Treatise on INVERTEBRATE PALEONTOLOGY *Moore, Editor* (C) Protista 2 (1) *Geological Society of America*
University of Kansas Press

TREATISE ON
INVERTEBRATE PALEONTOLOGY

Prepared under Sponsorship of
The Geological Society of America

The Paleontological Society *The Society of Economic Paleontologists and Mineralogists*
The Palaeontographical Society *The Palaeontological Association*

Directed and Edited by
RAYMOND C. MOORE

Part C

PROTISTA 2

SARCODINA
CHIEFLY "THECAMOEBIANS" AND FORAMINIFERIDA

By ALFRED R. LOEBLICH, JR., and HELEN TAPPAN
with some systematic descriptions of Foraminiferida by R. WRIGHT BARKER, W. STORRS COLE, R. C. DOUGLASS, MANFRED REICHEL, and M. L. THOMPSON

VOLUME 1

THE GEOLOGICAL SOCIETY OF AMERICA
and
THE UNIVERSITY OF KANSAS PRESS

1964

Library of Congress Catalogue Card
Number: 53-12913

Text Composed by
THE UNIVERSITY OF KANSAS PRESS
Lawrence, Kansas

Illustrations and Offset Lithography
MERIDEN GRAVURE COMPANY
Meriden, Connecticut

Binding
RUSSELL-RUTTER COMPANY
New York City

Address all communications to The Geological Society of America, 231 East 46 Street, New York 17, N.Y.

The *Treatise on Invertebrate Paleontology* has been made possible by (1) grants of funds from The Geological Society of America through the bequest of Richard Alexander Fullerton Penrose, Jr., for preparation of illustrations and partial defrayment of organizational expense and the United States National Science Foundation, in December, 1959, for completion of the *Treatise* project; (2) contribution of the knowledge and labor of specialists throughout the world, working in co-operation under sponsorship of The Geological Society of America, The Paleontological Society, The Society of Economic Paleontologists and Mineralogists, The Palaeontographical Society, and The Palaeontological Association; and (3) acceptance by The University of Kansas Press of publication without cost to the Societies concerned and without any financial gain to the Press.

TREATISE ON INVERTEBRATE PALEONTOLOGY

Directed and Edited by
RAYMOND C. MOORE

Assistants: DORIS E. NODINE ZELLER, LAVON McCORMICK, ROGER B. WILLIAMS, SHELIA M. KELSEY

Advisers: AGNES CREAGH (The Geological Society of America, *Executive Director*), G. ARTHUR COOPER (The Paleontological Society), N. D. NEWELL (The Society of Economic Paleontologists and Mineralogists), C. J. STUBBLEFIELD (The Palaeontographical Society), T. NEVILLE GEORGE (The Palaeontological Association), CLYDE K. HYDER (The University of Kansas Press, Editor).

PARTS

Parts of the *Treatise* are distinguished by assigned letters with a view to indicating their systematic sequence while allowing publication of units in whatever order each may be made ready for the press. The volumes are cloth-bound with title in gold on the cover. Copies are available on orders sent to the Publication Department of The Geological Society of America at 231 East 46th Street, New York 17, N.Y. The prices quoted very incompletely cover costs of producing and distributing the several volumes, but on receipt of payment the Society will ship copies without additional charge to any address in the world. Special discounts are available to members of sponsoring societies under arrangements made by appropriate officers of these societies, to whom inquiries should be addressed.

VOLUMES ALREADY PUBLISHED

(Previous to 1963)

Part D. PROTISTA 3 (chiefly Radiolaria, Tintinnina), xii+195 p., 1050 fig., 1954.
Part E. ARCHAEOCYATHA, PORIFERA, xviii+122 p., 728 fig., 1955.
Part F. COELENTERATA, xvii+498 p., 2700 fig., 1956.
Part G. BRYOZOA, xii+253 p., 2000 fig., 1953.
Part I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii+351 p., 1732 fig., 1960.
Part L. MOLLUSCA 4 (Ammonoidea), xxii+490 p., 3800 fig., 1959.
Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix+560 p., 2880 fig., 1959.
Part P. ARTHROPODA 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii+181 p., 565 fig., 1955.
Part Q. ARTHROPODA 3 (Crustacea, Ostracoda), xxiii+442 p., 3476 fig., 1961.
Part V. GRAPTOLITHINA, xvii+101 p., 358 fig., 1955.
Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv+259 p., 1058 fig., 1962.

THIS VOLUME

Part C. PROTISTA 2 (Sarcodina, chiefly "Thecamoebians" and Foraminiferida), xxxi+900 p., 5311 fig., 1964.

VOLUMES IN PREPARATION (1963)

Part A. Introduction.
Part B. Protista 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, etc.).
Part H. Brachiopoda.
Part J. Mollusca 2 (Caenogastropoda, Opisthobranchia).
Part K. Mollusca 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea). [Ready for press.]
Part M. Mollusca 5 (Endocochlia).
Part N. Mollusca 6 (Bivalvia).
Part R. Arthropoda 4 (Crustacea, Branchiopoda, Cirripedia, Malacostraca; Myriapoda; Hexapoda).
Part S. Echinodermata 1 (Echinodermata General Features, Carpoidea, Cystoidea, Cyclocystoidea, Paracrinoidea, Eocrinoidea, Edrioblastoidea, Blastoidea, Edrioasteroidea).
Part T. Echinodermata 2 (Crinoidea).
Part U. Echinodermata 3 (Echinozoa, Asterozoa).
Part X. Addenda, Index.

CONTRIBUTING AUTHORS

(Arranged by countries and institutions. Accompanying numbers are for cross reference from alphabetically arranged list, which follows.)

Australia.—*Univ. ADELAIDE,* (1) M. F. Glaessner; *NATIONAL Univ.,* Canberra, (2) D. A. Brown; *Univ. QUEENSLAND,* Brisbane, (3) Dorothy Hill; *SOUTH AUSTRALIA Geol. Survey,* Adelaide, (4) N. H. Ludbrook.

Belgium.—*Univ. LIÈGE,* (5) Georges Ubaghs; *Univ. LOUVAIN,* (6) Marius Lecompte.

Canada.—*Univ. BRITISH COLUMBIA,* Vancouver, (7) V. J. Okulitch; *Geol. Survey CANADA,* Ottawa, (8) J. A. Jeletzky, (9) G. W. Sinclair.

Denmark.—*Univ. COPENHAGEN,* (10) Chr. Poulsen, (11) H. W. Rasmussen.

France.—*Coll. ANTHROPOLOGIE,* Paris, (12) André Chavan; *BRITISH EMBASSY,* Paris, (13) R. V. Melville; *Univ. PARIS (Sorbonne),* (14) Colette Dechaseaux.

Germany.—*Univ. BERLIN,* (15) K. J. Müller; *Univ. BONN,* (16) H. K. Erben; *HAMBURG Staats Inst.,* (17) Walter Häntzschel; *SENCKENBERG Mus.,* Frankfurt a.M., (18) Herta Schmidt, (19) Wolfgang Struve; *Univ. TÜBINGEN,* (20) O. H. Schindewolf; *Univ. WÜRZBURG,* (21) Klaus Sdzuy; *Unattached,* (22) Hertha Sieverts-Doreck, Stuttgart-Möhringen.

Italy.—*Univ. MODENA,* (23) Eugenia Montanaro Gallitelli.

Japan.—*TOHOKU Univ.,* Sendai, (24) Kotora Hatai; *Univ. TOKYO,* (25) Tetsuro Hanai.

Netherlands.—*Univ. LEIDEN,* (26) H. Boschma, (27) L. B. Holthuis.

New Zealand.—*AUCKLAND Mus.,* (28) A. W. B. Powell; *DOMINION Mus.,* Wellington, (29) R. K. Dell; *NEW ZEALAND Geol. Survey,* Lower Hutt, (30) C. A. Fleming, (31) J. Marwick; *VICTORIA Univ. WELLINGTON,* (32) H. B. Fell, (33) David Pawson.

Norway.—*Univ. OSLO,* (34) Gunnar Henningsmoen, (35) T. Soot-Ryen, (36) Leif Størmer.

Poland.—*WARSZAWA Acad. Sci.,* (37) Gertruda Biernat.

Sweden.—*Univ. LUND,* (38) Gerhard Regnéll; *Univ. STOCKHOLM,* (39) Ivar Hessland, (40) R. A. Reyment; *UPPSALA Univ.,* (41) Valdar Jaanusson.

Switzerland.—*Univ. BASEL,* (42) Manfred Reichel.

United Kingdom.—*Univ. BIRMINGHAM,* (43) L. J. Wills; *BRITISH MUS. (Nat. History),* London, (44) Leslie Bairstow, (45) L. R. Cox, (46) Isabella Gordon, (47) S. M. Manton, (48) H. M. Muir-Wood; *BRITISH PETROLEUM Co.,* Middlesex, (49) F. E. Eames; *Univ. CAMBRIDGE,* (50) O. M. B. Bulman,

(51) M. J. S. Rudwick; *Univ. GLASGOW,* (52) W. D. I. Rolfe, (53) John Weir, (54) C. M. Yonge; *Geol. Survey GREAT BRITAIN, London,* (55) Raymond Casey, (56) C. J. Stubblefield; *IRAQ PETROLEUM Co.,* London, (57) G. F. Elliott; *Univ. LEICESTER,* (58) P. C. Sylvester-Bradley; *Univ. LONDON,* (59) D. V. Ager; *Univ. NOTTINGHAM,* (60) A. J. Rowell; *QUEEN'S Univ. BELFAST,* (61) Alwyn Williams, (62) A. D. Wright; *Univ. READING,* (63) H. L. Hawkins; *Univ. SWANSEA,* (64) F. H. T. Rhodes; *Unattached,* (65) Dennis Curry, Middlesex, (66) R. P. Tripp, Seven Oaks, Kent, (67) C. W. Wright, London.

United States of America.—*AMERICAN MUS. NAT. HISTORY,* New York, (68) R. L. Batten, (69) W. K. Emerson, (70) L. H. Hyman, (71) N. D. Newell; *CALIFORNIA ACAD. SCI.,* San Francisco, (72) G. D. Hanna, (73) L. G. Hertlein, (74) A. G. Smith; *CALIFORNIA INST. TECHNOLOGY,* Pasadena, (75) A. J. Boucot, (76) J. G. Johnson, (77) H. A. Lowenstam; *CALIFORNIA RESEARCH CORP.,* La Habra, Calif., (78) A. R. Loeblich, Jr.; *Univ. CALIFORNIA, Berkeley,* (79) J. W. Durham, (80) A. R. Loeblich, III, (81) C. D. Wagner; *Univ. CALIFORNIA,* Los Angeles, (82) W. D. Popenoe, (83) Helen Tappan; *Univ. CALIFORNIA,* San Diego (La Jolla), (84) M. N. Bramlette; *CHICAGO NAT. HISTORY MUS.,* (85) Fritz Haas; *Univ. CHICAGO,* (86) J. M. Weller; *Univ. CINCINNATI,* (87) K. E. Caster; *CORNELL Univ.,* Ithaca, N.Y., (88) W. S. Cole, (89) J. M. Wells; *FLORIDA Geol. Survey,* Tallahassee, (90) H. S. Puri; *Univ. FLORIDA,* Gainesville, (91) H. K. Brooks; *HARVARD Univ.,* Cambridge, Mass., (92) F. M. Carpenter, (93) Bernhard Kummel, (94) W. A. Newman, (95) R. D. Staton, (96) Ruth Turner, (97) H. B. Whittington; *HUMBLE OIL & REFINING Co.,* Houston, Tex., (98) H. H. Beaver, (99) R. M. Jeffords, (100) S. A. Levinson, (101) Joan Stough; *ILLINOIS Geol. Survey,* Urbana, (102) M. L. Thompson; *Univ. ILLINOIS,* Urbana, (103) H. W. Scott; *INDIANA Geol. Survey,* Bloomington, (104) R. H. Shaver; *State Univ. IOWA,* Iowa City, (105) W. M. Furnish, (106) B. F. Glenister; *JERSEY PRODUCTION Co.,* Tulsa, Okla., (107) J. S. Van Sant; *JOHNS HOPKINS Univ.,* Baltimore, Md., (108) Franco Rasetti; *Univ. KANSAS,* Lawrence, (109) R. H. Benson, (110) A. B. Leonard, (111) R. C. Moore, (112) C. W. Pitrat, (113) R. H. Thompson, (114) D. E. Nodine Zeller; *LOUISIANA State Univ.,* Baton Rouge, (115) W. A. van den Bold, (116) H. V. Howe; *Univ. MICHIGAN,* Ann Arbor, (117) R. V. Kesling, (118) E. C. Stumm; *Univ. MINNESOTA,* Minneapolis, (119) F. M. Swain; *Univ. MISSOURI,* Columbia, (120) R. E. Peck; *MISSOURI School of Mines,* Rolla, (121) Harriet Exline & D. L. Frizzell; *NEW MEXICO Inst. Mining & Geology,* Socorro, (122) Christina Lochman-Balk; *NEW YORK State Mus.,* Albany, (123) D. W. Fisher; *OHIO State Univ.,* Columbus, (124) Aurèle La Rocque, (125) W. C. Sweet; *OKLAHOMA Geol. Survey,* Norman, (126) T. W. Amsden, (127) R. O. Fay; *Univ. OKLAHOMA,* Norman, (128) C. C. Branson; *Coll. of PACIFIC,* Dillon Beach, Calif., (129) Joel Hedgpeth; *PALEONTOLOGICAL RESEARCH Inst.,* Ithaca, N.Y., (130) K. V. W. Palmer; *PHILADELPHIA Acad. Nat. Sci.,* (131) A. A. Olsson, (132) Robert Robertson; *PRINCETON Univ.,* Princeton, N. J., (133) A. G. Fischer, (134) T. G. Gibson, (135) B. F. Howell; *RADFORD Coll.,* Blacksburg, Va., (136) R. L. Hoffman; *ST. MARY'S Coll.,* St. Mary's College, Calif., (137) A. S. Campbell; *SHELL DEVELOPMENT Co.,* Houston, Tex., (138) R. W. Barker, (139) H. B. Stenzel, (140) John Wainwright; *SINCLAIR OIL & GAS Co.,* Tulsa, Okla., (141) A. L. Bowsher; *STANFORD Univ.,* Stanford, Calif., (142) A. Myra Keen; *TENNESSEE GAS TRANSMISSION Co.,* Houston, Tex., (143) H. J. Harrington; *TULANE Univ.,* New Orleans, La., (144) H. E. Vokes; *UNITED STATES Geol. Survey,* Washington, D.C., (145) J. M. Berdan, (146) R. C. Douglass, (147) MacKenzie Gordon, Jr., (148) K. E. Lohman, (149) A. R. Palmer, (150)

I. G. Sohn, (151) Curt Teichert, (152) E. L. Yochelson; *UNITED STATES Natl. Mus.*, Washington, D.C., (153) F. M. Bayer, (154) R. S. Boardman, (155) G. A. Cooper, (156) R. E. Grant, (157) P. M. Kier, (158) J. P. E. Morrison, (159) H. A. Rehder, (160) Joseph Rosewater; *WESTERN RESERVE Univ.*, Cleveland, O., (161) F. G. Stehli; *Univ. WICHITA*, Wichita, Kans., (162) Paul Tasch; *WOODS HOLE OCEANOGRAPHIC Inst.*, Woods Hole, Mass., (163) R. R. Hessler; *YALE Univ.*, New Haven, Conn., (164) A. L. McAlester, (165) Alexander Petrunkevitch.

Deceased.—(166) W. J. Arkell, (167) R. S. Bassler, (168) L. M. Davies, (169) Julia Gardner, (170) W. H. Hass, (171) J. B. Knight, (172) M. W. de Laubenfels, (173) A. K. Miller, (174) Emma Richter, (175) Rudolf Richter, (176) W. K. Spencer, (177) M. A. Stainbrook, (178) L. W. Stephenson, (179) O. W. Tiegs, (180) Johannes Wanner, (181) T. H. Withers, (182) Arthur Wrigley.

Alphabetical List

(Numbers refer to preceding list arranged by countries and institutions.)

Ager, D. V. (59)
Amsden, T. W. (126)
Arkell, W. J. (166)
Bairstow, Leslie (44)
Barker, R. W. (138)
Bassler, R. S. (167)
Batten, R. L. (68)
Bayer, F. M. (153)
Beaver, H. H. (98)
Benson, R. H. (109)
Berdan, J. M. (145)
Biernat, Gertruda (37)
Boardman, R. S. (154)
Bold, W. A. van den (115)
Boschma, H. (26)
Boucot, A. J. (75)
Bowsher, A. L. (141)
Bramlette, M. N. (84)
Branson, C. C. (128)
Brooks, H. K. (91)
Brown, D. A. (2)
Bulman, O. M. B. (50)
Campbell, A. S. (137)
Carpenter, F. M. (92)
Casey, Raymond (55)
Caster, K. E. (87)
Chavan, André (12)
Cole, W. S. (88)
Cooper, G. A. (155)
Cox, L. R. (45)
Curry, Dennis (65)
Davies, L. M. (168)
Dechaseaux, Colette (14)
Dell, W. K. (29)
Douglass, R. C. (146)
Durham, J. W. (79)
Eames, F. E. (49)
Elliott, G. F. (57)
Emerson, W. K. (69)
Erben, H. K. (16)
Exline, Harriet (121)
Fay, R. O. (127)
Fell, H. B. (32)
Fischer, A. G. (133)
Fisher, D. W. (123)
Fleming, C. A. (30)
Frizzell, D. L. (121)
Furnish, W. M. (105)
Gardner, Julia (169)
Gibson, T. G. (134)
Glaessner, M. F. (1)
Glenister, B. F. (106)
Gordon, Isabella (46)
Gordon, Mackenzie, Jr. (147)
Grant, R. E. (156)
Haas, Fritz (85)
Hanai, Tetsuro (25)
Hanna, G. D. (72)
Häntzschel, Walter (17)
Harrington, H. J. (143)
Hass, W. H. (170)
Hatai, Kotora (24)
Hawkins, H. L. (63)
Hedgpeth, Joel (129)
Henningsmoen, Gunnar (34)
Hertlein, L. G. (73)
Hessland, Ivar (39)
Hessler, R. R. (163)
Hill, Dorothy (3)
Hoffman, R. L. (136)
Holthuis, L. B. (27)
Howe, H. V. (116)
Howell, B. F. (135)
Hyman, L. H. (70)
Jaanusson, Valdar (41)
Jeffords, R. M. (99)
Jeletzky, J. A. (8)
Johnson, J. G. (76)
Keen, A. Myra (142)
Kesling, R. V. (117)
Kier, P. M. (157)
Knight, J. B. (171)
Kummel, Bernhard (93)
La Rocque, Aurèle (124)
Laubenfels, M. W. de (172)
Lecompte, Marius (6)
Leonard, A. B. (110)
Levinson, S. A. (100)
Lochman-Balk, Christina (122)
Loeblich, A. R., Jr. (78)
Loeblich, A. R., III (80)
Lohman, K. E. (148)
Lowenstam, H. A. (77)
Ludbrook, N. H. (4)
McAlester, A. L. (164)
Manton, S. M. (47)
Marwick, J. (31)
Melville, R. V. (13)
Miller, A. K. (173)
Montanaro Gallitelli, Eugenia (23)
Moore, R. C. (111)
Morrison, J. P. E. (158)
Muir-Wood, H. M. (48)
Müller, K. J. (15)
Newell, N. D. (71)
Newman, W. A. (94)
Okulitch, V. J. (7)
Olsson, A. A. (131)
Palmer, A. R. (149)
Palmer, K. V. W. (130)
Pawson, David (33)
Peck, R. E. (120)
Petrunkevitch, Alexander (165)
Pitrat, C. W. (112)
Popenoe, W. D. (82)
Poulsen, Chr. (10)
Powell, A. W. B. (28)
Puri, H. S. (90)
Rasetti, Franco (108)
Rasmussen, H. W. (11)
Regnéll, Gerhard (38)
Rehder, H. A. (159)
Reichel, Manfred (42)
Reyment, R. A. (40)
Rhodes, F. H. T. (64)
Richter, Emma (174)
Richter, Rudolf (175)
Robertson, Robert (132)
Rolfe, W. D. I. (52)
Rosewater, Joseph (160)
Rowell, A. J. (60)
Rudwick, M. J. S. (51)
Schindewolf, O. H. (20)
Schmidt, Herta (18)
Scott, H. W. (103)
Sdzuy, Klaus (21)
Shaver, R. H. (104)

Sieverts-Doreck, Hertha (22)
Sinclair, G. W. (9)
Smith, A. G. (74)
Sohn, I. G. (150)
Soot-Ryen, T. (35)
Spencer, W. K. (176)
Stainbrook, M. A. (177)
Staton, R. D. (95)
Stehli, F. G. (161)
Stenzel, H. B. (139)
Stephenson, L. W. (178)
Størmer, Leif (36)
Stough, Joan (101)
Struve, Wolfgang (19)
Stubblefield, C. J. (56)
Stumm, E. C. (118)
Swain, F. M. (119)
Sweet, W. C. (125)
Sylvester-Bradley, P. C. (58)
Tappan, Helen (83)
Tasch, Paul (162)
Teichert, Curt (151)
Thompson, M. L. (102)
Thompson, R. H. (113)
Tiegs, O. W. (179)
Tripp, R. P. (66)
Turner, Ruth (96)
Ubaghs, Georges (5)
Van Sant, J. F. (107)
Vokes, H. E. (144)
Wagner, C. D. (81)
Wainwright, John (140)
Wanner, Johannes (180)
Weir, John (53)
Weller, J. M. (86)
Wells, J. M. (89)
Whittington, H. B. (97)
Williams, Alwyn (61)
Wills, L. J. (43)
Withers, T. H. (181)
Wright, A. D. (62)
Wright, C. W. (67)
Wrigley, Arthur (182)
Yochelson, E. L. (152)
Yonge, C. M. (54)
Zeller, D. E. Nodine (114)

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 will bear the assigned index letter joined with numbers beginning with 1 and running consecutively to the end of the part. When the parts ultimately are assembled into volumes, no renumbering of pages and figures is required.

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 the Joint Committee on Invertebrate Paleontology representing 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.

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. 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 comes 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.

FORM OF ZOOLOGICAL NAMES

Many questions arise in connection with the form of zoological names. These include such matters as adherence to stipulations concerning Latin or Latinized nature of words accepted as zoological names, gender of generic and subgeneric names, nominative or adjectival form of specific names, required endings for some family-group names, and numerous others. Regulation extends to capitalization, treatment of particles belonging to modern proper names, use of neo-Latin letters, and approved methods for converting diacritical marks. The magnitude and complexities of nomenclatural problems surely are enough to warrant the complaint of those who hold that zoology is the study of animals rather than of names applied to them.

CLASSIFICATION OF ZOOLOGICAL NAMES

In accordance with the "Copenhagen Decisions on Zoological Nomenclature" (London, 135 p., 1953), zoological names may be classified usefully in various ways. The subject is summarized here with introduction of designations for some categories which the *Treatise* proposes to distinguish in systematic parts of the text for the purpose of giving readers comprehension of the nature of various names together with authorship and dates attributed to them.

CO-ORDINATE NAMES OF TAXA GROUPS

Five groups of different-rank taxonomic units (termed *taxa,* sing., *taxon*) are discriminated, within each of which names are treated as co-ordinate, being transferable from one category to another without change of authorship or date. These are: (1) species group (subspecies, species); (2) genus group (subgenus, genus); (3) family group (tribe, subfamily, family, superfamily; (4) suprafamilial group (suborder, order, subclass, class, subphylum, phylum). In groups (1), (2), and (3), the author of the first-published valid name for any taxon is held to be the author of all other taxa in the group which are based on the same nominate type and the date of publication for purposes of priority is that of the first-published name. Thus, if author A in 1800 introduced the family name X-idae to include 3 genera, one of which is *X-us*; and if author B in 1850 divided the 20 genera then included in X-idae into subfamilies called X-inae and Y-inae; and if author C in 1950 combined X-idae with other later-formed families to make a superfamily X-acea (or X-oidea, X-icae, etc.); the author of X-inae, X-idae and X-acea is A, 1800, under the Rules. Because taxonomic concepts introduced by authors B and C along with appropriate names surely are not attributable to author A, some means of recording responsibility of B and C are needed. This is discussed later in explaining use of *"nom. transl."* Taxa of group (4) are not regulated by the zoological Code (1961); they are discussed later under the heading "Suprafamilial Taxa."

The co-ordinate status of zoological names belonging to the species group is stipulated in Art. 46 of the present Rules; genus group in Art. 43 of the present Rules; family group in Art. 36 of the present Rules.

ORIGINAL AND SUBSEQUENT FORMS OF NAMES

Zoological names may be classified according to form (spelling) given in original publication and employed by subsequent authors. In one group are names which are entirely identical in original and subsequent usage. Another group comprises names which include with the original subsequently published variants of one sort or another. In this second group, it is important to distinguish names which are inadvertent changes from those constituting intentional emendations, for they have quite different status in nomenclature. Also, among intentional emendations, some are acceptable and some quite unacceptable under the Rules.

VALID AND INVALID NAMES

Valid names. A valid zoological name is one that conforms to all mandatory provisions of the Rules. Such names are divisible into groups as follows: (1) *"inviolate names,"* which as originally published not only meet all mandatory requirements of the Rules but are not subject to any sort of alteration (most generic and subgeneric names); (2) *"perfect names,"* which as they appear in original publication (with or without precise duplication by subsequent authors) meet all mandatory requirements and need no correction of any kind but which nevertheless are legally alterable under present Rules (as in changing the form of ending of a super- or suprafamilial name); (3) *"imperfect names,"* which as originally published and with or without subsequent duplication meet mandatory requirements but contain defects such as incorrect gender of an adjectival specific name (for example, *Spironema recta* instead of *Spironema rectum*) or incorrect stem or form of ending of a family-group name (for example, Spironemidae instead of Spironematidae); (4) *"transferred names,"* which are derived by valid emendation from either of the 2nd or 3rd groups or from a pre-existing transferred name (as illustrated by change of a family-group name from -inae to -idae or making of a superfamily name); (5) *"improved names,"* which include necessary as well as somewhat arbitrarily made emendations allowable under the Rules for taxonomic categories not now covered by regulations as to name form and alterations that are distinct from changes that distinguish the 4th group (including names derived from the 2nd and 3rd groups and possibly some alterations of 4th group names). In addition, some zoological names included among those recognized as valid are classifiable in special categories, while at the same time belonging to one or more of the above-listed groups. These chiefly include (7) *"substitute names,"* introduced to replace invalid names such as junior homonyms; and (8) *"conserved names,"* which are names that would have to be rejected by application of the Rules except for saving them in their original or an altered spelling by action of the International Commission on Zoological Nomenclature in exercising its plenary powers to this end. Whenever a name requires replacement, any individual may publish a "new name" for it and the first one so introduced has priority over any others; since newness is temporary and relative, the replacement designation is better called substitute name rather than new name.

It is useful for convenience and brevity of distinction in recording these groups of valid zoological names to introduce Latin designations, following the pattern of *nomen nudum, nomen novum,* etc. Accordingly, the groups are (1) *nomina inviolata* (sing., *nomen inviolatum,* abbr., *nom. inviol.*); (2) *nomina perfecta* (sing., *nomen perfectum,* abbr., *nom. perf.*); (3) *nomina imperfecta* (sing., *nomen imperfectum,* abbr., *nom. imperf.*); (4) *nomina translata* (sing., *nomen translatum,* abbr., *nom. transl.*); (5) *nomina correcta* (sing., *nomen correctum,* abbr., *nom. correct.*); (6) *nomina substituta* (sing., *nomen substitutum,* abbr., *nom. subst.*); (7) *nomina conservata* (sing., *nomen conservatum,* abbr., *nom. conserv.*).

Invalid names. Invalid zoological names consisting of originally published names that fail to comply with mandatory provisions of the Rules and consisting of inadvertent changes in spelling of names have no status in nomenclature. They are not available as replacement names and they do not preoccupy for purposes of the Law of Homonymy. In addition to *nomen nudum,* invalid names may be distinguished as follows: (1) *"denied names,"* which consist of originally published names (with or without subsequent duplication) that do not meet mandatory requirements of the Rules; (2) *"null names,"* which comprise unintentional alterations of names; and (3) *"vain or void names,"* which consist of invalid emendations of previously published valid or invalid names. Void names do have status in nomenclature, being classified as junior synonyms of valid names.

Proposed Latin designations for the indicated kinds of invalid names are as follows: (1) *nomina negata* (sing., *nomen negatum,* abbr., *nom. neg.*); (2) *nomina nulla* (sing., *nomen nullum,* abbr., *nom. null.*); (3) *nomina vana* (sing., *nomen vanum,* abbr., *nom. van.*). It is desirable in the *Treatise* to identify invalid names, particularly in view of the fact that many of the names (*nom. neg., nom. null.*) have been considered incorrectly to be junior objective synonyms (like *nom. van.*), which have status in nomenclature.

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 otherwise unacceptable under application of the Rules which is made valid, either with original or altered spelling, through procedures specified by the zoological Code (1961) or by action of ICZN exercising its plenary powers.

nomen correctum (nom. correct.). Name with intentionally altered spelling of sort required or allowable under the Rules but not dependent on transfer from one taxonomic category 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 categories not now fixed by Rules.)

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

nomen inviolatum (nom. inviol.). Name that as originally published meets all mandatory requirements of the Rules and also is uncorrectable 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 Rules, is not correctable to establish original authorship and date ("denied name").

nomen nudum (nom. nud.). Name that as originally published (with or without subsequent identical spelling) fails to meet mandatory requirements of the Rules 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 valid name, as *nom. inviol., nom. perf., nom. imperf., nom. transl.;* or invalid name, as *nom. neg., nom. nud., nom. van.,* or another *nom. null.*) ("null name").

nomen perfectum (nom. perf.). Name that as originally published meets all mandatory requirements of the Rules and needs no correction of any kind but which nevertheless is validly alterable ("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 category 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 emendations having status in nomenclature as junior objective synonyms ("vain or void name").

Except as specified otherwise, zoological names accepted in the *Treatise* may be understood to be classifiable either as *nomina 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, a few senior synonyms classifiable as *nomina negata* or *nomina nuda,* and numerous junior synonyms which include both objective (*nomina vana*) and subjective (all classes of valid names) types; effort to classify the invalid names as completely as possible is intended.

NAME CHANGES IN RELATION TO GROUP CATEGORIES

SPECIFIC AND SUBSPECIFIC 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 Rules (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.

GENERIC AND SUBGENERIC 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.

Examples in use of classificatory designations for generic 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 deLaub., *nom. subst.,* 1955 [*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.)].

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

The Rules now specify the form of endings only for subfamily (-inae) and family (-idae) but the Code defines all family-group assemblages (taxa) as co-ordinate, signifying that for purposes of priority a name published for a unit in any category and based on a particular type-genus shall date from its original publication for a unit in any category, retaining this priority (and authorship) when the unit 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 emendation 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 emendation. 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 Rules, 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 emendations 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 (*ex* Streptelasmidae Nicholson, 1889, *nom. imperf.*)]

Family PALAEOSCORPIIDAE Lehmann, 1944

[*nom. correct.* Petrunkevitch, 1955 (*ex* Palaeoscorpionidae Lehmann, 1944, *nom. imperf.*)]

Family AGLASPIDIDAE Miller, 1877

[*nom. correct.* Størmer, 1959 (*ex* Aglaspidae Miller, 1877, *nom. imperf.*)]

Superfamily AGARICIICAE Gray, 1847

[*nom. correct.* Wells, 1956 (*ex* 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 Rules. 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. According to the zoological Code, the family-group name requires replacement 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.

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. Conversely, a long-used family-group name founded on a junior objective synonym and having priority of publication is better continued in nomenclature than a replacement name based on the senior objective synonym.

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 as 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, crustacean, 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).

(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.

Order ENDOCERIDA Teichert, 1933

[*nom. correct.* Teichert, 1963 (*pro* order Endoceroidea Teichert, 1933)]

Suborder ENDOCERINA Teichert, 1933

[*nom. correct.* Teichert, 1963 (*pro* suborder Endoceracea Schindewolf, 1935, *nom. transl. ex* order Endoceroidea Teichert, 1933)]

Subclass ENDOCERATOIDEA Teichert, 1933

[*nom. transl.* Teichert, 1963 (*ex* superorder Endoceratoidea Shimanskiy & Zhuravleva, 1961, *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 of 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 containing definition of the genus which it serves as type; in such case, the initial letter of the generic name followed by the trivial 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 Rules, 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 a type-species originally may be classified as automatic if the new genus was introduced for a single species (monotypy), or if the names of species referred to the genus are objectively synonymous. In addition, fixation of a type-species originally may be established in several ways by original designation, as by explicit statement given by an author, by use of *typus* or *typicus* as a new specific name, and by absolute tautonymy (e.g., *Mesolobus mesolobus*). According to convention adopted in the *Treatise,* the absence of indication as to the manner of fixing the type-species is to be understood as signifying fixation of the type-species in one way or another originally. Where an author wishes to specify the mode of original fixation, however, this may be done by such abbreviations as "M" (monotypy), "OS" (objective synonymy), and "OD" (original designation), the first- and last-mentioned being most common and the other very rare.

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 2 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 Rules 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.

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 DELAUBENFELS, *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.

Homonyms by misidentification. When an author uses a generic name for species not congeneric with the type-species, it is needful to record the misuse of the generic name, even though this is only determinable subjectively. In the *Treatise* homonyms by misidentification are cited in synonymies as illustrated in the following example.

Asmussia PACHT, 1849 [**A. membranacea*] [=*Posidonomya* PACHT, 1852 (*non* BRONN, 1834); *Estheria* JONES, 1856 (*non* ROBINEAU-DESVOIDY, 1830; *nec* RUEPPELL, 1837)].

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 2 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

Aalen., Aalenian
aff., *affinis* (related to)
Afghan., Afghanistan
Afr., Africa, -an
aggl., agglutinated
Ala., Alabama
Alb., Albian
Alg., Algeria
Am., America, -n
apert., apertural
append., appendix
approx., approximately
Apt., Aptian
Aquitan., Aquitanian
Arch., Archipelago
Arct., Arctic
aren., arenaceous
Ariz., Arizona
Ark., Arkansas
art., article
Artinsk., Artinskian
AsiaM., Asia Minor
ASSR, Azerbaydzhan Soviet Socialist Republic
Atl., Atlantic
auctt., *auctorum* (of authors)
Aus., Austria
Auvers., Auversian
av., average
Avon., Avonian
Bajoc., Bajocian
Baluch., Baluchistan
Barrem., Barremian
Barton., Bartonian
Bathon., Bathonian
Bav., Bavaria
B.C., British Columbia
Belg., Belgium, Belgique
BMNH, British Museum (Natural History)
Boh., Bohemia
Br. Hond., British Honduras
Br.I., **Brit.I.**, British Isles
Brit., Britain, British
Bulg., Bulgaria
Burdigal., Burdigalian
C, Centigrade
C., Central
calc., calcareous
Calif., California
Callov., Callovian
C.Am., Central America
Cam., Cambrian
Campan., Campanian
Can., Canada
Caradoc., Caradocian
Carb., Carboniferous
Carib., Caribbean
Carn., Carnian
Carp., **Carpath.**, Carpathians
Cat., Catalog
Cenoman., Cenomanian
cf., *confer* (compare)
Chatt., Chattian
cm., centimeter
Coll., Collection
Colom., Colombia
Coniac., Coniacian
cosmop., cosmopolitan
Cr., Creek
Cret., Cretaceous
C.Z., Canal Zone
Czech., Czechoslovakia
Dan., Danian
Denm., Denmark
Dept., Department
Dev., Devonian
diagram., diagrammatic
diam., diameter
Distr., District
Dordon., Dordonian
E., East
Ecuad., Ecuador
ed., edition, editor
e.g., *exempli gratia* (for example)
emend., *emendatus* (*-a*)
Eng., England
Eoc., Eocene
Equat., Equatorial
equiv., equivalent
err., *errore* (by error)
Est., Estonia
et al., *et alii* (and others, persons)
etc., *et cetera* (and others, objects)
Eu., Europe
Exped., Expedition

ext., exterior
F., Formation
Falk.Is., Falkland Islands
fam., family
Famenn., Famennian
fig., figure, -s
Fla., Florida
Fr., France, French, Français, -e
Frasn., Frasnian
Ga., Georgia
Gasc., Gascony
G.Brit., Great Britain
Geol., Geology, Geological, Geologische, etc.
Ger., Germany, German
Givet., Givetian
gm., gram, -s
Gotl., Gotland
Gotland., Gotlandian
Gr., Group
Greenl., Greenland
Guat., Guatemala
Hauteriv., Hauterivian
Hemis., Hemisphere
hom., homonym
horiz., horizontal
Hung., Hungary, Hungarica
ICZN, International Commission on Zoological Nomenclature
i.e., *id est* (that is)
Ill., Illinois
Ind., Indiana
Ind.O., Indian Ocean
Indon., Indonesia
Indo Pac., Indo-Pacific
Infravalangin., Infravalanginian
Ire., Ireland
Is., Island, -s
Jackson., Jacksonian
jr., junior
Jur., Jurassic
Kans., Kansas
Kazakh., Kazakhstan
Kazan., Kazanian
Kimmeridg., Kimmeridgian
Kinderhook., Kinderhookian
km., kilometer, -s
L., **Low.**, Lower
La., Louisiana
Lab., Labrador
Landen., Landenian
lat., lateral
Lias., Liassic
Lith., Lithuania
Llandeil., Llandeilian
Llandov., Llandoverian
Llanvirn., Llanvirnian
loc., locality
loc. cit., *loco citato* (in the place cited)
long., longitudinal
Ls., Limestone
Ludlov., Ludlovian
Lutet., Lutetian
m., meter
M., **Mid.**, Middle
M, Monotypy
Maastricht., Maastrichtian
Madag., Madagascar
mag., magnification
med., median
Medit., Mediterranean
Meramec., Meramecian
Mesoz., Mesozoic
Mex., Mexico
mi., mile, -s
Midway., Midwayan
Mio., Miocene
Miss., Mississippi, Mississippian
ml., milliliter, -s
mm., millimeter, -s
MNHN, Muséum National d'Histoire Naturelle (Paris)
Mo., Missouri
Mont., Montana
Morav., Moravia
Moscov., Moscovian
Moz., Mozambique
Mts., **Mtns.**, Mountains
n., new
N., North
N.Am., North American
Namur., Namurian
NC., North Central
N.Car., North Carolina
NE., Northeast
Neb., Nebraska
Neth., Netherlands
Nev., Nevada
N.J., New Jersey
N.Mex., New Mexico
no., number
nom. conserv., *nomen conservatum* (conserved name)
nom. correct., *nomen correctum* (corrected or intentionally altered name)
nom. imperf., *nomen imperfectum* (imperfect name)
nom. neg., *nomen negatum* (rejected name)
nom. nov., *nomen novum* (new name)
nom. nud., *nomen nudum* (naked name)
nom. null., *nomen nullum* (null, void name)
nom. subst., *nomen substitutum* (substitute name)
nom. transl., *nomen translatum* (transferred name)
nom. van., *nomen vanum* (vain, void name)
NW., Northwest
N.Z., New Zealand
O., Ocean
obj., objective
OD, original designation
Okla., Oklahoma
Oligo., Oligocene
opp., opposite
Ord., Ordovician
Ore., Oregon
Oxford., Oxfordian
p., page, -s
Pa., Pennsylvania
Pac., Pacific
Pac.O., Pacific Ocean
Pak., Pakistan
Paleoc., Paleocene
Paleog., Paleogene
Palest., Palestine
pend., pending
Penin., Peninsula
Penn., Pennsylvanian
Perm., Permian
perpend., perpendicular
Philip. Is., Philippine Islands
Piacenz., Piacenzan
pl., plate, -s, plural
Pleist., Pleistocene
Pliensbach., Pliensbachian
Plio., Pliocene
Pol., Poland
Port., Portugal
Portland., Portlandian
Precam., Precambrian
Pref., Prefecture
Priabon., Priabonian
Prov., Province
Pt., Point
pt., part, -s
Purbeck, Purbeckian
Queensl., Queensland
Rec., Recent
reconstr., reconstructed, -ion
reg., region
Rep., Republic
Rhaet., Rhaetian
R.I., Rhode Island
S., South, Sea
S.Am., South America
Santon., Santonian
Sarmat., Sarmatian
Sask., Saskatchewan
SC., South Central
S.Car., South Carolina
Scot., Scotland
SD, subsequent designation
S.D., Survey District
SE., Southeast
sec., section, -s
Senon., Senonian
ser., series, serial, etc.
Sh., Shale
Sib., Siberia
Sil., Silurian
s.l., **s.lat.**, *sensu lato* (in the wide sense, broadly defined)
Somali., Somaliland
sp., species
spp., species (plural)
Sp., Spain
Spitz., Spitzbergen
sq., square
s.s., **s.str.**, *sensu stricto* (in the strict sense, narrowly defined)
SSR, Soviet Socialist Republics
Stamp., Stampian
Str., Strait, -s
subfam., subfamily
suppl., supplement
SW., Southwest
Switz., Switzerland

tang., tangential
Tasm., Tasmania
Tatar., Tatarian
Tenn., Tennessee
Tert., Tertiary
Tex., Texas
Thanet., Thanetian
Thuring., Thuringian
Toarc., Toarcian
Torton., Tortonian
Tournais., Tournaisian
transl., translated, translation
transv., transverse
Trenton., Trentonian
Trias., Triassic
trop., tropical
Turon., Turonian
U., **Up.**, Upper
Univ., Universidad, Università, Université, Universitets, University
U.S., United States
USA, United States (America)
USNM, United States National Museum
USSR, Union of Soviet Socialist Republics
v., volume, -s
Va., Virginia
Valangin., Valanginian
var., variety
Venez., Venezuela
vert., vertical
Vict., Victoria
Vindobon., Vindobonian
Virgil., Virgilian
Vracon., Vraconian
vs., *versus* (opposed to)
Wash., Washington
W. Indies, West Indies, West Indies Federation
Wolfcamp., Wolfcampian
Wyo., Wyoming
Ypres., Ypresian
Yugo., Yugoslavia
Z., Zone
Zech., Zechstein
ZF, Zoology (Foraminifera)

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).

List of Serial Publications

Academia Brazileira de Sciencias, Anñaes. Rio de Janeiro.
[R.[1]] Academia de Ciencias y Artes de Barcelona, Memorias.
Académie Impériale de Metz, Mémoires. Metz.
Académie Impériale des Sciences, St. Pétersbourg, Mémoires [Akademiya Nauk SSSR, Leningrad].
Académie Royale des Sciences, des Lettres et des Beaux-Arts de Belgique, Bulletin. Bruxelles.
Académie des Sciences de Paris, Comptes Rendus; Mémoires. Paris.
Académie des Sciences URSS, Comptes Rendus [Akademiya Nauk SSSR, Leningrad].
Académie Tchèque des Sciences, Bulletin International, Classe des Sciences Mathématiques, Naturelles et de la Médecine [Česká Akademie véd a umění v Praze].
Academy of Natural Sciences of Philadelphia, Proceedings.
Accademia Gioenia delle Scienze Naturali di Catania, Bollettino. Sicily.
[R.] Accademia dei Lincei, Classe di Scienze Fisiche, Matematiche e Naturali, Memorie. Roma.
[R.] Accademia Nazionale [Italia] dei Lincei, Atti Rendiconti delle Sedute Solenni. Roma.

---

[1] R. or K. preceding a serial title stands for all forms meaning royal, imperial, e.g., Royale, Reale, Königliche, Kaiserliche, Kongelig, etc.

[R.] Accademia Pontaniana, Atti. Napoli.
Accademia Pontificia dei Nuovi Lincei, Memorie. Roma.
Accademia Scientifica Veneto-Trentino-Istriana, Atti. Padova.
[R.] Accademia delle Scienze, Atti. Torino.
[R.] Accademia delle Scienze Fisiche e Matematiche, Atti. Napoli.
[R.] Accademia delle Scienze dell'Instituto di Bologna, Memorie.
[R.] Accademia di Scienze, Lettere ed Arti, Atti; Memorie. Modena.
[R.] Accademia di Scienze, Lettere ed Arti degli Zelanti, Classe di Scienze, Memorie. Acireale.
Acta Palaeontologica Polonica [Polska Akademia Nauk, Komitet Geologiczny]. Warszawa.
Acta Universitatis Carolinae Geologica. Praha.
Akademie der Wissenschaften und der Literatur, Mainz, mathematisch-naturwissenschaftliche Klasse, Abhandlungen.
Akademie der Wissenschaftlichen zu München, mathematische-physikalische Klasse, Sitzungsberichten.
[K.[1]] Akademie der Wissenschaften, St. Petersburg [Akademiya Nauk SSSR, Leningrad].
[K.] Akademie der Wissenschaften zu Wien, Mathematische-Naturwissenschaftliche Classe, Denkschriften; Sitzungsberichte.
Akademiej Umìejetności Wydzial Matematyczno Przyrodniczy w Krakówie, Rozprawy. Krakow.
Akademiya Nauk Azerbaydzhan SSR, Doklady.
Akademiya Nauk Belorusskoy SSR, Institut Geologicheskikh Nauk, Paleontologiya i Stratigrafiya, Sbornik; Trudy; Doklady. Minsk.
Akademiya Nauk Kazakhskoy SSR, Institut Zoologiy, Institut Nefti, Trudy. Alma Ata.
Akademiya Nauk Kirgizhoy SSR, Institut Geologiy, Trudy; Izvestiya. Frunze.
Akademiya Nauk SSSR, Trudy; Doklady; Izvestiya. Moskva, Leningrad.
Akademiya Nauk SSSR, Institut Geologicheskikh Nauk, Trudy (Geologicheskaya Seriya). Moskva.
Akedemiya Nauk SSSR, Institut Paleontologicheskikh, Trudy (Paleontologicheskaya Seriya); Paleontologicheskiy Zhurnal. Moskva.
Akademiya Nauk SSSR, Kazanskogo Filiala, Institut Kazan, Geologicheskikh, Izvestiya. Kazan.
Akademiya Nauk SSSR Tadzhikskogo Kompleksnaya Ekspeditsiya, Trudy. Moskva.
Akademiya Nauk SSSR, Uralskiy Filial, Gorno-Geologicheskiy Institut, Trudy. Leningrad.
Akademiya Nauk SSSR, Voprosy Mikropaleontologiy. Moskva.
Akademiya Nauk Ukranskoy SSR, Institut Geologicheskikh Nauk, Trudy (Stratigrafiy i Paleontologiy Seriya). Kiev.
Akademiya Nauk Uzbekskoy SSR, Doklady.
Allan Hancock Foundation, Publications; Report of Pacific Expedition. Los Angeles.
American Academy of Arts and Sciences, Proceedings. Boston.
American Association of Petroleum Geologists, Bulletin. Tulsa, Okla.
American Geologist. Minneapolis, Minn.
American Journal of Botany. Lancaster, Pa.
American Journal of Conchology. Philadelphia, Pa.
American Journal of Science. New Haven, Conn.
American Midland Naturalist. Notre Dame, Ind.
American Museum of Natural History, Bulletins; Novitates; Micropaleontology. New York.
American Philosophical Society, Proceedings; Memoirs. Philadelphia, Pa.
Amsterdam Naturalist.
Annales de Biologie Lacustre. Bruxelles.
Annales de Géologie et de Paléontologie. Palermo.
Annales d'Histoire Naturelle. Paris.
Annales de Protistologie. Paris.
Annales des Sciences Naturelles. Paris.
Annals and Magazine of Natural History. London.
Arbeiten aus dem Biologischen Institut. München.
Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin, Jahrgang. Leipzig.
Archiv für Mikroskopische Anatomie. Bonn.
Archiv für Naturgeschichte. Leipzig, Berlin.
Archiv für Protistenkunde. Jena.
Archiv für Zoologie und Zootomie. Berlin.
Archives de Musée Teyler. Haarlem.
Archives Néerlandaises de Zoologie. Leiden.
Archives de Zoologie Expérimentale et Générale, Notes et Revues. Paris.
Arkiv för Botanik. Uppsala.
Arquivos do Museu Paranaense. Curitiba,. Brazil.
Asociación Mexicana Geólogos Petroleros, Boletín. Mexico D.F.
Association Française pour l'Avancement Sciéntifique, Comptes Rendus. Reims.
Australia Bureau of Mineral Resources, Geology and Geophysics, Bulletins; Reports. Canberra.
Australian Journal of Science. Sydney.
Australian Museum, Records. Sydney.
[K.] Bayerische Akademie der Wissenschaften, Mathematische-Physikalische Klasse, Abhandlungen. München.
Beiträge Zur Chemischen Mineralogie, Petrographie und Geologie. Jena.
Beiträge zur Naturkundlichen Forschung in Südwestdeutschland. Karlsruhe.
Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients. Wien.
Belfast Naturalists' Field Club, Proceedings. Belfast.
Bernice Pauahi Bishop Museum, Bulletin. Honolulu.
Bijdragen tot de Dierkunde. Leiden.
Biological Society of Washington, Proceedings. Washington, D.C.
Biologiya Belogo Morya, Belomorskoy Biologicheskoy Stantsii MGU, Trudy. Archangelsk.
[K.] Böhmischen Gesellschaft der Wissenschaften, Mathematische-Naturwissenschaftliche Klasse Abhandlungen; Sitzungsberichte. Praha. (*See* Rozpravy Třídy mathematicko-přirodově-decké Královsjé České Společnosti Náuk.)
Bollettino di Pesca, di Piscicoltura e di Idrobiologia. Roma.
Boston Society of Natural History, Proceedings.
Botanisches Zentralblatt. Jena. Dresden.
(Brasil) Divisão de Geologia e Mineralogia do Brasil, Ministério da Agricultura, Departmento Nacional da Produção Mineral, Boletim. Rio de Janeiro (*see* Serviço Geológico e Mineralógico do Brasil).
Breviora (*see* Harvard University Museum of Comparative Zoology).
British Association for the Advancement of Science, Reports. London.
British Museum (Natural History), Bulletins; Memoirs. London.
"Brotheria" Revista de Sciencias Naturaes do Col-

legio de San Fiel, Serie Botanica e Zoologica. Lisbõa.
Buffalo Society of Natural Science, Bulletin. Buffalo, N.Y.
Bulletin des Sciences de Bourgogne. Dijon.
Bulletin of Zoological Nomenclature. London.
Bulletin of American Paleontology. Ithaca, N.Y.
Cahiers Géologiques de Seyssel (Ain).
California Academy of Sciences, Proceedings. San Francisco.
California, University of, Publications in Zoology. Berkeley.
California, University of, Scripps Institution of Oceanography, Technical Series Bulletins. La Jolla (San Diego).
Cambridge Philosophical Society, Biological Reviews, Cambridge, Eng.
Canada, Geological Survey of, Department of Mines and Resources, Mines and Geology Branch, Bulletins; Memoirs. Ottawa.
Canadian Alpine Journal. Winnipeg, Canada.
Canadian Naturalist. Montreal, Canada.
Carnegie Institution of Washington, Publications. Washington, D.C.
Carnegie Museum, Annals. Pittsburgh, Pa.
Carte Géologique Detaillée de France, Mémoires. Paris.
Česká Akademie Císaře Františka Josefa pro Vědy, Slovestnost a Umění v Praze (Palaeontographica Bohemiae). Praha.
[K.] České Společnosti Náuk, Třída Mathematicko-Přírodovědecká, Věstník. Praha.
Challenger. Report on the Scientific Results of the Exploring Voyage of HMS Challenger. Zoology. Edinburgh.
Chester Society of Natural Science, Proceedings. Chester, Eng.
Chicago Natural History Museum, Fieldiana, Geology; Fieldiana, Geology Memoirs.
Chile, Universidad de, Instituto Geológico, Publicaciónes. Santiago.
(Chinese) National Research Institute of Geology (Academia Sinica), Memoirs. Shanghai.
Cincinnati Society of Natural History, Journal.
Colorado School of Mines, Quarterly. Golden, Colo.
Colorado, University of, Studies, General Series. Boulder, Colo.
[R.] Comitato Geologico d'Italia, Bollettino. Roma.
Congreso Geológico Venezuelano, Boletín de Geología; Memorias. Caracas.
Connecticut Geological and Natural History Survey, Bulletin. Hartford.
Copenhagen, Université de, Muséum de Mineralogie et de Géologie, Communications Paléontologiques. København.
Current Science. Bangalore, India.
Danmarks Geologiske Undersøgelse, Skrifter. København.
Dansk Geologisk Forening, Meddelelser. København.
Davenport Academy of Sciences, Proceedings. Davenport, Iowa.
Decheniana. Verhandlungen des Naturhistorischen Vereins der Rheinlande und Westfalens. Bonn.
Denison University Bulletin, Journal of the Scientific Laboratories. Granville, Ohio.
Deutsche Botanische Gesellschaft, Berichte. Berlin.
Deutsche Geologische Gesellschaft, Zeitschrift. Berlin, Hannover.
Deutsche Zoologische Gesellschaft, Verhandlungen. Leipzig.
Eclogae Geologicae Helvetiae. Basel (*see* Schweizerische Geologische Gesellschaft).
Edinburgh Geological Society, Transactions.
Ergebnisse und Fortschritte der Zoologie. Jena.
Erman's Archiv der Wissenschaften Russlands. Berlin.
Essex Field Club, Special Memoirs. London.
Experientia. Basel.
Feuille des Jeunes Naturalistes, Annales. Paris.
Fieldiana, Field Museum of Natural History (*see* Chicago Natural History Museum).
Florida Geological Survey, Bulletins. Tallahassee, Fla.
Földtani Közlöny [Magyaroni Földtani Társulat, Folyóirata]. Budapest.
Folia Zoologica et Hydrobiologica. Riga.
Fortschritte der Geologie. Köln, Leipzig.
Fortschritte der Paläontologie. Berlin.
Freiberger Forschungshefte. Berlin.
[K.] Fysiografiska Sällskapet, Lund, Handlingar.
Gegenbaurs Morphologisches Jahrbuch. Leipzig.
Geographische en Geologische Mededeelingen. Utrecht.
Geologia Romana. Roma.
Geological Magazine. London, Hertford.
Geological and Polytechnical Society of West Riding, Yorkshire, Proceedings.
Geological Society of America, Bulletin; Special Paper; Memoir. New York.
Geological Society of China, Bulletin. Peiping.
Geological Society of Glasgow, Transactions.
Geological Society of Japan, Journal. Tokyo.
Geological Society of London, Memoirs; Proceedings; Quarterly Journal; Transactions.
Geologie. Berlin.
Geologie en Mijnbouw, [K.] Nederlandsch Geologisch-Mijnbouwkundig Genootschap, Tijdschrift. 's Gravenhage.
Geologisch Rijksmuseum in Leiden, Publication.
[K.K.] Geologische Bundesanstalt Wien, Abhandlungen; Verhandlungen; Jahrbuch.
Geologische Landesanstalt von Elsass-Lothringen, Mitteilungen. Strassburg.
[K.K.] Geologische Reichsanstalt Wien (*see* Geologische Bundesanstalt Wien).
Geologische Rundschau (Geologische Vereinigung). Stuttgart, Leipzig, Berlin.
Geologische Spezialkarte Elsass-Lothringen, Abhandlungen. Strassburg.
Geologiska Föreningen, Stockholm, Förhandlingar.
Geologist's Association, Proceedings. London.
Gesellschaft zur Beförderung der Gesammten Naturwissenschaften zu Marburg, Sitzungsberichte.
[K.] Gesellschaft der Wissenschaften zu Göttingen, Mathematische-Physikalische Klasse, Abhandlungen; Nachrichten.
Giornale di Geologia (Annali del Museo di Geologia). Bologna.
Giornale di Scienze Naturali ed Economiche di Palermo.
Godishnik na Sofiyskiya Universitet. Sofia.
Gosudarstvennyi Okeanograficheskiy Institut, Trudy. Leningrad.
Great Britain, Geological Survey of, and Museum of Practical Geology, Memoirs. London.
Grenoble, Université de, Annales.

Gulf Coast Association of Geological Societies, Transactions. Houston, Tex.

Hamburg Geologisches Staatsinstitut, Mitteilungen.

Hamburgische Wissenschaftliche Anstalten, Jahrbuch.

Harvard University, Museum of Comparative Zoology, Bulletins; Memoirs; Breviora. Cambridge, Mass.

Helminthological Society of Washington, Proceedings. Washington, D.C.

Hessisches Landesamt für Bodenforschung, Notizblatt; Abhandlungen. Wiesbaden.

Hiroshima University, Journal of Science.

Hokkaido University, Journal of the Faculty of Science.

Hydrobiologia, Acta Hydrobiologica, Limnologica, et Protistologica. Den Haag.

Illinois State Geological Survey, Report of Investigations; Bulletins; Memoirs. Urbana, Ill.

Imperial Academy [of Japan], Proceedings. Tokyo.

India, Geological Survey of, Bulletins; Records; Memoirs (Palaeontologia Indica). Calcutta.

India, National Institute of Sciences, Proceedings. New Delhi.

Indiana Department of Conservation, Geological Survey, Bulletins. Bloomington, Ind.

Ingenieur in Nederlandsch-Indië, Mijnbouw Geologie. Bandoeng.

Institut d'Egypte, Bulletin. Cairo.

Institut Genévois, Mémoires. Genéve.

Institut Océanographique de Monaco, Bulletin. Monte Carlo, Paris.

Institut Royal des Sciences Naturelles de Belgique; Bulletin; Mémoire (*see* Musée Royal d'Histoire Naturelle de Belgique).

Instituto Geológico y Minero de España, Boletín; Memorias; Notas y Communicaciones. Madrid.

Iowa, State University of, Laboratory of Natural History, Bulletins; University of Iowa Studies (in Natural History). Iowa City, Iowa.

Israel Geological Survey, Bulletin. Jerusalem.

Japan, Geological Survey of, Bulletin; Report. Kawasaki.

Japanese Journal of Geology and Geography (Science Council of Japan). Tokyo.

Jenaische Zeitschrift der Wissenschaften. Jena.

Johns Hopkins University, Studies in Geology. Baltimore, Md.

Journal of Anatomy and Physiology. London.

Journal de Conchyliologie. Paris.

Journal of Geology. Chicago.

Journal of Paleontology. Tulsa, Okla.

Journal de Physique, de Chimie, d'Histoire Naturelle Élémentaires. Paris.

Journal of Protozoology. Washington, D.C.

Kansas State Geological Survey, Bulletins, Volumes. Lawrence.

Kansas, University of, Paleontological Contributions, Articles. Lawrence.

Kieler Meeresforschungen. Kiel.

Komission für Untersuchungen der Deutschen Meere in Kiel, Jahresberichte.

Kyushu University Faculty of Science, Memoirs. Fukuoka.

Laboratoire Maritime de Dinard, Bulletin.

Leiden Rijksuniversiteit, Leidsche Geologische Mededeelingen. Leiden.

[K.] Leopoldischen Carolinischen Deutschen Akademie für Naturforschung, Nova Acta Leopoldina; Abhandlungen. Halle.

Linnean Society of London, Transactions.

Linnean Society of New South Wales, Proceedings. Sydney.

Louisiana Department of Conservation, Louisiana State Geological Survey, Geological Bulletins. Baton Rouge.

Lund Universitet, Årsskrift.

Lvovskogo Geologicheskogo Obshchestva pri Gosudarstvennom Universitete im Ivana Franko, Trudy. Lvov.

Lyon Faculté des Sciences, Laboratoire de Géologie, Travaux. Lyon.

Lyon, Université de, Annales.

Magazine of Zoology and Botany. Edinburgh, London.

Maygar Királyi Földtani Intezet Évkönyve. Budapest.

Manchester Literary and Philosophical Society, Memoirs and Proceedings. Manchester, Eng.

Marine Biological Association of the United Kingdom, Journal. Cambridge, Eng.

Maroc Service Géologique du Division des Mines et de la Géologie, Notes et Mémoires. Rabat.

Maryland Geological Survey. Baltimore.

Materialy po Geologii Poleznym Iskopaemym Azovo-Chernomorskoye Upravlenie, Moskva.

Materialy po Istorii Fauny in Flory Kazakhstana. Alma Ata.

Mathematische und Naturwissenschaftliche Berichte aus Ungarn. Leipzig.

Meddelelser om Grønland (Kommissionen Videnskabelige Undersøgelser i Grønland). København.

México Universidad Nacional, Paleontología Méxicana; Instituto de Geología Boletín. México, D.F.

Micropaleontology (American Museum of Natural History). New York.

Michigan, University of, Museum of Paleontology, Contributions. Ann Arbor.

Missouri Geological Survey and Water Resources, Bulletins; Reports of Investigations. Rolla.

Missouri, University of, Technical Series Bulletins. Columbia.

Moskovskogo Obshchestvo Ispytateley Prirody (Société Impériale des Naturalistes de Moscou, Bulletin).

Muséum National [France] d'Histoire Naturelle, Mémoires. Paris.

Musée royal d'Histoire naturelle de Belgique, Mémoires; Bulletin. Bruxelles.

Museo de Historia Natural de Mendoza, Revista.

Museo Libico di Storia Naturale, Annali. Tripoli.

Museo Nacional [España] de Ciencias Naturales, Trabajos. Madrid.

Napoli, Università di, Museo Zoologico, Annuario. Napoli.

Národního Musea v Praze, Sborník (Acta Musei Nationalis Praque). Praha.

National Academy of Science (*see* United States).

National Research Institute of Geology (*see* Chinese).

Natural History Review, London.

Natural History Society of New Brunswick, Bulletin. St. John.

Naturaliste. Paris.

Nature. London.

Naturforschende Gesellschaft in Basel, Verhandlungen.

Naturforschende Gesellschaft in Danzig, Schriften.
Naturforschende Gesellschaft zu Freiburg in Baden.
Naturforschender Verein in Brünn, Verhandlungen; Sitzungsberichte.
Naturhistorische Gesellschaft zu Hannover, Jahresbericht.
Naturhistorische Gesellschaft zu Nürnberg, Abhandlungen.
[K.K.] Naturhistorisches Hofmuseums, Annalen. Wien.
Naturhistorisk Tidsskrift. København.
[Die] Naturwissenschaften, Berlin.
Naturwissenschaftlicher Verein für Neu-Vorpommern und Rügen in Griefswald, Mitteilungen. Berlin.
Naturwissenschaftlicher Verein für Schleswig-Holstein, Schriften. Kiel.
Naturwissenschaftlicher Verein für Steiermark, Mitteilungen. Graz.
Naturwissenschaftliche Zeitschrift "Lotos." Praha.
Natuurhistorisch Maandblad. Maastricht.
Natuurhistorische Genootschap Limburg. Heerlen.
Natuurkundig Tijdschrift voor Nederlandsch-Indië. Batavia.
Natuurkundige Verhandelingen van de Hollandsche Maatschappij der Wetenschappen te Haarlem.
[The] Nautilus. Philadelphia, Boston.
[K.] Nederlandsch Geologisch-Mijnbouwkundig Genootschap, Verhandelingen, Geologische Serie. 's Gravenhage.
[K.] Nederlandse Akademie van Wetenschappen, Afdeeling Natuurkunde, Verhandelingen. Amsterdam.
Nederlandsche Dierkundige Vereenigung, Tijdschrift. Leiden.
Neues Jahrbuch für Geologie und Paläontologie (Neues Jahrbuch für Mineralogie, Geologie, und Paläontologie), Beilage-Band. Stuttgart.
Neues Jahrbuch für Mineralogie (Neues Jahrbuch für Mineralogie, Geologie und Paläontologie), Abhandlungen; Beilage-Bande; Monatshefte, Stuttgart.
Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde. Stuttgart.
New Biology. London.
New Jersey, Geological Survey of, Paleontology. Trenton, N.J.
New Mexico State Bureau of Mines and Mineral Resources, Bulletin; Circular; Memoir. Socorro.
New York Academy of Science, Annals; Scientific Survey of Porto Rico and Virgin Islands. New York.
New York State Geological Survey, Palaeontology of New York, Albany.
New York State Museum, Bulletin. Albany.
New Zealand Institute, Transactions and Proceedings. Wellington.
New Zealand Journal of Geology and Geophysics. Wellington.
New Zealand Journal of Science and Technology. Wellington.
Norsk Geologisk Tidsskrift. Oslo.
[K.] Norske Videnskabers Selskab, Skrifter; Forhandlinger. Trondhjem, Oslo.
Norske Videnskaps-Akademi, Oslo, Skrifter.
North Carolina Geological Survey, Report [now Department of Conservation and Development of the State of North Carolina, Division of Mineral Resources]. Raleigh.
Northwest Science. Cheney, Wash.
Nova Acta Leopoldina, Neue Folge. [Nova Acta Academiae Caesarae Leopoldino-Carolinae Germanicae naturae curiosorum]. Halle.
Nova Guinea Uitkomsten Nederlandsche Nieuw-Guinea Expeditie 1903. Leiden.
Nuovi Annali delle Scienze Naturali di Bologna.
Nytt Magasin av Zoologi. Oslo.
Offenbacher Vereins für Naturkunde, Bericht über die Tätigkeit des. Offenbach a. M.
Oklahoma Academy of Sciences, Proceedings. Stillwater, Okla.
Oklahoma Geological Survey, Bulletins; Circulars; Geology Notes. Norman, Okla.
Osnovy Paleontologiy, Spravochnik Dlya Paleontologov I Geologov SSSR. Yu. A. Orlov, ed. Akademiya Nauk SSSR. Moskva.
Österreichische Akademie der Wissenschaften, mathematisch-naturwissenschaftliche Klasse, Denkschriften. Wien.
Pakistan, Geological Survey of, Palaeontologia Pakistanica. Karachi.
Palaeobiologica. Wien.
Palaeontographia Italica (Memorie di Paleontologia). Pisa.
Palaeontographica, Abteilung A; Abteilung B. Stuttgart & Kassel.
Palaeontographica Bohemiae [Česká akademie věd a umění v Praze, Vydavá, Třída II]. Praha.
Palaeontographical Society, Memoirs. London.
Palaeontological Society of India, Journal. Lucknow.
Palaeontological Society of Japan, Transactions and Proceedings. Tokyo.
Paläontologische Zeitschrift. Berlin & Stuttgart.
Paläontologisches Zentralblatt. Leipzig.
Palaeontology (Palaeontological Association). London.
Paleontologicheskaya Laboratoriya Moskovskogo Gosudarstvennogo Universiteta, Etyudy po Mikropaleontologii. Moskva.
Paleontologicheskiy Zhurnal (*see* Akademiya Nauk SSSR, Paleontologicheskiy Institut).
Pamiętnik Towarzystwa Nauk Ścisłych w Paryżu. Poland.
Pan-American Geologist. Des Moines, Iowa.
Philippine Journal of Science. Manila.
Physikalisch-medizinische Sozietät in Erlangen, Sitzungsberichte.
Physikalisch-medezinische Gesellchaft zu Würzburg, Sitzungsberichte.
[K.] Physikalisch-ökonomische Gesellschaft zu Königsberg, Schriften.
Polskiego Towarzystwa Geologicznego z Roku, Rocznika. Warszawa.
[K.] Preussische Akademie der Wissenschaften, Abhandlungen; Monatsberichte. Berlin.
[K.] Preussische Geologische Landesanstalt, Abhandlungen. Berlin.
Protoplasma. Leipzig.
Quarterly Journal of Microscopical Science. London.
Quarterly Review of Biology. Baltimore, Md.
Ray Society Publications. London.
Revue de l'Institut Français du Pétrole et Annales des Combustibles Liquides. Paris.
Revue Magasin de Zoologie. Paris.
Revue de Micropaléontologie (Laboratoire de Micropaléontologie). Paris.

Revue Suisse de Zoologie; Annales de la Société Zoologique Suisse et du Muséum d'Histoire Naturelle de Genève.
Revue de Zoologie et de Botanique Africaines. Bruxelles.
Rivista Italiana di Paleontologia. Parma.
Rivista Italiana di Paleontologia e Stratigrafia. Milano.
Rivista Italiana di Scienze Naturali, Bollettino. Siena.
Royal Asiatic Society, Bombay Branch, Journal. Bombay.
Royal Irish Academy, Proceedings. Dublin.
Royal Microscopical Society of London, Journal.
Royal Society of Canada, Transactions. Ottawa.
Royal Society of Edinburgh, Transactions; Memoirs. Edinburgh.
Royal Society of London, Philosophical Transactions, Series A; Series B.
Royal Society of New South Wales, Journal. Sydney.
Royal Society of New Zealand, Transactions and Proceedings. Dunedin.
Royal Society of South Australia, Transactions; Memoirs; Proceedings. Adelaide.
Royal Society of Victoria, Proceedings. Melbourne.
Russiche-Kaiserliche mineralogische Gesellschaft zu St. Petersburg, Verhandlungen [Vserossiykoe Mineralogicheskoe Obshchestvo, Leningrad].
Saigon, Université de, Annales de la Faculté des Sciences. Saigon.
Saitama University [Japan], Science Reports.
San Diego Society of Natural History, Transactions. San Diego, Calif.
São Paulo, Universidade de, Faculdade de Filosofia, Ciências e Letras, Boletim.
Schlesische Gesellschaft für vaterländische Kulture, Jahresbericht. Breslau.
Schweizerische Paläontologische Gesellschaft, Abhandlungen (same as Société Paléontologique de la Suisse). Zurich.
Science. New York, Washington, D.C.
Sciences Naturelles, Annales. Paris.
Scotland, Geological Survey of, Memoirs. Edinburgh.
Senckenbergiana Letheae* [Senkenbergische Naturforschende Gesellschaft, Wissenschaftliche Mitteilungen] [*"Letheae" added to title, 1954]. Frankfurt am Main.
Senckenbergische Naturforschende Gesellschaft, Abhandlungen. Frankfurt am Main.
Service de la Carte Géologique de l'Algérie, Travaux des Collaborateurs, Publications, Alger.
Service Géologique de l'Indochine, Mémoires. Saigon.
Service Géologique du Maroc, Division des Mines et de la Géologie, Notes. Rabat.
Serviço Geológico e Mineralógico do Brasil, Ministerio da Agricultura, Monographias; Boletim, Rio de Janeiro.
Siebenburgischer Verein für Naturwissenschaften in Hermannstadt, Verhandlungen und Mitteilungen.
Smithsonian Contributions to Knowledge, Washington, D.C.
Smithsonian Institution, Harriman Alaska Series, Geology and Paleontology. Washington, D.C.
Smithsonian Miscellaneous Collections. Washington, D.C.
Sociedad de Ciencias Naturales "La Salle," Memorias. Caracas.
Sociedad Cubana de Historia Natural, Memorias. Habana.
Società Geologica Italiana, Bollettino. Roma.
Società Italiana delle Scienze, Memorie. Trento.
Società Italiana di Scienze Naturali, Atti. Milano.
Società Naturalisti in Napoli, Bolletino. Napoli.
Società Toscana di Scienze Naturali Residente in Pisa, Memorie.
Societatis Regiae Scientarum Gottingensis, Commentationis.
Société Belge de Géologie, de Paléontologie, et d'Hydrologie, Bulletin. Bruxelles.
Société de Biologie, Comptes Rendus Hebdomadaires des Séances et Mémoires. Paris.
Société Botanique de France, Bulletin. Paris.
Société Botanique de Genève, Bulletin. Switzerland.
Société Géologique de France, Bulletin; Mémoires; Comptes Rendus des Séances. Paris.
Société Géologique du Nord, Annales. Lille.
Société Helvétique des Sciences Naturelle, Travaux; Comptes Rendus. Lausanne, Switz.
Société d'Histoire Naturelle de l'Afrique du Nord, Bulletin. Alger.
Société d'Histoire Naturelle d'Autun, Bulletin.
Société d'Histoire Naturelle de Paris, Mémoires.
Société d'Histoire Naturelle de Toulouse, Bulletin.
Société Impériale des Naturalistes de Moscou, Bulletin [Moskovskogo Obshchestvo Ispytateley Prirody].
Société Linnéene de Lyon, Bulletin.
Société Linnéene de Normandie, Bulletin. Caen.
Société Paléontologique de la Suisse, Mémoires. (Same as Schweizerische Paläontologische Gesellschaft.) Zürich.
Société de Physique et d'Histoire Naturalle de Genève, Mémoires.
Société Royale Malacologique de Belgique, Annales; Mémoires. Bruxelles.
Société Vaudoise des Sciences Naturelles, Bulletin. Lausanne, Switz.
Société Zoologique de France, Bulletin. Paris.
Society of Economic Paleontologists and Mineralogists, Special Publications. Tulsa, Okla.
Southern California Academy of Sciences, Bulletin. Los Angeles.
Sovetskaya Geologiya. Moskva.
Stanford University, Contributions of the Department of Geology. Palo Alto, Calif.
Státního Geologického Ústavu Československe Republiky, Věstník. Praha.
Stockholm Contributions to Geology (Acta Universitatis Stockholmiensis). Stockholm.
Suomalaisen Tiedeakatemian Toimitukala (Annales de l'Académie Scientifique Fennicae). Helsinki.
Svensk Faunistick Revy [1955, Zoologisk Revy]. Stockholm.
[K.] Svenska Vetenskapsakademien, Handlingar, Förhandlingar, Stockholm.
Sveriges Geologiska Undersökning, Årsbok; Afhandlingar. Stockholm.
Systematic Zoology. Lawrence, Kans.
Tartu Ülikooli Geoloogia-Instituudi Toimestused, Acta et Commentationes Universitatis Tartuensis (Dorpatensis). Tartu, Estonia.
Tashkentskoy Gosudarstvennogo Universiteta im V. I. Lenina, Trudy. Tashkent.
Tennessee Department of Conservation and Com-

merce, Division of Geology, Bulletins. Nashville.
Termeszetrajzi Füzetek. Budapest.
Texas, University of, Bulletins; Publications. Austin, Tex.
Tohoku University, Institute of Geology and Paleontology, Short Papers; Scientific Reports. Sendai, Japan.
Tokyo Bunrika Daigaku, Science Reports.
Tokyo Kyoiku Daigaku, Science Reports.
Türkiye Jeoloji Kurumu (Geological Society of Turkey), Bülteni. Istanbul.
United States Geological and Geographical Survey of the Territories, Annual Reports. Washington, D.C.
United States Geological Survey, Bulletins; Professional Papers. Washington, D.C.
(United States) National Academy of Science, Proceedings; Memoirs. Washington, D.C.
United States National Museum, Bulletins; Proceedings. Washington, D.C.
[R.] Università Biologico Laboratorio, Ricerche. Roma.
Universitet Innsbruck, Schlernschriften, Veröffentlichungen zur Landeskunde von Südtirol. Innsbruck.
Ústřední Ústav Geologichky Svazek, Sborník; Věstnik. Praha.
Venezuela Ministerio de Minas y Hidrocarbúros, Boletín de Geología. Caracas.
Verein der Freunde der Naturgeschichte in Mecklenburg, Archiv. Güstrow.
Verein der Preussische Rheinlands Westfalens, Verhandlungen. Köln.
Verein für vaterländische Naturkunde in Württemberg, Jahreshefte. Stuttgart.
Victoria Department of Mines, Mining and Geological Journal. Melbourne.
Victoria, Geological Survey of, Bulletins; Memoirs; Records. Melbourne.
Victoria Institute of Trinidad, Proceedings. Trinidad, B.W.I.
Victoria, National Museum of, Memoirs. Melbourne.
Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København.
Videnskabsselskabet i Kristiania, Forhandlinger. Oslo.
Vsesoyuznyi Nauchno-Issledovatelskii Geologorazvedachnyi Neftyanoi Institut, Trudy. Moskva.
Vsesoyuznyi Nauchno-Issledovatelskii Institut Geofizicheskikh Metodov Razvedki, Trudy. Moskva.
Vsesoyuznyi Neftyanoi Nauchno-Issledovatelskii Geologo-Razvedochnyi Institut, Trudy. Leningrad, Moskva.
Vsesoyuznoe Paleontologicheskoe Obshchestvo, Ezhegodnik. Moskva.
Wagner Free Institute of Science of Philadelphia, Bulletin.
Washington Academy of Sciences, Journal. Washington, D.C.
Yale University, Peabody Museum of Natural History, Bulletins; Sears Foundation for Marine Research, Memoirs. New Haven, Conn.
Zeitschrift für Geschiebeforschung und Flachlandsgeologie. Berlin.
Zeitschrift für Mineralogie. Berlin.
Zeitschrift für Natur- und Heilkunde der K. Medicinisch-chirurgisch Akademie St. Petersburg.
Zeitschrift für Naturwissenschaften. Halle.
Zeitschrift für Wissenschaftliche Mikroskopie und Mikroskopische Technik. Leipzig.
Zeitschrift für Wissenschaftliche Zoologie. Leipzig.
Zentralblatt für Mineralogie, Geologie und Paläontologie. Stuttgart.
Zoological Journal. London.
Zoological Society of London, Proceedings; Transactions.
Zoologische Jahrbücher, Supplementen. Jena.
Zoologischer Anzeiger. Leipzig.
Zoologischer Jahresbericht. Berlin.
Zoologiska Bidrag från Uppsala. Uppsala, Stockholm.

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	NORTH AMERICA
ROCKS OF CENOZOIC ERA	**ROCKS OF CENOZOIC ERA**
NEOGENE SYSTEM[1]	**NEOGENE SYSTEM**[1]
Pleistocene Series (including Recent)	Pleistocene Series (including Recent)
Pliocene Series	Pliocene Series
Miocene Series	Miocene Series
PALEOGENE SYSTEM	**PALEOGENE SYSTEM**
Oligocene Series	Oligocene Series
Eocene Series	Eocene Series
Paleocene Series	Paleocene Series
ROCKS OF MESOZOIC ERA	**ROCKS OF MESOZOIC ERA**
CRETACEOUS SYSTEM	**CRETACEOUS SYSTEM**
Upper Cretaceous Series	**Gulfian Series (Upper Cretaceous)**
Maastrichtian Stage[2]	Navarroan Stage
Campanian Stage[2]	Tayloran Stage
Santonian Stage[2]	Austinian Stage
Coniacian Stage[2]	
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)
Bathonian Stage	Bathonian Stage
Bajocian 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 Series (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
CARBONIFEROUS SYSTEM	
Upper Carboniferous Series	**PENNSYLVANIAN SYSTEM**
Stephanian Stage	**Kawvian Series (Upper Pennsylvanian)**
	Virgilian Stage
	Missourian Stage
Westphalian Stage	**Oklan Series (Middle Pennsylvanian)**
	Desmoinesian Stage
	Bendian Stage
	Ardian Series (Lower Pennsylvanian)
	Morrowan Stage
	MISSISSIPPIAN SYSTEM
	Tennesseean Series (Upper Mississippian)
Namurian Stage	Chesteran Stage
Lower Carboniferous Series	
Viséan 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)**
Coblenzian Stage	Onesquethawan Stage
	Deerparkian Stage
Gedinnian Stage	Helderbergian Stage
SILURIAN SYSTEM	**SILURIAN SYSTEM**
Ludlow Series	**Cayugan Series** Includes age equivalents of middle and upper Ludlow (in New York)
Wenlock Series	**Niagaran Series** Includes age equivalents of upper Llandovery, Wenlock, and lower Ludlow (in New York)
Landovery Series	**Medinan Series** Includes age equivalents of lower and middle Llandovery (in New York)
ORDOVICIAN SYSTEM	**ORDOVICIAN SYSTEM**
	Cincinnatian Series (Upper Ordovician)
	Richmondian Stage
Ashgill Series	Maysvillian Stage
	Edenian Stage
Caradoc Series	**Champlainian Series (Middle Ordovician)**
	Mohawkian Stage
	Trentonian Substage
	Blackriveran Substage
Llandeilo Series	Chazyan Stage
Llanvirn Series	
Arenig Series	**Canadian Series (Lower Ordovician)**
Tremadoc Series	
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

---

[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 C

PROTISTA 2

SARCODINA CHIEFLY "THECAMOEBIANS" AND FORAMINIFERIDA

By Alfred R. Loeblich, Jr.,[1] and Helen Tappan[2]

with some systematic descriptions of Foraminiferida by R. Wright Barker, W. Storrs Cole, R. C. Douglass, Manfred Reichel, and M. L. Thompson as recorded

VOLUME 1

CONTENTS

[Volume 1, p. i-xxxi, 1-510a; Volume 2, p. 511-900]

---

[1] California Research Corporation.

[2] University of California Los Angeles.

INTRODUCTION

The Sarcodina comprise one of the four main subdivisions of protozoans, and include those forms which have a single-celled protoplasmic body, amoeboid in form and nonflagellate during its principal stage, the cell wall without a thick pellicle and capable of forming pseudopodia, the characteristic locomotor apparatus of the subphylum. Included in the Sarcodina are large groups of organisms found as microfossils—"thecamoebians," foraminifers and radiolarians—as well as many equally large groups of nonshelled forms, some of which, because of parasitic habit, are more important to zoologists than to paleontologists.

As recently discussed by us (*1181[1]), the Sarcodina may be subdivided into two major groups on the basis of types of pseudopodia and protoplasmic movements. One group is characterized by a protoplasmic movement based on differential pressure produced by contraction of a plasmagel cortex (semisolidified protoplasm), which results in a flow of plasmasol (liquefied protoplasm). This type of movement and lobose pseudopodia associated with it are characteristic of the orders Amoebida, Mycetozoida, and Arcellinida, which are regarded by us as belonging to the restricted class Rhizopodea. Remaining Sarcodina are characterized by a filament-streaming type of protoplasmic movement, regarded by JAHN & RINALDI (*984) as due to a shearing force between two adjacent, oppositely moving gel-like filaments within a pseudopod, and without the presence of a plasmagel cortex. Whether or not this explanation for the mechanism of movement is correct, there is an easily observed difference in the character of the pseudopodia, with their continual two-way movement of protoplasm, contrasting with the ebb and flow of protoplasmic movement in the Lobosia. The filament-streaming occurs in the subclasses Filosia and Granuloreticulosia of the Sarcodina, and also in the heliozoans, radiolarians, and acantharians (these last groups already covered in *Treatise* Part D), all of which were included as subclasses of the class Reticularea (*1181).

ACKNOWLEDGMENTS

In this work, involving a classification of a major part of the Rhizopodea, LOEBLICH & TAPPAN wish to acknowledge the generous assistance given by many colleagues. During 1953-1954 a year was spent in Europe studying types in various museums and institutions and collecting topotypes of type-species of various genera in England, France, Italy, Spain, Netherlands, Germany, and Austria. During this time, HELEN TAPPAN was a Fellow of the John Simon Guggenheim Foundation, and ALFRED R. LOEBLICH, JR., was on the staff of the U. S. National Museum, Smithsonian Institution. To both of these organizations we are greatly indebted for this opportunity to study and collect in Europe and thus settle many taxonomic problems, as well as broaden our general knowledge of the Foraminiferida.

We are especially grateful to the British Museum (Natural History), London, for courtesies extended to us during four months in London, and for their permission to study and reillustrate the types of BRADY, PARKER & JONES, and others, and to select and isolate lectotypes for many of these as noted in the following systematic descriptions. During this visit, an exchange was arranged through the Keeper of Zoology, Dr. W. H. PARKER, for specimens from the working slides of BRADY (not the figured or catalogued types) to be deposited in the U. S. National Museum in exchange for other identified types to be deposited in the British Museum. Certain of these exchange specimens were illustrated in the U.S. National Museum Bulletin 215 as BRADY paratypes in the U.S. National Museum. Because of later published comments by persons not connected with either institution (*79, p. 26) that there was no record of such an exchange and because the staffs of both museums had changed meanwhile, according to information given to us, the U.S. National Museum has returned

---

[1] Asterisk-marked numbers in the text correspond to index numbers given in the references to literature beginning on page C797.

these specimens to the British Museum; hence they are no longer in the U.S. National Museum.

Similarly, we express our appreciation to the Muséum National d'Histoire Naturelle, Paris, for permission to examine and restudy the d'Orbigny types on deposit there. Many lectotypes of the type-species of genera were also isolated with the assistance of Dr. P. Marie, and the permission of Dr. J. Roger, then of the Museum, and were so labeled during our studies in Paris in 1954. These are also indicated in the systematic descriptions.

While in Europe we received much assistance in the field or museums from the following persons. In Great Britain we were aided by Dr. T. Barnard, University College, London; Mr. D. Carter, Imperial College, London; Dr. R. Casey, Geological Survey, London; Dr. R. H. Cummings, Glasgow University; Mr. Dennis Curry, Middlesex; the late Mr. A. G. Davis, Dr. W. H. Parker, and Dr. N. Tebble, all of the British Museum (Natural History), London; Mr. G. Elliott, Dr. A. Smout and Dr. F. R. S. Henson, Iraq Petroleum Co., London; Dr. W. Pitcher, Imperial College, London; and Prof. A. Williams, Queens University, Belfast. In France valued help was received from Dr. P. Marie, Bureau des Recherches Géologiques et Minières, Paris; Dr. J. Roger, Muséum National d'Histoire Naturelle, Paris; Dr. J. Cuvillier, Laboratoire de Géologie Appliqué, Paris; Prof. R. Ciry, Dr. H. Tintant, and Dr. P. Rat, of the University of Dijon; Mme. Y. Gubler and Dr. M. Lys, of the Institut Français du Pétrole; M. V. Pérébaskine, Pau; Dr. J. M. Payard, Poitiers; Dr. M. Vignoux and M. Magne, University of Bordeaux; M. Duperieur, Biarritz; Prof. M. Casteras and Mlle. Villatte, University of Toulouse; and Prof. Corroy, Dr. S. Taxy-fabre, and Dr. Catzigras, of the University of Marseille. In Italy we were aided in the field by Dr. E. Di Napoli-Alliata, Rome; Prof. B. Accordi, of the University of Ferrara; Prof. R. Selli, University of Bologna; and Prof. E. Montanaro-Gallitelli, University of Modena. In Spain we were accompanied by Dr. J. R. Bataller, University of Barcelona. In the Netherlands, Drs. J. H. van Voorthuysen, S. van der Heide, and van der Vaals, of the Netherlands Geological Survey, and Dr. J. Hofker, The Hague, were extremely helpful. In Germany we were aided by Drs. H. Hiltermann and F. Schmid, Amt. für Bodenforschung, Hannover; Dr. H. Bartenstein, Mobil Oil, A. G., Celle; Dr. R. Giers, Hamm; Dr. E. Brand, Wintershall A. G. Kassel; Drs. H. Beckmann and F. Bettenstedt, Preussiche Bergwerks and Hutten A. G., Hannover; Dr. H. G. Knipscheer, then of the Bavarian Geological Survey, Munich; Dr. E. Buck, Würtemburg Geological Survey, and the late Dr. K. Feifel, Kirchheim u. Teck.

We have received specimens as gifts, exchanges, or loans, helpful to an understanding of many genera from Dr. H. V. Andersen, Louisiana State University, Baton Rouge; Dr. K. Asano, Tohoku University, Sendai, Japan; Dr. O. L. Bandy, University of Southern California, Los Angeles; Mr. D. J. Belford, Bureau of Mineral Resources, Canberra, Australia; Dr. P. J. Bermúdez, Ministerio de Minas e Hidrocarburos, Caracas, Venezuela; Prof. F. Bieda, Katedra Paleontologii A. G.-H., Krakow, Poland; Dr. H. Bolli, Shell Oil Company, Caracas, Venezuela; Dr. E. Boltovskoy, Buenos Aires, Argentina; Dr. F. Brotzen, Sveriges Geologiska Undersökning, Stockholm, Sweden; Mr. A. C. Collins, Geelong, Victoria, Australia; Miss I. Crespin, Bureau of Mineral Resources, Canberra, Australia; Dr. C. W. Drooger, Geological Institute, Utrecht, Netherlands; Dr. S. Geroch, Universytet Jagiellonski, Krakow, Poland; Dr. H. Hagn, University of Munich, Munich, Germany; Dr. A. F. M. M. Haque, Geological Survey of Pakistan, Quetta; Dr. H. Höglund, Havsfiskellaboratoriet, Lysekil, Sweden; Dr. N de B. Hornibrook, New Zealand Geological Survey, Lower Hutt, New Zealand; Dr. I. de Klaz, Société des Pétroles d'Afrique Equatoriale, Port-Gentil, Gabon; Dr. E. Kristan-Tollman, Geologische Bundesanstalt, Vienna, Austria; Dr. Yolande Le Calvez, Bureau des Recherches Géologique et Minière, Paris; Dr. J. Małecki, Katedra Paleontologii, A.G.-H., Krakow, Poland; Dr. T. Matsunaga, Teikoku Oil Company, Tokyo, Japan; Miss F. L. Parker, Scripps Institution of Oceanography, La Jolla, California; Dr. V. Pokorný, Charles University, Prague, Czechoslovakia; Dr. A. Ramovs, University of

Ljubljana, Jugoslavia; Prof. M. Reichel, Basel, Switzerland; Mr. J. B. Saunders, Trinidad Texaco Inc., Pointe-a-Pierre, Trinidad, West Indies; Dr. J. Sigal, Rueil Malmaison, France; Dr. Y. Takayanagi, Tohoku University, Sendai, Japan; Dr. J. C. Troelsen, Petrobrás Setex, Salvador, Brazil; Dr. T. Uchio, University of Tokyo, Bunkyo-Ku, Japan; Miss Mary Wade, University of Adelaide, Australia; Dr. R. T. D. Wickenden, Geological Survey of Canada, Calgary, Canada; and Prof. Z. Shchedrina, Zoological Institute, Academy of Sciences USSR, Leningrad.

We have had considerable assistance in obtaining literature from the USSR from Prof. D. Rauzer-Chernousova, Geological Institute, Academy of Sciences USSR, Moscow, who provided many papers and books and in addition photocopies of several papers not available in any library in the United States. Prof. B. V. Tkachenko, Director, Instituta Geologii Arktiki, Leningrad, and Dr. A. A. Gerke of the same institute, were very helpful in assisting us in obtaining several rare publications of that institute. Prof. N. N. Subbotina, Drs. N. K. Bykova, E. V. Myatlyuk, L. Dain, and N. A. Voloshinova obtained numerous Soviet articles for us, as well as photocopies of others. Drs. A. K. Bogdanovich, V. A. Krasheninnikov, R. L. Merklin, T. A. Moskalenko, V. G. Morozova, E. A. Reytlinger, M. Ya. Serova, and A. S. Stoliyarov, of the Geological Institute, Academy of Sciences USSR, Moscow, and Dr. I. S. Suleymanov, Tashkent, Uzbek SSR, were very helpful in providing needed literature and information. Profs. A. V. Fursenko, Minsk, and Zoya Shchedrina, Leningrad, provided much valuable information. We are indebted to Dr. E. V. Bykova, Geological Institute, Kazakhaya Academy of Sciences, Alma-Ata, for also providing for use in the *Treatise* many original photographic negatives of specimens described by her from Kazakhstan. Prof. A. D. Miklukho-Maklay, Leningrad University, was very helpful in providing references to several genera described in the USSR and in aiding us in obtaining this material. Dr. K. V. Miklukho-Maklay, of the same institution, was also helpful in providing literature. Drs. D. M. Khalilov and Ch. A. Tairov, of the Geological Institute, Academy of Science, Azerbaidzhan SSR; Dr. O. K. Kaptarenko-Chernousova, Geological Institute, Academy of Science Ukraine RSR; and Dr. Kh. M. Saidova, Oceanological Institute, Academy of Sciences, Moscow, furnished much useful information. Without this help from our colleagues in the Soviet Union we would not have had as complete a coverage of the genera described from the USSR represented in our portion of the *Treatise*.

The later stages of this work have also been greatly facilitated by the excellent interlibrary loan staff at the University of California, Los Angeles; in particular, Mrs. Esther Euler, Mr. E. Mignon, and Mr. P. Warshaw are to be commended for the personal interest they took in our problems in preparing chapters in this volume of the *Treatise*. Without their willing efforts in obtaining many rare and old publications our task would have been immeasurably more difficult. The Department of Geology at the University of California Los Angeles also allowed us nearly full-time assistance of the departmental photographer for some months in preparation of certain of the illustrations.

We have benefited from discussion with members of the staff at the La Habra Laboratory of California Research Corporation and have had much help from Drs. M. A. Furrer, D. Levandowski, and R. W. Rex in preparation of our typescript.

Finally we wish to express our appreciation to California Research Corporation and especially to Mr. R. F. Faull, Vice-President, San Francisco; Mr. A. Hildebrand, Laboratory Director, La Habra; Dr. N. A. Riley, Assistant Laboratory Director, La Habra; and to Dr. W. J. Plumley, Geological Supervisor, La Habra; for their appreciation of basic science and for their encouragement and generous assistance given to the preparation of this volume, not only in nearly full-time work by A. R. Loeblich, but support in preparation of illustrations, X-ray and petrographic determinations and typing. Without such support, preparation of this volume would have been greatly delayed to say the least.

In the systematic sections which follow, the various groups are covered in the normal zoological order, with brief diagnoses and synonymies given only to the subfamily level for the naked Sarcodina. Introductory discussions, glossaries, and references are given with each of the major sections devoted to groups that may be preserved in the fossil record. Morphological terms used in the diagnoses of the naked forms will be found in the glossaries of the related testaceous forms.

SARCODINA, RHIZOPODEA, LOBOSIA

Subphylum SARCODINA Schmarda, 1871

[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}subphylum, ^{2}class, ^{3}grade, ^{4}section, ^{5}division, dagger (†) indicates *partim*)]——[=^{5}Sarcodea Schmarda, 1871, p. 156; =^{2}Sarkodina Hertwig & Lesser, 1874, p. 43; =^{2}Sarcodina Lütken, 1876, p. 537; =^{1}Sarcodina Calkins, 1909, p. 38; =^{2}Sarcodina (Rhizopoda *s.l.*) Hoogenraad & De Groot, 1940, p. 24]——[=^{3}Gymnomyxa Lankester, 1878 *fide* Lankester, 1885, p. 838, 839; =^{4}Pantostomata Kent, 1880, p. 34, 36, 37; =^{1}Mastigamoebaea† Corliss, 1960, p. 172, 187]

Unicellular organisms with amoeboid, nonflagellate principal stage, without a thick pellicle and capable of forming pseudopodia; majority not parasitic; cytoplasm differentiated, commonly into ecto- and endoplasm; some naked, others may have external or internal test, which may be membranous or chitinous, of secreted calcite, aragonite, silica, or strontium sulphate, or of agglutinated foreign matter held by ferruginous, calcareous or siliceous cement; reproduction by asexual division, or sexual reproduction with flagellate gametes, or more rarely amoeboid gametes. *?Precam., Cam.-Rec.*

Class RHIZOPODEA von Siebold, 1845

[*nom. correct.* T. L. Jahn & F. F. Jahn, 1949, p. 108 (*pro* class Rhizopoda von Siebold, 1845]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}subphylum, ^{2}superclass, ^{3}class, ^{4}subclass, ^{5}section, ^{6}subsection, ^{7}family; dagger (†) indicates *partim*)]——[=Rhizopodes Dujardin, 1835, p. 314 *(nom. neg.)*; =^{7}Rhizopodes Dujardin, 1841, p. 126, 240 *(nom. neg., nom. nud.)*; =^{3}Rhizopoda von Siebold in von Siebold & Stannius, 1845, p. 3; =^{6}Rhizopoda Pritchard, 1861, p. 201; =^{3}Rhizopodia Delage & Hérouard, 1896, p. 59; =^{3}Rizópodos Fernández Galiano, 1921, p. 19 *(nom. neg.)*; =^{4}Rhizopoda Kudo, 1931, p. 177; =^{2}Rhizopodes Deflandre in Grassé, 1953, p. 3 *(nom. neg.)*; =Rhizopoda Deflandre in Edmondson, 1959, p. 233]——[=Symplectomeres Dujardin, 1835, p. 109 *(nom. neg.)*; =Gymnica† Stein, 1857, p. 41; =Monocyphia Stein, 1857, p. 42; =Acyttaria Haeckel, 1862, p. 211; =Monothalamia Haeckel, 1862, p. 211; =Monothalamia Rhizopoda Hertwig & Lesser, 1874, p. 110; =^{5}Pantostomata† Kent, 1880, p. 36; =^{1}Plasmodroma† Doflein, 1902, p. 171; =^{1}Plasmodromata Hartmann, 1907, p. 140]

Pseudopodia lobose, very rarely filiform or anastomosing, naked forms with protoplasm differentiated into endoplasm and ectoplasm, and shelled forms with zonal differentiation of protoplasm frequent. Plasmodia may develop by fusion of individual amoebulae in some forms. Protoplasmic movement by means of a flow of plasmasol caused by differential pressure due to contraction of plasmagel cortex (*984, p. 101). *Miss.-Rec.*

Subclass LOBOSIA Carpenter, 1861

[*nom. correct.* Loeblich & Tappan, 1961, p. 251 (*pro* subclass Lobosa Chatton, 1925, *nom. transl. ex* order Lobosa Carpenter, 1861]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by author (^{1}class, ^{2}subclass, ^{3}section, ^{4}order, ^{5}suborder, ^{6}family; dagger (†) indicates *partim*)]——[=^{4}Lobosa Carpenter, 1861, p. 467; =^{5}Lobosa Leidy, 1879, p. 23; =^{3}Lobosa Lankester, 1885, p. 838; =^{1}Lobosa Lankester, 1885, p. 838, 841; =^{6}Lobosa West, 1901, p. 309 *(nom. nud.)*; =^{2}Lobosa Chatton, 1925, p. 76]——[=^{4}Rhizopoda sphygmica Haeckel, 1862, p. 211; =Protoplasta† Haeckel, 1870, p. 56; =Monothalamia Lobosa Hertwig & Lesser, 1874, p. 93; =^{4}Protoplasta† Leidy, 1879, p. 23; =^{2}Chaoinea† Poche, 1913, p. 168]——[=^{2}Amoebiae Delage & Hérouard, 1896, p. 89; =^{2}Amebea Calkins, 1909, p. 39; =^{4}Diffluentia Rhumbler, 1913, p. 339; =^{4}Addiffluentia Rhumbler, 1913, p. 339 *(nom. van.)*; =^{2}Amoebina Kühn, 1926, p. 107, 108; =^{2}Amoebaea Calkins, 1926, p. 324; =^{2}Amoebina (Rhizopoda *s.s.*) Hoogenraad & De Groot, 1940, p. 24]

With characters of the class. *Miss.-Rec.*

AMOEBIDA

Order AMOEBIDA Ehrenberg, 1830

[*nom. correct.* Haeckel, 1862, p. 211 (*pro* Amoebaea Ehrenberg, 1830)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}section; dagger (†) indicates *partim*)]——[=Amoebaea Ehrenberg, 1830, p. 59; =^{2}Amoebina Claus, 1872, p. 116; =^{1}Amoeboidea Lankester, 1877, p. 442; =^{1}Amoebina Kent, 1880, p. 36; =^{2}Amoebaea† Bütschli in Bronn, 1880, p. 176; =^{1}Amoebinen Hertwig, 1893, p. 149 *(nom. neg.)*; =^{2}Amöboea Blochmann, 1895, p. 12; =^{1}Amibos Fernández Galiano, 1921, p. 23 *(nom. neg.)*; =^{1}Amoebae Chatton, 1925, p. 76; =^{1}Amoebida (Gymnamoebida) Calkins, 1926, p. 337; =^{1}Ameboideos Gadea Buisán, 1947, p. 7 *(nom. neg.)*; =^{1}Amoebaea Deflandre in Grassé, 1953, p. 123; =^{2}Amoeboidina Bovee, 1957, p. 65]——[=^{1}Nuda Ehrenberg, 1832, p. 39; =^{2}Nuda Calkins, 1901, p. 106; =^{3}Nuda Minchen, 1912, p. 217; =^{1}Nuda (Gymnamoeba) Hoogenraad & De Groot, 1940, p. 24 (*non* family Nuda Claus, 1872, p. 108, =Protomyxidae Poche, 1913)]——[=^{1}Les Infusoires Homogénes Cuvier, 1817, p. 92 (*nom. neg.*); =^{1}Monostega† Diesing, 1848, p. 497; =^{1}Homogenea† Cuvier, 1851, p. 600, 707; ^{1}Proteina† Claparède & Lachmann, 1859, p. 435; =^{1}Athalamia† Schmarda, 1871, p. 160; =^{1}Monostegia† Haeckel, 1894, p. 164; =^{1}Chaidea Poche, 1913, p. 170]——[=Gymnamoebida Delage & Hérouard, 1896, p. 89; =^{2}Gymnamoebina Calkins, 1901, p. 105; =^{1}Gymnamoebaea Kühn, 1926, p. 108; =^{2}Gimnameboideos Gadea Buisán, 1947, p. 15 *(nom. neg.)*]——[=^{1}Testamoebida Epsteyn, 1926, p. 200, 208]

No thick pellicle or test; cytoplasm differentiated into hyaline and homogeneous ectoplasm and granulated or vacuolated endoplasm; pseudopodia blunt and broad (lobopodia); typically with single nucleus; flagellate stage may occur; reproduction asexual, commonly by binary fission; free-living in fresh or salt water, soil, or parasitic. *Rec.*

Superfamily PELOMYXACEA Schulze, 1877

[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}suborder, ^{2}superfamily)]——[=^{2}Pelomyxacea LOEBLICH & TAPPAN, 1961, p. 252 (*nom. transl. ex* family Pelomyxidae SCHULZE, 1877); =^{1}Amastigogenina CHATTON in GRASSÉ, 1953, p. 54; =^{1}Hartmannellina, ^{1}Chaosina, ^{1}Mayorellina, ^{1}Flabellulina, ^{1}Thecamoebina BOVEE, 1960, p. 355 (*non* Thecamoebina CALKINS, 1901)]

No flagellate stage in life history, life cycle limited to amoeboid stage and a cyst. *Rec.*

Family PELOMYXIDAE Schulze, 1877

[All names referred to are of family rank; dagger(†) indicates *partim*]——[Pelomyxidae SCHULZE, 1877, p. 26]——[=Amoebaea EHRENBERG, 1838, p. 125; =Amoebées EHRENBERG, 1838, p. 125 (*nom. neg.*); =Amibiens DUJARDIN, 1841, p. 226 (*nom. neg.*); =Amoebeae DIESING, 1848, p. 495; =Amoebea MAITLAND, 1851, p. 3; =Amoebina PERTY, 1852, p. 188; =Amoebidae BRONN, 1859, p. 67; =Amoebida SCHMARDA, 1871, p. 160; =Amoebaea lobosa BÜTSCHLI in BRONN, 1880, p. 176; =Amébidos GADEA BUISÁN, 1947, p. 15 (*nom. neg.*)]——[=Monamoebina HAECKEL, 1894, p. 164 (*nom. nud.*); =Monamoebidae CHATTON, 1925, p. 76 (*nom. nud.*)]——[=Chaidae POCHE, 1913, p. 171; =Chaosidae CHATTON in GRASSÉ, 1953, p. 54; =Schizopyrenidae SINGH, 1951, p. 584 (*nom. nud.*); =Lobosa† BLOCHMANN, 1895, p. 12: =Wechselthierchen EHRENBERG, 1838, p. 125 (*nom. neg., nom. nud.*)]

Amoebae commonly of large size, possessing one or more nuclei; movement by means of indeterminate pseudopodia (may appear in any position on the body), involving streaming of granular endoplasm; multiplication by binary or multiple fission. [Generally free-living, but a few are parasitic. Fresh or salt water or damp soil.] *Rec.*

The family name Amoebidae would have priority, except that the generic name *Amoeba* EHRENBERG, 1830 (*pro Amiba* BORY DE ST. VINCENT, 1822), is a junior synonym of *Chaos* LINNÉ, 1767. The family name Pelomyxidae has priority over the name Chaosidae, proposed as a substitute name for the Amoebidae. A representative species is illustrated in Figure 1.

Family THECAMOEBIDAE Chatton, 1925

[All names referred to are of family rank]——[Thecamoebidae CHATTON, 1925, p. 76 (*non* order *Thecamoebida* DELAGE & HÉROUARD, 1896); Thecamoebida COPELAND, 1956, p. 201, 202 (*nom. van.*)]

Body commonly ovoidal to circular in outline, and without formation of pseudopodia during locomotion; surface covered with

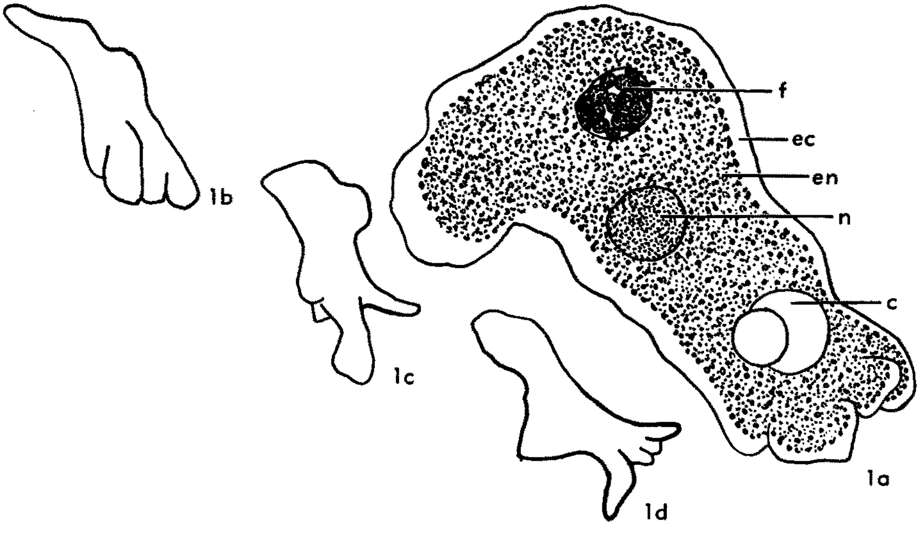


FIG. 1. Pelomyxidae; *1, Chaos diffluens* MÜLLER, a representative pelomyxid protistan; *1a,* living specimen enlarged to show ectoplasm *(ec),* endoplasm *(en),* nucleus *(n),* food vacuole *(f),* and contractile vacuole *(c)*; *1b-d,* outline views showing successive positions of pseudopodia during movement of an individual (*2117).

double-layered impermeable pellicle which may be longitudinally ridged. [Habitat subaerial, fresh water.] *Rec.*

The family Thecamoebidae, based on the genus *Thecamoeba* Fromentel (order Amoebida) is not related to the protozoans placed in the order Thecamoebida Delage & Hérouard, 1896 (=Testacea Schultze, 1854, Testacealobosa de Saedeleer, 1934, etc.).

Family HYALODISCIDAE Poche, 1913

[All names referred to are of family rank]——[Hyalodiscidae Poche, 1913, p. 182; Hyalodiscida Copeland, 1956, p. 201, 202 *(nom. van.)*]

Discoidal body with granular endoplasm and thin layer of homogeneous ectoplasm, no pellicle, pseudopodia indeterminate (may appear in any position). [Marine and fresh water.] *Rec.*

Family HARTMANNELLIDAE Volkonsky, 1931

[Hartmannellidae Singh, 1951, p. 584 *(nom. transl. ex* subfamily Hartmannellinae Volkonsky, 1931, p. 330]

Amoebae of small size, free-living in soil, coprophilous or parasitic. Separated by type of mitotic division (mesomitosis). *Rec.*

Family CHAETOPROTEIDAE Poche, 1913

[All names referred to are of family rank]——[Chaetoproteidae Poche, 1913, p. 172; =Chaetoproteida Copeland, 1956, p. 163 *(nom. van.)*]——[=Mayorellidae Schaeffer, 1926, p. 12, 47; =Mayorellida Copeland, 1956, p. 201, 202 *(nom. van.)*; =Flabellulidae Bovee, 1960, p. 355]

Amoebae of medium to large size; conical or tapering determinate pseudopodia (always appear in the same place on the body), anterior pseudopodium of clear, nongranular cytoplasm. [Fresh water and marine.] *Rec.*

Family ENTAMOEBIDAE Chatton, 1925

[Superscript numbers denote taxonomic rank assigned by authors (^{1}family; ^{2}subfamily)]——[^{1}Entamoebidae Chatton, 1925, p. 76; =^{2}Entamoebinae Chatton in Grassé, 1953, p. 65 *(nom. transl.)*]——[=^{1}Endamoebidae Calkins, 1926, p. 338; =^{2}Endamoebinae Chatton in Grassé, 1953, p. 62 *(nom. transl.)*; =^{1}Endamoebida Copeland, 1956, p. 201, 202 *(nom. van.)*]——[=^{1}Testamoebidae Epsteyn, 1926, p. 200, 208; =^{1}Dientamoebidae Grassé, 1953, p. 50]

Parasitic amoebae, vegetative form small, generally occurring in the alimentary canal of the host, multiplication by binary fission, encystment common. *Rec.*

Previously regarded as synonymous, the genera *Endamoeba* Leidy, 1879, and *Entamoeba* Casagrandi & Barbagallo, 1895, are now separated on the basis of nuclear characters.

Family PANSPORELLIDAE Chatton, 1953

[Pansporellidae Chatton in Grassé, 1953, p. 78; =Sporamoebidae Chatton, 1925, p. 75, 76 *(nom. nud.)*]

Amoebae parasitic in arthropods, cysts give rise to spores from which arise binucleate amoebulae which develop into vegetative stage. Spores differ from those of the Sporozoa in being permeable. *Rec.*

Superfamily TETRAMITACEA Kent, 1880

[*nom. transl.* Loeblich & Tappan, 1961, p. 253 (*ex* family Tetramitidae Kent, 1880]——[In synonymic citations ,superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}family group; dagger(†) indicates *partim)*]——[=^{1}Rhizo-Flagellata† Kent, 1880, p. 220; =^{3}Polystomata† Rhumbler, 1928, p. 4 (*non* Polystomata Averintsev, 1906); =^{2}Mastigogenina Chatton in Grassé, 1953, p. 37; =^{1}Rhizomastigina Kudo, 1939, p. 235; =^{1}Rhizomastigida Bovee, 1960, p. 355]

Life cycle includes both flagellate and amoeboid stage. Originally classed with class Flagellata, or considered as separate order of the subclass Zoomastigina (*1064, p. 333), but due to possession of pseudopodia and loss of the flagellum during part of the life cycle they are here classed with the Amoebida. *Rec.*

Family TETRAMITIDAE Kent, 1880

[Tetramitidae Kent, 1880, p. 312]——[=Vahlkampfidae Jollos, 1917, p. 261, & de Zulueta, 1917, p. 12; =Vahlkampfiidae Chatton in Grassé, 1953, p. 46]——[=Bistadiidae Doflein, 1916, p. 667 *(nom. nud.)*; =Dimastigamoebidae Wenyon, 1926, p. 160, 174, 260; =Dimastigamébidos Gadfa Buisán, 1947, p. 16 *(nom. neg.)*; =Naegleriidae Kudo, 1954, p. 435; =Polymastigamoebidae Bovee, 1960, p. 355 *(nom. nud.)*]

Amoebae small, free or coprophilous, producing biflagellate forms, normally uninucleate, no spores, cysts very resistant. *Rec.*

Family MASTIGAMOEBIDAE Chatton, 1925

[All names referred to are of family rank; dagger(†) indicates *partim*]——[Mastigamoebidae Chatton, 1925, p. 76]——[=Rhizomastigina† Bütschli in Bronn, 1884, p. 810 *(nom. nud.)*; =Rhizomastigidae Calkins, 1901, p. 137; =Rizomastígidos Gadea Buisán, 1947, p. 16 *(nom. neg.)*; =Rhizoflagellates Chatton in Grassé, 1953, p. 37 *(nom. neg.)*]

Amoebae of medium to large size, with a flagellum during at least part of the life cycle, free or parasitic. *Rec.*

The family was credited to Goldschmidt (1907) by Chatton (*810, p. 37), but Goldschmidt (*806) used the terms Rhizomastiginen (p. 160) and Mastigamöben (p. 161) in the vernacular, not as latinized names, and none were used by Goldschmidt in the sense of family names. The family Rhizomastigina Bütschli (1884) and corrected name Rhizomastigidae Calkins (1901) are invalid, as *nomina nuda.* They were not based on the later described *Rhizomastix* Alexeieff, 1911. The term Rhizoflagellates is a vernacular reference (in the synonymy of the Mastigamoebidae) to the order Rhizo-Flagellata Kent (1880). The earliest valid family reference is that of Chatton (1925).

Family PARAMOEBIDAE Poche, 1913

[Paramoebidae Poche, 1913, p. 173; =Paramébidos Gadea Buisán, 1947, p. 15 *(nom. neg.)*]

Amoebae possessing a paranucleus in addition to the normal nucleus, may produce cysts which give rise to flagellate spores. *Rec.*

The authorship of this family was credited to Schaudinn by Chatton (*810, p. 42). However, Schaudinn only described the genus *Paramoeba* and gave no family. The family was first named by Poche (1913). Furthermore, Calkins (*269, p. 456) cites Doflein as the author of the family.

MYCETOZOIDA

CONTENTS

NATURE OF MYCETOZOANS

Mycetozoans (Myxomycetes or Myxogastres) have been observed and described for some 300 years, and have been regarded as lower fungi by botanists and as protozoans by zoologists.

The plasmodium was first recognized by Fries (1829) who regarded the organisms (myxogastres) as fungi. Wallroth substituted the name Myxomycetes (slime fungi) in 1833, which is still their common botanical designation. De Bary (1859) transferred them to the animal kingdom, changing their name to Mycetozoa, or fungus-animals, as he observed them in cultures.

Mycetozoans are characterized by the presence of a large multinucleate amoeboid body or plasmodium. Species are distinguished by the structures developed during spore formation, by the form and color of the sporangium and capillitium, and the color, size, and markings of the spores. Cosmopolitan in their distribution, they occur throughout the world wherever there is sufficient decaying vegetation and moisture for their support in decaying wood, stumps, dead branches, or decaying leaves or straw. Some are widely ranging, but others have a more limited distribution (e.g., tropics, alpine regions).

The Sorophorina are not always included in the Mycetozoida, as they have only a temporary plasmodium, formed at the time of sporulation, and not a truly vegetative plasmodium. Some form pseudospores rather than true spores in sporangia. Many are parasitic.

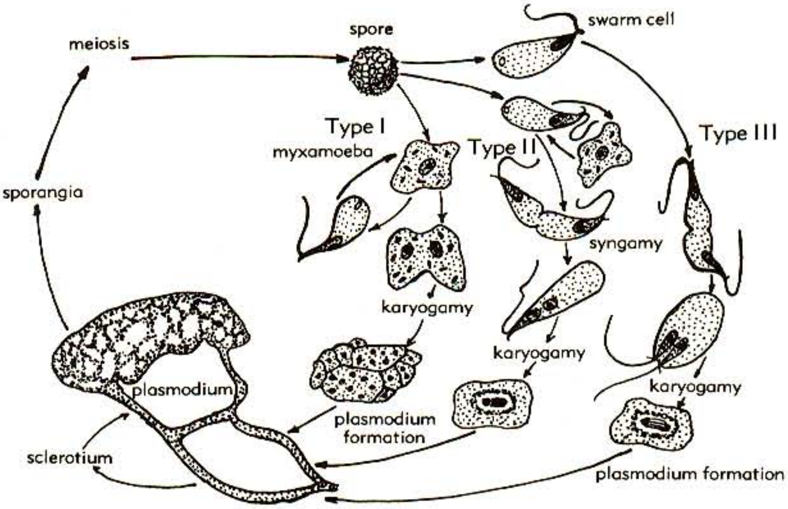


FIG. 2. Life cycle of Mycetozoida (diagrammatic) (*1585).

Eumycetozoina, or true mycetozoans, include three superfamilies, the Ceratiomyxacea (Exosporeae) and Stemonitacea and Trichiacea (Endosporeae). The Ceratiomyxacea develop colorless ovate spores on stalks arising from the fragile, white, branching and anastomosing filamentous structure on decayed wood. After dispersal, moistening causes the spore contents to swell, and the spore wall breaks apart, allowing the quadrinucleate protoplasmic contents to escape with an amoeboid movement. Nuclear division follows and the original spore contents divide into eight haploid uninucleate parts, each becoming a pyriform swarm cell by developing a flagellum. These probably fuse in pairs, although such fusion has not been observed in cultures. The resulting plasmodia are diploid, however, and live within decaying wood, only coming to the surface to produce the spores. Cushion-like aggregates appear at the surface, showing a dense network of protoplasm with granular streaming, the many nuclei then undergo a reduction division, and the protoplasm divides into numerous uninucleate "cells," each developing into a single-stalked spore. The nucleus within this spore divides twice to form a quadrinucleate spore, which detaches easily, and the gelatinous sporophore dries up.

The Stemonitacea and Trichiacea (Endosporeae) have a plasmodium of granular protoplasm, containing numerous nuclei or vacuoles, commonly white, yellow, or pink, but more rarely purple or green, the color being constant in a species. Some also contain calcium carbonate granules. The protoplasm circulates in a network of veins, flowing rapidly in one direction for a time, then slowing and reversing direction, with a rhythmic backward and forward flow, longer in the direction in which the plasmodium is creeping. Spores are spherical, of cellulose-like composition, with an inner hyaline layer and an outer colored layer with warts and ridges.

The life cycle is rather complex, recent studies by Ross (*1585) having shown the presence of three main types (Fig. 2). A briefly flagellate type (I), and a more persistent flagellate type (II) are both found in the Physaridae (in *Physarum, Fuligo* and *Physarella* of the Physarinae and in *Didymium* of the Didymiinae). A completely flagellate type (III) is found in the Stemonitidae (Stemonitacea) and the Liceidae and Trichiidae (Trichiacea).

In the briefly flagellate type (I) the germinating spores give rise to myxamoebae, which soon produce flagella, but the flagellate stage lasts less than two or three days, when the flagella are withdrawn and the cells become irreversibly amoeboid. After a vegetative stage of three to several days syngamy occurs between two nonflagellate myxamoebae (gametes), resulting in a diploid zygotic nucleus; the amoeboid zygotes remain solitary for several hours, feeding on bacteria, and then coalesce in large numbers to form multinucleate plasmodia.

In type II, the spores give rise to flagellate swarm cells directly, or almost immediately, and the flagellate stage lasts from 48 to 130 hours. Syngamy occurs by posterior fusion of two flagellate swarm cells, and karyogamy occurs while one set of flagella is still extended. Flagella are retracted and the zygote becomes amoeboid shortly afterward. Mitosis occurs, resulting in binucleate and then multinucleate plasmodia, which then may also fuse with other plasmodia, although coalescence is rare among zygotes of this type.

In type III the spores produce flagellate swarm cells, which last longer than in the other two types, posterior fusion in pairs follows, and flagella persist during and after karyogamy before the zygote becomes amoeboid. Later mitotic divisions result in formation of a 32- to 64-nucleus plasmodium, which then may also fuse with others.

Exposure of the plasmodium to dryness or cold is withstood by passing into a resting stage (sclerotium), the plasmodium aggregating in masses, discarding all refuse, and forming cyst walls around each mass containing 10 to 20 nuclei. The cysts dry to a horny consistency.

The plasmodium creeps to a dryer place before spores are formed. Sporangia develop a gelatinous wall, which becomes membranous. Each develops a stalk through which the protoplasm flows into the spherical head, a system of tubes (capillitium) forms within the sporangium, and some forms develop calcareous granules in the sporangium wall, in the tubes of the capillitium or stalk, or in all three. Sporangia may be solitary or clustered in an aethalium consisting of closely packed sporangia with imperfectly developed inner walls. Reduction division of nuclei occurs within the sporangia, each haploid daughter nucleus collecting protoplasm and developing spore walls. The capillitium may be modified to aid in spore dispersal.

GLOSSARY OF MORPHOLOGICAL TERMS

aethalium. Compound spore-bearing structure, formed by union of many sporangia, walls of inner sporangia being less developed.

amoebula. Small mass of protoplasm, containing single vesicular nucleus and contractile vacuoles; arises from germinating spore and by later development of flagellum gives rise to myxoflagellula or swarm spores.

capillitium. System of threads within sporangium, may be simple, branched, solid or tubular threads; assists in spore dispersal.

columella. Support for sporangium, attached to capillitium; solid or hollow, continuous with stalk of stalked sporangia.

cortex. Outer covering of aethalium.

elaters. Capillitium threads which are free, tubular, and marked with spiral bands (e.g., *Trichia*).

flagellum. Filamentous extension of cytoplasm, fine and threadlike and commonly in rapid motion; characteristic locomotor apparatus of Mastigophora, also found in swarm cells of Mycetozoa.

holozoic nutrition. Food supply consisting of ingested organisms (animals or plants).

karyogamy. Nuclear fusion, commonly associated with cytoplasmic fusion (plasmogamy), but not always simultaneous.

limax-form. Amoeboid body which under certain conditions may change to flagellate form.

lime-knots. Expansions in threads of capillitium containing granules of calcium carbonate.

meiosis. Reduction division in the nuclei, each half of nucleus then having half of chromosomes, resulting in haploid stage (as in gametes).

myxamoebae. Amoebulae which fuse to form plasmodium, without nuclear fusion.

myxoflagellula. Flagellate stage developing from myxamoebula, which arose from spore germination; myxoflagellulae may increase in number by binary fission and may ingest bacteria.

plasmodium. Multinucleate mass of naked protoplasm formed by fusion of swarm cells, with protoplasmic circulation; nuclei increase in number as plasmodium grows, but reduction division of nuclei occurs only at time of spore formation.

plasmogamy. Fusion of cytoplasm, as in union of gametes or association of amoebulae into plasmodium.

pseudocapillitium. Imperfectly developed walls of sporangia, resembling true capillitium.

pseudoplasmodium. Myxamoebae group before spore formation, but not fused to form true plasmodium (e.g., Sorophorina)

pseudospores. Formed directly from myxamoebae, without sporangia; have rigid walls but no thickening.

saprozoic nutrition. Food supply obtained from dissolved organic substance in water, ingested by osmosis through body surface.

sclerotium. Resting condition of plasmodium, consisting of numerous closely packed cellulose-walled cysts, each containing cytoplasm and 10 to 20 nuclei; may be formed when unfavorable conditions arise, and may last up to 3 years.

sporangium. Receptacle containing spores, developed by plasmodium commonly when food material is lacking.

spore. Commonly spherical, uninucleate bodies, 3 to 30 microns in diameter, formed by mitotic division of nuclei and division of cytoplasm within sporangium; provided with outer cellulose-like membrane; may germinate after moistening and give rise to amoebulae.

sporophore. Structure bearing spores on surface.

syngamy. Conjugation; fusion of 2 nuclei, accompanied by fusion of cytoplasm.

swarm cell. Myxoflagellula; pyriform, flagellate body, developed from amoeboid body (amoebula) arising from germinating spore.

SYSTEMATIC DESCRIPTIONS

Order MYCETOZOIDA de Bary, 1859

[*nom. correct.* Calkins, 1901, p. 18 (*pro* order Mycetozoa de Bary, 1859, p. 88; *non* Mycetozoida Schepotieff, 1912)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}division, ^{2}class, ^{3}subclass, ^{4}order, ^{5}suborder, ^{6}section; dagger(†) indicates *partim*)]——[=^{6}Myxogastres Fries, 1829, p. 3, 67; =^{4}Myxogasteres Schröter, 1886, p. 91, 98; =^{2}Myxogasteres (*eigentliche* Myxomyceten) Schröter, 1897, p. iii, 8; =^{5}Myxogastres MacBride, 1899, p. 20; =^{6}Myxogastres Morgan, 1900, p. 119; =^{6}Myxogasteres Doflein, 1911, p. 682]——[=Myxomycetes Wallroth, 1833 (*fide* Lister & Lister, 1925, p. xiii); =^{4}Myxomycetes Luerssen, 1879, p. 38; =Myxomyceten de Bary, 1884, p. 453 (*nom. neg.*); =Myxomyceteae Berlese in Saccardo, 1888, p. 323; =^{2}Myxomycetes Bennett & Murray, 1889, p. 401; =^{2}Myxomycetes MacBride, 1899, p.16; =Myxomyceten (Schleimpilze) Hertwig, 1919, p. 188 (*nom. neg.*); =Myxomyzeten Rhumbler in Kükenthal & Krumbach, 1923, p. 107 (*nom. van.*); =^{6}Mixomicetos Gadea Buisán, 1947, p. 28 (*nom. neg.*)]——[Mycetozoen de Bary, 1859, p. 88 (*nom. neg.*); =^{2}Mycetozoa Rostafiński, 1873, p. 1; =Mycetozoen (Eumycetozoen) Zopf, 1892, p. 45 (*nom. neg.*); =^{3}Mycetozoa Sedgwick, 1898, p. 15; =^{5}Mycetozoidea Doflein, 1901, p. 47; =^{4}Mycetozoen (Schleimtiere) Hertwig, 1919, p. 188 (*nom. neg.*); =Micetozoos Fernández Galiano, 1921, p. 39 (*nom. neg.*)]——[=^{4}Phytomyxini Schröter, 1886, p. 133; =^{4}Phytomyxinae MacBride, 1892, p. 111; =Phytomyxinae Schröter, 1897, p. iii, 5; =^{5}Phytomyxinae MacBride, 1899, p. 16; =^{6}Phytomyxinae Doflein, 1911, p. 672; =^{5}Phytomyxinea Poche, 1913, p. 197; =^{4}Phytomyxida Calkins, 1926, p. 328]——[=Myxothallophyta Schröter, 1897, p. iii; =Myxozoa† Schepotieff, 1912, p. 267; =Mixogasteros Fernández Galiano, 1921, p. 41 (*nom. neg.*); =^{1}Myxomycophyta Smith, 1955, p. 346; =^{4}Myxomycetales Bonner, 1959, p. 4; =^{4}Myxogastrales Bonner, 1959, p. 4]——[=Schleimpilze de Bary, 1859, p. 88 (*nom. neg.*); =^{4}Schleimpilze Rhumbler in Kükenthal & Krumbach, 1923, p. 106 (*nom. neg.*); =^{2}Zygosporeae Luerssen, 1879, p. 3; Monadinen (Monadineae)† Zopf, 1885, p. 98; =^{6}Plasmodiata Lankester, 1885, p. 838; =Eumycetozoa† Schepotieff, 1912, p. 267; =^{4}Pilztiere Rhumbler in Kükenthal & Krumbach, 1923, p. 106 (*nom. neg.*); =^{3}Archimycetes† Gaumann & Wynd, 1952, p. 13; =^{2}Plasmodiophoreae Smith, 1955, p. 356]

Holozoic or saprozoic organisms, previously regarded as related to fungi, but shown by their development to be protozoans. Large multinucleate body or plasmodium; cytoplasm granulated except for thin hyaline and homogeneous external layer, the granules in some forms consisting of calcium carbonate. Life cycle complex, with sexual reproduction. *Rec.*

Suborder SOROPHORINA Lankester, 1885

[*nom. correct.* Loeblich & Tappan, 1961, p. 255 (*pro* suborder Sorophora Minchen, 1912, p. 243, *nom. transl. ex* order Sorophora Lankester, 1885, p. 840)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}class, ^{2}subclass, ^{3}order, ^{4}suborder, ^{5}group, ^{6}family)]——[=^{6}Acrasiées Van Tieghem, 1880, p. 322 (*nom. neg.*); =Acrasieae de Bary, 1887, p. 421, 441; =Acrasieen de Bary, 1887, p. 475 (*nom. neg.*); =^{3}Acrasiei Schröter, 1886, p. 97; =^{1}Acrasieae Bennett & Murray, 1889, p. 405; =^{4}Acrasieae Zopf, 1892, p. 45; =Acrasidea Haeckel, 1894, p. 164; =^{3}Acrasieae Olive, 1902, p. 452; =^{3}Acrasiae Calkins, 1909, p. 38; =^{4}Acrasinea Poche, 1913, p. 175; =^{4}Acrasieos Fernández Galiano, 1921, p. 39 (*nom. neg.*); =^{3}Acrasida Calkins, 1926, p. 328; =^{3}Acrasiales Martin in Ainsworth & Bixby, 1950, p. 411; =^{4}Acrasina Hall, 1953, p. 227, 228; =^{3}Acrasiés Pavillard in Grassé, 1953, p. 493 (*nom. neg.*)]——[=^{5}Sorophoreen Zopf, 1885, p. 131 (*nom. neg.*); =Sorophoreae Berlese in Saccardo, 1888, p. 324; =^{3}Sorophoreen Zopf, 1892, p. 45 (*nom. neg.*); =^{2}Sorophora J. J. Lister in Lankester, 1909, p. 37; =^{3}Sorophorae Pavillard in Grassé, 1953, p. 493]——[=^{3}Pseudoplasmodiés Delage & Hérouard, 1896, p. 77 (*nom. neg.*); =^{3}Pseudoplasmodida Delage & Hérouard, 1896, p. 77; =^{3}Dictyosteliaceae J. J. Lister in Lankester, 1909, p. 37; =^{3}Guttulinaceae J. J. Lister in Lankester, 1909, p. 37]

Myxamoebae aggregate for spore formation, but without a true plasmodium; no flagellate stage. *Rec.*

Family SAPPINIIDAE Olive, 1901

[*nom. correct.* Doflein, 1909, p. 587 (*pro* family Sappiniaceae Olive, 1901, p. 334)]

Myxamoebae form pseudospores (with rigid but unthickened walls) directly, without fruiting bodies. *Rec.*

Family POCHEINIDAE Loeblich & Tappan, 1961

[*nom. subst.* Loeblich & Tappan, 1961, p. 256 (*pro* family Guttulinidae Doflein, 1909, p. 587, and family Guttulinacei Schröter, 1886, p. 97 (*nom. nud.*), based on *Guttulina* Cienkowski, 1873 (*non* d'Orbigny, 1839)]——[=Guttulineen Zopf, 1885, p. 132 (*nom. neg.*); =Guttulineae Berlese in Saccardo, 1888, p. 451 (*nom. nud.*); =Guttulinaceae Zopf, 1892, p. 45 (*nom. nud.*); =Guttuliniidae Kudo, 1931, p. 190 (*nom. van., nom. nud.*); =Guttulínidos Gadea Buisán, 1947, p. 27 (*nom. neg., nom. nud.*); =Guttulininae Doflein & Reichenow, 1952, p. 725 (*nom. transl., nom. nud.*); =Guttulinacea Copeland, 1956, p. 201, 203 (*nom. van., nom. nud.*)]

Plasmodium incomplete, myxamoebae of "limax" form, may form pseudospores or true spores in a fruiting body on a short, thick stalk. *Rec.*

Family DICTYOSTELIIDAE Rostafiński, 1873

[*nom. correct.* Kudo, 1931, p. 190 (*pro* family Dictyosteliaceae Rostafiński, 1875, p. 32, 86, 217, *nom. transl. ex* tribe Dictyosteliaceae Rostafiński, 1873, p. 4]——[=Acrasiées Van Tieghem, 1880, p. 322 (*nom. neg.*); =Acrasacées Van Tieghem, 1898, p. 21 (*nom. neg.*); =Acrasieae Hartog in Harmer & Shipley, 1906, p. x, 90; =Acrasidae Poche, 1913, p. 177; =Acrasíidos Gadea Buisán, 1947, p. 27 (*nom. neg.*)]——[=Dictyosteliaceen Zopf, 1885, p. 134 (*nom.

neg.); =Dictyosteliacei SCHRÖTER, 1886, p. 97; =Dictyostelidae DOFLEIN, 1909, p. 587, 588; =Dictiostélidos GADEA BUISÁN, 1947, p. 27 *(nom. neg.)*; =Dictyostelinae DOFLEIN & REICHENOW, 1952, p. 725 *(nom. transl.)*]——[=Pseudoplasmodidae DOFLEIN, 1901, p. 47 *(nom. nud.)*]

Pseudoplasmodium complete; myxamoebae with short, pointed pseudopodia. True spores formed in fruiting bodies with cellulose sheath. *Rec.*

Suborder PLASMODIOPHORINA Cook, 1928

[*nom. transl.* HALL, 1953, p. 227, 228 (*ex* order Plasmodiophorales COOK, 1928, *fide* KARLING, 1942, p. 2]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}class, ^{2}subclass, ^{3}order, ^{4}suborder, ^{5}superfamily; dagger(†) indicates *partim*)]——[=Monadineae zoosporae† ZOPF, 1885, p. 115; =Zoosporeae† BERLESE in SACCARDO, 1888, p. 453; =^{3}Chytridineae SCHRÖTER, 1893, *fide* FITZPATRICK, 1930, p. 38; =Mycetozoa† SCHEPOTIEFF, 1912, p. 267; =^{3}Protococcales† CLEMENTS & SHEAR, 1931, p. 30]——[=^{3}Phytomyxini† SCHRÖTER, 1886, p. 133; =^{4}Phytomyxinées TORREND, 1907, p. 37, 60 *(nom. neg.)*; ^{4}=Phytomyxinae DOFLEIN, 1911, p. 672; =^{4}Phytomyxinea POCHE, 1913, p. 197; =^{4}Fitomixinos FERNÁNDEZ GALIANO, 1921, p. 40 *(nom. neg.)*; =^{5}Fitomixinos GADEA BUISÁN, 1947, p. 28 *(nom. neg., nom. nud.)*; =^{2}Phytomyxinae HAGELSTEIN, 1932, p. 241; =^{1}Phytomyxinae SMITH, 1938, p. 360]

Large multinucleate amoeboid body. [Parasitic in plants, more rarely in animals.] *Rec.*

The genus *Phytomyxa* (basis for the order Phytomyxina) is not related to the Rhizopodea, and the order Chytridiales consists of true fungi. The earliest valid name is therefore the order Plasmodiophorales COOK, 1928, reduced to suborder rank by HALL, 1953.

Family PLASMODIOPHORIDAE Berlese, 1888

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 257 (*pro* family Plasmodiophoreae BERLESE in SACCARDO, 1888, p. 453]——[All names referred to are of family rank; dagger(†) indicates *partim*]——[=Plasmodiophoreen ZOPF, 1885, p. 129 *(nom. neg.)*; =Plasmodiophorinae DELAGE & HÉROUARD, 1896, p. 76; =Plasmodiophoraceae SCHEPOTIEFF, 1912, p. 267; =Plasmodiofóridos GADEA BUISÁN, 1947, p. 28 *(nom. neg., nom. nud.)*; =Plasmodiophorea COPELAND, 1956, p. 179 *(nom. neg.)*]——[=Gymnococcaceen ZOPF, 1885, p. 126 *(nom. neg.)*; =Gymnococcaceae BERLESE in SACCARDO, 1888, p. 453; =Gymnococcinae DELAGE & HÉROUARD, 1896, p. 75; =Gymnococcidae POCHE, 1913, p. 198]——[=Phytomyacei SCHRÖTER, 1886, p. 133; =Phytomyxidacées TORREND, 1907, p. 37, 39, 43, 60 *(nom. neg.)*; =Phytomyxaceae MIGULA, 1910, p. 6; =Phytomyxidae POCHE, 1913, p. 198]——[=Zoosporidae DOFLEIN, 1901, p. 41 (*non* Zoosporeae HARTOG, 1906, *nom. nud.*); =Azoosporeae† HARTOG in HARMER & SHIPLEY, 1906, p. x, 89 *(nom. nud.)*]

Characters of suborder. *Rec.*

Suborder EUMYCETOZOINA Poche, 1913

[*nom. correct.* HALL, 1953, p. 227, 230 (*pro* suborder Eumycetozoa POCHE, 1913, p. 199)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}class, ^{2}order, ^{3}suborder, ^{4}superfamily; dagger(†) indicates *partim*)]——[=^{2}Uterini veri FRIES, 1821, p. xliv; =^{3}Trichospermi FRIES, 1821, p. xliv; =^{2}Trichospermi FRIES, 1823, p. 276]——[=^{1}Gasteromycetes† FRIES, 1821, p. xxxv, xlviii; =^{2}Gasteromycetes genuina† FRIES, 1829, p. 1; =Gastromyzetes† RHUMBLER in KÜKENTHAL & KRUMBACH, 1926, p. 106; =Eumycetozoen† ZOPF, 1885, p. 131 *(nom. neg.)*; =^{4}Mixogastros GADEA BUISÁN, 1947, p. 28 *(nom. neg., nom. nud.)*; =^{2}Enteridiea COPELAND, 1956, p. 171]

Spores develop into myxamoebae or biflagellate swarm cells; either may fuse to form zygotes; zygotes from myxamoebae fuse to form plasmodia, whereas zygotes from swarm cells develop into plasmodia by nuclear division. *Rec.*

Superfamily CERATIOMYXACEA MacBride, 1892

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 258 (*pro* superfamily Ceratiomyxioidea PAVILLARD in GRASSÉ, 1953, p. 533, *nom. transl. ex* Ceratiomyxidae MACBRIDE, 1892)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}division, ^{2}class, ^{3}subclass, ^{4}cohors, ^{5}order, ^{6}series, ^{7}suborder, ^{8}subsuborder, ^{9}group, ^{10}section, ^{11}tribe)]——[=^{4}Exosporeae ROSTAFIŃSKI, 1873, p. 2; =^{2}Exosporeae ROSTAFIŃSKI, 1875, p. 83, 88; =^{9}Exosporeen ZOPF, 1885, p. 173; =^{5}Exosporea LANKESTER, 1885, p. 841; =^{7}Exosporei SCHRÖTER, 1886, p. 98, 100; =^{3}Exosporeae LISTER, 1894, p. 21, 25; =^{6}Exosporeae SEDGWICK, 1898, p. 17; =Exosporées TORREND, 1907, p. 37, 63 *(nom. neg.)*; ^{1}Exosporeae J. J. LISTER in LANKESTER, 1909, p. 37; =^{7}Exosporeae DOFLEIN, 1911, p. 683; ^{8}Exosporinei POCHE, 1913, p. 200; =^{6}Exosporales E. JAHN in ENGLER & PRANTL, 1928, p. 314; =^{11}Exosporeae KUDO, 1931, p. 187; =^{3}Exosporae MARTIN in AINSWORTH & BIXBY, 1950, p. 411; =^{7}Exosporés PAVILLARD in GRASSÉ, 1953, p. 532 *(nom. neg.)*]——[=^{5}Ceratiomyxaceae A. LISTER, 1894, p. 21, 25; =^{5}Ceratiomyxales COOKE, 1951, p. 173]——[=Ectosporeae SCHRÖTER, 1897, p. 15; =^{10}Ectosporeae MINCHEN, 1912, p. 242]

Spores developed outside a sporophore. *Rec.*

Family CERATIOMYXIDAE MacBride, 1892

[*nom. correct.* DOFLEIN, 1909, p. 599 (*pro* family Ceratiomyxaceae MACBRIDE, 1892, p. 113, *nom. subst. pro* family Ceratiaceae LUERSSEN, 1879, p. 41, *nom. transl. ex* tribe Ceratiaceae ROSTAFIŃSKI, 1873, p. 2, *nom. nud.*)]——[All taxa cited are of family rank]——[=Ceratiacei SCHRÖTER, 1886, p. 98, 101 *(nom. nud.)*; =Ceratieae DE BARY, 1887, p. 427; =Ceratiacées VAN TIEGHEM, 1898, p. 20 *(nom. neg.)*]——[=Ceratiomyxacées TORREND, 1907, p. 37, 39, 43, 63 *(nom. neg.)*; =Ceratomíxidos GADEA BUISÁN, 1947, p. 28 *(nom. neg.)*; =Ceratiomyxacea COPELAND, 1956, p. 177 *(nom. neg.)*]

Sporophores membranous, branched; spores white, borne singly on filiform stalks arising from an areolated sporophore. *Rec.*

Superfamily STEMONITACEA Fries, 1829

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 258 (*pro* superfamily Stemonitidides POCHE, 1913, p. 202, *nom. transl. ex* family Stemonitei FRIES, 1829)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}division, ^{2}class, ^{3}subclass, ^{4}cohors, ^{5}cohort, ^{6}order, ^{7}legion, ^{8}suborder, ^{9}subsuborder, ^{10}superfamily, ^{11}group, ^{12}section, ^{13}tribe; dagger(†) indicates *partim*)]——[=^{4}Endosporeae† ROSTAFIŃSKI, 1873, p. 2; =^{2}Endosporeae† ROSTAFIŃSKI, 1875, p. 83, 89; =^{11}Endosporeen† ZOPF, 1885, p. 136 *(nom. neg.)*; =^{6}Endosporea† LANKESTER, 1885, p. 840; =^{8}Endosporei† SCHRÖTER, 1886, p. 98, 101; =^{3}Endosporeae† A. LISTER, 1894, p. 21, 26; =^{6}Endosporeae† SEDGWICK, 1898, p. 17; =Endosporées† TORREND, 1907, p. 37 *(nom. neg.)*; =^{1}Endosporeae† J. J. LISTER in LANKESTER, 1909, p. 37; =^{12}Endosporeae† MINCHEN, 1912, p. 242; =^{9}Endosporinei† POCHE, 1913, p. 200; =Endosporeae (Myxogastres)† FITZPATRICK, 1930, p. 2; =^{13}Endosporeae† KUDO, 1931, p. 187; =^{8}Endosporées† PAVILLARD in GRASSÉ, 1953, p. 532 *(nom. neg.)*]——[=Trichophorae† ROSTAFIŃSKI, 1875, p. 83, 86, 91, 240; =^{13}Trichophorae POCHE, 1913, p. 201 *(nom. nud.)*]——[=Atrichae† ROSTAFIŃSKI, 1875, p. 83, 86, 90, 217; =Atrichées† TORREND, 1907, p. 37, 39 *(nom. neg.)*]——[=^{8}Amaurosporeae ROSTAFIŃSKI, 1875, p. 83, 90; =Amaurosporei† SCHRÖTER, 1886, p. 103; =^{6}Amaurosporae BERLESE in Saccardo, 1888, p. 323; =^{5}Amaurosporales A. Lister, 1894, p. 21, 26; =Amaurosporées Torrend, 1907, p. 38 (*nom. neg.*); =^{7}Amaurosporales Doflein, 1911, p. 685; =^{6}Amaurosporales A. Lister & G. Lister, 1925, p. 1]——[=^{6}Endotricheen† Zopf, 1885, p. 143 (*nom. neg.*); =^{8}Ystereonemeen Zopf, 1885, p. 143 (*nom. neg.*); =^{8}Endotricheat† Lankester, 1885, p. 841; =^{6}Euplasmodiés Delage & Hérouard, 1896, p. 77, 83 (*nom. neg.*); =^{6}Euplasmodida Delage & Hérouard, 1896, p. 77, 83; =^{10}Amaurochaetides Poche, 1913, p. 202; =^{10}Stemonitioidea Pavillard in Grassé, 1953, p. 533]

Spores violet-brown or purplish-gray and developed in a sporangium. *Rec.*

Family PHYSARIDAE Fries, 1829

[*nom. correct.* Doflein, 1909, p. 601 (*pro* family Physarei Fries, 1829, p. 75)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}subcohort, ^{4}sublegion, ^{5}superfamily, ^{6}family, ^{7}tribe, ^{8}subtribe)]——[=Physareen de Bary, 1864, p. 3 (*nom. neg.*); =^{7}Physaraceae Rostafiński, 1873, p. 9; =^{6}Physaraceae Rostafiński, 1875, p. 50, 84, 92; =^{6}Physareen Zopf, 1885, p. 144 (*nom. neg.*); =^{6}Physarea Lankester, 1885, p. 841; =^{6}Physaracei Schröter, 1886, p. 99, 120; =Physareae de Bary, 1887, p. 424, 431; =^{2}Physarae Massee, 1892, p. 30, 197, 262; =^{1}Physaraceae A. Lister, 1894, p. 21, 26; =^{7}Physarées Van Tieghem, 1898, p. 20 (*nom. neg.*); =^{6}Physareae MacBride, 1899, p. 21; =^{6}Physaracées Torrend, 1907, p. 38, 42, 52 (*nom. neg.*); =^{8}Physaroinae Poche, 1913, p. 202; =^{1}Physarales MacBride, 1922, p. 22; =^{2}Physariineae Hagelstein, 1944, p. 9; =^{6}Fisáridos Gadea Buisán, 1947, p. 29 (*nom. neg.*); =^{2}Physarina T. L. Jahn & F. F. Jahn, 1949, p. 138; =^{5}Physaroidea Pavillard in Grassé, 1953, p. 533]——[=^{1}Calcareae Rostafiński, 1873, p. 9; =Calcariaceen Zopf, 1885, p. 143 (*nom. neg.*); =^{3}Calcarineae A. Lister, 1894, p. 21, 26; =^{3}Calcarinae Penzig, 1898, p. 16; =Calcarinées Torrend, 1907, p. 37, 38 (*nom. neg.*); =^{4}Calcarineae Doflein, 1911, p. 685; =^{2}Calcarineae A. Lister & G. Lister, 1925, p. 1; =^{4}Calcarinea Kudo, 1931, p. 187]——[=^{7}Spumariaceae Rostafiński, 1873, p. 13; =^{6}Spumariaceae Rostafiński, 1875, p. 59, 84, 189; =^{6}Spumariaceen Zopf, 1885, p. 152 (*nom. neg.*); =^{6}Espumáridos Gadea Buisán, 1947, p. 29 (*nom. neg.*)]——[=^{7}Didymiaceae Rostafiński, 1873, p. 12; =^{6}Didymiaceae Rostafiński, 1875, p. 53, 84, 149; =^{6}Didymiaceen Zopf, 1885, p. 150 (*nom. neg.*); =^{2}Didymeae Massee, 1892, p. 30, 197; =^{1}Didymiaceae A. Lister, 1894, p. 21, 93; =^{7}Didymiées Van Tieghem, 1898, p. 20 (*nom. neg.*); =^{6}Didymieae MacBride, 1899, p. 21, 82; =^{6}Didymiacées Torrend, 1907, p. 38, 42, 51 (*nom. neg.*); =^{6}Didymidae Doflein, 1909, p. 601; =^{6}Didymiidae Poche, 1913, p. 202; =^{6}Didímos Gadea Buisán, 1947, p. 29 (*nom. neg.*); =^{6}Didymiacea Copeland, 1956, p. 177 (*nom. van.*)]——[=^{6}Aethalini Fries, 1829, p. 74; =^{7}Cienkowskiaceae Rostafiński, 1873, p. 9; =^{6}Cienkowskiaceae Rostafiński, 1875, p. 49, 84, 91; =^{1}Lithodermeae Massee, 1892, p. 30, 195, 197]

Sporangia containing secreted calcium carbonate. *Rec.*

Subfamily PHYSARINAE Fries, 1829

[*nom. correct.* Loeblich & Tappan, 1961, p. 260 (*pro* subfamily Physarei Schröter, 1886, p. 125, *nom. transl. ex* family Physarei Fries, 1829)]

Sporangia with calcium carbonate in form of minute round granules. *Rec.*

Subfamily DIDYMIINAE Rostafiński, 1873

[*nom. correct.* Loeblich & Tappan, 1961, p. 260 (*pro* subfamily Didymiei Schröter, 1886, p. 99, 121, *nom. transl. ex* tribe Didymiaceae Rostafiński, 1873)]——[=subfamily Spumariei Schröter, 1886, p. 99]

Calcium carbonate deposited in crystals outside of sporangium wall. *Rec.*

Family STEMONITIDAE Fries, 1829

[*nom. correct.* Doflein, 1909, p. 601 (*pro* family Stemonitei Fries, 1829, p. 75)]——[=In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}subcohort, ^{4}sublegion, ^{5}family, ^{6}tribe, ^{7}subtribe)]——[=Stemoniteen de Bary, 1864, p. xi (*nom. neg.*); =^{6}Stemonitaceae Rostafiński, 1873, p. 6; =Stemonitaceae Rostafiński, 1875, p. 38, 85, 193; =^{5}Stemonitaceaee Rostafiński, 1876, p. 24 (*nom. null.*); =^{5}Stemoniteen Zopf, 1885, p. 154 (*nom. neg.*); =^{5}Stemonitea Lankester, 1885, p. 841; =^{5}Stemonitacei Schröter, 1886, p. 99; =Stemoniteae de Bary, 1887, p. 427; =^{2}Stemonitae Massee, 1892, p. 30, 71, 72; =^{1}Stemonitaceae A. Lister, 1894, p. 21, 108; =^{6}Stemonitées Van Tieghem, 1898, p. 20 (*nom. neg.*); =^{5}Stemonitacées Torrend, 1907, p. 38, 41, 49 (*nom. neg.*); =^{1}Stemonitales MacBride, 1922, p. 22, 148; =^{5}Stemonitidaceae Hagelstein, 1944, p. 10 (*nom. van.*); =^{5}Estemonítidos Gadea Buisán, 1947, p. 28 (*nom. neg.*); =^{2}Stemonitina T. L. Jahn & F. F. Jahn, 1949, p. 139]——[=^{1}Amaurochaeteae Rostafiński, 1873, p. 6; =^{6}Amaurochaetaceae Rostafiński, 1873, p. 8; =^{1}Amaurochaete Rostafiński, 1875, p. 7; =^{5}Amaurochaetaceae Rostafiński, 1875, p. 46, 85, 210; =Amaurochaetaceen Zopf, 1885, p. 154 (*nom. neg.*); =^{1}Amaurochetene Berlese in Saccardo, 1888, p. 389; =^{3}Amaurochaetineae A. Lister, 1894, p. 21, 108; =^{1}Amaurochaetaceae A. Lister, 1894, p. 22, 134; =^{3}Amaurochaetinae Penzig, 1898, p. 51; =^{5}Amaurochaeteae MacBride, 1899, p. 107; =^{3}Amaurochaetineae J. J. Lister in Lankester, 1909, p. 37; =^{5}Amaurochaetidae Doflein, 1909, p. 601; =^{4}Amaurochaetineae Doflein, 1911, p. 685; =^{7}Amaurochaetoinae Poche, 1913, p. 201; =^{2}Amaurochaetineae A. Lister & G. Lister, 1925, p. 2; =^{5}Amaurochaetacées Pouchet, 1925, p. 55 (*nom. neg.*); =^{4}Amaurochaetinea Kudo, 1931, p. 187; =^{1}Amaurochaetales Hagelstein, 1944, p. 9; =^{5}Amaurochaetacea Copeland, 1956, p. 175 (*nom. van.*)]——[=^{6}Echinosteliaceae Rostafiński, 1873, p. 7; =^{5}Echinosteliaceae Rostafiński, 1875, p. 44, 85, 215; =^{5}Echinosteliidae Pavillard in Grassé, 1953, p. 533]——[=^{6}Enerthenemaceae Rostafiński, 1873, p. 8; =^{5}Enerthenemaceae Rostafiński, 1875, p. 43, 85, 203; =^{5}Enerthenemeen Zopf, 1885, p. 157 (*nom. neg.*); =^{5}Enerthenemea Lankester, 1885, p. 841]——[=^{6}Brefeldiaceae Rostafiński, 1873, p. 8; =^{5}Brefeldiaceae Rostafiński, 1875, p. 44, 86, 212; =^{5}Brefeldiacées Torrend, 1907, p. 38, 41, 49 (*nom. neg.*); =^{5}Brefeldiidae Poche, 1913, p. 202]——[=^{5}Raciborskiaceae Berlese in Saccardo, 1888, p. 324, 400; =^{2}Lamprodermae Massee, 1892, p. 30, 71, 94; =^{5}Lamprodermeae MacBride, 1899, p. 107, 136; =^{5}Lamprodermaceae MacBride, 1922, p. 148, 189]——[=Leptonemeae Schröter, 1897, p. 15; =^{1}Leptoneminées Torrend, 1907, p. 38 (*nom. neg.*)]——[=^{1}Columelliferae Morgan, 1900, p. 128; =^{1}Acalcarinées Torrend, 1907, p. 37, 38 (*nom. neg.*); =^{1}Collodermaceae G. Lister, 1918, p. 39; =^{5}Collodermaceae A. Lister & G. Lister, 1925, p. 2; =^{5}Collodermataceae Hagelstein, 1944, p. 10 (*nom. van.*); =^{5}Elaeomyxaceae Hagelstein, 1942, p. 594]

Sporangia without calcareous deposits. *Rec.*

Subfamily COLLODERMINAE A. Lister & G. Lister, 1925

[*nom. transl.* Loeblich & Tappan, 1961, p. 261 (*ex* family Collodermaceae Lister & Lister, 1925]

Sporangia distinct, sessile, with gelatinous outer wall. *Rec.*

Subfamily STEMONITINAE Fries, 1829

[*nom. correct.* Loeblich & Tappan, 1961, p. 262 (*pro* subfamily Stemonitei Schröter, 1886, p. 116, *nom. transl. ex* family Stemonitei Fries, 1829)]——[=subfamily Brefeldiei Schröter, 1886, p. 119]

Sporangia distinct, commonly with stalk and columella. *Rec.*

Subfamily AMAUROCHAETINAE Rostafiński, 1873

[*nom. transl.* Loeblich & Tappan, 1961, p. 262 (*ex* tribe Amaurochaetaceae Rostafiński, 1873, p. 8)]

Sporangia combined to form aethalium. *Rec.*

Superfamily TRICHIACEA Fries, 1821

[*nom. correct.* Loeblich & Tappan, 1961, p. 262 (*pro* superfamily Trichiides Poche, 1913, p. 201, *nom. transl. ex* family Trichocisti (Trichioidei) Fries, 1821, p. 1)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}division, ^{2}class, ^{3}subclass, ^{4}legion, ^{5}sublegion, ^{6}order, ^{7}suborder, ^{8}subsuborder, ^{9}cohors, ^{10}cohort, ^{11}subcohort, ^{12}group, ^{13}superfamily, ^{14}family, ^{15}section, ^{16}tribe; dagger(†) indicates *partim*)]——[=^{14}Fuliginoidei Fries, 1821, p. xlix, 1 *(nom. nud.)*; =^{9}Endosporeae† Rostafiński, 1873, p. 2; =^{2}Endosporeae† Rostafiński, 1875, p. 83, 89; =^{12}Endosporeen† Zopf, 1885, p. 136 *(nom. neg.)*; =^{6}Endosporea Lankester, 1885, p. 840; =^{7}Endosporei† Schröter, 1886, p. 98, 101; =^{3}Endosporeae† A. Lister, 1894, p. 21, 26; =^{6}Endosporeae† Sedgwick, 1898, p. 17; =Endosporées† Torrend, 1907, p. 37 *(nom. neg.)*; =^{1}Endosporeae† J. J. Lister in Lankester, 1909, p. 37; =^{15}Endosporeae† Minchen, 1912, p. 242; =^{3}Endosporinei† Poche, 1913, p. 200; =Endosporeae (Myxogastres)† Fitzpatrick, 1930, p. 2; =^{16}Endosporeae† Kudo, 1931, p. 187 *(nom. nud.)*; =^{7}Endosporées† Pavillard in Grassé, 1953, p. 532 *(nom. neg.)*]——[=^{6}Anemeae Rostafiński, 1873, p. 4; =^{11}Anemineae A. Lister, 1894, p. 22, 136; =^{5}Aneminea Doflein, 1911, p. 685; =^{7}Anemineae A. Lister & G. Lister, 1925, p. 2]——[=^{6}Calonemeae Rostafiński, 1873, p. 14; =^{11}Calonemineae A. Lister, 1894, p. 22, 161; =Calonemata Morgan, 1900, p. 126; =Caloneminées Torrend, 1907, p. 38, 39 *(nom. neg.)*; =^{5}Calonemineae Doflein, 1911, p. 686; =^{7}Calonemineae A. Lister & G. Lister, 1925, p. 3; =^{5}Caloneminea Kudo, 1931, p. 187; =^{7}Calonematineae Hagelstein, 1944, p. 11]——[=^{6}Enteridieae Rostafiński, 1873, p. 3; =^{6}Entheridieae Rostafiński, 1875, p. 7, 29; =^{6}Enteridiales E. Jahn, 1928, p. 16; =^{13}Enteridioidea Pavillard in Grassé, 1953, p. 533]——[=Trichophorae† Rostafiński, 1875, p. 83, 86, 91, 240; =Atriche† Rostafiński, 1875, p. 83, 86, 90, 217; =Atrichées Torrend, 1907, p. 37, 39 *(nom. neg.)*; =^{16}Atrichae Poche, 1913, p. 200 *(nom. nud.)*]——[=^{3}Lamprosporeae Rostafiński, 1875, p. 83, 217; =Lamprosporei Schröter, 1886, p. 102; =Lamprosporae Berlese in Saccardo, 1888, p. 324, 404; =^{10}Lamprosporales A. Lister, 1894, p. 22, 136; =Lamprosporées Torrend, 1907, p. 38 *(nom. neg.)*; =^{6}Lamprosporales A. Lister & G. Lister, 1925, p. 2; =^{4}Lamprosporales Doflein & Reichenow, 1929, p. 841]——[=^{7}Coelonemeen Zopf, 1885, p. 159 *(nom. neg.)*; =^{6}Endotricheen† Zopf, 1885, p. 143 *(nom. neg.)*; =^{7}Endotrichea Lankester, 1885, p. 841]——[=^{6}Peritricheen Zopf, 1885, p. 137 *(nom. neg.)*; =^{7}Peritrichea Lankester, 1885, p. 841; =^{6}Peritricheae Massee, 1892, p. 30, 32]——[=^{6}Calotricheae Massee, 1892, p. 30, 111, 112; =^{6}Euplasmodiés† Delage & Hérouard, 1896, p. 77, 83 *(nom. neg.)*; =^{6}Euplasmodida† Delage & Hérouard, 1896, p. 77, 83; =Platyneminées Torrend, 1907, p. 38, 39 *(nom. neg.)*; =^{4}Lamprosacrales Doflein, 1911, p. 685; =^{7}Dictydiineae Hagelstein, 1944, p. 10; =^{13}Trichioidea Pavillard in Grassé, 1953, p. 533; =^{13}Margaritoidea Pavillard in Grassé, 1953, p. 533]

Variously colored spores, but generally not violet brown or purplish gray, developed in sporangium. *Rec.*

Family LICEIDAE Fries, 1821

[*nom. correct.* Doflein, 1909, p. 601 (*pro* family Liceoidei Fries, 1821, p. xlix, 1)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}superfamily, ^{4}family, ^{5}tribe)]——[=Lycogaleen de Bary, 1864, p. xi *(nom. neg.)*; =^{5}Lycogalaceae Rostafiński, 1873, p. 3; =^{4}Lycogalaceae Luerssen, 1879, p. 41; =^{1}Lycogalaceae A. Lister, 1894, p. 23, 207; =^{4}Lycogalacées Torrend, 1907, p. 38, 40, 45 *(nom. neg.)*; =^{4}Lycogalidae Doflein, 1909, p. 602; =Lycogalactidae Poche, 1913, p. 201 *(nom. van.)*; ^{1}Lycogalales MacBride, 1922, p. 22, 232; =^{4}Lycogalactida Copeland, 1956, p. 175 *(nom. van.)*]——[=^{5}Liceaceae Rostafiński, 1873, p. 4; =^{4}Liceaceae Rostafiński, 1875, p. 32, 86, 218; =^{4}Liceaceen Zopf, 1885, p. 171 *(nom. neg.)*; =^{4}Liceacei Schröter, 1886, p. 98, 102; =^{4}Liceae MacBride, 1899, p. 145; =^{4}Liceacées Torrend, 1907, p. 37, 39, 43 *(nom. neg.)*; =^{4}Liceacae MacBride, 1922, p. 199 *(nom. null.)*; =^{1}Liceales E. Jahn, 1928, p. 16; =^{4}Liceidos Gadea Buisán, 1947, p. 28 *(nom. neg.)*; =^{2}Liceina T. L. Jahn & F. F. Jahn, 1949, p. 140; =^{4}Liceidae Pavillard in Grassé, 1953, p. 533; =^{3}Liceoidea Pavillard in Grassé, 1953, p. 533; =^{4}Liceacea Copeland, 1956, p. 175 *(nom. van.)*]——[=^{5}Cribrariaceae Rostafiński, 1873, p. 5; =^{4}Cribrariaceae Rostafiński, 1875, p. 35, 229; =^{4}Cribrariaceen Zopf, 1885, p. 139 *(nom. neg.)*; =^{4}Cribrariacei Schröter, 1886, p. 98, 102; =Cribrarieae de Bary, 1887, p. 421; =^{1}Cribrariae Massee, 1892, p. 30, 34, 44; =^{1}Cribrariaceae MacBride, 1899, p. 145; =^{4}Cribrarieae MacBride, 1899, p. 145, 159; =^{4}Cribrariacées Torrend, 1907, p. 37, 43, 44 *(nom. neg.)*; =^{4}Cribrariidae Poche, 1913, p. 201; =^{1}Cribrariales MacBride, 1922, p. 22, 199; =^{1}Cribriariales Plunkett, 1934, p. 44 *(nom. null.)*; =^{4}Cribáridos Gadea Buisán, 1947, p. 28 *(nom. neg.)*; =^{3}Cribrarioidea Pavillard in Grassé, 1953, p. 533; =^{4}Cribrariacea Copeland, 1956, p. 175 *(nom. van.)*]——[=^{1}Heterodermeae Rostafiński, 1873, p. 5; =^{1}Heterodermaceae A. Lister, 1894, p. 22, 136; =^{4}Heterodermaceae R. E. Fries, 1903, p. 67 *(nom. nud., non* based on *Heteroderma* Fitzinger, 1843, rept.); =^{4}Heterodermidae Doflein, 1911, p. 686 *(nom. nud.)*; =^{4}Heterodermacées Pouchet, 1925, p. 56 *(nom. neg., nom. nud.)*]——[=^{5}Liceathaliaceae Rostafiński, 1873, p. 4; =^{4}Liceathaliaceae Rostafiński, 1875, p. 33]——[=^{1}Reticularieae Rostafiński, 1873, p. 6 (*non* order Reticularia Carpenter, Parker & Jones, foram.); =^{5}Reticulariaceae Rostafiński, 1873, p. 6; =^{4}Reticulariaceae Rostafiński, 1875, p. 86, 240; =^{4}Reticulariaceen Zopf, 1885, p. 158 *(nom. neg.)*; =^{4}Reticulariacei Schröter, 1886, p. 99, 115; =^{1}Reticulariaceae Morgan, 1893, p. 10; =^{4}Reticularieae MacBride, 1899, p. 145, 149; =^{4}Reticulariacées Torrend, 1907, p. 38, 41, 49 *(nom. neg.)*; =^{4}Reticulariidae Doflein, 1911, p. 681 (*non* Reticulariidae Calkins, 1909, *nom. nud.*, foram.); =^{4}Reticulariacea Copeland, 1956, p. 175 *(nom. van.)*]——[=^{5}Dictydiaethaliaceae Rostafiński, 1873, p. 5; =^{4}Dictydiaethaliaceae Luersson, 1879, p. 43; =^{4}Dictydiaethaliacées Torrend, 1907, p. 37, 39, 43 *(nom. neg.)*; =^{4}Dictydiaethaliidae Poche, 1913, p. 201]——[=^{4}Clathroptychiaceae Rostafiński, 1875, p. 38, 86, 224; =^{4}Clathroptychiaceen Zopf, 1885, p. 137 *(nom. neg.)*; =^{4}Clathroptychiacei Schröter, 1886, p. 98, 108]——[=^{4}Protodermaceae Rostafiński, 1875, p. 90; =^{1}Protodermeae Rostafiński, 1875, p. 61, 83, 90; =^{1}Protodermieae Berlese in Saccardo, 1888, p. 328; =^{4}Protodermiaceae Berlese in Saccardo, 1888, p. 323 *(nom. van.)*]——[=^{1}Columelliferae Rostafiński, 1876, p. 32; =Tubulinae de Bary, 1887, p. 421; =^{2}Tubulinae Massee, 1892, p. 30, 34, 35; =^{1}Tubulinaceae A. Lister, 1894, p. 22, 152; =^{5}Tubulinées Van Tieghem, 1898, p. 20 *(nom. neg.)*; =^{4}Tubulinaceae R. E. Fries, 1903, p. 68 (based on *Tubulina* Persoon, 1794, junior synonym of *Tubifera* Gmelin, 1791); =^{4}Tubulinidae Doflein, 1909, p. 601; =^{4}Tubulinacées Pouchet, 1925, p. 57 *(nom. neg.)*]——[=^{4}Orcadellaceae Wingate, 1889, p. 280; =^{4}Orcadelleae MacBride, 1899, p. 145, 158; =^{4}Orcadellacées Torrend, 1907, p. 37, 39, 43 *(nom. neg.)*; =^{4}Orcadellidae Poche, 1913, p. 201]——[=^{4}Tubifereae MacBride, 1899, p. 145, 153; =^{4}Tubiferacées Torrend, 1907, p. 37, 40, 45 *(nom. neg)*; =^{4}Tubiferidae Poche, 1913, p. 201; =^{4}Tubiferaceae MacBride, 1922, p. 199, 203; =^{4}Tubiferida Copeland, 1956, p. 175 *(nom. van.)*]

Capillitium lacking or not forming system of uniform threads. *Rec.*

Subfamily CRIBRARIINAE Rostafiński, 1873

[*nom. transl.* Loeblich & Tappan, 1961, p. 265 (*ex* tribe Cribrariaceae Rostafiński, 1873, p. 6]

Capillitium absent, or not forming system of uniform threads; sporangium wall membranous, with minute round granules. *Rec.*

Subfamily LICEINAE Fries, 1821

[*nom. transl.* Loeblich & Tappan, 1961, p. 265 (*ex* family Liceoidei Fries, 1821, p. xlix, 1)]

Sporangia solitary, sessile or stalked, sporangium wall cartilaginous or membranous, capillitium absent. *Rec.*

Subfamily TUBIFERINAE MacBride, 1899

[*nom. transl.* Loeblich & Tappan, 1961, p. 265 (*ex* family Tubifereae MacBride, 1899, p. 145, 153)]

Capillitium absent, sporangium wall membranous, without granular deposits, sporangia clustered, cylindrical or ellipsoidal. *Rec.*

Subfamily RETICULARIINAE Rostafiński, 1873

[*nom. transl.* Loeblich & Tappan, 1961, p. 265 (*ex* tribe Reticulariaceae Rostafiński, 1873, p. 6)]

Sporangia closely compacted, generally fused to form large bodies (aethalia), sporangium walls incomplete and perforated; no true capillitium, or may have few branching strands. *Rec.*

Subfamily LYCOGALINAE Rostafiński, 1873

[*nom. transl.* Loeblich & Tappan, 1961, p. 265 (*ex* tribe Lycogalaceae Rostafiński, 1873, p. 3)]

Sporangia forming aethalium, pseudocapillitium consisting of branched colorless tubes. *Rec.*

Family TRICHIIDAE Fries, 1821

[*nom. correct.* Doflein, 1909, p. 602 (*pro* family Trichocisti (Trichioidei) Fries, 1821, p. 1)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}family, ^{4}tribe)]——[=^{3}Trichiacei Fries, 1829, p. 76; Trichiaceen de Bary, 1864, p. 18 (*nom. neg.*); =^{4}Trichiaceae Rostafiński, 1873, p. 14; =^{3}Trichiaceae Rostafiński, 1875, p. 62, 87, 243; =^{3}Trichiaceen Zopf, 1885, p. 159 (*nom. neg.*); =^{3}Trichinacea Lankester, 1885, p. 841; =^{3}Trichiacei Schröter, 1886, p. 98, 107; =Trichiae de Bary, 1887, p. 436; =^{2}Tricheae Massee, 1892, p. 30, 112; =^{1}Trichiaceae Morgan, 1893, p. 28; =^{3}Trichiacées Van Tieghem, 1898, p. 15 (*nom. neg.*); =^{4}Trichiées Van Tieghem, 1898, p. 20 (*nom. neg.*); =^{3}Trichieae MacBride, 1899, p. 179, 200; =^{1}Trichiales MacBride, 1922, p. 22, 236; =^{3}Tríquidos Gadea Buisán, 1947, p. 29 (*nom. neg.*); =^{3}Trichiacea Copeland, 1956, p. 176 (*nom. van.*)]——[=^{4}Perichaenaceae Rostafiński, 1873, p. 15; =^{3}Perichaenaceae Rostafiński, 1875, p. 73, 87, 291; =^{3}Perichaenaceen Zopf, 1885, p. 169 (*nom. neg.*); =^{1}Perichaenaceae Morgan, 1893, p. 19; =^{3}Perichaeneae MacBride, 1899, p. 179, 180; =^{3}Perichaenacea Copeland, 1956, p. 176 (*nom. van.*)]——[=^{4}Arcyriaceae Rostafiński, 1873, p. 15; =^{3}Arcyriaceae Rostafiński, 1875, p. 70, 87, 267; =^{3}Arcyriaceen Zopf, 1885, p. 162 (*nom. neg.*); =Arcyriae de Bary, 1887, p. 436; =^{2}Arcyriae Massee, 1892, p. 30, 113; =^{1}Arcyriaceae Morgan, 1893, p. 23; =^{3}Arcyrieae MacBride, 1899, p. 179, 186; =^{3}Arcyriacées Torrend, 1907, p. 38, 40, 45 (*nom. neg.*); =^{3}Arcyriidae Doflein, 1909, p. 602; =^{3}Arcyriacées Pouchet, 1925, p. 61 (*nom. neg.*) =^{3}Arcyriacea Copeland, 1956, p. 176 (*nom. van.*)]——[=^{1}Margaritaceae A. Lister, 1894, p. 23, 202 (*nom. nud.*, based on *Margarita* Lister, 1894, *non* Leach, 1814, *nec* Leach, 1819, *nec* Lea, 1836, *nec* Lea, 1838); =^{3}Margaritacées Torrend, 1907, p. 38, 40, 45 (*nom. neg.*, *nom. nud.*); =^{3}Margaritidae Doflein, 1909, p. 602 (*nom. nud.*); =^{3}Margaritaceae A. Lister & G. Lister, 1925, p. 3 (*nom. nud.*); =^{1}Margaritales E. Jahn, 1928, p. 16 (*nom. nud.*); =^{3}Margaritida Copeland, 1956, p. 176 (*nom. nud.*, *nom. van.*)]——[=^{3}Dianemeae MacBride, 1899, p. 179, 180 (*nom. nud.*, based on *Dianema* Rex, 1891, *non* Cope, 1871); =^{3}Dianemaceae MacBride, 1922, p. 237 (*nom. nud.*)]——[=^{3}Prototrichieae MacBride, 1899, p. 179, 199; =^{3}Prototrichiaceae MacBride, 1922, p. 237, 258; =^{3}Listerellaceae E. Jahn, 1928, p. 16]

Capillitium present as system of uniform or sculptured threads. *Rec.*

Subfamily TRICHIINAE Fries, 1821

[*nom. correct.* Loeblich & Tappan, 1961, p. 266 (*pro* subfamily Trichiei Schröter, 1886, p. 99, 111, *nom. transl. ex* family Trichocisti (Trichioidei) Fries, 1821, p. 1); subfamily Trichieae MacBride, 1892, p. 120, 128]

Capillitium distinct, consisting of system of tubular threads, either free and unbranched, or with open network having spiral or annular thickenings. *Rec.*

Subfamily ARCYRIINAE Rostafiński, 1873

[*nom. correct.* Loeblich & Tappan, 1961, p. 266 (*pro* subfamily Arcyriei Schröter, 1886, p. 99, *nom. transl. ex* tribe Arcyriaceae Rostafiński, 1873, p. 15)]——[All names referred to are of subfamily rank]——[=Perichaenei Schröter, 1886, p. 98, 107; =Arcyrieae MacBride, 1892, p. 120, 121; =Perichaeneae MacBride, 1892, p. 120]

Capillitium combined into elastic network of tubular threads branching at wide angles, threads smooth or with thickenings in form of cogs, rings, half-rings, spines or warts, or more rarely with free threads forming scanty network. *Rec.*

Subfamily PROTOTRICHIINAE MacBride, 1899

[*nom. transl.* Loeblich & Tappan, 1962, p. 107 (*ex* family Prototrichieae MacBride, 1899, p. 179, 199]——[=Dianemininae Loeblich & Tappan, 1961, p. 266 (*nom. subst.* and *nom. transl. ex* family Dianemeae MacBride, 1899, p. 179, 180, *nom. nud.*, based on *Dianema* Rex, 1891, *non* Cope, 1871, =*Dianemina* Loeblich & Tappan, 1961, p. 266, *nom. subst.*)]

Capillitium abundant, of solid threads, coiled and hairlike or nearly straight and attached to the sporangium wall, simple or branching at acute angles. Sporangia normally sessile. [Four genera are commonly assigned to this taxon, *Margarita* Lister, 1894 (upon which family Margaritidae Doflein, 1909, was based), *Dianema* Rex, 1891 (basis for family Dianemeae MacBride, 1899), *Prototrichia* Rostafiński, 1876 (basis for family Prototrichieae MacBride, 1899), and *Listerella* E. Jahn, 1906 (basis for family Listerellaceae E. Jahn, 1928). The family names based on *Dianema* and *Prototrichia* are the oldest, but as *Dianema* was a homonym it was renamed *Dianemina* and the subfamily name Dianemininae proposed by the writers (*1177, p. 266). However, the family group name based on *Prototrichia* has priority, hence was transferred to subfamily status (*1185). Of the remaining genera, *Margarita* Lister, 1894, is a junior homonym of *Margarita* Leach, 1814, and *M.* Leach, 1819, and *Margarita* Lea, 1836, and *M.* Lea, 1838, all proposed for mollusks. *Margarita* Lister, 1894, was renamed *Margaritellina* Loeblich & Tappan, 1962 (*1185, p. 108).] *Rec.*

"THECAMOEBIANS"

CONTENTS

NATURE OF ASSEMBLAGE

The orders Arcellinida and Gromida, together with part of the suborder Allogromiina of the order Foraminiferida, have been referred to collectively as Thecamoebians or Testacea by paleontologists. They include most of the fresh-water testaceous Rhizopodea. Zoological usage, however, has separated these groups for three-quarters of a century, primarily on characters of the pseudopodia, so that at present the Arcellinida are placed in the subclass Lobosia, class Rhizopodea, the Gromida in the subclass Filosia, and the Allogromiina in the subclass Granuloreticulosia; the latter two subclasses are assigned to the class Reticularea. Because of certain common characters observable to paleontologists, a single introduction may serve for all. The Allogromiina are herein discussed under the Foraminiferida.

Testaceans have been described and figured since the beginning of the nineteenth century. They are dominantly found in fresh water, on mosses, or in damp soil, but a few brackish or marine species occur. Some fossil forms have been found in lake deposits or in strata intercalated between coal seams. It seems probable that if more attention were given to these fresh-water forms, the number of genera reported as fossils would increase. The test is not as highly organized as that of the Foraminiferida, for commonly it consists of a simple unilocular saclike or saucer-shaped body which rarely exhibits modifications of the aperture and spinelike protuberances or other modifications. The test composition may be gelatinous, membranous, "chitinous," or agglutinated, or may consist of loosely arranged or closely imbricated siliceous plates or scales, or in a single genus may have secreted plates of calcite. As relates to fossil shells and those of Recent dead testaceans, for which information supplied by the pseudopodia and cytoplasmic nature is lacking, only the test composition and form can be utilized for taxonomic studies. Occasionally the tests of fresh-water forms have been obtained in near-shore marine deposits or as contamination in strata collected from outcrops in stream beds; they have then been described as foraminifers, because of their supposed marine occurrence. Such occurrences at the generic level are mentioned in the systematic section of this chapter.

The protoplasm of testaceans is similar to that of the nontestaceous rhizopods, showing a differentiation into ectoplasm and endoplasm. The number of nuclei varies in different genera.

Reproduction in the thecamoebians is commonly by simple fission, but some forms exhibit budding and a few also are reproduced sexually. Encystment may occur with the advent of unfavorable environmental conditions. Although not yet recognized as such in the fossil state, it is possible that the vegetative cysts may be preserved in sediments, particularly in intertongued marine and nonmarine strata or in strata associated with coals.

The food supply consists of other protistans, flagellates, ciliates, unicellular green algae, desmids, diatoms, and even fragments of moss and lichens. It is difficult to observe the ingestion of food in testaceans provided with an opaque test. *Paulinella* apparently does not ingest food but obtains the required nourishment from chromatophore-like symbiotic algae which are always associated with it.

The Lobosia are treated systematically first in order that they be kept with the remaining thecamoebians. They may, however, actually be more highly advanced than the foraminifers and radiolarians, since they are dominantly of fresh-water or terrigenous habitat; some have symbiotic relationships with algae and the nontestaceous forms include many that are parasitic.

GLOSSARY OF MORPHOLOGICAL TERMS

anisogamy. Fusion of 2 unlike gametes (classed as macrogametes and microgametes) to form zygote during sexual reproduction of Mastigophora, Sporozoa, and possibly some Lobosia.

aperture. Opening in test or shell for protrusion of pseudopodia.

blepharoplast. Basal granule where flagellum is inserted, observed in Mastigophora and gametes of some rhizopods.

chromidia. Extranuclear chromatin granules scattered throughout cytoplasm or restricted to region closely adjacent to nucleus.

contractile vacuole. Differentiated spherical part of cell that regulates osmosis, alternately filling and enlarging and discharging liquid from cell interior to outside; may be one or many, occur either in anterior portion of cytoplasm or near nucleus in thecamoebians (found in fresh-water forms).

cyst. Inert and resistant cover which envelops protoplasm and protects it from adverse environmental conditions; may be resting cysts or reproductive cysts; may form within test or just outside aperture; may give rise to uniflagellate spores which conjugate.

cytoplasm. Protoplasm, exclusive of nucleus, rich in proteids (albumen), poor in phosphorus.

diaphragm. Partial septum just below aperture or apertural neck, perforated for protrusion of pseudopodia (e.g., *Cucurbitella, Pontigulasia*).

diploid. Stage in life history in which nuclei contain full number of chromosomes; in sexual reproduction gametes contain half of this number, fusion of gametes to form zygote restoring diploid stage.

endolobopodia. Lobose pseudopodia in composition of which some endoplasm participates (e.g., Difflugiidae, Arcellidae).

ectoplasm. Hyaline, unequally thick peripheral region of cytoplasm with outer portion composed of relatively stationary particles of plasmasol and inner portion consisting of plasmagel.

endoplasm. Central dark granular part of cytoplasmic mass containing food vacuoles, contractile vacuoles, and nuclei; in Lobosia characterized by constant movement, flowing from back to front of cell body, changing from gel (plasmagel) to liquid (plasmasol) state.

epipods. Protoplasmic filaments (ectoplasm) extending from central mass of protoplasm to inner wall of test when latter is not completely filled; modified pseudopodia.

exolobopodia. Lobose pseudopodia composed entirely of ectoplasm (e.g., *Cochliopodium, Amphizonella, Pseudochlamys*).

filipodia. Elongate pseudopodia of ectoplasm which may anastomose, their rapid movement serving for locomotion and transport of food into body for digestion.

fission. Asexual reproduction, either by longitudinal fission or transverse division.

flagellum. Fine filamentous extension of cytoplasm which commonly displays rapid motion; characteristic locomotor apparatus of Mastigophora and found in gametes of some rhizopods, different groups having 1, 2, or 3 flagella.

granuloreticulose pseudopodia. Linear pseudopodia which anastomose and bifurcate readily, with more solid axis (stereoplasm) and outer fluid portion (rheoplasm) containing granules in continuous movement; may digest food outside of main body of protozoan.

haploid. Stage in life history in which nuclei have one-half of normal number of chromosomes, resulting from reduction division in nucleus; may be temporary (as in gametes) or represent a distinct generation (as in foraminifers).

holophytic nutrition. Plantlike maintenance of life by utilization of water, carbon dioxide and other inorganic substances for manufacture of food, found in Protozoa which possess chlorophyll, characteristic of some Mastigophora and some symbiotic rhizopod associations in which algae act as chromatophores for host (e.g., *Paulinella*).

holozoic nutrition. Animal-like maintenance of life by utilization of food consisting of ingested organisms (animals or plants).

hyaline. Glassy clear.

isogamy. Type of sexual reproduction in which 2 morphologically similar gametes fuse to form zygote.

lobopodia. Pseudopodia consisting of cytoplasmic mass with rounded termination which contains both ectoplasm and endoplasm (Lobosia), used for locomotion and transport of food into cell body for digestion.

lorica. Test or shell of thecamoebians.

meiosis. Reduction division in nuclei, each half of nucleus then having one-half of chromosomes, resulting in haploid stage (as in gametes).

mitosis. Nuclear division in which each half contains same number of chromosomes as parent nucleus; found in asexual reproduction or fission.

nucleus. More or less spherical, compact mass of chromatin surrounded by membrane, lying within cytoplasmic body and playing important part in development and functions of cell (e.g., digestion, test secretion); single individual may have one nucleus or many.

parasitic nutrition. Maintenance of life dependent on host, food being absorbed by osmosis from body fluid, digested food material, or cell substance of host.

peduncle. Mass of cytoplasm projecting from aperture, giving rise to pseudopodia; pseudopodial trunk.

pellicle. Membrane surrounding protozoan body, elastic and somewhat expansible.

plagiostome. Asymmetrically placed aperture or pseudostome (e.g., *Centropyxis, Plagiopyxis, Bullinularia*).

plasmagel. Outer, partially solidified, jelly-like cytoplasm; outer portion of plasmagel corresponds to ectoplasm.

plasmalemma. Elastic pellicle of plasmagel forming outer covering of amoeboid body.

plasmasol. Central fluid portion of cytoplasm.

plasmogamy. Fusion of 2 or more individuals commonly followed by encystment; results uncertain in thecamoebians, although nuclear divisions, sporulation, etc., have been reported.

protoplasm. Living matter comprising body of protozoan or other organism, divisible into cytoplasm and nucleus.

pseudochitin. Chitin-like substance composing some testacean tests, similar to keratin in containing sulfur, but also having inframicroscopic granules of opaline silica.

pseudopodia. Temporary or semipermanent cytoplasmic projections which serve for locomotion and food capturing; may occur as lobopodia (e.g., Lobosia), filopodia (e.g., Filosia), reticulopodia (e.g., Granuloreticulosia), or axopodia (e.g., Acantharia, Heliozoia).

pseudopodial trunk. Mass of cytoplasm projecting from aperture and giving rise to pseudopodia; peduncle.

pseudostome. Aperture in test from which pseudopodia protrude; may be simple opening or have definite structure (e.g., neck, oral apparatus, diaphragm).

reticulolobopodia. Lobose pseudopodia composed entirely of ectoplasm, rarely capable of anastomosing (e.g., *Phryganella, Cryptodifflugia*).

reticulopodia. Granuloreticulose pseudopodia which bifurcate and anastomose to form network.

rheoplasm. Granular outer fluid portion of granuloreticulose pseudopodia.

saprozoic nutrition. Maintenance of life by osmosis through cell wall of food consisting of organic substances dissolved in water.

sarcode. Protoplasm.

stercomata. Brown oval masses of debris within cytoplasm.

stereoplasm. Relatively solid axis of granuloreticulose pseudopodia, surrounded by granular rheoplasm.

symbiosis. Mutually beneficial life association of 2 organisms; green algae live within some Lobosia and Filosia, being always present in some genera but occasionally in others; symbiotic blue-green algae (Cyanophyceae) occur in one genus (*Paulinella*).

thecamoebian. General term for all testaceous rhizopods exclusive of Foraminiferida; commonly of fresh-water habitat, more rarely brackish to marine.

test. Shell or covering of protozoans; may be gelatinous, "chitinous," calcareous, or siliceous, composed of secreted platelets or solid wall, or formed of agglutinated foreign particles.

vacuoles. Globular inclusions in cytoplasm, may be contractile vacuoles or food vacuoles.

xanthosomes. Small refringent bodies, commonly very numerous, in cytoplasm.

zygote. Body formed by fusion of 2 gametes in course of sexual reproduction, zygote (diploid) containing twice as many chromosomes as each gamete (haploid).

GEOLOGICAL IMPORTANCE

Owing to the dominantly fresh-water habitat of thecamoebians and previous concentration of micropaleontologic studies on marine strata, few fossil occurrences of these organisms have been reported. Most, including *Arcella, Trigonopyxis, Hyalosphenia, Heleopera, Nebela,* and *Cryptodifflugia* among the Lobosia, have been described by protozoologists from Pleistocene deposits. *Silicoplacentina* has been found in the Pliocene, *Cyclopyxis* in the Miocene, *Difflugia* and *Pontigulasia* in the Eocene, and *Prantli-*

tina in the Mississippian. Among the Gromida, *Pseudodifflugia, Amphitrema, Archerella, Sphenoderia, Trinema,* and *Corythion* occur in Pleistocene deposits, *Tracheleuglypha* in Miocene strata, and *Euglypha* in Eocene beds.

Most living genera have wide geographic distribution and apparently some species occur in both hemispheres throughout a wide range of latitude. Their presence in marine strata (if not due to contamination) indicates the proximity of a shore line.

Order ARCELLINIDA Kent, 1880

[Arcellinida KENT, 1880, p. 36]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}section, ^{2}order, ^{3}suborder, ^{4}Gruppe; dagger(†) indicates *partim*)]——[=^{2}Monostega† DIESING, 1848, p. 497; =^{2}Monostegia† HAECKEL, 1894, p. 164]——[=^{2}Loricata EHRENBERG, 1832, p. 40; =Testacea SCHULTZE, 1854, p. 52 (*non* Testacea LINNÉ, 1758, p. 667); =^{3}Testacea BÜTSCHLI in BRONN, 1880, p. 181; =^{2}Testacea LANKESTER, 1885, p. 842; =^{1}Testacea MINCHEN, 1912, p. 217; =^{3}Testacea (Thecamoebaea) RHUMBLER in KÜKENTHAL & KRUMBACH, 1923, p. 69; =^{2}Testacida T. L. JAHN & F. F. JAHN, 1949, p. 42]——[=Lepamoebae† HAECKEL, 1870, p. 56; =^{2}Athalamia† SCHMARDA, 1871, p. 160; =Monothalamia monostomata HERTWIG & LESSER, 1874, p. 91; =^{2}Arcellina (Thecolobosa) HAECKEL, 1894, p. 164; =^{2}Thecamoebida DELAGE & HÉROUARD, 1896, p. 101; =^{3}Thecamoebina CALKINS, 1901, p. 106; =^{2}Conchulina† CASH, 1904, p. 224; =Rhizopoda lobosa testacea SCHOUTEDEN, 1906, p. 329; =^{2}Thecamoebaea (Testacea) KÜHN, 1926, p. 118; =^{3}Testacealobosa DE SAEDELEER, 1934, p. 5; =^{3}Tecameboideos GADEA BUISÁN, 1947, p. 16 (*nom. neg.*); =^{2}Testacealobosa DEFLANDRE in GRASSÉ, 1953, p. 123; =^{3}Testalobosina BOVEE, 1960, p. 355; =^{2}Lampramoebae COPELAND, 1956, p. 205; =^{4}Imperforata† BLOCHMANN, 1895, p. 14]

Test or rigid external membrane present, with definite aperture for protrusion of lobose pseudopodia. *Miss.-Rec.*

Superfamily ARCELLACEA Ehrenberg, 1832

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 267 (*ex* sectio Arcellina EHRENBERG, 1832, p. 40]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}suborder, ^{2}family group, ^{3}legion; dagger(†) indicates *partim*)]——[=^{2}Polystomata† RHUMBLER, 1928, p. 4 (*non* AVERINTSEV, 1906); =^{3}Eulobosa DE SAEDELEER, 1934, p. 5, 11; =^{1}Eulobosa DEFLANDRE in GRASSÉ, 1953, p. 123]

Pseudopodia finger-like, not anastomosing. *Miss.-Rec.*

Family COCHLIOPODIIDAE Taránek, 1882

[*nom. correct.* HICKSON in LANKESTER, 1909, p. 88 (*pro* Cochliopodidae TARÁNEK, 1882, p. 223]——[=Pseudonebelinae WAILES in CASH, WAILES & HOPKINSON, 1919, p. 66 (*nom. nud.*); =Cochliopodiinae DE SAEDELEER, 1934, p. 11]

Test reduced to flexible or semirigid membrane, without definite aperture. [Possibly intermediate between Amoebida and Arcellinida.] *Rec.*

Cochliopodium HERTWIG & LESSER, 1874, *921, p. 77 [**C. pellucidum* HERTWIG & LESSER, 1874, p. 66; SD LOEBLICH & TAPPAN, herein (=**Amoeba bilimbosa* AUERBACH, 1856, *55, p. 374)] [=*Kochliopodium* VALKANOV, 1932, *1972, p. 176) (*nom. null.*)]. Test a flexible membrane without included foreign matter (diam., 24-56μ), ornamented with granulations or may have spines, subglobular or slightly flattened against substratum; conical pseudopodia of ectoplasm, lacking granules, rarely divided, protruding in group from constantly dilatable aperture; single nucleus toward aboral end; vacuoles numerous. [Fresh water.] *Rec.,* Eu.-N.Am.——FIG. 3,*1*. **C. bilimbosum* (AUERBACH), Eu.; *1a,* side view, with sec. of test, enlarged; *1b,* top view, enlarged (*921).

Chlamydamoeba COLLIN, 1912, *373, p. lxxxviii [**C. tentaculifera;* OD]. Gelatinous, easily deformed test (diam., 30-60μ), generally rounded, covering even pseudopodia except at extremities; protoplasm consisting of opaque, hyaline band of ectoplasm surrounding granular, inclusion-bearing endoplasm; nucleus central; one contractile vacuole; pseudopodia absent entirely or short and blunt, may have central canals extending from tips into central area, movement extremely slow. [Marine.] *Rec.,* Eu.——FIG. 3,*3*. **C. tentaculifera,* Fr.; *3a,b,* varying forms showing thin test, differentiated endo- and ectoplasm and pseudopodial extensions, ×600 (*373).

Gocevia VALKANOV, 1932, *1972, p. 175, 187 [**G. pontica;* OD]. Test highly flexible (diam., 25-30μ), covered with foreign matter, protoplasmic body tending to spread out over substratum, as in *Cochliopodium;* test somewhat loosely covering protoplasm which is not differentiated into ecto- and endoplasm. [Marine.] *Rec.,* Eu.——FIG. 3,*2*. **G. pontica; 2a,* diagram. sec.; *2b,* ext.; *2c,* sec.; approx. ×2,000 (*1974).

Family MICROCORYCIIDAE de Saedeleer, 1934

[*nom. transl. et correct.* DEFLANDRE in GRASSÉ, 1953, p. 125 (*ex* Mikrocoryciinae DE SAEDELEER, 1934, p. 5, 18); tribus Mikrocoryciini DE SAEDELEER, 1934, p. 5, 18]——[tribus Microchlamyini DE SAEDELEER, 1934, p. 5, 18]——[=family Corycina STEIN, 1857, p. 42]

Test membranous, in part rigid or semirigid, thinning and becoming more pliable toward variously shaped aperture; one or many nuclei. *Rec.*

Microcorycia COCKERELL, 1911, *352, p. 137 [**Amphizonella flava* GREEFF, 1866, *813, p. 329; OD] [=*Corycie* DUJARDIN, 1852, *637, p. 241 (*nom. neg.*); =*Corycia* REUSS, 1862, *1552, p. 363 (*non Corycia* HUEBNER, 1823; *nec* HUEBNER, 1825; *nec* DUPONCHEL, 1829; *nec* BALY, 1864); *Coryzia* STEIN, 1867, *1836, p. 4 (*nom. van.*)]. Test yellowish, membranous, flexible, with agglutinated foreign matter (diam., 80-100μ), clear, hyaline, and fringelike at margins, attached to substratum or vegetal debris, hemispherical or ovoid, more rarely subglobular or free, with diaphanous margin infolded or closed, resulting in radial folds or ridges around apertural opening;

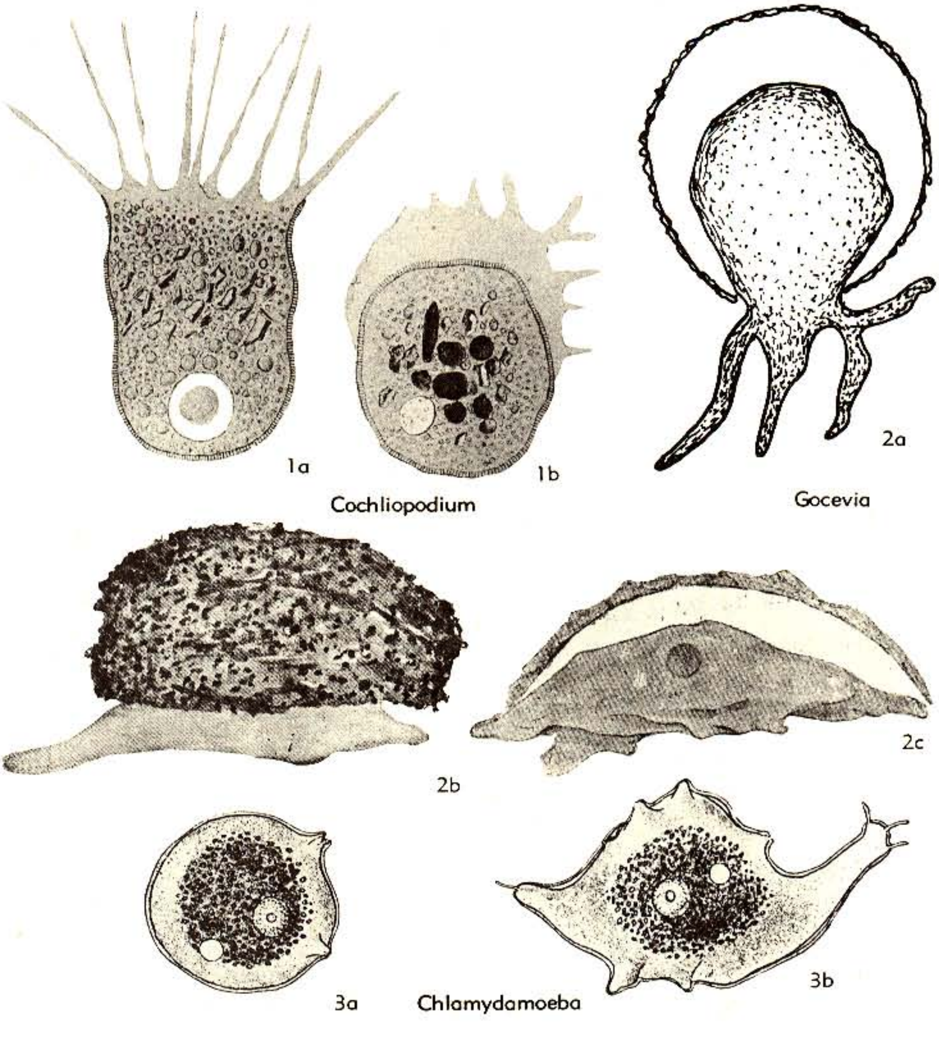


FIG. 3. Cochliopodiidae; *1, Cochliopodium; 2, Gocevia; 3, Chlamydamoeba* (p. C19).

pseudopodia lobular or digitate; protoplasm not completely filling test; with 1 or 2 nuclei. [Fresh water.] *Rec.,* Eu.——FIG. 4,*1*. **M. flava* (GREEFF); side view showing subglobular form with pendent membranous margin, ×350 (*1435).

Amphizonella GREEFF, 1866, *813, p. 323 [**A. violacea;* OD]. Test double, inner layer membranous or chitinoid, outer layer thick and mucilaginous (diam., approx. 0.16 mm.); protoplasm dense, granular, violet in color; pseudopodia blunt to subconical, radiating from aperture; single nucleus and clear vacuoles. [Fresh water.] *Rec.,* Eu.——FIG. 4,*2*. **A. violacea;* specimen showing subconical pseudopodia, approx. ×280 (*813).

Diplochlamys GREEFF, 1888, *814, p. 104 [**D. leidyi;* OD]. Test hemispherical or cup-shaped (diam., 80-100μ), double, inner layer consisting of hyaline membrane with variable aperture, external covering of loosely attached foreign matter; aperture large, nuclei numerous (as many as 100). [Fresh water.] *Rec.,* Eu.——FIG. 4,*3*. **D. leidyi;* ×400 (*302b).

Microchlamys COCKERELL, 1911, *352, p. 136 [**Pseudochlamys patella* CLAPARÈDE & LACHMANN, 1859, *345, p. 443; OD] [=*Pseudochlamys* CLAPARÈDE & LACHMANN, 1859, *345, p. 443) (*non* LACORDAIRE, 1848) (obj.)]. Test discoidal or cup-shaped (diam., 40-45μ), hyaline and flexible in young, rigid and brownish in adult, and may be punctate dorsally; pseudopodia short, lobose; with central nucleus and several contractile vacuoles. [Fresh water.] *Rec.*, Eu.——FIG. 4,6. **M. patella* (CLAPARÈDE & LACHMANN); *6a*, specimen with digitate pseudopod; *6b*, top view; ×500 (*300).

Parmulina PENARD, 1902, *1435, p. 206 [**P.*

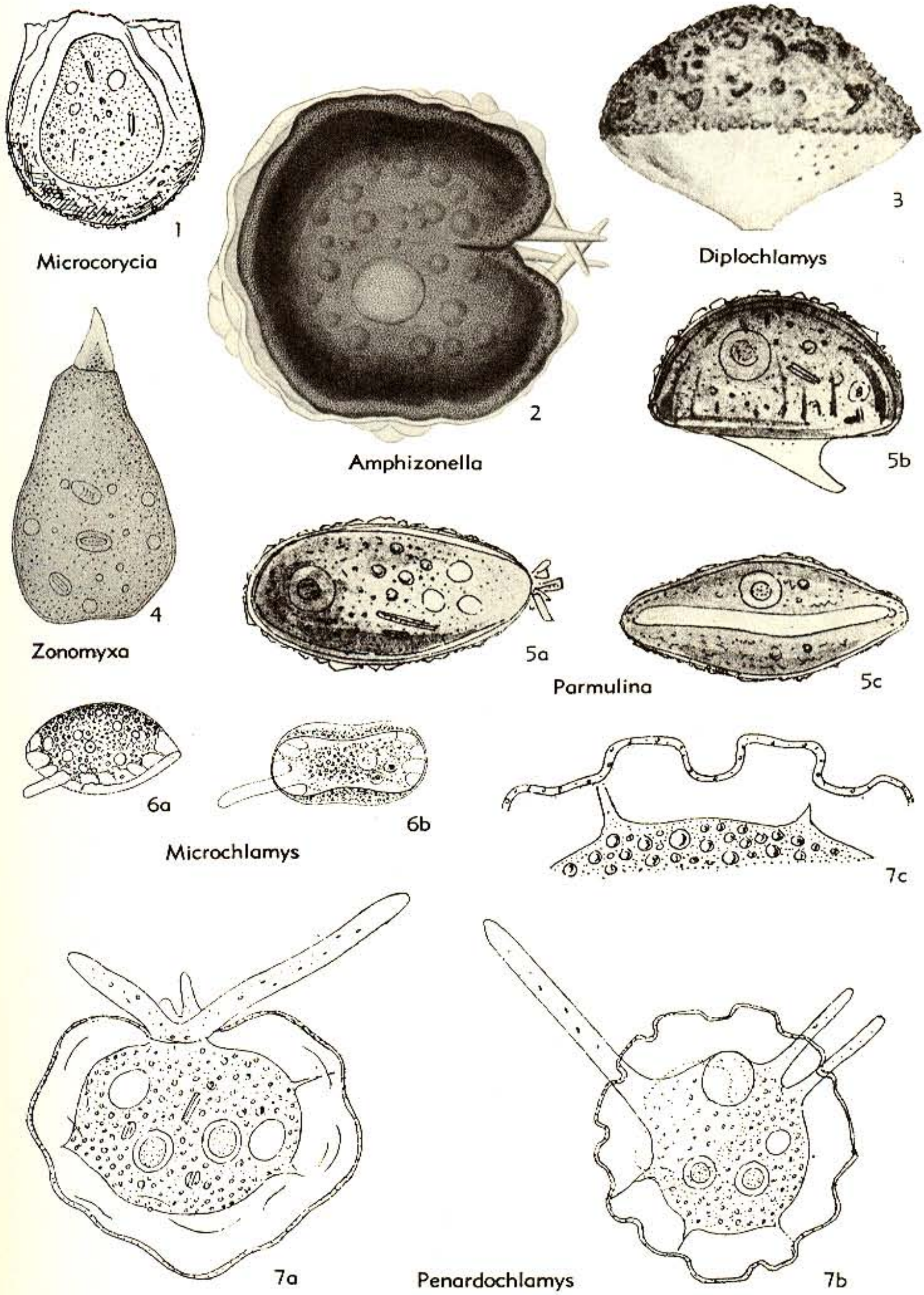


FIG. 4. Microcoryciidae; *1, Microcorycia; 2, Amphizonella; 3, Diplochlamys; 4, Zonomyxa; 5, Parmulina; 6, Microchlamys; 7, Penardochlamys* (p. C19-C22).

cyathus Penard, 1902; SD Penard, 1909, *1439, p. 286]. Test elongate, fusiform when viewed from above (length, 45-55µ), grayish to yellowish, thick and chitinoid, with some agglutinated foreign matter producing rugose surface; lower surface with elongate slitlike area where test becomes thin and supple, internal envelope not seen; pseudopodia not seen; numerous contractile vacuoles, one nucleus (diam., approx. 8µ), somewhat eccentric in position. [Fresh water.] *Rec.*, S.Am.-Eu.——Fig. 4,*5*. **P. cyathus; 5a-c,* top, side and basal views, approx. ×700 (*1439).

Penardochlamys Deflandre in Grassé, 1953, *810, p. 126 [**Pseudochlamys arcelloides* Penard, 1904, *1436, p. 408; OD(M)]. Test saclike (diam., 60-70µ), very thin, chitinoid, deformable, colorless or slightly yellowish, recurved at aperture; surface punctate, marked by broad undulations, changing slightly in form and place, test with single large opening at one end through which few large and lobate pseudopodia extend; protoplasm grayish, enclosing 2 large nuclei with central nucleoli, and one or many contractile vacuoles. [Fresh water.] *Rec.*, Eu.——Fig. 4,*7*. **P. arcelloides* (Penard); *7a,b,* side and bottom views, approx. ×750; *7c,* enlargement of margin shown in *7b* (*1436).

Zonomyxa Nüsslin, 1884, *1366, p. 697 [**Z. violacea;* OD]. Test a supple chitinoid membrane (length up to 250µ), pyriform in motion, discoid in repose, narrowing toward aperture, differing from *Amphizonella* in being multinucleate and in lacking outer mucilaginous covering, violet-colored; with single, lobular simple pseudopodium; protoplasm granular, several nuclei, numerous clear vacuoles. [Fresh water on sphagnum.] *Rec.*, Eu.——Fig. 4,*4*. **Z. violacea*; individual in movement, ×150 (*301).

Family ARCELLIDAE Ehrenberg, 1832

[*nom. transl. et correct.* Schulze, 1877, p. 26 (*pro* sectio Arcellina Ehrenberg, 1832, p. 40]——[In synonymic citations superscript numbers refer to taxonomic rank assigned bv authors (^{1}family, ^{2}subfamily; dagger(†) indicates *partim*)]——[=^{1}Arcellina, ^{1}Arcellinés Ehrenberg, 1838, p. 129; =^{1}Arcellinea, Arcellineae Diesing, 1848, p. 495, 497; =^{1}Arcellida Schmarda, 1871, p. 163; =^{2}Arcellinae Vejdovský, 1881, p. 138; =^{1}Arcélidos Gadea Buisán, 1947, p. 16 (*nom. neg.*)]——[=^{1}Pseudopodia† Ehrenberg, 1832, p. 39 (*nom. nud.*); =^{1}Kapselthierchen Ehrenberg, 1838, p. 129 (*nom. nud., nom. neg.*); =^{1}Monothalamia Pritchard, 1861, p. 201 (*nom. nud.*); =Monocyphia† Vejdovský, 1881, p. 138; =^{1}Lobosa Blochmann, 1895, p. 12]

Test chitinous, rigid, aperture ventral, always with edge infolded; commonly with 2 nuclei, may have many, rarely only one. *Pleist.-Rec.*

Arcella Ehrenberg, 1832, *664, p. 40 [**A. vulgaris;* OD] [=*Pyxidicula* Ehrenberg, 1834, *665, p. 295 (type, *Frustrulia operculata* Agardh, 1827, *4, p. 627); =*Arcellina* Carter, 1856, *286, p. 224, 247 (*nom. van.*); =*Arcella (Sticholepis)* Ehrenberg, 1872, *688, p. 244 (obj.); =*Cyphidium* Ehrenberg, 1837, *666, p. 172 (type, *C. aureolum* Ehrenberg, 1837); =*Arcella (Cyphidium)* Ehrenberg, 1872, *688, p. 245 (obj.); =*Arcella (Heterocosmia)* Ehrenberg, 1872, *688, p. 245 (type, *Arcella (Heterocosmia) peristicta* Ehrenberg, 1872 =*A. peristicta* Ehrenberg, 1854, SD Loeblich & Tappan, herein); =*Leptocystis* Playfair, 1918, *1459, p. 641 (type, *L. arcelloides* Playfair, 1918); =*Arcella (Euarcella)* Deflandre, 1928, *569, p. 209 (obj.); =*Arcella (Antarcella)* Deflandre, 1928, *569, p. 209 (type, *Arcella atava* Collin, 1914, *374, p. 85; =*Antarcella* Deflandre in Grassé, 1953, *810, p. 127]. Test membranous, transparent, chitinoid, punctate or minutely cancellate, rarely spinose, hemispherical, recurved at circular to crenulate aperture (av. diam., 70µ), young tests hyaline, adult brown; protoplasm centrally placed, attached to interior of test by threads of ectoplasm, may secrete gas vacuoles, to serve hydrostatic function, allowing individual to float, and later resorb vacuoles in order to settle; pseudopodia few, lobose, blunt; commonly binucleate, but in some species as many as 200 nuclei occur; 4 or more small contractile vacuoles; reproduction by "budding." [*Leptocystis* Playfair was separated from *Arcella* by its minute size (diam., 20µ) and absence of any surface markings. Only empty tests were seen. As young specimens of *Arcella* show all these characters, *Leptocystis* appears to represent only the early growth stage or a small species of *Arcella*. *Antarcella* was originally described as a subgenus, later raised to generic rank, differing in having a single nucleus, whereas *Arcella* commonly had two, more rarely 3 to 40 or up to 200. Specimens with a single nucleus are rare, only one or two species being included, and as the number appears to vary even within a species, *Antarcella* is here regarded as synonymous. *Pyxidicula* was originally described as a subgenus of the diatom genus *Gallionella* and the type-species was first described as a *Frustrulia*, later variously referred to *Cymbella* and *Cyclotella*. It differs from *Arcella* only in being extremely small, in having a very wide aperture, a single nucleus and in lacking ornamentation, all features which may be characteristic of young *Arcella*. The type-species is approximately 20µ in diameter, about the size of the smallest *Arcella vulgaris*.] [Brackish to fresh water.] *Pleist.-Rec.*, cosmop.——Fig. 5,*1*,*2*. **A. vulgaris,* Rec., Eng.; *1a,* young individual in movement; *1b,c,* basal and side views of young, empty transparent tests, ×300 (*300); *2,* top view of adult showing outstretched pseudopodia and cancellate test, ×200 (*2005).——Fig. 5,*3*. *A. arcelloides* (Playfair), Rec., Australia; *3a,b,* side and top views, ×900 (*1459).——Fig. 5,*4*. *A. atava* Collin, Rec., Fr.; *4a,b,* side and basal views, ×720 (*374).——Fig. 5,*5*. *A. operculata* (Agardh), Rec., Switz.; *5a,b,* side and top views, ×1,200; *5c,* enlarged margin, ×4,800 (*1435).

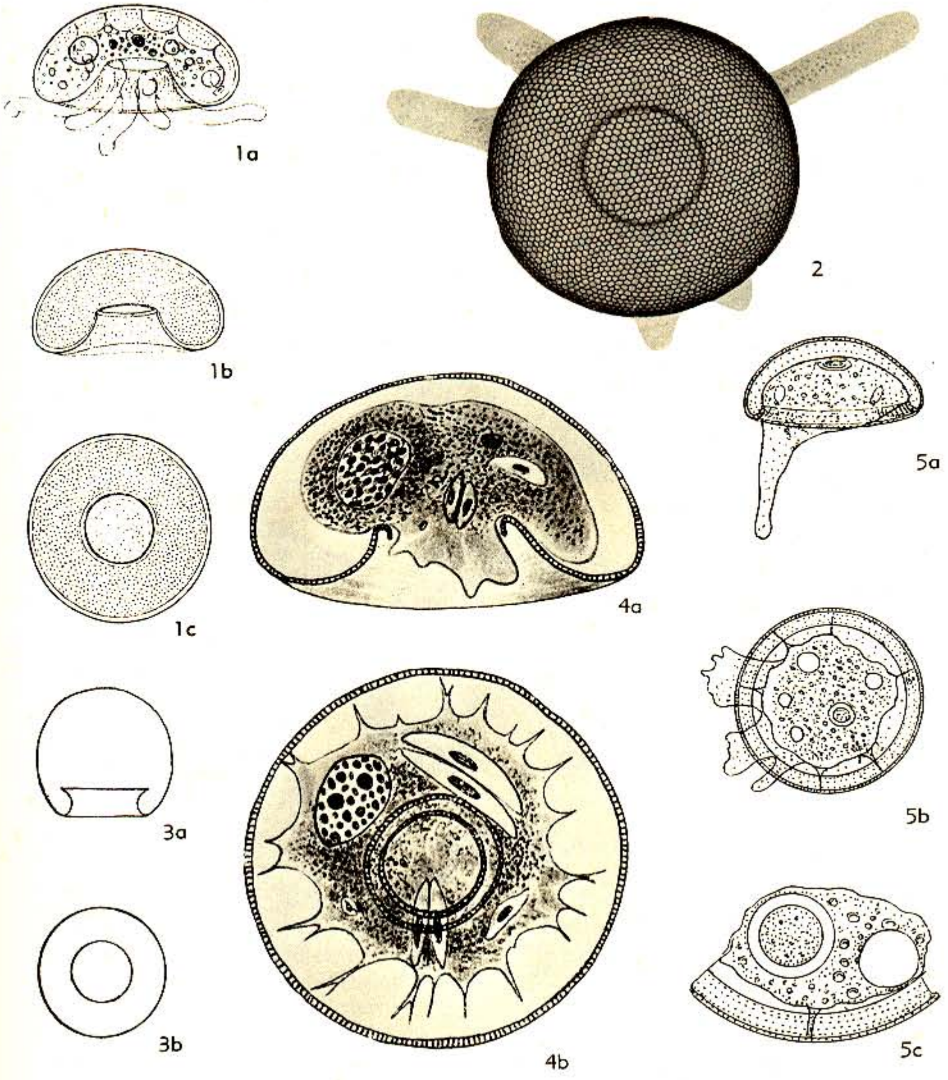


FIG. 5. Arcellidae; *1-5, Arcella* (p. C22).

Family CENTROPYXIDAE Jung, 1942

[Centropyxidae JUNG, 1942, p. 255; family Monocyphia VEJDOVSKÝ, 1881, p. 138 *(nom. nud.) (partim)*; family Conchulina WAILES, 1927, p. 153 *(nom. nud.)*]

Test chitinous, enclosing some foreign material, or with sandy layer, generally with dorsoventral symmetry; aperture ventral, with recurved margin, eccentric; single nucleus. *Pleist.-Rec.*

Centropyxis STEIN, 1859, *1835, p. 43 [**Arcella aculeata* EHRENBERG, 1832, *664, p. 40; OD] [=*Echinopyxis* CLAPARÈDE & LACHMANN, 1859, *345, p. 447 (obj.); *Arcella (Centropyxis)* EHRENBERG, 1872, *688, p. 245 (obj.); =*Millettella* RHUMBLER, 1904, *1569, p. 250 (type, *Reophax pleurostomelloides* MILLETT, 1899, *1284(c), p. 253; *Armillettum* RHUMBLER, 1913, *1572(b), p. 349 (*nom. van. pro Millettella,* obj.)]. Test chitinoid, colorless to brown, with or without some agglutinated material, discoid, circular or oval (diam., 0.1-0.4 mm.), may be ornamented with simple or bifid spines; aperture eccentric, circular or ovate; pseudopodia digitate. [Fresh water, but may be washed into shallow marine sediments.] *Pleist.-Rec.*, cosmop.——FIG. 6,*1-3*. **C. aculeata* (EHRENBERG), Rec., Eng.; *1a,b,* base and edge

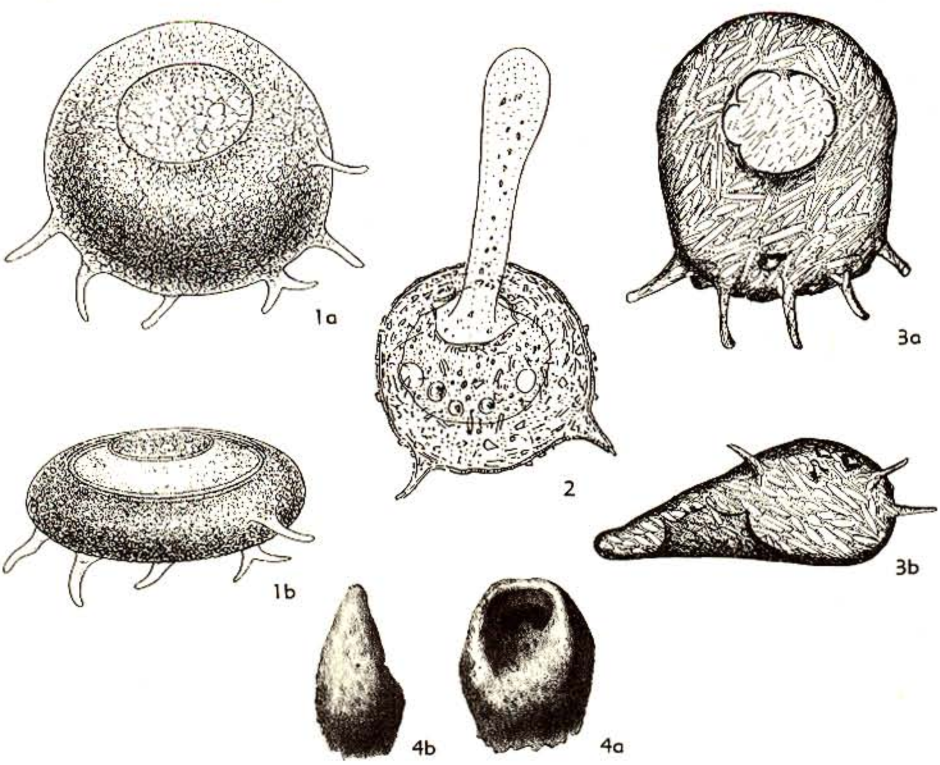


FIG. 6. Centropyxidae; *1-4, Centropyxis* (p. C23-C24).

views, ×300 (*300); *2,* specimen showing pseudopod (*1435); *3a,b,* basal and edge views, ×300 (*957).——FIG. 6,*4*. *C. pleurostomelloides* (Millett), Rec., shallow marine sediments, Malay Arch.; *4a,b,* basal and edge views, ×110 (*1284c).

