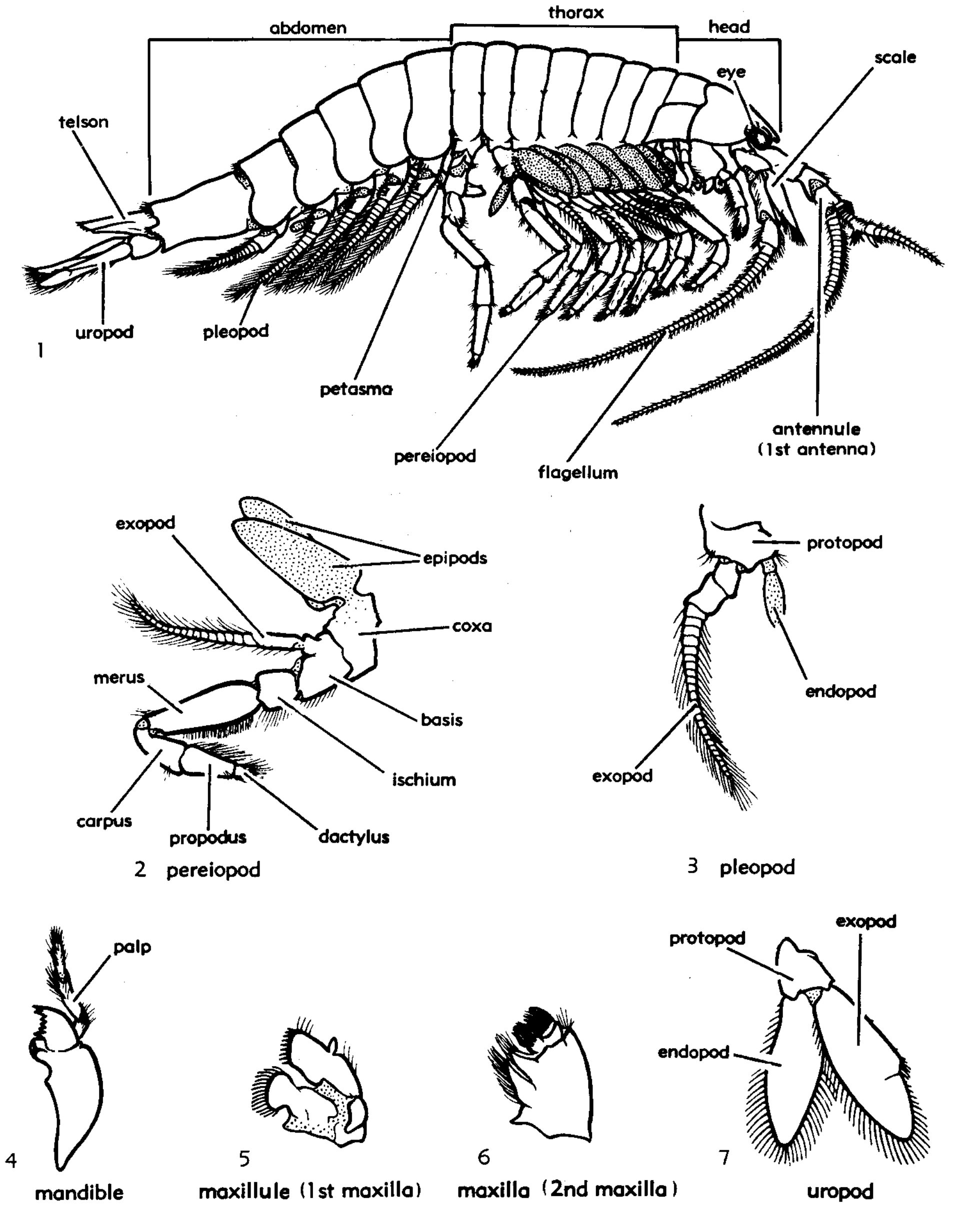


Fig. 162. Morphological features of syncarids illustrated by a generalized anaspidacean, *Anaspides tasmaniae* (Thomson), Rec., Australia.——*1*. Lateral view of male, ×3.——*2*. Second thoracic appendage, ×6.——*3*. Second abdominal appendage, ×6.——*4*. Mandible, ×10.——*5*. Maxillule, ×10.——*6*. Maxilla, ×10.——*7*. Uropod, ×6 (55).

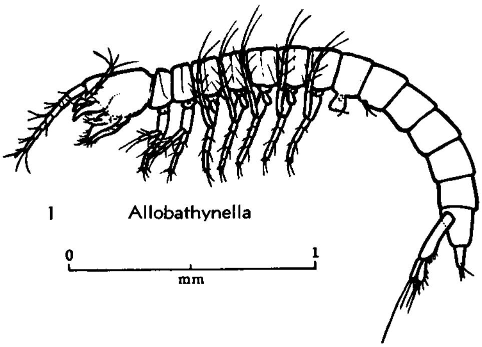


FIG. 163. Vestiges of furca in syncarids shown by bathynellacean *Allobathynella japonica* MORIMOTO & MIURA, male, Rec., Japan, ×32 (290).

posed the name Syncarida for them. Subsequent discoveries of fossils and extant species have greatly enlarged our knowledge of these relics of the past. The taxon is now recognized as being distinct from the Peracarida and the Eucarida. It is best defined by three morphological features which individually are not definitive, but taken together provide a valid basis for systematic differentiation. These characteristics are biramous thoracopods, absence of a carapace, and absence of a marsupium on mature females.

MORPHOLOGY

The syncarid body is constructed upon the basic eumalacostracan plan (Fig. 162,*1*). Tagmosis of the 19 appendage-bearing somites is into (1) a **head,** bearing two pairs of antennae **(antennules, antennae),** a pair of **mandibles** and two pairs of maxillae **(maxillules, maxillae),** (2) a **thorax** composed of eight somites, each bearing a pair of **pereiopods,** and (3) an **abdomen** composed of six somites, of which the first five bear **pleopods** and the last one a pair of **uropods.** The terminal body unit is a **telson.** The uropods and telson form a **caudal fan.** In the primitive extant Bathynellacea (Fig. 163) and in the recently discovered representative of a new family, the Stygocarididae (215) (Fig. 164), diminutive vestiges of **furca** are found. Cephalization has resulted in fusion of the first thoracic somite with the head in the Anaspidacea, whereas in the Bathynellacea the sixth abdominal somite is fused with the telson. All eight thoracic somites and six abdominal somites of the extinct Paleozoic order Palaeocaridacea (56) have retained their identity (Fig. 165).

No carapace or vestige of a carapace is found on any known syncarid, fossil or Recent. *Anthracocaris scotica* (PEACH) and *Acadiocaris novascotica* (COPELAND) (55) are peracarids with diminutive carapaces

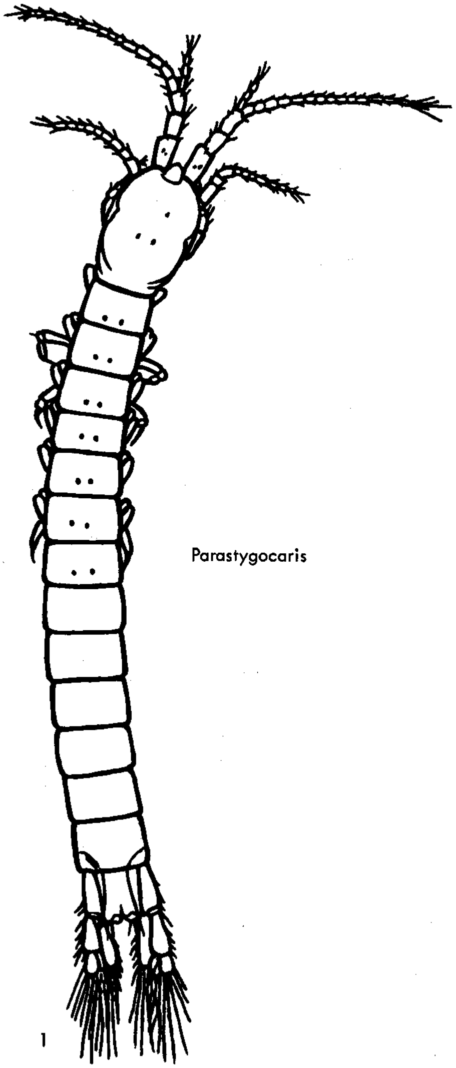


FIG. 164. Vestiges of furca in syncarids shown by stygocaridacean *Parastygocaris andina* NOODT, male, Rec., Argentina, ×60 (215).

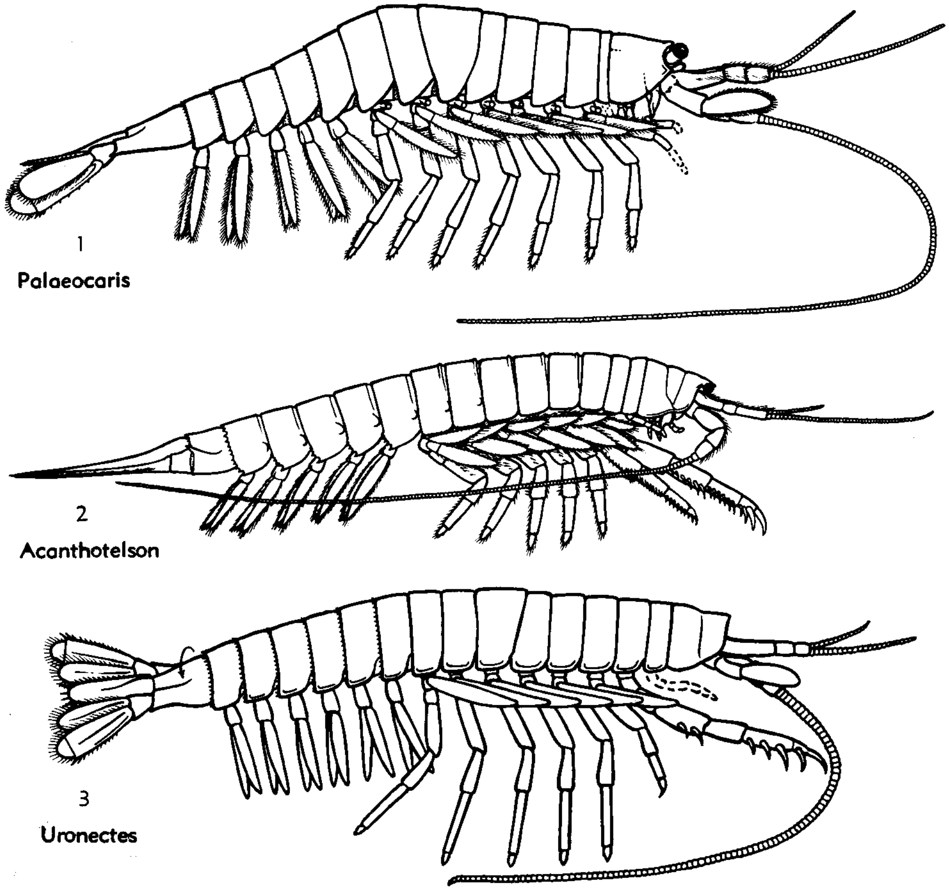


FIG. 165. Morphological features of syncarids shown by palaeocaridaceans (reconstr.).——*1. Palaeocaris typus* MEEK & WORTHEN, Penn., Ill., ×3.——*2. Acanthotelson stimpsoni* MEEK & WORTHEN, Penn., Ill., ×2.——*3. Uronectes fimbriatus* (JORDAN), Perm., Ger., ×3 (55).

occurring in Lower Carboniferous deposits of Scotland and Canada. Though both of these species were originally assigned to the syncarid *Palaeocaris,* their affinities are probably with the Tanaidacea or Spelaeogriphacea (55).

For purposes of homologous comparison between the different Eumalacostraca, the appendages of *Anaspides* (Rec., Tasmania) are most instructive (Fig. 162). The biramous thoracic legs are believed to have retained a primitive structure.

Each of the **antennules** consists of a **protopod** of three segments and two multiarticulate **flagella** (Fig. 162,*1*). Upon the proximal segment of this appendage is a slitlike pore, which is the external opening of a **statocyst.**

The antennae have a two-segment protopod, a bladelike exopod, a **scaphocerite** (antennal scale), and two-segment endopod, and a flagellum (Fig. 162,*1*). In some of the benthonic Paleozoic species (e.g., *Acanthotelson stimpsoni*) the caridoid eumalacostracan bladelike exopod has been lost (Fig. 166,*1*).

It is frequently stated that the retention of only two segments in protopods of the antennae is a feature distinctive of the Syncarida and the Eucarida, the latter having the **nephropore** of an antennal gland upon the proximal segment. For extant species this observation is correct, but *Palaeocaris typus* (Penn., Ill.) probably had three distinct segments in protopods of its antennae (55, p. 244). It is definite that *Acanthotelson stimpsoni* (Penn., Ill.) had a nephropore on the basal segment (55, p. 235) of its antennae (Fig. 166,*1*).

The body of the mandible of *Anaspides* is stout, with **gnathal lobe** differentiated into a thick **molar process** and distal toothed **incisor process** (Fig. 162,*4*). A three-segment **palp** arises on the outer surface of the body of the mandible. Calman (65, p. 148) and others have emphasized the absence of a lacinia mobilis on the mandibles of Syncarida. Bristles that may be homologous to this peracarid feature have been reported recently in species of *Parastygocaris* and *Stygocaris* (Rec., S.Am.) by Noodt (215, p. 571).

Both the maxillules and maxillae of *Anaspides* are small and highly specialized to

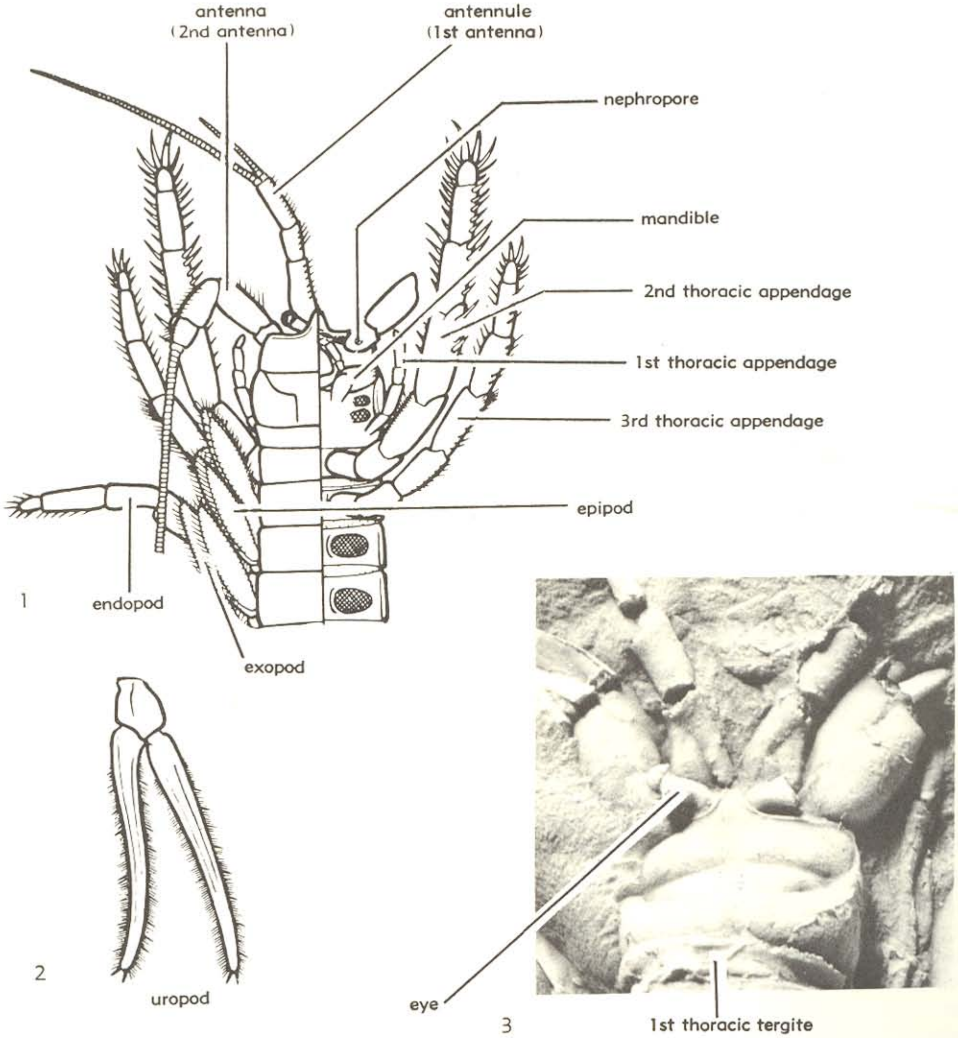


Fig. 166. Morphological features of syncarids shown by palaeocaridacean *Acanthotelson stimpsoni* Meek & Worthen, Penn., Ill.——*1*. Anterior portion of body, dorsal and ventral views, ×4.——*2*. Uropod, dorsal view, ×4.——*3*. Head and first thoracic tergite, dorsal view, ×8 (Brooks, n).

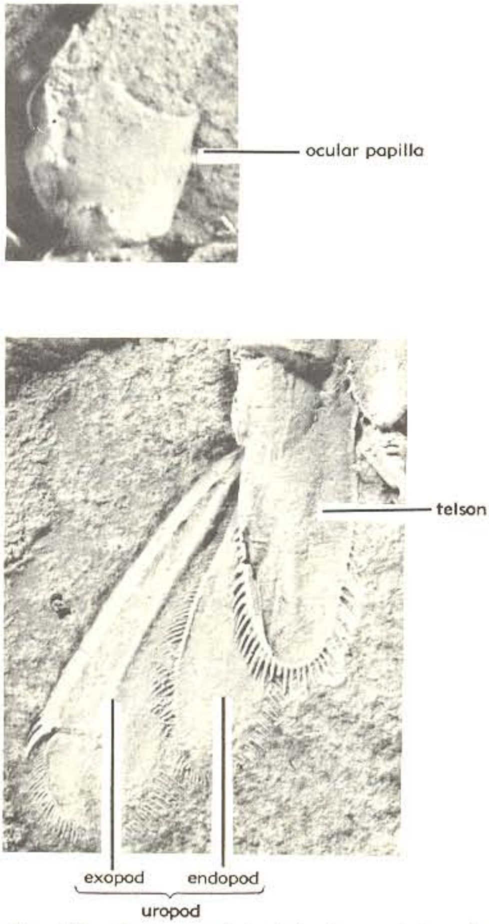


FIG. 167. Some morphological characteristics of *Palaeocaris typus* MEEK & WORTHEN, Penn., Ill. (Brooks, n).——*1*. Peduncle of left eye with base of ocular papilla, ×14.——*2*. Uropod (left) and telson, ×10.

assist in food manipulation during mastication. They have little resemblance to legs. The maxillules have a small basal segment which gives rise to two plates that constitute the greater part of the appendage (Fig. 162,*5*).

A broad **endite** extends mesially. On the outer edge of the lateral plate is a small lobe that might represent the vestige of an endopod or exopod. A single segment constitutes the greater part of each of the maxillae (Fig. 162,*6*). The mesial margin bears two small setiferous endites, whereas a movable bilobed structure with bristles is borne at its terminus.

The first pair of pereiopods of *Anaspides* are modified as **maxillipeds.** Their **endopod** is adapted for grasping, but otherwise is unaltered from the plan of that of the succeeding pereiopods. The **exopod** and **epipods** are reduced on the maxillipeds, but endites are present. The succeeding five pairs of appendages of *Anaspides* have retained their primitive structures, whereas the seventh pair have the epipods aborted and the exopods reduced. The last pair of thoracic appendages have also lost all traces of exopods.

The unmodified thoracopods of *Anaspides* are biramous, with an exopod rising from the second distinct segment (basis) of the protopod (Fig. 162,*2*). Only HANSEN (1925) has claimed to have detected the evasive theoretical precoxal segment. From the basal segment (coxa) of the appendage, two lobate, membranous epipods originate. As previously noted, an exopod arises from the basis; it consists of a proximal **stipe** and beyond this an annulate **flagellum.** The endopod is divided into five segments designated as in other crustaceans ischium, merus, carpus, propodus, and dactylus. The "knee" is between the merus and carpus. Three segments are distal to it.

FIG. 168. Portion of caudal fan of *Clarkecaris brasilicus* (CLARKE), Perm., Brazil, showing telson and right furcal lobe, ×6 (Brooks, n).

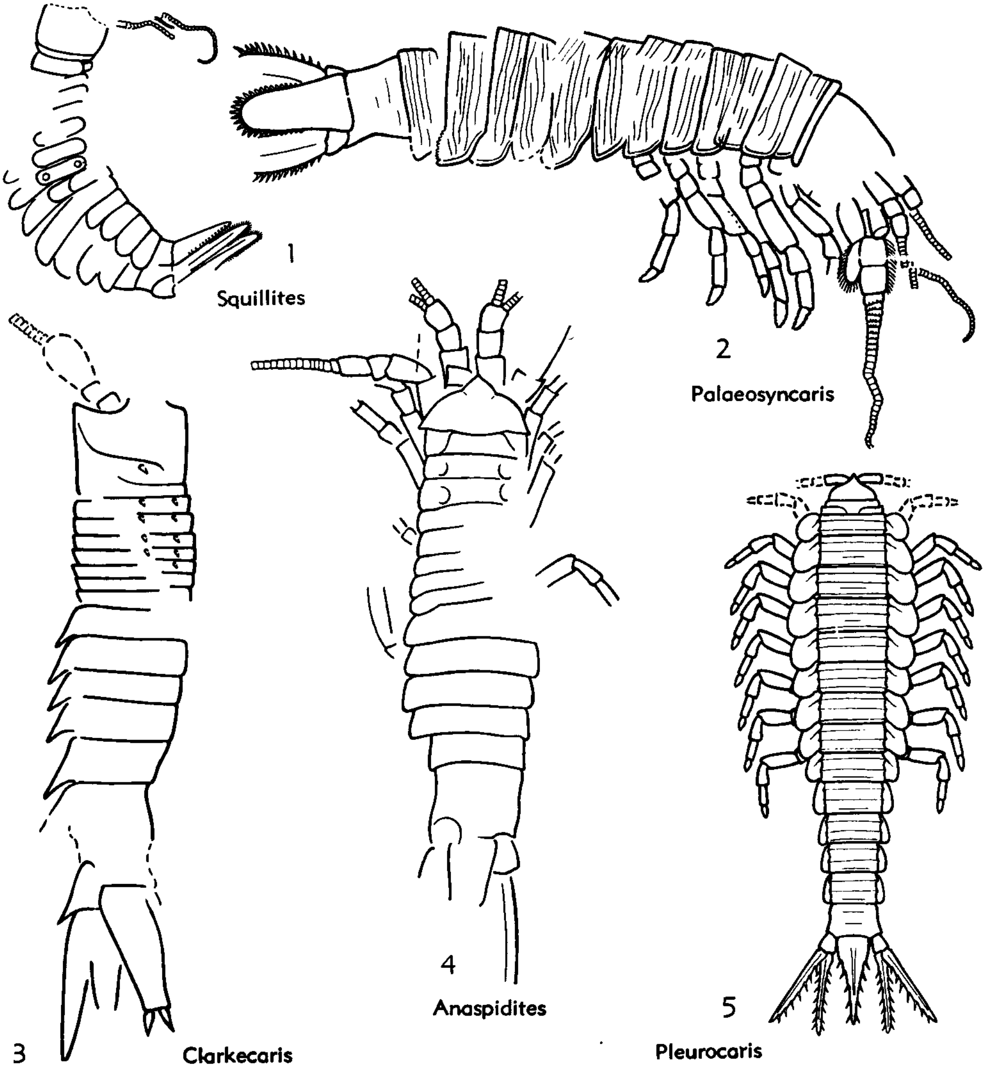


FIG. 169. Morphological features of fossil syncarids that are incompletely known (Brooks, n).——*1. Squillites spinosus* SCOTT, Miss., USA(Mont.), ×5.——*2. Palaeosyncaris dakotensis* BROOKS, Miss., USA(N. Dak.), ×2.——*3. Clarkecaris brasilicus* (CLARKE), Perm., Brazil, ×3.——*4. Anaspidites antiquus* (CHILTON), Trias., Australia, ×1.5.——*5. Pleurocaris annulata* CALMAN, U.Carb., Eng., ×7.

The pereiopods of Paleozoic syncarids have an identical structure (Fig. 165). In most species no maxillipeds are present, but *Acanthotelson stimpsoni* (Penn., Ill.) has massive grasping legs, as does *Uronectes fimbriatus* (Perm., Eu.). In both species they are the second pair of pereiopods.

Traces of the membranous epipods are rarely found on fossils, but remains of them have been reported for *Palaeocaris typus* and *Acanthotelson stimpsoni* (55). Though the preservation of the fossils is not adequate for positive proof, it appears that the exopods were not flagellate in the Paleozoic fossils, but rather spatulate lobes somewhat resembling epipods (Fig. 166,*1*).

In the minute Recent Bathynellacea, adapted for living in interstitial spaces in sand, the antennae and thoracic appendages are reduced and simplified (Fig. 163).

As to the pleopods and uropods of *Anaspides,* no morphological features of special importance call for notice. The pleopods of the first and second abdominal somites of males differ from those that follow and from female pleopods in that the endopods are produced as strong armlike gonapophyses—the petasma of stomatopods and eucarids—which projects forward between the last pair of thoracopods. The typical pleopod has a large basal segment (protopod), a much-reduced, soft lobate endopod, and an exopod consisting of two proximal segments followed by a long annulate, hairy flagellum (Fig. 162,*3*). In Recent syncarids adapted for living in interstitial spaces, the pleopods are reduced or aborted. Among Paleozoic fossils in which pleopods are known, the two rami are spatulate lobes of approximately equal size (Fig. 165).

The uropods are biramous on all known syncarids. Those of *Anaspides* (Fig. 162,*1*) and *Palaeocaris* (Fig. 167,*2*) are spatulate, but in many forms the rami are variously modified as styli (Fig. 166,*2*). A statocyst was reported by FRITSCH (97) in the basal segment of the uropod of *Uronectes fimbriatus.* Diligent restudy of the fossils has proved this observation to be in error.

The telson of *Anaspides* is a simple, spatulate terminal body unit with the anus situated on its ventral surface. In the Bathynellacea (Fig. 163) and Stygocaridacea (Fig. 164) are two small lobes representing rudiments of a furca. *Clarkecaris* (Perm., S.Am.), a primitive stygocarid, is the only Paleozoic fossil known to have preserved this fundamental crustacean structure (Fig. 168; 169,*3*).

The **compound eyes** of *Anaspides* are stalked, whereas those of *Koonunga* are sessile. The Bathynellacea are blind. All known fossil syncarids have stalked compound eyes (Fig. 166,*3*). A discovery of special interest on the peduncle of the eyes of *Palaeocaris typus* (55, p. 243) is an **ocular papilla** similar to that of the Mysidacea (Fig. 167,*1*).