Family PLAGIOPYXIDAE Bonnet, 1959

[Plagiopyxidae Bonnet, 1959, p. 2619]

Test pseudochitinous, with foreign matter, bilaterally symmetrical, aperture with strongly overlapping margins; pseudopodia consisting of "exolobopodia" which arise from ectoplasmic layer and protrude from aperture; single nucleus; may have provisory encystment during temporary desiccation with formation of spheroidal precyst of very thin hyaline cuticle enclosing active cytoplasm, precyst rapidly dehisced when favorable conditions reappear; encystment normal if dehydration is prolonged, precyst membrane thickening and enclosed cytoplasm becoming inactive. *Rec.*

Only *Plagiopyxis,* characterized by ectoplasmic pseudopodia, was originally included in this family. The additional genera here included correspond to *Plagiopyxis* in test morphology, but information as to details of their pseudopodia is lacking.

Plagiopyxis Penard, 1910, *1440, p. 936 [**P. callida;* OD]. Test rounded to oval (length, 0.09-0.13 mm.), with gray, yellow to brown agglutinated wall, aperture as in *Bullinularia* with lower lip extended within and parallel to outer upper lip for approximately one-third circumference of test; pseudopodia short, large and pointed, rarely observed. [In moss.] *Rec.,* N.Am.-S.Am.-Eu.-Australia.——FIG. 7,*5*. **P. callida,* Rec., Switz.; *5a,b,* dorsal and ventral views; *5c,* diagram. long. sec. (*1440).

Bullinularia Penard in Grassé, 1953, *810, p. 127 [**Bulinella indica* Penard, 1907, *1438, p. 277; OD] [=*Bulinella* Penard, 1907, *1438, p. 277 (obj.) (*non* Fischer, 1898); *Bullinula* Penard, 1911, *1441, p. 225 (obj.) (*non* Sowerby, 1839)]. Test plano- to concavo-convex, elliptical as seen from above (diam., 0.16-0.2 mm.), composed of siliceous material in chitinoid cement, most finely granular near aperture; aperture eccentric elongate slit with smooth, depressed lower lip and overhanging, perforate upper lip (pore diam. 2-3μ); character of pseudopodia unknown. [Fresh water.] *Rec.*, Eu.-N.Am.-N.Z.-Asia-Java.——FIG. 7,*1-3*. **B. indica* (PENARD), Netherlands; *1*, basal view, ×270 (*955); *2a,b*, Brit. Isles; basal and end view, ×200 (*302b); *3a*, India, long. sec. showing apertural overlap; *3b*, outline of aperture with overhanging upper lip shown as heavy line, lower lip as thin line (*1438).

Hoogenraadia GAUTHIER-LIÈVRE & THOMAS, 1958, *774, p. 352 [**H. africana*; OD]. Test similar to *Plagiopyxis* but ovate to pyriform in outline (length, 95-150μ); wall of siliceous platelets in

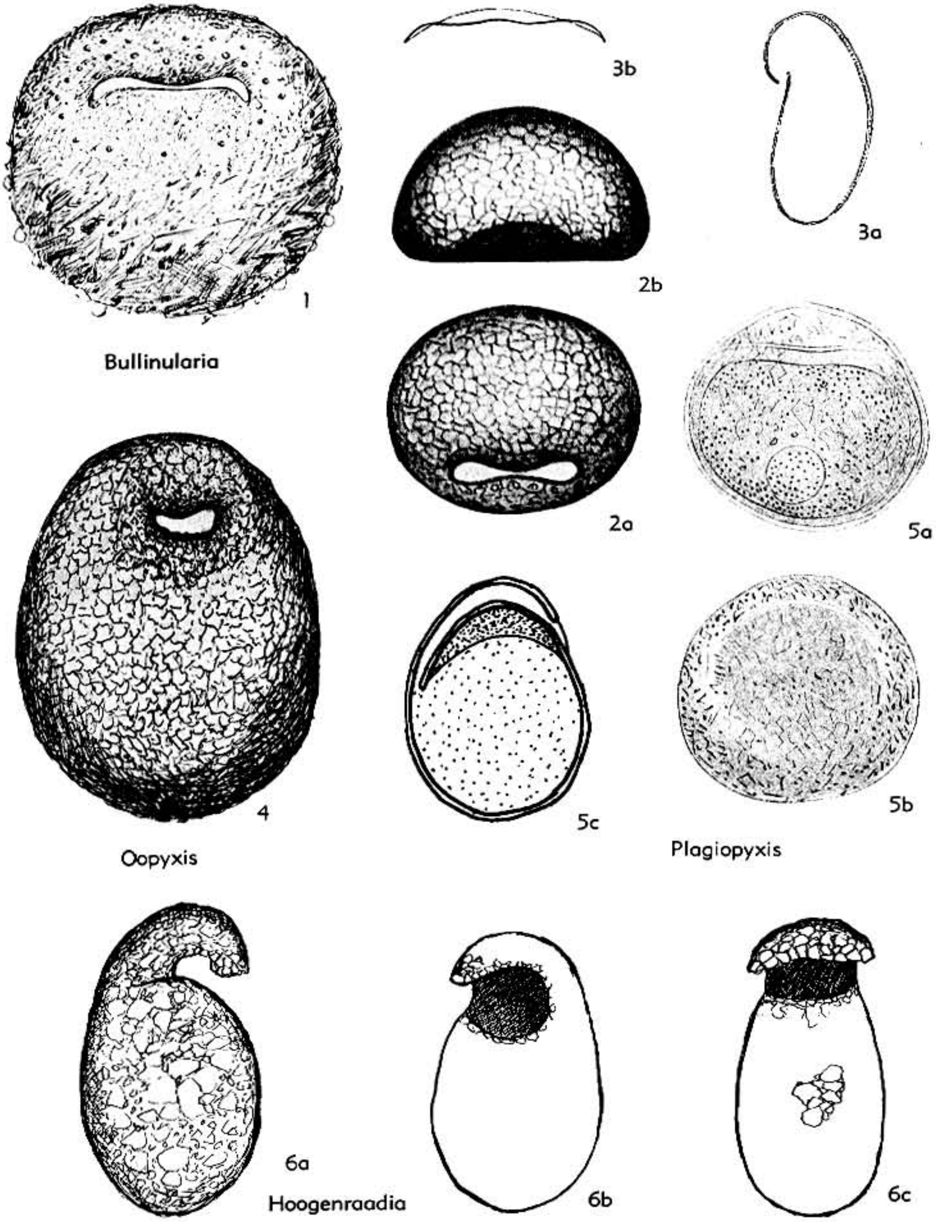


FIG. 7. Plagiopyxidae; *1-3*, *Bullinularia*; *4*, *Oopyxis*; *5*, *Plagiopyxis*; *6*, *Hoogenraadia* (p. C24-C26).

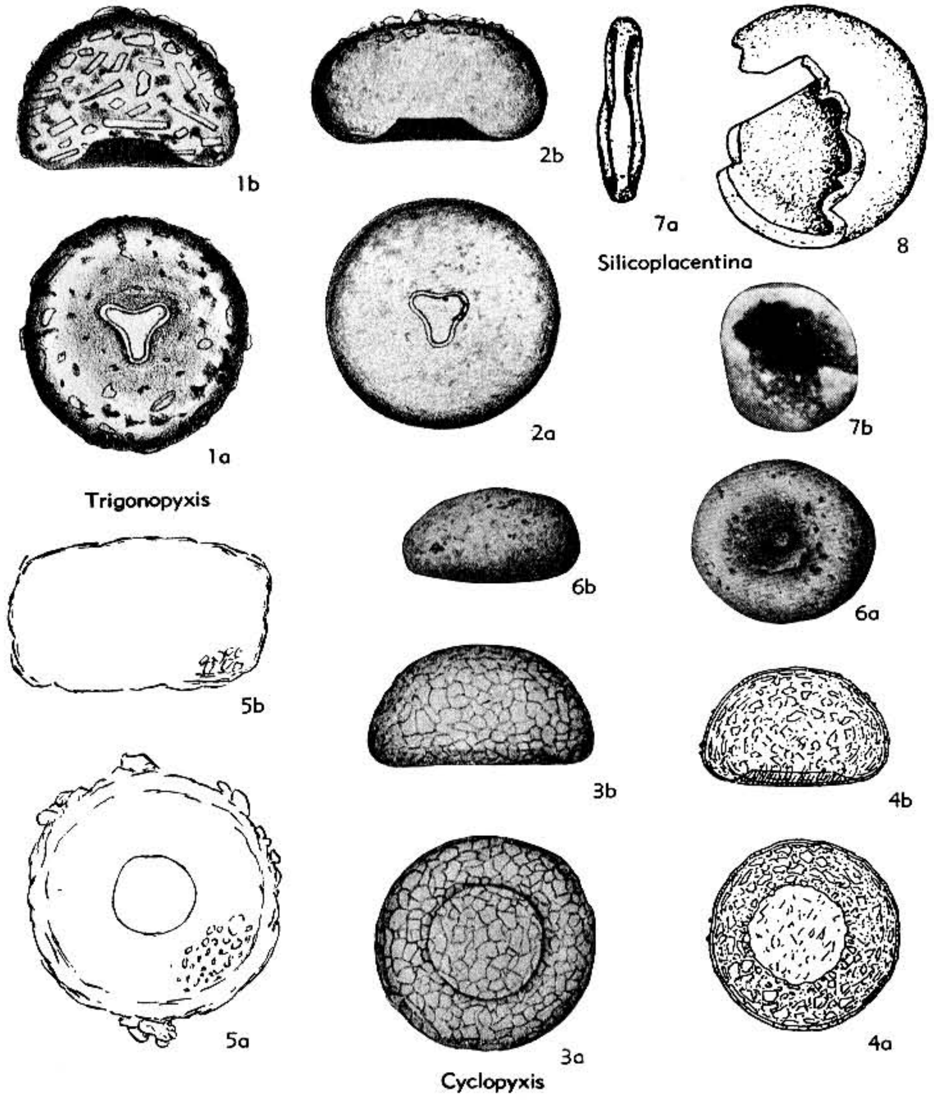


FIG. 8 Trigonopyxidae; _1,2, Trigonopyxis; 3-6, Cyclopyxis; 7,8, Silicoplacentina_ (p. C26-C27).

chitinoid cement; broad open aperture with lower margin incurved and strongly overhanging upper margin; living animal not observed. _Rec.,_ Afr.——FIG. 7,6. _*H. africana,_ middle Congo; _6a-c,_ side, oblique, and apert. views, ×345 (*774).

Oopyxis JUNG, 1942, *1005, p. 294 [_*O. cophostoma;_ OD]. Similar to _Centropyxis_ but with much reduced aperture, and to _Bullinularia_ but without apertural overlap. [Fresh water.] _Rec.,_ S.Am.——FIG. 7,4. _*O. cophostoma;_ basal view, ×618 (*1005).

Family TRIGONOPYXIDAE Loeblich & Tappan, n. fam.

Test pseudochitinous, with added foreign matter, radially symmetrical as in Difflugiidae but with flattened or invaginated apertural margin, without external neck. _Mio.-Rec._

Trigonopyxis PENARD, 1912, *1442, p. 9 [_*Difflugia arcula_ LEIDY, 1879, *1127, p. 116; OD(M)] [=_Cystidina_ P. VOLZ, 1929, *2023, p. 375 (obj.);

=*Trigonopsis* Scheffelt, 1920, *1642, p. 168 *(nom. null.)* (obj.) (*non* Perty, 1833)]. Test hemispherical (diam. approx. 90μ), consisting of parchment-like membrane with included foreign mineral and vegetable matter; aperture triangular or triradial, rarely quadrangular or irregular; pseudopodia unknown; nucleus large, spherical. *Pleist.-Rec.,* N.Am.-S.Am.-Eu.-N.Z.-Java-Sumatra. ——Fig. 8,*1,2*. **T. arcula* (Leidy), Rec.; *1a,b,* Pa., basal, edge views; *2a,b,* N.J., basal, edge views; ×250 (*1127).

Cyclopyxis Deflandre, 1929, *572, p. 330 [**Centropyxis arcelloides* Penard, 1902, *1435, p. 309; OD] [=*Centropyxis (Cyclopyxis)* Deflandre, 1929, *572, p. 330; =*Centropyxis (Cylindropyxis)* Kufferath, 1932, *1065, p. 56 *(nom. nud.)*; =*Leptodermella* Rhumbler, 1935, *1574, p. 177 (type, *Pseudarcella arenata* Cushman, 1930, *445, p. 15)]. Test plano-convex with radial symmetry, rarely with truncated margin (diam., 0.06-0.30 mm.); aperture circular, large, symmetrical; differing from *Centropyxis* in radial symmetry and from *Trigonopyxis* in large rounded, symmetrical aperture. [*Cylindropyxis* was defined as a subgenus to include species with truncate margins, resulting in a quadrate end view. *Leptodermella* differs only in its somewhat larger size.] [Fresh water.] *Mio.-Rec.,* Java-S.Am.-N.Am.-Afr.-Eu.——Fig. 8,*3,4*. **C. arcelloides* (Penard), Rec.; *3a,b,* Brit. Isles, basal and side views, ×300 (*302b); *4a,b,* Switz., basal and side views, enlarged (*1435).——Fig. 8,*5*. *C. cylindrica* (Kufferath), Rec., Afr.(Congo); *5a,b,* basal and edge views, approx. ×450 (*1065).——Fig. 8,*6*. *C. arenata* (Cushman), Mio., USA(Fla.); *6a,b,* basal and edge views, ×85 (*445).

Silicoplacentina Kőváry, 1956, *1049, p. 269 [**S. hungarica;* OD]. Test flattened, discoidal, larger forms somewhat elongate, commonly crushed in preservation (diam. 0.25-1.2 mm.); interior of chamber simple; wall thick, siliceous, granular in appearance, surface wrinkled, white; aperture at end of short projection, somewhat eccentric. *Plio.,* Eu.(Hung.).——Fig. 8,*7*. **S. hungarica; 7a,* edge view, ×38; *7b,* photograph of specimen, ×40 (*1049).——Fig. 8,*8*. *S.* sp., Pannonian; fragment, ×62 (*1049).

Family HYALOSPHENIIDAE Schulze, 1877

[*nom. correct.* Jung, 1942a, p. 256 (*pro* family Hyalospheniidae Schulze, 1877, p. 26]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}family, ^{2}subfamily, ^{3}tribus)]——[=^{1}Quadrulidae Schulze, 1877, p. 26, based on *Quadrula* Schulze, 1875 (=*Quadrulella* Cockerell, 1909) (*non Quadrula* Rafinesque, 1820); =^{1}Quadrulina (Euglyphina) Haeckel, 1894, p. 164; =^{2}Quadrulellinae de Saedeleer, 1934, p. 6]——[=^{1}Nebelidae Tarának, 1882, p. 230; =^{2}Nebelina Cash & Hopkinson, 1909, p. 80; =^{2}Nebelinae Wailes in Cash, Wailes & Hopkinson, 1919, p. 55; =^{3}Nebelini Jung, 1942, p. 387; =^{1}Nebelida Copeland, 1956, p. 205 *(nom. van.)*]——[=^{1}Heleoperidae Jung, 1942, p. 255; =^{2}Heleoperinae Jung, 1942, p. 385, 387; =^{1}Lecquereusiidae Jung, 1942, p. 257; =^{3}Physochilini Jung, 1942, p. 387]

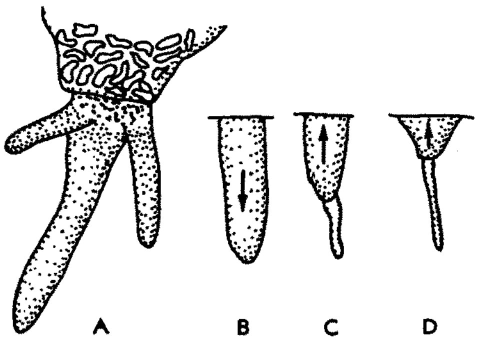


Fig. 9. Hyalospheniidae; *A-D,* successive stages in pseudopodial movement of *Lesquereusia spiralis* (p. *C*30-*C*31).

Test pseudochitinous, with siliceous plates or scales, rounded or angular, may have added foreign matter; aperture elongate or rounded; single nucleus; pseudopodia largely composed of ectoplasm, but may have slight penetration of endoplasm near base (endolobopodia), rounded terminally during advance and retraction, but when retracting temporarily leave behind fine, structureless, hyaline pellicle (e.g., *Nebela, Lesquereusia*) which tapers to point, resembles ectoplasm in appearance, and later pulls away from substratum to be resorbed. *M.Eoc.-Rec.*

The "pellicle" which is left behind by retreating pseudopodia but which never precedes advancing ones has been observed only in the Hyalospheniidae. Possibly such extensions have been mistaken in certain cases for pointed pseudopodia. The general appearance of the pseudopodia in *Lesquereusia spiralis* is shown in Figure 9,*A*; they are composed largely of ectoplasm but contain a slight extension of the endoplasm (entire animal not shown). The appearance of an advancing pseudopod with rounded margin (Fig. 9,*B*) and of a regressing pseudopod (Fig. 9,*C,D*) is illustrated. The regressing pseudopod continues to display a rounded margin but leaves behind a thin, attenuated pellicle that is retracted slowly (*909).

Hyalosphenia Stein, 1859, *1835, p. 42 [**H. cuneata* Stein in Schulze, 1875, *1698b, p. 335 (*=*Difflugia ligata* Tatem, 1870, *1879, p. 313); SD Loeblich & Tappan, herein] [=*Catharia* Leidy, 1874, *1123, p. 79 (type, *Difflugia ligata*

TATEM, 1870, *1879, p. 313) (*non Catharia* LEDERER, 1863)]. Test ovoid or pyriform (length, 15-150μ), compressed, membranous, hyaline, surface may be pitted but never includes foreign matter; aperture terminal, elliptical; protoplasm pale and granular, occupying interior of shell and at-

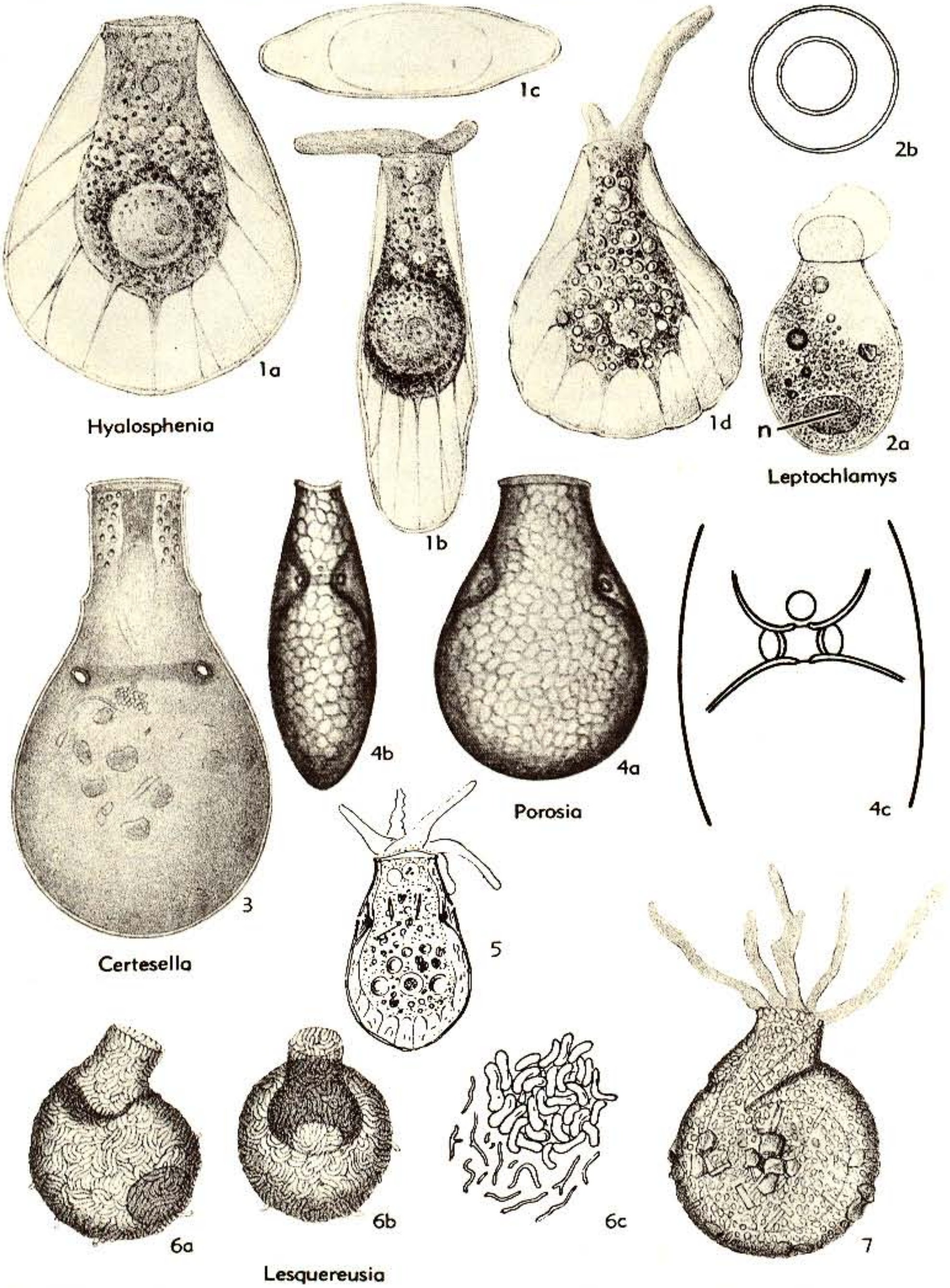


FIG. 10. Hyalospheniidae; *1, Hyalosphenia; 2, Leptochlamys; 3, Certesella; 4,5, Porosia; 6,7, Lesquereusia* (p. C27-C32).

tached to it by divergent threads of ectoplasm, which may appear to indent test margin by their tension; nucleus large, central; with several contractile vacuoles; pseudopodia few, digitate. [Fresh water.] *Pleist.-Rec.*, cosmop.——Fig. 10,*1*. **H. ligata* (Tatem), Rec., USA; *1a,b,* side and edge views, ×665; *1c,* outline of top, ×665; *1d,* side, showing indentation of test margin by tension of ectoplasmic threads, ×500 (*1127).

[Seemingly a type-species has not been selected previously for this genus, since it has commonly but erroneously been regarded as fixed by monotypy. Stein's original description of *Hyalosphenia* contains no mention of a specific name. The type reference has been cited both as a publication in the Transactions of the Czechoslovakian Academy for 1857 and as published in the *Bericht* of the Academy in 1859. Some bibliographies have listed these as two separate publications of differing date but with identical titles and pagination. In January, 1857, Stein orally presented a classification of the fresh-water Rhizopodea before the Academy in Prague, describing several genera, including *Hyalosphenia.* No formal paper was published and the transactions of meetings of this academy were first published in 1859 (including those of 1857 and other years), in the *Bericht.* Stein's only published reference to *Hyalosphenia* was in the transactions of the Academy meeting of 1857, published in 1859. No specific name was given to the form described, hence the genus remained without valid species. About 20 years later Schulze found a species in Germany which he believed to fit the description of Stein's still unnamed and unfigured species of *Hyalosphenia* from Prague. Schulze and Stein exchanged illustrations of their respective forms, believed by both workers to represent distinct species, and Schulze, 1875 (*1698b), described his as *Hyalosphenia lata,* comparing it in publication to "*Hyalosphenia cuneata* Stein." The latter name must have been included on Stein's unpublished sketches of the unnamed species that he had earlier described, but was first introduced into the literature by Schulze in 1875. Owing to the rarity of the publication containing Stein's description, later workers have referred only to Schulze's publication, and all subsequent texts and treatises have cited *H. cuneata* Stein, although Stein (*1835, p. 52) gave only the description and generic name, without any mention of the specific name *cuneata. Hyalosphenia* dates from 1859 (date of publication of the transactions of the 1857 meeting), but remained without included species until 1875, when the specific name *H. cuneata* was published, and *H. lata* was described by Schulze. Either of these nominal species is thus available for selection as type of the genus. In the intervening years Tatem, 1870 (*1879) had described *Difflugia ligata,* which was made the basis for the genus *Catharia* Leidy, 1874 (*1123). After Schulze's paper appeared, Tatem (*1880) stated that *Hyalosphenia lata* Schulze was a junior synonym of *D. ligata. Catharia* Leidy was also a homonym of *Catharia* Lederer, 1863. Leidy, 1879 (*1102, p. 131) stated that he had not seen Stein's publication, but the description quoted by Schulze from Stein did not give "sufficient difference to distinguish two species," and added that "the specific names of *cuneata, ligata* and *lata* are expressive of characters common to any or all the examples described by Stein, Tatem, Schulze, and myself." Leidy recognized the species as *H. cuneata,* but this name was not published until 1875 by Stein in Schulze, which postdated Tatem's publication. Hence the valid name for the type-species is *Hyalosphenia ligata* (Tatem), and *H. cuneata* Stein in Schulze and *H. lata* Schulze, 1875, are both junior synonyms.]

Apodera Loeblich & Tappan, 1961, *1181, p. 215 [**Nebela vas* Certes, 1891, *307, p. L15; OD] [=*Apodera* Jung, 1942, *1005, p. 256; *1006, p. 369, 380 *(nom. nud.)*]. Test (length, 130-210μ), with subspherical body separated from narrowed neck by distinct constriction, represented in interior by a pseudochitinous girdle; wall composed of large, regular, oval plates. *Rec.*, S.Hemis.-S.Am.-Australia-Hawaii-Java-Afr.——Fig. 11,*3*. **A. vas* (Certes), Cape Horn *(3a)*, Chile *(3b)*; *3a,* side view, approx. ×350 (*307); *3b,* edge view, ×470 (*1005).

Awerintzewia Schouteden, 1906, *1675, p. 356, 357 [**Heleopera cyclostoma* Penard, 1902, *1435, p. 390); OD(M)] [=*Averintzia* Wailes in Cash, Wailes & Hopkinson, 1919, *302b, p. 64 *(nom. van.)*; =*Awerintzia* Calkins, 1926, *268, p. 341 *(nom. van.)*; =*Awerintzevia* Neave, 1939, *1348a, p. 374 *(nom. van.)*; =*Averinzia* Jung, 1942, *1006, p. 385 *(nom. van.)*; =*Averincevia* Jírovec, 1953, *994, p. 321 *(nom. van.)*; ?=*Physochila* Jung, 1942, *1005, p. 256, 301; *1006, p. 369, 370 *(nom. nud.)*]. Test ovate and compressed (length, 135-180μ), composed of numerous, large, siliceous plates on pseudochitinous base with very small plates in intervening spaces, possibly with some foreign material at aboral end; aperture ovate, terminal, surrounded by distinctly thickened border. [In aquatic moss and sphagnum.] *Rec.*, Eu.-N. Am.-S. Am.-W. Ind. O.(Seychelles).——Fig. 11,*1,2*. **A. cyclostoma* (Penard), G.Brit. (1), Switz. (2); *1a,b,* side and top views, ×240 (*302b); *2a,b,* side view and vert. sec. showing thickening near aperture, ×240 (*1435).

Certesella Loeblich & Tappan, 1961, *1181, p. 215 [**Nebela martiali* Certes, 1891, *307, p. L14); OD] [=*Penardiella (Nebela)* Jung, 1942, *1005, p. 256, 317; *1006, p. 381 *(nom. nud.)* *(non Penardiella* Kahl, 1930)]. Test pseudochitinous, flask-shaped (length 80-200μ) with large, very thin, almost transparent, polygonal plates; 6 large pores arranged in pairs, first pair about midway on neck, other pairs perpendicular to these at base of neck, additional small pores occurring near aperture. [On moss.] *Rec.*, S.Am.-S.Hemis.——Fig. 10,*3*. **C. martiali* (Certes), Cape Horn; approx. ×300 (*307).

Heleopera Leidy, 1879, *1127, p. 162 [**H. picta* Leidy, 1879 (=**Difflugia (Nebela) Sphagni* Leidy, 1875, *1125, p. 157); OD]. Test ovate, compressed, transparent, amorphous scales covering chitinoid membrane and presenting reticulated appearance, may have agglutinated foreign material at base; aperture, narrow, elliptical, giving notched appearance in edge view; nucleus single, posterior; pseudopodia numerous, thin, bifurcating. *Pleist.-Rec.*, Eu.-N.Am.-S.Am.-E.Indies. ——Fig. 12,*4*. **H. sphagni* (Leidy), Rec., USA (N.J.); *4a-c,* side, edge and top view of empty test, showing form of test and aperture; *4d,* side view showing character of pseudopodia, ×330 (*1127).——Fig. 12,*5,6*. *H. petricola* Leidy, Rec., USA(N.J.); empty tests, showing siliceous plates, and agglutinated foreign matter near base; *5a,6,* side views; *5b,* edge; ×115 (*1127).

Jungia Loeblich & Tappan, 1961, *1181, p. 216 [**J. sundanensis* Van Oye, 1949, *1976, p. 331; OD] [=*Jungia* Van Oye, 1949, *1976, p. 330 *(nom. nud.)*]. Test saclike, globular to ovate, not compressed, of polygonal or elongate plates with rim of sand grains around aperture forming collar; aperture round, central. [On moss.] *Rec.*, Java-S.Am.(Venez.).——Fig. 12,*7*. **J. sundanensis* Van Oye, Java; side view, ×430 (*1976).

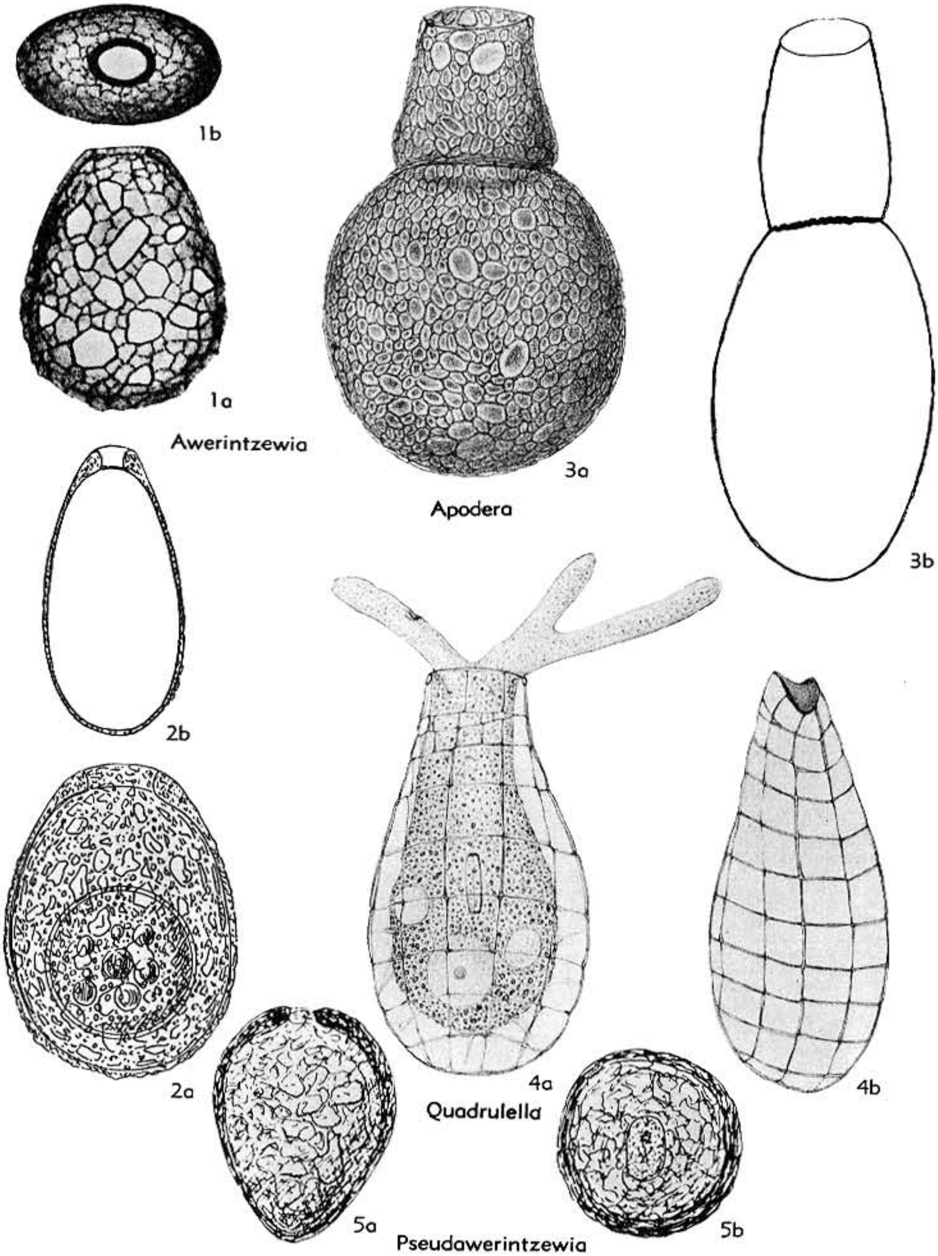


FIG. 11. Hyalospheniidae; *1,2, Awerintzewia; 3, Apodera; 4, Quadrulella; 5, Pseudawerintzewia* (p. *C29, C32*).

Leptochlamys WEST, 1901, *2046, p. 325 [**L. ampullacea*; OD(M)]. Shell ovoid, thin, transparent, chitinoid, circular in section (length, 48-55μ), aperture circular, slightly eccentric; test filled by protoplasm; nucleus large, vacuoles absent; single, short, expanded pseudopodium. [Fresh water.] *Rec.*, Eu.——FIG. 10,2. **L. ampullacea*, Wales; *2a*, side view showing subglobular pseudopodium and large nucleus (*n*); *2b*, outline from above, showing circular aperture and rounded sec., ×520 (*2046).

Lesquereusia SCHLUMBERGER, 1845, *1669, p. 255

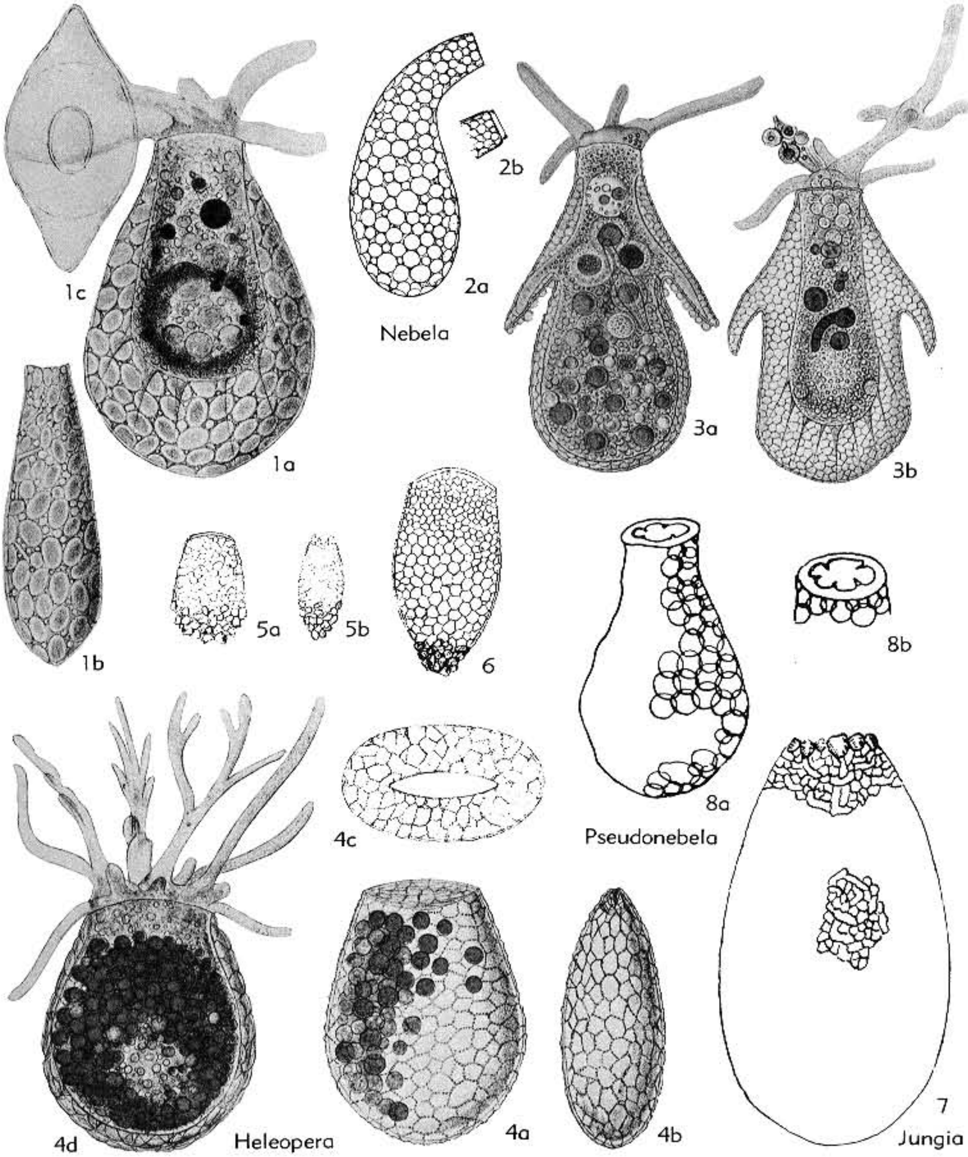


FIG. 12. Hyalospheniidae; *1-3, Nebela; 4-6, Heleopera; 7, Jungia; 8, Pseudonebela* (p. C29, C32).

[**L. jurassica;* OD(M)] [=*Lecquereusia* SCHLUMBERGER, 1845, *1669, p. 255 (obj.) *(nom. imperf.)*; *Lesquereusia* AGASSIZ, 1846, *6, p. 203, 208 *(nom. correct.)*]. Test compressed, ovoid or globose with asymmetrical neck, giving the appearance of a semispiral, up to 135μ in length, wall a transparent chitinous membrane with closely interwoven vermiform pellets or more rarely agglutinated foreign matter; protoplasm partially filling the test with a narrow band of ectoplasm extending up through the neck to the rounded aperture; nucleus single, posterior in position; pseudopodia long, blunt, simple or bifid. [As brought out by CASH & HOPKINSON (301, p. 66) the correct name for the species with vermiform pellets is *L. jurassica* SCHLUMBERGER, and *L. spiralis* (EHRENBERG) correctly refers to the agglutinated species.] [Fresh water.] *Rec.,* cosmop.——Fig. 10,*6*. **L. jurassica,* N.J.*(6a,b),* Switz.*(6c)*; *6a,b,* side and edge view, ×250 (*1127); *6c,* enlargement of pellets ca. ×350 (*1435).——Fig. 10,*7*. *L. spiralis* (Ehrenberg), USA(N.J.); side view showing agglutinated test and elongate pseudopodia, ×250 (*1127).

Nebela Leidy, 1875, *1125, p. 156 [**Difflugia (Nebela) numata* Leidy, 1875; SD Loeblich & Tappan, herein, =**Difflugia collaris* Ehrenberg, 1848, *676, p. 218, =*Nebela collaris* (Ehrenberg) Leidy, 1879, *1127, p. 150] [=*Difflugia (Reticella)* Ehrenberg, 1872, *688, p. 247 (type, *Difflugia (Reticella) collaris* Ehrenberg, 1872, =*Difflugia collaris* Ehrenberg, 1848, SD Loeblich & Tappan, herein) (*non Reticella* Gray, 1870); =*Cyphoderiopsis* Playfair, 1918, *1459, p. 669 (type, *Nebela longicollis* Penard, 1890, *1433, p. 158; =*Nebella* Bartoš, 1938, *96, p. 346 *(nom. null.)*; =*Argynnia* Jung, 1942, *1005, p. 256, 302; *1006, p. 369, 371 *(nom. nud.)*; =*Leidyella* Jung, 1942, *1006, p. 369, 384 *(nom. nud.)*; =*Umbonaria* Jung, 1942, *1005, p. 256; *1006, p. 370, 382 *(nom. nud.)*; =*Pterygia* Jung, 1942, *1005, p. 313; *1006, p. 370, 382 (type, *P. carinulata* Jung, 1942 (*non Pterygia* Bolten, 1798, *nec* Laporte, 1832); =*Schaudinnia* Jung, 1942, *1005, p. 311; *1006, p. 369, 379 *(nom. nud.)* (*non* Schulze, 1900); =*Deflandria* Jung, 1942, *1005, p. 256, 307; *1006, p. 369, 373 *(nom. nud.)*]. Test thin, pseudochitinous, transparent, ovate, pyriform or elongate, compressed (length to 180μ), may have lateral chamber extensions; surface with numerous oval or circular plates or scales of variable size, or rarely rectangular or rodlike plates; protoplasm granular, colorless, but may contain colored food vacuoles; single nucleus; pseudopodia variable in number, blunt, rarely bifid, protoplasmic body attached to test interior by strands or bands of ectoplasm. [The type-species was stated by Deflandre (*576) to be *Nebela collaris* (Ehrenberg) Leidy, but this species was not among the six originally included by Leidy (*1125) and accordingly is ineligible to be the type. The type is here designated as *Difflugia (Nebela) numata* Leidy, which is, however, a junior subjective synonym of *N. collaris*.] *Pleist.-Rec.,* cosmop.——Fig. 12,*1*. **N. collaris* (Ehrenberg). Rec., USA(N.J.); *1a-c,* side, edge and top views, ×330 (*1127).——Fig. 12,*2*. *N. longicollus* Penard, Rec., Australia; *2a,b,* lat. view and detail of aperture, ×440 (*1459).——Fig. 12,*3*. *N. ansata* Leidy, Rec., USA(N.J.); *3a,* active individual with protoplasm filling shell, ×115; *3b,* contracted protoplasm attached to shell by ectoplasmic threads, ×115 (*1127).

Porosia Jung, 1942, *1006, p. 369, 380 [**Nebela bigibbosa* Penard, 1890, *1433, p. 161; OD(M)] [=*Alocodera (Nebela)* Jung, 1942, *1005, p. 256, 313; *1006, p. 369, 380 (type, *Hyalosphenia cockayni* Penard, 1910, *1441, p. 238)]. Like *Certesella,* with large lateral pores which may be connected by internal tubes, but without smaller perforations in region of neck; oval, round, or elongate scales. *Rec.,* Eu.——Fig. 10,*4,5*. **P. bigibbosa* (Penard); *4a,b,* side and edge views, G.Brit., ×300 (*302b); *4c,* detail of large pores from test edge, G.Brit., ca. ×800 (*2031); *5,* side view, showing protoplasm, pseudopodia and lat. pores, Switz., *ca.* ×200 (*1433).

Pseudawerintzewia Bonnet, 1959, *169, p. 186 [**P. calcicola;* OD(M)]. Test similar to *Awerintzewia* but circular rather than compressed in section; wall progressively thicker from base to oral region, with amorphous siliceous scales in abundant chitinoid cement, aperture elliptical, commonly with chitinoid epiphragm. [Neither living animal nor cysts have been observed. The "epiphragm" is similar to that of the Phryganellidae, but may be only dried cytoplasm at the opening. Because of the similarity of test features, *Pseudawerintzewia* is here placed in the Hyalospheniidae.] *Rec.,* Eu.(Fr.).——Fig. 11,*5*. **P. calcicola*; *5a,* optical sec., showing wall thickening toward aperture, ×440; *5b,* apert. view showing circular sec. and ovate aperture with epiphragm, ×440 (*169).

Pseudonebela Gauthier-Lièvre, 1954, *773, p. 363 [**P. africana*; OD(M)]. Test lagenoid (length, 90-100μ), with elongate neck; wall transparent, of secreted oval or circular plates in a chitinoid cement with some foreign matter; aperture terminal, round, with thickened rim from which project 3 to 5 denticulations formed by small triangular platelets. [Fresh water.] *Rec.,* Afr.——Fig. 12,*8*. **P. africana; 8a,b,* side view of test and oblique view of aperture showing teeth, ×400 (*773).

Quadrulella Cockerell, 1909, *351, p. 565 [**Difflugia proteiformis* var. *symmetrica* Wallich, 1863, *2034, p. 458; OD] [=*Quadrula* Schulze, 1875, *1698b, p. 329, 330 (obj.)(*non* Rafinesque, 1820)]. Test compressed, pyriform (length, approx. 85-100μ), transparent, with large, thin, square chitinoid plates in transverse to slightly oblique series, adjacent but not overlapping; aperture terminal, oval; protoplasm colorless, granular, with single nucleus; pseudopodia few, broad, digitate, rarely bifid. [Deflandre & Deflandre-Rigaud (*577, p. 229) have stated that *Difflugia? marina* Bailey, 1856, is identical with *Quadrulella symmetrica* (Wallich), 1863, yet regard the older name as the rejected synonym. If the two are identical, the oldest name must be the valid one, regardless of its applicability to a fresh-water form, and regardless of the length of time that has lapsed without such recognition. We do not regard the two species as identical, however, although they are undoubtedly congeneric. The species differ in relative size and number of plates (*Quadrulella marina* having fewer, larger, and less regularly arranged plates), and in test size and proportions (*Q. marina* being much smaller and having a more pyriform outline and more distinctly separated neck).] [On sphagnum and moss.] *Eoc.-Rec.,* Eu.-N.Am.-S.Am.-Ind.O. (Seychelles)-MalayArch.(Borneo)-Afr.——Fig. 11,

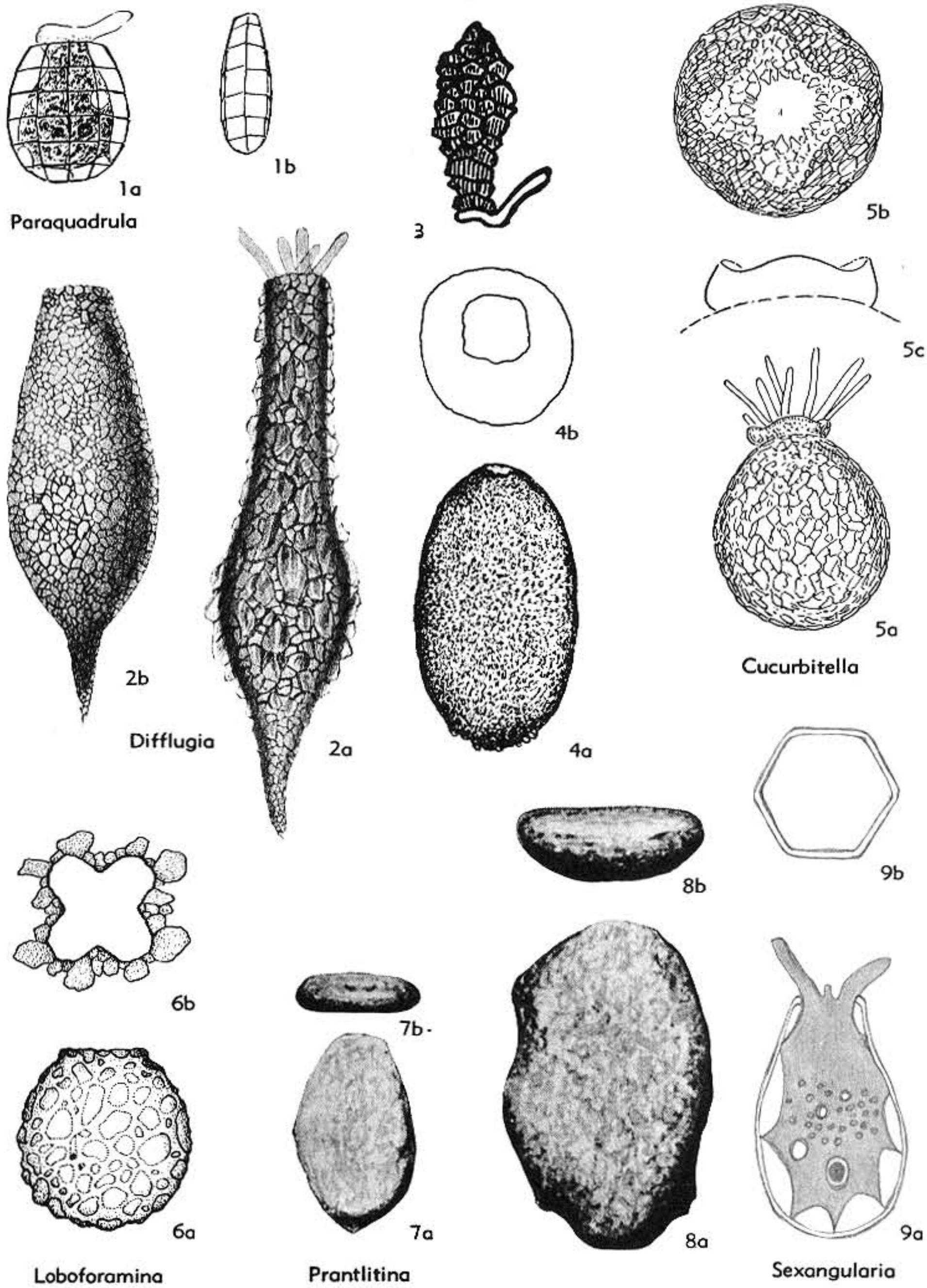


Fig. 13. Paraquadrulidae; *1, Paraquadrula;* Difflugiidae; *2-4, Difflugia; 5, Cucurbitella; 6, Loboforamina; 7,8, Prantlitina; 9, Sexangularia* (p. C34-C37).

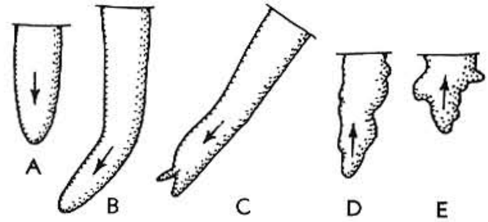


FIG. 14. Diagrams indicating the nature of pseudopodial movement in *Difflugia oviformis*, Rec. (entire animal not shown, arrows marking direction of movement); *A,B*, advance of lobose pseudopodium; *C*, bifurcating pseudopodium; *D,E*, retraction of pseudopodium showing undulatory margin, loss of rigidity, and gradual diminution without residual pellicle (*909).

4. **Q. symmetrica* (WALLICH), Rec., Ger.; *4a,b*, living individual showing pseudopodia and edge view of empty test, ×400 (*1698b).

Family PARAQUADRULIDAE Deflandre, 1953

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 268 (*ex* subfamily Paraquadrulinae DEFLANDRE in GRASSÉ, 1953, p. 130)]

Test with quadrangular calcite plates covering a thin pseudochitinous pellicle; aperture ovate; one nucleus. *Rec.*

Paraquadrula DEFLANDRE, 1932, *573, p. 1346 [**Quadrula irregularis* ARCHER, 1877, *34a, p. 113; OD]. Test minute (length, 30-38μ), subglobular to discoid, without neck or thickened apertural rim; wall a transparent chitinous membrane with surface of closely set, quadrangular calcareous plates which may have thickened rims; aperture ovate to slitlike; protoplasm colorless, granular; pseudopodia few, simple. [On moss.] *Rec.*, W.Eu.-Spitz.——FIG. 13,*1*. **P. irregularis* (ARCHER), Neth.; *1a,b*, side and edge views, ×360 (*957).

Family DIFFLUGIIDAE Wallich, 1864

[*nom. transl. et correct.* TARÁNEK, 1882, p. 225 (*ex* subfamily Difflugidae WALLICH, 1864)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}family, ^{2}subfamily); dagger(†) indicates *partim*]——[=^{2}Difflugiinae VEJDOVSKÝ, 1881, p. 138; =^{1}Difflugina STEIN, 1859, p. 42; =^{2}Difflugina CASH & HOPKINSON, 1909, p. 2; =^{2}Diffluginae WAILES in CASH, WAILES & HOPKINSON, 1919, p. 36; =^{1}Difflugiidae (Lobosa) HOOGENRAAD & DE GROOT, 1940, p. 24; =^{1}Diflúgidos GADEA BUISÁN, 1947, p. 16 (*nom. neg.*); =Difflugiida COPELAND, 1956, p. 205 (*nom. van.*)]——[=^{1}*Monocyphia*† VEJDOVSKÝ, 1881, p. 138; =^{1}Adjungentiidae† RHUMBLER, 1895a, p. 93, 95 (*nom. nud.*); =^{1}Protrudentiidae† RHUMBLER, 1895, p. 94, 95 (*nom. nud.*); =^{1}Pontigulasiidae JUNG, 1942, p. 257; =^{2}Cingodifflugiinae JUNG, 1942, p. 387, 388; =^{2}Planodifflugiinae JUNG, 1942, p. 388]

Test rarely pseudochitinous, generally composed of foreign particles, not of secreted plates; form variable but with axial symmetry and terminal aperture; one or many nuclei; pseudopodia rigid during progression, with movement normal, if extremely elongated they may become attenuated or abruptly change in diameter; when advance ceases, pseudopodia lose rigidity and become pliable and may bifurcate, margin becomes undulating, and pseudopod is then retracted to fuse with remaining cytoplasm, no pellicle remaining behind such as found in *Nebela*. *Miss.-Rec.*

Pseudopodial movement in the Difflugiidae is illustrated diagrammatically in Figure 14.

Difflugia LECLERC in LAMARCK, 1816, *1088, p. 95 [**D. protoeiformis* LAMARCK, 1816; OD(M)] [=*Difflugie* LAMARCK, 1816, *1088, p. 94, and LECLERC, 1816, *1116, p. 474 (*nom. neg.*); *Difflugia (Eudifflugia)* DIESING, 1848, *596, p. 497 (type, *Difflugia protoeiformis* LAMARCK, 1816, =*Difflugia (Eudifflugia) proteiformis* LAMARCK, DIESING, 1848, *596, p. 502 (obj.), SD LOEBLICH & TAPPAN, herein); =*Difflugia (Corticella)* EHRENBERG, 1872, *688, p. 247 (type, *Difflugia (Corticella) proteiformis* LAMARCK, EHRENBERG, 1872, =*Difflugia protoeiformis* LAMARCK, 1816 (obj.), SD LOEBLICH & TAPPAN, herein); *Odontodictya* EHRENBERG, 1872, *688, p. 247 (type, *Difflugia (Reticella) globularis* WALLICH, EHRENBERG, 1872, =*Difflugia globularis* WALLICH, 1864, SD LOEBLICH & TAPPAN, herein); =*Acipyxis* JUNG, 1942, *1005, p. 255, 278 (*nom. nud.*); =*Planodifflugia* JUNG, 1942, *1005, p. 255, 280 (*nom. nud.*); =*Pycnochila* JUNG, 1942, *1005, p. 255, 282 (*nom. nud.*) (*non* HORN, 1905); =?*Schwabia* JUNG, 1942, *1005, p. 255, 284 (type, *S. regularis*

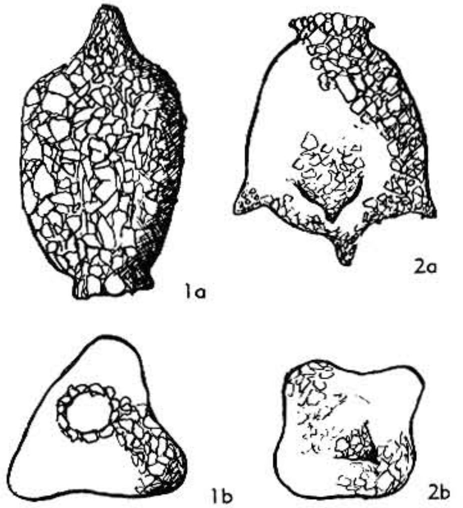


FIG. 15. Difflugiidae; *1,2, Difflugia* (p. C34-C35).

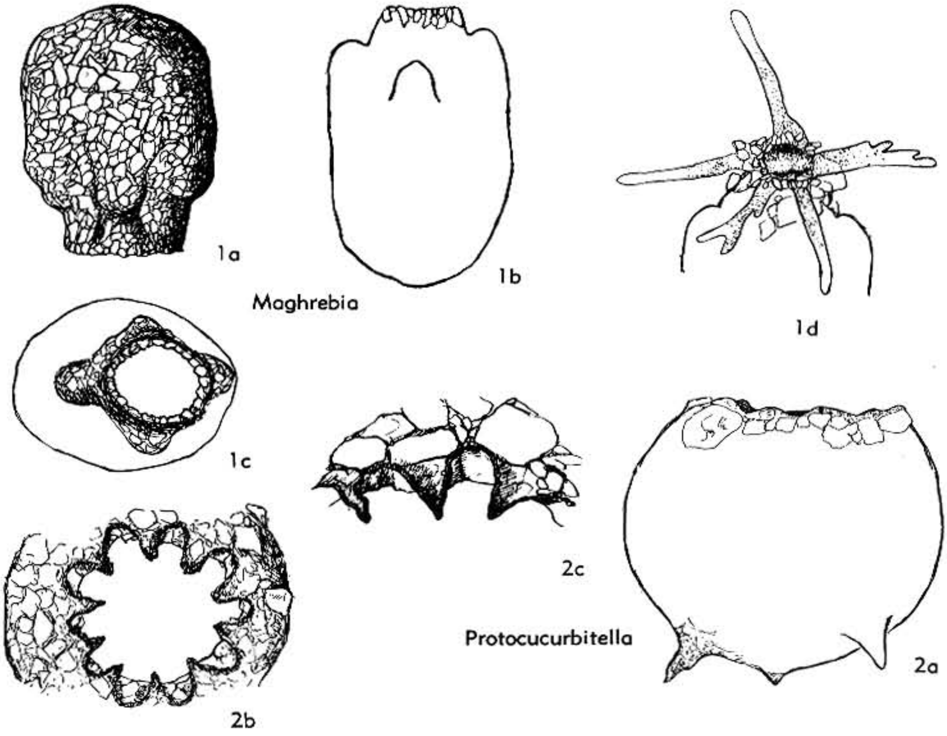
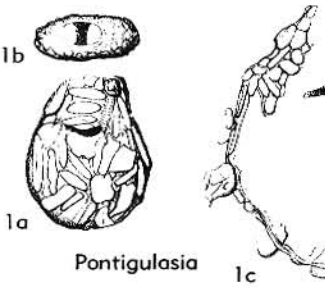


Fig. 16. Difflugiidae; *1, Maghrebia; 2, Protocucurbitella* (p. *C*36).

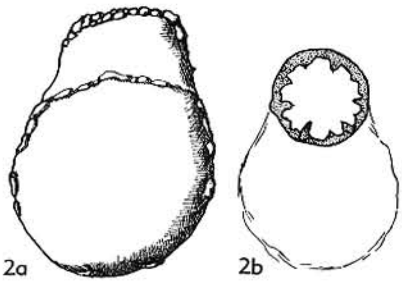
Jung, 1942); =*Globonota* Jung, 1942, *1005, p. 254, 275 *(nom. nud.)*; =*Pentagonia* Gauthier-Lièvre & Thomas, 1958, *774, p. 349 (type, *P. maroccana*) (*non Pentagonia* Cozzens, 1846)]. Test globular, elongate, pyriform, or acuminate, typically circular in section (length 15-450μ, av. approx. 100μ); wall with pseudochitinous base and variable amounts of agglutinated material; aperture rounded, may be somewhat produced; protoplasm occupying most of test, attached internally to it by threads of ectoplasm; nucleus large, single; one or more contractile vacuoles; pseudopodia few, simple or bifid, of colorless ectoplasm, more rarely including some granular endoplasm. [Fresh-water lakes and ponds.] *M. Eoc.-Rec.*, cosmop.——Fig. 13,*2,3*. **D. protoeiformis* Lamarck, Rec.; USA(N.J.), *2a*, elongate individual with projecting pesudopodia, ×200; USA(Pa.), *2b*, empty test of common form, ×200 (*1127); Eu., *3*, lectotype, here designated (*1116, pl. 17, fig. 5).——Fig. 13,*4*. *D. regularis* (Jung), Rec., S.Am.(Chile); *4a,b*, side and top views, ×580 (*1005).——Fig. 15,*1,2*. *D. maroccana* (Gauthier-Lièvre & Thomas), Rec., Afr.(Morocco); *1a*, side view of slightly angular specimen, aperture down; *1b*, apertural view; *2a*, side view of quadrangular specimen with spinelike projections; *2b*, basal view; all ×490 (*774).

[Leclerc originally described *Difflugia*, illustrating it with a plate of six figures, but gave no specific names. Before this article was published (Sept., 1816), Lamarck gave a generic description (Mar., 1816), citing "*Difflugia* LeClerc, mém. mss." as a synonymic reference. He named the species *D. protoeiformis* and his description (without figures) closely followed that of Leclerc (1816), and was based on Leclerc's manuscript. The genus should therefore be credited to Leclerc in Lamarck (1816), and the type-species (by monotypy it can only be *D. protoeiformis*) to Lamarck alone. The descriptions and figures given by Leclerc represent forms now included in both *Difflugia* and *Lesquereusia*. Leidy, 1879 (*1127) referred Leclerc's fig. 1 and 4 to *D. spiralis* Ehrenberg, 1840 [=*Lesquereusia*], his fig. 2 and 3 to *D. pyriformis* Perty, 1848, and his fig. 5 to *D. acuminata* Ehrenberg, 1838. Cash & Hopkinson (*301) referred Leclerc's fig. 1*a* to *Lesquereusia modesta* Rhumbler, 1895, fig. 1 and 4 to *L. spiralis* (Ehrenberg), 1840, fig. 3 to *D. oblonga* Ehrenberg, 1838 and fig. 5 to *D. acuminata* Ehrenberg, 1838. Thus the type figures have been later placed in five species, all of later date. Leclerc's plate description indicates that he regarded his fig. 1-4 as the same form, and in fact indicates that they are variant views of the same specimen, his fig. 2 and 3 representing edge views of the *spiralis* type shown in side view in his fig. 1 and 1*a*. His fig. 1 is apparently merely a diagrammatic representation to show the "spire," as he states the next figure to be "la même coquille en partie recouverte de petits grains de sable." As no lectotype has yet been designated, we here designate as lectotype of *D. protoeiformis* Lamarck the specimen illustrated on pl. 17, fig. 5 of Leclerc (*1116), here refigured and unquestionably *Difflugia* as generally understood. *D. acuminata* Ehrenberg, 1838, is thus a junior synonym of *D. protoeiformis* Lamarck, 1816. All remaining figures of Leclerc represent *Lesquereusia*.]

Cucurbitella Penard, 1902, *1435, p. 310 [**C. mespiliformis*; OD(M)] [=*Cingodifflugia* Jung, 1942, *1005, p. 255, 283 *(nom. nud.)*; =*Eustoma* Jung, 1942, *1005, p. 255, 283 *(nom. nud.)* (*non*



Pontigulasia



Pseudopontigulasia

FIG. 17. Difflugiidae; *1, Pontigulasia; 2, Pseudopontigulasia* (p. *C*36).

PIETTE, 1855, *nec* BENEDEN, 1871, *nec* GIRARD, 1893)]. Test subglobular, agglutinated (length, approx. 140μ); aperture terminal, irregularly circular, surrounded by 3- to 4-lobed collar, internal diaphragm just below collar with rounded and restricted opening, diaphragm commonly partially visible through lobes of main aperture; protoplasm granular; single large nucleus, one or more contractile vacuoles and commonly containing symbiotic algal cells; pseudopodia numerous, thin and digitate. [Fresh water.] *Rec.*, Eu.-N.Am.——FIG. 13,*5*. **C. mespiliformis*, Switz.; *5a*, side view showing pseudopodia, ×250; *5b*, top view, showing quadrilobed apert. collar, ×250; *5c*, enlarged side view of apert. collar (*1435).

Loboforamina JUNG, 1942, *1005, p. 255, 282 [**Difflugia lobostoma* LEIDY var. *globulus* PLAYFAIR, 1918, *1459, p. 644, =*Loboforamina playfairi* LOEBLICH & TAPPAN, *nom. nov.*, herein (*non Arcella globulus* EHRENBERG, 1848, =*Difflugia globulus* (EHRENBERG) CASH & HOPKINSON, 1909, *301, p. 33); OD(M)] [=*Corona* VEJDOVSKÝ, 1881, *1999, p. 137 (type, *C. cornula*, =*Difflugia proteiformis* subsp. *globularis* var. *corona* WALLICH, 1864, *2035, p. 241) (*non Corona* ALBERS, 1850, *nec* RECLUZ, 1850, *nec* BARRANDE in WAAGEN & JAHN, 1899; *nec* JEKELIUS, 1932); =*Difflugia (Pseudocucurbitella)* GAUTHIER-LIÈVRE & THOMAS, 1960, *775, p. 589, 591 (*nom. nud.*)]. Similar to *Difflugia* but with 3- to 6-lobed aperture; differs from *Cucurbitella* in lacking lobed collar; 60-80μ in length. [Fresh water.] *Rec.*, N.Am.-S.Am.-Australia-Eu.——FIG. 13,*6*. **L. playfairi* LOEBLICH & TAPPAN, Australia; *6a*, side view, ×400; *6b*, apert. region, ×660 (*1459).

Maghrebia GAUTHIER-LIÈVRE & THOMAS, 1958, *774, p. 350 [**M. spatulata;* OD]. Test agglutinated (length 95-125μ), similar to *Difflugia* but with large protuberances (commonly 4) at apertural shoulder, directed toward aperture; aperture rounded, with border of closely spaced sand grains; pseudopodia elongate, lobose. [Marshes.] *Rec.*, Afr.(Algeria).——FIG. 16,*1*. **M. spatulata; 1a,b*, side views; *1c*, apert. view; *1d*, apert. area showing pseudopodia; all ×225 (*774).

Pontigulasia RHUMBLER, 1895, *1568b, p. 105 [**P. compressa* RHUMBLER, 1905; SD LOEBLICH & TAPPAN, herein, =*P. rhumbleri* HOPKINSON in CASH & HOPKINSON, 1909, *301, p. 162 (*non Difflugia compressa* CARTER, 1864, *288, p. 22, =*Pontigulasia compressa* (CARTER) CASH & HOPKINSON, 1909, *301, p. 62)]. Like *Difflugia* but with constriction forming neck and internal transverse diaphragm at position of constriction, with perforations for extrusion of pseudopodia around or through internal diaphragm; test 120-170μ in length; nucleus single; pseudopodia lobose. [On moss, in lakes.] *Eoc.* (*1984, p. 334), *Rec.*, Eu.-N.Am.-S.Am.-Afr.——FIG. 17,*1*. **P. rhumbleri* HOPKINSON, Rec., Ger.; *1a,b*, lat., apert. views, ×144; *1c*, long. sec. showing internal diaphragm, ×238 (*1568b).

Prantlitina VAŠÍČEK & RŮŽIČKA, 1957, *1984, p. 334 [**P. prantli*; OD] [=*Prantlitina (Prantlitinopsis)* VAŠÍČEK & RŮŽIČKA, 1957, *1984, p. 337 (type, *P. (Prantlitinopsis) sturi)*]. Test ovate, flattened, agglutinated (length, 0.31-0.65 mm.), probably on pseudochitinous base as deformation is common, thick-walled, inner cavity of test simple; aperture simple, elongate, terminal slit. [Fresh-water deposits.] *U.Carb.(Namur.)*, Eu. (Czech.).——FIG. 13,*7*. *P. sturi* VAŠÍČEK & RŮŽIČKA; *7a,b*, lat., apert. views, ×70 (*1984).——FIG. 13,*8*. **P. prantli; 8a,b*, lat., apert. views, ×70 (*1984).

Protocucurbitella GAUTHIER-LIÈVRE & THOMAS, 1960, *775, p. 593 [**P. coroniformis;* OD]. Test 200-230μ in length, similar in appearance to *Loboforamina* but with slight constriction below lobate aperture similar to diaphragm of *Cucurbitella*, broad opening in irregular diaphragm. [Marshes and swamps.] *Rec.*, Afr.-Madag.——FIG. 16,*2*. **P. coroniformis*, Afr.; *2a,b*, lat., apert. views, ×170; *2c*, detail of aperture, ×380 (*775).

Pseudopontigulasia VAN OYE, 1956, *1977, p. 347 [**P. gessneri;* OD(M)]. Similar to *Loboforamina* but with numerous projecting toothlike infoldings of pseudochitinous apertural margin rather than infolding of entire margin into few large lobes; about 60μ in length. [Fresh water.] *Rec.*, S.Am.——FIG. 17,*2*. **P. gessneri*, Venez.; *2a,b*, side and oblique views showing apert. teeth; approx. ×550 (*1977).

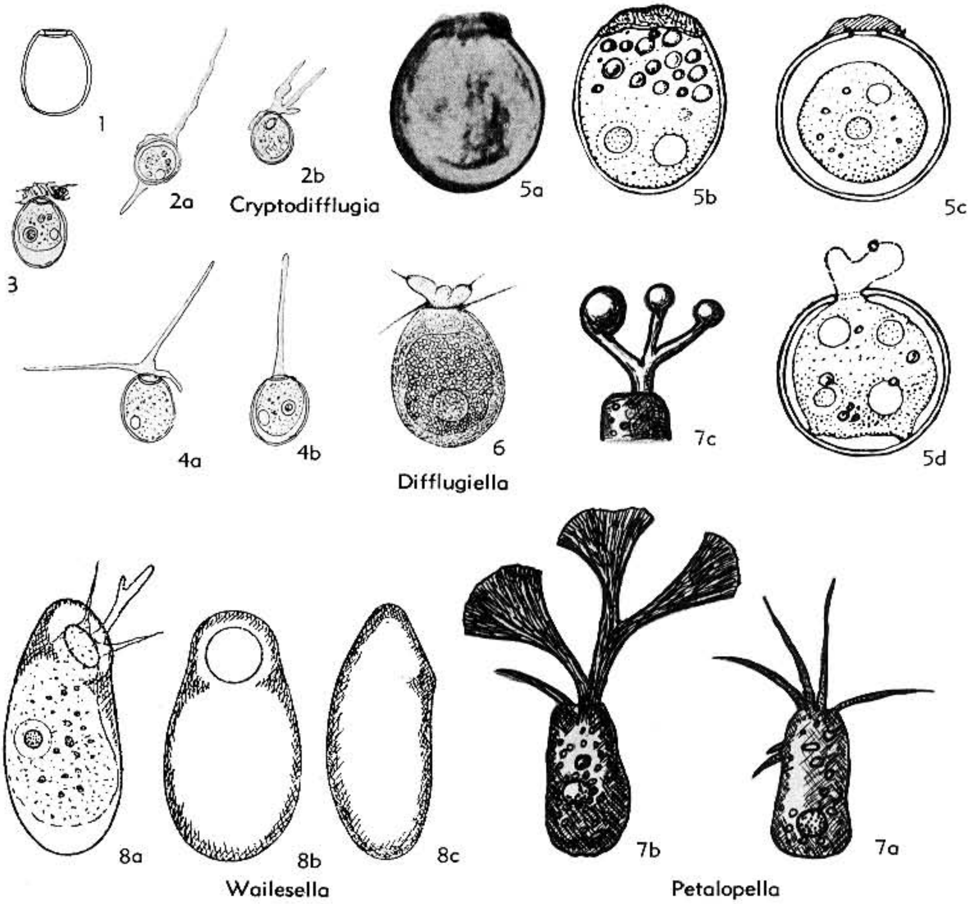


FIG. 18. Cryptodifflugiidae; *1-5, Cryptodifflugia; 6, Difflugiella; 7, Petalopella; 8, Wailesella* (p. C37-C38).

Sexangularia AVERINTSEV, 1906, *59, p. 163 [**S. parvula;* OD(M)]. Test elongate (length 0.12-0.18 mm.), lagenoid in outline, hexagonal in section; wall chitinoid, with rare agglutinated material; pseudopodia short and lobose; protoplasm attached to interior by strands of ectoplasm. [Fresh water.] *Rec.,* Eu.——FIG. 13,9. **S. parvula; 9a,b,* side view showing protoplasm and transv. sec. of test, ×275 (*59).

Superfamily CRYPTODIFFLUGIACEA Jung, 1942

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 269 (*ex* family Cryptodifflugiidae JUNG, 1942, p. 257)] [=legio Reticulolobosa DE SAEDELEER, 1934, p. 6, 21; =suborder Reticulolobosa DEFLANDRE in GRASSÉ, 1953, p. 132; =suborder Testareticulosina BOVEE, 1960, p. 355]

Pseudopodia of ectoplasm, pointed or bifurcating, anastomosing. *Pleist.-Rec.*

Family CRYPTODIFFLUGIIDAE Jung, 1942

[Cryptodifflugiidae JUNG, 1942, p. 257]

Test membranous to pseudochitinous. *Pleist.-Rec.*

Cryptodifflugia PENARD, 1890, *1433, p. 168 [**C. oviformis;* OD(M)] [=*Geococcus* FRANCÉ, 1913, *737, p. 28 (type, *G. vulgaris* FRANCÉ, 1913) (*non Geococcus* GREEN, 1902)]. Test chitinoid, ovoid, tiny, 15-18μ in maximum diameter, round in section; small rounded aperture at slightly narrowed end which may have internal ridge at its margin, producing invaginated appearance; protoplasm clear, filling test or leaving gap at aboral end; nucleus rounded, clear; single contractile vacuole; few pseudopodia, narrow and elongate. [Fresh water and soil.] *Pleist.-Rec.,* Eu.——FIG. 18,*1-4.* **C. oviformis,* Rec., Ger.; *1,*

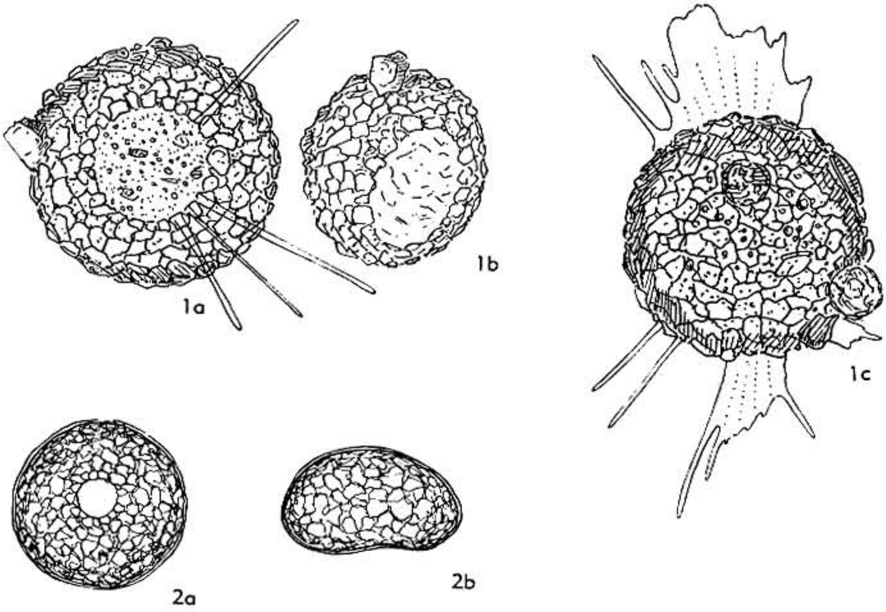


FIG. 19. Phryganellidae; *1,2, Phryganella* (p. *C*38-*C*39).

empty test; *2a,b,* individual showing pseudopodia and contractile vacuole, same 5 minutes later; *3,* specimen with detritus in apert. region; *4a,b,* specimens showing contractile vacuole, elongate pseudopodia, and nucleus with dark, round nucleolus; all approx. ×600 (*1433).——FIG. 18,*5*. *C. vulgaris* (FRANCÉ), Rec., Ger.; *5a,* photomicrograph; *5b,c,* encysted individuals; *5d,* beginning of pseudopodial extrusion; all ×400 (*737).

Difflugiella CASH, 1904, *299, p. 218, 224 [**D. apiculata;* OD]. Test up to 40μ in length, ovoid, circular in section, pseudochitinous, flexible, transparent; protoplasm colorless, granular; with 2 or 3 vacuoles and inconspicuous nucleus; pseudopodia of 2 kinds, active lobular or digitate ones with short, acute apiculate terminations protruding centrally from aperture, other pseudopodia longer, narrower, tapering, projecting from each side and showing less tendency to alteration. [Fresh water.] *Rec.,* Eu.——FIG. 18,*6*. **D. apiculata,* Eng.; side view, ×500 (*299).

Petalopella LOEBLICH & TAPPAN, 1961, *1181, p. 216 [**Petalopus diffluens* CLAPARÈDE & LACHMANN, 1859, *345, p. 442; OD] [=*Petalopus* CLAPARÈDE & LACHMANN, 1859, *345, p. 442 (obj.), (*non* KIRBY & SPENCE, 1828, *nec* MOTSCHOULSKY, 1845)]. Test ?membranous, ovoid, region of pseudopodial origin truncate; nucleus not observed; pseudopodia variable, may have single pseudopod which ramifies into many branches, or number of thickened pseudopodia spreading and flabelliform or clavate at their extremities and retractable into body. [Known only from the original description, the nominal genus (a homonym) was renamed, since the pseudopodial character differentiates it from other described genera.] [Fresh water.] *Rec.,* Eu.——FIG. 18,*7*. **P. diffluens* (CLAPARÈDE & LACHMANN), Ger.; *7a-c,* views showing different pseudopodial characters, approx. ×300 (*345).

Wailesella DEFLANDRE, 1928, *570, p. 37 [**Cryptodifflugia eboracensis* WAILES in WAILES & PENARD, 1911, *2031, p. 24; OD]. Test small, (length, 28-28μ), transparent, smooth, chitinoid, elongate ovate, slightly compressed; aperture circular, placed somewhat obliquely in relation to the longitudinal axis; protoplasm colorless, granular; single nucleus with large nucleolus,1-2 contractile vacuoles; pseudopodia few, short, pointed or digitate. [On sphagnum.] *Rec.* Eu.-E.USA.-Alaska-Can.——FIG. 18,*8*. **W. eboracensis* (WAILES), Ire.; *8a,* oblique view of living specimen; *8b,c,* apert. and side views, ×1,300 (*2031).

Family PHRYGANELLIDAE Jung, 1942

[Phryganellidae JUNG, 1942, p. 257]

Test arenaceous. *Pleist.-Rec.*

Phryganella PENARD, 1902, *1435, p. 418 [**P. nidulus* PENARD, 1902; SD LOEBLICH & TAPPAN, herein] [=*Phryanella* NEAVE, 1940, *1348c, p. 733 *(nom. null.)*; =?*Geopyxella* BONNET & THOMAS, 1955, *171, p. 419 (type, *G. sylvicola*)]. Similar to *Difflugia,* 0.16-0.22 mm. in length, but with pseudopodia varying from broad lobate ex-

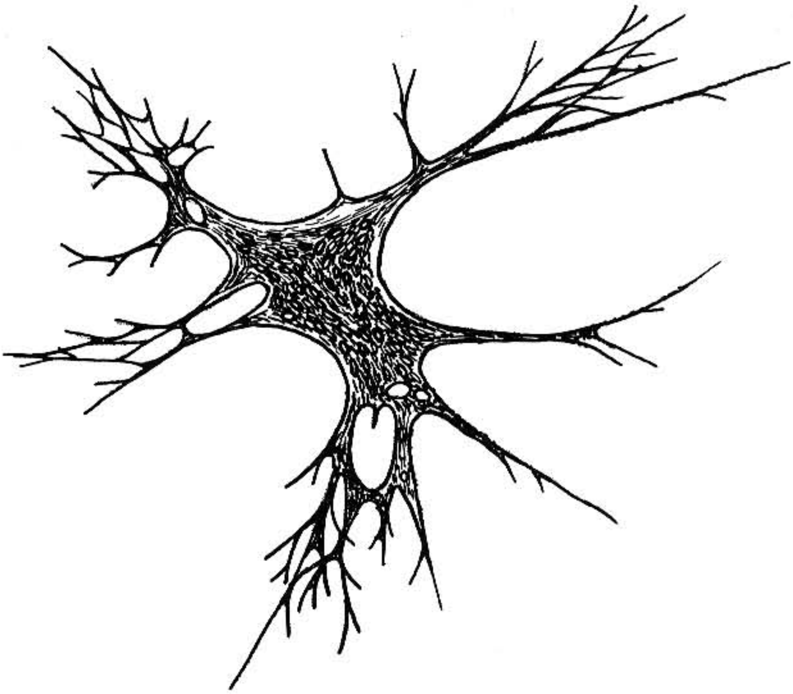


FIG. 20. Penardiidae; *Penardia* (p. C40).

pansions to narrow, digitate and pointed, extending radially; multinucleate, up to 400. [Only the test of *Geopyxella* was described. This seems analogous to *Phryganella*, but the synonymy can only be proven by a study of pseudopodial and other characters]. [On moss.] *Pleist.-Rec.*, India-W.Eu.-N.Am.——FIG. 19,*1*. **P. nidulus*, Rec., Switz.; *1a-c*, apert., oblique, and aboral views, approx. ×170 (*1435).——FIG. 19,*2*. *P. sylvicola* (Bonnet & Thomas), Rec., Fr.; *2a,b*, apert. and edge views, ×320 (*171).

Class RETICULAREA Lankester, 1885

[*nom. correct.* Loeblich & Tappan, 1961, p. 216 (*pro* class Reticularia Lankester, 1885, p. 845)]——[=Rhizopoda asphycta Haeckel, 1862, p. 211]

Unicellular organisms with amoeboid principal stage; pseudopodia in form of filopodia, reticulopodia, or axopodia; may have secreted or agglutinated skeleton; protoplasmic movement by active shearing or sliding between adjacent gel-like filaments moving in opposite directions in same pseudopod, and in absence of a plasmagel cortex (*984). [The class Reticularea, as redefined, includes the subclasses Filosia, Granuloreticulosia, Radiolaria, Heliozoia, and Acantharia (*1181, p. 216).] *?Precam., Cam.-Rec.*

Subclass FILOSIA Leidy, 1879

[*nom. transl.* Loeblich & Tappan, 1961, p. 269 (*ex* suborder Filosa Leidy, 1879, p. 23, 189)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}class, ^{2}section, ^{3}order); dagger(†) indicates *partim*]——[=^{2}Filosa† Lankester, 1885, p. 838; =Filosa monostomata Averintsev, 1907, p. 100; =Filosa Chatton, 1925, p. 76; =^{3}Filosa Rhumbler, 1913, p. 339; =^{3}Affilosia Rhumbler, 1913, p. 339 *(nom. van.)*; =^{1}Filosa Deflandre in Grassé, 1953, p. 132]——[=Protoplasta† Haeckel, 1870, p. 56; =^{3}Protoplasta† Leidy, 1879, p. 23; =Monothalamia filosa Taránek, 1882, p. 232]

Pseudopodia filiform, tapering, branching and rarely or not anastomosing. *M.Eoc.-Rec.*

Order ACONCHULINIDA de Saedeleer, 1934

[*nom. correct.* Loeblich & Tappan, 1961, p. 269 (*pro* order Aconchulina Deflandre in Grassé, 1953, p. 92, *nom. transl. ex* suborder Aconchulina de Saedeleer, 1934, p. 6, 24)]

Naked amoebae with filiform pseudopodia. *Rec.*

Family PENARDIIDAE Loeblich & Tappan, 1961

[Penardiidae Loeblich & Tappan, 1961, p. 269; =family Reticulosa Cash, 1904, p. 222 *(partim)* (*non* Reticulosa Carpenter, Parker & Jones, 1862, *nom. nud.*)]

Characters as in the order. *Rec.*

Penardia Cash, 1904, *299, p. 223 [**P. mutabilis;* OD(M)]. Round to ovoid body when at rest, during progression expanded and mobile, with widespread network of slender, branching and anastomosing pseudopodia; endoplasm deep green with symbiotic algae, ectoplasm granular, gray to colorless; single nucleus; one or more contractile vacuoles; up to 400μ in maximum diameter. [In sphagnum.] *Rec.*, Eu.——Fig. 20. **P. mutabilis,* Eng.; active individual, ×350 (*299).

Order GROMIDA Claparède & Lachmann, 1859

[Gromida Claparède & Lachmann, 1859, p. 464]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}subclass, ^{2}order, ^{3}suborder, ^{4}group); dagger(†) indicates *partim*]——[=^{2}Gromiidea Lankester, 1885, p. 845; =^{3}Gromidae Delage & Hérouard, 1896, p. 109; =^{2}Gromiida Calkins, 1909, p. 38]——[=Monostègues† d'Orbigny in de la Sagra, 1839, p. xxxvii, 1 *(nom. neg.)*; =Lepamoebae† Haeckel, 1870, p. 56; =^{2}Rhizopoda imperforata† Schmarda, 1871, p. 162; =^{1}Imperforata† Lankester, 1885, p. 845; =^{3}Testacea† Blochmann, 1895, p. 14; =^{4}Imperforata Blochmann, 1895, p. 14; =Monostomata Averintsev, 1906, p. 258; =Rhizopoda filosa testacea Schouteden, 1906, p. 358; =^{4}Amphistomata Schouteden, 1906, p. 372; =^{2}Solenopoda Zarnik, 1908, p. 78; =^{3}Testaceafilosa de Saedeleer, 1934, p. 6, 27; =^{3}Monotálamos† Gadea Buisán, 1947, p. 17 *(nom. neg.)*; =^{2}Testaceafilosa Deflandre in Grassé, 1953, p. 133; =^{3}Testafilosina Bovee, 1960, p. 355]

Amoebae with filopodia, shell or lorica always with distinct aperture. Uniflagellate gametes (*Gromia*). *M.Eoc.-Rec.*

Superfamily GROMIACEA Reuss, 1862

[*nom. correct.* Loeblich & Tappan, 1961, p. 269 (*pro* superfamily Gromiides Poche, 1913, p. 173, *nom. transl. ex* family Gromidea Reuss, 1862, p. 362)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}superfamily, ^{2}family group); dagger(†) indicates *partim*]——[=Foraminifera Monomera† Reuss, 1862, p. 362 (*non* Monomera Latreille, 1825, p. 408); =^{1}Cystoforaminifera (Vesiculata)† Eimer & Fickert, 1899, p. 67 *(nom. nud.)*; =Amphistomata† Averintsev, 1906, p. 316; =^{1}Amphitrematides Poche, 1913, p. 174; =^{2}Monostomata† Rhumbler, 1928, p. 3 *(nom. nud.)*]

Test chitinous, without distinct siliceous scales or plates, but commonly with agglutinated foreign material. *Pleist.-Rec.*

Family GROMIIDAE Reuss, 1862

[*nom. correct.* Eimer & Fickert, 1899, p. 670 (*pro* family Gromidea Reuss, 1862, p. 362)]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}family, ^{2}subfamily); dagger(†) indicates *partim*]——[=^{1}Gromida Carpenter, 1861, p. 470; =^{1}Gromidae Claus, 1872, p. 108; =^{1}Gromidee Schwager, 1876, p. 484; =^{1}Gromiina Bütschli in Bronn, 1880, p. 186; =^{1}Grominae Delage & Hérouard, 1896, p. 116; =^{2}Gromiinae de Saedeleer, 1934, p. 6, 47; =^{1}Grómidos Gadea Buisán, 1947, p. 17 *(nom. neg.)*]——[=^{1}Pamphagidae Taránek, 1882, p. 232; =^{1}Pseudodifflugiidae Taránek, 1882, p. 233; =^{2}Pseudodifflugiinae de Saedeleer, 1934, p. 6, 44; =^{1}Chamydophryidae Taránek, 1882, p. 235; =^{2}Chlamydophryinae de Saedeleer, 1934, p. 6, 32; =^{1}Monostomina† Lankester, 1885, p. 845 *(nom. nud.)*; =^{2}Monostominae† Calkins, 1901, p. 106 *(nom. nud.)*; =^{1}Adjungentiidae† Rhumbler, 1895, p. 93, 95 *(nom. nud.)*; =^{1}Nuditestiidae Rhumbler, 1895, p. 93, 94 *(nom. nud.)*; =^{2}Pseudo-Gromiinae Wailes in Cash, Wailes & Hopkinson, 1915, p. 100 *(nom. nud.)*; =^{2}Pseudogromiinae Calkins, 1926, p. 361 *(nom. nud.)*] [Also =^{1}Gromiada Haeckel, 1894, p. 190]

Test membranous or pseudochitinous, rigid or slightly flexible, without distinct plates or scales, but with some siliceous elements, and commonly with foreign material. *Pleist.-Rec.*

Gromia Dujardin, 1835, *632, p. 338 [**G. oviformis* Dujardin, 1835, *634(a), p. 345; SD (SM), Dujardin, 1835] [=*Arcellina* DuPlessis, 1876, *1460, p. 100 (type, *A. marina*) (*non Arcellina* Carter, 1856); =*Hyalopus* Schaudinn, 1894, *1641, p. 14) (type, *Gromia dujardinii* Schultze, 1854, *1695, p. 55)]. Test basically spherical to ovoid (diam., 0.15-3.0 mm.), may be deformed and lobate when living in dense growth, or flattened at extremities; wall transparent to colorless or apertural rim may be brownish, regarded as consisting of 2 layers (Jepps, *990; Hedley, *891), inner structureless membrane and outer perforated layer originally described as having irregularly prismatic structure (chitinoid?), 2-20μ in length and insoluble in HCl, but dissolved in caustic potash, perforations shown to be radial canals under electron microscope, and the inner layer shown to be finely granular ectoplasm (*892); aperture broad, round or oval, terminal, surrounded by apertural apparatus which consists of narrow tubuliferous ring at outer margin of base of conspicuous, hyaline, flexible collar, the area surrounding the oral capsule lacking perforations in electron micrographs, 9 to 20 simple lobes or fimbriate septal bars radiate inward from edges of collar, restricting the opening; the oral capsule has numerous fine tubules or fibrils as seen by electron microscope; granular protoplasm filling test, contains food particles, numerous small refringent bodies (xanthosomes), sand grains and abundant brown oval masses of debris (stercomata) which results in opaque brown color; multinucleate, spherical nuclei (diam., 3.5-5μ); pseudopodia arising from clear ectoplasm in pseudopodial trunk are thick, very elongate, hyaline and nongranular; asexual and sexual reproduction, uniflagellate flagellulae having been variously referred to as gametes (*1106) which fuse, or as asexual "swarm spores" (*990). [Valkanov, 1938, reported fusion of gametes, and dimorphism in size of adults, resulting from the sexual and asexual generations in *G. dujardinii* (*1973). [Marine.] *Rec.*, Eu.-N.Am.——Fig. 21,*1-4*. **G. oviformis; 1,* living animal showing pseudopodia, Fr.; ×10 (*632); *2a,b,* thick perforated layer with thinner supposed membranous layer and surface view showing perforated "prisms," Eng.; ×1,750; *3,* flagellate gamete, Eng.; ×4,000 (*1106); *4a,b,* oral apparatus, top view and vert. sec., USA(Calif.); ×50 (*41).——Fig. 21,*5*. *G. dujardinii* Schultze, Italy; ×36 (*1695).——Fig. 22,*1-3*. **G. oviformis,* electron micrographs (*892); *1,* section of shell showing canal passing radially through wall, ×15,800; *2*, oblique section of shell (dark area in upper right), showing honeycomb membrane that extends diagonally across figure and cytoplasm (lower left), ×137,000; *3*, section of oral capsule showing tubules of which it is composed, with connecting filaments, ×82,000.

Amoebogromia Giard, 1900, *787, p. 377 [**A. cinnabarina* OD(M)]. Solitary or in small colonies

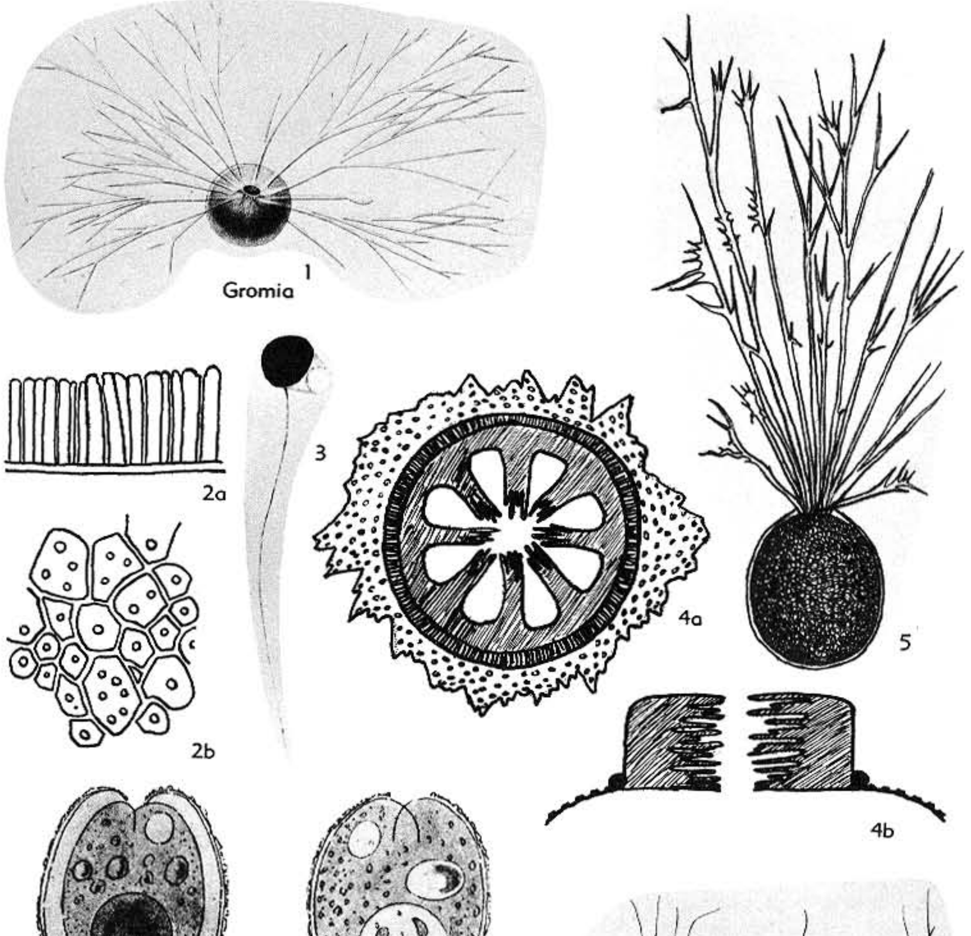


Fig. 21. Gromiidae; *1-5, Gromia; 6,7, Capsellina; 8, Bargoniella* (p. C40-C42).

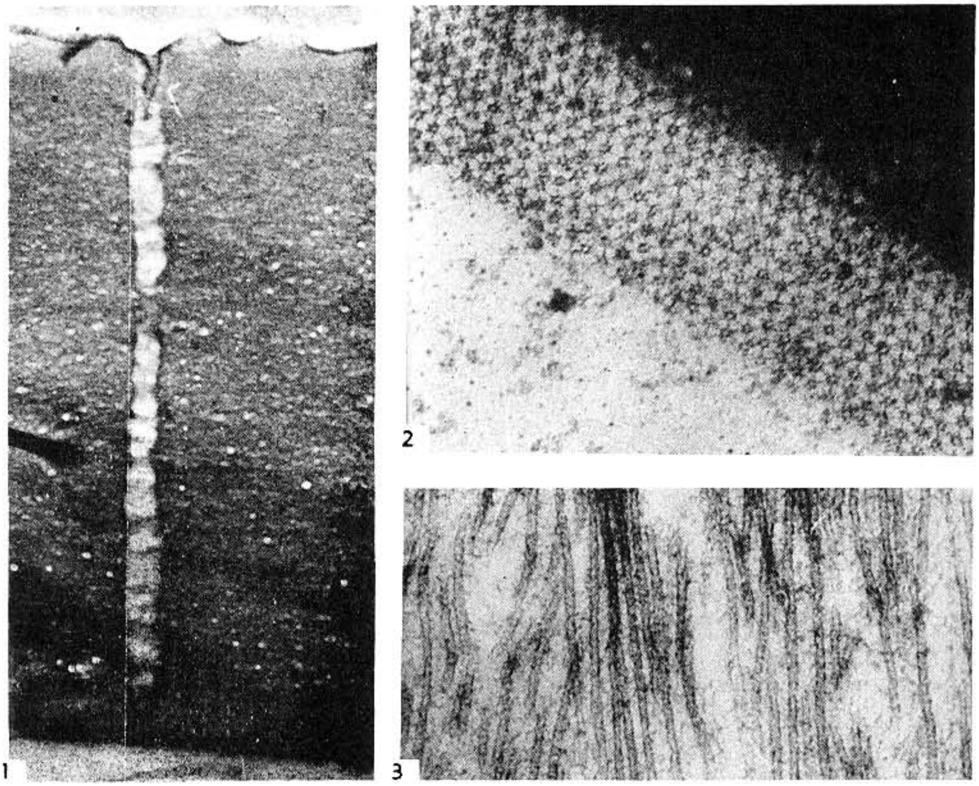


FIG. 22. Gromiidae; *1-3, Gromia oviformis,* electron micrographs (p. *C*40).

of 10 to 12; test irregularly ovoid, but variable during movement (length to 2 mm.), with hyaline, elastic test completely filled by homogeneous, finely granular, red protoplasm; nucleus spherical, eccentric, large (diam., 160μ); pseudopodia extended from single opening, elongate; never figured. [Marine, associated with cirripeds.] *Rec.,* Eu.(Fr.).

Bargoniella LOEBLICH & TAPPAN, 1961, *1181, p. 216 [**Salpicola amylacea* BARGONI, 1894, *80, p. 43; OD] [=*Salpicola* BARGONI, 1894, *80, p. 43 (obj.) (*non* RICHIARDI, 1880)]. Test ovoid with "cellulose" wall; aperture terminal with thickened collar from which pseudopodial trunk emerges; protoplasm granular, filling test, pale in young but opaque in adult; nucleus large; reproduction by binary fission; pseudopodia elongate, bifurcate, probably filose, and ramifying in tunicate *Salpa* upon which it is parasitic. [Originally regarded as a parasitic foraminifer, this genus was referred to the Filosa (*1569, p. 202) because of its evident filose pseudopodia. A search for type material on the tunicates *Salpa mucronata* and *S. democratica* in the region of Messina, Sicily, could determine without doubt the systematic position of this genus.] [Marine.] *Rec.,* Eu.(Italy).——FIG. 21,*8*. **B. amylacea* (BARGONI), Sicily; enlarged (*700).

Capsellina PENARD, 1909, *1439, p. 290 [**C. bryorum*; OD] [=*Rhogostoma* BĚLAŘ, 1921, *107, p. 305 (type, *R. schuessleri* BĚLAŘ). Test ovoid, slightly compressed laterally (diam., 12-40μ); wall of 2 layers, outer one membranous, grayish to dark brown, with small chitinous or siliceous agglutinated particles, inner one transparent, pearl-gray, flexible; aperture narrow elongate slit in depression; one or many contractile vacuoles; nucleus very large, single, with 3 to 6 nucleoli; reproduction by division; pseudopodia filopodia, without anastomosing. [On moss.] *Rec.,* Eu.——FIG. 21,*6*. **C. bryorum,* Switz.; *6a-c,* broad side with contracted protoplasm showing large nucleus; oblique and apert. views, ×750 (*1439).——FIG. 21,*7*. *C. schuessleri* (BĚLAŘ), Ger.; side view showing pseudopodia, ×1,700 (*107).

Chlamydophrys CIENKOWSKI, 1876, *341, p. 39 [**C. stercorea;* OD]. Test ovoid, hyaline, with short neck, rather rigid but capable of deformation; protoplasm divided into 2 zones by dark equatorial zone of granules, oral area of protoplasm being rich in vacuoles, aboral end with transparent protoplasm containing single nucleus with nucleolus; pseudopodial trunk arising from neck, from which numerous, fine, nongranular

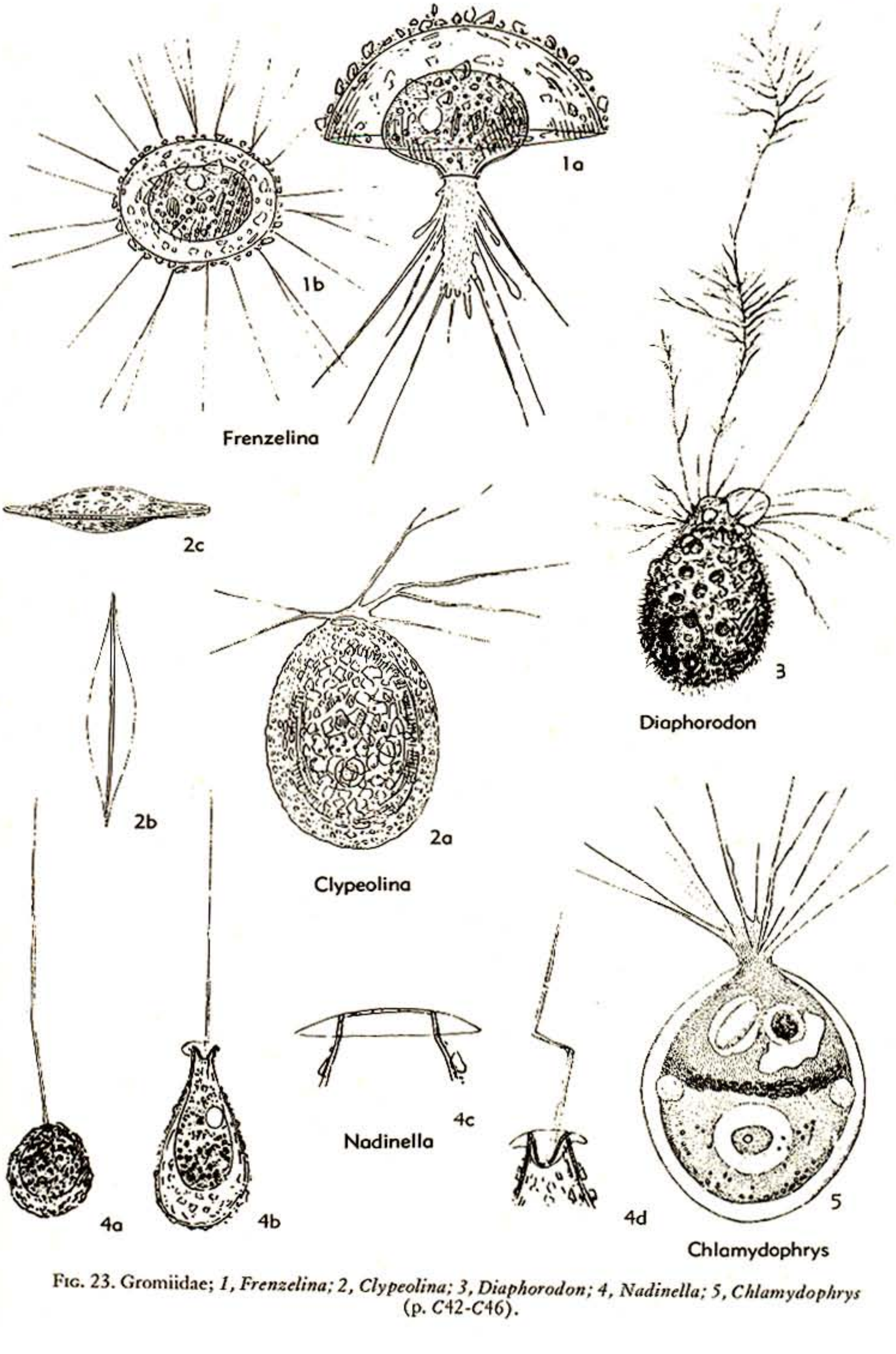


FIG. 23. Gromiidae; *1, Frenzelina; 2, Clypeolina; 3, Diaphorodon; 4, Nadinella; 5, Chlamydophrys* (p. C42-C46).

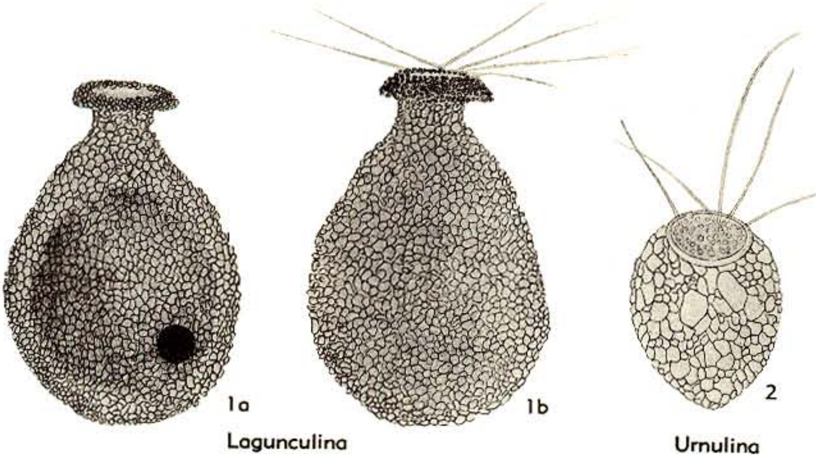


FIG. 24. Gromiidae; *1, Lagunculina; 2, Urnulina* (p. C44, C46-C47).

pseudopodia extend. [Fresh water.] *Rec.*, Eu.——FIG. 23,*5*. **C. stercorea*, Ger.; side view showing dark equat. zone, large nucleus, and delicate pseudopodia, ×760 (*341).

Clypeolina PENARD, 1902, *1435, p. 459 [**C. marginata;* OD(M)]. Test grayish, oval or elliptical (length, 80-140μ), composed of 2 layers, outer cover of 2 strongly compressed chitinoid valves with distinct border flange, bearing flat, irregular, siliceous scales which are larger toward center of test and separated by smaller scales, inner cover consisting of membranous sac; aperture elliptical to linear; nucleus large, round, with large nucleolus, single contractile vacuole; pseudopodia filiform, elongate, narrow, branching; reproduction by binary fission, each half appropriating one of outer valves and secreting another new one. [Fresh water.] *Rec.*, Eu.——FIG. 23,*2*. **C. marginata*, Switz.; *2a-c*, side, edge, and top views approx. ×250 (*1435).

Diaphorodon ARCHER, 1869, *31, p. 394 [**D. mobile;* OD]. Test large, ovoid (length, 60-113μ), membranous, with agglutinated cover and with thick covering of fine, rigid, hyaline, apparently pseudochitinous bristles which were originally thought to be pseudopodia; pseudopodia long, filose, branching; single nucleus, placed posteriorly; aperture terminal, of varying shape; 1 or 2 contractile vacuoles toward apertural end. [Fresh water.] *Rec.*, Eu.——FIG. 23,*3*. * *D. mobile*, G. Brit.; ×200 (*302a).

Frenzelina PENARD, 1902, *1435, p. 463 [**F. reniformis;* OD(M)]. Test thin, hemispherical (diam., 26-30μ), with some siliceous particles, aperture equal to diameter of test; protoplasmic body rounded, ovoid, slightly reniform, covered by thin, flexible membrane, with considerable separation between this and outer test; apertural orifice of inner membrane narrowed, round, and may protrude slightly; nucleus central, one contractile vacuole, numerous very fine pseudopodia, rigid, simple or bifurcate, leading from pseudopodial trunk. [Fresh water.] *Rec.*, Eu.-Australia.——FIG. 23,*1*. **F. reniformis*, Switz.; *1a*, side view showing pseudopodial trunk, outer test and inner membrane, approx. ×1,000; *1b*, top view, approx. ×700 (*1435).

Lagunculina RHUMBLER, 1904, *1569, p. 248 [**Ovulina urnula* GRUBER, 1884, *833, p. 497; OD(M)] [=*Ovulina* GRUBER, 1884, *833, p. 497 (obj.) (*non* EHRENBERG, 1845); =*Arlagunculum* RHUMBLER, 1913, *1572b, p. 349 (obj.) (*nom. van.*)]. Test flask-shaped (length, 0.15 mm.), with everted phialine apertural neck; wall finely arenaceous, finer-grained and less densely packed in apertural region; one nucleus. [Similar in general appearance to *Urnulina* GRUBER, but in view of the questionable pseudopodial characters of both genera, they are left distinct for the present.] [Shallow marine, on wood and rocks.] *Rec.*, Eu.——FIG. 24,*1*. **L. urnula* (GRUBER), Italy(Genoa Harbor); *1a,b*, side view of stained test and living specimen showing pseudopodia, ×300 (*833).

Lecythium HERTWIG & LESSER, 1874, *921, p. 117 [**Arcella? hyalina* EHRENBERG, 1838, *668, p. 134; OD(M)] [=*Pamphagus* BAILEY, 1853, *66, p. 347 (type, *P. mutabilis* BAILEY, 1853) (*non Pamphagus* THUNBERG, 1815); =*Baileya* AVERINTSEV in SCHOUTEDEN, 1906, *1675, p. 382 (*pro Pamphagus* BAILEY, 1853); =*Troglodytes* GABRIEL, 1876, *759, p. 536 (type, *T. zoster*) (*non Troglodytes* MOEHRING, 1758, *nec* GEOFFROY, 1812); =*Phonergates* BUCK, 1878, *251, p. 20 (type, *P. vorax* BUCK, 1878 (*non Phonergates* STÅL, 1853)]. Test spherical to pyriform (length, 30-45μ), thin, flexible, colorless or translucent, no foreign matter; aperture terminal, circular, on short neck; protoplasm colorless, granular, filling test; nucleus large, with central nucleolus, posterior in position; one contractile vacuole; pseudopodia numerous, narrow, elongate, branching. [Fresh water on moss.] *Rec.*, Eu.-N.Am.——Fig. 25,2. **L. hyalinum* (Ehrenberg), Ger.; *2a,b*, side and aboral views, approx. ×500 (*921).

Nadinella Penard, 1899, *1434, p. 82 [**N. tenella*; OD]. Test flask-shaped (length, 50-55μ), pseudochitinous, with small agglutinated scales par-

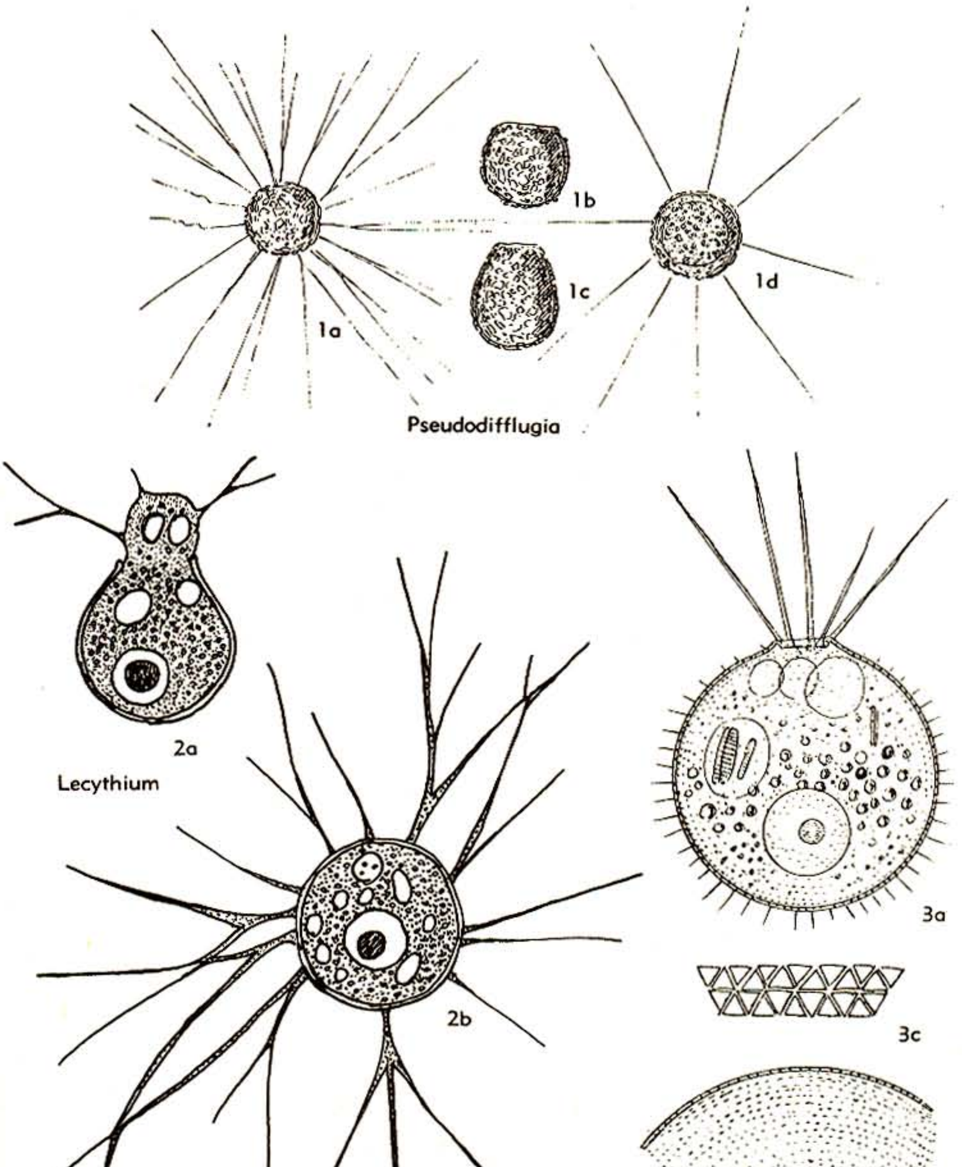


Fig. 25. Gromiidae; *1*, *Pseudodifflugia*; *2*, *Lecythium*; *3*, *Penardeugenia* (p. C44-C46).

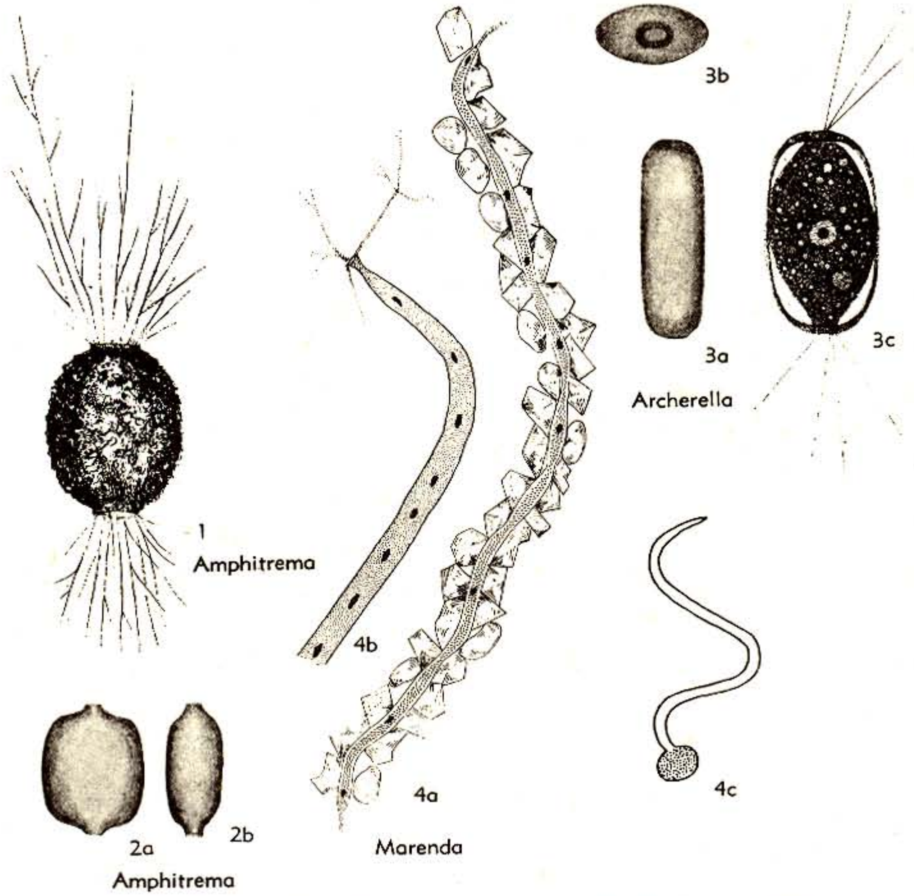


FIG. 26. Amphitrematidae; *1, 2, Amphitrema; 3, Archerella; 4, Marenda* (p. C47).

ticularly at aboral end, compressed; aperture narrow, grooved at each side with broad hyaline collar surrounding aperture; protoplasm clear, not completely filling test; nucleus at aboral end; one contractile vacuole; pseudopodia elongate, narrow, filiform. [Fresh water.] *Rec.*, Eu.——FIG. 23,*4*. _*N. tenella,_ Switz.; *4a,b,* aboral and side views, approx. ×500; *4c,d,* aperture from larger side and from edge, enlarged (*1434).

Penardeugenia DEFLANDRE in DEFLANDRE-RIGAUD, 1958, *578, p. 29 [_*Pamphagus bathybioticus_ PENARD, 1904, *1436, p. 413; OD] [=*Eugenia* AVERINTSEV, 1906, *59, p. 263 (obj.) (*non* GOULD, 1855, *nec* MARTENS, 1860; *nec* ROBINEAU-DESVOIDY, 1863; *nec* HALL, 1867)]. Test globular (diam., 35-45μ), thin-walled, hyaline, with small, triangular, siliceous platelets regularly arranged, test covered by short pointed siliceous bristles, enlarged at their base; aperture terminal, round to elliptical owing to rather flexible margin; protoplasm granular, colorless, with large nucleus containing small nucleolus at aboral end of test; large, round, active contractile vacuoles near aperture; pseudopodia filiform, tapering. [Fresh water.] *Rec.*, Eu.——FIG. 25,*3*. _*P. bathybiotica_ (PENARD), Switz.; *3a,* side view, approx. ×875; *3b,* apert. area, enlarged; *3c,* detail of plate arrangement, approx. ×1,700 (*1436).

Pseudodifflugia SCHLUMBERGER, 1845, *1669, p. 256 [_*P. gracilis;_ OD(M)]. Test ovoid to globular (length, 20-65μ), pseudochitinous, usually rigid, with some foreign matter; aperture large, rounded, terminal; single nucleus and single contractile vacuole; pseudopodia filiform, very elongate, simple or branching. [Fresh water.] *Pleist.-Rec.*, Eu.——FIG. 25,*1*. _*P. gracilis,_ Rec., Switz.; *1a-d,* aboral, side and apert. views of variously shaped tests, ×250 (*1435).

Urnulina GRUBER, 1884, *833, p. 496 [_*U. difflugiaeformis_; OD] [=*Arurnulum* RHUMBLER, 1913, *1572b, p. 349 (obj.) (*nom. van.*)]. Test ovate (length, approx. 0.8 mm.), somewhat narrowed at aboral end; wall of foreign matter and densely packed siliceous grains, some of which may be secreted by animal; aperture broad, at flattened end of test, with clear rim; pseudopodia originally illustrated as filose and hyaline, but only observed once, and description leaves doubt as to their true character. [Marine.] *Rec.*, Eu.(Medit.-N.Sea).——Fig. 24,*2*. **U. difflugiaeformis*, Italy(Genoa Harbor); ×30 (*833).

Family AMPHITREMATIDAE Poche, 1913

[Amphitrematidae Poche, 1913, p. 174]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}family, ^{2}subfamily, ^{3}tribus); dagger(†) indicates *partim*]——[=Monothalamia amphistomata† Hertwig & Lesser, 1874, p. 137 *(nom. nud.)*; =^{1}Amphistominat† Bütschli in Bronn, 1880, p. 188 *(nom. nud.)*; =^{1}Amphistominae† Delage & Hérouard, 1896, p. 116 *(nom. nud.)*; =^{1}Amphistominidae† Schouteden, 1906, p. 358 *(nom. nud.)*; =^{2}Amphitreminae Galloway, 1933, p. 45; =^{3}Amphistominit de Saedeleer, 1934, p. 8, 86 *(nom. nud.)*; =^{1}Amphitremidae Grospietsch, 1958, p. 35]

Test chitinous and may include foreign material; apertures at both poles of test. *Pleist.-Rec.*

Amphitrema Archer, 1867, *28, p. 174 [**A. wrightianum* Archer, 1869, *31, p. 397, expl. pl. 20; SD(SM) Archer, 1869]. Test ovoid, symmetrical (length, 55-100μ), transparent membrane covered with foreign matter, with distinct aperture at each end, produced on short, rimlike neck; protoplasm colorless, granular, may contain symbiotic algae; nucleus single, large, central in position and containing several nucleoli; 1 or 2 contractile vacuoles; numerous slender, filose pseudopodia arising in dense tuft from each aperture and rarely branching. [Fresh water.] *Pleist.-Rec.*, Eu.——Fig. 26,*1,2*. **A. wrightianum*; *1*, living specimen, Rec., Ire., ×400 (*31); *2a,b*, fossil tests from which agglutinated material has been lost, peat deposit, Pleist., Ire., ×250 (*302a).

Archerella Loeblich & Tappan, 1961, *1181, p. 217 [**Ditrema flavum* Archer, 1877, *33, p. 103; *34b, p. 336; OD] [=*Ditrema* Archer, 1877, *33, p. 103; *34b, p. 336 (obj.) (*non* Temminck & Schlegel in von Siebold, 1844, p. 77)]. Similar to *Amphitrema* but test thick and pseudochitinous (length, 45-77μ), devoid of foreign matter; pseudopodia few. [Fresh water on sphagnum.] *Pleist.-Rec.*, Eu.-N.Am.——Fig. 26,*3*. **A. flavum* (Archer), Rec., Br.I.; *3a-c*, edge, top, and side views showing living animal and test, ×500 (*302a).

Marenda Nyholm, 1951, *1373, p. 91 [**M. nematoides*; OD]. Test elongate, tubular, flexible, especially at ends, somewhat tapering at both ends (length, to 9 mm.), wall pseudochitinous membrane which may be slightly constricted at various places, without agglutinated covering; protoplasm opaque and white, containing numerous nuclei and some vacuoles (not contractile); pseudopodia, filose, protruding from apertures at each end of test; encystment occurs by collection of globular mass of protoplasm outside one of apertures and secretion of protective membrane. [Marine (depth, 8-20 m.)] *Rec.*, Eu.(Medit., Fr.)——Fig. 26,*4*. **M. nematoides*, Fr.; *4a*, specimen flat on sandy bottom (not a test) showing irregular constrictions and numerous nuclei, ×12.5; *4b*, one end of tube showing pseudopodia, ×20; *4c*, specimen showing encystment, enlarged (*1373).

Superfamily EUGLYPHACEA Wallich, 1864

[*nom. transl.* Loeblich & Tappan, 1961, p. 270 (*ex* subfamily Euglyphidae Wallich, 1864, p. 217, 240)]——[=Monostomata Schulze, 1877, p. 28 *(partim)*; =family group Monostomata Rhumbler, 1928, p. 3 *(partim)*]

Test composed of variously shaped siliceous scales. *M.Eoc.-Rec.*

Family EUGLYPHIDAE Wallich, 1864

[*nom. transl.* Schulze, 1877, p. 28 (*ex* subfamily Euglyphidae Wallich, 1864, p. 217, 240)]——[=Euglyphina Bütschli in Bronn, 1880, p. 185; =Euglyphinae Delage & Hérouard, 1896, p. 112; =Euglífidos Gadea Buisán, 1947, p. 16 *(nom. neg.)*; =Euglyphida Copeland, 1956, p. 191 *(nom. van.)*]——[=Monocyphia Vejdovský, 1881, p. 138 *(partim)*; =Monostomina Lankester, 1885, p. 845 *(partim) (nom. nud.)*; =Protrudentiidae Rhumbler, 1895a, p. 94, 95 *(partim) (nom. nud.)*; =^{1}Trinemidae (Euglyphina) Hoogenraad & de Groot, 1940, p. 24; =Assulinidae Jung, 1942a, p. 257]

Test hyaline, symmetrical, elongate, composed of rounded siliceous scales, aperture rounded to elongate; one nucleus. *M.Eoc.-Rec.*

Subfamily EUGLYPHINAE Wallich, 1864

[*nom. correct.* Vejdovský, 1881, p. 138 (*pro* subfamily Euglyphidae Wallich, 1864, p. 217, 240); tribus Euglyphini de Saedeleer, 1934, p. 6, 27]

Test radially symmetrical with centrally placed aperture. *M.Eoc.-Rec.*

Euglypha Dujardin, 1840, *635, p. 285 [**E. tuberculata* Dujardin, 1841, *636, p. 251; SD Loeblich & Tappan, herein] [=*Crossopyxis* Ehrenberg, 1872, *688, p. 245 (type, *Difflugia (Exassula) laevigata* Ehrenberg, 1872, =*Difflugia laevigata* Ehrenberg, 1842, SD Loeblich & Tappan herein); =*Difflugia (Setigerella)* Ehrenberg, 1872, *688, p. 247 (type, *Difflugia (Setigerella) setigera* (Perty) Ehrenberg, 1872, =*Euglypha setigera* Perty, 1849, SD Loeblich & Tappan, herein); =*Pareuglypha* Penard, 1902, *1435, p. 492, type, *P. reticulata*)]. Test hyaline, elongate (length, 20-140μ), ovate to acuminate, rounded in section, consisting of circular, oval or scutiform siliceous plates in regularly alternating rows and in some forms with siliceous spines which are modified scales; aperture terminal, rounded, with apertural plates denticulate; protoplasm colorless, not completely filling test; nucleus large; 1 or 2 contractile vacuoles; pseudopodia filose and branching; encystment may occur.

[Fresh water in moss, sphagnum and submerged vegetation.] *M.Eoc.-Rec.*, cosmop.——Fig. 27,*1-4*. **E. tuberculata* Dujardin; *1*, side view of test referred by Dujardin to *E. alveolata*, Rec., Fr.; ×340 (*636); *2*, side view showing pseudopodia, Rec., Br.I., ×400 (*302a); *3a,b*, side and apert.

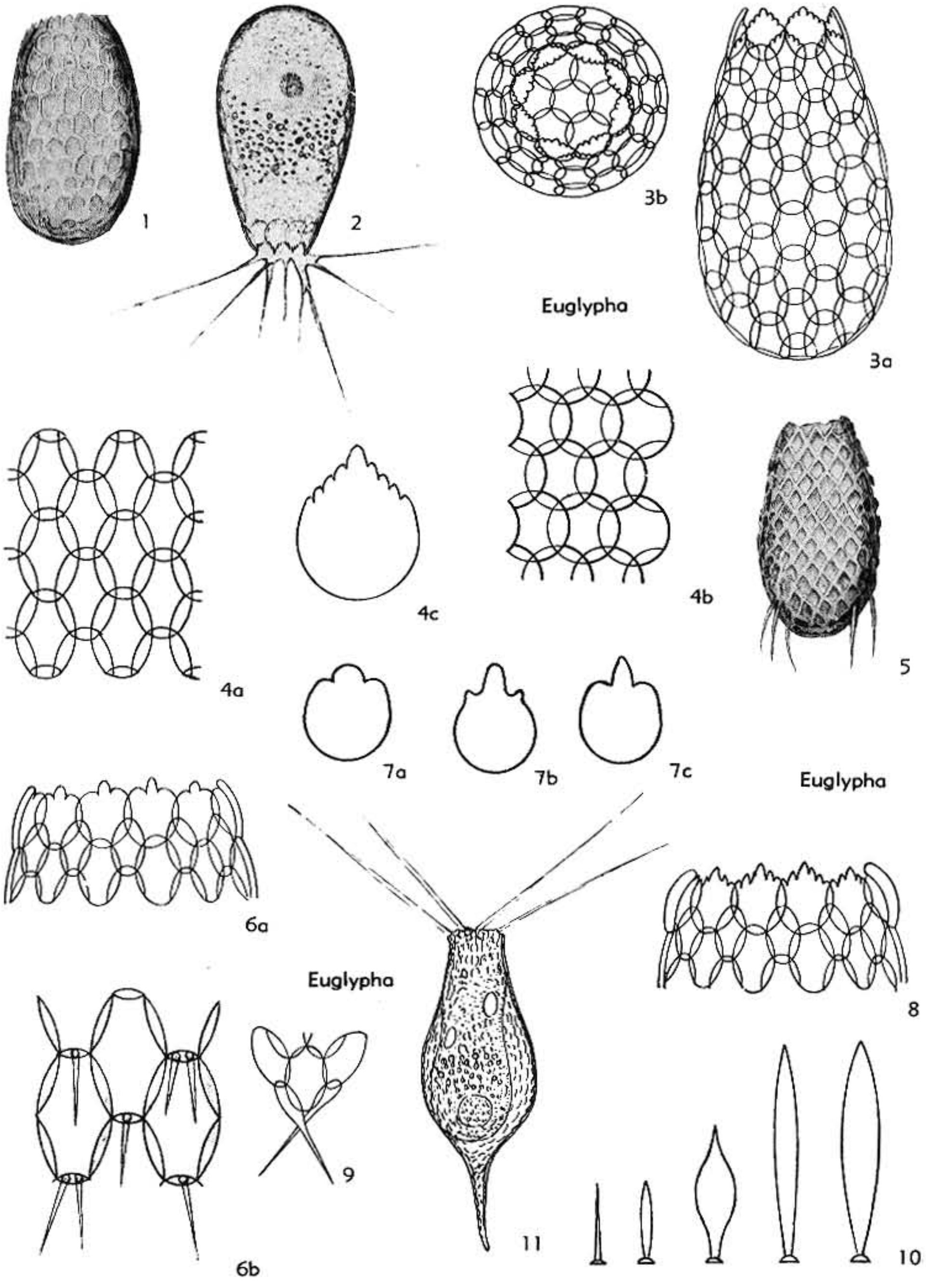


Fig. 27. Euglyphidae (Euglyphinae; *1-10, Euglypha*) (p. C47-C49).

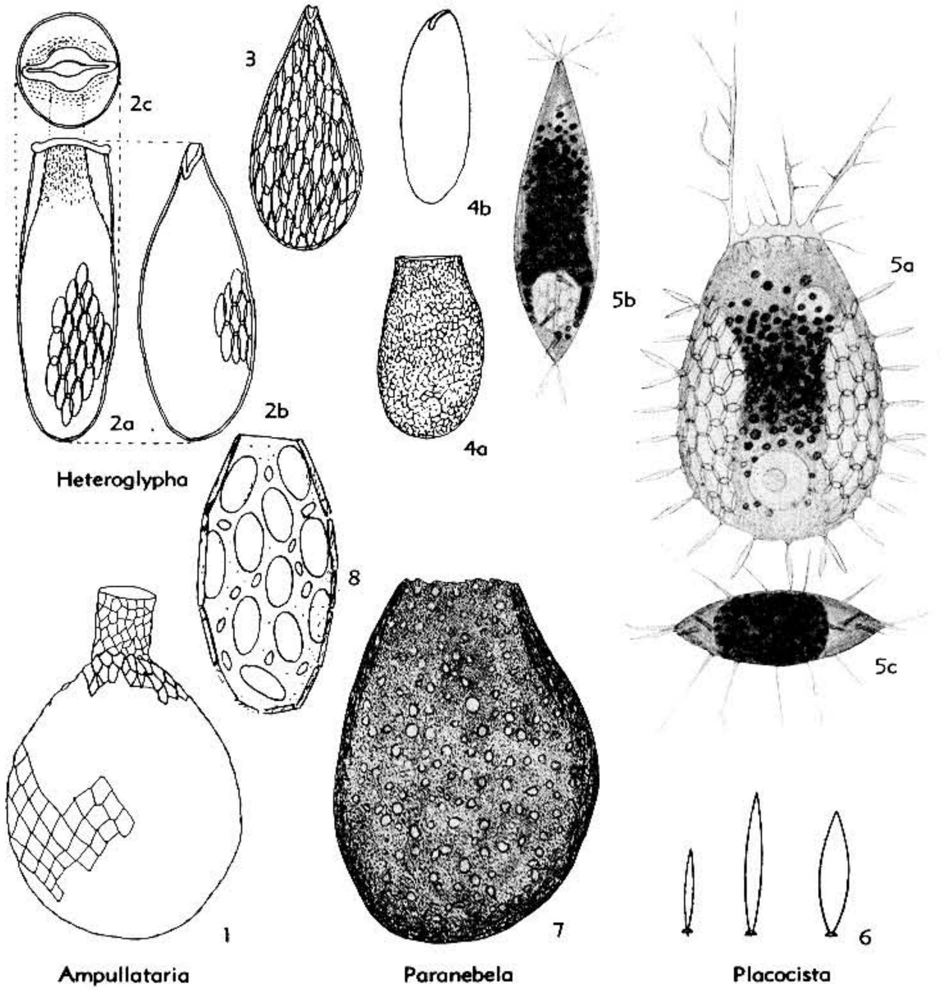


Fig. 28. Euglyphidae (Euglyphinae; *1, Ampullataria; 2-4, Heteroglypha; 5, 6, Placocista; 7, 8, Paranebela*) (p. C49-C50).

views showing plate arrangement, Rec., Br.I., ×600 (*302a); *4a,b,* oval and circular body scales, ×1,000; *4c,* apert. scale, ×2,000, Rec., Br.I.——Fig. 27,*5*. *E. alveolata* Dujardin, Rec., Fr.; lectotype (*636, pl. 2, fig. 9) herein designated, ×340.——Fig. 27,*6*. *E. ciliata* Ehrenberg, Rec., Br.I.; *6a,* apert. scales, ×1,600; *6b,* body scales and spines, ×2,000 (*302a).——Fig. 27,*7*. *E. rotunda* Wailes, Rec., Br.I.; *7a-c,* apert. scales, ×1,000 (*302a).——Fig. 27,*8*. *E. strigosa* Ehrenberg, Rec., Br.I.; apert. scales, ×1,600 (*302a).——Fig. 27,*9*. *E. mucronata* Leidy, Rec., Br.I.; terminal spines, ×1,000 (*302a).——Fig. 27,*10*. *E. compressa* Carter, Rec., Br.I.; spines, ×1,000 (*302a).——Fig. 27,*11*. *E. reticulata* (Penard), Rec., Switz.; approx. ×630 (*1435).

Ampullataria Van Oye, 1956, *1977, p. 353 [**A. rotunda;* OD(M)]. Test lagenoid (length, 110μ), circular in section, with elongate tubular neck distinctly separated from ovate body; small oval plates overlapping to appear hexagonal, plates of neck smaller, irregular and not overlapping, capable of movement; aperture terminal, rounded; protoplasmic details unknown. [Fresh water.] *Rec.,* S.Am.(Venez.).——Fig. 28,*1*. **A. rotunda;* ×400 (*1977).

Heteroglypha Thomas & Gauthier-Lièvre, 1959, *1909, p. 205 [**H. delicatula;* OD(M)] [=?*Hyalina* Jung, 1942, *1005, p. 328 (type, *H. neta* Jung, 1942) (*non Hyalina* Schumacher, 1817, *nec* Studer, 1820, *nec* Albers, 1850, *nec* Rambur, 1866)]. Like *Sphenoderia* but with thin chitinoid lip rather than denticulate apertural margin; test covered with elongate oval scales (length, 40-75μ), imbricated as in _Euglypha;_ living animal unknown. [_Hyalina_ Jung was described as having a netlike surface rather than imbricate scales. Its similarity to _Heteroglypha_ in appearance suggests that the network may actually denote the presence of scales; hence the genus is regarded as probably synonymous]. [Fresh water on sphagnum.] _Rec.,_ Afr.-S.Am.——Fig. 28,_2,3._ *_H. delicatula,_ Congo; _2a-c,_ side, edge, and top views, ×580 (*1909); _3,_ edge view showing plate arrangement, ×580 (*1909).——Fig. 28,_4._ _H. neta_ (Jung), Chile; _4a,b,_ side and edge views, ×583 (*1005).

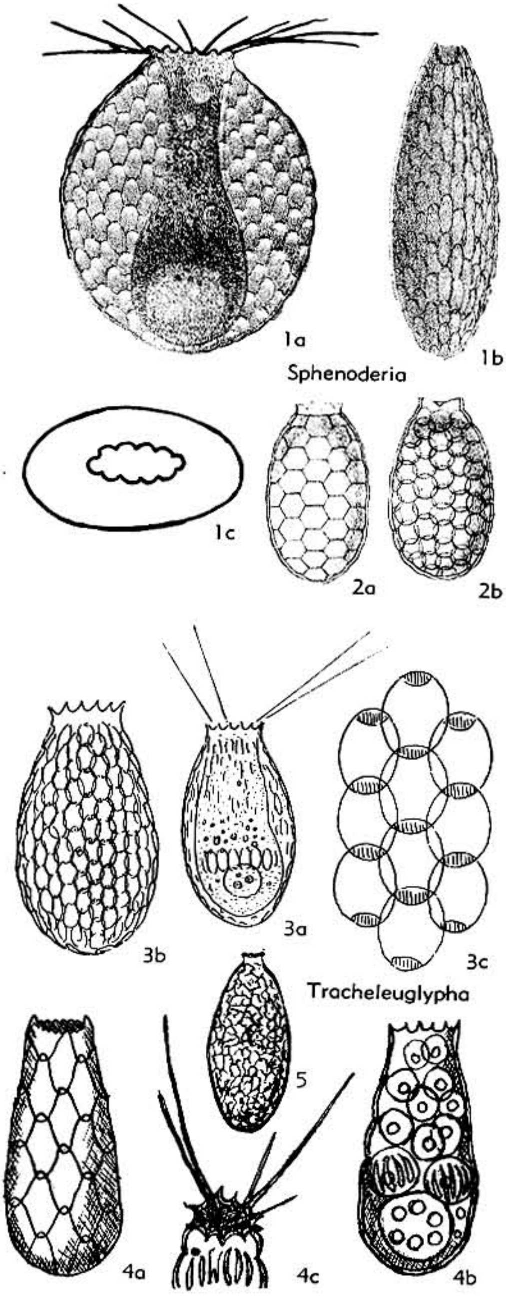


Fig. 29. Euglyphidae (Euglyphinae; _1,2, Sphenoderia; 3-5, Tracheleuglypha_) (p. _C50-C53_).

Paranebela Jung, 1942, *1005, p. 257, 327 [*_P. dentatula;_ OD] [=_Euglyphidion_ Bonnet, 1960, *170, p. 1 (type, _E. enigmaticum_)]. Test ovate, compressed (length, 30-172μ), with granular, medium to dark brown wall in which scattered irregular rounded plates are embedded; aperture rounded, with slightly thickened lip and finely scalloped or weakly dentate margin; living animal unknown. [Fresh water.] _Rec.,_ S.Am.-Eu.——Fig. 28,_7._ *_P. dentatula,_ Chile; side view, ×310 (*1005).——Fig. 28,_8._ _P. enigmatica_ (Bonnet), Fr.(Hautes-Pyrénées); side view showing siliceous scales of 2 sizes, ×1,320 (*170).

Placocista Leidy, 1879, *1127, p. 221 [*_Euglypha spinosa_ Carter, 1865, *289, p. 290; OD] [=_Placocysta_ Blochmann, 1886 (_fide_ *302a, p. 42) (_nom. van._)]. Test ovate (length, 65-175μ), compressed, lenticular in section, composed of oval to circular imbricated siliceous scales; aperture elongate, with flexible border, without toothed apertural scales of _Euglypha_ or denticulate pseudochitinous margin of _Sphenoderia;_ protoplasm gray to colorless, granular, particularly in central area, and may contain symbiotic algae; nucleus large, posterior; 2 or more contractile vacuoles; pseudopodia filose and branching, generally arising from protruding pseudopodial trunk. [Fresh water on sphagnum.] _Rec.,_ Eu.-N.Am.——Fig. 28,_5,6._ *_P. spinosa_ (Carter), Br.I.; _5a-c,_ side, edge and basal views, ×300 (*302a); _6,_ spines, ×800 (*302a).

Sphenoderia Schlumberger, 1845, *1669, p. 256 [*_S. lenta;_ OD(M)] [=_Assulina_ Ehrenberg, 1872, *688, p. 246 (type, _Difflugia seminulum_ Ehrenberg, 1848, *677, p. 379, SD Loeblich & Tappan, herein); =_Hologlypha_ Ehrenberg, 1872, *688, p. 246 (type, _Difflugia (Assulina) lenta_ Schlumberger, Ehrenberg, 1872, =_Sphenoderia lenta_ Schlumberger, 1845, obj., SD Loeblich & Tappan, herein)]. Test ovoid to globular (length, 30-150μ), compressed, hyaline, colorless to brown, membranous, covered with regularly arranged, circular, oval, or hexagonal siliceous scales, which do not extend to cover neck, as in _Euglypha,_ but leave bare a thin chitinous dentate membrane or collar around oval or elliptical terminal aperture; protoplasm commonly colorless to gray; nucleus large, toward posterior end; 1 or 2 contractile vacuoles; pseudopodia filose, may bifurcate. [Fresh water on

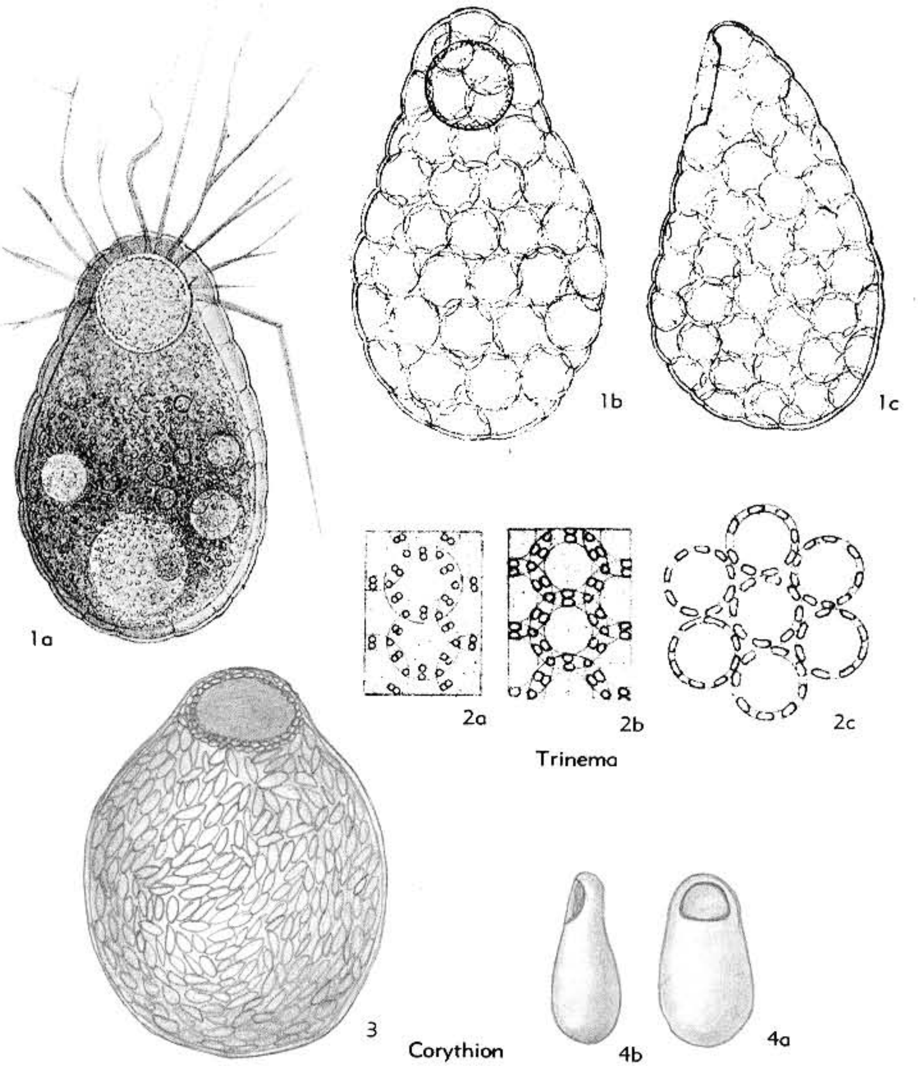


FIG. 30. Euglyphidae (Trinematinae; *1,2, Trinema; 3,4, Corythion*) (p. C53).

sphagnum.] *Pleist.-Rec.*, Eu.-N.Am.-Afr.-Australia. ——FIG. 29,*1*. *S. seminulum* (EHRENBERG), Rec., USA(N.J.); *1a-c*, side, edge, and top views (*1a*, living specimen), ×500 (*1127).——FIG. 29,*2*. **S. lenta*, USA(N.J.); *2a,b*, side views of empty tests, ×500 (*1127).

Tracheleuglypha DEFLANDRE, 1928, *570, p. 40 [**Euglypha dentata* VEJDOVSKÝ, 1882, *2000, pl. 2, figs. 1F, 1J, 1K; OD] [=?*Geamphorella* BONNET, 1959, *169, p. 180 (type, *G. lucida*)]. Like *Euglypha* but without apertural scales; like *Sphenoderia* but aperture circular rather than elongate; length of test, 35-100μ. [PENARD (*1435) described *Euglypha dentata* as having only rounded scales, with a denticulate membranous collar projecting above the last row of scales, and this character was regarded as of generic importance by DEFLANDRE (*570). However, the original figures of VEJDOVSKÝ (here redrawn, Fig. 29,*4a-c*) show dentate apertural scales. Either these original figures are erroneous or the genus is a synonym of *Euglypha*. Only a study of topotype material can solve the problem]. [Fresh water, on moss and sphagnum.]

Mio.-Rec., Eu.-Afr.-N.Am.-S.Am.-Asia-Ind.O. (Seychelles)-Australia.——FIG. 29,*3,4*. **T. dentata* (VEJDOVSKÝ), Rec.; *3a,b*, side views of living specimen and empty test; Switz., approx. ×600, *3c*, arrangement of scales, showing cementing material at scale extremities, enlarged (*1435); *4a-c*, exterior, interior after reproductive fission, and apertural area showing pseudopodia, Czech.,

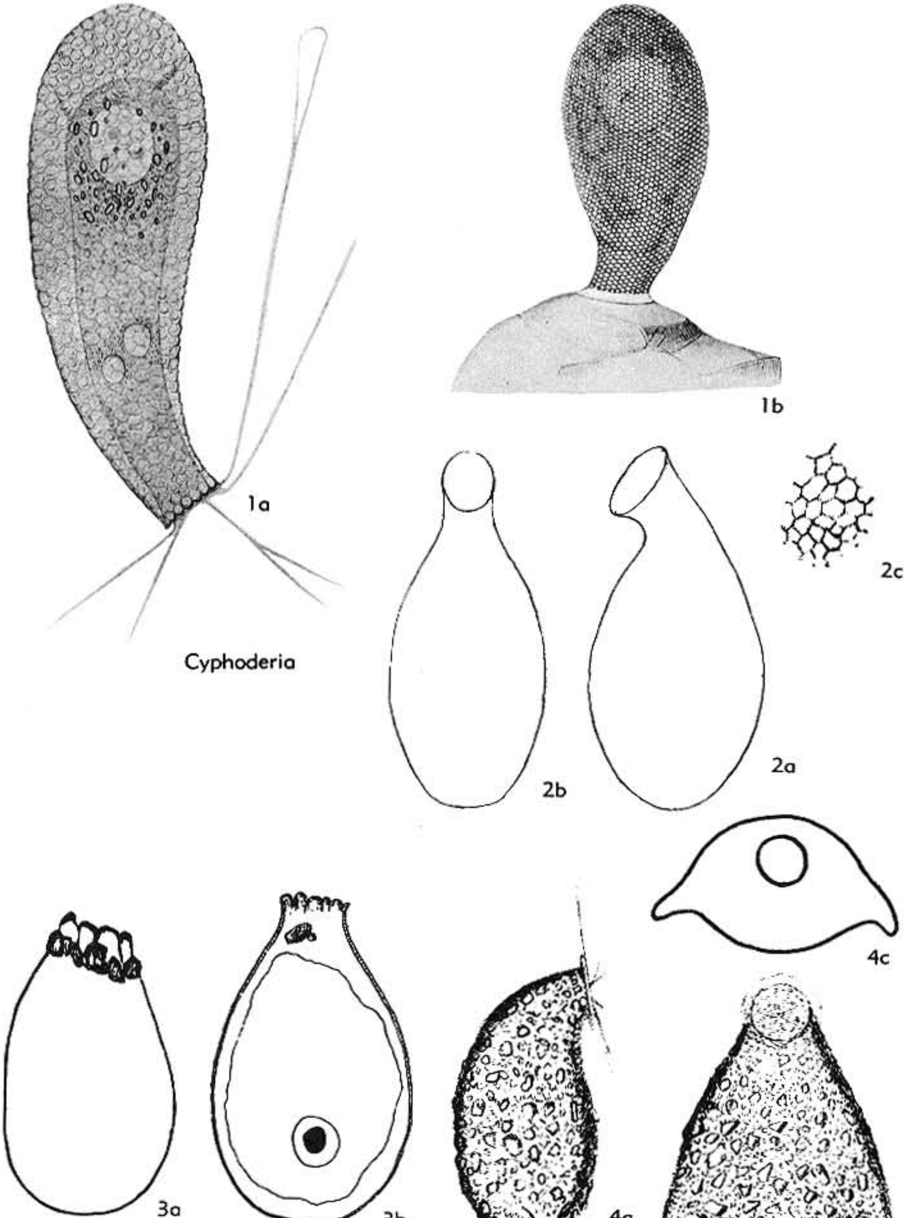


FIG. 31. Cyphoderiidae; *1-3, Cyphoderia; 4, Campascus* (p. C53-C54).

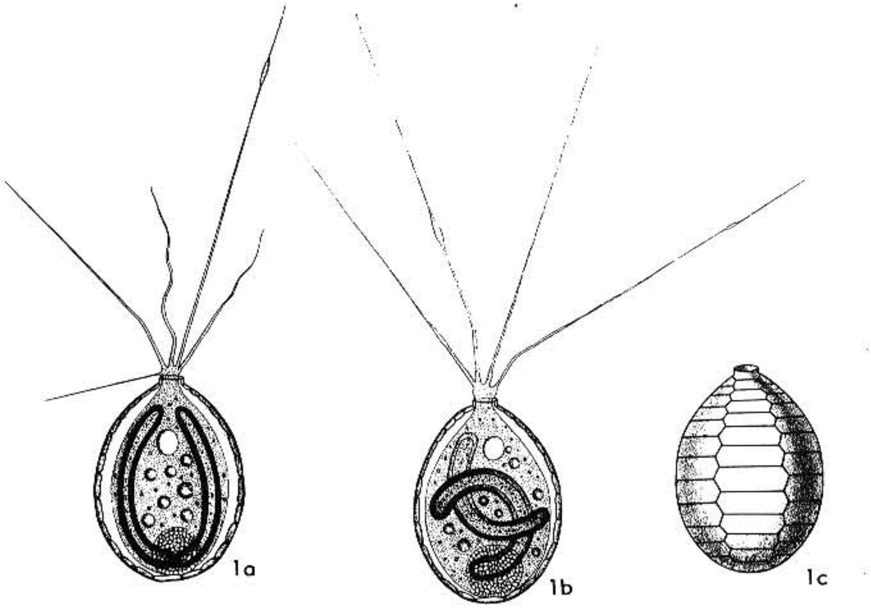


Fig. 32. Paulinellidae; *1, Paulinella* (p. *C*54).

approx. ×600 (*2000).——Fig. 29,*5*. *T. lucida* (Bonnet), Rec., Fr.; side view, ×440 (*169).

Subfamily TRINEMATINAE Hoogenraad & de Groot, 1940

[*nom. correct.* Loeblich & Tappan, herein (*ex* Trineminae (Monostomina) Hoogenraad & de Groot, 1940, p. 24)]

Test with bilateral symmetry and eccentric aperture. *Pleist.-Rec.*

Trinema Dujardin, 1841, *636, p. 249 [**T. acinus,* =*Difflugia enchelys* Ehrenberg, 1838, *668, p. 132; OD(M)] [=*Trinème* Dujardin, 1836, *634b, p. 198 *(nom. neg.)*; *Arcella (Homoeochlamys)* Ehrenberg, 1872, *688, p. 244 (type, *Arcella (Homoeochlamys) enchelys* Ehrenberg, 1838, =*Difflugia enchelys* Ehrenberg, 1838, SD Loeblich & Tappan, herein)]. Test small (length, 20-100μ, av. 50μ), hyaline, elongate ovate, with overlapping circular siliceous plates; aperture circular, lateral at narrowed end of test and somewhat invaginated; protoplasm colorless; nucleus posterior with one or more nucleoli; pseudopodia filose, very narrow, few. [Fresh water.] *Pleist.-Rec.,* Eu.-N.Am.-S.Am.-Australia.——Fig. 30,*1,2*. **T. enchelys* (Ehrenberg), Rec., *1a-c,* living animal, side and edge views of empty tests, USA (N.J.), ×500 (*1127); *2a-c,* portions of test showing different types of scales, Br.I., ×1,000 (*302a).

Corythion Taránek, 1882, *1876, p. 232 [**C. dubium;* OD]. Like *Trinema* but with nonimbricated oval siliceous plates, length of test, 25-65μ. [Fresh water.] *Pleist.-Rec.,* Eu.-S.Am.-N. Am.——Fig. 30,*3,4*. **C. dubium, Rec.,* Czech.; *3,* empty test, ×1,000 (*1876); *4a,b,* side and edge views, ×500 (*1876).

Family CYPHODERIIDAE de Saedeleer, 1934

[*nom. transl.* Jung, 1942a, p. 257 (*ex* tribus Cyphoderini de Saedeleer, 1934, p. 6); family Revolventiidae Rhumbler, 1895a, p. 94, 95 *(nom. nud.)*]

Test elongate, generally recurved near anterior end, composed of very small rounded siliceous scales, aperture simple or with a thin, hyaline, disc-shaped collar. *Rec.*

Cyphoderia Schlumberger, 1845, *1669, p. 255 [**C. margaritacea,* =**Difflugia ampulla* Ehrenberg, 1840, *669, p. 199; OD(M)] [=*Allodictya* Ehrenberg, 1872, *688, p. 247 (type, *Difflugia (Reticella) lagena* Ehrenberg, 1872, =*Difflugia lagena* Ehrenberg, 1843, SD Loeblich & Tappan, herein); =*Ampullaria* Werneck in Ehrenberg, 1872, *688, p. 234 (type, *Difflugia ampulla* Ehrenberg, 1840); =*Schaudinnula* Averintsev, 1906, *60, p. 311 (type, *S. arcelloides*); =*Feuerbornia* Jung, 1942, *1005, p. 257, 326 (type, *F. lobophora*)]. Test flask- or retort-shaped, with curved neck, rounded to triangular in section, 60-190μ in length, commonly about 100μ, with thin pseudochitinous, yellowish to colorless wall covered with cemented siliceous discs or imbricated scales; aperture terminal, oblique, circular in outline; protoplasm granular, grayish, with crystalline inclusions, not completely filling test; nucleus large, posterior; 1 or 2 contractile vacuoles near aperture; pseudopodia few, long, filose,

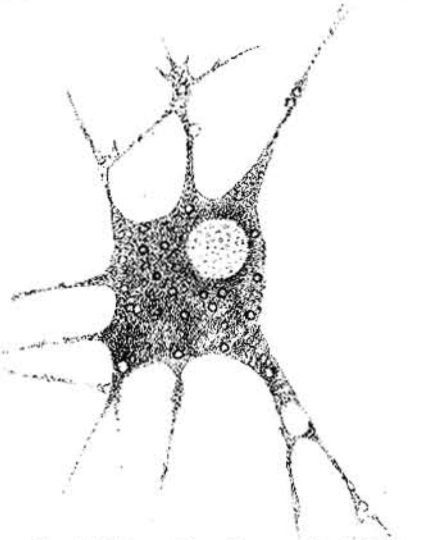


FIG. 33. Biomyxidae; *Biomyxa* (p. C54).

simple, bifurcating. [Fresh water, on sphagnum.] *Rec.*, Eu.-N.Am.-S.Am.——FIG. 31,*1*. **C. ampulla* (EHRENBERG), Ger.; *1a*, living animal showing light-colored nucleus, 2 contractile vacuoles and imbricated plates, ×600 (*1698b); *1b*, specimen with apert. membrane attached to sand grain, ×400 (*1698b). —— FIG. 31,*2*. *C. arcelloides* (AVERINTSEV), USSR; *2a,b*, side and edge views, ×470 (*669); *2c*, detail of surface, enlarged (*669).——FIG. 31,*3*. *C. lobophora* (JUNG), Chile; *3a,b*, side views, *3b* showing protoplasm, nucleus, and scalloped apert. margin, ×470, ×588 (*1005).

Campascus LEIDY, 1877, *1126, p. 294 [**C. cornutus;* OD(M)]. Similar to *Cyphoderia*, but pseudochitinous pellicle covered with amorphous scales lacking uniformity of shape or arrangement (*302a, p. 83) or with scattered sand particles (*1127, p. 205) (length of test, 50-140μ). [Fresh water.] *Rec.*, N.Am.-Eu.——FIG. 31,*4*. **C. cornutus* LEIDY, USA(Utah); *4a-c*, side, edge, and apert. views, ×250 (*1127).

Family PAULINELLIDAE
de Saedeleer, 1934

[*nom. transl.* DEFLANDRE in GRASSÉ, 1953, p. 135 (*ex* Paulinellinae DE SAEDELEER, 1934, p. 6, 31)]

Test symmetrical, composed of very elongate siliceous rectangular plates with rounded margins, arranged in alternating transverse rows, their imbrication resulting in hexagonal appearance; aperture elongate; commonly with symbiotic algae. *Rec.*

Paulinella LAUTERBORN, 1895, *1098, p. 537 [**P. chromatophora;* OD]. Test small (length, 25-42μ), ovate, consisting of curved siliceous plates with rounded ends, in alternating rows; aperture terminal, oval, surrounded by single pentagonal plate which is produced centrally into a necklike rim; protoplasm clear, somewhat bluish; nucleus single, posterior in position; one contractile vacuole toward oral end; in type-species always with 2 horseshoe-shaped symbiotic algae; pseudopodia few, straight, radiating; reproduction by fission. [Fresh water.] *Rec.*, Eu.——FIG. 32,*1*. **P. chromatophora*, Ger.; *1a,b*, living animal showing pseudopodia, nucleus, and symbiotic algae; *1c*, exterior of empty test showing plate arrangement; all approx. ×1,000 (*1098). [The genus *Paulinella*=*Cyanospira* CHODAT, 1920, *337A, p. 298 (type, *C. aeruginosa*).]

Subclass
GRANULORETICULOSIA
de Saedeleer, 1934

[*nom. transl. et correct.* LOEBLICH & TAPPAN, 1961, p. 271 (*ex* order Granuloreticulosa DE SAEDELEER, 1934, p. 7, 50); class Granuloreticulosa DEFLANDRE in GRASSÉ, 1953, p. 139]

Pseudopodia delicate and reticulate; cytoplasm minutely granular. *?Precam., ?Cam., Ord.-Rec.*

Order ATHALAMIDA Haeckel,
1862

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 271 (*pro* order Athalamia HAECKEL, 1862, p. 211)]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}order, ^{2}suborder); dagger(†) indicates *partim*]——[^{1}Homogenea LANKESTER, 1877, p. 442; =^{2}Amoebaea† BÜTSCHLI in BRONN, 1880, p. 176; =^{1}Acystosporés† DELAGE & HÉROUARD, 1896, p. 66 (*nom. neg.*); =^{1}Acystosporidia† DELAGE & HÉROUARD, 1896, p. 66; =^{2}Arnudia RHUMBLER, 1913, p. 339; =^{2}Athalamia DE SAEDELEER, 1934, p. 7, 50]

Lacking test or shell, pseudopodia may arise from any position on surface. *Rec.*

Family BIOMYXIDAE
Loeblich & Tappan, 1961

[Biomyxidae LOEBLICH & TAPPAN, 1961, p. 271; =family Amoebaea reticulosa BÜTSCHLI in BRONN, 1880, p. 178 (*partim; nom. nud.*); =family Reticulosa BLOCHMANN, 1895, p. 14 (*nom. nud.*) (*non* Reticulosa CARPENTER, PARKER & JONES, 1862)]

Cytoplasm granular, without division into ectoplasm and endoplasm. [Only the type genus of this nontestaceous family is discussed.] *Rec.*

Biomyxa LEIDY, 1875, *1124, p. 125 [**B. vagans;* OD(M)]. Naked protistans of variable size and extremely variable form, constantly motile; protoplasm finely granular and colorless, with numerous minute contractile vacuoles and oil globules; nucleus large, distinct; pseudopodial prolongations filamentous, freely branching, anastomosing and reticulose, with pronounced granular streaming throughout body and pseudopodia. *Rec.*, N. Am.——FIG. 33. **B. vagans*, USA(N.J.); specimen on sphagnum, ×250 (*1127).

FORAMINIFERIDA

CONTENTS

GENERAL FEATURES

INTRODUCTION

The next following paragraphs, quoted from the preface to an "Introduction to the Study of Foraminifera" (*281, p. vii-ix), published a century ago, serve well as initial statements chosen for description of these organisms in the present volume.

> The study of the Rhizopod type in general, and of the Foraminifera in particular, has peculiar features of interest to the Physiologist, the Zoologist, and the Geologist. . . . The Physiologist has here a case in which those vital operations which he is accustomed to see carried on by an elaborate apparatus, are performed without any special instruments whatever, a little particle of apparently homogeneous jelly changing itself into a greater variety of forms than the fabled Proteus, laying hold of its food without members, swallowing it without a mouth, digesting it without a stomach, appropriating its nutritious material without absorbent vessels or a circulating system, moving from place to place without muscles, feeling (if it has any power to do so), without nerves, propagating itself without genital apparatus, and not only this, but in many instances forming shelly coverings of a symmetry and complexity not surpassed by those of any testaceous animals.
>
> Again, there are certain peculiarities about the Foraminifera which make this group singularly adapted for that kind of comparison, at once minute and comprehensive, amongst large numbers of individual forms, which should be the basis of all Zoological systematization. . . .
>
> . . . the special feature of interest which this group has for the Geologist [is] that there is strong reason to regard a large proportion of the existing Foraminifera as the direct lineal descendants of those of very ancient geological periods. . . . It may at once be conceded that no other group affords anything like the same evidence, on the one hand of the derivation of a multitude of distinguishable forms from a few primitive types, and on the other of the continuity of those types through a vast succession of geological epochs.

Foraminifers were first recorded in the literature in the 5th century B.C. by Herodotus, who noted the nummulites in the rocks of which the Egyptian pyramids were constructed, but not until nearly 2,000 years later were they recognized as being the fossil remains of organisms. This was by Agricola (1558 A.D.). The smaller foraminifers were first described by Beccarius in 1731, but then, and for the next century, all those described were variously regarded as worms, cephalopods, gastropods, or corals, and many species were described originally as belonging to *Nautilus, Orthocera,* or *Serpula.*

The early foraminiferal literature of the late 18th and early 19th centuries (Batsch, de Blainville, Bosc, Breyn, Broderip, Bruguière, Cuvier, von Fitchel & von Moll, de Haan, Lamarck, Latreille, Montagu, de Montfort, Soldani, Schröter, Walker) is concerned with conchology and refers to Mollusca (Testacea), Cephalopoda, Zoophytes, Radiata (corals), and Vers (worms). Numerous generic, specific, and familial names now recognized for the Foraminiferida actually antedate the general recognition of these organisms as Protozoa, yet many of the generic distinctions were valid and remain so today. Both of the later commonly applied designations for this large group of protozoans were first proposed under the assumption that they were actually cephalopods. The class Polythalamiis BREYN, 1732 (=Polythalamia of many later publications), was originally defined as a new class of the molluscan Testacea (not the later protozoan Testacea or Thecamoebida) and LINNÉ later considered the Polythalamia among the nautiloids. The name Foraminifera also was originally proposed by D'ORBIGNY, 1826, as an order, to separate the Cephalopodes Foraminifères, whose shells merely had openings in the septa, from the Cephalopodes Siphonifères, whose shells had an intercameral siphon.

DUJARDIN first demonstrated the protozoan nature of these organisms in 1835, yet even after acceptance of this relationship was general, some species and even genera now placed in the Foraminiferida were still variously described originally as gastropods, bryozoans, corals, worms, or algae; also others, the true affinities of which lie with these above-mentioned groups or others, were described as foraminifers.

The first large-scale systematic work was that of D'ORBIGNY, 1826, in which 5 families, 52 genera, and 544 species were recognized. Because D'ORBIGNY worked with many fossil-bearing strata, he was strongly impressed with the changes in microfauna throughout geologic time. Since he defined genera and species within narrow limits and cited their geologic occurrence as well, this early taxonomic work also represents the earliest biostratigraphic application of this group of organisms. A relatively large number of D'ORBIGNY'S type-specimens are preserved in the Muséum National d'Histoire Naturelle, Paris, and studies of them by us have attested to the general accuracy and reliability of his observations. With this auspicious beginning, the development of the stratigraphic use of foraminifers closely paralleled the taxonomic studies in Europe.

While the early Continental workers concentrated on stratigraphic application of the Foraminiferida and description of the faunas (e.g., D'ORBIGNY, REUSS, TERQUEM, BERTHELIN) the English workers in general concentrated on morphologic studies and description of Recent faunas (e.g., BRADY, CARTER, WILLIAMSON, HERON-ALLEN, EARLAND). Because of the necessity of using a microscope in their study, many early students of foraminifers were professional physicians, surgeons, and pharmacists, and morphological details were described with great accuracy and illustrated with meticulous care and beauty. In fact, it is difficult to find a "modern innovation" in the technique of study of the Foraminiferida that was not foreshadowed by these early publications—life cycles, wall composition and structure, lamellar character, canal systems, dimorphism, tooth plates, protoplasmic streaming, and other features. Only the interpretations and relative importance of the various factual data have changed. The English laid less importance on the stratigraphic occurrence of foraminifers, however, and allowed a greater range of variability for all taxonomic categories of these "primitive" forms, a tendency existing to this day among English protozoologists who still use the 1884 classification of families proposed in BRADY'S *Challenger* monograph (*993).

In the late 19th century the German protozoologists studied living foraminifers and based their "natural" classifications on the biology of these organisms, as well as on general morphology of the tests (e.g., NEUMAYR, RHUMBLER, EIMER & FICKERT, SCHUBERT) and utilized to varying extent the geologic occurrence and law of recapitulation to determine ancestries and relationships.

Although the stratigraphic and geologic use of foraminifers had been recognized since the time of D'ORBIGNY, economic importance of the group was not recognized until about 1917, when micropaleontology was first applied to exploration for petroleum. This importance has come to be a somewhat mixed blessing. The focus of attention on the group led to a "population explosion" of micropaleontologists and foraminiferologists. Though it supplied an incentive for the study of foraminifers by a great number of excellent and competent workers, it led to an almost overwhelming quantity of publications, with resultant multiplicity of names, repetition of effort, and a tendency in some quarters to regard foraminifers as stratum labels—merely objects of use for identification of geologic age or local beds. This had two unfortunate results. Many of the hastily prepared generic and specific descriptions are almost completely useless, because workers did little more than give names (often improper or incorrect ones) to useful stratigraphic curiosities. They left the task of preparing needed careful morphological descriptions, determining the nature of intraspecific variations, and the like for later revisers who undertake the examination of type specimens, topotypes, and other comparative material. The decline in careful morphological studies was accompanied by a similar decline in quality of illustration. With amazement and chagrin one compares the hand-colored drawings and lithographs of BRADY, CARPENTER, GÜMBEL, VON MÖLLER, and SCHULTZE, and the beautiful photographs of thin sections published by DOUVILLÉ, SCHLUMBERGER, and others of the late 19th century with the caricatures and out-of-focus photographs found in many modern systematic publications. Fortunately, some outstanding modern exceptions do not merit these criticisms.

A second unfortunate aspect of economic interest in the Foraminiferida and the resultant deluge of faunal-stratigraphic literature is its very abundance, which is enough to overwhelm even conscientious specialists. Numerous articles have been published with a provincial outlook and little reference to what had been done previously or was being done on similar faunas elsewhere. The resultant multiplicity of names proposed in different areas for a single organism hampers the very use in correlation which had originally supplied the impetus for studies of the group. A small assemblage of planktonic species from the mid-Cretaceous recently restudied (LOEBLICH & TAPPAN, 1961, *1183) showed, on the basis of topotypes and comparison of original types, that for 60 specific names proposed, 27 were valid, the remainder synonyms, and during the year or so the article was in press before publication, another half dozen articles appeared describing additional "species" of these stratigraphically important forms.

Probably in large part because of their geologic application, the great majority of current publications on foraminifers, whether taxonomic, morphologic, or stratigraphic, are written by paleontologists rather than zoologists. The protozoologists have more and more concerned themselves with the fresh-water and parasitic protozoans and their biochemical, physiological, and ecological nature, and less and less interested themselves in the Foraminiferida, or, indeed, in protozoan taxonomy generally. This is well illustrated by contrasting the articles on foraminifers given in the 9th edition of the Encyclopaedia Britannica (1879) with those of three-quarters of a century later. In 1879 CARPENTER's coverage of the assemblage occupied 17 double-columned quarto pages, which contained detailed discussion of their taxonomy, morphology, and living habits as known to that date (before the appearance of the monumental *Challenger* volume of BRADY in 1884). In 1956, despite the great quantity of information supplied by an average of 500 articles annually on foraminifers, the enlarged Encyclopaedia Britannica devoted less than four pages to these animals, and about one-half of that was concerned with their role in historical and petroleum geology!

The stress on stratigraphic application of foraminifers is unfortunate. Because most paleontologists have geological rather than biological training, not only have they been lax at times in adhering to the rules of nomenclature but they have seemed to disregard the zoological meaning of binary nomenclature. Clearly, some have had scant recognition of the zoologists' concept of species. Numerous specimens have been named as representatives of a new species when obviously they have been selected from a variable population; commonly the selected specimens are growth stages of a single form, isolated from a single sample of rock or dredged from the sea floor. Similarly, some species or genera have been regarded as ancestral to others which actually appeared earlier in the geologic record than the supposed ancestor. Biological information has not been greatly utilized in classification and too little experimental work or life studies have been made on foraminifers. Although thousands of species and genera are named, the complete life history of but a handful is known. It is only in recent years that paleontologists have begun to realize the importance of more information about the living animals, their present-day ecology, and the factors controlling their distribution. More emphasis is again being placed on their biology and detailed morphology, instead of their geologic occurrence only, and many of the promising lines of research hinted at by Carpenter, Lankester, Brady and others are now being realized.

It is hoped that the present volume summarizes the state of present knowledge on the Foraminiferida, and if many facts of seeming unimportance are included, it is because we firmly believe that advances in the future may be in directions or along lines scarcely glimpsed today, but which may nevertheless be suggested by the work of some earlier investigator.

MORPHOLOGY AND BIOLOGY

TERMINOLOGY

At the outset of discussions of morphological and biological aspects of the Foraminiferida, it is desirable to introduce the rather numerous terms which have come to be employed in studies of these protistans. For this purpose a glossary of the terms, alphabetically arranged, is inserted here.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO FORAMINIFERIDA

aboral. Opposite to oral side or end.

A_1 generation. Plurinucleate megalospheric forms.

A_2 generation. Uninucleate megalospheric forms.

acanthus (pl., **acanthi**). Secondary deposit in endothyrid chamber floor, sharply pointed but not curved toward anterior.

accessory apertures. Test openings that do not lead directly into primary chambers but extend beneath or through accessory structures (e.g., bullae, tegilla), found in planktonic foraminifers.

acervuline. Chambers in irregular clusters (e.g., *Acervulina*).

adventitious. Formed of foreign particles (e.g., in agglutinated test).

agglutinated. Foreign particles bound together by cement.

alar projection. Winglike extension of test.

alveolus (pl., **alveoli**). Minute blind cavity in shell wall (e.g., in keriotheca of some fusulinids) or blind chamberlet opening only toward back, opposite to direction of coiling (e.g., Alveolinidae).

alveolar. Having numerous honeycomb-like small cavities (e.g., Fusulinacea).

amoeboid. Having form of *Amoeba,* with lobopodia.

annular. Cyclical or ringlike.

annulus (pl., **annuli**). Ring or circle of chambers.

anterior. Direction toward aperture.

antetheca. Final septal face in fusulinaceans.

aperture. Opening or openings from chamber of test to exterior.

arborescent. Branching in treelike manner.

areal aperture. Aperture in face of final chamber of test.

areal bulla (pl., **bullae**). Blister-like structure covering multiple areal apertures (e.g., *Globigerinatella*).

arenaceous. Composed of sand or other foreign particles (e.g., in some agglutinated tests).

areolate. Divided into small spaces on larger surface.

argillaceous. Composed of clay or mud (e.g., in some agglutinated tests).

attic. Very small, uppermost (abaxial) chamberlet in superposed chamberlets of a shell volution (e.g., *Flosculinella, Alveolinella*).

autogamy. Fertilization of gametes from same parent.

axial fillings. Deposits of dense calcite, developed in axial regions of some fusulinaceans, formed probably at same time as excavation of tunnel or foramina and formation of chomata and parachomata.

axial section. Slice bisecting test in plane coinciding with axis of coiling and intersecting proloculus (e.g., fusulinaceans, alveolinids, nummulitids).

axial septulum (pl., **septula**). Secondary or tertiary septum located between primary septa (e.g., Verbeekinidae), its plane approximately parallel to axis of coiling, and thus observable in sagittal (equatorial), parallel, and tangential sections; includes primary axial septula and secondary axial septula.

axis. Imaginary line around which spiral or cyclical shell is coiled, transverse to plane of coiling.

axostyle. Internal extension from blepharoplast to extremity in gametes of Miliolacea.

B-form. Microspheric form.

basal layer. Varyingly thick, comparatively uniform deposit of shell substance in adaxial part of test volution, adherent to abaxial wall (roof) of preceding volution (e.g., Alveolinidae).

biconvex. Having both sides convex or more or less inflated.

bifid. Divided into 2 branches.

biforaminate. Having both protoforamen (primary aperture) and deuteroforamen (secondary aperture) (e.g., *Discorbis*).

biformed. Proposed by Lister as substitute for *dimorphic,* referring to shells with growth plan that changes during ontogeny.

bilamellar. Walls of each chamber consisting of 2 primarily formed layers.

biloculine. Shaped like *Pyrgo* ("*Biloculina*"), with 2-chambered exterior part of test.

biserial. Having chambers arranged in 2 rows.

biumbilicate. Having central depression (umbilicus) on each side of test (e.g., planispiral forms).

biumbonate. Having 2 raised umbonal bosses (e.g., *Lenticulina*).

blepharoplast. Small compact granule, in which flagella are inserted (in flagellate gametes of foraminifers).

boss. Round and raised or knoblike ornamental structure.

buccal aperture. Tunnel opening between chambers of fusulinids; foramen.

buccal apparatus. Oral or apertural structure (e.g., *Gromia, Allogromia*).

bulla (pl., **bullae**). Blister-like structure that partially or completely covers primary or secondary apertures, not closely related to primary chambers; may be umbilical, sutural, or areal in position and may have one or more accessory marginal apertures (in planktonic foraminifers).

"calcite eyes." Rounded bodies of clear calcite occurring sporadically in radial zone and central area of Orbitolinidae.

cameral aperture. Opening of chamber.

canaliculate. Possessing series of fine tubular cavities.

cancellate. Having honeycomb-like surface.

carina. Keel or flange.

carinal band. Imperforate marginal area (poreless margin) between keels of test (e.g., Globotruncanidae).

cellules. Subdivision of marginal chamberlets in outer part of marginal zone, formed by primary and secondary partitions (e.g., Orbitolinidae).

central complex. Core or central zone in which chamber passages bifurcate and anastomose in reticulate pattern (e.g., Orbitolinidae).

central section. Slice bisecting central chambers of test.

chamber. Test cavity and its surrounding wall, formed at single short growth stage in multilocular forms; variously shaped inclosure within test that invariably is connected by pores, intercameral foramina, or other passages leading to similar inclosures or to exterior.

chamber passages. Radial corridors consisting of centrally directed extensions of marginal chamberlets (e.g., Orbitolinidae).

chamberlet. Subdivision of chamber produced by axial or transverse septula.

chitin. Horny substance occurring in some invertebrates (e.g., arthropods), erroneously reported in foraminifers.

choma (pl., **chomata**). Revolving ridgelike deposit of dense shell substance delimiting tunnel (e.g., Fusulinidae).

chromidia. Extranuclear chromatin granules, scattered throughout cytoplasm or clustered around nucleus.

clavate. Club-shaped, inflated terminally.

convolute. Evolute, enrolled, referring to test with all whorls visible.

cornuspirine. Having tubelike planispirally coiled test (e.g., *Cyclogyra*="*Cornuspira*").

costa. Raised ridge or rib.

costate. Having raised ridges or costae.

cribrate. Perforated with round holes, sievelike.

cuniculus (pl., **cuniculi**). Tunnel-like continuous cavity formed by strong septal fluting, opposed folds of adjacent septa meeting to form continuous spiral sutures with vaulted arches between, serving to connect adjoining chambers from one foramen to next (e.g., Verbeekinidae).

cyclogyrine. Having tubelike planispirally coiled test (e.g., *Cyclogyra*).

cyclomorphosis. Changes in form during life cycle (ontogeny).

cyst. Resistant cover over entire foraminifer, commonly formed of agglutinated debris, for protection during chamber formation or asexual reproduction, or may enclose 2 or more individuals in plastogamic sexual reproduction (first reported by Brady in *Cibicides*, but common to many other forms).

cytoplasm. Protoplasm, exclusive of nucleus, rich in proteids (albumen), poor in phosphorus.

dendritic. Branched, treelike.

deuteroconch. Chamber immediately adjoining proloculus and formed next after it.

deuteroforamen. Aperture independent of tooth plate in some enrolled foraminifers.

deuteropore. Groups of protopores fusing into single larger pore cavity in outer wall.

diagonal section. Slice cutting axis of coiling obliquely.

diaphanotheca. Relatively thick, light-colored to transparent layer of spirothecal wall next below tectum in fusulinid foraminifers.

dimorphism. Occurrence in single species of 2 distinct forms; megalospheric and microspheric tests (gamont and schizont generations).

diploid. Stage in life history in which nuclei contain full number of chromosomes, gamont generation in foraminifers containing half of this number and fusion of gametes to form zygote restoring diploid stage of schizont generation.

distal. Direction away from proloculus in direction of growth.

dorsal. Opposite to ventral side; spiral side of trochoid forms.

ectoparasitic. Externally parasitic.

ectoplasm. Outer zone of protoplasm, hyaline and homogeneous.

ectosolenian. Having external tubelike neck (e.g., *Lagena*).

embryonic apparatus. Group of chambers at center of some megalospheric tests, larger in size and different in shape and arrangement from other chambers; nucleoconch.

endoplasm. Central part of cytoplasmic mass, commonly granulated.

entosolenian. Having internal tubelike apertural extension (e.g., *Oolina*).

ephebic. Pertaining to adult stage in ontogeny.

epidermal layer. Imperforate outer layer, commonly present in Lituolidae.

epitheca. Secondary deposit in inner wall of some fusulinids; tectorium.

equatorial. Located in median plane normal to axis of coiling.

equatorial aperture. Symmetrical opening of planispiral test, commonly interiomarginal but may be areal or peripheral.

equatorial section. Slice of test in equatorial plane (sagittal section).

equitant. Inverted V-shaped.

evolute. Tending to uncoil; chambers nonembracing.

exogenous. Added to outside.

external furrow. Linear depression on outer surface of test where wall bends downward (adaxially) into septum; coincides in position with septal suture (e.g., Fusulinidae, Alveolinidae) (syn., septal furrow).

extraumbilical aperture. Opening in final chamber of test not connecting with umbilicus, commonly sutural midway between umbilicus and periphery.

extraumbilical-umbilical aperture. Opening in final chamber of test that extends along its forward margin from umbilicus toward periphery, thus reaching extraumbilical point (outside umbilicus) (e.g., *Globorotalia*).

filamentous. Threadlike, composed of filaments.

filose. Threadlike.

fimbriate. Having fringed appearance.

fissure. Deep cleft, as in test of *Fissurina.*

fistulose. Having tubular irregular growth in apertural region (common in polymorphinids).

flabelliform. Shaped like fan.

flagellum (pl., **flagella**). Whiplike structure, used in locomotion in Mastigophora and found in gametes of some foraminifers; gametes either biflagellate or triflagellate.

flange. Platelike marginal extension along chambers (e.g., *Sphaeroidinella*) or bordering aperture as highly developed apertural lip (e.g., *Hantkenina*).

flexostyle. Tubular enrolled chamber of test immediately following proloculus (e.g., *Amphisorus* and other Miliolacea).

floor. Bottom wall of superposed chamberlet (e.g., Alveolinidae).

fluting. *See* septal fluting.

foramen (pl., **foramina**). Opening between chambers located at base of septa (e.g., Fusulinidae) or areal in position; in various foraminifers may represent previous aperture or be formed secondarily (not equivalent to pore of perforate test (*see* perforate).

fossettes. Grooves paralleling periphery (e.g., on surface of *Elphidium* tests).

fusiform. Spindle-shaped, tapering at each end.

gamete. Reproductive cell with haploid chromosome number, capable of fusing in pairs to form new individual (zygote); observed in foraminifers are amoeboid gametes, biflagellate gametes, and triflagellate gametes, each characteristic of distinct groups of genera or families.

gamont. Generation which forms gametes in sexual reproduction, commonly with megalospheric test (A-forms).

gerontic. Senile stage in ontogeny.

glomospirine. Having irregularly wound coiled tubular chamber (e.g., *Glomospira*).

granular hyaline wall. Perforate, lamellar part of test composed of minutely granular calcite, seen between crossed nicols as multitude of tiny flecks of color; granules equidimensional, variously oriented.

granuloreticulose pseudopodia. Bifurcating and anastomosing extensions of protoplasm with relatively solid axis (stereoplasm) and granular fluid outer portion (rheoplasm) with granules in continuous movement; may digest food outside main body of animal.

hamulus (pl., **hamuli**). Hook-shaped secondary deposit on chamber floor in endothyrids, point of hook directed toward aperture of test.

haploid. Stage in life history in which nuclei have one-half normal number of chromosomes; resulting from reduction division in nucleus, may be temporary (only in gametes) or represent a distinct generation (in foraminifers).

hemisepta. Partial septa between normal ones and subdividing chambers (e.g., some Lituolacea).

heterokaryotic. Having nuclei of differing types (e.g., vegetative and reproductive).

hispid. Covered with fine, short hairlike spines.

hologamic. Having biflagellate gametes, all similar, emitted by isolated parents, not associated in pairs (plastogamy) or groups (syzygy); gametes may be free-living for many days before fusing to produce zygotes.

hyaline. Glassy clear, transparent.

hypodermis. Reticulate layer beneath outer imperforate layer in wall of some Lituolacea (e.g., *Cyclammina*).

imperforate. Without pores, sometimes used for porcelaneous tests (e.g., Miliolacea), and in describing ornamentation (e.g., pillars, keels, carinal band) of normally perforate forms.

infralaminal accessory aperture. Opening in planktonic foraminiferal test leading to cavity beneath accessory structures (bullae, tegilla), and at margin of these structures (e.g., *Catapsydrax*).

inframarginal sulcus. Deep indentation of apertural face of test (e.g., *Alabamina*); infundibulum; *scrobis septalis.*

infundibulum. Deep indentation of *scrobis septalis* or basal indentation of apertural face of test (e.g., *Alabamina*); inframarginal sulcus.

instar. Single episode of shell formation, commonly of single chamber.

intercameral. Located between chambers.

intercameral foramen. Opening between successive chambers, may be secondarily formed or represent earlier aperture.

interio-areal aperture. Opening in chamber face, not at its base; areal.

interiomarginal aperture. Basal opening in test at margin of final chamber, along final suture; in coiled forms may be umbilical, extraumbilical, or equatorial in position.

interseptal. Located between septa.

intralaminal accessory aperture. Opening in planktonic foraminiferal test leading through accessory structures (bullae, tegilla) into cavity beneath them, not directly into chamber cavity (e.g., *Rugoglobigerina*).

intraseptal. Located within septum (e.g., canal system).

intraumbilical aperture. Opening of test located in umbilicus but not extending outside of it.

involute. Strongly overlapping; in enrolled forms, later whorls completely enclosing earlier ones.

isogamy. Conjugation of two morphologically similar gametes to form zygote in sexual reproduction.

isogenotypic. Generic names proposed for same type-species; thus synonymous.

juvenarium. Proloculus and first few chambers of foraminifer; embryonic apparatus.

keriotheca. Relatively thick shell layer with honeycomb-like structure in wall of some fusulinids, occurring next below tectum and forming part of spirotheca (e.g., *Triticites*); may be divisible into lower and upper keriothecal layers.

labial aperture. Opening formed by free parts of apertural lip, not directly opening to chamber of test; accessory aperture.

labyrinthic. Having complex spongy wall with interlaced dendritic channels perpendicular to surface, characteristic of some agglutinated foraminifers; alveolar, vacuolar, vesicular.

lamellar. Composed of thin platelike layers of aragonite or calcite, one layer being formed with addition of each new chamber and covering whole previously formed test.

lanceolate. Flat, narrow, and tapering to point.

lenticuline. Lens-shaped, similar in form to *Lenticulina.*

limbate. Referring to thickened border or edge of chamber, commonly at suture, may also be elevated.

lip. Elevated border of aperture, may be small and at one side of aperture or completely surround it.

lobopodia. Pseudopodia with rounded termination, containing both ectoplasm and endoplasm, used for locomotion in Lobosia and found in gametes of some foraminifers (e.g., Spirillinidae).

loculus. Chamber.

lower keriotheca. Adaxial (lower) part of keriotheca characterized by coarse alveolar structure (e.g., *Schwagerina*).

lower tectorium. Adaxial secondary layer of spirotheca next below diaphanotheca or tectum (e.g., *Profusulinella*).

main partitions. Radial walls of test extending from marginal zone toward center of chamber and may be simple transverse septa (e.g., Orbitolinidae).

marginal chamberlets. Simple subdivisions of primary chambers in marginal zone of chamber, formed by main partitions only (e.g., Orbitolinidae).

marginal cord. Thick spiral structure beneath surface at periphery of test (e.g., Nummulitidae).

marginal zone. Peripheral portion of chambers, where chamberlets are subdivided by primary and secondary partitions (e.g., Orbitolinidae).

meandrine. Tortuous, winding, meandriform.

median section. Slice in central sagittal position, perpendicular to axis of coiling.

megalospheric. Having large proloculus, commonly representing gamont generation, adult test smaller than agamont.

microgranular. Microscopically granulose, referring to wall composed of minute calcite crystals (e.g., Parathuramminacea, Endothyracea), probably originally granular but possibly recrystallized; granules may be aligned in rows perpendicular to outer wall, resulting in fibrous structure.

microsomes. Fine refringent, colorless, slightly elongate granules in central area of cytoplasm; slightly tinted gray by ferric hematoxyline and brown-violet by feulgen (e.g., *Cibicides, Peneroplis, Planorbulina, Elphidium*).

microspheric. Having small proloculus, commonly agamont (schizont) generation, adult test large.

milioline. Formed as in Miliolacea, commonly with narrow elongate chambers, two to whorl, added in differing planes of coiling.

mitosis. Nuclear division in which each resultant half contains same number of chromosomes as parent nucleus; characteristic of asexual reproduction, fission, schizogony.

monolamellid. Referring to lamellar hyaline tests with single-layered septa and wall of last-formed chamber.

multilocular. Many-chambered test of unicellular organism.

multiple tunnels. Series of openings in test chamber produced by resorption of lower (adaxial) parts of septa.

murus reflectus. Sutural indentation of apertural face of test, longitudinally and obliquely folded below aperture (e.g., *Osangularia*).

neanic. Youthful stage in ontogeny.

nepionic. Stage immediately after embryonic stage in ontogeny.

nucleoconch. *See* embryonic apparatus.

nucleolus. Small spherical body within nucleus, which has characteristic reaction to some stains.

nucleus. More or less spherical, compact mass of chromatin surrounded by membrane, lying within cytoplasmic body and having important part in development and functions of cell (e.g., digestion, test secretion); single cell may have one nucleus or many.

oblique section. Slice through test cut in direction neither parallel to axis of coiling nor normal to it.

orifice. Aperture or other opening in test.

palmate. Flat, resembling hand with outspread fingers.

parachomata. Ridges of dense calcite developed between adjacent foramina in tests having multiple foramina, developed in some fusulinaceans (e.g., Verbeekinidae, Neoschwagerininae).

parallel section. Slice through test in plane normal to axis of coiling but not through proloculus.

peneropline. Having form of *Peneroplis.*

perforate. Punctured, referring to walls of test pierced by numerous pores that are distinct from apertures, foramina, and canals; characteristic of calcareous hyaline tests, although some others may exhibit it.

periembryonic chambers. Nepionic parts of test formed on ventral side partially surrounding proloculus (e.g., Orbitolinidae).

peristome. Raised rim around aperture of test.

phialine. Having everted rim on apertural neck, as on neck of vial or bottle.

phrenothecae. Thin, dense, diaphragm-like partitions that extend across chambers of test at various angles and in various parts of chamber (e.g., *Pseudofusulina*).

planispiral. Coiled in single plane.

plastogamy. Fusion of adults by umbilical surface at time of sexual reproduction, ensuring fertilization of gametes.

plectogyral. Coiling in different planes; streptospiral.

plicate. Having folds, ribs, or ridges.

podostyle. Pseudopodial trunk that comprises mass of cytoplasm projecting from aperture of monothalamous foraminifers for giving rise to pseudopodia.

polymorphine. Similar in shape to *Polymorphina.*

polymorphism. Morphologically different forms of same species which may be result of different generations.

polythalamous. Composed of numerous chambers.

polyvalent individuals. Vegetative association, accidental, and probably due to crowding, results in specimens with two or more embryonal apparatuses always of same generation (micro- or megalospheric) and of approximately same age; not related to plastogamy.

porcelaneous. Having calcareous, white, shiny, and commonly imperforate wall resembling porcelain in surface appearance; shows low polarization tints between crossed nicols and has majority of crystals with *c*-axes tangential, or more rarely arranged radially; commonly brown in transmitted light.

pore plug. Minute, single, organic, microporous plates lying at base of external pores in certain foraminifers.

porticus (pl., **portici**). Distinctly asymmetrical apertural flaps, originally defined as being imperforate (e.g., *Ticinella, Praeglobotruncana*).

postseptal passage. Opening that interconnects all chamberlets of same chamber, located between wall and septum at back of chamber (e.g., Alveolinidae).

preseptal passage. Opening that interconnects all chamberlets of same chamber, located in anterior part of chamber (e.g., Alveolinidae).

primary aperture. Main opening of test, may be only one or accompanied by secondary (accessory) apertures (protoforamen of Hofker).

primary axial septulum (pl., **septula**). Major partition of chamberlet with plane approximately parallel to axis of coiling, seen in sagittal sections (e.g., *Lepidolina, Yabeina*).

primary septulum (pl., **septula**). Major partition of chamberlet; includes primary axial and primary transverse septula (e.g., Neoschwagerininae).

primary transverse septulum (pl., **septula**). Major partition of chamberlet with plane approximately normal to axis of coiling, seen in axial sections (e.g., *Lepidolina, Yabeina*).

proloculus (pl., **proluculi**). Initial chamber of foraminiferal test.

proloculus pore. Single circular opening in proloculus leading to next-formed chamber of test (e.g., Fusulinidae).

protheca. Primary elements of fusulinid wall, comprising diaphanotheca and tectum.

protoforamen. Opening of test associated with fully developed or rudimentary tooth plate.

protoplasm. Living matter comprising body of protozoan, as well as cells of other organisms; consists of cytoplasm and nucleus.

protoplast. Protoplasmic body.

protopore. Single fine opening which is rounded at least on inner wall; perforation.

proximal. Nearer to proloculus in direction of growth.

pseudocarina. Perforate, ridgelike thickening of peripheral part of chamber wall, approximately in plane of coiling.

pseudochambers. Partially subdivided test cavity, indicated by slight protuberances or incipient septa (e.g., Tournayellidae).

pseudochitin. Chitin-like proteinaceous material which comprises some protozoan tests, similar to keratin in containing sulfur but including inframicroscopic granules of opaline silica.

pseudopodia. Temporary or semipermanent cytoplasmic projections serving for locomotion, attachment, and capture of food; in foraminifers have form of reticulopodia.

pseudopodial trunk. Podostyle, comprising mass of cytoplasm that projects from aperture, giving rise to pseudopodia, present in monothalamous forms only.

pseudoumbilicus. Wide or narrow, deep depression between inner umbilical chamber walls, where sharply angled umbilical shoulder occurs (e.g., in *Globorotalites*).

pycnotheca. Dense layer of wall penetrated by septal pores, wedged between tectum and keriotheca of septal face (antetheca) of some fusulinids (e.g., Schwagerininae).

quinqueloculine. Having five externally visible chambers as result of growth in varying planes about elongate axis (e.g., *Quinqueloculina*).

radial. Direction from pole or axis to any part of circumference of test (e.g., radial septa).

radial microstructure. Construction of calcareous tests consisting of calcite or aragonite crystals with *c*-axes perpendicular to surface; between crossed nicols shows black cross with concentric rings of color mimicking negative uniaxial interference figure.

radial zone. Chamber portion between marginal zone and central complex of test with essentially radial elements (e.g., Orbitolinidae).

radiate aperture. Opening associated with numerous diverging slits (e.g., Nodosariacea).

rectilinear. Growing in a straight line.

relict apertures. Short radial slits around umbilicus of test which remain open when umbilical portions of equatorial aperture are not covered by succeeding chambers (e.g., Planomalinidae); even when secondarily closed, elevated apertural lips or flanges remain visible around umbilicus (e.g., *Planomalina, Hastigerinoides*).

reniform. Kidney-shaped.

reticulate. Like network, referring to ornamental ridges at surface of test or inner meshwork (e.g., *Cyclammina*).

retral processes. Backward-pointing extensions of chamber cavity and enclosed protoplasm, located beneath external ridges on chamber wall and ending blindly at chamber margins (e.g., *Elphidium*).

rhizopodia. Bifurcating and anastomosing pseudopodia.

rugose surface. Rough irregular ornamentation, may form ridges (e.g., *Rugoglobigerina*).

sagittal section. Slice through test perpendicular to axis of coiling and passing through proloculus (equivalent to equatorial section).

sarcode. Protoplasm of protozoan.

schizogamy. Formation of embryos asexually by division of plurinucleate schizont; same as schizogony, agamogony.

schizont. Generation which divides asexually to form embryos; commonly with microspheric test (B-form); agamont.

scrobis septalis. Inframarginal asymmetrical indentation or concave surface of apertural face of test, may be deep (e.g., *Alabamina*); infundibulum, inframarginal sulcus.

secondary apertures. Additional or supplementary openings into main chamber cavity, may be areal, sutural, or peripheral in position.

secondary axial septulum (pl., **septula**). Minor partition of chamberlet reaching short distance downward (adaxially) from spirotheca, with plane approximately parallel to axis of coiling, located between primary axial septula (e.g., Neoschwagerininae).

secondary septulum (pl. **septula**). Minor partition of chamberlet reaching downward (adaxially) from spirotheca (e.g., Neoschwagerininae).

secondary transverse septulum (pl., **septula**). Minor partition of chamberlet with plane approximately normal to axis of coiling (e.g., Neoschwagerininae).

septal flap. Extension of each lamella in Rotaliacea, formed on inner side of chamber over distal face of previous chamber, resulting in secondarily doubled septa.

septal fluting. Folding or corrugation of septum (and antetheca) transverse to axis of coiling, generally strongest in lower (adaxial) part of septum and toward poles.

septal foramen. Intercameral opening, may be homologous with aperture or secondarily formed.

septal furrow. Same as external furrow.

septal pore. Small perforation in septum (and antetheca) in fusulinids.

septulum (pl., **septula**). Ridge extending downward adaxially, from lower surface of spirotheca so as to divide chambers partially (e.g., Neoschwagerininae).

septum. Partition between chambers, commonly consisting of previous outer wall or apertural face, may have single layer (monolamellid), be secondarily doubled enclosing canal systems (e.g., rotalids), or be primarily double (bilamellid).

sessile. Attached, sedentary.

sieve-plate. (1) Minute discoidal plate with numerous circular, triangular, and polygonal micropores arranged in concentric rows, contained in pore canal of certain foraminifers. (2) Equivalent to trematophore.

sigmoid. S-shaped.

sigmoiline. Sigmoid or with sigmoid axis (e.g., *Sigmoilina*).

siphon. Internal tube extending inward from aperture, entosolenian (e.g., *Oolina*).

somatic nucleus. Vegetative nucleus not taking part in reproduction, found in heterokaryotic foraminifers.

spinose. Having fine elongate solid spines on surface of test (e.g., *Hastigerinella*), each spine comprising single calcite crystal, elongated along *c*-axis.

spiral canals. Part of canal system in umbilical region, parallel and inside lateral chamber margins (e.g., *Elphidium*).

spiral side. Part of test where all whorls are visible (e.g., trochospiral forms), also commonly called dorsal side.

spirilline. Comprising planispiral nonseptate tube enrolled about globular proloculus (e.g., *Spirillina*).

spirotheca. Outer or upper wall of test in fusulinaceans.

spiroumbilical. Interiomarginal aperture extending from umbilicus to periphery and finally onto spiral side.

stercomata. Brown oval masses of debris within cytoplasm; fecal pellets.

stereoplasm. Axis of granuloreticulose pseudopodia, relatively solid, surrounded by granular rheoplasm; noted in *Peneroplis, Elphidium,* not visible in most agglutinated types.

stolon. Prolonged extension of body, commonly tubelike projections connecting chambers in orbitoids.

stomostyle. Thickened outer membrane invaginated in cytoplasm of apertural region from which pseudopodial trunk emerges.

streptospiral. Coiled like ball of twine.

striate. Marked by parallel grooves or lines.

subseptate. Having slight protuberances or incipient septa that form pseudochambers (e.g., Tournayellidae).

supplementary apertures. Secondary openings in test which may be additional to primary aperture and thus independent of it; in some forms may completely replace primary aperture.

supplementary multiple areal apertures. Subordinate openings in tests, may have primary equatorial aperture associated with supplementary areal apertures which are thus shown to be secondary (e.g., *Cribrohantkenina*).

supraembryonic area. Circular apical area over megalospheric proloculus in some orbitolinids; central boss mamilla.

sutural supplementary apertures. Relatively small sutural openings, which may be single or one per suture (e.g., *Rotalipora*), or multiple, with many openings along the sutures (e.g., *Candeina*); may be restricted to spiral side (e.g., *Truncorotaloides*), restricted to umbilical side (e.g., *Rotalipora*), or present on both sides (e.g., *Candeina*).

suture. Line of union between two chambers or between two whorls (spiral suture).

symbiosis. Life association mutually beneficial to both organisms; commonly refers to green or blue green algae or yellow cryptomonads symbiotic with some foraminifers (*Globigerina* has symbiotic zooxanthellae).

syzygy. Association of two or more gamonts in common reproductive cyst for emission and fusion of gametes.

tangential section. Slice through part of test parallel to axis of coiling or growth but not through proloculus.

tectine. Albuminoid organic substance having appearance of chitin but distinct chemically.

tectorium (pl., tectoria). Internal lining of chamber, composed of dense calcite formed at or near same time as that in which tunnel in test is excavated (e.g., Fusulininae); may include lower and upper tectoria.

tectum. (1) Thin, dense outer layer of spirotheca (e.g., Fusulinacea). (2) Marginal prolongation of chamber in trochospirally coiled tests making sutures of spiral side more inclined than on umbilical side (so used by BROTZEN, but because of prior adoption for fusulinids, should not be used in this sense).

tegillum (pl., **tegilla**). Umbilical coverings in planktonic foraminiferal tests comprising extensions from chambers comparable to a highly developed apertural lip but extending across umbilicus, thus completely covering primary aperture, attached at their farther margin or at tegilla of earlier chambers (e.g., *Globotruncana, Rugoglobigerina*); may have small openings along their margins or be pierced centrally, communicating with primary umbilical apertures and umbilical area.

test. Shell or skeletal covering, may be secreted, gelatinous, chitinous, calcareous or siliceous, composed of platelets, solid walls, agglutinated foreign particles, or combination of two or more of these.

tooth. Projection in aperture of test, may be simple or complex, single or multiple.

tooth plate. Internal, apertural modification commonly consisting of contorted plate that extends from aperture through chamber to previous septal foramen (e.g., Buliminidae); one side may be attached to chamber wall or base attached to proximal border of foramen, opposite side being free and folded. [Many internal features have been regarded as homologous and interpreted as modified tooth plates by HOFKER.]

transverse septulum (pl., **septula**). Minor partitions of chambers oriented transverse to axis of coiling, seen in sagittal and parallel sections (e.g., Verbeekinidae).

trematophore. Perforated plate over aperture of some miliolids, sometimes referred to as sieve-plate.

triloculine. Having three externally visible chambers, resembling *Triloculina* in form and chamber plan.

trimorphism. Defined to indicate that some megalospheric forms were plurinucleate and reproduced asexually (as schizonts); originally thought to be represented by three forms in all species (schizont, uninucleate "gamont," plurinucleate "gamont," respectively indicated as B, A_1 and A_2 generations) but this has never been demonstrated in cultures.

triserial. Chambers arranged in three columns, high trochospiral with three chambers in each whorl.

trochoid. Trochospiral, rotaloid, rotaliform; chambers coiled spirally, evolute on one side, involute on other.

trochospiral. Trochoid, rotaliform; spirally coiled chambers, evolute on one side of test, involute on opposite side.

tuberculate. Covered with tubercles or small rounded prominences.

tubulospine. Chamber produced radially into long hollow extension (e.g., *Schackoina*).

tumulus (pl., **tumuli**). Secondary deposit on chamber floor appearing in cross section as more or less symmetrical node with rounded summit (e.g., endothyrids).

tunnel. Resorbed area at base of septa in central part of test in many fusulinids, facilitating communication between adjacent chambers.

umbilical depression. Closed, shallow, axial depressed area formed by curvature of overlapping chamber walls in involute spire; may be filled by thickenings or knob.

umbilical side. Involute side in trochospiral forms, with only chambers of final whorl visible around umbilicus; also called ventral side; commonly with aperture.

umbilical teeth. Triangular modification of apertural lip, those of successive chambers in forms with umbilical aperture giving characteristic serrate border to umbilicus (e.g., *Globoquadrina*).

umbilicate. Having one or more umbilici.

umbilicus (pl., **umbilici**). Space formed between inner margins of umbilical walls of chambers belonging to same whorl; may be restricted by apertural lips or prolongations of chamber margins or by pillars or plugs.

umbo. Central round, elevated structure in discoidal forms; commonly due to lamellar thickening (e.g., *Lenticulina*), may occur on one or both sides of test.

umbonate. Having umbo, on one or both sides (biumbonate).

unilocular. Monothalamous, single-chambered.

uniserial. Having chambers arranged in a single row.

upper keriotheca. Abaxial (upper) part of keriotheca characterized by fine alveolar structure (e.g., *Schwagerina*).

upper tectorium. Abaxial secondary layer of spirotheca next above tectum (e.g., *Profusulinella*).

vacuole. (1) Globular inclusion in cytoplasm; includes contractile vacuoles, food vacuoles. (2) Cavities, especially irregularly shaped ones, in test wall.

ventral. Pertaining to inferior side of test, commonly used for umbilical side; opposite to dorsal; commonly apertural side.

vitreous. Hyaline, having appearance and luster of glass.

whorl. Single turn or volution of coiled test (through 360 degrees).

xanthosome. Small refringent, brown or yellowish, globular inclusions in cytoplasm, commonly very numerous, possibly products of excretion.

zygote. Result of fusion of two gametes in process of sexual reproduction, zygote (diploid) containing twice as many chromosomes as each gamete (haploid).

THE LIVING ANIMAL

Although foraminifers are unicellular or acellular organisms, this is no longer regarded as synonymous with simple or primitive. Considerable variation exists among living forms in size, habit, habitat, life cycles, pseudopodial character, and test morphology. In extinct genera represented by fossils, morphology of the test affords the only basis for identification and classification, but as this appears to be closely related to living functions, a comparison with similar living forms may be used for determining relationships. Discussion of the characters of the test is given in the following chapter, but because much important information can also be obtained from living forms, a summary of present knowledge of living foraminifers is introduced here with notice of subjects likely to be of use or interest to paleontologists and taxonomists.

PROTOPLASMIC BODY

As in the Amoebida, the protoplasm is differentiated into an outer layer of relatively clear ectoplasm and an inner, darker-colored endoplasm. In forms with a single aperture, the ectoplasm may be condensed into a single apertural plug (stomostyle). In those with multiple apertures or perforations, the ectoplasm may be more dispersed and less evident, forming only a thin outer layer. The test is always a secretion of the ectoplasm and pseudopodia. The endoplasm is restricted to the already-constructed chambers. It may be variously colored in shades of yellow, yellowish-brown, greenish-brown, salmon-rose, orange-red, or crimson, some of the colors being due to pigments and others to various inclusions or symbionts.

The peripheral zone, or outer few chambers of multilocular forms, lacks microsomes but is crowded with exogenous inclusions consisting of nutritive particles or prey, debris of objects that have served as food (e.g., empty frustrules of diatoms), various mineral grains, symbionts, and parasites. Other inclusions result directly from the metabolic activity, such as the pigments, which may be dissolved in fat globules, the brownish globular xanthosomes that are probably products of excretion, and the granules. The protoplasm external to the test in many planktonic forms is highly areolated, and contains numerous fat globules as an aid in buoyancy. In the multilocular forms, a central area of dense plasma which surrounds the nucleus contains an abundance of tiny refringent granules or microsomes, numerous small vacuoles, pigments, and fat globules. In young individuals the vegetative outer zone is dominant, for the animals eat much and grow rapidly. In adults the dense central area is proportionately greater, finally comprising the entire protoplasmic body just before reproduction occurs.

In unilocular forms, the endoplasm is relatively homogeneous and the various inclusions uniformly spaced, although the proportion of excretory products and metabolic debris may be comparatively large.

NUCLEUS

All foraminifers have one or more nuclei. The nuclei are typically spherical, those of agglutinated or pseudochitinous unilocular genera having a thick membrane and being never deformed. Nuclei of higher forms are apparently more plastic, particularly in species having numerous relatively narrow foramina. The nuclei increase in size with growth of the individual, the largest recorded one being visible to the naked eye and up to 0.6 mm. in diameter (*Bathysiphon filiformis*, with tests up to 50 mm. in length).

Recent studies by GRELL (1956, *819) have shown that some forms (e.g., *Glabratella, Rubratella*) are heterocaryotic. In such genera, some of the nuclei are wholly vegetative (somatic), taking part only in normal day-to-day existence, but later they disintegrate and do not enter into nuclear divisions (generative) at time of reproduction. Those that are homokaryotic (all nuclei similar in form and function) include *Patellina* and *Spirillina.*

The nuclear structure and processes of nuclear divisions have been described minutely for some species, but because of their relative unimportance for the paleontologist, they are not here discussed in detail (see works of ARNOLD, GRELL, LE CALVEZ, MYERS, and RHUMBLER).

A nuclear dimorphism also exists, the megalospheric (gamont) generation being uninucleate and the microspheric (schizont) generation being more commonly plurinucleate. The mononucleate forms are most frequent, however, and probably represent the most primitive form. The simplest foraminifers, such as the unilocular forms with agglutinated or pseudochitinous test, are mononucleate throughout the vegetative existence of both the gamont and schizont forms. Some more highly organized species also are not known to have more than one nucleus at any time (e.g., *Globigerina,* apogamic *Oolina,* and *Neoconorbina*).

Plurinucleate forms, when present, are always schizont, the many nuclei arising from an early multiplication of nuclei from the original zygote. The monothalamous forms have a very short multinucleate stage, as the nuclear division occurs just preceding the asexual cytoplasmic division. The schizonts of more highly organized forms (e.g., *Planorbulina, Elphidium, Peneroplis*), with flagellate gametes in the reproductive stage, have early nuclear divisions which continue repeatedly throughout vegetative life. The plastogamic genera with amoeboid gametes (e.g., *Patellina*) develop four nuclei early in the schizont stage but show no further nuclear activity until just before the reproductive stage.

PSEUDOPODIA

The most important functions of the pseudopodia are concerned with capturing and digesting prey and expelling debris. Other functions are those of constructing the test, forming protective cysts, and making temporary or semipermanent attachment to the substratum.

The pseudopodia of foraminifers are invariably of granuloreticulose type, comprising very elongate linear extensions of the protoplasm which readily bifurcate and anastomose. The pseudopodia are but little thicker than the granules of plasmatic origin streaming along them. Commonly they have

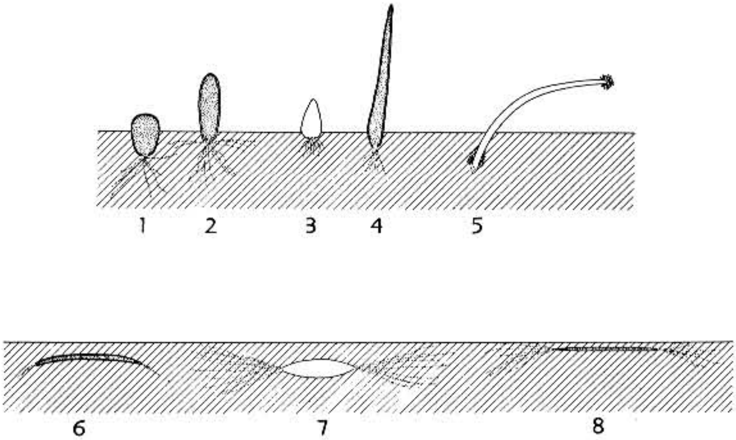


Fig. 34. Pseudopodial function in Foraminiferida.——*1-5.* Erect, rigid pseudopodia; *1,2,* Allogromiidae; *3, Hippocrepina; 4, Micrometula; 5, Bathysiphon.*——*6-8,* Prostrate, fragile, anastomosing pseudopodia; *6, Shepheardella; 7, Phainogullmia; 8, Nemogullmia* (*1379).

a relatively solid axis (stereoplasm) surrounded by a more fluid layer (rheoplasm). The solid axis and granular streaming are the most characteristic features, since variation in the amount of anastomosing occurs. The movement of the pseudopodia is characteristically rapid but it varies somewhat in different forms and at different times in the life cycle of an individual. Protruding from the aperture in many of the monothalamous genera is a distinct pseudopodial trunk (podostyle) from which the finer pseudopodia extend.

Some of the Lagynacea with podostyle are nearly immobile. They (e.g., *Amphitrema, Microcometes, Diplophrys*) have fewer granules and less active pseudopodia, with less prominent anastomosing and less pronounced streaming, than others (e.g., *Lieberkuehnia*) with thicker pseudopodia, more numerous granules, and motile pseudopodia, as in the higher forms of foraminifers.

Many agglutinated species exhibit no visible axis in the pseudopodia, but an increase in the amount of available potassium may cause it to appear.

The granular streaming was first observed by Dujardin (1835) and well described by many later workers (e.g., Schultze, 1863; Leidy, 1879; Brady, 1884) who carefully distinguished this type of pseudopodial movement from the amoeboid movements of the Amoebida and Arcellinida. Leidy was the first to separate the three groups called Lobosa, Filosa, and Foraminifera (with granuloreticulose pseudopodia) using their pseudopodial nature as basis.

Certain benthonic forms have relatively rigid pseudopodia, which help to anchor the specimens in soft sediments, allowing them to stand erect (e.g., *Hippocrepina*) (Fig. 34). Others, with fragile pseudopodia, and those with apertures at both ends, lie horizontally, their anastomosing pseudopodia apparently playing an important role in binding detritus of loose sedimentary bottoms (*1379).

In highly spinose planktonic species the pseudopodia extend along the radiating spines and the protoplasmic granules appear to stream up and down their surface.

Pseudopodial form may also vary in different growth stages. The pseudopodia of the sessile adult *Iridia,* which arise from a pseudopodial trunk, are very elongate, homogeneous, and without apparent axis in the adult; they anastomose, display rapid granular circulation of 400-500μ per minute, and show rapid movement of the pseudopodial extremities. The young embryo resulting from asexual reproduction, which has a temporarily pelagic existence, possesses a globular body with elongate, radiating and nonanastomosing pseudopodia. Only with retraction of the elongate rigid pseudopodia does it become benthonic and attached and begin to develop a test.

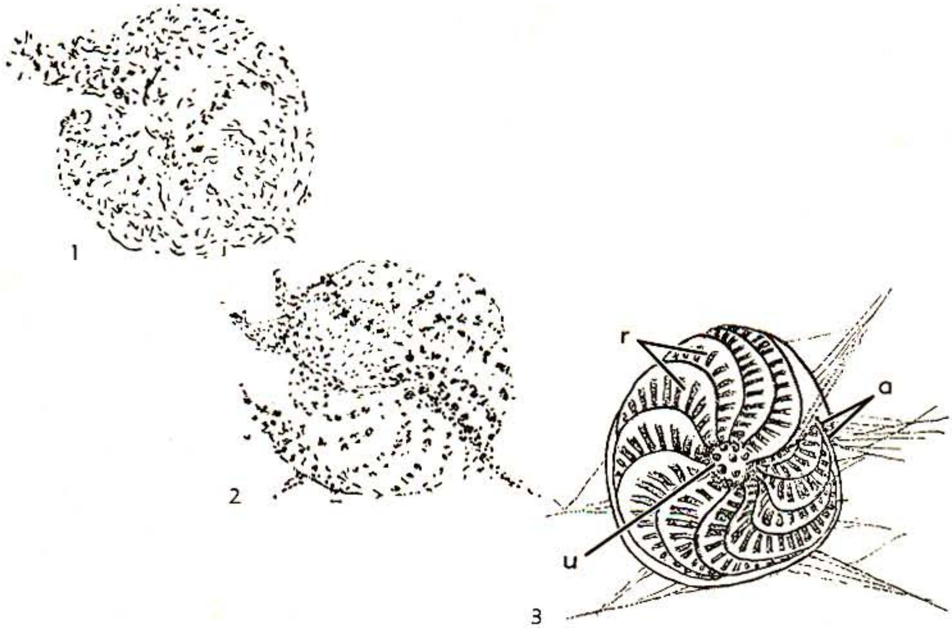


FIG. 35. Feeding cysts in *Elphidium*. Two successive feeding cysts *(1,2)* are shown with *Elphidium (3)* moving to a new location. The cysts are composed of empty diatom frustrules and xanthosomes deposited outside canal openings and along pseudopodial tracks (aperture, *a*; umbo with openings of spiral canal, *u*; retral processes, *r*), enlarged (*1380).

GAMETES

During the sexual phase of reproduction, gametes are produced. In a few genera all of the parent nuclear material is utilized in making them, the resultant gametes being relatively large (40-50μ in diameter) and amoeboid both in appearance and mode of locomotion. This is true only in rather few genera (e.g., *Allogromia* and plastogamic forms such as *Patellina, Spirillina,* and *Rubratella*). Other plastogamic forms (e.g., *Glabratella*) have triflagellate gametes about 8μ in diameter. The great majority of foraminifers yet studied are hologamic. They produce extremely small and numerous, unequally biflagellate gametes. The gametes of different genera are similar in having two flagella of unequal length inserted in a blepharoplast; they contain a single nucleus and one or more fatty inclusions, commonly one but two in *Hemisphaerammina bradyi.* Differences in the gametes of different species are in body size of the gamete, length of the two flagella, number of fatty inclusions, and presence or absence of an axostyle (present in the Miliolacea). The gametes vary in size from 2μ in length and 1.2μ in breadth *(Iridia diaphana)* to 6μ in length and 3.5μ in width *(Hemisphaerammina crassa)*. The two flagella vary in size from 3μ (length of smaller) and 8μ (length of larger) (e.g., *Planorbulina mediterranensis*), to 5μ and 20μ respectively (e.g., *Hemisphaerammina crassa*). The majority of hyaline calcareous genera have gametes about 3μ long, the larger flagellum being approximately three times the body length. The agglutinated and pseudochitinous, unilocular genera commonly have larger gametes (3-6μ in length) with flagella three to four times the gamete body length.