For the most part, features of the internal morphology of the Syncarida are primitive. Especially noteworthy is the so-called pars ampullaris on the entrance of the caeca into the pyloric chamber of the stomach, which is homologous to a similar structure in the Stomatopoda (275, p. 95). The stomach is small. A large number of liver caeca enter the stomach ventrally. Except for two small dorsal diverticula in the abdomen, the intestine is simple. In all Recent syncarids the excretory organs are maxillary nephridia, but in *Acanthotelson stimpsoni* nephropores are associated with the antennae (55, p. 235). Publications by SMITH (278) and SIEWING (273) give details of the internal morphology of the Recent Syncarida.

ONTOGENY

The eggs of Recent Syncarida are deposited, not carried by the mother. The nauplius and other ontogenetic stages are developed in the egg. No metamorphosis occurs, though the newly hatched animal is not completely developed; for example, in *Anaspides* the eyes are sessile and only two hepatic caeca are present (146). Whereas *Anaspides* is hatched with a full complement of body somites, *Bathynella* has only three abdominal somites (16).

ECOLOGY

It is customary to refer to the Syncarida as fresh-water Crustacea. Though all extant species, except *Thermobathynella amyxi* SIEWING, from brackish waters at the mouth of the Amazon, do live in fresh water, it is definite that many fossil syncarids were marine. In evaluating the paleontological environmental occurrence of animals with a chitinous exoskeleton, one must not neglect the fact that fossil arthropods without mineral-reinforced skeletons are practically unknown from marine deposits. This does not mean that highly diverse arthropods were lacking in seas of the past, but only that remains of those with chitinous exoskeletons were destroyed by normal biological and physicochemical vicissitudes during accumulation and diagenesis of the sediments.

It is believed that all Carboniferous syncarids were marine, but it is possible that some Permian species normally inhabited fresh water. *Clarkecaris brasilicus* (Perm., S.Am.), from the Irati Shales, is from a marine lithotope (Fig. 168; 169,*3*). On the other hand, stratigraphic evidence and the associated fossils of *Anaspidites antiquus,* from the Triassic of Australia, suggest a fresh-water habitat (Fig. 169,*4*).

Paranaspides lacustris, a shrimplike syncarid, is nektonic, whereas *Anaspides tasmaniae* is benthonic. These relatively unspecialized Crustacea are from lakes and rivers of Tasmania. Species of *Koonunga* and *Micraspides* have been found in bottom detritus of lakes and pools in Australia and are intermediate between the true surface-dwellers mentioned above and highly specialized subterranean species. *Koonunga* has small sessile eyes and shuns strong light, whereas *Micraspides* lacks eyes. Species adapted for existence in interstitial spaces in sediment are geographically widespread, for North America and Australia are the only continents from which members of the Bathynellacea have not been reported. Fossil and extant members of the Stygocaridacea have been found only in South America.

Some syncarids are microphagous feeders. *Anaspides,* on the other hand, has maxillipeds adapted for grasping large detritus and prey. It has been observed to be carnivorous (213, p. 15). No question exists as to the predaceous habits of the extinct *Acanthotelson* and *Uronectes,* which possessed strong raptorial maxillipeds.

STRATIGRAPHIC OCCURRENCE

None of the Syncarida have carapaces strengthened by mineral matter. Chitinous exoskeletons rapidly decompose upon death of animals except when unusual physicochemical conditions exist to prevent destruction. Such fossils are found as compressions in black shales and in clay ironstone concretions from dark gray to black siltstone and shales. *Anaspidites antiquus* (Trias., Australia) is from a variegated gray to brick red, laminated lacustrine deposit (Fig. 169,*4*).

Though *"Palaeocaris"* has been reported from the Devonian of Belgium (Van Straelen, 1943) and New York (Wells, 1957), these fossils were misinterpreted (57). The original determinations were based on absence of a carapace in the fossils, but this is due to poor preservation. The oldest true syncarids are *Squillites spinosus* and *Palaeosyncaris dakotensis,* from the Heath Shale, of Late Mississippian age, in Montana and North Dakota (55) (Fig. 169,*1*,*2*). A large number of specimens are known from Carboniferous deposits in North America and Europe. Permian species are known from Europe and South America. The Paleozoic northern hemisphere species are all members of the order Palaeocaridacea, whereas *Clarkecaris,* from Brazil, is a primitive stygocaridacean. A single specimen of *Anaspidites antiquus* has been found in Triassic shales of Australia (Fig. 169,*4*). It is doubtful that *Triasocaris* (Bill, 1914), from the Triassic of France, has been interpreted correctly.

PHYLOGENY

Misinformation and insufficient knowledge of the morphology of fossil syncarids have resulted in many misconceptions of their phylogenetic relationships. Because of the erroneous interpretation of *Acanthotelson* by Packard (1886), many authors have postulated a relationship between the Syncarida and Isopoda (Nicholls, 1929; Calman, 1934; Glaessner, 1957). Siewing (275, p. 95) has cited the presence of a seventh abdominal somite and the occurrence of statocysts in uropods of *Uronectes* (Fritsch, 1901) as evidence for an affinity of syncarids with the Mysidacea, although it has been proved that Fritsch was mistaken in reporting both of these morphological features (55, p. 239). In the light of present knowledge of Recent and extinct Crustacea, the Syncarida possess characteristics considered to be diagnostic of one or more of all other eumalacostracan taxa; thus they are of great phylogenetic interest.

The furca on the telson of Recent Bathynellacea and Stygocaridacea is a primitive crustacean feature that has been lost by most Eumalacostraca. Rudiments of a furca are present on some euphausiaceans and in larval stages of the Eucarida. All known species of the extinct Eocarida have a furca or furcal lobes on the telson. None of the Paleozoic syncarids of the extinct order Palaeocaridacea are known to have had a furca. Restudy of the type specimens of *Clarkecaris brasilicus*, a primitive stygocaridacean from South America, proves it to have had a furca (Fig. 168). These crustaceans, not the palaeocarids, must be closest to the ancestral syncarid stock.

The digestive tract, nervous system, reproductive system, and excretory system of Recent syncarids are those of a generalized eumalacostracan. This is true also for the stomatopods (275, p. 93), but the characteristics in each were inherited independently from the ancestral eumalacostracan stock.

Until nephropores were discovered in *Acanthotelson*, it was believed that all syncarids had maxillary glands. This, in addition to the presence of biramous pereiopods and stalked or sessile compound eyes coupled with lack of a carapace and of an appendix interna on the pleopods of syncarids, has been construed as indicative of their affinities with Peracarida. Features that syncarids have in common with the Eucarida invalidate this interpretation. Female syncarids lack oöstegites and the mature males have a petasma. These are characteristic of both the Stomatopoda and Eucarida. Characteristics that are distinctly eucarid in nature are presence of a statocyst in the basal antennal segments and presence of a seminal receptacle in females. The correlative morphological features mentioned above must be homeomorphic.

The evidence presented supports the conclusion that syncarid evolution has followed four distinct lines. These have led to differentiation of the groups now ranked as orders—Palaeocaridacea, Anaspidacea, Bathynellacea, and Stygocaridacea. The archaic syncarid, which is unknown, must have had all thoracic and abdominal somites free, lacked a carapace, had biramous thoracic appendages, and possessed a furca on the telson.

The Palaeocaridacea are the oldest syncarid fossils yet discovered. Even so, they cannot be considered the ancestral stock of the Syncarida, as Noodt (1964) has postulated. Though highly specialized, the extant members of the orders Bathynellacea and Stygocaridacea have retained more fundamental primitive characteristics. These two orders must have been early derivatives of the original syncarids which thus far are unknown. The Stygocaridacea are restricted to the South American continent with the oldest known fossil, *Clarkecaris*, occurring in Permian strata. It is possible that the Anaspidacea of Australia and Tasmania are their descendants.

The relationships of the Syncarida have been confused by the evolution of homeomorphic features. There is no proof of a relationship with any of the other Eumalacostraca other than through a common ancestor.

CLASSIFICATION

The Syncarida was originally defined by Packard (1885) as including only the Pennsylvanian fossil, *Acanthotelson stimpsoni*, believed to be closely related to the Isopoda and Amphipoda. With the discovery of the Recent "Tasmanian mountain shrimp," *Anaspides tasmaniae* (Thomson), Calman (1896) established the Syncarida as an order and extended it to include fossils such as *Palaeocaris*. Subsequently, several additional Recent genera have also been discovered. In his last published classification of these Crustacea, Calman (1909, p. 162) raised the Syncarida to division rank (i.e., superorder).

The attempts of Chappuis (1915), Cockerell (1916), Siewing (1959), and Vandenberghe (1960) to establish a systematic classification of the Syncarida have failed because they were based upon erroneous interpretation of the Paleozoic fossils. Brooks (55, 56) has restudied the fossils and proposed that three orders be recognized on the basis of fusion or lack of fusion of somites. One additional order (Stygocaridacea) subsequently has been defined by Noodt (1964, p. 96).

The Palaeocaridacea have all eight thoracic somites and six abdominal somites free. There is no furca. The known Anaspidacea have the first thoracic somite fused with the head and in the Clarkecarididae and Stygocarididae the first thoracic somite is fused with the head, but rudiments of a furca are present. The order Stygocaridacea, established for the extant forms (NOODT, 1964), should include also the extinct Clarkecarididae, which possess the same characteristics. The aberrant Bathynellacea all have a furca, and although their eight thoracic somites are free, the last abdominal somite is fused with the telson. Families are distinguished on the basis of their adaptive trends.

A tabulation of suprageneric divisions of the Syncarida showing their stratigraphic occurrence and numbers of contained genera is given on page *R*114.

SYSTEMATIC DESCRIPTIONS

Superorder SYNCARIDA Packard, 1885

[*nom. transl.* CALMAN, 1904 (*ex* Syncarida PACKARD, 1885, *partim*)] [=Anomostraka VON GROBBEN, 1910]

Carapace absent, pereiopods biramous, with one or two epipods; seminal receptacle may be present but no oöstegites. *U.Miss.-Rec.*

Order PALAEOCARIDACEA Brooks, 1962

[=Gampsonychidae SIEWING, 1959 (*pro* Gampsonychidae PACKARD, 1886, *partim*); Anaspidacea CALMAN, 1904 (*partim*)]; Simplicipoda FRITSCH, 1901 (*partim*)]

First thoracic somite not incorporated into cephalon; compound eyes stalked; caudal furca lacking. *U.Miss.-Perm.*

Family PALAEOCARIDIDAE Meek & Worthen, 1865

[*non* Palaeocaridae SIEWING, 1959] [=Nectotelsonides BROCCHI, 1880; Eilecticidae VANDENBERGHE, 1960]

No thoracic endopods modified as raptorial appendages; rami of uropods lobate; telson spatulate. *U.Miss.-Perm.*

Palaeocaris MEEK & WORTHEN, 1865, p. 48 [**P. typus*; OD] [=*Nectotelson* BROCCHI, 1880; *Palaeoorchestia* ZITTEL, 1882; *Gasocaris* FRITSCH, 1901; *Praeanaspides* WOODWARD, 1908]. Thoracic and abdominal pleural lobes rounded anteriorly, posterior edge straight, without spines. *U.Carb. (Westphalian) - Perm.*, N. Am.(Ill.-N. Scotia)-Eu. (Eng.-Fr.-Belg.-Neth.).——FIG. 165,*1*; 170,*1a*. **P. typus*, Penn., Ill.; 165,*1*, ×3; 170,*1a*, ×2 (55).——FIG. 170,*1b*. *P. krejcii* (FRITSCH), Perm., Eu.; ×4 (Brooks, n).——FIG. 170,*1c*. *P. rochi* (BROCCHI), Perm., Eu.; ×4 (Brooks, n).

Palaeosyncaris BROOKS, 1962, p. 250 [**P. dakotensis*; OD]. Thoracic and abdominal pleural lobes progressively larger, posterior margin at last thoracic and abdominal lobes rounded, spines on abdominal pleural lobes. *U.Miss.* or *L.Penn.*, N. Am.(N.Dak.).——FIG. 169,*2*; 170,*2*. **P. dakotensis*, 169,*2*; 170,*2*, both ×2 (55).

Squillites SCOTT, 1938, p. 508 [**S. spinosus*; OD]. First thoracic tergite reduced; uropods with narrow spatulate rami; telson wedge-shaped. *U.Miss.*, N.Am.(Mont.).——FIG. 169,*1*; 170,*3*. **S. spinosus*; 169,*1*, ×5; 170,*3*, ×6 (55).

Family URONECTIDAE Cockerell, 1916

[=Gampsonychidae PACKARD, 1886]

Endopods of second thoracic appendages raptorial; rami of uropods and telson spatulate; antennae without scaphocerites. *L. Perm.*

Uronectes BRONN, 1850, p. 575 [**Gampsonyx fimbriatus* JORDAN, 1847; OD] [=*Gampsonyx* JORDAN, 1847 (obj.); *Carcinurus* BRONN, 1850; *Gampsonychus* BURMEISTER, 1855 (obj.)]. First thoracopods reduced; pleura truncate and posterior margin of abdominal tergites serrate. *L.Perm.*, Eu. (Saar B.).——FIG. 165,*3*; 173,*1*. **U. fimbriatus* (JORDAN); 165,*3*, ×3; 173,*1*, ×4.5 (Brooks, n).

Family ACANTHOTELSONIDAE Meek & Worthen, 1865

[*non* COCKERELL, 1916]

Second and third pereiopods raptorial; rami and uropods and telson styloid. *Penn.*

Acanthotelson MEEK & WORTHEN, 1865, p. 399 [**A. stimpsoni*; OD]. Thoracic pleura truncate, posterior margin of abdominal pleural lobes serrate; length of all abdominal somites approximately equal. *Penn.*, N.Am.(Ill.).——FIG. 165,*2*; 171,*1*. **A. stimpsoni*; 165,*2*, ×2; 171,*1*, ×4.5 (Brooks, 1962).

Family PLEUROCARIDIDAE Chappuis, 1915

[*nom. correct* BROOKS, 1962 (*ex* Pleurocaridae CHAPPUIS, 1915)] [*non* Eileticidae VANDENBERGHE, 1960]

No pereiopods specialized for raptorial purposes; thoracic pleura large; rami of uropods and telson styloid. *Penn.*

Pleurocaris CALMAN, 1911, p. 156 [**P. annulatus*; OD]. Head small, 2 cephalic grooves not joining laterally; margins of uropod rami and telson spinose. *Penn.*, Eu.(Eng.-?Fr.).——FIG. 169,*5*; 172,*1*. **P. annulatus*, Eng.; 169,*5*, ×7; 172,*1*, ×9 (Brooks, n).

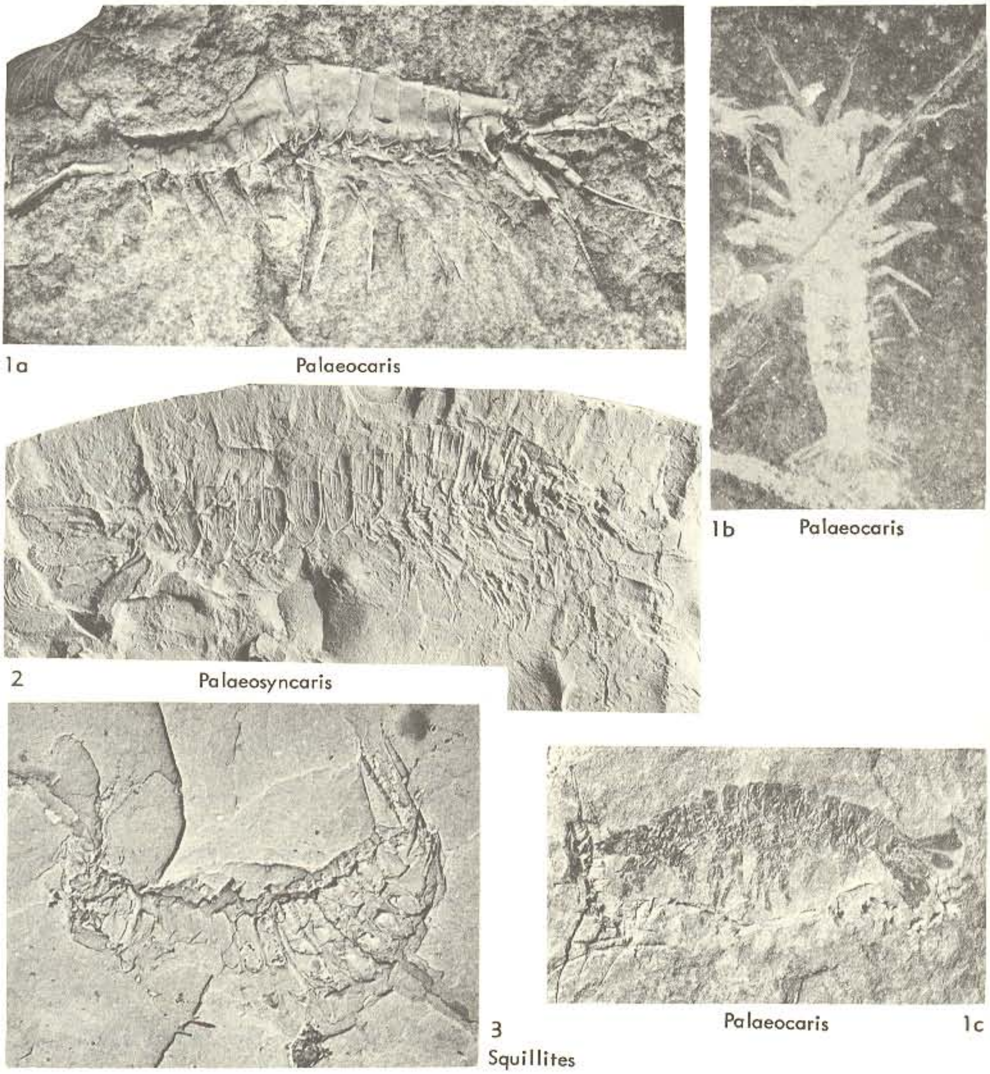


FIG. 170. Palaeocaridacea, Palaeocarididae (p. *R*355).

Order ANASPIDACEA Calman, 1904

[*nom. transl.* SIEWING, 1959]

First thoracic somite incorporated into cephalic tagma; seminal receptacle present. *Trias.-Rec.*

Family ANASPIDIDAE Thomson, 1894

Exopods on thoracic appendages *1* to *7;* endopods of pleopods reduced; with stalked compound eyes. *Trias.-Rec.*

Anaspides THOMSON, 1894, p. 285 [**Anaspis tasmaniae* THOMSON, 1892; OD]. Thoracic somites increasing only slightly in length posteriorly; antennal scales shorter than 1st 2 joints of endopod. *Rec.,* Tasmania.——FIG. 162,*1*. **A. tasmaniae* (THOMSON); ×3 (Brooks, n).

Paranaspides SMITH, 1908, p. 465 [**P. lacustris*; OD]. Thoracic somites increasing in length pos-

1 **Acanthotelson**

FIG. 171. Palaeocaridacea, Acanthotelsonidae (p. *R*355).

teriorly and body flexed at 1st abdominal somite, which is largest; antennal scales longer than 1st 2 joints of endopod. *Rec.*, Tasmania.

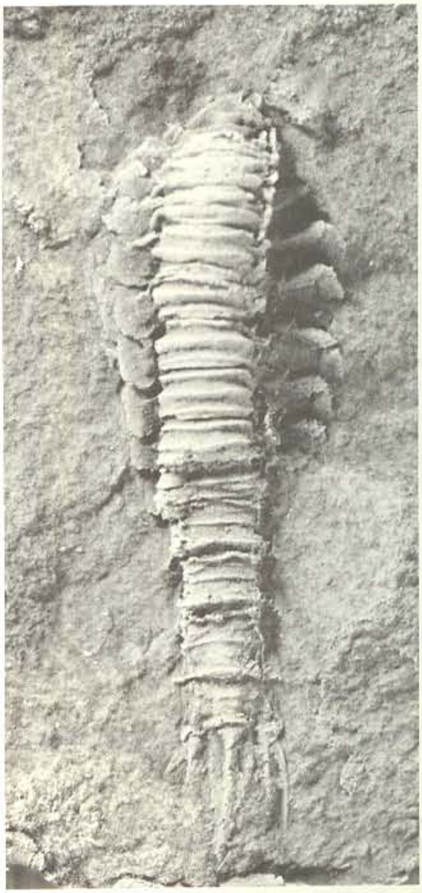
Anaspidites BROOKS, 1962, p. 234 [**Anaspides antiquus* CHILTON, 1929; OD]. Rostrum with broad base; thoracic somites reduced but position of origin of thoracic legs relatively widespread; scaphocerites with straight outer edge. *Trias.*, Australia.——FIG. 169,*4*; 174,*1*. **A. antiquus* (CHILTON); 169,*4*, ×1.5; 174,*1*, ×2 (Brooks, n).

Family KOONUNGIDAE Sayce, 1908

Eyes sessile, antennae lacking scaphocerites; last two pereiopods uniramous, pleopods all uniramous except first two in males, which are copulatory organs. *Rec.*

Koonunga SAYCE, 1908, p. 353 [**K. cursor*; OD]. Eyes sessile. *Rec.*, Australia.

Micraspides NICHOLLS, 1931, p. 475 [**M. calmani*; OD]. Blind. *Rec.*, Tasmania.



1 **Pleurocaris**

FIG. 172. Palaeocaridacea, Pleurocarididae (p. *R*355)

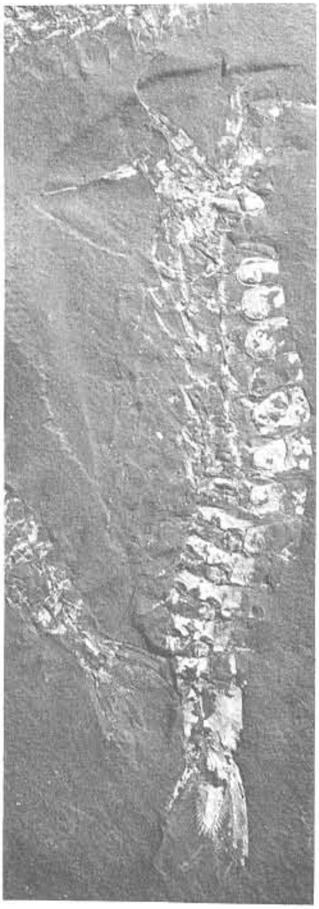


FIG. 173. Palaeocaridacea, Uronectidae (p. *R*355).

Order BATHYNELLACEA Chappuis, 1915

[*nom. transl.* SIEWING, 1959]

Aberrant subterranean syncarids having last abdominal somite fused with telson; pleopods reduced or absent; furca present. *Rec.*

Family BATHYNELLIDAE Chappuis, 1915

Characters of order. *Rec.*

Bathynella VEJDOVSKY, 1882, p. 65 [**B. natans*; OD]. Pleopods 2-jointed, antennae with 5 or more joints; exopods present on pereiopods *1* to *7*. *Rec.*, Eu.-Japan.

Allobathynella MORIMOTO & MIURA, 1957, p. 145 [**A. japonica*; OD]. Pleopods single-jointed, rudimentary. *Rec.*, Japan.——FIG. 163,*1*. **A. japonica*; ×32 (290).

Brazilibathynella JAKOBI, 1961, p. 27 [**B. florianopolis* JAKOBI, 1958; OD]. Pleopods absent; 1st antennae with 6 joints; exopods of thoracopods with 2 joints. *Rec.*, S.Am.(Brazil).

Parabathynella CHAPPUIS, 1926, p. 7 [**P. stygia*; OD]. Pleopods entirely absent; antennae with 5 or fewer joints; exopods of pereiopods *2* to *7*, 2- or 3-jointed. *Rec.*, Eu.-Malay.Arch.-Japan-Madag.

Thermobathynella CAPART, 1951, p. 1 [**T. adami*; OD]. Pleopods entirely absent; antennae with 5 joints; exopods of pereiopods *1* to *7* with only single joint. *Rec.*, Afr.-S.Am.

Order STYGOCARIDACEA Noodt, 1964

First thoracic somite fused with head; telson bearing furcal rudiment; petasma and antennal statocysts present. *Perm.-Rec.*

Family STYGOCARIDIDAE Noodt, 1962

[*nom. correct.* NOODT, 1964 (*pro* Stygocaridae NOODT, 1962)]

Specialized for living interstitially, eyes and pleopods aborted. First pereiopods specialized as maxillipeds; antennae lacking exopod scaphocerites; rudiments of furca on telson. *Rec.*

Stygocaris NOODT, 1962, p. 577 [**S. gomezmillasi* NOODT, 1962; OD]. Exopods on pereiopods aborted; segments of both antennules and antennae reduced in number. *Rec.*, S.Am.(Chile).

Parastygocaris NOODT, 1962, p. 576 [**P. andina* NOODT, 1962; OD]. Exopods on thoracic appendages *2* to *6;* exopods of uropod divided into 2 segments. *Rec.*, S.Am.(Arg.).——FIG. 164,*1*. **P. andina*; ×50 (215).

Family CLARKECARIDIDAE Brooks, 1962

Suture between head and first thoracic tergite vestigial; anterior sulcus on cephalon sigmoidal; abdominal pleura spinelike; furca present. *Perm.*

Clarkecaris MEZZALIRA, 1952, p. 47 [**Gampsonyx brasilicus* CLARKE, 1920; OD] [=*Gampsonyx* CLARKE, 1920 (obj.)]. Thoracic somites shorttened, paired dorsal spines on thoracic tergites. *Perm.*, S.Am.(Brazil).——FIG. 169,*3*; 174,*2*. **C. brasilicus* (CLARKE), 169,*3*, ×3; 174,*2*, ×6 (Brooks, n).

Order and Family UNCERTAIN

Triasocaris BILL, 1914, p. 323 [**T. peachi;* OD] (*nom. dub.). Trias.*, Eu.(Fr.).

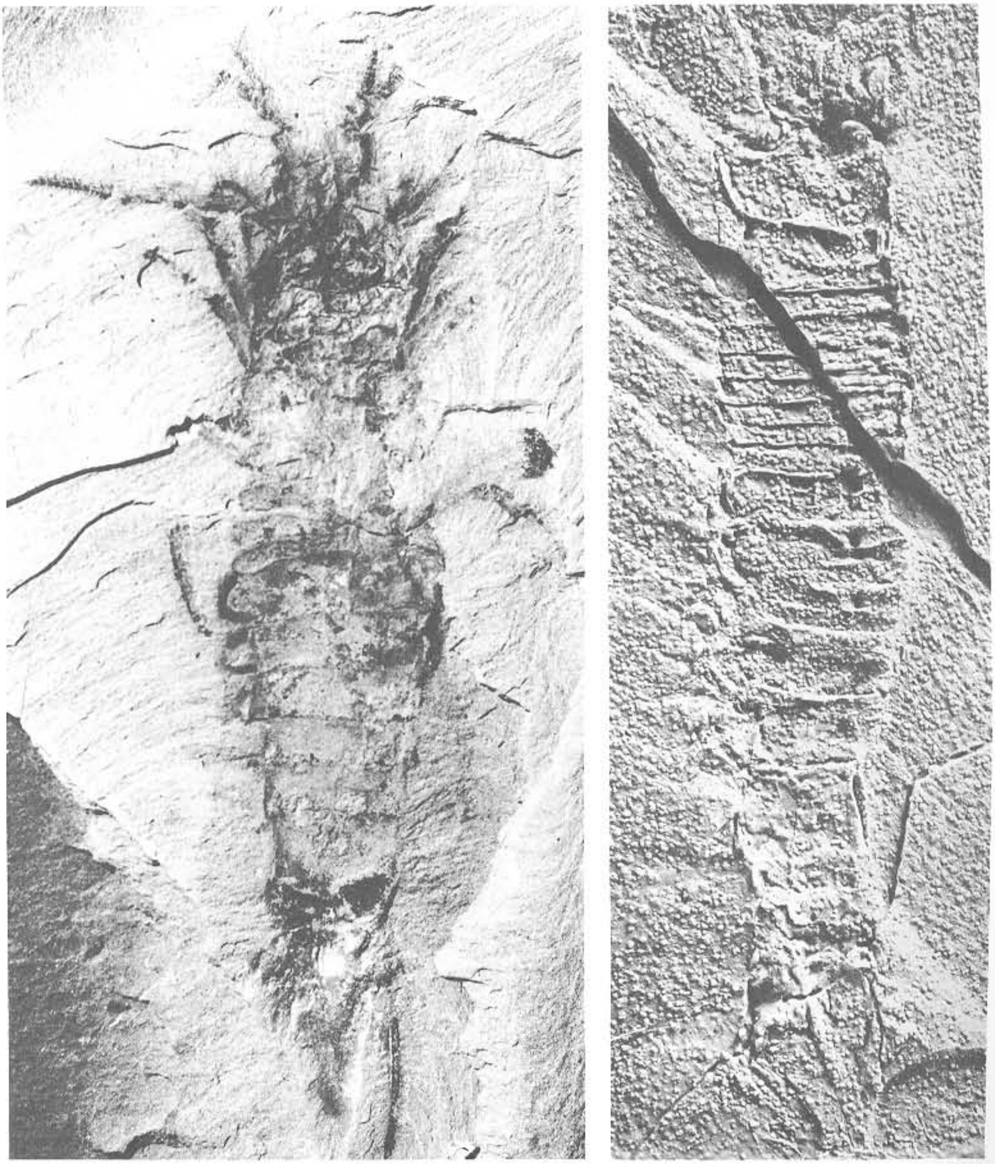


FIG. 174. Anaspidacea (Anaspididae) *(1)*; Stygocaridacea (Clarkecarididae) *(2)* (p. *R*357-*R*358).

PERACARIDA

By Robert R. Hessler

[Woods Hole Oceanographic Institution] [Acknowledgments are made to Dr. Edward L. Bousfield, National Museum of Canada, and to Dr. Eric L. Mills, Queen's University, Ontario, Canada, for their advice on taxonomic placement of fossil amphipods. Appreciation also is expressed to Dr. Isabella Gordon, British Museum (Natural History), London, and Dr. W. D. I. Rolfe, Hunterian Museum, University of Glasgow, for their criticism of the typescript. Work for the *Treatise* has been supported partly by the National Science Foundation under grants G-10744 and GB-563. This is contribution 1445 of the Woods Hole Oceanographic Institution.]

CONTENTS

Superorder PERACARIDA Calman, 1904

First thoracomere invariably fused to cephalon; carapace fold (when present) never fused to all thoracomeres; protopod of antenna typically three-segmented; mandible with lacinia mobilis in all expect parasitic and other specialized forms (Fig. 175); first thoracopod modified as maxilliped; major flexure ("knee") of endopods of second to eighth thoracopods between merus and carpus; eggs and young nearly always carried in marsupium formed by medial lamellar outgrowths (oöstegites) of coxae of two to seven pairs of thoracopods (Fig. 176); pleopods without appendix interna; young liberated from marsupium at late stage of development, not as nauplii. Hepatic caeca few and simple; heart usually elongate, extending through greater part of thorax or displaced into abdomen; spermatozoa usually threadlike. *Perm.-Rec.*

In both isopods and amphipods the coxae of the pereiopods tend to be flattened and platelike, and may be quite large. These plates, called **epimeres** or coxal plates, are broadly joined to edges of the tergites and are the functional equivalent of pleura (lateral outfoldings of tergites), commonly fold-

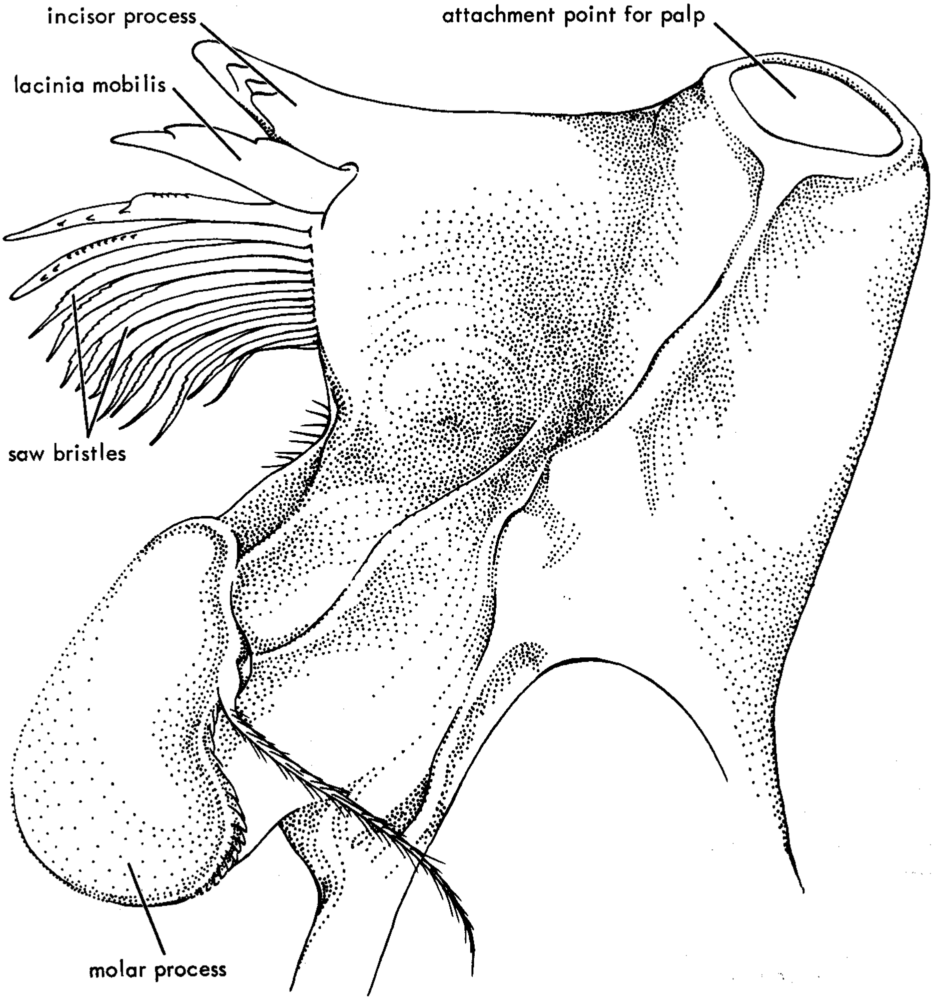


FIG. 175. Right mandible of the amphipod ***Leptocheirus pinguis*** (STIMPSON) (1853), dorsal view, showing the characteristic gnathic structures found in the Peracarida. The mandibular palp has been removed (Hessler, n).

ing down laterally over the basal portion of the rest of the limb (Fig. 176). The line of juncture of coxal plate and tergite may remain distinct, as in the Gammaridea or may be completely obscured through fusion, as in most Oniscoidea (GRUNER, 1953). Epimeres are never developed on the pleon, where pleura of considerable size may occur instead.

Among many varied attempts at classifying the Malacostraca, only the few major systems having direct importance to the Peracarida are considered here.

LEACH (1815) divided the Malacostraca into groups named Edriophthalma, having sessile eyes, and Podophthalma, with movable stalked eyes. Nearly coincident with this system is BURMEISTER'S (1834) division into Thoracostraca, having a carapace fold, and Arthrostraca, without one. Although most orders fall into either the edriophthalmid-arthrostracid or podophthalmid-thoracostracid assemblages, the living Tanaidacea, which possess a carapace and lack stalked eyes, and the equally equivocal Cumacea make such a bipartite division indefensible (1).

The Schizopoda of LATREILLE (1817), in-

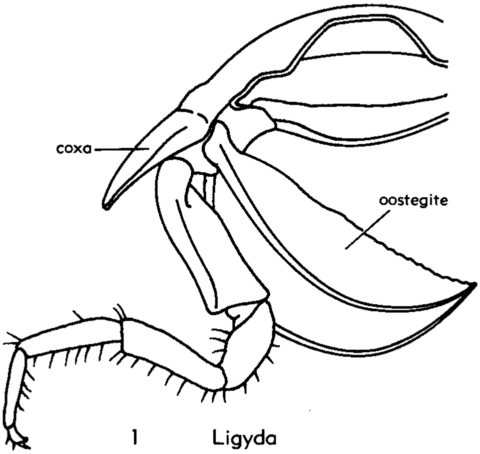


FIG. 176. Thoracic segment of *Ligyda exotica* ♀ showing one of oöstegites which make up brood pouch, also illustrating how the coxa has become fused to the trunk, becoming modified as an epimeral plate, enlarged (379).

cluding the Mysidacea and Euphausiacea, is another taxonomic unit which existed for many years in good standing. BOAS (1883) pointed out the many differences between mysidaceans and euphausiids and discarded this grouping. HANSEN (1893) concurred with BOAS and united the mysidaceans with the cumaceans, tanaidaceans, isopods, and amphipods. CALMAN (1904) called this large group the Peracarida.

The Tanaidacea have had a very unsettled systematic position in the past. Early workers often included them with the amphipods, whereas G. O. SARS and other late 19th century taxonomists placed them in the isopods. CALMAN and HANSEN followed CLAUS (1888) in considering the Tanaidacea as an independent order.

The Peracarida, in addition to containing orders with highly unique morphologies, includes one group, the Mysidacea, which shares with a number of nonperacaridan orders a collection of important characters known as the caridoid facies (further noted in discussion of the mysidaceans). Unless one is willing to assume that the caridoid facies was acquired convergently, he is forced to conclude that mysidaceans are the most primitive living pericaridan group. Other primitive mysidacean features are the presence of seven abdominal segments and a caudal furca in the embryo, large number of oöstegites in lophogastrids, free telson, first maxillipeds not fused basally and not strongly differentiated from other thoracic limbs, and nature of the filter-feeding mechanism.

The Amphipoda and Isopoda, which comprise the heart of BURMEISTER'S Arthrostraca, have been thought by many (e.g., REIBISCH, 1927) to be closely related, having in common sessile eyes and thoracic epimeres (see below), and lacking a carapace fold. However, CALMAN (65) and SIEWING (274) have considered these similarities to be superficial. Far more important differences in the excretory organs, respiratory and circulatory systems, modes of reproduction and development, structure of abdominal appendages, and morphology of the digestive tract indicate that these orders are the end products of two distinct lines of specialization which diverged from some mysidacean-like ancestor (Fig. 177).

The Cumacea and Tanaidacea are considered to represent intermediate grades of development in the evolution of the isopodan condition (274). Important facets of this evolution are the progressive reduction of the carapace fold, specialization of the first maxilliped (especially in relating cumaceans and tanaidaceans), and gradual loss of pereiopodal exopods. SIEWING has mentioned changes in the structure of the digestive tract and shift in the respiratory organs, as well as similarity to the isopods

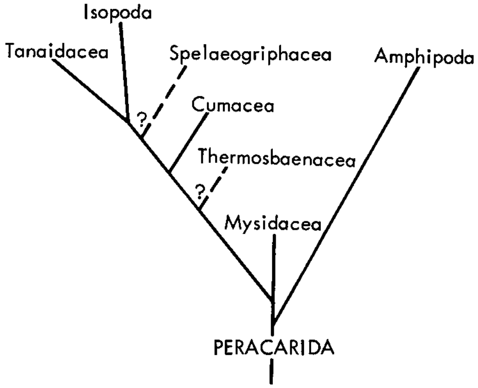


FIG. 177. Phylogeny of Recent Peracarida as interpreted by SIEWING (274) and modified by FRYER (101).

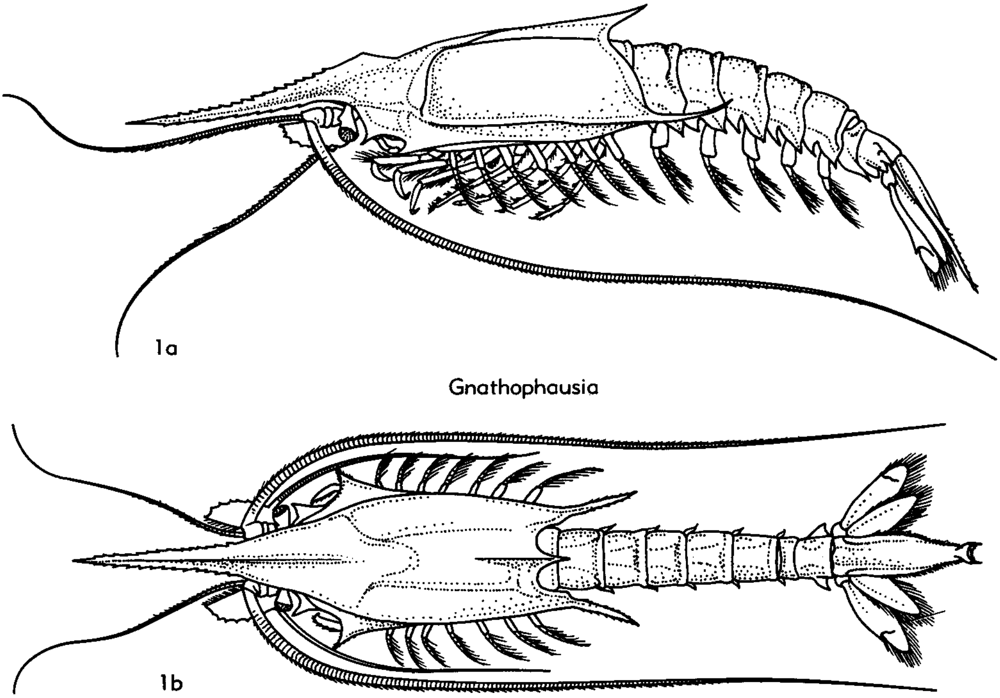


FIG. 178. Lophogastrida: *Gnathophausia calcarata* G. O. SARS; *1a,b,* lateral and dorsal views, ×0.8 (377c).

in such characters as distinguish the latter group from the amphipods.

The Spelaeogriphacea is clearly a primitive order, but its exact position within the Peracarida is uncertain.

A tabulation of suprageneric divisions of the Peracarida showing their stratigraphic occurrence and numbers of genera contained in each is given on page *R*114.

The Thermosbaenacea, included in the Peracarida in this volume, are probably the result of an early divergence in peracaridan evolution. SIEWING has considered the order to be a closely related but independent division.

Quite different from the above scheme, in which the Peracarida is construed to be a natural phyletic unit, is GLAESSNER'S (1957) suggestion that the Tanaidacea, Isopoda, and Amphipoda are related to the early Syncarida by way of the Acanthotelsonidae, and that the Mysidacea, Cumacea, Eucarida, and Hoplocarida are all derived from the Pygocephalomorpha. The Acanthotelsonidae and Pygocephalomorpha then would be interpreted as derived from a common Paleozoic caridoid malacostracan. As such, the Peracarida would be a diphyletic group. TIEGS & MANTON (288), BIRSHTEYN (43), and SIEWING (275) do not agree to the syncarid origin of part of the Peracarida.

Order MYSIDACEA Boas, 1883

Exhibiting caridoid facies; carapace fold more or less enveloping thoracic region; eyes stalked, movable; antennule (first antenna) biramous; antenna (second antenna) with scalelike exopod; thoracopods bearing natatory exopods; abdomen large, elongate, ventrally flexed, terminating in tail fan formed by lamellar rami of uropods and telson; first one, two, three, or rarely four thoracomeres fused to cephalon; first one or two pairs of thoracopods modified as maxillipeds, in some forms lacking exopods, first with leaflike epipod; ramified gills at base of some or all thoracopods. Young

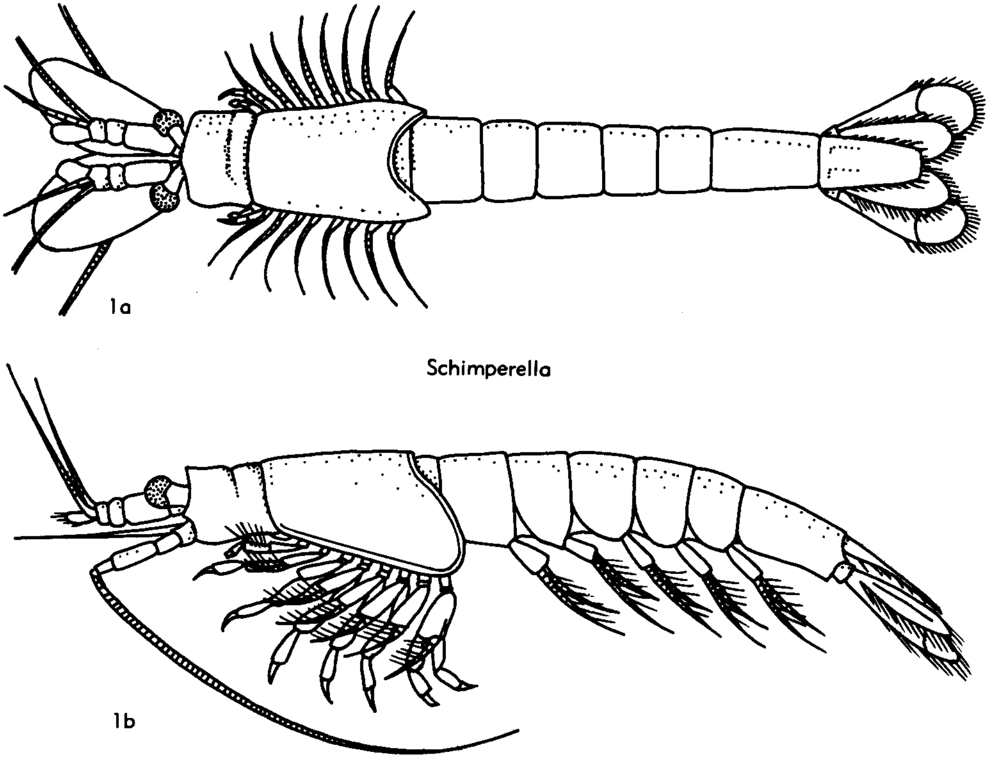


Fig. 179. Mysida: *Schimperella beneckei* Bill; *1a,b,* dorsal and lateral views, ×7 (39).

leave marsupium with full complement of limbs. *Trias.-Rec.*

Among peracarids, the Mysidacea can be recognized at a glance because they possess the caridoid facies, but it is sometimes more difficult to distinguish members of this order from nonperacaridan forms (e.g., Euphausiacea, and lower Decapoda) which also exhibit the caridoid facies. This is particularly true of fossils in which diagnostic peracaridan traits usually are not preserved.

A number of Paleozoic genera have been included in the Mysidacea (299) in the past, some (e.g., *Pygocephalus, Tealliocaris, Crangopsis*) because of the presence of oöstegites. Brooks (55) has pointed out that all of these genera differ from any of the Recent eumalacostracan superorders in having an unsegmented sympod and caudal furca on which account he has included them in a new division named Eocarida. Accepting this classification, at the present time no mysidaceans are known from the Paleozoic.

Of the two mysidacean suborders, the Lophogastrida are considered to be the more primitive in that all have seven pairs of oöstegites, well-developed unspecialized pleopods, and no uropodal statocysts. The Lophogastridae are especially primitive in that some show indications of a seventh abdominal segment (Fig. 178) and in having *(Gnathophausia)* a two-jointed maxillulary palp, which is reflected into the branchial cavity.

Mysidaceans are found primarily in marine environments, but some species are markedly euryhaline, and a few live in fresh water. As a whole, the group is essentially pelagic, although commonly epibenthic. Species which exhibit vertical migration may be found on the bottom or even burrowed into it during the daytime.

Both carnivorous and detritus-feeding habits are characteristic. The detritus-feeders may filter fine particles from the water or pick up larger bits from the bottom.

The Mysidacea, including both suborders Lophogastrida and Mysida, are a very cosmopolitan assemblage.

Suborder LOPHOGASTRIDA Boas, 1883

Ramified branchiae well developed on second to seventh thoracopods but rudimentary or absent on eighth; seven pairs of oöstegites; pleopods biramous, natatory, well developed in both sexes, may be slightly modified in males. No statocyst in endopod of uropods (Fig. 178). *Rec.*

Suborder MYSIDA Boas, 1883

Thoracopods lacking branchiae; usually two or three pairs of oöstegites present, rarely seven pairs; pleopods usually rudimentary in females, biramous and natatory in some males but more commonly with one or more pairs modified as accessory copulatory organs; uropodal endopod usually with statocyst. *Trias.-Rec.*

Family UNCERTAIN

Schimperella Bill, 1914, p. 310 [**S. beneckei*; SD Hessler, herein]. No obvious rostrum; carapace fold extended posteriorly to cover most of last pereionite, rounded posterolaterally, only moderately emarginate posteriorly; eyes well developed. Antennule wih distal end of last peduncular segment modified in males; scaphocerites of antennae very large, broad; pereiopods normal, more or less similar where known. Abdomen without evident pleura; telson elongate, truncate, entire; pleopods large, subequal, natatory, apparently unmodified. Uropodal rami broadly rounded posteriorly; exopod with transverse suture; no apparent statocyst. *Trias.*, Eu.(Alsace).——Fig. 179,*1*. **S. beneckei; 1a,b,* dorsal, lat. views (reconstr.), ×7 (39).

[*Schimperella* is tentatively placed in the suborder Mysida on the basis of its general body form, especially that of the carapace, and the presence of an *appendix masculina* on the first antenna. The well-developed, unmodified pleopods and pereiopods and the absence of a statocyst in the uropods suggest that this genus may be relatively primitive. It differs from some of the Lophogastridae in that no suture subdivides the last pleonite indicates fusion of the 6th and 7th abdominal somites.]

Francocaris Broili, 1917, p. 429 [**F. grimmi*; OD]. Cephalon strongly produced anteriorly into long

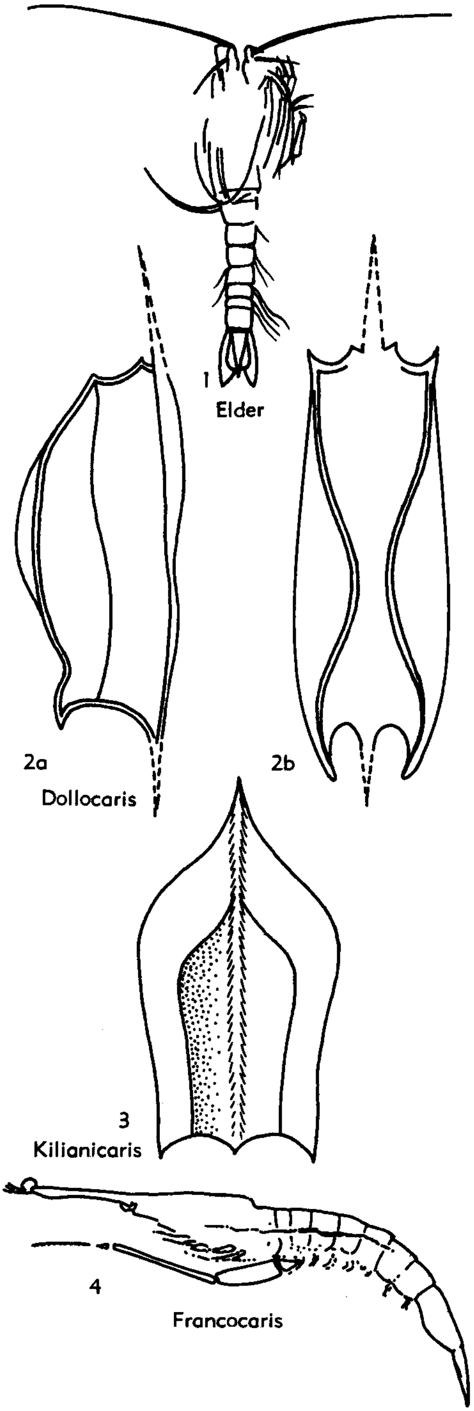


Fig. 180. Mysidacea, Family Uncertain *(4)*, Suborder and Family Uncertain *(1-3)* (p. *R*365-*R*366).

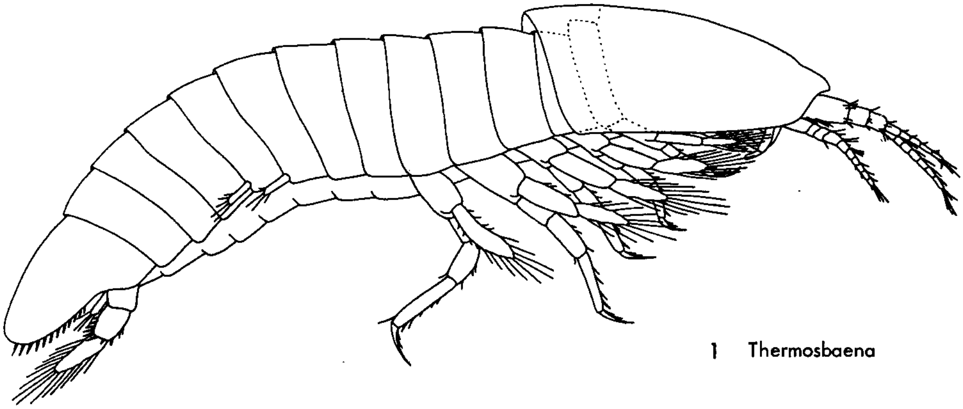


Fig. 181. *Thermosbaena mirabilis* Monod, adult female, lateral view, ×30 (347).

slender process with eyes at anterior end; carapace not strongly sclerotized; 8th thoracopods extremely long, with large basal segment. [Broili placed *Francocaris* among the Mysidacea because its carapace appears to be fused only to the anterior thoracic segments.] *U.Jur.*, Eu.(Ger.).——Fig. 180,*4*. **F. grimmi;* lat., ×1.4 (346a).

Suborder and Family UNCERTAIN

Dollocaris Van Straelen, 1923, p. 432 [**D. ingens*; OD]. Carapace with weak marginal furrow; dorsomedial carina running from posteromedial spine forward onto long rostrum; marked lateral carina halfway between dorsal mid-line and lateral edge, running length of carapace; posterolateral spines present. *U.Jur.*, Eu.(Fr.).——Fig. 180,*2*. **D. ingens*; *2a,b,* carapace; lat., dorsal, ×0.6 (383).