CYSTS

Cysts are formed at many stages in the life of most benthonic foraminifers. Temporary cysts are formed for protection during secretion of new chambers, for protection in schizogony (multiple fission cysts), and over pairs of gamont tests in syzygy or groups of these in association during gamogony. Even irregular feeding cysts may develop; these consist largely of debris resulting from the feeding process (Fig. 35).

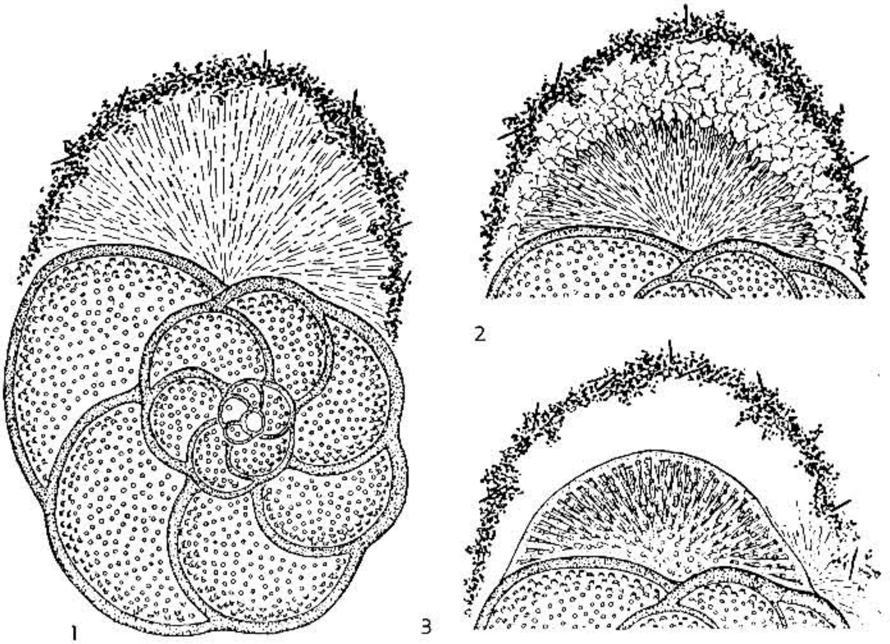


Fig. 36. Chamber formation in *Discorbinella bertheloti*; *1*, pseudopodia forming protective cyst; *2*, main pseudopodia retracted to position of future wall; *3*, formation of pseudochitinous pellicle with perforations, before calcification; all ×60 (*1109).

These growth cysts have erroneously been referred to as a variable form of test (*1380) and have probably even been described as distinct agglutinated species or genera. Because of their relatively loose agglomeration of material, such cysts are, however, unlikely to be preserved as fossils.

CHAMBER FORMATION

The process of chamber formation has been described in *Patellina* (*1335), *Glabratella* (*1339), and *Discorbinella* (*1109). In each of these genera the protective cyst which is formed and sealed to the substratum, consists of a thin membrane and debris collected by the pseudopodia. When the cyst is completed, the pseudopodia withdraw; the test and cyst then are separated opposite the last chamber by an expanding mass of clear cytoplasm which extends the width of a chamber below and beyond the margin. Indication of calcification of the surface membrane of the forming chamber first appears as bright points in reflected light. Pseudopodia extend through minute pores along the margin and the calcification gradually increases, shown as an increase in the amount of light reflected from its surface. In *Patellina* about 5 hours is required for completion of a chamber (*1335). In *Glabratella* it can be seen that a new layer of calcite is added to the entire test at the time of formation of the new chamber. In *Tretomphalus* it has been observed that the pores are due to deposition of shell material around the base of short pseudopodia extending through the pseudochitinous membrane to the wall of the cyst and that they are not formed secondarily after the wall is completed. About 12 hours is required for making an adult chamber in *Glabratella* (*1339).

In *Discorbinella* (Fig. 36) chamber formation is similar; the test and growth cyst around the margin are shown (Fig. 36,*1*), with pseudopodia extending out to the cyst margin. Rapid circulation of granules occurs at this time. The main pseudopodia then retract, leaving only fine extensions to the cyst (Fig. 36,*2*), and the border changes in refringence, with perforations of a thin pseudochitinous pellicle that appears, showing as small, conical spaces (Fig. 36,*3*). This pellicle, which is the first element of the test, first becomes enriched with lime salts at tiny points (e.g., *Patellina*), which by gradual coalescence produce the calcareous test. The pseudopodia then protrude from

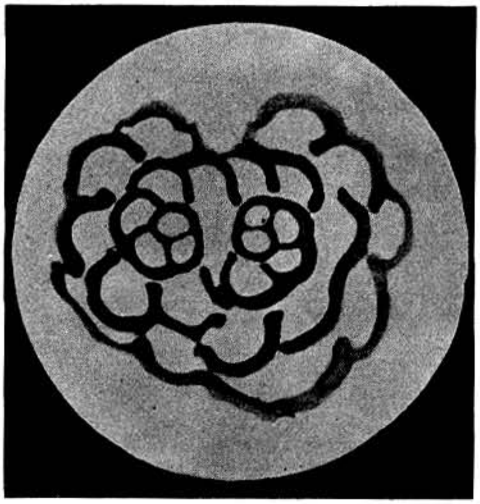


FIG. 37. Polyvalence in juvenile *Planorbulina mediterranensis*, enlarged (*1109).

the new aperture and the completed chamber fills with ectoplasm. About 8 hours is required for making a chamber in *Patellina*. The test is secreted by the ectoplasm and the pseudopodia, the endoplasm being found only in previously constructed chambers (*1109).

POLYVALENCE

In some large discoidal species, a random specimen may exhibit two or more embryonal stages (Fig. 37). This is an accidental vegetative association, not equivalent to the plastogamy found in the reproductive cycle of some species. The polyvalent specimens always are of the same generation and of approximately the same size, probably because of crowding in the growth cyst. In this type of individual the cytoplasm fuses, whereas the nuclei do not. The first chamber developed after fusion is twice the normal size for that stage (*1109).

SYMBIONTS

Various species of foraminifers have symbiotic zooxanthellae consisting of unicellular blue-green or green algae, which aid in food production by means of photosynthesis. *Peneroplis* and *Globigerina* contain such zooxanthellae (Fig. 38, *2068). The ciliate *Stylonychia* reportedly swims around the pseudopodia and shell of *Peneroplis*, or even into its last chamber, without being disturbed by the foraminiferal pseudopodia; apparently it helps to keep the foraminifer clean (*1627).

PARASITES

Some foraminifers may have other protozoans as parasites. *Elphidium crispum* has been reported to have the coccidian *Trophosphaera planorbulinae* (Le Calvez) in the protoplasm of larger chambers or extending throughout the test, so that eventually the *Elphidium* is destroyed. Nematode worms may also be parasitic on them (*1340). Various Recent and fossil tests may be observed with large, irregularly spaced perforations in the walls, the punctures being due to parasites or predators of some sort. One foraminifer *(Oolina marginata)* is itself a parasite on other species and captures and ingests the circulating protoplasmic granules of the host.

LIFE HISTORY

Probably no other group of organisms can compete with the Foraminiferida in low percentage of described living species in which the life history is known. Only 15 to 20 species have been thoroughly studied, though some information is available for about twice as many. A few generalizations may be made, however.

A paleontologist is gratified to learn that generic and suprageneric separations made almost solely on morphology and structure of the test generally accord with available information on life histories. Thus, simpler genera with a single-chambered test of pseudochitin or pseudochitin combined with agglutinated particles also have simpler life histories. They are commonly mononucleate in both the schizont and gamont forms until just before the reproductive process.

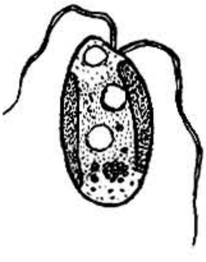


FIG. 38. *Cryptomonas schaudinni* Winter, symbiotic zooxanthella found in *Peneroplis*, ×2,250 (*2068).

The more complex life cycles and higher degree of nuclear differentiation and dimorphism, accompanied by the occurrence of flagellate gametes, are found in genera with more complex multilocular tests.

Patellina and *Spirillina,* in which differentiation of the test and its unusual wall structure originally led to placing them in a distinct family, also show distinctive nuclear characters; they have quadrinucleate schizonts, a syzygial reproductive phase, and amoeboid gametes.

All Miliolacea yet studied, classified in this group because of their distinctive porcelaneous test, have a distinctive form of gamete with axostyle.

Because such information may aid in constructing a truly natural classification, present knowledge of life cycles of foraminifers is here briefly summarized. It would be helpful to have life studies of many foraminifers, particularly of genera belonging to superfamilies as yet unstudied. For example, no life history of a species with aragonite test (Robertinacea) now is available and none of the perforate granular Cassidulinacea (e.g., *Pleurostomella, Fursenkoina, Nonion, Anomalina, Cassidulina*) are known in detail. Complete life histories of the planktonic genera are unkown. None of the Buliminacea have been studied and very little is known of the Nodosariacea (except the aberrant parasitic *Oolina*), or of multilocular agglutinated forms. In view of the great variety exhibited by those studied to date, it is almost certain that equally important distinctions will be observed when representatives of some of these other large groups are studied.

In general, two methods of reproduction are known in the foraminifers and normally these alternate in occurrence. An asexual reproduction consists of simple multiple fission (schizogony), in which the entire protoplasmic content of the parent test normally is utilized. The adult that eventually produces these asexually formed embryos is variously termed the schizont or agamont. Because asexually formed embryos normally are larger than the sexually formed ones, they develop a larger first chamber of the test (proloculus) and grow to form the adult megalospheric test of the gamont generation. The megalospheric gamont later produces gametes, the fusion of which to form a zygote produces a young schizont with microspheric test. A nuclear dimorphism is also present, the schizont having a diploid chromosome number, whereas the gamont is haploid. This alternation of morphologically similar diploid and haploid generations parallels the alternation of generations in lower plants and is unlike any other animals, which normally have cell nuclei with diploid chromosomes, and only haploid gametes. Various modifications of this general pattern of alternation of generations are observed. Reproduction by simple fission or by fragmentation and regeneration may occur, especially in some large agglutinated forms, but this is not part of the usual dimorphic cycle; it is discussed under "Life Habits."

REPRODUCTIVE CYCLE OF "PRIMITIVE" FORMS

The simplest kinds of foraminifers possess pseudochitinous or agglutinated unilocular tests. Genera studied in relative detail include *Iridia* (Le Calvez, 1936, *1104), *Nemogullmia* (Nyholm, 1956, *1378), and *Myxotheca* (Føyn, 1936, *736; Grell, 1958, *821) of the Lagynidae, which are alike in having biflagellate gametes, and *Allogromia* (Arnold, 1955, *45) of the Allogromiidae, which has amoeboid gametes.

The least complex cycle is probably that characteristic of *Myxotheca* (Fig. 39). The adult schizont with diploid nuclei has a reduction division (meiosis) prior to the onset of asexual reproduction. The protoplasm also is divided among the resultant nuclei for making the young gamont embryos. Upon escape from the parent, the young gamont has a vegetative period of growth, the resultant adult gamont being similar to the adult schizont until the reproductive phase begins. At this time a great many tiny, biflagellate gametes are formed. These are released into the open sea, and conjugation occurs outside the parent test, although not necessarily with those from another adult, for in isolated cultures, gametes from a single parent have been observed to fuse. The zygote thus formed, with diploid chromosome number, then grows into the adult schizont. In this form, no sexual differentiation of the gamonts is seen, the form being monoecious (gametes of a single parent may fuse).

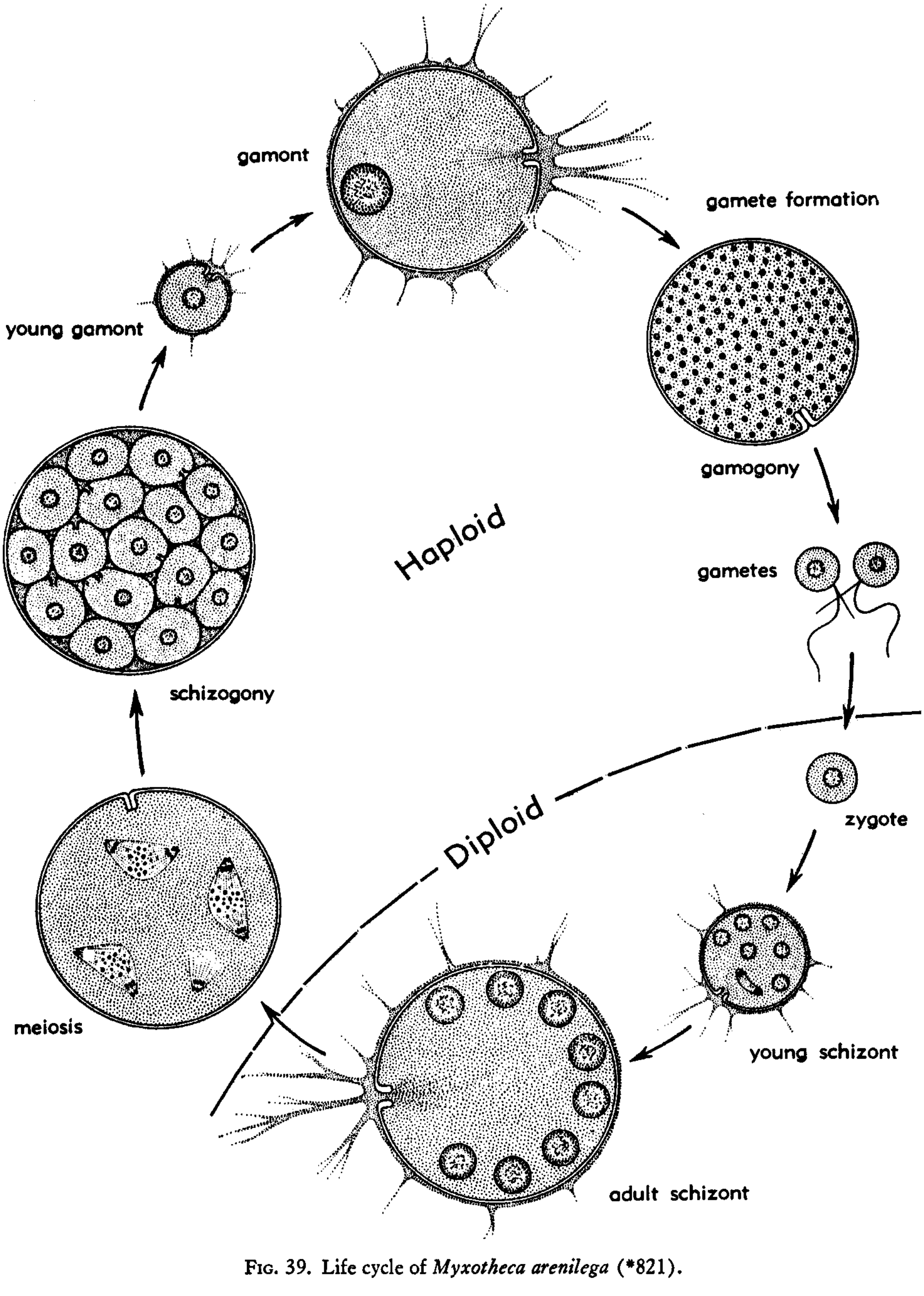


FIG. 39. Life cycle of *Myxotheca arenilega* (*821).

A modification of this life cycle is shown by *Iridia* (Fig. 40). The adult diploid schizont is uninucleate and is relatively scarce in nature. With onset of schizogony, a cytoplasmic purification occurs, debris and waste products being excreted before the occurrence of nuclear divisions which yield approximately 40 daughter nuclei. The parent cytoplasm is divided among these nuclei to form the young haploid mononucleate embryos. The parent test is commonly dissolved for their dispersal. At least in some

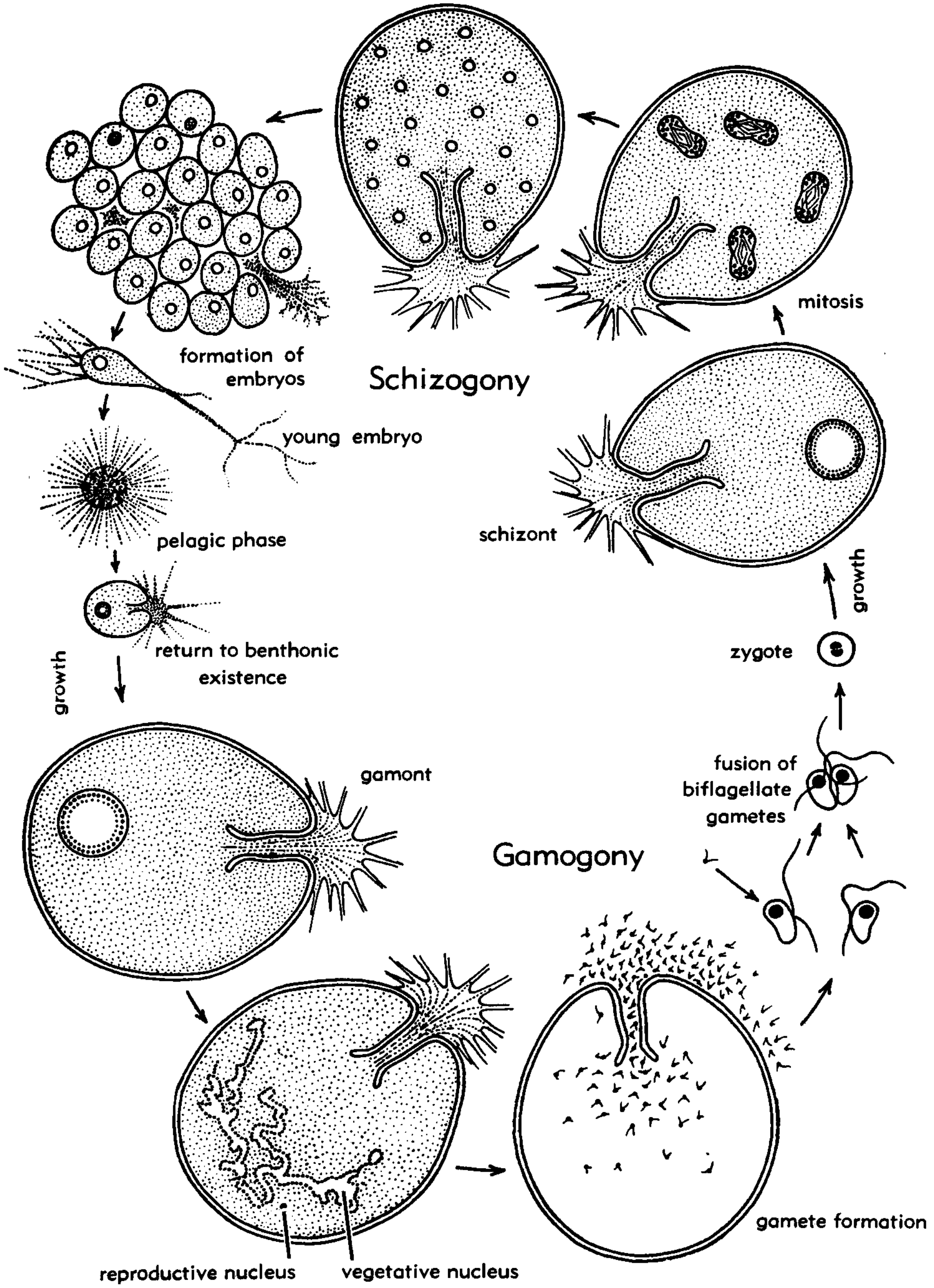


FIG. 40. Life cycle of *Iridia lucida* (*810).

species the embryo soon retracts the originally reticulose pseudopodia, contracts to a spherical form, puts forth many elongate, nonanastomosing pseudopodia, and becomes pelagic for a few hours or a day, doubtless in order better to insure their dispersal. Then the radiate pseudopodia retract, the animal becomes benthonic, attaches to the

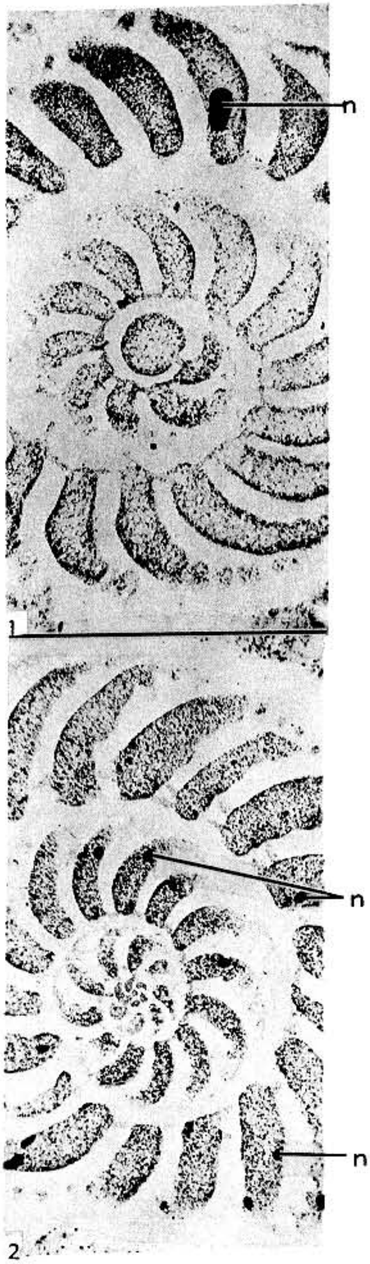


FIG. 41. Horizontal sections of *Elphidium crispum*, enlarged (*1340).——*1*. Megalospheric gamont, with large proloculus and single large nucleus (*n*).——*2*. Microspheric schizont, with minute proloculus and many nuclei (*n*).

substratum, and develops a pseudochitinous test. The adult gamont of these unilocular forms is identical in appearance to the adult schizont, although the gamonts are far more abundant. Gamogony begins with cytoplasmic purification, followed by disintegration of the large nucleus and development of the micronucleus, its numerous nuclear divisions resulting in many millions of tiny gametes, each with a nucleus, an oil inclusion, and two flagella of unequal length. The gametes are emitted at night, fusing with those of other adults to form zygotes, the young schizonts. Culture data indicate a primitive sexuality, and unlike *Myxotheca,* the gametes of a single parent will not combine to form zygotes, two parents being required (dioecious). The complete cycle requires about a year, schizogony occurring in winter and gamogony in summer.

Cytoplasmic purification of the uninucleate gamont at the onset of gamogony in *Nemogullmia* closes both apertures with balls of detrital material. The cytoplasmic and nuclear divisions to form gametes occur first in the central areas of the elongate test and then spread to both ends. The escape of the gametes is not through the original apertures but through openings formed in the pseudochitinous test; commonly large groups of gametes are extruded at one time in lumps of cytoplasm containing oil droplets. These break apart within an hour or so, liberating the free-swimming, biflagellate gametes. The entire protoplasmic content is consumed in the production of gametes. The schizont is multinucleate (*1378).

In *Allogromia laticollaris* both schizont and gamont are multinucleate, gametes are amoeboid, and fusion may occur autogamously within the parent test (both gametes from the same parent as in *Myxotheca,* i.e. monoecious); the zygote enlarges and only finally emerges as multinucleate diplonts. The cycle is complicated in that a series of haploid schizont generations may be produced before schizogony occurs and a series of diploid generations may be produced by schizogony before gamogony occurs. Asexual budding may also take place (*45).

Unilocular agglutinated species (e.g., *Hemisphaerammina bradyi,* Ammodiscacea) have a similarly simple life cycle, with biflagellate gametes. The young embryos formed in schizogony leave the parent test with only a pseudochitinous cover; the agglutinated test is developed later.

DOMINANT REPRODUCTIVE CYCLE OF MULTILOCULAR FORAMINIFERS AND SOME MODIFICATIONS

The most commonly occurring cycle is characterized by isolated adult gamonts (hologamic) having numerous nuclear divisions. The many resulting biflagellate gametes are released into the open sea and may be free-swimming for a number of days before they fuse in pairs to form zygotes. The young diploid schizont has three to five nuclear divisions early in its existence, hence is multinucleate. The adult schizont has a larger test than the gamont. At the beginning of schizogony an agglutinated protective covering cyst is formed over the animal, and nuclear reduction division occurs so that the gamont embryos, adult, and gametes are all haploid and the schizont diploid. In species with an annual cycle, the schizont is most common during the winter and the gamont, of shorter life span, is found during the summer months. Other species may require two to four years for a complete cycle. Some modifications of this general form are shown by *Elphidium, Ammonia, Discorbis, Tretomphalus* and *Planorbulina,* almost as many variations being known as species studied.

Elphidium crispum (Rotaliacea)

The common species, *Elphidium crispum,* occurs in large numbers near Plymouth, England, and on account of its availability was one of the earliest to be studied. The life cycle was first observed by LISTER (1895, *1149) and the true meaning of dimorphism in foraminifers elucidated thereby. Later investigations by JEPPS (1942, *992) and MYERS (1943, *1340) added details to the original study. Now it is known that the multinucleate adult schizont has a microspheric test with small proloculus (diam., approx 10μ) (Fig. 41,*2*, 42). Asexual division of the schizont results in many young megalospheric uninucleate gamonts, each with a proloculus of 50 to 70μ in diameter. Commonly two chambers are developed before the gamont escapes from the parent test to grow into the adult (Fig. 41,*1*). At the beginning of gamogony the animal ceases to feed, all waste matter is discarded, the

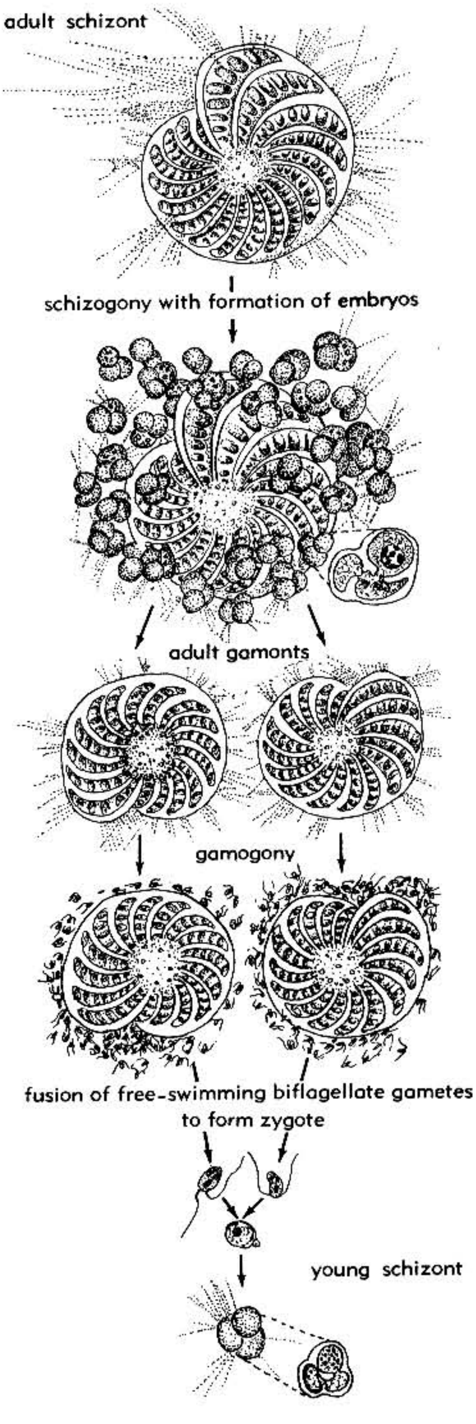


FIG. 42. Life cycle of *Elphidium crispum* (*1338).

vegetative nucleus disappears, and successive nuclear divisions of the generative micronucleus result in the development of many biflagellate gametes. These are released into the open ocean in large numbers and conjugate with those from other parents, resorbing the flagella to form the young schizont. Rapid nuclear divisions

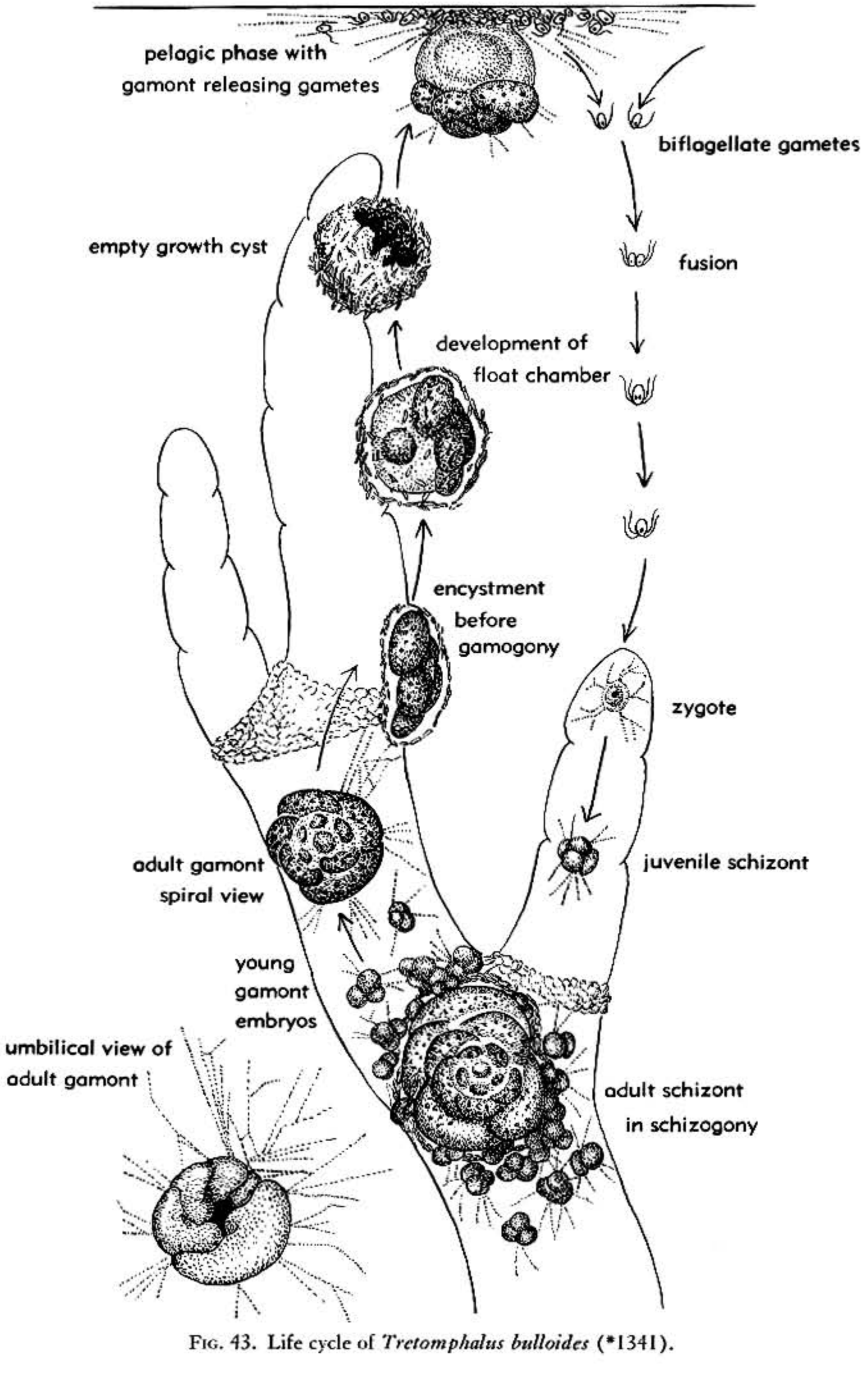


FIG. 43. Life cycle of *Tretomphalus bulloides* (*1341).

occur so that the schizont is multinucleate throughout its existence. In temperate regions the life span of each individual is about a year and the complete cycle requires two years in tide pools, whereas below low tide level three to four years may be required, the specimens being larger and having more numerous chambers in this environment. In tropical regions the life span is about six months and the complete cycle requires one year. Growth and reproduction are largely confined to the spring months. An occasional schizont fails to have the normal nuclear reduction division and remains diploid, resulting in a megalospheric form which reproduces asexually as a schizont. This is a form of trimorphism, but is not an obligatory part of the cycle.

Ammonia beccarii has a similar cycle, which may be termed holotrimorphic, as the gamont may produce microspheric schizonts, which give rise to megalospheric schizonts that in turn produce gamonts.

Some forms with intralocular schizogony (e.g., *Discorbis vilardeboanus* auctt., *non* d'Orbigny) have developing embryos that dissolve much of the interior and ventral face of the parent schizont test before they escape. For this reason many such microscopic tests are destroyed during the reproductive cycle and accordingly are rare in the fossil record, being preserved only when the living animal met death before completion of the cycle.

Tretomphalus bulloides (Discorbacea)

The alternation of generations is complicated in this form by development of a pelagic stage (Fig. 43). The microspheric schizont has 16 to 24 chambers and contains 18 to 20 nuclei. It is usually protected beneath a cystlike structure; hence, the closely appressed lower or umbilical surface commonly is deformed to agree with the surface of the substratum. A "growth" cyst is also formed when schizogony commences. In about three days the 80 to 225 young embryos have each developed two or three chambers. They then dissolve the umbilical surface of the parent to make their escape. An additional chamber or two is formed the next day, by which time the young have dispersed from the empty, now disintegrated parent test. After developing 13 to 18 chambers, the gamont again forms a growth cyst, ectoplasm extruded from the ventral surface expands to a globular form and finally secretes a large hemispherical float chamber over the entire umbilical surface. The cytoplasm simultaneously develops a large gas bubble which occupies most of the chamber and the animal then pushes out of the cyst to float to the surface. The development of the planktonic stage requires 18 to 24 hours and biflagellate gametes are simultaneously developed within the cytoplasm. The floating gamonts move slowly beneath the surface film by means of long pseudopodia and when two individuals approach closely, their pseudopodia anastomose, bringing the tests together with their float chambers facing each other. The gametes are then discharged in streams from the floating tests through the larger pores of the float chambers and they fuse to form young schizonts. About 12 hours later the float fills with water and the empty test sinks to the bottom. The young schizont also sinks to the bottom and grows to form the benthonic microspheric adult.

Planorbulina mediterranensis (Orbitoidacea)

This is an attached form, and unlike *Elphidium,* dimorphism is not reflected in test size but only in size of the proloculus, which is 11 to 14μ in diameter in the microspheric schizont (about 4 per cent of the specimens) and 23 to 56μ in diameter in the megalospheric form (about 96 per cent). Just before schizogony the protective crust over the test is reinforced by excreted debris. During schizogony only a small part of the parent protoplasm is used for the developing embryos. The 60 to 100 young embryos at first have only a pseudochitinous membrane, which becomes calcified after the embryo has developed four chambers, by which time much of the parent test has been dissolved. After formation of the fifth chamber, the young dislodge the protective covering or cyst and escape, moving some millimeters away before attaching to the substratum and proceeding with growth. In this species occasional trimorphism occurs, with some uninucleate and some multinucleate gamonts, but this is not reflected in size of the proloculus; hence, no trimorphism of the test is seen, only of the nuclei. According to Le Calvez (*1106) the microspheric forms in cultures produce only typical uninucleate gamonts. The adult gamont in gamogony has rapid nuclear divisions, producing many biflagellate gametes which escape in a cloud, commonly at night, into the open sea and may be free-swimming for many days before fusion. The cycle of *Planorbulina* is somewhat more complex than that of *Ammonia* and may be termed paratrimorphic. Thus, the schizont may produce either uninucleate or multinucleate diploid megalospheric forms, each of which may produce schizonts or the multinucleate one may produce uninucleate forms first.

The life cycle of imperforate, porcelaneous foraminifers is similar. That of *Peneroplis pertusus* (FORSKÅL) was studied early by WINTER (1907, *2068) (Fig. 44). The adult schizont with about 40 chambers divides asexually to form many small embryo gamonts, which develop a spherical proloculus and tubular enrolled second chamber or spiral passage before breaking free. The proloculus of the young schizont is distinctly perforate, similar to hyaline calcareous forms, but later chambers have the characteristic imperforate porcelaneous wall. This species also has many tiny symbiotic algae or zooxanthellae (*Cryptomonas*). The gamont grows to maturity (about 21 chambers) and then produces numerous flagellate gametes. These were originally described as uniflagellate. According to LE CALVEZ (*1106), the long blepharoplast characteristic of the miliolacean gametes may have been mistaken for a flagellum, and the two very fine true flagella were not seen by WINTER. Fusion of the gametes results in the production of a new schizont generation.

An interesting variation to the general rule that all parent cytoplasm is utilized in producing the next generation was observed in a small miliolid, referred to *Spiroloculina,* kept in isolation cultures. In schizogony, part of the parent protoplasm moved outside the test into the reproductive cyst to produce the embryonic young, but some of the protoplasm remained in the parent test and then resumed feeding in a normal vegetative existence. After some time (three days to a month) another group of young was produced by schizogony from the same adult (*44).

Other species that have been studied and found to have similar life cycles include *Nubecularia lucifuga, Quinqueloculina seminulum, Q. suborbicularis, Triloculina circularis, T. rotunda, Discorbinella bertheloti, Cibicides lobatulus, Cyclocibicides vermiculatus,* and *Eponides repandus.* Of these, the Miliolacea are characterized by a distinctive type of gamete, with long axostyle. The young gamonts have also been observed in other genera, although complete cycles and gametes have not been identified for all of these.

REPRODUCTIVE CYCLE OF PLASTOGAMIC SPECIES WITH TRIFLAGELLATE GAMETES

Plastogamic genera that have triflagellate gametes are here included in the Glabratellidae, with such genera represented as *Glabratella* (synonym, *Conorbella*) and *Angulodiscorbis.* Most of these species had previously been placed in *Discorbis,* but the generic separation, originally based solely on test morphology, here also is upheld by distinctive reproductive characters. The pairing or association of tests which precedes gamogony had been noted long before its true nature was determined, for it was variously thought to be plastogamy (a modified asexual reproduction), or a reproduction by budding (HERON-ALLEN, 1915, *904). MYERS (1933, *1334) used the term syzygy, to which JEPPS (*993) objected because of its prior use in a somewhat different sense in the minute wormlike sporozoans known as gregarines. This has been observed in *Glabratella patelliformis, G. pulvinata, G. ornatissima, G. opercularis* and *G. parisiensis* (MYERS, 1940, *1339), *G. mediterranensis* (LE CALVEZ, 1950, *1109), and *G. sulcata* (GRELL, 1958, *820c).

The multinucleate schizont reaches maturity at about two to two and a half months of age, the final chamber commonly being smaller than several which had preceded it (Fig. 45). Schizogony begins with the development of a rigid protective cyst composed of diatom frustrules and other debris, the nuclei moving through chambers farther from the proloculus, the larger nuclei dividing in *Glabratella patelliformis* and all nuclei doing so in *G. opercularis.* Globules of cyotoplasm then separate around each nucleus to form about 30 to 120 young schizonts, the number varying somewhat in different species. Not all of the parent cytoplasm is utilized in forming the mononucleate embryos, which develop a plasma membrane, then an outer ectoplasmic layer; moving about within the parent test by means of pseudopodia, they consume this remaining cyotoplasm and much of the calcium walls and septa of the parent test. A

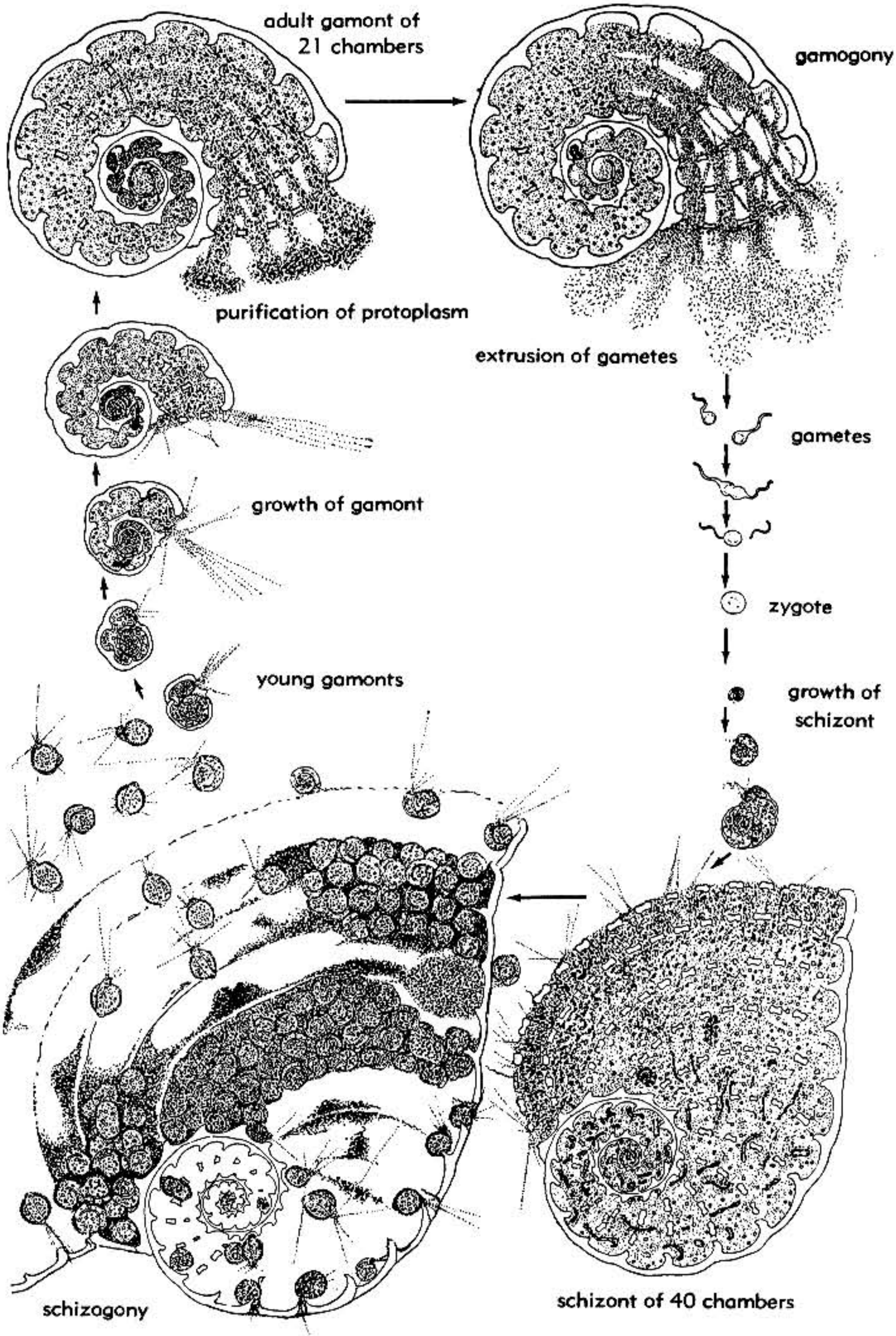


FIG. 44. Life cycle of *Peneroplis pertusus* (*2068).

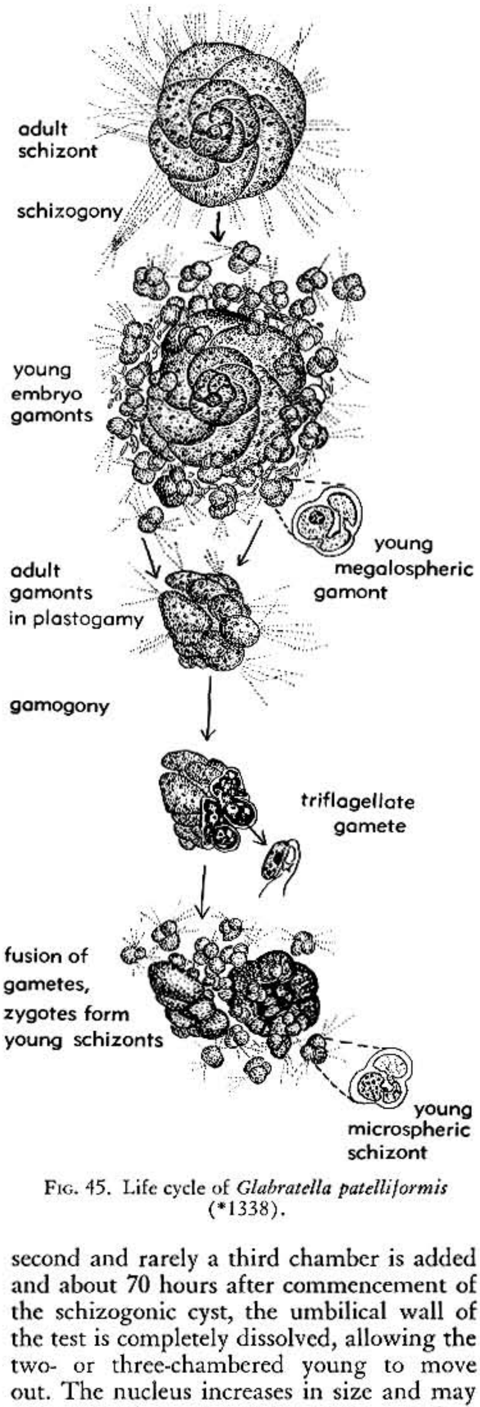


FIG. 45. Life cycle of *Glabratella patelliformis* (*1338).

second and rarely a third chamber is added and about 70 hours after commencement of the schizogonic cyst, the umbilical wall of the test is completely dissolved, allowing the two- or three-chambered young to move out. The nucleus increases in size and may remain in the proloculus or move to whatever chamber is approximately central in the series. The adult gamonts may have from 6 to 16 chambers. These associate in pairs, fusing by the umbilical surfaces commonly in such position that the apertures are opposed, moving and rotating for this purpose by means of the pseudopodia. The fused pairs may move for some distance over the substratum, then become cemented to it. At times three or four tests of varying size may associate at once. The septa and umbilical surface are resorbed and the protoplasts fuse in the intervening space. Multiple nuclear divisions rapidly produce the numerous (250 to 300 per gamont) small spherical triflagellate gametes. Two of the flagella are of equal length and beat in unison, the third being somewhat longer and trailing. Only about 10 per cent of the gametes fertilize; the remainder are consumed by those which develop. The zygote retains the flagella until it has enlarged to about two-thirds the size of the protoplasmic mass in a schizont proloculus. An ectoplasmic layer develops and a thin perforate test wall forms within it, the proloculus diameter depending on the amount of growth occurring before its secretion. Two or three chambers are formed before the cement attaching the associated tests is dissolved for dispersal of the young. From 18 to 32 young schizonts normally develop from an associated pair of tests.

Megalospheric tests of *Glabratella patelliformis* are sinistrally coiled, whereas microspheric ones are dextrally coiled. Among the plastogamic species in general, the schizont form is relatively large and low-spired, the gamont being smaller and more conical. LE CALVEZ (1952, *1110) noted that different specific names have been applied to the two generations in many instances. The complete cycle with alternation of generations in this species requires 64 days or more (*1339). Because certain specimens would fuse only with certain others in laboratory experiments, possible sexuality is suggested even though no morphologic differences could be observed (*1109). This type of reproduction has apparently occurred in the foraminifers since Eocene times, for according to LE CALVEZ (*1109) fossilized species from the Lutetian of the Paris basin show the open umbilical area similar to the present-day empty tests that have separated after resorption of the septa and umbilical surface during the plastogamic process.

REPRODUCTIVE CYCLE OF PLASTOGAMIC AND SYZYGIAL SPECIES WITH AMOEBOID GAMETES

This type of reproduction is characteristic of the Spirillinacea and has been thoroughly described for *Spirillina vivipara* by MYERS (1936, *1337) and for *Patellina corrugata* by MYERS (1935, *1336), LE CALVEZ (1938, *1106), and GRELL (1958, *821; 1959, *820d). It also occurs in *Rubratella* and was described by GRELL (1958, *820b, *821). In most species with amoeboid gametes the microspheric and megalospheric tests are reversed as compared with the majority of foraminifers with flagellate gametes, because the gamont generation commonly has a small proloculus (hence microspheric), and the schizont generation a large one (therefore megalospheric).

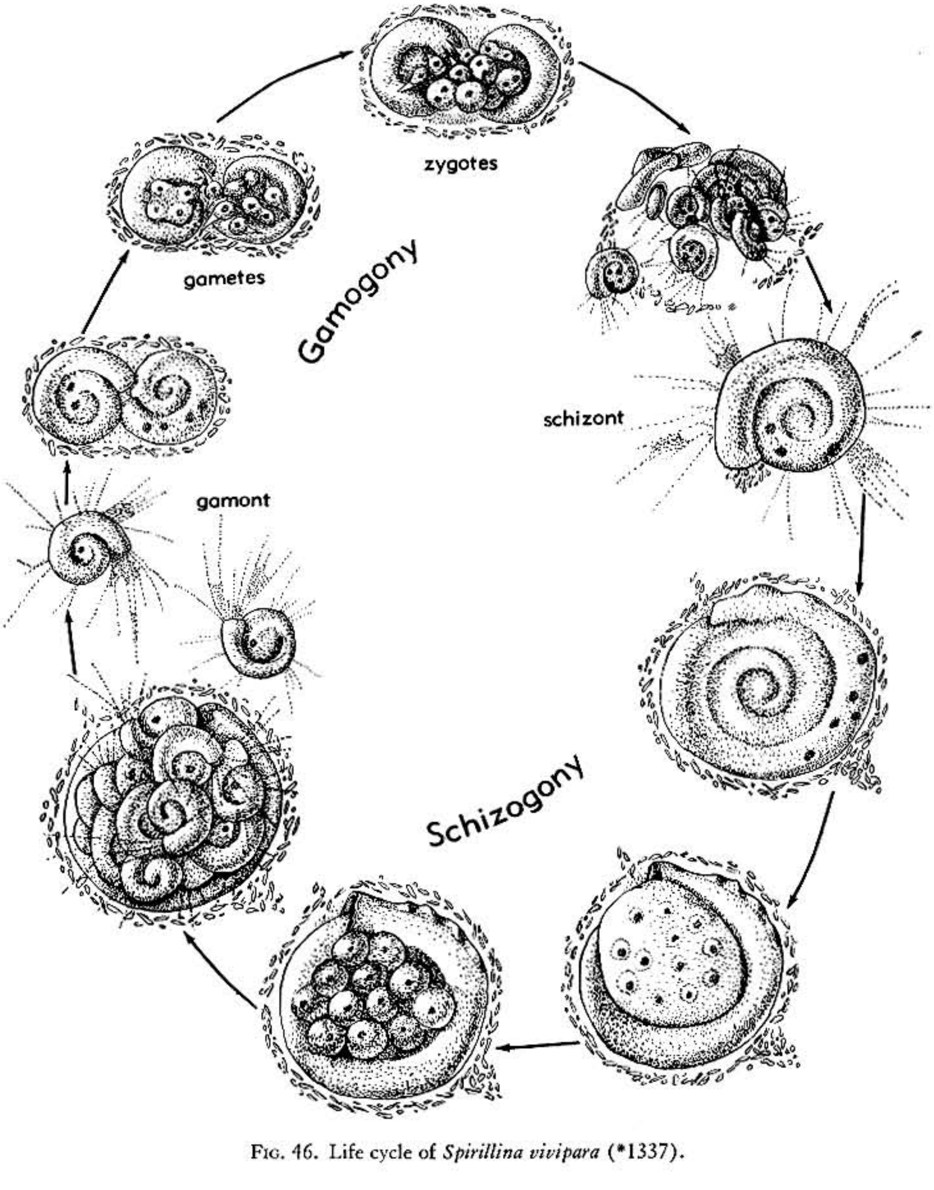


FIG. 46. Life cycle of *Spirillina vivipara* (*1337).

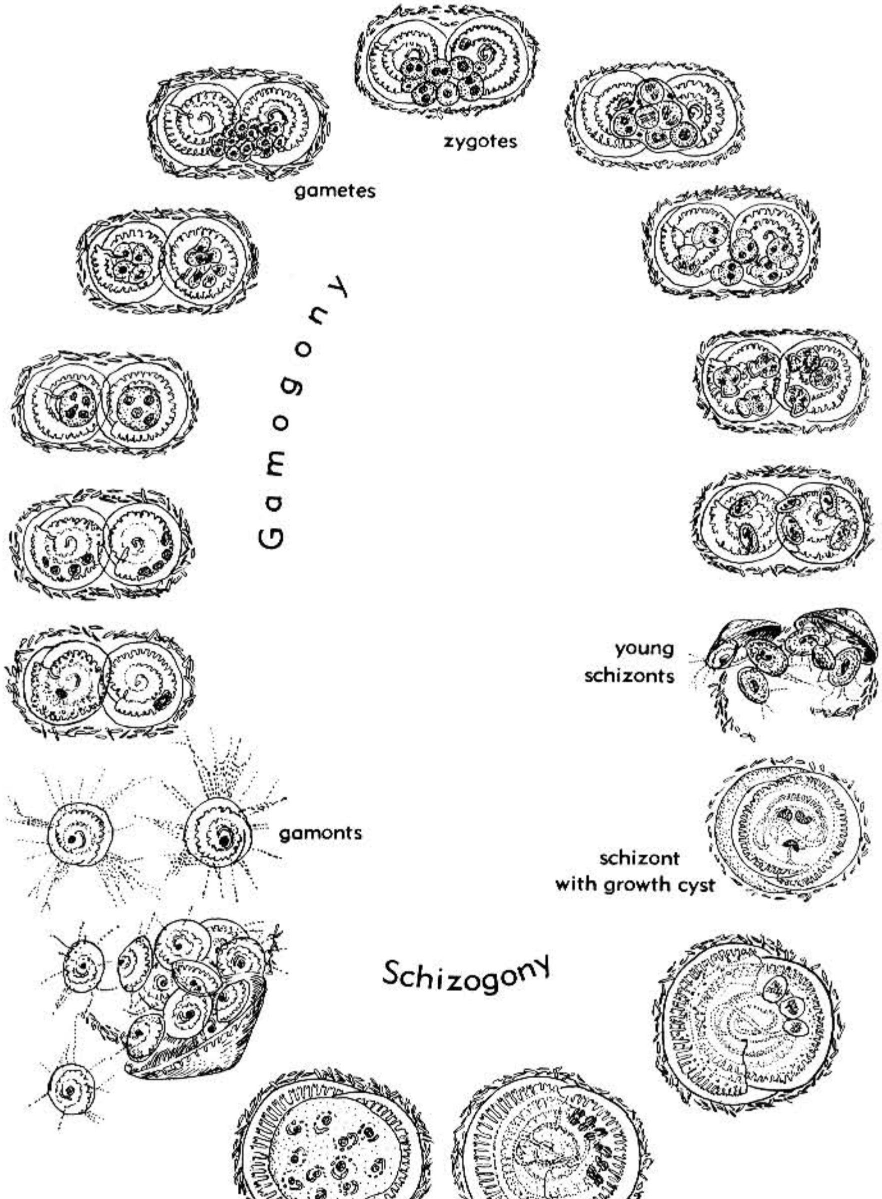


FIG. 47. Life cycle of *Patellina corrugata* (*1336).

The species *Spirillina vivipara* probably has the least complex type of life cycle (Fig. 46). In this form no definite period of chamber development is recognized, growth and secretion of the test being more or less continuous during vegetative existence. The multinucleate schizont commonly has a larger test (diam., 125-152μ), consisting of two and three-fourths to three and one-half whorls, an ovoid proloculus, and a somewhat constricted early part of the spirally wound chamber. In some specimens the final whorl may have a sharp bend so that the tubular chamber turns toward the umbilical depression. At maturity a reproductive cyst is formed from debris collected by the pseudopodia from the immediate vicinity and plastered over the dorsal side of the test, laterally sealing it to the substratum. Two nuclear divisions follow, all nuclei dividing at once so as to commonly form 12 young, or more rarely 16. This nuclear division is followed by migration of the multinucleate cytoplasm from the test into the cyst or brood chamber. Cytoplasmic differentiation and multiple fission follow, each nucleus forming a new mononucleate juvenile gamont. The proloculus of the young test is secreted immediately, its development beginning even before the multiple fission. When about three-fourths of the first whorl of the coiled chamber is complete, the cyst is ruptured and the 12 to 16 young gamonts escape. The adult gamont commonly has only one and a half whorls and an average diameter of 60 to 78μ; the proloculus is subglobose and the spiral chamber is uniformly graduated from the proloculus. At maturity, two to four of the gamont tests group in association, or syzygy, and form a fertilization cyst over the entire group, in the same manner as the cyst was formed by the schizont before reproduction. The nucleus of each gamont then divides, two or three successive divisions producing four to eight gametocytes which move out into the cyst. An additional fission gives rise to 8 to 16 gametes from each original gamont. The large gametes (diam., 40-50μ), of the various specimens in association then fuse in pairs and secrete a proloculus about the zygote, and two nuclear divisions follow, resulting in a quadrinucleate schizont. When about three-fourths of a whorl of the tubular test has developed, the young escape from the cyst. Twelve chromosomes are present in *Spirillina* in the diploid stage. The minimum length of time required for a complete cycle is about 18 days, but if association of the gamonts in syzygy is somewhat delayed, growth and test secretion may continue for a longer time. Similarly the schizogony, under less favorable conditions, may also be delayed for several weeks.

The earliest investigation showing complete cytological development in the alternation of generations of a foraminifer was by Myers (1935, *1336) in a study of *Patellina corrugata* (Fig. 47). For a time this raised doubts as to the correctness of interpretation of flagellate gametes in *Peneroplis, Elphidium,* and other genera, an interpretation which subsequently has been proven cytologically. The alternation of generations was shown to be similar to those described above, the amoeboid gametes being similar to those of *Spirillina.* The early stage has an undivided coil as in *Spirillina,* but later chambers are biserially arranged. A temporary protective growth cyst is formed each time a new chamber is added. The adult schizont rests with the umbilical side on the substratum and forms an agglutinated protective cyst when about to undergo schizogony. The number of nuclei is somewhat variable, but two successive mitoses form quadruple the number of nuclei. These collect cytoplasm after moving out of the test into the cyst cavity and form the uninucleate embryo gamonts. After about two days the young gamonts escape, having resorbed most of the ventral wall and septa of the parent test as a source of calcium carbonate. The new embryonic tests consist of the proloculus and a spiral chamber of about one and three-fourths whorls. After growth these gamonts associate in a reproductive cyst in groups of two to nine, with synchronous development of the gamogony. Nuclear divisions result in eight large amoeboid gametes within each test, the haploid number of chromosomes being 12. These gametes fuse inside the cyst with gametes from other parent tests to form the zygotes, and any that fail of fertilization are consumed as food by the successful ones. Nuclear divisions, cytoplasmic reorganization, and test secretion follow to complete the cycle. According to Grell (1958, *821), a sexual differentiation occurs in the adult gamonts and no association will develop unless at least one of each "sex" is present. Furthermore, in an association of three tests (common in nature), the total number of zygotes will be only that of the lesser number of gametes of one sex. If two plus-individuals (each with three nuclei originally) and one minus-individual (with originally four nuclei) associate, the former developing 12 plus-gametes and the latter eight minus-gametes, the number of embryos will

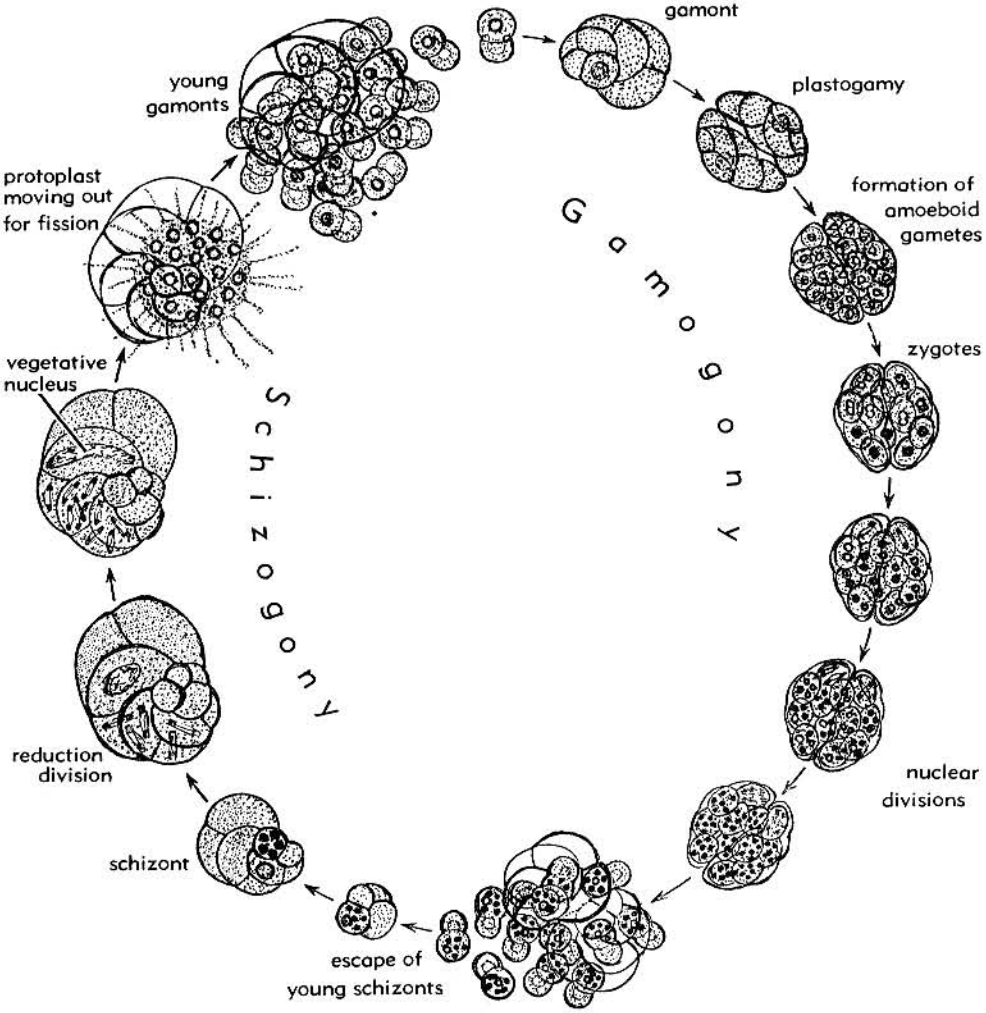


FIG. 48. Life cycle of *Rubratella intermedia* (*821).

be eight, the remaining plus-gametes not developing. GRELL noted that in *Patellina,* the gamonts and gametes of the plus-sex were somewhat more compactly built than the minus-sex. He also noted that the reduction division from diploid to haploid chromosome number occurs at the beginning of schizogony, so that the gamont generation is always haploid.

Rubratella intermedia is a very tiny species with only a few thin-walled chambers, each with internal radial partition formed simultaneously with the chamber (Fig. 48). The adult schizont normally has four to seven chambers, the gamont one to five. This species is heterokaryotic, having one somatic or vegetative nucleus and commonly five generative nuclei, or more rarely only one to as many as seven generative ones. The inner chamber walls of the schizont are dissolved when the protoplast moves out of the test for multiple fission, and formation of the young embryos occurs outside the parent test. The gamont always has only a single nucleus occupying the proloculus, which commonly is larger than that of the schizont, although size varies somewhat in both generations. With the beginning of gamogony, the inner walls are dissolved and two tests fuse by their umbilical surfaces in plastogamy. The somatic nucleus disintegrates and the remaining nuclei divide to form the amoeboid gametes. These fuse to form the new schizont generation (*820b). This reproductive cycle is like that of the Glabratellidae in showing plastogamy and like the Spirillinidae in having amoeboid gametes. Sexuality is also shown in *Rubratella* (Fig. 49). In plastogamic pairs where one gamont is larger than the other the resultant gametes are of proportional size and the resultant zygotes without exception show pairing of gametes and nuclei of dissimilar size (*821).

REPRODUCTION OF SPECIES WITH AUTOGAMOUS FERTILIZATION OF AMOEBOID GAMETES

The life cycle of species of *Rotaliella* have been described by GRELL (1954, *818; 1957, *820a). Similar to the Spirillinidae in having a quadrinucleate schizont generation and in the development of amoeboid gametes, they differ in lacking the plastogamic habit and in having autogamous fertilization within a single parent test (Fig. 50). The schizont nuclei are of two types, one being larger and one smaller. The larger type is vegetative in character and apparently of use only in growth and development of the individual, not taking part in the reproductive phase. The three smaller generative nuclei each have two nuclear divisions which form 12 new embryonic gamonts, and at this time the larger vegetative nucleus disintegrates. The young and adult gamonts are uninucleate, the nucleus being situated in the proloculus. In gamogony this nucleus divides and forms large amoeboid gametes which then fuse in pairs within the same parent test (autogamy). Both generations in species of *Rotaliella* are characterized by a small number of chambers (five or six only) (*818).

REPRODUCTION IN APOGAMIC SPECIES

A few species have been studied which apparently have lost the sexual reproductive stage and only reproduce by simple fission. Among these is *Neoconorbina orbicularis*. LE CALVEZ (1950, *1109) observed eight successive schizogonic generations in cultures of this species without the appearance of gamogony. The specimens are invariably mononucleate and the number of embryos formed is never large.

Another aberrant form without sexual reproduction is *Oolina marginata*. It is an ectoparasite on various discorbid species (e.g., *Rosalina*). At the time of reproduction, *Oolina* leaves the host, moving outside the ring of debris which normally surrounds *Rosalina*. Lying on its side, *Oolina* constructs a large hemispherical chitinoid cyst around the apertural region; then the cytoplasm dissolves the internal entosolenian tube and moves out of the test into the cyst. Schizogony occurs, the single nucleus and protoplasm divide into two to six fragments, each of which secretes a separate test, breaks free from the parent test, and returns to reinfest the host. This cycle is repeated about every ten days.

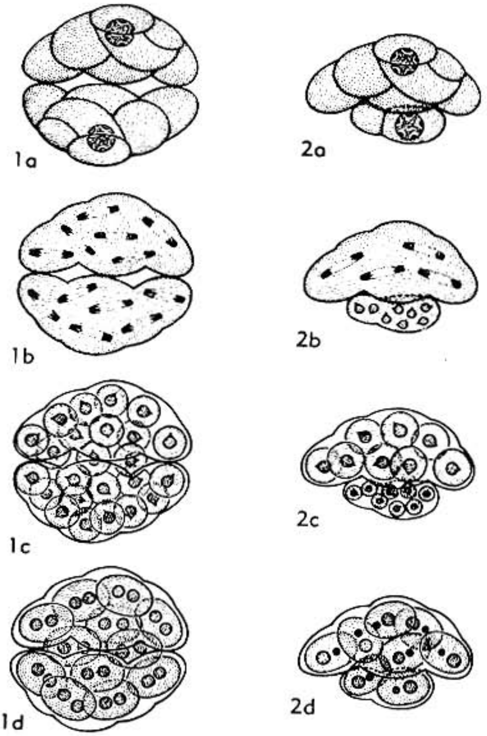


FIG. 49. Plastogamy in *Rubratella intermedia*; *1*, gamonts of similar size; *2*, gamonts of dissimilar size (*1a,2a*, pairing of gamonts; *1b,2b*, nuclear division; *1c,2c*, formation of gametes, those of unequal-sized gamonts being also dissimilar in size and with differing size of nuclei; *1d,2d*, zygotes resulting from pairing of gametes, unequal sizes of fusing nuclei demonstrating that only gametes from different tests fuse) (*821).

Although they reproduce only asexually, without production of gametes, adult specimens of both *Neoconorbina* and *Oolina* are uninucleate. The single nucleus and the small size and simple test of *Oolina* all are

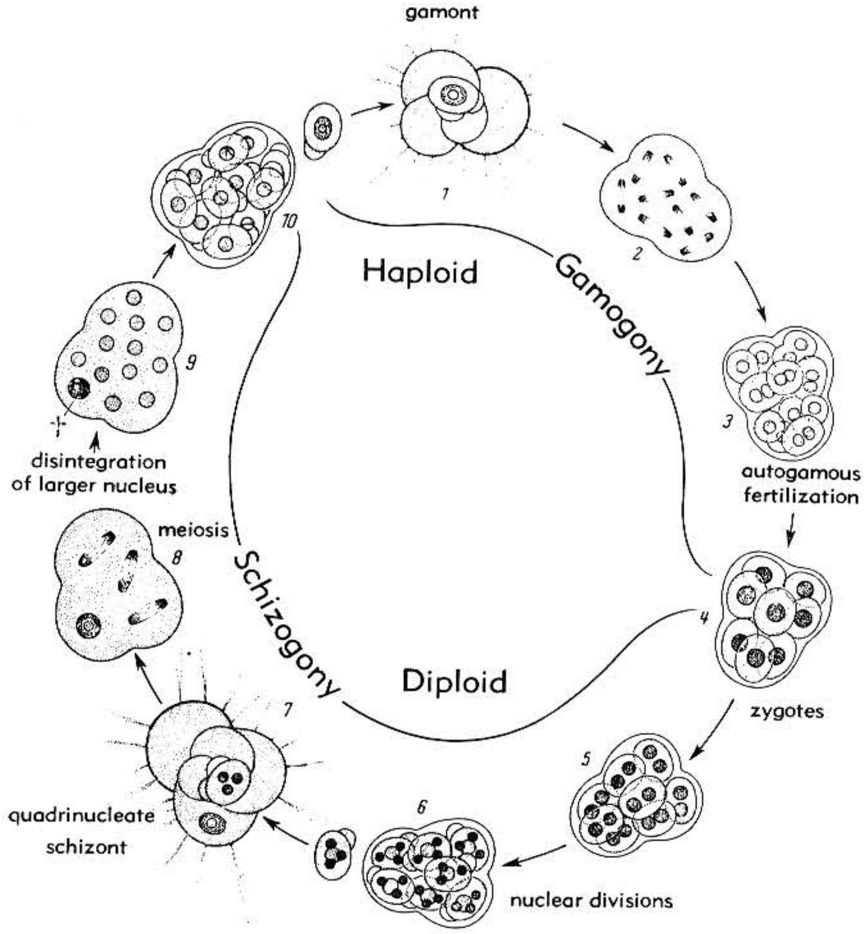


FIG. 50. Life cycle of *Rotaliella heterocaryotica* (*821).

suggestive of the gamont generation; hence, these apogamic genera may actually be represented by a gamont generation that reproduces by haploid parthenogenesis, so that the unilocular *Oolina* may be the megalospheric form and the microspheric generation may no longer exist. Bisexuality occurs in some foraminiferal species and disappearance of the gamonts of one sex may have resulted in the loss of sexual reproduction.

BUDDING AND FRAGMENTATION

In addition to reproductive cycles characterized by alternation of generations, some genera are reproduced by other methods. Fragmentation is especially characteristic of large agglutinated species (e.g., *Bathysiphon, Astrorhiza*). In *Bathysiphon* fragmentation occurs periodically and growth commonly occurs only at one end of the test. In accidental fragmentation, observed in some species, the missing parts may be regenerated and thus many specimens with repaired or restored tests are found in fossil assemblages.

Budding has been reported in certain calcareous genera, but the paired tests were interpreted erroneously as denoting plastogamic reproduction. True budding has been reported in *Halyphysema*. One or more swollen areas develop at the free end of the attached test; these gradually detach and fall to the substratum as subspherical forms with walls of sponge spicules and detritus. The scars left by detachment from the parent are soon repaired and the globular specimens move over the substratum by means of fine elongate pseudopodia. After about two days, a basal disc develops, resulting in the normal attached form.

LIFE HABITS

HABITAT

Foraminiferida are aquatic, dominantly marine protozoans, but some Lagynacea occur in fresh waters. Others are relatively tolerant and live in either brackish or marine water. Most genera are benthonic, occurring from tide pools to all known depths. Some are free-living and move slowly about over the bottom or along their algal supports by means of their elongate pseudopodia. Others occur on sandy or gravelly bottoms, where their pseudopodia may anastomose in the substratum and act as a binding agent. Some attach themselves permanently or temporarily to various seaweeds, corals, or other organisms such as mollusks, and can be found even on fragments of these organisms. Permanent attachment by means of a cement persists after death of the animal and fossil adherent foraminifers are commonly found attached to pelecypod fragments. Others may hold positions only temporarily or may be well attached during life to an alga or other readily decayable matter. These are commonly freed by its disintegration so that the specimens appear free, the attachment during life being indicated by a flattened or irregularly contorted appearance of the formerly attached side. Some foraminifers live within empty tests of other foraminifers or in polychaete worm tubes, and a few are actually parasitic on other foraminifers. A small number of genera are planktonic (Globigerinacea); some may have short pelagic stages in various parts of their life history (e.g., *Iridia, Tretomphalus*). The flagellate gametes of some species are pelagic. Foraminiferida occur in all latitudes, although some genera and species are restricted to tropical latitudes and others to polar regions.

The distribution of foraminiferal species probably is controlled by temperatures required both for existence and for reproduction. Some species tolerate temperatures from near freezing to 34°C, but the lower limit for reproductive activity is approximately 25°C. Laboratory experiments have shown that optimum temperatures for some species differ slightly from those in which they occur in nature, suggesting that such occurrences are near the limit for successful maintenance of the species. In general, a greater variety of forms occurs in warm, shallow waters, but approximately equal numbers of specimens may be found in many different environments. They have even been reported from fresh, brackish and salt water in the Sahara, at some distance from the present coast.

FEEDING HABITS

Food utilized by foraminifers consists dominantly of diatoms when these are available. Other organisms, both vegetable (algae) and animal (e.g., small crustaceans) may also be utilized. In some species (e.g., *Elphidium, Peneroplis*) a paralyzing effect of the pseudopodia on the prey has been reported but in others (e.g., *Myxotheca*) the prey may struggle for some time after capture. *Calcituba* feeds on filamentous algae. *Patellina* utilizes diatoms, infusoria, copepods, and nauplius larvae. *Peneroplis* consumes diatoms and algae, spores, small crustaceans, flagellates, and ciliates. *Globigerina* relies upon symbiotic zooxanthellae but also captures copepods. *Globorotalia* utilizes both radiolarians and diatoms as food (*1627). *Astrorhiza* has been noted to have extremely adhesive pseudopodia when feeding, capable of capturing and holding a wide variety of small organisms. It appears that the prey of this organism may be killed by exhaustion or suffocation, rather than by any paralyzing effect (*249). In some large species (e.g., *Elphidium*) the digestion of the food is carried on by the pseudopodia outside of the test. In others, especially unilocular species and those with a relatively large aperture (e.g., Miliolidae), the prey is drawn into the animal for digestion. Waste products (e.g., empty diatom frustrules) may remain in the cytoplasm until just before reproduction occurs or the waste may be condensed into small pellets (stercomata) as in *Peneroplis*. The tiny brown xanthosomes also appear in the protoplasm after feeding and are excreted from time to time. During feeding a mucus-

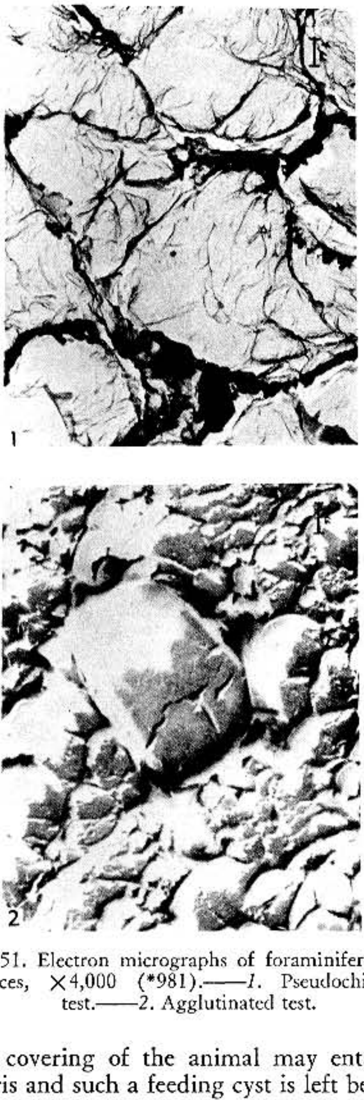


FIG. 51. Electron micrographs of foraminiferal test surfaces, ×4,000 (*981).——*1.* Pseudochitinous test.——*2.* Agglutinated test.

like covering of the animal may entangle debris and such a feeding cyst is left behind when the foraminifer moves on to another area. Feeding cysts left behind by *Elphidium* (Fig. 35) are composed of empty diatom frustrules, xanthosomes and other debris which commonly occurs in clusters near canal openings and in the pseudopodial tracks, suggesting that the purpose of the canal system in the Rotaliacea may be for the extrusion of the xanthosomes (*993, p. 71).

TEST

The test or shell of foraminifers may be relatively simple or, on the other hand, extremely complex. Adults may range in diameter from 0.02 to 110.0 mm. The wall may be membranous or pseudochitinous, constructed of agglutinated fragments held in organic, ferruginous, calcareous, or siliceous cement, or composed of secreted calcite or aragonite of varying microstructure. Because only the test occurs fossilized and because a majority of all foraminiferids have been described by paleontologists, many living species and genera have been differentiated largely or entirely by features of the shell. Mostly features of test morphology are paralleled by similarly important differences in the soft parts, cytoplasm, and nuclei, or by distinctive living habits and reproductive processes. Hence, classification based on shell characters seems not too far from a "natural" one. Mentioned briefly under different taxonomic headings in the systematic section, features of wall composition, structure, and test morphology are here outlined as a basis for later discussions.

WALL COMPOSITION AND MICROSTRUCTURE

Pseudochitinous Tests. Some of the most primitive single-chambered species have thin, easily deformable test walls that have been variously regarded as chitinous, chitinoid, pseudochitinous, keratinous, proteinaceous or tectinous. The organic material in the test of *Peneroplis* has been shown to give a protein (albuminoid) chemical reaction; hence, it is unrelated to true chitin (AVERINTSEV, 1903, *58). Many later studies have confirmed this early work. HEDLEY (1958, *889) stated that the organic matrix of the agglutinated wall of *Halyphysema* contains an acid mucopolysaccharide containing sulfuric acid groups. An organic sheath underlying the test wall gives the reaction of a carbohydrate, and apparently a protein is also present; hence, it is regarded as a mucopolysaccharide or mucoprotein.

A proteinaceous or pseudochitinous wall is present in many thecamoebians and is characteristic of the foraminiferal superfamily Lagynacea (Fig. 51,*1*). Many genera with this type of test are known in present-day faunas, but owing to their fragility they are scarce in the fossil record. A number of "chitinous" forms have been reported from acid residues of limestones (e.g., Paleozoic of the Baltic region) and are here included in the Lagynacea. Because of the method of extraction, however, it is uncertain whether or not these may have also had an additional layer of calcite or agglutinated particles which was destroyed by the acidizing. Such a basal organic layer is present in agglutinated, hyaline, and porcelaneous calcareous secreted tests, and, as mentioned under discussion of chamber formation, is usually the originally formed wall layer, which then becomes calcified or adds foreign matter to its surface. It is preserved in decalcified preparations of living forms and in some fossil ones as well, as for example in so-called microforaminifera (WETZEL, 1957, *2049).

Agglutinated Tests. Many foraminifers have tests which are partially formed organically but which also include a varying proportion of extraneous matter. Variations in this type of test wall may be shown in degree of selectivity of the foreign matter utilized, in composition of the material in which it is embedded, and in presence or absence of structures in the agglutinated or secreted layer. The foreign particles utilized in test construction reflect to some extent the local environment, so that in carbonate facies the agglutinated species may utilize carbonate grains. The density, specific gravity, and surface texture of the grains are apparently the important factors in selection of grains (*1627). Material commonly utilized includes quartz grains, various heavy minerals, clay or carbonate fragments or grains, and organic debris, including tests of smaller foraminifers, radiolarians, coccoliths, fragments of molluscan shells (e.g., *Inoceramus prisms*), and sponge spicules (Fig. 51,2).

The type of material utilized has been regarded as a feature of taxonomic importance by some authors (HOFKER, 1953, *940; AVNIMELECH, 1952, *63). Noting that some species and genera are selective in the construction of their agglutinated tests, they have used its components as a basis for generic and specific differentiation. Such procedure is not to be recommended, because variations in selection of materials are indicated both in natural occurrences and in laboratory experiments. Thus SLAMA (1954, *1798) raised several species of *Ammobaculites* in cultures that in nature had tests of silt-sized or smaller particles or some fine sand grains. When placed in aquaria with quartz beach sand, this material was utilized for building the test. When silicon carbide abrasive powder was added to the substratum, this was immediately incorporated in later chambers of tests with a coarse-grained early portion. BUCHANAN & HEDLEY (1960, *249) have noted that *Astrorhiza limicola,* found on differing types of substrate, utilized these differing materials in their tests. In cultures it readily used powdered glass and "Perspex" shavings for test construction and repair.

Similar conclusions may be reached by a mineralogical comparison of substratum (or enclosing strata) and foraminiferal test walls. LACROIX (1926, *1073) has reported that dredgings from an area in the Faroe Islands supplied specimens of numerous common species that normally have finely arenaceous tests (e.g., *Cystammina pauciloculata, Haplophragmoides canariensis, Trochammina squamata, T. rotaliformis, T. globigeriniforme, Spiroplectammina biformis*) all of which utilized calcareous coccoliths as extraneous material. The coccoliths could be dissolved in acid, leaving only the pseudochitinous base. The test of *Discammina* was observed by LACROIX (*1077) to be composed of sand in some localities, of sponge spicules in others, and to include black grains of volcanic glass in the Azores. DICK (1928, *592) found *Bathysiphon argenteus* in the Clyde estuary to contain numerous needles of rutile and flakes of mica in its test, the rutile crystals being regularly laid at right angles to the long axis of the shell. Similar rutile-bearing tests were located around the Scottish coast and across the North Sea as far as Norway, apparently coinciding with a disintegrating outcrop of rutiliferous schist on the sea floor; this schist was recognized to occur in the first-mentioned area.

GIGNOUX & MORET (*788) and BONTE (*172) also have noted that in many genera considered to have granular calcareous tests the wall structure actually was finely agglutinated; the calcareous grains derived from local lime-mud depositional environments were difficult to recognize because the cementing material also was calcareous. VENGLENSKIY (1960, *2003) has reported Miocene species with tests constructed of chalcedony grains (similar grains occurring in the local clays). We have observed that *Flabellammina washitensis* in the Oklahoma and Texas Lower Cretaceous (Albian) has an arenaceous test in sandy strata and utilizes coarse shell fragments in the "oyster beds" of *Gryphaea washitaensis*; in the Duck Creek Formation the test consists largely of agglutinated minute calcareous spheres (so-called *Oligostegina*).

In making X-ray analyses SWITZER & BOUCOT (1955, *1859) determined that agglutinated foraminifers include calcite, aragonite, quartz, feldspar, pyroxene, magnetite, hornblende, biotite and volcanic glass in their tests. They concluded (*1859, p. 533) that "although certain genera may choose sponge spicules rather than sand grains, they do so through a preference for certain shapes. It is most unlikely that sand grains of the same shape and size but different mineralogical composition can be distinguished by the organism. . . . The percentage of these minerals pyroxene, hornblende, and feldspar in each test is variable probably being a function of the random distribution of the mineral grains on the sea bottom."

Although the actual material used for test construction appears variable, many species have characteristic ways of orienting the fragments, such as the lengthwise alignment of sponge spicules in *Marsipella* and *Halyphysema,* the perpendicular alignment of rutile crystals in *Bathysiphon,* and the well-known example of *Psammosphaera* with a single elongate spicule carefully centered across its test. Specimens of *Gaudryina nanushukensis* in the Lower Cretaceous of Alaska and Canada commonly have finely agglutinated tests with dark mineral grains aligned along the sutures and outlining the chambers.

SULEYMANOV (1960, *1856), in a study of Upper Cretaceous *Textularia,* concluded that some species had different selective power in the same biotope, but that the species showed some variation in particles utilized according to different biotopes, and were influenced by the availability of materials. BUCHANAN & HEDLEY (1960, *249) have reported that when *Astrorhiza limicola* tests were disintegrated, the size range of particles used in the test was almost exactly the same as that of a sample of the bottom sediment from which it came and varied similarly from one locality to the next. In cultures, a portion of the test wall was removed from specimens that were then left in a container without any available grains. A membrane was secreted to cover the damaged area. If sediment was then made available, it would be added over the membrane.

The extraneous material used in test construction may be variously cemented by organic cement, calcium carbonate, hydroxides or carbonates of iron, and possibly also hydrates of silica.

In *Astrorhiza,* the organic cement has the consistency of a rigid gel. Apparently it is composed of a protein-carbohydrate material with at least some acid mucopolysaccharide (*249).

A similar composition was noted for *Halyphysema* (*889). A chitinoid or pseudochitinous lining has been reported for many agglutinated forms, but apparently is not present in all (e.g., *Astrorhiza*). In desiccated specimens dried and shriveled protoplasm may coat the interior surface of tests and appear to be an organic lining. It is not present in fresh material, although an organic membrane may be formed in repairing damage to the test. An inner organic sheath present in *Halyphysema* consists of a protein and carbohydrate complex, either a mucopolysaccharide or mucoprotein.

Iron has been reported in the tests of many agglutinated forms, either as iron salts in the organic layer (LACROIX, *1073), iron phosphate cement (CARPENTER, *277), iron oxide, or iron carbonate cement (FAURÉ-FREMIET, 1911, *713; VINOGRADOV, 1953, *2007). Iron is especially dominant in *Cyclammina cancellata* and *Cribrostomoides latidorsatum,* resulting in a characteristic red-brown color. *Rhabdammina* is high in Fe_2O_3 and occurs in abundance in the Barents Sea, where it may be an agent in iron enrichment of the sediments.

The presence of iron in the test is undoubted, but the question remains as to whether this is secreted by the animal. It is yet unproved, but the iron possibly may have been present already on sand grains of the sediment which was utilized in test construction (*249).

Siliceous cement has been reported in various members of the Rzehakinidae (e.g., *Miliammina*).

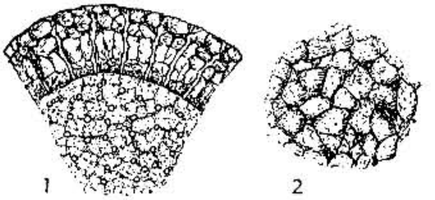


FIG. 52. Wall structure of *Textularia agglutinans* (*1075).——*1.* Fragment of wall showing internal surface of chamber with perforations at bottom and section through wall with irregular perforations, ×100.——*2.* Exterior surface of fragment showing tiny pores between sand grains, ×500.

The microstructure of agglutinated foraminiferal walls has not been much studied. Some forms are known to have a simple layering, with smoothly finished inner wall, coarser-grained central portion, and finer-grained surface covering. In addition, many agglutinated tests have fine tubules piercing the wall, which give a fibrous appearance in section (MOEBIUS, 1880, *1293). The tubules may be slightly irregular, branching or anastomosing and opening at the outer surface as tiny perforations (Fig. 52). The tubules and perforations are 1 to 4μ in diameter, but they end blindly at the inner pseudochitinous membrane; hence they are not comparable to the perforations of calcareous foraminifers. A possible osmotic connection through the pseudochitinous layer has been postulated (*1075). However, some agglutinated genera apparently do have pseudopodial connections through the wall perforations (e.g., *Psammosphaera*).

Porcelaneous Tests. The terms porcelaneous and hyaline were first used by WILLIAMSON (1858, *2065), the porcelaneous wall being described as "an opaque calcareous substance having a porcelainous aspect, and presenting, when seen by transmitted light, a rich brown or amber colour."

CARPENTER (1856, *271a) separated some of the same groups of foraminifers on the basis of the presence or absence of perforations in the wall for extrusion of pseudopodia. Those lacking such perforations, called Imperforata, had pseudopodia extending only from the aperture, whereas the Perforata commonly had pseudopodia protruding from the perforations in all visible chambers, as well as from the main aperture. REUSS (1862, *1552) and CARPENTER (1861, *272) included both porcelaneous and arenaceous foraminifers in the Imperforata, CARPENTER adding the membranous forms to the group. The presence of perforations was soon demonstrated in the agglutinated foraminifers, however, and RHUMBLER (1894, *1567) also showed that the embryonic chamber of *Peneroplis* was perforated, though the adult test is typically porcelaneous (Fig. 53). This was later observed also in the alveolinellids and *Keramosphaera*. Nevertheless, it has been conceded generally that the porcelaneous tests have a distinct structure. CORNISH & KENDALL (1888, *387) suggested that the porcelaneous ones were probably composed of aragonite rather than calcite, because they typically exhibit an opaque chalky appearance. Attempts to check this on the basis of specific gravity were inconclusive. They stated that porcelaneous foraminifers were less resistant to carbonic acid than calcareous ones, that the resistance was related to shell structure, and that opacity in fossils accompanied instability of the test in carbonated water. Others disagreed and CHAPMAN (1904, *318) stated that the porcelaneous wall was probably not aragonite, since porcelaneous species were found in the Australian Permo-Carboniferous. Because of the instability of aragonite, it would not be expected to be found in strata so old.

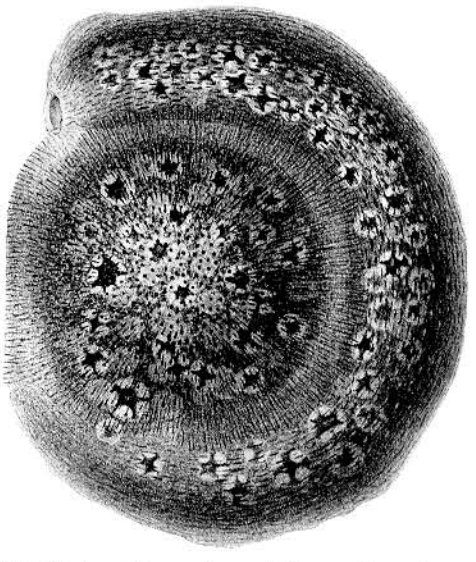


FIG. 53. Juvenile specimen of *Peneroplis pertusus* with globular, finely perforate proloculus and enrolled spiral passage, ×850 (*2068).

He added that "traces of anomalous biaxial figures under convergent polarized light" were not suggestive of calcite, and believed the porcelaneous test probably to be a mixture of organic matter and lime carbonate ("conchite"). X-ray studies by MAYER (1932, *1238) definitely showed that porcelaneous tests (e.g., *Orbitolites, Peneroplis, Quinqueloculina*) were composed of calcite and not aragonite.

Magnesium carbonate was reported to occur with calcite in many foraminiferal tests (VINOGRADOV, 1953, *2007), and a higher percentage (5-12.5 per cent) of the test was found to be $MgCO_3$ in porcelaneous tests (e.g., *Orbitolites, Pyrgo*). It is not present as dolomite, for it was never found in the correct ratio of $MgCO_3$ to $CaCO_3$; the form in which it does occur is unknown. CHAVE (1954, *328) analyzed a number of porcelaneous and hyaline tests for $MgCO_3$. The percentage of $MgCO_3$ was found to be highest in tests from warm waters. Unfortunately, the specimens examined were not identified specifically. Most of the porcelaneous forms were from Bermuda, Florida Keys, and Palau (water temperatures 23.0° to 28.0°C) and contained 11.5 to 15.9 per cent of $MgCO_3$. One specimen of *Triloculina* from Maine (water temperature 6.0°C) had only 6.7 per cent $MgCO_3$. Most of the hyaline species examined were from colder water. He concluded that three factors influenced the magnesium content—skeletal mineralogy, water temperature, and "phylogenetic level of the organism." VINOGRADOV (1953, *2007) regarded the occurrence of $MgCO_3$ as a characteristic of porcelaneous foraminifers (5-12.5 per cent) in contrast to hyaline calcareous ones (3-5 per cent). This was based on a total of 17 species examined by VINOGRADOV, as compared with 23 species studied by CHAVE. In view of the small amount of data yet available, the relative importance of these factors is still undetermined. It is not known whether magnesium is an important genetic factor of the porcelaneous wall or an accidental inclusion, perhaps resulting from environmental factors.

LACROIX (1923, *1072) described a "chitinous" base to the porcelaneous test, stating that when Recent specimens were decalcified the residue was a fine transparent membrane which completely lined the chamber interior. Slightly yellowish in thicker areas, it is resistant both to dilute and concentrated acetic acid, hydrochloric acid, sulfuric acid, and nitric acid, and it is not attacked by ammonium, potassium or sodium hydroxides. However, hypochlorites (Javel water, liqueur of Labarraque) rapidly dissolved it. He regarded the substance as similar to insect wings and therefore composed of chitin. He noted that it is alterable like an albuminoid substance and might be destroyed in dead specimens. Porcelaneous species become membranous or "chitinous" in low-salinity areas (e.g., estuaries, brackish-water lagoons); hence, the "chitinous" membrane was regarded as the basis, which is normally impregnated with calcareous salts. It has been concluded that true chitin does not occur in protozoans, the substance being proteinaceous instead. Protein was reported by VINOGRADOV (1953, *2007) to be present in the tests of Miliolidae. CUSHMAN & WARNER (1940, *533) reported the presence of cryptocrystalline calcite and chitin mixed throughout the wall of *Cornuspira* (=*Cyclogyra*), *Sigmoilina, Massilina* (with some foreign matter also), *Peneroplis, Sorites, Archaias, Marginopora,* and *Alveolinella.*

WOOD (1949, *2073) studied porcelaneous tests optically and stated that in ordinary light they appear to be homogeneous, and "between crossed nicols the test invariably shows low polarization tints, greys and yellows of the first order, whatever the thickness of the section. . . . In a number of forms . . . a multitude of tiny flecks may be observed between crossed nicols, which are the individual crystals of the wall." The crystals are roughly equidimensional, subangular, and not elongated, approximately 1.5μ in diameter, and without constant crystal orientation (which explains the low polarization colors, since the crystals compensate for each other within the thickness of the section), although in some forms a preferred orientation seemed recognizable in specimens from the same locality. The porcelaneous test also shows a tendency toward recrystallization, the crystals becoming slightly larger and the characteristic brown color disappearing. The test remains opaque, however, "the light being lost by scattering and total internal reflection at the multitude of boundaries."

The cause of brown color in Recent porcelaneous foraminifers was thought by SOLLAS (1921, *1811) to be due to scattering of light by the tiny crystals and by CUSHMAN & WARNER (1940, *533) to be caused by organic matter (pseudochitin). WOOD (1949, *2073) commented that the organic matter left in decalcified specimens was colorless. On the basis of spectrographic and X-ray analysis of Recent and fossil specimens, he noted that a Recent specimen in X-ray showed smaller lattice spacings and a crystal size between 0.5 and 5μ. The smaller spacing was regarded as possibly due to some magnesium or iron substituted for the calcium. In the fossil form the lattice spacing is identical to that of pure $CaCO_3$ and the crystal size greater than 5μ. Spectographic analysis showed that lead was present in Recent but not fossil tests, suggesting that the brown color might be due to traces of lead.

Some porcelaneous genera and species may have a surficial arenaceous coating over the characteristic porcelaneous wall (e.g., *Ammomassilina, Dentostomina, Nodobacularia, Nubeculina, Schlumbergerina, Sigmoilopsis, Siphonaperta,* some *Quinqueloculina*).

Microgranular Tests. Paleozoic calcareous foraminifers belonging to the Parathuramminacea, Endothyracea, and Fusulinacea have a distinctive wall structure. It consists of very tiny calcite crystals which are equidimensional, subangular, and tightly packed. In thin sections the wall commonly appears dark, because of loss of light by reflection and internal refraction. The crystals are of similar size in specimens from different areas and not comparable to grain size of the surrounding matrix; hence, the granularity seems to be a characteristic of the shell itself rather than predominantly an agglutination of calcium carbonate particles from the sea bottom, although some foreign matter may be included. Secreted secondary deposits also occur in older chambers, further suggesting a secreted origin of the entire test. When the granules are regularly aligned, the resultant wall is fibrous or pseudofibrous in appearance. Various genera may have more than one wall layer (up to four layers) in differing combinations of microgranular and fibrous layers. Recrystallization may obscure the different layers.

Microstructure of the sort just noted was first described by BRADY (1876, *193), who regarded it as agglutinated calcareous grains in a calcareous cement. He was followed in this belief by others, including CUSHMAN (1948, *486). VON MÖLLER, 1878 (*1568b), stated that *Endothyra* was not arenaceous but perforate. Others described the endothyroid test as arenaceous or subarenaceous. GALLOWAY & HARLTON (1928, *763) regarded calcareous species as primitive and arenaceous ones as derived later, describing the wall of *Endothyra* as "calcareous, thick, opaque, imperforate, without or with inner, meshwork layer, not of agglutinated particles," and stating that the "exceedingly fine calcite crystals . . . resulted from the crystallization of the original calcareous walls. . . ." WOOD (1949, *2073) noted the resemblance of the granular endothyroid wall to that of recrystallized alveolinids and regarded as uncertain "whether the test of an *Endothyra* has recrystallized from a minutely crystallized secreted test or was secreted in nearly its present state." It was probably not agglutinated and not recrystallized from the radial hyaline type of wall, since crystals tend to increase in grain size when recrystallization occurs. Some genera seem to be particularly susceptible to such recrystallization (e.g., *Loeblichia*) (CUMMINGS, *398; FOMINA, *728).

REYTLINGER (1950, *1560) divided Paleozoic smaller foraminifers into six groups based on wall structure, as follows: (1) dark micrograined walls with very fine calcite grains and fine perforations; (2) walls of gray or yellow color, consisting of small, elongate, light-colored grains resulting in a fibrous appearance, and including some large angular grains, such walls being susceptible to differentiation into two layers; (3) coarse-grained and agglutinated walls with much calcareous cement; (4) coarsely perforated walls (e.g., *Bradyina*) with simple to dentritic pores and possibly with agglutinated material; (5) hyaline-radial perforate walls which may have an interior darker layer (e.g., Archaediscidae, some Nodosariidae); and (6) micrograined walls of grayish, yellowish or brownish color (e.g., *Agathammina*). REYTLINGER regarded only groups 1, 5, and 6 as secreted, the others being walls consisting of mixed agglutinated and secreted material. She concluded that wall structure was not a stabilized feature but might vary according to local conditions. All of the above-mentioned wall variations are found in the suborder Fusulinina, as here recognized, the more complex walls of numerous layers characterizing the more advanced genera.

Hyaline Calcareous Tests with Perforate Radial Walls. Foraminiferida with hyaline calcareous perforate walls have long been recognized as having differing optical characteristics when viewed with polarized light. SORBY (1879, *1813, p. 64) stated, "Their shell is often composed of small prisms of calcite having their principal axis perpendicular to the surface of the shell. The result is that each cell gives rise to a black cross and colored rings when seen with polarized light. In some cases, however, the calcite has not been deposited symmetrically round each cell, but occurs in smaller radiate groups, and occasionally nothing can be seen but granules without definite optical arrangement." Not until 70 years later were these differences regarded as significant in classification. WOOD (1949, *2073) systematically examined hundreds of species from many families under polarized light and found that the larger percentage of hyaline tests had a perforate radial microstructure and that most of those with perforate granular structure were dominantly members of a few families. In the dozen years since then an increasing number of descriptions have included such optical characteristics as part of the diagnoses. Additional studies (both published and previously unpublished observations herein included) have resolved many of the seeming anomalous situations noted by WOOD.

WOOD examined intact small specimens (e.g., *Lagena*) which between crossed nicols showed a black cross with concentric rings of color, "closely mimicking a typical (negative) uniaxial interference figure . . . the test is built of crystals of calcite with their *c*-axes normal to the spherical surface." Each spine of *Globigerina* is a single crystal of calcite and because of its elongation along the *c*-axis of the crystal, extinction in polarized light is absolutely straight. The hyaline appearance thus is due to the radial wall structure, but radially built tests are only hyaline in appearance when thin-walled and finely perforate. The hyaline appearance is less noticeable in forms with a considerably thickened test or with coarser pores (which bend the light rays, reflecting and refracting the light). Larger or thicker specimens must be crushed or thin-sectioned in order to obtain required information. In the systematic part of the present work, generic descriptions state that the test is granular or radial only if the type-species has been examined to determine this character. We have checked this by the method of crushing specimens, believing it to be the most reliable. Although placement in one or another family or superfamily should so indicate, it has been impossible to obtain specimens for examination of all type-species and because superficially similar species may actually not be congeneric, the use of some other species is inconclusive for placement of a genus.

KRASHENINNIKOV (1960, *1052) divided radial microstructure into coarsely radial, finely radial, and indistinctly radial types, noting that some modification of the structure might occur in the ornamentation and that the inner part of the wall best shows the permanent or characteristic microstructure.

Hyaline foraminiferal species, unlike microgranular-fibrous or porcelaneous ones, do not include agglutinated matter in the wall except for particles accidentally intruded during chamber formation. The species described as *Globulina arenacea* BROTZEN (1948, *241) and reported by BIGNOT & NEUMANN (1962, *138) as possessing a hyaline test with superficial agglutinated layer, does not belong to this genus, but should be referred to *Nouria, Uvigerinammina,* or some similar form.

As noted below, not only are hyaline radial walls commonly composed of calcite crystals, as stated by WOOD, but aragonite-walled genera also have such a radial microstructure, some having an almost porcelaneous appearance because of their thicker walls (e.g., *Epistomina*). In some perforate, radial-walled genera portions of the wall may be imperforate (septa, supplementary deposits) but the microstructure is radial, nevertheless.

Hyaline Calcareous Test with Monocrystalline Walls. The Spirillinidae tend to have tests composed of a single crystal of calcite, or more rarely consisting of several large crystals with irregular boundaries.

They are not of radial hyaline appearance. The pores pass through the single crystal, not between crystals as in the hyaline radial forms, hence are angular in outline and irregularly distributed.

Hyaline Calcareous Tests with Perforate Granular Walls. As originally noted by SORBY (1879, *1813) not all foraminiferal tests show a characteristic black cross in polarized light, but instead, some have a granular appearance. WOOD (1949, *2073) stated, "Seen between crossed nicols such forms show a multitude of tiny flecks of colour." Their minutely granular nature is visible in thin section, the granules being equidimensional and sutured together. A faint speckled appearance of the surface is noted in polarized light, owing to different grain orientations and resultant differences of refractive index. Some granular forms may even appear granular in reflected light, whereas others are so thin-walled as to appear hyaline; accordingly, the only reliable method of determining wall structure is by crushing or sectioning a specimen and viewing it with polarized light.

Ehrenbergina hystrix BRADY was stated by WOOD (1949, *2073) to have a radially built wall, whereas *E. hystrix glabra* HERON-ALLEN & EARLAND was described as having granular microstructure. This has been cited commonly as proof of the unreliability of this wall character for taxonomy. Interestingly, *E. hystrix* was stated by HOFKER (1951, *928c) to be biserial throughout and to have apertural furrows and a complex tooth plate similar to that of *Buliminella*; hence, relationship to that genus was postulated. Other species of *Ehrenbergina* (e.g., *E. pacifica*) do not have such apertural furrows and were said to have a triserial base of two whorls before the biseriality developed and to have a tooth plate similar to *Cassidella* (=?*Fursenkoina*). The apertural appearance of *E. hystrix glabra* as originally illustrated also appears much closer to the Caucasinidae and Cassidulinidae—in fact HERON-ALLEN & EARLAND themselves (1932, *916, p. 360) stated that they regarded it as "merely spinose variations of the dominant local species *E. pupa* . . . and that it would have been more correctly placed as var. *spinosa* of *E. pupa*, than as var. *glabra* of *E. hystrix*." According to WOOD (1949, *2073), the wall of *E. pupa* is granular in structure. Apparently here also species of two distinct genera were erroneously associated and incorrect relationships postulated because of their nomenclatural association.

Spicular Tests. *Carterina*, the only known representative of this wall type, has a test composed of numerous elongate fusiform spicules each consisting of a single crystal of calcite, with its *c*-axis parallel to the length of the spicule.

Mineralogical Composition of Calcareous Walls. As previously noted, hyaline calcareous foraminifers may have a perforate radial, perforate granular, monocrystalline or spicular microstructure. They may also be divided into two main groups on the basis of their mineralogical nature, that is, composed of calcite (hexagonal crystal form of $CaCO_3$) or aragonite (orthorhombic form). In early studies porcelaneous forms were thought to be aragonitic, but later this was disproved.

Investigations of tests of *Globigerina* and *Amphistegina* by BÜTSCHLI (1908, *256) have indicated that they consist of calcite. CLARKE & WHEELER (1922, *346) tested *Polytrema* with cobalt nitrate (Meigen's reaction) and SCHMIDT (1924, *1673) examined *Lagena* and *Globigerina*, this work showing that all have calcitic shells.

MAYER (1932, *1238) X-rayed various porcelaneous species as well as the hyaline *"Globigerina cretacea," G. marginata* (=*Globotruncana*), *Nummulites laevigatus, Operculina ammonoides,* and *Fusulina* sp., proving that all have walls composed of calcite.

Nevertheless, BANDY (1954, *73) determined that a few genera were aragonitic, using Meigen's reaction. These included *Hoeglundina, Ceratobulimina, Pseudobulimina, Lamarckina* and *Colomia,* as well as *Bigenerina irregularis* from the Gulf of Mexico. Of approximately 2,000 species contained in the 35 samples treated, only 11 were found to have aragonite tests (4, Cretaceous; 4, Eocene; 3, Recent). A few Miocene specimens of *Hoeglundina* did not give a good reaction. The *Colomia* was also checked by X-ray analysis. BANDY concluded that "(1) aragonite is quite stable in the shells of mollusks, (2) the cementing material in some arenaceous Foraminifera may prove to be aragonite, and (3) there is no very close relationship between the genera represented by the aragonitic species in the study."

TROELSEN (1955, *1952) believed that a systematic value of test composition was indicated, because (excepting *Colomia* and *Bigenerina*) the foraminifers examined by BANDY and found to be aragonitic all belong to the Ceratobuliminidae and Robertinidae. TROELSEN made additional tests for aragonite, also by Meigen's reaction, using samples from Lower Cretaceous, Paleocene, lower Eocene, middle Oligocene, lower Miocene, upper Pliocene, Pleistocene, and Recent deposits. Ten samples and additional isolated specimens included some 28 species found to be aragonitic, all belonging to these two families. Genera identified by TROELSEN as aragonitic include *Lamarckina, Ceratobulimina (Ceratobulimina), C. (Ceratolamarckina), C. (Ceratocancris), Cerobertina, Epistomina, Epistominoides, Robertina, Robertinoides, Geminospira, Alliatina,* and *Cushmanella.* Specimens of *Alabamina, Osangularia, Pulsiphonina, Eponidella, Asterigerina,* and *Asterigerinata,* all of which had been referred to the Ceratobuliminidae but previously stated by TROELSEN to be unrelated to this family on the basis of internal structure, when examined by Meigen's reaction, were found to have calcitic tests, thus upholding earlier morphologic separation.

BRAY (1944, *204) regarded Meigen's reaction as less reliable than X-ray analysis, stating that calcite of small particle size might give an aragonite reaction. In addition, small amounts of magnesium at times gave an erroneous aragonite reaction, both with Meigen's reaction (cobalt nitrate test) and by means of Feigl's reagent (manganous sulfate solution containing silver sulfate). BRAY cited other methods for testing calcite and aragonite, such as specific gravity (2.72 for calcite, 2.93 for aragonite), solubility in H_2CO_3, and optical methods (calcite being optically uniaxial, aragonite biaxial), but regarded results obtained from these as unreliable. The chemical methods are particularly unreliable if the material has a slightly chalky consistency. Possibly these reasons explain the aragonite reaction of *Bigenerina* noted by BANDY, using the cobalt nitrate method. Erroneous results may have been due to small particle size of the cement or agglutinated grains, or the agglutinated particles might have been aragonitic. No sufficient proof seems to indicate that the cement itself is aragonitic and an X-ray determination would be of interest in this connection.

A discussion of the X-ray powder diffraction method has been given by SWITZER & BOUCOT (1955, *1859), with data on a number of genera tested by them. They noted that all porcelaneous forms examined were calcitic, as had been observed earlier, that most hyaline forms also were calcitic, and that aragonitic ones included only those previously noted by BANDY & TROELSEN (*Colomia, Hoeglundina, Ceratobulimina*). A Recent *Textularia* was found to contain both calcite and aragonite, and a few calcitic forms were found to be replaced or filled with heulandite.

TODD & BLACKMON (1956, *1939) substantiated TROELSEN's statement as to the generic significance of mineralogical composition, concluding that aragonitic genera are related at the family level. A description was given of their method. In a few instances the X-ray analysis of an unbroken specimen indicated the presence of minor amounts of aragonite with the calcite. After specimens were dissected and detrital material removed from the interior, diffraction patterns were taken of the cleaned test fragments. Each such fragment was found to consist of only one of the minerals.

Although secretion of calcite and aragonite may be variable in some higher organisms, or both may be secreted in different shell layers in some forms, this does not apply to the foraminifers. Specimens of an aragonitic genus are invariably aragonitic, regardless of ecologic or geologic occurrence, those tested by TODD & BLACKMON ranging in depth from 27 to 494 fathoms and in latitude from the tropics to the Arctic.

In 1879 SORBY (*1813) stated, "Rose long ago suggested that the presence of well-preserved shells of some genera along with mere casts of other genera might be attributed to the fact that those which are preserved were calcite and those removed were aragonite." Sorby also noted that living *Mytilus edulis* has a shell wall with an outer calcitic layer and an inner aragonitic layer. In raised beaches the shells of this species showed the outer calcitic layer well preserved, whereas the inner layer (aragonite) had been completely removed. He added, "If this is the case in different layers of the same shell, why should it not happen in different shells which are composed entirely of the one or of the other mineral?" We have examined many specimens of foraminifers of many ages and from many localities, without ever having seen a specimen of a normally aragonitic genus that was converted to calcite; included are fossils as old as Early Jurassic *(Reinholdella)*. From strata of any age, specimens referable on a purely morphologic basis to the Epistomininae, Ceratobuliminininae, and Robertinidae have always been found to be aragonitic if any shell material is preserved. Under conditions unfavorable for preservation of aragonite, the wall is dissolved or otherwise destroyed, so that only a steinkern remains (e.g., *Epistomina*), although normally calcitic genera are preserved as complete tests. Possibly size or shell structure may have an effect in accentuating this factor in preservation of foraminifers.

Chemical Composition of Calcareous Walls. Very few detailed analyses have been made of the tests of foraminifers. A few were given by Brady (1884, *200) and Clarke & Wheeler (1922, *346); these have been summarized in tabular form by Vinogradov (1953, *2007) (Table 1). At that time only 17 analyses of calcareous foraminifers, including both hyaline and porcelaneous species had been published. Benthonic species were shown to have up to 12.52 per cent of $MgCO_3$, but planktonic species had less. He also noted that early stages of *Sphaeroidinella dehiscens* and *Globorotalia menardii* were low in $MgCO_3$, as in *Globigerina*. Chave's (*328) examina-

Table 1. *Composition of Tests of Calcareous Foraminiferida*[1]

Species[2]	$CaCO_3$	$MgCO_3$	Fe_2O_3	SiO_2	Family	Locality	Author[3]
Globigerina bulloides	93.14	0.57	1.72	1.57	Globigerinidae	....	*200
G. bulloides	91.32	0.30	2.72	1.83	Globigerinidae	....	*200
G. bulloides	92.54	0.87	1.25	1.36	Globigerinidae	....	*200
Pulvinulina menardii [*Globorotalia*]	77.02	3.67	3.98	(15.33)	Globorotaliidae	40°34'N, 66°09'W	*346
Operculina complanata	93.60	4.8	0.1	0.9	Nummulitidae	....	*200
Sphaeroidina dehiscens [*Sphaeroidinella*]	84.38	1.79	4.94	8.89	Globigerinidae	Philippine Is.	*346
Amphistegina lessonii	92.85	4.9	trace	0.3	Amphisteginidae	Cape Verde Is.	*200
Orbitolites complanata laciniata [*Marginopora vertebralis*]	86.46	12.52	0.68	0.58	Soritidae	Fiji, Pacific	*200
O. complanata laciniata [*M. vertebralis*]	88.2	8.8	......	0.3	Soritidae	Fiji, Pacific	*200
O. complanata laciniata [*M. vertebralis*]	88.74	9.55	......	0.14	Soritidae	Fiji, Pacific	*200
O. complanata laciniata [*M. vertebralis*]	87.91	10.50	......	0.11	Soritidae	Fiji, Pacific	*200
O. marginatis [*Sorites marginalis*]	89.01	10.55	0.13	0.31	Soritidae	Tortugas, Fla.	*346
Orbiculina adunca [*Archaias angulatus*]	89.76	10.04	0.09	0.11	Soritidae	Key West, Fla.	*346
Quinqueloculina auberiana	90.11	9.33	0.56[4]		Miliolidae	Tortugas, Fla.	*346
Polytrema mineaccum [*Miniacina miniacea*]	88.76	11.22	0.02[4]		Homotremidae	Bahamas	*346
Tinoporus baculatus [*Baculogypsina sphaerulata*]	88.70	11.08	0.19	0.03	Calcarinidae	Australia	*346
Biloculina sp.	92.05	......	......	......	Miliolidae	....	*200

---

[1] Given as percentages of ash.

[2] Currently recognized specific names given in square brackets.

[3] Index numbers refer to authors in "References" (p. 797).

[4] Combined Fe_2O_3 and SiO_2.

TABLE 2. *Grouped Percentages of Elements in Tests of Calcareous Foraminiferida*

	>10	10-1	1-0.1	0.1-0.01	0.01-0.001	<0.001
Amphistegina radiata (Red Sea)	Ca	Si, Mg, Na, Sr	Al	Mn, Fe	Ti, Pb, Sn, Cr, V, Cu, Ag, Ba, B	
Amphistegina radiata (Bikini)	Ca	Mg, Sr	Si, Na	Al, Fe	Mn, Ti, Cr, V, Cu, Ba, B	Pb, Ag
Calcarina defrancii (Bikini)	Ca	Mg, Na, Sr	Si	Al	Mn, Ti, V, Cu, Ba, Fe, B	Pb, Ag, Cr
Amphisorus hemprichii (Red Sea)	Ca	Si, Mg, Sr, Na		Al	Mn, Ti, Cr, V, Cu, Fe, Ba, B	Pb, Ag

tion of 23 species gave the percentage of $MgCO_3$ in each (ranging from 0.33 per cent in Alaskan *Elphidium* to 15.9 per cent in an *Orbitolites* from Palau). No specific determinations were given of the forms tested and the small number makes it uncertain whether the presence of $MgCO_3$ is related to the taxonomic position of the specimens, to water temperature, or to microstructure of the wall. CHAVE believed the temperature to be a controlling factor in contrast to VINOGRADOV, who judged that the porcelaneous *vs.* hyaline nature of the test is more important.

SAID (1951, *1614) made spectrographic analyses of three Recent species from the Red Sea and from Bikini atoll. Seventeen elements were recorded, a large percentage consisting of alkaline earth metals (Ca, Sr, Ba). The strontium (1 to 5 per cent) is higher than in any other recorded marine invertebrate except for the Acantharia. Potassium is rare (less than 0.01 per cent), but sodium is recorded in high quantities (0.5 to 7 per cent), silicon ranged from 1 to 5 per cent, and magnesium was present in rather large quantities. "It was noted that the amount of magnesium varies considerably with little range in temperature." Boron was present in minor quantities (0.001 to 0.003 per cent), and aluminum, iron, vanadium, lead, and silver occur. *Amphistegina radiata* was examined from both areas and was found to have a different composition in the two areas (Table 2). SAID concluded that "chemical composition of the test cannot be used in classifying Foraminifera or in tracing evolutionary lines."

Spectrographic and X-ray analyses of 11 species of planktonic foraminifers have been made by EMILIANI (1955, *704), who found the shell material to be nearly pure calcite, with about 0.11 per cent of strontium substituted for calcium in the calcite structure. Small amounts of several elements were present, but most of these apparently were contaminants, only the silica and manganese being regarded as possibly associated with the shell material. Manganese incrustations were observed on the surface of some tests; hence this may also be a contaminant even when no incrustations are visible. Trace elements were examined in planktonic foraminifers by KRINSLEY (1960, *1056). Of seven elements studied (Mn, Ti, Al, Mg, Sr, Cu, Ni) manganese concentration seemed to be related to locality and possibly to age rather than to species; the amount of magnesium observed was complicated by sedimentary magnesium that could not be successfully removed from the sample; the aluminum and titanium were also regarded as contaminants; the copper appeared constant with respect to geographic location, but not to species; and the strontium appeared to be biogenic and relatively stable from one sample to another.

Walls of Lamellar Character. Foraminiferal tests of agglutinated, microgranular, and porcelaneous microstructure commonly are nonlamellar, each chamber being added separately, commonly without noticeable overlap of earlier formed chambers by later ones. In contrast, hyaline calcareous forms are lamellar, for with each new chamber added a layer (lamella) is added over the exterior of the entire previously formed test, so that the early chambers have much thicker walls than late ones, with the distinct layers visible in section. This has been recognized by workers for more than a century. Recently the lamellar character has been restudied and three distinct types were noted. SMOUT (1955, *1804) observed that the Rotaliidae have a lamellar test, lamellae being added also against the face of the previously formed chamber but enclosing a space between the septal layers which functions as a canal system. He separated from the superfamily Rotaliidea (=Rotalîacea) the forms with single-layered septa, which he placed in the superfamily Discorbidea (=Discorbacea). REISS (1958, *1530) substantiated this division but added a third (bilamellid) type of wall, with primarily doubled septa. REISS regarded the lamellar characters as more reliable than wall microstructure (hyaline perforate, radial, granular) or than apertural features (utilized in suprageneric classification by HOFKER, 1951, *928c). Both microstructure and lamellar characters are cited in the classification here used. Unfortunately, not all genera have been checked to date as to lamellar characters or microstructure, and the placement of some may need to be changed when additional information is available. All genera for which this is known have statements to that effect in the generic descriptions. Lamellar nature is best demonstrated in thin sections of tests with perforate radial wall structure, those with granular walls showing less distinct parting lines between successive lamellae. In any form recrystallization in preservation may obliterate visible layering.

The simplest type of septa and test wall in multilocular foraminifers was defined by CARPENTER, PARKER & JONES (1862, *281) as having the septum "that divides each chamber from its successor being formed solely by the anterior wall of the older, which serves as the posterior wall of the newer." In agglutinated species and most microgranular and porcelaneous calcareous genera the new chamber attaches to the previous one, but little overlap or layering occurs (Fig. 54). In some porcelaneous forms (e.g., *Planispirinella*) an involute coil may result in the appearance of layering in axial sections, but equatorial sections show the test to be nonlamellar.

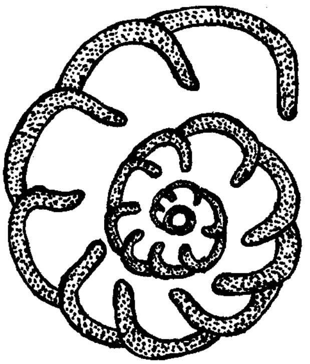


FIG. 54. Diagrammatic section of nonlamellar test (*2117).

In hyaline calcareous species, a layer of shell material is added over all exposed parts of the test at the time each new chamber is added, earlier parts of the test thus developing a secondarily thickened wall (supplementary skeleton or secondary deposits). The septa remain unthickened (Fig. 55,*1*). This monolamellar wall is characteristic of the Nodosariacea, Buliminacea, and Robertinacea of present classification, and is also found in simpler families of the Cassidulinacea (e.g., Nonionidae, Caucasinidae, Pleurostomellidae).

Calcareous foraminifers having a rotaliid type of lamellar wall structure are distinguished by the presence of doubled septa. In addition to the new chamber and layer of shell material deposited over the test exterior, a septal flap is formed against the previous apertural face, resulting in a double septum. The new apertural face is monolamellar, the earlier septa being secondarily doubled; a cavity remains between the two septal layers forming part of a canal system. This canal system and the secondarily doubled septa were first utilized taxonomically by CARPENTER, PARKER & JONES (1862, *281), as a basis for generic separation of the larger discoidal foraminifers. More recently SMOUT (1955, *1804) separated the superfamilies Discorbidea and Rotaliidea on the basis of distinction between monolamellar and rotaliid septa with enclosed canal system (Fig. 55,*2*).

In foraminifers with bilamellar structure, the wall of each new chamber is double, with an outer layer covering the new cham-

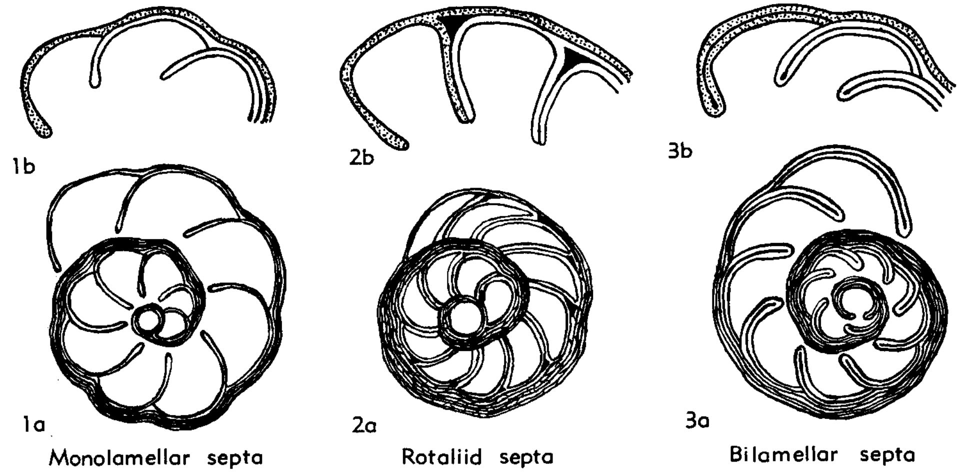


FIG. 55. Diagrammatic sections of lamellar tests.——*1a,2a,3a*. Equatorial sections showing lamellar development.——*1b,2b,3b*. Final three chambers showing their lamellar character (last added chamber and lamella indicated by stippled pattern) (*2117).

ber and entire previously formed test, similar to the entire monolamellar wall but with a second and inner layer lining only the newly formed wall of the new chamber. This adheres to the margin of the previous septum and previous whorl where overlapped by the new chamber. The septa are thus primarily double and the apertural face of the final chamber is also doubled. This type of wall may also enclose a canal system. It is characteristic of the radiate-walled superfamily Orbitoidacea and of some families of the granular-walled Cassidulinacea (Osangulariidae, Anomalinidae) (Fig. 55,*3*). The so-called "three-layered" foraminiferal walls of HANZAWA (1962, *875) include both bilamellid and rotaliid septal types, the parting lines and canal system which appear as a dark line in sections being regarded as a third layer by HANZAWA. Others have considered it to represent an original pseudochitinous membrane. According to REISS (1958, *1530, p. 55) "the dark lines produced at the contact surfaces of consecutive main lamellae in thickened parts of the test cannot be compared with the dark lines between the outer or main lamella and the inner lining in the Bilamellidea." The latter spaces were regarded by REISS as not representing original hollows or the position of a former pseudochitinous membrane. He believed the spaces between the main lamella and inner lining in bilamellid forms to have been filled originally by protoplasmic matter communicating through the walls by means of canalicules. They are located within the walls of individual chambers and therefore are canal systems. The interlamellar dark lines between laminae in thickened areas of the test are of different origin and represent parting lines or contact surfaces.

TEST, CHAMBER FORM AND ARRANGEMENT

Chamber form and arrangement and resultant test form are extremely varied in the Foraminiferida. Chamber form may be globular or spherical, ovate, pyriform, tubular, cyclical, hemsipherical, clavate, radial elongate, tubulospinate, angular (conical, rhomboid, truncate) or fistulose (Fig. 56).

Chamber arrangement may be rectilinear, arcuate, zigzag, planispiral (evolute, involute), peneropline, low or high trochospiral, biconvex, plano-convex, with elevated spiral side (spiroconvex) or elevated umbilical side (umbilicoconvex), streptospiral, milioline, uniserial, biserial, triserial, quadriserial, or multiserial. Biformed or triformed tests may result from various combinations of these (Fig. 57).

According to form of the chamber itself unilocular tests may be irregular in outline, tubular, globular, hemispherical, conical, enrolled, dendritic, arborescent, stellate, radiate, or bifurcating (Fig. 58). Multilocular tests may have any of the above forms, or be flabelliform, lanceolate or palmate, lenticular, umbilicate, umbonate, discoidal or

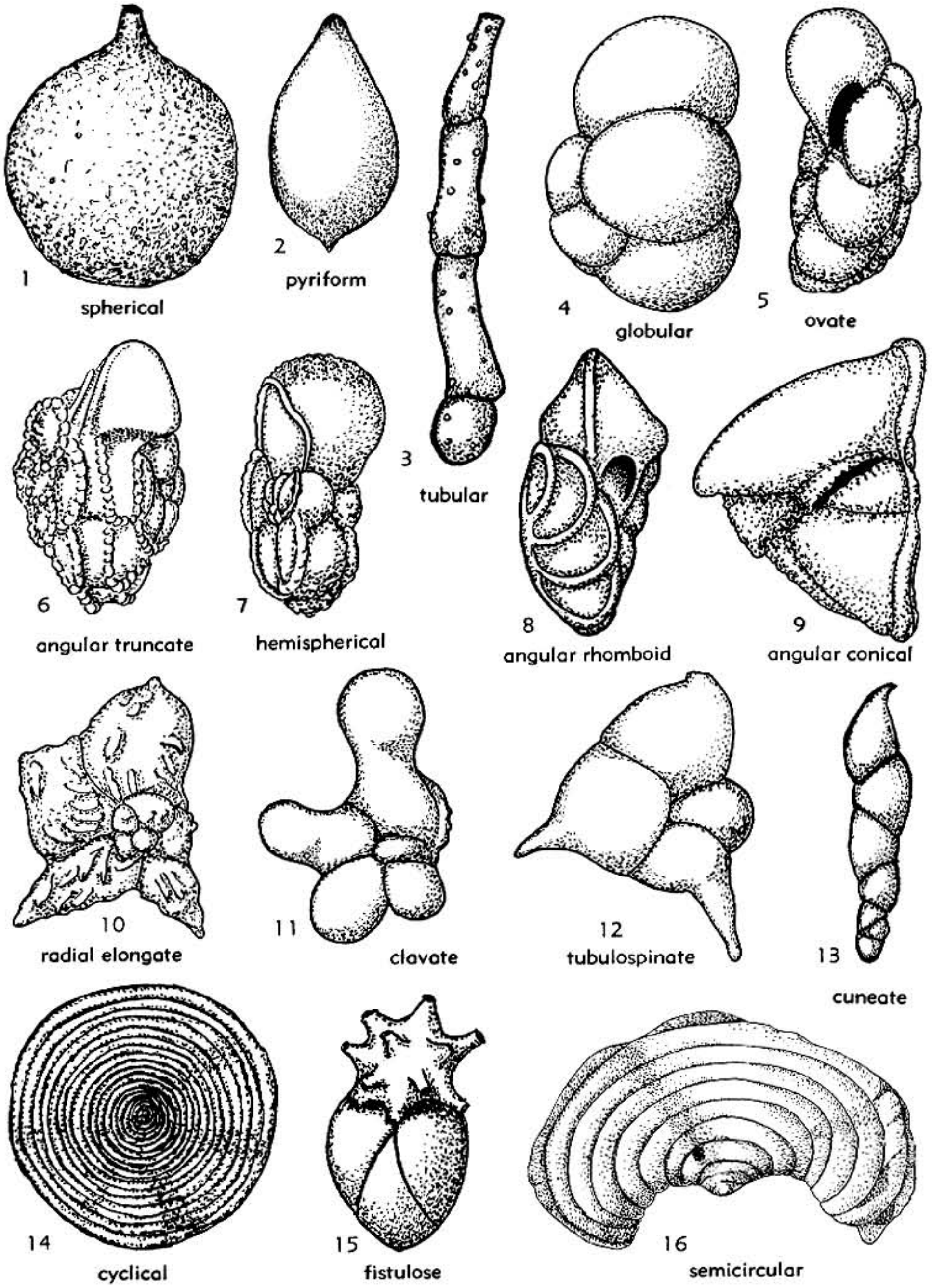


Fig. 56, *1-16*. Shapes of chambers in foraminiferal tests (*2117).

fusiform (Fig. 59). Chamber form and arrangement are not always visible externally, although a knowledge of this is required in any detailed study of foraminifers. When not externally visible, the chamber arrangement may be determined in various in-

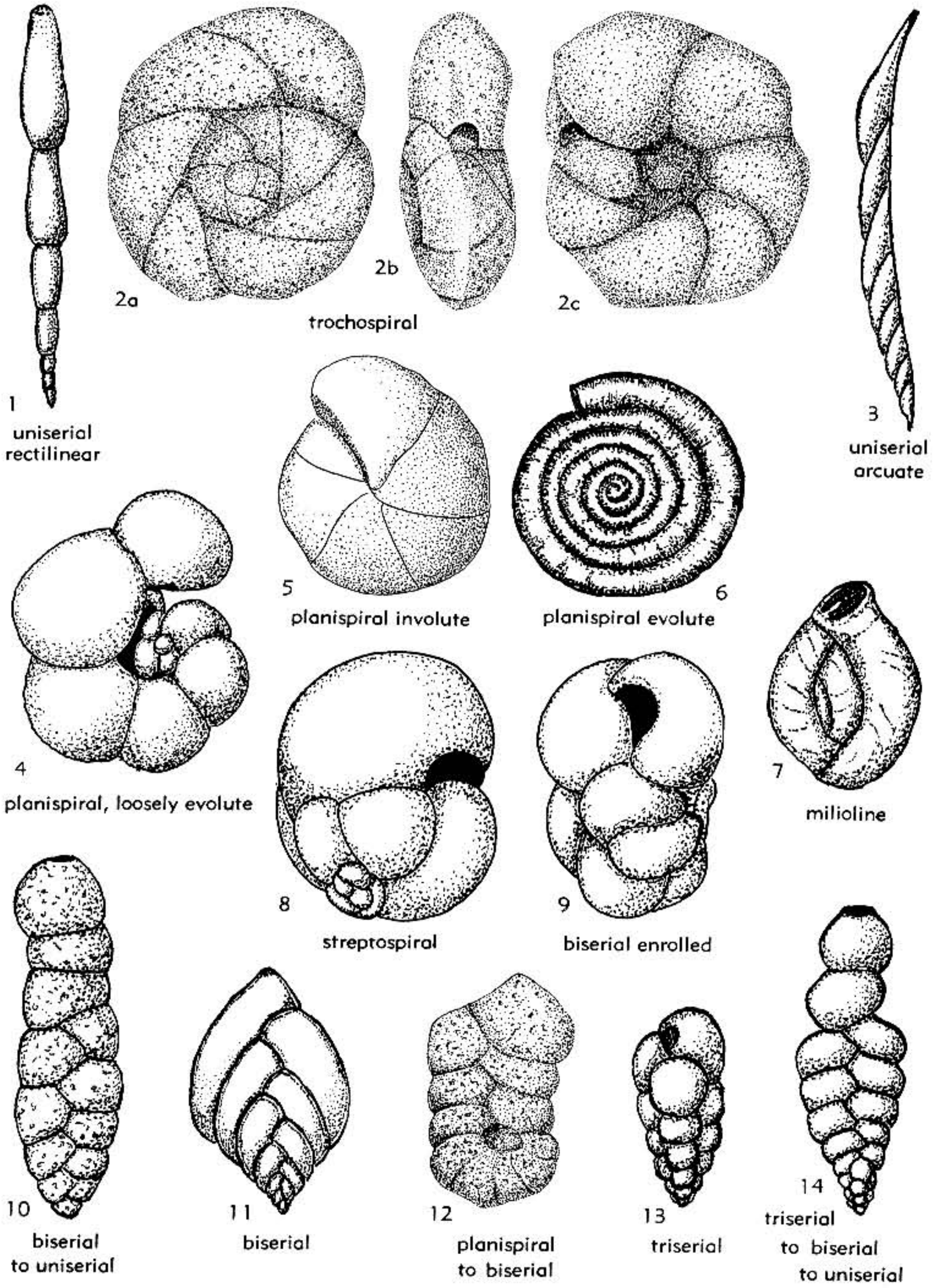


FIG. 57, *1-14*. Arrangement of chambers in foraminiferal tests (*2117).

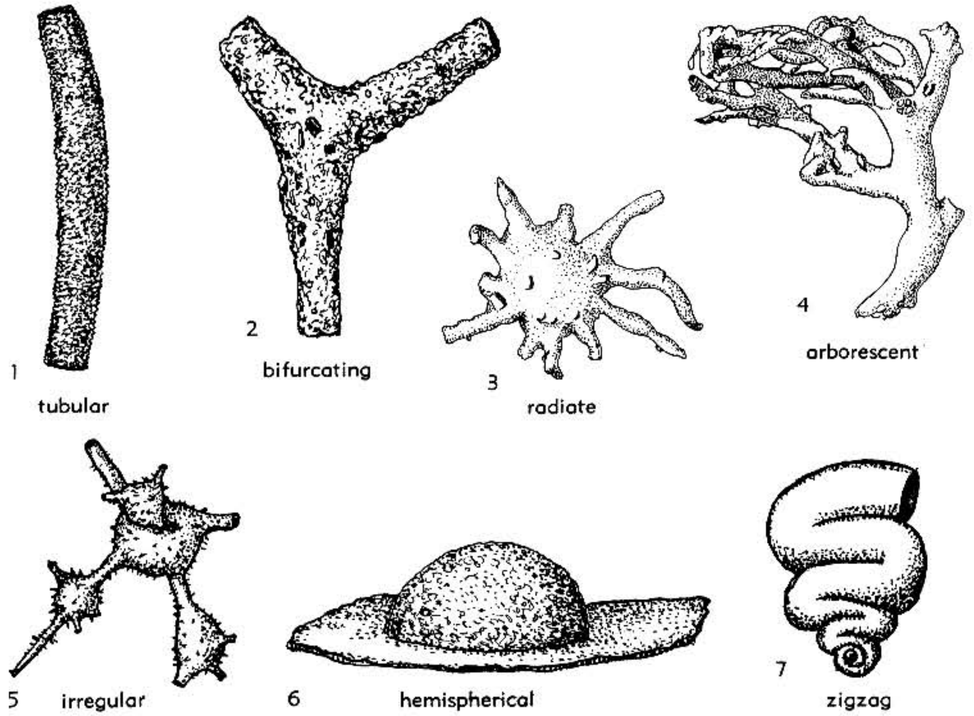


FIG. 58, *1-7*. Shapes of foraminiferal tests (*2117).

stances by viewing the test in transmitted light (in balsam, or immersed in oils such as castor oil), by thin sectioning, by microdissections—both by physical means and by selective dissolution using a mixture of hydrochloric acid and gum tragacanth solution as described by TROELSEN (1954, *1951), by decalcification—all shown by examples in the systematic section of this volume—or by microradiography (X ray) (Fig. 60).

Various theories have been proposed to account for chamber form and arrangement mechanically on the basis of surface tension of the protoplasm, environmental characters, apertural position and volume and shape of previous chambers; various formulas have been presented in explanation of these theories by RHUMBLER (1911, *1572a), REDMOND (1953, *1510), and HOFKER (1954, *941). Regardless of the mechanics of their formation, both a particular chamber form and arrangement are characteristic of species, genera, and suprageneric categories.

DIMORPHISM

The alternation of sexual and asexual generations in the life cycle of foraminifers has been discussed above in treating the life history. The resultant dimorphism may be of various kinds. Morphologic dimorphism of the test is most commonly indicated by the term *dimorphism,* referring to megalospheric and microspheric tests. Such dimorphism was known before its cause was determined.

A nuclear dimorphism occurs in foraminifers also, the microspheric form commonly being plurinucleate and the megalospheric one uninucleate.

Evolutive dimorphism consists of the alternation of a microspheric schizont, which by asexual division results in megalospheric embryos that develop into the adult gamont. The megalospheric gamont has sexual reproduction, production of gametes and fertilization resulting in a new microspheric generation.

The three forms of dimorphism are not entirely compatible in all foraminifers, morphologic dimorphism being true only in multilocular forms with flagellate gametes and nonplastogamic reproduction. As shown in the life history of *Patellina,* the megalospheric and microspheric tests (as indicated by size of proloculus) are not indicative of the gamont and schizont generations, as they were in *Elphidium*. Even

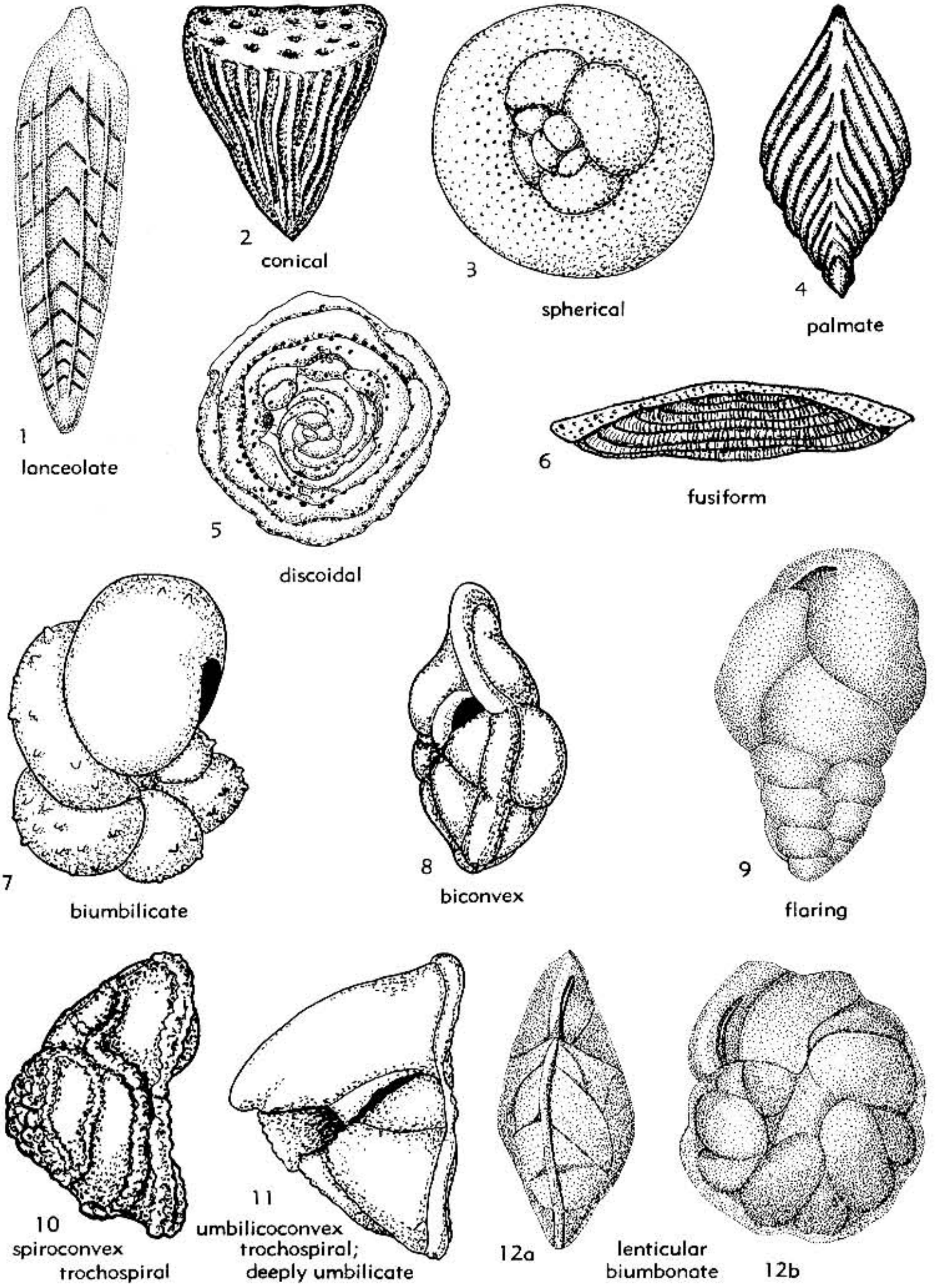
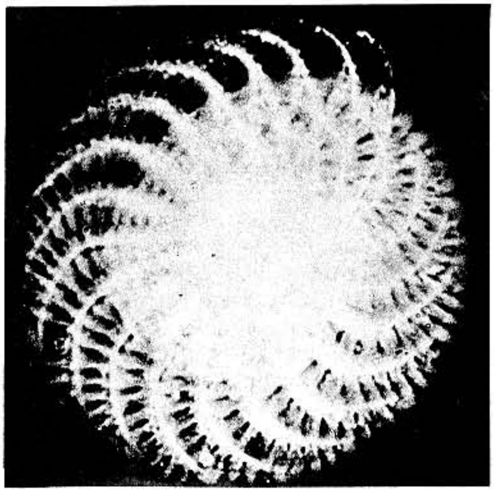


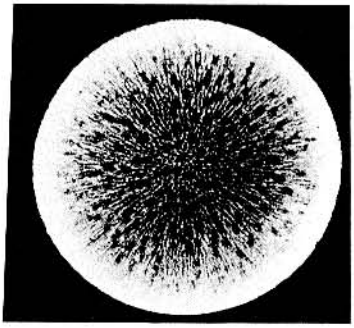
Fig. 59, *1-12*. Shapes of foraminiferal tests (*2117).

nuclear dimorphism is not constant, since some species have uninucleate schizonts during their entire vegetative life.

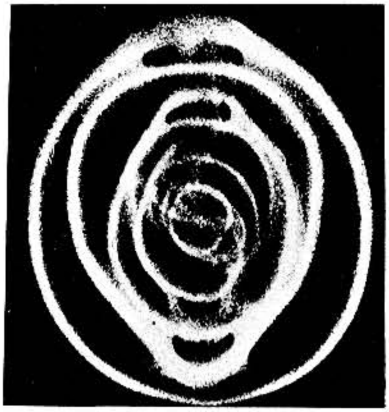
In addition to two characteristic generations it was observed that megalospheric tests may occur with differing proloculus sizes. This was thought to represent a sexual differentiation (male and female) in the gamont generation. It was determined later that in certain species, some "megalospheric" forms may be plurinucleate and reproduce asexually as schizonts, whereas other megalospheric specimens were uninucleate and reproduced sexually. This was



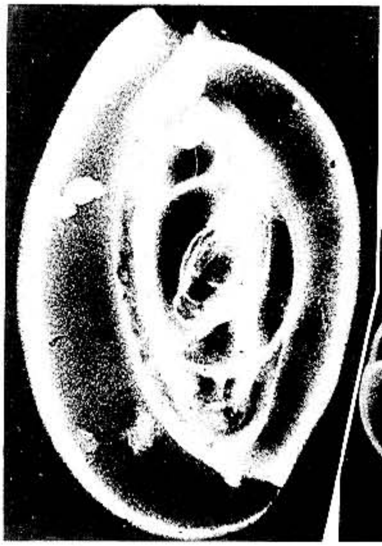
1 Elphidium



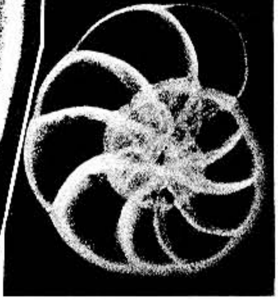
2 Orbulina



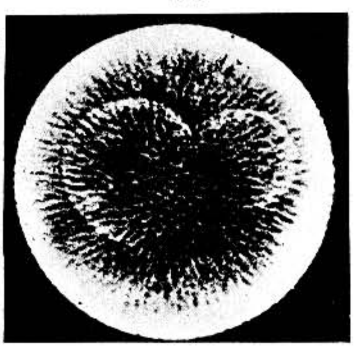
3 Pyrgo



4 Quinqueloculina



5 Nonion



6 Orbulina

Fig. 60, *1-6*. Structure of foraminiferal tests indicated by microradiographs, enlarged (*888).

then thought to represent three distinct generations in the life cycle and was described by HOFKER (1925, *926) as trimorphism. It was assumed to be obligatory in all species, the two megalospheric forms being referred to as the A_1 and A_2 generations and the microspheric as the B generation. HOFKER (1930, *928b, p. 104) stated, "No student in living or fossil Foraminifera must be content, when describing Foraminifera, if he describes not at least three forms of a single species." With additional information available from culturing, it has been shown that these three generations do not occur regularly and are never present in some species. In others sexual reproduction may even be lost entirely, resulting in an apogamic cycle. Simple dimorphism may be difficult to recognize among fossils, for gamogony in some genera results in destruction of the parent test; hence, the microspheric generation is much rarer in dead populations or fossil assemblages than in living populations. Measurements of proloculus size (LE CALVEZ, 1938, *1106) in very numerous juvenile specimens produced asexually from the same parent test showed that young sister gamonts of *Planorbulina mediterranensis* exhibited proloculus variation of 31 to 54μ, and the proloculi of the parent schizonts varied from 27 to 44μ. Adult gamonts producing gametes showed a proloculus size range of 28 to 48μ. Thus, no trimorphism is indicated and even the microspheric and megalospheric generations cannot be determined solely by size of proloculus in this species. LE CALVEZ concluded that the size of the proloculus and the size of the embryonic form is defined at schizogony and depends exclusively on the ratio of volume of maternal protoplasm to number of daughter nuclei. The size of later chambers formed in free life depends on constant genetic factors of the individual species and two variables—surface tension of the protoplasm and that of the surrounding medium (water). Examination of numbers of individuals at different times in the year suggest that seasonal modifications (temperature, salinity, density) had relatively little effect on chamber form.

The variations known to occur in the life cycle of a living species complicates the problem of systematics. Whereas statistical analysis of certain measurements in some invertebrates can determine the validity of species, the information available to date shows that so great variability occurs in foraminifers that HOFKER (1930, *928b), was led to state, "A specific name may never be based upon . . . differences in the shape and measures of the chambers."

An interesting feature of microspheric forms (with smaller proloculus) is their more varied test morphology. A species with wholly biserial megalospheric form may be represented by a microspheric form with basal planispiral coil, or early triserial or trochospiral development. Relationships to other genera in the same family are commonly indicated by the earliest-formed chambers of the microspheric test. This has been regarded as a recapitulation of ancestral characters by some specialists, but by others thought to indicate the direction of evolution and to suggest the adult characters of the descendants to come. Morphologic information and the geologic record must both be utilized in order to determine which is correct.

In contrast to the suggestion that varying forms were the result of a trimorphic cycle, LE CALVEZ concluded that in foraminifers of regular growth, the volume of any chamber is proportional to the quantity of protoplasm occupying pre-existing chambers, whatever the number of chambers and the form considered. In megalospheric *Pyrgo* the proloculus has a diameter of 400μ. For this quantity of protoplasm a microspheric test would have 12 chambers and show an early quinqueloculine coiling followed by a triloculine stage. The second chamber of megalospheric *Pyrgo* would bypass these stages and have the same form and position as the thirteenth chamber of the microspheric test. A megalospheric specimen with proloculus diameter of 150μ (similar in volume to a microspheric test of eight chambers) would have a triloculine arrangement of the first three chambers and then a biloculine development. LE CALVEZ did not consider the microspheric stages as a recapitulation of their geologic history but merely a specific character and regarded it as the more stable form having a maximum number of morphological characters. Thus (*1106, p. 315) a megalospheric form of any size, when commencing free life and growth, will organize its consecutive chambers in approximately the way that would follow in the microspheric test with initial portion of the same plasmic volume. He restricted the term trimorphism to indicate

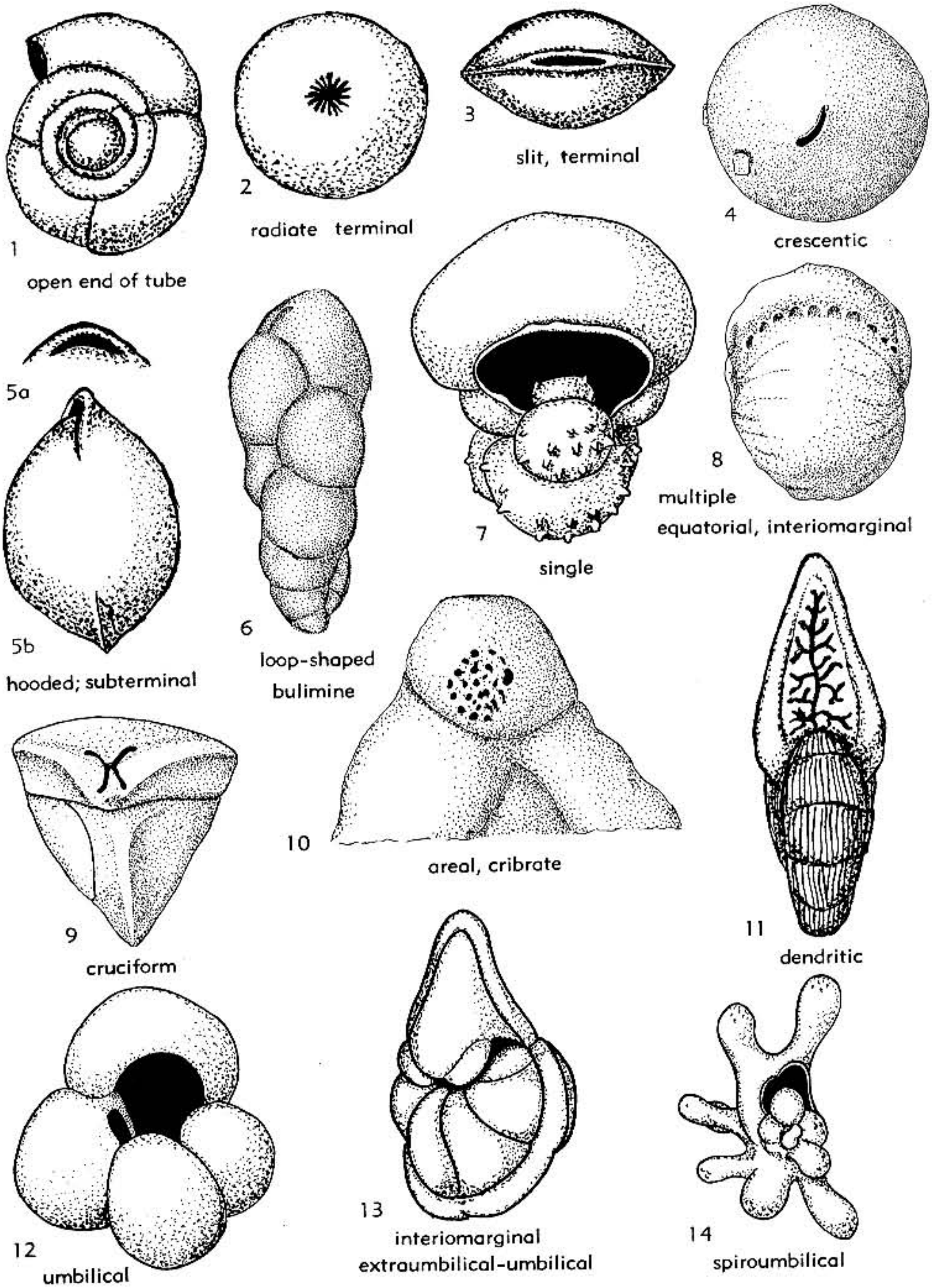


FIG. 61, *1-14*. Location and form of primary apertures in foraminiferal tests (*2117).

only test morphology where it was occasionally recognizable, saying that this was not intended to indicate any biologic conclusions.

TEST OPENINGS

A foraminiferal test may have various intercameral openings as well as openings to the exterior. These include primary, secondary, or accessory apertures and their modifications, canal openings and stolons, and tiny perforations in the wall.

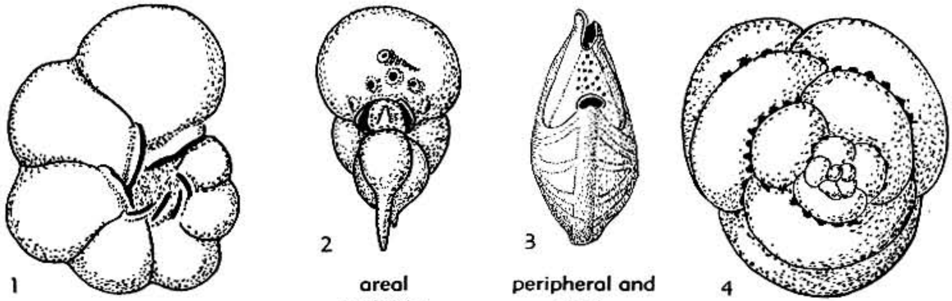
Apertural Form, Position, and Modifications. Apertural openings include the primary aperture or main opening or openings in unilocular tests or in the final chamber of multilocular tests, as well as various secondary or accessory apertures which may be present. The aperture may consist of a single opening or of many openings which differ in shape and position. The aperture may be single or multiple, and rounded, slitlike, arcuate, radiate, loop-shaped, cruciform, dendritic, or cribrate. The apertural position may be at the open end of the chamber, terminal, subterminal, interiomarginal (basal), areal, equatorial, peripheral, umbilical, extraumbilical-umbilical or spiroumbilical (Fig. 61).

The additional openings which are formed by folding of the attached portion of the tooth plate in some genera (e.g., especially *Robertinoides, Pseudobulimina*), and which are always connected with canals in the tooth plate were termed supplementary foramina by Hofker. These and other supplementary openings may be areal, peripheral, sutural (single or multiple), may be relict apertures, or may be connected with internal partitions or canal systems. Accessory apertures are those which do not open directly into the chamber cavity but into cavities formed by various modifications of the aperture, such as bullae or tegilla. They may be infralaminal or intralaminal in position (Fig. 62).

Apertural external modifications include presence of an apertural lip, flange, bulla, tegilla, phialine lip, an apertural tooth, simple, bifid or complex, apertural flap, or valvular tooth and umbilical teeth (Fig. 63). Internal modifications consist of entosolenian tube, hemicyclindrical siphon, tooth plates, and secondary partitions.

Many hyaline foraminifers have internal partitions or tooth plates associated with the aperture. When these are present the aperture connected with the tooth plate was termed the protoforamen by Hofker (1951, *928c, *936). When two main openings are present, that not associated with the tooth plate was termed a deuteroforamen. Other (biforaminate) foraminifers were regarded as originally having had both a protoforamen and deuteroforamen, but if the protoforamen and tooth plate are reduced or lost, this leaves only the deuteroforamen. Although such features undoubtedly have occurred in some forms, it is not possible to be certain in every instance whether a protoforamen or deuteroforamen is present; hence these terms, which express theoretical concepts, are not here used in the morphologic descriptions, since to do so would require acceptance of supposed relationships that are doubtful or even strongly controversial. A solely morphological terminology is therefore preferable. Some relationships originally postulated by Hofker on the basis of tooth plates, protoforamen, and deuteroforamen have later been upheld by study of life cycles, cytology, test mineralogy, and microstructure; hence this feature is certainly of major importance, though function of the tooth plate in the living animal is not yet known. Problematical also is the question as to whether all so-called "tooth plate foraminifera" are closely related, as postulated by Hofker. If related to a physiologic function of the animal, a tooth plate may have developed at more than one time, just as similar test form, chamber arrangement, or apertural character may appear in agglutinated, porcelaneous, or hyaline lineages. In the *Treatise* classification, apertural "tooth plate" development is regarded as an advanced apertural feature which developed independently in various lines. Thus, the entosolenian tube in the Glandulinidae, the internal siphon in the Pleurostomellidae, and the tooth plates of the Buliminidae, Bolivinitidae, and Caucasinidae, or the internal partitions of the Ceratobuliminidae and Robertinidae are here regarded as convergent rather than divergent features. Each of these groups may be more closely related to other types that lack tooth plates than to families that possess them (Fig. 64).

Canal System and Stolons. Canal systems found in the Rotaliacea and Orbitoidacea are complexes of essentially tubular cavities within the shell material, commonly occurring between the two layers of the septal wall (intraseptal canals). Fissures are homologous with canals. Canals may be described according to their position (e.g.,

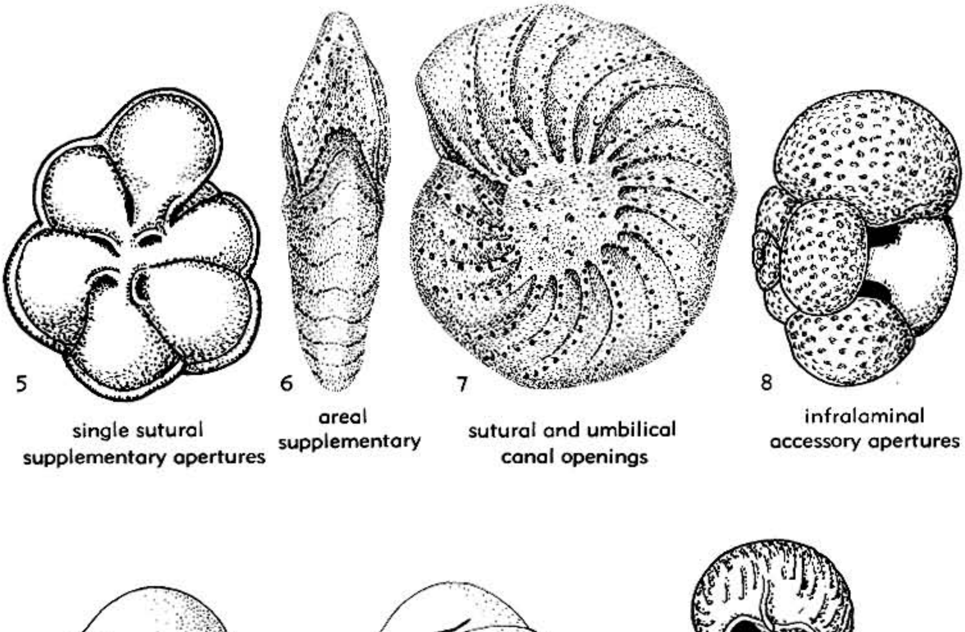


relict

areal multiple

peripheral and areal

multiple sutural

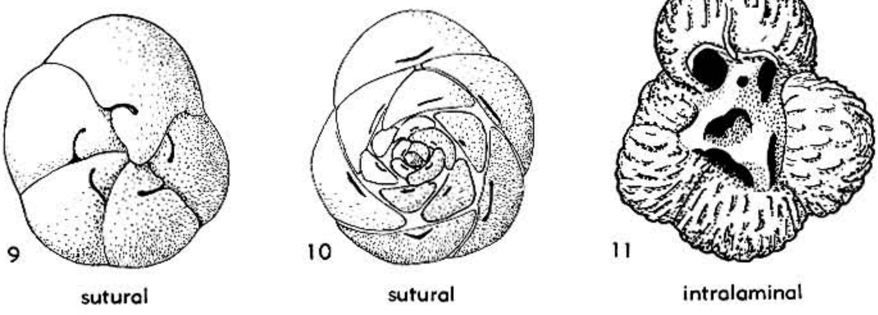


single sutural supplementary apertures

areal supplementary

sutural and umbilical canal openings

infralaminal accessory apertures



sutural

sutural

intralaminal

FIG. 62. Type of supplementary apertures *(1-6)* and accessory apertures *(7-11)* in foraminiferal tests (*2117).

intraseptal, marginal, lateral, or umbilical) and they may vary a great deal in complexity and ramification. They are presumed to result from protoplasmic currents which cause open spaces to remain when shell laminae are formed (Fig. 65). Stolons may

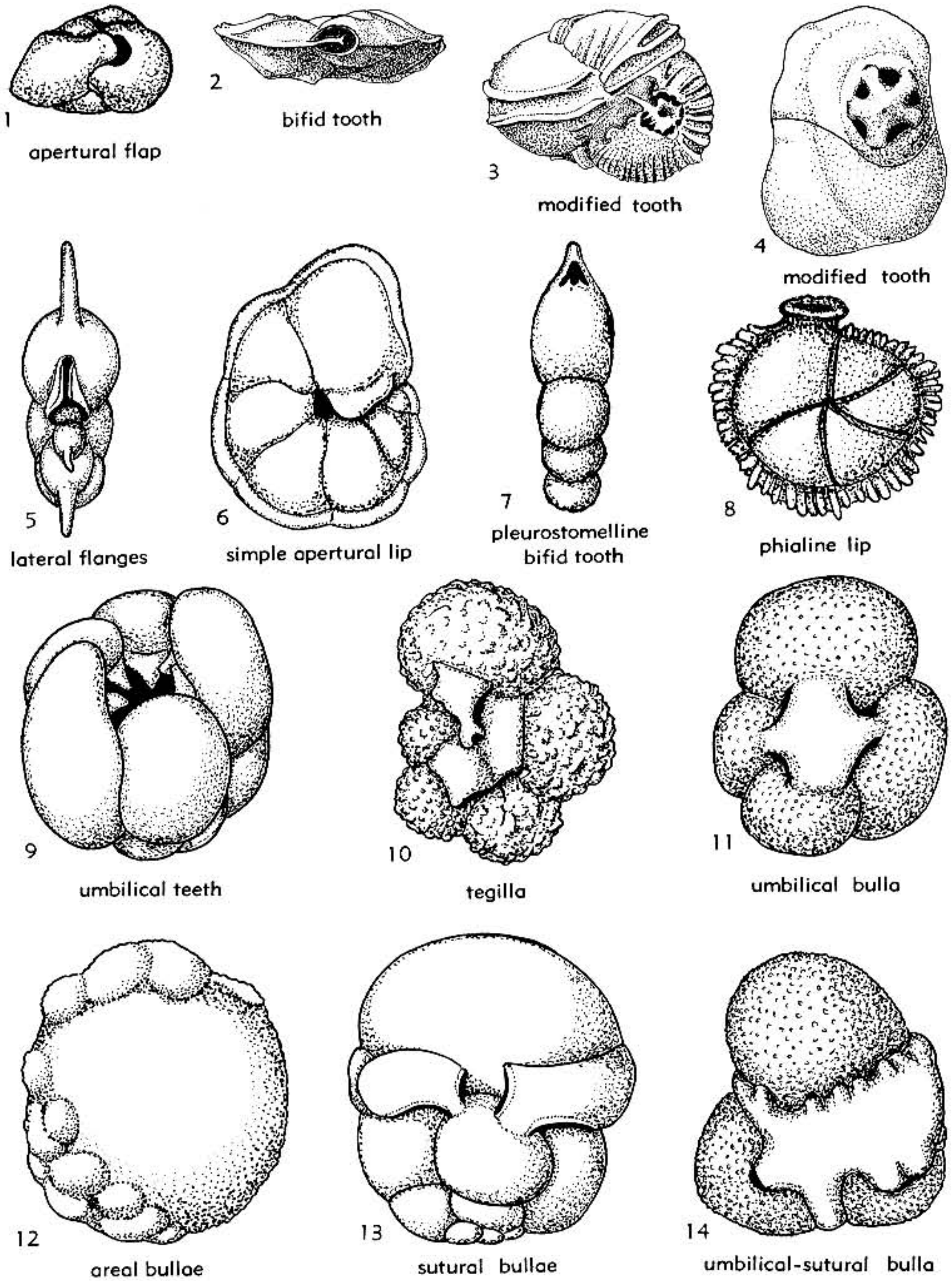


FIG. 63, *1-14*. Modifications of apertures in foraminiferal tests (*2117).

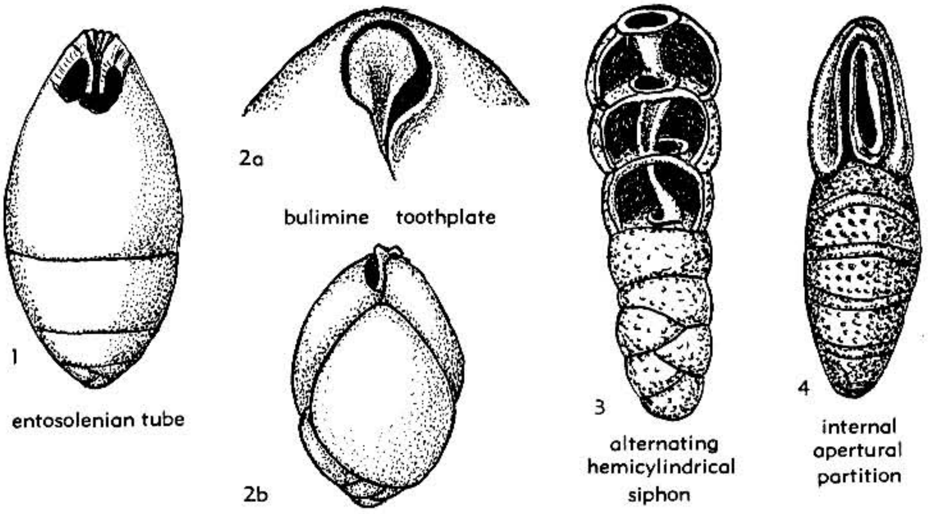


Fig. 64, *1-4*. Internal apertural modifications in foraminiferal tests (*2117).

result from simple radial canals that become intercameral connections.

Perforations and Pore Plates. Perforations occur in the walls of most hyaline foraminifers and in some agglutinated forms, serving for the passage of pseudopodia. The size, arrangement, and placement of the pores seem to be an important systematic characteristic, as is the area of the test that is perforate or imperforate—for example, only the lower portion of the chambers of certain Buliminidae and Bolivinitidae is perforate, the apertural area and apertural face is nonperforate in many genera, and the tooth plates always lack pores. Hofker (1951, *934, p. 38) stated that "within a particular species they are of constant size and distribution over the wall, so that many closely related species . . . can be distinguished very easily by means of the size of their pores." He has described the pore size or pore-index of many species. The geologically older species are commonly more finely perforate, the younger ones having coarser pores. The same may be found in an individual ontogeny, early chambers being finely perforate and later ones more coarsely perforate. The primitive simple pores were termed protopores by Hofker (1951, *928c). Besides protopores, secondary test thickening in lamellar foraminifers may enclose a number of protopores, so that many pores open in the interior of the test but converge in the walls to fewer larger pores at the outer surface (deuteropores). All deuteropores have a diameter greater than 2μ and are commonly irregular in shape. They may be restricted to only one side of the test or may be interspersed among the protopores. Considerable variation may occur in size and shape of pores in an individual specimen, but the pore pattern is characteristic of the species.

Dark discs within pores at the level of each successively formed lamina were noted by Le Calvez (1947, *1108) and similar discs were described by Jahn (1953, *981) as sieve plates and by Arnold (1954, *42), as pore plugs which have a diameter of 2 to 6μ and thickness of 0.5 to 3μ. They may serve a filtering purpose for the pseudopodia (*43). The sieve plates may be seen in decalcified specimens and are particularly well shown in electron micrographs (Fig. 66).

Ornamentation. In hyaline foraminifers ornamentation may consist of pillars, ribs, ridges, cancellations, keels, flanges, spines, nodes, etc., largely consisting of thickened, imperforate shell matter of various forms, or modifications of the apertures or wall perforations (Fig. 67).

Pillars were considered by Smout (1954, *1803) to be formed in different ways, most

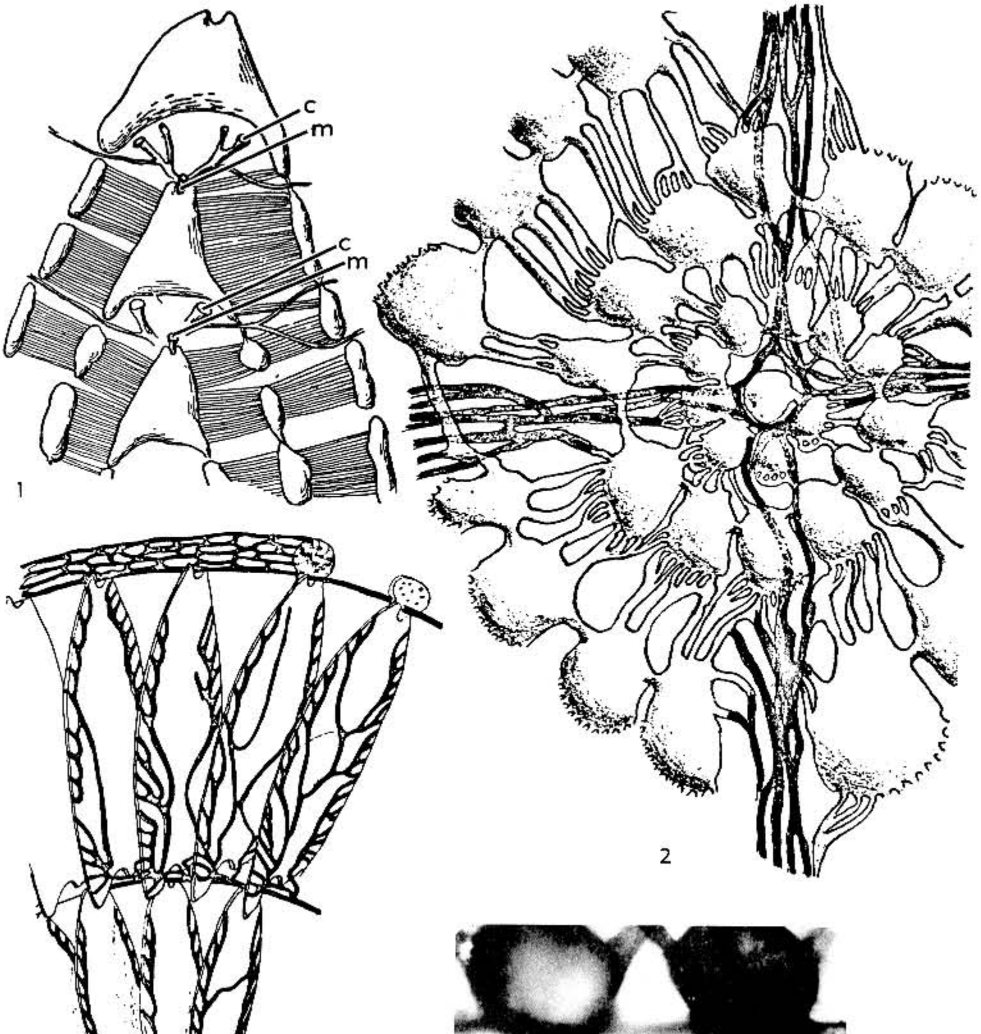


FIG. 65. Canal systems and stolons in foraminifers.——*1.* Portion of axial section of *Nummulites laevigatus* showing marginal cord *(m)* and spiral canal *(c)*, enlarged (*928a).——*2.* Equatorial section of decalcified *Calcarina spengleri*, canal system shown dark, located in region of spines, ×95 (*928a).——*3.* Canal system of *Nummulites complanatus*, diagrammatic (*928a).——*4.* Decalcified section of *Lepidocyclina favosa* showing diagonal and annular stolons, enlarged (*1998).

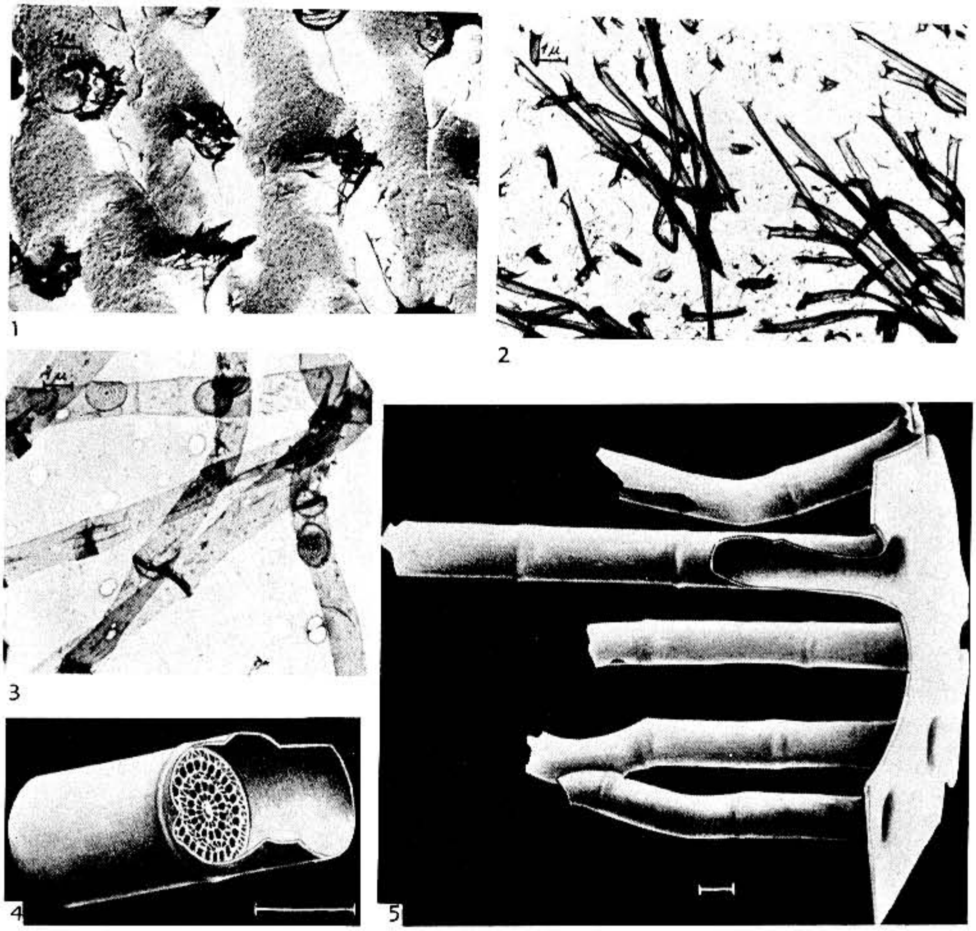


Fig. 66. Electron micrographs of decalcified foraminiferal tests and reconstruction of pore canals and sieve plates.——*1*. Organic wall layer.——*2*. Organic canals.——*3*. Decalcified specimen showing pseudochitinous lining of pores and regularly spaced sieve plates, all ×4,000.——*4*. Reconstruction of single canal and sieve plate.——*5*. Reconstruction of part of wall showing organic layer of canals (length of line on figure equals 1μ) (*981).

other types of ornamentation being ascribable to one or another of these modes of origin (Reiss, 1958, *1530). (1) *Inflational.* Pillars formed by local thickening of imperforate shell material along lines radiating from the center or axis of the test, each lamina adding to the thickening; most papillae, spines, striae, costae, ribs, and keels are similarly formed (Fig. 68,*1*), (2) *Textural.* Some pillars and keels or carinal bands may be differentiated only by a distinctive appearance of the shell material, such as lack of perforation or tubulation; some ornamentation may be formed by combinations of inflational and textural types (Fig. 68,*2*). (3) *Incised.* Fissures may isolate some portions of shell material at the surface and intercept a number of laminae. Incised pillars may appear externally as granules, less rounded in form than inflational pustules, and incised inflational pillars may be distinguished (Fig. 68,*3*).

Coiling Ratios. In 1938 Cosijn (*388) made a series of statistical studies on foraminifers, one of which was based on the observation that trochospirally coiled shells may vary in direction of coiling (dextral, sinistral). Specimens of *Globorotalia menardii* were studied from five well samples and one Recent dredging from the Kei Islands, Netherlands East Indies, with results summarized in Table 3.

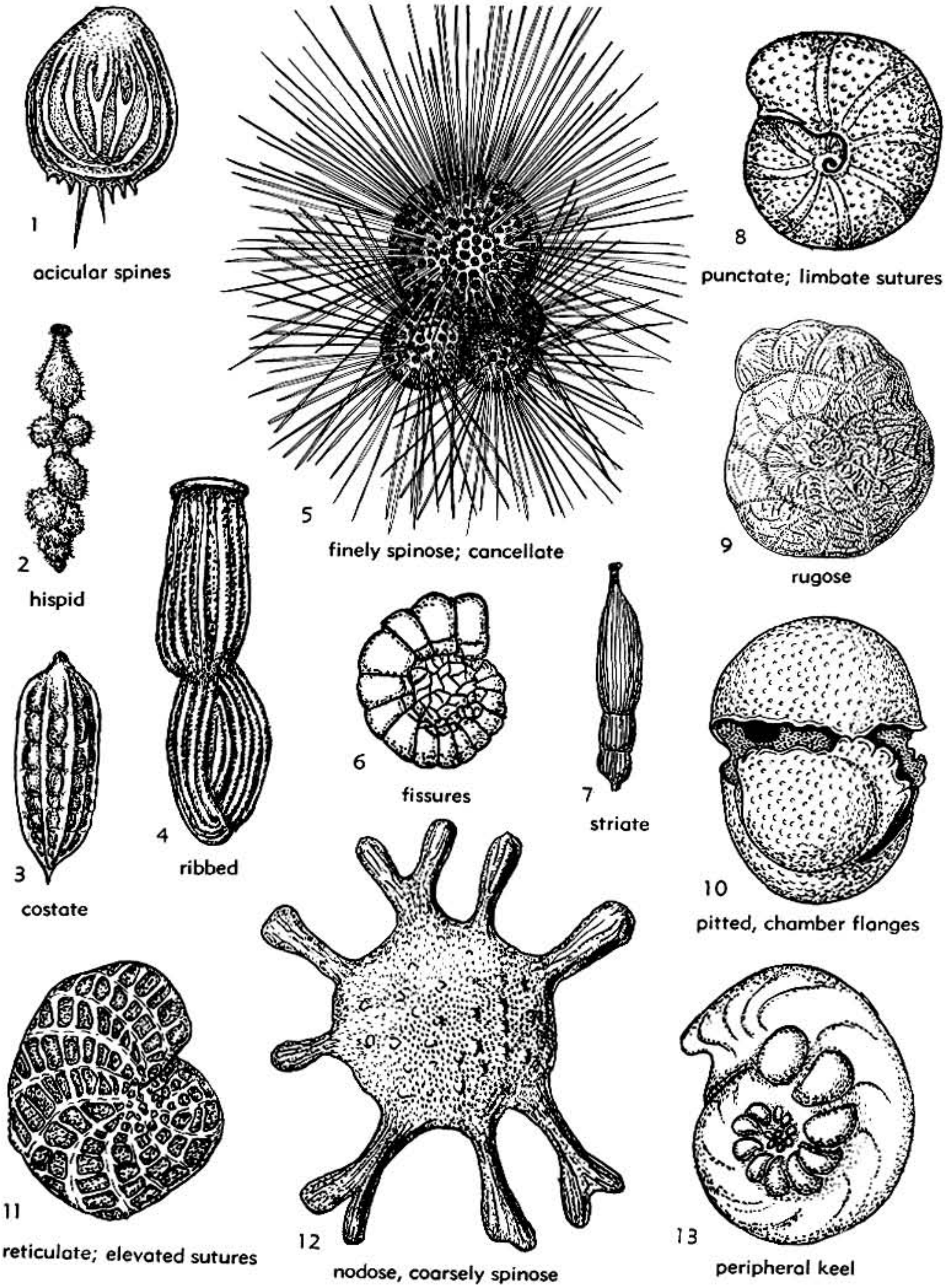


FIG. 67, *1-13*. Ornamentation of foraminiferal tests (*2117).

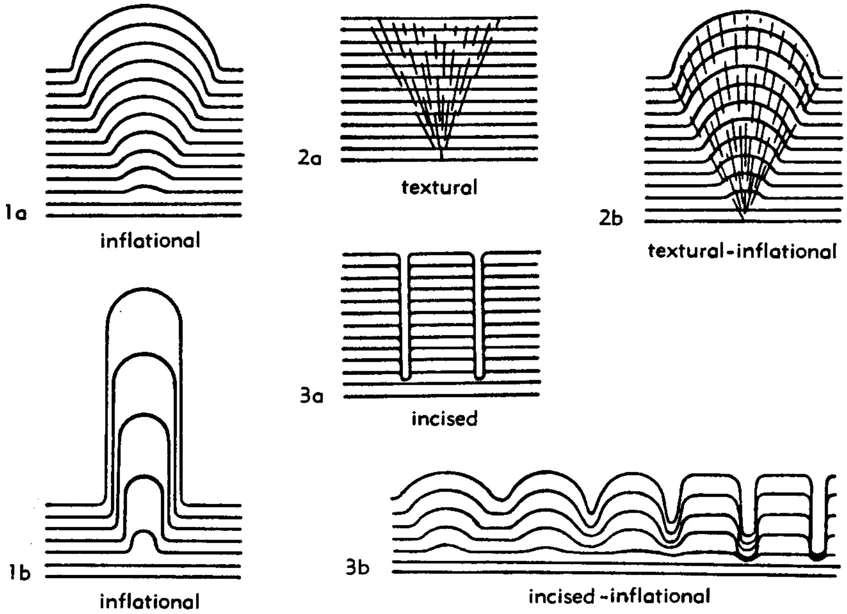


FIG. 68. Development of pillars in foraminiferal tests.——*1a,b.* Inflational pillars.——*2a,b.* Textural pillars.——*3a,b.* Incised pillars (*1803).

TABLE 3. *Direction of Coiling in Foraminiferal Tests*

Sample (depth in m.)	Sinistral (per cent)	Dextral (per cent)
Sub-Recent (dredged)	99	1
201-209 211-215	8	92
401-404	98.5	1.5
604	97	3
1007	90	10
1627	89	11

Dominantly sinistral coiling was observed, except in specimens from a depth of approximately 200 m., where dominantly dextral coiling was observed.

GANDOLFI (1942, *768) noted that geologically older tests of *Rotalipora appenninica* exhibited random coiling (approximately equal numbers of dextral and sinistral), whereas geologically younger ones were dominantly dextral.

BOLLI (1950, *157), who studied coiling directions in various species of *Globorotalia* and *Globotruncana,* observed random coiling in geologically earliest representatives of a species, whereas later ones developed a preference for either dominantly right or left coiling. He observed that species of *Globotruncana* and *Rugoglobigerina* tended to be dextrally coiled, whereas species of *Globorotalia* tended toward sinistral coiling. He postulated that, in a limited region, coiling ratios might give an indication of relative stratigraphic position of isolated outcrops. Some species of the Globigerinidae developed sinistral coiling, but others became dextrally coiled (Figs. 69, 70).

VAŠÍČEK (1953, *1982) made similar studies of coiling ratios of foraminifer tests in the Tortonian of Moravia. He postulated that the coiling ratio might differ in different generations of a species. Because of seasonal or other factors affecting relative numbers of microspheric and megalospheric forms produced, regular fluctuations in coiling ratios might result. Coiling ratios were plotted from various well samples, the resultant oscillations being regarded as possibly due to local influx of materials from a different source. The coiling changes seem to be limited to megalospheric specimens and the changes are distributed both stratigraphically and geographically.

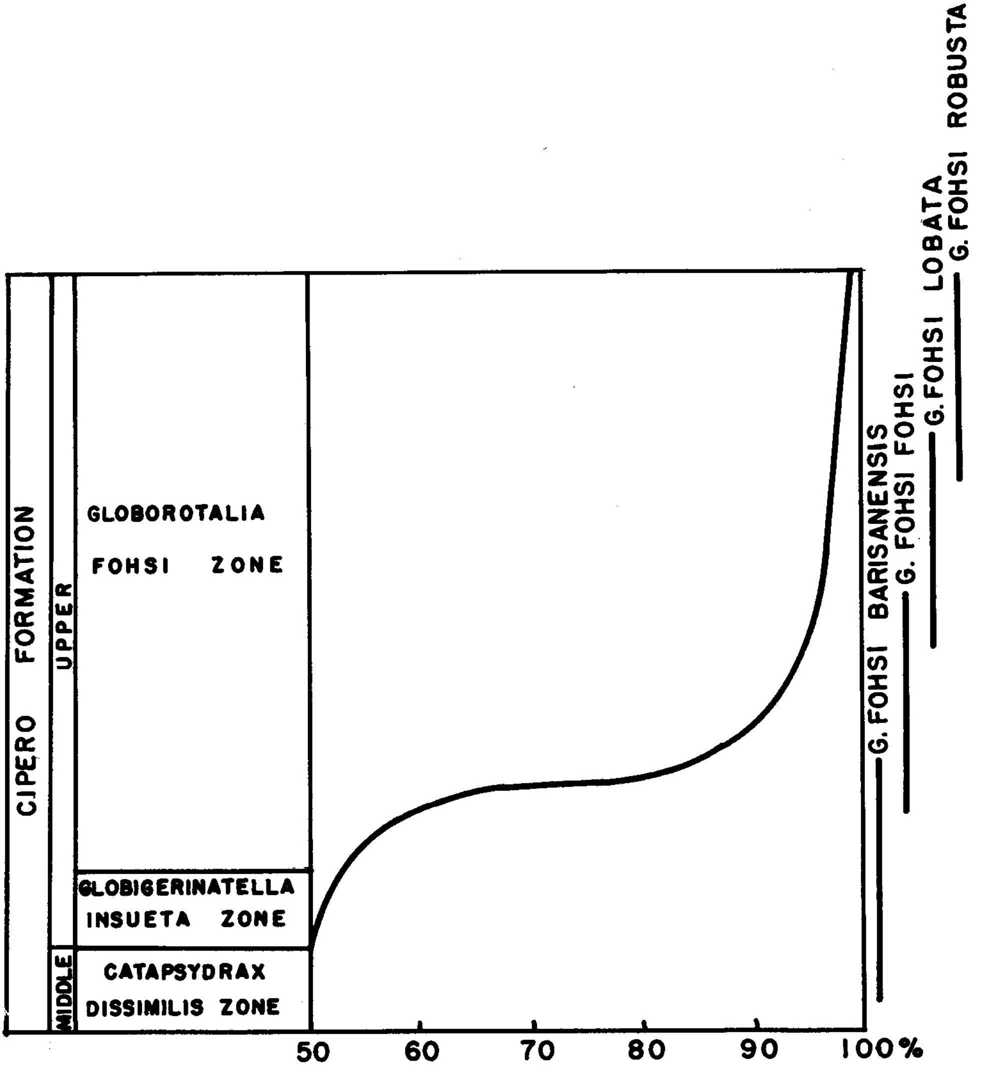


Fig. 69. Percentages of sinistrally coiled *Globorotalis fohsi* in the Miocene of Trinidad, showing change from random to dominantly sinistral tests with lapse of geologic time (*164).

Geographic variation in coiling ratios in Recent North Atlantic *Globorotalia truncatulinoides* has been demonstrated by Ericson, Wollin & Wollin (1954, *708) (Fig. 71). According to evidence from submarine cores, the provinces indicated appear to have long been in existence, the southern right-coiling province for some 10,000 years. The central left-coiling province apparently came into existence in Recent time during the last 2,000 years. It was also noted that *G. truncatulinoides* was dominantly coiled sinistrally during the Pleistocene.

Although no explanation was given originally as to the cause of these provinces defined by dissimilar coiling of foraminiferal tests, Bandy (*75) suggested that temperature controls were probably effective and that the Gulf Stream carried dextral populations northward along the eastern coast of North America.

Our comparison of the indicated locations of the provinces with distribution of cold and warm currents suggests that the right-coiling provinces reflect the presence of warm currents (e.g., Guinea Current, North Equatorial Current, Gulf Stream, the West Wind Drift and North Atlantic

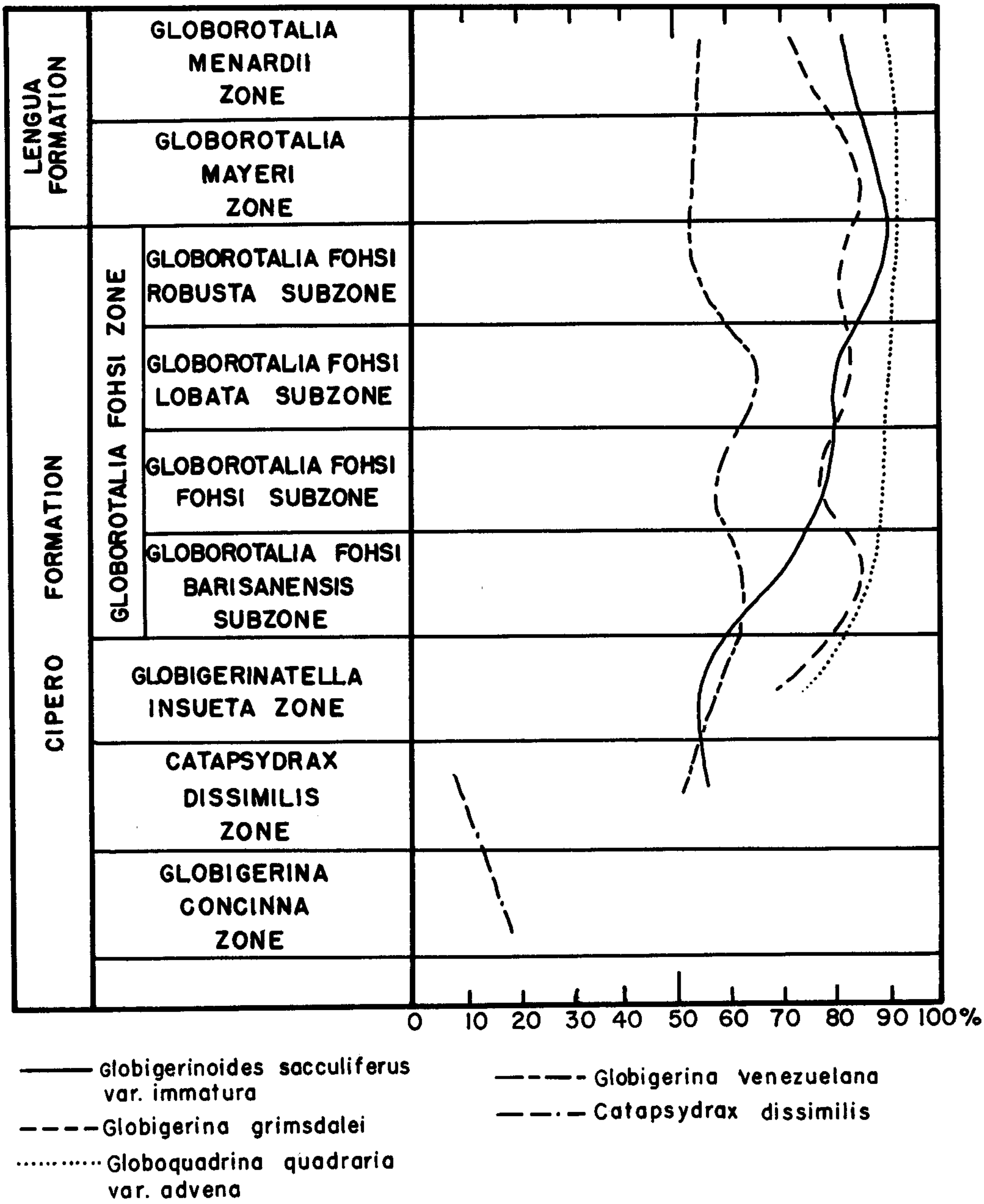


FIG. 70. Percentage of sinistrally coiled globigerinid tests in Oligocene-Miocene deposits (*164).

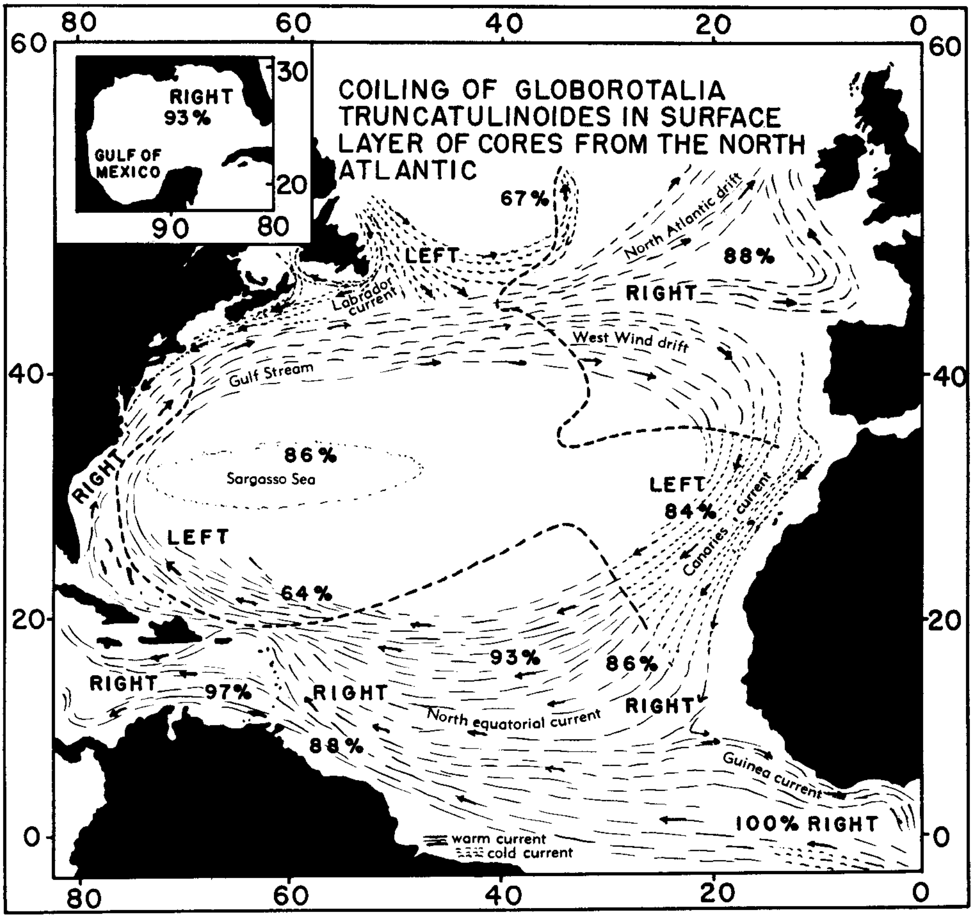


Fig. 71. Provinces of living *Globorotalia truncatulinoides* defined by distribution of dominantly sinistral- and dextral-coiled tests, respectively. Warm currents (solid lines) and cold currents (dotted lines) have been added to indicate possible influencing factors (*708, modified).

Drift). The last two can thus be correlated with the two indentations of the right-coiling province in the central North Atlantic (Fig. 71).

The provinces indicated by left-coiled tests are placed in areas of cold currents (e.g., Canaries Current, Labrador Current). Cold Labrador waters apparently extend their influence across the Gulf Stream into the central Atlantic. The dominantly sinistral coiling during Pleistocene time agrees with this suggested hypothesis based on tests of *G. truncatulinoides*. Low temperatures are known to affect reproduction in various genera of foraminifers and this may be a factor in the effect of temperature on the distribution of test coiling.

Bandy (1960, *75) noted changes in coiling ratios of *Globigerina pachyderma* tests in Pliocene and Pleistocene deposits of southern California. In the Arctic and Antarctic area coiling in this species is dominantly (98 per cent) sinistral, whereas in temperate and tropical areas it is dominantly (up to 98 per cent) dextral. Modern populations off southern California, which have been dextral for about 11,000 years, as indicated by radiocarbon dating, were preceded by sinistral populations of the late Pleistocene. Pliocene strata have dominantly dextral populations; hence, change in coiling ratios of foraminiferal tests may be used for placement of the Pleistocene-Recent boundary.

A similar use of coiling ratio fluctuations was made by NAGAPPA (1957, *1344) to determine the Laki-Ranikot boundary (Paleocene-Eocene) in Pakistan.

ECOLOGY AND PALEOECOLOGY

GENERAL DISCUSSION

Foraminiferida occur at present in nearly all marine and brackish-water environments, as well as more rarely in fresh water (Allogromiidae). They are abundant in present-day sediments, varying in abundance from about 1,000 to 2,500,000 living individuals to a square meter of the sea floor, averaging about 10,000 per sq. m. in the outer shelf of the Gulf of Mexico to 90,000 per sq.m. in the Mississippi delta region. Some species have a seasonal abundance, varying in accordance with their respective reproductive cycles. Others are present in about the same abundance and size range throughout the year (*1454).

Because of their wide geographic range and large numbers, as well as long geologic history, foraminifers afford an excellent source of paleoenvironmental data.

In general, broad latitudinal zones of temperature affect distribution of foraminifers and on open coastlines faunal zones also correspond roughly to depth, with some fluctuations due to unusual higher- or lower-than-normal salinity. In uniformly shallow or partially enclosed basins, such as probably were represented in geosynclinal deposits in the geologic past, presumably lessened variations of temperature and depth would reduce the importance of these factors, so that limiting controls could be, in varying proportions, character of the substratum, salinity, and availability of food and oxygen.

The oceanographic condition of the basin was considered primary in importance to foraminiferal distribution by SAID (1951, *1615). In the most common type, where the bottom waters are aerated by sinking of the surface waters, distribution of foraminifers was stated to be controlled by the amount of food and texture of the substratum. These factors may also account for the apparent depth zonation. In basins where the bottom water is stagnant and non-oxygenated, as in the Black Sea, the sediments are black and amount of oxygen is the limiting factor.

The occurrence of benthonic species is controlled to a great extent by physical factors of depth, temperature, amount of light, turbidity and turbulence of the water, character of the bottom sediments, chemical factors of water salinity and available elements, and biological factors of available food supply, symbiotic organisms, parasites, and predators. Planktonic foraminifers are influenced by the same chemical and biologic factors, but the important physical influences are temperature, currents, turbulence, and turbidity. Benthonic fossils thus aid in determining the paleoenvironmental factors of depth, temperature, salinity, bottom conditions, and to a lesser extent amount of light. An important use of faunal assemblages is in the recognition of ancient near-shore, lagoon or marsh deposits and determination of ancient shore lines.

Knowledge of the characteristic depths of various faunas also allows use of them to identify displaced faunas (displaced into deeper water), as in the San Diego Trough and Sigsbee Deep (*1453, *1961), or changes in sea level and resultant depth of water (*1961) and may aid in determining paleocurrents and water masses. The ratio of living specimens to total assemblage of benthonic foraminifers may suggest relative rates of deposition of sediment. Large populations of empty tests in unit amounts of sediment suggest slow sedimentation, whereas small populations indicate rapid deposition.

According to KRASHENINNIKOV (1960, *1053) different faunal facies occur at the same depths, depending on rate of sedimentation and bottom characters. Thus, with mobile water and rapid sedimentation at shallow depths the Elphidiidae predominate, whereas with quiet water and slower sedimentation at the same depth porcelaneous forms are most abundant (e.g., Miliolidae, Peneroplidae), as well as at-

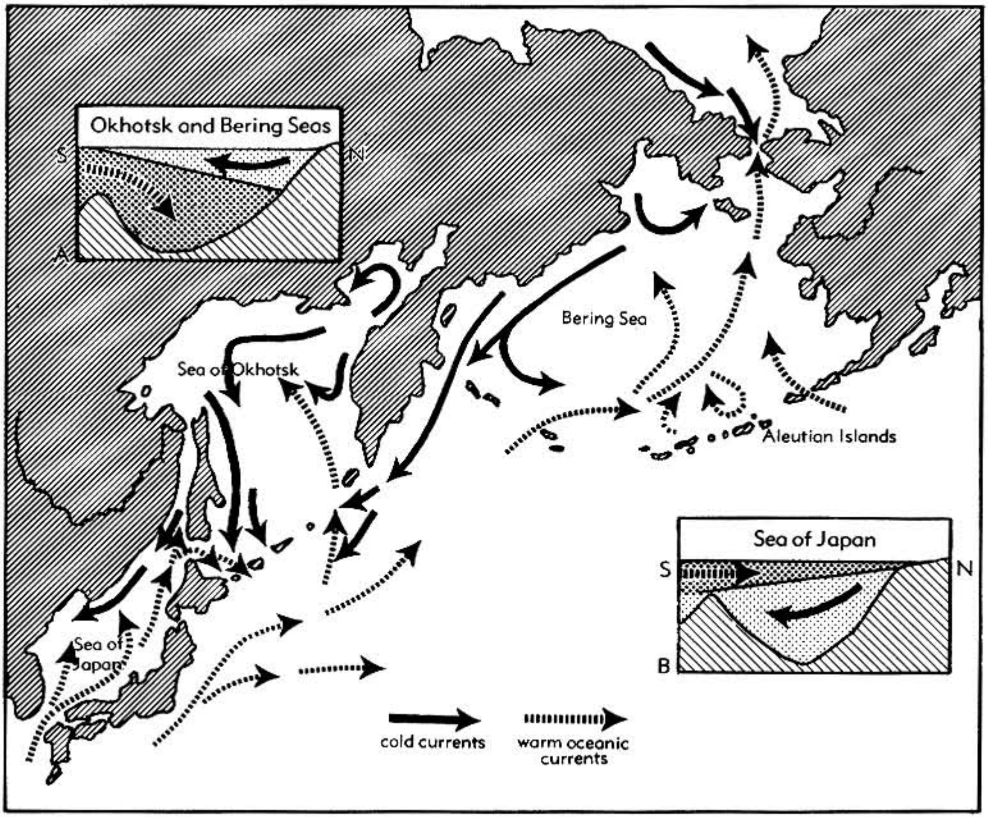


FIG. 72. Distribution of warm and cold waters in Sea of Okhotsk and Bering Sea, with inset figures indicating vertical interchange of warm-water (heavy stippled pattern) and cold-water (light stippled pattern) masses in the Okhotsk-Bering Sea areas *(A)* and Sea of Japan area *(B)* (P. V. Ushakov in *1431).

tached forms (e.g., *Nubecularia, Planorbulina*). In clastic deposits (sandy clays) dominant families are the Textulariidae, Discorbidae, Rotaliidae, Elphidiidae, and Nonionidae. In shallow waters of algal facies, *Cibicides* is abundant, along with the Polymorphinidae, Cassidulinidae, Discorbidae, and Textulariidae. With increased depth, where algae are less abundant, the Cassidulinidae increase and representatives of the Buliminidae and Chilostomellidae appear. Genera of the latter two families occur also in still deeper water where algae are absent, as do the Nodosariidae and planktonic families. In reefy facies many attached foraminifers are found and others adapted to living in reef cavities occur. Studies of these facies in Miocene strata of a broad area on the Russian Platform have led to correlation of zones distinguished in deposits of different facies.

Planktonic species may be found in a great variety of lithofacies, as their occurrence is limited largely by temperature and character of the water masses and currents. They may indicate broad latitudinal temperature zones, allowing recognition of low-latitude, mid-latitude, and high-latitude assemblages. Mixed planktonic faunas were stated by PHLEGER (1960, *1454) to occur in areas where water masses converge or where part of the fauna or empty tests representing it were relict from a previous environment. Abundant planktonic faunas are characteristic of offshore oceanic water masses. Ratios of total benthonic to total planktonic population may be directly related to depth and distance from shore.

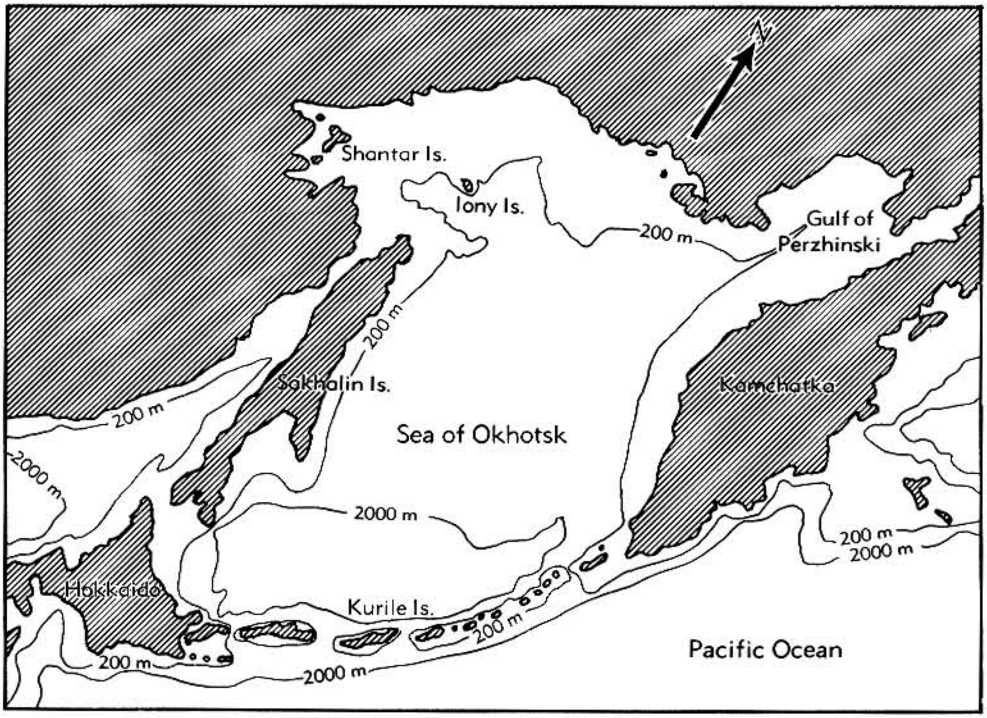


FIG. 73. Generalized water depths in Sea of Okhotsk, for comparison with distribution of faunal zones (Fig. 74) (*2117).

This is modified by bottom topography, however, since numbers of benthonic foraminifers increase over submarine highs.

Modern ecologic studies have commonly recorded depth and temperature data, as well as information on salinity and currents to some extent. Less information is available as to sediments and nature of substrates. Almost nothing is known of the influence of biologic factors such as food supply, symbionts, and parasites. Actual controlling factors in distribution are not always certain, in part because of paucity of data from controlled laboratory experimentation as to the tolerance limits of foraminifers, except for salinity and temperature effects.

The complexity of the problem of foraminiferal distribution is well illustrated by recent detailed ecologic studies by SAIDOVA (1960, *1617; 1961, *1618) in the Okhotsk Sea (Table 4). In this area temperature variations reflect a mixing of warm and cold currents which is not correlative with depth (Fig. 72, 73). Twenty-one distinct foraminiferal assemblages were recognized, based on 650 surface samples and cores (Fig. 74). Each assemblage was characteristic of certain depth, temperature, and bottom sediment. Nine of the assemblages are characteristic of the shelf area, nine of the shelf slope, and three of the deeper central area.

Of the nine shelf-area assemblages, depths were all less than 250 feet, yet the assemblages varied greatly in species and specimens (the latter from 50 to more than 800 in 50 grams), and they varied also from approximately equal calcareous and arenaceous species to nearly 100 per cent calcareous species. On the average, finer bottom sediment (e.g., area of assemblage 8) had the poorest faunas and coarser sediment (e.g., area of assemblage 2) of the same depth and temperature had a much more abundant fauna.

TABLE 4. *Foraminiferal assemblages of the Okhotsk Sea*
[Compiled from SAIDOVA (*1617, *1618)]

	Depth in Meters	Bottom Character	Temperature °C	Salinity (‰)	Number Specimens in 50 gm.
1-9. SHELF ASSEMBLAGES					
1. Shantar Island assemblage: *Quinqueloculina seminulum, Q. arctica, Pseudopolymorphina atlantica, Elphidium orbiculare, E. clavatum, Elphidiella arctica*	20-80	coarse and fine sand	variable		100 (calc.)
2. West and central coast assemblage: *Textularia gracillima, Verneuilina advena, Nonionellina labradorica, Elphidium orbiculare, E. clavatum,* E. sp. 1	30-120	sand, coarse silt	−1.5° to 5°C	30.0	300-500 (calc.) 50- (aren.)
3. Northeast and Kamchatka coast assemblage: *Nonion grateloupi, Elphidium clavatum, Ammobaculites foliaceus, Textularia gracillima, Verneuilina advena, Adercotryma glomerata*	200	sand, coarse silt	+1.5 to 3°C	33.25	100-300 (calc.) aren. isolated occurrence
4. North Sakhalin coast assemblage: *Islandiella californica, Nonion grateloupi, Elphidium clavatum*	200	sand	0 to +5°C	less than 33.5	100-200 (calc.) few (aren.)
5. South Sakhalin and Hokkaido coast assemblage: *Nonionellina labradorica, Elphidium clavatum, Recurvoides contortus*	200	sandy silt	0 to 1.5°C	33.5	50-100 (aren.-calc.)
6. Kurile Island coast assemblage: *Cibicides variabilis, Islandiella californica, Angulogerina angulosa*	150	sandy	+2°	33.5	300+ (aren.-calc.)
7. Northern shelf assemblage: *Islandiella californica, Cassidulina* sp., *Angulogerina angulosa*	100-250	silty clay and fine to coarse silt mud	−1.5 to 0°C	33.25 to 33.5	100-800 (calc.) 25-100 (aren.)
8. Central northern shelf assemblage (north of Iony Island and Kashevarova shoals): *Nonion grateloupi, Cassidulina* sp., *Islandiella californica, Miliammina herzensteini* (eurybiotic sp.)	150	fine mud	−1.5	33.0 to 33.5	less than 100 (calc.) aren. as single specimens
9. Iony Island region assemblage (confluence of Pacific and Okhotsk water masses): Eurybiotic species only, but abundant, *Islandiella californica, Uvigerina peregrina, Angulogerina angulosa*		sand, pebbles	−1.5 to 2.3°C	33.5 to 34.5 nutrients high; oxygen up to 5 ml/1	800 (calc.) (aren. rare)
10-18. SHELF-SLOPE ASSEMBLAGES					
10. North slope, north of Kashevarova shoals assemblage (cold Okhotsk water, slope to greater depth): eurybiotic species, *Islandiella californica, Angulogerina angulosa, Uvigerina peregrina, U.* spp., *Elphidium* sp. 1	250-750	fine silt-clay mud	0 to +1.5°C	33.5 to 33.75	50-85 calc. Aggl. absent

11. Tinro Valley region assemblage: *Angulogerina angulosa, Adercotryma glomerata, Haplophragmoides columbiensis, Bolivina decussata, Uvigerina peregrina, Valvulineria ochotica*	200-800	sand, fine to coarse silt, silty clay, clay diatomaceous ooze	+1° to +2°C	33.5 to 33.75	100- (calc.) 15- (aren.)
12. South Kamchatka slope assemblage: *Stainforthia concava, Uvigerina peregrina, Elphidium* sp. 2, *Nonion scaphum, Chilostomellina fimbriata, Globobulimina pacifica*	250-1000	coarse silt, fine silt, silty clay mud	+1.5 to +2.35°C	33.5 to 34.25	300 (calc.) 10-15 (aren.)
13. North Sakhalin Island slope assemblage: *Uvigerina peregrina, Elphidium* sp. 2, *Nonion scaphum, Islandiella norcrossi*	150-750	coarse silt, fine silt, silty clay ooze	+2° to 0°C	33.5 to 34.0	100-300 (calc.) aren. as single specimens
14. Shmidta Trough west slope assemblage: Eurybiotic species, *Bolivina subspinescens, Islandiella norcrossi, Valvulineria ochotica*	600-1250	silt clay or diatomaceous clay ooze	+1.5 to 2.3°C	34.0	100+ (calc.) 25- (aren.)
15. Lebedia Trough assemblage: *Valvulineria ochotica, Islandiella norcrossi, Uvigerina peregrina*	400-900	silt clay, diatomaceous clay ooze	+1.5 to 2.3°C	33.75 to 34.25	100-300 (calc.) aren. as single specimens
16. South Kamchatka base of slope assemblage: *Stainforthia concava, Angulogerina angulosa, Adercotryma glomerata, Pullenia subcarinata, Bolivina subspinescens, Islandiella norcrossi, Valvulineria ochotica, Globobulimina pacifica*	550-1250	silty clay, diatomaceous clay ooze	+2 to 2.4°C	34.0 to 34.25	500+
17. South Sakhalin and Hokkaido slope assemblage: *Haplophragmoides columbiense, Islandiella norcrossi, Globobulimina pacifica*	200-250 to 1500	fine silt, silty clay mud	+1.5 to 0°C	33.5 to 34.0	100-300
18. Kurile Islands slope assemblage: *Angulogerina angulosa* and rare specimens of other species	200-3000	coarse silt, fine mud silt	+2°C	34.6	100-300 (calc.) aren. as single specimens
19-21. CENTRAL OKHOTSK SEA ASSEMBLAGES					
19. Central Okhotsk Sea submerged platform assemblage: *Uvigerina ochotica, Gyroidina soldanii, G. orbicularis, Cassidulina delicata, Islandiella norcrossi, Valvulineria ochotica, Bulimina buchiana*	600-1500	silt, diatomaceous clay ooze	+2 to 2.4°C	34.0 to 34.5	300+ (calc.) aren. as single specimens
20. Deryugina Depression assemblage: *Pyrgo fischeri, Bulimina inflata, Cyclammina cancellata, Bolivina subaenariensis*	1300-1740	diatomaceous clay ooze	2.3°C	34.5	50- (calc.) aren. as single specimens
21. Southern deepwater trough assemblage: *Melonis pompilioides, Miliolina reussi, Reophax guttifer*	1500-3300	silty clay, diatomaceous clay ooze	+1.8° to +2°C	34.5 to 34.7	5- (calc.) aren. rare to 0.

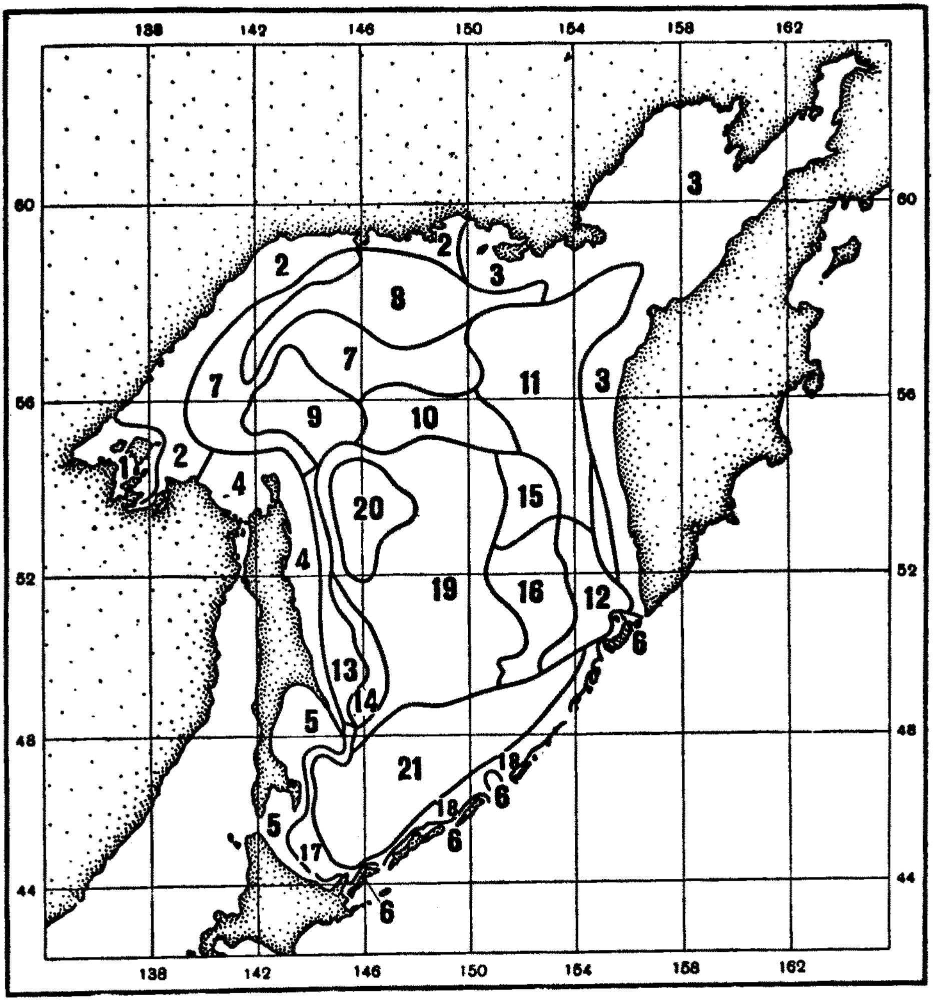


Fig. 74. Distribution of faunal assemblages in Sea of Okhotsk (*1617).

Arenaceous species were found to be extremely rare even in the deeper assemblages, despite size of the sea and water depths. The Sea of Okhotsk has approximately the same area and maximum depth as the Gulf of Mexico; yet no planktonic species were observed, the Kurile Island chain apparently serving as an effective barrier.

Because of difficulties inherent in attempting to reproduce marine environments in the laboratory, most of the ecological data available is based on "field studies" of living foraminiferal populations, recently summarized by Phleger (1960, *1454).

TEMPERATURE

On present continental shelves three bathymetric water layers are distinguished —a seasonal layer of greatest temperature variation, a permanent thermocline with gradual change in temperature, and a deep-bottom water layer (Fig. 75). Measurements of surface-water temperature alone, therefore, do not necessarily define thermal characteristics of the water mass. In partially enclosed basins, temperature has a lessened effect on faunal distribution (*1615). Variations in distribution with depth in such areas are not a function of

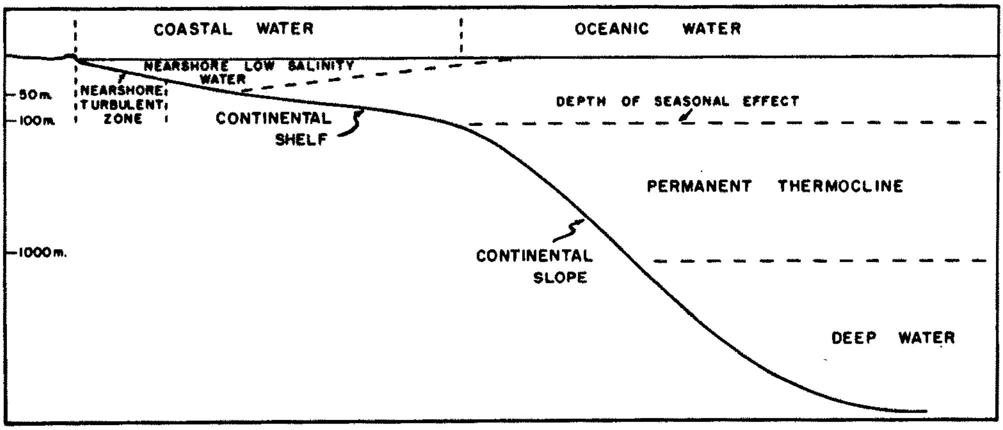


Fig. 75. Classification and distribution of coastal and oceanic waters near area of high runoff from land (*1454).

temperature; for example, in the Red Sea an approximate difference of only 2°C is found in the temperature of top and bottom waters (*1613), and in the Java Sea only 0.5°C temperature variation in the water column is measured.

Laboratory studies have shown that minimum and maximum temperatures affect the survival of a species, as well as its reproduction and repopulation. Within these limits an effect of seasonal variations, varying according to the species, may be observed. Some species can withstand wide temperature variations and show no seasonal change in size range. Others apparently are more strongly controlled by temperature and reproduce only in the warmer seasons. Species most strongly influenced by seasonal variations are benthonic forms living in shallow waters and planktonic forms living within the seasonal water layer. The present latitudinal control of planktonic species results in recognizable low-latitude, mid-latitude, and high-latitude assemblages. Similar temperature variations occurring in the geologic past may somewhat complicate long-range correlation by means of planktonic species. Bradshaw (1959, *185) noted four planktonic assemblages in the northern and equatorial Pacific (Fig. 76, 77). These assemblages roughly agree with latitudes, but are even more closely related to sea surface temperature, affected by major currents.

Experimental laboratory cultures have shown that growth and reproduction occur as long as environmental factors are favorable, but as these (e.g., temperature, salinity) depart from optimal values, rate of growth and frequency of reproduction decline. Cultures of *"Streblus beccarii* var. *tepida"* showed that at least 13 chambers were developed before reproduction occurred, but if temperature and salinity were unfavorable the specimen might continue growth and chamber addition for longer times. "The specimen may thus finally reproduce at a larger size and with a greater number of chambers than would be true under more favorable circumstances. . . . [Thus] larger specimens of the same species would be expected in the unfavorable environments and the smaller specimens under the most favorable conditions" (Bradshaw, 1957, *184). Phleger (1960, *1454) noted that in areas of optimum conditions and large living populations small specimen size "does *not* indicate a 'depauperate' fauna, but indicates unusually favorable conditions and therefore rapid reproduction." Concurrent rapid sedimentation might result in the accumulation of only a meager population in the sediment. "Unusually large specimen size may, therefore, indicate growth under marginal conditions." The occurrence of extremely large "species" of *Haplophragmoides* (e.g., *H. gigas, H. topagorukensis*) in the Canadian and Alaskan Cretaceous shallow-water deposits may

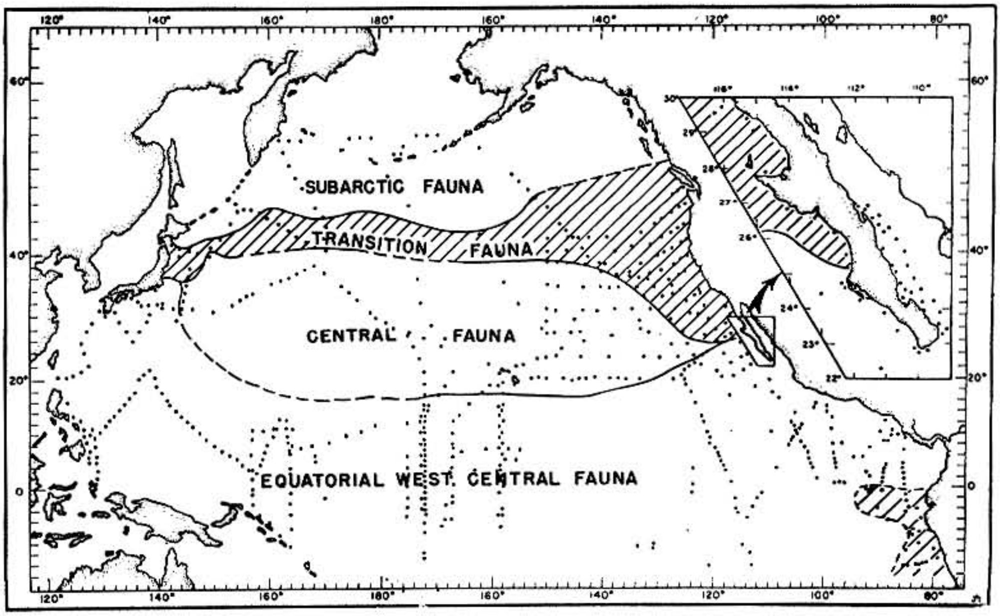


FIG. 76. Generalized distribution of planktonic assemblages of organisms in central and northern Pacific region (extent of sampling indicated by dots) (*185).

have been due to inhibiting temperatures or other unfavorable conditions. The occurrence of smaller forms in more offshore strata may thus not be a replacement by different species, but merely environmental size control. Restraint must be used in species delimitation with such marginal populations, as size characteristics are relatively unreliable.

Similarly, ecologically produced "dwarfed faunas" of invertebrates (as opposed to the pseudo-dwarfed faunas due to sorting ("pebble necrocoenosis" of Tasch, 1953, *1878) should contain relatively large foraminiferal specimens. The giant forms of *Endothyra* in the Salem and St. Louis Limestones associated with a "dwarfed" invertebrate fauna of brachiopods and gastropods would therefore seem to be normal for a highly unfavorable environment, instead of an anomalous occurrence, and thus not necessarily proof that true dwarfing did not occur, as suggested by Tasch. The size of *Endothyra* probably bears no relationship to cannibalism in ciliates that results in gigantism, as suggested by Lalicker (1948, *1080), especially as foraminifers are dominantly vegetarian, feeding largely on diatoms and other microscopic plant life.

DEPTH

Phleger (1960, *1454) regarded depth as the most important environmental factor, stating that "benthonic foraminiferal faunas are zoned offshore according to depth of water." A marked boundary in mid-latitudes at approximately 70-125 m. depth is found world-wide, marking the lower limit of the seasonal temperature layer. Other recognizable faunal-depth boundaries on the continental shelf are at 20-30 m. and at 50 m., and at 1,000 m. and possibly at 2,000 m. on the continental slope. That at about 1,000 m. may be at the bottom of the permanent thermocline, and that at 2,000 m. possibly may be due to hydrostatic pressure, since pressure at this depth is approximately 200 atmospheres, a suggested tolerance limit for some bacteria and possibly for other organisms as well. The other boundaries were considered by Phleger more difficult to explain physically. Probably they are related to the substrate.

Distinct faunas occur in each of the minor environments. Those of coastal lagoons can be distinguished from adjacent near-shore open-ocean assemblages. Deltaic marshes with rapid sedimentation have a characteristic fauna which is surprisingly similar throughout a wide geographic range, whether brackish or hypersaline in character. Sand lagoon barriers may have a mixture of species representing open-ocean, lagoon, and marsh benthonic environments, those from the open ocean commonly showing physical sorting.

Although some genera have limited depth ranges, use of individual species allows better zonation. A few species have almost world-wide occurrence within their depth zones.

The depth zonation in the Red Sea was stated by SAID (1950, *1613) to be controlled by organic content of the water and nature of the substrate and not by temperature variation. Furthermore, he reported that benthonic species are abundant near coast lines regardless of depth. Bottom topography has some effect, however, as unusually large foraminiferal numbers were found to be associated with submarine hills.

WATER-COLUMN DISTRIBUTION OF PLANKTONIC SPECIES

Planktonic species may occur at different depths within the water column. Also, they may migrate up or down in the water column diurnally or with growth and may live at different depths in different areas in order to adjust to local water temperature and density.

BRADSHAW (1959, *185) noted that planktonic specimens are less abundant in samples collected directly from the sea surface than from slightly deeper tows. The highest concentration occurs at depths of 6 to 30 m. and the greatest number never below 100 m. Most pronounced decrease in number with depth occurs between 50 and 100 m.; relatively few specimens were noted below 200 m.

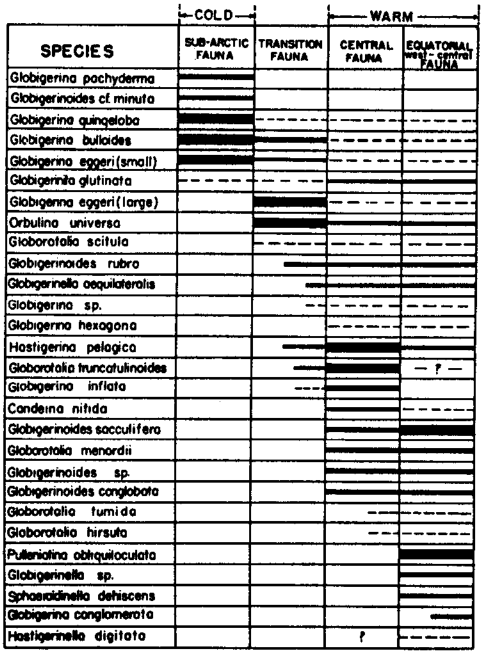


FIG. 77. Generalized distribution of planktonic foraminifers showing composition of assemblages in warm, transitional, and cold environments (*185).

Some diurnal migration apparently occurs, concentration at the surface being greater during daytime in the North Atlantic, off Bermuda, and in the Pacific (*185), suggesting that foraminifers migrate upward during the day and descend at night, possibly owing to effects of oxygen production by symbiotic algae. This may also be the reason for the greatest plankton populations in the uppermost 30 m. zone. Largest specimens of many species are commonly found in the deepest samples, which possibly is explained by their delayed reproduction and continued vegetative growth, as discussed more fully in considering temperature effects.

The temperature data derived from oxygen isotope ratios in tests of foraminifers by EMILIANI (1954, *703) and assumed to indicate depth at which the shell was formed have been questioned by BRADSHAW (1959, *185), because symbiotic zooxanthellae may influence the nature of the calcium carbonate deposited. The composite nature of EMILIANI's sample (several hundred tests for each determination, taken from several centimeters of core and thus possibly representing an extensive time span) also allows possibility of error, for final determinations give only an average; climatic fluctuations during the period of time represented by the material is unknown. Some seasonal changes in fauna occur even within a single year. Production of specimens in laboratory cultures under controlled temperature conditions might give data as to whether the oxygen-isotope method is valid for foraminiferal shells, reducing the number of variables in using large numbers of specimens for a single determination.

CHARACTER OF SUBSTRATE

PHLEGER (1960, *1454) regarded character of the substrate as a relatively unimportant environmental factor except for foraminifers requiring a surface for attachment (e.g., *Cibicides*) and for those associated with calcareous bioherms. Otherwise he regarded depth as the controlling factor. However, most published environmental studies are based on continental shelf areas adjacent to open coasts. No experimental evidence is available concerning effects of the substrate, though they appear to be important in some regions. PHLEGER stated that "although temperature has an importance rôle in influencing the distribution of species in the open seas with a large thermocline, it apparently does not influence zonation in shallow or partially enclosed basins. . . . In basins without a marked thermocline the availability of food, oxygen, the character of the substratum, or the salinity may be the dominant factor, either singly or in combination." Thus, in the Java Sea, where temperature does not vary more than half a degree between the surface and bottom at 30 to 50 m., just as distinct a zonation is found as off California, where the depth range amounts to 2,000 m. and temperature variations of 15°C occur (MYERS & COLE, 1957, *1343).

MYERS (1945, *1342) reported that at shallow depths in the Java Sea, in an area of dominantly carbonate facies, "each type of bottom produces a distinct population of Foraminifera." Only species living on seaweeds or attached to dead corals occur in the lagoons and platforms back of reef areas, as a result of scouring action of the surf. In the zone of living corals below low-tide level, living foraminifers are also associated only with seaweed or dead corals. On sandy mud bottoms immediately adjacent to the reefs a totally different population occurs; this consists of particularly large species. On heavy mud bottoms even larger species with more flattened tests are found, for these are adapted to glide over soft sediments. Farther from land only the smallest species occur, because the fine muds are almost a water suspension. In this environment larger or heavier species would sink below the surface muds. Coarse quartz sand bottoms indicate current sorting and species are commonly small forms with a brief life span. MORISHIMA (1948, *1314) found similar bottom control in shallow bays of the Inland Sea of Japan. Since maximum depth was 30.5 m. and maximum temperature fluctuation within the water column only 1 to 2°C, depth and temperature were unimportant factors, salinity and bottom characters being the controlling elements.

SAID (1950, *1613) noted a directly proportional relationship of foraminiferal number and median diameter of sediment in the Red Sea, coarser sediments containing the greater concentrations of benthonic foraminifers. Also directly proportional was the amount of total organic content. In another limited region—a lagoonal marsh off North Carolina—D. N. MILLER (1953, *1282) noted that "substratum conditions appear to have the most effect on faunal population. Shifting sands produced the highest arenaceous/calcareous ratio for Foraminifera. Compact, organic, argillaceous sands produced depauperate fauna. Fine clean sands carried the most abundant populations." A similar substrate control was observed in Recent Arctic foraminiferal faunas off Point Barrow, Alaska, by LOEBLICH & TAPPAN (1953, *1162) where faunas were most abundant and diversified in an offshore zone with gravelly bottom, and much restricted in the nearer shore mud zone. Heavy winter storms during 1949-1950 carried large quantities of mud over some previously observed gravel zones. In samples dredged after this influx of mud only dead invertebrates were found and the foraminiferal fauna was much reduced, probably to a greater extent than was indicated by the number of specimens found, since no information was available as to whether or not the observed foraminiferal tests contained protoplasm or were dead shells, either antedating the catastrophe, or later transported into the area.

SALINITY, OXYGEN, TRACE ELEMENTS

Species of foraminifers that can tolerate wide limits of salinity, such as those found in marshes, are found in both brackish and hypersaline waters. With lowered salinity the number of species is reduced, but the number of specimens of stenohaline forms is very great, either owing to lessened competition or increased available organic matter.

The limiting effect of salinity on growth and reproduction has been mentioned in connection with experimental data on temperature control. Either too high or too low salinities for a given species tend to retard its reproductive cycle. In brackish water in the Etang de Canet, France, general size and variety of foraminifers were found to decrease inland. The number of species in the brackish water was greatly restricted (only seven), all with calcareous relatively thin tests and lessened ornamentation. The number of individuals was high, however (J. LE CALVEZ & Y. LE CALVEZ, 1951, *1111).

Some foraminifers have even been reported from continental saline waters, when these contain chlorides of sodium or magnesium. They have been recorded from springs in the Kara-Kum desert in central Asia. Living foraminifers were found in fresh-, brackish-, and salt-water springs, irrigation ditches, and drainage canals of the Oued Rhir, a continental desert in Algeria, more than 400 km. (250 mi.) from the nearest coast, the species being euryhaline forms now present along the coasts. Genera reported include *Ammodiscus, Miliammina* and *Trochammina* (all common), *Anomalina* (varying abundance), and rare *Nonion, Cibicides,* and *Ophthalmidium*. *Trochammina* was found even in springs where the water was potable (pH of 7.2). The occurrence is difficult to explain except as a possible remnant of an earlier inland sea (GAUTHIER-LIÈVRE, 1935, *772).

In some enclosed basins, such as the Black Sea, where little exchange between surface and bottom waters exists, the bottom water is stagnant and unoxygenated, bottom sediment is black, and decomposing phytoplankton releases H_2S and NH_4 under almost anaerobic conditions. Oxygen becomes the limiting factor. Both number of species and total benthonic foraminiferal number (number of specimens in one gram) is reduced, and the specimens are small. This may be an instance of retardation of growth due to lower metabolism (SAID, 1951, *1615). The known inhibiting effect of H_2S on nuclear fission in *Amoeba* also suggests a possible retardation of the orderly succession of generations in foraminifers, resulting in their decreased abundance. A similar occurrence of a depauperate fauna in organic clays under anaerobic conditions was noted by D. N. MILLER (1953, *1282), many specimens containing pyrite grains inside the chambers.

J. LE CALVEZ & Y. LE CALVEZ (1951, *1111) noted that within the brackish waters of the Etang de Canet, the greatest influence on vitality of foraminifers and their ability to multiply was the oxygenated nature of the bottom. Thus, black putrid clays at 0.90 m. and salinity of 23.37 contained no foraminifers, whereas sandier, cleaner samples at the same depth and salinity from locations farther inland contained up to 256 individuals in a cubic centimeter.

"Dwarfed" thin-shelled specimens of *Heterostegina* 1.5 mm. in diameter which occur in down-dip shales of the Anahuac formation ("Oligocene") of Texas, noted by LALICKER (1948, *1080), may have been due to a similar environment. Tests belonging to this genus normally have a diameter of 4.3 mm. in the usual calcareous sand facies formed in a clean, shallow-water environment.

SAID (1950, *1613) noted that in the well-oxygenated Red Sea total numbers of benthonic foraminifers are directly proportional to nitrogen percentage (organic content). In the Red Sea basin an increase in oxygen resulted in even fewer foraminifers, probably owing to lessened organic content.

The inverse ratio in abundance of radiolarians and foraminifers in modern seas

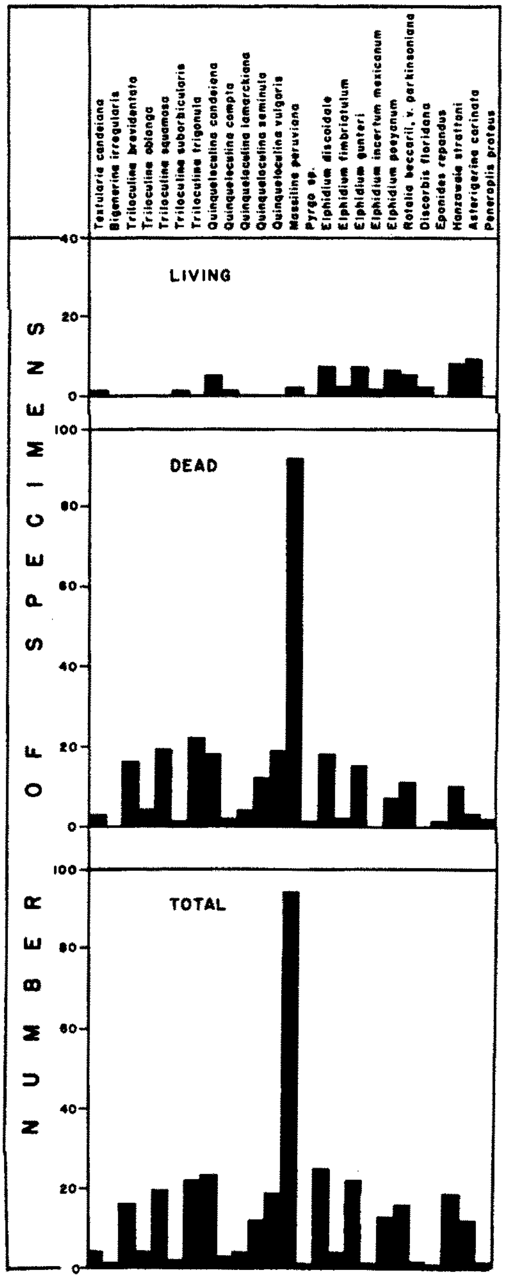


Fig. 78. Histograms showing foraminiferal populations on sandy shell bank in northwestern Gulf of Mexico. The large numbers of dead *Massilina peruviana* and other miliolids suggest post-mortem transportation of tests (*1733).

and in fossil assemblages may be due to the amount of dissolved silica available, since radiolarian deposits commonly are associated with areas of volcanic activity or with bentonite deposits. The turbidity factor of ash falls would restrict benthonic foraminiferal assemblages, but the limitation of the planktonic species may be chemically controlled in this instance.

Very few data are available as to effect of the presence or absence of trace elements. Boltovskoy (1956, *165) noted a depauperate foraminiferal fauna on the Argentine shelf between the Straits of Magellan and San Julián. As no other cause was apparent, an investigation of the shells of some species was made to determine the presence of unusual elements. Specimens of two species (*Quinqueloculina seminulum, Buccella frigida*) were examined from the depauperate fauna and from a more normal area south of Tierra del Fuego. Elements found in the shells of both species in both regions include Ca, Fe, Mg, Si, Sr, and Ti; *Buccella* also had Al and *Quinqueloculina* also had Mn and Sn at both localities. The sole element found only in San Blas Bay (depauperate zone) specimens of both species was Pb. Lead salts may decrease the plant (diatom) productivity, and the reduced food supply result in impoverished foraminiferal faunas.

CURRENTS

Because of their small size, empty tests of foraminifers may be sorted, reworked, and transported by currents or gravity in the same way as are mineral grains of similar size and conformation. They may be carried into areas in which they were not living and similarly may live in areas where empty tests, because carried away, are not deposited. Currents aid in dispersal of species, especially of planktonic forms; they also transport the flagellate gametes and young embryonic individuals of various species. In some studies of present-day assemblages comparison of specimens actually containing protoplasm with those found only as empty shells has aided in determining relationships of biocoenoses to thanatocoenoses. Shifflett (1961, *1733) from a study of living and dead populations in the Gulf of Mexico based on 12

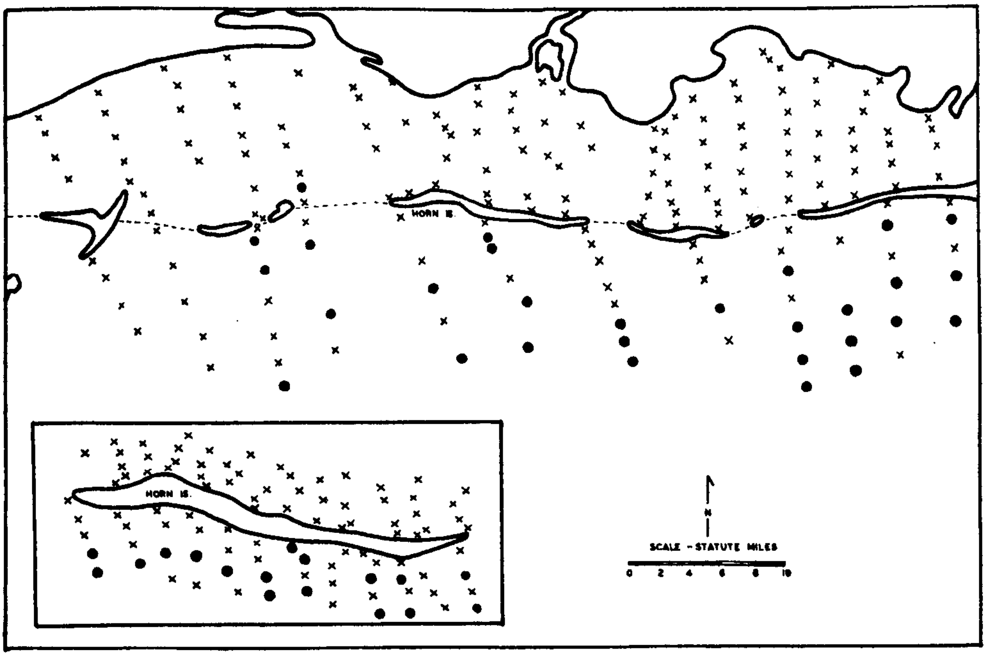


FIG. 79. Occurrence of planktonic and benthonic foraminifers in Mississippi Sound (blackened circles indicating samples that contain planktonic species and crosses those that contain only benthonic species). Planktonic forms are restricted to open Gulf areas, since the barrier islands effectively prevent their transportation inland (*1800).

shallow-water samples noted that faunal variations are great in short lateral distances. Comparison of living and dead assemblages so observed yields information on changing conditions and possible displaced faunas (Fig. 78).

D. J. CARTER (1951, *283) noted that in current-controlled assemblages the size ratios of foraminiferal specimens are similar to size ratios of sediments, the foraminiferal shells behaving as an integral part of the sediment. Foraminifers in the Coralline Crag of Suffolk (England) were shown to be a current-drifted faunal assemblage, only a few species (e.g., *Cibicides lobatulus, Planorbulina mediterranensis*) not being related directly to the sedimentary size fraction. The latter species live attached to algae, hence were probably indigenous to the locality.

F. D. SMITH (1955, *1800) made a study of the ratio of planktonic specimens to the total assemblage in the Gulf of Mexico and Mississippi Sound, for the purpose of testing its value as an indication of nearness to shore line, depth of water, and topographic anomalies such as offshore islands. In an unobstructed area of the Gulf a correlation between depth and percentage of planktonic specimens to total foraminiferal number was found. Use of similar methods in fossil sediments would indicate the direction of the shore line. Where islands occur in the Mississippi Sound, they obstructed the transportation of planktonic tests. A sharp decrease in percentage of planktonic species in adjoining areas in fossil material might indicate the presence of former reefs or barrier islands (Fig. 79).

A depth oscillation chart was devised by ISRAELSKY (1949, *979) by determining percentages of calcareous benthonic species of foraminifers in assemblages from varying depths. The depth significance of species obtained from a well penetrating Miocene sediments in Louisiana was determined by their relative abundance as compared to that of *Ammonia beccarii* (as indicator of shallow to brackish environment) and *Uvigerina* spp. (regarded as indicating deeper

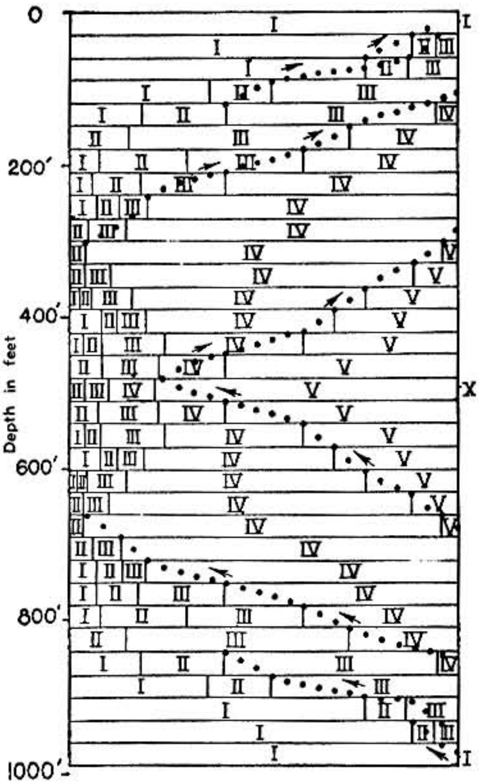
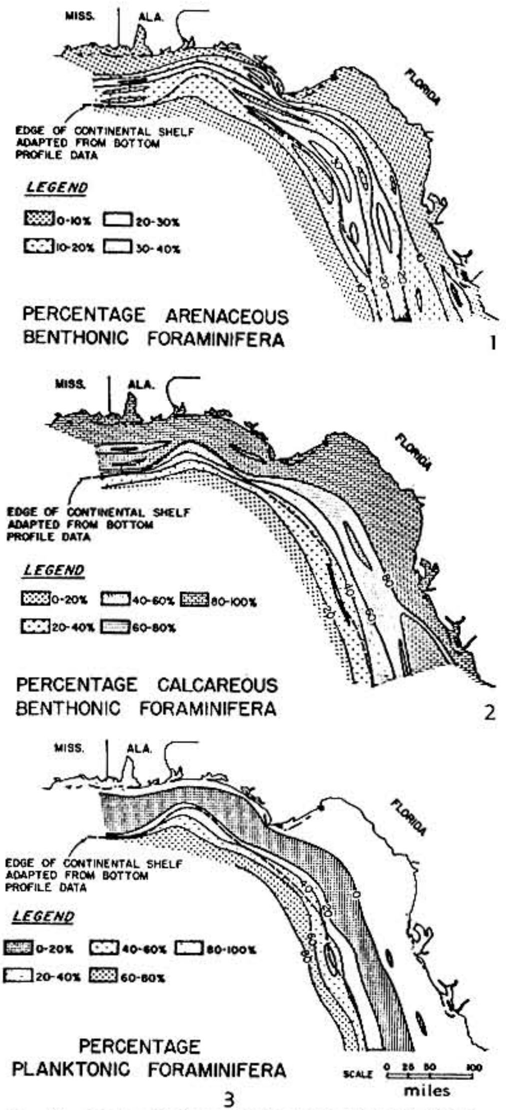


Fig. 80. Hypothetical marine cycle shown by depth oscillation chart. [Explanation: I, brackish-water assemblage; II, beach assemblage; III, seaweed-zone assemblage; IV, V, successively deeper water assemblages. Leftward shift of numbers in upward succession and left-pointing arrows indicates deepening water, and the opposite indicates shallowing water. The stratigraphic position of the deepest water assemblage (X) may be used to define a time plane] (*979).

water). Five assemblages interpreted to represent certain depths were distinguished and percentages of each assemblage in the various samples were plotted in order to identify marine cycles of deepening or shoaling water (Fig. 80). These oscillations could be adapted for correlation within a limited area, and with enough points of control, could be used to determine true time planes in a region (marked by stratigraphic position of deepest assemblages in different places or of shallowest assemblages in wholly marine sequences).

Biofacies maps have been constructed by Upshaw & Stehli (1962, *1971) by plotting percentages of planktonic specimens in foraminiferal assemblages, using these to indicate direction toward a coastline and fluctuations in distance to it (Fig. 81). A "departure map" was prepared for the same area by plotting percentages of specimens of planktonic, calcareous benthonic, and



PERCENTAGE ARENACEOUS BENTHONIC FORAMINIFERA

PERCENTAGE CALCAREOUS BENTHONIC FORAMINIFERA

PERCENTAGE PLANKTONIC FORAMINIFERA

Fig. 81. Marine biofacies indicated by foraminiferal assemblages in northeastern Gulf of Mexico.——*1.* Biofacies defined by percentages of arenaceous benthonic foraminifers.——*2.* Biofacies defined by percentages of calcareous benthonic foraminifers. ——*3.* Biofacies defined by percentages of planktonic foraminifers in total assemblage, decrease indicating direction toward shore (*1971).

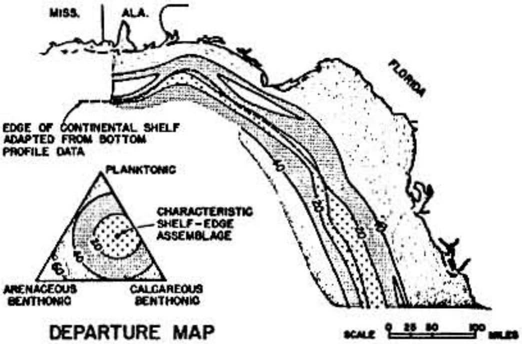


FIG. 82. "Departure map" based on shelf-edge foraminiferal assemblages, showing optimum assemblage for a selected environment and distances both shoreward and seaward from its location (*1971).

arenaceous benthonic foraminifers (Fig. 82). In the example used, the edge of the continental shelf off the west coast of Florida was regarded as a selected target environment comprising a sandy zone in a region of carbonate facies; in buried sediments it could serve as a potential petroleum reservoir. By plotting percentages of the three foraminiferal assemblages on a triangular diagram (Fig. 83) the optimum percentages for this environment were determined to be 16 per cent arenaceous benthonic foraminifers, 43 per cent calcareous benthonic, and 41 per cent planktonic specimens (square marked "F" in Fig. 83). When additional samples were plotted, departure from the optimum could be determined by distance from F, regardless of direction. The data plotted on a map (Fig. 82) indicate the departure from the optimum environment both seaward and shoreward; it marks the location of the continental shelf margin. Similar local maps could be utilized to locate ancient offshore bars or submarine highs. This method has the advantage of not requiring specific identifications for preparation of the graph and map.

TURBIDITY

The depth to which light penetrates in the sea is limited by turbidity of near-surface waters, which depends on the amount of material carried by it in suspension. In relatively clear water, photosynthesis probably occurs to a depth of about 50 m., thus to some extent limiting the production of the food supply (diatoms and other unicellular algae), as well as symbiotic zooxanthellae known to occur in some foraminifers. In highly turbid water suspended matter reduces the depth of light penetration, with corresponding reduction of the food supply and growth of symbiotic algae found especially in planktonic and some benthonic calcareous species. Arenaceous foraminifers seem to be less affected by turbidity than others, and STAINFORTH (1952, *1834, p. 43) has even suggested that assemblages of them dominated by large robust species, are turbidity-controlled. The robust *Haplophragmoides, Verneuilinoides,* and *Uvigerinammina* assemblages found in many Cretaceous deposits of northern Alaska and the Carpathian flysch appear to be at least partially turbidity-controlled. The turbidite nature of enclosing sediments substantiates this assumption. As mentioned in discussion of temperature, unusually robust foraminifers may indicate delayed reproduction and marginal living conditions, such as the limited faunas in this facies suggest.

Bentonitic sediments and other highly siliceous rocks commonly contain radiolarians and diatoms. These organisms occur in inverse ratio to numbers of foraminifers, suggesting that ash falls may have been important contributors to the turbidity, allowing survival of planktonic siliceous

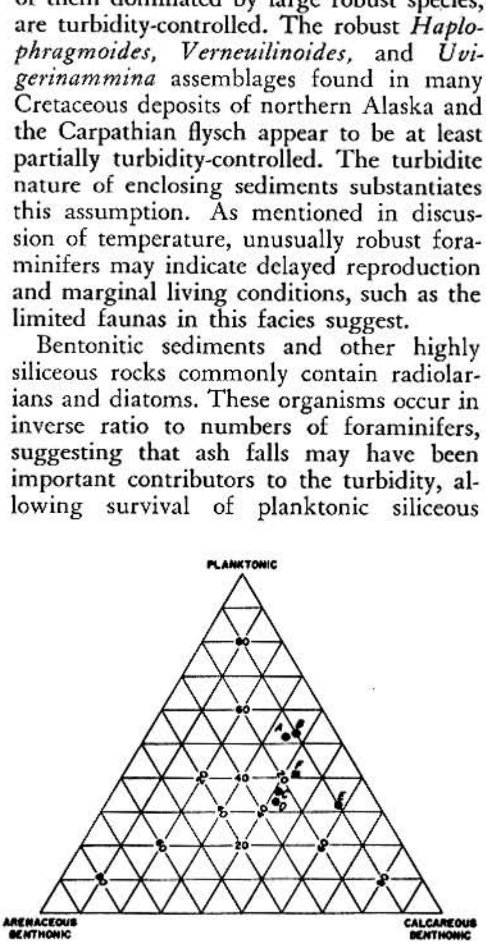


FIG. 83. Triangular graph showing selected target environment and its optimum point, based on analysis of foraminiferal assemblages. [Solid dots indicate percentages of different assemblages found along different traverses; solid square *(F)* represents average of these and the optimum point] (*1971).

forms but greatly reducing the calcareous foraminiferal faunas.

Phleger (1960, *1454, p. 113) has stated that no direct evidence is available concerning an effect of turbidity on foraminiferal distribution, but the very similar arenaceous faunas found in flysch-type deposits of Trinidad, northern Alaska, and the Carpathian Mountains strongly suggest that such a factor is important.

TURBULENCE

Strong surface winds produce turbulence of water bodies which agitates the bottom of shallow waters and makes them turbid. Water mixing is general. Replenishment of nutrients in upper water layers allows an increased production of phytoplankton. Turbulence in fine-grained sediments may bury foraminifers and hence restrict their occurrence. A faunal boundary in the region of San Diego, California, at a depth of about 13-20 fathoms was interpreted by Uchio (1960, *1961) as base of the turbulent zone.

RELATION OF FORM OF TEST TO HABITAT

Myers (1945, *1342) noted that many foraminifers show a relationship between form of the test and environment. Heavily spined shells are characteristic of tropical or subtropical climates in protected bays or seas affected by infrequent storms. In the Java Sea species living in quiet water attached to seaweeds are commonly strongly spinose, the spines protruding in all directions. Thin discoidal tests may be found on seaweeds and may show evidence of attachment (e.g., *Planorbulina*). Species that move about over a firm muddy bottom commonly are discoidal or much-flattened trochospiral or may have spines in a single plane. On soft muddy bottoms the spines tend to be long and attenuated in one plane. The tests of species living on firmer sandy bottoms may have a much-thickened central area. Lenticular forms occur on algal fronds and on heavy mud bottoms. The shape of tiny species seems to be less influenced by environment and their distribution may be extended by turbulence and current action. Planktonic forms commonly have globular chambers, bear numerous spines, or have broad flat carinate tests.

A similar general correlation of test form with depth was suggested by Bandy (1960, *74). Among agglutinated foraminifers the simpler forms are characteristic of bays and lagoons, whereas labyrinthic forms and those with siphonate chambers are found in central and outer parts of shelf areas and bathyal zones. Among porcelaneous forms, diverse miliolids are abundant in bays and the inner shelf but large biloculine types occur in bathyal depths. Discoidal and fusiform types inhabit the inner and central shelf, those with internal chamberlets more commonly in the central and outer shelf.

Calcareous perforate species with pillars (e.g., Rotaliidae, Calcarinidae) occur in the inner shelf; those with striae and costae are common in the outer shelf or bathyal zone. Coarser ornamentation and larger size are characteristic of deeper water assemblages.

STRATIGRAPHIC DISTRIBUTION

Although foraminifers are unicellular and therefore theoretically belong among more primitive forms of animal life, many higher invertebrates have an earlier geologic record. It seems probable that earliest foraminifers were similar to the present-day Lagynidae and Allogromiidae, with membranous or pseudochitinous tests. Agglutinated matter may have been gradually added to this as in living *Myxotheca,* but the fragility of such tests has prevented their preservation in the Precambrian geological record. According to Vinogradov (1953, *2007), the absence of Precambrian animals with calcareous skeletons possibly is due to a greater amount of CO_2 in the atmosphere and ocean water of early earth history, increasing the solubility of $CaCO_3$. Some Precambrian calcareous algae are known, but since these may take CO_2, CO_3, and HCO_3 from the water, they would be enabled to precipitate the $CaCO_3$. Vinogradov postulated that the most ancient Proterozoic animals were probably naked and planktonic (similar to present-day invertebrate larvae); he suggested that earliest coverings of the body may have been of organic protein, cellulose, or chitin.

CAMBRIAN AND ORDOVICIAN

The geologically oldest pseudochitinous foraminifers yet described apparently are the allogromiid genera *Chitinodendron* (U. Cam.), *Archaeochitosa* (Ord.), and *Chitinolagena, Labyrinthochitinia,* and *Maylisoria* (U.Ord.). The oldest recorded agglutinated forms belong to Cambrian and Ordovician Astrorhizidae—*Bathysiphon* (L. Cam.), *Hyperammina* (L.Ord.), *Astrorhiza* (M.Ord.), and *Rhabdammina* (U.Ord.)—and Ordovician Saccamminidae *(Ordovicina, Kerionammina, Psammosphaera, Pseudastrorhiza, Stegnammina, Tholosina).* The oldest known calcareous foraminifer is of Ordovician age, and belongs to the Parathuramminacea, family Moravamminidae *(Saccamminopsis).*

All of these early representatives, regardless of test composition, are simple forms having a single chamber or clusters of chambers, the original shape of which is doubtful, since irregular form of the fossils may be due to crushing of the soft pseudochitinous or weakly reinforced test. The pseudochitinous forms have a scattered geologic record from Cambrian to the present, but as they have mainly been obtained from acid residues, the pseudochitinous material alone being preserved, they may in life have been further protected by a calcareous or agglutinated test. The earliest calcarous forms known have been found in thin-sectioned limestones; greater search for them by similar methods of examination may show that they have much wider occurrence in early Paleozoic limestones than present records suggest.

SILURIAN

By Silurian time a fairly diverse assemblage of foraminifers is known, representing in addition to above-mentioned forms, in the Allogromiidae, *Archaeochitinia* and *Xenotheka* and in the Saccamminidae, *Blastammina, Sorosphaera, Saccammina, Lagenammina, Stomasphaera, Thurammina, Amphicervicis,* and *Colonammina.* The first enrolled tubular forms, grouped in the Ammodiscidae, appear in the Silurian, with *Ammodiscus, Glomospira, Turritellella, Tolypammina, Lituotuba,* and *Ammolagena.* The Silurian also saw a further expansion of microgranular calcareous genera and the appearance of the earliest Nodosinellidae *(Illigata, Eolagena).*

DEVONIAN

A few additional agglutinated genera of the Astrorhizidae *(Hippocrepina),* Saccamminidae *(Ceratammina, Hemisphaerammina, Webbinelloidea, Weikkoella),* and Ammodiscidae *(Psammonyx, Trepeilopsis)* appeared first in the Devonian, but this period is characterized largely by great expansion of microgranular forms with first appearance of the Parathuramminidae *(Parathurammina, Archaesphaera, Bisphaera, Cribrosphaeroides, Irregularina, Quasituberitina, Rauserina, Uralinella).* All of the Devonian parathuramminids, except for *Palachemonella* reported from Germany, are known only from Russia, where they have been studied extensively in thin-sectioned limestones. The Caligellidae are represented by *Caligella* and *Shuguria,* both from the Russian platform, the Moravamminidae by *Earlandia, Paratikhinella, Pseudoglomospira, Moravammina, Kettnerammina,* and *Vasicekia,* all known from the west European and Russian Devonian; the Nodosinellidae are represented by the earliest *Tuberitina, Tubeporina, Umbellina, Eovolutina, Nodosinella, Frondilina, Hipporina, Lunucammina;* the Colaniellidae by *Multiseptida,* and the Ptychocladiidae by *Tscherdyncevella.* The family Semitextulariidae appeared in the Devonian and is restricted to it *(Semitextularia, Paratextularia, Pseudopalmula)*; and the earliest Tournayellidae *(Tournayella, Brunsiina, Septabrunsiina)* and first Endothyridae *(Nanicella, Rhenothyra, Quasiendothyra, Rectoseptaglomospiranella)* are found here also.

MISSISSIPPIAN AND PENNSYLVANIAN

In Carboniferous times foraminifers began to appear in sufficient abundance locally to be of importance in rock-making, endothyrid limestones occurring in the Mississippian and fusulinid beds throughout the Permo-Carboniferous. A few additional simple agglutinated genera appeared in the Carboniferous (especially Ammodiscidae), but the most important developments were in beginnings of the more complex agglutinated forms (Lituolacea), the earliest porcelaneous calcareous genera, and the great expansion of microgranular calcareous genera, especially Endothyracea and Fusulinacea, the latter first appearing in the Late Mississippian (Chesteran). Among important first appearances were the Hormosinidae *(Reophax)*, Lituolidae *(Haplophragmoides, Trochamminoides, Ammobaculites)*, Textulariidae *(Spiroplectammina, Textularia)*, Trochamminidae *(Trochammina)*, and Ataxophragmiidae *(Mooreinella)*. Among newly introduced porcelaneous foraminifers, the tubular enrolled Fischerinidae first appeared in the Mississippian *(Cyclogyra, Agathammina, Hemigordius)* and additional genera arose in the Pennsylvanian, particularly attached types *(Orthovertella, Calcivertella, Calcitornella, Plummerinella)*. The first chambered genus to appear was *Eosigmoilina* (Ophthalmidiinae).

The dominant members of Carboniferous assemblages were microgranular calcareous genera (especially the Endothyracea and Fusulinacea). A few simpler genera also made their first appearance including Moravamminidae *(Earlandinita, Lugtonia, Turrispiroides)*, Ptychocladiidae *(Ptychocladia, Aoujgalia, Stacheia, Stacheoides, Fourstonella, Palaeonubecularia)*, Palaeotextulariidae *(Palaeotextularia, Climacammina, Cribrogenerina, Deckerellina, Palaeobigenerina)*, Tetrataxidae *(Tetrataxis, Polytaxis, Valvulinella)*, Biseriamminidae *(Biseriammina, Globivalvulina)*, new Tournayellidae *(Forschia, Forschiella, Glomospiroides, Lituotubella)*, Endothyridae *(Loeblichia,* undoubted *Endothyra, Endothyranella, Paraendothyra, Paraplectogyra, Haplophragmella, Cribrospira, Klubovella, Endothyranopsis, Chernyshinella, Bradyina, Glyphostomella, Janischewskina)*, early Archaediscidae *(Archaediscus, Brunsia, Permodiscus)*, and Lasiodiscidae *(Lasiodiscus, Howchinia, Monotaxinoides)*.

The most characteristic and striking of the late Paleozoic foraminifers are the fusulinids, which arose as close-coiled forms with short axis in the Upper Mississippian (Chesteran), derived from an endothyrid ancestor. The fusulinids rapidly increased in diversity, length of coiling axis, and internal complexity.

PERMIAN

The agglutinated, microgranular, and porcelaneous types of foraminifers were all represented by additional genera in the Permian, probably the more striking of these being those with internal complexity such as the agglutinated *Oryctoderma*, the microgranular *Colaniella* (Colaniellidae), *Pachyphloia* (Nodosinellidae), and *Lasiotrochus* (Lasiodiscidae). The porcelaneous genera with enrolled zigzag chambers *(Flectospira, Meandrospira)* and others with complex interior *(Pseudovermiporella)* appeared in the Permian. The final expansion of the Fusulinacea occurred, many developing long, attenuated tests and highly fluted septa. All became extinct at the close of the Permian.

A minor but important constituent of the Permian foraminiferal fauna comprise forerunners of the perforate hyaline groups, which are earliest representatives of the Nodosariidae *(Nodosaria, Astacolus, Dentalina, Frondicularia, Pseudonodosaria, Pseudotristix, Lingulina, Lingulonodosaria)*.

TRIASSIC

The known Triassic faunas are mostly from latest Triassic rocks, very little being known of the earlier Triassic. The oldest representatives of the arenaceous Schizamminidae *(Schizammina)*, Verneuilininae *(Gaudryina)* and Valvulininae *(Valvulina)*, the first porcelaneous Soritidae *(Triasina)*, and last of the microgranular forms *(Tetrataxis)* occur in the Triassic. The faunas known are dominated by the Nodosariidae, mostly the same genera that began in the Permian but in the Triassic represented by more ornamented forms, as well as the additional genera *Lenticulina, Marginulina, Vaginulina*, and *Vaginulinopsis*.

The earliest representatives of several families were Triassic species of Polymorphinidae *(Pyrulinoides, Sagoplecta)*, Bolivinitidae *(Brizalina)*, Involutinidae *(Involutina, Aulotortus, Paalzowella, Semiinvoluta, Trocholina)*, and questionably Spirillinidae *(Spirillina)* and Ceratobuliminidae *(Epistomina)*. In addition, a peculiar mid-Triassic fauna from Austria has been reported to contain the oldest Discorbidae *(Diplotremina, Duostomina, Variostoma)* and Anomalinidae *(Asymmetrina, Involvina, Plagiostomella)*, although nothing is known of the microstructure or lamellar character of these genera. If additional study upholds these reported occurrences, we may say that by Triassic time most of the superfamilies of calcareous foraminifers had been introduced (but not the Rotaliacea, Globigerinacea, and Orbitoidacea).

JURASSIC

During the Jurassic Period dominant members of the faunas were the Nodosariacea, represented by many genera, many with ornately ribbed surfaces, but with such great intraspecific variation that generic limits are difficult to delineate. The earliest attached Polymorphinidae also are found in the Jurassic, as are the first Glandulinidae.

In some areas a great expansion of the Lituolidae, Pavonitinidae, and Dicyclinidae occurred, with first appearance of many forms having a complex interior. Among porcelaneous forms were the earliest Nubeculariinae, Nodobaculariinae, Miliolidae *(Quinqueloculina)*, and Rhapydionininae. The Turrilinidae began in the Jurassic *(Praebulimina)*, as did the first of many genera of the Spirillinidae *(Spirillina, Conicospirillina, Miliospirella, Planispirillina, Terebralina, Turrispirillina)*.

The earliest planktonic foraminifers apparently were Jurassic forms representing the Guembelitriinae *(Gubkinella)*. The first Nonionidae *(Allomorphina)* and Ceratobulimininae *(Conorboides, Praelamarckina, Pseudolamarckina)* appeared. Additional genera of the Epistomininae, which in large part are characteristic of Jurassic strata *(Epistominita, Epistominoides, Garantella, Hoeglundina, Rectoepistominoides,* and *Reinholdella)*, are recorded.

CRETACEOUS

Foraminiferal limestones of Cretaceous age include the earliest miliolid limestones belonging to the Lower Cretaceous and orbitolinid, alveolinid, and orbitoidid limestones occurring in the Upper Cretaceous. Locally, various agglutinated genera also appeared in great numbers (e.g., *Cribratina* in the Texas mid-Cretaceous) and the earliest fossil planktonic oozes are Early Cretaceous in age. Numerous additional agglutinated genera are noteworthy, including some with labyrinthic interior (e.g., *Cribratina, Haplostiche,* Hormosinidae). The first Rzehakinidae *(Rzehakina, Miliammina, Psamminopelta, Silicosigmoilina)* are found in Cretaceous beds and many new Lituolidae *(Ammobaculoides, Ammotium, Buccicrenata, Bulbophragmium, Cyclammina, Daxia, Choffatella, Flabellammina, Hemicyclammina, Martiguesia, Navarella, Pseudochoffatella, Spirocyclina, Sornayina, Coscinophragma, Manorella, Loftusia, Phenacophragma, Stomatostoecha, Acruliammina, Arenonina)*. A similar great expansion, with appearance of a great many additional genera, occurred in the Ataxophragmiidae, Pavonitinidae, Dicyclinidae, and Orbitolinidae (locally limestone-forming), the orbitolinids being represented by *Orbitolina, Dictyoconus, Iraqia,* and *Simplorbitolina.*

Among imperforate calcareous forms were the earliest Spiroloculininae *(Spiroloculina)* and many genera of the Miliolidae (including earliest Miliolinae and Fabulariinae), additional Soritidae (earliest Meandropsininae) and earliest Alveolinidae, all of Late Cretaceous age. These became extremely abundant and important in forming limestone.

The hyaline calcareous foraminifers of the Cretaceous are characterized by a great expansion of coiled genera representing most of the superfamilies. In the Buliminacea, new forms of the Turrilinidae include *Buliminella, Neobulimina, Pyramidina, Rectobulimina, Sporobulimina, Sporobuliminella,* and *Lacosteina;* in the Bolivinitidae are *Bolivina, Bolivinoides* (especially in the later Cretaceous), *Gabonella, Grimsdaleinella, Loxostomoides,* and *Tappanina.* The Eouvigerinidae first appeared in the Early Cretaceous *(Eouvigerina)* and became important in the Late Cretaceous *(Siphogenerinoides)*. In the Uvigerinidae earliest genera are the Late Cretaceous *Orthokarstenia* and *Pseudouvigerina.* New Discorbidae are *Conorbina, Eoeponidella, Epistominella, Eurycheilostoma, Baggina,* and *Valvulineria.* The oldest known Patellininae occur in Lower Cretaceous rocks; also, the oldest Rotaliacea, represented by the Rotaliidae *(Rotalia, Kathina, Pararo-*

talia, Smoutina, Arnaudiella, Fisseolphidium, Pokornyellina, Pseudosiderolites), Calcarinidae *(Calcarina?, Siderolites),* and Nummulitidae *(Sulcoperculina),* are Cretaceous.

The first important planktonic foraminifers are Cretaceous assemblages. New Early Cretaceous genera belong to the Heterohelicidae *(Guembelitria, Heterohelix, Bifarina),* Planomalinidae *(Planomalina, Biglobigerinella, Globigerinelloides, Hastigerinoides),* Schackoinidae *(Schackoina, Leupoldina),* and Rotaliporidae *(Hedbergella, Clavihedbergella, Praeglobotruncana, Rotalipora, Ticinella).* Additional new forms appearing in the Late Cretaceous and restricted to it represent the Heterohelicidae *(Guembelitriella, Gublerina, Planoglobulina, Pseudoguembelina, Pseudotextularia, Racemiguembelina)* and Globotruncanidae *(Globotruncana, Abathomphalus, Plummerita, Rugoglobigerina, Trinitella).* In addition, the earliest Globigerinidae *(Globorotaloides)* appeared in latest Maastrichtian deposits, but this family is more characteristic of the early Cenozoic.

The bilamellid Orbitoidacea entered the fossil record in the Late Cretaceous with beginning of the Cibicididae *(Planulina* and *Cibicides),* Cymbaloporidae *(Cymbalopora),* Homotrematidae *(Carpenteria),* Pseudorbitoididae (all genera), and Orbitoididae (most genera, including *Orbitoides, Lepidorbitoides, Omphalocyclus*). New Pleurostomellidae appeared in the Early Cretaceous with the earliest Caucasinidae *(Fursenkoina, Cassidella, Coryphostoma, Caucasina),* Loxostomidae *(Loxostomum, Trachelinella),* Alabaminidae *(Alabamina)* and Osangulariidae *(Osangularia, Charltonina, Conorotalites, Globorotalites, Goupillaudina, Gyroidinoides).* New Nonionidae *(Chilostomella, Allomorphinella, Quadrimorphina, Nonion, Nonionella, Pullenia)* and last of the Involutinidae are recorded from Late Cretaceous strata.

Especially characteristic of the Cretaceous are the coarsely perforate Anomalinidae *(Gavelinella, Anomalinoides, Angulogavelinella, Heterolepa, Karreria, Pulsiphonina, Stensioina).* New Ceratobuliminidae (including *Ceratobulimina, Ceratolamarckina, Lamarckina)* and the earliest Robertinidae *(Colomia)* appeared in the Late Cretaceous.

PALEOCENE

The Paleocene has a truly transitional foraminiferal fauna which includes many genera and species of smaller foraminifers that were present in the Late Cretaceous (Maastrichtian) and persisted into the earliest Paleocene (Danian). Many new forms (especially planktonic genera and larger foraminifers) had their beginning in the Paleocene, however, and many characteristic Cretaceous forms had then completely disappeared.

Among new larger foraminifers are the porcelaneous *Fasciolites* and *Orbitolites,* together with the earliest *Nummulites, Miscellanea* (Nummulitidae), *Discocyclina,* and *Pseudophragmina* (Discocyclinidae). Among smaller foraminifers, new nodosariacean genera *(Polymorphina, Glandulina)* and buliminacean genera (including the earliest Buliminidae, *Bulimina, Globobulimina, Praeglobobulimina*) appeared. With them are new Rotaliacea (first Elphidiidae, *Protelphidium, Elphidiella, Laffitteina,* and new Rotaliidae, *Lockhartia, Thalmannita*). Other additions to the fauna include the granular-walled *Florilus* (Nonionidae), *Gyroidina* (Alabaminidae), and *Boldia, Coleites,* and *Melonis* (Anomalinidae).

The most striking change with advent of Paleocene time was in the character of planktonic assemblages. The abundant Cretaceous families Rotaliporidae, Globotruncanidae, and Schackoinidae disappeared completely at the close of the Maastrichtian, as did nearly all of the Heterohelicidae (only *Heterohelix* and *Bifarina* remaining). Two new forms *(Woodringina, Chiloguembelina)* appeared in the Danian. The Globigerinidae became the most important planktonic family in Paleocene time, when they were represented by *Globigerina, Globoconusa,* and *Subbotina.* The earliest Hantkeninidae *(Globanomalina)* and Globorotaliidae *(Turborotalia* and *Globorotalia)* also appeared.

EOCENE

Eocene time was marked by a great expansion of many groups of foraminifers. The Nummulitidae became abundant, forming limestones, their characteristic occurrence in rocks of this age leading to the common use of the term "Nummulitic" *(Nummulitique)*, synonymous with "Paleogene" throughout much of Europe. The Lepidocyclinidae *(Lepidocyclina, Pseudolepidina, Helicolepidina,* and *Helicostegina)* began in the Eocene. Alveolinid limestones were also formed in the early and middle Eocene, and miliolid limestones were deposited in the Eocene of France. Many shallow-water genera made their first appearance in the Paris Basin in Eocene time.

Other genera which appeared in the Eocene were the ataxophragmiid genera *Clavulina* and *Liebusella,* a number of miliolids with complex apertures or interiors *(Miliola, Hauerina, Austrotrillina, Fabularia, Articulina),* and new soritids *(Dendritina, Archaias, Spirolina, Somalina, Yaberinella).* The Plectofrondiculariinae (Nodosariidae) first appeared, with *Amphimorphina, Plectofrondicularia,* and *Bolivinella* represented. Among the Buliminacea were new forms of Turrilinidae *(Turrilina, Baggatella, Buliminellita),* Eouvigerinidae *(Siphonodosaria),* Sphaeroidinidae *(Sphaeroidina),* Pavonininae *(Reussella, Chrysalidinella, Tubulogenerina),* and Uvigerinidae *(Uvigerina, Euuvigerina, Hopkinsina, Kolesnikovella, Rectuvigerina, Siphogenerina, Trifarina, Uvigerinella).*

New Discorbidae *(Discorbis, Cancris, Pijpersia),* Glabratellidae *(Glabratella, Heronallenia),* first Siphoninidae *(Siphonina, Siphonides, Siphoninella),* and new Epistomariidae *(Epistomaria, Elphidioides, Nuttallides)* are recorded from Eocene deposits. Among the Rotaliacea were the first *Biarritzina, Dictyoconoides, Chapmanina, Ferayina* (Rotaliidae), *Elphidium, Polystomellina,* and *Porosorotalia* (Elphidiidae). New bilamellid genera include Eponides (Eponididae), the Planorbulinidae *(Planorbulina, Linderina, Planorbulinella), Gypsina* (Acervulinidae), many Cymbaloporidae *(Cymbaloporella, Fabiania, Gunteria, Halkyardia),* and Homotrematidae *(Sporadotrema, Victoriella, Eorupertia).* Among the granular-walled forms were the first *Cassidulina, Ehrenbergina, Globocassidulina* (Cassidulinidae), *Almaena, Ganella,* and *Queraltina* (Almaeninae). New aragonitic forms include *Stomatorbina* and *Schlosserina* (Epistominidae) and *Robertina, Cerobertina,* and *Pseudobulimina* (Robertinidae).

New planktonic genera of the Globigerinidae include *Globigerinoides, Globoquadrina, Globigerapsis,* and *Porticulasphaera,* and genera that developed apertural bullae *(Catapsydrax, Globigerinatheka)* appeared in the middle Eocene. In middle and late Eocene time the planktonic genera *Hantkenina, Cribrohantkenina,* and *Clavigerinella* are represented.

OLIGOCENE AND MIOCENE

Some larger foraminifers are particualrly characteristic of mid-Tertiary formations, among them the Miogypsinidae *(Miogypsina, Miogypsinoides),* which are restricted to Oligocene and early Miocene strata, and the Lepidocyclinidae, which also were locally abundant. A number of additional genera appeared in the Miocene, among them complex Soritidae *(Sorites, Amphisorus, Marginopora)* some Rotaliidae *(Ammonia, Pegidia, Rupertina),* Bolivinitidae *(Bolivinita),* Calcarinidae *(Baculogypsina),* and Anomalinidae *(Discanomalina, Hanzawaia, Holmanella).*

Planktonic foraminifers developed a modern aspect with the first appearance of many additional genera of the Hantkeninidae *(Hastigerina, Beella, Cassigerinella)* and Globigerinidae *(Orbulina, Candeina, Sphaeroidinella, Sphaeroidinellopsis, Globigerinatella, Globigerinita, Globigerinoita, Tinophodella).*

PLIOCENE AND PLEISTOCENE

A few additional genera first appeared in the Pliocene, among them *Pseudorotalia* (Rotaliidae), *Cellanthus* (Elphidiidae), *Pulleniatina* (Globigerinidae), *Sestronophora* (Eponididae), *Caribeanella* (Cibicididae), and *Alliatina, Alliatinella,* and *Geminospira* (Robertinidae). In the Pleistocene *Asterorotalia* (Rotaliidae) and *Hyalinea* (Cibicididae) have been reported.

Many generic and suprageneric ranges are still imperfectly known. Because of rapid changes in taxonomy based on more detailed morphology and newer methods of study it has been impossible to reallocate all previously described species. Many need additional study in order to determine true relationships and correct placement; hence, many generic and familial ranges will undoubtedly be extended somewhat eventually.

CLASSIFICATION

INTRODUCTION

"Classifications may be complex but the process of classifying is essentially simple. . . . Man has discriminative capacities far beyond his ability to remember the details and he escapes from this dilemma only by classifying his concepts" (BLACKWELDER, 1959, *140, p. 204). According to WHITTAKER (1959, *2057) a natural classification should consist of internally coherent taxa, subject to clear definition and delimitation, and based on the consideration of a maximum number of characteristics. A supposed evolutionary unit (common descent) should underlie the classification, whose organization (number, arrangement, and ranking of taxa) should embody our understanding of major relationships, summarize existing knowledge, and express evolutionary relations.

Foraminiferida are one of the few living animal groups, classification of which has been largely constructed on the basis of shell morphology, a fact which may have convenience for paleontologists who have only skeletal parts with which to work but which has handicapped serious students in attempts to understand natural relationships, as in the matter of dimorphism. In spite of their abundance, ease of culture, and relatively large size, foraminifers are among the most neglected of protozoans by zoologists, inasmuch as "They make no dramatic impact on human life like the famous parasites" (SANDON, 1957, *1628, p. 7). Hence, not only taxonomic description of species and genera but also major attempts at classification have largely been made by paleontologists. Zoological and protozoological texts commonly have followed one or another recent classification, though some have objected to the number of subdivisions recognized, as did JEPPS (1956, *993, p. 87), who wrote: "It seems better then for the present that a zoologist should adhere to Brady's simpler classification, remembering always that it certainly needs modification in accordance with the characteristics of the living organisms."

Fortunately, not all protozoologists are so narrow in outlook as to ignore three-quarters of a century of studies since the appearance of BRADY's *Challenger* Report, and instead of deploring the erection of a classification based in large part on the fossil record, they regard this as a unique opportunity to use evolutionary data, which is all too rare for a majority of the Protozoa. An apparently common misconception among paleontologists is that the Protozoa are to be regarded as "simple" forms, as indicated by the recent statement "More than 20,000 Recent and fossil species, subspecies and varieties of Foraminifera have been named, and they are arranged under a most elaborate and complex classification of superfamilies, families, and genera. Note that this group of organisms belongs to the one-celled Protozoa. They are the simplest forms in the animal kingdom, and, so far as known, they did not give rise to any of the more complex forms" (RAINWATER, 1960, *1497, p. 47).

By way of contrast are following recent statements by protozoologists: "The Protozoa can not be considered simple in any sense of the word. Each individual is complete in that it contains often within a single cell the facilities for performing all of the body functions for which a vertebrate possesses many organ systems. This concentration of functions into a small bit of protoplasm does not result in simplicity, but only in a reduction of the fundamental problem to a state where the machinery for performing each body function is not so readily visible. The fact that the machinery is not so visible does not imply that it does not exist or that if it does, it is simpler in nature" (JAHN & JAHN, 1949, *983, p. 3). "Through the processes of organic evolution, they [Protozoa] have undergone cytological differentiation and the Metazoan histological differentiation" (KUDO, 1954, *1064, p. 5). Although foraminifers may have been an "end-of-the-line" development within the Protozoa or Protista, other living Protozoa are regarded as being very similar to the forerunners of all present living organisms. "The modern view holds that photosynthetic phytoflagellates, . . . were probably ancestral not only to the Protozoa proper but also to the entire plant and animal kingdoms . . . the curious choanoflagellates have been considered progenitors of the . . . sponges by a number of systematists" (*385, p. 183). "Whether Protozoa are considered unicellular or acellular, there is practically universal agreement among biologists that they must have served as the source from which the Eumetazoa arose" (*385, p. 184). "The Eumetazoa may have arisen from either a colonial phytoflagellate of some sort or a ciliate-like progenitor. The primitive eumetazoan is postulated to have been a hydrozoan cnidarian in the first case, an acoel turbellaria in the second" (*385, p. 187).

In some more recent discussions certain flagellates are regarded as most primitive, the rhizopods representing one branch of evolution from these, the ciliates and Metazoa another. The same primitive flagellate type doubtless gave rise to the higher plants along another line of evolution.

Corliss (1962, *386, p. 37) stated that the science of systematics is divisible into three phases: "*alpha* taxonomy, the first or earliest stage, essentially limited to production of conventional descriptions of species and groups of species; *beta* taxonomy, the synthetic phase, concerned with proposals and treatment of schemes of natural classification embracing all levels in the taxonomic hierarchy; and finally the *gamma* stage, presumably the ultimate goal of all taxonomy, devoted principally to problems of evolutionary relationships at intraspecific populational levels." He added that "in general, the protozoologist is still in the dark ages of stage one, although for practical reasons . . . he must attempt a bit of *beta* taxonomy concomitantly."

As the study of microscopic organisms began somewhat later than that of larger ones, the past 150 years has been largely devoted to the *alpha* taxonomy of Corliss, namely, description of the many species in living and fossil faunas. Not all work is of equivalent quality in descriptions currently appearing or in comparison with earlier and later studies. Much careless descriptive work, with disregard of the species concept and lack of sufficient examination of previous publications has led to an unquestionably large number of synonyms in some groups, although "lumping" has persisted in others. Either extreme obscures relationships and destroys usefulness of the forms for ecologic, taxonomic, or stratigraphic purposes. Monographic treatments of any group will bring out many examples of synonymy but will also show unjustified use of the same name with too-wide limits and it is safe to assume that undoubtedly many valid species and genera remain yet to be described.

Blackwelder (1959, *140) noted that 95 per cent of all described animals are invertebrates and that the Protozoa alone represent 5 per cent of all known animals, being roughly equivalent in number to all known vertebrates. The foraminifers represent about half of all known Protozoa (Levine, 1962, *1132), or about 2.5 per cent of all known organisms. No one would recommend placing all vertebrates, living and fossil, in a mere 10 families, as Jepps (1956, *993) recommended for the foraminifers, yet the vertebrates are a far more compact group in mode of reproduction or in chemical composition of the skeleton, and shorter in geologic duration than foraminifers. The classification adopted herein includes 95 families of Foraminiferida, of which 33 are extinct. If this number of families seems excessive, one may point out that it includes 21,433 Recent and fossil species (up to 1958), according to a recent estimate given by Levine (1962, *1132), based on published indices and the Zoological Record. This is undoubtedly too low a figure, since none of these has a representative coverage of species or genera published in the Soviet Union. [As example, some 67 foraminiferal genera omitted from the Zoological Record for the years 1957-1958 are included in the present *Treatise* volume. We have made no attempt to check the coverage of specific names.] Nevertheless, Levine's figures are a fair estimate. In comparison, Levine recorded 4,790 species for ciliated Protozoa (approximately one-fifth as many as for foraminifers), although interestingly enough, numbers of living foraminifers and living ciliates are very close (4,163 foraminifers, 4,776 ciliates). In contrast to the 62 families here recognized for living foraminifers, Corliss (1962, *386) stated that the ciliates are organized in 130 families. A similar ratio for classification of living and fossil foraminifers would allow for 750 families!

PREVIOUS CLASSIFICATIONS

"As is the case with all other groups of organic beings, few authorities agree in the classification of the Rhizopods . . ." (Leidy, 1879, *1127, p. 6). This is certainly true of the foraminifers. From the five families originally recognized by d'Orbigny (1826, *1391) to the 50 used by Cushman (1948, *486), 62 by Sigal in Piveteau (1952, *1458), or the 72 utilized in Osnovy Paleontologiy by Rauzer-Chernousova & Fursenko (1959, *1509) considerable variation is indicated in relative importance assigned to the characters utilized and in the resultant number of taxonomic divisions.

DE BLAINVILLE, 1825

The earliest classification of foraminifers using latinized group names was that of de Blainville (1825, *142) in which these names were classed as included with cephalopods. Each of the ten families, assigned to two orders, was based largely on shape of the test and included genera from two groups (Orthocerata, for example, including *Belemnites, Orthoceras,* and *Hippurites* with the foraminiferan *Nodosaria*). Statement of de Blainville's classification is given in Table 5.

Table 5. *Classification of Foraminiferida by de Blainville, 1825 (*142)*

Type Malacozoa (Malacozoaires)
Class Cephalophora (Céphalophores)
Order Cellulacea (Cellulacés)
Families Spherulacea (Sphérulacés)——Planulacea (Planulacés)——Nummulacea (Nummulacés)
Order Polythalamacea (Polythalamacés)
Families Orthocerata (Orthocérés)——Lituacea (Lituacés)——Cristacea (Cristacés)——Ammonacea (Ammonacés)——Nautilacea (Nautilacés)——Turbinacea (Turbinacés)——Turriculacea (Turriculacés)

D'ORBIGNY, 1826

D'Orbigny (1826, *1391) first utilized the term "foraminifères," although only in French vernacular, to subdivide the Cephalopoda into two orders, those with siphons (Order Siphonifères) and those lacking siphons (Order Foraminifères). The families were based upon chamber arrangement (uniserial; bi- or triserial; enrolled trochospiral or planispiral; milioline, and biserial enrolled, in the order given). Names of the several groups are given in Table 6.

Table 6. *Classification of Foraminiferida by d'Orbigny, 1826 (*1391)*

Order Foraminifères, nov.
Families Les Stichostègues, nov.——Enallostègues, nov.——Hélicostègues, nov. (Sections Turbinoïdes, nov.; Ammonoïdes, nov.)——Les Agathistègues, nov.——Les Enthomostègues, nov.

CROUCH, 1827

A classification by Crouch (1827, *397) closely followed that of de Blainville but transferred the Spherulacea to the Polythalamia and changed the family terminations, as indicated in Table 7.

Table 7. *Classification of Foraminiferida by Crouch, 1827 (*397)*

Order Cephalopoda
Division I. Polythalamous Cephalopoda
Families Orthocerata——Lituolata—Cristata——Sphaerulata——Radiolata——Nautilacea——Ammoneata

D'ORBIGNY, 1839

In 1839 d'Orbigny in de la Sagra (*1611) elevated his original families based on chamber arrangement to the rank of orders, adding the Monostègues for unilocular forms and erecting ten families within these orders, some based on generic names and others merely on descriptive terms. D'Orbigny's classification of 1839 appears in Table 8.

Table 8. *Classification of Foraminiferida by d'Orbigny, 1839 (*1611)*

Class Foraminifères
Order Monostègues
Order Stichostègues
Families Equilateralidae——Inequilateralidae
Order Hélicostègues
Families Nautiloidae——Turbinoidae
Order Entomostègues
Families Asterigerinidae——Cassidulinidae
Order Énallostègues
Families Polymorphinidae——Textularidae
Order Agathistègues
Families Miliolidae——Multiloculidae

SCHULTZE, 1854

Schultze (1854, *1695) gave the following classification of the Rhizopoda (Table 9).

Table 9. *Classification of Foraminiferida by Schultze, 1854 (*1695)*

Nuda
Testacea
  Monothalamia
    Families Lagynidae —— Orbulinida —— Cornuspirida
  Polythalamia
    Group Helicoidea
      Families Miliolida——Turbinoida (Subfamilies Rotalida; Uvellida; Textilarida; Cassidulinida) ——Nautiloida (Subfamilies Cristellarida; Nonionida; Peneroplida; Polystomellida)——Alveolinida——Soritida
    Group Rhabdoidea
      Family Nodosarida
    Group Soroidea
      Family Acervulinida

CARPENTER, PARKER & JONES, 1862

In 1862, two classifications appeared almost simultaneously, one by Carpenter, Parker & Jones (*281) in England, and the other, based largely on fossil faunas, by Reuss (*1552) in Austria. The former divided the Rhizopoda into three orders, that referring to foraminifers being termed the order Reticularia. Major subdivisions were based on test structure, the Imperforata (Table 10) including pseudochitinous, porcelaneous, and arenaceous "families," and the Perforata including a hyaline, perforate family, another incorporating planktonic forms and a third comprising tests with canal systems.

Table 10. *Classification of Foraminiferida by Carpenter, Parker & Jones, 1862 (*281)*

Order Reticularia
  Suborder Imperforata
    Families Gromida——Miliolida——Lituolida
  Suborder Perforata
    Families Lagenida——Globigerinida (Subfamilies Globigerinae; Textularinae; Rotalinae)——Nummulinida

REUSS, 1862

A more detailed classification was given by Reuss (*1552) with many additional family names, as outlined in Table 11.

Table 11. *Classification of Foraminiferida by Reuss, 1862 (*1552)*

Foraminifera d'Orbigny
  Foraminifera Monomera, nov.
    Families Gromidea Claparède——Lagenidea, nov. ——Spirillinidea, nov. —— Squamulinidea, nov. ——Ovulitidea, nov.——Cornuspiridea Schultze ——Ammodiscinea, nov.
  Foraminifera Polymera, nov.
    Families Rhabdoidea Schultze (Subfamilies Nodosaridea, nov.; Vaginulinidea, nov.; Frondicularidea, nov.; Glandulinidea, nov.; Pleurostomellidea, nov.)——Cristellaridea Schultze——Polymorphinidea (d'Orbigny), nov.——Cryptostegia, nov. ——Textilaridea Schultze —— Cassidulinidea d'Orbigny——Miliolidea Schultze (Miliolidea genuina, nov.; Fabularidea d'Orbigny)——Orbitulitidea, nov.——Peneroplidea Schultze——Lituolidea, nov.——Uvellidea (Ehrenberg), nov.——Rotalidea——Polystomellidea, nov.——Nummulitidea, nov.

A postscript to Reuss (1862, *1552, p. 394) gave a revised classification based also on test composition and structure. In this classification (Table 12) the Gromidea were omitted, being transferred to the testacean groups.

Table 12. *Classification of Foraminiferida by Reuss (*1552, p. 394, postscript)*

Foraminifera with imperforate shell
  With agglutinated test
    Lituolidea——Uvellidea
  With porcelaneous calcareous test
    Squamulinidea? —— Miliolidea (Cornuspiridea; Miliolidea genuina; Fabularidea)——Peneroplidea ——Orbitulitidea
Foraminifera with porous shell
  With glassy, finely porous calcareous test
    Spirillinidea——Ovulitidea——Rhabdoidea (Lagenidea; Nodosaridea; Vaginulinidea; Frondicularidea; Glandulinidea; Pleurostomellidea)—— Cristellaridea —— Polymorphinidea——Cryptostegia——Textilaridea——Cassidulinidea
  With very finely perforate calcareous test
    Rotalidea
  With calcareous test with canal system
    Polystomellidea——Nummulitidea

JONES, 1875

Jones in Griffith & Henfrey (1875, *824) removed arenaceous foraminifers from the Imperforata of Carpenter, Parker & Jones (1862, *281), and added more subdivisions as shown in Table 13.

Table 13. *Classification of Foraminiferida by Jones (*824)*

Imperforate or porcelaneous Foraminifera
  Families Nubecularida——Miliolida——Peneroplida——Orbiculinida——Dactyloporida
Arenaceous Foraminifera
  Parkeriada——Lituolida
Perforate or hyaline Foraminifera
  Lagenida——Polymorphinida——Buliminida —— Textilarida —— Globigerinida (Globigerinina; Rotalina; Polystomellina; Nummulinina)

SCHWAGER, 1877

In Schwager's classification (1877, *1705) test composition and chamber arrangement were combined. The first four subdivisions of the perforate calcareous forms were those with uniserial chambers in one plane, the next three had uniserial chambers in a spire, the eighth had two or more series of chambers, and the ninth was complex. A similar subdivision of the agglutinated forms had three uniserial groups, and one with two or more rows of chambers. In imperforate tests, the first two had chambers in a single series of cyclical arrangement, the third had chambers in more than one series, and the fourth had a complex structure. Schwager's classification is recorded in Table 14.

Table 14. *Classification of Foraminiferida by Schwager, 1877 (*1705)*

Perforate calcareous
Families Lagenoidea—Rhabdoidea—Dentalinoidea (Subfamilies Dentalinidae; Pullenidae; Nummulitidae)—Cristellaroidea—Polymorphinidea—Buliminidea (Buliminidae; Rotalidae)—Globigerinidea (Globigerinidae; Planorbulinidae)—Textilaridea (Textilaridae; Cryptostegia)—Tinoporidea
Agglutinated
Trochamminidea—Lituolidea—Ataxophragmidea—Plecanioidea
Calcareous imperforate
Cornuspiridea—Peneroplidea—Miliolidea—Dactyloporidea—Receptaculitidea
Chitinous
Gromidea

BRADY, 1884

Brady's classification in the "Challenger" Report (1884, *200), was based largely on his incomparable studies of Recent foraminifers. Although he discarded the suborders Imperforata and Perforata, his 10 families were similar to the 6 families and 3 subfamilies used by Carpenter, Parker & Jones (1862, *281), with addition of the Astrorhizidae and Chilostomellidae. Most of these were subdivided into additional subfamilies. The major groupings of families by Brady, as shown in Table 15, bear considerable resemblance to those here regarded as superfamilies or suborders.

The classification used by Lankester (1885, *1093) in the Encyclopaedia Britannica followed that of Brady, but changed the family and subfamily terminations.

Table 15. *Classification of Foraminiferida by Brady, 1884 (*200)*

Subkingdom Protozoa
Class Rhizopoda
Order Foraminifera (Reticularia)
Families Gromidae—Miliolidae (Subfamilies Nubecularinae; Miliolininae; Hauerininae; Peneroplidinae; Alveolininae; Keramosphaerinae)—Astrorhizidae (Astrorhizinae; Pilulininae; Saccammininae; Rhabdammininae)—Lituolidae (Lituolinae; Trochammininae; Endothyrinae; Loftusinae)—Textularidae (Textularinae; Bulimininae; Cassidulininae)—Chilostomellidae—Lagenidae (Lageninae; Nodosarinae; Polymorphininae; Ramulininae)—Globigerinidae—Rotalidae (Spirillininae; Rotalinae; Tinoporinae)—Nummulinidae (Fusulininae; Numulitinae; Cycloclypeinae; ?Eozoöninae).

RHUMBLER, 1895

Rhumbler (1895, *1568A) further subdivided the arenaceous families, removed the Endothyrinae from the Lituolidae and Fusulininae from the Nummulinidae of Brady, combining them in a single family; he also removed the Spirillininae from the Rotaliidae (early recognizing the distinctiveness of this group), and combined the remainder of Brady's Globigerinidae, Rotaliidae, and Nummulinidae into a single family. His arrangement of foraminifer assemblages is shown in the following outline (Table 16).

Table 16. *Classification of Foraminiferida by Rhumbler, 1895 (*1568A)*

Families Rhabdamminidae (Subfamilies Myxothecinae; Astrorhizinae; Saccammininae; Rhizammininae; Rhabdammininae; Hippocrepininae; Girvanellinae)—Ammodiscidae—Spirillinidae—Nodosinellidae—Miliolinidae (Nubecularinae; Miliolinae; Hauerininae)—Orbitolitidae—Textularidae (Textularinae; Buliminae; Cassidulinae)—Nodosaridae (Nodosarinae; Lageninae; Cristellarinae; Polymorphininae)—Endothyridae (Endothyrinae; Fusulininae)—Rotalidae (Rotalinae; Tinoporinae; Globigerininae; Polystomellinae; Nummulitinae)

DELAGE & HÉROUARD, 1896

Delage & Hérouard (1896, *580) combined Carpenter's Imperforata and Perforata (as orders) with Brady's classification within the subclass Foraminiferiae, elevating Brady's families to tribes or suborders and his subfamilies to families, resulting in a total of 24 families (Table 17).

TABLE 17. *Classification of Foraminiferida by Delage & Hérouard, 1896 (*580)*

Subclass FORAMINIFERIAE
Order IMPERFORIDA
Suborder GROMIDAE
Suborder MILIOLIDAE
Families Hauerinae—Peneroplinae—Alveolininae—Keramosphaerinae
Suborder ARENACIDAE
Tribe Astrorhizina
Families Astrorhizinae—Saccamminae—Rhabdamminae
Tribe Lituolina
Families Lituolinae—Trochamminae—Endothyrinae
Order PERFORIDA
Suborder LAGENIDAE
Families Lageninae — Nodosarinae—Polymorphinae—Ramulinae
Suborder CHILOSTOMELLIDAE
Suborder TEXTULARIDAE
Families Textularinae—Buliminae—Cassiduline
Suborder GLOBIGERINIDAE
Suborder ROTALIDAE
Families Spirillinae—Rotalinae—Tinoporinae
Suborder NUMMULITIDAE
Families Fusulininae — Polystomellinae—Nummulitinae—Cycloclypeinae

EIMER & FICKERT, 1899

EIMER & FICKERT (1899, *692) redefined many of the earlier proposed families, and erected many descriptive names that were not based on those of included genera, as follows (Table 18).

TABLE 18. *Classification of Foraminiferida by Eimer & Fickert, 1899 (*692)*

ASTRORHIZIDAE
Families Protocystidae—Astrorhizidae
SIPHONOFORAMINIFERA (TUBULATA)
Families Rhabdamminidae—Dendrophryidae—Saccorhizidae
CYSTOFORAMINIFERA (VESICULATA)
Families Gromiidae — Psammosphaeridae—Saccamminidae—Kyphamminidae
ASCOFORAMINIFERA (UTRICULATA)
Families Ammoasconidae—Serpuleidae
STICHOSTEGIA
PSAMMATOSTICHOSTEGIA
Families Hyperamminidae—Aschemonellidae
TITANOSTICHOSTEGIA
Family Nodosaridae
TEXTULARIDAE
Families Opistho-Dischistidae (Cribrosa; Oculosa)—Pavoninidae—Dichistidae (Cribrosa; Oculosa) — Opistho-Trichistidae (Cribrosa; Oculosa) — Trichistidae—Buliminidae — Frondicularidae
ENCLINOSTEGIA
Family Cassidulinidae
ORTHOKLINOSTEGIA
CORNUSPIRENSTAMM
Families Cornuspiridae—Miliolidae—Orbitoididae—Alveolinidae—Chilostomellidae
ENDOTHYRANSTAMM
Families Haplophragmidae—Endothyridae—Polystomellidae—Rotalidae — Cyclospiridae—Acervulinidae—Calcarinidae—Globigerinidae—Fusulinidae—Nummulitidae

LISTER, 1903

LISTER in LANKESTER (1903, *1094) used a classification similar to that of BRADY but elevated families to the rank of orders and subfamilies to families, the only exceptions being that the subfamilies Cycloclypeinae and Eozooninae were omitted. LISTER also gave a long discussion of the features of dimorphism, which he recognized as occurring in nearly all families.

SCHUBERT, 1921

SCHUBERT (1921, *1694) proposed a classification with families similar to those of BRADY but with additions which included six main groups, Protammida and Metammida for unilocular and multilocular agglutinated forms, the Porcellanea for porcelaneous forms, and Basistoma, Telostoma, and Schizostoma, based on apertural features. The Basistoma have an interiomarginal or basal aperture, the Telostoma a terminal aperture that is radiate, simple, rounded or specialized. The Schizostoma have a slitlike aperture (e.g., *Valvulina*) or a modified one (e.g., *Bulimina*), or cribrate ones developed from these. SCHUBERT's classification is as follows (Table 19).

TABLE 19. *Classification of Foraminiferida by Schubert, 1921 (*1694)*

PROTAMMIDA
METAMMIDA
BASISTOMA
Families Endothyridae (Endothyrinae; Fusulininae)—Rotalidae (Truncatulininae; Pulvinulininae; Globigerininae; Rotalinae; Discorbininae; Patellininae)—Orbitoididae—Nummulitidae
PORCELLANEA
Families Cornuspiridae—Miliolidae—Nubeculaoridae—Orbitolitidae (Orbitolitinae; Orbiculininae)—Keramosphaeridae—Alveolinidae
TELOSTOMA
Families Nodosaridae (Nodosarinae; Cristellarinae)—Polymorphinidae
SCHIZOSTOMA
Families Valvulinidae (Valvulininae; Textularinae)—Buliminidae (Bulimininae)

CUSHMAN, 1925

Cushman followed Brady in classification of the foraminifers in his early publications on these protozoans of the Atlantic and Pacific Oceans, and as late as 1925 this differed only by addition of a few subfamilies. Cushman's arrangement is shown in Table 20.

Table 20. *Classification of Foraminiferida by Cushman, 1925* (*420)

Families Gromidae——Astrorhizidae (Subfamilies Astrorhizinae; Saccammininae; Hyperammininae)——Lituolidae (Aschemonellinae; Reophacinae; Trochammininae; Neusininae; Orbitolininae; Endothyrinae)——Textulariidae (Spiroplectinae; Textulariinae; Verneulininae; Buliminnae; Cassidulininae)——Lagenidae (Lageninae; Nodosariinae; Polymorphininae; Uvigerininae; Ramulininae)——Chilostomellidae——Globigerinidae——Rotaliidae (Spirillininae; Rotalinae)——Nummulitidae (Fusulininae; Polystomellinae; Cycloclypeinae)——Miliolidae (Cornuspirininae; Quinqueloculininae)

CUSHMAN, 1927

In 1927 Cushman replaced the Gromidae by the Allogromiidae, and elevated various subfamilies to family status, with the result that 15 arenaceous families (instead of three), and six porcelaneous families (instead of one) were distinguished. The calcareous and agglutinated subfamilies of the Textulariidae were separated, with recognition of the Heterohelicidae, Buliminidae, and Cassidulinidae, and trochospiral hyaline forms were divided into a number of families and subfamilies. The previously recognized ten families were increased to 45. Cushman's 1927 classification is summarized in Table 21.

Table 21. *Classification of Foraminiferida by Cushman, 1927* (*431)

Order Foraminifera

Families Allogromiidae (Myxothecinae; Allogromiinae)——Astrorhizidae——Rhizamminidae—Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae)——Hyperamminidae (Hyperammininae; Dendrophryinae)——Reophacidae (Aschemonellinae; Reophacinae)——Ammodiscidae——Lituolidae (Haplophragmiinae; Lituolinae) —— Textulariidae (Spiroplectammininae; Textulariinae)——Verneuilinidae —— Valvulinidae—Fusulinidae (Fusulininae; Verbeekininae) Loftusiidae——Neusinidae —— Silicinidae——Miliolidae——Opthalmidiidae (Cornuspirinae; Nodobaculariinae; Opthalmidiinae; Nubeculariinae) —— Fischerinidae —— Trochamminidae (Trochammininae; Globotextularinae; Ammosphaeroidininae)——Placopsilinidae (Placopsilininae; Polyphragminae) —— Orbitolinidae——Lagenidae (Nodosariinae; Lageninae)——Polymorphinidae (Polymorphininae; Ramulininae)——Nonionidae——Nummulitidae ——Peneroplidae (Spirolininae; Archaisinae [*sic*]; Orbitolitinae)——Alveolinellidae —— Keramosphaeridae——Heterohelicidae (Heterohelicinae; Pavonininae; Guembelininae; Bolivinitinae; Spiroplectininae; Plectofrondicularinae; Eouvigerininae)——Hantkeninidae——Buliminidae (Terebralininae; Turrilininae; Bulimininae; Virgulininae; Reussiinae; Uvigerininae) —— Ellipsoidinidae——Rotaliidae (Spirillininae; Turrispirillininae; Discorbisinae; Rotaliinae; Bagginінae)——Amphisteginidae——Calcarinidae——Cymbaloporidae —— Cassidulinidae (Ceratobulimininae; Cassidulininae; Ehrenbergininae) —— Chilostomellidae (Allomorphininae; Chilostomellinae; Seabrookiinae; Allomorphinellinae; Sphaeroidininae)——Globigerinidae (Globigerininae; Orbulininae; Pulleniatininae; Candeininae)——Globorotaliidae —— Anomalinidae (Anomalininae; Cibicidinae) —— Planorbulinidae——Rupertiidae——Homotremidae——Orbitoididae

GALLOWAY, 1933

The classification of Galloway (1933, *762) recognized 35 families and his was the first attempt to cite authors and dates for the family categories, as well as to recognize priority in suprageneric classification. Thus, some family names differed from the previous classifications even when included genera were the same. Many features were similar to the classification of Rhumbler (1895), which recognized the Spirillinidae, Endothyridae, and Nodosinellidae as separate families. Greater subdivision of the hyaline calcareous families was made although with somewhat different grouping as compared with Cushman's classification. Galloway's arrangement is outlined in Table 22.

Table 22. *Classification of Foraminiferida by Galloway, 1933* (*762)

Order Foraminifera d'Orbigny, 1826

Families Lagynidae Schultze, 1854 (Subfamilies Lagyninae Galloway, n. subfam.; Amphitreminae Galloway, n. subfam.; Myxothecinae Rhumbler, 1895; Allogromiinae Rhumbler, 1904; Rhynchogromiinae Galloway, n. subfam.)——Astrorhizidae Brady, 1881 (Saccammininae Brady, 1884; Proteonininae Galloway, n. subfam.; Astrorhizinae

Brady, 1884; Hyperammininae Cushman, 1910) ——Spirillinidae Reuss, 1861 (Spirillininae Brady, 1884; Problematininae Rhumbler, 1913; Patellininae Rhumbler, 1906)——Ammodiscidae Rhumbler, 1895——Miliolidae d'Orbigny, 1839 (Cornuspirinae Reuss, 1861; Nubeculariinae Brady, 1884; Miliolinae Reuss, 1861; Hauerininae Brady, 1884)——Soritidae Ehrenberg, 1840 (Peneroplinae Schultze, 1854; Orbitolitinae Brady, 1881)——Alveolinellidae Cushman, 1928 (Alveolinellinae Galloway, n. name; Keramosphaerinae Brady, 1884)——Endothyridae Rhumbler, 1895 (Endothyrinae Brady, 1884; Tetrataxinae Galloway, n. subfam.) —— Nodosinellidae Rhumbler, 1895——Reophacidae Cushman, 1927 ——Trochamminidae Schwager, 1877 (Trochammininae Brady, 1884; Placopsilininae Cushman, 1927)——Lituolidae Reuss, 1861 (Lituolinae Brady, 1884; Neusininae Cushman, 1910)—— Orbitolinidae Martin, 1890 —— Ataxophragmiidae Schwager, 1877 (Ataxophragmiinae Galloway, n. subfam.; Verneuilininae Cushman, 1911)——Textulariidae d'Orbigny, 1846 (Palaeotextulariinae Galloway, n. subfam.; Textulariinae Schultze, 1854)——Nodosariidae Schultze, 1854 (Frondiculariinae Reuss, 1861; Nodosariinae Reuss, 1861; Robulinae Galloway, n. subfam.)—— Polymorphinidae d'Orbigny, 1846 (Polymorphininae Brady, 1881; Ramulininae Brady, 1884)—— Nonionidae Reuss, 1860 (Nonioninae Schultze, 1854; Elphidiinae Galloway, n. subfam.)—— Rotaliidae Reuss, 1860 (Rotaliinae Schultze, 1854; Discorbinae Cushman, 1927; Cibicidinae Galloway, n. subfam.; Planorbulininae Galloway, n. subfam.)——Acervulinidae Schultze, 1854 (Rupertiinae Galloway, n. subfam.; Acervulininae Galloway, n. subfam.)——Tinoporidae Schwager, 1877—Asterigerinidae d'Orbigny, 1839—— Chapmaniidae Galloway, n. fam.——Chilostomellidae Brady, 1881——Orbulinidae Schultze, 1854——Pegidiidae Heron-Allen & Earland, 1928 ——Heterohelicidae Cushman, 1927 (Heterohelicinae Cushman, 1927; Gümbelininae Cushman, 1927; Bolivinitinae Cushman, 1927)—— Buliminidae Jones, 1876 (Turrilininae Cushman, 1927; Bulimininae Brady, 1884)——Cassidulinidae d'Orbigny, 1839——Uvigerinidae Galloway & Wissler, 1927 (Uvigerininae Cushman, 1913; Angulogerininae Galloway, n. subfam.)——Pleurostomellidae Reuss, 1860——Fusulinidae Möller, 1878 (Fusulininae Rhumbler, 1895; Schwagerininae Dunbar & Henbest, 1930; Verbeekininae Staff & Wedekind, 1910)——Camerinidae Meek & Hayden, 1865 (Camerininae Galloway, n. name; Heterosteginae Galloway, n. subfam.)——Orbitoididae Schubert, 1920 (Orbitoidinae Prever, 1904; Miogypsininae Vaughan, 1928; Omphalocyclinae Vaughan, 1928)——Cycloclypeidae Galloway, n. fam. (Cycloclypeinae Bütschli, 1880; Discocyclininae Galloway, 1928)

CHAPMAN & PARR, 1936

Chapman & Parr in 1936 (*325) grouped 33 families into 3 superfamilies, one for the pseudochitinous Allogromiidae, one for all perforate hyaline calcareous families, and one for remaining arenaceous and porcelaneous forms. The families were similar to those of Cushman's 1927 classification, but among the agglutinated group, the Neusinidae were omitted and Placopsilinidae and Orbitolinidae reduced to subfamily status, and the calcareous Nonionidae, Hantkeninidae, Amphisteginidae, Calcarinidae, Cymbaloporidae, Globorotaliidae, Anomalinidae, Planorbulinidae, Rupertiidae, and Homotremidae of Cushman were reduced to subfamilies. The classification of Chapman & Parr is given in Table 23.

Table 23. *Classification of Foraminiferida by Chapman & Parr, 1936 (*325)*

Order Foraminifera
 Superfamily Allogromioidea
  Allogromiidae (Subfamilies Myxothecinae; Allogromiinae)
 Superfamily Spirillinoidea
  Spirillinidae——Nodosariidae (Nodosariinae; Lageninae) —— Polymorphinidae (Polymorphininae; Ramulininae)——Buliminidae (Turrilininae; Bulimininae; Virgulininae; Reussellinae; Uvigerininae)——Cassidulinidae —— Pleurostomellidae——Heterohelicidae (Heterohelicinae; Gümbelininae; Bolivinitinae; Plectofrondiculariinae; Eouvigerininae)——Rotaliidae (Discorbinae; Cymbaloporinae; Rotaliinae; Pegidiinae; Siphonininae; Bagginae; Cibicidinae; Planorbulininae; Rupertiinae; Homotreminae; Amphisteginae; Calcarininae)——Chilostomellidae (Chilostomellinae; Seabrookiinae; Allomorphinellinae; Sphaeroidininae)——Orbulinidae (Globigerininae; Orbulininae; Pulleniatininae; Candeininae; Hantkenininae; Globorotaliinae) ——Orbitoididae (Lepidorbitoidinae; Orbitoidinae; Omphalocyclinae; Miogypsininae; Discocyclininae)——Nummulitidae (Nonioninae; Nummulitinae)
 Superfamily Ammodiscoidea
  Ammodiscidae (Ammodiscinae; Tolypammininae)——Hyperamminidae (Hyperammininae; Dendrophryinae)——Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae; Webbinellinae)——Rhizamminidae (Rhizammininae; Botellininae) —— Astrorhizidae——Opthalmidiidae (Cornuspirinae; Nodobaculariinae; Opthalmidiinae; Nubeculariinae) —— Miliolidae—— Fischerinidae —— Soritidae (Peneroplinae; Archaiasinae; Orbitolitinae)——Alveolinellidae

——Keramosphaeridae——Silicinidae (Silicininae; Rzehakininae)——Lituolidae (Endothyrinae; Haplophragmiinae; Lituolinae; Placopsilininae; Polyphragminae) —— Loftusiidae —— Reophacidae (Nodosinellinae; Reophacinae; Aschemonellinae; Sphaerammininae)——Textulariidae —— Trochamminidae (Trochammininae; Globotextulariinae; Ammosphaeroidininae; Nouriinae) —— Valvulinidae (Tetrataxinae; Valvulininae; Orbitolininae)——Verneuilinidae ——Fusulinidae (Fusulininae; Schwagerininae; Verbeekininae; Neoschwagerininae)

GLAESSNER, 1945

Glaessner (1945, *796) recognized 37 families, grouped into seven superfamilies. Two arenaceous superfamilies were distinguished, one of unilocular and the other of multilocular families. Another superfamily included the Endothyridae and Fusulinidae and still another included porcelaneous forms; the hyaline families were divided into three superfamilies, one for the Lagenidae and Polymorphinidae, one for most biserial and elongate genera, and a third for all spirally enrolled and discoidal forms. Most families were similar to those of Cushman's 1927 classification except that the Spirillinidae and Discorbidae were recognized as distinct families and the Hantkeninidae, Anomalinidae, Rupertiidae, and Homotremidae were included in other families. Glaessner's arrangement of foraminifer suprageneric taxa is shown in Table 24.

Table 24. *Classification of Foraminiferida by Glaessner, 1945 (*796)*

Superfamily Astrorhizidea

Astrorhizidae (Astrorhizinae; Rhizammininae; Hyperammininae)——Saccamminidae (Psammosphaerinae; Saccammininae)——Ammodiscidae

Superfamily Lituolidea

Reophacidae——Lituolidae (Haplophragmiinae; Lituolinae; Loftusiinae)——Orbitolinidae——Textulariidae——Trochamminidae (Trochammininae; Tetrataxinae)——Verneuilinidae (Verneuilininae; Eggerellinae; Ataxophragmiinae; Valvulininae)

Superfamily Endothyridea

Endothyridae —— Fusulinidae (Fusulininae; Schwagerininae; Verbeekininae; Neoschwagerininae)

Superfamily Miliolidea

Miliolidae——Ophthalmidiidae——Peneroplidae——Alveolinidae

Superfamily Lagenidea

Lagenidae——Polymorphinidae

Superfamily Buliminidea

Buliminidae (Turrilininae; Bulimininae; Reussellinae; Uvigerininae; Plectofrondiculariinae; Bolivininae) —— Cassidulinidae —— Ellipsoidinidae ——Chilostomellidae

Superfamily Rotaliidea

Spirillinidae (Spirillininae; Patellininae) —— Discorbidae (Discorbinae; Siphonininae; Anomalininae) —— Globigerinidae (Globigerininae; Hantkenininae)——Globorotaliidae —— Gümbelinidae——Planorbulinidae (Planorbulininae; Rupertiinae)——Cymbaloporidae——Nonionidae Ceratobuliminidae —— Amphisteginidae —— Rotaliidae —— Calcarinidae——Miogypsinidae Orbitoididae (Omphalocyclinae; Orbitoidinae; Helicolepidininae) —— Discocyclinidae —— Camerinidae (Camerininae; Heterosteginae)

CUSHMAN, 1948

In the last edition of his text, Cushman (1948, *486) recognized 50 families, adding five to the 45 families of his 1927 classification. Changes in subfamilies were made. Table 25 lists only families in which additional subfamilies were recognized (marked by an asterisk) or subfamilies were omitted (indicated by enclosure within square brackets), together with the five added families (marked by two asterisks).

Table 25. *Family-group Taxa of Foraminiferida added by Cushman (1948, *486) to his 1927 Classification*

Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae; *Webbinellinae)——Reophacidae (Aschemonellinae; Reophacinae; *Sphaerammininae) —— Ammodiscidae (*Ammodiscinae; *Tolypammininae)——Lituolidae (Haplophragmiinae; *Endothyrinae; Lituolinae)——Valvulinidae (*Valvulininae; *Eggerellinae)—— Fusulinidae Möller, 1878 (Fusulininae Rhumbler, 1895 [Verbeekininae]; *Schwagerininae Dunbar & Henbest, 1930)——**Neoschwagerinidae Dunbar, nov. (Verbeekininae Staff & Wedekind, 1910; *Neoschwagerininae Dunbar & Condra, 1927)——Silicinidae (*Involutininae; *Rzehakininae)——Ophthalmidiidae (Cornuspirinae; [Nodobaculariinae]; *Nodophthalmidiinae; Ophthalmidiinae; Nubeculariinae) —— Trochamminidae (Trochammininae; Globotextularinae; Ammosphaeroidininae; *Tetrataxinae)——**Camerinidae [Nummulitidae] (*Archaediscinae; *Camerininae) —— Heterohelicidae (Heterohelicinae; [Pavonininae]; Gümbelininae; Bolivinitinae; [Spiroplectininae]; Plectofrondiculariinae; Eouvigerininae)——Buliminidae (Terebralininae; Turrilininae; Bulimininae; Virgulininae; *Reussellinae; [Reussiinae]; Uvigerininae) —— Rotaliidae (Spirillininae; Turrispirillininae; *Discorbinae;

[Discorbisinae]; Rotaliinae; *Siphonininae; Baggininae) —— **Pegidiidae——**Victoriellidae ——Orbitoididae Schubert, 1920 (Pseudorbitoidinae M. G. Rutten; *Orbitoidinae Prever; *Lepidocyclinae Tan; *Helicolepidinae Tan)——**Discocyclinidae Vaughan & Cole——**Miogypsinidae Tan

HOFKER, 1951

The next major revision of foraminiferal classification was by Hofker (1951, *928c) in the third part of his report on the "Siboga" foraminifers. Some of the non-perforate agglutinated and porcelaneous genera were treated in the earlier reports, but in the third part the agglutinated forms with apertural tooth (Valvulinidae) were regarded as the source of most hyaline foraminifers, and all were considered to belong to the order Dentata of the subclass Foraminifera. In this classification major partition into suborders was on the basis of apertural characters, the Protoforaminata having a single aperture (protoforamen) with internal tooth plate, the Biforaminata having an additional second aperture (deuteroforamen), and the Deuteroforaminata having only the deuteroforamen, the original protoforamen having been reduced. Attention was focused on the previously neglected tooth plates and internal partitions as important guides in determining relationships. A number of new families were erected for different trochospiral hyaline groups, a total of 23 families being included in the three suborders. Hofker's classification is recorded in Table 26.

Table 26. *Classification of Foraminiferida by Hofker (1951, *928c)*

Subclass Foraminifera
 Order Dentata
  Suborder Protoforaminata
   Families Valvulinidae——Bolivinidae——Buliminellidae —— Buliminidae —— Uvigerinidae Cassidulinidae
  Suborder Biforaminata
   Ceratobuliminidae——Cibicidae —— Eponidae —— Epistominidae——Laticarinidae —— Alabaminidae——Robertinidae——Camerinidae
  Suborder Deuteroforaminata (or Conorbida)
   Conorbidae —— Rotalidae —— Pulvinulinidae —— Marginolamellidae —— Amphisteginidae ——Cymbaloporettidae —— Valvulineridae—— Tinoporidae——Globigerinidae

SIGAL, 1952

The classification used by Sigal (*1458) divided the foraminifers into three suborders, one for single-chambered forms, one for tubular forms—both straight tubular and enrolled ones with agglutinated, porcelaneous, or hyaline tests—and a third for remaining chambered forms, making this suborder comparable to the so-called "polythalamians" of 18th and 19th century usage. The third suborder was divided into six superfamilies, one containing agglutinated forms, one the fusulinids, one the porcelaneous groups, and three the hyaline perforate foraminifers (Lagenidea, Buliminidea, Rotaliidea). Fewer subfamilies were recognized, but a total of 62 families was included. Sigal's classification is presented in Table 27.

Table 27. *Classification of Foraminiferida by Sigal in Piveteau (1952, *1458)*

Order Foraminifera
 Suborder Uniloculinidea
  Superfamily Lagynidea
  Superfamily Astrorhizidea
   Families Saccamminidae —— Rhizamminidae ——Astrorhizidae
 Suborder Biloculinidea
  Hyperamminidae —— Ammodiscidae ——Cornuspiridae——Spirillinidae——Involutinidae
 Suborder Pluriloculinidea
  Superfamily Lituolidea
   Reophacidae——Haplophragmiidae —— Textulariidae —— Silicotextulinidae —— Trochamminidae (Trochammininae; Textrataxinae)—— Placopsilinidae——Ptychocladiidae ——Verneuilinidae (Eggerellinae; Valvulininae; Verneuilininae; Ataxophragmiinae)——Neusinidae [appendix]——Lituolidae (Lituolinae; Loftusinae) ——Orbitolinidae——Endothyridae
  Superfamily Fusulinoidea (by R. Ciry)
   Fusulinidae (Fusulininae; Schwagerininae)—— Neoschwagerinidae (Verbeekininae; Neoschwagerininae)
  Superfamily Miliolidea
   Ophthalmidiidae (Nodophthalmidiinae; Ophthalmidiinae; Nubeculariinae) —— Miliolidae ——Fischerinidae —— Peneroplidae (Spirolininae; Meandropsininae; Orbitolitinae; Keramosphaerinae [appendix]) —— Alveolinidae —— Paramiliolidae [appendix]
  Superfamily Lagenidea
   Lagenidae (Lenticulininae; Lageninae; Stilostomellinae)——Polymorphinidae (Polymorphininae; Ramulininae)——Enantiomorphinidae
  Superfamily Buliminidea
   Buliminidae (Turrilininae; Buliminae; Reus-

sellinae; Bolivininae; Uvigerininae; Robertininae; Lacosteininae)——Cassidulinidae——Ellipsoidinidae——Chilostomellidae——Nonionidae——Heterohelicidae
Superfamily Rotaliidea
Discorbidae (Patellininae; Discorbinae; Cancrininae; Discorbinellinae; Chapmanininae)——Anomalinidae —— Epistominidae—Ceratobuliminidae —— Globigerinidae (Globigerininae; Orbulininae; Pulleniatininae; Candeininae)——Hantkeninidae —— Globorotaliidae —— Gümbelinidae —— Elphidiidae —— Planorbulinidae ——Rupertiidae —— Victoriellidae — Homotremidae —— Pegidiidae —— Cymbaloporidae ——Rotaliidae —— Calcarinidae —— Miscellaneidae —— Nummulitidae (Nummulitinae; Siderolitinae; Heterosteginae) —— Miogypsinidae —— Orbitoididae (Omphalocyclinae; Orbitoidinae; Pseudorbitoidinae; Clypeorbinae; Lepidorbitoidinae)——Discocyclinidae (Discocyclininae; Orbitoclypeinae)——Amphisteginidae——Helicolepidinidae——Lepidocyclinidae

POKORNÝ, 1958

Pokorný (1958, *1478) recognized nine superfamilies, adding to those of Sigal the Spirillinidea, distinguished as a separate superfamily. Among his 60 families were included the Semitextulariidae, Tournayellidae, Lasiodiscidae, Archaediscidae, and Loftusiidae. His classification is summarized in Table 28.

Table 28. *Classification of Foraminiferida by Pokorný (1958, *1478)*

Class Granuloreticulosa de Saedeleer, 1934
  Order Foraminifera d'Orbigny, 1826
    Superfamily Allogromiidea
    Superfamily Astrorhizidea
      Families Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae)——Astrorhizidae——Rhizamminidae——Hyperamminidae (Hyperammininae; Earlandiinae; Dendrophyrinae; Moravammininae)——Reophacidae—— Ammodiscidae (Ammodiscinae; Rzehakininae) —— Tournayellidae —— Lasiodiscidae —— Archaediscidae
    Superfamily Lituolidea
      Lituolidae —— Loftusiidae —— Textulariidae —— Semitextulariidae —— Trochamminidae ——Tetrataxidae (Tetrataxinae; Globivalvulininae)——Verneuilinidae (Verneuilininae; Valvulininae; Ataxophragmiinae)——Orbitolinidae ——Endothyridae (Endothyrinae; Bradyininae)
    Superfamily Fusulinidea
      Fusulinidae (Schubertellinae; Staffelininae [*sic*]; Boultoniinae; Fusulininae; Schwagerininae)——Neoschwagerinidae (Verbeekininae; Neoschwagerininae)
    Superfamily Miliolidea
      Ophthalmidiidae (Cornuspirinae; Ophthalmidiinae; Nubeculariinae)——Miliolidae——Peneroplididae —— Alveolinidae —— Keramosphaeridae
    Superfamily Nodosariidea
      Nodosariidae——Polymorphinidae —— Enantiomorphinidae
    Superfamily Buliminidea
      Buliminidae (Turrilininae; Bulimininae; Reussellinae; Uvigerininae; Plectofrondiculariinae; Bolivininae)——Cassidulinidae —— Chilostomellidae——Nonionidae——Ellipsoidinidae
    Superfamily Spirillinidea
      Spirillinidae (Spirillininae; Patellininae)
    Superfamily Rotaliidea
      Discorbidae (Discorbinae; Siphonininae; Bagginninae; Anomalininae)——Planorbulinidae —— Rupertiidae (Rupertiinae; Homotrematinae)——Pegidiidae——Cymbaloporidae —— Ceratobuliminidae——Epistominidae——Robertinidae——Orbulinidae —— Hantkeninidae —— Globorotaliidae —— Heterohelicidae —— Amphisteginidae —— Elphidiidae —— Rotaliidae —— Baculogypsinidae —— Miscellaneidae——Nummulitidae (Nummulitinae; Heterosteginae) —— Orbitoididae —— Pseudorbitoididae —— Lepidorbitoididae——Discocyclinidae——Orbitoclypeidae —— Helicolepidinidae —— Lepidocyclinidae —— Miogypsinidae

REISS, 1958

Reiss (1958, *1530) published a revised classification of perforate hyaline foraminifers based on the lamellar character of the walls and septa. In addition to five superfamilies with nonlamellar tests (these groups not being subdivided or discussed), he recognized five superfamilies of lamellar-shelled foraminifers, although the Monolamellidea and Bilamellidea (and Biloculinidea) were invalid according to rules of nomenclature since they were not based on the name of an included genus. In part, families were those proposed by Hofker, but some invalid families were indicated (e.g., Hyalovirgulinidae) and others were placed conflictingly in two superfamilies (i.e., Orbitoididae, "Pulvinulinidae"). In spite of these defects, Reiss's studies re-emphasized the importance of wall structures in many of the smaller foraminifers as well as in the so-called "larger foraminifera." The classification is recorded in Table 29.

TABLE 29. *Classification of Foraminiferida by Reiss (1958, *1530)*

NONLAMELLAR TESTS
  Superfamily ASTRORHIZIDEA (agglut., pseudochitin.)
  Superfamily ENDOTHYRIDEA (calc. complex)
  Superfamily LITUOLIDEA (pseudochitin., agglut., "fibrous," microgran.)
  Superfamily MILIOLIDEA (cryptocrystalline, "porcelan.")
  Superfamily BILOCULINIDEA (agglut., porcelan., radiate)
LAMELLAR, CALCAREOUS PERFORATE TESTS
  Superfamily LAGENIDEA (radiate microstructure)
    Families Lagenidae——Polymorphinidae——Enantiomorphinidae
  Superfamily BULIMINIDEA (PROTOFORAMINATA) (radiate and granular microstructure)
    Buliminidae —— Buliminellidae —— Virgulinidae —— Hyalovirgulinidae —— Uvigerinidae ——Bolivinidae —— Cassidulinidae —— Chilostomellidae
  Superfamily MONOLAMELLIDEA (radiate and granular microstruct.)
    (A) BIFORAMINATE
      Ceratobuliminidae[1] —— Epistominidae[1] —— Robertinidae[1] —— Nonionidae —— Alabaminidae —— Eponididae —— Parrelloididae —— Siphoninidae
    (B) DEUTEROFORAMINATE
      Conorbidae —— "Pulvinulinidae" *(pars)* —— Valvulineriidae —— Asterigerinidae —— Planorbulinidae
  Superfamily ROTALIIDEA (bi- and deuteroforaminata, radiate)
    Rotaliidae — Rupertiidae —— Miscellaneidae ——Nummulitidae —— Baculogypsinidae —— Elphidiidae —— Miogypsinidae —— Orbitoididae
  Superfamily BILAMELLIDEA (deuteroforaminata, radiate and granular)
    Gavelinellidae —— "Pulvinulinidae" *(pars)*—— Anomalinidae —— Globigerinidae —— Hantkeninidae —— Gümbelinidae —— Globorotaliidae —— Cymbaloporettidae —— Amphisteginidae —— Helicolepidinidae —— Discocyclinidae ——Orbitoididae *(pars)*

RAUZER-CHERNOUSOVA & FURSENKO, 1959

In 1959 a classification of foraminifers directed by RAUZER-CHERNOUSOVA & FURSENKO (*1509) and including the work of many Soviet micropaleontologists was published in *Osnovy Paleontologii.* This classification utilized 13 orders, 14 superfamilies, and 72 families. Major differences from other published arrangements consisted in the addition of numerous families and some superfamilies (Parathuramminidea, Tournayellidea, Endothyridea) for Paleozoic genera which had been studied in detail. The ten families of BRADY were elevated to the rank of orders in this classification, as they had been by LISTER in LANKESTER (1903, *1094), except that the Chilostomellidae remained a family and the Globigerinidae was raised only to superfamily rank. Five additional orders were introduced—Ammodiscida, Endothyrida, Fusulinida, Ataxophragmida, and Heterohelicida.

The Soviet publication also cited authors and dates for family-group names, although the Lagynidae of SCHULTZE, 1854 (based on *Lagynis,* a pseudochitinous form) was mistaken for the Lagenidae (=Nodosariidae). Many new genera were included, although coverage at this level was limited largely to genera known from the USSR. Because of the relative inaccessibility of many of the original publications, it is an excellent record for other genera published in the Soviet Union prior to 1956, when this volume apparently went to press. The classification is outlined in Table 30.

TABLE 30. *Classification of Foraminiferida in Osnovy Paleontologii (1959, *1509)*

Subclass FORAMINIFERA
  Order ALLOGROMIIDA
  Order ASTRORHIZIDA
    Superfamily ASTRORHIZIDEA H. B. Brady, 1881
      Families Astrorhizidae H. B. Brady, 1881—— Rhizamminidae H. B. Brady, 1879——Saccamminidae H. B. Brady, 1884 (Psammosphaerinae Cushman, 1927; Saccammininae H. B. Brady, 1884; Webbinellinae Cushman, 1927)——Hyperamminidae Eimer & Fickert, 1899 (Hyperammininae Eimer & Fickert, 1899; Dendrophryinae Cushman, 1927)——Reophacidae Cushman, 1927
    Superfamily PARATHURAMMINIDEA E. V. Bykova, 1955
      Parathuramminidae E. V. Bykova, 1955—— ——Caligellidae Reytlinger, fam. nov.
    ASTRORHIZIDA incertae sedis
      Neusinidae Cushman, 1927——Familiae incertae
  Order AMMODISCIDA
    Superfamily AMMODISCIDEA Rhumbler, 1895
      Ammodiscidae Rhumbler, 1895 (Ammodiscinae Rhumbler, 1895; Tolypammininae Cushman, 1929)
    Superfamily TOURNAYELLIDEA Daïn, 1953
      Tournayellidae Daïn, 1953 (Tournayellinae Daïn, 1953; Forschiinae Daïn, 1953)

---

[1] Aragonitic in part.

Superfamily Lituolidea Reuss, 1861

Lituolidae Reuss, 1861 (Haplophragmellinae Reytlinger, subfam. nov.; Lituolinae Reuss, 1861; Subfamiliae incertae)——Silicinidae Cushman, 1927 (Involutininae Cushman, 1940; Rzehakininae Cushman, 1940)

Order ENDOTHYRIDA

Endothyridae H. B. Brady, 1884 (Endothyrinae H. B. Brady, 1884; Chernyshinellinae Reytlinger, subfam. nov.; Plectogyrinae Reytlinger, subfam. nov.; Endothyranopsinae Reytlinger, subfam. nov.)——Bradyinidae Reytlinger, 1950 ——Mesoendothyridae Voloshinova, fam. nov. ——Spirocyclinidae Munier-Chalmas, 1887

Order FUSULINIDA

Superfamily FUSULINIDEA von Möller, 1878

Ozawainellidae Thompson & Foster, 1937 (Staffellinae A. D. Miklukho-Maklay, 1949; Ozawainellinae Thompson & Foster, 1937)—— Fusulinidae von Möller, 1878 (Fusulinellinae Staff & Wedekind, 1910; Fusulininae von Möller, 1878; Eofusulininae Rauzer-Chernousova & Rosovskaya, subfam. nov.)——Schubertellidae Skinner, 1931 (Schubertellinae Skinner, 1931; Boultoniinae Skinner & Wilde, 1954)—— Schwagerinidae Dunbar & Henbest, 1930 (Schwagerininae Dunbar & Henbest, 1930; Polydiexodininae A. D. Miklukho-Maklay, 1953)

Superfamily VERBEEKINIDEA Staff & Wedekind, 1910

Verbeekinidae Staff & Wedekind, 1910——Neoschwagerinidae Dunbar & Condra, 1927

Order TEXTULARIIDA

Textulariidae d'Orbigny, 1846 (Palaeotextulariinae Galloway, 1933; Textulariinae d'Orbigny, 1846)

Order ATAXOPHRAGMIIDA

Trochamminidae Schwager, 1877——Ataxophragmiidae Schwager, 1877 (Verneuilininae Cushman, 1911; Valvulininae Cushman, 1927; Ataxophragmiinae Schwager, 1877)——Orbitolinidae Martin, 1890——Placopsilinidae Cushman, 1928 (Placopsilininae Cushman, 1928; Coscinophragminae Thalmann, 1950)——Tetrataxidae Galloway, 1933——Biseriamminidae N. E. Chernysheva, 1941

Order MILIOLIDA

Superfamily MILIOLIDEA d'Orbigny, 1839

Cornuspiridae Reuss, 1861——Ophthalmidiidae Cushman, 1927——Miliolidae d'Orbigny, 1839 ——Familiae incertae

Superfamily ALVEOLINIDEA Schultze, 1854

Peneroplidae Schultze, 1854——Alveolinidae Schultze, 1854

Order LAGENIDA

Lagenidae Schultze, 1854 (Umbellinae Fursenko, subfam. nov.; Lageninae Schultze, 1854; Colaniellinae Fursenko, subfam. nov.; Nanicellinae Fursenko, subfam. nov.; Lenticulininae Sigal, 1952) —— Enantiomorphinidae Marie, 1941——Polymorphinidae d'Orbigny, 1846 (Polymorphininae d'Orbigny, 1846; Ramulininae H. B. Brady, 1884)——Pseudopalmulidae E. V. Bykova, fam. nov.

Order ROTALIIDA

Superfamily DISCORBIDEA Cushman, 1927

Discorbidae Cushman, 1927 (Discorbinae Cushman, 1927; Baggininae Cushman, 1927; Eponidinae Hofker, 1951)——Siphoninidae Cushman, 1928 (Siphonininae Cushman, 1927; Almaeninae Myatlyuk, subfam. nov.)——Pseudoparrellidae Voloshinova, 1952——Chapmaniidae Galloway, 1933

Superfamily CERATOBULIMINIDEA Glaessner, 1937

Epistominidae Brotzen, 1942——Ceratobuliminidae Glaessner, 1937——Robertinidae Sigal, 1952——Asterigerinidae d'Orbigny, 1839

Superfamily NONIONIDEA Schultze, 1854

Anomalinidae Cushman, 1927 (Anomalininae Cushman, 1927; Cibicidinae Cushman, 1927) ——Nonionidae Schultze, 1854 (Nonioninae Schultze, 1854; Nonionellinae Voloshinova, 1958; Melonisinae Voloshinova, 1958)—— Planorbulinidae Cushman, 1927——Rupertiidae Cushman, 1927——Victoriellidae Chapman & Crespin, 1930 —— Homotremidae Cushman, 1927——Cymbaloporettidae Cushman, 1927

Superfamily GLOBIGERINIDEA Carpenter, 1862

Globigerinidae Carpenter, 1862 (Globigerininae Carpenter, 1862; Orbulininae Schultze, 1854; Pulleniatininae Cushman, 1927; Candeininae Cushman, 1927)——Hantkeninidae Cushman, 1924——Globorotaliidae Cushman, 1927 (Globotruncaninae Brotzen, 1942; Globorotaliinae Cushman, 1927; Rugoglobigerininae Subbotina, subfam. nov.)

Superfamily ROTALIIDEA Reuss, 1860

Rotaliidae Reuss, 1860——Elphidiidae Galloway, 1933 (Elphidiinae Galloway, 1933; Cribroelphidiinae Voloshinova, 1958)

Order NUMMULITIDA

Nummulitidae Carpenter, 1859 (Nummulitinae Carpenter, 1859; Miscellaneinae Sigal, 1952; Siderolitinae Sigal, 1952; Heterostegininae Galloway, 1933)——Miogypsinidae Tan Sin Hok, 1936——Orbitoididae Prever, 1904 (Omphalocyclininae Vaughan, 1920; Orbitoidinae Prever, 1904; Pseudorbitoidinae Rutten, 1935; Lepidorbitoidinae Silvestri, 1907) ——Discocyclinidae Vaughan & Cole, 1940 (Discocyclininae Vaughan & Cole, 1940; Orbitoclypeinae Brönnimann, 1946) —— Lepidocyclinidae Scheffen, 1932 (Helicolepidininae Tan Sin Hok, 1936; Lepidocyclininae Tan Sin Hok, 1936)

Order BULIMINIDA

Buliminidae Jones, 1876 (Buliminellinae N. K. Bykova, subfam. nov.; Virgulininae Cushman, 1927; Baggatellinae N. K. Bykova, subfam. nov.; Bulimininae Jones, 1876; Reussellinae Cushman, 1933; Caucasininae N. K. Bykova, subfam. nov.; Uvigerininae Cushman, 1913)——Pleurostomellidae Reuss, 1860——Cassidulinidae d'Orbigny, 1839

Order HETEROHELICIDA

Bolivinitidae Cushman, 1927 (Bolivininae Glaessner, 1937; Bolivinitinae Cushman, 1927; Plectofrondiculariinae Glaessner, 1945; Lacosteininae Sigal, 1952)——Heterohelicidae Cushman, 1927

Foraminifera. Familiae incertae sedis

Chilostomellidae H. B. Brady, 1881 (Allomorphininae Cushman, 1928; Chilostomellinae H. B. Brady, 1881; Seabrookiinae Cushman, 1928; Allomorphinellinae Cushman, 1928; Sphaeroidininae Cushman, 1928)——Archaediscidae N. E. Chernysheva, 1948——Lasiodiscidae Reytlinger, fam. nov.——Spirillinidae Reuss, 1861 (Spirillininae Reuss, 1861; Patellininae Rhumbler, 1906)

CLASSIFICATION ADOPTED IN TREATISE

Ideally, classification of the Foraminiferida, as of other animals, should be based on complete morphological data (e.g., characters of the test, protoplasm, inclusions in the protoplasm, nucleus), obtained by all known suitable techniques, as well as on information concerning reproductive processes (e.g., modifications of the alternation of generations, gametes), life habits and habitat, geologic ranges, and ontogenetic changes. As far as knowledge is available, we have attempted to follow this procedure in the present classification. Because of the paucity of information yet available on living foraminifers, the taxonomic divisions are necessarily based largely on characters of the test, though additional data of all sorts are included and utilized when possible.

Wall composition and microstructure of the test are regarded by us as primary in importance for classifying the Foraminiferida, for these skeletal features are determined by the nature of the secreting protoplasm. Thus, the basic chemical composition, and radial or granular arrangement of the crystals is utilized for distinguishing characters judged to have most significance for definition of suborders and superfamilies. Within a suborder, the unilocular or multilocular nature of the test is considered important (superfamily rank) in the lower groups (agglutinated and microgranular forms), but the few unilocular tests among hyaline calcareous forms appear in each case to be probably secondarily simplified, as also evidenced in *Oolina,* for example, by its parasitic habit and loss of the sexual generation in reproduction.

Of secondary importance is mode of chamber and septal addition (lamellar nature of hyaline tests), and whether chambers are added in uniserial, planispiral, or low to high trochospiral arrangement, or modifications or combinations of these.

In interpreting wall composition to be primary in importance, we conclude that the same chamber arrangement and form of test may have developed in independent lineages by parallel evolution, without indicating interrelationship of the similarly shaped shells. Thus, planispiral (or uniserial, or biserial, or trochospiral) forms may have developed independently in forms with arenaceous, porcelaneous, microgranular, hyaline radial (calcitic or aragonitic), and hyaline granular walls. The development of bilamellar septal structure also seems to have occurred independently in forms with radial and granular walls.

Apertural characters and modifications of them are regarded as next in importance. The Nodosariacea, for example, dominantly have radiate apertures, some with modifications such as the entosolenian tubes of the Glandulinidae. The Buliminacea possess a basically loop-shaped aperture and internal tooth plate, but modifications in the direction of terminal or even multiple apertures occur with differing form and arrangement of the chambers.

Chamber form and arrangement are considered to be third in importance, followed by the free-living or attached nature of the animal.

The classification incorporates many features utilized in previous ones which differ from one another mainly because of the dissimilar emphasis placed by different workers on features such as wall composition, perforation, microstructure, layering, test shape, chamber number, chamber form and arrangement, apertural position, and modifications of these.

We believe that a relatively detailed supra-generic classification, with suborders, superfamilies, families, and subfamilies should aid in grouping like forms. By utilizing critically as many characters as possible in constructing this classification, it is hoped to emphasize the need for more detailed descriptions of all new species and genera, as well as redescription whenever possible of inadequately treated earlier ones.

The *Treatise* classification of Foraminiferida recognizes five suborders of these protistans, defining them mainly on the basis of wall composition of their test. The suborders are named Allogromiina (membranous and pseudochitinous tests), Textulariina (agglutinated tests), Fusulinina (calcareous microgranular tests), Miliolina (porcelaneous calcitic tests), and Rotaliina (hyaline perforate calcareous tests). Seventeen superfamilies are distinguished within these suborders on the basis of the unilocular or multilocular nature of tests (Textulariina, Fusulinina) and character of wall microstructure (Fusulinina, Rotaliina). The Rotaliina include ten superfamilies—Nodosariacea, with monolamellar walls of radially built calcite and radiate terminal apertures; Buliminacea, with monolamellar walls of radially built calcite forming a high-spired test with loop-shaped aperture and internal tooth plate; Discorbacea, with enrolled trochospiral tests and monolamellar walls of radially built calcite; Spirillinacea, also with monolamellar walls and with test commonly forming a single crystal, reproduction in association, with amoeboid gametes; Rotaliacea, with walls of radially built calcite and secondarily doubled septa making a canal system; Globigerinacea, foraminifers of planktonic habit with walls of radially built calcite forming a coarsely perforate test with bilamellid septa; Orbitoidacea with walls of radially built calcite and bilamellid septa; Cassidulinacea, with walls of granular calcite, some families monolamellid, others bilamellid; Carterinacea, with walls composed of calcite spicules, each consisting of a single crystal; and Robertinacea, with walls of radially arranged aragonite forming internally subdivided chambers.

Although many genera are definitely placed within this framework, others have been insufficiently described to allow unquestioned assignment of them without restudy. When possible, such restudy has been undertaken, but specimens of some type-species have not been available for sectioning and X-ray or petrographic analysis in order to determine the wall microstructure, chemical composition, and lamellar character. Since the generic assignment of other species presumed to belong in a given genus may be questionable it was considered necessary always to check the type-species in order to determine reliably the wall structure of each genus. When these features are known, they are indicated in the generic diagnoses, but if not, statements concerning wall structure are omitted, indicating that its characters have yet to be studied. Some genera may require transfer to other families and superfamilies after the walls of their tests have been properly investigated. Generic and specific identification of them commonly does not necessitate recourse to these methods, but original placement within suprageneric categories requires it.

OUTLINE OF CLASSIFICATION

The following outline of the classification of the Foraminiferida summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each family group and higher-rank taxon. Where a single number is given, it refers to genera; where two numbers are given, the second indicates subgenera. Authorship of the systematic descriptions is also indicated by recording with each division the initial letters of the author's name (B for Barker, C for Cole, D for Douglass, L-T for Loeblich & Tappan, R for Reichel, TH for Thompson).

The stratigraphic distribution of suborders, superfamilies, families, and subfamilies of Foraminiferida recognized in the *Treatise* is indicated graphically in Fig. 83A. Stratigraphic distribution of families plotted in order of first known appearance in the geologic record is shown graphically in Fig. 83B.

Main Divisions of Foraminiferida

- Allogromiina *(suborder)* (47). *U.Cam.-Rec.* (L-T)
  - Lagynacea *(superfamily)* (47). *U.Cam.-Rec.* (L-T)
    - Lagynidae (18). *Rec.* (L-T)
    - Allogromiidae (29). *U.Cam.-Rec.* (L-T)
- Textulariina *(suborder)* (293). *Cam.-Rec.* (D,L-T)
  - Ammodiscacea *(superfamily)* (84). *Cam.-Rec.* (L-T)
    - Astrorhizidae (22). *L.Cam.-Rec.* (L-T)
      - Astrorhizinae (5). *M.Ord.-Rec.* (L-T)
      - Rhizammininae (3). *L.Cam.-Rec.* (L-T)

- Hippocrepininae (7). *L.Ord.-Rec.* (L-T)
- Botellininae (1). *Rec.* (L-T)
- Dendrophryinae (6). *Pleist.-Rec.* (L-T)
- Schizamminidae (2). *?Trias., Rec.* (L-T)
- Saccamminidae (41). *Ord.-Rec.* (L-T)
  - Psammosphaerinae (8). *M.Ord.-Rec.* (L-T)
  - Saccammininae (12). *Ord.-Rec.* (L-T)
  - Hemisphaeramminae (10). *Ord.-Rec.* (L-T)
  - Diffusilininae (11). *M.Ord.-Rec.* (L-T)
- Ammodiscidae (19). *Sil.-Rec.* (L-T)
  - Ammodiscinae (12). *Sil.-Rec.* (L-T)
  - Tolypammininae (7). *Sil.-Rec.* (L-T)
- Lituolacea *(superfamily)* (209). *Miss.-Rec.* (D,L-T)
  - Hormosinidae (13). *Miss.-Rec.* (L-T)
    - Aschemonellinae (2). *Cret.-Rec.* (L-T)
    - Hormosininae (9). *Miss.-Rec.* (L-T)
    - Cribratininae (2). *Cret.* (L-T)
  - Nouriidae (1). *?Eoc., Rec.* (L-T)
  - Rzehakinidae (8). *L.Cret.-Rec.* (L-T)
  - Lituolidae (57). *Carb.-Rec.* (L-T)
    - Haplophragmoidinae (9). *Carb.-Rec.* (L-T)
    - Sphaeramminae (3). *Rec.* (L-T)
    - Cyclammininae (11). *Jur.-Rec.* (L-T)
    - Spirocyclininae (4). *Jur.-U.Cret.* (L-T)
    - Loftusiinae (2). *Jur.-Cret.* (L-T)
    - Lituolinae (18). *Carb.-Rec.* (L-T)
    - Placopsilininae (7). *Miss.-Rec.* (L-T)
    - Coscinophragmatinae (3). *U.Cret.-Rec.* (L-T)
  - Textulariidae (21). *Carb.-Rec.* (L-T)
    - Spiroplectammininae (5). *Carb.-Rec.* (L-T)
    - Textulariinae (7). *Penn.-Rec.* (L-T)
    - Pseudobolivininae (4). *M.Jur.-Rec.* (L-T)
    - Plectorecurvoidinae (1). *L.Cret.* (L-T)
    - Tawitawiinae (4). *Eoc.-Rec.* (L-T)
  - Trochamminidae (15). *Carb.-Rec.* (L-T)
    - Trochammininae (14). *Carb.-Rec.* (L-T)
    - Remaneicinae (1). *Rec.* (L-T)
  - Ataxophragmiidae (61). *Penn.-Rec.* (L-T)
    - Verneuilininae (17). *U.Trias.-Rec.* (L-T)
    - Globotextulariinae (14). *Penn.-Rec.* (L-T)
    - Valvulininae (14). *U.Trias.-Rec.* (L-T)
    - Ataxophragmiinae (16). *L.Cret.-Rec.* (L-T)
  - Pavonitinidae (15). *U.Jur.-Rec.* (L-T)
    - Pfendererininae (8). *U.Jur.-U.Cret.* (L-T)
    - Pavonitininae (7). *L.Cret.-Rec.* (L-T)
  - Dicyclinidae (13). *?U.Trias., Jur.-M.Eoc.* (L-T)
    - Cyclolininae (3). *L.Cret.-U.Cret.* (L-T)
    - Dicyclininae (10). *?U.Trias., Jur.-M.Eoc.* (L-T)
  - Orbitolinidae (5). *L.Cret.-Eoc.* (D,L-T)
- Fusulinina *(suborder)* (183;2). *Ord.-Trias.* (L-T,TH)
  - Parathuramminacea *(superfamily)* (23). *Ord.-Carb.* (L-T)
    - Parathuramminidae (11). *Dev.-L.Carb.* (L-T)
    - Caligellidae (2). *U.Dev.-L.Carb.* (L-T)
    - Moravamminidae (10). *Ord.-Carb.* (L-T)
      - Earlandiinae (6). *Ord.-Carb.* (L-T)
      - Moravammininae (4). *M.Dev.-M.Carb.* (L-T)
  - Endothyracea *(superfamily)* (72). *L.Sil.-Trias.* (L-T)
    - Nodosinellidae (11). *L.Sil.-Perm.* (L-T)
      - Tuberitininae (3). *L.Sil.-U.Carb.* (L-T)
      - Umbellininae (3). *Sil.-Dev.* (L-T)
      - Nodosinellinae (5). *U.Dev.-Perm.* (L-T)
    - Colaniellidae (2). *U.Dev.-U.Perm.* (L-T)
    - Ptychocladiidae (7). *Dev.-Perm.* (L-T)
      - Ptychocladiinae (1). *U.Penn.* (L-T)
      - Stacheiinae (6). *Dev.-Perm.* (L-T)
    - Palaeotextulariidae (5). *Carb.-Perm.* (L-T)
    - Semitextulariidae (3). *Dev.* (L-T)
    - Tetrataxidae (3). *Miss.-Trias.* (L-T)
    - Biseriamminidae (3). *L.Carb.-Perm.* (L-T)
    - Tournayellidae (8). *U.Dev.-U.Perm.* (L-T)
    - Endothyridae (23). *Dev.-Perm.* (L-T)
      - Loeblichiinae (5). *Dev.-Perm.* (L-T)
      - Endothyrinae (10). *U.Dev.-Perm.* (L-T)
      - Haplophragmellinae (3). *L.Carb.-M.Carb.* (L-T)
      - Endothyranopsinae (2). *L.Carb.* (L-T)
      - Bradyininae (3). *Carb.* (L-T)
    - Archaediscidae (3). *L.Carb.-Perm.* (L-T)
    - Lasiodiscidae (4). *L.Carb.-U.Perm.* (L-T)
  - Fusulinacea *(superfamily)* (88;2). *U.Miss.-U.Perm.* (TH)
    - Ozawainellidae (7). *U.Miss.-U.Perm.* (TH)
    - Staffellidae (5). *L.Penn.-Perm.* (TH)
    - Fusulinidae (50;2). *U.Carb.(M.Penn.)-U.Perm.* (TH)
      - Schubertellinae (10). *U.Carb.(M.Penn.)-U.Perm.* (TH)
      - Fusulininae (20). *U.Carb.(M.Penn.)-U.Perm.* (TH)
      - Schwagerininae (20;2). *U.Carb.(M.Penn.)-U.Perm.* (TH)
    - Verbeekinidae (12). *Perm.* (TH)
      - Verbeekininae (5). *Perm.* (TH)
      - Neoschwagerininae (7). *U.Perm.* (TH)
    - Nominal Fusulinacean Genera of Uncertain Status (14). *Carb.-Perm.* (TH)
    - Nomina Nuda (5). (TH)
    - Nomen Inquirendum (1). (TH)
- Miliolina *(suborder)* (145;4). *Carb.-Rec.* (L-T,R)
  - Miliolacea *(superfamily)* (145;4). *Carb.-Rec.* (L-T,R)
    - Squamulinidae (1). *Rec.* (L-T)
    - Fischerinidae (21). *Carb.-Rec.* (L-T)
      - Cyclogyrinae (12). *Carb.-Rec.* (L-T)
      - Fischerininae (4). *Jur.-Rec.* (L-T)
      - Calcivertellinae (5). *Penn.-Jur.* (L-T)
    - Nubeculariidae (28). *M.Carb.-Rec.* (L-T)
      - Nubeculariinae (7). *Jur.-Rec.* (L-T)
      - Ophthalmidiinae (10). *M.Carb.-Rec.* (L-T)
      - Spiroloculininae (3). *U.Cret.-Rec.* (L-T)
      - Nodobaculariinae (7). *Jur.-Rec.* (L-T)
      - Discospirininae (1). *M.Mio.-Rec.* (L-T)
    - Miliolidae (48). *Jur.-Rec.* (L-T)
      - Quinqueloculininae (19). *Jur.-Rec.* (L-T)
      - Miliolinellinae (4). *Eoc.-Rec.* (L-T)
      - Miliolinae (12). *U.Cret.-Rec.* (L-T)
      - Fabulariinae (8). *U.Cret.-Rec.* (L-T)
      - Tubinellinae (5). *M.Eoc.-Rec.* (L-T)

Barkerinidae (4). *L.Cret.-U.Cret.* (L-T)
Soritidae (33). *U.Trias.-Rec.* (L-T)
Peneroplinae (8). *U.Trias.-Rec.* (L-T)
Meandropsininae (8). *U.Cret.-Paleoc.* (L-T)
Rhapydionininae (5). *Jur.-Rec.* (L-T)
Archaiasinae (3). *M.Eoc.-Rec.* (L-T)
Soritinae (7). *Eoc.-Rec.* (L-T)
Keramosphaerinae (2). *Mio.-Rec.* (L-T)
Alveolinidae (10;4). *L.Cret.-Rec.* (R)
Rotaliina *(suborder)* (532;19). *Perm.-Rec.* (B,C, L-T)
Nodosariacea *(superfamily)* (87). *Perm.-Rec.* (L-T)
Nodosariidae (49). *Perm.-Rec.* (L-T)
Nodosariinae (37). *Perm.-Rec.* (L-T)
Plectofrondiculariinae (3). *Eoc.-Rec.* (L-T)
Lingulininae (9). *Perm.-Rec.* (L-T)
Polymorphinidae (25). *Trias.-Rec.* (L-T)
Polymorphininae (17). *Trias.-Rec.* (L-T)
Webbinellinae (4). *Jur.-Rec.* (L-T)
Ramulininae (4). *Jur.-Rec.* (L-T)
Glandulinidae (13). *Jur.-Rec.* (L-T)
Glandulininae (9). *Jur.-Rec.* (L-T)
Seabrookiinae (1). *U.Cret.-Rec.* (L-T)
Oolininae (3). *Jur.-Rec.* (L-T)
Buliminacea *(superfamily)* (67). *U.Trias.-Rec.* (L-T)
Turrilinidae (15). *M.-Jur.-Rec.* (L-T)
Turrilininae (13). *M.Jur.-Rec.* (L-T)
Lacosteininae (2). *U.Cret.-U.Eoc.* (L-T)
Sphaeroidinidae (2). *U.Cret.-Rec.* (L-T)
Bolivinitidae (12). *U.Trias.-Rec.* (L-T)
Islandiellidae (4). *?U.Cret., Paleoc.-Rec.* (L-T)
Eouvigerinidae (5). *L.Cret.-Rec.* (L-T)
Buliminidae (14). *Paleoc.-Rec.* (L-T)
Bulimininae (5). *Paleoc.-Rec.* (L-T)
Pavonininae (9). *Eoc.-Rec.* (L-T)
Uvigerinidae (15). *U.Cret.-Rec.* (L-T)
Discorbacea *(superfamily)* (56). *M.Trias.-Rec.* (B,L-T)
Discorbidae (34). *M.Trias.-Rec.* (L-T)
Discorbinae (29). *M.Trias.-Rec.* (L-T)
Baggininae (5). *L.Cret.-Rec.* (L-T)
Glabratellidae (5). *Eoc.-Rec.* (L-T)
Siphoninidae (4). *Eoc.-Rec.* (L-T)
Asterigerinidae (4). *Cret.-Rec.* (B)
Epistomariidae (9). *U.Cret.-Rec.* (L-T)
Spirillinacea *(superfamily)* (11). *?Trias., Jur.-Rec.* (L-T)
Spirillinidae (10). *?Trias., Jur.-Rec.* (L-T)
Spirillininae (8) *?Trias., Jur.-Rec.* (L-T)
Patellininae (2). *L.Cret.-Rec.* (L-T)
Rotaliellidae (1). *Rec.* (L-T)
Rotaliacea *(superfamily)* (59;5). *U.Cret.-Rec.* (C,L-T)
Rotaliidae (31). *U.Cret.-Rec.* (C,L-T)
Rotaliinae (12). *U.Cret.-Rec.* (L-T)
Cuvillierininae (11). *U.Cret.-Mio.* (C,L-T)
Chapmanininae (4). *M.Eoc.-Mio.* (L-T)
Pegidiinae (2). *Mio.-Rec.* (L-T)
Rupertininae (2). *?Eoc., Mio.-Rec.* (L-T)
Calcarinidae (5). *U.Cret.-Rec.* (L-T)
Elphidiidae (13). *Paleoc.-Rec.* (L-T)
Elphidiinae (9). *Paleoc.-Rec.* (L-T)
Faujasininae (4). *M.Eoc.-Rec.* (L-T)
Nummulitidae (8;3). *U.Cret.-Rec.* (C)
Nummulitinae (5). *U.Cret.-Rec.* (C)
Cycloclypeinae (3;3). *Eoc.-Rec.* (C)
Miogypsinidae (2;2). *M.Oligo.-L.Mio.* (C)
Globigerinacea *(superfamily)* (60). *M.Jur.-Rec.* (L-T)
Heterohelicidae (12). *M.Jur.-Oligo.* (L-T)
Guembelitriinae (4). *M.Jur.-Eoc.* (L-T)
Heterohelicinae (8). *L.Cret.-Oligo.* (L-T)
Planomalinidae (4). *L.Cret.-Paleoc.* (L-T)
Schackoinidae (2). *L.Cret.-U.Cret.* (L-T)
Rotaliporidae (5). *Cret.* (L-T)
Hedbergellinae (3). *L.Cret.-U.Cret.* (L-T)
Rotaliporinae (2). *L.Cret.-U.Cret.* (L-T)
Globotruncanidae (5). *U.Cret.* (L-T)
Hantkeninidae (7). *Paleoc.-Rec.* (L-T)
Hastigerininae (4). *Paleoc.-Rec.* (L-T)
Hantkenininae (2). *Eoc.* (L-T)
Cassigerinellinae (1). *Oligo.-Mio.* (L-T)
Globorotaliidae (3). *Paleoc.-Rec.* (L-T)
Globorotaliinae (2). *Paleoc.-Rec.* (L-T)
Truncorotaloidinae (1). *L.Eoc.-M.Eoc.* (L-T)
Globigerinidae (22). *U.Cret.-Rec.* (L-T)
Globigerininae (10). *U.Cret.-Rec.* (L-T)
Sphaeroidinellinae (2). *Mio.-Rec.* (L-T)
Orbulininae (4). *Eoc.-Rec.* (L-T)
Catapsydracinae (6). *M.Eoc.-Rec.* (L-T)
Orbitoidacea *(superfamily)* (71;14). *Cret.-Rec.* (B,C,L-T)
Eponididae (13). *Paleoc.-Rec.* (L-T)
Amphisteginidae (4). *?U.Cret., Eoc.-Rec.* (B)
Cibicididae (14). *Cret.-Rec.* (L-T)
Planulininae (3). *U.Cret.-Rec.* (L-T)
Cibicidinae (11). *Cret.-Rec.* (L-T)
Planorbulinidae (4). *Eoc.-Rec.* (L-T)
Acervulinidae (6). *Eoc.-Rec.* (L-T)
Cymbaloporidae (9). *U.Cret.-Rec.* (L-T)
Homotrematidae (7). *U.Cret.-Rec.* (L-T)
Homotrematinae (3). *Eoc.-Rec.* (L-T)
Victoriellinae (4). *U.Cret.-Rec.* (L-T)
Orbitoididae (4;4). *U.Cret.-Paleoc.* (C)
Discocyclinidae (3;6). *Paleoc.-Eoc.* (C)
Lepidocyclinidae (4;4). *M.Eoc.-M.Mio.* (C)
Lepidocyclininae (2;4). *M.Eoc.-M.Mio.* (C)
Helicolepidininae (2). *M.Eoc.-U.Eoc.* (C)
Pseudorbitoididae (3). *U.Cret.* (C)
Cassidulinacea *(superfamily)* (89). *U.Trias.-Rec.* (L-T)
Pleurostomellidae (13). *?Jur., L.Cret.-Rec.* (L-T)
Pleurostomellinae (11). *?Jur., L.Cret.-Rec.* (L-T)
Wheelerellinae (2). *U.Cret.* (L-T)
Annulopatellinidae (1). *Mio.-Rec.* (L-T)
Caucasinidae (7). *U.Cret.-Rec.* (L-T)
Fursenkoininae (6). *U.Cret.-Rec.* (L-T)
Caucasininae (1). *U.Cret.-Mio.* (L-T)

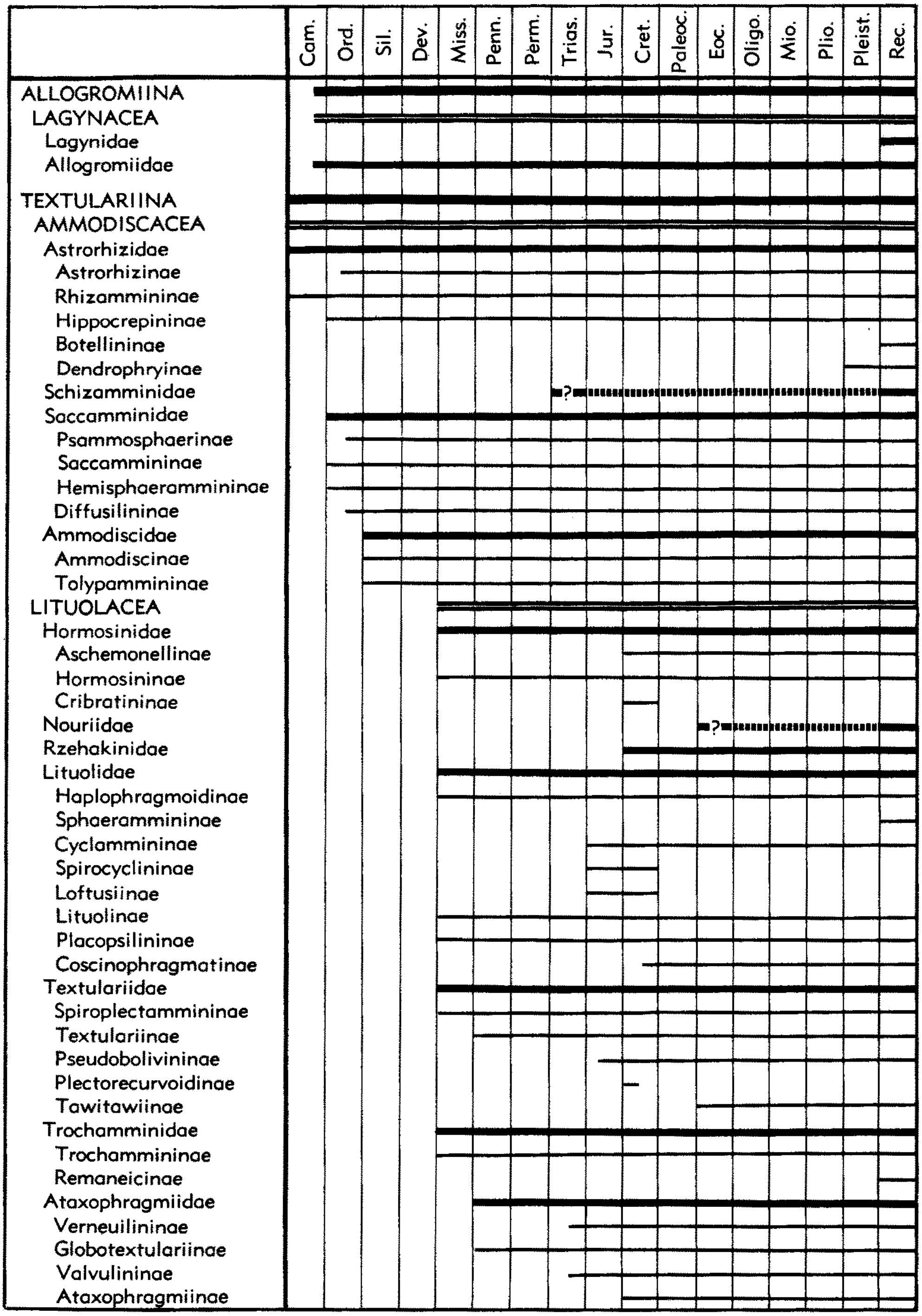


FIG. 83A. Stratigraphic distribution of suprageneric taxa of Foraminiferida (*2117).

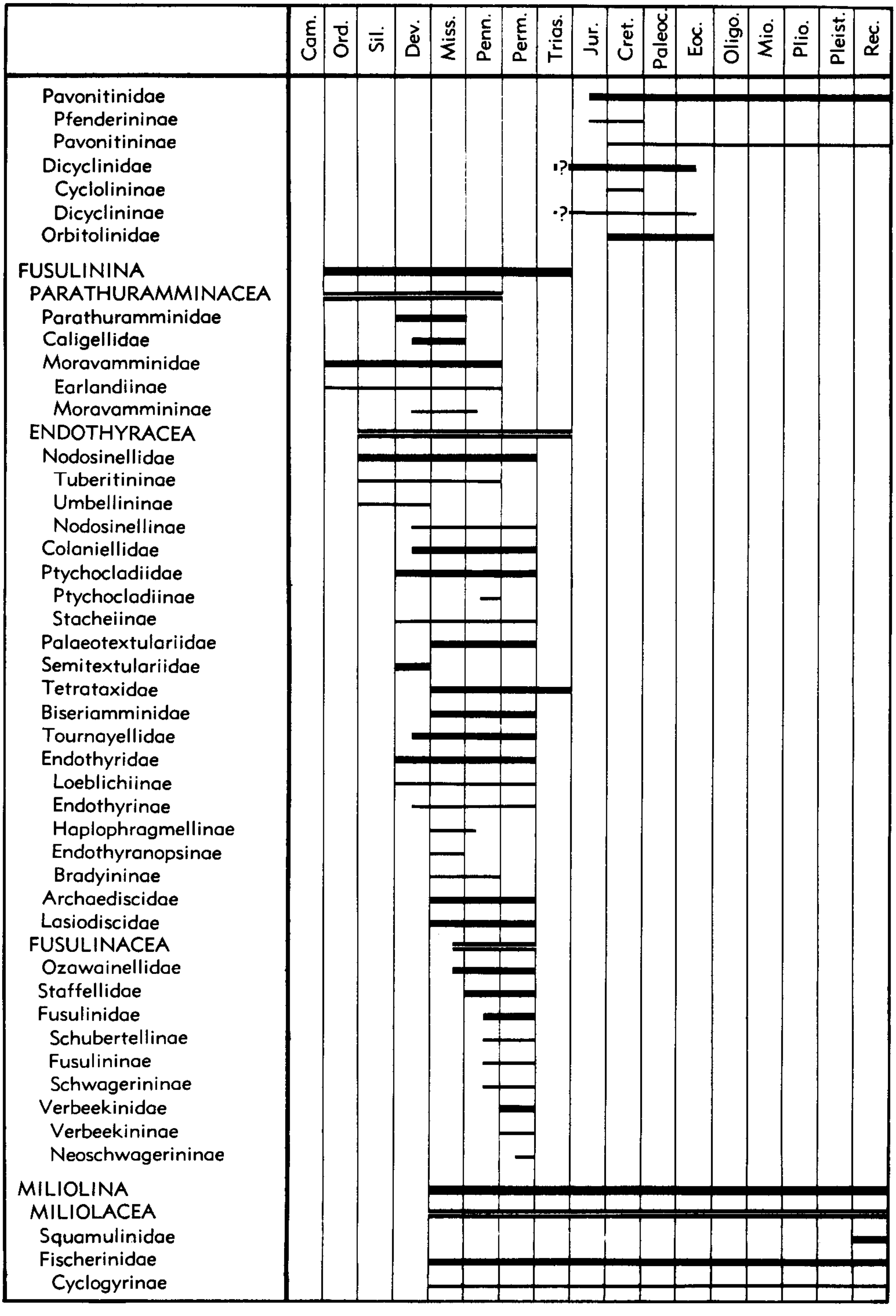


FIG. 83A *(continued)*.

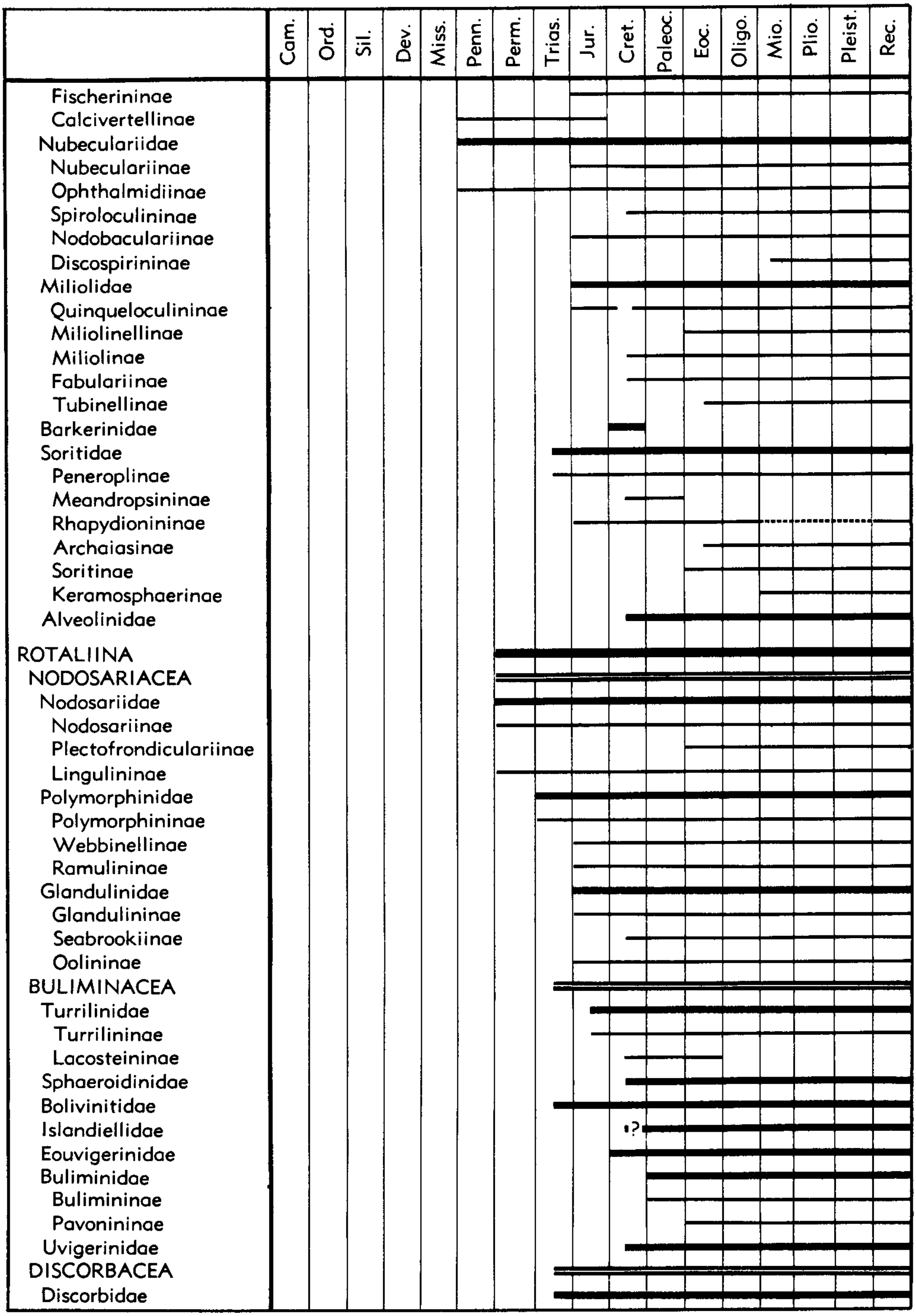


FIG. 83A *(continued)*.

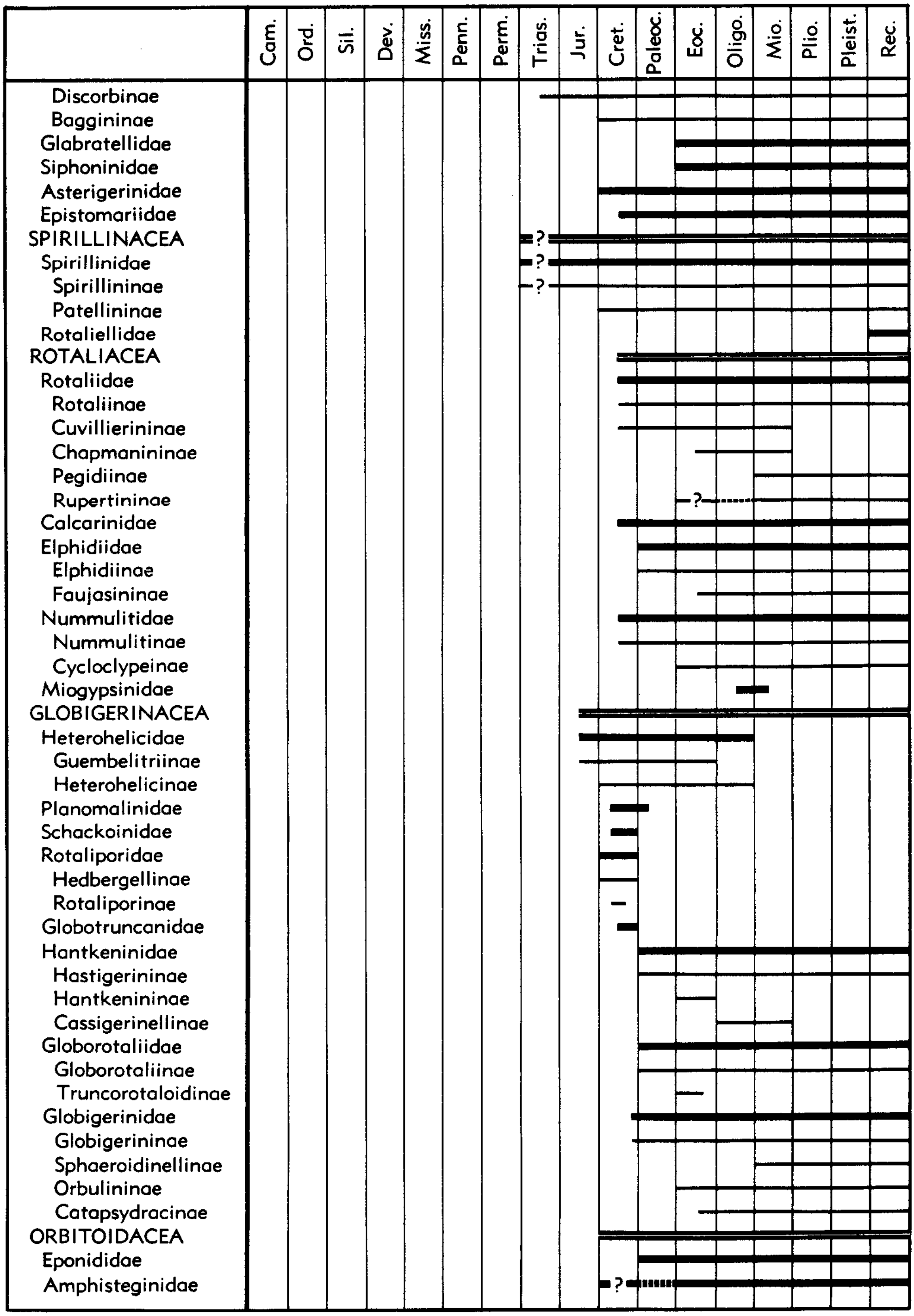


FIG. 83A *(continued)*.

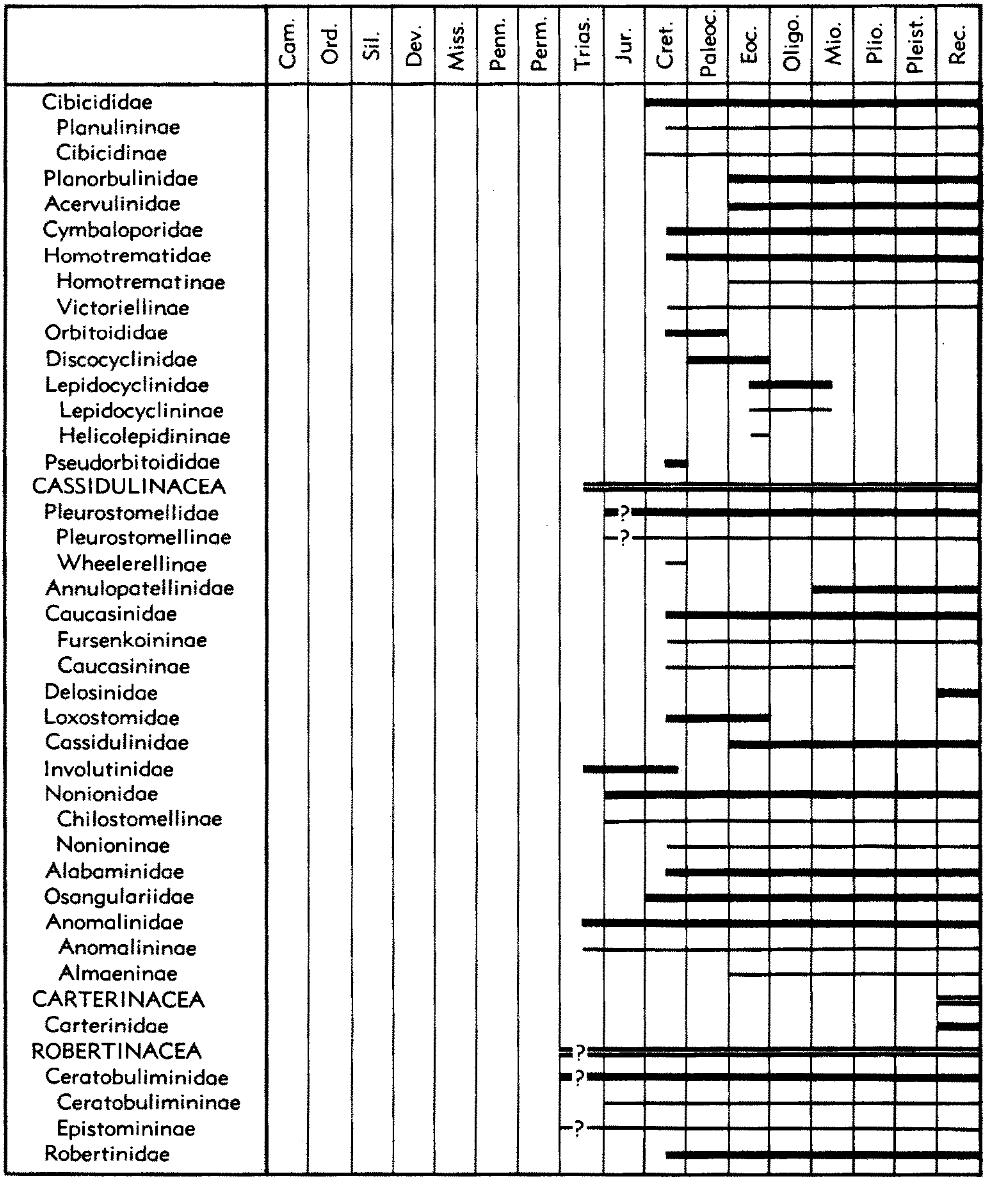


FIG. 83A *(continued).*

Delosinidae (1). *Rec.* (L-T)
Loxostomidae (3). *U.Cret.-Eoc.* (L-T)
Cassidulinidae (6). *Eoc.-Rec.* (L-T)
Involutinidae (6). *U.Trias.-U.Cret.* (L-T)
Nonionidae (15). *Jur.-Rec.* (L-T)
Chilostomellinae (5). *Jur.-Rec.* (L-T)
Nonioninae (10). *U.Cret.-Rec.* (L-T)
Alabaminidae (6). *U.Cret.-Rec.* (L-T)
Osangulariidae (7). *L.Cret.-Rec.* (L-T)
Anomalinidae (24). *U.Trias.-Rec.* (L-T)
Anomalininae (20). *U.Trias.-Rec.* (L-T)
Almaeninae (4). *Eoc.-Rec.* (L-T)
Carterinacea *(superfamily)* (1). *Rec.* (L-T)
Carterinidae (1). *Rec.* (L-T)
Robertinacea *(superfamily)* (31). *?Trias., Jur.-Rec.* (L-T)

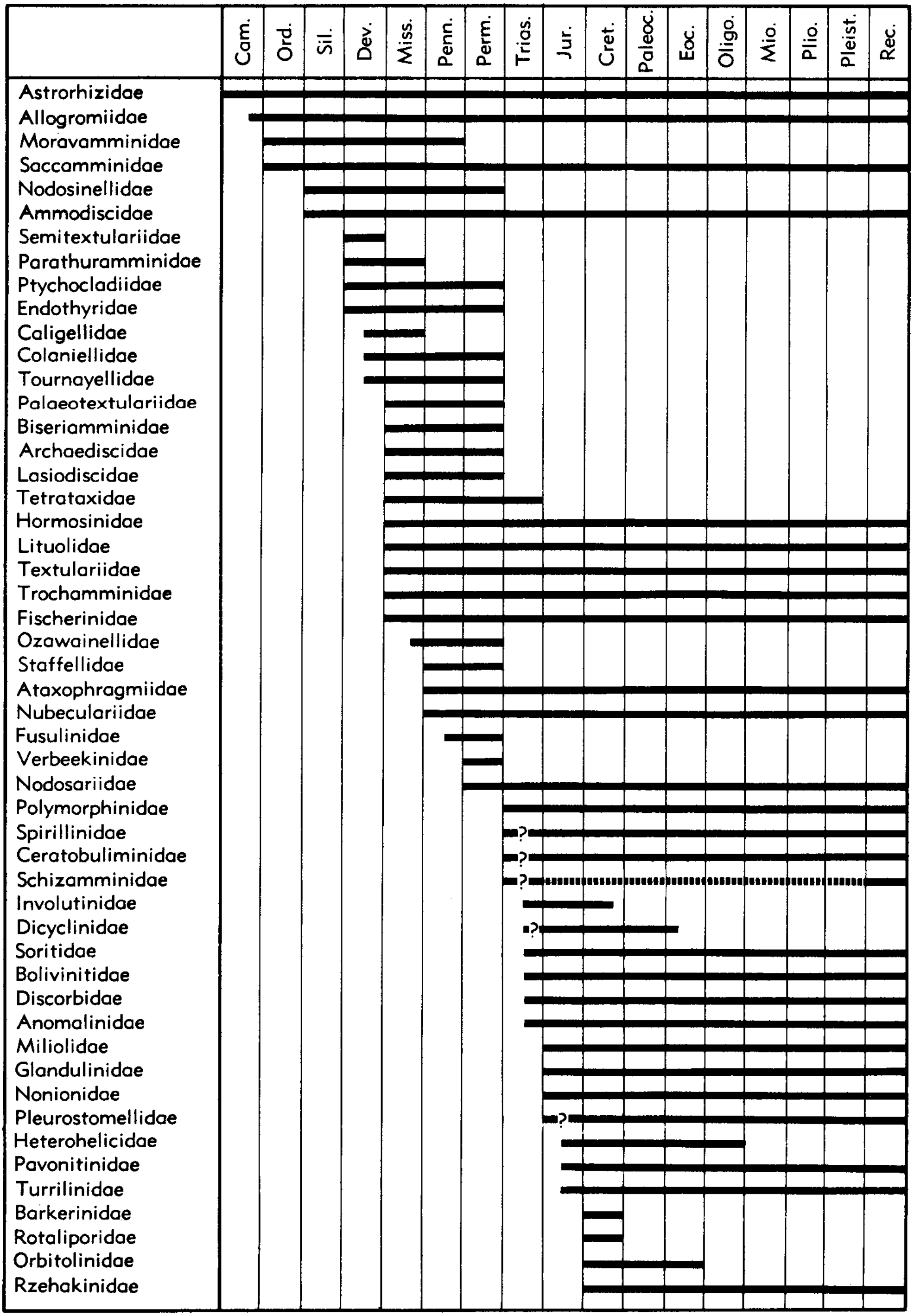


FIG. 83B. Graph showing stratigraphic distribution of families of Foraminiferida plotted according to relative time values (*2117).

Ceratobuliminidae (21). *?Trias., Jur.-Rec.* (L-T)
Ceratobulimininae (10). *Jur.-Rec.* (L-T)
Epistomininae (11). *?Trias., Jur.-Rec.* (L-T)
Robertinidae (10). *U.Cret.-Rec.* (L-T)

Nomina Nuda (68). (L-T)
Unrecognizable Genera (90). (L-T)
Generic names erroneously applied to Foraminiferida (39). (L-T)

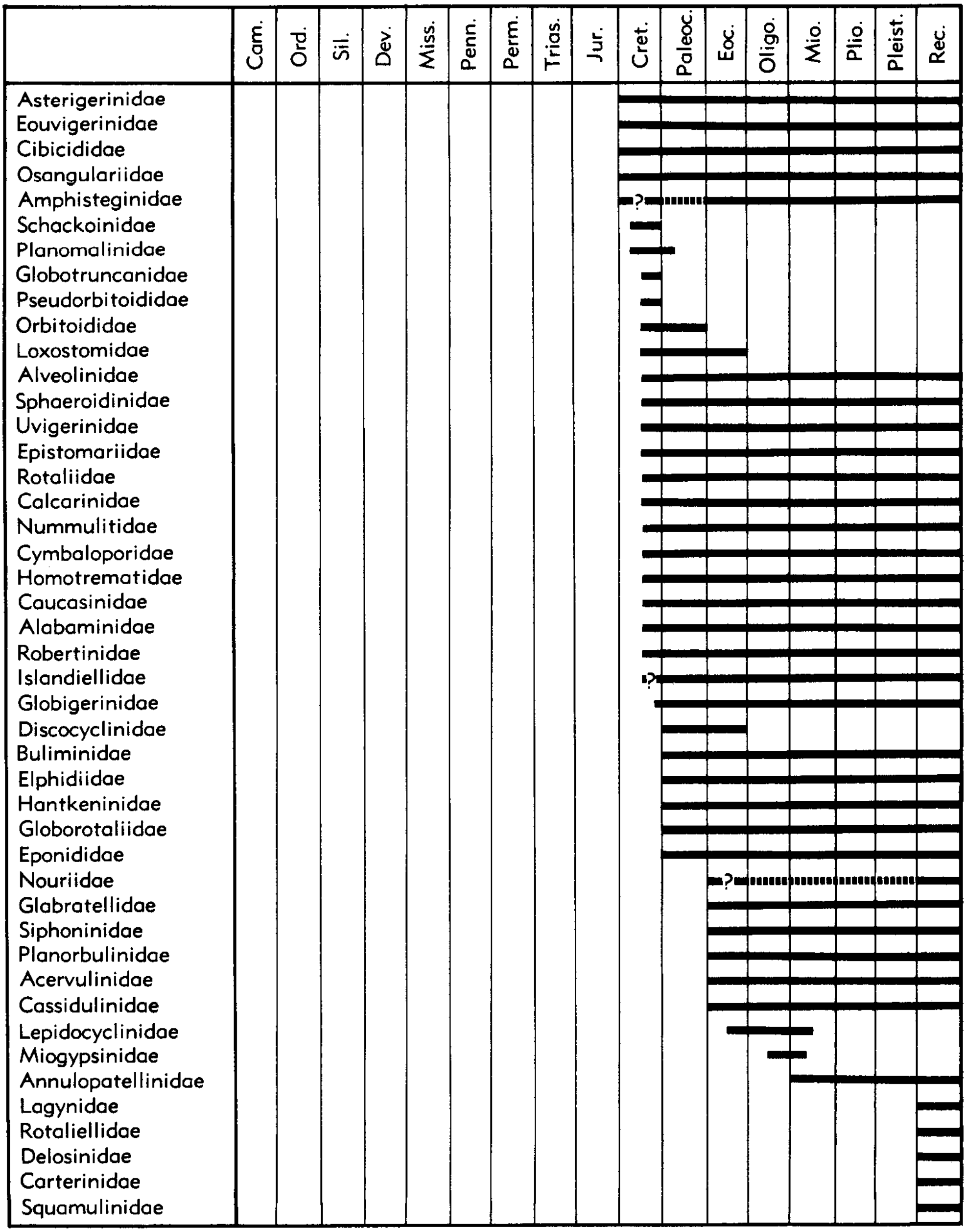


FIG. 83B *(continued)*.

SYSTEMATIC DESCRIPTIONS

Order FORAMINIFERIDA Eichwald, 1830

[*nom. correct.* T. L. Jahn & F. F. Jahn, 1949, p. 128 (*pro* order Foraminifera Claparède & Lachmann, 1859, p. 432, 434; Eichwald, 1830 (Zoologia Specialis, v. 2) p. 21)]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}class, ^{2}subclass, ^{3}division, ^{4}order, ^{5}suborder, ^{6}section, ^{7}family); dagger (†) indicates *partim*]——[^{4}Foraminifères d'Orbigny, 1826, p. 131 (*nom. neg.*); =^{1}Foraminifères d'Orbigny in de la Sagra, 1839, p. xxxi (*nom. neg.*); =^{7}Foraminifera Pritchard, 1861, p. 201 (*nom. nud.*); =^{2}Foraminiferiae Delage & Hérouard, 1896, p. 107; =^{2}Foraminifera Calkins, 1909, p. 38; =^{4}Foraminíferos Fernández Galiano, 1921, p. 26 (*nom. neg.*); =^{4}Foraminiferae Chatton, 1925, p. 76; =^{5}Foraminifera Marks, 1951, p. 377]——[=^{1}Polythalamiis Breyn, 1732 (*fide* Sherborn, 1888, p. 18); =^{4}Polythalamacea† de Blainville, 1825, p. 375; =^{4}Polythalamia Ehrenberg, 1838, p. 197, 200; =^{3}Polythalamia Marriott, 1878, p. 30; =Polythalamien Hertwig, 1893, p. 158 (*nom. neg.*); =^{5}Polythalamia Doflein, 1911, p. 633; =^{5}Politálamos Fernández Galiano, 1921, p. 29 (*nom. neg.*)]——[=^{4}Reticularia Carpenter, 1861, p. 466; =^{4}Reticulosa Carpenter, Parker & Jones, 1862, p. 17; =^{4}Reticulariida† Calkins, 1901, p. 106; =Reticulariidae Calkins, 1909, p. 25]——[=Monothalamia† Haeckel, 1862, p. 211; =^{5}Monothalamia† Fernández Galiano, 1921, p. 28; =^{6}Monotálamos† Fernández Galiano, 1921, p. 28 (*nom. neg.*)]——[=^{4}Polypes à rayons† Lamarck, 1801, p. 360 (*nom. neg.*); =^{6}Polypes coralligenes† Lamarck, 1801, p. 365 (*nom. neg.*); =Asiphoidea de Haan, 1825, p. 20; =Monosomatia Ehrenberg, 1839, table opp. p. 120; =Polysomatia Ehrenberg, 1839, table opp. p. 120; =Testacea† Schultze, 1854, p. 52; =^{4}Athalamia† Schmarda, 1871, p. 160; =^{4}Rhizopoda imperforata† Schmarda, 1871, p. 162; =Thalamophora† Hertwig, 1876, p. 53; =^{4}Thalamophoren Hertwig, 1893, p. 156 (*nom. neg.*); =^{5}Amoebaea† Bütschli in Bronn, 1880, p. 176; =Rhizopoda reticulosa testacea Schouteden, 1906, p. 376; =^{5}Arforaminiferia Rhumbler, 1913, p. 341; =^{4}Arreticularia Rhumbler, 1913, p. 339 (*nom. van.*); =^{4}Thalamia Deflandre in Grassé, 1953, p. 139]

Protoplasmic body protected by test composed of one or more interconnected chambers; wall may be imperforate, finely or coarsely perforate, primitively "chitinous," but may be variously modified, and composed of agglutinated particles, or of secreted material, rarely of silica or aragonite, more commonly of calcite, which may be porcelaneous, fibrous, or granular, hyaline-microgranular, or hyaline-radiate in structure, consisting of single layer or with two or more layers and may have canal system of varying complexity; commonly with one or more large openings or apertures in addition to smaller wall perforations which may be present; granuloreticulose pseudopodia protrude from apertures and perforations; reproduction characterized by alternation of asexual and sexual generations, although one generation may be secondarily repressed; gametes commonly flagellate (2-3 flagella) or more rarely amoeboid. [Habitat almost entirely marine to brackish waters but a few may occur in fresh waters; free-living, benthonic or pelagic, or attached to a substratum, rarely parisitic.] *?Precam., Cam.-Rec.*

Suborder ALLOGROMIINA Loeblich & Tappan, 1961

[Allogromiina Loeblich & Tappan, 1961, p. 217]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}division, ^{3}suborder); dagger (†) indicates *partim*]——[Monothalamia† Schultze, 1854, p. 52; =Monostomata† Schulze, 1877, p. 28; ^{2}Monothalamia† Marriott, 1878, p. 30; =Monothalamien Hertwig, 1893, p. 157 (*nom. neg.*); ^{1}Monothalamia† Haeckel, 1894, p. 164; =Monothalamia† Fernández Galiano, 1921, p. 21; =Monotálamos Fernández Galiano, 1921, p. 28 (*nom. neg.*); =^{1}Archi-Monothalamida Calkins, 1926, p. 354; =^{1}Monosomatia† Copeland, 1956, p. 183]——[=^{1}Acystosporés† Delage & Hérouard, 1896, p. 66 (*nom. neg.*); =^{1}Acystosporidia† Delage & Hérouard, 1896, p. 66; =Amphistomata† Averintsev, 1906, p. 316; =^{3}Uniloculinidea† Sigal in Piveteau, 1952, p. 154]——[=^{1}Allogromidiaceae Hartog in Harmer & Shipley, 1906, p. 58; =^{1}Allogromiida Fursenko, 1958, p. 22]

Test membranous or pseudochitinous, may have ferruginous encrustations or more rarely small quantities of agglutinated material. *U.Cam.-Rec.*

Superfamily LAGYNACEA Schultze, 1854

[*nom. correct.* Loeblich & Tappan, 1961, p. 274 (*pro* superfamily Lagynidea Sigal in Piveteau, 1952, p. 154)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}legio, ^{2}family group, ^{3}superfamily); dagger(†) indicates *partim*]——[=^{2}Archi-Monothalamidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 85; =^{2}Monostomata† Rhumbler, 1928, p. 3; =^{3}Microcometides Poche, 1913, p. 175]——[=^{1}Allogromiidia De Saedeleer, 1934, p. 7, 52; =^{3}Allogromioidea Chapman & Parr, 1936, p. 141; =^{3}Allogromiidea Pokorný, 1958, p. 158]

Characters of the suborder. *U.Cam.-Rec.*

Within this superfamily some genera are known to possess flagellate gametes and others amoeboid gametes. As so few have yet been studied in culture, the genera are separated into families on the basis of test composition, although, in addition, all those known to have flagellate gametes are placed in the Lagynidae and those with amoeboid gametes in the Allogromiidae.

Family LAGYNIDAE Schultze, 1854

[*nom. correct.* Carpenter, 1861, p. 458 (*pro* family Lagynida Schultze, 1854, p. 52)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}group, ^{2}family, ^{3}subfamily, ^{4}tribe); dagger(†) indicates *partim*] —— [=^{3}Lagyninae Galloway, 1933, p. 41]——[=Monothalamia amphistomata† Hertwig & Lesser, 1874, p. 137 (*nom. nud.*); =^{2}Monostomina† Lankester, 1885, p. 845 (*nom. nud.*); [=^{3}Monostominae Calkins, 1901, p. 106 (*nom. nud.*)]——[=^{2}Amoebaea reticulosa† Bütschli in Bronn, 1880, p. 178 (*nom. nud.*); =^{2}Monocyphia† Vejdovský, 1881, p. 138; =^{3}Plagiophryiinae Vejdovský, 1881, p. 138; =^{2}Diplophryidae Taránek, 1882, p. 235; =^{3}Nuditestiidae† Rhumbler, 1895, p. 93, 94 (*nom. nud.*); =^{3}Myxothecinae Rhumbler, 1895, p. 79; =^{3}Armyxothecnia Rhumbler, 1913, p. 343 (*nom. van.*); =^{1}Perforata Blochmann, 1895, p. 20; =^{4}Belariini De Saedeleer, 1934, p. 7, 79; =^{4}Heterogromiini De Saedeleer, 1934, p. 7, 82]——[^{2}Amphistomina† Bütschli in Bronn, 1880, p. 188 (*nom. nud.*); =^{2}Amphistominae† Delage & Hérouard, 1896, p. 116 (*nom. nud.*); =^{2}Amphistomidae† Schouteden, 1906, p. 358 (*nom. nud.*); =^{3}Amphistominae Calkins, 1933, p. 470 (*nom. nud.*); =^{3}Amphistomini De Saedeleer, 1934, p. 8, 86 (*nom. nud.*); =^{2}Anfistómidos Gadea Buisán, 1947, p. 16 (*nom. null., nom. neg., nom. nud.*)]——[=Polystomata Averintsev, 1906, p. 129, 322 (*nom. nud.*); =^{1}Polystomata Schouteden, 1906,

p. 373; =^{2}Polystomidae Schouteden, 1906, p. 358 (*nom. nud.*); =^{3}Polystominae De Saedeleer, 1934, p. 8 (*nom. nud.*); =^{4}Polystomini De Saedeleer, 1934, p. 8, 83 (*nom. nud.*)]——[=^{2}Microcometidae Poche, 1913, p. 175; =^{2}Microcometesidae Grospietsch, 1958, p. 35, 57; =^{2}Mikrogromiidae De Saedeleer, 1934, p. 7, 68; =^{4}Mikrogromiini De Saedeleer, 1934, p. 7, 68; =^{2}Microgromiidae Doflein & Reichenow, 1952, p. 730 (*nom. van.*)]

Test small, membranous to pseudochitinous and may have ferruginous encrustations or rarely agglutinated matter; may form colonies; aperture single, or numerous apertures not localized; gametes biflagellate

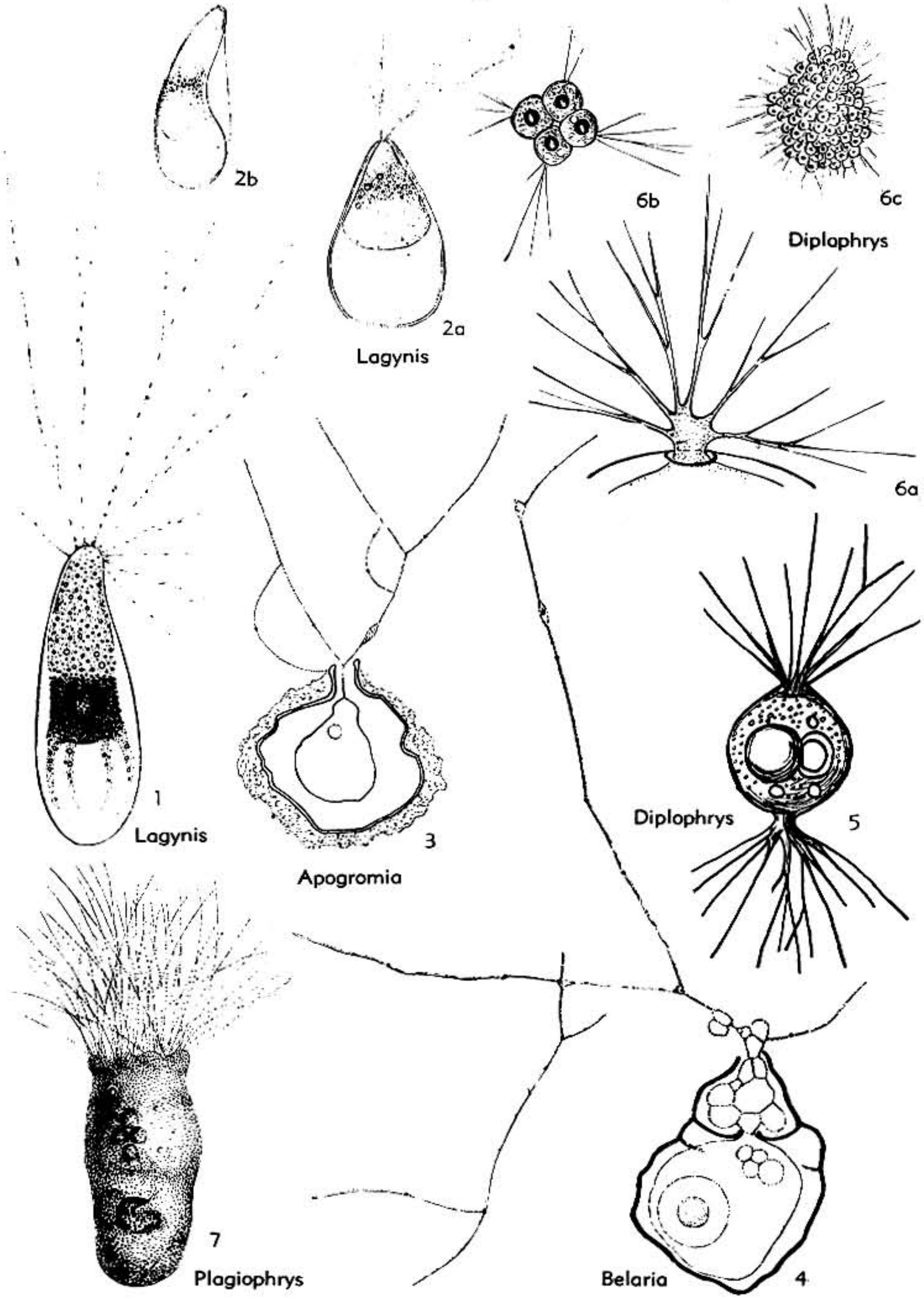


Fig. 84. Lagynidae; *1, 2, Lagynis; 3, Apogromia; 4, Belaria; 5, 6, Diplophrys; 7, Plagiophrys* (p. *C*166, *C*170).

(Myxotheca, Nemogullmia, Iridia, Cystophrys?). Rec.

Lagynis Schultze, 1854, *1695, p. 56 [*_L. baltica;_ OD] [=_Difflugia (Exassula)_ Ehrenberg, 1872, *688, p. 245 (type, _Difflugia (Exassula) baltica_ Schultze, Ehrenberg, =_Lagynis baltica_ Schulze, 1854, SD Loeblich & Tappan, herein, (obj.); _Platoum_ Schulze, 1875, *1698a, p. 115 (type, _P. parvum_ Schulze, 1875)]. Test transparent, membranous, hyaline, elastic, elongate and ovate in shape or may be slightly flattened at one side, length 0.05 mm.; aperture small, rounded, terminal to slightly eccentric, with narrow lip; protoplasm not completely filling test, granular, central zone containing dark granules, oral portion being light in color; one or two small contractile vacuoles; nuclei large, light-colored and spherical, nearly filling width of test and located near aboral end; pseudopodia thin, elongate, branching and granular. [Marine.] _Rec._, Eu.——Fig. 84,_1_. *_L. baltica,_ Baltic Sea; showing granular protoplasm with band of dark granules, posterior end with only a few bands of protoplasm, not filling test, and elongate granular pseudopodia, ×180 (*1695).——Fig. 84,_2_. _L. parva_ (Schulze), Baltic Sea; _2a,b,_ side and edge views showing test form, large, oval, light-colored nucleus, and dark, granular band of protoplasm, ×800 (*1698a).

Apogromia De Saedeleer, 1934, *1609, p. 76 [*_Microgromia mucicola_ Archer, 1877, *34a, p. 121, =_Mikrogromia mucicola_ Archer, De Saedeleer, *1609, p. 76; OD]. Test 8-15μ in length, like _Cystophrys_ but without internal septum at neck and therefore with symmetrical pseudopodial trunk. [Fresh water; marine species referred to this genus by some authors belong to _Kibisidytes._] _Rec.,_ Eu.——Fig. 84,_3_. *_A. mucicola_ (Archer), Belg.; with ferruginous coating, ×2,000 (*1609).

Belaria De Saedeleer, 1934, *1609, p. 79 [*_B. bicorpor_; OD(M)]. Test 13-16μ in length, like _Cystophrys_ but with symmetrical septum at base of neck and central perforation for extrusion of pseudopodial trunk; one contractile vacuole. [Fresh water.] _Rec.,_ Eu.——Fig. 84,_4_. *_B. bicorpor,_ Belg.; ×2,000 (*1609).

Boderia Wright, 1867, *2082, p. 335 [*_B. turneri;_ OD] [=_Arboderium_ Rhumbler, 1913, *1572b, p. 343 (obj.) _(nom. van.)_]. Test conical to platelike, membranous, colorless, length, 1.5-6.0 mm.; protoplasm brown or orange; single large nucleus or more rarely as many as 9 or 10 grouped in 2 clusters; pseudopodia few, commonly 3 or 4, protruding in bundles from openings at angles of platelike membrane; exhibits strong protoplasmic streaming. [Marine.] _Rec.,_ N.Sea.——Fig. 90,_2_. *_B. turneri;_ platelike test and long reticulose pseudopodia; approx. ×3 (*2082).

Cystophrys Archer, 1869, *29, p. 259, pl. 17 [*_C. haeckeliana_=_Gromia socialis_ Archer, 1869, *30, p. 322, *31, p. 390; OD] [=_Mikrogromia_ Hertwig, 1874, *917, p. 33 (type, _Gromia socialis_ Archer, 1869) (obj.); _Microgromia_ Archer 1876, *32, p. 343 _(nom. van.)_]. Test small, length 25-35μ, spherical to pyriform, circular in section, may occur in colonies or small groups; aperture circular, terminal, commonly produced on short neck which is internally provided with asymmetrical septum resulting in asymmetrical development of pseudopodial trunk; protoplasm granular, only partially filling test; one contractile vacuole; pseudopodia elongate, may bifurcate or anastomose and arise from a distinct pseudopodial trunk; reproduction by longitudinal or transverse division and also by development of biflagellate "zoospores." [Although commonly referred to _Mikrogromia_ (or its erroneous emendation _Microgromia_) the generic name _Cystophrys_ clearly has priority. Archer originally included two species, _C. haeckeliana_ and _C. oculea,_ and although the type was not designated in the text it was effectively determined in the original publication by the citation as _gen. et sp. nov._ for _C. haeckeliana_ and only _sp. nov._ for _C. oculea_ on the explanation for plate 17.] [Fresh water.] _Rec.,_ Eu.——Fig. 85,_1-3_. *_C. haeckeliana_; Brit.I. _(1),_ Belg. _(2),_ Ger. _(3)_; _1a,_ solitary individual, ×300; _1b,_ colony, ×250 (*302a); _2,_ individual showing internal septum, ×2,000 (*1609); _3,_ loosely aggregated colony with one specimen _(a)_ showing transverse division, approx. ×250 (*917).

Diplophrys Barker, 1868, *81, p. 123 [*_D. archeri;_ OD (M)]. Test thin, hyaline, spherical and homogeneous, diam., 8-20μ, with simple circular aperture at each pole, may form colonies up to 30-60μ diam. which have amoeboid movement and may divide; protoplasm colorless, transparent, granular; single nucleus with single nucleolus; several contractile vacuoles and oil globules always present; pseudopodia elongate, radiating, straight or bifurcating, protruding from both apertures; reproduction by fission or tetrad division. [Fresh water.] _Rec.,_ Eu.——Fig. 84,_5,6_. *_D. archeri,_ Ger. _(5),_ Neth. _(6)_; _5,_ side view of single specimen, approx. ×1,000 (*921); _6a,_ apert. part of test with pseudopodia, ×1,500; _6b,_ tetrad division, ×600; _6c,_ colony of small embryonic individuals, ×600 (*957).

Echinogromia Schröder, 1907, *1676, p. 345 [*_E. multifenestrata;_ OD] [=_Arechinogromium_ Rhumbler, 1913, *1572b, p. 344 (obj.) _(nom. van.)_]. Test spherical, or rarely blunt-triangular, wall membranous, hyaline, thickness approx. 2μ; diam., 0.5-1.0 mm.; 4 to 8 circular apertures with rim 16-20μ thick, outer secondary sheath with diam. approx. 3 mm., not closely attached to test, composed of abundant sponge spicules which show traces of protoplasm, probably from pseudopodia; protoplasm completely filling test, not differentiated into ecto- and endoplasm; 1 to 4 nuclei, approximately 0.2 mm. diam., no nucleoli; pseu-

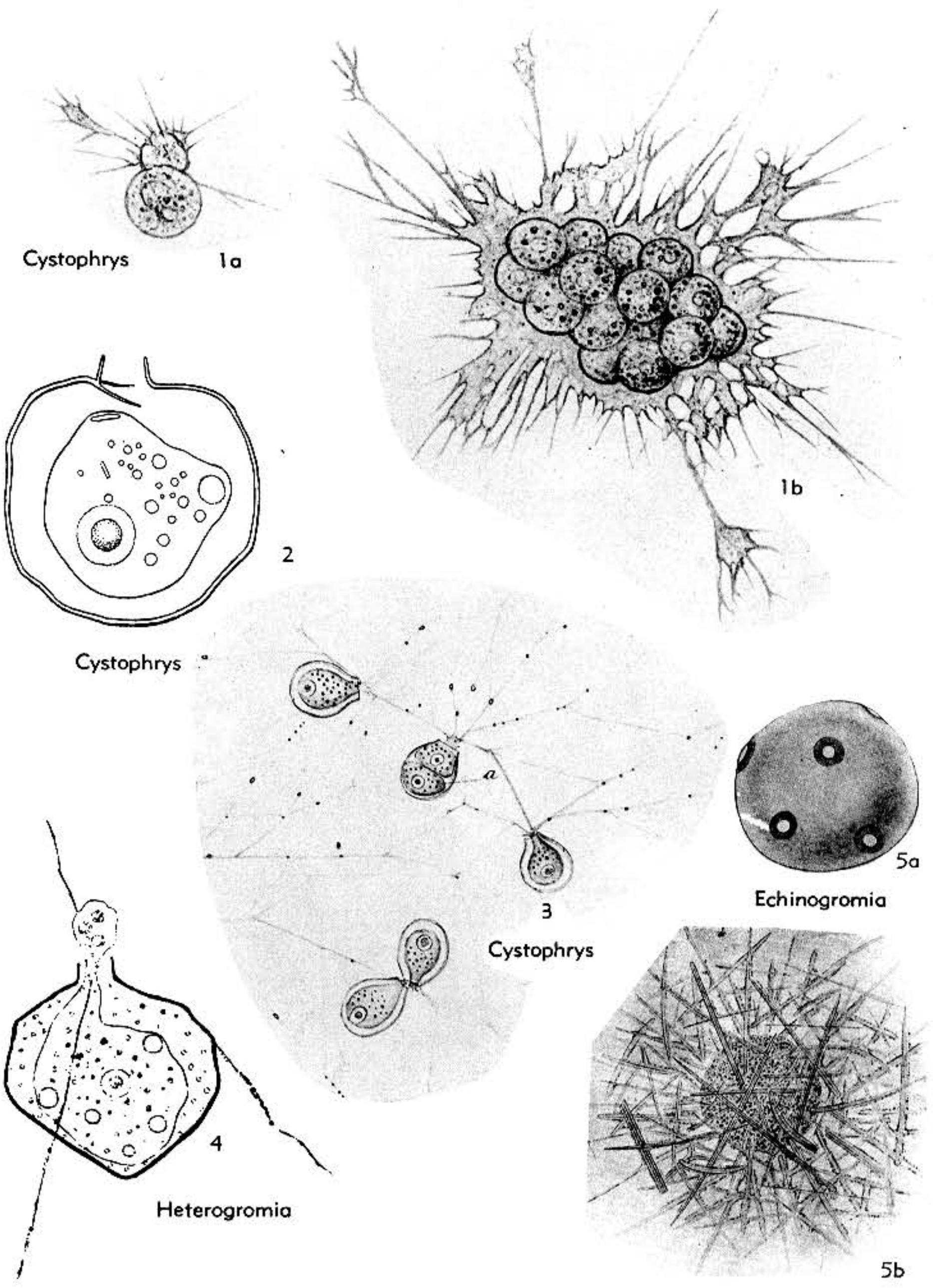


FIG. 85. Lagynidae; *1-3, Cystophrys; 4, Heterogromia; 5, Echinogromia* (p. C166-C167).

dopodial character unknown. [Marine.] *Rec.*, Antarctic.——FIG. 85,*5*. **E. multifenestrata; 5a,* test showing apertures, ×25; *5b,* specimen with outer sheath, ×15 (*1676).

Heterogromia De Saedeleer, 1934, *1609, p. 82 [**H. intermedia;* OD]. Test 9-11μ in length, like *Apogromia* but with numerous peripheral contractile vacuoles. [Fresh water.] *Rec.*, Eu.——FIG. 85,*4*. **H. intermedia,* Belg.; ×2,000 (*1609).

Iridia Heron-Allen & Earland, 1914, *910a, p. 371 [**I. diaphana;* OD]. Test attached, hemispherical or irregularly dome-shaped chamber with short irregularly tubular or branching projections; wall pseudochitinous or with some agglutinated material on pseudochitinous base; apertures at ends of tubular projections; pseudopodia in adult elongate, bifurcating, and arising from stomostyle; reproductive cycle with asexual division, young developing free or pelagic stage ensuring their dispersion, during which globular body has non-

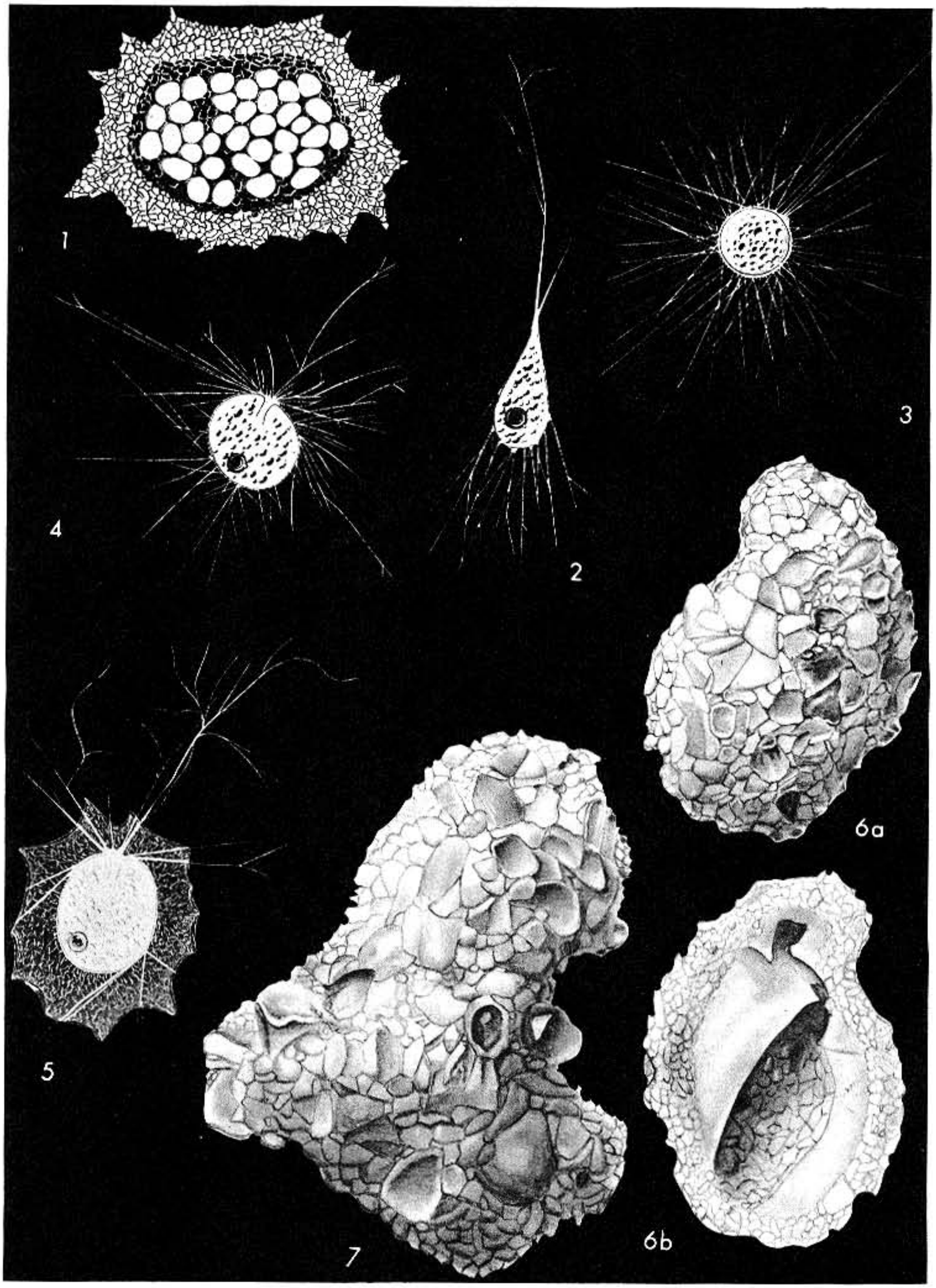


Fig. 86. Lagynidae; *1-7, Iridia* (p. C167-C169).

anastomosing, elongate, radiating pseudopodia; within few to 24 hours young become benthonic, resorb pseudopodia, attach to substratum, and develop test; this stage gives rise to biflagellate gametes (flagella unequal in length) which after fusion give rise to adult schizont indistinguishable from gamont (*1104). [Previously this genus has been placed with attached Saccamminidae (*486) or Astrorhizidae (*762). Here it is assigned to the Lagynidae because of its basically pseudochitinous test, stomostyle, and biflagellate gametes. Somewhat similar Allogromiidae have amoeboid gametes.] *Rec.*, Afr.-Carib.-Medit.——Fig. 86,*1-5*. **I. diaphana*, Medit.; *1*, detached adult schizont from beneath, showing asexually formed young, ×25; *2*, embryo after leaving parent test, showing pseudopodial trunk, ×135; *3*, pelagic stage with radiating pseudopodia, ×150; *4*, beginning of benthonic sedentary stage, showing stomostyle and normal pseudopodia, ×115; *5*, attached stage with small pseudopodia in process of test construction, normal pseudopodia extending beyond, ×115 (*1104). Fig. 86,*6,7*. **I. diaphana*, Madag.Str. (Kerimba Arch.); *6a,b*, upper and lower surfaces of empty test, showing agglutinated covering; *7*, irregular test, ×49 (*2117).——Fig. 87. *I. lucida* Le Calvez, Medit.; biflagellate gamete. ×6,000 (*1103).

Kibisidytes Jepps, 1934, *991, p. 125 [**K. marinus;* OD (M)]. Test small, saclike, brown, length, 10-14μ, commonly with ferruginous surface encrustation; aperture single, rounded; protoplasm opaque, only partially filling test; nucleus single; no contractile vacuole; pseudopodia delicate; granular, branching, but fairly short; reproduction by binary fission. [Lives in surface film of sea water or attached to floating objects in sea.] *Rec.*, Eu.——Fig. 88,*5*. **K. marinus*, Scot.; *5a,b*, living specimens showing test variation; *5c*, stained specimen showing nucleus, ×1,575 (*991).

Microcometes Cienkowski, 1876, *341, p. 46 [**M. paludosa;* OD]. Simple, rounded, membranous, transparent and pliable test which may have irregular, brown ferruginous crust, diam. 7-22μ, with 3 to 5 openings; protoplasm opaque, occupying about half interior of test and containing food inclusions; central nucleus; 1 to 6 contractile vacuoles; pseudopodia long, delicate, branching, granular. [Fresh water, among algae.] *Rec.*, Eu.——Fig. 88,*1,2*. **M. paludosa*, USSR *(1)*, Brit.I. *(2)*; *1*, ×1,000 (*341); *2*, ×1,450 (*991).

Myxotheca Schaudinn, 1893, *1640, p. 18 [**M. arenilega;* OD]. [=*Armyxothecum* Rhumbler, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Basically spherical to hemispherical form, diam., 0.16-0.56 mm., with gelatinous covering; commonly with loosely attached sand grains or other foreign matter; protoplasm granular, reddish, lacking separation into ecto- and endoplasm; single, large nucleus (39-75μ diam.); pseudopodia may appear at any position, up to 4 or 5 cm. in length, granular, and exhibit streaming. [Marine.] *Rec.*, Eu.——Fig. 89,*1*. **M. arenilega*, Adriatic Sea; *1a*, contracted specimen showing partially agglutinated upper surface covering; *1b*, same with altered form, from opposite lower side, showing extended pseudopodia and central nucleus; *1c*, transv. sec. showing nucleus, agglutinated upper surface, and clear lower surface, approx. ×300 (*1640).

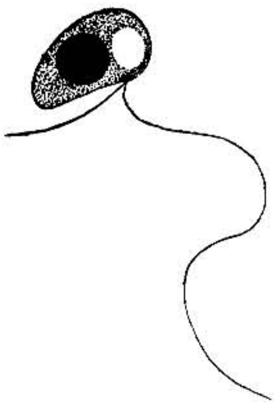


Fig. 87. Lagynidae; *Iridia* (p. C167-C169).

Nemogullmia Nyholm, 1953, *1375, p. 105 [**N. longevariabilis;* OD]. Test free or in empty worm tubes and foraminiferal tests, elongate, 1.6-19.0 mm. in length, smooth, transparent, white or pale red, chitinoid, straight or convoluted, may have constrictions in wall and bear some agglutinated detritus; temporary small apertures at ends of test; protoplasm opaque, commonly containing oil droplets; one or more nuclei; pseudopodia reticulose; reproduction by means of biflagellate gametes which develop within test after apertures are temporarily closed, multinucleate individuals reproducing by fission, specimens with single nucleus giving rise to gametes. [Marine.] *Rec.*, Eu.——Fig. 90,*4,5*. **N. longevariabilis*, Sweden (Gullmar Fjord); *4*, agglutinated detritus on elongate test, ×5 (*1378); *5*, specimen showing pseudopodia extending from apertures at ends of test, ×1.4 (*1375).

Ophiotuba Rhumbler, 1894, *1568a, p. 604 [**O. gelatinosa*; OD] [=*Arophiotubum* Rhumbler, 1913, *1527b, p. 350 (obj.) *(nom. van.)*]. Test, 2-5 mm. in length, firm convoluted membrane, rigid and chitinoid in appearance, without agglutinated matter, filling large empty tests of other foraminifers in which they are suspended by threadlike filaments, end of tube extending through aperture of sheltering test, with numerous radiating branches which are also protected by rigid membrane and may be individually convoluted; protoplasm reticulate under high magnification; nuclei small and numerous. [Marine.]

Rec., N.Atl.-N.Sea.——FIG. 90,*3*. **O. gelatinosa*, N.Atl.; convoluted body within empty test (*s*) of *Saccammina*, showing threadlike filaments (*f*) by which it is suspended and branching terminus of test (*t*), ×50 (*1568a).

Plagiophrys CLAPARÈDE & LACHMANN, 1859, *345,

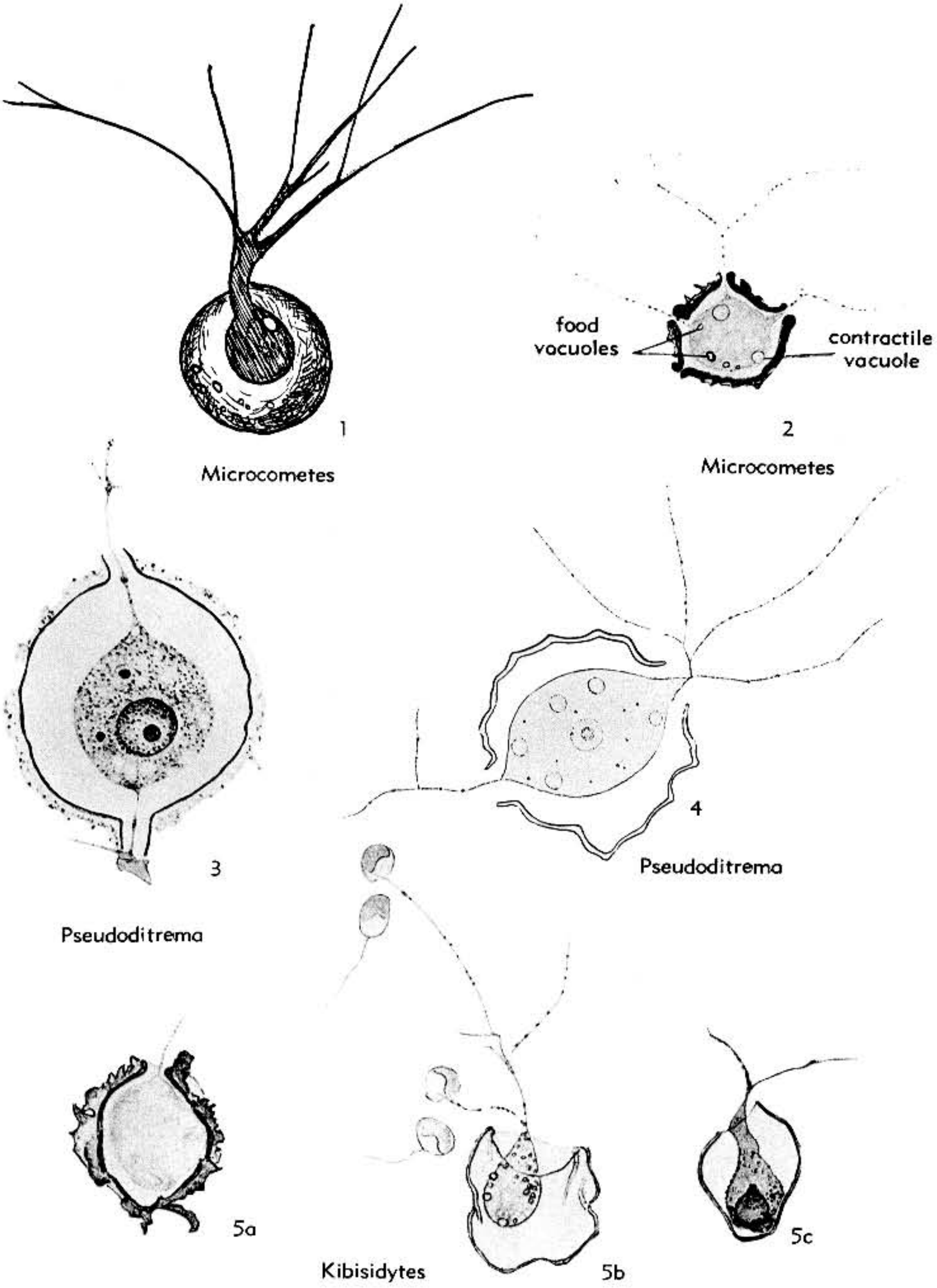


FIG. 88. Lagynidae; *1,2, Microcometes; 3-4, Pseudoditrema; 5, Kibisidytes* (p. C169, C172).

p. 453 [**P. cylindrica*; SD RHUMBLER, 1904, *1569, p. 200] [=*Arplagiophrum* RHUMBLER, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Test membranous, flexible, approx. 0.13 mm. in length, elongate, sides subcylindrical, apertural margin scalloped; pseudopodia numerous, filose, granular; nucleus and contractile vacuole unknown. [?Fresh water.] *Rec.*, ?Ger.——FIG. 84,7. **P. cylindrica;* side view, approx. ×160 (*700).