Elder Münster, 1839, p. 77 [**E. ungulatus*; SD Oppel, 1862] [=*Saga* Münster, 1839]. Cephalothorax of relatively delicate composition, rarely preserved in fossils where all other parts are in the proper relationship to each other; flagellum of antennae as long as body, much longer than those of antennules; pereiopods with distinct distal claw. *U.Jur.*, Eu.(Ger.).——Fig. 180,*1*. **E. ungulatus;* dorsal, ×0.8 (369).

Kilianicaris Van Straelen, 1923, p. 434 [**K. lerichei*; OD]. Carapace angular, subquadrate posteriorly, with strong dorsomedial and weak lateral carinae; rostrum broad; posteromedial and posterolateral spines weakly produced. *U.Jur.*, Eu.(Fr.).——Fig. 180,*3*. **K. lerichei;* carapace, lat., ×1.1 (383).

[Van Straelen (383) put *Dollocaris* and *Kilianicaris* in a new family, the Dollocaridae, which he placed near the Lophogastridae, but which differ in lack of a cervical furrow, in general form of the carapace, and in position of the carinae. *Dollocaris* and *Kilianicaris* are based on the carapace alone. Although in both this structure is much like that of *Gnathophausia*, not enough is known of these two fossil genera to demonstrate that they are definitely mysidaceans (287).]

Order THERMOSBAENACEA Monod, 1927

No oöstegites; instead eggs and embryos carried in dorsal brood pouch formed by shell fold. Maxilliped with two protopodal endites, most distal of which is very large, quadrate; epipod leaflike; slender exopod usually present in both sexes; slender endopod found in males of some species and female of one. Shell fold fused to first thoracomere, small, covering no more than next two somites. Eyes rudimentary or absent. Antennule biramous; antenna lacking exopod. Pereiopods with exopods. Pleopods on first two pleonites only. Uropod biramous, flattened. Young leave brood pouch before pereiopods 6 and 7 have developed. *Rec.*

Stella (1953) and Taramelli (1954) placed the Thermosbaenacea between the Peracarida and Syncarida. Siewing (272) noted the close relationship to the Peracarida, but concluded that the unique mode of brooding young and the different form of the maxilliped were of sufficient importance to warrant placing thermosbaenaceans in a separate, new division, the Pancarida. Subsequently, Gordon (1958), Barker (14), and Fryer (101) have minimized the importance of these differences and have followed Monod's original designation.

Thermosbaenaceans have been recorded from thermal springs, fresh and brackish subterranean lakes, and brackish coastal

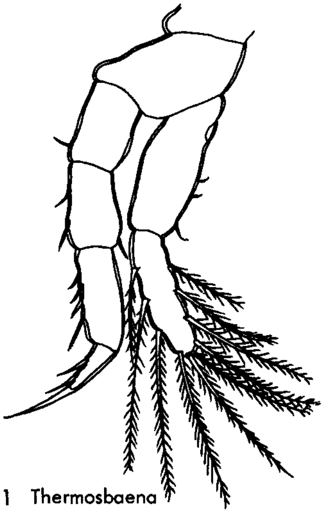


Fig. 182. Third pereiopod of *Thermosbaena mirabilis* Monod, ×90 (206).

ground water. Karaman (163) and others consider the ancestors of this group to have been marine, thermosbaenaceans having invaded continental environments through the intermediate marine or brackish coastal ground water.

Family THERMOSBAENIDAE Monod, 1927

Characters of order. *Rec.*

Thermosbaena Monod, 1924, p. 58 [**T. mirabilis*; OD]. Body short and stocky; pereiopods absent from last 2 pereionites; endopod of uropod reduced; telson fused to pleonite 6. *Rec.*, N.Afr.——Fig. 181,*1*; 182,*1*. **T. mirabilis*, Tunisia; 181,*1*, adult female, lat., ×30 (347); 182,*1*, 3rd pereiopod, ×90 (206).

Monodella Ruffo, 1949, p. 45 [**M. stygicola;* OD]. Body slender, elongate; pereiopods on all pereionites; uropod with well-developed endopod; telson free. *Rec.*, USA(Tex.)-Italy-Yugosl.-Israel. ——Fig. 183,*1*. *M. halophila* Karaman, Yugosl.; maxilliped of male, ×90 (163).

Order SPELAEOGRIPHACEA Gordon, 1957

Body elongate, subcylindrical; carapace short, fused dorsally to first thoracic somite, covering most of second to form lateral branchial cavities; trunk segments other than first thoracomere free, including telson; pleon long; ocular lobe movable, but without visual elements. Antennules biramous; antennae with small exopodal scaphocerite and four-jointed peduncle; mandible with unjointed palp; maxilliped having large cup-like branchial epipod located in branchial chamber; thoracopods two to four with two-segmented natatory exopods, next three (in some forms four) pairs with unjointed branchial exopods; first four pleopods well developed, biramous, natatory, fifth pleopods vestigial; uropods biramous, flattened. *Rec.*

This order is known only from a cave at Table Mountain, South Africa, where its single known species was found in a fresh-water pool. Because *Spelaeogriphus* possesses a lacinia mobilis and oöstegites Gordon (121) included it in the Peracarida. Nevertheless, some of its features (e.g., large number of exopods, some respiratory) are reminiscent of the Syncarida. Although almost all characters of *Spelaeogriphus* are found in other peracaridan orders, in combination they are unique; the small carapace fold fused to a single thoracomere, the well-developed abdomen bearing large, natatory pleopods, and the movable ocular lobes are among the most important of these (Fig. 184). Gordon (1960) has placed *Spelae-*

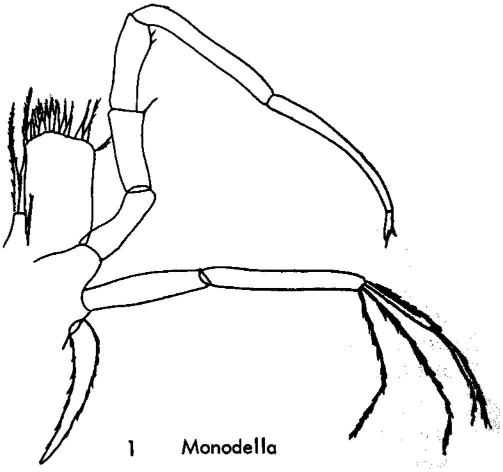


Fig. 183. *Monodella halophila* Karaman, maxilliped of adult male, ×90 (163).

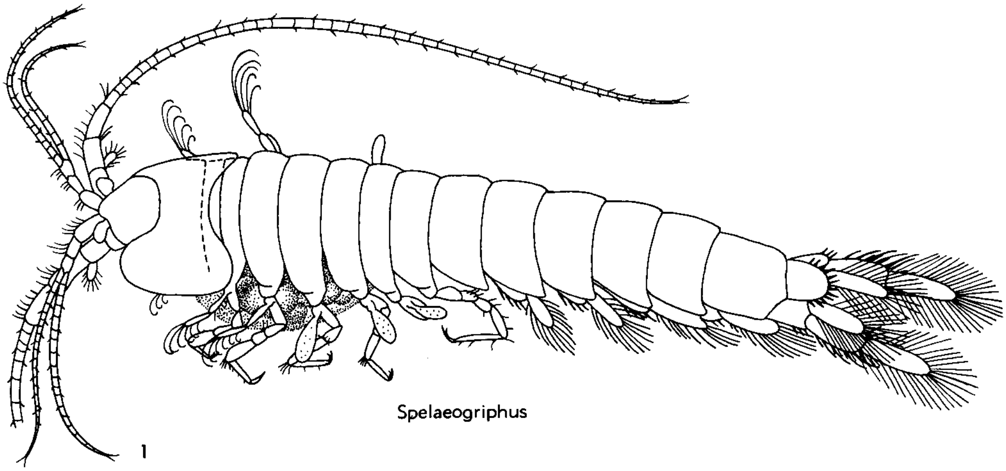


FIG. 184. *Spelaeogriphus lepidops* GORDON; dorsolateral view of adule female carrying eggs, ×7.5 (358).

ogriphus closest to the Tanaidacea, mainly because of its small carapace, two-jointed antennal protopod, and the cuplike branchial epipod of the maxillipeds.

Order CUMACEA Kröyer, 1846

[=Sympoda STEBBING, 1900]

Carapace fold fused to at least three thoracomeres, in some to four, and very rarely to as many as six thoracomeres thus forming lateral branchial chambers which contain branchial epipodite of first maxilliped; anterolateral portions produced anteriorly, usually meeting in front of cephalon to form pseudorostrum. Eyes (when present) nearly always forming unpaired dorsomedial organ; antennules may be biramous; antennae lacking exopod; first three thoracopods modified as maxillipeds; natatory exopods may be present on thoracopods *3* to *7;* pleon slender, long, usually defined distinctly from bulkier unit formed by cephalon and thorax; pleopods absent on female, present in varying numbers on male; uropods large, styliform; telson may or may not be fused to last pleomere. *U.Perm.-Rec.*

Cumaceans are easily recognized by the long, slim, subcylindrical pleon which is usually strongly differentiated from the broad, commonly inflated pereion and cephalon. The shape of the anterior end of the cephalon is also distinctive (Fig. 185). The sessile eyes usually form an unpaired dorsal visual organ situated between the rostrum and pseudorostrum; this probably results from a dorsomedial migration of the originally lateral eyes in response to development of the pseudorostrum. Also contributing to the characteristic shape are the large, obvious uropods, each with its long, slender peduncle. Cumaceans are rarely more than 3.5 cm. long.

The inflated form of the carapace is mostly a result of the large, lateral branchial chambers. These serve respiration in being lined with a respiratory epithelium, and far more importantly, in housing a large branchial epipod of the maxillule. This epipod is subdivided into a complicated, posteriorly directed gill and an anteriorly directed exhalant siphon. The latter projects forward under the pseudorostral lobe and forms the siphonal apparatus, either in conjunction with this lobe or independently.

The Cumacea are dominantly marine, but some brackish and fresh-water forms exist. Although cumaceans, particularly reproductive males, can swim, they spend most of their time buried in the substrate. Many species are selective as to grain size of particles comprising this substratum. Cumaceans occur from intertidal to abyssal depths, and many species are quite eurybathic. For the most part, cumaceans are selective deposit-feeders.

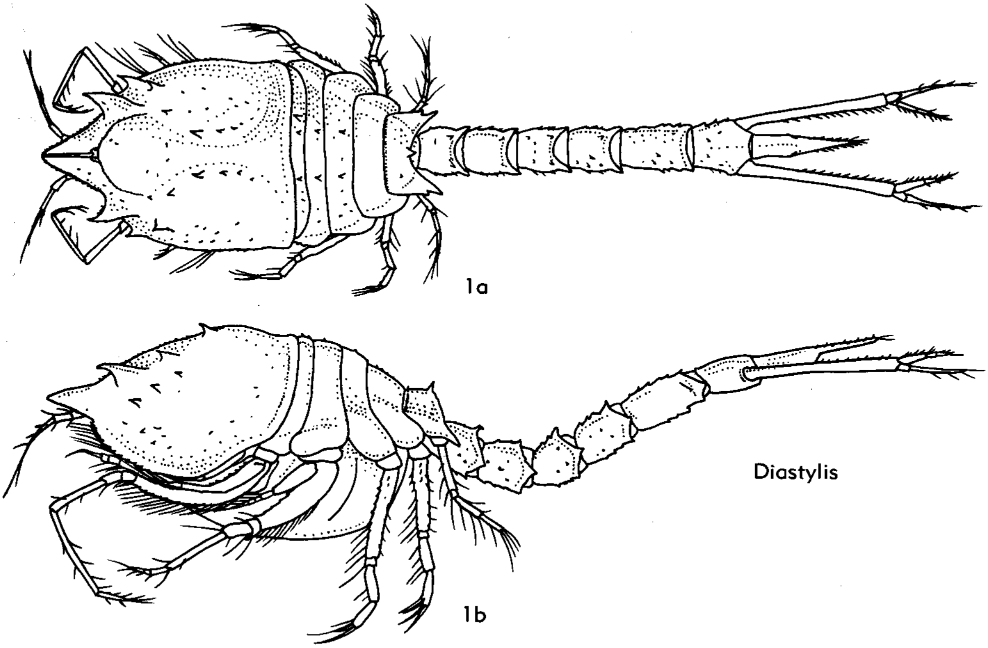


FIG. 185. *Diastylis cornuta* (BOECK, 1863), Rec.; *1a,b,* adult female, dorsal, lateral views, ×7.5 (377d).

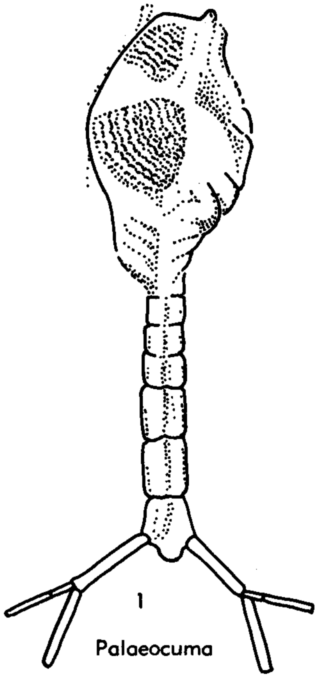


FIG. 186. Cumacea, Family Uncertain (p. *R*369).

ZIMMER (338) has divided the Cumacea into seven families, which, according to JONES (1960), contain 78 genera and about 645 species.

MALZAHN (personal communication; also see ROLFE, this volume, p. *R*313) has found cumacean remains in Upper Permian beds of Germany.

Family UNCERTAIN

Palaeocuma BACHMAYER, 1960, p. 422 [**P. hessi*; OD]. Telson small; cephalothorax egg-shaped, somewhat truncate anteriorly; pleonites 1 to 5 cylindrical, with strong dorsomedial keel; pleon only slightly longer than cephalothorax; exopod of uropods weaker, somewhat shorter than endopod. *M.Jur.,* Eu.(Fr.).——FIG. 186,*1*. **P. hessi*; dorsal, ×2.5 (9).

Order TANAIDACEA Dana, 1853

[=Chelifera G. O. SARS, 1882; Anisopoda CLAUS, 1888]

Carapace fold short, covering first two thoracomeres to which it is fused dorsally, forming small lateral branchial cavities; body generally subcylindrical or tapering evenly posteriorly; pleon short; telson fused

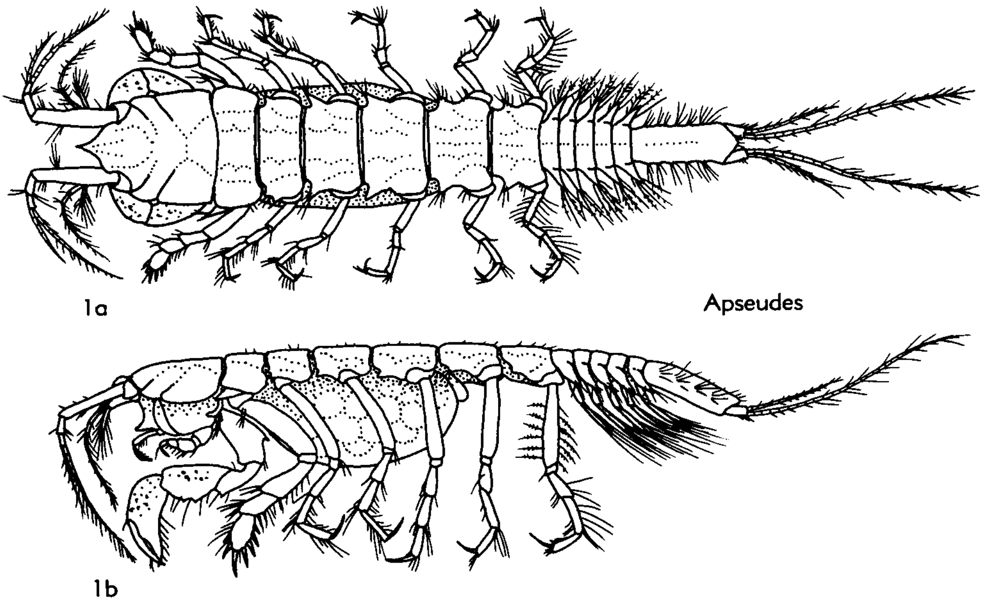


FIG. 187. Monokonophora: *Apseudes spinosus* (M. SARS); *1a,b,* dorsal and lateral views, ×10 (261b).

to sixth pleonite; eyes (when present) set on short immovable lobes (except in *Ophthalmapseudes*). First thoracopods modified as maxillipeds having branchial epipodite; second thoracopods chelate, usually enlarged; vestigial exopods present in some forms on second and third thoracopods of adults; more posterior thoracopods with or without exopod in manca-stage larvae; pleopods usually present, biramous; uropods small, slender. *Perm.-Rec.*

The cylindrical or somewhat depressed body is generally slender and long. The pleon is commonly quite abbreviated, although its individual segments are almost never fused together. In the Monokonophora the body gradually narrows posteriorly, whereas in the Dikonophora it is common for body width hardly to vary. This body shape, in combination with the tagmosis and usually enlarged chelipeds, gives the tanaidaceans an appearance which is difficult to mistake. Tanaidaceans are small, rarely attaining a length of 2.5 cm.

In many differences between the two suborders, the Dikonophora consistently prove to be more degenerate than the Monokonophora. Both antennules and antennae are biramous in the latter but uniramous in the former. In the Dikonophora a mandibular palp is lacking, the maxillules bear only a single endite and the maxillae are rudimentary. Indeed, in males of many Dikonophora most of the mouth parts are vestigial or absent. The monokonophoran maxillipeds bear a much larger, more complicated branchial epipodite. In the Dikonophora the coxae and even the bases of the maxillipeds tend to fuse. Small exopods may be present on some thoracopods of monokonophorans, but are always absent in the Dikonophora. The marsupium of the Tanaidae (Dikonophora) is formed by only a single pair of oöstegites. Finally, the uropodal rami tend to be shorter in the Dikonophora, and the exopod may even be absent. SIEWING (1954) has compared the internal anatomy of Apseudidae (Monokonophora) and Paratanaidae (Dikonophora) and has found the latter to be reduced in a number of respects.

Tanaidaceans live almost exclusively in marine or brackish waters, from littoral to hadal depths (more than 6,000 m.). They are benthic organisms and burrow in mud, crawl in rock crevasses, or live among plant or animal colonies. Some secrete a filamentous, feltlike mass in which they live; others build tubes. Walking is the predominant form of locomotion; a few also swim, but very poorly.

Both suborders of the Tanaidacea are very widespread, cosmopolitan crustacean groups.

Suborder MONOKONOPHORA Lang, 1956

Antennules with two flagella; mandibles with palp; maxillules with two endites; marsupium formed by four pairs of oöstegites; males with one genital cone (Fig. 187). *Perm.-Rec.*

Family UNCERTAIN

Ophthalmapseudes Glaessner, in Glaessner & Malzahn, 1962, p. 259 [**Decapoda* cf. *Macrura rhenana* Malzahn, 1957; OD]. General aspect of carapace and abdomen as in Apseudidae (Fig. 187); eyes on elongate, apparently movable stalks. *U.Perm.-M.Jur.*, Eu.(Ger.).——Fig. 188,*1*. **O. rhenanus* (Malzahn); *1a,b*, cephalic shield (reconstr.), lat., dorsal, showing eyestalks, ×30 (186).

Suborder DIKONOPHORA Lang, 1956

Antennules with single flagellum; mandibles without palp; marsupium formed by one or four pairs of oöstegites; males with two genital cones (Fig. 189). *Rec.*

Suborder and Family UNCERTAIN

Palaeotanais Reiff, 1936, p. 86 [**P. quenstedti*; OD]. Pereionites well vaulted, each with pair of dorsolateral furrows; basis of third thoracopods long, broad; pleonites narrower, not vaulted, each pointed posterolaterally. *L.Jur.*, Eu.(Ger.).——Fig. 188,*2*. **P. quenstedti*; holotype, *2a*, dorsal, as figured by Quenstedt, ×5 (374); *2b*, same fossil, dorsal, refigured by Reiff, ×5 (375).

[Reiff (375) has commented that the single known specimen is less complete than when Quenstedt (374) first figured it. The fossil originally consisted of seven large somites, of which the first was rounded off anteriorly, and four small posterior somites, the posterior end being missing. Assuming the first somite to be the cephalon, Reiff concluded that the fossil was most similar to tanaidaceans because of identical tagmosis, similar size and body form, and similar morphology of sole remnant limb fragment.]

Charassocarcinus (see p. *R*532 and p. *R*628).

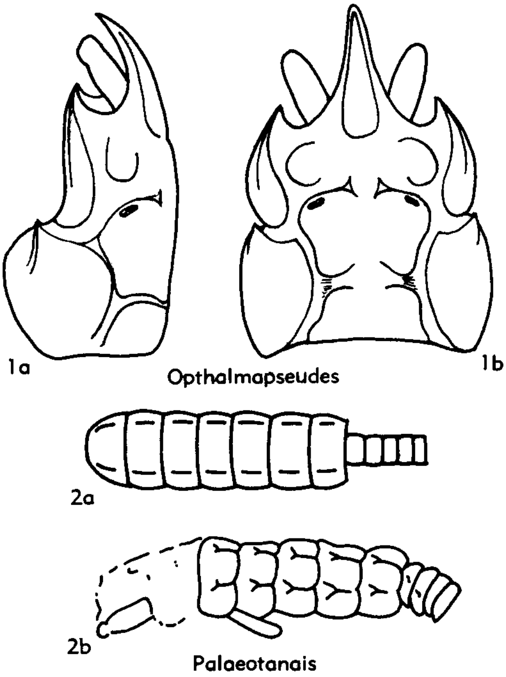


Fig. 188. Tanaidacea: Monokonophora, Family Uncertain *(1)*; Suborder and Family Uncertain *(2)* (p. *R*371).

Order ISOPODA Latreille, 1817

First thoracomere fused to cephalon, and rarely second as well; no distinct carapace fold; body most commonly somewhat depressed; pleon short, in many with segments fused; telson nearly always fused with last pleonite; eyes sessile, not stalked. Antennules usually uniramous; antennae nearly always lacking exopod; pereiopods without exopods, coxae always short; first thoracopods modified as maxilliped with epipod (when present) not enclosed in branchial chamber; second thoracopods rarely also modified as mouth parts; pleopods biramous, specialized for respiration; heart located in pleon. [Young leave marsupium before appearance of last pair of thoracopods (manca stage).] *Trias.-Rec.*

Many different body shapes are found in this order. Most commonly isopods are somewhat depressed, as in the Oniscoidea (Fig. 202) or Flabellifera (Fig. 192). This

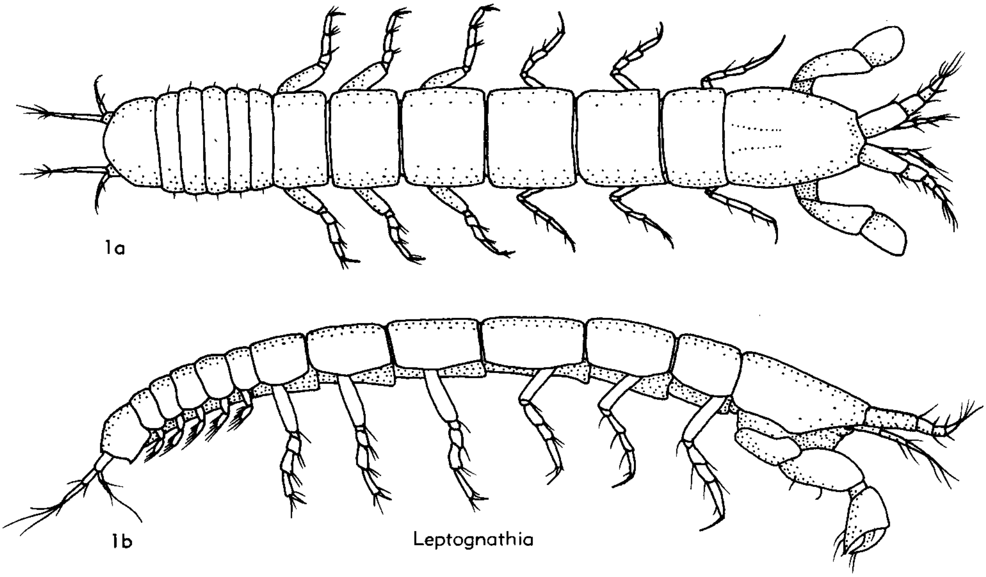


FIG. 189. Dikonophora: *Leptognathia longiremis* (LILLJEBORG); *1a,b,* dorsal and lateral views, ×30 (261b).

form is carried to the extreme in the Serolidae (Fig. 197). Some of the Phreatoicidea (Fig. 203) exhibit the opposite pattern, appearing to be compressed laterally and are remarkably similar to the gammaridean amphipods. Many of the Asellota are cylindrical, as are the Anthuridea (Fig. 191) and Arcturidae (Valvifera). The latter two groups are, in addition, conspicuously elongate, this being achieved in the arcturids by lengthening of but a single segment.

As pointed out by ZIMMER (337), the name Isopoda is somewhat of a misnomer. Except in the Epicaridea, which are truly isopodous, pereiopods one to three are directed anteriorly and pereiopods five to seven point posteriorly, whereas the fourth pereiopod commonly occupies an intermediate position. This is true even in the Oniscoidea, Limnoriidae (Flabellifera), and Gnathiidea, where the limbs are otherwise essentially alike.

More commonly the pereiopods are specialized in blocks. A frequent pattern is one in which the posteriorly turned limbs are significantly longer than others and are "ambulatory" in form as in the Aegidae (Flabellifera). In many groups the first three pereiopods are hooked or subchelate; the Anthuridea and many Idotheidae are examples of this. In the Phreatoicidea and many Asellota only the first pereiopod is subchelate. The most extreme pereiopodal specialization is seen in the Munnopsidae (Asellota). Here the first two pereiopods are short and slender, the second two are thin and extremely elongate, while the last three are short paddles.

Because of the primarily respiratory function of all or part of a number of the pleopods, a variety of different adaptations serves to protect these delicate structures. For example, in many Cymothoidae the exopod of each pleopod protects the respiratory endopod. The first pleopods of some Anthuridea fold back over the rest. In female Paraselloidea (Asellota) the second pleopods form an unpaired operculum covering a ventral chamber in which the other pleopods lie. In the Valvifera the uropods are modified to form a pair of laterally hinged ventral plates which cover the ventral surface of the pleon. In addition to this respiratory or protective function, pleopods may also serve in locomotion or be modified for copulation.

The uropods may vary in form from valvelike opercula described above to relatively simple caudal processes, as found in the Asellota or Oniscoidea. A fanlike form, such as that of the caridoid facies, appears in many Flabellifera and in the Gnathiidae.

The order Isopoda is the largest of the peracaridan orders. The majority of species are marine where they are found at all depths. Nevertheless they are well represented on land, primarily by the large suborder Oniscoidea. Members of the Asellota, Valvifera, Flabellifera, Anthuridea, and all of the Phreatoicidea (except for a few terrestrial forms) may be found in fresh water and may even occur in interstitial and subterranean environments.