[*Plagiophrys* was described in Berlin from a bottle of water and algae of unknown source; two originally included species were *P. cylindrica* and *P. spherica*. Some later references to the type-species seem questionable. **PENARD** (1902, *1435, p. 442) stated that *P. cylindrica* might belong to *Diaphorodon* and that *P. spherica* was identical to *Pamphagus hyalinus* (=*Lecythium*), but de-

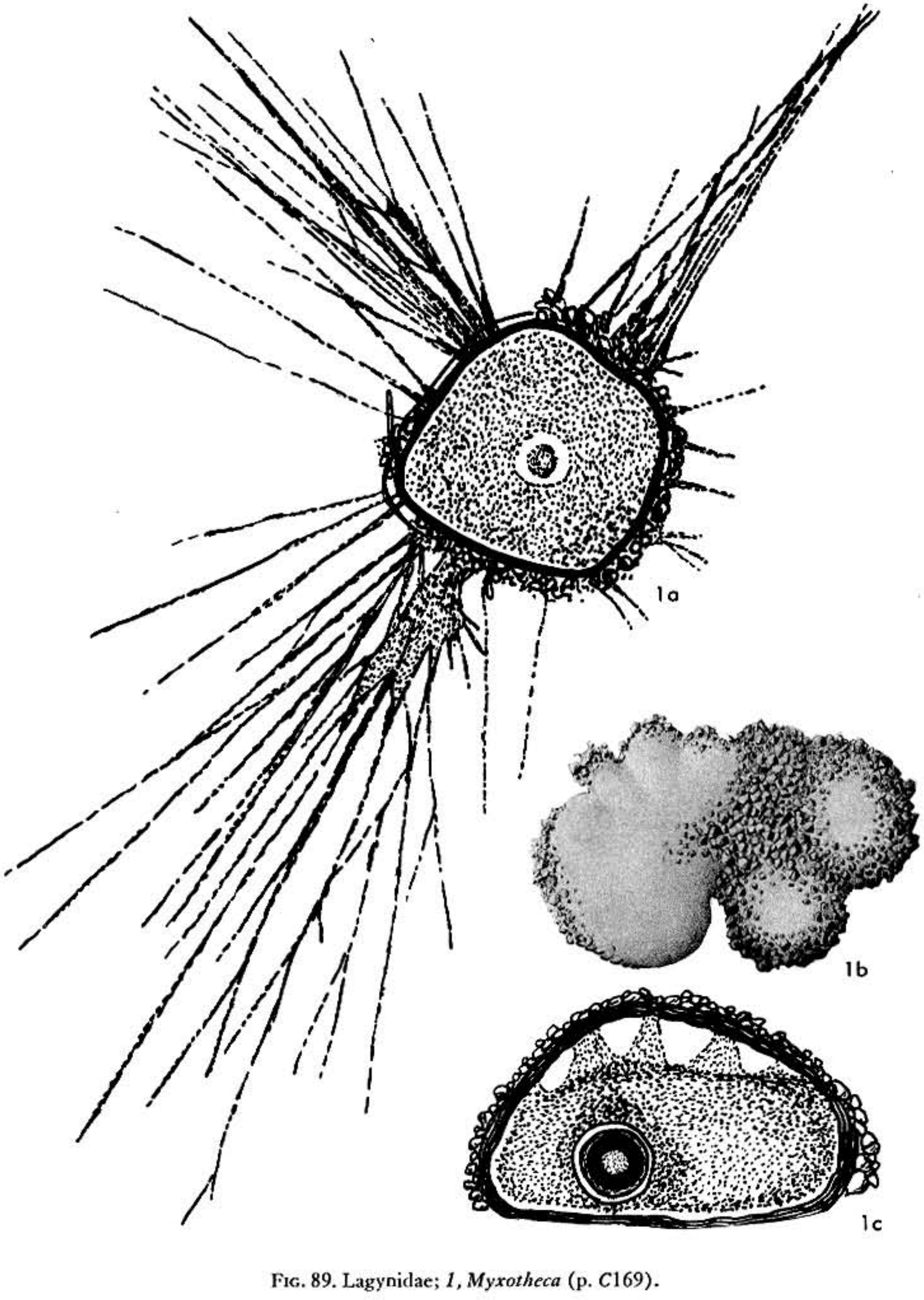


FIG. 89. Lagynidae; *1, Myxotheca* (p. C169).

scribed a new species as *Plagiophrys parvipunctata*. DEFLANDRE in GRASSÉ (1953, *810, p. 137) regarded *P. parvipunctata* as the only species belonging to the genus, but this species was not in the original list of species. RHUMBLER was correct in designating *P. cylindrica* as type.]

Pseudoditrema DEFLANDRE in GRASSÉ, 1953, *810, p. 143 [**Ditrema mikrous* DE SAEDELEER, 1934, *1609, p. 89; OD]. Similar to *Microcometes* but with only 2 opposite apertures; test 9-25μ in

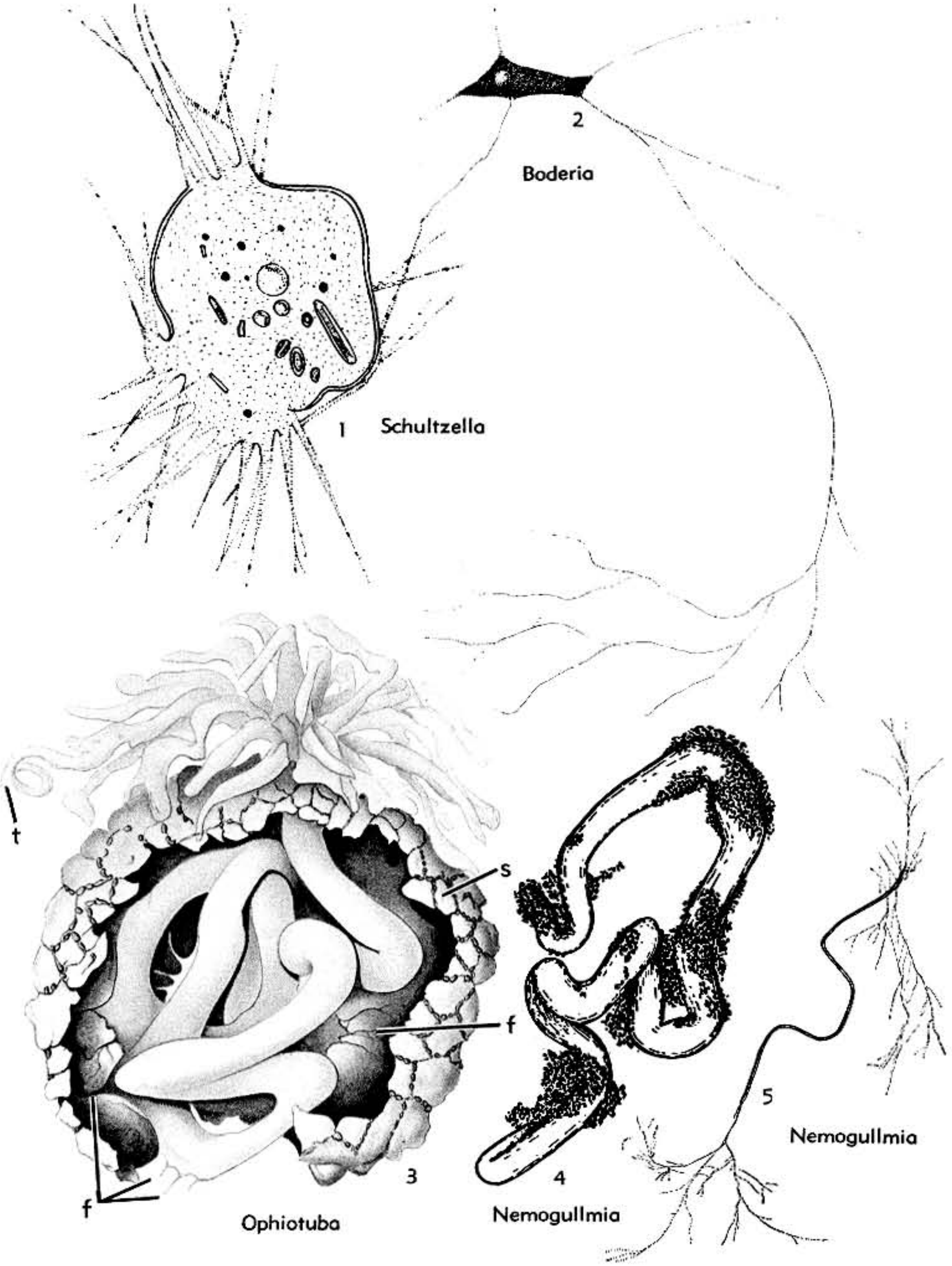


FIG. 90. Lagynidae; *1, Schultzella; 2, Boderia; 3, Ophiotuba; 4,5, Nemogullmia* (p. C166, C169-C170, C173).

length, ferruginous coating may occur; protoplasm partly filling test, containing numerous granules and contractile vacuoles; pseudopodia very thin, elongate, bifurcating and anastomosing. [Fresh water.] *Rec.*, Eu.——FIG. 88,*3,4*. **P. mikrous* (DE SAEDELEER), Eng. *(3)*, Belg. *(4)*; *3*, living specimen (regarded as *Microcometes paludosa*); ×1,450 (*991); *4*, living specimen, ×2,000 (*1609).

Rhumblerinella SCHMIDT, 1929, *1674, p. 353 [**R. bacillifera;* OD]. Test irregular, ellipsoidal or spherical, 0.7 mm. in length; superficial layer of protoplasm contains numerous small, elongate, calcite spicules approx. 5μ long secreted by animal, densely packed and apparently without binding cement, some foreign matter may be agglutinated outside this plasma layer; no distinct aperture; large round nucleus with firm birefractive membrane; pseudopodia elongate, fine, with pronounced granular streaming, may be produced from any portion of test, but are predominantly around lateral margins. [Marine.] *Rec.*, Eu. (N.Sea).——FIG. 91,*1*. **R. bacillifera*, Helgoland; *1a*, entire specimen, ×47; *1b*, margin with pseudopodia, ×80; *1c*, isolated calcite spicules in polarized light, ×800 (*1674).

Schultzella RHUMBLER, 1904, *1569, p. 197 [**Lieberkühnia diffluens* GRUBER, 1884, *833, p. 484; OD] [=*Schultzia* GRUBER, 1888, *834, p. 36 (obj.) (*non* GRIMM, 1876; *nec* GRAFF, 1882); *Arschultzellum* RHUMBLER, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Test globular or hemispherical, diam. 0.22 mm., gelatinous, without foreign material; protoplasm finely granular, colorless; nuclei small, numerous; several vacuoles and oil globules; pseudopodia may protrude in any position through irregular holes in gelatinous cover. [Marine.] *Rec.*, Eu.——FIG. 90,*1*. **S. diffluens* (GRUBER), Italy; ×150 (*1569).

Family ALLOGROMIIDAE Rhumbler, 1904

[*nom. correct.* SCHOUTEDEN, 1906, p. 374 (*pro* family Allogromida AVERINTSEV, 1906, p. 324, *nom. transl. ex* subfamily Allogromiinae RHUMBLER, 1904, p. 202)]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}family, ^{2}subfamily, ^{3}tribus); dagger(†) indicates *partim*]——[=^{1}Monostomina† LANKESTER, 1885, p. 845 *(nom. nud.)*; ^{1}Nuditestiidae† RHUMBLER, 1895, p. 93, 94 *(nom. nud.)*; =^{2}Monostominae† CALKINS, 1901, p. 106 *(nom. nud.)*; =^{2}Craterininae RHUMBLER, 1904, p. 196 (=Allogromiinae); =^{2}Arrogromnia RHUMBLER, 1913, p. 343 *(nom. van.)*; =^{2}Rhynchogromiinae GALLOWAY, 1933, p. 52; =^{2}Lieberkuehniinae DE SAEDELEER, 1934, p. 7, 64; =^{3}Lieberkuehniini DE SAEDELEER, 1934, p. 7, 64; =^{3}Pleurophryini DE SAEDELEER, 1934, p. 7, 60; =^{3}Allelogromiini DE SAEDELEER, 1934, p. 7, 67; =^{1}Allogromidae DOGEL, 1951, p. 464 *(nom. van.)*; =^{1}Allogromiida COPELAND, 1956, p. 183 *(nom. van.)*; =^{1}Alexandrellidae E. V. BYKOVA, 1958, p. 881 *(nom. nud.)*; =^{1}Maylisoriidae E. V. BYKOVA, 1961, p. 20]

Test pseudochitinous or with agglutinated matter on pseudochitinous base; forms known to show alternation of generations (e.g., *Allogromia*) have amoeboid gametes. *U.Cam.-Rec.*

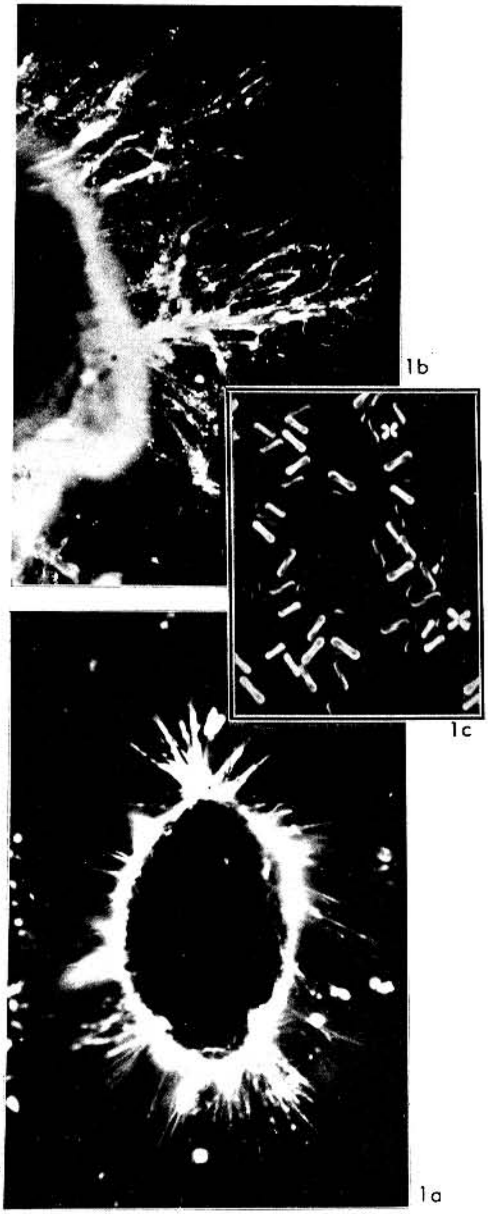


FIG. 91. Lagynidae; *1, Rhumblerinella* (p. C173).

Allogromia RHUMBLER, 1904, *1569, p. 203 [**Craterina mollis* GRUBER, 1884, *833, p. 488; OD] [=*Craterina* GRUBER, 1884, *833, p. 488 (obj.) (*non* CURTIS, 1826; *nec* BORY DE ST. VINCENT, 1827); *Arrogromium* RHUMBLER, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Test free, ovate to spherical, with thin pseudochitinous test, 0.08-0.5 mm. in length, may have agglutinated foreign matter; aperture terminal, rounded, with entosolenian tube serving as sheath for pseudopodial trunk; pseudopodia granular, much elongate and anastomosing, with typical protoplasmic streaming; reproduction both by asexual schizogamy and sexual, with production of amoeboid

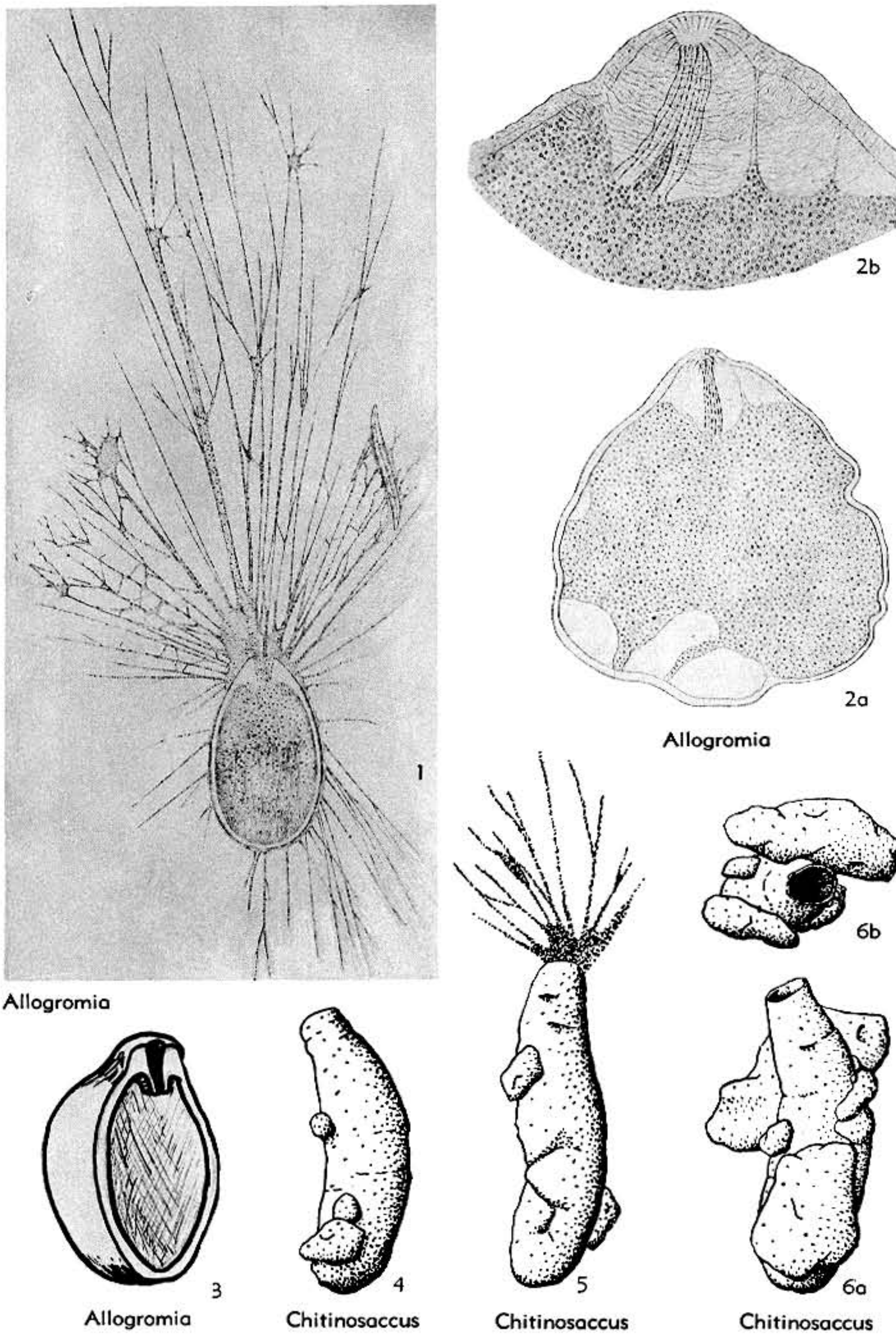


Fig. 92. Allogromiidae; *1-3, Allogromia; 4-6, Chitinosaccus* (p. *C*173-*C*176).

gametes but haploid and diploid adults morphologically similar. [Marine and fresh water.] *Rec.*, Eu.-N.Am.——FIG. 92,*1*. *A. ovoidea* RHUMBLER, Adriatic Sea; anastomosing pseudopodia arising from pseudopodial trunk, ×35 (*1695).——FIG. 92,*2*. **A. mollis* (GRUBER), Italy; *2a*, living example, ×100; *2b*, enlargement showing inverted aperture (*833).——FIG. 92,*3*. *A. laticollare* ARNOLD, USA(Fla.); diagram. sec. of test to show entosolenian tube or peduncular sheath, enlarged (*40).

[WAILES in CASH, WAILES and HOPKINSON (1915, *302a, p. 138) stated that DUJARDIN's *Gromia fluvialis*, 1837, should be considered as type of *Allogromia*. DE SAEDELEER (1934, *1609, p. 55) concluded that *G. fluvialis* DUJARDIN, 1837, was also typically filose and thus belonged to the Gromiidae and he designated the granuloreticulose *G. fluviatilis* DUJARDIN, 1841, as type-species of *Allogromia*. However, RHUMBLER (1904, *1569, p. 203) did not describe a new genus, but specifically stated that *Allogromia* was a *nom. nov.* for *Craterina* GRUBER. The type-species must therefore be the same as that of *Craterina* GRUBER (*C. mollis* GRUBER) as stated by RHUMBLER (*1569, p. 204).]

Archaeochitinia EISENACK, 1954, *694, p. 54 [**A. gotlandica;* OD]. Test free, unilocular, semiglobular; wall chitinous; aperture consisting of small pores or openings at end of short tubuli. *L.Sil.*, Eu.——FIG. 93,*1*. **A. gotlandica*, Llandov., Sweden(Gotl.); *1a*, side view, ×140; *1b*, apertures, enlarged (*694).

Archaeochitosa EISENACK, 1959, *695, p. 91 [**A. lobosa*; OD]. Test pseudochitinous membrane, forming single irregular chamber; one or more circular to oval apertures at ends of tubular extensions from central portion. *Ord.-Jur.*, Eu.——FIG. 93,*2*. **A. lobosa*, Ord. (Echinosphaeritenkalk), Est.; ×50 (*695).

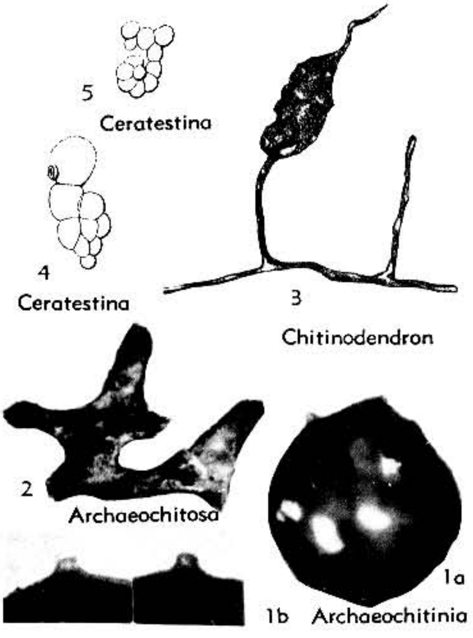


FIG. 93. Allogromiidae; *1, Archaeochitinia; 2, Archaeochitosa; 3, Chitinodendron; 4, 5, Ceratestina* (p. C175).

FIG. 94. Allogromiidae; *Chitinolagena* (p. C175).

Ceratestina CARTER, 1880, *296, p. 448 [**C. globularis;* SD GALLOWAY, 1933, *762, p. 294]. Similar to *Placopsilinella* in having dark brown pseudochitinous wall and attached, subglobular, irregularly arranged chambers, but differing in presence of stoloniferous intercameral connections and stoloniferous extensions from final chamber; differs from *Hospitella* in being attached but not parasitic, and in having more closely, less regularly arranged chambers. *Rec.*, Ind.O.——FIG. 93,*4,5*. **C. globularis*, *4,5*, entire individuals, approx. ×25 (*296).

[The original figures and description of this genus are quite similar to *Placopsilinella*, but as the types of *Ceratestina* were not found (stated to be in Liverpool Free Museum, but apparently destroyed during World War II) both genera are tentatively recognized, though additional material may prove their identity. Specimens of the type-species of *Placopsilinella* do not show the stoloniferous features described for *Ceratestina*.]

Chitinodendron EISENACK, 1937, *693b, p. 236 [**C. bacciferum;* OD]. Thin pseudochitinous branching tubes, which terminate in oval saclike chambers that commonly are axially symmetrical. *U.Cam.-Sil.*, USA-Eu.(Est.-Ger.).——FIG. 93,*3*. **C. bacciferum*, M.Ord.(Llanvirn.), Est.; ×60 (*693b).

Chitinolagena E. V. BYKOVA, 1961, *260, p. 31 [**C. gutta;* OD]. Test unilocular, with inflated base and wide elongated neck; wall chitinoid, dark brown, of labyrinthine structure; aperture terminal. [*Chitinolagena* is here recognized as a foraminifer, as interpreted by BYKOVA, but possibly should be placed with the Chitinozoa which it strongly resembles in form.] *U.Ord.(Caradoc.)*, USSR(Kazakh.).——FIG. 94. **C. gutta;* holotype, long. sec., ×330 (*2112).

Chitinosaccus SMITTER, 1956, *1802, p. 285 [**C. zuluensis;* OD]. Test irregular, elongate, cylindrical sac, 0.65 mm. in length; pseudochitinous, somewhat flexible, with some foreign matter, colorless to reddish-brown; aperture terminal, rounded, single; protoplasm filling test; pseudopodia branching and anastomosing. [Brackish water, sublittoral.] *Rec.*, S.Afr.——FIG. 92,*4-6*. **C. zuluensis*, Zululand; *4,5*, empty test and one with protruding pseudopodia; *6a,b*, side, top views, approx. ×60 (*1802).

Dactylosaccus RHUMBLER, 1894, *1568a, p. 601

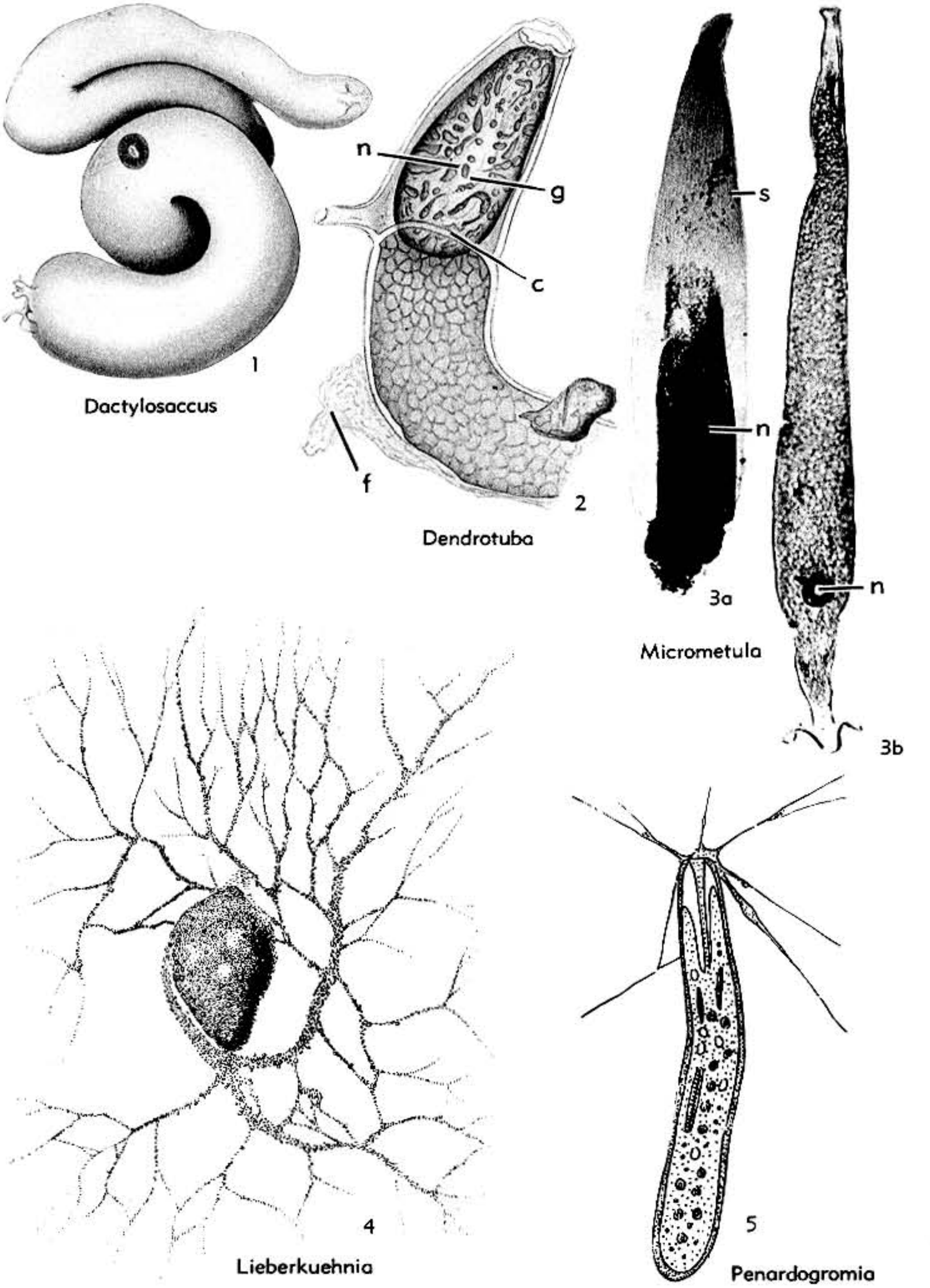


FIG. 95. Allogromiidae; *1, Dactylosaccus; 2, Dendrotuba; 3, Micrometula; 4, Lieberkuehnia; 5, Penardogromia* (p. C176-C177, C179, C181).

[**D. vermiformis;* OD] [=*Ardactylosaccum* Rhumbler, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Free-living or inhabiting empty foraminiferal tests; elongate, to 4 mm. in length, hyaline, chitinoid; sausage-shaped or convoluted tube, enlarging somewhat toward apertural end, from which lobose protuberances extend giving rise to pseudopodia; protoplasm with small vacuoles; 1 or 2 globular nuclei. [Marine, 40-250 m.] *Rec.,* N.Atl.-N.Sea.——Fig. 95,*1*. **D. vermiformis,* N.Atl.; ×45 (*1568a).

Dendrotuba Rhumbler, 1894, *1568a, p. 606 [**D. nodulosa;* OD] [=*Ardendrotubum* Rhumbler, 1913, *1572b, p. 350 (obj.) *(nom. van.)*]. Test, 0.7-5.0 mm. in length, growing inside empty foraminiferal tests and attached by rigid and tough threadlike filaments, tube much convoluted, may be branched, even in size except for some knotlike swellings; wall resistant, chitinoid sheath with ringlike constrictions; ends of tube tapering or clavate; nucleus single, large, approximately as wide as protoplasmic body, diam. 87-138μ, variable in position. [Marine, cold water.] *Rec.,* N.Atl.——Fig. 95,*2*. **D. nodulosa;* portion of tube with central constriction *(c)*, threadlike filaments *(f)*, large ovoid nucleus *(n)* and chromatin granules in nucleus *(g)*, ×250 (*1568a).

Diplogromia Rhumbler, 1904, *1569, p. 214 [**Gromia brunneri* Blanc, 1886, *145, p. 362; SD Cushman, 1928, *439, p. 60] [=*Ardiplogromium* Rhumbler, 1913, *1572b, p. 344 (obj.) *(nom. van.)*; *Allelogromia* De Saedeleer, 1934, *1609, p. 67 (obj.)]. Test free, ovoid or pyriform, length, 0.06-0.25 mm.; wall 0.02 mm. thick, composed of small siliceous particles and foreign matter held in gelatinous cement; aperture terminal, round, extensible; protoplasm yellowish and extending from aperture in asymmetrical pseudopodial peduncle, protoplasmic body covered with fairly thick mucilaginous layer which separates it from external test and which apparently was originally regarded as an inner hyaline layer, though no trace of such 2-layered character can be seen in thin sections (*1437, p. 69); nucleus large, spherical, may have many smaller nuclei; vacuoles small, generally numerous; pseudopodia numerous, long, commonly anastomosing. [Fresh water.] *Rec.,* Eu.——Fig. 96,*1*. **D. brunneri* (Blanc), Switz.; ×110 (*1569).

Hospitella Rhumbler, 1911, *1572a, p. 92, 227 [**H. fulva*; OD (M)] [=*Arhospitellum* Rhumbler, 1913, *1572b, p. 440 (obj.) *(nom. van.)*; *Hospitellum* Rhumbler, 1913, *1572b, p. 468 (obj.) *(nom. van.)*]. Test attached, pseudochitinous, brownish, imperforate, commonly occurring in empty tests of other foraminifers; chambers globular to ovate or flask-shaped with stoloniferous necks, in uniserial or irregularly branching arrangement, or may be closely piled on each other, influenced by size and shape of cavities in occupied test, neck and aperture may pierce shell of this test. [Differs from *Placopsilinella* in flask-shaped chambers and apparently parasitic habit. The type-species, regarded as fixed by monotypy as *H. fulva,* is the only described species included by Rhumbler; *H. fusca* was mentioned (*1572a, p. 227) but not described and thus is a *nomen nudum.*] *Rec.,* Atl.——Fig. 97,*2*. **H. fulva;* ×95 (*1572a).

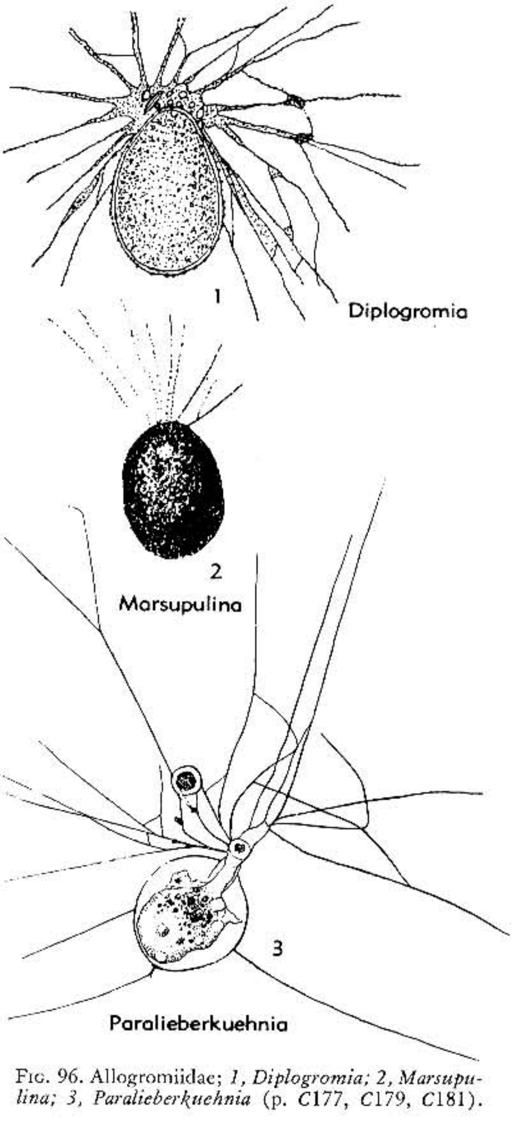


Fig. 96. Allogromiidae; *1, Diplogromia; 2, Marsupulina; 3, Paralieberkuehnia* (p. C177, C179, C181).

Labyrinthochitinia E. V. Bykova, 1961, *260, p. 58 [**L. tastikoliensis;* OD]. Test free or attached, subglobular to subellipsoidal, with inner partitions resulting in numerous somewhat indistinct chamberlets that intercommunicate by labyrinthine canals; wall thin, dark brown, chitinoid, labyrinthic in structure; no aperture other than canal-like wall openings. *U.Ord.(Caradoc.)*, USSR(N. Kazakh.).——FIG. 98,*1,2*. *_L. tastiḳoliensis; 1,_ holotype, *2*, paratype, ×330 (*2112).

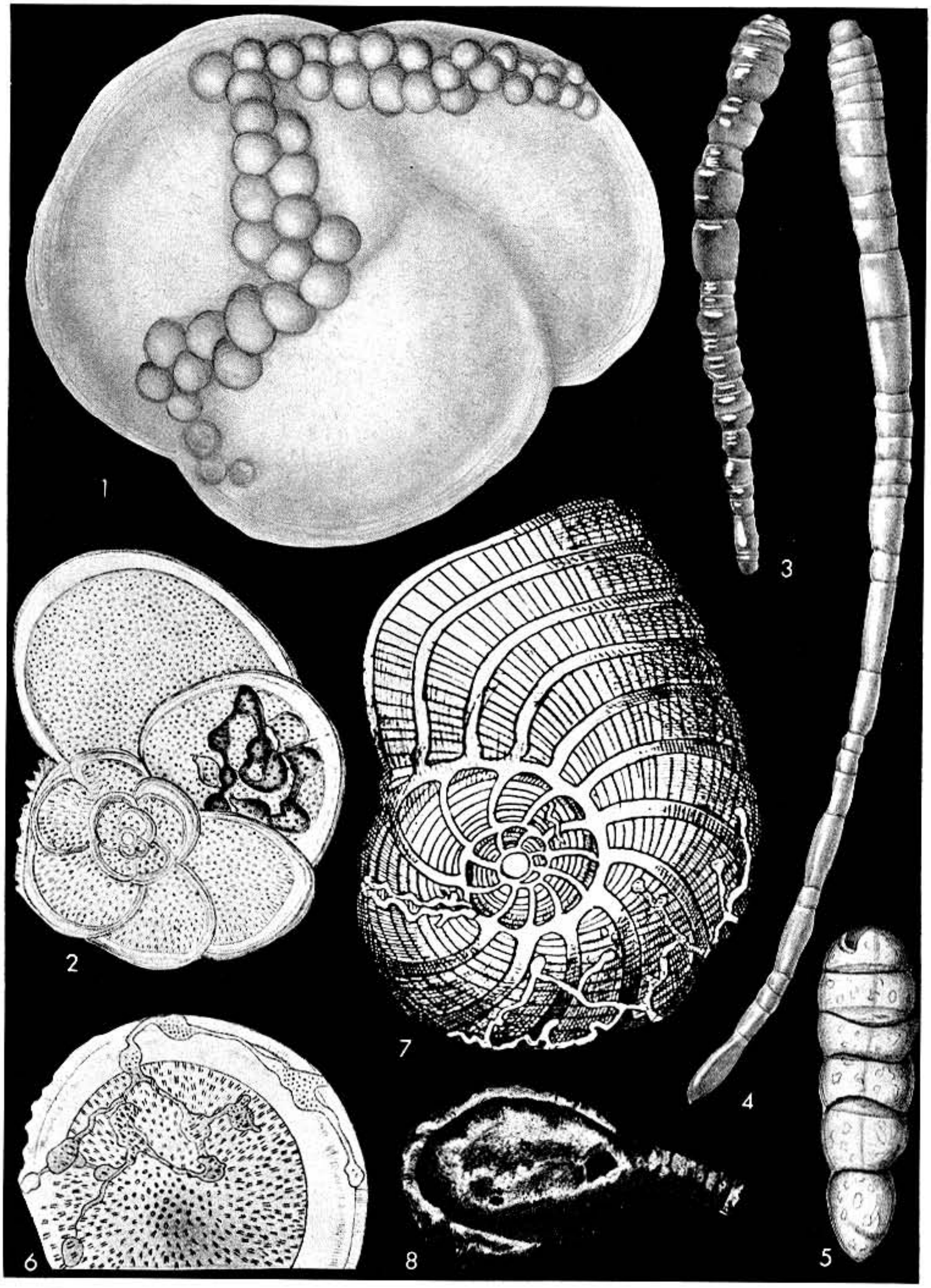


FIG. 97. Allogromiidae; *1, Placopsilinella; 2, Hospitella; 3, 4, Nodellum; 5, Turriclavula; 6, 7, Thalamophaga; 8, Xenotheḳa* (p. C177, C179-C181, C183).

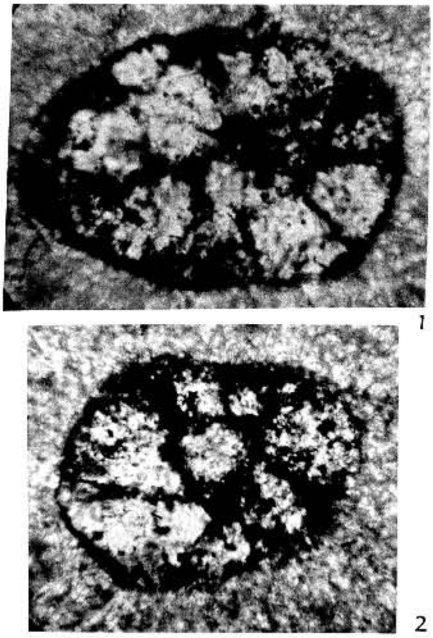


FIG. 98. Allogromiidae; *1,2, Labyrinthochitinia* (p. C177-C178).

Lieberkuehnia Claparède & Lachmann, 1859, *345, p. 464 [**L. wagneri*; OD (M)] [=*Arlieberkuehnium* Rhumbler, 1913, *1572b, p. 343 (obj.) *(nom. van.)*]. Test 60-350μ in length, oval or spherical, membranous, smooth or thinly covered with foreign matter; aperture single, lateral or subterminal, may be narrow slit; protoplasm clear, slightly yellowish, distinctly granular with ribbonlike pseudopodial trunk extending through aperture and giving rise to pseudopodia or layer of protoplasm that may almost envelop test; one to many spherical nuclei, 80-150 in type-species; numerous contractile vacuoles; pseudopodia elongate, anastomosing, with pronounced granular streaming; reproduction by fission. [Fresh water and marine.] *Rec.*, Eu.——FIG. 95,*4*. **L. wagneri* (bottle of water in Berlin from unknown source); approx. ×100 (*281).

Marsupulina Rhumbler, 1904, *1569, p. 249 [**M. schultzei*; OD (M)] [=*Armarsupium* Rhumbler, 1913, *1572b, p. 349 *(nom. van.)* (obj.)]. Test ovate, ellipsoid or reniform, 0.2 mm. in length; wall chitinoid, may be partially or wholly covered with deposit of amorphous, granular calcite; aperture rounded, eccentric; nucleus single; pseudopodia granulose. [Marine.] *Rec.*, Eu.——FIG. 96,*2*. **M. schultzei*, Medit.(Italy); ×60 (*1569).

Maylisoria E. V. Bykova, 1961, *260, p. 31 [**M. pseudoscheda*; OD] [=*Alexandrella* E. V. Bykova, 1958, *259, p. 880 *(nom. nud.)* (*non* Chevreux, 1911; *nec* Tonnoir, 1926)]. Test free, irregularly ovate; wall thick, yellowish or brownish-gray, chitinoid and microgranular, labyrinthine in structure, pierced by narrow tubular pores or canals; without aperture other than tubular canals. *U.Ord. (Caradoc.)*, USSR(C.Kazakh.).——FIG. 99,*1,2*. **M. pseudoscheda; 1a,* holotype, ×330; *1b,* diagram showing structure; *2,* paratype, ×330 (*2112).

Micrometula Nyholm, 1952, *1374, p. 15 [**M. hyalostriata;* OD]. Test elongate, 0.7-1.2 mm. in length, tapering, imperforate, hyaline and chitinoid with fine longitudinal striations; rounded aperture at larger end, smaller temporary opening may be present at opposite end; cytoplasm without inclusions, although some detrital particles may accumulate at aperture; one nucleus. [Marine.] *Rec.*, Eu.——FIG. 95,*3*. **M. hyalostriata*, Sweden(Gullmar Fjord); *3a,* side view showing striated test *(s)* and nucleus *(n)*, ×100; *3b,* long. sec. showing nucleus *(n)*, ×110 (*1374).

Nodellum Rhumbler, 1913, *1572b, p. 443, 473 [**Reophax membranacea* Brady, 1879, *196a, p. 53; OD] [=*Arnodellum* Rhumbler, 1913, *1572b, p. 443 (obj.) *(nom. van.)*; *Chitinosiphon* Thalmann & Bermúdez, 1954, *1906, p. 53 (type, *C. rufescens* Thalmann & Bermúdez, 1954)]. Test free; oval proloculus followed by elongate, curved, and slightly enlarging tube with irregularly spaced transverse constrictions; wall thin, translucent, brown, pseudochitinous; aperture rounded, at slightly constricted end of tube. *Rec.*,

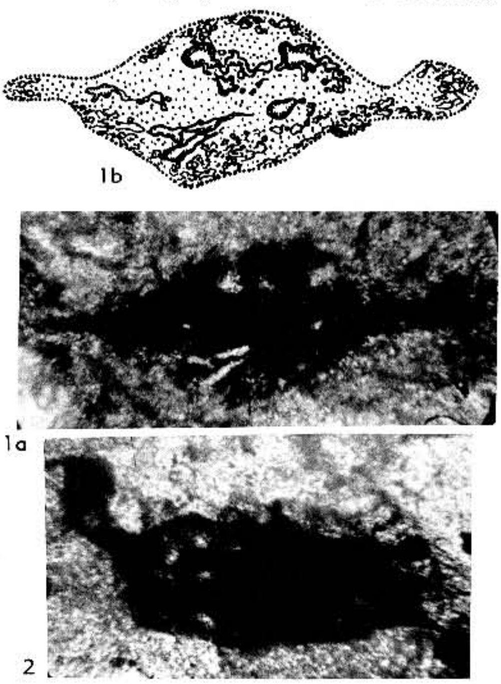


FIG. 99. Allogromiidae; *1,2, Maylisoria* (p. C179).

Atl.O.——Fig. 97,*3,4*. **N. membranacea* (Brady); *3*, topotype, S.Atl.; ×65 (*2117); *4*, holotype, refigured, of *C. rufescens* Thalmann & Bermúdez, ×50 (*2117).

[Because *Nodellum* was described as chambered and with sand grains attached to chitinoid wall, *Chitinosiphon* was recently proposed. Not only are the genera synonymous, but their type-species are identical. No attached sand occurs on topotypes of *Reophax membranacea*, hence pos-

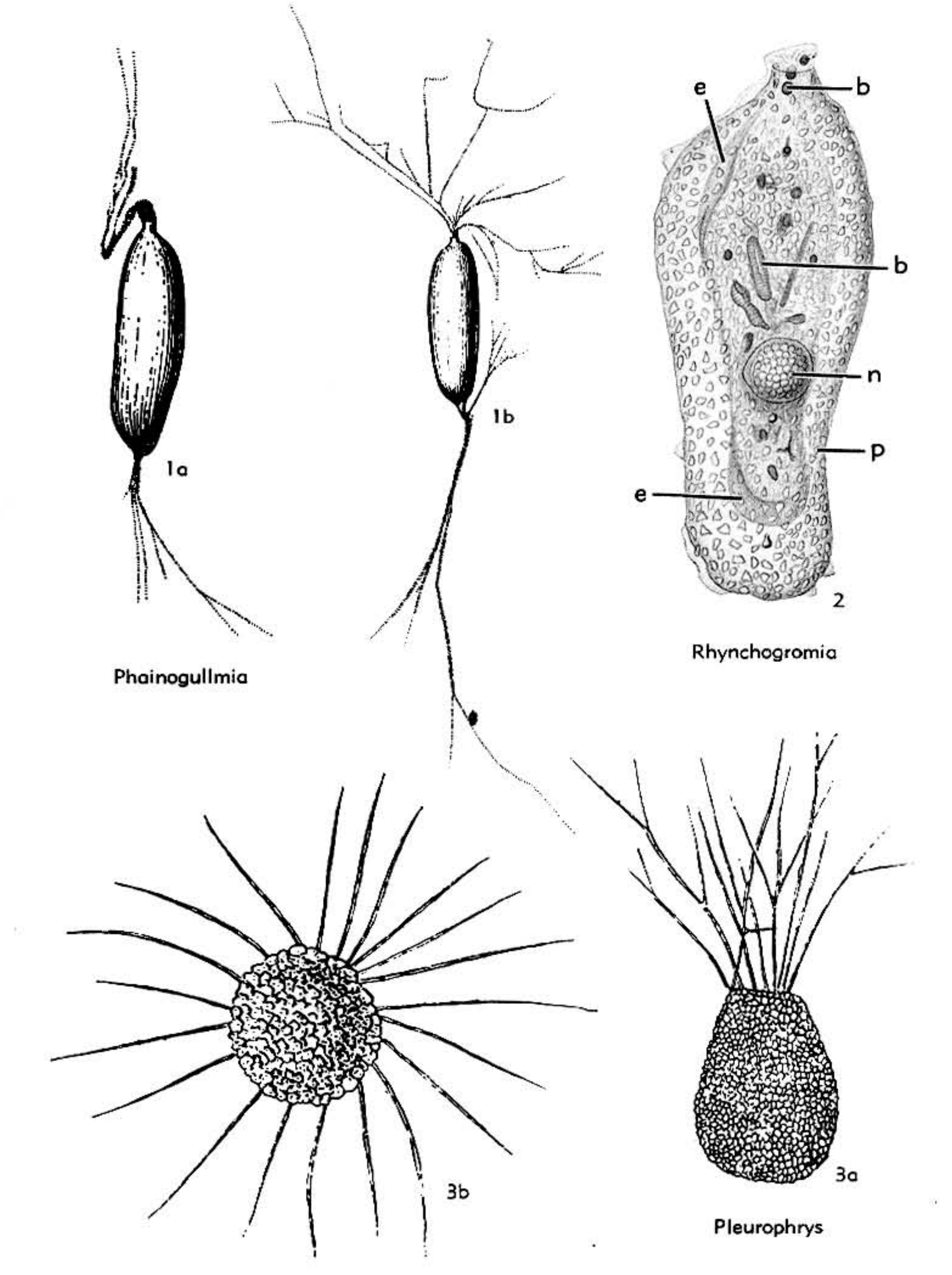


Fig. 100. Allogromiidae; *1, Phainogullmia; 2, Rhynchogromia; 3, Pleurophrys* (p. C181).

sibly extraneous material was originally mistaken for an agglutinated test. The specimens illustrated for *Chitinosiphon* include the holotype of *C. rufescens*, 3.14 mm. in length, and paratypes 1.49 to 2.9 mm. in length, the type of *R. membranacea* being about 1.4 mm. in length. Both type-species were described from deep water in the Atlantic.]

Paralieberkuehnia DE SAEDELEER, 1934, *1609, p. 52 [**Microgromia elegantula* PENARD, 1904, *1436, p. 416, OD] [=*Faralieberkuehnia* DE SAEDELEER, 1932, *1375, p. 619 *(nom. nud.)*]. Test, 20-25μ in length, thin, hyaline, pseudochitinous, rounded; protoplasm encloses brilliant grains, only partially filling test as globular mass, restricted toward aperture into pseudopodial trunk; nucleus subcentral; very large contractile vacuole near base of pseudopodial trunk; pseudopodia very fine, straight, long, granular and exhibit slow granular streaming. [Fresh water.] *Rec.*, Eu.——FIG. 96,*3*. **P. elegantula* (PENARD), Belg.; specimen with strong pseudopodial trunk and elongate pseudopodia, ×500 (*1609).

Penardogromia DEFLANDRE in GRASSÉ, 1953, *810, p. 140 [**Gromia linearis* PENARD, 1902, *1435, p. 567; OD (M)]. Test elongate, 220-230μ in length, tubular or fusiform, straight to slightly arcuate, thin, delicate, translucent, yellowish, consisting of extremely small platelets in clear groundmass, suggesting small longitudinal striations; aperture terminal; protoplasm yellowish, constricted toward aperture into distinct pseudopodial trunk; nucleus spherical, with large nucleoli, more rarely as many as 20 nuclei; small contractile vacuole; pseudopodia anastomosing and filamentous, extending from trunk. [DEFLANDRE cited the type-species as *"Gromia linearis* var. Penard, 1902," but in 1902 PENARD described no form under this name, only *"Gromia linearis* spec. nov."] [Fresh water.] *Rec.*, Eu.——FIG. 95,*5*. **P. linearis* (PENARD), Switz.; approx. ×250 (*1435).

Phainogullmia NYHOLM, 1955, *1377, p. 466 [**P. aurata;* OD]. Test cylindrical, 0.2-1.4 mm. in length, tapering at both ends, yellowish-brown, glossy, opaque, consisting of chitinoid lamellae; aperture at each end of test; food vacuoles in protoplasm; single nucleus; pseudopodia reticulose, extending from both apertures; asexual reproduction by formation of numerous nuclei, each accumulating protoplasm and becoming a new embryo, no sexual reproduction observed. [Marine.]*Rec.*, Eu.——FIG. 100,*1*. **P. aurata*, Sweden (Gullmar Fjord); *1a,b*, partially and fully extended pseudopodia, ×75 (*1377).

Placopsilinella EARLAND, 1934, *653, p. 95 [**P. aurantiaca;* OD]. Test tiny, commonly attached to other foraminifers; wall pseudochitinous, with some ferruginous cement; numerous rounded, plano-convex chambers, commonly arranged in double row, single row, or rarely with 3 chambers abreast, but without regularity in mode of increase or decrease, and without definite arrangement; no visible aperture nor evidence of communication between chambers. *Rec.*, Atl.——FIG. 97,*1*. **P. aurantiaca* (hypotype BMNH ZF3659), ×218 (*2117).

[A single specimen found by EARLAND showed an apparent early spiral development of the chambers, and he therefore considered the genus related to *Placopsilina*. However, this was apparently an accidental arrangement, since none of the other specimens show any indication of coiling. The composition of the wall also seems to exclude this genus from the Placopsilinidae, as likewise absence of an aperture or opening between chambers, and the complete absence of regularity of chamber arrangement. Because of the pseudochitinous wall, it is here placed in the Allogromiidae. It differs from *Ceratestina* and *Hospitella* in the absence of any visible aperture or stoloniferous intercameral necks.]

Pleurophrys CLAPARÈDE & LACHMANN, 1859, *345, p. 454 [**P. sphaerica*; OD (M)]. Test ovate, length, 30-72μ, of organic matter in which small foreign bodies and sand grains are cemented; aperture rounded; protoplasm wholly filling test; pseudopodia reticulose, granular. [*Lithocolla* SCHULTZE, 1874, regarded as a synonym of this genus (*762, p. 45), is now considered to be a heliozoan]. [Fresh water and marine.] *Rec.*, Eu. ——FIG. 100,*3*. **P. sphaerica,* Ger.; *3a,b,* side and basal views, approx. ×300 (*1609).

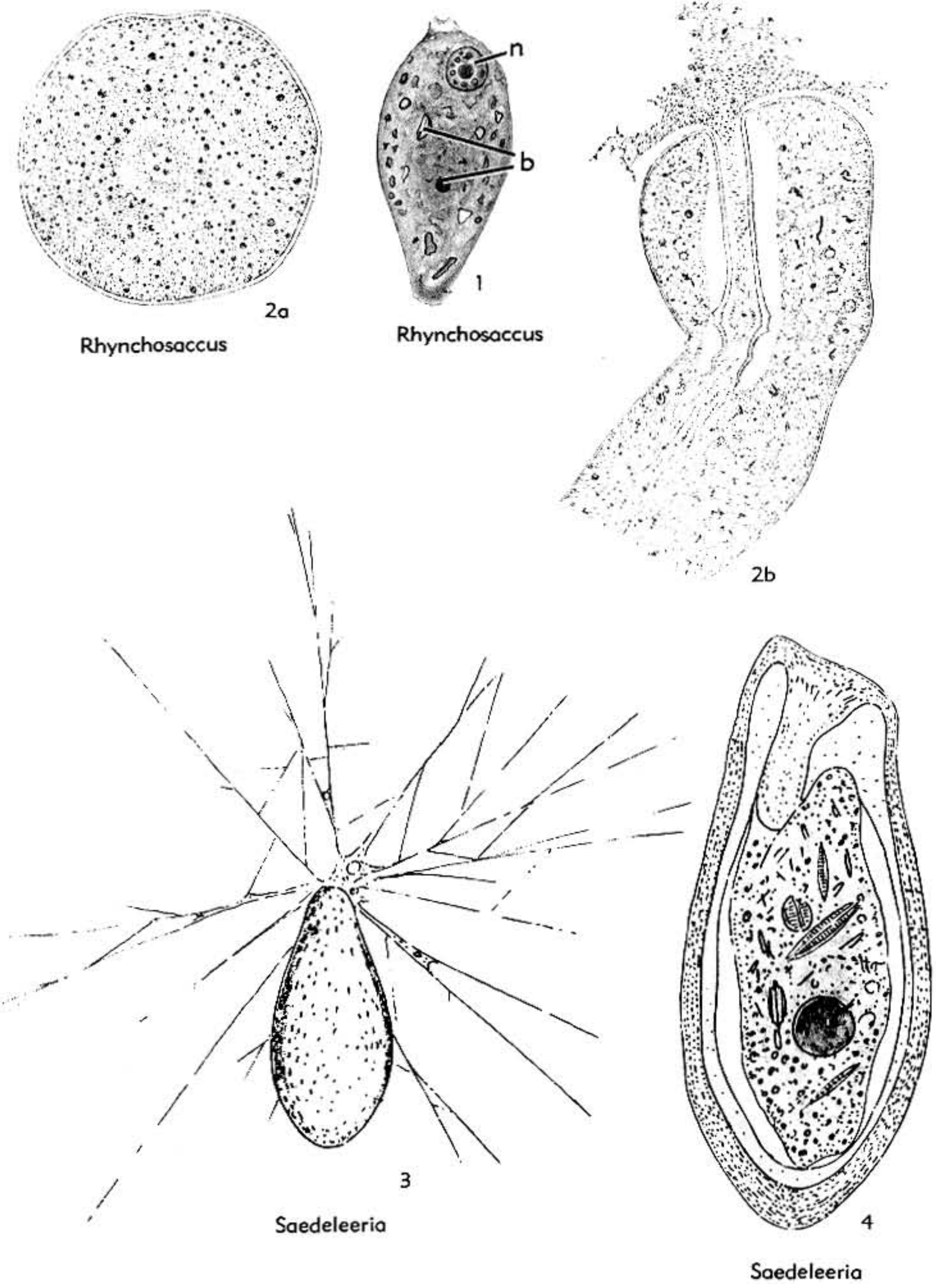
Rhynchogromia RHUMBLER, 1894, *1568a, p. 590 [**R. variabilis;* OD] [=*Arrhynchogromium* RHUMBLER, 1913, *1572b, p. 344 (obj.) *(nom. van.)*]. Test elongate-ovate, 0.28-0.92 mm. in length; wall single-layered, containing numerous elongate or platelike secreted bodies and some foreign matter; living in tests of other foraminifers; aperture at one end of test, second aperture rarely at opposite end; 1 to 3 globular nuclei. [Marine.] *Rec.*, N.Sea-N.Atl.——FIG. 100,*2*. **R. variabilis*, N.Atl.; showing nucleus *(n)*, ectoplasm *(e)*, foreign bodies *(b)* and secreted platelets *(p)*, ×220 (*1568a).

Rhynchosaccus RHUMBLER, 1894, *1568a, p. 595, 600 [**R. immigrans;* OD] [=*Arrhynchosaccum* RHUMBLER, 1913, *1572b, p. 344 (obj.) *(nom. van.)*]. Test ovate to elongate, length, 0.24-0.9 mm., rounded at ends, may be somewhat inflated toward apertural margin; wall thin, elastic, homogeneous, thickened toward aperture and with inverted entosolenian tube; similar apertures may occur at both ends; parasitic in tests of larger foraminifers or may occur in empty tests; nucleus globular. [Marine.] *Rec.*, N.Atl.-N.Sea.——FIG. 101,*1,2*. **R. immigrans*, N.Atl. *(1)*, France *(2)*; *1*, showing nucleus *(n)* and foreign bodies *(b)*, ×64 (*1568a); *2a,b*, transv. and long. secs. of apert. end showing entosolenian tube, ×200 (*1102).

Saedeleeria LOEBLICH & TAPPAN, 1960, *1175, p. 196 [**Gromia gemma* PENARD, 1899, *1434, p. 86; OD]. Test ovate to pyriform, 0.2-0.6 mm. in length, with thick, white, double-layered wall, outer layer with cemented, granular siliceous inclusions and inner, hyaline layer, homogeneous and thickened at aperture which is rounded, terminal, asymmetrical, and inverted; protoplasm yellowish, clear and colorless toward aperture where it extends as pseudopodial trunk; single large spherical nucleus, to 50μ in diam., or, rarely, more than one; pseudopodia long, numerous, anastomosing. [Fresh water.] *Rec.*, Eu. ——FIG. 101,*3,4*. **S. gemma* (PENARD), Switz.

(Lake Leman); *3*, exterior showing pseudopodia, approx. ×100; *4*, sectioned specimen showing 2-layered wall, protoplasmic body, and inverted neck, enlarged (*1434).

Shepheardella SIDDALL, 1880, *1737, p. 131 [**S. taeniformis*; OD] [=*Shepheardia* SIDDALL, 1880, *1737, pl. 15 *(nom. null.)*; *Arshepheardellum* RHUMBLER, 1913, *1572b, p. 343 (obj.) *(nom. van.)*; *Tinogullmia* NYHOLM, 1954, *1376, p. 36 (type, *T. hyalina*)]. Test elongate, 1.0-7.5 mm. in length, tubular, straight to slightly arcuate, tapering at both ends, wall firm, flexible, trans-



Rhynchosaccus

Rhynchosaccus

Saedeleeria

Saedeleeria

FIG. 101. Allogromiidae; *1, 2, Rhynchosaccus; 3, 4, Saedeleeria* (p. C181-C182).

parent, colorless, chitinoid; small aperture at each end; protoplasm yellowish, coarsely granular, with pronounced streaming, accumulating in small lump at each end and thinly coating exterior of test also; pseudopodia extending in outspread network from both apertures, rapid streaming within pseudopodia. [SIDDALL described the central oval body as a nucleus, but NYHOLM stated that the similar oval body in *Tinogullmia* was a vacuole and that the nucleus was visible only in sections.] [Marine.] *Rec.*, Eu.——FIG. 102,*1*. **S. taeniformis*, Eng.; *1a*, side view of slender test and long, branched pseudopodia, ×12; *1b*, aperture, ×170 (*1737).

Thalamophaga RHUMBLER, 1911, *1572a, p. 229 [**T. ramosa;* SD LOEBLICH & TAPPAN, herein] [=*Orbitophage* SCHLUMBERGER, 1903, *1663, p. 276 *(nom. neg.)*; *Orbitophaga* RHUMBLER, 1911, *1572a, p. 230 (type, *O. ramosa*, =*Thalamophaga ramosa* RHUMBLER, 1911, SD, LOEBLICH & TAPPAN, herein, obj.); *Marsupophaga* RHUMBLER, 1911, *1572a, p. 231 (type, *M. ramosa*, =*Thalamophaga ramosa* RHUMBLER, 1911, SD, LOEBLICH & TAPPAN, herein, obj.); *Tubophaga* RHUMBLER, 1911, *1572a, p. 232 (type, *T. ramosa*, =*Thalamophaga ramosa* RHUMBLER, 1911, SD, LOEBLICH & TAPPAN, herein, obj.); *Nummophaga* RHUMBLER, 1911, *1572a, p. 232 (type, *N. ramosa*, =*Thalamophaga ramosa* RHUMBLER, 1911, SD, LOEBLICH & TAPPAN, herein, obj.); *Arthalamophagum* RHUMBLER, 1913, *1572b, p. 440 (obj.)]. Attached forms which burrow in test of other foraminifers and consist of inflated, irregular chambers 2-8μ in diam., connected by stolon-like tubes which may branch and may resorb calcite of occupied test so that very thin chitinoid wall of "parasite" merely lines such burrows. [The names *Orbitophaga, Nummophaga, Marsupophaga,* and *Tubophaga,* used by RHUMBLER to indicate burrowing foraminifers of *Thalamophaga* type found on different shells (e.g., *Orbitolites, Nummulites*), were not accompanied by any named species.] *Rec.*, Atl.——FIG. 97,*6*. **T. ramosa;* enlarged (*1572a).——FIG. 97,*7*. *T. incerta* (RHUMBLER); ×80 (*1572a).

Turriclavula RHUMBLER, 1911, *1572a, p. 85 [**T. interjecta;* OD]. Test small, approx. 0.15 mm. in length; wall membranous or with small inclusions; chambers few, uniserial, rectilinear; aperture terminal, ?slitlike. *Rec.*, Atl.——FIG. 97,*5*. **T. interjecta*, Cape Verde Is.; ×320 (*1572a).

Xenotheka EISENACK, 1938, *693b, p. 239 [**X. klinostoma;* OD]. Test attached, consisting of globular chamber with long tubular neck; wall pseudochitinous; rounded aperture at end of tubular neck. [This genus is similar to *Ammolagena* of the Tolypammininae, but has a pseudochitinous wall. Since the tests were from acid residues, an outer agglutinated layer may have been present but destroyed, and if so, the genus would be a synonym of *Ammolagena*. Lacking evidence of such an agglutinated layer in *Xenotheka* it is here recognized as belonging to the Allogromiidae.] *Sil.*, Eu.——FIG. 97,*8*. **X. klinostoma*, E. Prussia [Poland]; paratype, ×60 (*700).

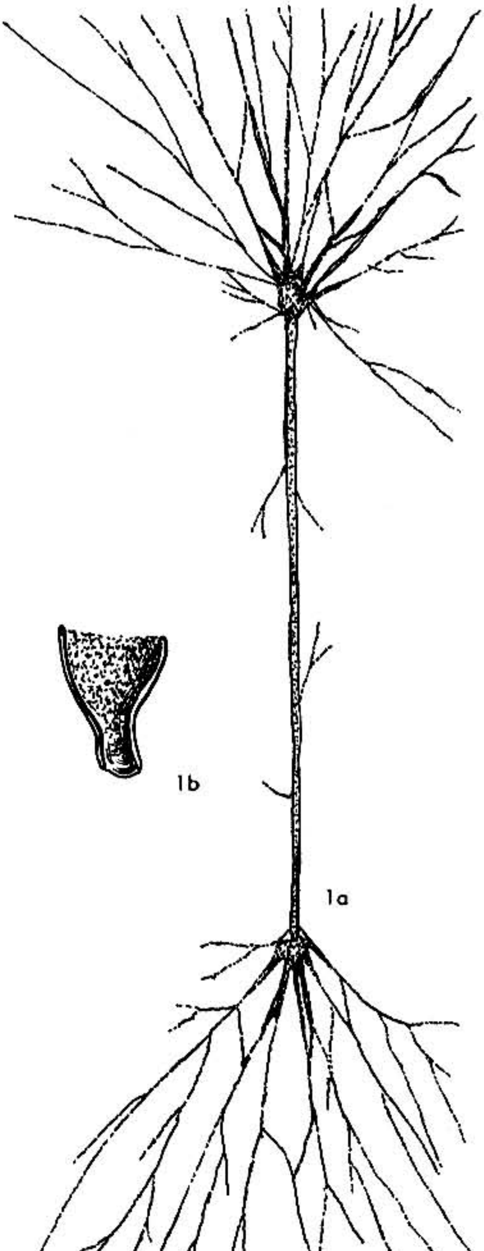


FIG. 102. Allogromiidae; *1*, *Shepheardella* (p. C182-C183).

Suborder TEXTULARIINA Delage and Hérouard, 1896

[*nom. correct.* Loeblich & Tappan, 1961, p. 217 (*pro* suborder Textularidae Delage & Hérouard, 1896, p. 139)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}class, ^{2}subclass, ^{3}order, ^{4}suborder, ^{5}group, ^{6}tribu); dagger(†) indicates *partim*]——[=^{4}Monosomatia† Ehrenberg, 1839, table opp. p. 120; =Foraminifera Monomera† Reuss, 1862, p. 362 (*non* Monomera Latreille, 1825, p. 408); =^{3}Archimonothalamia Kühn, 1926, p. 127; =^{4}Monothalamia De Saedeleer, 1934, p. 7, 52 (*non* Monothalamia Schultze, 1854); =^{4}Monothalamia Avnimelech, 1952, p. 63 (*non* Monothalamia Schultze, 1854, *nec.* Marriott, 1878, *nec* Haeckel, 1894, *nec* De Saedeleer, 1934); =^{4}Uniloculinidea† Sigal in Piveteau, 1952, p. 154; =^{3}Monosomatia† Copeland, 1956, p. 183]——[=^{3}Helicostègues† d'Orbigny in de la Sagra, 1839, p. xxxviii, 27 (*nom. neg.*); =Helicostegia† Reuss, 1860, p. 151, 205; =^{5}Helicoidea Schultze, 1854, p. 53; =^{3}Cyclostègues† d'Orbigny, 1851, p. 192 (*nom. neg.*); =^{3}Énallostègues† d'Orbigny in de la Sagra, 1839, p. xxxix, 125 (*nom. neg.*); =Enallostegia† Reuss, 1860, p. 151, 231; =Turbinoidea† Reuss, 1860, p. 151; =Foraminifera Polymera† Reuss, 1862, p. 365; =^{3}Polystegia† Haeckel, 1894, p. 164; =^{4}Biloculinidea† Sigal in Piveteau, 1952, p. 157; =^{4}Pluriloculinidea† Sigal in Piveteau, 1952, p. 160]——[=^{2}Perforata† Lankester, 1885, p. 847; =^{4}Perforina† Calkins, 1901, p. 108; =^{3}Orthostili (Perforata)† Silvestri, 1937, p. 89]——[=^{5}Imperforata† Claus, 1872, p. 108; =^{2}Imperforata† Lankester, 1885, p. 845; =^{4}Imperforina† Calkins, 1901, p. 106]——[=^{6}Orthocerata† Latreille, 1825, p. 162; =^{3}Physemaria† Haeckel, 1877, p. 221; =^{1}Gastraeada† Haeckel, 1877, p. 221; =Arenacea Carpenter, 1879, p. 375; =^{4}Arenacidae Delage & Hérouard, 1896, p. 127; =Protammida Schubert, 1921, p. 145; =Schizostoma† Schubert, 1921, p. 179; =Metammida Schubert, 1921, p. 146; =^{3}Dentata† Hofker, 1951, p. 14; =^{4}Protoforaminata† Hofker, 1951, p. 42; =^{3}Hellenoidea† Wedekind, 1937, p. 79]——[=^{3}Astrorhizidea Lankester, 1885, p. 846; =^{3}Astrorhizidaceae Hartog in Harmer & Shipley, 1906, p. 59; =^{3}Astrorhizida Calkins, 1909, p. 38; =^{4}Astrorhizidea Jírovec, 1953, p. 334]——[=^{3}Lituolidea Lankester, 1885, p. 847; =^{3}Lituolidea Lister in Lankester, 1903, p. 142; =^{3}Lituolidaceae Hartog in Harmer & Shipley, 1906, p. 59; =^{3}Lituolida Calkins, 1909, p. 39]——[=^{3}Textularidea Lankester, 1885, p. 847; =^{4}Textularidae Delage & Hérouard, 1896, p. 139; =^{3}Textularidea Lister in Lankester, 1903, p. 143; =^{3}Textulariaceae Hartog in Harmer & Shipley, 1906, p. 59; =^{3}Textularida Calkins, 1909, p. 39; =^{3}Textulinida† Calkins, 1926, p. 356; =^{3}Textularidia Kühn, 1926, p. 150; =^{4}Textulariacea Wedekind, 1937, p. 84; =^{4}Textulariidea Jírovec, 1953, p. 335; =^{3}Textulariida Fursenko, 1958, p. 23]——[=^{3}Rotaliaridia† Kühn, 1926, p. 152; =^{3}Nodosalidia† Calkins, 1926, p. 355; =Sektion Neohellenoidea† Wedekind, 1937, p. 72, 84; =^{4}Haplophragmiacea Wedekind, 1937, p. 111; =^{3}Ammodiscida Fursenko, 1958, p. 23; =^{3}Ataxophragmiida Fursenko, 1958, p. 23]

Test composed of agglutinated foreign matter held by various cements. *Cam.-Rec.*

Superfamily AMMODISCACEA Reuss, 1862

[*nom. correct.* Loeblich & Tappan, 1961, p. 275 (*pro* superfamily Ammodiscoidea Chapman, Parr & Collins, 1934, p. 556)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}superfamily, ^{2}tribe, ^{3}family group, ^{4}legio); dagger(†) indicates *partim*]——[=^{2}Astrorhizina Delage & Hérouard, 1896, p. 128; =^{1}Astrorhizidea Glaessner, 1945, p. 88; =Astrorhizidae Eimer & Fickert, 1899, p. 593; =^{1}Astrorhizicae Easton, 1960, p. 65]——[Arenacea Carpenter, 1879, p. 375; =Stichostegia† Eimer & Fickert, 1899, p. 674 (*non* Stichostègues d'Orbigny, 1826), (*nom. nud.*); =Psammatostichostegia Eimer & Fickert, 1899, p. 674 (*nom. nud.*); =Ascoforaminifera Eimer & Fickert, 1899, p. 673 (*nom. nud.*); =Cystoforaminifera (Vesiculata)† Eimer & Fickert, 1899, p. 670 (*nom. nud.*); =Siphonoforaminifera (Tubulata) Eimer & Fickert, 1899, p. 667 (*nom. nud.*); =^{3}Archi-Monothalamidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 85; =^{4}Archithalamia De Saedeleer, 1934, p. 7]——[=^{1}Ammodiscidea Dain in Rauzer-Chernousova & Fursenko, 1959, p. 180]

Test irregular, spheroidal or tubular and straight, branching or enrolled; nonseptate or only irregularly constricted; wall agglutinated, simple or labyrinthic; aperture simple. *Cam.-Rec.*

Family ASTRORHIZIDAE Brady, 1881

[All names of family rank; dagger(†) indicates *partim*]——=Astrorhizidae Brady, 1881, p. 41, 43; =Astrorhizina Lankester, 1885, p. 846; =Astrorhizinae Delage & Hérouard, 1896, p. 129; =Astrorhizida Haeckel, 1894, p. 185)]——[=Arenacea† Bütschli in Bronn, 1880, p. 193 (*nom. nud.*); =Ammodinetta Haeckel, 1894, p. 164 (*nom. nud.*); =Ammoasconidae Eimer & Fickert, 1899, p. 673 (*nom. nud.*); =Serpuleidae Eimer & Fickert, 1899, p. 674 (*nom. nud.*)]——[=Rhabdamminina Lankester, 1885, p. 846; =Rhabdamminidae Rhumbler, 1895, p. 79; =Rhabdamminae Delage & Hérouard, 1896, p. 130; =Arrhabdammidia Rhumbler, 1913, p. 342 (*nom. van.*)]——[=Dendrophryida Haeckel, 1894, p. 185; =Dendrophyridae Eimer & Fickert, 1899, p. 669; =Saccorhizidae Eimer & Fickert, 1899, p. 670; =Rhizamminidae Wiesner, 1931, p. 79; =Botellinidae Loeblich & Tappan, 1961, p. 277]

Test free or attached, nonseptate, tubular or branching, not enrolled; wall simple, with pseudochitinous inner layer and agglutinated outer layer; aperture absent or terminal, rounded. *L.Cam.-Rec.*

Subfamily ASTRORHIZINAE Brady, 1881

[*nom. transl.* Brady, 1884, p. 61 (*ex* Astrorhizidae Brady, 1881, p. 41, 43)]——[All names of subfamily rank]——[=Rhabdammininae Brady, 1884, p. 64; =Arastrorhiznia Rhumbler, 1913, p. 344 (*nom. van.*); =Arrhabdamnia Rhumbler, 1913, p. 350 (*nom. van.*)]

Test free, with simple or branching tubes extending from central chamber; aperture at open ends of tubes. *M.Ord.-Rec.*

Astrorhiza Sandahl, 1858, *1625, p. 301 [**A. limnicola*; OD (M)] [=*Arenistella* Fischer in de Folin & Périer, 1875, *727Aa, p. 52 (type, *A. agglutinans*, =?*Ammodiscus lindahli* Carpenter & Jeffreys, 1870, *279, p. 159; *Astrodiscus* Schulze, 1875, *1697, p. 113 (type, *A. arenaceus, non Astrodiscus* Ludwig, 1866); *Haeckelina* Bessels, 1875, *136, p. 265 (type, *H. gigantea*); *Astrorhiza* Eimer & Fickert, 1899, *692, p. 594 (type, *A. limnicola* Sandahl, 1858, *1625, p. 301, SD Loeblich & Tappan, herein, obj.); *Arastrorhizum* Rhumbler, 1913, *1572b, p. 345 (obj.) (*nom. van.*)]. Test free, flattened, consisting of hollow central disc from which numerous tubular arms radiate; wall agglutinated of poorly cemented mud and sand, with little selectivity shown as to size or type of material used; interior of wall with pseudochitinous lining; apertures at ends of tubular arms. [Differs from *Astrammina* Rhumbler, 1931, in the discoid rather than inflated central chamber and in being completely encircled by radial arms.] *M.Ord.-Rec.*, cosmop.——Fig. 103,*1*. **A. limnicola*, Rec., N. Sea(Norway); ×8 (*2117).

Astrammina Rhumbler in Wiesner, 1931, *2063, p. 77 [**A. rara*; OD (M)] [=*Armorella* Heron-Allen & Earland, 1932, *914d, p. 256 (type, *A. sphaerica*)]. Test free, spherical, consisting of single chamber with few radiating tubular extensions; wall agglutinated, incorporating sand and sponge spicules with much cement; apertures at open ends of tubular extensions. [Differs from *Astrorhiza* in having a globular instead of discoid center and only a few irregularly placed tubular arms.] *Rec.*, Atl.——Fig. 103,*2*. **A. rara*, Antarctic; ×14 (*2063).——Fig. 103,*3,4*. *A. sphaerica* (Heron-Allen & Earland), S.Atl.(S. Georgia Is.); *3*, lectotype, here designated and refigured (*914d, pl. 2, fig. 5), ×48; *4*, coarse-textured paratype refigured (*914d, pl. 2, fig. 10), ×48 (*2117).

Radicula Christiansen, 1958, *338, p. 51 [**R. limosa;* OD]. Test free, large, to 15 mm. in length, with numerous (to 15) very elongate, tubular, irregularly bifurcating and tapering arms, to 0.8 mm. max. diam., but lacking distinct central chamber; wall with pseudochitinous lining and outer very fine-grained agglutinated layer; apertures at open ends of tapering arms. *Rec.*, Eu.——Fig. 104,*1*. **R. limosa*, Dröbak Sound, Oslo Fjord, Norway; holotype, ×8 (*338).

Rhabdammina M. Sars in Carpenter, 1869, *274, p. 61 [**R. abyssorum;* OD] [=*Rhabdammina* M. Sars, 1869, *1629, p. 248 *(nom. nud.)*; *Rhabdammina* M. Sars in Carpenter, 1868, *273, p. 171, 172 *(nom. nud.)*; *Rhabdammina* Eimer & Fickert, 1899, *692, p. 595 (type, *R. linearis* Brady, 1879, *196a, p. 37, SD Loeblich & Tappan, herein); *Arrhabdammum* Rhumbler, 1913,

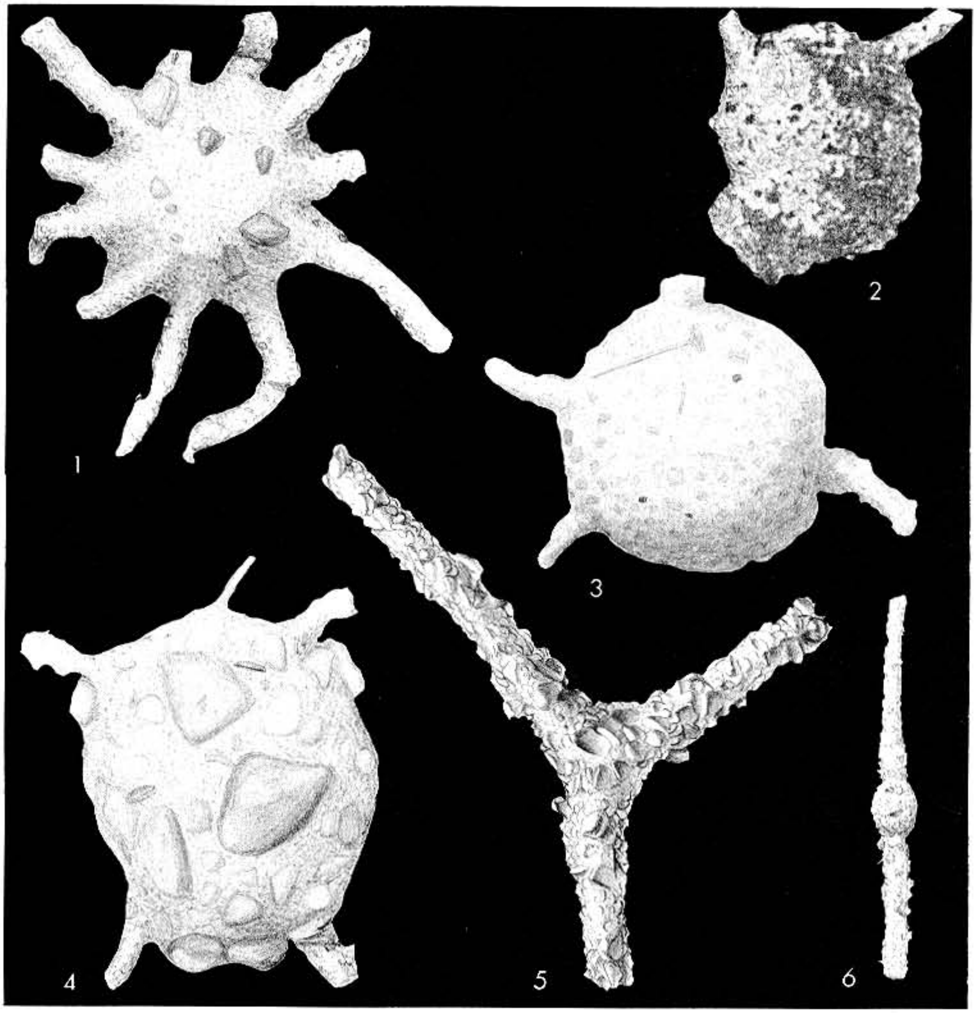


Fig. 103. Astrorhizidae (Astrorhizinae; *1, Astrorhiza; 2-4, Astrammina; 5,6, Rhabdammina*) (p. *C*184-*C*186).

*1572b, p. 351 (obj.) *(nom. van.)*; *Oculosiphon* Avnimelech, 1952, *63, p. 65 (type, *Rhabdammina linearis* Brady, 1879)]. Test free, large, to 20 mm. in length, with elongate tubular arms radiating from relatively small central chamber; wall agglutinated; apertures at open ends of tubular arms. *U.Ord.-Rec.*, cosmop.——Fig. 103,*5*. **R. abyssorum*, Rec., N.Atl., ×10 (*2117).——Fig. 103,*6*. *R. linearis* Brady, Rec., N.Atl., ×11 (*2117).

Vanhoeffenella Rhumbler, 1905, *1570, p. 105 [**V. gaussi;* OD] [=*Arvanhoeffenum* Rhumbler, 1913, *1572b, p. 345 (obj.) *(nom. van.)*]. Test free, large, 0.4-2.6 mm. in length, discoidal to fusiform, with angular framework consisting of hollow agglutinated tube, with opposite pseudochitinous, nonagglutinated sides; apertures at ends of short tubular extensions at angles of test. *Rec.*, Antarctic-Ind.O.-Norway. —— Fig. 104,*2*,*3*. **V. gaussi*, Antarctic *(2)*, Norway, Oslo Fjord *(3)*; *2a,b*, typical discoidal form showing clear chitinoid sides and agglutinated framework, ×40 (*1570); *3a,b*, side and edge views of elongate form, pseudopodia protruding from apertures, ×40 (*338).

Subfamily RHIZAMMININAE Rhumbler, 1895

[Rhizammininae Rhumbler, 1895, p. 82]——[All names of subfamily rank]——[=Arrhizamnia Rhumbler, 1913, p. 350 *(nom. van.)*; =Psammosiphonellinae Avnimelech, 1952, p. 64; =Argillotubinae Avnimelech, 1952, p. 64; =Micatubinae Avnimelech, 1952, p. 65; =Bathysiphoninae Avnimelech, 1952, p. 66; =Testulosiphoninae Avnimelech, 1952, p. 66]

Test tubular, both ends open. *L.Cam.-Rec.*

Rhizammina Brady, 1879, *196a, p. 39 [**R. algaeformis*; OD (M)] [=*Rhizammina* Eimer & Fickert, 1899, *692, p. 595 (type, *R. algaeformis* Brady, 1879, SD Loeblich & Tappan, herein, obj.); *Arrhizammum* Rhumbler, 1913, *1572b, p. 350 (obj.) *(nom. van.)*; *Testulorhiza* Avnimelech, 1952, *63, p. 66 (type, *Rhizammina globigerinifera* Hofker, 1930, *928b, p. 117); *Testulosiphon* Avnimelech, 1952, *63, p. 66 (type, *Rhizammina indivisa* Brady, 1884, *200, p. 277)]. Test simple or branching tube; wall thin, with finely arenaceous groundmass and irregular covering of larger fragments, which may consist of larger sand grains, radiolarians, *Globigerina* shells, and other foreign matter (e.g., *Challenger* locs. 146, 299); apertures at open ends of tubular branches. *Rec.*, cosmop.——Fig. 105,*2*. **R. algaeformis*, Ind.O.; ×18 (*2117).——Fig. 105,*3*. *R. indivisa* Brady, N.E.Atl.O.; ×7.5 (*2117).

[The type of wall is distinctly affected by type of substratum, varying from an arenaceous wall with some radiolarian tests, to a wholly calcareous covering of tiny specimens of *Globigerina*. The genera *Testulorhiza* and *Testulosiphon* were introduced for forms with wall composed of tests of other foraminifers agglutinated on a chitinoid base. Since the type-species of *Rhizammina* commonly contains large quantities of tests of *Globigerina* (as in the specimen figured), the mentioned forms are regarded as congeneric.]

Bathysiphon M. Sars in G. O. Sars, 1872, *1630, p. 251 [**B. filiformis;* OD] [=*Rhabdamminella* de Folin, 1881, *724, p. 140 *(nom. nud.)*; *Rhabdamminella* de Folin, 1887, *726a, p. 115 (type, *R. prismaeginosa*); *Arbathysiphum* Rhumbler, 1913, *1572b, p. 352 *(nom. van.)*; *Hippocrepinella* Heron-Allen & Earland, 1932, *914d, p. 254 (type, *H. hirudinea*); *Arenosiphon* Grubbs, 1939, *832, p. 544 (type, *A. gigantea*); *Psammosiphonella* Avnimelech, 1952, *63, p. 64 (type, *Bathysiphon arenacea* Cushman, 1927, *435, p. 129); *Micatuba* Avnimelech, 1952, *63, p. 65 (type, *Bathysiphon flexilis* Höglund, 1947, *924, p. 42); *Argillotuba* Avnimelech, 1952, *63, p. 64 (type, *Astrorhiza vermiformis* Goës, 1896, *805, p. 20]. Test free, large, to 50 mm. in length, elongate, narrow, more or less flexible tube, which may have annular constrictions; wall agglutinated, commonly of siliceous sponge spicules and fine sand or other mineral matter in calcareous cement; aperture at one of open ends; protoplasm multinucleate, protoplasmic movement very sluggish, pseudopodia protruding only from one end of test where growth occurs, opposite end may be secondarily closed by secreted disc and contain intensely black matter consisting of waste rejected by protoplasm and packed into aboral end of test, additional disc secreted periodically to seal off such debris, filled sections of test eventually becoming detached (*1107). *L.Cam.-Rec.*, cosmop. ——Fig. 105,*4*. **B. filiformis*, Rec., Pac.O., ×8 (*2117).——Fig. 105,*5*. *B. gigantea* (Grubbs), Sil. (Niagaran), USA(Ill.); ×16 (*2117).——Fig. 105,*6*. *B. arenacea* Cushman, Rec., Pac.O.; holotype, refigured, ×39 (*2117).——Fig. 105,*7*. *B. flexilis* Höglund, Rec., N.Sea; long. sec. showing imbricated layers of ?mica grains in fine-grained groundmass, ×880 (*924).——Fig. 105,*8-10*. *B. hirudinea* (Heron-Allen & Earland), Rec., S. Atl.(S.Georgia Is.); *8*, lectotype, here designated and figured, one of original syntypes but not figured previously (BMNH-ZF 3300); *9*, top view of paratype, also figured by Heron-Allen & Earland (*914d, pl. 1, fig. 10) (BMNH-ZF 3300); *10*, paratype, long. sec. redrawn, specimen figured (*914d, pl. 1, fig. 9) (BMNH-ZF 3301); all ×41 (*2117).

[*Bathysiphon* differs from *Rhizammina* in having a regular or slightly tapered, nonbranching tubular test. *Hippocrepinella* was defined as having slightly constricted apertures and a smoothly finished, transversely wrinkled wall. None of these characters serve to separate it from *Bathysiphon*. Furthermore, sectioned specimens of *Hippocrepinella* described by Heron-Allen & Earland (*914d, p. 258) showed the cavity "more or less completely filled with an ingested mass of foodstuffs, principally diatoms, and it depends upon the compactness of this mass whether the test preserves its outline after death, or suffers distortion and compression." This seems also to indicate congeneric status with *Bathysiphon*, since these filled sections were probably discarded waste-filled sections of the test, similar to those described in the type-species of *Bathysiphon*. The "apertural constrictions" may be due to contraction of the semiflexible test when dried.]

Marsipella Norman, 1878, *1363, p. 281 [**M. elongata*; OD (M)] [=*Armarsipellum* Rhumbler, 1913, *1572b, p. 351 (obj.) *(nom. van.)*]. Test free, consisting of single undivided tubular, cylindrical, or elongate-fusiform chamber, which may be slightly twisted; wall of agglutinated sand, sponge spicules, or tests of other foraminifers; apertures at open ends of tube. *U.Ord.-Rec.*, cosmop.——FIG. 105,*1*. **M. elongata*, Rec., N.Atl., ×14 (*2117).

Subfamily HIPPOCREPININAE Rhumbler, 1895

[Hippocrepininae RHUMBLER, 1895 (*1568A, p. 83)]——[All names are of subfamily rank]——[=Hyperammininae CUSHMAN, 1910, p. 59; =Arhippocrepnia RHUMBLER, 1913, p. 352 (*nom. van.*)]

Test free, globular proloculus continuing

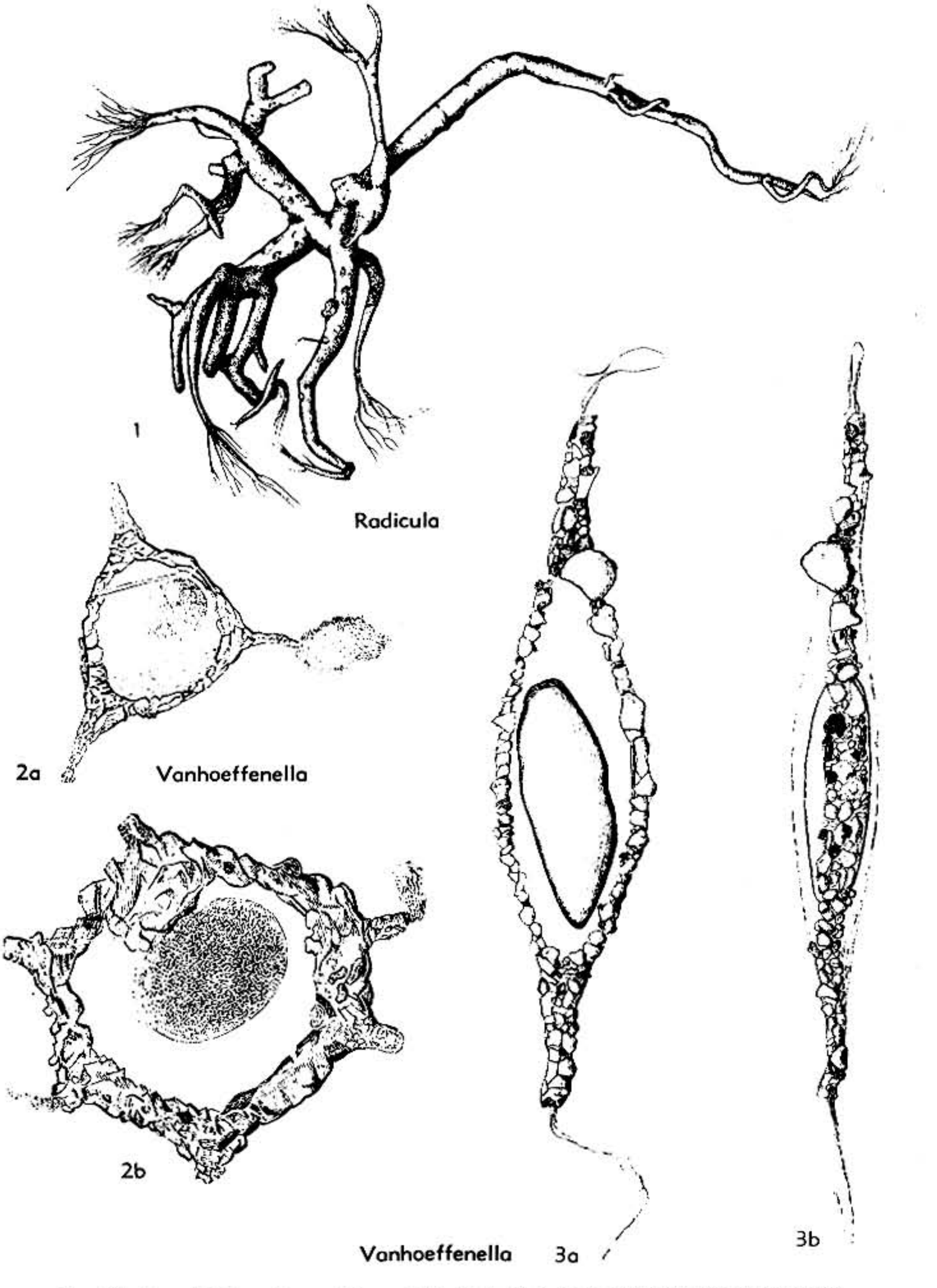


FIG. 104. Astrorhizidae (Astrorhizinae; *1*, *Radicula; 2,3, Vanhoeffenella*) (p. *C*185-*C*186).

into nonseptate tube; aperture at open end of tube. *L.Ord.-Rec.*

Hippocrepina Parker in G. M. Dawson, 1870, *565, p. 177 [*H. indivisa; OD] [=*Arhippocrepum* Rhumbler, 1913, *1572b, p. 352 (obj.) (*nom. van.*); *Hyperamminella* Cushman & Wa-

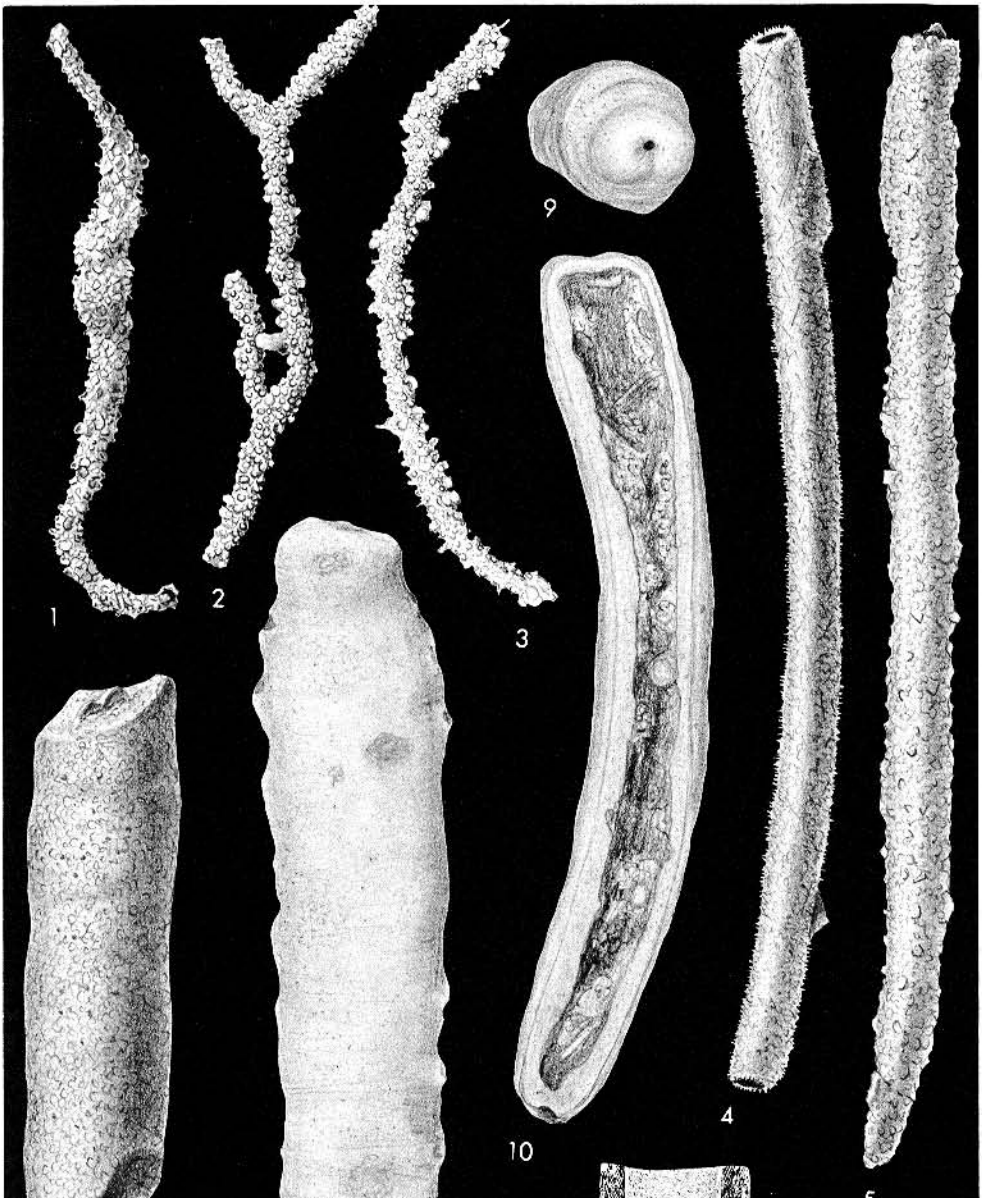


Fig. 105. Astrorhizidae (Rhizammininae; *1, Marsipella; 2,3, Rhizammina; 4-10, Bathysiphon*) (p. *C*186-*C*187).

TERS, 1928, *535, p. 36 (type, *H. elegans*) (*non* DE FOLIN, 1881, 1887); *Hyperamminoides* CUSHMAN & WATERS, 1928, *537, p. 112 (*nom. subst. pro Hyperamminella* CUSHMAN & WATERS, 1928, *non* DE FOLIN)]. Test free, elongate, tapering, may have irregularly spaced transverse constric-

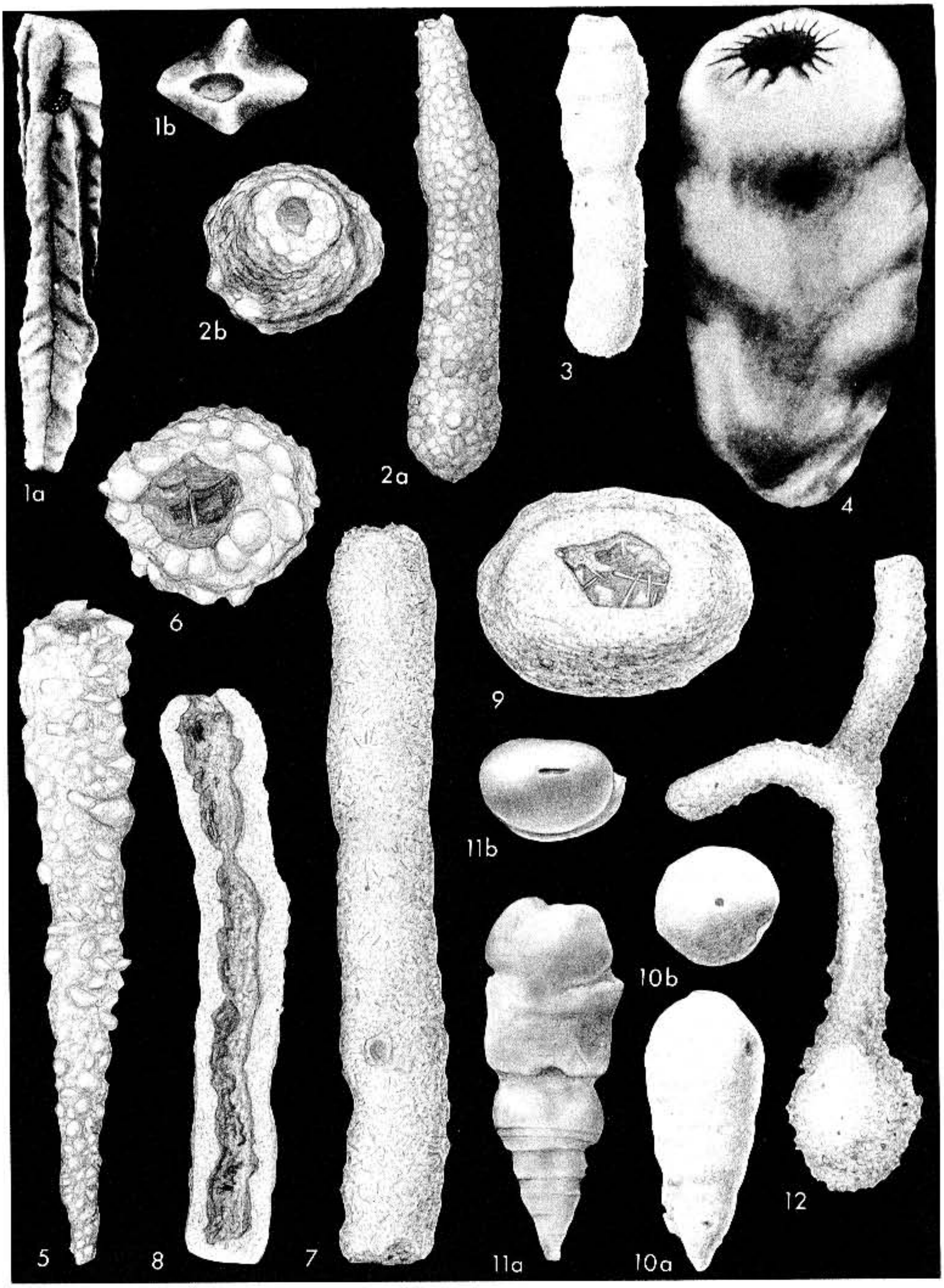


FIG. 106. Astrorhizidae (Hippocrepininae; *1, Giraliarella; 2, 3, Hyperammina; 4, Pseudohyperammina; 5, 6, Jaculella; 7-9, Protobotellina; 10, 11, Hippocrepina; 12, Saccorhiza*) (p. *C*188-*C*190).

tions but no internal septa, contracted and broadly rounded at apertural end; wall finely agglutinated, may have siliceous cement; aperture small, terminal, rounded, may have slightly raised margin. *U.Dev.-Rec.*, Eu.-N.Am.——Fig. 106,*10*. **H. indivisa,* Rec., N.Alaska(off Pt.Barrow); *10a,b,* side and top views, ×44 (*2117).——Fig. 106, *11*. *H. elegans* (Cushman & Waters), U.Penn. (Cisco), USA(Tex.); *11a,b,* side and top views of holotype (redrawn), ×32 (*2117).

[Late Paleozoic species have been referred to *Hyperamminoides* but without morphologic basis for separation from *Hippocrepina*. The "elongate" aperture reported in some fossil species is due to compression of the tests in preservation. Conklin (*378, p. 168) regarded *Hyperamminoides* as a synonym of *Hyperammina*, but the latter has a bulbous base and narrowed later portion, whereas typical *Hyperamminoides* has a finely arenaceous flaring test characteristic of the type-species of *Hippocrepina*.]

Giraliarella Crespin, 1958, *394, p. 56 [**G. angulata;* OD]. Similar to *Hippocrepina* but with triangular to quadrate section; wall finely agglutinated with siliceous cement. *Perm.*, W.Australia.——Fig. 106,*1*. **G. angulata; 1a,b,* side and top views of holotype, ×40, ×104 (*394).

Hyperammina Brady, 1878, *195, p. 433 [**H. elongata*; OD (M)] [=*Rhabdopleura* G. M. Dawson, 1870, *565, p. 175 (type, *R. abyssorum*) (*non* Allman, 1869; *nec* deKoninck, 1881); *Hyperammina* Eimer & Fickert, 1899, *692, p. 603 (type, *H. friabilis* Brady, 1884, *200, p. 258, SD Loeblich & Tappan, herein); *Bactrammina* Eimer & Fickert, 1899, *692, p. 673 (obj.); *Arhyperammum* Rhumbler, 1913, *1572b, p. 351 (obj.) (*nom. van.*)]. Test free, elongate, cylindrical, consisting of bulbous proloculus and long tubular second chamber generally somewhat smaller than proloculus in diameter; wall agglutinated, commonly of angular quartz fragments with small amount of calcareous or ferruginous cement; aperture terminal, rounded, constricted. [*Hyperammina* differs from *Hippocrepina* in being more coarsely agglutinated and in having an inflated base and narrowed later portion.] *L.Ord.-Rec.*, cosmop.——Fig. 106,*2*. **H. elongata,* Rec., Cape Frazer (N.Polar Exped. 1875-76); *2a,b,* side and top views of lectotype (here designated and redrawn, BMNH-ZF 3604), ×28, ×48 (*2117).——Fig. 106,*3*. *H. abyssorum* (G. M. Dawson), Rec., Canada (Lab.); ×7 (*2117).

Jaculella Brady, 1879, *196a, p. 35 [**J. acuta*; OD (M)] [=*Arjaculum* Rhumbler, 1913, *1572b, p. 352 (obj.) (*nom. van.*)]. Test free, elongate, conical, nonseptate tube; wall coarsely arenaceous, thick, firmly cemented, coarsely finished both on exterior and interior; rounded aperture at larger, open end of tube. [The genus has been stated to have a chitinoid interior lining (*486, p. 85), but this is not evident in Brady's type specimens. It has also been stated to be smoothly finished inside (*762, p. 75), but specimens of the type-species are equally roughened inside and out. *Jaculella* differs from *Protobotellina* in being conical rather than cylindrical.] *L.Jur.-Rec.*, cosmop.——Fig. 106,*5,6*. **J. acuta;* Rec., S.Atl.(off S.Am.); *5,* lectotype (here designated and redrawn from Brady, *196a, pl. 3, fig. 12, BMNH-ZF 1602), ×10; *6,* apert. view of paratype (Brady, *200, pl. 22, fig. 18, BMNH-ZF 1603), ×22 (*2117).

Protobotellina Heron-Allen & Earland, 1929, *914b, p. 326 [**P. cylindrica;* OD]. Test free, tubular, irregularly cylindrical, nonseptate, open only at one end; wall agglutinated, nonlabyrinthic, composed of broken sponge spicules and fine sand with little visible cement, exterior smoothly finished, inner surface rough, with numerous irregular cavities and projecting sponge spicules; aperture terminal, irregular in shape, with constricting grains and sponge spicules partially closing open end of tube. *Rec.*, Antarctic.——Fig. 106,*7-9*. **P. cylindrica,* S.Atl.; *7,* side view of lectotype (here designated and redrawn), ×5; *8,* sectioned paratype (redrawn, *914b, pl. 2, figs. 10, 11), ×5; *9,* top view of paratype (redrawn, *914b, pl. 2, fig. 12) ×10 (*2117).

[*Protobotellina* differs from *Botellina* in having a nonlabyrinthic interior, in being cylindrical, and in lacking an inflated bulbous base. It differs from *Jaculella* in its cylindrical instead of conical, flaring form. It is very like *Bathysiphon* except for being closed at one end. Sectioned specimens contained a black "protoplasm" reminiscent of the waste-filled discarded sections of *Bathysiphon,* but the closed base of agglutinated material and single aperture serve to separate *Protobotellina* from *Bathysiphon*.]

Pseudohyperammina Crespin, 1958, *394, p. 55 [**P. radiostoma*; OD]. Test similar to *Hippocrepina* but with less rapid flaring and subovate outline; wall thin, finely agglutinated; aperture ovate, with thickened border and radially arranged elongate grooves extending outward from apertural opening. *Perm.*, W.Australia.——Fig. 106,*4*. **P. radiostoma;* ×45 (*394).

Saccorhiza Eimer & Fickert, 1899, *692, p. 670 [**Hyperammina ramosa* Brady, 1879, *196a, p. 33; OD (M)]. Test free, with subglobular proloculus and long dichotomously branching tubular undivided chamber of nearly uniform diameter throughout; wall thick, agglutinated, consisting of medium to fine sand grains, commonly with abundant sponge spicules fastened almost at right angles to outer surface, giving very spinose, bristling appearance; apertures formed by open ends of tubes. [*Saccorhiza* differs from *Hyperammina* in its branching character.]. *L.Miss.-Rec.*, Atl.-Pac.——Fig. 106,*12*. **S. ramosa* (Brady), Rec., N.Pac.; lectotype (here designated and redrawn, BMNH-ZF 3602), ×22 (*2117).

Subfamily BOTELLININAE
Chapman & Parr, 1936

[Botellininae Chapman & Parr, 1936, p. 146]

Globular proloculus with nonlabyrinthic interior followed by elongate, tubular, undivided chamber with labyrinthic interior; wall agglutinated, with inner pseudochitinous lining. *Rec.*

Botellina Carpenter, Jeffreys & Thomson, 1870, *280, p. 443 [**B. labyrinthica* Brady, 1881; SD (SM) Brady, 1881, *196c, p. 48] [=*Arbotellum* Rhumbler, 1913, *1572b, p. 351 (obj.) (*nom. van.*)]. Test elongate, cylindrical, with bulbous proloculus and undivided tubular later portion nearly filled with arenaceous, labyrinthic mate-

Fig. 107. Astrorhizidae (Botellininae; *1-3, Botellina*); Schizamminidae; *4, 5, Jullienella; 6-10, Schizammina* (p. *C*190-*C*194).

rial; may exhibit irregular growth constrictions; wall agglutinated, composed of sand grains and sponge spicules with comparatively little cement, rather smoothly finished inside of initial bulbous portion, but very rough, labyrinthic, and thick in tubular portion; apertures consisting of very slightly constricted open end of tube. *Rec.*, Atl.-Pac.-Antarctic.——Fig. 107,*1-3*. **B. labyrinthica*, N.Atl.(Faröe Channel); *1-3*, ext. view, long. sec., apert. view (all syntypes), ×8 (*2117).

Subfamily DENDROPHRYINAE
Haeckel, 1894

[*nom. transl.* Cushman, 1927, p. 14 (*ex* Dendrophryida Haeckel, 1894, p. 185)]

Test attached, commonly branching or occurring in clusters. *Pleist.-Rec.*

Dendrophrya T. S. Wright, 1861, *2081, p. 122 [**D. erecta;* SD Cushman, 1918, *411a, p. 85] [=*Psammatodendron* Norman in Brady, 1881, *197, p. 98 (type, *P. arborescens*); =*Ardendrophyrum* Rhumbler, 1913, *1572b, p. 345 (obj.) (*nom. van.*); *Dendrophyra* Cushman, 1917, *407, p. 652 (*nom. null.*)]. Test attached by proloculus, later elongate, nonseptate, branching tubular portion growing erect and spreading; wall with pseudochitinous lining and outer agglutinated layer, may have ferruginous cement; apertures at open ends of tubular branches. [*Psammatodendron* has been recognized for some delicately branched species, but the differences are of only specific nature.] *Pleist.-Rec.*, Atl.——Fig. 108,*1*. **D. erecta*, Rec., N.Atl.(off Scot.); ×18 (*2117).——Fig. 108,*2*. *D. arborescens* (Norman), Rec., N.Atl. (off Scot.); ×13 (*2117).

Dendronina Heron-Allen & Earland, 1922, *911, p. 78 [**D. arborescens;* SD Cushman, 1928, *439, p. 87]. Test commonly attached, with early expanded basal chamber or pad containing ramifying passages which converge to central cavity, or may grow free, with bulbous early portion, later development consisting of elongate tube which may branch dichotomously, or more than one such nonseptate tube may arise from basal expansion; wall fragile, consisting of fine sand grains and sponge spicules aligned in direction of test growth, upon pseudochitinous base; apertures are simple terminal openings at slightly constricted ends of branches, with spicules projecting somewhat beyond remainder of wall. [The "crown" of projecting spicules is somewhat less prominent in actual specimens than in restoration figured by Heron-Allen & Earland (*911, pl. 2, fig. 12), which has been recopied as representing a complete specimen. The actual types show fragmental material such as that here illustrated.] *Rec.*, S.Pac.——Fig. 108,*3,4*. **D. arborescens*, Rec., off N.Z.; *3*, lectotype (here designated and redrawn, BMNH-ZF 3608), showing basal expansion; *4*, paratype (BMNH-ZF 3609), showing branching, both ×22 (*2117).

Halyphysema Bowerbank, 1862, *183, p. 1105 [**H. tumanowiczii*; OD (M)] [=*Gastrophysema* Haeckel, 1877, *849, p. 4, 8, 24 (type, *Squamulina scopula* Carter, 1877, *290, p. 311) (*nom. subst. pro Halyphysema tumanowiczii* Bowerbank, 1862) SD Loeblich & Tappan, herein (obj.); *Haliphysema* Haeckel, 1877, *849, p. 1 (*nom. van.*); *Arhaliphysemum* Rhumbler, 1913, *1572b, p. 352 (*nom. van.*)]. Test attached, with internally subdivided, spreading basal expansion and later erect conical or clavate chamber, which is tubular and even bifurcating in some species; wall agglutinated, that of basal expansion fine-grained and may include fragments of sponge spicules, erect portion with sand, other foraminiferal tests, or numerous elongate sponge spicules oriented in direction of test growth; aperture terminal and rounded, may be obscured by cluster of spicules; pseudopodial network with pronounced graunlar streaming, many nuclei. *Rec.*, Atl.-Carib.-Pac.——Fig. 108,*6,7*. **H. tumanowiczii*, Eng.(Sussex); *6*, lectotype (BMNH-ZF 3652), ×57; *7*, several paratypes showing attachment, ×17 (*1153).——Fig. 109, living specimen, showing pseudopodial network, ×70 (*1034).

Normanina Cushman, 1928, *436, p. 7 [**Haliphysema confertum* Norman, 1878, *1363, p. 279; OD]. Test free, consisting of central mass from which tubular portions radiate, individual tubes expanding distally into globular or conical masses; wall of tubular portion flexible, agglutinated, composed of medium-sized grains; apertures not observed in type-species. *Rec.*, Atl.——Fig. 108,*8*. **N. conferta* (Norman), off Greenl.; *8a*, holotype (redrawn, BMNH-ZF 3657), entire specimen, ×48; *8b*, single individual, ×105 (*2117).

Nubeculariella Averintsev, 1911, *62, p. 8 [**N. birulai;* OD]. Pseudochitinous tube with agglutinated coating, some grains so large as to suggest attachment to substratum; rounded aperture at somewhat flaring open end of tube. *Rec.*, Arctic O.——Fig. 108,*5*. **N. birulai*; approx. ×28 (*62)

Syringammina Brady, 1883, *199, p. 159 [**S. fragilissima*; OD] [=*Arsyringammum* Rhumbler, 1913, *1572b, p. 345 (obj.) (*nom. van.*)]. Test free or attached, consisting of bulbous base with many branching or anastomosing tubes forming rounded mass; wall finely agglutinated; apertures at ends of tubular portions. *Rec.*, N.Atl.(Faroe Channel).——Fig. 108,*9*. **S. fragilissima*; ×3.3 (*2117).

Family SCHIZAMMINIDAE
Nørvang, 1961

[Schizamminidae Nørvang, 1961, p. 171]

Test free, nonseptate, tubular, and dichotomously branching or spheroidal, may be flattened, interior cavity not subdivided;

wall agglutinated with organic cement, nonporous but with interstitial canals filled by protoplasm, no inner lining, but outer covering of tectine present; apertures consisting of simple rounded openings at ends of branches. *?Trias., Rec.*

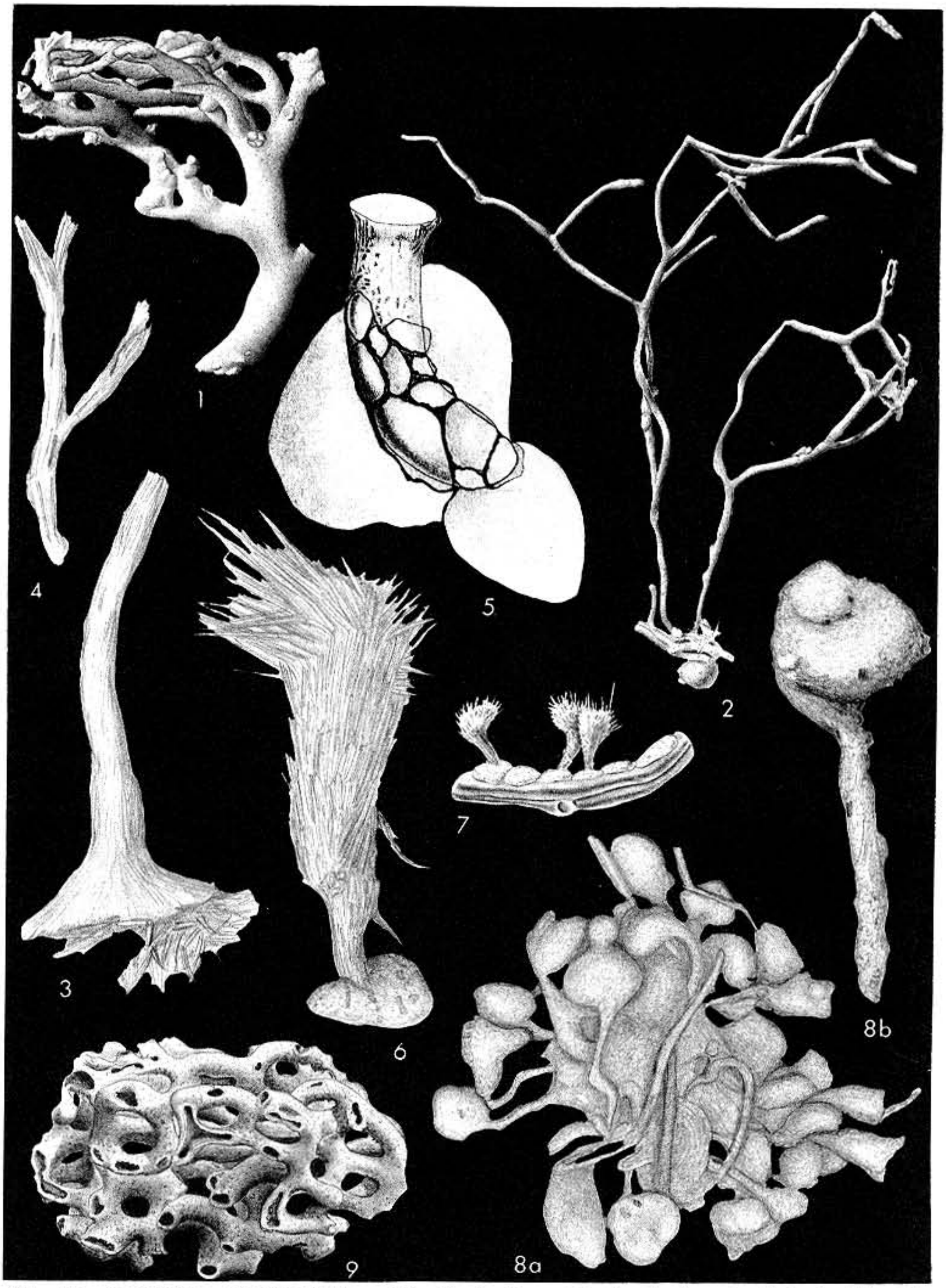


FIG. 108. Astrorhizidae (Dendrophryinae; *1,2, Dendrophrya; 3,4, Dendronina; 5, Nubeculariella; 6,7, Halyphysema; 8, Normanina; 9, Syringammina*) (p. C192).

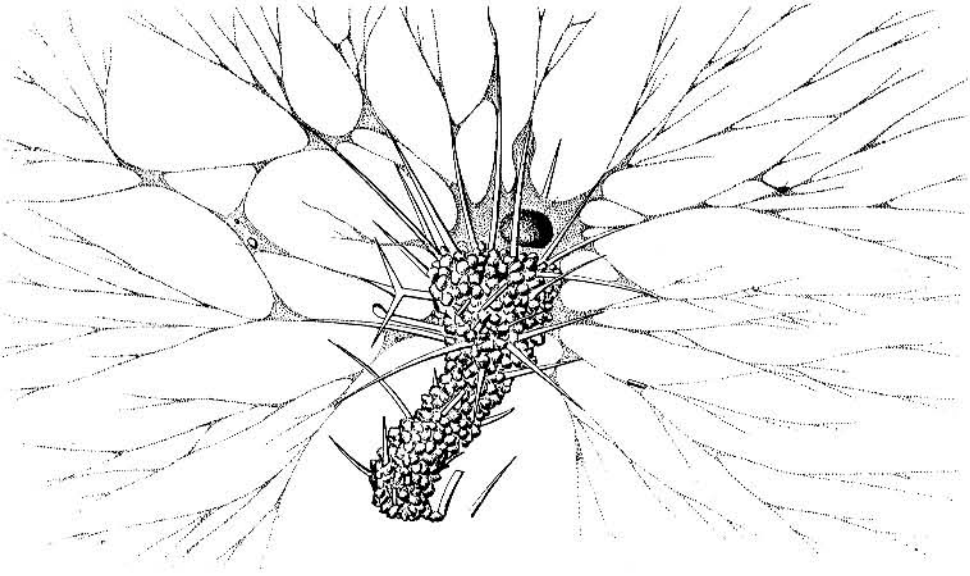


FIG. 109. Astrorhizidae (Dendrophryinae; *Halyphysema*) (p. C192).

Schizammina HERON-ALLEN & EARLAND, 1929, *914a, p. 103 [**S. labyrinthica*; SD CUSHMAN, 1930, *447, p. 73] [=*?Psammosiphon* RHUMBLER, 1911, *1572a, p. 43 (type, *Nodosinella wedmoriensis* CHAPMAN, 1895, *312, p. 320) (*non Psammosiphon* VINE, 1882); *Arpsammosiphoum* RHUMBLER, 1913, *1572b, p. 440 (*nom. van.*)]. Test free, consisting of nonseptate tube, dichotomously branching in single plane; wall finely agglutinated, exterior smoothly finished, interior labyrinthic but chamber cavity rather smoothly finished between pore openings, exterior with few transverse wrinkles; apertures at open ends of tubular chamber. [Differs from *Rhizammina* in possessing a labyrinthic wall.] *?Trias. (Rhaet.)*, Eng.; *Rec.*, Atl.——FIG. 107,*6,7*. **S. labyrinthica*, Rec., off French Equat. Afr. *(6)*, off Gabon *(7)*; *6*, lectotype (here designated and redrawn, BMNH-ZF 3653), ×5.2 (*2117); *7*, sectioned paratype, ×10 (*2117).——FIG. 107,*8-10*. *S. wedmoriensis* (CHAPMAN), Trias. (Rhaet.), Eng.; *8,9*, ext. views, ×5; *10*, long. sec., ×5 (*1572a).

Julliennella SCHLUMBERGER, 1889, *1653, p. 213 [**J. foetida*; OD (M)]. Test large, flabelliform, or may have large fan-shaped portions extending in 2 directions from central attachment, margin produced into numerous tubules; wall firm, finely agglutinated, with much ferruginous cement, insoluble in hydrochloric acid, labyrinthic, surface transversely wrinkled, interior irregularly subdivided by series of intermittent radiating ridges which are not reflected on exterior; interior surface with many large pores which constrict within wall to connect with smaller openings at outer surface; apertures numerous, comprising small rounded openings at ends of tubular extensions along periphery; reddish-brown. *Rec.*, Afr.(Liberia).——FIG. 107,*4,5*. **J. foetida*, topotypes; *4*, ext., showing flabelliform test, growth ridges, and apertures on tubular extensions, ×2; *5a,b*, fragments of surface and int., with discontinuous radiating ridges and large pores, ×10 (*1166).

Family SACCAMMINIDAE
Brady, 1884

[*nom. correct.* EIMER & FICKERT, 1899, p. 671 (*pro* family Saccamminina LANKESTER, 1885, p. 846, *nom. transl. ex* subfamily Saccammininae BRADY, 1884, p. 64)]——[All names of family rank; dagger(†) indicates *partim*]——[=Arenacea† BÜTSCHLI in BRONN, 1880, p. 193 *(nom. nud.)*; =Arenácidos GADEA BUISÁN, 1947, p. 17 *(nom. neg.)*; =Protocystidae EIMER & FICKERT, 1899, p. 665 *(nom. nud.)*; =Kyphamminidae EIMER & FICKERT, 1899, p. 672 *(nom. nud.)*; =Ammoasconidae† EIMER & FICKERT, 1899, p. 673 *(nom. nud.)*]——[=Pilulinina LANKESTER, 1885, p. 846; =Pilulinida HAECKEL, 1894, p. 190; =Pilulinidae LISTER in LANKESTER, 1903, p. 141; =Saccamminae DELAGE & HÉROUARD, 1896, p. 130; =Psammosphaerida HAECKEL, 1894, p. 185; =Psammosphaeridae EIMER & FICKERT, 1899, p. 670; =Stegnamminidae MOREMAN, 1930, p. 48]

Test free or attached, subglobular, or in groups; aperture absent, single, or multiple. *Ord.-Rec.*

Subfamily PSAMMOSPHAERINAE
Haeckel, 1894

[*nom. transl.* CUSHMAN, 1927, p. 11 (*ex* family Psammosphaerida HAECKEL, 1894, p. 185)]——[All names of subfamily rank]——[=Stegnammininae MOREMAN, 1930, p. 48; =Thekammininae DUNN, 1942, p. 326]

Test free, globular or with several loosely joined chambers, no aperture. *M.Ord.-Rec.*

Psammosphaera SCHULZE, 1875, *1697, p. 113 [**P. fusca*; OD] [=*Arpsammosphaerum* RHUMBLER, 1913, *1572b, p. 347 (obj.) *(nom. van.)*; *Psammella* RHUMBLER, 1935, *1574, p. 167 (type, *P. frankei*) (*non* LENDENFELD, 1887, *nom. nud.*); *Pilalla* RHUMBLER, 1935, *1574, p. 150 (type, *P. exigua*)]. Test free, single chamber, commonly globular; wall with thin pseudochitinous inner layer and outer, firmly cemented agglutinated layer; aperture indefinite. [Separate generic names have been proposed for forms with varying proportions of pseudochitin and sand and with varying grain size in the agglutinated wall. These are regarded here as of specific value only.] *M.Ord.-Rec.*, N.Am.-S.Am.-Eu.-Australia-Antarctic.——FIG. 110,*1*. **P. fusca*, Rec., Atl.; *1a,b*, ext. views, with side broken to show interior, ×30 (*2117).——FIG. 111,*1*. *P. frankei* (RHUMBLER) *forma sphaeroides* RHUMBLER, Rec., Ger.(Kieler Bucht); test broken open, showing remains of protoplasmic body, ×50 (*1574).——FIG. 111,*2*. *P. frankei* (RHUMBLER) *forma ellipsoides* (RHUMBLER), ext., ×50, Rec., Ger.(Kieler Bucht); ext., ×50 (*1574).——FIG. 111,*3*. *P. exigua* (RHUMBLER), Rec., Ger.(Kieler Bucht); in balsam, ×180 (*1574).

Amphifenestrella RHUMBLER, 1935, *1574, p. 169 [**A. wiesneri*; OD]. Test free, discoidal, flat sides of transparent pseudochitin, with peripheral area of agglutinated material; no definite apertures or tubular extensions of chamber. [Differs from *Vanhoeffenella* in lacking tubular extensions at angles of the test and in lacking definite apertures.] *Rec.*, Ger.——FIG. 111,*4*. **A. wiesneri*, Kieler Bucht; peripheral agglutinated border and transparent pseudochitinous side through which protoplasmic contents can be seen, ×50 (*1574).

Blastammina EISENACK, 1932, *693a, p. 261 [**B. polymorpha*; OD]. Test free, consisting of one or rarely more than one hemispherical rounded to subangular chamber, may be irregularly grooved or infolded; wall with brown, pseudochitinous layer sparsely covered with mosaic of sand grains; no distinct aperture. *Sil.*, Eu.——FIG. 111,*5-7*.

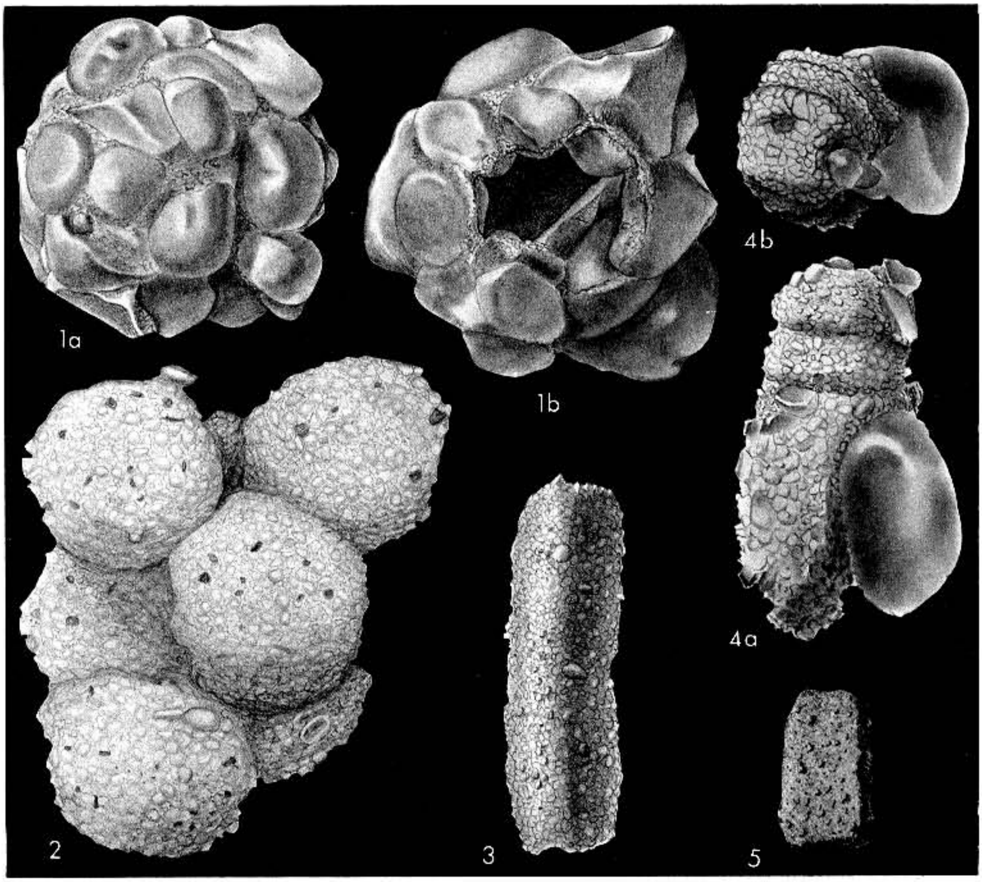


FIG. 110. Saccamminidae (Psammosphaerinae; *1, Psammosphaera; 2, Sorosphaera; 3-5, Stegnammina*) (p. C195-C196).

**B. polymorpha,* Sweden(Gotl.); *5,* neotype, X67 (*694); *6,* hemispherical form, X58 (*693a); *7,* irregularly grooved, X40 (*693a).

Ceratammina Ireland, 1939, *976, p. 194 [**C. cornucopia*; OD]. Test free, unilocular, conical and slightly curved; wall agglutinated of fine, well-cemented sand grains; aperture not apparent. *L.Dev.,* N.Am.——Fig. 111,*8.* **C. cornucopia,* Helderberg., USA(Okla.); X40 (*976).

Pseudastrorhiza Eisenack, 1932, *693a, p. 259 [**P. silurica*; OD] [=*Parvistellites* O. Wetzel, 1951, *2048, p. 113 (type, *P. hospitalis*)]. Test of agglutinated quartz grains, with numerous (commonly 3-7) short, thick radiating arms, which are closed terminally, thus differing from *Astrorhiza*; aperture not visible. *Ord.-Paleoc.,* Eu.(Ger.-Est.)-N.Am.(Ill.).——Fig. 111,*9.* **P. silurica,* Ord., Est.; neotype, X50 (*694).——Fig. 111,*10.* *P. hospitalis* (Wetzel), Paleoc. (Dan.), Ger., X115 (*2048).

Sorosphaera Brady, 1879, *196a, p. 28 [**S. confusa*; OD (M)] [=*Thuramminopsis* Haeusler, 1883, *853, p. 69 (type, *T. canaliculata*); *Arsorophaerum* Rhumbler, 1913, *1572b, p. 347 (obj.) *(nom. van.)*; *Sorophaera* Rhumbler, 1913, *1572b, p. 347 (obj.) *(nom. null.)*; *Psammophax* Rhumbler in Wiesner, 1931, *2063, p. 80 (type, *P. consociata*); *Arenosphaera* Shchedrina, 1939, *1724, p. 95 (type, *A. perforata*); *Danubica* Frentzen, 1944, *747, p. 325 (type, *D. gracilis*)]. Test free, consisting of variously arranged globular chambers with no apparent order of development; wall agglutinated of rather coarse grains and loosely cemented so that tests are easily broken; no distinct aperture apparent, communication of protoplasm with exterior probably between loosely cemented grains. [*Sorosphaera* differs from *Psammosphaera* in consisting of numerous loosely joined chambers. The type specimen of *S. confusa,* in the British Museum (Natural History) has disintegrated since its original description, probably owing to its extremely fragile nature.] *Sil.-Rec.,* Eu.-N.Am.-Arctic-Antarctic.——Fig. 110,*2.* **S. confusa,* Rec., Atl.; X22 (*2117).——Fig. 111,*11.* *S. consociata* (Rhumbler), Rec., Antarctic; X23.5 (*2063).——Fig. 111,*12.* *S. gracilis* (Frentzen), Jur., Ger.; approx. X30 (*747).——Fig. 111,*13.* *S. robusta* (Frentzen), Jur., Ger.; holotype, approx. X20 (*747).——Fig. 111,*14.* *S. perforata* (Shchedrina), Rec., USSR(Kara Sea); *14a,* 3-chambered specimen with last one broken; *14b,* portion of test wall, X40 (*1724).

Stegnammina Moreman, 1930, *1309, p. 49 [**S. cylindrica*; OD] [=*Raibosammina* Moreman, 1930, *1309, p. 50 (type, *R. mica*); *Thekammina* Dunn, 1942, *648, p. 326 (type, *T. quadrangularis*)]. Test free, subcylindrical to angular, straight to curved; wall thin, agglutinated, well cemented; without definite aperture. [Modifications of chamber shape are not regarded as generic in importance. *Thekammina* was defined for a subquadrangular species, but one species of *Stegnammina* is triangular; hence, they are believed to be congeneric. *Raibosammina* was regarded as being slightly irregular and in having a chamber interior of varying diameter.] *Ord.-Dev.,* N.Am.——Fig. 110,*3.* **S. cylindrica,* Sil., USA(Okla.); lectotype (here designated and redrawn), X62 (*2117).——Fig. 110,*4.* *S. mica* (Moreman), Ord., USA(Okla.); *4a,b,* side and end view, X83 (*2117).——Fig. 110,*5.* *S. quadrangularis* (Dunn), Sil., USA(Ill.); X24 (*648).

Storthosphaera Schulze, 1875, *1697, p. 113 [**S. albida*; OD] [=*Titanopsis* de Folin, 1881, *724, p. 138 *(nom. nud.)*; *Titanopsis* de Folin, 1887, *726a, p. 114 (type, *T. irregularis*); *Arstorthosphaerum* Rhumbler, 1913, *1572b, p. 347 (obj.) *(nom. van.)*]. Single, free, irregular chamber; wall finely arenaceous, loosely cemented; aperture indefinite. *Rec.,* Atl.-Antarctic.——Fig. 111,*15-17.* **S. albida,* off Norway; *15,16,* side views, X20; *17,* sectioned specimen showing wall thickness, X20 (*200).

Subfamily SACCAMMININAE Brady, 1884

[Saccammininae Brady, 1884, p. 64]——[All names of subfamily rank]——[=Arsaccamnia Rhumbler, 1913, p. 347 *(nom. van.)*; =Pilulininae Brady, 1884, p. 63; =Pelosininae Cushman, 1927, p. 12]

Test free, definite aperture. *Ord.-Rec.*

Saccammina M. Sars in Carpenter, 1869, *274, p. 61 [**S. sphaerica* Brady, 1871, *188, p. 183; SD Cushman, 1928, *439, p. 72 (see Loeblich & Tappan, 1961, *1180)] [=*Saccamina* Carpenter, 1869, *274, p. 61 *(nom. null.)*; *Saccammina* M. Sars, 1869, *1629, p. 248 *(nom. nud.)*; *Arsaccammum* Rhumbler, 1913, *1572b, p. 347 (obj.) *(nom. van.)*; *Placentammina* Majzon, 1943, *1203, p. 62 (type, *Reophax placenta* Grzybowski, 1897, *836, p. 276)]. Test free, single globular chamber; wall with pseudochitinous base and outer agglutinated layer, firmly cemented; aperture rounded, may be produced on short neck. *Sil.-Rec.,* N.Am.-Eu.-Atl.-Pac.-Antarctic.——Fig. 112,*1.* **S. sphaerica,* Rec., Atl.; X47 (*2117).

Brachysiphon Chapman, 1906, *319, p. 83 [**B. corbuliformis*; OD] [=*Arbrachysiphum* Rhumbler, 1913, *1572b, p. 351 (obj.) *(nom. van.)*; *Sacculinella* Crespin, 1958, *394, p. 43 (type, *S. australe*); *Hyperamminita* Crespin, 1958, *394, p. 54 (type, *Hyperammina(?) rudis* Parr, 1942, *1425, p. 105)]. Test free, elongate, subcylindrical; wall agglutinated, incorporating small foraminifers, shell fragments and mineral grains on pseudochitinous base or internal lining; aperture irregular opening at slightly constricted end of tube. [*Brachysiphon* differs from *Saccammina* in the elongate cylindrical form and from *Lagenammina* in having parallel sides and in lacking a constricted neck. It differs from *Bathysiphon* in being relatively short and closed at one end.] *Perm.-Rec.,* N.Z.-Australia.——Fig. 112,2. **B. corbuliformis,* Rec., N.Z.(off Great Barrier Is.); *2a,b,* side and top views of topotype, ×28 (*2117).——Fig. 112,*3*. *B. rudis* (Parr), Perm.,

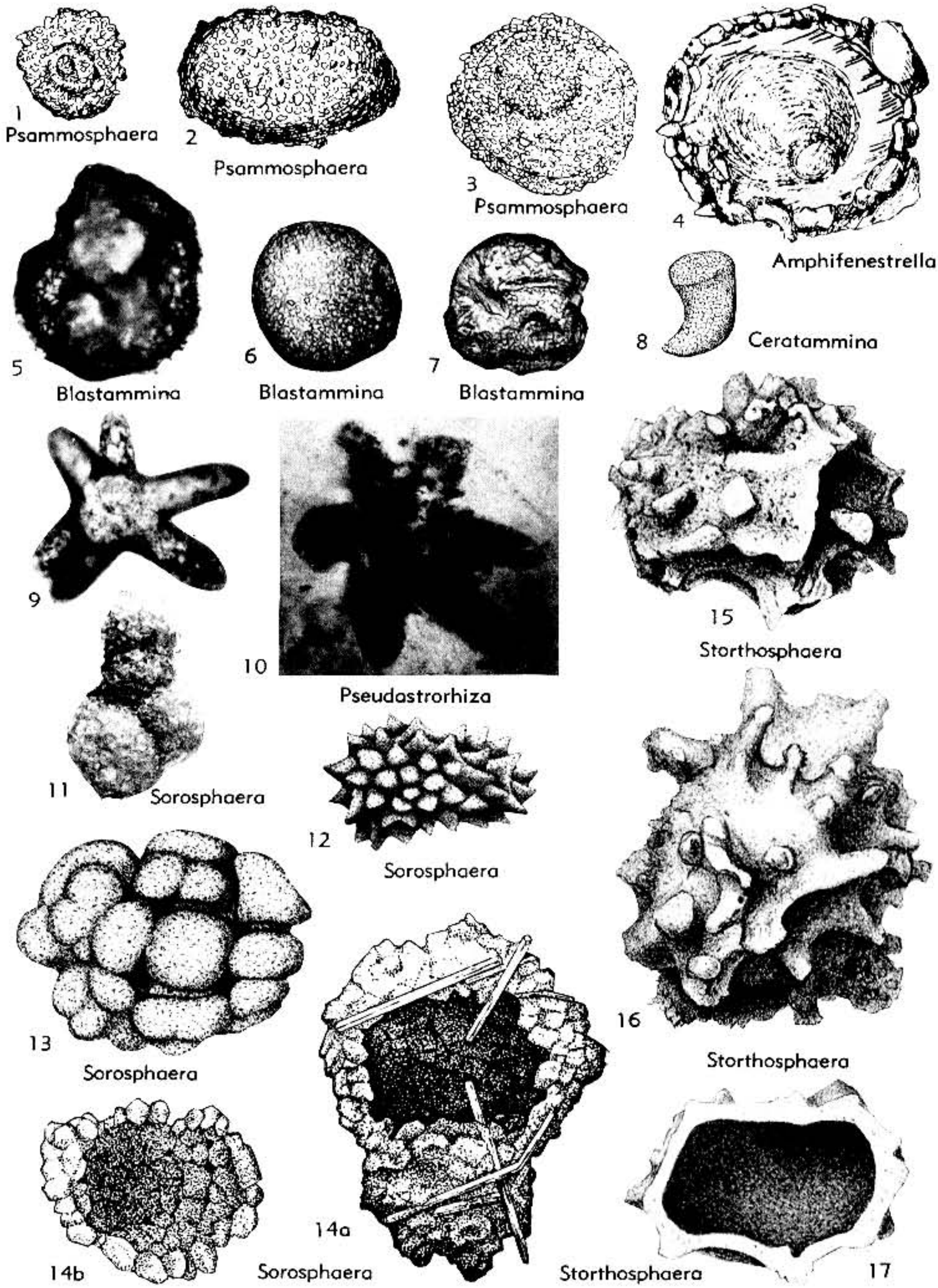


Fig. 111. Saccamminidae (Psammosphaerinae; *1-3, Psammosphaera; 4, Amphifenestrella; 5-7, Blastammina; 8, Ceratammina; 9,10, Pseudastrorhiza; 11-14, Sorosphaera; 15-17, Storthosphaera*) (p. C195-C196).

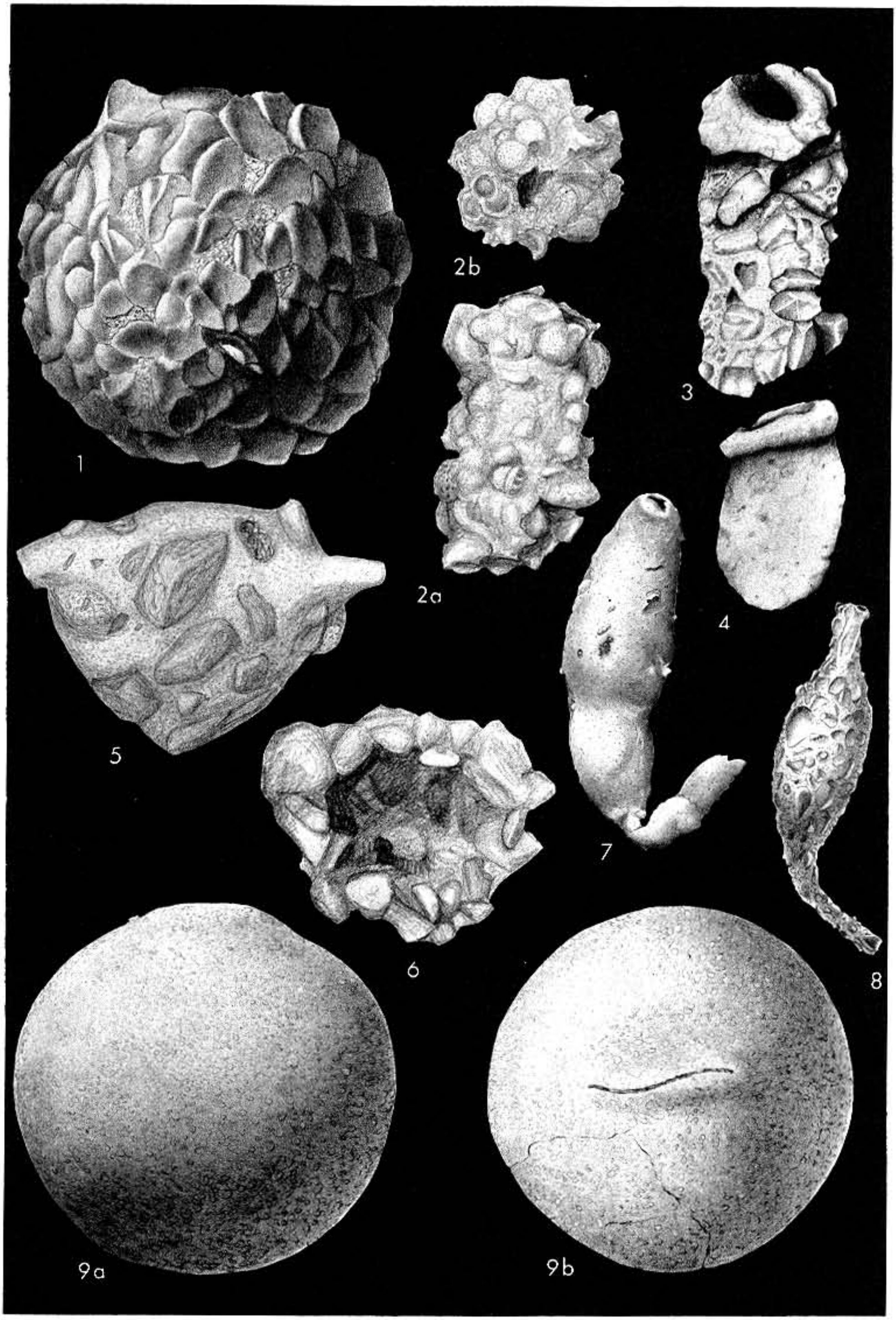


Fig. 112. Saccamminidae (Saccammininae; *1, Saccammina; 2-4, Brachysiphon; 5,6, Pelosphaera; 7,8, Pelosina; 9, Pilulina*) (p. C196-C201).

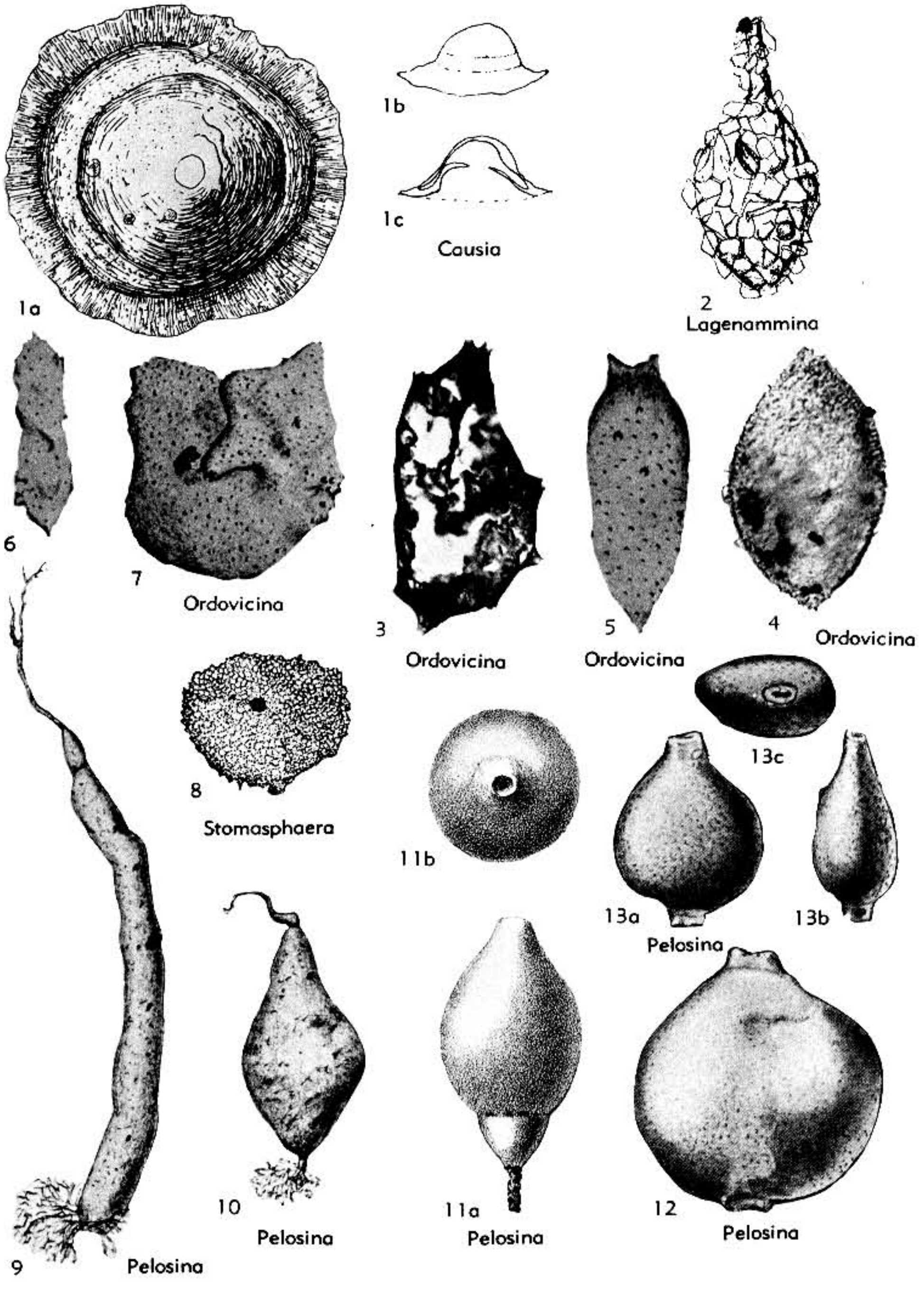


Fig. 113. Saccamminidae (Saccammininae; *1, Causia; 2, Lagenammina; 3-7, Ordovicina; 8, Stomasphaera; 9-13, Pelosina*) (p. C200-C202).

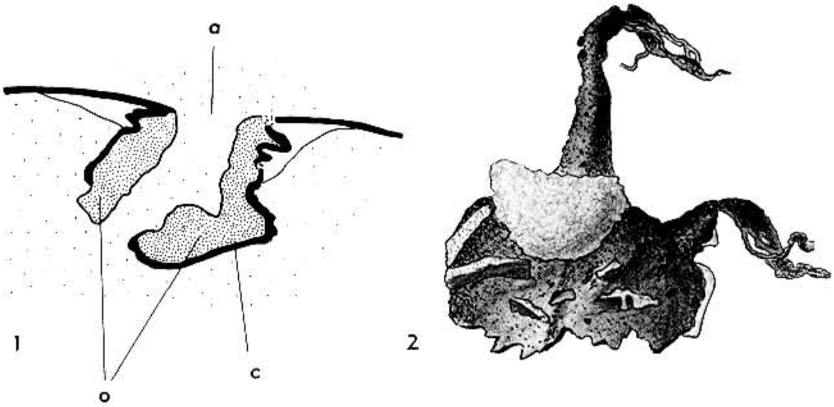


Fig. 114. Saccamminidae (Saccammininae; *1,2, Pelosphaera*) (p. *C*201).

Australia; ×28 (*394).——Fig. 112,*4*. *B. australe* (Crespin), Perm., W.Australia (Carnavon Basin); ×39 (*394).

Causia Rhumbler, 1938, *1576, p. 171 [**C. injudicata*; OD]. Test free, unilocular, circular in plan, convex above and concave below, may have marginal flange; wall of pseudochitin with small amount of fine-grained agglutinated foreign matter; aperture small, rounded, at center of concave lower side. *Rec.*, N.Sea.——Fig. 113,*1*. **C. injudicata*, Helgoland; *1a*, dorsal view, but with small rounded ventral aperture visible through semitransparent pseudochitinous wall, ×200; *1b*, diagram. edge view of marginal flange, ×110; *1c*, diagram. vert. sec., ×110 (*1576).

Lagenammina Rhumbler, 1911, *1572a, p. 92, 111 [**L. laguncula*; OD(M)] [=*Arlagenammum* Rhumbler, 1913, *1572b, p. 348 (obj.) *(nom. van.)*]. Test single flask-shaped chamber; wall with pseudochitinous inner layer, densely covered with agglutinated material; aperture terminal, produced on neck. *Sil.-Rec.*, N.Am.-Atl.——Fig. 113,*2*. **L. laguncula*, Rec., N.Atl., ×218 (*1572a).

Ordovicina Eisenack, 1938, *693b, p. 234 [**O. oligostoma*; OD] [=*Amphitremoida* Eisenack, 1938, *693b, p. 235 (type, *A. citroniforma*); *Amphitremoidea* Thalmann, 1941, *1897e, p. 648 *(nom. van.)*; *Shidelerella* Dunn, 1942, *648, p. 328 (type, *S. bicuspidata*); *Croneisella* Dunn, 1942, *648, p. 334 (type, *C. typa*); *Gastroammina* Dunn, 1942, *648, p. 335 (type, *G. williamsae*)]. Test free, single ovate to irregularly shaped chamber, wall with pseudochitinous base and agglutinated outer layer; one or more apertures at ends of slight projections. [Because of the dominantly pseudochitinous wall and thin agglutinated layer, the fossil tests are commonly somewhat distorted, suggesting that restricted generic limits should not be based on test shape alone.] *Ord.-Sil.*, N.Am.-Eu.——Fig. 113,*3*. **O. oligostoma*, Ord., Est.; ×95 (*694).——Fig. 113,*4*. *O. citroniforma* (Eisenack), Ord., Baltic; hypotype, ×140 (*694).——Fig. 113,*5*. *O. bicuspidata* (Dunn), Sil., USA(Ill.); ×35 (*648).——Fig. 113,*6*. *O. typa* (Dunn), Sil., USA(Ill.); ×27 (*648).——Fig. 113,*7*. *O. williamsae* (Dunn), Sil., USA (Mo.); ×27 (*648).

Pelosina Brady, 1879, *196a, p. 30 [**P. variabilis;* SD Cushman, 1910, *404a, p. 45] [=*Arpelosum* Rhumbler, 1913, *1572b, p. 348 (obj.) *(nom. van.)*; *Pelosinella* Parr, 1950, *1429, p. 261 (type, *P. bicaudata*); *Globosiphon* Avnimelech, 1952, *63, p. 65 (type, *Pelosina variabilis* Brady var. *sphaeriloculum* Höglund, 1947, *924, p. 61); *Millettina* Avnimelech, 1952, *63, p. 64 (type, *Pelosina distoma* Millett, 1904, *1284f, p. 608); *Caudammina* Montanaro Gallitelli, 1955, *1301, p. 178 (type, *Saccammina? caudata* Montanaro Gallitelli, 1955, *1301, p. 178)]. Test free, subcylindrical, elongate, fusiform, nonseptate; wall thick, may be irregularly constricted, finely agglutinated, with thin, pseudochitinous base, well-preserved specimens with fine tubular extensions at either end; pseudochitinous lining may protrude farthest at one end; apertures at open end of tubular extension at one or both ends. *Cret.-Rec.*, Eu.-Sib.-Atl.-Pac.-Arctic-Antarctic.——Fig. 112,*7*; 113,*9*. **P. variabilis*, Rec., off N.Z. (112,*7*), off Sweden (113,*9*); 112,*7*, topotype, ×8 (*2117); 113,*9*, specimen showing membranaceous dendritic "appendages," probably preserved pseudopodia, ×17 (*924).——Fig. 112,*8*. *P. bicaudata* (Parr), Rec., off Kerguelen Is.; ×44 (*1429).——Fig. 113,*10*. *P. sphaeriloculum* Höglund, Rec., off Sweden; ×17 (*924).——Fig. 113,*11*. *P. distoma* Millett, Rec., Malay Arch.; *11a,b*, side and apert. views, ×115 (*1284f).——Fig. 113,*12,13*. *P. caudata* (Montanaro Gallitelli), Cret., N.Italy; *12*, holotype,

×100; *13a-c*, side, edge, and top views of paratype, ×100 (*1304).

HÖGLUND (*924) regarded the broader end of the test as apical and the smaller end as oral. In well-preserved specimens extremely delicate dendritic "appendages" at the broad end were regarded as holdfasts, though he also stated that they might be preserved threads of pseudopodia with adherent particles of bottom sediment, since his material was preserved in alcohol immediately after sampling. The latter explanation seems to us more likely, the broader end then appearing to be the apertural end, and in dried specimens (such as the illustrated topotype) it contains an opening. The opposite end had a few thin dendritic tubes in HÖGLUND's material, which could well have served as holdfasts. *Pelosinella*, *Millettina*, and *Caudammina* all were defined for species with openings at both ends, but because of the delicate nature of the tests, this is doubtless due to the state of preservation of the dried or fossil material upon which the species were based. Simple saclike species previously placed in *Pelosina* should be referred to *Saccammina*.]

Pelosphaera HERON-ALLEN & EARLAND, 1932, *914d, p. 255 [**P. cornuta*; OD(M)]. Test free, roughly spherical, with 2 or more projecting fragile, flexible, conical tubes of fine mud, equal in length to test diameter, repeatedly bifurcating near extremity, as in *Pelosina*, tubes commonly destroyed in dead specimens, so that test resembles *Saccammina*; wall with inner imperforate pseudochitinous layer and outer agglutinated layer; cement soft, flexible on surface but firm and smooth internally and may appear somewhat fibrous between grains in interior; aperture single, with distinctive oral apparatus consisting of pseudochitinous entosolenian tube with inner gel-like capsule. *Rec.*, S.Georgia Is.-Antarctic.——FIG. 112,*5,6*; 114,*1,2*. **P. cornuta*, off S.Georgia (112,*5,6*), Antarctic (114,*1,2*); 112,*5*, lectotype (here designated, *914d, pl. 2, fig. 14, and redrawn), ×10 (*2117); 112,*6*, paratype (*914d, pl. 2, fig. 15, redrawn), broken to show interior, ×10 (*2117); 114,*1*, diagram. sec. through apertural region (*a*) and showing chitinous layer (*c*), entosolenian tube with gel-like oral capsule (*o*), ×155 (*890); 114,*2*, fragment of alcohol-preserved test, showing fine-grained, repeatedly bifurcating, tubular extensions, ×12.5 (*653).

Pilulina CARPENTER, 1870, *275, p. 5 [**P. jeffreysii* CARPENTER, 1875, *276, p. 532; SD (SM) CARPENTER, *276, p. 532] [=*Arpilulum* RHUMBLER, 1913, *1572b, p. 349 (*nom. van.*)]. Test free, globular; wall thick, of agglutinated loosely aggregated sand and sponge spicules, resulting in delicate test; aperture elongate slit, somewhat as in *Fissurina*, elevated on very slightly produced ridge. [Differs from *Saccammina* in the elongate slitlike aperture.] *Rec.*, Atl.-Pac.-Antarctic.——FIG. 112,*9*. **P. jeffreysii*, N.Atl.; *9a,b*, side, apert. views, ×13 (*2117).

Saccamminoides GEROCH, 1955, *783, p. 54, 57, 60 [*non* IRELAND, 1956] [**S. carpathicus*; OD]. Test free, consisting of few rapidly enlarging, irregularly arranged chambers; wall agglutinated, with siliceous cement; apertures rounded in each of last 2 or 3 chambers, may be slightly produced. [This genus is very similar to *Sorosphaera* except

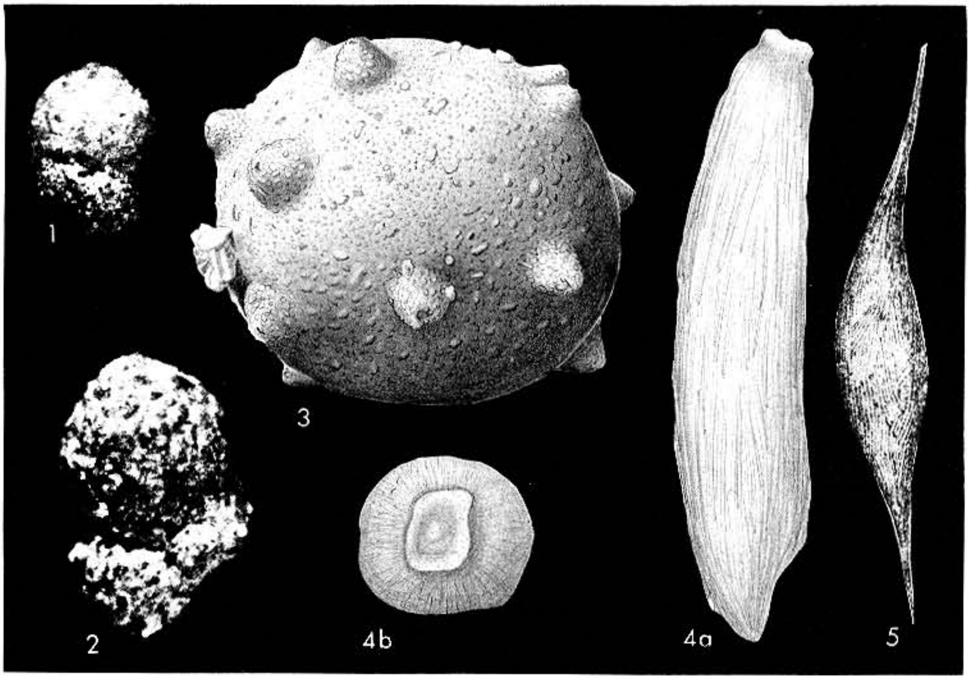


FIG. 115. Saccamminidae (Saccammininae; *1,2*, *Saccamminoides*; *3*, *Thurammina*; *4,5*, *Technitella*) (p. C201-C202).

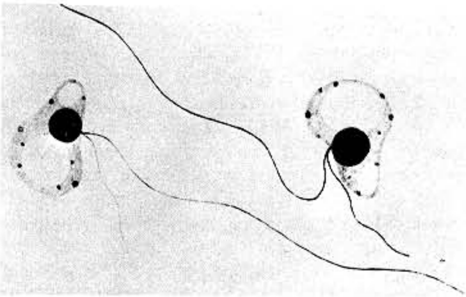


FIG. 116. Saccamminidae (Hemisphaeramminninae; *Hemisphaerammina*) (p. *C*202).

for the presence of distinct apertures in the chambers.] *L.Eoc.*, Eu.(Pol.)——FIG. 115,*1,2*. **S. carpathicus*, W. Carpathians; *1,2*, holotype and paratype, ×33 (*783).

Stomasphaera MOUND, 1961, *1321, p. 28 [**S. brassfieldensis*; OD]. Test free, single subspherical or somewhat subangular chamber; wall agglutinated, medium to coarsely arenaceous, poorly to well cemented, surface rough; aperture single small, rounded opening. *L.Sil.*, N.Am.——FIG. 113,*8*. **S. brassfieldensis*, USA(Ind.); holotype, ×100 (*1321).

Technitella NORMAN, 1878, *1363, p. 279, 281 [**T. legumen*; SD CUSHMAN, 1910, *404a, p. 47] [=*Dioxeia* DE FOLIN, 1887, *726a, p. 115 (type, *D. richardi*); *Hyperamminella* DE FOLIN, 1881, *724, p. 140 (*non* CUSHMAN & WATERS, 1928) (*nom. nud.*); *Hyperamminella* DE FOLIN, 1887, *726a, p. 114 (*non* CUSHMAN & WATERS, 1928), no species named; *Artechnitum* RHUMBLER, 1913, 1572b, p. 350 (obj.) (*nom. van.*)]. Test free, consisting of single elongate, oval, fusiform or cylindrical chamber; wall thin, composed of longitudinally aligned sponge spicules, with some sand grains; aperture terminal, rounded, may be on short neck. [*Technitella* differs from *Pelosina* in having a thin wall composed largely of sponge spicules, instead of a thick layer of fine agglutinated material on a pseudochitinous inner layer.] *Oligo.-Rec.*, S.Am.-Australia-Atl.-Antarctic.——FIG. 115,*4*. **T. legumen*, Rec., off Ire.; *4a,b*, side and top views of holotype (here refigured, BMNH ZF3628), ×64 (*2117).——FIG. 115,*5*. *T. richardi* (DE FOLIN), loc. and mag. not given (*726a).

Thurammina BRADY, 1879, *196a, p. 45 [**T. papillata*; SD CUSHMAN, 1910, *404a, p. 57] [=*Thyrammina* RHUMBLER, 1904, *1569, p. 236 (obj.) (*nom. van.*); *Arthyrammum* RHUMBLER, 1913, *1569, p. 347 (obj.) (*nom. van.*). Test free, single, nearly globular chamber; wall thin, finely agglutinated, surface smoothly finished; apertures several, commonly situated on small mammillate protuberances. [Differs from *Saccammina* in possessing numerous apertures on short protuberances.] *Sil.-Rec.*, N.Am.-Eu.-Atl.-Pac.-Indon.-Antarctic.——FIG. 115,*3*. **T. papillata*, Rec., S.Atl.; ×48 (*2117).

Subfamily HEMISPHAERAMMININAE
Loeblich & Tappan, 1961

[Hemisphaeramminnae LOEBLICH & TAPPAN, 1961, p. 277]

Test attached, consisting of one or more subglobular or hemispherical chambers. *Ord.-Rec.*

Hemisphaerammina LOEBLICH & TAPPAN, 1957, *1172, p. 223 [**H. batalleri*; OD] [=*Fairliella* SUMMERSON, 1958, *1858, p. 555 (type, *F. dicantha*); *Iridiella* SHCHEDRINA, 1962, *1726A, p. 57 (type, *I. marisalbi*)]. Test attached, consisting of single hemispherical chamber, may have bordering flange; wall agglutinated, with considerable cement; no apparent aperture. [This genus includes the agglutinated species previously referred to *Webbinella*, as the type-species of *Webbinella*, *W. hemispherica* PARKER, JONES & BRADY, is an attached polymorphinid (*1172).] *M.Dev.-Rec.*, Eu.-USSR-N.Am.-Atl.——FIG. 117,*1*. **H. batalleri*, U.Cret.(U.Santon.), Sp.; holotype, ×12 (*1172).——FIG. 117,*2*. *H. bradyi* LOEBLICH & TAPPAN, Rec., off Eng.; holotype, ×33 (*1172).——FIG. 117,*3*. *H. marisalbi* (SHCHEDRINA), Rec., White Sea; *3a*, dorsal view; *3b*, ventral view, ×30 (*1726A).——FIG. 116. *H. crassa* (LE CALVEZ), Rec., Atl.; biflagellate gametes, ×3,000 (*1106).

Ammopemphix LOEBLICH, 1952, *1152, p. 82 [**Urnula quadrupla* WIESNER, 1931, *2063, p. 82; OD] [=*Urnula* WIESNER, 1931, *2063, p. 82 (obj.) (*non* CLAPARÈDE & LACHMANN, 1857)]. Test attached when living, nearly circular in outline, flat on attached side, convex above, commonly consisting of 4 or more nearly equal chambers, usually symmetrically arranged, with few chambers in single whorl, or with outer ring of chambers; sutures depressed, septa visible from base on unattached specimens, thickness nearly equal to that of outer wall, which is finely arenaceous and white to yellowish, attachment wall very thin, delicate, translucent, and may be broken off when loosened from attachment, leaving chambers open ventrally; apertures rounded, dorsal, one at summit of each chamber. *Rec.*, Antarctic-Arctic.——FIG. 117,*7*. **A. quadrupla* (WIESNER), Antarctic (Weddell Sea); ×146 (*2117).

Amphicervicis MOUND, 1961, *1321, p. 29 [**A. elliptica*; OD]. Test attached, hemispherical, elliptical to circular in outline, with 3 chambers internally similar to *Psammosphaera* but completely enveloped by large final chamber, base flattened to concave; wall thick, agglutinated, fine- to medium-grained and well-cemented, surface smooth; 2 apertures, each a simple, round

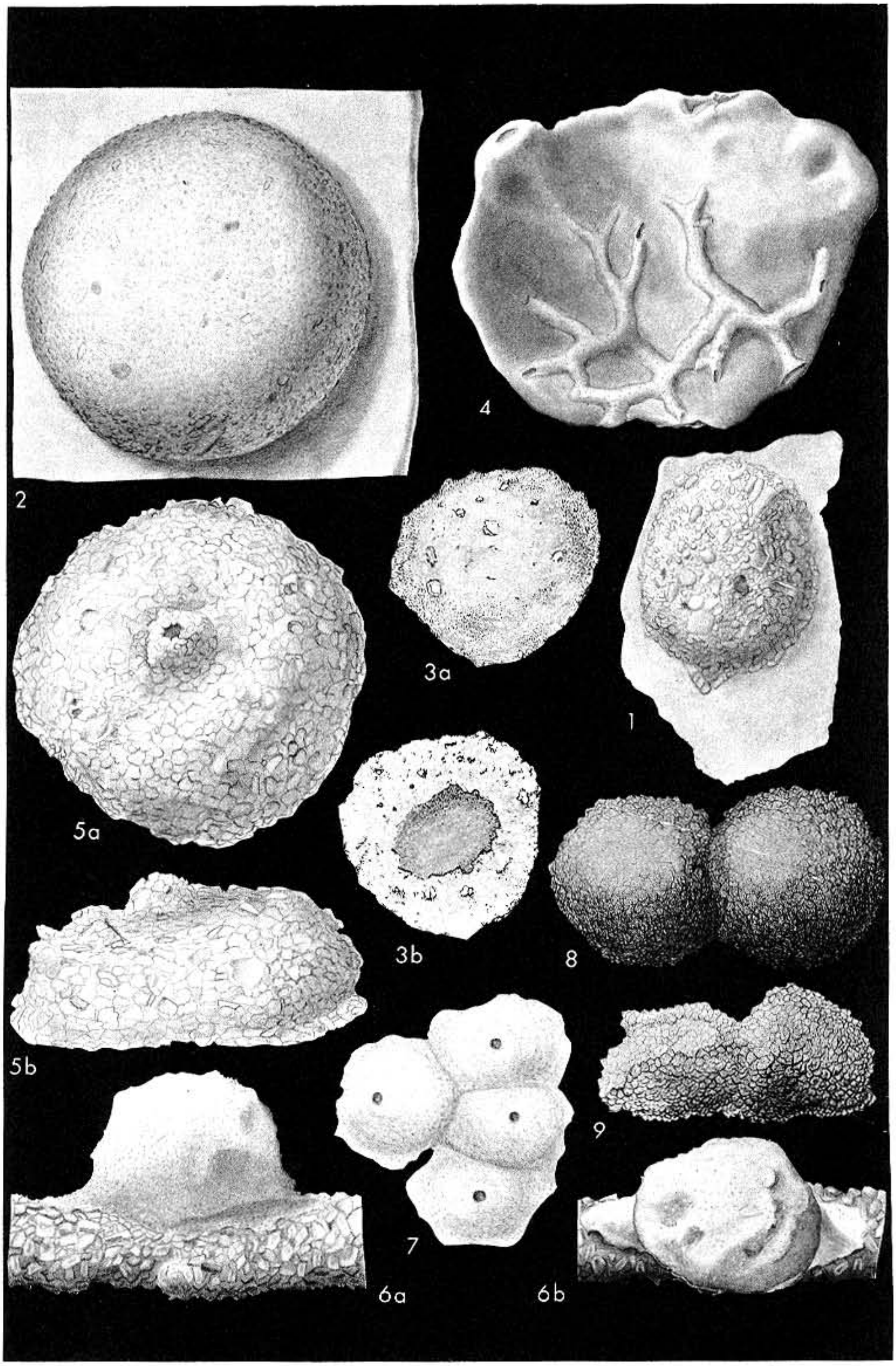


FIG. 117. Saccamminidae (Hemisphaerammininae; *1-3, Hemisphaerammina; 4, Sagenina; 5, Colonammina; 6, Tholosina; 7, Ammopemphix; 8,9, Webbinelloidea*) (p. C202, C204-C205).

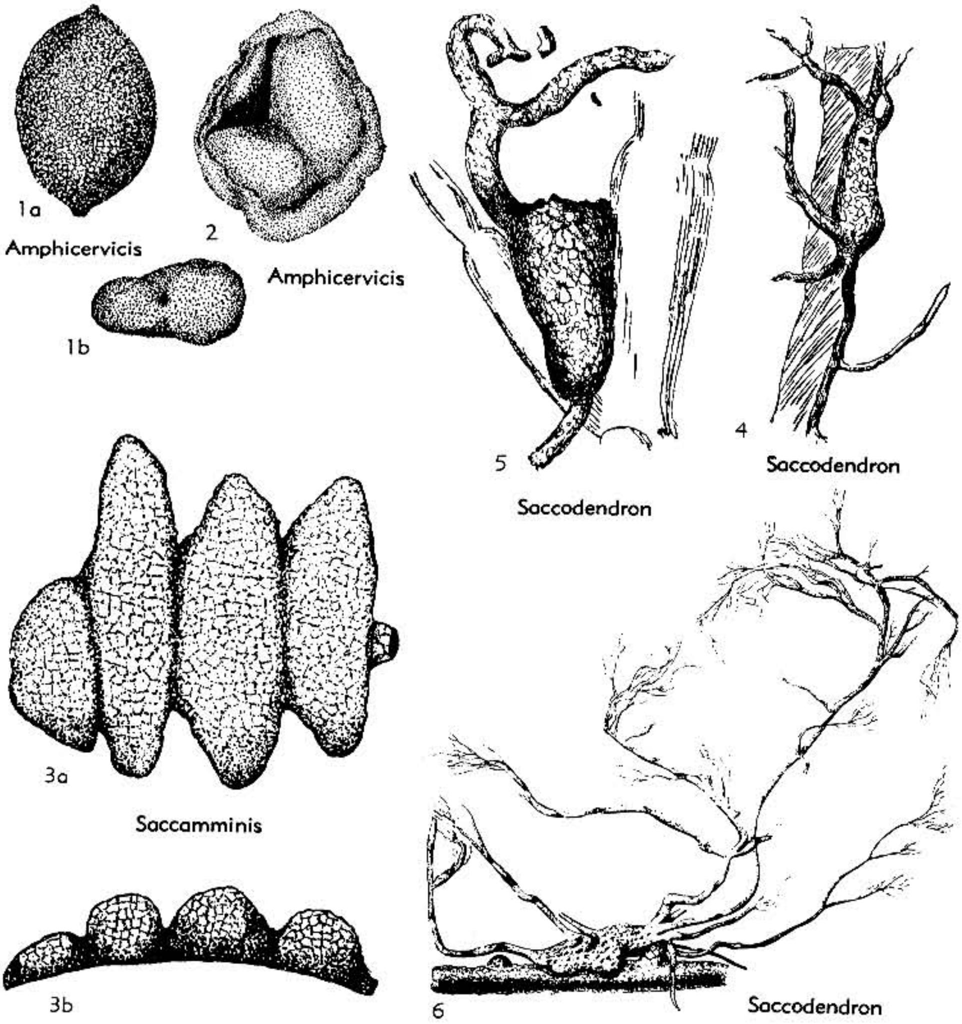


FIG. 118. Saccamminidae (Hemisphaeramminínae; *1,2, Amphicervicis; 3, Saccamminis; 4-6, Saccodendron*) (*C*202-*C*205).

opening somewhat produced, and at opposite extremities of test. *L.Sil.*, N.Am.——FIG. 118,*1,2*. **A. elliptica*, USA(Ind.); *1a,b*, side and end view of holotype; 2, paratype showing 3-chambered interior; both ×100 (*1321).

Colonammina MOREMAN, 1930, *1309, p. 55 [**C. verruca*; OD] [=*Psammoscene* RHUMBLER in WIESNER, 1931, *2063, p. 85 *(nom. nud.)*; *Psammoscene* THALMANN, 1934, *1896, p. 243 (type, *P. craterula* RHUMBLER, 1931)]. Similar to *Ammopemphix*, but consisting of solitary chambers only, may have surrounding flange; single aperture at summit of chamber. *Sil.-Rec.*, N.Am.-Antarctic.——FIG. 117,*5*. **C. verruca*, Sil., USA(Okla.); *5a,b*, top and edge views, ×162 (*2117).

Goatapitigba NARCHI, 1962 (see p. *C*795).

Saccamminis IRELAND, 1960, *978, p. 1217 [*pro Saccamminoides* IRELAND, 1956, *977, p. 841 *(non* GEROCH, 1955)] [**Saccamminoides multicellus* IRELAND, 1956, *977, p. 841; OD]. Attached, similar to *Tholosina*, but with more than one hemispherical chamber, commonly in linear series; aperture terminal, at end of slight protuberance, against attachment. *U.Penn.*, N.Am. ——FIG. 118,*3*. **S. multicellus* (IRELAND), Virgil., USA(Kans.); *3a,b*, top and edge views, ×80 (*977).

Saccodendron RHUMBLER, 1935, *1574, p. 173 [**S. heronalleni*; OD]. Test attached, hemispherical to ovate chamber with one or more elongate, bifurcating, tubular extensions arising from peripheral area; may grow free of attachment; wall agglutinated; apertures at ends of tubes. *Rec.*, Eu.——FIG. 118,*4-6*. **S. heronalleni*, Ger. (*4,5*, figured as *S. heronalleni* RHUMBLER *forma latericium* RHUMBLER, 1935), Sweden (*6*); *4,5*, side views, ×40, ×50 (*1574); *6*, specimen attached to *Rhabdammina*, ×7.5 (*924).

Sagenina CHAPMAN, 1900, *314, p. 4 [*pro Sagenella* BRADY, 1879, *196a, p. 41 (*non* HALL, 1851] [**Sagenella frondescens* BRADY, 1879, *196a, p. 41; OD(M)] [=*Arsagenum* RHUMBLER, 1913, *1572b, p. 345 (obj.) (*nom. van.*)]. Test attached throughout, consisting of dichotomously or irregularly branching tubes, finely agglutinated; apertures at open ends of tubes. *Eoc.-Rec.*, Philip.-Japan-S.Pac.——FIG. 117,*4*. **S. frondescens* (BRADY), topotype, Rec., S.Pac.(Admiralty Is.); ×10 (*2117).

Tholosina RHUMBLER, 1895, *1568A, p. 82 [**Placopsilina bulla* BRADY, 1881, *196c, p. 51; SD CUSHMAN, 1918, *411a, p. 63] [=*Pseudoplacopsilina* EIMER & FICKERT, 1899, *692, p. 672 (obj.); *Artholosum* RHUMBLER, 1913, *1572b, p. 346 (obj.) (*nom. van.*)]. Similar to *Hemisphaerammina*, but with 2 or more apertures flush with attachment or commonly at ends of irregular protuberances, just above base of test. *Ord.-Rec.*, Atl.-Antarctic-N.Am.-Eu.——FIG. 117,*6*. **T. bulla* (BRADY), Rec., Atl.; *6a,b*, side and top views, ×20 (*2117).

Webbinelloidea STEWART & LAMPE, 1947, *1838, p. 534 [**W. similis*; OD] [=*Sorosphaeroidea* STEWART & LAMPE, 1947, *1838, p. 534 (type, *S. polygonia*)]. Test attached, without visible aperture as in *Hemisphaerammina*, but with numerous chambers in linear or spreading arrangement, as in *Ammopemphix* or *Saccamminis*. *M.Dev.*, N.Am.——FIG. 117,*8*. **W. similis*, USA (Ohio); ×40 (*1838).——FIG. 117,*9*. *W. polygonia* (STEWART & LAMPE), USA(Ohio); ×40 (*1838).

Subfamily DIFFUSILININAE Loeblich & Tappan, n. subfam.

Test free or attached, with interior partially subdivided into chamberlets. *M.Ord.-Rec.*

Diffusilina HERON-ALLEN & EARLAND, 1924, *912, p. 614 [**D. humilis*; OD]. Test attached, commonly to algae, irregular in outline, consisting of mass of intricately ramifying tubes with finely agglutinated wall; apertures inconspicuous at ends of 1 to 4 small pustules on outer surface; dark-colored protoplasm completely filling test. [Differs from *Verrucina* in its very irregular character and unevenly spaced apertures.] *Rec.*, S.Pac.-Atl.——FIG. 119,*1,2*. **D. humilis*, S.Pac.(Lord Howe Is.); *1,2*, top views, ×26 (*2117).

Crithionina GOËS, 1894, *804, p. 14 [**C. mamilla*; SD RHUMBLER, 1904, *1569, p. 229] [=*Arcrithionum* RHUMBLER, 1913, *1572b, p. 346 (obj.) (*nom. van.*)]. Test attached, commonly to *Rhabdammina*, or later detached, subspherical to hemispherical, single chamber incompletely divided by ingrowth of wall which appears to form partial septum; wall thick, finely agglutinated, of sand, sponge spicules and foraminiferal tests, surface commonly roughened owing to dislodgement of some larger fragments embedded in wall; no apparent aperture in globular forms but tubular chitinoid or agglutinated projection which terminates in rounded aperture may occur at one side, probably at only one stage in life history (*924). [Redescription of the type-species by HÖGLUND (*924) based on the original material of GOËS requires modification of the generic definition.] *Rec.*, Atl.-Pac.-Carib.-N.Sea.——FIG. 120,*1-4*. **C. mamilla*, N.Sea(Skagerak); *1,2*, ext. and sec. showing internal septum, ×17; *3*, sec. of another specimen, ×30; *4*, specimen with tubular projection and rounded aperture, ×17 (*924).

Daitrona LOEBLICH & TAPPAN, 1961, *1181, p. 218 [**Crithionina lens* GOËS, 1896, *805, p. 24; OD]. Test free, 2-4 mm. diam., lenticular in section, rounded to oblong in plan; single chamber subdivided by radial semisepta or secondary partitions, projecting inward from wall, may subdivide test almost completely; wall finely agglutinated, loosely cemented; no localized aperture. [Differs from *Crithionina* in being free and in having numerous radiating secondary partitions subdividing the chamber. Differs from *Oryctoderma* in having a thin wall with secondary partitions nearly completely segmenting the test, rather than a thick wall with labyrinthine passages connecting the smoothly finished inner cavity to the exterior.] *Rec.*, Pac.——FIG. 120,*5-7*. **D. lens* (GOËS); *5a,b*, side, edge views; *6,7*, horiz. and vert. secs., ×11 (*805).

Discobotellina COLLINS, 1958, *375, p. 342 [**D. biperforata*; OD). Test discoidal, single chamber, with concentric growth rings; 2 distinct forms in type-species (may represent alternating generations), one discoidal with central inflated area, other slightly elliptical in outline, with 2 eccentric slotlike perforations which pass through test, apparently migrating outward by resorption and regrowth at margins as test enlarges; wall agglutinated, with thick inner layer of loosely cemented large grains, and thin, fine-grained, well-cemented outer layer, imperforate except at peripheral margin where interstitial spaces communicate with labyrinthic interior. *Rec.*, Australia.——FIG. 119, *6-8*. **D. biperforata*; S.Queensl.(*6*), Great Barrier Reef(*7,8*); *6a,b*, side, edge views of holotype (perforated form), ×1.8 (*375); *7a,b*, side, edge views

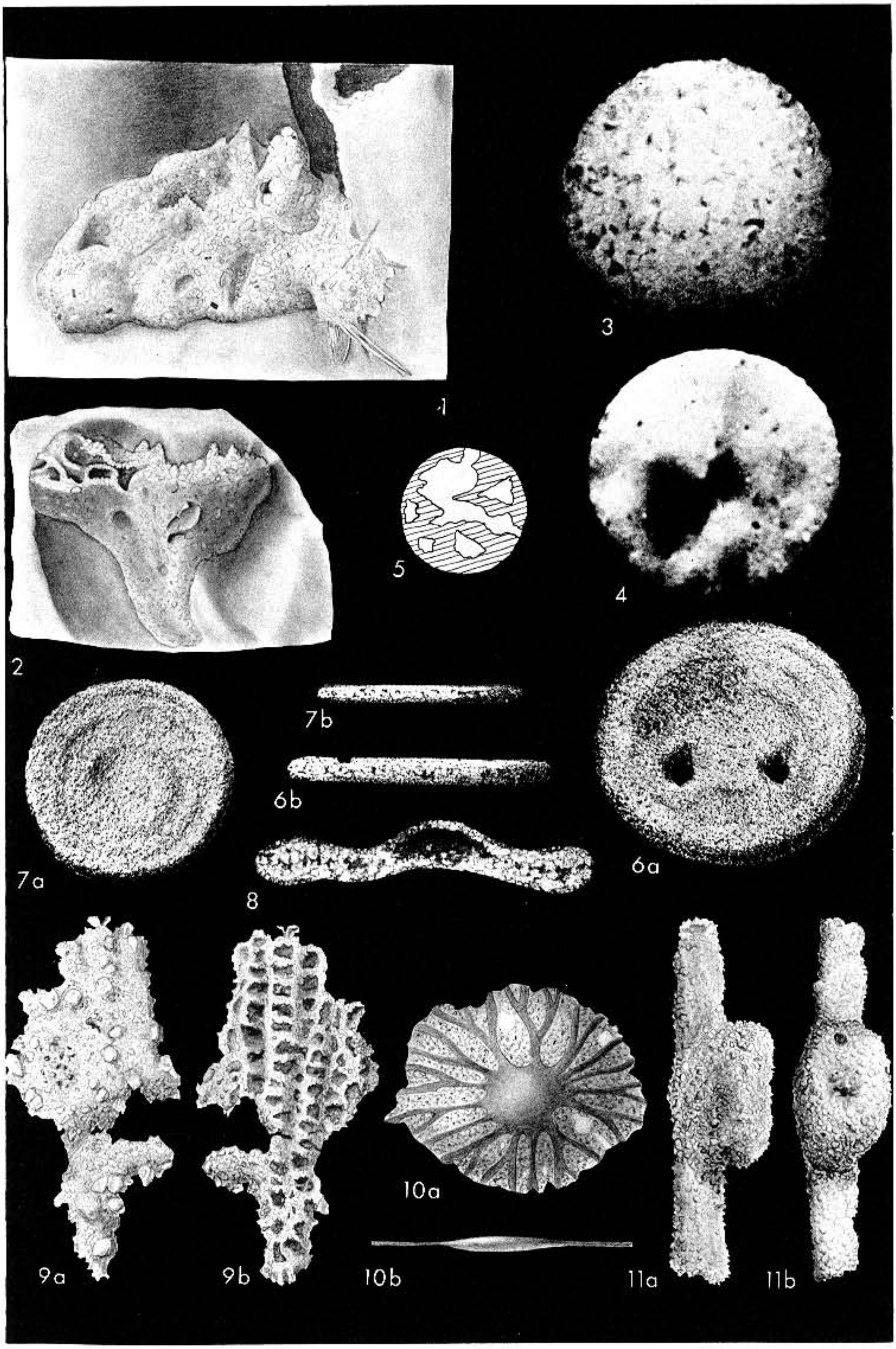


FIG. 119. Saccamminidae (Diffusilininae; *1,2, Diffusilina; 3-5, Weikkoella; 6-8, Discobotellina; 9, Kerionammina; 10, Masonella; 11, Verrucina*) (p. C205-C210).

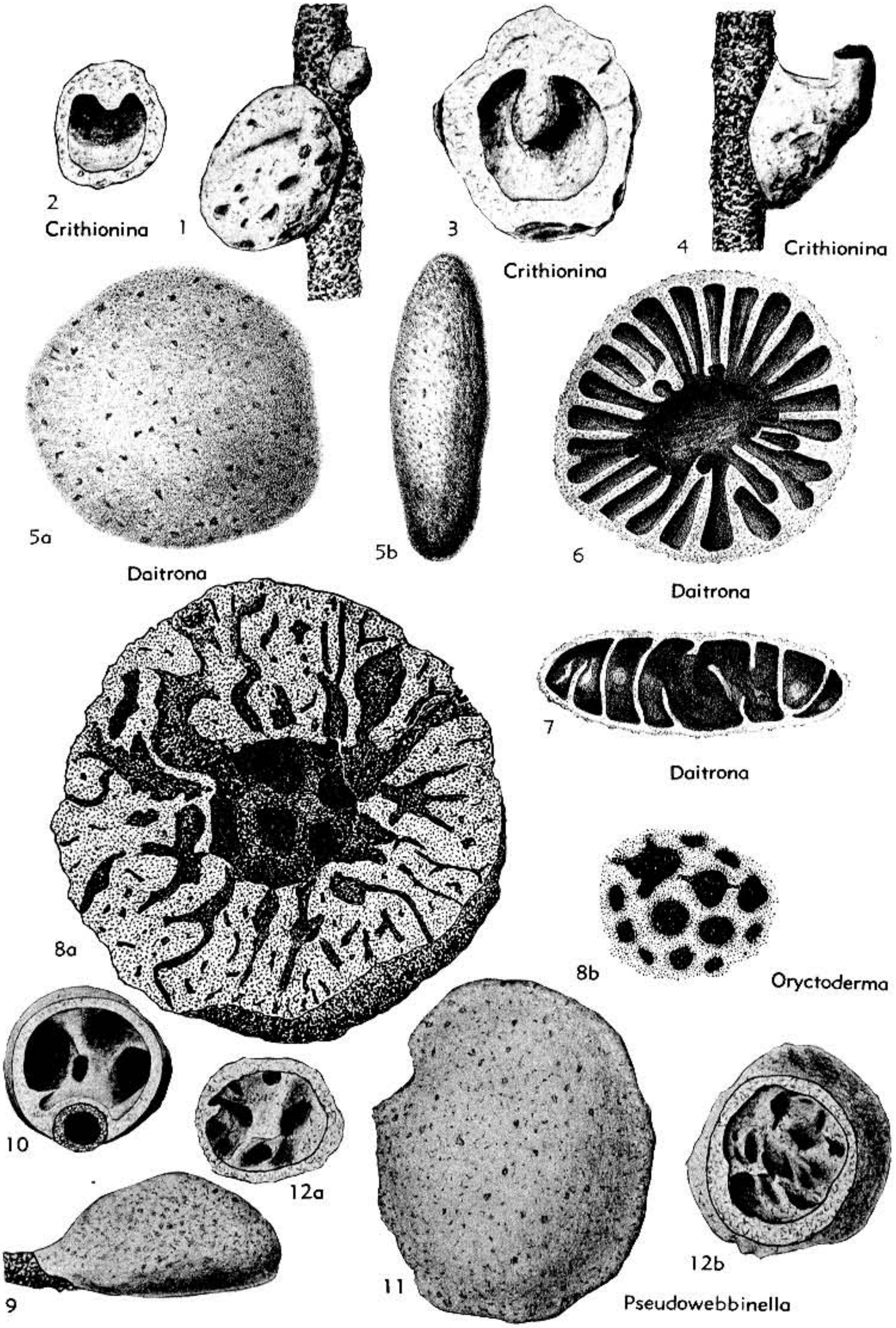


FIG. 120. Saccamminidae (Diffusilininae; *1-4, Crithionina; 5-7, Daitrona; 8, Oryctoderma; 9-12, Pseudowebbinella*) (p. C205, C208).

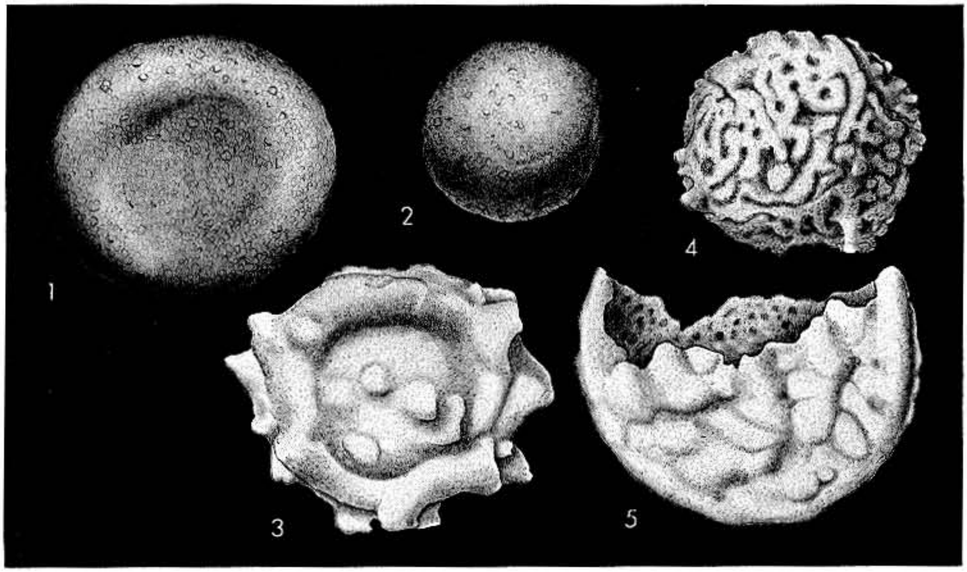


FIG. 121. Saccamminidae (Diffusilininae; *1-5, Thuramminoides*) (p. C208-C210).

of paratype, ×3 (*375); *8*, specimen broken to show internal structure, ×4 (*375).

Kerionammina MOREMAN, 1933, *1310, p. 397 [**K. favus*; OD]. Test attached, irregularly spreading; wall agglutinated, with labyrinthic interior, subdivided into more or less regular chamberlets; apertures rounded, at ends of tubular extensions from peripheral margin. [Originally placed in the family Neusinidae because of its labyrinthic character, later it was removed to the Saccamminidae (*486). *Neusina* is a junior synonym of *Stannophyllum* and belongs to the Xenophyophorida rather than to the Foraminiferida.] *M.Ord.*, N.Am.——FIG. 119,*9*. **K. favus*, Trenton., USA (Okla.); *9a,b*, dorsal and ventral sides, ×26 (*2117).

Masonella BRADY, 1889, *201, p. 295 [**M. planulata;* SD CUSHMAN, 1927, *433, p. 188] [=*Armasonellum* RHUMBLER, 1913, *1572b, p. 345 (obj.) *(nom. van.)*]. Test discoidal, compressed, central cavity with fine, branching tubules extending to periphery; wall finely agglutinated; aperture at open ends of tubules. *Rec.*, Ind.O. ——FIG. 119,*10*. **M. planulata*, Bay of Bengal; *10a,b*, side, edge views, ×7 (*201).

Oryctoderma LOEBLICH & TAPPAN, 1961, *1181, p. 217 [**Crithionina rotundata* CUSHMAN, 1910, *404a, p. 56; OD]. Test free, large, globular, unilocular; central cavity relatively small, simple, spherical; wall agglutinated, very thick and loosely cemented, with numerous ramifying canals leading from central cavity to exterior, margins of canals being relatively firmly cemented; apertures consisting of numerous circular to polygonal openings on surface which lead into these canals. *Perm.-Rec.*, Atl.-Pac.-Australia.——FIG. 120,*8*. **O. rotundata* (CUSHMAN), Rec., Pac.(off San Diego, Calif.); *8a*, int., ×10; *8b*, part of surface, ×25 (*404a).

Pseudowebbinella SHCHEDRINA, 1962, *1726A, p. 54 [**Crithionina goesi* HÖGLUND, 1947, *924, p. 36; OD]. Test attached, consisting of single hemispherical chamber, internally partially subdivided by short radial partitions projecting inward from the peripheral margin; wall agglutinated; no distinct aperture. [*Pseudowebbinella* resembles *Crithionina* externally, but has a more complex internal subdivision. It resembles *Daitrona* in the inner structure but differs in the attached character.] *Rec.*, Eu.(N. Sea)-USSR(White Sea).——FIG. 120,*9-12*. **P. goesi* (HÖGLUND), N. Sea; *9*, ext. of specimen attached to *Rhabdammina*; *10*, sectioned specimen showing internal subdivision; *11*, surface of discoidal specimen; *12a,b*, transversely sectioned specimen, ×17 (*924).

Thuramminoides PLUMMER, 1945, *1468, p. 218 [**T. sphaeroidalis*; OD]. Test free, subglobular to compressed; wall finely agglutinated, interior labyrinthic; no visible aperture, or with openings at ends of short protuberances. *L.Penn.-M.Penn.*, N.Am.; *Mesoz.*, USSR.——FIG. 121,*1-5*. **T. sphaeroidalis*, L.Penn., Tex.*(2)*, M.Penn., Tex. *(1,3-5)*; *1*, holotype; *2*, small globular paratype; *3-5*, paratypes with large protuberances, labyrinthic test, broken specimen showing pitted inner surface; all ×48 (*2117).

[This genus was defined as having a labyrinthic or spongy interior, and in the type-species varying from a smooth surface to a papillate one. Examination of the original types strongly suggests that these include more than one species and possibly more than one genus. The holotype and one paratype have a compressed circular form, with smoothly finished surface; another paratype shows large protuberances bearing small rounded openings.

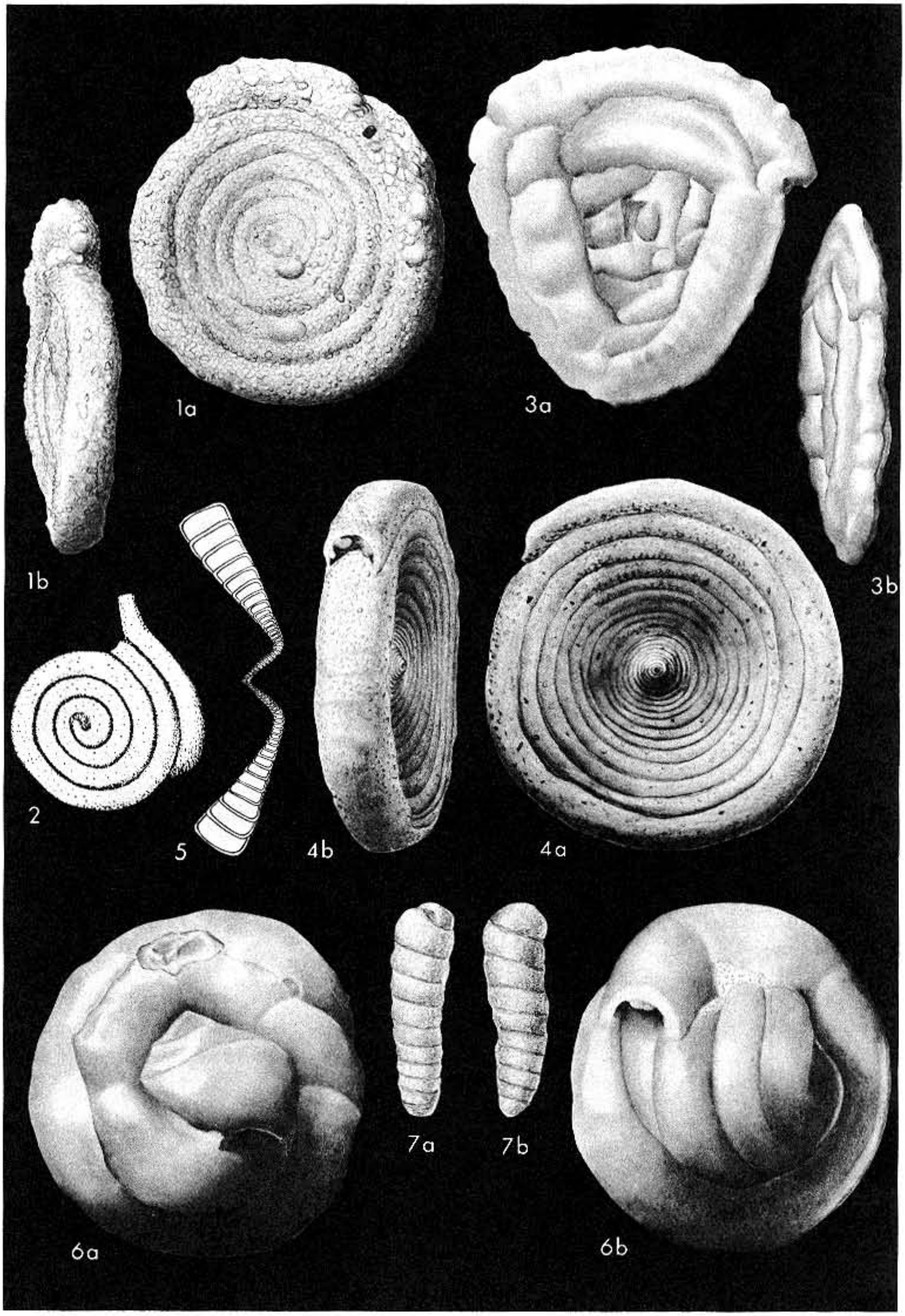


FIG. 122. Ammodiscidae (Ammodiscinae; *1,2, Ammodiscus; 3, Glomospirella; 4,5, Ammodiscoides; 6, Glomospira; 7, Turritellella*) (p. C210, C212).

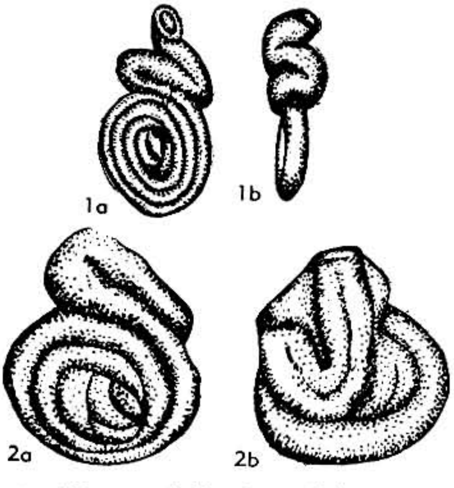


Fig. 123. Ammodiscidae (Ammodiscinae; *1,2, Ammovertellina*) (p. *C*210).

Other specimens with irregular surfaces show roughened internal walls which suggest a labyrinthic structure. However, the globular paratype Plummer figured as an internal cast, showing the spongy interior, we believe to be a complete specimen, as it shows an agglutinated wall and is not a secondarily formed internal cast. It is a globular specimen with exterior labyrinthic wall and seems quite distinct from the smooth-walled, compressed holotype. The interior of a large number of smooth forms must be examined in order to determine if they do represent a single species, and if the genus does include all specimens here included by Plummer.]

Verrucina Goës, 1896, *805, p. 25 [**V. rudis*; OD(M)] [=*Arverrucum* Rhumbler, 1913, *1572b, p. 346 (obj.) *(nom. van.)*]. Test attached, hemispherical to ovoid; coarsely agglutinated, interior partially subdivided into chamberlets; aperture in depressed area at summit of test. [Similar to *Colonammina* but with complex interior.] *Rec.*, E.Pac.——Fig. 119,*11*. **V. rudis*, off Mex.; *11a,b*, edge and top views, ×7 (*2117).

Weikkoella Summerson, 1958, *1858, p. 548 [**W. sphaerica*; OD]. Test similar to *Thuramminoides*, but without definite central cavity, entire test consisting of labyrinthic agglutinated material with ramifying cavity. *M.Dev.*, USA(Ohio).——Fig. 119,*3-5*. **W. sphaerica*; *3*, ext. of holotype, ×53; *4*, broken specimen showing inter., ×53; *5*, diagram. sec. showing labyrinthine chamber cavity, ×26 (*1858).

Family AMMODISCIDAE Reuss, 1862

[*nom. correct.* Rhumbler, 1895, p. 83 (*pro* family Ammodiscinea Reuss, 1862, p. 365]——[All names of family rank]——[=Ammodisculinidae Rhumbler, 1913, p. 339 *(nom. van.)*; =Arammodisclidia Rhumbler, 1913, p. 341 *(nom. van)*; =Ammodiscida Haeckel, 1894, p. 185; =Tolypamminidae Loeblich & Tappan, 1954, p. 308]

Test free or attached, proloculus followed by nonseptate enrolled tubular second chamber, aperture formed by open end of tube. *Sil.-Rec.*

Subfamily AMMODISCINAE Reuss, 1862

[*nom. transl.* Rhumbler, 1904, p. 275 (*ex* family Ammodiscinea Reuss, 1862)] [=Arammodiscinia Rhumbler, 1913, p. 385 *(nom. van.)*; Baissunellinae Arapova, 1961, p. 151]

Test free, planispiral, or irregularly coiled. *Sil.-Rec.*

Ammodiscus Reuss, 1862, *1552, p. 365 [**Ammodiscus infimus* Bornemann, 1874, *174, p. 725 (*non Orbis infimus* Strickland, 1846); =*Involutina silicea* Terquem, 1862, *1883, p. 450; SD Loeblich & Tappan, 1954, *1165, p. 306; Gerke, 1960, *781, p. 7; Loeblich & Tappan, 1961, *1176, p. 191] [=*Arammodiscum* Rhumbler, 1913, *1572b, p. 387 (obj.) *(nom. van.)*; *Bifurcammina* Ireland, 1939, *976, p. 201 (type, *B. bifurca*)]. Test free, discoidal, proloculus followed by undivided planispirally enrolled tubular chamber, which may show transverse growth constrictions but no internal partitions; wall agglutinated; aperture at open end of tubular chamber. [Gerke, 1960, *781, p. 7, and Loeblich & Tappan, 1961, *1176, p. 191, independently arrived at similar conclusions as to the type-species and status of *Ammodiscus*. The occasional double chamber, basis for the genus *Bifurcammina*, is an accidental occurrence in many species, from Paleozoic to Recent, and does not warrant separate generic status.] *Sil.-Rec.*, cosmop.——Fig. 122,*1*. **A. siliceus* (Terquem), L.Jur.(Lias.), Fr.; *1a,b*, side and edge views of lectotype, ×44 (*1165).——Fig. 122,*2*. *A. bifurca* (Ireland), Sil., USA (Okla.); ×53 (*976).

Ammovertellina Suleymanov, 1959, *1854, p. 19 [**A. prima*; OD]. Test free, with tubular chamber streptospirally coiled in early stage, later planispiral, as in *Glomospirella*, but with final stage uncoiled and zigzag growth as in *Ammovertella*; wall agglutinated of angular quartz grains in insoluble cement; aperture simple, at open end of tube. *Paleoc.*, *?Rec.*, USSR(Uzbek, Kyzylkumov).——Fig. 123,*1,2*. **A. prima*; *1a,b*, side and edge views of holotype; *2a,b*, opposite sides of paratype, ×68 (*1854).

Ammodiscoides Cushman, 1909, *402, p. 424 [**A. turbinatus*; OD] [=*Arammodiscodum* Rhumbler, 1913, *1572b, p. 387 (obj.) *(nom. van.)*]. Early stage regularly trochospiral as in *Arenoturrispirillina*, later planispiral as in *Glomospirella* or *Ammodiscus*; aperture at open end of tubular chamber. *Penn.-Rec.*, Eu.-N.Am.-Atl.-Carib.——Fig. 122,*4,5*. **A. turbinatus*, Rec., Carib.; *4a,b*, side and edge views, ×16 (*2117); *5*, diagram. sec. showing plan of coiling, ×40 (*402).

Arenoturrispirillina Tairov, 1956, *1861, p. 115 [**A. aptica* Tairov & Kuznetsova, 1956, *1861, p. 115; OD]. Test conical, similar in plan to *Ammodiscus* but with regular trochospiral coil,

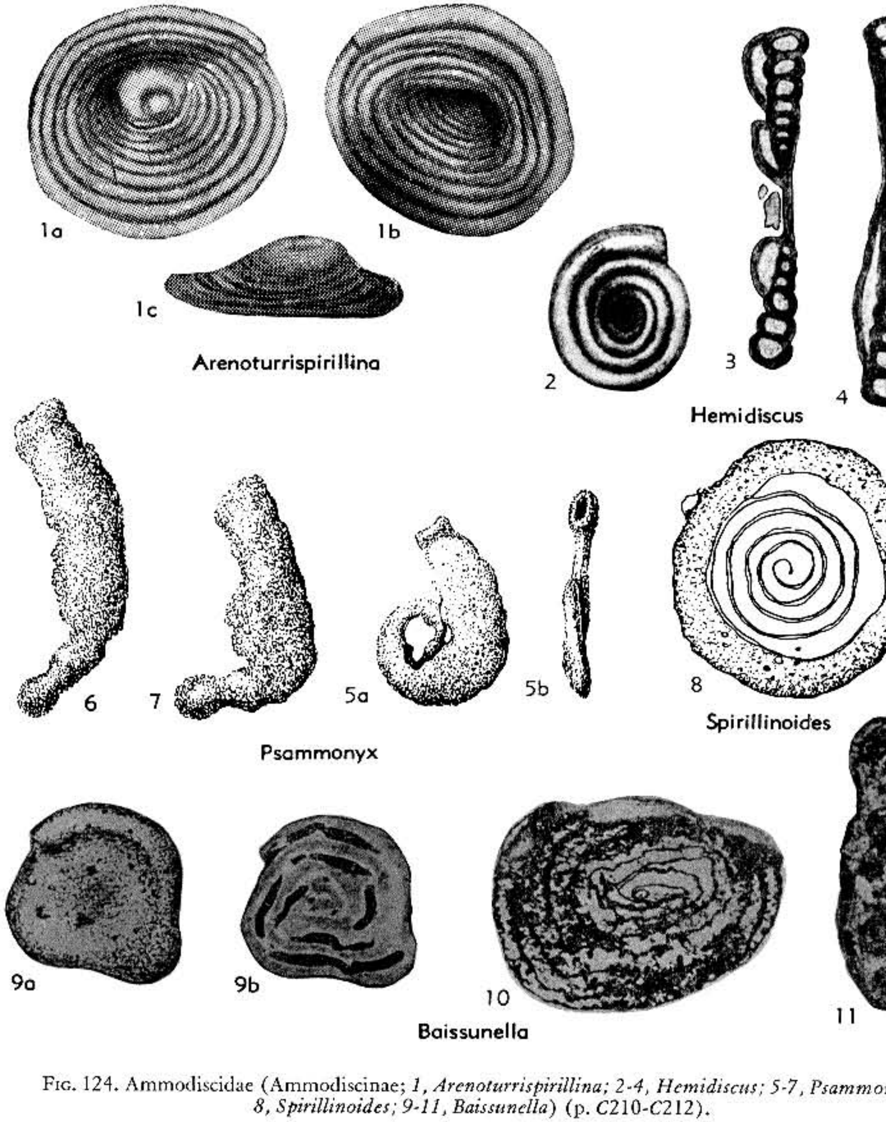


FIG. 124. Ammodiscidae (Ammodiscinae; *1, Arenoturrispirillina; 2-4, Hemidiscus; 5-7, Psammonyx; 8, Spirillinoides; 9-11, Baissunella*) (p. C210-C212).

as in early stage of *Ammodiscoides,* evolute and not close-coiled or high-spired as in *Turritellella,* aperture at open end of tube. *Cret.-Eoc.,* Eu.-N. Am.——FIG. 124,*1.* **A. aptica* TAIROV & KUZNETSOVA, L.Cret., USSR; *1a-c,* approx. ×100 (*1861).

Baissunella ARAPOVA, 1961, *27A, p. 151 [**B. mirkamalovae;* OD]. Test free, large, to 6.0 mm. diam., discoidal, periphery rounded; oval proloculus followed by tubular second chamber, which in section is seen to have slight growth constrictions giving appearance of pseudochambers, plane of coiling may vary slightly with growth; spiral suture obscure; wall of 2 layers, inner one with angular quartz grains in large amount of calcareous cement, exterior layer of microgranular calcite; aperture a rounded areal opening. *U.Cret. (U.Cenom.),* USSR(Uzbek).——FIG. 124,*9-11.* **B. mirkamalovae,* Baisun-Tau, Uzbek SSR; *9a,b,* ext. (paratype) (stated to be lateral views, but one drawing apparently reversed, or that of fig. 9b may be in transmitted light), ×5; *10,* transv. sec. showing growth constrictions in early coil, ×8; *11,* long. sec. showing change in plane of coiling which produces sigmoid appearance, ×9 (*27A).

[This genus was made the monotypic representative of a new subfamily Baissunellinae, because of the "two layered" wall and "pseudochambers." As the proportions of cement and agglutinated matter vary in many Ammodisci-

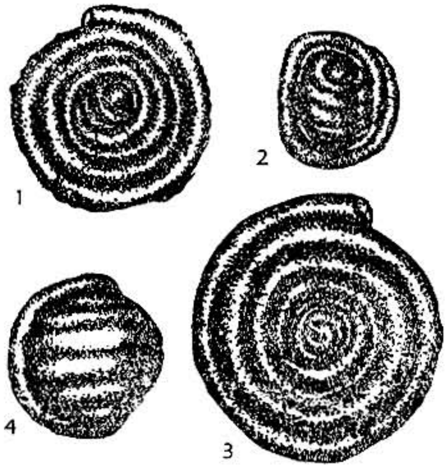


FIG. 125. Ammodiscidae (Ammodiscinae; *1-4*, *Usbekistania*) (p. C212).

nae, it is here placed in this subfamily. The genus is tentatively recognized, although the large size of the test is unusual for Cretaceous Ammodiscidae; possibly examination may prove it to be a calcareous worm tube. It was described from Upper Cretaceous (lower Turonian) in the *Inoceramus labiatus* zone where it is associated with *Praeglobotruncana stephani*. It is regarded by us as late Cenomanian in age.]

Glomospira Rzehak, 1885, *1600, p. 126 [**Trochammina squamata* Jones & Parker, *var. gordialis* Jones & Parker, 1860, *998, p. 304; OD (M)] [=*Seguenza* O. Silvestri, 1889, *1792, p. 57 (type, *Seguenza anomala* Silvestri, 1889); *Gordiammina* Rhumbler, 1895, *1568A, p. 84 (obj.); *Arglomospirum* Rhumbler, 1913, *1572b, p. 387 (obj.) *(nom. van.)*; *Tolypamminella* Marie in Deleau & Marie, 1961, *580A, p. 83 (type, *T. vermiculare* Marie, 1961); *Hemigordiellina* Marie in Deleau & Marie, 1961, *580A, p. 76 (type, *Glomospira diversa* Cushman & Waters, 1930, *539A, p. 42)]. Test similar to *Ammodiscus*, but coiling streptospiral or irregular; aperture at end of tube. *Sil.-Rec.*, cosmop.——Fig. 122,*6*. **G. gordialis* (Jones & Parker), Rec., Atl.; *6a,b*, opposite sides of test, ×116 (*2117).

Glomospirella Plummer, 1945, *1468, p. 233 *(non Glomospirella* Reytlinger, 1950) [**Glomospira umbilicata* Cushman & Waters, 1927, *534, p. 148; OD] [=*Brunsiella* Reytlinger, 1950, *1560, p. 16 (type, *Glomospira ammodiscoidea* Rauzer-Chernousova, 1938, *1501, p. 93, 151)]. Test free, discoidal, early stage as in *Glomospira*, later planispiral as in *Ammodiscus*; wall very finely agglutinated, smoothly finished; aperture at open end of tube. *U.Carb.(L.Penn.-M.Penn.)-Cret.*, N.Am.-Eu.——Fig. 122,*3*. **G. umbilicata* (Cushman & Waters), L.Penn., USA(Tex.); *3a,b*, side and edge views of holotype, ×68 (*2117).

Hemidiscus Schellwien, 1898, *1644, p. 265 [**Ammodiscus (Hemidiscus) carnicus*; OD] [=*Arhemidiscum* Rhumbler, 1913, *1572b, p. 387 (obj.) *(nom. van.)*]. Test similar to *Ammodiscus* but later coiling irregular on one side; wall finely agglutinated; aperture at open end of tubular chamber. *U.Carb.-Perm.*, Eu.——Fig. 124,*2-4*. **H. carnicus*, U.Carb., Italy; *2*, side view, ×100; *3,4*, cross secs., ×100 (*1644).

Psammonyx Döderlein, 1892, *598, p. 145 [**P. vulcanicus*; OD] [=*Arpsammonyxum* Rhumbler, 1913, *1572b, p. 386 (obj.) *(nom. van.)*]. Test similar to *Ammodiscus*, but with tubular chamber compressed, evolute and tending to uncoil; aperture terminal, may have slight bordering lip. *Dev.*, USA(Okla.); *Rec.*, Japan.——Fig. 124,*5-7*. **P. vulcanicus*, Rec., Japan; *5a,b*, side and edge views of enrolled form; *6,7*, uncoiled forms; all ×1.7 (*1570).