The feeding types found among the isopods are equally diverse. Most are detritus-feeders. Some are herbivorous, including wood-eaters, and yet others are carnivores, ranging in degree from predators to highly specialized parasites. Most of the nonparasitic isopods are primarily benthic.

Isopods are almost ubiquitous crustaceans, for each of the suborders can be classed as cosmopolitan, with qualification that living Phreatoicidea now are known only from New Zealand, Australia, northern India, and South Africa.

Suborder GNATHIIDEA Leach, 1814

Second thoracomere fused to cephalon and its appendage modified to act as mouth part; eighth thoracomere and its appendage absent; as result, only five free thoracomeres and the same number of pereiopods occur; peduncles of antennae consisting of four segments; pleonites not fused; uropods flattened, biramous, forming caudal fan in conjunction with pleotelson. Extraordinary sexual dimorphism and extensive metamorphosis; larvae parasitic and provided with suctorial mouth parts; those of adult male reduced to large, anteriorly protruding, pincer-like mandibles and modified maxillipeds, while in adult female only maxillipeds remain (Fig. 190). *Rec.*

Suborder ANTHURIDEA Leach, 1814

Body slender, elongate. Some forms with anterior pleonites fused but last somite never fused to telson; peduncle of antenna with five segments; mouth parts suctorial in some forms; second, third, fourth thoracopods subchelate, second being enlarged; pleopods branchial, first long, somewhat opercular; uropods broad, flat, biramous, with exopod arching over telson (Fig. 191). *Rec.*

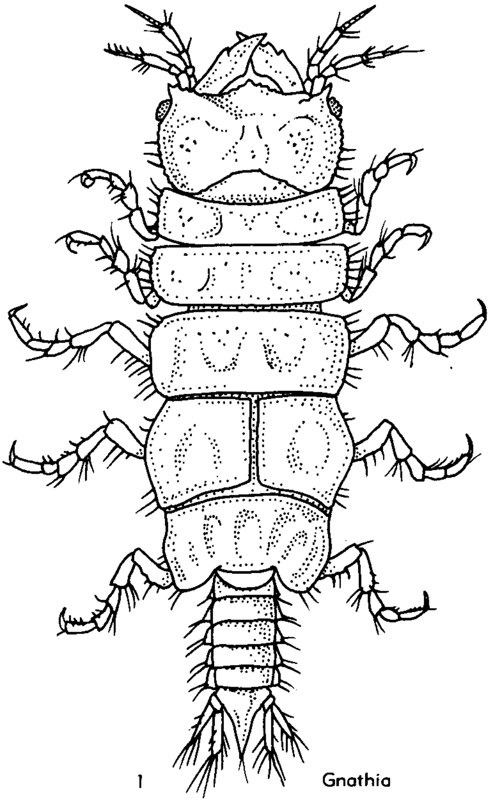


FIG. 190. Gnathiidea: *Gnathia elongata* (KRÖYER); ♂, dorsal view, ×18 (261b).

Suborder FLABELLIFERA G. O. Sars, 1882

Body more or less depressed; pleonites free or fused. Peduncle of antennae with five or six joints; mouth parts normal or suctorial; mandibles usually with reduced or modified molar process; coxae of pereiopods developed as epimeres, in many forms partly or completely fused to thoracomeres;

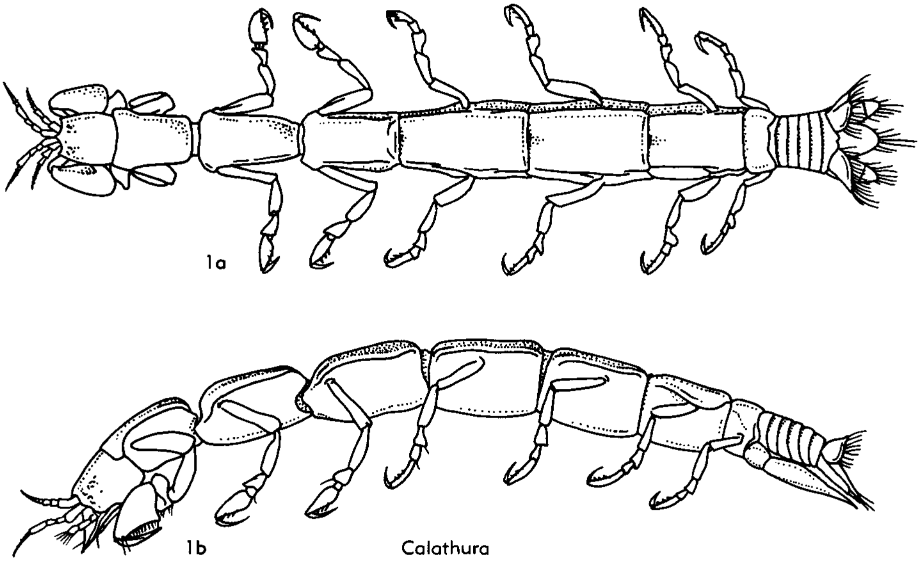


FIG. 191. Anthuridea: *Calathura norvegica* (G. O. SARS); *1a,b,* dorsal and lateral views of female, ×9 (261b).

uropods biramous, usually flattened and forming caudal fan in conjunction with pleotelson. *Trias.-Rec.*

Family CIROLANIDAE Hansen, 1890

Body ovoid; subsemicircular in cross section; labrum large; eyes usually small. Antennules and antennae unequal in length, with well-defined peduncles and flagella; mandibles with large lacinia mobilis; maxillipeds and both pairs of maxillae well developed, palp of former without hooks; well-developed epimeres defined on all pereionites except first; pereiopods *1* to *3* prehensile, *4* to *7* ambulatory; all six pleonites distinct from each other, but last one fused to telson; biramous uropods lateral, forming caudal fan with flattened pleotelson. Free-living. *?Mio., Rec.*

Bathynomus MILNE-EDWARDS, 1879, p. 21 [**B. giganteus*; OD]. Peduncle of antenna with 5 joints; rudimentary scaphocerite attached to distal end of peduncle of antennule; maxilliped with hooks on endite of basis; all 6 pleonites distinct; pleopods with accessory branchial rami on endopods. [IMAIZUMI (1953) has placed a fragmentary pleon from the Miocene of Japan in this genus and has claimed that specimens included in *Palaega* WOODWARD (1870) more properly belong here.] *?Mio., Rec.,* Carib.-Gulf Mex.-Indian O.-W. Pac.——FIG. 192,*1*. **B. giganteus*; *1a,b,* dorsal, lat., ×0.6 (368).

Family SPHAEROMIDAE White, 1847

Body ovoid, well vaulted, capable of partial or complete enrollment. Antennules and antennae multiarticulate, clearly divided into peduncle and flagellum; mandibles with palp; epimeres firmly fixed to all pereionites, defined by furrow on all but first; pleon biarticulate, composed of large pleotelson and smaller anterior unit which is product of at least two fused pleonites; uropods lateral; endopod fused to protopod; exopod absent in some forms. *Trias.-Rec.*

The relationships between the modern genera of the Sphaeromidae are extremely subtle and difficult to interpret (142). This is in part a result of extensive sexual dimorphism. As usual in Recent groups, much of the systematics is based on structures seldom preserved in fossils. For all of these reasons the reference of fossil forms to Recent genera (e.g. *Sphaeroma, Cymodoce*) should be suspected and considered only tentative.

Group SPHAEROMIDAE HEMIBRANCHIATAE Hansen, 1905

Body never strongly depressed; ability to enroll well developed; lateral margin of pereion not continuous. Proximal portion of antennae never protruding with free expansions in front of cephalon, fitted into oblique excavations. Pleopods *4* and *5* with thick fleshy endopods having deep transverse folds; exopods submembranous, rather pellucid, with two segments; neither ramus with plumose marginal setae; exopod of fifth pleopod with subapical squamiferous protuberance of lower surface very high; pleopod three with both rami having long closely set plumose setae, at least on distal

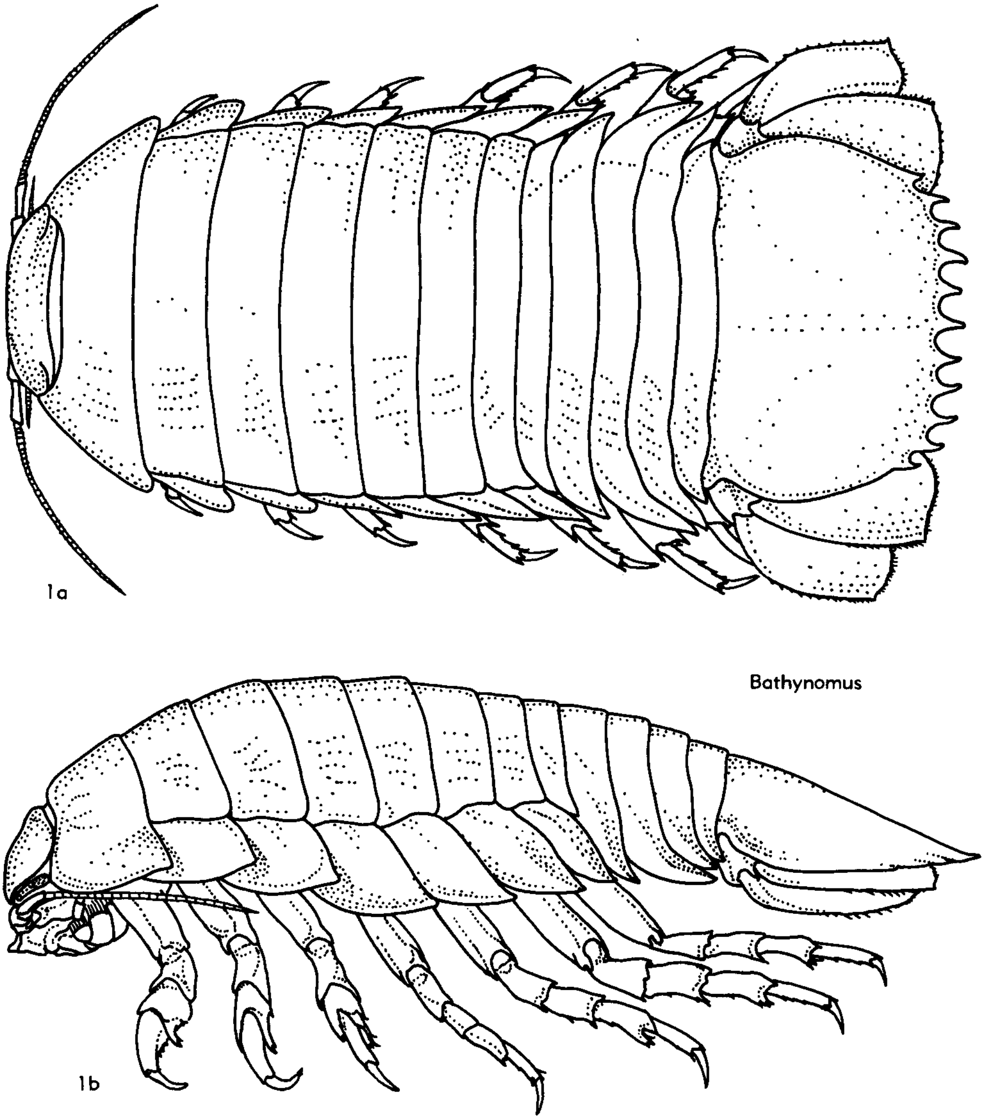


FIG. 192. Flabellifera, Cirolanidae: *Bathynomus giganteus* MILNE-EDWARDS; *1a,b*, ♂ dorsal and lateral views, ×0.5 (368).

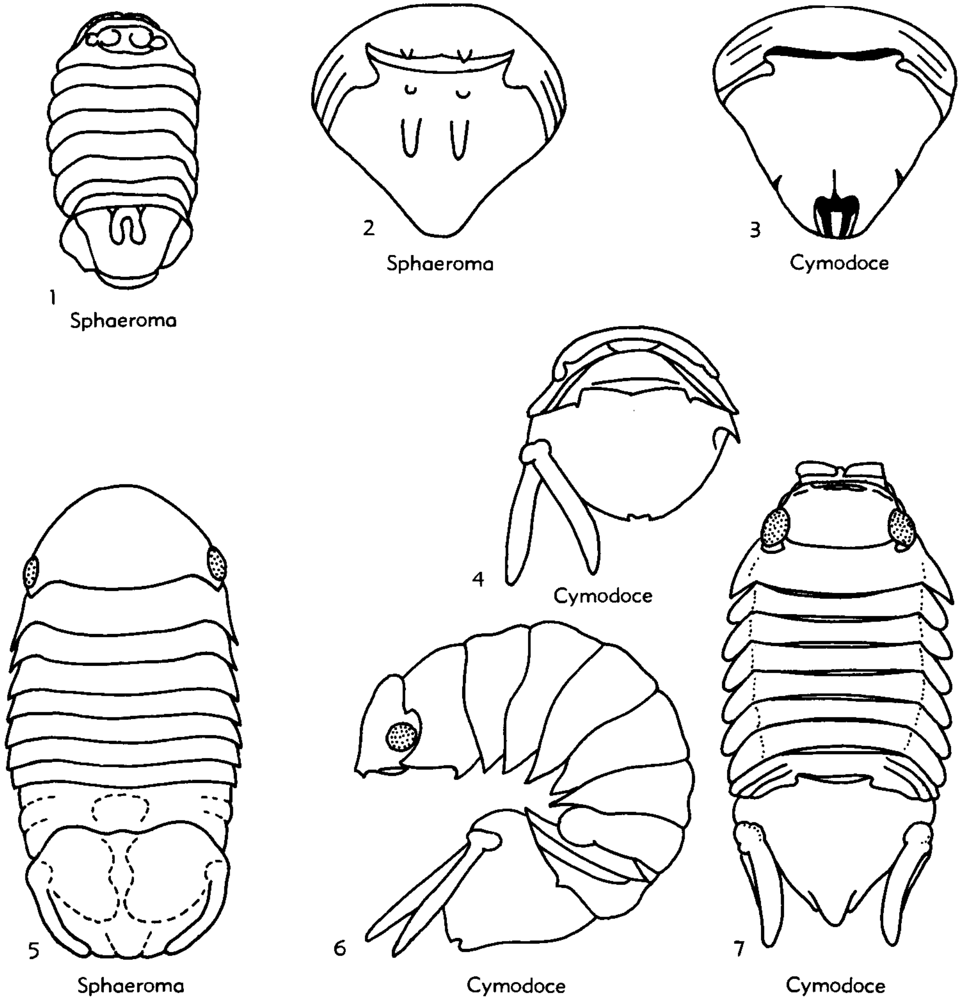


Fig. 193. Flabellifera, Sphaeromidae (p. *R*376-*R*377).

margin; pleopod one with rather broad endopod (scarcely ever 1.5 times longer than wide); uropods always with exopods, which may be exceedingly small. Brood develops in ventral pockets. *?Mio., Rec.*

Tribe CYMODOCINI Hansen, 1905

End of pleon in both sexes with notch which is semicircular in some forms but most commonly bilobed, being divided by mesial process, which rarely is large enough to overlap lateral teeth limiting notch, so that lateral teeth are visible only from side; mouth parts strongly metamorphosed in female; maxillipeds with long lobes on joints *2* to *4* of palp; oöstegites overlapping at mid-line; pleopod *3* with two-jointed exopod. *?Mio., Rec.*

Cymodoce Leach, 1814, p. 433 [**C. truncata*; OD] [=*Cymodocea* Leach, 1818; *Cymodice* Leach, 1815]. Epistome without free process anteriorly; notch at posterior end of pleotelson at least with vestige of mesial lobe which generally is well developed, being commonly large or even very large; no medial process on anterior unit of pleon in male; rami of uropod generally well developed; exopod not able to fold under endopod. *?Mio., Rec.*, cosmop.——Fig. 193,*4,6-7*. *C.? exors* (Von Eichwald), Mio., Eu. (Rumania-S. USSR); *4*, pleon, dorsal, ×3 (4); *6*, lat. (reconstr.), ×3.5 (4); *7*, dorsal (reconstr.), ×6 (276).——Fig. 193,

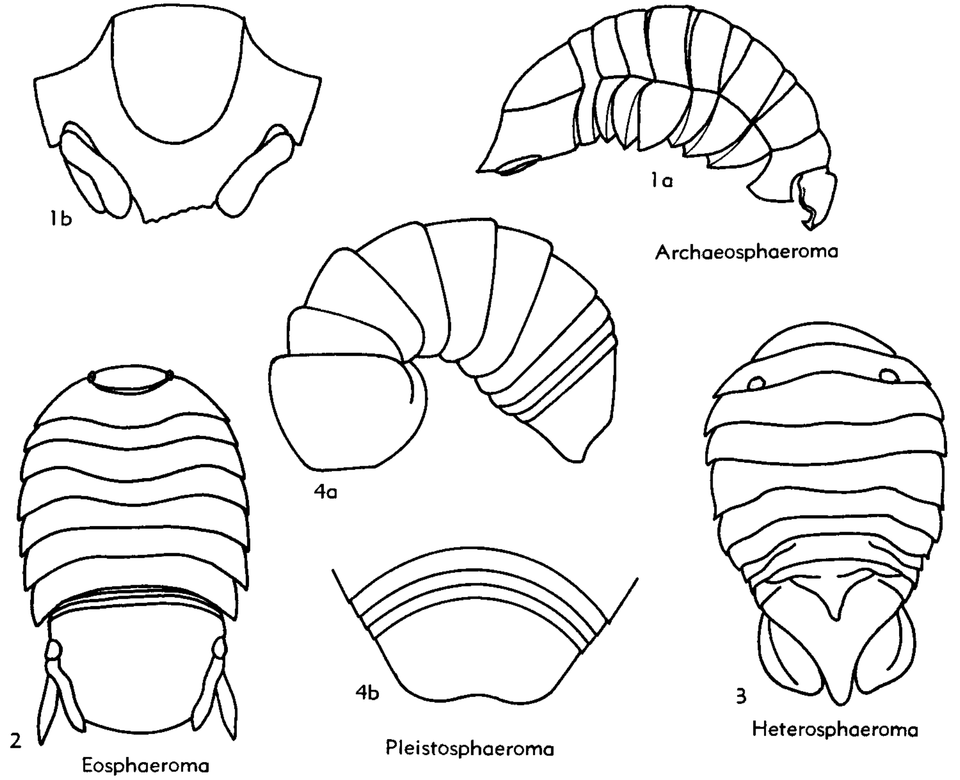


FIG. 194. Flabellifera, Sphaeromidae (p. *R*377-*R*378).

3. C.? oroszyi BACHMAYER, M.Mio., Aus., pleon, dorsal, ×6 (341a).

Tribe SPHAEROMINI Hansen, 1905

End of pleon in female rounded or somewhat produced and more or less acute, without notch; in some forms end much produced, with pair of lateral notches, so that mesial part is shaped as process narrowed at base. Mouth parts similar in both sexes. *?Mio., Rec.*

Sphaeroma LATREILLE, 1804, p. 41 [**Cymothoa serrata* FABRICIUS, 1793; OD]. Body capable of complete enrollment. Mandible normal, incisor process not elongate, its end obtuse or with some small teeth; maxillipeds with low or rudimentary lobes on segments *2* to *4* of palp; 3 anterior pereiopods with closely spaced, exceedingly long, stiff, plumose setae on outer margin of segments *3* and *4;* oöstegites overlapping at mid-line; pleon with side not expanded below lateral margin of pereion, tip rounded, not triangular or subacute; exopod of 3rd pleopod unjointed; uropodal rami subsimilar; exopod denticulate laterally, capable of folding under endopod, which is immovably fixed to side of pleotelson. *?Mio., Rec.*, cosmop.——FIG. 193,*2*. *S. weinfurteri* BACHMAYER, M.Mio., Ger.; pleon, dorsal, ×11 (341).——FIG. 193,*5*. *S.? bachmayeri* TAUBER, M.Mio., Austria; dorsal, ×9 (381).——FIG. 193,*1*. *S.? burkartii* BARCENA, Tert., Mex.; dorsal, ×4.5 (342).

Group UNCERTAIN

Archaeosphaeroma NOVAK, 1872, p. 45 [**A. friči;* OD]. Body strongly vaulted, not capable of complete enrollment; epimeres transversely elongate, pointed, imbricating anteriorly and posteriorly from 5th pereionite; uropods with elongate, rounded, subequal rami much shorter than pleotelson, which tapers posteriorly and is strongly emarginated laterally to accommodate uropods. *Mio.*, Czech.——FIG. 194,*1*. **A. frici; 1a,* lat., ×4.5; *1b,* pleon, dorsal, ×6 (370a).

Cyclosphaeroma WOODWARD, 1890, p. 530 [**C. trilobatum*; OD] [=*Palaeosphaeroma* REMES, 1903]. Body broad, strongly vaulted; cephalon also quite broad, but short, trilobate, only slightly surrounded by 1st pereionite; eyes large. Epimeres fused to pereionites, but still defined by

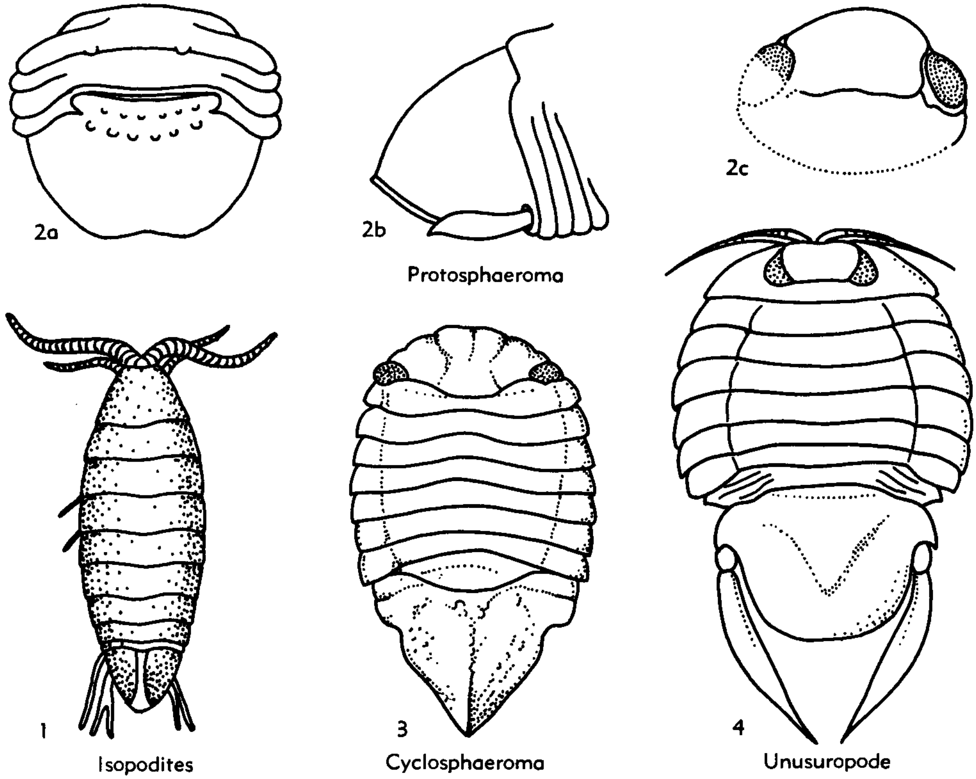


FIG. 195. Flabellifera, Sphaeromidae (p. *R*377-*R*379).

furrows except on 1st. Pleotelson triangular, pointed posteriorly, with lateral emargination for uropods; pleura of single fused pleonite defined by lateral furrows anteriorly; with strong medial ridge; pleura of anterior pleonal unit apparently obsolete, pleotelson and last pereionite coming together laterally. *Jur.*, Eng.-Czech.-Austria.——FIG. 195,*3*. **C. trilobatum*, Eng.; dorsal, ×1 (386b).

Eosphaeroma WOODWARD, 1879, p. 346 [**E. fluviatile*; SD VAN STRAELEN, 1931] [=*Palaeoniscus* MILNE-EDWARDS, 1843]. Body broad, ovoid; cephalon small, much narrower than width of pereion, surrounded posterolaterally by 1st pereionite. Pleotelson subsemicircular, broadly rounded posteriorly; uropods biramous; rami subequal, sickle-shaped. *Oligo.*, Eng.-Fr.-Ger.——FIG. 194,*2*. *E. margarum* (DESMAREST), Fr.-Ger., dorsal, ×3.5 (298).

Heterosphaeroma MUNIER-CHALMAS, 1872, p. 166 [**Sphaeroma priscum* MILNE-EDWARDS, 1868; OD]. Body broad; anterior pleonal unit with single pair of transverse lateral furrows; pleotelson subtriangular, strongly pointed posteriorly, with single pair of lateral furrows anteriorly; uropods apparently uniramous, broad, rounded posteriorly. *L.Eoc.*, Fr.——FIG. 194,*3*. **H. priscum* (MILNE-EDWARDS), dorsal, ×4 (298).

[VAN STRAELEN (298) has misinterpreted the specimen at his disposal. His photograph (Fig. 9 of plate) shows clearly that what he called the fused 6th and 7th pereionites is actually the anterior unit of the pleon, and the part identified by him as cephalon is the 2nd pereionite; the specimen actually lacks a cephalon.]

Isopodites VON AMMON, 1882, p. 536 [**Sphaeroma triasina* PICARD, 1858; OD]. Body elongate, ovoid; cephalon relatively elongate, not surrounded posteriorly by pereionite *1;* pleotelson subtriangular, with median carina; apparently no lateral emargination for uropods, which are biramous, scissors-like. *Trias.*, Ger.——FIG. 195,*1*. **I. triasinus* (PICARD), dorsal, ×4 (373).

[VAN STRAELEN (298) has stated that this species is unrelated to the Sphaeromidae, being more like the Cymothoidae. However, the presence of only a single free pleonal unit anterior to the pleotelson is a strong argument for affinity to the Sphaeromidae.]

Pleistosphaeroma STROUHAL, 1954, p. 57 [**P. hundsheimensis*; OD]. Body strongly vaulted; 1st pereionite with posterolateral furrow which accommodates anterior edge of following pereionite during enrollment; epimeres completely fused to pereionites, rounded laterally; 3 free pleonal somites anterior to pleotelson, which is short, subtrapezoidal, and rounded posterolaterally. *Pleist.*, Austria.——Fig. 194,*4*. **P. hundsheimensis*; *4a*, lat., ×8; *4b*, pleon, dorsal, ×12 (380).

Protosphaeroma Bachmayer, 1949, p. 264 [**P. ernstbrunnense*; OD]. Body strongly vaulted; eyes well developed. Anterior pleonal unit with lateral furrows which demark fused segments that curve anteriorly at their lateral ends; pleotelson short, rounded posteriorly. *Jur.*, Czech.-Austria. ——Fig. 195,*2*. **P. ernstbrunnense*, Austria; *2a,b*, pleon, dorsal, lat., ×13; *2c*, cephalon, dorsal, ×10 (7).

Unusuropode Duarte & Santos, 1962, p. 58 [**U. castroi*; OD]. Cephalon small, set deeply back into pereionite *1;* eyes large; epimeres defined on pereionites *2* to *7;* anterior pleonal unit with 3 pairs of lateral sutures; pleotelson smoothly rounded posteriorly, entire, well vaulted, with strong anteromedial elevation; uropods apparently uniramous, very long, saber-like. *U.Cret.*, Brazil. ——Fig. 195,*4*. **U. castroi*; dorsal, ×10 (83).

Family ARCHAEONISCIDAE Haack, 1918

Characters of type genus. *Jur.*

Archaeoniscus Milne-Edwards, 1843, p. 328 [**A. brodiei*; OD]. Body broad, oval, only moderately vaulted; cephalon subquadrate, sunk deeply into 1st pereionite; eyes located dorsolaterally, of moderate size, prominent; 7 pereionites alike except for 1st; epimeres not defined; pleon as wide as pereion; 4 free pleonites subequal, essentially like pereionites; pleotelson large, subsemicircular. *Jur.*, Eng.-Ger.——Fig. 196,*1*. **A. brodiei*; dorsal, ×2.5 (136).

[The broad, oval body, prominent eyes, absence of defined epimeres, and presence of only 4 free pleonites justifies placement of this monotypic genus in its own family. These are all features commonly occurring in the Oniscoidea, but as Haack (136) has pointed out, the large pleotelson, well-developed antennules and form of antennae and uropods exclude *Archaeoniscus* from the latter suborder.]

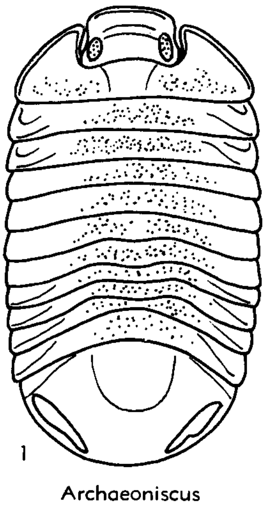


Fig. 196. Flabellifera, Archaeoniscidae (p. *R*379).

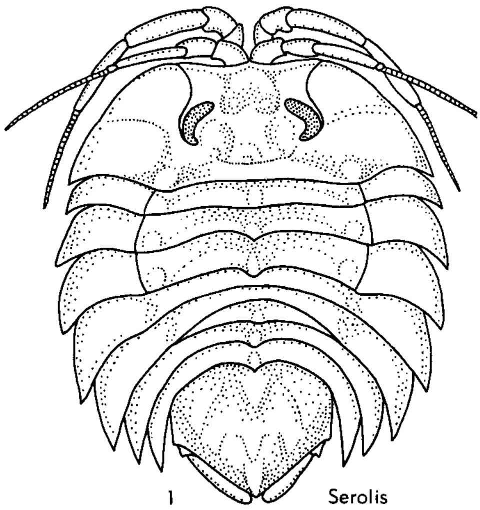


Fig. 197. Flabellifera, Serolidae: *Serolis kempi* Sheppard; ♂, dorsal view, ×3.4 (378).

Family SEROLIDAE Dana, 1852

Body strongly flattened, broad; cephalon sunk deeply into first pereionite and fused to it posteriorly. Both antennules and antennae with well-defined peduncle and multiarticulate flagellum; mandible with palp; maxilliped with three-segmented palp; epimeres of pereionites extensive; tergum of last thoracomere usually absent; second pereiopod in both sexes, third pereiopod in male modified as prehensile organ; pleon composed of four units, three relatively subequal pleonites and one large pleotelson; first three pleopods natatory; fourth and fifth branchial, with outer pair of fourth forming operculum; uropod lateral, with free rami (Fig. 197). *Rec.*, S.Hemis.-N.Pac.-N.Atl.

Family UNCERTAIN

Anhelkocephalon Bill, 1914, p. 338 [**A. handlirschi*; OD]. Much like Serolidae, with number of pleonites reduced; terminal segment large, cephalon deeply embedded in 1st pereionite. *M. Trias.*, Fr.(Alsace).

[This monotypic genus is vaguely characterized and has not been figured. Van Straelen (298) doubted that it should be put in the Serolidae.]

Cymatoga von Eichwald, 1863, p. 416 [**C. jazy-*

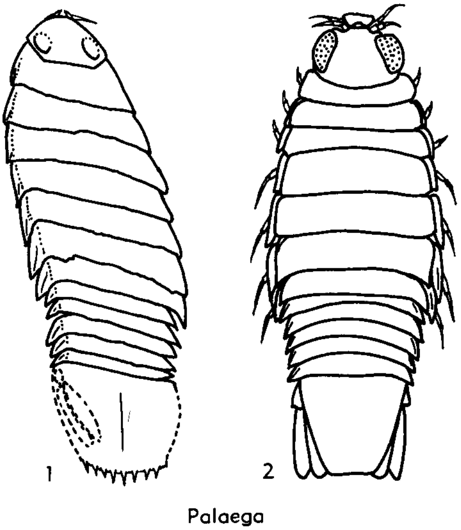


FIG. 198. Flabellifera, Family Uncertain (p. R380).

kowii; OD]. Body very elongate (cephalon lacking); 7 pereionites and 6 free subequal pleonites; pleon narrower than pereion; telson large. *Cret.*, Eu.(USSR).

[This monotypic genus has not been figured. VON EICHWALD claimed that it belongs to the Cymothoidae, and therefore it may be assumed that its body is of the same general facies as seen in *Palaega*.]

Palaega WOODWARD, 1870, p. 496 [*emend.* HESSLER, herein] [**P. carteri*; OD] [=*Aegites* VON AMMON, 1882]. Body elongate, oval; eyes large (where known). Seven free pereionites (where known), not necessarily subequal; epimeres distinct on all but first; pereiopods slender, ambulatory (where known); pleon not abruptly narrower than pereion, may taper posteriorly; five free pleonites subequal, with posteriorly pointed pleura; pleotelson large, commonly with median carina and rounded, posterior margin which may be denticulate; uropods biramous, lamellar. *Jur.-Plio.*, Eu.-N.Am.-Australia. ——FIG. 198,*1*. *P. scrobiculata* VON AMMON, U. Oligo., Austria; dorsal, ×0.5 (340).——FIG. 198, *2*. *P. kessleri* REIFF, L.Jur., Ger.; dorsal (reconstr.), ×2 (375).

[Virtually all fossil flabelliferans having 7 free pereionites and 5 free pleonites have been included in *Palaega*. These fossils cover a range from Jurassic through Pliocene. Many of the species are based on the posterior half of the body, but in *P. kunthi* (VON AMMON) (1882), *P. scrobiculata* VON AMMON (1882), *P. maccoyi* CARTER (1899), *P. jurassica* STOLLEY (1910), *P. danica* VAN STRAELEN (1928), *P. suevica* REIFF (1936), and *P. kessleri* REIFF (1936), the general form of the whole body is known. This body form, particularly that of pleon, is essentially the same in all and plays the major role in diagnosis of the genus. However, this very same body form is found in numerous families of modern flabelliferans (Cirolanidae, Exocorallanidae, Corallanidae, Aegidae, Cymothoidae) (251). These modern groups are discriminated mainly on the basis of appendages which are almost unknown in the fossils. Therefore, it is quite likely that *Palaega* is no more than a form genus. ¶From the literature it appears that *Palaega* can be divided into two groups on the basis of the cephalon. In one, characterized by *P. scrobiculata* (Fig. 198,*1*), *P. kunthi*, *P. jurassica*, and *P. danica*, the cephalon is distinctly sunk back into the first pereionite. Its eyes are dorsally placed. In the other, composed of *P. maccoyi*, *P. suevica*, and *P. kessleri* (Fig. 198,2), the cephalon is smoothly rounded and at the very most is only slightly engulfed by the 1st pereionite. Its eyes are anterolateral. In the 3 latter species the labrum protrudes strongly in front of the cephalon and where known is accompanied by a pair of scythelike mandibles. The palaegids which possess these protruding mouth parts are strongly reminiscent of the Urdidae, differing only in size of the eyes and number of pereionites. REIFF (375) has noted that the mandibles are formed as in the Exocorallanidae, but that the pleotelson differs. ¶VAN STRAELEN (1930) has reported a poorly preserved isopod from the Eocene of Jutland. This he placed in the vicinity of *Aega* LEACH (1815), on the basis of the pleotelson. Such an assignment makes the systematic position of this individual as vague as is that of *Palaega*.]

Suborder VALVIFERA
G. O. Sars, 1882

Uropods modified to form laterally hinged opercula which fold over branchial pleopods like pair of swinging doors. Pleonites more or less fused; peduncle of antennae consisting of five segments; mouth parts normal but mandible usually without palp, and maxilliped commonly with reduced

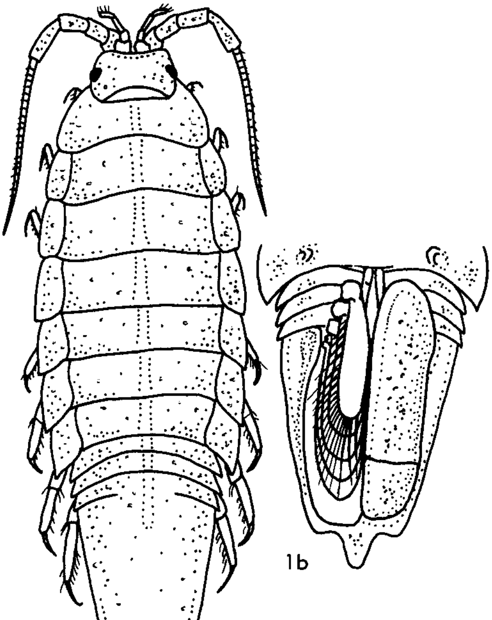


FIG. 199. Valvifera: *Idotea baltica* (PALLAS); *1a*, ♂, dorsal view, ×1.6; *1b*, ventral surface of pleon, with uropod removed to show branchial pleopods in respiratory chamber, ×2 (261b).

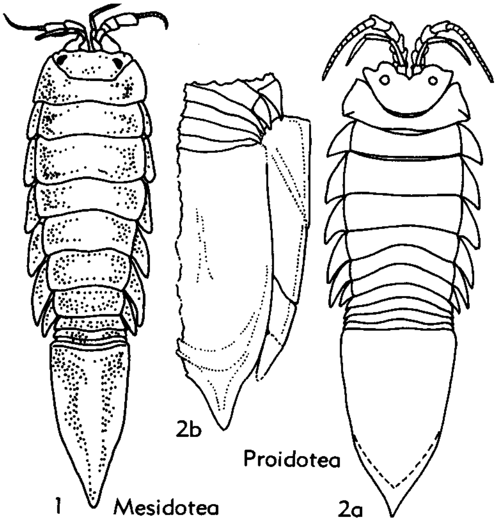


FIG. 200. Valvifera: Idotheidae (Mesidoteinae) (p. *R*381).

number of segments; coxae of pereiopods usually developed as epimeres which are commonly fused to pereion. *Oligo.-Rec.*

Family IDOTEIDAE Leach, 1813

Body somewhat depressed. Pereionites subequal; epimeres distinct in some forms but fused to somites in others; some or all pleonites fused to form large pleotelson; antennule with uniarticulate flagellum; antenna much longer than antennule, with multiarticulate flagellum; mandibular palp lacking; pereiopods increasing in length posteriorly, first four subchelate on some forms, otherwise pereiopods similar to each other (Fig. 199). *Oligo.-Rec.*

Subfamily MESIDOTEINAE Racovitza & Sevastos, 1910

[*nom. correct.* Hessler, herein (*pro* subfamily Mesidoteini Racovitza & Sevastos, 1910)]

Anterolateral angles of cephalon produced into flattened lobes having submedial cleft; eyes dorsal. First pereionite strongly enveloping cephalon laterally; epimeres defined on all pereionites except first; pereiopods distinctly dimorphic, first four subchelate, others ambulatory and longer; first three or four pleonites free; pleotelson more than 0.25 length of body; protopod of uropod at least 0.6 total length of limb, exopod present, rudimentary. *Oligo.-Rec.*

Mesidotea Richardson, 1905, p. 347 [*?type sp.]. Flagellum of antennule with single segment, that of antenna multiarticulate; palp of maxilliped with five segments; pleonite four fused to pleotelson, but distinctly defined; protopod of uropod at least 0.8 total length of limb. *Pleist.-Rec.*, Holarctic-N. Atl.-NE. Pac.-Baltic-Caspian.——Fig. 200,*1*. *M. sabini* Krøyer, dorsal, ×0.7 (359).

Proidotea Racovitza & Sevastos, 1910, p. 194 [**P. haugi*; OD]. Body elongate, tapering only slightly posteriorly; first four pleonites distinctly defined and probably free; protopod of uropod only 0.6 total length of limb. *L.Oligo.-M.Oligo.*, Romania-Pol.——Fig. 200,*2*. **P. haugi*; *2a*, dorsal (reconstr.), ×2.25; *2b*, post. portion of body with uropod, dorsal, ×3 (230).

Suborder ASELLOTA Latreille, 1803

Telson and last five (rarely four or six) pleonites fused into a single unit; anterior pleonites, when free, strongly reduced; one or two of more anterior pleopods forming posteriorly directed operculum over the other pleopods which are branchial in function. Various thoracomeres in some forms fused to each other or to pleotelson; peduncle of antenna consisting of six segments; mouth parts normal; coxae of pereiopods small; uropods subterminal, styliform, commonly biramous (Fig. 201). *Rec.*

Suborder ONISCOIDEA Latreille, 1803

[*emend.* G. O. Sars, 1882]

Body more or less depressed; pleonites rarely fused. Antennules very small, never with more than three segments; peduncle of antennae with five segments; mouth parts normal, but mandible lacking palp and terminal portion of maxilliped reduced; coxae of pereiopods expanded into epimeres which are usually not differentiated from tergites; uropods subterminal, styliform, generally biramous. Terrestrial, pleopods fitted for air-breathing. *Eoc.-Rec.*

Family TRICHONISCIDAE G. O. Sars, 1899

Cannot enroll. Cephalon without frontal line or occipital furrow; supra-antennary

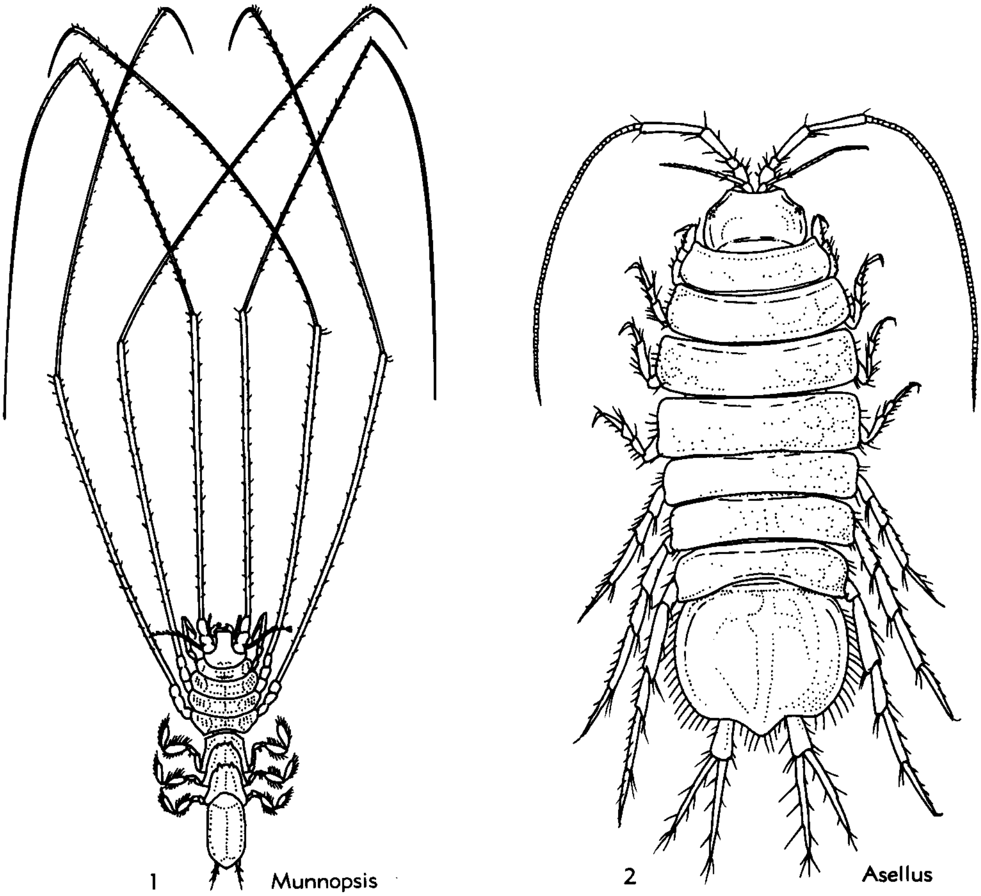


FIG. 201. Asellota: *1, Munnopsis typica* M. SARS; ♂, dorsal view, ×2.7 (261b); *2, Asellus aquaticus* LINNÉ, ♀, dorsal view, ×8 (261b).

line projecting broadly down between antennae nearly to clypeus, and also defining projecting antennary tubercles laterally; marginal line horizontal; clypeus flat, projecting strongly forward; mandible with well-developed molar process; genital apophysis unpaired, with single duct; no pseudotrachea. *U.Eoc.-Rec.*

Subfamily TRICHONISCINAE Verhoeff, 1908

Body smooth or tuberculate, but lacking costae; pleura of pleonites short (transverse) so that pleon is abruptly narrower than pereion. *U.Eoc.-Rec.*

Trichoniscus BRANDT, 1833, p. 174 [**T. pusillus*; OD] [=*Spiloniscus* RACOVITZA, 1908]. Cuticle smooth or scaly, but not granular. Eyes triangular, with 3 ommatidia, rarely reduced. Flagellum of antennae with 3 or 4 poorly defined segments; left mandible with 2 penicilli, right with 1; pleopod *1* of male with triangular exopod lacking setae; endopod developed as 2-jointed paracopulatory organ; pleotelson with narrowly truncate tip. *U.Eoc.-Rec.*, Eu.-N.Afr.-N.Am.——FIG. 202,*3*. **T. pusillus*; dorsal, ×11 (261b).

Family ONISCIDAE Dana, 1852

[*emend.* VERHOEFF, 1918]

Cannot enroll (with rare exceptions). Eyes generally well developed; triturating molar process of mandible replaced by brushlike setae; genital apophysis unpaired, with paired ducts and exit pores; pseudotrachea absent; uropod extending beyond posterior end of body; tip of pleotelson conically produced. *U.Eoc.-Rec.*

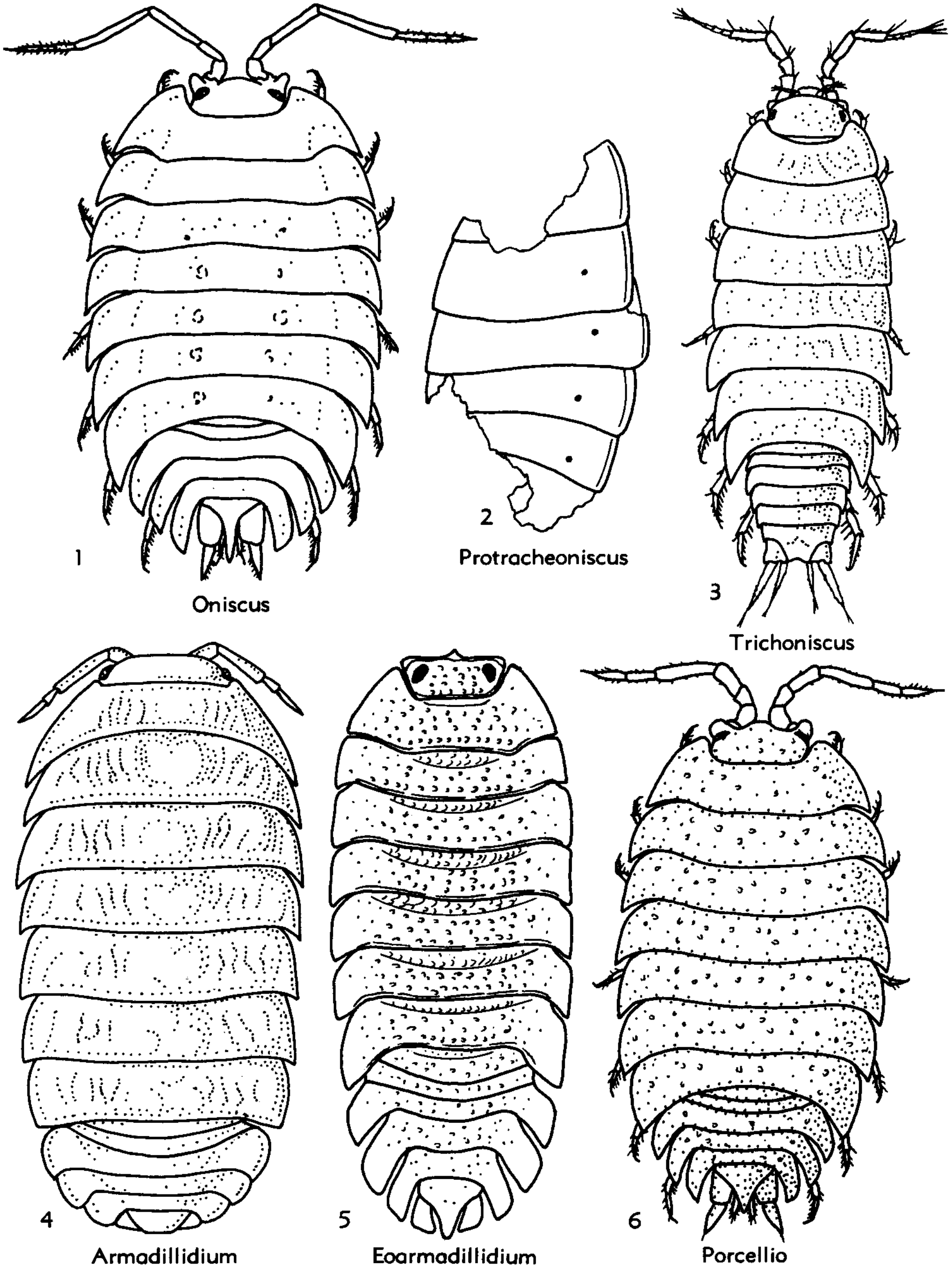


FIG. 202. Oniscoidea; Trichoniscidae (Trichoniscinae) *(3)*; Oniscidae (Oniscinae) *(1)*; Porcellionidae *(2,6)*; Armadillidiidae *(4-5)* (p. *R*382-*R*384).

Subfamily ONISCINAE Vandel, 1952

Cephalon with strongly developed frontal line defining pair of lateral lobes and single median frontal lobe. Flagellum of antennae with three segments; glandular field on epimeres generally ovoid and reduced; pleura of pleonites large, causing outline of pleon to be continuous with that of pereion; genital apophysis simple. *U.Eoc.-Rec.*

Oniscus LINNÉ, 1758, p. 636 [**O. asellus;* SD DESMAREST, 1859]. Cephalon with indistinct supra-antennary line. Mandible with 3 to 5 penicilli; posterior margin of anterior pereionites strongly sinuous, forming acute posterolateral angles; epimeres large; articular process on pereionites *1-4;* lateral edge of pleopodal exopods bearing well-differentiated respiratory region; pleotelson tapering to long narrow point. *U.Eoc.-Rec.,* Eu.——FIG. 202,*1*. **O. asellus*; dorsal, ×2.7 (261b).

Family PORCELLIONIDAE Verhoeff, 1918

Usually cannot enroll; where enrollment is possible, system is primitive. Flagellum of antennae with two or three segments; molar process of mandible reduced to brushlike setae; genital apophysis unpaired, with paired ducts and exit pores; pseudotrachea present; uropods extending beyond posterior end of body; tip of pleotelson conically produced. *U.Eoc.-Rec.*

Porcellio LATREILLE, 1804, p. 45 [**P. scaber*; SD ICZN Opinion 104, 1928]. Cuticular granulation distinct to absent. Cephalon without supra-antennary line; frontal line distinct, defining more or less developed median lobe and well-developed lateral lobes; eyes large; antennae long. Pleura of pleonites large, so that margin of pleon is continuous with that of pereion; pseudotrachea on exopods of pleopods *1* and *2* only; produced terminal portion of pleotelson usually distinctly defined from basal portion. *U.Eoc.-Rec.,* N.Am.-Central Am.-Eu.-N.Afr.-AsiaM.——FIG. 202,*6*. **P.* scaber; dorsal, ×3.3 (261b).

Protracheoniscus VERHOEFF, 1917, p. 211 [*?type-sp.]. Tergites smooth, not granulate. Cephalon without supra-antennary line; frontal line defining pair of small or medium-sized lateral lobes; median lobe not developed. Posterior margin of pereionites *1* and *2* rounded, not sinuous; all pleopodal exopods with weakly developed pseudotracheal system; exopod of pleopod *1* in male longer than wide. *?Pleist.-Rec.,* Asia-Japan-Philippines-Eu.——FIG. 202,*2*. *P.* sp. cf. *P. amoenus* KOCH, Pleist., Austria; fragment of pereion, dorsal, ×7.5 (380).

Family ARMADILLIDIIDAE Brandt, 1833

Median genital apophysis with paired ducts and exit pores; pseudotrachea in exopods of pleopods one and two only. Capable of complete enrollment and possessing many specializations related to this function: body very convex; cephalon enlarged transversely so that insertions of antennules and antennae widely separated; in enrollment two-jointed antennae rest against median scutellar lobe and in grooves formed by pair of lateral antennary lobes; primary marginal line almost completely obliterated in favor of secondary one; pleurepimeres fitted with specialized tongue-and-groove system; pleotelson broadly triangular or truncate; appendages generally short; uropodal exopod enlarged and flattened to fill gap between pleonite five and pleotelson. *Mio.-Rec.*

Armadillidium BRANDT, 1833, p. 184 [**Armadillo vulgare* LATREILLE, 1804; SD ICZN Opinion 104, 1928] [=*Uropodias* RICHARDSON, 1902; *Armadillo* CUVIER, 1792]. Cephalon with vertex separated from frontal region by parallel frontal and postscutellar lines. Posterior edge of epimere of pereionite *1* rarely with horizontal cleft (schisma); uropodal endopod short, not extending beyond posterior border of telson. *Mio.-Rec.,* Medit.-C.Eu. ——FIG. 202,*4*. **A. vulgare* (LATREILLE); dorsal, ×3.7 (261b).

?**Eoarmadillidium** DOLLFUS, 1904, p. 146 [**E. granulatum*; OD]. Body moderately convex, slightly spread out laterally; cephalon with triangular median lobe. Pleotelson triangular; uropod with platelike exopod. *Pleist.,* Fr.——FIG. 202,*5*. **E. granulatum*; dorsal, ×5.4 (354).