Spirillinoides Rhumbler, 1938, *1576, p. 174 [**S. circumcinctus*; OD]. Test consisting of a planispiral and evolute to slightly trochospirally coiled undivided tubular chamber; wall pseudochitinous, imperforate, with the outer whorl bordered by an agglutinated layer; aperture at the open end of the tubular chamber. *Rec.*, N.Sea.——Fig. 124, *8*. **S. circumcinctus*, Helgoland, ×200 (*1576).

Turritellella Rhumbler, 1904, *1569, p. 283 [*pro Turitellopsis* Rhumbler, 1895, *1568A, p. 84 *(nom. null., fide* Rhumbler, 1904, *1569, p. 289, corr. *Turritellopsis* Rhumbler) *(non* Sars, 1878)] [**Trochammina shoneana* Siddall, 1878, *1736, p. 46; SD Schellwien, 1898, *1644, p. 265] [=*Arturritellum* Rhumbler, 1913, *1572b, p. 387 (obj.) *(nom. van.)*]. Test free, elongate, high-spired; proloculus followed by long undivided close-coiled tubular 2nd chamber; wall finely agglutinated, reddish or yellowish, grading from more deeply colored proloculus to lighter terminal portion; aperture at open end of tube. *Sil.-Rec.*, Eu.-N.Am.-Arctic-Antarctic. —— Fig. 122,*7*. **T. shoneana*, Rec., N.Am.(off Baffin Is); *7a,b*, opposite sides of test, ×100 (*1162).

[Rhumbler, 1895 (*1568A, p. 84) described *Turitellopsis* as being "turitellaartig," spelling both the new generic name and that of the gastropod genus with one "r." Comparison to the gastropod genus, also misspelled, is regarded as evidence of erroneous spelling in the original publication (Code, Art. 32,a,ii), hence Rhumbler's name was a homonym of *Turritellopsis* Sars. It was renamed by Rhumbler, 1904 (*1569, p. 283) as *Turritellella*.]

Usbekistania Suleymanov, 1960, *1855, p. 18 [**Glomospirella (Usbekistania) mubarekensis*; OD] [=*Glomospirella (Usbekistania)* Suleymanov, 1960, *1855, p. 18 (obj.)]. Test free, consisting of spherical proloculus and undivided tubular 2nd chamber coiled in high spire around vertical axis, with final stage planispirally coiled at axis nearly perpendicular to original axis; wall agglutinated, of minute quartz grains in insoluble, probably siliceous cement; aperture at open end of tube. *Jur.-Rec.*, USSR(Uzbek).——Fig. 125, *1-4*. **U. mubarekensis*, Paleoc., Bukhara *(1-3)*, U.Eoc., Amu Darya Basin *(4)*; *1-3*, holotype and paratypes; *4*, paratype; all ×100 (*1855).

Subfamily TOLYPAMMININAE Cushman, 1928

[Tolypammininae CUSHMAN, 1928, p. 103]

Test attached, proloculus followed by tubular second chamber, coiled or irregular. _Sil.-Rec._

Tolypammina RHUMBLER, 1895, *1568A, p. 83 [*_Hyperammina vagans_ BRADY, 1879, *196a, p. 33; OD(M)] [=_Serpulella_ EIMER & FICKERT, 1899, *692, p. 674 (obj.); _Adhaerentina_ PAALZOW, 1935, *1406, p. 28 (type, _Adhaerentina permiana_ PAALZOW, 1935)]. Test attached, large globular proloculus followed by long undivided tubular 2nd chamber of smaller diameter which winds irregularly over surface of attachment; wall agglutinated with considerable cement, commonly reddish; aperture at open end of tubular chamber. [Differs from _Lituotuba_ in lacking the early streptospiral coil and in having an irregularly winding later stage.] _U.Sil.-Rec._, Eu.-N.Am.-N.Z.-Australia-Antarctic-Atl.-Pac.——FIG. 126,_1_. *_T. vagans_ (BRADY), Rec., S.Atl.; ×19 (*2117).——FIG. 126, _2_. _T. permiana_ (PAALZOW), Perm.(Zech.), Ger.; ×8 (*1406).

Ammodiscella IRELAND, 1956, *977, p. 845 [*_A. virgilensis_; OD]. Similar to _Hemidiscus_, but attached. _U.Penn.(Virgil.)_, USA(Kans.).——FIG. 126,_7_. *_A. virgilensis_; _7a_, top view; _7b_, attached side; _7c_, cross sec.; all ×53 (*977).

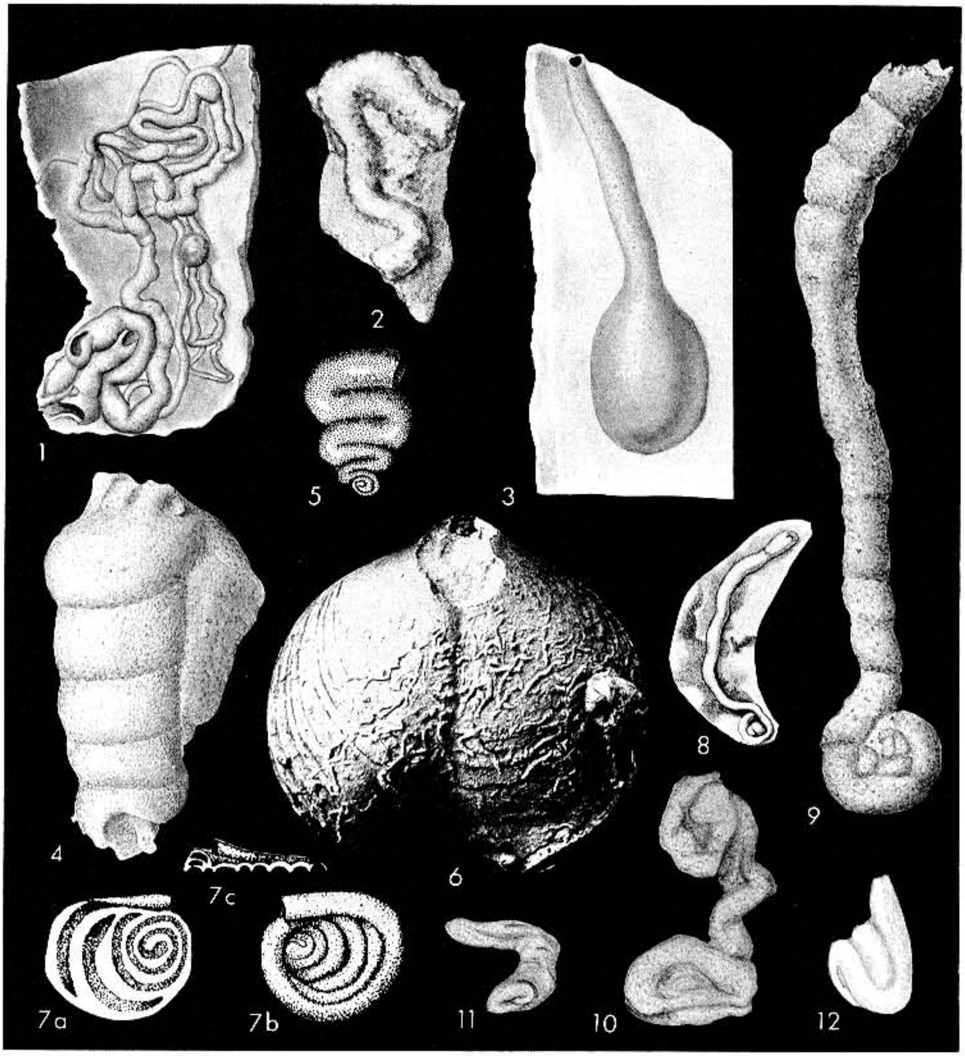


FIG. 126. Ammodiscidae (Tolypammininae; _1,2_, _Tolypammina_; _3_, _Ammolagena_; _4_, _Trepeilopsis_; _5_, _Ammovertella_; _6_, _Serpulopsis_; _7_, _Ammodiscella_; _8-12_, _Lituotuba_) (p. C213-C214).

Ammolagena Eimer & Fickert, 1899, *692, p. 673 [**Trochammina irregularis* (d'Orbigny) var. *clavata* Jones & Parker, 1860, *998, p. 304; OD (M)] [=*Arammlagenum* Rhumbler, 1913, *1572b, p. 346 (obj.) (*nom. van.)*]. Test attached, lagenoid, with elongate tubular neck; wall with pseudochitinous inner layer and finely agglutinated outer layer; aperture terminal, rounded. *Sil.-Rec.,* Ger.-Atl.-Carib.-Medit.——Fig. 126,*3*. **A. clavata* (Jones & Parker), Rec., Gulf Mex.; ×20 (*2117).

Ammovertella Cushman, 1928, *436, p. 8 [*pro Ammodiscus (Psammophis)* Schellwien, 1898, *1644, p. 265 (*non Psammophis* Fitzinger, 1826)] [**Ammodiscus (Psammophis) inversus* Schellwien, 1898, *1644, p. 266; OD] [=*Arpsammophoum* Rhumbler, 1913, *1572b, p. 387 (obj.) (*nom. van.)*]. Test attached, proloculus followed by elongate undivided tubular 2nd chamber which progresses in zigzag fashion, later bends closely adjacent to earlier ones; wall agglutinated, with considerable cement; aperture at open end of tube. *Penn.-Rec.,* Eu.-N.Am.-Carib.——Fig. 126,*5*. **A. inversa* (Schellwien), U. Carb., Eu.(Carnic Alps), enlarged (*1509).

Lituotuba Rhumbler, 1895, *1568A, p. 83 [**Serpula filum* Schmid, 1867, *1672, p. 583; SD Schellwien, 1898, *1644, p. 265] [=*Ammonema* Eimer & Fickert, 1899, *692, p. 685 (obj.); *Arlituotubum* Rhumbler, 1913, *1572b, p. 386 (obj.) (*nom. van.)*; *Thalmannina* Majzon, 1943, *1203, p. 64, 154 (type, *T. nothi*)]. Test free or attached, early stage irregularly coiled undivided tube as in *Glomospira,* later stage uncoiling and becoming rectilinear; aperture at end of tube. [Specimens with irregular early coil are found in many assemblages, and do not warrant generic separation.] *Sil.-Rec.,* cosmop.——Fig. 126,*8*. **L. filum* (Schmid), Perm.(Zech.), Ger.; enlarged (*193).——Fig. 126,*9*. *L. lituiformis* (Brady), Rec., Carib.; ×20 (*2117).——Fig. 126,*10,11*. *L. irregularis* Tappan, L.Jur., N.Alaska; *10,* test showing irregular character, ×48 (*1874); *11,* irregular specimen, ×28 (*1874).——Fig. 126,*12*. *L. nothi* (Majzon), Flysch, Hung.; ×36 (*1203).

Serpulopsis Girty, 1911, *790, p. 124 [**Serpula insita* White, 1878, *2054, p. 37; OD] [(*non Serpulopsis* Kittl, 1913)]. Test free or attached, may be somewhat embedded in host; proloculus followed by close-coiled tube of 1 or 2 volutions, then with tube of irregular growth, enlarging slowly; wall agglutinated; aperture at open end of tube. [Originally regarded as an annelid, *Serpulopsis* (*Treatise* Part W, p. 160) was considered by Henbest (1960, *898, p. B386) to be a foraminifer.] *Penn.,* USA(Okla.-Ind.).——Fig. 126,*6*. **S. insita* (White), USA(Okla.); attached tubes on surface of brachiopod, ×1.3 (*791).

Trepeilopsis Cushman & Waters, 1928, *535, p. 38 [**Turritellella grandis* Cushman & Waters, 1927, *534, p. 149; OD]. Test tubular undivided chamber in high trochospiral coil as in *Turritellella* but attached commonly to spines of "*Productus,*" with final portion of tubular chamber reverting and growing straight across previous whorls; aperture at open end. *U.Dev.-Perm.,* N.Am.-Eu.——Fig. 126,*4*. **T. grandis* (Cushman & Waters), M. Penn., USA(Tex.); high-spired test and reverted tubular chamber which may have been attached to algae, as central area is open, ×53 (*2117).

Superfamily LITUOLACEA
de Blainville, 1825

[*nom. correct.* Loeblich & Tappan, 1961, p. 277 (*pro* superfamily Lituolidea Glaessner, 1945, p. 93, *ex* family Lituacea de Blainville, 1825)]——[In synonymic citations superscript numbers refer to taxonomic rank assigned by authors (^{1}tribu, ^{2}family group, ^{3}superfamily); dagger(†) indicates *partim*]——[=^{1}Lituolina Delage & Hérouard, 1896, p. 132; =^{3}Lituolicae Brönnimann, 1958, p. 176]——[=^{3}Enclinostegia† Eimer & Fickert, 1899, p. 682; =^{3}Orthoklinostegia† Eimer & Fickert, 1899, p. 685; =^{2}Textulinidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 88; =^{2}Nodosalidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 86; =^{2}Rotaliaridia† Rhumbler in Kükenthal & Krumbach, 1923, p. 88]

Multilocular, typically coiled spirally or uncoiled or straight, reduction of chambers in each whorl may result in triserial or biserial arrangement; chambers simple or labyrinthic; wall siliceous or agglutinated, with calcareous, siliceous, or ferruginous cement; aperture single or multiple. *Miss.-Rec.*

Family HORMOSINIDAE
Haeckel, 1894

[*nom. correct.* Loeblich & Tappan, herein, *pro* Hormosinida Haeckel, 1894, p. 185]——[All names of family rank; dagger(†) indicates *partim*]——[=Arenacea Bütschli in Bronn, 1880, p. 193 (*nom. nud.*); =Aschemonellidae Eimer & Fickert, 1899, p. 676; =Nodosamminidae† Rhumbler, 1913, p. 339 (*nom. nud.*); =Arnodosammidia† Rhumbler, 1913, p. 341 (*nom. van.*); =Reophacidae Cushman, 1927, p. 15; =Silicinidae Cushman, 1927, p. 29; =Reophacida Copeland, 1956, p. 186 (*nom. van.*)]

Test free, chambers arranged in straight or curved series; wall agglutinated, aperture terminal. *Miss.-Rec.*

Subfamily ASCHEMONELLINAE
Eimer & Fickert, 1899

[*nom. transl.* Cushman, 1910, p. 80 (*ex* family Aschemonellidae Eimer & Fickert, 1899)] [=Araschemonellinia Rhumbler, 1913, p. 439 (*nom. van.*)]

Irregular chambers in rectilinear arrangement. *Cret.-Rec.*

Aschemonella Brady, 1879, *196a, p. 44 [**A. scabra;* OD (M)] [=*Araschemonellum* Rhumbler, 1913, *1572b, p. 440 (*nom. van.*)]. Test free, consisting of tubular or inflated chambers in single or commonly branching series; wall thin, finely to coarsely agglutinated, firmly cemented; apertures several, rounded, at ends of tubular necks. *Cret.-Rec.,* Atl.-Pac.-Eu.——Fig. 127,*1*. **A. scabra,* Rec., N.Pac. (*Challenger* Sta-

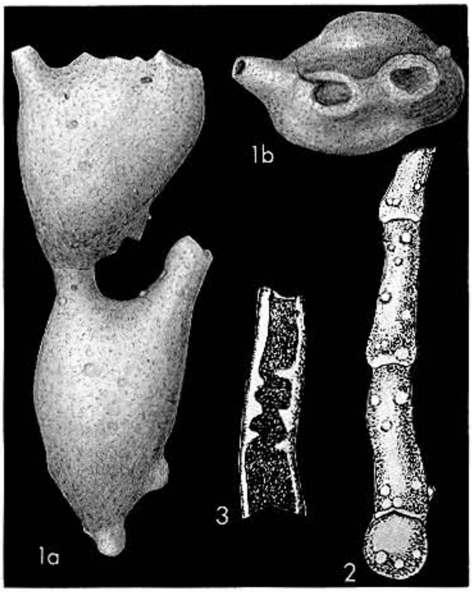


Fig. 127. Hormosinidae (Aschemonellinae; *1, Aschemonella; 2,3, Kalamopsis*) (p. *C*214-*C*215).

tion 244, lat. 35°22′N., long. 169°53′E., 2,900 fathoms); *1a,b,* side and top views of lectotype here designated (BMNH-ZF 1102), ×10 (*2117).

[Brady (1884, *200) considered *A. scabra* to be a synonym of *Astrorhiza catenata* Norman, 1876, but the two species are distinct. *Aschemonella catenata* is a much smaller, delicate species, with chambers tending to be bulbous rather than elongate as in *A. scabra.* The name of the type-species thus remains *A. scabra. Aschemonella* differs from *Kalamopsis* in its inflated chambers which may branch and in having more than one aperture to each chamber.]

Kalamopsis de Folin, 1883, *725, p. 320 [**K. vaillanti;* OD (M)] [=*Arkalamopsum* Rhumbler, 1913, *1572b, p. 352 *(nom. van.)*]. Test with globular proloculus and tubular later chambers, which are separated internally by partial septa not always reflected by external sutures. *Rec.,* Atl.-Pac.——Fig. 127,*2,3.* **K. vaillanti,* Gulf Gasc.; *2,3,* side view and long. sec., enlarged (*1569).

Subfamily HORMOSININAE Haeckel, 1894

[*nom. transl.* Loeblich & Tappan, herein, *ex* family Hormosinida Haeckel, 1894, p. 185]——[=Reophacinae Cushman, 1910, p. 81; =Arreophaxnia Rhumbler, 1913, p. 440 *(nom. van.)*; =Reophacidinae Silvestri, 1950, p. 44 *(nom. van.)*; =Proteonininae Galloway, 1933, p. 65; =Silicininae Cushman, 1933, p. 143]

Chambers typically in regular rectilinear series; wall agglutinated, interior simple; aperture single or multiple. *Miss.-Rec.*

Hormosina Brady, 1879, *196a, p. 56 [**H. globulifera;* SD Cushman, 1910, *404a, p. 93] [=*Arhomosum* Rhumbler, 1913, *1572b, p. 441 *(nom. van.)*]. Test similar to *Reophax* but with very large globular chambers; wall finely arenaceous, with abundant cement and smoothly finished; aperture on produced neck. *Jur.-Rec.,* Atl.-Pac.-Eu.-Carib.-Medit.-Antarctic.——Fig. 128,*4,5.* **H. globulifera,* Rec., Atl.; *4a,* side view of microspheric form; *4b,* top view; *5,* side view of single-chambered specimen; all ×20 (*2117).

Auerinella Frenguelli, 1953, *746, p. 46 [**A. fuegiae;* OD]. Test similar to *Reophax,* but very small, about 0.175 mm. long, insoluble in HCl, somewhat roughened surface; aperture elliptical, on subcylindrical neck. *Pleist.,* S.Am.——Fig. 129, *1.* **A. fuegiae; 1a,* photograph of surface; *1b,* median plane; *1c,* outline drawing, all ×600 (*746).

Nodosinum Hofker, 1930, *928b, p. 121 [**Nodosinella gaussica* Rhumbler, 1913, *1572b, p. 453, 459, 460, 461; (=*Arnodosinum py-gaussicum* Rhumbler, 1913, *1572b, p. 452, 453, 459, 460, 461, *nom. van.)*; OD]. Similar to *Reophax* but with radiate aperture owing to ribs that protrude inward from apertural opening and extend internally length of neck. *Rec.,* Malay Arch. (Indon.).——Fig. 129,*3-6.* **N. gaussicum* (Rhumbler); *3,4,* side views, ×4.5; *5,* apert. view, enlarged; *6,* long. sec. of final chamber, enlarged (*928b).

[The type-species was stated by Thalmann (1961, *1905, p. 232) to be *Arnodosinum py-gassicum* Rhumbler, 1913 *(sic)*. However, it was named *Nodosinella gaussicum* by Rhumbler (followed by the added "new nomenclature" he was then proposing). Hofker stated (*928b, p. 122) that he gave the species the name *Nodosinum gaussicum*; hence the specific name *py-gaussicum* is merely a *nomen vanum* synonym.]

Polychasmina Loeblich & Tappan, 1946, *1154, p. 242 [**P. pawpawensis*; OD]. Test free, flattened, composed of linear series of chambers; wall thick, coarsely arenaceous; aperture terminal, consisting of single row of elongate slits, paralleling flattened sides of test. *L.Cret.(Alb.),* USA(Tex.).——Fig. 128,*6,7.* **P. pawpawensis; 6a,b,* side and top views of broad, flattened specimen; *7,* side view of narrower form, ×10 (*2117).

Protoschista Eimer & Fickert, 1899, *692, p. 605, 677 [**Lituola findens* Parker, 1870, *565, p. 176; OD (M)]. Test free, consisting of series of chambers which are normally regularly uniserial, commonly branching from proloculus and forming 2 or 3 uniserial series of slightly inflated chambers, nearly equal in size throughout; wall agglutinated, with comparatively little cement, surface rough; aperture circular, at ends of series of chambers. [*Protoschista* differs from *Reophax* in developing a branching habit of growth.] *Rec.,* Atl.-Arctic.——Fig. 130,*4.* **P. findens* (Parker), Alaska; ×66 (*1162).

Psammolingulina Silvestri, 1904, *1760, p. 247 [**Lingulina papillosa* Neugeboren, 1856, *1351, p. 97; OD]. Test elongate, uniserial, similar to *Reophax* with agglutinated wall but with elongate, arcuate terminal aperture. *U.Cret.-Plio.,* Eu.——Fig. 129,*2.* **P. papillosa* (Neugeboren), Mio.-Plio., Rumania; *2a,b,* side, top views, enlarged (*700).

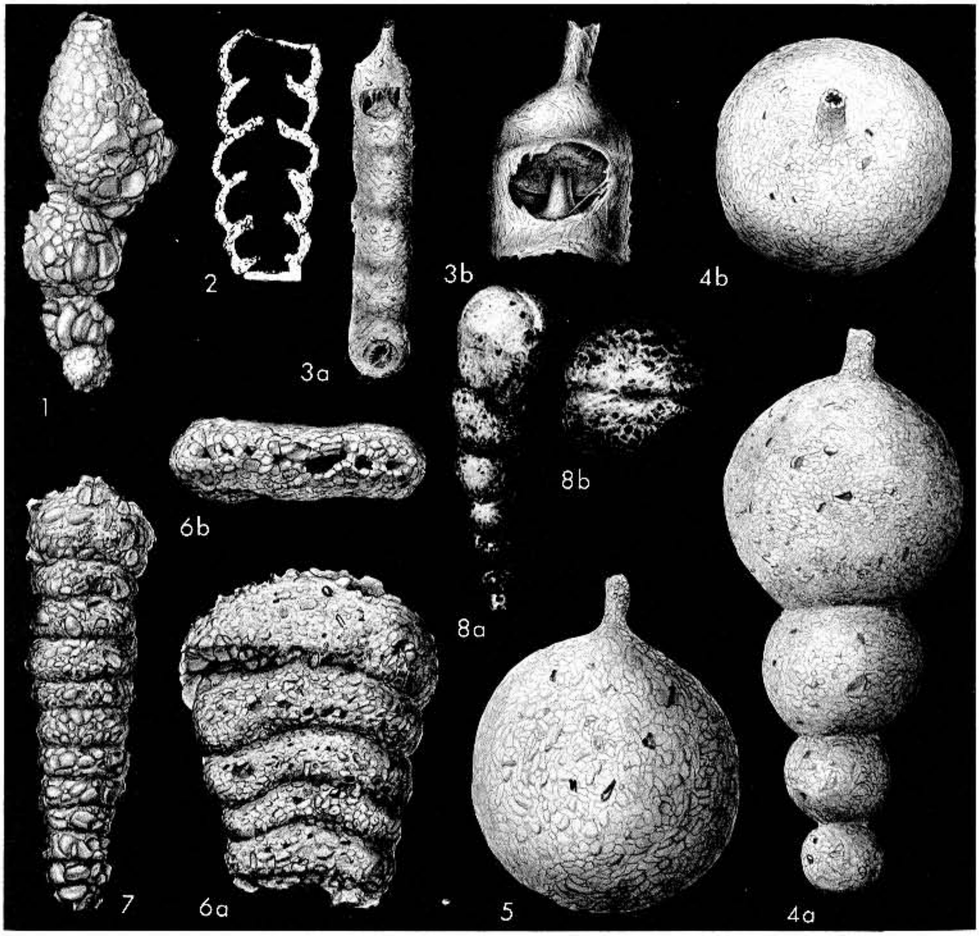


FIG. 128. Hormosinidae (Hormosininae; *1-3, Reophax; 4,5, Hormosina; 6,7, Polychasmina; 8, Sulcophax*) (p. *C*215-*C*217).

Reophax MONTFORT, 1808, *1305, p. 331 [**R. scorpiurus;* OD (M)] [=*Reophagus* AGASSIZ, 1844, *5, p. 22 *(nom. van.)*; *Proteonina* WILLIAMSON, 1858, *2065, p. 1 (type, *P. fusiformis*); *Silicina* BORNEMANN, 1874, *174, p. 731 (type, *Involutina polymorpha* TERQUEM, 1864, *1885, p. 432); *Lituolina* GOËS, 1881, *800, p. 33 (obj.); *Reophaxopsis* DE FOLIN, 1887, *129, p. 127 (type, *R. elegans*); *Nodulina* RHUMBLER, 1895, *1568A, p. 82, 85 (type, *Reophax dentaliniformis* BRADY, 1881, *196c, p. 49, SD LOEBLICH & TAPPAN, herein); *Rheophax* EIMER & FICKERT, 1899, *692, p. 603 *(nom. van.)*; *?Ammofrondicularia* SCHUBERT, 1902, *1681, p. 24 (type, *A. angusta*); *Arreophaxum* RHUMBLER, 1913, *1572b, p. 441 *(nom. van.)*; *Arproteonum* RHUMBLER, 1913, *1572b, p. 348 *(nom. van.)*; *Arsilicoum* RHUMBLER, 1913, *1572b, p. 389 *(nom. van.)*; *Ginesina* BERMÚDEZ & KEY, 1952, *129, p. 72 (type, *G. delicatula*)]. Test free, elongate, nearly straight or arcuate; chambers few, increasing in size as added; sutures nearly horizontal, obscure to moderately constricted; wall agglutinated, with comparatively little cement, surface rough; aperture terminal, rounded, at end of distinct tubular neck. *Miss.-Rec.*, cosmop.——FIG. 128,*1*. **R. scorpiurus*, Rec., Gulf Mex.; side view, ×45 (*2117).——FIG. 128, *2*. *R. angusta* (SCHUBERT), L.Oligo., S.Tirol; holotype, sectioned, ×66 (*700).——FIG. 128,*3*. *R. delicatula* (BERMÚDEZ & KEY), Rec., Carib.; *3a*, side view, portion of penultimate chamber wall removed to show interior, ×13; *3b*, terminal portion, ×28 (*2117).

[*Reophax* differs from *Hormosina* in lacking the very distinct apertural neck and globular chambers of the latter. From *Protoschista* it is distinguished by its lack of branching habit of growth. *Proteonina* WILLIAMSON has been shown to be a *Reophax* (*1166, p. 7), as based on the type-species. *Silicina* was shown (*1875, p. 210) to be unrecognizable, as two of the three original specimens of TERQUEM were indeterminate fragments and the last was a fragment of *Reophax*. *Ammofrondicularia* was based on a fragment in section, and although the base was not present on the type, it apparently also belongs to *Reophax*. *Ginesina* was originally distinguished from *Reophax* by the presence of an internal tube (*129). Restudy of the holotype shows that the "internal tube" merely represents the apertural neck of earlier chambers preserved within succeeding chambers, hence is not a valid basis for separation.]

Sulcophax Rhumbler in Wiesner, 1931, *2063, p. 93 [**S. claviformis;* OD (M)]. Test similar to *Reophax* but aperture curved slit, which may be in slight depression on terminal face. *Rec.*, Antarctic-N.Am.——Fig. 128,*8*. **S. claviformis; 8a,b,* side and apert. views, ×40, ×70 (*2063).

Thomasinella Schlumberger in Thomas, 1893, *1908, p. 5 [**T. punica* Schlumberger, 1893; SD Schlumberger in Peron, 1893, *1446, explanation pl. 14] [=*Thomasinella* Schlumberger, 1889, *1652, p. 425 *(nom. nud.)*; *Bireophax* Bolli, 1961, *163, p. 494 (type, *B. guaricoensis*)]. Test large, arborescent, branches composed of numerous cylindrical chambers somewhat

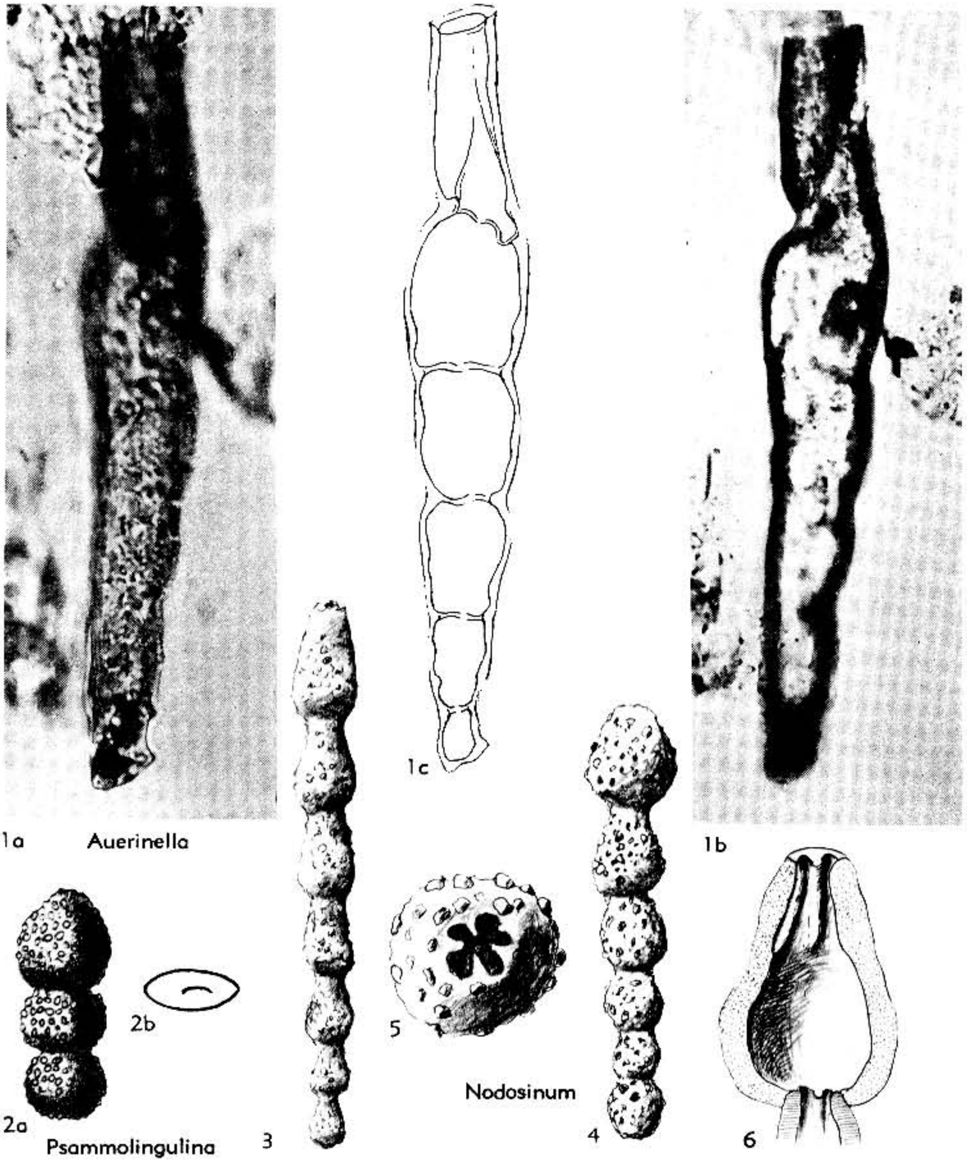


Fig. 129. Hormosinidae (Hormosininae; *1, Auerinella; 2, Psammolingulina; 3-6, Nodosinum*) (p. *C*215).

broader than high, arranged in single series, but regularly bifurcating so that adult test is composed of numerous dichotomously bifurcating and chambered branches; sutures distinct, horizontal, slightly constricted; wall agglutinated, very thick, traversed by large radially arranged pores which can be seen in broken specimens; apertures terminal on ends of branches, usually single, but

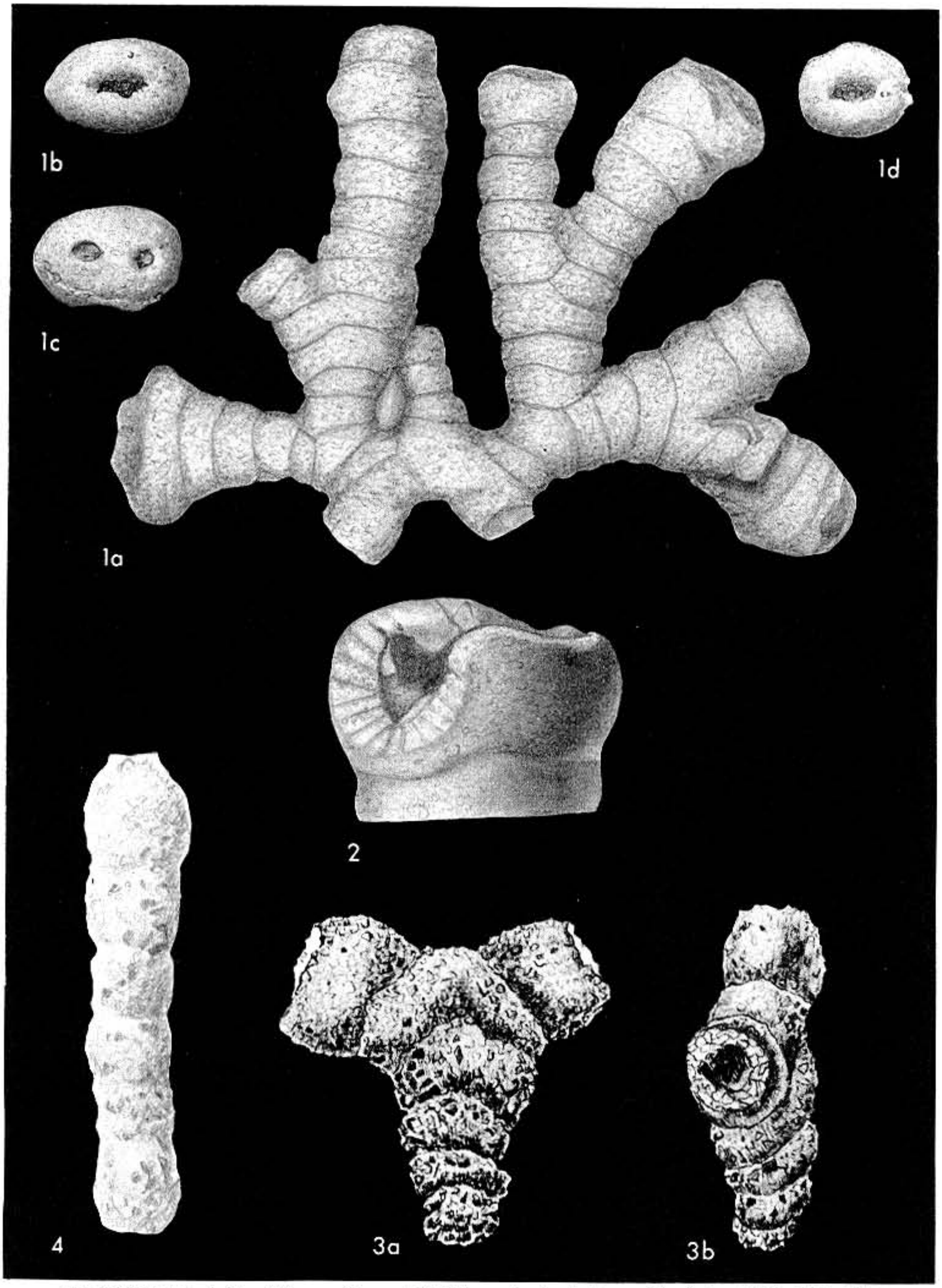


FIG. 130. Hormosinidae (Hormosininae; *1-3, Thomasinella; 4, Protoschista*) (p. C215, C217-C219).

rarely double, probably in later chambers just prior to bifurcation. *U.Cret.(Cenoman.)*, Alg.-Tunisia-Egypt-Venez.——Fig. 130,*1,2*. **T. punica*, Tunisia; *1a*, holotype, ×15.5; *1b-d*, apert. views, ×15.5; *2*, enlarged portion of broken specimen, canals perforating wall, ×30 (*2117).——Fig. 130,*3*. *T. guaricoensis* (Bolli), M.Cret., Venez.; *3a,b*, side and edge views of holotype, ×26 (*163).

[Although well described and figured nearly 70 years ago, this genus was generally overlooked because of the relative inaccessibility of the publications until the figures and description were copied by Ellis & Messina (*700). The first placement of the genus in a specific family was that by Sigal (1956, *1748, p. 104) who placed it in the "Haplophragmiidae (fam. Lituolidae, sousfamille Haplophragmoidinae pour Mayne)," regarding it as related to *Ammobaculites* and *Flabellammina*. Approximately three months later Omara (*1389, p. 885) independently published a redescription of the genus and placed it in the Reophacidae on the basis of an ontogenetic series he obtained from Egypt.]

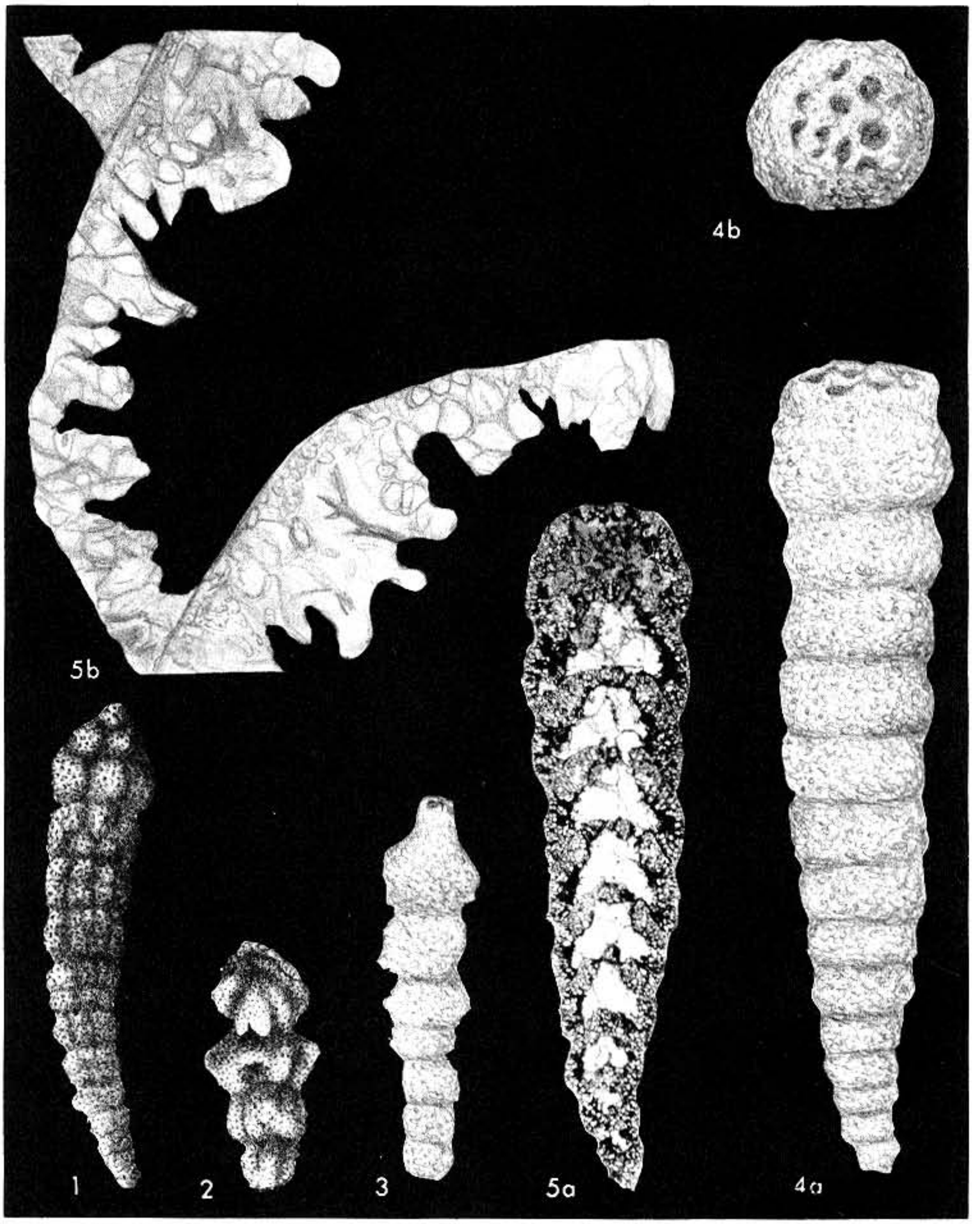


Fig. 131. Hormosinidae (Cribratininae; *1,2*, *Haplostiche; 3-5*, *Cribratina*) (p. C220).

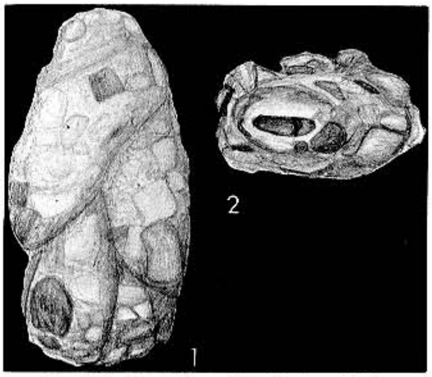


FIG. 132. Nouriidae; *Nouria* (p. C220).

Subfamily CRIBRATININAE
Loeblich & Tappan, n. subfam.

Test free, elongate; chambers in a rectilinear series; wall agglutinated; interior labyrinthic; aperture terminal. *Cret.*

Cribratina Sample, 1932, *1624, p. 319 [**Nodosaria texana* Conrad in Emory, 1857, *705, p. 159; OD]. Test free, large, to 10 mm. in length, elongate, uniserial and rectilinear, chambers closely appressed, sutures straight, horizontal, constricted; wall agglutinated, medium- to coarse-grained, with calcareous or ferruginous cement, labyrinthic; aperture terminal, cribrate, with numerous irregular, subangular openings on produced portion of terminal face. [Although previously regarded as a synonym of *Haplostiche*, the present genus differs in having a multiple aperture.] *L.Cret.(Alb.)-U.Cret.(Cenom.)*, N.Am.——Fig. 131,*3-5*. **C. texana* (Conrad); L.Cret. (Alb.), USA(Tex.); *3*, megalospheric specimen; *4a,b*, side and apert. views of microspheric specimen, ×11.5; *5a*, long. sec., ×12; *5b*, portion of long. sec. enlarged to show labyrinthic interior, ×72 (*2117).

Haplostiche Reuss, 1861, *1549, p. 15 [**Dentalina foedissima* Reuss, 1860, *1548, p. 189; OD] [=*Arhaplostichoum* Rhumbler, 1913, *1572b, p. 446 (obj.) *(nom. van.)*]. Test free, large, elongate, up to 7 or 8 mm. in length, consisting of numerous, uniserially arranged, gradually enlarging and closely appressed chambers; sutures horizontal, constricted; wall agglutinated, interior labyrinthic; aperture terminal, rounded, somewhat produced. *U.Cret.*, Eu.——Fig. 131,*1,2*. **H. foedissima* (Reuss), Ger.; approx. ×10 (*1549).

[*Haplostiche* is here restricted to include only species with single terminal aperture, as in the type-species. It differs from *Reophax* in its much larger size, labyrinthic interior, and closely appressed chambers. Small species with a single aperture and simple interior belong to *Reophax*, those with slitlike aperture are placed in *Psammolingulina*, and those with a terminal multiple aperture and labyrinthic interior are referred to *Cribratina*.]

Family NOURIIDAE
Chapman & Parr, 1936

[*nom. transl.* Loeblich & Tappan, 1961, p. 279 (*ex* subfamily Nouriinae Chapman & Parr, 1936, p. 149)]

Chambers in loose spiral or biserial, strongly overhanging laterally; aperture terminal. *?Eoc.,Rec.*

Nouria Heron-Allen & Earland, 1914, *910a, p. 375 [**N. polymorphinoides*; SD Cushman, 1927, *433, p. 189]. Test free, elongate, rounded in section; 2 to 5 elongate chambers which are first arranged in polymorphine spiral, later biserial; sutures obscure, little depressed; wall thin, externally smooth, rough within, of mineral grains, shell fragments, or sponge spicules; aperture terminal, round or oval, some with slight lip. *?Eoc., Rec.*, Eu.-Pac.-Carib.-Kerimba Arch.-N.Sea-Atl.——Fig. 132,*1,2*. **N. polymorphinoides*, Rec., Kerimba Arch.; *1*, side view of lectotype (here designated, BMNH-ZF 3622, *910a, pl. 37, fig. 7); *2*, top view of paratype, ×36 (*2117).

Family RZEHAKINIDAE
Cushman, 1933

[*nom. transl.* Tappan, 1957, p. 210 (*ex* subfamily Rzehakininae Cushman, 1933, p. 144)]——[=subfamily Silicininae Earland, 1933, p. 89 (*non* Silicininae Cushman, 1933); =Silicinidae Cushman, 1927 *(nom. nud.)*; =Paramiliolidae Sigal in Piveteau, 1952, p. 208 *(nom. nud.)*]

Test free, proloculus followed by tubular chambers, about half coil in length and added in various planes, as in calcareous imperforate Miliolidae; wall siliceous or agglutinated, generally insoluble in acid. *L.Cret.-Rec.*

Rzehakina Cushman, 1927, *431, p. 31 [**Silicina epigona* Rzehak, 1895, *1605, p. 214; OD]. Test ovate in outline, compressed; chambers a half coil in length, planispiral and involute; aperture at open end of chamber, somewhat constricted. *U. Cret.-Paleoc.*, cosmop.——Fig. 133,*1-3*. **R. epigona* (Rzehak), ?Paleoc., Eu.(Aus.); *1a,b, 2a,b*, side and top views, ×60 (*2117); *3*, long. sec., enlarged (*1605).

Ammoflintina Earland, 1934, *653, p. 98 [**A. trihedra*; OD]. Test free, roughly triangular in outline, planispiral, evolute; chambers 3 to whorl, wedge-shaped; aperture large, simple, at end of final chamber. [*Ammoflintina* was originally considered to belong to the Ammodiscinae, close to *Lituotuba*. It differs from *Lituotuba* in being distinctly chambered and coiled throughout.] *Rec.*, Antarctic.——Fig. 133,*7*. **A. trihedra*; lectotype (here designated, *653, pl. 3, fig. 22, BMNH-ZF 400); *7a,b*, opposite sides; *7c*, edge view, ×105 (*2117).

Miliammina Heron-Allen & Earland, 1930, *914c, p. 41 [**Miliolina oblonga* (Montagu) var. *arenacea* Chapman, 1916, *320, p. 59; SD Cockerell, 1930, *353, p. 975]. Chambers arranged in quinqueloculine plan; wall siliceous, insoluble in hydrochloric acid; aperture rounded, with infolding of wall to form tooth. *L.Cret.-Rec.*, N.Am.-Antarctic.-Eu.——Fig. 134,*1,2*. *M. earlandi* Loeblich & Tappan, Rec., S.Atl.(S.Georgia Is.); *1a-c*, lectotype; *1a,b*, opposite sides; *1c*, top view; *2*, sectioned specimen to show quinqueloculine plan, ×105 (*1166).

Psamminopelta Tappan, 1957, *1875, p. 211 [**P.*

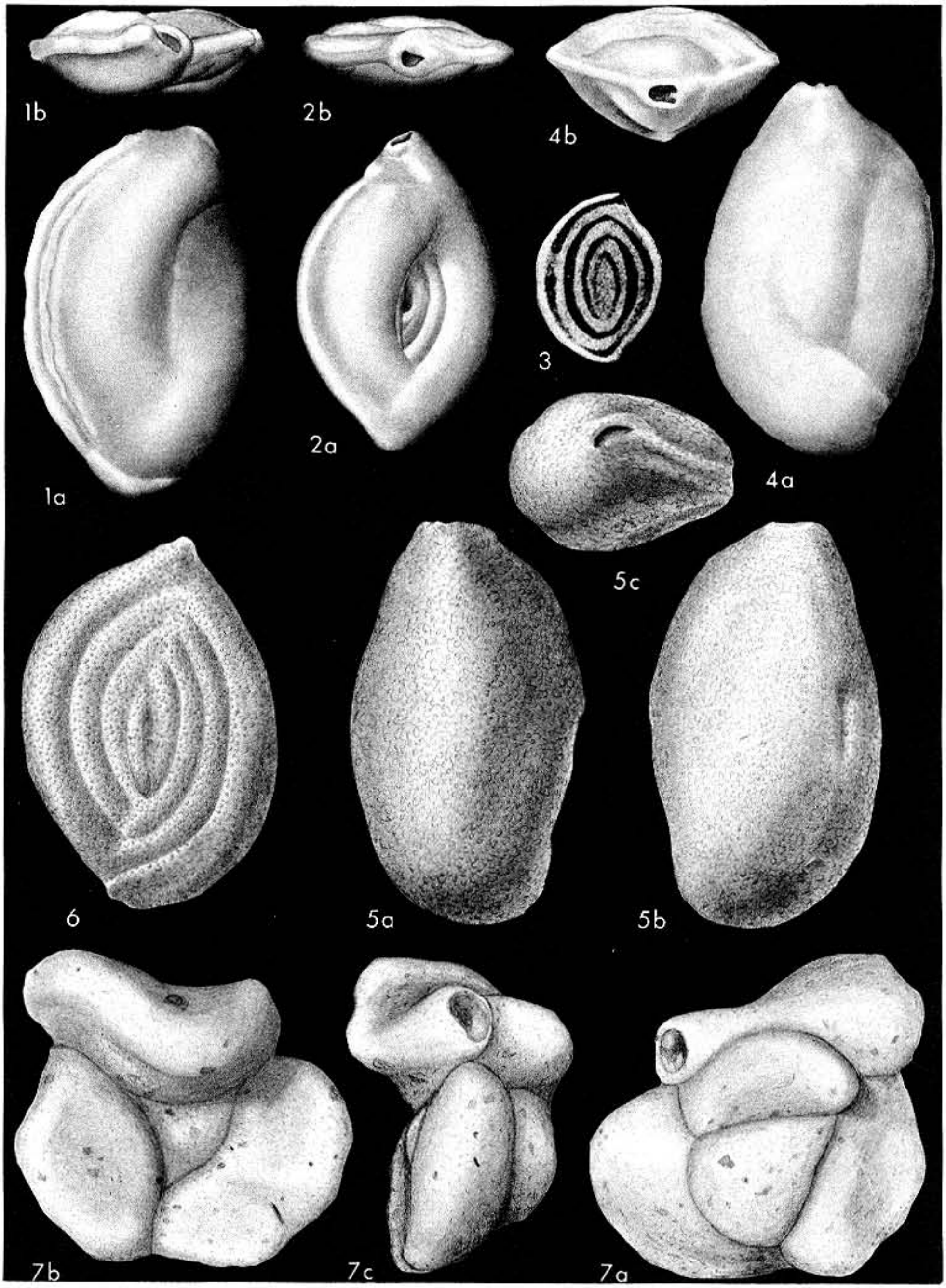


Fig. 133. Rzehakinidae (Rzehakininae; *1-3, Rzehakina; 4,5, Silicosigmoilina; 6, Psamminopelta; 7, Ammoflintina*) (p. C220-C222).

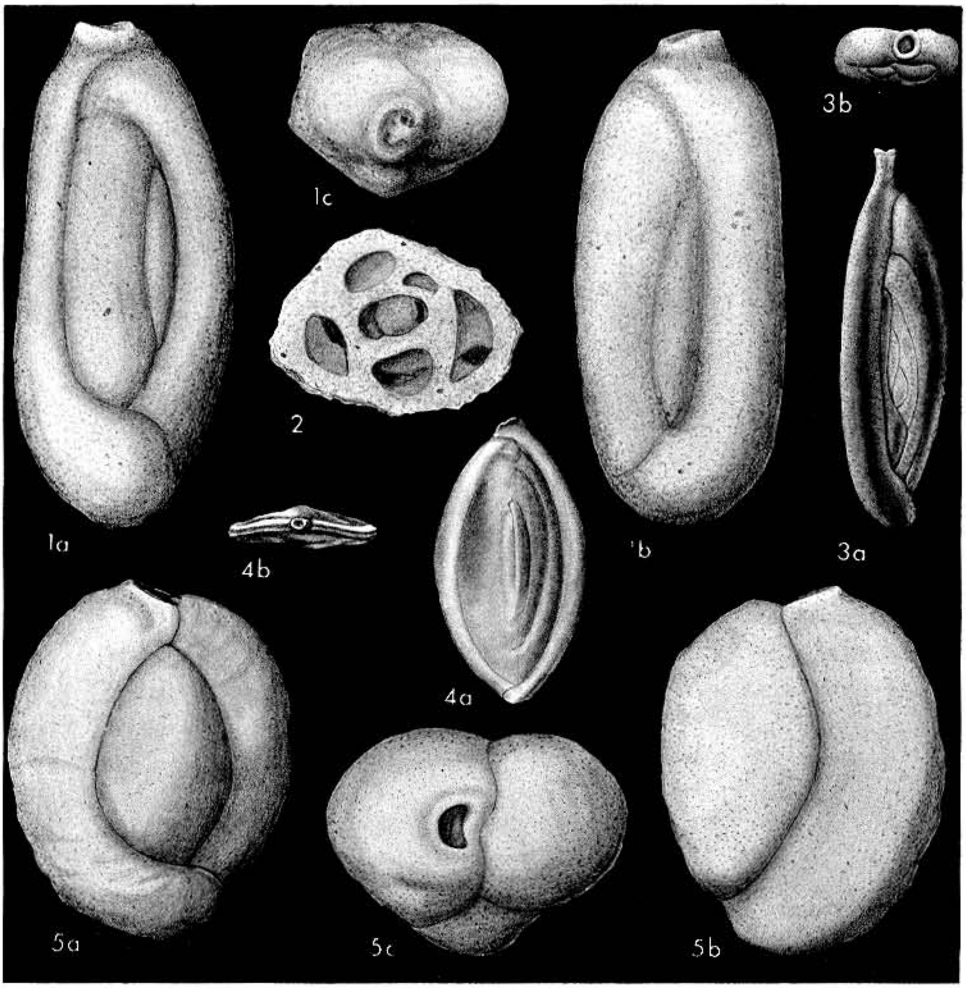


FIG. 134. Rzehakinidae (Rzehakininae; *1,2, Miliammina; 3, Spirolocammina; 4, Spirosigmoilinella; 5, Trilocularena*) (p. C220-C224).

bowsheri; OD]. Similar to *Spirosigmoilinella* but planispiral and evolute throughout and without any sigmoid development; aperture without tooth. [Differs from *Rzehakina* in being evolute and symmetrically planispiral in coiling.] *L.Cret.-U.Cret.*, N.Am.(Alaska).——FIG. 133,*6*. **P. bowsheri*, side view of holotype, ×62 (*2117).

Silicosigmoilina CUSHMAN & CHURCH, 1929, *500, p. 502 [**S. californica;* OD] [=*Silicosigmoilina (Bramletteia)* ISRAELSKY, 1951, *980, p. 10 (type, *S. (B.) perplexa)*]. Test with chambers half coil in length, planispirally arranged in early stages, later sigmoid; aperture described as lacking tooth, but small tooth or infolding of inner margin occurs in young specimens, slight compression of aperture in later stages obscuring its character somewhat. [*Bramletteia* was described as a subgenus for the species with a "toothlike" projection at the aperture. As this is also found in the type-species of *Silicosigmoilina*, the generic definition only requires modification and *Bramletteia* is a synonym.] *U.Cret.-Paleoc.*, N.Am.-S.Am.-Japan-Eu. —— FIG. 133,*4*. **S. californica*, U.Cret., USA(Calif.); *4a,b*, side and top views of paratype showing aperture and short toothlike projection, ×66 (*2117).——FIG. 133,*5*. *S. perplexa* ISRAELSKY, Paleoc., USA (Calif.); *5a-c*, opposite sides and top view of holotype, ×143 (*2117).

Spirolocammina EARLAND, 1934, *653, p. 109 [**S. tenuis;* OD]. Test minute, elongate; chambers evolute and nearly planispiral, but with slight sigmoid curve of long axis; aperture produced on neck, without tooth. *Rec.*, Antarctic.——FIG. 134, *3*. **S. tenuis; 3a,b*, side and top views, ×102 (*2117).

Spirosigmoilinella MATSUNAGA, 1955, *1237, p. 49

[**S. compressa;* OD]. Early stage sigmoid in development as in *Silicosigmoilina,* later chambers in single plane; aperture rounded, on short neck, and lacking tooth. *L.Mio.-M.Mio.,* Japan.——Fig. 134,4. **S. compressa; 4a,b,* side and top views showing rounded aperture and slightly inflated central portion due to early sigmoid development, ×62 (*2117).

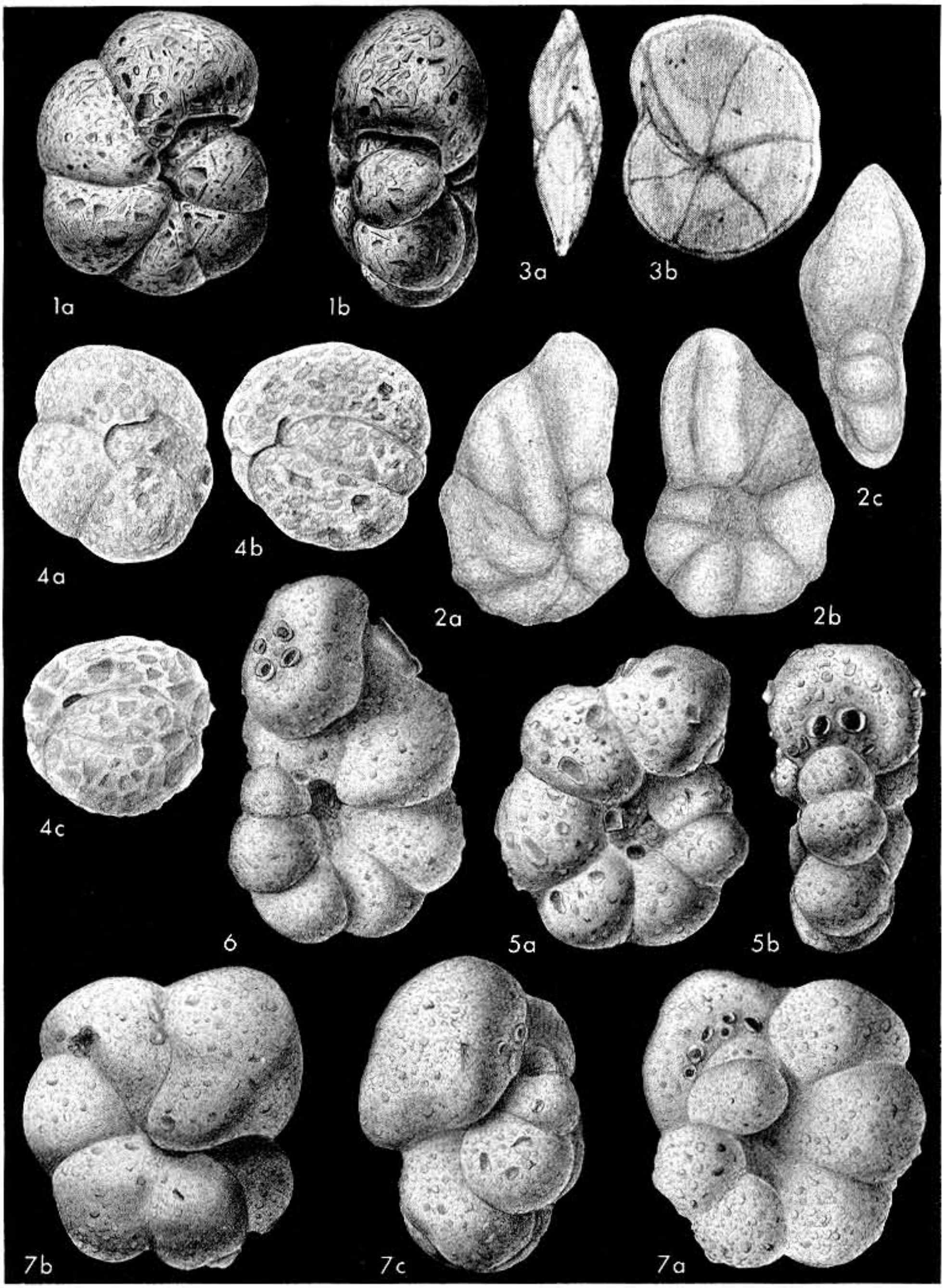


Fig. 135. Lituolidae (Haplophragmoidinae; *1-3, Haplophragmoides; 4, Adercotryma; 5-7, Trochamminita*) (p. *C*225-*C*227).

Trilocularena Loeblich & Tappan, 1955, *1166, p. 13 [**Miliammina circularis* Heron-Allen & Earland, 1930, *914c, p. 44; OD]. Chambers in triloculine arrangement; aperture with broad shallow tooth formed by infolding of margin. *Rec.*, Antarctic.——Fig. 134,5. **T. circularis*

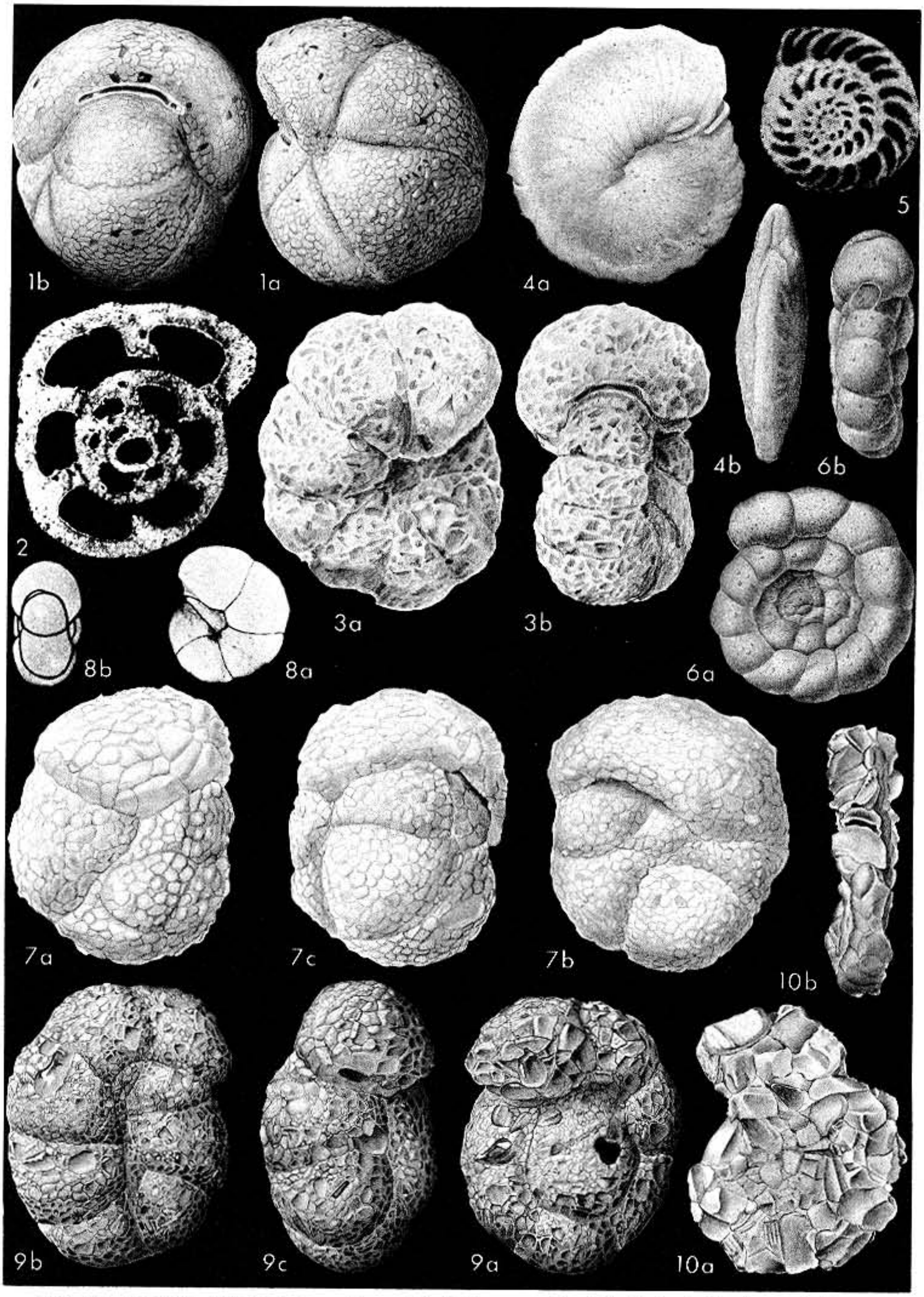


Fig. 136. Lituolidae (Haplophragmoidinae; *1-3, Cribrostomoides; 4,5, Daxia; 6, Trochamminoides; 7,8, Thalmannammina; 9, Recurvoides; 10, Discammina*) (p. *C225-C227*).

(Heron-Allen & Earland); *5a,b,* opposite sides; *5c,* top view, ×36 (*1166).

Family LITUOLIDAE de Blainville, 1825

[*nom. correct.* Schulze, 1877, p. 28 (*pro* family Lituacea and Lituacés de Blainville, 1825, p. 380)]——[All names of family rank; dagger(†) indicates *partim*]——[=Les Lituolacées Lamarck, 1809, p. 323 (*nom. neg.*); =Lituolata Crouch, 1827, p. 40; =Lituolitidae Broderip, 1839, p. 321; =Lituolacea Agassiz, 1844, p. 15; =Lituolidea Reuss, 1862, p. 308; =Lituolida Carpenter, 1861, p. 470; =Lituolidee Schwager, 1876, p. 482; =Lituolideae Gümbel, 1868, p. 22; =Lituolina Lankester, 1885, p. 847; =Lituoletta Haeckel, 1894, p. 164; =Lituolinae Delage & Hérouard, 1896, p. 132]——[=Polythalama† Latreille, 1825, p. 161 (*nom. nud.*); =Nautiloidae† d'Orbigny in de la Sagra, 1839, p. xxxviii, 38 (*nom. nud.*); =Nautiloida† Schultze, 1854, p. 53 (*nom. nud.*); =Loftusina Lankester, 1885, p. 847; =Loftusiidae Lister in Lankester, 1903, p. 142]——[=Spirocyclinidae Munier-Chalmas, 1887, p. xxxi; =Haplophragmidae Eimer & Fickert, 1899, p. 693; =Placopsilinidae Cushman, 1927, p. 41; =Polyphragmidae Hofker, 1930, p. 124; Haplophragmiidae Sigal in Piveteau, 1952, p. 162; =Mesoendothyridae Voloshinova, 1958, p. 19]

Test free or attached, early stage coiled, later may be uncoiled, irregular or annular; wall agglutinated, with calcareous cement or microgranular calcite, interior simple to labyrinthic, epidermal layer imperforate; aperture single or multiple. *Carb.-Rec.*

Subfamily HAPLOPHRAGMOIDINAE Maync, 1952

[Haplophragmoidinae Maync, 1952, p. 43]

Test free, coiled, interior simple, not labyrinthic, no alveolar hypodermis. *Carb.-Rec.*

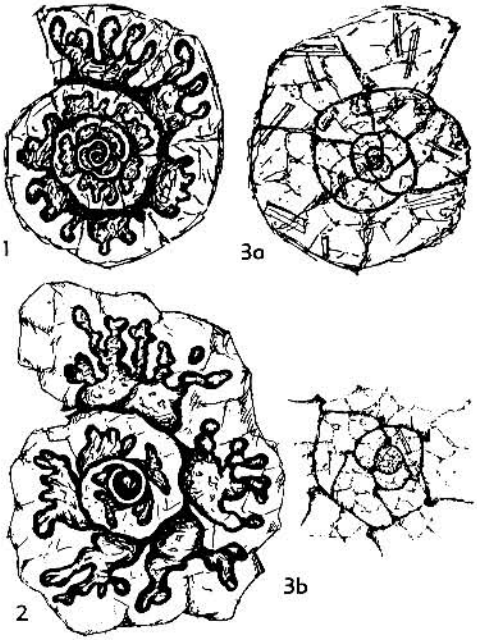


Fig. 137. Lituolidae (Haplophragmoidinae; *1-3, Discammina*) (p. *C226*).

Haplophragmoides Cushman, 1910, *404a, p. 99 [**Nonionina canariensis* d'Orbigny, 1839, *86, p. 128; OD] [=*Robulammina* Montanaro Gallitelli, 1947, *1299A, p. 189 (type, *Haplophragmoides? robulus*); *Asanospira* Takayanagi, 1960, *1863, p. 74 (type, *Lenticulina? teshioensis* Asano, 1950, *51, p. 21)]. Test planispirally coiled, involute; wall agglutinated, aperture an equatorial interiomarginal slit. [*Robulammina* was based on a very small species in flysch sediments of the Apennines where compression of the agglutinated species results in a considerable amount of distortion. *Asanoina* was separated on the basis of its siliceous cement, but as the type-species occurs in Cretaceous mud and siltstones, possibly the cement is a product of replacement in fossilization.] *Carb.-Rec.,* cosmop.——Fig. 135,*1*. **H. canariensis* (d'Orbigny), Rec., Philip.; *1a,b,* side and edge views, ×44 (*2117).——Fig. 135,*2*. *H. robulus* (Montanaro Gallitelli), U.Cret., Italy (Apennines); *2a,b,* opposite sides of lectotype (here designated, *1299A, figs. 1(9), 2(5); *2c,* edge view, ×212 (*2117).——Fig. 135,*3*. *H. teshioensis* (Asano), U.Cret., Japan; *3a,b,* edge and side views, ×26 (*1863).

Adercotryma Loeblich & Tappan, 1952, *1159, p. 141 [**Lituola glomerata* Brady, 1878, *195, p. 433; OD]. Test free, planispiral, subglobular or ovate, elongate in direction of coiling axis, slightly asymmetrical; aperture interiomarginal, forming low slit or arch near umbilicus on one side, and closer to umbilicus than to periphery, or may be lacking in final chamber. [*Adercotryma* differs from *Haplophragmoides* in being somewhat asymmetrical, completely involute rather than slightly evolute, in having the greatest dimension in the axis of coiling, and in the asymmetrically placed aperture, which is found near the umbilicus on one side rather than in the plane of coiling at the periphery, or it may even be lacking completely in the final chamber.] *Rec.,* Atl.-Pac.——Fig. 135,*4*. **A. glomerata* (Brady), Greenl.; *4a-c,* side and edge views, ×100 (*1159).

Cribrostomoides Cushman, 1910, *404a, p. 108 [**C. bradyi* (=*Lituola subglobosum* G. O. Sars, 1871); OD] [=*Labrospira* Höglund, 1947, *924, p. 141, 145 (type, *Haplophragmium crassimargo* Norman, 1892, *1364, p. 17)]. Similar to *Haplophragmoides* but with areal aperture consisting of single elongate slit in young, and dentate slit or row of areal pores in very large individuals. [The original types of both *Cribrostomoides* and *Labrospira,* here regarded as synonymous, have been restudied by us, and a lectotype is here designated for *Haplophragmium crassimargo* Norman (BMNH-ZF 3640, from Bog Fjord, East Finmark at 100-110 fathoms). As *Cribrostomoides bradyi* Cushman is a synonym of *Lituola subglobosum* G. O. Sars (*653, p. 89) the type-species should be referred to *Cribrostomoides subglobosum.*] *U. Cret.-Rec.,* Atl.-Pac.-N.Am.-Carib.-Japan-Eu.——Fig. 136,*1,2*. **C. subglobosum* (G. O. Sars), Rec.,

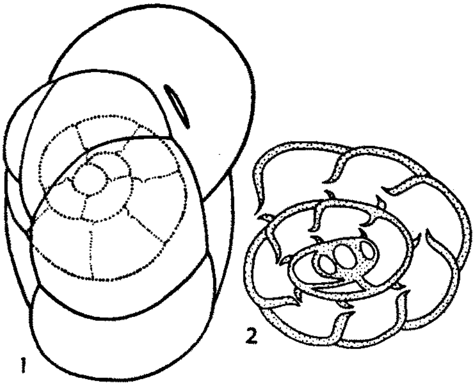


Fig. 138. Lituolidae (Haplophragmoidinae; *1,2, Recurvoides*) (p. *C226*).

Philip.; *1a,b,* side, edge views, ×26 (*2117); *2,* sagittal sec., ×20 (*894).——Fig. 136,*3. C. crassimargo* (Norman), Rec., Arctic; *3a,b,* side, edge views, ×17 (*1162).

Daxia Cuvillier & Szakall, 1949, *544, p. 8 [**D. cenomana;* OD]. Test planispiral and involute as in *Haplophragmoides* but having numerous broad low chambers with simple interior forming compressed lenticular test; wall finely agglutinated with calcareous cement; aperture elongate slit extending somewhat up face of final chamber. [*Daxia* superficially resembles *Cyclammina* but lacks the complex internal structure of that genus.] *U.Cret.(Cenom.),* Fr.——Fig. 136,*4,5.* **D. cenomana; 4a,b,* side and edge views of topotype, ×22 (*2117); *5,* sectioned specimen, ×10 (*544).

Discammina Lacroix, 1932, *1076, p. 2 [**D. fallax* Lacroix, 1932 (=*Lituolina irregularis* var. *compressa* Goës, 1882, *801, p. 141, =*Haplophragmium emaciatum* Brady, 1884, *200, p. 305); OD (M)]. Test planispiral, slightly evolute, to 1.5 mm. in diam., interior divided by thin straight septa, which may show at surface as sutural constrictions or be obscured by coarse wall texture; wall coarsely agglutinated on pseudochitinous membrane? and may include quartz grains, sponge spicules, or volcanic fragments in ferruginous cement; aperture low interiomarginal equatorial opening. *Rec.,* Medit.-Atl.-Pac.-Carib.——Fig. 136, *10*; 137,*1-3.* **D. compressa* (Goës), Atl. (136, *10*), Fr.(Gulf Gasc.) (137); 136,*10a,b,* side and edge views of specimen identified by Lacroix, ×45 (*2117); 137,*1,2,* microspheric and megalospheric specimens injected with air and viewed in transmitted light, showing pseudolabyrinthic appearance, ×67 (*1077); 137,*3a,* microspheric specimen filled with "essence de girofle," showing distinct septa, ×67 (*1077); 137,*3b,* central area showing slightly elevated apertures in straight, thin septa, ×133 (*1077).

[Brönnimann (1951, *225, p. 103) considered that *Discammina,* because of its supposedly nonseptate, undivided second chamber, belongs in the Ammodiscidae, as originally placed by Lacroix. Brönnimann noted that septa seemed to be shown in Lacroix's text-fig. *a,* but later Maync (1953, *1242, p. 148) indicated that neither true septa nor semisepta are present in *Discammina;* also, he did not consider it to have a truly labyrinthic wall. Nevertheless, *Discammina* was shown by Lacroix (1935, *1077) to be distinctly septate, the thin septa resembling those of *Ammoscalaria,* as shown by the figures here reproduced. The difference in interpretation of wall structure is due to the different methods used for study. Lacroix illustrated specimens that had been injected with air, colored liquids, or a clarifying liquid (such as "essence de girofle") after treatment in alcohol. These methods produced an appearance completely different from that obtained by thin sectioning. Bubbles introduced by the air-injection method gave specimens a complex appearance. In transmitted light, however, shells identified by Lacroix are nearly transparent because of large clear quartz grains in the walls, which give no indication of truly labyrinthic structure. Hence the genus does not belong with *Cyclammina,* as suggested by Lacroix (1935, *1077) or with *Ammodiscus,* as he concluded earlier (1932, *1076). Although here placed in the Haplophragmoidinae, *Discammina* is regarded as distinct from *Haplophragmoides* in having thin transverse septa (as in *Ammoscalaria*), which do not appear analogous to the apertural face. During the injection treatment Lacroix noted that the test was apparently imperforate, since the glycerin entered only at the aperture. This was regarded as evidence for a pseudochitinous base to the agglutinated test. The type-species was noted by Lacroix (*1077) to be a junior synonym of both *Lituolina irregularis* var. *compressa* Goës, 1882, and *Haplophragmium emaciatum* Brady, 1884. Although *Rhaphidohelix elegans* Möbius, 1880, was also regarded as identical, this last appears to be distinct, and is probably a trochospiral rather than planispiral form. The correct name for the type-species thus is *Discammina compressa* (Goës).]

Recurvoides Earland, 1934, *653, p. 91 [**R. contortus;* OD]. Test free, subglobular; coiling streptospiral, with few chambers in each whorl, later whorls in differing planes so that exterior somewhat resembles *Trochammina,* although only earlier periphery and not all earlier whorls are visible from spiral side; wall agglutinated, thin; aperture small, areal, with distinct bordering lip. [Coiling may vary from distinctly streptospiral throughout to nearly planispiral, with an abrupt change of 90° in the plane of coiling during development.] *Mio.-Rec.,* Antarctic-Carib.-Eu.-N. Am.-Atl.-Pac.——Fig. 136,*9.* **R. contortus,* Rec., Antarctic; *9a,b,* opposite sides; *9c,* edge view; all ×44 (*2117).——Fig. 138,*1. R. trochamminiforme* Höglund, Rec., Sweden; diagram of progressive change in coiling plan, ×175 (*924).——Fig. 138,*2. R. laevigatum* Höglund, Rec., Sweden; sectioned specimen showing position of aperture and change in direction of coiling, ×155 (*924).

Thalmannammina Pokorný, 1951, *1473, p. 477 [**Haplophragmium subturbinatum* Grzbowski, 1897, *836, p. 280; OD] [=*Recurvoidella* Uchio, 1960, *1961, p. 53 (type, *R. parkerae*)]. Similar to *Recurvoides,* but with interiomarginal aperture, not areal in position. *Eoc.-Rec.,* Eu.-Atl.-Pac.——Fig. 136,*7.* **T. subturbinata* (Grzbowski), Eoc., Eu.; *7a,b,* opposite sides; *7c,* edge view, ×105 (*2117).——Fig. 136,*8. T. parkerae* (Uchio), Rec., Calif.; *8a,* side view; *8b,* edge view showing interiomarginal aperture, ×50 (*1961).

Trochamminita Cushman & Brönnimann, 1948, *498, p. 17 [**T. irregularis;* OD]. Test free, enrolled, early portion planispiral, later portion may develop irregular inflated chambers; sutures radial in planispiral portion; wall agglutinated; apertures

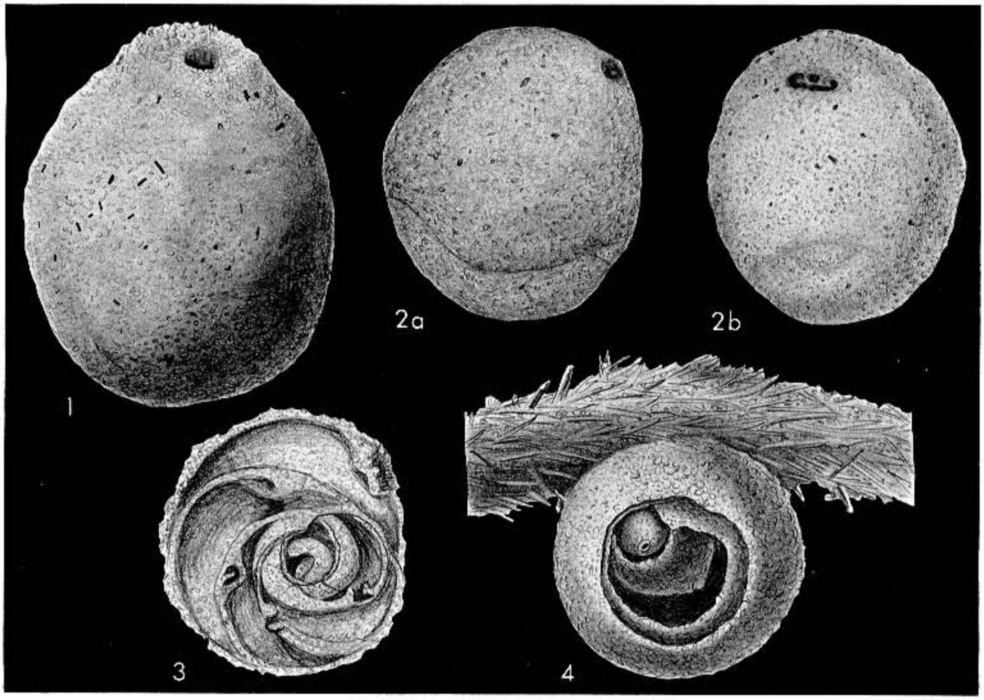


FIG. 139. Lituolidae (Sphaeramminiae; _1-3, Sphaerammina; 4, Ammosphaerulina_) (p. C227-C228).

areal, single or multiple in planispiral portion, variable in position on irregular later chambers, surrounded by prominent raised lips. [_Trochamminita_ differs from _Trochammina_ in being planispiral in the early stage and in having multiple areal apertures in the adult.] _Rec._, Carib.-USA (La.).——FIG. 135,_5-7_. *_T. irregularis_, Trinidad, W. Indies; _5a,b_, side and edge views, ×112; _6_, side view, ×82; _7a-c_, opposite sides and edge view, ×82 (*1631).

Trochamminoides CUSHMAN, 1910, *404a, p. 97 [*_Trochammina proteus_ KARRER, 1866, *1021, p. 494; OD]. Similar to _Haplophragmoides_ but coiling involute, aperture large, interiomarginal, with slightly thickened lip. _Carb.-Rec._, cosmop. ——FIG. 136,_6_. *_T. proteus_ (KARRER), Rec., Gulf Mex.; _6a,b_, side, edge views, ×17 (*2117).

Subfamily SPHAERAMMININAE Cushman, 1933

[Sphaeramminiae CUSHMAN, 1933, p. 87]

Test planispiral and involute, with later chambers almost completely overlapping and enclosing earlier ones; wall agglutinated; aperture areal, with incurved rim and projecting tooth. _Rec._

Sphaerammina CUSHMAN, 1910, *403, p. 439 [*_S. ovalis_; OD]. Test large, 1-2 mm. in length, consisting of planispiral series of strongly overlapping chambers, with little other than final chamber visible externally; wall finely arenaceous; aperture areal, slitlike to rounded, with simple to elongate tooth. [The generic definition is here emended to delineate planispiral instead of rectilinear development, as evidenced by dissected topotypes of the type-species.] _Rec._, Philip.——FIG. 139,_1-3_; 140,_1_. *_S. ovalis_; 139,_1_, holotype, ×35; 139,_2a,b_, side and edge views of topotype, chambers strongly overlapping, aperture areal, ×28; 139,_3_, horiz. half-section, showing planispiral coiling with approximately 5 chambers to each whorl but strong chamber overlap, so that only 3 are visible externally, apert. margin incurved, distinct apert. tooth seen in 3 chambers, ×28; 140,_1a-d_, apert. variation in specimens of _S. ovalis_, showing tooth and modifications, ×40 (all *2117).

Ammosphaerulina CUSHMAN, 1912, *405, p. 228 [*_A. adhaerens_; OD]. Test attached, otherwise

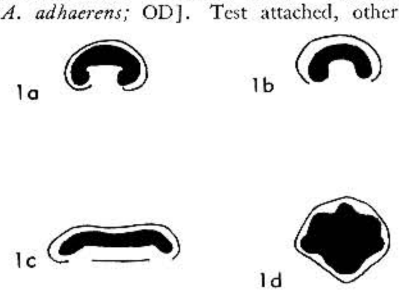


FIG. 140. Lituolidae (Sphaeramminiae; _1, Sphaerammina_) (p. C227).

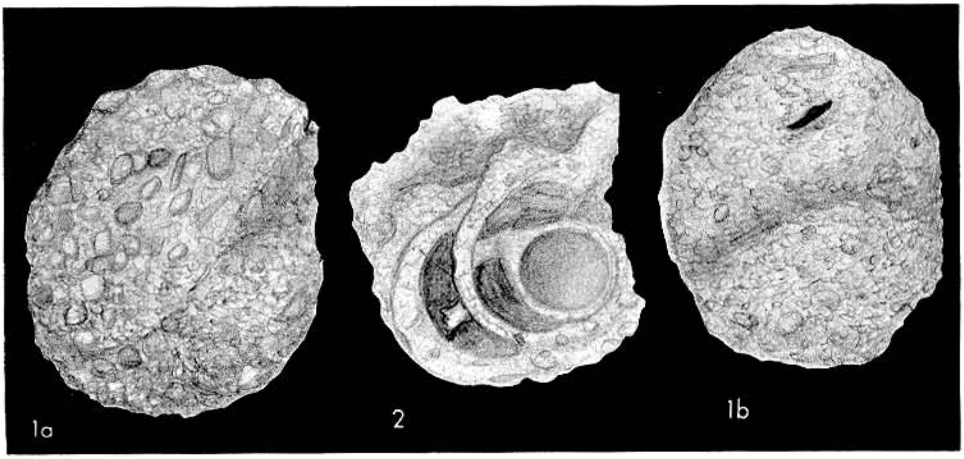


FIG. 141. Lituolidae (Sphaeramminiae; *1,2, Canepaia*) (p. *C*228).

similar to *Sphaerammina,* with completely overlapping chambers, approx. 0.75 mm. in diam. *Rec.,* Malay Arch.(Indon.).——FIG. 139,*4*. **A. adhaerens;* holotype attached to *Saccorhiza,* partially broken to show enveloping spherical chambers, ×44 (*2117).

Canepaia BOLTOVSKOY, 1961, *166, p. 74 [**C. brasiliensis;* OD]. Test free, subspherical, with strongly overlapping chambers, commonly only last 1 or 2 chambers visible externally, chamber arrangement asymmetrical, apparently planispiral as in *Sphaerammina;* wall agglutinated, septa in inner portion of wall very fine-grained, outer wall with some larger grains in fine-grained base; aperture small, rounded to irregularly elongate, with inward projecting lip which in broken specimens may give appearance of interseptal pillar. [*Canepaia* differs from *Sphaerammina* as herein redefined in the simple nondentate aperture. Because of strong similarity to *Sphaerammina* and absence of a rectilinear development, *Canepaia* is here transferred from the Reophacidae, where it was placed originally, to the Sphaeramminidae.] *Rec.,* S.Am.(Brazil).——FIG. 141,*1,2*. **C. brasiliensis; 1a,b,* side and apert. views of topotype with strongly overlapping chambers and elongate aperture; *2,* dissected specimen showing globular proloculus, overlapping later chambers with portions of inner entosolenian apertural necks appearing as interseptal pillars, ×72 (*2117).

Subfamily CYCLAMMININAE Marie, 1941

[Cyclammininae MARIE, 1941, p. 257] [=Choffatellinae MAYNC, 1958, p. 1]

Planispiral to uncoiling; wall with reticulate near-surface meshwork beneath imperforate epidermal coating and commonly with labyrinthic interior; aperture single or multiple. *Jur.-Rec.*

Cyclammina BRADY, 1879, *196a, p. 62 [**C. cancellata;* OD (M)] [=*Cyclammina* BRADY in NORMAN in JEFFREYS, 1876, *987, p. 214 *(nom. nud.)*]. Test planispirally coiled, involute; chambers low, broad, numerous, with complex interior, reticulate hypodermis beneath imperforate outer layer; wall finely agglutinated, both walls and septa strongly labyrinthic, with intricate network of branching and anastomosing passages; aperture consisting of equatorial interiomarginal slit and series of rounded pores with raised margins scattered over face. *Cret.-Rec.,* cosmop.——FIG. 142, *1-4*. **C. cancellata,* Rec., Atl. *(1-3),* Rec., Philip. *(4)*; *1a,b,* side and edge views, ×14 (*2117); *2,3,* equat. and axial secs., ×18 (*1248); *4,* equat. sec., ×20 (*894).

Alveolophragmium SHCHEDRINA, 1936, *1723, p. 312 [**A. orbiculatum;* OD]. Test planispiral, involute, similar to *Haplophragmoides,* but with complex interior; wall with inner alveolar structure below imperforate outer layer; aperture equatorial and areal, with bordering lips. *Rec.,* Arctic-Sea of Japan.——FIG. 143,*1,2*. **A. orbiculatum,* Sea of Japan; *1a,b,* side, edge views, ×12; *2,* sec. showing labyrinthic interior, ×25 (*1509).

Choffatella SCHLUMBERGER, 1905, *1665, p. 763 [**C. decipiens;* OD]. Test planispiral, involute, chambers numerous, broad and low, tending to increase in breadth somewhat in adult so that whorls are higher; wall with imperforate outer layer and alveolar inner layer, regularly spaced partitions; aperture linear series of pores in slight depression extending vertically up apertural face. *L.Cret.,* Medit.-USA-Mex.-Carib.-S. Am.(Venez.)-Afr.-W.Eu.——FIG. 143,*3-6*. **C. decipiens;* Port. *(3),* Venez. *(4,6),* Switz. *(5)*; *3a,b,* side and edge views of paratype, matrix attached to one side, ×24 (*2117); *4,* tang. sec.; *5,* median sec., microspheric; *6,* equat. sec., megalospheric; *4-6,* ×30 (*1239).

Feurtillia MAYNC, 1958, *1245, p. 1 [**F. frequens;* OD]. Test coiled to uniserial, like *Ammobaculites* but wall complex, with reticulate subepidermal meshwork; aperture elongate vertical slit in plane of coiling. *Jur.(Purbeck.)-L.Cret.(U.Valang.)*, Eu. (Switz.).——FIG. 144,*1-3*. **F. frequens*, Jur., Switz.; *1a-c*, holotype, opposite sides, and apert. views; *2,3*, median and axial secs. of paratypes showing thick septa, ×64 (*1245).

Hemicyclammina MAYNC, 1953, *1242, p. 148 [**H. sigali*; OD]. Test planispiral, involute, interior

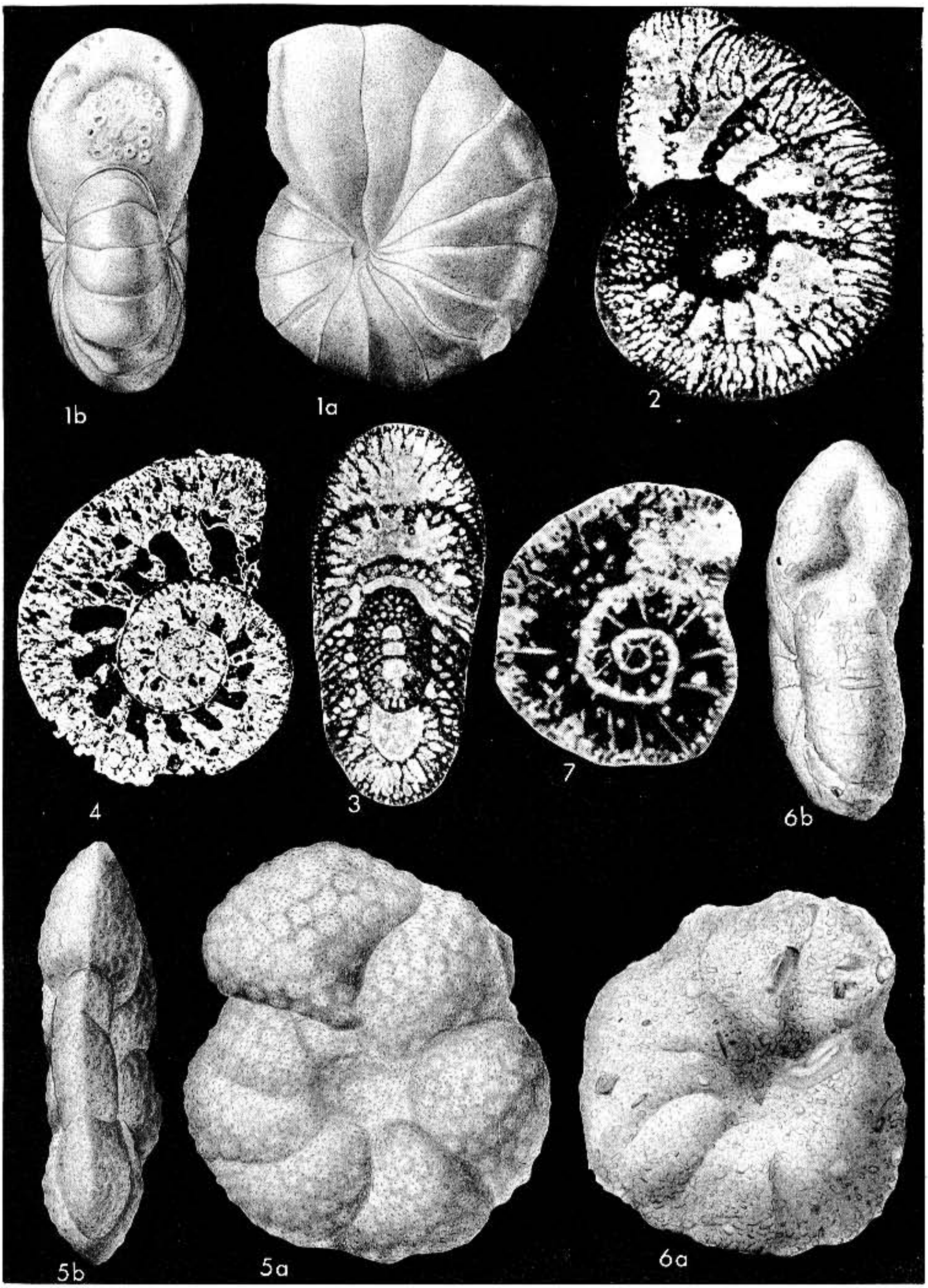


FIG. 142. Lituolidae (Cyclammininae; *1-4*, *Cyclammina*; *5*, *Reticulophragmium*; *6,7*, *Hemicyclammina*) (p. C228-C231, C233).

incompletely divided by "semisepta," or discontinuous septa projecting 0.5-0.8 distance across chamber cavity; outer wall labyrinthic, septal walls simple; aperture obscure in type-species, but apertural face depressed. *U.Cret.(M.Cenoman.)*, N.Afr. (Alg.).——FIG. 142,*6*,*7*. **H. sigali*; *6a,b*, side

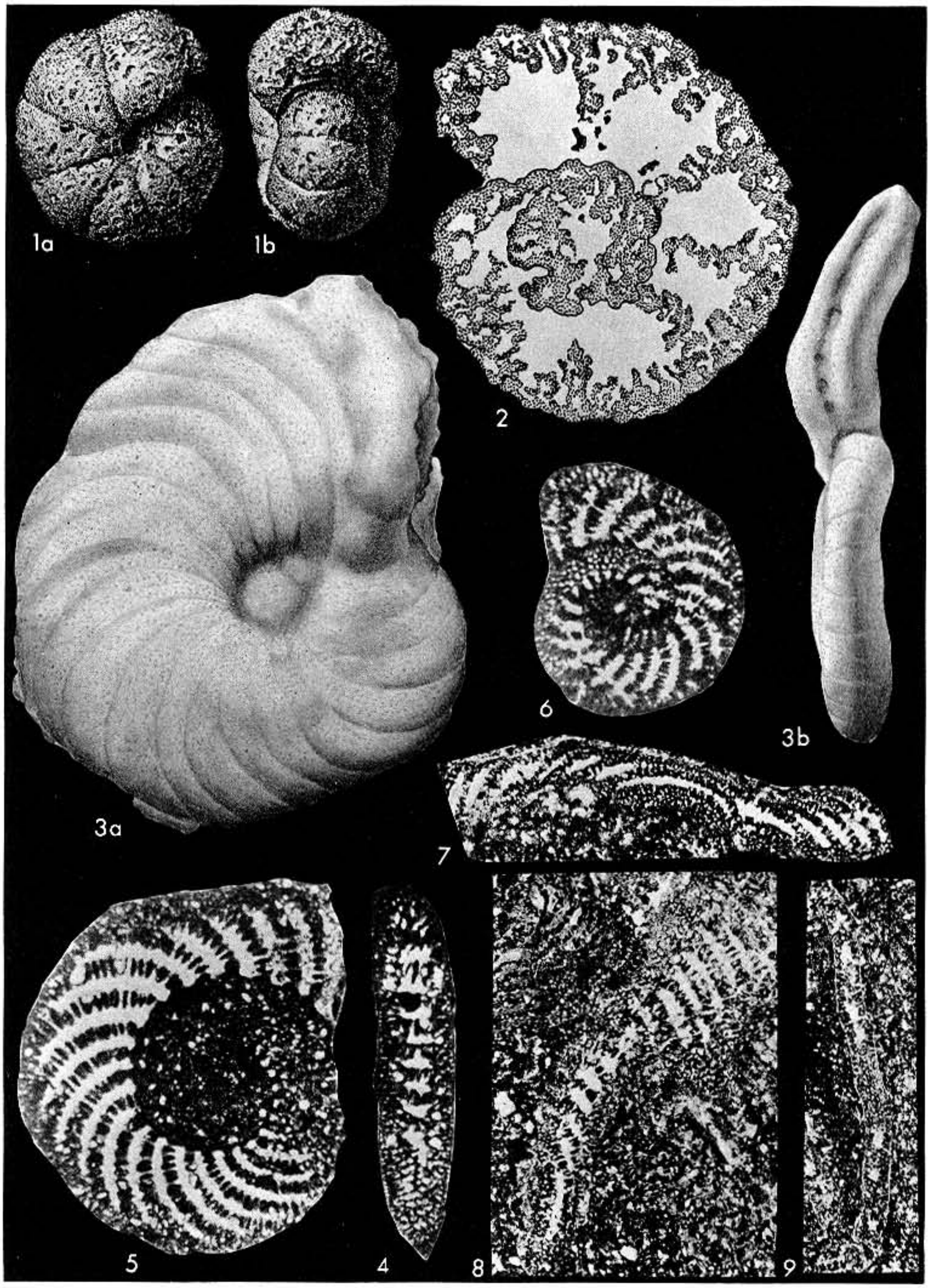


FIG. 143. Lituolidae (Cyclammininae; *1,2*, *Alveolophragmium*; *3-6*, *Choffatella*; *7-9*, *Pseudochoffatella*) (p. *C*228, *C*233).

and edge views of holotype, ×58 (*2117); 7, sec. showing labyrinthic wall and semisepta, ×35 (*1242).

Martiguesia Maync, 1959, *1248, p. 21 [*M. cyclamminiformis; OD]. Test planispiral in early stage, later tending to uncoil, wall with outer imperforate layer over alveolar subepidermal layer, which forms labyrinthic spongy mass filling cham-

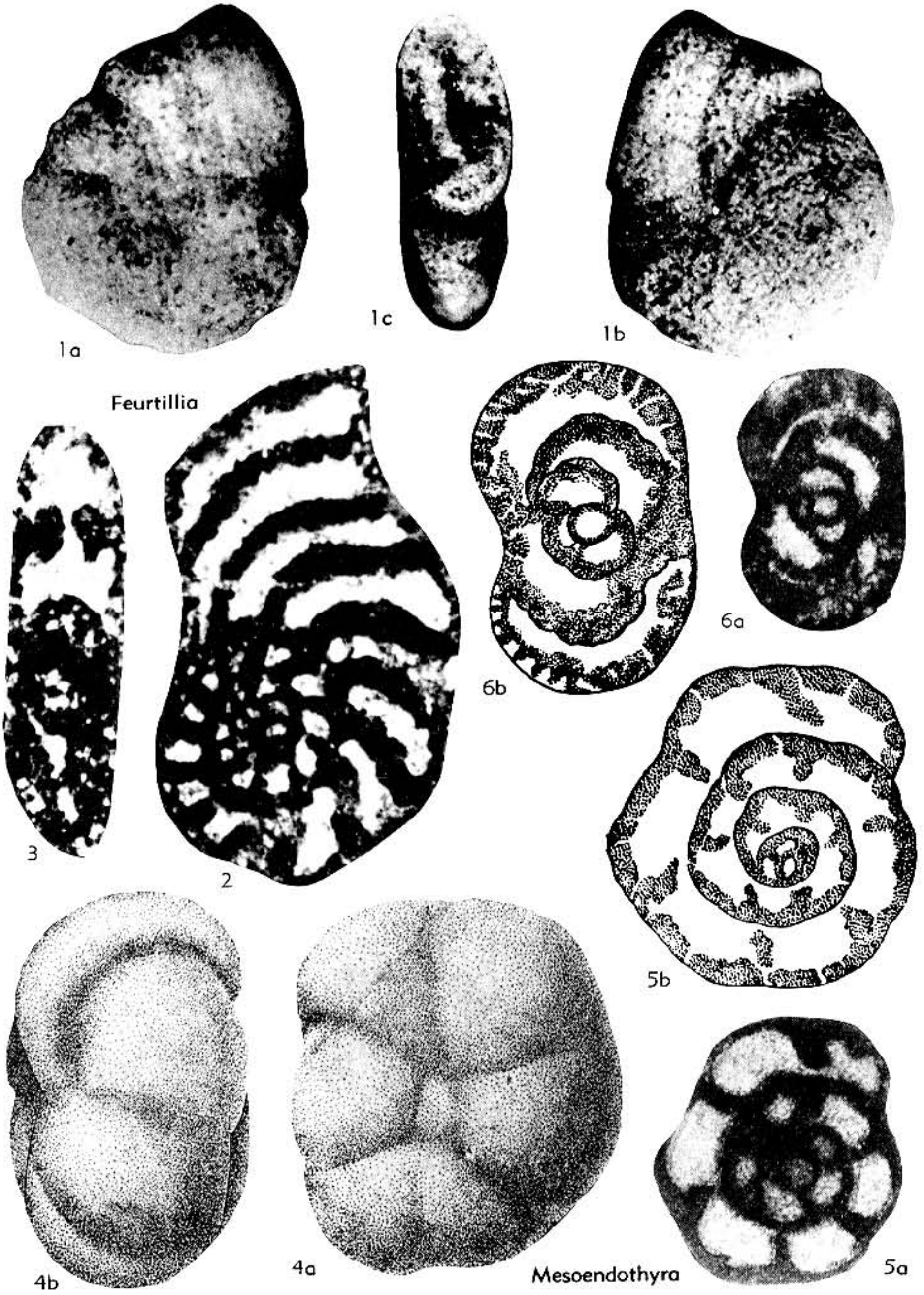


Fig. 144. Lituolidae (Cyclammininae; *1-3, Feurtillia; 4-6, Mesoendothyra*) (p. C228-C229, C232-C233).

ber; aperture terminal, cribrate. *U.Cret.(Santon.)*, Eu.(Fr.).——FIG. 145,*1-3*. **M. cyclamminiformis; 1,* side view of holotype, ×40; *2,* axial sec. megalospheric paratype; *3,* equat. sec. microspheric paratype; *2,3,* ×20 (*1248).

Mesoendothyra DAIN, 1958, *265, p. 19 [**M. izu-*

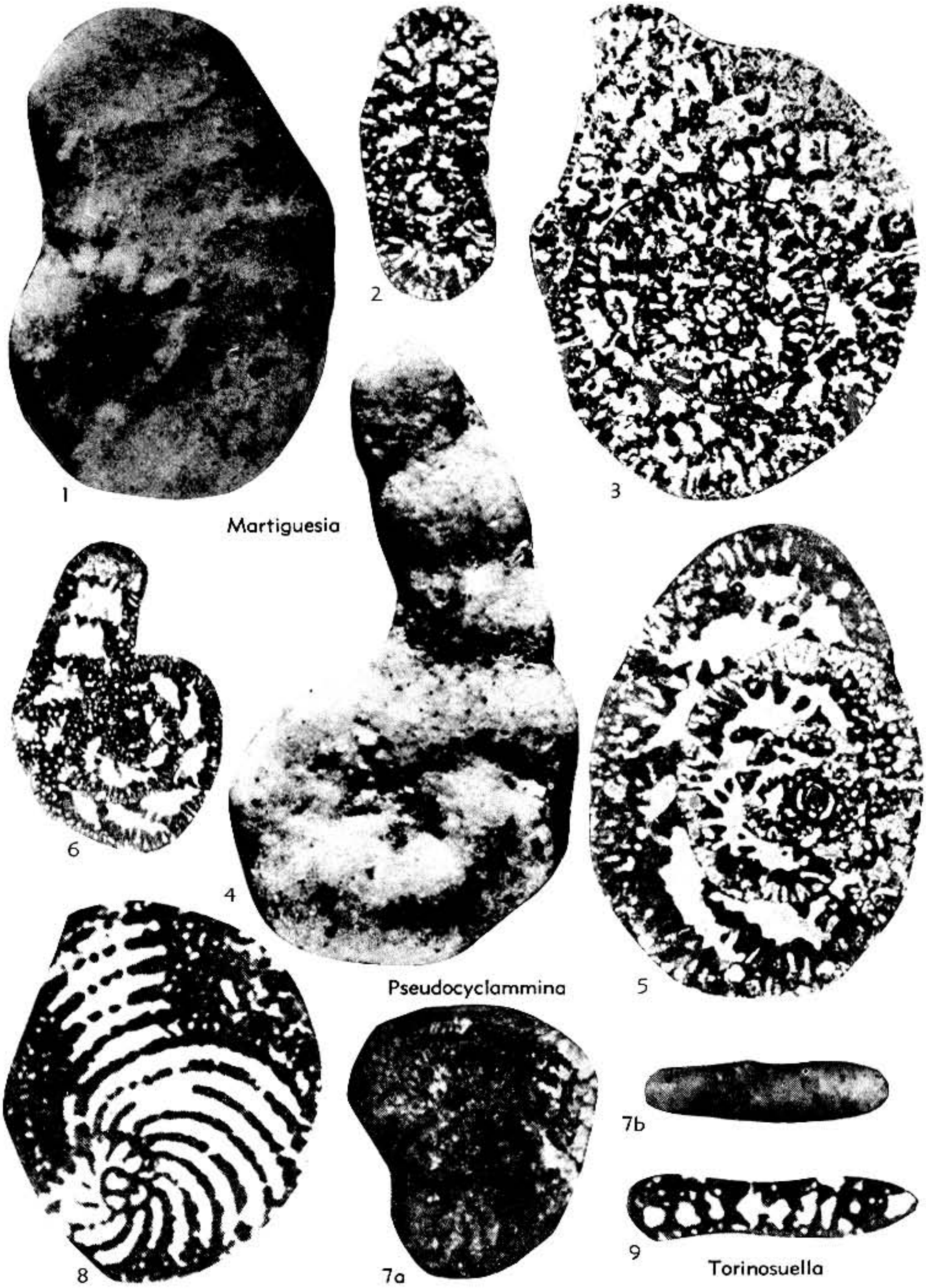


FIG. 145. Lituolidae (Cyclammininae; *1-3, Martiguesia; 4-6, Pseudocyclammina; 7-9, Torinosuella*) (p. *C*231-*C*233).

miana; OD]. Test enrolled and involute, early coiling plectogyral; wall agglutinated, outer layer imperforate and interior coarsely alveolar, septa with single imperforate layer; aperture an interiomarginal slit. *U.Jur.(Kimmeridg.),* Eu.(Ukraine).——FIG. 144,*4-6*. **M. izumiana; 4a,b,* side, edge views of holotype, ×72 (*265); *5a,6a,* median and vert. secs., ×50 (*265); *5b,6b,* median and vert. secs. redrawn, ×68 (*1509).

Pseudochoffatella DELOFFRE, 1961, *582, p. 105 [**P. cuvillieri;* OD] [*non* LEUPOLD & MAYNC, 1935, *1131, p. 132 *(nom. nud.)*]. Test free, large, compressed, 7-12 mm. long, 0.9-1.2 mm. thick, early stage enrolled, later uncoiled; chambers numerous, interior labyrinthic, chambers only partially subdivided; wall agglutinated, with quartz grains embedded in much calcareous cement; aperture undetermined. [*Pseudochoffatella* is known only from nonoriented sections, hence certain important characters are yet unknown.] *L.Cret.(Apt.),* Eu.(Fr.-Sp.).——FIG. 143,*7-9*. **P. cuvillieri,* Fr.; *7,8,* oblique horiz. sec.; *9,* transv. sec. showing large size and labyrinthic wall, all ×17 (*582).

Pseudocyclammina YABE & HANZAWA, 1926, *2091, p. 10 [**Cyclammina lituus* YOKOYAMA, 1890, *2096, p. 26; OD] [=*Pseudochoffatella* LEUPOLD & MAYNC, 1935, *1131, p. 132 *(nom. nud.) (non* DELOFFRE, 1961)]. Test enrolled in early stage, later uncoiling as in *Lituola,* but with irregular reticulate outer layer and thick, conspicuous labyrinthic inner layer in both walls and septa; aperture cribrate, of numerous irregularly spaced openings on terminal face. [Differs from *Lituola* in its complex wall, and from *Choffatella* in its cribrate aperture, rather than vertical series of pores.] *U.Jur.-U.Cret.(Santon.),* Japan-Eu.-Carib.-Malay Arch.(Sumatra).——FIG. 145,*4-6*. **P. lituus* (YOKOYAMA), U.Jur.(Kimmeridg.), Japan *(5,6),* U.Jur.(Kimmeridg.-Portland.), Pol. *(4); 4,* side view, ×20; *5,* median sec., ×20; *6,* equat. sec., ×12 (all *1247).

Reticulophragmium MAYNC, 1955, *1244, p. 557 [**Alveolophragmium venezuelanum* MAYNC, 1952, *1241, p. 142; OD]. Similar to *Alveolophragmium,* but with interiomarginal aperture, bordered only by lip at upper margin. *Mio.-Rec.* S. Am.(Venez.)-Malay Arch.(Java).——FIG. 142,*5*. **R. venezuelanum* (MAYNC), Mio., Venez.; *5a,b,* side and edge views, surface meshwork reflecting internal reticulate layer, ×62 (*2117).

Torinosuella MAYNC, 1959, *1250, p. 6 [**Choffatella peneropliformis* YABE & HANZAWA, 1926, *2091, p. 11; OD]. Planispiral, similar to *Choffatella* in early stage but uncoiling and with broad low uniserial chambers in later stage; wall finely arenaceous, with imperforate outer layer and inner alveolar layer forming meshwork; aperture terminal, cribrate. *U.Jur.(Kimmeridg.)-L.Cret.(Hauteriv.),* Japan-Eu.(Port.-Switz.-Yugo.). —— FIG. 145,*7-9*. **T. peneropliformis* (YABE & HANZAWA), U.Jur.(Kimmeridg.), Port. *(7),* U.Jur., Japan *(8,9); 7a,b,* side, top views, ×40 (*1250); *8,9,* median and transv. secs., ×40 (*1250).

Subfamily SPIROCYCLININAE
Munier-Chalmas, 1887

[*nom. transl.* MAYNC, 1950, p. 538 (*ex* family Spirocyclinidae MUNIER-CHALMAS, 1887)]

Septa simple, chambers subdivided by secondary radial septula into chamberlets, interior labyrinthic, walls and septa divided by ramifying, anastomosing channels, alveolar-reticulate hypodermis beneath epidermal coating. *Jur.-U.Cret.*

Spirocyclina MUNIER-CHALMAS, 1887, *1325, p. xxxi [**S. choffati;* OD]. Test free, coiled, large, slightly trochospiral, nearly involute; chambers broad, low, increasing rapidly in breadth, subdivided internally by numerous transverse radial partitions beneath alveolar layer, forming secondary chamberlets which show at surface as reticulations when specimen is dampened; wall agglutinated, fine-grained, with much cement; aperture consisting of 2 vertical rows of pores in slight depression at either side of apertural face. *U.Cret.(Senon.),* Eu.(Fr.).——FIG. 146,*1,2*. **S. choffati; 1a-c,* opposite sides and edge of lectotype (designated by MAYNC, *1247), showing double row of apertural pores, ×17 (*2117); *2,* sectioned specimen, ×14 (*1247).

Anchispirocyclina JORDAN & APPLIN, 1952, *1003, p. 3 [**A. henbesti* JORDAN & APPLIN, 1952 (=*Dicyclina lusitanica* EGGER, 1902, *660, p. 585); OD] [=*Trematocyclina* CHOFFAT, 1885, *337B, p. 23 *(nom. nud.); Iberina* MUNIER-CHALMAS, 1902, *1327, p. 350 (type, *Dicyclina lusitanica* EGGER, 1902, *660, p. 585) *(non Iberina* SIMON, 1881)]. Test enrolled, spreading, reniform or discoidal; broad, low chambers planispiral in early stage, increasing in breadth and curvature, especially in microspheric forms, becoming peneropline to reniform in outline, or chambers may become cyclical, resulting in discoidal test; chambers internally subdivided by somewhat irregular interseptal pillars, which project backward from each septum toward previous one, septa with numerous openings (as in *Choffatella*) spaced among interseptal pillars; wall with imperforate outer layer and alveolar subepidermal layer, and may have undivided chamber cavity immediately beneath this layer, with interior intricately divided by numerous interseptal pillars forming distinctly labyrinthic appearance; aperture cribrate. [MAYNC (1959, *1249, p. 39-40) noted the synonymy of *Iberina* and *Anchispirocyclina,* suppressing the latter as junior synonym. As *Iberina* MUNIER-CHALMAS, 1902, is a junior homonym of *Iberina* SIMON, 1881, *Anchispirocyclina* is here re-instated as the valid name of this genus.] *U.Jur.(Kimmeridg.)-L.Cret.(L.Valang.),* S.Eu.-N.Afr.-SE. USA-Carib. (Cuba).——FIG. 147,*1-10*. *A. lusitanica* (EGGER),

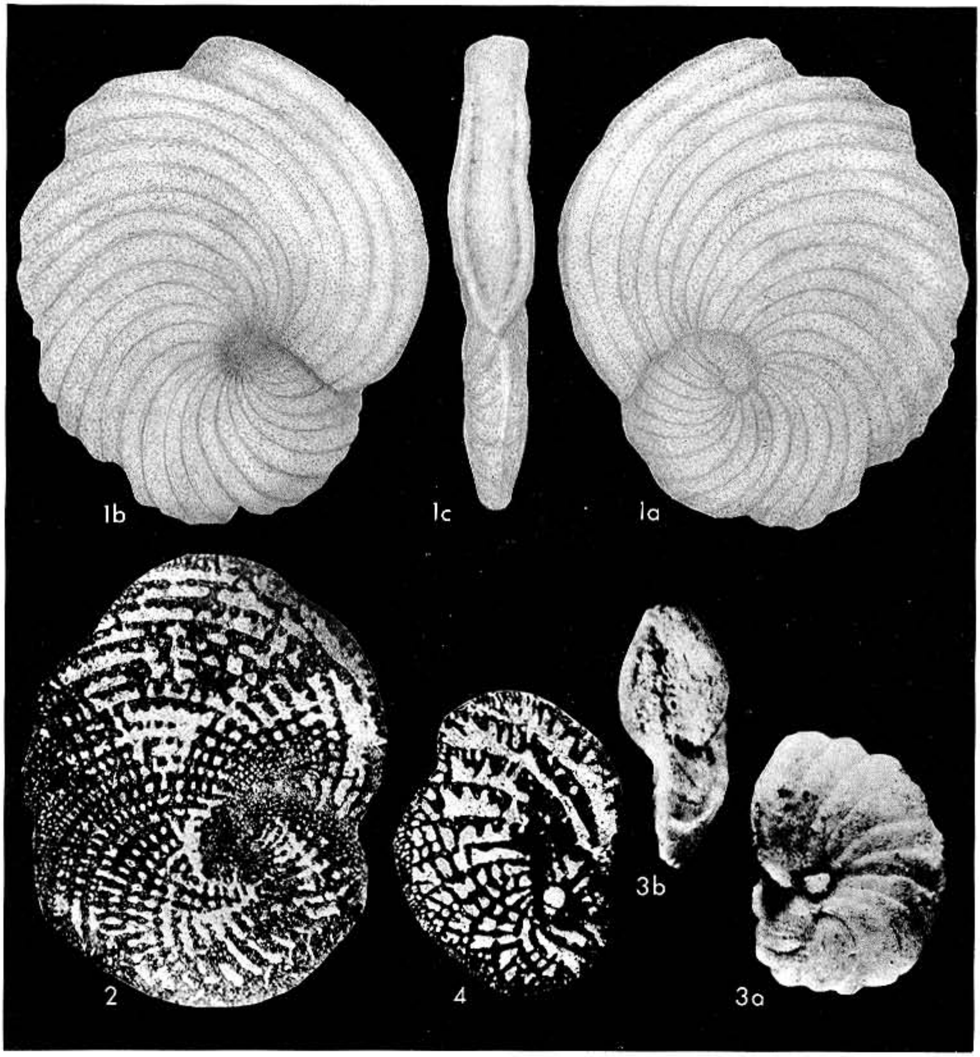


Fig. 146. Lituolidae (Spirocyclininae; *1,2, Spirocyclina; 3,4, Sornayina*) (p. *C233, C236*).

U.Jur., Port. *(1,3,5,6)*, U.Jur., USA(N.Car.) *(7-10)*, L.Cret.(L.Valang.), Port. *(2,4)*; *1a-c*, opposite sides and edge of neotype, ×3.2; *1d*, edge enlarged to show apertural pores, ×15; *2*, megalospheric form, ×24; *3*, megalospheric section, ×24; *4*, median sec. of microspheric form, ×7; *5*, portion of median sec. of microspheric form, ×14; *6*, trans. sec. of microspheric form, ×8.3; *7*, sec. of microspheric test, holotype of "*A. henbesti*," ×64; *8*, sec. of megalospheric form, paratype of "*A. henbesti*," ×20; *9, 10*, oblique equat. sec. and subaxial sec. of microspheric form, ×18 *(1-6*, *1249; *7-10*, *1003).

Orbitammina Berthelin, 1893, *135, p. lxxiii [**Orbicula elliptica* d'Archiac, 1843, *36, p. 375; OD]. Test large, compressed, reniform, with lateral borders recurved and overlapping to give discoidal appearance, to 22 mm. in diam., surface with fine concentric striae when slightly abraded, primary chambers broad, low and semiannular, subdivided into secondary chamberlets approx. 0.06 mm. in diam., with one or more perforations connecting successive chamberlets, chamber subdivisions not quite extending to outer lamella, so that opening connects all chamberlets of single chamber adjacent to outer wall, which is granular-calcareous, probably agglutinated with calcareous cement, imperforate. [Differs from *Spirocyclina* in the absence of a subepidermal alveolar layer.] *U.Jur.(Bathon.)*, Eu.(Fr.).——Fig. 148, *1-3*. **O. elliptica* (d'Archiac); *1a*, neotype, ×2;

1b, same specimen with early peneropline stage restored, ×1.7; 2, part of equat. sec., ×20; *3a*, schematic drawing of axial sec. along line AB of *3b*, showing chambers of secondary chamberlets and connecting perforations; *3b*, superficial equat. sec. along line XY of *3a*, ×87 (all *172).

Fig. 147. Lituolidae (Spirocyclininae; *1-10, Anchispirocyclina*) (p. *C*233-*C*234).

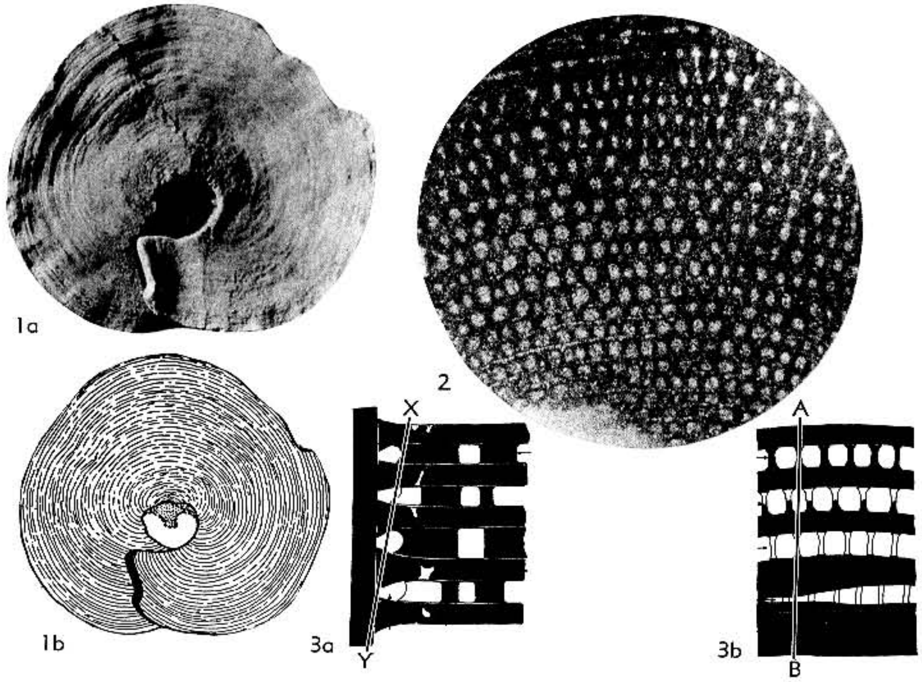


FIG. 148. Lituolidae (Spirocyclininae; *1-3, Orbitammina*) (p. *C*234-*C*235).

Sornayina Marie, 1960, *1224, p. 320 [**S. foissacensis;* OD]. Test free, planispiral to asymmetrical, trochospiral, chambers numerous, low and broad, tending to uncoil slightly in later stages; wall agglutinated with considerable cement, imperforate epidermal layer overlying subepidermal alveolar zone, primary chambers subdivided by somewhat irregular transverse partitions perpendicular to septa below alveolar zone, septula progressively reduced to pillars or knobs farther inward, nearly continuous median partition at center dividing test equally; aperture cribrate, filling most of apertural face. [*Sornayina* differs from *Spirocyclina* in its less regularly spaced secondary septula, smaller number of chambers in each whorl, and in having a cribrate aperture, instead of a double vertical row of pores.] *U.Cret.* *(Coniac.)*, Eu.(Fr.).——Fig. 146,*3,4*. **S. foissacensis; 3a,b,* side and edge of holotype, ×17 (*1224); *4,* median sec. of megalospheric topotype, showing reticulate subepidermal layer and primary chambers partially subdivided by secondary septula, ×18 (*1251).

Subfamily LOFTUSIINAE Brady, 1884

[*nom. correct.* Loeblich & Tappan, 1961, p. 280 (*pro* subfamily Loftusinae Brady, 1884, p. 67)]

Test fusiform, planispiral, involute, with numerous low whorls; wall agglutinated, interior labyrinthic; aperture multiple, along base of apertural face. *Jur.-Cret.*

Loftusia Brady in Carpenter & Brady, 1870, *278, p. 739, 751 [**L. persica;* OD (M)]. Test large, to 80.0 mm. in length, free, fusiform, planispirally enrolled, with elongate axis of coiling; primary septa strongly oblique to regularly enrolled spiral lamina, secondary septula perpendicular to primary septa; wall agglutinated, enclosing tests of smaller foraminifers and mineral fragments in calcareous cement, thin spiral lamina largely of calcareous granules closely cemented. *U.Cret.* *(Maastricht.)*, SW.Asia-Eu.(Balkans.). —— Fig. 149,*1-4*. **L. persica,* Iran; *1,* ext., ×1; *2,* tang. long. sec. in reflected light, showing alveolar appearance of layer beneath thin epidermis, ×22.5; *3,* transv. sec., part showing separate epidermal layer, alveolar subepidermal layer, and secondary septula, ×33; *4,* transv. sec. in Canada balsam, in transmitted light, ×5 (*278).

Paracyclammina Yabe, 1946, *2086, p. 259 [**Loftusia bemmeleni* Silvestri, 1932, *1786, p. 89; OD]. Test to 10 mm. in diam., short axis of coiling, numerous low whorls; septa oblique, thick, perforate, no secondary septa; wall agglutinated, with much cement, coarsely alveolar layer near surface. [*Paracyclammina* differs from

Pseudocyclammina in the large number of its closely coiled whorls and strongly oblique septa, like those of *Loftusia*. It differs from *Loftusia* in its short axis of coiling and absence of secondary septa or pillars.] *U.Jur.-L.Cret.*, Malay Arch. (Sumatra).——FIG. 150,*1-3*. **P. bemmeleni*

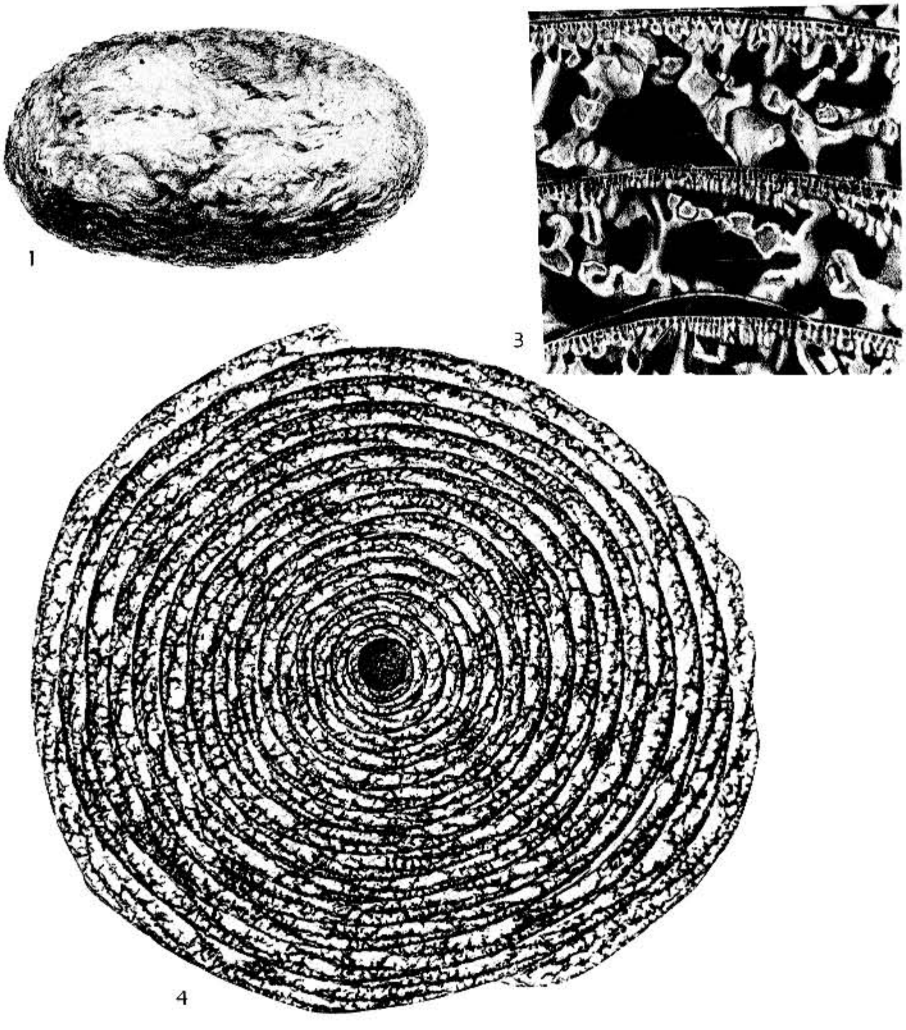


FIG. 149. Lituolidae (Loftusiinae; *1-4, Loftusia*) (p. *C*236).

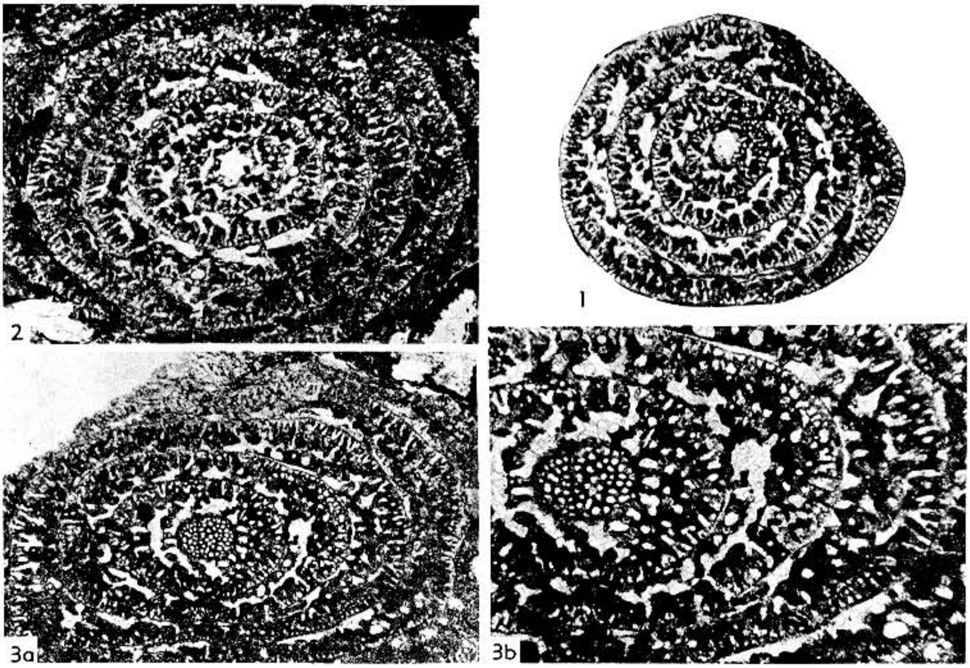


FIG. 150. Lituolidae (Loftusiinae; *1-3, Paracyclammina*) (p. *C236-C238*).

(SILVESTRI), L.Cret.; *1*, megalospheric juvenile, sec. in plane of symmetry, ×14; *2*, slightly oblique long. sec. of megalospheric adult, ×14; *3a*, long. sec. perpend. to plane of symmetry of megalospheric adult, ×14; *3b*, central part of *3a*, ×24 (all *1786).

Subfamily LITUOLINAE de Blainville, 1825

[*nom. transl.* BRADY, 1884, p. 65 (*ex* family Lituacea DE BLAINVILLE, 1825)] [=Haplophragmiinae CUSHMAN, 1927, p. 19]

Similar to Haplophragmoidinae but spire uncoiling in adult, or cyclical, interior simple. *Carb.-Rec.*

Lituola LAMARCK, 1804, *1085b, p. 242 [**L. nautiloidea* LAMARCK, 1804 (=*Lituolites nautiloidea* LAMARCK, 1804, *1085b, p. 242); SD CUSHMAN, 1920, *411b, p. 69] [=*Lituolites* LAMARCK, 1804, *1085b, p. 242 (obj.); *Stylolina* KARRER, 1877, *1023, p. 371 (type, *S. lapugyensis*); *Cribrospirella* MARIE, 1941, *1215, p. 28 (type, *Lituolites difformis* LAMARCK, 1804, *1085b, p. 243)]. Test large, early portion planispirally coiled, later rectilinear; wall agglutinated, with interior structure of walls and septa simple; aperture terminal, cribrate. [Differs from *Ammobaculites* in having a multiple aperture and from *Haplophragmium* in having an early planispiral, rather than streptospiral, coil. *Stylolina* has been regarded as a synonym of *Haplophragmium* (*762), but because of its multiple aperture, is here classed as a synonym of *Lituola*.] *U.Trias.-Rec.*, cosmop.——FIG. 151,*1-3*. **L. nautiloidea*, U.Cret.(Campan.), Eu.(Fr.); *1a,b*, side, edge views of neotype, ×16 (*2117); *2a,b*, side, top views of topotype, ×16 (*2117); *3*, median sec., showing simple walls and septa, ×17 (*1240).

Ammoastuta CUSHMAN & BRÖNNIMANN, 1948, *498, p. 17 [**A. salsa*; OD] [=*Praeammoastuta* BURSCH, 1952, *255, p. 915 (type, *P. alberdingi*)]. Ovate to flabelliform, compressed test with low, rapidly broadening chambers in curved, semienrolled series, similar to calcareous isomorph *Astacolus*; wall finely agglutinated on inner pseudochitinous layer, interior simple; aperture transverse areal slit near center of terminal face of final chamber, secondary apertures consisting of cribrate openings at lower end of final chamber (nearest proloculus). *U.Eoc.-Rec.*, N.Am.(USA)-W.Indies(Trinidad)-S. Am.(Venez.-Ecuad.)-C. Am.(Panama). —— FIG. 151,*4*. **A. salsa*, Rec., USA(La.); *4a,b*, side and edge views, ×130 (*2117).——FIG. 151,*5*. *A. alberdingi* (BURSCH), Oligo., Venez.; *5a,b*, side, edge views, ×174 (*2117).

[MAYNC (*1240, p. 43) stated that the genus lacks an early coiled portion and is therefore "not a lituolid foraminifer." BURSCH (*255, p. 915) placed it in the Reophacinae. As it shows apparent derivation from a coiled form, however, we regard it as closely related to such forms as *Flabellammina* and retain it within this subfamily. It shows no affinity to the uniserial Reophacidae. The presence of cribrate apertures in *Praeammoastuta alberdingi* BURSCH was noted by SAUNDERS (*1633, p. 84), who therefore classed that genus as a synonym of *Ammoastuta*.]

Ammobaculites CUSHMAN, 1910, *404a, p. 114 [**Spirolina agglutinans* D'ORBIGNY, 1846, *1395, p. 137; OD]. Test free, early portion close coiled, later uncoiled and rectilinear, rounded in section;

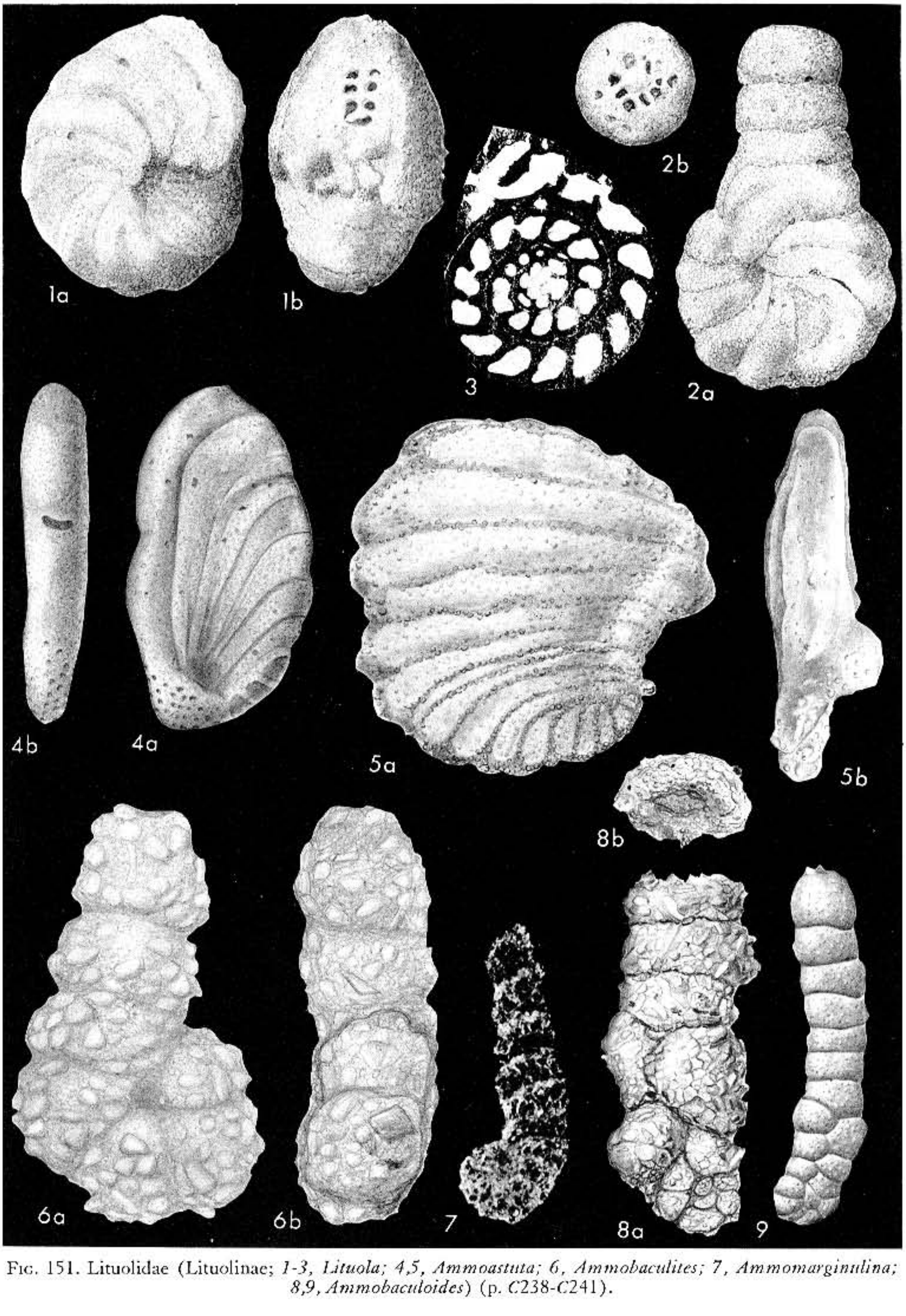


FIG. 151. Lituolidae (Lituolinae; *1-3, Lituola; 4,5, Ammoastuta; 6, Ammobaculites; 7, Ammomarginulina; 8,9, Ammobaculoides*) (p. C238-C241).

wall agglutinated, interior simple; aperture terminal, rounded. [*Ammobaculites* differs from *Haplophragmium* in its early planispiral, rather than streptospiral coil, from *Ammomarginulina* in its straight sutures and centrally placed aperture, and from *Ammoscalaria* in its thicker septa, which

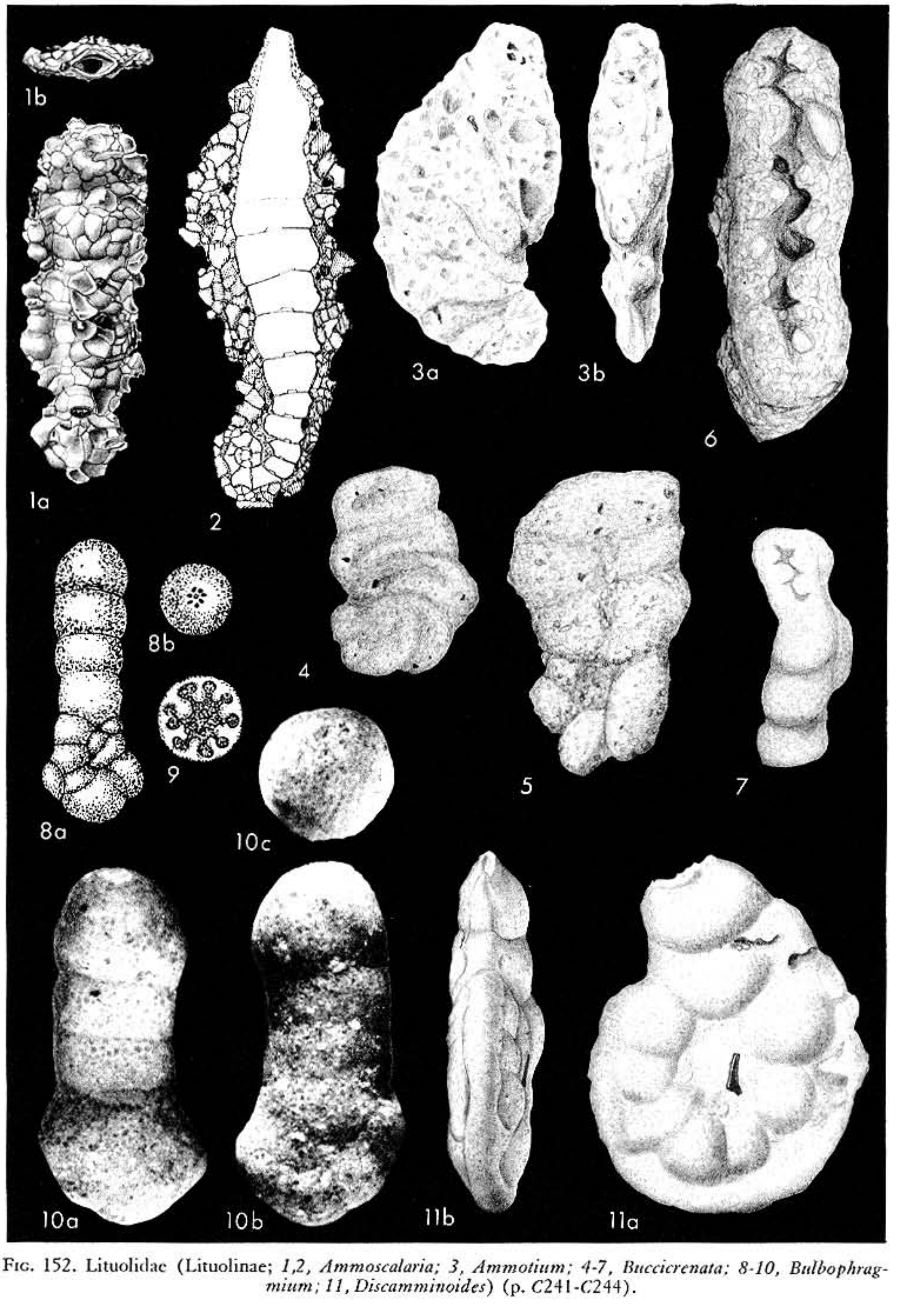


Fig. 152. Lituolidae (Lituolinae; *1,2, Ammoscalaria; 3, Ammotium; 4-7, Buccicrenata; 8-10, Bulbophragmium; 11, Discamminoides*) (p. C241-C244).

represent apertural faces of previous chambers, rather than being pseudochitinous and of secondary origin.] *Carb.-Rec.*, cosmop.——FIG. 151, *6*. **A. agglutinans* (D'ORBIGNY), Mio., Eu.(Aus.); *6a,b*, side, edge views of lectotype, ×48 (*2117).

Ammobaculoides PLUMMER, 1932, *1465, p. 87 [**A. navarroensis;* OD] [=*Spiroplectella* EARLAND, 1934, *653, p. 113 (type, *S. cylindroides)*]. Test free, elongate, ovate to rounded in section; early chambers in planispiral coil, later biserially arranged and finally uniserial; wall agglutinated, insoluble in acid; aperture at base of final chamber of early portion, becoming terminal in adult. *L.Cret.-Rec.*, N.Am.-Eu.-Antarctic.——FIG. 151,*8*. **A. navarroensis*, U.Cret., USA(Tex.); *8a,b*, side, top views, ×80 (*2117).——FIG. 151,*9*. *A. cylindroides* (EARLAND), Rec., Antarctic, side view, ×166 (*2117).

[The type-species of *Spiroplectella* differs from that of *Ammobaculoides* only in being smaller and more regular in size, breadth of the coil being approximately equal to that of the biserial stage and the final uniserial portion. In *A. navarroensis* the biserial stage is widest. These differences are of specific rather than generic importance, however. Since both develop from coiled to biserial to uniserial, having agglutinated tests insoluble in HCl, they are here considered synonymous.]

Ammomarginulina WIESNER, 1931, *2063, p. 97 [**A. ensis;* OD (M)]. Test planispiral in early stage, later rectilinear, strongly compressed; sutures oblique; wall agglutinated, with very little cement; aperture terminal, eccentric, at dorsal angle of test. [MAYNC (*1240) stated that *Ammobaculites compressa* CUSHMAN & WATERS (M. Penn., Mich.) "should be referred to *Ammomarginulina*" and thus would extend the range of the genus to the Pennsylvanian. As *A. compressa* has neither the eccentric aperture at the dorsal angle nor the oblique sutures which characterize *Ammomarginulina*, we regard it as a true *Ammobaculites*.] *Jur.-Rec.*, Antarctic-Afr.-N.Am.-Eu. ——FIG. 151,*7*. **A. ensis*, Rec., Antarctic; holotype, ×66 (*2063).

Ammoscalaria HÖGLUND, 1947, *924, p. 151 [**Haplophragmium tenuimargo* BRADY in TIZARD & MURRAY, 1882, *1936, p. 715; OD]. Test free, elongate, early portion planispiral, later uncoiling and rectilinear, original development as tubular test with secondarily formed septa and resultant chamber development; sutures indistinct at surface, internal septa extremely thin, straight and pseudochitinous; exterior wall coarsely agglutinated, thick; aperture rounded to slightly elongate, may be produced on distinct neck, which is apparently temporary structure resorbed in formation of next succeeding chamber, foramina of secondarily formed septa not correlative with terminal aperture, but consisting of slight tubular projection from center of each pseudochitinous septum. [*Ammoscalaria* differs from *Ammobaculites* in its secondarily formed thin, pseudochitinous septa.] *Rec.*, Atl.-Pac.——FIG. 152,*1,2*. **A. tenuimargo* (BRADY), Atl. *(1)*, N.Sea *(2)*; *1a,b*, side, top view of topotype, ×23 (*2117); *2*, sec. showing nature of septa, ×37 (*924).

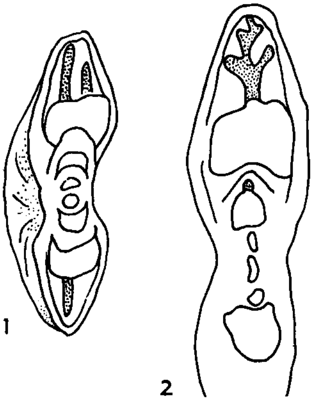


FIG. 153. Lituolidae (Lituolinae; *1,2, Discamminoides*) (p. C242-C244).

Ammotium LOEBLICH & TAPPAN, 1953, *1162, p. 33 [**Lituola cassis* PARKER in DAWSON, 1870, *565, p. 177; OD]. Test free, compressed, ovate in outline, chambers planispirally coiled and evolute, later chambers tending to uncoil but reaching backward toward coil at inner margin; wall agglutinated; aperture simple, rounded, terminal, at dorsal angle of final chamber. [*Ammotium* differs from *Ammobaculites* in becoming only partially uncoiled, the later portion being flattened rather than rounded in section and the chambers reaching far back toward the coil at the inner margin.] *Cret.-Rec.*, Atl.-Pac.——FIG. 152,*3*. **A. cassis* (PARKER), Rec., Alaska; *3a,b*, side, edge views, ×28 (*1162).

Buccicrenata LOEBLICH & TAPPAN, 1949, *1156, p. 252 [**Ammobaculites subgoodlandensis* VANDERPOOL, 1933, *1975, p. 407); OD]. Test free, flattened, early stage planispiral, later portion uncoiled and straight; wall agglutinated, aperture interiomarginal in the early stage, becoming terminal in uncoiled portion, elongate, with series of lateral toothlike projections. [*Buccicrenata* differs from *Ammobaculites* in its elongate, crenulate aperture instead of a simple one.] *L.Cret.(Alb.)*, USA(Tex.-Okla.).——FIG. 152,*4-7*. **B. subgoodlandensis* (VANDERPOOL); *4,5*, side view of lectotype and topotype, ×10; *6,7*, apert. views of topotypes, ×22 (*1156).

Bulbophragmium MAYNC, 1952, *1240, p. 46 [**Haplophragmium aequale* REUSS, 1860, *1548, p. 218, pl. 11, fig. 2a *(non Spirolina aequalis* ROEMER, 1841, *1583, p. 98) (=*Bulbophragmium aequale* MAYNC, 1952, see *1164, p. 33, =*Lituola westfalica* BARTENSTEIN, 1952, *91, p. 323); OD]. Test similar to *Lituola*, but early stage streptospirally coiled rather than planispiral; interior simple; aperture cribrate. *Cret.*, Eu.——FIG. 152, *8-10*. **B. aequale* MAYNC, U.Cret.(Campan.), Ger.; *8a,b*, side and top views; *9*, sec. of specimen; *10a-c*, opposite sides and top view of neotype, ×10 (*91).

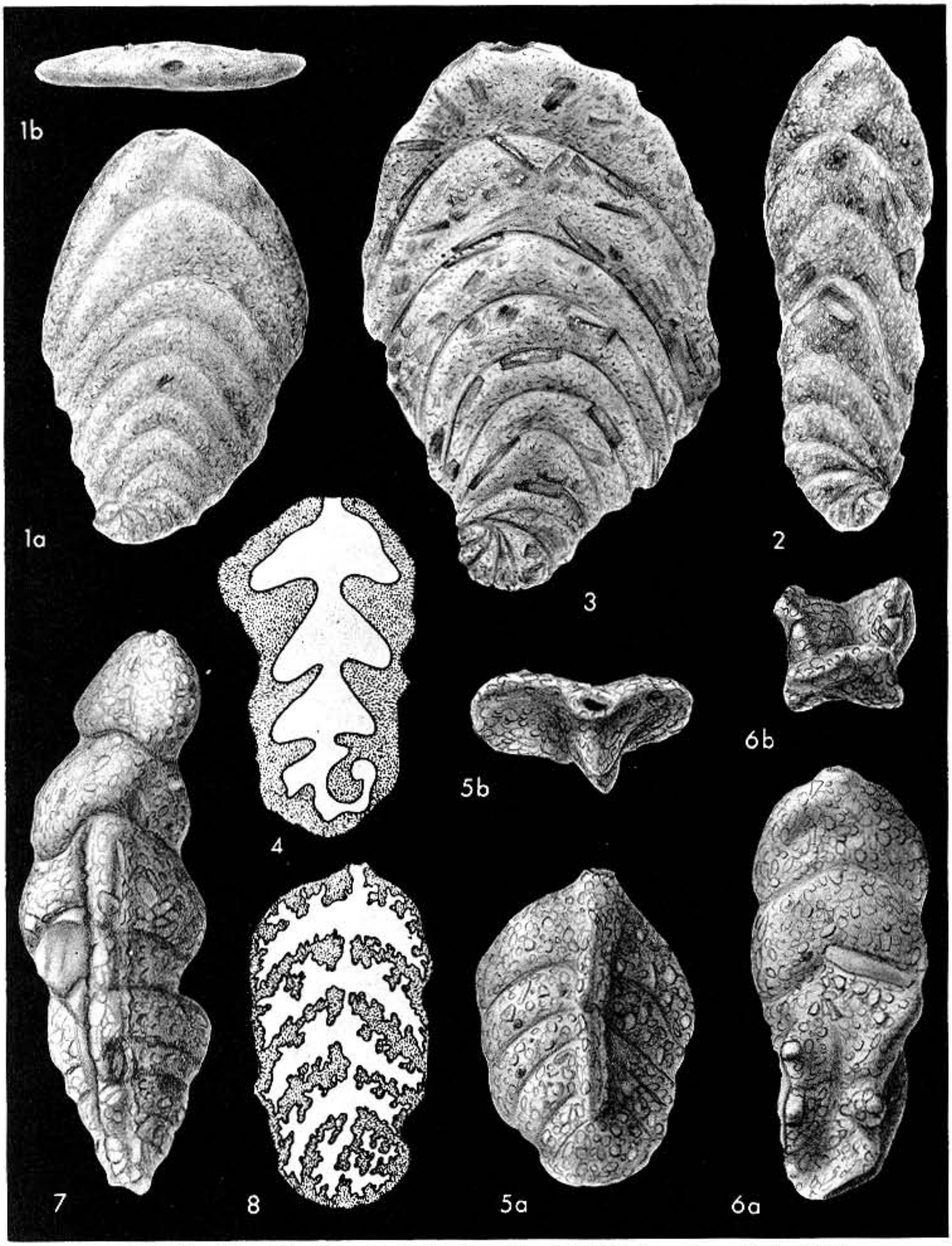


Fig. 154. Lituolidae (Lituolinae; *1-4, Flabellammina; 5-8, Flabellamminopsis*) (p. *C244*).

[The involved nomenclature of the type-species is discussed by Loeblich & Tappan (*1164). The type-species was stated originally to be *Haplophragmium aequale* Reuss, 1860 (*non Spirolina aequalis* Roemer, 1841). As this is a type without a valid specific name, the Rules state that in such cases the old specific name is to be used with the new generic name as a new species, with authorship and date that of the author of the genus, in this instance, *Bulbophragmium aequale* Maync. The later-proposed name *Lituola westfalica* Bartenstein is therefore a junior synonym.]

Discamminoides Brönnimann, 1951, *225, p. 103 [**D. tobleri*; OD]. Planispiral early stage, becoming uniserial in later development; septa thin, curved, nonalveolar; wall agglutinated, peripheral area of chamber cavity with spongy alveolar filling of fine-grained arenaceous material, alveolar openings perpendicular to outer wall but not perforating it, no true labyrinthic layer developed; aperture interiomarginal in early stage, terminal in later stage (whether single or multiple being unknown). [This genus is only provisionally recognized as distinct, for according to MAYNC (*1240, p. 48) the alveolar structure is not pres-

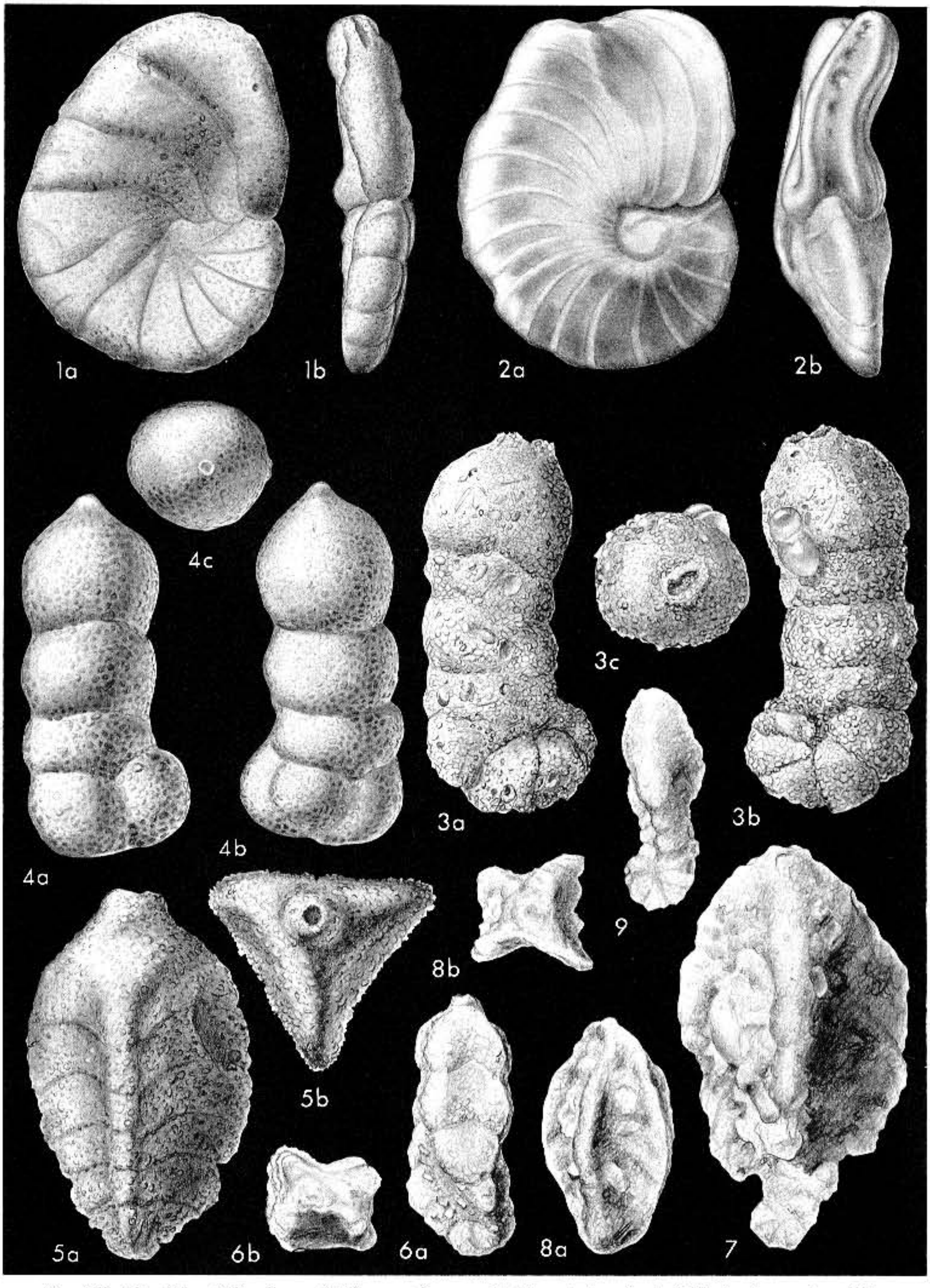


FIG. 155. Lituolidae (Lituolinae; *1, Phenacophragma; 2, Stomatostoecha; 3,4, Haplophragmium; 5-9, Triplasia*) (p. C244-C247).

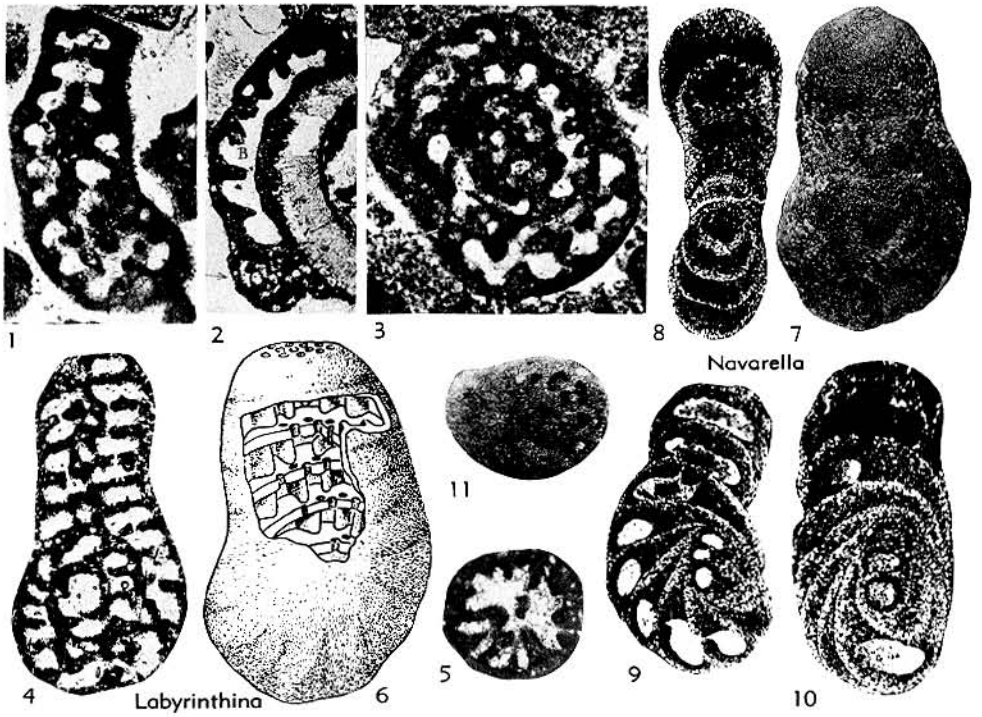


FIG. 156. Lituolidae (Lituolinae; _1-6, Labyrinthina; 7-11, Navarella_) (p. C245).

ent in all specimens. If this is not a constant feature of the genus, _Discamminoides_ would appear to be a synonym of _Ammobaculites_ or _Lituola,_ depending on the presence of a single or multiple aperture, not yet described.] _U.Oligo.-L.Mio.,_ W.Indies(Trinidad).——FIG. 152,_11_; 153, _1,2_. *_D. tobleri,_ Mio.; 152,_11a,b,_ side, edge views of holotype, ×39 (*2117); 153,_1,2,_ megalospheric paratypes, nearly axial sec. _(1)_, showing straight alveoles (shaded), and sec. parallel to axis _(2)_ showing branching alveole, ×35 (*225).

Flabellammina CUSHMAN, 1928, *436, p. 1 [*_F. alexanderi;_ OD]. Test elongate, compressed, early stage coiled, later uniserial, with broad, low chevron-shaped chambers; wall coarsely agglutinated, simple walls and septa; aperture terminal, rounded to ovate. [_Flabellammina_ differs from _Ammobaculites_ in having compressed, equitant uniserial chambers.] _L.Cret.-U.Cret.,_ N.Am.-Eu. ——FIG. 154,_1-3_. *_F. alexanderi,_ L.Cret.(Alb.), USA(Tex.); _1a,b,_ side, top views of microspheric, finely agglutinated specimen, ×33; _2,3,_ side views of coarsely agglutinated microspheric and megalospheric specimens, ×72 (*2117).——FIG. 154,_4_. _F. rugosa_ ALEXANDER & SMITH, L.Cret.(Alb.), USA(Tex.), long. sec. showing simple interior, ×52 (*11).

Flabellamminopsis MALECKI, 1954, *1209, p. 104, 112, 117 [*_F. variabilis;_ OD]. Test enrolled to uniserial, similar in form to _Triplasia,_ with flattened, triangular or quadrate tests, but with pseudolabyrinthic, quite irregular internal structure, although lacking true alveolar layer; aperture terminal, rounded. [This variable form may have flattened, triangular, or quadrate specimens or a succession of these stages in a single specimen.] _M.Jur.,_ Eu.(Pol.).——FIG. 154,_5-8_. *_F. variabilis;_ _5a,b,_ side, top views of triangular specimen; _6a,b,_ side, top views of quadrate specimen; _7,_ triangular form, rounded in later portion, ×33 (*2117); _8,_ sec. showing pseudolabyrinthic structure, enlarged (*1210).

Haplophragmium REUSS, 1860, *1548, p. 217 [*_Spirolina aequalis_ ROEMER, 1841, *1583, p. 98; SD CUSHMAN, 1920, *411b, p. 67] [=_Bulbobaculites_ MAYNC, 1952, *1240, p. 47 (type, _Ammobaculites lueckei_ CUSHMAN & HEDBERG, 1941, *507, p. 83)]. Early portion streptospirally coiled, as in _Bulbophragmium,_ later rectilinear; interior simple; aperture rounded, single, terminal. [_Haplophragmium_ differs from _Ammobaculites_ in its early streptospiral coil.] _M.Jur.-U.Cret.,_ Eu.-N. Am.-S.Am.——FIG. 155,_3_. *_H. aequale_ (ROEMER), L.Cret.(Hauteriv.), Ger.; _3a-c,_ opposite sides and top view of topotype, ×20 (*2117).——FIG. 155,_4_. _H. lueckei_ (CUSHMAN & HEDBERG), U.Cret., S.Am.(Colom.); _4a-c,_ opposite sides and top of holotype, ×124 (*2117).

Labyrinthina Weynschenk, 1951, *2051, p. 793 [**L. mirabilis*; OD] [=*Lituosepta* Cati, 1959, *303, p. 2 (type, *L. recoarensis*)]. Test elongate, subcylindrical, enrolled in early stage, later uncoiling, wall agglutinated of calcareous particles in calcareous cement, nonlabyrinthic, as in *Lituola,* but with secondary transverse septa projecting short distance inward from outer wall; aperture terminal, cribrate. *U.Trias.-L.Jur.(Lias.),* Eu.(Aus.)-Italy.——Fig. 156,*1-3*. **L. mirabilis,* U.Trias., Aus.; *1,* long. sec. showing parts of secondary transverse septa in central portion of test; *2,* long. sec. showing supposed attachment; *3,* transv. sec., ×33 (*2051).——Fig. 156,*4-6*. *L. recoarensis* (Cati), L.Jur.(Lias.), Italy; *4,* long. equat. sec. of holotype showing early coil and later rectilinear development, with portions of transv. septa visible where intersected near center of test; *5,* transv. sec. of paratype showing transv. septa, ×40; *6,* reconstr. showing internal and external charatcers, ×55 (*303).

[*Labyrinthina* and its synonym *Lituosepta* were both originally placed in the Lituolidae because of the similarity to *Lituola* and the nature of the embryonal portion, although the secondary septa of *Lituosepta* were regarded as similar to the Meandropsinidae. Maync (*1240, p. 51) suggested the placement of *Labyrinthina* with the Placopsilinidae because of some supposedly attached specimens. These were obtained only from thin sections in limestone and the presumed attached nature seems uncertain from the evidence available. The majority of specimens were unquestionably free-living.]

Navarella Ciry & Rat, 1951, *343, p. 85 [**N. joaquini;* OD]. Test large, early stage streptospirally enrolled, later portion uncoiled, in wide spire; septa strongly arched; wall agglutinated, with calcareous cement; aperture in early coil interiomarginal arched slit, later with small circular pores in addition to interiomarginal opening, and in uncoiled stage only scattered circular pores occur on terminal surface. *U.Cret.(Maastricht.),* Eu.(Sp.-Switz.-Fr.).——Figs. 156,*7-11*. **N. joaquini,* Sp.; *7,* side view of topotype, ×8; *8,9,* axial and equat. secs., ×8; *10,* somewhat oblique sec. showing early spire and arched septa, ×10; *11,* sec. near surface showing cribrate aperture, ×15 (*1243).

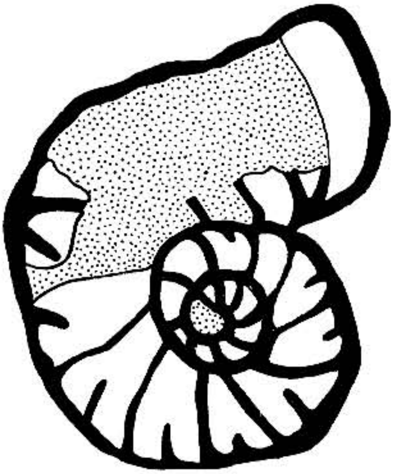


Fig. 157. Lituolidae (Lituolinae; *Phenacophragma*) (p. C245).

Fig. 158. Lituolidae (Lituolinae; *Stomatostoecha*) (p. C245).

Phenacophragma Applin, Loeblich & Tappan, 1950, *27, p. 78 [**P. assurgens;* OD]. Test free, planispiral, somewhat evolute, with slight tendency to uncoil; chambers numerous; septa of 2 types, complete normal septa alternating with hemisepta which project only slightly into chamber cavities; wall calcareous, imperforate, and microgranular, with some additional material incorporated in epidermal layer, interior simple, not labyrinthic, and with no transverse partitions; aperture slitlike, terminal. *L.Cret.(Alb.),* USA (Tex.).——Fig. 155,*1;* 157. **P. assurgens;* 155, *1a,b,* side, edge views of holotype, ×83 (*2117); 157, sec. of paratype showing true septa and hemisepta, ×95 (*27).

Stomatostoecha Applin, Loeblich & Tappan, 1950, *27, p. 76 [**S. plummerae;* OD]. Test free, planispiral, not completely involute; chambers numerous; wall composed of calcareous detrital material, interior simple, not labyrinthic, and with neither transverse nor parallel partitions; aperture single series of pores in linear depression on apertural face of final chamber. [*Stomatostoecha* differs from *Choffatella* in lacking any transverse or parallel partitions and from *Phenacophragma* in lacking hemisepta and in having a multiple aperture.] *L.Cret.(Alb.),* USA(Tex.).——Fig. 155,*2;* 158. **S. plummerae;* 155,*2a,b,* side, edge views of holotype, ×44 (*2117); 158, sec. of paratype showing simple interior, ×64 (*27).

Triplasia Reuss, 1854, *1543, p. 65 [**T. murchisoni;* OD (M)] [=*Rhabdogonium* Reuss, 1860, *1548, p. 198 (type, *Triplasia murchisoni* Reuss, 1854, SD Loeblich & Tappan, herein, obj.); *Frankeina*

CUSHMAN & ALEXANDER, 1929, *487, p. 61 (type, *F. goodlandensis*); *Centenarina* MAJZON, 1948, *1204, p. 24 (type, *C. hungarica*); *Tetraplasia* BARTENSTEIN & BRAND, 1949, *94, p. 672 (type, *T. georgsdorfensis*); *Centenaria* THALMANN, 1950, *1897i, p. 743 (*nom. null.*)]. Test free, early

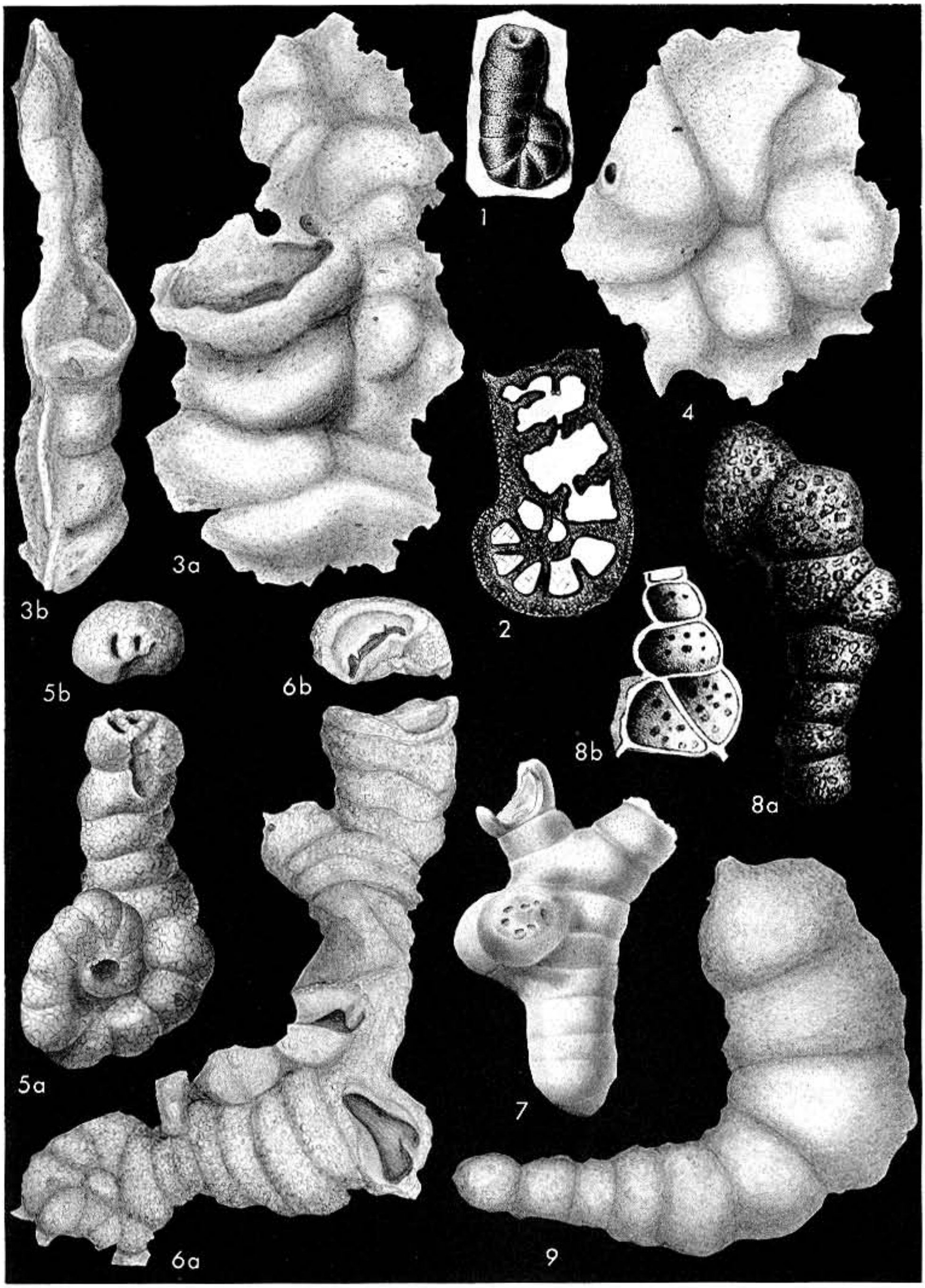


FIG. 159. Lituolidae (Placopsilininae; *1-4, Placopsilina; 5, Acruliammina; 6, Haddonia; 7, Manorella; 8,9, Subbdelloidina*) (p. C247-C248).

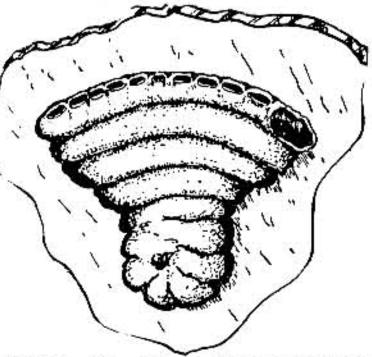


Fig. 160. Lituolidae (Placopsilininae; *Arenonina*) (p. *C*247).

portion may be planispiral, especially in microspheric forms, later portion uniserial or may be uniserial throughout, uniserial portion rhomboid in section, most commonly triangular, but some quadrate specimens occur in most species; sutures somewhat arched on faces of test, recurved at angles; wall agglutinated, composition and size of fragments extremely variable in same species; aperture terminal, round to elongate, may be produced on short neck. [*Triplasia* differs from *Flabellammina* in being triangular or quadrate in section in the uniserial stage. Most species contain some quadrate specimens; hence, this feature is not regarded as generic in importance in this lineage (*1161).]. *L.Jur.-Rec.,* N.Am.-Eu.-Pac.——Fig. 155,*5*. **T. murchisoni,* U.Cret.(Coniac.-L.Santon.), Aus.; *5a,b,* side, apert. views of topotype, ×48 (*2117).——Fig. 155,*6*. *T. georgsdorfensis* (Bartenstein & Brand), L.Cret.(Valang.), Ger.; *6a,b,* side, top views, ×22 (*1161).——Fig. 155,*7-9*. *T. goodlandensis* (Cushman & Alexander), L.Cret.(Alb.), USA(Tex.); *7,* side view of triangular microspheric topotype; *8a,b,* side, top views of quadrate topotype; *9,* megalospheric topotype; all ×55 (*1161).

Subfamily PLACOPSILININAE Rhumbler, 1913

[Placopsilininae Rhumbler, 1913, p. 444] [=Arplacopsinia Rhumbler, 1913, p. 444 *(nom. van.)*]

Test attached, early chambers may be enrolled, later uncoiling; wall simple. *Miss.-Rec.*

Placopsilina d'Orbigny, 1850, *1397a, p. 259 [**P. cenomana;* SD Cushman, 1920, *411b, p. 70] [=*Ammocibicides* Earland, 1934, *653, p. 106 (type, *A. proteus*)]. Test attached, early stage planispirally coiled, later uncoiling and rectilinear; wall agglutinated, nonlabyrinthic; aperture terminal, rounded, may have slight lip. *M.Jur.-Rec.,* cosmop.——Fig. 159,*1,2*. **P. cenomana,* U.Cret.(Cenoman.), Czech.; *1,* attached specimen, ×10; *2,* sec. of early portion showing nonlabyrinthic walls, ×28 (*1445).——Fig. 159,*3,4*. *P. proteus* (Earland), Rec., S.Am.(Drake Straits); *3,* syntype of Earland (*653, pl. 4, fig. 5) here designated as lectotype; *3a,b,* side and edge views showing flattened area where attached, ×48; *4,* small paratype (*653, pl. 4, fig. 1), ×105 (*2117).

[*Ammocibicides* was stated by Cushman (1948, *486, p. 204) to be trochoid in the early stage, "probably attached in the early stages, later becoming free." An examination of the original types in the British Museum (Natural History) (here redrawn), shows this form to be wholly attached, planispiral, and in no way distinguishable from *Placopsilina*. The irregular margin of *A. proteus* was not regarded by Earland as of generic importance, as he also described *A. pontoni* from the Eocene of Alabama, which shows as regular an outline as *P. cenomana*. *Ammocibicides* is here suppressed as a synonym of *Placopsilina*.]

Acruliammina Loeblich & Tappan, 1946, *1154, p. 252 [**Placopsilina longa* Tappan, 1940, *1871, p. 100; OD]. Test attached, at least in early portion; early stage close coiled, later uncoiling, only few chambers of coiled portion may be attached or all of coiled portion and much of uniserial portion may be attached, later portion of test usually growing free from attachment and uniserial part becoming cylindrical; wall agglutinated; aperture terminal, single low slit at attachment in early stages, later divided by median septum and finally cribrate. [*Acruliammina* differs from *Placopsilina* in having a cribrate rather than simple aperture.] *L.Cret.(Alb.)-U.Cret.(Campan.),* USA (Tex.-Okla.).——Fig. 159,*5*. **A. longa* (Tappan), L.Cret.(Alb.), Tex.; *5a,b,* side, apert. views, ×22 (*2117).

Arenonina Barnard, 1958, *87, p. 118 [**A. cretacea;* OD]. Test attached, early stage planispirally enrolled, later uncoiled and with broad, low chambers resulting in flabelliform test; wall finely agglutinated, with considerable calcareous cement; aperture terminal slit in early stage, multiple in adult flabelliform portion, with single row of large rounded openings extending across breadth of final chamber, each aperture with distinct lip. [*Arenonina* differs from *Placopsilina* in its spreading chambers and flabelliform test and in having a multiple aperture consisting of a single row of openings.] *U.Cret.(Senon.),* Eng.——Fig. 160. **A. cretacea;* ×30 (*87).

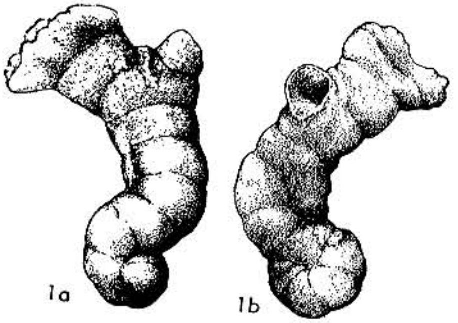


Fig. 161. Lituolidae (Placopsilininae; *1, Manorella*) (p. *C*248).

Fig. 161A. Lituolidae (Placopsilininae; *Oxinoxis*) (p. C248).

Haddonia Chapman, 1898, *313, p. 453, 455 [**H. torresiensis;* OD] [=*Arhaddonium* Rhumbler, 1913, *1572b, p. 448 (obj.) *(nom. van.)*]. Test large, attached, early portion coiled, later uniserial or branching; chambers broad, low, irregular in size and shape; sutures depressed; wall coarsely agglutinated, with much calcareous cement, interior smoothly finished, although pitted and traversed by large canals; aperture terminal, arched and slitlike, with projecting teeth. *Eoc.-Rec.*, Pac.-W.Indies(Cuba).——Fig. 159,*6*. **H. torresiensis*, Rec., N.Australia(Torres Straits); *6a*, side view of lectotype (here designated and redrawn, BMNH Cat. No. 97.11.20.1, specimen figured by Chapman, *313, pl. 28, fig. 2), illustration here published showing more of test than original figures, which did not show complete specimen; *6b*, top view of final chamber showing slitlike aperture and projecting teeth of penultimate chamber, with broken wall of final chamber showing straight transverse canals or pores, ×5.2 (*2117).

[This form was originally described as having a labyrinthic interior, but the inner wall is very smoothly finished as can be seen where branches are broken. Possibly straight pores in the wall were mistaken for a labyrinthic interior. No sections or additional material were available to check this. *Haddonia* differs from *Placopsilina* in its branching character, coarsely perforate wall, and elongate, slitlike aperture, instead of rounded aperture. *Coscinophragma* differs in having a labyrinthic interior and cribrate aperture.]

Manorella Grice, 1948, *823, p. 223 [**M. proteus;* OD]. Test free, early stage may be trochospirally coiled, later uniserial, with closely appressed chambers, rarely branching; wall agglutinated on pseudochitinous base, with calcareous particles in calcareous cement, coarsely perforate, interior simple; aperture multiple, with few ovate to slitlike openings on slight collar-like projections, paralleling periphery on terminal face. *U.Cret.*, USA (Tex.).——Fig. 159,7; 161,*1*. **M. proteus*; 159,*7*, holotype, with multiple apert. and coarse perforations, ×36 (*2117); 161,*1a,b*, opposite sides of paratype showing early coil and later branching, ×30 (*823).

Oxinoxis Gutschick, 1962, *844A, p. 1299 [**O. botrys*; OD]. Test large, up to 1.5 mm. in length, early portion attached and lacking basal wall against attachment, later growing free of attachment, with complete wall; proloculus ovate, followed by loosely coiled series of few subglobular chambers, later chambers uncoiled and rectilinear, each with distinct and tubular neck; wall agglutinated, of quartz and calcareous grains in siliceous cement; aperture rounded and terminal on short thick neck. *L.Miss.(Kinderhook.)*, USA(Mont.).——Fig. 161A,*1*. **O. botrys;* attached side of holotype, showing open base of early loosely coiled attached chambers, and free-growing later chambers broken open to show tubular necks, ×33 (*844A).

[Although originally placed in the "family Reophacidae, subfamily Aschemonellinae," *Oxinoxis* is here transferred to the Placopsilininae, because of its early coil and attached nature. It resembles *Subbdelloidina* Frentzen in the poorly developed coil, but differs in the distinctly globose chambers and tubular necks, and in the tendency to grow free of the attachment in the later stage.]

Subbdelloidina Frentzen, 1944, *747, p. 331 [**S. haeusleri;* OD] [=*Eoplacopsilina* Payard, 1947, *1432, p. 63 (type, *E. mariei*)]. Test attached, with bulbous proloculus followed by uniserial, rectilinear, arcuate, or somewhat irregular series of chambers, increasing gradually in size; wall agglutinated; aperture terminal, may be slightly produced. [Differs from *Placopsilina* in lacking an early coiled stage. *Eoplacopsilina* was originally stated (*1432) to have an internal spire within the spherical proloculus, but examination of the holotype (only known specimen) of the type-species shows that this appearance is due to an irregular chamber cavity, not a spiral stage of numerous chambers, as found in *Placopsilina*.] *L. Jur.(U.Lias.)-U.Jur.*, Eu.(Switz.-Ger.-Fr.).——Fig. 159,*8*. **S. haeusleri*, U.Jur., Switz.; *8a,b*, ext. and part of formerly attached side showing simple walls, enlarged (*854).——Fig. 159,*9*. *S. mariei* (Payard), L.Jur.(Toarc.), Fr.; holotype (redrawn), ×105 (*2117).

Subfamily COSCINOPHRAGMATINAE Thalmann, 1951

[*nom. correct.* Loeblich & Tappan, herein (*pro* Coscinophragminae Thalmann, 1951, p. 221) (*nom. subst. pro* Polyphragminae Rhumbler, 1913, p. 446, *nom. nud.*)] [=Arpolyphragmina Rhumbler, 1913, p. 446 *(nom. van.)*]

Test attached, wall labyrinthic. *U.Cret.-Rec.*

Coscinophragma Thalmann, 1951, *1899d, p. 221 [*pro Polyphragma* Reuss, 1871, *1556, p. 278 (*non* Quatrefages, 1866)] [**Lichenopora cribrosa* Reuss, 1846, *1538, p. 64; OD] [=*Arpolyphragmoum* Rhumbler, 1913, *1572b, p. 447 (obj.) *(nom. van.)*]. Test attached by base, with cylindrical and bifurcating branches composed of numerous broad low chambers; wall agglutinated, interior labyrinthic with coarsely agglutinated layer and inner thin perforate homogeneous layer lining alveolar openings; aperture terminal, cribrate, consisting of regularly spaced rounded openings. *U.Cret.(Cenoman.)*, Eu.(Czech.).——Fig. 162, *8,7*. **C. cribrosa* (Reuss); *6a,b*, side and top views of branched fragment, ×5, ×14; *7a*, sec. showing interior structure, ×22; *7b*, sec. of portion of wall, showing thick, compact arenaceous layer and thin perforate layer, ×400 (*1445).

Adhaerentia Plummer, 1938, *1467, p. 242 [**A. midwayensis;* OD]. Test elongate, attached by hemispherical proloculus, commonly to coiled calcareous foraminifers, later growing free, early chambers biserially arranged, later uniserial and cylindrical; sutures slightly depressed to indistinct; wall agglutinated, interior labyrinthic; aperture in biserial stage rounded and subterminal, in later stages becoming irregular in outline and finally terminal and multiple. [*Adhaerentia* was

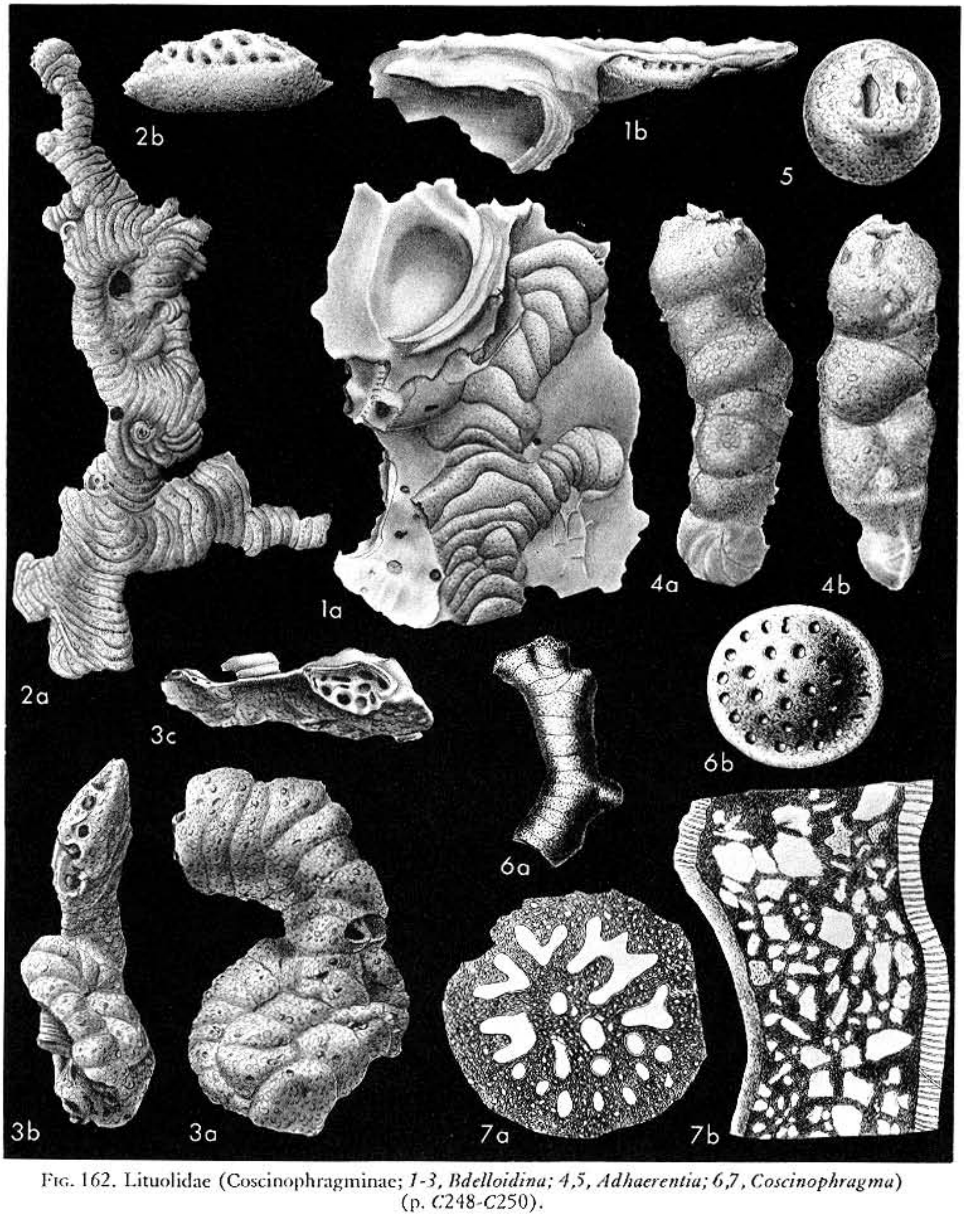


Fig. 162. Lituolidae (Coscinophragminae; *1-3, Bdelloidina; 4,5, Adhaerentia; 6,7, Coscinophragma*) (p. C248-C250).

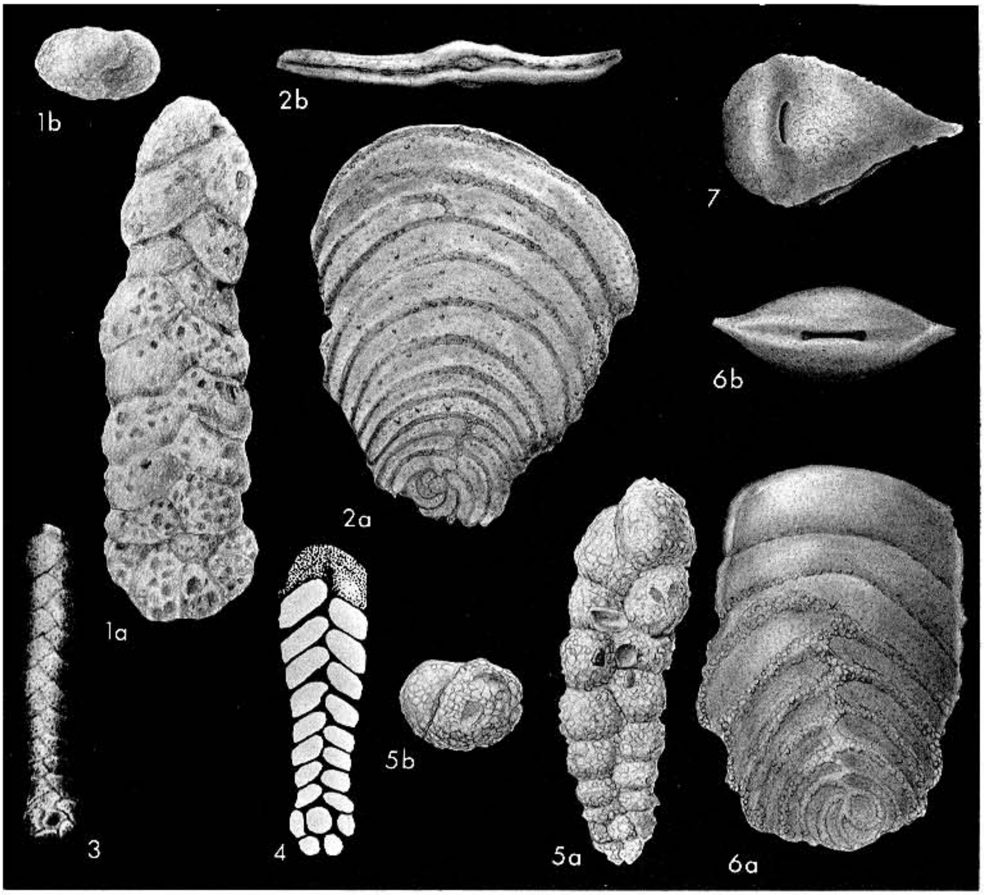


FIG. 163. Textulariidae (Spiroplectammininae; *1, Spiroplectammina; 2, Ammospirata; 3,4, Bolivinopsis; 5, Morulaeplecta; 6,7, Vulvulina*) (p. C251-C253).

placed in the Placopsilinidae by PLUMMER (1938, *1467), who regarded it as an advanced member of the family because of its reduced attached stage and labyrinthic interior.] *Paleoc.*, USA(Ala.).——FIG. 162,*4,5*. **A. midwayensis; 4a,b,* side, edge views of specimen attached to *Lenticulina; 5,* top view of another specimen showing double aperture; both ×26 (*2117).

Bdelloidina CARTER, 1877, *293, p. 201 [**B. aggregata;* OD] [=*Arbdelloidinum* RHUMBLER, 1913, *1572b, p. 448 (obj.) *(nom. van.)*]. Test attached, with numerous broad, low chambers in uniserial series or spreading and rarely branching; wall agglutinated, rough externally, smooth inside, with interior secondary septa vertically crossing chambers from base to top, numerous internal pores pitting interior and row of communicating pores through septal faces; aperture single or double row of pores against attachment on terminal face of last-formed chamber. *Paleoc. (Landen.)-Rec.,* Pac.-USA(N.J.).——FIG. 162,*1,2*. **B. aggregata,* Rec., Pac.(Bikini Atoll) *(1),* Ind. O. *(2)*; *1a,b,* side view of attached specimen and top view of branch showing multiple aperture, ×5.5; *2a,b,* side view of much branched specimen and top view of branch showing double row of pores, ×5, ×20 (*1166).——FIG. 162,*3*. *B. vincentownensis* HOFKER, Paleoc.(Landen.), N.J.; *3a,b,* side, edge views showing aperture as a single row of pores; *3c,* broken to show complex interior; all ×14 (*2117).

Family TEXTULARIIDAE Ehrenberg, 1838

[*nom. correct.* CHAPMAN, 1900, p. 9 (*pro* family Textularina EHRENBERG, 1838, p. 200)]——[All names referred to are of family rank; dagger(†) indicates *partim*]——[=Énallostègues† D'ORBIGNY, 1826, p. 260 *(nom. nud)*; =Turbinoida† SCHULTZE, 1854, p. 52 *(nom. nud.)*; =Uvellidea† REUSS, 1862, p. 318, 382 *(nom. nud.)*; =Uvellideae† GÜMBEL, 1870, p. 23 *(nom. nud.)*; =Plecanioidea SCHWAGER, 1877, p. 22; =Turbinida† MARRIOTT, 1878, p. 30 *(nom. nud.)*; =Opistho-Dischistidae† EIMER & FICKERT, 1899, p. 677 *(nom. nud.)*; =Dischistidae† EIMER & FICKERT, 1899, p. 678 *(nom. nud.)*]——[=Textularidae D'ORBIGNY in DE LA SAGRA, 1839, p. 140; =Textilarina AGASSIZ, 1844, p. 4; =Textilarideae REUSS, 1860, p. 231; =Textilaridea REUSS, 1862, p. 320; =Textularida SCHMARDA, 1871, p. 164; =Textilarida JONES in GRIFFITH & HENFREY, 1875, p. 320; =Textilariidae JONES, 1895, p. 140; =Textularinae Delage & Hérouard, 1896, p. 140; =Textulinidae Rhumbler, 1913, p. 339 (*nom. van.*); =Artextulidia Rhumbler, 1913, p. 342 (*nom. van.*); =Textuláridos Gadea Buisán, 1947, p. 18 (*nom. neg.*)]

Test free or attached, may have early planispiral coil, generally biserial and may become uniserial; wall agglutinated; aperture simple, basal or terminal, single to multiple. *Carb.-Rec.*

Subfamily SPIROPLECTAMMININAE
Cushman, 1927

[Spiroplectammininae Cushman, 1927, p. 21]

Early stage planispiral, later biserial. *Carb.-Rec.*

Spiroplectammina Cushman, 1927, *431, p. 23 [**Textularia agglutinans* d'Orbigny var. *biformis* Parker & Jones, 1865, *1418, p. 370; OD]. Test free, elongate, early portion in planispiral coil of few chambers, later chambers biserially arranged; wall agglutinated; aperture low arch at inner margin of final chamber. [*Spiroplectammina* differs from *Textularia* in having a distinct and well-developed initial coil. The lectotype of *Textularia agglutinans* var. *biformis* Parker & Jones is here designated (BMNH-ZF 3639, *ex* 94.4.3.194, at 60-70 fathoms off Hunde Island, Davis Straits).] *Carb.-Rec.*, cosmop.——Fig. 163, *1*. **S. biformis* (Parker & Jones), Rec., Alaska (Chukchi Sea); *1a,b*, side, top views, ×100 (*1162).

Ammospirata Cushman, 1933, *458, p. 32 [**Pavonina mexicana* Cushman, 1926, *422, p. 22; OD]. Test free, palmate, compressed; globular proloculus followed by few narrow, elongate chambers in planispiral coil of single whorl, chambers with considerable overlap of preceding chambers at periphery, coiled stage followed by short biserial stage of very low, broad chambers, which extend back around coil at each margin of test, followed by well-developed uniserial stage of many broad, low-arched chambers (as many as 14 uniserial chambers present in topotype specimens of type-species); sutures thickened, slightly elevated; wall finely agglutinated, smoothly finished; aperture terminal, consisting of series of small pores in narrow depression extending along entire upper margin of chamber. [*Ammospirata* differs from *Spiroplectammina* in its palmate shape, strongly arched chambers and extremely broad, low chambers, showing considerable overlap of earlier ones at their outer margin in the later uniserial stage, and in the multiple aperture.] *Oligo.*, Mex.——Fig. 163,*2*. **A. mexicana* (Cushman); *2a,b*, side, top views of topotype showing pores in terminal groove, ×42 (*2117).

Bolivinopsis Yakovlev, 1891, *2095, p. 349 [**B. capitata*; OD] [=*Spiroplectoides* Cushman, 1927, *428, p. 77 (type, *Spiroplecta rosula* Ehrenberg, 1854, *680, p. xxxii)]. Test with large planispiral coil in early stage and later long, narrow biserial stage, similar in plan to *Spiroplectammina*; wall calcareous, possibly of agglutinated fine-grained calcareous particles. *U.Cret.*, Eu.-N.Am.-S.Am.——Fig. 163,*3*. **B. capitata*, USSR; ×120 (*1197).——Fig. 163,*4*. *B. rosula* (Ehrenberg), USA(Miss.); ×39 (*484).

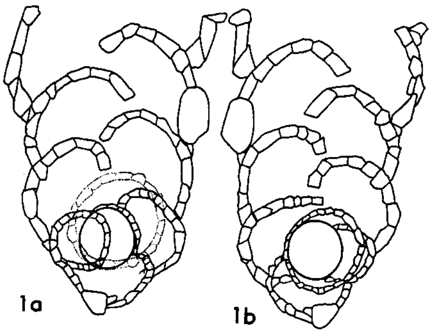


Fig. 164. Textulariidae (Spiroplectammininae; *1*, *Morulaeplecta*) (p. C251).

[The nature of the wall of the type-species is somewhat doubtful. Macfadyen (1933, *1197) noted that *B. capitata* had originally been included in the perforate calcareous group by Yakovlev and on this basis, as well as general form, assumed it to be identical with *Spiroplecta rosula* Ehrenberg. Thus *Spiroplectoides* was regarded as a junior synonym of *Bolivinopsis*. Frizzell (1943, *750, p. 338) stated that the synonymy was not positive. As the original description was based on a single specimen mounted in balsam, details of wall characters were uncertain and Frizzell stated that it is commonly difficult to distinguish between finely agglutinated tests and secreted calcareous ones. He added that a study of topotypes would be necessary to settle the problem. Cushman (1946, *484, p. 102, 103) regarded *B. rosula* as "calcareous, finely perforate," and *B.? clotho* (Grzybowski) (=*Spiroplectammina grzybowskii* Frizzell) as "entirely siliceous." Glaessner (1947, *796, p. 98) stated that *Bolivinopsis* should replace *Spiroplectammina*, as the type-species was said to be arenaceous. Shlykova in Rauzer-Chernousova & Fursenko (1959, *1509, p. 219) recognized both *Spiroplectammina* and *Bolivinopsis*, placing both in the Textulariinae. As we have been unable personally to examine topotype material of *B. capitata*, we follow this latter usage and recognize both genera. Shlykova stated that the wall of *Bolivinopsis* is calcareous but by placement in this family would seem to indicate that it may be of agglutinated calcareous particles.]

Morulaeplecta Höglund, 1947, *924, p. 165 [**M. bulbosa;* OD]. Test streptospirally coiled in initial portion, completely enclosing bulbous proloculus, later portion biserial; proloculus pseudochitinous, remainder of wall agglutinated; aperture interiomarginal arch. [*Morulaeplecta* differs from *Spiroplectammina* in its early streptospiral rather than planispiral coil.] *Rec.*, Sweden.——Fig. 163,*5*; 164,*1*. **M. bulbosa;* 163,*5a,b*, side, top views of paratype, ×123 (*2117); 164,*1a,b*, optical secs., ×250 (*924).

Vulvulina d'Orbigny, 1826, *1391, p. 264 [**V. capreolus;* SD Cushman, 1928, *439, p. 118] [=*Schizophora* Reuss, 1861, *1551, p. 12 (type, *S. neugeboreni*); *Venilina* Gümbel, 1870, *840, p. 648 (type, *V. nummulina*); *Trigenerina* Schubert, 1902, *1681, p. 26 (obj.)]. Test free, flaring or elongate, lozenge-shaped or rhomboidal in section, lateral margins acutely angled; chambers increasing rapidly in size, early portion coiled at least in microspheric generation, later chambers biserially arranged, broad and low, somewhat arched over early coil, recurved laterally, final chambers uniserial in best-developed specimens of most species, but some may show only biserial development; sutures distinct, commonly thickened and elevated in early portion, later

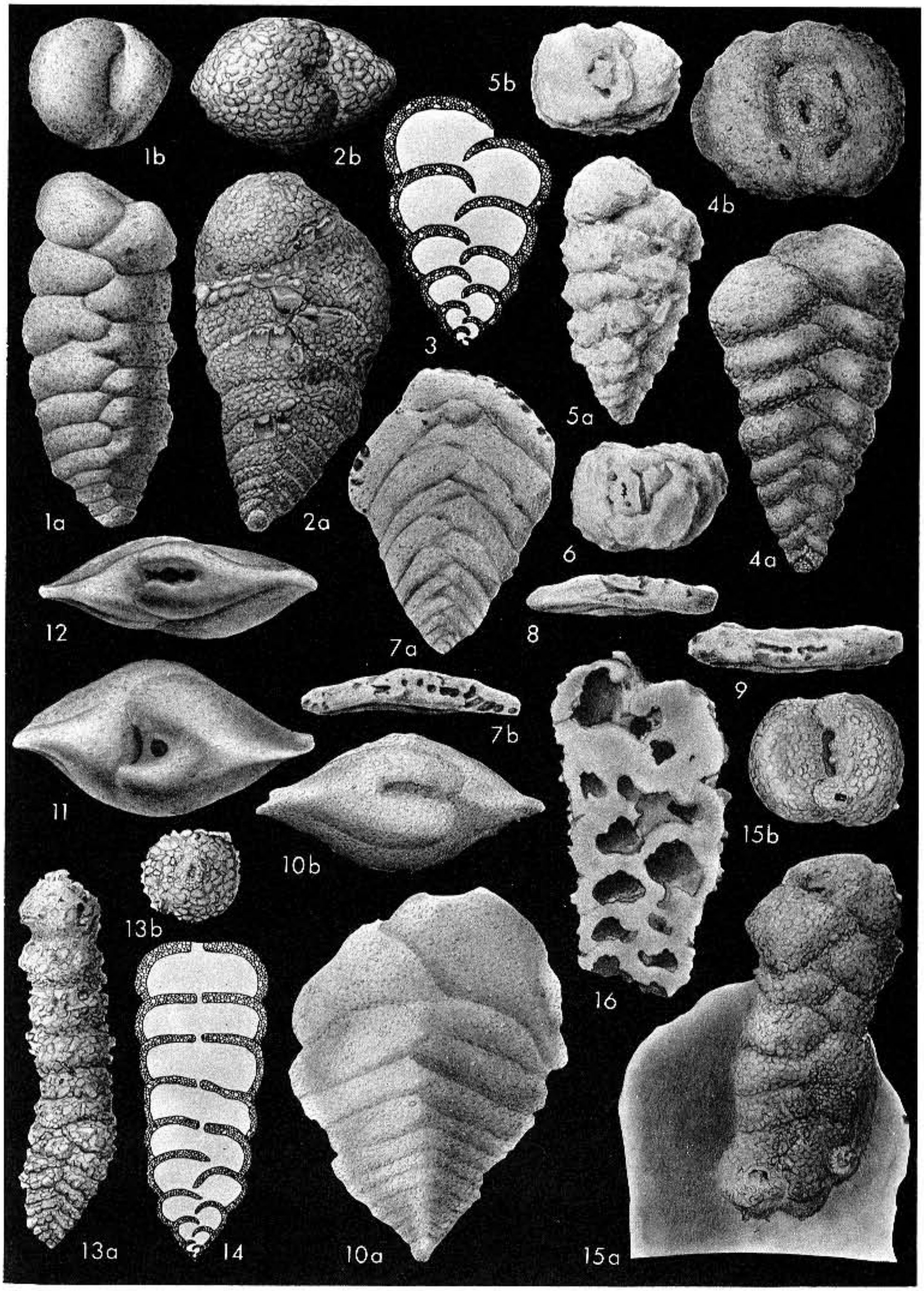


FIG. 165. Textulariidae (Textulariinae; *1-3, Textularia; 4-6, Olssonina; 7-9, Poritextularia; 10-12, Semivulvulina; 13-14, Bigenerina; 15,16, Textularioides*) (p. C253-C255).

moderately depressed; wall agglutinated, but very finely grained and smoothly finished, of calcareous, arenaceous, or other mineral grains; aperture in early stage broad, low interiomarginal arch, in uniserial stage becoming elongate, narrow terminal slit. [*Vulvulina* differs from *Ammospirata* in having a single terminal aperture rather than a row of pores in the uniserial stage and in the uniserial portion being of equal or lesser breadth than the preceding biserial stage, whereas in *Ammospirata* the uniserial portion is broad, resulting in a distinctly palmate test.] *U.Cret. (Campan.)-Rec.,* cosmop.——Fig. 163,*6,7*. *V. pennatula* (Batsch), Rec., Italy, topotypes; *6a,b,* side, top views of adult test showing early coil, later biserial stage, and final uniserial development with terminal slitlike aperture; *7,* top view showing basal aperture in biserial stage; all ×40 (*2117).

Subfamily TEXTULARIINAE Ehrenberg, 1838

[*nom. correct.* Chapman, 1900, p. 9 (*pro* subfamily Textularinae Carpenter, Parker & Jones, 1862, p. 189)]——[All names referred to are of subfamily rank]——[=Textilarida Schultze, 1854, p. 52; =Textilaridae Schwager, 1877, p. 21; =Textilaria Marriott, 1878, p. 30; =Textularidae Bütschli in Bronn, 1880, p. 203; =Textilariinae Jones, 1895, p. 141]

Test biserial, at least in early stage, may become uniserial. *Penn.-Rec.*

Textularia Defrance in de Blainville, 1824, *141a, p. 177 [**T. sagittula;* OD (M)] [=*Textilaria* Ehrenberg, 1839, *667, opposite p. 120 (obj.) *(nom. van.)*; *Plecanium* Reuss, 1862, *1552, p. 383 (type, *Textularia labiata* Reuss, 1862); *Textillaria* Schwager, 1864, *1702, p. 200 *(nom. van.)*; *Pleurostomelloides* Majzon, 1943, *1203, p. 157 (type, *P. andreasi*)]. Test free, elongate, biserial, generally more or less compressed in plane of biseriality or rarely oval to circular in cross section; chambers numerous, generally closely appressed; wall agglutinated, simple; aperture single low arch at base of last chamber. *Penn.-Rec.,* cosmop.——Fig. 165,*1,2*. **T. sagittula,* Plio.(Piacenz.), Italy (Siena, *1a,b;* Castel-Arquato, *2a,b*); *1a,b,* side, top views of topotype, ×26 (*2117); *2a,b,* side, top views, ×64 (*2117).——Fig. 165,*3*. *T.* sp., long. axial sec. showing simple wall construction, enlarged (*401).

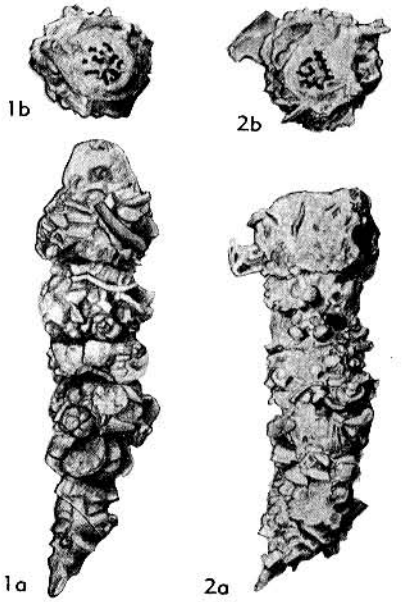


Fig. 166. Textulariidae (Textulariinae; *1,2, Cribrobigenerina*) (p. *C*254).

[Defrance (*141a, p. 177) described *Textularia* with *T. sagittula* Defrance as type-species. No localities were cited, for the author stated only that his fossils came from Italy. Defrance's illustrations (1824, *141b, pl. 13, figs. 5, 5a,b) indicate that the species is a very large form (3 mm. in length) and show that it definitely is biserial in the early stages. Later, Defrance (1828, *579f, p. 345) reported the occurrence of this species as "fossile près de Sienne, de Castel-Arquato, et vivant sur les bords de la Mediterranée. d'Orbigny, loc. cit.)." Lacroix (1929, *1074, p. 2) stated that he had examined many thousand examples of *T. sagittula* from dredgings in the Bay of Biscay (Gulf of Gascony), the English Channel, and the Mediterranean, and that a true biserial specimen did not exist. All complete specimens seen by him exhibited an early coiled stage, although in some less perfect specimens this portion was broken or abraded so as to give a pseudobiserial appearance. On the basis of dimorphism and of a statistical study Lacroix believed that a biserial form would be impossible in this species as he observed both "A and B forms" with distinct coils. Following Lacroix's work, some later investigators have considered *Textularia* and *Spiroplectammina* to be synonymous, although Lacroix considered both genera valid, differing only in relative importance of the coiled portion of the test. Bandy (1949, *71) noted that some workers even placed the type-species of *Textularia* in *Spiroplectammina,* which *Textularia* antedated by more than a century.

In order to settle definitely the status of this genus we attempted to re-examine Defrance's types, conducting a prolonged search for them while in France during 1953-54. Since no trace of his collection could be found, the types are presumed to be lost. As noted above, Defrance's original description gave no definite localities, whereas his later publication cited three localities in Italy—near Siena, at Castel-Arquato, and off the Italian coast living in the Mediterranean. The Mediterranean is excluded from consideration as a source of topotype material, as too vague and not qualifying as a producer of "fossil from Italy." Both Castel-Arquato and Siena have excellent exposures of the Piacenzan (Pliocene), and both contain numerous textularians. Specimens closest in appearance to the type description and figures were found at Siena. Cushman (1945, *481) figured two specimens from Castel-Arquato, which he referred to "*Spiroplectammina sagittula*" but, like the majority of specimens at Castel-Arquato, they were only about 1 mm. in length, and thus only one-third the length of Defrance's figured type. Much more typical specimens occur at Siena and for this reason, as well as the fact that the Siena locality was the first cited by Defrance, we consider it to be the type locality.

Specimens of the species from Siena were found to be truly biserial, as described for the genus, and they range from approximately 1.35 to 2.57 mm. in length. It is quite possible that for the species Lacroix described, no completely biserial form exists, but he was not studying Defrance's *Textularia sagittula.* Lacroix's specimens were all obtained from Recent dredgings in areas remote from the type locality of *T. sagittula* in the Pliocene (Piacenzan) of northern Italy. Furthermore, Lacroix's specimens (fig. 2,3) were approximately 1 mm. long, much compressed, and with a rounded base, whereas Defrance's figured type has a length of 3 mm. ("un ligne et demi"), the base is quite pointed, and the original illustration shows considerable inflation of the test. It seems obvious, therefore, that Lacroix was dealing with a completely different species and genus, his form being a true *Spiroplectammina*; hence, it has little or no bearing on understanding of *Textularia*.]

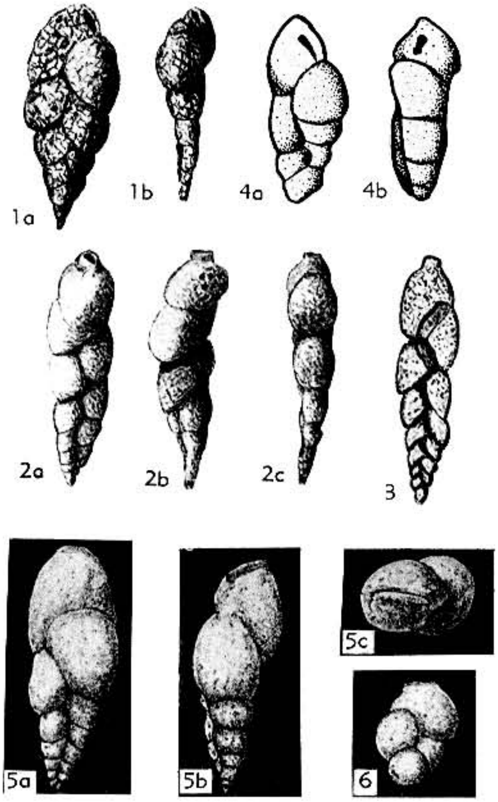


FIG. 167. Textulariidae (Pseudobolivininae; *1-6, Pseudobolivina*) (p. C255).

Bigenerina D'ORBIGNY, 1826, *1391, p. 261 [**B. nodosaria;* SD CUSHMAN, 1911, *404b, p. 27] [=*Bigenerina (Gemmuline)* D'ORBIGNY, 1826, *1391, p. 262 *(nom. neg.); Gemmulina* D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. 141 (type, *Bigenerina (Gemmuline) digitata* D'ORBIGNY, 1826, *1391, p. 262)]. Test free, elongate, early portion biserial with basal aperture as in *Textularia,* later uniserial with terminal and rounded aperture. *Jur.-Rec.,* cosmop.——FIG. 165,*13.* **B. nodosaria,* Rec., Eu.(Fr.); *13a,b,* side, top views, ×35 (*2117).——FIG. 165,*14. B.* sp., long. sec., showing simple agglutinated wall and change in apert. position with growth, enlarged (*401).

Cribrobigenerina ANDERSEN, 1961, *18, p. 26 [**C. parkerae;* OD]. Test large, elongate, early stage biserial, later uniserial; chambers somewhat inflated; sutures indistinct in early stage, slightly constricted in adult; wall coarsely agglutinated with much cement, surface rough; aperture terminal, cribrate, with irregularly shaped openings. *Rec.,* USA(La.).——FIG. 166,*1,2.* **C. parkerae; 1a,b,* side, top views of holotype; *2a,b,* paratype; all ×20 (*18).

Olssonina BERMÚDEZ, 1949, *124, p. 99 [**O. cribrosa;* OD] [=*Cribrotextularia* LOEBLICH & TAPPAN, 1952, *1158, p. 79 (type, *Textularia coryensis* COLE, 1941, *357, p. 21)]. Test free, elongate, flaring, ovate to quadrangular in section; chambers biserially arranged throughout; wall agglutinated, simple, not labyrinthic; aperture in early stages consisting of arch at base of last chamber and in addition symmetrical series of pores, usually in ring, on face of chamber, arched aperture partially closed in later chambers and represented by series of openings at base of final chamber additional to terminal cribrate apertures. *M.Eoc.,* W.Indies(Dominican Republic) - USA (Fla.).——FIG. 165,*4.* **O. cribrosa,* Dominican Republic; *4a,b,* side, top views, ×48 (*2117).——FIG. 165,*5,6. O. coryensis* (COLE), USA(Fla.); *5a,b,* side and top views of hypotype showing terminal cribrate aperture; *6,* top view of specimen with broken final chamber showing part of multiple aperture in addition to basal aperture, ×22 (*1158).

[The synonymy of *Cribrotextularia* and *Olssonina* was noted by LOEBLICH & TAPPAN (1953, *1163). *Olssonina* differs from both *Climacammina* and *Cribrostomum* in being wholly biserial and in lacking any uniserial development, in having a simple and distinctly agglutinated wall, rather than a double-layered fibrous calcareous one, and in lacking any development of pillars supporting the terminal chamber as in *Cribrostomum.*]

Poritextularia LOEBLICH & TAPPAN, 1952, *1160, p. 264 [**P. mexicana;* OD]. Test free, compressed, biserial throughout; wall agglutinated, interior simple; aperture consisting in early stages of elongate slit at base of last chamber, paralleling sides of test, and in adult comprising a linear series of openings across terminal portion of final chamber, formed by development of pillars across original slit. *Rec.,* Pac.(off Mex.).——FIG. 165,*7-9.* **P. mexicana; 7a,b,* side and top views of holotype showing multiple aperture; *8,9,* top views of paratypes showing basal aperture and later development of terminal aperture, ×22 (*1160).

[*Poritextularia* resembles *Textularia* DEFRANCE in its biserial agglutinated test but differs in having a multiple aperture. It resembles *Tawitawia* in the large flattened biserial test with rather extreme overlap of chambers and multiple aperture but differs in having a simple interior, lacking the internal pillars and labyrinthic structure of the latter genus, and in being completely biserial with no tendency to become uniserial. The aperture of *Tawitawia* is completely terminal and does not extend to the base of the final chamber as in *Poritextularia.*]

Semivulvulina FINLAY, 1939, *717a, p. 505 [**Textilaria capitata* STACHE, 1865, *1825, p. 270; OD] [=*Vulvulina (Semivulvulina)* FINLAY, 1939, *717a, p. 505 (obj.)]. Test free, flaring, rhomboidal in section, lateral margins acutely angled; chambers increasing rapidly in size, biserially arranged throughout, relatively low and broad; sutures distinct, depressed, oblique; wall finely agglutinated; aperture in early stages comprising interiomarginal arch, later with additional 1 or 2 areal openings above basal aperture, which in well-developed specimens fuse to form very high, narrow slit with scalloped margins reflecting its

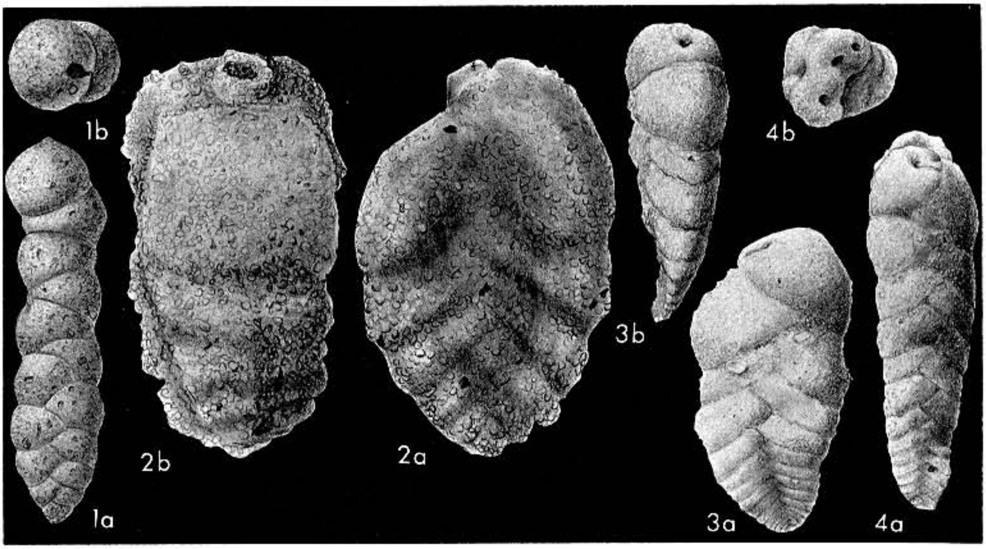


FIG. 168. Textulariidae (Pseudobolivininae; *1, Haeuslerella; 2, Siphotextularia; 3,4, Planctostoma*) (p. *C*256-*C*258).

development from separate openings, final elongate slit becoming nearly central in position and occupying nearly 0.3 of distance across terminal surface of test, though remaining open at base of chamber. [*Semivulvulina* differs from *Textularia* DEFRANCE in having a much elongated aperture with scalloped margin, which develops from 2 or more distinct openings, rather than having a single, low interiomarginal arch. *Semivulvulina* differs from *Vulvulina* in the absence of an early coil, in lacking a final uniserial stage, and in its more complex aperture.] *M.Eoc.-L.Mio.*, N.Z.——FIG. 165,*10-12*. **S. capitata* (STACHE), L.Oligo. *(10)*, Tert. *(11,12)*; *10a,b,* side, top views; *11,12,* apert. views showing varying apert. forms; all ×48 (*2117).

Textularioides CUSHMAN, 1911, *404b, p. 26 [**T. inflata;* OD]. Test attached at least in early stages; chambers in biserial textularian arrangement, somewhat flattened against attachment, later portion may grow free of attachment; wall agglutinated, with coarse grains embedded in fine ground mass, numerous tiny pores piercing wall; aperture low arch or slit at base of final chamber. [*Textularioides* differs from *Textularia* in being attached during at least part of its development.] *Rec.,* N.Pac.——FIG. 165,*15,16*. **T. inflata; 15a,b,* side, top views of topotype; *16,* attached side of topotype showing radial perforations of agglutinated wall; all ×33 (*1166).

Subfamily PSEUDOBOLIVININAE Wiesner, 1931

[Pseudobolivininae WIESNER, 1931, p. 98]

Test biserial, aperture comprising elongate terminal slit or may be produced on neck. *M.Jur.-Rec.*

Pseudobolivina WIESNER, 1931, *2063, p. 99 [**P. antarctica* (=*Bolivina punctata* D'ORBIGNY var. *arenacea* HERON-ALLEN & EARLAND, 1922, *911, p. 133) (*non B. variabilis* var. *arenacea* H.-A. & E., 1922; *nec. B. textilarioides* var. *arenacea* H.-A. & E., 1922; *nec B. inflata* var. *arenacea* H.-A. & E., 1922; *nec. B. tortuosa* var. *arenacea* H.-A. & E., 1922); OD (M)] [=*Plectinella* MARIE, 1956, *1221, p. B240 (type, *P. virgulinoides*); *Parvigenerina* VELLA, 1957, *2001, p. 18 (type, *Bifarina porrecta* (BRADY) var. *arenacea* H.-A. & E., 1922, *911, p. 132); *Arenovirgulina* SAID & BARAKAT, 1958, *1616, p. 243 (type, *A. aegyptica*); *Bimonilina* EICHER, 1960, *690, p. 65 (type, *B. variana*)]. Test biserial, tending to become uniserial, axis slightly twisted; aperture high narrow slit, interiomarginal in early biserial stage, becoming nearly terminal in later stage. *M.Jur.(Callov.)-Rec.,* Antarctic-N.Z.-Pac.-Eu.-Atl.-N.Afr.-N.Am.——FIG. 167,*1-3*. **P. antarctica;* Rec., Antarctic *(1)*, N.Z.*(2)*; *1a,b,* side and edge views of type-specimen of *Bolivina punctata* var. *arenacea* H.-A. & E., ×90 (*911); *2a-c,* opposite sides and edge of type-specimen of *Bifarina porrecta* var. *arenacea* H.-A. & E., type-species of *Parvigenerina; 3,* specimen mounted in balsam and viewed in transmitted light; all ×70 (*911). ——FIG. 167,*4*. *P. aegyptica* (SAID & BARAKAT), M.Jur.(Callov.), Egypt; *4a,b,* ×80 (*1616).——FIG. 167,*5,6*. *P. variana* (EICHER), L.Cret., USA (Wyo.); *5a-c,* opposite sides and top view of microspheric holotype; *6,* megalospheric paratype, all ×83 (*690).

[The type-species of *Pseudobolivina* and *Parvigenerina* were both described from specimens obtained by the Terra Nova Expedition. They are nearly identical in size and appearance, except that those with the better uniserial develop-

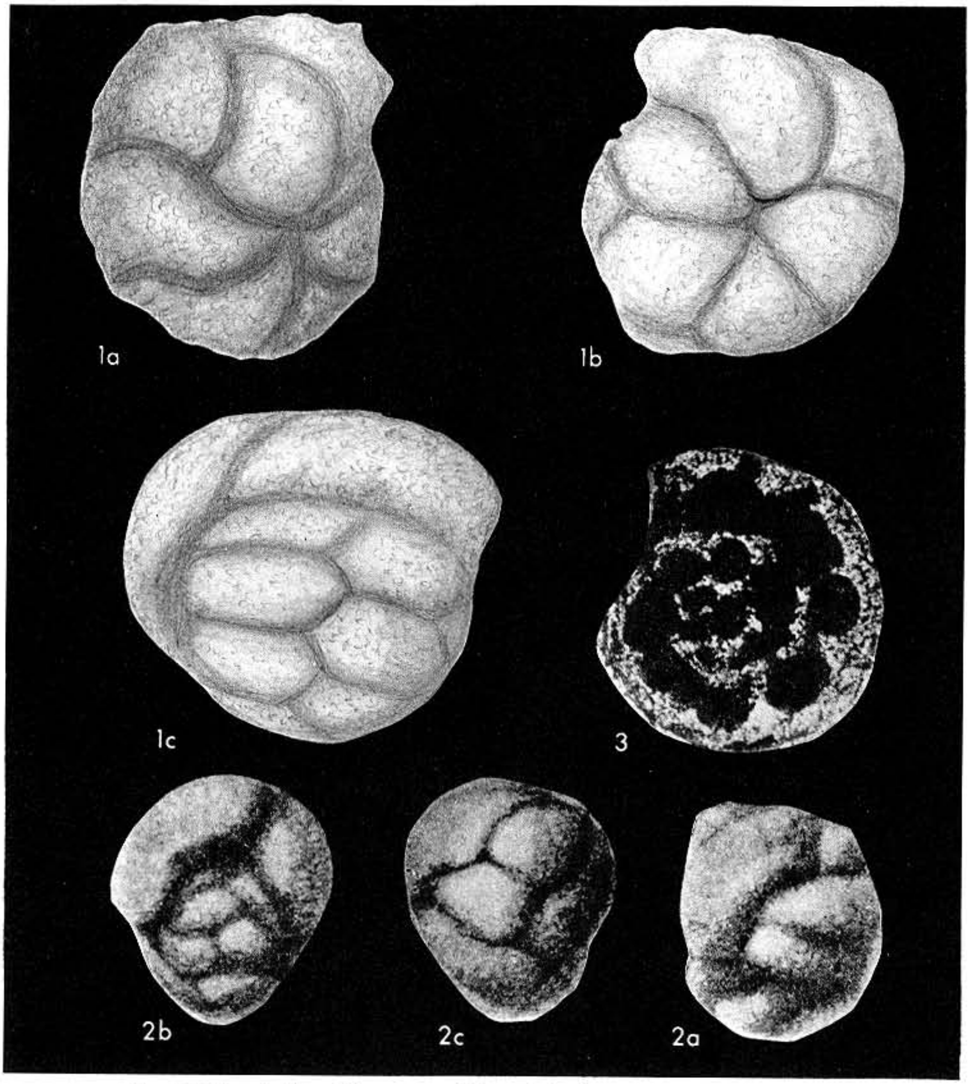


Fig. 169. Textulariidae (Plectorecurvoidinae; *1-3, Plectorecurvoides*) (p. C258).

ment (*"Bifarina"*) were somewhat larger (0.40-0.45 mm.) than the wholly biserial forms (0.35 mm.). They are here regarded as conspecific, as well as congeneric. *Pseudobolivina* differs from *Textularia* in the high slitlike aperture and tendency to become uniserial.]

Haeuslerella Parr, 1935, *1423, p. 82 [**H. pukeuriensis;* OD (M)]. Test free, elongate, chambers numerous, biserial in early portion, later chambers cuneate and alternating in loosely biserial arrangement; sutures distinct, depressed, early ones nearly horizontal, later ones oblique; wall agglutinated, surface smoothly finished; aperture nearly terminal, rounded, slightly eccentric, on upper surface of cuneate chamber. [*Haeuslerella* differs from *Textularia* in possessing the loosely biserial, cuneate-chambered later portion, and terminal aperture. It differs from *Bigenerina* in having an eccentric aperture and in lacking a distinct uniserial development. *Planctostoma* differs in the absence of a loosely biserial stage, and in having a terminal aperture on the typically biserial chambers.] *L.Mio.-L.Plio.,* N.Z.——Fig. 168,*1*. **H. pukeuriensis,* Mio.; *1a,b,* side, top views of topotype, ×42 (*2117).

Planctostoma Loeblich & Tappan, 1955, *1166, p. 8 [**Textularia luculenta* Brady, 1884, *200, p. 364; OD]. Test free, elongate, chambers biserially arranged, only very rarely with final uniserial development; wall agglutinated, simple in structure; aperture basal in young stage, later and typically consisting of rounded opening in terminal face, commonly somewhat eccentric and may become multiple with 2 or 3 rounded openings. *Rec.*, N.Atl.-S.Atl.-Carib.——Fig. 168,*3,4*. **P. luculenta* (Brady), Carib.; *3a,b*, side, edge views of hypotype; *4a,b*, side and apert. views of hypotype showing multiple aperture; all ×22 (*1166).

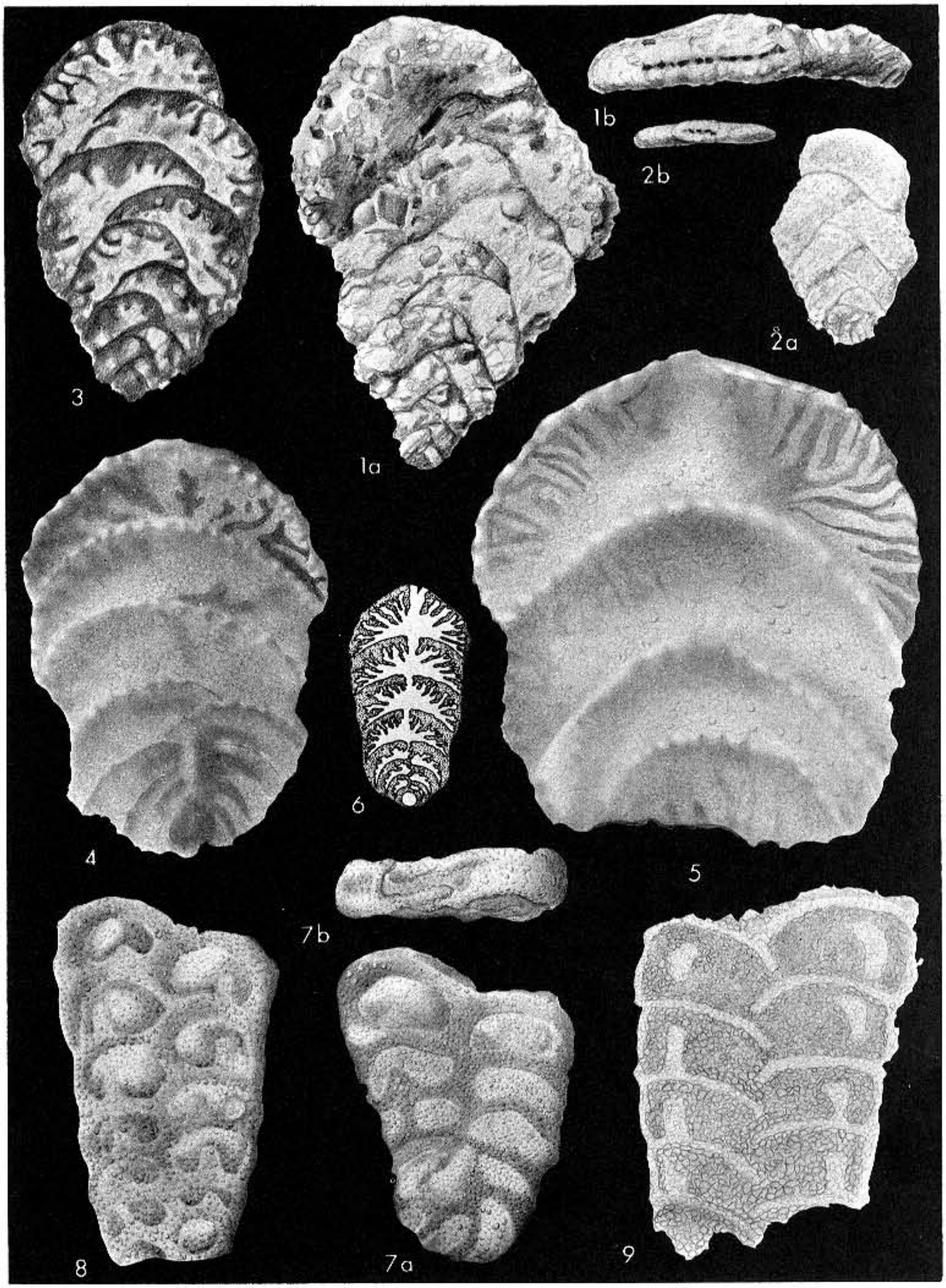


Fig. 170. Textulariidae (Tawitawiinae; *1-3*, *Tawitawia*; *4-6*, *Phyllopsamia*; *7-9*, *Septigerina*) (p. C258-C259).

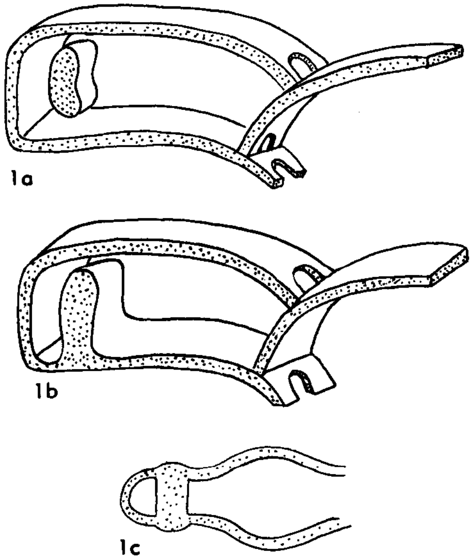


Fig. 171. Textulariidae (Tawitawiinae; *1, Septigerina*) (p. *C*258-*C*259).

[*Planctostoma* differs from *Textularia* in having a terminal aperture rather than a basal one. It is differentiated from *Bigenerina* in generally lacking a uniserial stage and in its terminal single or multiple aperture. It lacks the quadrangular outline of *Siphotextularia* and has a rounded aperture, which may be multiple instead of a terminal slitlike aperture with a projecting rim.]

Siphotextularia Finlay, 1939, *717a, p. 510 [**S. wairoana;* OD]. Test free, quadrangular in section, chambers biserially arranged throughout; aperture nearly terminal, rounded, in face of final chamber and produced on short neck. *Paleoc.-Rec.*, cosmop.——Fig. 168,*2*. **S. wairoana*, L. Plio., N.Z.; *2a,b,* side and edge views showing terminal elevated aperture, ×109 (*2117).

[*Siphotextularia* differs from *Textularia* in having a subterminal slitlike aperture which is areal rather than basal, and in the aperture being produced on a distinct neck. It differs from *Planctostoma* in having a quadrangular section, in having a slitlike rather than a rounded aperture, in having an apertural neck, and in having only a single apertural opening.]

Subfamily PLECTORECURVOIDINAE
Loeblich & Tappan, n. subfam.

Test biserial, with biserial axis planispirally enrolled, so that test is isomorph of *Cassidulina* in development. *L.Cret.*

Plectorecurvoides Noth, 1952, *1365, p. 117 [**P. alternans;* OD]. [=*Globivalvulinella* Bukalova, 1957, *252, p. 185 (type, *G. grossheimi*)]. Test planispirally enrolled, biserial; wall agglutinated; aperture not observed but intercameral openings are interiomarginal. *L.Cret.(Alb.),* Eu.(Aus.-Czech.-USSR).——Fig. 169,*1*. **P. alternans,* Aus.; *1a-c,* opposite sides and apert. views, ×158 (*2117).——Fig. 169,*2,3*. *P. grossheimi* (Bukalova), USSR; *2a-c,* side, apert., periph. views of holotype, ×70; *3,* sec. of paratype showing interior, ×100 (*252).

Subfamily TAWITAWIINAE
Loeblich & Tappan, 1961

[Tawitawiinae Loeblich & Tappan, 1961, p. 282]

Biserial, with vertical pillars subdividing chambers; aperture multiple, terminal. *Eoc.-Rec.*

Tawitawia Loeblich, 1952, *1151, p. 190 [**Textularia immensa* Cushman, 1913, *406, p. 633; OD]. Test large, flattened, biserial; chambers numerous, low, strongly overlapping in line of biseriality; wall coarsely agglutinated, thick, with pillars projecting downward into interior from roof of chambers, resulting in labyrinthine interior; aperture terminal, consisting of elongate series of irregular slits separated completely by pillars across opening or only partially by projections from one side, aperture not extending as far as inner margin of chamber. *Rec.*, N.Pac.O.(Philip.).——Fig. 170,*1-3*. **T. immensa* (Cushman); *1a,b,* side and top views of microspheric hypotype, ×10; *2a,b,* side and top views of megalospheric hypotype, ×10; *3,* long. sec. showing vertical pillars projecting downward from chamber roofs, ×22 (*1151).

[*Tawitawia* differs from *Textularia* in its labyrinthine interior, internal pillars, and terminal multiple aperture. *Septigerina* has vertical internal pillars, but these are much fewer, the test has a coiled base, and the aperture is typically textularian. *Tawitawia* differs from *Olssonina* in having a single row of apertural slits, rather than scattered pores over the apertural surface, and in having a labyrinthic interior.]

Phyllopsamia Małecki, 1954, *1210, p. 503, 507, 511 [**P. adanula;* OD]. Test compressed, palmate; early stage biserial, later uniserial; interior as in *Tawitawia;* wall agglutinated; aperture one or more slits in terminal groove. [Originally placed in the Lituolidae (Lituolinae), this genus is here referred to the Textulariidae because of its biserial early stage. *Phyllopsamia* differs from *Tawitawia* in having a final uniserial stage.] *Mio.*, Eu.(Pol.).——Fig. 170,*4-6*. **P. adanula; 4,5,* ext. views, ×52 (*2117); *6,* sec. showing interior, approx. ×28 (*1210).

Septigerina Keijzer, 1941, *1028, p. 1006 [**S. dalmatica;* OD]. Test free, elongate, flattened; early portion planispiral, later biserial, with horizontal partition extending through later chambers near their outer margin from one wall to that opposite, projection attached also to preceding septum in earlier biserial chambers, but extending only as horizontal pillar across central part of final chamber; wall agglutinated; aperture comprising arch at base of final chamber. *M.Eoc.*, Eu.(Yugo., Dalmatia).——Fig. 170,*7-9*; 171,*1*. **S. dalmatica;* 170,*7a,b,* side and top views of lectotype showing basal coil; 170,*8*, side view of paratype showing later development of pillars, ×116; 170,*9,* long. sec., ×86 (*2117); 171,*1a,b,*

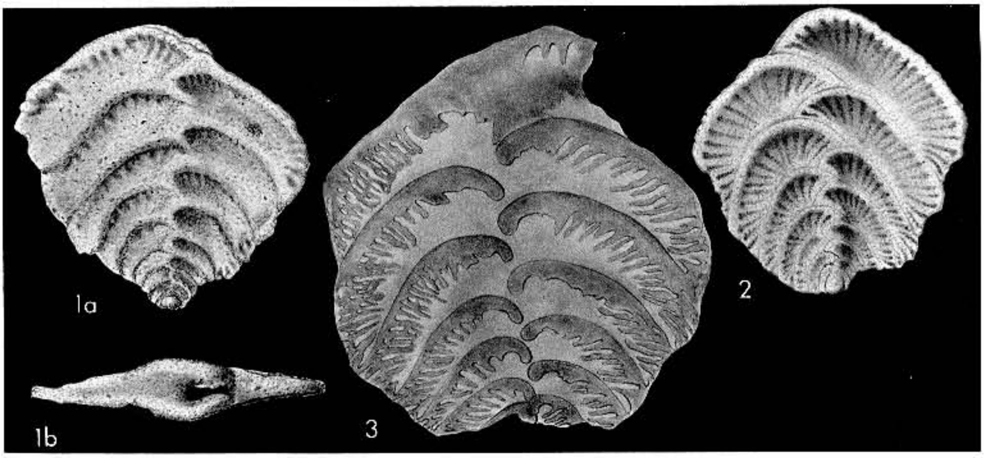


Fig. 172. Textulariidae (Tawitawiinae; *1-3, Zotheculifida*) (p. *C*259).

diagram of long. sec. showing internal pillar within a chamber; 171,*1c*, diagram of horiz. sec. showing pillar extending across chamber, enlarged (*1028).

[*Septigerina* differs from *Spiroplectammina* in the presence of secondary pillars extending across the outer portions of the biserial chambers. Three of the original syntypes of the type-species (collection of the Rijks Universitiet, Utrecht, Netherlands) were redrawn, the specimens having been generously loaned to us by the Rijks Universitiet. That in Fig. 170,*7* is here designated as lectotype.]

Zotheculifida Loeblich & Tappan, 1957, *1172, p. 224 [**Textularia lirata* Cushman & Jarvis, 1929, *509, p. 6; OD]. Test free, compressed, elongate or palmate, chambers numerous, biserially arranged, with internal incomplete partitions extending obliquely downward from septa, visible externally only when outer surface has either been dampened or somewhat abraded, and in rare specimens secondary partitions visible externally as slightly darker than intervening spaces; wall agglutinated, fine-grained, rather smoothly finished; aperture comprising high narrow arch at base of final chamber. *Mio.*, W.Indies(Trinidad).——Fig. 172,*1-3*. **Z. lirata* (Cushman & Jarvis); *1a,2,* side views of hypotypes; *1b,* top view; *3,* long. sec.; all ×34 (*1172).

[*Zotheculifida* differs from *Tawitawia* in its more numerous and regularly arranged internal partitions and in possessing a single textularian aperture, rather than a terminal linear series of pores. The type-species was originally described from the "*Sagrina* beds," Trinidad Point, Oropouche Lagoon, Trinidad, West Indies, which were then thought to be Eocene in age, but are now regarded as Miocene.]

Family TROCHAMMINIDAE
Schwager, 1877

[*nom. correct.* Lister in Lankester, 1903, p. 142 (*pro* family Trochamminidea Schwager, 1877, p. 21)]——[In synonymic citations dagger(†) indicates *partim*]——[=Arenacea Bütschli in Bronn, 1880, p. 193 *(nom. nud.)*; =Dischistidae† Eimer & Fickert, 1899, p. 678 *(nom. nud.)*; =Trochammina Lankester, 1885, p. 847; =Trochamminae Delage & Hérouard, 1896, p. 133; =Artrochammidia Rhumbler, 1913, p. 342 *(nom. van.)*; =Trochamminida Haeckel, 1894, p. 185]

Test free or attached, trochospiral; wall agglutinated; aperture interiomarginal or areal, single or multiple. *Carb.-Rec.*

Subfamily TROCHAMMININAE Schwager, 1877

[*nom. transl.* Brady, 1884, p. 66 (*ex* family Trochamminidea Schwager, 1877)] [=Ammosphaeroidininae Cushman, 1927, p. 40]

Test free or attached, trochospiral; wall agglutinated, interior simple; aperture interiomarginal or areal. *Carb.-Rec.*

Trochammina Parker & Jones, 1859, *1417b, p. 347 [**Nautilus inflatus* Montagu, 1808, *1299, p. 81; OD (M)] [=*Rhaphidohelix* Möbius, 1880, *1293, p. 76 (type, *R. elegans*); *Raphidohelix* Goës, 1882, *801, p. 140 *(nom. van.)*; *Trochamina* Deecke, 1884, *568, p. 21 *(nom. null.)*; *Reussina* Grzybowski, 1896, *835, p. 278 (*non Reussina* Neviani, 1896); *Ammoglobigerina* Eimer & Fickert, 1899, *692, p. 704 (type, *A. bulloides*, =*Lituola nautiloidea* Lamarck var. *globigeriniformis* Parker & Jones, 1865, *1418, p. 407); *?Glomerina* Franke, 1928, *740, p. 164 (type, *Lituola globigerinoides* Perner, 1892, *1445, p. 52)]. Test free, trochospiral; globular to ovate chambers increasing gradually in size; wall agglutinated; aperture low interiomarginal extraumbilical-umbilical arch which may have narrow bordering lip. *Carb.-Rec.*, cosmop.——Fig. 173,*1*. **T. inflata* (Montagu), Rec., N.Atl.; *1a-c,* spiral and umbilical sides and edge view, ×86 (*2117).——Fig. 173,*2*. *T. globigeriniformis* (Parker & Jones), Rec., N.Atl.; *2a-c,* opposite sides and edge view of lectotype (here designated and refigured) of *Lituola nautiloidea* Lamarck var. *globigeriniformis* Parker & Jones (1865, *1418, pl. 17, fig. 96), ×146 (*2117).

Ammosphaeroidina Cushman, 1910, *404a, p. 128 [**Haplophragmium sphaeroidiniformis* Brady, 1884, *200, p. 313; OD]. Test globose, streptospirally coiled with few embracing chambers, only 3 of final whorl visible at exterior; wall agglutinated; aperture low interiormarginal arch. *Eoc.-Rec.*, Pac.-Medit.-Antarctic-W.Indies(Cuba).——FIG. 174,*1*. **A. sphaeroidiniformis* (BRADY), Rec., Pac.; *1a-d*, opposite sides, edge view, and oblique view to show aperture, ×33 (*2117).

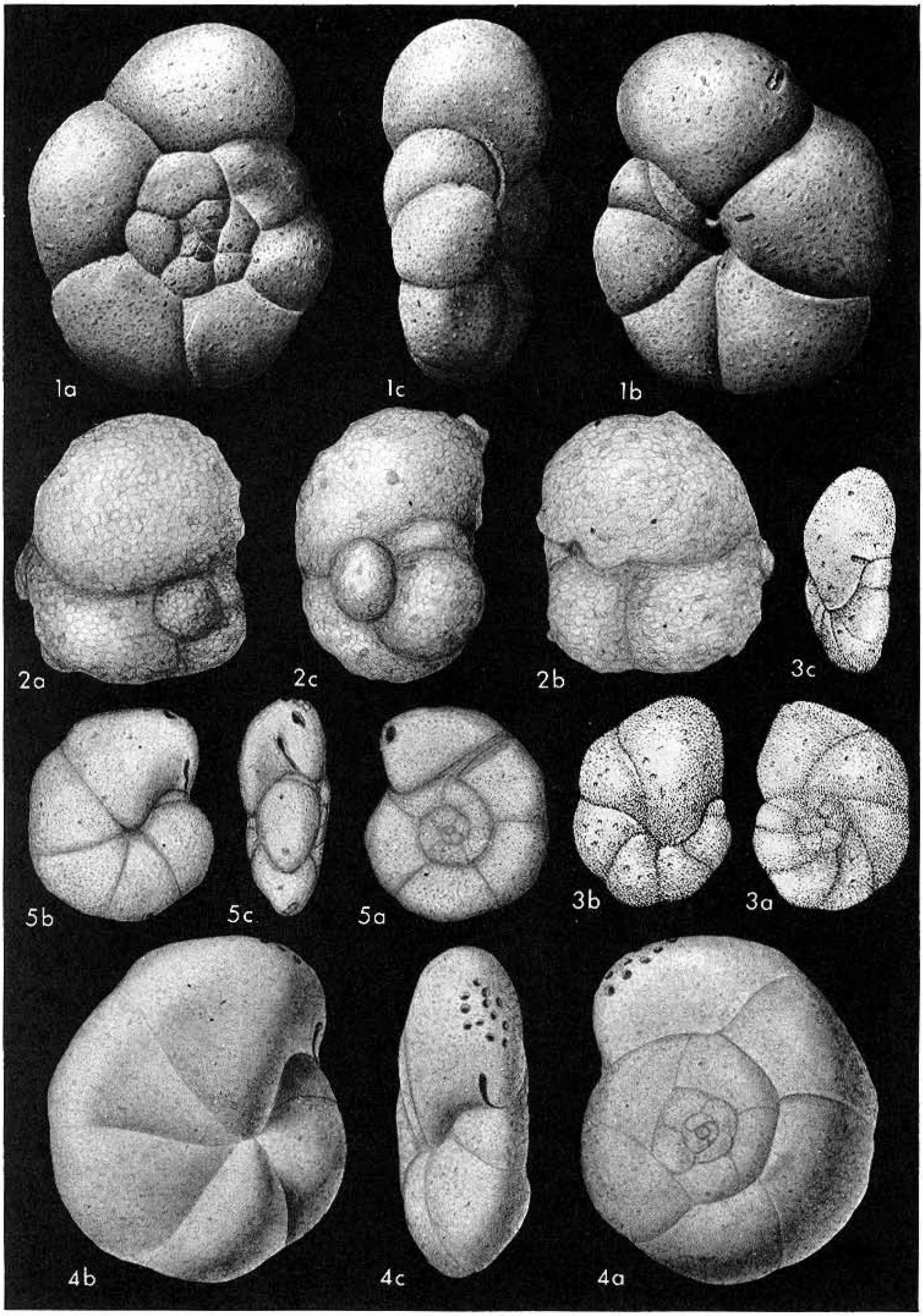


FIG. 173. Trochamminidae (Trochammininae; *1,2, Trochammina; 3, Trochamminula; 4,5, Arenoparrella*) (p. C259, C262, C266).

Arenonionella Marks, 1951, *1225, p. 377 [**A. voutei*; OD]. Test free, slightly trochospiral; chambers low and broad, all partially visible on spiral side, but with prominent lobe overhanging umbilicus on opposite side; wall thin, somewhat flexible and easily distorted, agglutinated with calcareous cement on pseudochitinous base, interior simple; aperture low interiomarginal, equatorial slit. [*Arenonionella* resembles the calcareous genus *Nonionella* in character of coiling, the overhanging chamber on one side, and equatorial location of the aperture but differs in having an agglutinated

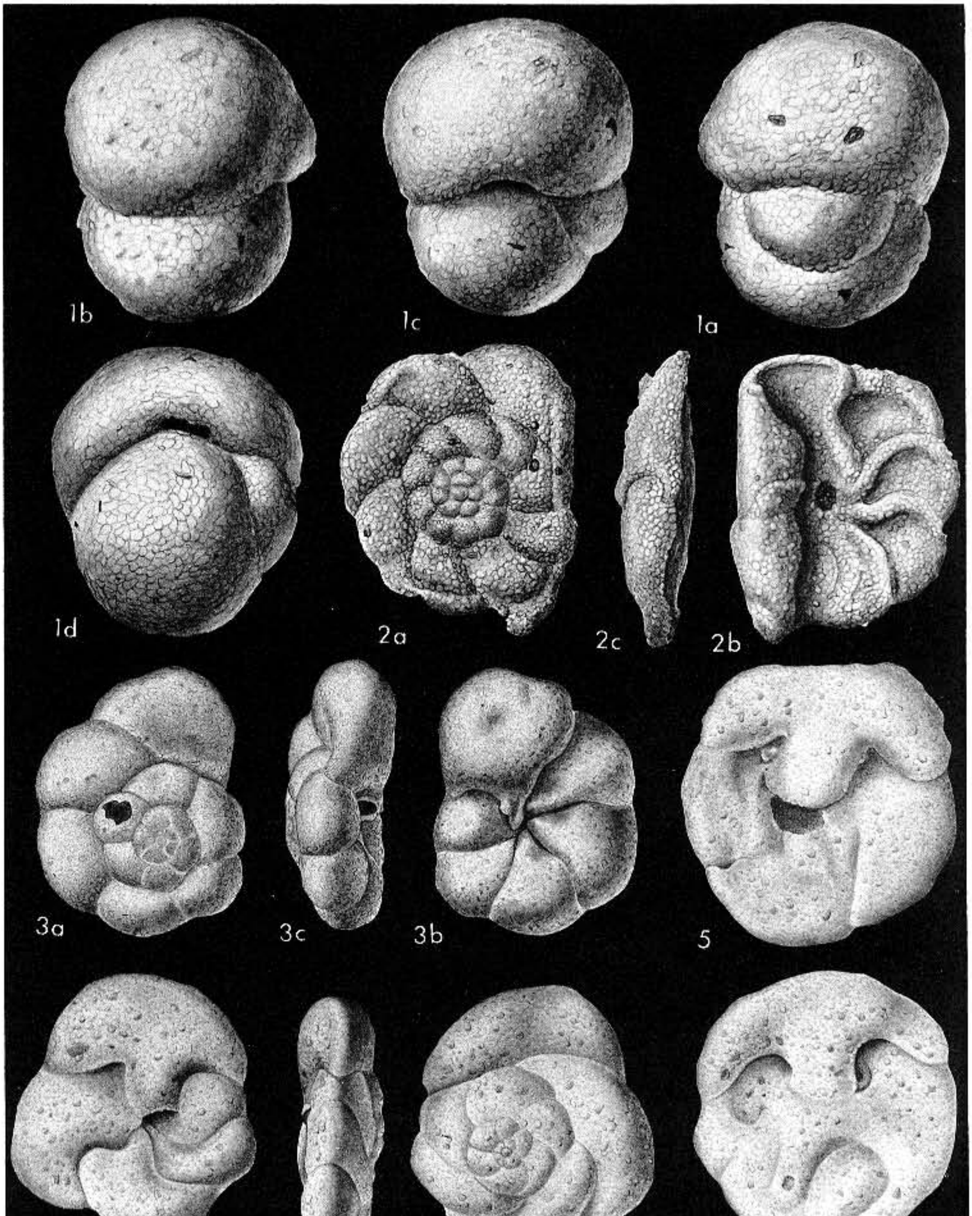


Fig. 174. Trochamminidae (Trochammininae; *1, Ammosphaeroidina; 2, Rotaliammina; 3, Siphotrochammina; 4-6, Tiphotrocha*) (p. C259-C260, C265-C266).

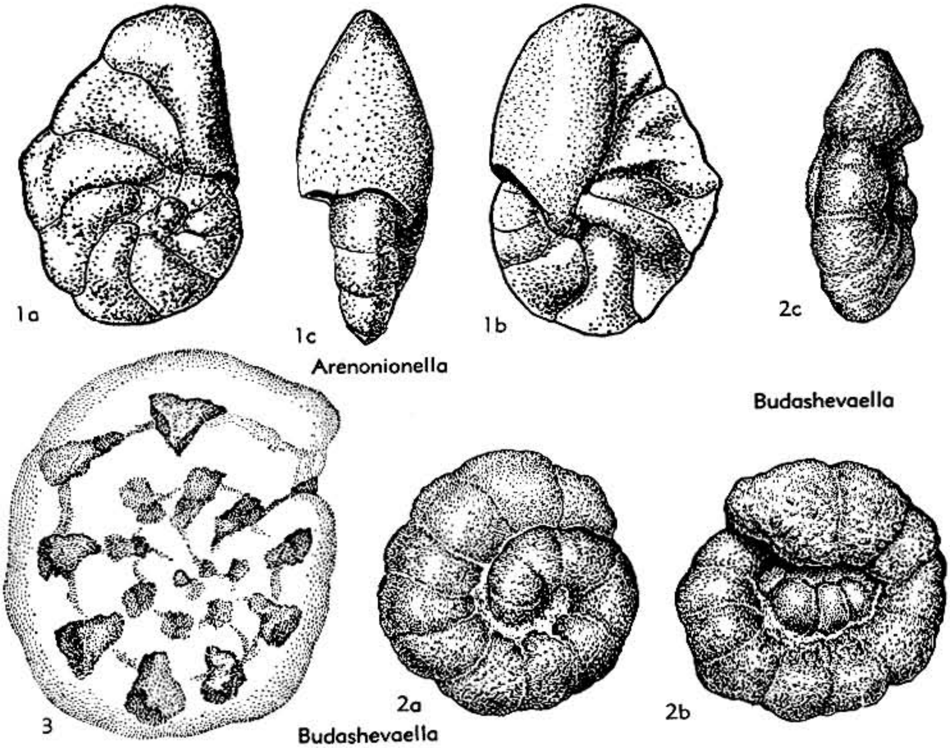


FIG. 175. Trochamminidae (Trochammininae; *1, Arenonionella; 2,3, Budashevaella*) (p. C261-C262).

wall. Because of the trochospiral coiling, it is here removed from the Haplophragmoidinae to the Trochamminidae. A junior synonym of *Arenonionella* is *Mendesia* PETRI, 1962, *1447A, p. 56 (type, *M. minuta) (non Mendesia* DE JOANNIS, 1902).] *U.Cret.(Maastricht.),* S.Am.(Brazil)*-Mio. (Vindob.),* N.Afr.(Algeria).——FIG. 175,*1*. **A. voutei; 1a-c,* opposite sides and edge, ×124 (*1225).

Arenoparrella ANDERSEN, 1951, *15, p. 31 [**Trochammina inflata* (MONTAGU) var. *mexicana* KORNFELD, 1931, *1048, p. 86; OD]. Test free, trochospiral, spiral side convex, umbilical side with small closed umbilicus; chambers increasing gradually in size; sutures radial; wall agglutinated; primary aperture elongate slit extending up face of final chamber approximately paralleling plane of coiling, supplementary cribrate aperture consisting of numerous circular openings near apex of final chamber. [*Arenoparrella* differs from *Jadammina* in having a vertical slitlike primary aperture and supplementary cribrate openings at the apex of the chamber, whereas in *Jadammina* the primary aperture is a low interiomarginal equatorial aperture with cribrate openings just above in the face of the chamber.] *Mio.-Rec.,* USA(La.) - W. Indies(Trinidad) - S. Am.(Venez.).——FIG. 173,*4,5*. **A. mexicana* (KORNFELD), Rec., Trinidad *(4),* USA(La.) *(5)*; *4a-c,* opposite sides and edge view of hypotype showing loop-shaped, nearly vertical slitlike primary aperture, and secondary apertural openings at peripheral angle, ×109 (*1631); *5a-c,* opposite sides and edge of hypotype, ×64 (*16).

Budashevaella LOEBLICH & TAPPAN herein [*nom. nov. pro Circus* VOLOSHINOVA & BUDASHEVA, 1961, *2021, p. 199, *non Circus* DE LACEPÈDE, 1799] [**Circus multicameratus* VOLOSHINOVA & BUDASHEVA, 1961, *2021, p. 201, here designated as type-species]. Test free, enrolled, early chambers streptospiral, later planispiral and partially evolute; chambers numerous; sutures curved to sinuate, radial, depressed; wall agglutinated, simple, nonalveolar, with considerable amount of siliceous cement; aperture interiomarginal. [Differs from *Trochamminoides* in its early streptospiral coil and from *Recurvoides* in its evolute coiling and interiomarginal aperture.] *U.Eoc.-Mio.,* USSR (Sakhalin Is.-Kamchatka).——FIG. 175,*2,3*. **B. multicamerata* (VOLOSHINOVA & BUDASHEVA), L. Mio., Sakhalin Is.; *2a-c,* opposite sides and edge view of paratype, ×47; *3,* specimen partially clarified in oil to show chamber arrangement, ×72 (*2021).

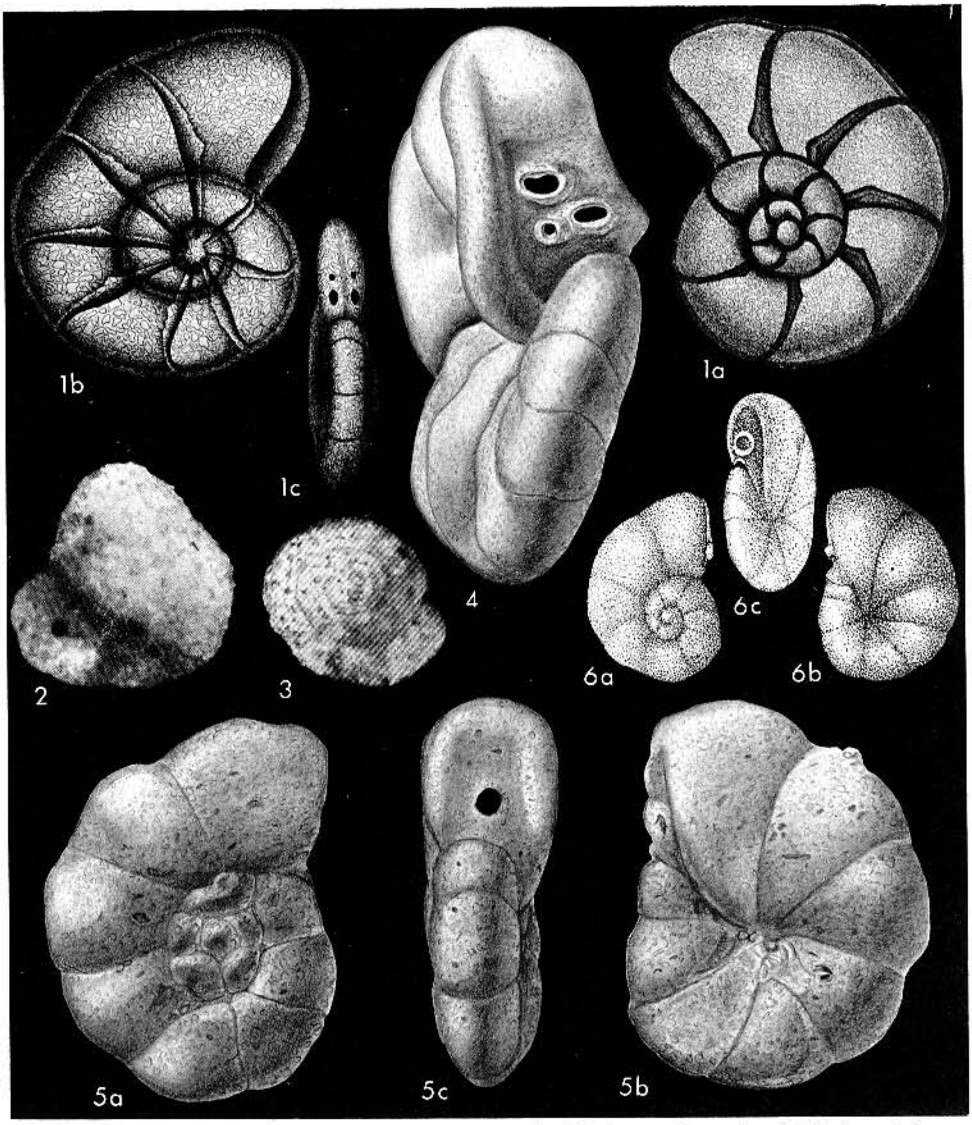


FIG. 176. Trochamminidae (Trochammininae; *1, Entzia; 2,3, Conotrochammina; 4-6, Jadammina*) (p. *C263-C265*).

Conotrochammina FINLAY, 1940, *717d, p. 448 [**C. whangaia*; OD]. Test with high trochospiral coil, deeply umbilicate, with nonconstricted sutures; aperture small rounded areal opening. [*Conotrochammina* differs from *Trochammina* in having an areal instead of interiomarginal aperture. Originally placed in the Ammodiscidae, it is here regarded as closely related to *Trochammina,* because of its distinctly chambered character and a restricted areal aperture.] *U.Cret.(Campan.)-Paleoc.,* N.Z.——FIG. 176,*2,3*. **C. whangaia,* Campan.; *2,* holotype, edge view showing elevated spire; *3,* spiral view of paratype, ×30 (*717d).

Cystammina NEUMAYR, 1889, *1355, p. 167 [**Trochammina pauciloculata* BRADY, 1879, *196a, p. 58; SD GALLOWAY, 1933, *762, p. 186] [=*Ammochilostoma* EIMER & FICKERT, 1899, *692, p. 692 (type, *Trochammina pauciloculata* BRADY, 1879, SD CUSHMAN, 1910, *404a, p. 126) obj.)]. Test free, trochoid, chambers few, high, inflated; sutures distinct, depressed; wall finely agglutinated with considerable cement; aperture comprising slit in face of final chamber, paralleling

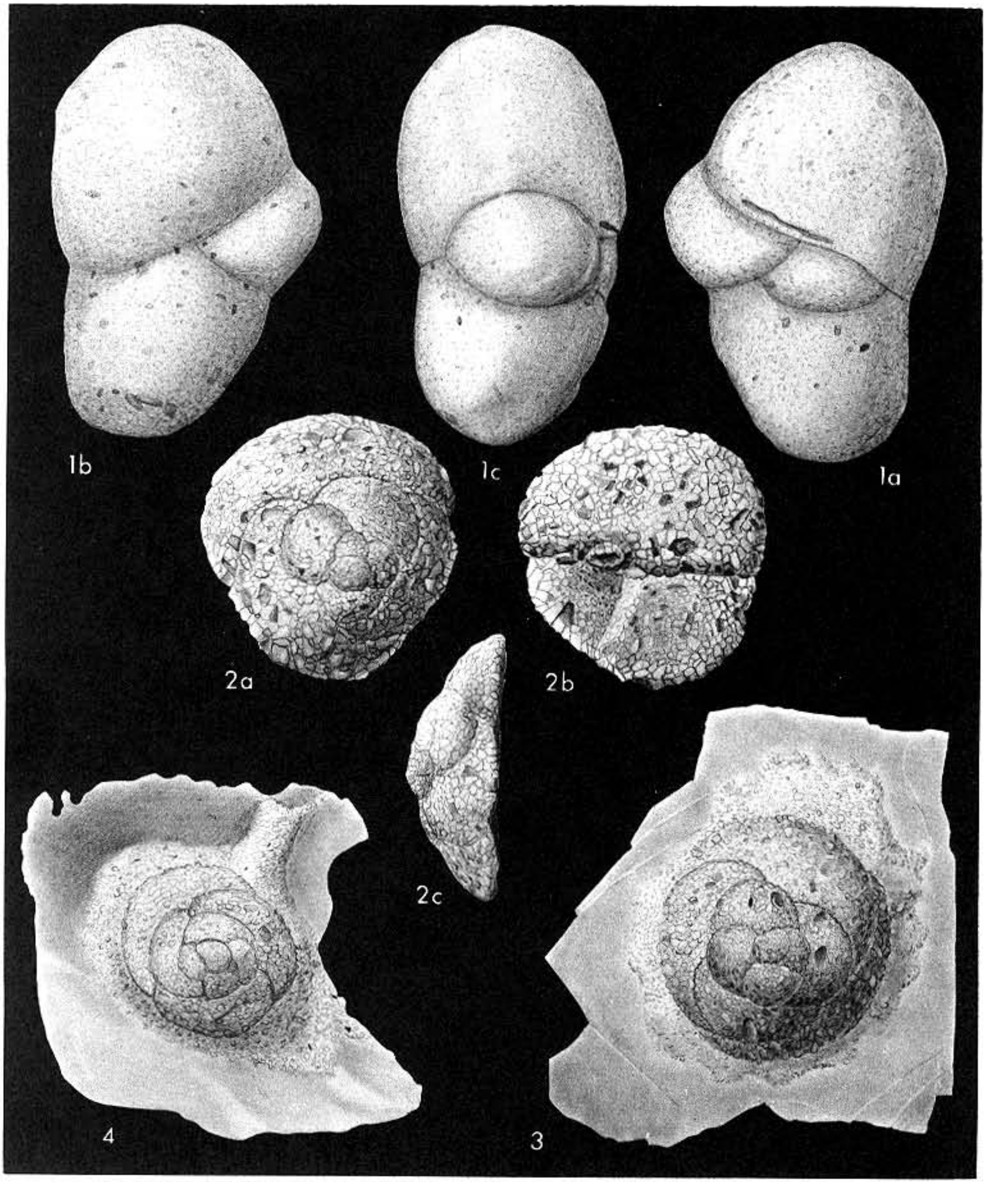


FIG. 177. Trochamminidae (Trochammininae; *1, Cystammina; 2-4, Tritaxis*) (p. C263-C264, C266).

and near basal margin, on ventral side. [*Cystammina* differs from *Trochammina* in having high and inflated chambers and in having a slitlike areal aperture in the ventral face, instead of a basal one.] *Eoc.-Rec.*, Pac.-Atl.-Eu.-Carib.-Antarctic.——FIG. 177,*1*. **C. pauciloculata* (BRADY), Rec., Pac.; *1a-c*, opposite sides and edge view showing areal slitlike aperture of lectotype (BMNH-ZF 2508) (here designated and redrawn), ×105 (*2117).

Entzia DADAY, 1883, *548, p. 209 [**E. tetrastomella*; OD (M)] [*non Entzia* LEBOUR, 1922]. Test in low trochospiral coil; wall pseudochitinous, with small amount of siliceous material; aperture areal, with 2 pair of openings somewhat produced and symmetrically placed in lower half of apertural face, lower pair larger and ovate, upper pair smaller and rounded. [*Entzia* differs from *Jadammina* in lacking an interiomarginal aperture in addition to the areal openings.] *Rec.*, Rumania (salt pools).——FIG. 176,*1*. **E. tetrastomella*; *1a-c*, opposite sides and edge view, approx. ×120 (*548).

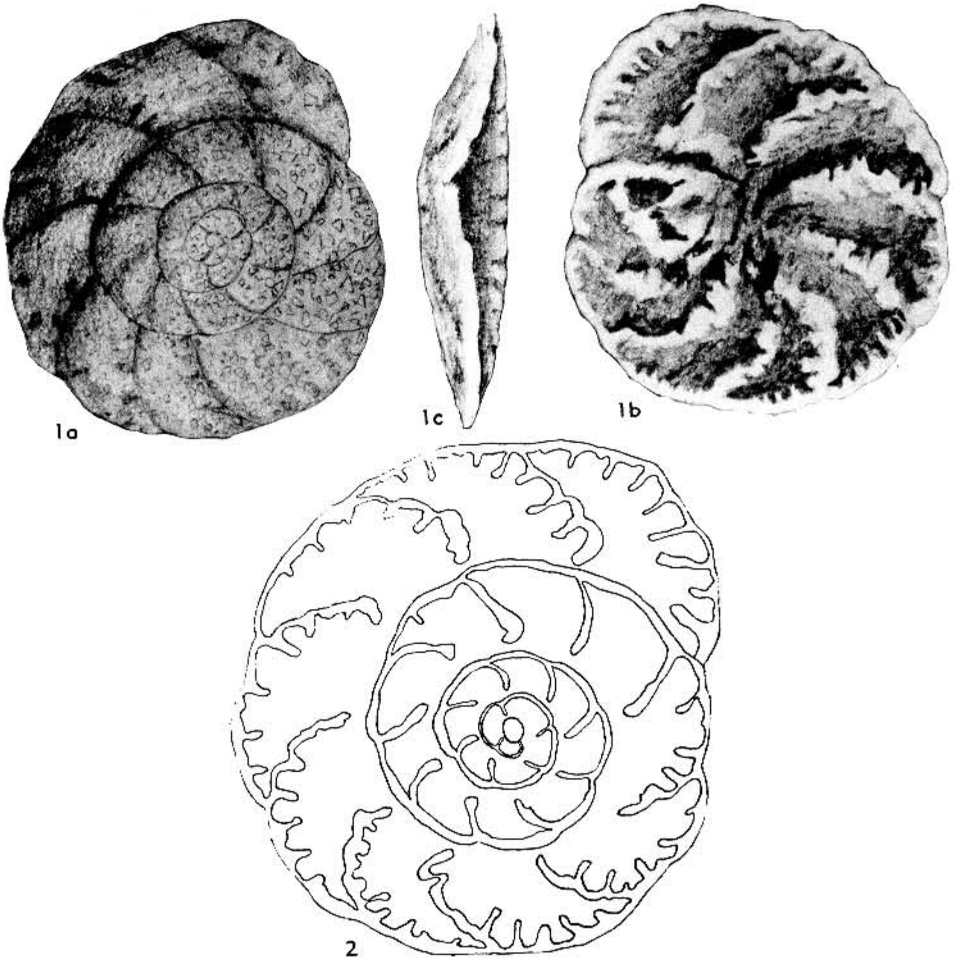


FIG. 178. Trochamminidae (Remaneicinae; *1,2, Remaneica*) (p. *C*266-*C*268).

Jadammina BARTENSTEIN & BRAND, 1938, *93, p. 381 [**J. polystoma*; OD] [=*Borovina* SHMALGAUSEN, 1950, *1735, p. 869 (type, *B. zernovi*); *Trochamminisca* SHCHEDRINA, 1955, *1726, p. 7 (type, *T. cyclostoma*)]. Test free, trochospiral, lenticular to flattened, sutures radial to slightly curved; wall agglutinated, imperforate, with few grains on pseudochitinous base; primary aperture low interiomarginal, equatorial slit, with supplementary cribrate areal aperture consisting of rounded openings in lower portion of final chamber face, with projecting lips. *Rec.*, Eu.-N.Am.——FIG. 176,*4,5*. **J. polystoma*, Ger.; *5a-c*, opposite sides and edge of small specimen with single areal aperture; *4*, edge view of larger specimen showing multiple areal aperture; all ×200 (*2117).——FIG. 176,*6*. *J. cyclostoma* (SHCHEDRINA), USSR(White Sea); *6a-c*, opposite sides and oblique edge view to show mode of coiling and 2 apertural forms, ×66 (*1726).

[*Jadammina* differs from *Trochammina* in having an equatorial primary aperture, rather than one on the umbilical side, and in having supplementary cribrate areal openings. *Trochamminisca* was described as having 2 apertures, the primary aperture an arched equatorial slit extending slightly to the ventral side and bordered by a lip, the secondary aperture a single rounded areal opening with a bordering collar. As many specimens of the type-species of *Jadammina* also show only a single areal opening in addition to the equatorial opening, *Trochamminisca* is regarded as a synonym.]

Rotaliammina CUSHMAN, 1924, *418, p. 11 [**R. mayori*; OD]. Test attached, trochoid, all chambers visible on spiral side, only those of final whorl seen from attached umbilical side; wall very thin, flexible, agglutinated, with fine sand held in small amount of cement; aperture indistinct, probably against attachment. [*Rotaliammina* differs from *Trochammina* in its attached character, thin flexible walls, and obscure aperture, probably against the attachment, rather than a conspicuous arched extraumbilical-umbilical one.] *Rec.*, Pac.——FIG. 174,*2*. **R. mayori; 2a-c*, opposite sides and edge view of holotype, ×118 (*1166).

Siphotrochammina SAUNDERS, 1957, *1631, p. 9 [**S. lobata;* OD]. Test free, trochospiral, spiral side convex, umbilical side depressed; chambers ovate, increasing gradually in size; sutures curved on spiral side, radial on umbilical side; wall agglutinated; aperture consisting of forward-directed, rounded opening at end of siphon-like lobe which projects from umbilical margin of final chamber, former aperture of penultimate chamber opening into siphon of final chamber. [*Siphotrochammina* differs from *Trochammina* in having a rounded aperture at the end of a siphon-like extension of the final chamber, rather than a simple interiomarginal slit.] *Rec.*, W.Indies(Trinidad).——FIG. 174, *3*. **S. lobata; 3a-c*, opposite sides and edge of paratype showing apertural siphon, ×110 (*1631).

Tiphotrocha SAUNDERS, 1957, *1631, p. 11 [**Trochammina comprimata* CUSHMAN & BRÖNNIMANN, 1948, *498A, p. 41; OD]. Test free, trochospiral, spiral side flat to convex, umbilical side somewhat excavated, with small, open umbilicus; chambers enlarging rapidly as added, resulting in decreasing number in each whorl, later chambers crescentic, with prominent central lobe on umbilical side; sutures depressed, curved on spiral side, strongly and doubly sinuate on umbilical side; wall agglutinated, thin and fragile, with little cement; aperture interiomarginal in young specimens, extraumbilical-umbilical in position, in re-entrant just forward from umbilical lobe of final chamber, and in well-developed adult specimens secondary opening seemingly occurs in posterior re-entrant behind umbilical lobe, its margin free with opening beneath it, or lobe may cross umbilicus and fuse with opposite side, effecting complete closure of opening. [*Tiphotrocha* differs from *Trochammina* in its open umbilical apertures, and umbilical lobe of the final chamber, which may also have a secondary opening. It is similar in apertural features to the calcareous genus *Neoconorbina*, differing in its agglutinated wall character.] *Mio.-Rec.*, W.Indies(Trinidad)-USA(La.).——FIG. 174,*4-6*. **T. comprimata* (CUSHMAN & BRÖNNIMANN), Rec., Trinidad; *4a-c*, opposite sides and edge views of hypotype showing crescentic chambers and apertural openings into umbilicus from each chamber of final whorl; *5*, ventral view of hypotype showing large ventral lobe of final chamber partially covering umbilicus; *6*, hypotype showing fused umbilical covering obscuring apertures; all ×71 (*1631).

Tritaxis SCHUBERT, 1921, *1694, p. 180 [**Rotalina fusca* WILLIAMSON, 1858, *2065, p. 55; SD CUSHMAN, 1928, *439, p. 171] [=*Trochamminella* CUSHMAN, 1943, *477, p. 95 (type, *T. siphonifera*)]. Test low trochoid spire, free-living in early stage, later becoming attached by ventral surface with irregular spreading mass surrounding regularly coiled early portion; early chambers subglobular, later increasing rapidly in relative breadth and developing low crescentic outline as seen on spiral side, much overlapping on umbilical side, with final chamber comprising approximately half of test; sutures distinct, slightly depressed; wall agglutinated, comparatively coarse-grained, surface roughened in appearance; aperture on umbilical side, free specimens with ovate opening at base of last-formed chamber near umbilicus, surrounded by distinct lip, not always visible in attached later stages, but may occur as openings on tubular projections at outer margins of attached portion. [*Tritaxis* differs from *Trochammina* in possessing in the free stage an ovate aperture on the umbilical side, rather than an extraumbilical-umbilical aperture, and in having a later attached stage with tubular-like openings at outer margins of the attached portion.] *Rec.*, Brit. I.(Ire.)-Puerto Rico.——FIG. 177,*2,3*. **T. fusca* (WILLIAMSON), Ire.; *2a-c*, opposite sides and edge of free specimen; *3*, attached specimen; all ×48 (*1166).——FIG. 177,*4*. *T. siphonifera* (CUSHMAN), Puerto Rico; ×44 (*1166).

Trochamminula SHCHEDRINA, 1955, *1726, p. 5 [**T. fissuraperta* = *Trochammina fissuraperta* SHCHEDRINA, 1953 *(nom. nud.)*, *1725, p. 15; OD]. Test similar to *Trochammina* but with 2 types of apertures—interiomarginal, extending from periphery nearly to umbilicus on ventral side and elongate aperture extending somewhat obliquely up face of final chamber on periphery; wall finely agglutinated, with ferruginous cement. [*Trochamminula* resembles *Arenoparrella* in having a vertical aperture in the face but has an interiomarginal aperture and lacks secondary pores near the peripheral angle.] *Rec.*, Arctic(Barents Sea-Okhotsk Sea-Bering Sea).——FIG. 173,*3*. **T. fissuraperta*, Arctic; *3a-c*, opposite sides and edge to show 2 forms of aperture, ×66 (*1726).

Subfamily REMANEICINAE
Loeblich & Tappan, n. subfam.

Test attached, trochospiral, chambers internally subdivided by infoldings of wall. *Rec.*

Remaneica RHUMBLER, 1938, *1576, p. 194 [**R. helgolandica;* OD] [=*Trochammina (Remaneica)* HÖGLUND, 1947, *924, p. 212 (obj.)]. Test small, attached, low trochospiral coil; chambers with secondary infoldings or plications of wall, which may show at surface as septal slits; wall brown, pseudochitinous, imperforate and flexible, with varying amount of agglutinated matter, exterior surrounded by "buffer zone" of agglutinated matter; aperture not observed. *Rec.*, Ger.(Helgoland)-

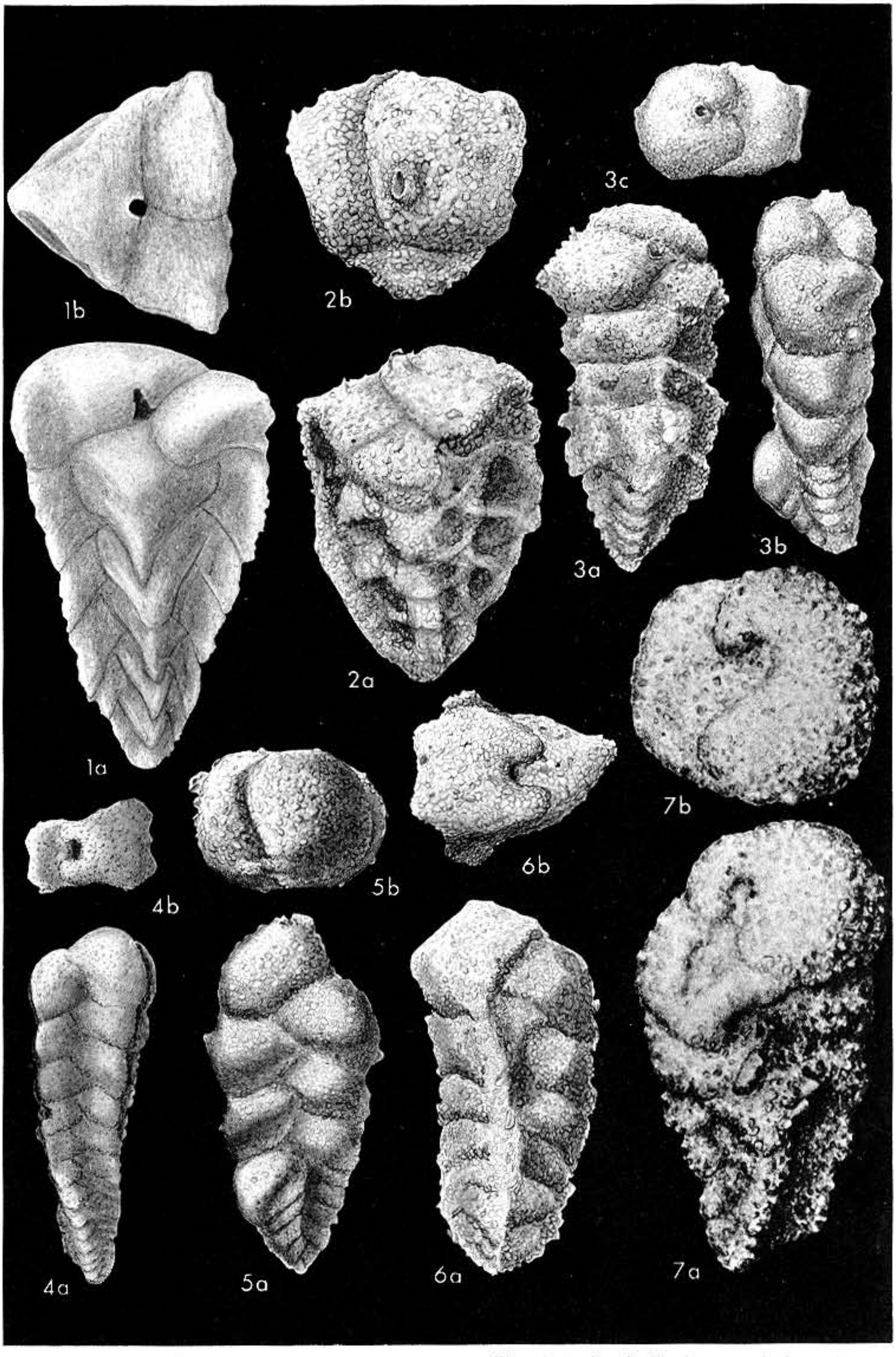


FIG. 179. Ataxophragmiidae (Verneuilininae; *1*, *Verneuilina*; *2*, *Barbourinella*; *3*, *Bermudezina*; *4-7*, *Gaudryina*) (p. C268-C269).

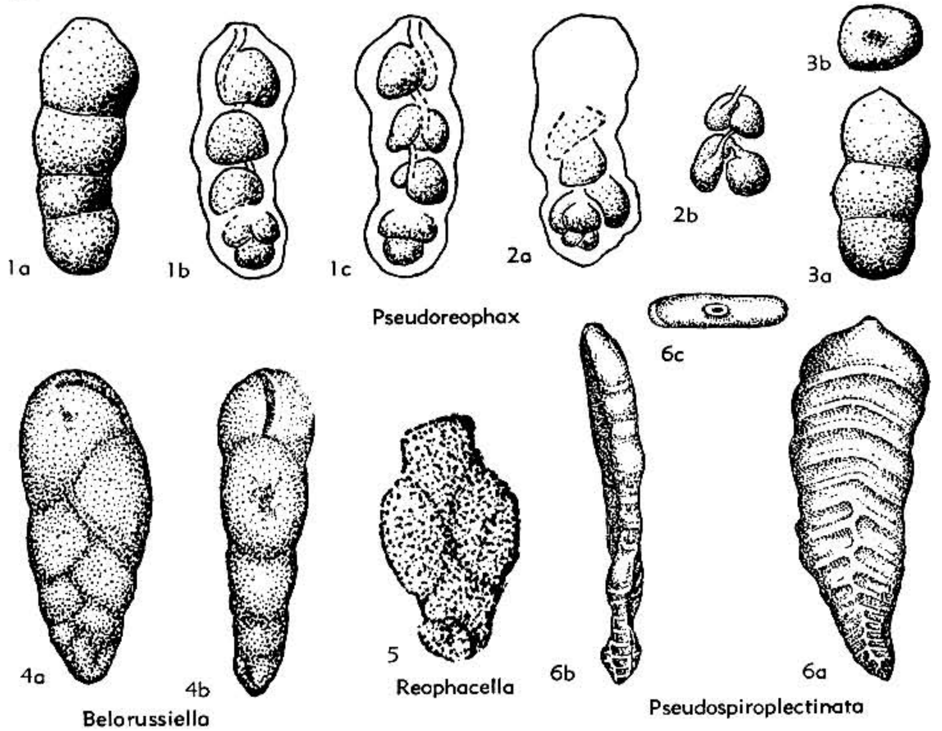


FIG. 180. Ataxophragmiidae (Verneuilininae; *1-3, Pseudoreophax; 4, Belorussiella; 5, Reophacella; 6, Pseudospiroplectinata*) (p. *C*269-*C*272).

Fr.-Sweden.——FIG. 178,*1*,*2*. **R. helgolandica,* Sweden; *1a-c,* opposite sides and edge view, ×210; *2,* optical sec. showing secondary chamber plications, ×230 (*924).

[*Remaneica* differs from *Rotaliammina* in having secondary plications within the chambers. *Remaneica* is regarded as adapted to life on a movable substratum, its scalelike form, protective coating, and chamber plications tending to make it resistant to deformation. Specimens referred to *Remaneica* from the western Atlantic do not appear congeneric, as they lack the characteristic chamber plication.]

Family ATAXOPHRAGMIIDAE Schwager, 1877

[*nom. correct.* GALLOWAY & HEMINWAY, 1941, p. 320 (*pro* family Ataxophragmidea SCHWAGER, 1877, p. 22)]——[All names are of family rank; dagger(†) indicates *partim*]——[=Hélicostègues† D'ORBIGNY, 1826, p. 268 *(nom. nud.)*; =Uvellina† EHRENBERG, 1839, table opposite p. 120 *(nom. nud.)*; =Turbinoidae† D'ORBIGNY in DE LA SAGRA, 1839, p. xxxviii, 71 *(nom. nud.)*; =Turbinoida† SCHULTZE, 1854, p. 52 *(nom. nud.)*; =Helicostegia† REUSS, 1860, p. 151, 205 *(nom. nud.)*; =Uvellidae† REUSS, 1860, p. 203 *(nom. nud.)*; =Uvellidea† REUSS, 1862, p. 318, 382 *(nom. nud.)*; =Uvellideae† GÜMBEL, 1870, p. 23 *(nom. nud.)*; =Turbinida† MARRIOTT, 1878, p. 30 *(nom. nud.)*; =Trischistidae EIMER & FICKERT, 1899, p. 680 *(nom. nud.)*];——[=Valvulinidae BERTHELIN, 1880, p .16; =Opistho-Trischistidae EIMER & FICKERT, 1899, p. 680 *(nom. nud.)*; =Textulinidae† RHUMBLER, 1913, p. 339 *(nom. van.)*; =Verneuilinidae CUSHMAN, 1927, p. 25; =Eggerellidae HOFKER, 1957, p. 35]

Test free, trochospiral, uncoiling or uniserial; wall agglutinated; aperture a basal slit in the early stage, later may become terminal, cribrate or toothed. *Penn.-Rec.*

Subfamily VERNEUILININAE Cushman, 1911

[Verneuilininae CUSHMAN, 1911, p. 52]——[All names of subfamily rank; dagger(†) indicates *partim*]——[=Uvellida† SCHULTZE, 1854, p. 52 *(nom. nud.)*; =Spiroplectininae CUSHMAN, 1927, p. 62; =Spiroplectinatinae CUSHMAN, 1928, p. 235]

Triserial in early stage, later biserial or uniserial in some forms; number of chambers to whorl tending to decrease with growth; aperture simple. *U.Trias.-Rec.*

Verneuilina D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. 104 [**V. tricarinata;* SD (SM) D'ORBIGNY, 1840, *1394, p. 39] [=*Verneulina & Verneolina* COSTA, 1856, *392, p. 263 *(nom. null.)*]. Test free, elongate, triangular, with angles of test sharp, nearly carinate, chambers triserially arranged throughout; wall agglutinated, with much calcareous cement; aperture a low arch at inner face of final chamber. *Jur.-Rec.,* cosmop.——FIG. 179, *1.* **V. tricarinata,* U.Cret.(Senon.), Eu.(Fr.); *1a,b,* side and top views of lectotype, here designated and redrawn (MNHN), ×80 (*2117).

Barbourinella BERMÚDEZ, 1940, *122, p. 410 [*pro Barbourina* BERMÚDEZ, 1939, *121a, p. 9 (*non* AMARAL, 1924)] [**Barbourina atlantica* BERMÚDEZ, 1939, *121a, p. 9; OD]. Test triserial and triangular throughout as in *Verneuilina,* but with terminal rounded aperture which may be slightly produced. *Mio.-Rec.,* Carib.——FIG. 179,*2*. **B.*

atlantica (Bermúdez), Rec., Carib.; *2a,b,* side, top views of holotype, ×56 (*2117).

Belorussiella Akimets, 1958, *9, p. 35 [**B. bolivinaeformis;* OD]. Test elongate, with short, early triserial and triangular stage followed by better-developed biserial stage with more inflated chambers and ovate section; sutures indistinct in triserial portion, depressed and oblique in biserial stage; wall agglutinated, of fine-grained calcareous particles in calcareous cement, surface roughened; aperture elongate loop-shaped slit extending up face of final chamber to its apex. [Differs from *Gaudryina* in its elongate vertical apertural slit.] *U.Cret.(Turon.-U.Santon.),* USSR(Belorusskaya SSR).——Fig. 180,*4*. **B. bolivinaeformis,* U. Santon.; *4a,b,* side, edge views, ×104 (*10).

Bermudezina Cushman, 1937, *470, p. 102 [**Heterostomella (?) cubensis* Palmer & Bermúdez, 1936, *1412, p. 244; OD]. Test similar to *Gaudryina* but with terminal circular aperture on short neck. *U.Eoc.-Mio.,* Carib.-Eu.(Bulg.).——Fig. 179,*3*. **B. cubensis* (Palmer & Bermúdez), L.Oligo., Cuba; *3a-c,* side, edge, and top views of lectotype (here designated, USNM-498781), ×94 (*2117).

Flourensina Marie, 1938, *1214, p. 91 [**F. douvillei;* OD]. Test triserial, with chambers strongly inflated into spinose projections; aperture a loop in face of final chamber, extending upward from basal suture. [*Flourensina* differs from *Verneuilina* in its strongly laterally produced chambers and high narrow aperture.] *L.Cret.(U. Vracon.),* Eu. (Fr.).——Fig. 181,*1*. **F. douvillei;* side, top views of paratype, ×50 (*2117).

Gaudryina d'Orbigny in de la Sagra, 1839, *1611, p. 112 [**G. rugosa* d'Orbigny, 1840, *1394, p. 44; SD Cushman, 1911, *404b, p. 62] [=*Gaudryna* d'Orbigny, 1839, *1611, p. 219 *(nom. null.); Gaudryina (Siphogaudryina)* Cushman, 1935, *466, p. 3 (type, *Gaudryina stephensoni* Cushman, 1928, *438, p. 108); *Gaudryina (Pseudogaudryina)* Cushman, 1936, *468, p. 12 (type, *Textularia atlantica* Bailey, 1851, *65, p. 12); *Valvoreussella* Hofker, 1957, *948, p. 87 (type, *Verneuilina bronni* Reuss, 1846, *1538, p. 38)]. Test free, elongate, early stage triserial and commonly triangular, later portion biserial; aperture interiomarginal. *U.Trias.-Rec.,* cosmop.——Fig. 179,*5*. **G. rugosa,* U.Cret., Ger.; *5a,b,* side, top views of hypotype, ×39 (*2117).——Fig. 179,*6*. *G. atlantica* (Bailey), Mio., W.Indies(Jamaica); *6a,b,* side, top views, ×20 (*2117).——Fig. 179, *4*. *G. stephensoni* Cushman, U.Cret., USA(Tex.); *4a,b,* side, top views of paratype, ×86 (*2117). ——Fig. 179,*7*. *G. bronni* (Reuss), U.Cret. (Plänermergel), Eu.(Boh.); *7a,b,* side, top views of topotype, ×66 (*470).

[The subgenus *Pseudogaudryina* was based on forms with few biserial chambers that had retained the triangular section of the test, but as this angularity commonly becomes less pronounced with increased length of biserial development, it is regarded as a developmental feature and not of taxonomic importance. The subgenus *Siphogaudryina* is based on *Gaudryina stephensoni,* which does not show the fistulose processes described for that subgenus, worn angles of poorly preserved specimens being so mistaken. *Valvoreussella* was stated to have a normally loop-shaped aperture, although some specimens have a terminal aperture in the biserial stage. Many species of *Gaudryina* show a tendency toward *Tritaxia,* by developing a random uniserial chamber and terminal aperture in gerontic specimens (Tappan, 1943, *1872, p. 78). The characters shown by the major part of the species population must determine the generic placement, however. All specimens of *Verneuilina bronni* illustrated by Reuss (*1538), Cushman (*470), and others show typical characters of *Gaudryina,* as do all but one of those figured by Hofker (*948). *Valvoreussella* is therefore regarded as a synonym of *Gaudryina.* Bowen (1955, *182) regarded *Heterostomella, Plectina, Dorothia, Marssonella, Karreriella, Bermudezina,* and *Migros* as synonyms of *Gaudryina,* recognizing as generic characters neither the number of chambers to a whorl (triserial or multilocular trochospiral) nor the position and character of the aperture. Both features are regarded as of generic value by us. *Bermudezina* and *Heterostomella* are here regarded as valid genera of the Verneuilininae, *Karreriella* and *Dorothia* as valid genera of the Eggerellinae (with *Marssonella* a synonym of *Dorothia*), and *Plectina* as a valid genus in the Valvulininae.]

Gaudryinella Plummer, 1931, *1464, p. 341 [**G. delrioensis;* OD]. Test elongate, early stage triserial and triangular in section, later irregularly and loosely biserial; inflated, cuneate chambers progressively more loosely appressed, becoming semiuniserial; wall agglutinated; aperture interiomarginal in early stage, rounded and terminal in adult. *L.Cret.(Alb.)-U.Cret.(Maastricht.),* N.Am.-Eu.——Fig. 181,*5,6*. **G. delrioensis,* U.Cret.(L. Cenoman.), USA(Tex.); topotypes, ×100 (*2117).

[*Gaudryinella* was considered a possible synonym of *Spiroplectinata* by Hofker (1951, *935, p. 4) but is here recognized as being triserial in the early stage, then loosely biserial to semiuniserial with cuneate chambers. *Spiroplectinata* has a distinct and regular biserial stage following a reduced triserial stage, succeeded by regularly developed uniserial chambers. The Eocene *G. cubana* Cushman & Bermúdez is here regarded as a *Tritaxia.*]

Heterostomella Reuss, 1866, *1555, p. 448 [**Sagrina rugosa* d'Orbigny, 1840, *1394, p. 47; OD (M)]. Test free, early stages triserial, roughly triangular in section, later biserial, becoming roughly quadrangular in section, ridges formed by fistulose angles; wall agglutinated, in type-species, coarsely arenaceous with calcareous cement; aperture in adult terminal on short neck. [*Heterostomella* differs from *Gaudryina* in having fistulose angles and a terminal aperture.]. *U.Cret.(Senon.),* Eu.-N.Am.——Fig. 181,*2*. **H. rugosa* (d'Orbigny), Senon., Fr.; *2a,b,* side and top views of lectotype, here designated and redrawn (MNHN), ×64 (*2117).

Migros Finlay, 1939, *717c, p. 312 [**Gaudryina medwayensis* Parr, 1935, *1423; p. 83; OD] [=*Paleogaudryina* Said & Barakat, 1958, *1616, p. 243 (type, *P. magharaensis*)]. Test similar to *Gaudryina* but with high, loop-shaped, instead of low, basal aperture. *M.Jur.-Mio.,* N.Z.-Australia-Eu.-Egypt.——Fig. 181,*3*. **M. medwayensis* (Parr), M.Mio., N.Z.; *3a,b,* side and top views, ×36 (*2117).——Fig. 181,*4*. *M. magharaensis* (Said & Barakat), U.Jur.(Kimmeridg.), Egypt (Sinai); *4a-c,* holotype, ×55 (*1616).

Pseudoreophax Geroch, 1961, *785, p. 159 [**P.*

cisovnicensis; OD]. Test elongate, straight or arcuate, circular to ovate in section, trochospiral in early stage of microspheric forms and later uniserial, megalospheric forms uniserial throughout; chamber internal cavity semicircular in plane perpendicular to axis of test and arched upward

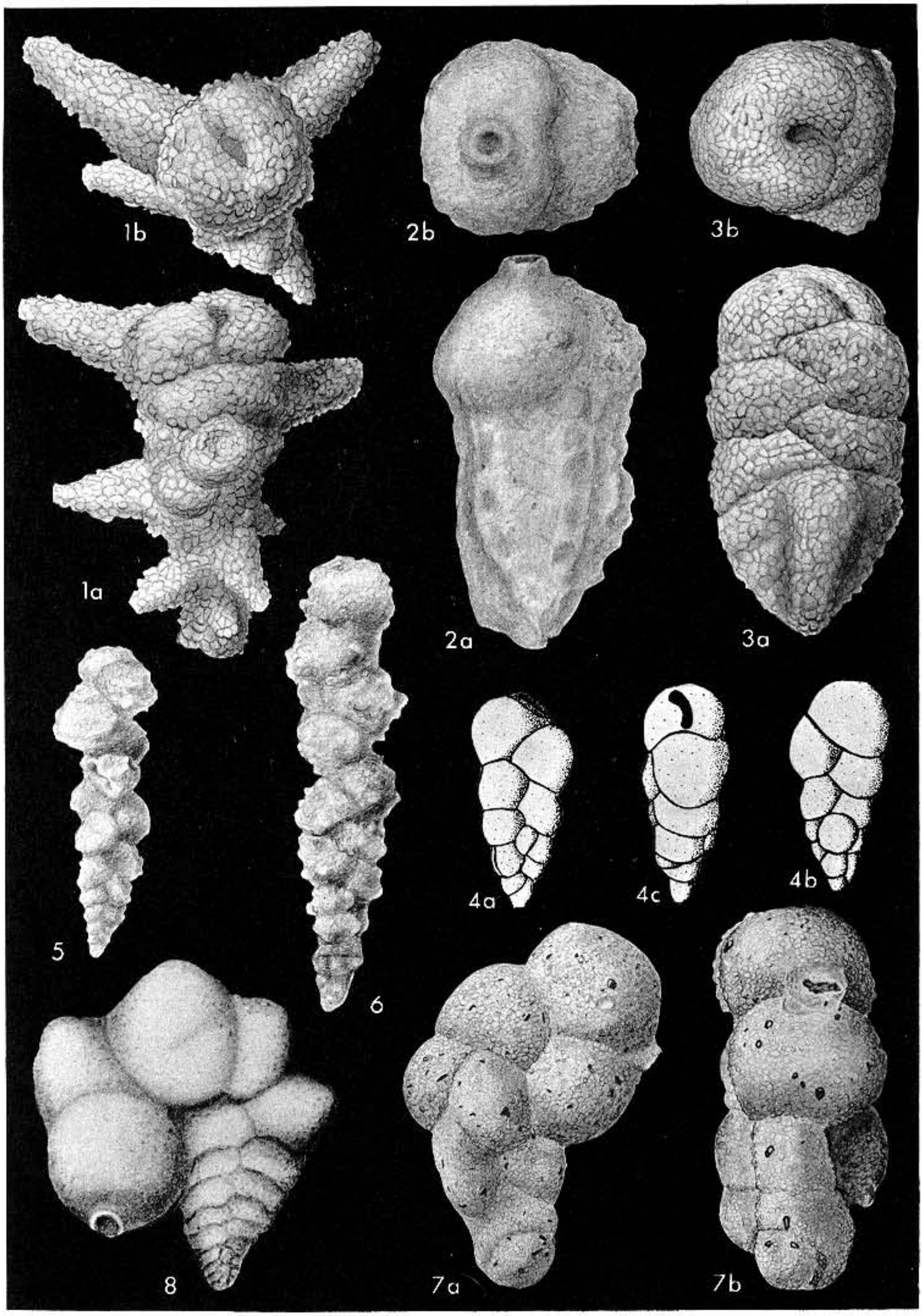


FIG. 181. Ataxophragmiidae (Verneuilininae; *1, Flourensina; 2, Heterostomella; 3,4, Migros; 5,6, Gaudryinella; 7,8, Rudigaudryina*) (p. C269, C272).

from base; sutures depressed; horizontal in uniserial stage; wall very finely agglutinated, surface smoothly finished; aperture terminal, rounded, may be slightly eccentric. *L.Cret.(Valang.-L. Barrem.)*, Carpathians(Pol.).——Fig. 180,*1-3*. **P. cisovnicensis*, Valang.-Hauteriv. *(1,2)*, Barrem.

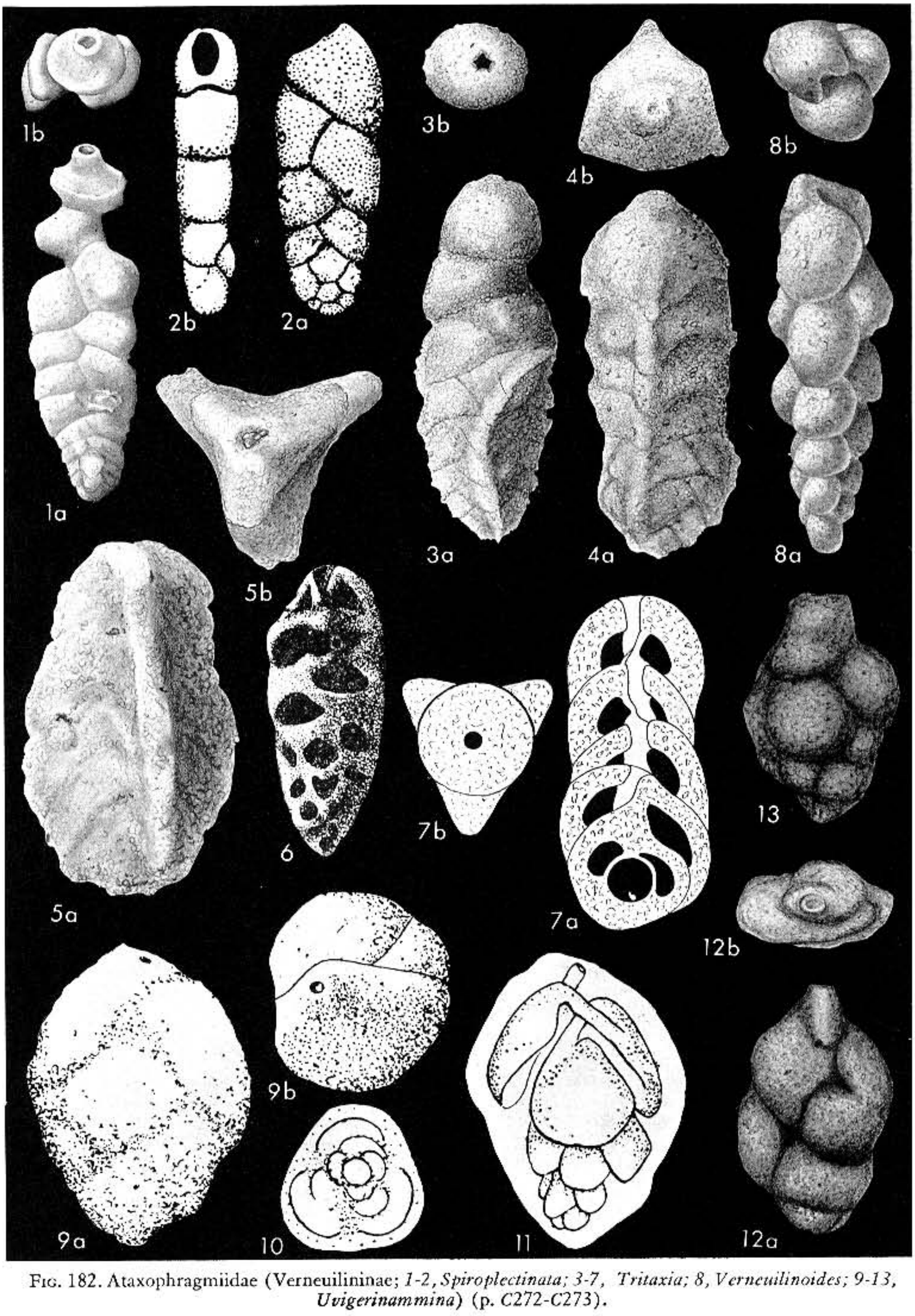


Fig. 182. Ataxophragmiidae (Verneuilininae; *1-2, Spiroplectinata; 3-7, Tritaxia; 8, Verneuilinoides; 9-13, Uvigerinammina*) (p. C272-C273).

(3); 1a-c, side view and opposite sides of megalospheric holotype viewed in immersion oil to show chamber cavities; *2a,b,* microspheric form viewed in immersion oil to show early trochospiral development and chamber arrangement in transition to uniserial stage; *3a,b,* side, top views of megalospheric paratype, ×65 (*785).

Pseudospiroplectinata Gorbenko, 1957, *808, p. 879 [**P. plana;* OD]. Test elongate, broad and flattened; chambers of early stage triserially arranged, later biserial, and finally uniserial; aperture terminal, rounded, on short neck. [*Pseudospiroplectinata* differs from *Spiroplectinata* in having a broad, flat, and regularly uniserial later stage, rather than cuneate chambers in an irregular, short uniserial stage. The genus and type species were incorrectly described as new in a second publication in 1960 (*808A, p. 71).]. *U. Cret.(U.Cenoman.),* USSR(Donets Basin).——Fig. 180,*6.* **P. plana; 6a-c,* side, edge, and top views, approx. ×40 (*808).

Reophacella Kaptarenko-Chernousova, 1956, *1017, p. 32 [**R. compressa;* OD (M)]. Test free, elongate, somewhat flaring, chamber arrangement indistinct in early portion, later with apparently paired chambers; wall arenaceous; aperture terminal, rounded on broad neck. [Similar to *Uvigerinammina* but lacks the early distinctly triserial development.] *U.Eoc.(Kiev Stage),* USSR (Ukraine).——Fig. 180,*5.* **R. compressa;* side view of holotype, ×70 (*1017).

Rudigaudryina Cushman & McCulloch, 1939, *511, p. 94 [**R. inepta;* OD]. Test triserial in early stage, later portion biserial, as in *Gaudryina,* but with final chambers irregularly spreading; aperture terminal, rounded, with short neck or lip. *Rec.,* Pac.——Fig. 181,*7,8.* **R. inepta; 7a,b,* side, edge views of megalospheric paratype, ×86 (*2117); *8,* microspheric paratype, ×55 (*511).

Spiroplectinata Cushman, 1927, *431, p. 62 [*pro Spiroplectina* Cushman, 1927, *428, p. 78 (non Schubert, 1902)] [**Textularia annectens* Parker & Jones, 1863, *1417e, p. 92; OD] [=*Paragaudryina* Suleymanov, 1958, *1853, p. 19 (type, *P. inornata)*]. Test free, elongate, triserial in early portion, later biserial, and finally uniserial; sutures slightly depressed in early development, more strongly constricted in uniserial portion; wall agglutinated; aperture terminal, rounded. *L.Cret.-U.Cret.,* Brit. I.-Eu.-N.Am.-USSR.——Fig. 182,*1.* **S. annectens* (Parker & Jones), L.Cret. (Alb.), Eng.; *1a,b,* side, top views of topotype, ×74 (*2117).——Fig. 182,*2. S. inornata* (Suleymanov), U.Cret.(L.Turon.), USSR(Fergana); *2a,b,* side, edge views of holotype, ×55 (*1857). [Originally described (1927) as having an early planispiral stage and calcareous wall, *Spiroplectinata* was redescribed (Cushman, *461, p. 114), placed in the Verneuilinidae, and said to have a triserial beginning and arenaceous wall. Earland (1934, *653, p. 114) stated that he considered the early development as planispiral, with edges of the spiral toward the face of the test. The original types of Parker & Jones were examined by us in 1953 and a lectotype from the Gault at Biggleswade, Bedfordshire, England, was chosen; it is here designated (BMNH-P41668). The types and all other specimens seen by us show a very short but distinctly triserial and triangular early stage of about 3 series of chambers. Some species that previously were placed in *Gaudryinella—G. pseudoserrata* Cushman— or *Pseudogaudryinella— P. mollis* (Cushman)— should be placed in *Spiroplectinata.*]

Tritaxia Reuss, 1860, *1548, p. 227 [**Textularia tricarinata* Reuss, 1844, *1537, p. 215 (=*Verneuilina dubia* Reuss, 1851, *1542, p. 40; OD (M)] [=*Tritaxiopsis* Rzehak, 1895, *1605, p. 217 (type, *Tritaxia pleurostoma* Rzehak, 1895); *Pseudogaudryinella* Cushman, 1936, *468, p. 23 (type, *Gaudryinella capitosa* Cushman, 1933, *459, p. 52); *Clavulinoides* Cushman, 1936, *468, p. 20 (type, *Clavulina trilatera* Cushman, 1926, *423, p. 588); *?Siphonclavulina* Silvestri, 1948, *1790, p. 1 (type, *S. trigona)*]. Test triserial and triangular in section in early stage, later portion uniserial and commonly triangular, more rarely compressed; aperture interiomarginal in triserial stage, terminal in adult, with thick-walled internal tube connecting apertures of last 1 or 2 chambers (*88). [The type-species of *Clavulinoides* is not distinguishable generically from *Tritaxia.* A less typical species, *Clavulina compressa* Cushman, shows a compressed and almost palmate uniserial stage, but rare specimens have a distinct third angle; hence, this species is also regarded as *Tritaxia.*] *L.Cret.-Rec.,* cosmop.——Fig. 182, *5,6.* **T. tricarinata* (Reuss), U.Cret., Eu.(Boh.); *5a,b,* side, top views of topotype, ×58 (*2117); *6,* abraded specimen showing internal tube in final chamber, ×24 (*88).——Fig. 182,*3. T. capitosa* (Cushman), U.Cret., USA(Miss.); *3a,b,* side, top views of holotype, ×31 (*2117).——Fig. 182,*4. T. trilatera* (Cushman), Paleoc., N.Am.(Mex.); *4a,b,* side, top views of hypotype, ×54 (*2117).——Fig. 182,*7. T. trigona* (Silvestri), Eoc., Eu.(Italy); *7a,b,* long. sec. and top view, ×40 (*1790).

Uvigerinammina Majzon, 1943, *1203, p. 68 [**U. jankoi;* OD (M)]. Test in trochoid spire of 3 chambers to whorl and thus triserial throughout, but chambers not in parallel rows, as in *Verneuilina,* chambers increasing rapidly in size; wall agglutinated, thick, chamber cavities saclike with internal necklike connections between adjacent chambers; aperture terminal, may be flush or somewhat produced on external neck. [*Uvigerinammina* is apparently a strongly facies-controlled form, commonly occurring in flysch-type sediments.] *L.Cret.(Alb.)-U.Cret., ?Paleoc.,* USSR (Carpathians)-N.Am.(Can.-Alaska).——Fig. 182, *9-11.* **U. jankoi,* Cret., Carp.; *9a,b,* side and apert. views; *10,* specimen in clove oil showing chamber arrangement in basal view; *11,* specimen viewed from side in clove oil showing internal cavities and stolon-like necks between chamber cavities, ×36 (*784).——Fig. 182,*12,13. U. manitobensis* (Wickenden), L.Cret.(Alb.), Alaska; *12a,b,* side, top views of hypotype, ×64; *13,* side view of another hypotype, ×47 (*2117).

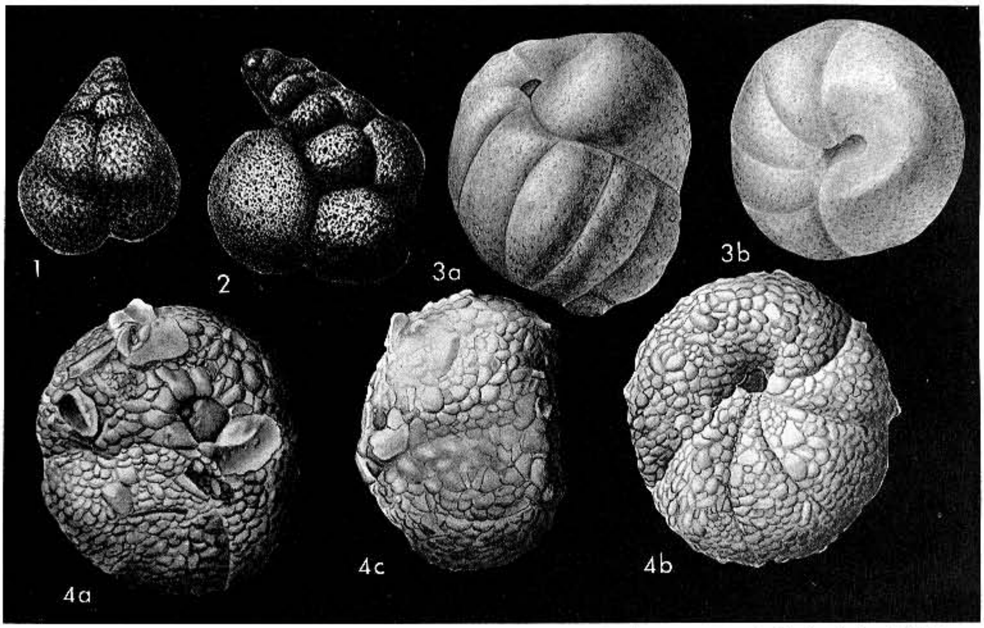


FIG. 183. Ataxophragmiidae (Globotextulariinae; *1,2, Globotextularia; 3,4, Arenobulimina*) (p. C273).

Verneuilinoides LOEBLICH & TAPPAN, 1949, *1155, p. 91 [**Verneuilina schizea* CUSHMAN & ALEXANDER, 1930, *488, p. 9; OD]. Test free, elongate, triserial throughout, with rounded angles; loosely appressed chambers increasing in size toward apertural end; sutures generally distinct and depressed; wall arenaceous, aperture an arch at base of final chamber. [*Verneuilinoides* differs from *Verneuilina* in being rounded in section with loosely appressed chambers rather than triangular in section, and elongate and narrow rather than pyramidal in shape.] *Jur.-Cret.*, N.Am.-Eu.——FIG. 182,*8*. **V. schizea* (CUSHMAN & ALEXANDER), L.Cret.(Alb.), USA(Tex.); *8a,b,* side, top views of holotype, ×100 (*2117).

Subfamily GLOBOTEXTULARIINAE Cushman, 1927

[Globotextulariinae CUSHMAN, 1927, p. 40; Eggerellinae CUSHMAN, 1937, p. 30]

Test trochoid, 3 or more chambers to whorl, number of chambers to whorl tending to decrease with growth to 2 or 1; aperture single interiomarginal opening or cribrate. *Penn.-Rec.*

Globotextularia EIMER & FICKERT, 1899, *692, p. 679 [**Haplophragmium anceps* BRADY, 1884, *200, p. 313; OD]. Test high trochospiral, chambers inflated and subglobular, commonly 4 in final whorl; wall coarsely agglutinated; aperture interiomarginal. *Rec.*, N.Atl.-S.Atl.-S.Pac. [Deep water.]——FIG. 183,*1,2*. **G. anceps* (BRADY), S. Pac. *(1)*, S.Atl. *(2)*; *1,* quadriserial form, here designated lectotype; 2, aberrant form; both ×10 (*200).

Arenobulimina CUSHMAN, 1927, *428, p. 80 [**Bulimina presli* REUSS, 1846, *1538, p. 38; OD] [=*Hagenowella* CUSHMAN, 1933, *456, p. 21 (type, *Valvulina gibbosa* D'ORBIGNY, 1840, *1394, p. 38); *Ataxophragmoides* BROTZEN, 1948, *241, p. 35 (type, *A. frankei*)]. Test trochospiral, similar to *Valvulammina* in chamber arrangement; wall agglutinated, interior of chambers simple; aperture an interiomarginal arch or loop, without apertural tooth. *L.Cret.(Alb.)-L.Paleoc.*, Eu.-N. Am.——FIG. 183,*3*. **A. presli* (REUSS), U.Cret., Boh.; *3a,b,* side, apert. views of hypotype, ×100 (*2117).——FIG. 183,*4*. *A. frankei* (BROTZEN), L.Paleoc., Sweden; *4a-c,* opposite sides and edge view, ×48 (*2117).

[*Arenobulimina* is similar to *Ataxophragmium*, but does not have internal pillars. *Hagenowella* was described as having internal radial partitions, but was based on misidentified material of the type-species, as was noted by MARIE (1941, *1215, p. 41). As the type-species has a simple interior, *Hagenowella* was suppressed (*1182, p. 242) as a junior synonym of *Arenobulimina*. The specimens erroneously referred to *Hagenowella gibbosa* (D'ORBIGNY) should be referred to *Valvulina quadribullata* VON HAGENOW, the type-species of *Hagenowina* LOEBLICH & TAPPAN, 1961.]

Cribrogoesella CUSHMAN, 1935, *466, p. 4 [**Bigenerina robusta* BRADY, 1881, *196c, p. 53; OD]. Test free, elongate, early trochospiral stage with up to 5 chambers in whorl, reducing rapidly to 3, followed by biserial stage and becoming uniserial in adult; wall agglutinated, thick, fibrous; aperture of biserial stage at base of last-formed chamber, in adult becoming terminal and cribrate. [*Cribrogoesella* differs from *Goesella* in having a multiple aperture instead of a simple one with tooth.] *Mio.-Rec.*, Carib.-Pac.O.-Atl.O.——Fig. 184,*1-3*. **C. robusta* (Brady), Rec., Atl.; *1a,b*, *2*, side, top views of paratypes; *3*, sectioned specimen showing fibrous wall, paratype (*200, pl. 45, fig. 13) redrawn, ×17 (*2117).

Digitina Crespin & Parr, 1940, *396, p. 306 [**D. recurvata;* OD]. Test trochospiral in early stage, later irregularly biserial, similar to *Mooreinella*, but with basal rather than subterminal aperture. [The Cenozoic *Plectotrochammina* differs in having a highly developed trochoid stage and reduced biserial development.] *Perm.*, Australia (New S.Wales).——Fig. 185,*7*. **D. recurvata;*

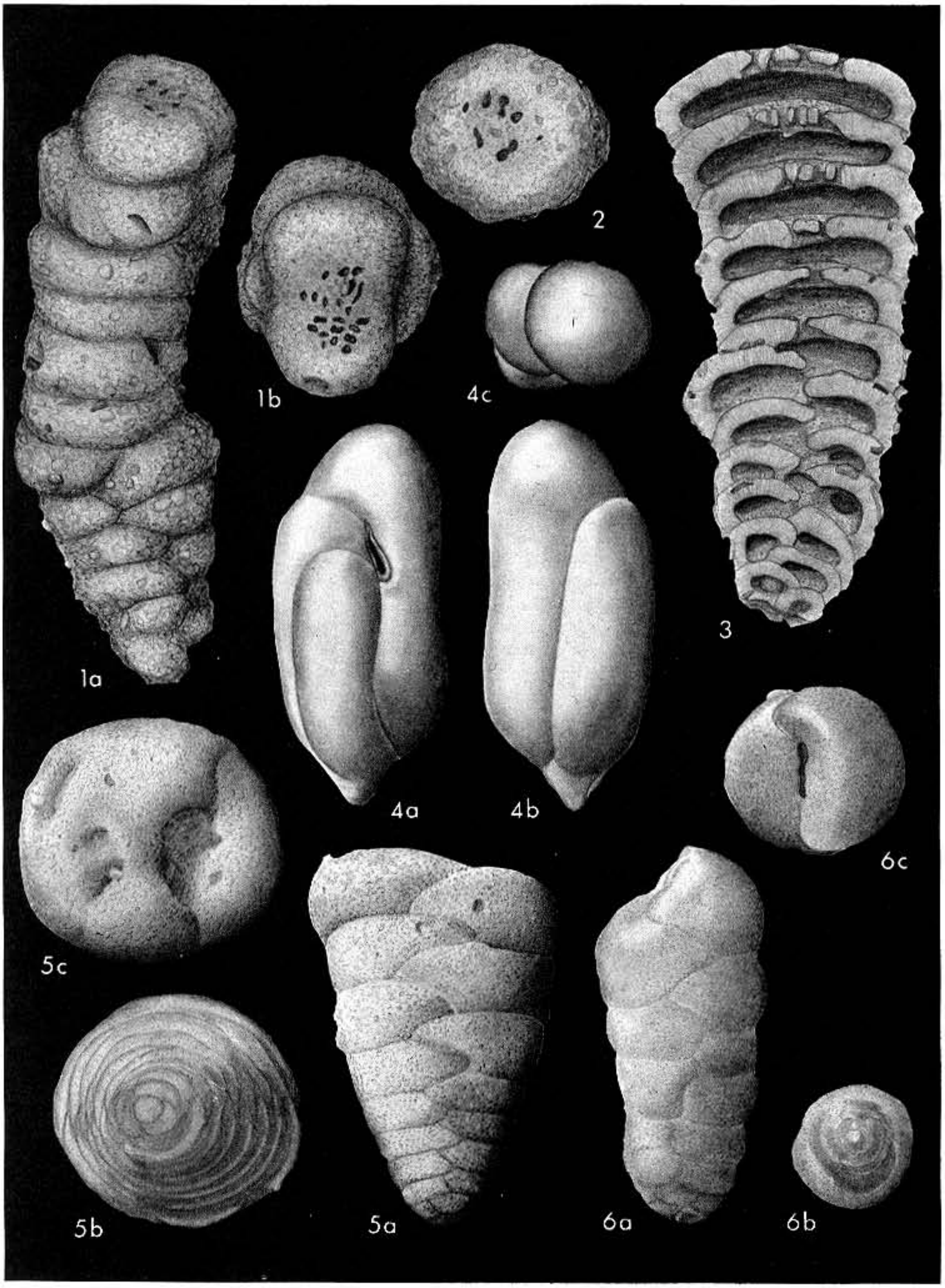


Fig. 184. Ataxophragmiidae (Globotextulariinae; *1-3, Cribrogoesella; 4, Eggerina; 5,6, Dorothia*) (p. *C273-C275*).

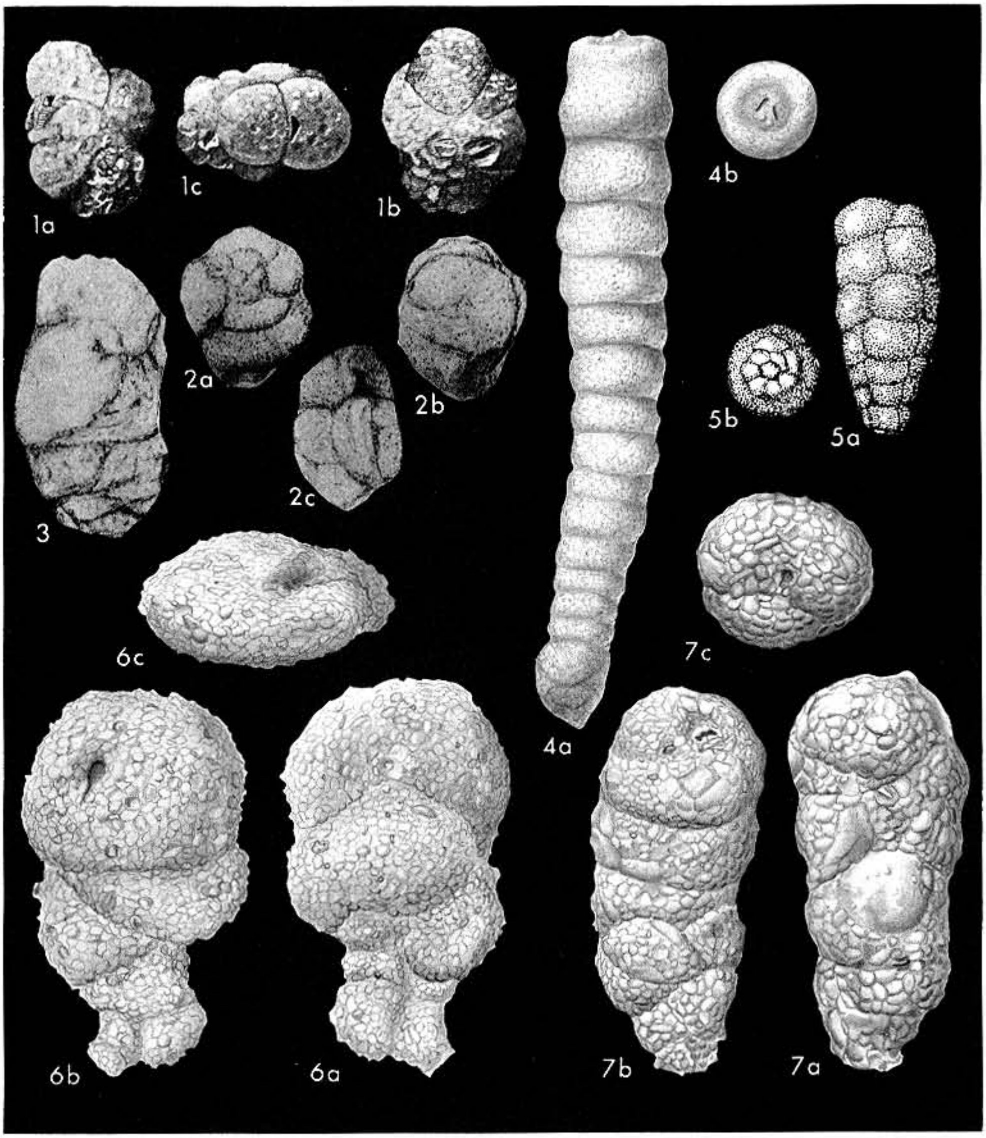


FIG. 185. Ataxophragmiidae (Globotextulariinae; *1-3, Plectotrochammina; 4, Multifidella; 5, Orientalia; 6, Mooreinella; 7, Digitina*) (p. C274, C277-C279).

7a-c, opposite sides and apert. view of topotype, ×52 (*2117).

Dorothia PLUMMER, 1931, *1463, p. 130 [*Gaudryina bulletta* CARSEY, 1926, *282, p. 28; OD] [=*Marssonella* CUSHMAN, 1933, *458, p. 36 (type, *Gaudryina oxycona* REUSS, 1860, *1548, p. 229)]. Early stage trochospiral, with 4 or more chambers to whorl, later stage reduced to biserial; wall agglutinated, may be of calcareous particles on pseudochitinous lining; aperture an interiomarginal slit. [*Marssonella* was placed in the synonymy of *Dorothia* by TRUJILLO (1960, *1954, p. 308) and with this we agree. The congeneric status of *Dorothia, Marssonella,* and *Gaudryina,* as suggested by BOWEN (1955, *182, p. 363) is not upheld by our studies.] *L.Cret.(Alb.)-Rec.,* cosmop.——FIG. 184,6. **D. bulletta* (CARSEY), U. Cret., USA(Tex.); *6a-c,* side, basal, and apert. views of topotype, ×68 (*2117).——FIG. 184,5. *D. oxycona* (REUSS), U.Cret., Eu.(Ger.); *5a-c,* side, basal, and apert. views, ×62 (*2117).

Eggerella CUSHMAN, 1933, *458, p. 33 [**Verneuilina bradyi* CUSHMAN, 1911, *404b, p. 54; OD]. Test in trochospiral coil, with 5 chambers to whorl in early stage of microspheric form, gradually reduced to 3 to whorl in adult; wall finely agglutinated on pseudochitinous base, may be of calcareous particles in calcareous cement; aperture a low interiomarginal slit. *?U.Cret.*, *Eoc.-Rec.*, cosmop.——FIG. 186,*1*. **E. bradyi* (CUSHMAN), Rec., Pac.O.; *1a,b*, side, top views of holotype, ×65 (*2117).

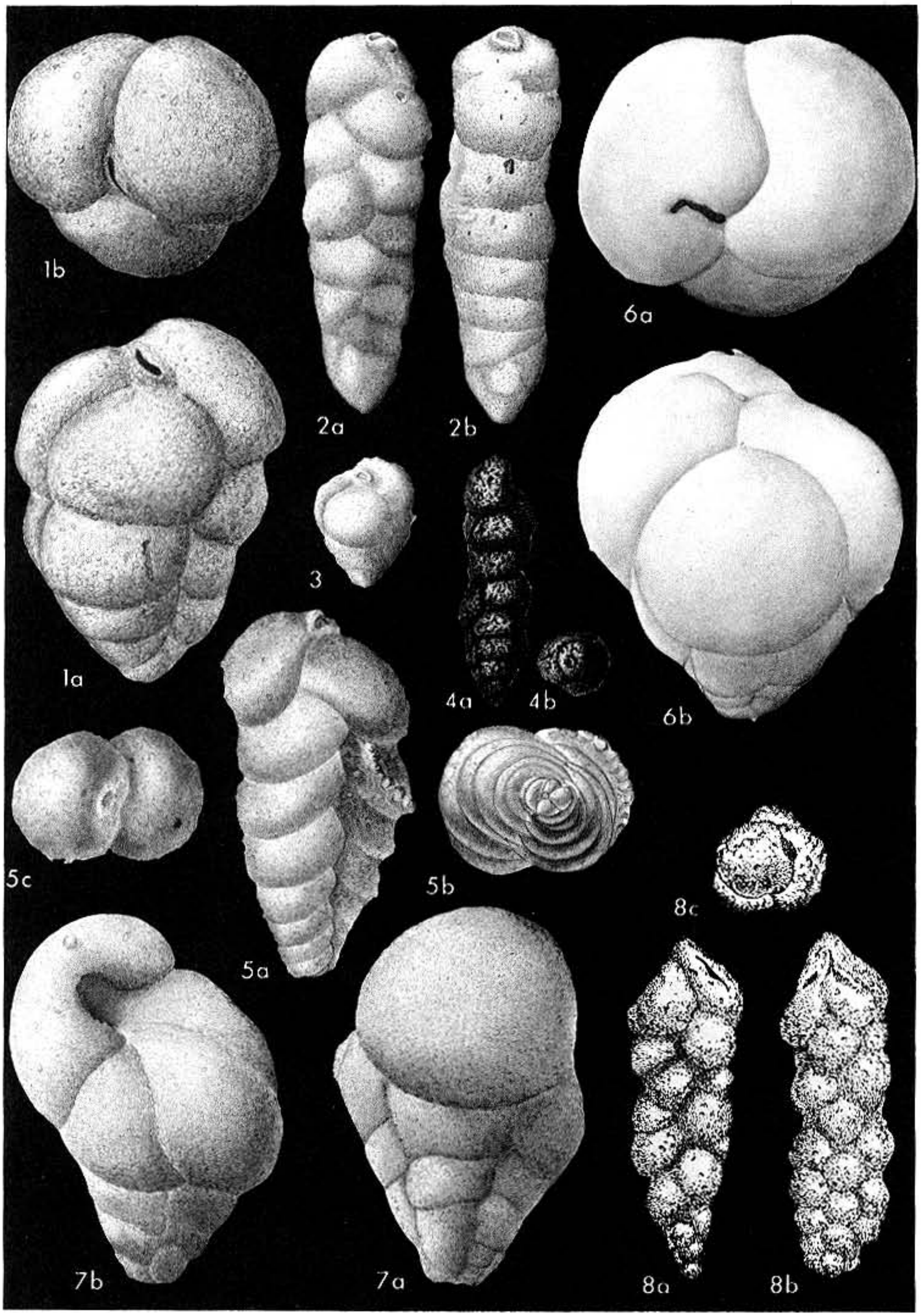


FIG. 186. Ataxophragmiidae (Globotextulariinae; *1, Eggerella; 2-5, Karreriella; 6, Eggerellina; 7,8, Gravellina*) (p. *C275-C277*).

[*Eggerella* differs from *Dorothia* in being triserial, rather than biserial, in the adult. It is apparently restricted to the Tertiary. The two species referred to *Eggerella* by Cushman (*471) include *Globigerina trochoides* Reuss, 1845, and *Valvulina inflata* Franke, 1928. The generic character of Reuss' species is extremely doubtful—in fact, in 1946 Cushman (*484, p. 42) referred it to *Eggerella? trochoides* (Reuss), and in the same publication (p. 145) also referred it to *Allomorphina trochoides* (Reuss), illustrating and describing it under both generic names without comment. A restudy of the original types or topotypes should determine its generic status. *"Valvulina" inflata* Franke is probably very similar to *"Globigerina" trochoides. Eggerella columna* Finlay (1940, *717d), from the uppermost Cretaceous of New Zealand, may possibly belong to the present genus.]

Eggerellina Marie, 1941, *1215, p. 31 [**Bulimina brevis* d'Orbigny, 1840, *1394, p. 41; OD]. Test free, conical or ovoid, triserial, with inflated and embracing chambers; wall agglutinated, of calcareous particles with considerable cement; interior simple; aperture narrow, hook-shaped, interiomarginal and extending short distance up face. *U.Cret.(Senon.),* Eu.(Fr.).——Fig. 186,*6*. *E. brevis* (d'Orbigny) *conica* Marie; *6a,b,* top and side views of hypotype, personal collection of P. Marie, no. 6028, Paris (*1215, pl. 7, fig. 70), redrawn, probably microspheric form of *E. brevis* (d'Orbigny), ×64 (*2117).

[Cushman (1948, *486, p. 130) regarded d'Orbigny's species as a true *Bulimina* with perforate calcareous wall. The wall is agglutinated, but composed of calcareous particles; hence the genera are distinct, and *Eggerellina* is placed with the agglutinated genera. It differs from *Eggerella* in having a high loop- or hook-shaped aperture, instead of a low interiomarginal slit. The aperture thus resembles that of *Hagenowina,* which differs in having secondary septa and a complex interior.]

Eggerina Toulmin, 1941, *1944, p. 573 [**E. cylindrica*; OD]. Test high trochospiral coil, 3 strongly enveloping chambers to whorl; wall agglutinated, may be of calcareous particles and with much calcareous cement; aperture a low interiomarginal umbilical arch with slight lip. [*Eggerina* differs from *Eggerella* in its elongated chambers along the axis of coiling.] *U.Paleoc.,* USA(Ala.).——Fig. 184,*4*. **E. cylindrica; 4a-c,* opposite sides and top view of holotype, redrawn, ×74 (*2117).

Gravellina Brönnimann, 1953, *229, p. 87 [**G. narivaensis;* OD] [=*Verneuilinella* Tairov, 1956, *1861, p. 113 (type, *V. azerbaidjanica*)]. Test quadriserial throughout; wall finely agglutinated; aperture an interiomarginal arch. [*Verneuilinella* Tairov is based on a somewhat more elongate species, but the test shape is not regarded as generic in importance.] *L.Cret.(Apt.)-Mio.,* USSR-W.Indies(Trinidad).——Fig. 186,*7*. **G. narivaensis,* Mio., Trinidad; *7a,b,* opposite sides of holotype, redrawn, ×80 (*2117).——Fig. 186,*8*. *G. azerbaidjanica* (Tairov), L.Cret., Apt., USSR (Azerbaidzhan); *8a-c,* opposite sides and top view of holotype, ×85 (*1509).

Karreriella Cushman, 1933, *458, p. 34 [**Gaudryina siphonella* Reuss, 1851, *1541, p. 78; OD] [=*Karrerulina* Finlay, 1940, *717d, p. 450 (type, *Gaudryina apicularis* Cushman, 1911, *404b, p. 69); *Valvotextularia* Hofker, 1951, *928c, p. 30 (type, *Textularia catenata* Cushman, 1911, *404b, p. 23)]. Test free, elongate, early chambers in trochoid spire of one or more whorls, followed by well-developed biserial stage, which may be slightly twisted about its axis; wall finely agglutinated, smoothly finished; aperture rounded, in terminal face of final chamber, bordered by lip or produced on distinct slender neck. *Paleoc.-Rec.,* cosmop.——Fig. 186,*2,3*. **K. siphonella* (Reuss), M.Oligo., Eu.(Ger.); *2a,b,* side and edge views of large microspheric topotype; *3,* side view of megalospheric topotype; all ×40 (*2117).——Fig. 186,*4*. *K. apicularis* (Cushman), Rec., Pac.O.; *4a,b,* side, top views, ×42 (*200).——Fig. 186, *5*. *K. catenata* (Cushman), Rec., Pac.O.; *5a-c,* side, base, and top views, ×112 (*2117).

[No generic or subgeneric distinction is recognized for *Karrerulina,* which is here regarded as a synonym of *Karreriella*. Finlay (1939, *717a, p. 510) placed the type-species of *Valvotextularia, Textularia catenata,* in his genus *Siphotextularia,* stating that it had a typical siphotextularian aperture in the face of the final chamber and produced on a neck. It differs from *Siphotextularia* in having the early trochoid stage of about 4 chambers in the first whorl, hence is here referred to *Karreriella. Karreriella* differs from *Dorothia* in having the terminal aperture.]

Mooreinella Cushman & Waters, 1928, *535, p. 50 [**M. biserialis;* OD]. Test trochospiral in early stage, later irregularly biserial; wall coarsely agglutinated; aperture becoming rounded and terminal in biserial stage. [*Mooreinella* is irregularly biserial in the adult and has a relatively inconspicuous trochospiral development. *Plectotrochammina* differs from it in its highly developed trochospiral stage, and regular but reduced biserial stage, with slitlike areal aperture near the base of the apertural face rather than terminal in position.] *Penn.,* USA(Tex.).——Fig. 185,*6*. **M. biserialis; 6a-c,* opposite sides and top view of holotype, ×45 (*2117).

Multifidella Loeblich & Tappan, 1961, *1181, p. 218 [**Clavulina communis* d'Orbigny var. *nodulosa* Cushman, 1922, *411c, p. 85; OD]. Test free, elongate, early portion trochospiral with 4 or 5 chambers to whorl, progressively reducing to triserial, biserial and uniserial, uniserial stage comprising large proportion of adult test; wall finely agglutinated, aperture terminal, cribrate, consisting of variously aligned, elongate slits with bordering lips. [*Multifidella* differs from *Cribrogoesella* in its slender test with elongate uniserial stage and in having a multiple aperture consisting of slits with bordering lips.] *Mio.-Rec.,* Atl.O.-Carib.-W.Indies(Trinidad).——Fig. 185,*4*. **M. nodulosa* (Cushman), Rec., Atl.; *4a,b,* side and apert. views of lectotype, × 20 (*2117).

Orientalia N. K. Bykova, 1947, *262, p. 229 [**O. exilis;* OD]. Test elongate, early stage trochospiral, with 6 or 7 chambers to whorl, later reduced to quadriserial, with chambers in 4 vertical rows; wall finely agglutinated with large amount of cement; aperture an interiomarginal slit. [*Orientalia* differs from *Dorothia* in its later

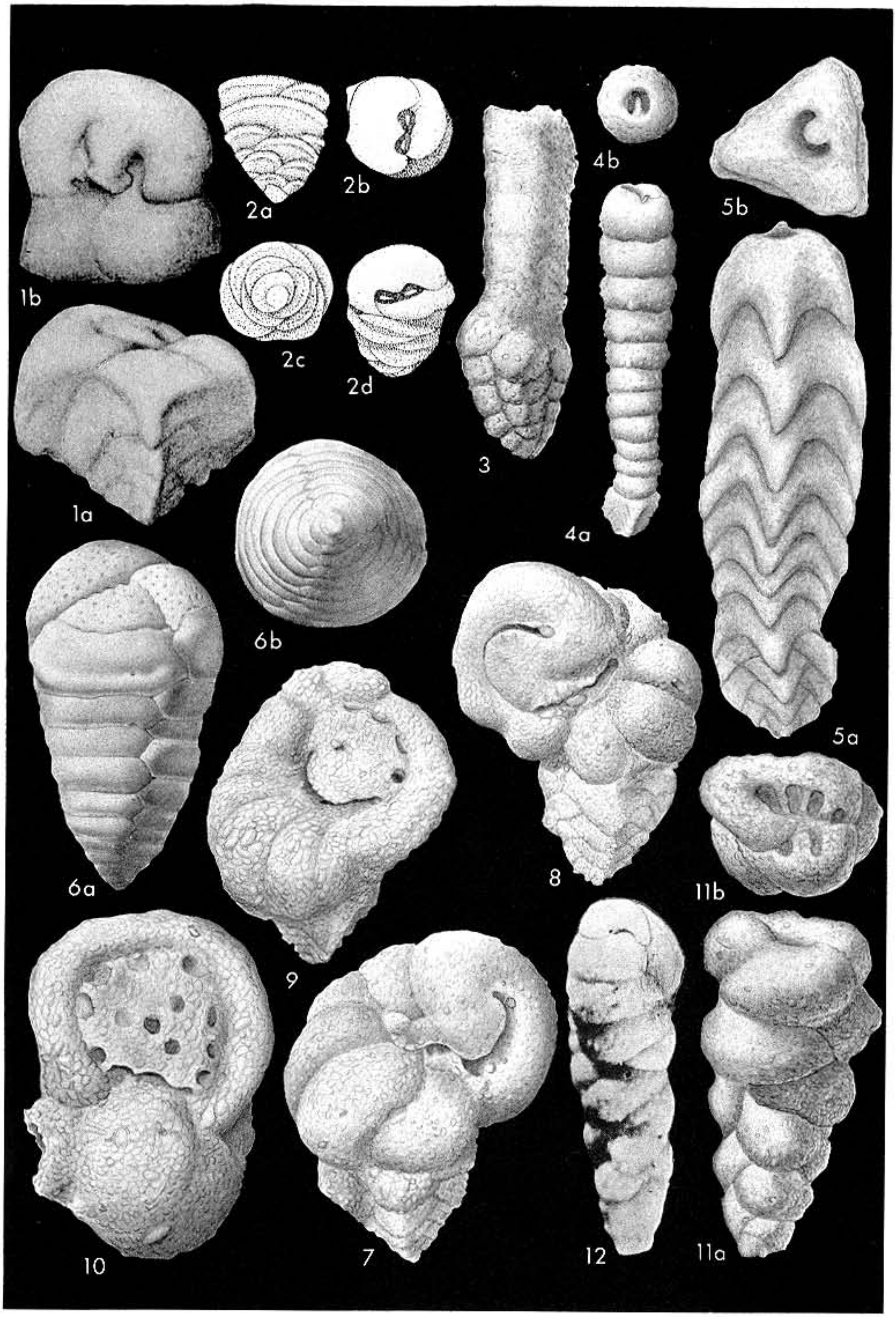


Fig. 187. Ataxophragmiidae (Valvulininae; *1,2, Valvulina; 3-5, Clavulina; 6, Chrysalidina; 7-10, Cribrobulimina; 11,12, Cribroturretoides*) (p. C279-C281).

quadriserial stage, and from *Gravellina* in having an early trochospiral stage of more than 4 chambers in each whorl, rather than being quadriserial throughout.] *U.Cret.(Cenoman.),* USSR (Guzar-Dari, Bukhara).——Fig. 185,*5*. **O. exilis; 5a,b,* side and basal views of holotype, ×66 (*262).

Plectotrochammina Parr, 1950, *1429, p. 280 [**P. subglobosa*; OD] [=*Poronaia* Ujiié & Watanabe, 1960, *1965, p. 133 (type, *Plectina poronaiensis* Asano, 1952, *53, p. 33)]. Test free, early chambers in high trochoid spire similar to *Trochammina,* later portion becoming biserial; wall coarsely agglutinated; aperture an arched areal slit, slightly above base of final chamber. [*Poronaia* was also described as trochospiral, as in *Trochammina,* with later biserial stage and was placed in the Eggerellinae. It is here regarded as a junior synonym of *Plectotrochammina* which is transferred to the Globotextulariinae.] *U.Eoc.-Rec.,* Antarctic-Japan. ——Fig. 185,*1*. **P. subglobosa,* Rec., Antarctic; *1a,b,* opposite sides showing early trochoid coil followed by pair of biserial chambers; *1c,* view of top of biserial pair of chambers showing aperture, ×25 (*1429).——Fig. 185,*2,3*. *P. poronaiensis* (Asano), ?U.Eoc., Japan; *2a-c,* opposite sides and edge showing early trochoid spire; *3,* crushed specimen with well-developed biserial stage; all ×33 (*1965).

Subfamily VALVULININAE Berthelin, 1880

[*nom. transl.* Schubert, 1920, p. 179 (*ex* family Valvulinidae Berthelin, 1880)] [=Uvellida Schultze, 1854, p. 52 (*partim*) (*nom. nud.*)]

Three chambers in early whorls, later increasing in number or becoming uniserial; aperture with valvular tooth, interiomarginal at least in early stage, but may become terminal and modified to multiple aperture. *U.Trias.-Rec.*

Valvulina d'Orbigny, 1826, *1391, p. 268, 270 [**V. triangularis;* SD Parker, Jones & Brady, 1865, *1419, p. 35] [=*Duotaxis* Kristan, 1957, *1057, p. 294 (type, *D. metula*)]. Test free, triserial in early stages, may be triangular in section, later may have more than 3 chambers to whorl; wall agglutinated; aperture at base of final chamber, with large valvular tooth. *U.Trias.(Rhaet.)-Rec.,* cosmop.——Fig. 187,*1*. **V. triangularis,* Eoc., Eu.(Fr.); *1a,b,* side, top views, ×33 (*471). ——Fig. 187,*2*. *V. metula* (Kristan), U.Trias. (Rhaet.), Eu.(Aus.); *2a-d,* side, top, base, and oblique views of holotype, ×22 (*1057).

Chrysalidina d'Orbigny in de la Sagra, 1839, *1611, p. 109 [**C. gradata;* OD (M)] [=*Pupina* d'Orbigny in de la Sagra, 1839, *1611, p. 29 (*non* Vignard, 1829)]. Test large, elongate, triserial throughout; wall agglutinated; aperture of numerous pores in terminal face, those of all chambers of last whorl remaining open. [Cushman (1937, *471, p. 54) stated "early stages unknown," and "all of the figures given of the type species are based upon d'Orbigny's originals." The figures here given are of topotype specimens and show the species to be triserial throughout.] *U. Cret.(Cenoman.),* Eu.(Fr.).——Fig. 187,*6*. **C. gradata; 6a,b,* side, basal views of topotype, ×12 (*2117).

Clavulina d'Orbigny, 1826, *1391, p. 268 [**C. parisiensis;* SD Cushman, 1911, *404b, p. 72] [=*Pseudoclavulina* Cushman, 1936, *468, p. 16 (type, *Clavulina clavata* Cushman, 1926, *423, p. 589)]. Test free, triangular in section, early portion with chambers triserially arranged, later uniserial; chambers numerous, low, broad; wall agglutinated, with much calcareous cement; aperture terminal, rounded, with valvular tooth. [*Clavulina* differs from *Valvulina* in possessing a final uniserial stage and terminal aperture.] *Paleoc.-Rec.,* cosmop.——Fig. 187,*4*. **C. parisiensis,* M.Eoc.(Lutet.), Eu.(Fr.); *4a,b,* side, top views, ×35 (*2117).——Fig. 187,*5*. *C. angularis* d'Orbigny, Rec., Medit.Sea(Corsica); *5a,b,* side, top views of holotype (MNHN, labeled "Tableau Methodique Modèle"), ×48 (*2117).——Fig. 187,*3*. *C. clavata* Cushman, Paleoc., Mex.; side view of holotype, ×51 (*2117).

Cribrobulimina Cushman, 1927, *428, p. 80 [**C. mixta* Cushman, 1927 (=*Valvulina mixta* Parker & Jones, 1865, *1418, p. 438, *nom. nud,* =*Valvulina polystoma* Parker & Jones, 1865, *1418, p. 437, *nom. nud.,* =*Valvulina* sp. Carpenter, Parker & Jones, 1862, *281, p. 146, pl. 11, figs. 19-26); OD]. Test free, early stages triserial and triangular in section, later in loose spiral of 5 or more chambers in each whorl; wall agglutinated, with 2 layers, inner layer distinctly perforated, relatively thick, commonly of calcareous particles embedded in calcareous cement, covered by thin outer layer of quartz sand; aperture in young as in *Valvulina,* in later development plate-like tooth attaches to opposite wall and develops series of openings at its margin and others scattered over its surface. *Rec.,* Australia.——Fig. 187, *7-10*. **C. mixta; 7,8,* specimens showing valvular tooth with only early indication of pores at its margin; *9,10,* specimens with tooth attached for most of its margin and strong development of pores both at edge and in central area of tooth, ×45 (*2117).

[Carpenter, Parker & Jones (1862, *281, p. 146-148) described *Valvulina,* stating (p. 146) that in it all the principal modifications could be referred to "one central type; the *Valvulina triangularis* of d'Orbigny being the form of which the rest may be regarded as varieties." The description of the "varieties" followed, but they gave no name to any of these, other than the generic name of *Valvulina.* In 1865 Parker & Jones (*1418) used the names *Valvulina polystoma* (table, p. 437) and *Valvulina mixta* (table, p. 438), but without any description. Footnotes referred to the illustrations in Carpenter, Parker & Jones (1862, *398, pl. 11, fig. 21, 24 for *V. polystoma* and pl. 11, figs. 19, 20,

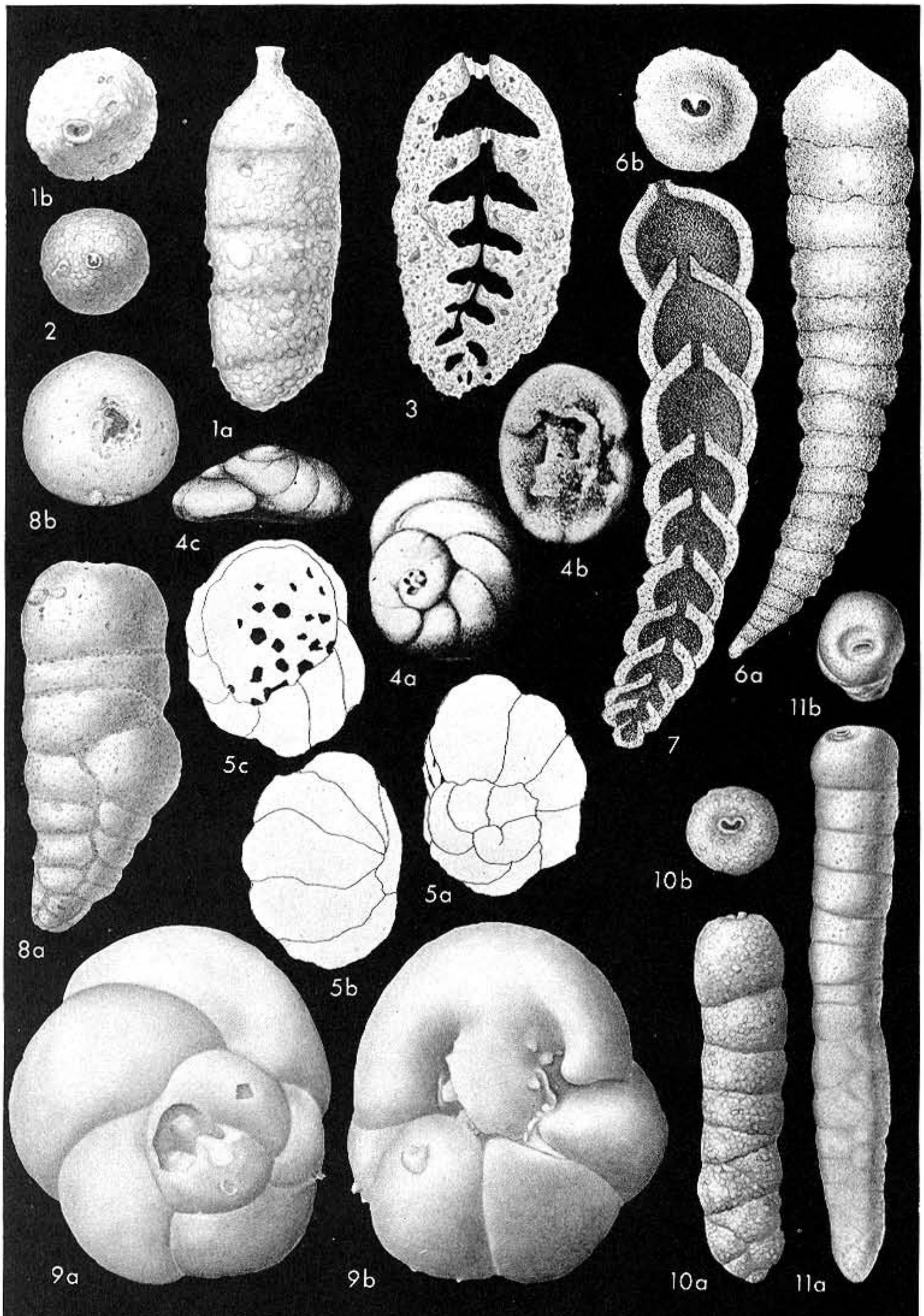


FIG. 188. Ataxophragmiidae (Valvulininae; *1-3, Cylindroclavulina; 4,5, Discorinopsis; 6,7, Dusenburyina; 8, Goesella; 9, Valvulammina; 10,11, Martinottiella*) (p. C281-C283).

25, 26 for *V. mixta*) but did not refer to any description. The descriptions for these species quoted in Ellis & Messina (1940, *700) are from Carpenter, Parker & Jones' discussion of unnamed *Valvulina*. Both names were *nomina nuda* in the 1865 publication. The first validated reference to a specific name for this form is apparently that of Cushman (1927, *428), where for the first time a description was given with the specific name. The type-species is therefore correctly cited as *Cribrobulimina mixta* Cushman, 1927. The page priority of *Valvulina polystoma* Parker & Jones, 1865, over *V. mixta* Parker & Jones, 1865, accepted by Parr (1932, *1421, p. 6) and Cushman (1937, *471, p. 27) is invalid, as both names were *nomina nuda* in 1865, and *V. polystoma* was not mentioned by Cushman in 1927. A lectotype is here designated for *Cribrobulimina mixta* Cushman (=*Valvulina mixta* Parker & Jones, 1865, *nom. nud.*) (BMNH-ZF 3591). Paratypes in the British Museum (Natural History) are labeled *Valvulina mixta* Parker & Jones (BMNH-ZF 3590). A lectotype was also selected and so labeled by us (and is here designated) for *Valvulina polystoma* Parker & Jones (BMNH-ZF 3593) and paratypes (ZF 3592). All are from Recent shore sands at Melbourne, Australia. The name *Valvulina polystoma* (*nomen nudum*, Parker & Jones) was validated by Parr (1932, *1421). The two are conspecific. *Cribrobulimina* differs from *Valvulina* in the development of a multiple aperture on the large platelike tooth.]

Cribroturretoides Smith, 1949, *1799, p. 56 [**C. miocenica;* OD] [=*Neoclavulina* Puri, 1957, *1488, p. 106 (type, *Valvulina intermedia* Applin & Jordan, 1945, *26, p. 134)]. Test free, elongate, triserial, with chambers rounded as in *Verneuilinoides;* wall agglutinated; aperture terminal, cribrate, with few relatively large, irregular openings apparently developed from valvuline tooth. *Eoc.-Mio.*, USA(La.-Fla.).——Fig. 187,*11*. **C. miocenica,* Mio., USA(La.); *11a,b,* side, top views of holotype, ×173 (*2117).——Fig. 187, *12*. *C. intermedia* (Applin & Jordan), M.Eoc., USA(Fla.); side view of holotype, ×30 (*26).

[*Neoclavulina* was stated by Puri to have a terminal rounded or elliptical aperture, "with or without a valvular tooth." The type-species, *Valvulina intermedia,* has a distinct tooth, "which is broadened on mature specimens to form small, rounded, plate-like structure with series of small openings along edge" (*26). As based on the type-species, *Neoclavulina* is thus a junior synonym of *Cribroturretoides.* If other species placed in *Neoclavulina* do not have a valvular tooth, they would not be referrable to the present subfamily, and probably would be assigned to *Verneuilina.*]

Cylindroclavulina Bermúdez & Key, 1952, *129, p. 76 [**Clavulina bradyi* Cushman, 1911, *404b, p. 73; OD]. Test free, large, robust, cylindrical, earliest portion triserial, then biserial and finally uniserial, with multiserial stage much reduced; wall agglutinated, very thick, leaving much diminished chamber cavity; aperture terminal, produced on distinct neck, with tooth projecting from one margin. [*Cylindroclavulina* differs from *Clavulina* d'Orbigny in being cylindrical throughout, rather than triangular in the early triserial stage. Also, *Cylindroclavulina* has a biserial stage between the triserial and uniserial stages.] *Oligo.-Rec.*, Pac.O. - Eu.(Hung.-Italy).——Fig. 188,*1-3*. **C. bradyi* (Cushman), Rec., Pac.; *1a,b,* side, top views of holotype, ×24 (*2117); *2,* top view showing well-developed tooth, ×14; *3,* sectioned specimen showing thick wall, ×10 (*200).

Discorinopsis Cole, 1941, *357, p. 36 [**D. gunteri;* OD] [=*Arenagula* Bourdon & Lys, 1955, *177, p. 336 (type, *A. globula*); *Arenaglobula* Thalmann, 1958, *18971, p. 752 (obj.) (*nom. null.*)]. Test low, spiral, early stage with about 5 chambers to each whorl, increasing to as many as 7 chambers in final whorl of microspheric form with early development as in *Valvulammina;* wall agglutinated, of calcareous particles in calcareous cement; aperture umbilical in young, with broad valvular tooth, which in adult becomes attached and perforated throughout with large openings, as in *Cribrobulimina. M.Eoc.-Oligo.*, USA(Fla.)-Eu.(Fr.).——Fig. 188,*4*. **D. gunteri,* M.Eoc., USA (Fla.); *4a-c,* opposite sides and edge of holotype showing low multilocular spire and cribrobulimine aperture, ×10 (*357).——Fig. 188,*5*. *D. globula* (Bourdon & Lys), Oligo.(Stamp.), Fr.; *5a-c,* opposite sides and edge, showing low spire and multiple aperture, ×24 (*177).

[*Discorinopsis* was originally described as calcareous and related to *Discorbis.* Thin sections of the type-species made by us showed it to be agglutinated (*1162, p. 117), and it is here placed with the Valvulininae. The species described as *Valvulina floridana* Cole, 1941, from the same sample as the type-specimens of *D. gunteri,* is probably a young megalospheric form of this species, being smaller, with only 3 chambers in each whorl and with a simple valvular tooth. *Discorinopsis* has an apertural development as in *Cribrobulimina* but differs from that genus in having a low trochospiral coil, whereas *Cribrobulimina* has an early triserial and triangular, high-spired stage and a later stage with many chambers in a whorl. *Arenagula* is identical in all characteristics to *Discorinopsis* as here redefined on the basis of the type-species.]

Dusenburyina Bermúdez & Key, 1952, *129, p. 73 [**Clavulina procera* Goës, 1889, *802, p. 9; OD]. Test free, elongate, uniserial, rounded in section; wall agglutinated, of calcareous particles with considerable cement; aperture terminal, rounded to ovate, with projecting tooth that, when relatively broad, may appear semilunate. [*Dusenburyina* differs from *Reophax* in possessing an apertural tooth. It differs from *Clavulina* d'Orbigny in lacking an early triserial development and in being uniserial throughout.] *Rec.*, Carib.——Fig. 188,*6,7*. **D. procera* (Goës); *6a,b,* side, apert. views of microspheric specimen; *7,* sectioned megalospheric specimen, ×8 (*801).

Goesella Cushman, 1933, *458, p. 34 [**Clavulina rotundata* Cushman, 1913, *406, p. 635; OD]. Test elongate, early stage with 4 or 5 chambers in whorl, then progressively reduced to triserial, biserial, and finally uniserial; wall thick, agglutinated, of fine sand with considerable cement; aperture terminal, rounded or irregular, with tooth projecting from one side. *U.Cret.(Senon.)-Rec.*, cosmop.——Fig. 188,*8*. **G. rotundata* (Cushman), Rec., Philip. Is.; *8a,b,* side and top views of holotype (redrawn), ×20 (*2117).

[*Goesella* differs from *Martinottiella* in having a rounded aperture with a tooth instead of a slitlike or arcuate aperture, with bordering lip or produced neck. The uniserial development is commonly more pronounced in *Martinottiella,* resulting in a narrower, more elongate test. The original description of *Goesella* did not mention the apertural tooth, but this is seen in the holotype of the type-species, as well as in many others. Species such as *G. parri* Cushman should be placed in *Martinottiella,* as they have a slitlike or arcuate aperture, and slender test with pronounced uniserial development.]

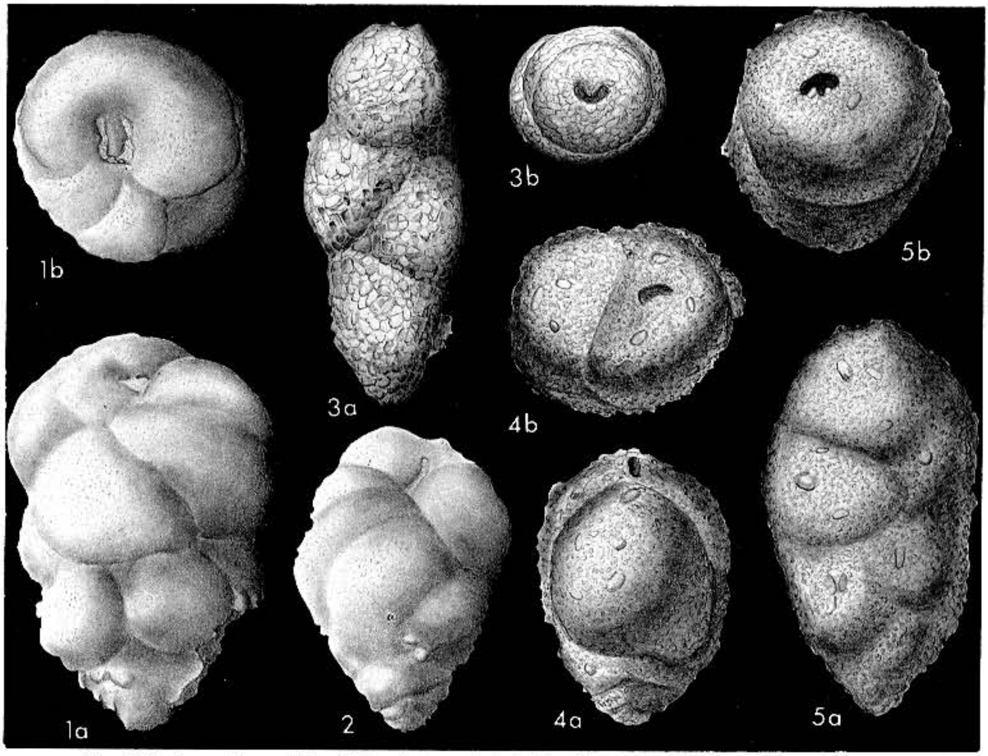


FIG. 189. Ataxophragmiidae (Valvulininae; *1,2, Makarskiana; 3-5, Plectina*) (p. C282-C283).

Makarskiana Van Soest, 1942, *1808, p. 27 [**M. trochoidea;* OD]. Similar to *Valvulammina* in having 4 or 5 chambers in early whorls, later with 3 or 4, but differs in having high trochospiral coil; aperture with small narrow valvuline tooth. *Eoc.,* Eu.(Yugo., Dalmatia).——FIG. 189, *1,2.* **M. trochoidea; 1a,b,* side, top views of holotype (redrawn); 2, paratype, all ×32 (*2117).

Martinottiella Cushman, 1933, *458, p. 37 [**Clavulina communis* d'Orbigny, 1826, *1391, p. 268; OD] [=*Listerella* Cushman, 1933, *458, p. 36 (type, *Clavulina primaeva* Cushman, 1913, *406, p. 635) (*non Listerella* Jahn, 1906); *Schenckiella* Thalmann, 1942, *1900, p. 458 (type, *Clavulina primaeva* Cushman, 1913, *406, p. 635) (*nom. subst. pro Listerella* Cushman, 1933, *non* Jahn, 1906)]. Test free, elongate, cylindrical, early chambers trochospiral with 4 or 5 to whorl, progressively reduced to triserial, biserial, and uniserial, adult with relatively elongate uniserial development; wall finely agglutinated; aperture terminal, elongate slit, commonly arcuate, with bordering lip. *Paleoc.-Rec.,* cosmop.——FIG. 188,*10.* **M. communis* (d'Orbigny), Rec., Eu.(Italy); *10a,b,* side, top views of hypotype, ×28 (*2117). ——FIG. 188,*11. M. primaeva* (Cushman), Rec., Pac.O.; *11a,b,* side, top views of holotype, ×28 (*2117).

[*Martinottiella* differs from *Goesella* in its more pronounced uniserial development and resultant elongate test, and in having a slitlike aperture with bordering lip, rather than a depressed rounded aperture with projecting tooth. Cushman (1937, *471, p. 138) placed *Martinottiella* in the synonymy of *Listerella,* stating that their type-species were congeneric. In 1942, Thalmann (*1900) noted that *Listerella* Cushman was a homonym of *Listerella* Jahn and proposed *Schenckiella* as a replacement name. Cushman (1947, *485, p. 48) recognized both *Schenckiella* and *Martinottiella,* using the latter name for "those species, formerly placed under *Listerella,* in which the biserial stage is much reduced or wanting." As the proportionate length of the biserial stage is quite variable in many species, *Martinottiella* is here regarded as the valid name and *Schenckiella* is suppressed as a junior synonym.]

Minouxia Marie, 1955, *1220, p. 119 [**M. gumbelitrioides;* OD] [=*Bermudezita* Seiglie, 1961, *1715, p. 342 (type, *B. borroi*)]. Test triserial throughout; wall agglutinated; primary aperture interiomarginal, umbilical region covered by trematophore (separate plate with numerous perforations). [The original illustrations of this genus appear similar to *Chrysalidina* but the aperture is described as having a distinct trematophore plate; the genus therefore is recognized on that basis until type material can be examined.] *U.Cret. (Dordon.),* Eu.(Fr.)-W.Indies(Cuba). —— FIG. 190,*1.* **M. gumbelitrioides,* Fr.; *1a-c,* opposite sides and apert. view, ×85 (*1220).——FIG. 190, *2. M. dordonica* Marie, Fr.; side view, ×54 (*1220).

Plectina Marsson, 1878, *1228, p. 160 [**Gaudryina ruthenica* Reuss, 1851, *1542, p. 41; SD Cushman, 1928, *439, p. 127] [=*Arenodosaria* Finlay, 1939, *717b, p. 95 (type, *Clavulina robusta* Stache, 1865, *1825, p. 169)]. Test elongate, up to 5 chambers to whorl in early stage, later reducing to loosely biserial; wall agglutinated, with considerable cement; aperture interiomarginal in early stage, later terminal, rounded, with small valvular tooth. [*Arenodosaria* was regarded as being uniserial in final development, but the type-species of *Plectina* and *Arenodosaria* both are loosely biserial to nearly uniserial with cuneate chambers, not truly rectilinear and uniserial. The two generic names are regarded as synonymous.] *U.Cret.(Senon.)-Rec.*, cosmop.——Fig. 189,*3*. **P. ruthenica* (Reuss), U.Cret.(Senon.), Eu.(Ger.); *3a,b*, side, top views of hypotype, ×32 (*2117).——Fig. 189,*4,5*. *P. robusta* (Stache), L.Oligo., N.Z.; *4a,b*, *5a,b*, side, top views, ×32 (*2117).

Valvulammina Cushman, 1933, *458, p. 37 [**Valvulina globulosa* d'Orbigny, Cushman, 1933 *err. pro Valvulina globularis* d'Orbigny, 1826, *1391, p. 270; OD]. Test low trochospiral coil, with more than 3 chambers to whorl, ventral side umbilicate; wall agglutinated, of calcareous fragments in calcareous cement with pseudochitinous lining in at least early portion; aperture umbilical, partially covered by large rounded tooth. [*Valvulammina* differs from *Valvulina* in having more than 3 chambers to a whorl throughout development and in its low trochospiral coil.] *Paleoc., ?Mio.*, N.Am.-Carib.-Eu.(Fr.).——Fig. 188,*9*. **V. globularis* (d'Orbigny), Eoc., Fr.; *9a,b*, opposite sides, ×50 (*2117).

Subfamily ATAXOPHRAGMIINAE Schwager, 1877

[*nom. transl.* Galloway, 1933, p. 211 (*ex* family Ataxophragmidea Schwager, 1877)]

Early stage with 3 or more chambers in each whorl but increasing in number with growth or uncoiling and spreading to form low conical test; interior with internal pillars and partitions. *L.Cret.-Rec.*

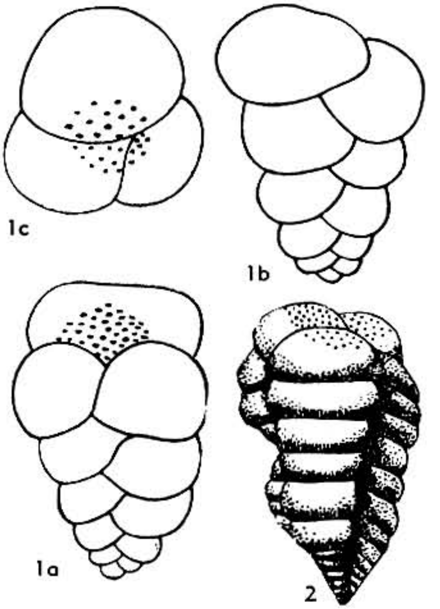


Fig. 190. Ataxophragmiidae (Valvulininae; *1,2*, *Minouxia*) (p. *C*282).

Ataxophragmium Reuss, 1860, *1546, p. 52 [**Bulimina variabilis* d'Orbigny, 1840, *1394, p. 40; SD Cushman, 1928, *439, p. 129] [=*Pernerina* Cushman, 1933, *456, p. 19 (type, *Bulimina depressa* Perner, 1892, *1445, p. 55); *Ataxogyroidina* Marie, 1941, *1215, p. 53, 255, 258 (obj.)]. Test free, trochospiral, tending to become streptospiral in coiling; chambers low and broad, with internal partitions; wall agglutinated; aperture interiomarginal slit or loop, umbilical in position. *U.Cret.(Cenom.-Maastricht.)*, Eu.——Fig. 191,*1,2*. **A. variabile* (d'Orbigny), Senon., Eng.; *1a,b*, edge, apert. views of hypotype, ×50; *2a-c*, opposite sides and apert. view of hypotype (P. Marie Coll. 6051), Senon., Fr.; ×39 (*2117).——Fig. 191,*3,4*. *A. depressum* (Perner), Cenoman., Czech. *(3)*, Turon., Ger. *(4)*; *3a-c*, side, edge, apert. views of topotype, ×45 (*2117); *4*, apert. view of hypotype, abraded to show internal partitions, ×45 (*2117).

[The nomenclature of this form has been confused in the past, and specimens with simple interior, as well as those with internal partitions, have been variously referred to the type-species, as have both enrolled and uniserial forms. At least 3 revisions have been made which resulted in the description of new generic names for one or another of these forms, but as the type-species was not firmly based, the results were not conclusive. d'Orbigny described *Bulimina variabilis* in 1840, stating that it was extremely variable in form, figuring 3 specimens. It was stated to be common at Sens, rare at Meudon and Saint Germain, and in England. Of specimens figured, that shown on his plate 4, fig. 9, 10 (*1394) was stated to be a "regular individual" (figures reproduced by Cushman, 1937, *471, pl. 21, figs. 10a,b), that in fig. 11 regarded as a deformed individual, and that in fig. 12 stated to be an exaggerated form of the type of fig. 11. As the original of figs. 9, 10 was regarded as the normal form, it is here designated as lectotype. The uncoiled specimens, such as d'Orbigny's fig. 12, were stated by Marie (1941, *1215, p. 54) to belong to a different species and genus *(Orbignyna)*, although these dissimilar forms have been repeatedly referred to the same species. Of the specimens illustrated by Cushman (1937, *471, pl. 21) as *Ataxophragmium variabile*, those of figs. 10 and 13 are definitely *A. variabile;* those of figs. 11 and 15 and possibly 14 are *Orbignyna*. Noting that 2 forms were originally included by d'Orbigny, and referring the uncoiled specimens to *Orbignyna*, Marie (1941) proposed *Ataxogyroidina* as a new generic name for the close-coiled specimens but designated *Bulimina variabilis* d'Orbigny as type-species. Hence *Ataxogyroidina* is a junior isogenotypic synonym of *Ataxophragmium*. Barnard in Barnard & Banner (1953, *88, p. 177, 206) recognized the generic name *Ataxogyroidina* for specimens without internal partitions and *Arenobulimina* for those with internal partitions, although this is exactly contrary to conditions shown in the type-species and descriptions of the 2 forms. Marie's original definition of *Ataxogyroidina* (*1215, p. 53) stated (translation) that the chambers were "occupied in their interior by a series of buttresses, more or less developed, localized at the contact of the suture below." Furthermore, *Ataxophragmoides* Brotzen, 1948, was described for forms without internal partitions but

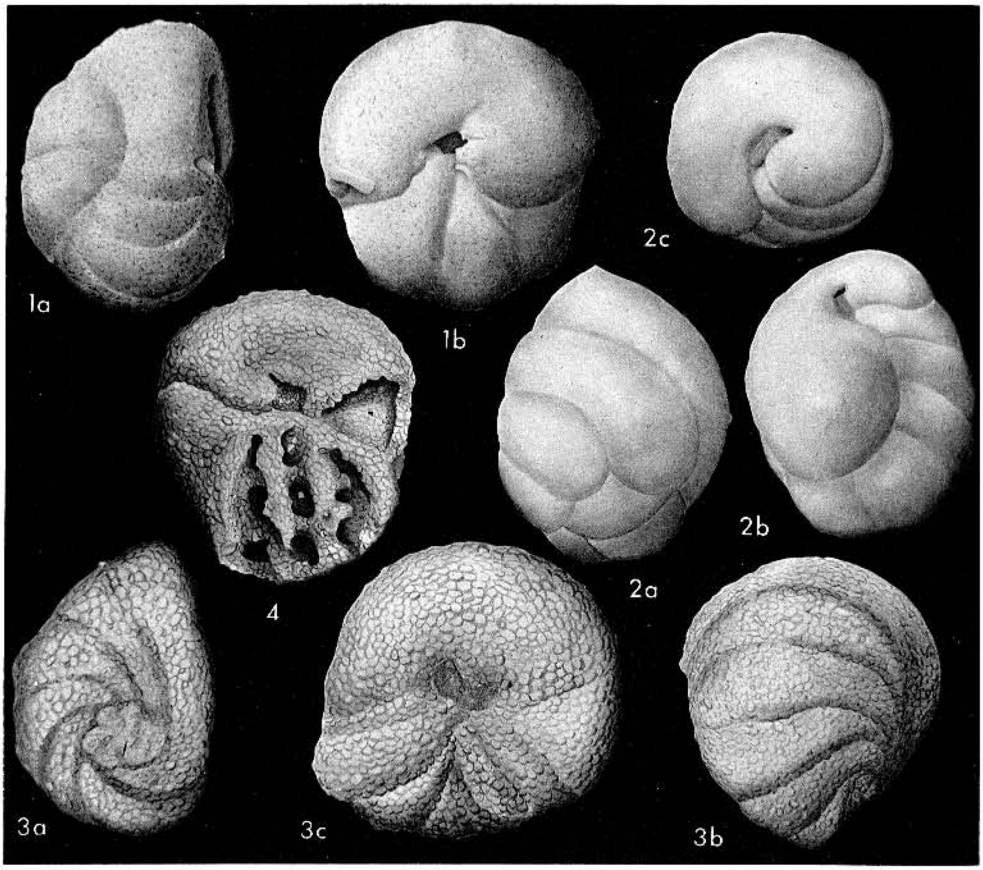


Fig. 191. Ataxophragmiidae (Ataxophragmiinae; *1-4, Ataxophragmium*) (p. C283-C284).

superficially similar to *Ataxophragmium*. Voloshinova & Balakhmatova in Rauzer-Chernousova & Fursenko (1959, *1509, p. 226-227) recognize *Arenobulimina* and *Ataxophragmium* as having simple chambers, and *Pernerina* and *Orbignyna* with internal partitions, and proposed *Beisselina* (a homonym of *Beisselina* Canu, 1913) for the uncoiled forms with internal partitions. As here redefined on the basis of their type-species, *Ataxophragmium* (with *Pernerina* and *Ataxogyroidina* as synonyms) includes coiled species with internal chamber partitions and interiomarginal aperture; *Arenobulimina* (with *Ataxophragmoides* as a synonym) includes similar forms without internal partitions; *Orbignyna*, partially uncoiled, with partitions and a terminal aperture, and *Voloshinovella* Loeblich & Tappan (*nom. nov. pro Beisselina* Voloshinova & Balakhmatova, 1959, *non Beisselina* Canu, 1913) include forms with internal partitions, later completely uncoiled and rectilinear stage and terminal aperture.]

Camagueyia Cole & Bermúdez, 1944, *370, p. 335 [**C. perplexa;* OD]. Early stage trochospiral, later with fewer chambers to whorl; wall thick, finely agglutinated, with considerable cement, septa not completely extending across test, as vertical pillars fill central area; aperture terminal, in center of truncate apertural face, with inward-projecting teeth, as in *Tritaxilina*. [*Camagueyia* is poorly known from original materials and needs further study. No information is available as to number of chambers in a whorl or changes in development. It was originally placed in the Valvulinidae but is here tentatively transferred to the Ataxophragmiinae because of the presence of vertical pillars.] *M.Eoc.*, W.Indies(Cuba).——Fig. 192,*1,2*. **C. perplexa; 1a-d,* ext. of 4 cotypes, ×10; *2*, axial sec. of "paratype," ×41 (*370).

Coprolithina Marie, 1941, *1215, p. 37 [**C. subcylindrica*; OD]. Test free, subcylindrical, trochospirally coiled in single whorl in early stage, forming bulbous base, though with little external evidence of coil, later with cylindrical uniserial portion, with diameter nearly equal to that of coil; chambers subdivided internally by 8 to 14 vertical radial partitions, extending inward from wall approximately half the distance to center; sutures in early portion indistinct, later ones slightly depressed and horizontal; wall thick, coarsely agglutinated, with much calcareous cement; aperture in early stage comprising interiomarginal slit, multiple in adult, consisting of 5 or 6 rounded pores in central portion of terminal face. [*Coprolithina* differs from *Orbignyna* in having a multiple aperture instead of a single large, central

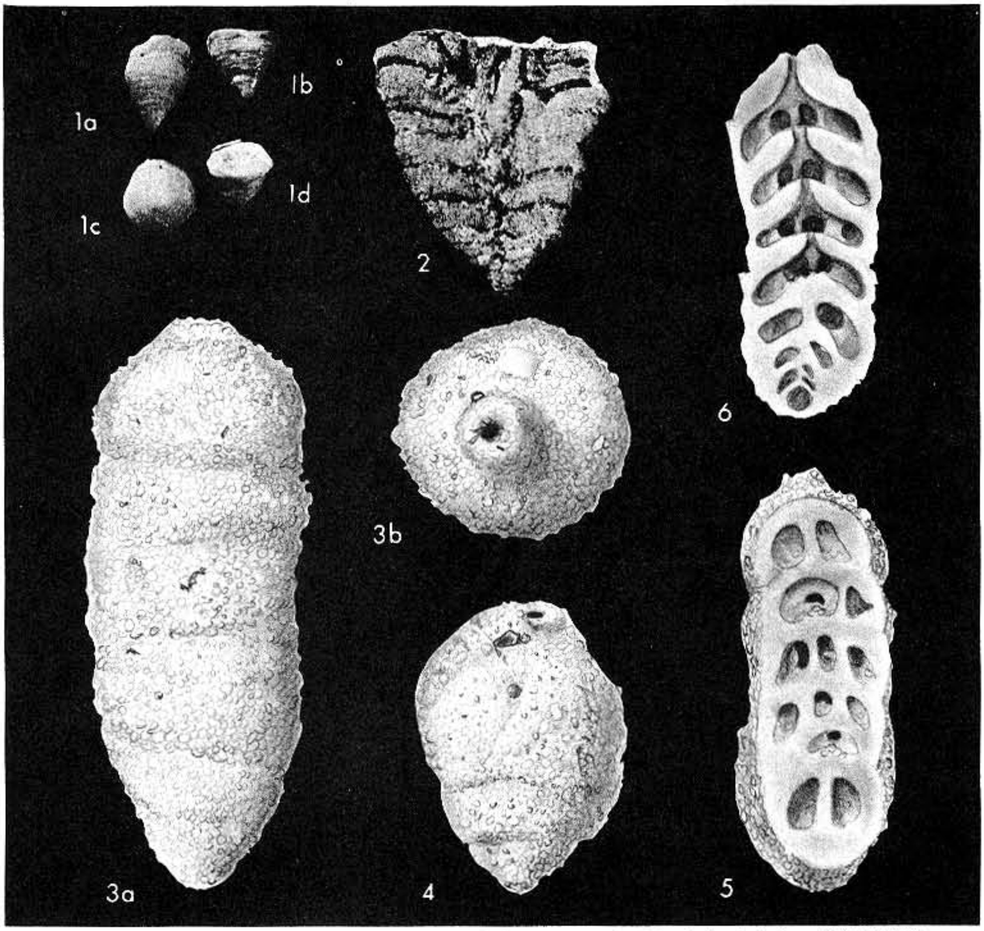


FIG. 192. Ataxophragmiidae (Ataxophragmiinae; _1,2, Camagueyia; 3-6, Cubanina_) (p. C284-C285).

aperture in a terminal depression.] _U.Cret. (Senon.)_, Eu.(Fr.-Eng.).——FIG. 193,_3-5_. _*C. subcylindrica_, Fr. (_3_), Eng. (_4,5_); _3a,b_, side, top views of holotype (P. MARIE Coll., Paris), ×20; _4,5_, horiz. and long. sectioned hypotypes, ×22 (*2117).

Cubanina PALMER, 1936, *1409, p. 123 [_*C. alavensis;_ OD]. Test elongate, early portion triserial, later uniserial, as in _Clavulina_, but with interior of chambers partially subdivided by narrow vertical partitions projecting somewhat inward from agglutinated wall; aperture terminal, rounded, somewhat produced. [_Cubanina_ differs from _Matanzia_ in the uniserial, rather than biserial, final stage.] _L.Oligo._, W.Indies(Cuba).——FIG. 192,_3-6_. _*C. alavensis; 3a,b_, side, top views of lectotype (here designated, USNM 498772); _4_, side view of juvenile paratype (USNM 498773); _5,6_, tang. and axial long. secs. of paratypes (USNM 498849, 498850) showing internal partitions, ×30 (*2117).

Cuneolina D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. 150 [_*C. pavonia_ D'ORBIGNY, 1846, *1395, p. 253; SD (SM)] [=_Cuneolinella_ CUSHMAN & BERMÚDEZ, 1941, *492, p. 101 (type, _C. lewisi_)]. Test subcylindrical to flabelliform, trochospiral in early stage, later with arcuate biserially arranged chambers, increasing rapidly in size in plane of biseriality; internal structure as in _Dicyclina;_ wall agglutinated, with considerable cement and imperforate outer layer; aperture series of rounded interiomarginal openings. _L.Cret.(Alb.)-Mio._, Eu.-N. Am.-C. Am. - SW. Asia - W. Indies(Dominican Rep.).——FIG. 193,_1_. _*C. pavonia_, U.Cret. (Cenoman.), Fr.; _1a,b_, side, edge views of topotype, ×48 (*2117).——FIG. 193,_2_. _C. lewisi_ (CUSHMAN & BERMÚDEZ), Mio., Dominican Republic; _2a-c_, side, basal, apert. views of paratype, ×7 (*2117). [See also Fig. 210.]

Dictyopsella MUNIER-CHALMAS in SCHLUMBERGER, 1900, *1660, p. 462 [_*D. kiliani;_ SD CUSHMAN, 1928, *439, p. 111]. Test trochospiral; chambers

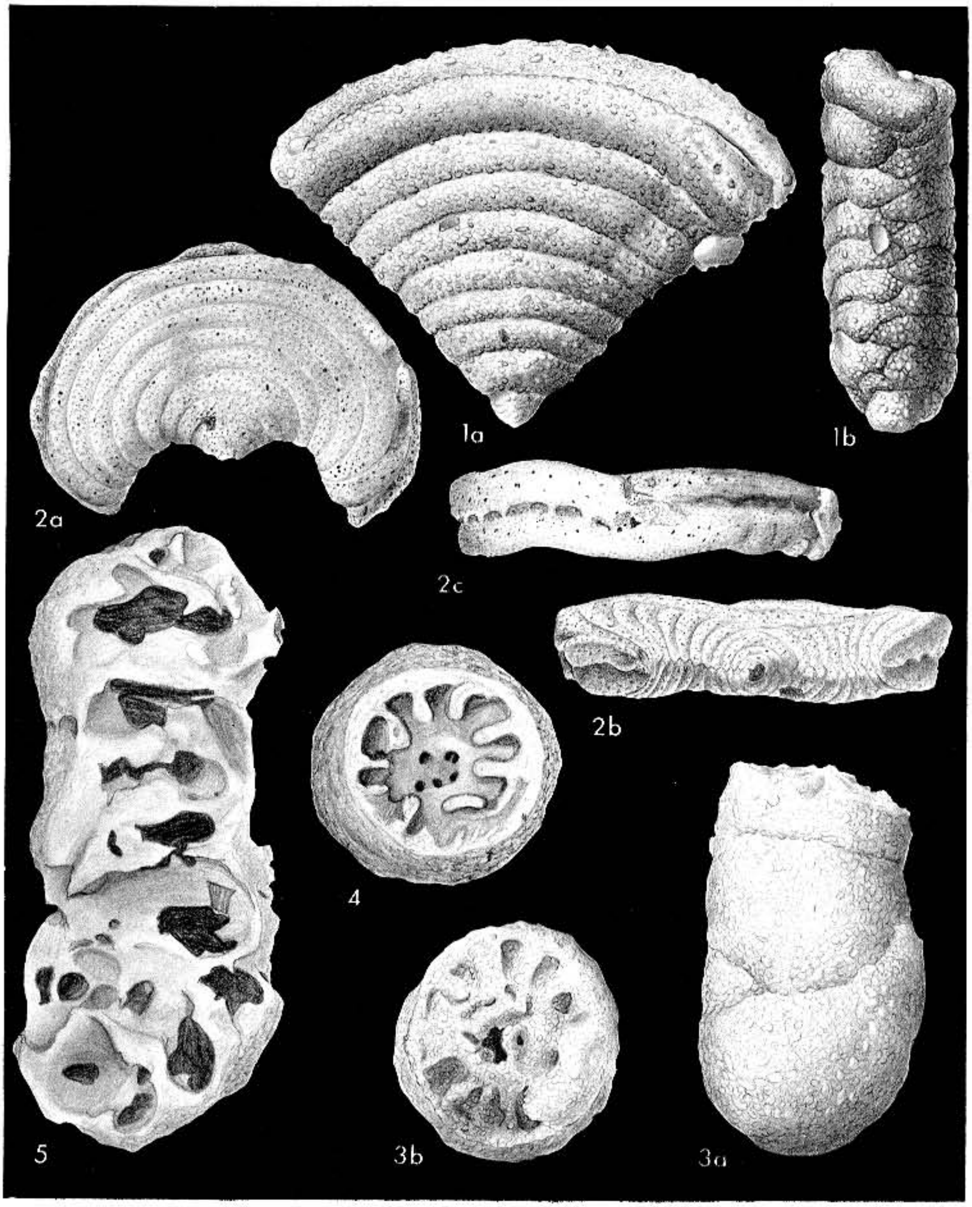


FIG. 193. Ataxophragmiidae (Ataxophragmiinae; *1,2, Cuneolina; 3-5, Coprolithina*) (p. C284-C285).

subdivided by secondary radial partitions between radial septa and partial transverse subepidermal partitions giving superficially cancellate appearance; wall largely of calcareous material, probably agglutinated calcareous particles, with some extraneous material in outer layer; aperture umbilical, interiomarginal. *U.Cret.(Cenoman.-Santon.)*, Eu.(Sp.)-Asia(Arabia).——FIG. 194,*1-3*. **D. kiliani*, Santon., Sp.; *1a-c*, opposite sides and edge of topotype, *1a*, ×33, *1b,c*, ×34 (*2117); *2,3*, long. and transv. secs., ×33 (*1660).

Hagenowina LOEBLICH & TAPPAN, 1961, *1182, p. 242 [**Valvulina quadribullata* VON HAGENOW, 1842, *858, p. 570; OD]. Test trochospiral, 3 or more chambers to whorl as in *Eggerella*, but with interior subdivided by partial radial partitions similar to those of *Ataxophragmoides* and *Orbignyna;* aperture interiomarginal slit, with indistinct tooth. *U.Cret.(U.Senon.)*, Ger.(Rügen).——FIG. 194,*4,5*. **H. quadribullata* (VON HAGENOW), topotypes (USNM, CUSHMAN Coll. 21213) previously illustrated as *Hagenowella gibbosa*, redrawn; *4a,b*,

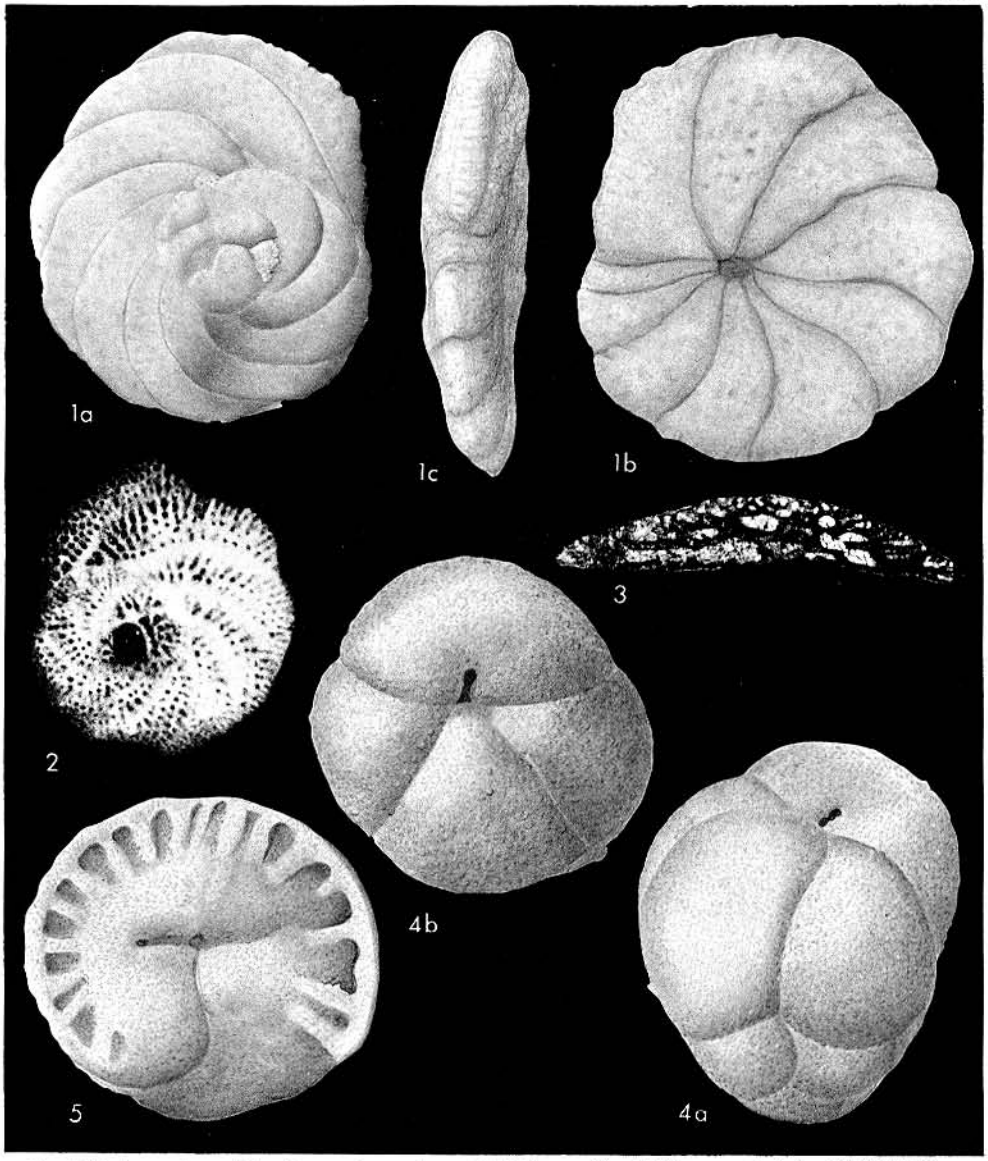


FIG. 194. Ataxophragmiidae (Ataxophragmiinae; *1-3, Dictyopsella; 4,5, Hagenowina*) (p. C285-C287).

side, apert. views; *5*, sectioned specimen showing internal partitions, ×49 (*2117).

[*Hagenowina* includes forms referred to *Hagenowella* that show internal radial partitions. The type-species of *Hagenowella* (*Valvulina gibbosa* D'ORBIGNY, 1840) has a simple interior cavity and thus is referred to *Arenobulimina*. Specimens referred to *Hagenowella gibbosa* from England and France must be checked internally to determine whether they should be placed in species of *Hagenowina* or *Arenobulimina*.]

Jarvisella BRÖNNIMANN, 1953, *229, p. 88 [**J. karamatensis*; OD]. Test trochospirally coiled in early stage, becoming triserial in adult; chambers partially subdivided by vertical infolding of walls at lower edge; wall finely agglutinated, thin; aperture interiomarginal arch with bordering lip. [*Jarvisella* is similar in general appearance to *Remesella* but is triserial rather than biserial in the adult.] *Oligo.-Mio.*, W.Indies(Trinidad).——FIG. 195,*1,2*. **J. karamatensis; 1a-d*, opposite sides, base and top of holotype, ×80 (*2117); *2*, specimen with outer wall removed to show infolding of basal portion of chamber walls, ×24 (*229).

Liebusella CUSHMAN, 1933, *458, p. 36 [**Lituola soldanii* JONES & PARKER, 1860, *998, p. 307; OD]. Test with early trochospiral portion of 4 or 5 chambers to whorl, rapidly reducing to uniserial in adult; interior of chambers subdivided by radial vertical partitions; wall coarsely agglutinated, commonly of calcareous particles; aperture terminal, slightly produced and may be irregular or multiple. [*Liebusella* differs from *Tritaxilina* in its coarse-textured, homogeneous wall, rather than distinctly perforate wall.] *Eoc.-Rec.*, Eu.-N.Am.-

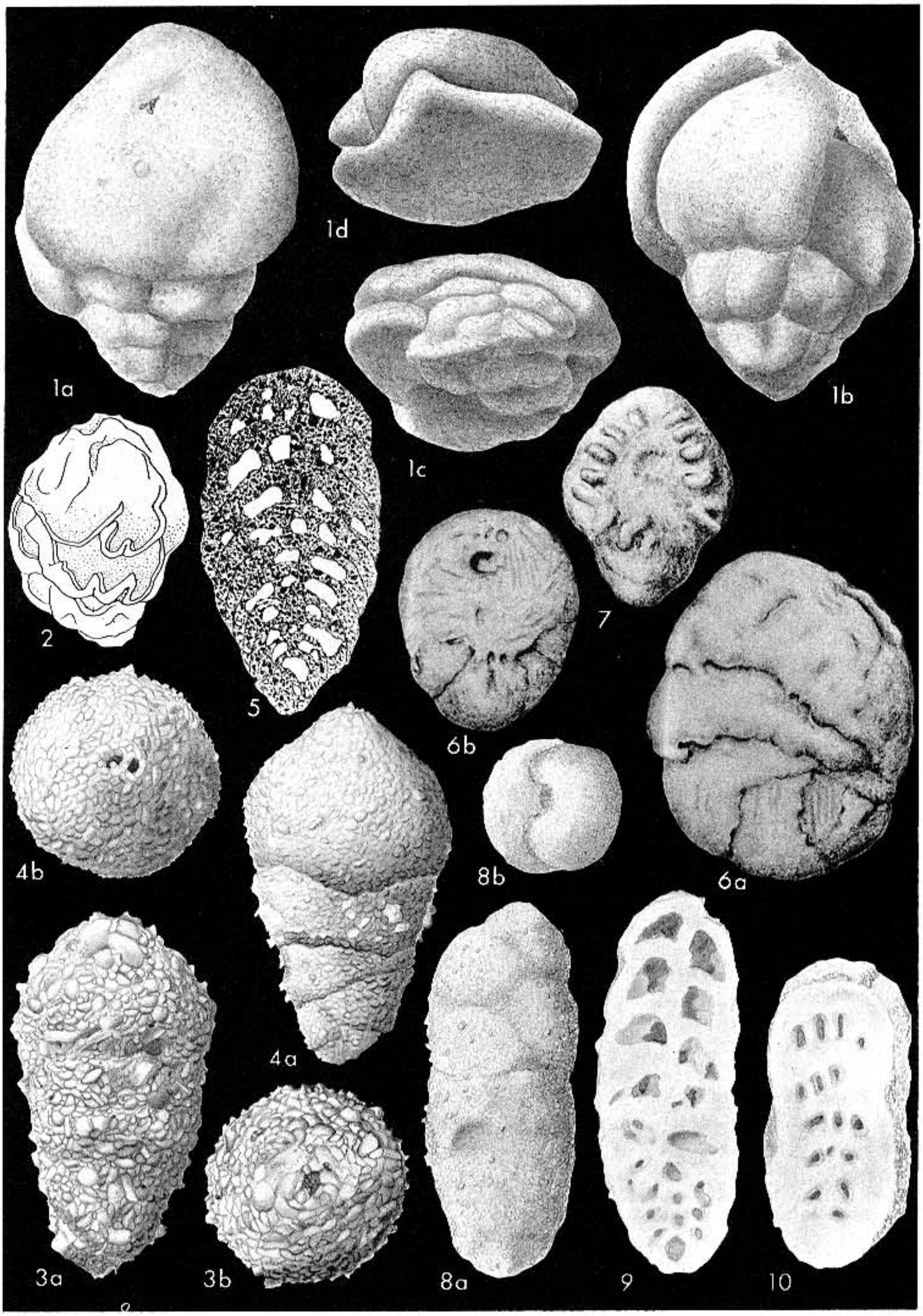


FIG. 195. Ataxophragmiidae (Ataxophragmiinae; *1,2, Jarvisella; 3-5, Liebusella; 6,7, Orbignyna; 8-10, Matanzia*) (p. C287-C290).

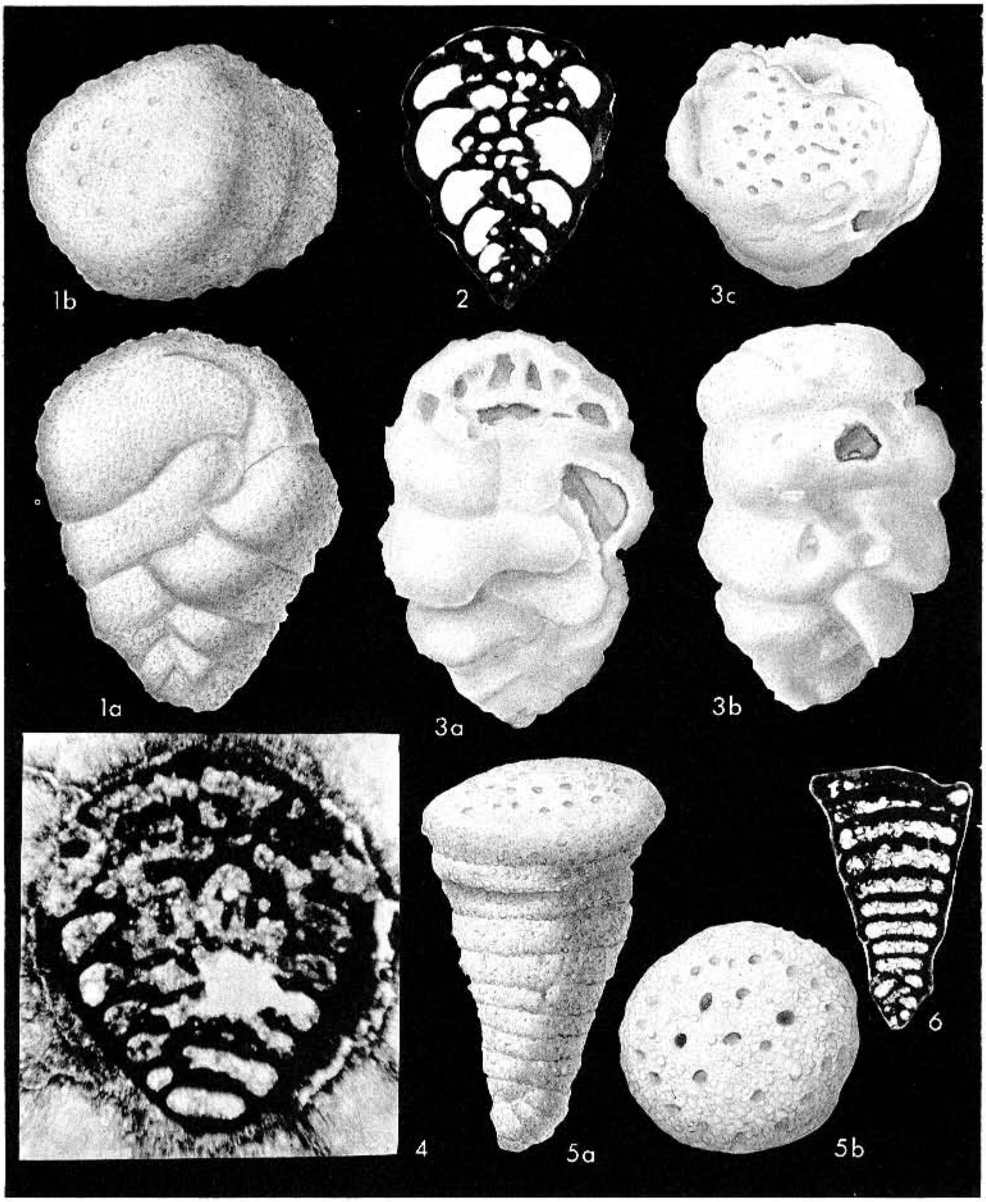


FIG. 196. Ataxophragmiidae (Ataxophragmiinae; *1-4, Pseudochrysalidina; 5,6, Pseudolituonella*) (p. *C*290).

W.Indies-Pac.O.-N.Z.-Australia. —— FIG. 195,*3-5*. **L. soldanii* (JONES & PARKER), Mio., Jamaica *(3)*, Rec., Cuba *(4)*, Rec., Carib. *(5)*; *3a,b,* side, top views of hypotype, ×23; *4a,b,* side, top views, ×23; *5,* sectioned specimen, ×10 (*2117).

Matanzia PALMER, 1936, *1409, p. 125 [**M. bermudezi;* OD]. Test trochospiral in early stages, later reducing to biserial; chambers partially subdivided internally by vertical partitions projecting inward from outer wall; wall agglutinated, of calcareous particles in considerable cement; aperture interiomarginal. *L.Oligo.-Mio.,* Carib.(Cuba)-?N.Z.——FIG. 195,*8-10*. **M. bermudezi,* L.Oligo., Cuba; *8a,b,* side, top views of lectotype (here designated, USNM 498771, specimen figured by PALMER); *9,10,* sectioned paratypes (USNM 498845, 498847), ×29 (*2117).

Orbignyna VON HAGENOW, 1842, *858, p. 573 [**O. ovata;* OD (M)] [=*Orbignyina* BRONN, 1853, *214a, p. 84 *(nom. van.)*].Early stage planispiral,

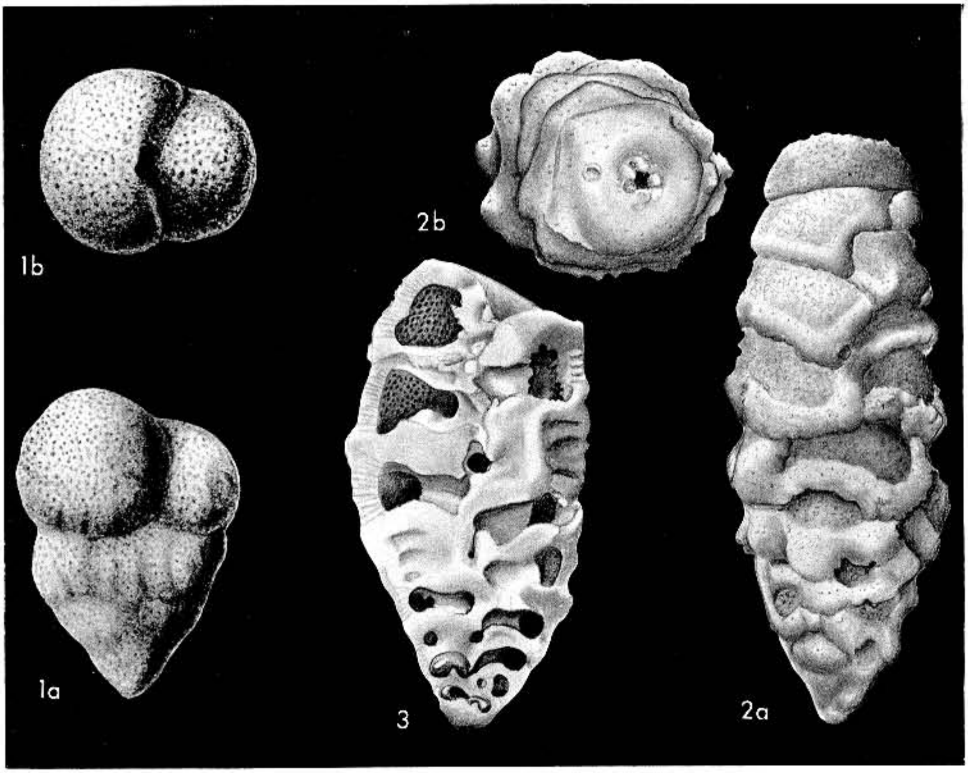


FIG. 197. Ataxophragmiidae (Ataxophragmiinae; *1, Remesella; 2,3, Tritaxilina*) (p. C290-C291).

later somewhat uncoiling, but compressed and not completely uncoiled; interior of chambers subdivided by vertical radial partitions extending inward from outer agglutinated wall, which may include calcareous particles and shell fragments; aperture interiomarginal in earliest coiled stage and rounded or irregular areal opening in adult. *U.Cret.(U.Senon.-Maastricht.),* Eu.——FIG. 195, *6,7. *O. ovata,* Maastricht., Ger.; *6a,b,* side, apert. views; *7,* eroded specimen showing internal divisions; all ×47 (*471).

Pseudochrysalidina COLE, 1941, *357, p. 35 [**P. floridana;* OD] [=*Pseudogoesella* KEIJZER, 1945, *1030, p. 190 (type, *P. cubana*); *Dukhania* HENSON, 1948, *901, p. 609 (type, *D. conica*)]. Test high trochospiral, with gradual reduction in number of chambers to whorl, later portion tending to become biserial; wall agglutinated, may be of calcareous particles; interior with vertical pillars subdividing central area of chambers; aperture interiomarginal in early stage, cribrate over terminal surface in adult. [*Pseudogoesella* was shown by BERMÚDEZ (1949, *124, p. 100) to be a synonym of *Pseudochrysalidina.*] *L.Cret.-Eoc.,* Carib.(Cuba)-USA (Fla.) - W. Indies (Dominican Rep.)-Arabia(Qatar Penin.).——FIG. 196,*1,2. *P. floridana,* M.Eoc., USA(Fla.); *1a,b,* side, top views of paratype, ×33 (*2117); *2,* long. sec. showing internal vertical pillars, ×29 (*357).——FIG. 196, *3. P. cubana,* Eoc., Cuba; *3a-c,* opposite sides and apert. view of holotype (Univ. Utrecht Coll.), ×39 (*2117).——FIG. 196,*4. P. conica* (HENSON), M.Cret., Qatar Penin.; slightly oblique sec., ×28 (*2115).

Pseudolituonella MARIE, 1955, *1220, p. 117 [**P. reicheli;* OD]. Test elongate, conical, early portion trochospiral, later uniserial, with broad low chambers; interior of chambers with sporadic hollow interseptal pillars extending from edge of circular openings at base of chambers toward apertures at opposite end of chamber; wall of agglutinated calcite, single-layered, imperforate; aperture cribrate in center of terminal face with nonperforate marginal area. [*Pseudolituonella* differs from *Lituonella* in the sporadic and rudimentary nature of the interseptal pillars and from *Minouxia* in the later uniserial stage.] *U.Cret.(U.Cenoman.),* Eu.(Fr.)-SW.Asia(Israel).——FIG. 196,*5,6. *P. reicheli,* Fr.; *5a,b,* side, top views of topotype, ×37 (*2117); *6,* axial sec. of topotype showing portions of interseptal pillars, ×29 (*1532).

Remesella VAŠÍČEK, 1947, *1981, p. 246 [**R. mariae;* OD]. Early portion triserial, later biserial as in *Gaudryina* but with incomplete secondary vertical partitions, visible as grooves at test surface; wall agglutinated, with considerable cement, surface rough; aperture interiomarginal. [Originally known only from the type-species, Eocene, *Matan-*

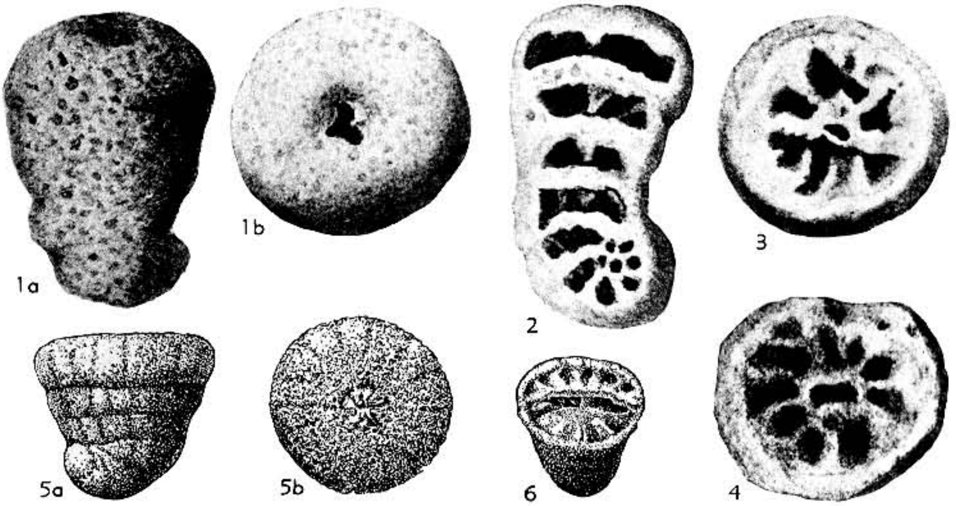


Fig. 198. Ataxophragmiidae (Ataxophragmiinae; *1-6, Voloshinovella*) (p. C291).

zia simulans Finlay, from the Whangai beds (U. Cret.) of Dannevirke area, Mangaotoro S.D., New Zealand, apparently belongs to *Remesella*.] *U. Cret.-Eoc.*, Eu.-N.Z.——Fig. 197,*1*. **R. mariae*, Eoc., Czech.; *1a,b*, side, top views of holotype, ×47 (*1981).

Tritaxilina Cushman, 1911, *404b, p. 71 [**Clavulina caperata* Brady, 1881, *196c, p. 54; OD] [=*Clavulinella* Schubert, 1921, *1694, p. 181 (obj.)]. Test free, elongate, in high trochospiral coil, early stage with up to 5 chambers in whorl, successively reduced to 4, 3, and 2 to whorl, and finally rectilinear; chambers internally subdivided; wall agglutinated, thick, with pseudochitinous lining and distinct pores in wall; aperture interiomarginal in early stages, becoming terminal and rounded in adult, with slight lip, and series of projecting teeth which partially close opening. *Eoc.-Rec.*, Pac.O.-Atl.O.-Eu.-N.Am.-C.Am.——Fig. 197,*2,3*. **T. caperata* (Brady), Rec., Philip. Is.; *2a,b*, side, top views of hypotype; *3*, sec. of hypotype, ×32 (*2117).

Voloshinovella Loeblich & Tappan, *nom. nov.*, herein [*pro Beisselina* Voloshinova & Balakhmatova in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 227 (*non* Canu, 1913)] [**Lituola aequisgranensis* Beissel, 1891, *106, p. 12; here designated as type-species]. Test similar to *Orbignyna* in early stage, but uncoiling and with rounded section in adult; wall agglutinated, with vertical radial partitions subdividing chambers; aperture terminal, irregular in outline. *U.Cret.(Senon.)*, Eu.——Fig. 198,*1-6*. **V. aequisgranensis* (Beissel); U.Senon., Ger. *(1-4)*, USSR *(5,6)*; *1a,b*, side, top views; *2*, long. sec.; *3,4*, horiz. secs. showing internal pillars, ×14 (*106); *5a,b*, side, top views; *6*, oblique view of sectioned specimen, ×23 (*1509).

Family PAVONITINIDAE
Loeblich & Tappan, 1961

[*nom. transl.* Loeblich & Tappan, herein (*ex* Pavonitininae Loeblich & Tappan, 1961, p. 283)] [=Pfenderinidae Smout & Sugden, 1962, p. 582]

Test trochospiral, at least in early stage, with 3 to many chambers to whorl, later may be reduced in number of chambers to biserial or uniserial, chambers may be subdivided by pillars or partitions; wall of agglutinated calcareous fragments or microgranular. *U.Jur.-Rec.*

Subfamily PFENDERININAE
Smout & Sugden, 1962

[*nom. transl.* Loeblich & Tappan, herein (*ex* Pfenderinidae Smout & Sugden, 1962, p. 582)]

Test trochospiral, in later stage may have reduction in number of chambers to whorl, interior subdivided by vertical or horizontal partitions, or both; wall calcareous and microgranular, or of agglutinated calcareous grains. *U.Jur-U.Cret.(Senon.)*.

Pfenderina Henson, 1948, *901, p. 609 [**Eorupertia neocomiensis* Pfender, 1938, *1452, p. 236; OD]. Test trochospiral; chambers numerous, with axial region of thickened shell material which may show irregular, reticulate texture in sections; septa more or less perpendicular to spiral axis and oblique to axis of test; wall calcareous, microgranular, imperforate; aperture consisting of numerous pores in center of apertural face, secondary intercameral foramina about equidistant from ends of chamber spaces, along central columella and appear there as spiral groove. [*Pfenderina* differs from *Kurnubia* in the absence of subepidermal

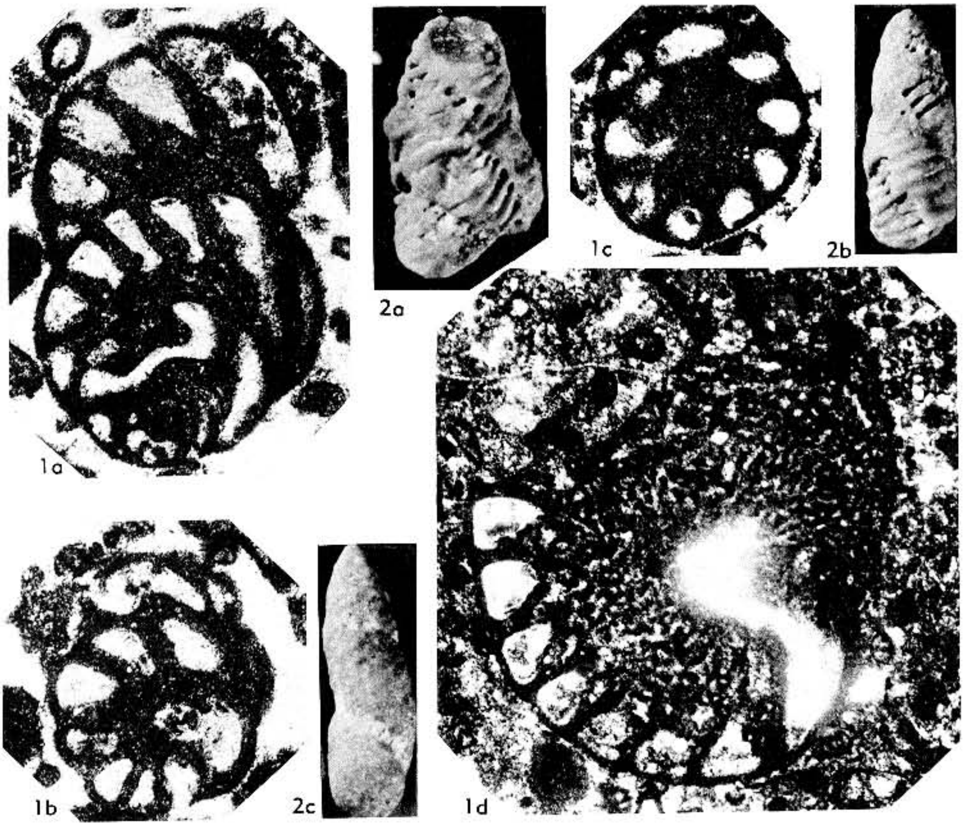


Fig. 199. Pavonitinidae (Pfenderininae; *1,2*, *Pfenderina*) (p. C291-C292).

partitions.] *U.Jur.-U.Cret.(Cenoman.)*, Eu.-SW. Asia.——Fig. 199,*1,2*. **P. neocomiensis* (Pfender), L.Cret.(Neocom.), Fr. *(1)*; M.Jur.(Bathon.), Arabia *(2)*; *1a*, subaxial sec.; *1b*, sec. through early coil; *1c*, transv. sec. showing central thickened area; *1d*, reticulate appearance of central thickened area, ×40 (*1452); *2a-c*, ext. of isolated specimens, partially decorticated, secondary foramina visible in *2a,b*, entire apert. face shown in *2c*, perforate, but without basal primary aperture, ×20 (*1807).

Accordiella Farinacci, 1962 (see p. C795).

Hensonia Marie, 1955, *1220, p. 121 [**H. tricarinata*; OD]. Test triangular and triserial, similar to *Verneuilina* but with internal plates resulting in reticular subepidermal area of chambers; wall agglutinated; aperture multiple, terminal on final chamber. *U.Cret.(Senon.)*, Eu.(Fr.).——Fig. 200, *2*. **H. tricarinata*; side view, ×50 (*1220).

Kilianina Pfender, 1933, *1449, p. 245 [**K. blancheti*; OD] [=*Lituonelloides* Henson, 1948, *902, p. 26 (type, *L. compressus*)]. Test conical in form, early chambers trochospirally arranged, later uniserial; outer portion of chambers without subepidermal partitions, central area with lamelliform interseptal buttresses, which may coalesce to form irregular partitions; wall of agglutinated calcareous particles, with some sandy material, imperforate; aperture consists of large perforations in oral face of central portion. [*Kilianina* commonly has been placed in the Orbitolinidae, but was deleted from that family by Douglass (*611, p. 260) and regarded by Smout & Sugden, 1962 (*1807), as belonging to the Tetrataxinae. Chamber arrangement, wall structure and multiple aperture suggest its present placement in the Pfenderininae.] *M.Jur.(Bathon.)-U.Cret.(Maastricht.)*, Eu.-SW.Asia.——Fig. 201, *1-4*. **K. blancheti*, M.Jur.(Bathon.), Fr.; *1*, sec. parallel to axis, ×40; *2*, same, ×35; *3*, basal sec., ×35; *4*, oblique sec. through early spiral portion, ×35 (*1449).——Fig. 201,*5*. *K. compressa* Henson, U.Cret.(Maastricht.), Qatar Penin., Arabia; subaxial sec. of paratype (BMNH P35876), ×39 (*2115).

Kurnubia Henson, 1948, *901, p. 608 [**K. palasti-*

niensis; OD]. Test elongate, with early stage trochospiral about central column, gradually becoming rectilinear, uniserial stage being more or less prominent in different species; wall probably agglutinated calcareous, outer layer imperforate, reticulate subepidermal layer formed by inter-

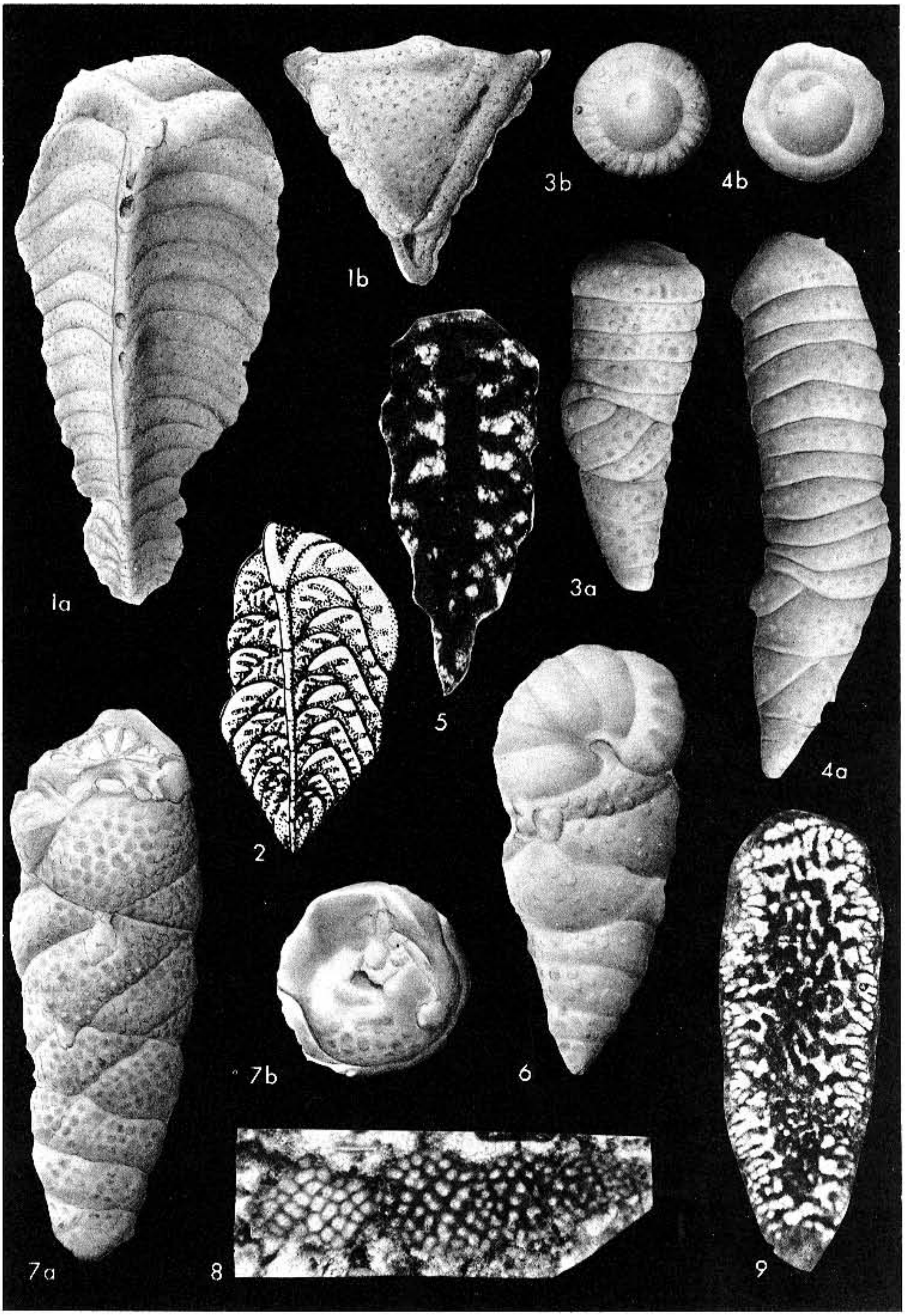


FIG. 200. Pavonitinidae (Pfenderininae; *1, Marieita; 2, Hensonia; 3-9, Kurnubia*) (p. C292-C294).

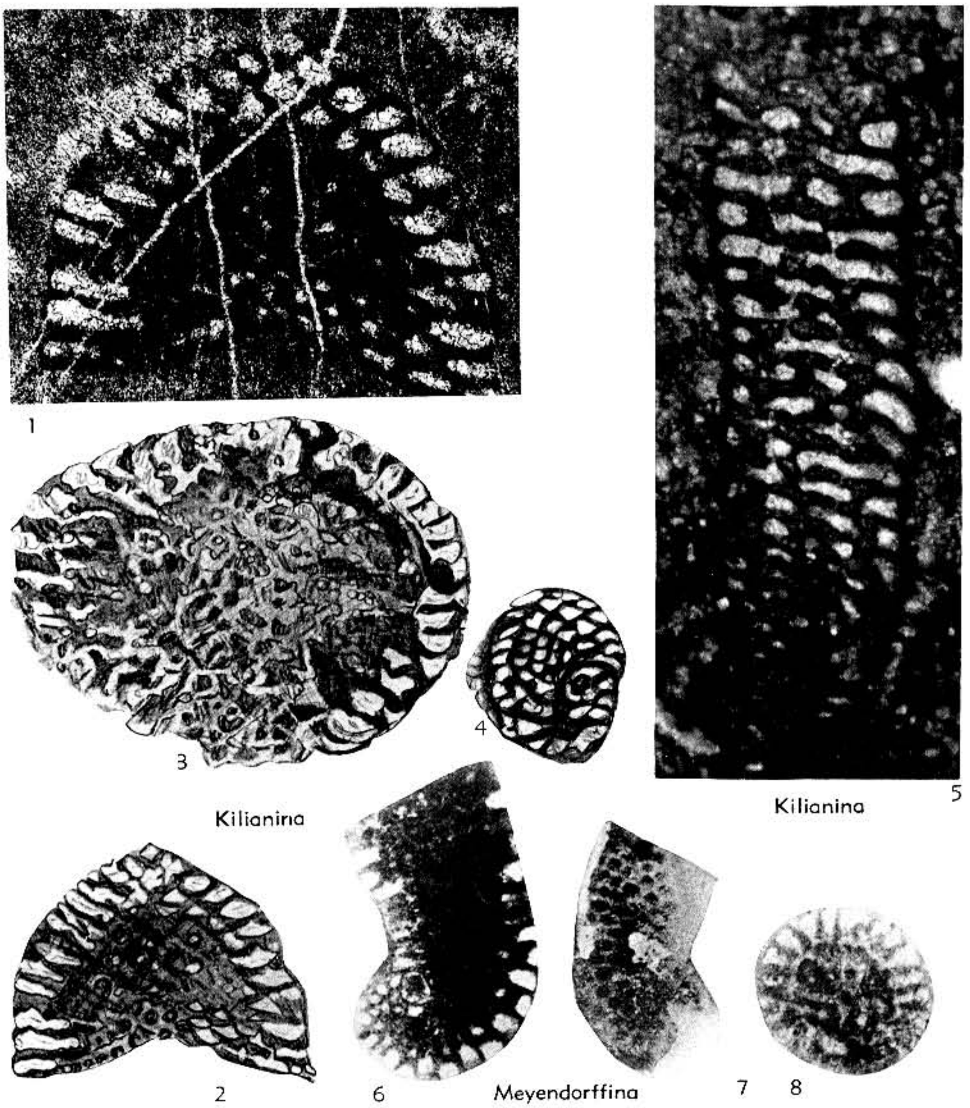


FIG. 201. Pavonitinidae (Pfenderininae; *1-5, Kilianina; 6-8, Meyendorffina*) (p. *C*292, *C*295).

secting short partitions projecting inward from outer wall; oral face convex, aperture interiomarginal in early stage, becoming terminal in later stage, probably multiple around central core but not distinct in specimens observed. [*Valvulinella jurassica* HENSON is here regarded as belonging to *Kurnubia*. It occurs with and was said to intergrade with *K. palastiniensis*, although lacking the elongate uniserial development.] *U.Jur.*, SW.Asia.——FIG. 200,*3-5*. **K. palastiniensis*, Palest.; *3a,b, 4a,b*, side and top views of paratypes, ×52 (*2117); *5*, vert. sec., ×70 (*2115).——FIG. 200,*6-9*. *K. jurassica* (HENSON), U.Jur., Palest.; *6,7a*, side views of paratypes, showing coiling and reticulate subepidermal layer of worn specimen; *7b*, top view, ×60 (*2117); *8,9*, tang. sec. showing subepidermal layer and deeper long. sec. showing internal pillars, ×36 (*2115).