[This genus may not be a member of the Armadillidiidae in spite of its spatulate uropods. The flattened body and the form of the cephalon are more reminiscent of *Porcellio* than of *Armadillidium* (291).]

Suborder PHREATOICIDEA Stebbing, 1893

Body more or less laterally flattened. Pleonal somites free, but telson fused to last somite; mouth parts normal; peduncle of antennae with five segments; second thoracopod subchelate; second to fifth thoracopods directed forward, sixth to eighth directed backward; coxae of thoracopods not expanded into epimeral plates; pleopods subequal, natatory as well as respiratory; uropod posterolateral, biramous, locomotory. *Perm.-Rec.*

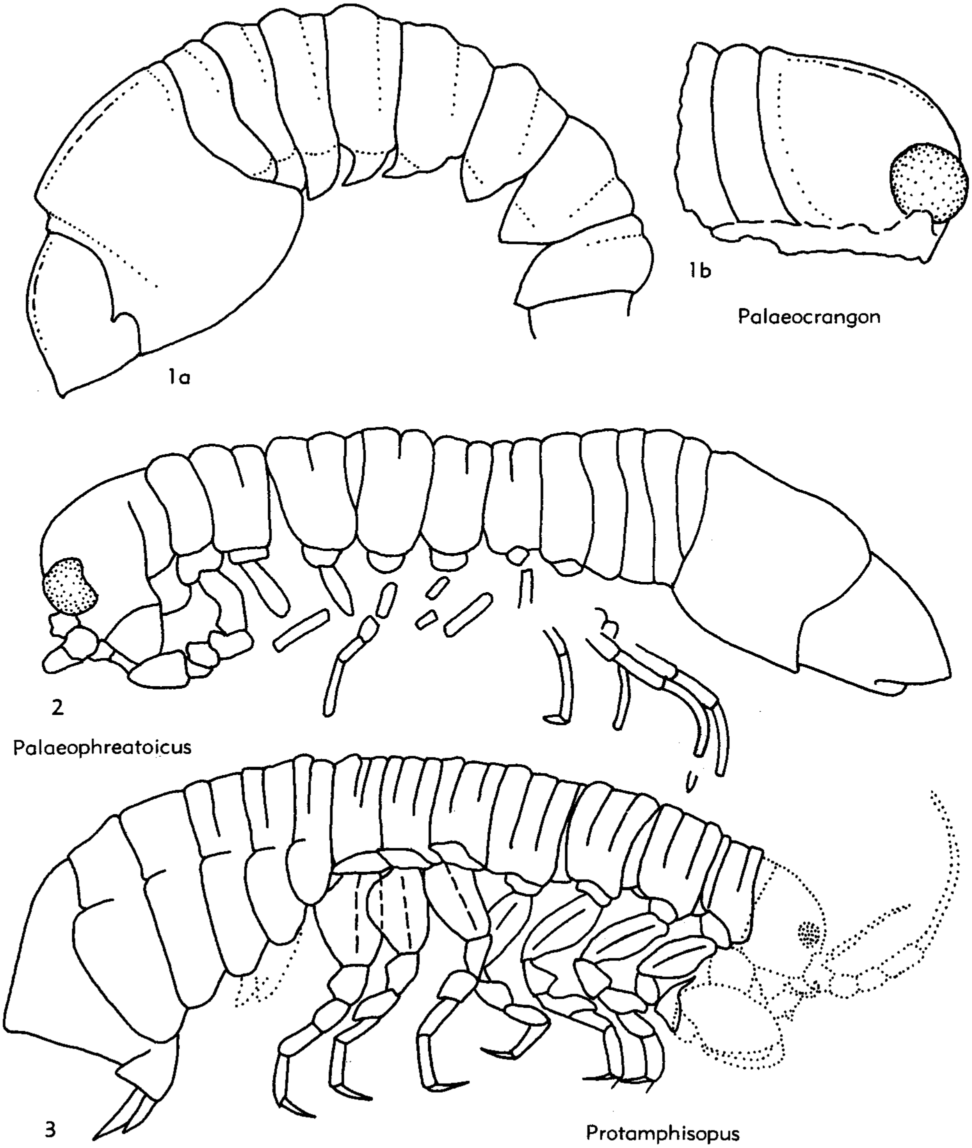


FIG. 203. Phreatoicidea; Amphisopidae *(3)*; Palaeophreatoicidae *(1-2)* (p. *R*385-*R*386).

Family AMPHISOPIDAE Nicholls, 1943

Lacinia mobilis on both mandibles. Head relatively short; eyes (when present) prominent, many-faceted. Telson only slightly produced into terminal projection or not at all; coxae of pereiopods generally fused with pleura; basis of more posterior pereiopods usually well expanded. *Trias.-Rec.*

Protamphisopus NICHOLLS, 1943, p. 109 [**Phreatoicus wianamattensis* CHILTON, 1917; OD]. Pereionites deeper than long, some with marked transverse ridge; transition to pleon abrupt, pleonites being extremely deep; bases of at least last 5 pereiopods well expanded; ischia relatively shorter than in Recent forms; merus produced strongly downward on 3rd and 4th pereiopods; 3rd to 6th pereiopods apparently subequal; uropod very short,

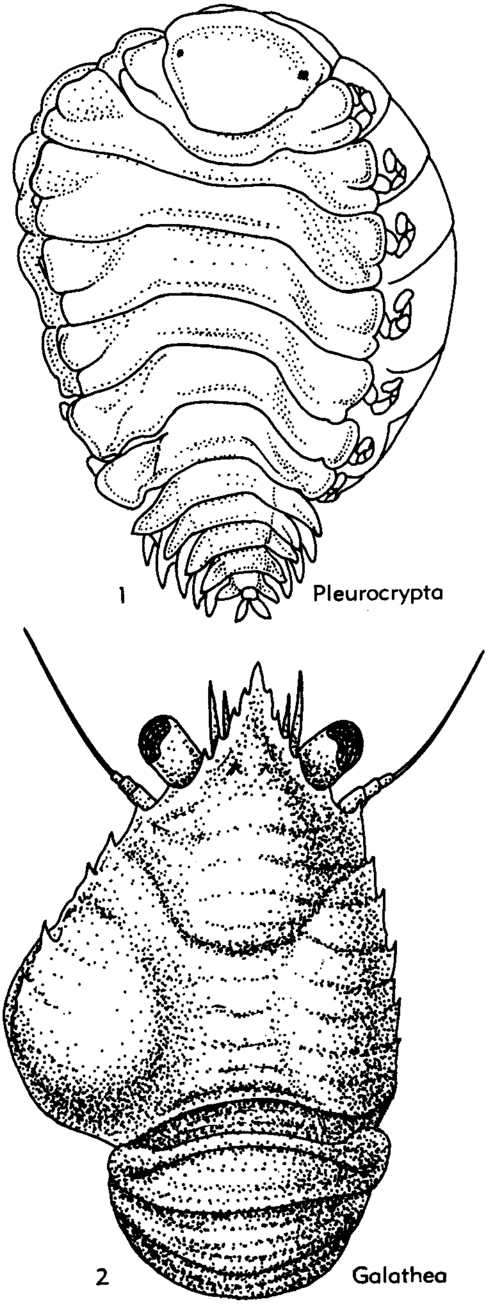


Fig. 204. Epicaridea: 1, *Pleurocrypta microbranchiata* G. O. Sars; ♀, dorsal view, ×12 (261b); *2*, dorsal view of decapod *Galathea intermedia* Lilljeborg showing left branchial cavity swollen to accommodate an individual of the epicaridean species *Pleurocrypta microbranchiata,* enlarged (261b).

with short peduncle expanded distally. *Trias.,* Australia.——Fig. 203,*3*. **P. wianamattensis* (Chilton); lat. (reconstr.), ×2.4 (211).

Family PALAEOPHREATOICIDAE Birshteyn, 1962

Head relatively long, with deep vertical cervical furrow; eyes very large, protruding anteriorly. First pereionite not expanded ventrolaterally; coxae of pereiopods not fused to pleura; fifth pleonite extremely enlarged; pleotelson large, pointed, but telsonic projection not defined. *Perm.*

Palaeophreatoicus Birshteyn, 1962, p. 66 [**P. sojanensis;* OD]. Body cylindrical; pleonites *1* to *4* shorter than pereionites, which bear transverse furrows. *U.Perm.,* Eu.(Ger.-USSR).——Fig. 203, *2*. **P. sojanensis,* lat. (holotype), ×8 (43).

Palaeocrangon von Schauroth, 1854, p. 560 [**Trilobites problematicus* von Schlotheim, 1820; OD] [=*Prosoponiscus* Kirkby, 1857 (*non Palaeocrangon* Salter, 1861)]. Body laterally compressed, with mid-dorsal keel; pereionites and 1st 4 pleonites subequal in length; anterior pleonites with triangular pleurae. *Perm.,* Eu.(Eng.-Ger.).——Fig. 203,*1*. **P. problematicus* (Schlotheim); *1a,* pleon and posterior portion of pereion (composite reconstr.), ×7.2 (356); *1b,* cephalon and 1st 2 pereonites, lat., ×6.4 (362).

[The systematic position of this monotypic genus has been the subject of much disagreement. Indeed, it has been placed with the trilobites, decapods, amphipods, and isopods. Most recently Glaessner (1957) and Birshteyn (43) have argued for phreatoicid affinities.]

Suborder EPICARIDEA Latreille, 1831

[=Bopyroidea Richardson, 1904]

Ectoparasitic on other Crustacea (Copepoda, Ostracoda, Mysidacea, Euphausiacea, Isopoda, Amphipoda, parasitic Cirripedia, and Decapoda). Sexual dimorphism marked, female greatly modified, often asymmetrical and some lacking segmentation or appendages; male comparatively diminutive. Mouth parts suctorial and reduced or absent; thoracopods (when present) are prehensile; pleopods of adult all branchial. Development in form of regressive metamorphosis (Fig. 204). *?U.Jur., Rec.*

Adult female Epicaridea may be so specialized that in some groups they are no more than nearly formless sacs of eggs. Adult males and larvae of both sexes are more normal in form and are much like

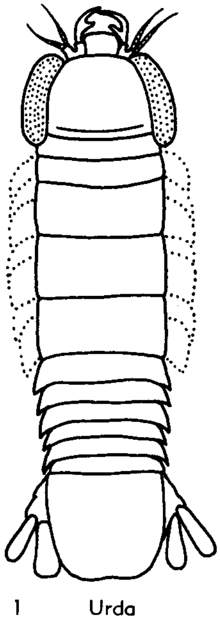


FIG. 205. Isopoda Suborder Uncertain; Urdidae (p. *R*387).

Flabellifera. Epicarideans exhibit a degree of host specificity. For instance, the Bopyridae are parasitic on Decapoda, and the various genera of Cryptoniscidae parasitize Ostracoda, Cirripedia, Mysidacea, Cumacea, Isopoda, or Amphipoda (337).

Where found in the branchial cavity of the host, the carapace of the latter may become asymmetrical distended to accommodate the parasite (Fig. 204,2). Such abnormally swollen carapaces have been found in a number of species of Decapoda from the Upper Jurassic and the Cretaceous of England, Germany, France, and Czechoslovakia. They are regarded as indicating the presence of epicarideans during these periods (6, 298, 314b).

Suborder UNCERTAIN

Family URDIDAE Kunth, 1870

[*nom. correct.* HESSLER, herein (*pro* Urdaidae KUNTH, 1870)]

Characters of type genus. *Jur.-Cret.*

KUNTH (1870) placed this family between the Anceidae (=Gnathiidea) and Cymothoidea (Flabellifera). MONOD (205) denied its affinity to the Gnathiidae, claiming that the missing pereionites of *Urda* are probably merely hidden from view. He included the Recent genus *Gnatholana* BARNARD (1920) in the Urdidae because it also possesses protruding mandibles and labrum, and he placed the family close to the cymothoids. MENZIES (1962) has considered the Gnathiidae to be derived from a cirolanid ancestor, with *Urda* being related to an intermediate form; *Gnatholana* was judged to be a relict that descended from this *Urda*-like ancestor.

Urda MÜNSTER, 1840, p. 21 [*emend.* HESSLER, herein] [**U. rostrata*; SD OPPEL, 1862] [=*Reckur* MÜNSTER, 1842]. Body elongate, with subparallel sides; cephalon large, not surrounded posteriorly by 1st pereionite; eyes lateral and very large, usually equal to the length of cephalon; labrum extending anterior to cephalon. Mandibles prominent, pincer-like, extending anteriorly beyond labrum; 6 pereionites; epimeres free; pleon slightly narrower than pereion, with 5 free, subequal pleonites and large, flat pleotelson; uropods biramous, lamellar. *Jur.-Cret.*, Eu.(Fr.-Ger.-Czech.).——FIG. 205,*1*. **U. rostrata*, dorsal, ×2.2 (363).

[MÜNSTER (1840), KUNTH (1870), REMES (1912) and VAN STRAELEN (298) claim that *Urda* has only 5 free pereionites. The first-mentioned three authors stated that the pleon has 6 free pleonites. STOLLEY (285) reported 6 pereionites and 5 free pleonites on *U. cretacea*, the last pereionite being smaller than the 5th and such that it might be confused as a pleonite in poorly preserved material.]

ISOPODA INCERTAE SEDIS

Two fossil isopod species, both from the Jurassic of Bavaria, which have never been figured and are too poorly described to be diagnosed are *Sphaeroma antiqua* DESMAREST (1822) and *Neosoma edwardsii* OPPEL (1865). The latter genus is monotypic.

Order AMPHIPODA Latreille, 1816

First and second thoracomeres in some fused to cephalon; no distinct carapace fold; eyes sessile, unstalked (except in Ingolfiellidea). Antennules commonly biramous; antennae uniramous, with five-segmented peduncle. Thoracopods lacking exopods, some with branchiae; coxae short, but they may be expanded into plates which are more or less fused to body; first thoracopods modified as maxillipeds, next two commonly subchelate gnathopods; forms with pleon not reduced bearing pleopods with multiarticu-

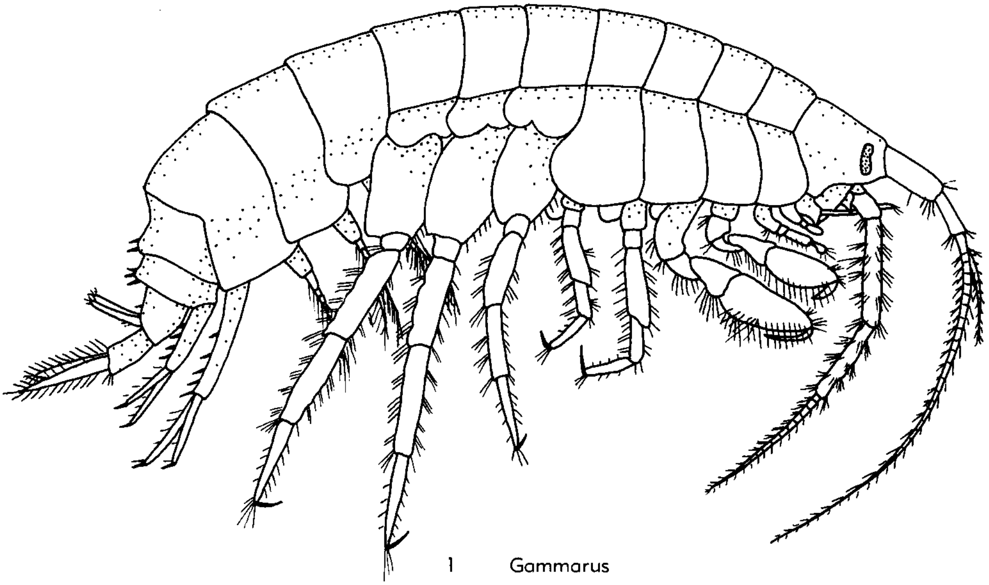


FIG. 206. Gammaridea, Gammaridae (p. R390).

late rami on first three somites and usually uropods with unsegmented rami on last three somites; telson usually not fused to last pleonite. Young leave marsupium with full number of appendages. *U.Eoc.-Rec.*

Amphipods are dominantly marine, occurring at all depths. Of the three major suborders, only the Gammaridea include freshwater and even terrestrial representatives. More than one-third of the known freshwater forms are found in Lake Baikal. Because of the long history and isolation of this lake, a small initial gammaridean stock located there is judged to have undergone extensive taxonomic differentiation, resulting in more than 290 species which live in Lake Baikal today (59).

The Hyperiidea are exclusively pelagic and commonly live a predaceous existence. Within the Caprellidea, the Cyamidae live as ectoparasites on whales, whereas the Caprellidae are epifaunal, being found on seaweed, hydroids, and other living substrata. A few Gammaridea are truly pelagic; most are benthic, but possess the ability to swim. The majority of these benthic forms are detritus- or filter-feeders and may build a large variety of burrows or tubes in pursuit of these ends. Gammarideans may also be epifaunal herbivores.

About 4,000 species of amphiopods are known, and by far the greatest majority of these are gammarideans. This suborder is striking because, in relation to its large species composition and wide range of environments occupied, it displays a relatively small degree of morphological diversity. Thus, in the taxonomy of the Gammaridea minor structural differences play an important role, even at high taxonomic levels. This fact should be kept in mind when evaluating the placement of fossil forms in Recent genera.

Most amphipod groups are cosmopolitan in distribution but the Ingolfiellidea are as yet known only from Europe, North Atlantic, South America, Africa, and the South China Sea.

Suborder GAMMARIDEA Latreille, 1803

[=Crevettina CLAUS, 1880 (*pro* Crevettines MILNE-EDWARDS, 1830)]

First thoracomere only fused to cephalon; maxillipeds with palp; coxae of thoracopods two to eight usually giving rise to large plates; body usually appearing to be laterally flattened; all pleonites well developed, free; three pairs of pleopods and three pairs of uropods well developed; eyes rarely very large. *U.Eoc.-Rec.*

Family GAMMARIDAE Leach, 1814

Body more or less slender; pleonites four to six usually well defined. Antennules and antennae generally rather slender, usually similar in both sexes; accessory flagellum of antennule well developed in many forms but may be reduced or absent; mouth parts normal; labrum with distal border rounded, entire, or only slightly emarginate; labium with inner lobes well developed, poorly defined, or absent; mandibles with well-developed gnathic structures and three-segmented palp, second segment of palp almost never smaller than first; maxillules with both endites and palp well developed; gnathopods generally rather powerful, rarely less than subchelate; pereiopods more or less slender,

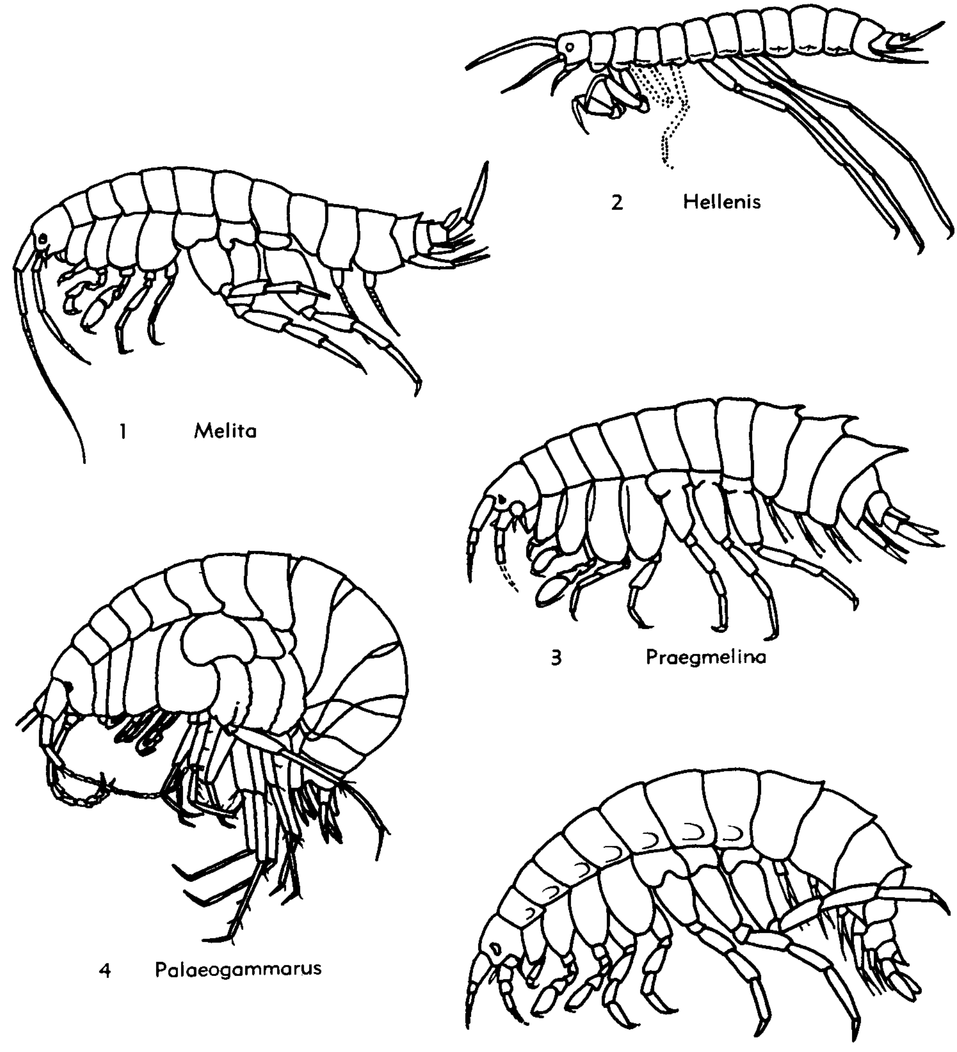


Fig. 207. Gammaridea, Gammaridae (p. *R*390).

few with basis little expanded in last three pereiopods; pleopods only rarely uniramous; uropod *3* rarely losing one or both rami, which are often foliaceous, usually projecting beyond uropods *1* and *2;* telson either entire, partially cleft, or cleft to base, in some forms sexually dimorphic. *U.Eoc.-Rec.*

Gammarus Fabricius, 1775, p. 418 [**Cancer pulex* Linné, 1758; SD ICZN Opinion 104, 1928]. Cephalon without distinct rostrum; body lacking carinae, teeth, and tubercles; dorsal spicules in median and lateral groups on pleonites *4* to *6*. Antennules usually longer than antennae but with shorter peduncle; accessory flagellum with 1 to 4 segments; basal endite of maxillules with continuous row of strong, plumose setae on inner margin; outer lobe with 10 or 11 serrate spines; tip of right palp with short thick spines, those of left palp being longer, thinner; coxal plates *1* to *4* usually deep, 4th with distinct lobe occupying distal portion of posterior border, gnathopods subchelate, 2nd usually larger than 1st, both stronger in male; 3rd uropods large, biramous; exopods with 2 segments, 2nd being short; telson deeply cleft. Branchiae simple. [Boreal-temperate-subtropical.] *?U.Eoc.,* Rec.——Fig. 206,*1*. *G. locusta* (Linné); lat., ×6 (261a).

[None of the various reports compiled by Van Straelen (299) and Maïkovsky (185) claiming the occurrence of *Gammarus* in the fossil record is convincing. Undoubtedly the fossils in question belong to the Gammaridea but need to be studied in far greater detail before trustworthy generic determinations can be made.]

Andrussovia Derjavin, 1927, p. 190 [**A. sokolovi*; SD Birshteyn, 1960]. Rostrum small; 1st 3 pleonites and in one species posterior pereionites dorsally carinate; pleonites *2* and *3* with subquadrate posterolateral corners; antennules and antennae short, subequal, accessory flagellum apparently absent; gnathopods alike, subchelate; coxal plates *1* to *4* large, deep; basis of last 3 pereiopods scarcely expanded; uropod *3* comparatively long, endopod well developed. *M.Mio.,* USSR (Caspian).——Fig. 207,*5*. **A. sokolovi,* lat., ×5.4 (353).

Hellenis Petunnikov, 1914, p. 153 [**H. saltatorius*; OD] [=*Prionchelius* Petunnikov, 1914; *Tetrachelius* Petunnikov, 1914]. Body slender; antennules and antennae short, antennules being longer; coxal plates *1* to *4* small, shallow; gnathopods subequal, large with proximal end of propodus slender; last 3 pereiopods long, slender; uropod *2* short; uropod *3* much longer. *L.Mio.,* USSR(Caspian).——Fig. 207,*2*. **H. saltatorius,* lat., ×15 (345).

Melita Leach, 1814, p. 403 [**Cancer palmatus* Montagu, 1804; OD]. Cephalon not rostrate. Pereion smooth; pleon usually with one or more segments dorsally dentate and armed with bristles; antennules longer, more slender than antennae, with accessory flagellum; mouth parts normal; several setae on basal endite of maxillules, 11 setae on more distal endite; 1st gnathopods small, subchelate, 2nd larger, in some species with left and right unequal in males, in some nearly chelate; 4th coxal plate largest, emarginate posteriorly; basis of last 3 pereiopods well expanded, last 2 subequal, longer than others; 2nd uropod shortest; 3rd largest by far, with very large exopod and tiny endopod; telson small, deeply cleft. [Maïkovsky (185) has reported *M. palmata* from the Lower Oligocene of Alsace.] *L.Oligo.-Rec.,* cosmop.——Fig. 207,*1*. **M. palmata* (Montagu), L.Oligo., Rec., lat., ×7 (261a).

Palaeogammarus Zaddach, 1864, p. 10 [**P. sambiensis*; OD]. Antennules longer than antennae, with thick 1st peduncular segment and accessory flagellum of 2 segments; coxal plates *1* to *4* very deep; gnathopods subequal, subchelate; propodus rounded; last pereiopod shorter than preceding one; basis of last 3 pereiopods expanded, oval; 4th and 5th pleonites with marginal denticles posteriorly; uropod 3 short, biramous; endopod reduced; telson deeply cleft. [According to Bousfield (personal communication) this genus is much like *Crangonyx* Bate.] *U.Eoc.(Baltic amber).*——Fig. 207,*4*. *P. balticus* Lucks; lat., ×15 (365).

Praegmelina Derjavin, 1927, p. 187 [**P. andrussovi*; SD Birshteyn, 1960]. Cephalon without conspicuous rostrum; pereion with pair of low lateral ridges formed from single pair of prominences on each somite; 1st 3 pleonites dorsally carinate; 2nd and 3rd with acutely produced posterolateral corners; antennules and antennae short, subequal, accessory flagellum not obvious; mouth parts apparently normal; gnathopods subequal, subchelate, small; coxal plates large and deep; basis of last 3 pereiopods not expanded; uropod *3* of moderate size with well-developed endopod. *M.Mio.,* USSR(Caspian).——Fig. 207,*3*. **P. andrussovi,* lat., ×2.5 (353).

Suborder CAPRELLIDEA Leach, 1814

[=Laemodipoda Latreille, 1817]

First and second thoracomeres fused to cephalon; palp of maxilliped usually present; thoracopods four and five nearly always vestigial or absent; coxae of thoracopods small, commonly fused to body; pleon strongly reduced, with appendages vestigial or absent; body either slender and very elongate, or dorsoventrally flattened; eyes small. *Rec.*

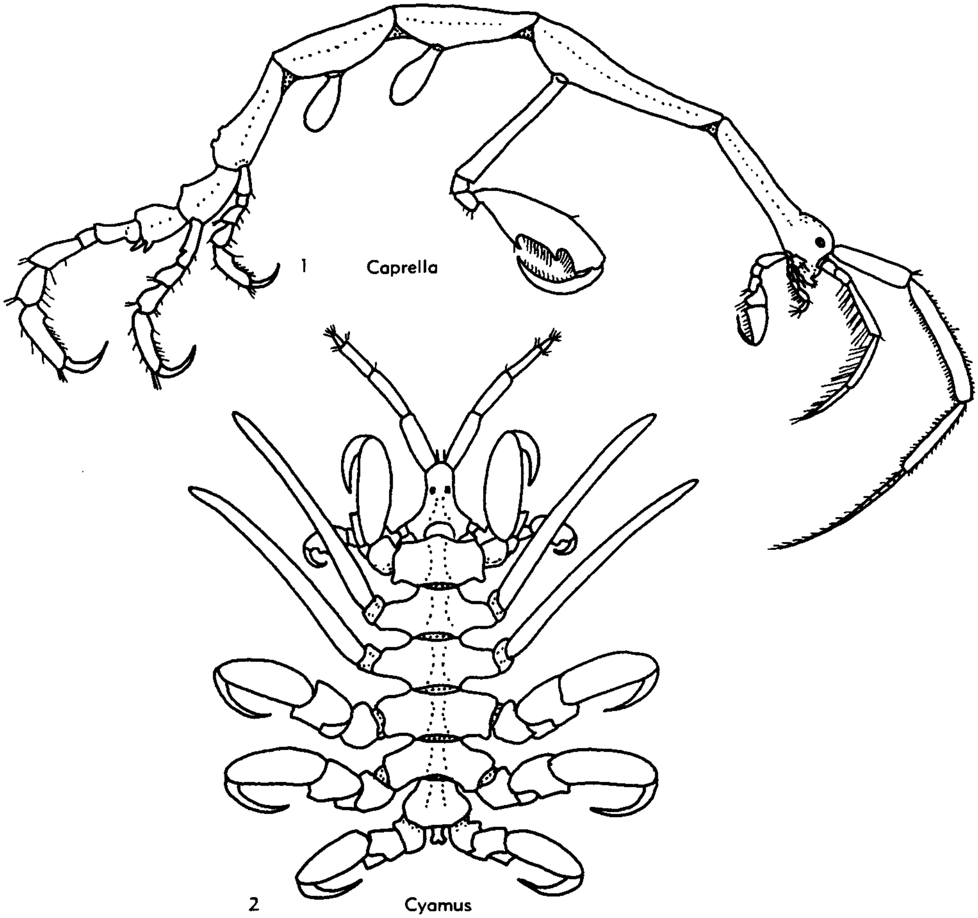


FIG. 208. Caprellidea: *1, Caprella linearis* (LINNÉ) (Caprellidae); ♀, lat. view, ×5.2 (261a); *2, Cyamus boopis* LÜTKEN (Cyamidae); ♂, dorsal view, ×3 (261a).

This suborder consists of two families, the Caprellidae DANA (1852), which are free-living forms (Fig. 208,*1*), and the Cyamidae WHITE (1847), which are ectoparasites on whales (Fig. 208,*2*).

Suborder HYPERIIDEA Latreille, 1831

First thoracomere fused to cephalon; maxilliped without palp; coxae of thoracopods two to eight small or fused to body; head usually enlarged, conspicuous; eyes generally very large, commonly covering most of surface of head; pleon well developed; pleonites generally free with appendages well developed (Fig. 209). *Rec.*

Suborder INGOLFIELLIDEA Hansen, 1903

First thoracomere fused to cephalon; maxillipeds with palp; coxae of thoracopods two to eight small; body elongate; articulated eye lobes may occur, but without visual surfaces; pleon well developed; pleonites free; pleopods one to three and uropod three vestigial (Fig. 210). *Rec.*

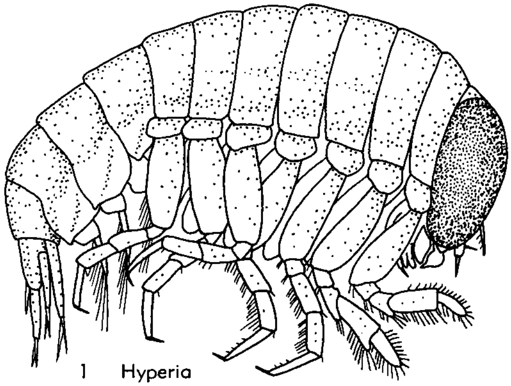


Fig. 209. Hyperiidea: *Hyperia medusarum* Müller; ♀, lat. view, ×3.9 (261a).

Suborder UNCERTAIN

Tracks or burrows supposed to have been made by amphipods have been reported from the Devonian (Dahmer, 1938), Triassic (Rücklin, 1938), and Jurassic (Putzer, 1938; Weiss, 1940) of Germany.

Order ANTHRACOCARIDACEA Brooks, 1962

Carapace short, covering only first two thoracomeres; sixth pleonite not fused to telson. *Miss.*

Brooks (55), following Calman (1933), has placed this order tentatively in the Peracarida. The general form of its carapace and body suggests possible affinity with the Tanaidacea, Spelaeogriphacea, or Thermosbaenacea and indeed may prove eventually to belong to one of the extant orders.

Family ANTHRACOCARIDIDAE Brooks, 1962

Characters of order. *Miss.*

Anthracocaris Calman, 1933, p. 562 [**Palaeocaris scoticus* Peach, 1882; OD]. Posterolateral expansions of cephalic shield defined by dorsolateral furrows, indicating probable branchial chambers; pleon not abbreviated, not clearly differentiated from pereion; telson large, styliform. *L.Carb.*, Scot.——Fig. 211,*1*. **A. scotica* (Peach); dorsal, ×3 (348b).

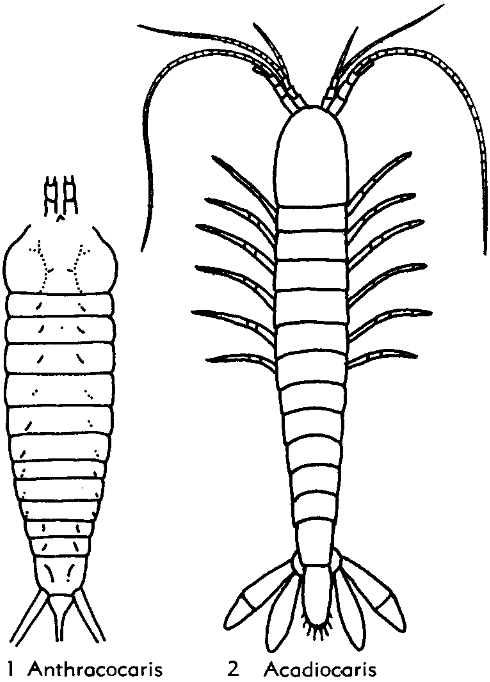


Fig. 211. Anthracocaridacea; Anthracocarididae (p. *R*392-*R*393).

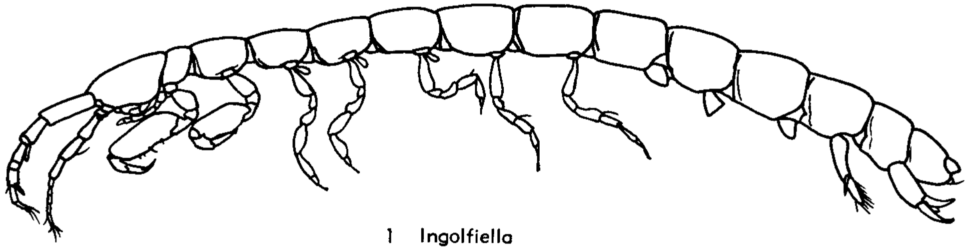


Fig. 210. Ingolfiellidea: *Ingolfiella abyssi* Hansen; lat. view, ×33 (360).

Acadiocaris Brooks, 1962, p. 273 [**Palaeocaris novascotica* Copeland, 1957; OD]. Telson spatulate; uropods with narrow, lobate, leaflike rami. *M.Miss.*, Can.——Fig. 211,2. **A. novascotia* (Copeland); dorsal (reconstr.), ×5 (Hessler, n).

PERACARIDA INCERTAE SEDIS

A number of fossils from Europe and North America which have been referred to peracaridan orders either clearly do not belong to them or they are so fragmentary that the evidence for classifying them is insufficient (55, 299). Such fossils are: *Houghtonites* [*Mollisonia*] *gracilis* Walcott (1912) from the Cambrian; *Necrogammarus salwayi* Woodward (1871), from the Silurian; *Oxyuropoda ligioides* Carpenter & Swain (1908), *Gitocrangon granulatus* Richter (1848), *Praearcturus gigas* Woodward (1871), and *Palaeoisopus problematicus* Broili (1928) from the Devonian; *Camptophyllia eltringhami* Gill (1924), *Diplostylus dawsoni* Salter (1863), and *Amphipeltis paradoxus* Salter (1863) from the Carboniferous; *Diaphanosoma rare* Bill (1914) from the Triassic; *Mysis steinlai* Geinitz (1843) from the Cretaceous; and *Opsipedon gracilis* Heer (1865) and *Norna lithophila* Münster (1840) from the Jurassic.

EUCARIDA

By R. C. Moore

Superorder EUCARIDA Calman, 1904

Highly developed eumalacostracans having carapace fused dorsally with all thoracic somites, compound eyes located on movable stalks, adults without lacinia mobilis on mandibles, eggs usually attached to abdominal appendages, young typically developing with metamorphosis, free-swimming nauplius stage in primitive forms. *Permotrias.-Rec.*

The Eucarida comprise the host of decapods—unnumbered kinds of shrimps, crayfishes, lobsters, and crabs—and the cosmopolitan oceanic nektonic crustaceans known as euphasiaceans, which are a very important food source for whales. Among decapods, the caridoid facies may be retained by adults, but the body shape and nature of appendages is greatly modified in crabs. The gills of decapods generally are developed in several series, all protected by the carapace. Three pairs of their thoracic limbs are specialized as maxillipeds. The young generally hatch at a postnauplius stage. In euphausiaceans the gills occur in a single exposed series and none of the pereiopods are developed as maxillipeds. Instead, all may be specialized for filter-feeding.

EUPHAUSIACEA

By ROBERT R. HESSLER
[Woods Hole Oceanographic Institution]

ADULT MORPHOLOGY

All euphausiaceans conform to a narrowly circumscribed morphological pattern. The general body form is prawnlike (Fig. 212). The carapace, which is fused to all thoracic somites, is usually divided by a cervical furrow and terminates anteriorly in a short or moderately produced rostrum. Pleura, in contrast to those of the Decapoda, are weakly developed and do not enclose branchial chambers. They occur on all but the last of the abdominal somites.

The antennules consist of two flagella and a three-segmented peduncle. The antennae are composed of a two-segmented protopod, endopodal flagellum, and exopodal scaphocerite. The uniramous mandibles usually are provided with three-segmented palps. Their gnathal lobes lack saw bristles and lacinia mobilis. The three-segmented main body of the maxillules is produced medially into two endites and rather commonly bear a pseudoexopod laterally. The palp of maxillules is unjointed in all genera except *Bentheuphausia*, where it consists of two segments. The maxillae are composed of a three-segmented protopod, with endites on the second and third segments, an exopod, and a palp. The palp is a single segment except in *Bentheuphausia* where it is three-segmented. Paragnaths are well developed.

All thoracic limbs are basically similar in structure (Fig. 213). Coxa and basis are distinct from each other and bear medial endites which are more strongly developed on the anterior thoracopods, but not to such a degree as to constitute gnathobases. Except where reduction has occurred, all limbs bear a leaflike, two-segmented exopod furnished with long, natatory setae. The five-segmented endopod is much larger and carries medially directed setae. Its knee occurs between the second and third segments. In all euphausiaceans except *Bentheuphausia* the eighth thoracopod is markedly reduced. The seventh thoracopod is also reduced in many members of the Euphausiidae.

Raptorial structures have been derived from the modification and elongation of the second thoracic endopod in *Thysanoessa* and *Nematoscelis*, the third thoracic endopod in *Nematobrachion* (Fig. 214) and

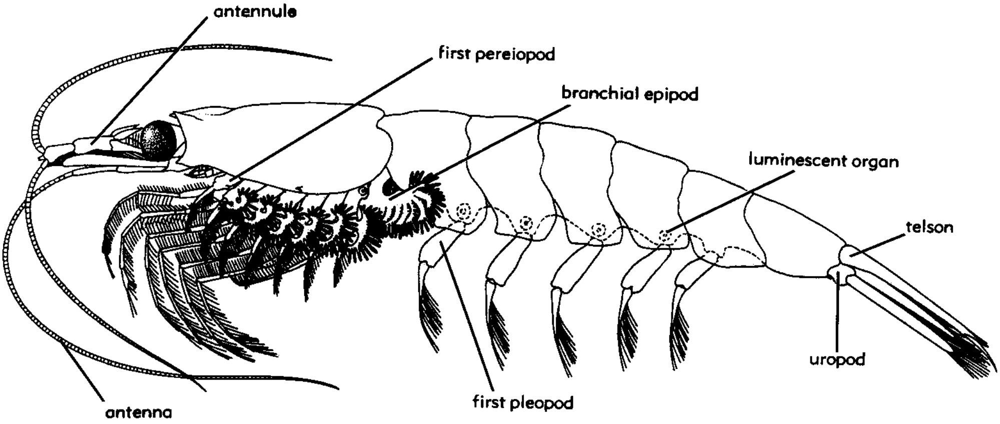


FIG. 212. Morphology of a typical euphausiid, *Meganyctiphanes norvegica* (M. SARS). Lateral view of adult, approx. ×7.8 (361).

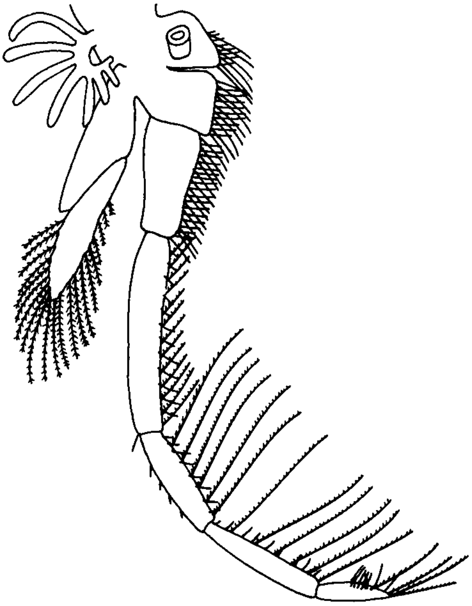


FIG. 213. Typical euphausiid second thoracopod, *Euphausia* sp. (=SARS' *E. pellucida*), ×25 (377a).

Stylocheiron, and both the second and third endopods in *Tessarabrachion.*

In general, all thoracic limbs are provided with branchial epipods. The branchiae are simple on the first thoracopods, but become progressively larger and more complexly ramified posteriorly. On forms having raptorial limbs, branchiae may be absent anteriorly, but posteriorly, even when the rest of the limb is reduced or absent they remain well developed.

The pleopods consist of a two-segmented protopod and flat unjointed exopod and endopod, the latter provided with an appendix interna. In males of all genera except *Bentheuphausia* endopods of the first and second pairs of pleopods bear an additional medial lobe, the appendix masculina, which functions in copulation. The form of this structure may be quite complex, and it figures importantly in systematics of lower categories.

The uropods are composed of an unjointed protopod and two elongate, unjointed rami, except in *Bentheuphausia,* where the exopod is indistinctly two-segmented (Fig. 215).

Luminescent organs are found in all euphausiaceans except *Bentheuphausia.* They are located in stalks of the compound eyes, coxae of the second and seventh thoracopods, and sternites of the first four abdominal somites. In *Stylocheiron* many of these organs have disappeared.

The telson is provided with a pair of pointed, subapical spines (Fig. 215), which, although reminiscent of the caudal rami of the phyllocarids and many lower Crustacea, are actually enlarged marginal setae (Fig. 216).

The paired compound eyes are stalked and movable. In genera in which the second or third thoracic limb, or both of these limbs, has become modified into a raptorial structure, the visual surfaces of the compound eyes are divided into dorsoanterior and lateral portions (Fig. 214).

Euphausiaceans range in length from less than 7 mm. to almost 5 cm.

DEVELOPMENT

Euphausiacean development (Fig. 216) is divided into six smoothly intergrading stages designated as nauplius, metanauplius, calyptopis, furcilia, cyrtopia, and postlarval.

The oval, unsegmented body of the nauplius (Fig. 216,*1*) lacks compound eyes or mouth. Antennules, antennae, and mandibles are present, the latter two pairs being biramous and natatory.

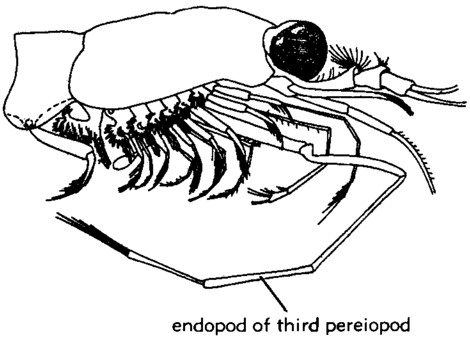


FIG. 214. *Nematobrachion boopis* (CALMAN); lateral view of anterior portion of adult, showing elongation of third pereiopod and subdivision of compound eye, approx. ×5.5 (348a).

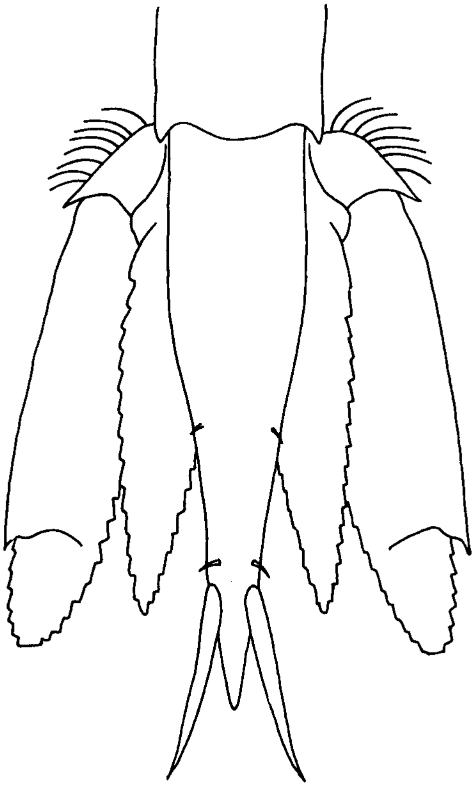


FIG. 215. *Bentheuphausia ambylops* (G. O. SARS), dorsal view of posterior end, showing uropods and telson (note paired subapical spines and compare with Fig. 216), ×25 (377a).

In the metanauplius (Fig. 216,*2*) rudiments of the maxillules, maxillae, and first thoracopods appear, while the mandibular palp is lost.

The abdomen becomes distinct from the rest of the body in the calyptopis stage (Fig. 216,*3,4*). Compound eyes develop, but they are immobile and covered by the newly developing carapace. The mandible, maxillules, maxillae, and first thoracopods develop further, and uropods appear.

In the furcilia stage (Fig. 216,*5*) the compound eyes become movable and project beyond the sides of the carapace, while the anterior thoracic limbs and the pleopods develop.

Up to this point the antennae have retained their naupliar form and natatory function, but beginning with the cyrtopia stage they assume the basic adult morphology and no longer serve in locomotion. The posterior thoracic limbs develop.

In the postlarval stage further details of adult form are attained gradually.

MODE OF LIFE

Euphausiaceans invariably are members of the marine zooplankton, where they are second only to copepods in importance as part of the food chain. The vast majority of species are found in the open ocean, but some, particularly species of *Nyctiphanes, Meganyctiphanes,* and *Pseudeuphausia,* live in coastal waters. Most species occur at or near the ocean surface, and these usually exhibit diurnal migration. *Bentheuphausia,* on the other hand, is an abyssal form with vestigial eyes.

Temperature is probably the most important physical factor determining distribution. This being so, depth in the water column is as important as latitude as a distributional parameter (87).

Most euphausiaceans are filter-feeders, with detritus, algae, and copepods (?passively captured) making up the bulk of their stomach contents. Where copepods form a significant percent of the diet, such as that of *Meganyctiphanes,* active predation may occur (MACDONALD, 1927). Genera with raptorial limbs are considered to be more wholly predaceous, and with this is correlated specialized eyes and a modified or enlarged stomach (339). However, one representative of this group *(Thysanoessa raschi)* is known to feed on detritus, possibly using its elongate limbs to stir up mud.

FOSSIL RECORD

PEACH (226) has included the Carboniferous genera *Anthracophausia* and *Crangopsis* in the Euphausiacea. Most subsequent authors have not concurred, although ZIMMER & GRUNER (339) agree that *Anthracophausia* is a euphausiacean. Since PEACH clearly illustrated and described the eighth thoracic somite of *Anthracophausia* as being a complete, sclerotized ring, free from the carapace, this genus cannot be a euphausiacean, although it may very well be related to a precursor of the order. An additional reason for the exclusion of these genera from the Euphausiacea is their possession of an unjointed sympod (55).

A tabulation of the suprageneric divisions of the Euphausiacea showing their stratigraphic occurrence and numbers of contained genera is given on page *R*114.

SYSTEMATIC DESCRIPTIONS

Order EUPHAUSIACEA Dana, 1852

Eucarida retaining primitive caridoid facies, no thoracopods modified as maxillipeds, all with branchial epipodites which are not covered by carapace; exopod present on thoracopods which are not reduced; luminescent organs nearly always present. Young hatch as nauplii. *Rec.*

Family BENTHEUPHAUSIIDAE Colosi, 1917

Characters of type genus. *Rec.*

Bentheuphausia G. O. SARS, 1885, p. 108 [**Thysanopoda(?) ambylops* G. O. SARS, 1883; OD]. Eighth thoracopod reduced but with complete structure; endopods of maxillules 2-segmented, whereas those of maxillae are 3-segmented; 1st and 2nd pleopods not strongly modified for copulation; luminescent organs absent; eyes reduced. *Rec.*, cosmop.——FIG. 215. **B. ambylops* (G. O. SARS), cosmop.; telson and uropods, dorsal, ×25 (377a).

Family EUPHAUSIIDAE Dana, 1850

[*nom. correct.* WILLEMOES SUHM, 1875 (*pro* Euphausidae DANA, 1850)]

Eighth and commonly seventh thoracopods reduced and simplified; endopods of

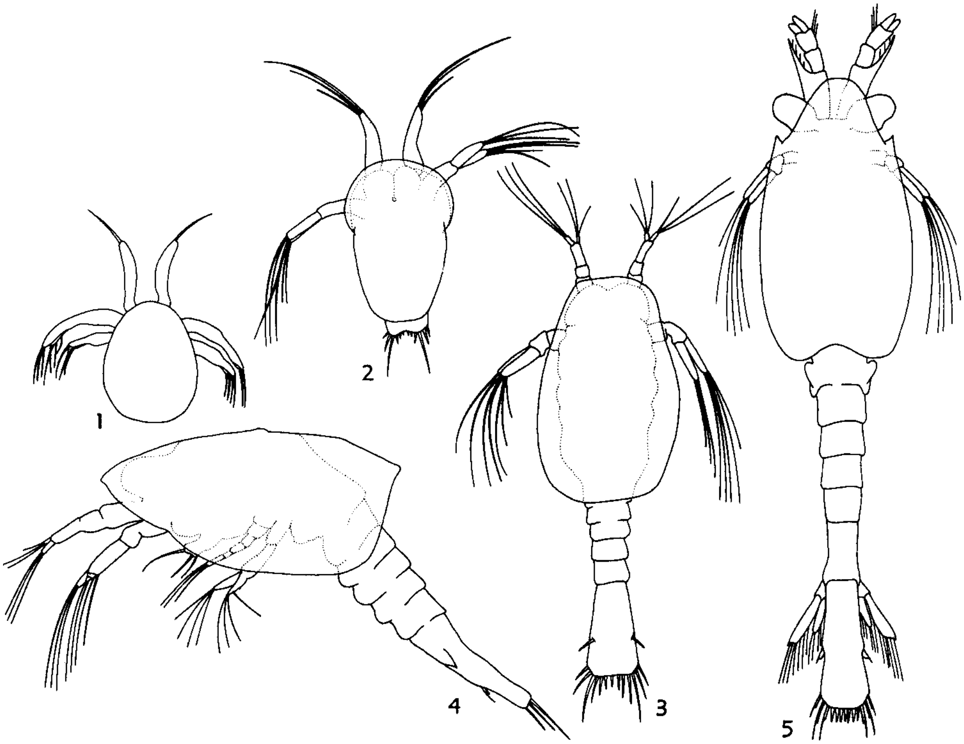


FIG. 216. Developmental stages of larval *Euphausia superba* DANA: *1*, first nauplius, dors., ×25; *2*, metanauplius, dors., ×25; *3*, second calyptopis, dors., ×20; *4*, second calyptopis, lat., ×25; *5*, second furcilia, dors., ×35 (97).

maxillules and maxillae unjointed; first and second pleopods of male strongly modified for copulation; luminescent organs present; eyes well developed. *Rec.,* cosmop.

Ten genera are recognized in this family, three representative ones being described and figured here.

Euphausia DANA, 1850, p. 130 [**E. superba*; SD HANSEN, 1905]. First 6 thoracopods approximately equal in length; eyes spherical; 7th and 8th thoracopods rudimentary in both sexes, forming small, unjointed, setose processes; antennulary peduncle almost invariably alike in both sexes; first pleopods of male with setae on setiferous lobe of endopod. *Rec.,* cosmop. except high Arctic. ——FIG. 213. *E.* sp. (=*E. pellucida* SARS, 1885; see HANSEN, 1905); 2nd thoracopod, ×25 (377a). ——FIG. 216,*1-5*. **E. superba* DANA, Antarctic; *1-5,* developmental stages (97).

Meganyctiphanes HOLT & TATTERSALL, 1905, p. 103 [**Thysanopoda norvegica* M. SARS, 1857; OD]. Only 8th thoracopod rudimentary; 6th and 7th thoracopods with exopod in both sexes; both terminal and proximal processes of appendix masculina developed. *Rec.,* N.Atl., Medit.——FIG. 212. **M. norvegica* (M. SARS), N.Atl., Medit.; adult showing morphological features, lat., approx. ×5.5 (361).

Nematobrachion CALMAN, 1905, p. 153 [**Nematodactylus boöpis* CALMAN, 1896; OD]. Third thoracopod elongate, 7th with 5 endopodal segments; full complement of luminescent organs; branchiae well developed. *Rec.,* trop.-temp.Atl.-Pac.-Ind.O.——FIG. 214. **N. boopis* (CALMAN); anterior half of body, lat., approx. ×5.5 (348a).