Maricita LOEBLICH & TAPPAN, *nom. nov.*, herein, [*pro Reichelina* MARIE, 1955, *1220, p. 122 (*non* ERK, 1942)] [**Reichelina prismatica* MARIE, 1955, *1220, p. 123; here designated as type-species]. Test elongate, pyramidal, triangular in section, early stage probably triserial, adult with broad,

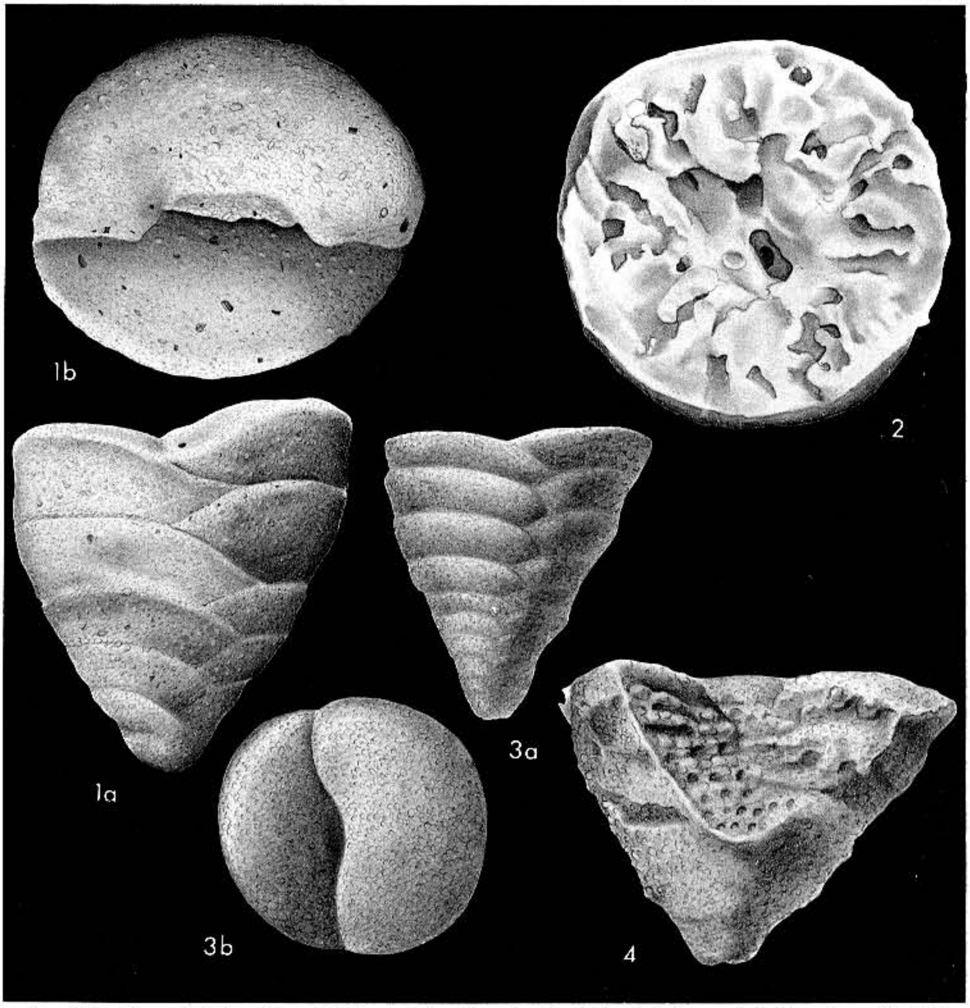


FIG. 202. Pavonitinidae (Pavonitininae; *1,2, Textulariella;* Pfendernininae; *3,4, Pseudotextulariella*) (p. *C*295, *C*299-*C*300).

low, uniserial chambers with labyrinthic interior; sutures slightly depressed, moderately arched at center of flat sides of test; wall agglutinated, with reticulate subepidermal meshwork; aperture cribrate, with small circular openings scattered over flattened terminal face of test. *U.Cret.(Senon.)*, Eu.(Fr.).——FIG. 200,*1*. **M. prismatica* (MARIE); *1a,b,* side, apert. views, ×53 (*2117).

Meyendorffina AUROUZE & BIZON, 1958, *56, p. 72 [**M. bathonica;* OD]. Test planispiral in early stage, later uncoiling and uniserial, chambers subdivided by vertical radial partitions in peripheral area, and pillars in internal zone; wall of microgranular calcite; aperture multiple, openings lying between peripheral and internal zones where they are irregularly interspersed between pillars. *Jur.(Bathon.),* Eu.(Fr.).——FIG. 201,*6-8*. **M. bathonica; 6,* long. sec. of paratype, ×50; *7,* exterior of holotype, ×30; *8,* transv. sec. of paratype, ×40 (*56).

Pseudotextulariella BARNARD in BARNARD & BANNER, 1953, *88, p. 177, 198 [**Textulariella cretosa* CUSHMAN, 1932, *454, p. 97; OD]. Test subconical, early stage triserial, later biserial; interior of chambers with vertical and horizontal partitions forming partial chamberlets; wall agglutinated; aperture interiomarginal. *U.Cret.(Cenoman.),* Eu.——FIG. 202,*3,4*. **P. cretosa* (CUSHMAN), Eng.; *3a,b,* side, top views; *4,* specimen with broken exterior to show peripheral chamberlets, all ×47 (*2117).

Subfamily PAVONITININAE
Loeblich & Tappan, 1961

[Pavonitininae LOEBLICH & TAPPAN, 1961, p. 283]

Early stage trochospiral, with 3 or more chambers to whorl, later may be biserial or uniserial, secondary septa or vertical pillars projecting downward from chamber roof. *L.Cret.-Rec.*

Pavonitina Schubert, 1914, *1692, p. 143 [**P. styriaca;* OD] [=*Pseudotriplasia* Małecki, 1954, *1210, p. 499, 509 (type, *P. elongata*)]. Test

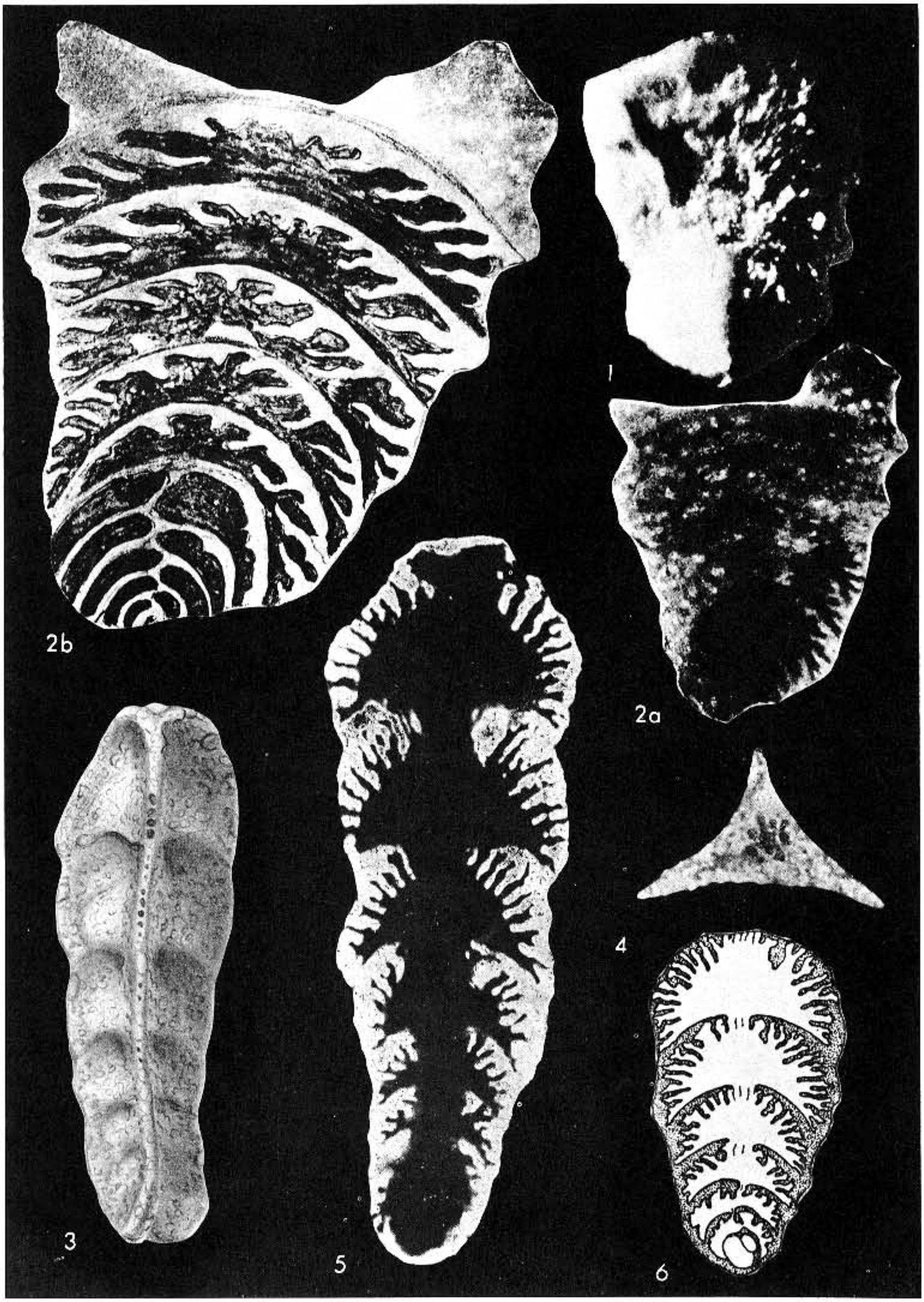


Fig. 203. Pavonitinidae (Pavonitininae; *1-6, Pavonitina*) (p. C296-C298).

elongate, early stage triserial, later uniserial, later stage compressed or may be triangular throughout; interior of chambers with irregular secondary partitions projecting inward and downward from outer agglutinated wall; aperture terminal, cribrate. *Mio.*, Eu.——Fig. 203,*1,2*. **P.*

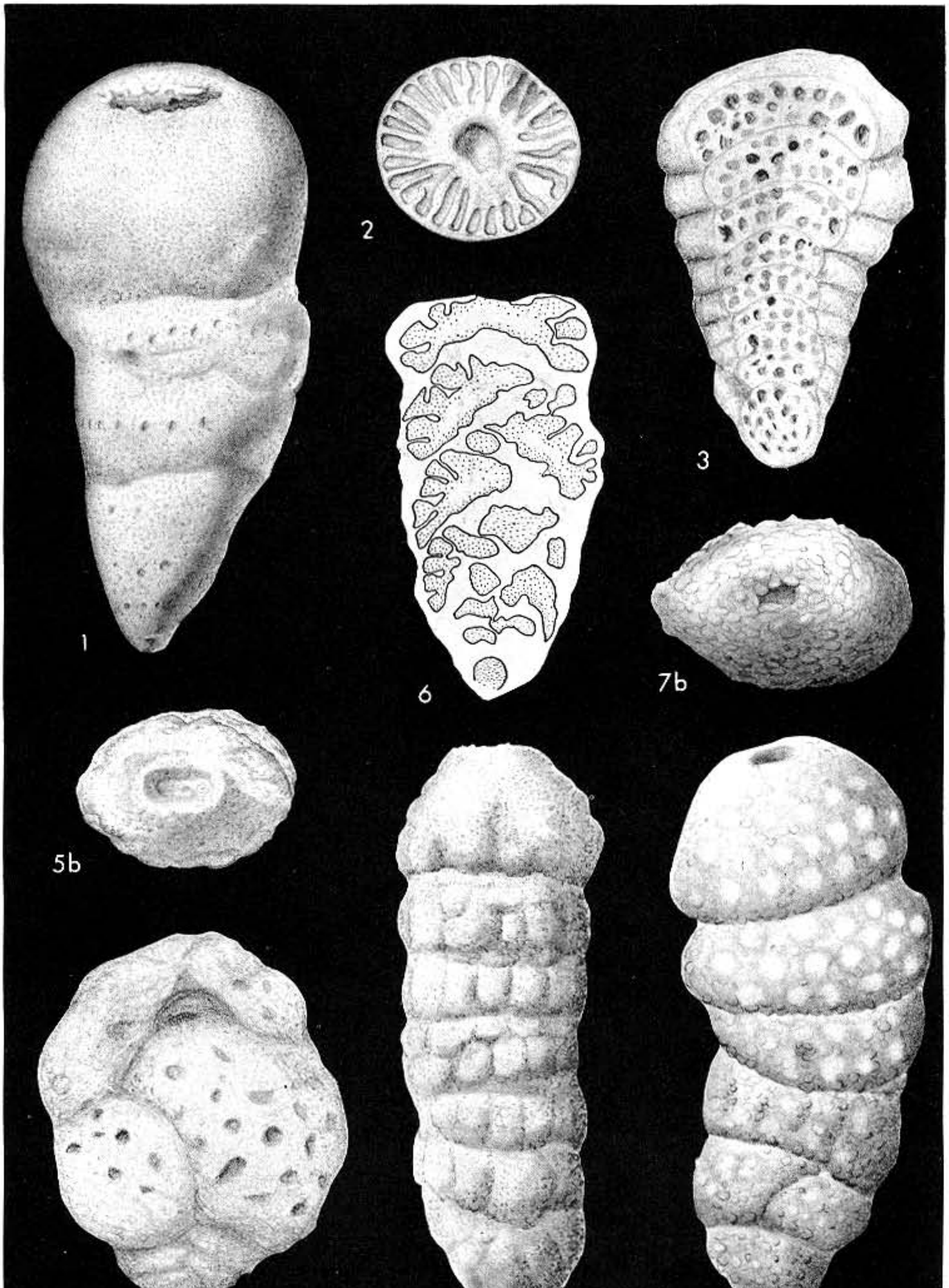


Fig. 204. Pavonitinidae (Pavonitininae; *1-3, Guppyella; 4, Alveovalvulina; 5-7, Alveovalvulinella*) (p. C298).

Fig. 205. Pavonitinidae (Pavonitininae; *Alveovalvulina*) (p. *C*298).

styriaca, Aus.; *1*, exterior, ×60; *2a*, unretouched photograph of specimen mounted in glycerin seen in transmitted light, ×70; *2b*, same specimen retouched to show chamber arrangement, ×100 (*1692).——Fig. 203,*3-6*. *P. elongata* (Małecki), Pol.; *3*, side view, ×40 (*2117); *4*, top view of another specimen; *5*, long. sec. showing partial subdivisions, ×40; *6*, same, diagram. (*1210).

[*Pavonitina* was originally described as having an agglutinated shell but was placed with the perforate calcareous *Pavonina* by Galloway (1933, *762), and not mentioned at all in other texts and treatises on foraminifers. Although Schubert described only 2 rows of chambers in the early stage (determined from specimens mounted in glycerin and seen in transmitted light) his photographic figures clearly show the early triangular stage. No sections were made. The one figure that shows distinct "biseriality" of the base is the only one that was retouched. It seems probable from the illustrations, age, and locality that *Pseudotriplasia plana* or *P. robusta* Małecki, or both, may be junior synonyms of *Pavonitina styriaca* Schubert.]

Alveovalvulina Brönnimann, 1951, *225, p. 100 [**A. suteri*; OD]. Early stage trochospiral, reducing in number of chambers in whorl to 3 or 4 in adult, chambers overlapping, outer portions subdivided by irregular horizontal and vertical plates projecting inward, resulting in alveolar or reticulate peripheral area; wall agglutinated; aperture interiomarginal. *Mio.*, W.Indies(Trinidad).——Fig. 204,*4*; 205. **A. suteri*; 204,*4*, exterior of holotype showing surface pits which reflect internal alveoli, ×72 (*2117); 205, axial sec., ×44 (*225).

Alveovalvulinella Brönnimann, 1953, *229, p. 90 [**Liebusella pozonensis* Cushman & Renz, 1941, *523, p. 9; OD]. Test elongate, early chambers trochospiral, later triserial, biserial, and finally uniserial; interior of chambers peripherally subdivided by transverse and longitudinal plates, forming alveoles, as in *Alveovalvulina;* wall agglutinated; aperture terminal, rounded in adult. [*Alveovalvulinella* differs from *Alveovalvulina* in the later uniserial stage and terminal aperture.] *Oligo-Mio.*, W. Indies(Trinidad)-S. Am.(Venez.)-Costa Rica.——Fig. 204,*5-7*. **A. pozonensis* (Cushman & Renz), Venez.; *5a,b*, side, top views of paratype, ×88 (*2117); *6*, long. sec., ×40 (*229); *7a,b*, side, top views of holotype, ×62 (*2117).

Coskinolina Stache, 1875, *1826, p. 337 [**C. liburnica*; OD (M)]. Early portion trochospiral, later conical, with vertical interseptal pillars as in *Lituonella* but marginal zone subdivided by radial partial partitions, terminal face with nonperforate marginal area; wall finely agglutinated; aperture multiple, in central area of terminal face. *L.Cret.-M.Eoc.*, Eu.-N.Am.-S.Am.-Asia.——Fig. 206,*4-6*. **C. liburnica*, M.Eoc., Istria-Dalmatia; *4a,b*, ext. views, ×7; *5*, axial section, ×16 (*1690); *6a*, part of axial sec. of topotype showing spongy or fibrous wall, ×66; *6b*, part of basal sec., ×66 (*611).——Fig. 206,*7*. *C. balsilliei* Davies, L.Eoc., Baluch.; *7a*, basal sec. showing interseptal pillars in central area and radial partitions subdividing marginal zone, ×18; *7b*, part of marginal zone, ×48 (*560).

Guppyella Brönnimann, 1951, *225, p. 98 [**Goesella miocenica* Cushman, 1936, *468, p. 33; OD]. Test elongate, early stage trochospiral, with 4 to 6 chambers in whorl, later reduced to triserial, biserial, and finally uniserial; chambers peripherally subdivided into alveolar cavities formed by vertical and horizontal partitions extending nearly to center of test; wall agglutinated; aperture interiomarginal slit in early stage, becoming terminal and ovate in uniserial stage. *Mio.*, W.Indies(Trinidad).——Fig. 204,*1-3*. **G. miocenica* (Cushman); *1*, holotype, showing exterior and terminal aperture; *2*, transv. sec. of hypotype; *3*, long. tang. sec. showing alveolar appearance, ×35 (*2117).

Lituonella Schlumberger in Schlumberger & Douvillé, 1905, *1667, p. 297, 303 [**L. roberti;* OD]. Test conical, early chambers in asymmetrical spire somewhat to one side of apex of test, later chambers broad, saucer-shaped, nearly circular in plan, with marginal ridge, sutures curved in early portion, nearly straight in uniserial portion and slightly depressed; outer wall compact, imperforate, central portion of basal surface with spongy texture and containing large perforations, each of which is bordered by hemicylindrical, pillar-like interseptal buttresses, those of outer ring of perforations with buttress external to opening, marginal area outside rows of perforations without subdivision. [The depository for types of *Lituonella roberti* was not stated originally; the lectotype and paratypes are in the Sorbonne collections, Paris.] *Eoc.*, Eu.(Fr.)-Asia (India).——Fig. 206,*1,2*. **L. roberti*, M.Eoc. (Lutet.), Fr.; *1a-c*, side, spiral, and apert. views of topotype showing asymmetrical spire and large perforations of terminal face, ×17 (*2117); *2*, axial sec., ×15 (*1780).——Fig. 206,*3*. *L. douvillei* Davies, L.Eoc., Baluch.; *3a*, horiz. sec. showing undivided outer marginal zone and interseptal buttresses in central area, ×18; *3b*, marginal portion, ×48 (*560).

Textulariella CUSHMAN, 1927, *431, p. 24 [**Textularia barrettii* JONES & PARKER, 1876, *1001, p. 99 (=*Textularia barrettii* JONES & PARKER, 1863, *1000, p. 80, *nom. nud.*); OD]. Test subconical, early stage trochospiral with 3 or more chambers in whorl, later biserial as in *Dorothia* but interior

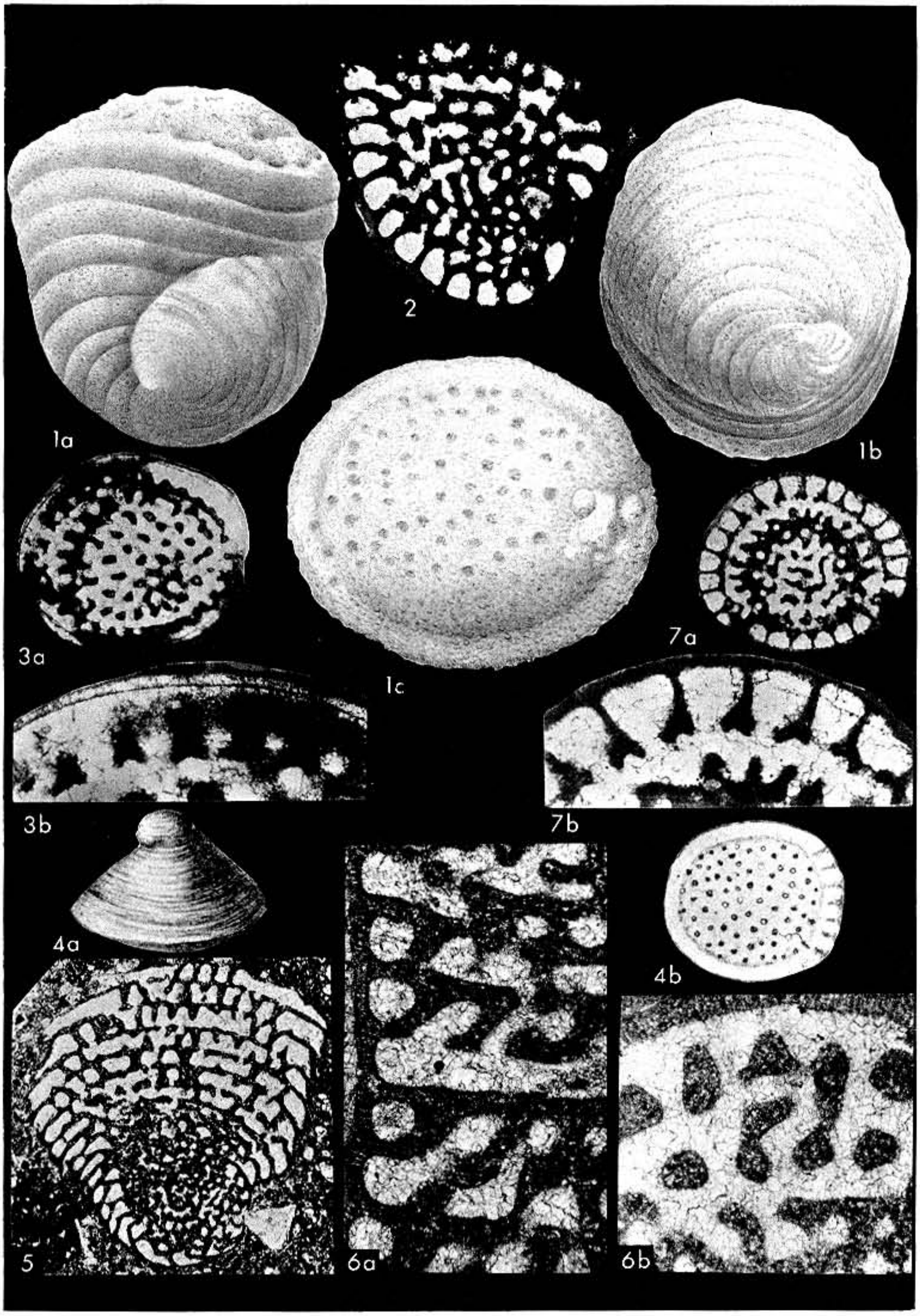


FIG. 206. Pavonitinidae (Pavonitininae; *1-3, Lituonella; 4-7, Coskinolina*) (p. C298).

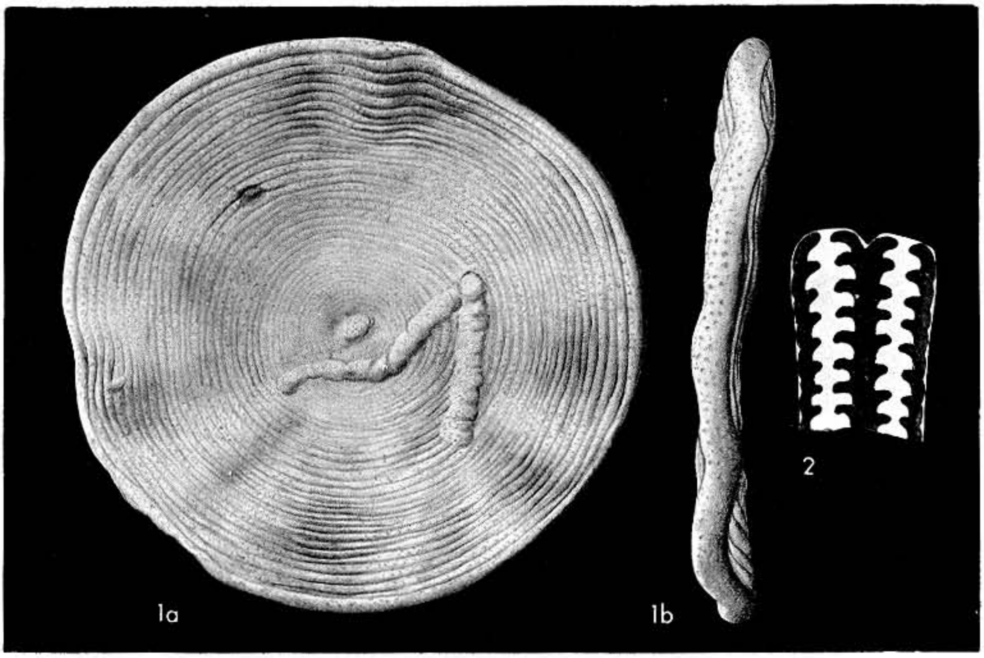


FIG. 207. Dicyclinidae (Cyclolininae; *1, Cyclolina; 2, Cyclopsinella*) (p. C301-C302).

labyrinthic; aperture low interiomarginal arch. [The original types in the British Museum (Natural History) were segregated by us. A lectotype (BMNH-ZF3635) and paratype (BMNH-ZF3636) are here designated from Recent deposits off Jamaica, West Indies, at 100-250 fathoms.] *Paleoc.-Rec.*, Carib.-N.Am.-Afr.-Eu.-Pac.-Atl.——FIG. 202,*1,2*. **T. barrettii* (JONES & PARKER), Rec., USA(Fla.); *1a,b,* side, top views; *2,* specimen broken to show interior, ×33 (*2117).

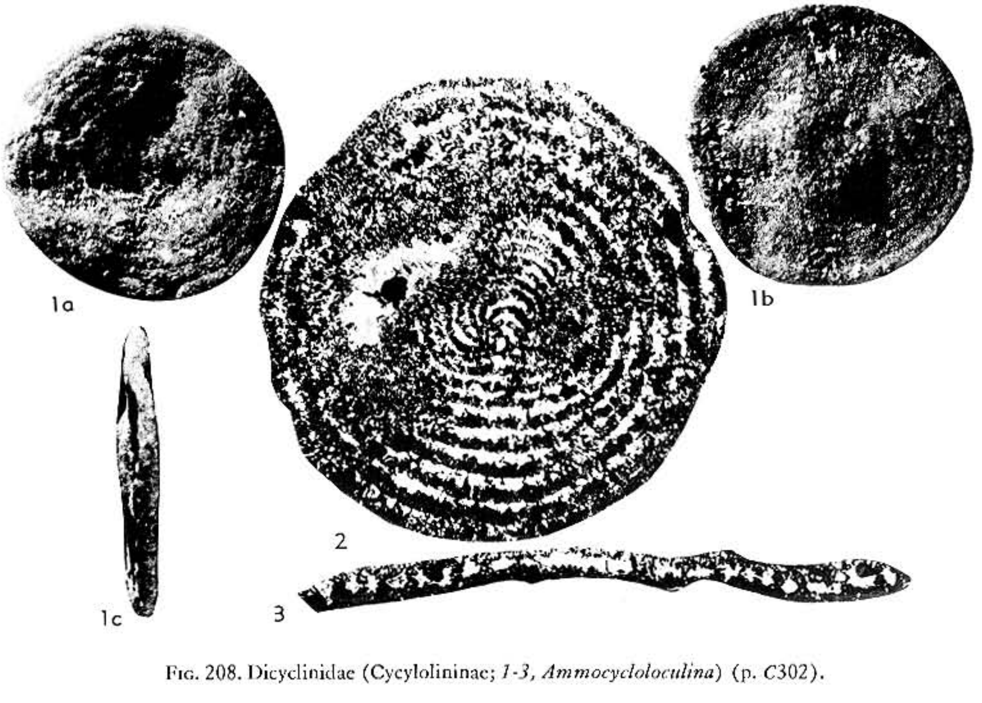


FIG. 208. Dicyclinidae (Cycylolininae; *1-3, Ammocycloloculina*) (p. C302).

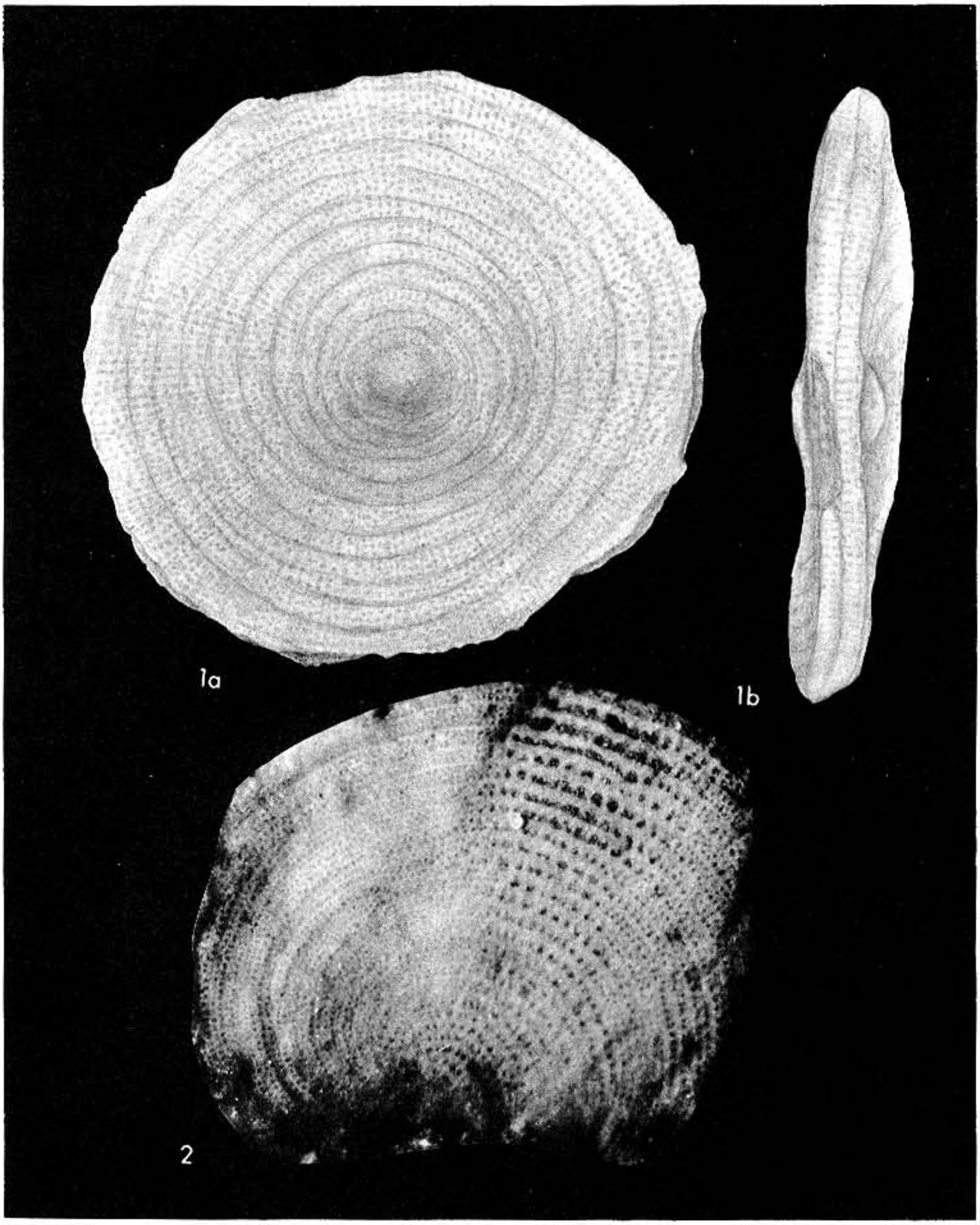


FIG. 209. Dicyclinidae (Dicyclininae; *1, Dicyclina; 2, Broeckinella*) (p. *C*303-*C*304).

Family DICYCLINIDAE
Loeblich & Tappan, n. fam.

Test free, discoidal or depressed conical, chambers cyclical; wall of finely agglutinated calcareous particles, with imperforate epidermis; aperture multiple, peripheral. *?U.Trias., Jur.-M.Eoc.*

Subfamily CYCLOLININAE
Loeblich & Tappan, n. subfam.

Cyclical chambers not subdivided by radial partitions. *L.Cret.-U.Cret.*

Cyclolina D'ORBIGNY, 1846, *1395, p. 139 [**C. cretacea;* OD (M)]. Test free, discoidal, with undivided annular chambers; wall finely agglutin-

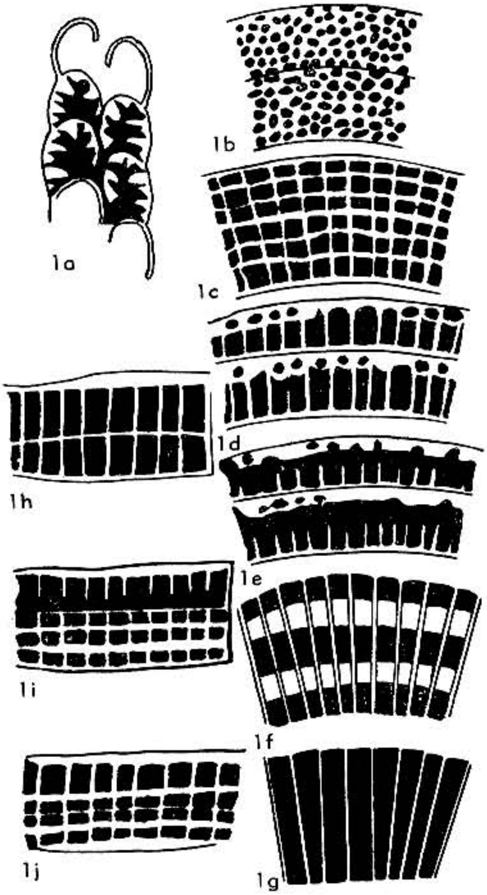


FIG. 210. Dicyclinidae (Dicyclininae; *1, Dicyclina*) (p. *C*303-*C*304).

ated; aperture multiple, with numerous pores on periphery. [The lectotype and two paratypes are in MNHN, Paris.] *U.Cret.(Cenoman.-Senon.),* Eu. ——FIG. 207,*1*. **C. cretacea,* U.Cret.(Cenoman.), Fr.; *1a,b,* side, edge views of topotype, ×17 (*2117).

Ammocycloloculina Maync, 1958, *1246, p. 53 [**Spirocyclina erratica* Joukowsky & Favre, 1913, *1004, p. 491; OD]. Test discoidal, to 15 mm. diam.; early chambers planispirally arranged in spire of about 6 chambers, later strongly embracing, with flabelliform outline, and finally cyclical; wall thick, coarsely agglutinated, with calcareous cement, thin imperforate outer layer with microgranular texture, thick walls irregularly perforated by tubular openings or interstitial spaces between foreign matter but without development of radially arranged pillars; aperture indistinct, probably consisting of peripheral pores. [Differs from the Cyclammininae and Spirocyclininae in lacking a subepidermal alveolar layer.] *L.Cret. (Infravalangin.),* Eu.(Fr.).——FIG. 208,*1-3*. **A. erratica* (Joukowsky & Favre); *1a-c,* opposite sides and edge of paratype, ×5.5; *2,3,* median and axial secs., ×11 (*1246).

Cyclopsinella Galloway, 1933, *762, p. 138 [**Cyclopsina steinmanni* Munier-Chalmas, 1887, *1325, p. xxx; OD] [=*Cyclopsina* Munier-Chalmas, 1887, *1325, p. xxx (obj.) (*non* Milne-Edwards, 1840); *Cycloclypsinella* Thalmann, 1935, *1897a, p. 734 *(nom. null.)*]. Test discoidal, with 2 layers of annular chambers separated by median partition, with intercameral pores between chambers of single layer but no communication between 2 layers; wall agglutinated. *U.Cret.(Cenoman.),* Eu.——FIG. 207,*2*. **C. steinmanni* (Munier-Chalmas), diagram. transv. sec. showing 2 layers of chambers, ×40 (*1666).

[*Cyclopsinella* was originally described as similar to 2 superposed *Cyclolina.* The original material, now in the Sorbonne, Paris, was from the Upper Cretaceous (Cenomanian) of Île Madame, France, and included a longitudinal and a transverse section. In addition, a longitudinal section is included from Les Martigues, France. All sections were poor and none have been figured.]

Subfamily DICYCLININAE
Loeblich & Tappan, n. subfam.

Chambers partially subdivided by radial transverse partitions or both into numerous small chamberlets. *?U.Trias., Jur.-M.Eoc.*

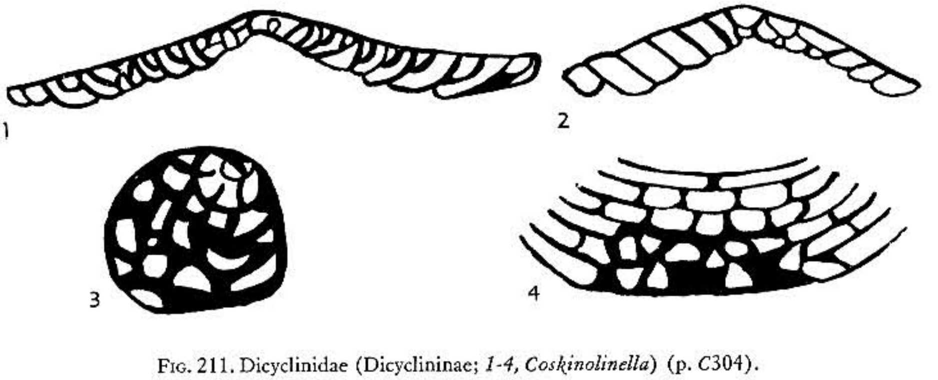


FIG. 211. Dicyclinidae (Dicyclininae; *1-4, Coskinolinella*) (p. *C*304).

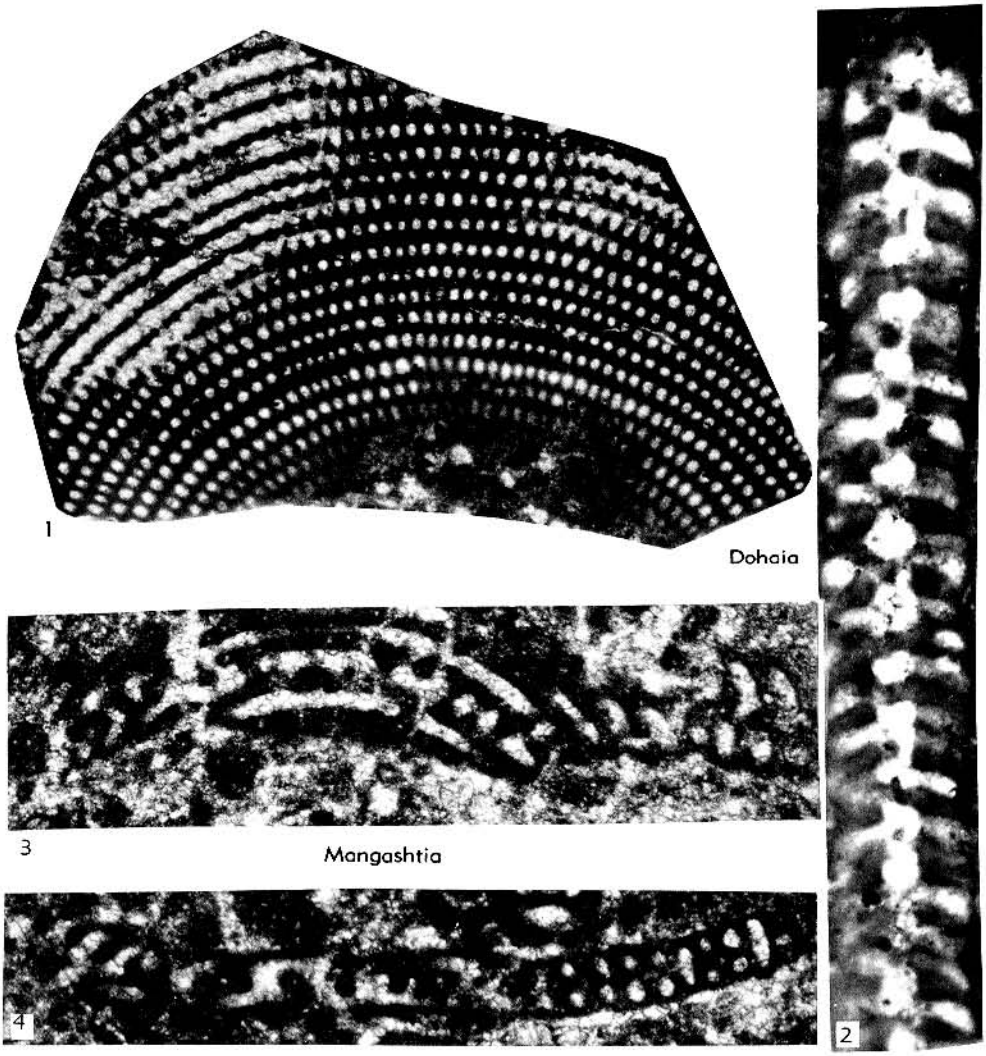


FIG. 212. Dicyclinidae (Dicyclininae; *1,2, Dohaia; 3,4, Mangashtia*) (p. *C*304-*C*307).

Dicyclina MUNIER-CHALMAS, 1887, *1325, p. xxx [**D. schlumbergeri*; OD]. Test free, flattened, discoidal, early planispiral chambers in 2 parallel layers forming raised central knob, remainder consisting of 2 layers of annular chambers which are subdivided by radial partitions into chamberlets; wall agglutinated, of calcareous fragments with imperforate epidermis, walls of the primary chambers recurved in section toward center of test, not meeting peripheral wall of preceding chamber or that of opposite layer, leaving median zone between incurved ends of opposing primary chambers; interior subdivided by numerous, thin radial partitions perpendicular to median layer and in alignment from one primary chamber to next, dividing primary chamber into rectangular chamberlets which may be resubdivided by 3 or 4 partial partitions in each chamberlet, those of same cycle communicating by means of large pore through each radial partition; aperture comprising single median row of openings in slight depression at peripheral margin. [The types of *D. schlumbergeri,* from the Cenomanian of Île Madame, France, are in the Sorbonne Collections, Paris. Four specimens on the original slide have about the same size as that refigured here, and 2 fragments would have been approximately twice as large.] *U.Cret.(Cenoman.)*, Eu.——FIG. 209,*1*. **D. schlumbergeri,* Île Madame,; *1a,b,* side, edge views of lectotype (here designated, Sorbonne

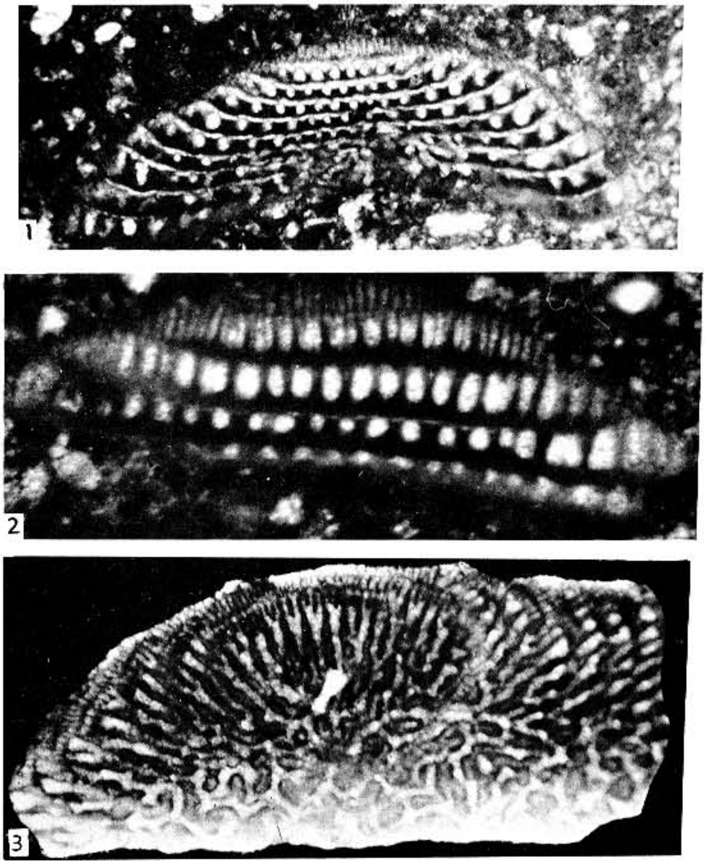


FIG. 213. Dicyclinidae (Dicyclininae; *1-3, Orbitolinella*) (p. C308).

Coll., Paris), ×33 (*2117).——FIG. 210,*1*. Internal structure of *Dicyclina* and *Cuneolina* (diagram.); *1a*, transv. sec. along radius; *1b-g*, secs. parallel to plane of development cut progressively from surface *(1b)* to median layer *(1g)*; *1h-j*, transv. secs. perpend. to radius (*901).

Broeckinella HENSON, 1948, *902, p. 92 [**B. arabica*; OD]. Test compressed, early stages planispiral, later flabelliform, tending to become cyclical; chambers arcuate, in single layer, undivided in median plane but with subepidermal transverse and parallel partial partitions, giving reticulate subepidermal layer, transverse partitions of succeeding chambers in alignment; successive chambers connected by apertures which appear on oral face as single median row of circular openings. [*Broeckinella* differs from *Broeckina* in having both parallel and transverse subepidermal plates. The genus and type-species are known from a single specimen.] *U.Cret.(Maastricht.)*, Asia (Qatar Penin., Arabia).——FIG. 209,*2*. **B. arabica*, exterior of holotype, ×30 (*2115).

Coskinolinella DELMAS & DELOFFRE, 1961, *581, p. 167 [**C. daguini*; OD]. Test free, small, low conical, early chambers indistinct, possibly trochospiral, later chambers discoidal, apparently not subdivided; septa not extending entirely to axis but leave unpartitioned open central area; wall finely agglutinated, of calcareous fragments. [The genus is known only from sections and originally was regarded as belonging to the Orbitolinidae. Because of the simple interior, it is here transferred to the Dicyclininae.] *L.Cret.(Alb.)*, Eu. (Fr.).——FIG. 211,*1-4*. **C. daguini*; *1*, transv. sec., ×42; *2*, transv. sec., ×40; *3*, tang. sec. through apex, ×60; *4*, tang. sec., ×42 (*581).

Dohaia HENSON, 1948, *902, p. 101 [**D. planata*; OD]. Test discoidal, early stage planispiral and evolute, later chambers cyclical; chambers undivided in median plane but outer portions of chambers have transverse subepidermal partitions, forming rectangular subepidermal incomplete chamberlets; wall calcareous, agglutinated; apertures numerous, in 2 rows, one at each side of

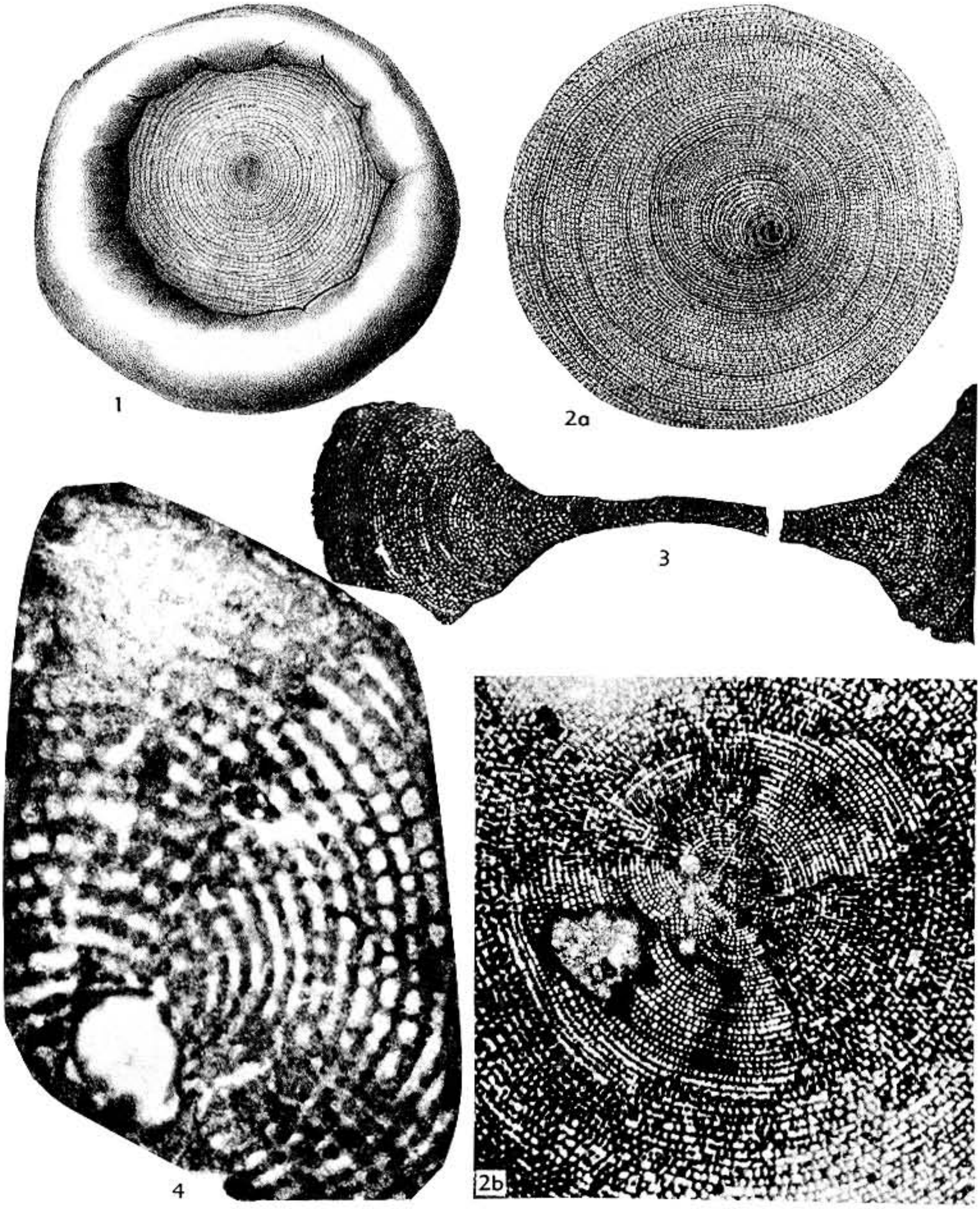


FIG. 214. Dicyclinidae (Dicyclininae; *1-4, Orbitopsella*) (p. C308).

median plane. [Differs from *Qataria* in the chamberlets alternating in position from one annulus to the next, whereas they are in radial alignment in *Qataria*.] *U.Cret.(U.Cenoman.-Turon.)*, SW. Asia.——FIG. 212,*1*,*2*. **D. planata*, Qatar Penin., Arabia; *1*, slightly oblique subequat. sec., ×30; *2*, axial sec. of paratype, ×58 (*2115).

Mangashtia HENSON, 1948, *902, p. 94 [**M. viennoti*; OD]. Test compressed, operculiform or flabelliform, early chambers spirally arranged; later stages with interseptal pillars perpendicular to septa in median plane of test, and aligned from one chamber to next; wall agglutinated, of calcareous particles in calcareous cement; aperture

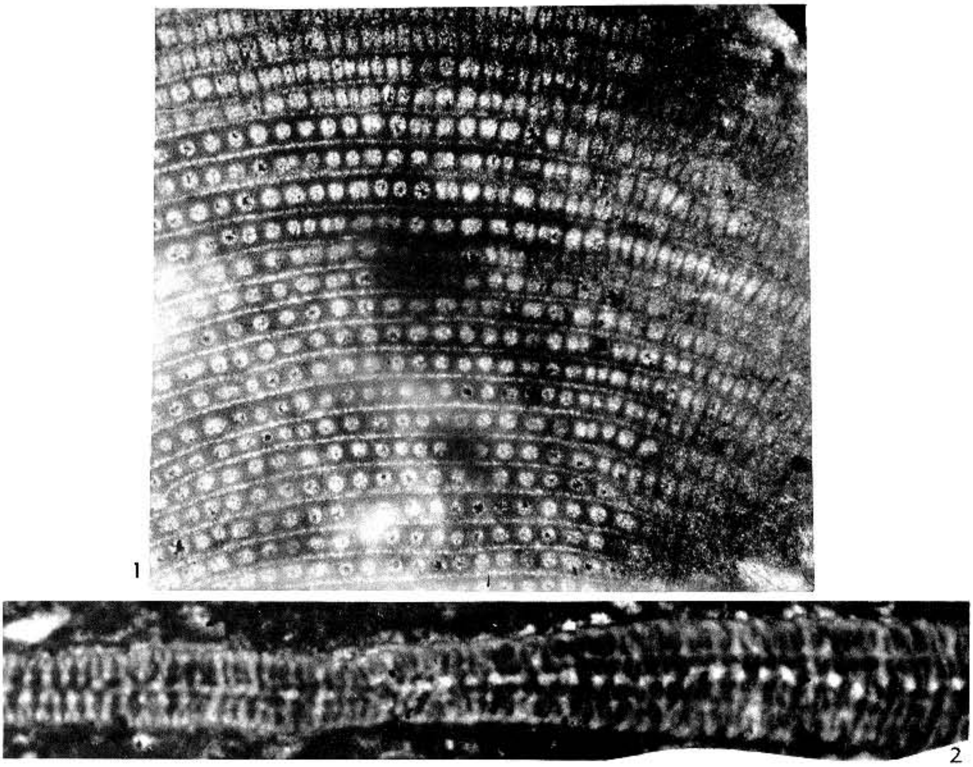


FIG. 215. Dicyclinidae (Dicyclininae; *1,2, Qataria*) (p. C308).

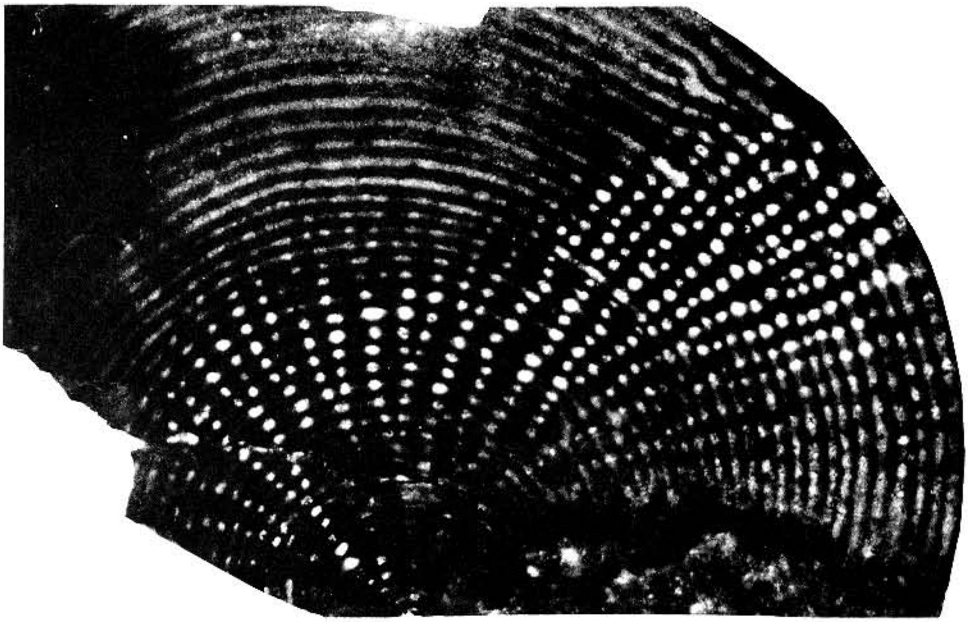


FIG. 216. Dicyclinidae (Dicyclininae; *1, Zekritia*) (p. C308).

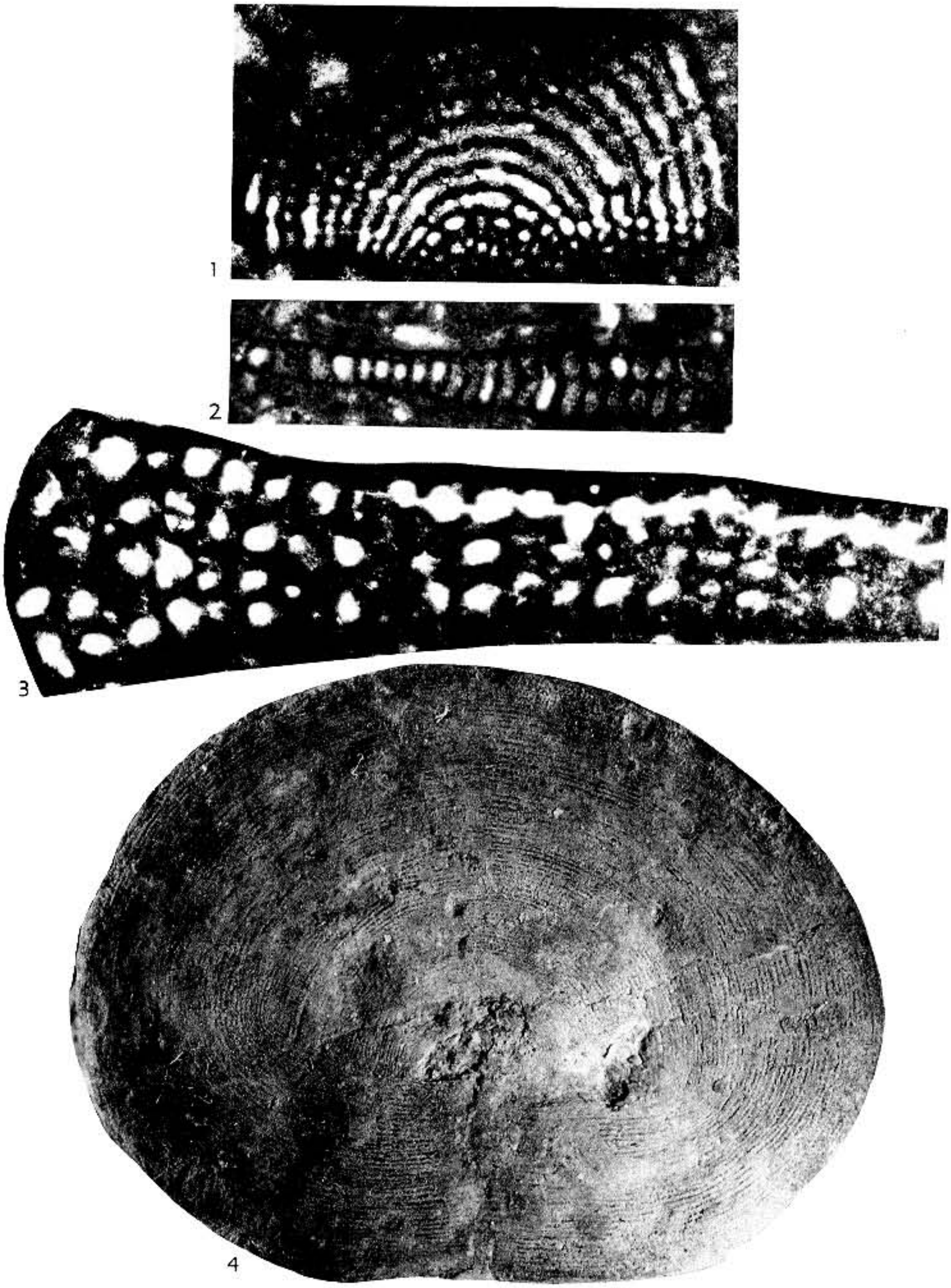


FIG. 217. Dicyclinidae (Dicyclininae; *1-4, Saudia*) (p. C308).

multiple, consisting of perforations in septa between interseptal buttresses. [This genus is known only from 12 random sections of the type-species. It differs from *Cyclolina* in the development of interseptal pillars.] *U.Cret.(Cenoman.-Turon.)*, Asia(Iran).——FIG. 212,*3,4*. **M. viennoti*, Kuh-i-Mangasht, Iran, syntypes (BMNH-P35881); *3*, subaxial sec. parallel to septum in center of sec., showing interseptal pillars and transverse to septa at ends of section, ×60; *4*, slightly oblique equat.

sec. showing irregular interseptal buttresses, apertures, and undivided chambers at each side of median plane, ×60 (*2115).

Orbitolinella Henson, 1948, *902, p. 90 [**O. depressa*; OD]. Test conical, chambers arranged as in *Orbitolina* and subdivided by numerous subepidermal partitions, perpendicular to septa and outer walls and those of succeeding chambers in alignment, partitions becoming irregular toward center of chamber, forming reticulate zone; intercameral communication by means of pores in radial and inner reticulate zones but not in marginal area; wall granular or agglutinated calcareous, with vitreous layer over oral face (possibly originally pseudochitinoid). *U.Cret.(U. Cenoman.* or *Turon.),* Asia(Qatar Penin., Arabia).——Fig. 213,*1-3*. **O. depressa; 1,* subaxial sec. of syntype, ×38; *2,* oblique tang. sec. showing more numerous partitions in outer layer (at top of figure), ×60; *3,* oblique transv. sec. of syntype intersecting 6 chambers at outer edge and showing reticulate appearance of central part, ×30 (*2115).

Orbitopsella Munier-Chalmas, 1902, *1328, p. 351 [**Orbitulites praecursor* Gümbel, 1872, *841, p. 256 (=*Orbitulites circumvulvata* Gümbel, 1872, *841, p. 259); OD] [=*Coskinolinopsis* Henson, 1948, *902, p. 27 (type, *C. primaevus*)]. Test discoidal, to 18 mm. diam., may have thickened margin; early coiled stage reduced, chambers spreading in peneropline form, followed by reniform stage and later by annular chambers, at least in microspheric form; incomplete secondary septa forming chamberlets which are regularly developed and perpendicular to spiral lamella in outer layer, but irregular and in form of pillars in deeper zone of each chamber; no true alveolar structure; circular canals aligned beneath surface may be seen in axial sections as undivided portions of circular chamber occurring between outer reticulate zone and inner regularly pillared zone; aperture consisting of irregularly distributed openings on peripheral margin. *?U.Trias., L.Jur.,* Eu.-SW.Asia.——Fig. 214,*1-3*. **O. praecursor* (Gümbel), L.Jur.(Lias.), Roveredo Tyrol Alps; *1,* ext. (as *O. circumvulvata*), ×10 (*841); *2a,* equat. sec., ×10 (*841); *2b,* central portion of equat. sec., ×14 (*788); *3,* axial sec., ×9 (*788).——Fig. 214,*4*. *O. primaeva* (Henson), U.Trias. or L.Jur., SW.Asia(Oman); probably megalospheric syntype (BMNH P35788), ×60 (*2115).

Qataria Henson, 1948, *902, p. 98 [**Q. dukhani*; OD]. Test discoidal, early stage planispiral; later chambers cyclical; outer margins of chambers subdivided by numerous parallel and transverse subepidermal partitions; lateral chamberlets in radial rows from center to periphery; aperture multiple; small perforations in outer wall in rows corresponding to opposing pairs of lateral chamberlets. *U.Cret. (U. Cenoman.* or *Turon.),* Asia(Qatar Penin., Arabia).——Fig. 215,*1,2*. **Q. dukhani; 1,* fragment of superficial sec., parallel to equatorial plane, ×67; *2,* subaxial sec. of paratype showing lateral chamberlets, ×59 (*2115).

Saudia Henson, 1948, *902, p. 97 [**S. discoidea;* OD]. Test discoidal, early stage with spiral development probably not subdivided, later flabelliform with arcuate uniserial stage, followed by cyclical chambers with margins partially divided by secondary transverse and parallel subepidermal partitions, projecting inward from outer wall, radial interseptal pillars also occurring in median plane in later, thicker parts of test, pillars being aligned from one cycle to next; interseptal communication by means of apertures between interseptal pillars. *Paleoc.-M.Eoc.,* SW.Asia.——Fig. 217,*1-3*. **S. discoidea,* M.Eoc.(Lutet.), Ansab, between Iraq and Saudi Arabia; *1,* young megalospheric flabelliform paratype, ×40; *2,* subaxial sec. through early stage of paratype showing interseptal pillars in outer zone, ×40; *3,* subaxial sec. of paratype showing numerous pillars, ×37 (*2115).——Fig. 217,*4*. *S. labyrinthica* Grimsdale, Paleoc., N.Iraq; ext., ×5 (*2115).

Zekritia Henson, 1948, *902, p. 95 [**Z. langhami;* OD]. Test compressed, flabelliform; chambers of early stages probably evolute planispiral, later uniserial and arcuate, chambers in 2 layers partially subdivided by interseptal partitions and pillars in median plane; wall calcareous, agglutinated; aperture cribrate in rows at either side of median partition, with intercameral connections between chambers of 2 layers. [*Zekritia* differs from *Cyclopsinella* in having connections between the 2 layers of chambers. The type-species is known from a single sectioned specimen.] *U.Cret. (?Turon.),* Asia(Qatar Penin., Arabia).——Fig. 216. **Z. langhami,* slightly oblique sec. of holotype, ×39 (*2115).

ORBITOLINIDAE

By R. C. Douglass,[1] A. R. Loeblich, Jr.,[2] and Helen Tappan[3]

[[1]United States Geological Survey, [2]California Research Corporation, [3]University of California at Los Angeles]

Family ORBITOLINIDAE Martin, 1890

[Orbitolinidae Martin, 1890, p. 226] [=subfamily Orbitolininae Cushman in Eastman, 1913, p. 27; =family Arorbitolidia Rhumbler, 1913, p. 342 *(nom. van.)*; =family Orbitolinida Copeland, 1956, p. 186 *(nom. van.)*]

Relatively large conical shells varying from high cone with pointed apex to broad shield or disc. Test with single series of shallow cuplike chambers that increase in diameter more or less regularly, initial chambers of some tests developed in spiral form at angle to adult portion of test; chambers divided by vertical and, in some genera,

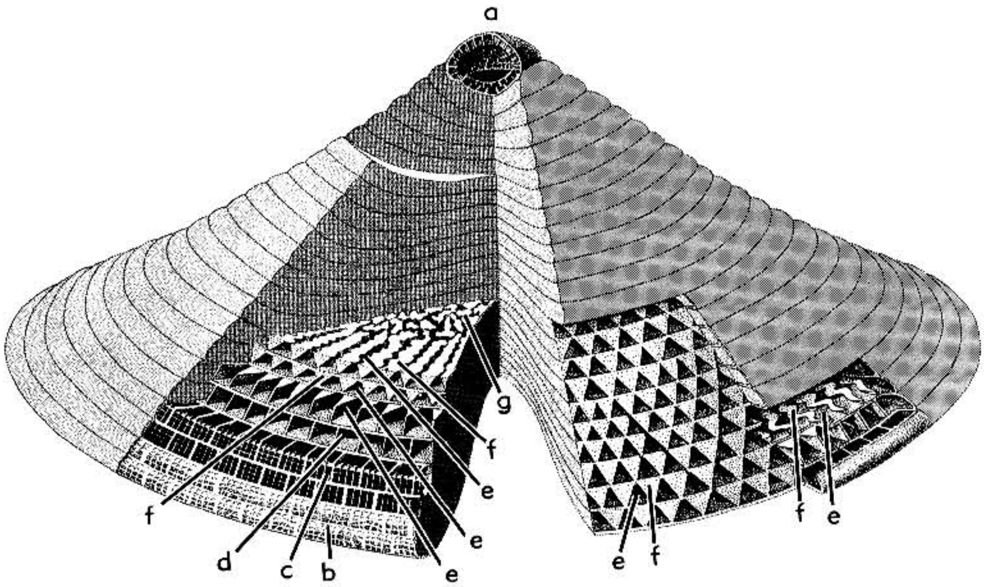


FIG. 218. Orbitolinidae. Reconstruction of *Orbitolina* with parts cut away to show internal structures. [Explanation: *a*, megalospheric embryonic apparatus; *b*, slightly abraded surface showing cellules; *c*, marginal zone beneath cut-away surface; *d*, inframarginal zone exposing chamberlets; *e*, radial passages between chambers; *f*, slightly zigzag main radial partitions showing triangular cross section; *g*, central complex] (*611).

horizontal plates, with central area divided by either vertical partitions or pillars, or combination of both (Fig. 218, 219); communication between chambers by septal or apertural pores. Test wall of 2 parts, outer layer forming dorsal surface of test and continuing as ventral surface of each septum, inner layer continuous with partitions or pillars and plates; inner layer, at least, agglutinate and may contain abundant grains of detrital material. [The family lived in shallow, warm marine waters in a circumglobal northern equatorial belt.] *L.Cret.-Eoc.*

Orbitolina D'ORBIGNY, 1850, *1397b, p. 143 [**Orbulites lenticulata* LAMARCK, 1816, *1088, p. 197 (=*Madreporites lenticularis* BLUMENBACH, 1805, *150b, p. lxxx); OD (M)] [=*Orbitulina* BRONN in BRONN & ROEMER, 1853, *214a, p. 93 (obj.) *(nom. van.)*; *Orbitolinopsis* SILVESTRI, 1932, *1787A, p. 160 *(nom. nud.)*; *Orbitolinopsis* HENSON, 1948, *902, p. 67 (type, *Orbitolina? kiliani* PREVER in SILVESTRI, 1932, *1787A, p. 159); *Orbitolinoides* VAUGHAN, 1945, *1995, p. 22 (type, *O. senni*); *Birbalina* SAHNI & SASTRI, 1957, *1612, p. 28 (type, *B. pulchra*); *Abrardia* NEUMANN & DAMOTTE, 1960, *1353, p. 60 (type, *Dictyoconus mosae* HOFKER, 1955, *944, p. 115); *Orbitolina (Mesorbitolina)* SCHRÖDER, 1962, *1676A, p. 181 (type, *Orbitulites texanus* ROEMER, 1852, *1580A, p. 86)]. Test to 30 mm. diam.; main partitions zigzag, continuous through marginal and radial zones, thickened in upper portion of chambers; partitional pores prominent in some species, tending to interrupt partitions to form pillar-like structures in central area; marginal zone divided by partitions and one or more series of vertical and horizontal plates. *L.Cret.(Barrem.) - U.Cret. (Maastricht.)*, equat. region, cosmop.——FIG. 220, *1-4*. **O. lenticularis* (BLUMENBACH), L.Cret. (Apt.), Fr.; *1,2*, dorsal, ventral sides of topotypes,

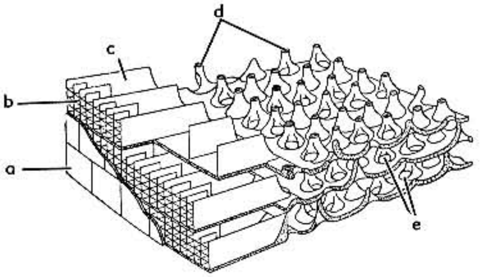


FIG. 219. Orbitolinidae. Reconstruction of a small portion of the test of *Dictyoconus* near its base with parts cut away to show internal structure. [Explanation: *a*, outer surface indicating placement of septa and main partitions; *b*, cellules; *c*, chamberlets; *d*, pillars partially encircling apertural pores; *e*, apertural pores] (*562).

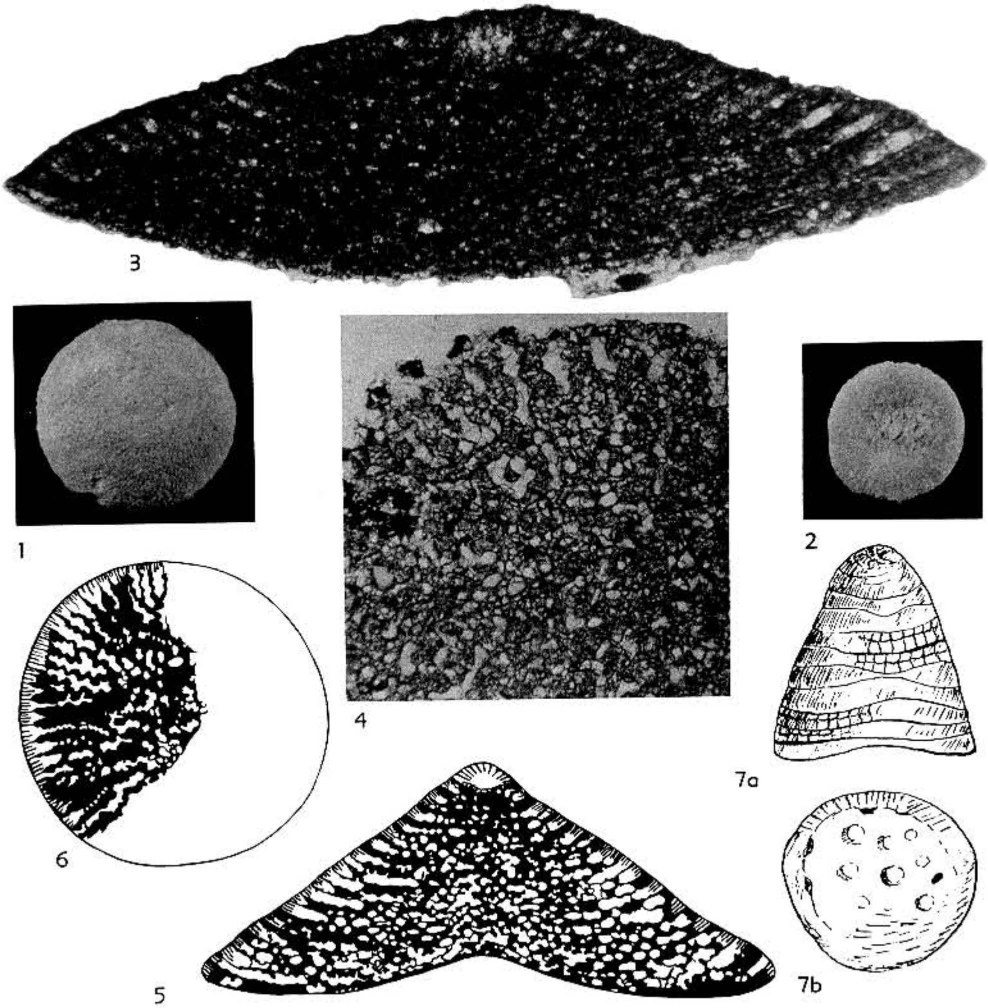


FIG. 220. Orbitolinidae; *1-7, Orbitolina* (p. C309-C310).

×6.6; *3,* slightly oblique axial sec., ×20; *4,* portion of basal sec., ×50 (*2114).——FIG. 220,*5,6*. *O. texana* (ROEMER), L.Cret.(Alb.), USA(Tex.); ×20 (*611).——FIG. 220,*7*. *O. mosae* (HOFKER), U.Cret.(Maastricht.), Fr.; *7a,b,* side and basal views, approx. ×33 (*1353).

Coskinolinoides KEIJZER, 1942, *1029, p. 1016 [**C. texanus* (=*Coskinolina adkinsi* BARKER, 1944, *83, p. 206); OD]. Test minute, about 0.5 mm. diam.; main partitions simple planes extending from marginal zone to central area; marginal zone divided by main partitions and 1 or 2 sets of vertical plates only. *L.Cret.,* N.Am.-S.Am.——FIG. 221,*1-3*. **C. texanus,* Alb., USA(Tex.); *1,2,* basal and axial secs., ×66 (*2114); *3a,b,* side, basal views of exterior, ×50 (*2117).

Dictyoconus BLANCKENHORN, 1900, *146, p. 432 (*nom. conserv.,* ICZN, Op. 585) [**Patellina egyptiensis* CHAPMAN, 1900, *316, p. 11 (=*P. aegyptiensis* CHAPMAN, 1900, *nom. reject.,* ICZN, Op. 585); SD WOODRING, 1924, *2078, p. 608] [=*Dictyoconos* BLANCKENHORN, 1900, *146, p. 434 *(nom. reject.,* ICZN, Op. 585); *Cushmania* SILVESTRI, 1925, *1780, p. 52 (type, *Conulites americana* CUSHMAN, 1919, *414, p. 43); *Fallotella* MANGIN, 1954, *1212, p. 209 (type, *F. alavensis*)]. Test to about 7 mm. diam.; central area with interseptal pillars, separated slightly from marginal zone by marginal ridge in many species; marginal zone divided by partitions and may have one or more series of vertical and horizontal plates. *L.Cret.-U.Eoc.,* cosmop.——FIG. 221,*4*. **D.*

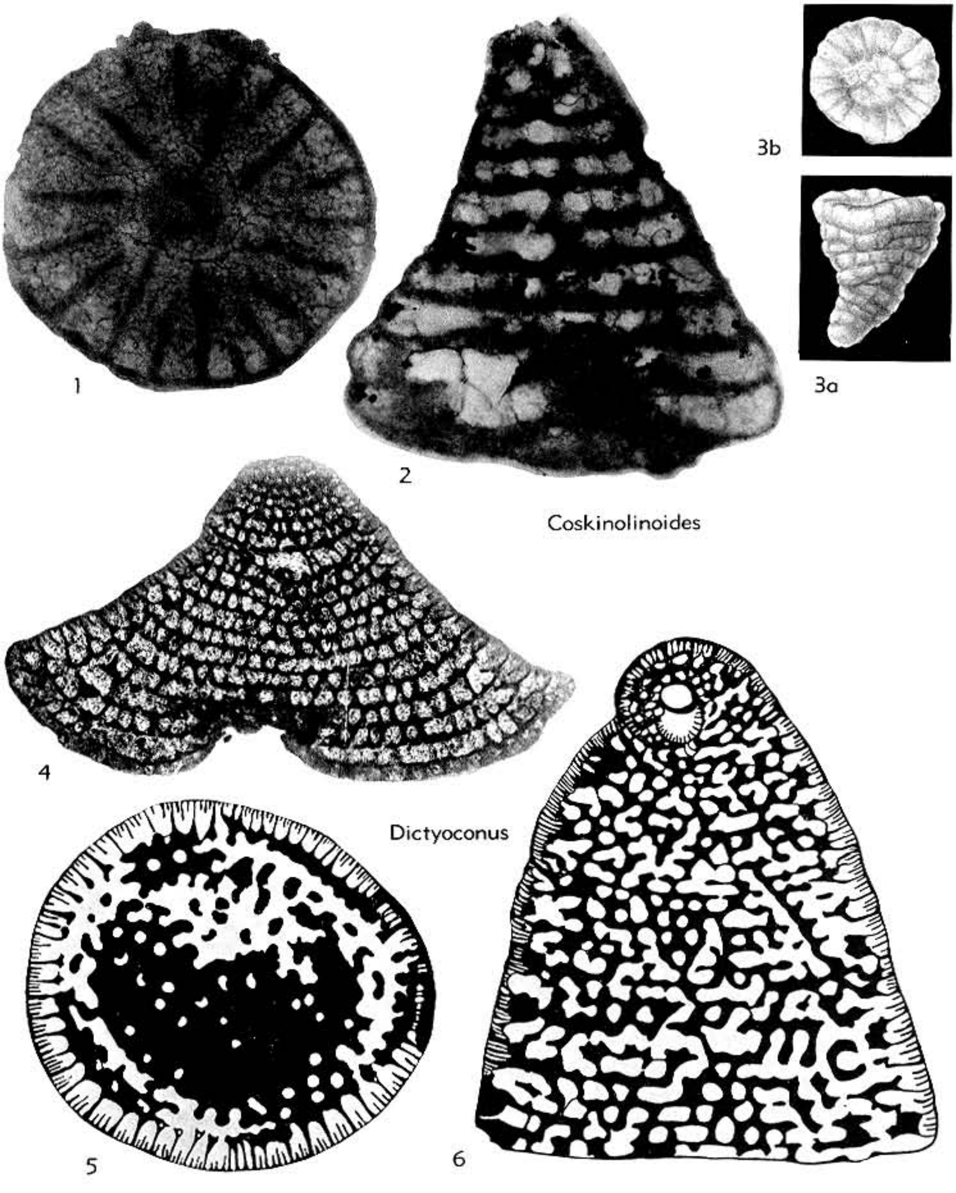


FIG. 221. Orbitolinidae; *1-3, Coskinolinoides; 4-6, Dictyoconus* (p. C310-C311).

egyptiensis (CHAPMAN), Eoc.(Lutet.), SW.Asia (Egypt); axial sec., ×10 (*1781).——FIG. 221, *5,6. D. indicus* DAVIES, L.Eoc., Baluch.; basal and axial secs., ×20 (*611).

Iraqia HENSON, 1948, *902, p. 69 [**I. simplex*; OD] [=*Dictyoconella* HENSON, 1948, *902, p. 24 (type, *D. complanata*)]. Test less than 2 mm. diam.; main partitions reticulate in central area; marginal zone divided by main partitions and may have one or more series of vertical and horizontal plates. *L.Cret.(Apt.-Alb.)-U.Cret. (Cenoman.-Maastricht.)*, Eu.-SC.Asia.——FIG. 222, *1-3. *I. simplex*, L.Cret.(Apt.), Iraq; *1a,b*, side and basal views, ×40 (*2117); *2*, axial sec.; *3*, horiz. sec., ×33 (*2115).——FIG. 222,*4-7. I. complanata* (HENSON), U.Cret.(Maastricht.), Arabia; *4*, side view of holotype, ×22 (*2117); *5*, oblique sec. of paratype nearly paralleling plane

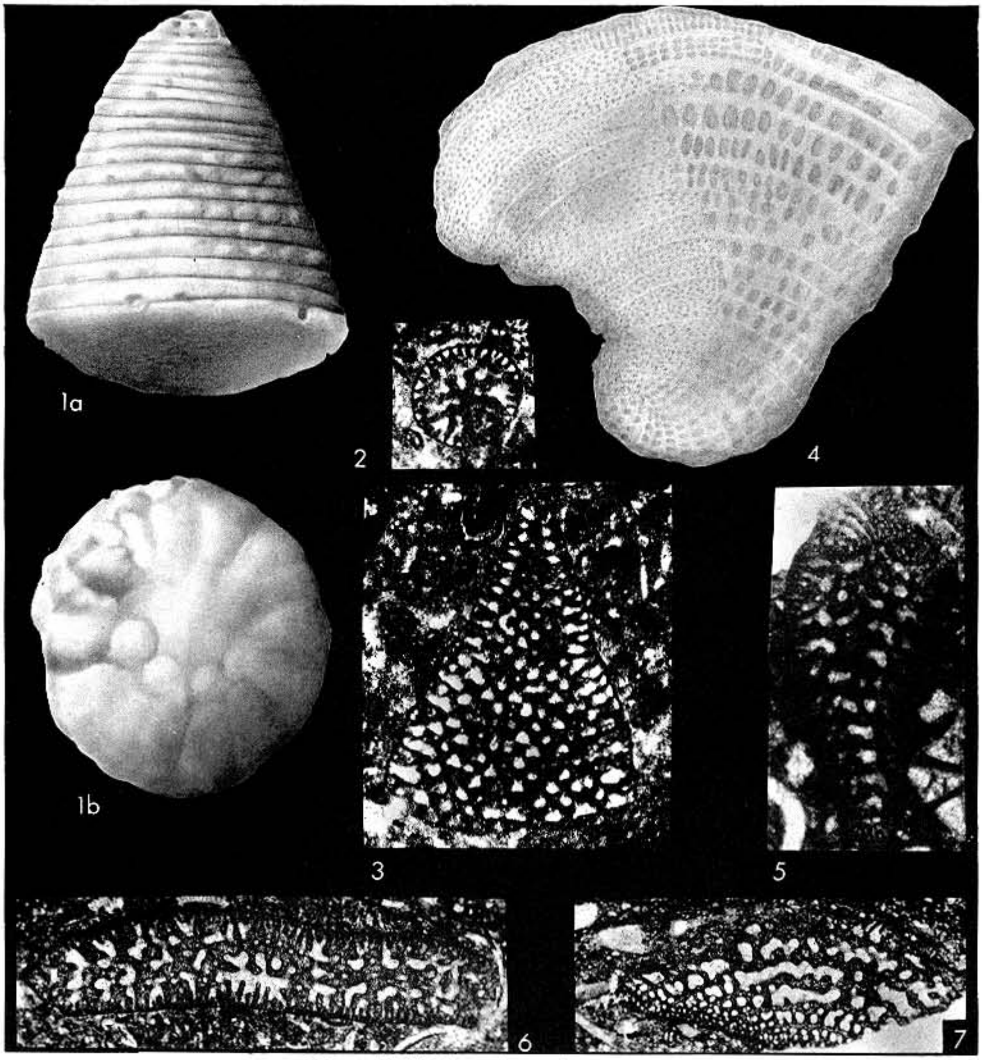


FIG. 222. Orbitolinidae; *1-7, Iraqia* (p. *C*311-*C*312).

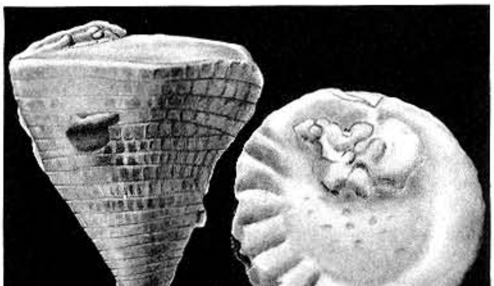


FIG. 223. Orbitolinidae; *1, Simplorbitolina* (p. *C*312-*C*313).

of compression, ×23; *6*, paratype, sec. perpend. to axis, ×20; *7*, oblique sec. showing subepidermal layer, left, and central zone, right, ×20 (*2115).

Simplorbitolina CIRY & RAT, 1953, *344, p. 85 [**S. manasi*; OD]. Test small, generally less than 3 mm. diam.; includes forms intermediate between *Orbitolina* and *Dictyoconus*, with main partitions extending from marginal zone into central area in zigzag manner as in *Orbitolina* but with lower part of each partition discontinuous in form of pillars as in *Dictyoconus;* marginal zone divided by main partitions and one or more series of plates. *L.Cret.*, Eu.(Spain)-Asia(Arabia).——FIG. 223,*1*; 224,*1-3*. **S. manasi*, Spain; 223,*1a,b*, side and basal views of exterior of topotype, ×35 (*2117); 224,*1a,b*, basal and axial sec., ×30

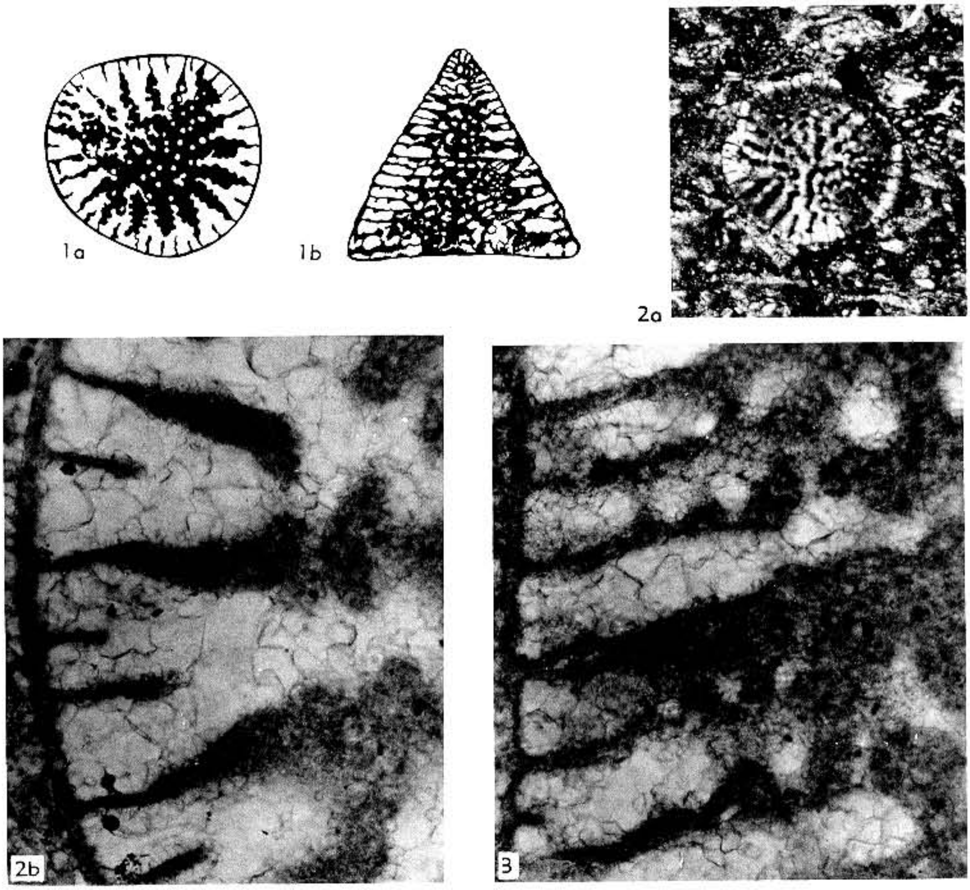


FIG. 224. Orbitolinidae; *1-3, Simplorbitolina* (p. C312-C313).

(*611); 224,*2a*, basal sec., ×20; 224,*2b*, portion of basal sec., ×100; 224,*3*, portion of axial sec., ×100 (*2114).

Suborder FUSULININA Wedekind, 1937

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 219 (*pro* suborder Fusulinacea WEDEKIND, 1937, p. 79)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder); dagger(†) indicates *partim*] —— [=^{2}Imperforina† CALKINS, 1901, p. 106; =^{2}Tinoporinae† CALKINS, 1901, p. 109; =^{1}Nodosaridia† KÜHN, 1926, p. 134; =^{1}Rotaliaridia† KÜHN, 1926, p. 152; =^{1}Textulinida† CALKINS, 1926, p. 356; =^{1}Nodosalidia† CALKINS, 1926, p. 355; =Sektion *Palaeohellenoidea* WEDEKIND, 1937, p. 72, 79; =^{1}*Hellenoidea*† WEDEKIND, 1937, p. 79; =^{2}*Cribrostomacea* WEDEKIND, 1937, p. 79; =^{2}Cribrospiracea WEDEKIND, 1937, p. 79; =^{2}Pluriloculinidea† SIGAL in PIVETEAU, 1952, p. 160; =^{1}Endothyrida FURSENKO, 1958, p. 23; =^{1}Fusulinida FURSENKO, 1958, p. 23]

Primitively of microgranular calcite, advanced forms with 2 or more differentiated layers in wall. *Ord.-Trias.*

Superfamily PARATHURAMMINACEA E. V. Bykova, 1955

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 283 (*pro* superfamily Parathuramminidea FURSENKO in RAUZER-CHERNOUSOVA & FURSENKO, 1959, p. 174)]

Single globular or tubular chamber or cluster of such chambers; wall simple, consisting of calcareous granules in calcareous cement; aperture simple. *Ord.-Carb.*

Family PARATHURAMMINIDAE E. V. Bykova, 1955

[Parathuramminidae E. V. BYKOVA in E. V. BYKOVA & POLENOVA, 1955, p. 15] [=Archaesphaeridae MALACHOVA, 1956, p. 87]

Globular chamber or cluster of chambers; aperture absent or multiple, at ends of tubular projections. *Dev.-L.Carb.*

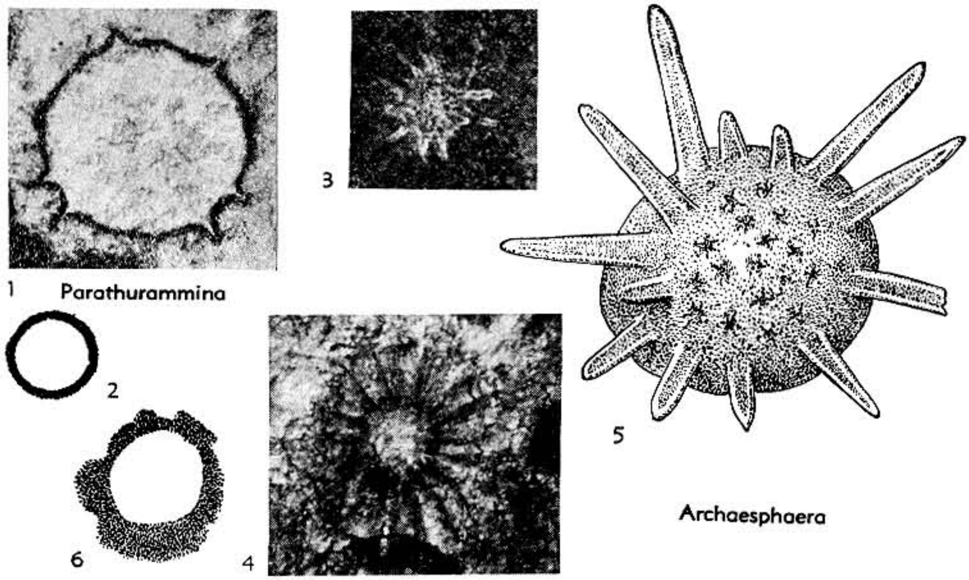


Fig. 225. Parathuramminidae; *1, Parathurammina; 2-6, Archaesphaera* (p. C314).

Parathurammina Suleymanov, 1945, *1851, p. 126 [**P. dagmarae*; OD] [=*Thurammina (Salpingothurammina)* Poyarkov in Purkin, Poyarkov & Rozhanets, 1961, *1490, p. 31 (type, *Parathurammina tuberculata* Lipina, 1950, *1142, p. 118)]. Test free, globular, 0.2 to 0.45 mm. diam.; wall calcareous, granular, may appear striate in section, surface with numerous tubular protuberances; apertures at ends of protuberances. *Dev.-L.Carb. (L.Tournais.)*, USSR(Volga-Ural area).——Fig. 225,*1*. **P. dagmarae*, U.Dev., USSR (W.Sib.); ×50 (*831).

[Poyarkov, 1961, *1490, regarded *Parathurammina* as composed of agglutinated calcareous particles and therefore a synonym of *Thurammina*, which has a similar shape. He did not regard the wall composition as having generic importance but subdivided *Thurammina* into 2 subgenera on the basis of apertural features. *Thurammina (Thurammina)* has papillate ("nipple-like") protuberances, whereas *Thurammina (Salpingothurammina)* has tubular projections upon which were situated the apertures. The species included in *Salpingothurammina* are those commonly placed in *Parathurammina*; hence a modified definition or emendation of that genus would have been sufficient. The new name proposed by Poyarkov is a junior synonym of *Parathurammina*, regardless of which criterion is considered for generic separation. Poyarkov stated that the apertural protuberances might reflect pseudopodial form, the papillate ones *(Thurammina)* formed by "lobopodia," and the tubular ones ("Salpingothurammina," =*Parathurammina*) due to "rhizopodia." No true Foraminiferida are known to have lobopodia, as these are found only in the Amoebida and Arcellinida; hence, the pseudopodial nature probably is not the cause of the different forms of apertural projections. *Parathurammina* is here considered to have a secreted granular wall, not an agglutinated one as in *Thurammina*.]

Archaesphaera Suleymanov, 1945, *1851, p. 126 [**A. minima*; OD] [=*Vicinesphaera* Antropov, 1950, *25, p. 22 (type, *V. squalida*)]. Test free, globular, 0.08-0.34 mm. in diam., surface smooth; wall thin, calcareous, dark, uniform, finely granular; no pores or aperture observed. *Dev.-L.Carb.*, USSR(Ukraine).——Fig. 225,*2-5*. **A. minima*, L.Carb.(Tournais.), Ukraine; *2*, sec., ×80 (*1851); *3,4*, ×100; *5*, restoration, ×330 (*261).——Fig. 225,*6*. *A. squalida* (Antropov), Dev. (Famenn.), Tataria; ×60 (*1509).

[The original description is as given above. The genus was emended by E. V. Bykova (1955, *261), who stated that the spherical test has numerous spines projecting from the surface layer and that the wall is composed of 2 layers, the outer one being thin, obscure, finely granular, porous and not generally preserved, whereas the inner layer is clear, homogeneous, and radially striate owing to the coarse perforation. *Vicinesphaera* was described as differing from *Archaesphaera* in its more irregular wall, but this seems probably to be a result of the preservation.]

Bisphaera Birina, 1948, *139, p. 159 [**B. malevkensis*; OD]. Test comprising single chamber but with central constriction suggesting tendency toward double-chambered form; wall single layered, of finely granular calcite, porous; no aperture observed. *M.Dev.-L.Carb.(Tournais.)*, USSR(W. Urals, Russian Platform).——Fig. 226,*1,2*. **B. malevkensis*, Dev., Bashkir, ASSR; *1*, sectioned specimen; *2*, reconstr., ×100 (*261).

Cribrosphaeroides Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 174 [**Cribrosphaera simplex* Reytlinger, 1954, *1561, p. 65; OD] [=*Cribrosphaera* Reytlinger, 1954, *1561, p. 65 (obj.) (*non Cribrosphaera* Popofsky, 1906); *Cribrosphaerella* Pronina, 1960, *1485, pl. 25, fig. 1 (expl. of pl. 25 given as *Cribrosphaeroides*); *Cribsophaeroides* Pronina, 1960, *1485, p. 140 *(nom. null.)*]. Test circular or irregular in form; wall granular, coarsely perforate; without apparent aperture. *Dev.(Frasn.)*, USSR(Russian Platform).——Fig. 226,*3*. **C. simplex* (Reytlinger); holotype, ×140 (*1561).

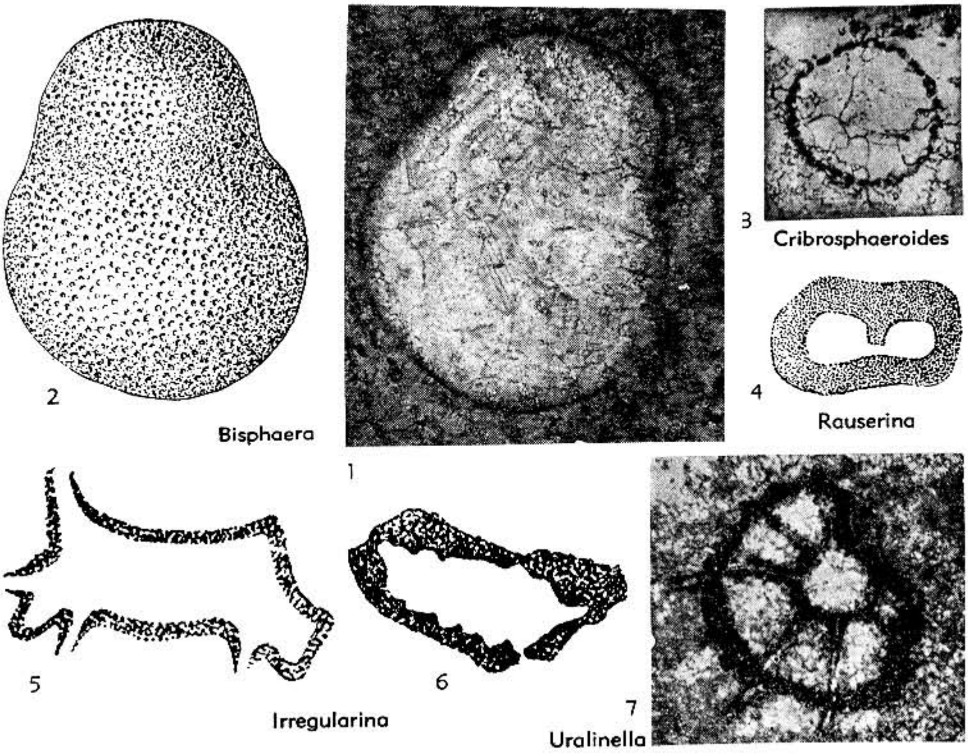


Fig. 226. Parathuramminidae; *1,2, Bisphaera; 3, Cribrosphaeroides; 4, Rauserina; 5,6, Irregularina; 7, Uralinella* (p. C314-C316).

Irregularina E. V. Bykova in Bykova & Polenova, 1955, *261, p. 21 [**I. karlensis* Vissarionova, 1950, *2010, p. 35; OD] [=*Irregularina* Vissarionova, 1950, *2010, p. 35 *(nom. nud.)*; *Corbis* Antropov, 1950, *25, p. 26 (type, *C. nodosus*) (*non* Cuvier, 1817); *Corbiella* Reytlinger, 1954, *1561, p. 62 *(nom. nud.)*; *Corbiella* Antropov in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 175 (*nom. subst. pro Corbis* Antropov, 1950, obj.)]. Test free, consisting of single irregular chamber; wall calcareous; aperture at ends of necklike projections. *U.Dev.(Givet.) - L.Carb. (Tournais.)*, C.Asia-USSR(Russian Platform).——Fig. 226,5. **I. karlensis*, Dev.(Givet.), Baskiri; sectioned specimen, ×150 (*1509).——Fig. 226, 6. *I. nodosa* (Antropov), U.Dev.(Frasn.), Tataria; sectioned specimen, ×120 (*1509).

[Vissarionova (1950, *2010) described *Irregularina* and included 3 species, *I. cardiformis, I. mopha* (listed as *I. morpha*, p. 30, and on figure explanation) and *I. karlensis* (as *Iiregularina karlensis* on p. 35). None was designated as type-species. The "genotype" species was stated to be *I. karlensis* by Bykova in Bykova & Polenova (1955, *261, p. 21); hence, the genus dates from 1955 and is credited to Bykova, according to the International Rules of Zoological Nomenclature. *Corbiella* was described as being irregular or boxlike, the aperture not being observed. Because of its irregular form, like that of *Irregularina*, it seems probable that nonoriented sections might not have intersected the aperture, and they are here regarded as synonymous.]

Palachemonella H. Beckmann, 1953, *104, p. 265 [**P. torleyi*; OD]. Test consisting of single ovate to globular or irregular chamber; wall of granular calcite, in sections with dark inner layer (pseudochitin?) and light outer layer, with small percentage of foreign matter?, apertures rounded, at ends of irregularly spaced necklike protuberances. *M.Dev.*, Eu.——Fig. 227. **P. torleyi*, Ger.; ×85 (*2117).

Petchorina Reytlinger, 1962 (see p. C796).

Quasituberitina Poyarkov in Purkin, Poyarkov & Rozhanets, 1961, *1490, p. 24 [**Q. magna;* OD] [=*Quasituberitina* Poyarkov, 1957, *1480, p. 33, 35 *(nom. nud.)*]. Test with small spherical proloculus followed by strongly enveloping larger second chamber, intercommunicating by means of relatively large opening; wall dark, finely granular, homogeneous and imperforate. [Originally placed in the Stegnamminidae, this genus is here transferred to the Parathuramminidae.] *Dev.(U. Famenn.)*, USSR.——Fig. 228. **Q. magna;* ×130 (*1490).

Rauserina Antropov, 1950, *25, p. 27 [**R. notata*; OD]. Test free, of 1 or 2 subglobular chambers; wall calcareous, finely granular; external aperture not observed but intercameral opening present. [*Rauserina* differs from *Archaesphaera* in having

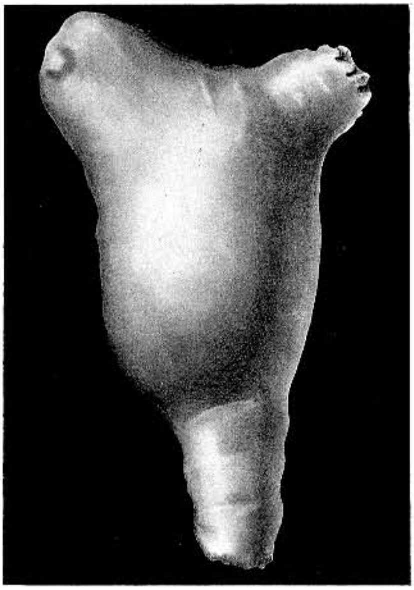


FIG. 227. Parathuramminidae; *Palachemonella* (p. C315).

2 chambers and from *Eovolutina* in the chambers being adjacent rather than concentric.] *M.Dev. (Givet.) - U.Dev.(Famenn.),* USSR(Russian Platform).——FIG. 226,*4*. **R. notata,* U.Dev.(Frasn.); sectioned specimen, ×140 (*1509).

Uralinella E. V. Bykova, 1952, *257, p. 15 [**U. bicamerata*; OD]. Test with 2 chambers, globular proloculus nearly completely surrounded by outer 2nd chamber; wall calcareous, finely granular; 5 to 8 apertures at periphery of proloculus, with elongate tubular necks which extend through interior of embracing 2nd chamber and continue as similar necks and openings at surface of final chamber. [Groups of specimens may be found closely adjacent in thin sections, suggesting possible colonial development.] *U.Dev.,* USSR(Urals: Bashkir-Tartar).——FIG. 226,*7*. **U. bicamerata;* thin section of holotype, ×100 (*257).

Uslonia Antropov, 1959, *25A, p. 28 [**U. permira*; OD]. Test consisting of single irregular chamber 0.5 to 2.0 mm. in length; wall calcareous, homogeneous, perforate; aperture not observed. *U.Dev. (U.Frasn.),* USSR(Bashkir - Tatar - Udmurt).——FIG. 228A,*1*. **U. permira*; *1a,* holotype, sec.; *1b,* paratype, ×14 (*25A).

[Originally placed in the Saccamminidae, the genus is known only from nonoriented sections of the type-species and was thought possibly to be an attached form. It is here transferred to the Parathuramminidae. The test is quite similar in appearance to that of the Devonian *Palachemonella,* and if additional material shows the presence of apertures at ends of the irregular projections it would probably be congeneric.]

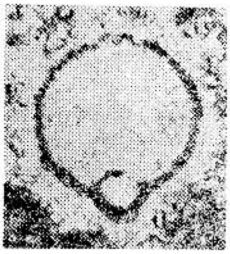


FIG. 228. Parathuramminidae; *Quasituberitina* (p. C315).

Family CALIGELLIDAE Reytlinger, 1959

[Caligellidae Reytlinger in Rauzer-Chernousova & Fursenko, 1959, p. 175]

Test tubular or enrolled, may have irregular constrictions or projections from wall, tending to become septate in advanced forms; aperture simple or irregular. *U.Dev.-L.Carb.*

Caligella Antropov, 1950, *25, p. 28 [**C. borovkensis*; OD] [=*Evlania* E. V. Bykova, 1952, *257, p. 20 (type, *E. transversa*); *Baituganella* Lipina, 1955, *1143, p. 19 (type, *B. chernyshinensis*); *Paracaligella* Lipina, 1955, *1143, p. 26 (type, *P. antropovi*)]. Test free? or attached, tubular, early portion may be slightly coiled, later portion uncoiling; partially divided by incomplete septa, or more rarely complete septa, into irregularly sized chambers; wall calcareous, aperture rounded, terminal, may have thickened margin or neck. [Modifications of the basic form have been the basis for 4 generic names, which include a total of 7 species, most of which are known only from thin sections. Their differences are here regarded as of only specific rather than generic importance.]

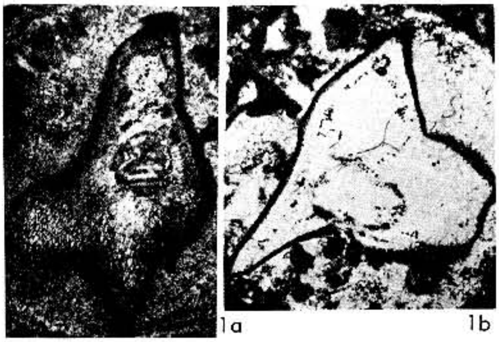


FIG. 228A. Parathuramminidae; *1, Uslonia* (p. C316).

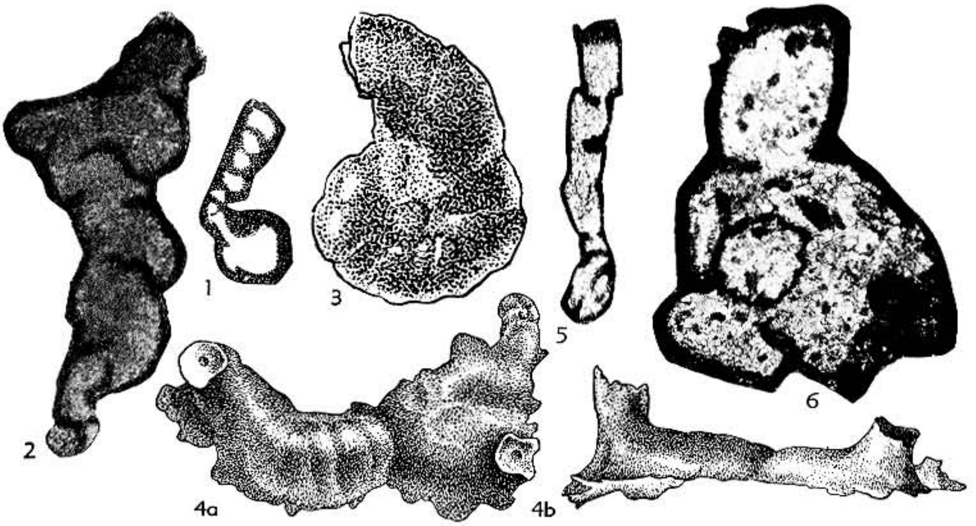


FIG. 229. Caligellidae; *1-6, Caligella* (p. C316-C317).

U.Dev.(Frasn.-Famenn.)-L.Carb.(Tournais.),USSR (Russian Platform-Volga-Ural Region).——FIG. 229,*1*. **C. borovkensis*, U.Dev., ×66 (*1509).——FIG. 229,*2-4*. *C. transversa* (E. V. BYKOVA), M. Dev., USSR(Voronez Distr.); *2*, holotype, ×66; *3*, paratype, early enrolled stage, ×160; *4a,b*, top, edge views of paratype, ×66 (*257).——FIG. 229, *5*. *C. antropovi* (LIPINA), U.Dev.; holotype, ×47 (*1143).——FIG. 229,*6*. *C. chernyshinensis* (LIPINA), L.Carb.(Tournais.), holotype, ×47 (*1143).

Shuguria ANTROPOV, 1950, *25, p. 30 [**S. flabelliformis;* OD]. Test free, flattened, flabelliform, to 0.84 mm. in length; chambers of early stage planispiral, later biserial and finally multiserial, with somewhat separated series; wall calcareous, structure obscure; apertures as openings at periphery. *U.Dev.(Frasn.)*, Russian Platform.——FIG. 230. **S. flabelliformis;* enlarged (*25).

Family MORAVAMMINIDAE Pokorný, 1951

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 283 (*ex* subfamily Moravammininae POKORNÝ, 1951)] [=Earlandiidae CUMMINGS, 1955, p. 227]

Test globular to tubular and nonseptate, free or attached; aperture simple and terminal. *Ord.-Carb.*

Subfamily EARLANDIINAE Cummings, 1955

[*nom. transl.* POKORNÝ, 1958, p. 169 (*ex* family Earlandiidae CUMMINGS, 1955)]

Test free, tubular or uniserial. *Ord.-Carb.*

Earlandia PLUMMER, 1930, *1462, p. 12 [**E. perparva*; OD] [=*Syzrania* REYTLINGER, 1950, *1560, p. 92 (type, *S. bella*)]. Test free, elongate, with globular proloculus followed by long nonseptate tubular chamber; wall of finely granular calcite; aperture at open end of tube. *Dev.-Penn.*, Brit.I.-USA(Tex.)-USSR.——FIG. 231,*1,2*. **E. perparva*, Penn., USA(Tex.); *1*, topotype, ×90 (*2117); *2*, diagram. long. sec., ×50 (*400).——FIG. 231,*3*. *E. bella* (REYTLINGER), U.Carb., USSR (Syzran); sectioned holotype showing nonseptate tube, ×96 (*1560).

Earlandinita CUMMINGS, 1955, *400, p. 230 [**Nodosinella perelegans* PLUMMER, 1930, *1462, p. 14; OD]. Test free, elongate, uniserial, straight or slightly arcuate; septa and chambers well defined; wall calcareous, finely granular; aperture terminal, rounded. [*Earlandinita* differs from *Paratikhinella* in having complete septa and from *Nodosinella* in its single-layered wall.] *L.Carb.(Avon.)*, Brit.I.; *Penn.*, USA(Tex.).——FIG. 231,*8-10*. **E. perelegans* (PLUMMER), Penn., USA(Tex.); *8,9*, holotype and paratype, ×100 (*1462); *10*, diagram. sec., ×90 (*400).

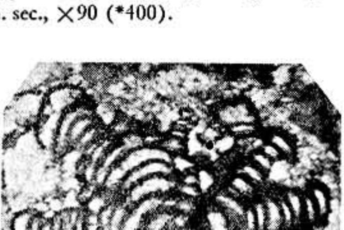


FIG. 230. Caligellidae; *Shuguria* (p. C317).

Lugtonia Cummings, 1955, *400, p. 231 [***Nodosinella concinna* Brady, 1876, *193, p. 106; OD]. Test free, small, tapering, globular chambers in rectilinear arrangement; sutures constricted, septa domed internally; original wall composition uncertain, replaced by amorphous or crystalline silica;

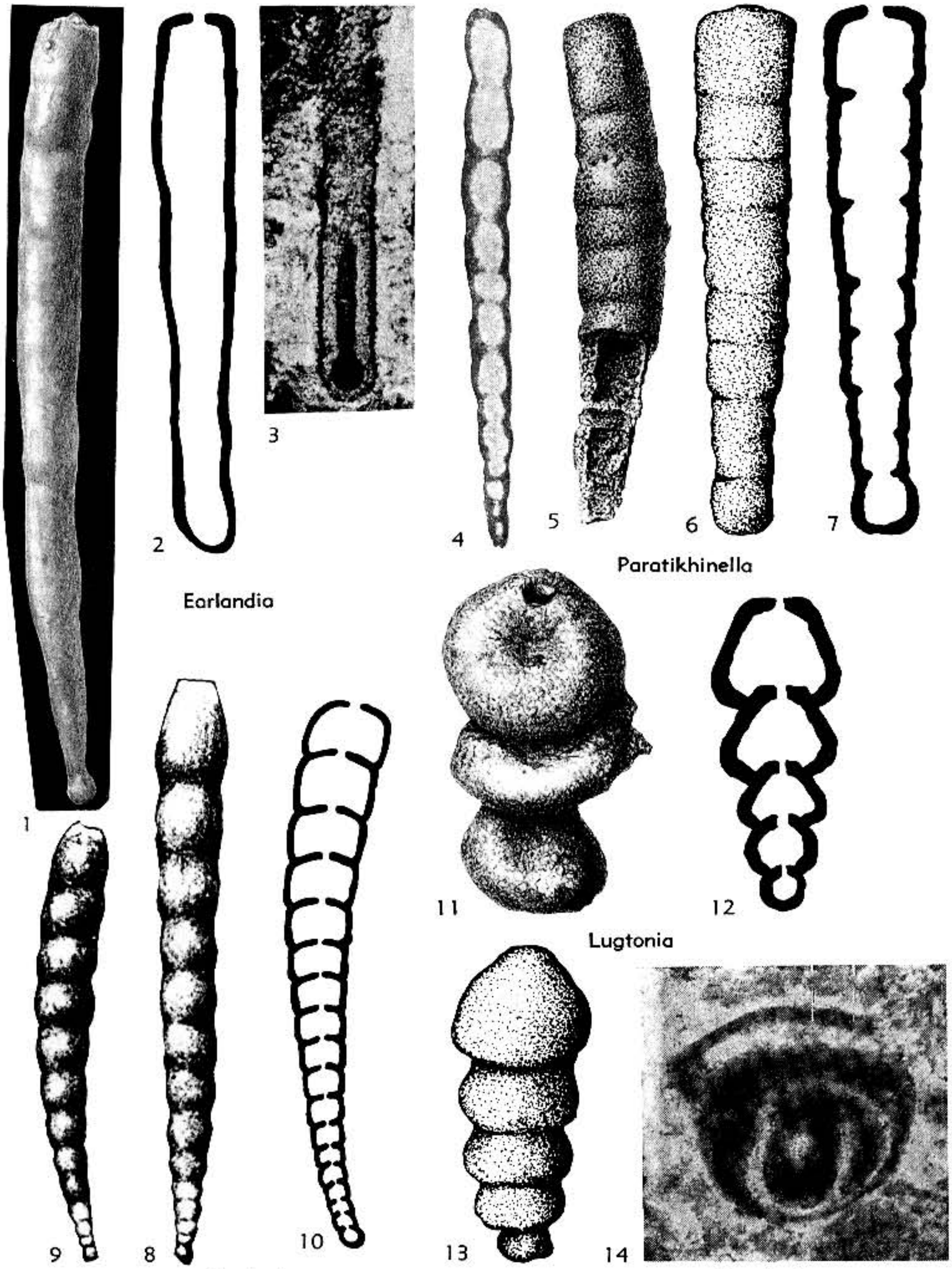


Fig. 231. Moravamminidae (Earlandiinae; *1-3, Earlandia; 4-7, Paratikhinella; 8-10, Earlandinita; 11-13, Lugtonia; 14, Pseudoglomospira*) (p. *C*317-*C*319).

aperture terminal, rounded. [Known only from sediments where secondary silicification has occurred, but there associated with secondarily silicified species belonging to the Parathuramminacea and Endothyracea.] *L.Carb.(Visean-Namur.)*, Brit. I.——Fig. 231,*11-13*. **L. concinna* (Brady); *11, 12*, side view and sectioned specimen, ×45 (*400); *13*, side view of holotype, ×50 (*193).

Paratikhinella Reytlinger, 1954, *1561, p. 71 [**Tikhinella cannula* E. V. Bykova, 1952, *257, p. 32; OD] [=*Earlandinella* Cummings, 1955, *400, p. 229 (type, *Nodosinella cylindrica* Brady, 1876, *193, p. 104)]. Test free, cylindrical, spherical proloculus followed by tapering tubular portion, partially subdivided by incomplete septa produced by inward thickenings of test wall, which is calcareous, finely granular; aperture terminal, rounded. *U.Dev.(Frasn.)*, USSR(Russian Platform); *L.Carb.(Avon.)*, Brit.I.——Fig. 231,*4*. **P. cannula* (E. V. Bykova), U.Dev.; USSR; holotype, ×100 (*257).——Fig. 231,*5-7*. *P. cylindrica* (Brady), L.Carb., Eng.; *5*, lectotype, ×30 (*193); *6,7*, side view and sectioned specimen, ×30 (*400).

Pseudoglomospira E. V. Bykova in E. V. Bykova & Polenova, 1955, *261, p. 30 [**P. devonica;* OD (M)]. Test consisting of globular proloculus and tubular undivided 2nd chamber which is streptospirally enrolled; wall calcareous, homogeneous, dark, and finely granular; aperture at open end of tube. *Dev.-Carb.*, USSR.——Fig. 231,*14*. **P. devonica*, Dev., Sartov Province; section of holotype, ×100 (*261).

Saccamminopsis Sollas, 1921, *1811, p. 193, 211 [**Saccammina carteri* Brady, 1871, *188, p. 177 (=*Nodosaria fusulinaformis* M'Coy, 1849, *1196, p. 131); OD (M)] [=*Carteria* Brady in C. Moore, 1870, *1306, p. 372 (type not designated) (*non Carteria* Diesing, 1866, *non* Gray, 1867; *nec* Signoret, 1874)]. Test free, uniserial, with globular to ovate chambers, and strongly constricted sutures, chambers commonly broken apart in preservation; wall thin, calcareous; aperture terminal, rounded. [Originally regarded as agglutinated, the type-species was restudied by Sollas, and shown to be originally calcareous, a secondary silicification and infilling having caused the labyrinthic appearance.] *Ord.-Carb.*, Brit.I.——Fig. 232,*1,2*. **S. fusulinaformis* (M'Coy); *1*, exterior of various specimens, ×2 (*193); *2*, sectioned specimen, ×16 (*1811).

Subfamily MORAVAMMININAE Pokorný, 1951

[Moravammininae Pokorný, 1951, p. 7]

Test attached, tubular. *M.Dev.-M.Carb.*

Moravammina Pokorný, 1951, *1472, p. 7 [**M. segmentata*; OD] [=*Litya* E. V. Bykova in E. V. Bykova & Polenova, 1955, *261, p. 27 (type, *L. sizranensis*)]. Test tubular, attached by proloculus, may be enrolled about attachment, later uncoiled and erect; chambers separated by equally spaced thin septa; wall calcareous, finely granular; aperture rounded, terminal. [*Litya* was regarded as differing from *Moravammina* in its slight tendency to coil in trochoid manner. Since both are coiled about an attachment, the spires vary considerably and they are here regarded as congeneric.] *M.Dev.(Givet.)*, Czech.; *U.Dev.(Frasn.)*, USSR.——Fig. 233,*1*. **M. segmentata*, M.Dev., Czech.; topotype, ×59 (*2117).——Fig. 233,*2-4*. *M. sizranensis* (E. V. Bykova), U.Dev., USSR; *2*, holotype; *3a,b*, side, edge views of paratype; *4*, sec. showing septation; all ×66 (*261).

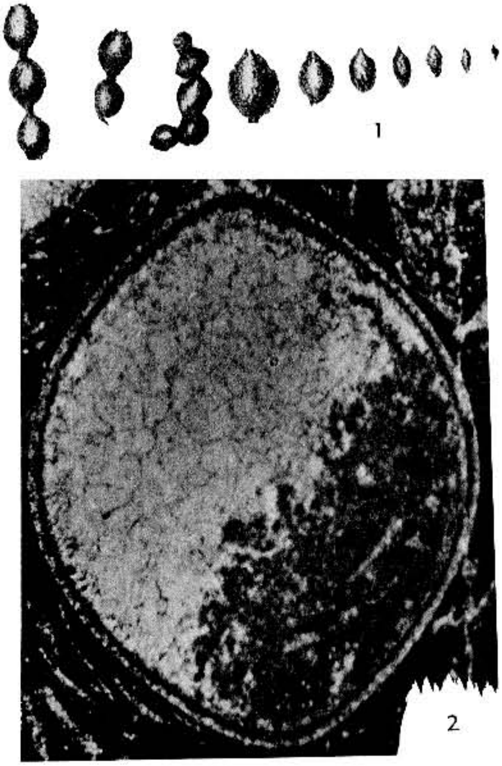


Fig. 232. Moravamminidae (Earlandiinae; *1,2*, *Saccamminopsis*) (p. *C*319).

Kettnerammina Pokorný, 1951, *1472, p. 3 [**K. givetiana*; OD] [=*Saccorhina* E. V. Bykova in E. V. Bykova & Polenova, 1955, *261, p. 33 (type, *S. trivirgulina*)]. Test similar to *Moravammina* but with globular proloculus followed by nonseptate tubular 2nd chamber with tendency to bifurcate. *M. Dev. (Givet.) - U. Dev. (Frasn.)*, Czech.-USSR (Russian Platform).——Fig. 233,*7*. **K. givetiana*, M.Dev.(Givet.), Czech.; topotype, ×28 (*2117).——Fig. 233,*8,9*. *K. trivirgulina* (E. V. Bykova), U.Dev.(Frasn.), USSR; *8*, holotype; *9*, paratype, ×66 (*261).

Turrispiroides Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 181 [*pro Turrispira*

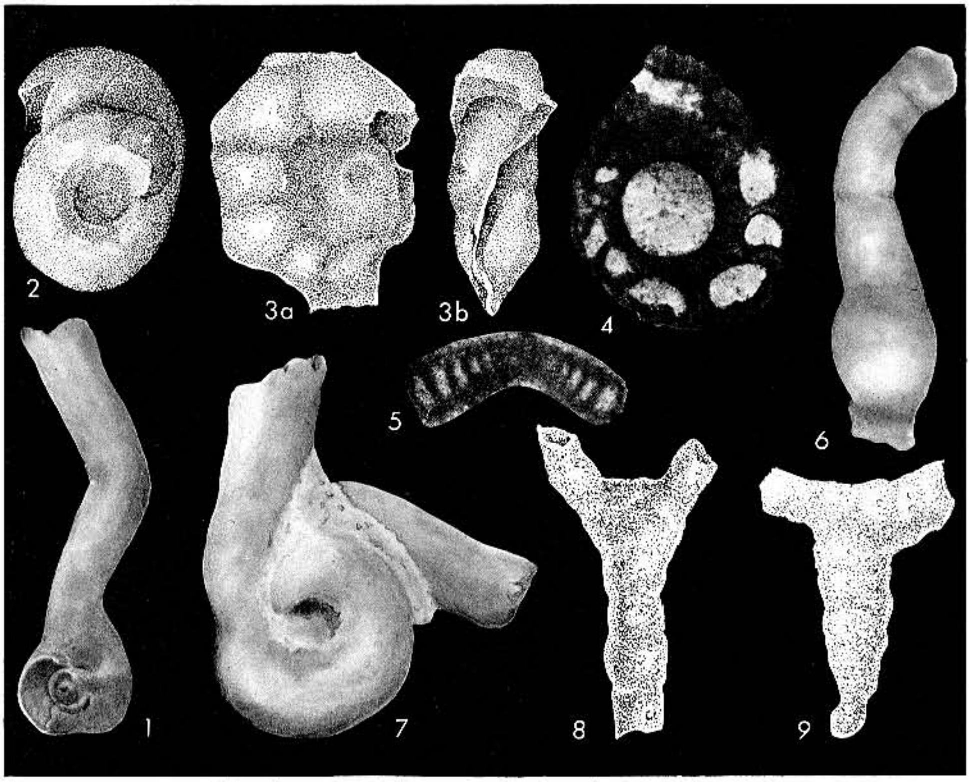


FIG. 233. Moravamminidae (Moravammininae; *1-4, Moravammina; 5, Turrispiroides; 6, Vasicekia; 7-9, Kettnerammina*) (p. *C*319-*C*320).

Reytlinger, 1950, *1560, p. 18 (*non* Conrad, 1866; *nec* Petho, 1906)] [**Turrispira mira* Reytlinger, 1950, *1560, p. 19; OD]. Text with proloculus followed by nonseptate tubular 2nd chamber, trochospirally coiled; wall calcareous, finely granular. *M.Carb.(L.Moscov.),* USSR(Russian Platform).——FIG. 233,*5*. **T. mira* (Reytlinger); holotype, sec. showing low spire, ×66 (*1509).

Vasicekia Pokorný, 1951, *1472, p. 11 [**V. moravica;* OD]. Test consisting of elongate tubular segments with bulbous inflated portion near one end, regarded as fragments of originally multilocular test; aperture at open end of tubular portion. [This genus was originally placed in the Reophacidae, but is nonagglutinated and composed of granular calcite, hence here transferred to the Moravammininae. *Vasicekia* is superficially similar to *Moravammina* but has very elongate chambers with swollen area near one extremity.] *M. Dev.(Givet.),* Czech.——FIG. 233,*6*. **V. moravica;* topotype, ×86 (*2117).

Superfamily ENDOTHYRACEA Brady, 1884

[*nom. correct.* Loeblich & Tappan, 1961, p. 284 (*pro* superfamily Endothyridea Glaessner, 1945, p. 107)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}superfamily, ^{2}family group); dagger(†) indicates *partim*]——[=^{1}Orthoklinostegia† Eimer & Fickert, 1899, p. 685; =Basistoma† Schubert, 1921, p. 148; =^{2}Archi-Monothalamidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 85; =^{2}Nodosalidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 86; =^{2}Rotaliaridia† Rhumbler in Kükenthal & Krumbach, 1923, p. 88; =^{2}Textulinidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 88; =^{1}Tournayellidea Dain in Rauzer-Chernousova & Fursenko, 1959, p. 183]

Tubular or with early trochospiral or irregular coil, biserial or uniserial; interior may be divided into chamberlets, but not labyrinthic; wall calcareous, fibrous or granular, with some arenaceous material included in primitive forms, commonly with 2 layers, finely perforate; aperture simple to multiple, basal or terminal. *L.Sil.-Trias.*

Family NODOSINELLIDAE Rhumbler, 1895

[Nodosinellidae Rhumbler, 1895, p. 85]——[All names are of family rank; dagger(†) indicates *partim*]——[=Nodosamminidae† Rhumbler, 1913, p. 339 (*nom. nud.*); =Nodosinellida Copeland, 1956, p. 186 (*nom. van.*); =Tuberitinidae Miklukho-Maklay, 1958, p. 134]

Test tubular or uniserial; wall structure compound, of microgranular calcite with inner fibrous layer. *L.Sil.-Perm.*

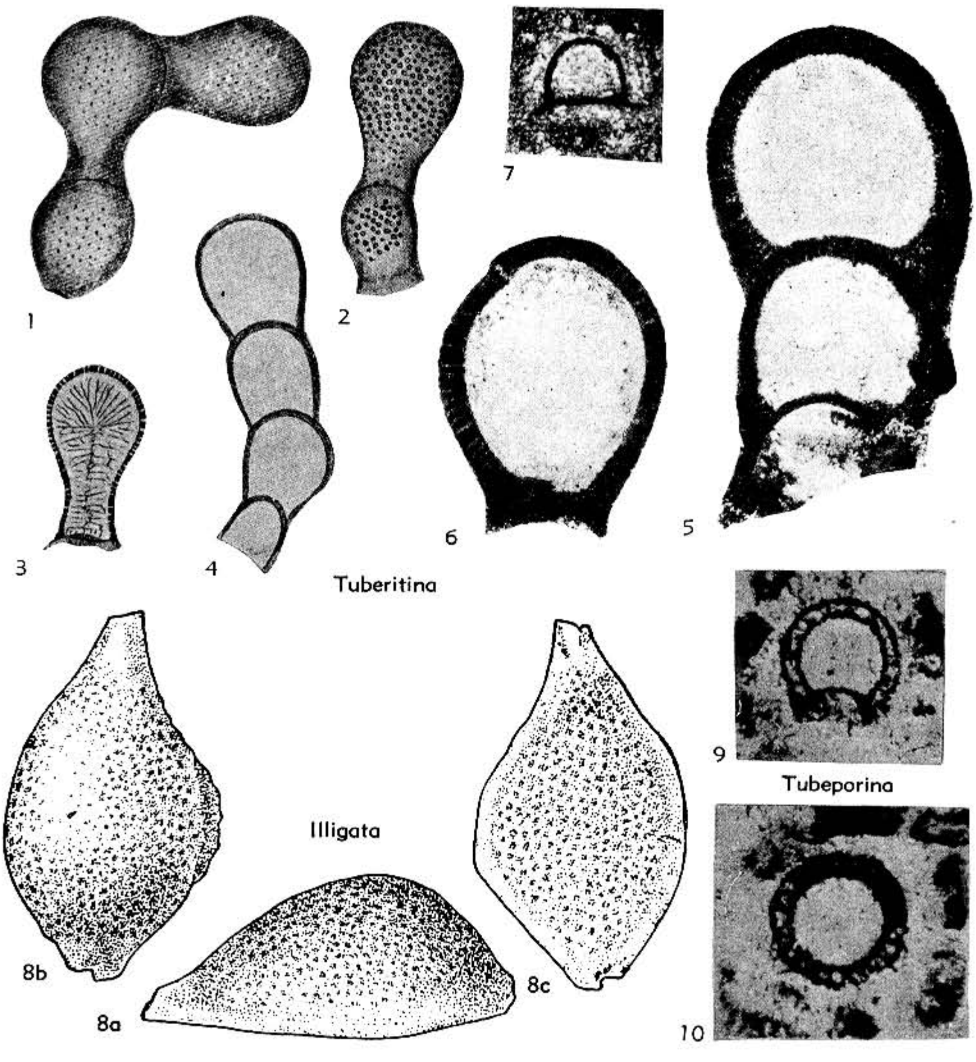


FIG. 234. Nodosinellidae (Tuberitininae; *1-7, Tuberitina; 8, Illigata; 9,10, Tubeporina*) (p. *C*321-*C*322).

Subfamily TUBERITININAE Miklukho-Maklay, 1958

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 284 (*ex* family Tuberitinidae MIKLUKHO-MAKLAY, 1958)]

Test attached, consisting of one or more subhemispherical chambers, no distinct aperture. *L.Sil.-U.Carb.*

Tuberitina GALLOWAY & HARLTON, 1928, *763, p. 346 [**T. bulbacea*; OD] [=*Capidulina* MASLOV, 1935, *1231, p. 11 (type, *C. hemispherica*); *Paratuberitina* A. D. MIKLUKHO-MAKLAY, 1957, *1267, p. 95 (type, *Tuberitina collosa* REYTLINGER, 1950, *1560, p. 89); *Neotuberitina* POYARKOV, 1957, *1480, p. 33, 36 *(nom. nud.)*; *Neotuberitina* A. D. MIKLUKHO-MAKLAY, 1958, *1269, p. 134 (type, *Tuberitina maljavkini* MIKHAYLOV, 1939, *1260, p. 48); *Eotuberitina* POYARKOV, 1957, *1480, p. 33, 35 *(nom. nud.)*; *Eotuberitina* A. D. MIKLUKHO-MAKLAY, 1958, *1269, p. 134 (type, *Tuberitina maljavkini* REYTLINGER, 1950, *1560, p. 88, *non Tuberitina maljavkini* MIKHAYLOV, 1939, =*Eotuberitina reitlingerae* A. D. MIKLUKHO-MAKLAY, 1958)]. Test attached, to 1.2 mm. in length; proloculus in form of basal disc, later bulbous chambers in rectilinear or curved series, increasing gradually in size as added; wall thick, calcareous, granular and finely perforate, surface commonly punctate; no aperture or intercameral connection except for wall perforations. *U.Dev.,*

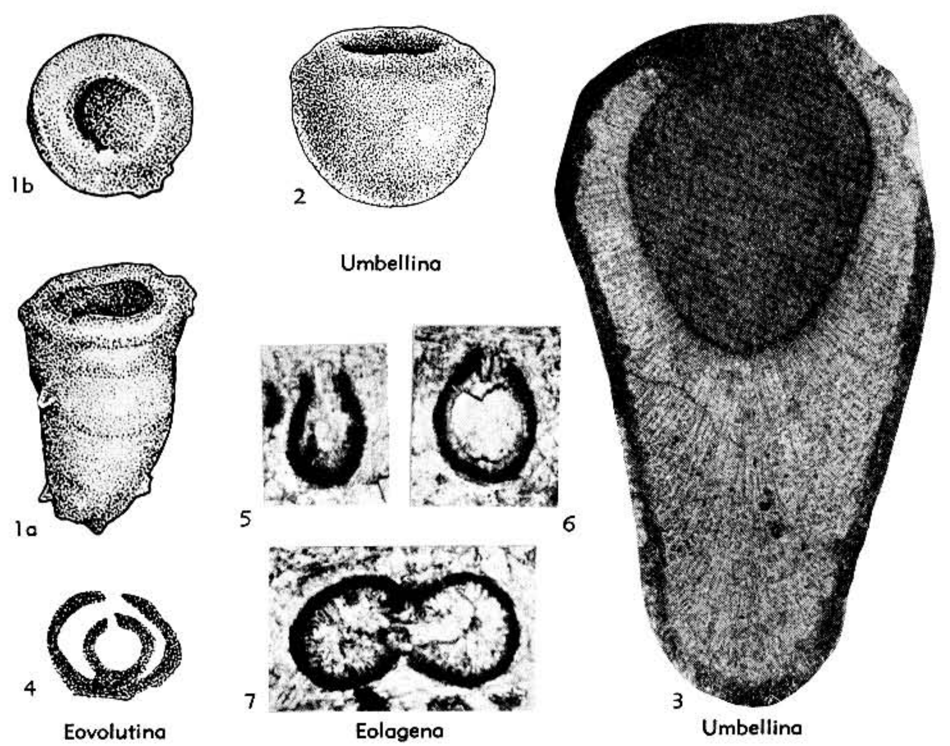


FIG. 235. Nodosinellidae (Umbellininae; _1-3, Umbellina; 4, Eovolutina; 5-7, Eolagena_) (p. _C322-C323_).

USSR; _U.Carb.(Penn.)_, N.Am.; _L.Perm._, USSR.——FIG. 234,_1-4_. *_T. bulbacea_, _Penn._, USA (Okla.); _1_, holotype; _2_, specimen showing distinctly punctate surface; _3,4_, thin secs. showing perforate wall; all ×35 (*763).——FIG. 234,_5,6_. _T. collosa_ Reytlinger, M.Carb.(U.Moscov.), USSR; holotype and paratype, ×90 (*700).——FIG. 234,_7_. _T. reitlingerae_ (A. D. Miklukho-Maklay), M.Carb., USSR; holotype, ×90 (*1560).

Illigata E. V. Bykova, 1956, *258, p. 21 [*_I. annae_; OD]. Test unilocular, ovate, attached by one side, shape and convexity of test influenced by substratum; wall calcareous, perforate, smooth; aperture rounded, somewhat produced, at one end of elongate test. _L.Sil._, Baltic.——FIG. 234,_8_. *_I. annae_, Lith.; _8a-c_, side, top, basal views, ×100 (*258).

[This genus was originally placed in the Lagenidae by Bykova, and transferred to the Umbellinae by Fursenko (1959, *1509, p. 249). Because of its attached nature and perforate wall, it is here placed with the Tuberitininae. Bykova (*258, p. 22) stated that _Thurammina echinata_ Dunn from the Silurian of North America appeared similar to _Illigata_. However, as _T. echinata_ was obtained from insoluble residues of limestones, its arenaceous nature seems undoubted. _Illigata_ is known only from Europe.]

Tubeporina Pronina, 1960, *1486, p. 51 [*_T. gloriosa_; OD]. Test attached, single hemispherical to subglobular chamber, with basal attachment disc; wall thick, calcareous, with 3 layers; aperture consisting of coarse perforations through wall. [_Tubeporina_ differs from _Tuberitina_ in having a 3-layered wall.] _M.Dev.(Givet.)_, USSR(Ural Mts.).——FIG. 234,_9-10_. *_T. gloriosa_; _9_, vert. sec. of holotype showing thick 3-layered chamber wall and attachment disc; _10_, horiz. sec., showing coarse perforations, ×150 (*1486).

Subfamily UMBELLININAE

Loeblich & Tappan, 1961

[Umbellininae Loeblich & Tappan, 1961, p. 284 (_nom. subst. pro_ subfamily Umbellinae Fursenko in Rauzer-Chernousova & Fursenko, 1959, p. 248)]

Test free, globular or flask-shaped. _Sil.-Dev._

Umbellina Loeblich & Tappan, 1961, *1177, p. 284 [_pro Umbella_ Maslov, 1955 in E. V. Bykova & Polenova, 1955, *261, p. 40 (_non_ d'Orbigny, 1841; _nec_ Scudder, 1882)] [*_Umbella bella_ Maslov in E. V. Bykova & Polenova, 1955, *261, p. 37; OD]. Test free, single globular to subconical chamber; wall calcareous, thick, with 2 layers, inner dark finely granular layer and outer radially perforated layer; aperture simple, rounded, may be slightly produced. _Dev._, USSR(Russian

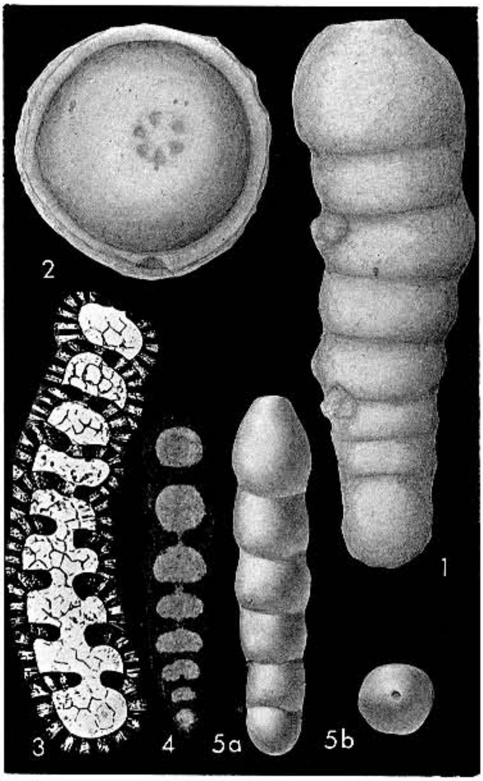


FIG. 236. Nodosinellidae (Nodosinellinae; *1-5*, *Nodosinella*) (p. *C*323-*C*324).

Platform-W.Urals-Kazakh.).——FIG. 235,*1-3*. **U. bella* (MASLOV); *1a,b,* side, top views of elongate specimen, ×85; *2,* side view of subglobular form, ×100; *3,* long. sec. of large specimen showing thick radially perforate wall, ×100 (*261).

Eolagena LIPINA, 1959, *1144, p. 825 [**E. minuta*; OD]. Test ovoid, pyriform, or flask-shaped; wall calcareous, with 2 layers, internal radial layer and outer finely granular layer, aperture simple rounded opening. [*Eolagena* is similar to *Umbellina* in general appearance but much smaller, and the wall structure is different. *Eolagena* is thinner walled, with thin radial internal layer, and thicker external granular layer, whereas *Umbellina* has an extremely thick wall, with thick outer radial layer and thin inner granular layer.] *U.Sil. (Ludlov.),* USSR(Sib.).——FIG. 235,*5-7*. **E. minuta*; *5,* long. sec. of holotype; 6,7, sectioned paratypes; all ×140 (*1144).

Eovolutina ANTROPOV, 1950, *25, p. 29 [**E. elementa*; OD]. Test globular, wtih 2 chambers, later (outer) chamber completely overlapping proloculus; wall calcareous; aperture simple, at one end of chamber. *M.Dev. (Givet.) - U.Dev. (Frasn.-Famenn.),* USSR.——FIG. 235,*4*. **E. elementa,* Frasn.; sectioned specimen, ×140 (*1509).

[Originally placed questionably in the Lagenidae, *Eovolutina* was later transferred to the Parathuramminidae. As the aperture is only at one end of the test, rather than absent or with multiple irregularly scattered openings, the genus is here placed tentatively in the Umbellininae. The characteristic fibrous wall of this group has not been noted for *Eovolutina;* the wall has been described as "obscure."]

Subfamily NODOSINELLINAE Rhumbler, 1895

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 285 (*ex* family Nodosinellidae RHUMBLER, 1895)]

Test free, uniserial; wall compound, of microgranular calcite with inner fibrous layer. *U.Dev.-Perm.*

Nodosinella BRADY, 1876, *193, p. 102 [**N. digitata;* SD MILLER, 1889, *1283, p. 161] [=*Monogenerina* SPANDEL, 1901, *1822, p. 179 (type, *M. atava*); *Arnodosinum* RHUMBLER, 1913, *1572b, p. 442 (type, *Nodosinella digitata* BRADY, 1876, *193, p. 103), SD LOEBLICH & TAPPAN, herein (obj.); *Nodosaroum* RHUMBLER, 1913, *1572b, p. 443 (type, *Nodosaria index* EHRENBERG, 1854, *680, p. xxxvii, xi); *Arnodosaroum* RHUMBLER, 1913, *1572b, p. 443 (type, *A. indictoum, nom. van. pro Nodosaria index* EHRENBERG, 1854); *Spandelina (Spandelinoides)* CUSHMAN & WATERS, 1928, *539, p. 367 (type, *S. (S.) nodosariformis*); *Eonodosaria* LIPINA, 1950, *1142, p. 126 (type, *E. evlanensis*); *Tikhinella* E. V. BYKOVA, 1952, *257, p. 29 (type, *T. measpis*); *Protonodosaria* GERKE, 1959, *779, p. 42 (type, *Nodosaria proceraformis* GERKE, 1952)]. Test free, uniserial, straight or arcuate; septa straight or slightly domed; wall calcareous, outer layer microgranular, inner layer radially striate or fibrous and finely perforate; aperture rounded, at open end of tube. *U.Dev.-Perm.,* Eu.-N.Am.——FIG. 236, *1,2*; 237,*1*. **N. digitata,* Perm., Eng.; 236,*1,* lectotype (BMNH-P41657) redrawn, ×48; 236,*2,* top view of broken paratype (BMNH-P41658) showing apparently multiple aperture in septum, not terminal face, ×48 (*2117); 237,*1a,* diagram.

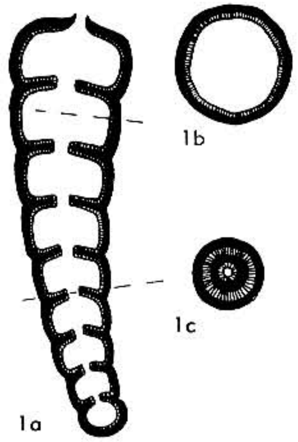


FIG. 237. Nodosinellidae (Nodosinellinae; *1*, *Nodosinella*) (p. *C*323-*C*324).

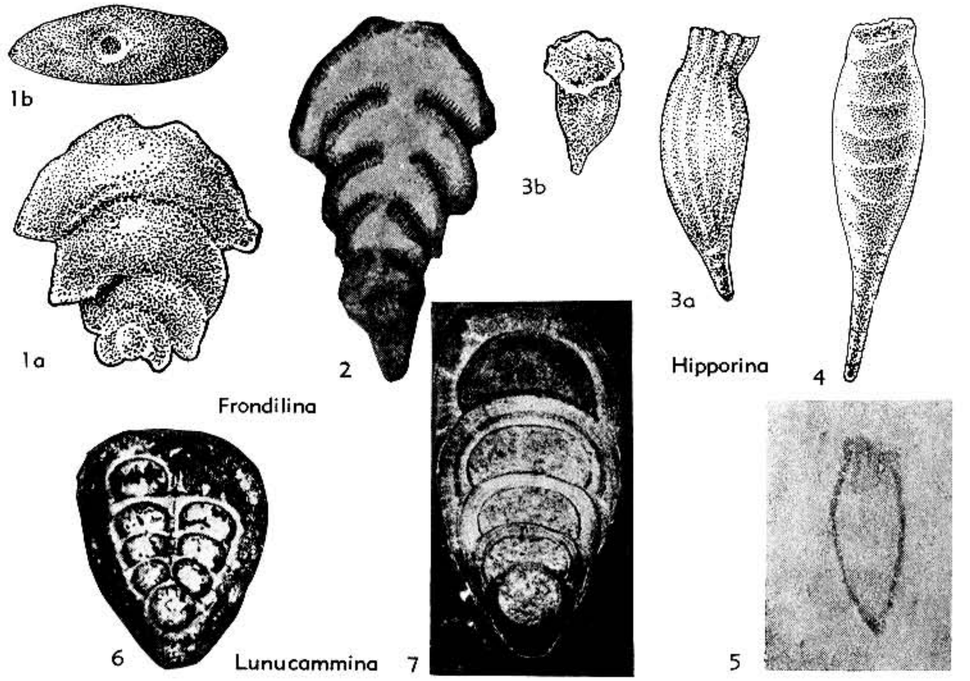


FIG. 238. Nodosinellidae (Nodosinellinae; *1,2, Frondilina; 3-5, Hipporina; 6,7, Lunucammina*) (p. *C*324-*C*326).

long. sec., ×25; 237,*1b,c,* transv. secs. through chamber and septum, ×25 (*400).——FIG. 236, *3. N. index* (EHRENBERG), L. Carb.(Kohlenkalk), USSR, sec. showing radially fibrous wall, approx. ×28 (*1572b).——FIG. 236,*4. N. measpis* (BYKOVA), U.Dev., USSR; long. sec. of holotype, ×80 (*257).——FIG. 236,*5. N. nodosariformis* (CUSHMAN & WATERS), Perm., USA(Tex.); *5a,b,* side, top views of paratype, ×47 (*2117).

[When restudying the original types of *N. digitata* in the British Museum (Natural History), we noted an apparent multiple aperture on the domed surface of one of the paratypes, a broken specimen, here redrawn. The true apertures of the terminal face appear only to be simple, however, and the apparent multiple aperture may be that of an abnormal specimen. CUMMINGS (*400, p. 225) noted that the outer microgranular layer of the wall might be altered to recrystallized calcite of irregular grain size, a feature which has led to statements that the test was agglutinated. *Nodosaroum* was defined by RHUMBLER for the calcareous *Nodosaria index*, as he believed *Nodosinella* to be an arenaceous genus. As redefined by CUMMINGS (*400) on the basis of the type-species, the wall of *Nodosinella* is calcareous and distinctly fibrous in appearance. *Spandelinoides* was originally described as a subgenus of *Spandelina*, but because of the rounded section is here regarded as synonymous with *Nodosinella*. *Spandelina* is a synonym of *Lunucammina*. *Tikhinella* was regarded by POKORNÝ (1958, *1478, p. 174) as similar to *Earlandinita*. The radial structure mentioned as occurring in a number of species of *Tikhinella* suggests the fibrous structure of *Nodosinella*, hence *Tikhinella* is here regarded as synonymous with *Nodosinella*.]

Frondilina E. V. BYKOVA, 1952, *257, p. 24 [**F. devexis*; OD]. Test similar to *Lunucammina,* with more strongly overlapping chambers, wall with dark, finely granular homogeneous outer layer and thicker, radially striate, light inner layer; septa with 3 layers, of which 2 are light and 1 dark. [The wall structure is the reverse of that found in *Lunucammina,* as the granular layer is the outer one in *Frondilina,* whereas the inner layer is granular in *Lunucammina*. Permian specimens referred to *Frondicularia* (*1264) belong to *Frondilina.*] *U.Dev.(Frasn.)-Perm.,* USSR (Urals).——FIG. 238,*1,2. *F. devexis*; *1a,b,* side, top views of holotype, ×100; 2, long. sec. of paratype, ×115 (*257).

Hipporina E. V. BYKOVA in E. V. BYKOVA & POLENOVA, 1955, *261, p. 36 [**H. hastila*; OD] [=*Hypporina* E. V. BYKOVA in E. V. BYKOVA & POLENOVA, 1955, *261, p. 36, 37 *(nom. null.)*]. Test free, elongate, fusiform, with uniserial arrangement of rapidly enlarging chambers, final chamber constricted toward aperture; wall calcareous, surface may be longitudinally ribbed; aperture cribrate on terminal surface. [Originally placed in the Lagenidae (=Nodosariidae), *Hipporina* is here tentatively placed with the Nodosinellidae, although details of the wall structure are unknown.] *U.Dev.(Frasn.),* USSR(Russian Platform-Urals).——FIG. 238,*3-5.* **H. hastila; 3a,b,* side and oblique top views of holotype; *4,* paratype; *5,* sectioned specimen; all ×100 (*261).

Lunucammina SPANDEL, 1898, *1821, p. 8 [**Geinitzella (Lunucammina) permiana;* OD] [=*Geinit-*

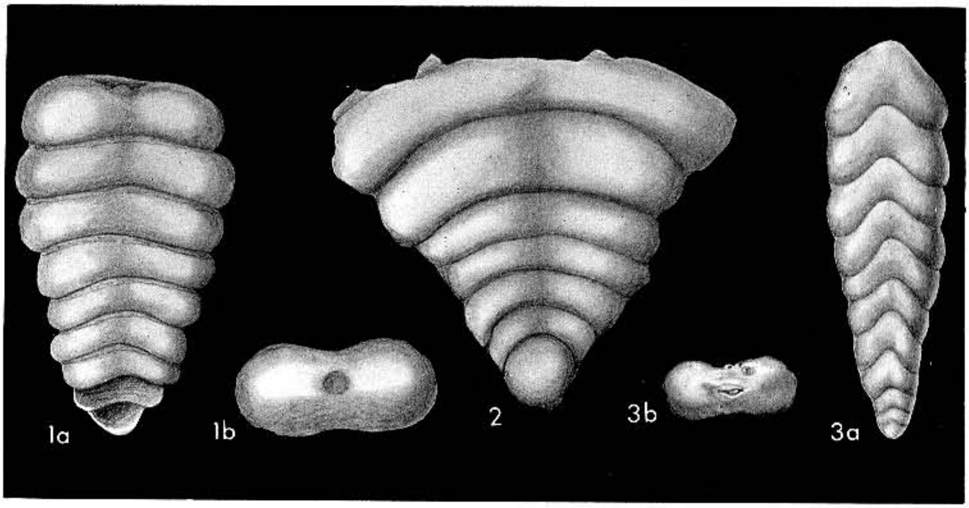


Fig. 239. Nodosinellidae (Nodosinellinae; *1-3, Lunucammina*) (p. *C324-C326*).

zella (Lunucammina) Spandel, 1898, *1821, p. 8 (obj.); *Geinitzella* Spandel, 1898, *1821, p. 7 (type, *Textularia cuneiformis* Jones in King, 1850, *1039A, p. 18 (*non Textularia cuneiformis* d'Orbigny, 1826), =*Textularia jonesi* Brady, 1876, *193, p. 133) (*non Geinitzella* Waagen & Wentzel, 1866); *Padangia* Lange, 1925, *1091, p. 228 (type, *P. perforata*) (*non Padangia* Babor, 1900; *nec* Werner, 1924); *Geinitzina* Spandel, 1901, *1822, p. 189 (*nom. subst. pro Geinitzella* Spandel, 1898); *Spandelina* Cushman & Waters, 1928, *539, p. 363 (type, *S. excavata*); *Eogeinitzina* Lipina, 1950, *1142, p. 124 (type, *E. devonica*); *Neogeinitzina* K. V. Miklukho-Maklay, 1954, *1277, p. 34 (type, *N. orientalis*)]. Test free, elongate, uniserial, compressed, commonly with median longitudinal depression which in slightly tangential sections gives pseudobiserial appearance; chambers broad, low, arched as in *Lingulina* or *Frondicularia;* wall calcareous, with microgranular inner layer and radially striate outer layer; aperture terminal, rounded to ovate. *U.Dev.-Perm.,* N.Am.-Eu.-Malay Arch.-Australia.——Fig. 239,*1*. **L. permiana* Spandel, Perm. (Zech.), Ger.(Thuringia); *1a,b,* side, top views of topotype (BMNH-P41666, labeled *Geinitzina jonesi*) partially embedded in limestone slab, ×105 (*2117).——Fig. 239,*2*. *L. jonesi* (Brady), Perm., Eng.; side view (BMNH-P35421), ×105 (*2117).——Fig. 239,*3*. *L. excavata* (Cushman & Waters), Perm., USA(Tex.); side, top views of holotype, ×86 (*2117).——Fig. 238,*6*. *L. orientalis* (K. V. Miklukho-Maklay), U.Perm., C.Caucasus; slightly tang. long. sec. of holotype, with median long. depression of test resulting in false suggestion of median septum or internal tube, ×65 (*1277).——Fig. 238,*7*. *L. perforata* (Lange), M.Perm., Indonesia; lat. long., but not axial sec., ×30 (*1091).

[*Lunucammina* was originally described as a subgenus of *Geinitzella,* differing in being slightly depressed only on one face, the other being slightly convex; it was regarded as a distinct genus by Lange (1925, *1091) and others. This minor difference is not considered to be generic, or even subgeneric, in importance. *Lunucammina* dates from 1898, and thus has priority over *Geinitzina,* described in 1901 as a replacement for the homonym *Geinitzella;* genera and subgenera are of equivalent status for purposes of priority. In the original description and in later publications by Spandel, this genus was described as uniserial. Brady, however, had thought *Textularia jonesi,* the type-species of *Geinitzella,* to be biserial, partially on the basis of very diagrammatic drawings of German specimens sent to him by Richter (*193, pl. 10, figs. 21-22). Brady stated (*193, p. 133), however, that "The singular feature of all, whether English or German, consists in the arrangement of the chambers, the two series being almost exactly opposite, instead of alternating with each other. This is so uniform a character that a doubt has more than once occurred to me whether the specimens were actually Textulariae—whether they might not belong to some unknown broad variety of one of the uniserial types, the depressed median line being in reality a fracture, the result of pressure on a very thin shell-wall." The type-specimen of *Textularia cuneiformis* Jones, 1850, is apparently not preserved. The German specimens of *Textularia jonesi* Brady, sent by Richter, now in the Brady collection of the British Museum (Natural History), do not show any biseriality. All are in limestone, but one (BMNH-P41666) (*193, pl. 10, fig. 20), here redrawn, was on the edge of a slab of limestone from the Permian Zechstein of Thuringia. Thus the end could be cleaned, and from the top a single chamber can be seen, slightly depressed on each side, the furrow giving the impression of a median septum in specimens broken open and seen from the interior, or in slightly tangential sections. The single English specimen in the Brady collection (BMNH-P35421) (*193, pl. 10, fig. 20) was embedded in limestone and could not be sectioned, but it also appears to be calcareous. It comes from the Lower Magnesian Limestone (Permian), Summerhouse, Durham, and is here redrawn. Cushman & Waters (1928, *539, p. 363) apparently followed Brady in considering *Geinitzina* biserial and described *Spandelina* for the uniserial species. It thus is synonymous wth *Lunucammina. Neogeinitzina* was differentiated on the basis of an "internal tube," but was described from thin sections. The original figures of the holotype appear to be of a somewhat tangential longitudinal section, the median external groove of the test giving the erroneous appearance of a median septum, or "apertural tube." Similar sections had led Brady to regard *Textularia jonesi* as "biserial." Illustrations of other new species *(Geinitzina tcherdynzevi)* sectioned by K. V. Miklukho-Maklay show merely a depressed central portion of the septa, reflecting the longitudinal depression in nearly central longitudinal sections. *Neogeinitzina* is thus regarded as a synonym of *Lunucammina.* Species re-

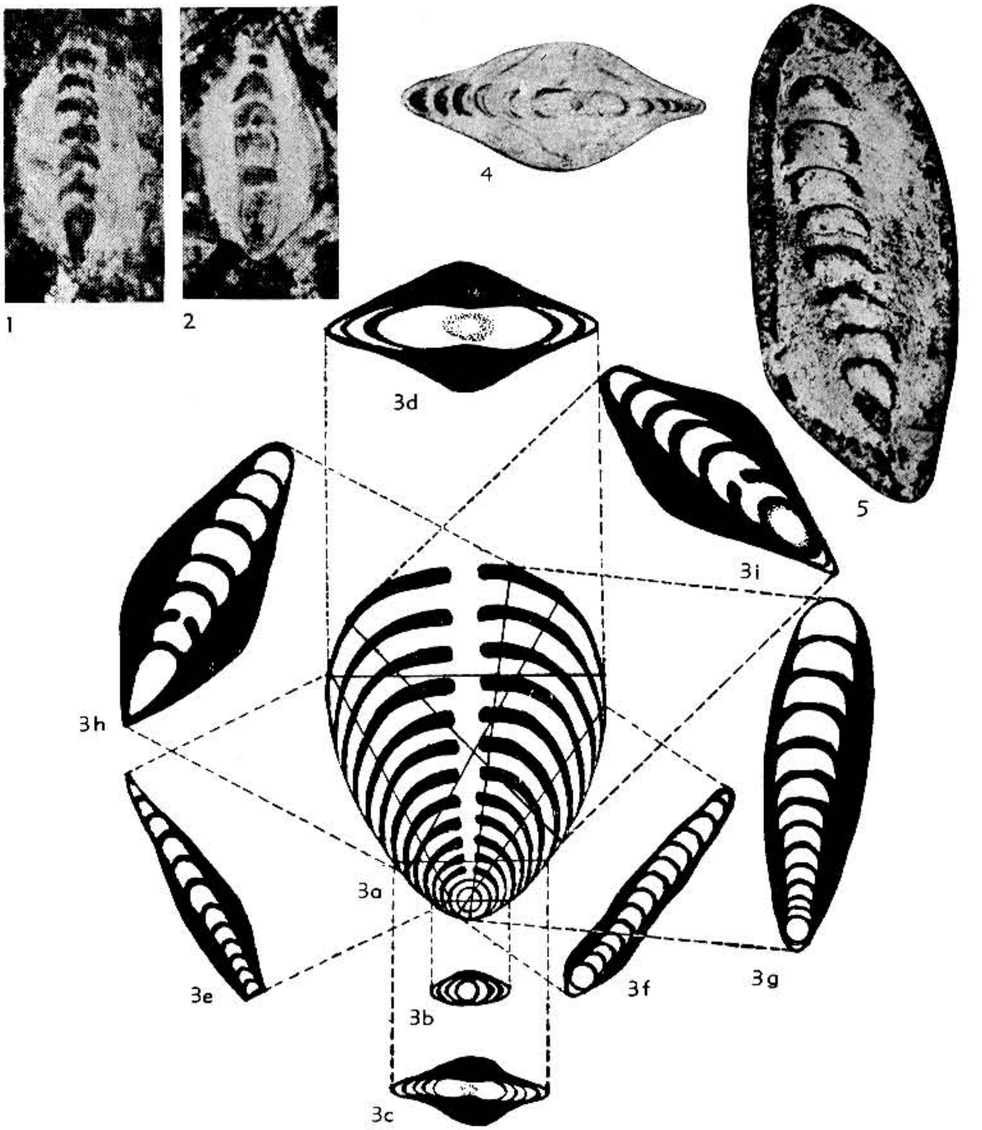


FIG. 240. Nodosinellidae (Nodosinellinae; *1-5*, *Pachyphloia*) (p. *C326-C328*).

ferred to "*Pseudoglandulina*" from the Permian (*1277) also belong here.]

Pachyphloia LANGE, 1925, *1091, p. 230 [**P. ovata*; SD GALLOWAY, 1933, *762, p. 172] [=*Parapermodiscus* A. D. MIKLUKHO-MAKLAY, 1953, *1262, p. 129 (type, *P. gefoensis*); *Parageinitzina* K. V. MIKLUKHO-MAKLAY, 1954, *1277, p. 61 (type, *P. depressa*); *Parapachyphloia* K. V. MIKLUKHO-MAKLAY, 1954, *1277, p. 57 (type, *P. asymmetrica*); *Pseudogeinitzina* K. V. MIKLUKHO-MAKLAY, 1954, *1277, p. 35 (type, *P. magna*)]. Test elongate, compressed, ovate in outline, regularly fusiform to sinuate in horizontal section, consisting of rectilinear series of very broad, low, strongly overlapping chambers; wall calcareous, with radial or fibrous structure, thickened and lamellar, epecially at lateral margins, which may be slightly curved, resulting in sinuate section, separate lamellae added with formation of successive chambers; aperture terminal, rounded and with appearance of radial grooves. *?L.Perm., U. Perm.*, Malay Arch.-USSR.——FIG. 240,*1,2*. **P. ovata*, M.Perm., Sumatra; original nonoriented

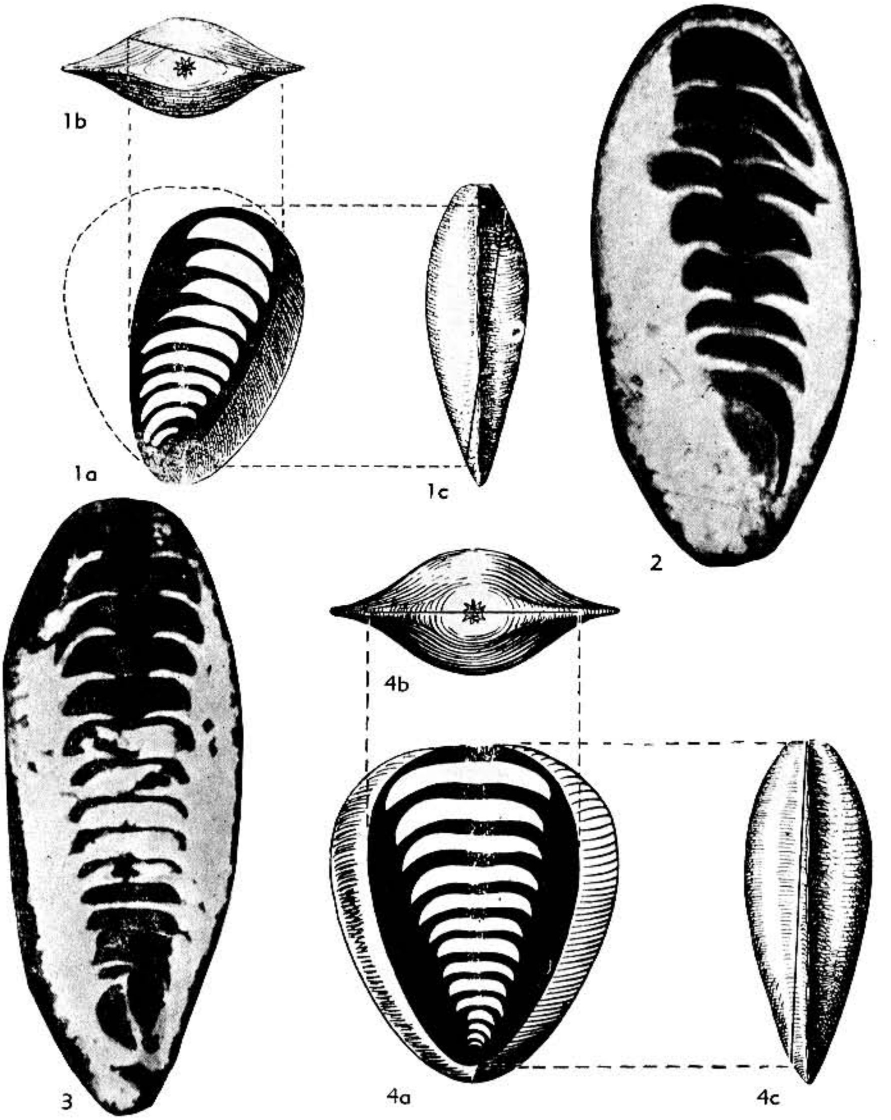


FIG. 241. Nodosinellidae (Nodosinellinae; *1-4, Pachyphloia*) (p. *C*326-*C*328).

lat. secs., ×90 (*1091).——FIG. 240,*3*. *P.* sp., diagram., showing different appearance of variously oriented sections; *3a,* long. sec.; *3b-d,* transv. secs. such as were made basis for *Parapermodiscus* and *Pararobuloides; 3e-g,* lat. secs., described as species of *Nodosaria* and *Pachyphloia; 3h,i,* lat. secs. through lamellar thickened area of test, such as original secs. of *Pachyphloia ovata* and those on which *Parapachyphloia* was based (*1818).——FIG. 240,*4*. *P. gefoensis* (A. D. MIKLUKHO-MAKLAY), U.Perm., C.Caucasus; transv. sec. (as in *3c*) but originally thought to represent axial sec. of a discoidal genus, ×47 (*1262).——FIG. 240,*5*. *P. asymmetrica* (K. V. MIKLUKHO-MAKLAY), U.Perm., C.Caucasus; holotype, slightly oblique lat. sec. (as in *3g,h*), ×47 (*1277).——FIG. 241,*1*. *P.* sp.; *1a-c,* diagram showing position of oblique long. secs. such as were made basis for *Parageinitzina* (*1818).——FIG. 241,*2*. *P. depressa* (K. V. MIKLUKHO-MAKLAY), U.Perm., C.Caucasus; holotype in oblique long. sec. (as in *1a*), ×47 (*1277),——FIG. 241,*3*. *P. magna* (K. V. MIKLUKHO-MAKLAY), U.Perm., C.Caucasus, tang. sec. of holotype (as in *4a*), ×65 (*1277).——FIG.

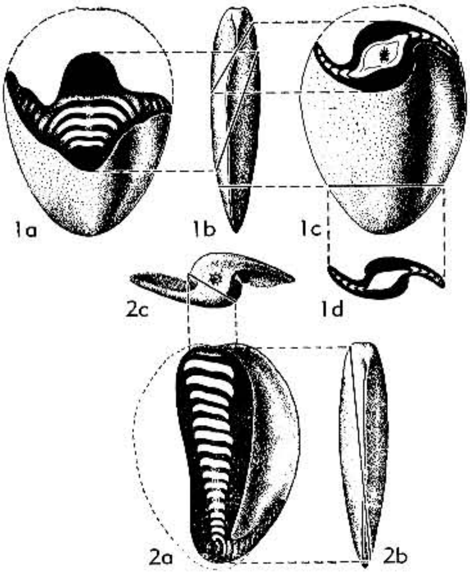


FIG. 242. Nodosinellidae (Nodosinellinae; *1,2*, *Pachyphloia*) (p. *C*326-*C*328).

241,*4*. *P*. sp.; *4a-c*, diagram showing position of slightly tang. long. secs. on which *Pseudogeinitzina* was based (*1818).——FIG. 242,*1,2*. *P*. sp.; *1a-d*, *2a-c*, diagrammatic figure of somewhat sinuate specimens showing asymmetry to be expected in nonoriented secs. (*1818).

[*Pachyphloia* differs from *Lunucammina* in its extremely thickened lamellar walls, and broad low, arcuate chambers. A detailed study of serial sections of *Pachyphloia* by SOSNINA (*1818, *1817) showed that nonoriented sections of this form have been referred to 8 different genera, *Nodosaria*, *Pararobuloides*, *Pachyphloia*, *Parapachyphloia*, *Pseudogeinitzina*, *Parageinitzina* and *Parapermodiscus*, of which the last 4 are synonyms of *Pachyphloia*.]

Family COLANIELLIDAE
Fursenko, 1959

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 285 (*ex* subfamily Colaniellinae FURSENKO in RAUZER-CHERNOUSOVA & FURSENKO, 1959, p. 251)]

Test uniserial, chambers strongly overlapping, internally subdivided by vertical radial partitions; wall of 2 layers, inner layer finely granular, outer layer vitreous; aperture rounded to radiate. *U.Dev.-U. Perm.*

Colaniella LIKHAREV, 1939, *1138, p. 31 [*pro Pyramis* COLANI, 1924, *354, p. 181 (*non* BOULTEN, 1798; *nec* SCHUMACHER, 1817; *nec* OTTO, 1821; *nec* BROWN, 1827; *nec* PUTZEYS, 1846; *nec* HAECKEL, 1887)] [**Pyramis parva* COLANI, 1924, *354, p. 181; OD] [=*Wanganella* SOSNINA in KIPARISOVA, *et al.*, 1956, *1040, p. 15 (type, *W. ussuriensis*)]. Test elongate, subfusiform to subcylindrical, uniserial and rectilinear, with broad, low and strongly domed chambers which are strongly overlapping for as much as half length of test; interior wtih radiating secondary interseptal partitions extending nearly to center of test; wall calcareous, finely perforate, and of radial or fibrous appearance; aperture terminal, radiate. *U.Perm.*, IndoChina-Greece-USSR(Caucasus-Pamir).——FIG. 243,*1-3*. **C. parva* (COLANI); *1*, reconstr. showing ext. and partial long. and horiz. secs., ×50; *2*, axial sec., ×100; *3*, transv. sec. near middle of test, strongly overlapping chambers resulting in appearance of small chamberlets, ×100 (*1517).——FIG. 243,*4,5*. *C. ussuriensis* (SOSNINA), USSR; *4*, long. sec. of holotype, slightly oblique at base, nearly tang. toward central part, and lat. oblique toward top of figure; *5*, slightly oblique transv. sec., ×50 (*1040).

Multiseptida E. V. BYKOVA, 1952, *257, p. 27 [**M. corallina*; OD]. Test elongate, uniserial; globular proloculus followed by broad, low, strongly overlapping chambers, as in *Glandulina;* interior of chambers with longitudinal radial partial partitions extending inward from outer wall, which is calcareous, outer wall 2-layered, outer one light colored, semitransparent, with radial striations, inner layer dark, finely granular, homogeneous, vertical partitions and internal thickening around aperture consisting of darker granular material; aperture terminal, rounded. [*Multiseptida* differs from *Colaniella* in its less strongly overlapping chambers, in narrower vertical partitions restricted to the inside wall of chambers, and in a rounded aperture, whereas in *Colaniella* the vertical partitions extend from top to bottom of chambers and the aperture is radiate.] *U.Dev.(Frasn.)*, USSR (Russian Platform).——FIG. 244,*1-3*. **M. corallina*; *1*, holotype, long. sec., ×133; *2*, paratype, horiz. sec. showing 2 layers of wall and vertical partial partitions, ×133; *3*, diagram. long. sec. showing light outer radial layer of wall, inner dark granular layer, thickened inner layer in ring at aperture, aperture, and radial partial long. partitions, approx. ×123 (*257).

Family PTYCHOCLADIIDAE Elias, 1950

[Ptychocladiidae ELIAS, 1950, p. 288]

Test attached, uniserial and branching or spreading; wall granular, calcareous, banded, with transverse tubuli; no distinct aperture. *Dev.-Perm.*

Subfamily PTYCHOCLADIINAE Elias, 1950

[*nom. transl.* LOEBLICH & TAPPAN, 1961, p. 285 (*ex* family Ptychocladiidae ELIAS, 1950)]

Test uniserial and dichotomously branching, or with branches laterally fused to become discoidal. *U.Penn.*

Ptychocladia ULRICH & BASSLER, 1904, *1966, p. 289 [**P. agellus*; OD]. Test attached, consisting of numerous radiating uniserial "branches" of uniserial chambers, extending from common center and bifurcating at irregular intervals; chambers broad and low, with domed septa, broader chambers may be subdivided internally by interseptal radial partitions; wall calcareous, finely granular, perforated, and with laminar "banding" of thin dark inner layer and thicker light-colored

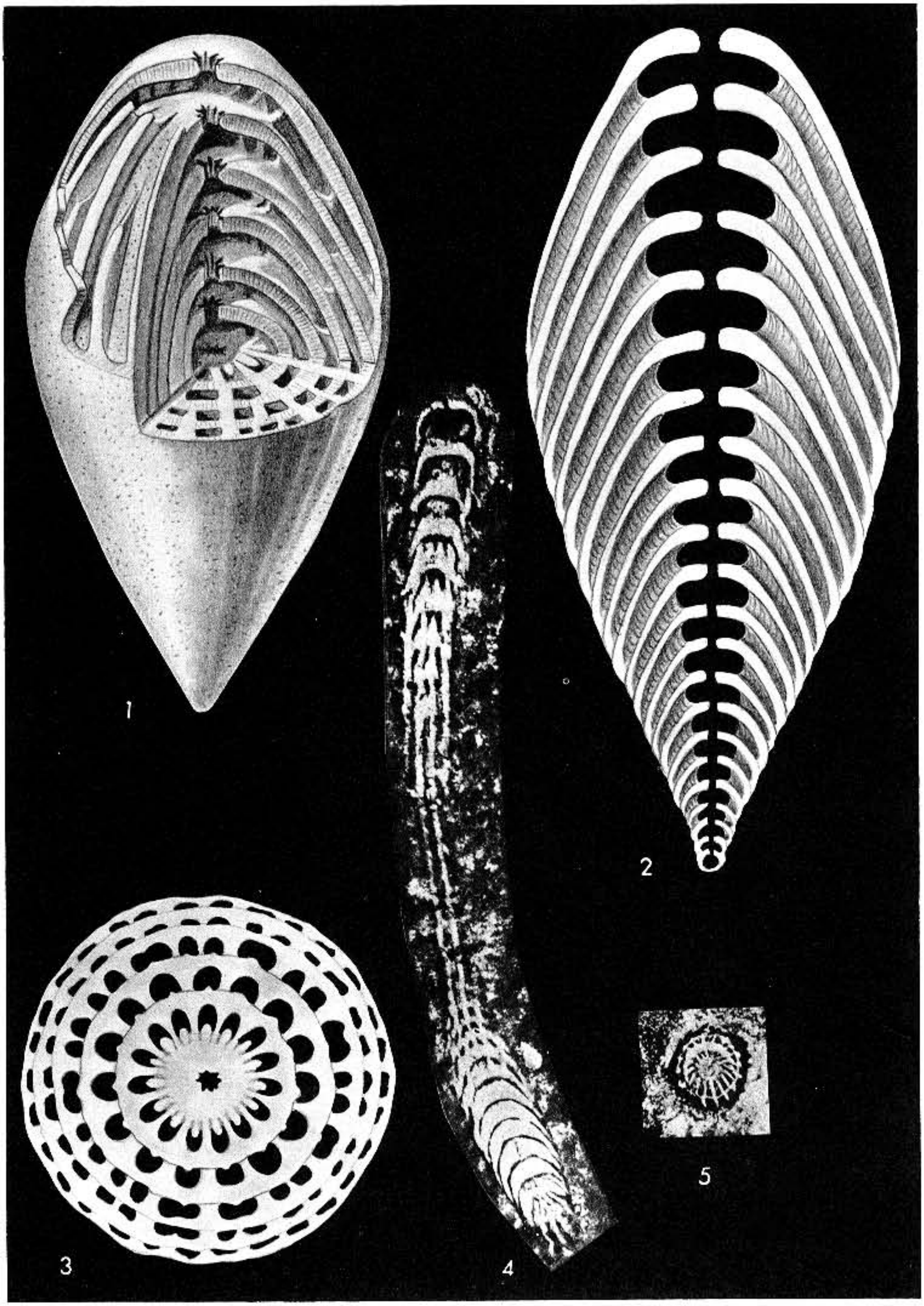


FIG. 243. Colaniellidae; *1-5, Colaniella* (p. C328).

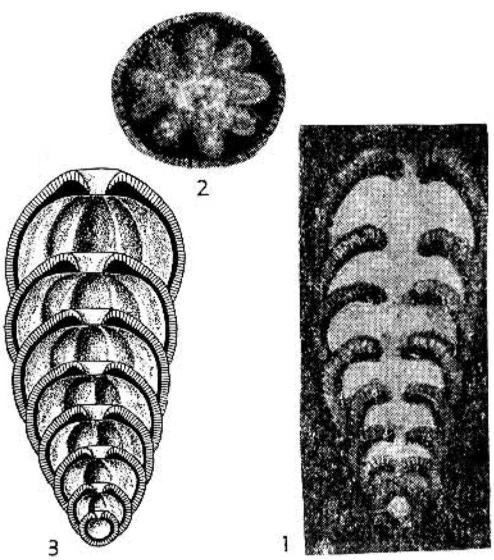


FIG. 244. Colaniellidae; *1-3, Multiseptida* (p. C328).

layer; no visible aperture. [Originally described as problematical, possibly bryozoan, alga, or foraminifera, *Ptychocladia* was transferred to the Foraminifera by ELIAS, 1950 (*696)]. *U.Penn.*, N.Am.——FIG. 245,*1-3*. **P. agellus*, USA(Ill.) *(1,2)*, USA(Neb.) *(3)*; *1,2*, holotype, paratype, ×9 (*1966); *3*, specimen, ×20 (*696).

Subfamily STACHEIINAE Loeblich & Tappan, 1961

[Stacheiinae LOEBLICH & TAPPAN, 1961, p. 285]

Test attached, spreading, with chambers in sheetlike layers. *Dev.-Perm.*

Stacheia BRADY, 1876, *193, p. 107 [**S. marginulinoides;* SD CUSHMAN, 1927, *433, p. 189] [=*Stacheya* DELAGE & HÉROUARD, 1896, *580, p. 134 *(nom. van.)* (obj.); *Arstachecoum* RHUMBLER, 1913, *1572b, p. 446 (obj.) *(nom. van.)*]. Test attached during at least part of its development, with central support indicated in some species; early portion spiraling, later uniserial, with low, somewhat embracing chambers that subdivide irregularly into chamberlets with secondary partitions perpendicular to transverse septa, partitions may branch and be so numerous that chamberlets mask basic uniserial structure; sutures of primary chambers show externally as transverse depressions; wall calcareous, granular; surface smooth to quite irregular; aperture simple and rounded, terminal. *L.Carb.*, Eu.-N.Am.——FIG. 246,*1,2*. **S. marginulinoides*, Yoredale, Eng. (Hurst) *(1)*, Eng.(?loc.)*(2)*; *1a,b*, side, top views of lectotype (BMNH-P41653 *ex* P35455, =*193, pl. 7, fig. 17), redrawn, ×64 (*2117); *2*, sectioned paratype (BMNH-P35507, =*193, pl. 7, fig. 21), redrawn, ×64 (*2117).

Aoujgalia G. TERMIER & H. TERMIER, 1950, *1882, p. 40 [**A. variabilis*; OD] [=*Aoujgalia* G. TERMIER & H. TERMIER, 1947, *1881, p. 146, 271, pl. 5, fig. 46 *(nom. nud.)*]. Test attached, subconical and flattened against attachment, with irregular

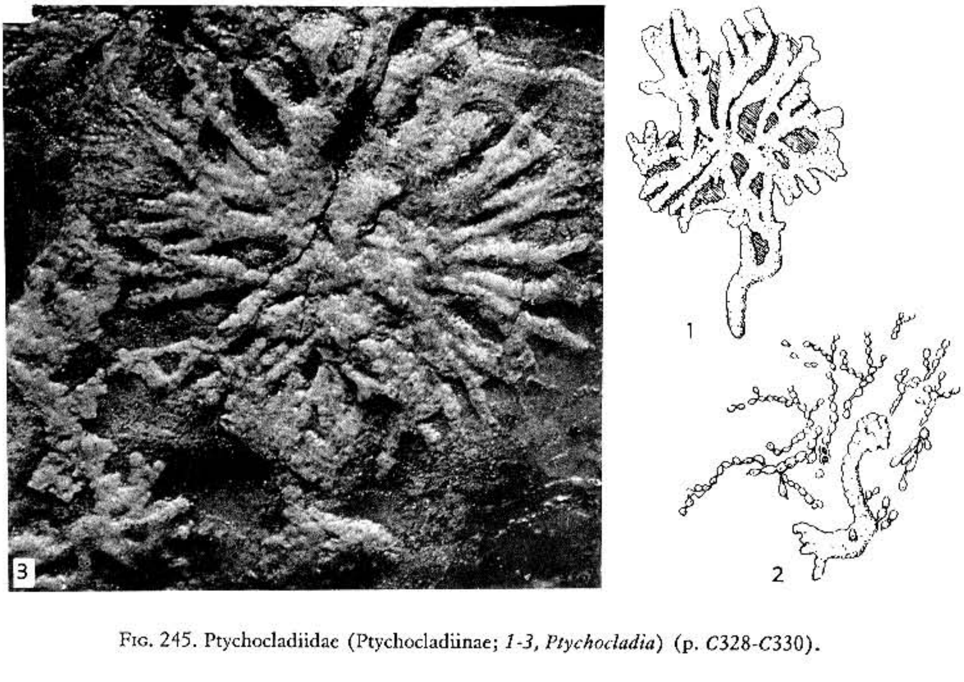


FIG. 245. Ptychocladiidae (Ptychocladiinae; *1-3, Ptychocladia*) (p. C328-C330).

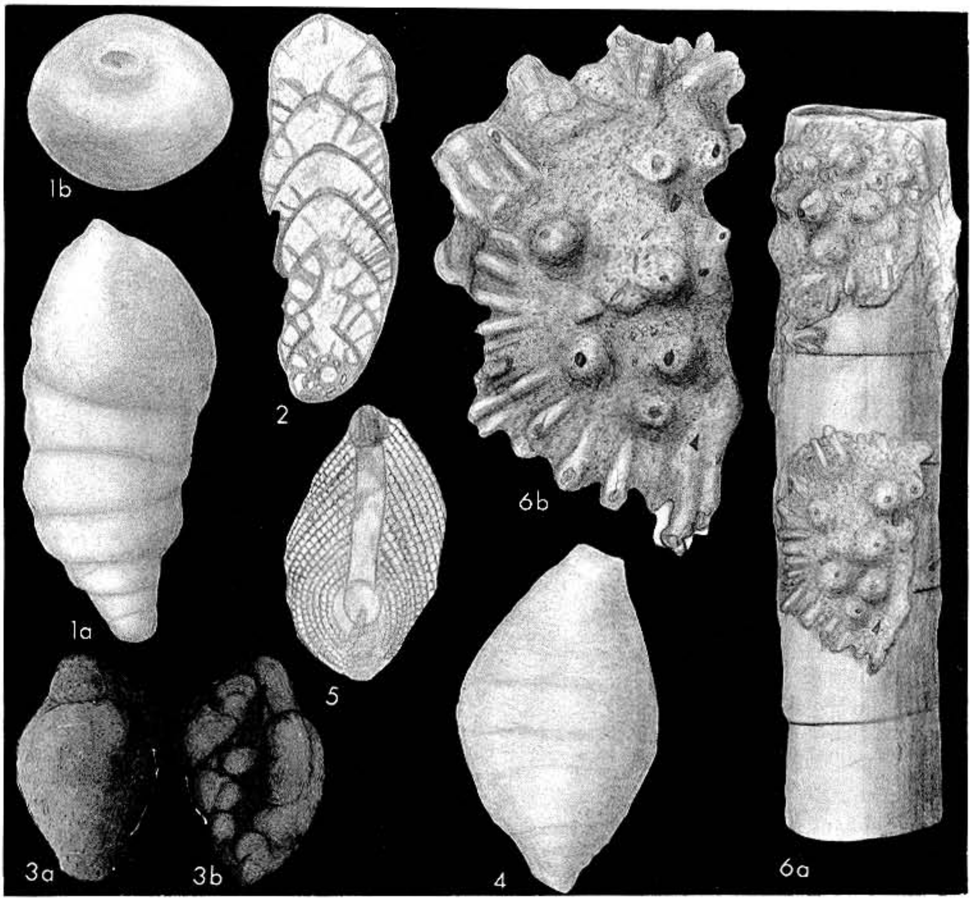


FIG. 246. Ptychocladiidae (Stacheiinae; *1,2, Stacheia; 3-5, Fourstonella; 6, Stacheoides*) (p. *C*330-*C*332).

layers of small chamberlets as in *Stacheoides*, early portion ?planispiral; wall calcareous, fibrous, aperture unknown. *L.Carb.(U.Visean)*, C.Morocco. ——FIG. 247,*1,2*. **A. variabilis*, nonoriented secs., ×40 (*1882).

[This genus is poorly known, very little information being available as to details of the wall structure or aperture. It was originally placed in the *Spirillinidae*, but none of that family show such attached, multichambered tests, nor are they composed of fibrous calcite. *Aoujgalia* seems closely related to *Stacheia, Stacheoides*, and *Fourstonella*. *Stacheia* has a similar irregular or acervuline growth habit, and both primary and secondary septal walls are of equal thickness to that of the chamber roofs and floors. *Stacheia* thus seems closest to *Aoujgalia* as far as its characters are known and would preoccupy it if they are found by additional study to be truly congeneric. *Fourstonella* has a distinctive fusiform shape, and regularly arranged chamberlets, the horizontal walls being of greater thickness than the vertical ones. *Stacheoides* has a low encrusting or sheetlike growth form, with mammilate protuberances and vertical chamberlet partitions of different thickness from floor and roofs. All occur in the Carboniferous.]

Fourstonella CUMMINGS, 1955, *398, p. 6 [**Stacheia fusiformis* BRADY, 1876, *193, p. 114; OD]. Test attached, commonly to crinoid stems or other thin columnar foreign objects, possibly encrusting algae, fusiform in outline; composed of many thin layers of small chambers, each layer nearly completely overlapping preceding one and subdivided into minute rectangular chamberlets, no external sutures visible; wall calcareous, finely granular, horizontal walls thicker than vertical secondary partitions, surface granular in appearance, with faint and irregular transverse grooves, possibly reflecting termination of layer of chambers; aperture not evident. [*Fourstonella* differs from *Stacheia* in its low, numerous layers of chambers and distinct chamberlets, with vertical walls thinner than those of horizontal layers. No early spire is present in *Fourstonella*.] *L.Carb. (Avon.)*, Eu.(Eng.).——FIG. 246,*3-5*. **F. fusiformis* (BRADY), Northumberland; *3a,b*, opposite sides of paratype (Glasgow Univ. Geology Coll. P1001), showing position of former attachment, ×44 (*398); *4*, lectotype (BMNH-P41654, *ex*

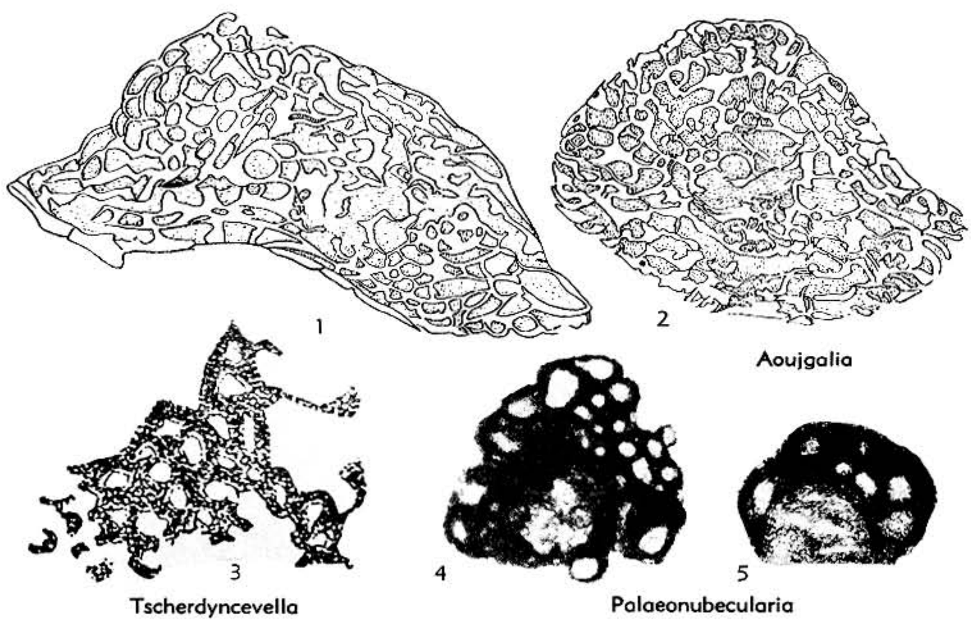


FIG. 247. Ptychocladiidae (Stacheiinae; *1,2, Aoujgalia; 3, Tscherdyncevella; 4,5, Palaeonubecularia*) (p. *C*330-*C*332).

P35458), redrawn; *5,* sectioned paratype (BMNH-P35509), redrawn; both ×65 (*2117).

Palaeonubecularia REYTLINGER, 1950, *1560, p. 91 [**P. fluxa*; OD]. Test attached, consisting of single chamber or of irregular aggregates of chambers; wall calcareous, microgranular, dark, compact. *M.Carb.(Moscov.)-Perm.,* USSR-USA (Kans.).——FIG. 247,*4,5.* **P. fluxa,* M.Carb., USSR(Moscov.); *4,* sec. of holotype, *5,* paratype, ×46 (*1560).

[Possibly *Palaeonubecularia* may be congeneric with *Aoujgalia,* but this is difficult to determine from published descriptions. Both genera were described in 1950, and the actual date (month and day) of publication has not been ascertained, to determine which has priority in the event they are found to be synonymous.]

Stacheoides CUMMINGS, 1955, *399, p. 343 [**Stacheia polytrematoides* BRADY, 1876, *193, p. 118; OD]. Test attached, encrusting mass irregular in outline, composed of numerous very tiny chamberlets with thickened partitions, small chamberlets clustered around random radiating tubules and forming mammilate protuberances; wall calcareous, finely granular, may have few quartz grains embedded in calcareous material, chamberlet partitions smaller in thickness than roofs and floors; apertures at ends of radiating tubules which form surface protuberances. *L.Carb.,* Eu.(Scot.).——FIG. 246,*6*; 248. **S. polytrematoides* (BRADY), Hosie Ls.; 246,*6a,b,* lectotype (here refigured, BMNH-P35405, =*193, pl. 9, figs. 10, 12), attached to crinoid stem, ×10, ×22 (*2117); 248, diagram. sec. of chamberlets on an attachment, ×18 (*399).

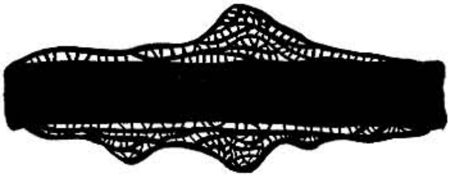


FIG. 248. Ptychocladiidae (Stacheiinae; *Stacheoides*) (p. *C*332).

[*Stacheoides* was described as related to *Nubecularia* of the Ophthalmidiidae. It differs from *Stacheia* in including adventitious material in the wall, in having chamberlet walls of different thickness than the roofs and floors, and in having numerous small apertures, instead of a single terminal aperture.]

Tscherdyncevella ANTROPOV, 1950, *25, p. 29 [**T. acervulinoides*; OD]. Test free or attached, irregular in form, consisting of one or many acervuline-arranged, successively added chambers; wall calcareous, structure obscure; apertures at base of chambers. *Dev.(Frasn.),* USSR(Russian Platform).——FIG. 247,*3.* **T. acervulinoides,* Tatar., USSR; sectioned specimen, ×120 (*1509).

Family PALAEOTEXTULARIIDAE
Galloway, 1933

[*nom. transl.* WEDEKIND, 1937, p. 79 (*ex* subfamily Palaeotextulariinae GALLOWAY, 1933, p. 221)]——[dagger(†) indicates *partim*]——[=Dischistidae† EIMER & FICKERT, 1899, p. 678 (*nom. nud.*); =Opistho-Dischistidae† EIMER & FICKERT, 1899, p. 677 (*nom. nud.*); =Cribrostomatidae WEDEKIND, 1937, p. 79]

Test biserial or may become uniserial; wall granular calcareous, with inner layer

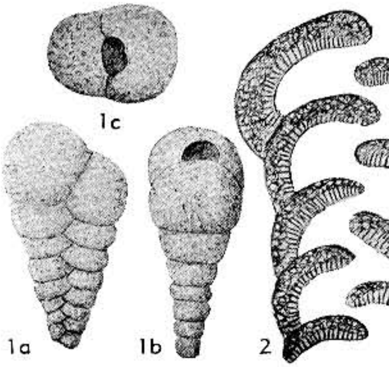


FIG. 249. Palaeotextulariidae; *1,2, Palaeotextularia* (p. *C*333).

and thin adventitious coating; aperture simple or multiple. *Carb.-Perm.*

Palaeotextularia Schubert, 1921, *1694, p. 183, 185 [**P. schellwieni* Galloway & Rynicker, 1930, *765, p. 20, =*Textularia textulariformis* (Möller) Schellwien, 1898, *1644, p. 268 (*non Cribrostomum textulariforme* Möller, 1879); SD Galloway & Rynicker, 1930, *765, p. 20]. Test free, biserial, as in *Textularia,* but with double-layered calcareous wall, outer finely granular layer and inner radial fibrous layer, and may have small amounts of embedded adventitious material in outer layer; aperture an interiomarginal arch. *Carb.-Perm.,* Eu.-N.Am.——Fig. 249,*1,2*. *P. grahamensis* (Cushman & Waters), Penn., USA (Okla.); *1a-c,* side, edge, and top views, ×35; *2,* portion of long. axial sec. showing 2 layers of wall, ×110 (*765).

Climacammina Brady in Etheridge, 1873, *711, p. 94 [**Textularia antiqua* Brady in Young & Armstrong, 1871, *2097, p. 13; OD (M)] [=*Cribrostomum* Möller, 1879, *1296, p. 39 (type, *C. textulariforme*); *Climaccamina* Scudder, 1882, *1709a, p. 77 *(nom. van.)*; *Moellerina* Eimer & Fickert, 1899, *692, p. 677 (type, *Cribrostomum gracile* Möller, 1879, *1296, p. 59, *non Moellerina* Ulrich, 1886; *nec* Schellwien, 1898); *Deckerella* Cushman & Waters, 1928, *538, p. 128 (type, *D. clavata*)]. Test free, large, early portion biserial, later with more or less well-developed uniserial portion; chambers increasing gradually in size, commonly broad, low, sutures depressed; wall calcareous, with 2 layers, inner layer radially fibrous, outer layer granular, and may have agglutinated particles; apertural face of chambers in late biserial and uniserial stages supported by irregular pillars between terminal wall and preceding septum, forming labyrinthic interior; aperture in earliest biserial chambers interiomarginal slit; in later chambers slit supplemented by one or more openings in septal face, gradually becoming nearly terminal in position, and in uniserial stage with 2 or more terminally placed openings, commonly very numerous and covering major portion of terminal face. *L.Carb.(U.Tournais.)-Perm.(Thuring.),* Eu.-N.Am.-Malay Arch.(Sumatra).——Fig. 250,*1*; 251,*1*. **C. antiqua* (Brady), L.Carb., Scot.; 250, *1a,b,* side, top views of hypotype, ×26 (*2117); 251,*1,* diagram. long. axial sec. showing chamber arrangement, 2-layered wall and multiple aperture (*401).——Fig. 250,*2*; 251,*2*. *C. clavata* (Cushman & Waters), Penn., USA(Tex.); 250,*2,* side, top views of holotype, ×30 (*2117); 251,*2,* long. axial sec., diagram. (*401).——Fig. 251,*3,4*. *C. textulariforme* (Möller), L.Carb.(Visean), USSR, side and long. axial sec., ×22 (*1509).

[Four generic names have been based on species which we consider to belong to *Climacammina.* Möller (1879) described *Cribrostomum* with 8 species, of which *C. textulariforme* Möller was later selected as type. Cushman separated *Cribrostomum* from *Climacammina* as being completely biserial, but later stated (*461, p. 111) "These may be only a stage in the development of *Climacammina.*" Plummer (1945, *1468, p. 244) stated that the "species" *Cribrostomum textulariforme* "is without doubt the immature form of one of the five biformed species in the group of eight 'species' recorded in the same paper with the description of *Cribrostomum. C. commune* Möller is recorded from the same localities as *C. textulariforme* and can well be the mature form of the species." Plummer considered *Cribrostomum* to differ from *Climacammina* in having irregular, more numerous, and irregularly spaced openings, whereas *Climacammina* had fewer, symmetrically shaped openings. As the original illustrations of *Cribrostomum* show only a few regularly spaced rounded pores which closely resemble those of the type-species of *Climacammina,* this distinction apparently fails to separate the two and we here consider *Cribrostomum* to be a synonym of *Climacammina. Moellerina* was defined by Eimer & Fickert, the type-species being later designated by Cushman (1928, *439, p. 120) as *Cribrostomum gracile* Möller. This species was originally placed in *Cribrostomum* and is typical of that genus. Furthermore, the

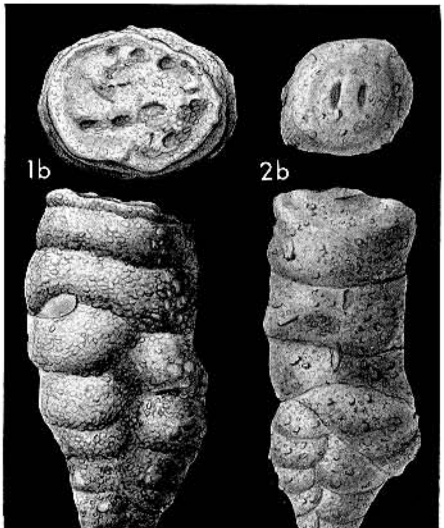


FIG. 250. Palaeotextulariidae; *1,2, Climacammina* (p. *C*333-*C*334).

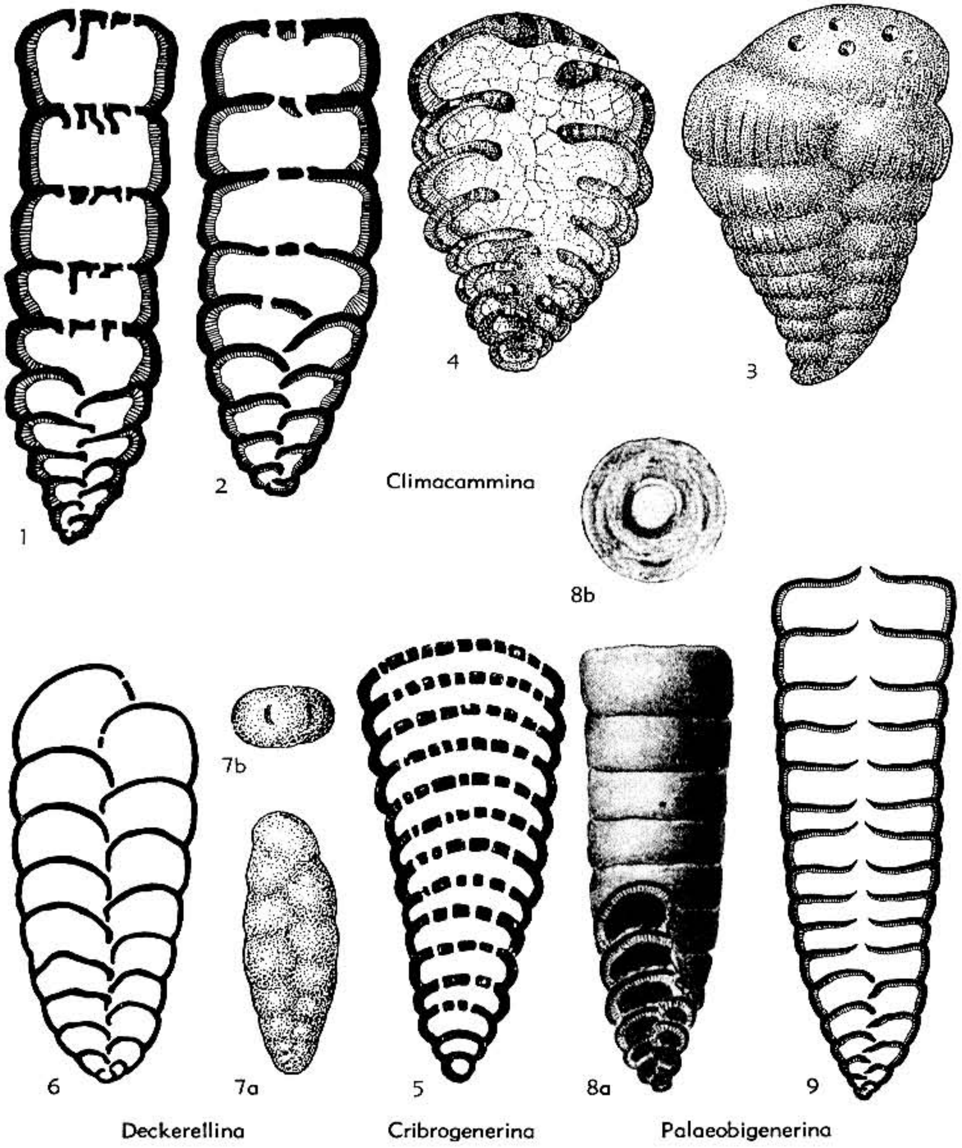


FIG. 251. Palaeotextulariidae; *1-4, Climacammina; 5, Cribrogenerina; 6,7, Deckerellina; 8,9, Palaeobigenerina* (p. *C333-C335*).

generic name *Moellerina* is a double homonym. *Deckerella* CUSHMAN & WATERS was defined as having only a paired aperture and not a truly multiple one. However, the type-species may have up to 4 openings and other species of *Climacammina* also may show relatively few openings; hence *Deckerella* is here regarded as a synonym of *Climacammina*.]

Cribrogenerina SCHUBERT, 1908, *1687, p. 245 [**Bigenerina sumatrana* VOLZ, 1904, *2024, p. 96 (=*B. sumatrensis,* *2024, p. 107, 108, 110); OD (M)]. Test free, elongate, uniserial and rectilinear, early portion biserial in microspheric generation, with 1 or 2 pairs of biserial chambers; chambers broad and low; wall calcareous, with outer granular layer and inner fibrous one; aperture terminal, cribrate, over most of terminal face. *?U.Carb., Perm.,* Asia(Sumatra-China).——FIG. 251,*5*. **C. sumatrana* (VOLZ), Perm., Sumatra, ×8 (*700).

[The validity of this genus is questionable. The species regarded by CUMMINGS (1956, *401) as belonging definitely to *Cribrogenerina* include 3 species described as *Bigenerina* by VOLZ (*B. sumatrana, B. leonhardi, B. wysogorskyi*). The last named shows a small biserial stage. The 2-layered

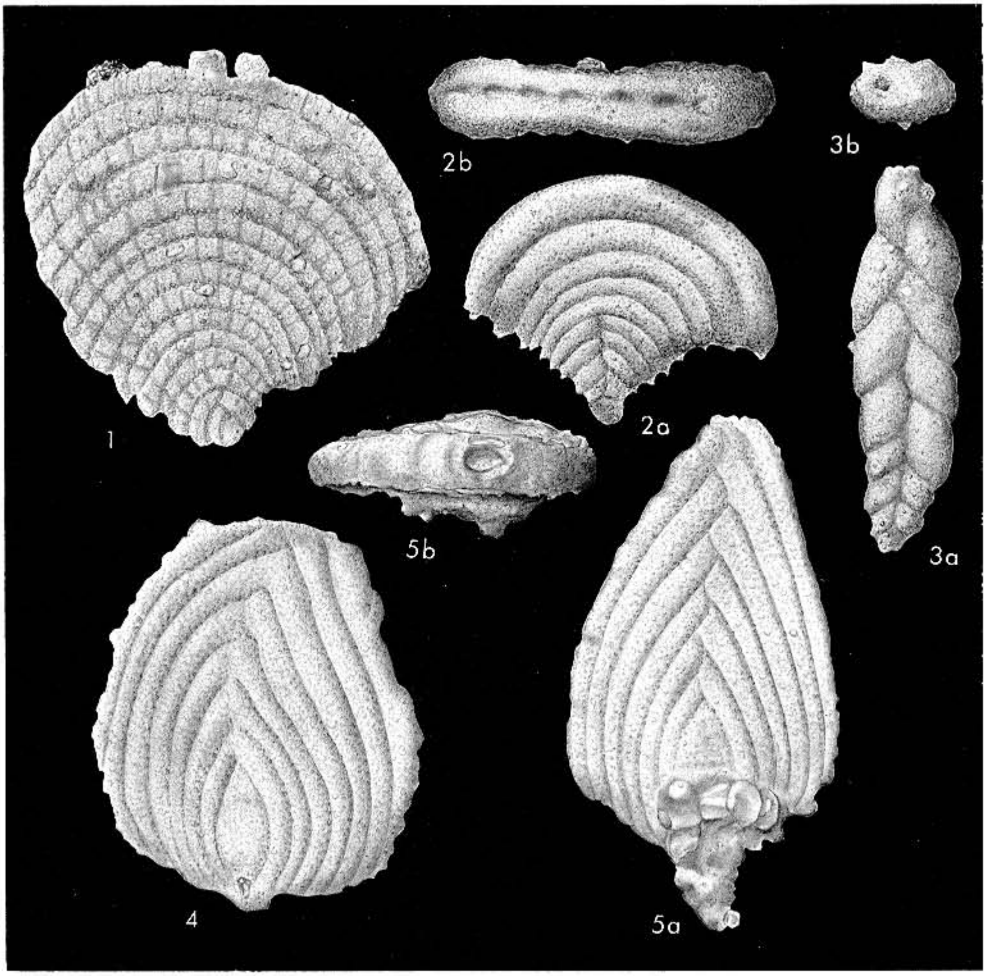


FIG. 252. Semitextulariidae; *1,2, Semitextularia; 3, Paratextularia; 4,5, Pseudopalmula* (p. *C*335-*C*337).

wall structure, as given by later workers, was not in the original definition of the species, and the only illustrations available are diagrammatic. *Cribrogenerina krizi* CUSHMAN, which has interseptal pillars and a well-developed biserial stage, should be referred to *Climacammina.* Other species distinguished from thin sections (and some on nonoriented sections) were regarded by CUMMINGS as needing further study.]

Deckerellina REYTLINGER, 1950, *1560, p. 57 [**D. istiensis;* OD]. Test biserial, as in *Palaeotextularia,* wall calcareous, finely granular, with radial layer poorly developed; aperture in earliest chambers interiomarginal, in later chambers with single supplementary lunate areal opening in addition. *L.Carb.(Visean),* Brit.I.; *M.Carb.(Moscov.),* USSR. ——FIG. 251,*6,7.* **D. istiensis,* M.Carb.(Moscov.), USSR; *7a,b,* side, top views, ×40 (*1560); *6,* diagram. long. sec. (*401).

Palaeobigenerina GALLOWAY, 1933, *762, p. 223 [**Bigenerina geyeri* SCHELLWIEN, 1898, *1644, p. 271; OD]. Test biserial in early stage, later uniserial, as in *Bigenerina* with relatively broad, low chambers; wall with 2 layers, as in *Palaeotextularia*; aperture terminal, rounded. *L.Carb. (Visean)-U.Perm.(Thuring.),* Eu.-N.Am.——FIG. 251,*8,9.* **P. geyeri* (SCHELLWIEN), U.Carb., Carnic Alps; *8a,b,* side, top views, ×25 (*700); *9,* diagram. long. axial sec. (*401).

Family SEMITEXTULARIIDAE Pokorný, 1956

[Semitextulariidae POKORNÝ, 1956, p. 284; Pseudopalmulidae E. V. BYKOVA in RAUZER-CHERNOUSOVA & FURSENKO, 1959, p. 264]

Test biserial or may become uniserial, compressed, chambers simple or with vertical pillars; aperture multiple. *Dev.*

Semitextularia A. K. MILLER & CARMER, 1933, *1281, p. 428 [**S. thomasi*; OD]. Test free, flattened, palmate, short early biserial portion with 2 to 4 pairs of broad, low alternating chambers, followed by more numerous, very broad, low,

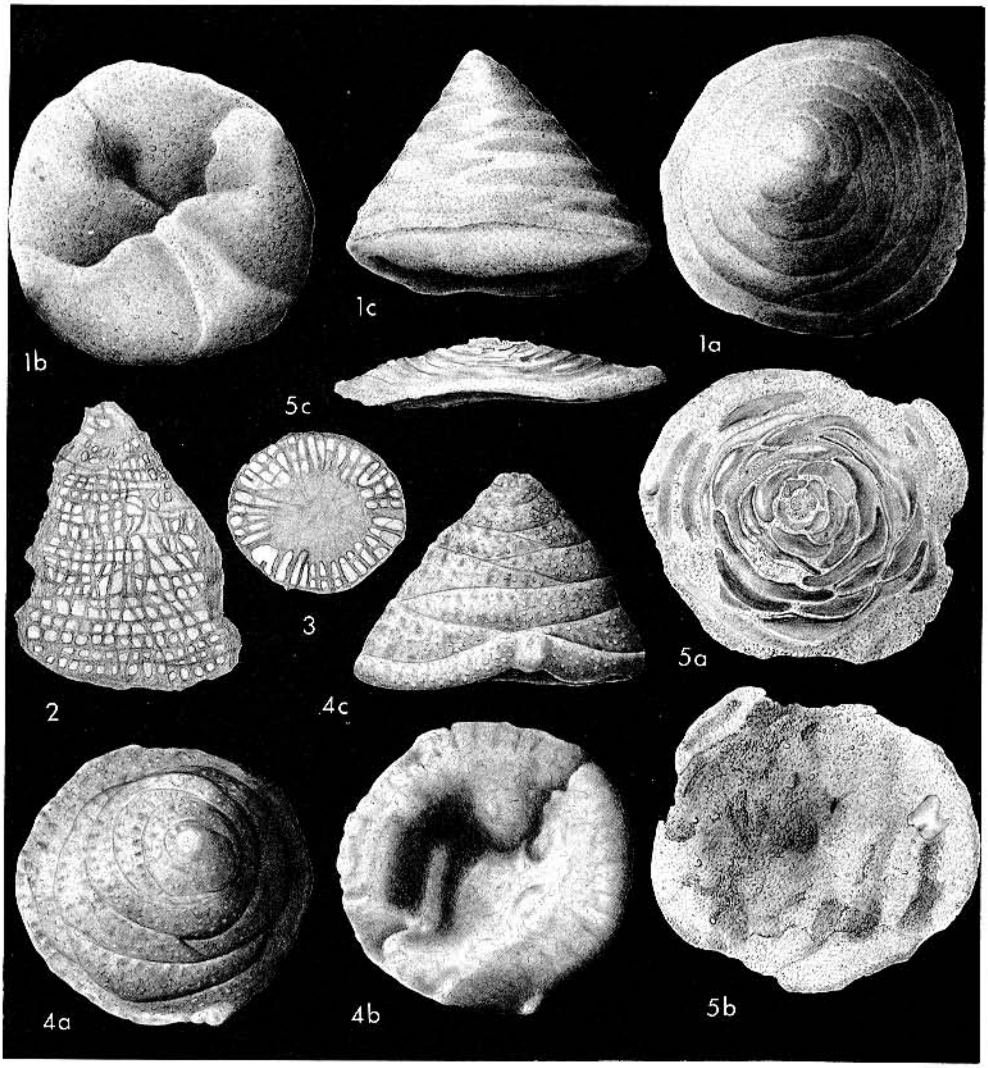


FIG. 253. Tetrataxidae; *1, Tetrataxis; 2-4, Valvulinella; 5, Polytaxis* (p. C337).

arched, uniserially arranged chambers somewhat overlapping and inflated laterally, may have lateral spinelike protuberances; interior of chambers with irregular vertical interseptal pillars, those of successive chambers not aligned; wall calcareous, finely granular; aperture consisting of single series of pores on outer margin of final chamber. *M. Dev.-U.Dev.*, N.Am.-Eu.——FIG. 252,*1,2*. **S. thomasi*, USA(Iowa); *1*, large specimen as seen when dampened to show interseptal pillars; *2a,b*, side, top views; all ×86 (*2117).

[The original description stated that the early portion was coiled, also that (p. 429) "the planispiral arrangement of these early chambers has been observed only in one of the better preserved specimens with the aid of transmitted light." Later workers have shown only biserial early development. We have examined a large number of specimens and have also found no trace of an early coil. Perhaps the poor preservation may have given an erroneous suggestion of this feature in the single specimen.]

Paratextularia POKORNÝ, 1951, *1472, p. 20 [**Textularia*(?) *proboscidea* CUSHMAN & STAINBROOK, 1943, *524, p. 78; OD] [=*Cremsia* E. V. BYKOVA, 1952, *257, p. 50 (obj.)]. Test free, elongate; chambers biserially arranged throughout, final chamber typically somewhat produced; wall calcareous, finely granular; aperture terminal, rounded, on prolongation of final chamber. *Dev.*, N.Am.-Eu.——FIG. 252,*3*. **P. proboscidea* (CUSHMAN & STAINBROOK), USA(Iowa); *3a,b*, side, top views, ×109 (*2117).

[*Paratextularia* and *Cremsia* were defined with the same type-species. *Paratextularia* differs from *Palaeotextularia* SCHUBERT, as described, in having a terminal aperture rather than an interiomarginal one. They may prove synonymous after a restudy of the original specimens or

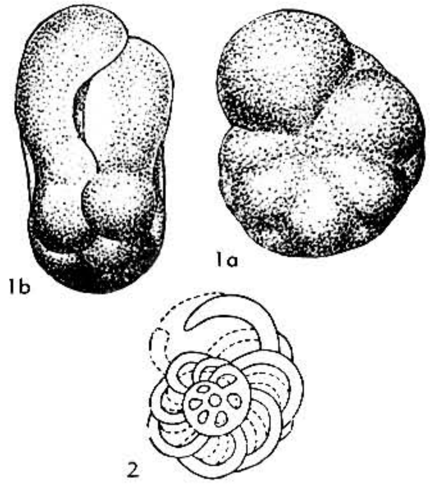


FIG. 254. Biseriamminidae; *1,2, Biseriammina* (p. *C*338).

topotypes of the type-species, *Palaeotextularia schellwieni* GALLOWAY & RYNIKER, 1930. Other species later referred to *Palaeotextularia* include both those with terminal aperture and others with a typical textularian aperture. If the type-species is found to have a terminal aperture and to be otherwise similar, SCHUBERT's name would have priority over *Paratextularia*. However, the original figures appear to be of an internal cast, and the apertural position is not well defined, so that both are here tentatively recognized.]

Pseudopalmula CUSHMAN & STAINBROOK, 1943, *524, p. 78 [*P. palmuloides; OD]. Test free, small, palmate, flattened; chambers biserially arranged throughout, low, very broad, extending far back toward proloculus on each side; wall calcareous, finely granular; aperture ovate on apertural face of final chamber, nearly terminal. [*Pseudopalmula* differs from *Paratextularia* in its palmate test and ovate aperture which is not produced on a neck.] *Dev.*, N.Am.-Eu.——FIG. 252, *4,5*. *P. palmuloides, USA(Iowa); *4*, holotype; *5a,b*, side, top views of paratype, ×127 (*2117).

Family TETRATAXIDAE Galloway, 1933

[*nom. transl.* POKORNÝ, 1958, p. 199 (*ex* subfamily Tetrataxinae GALLOWAY, 1933, p. 161); Tetrataxiinae REYTLINGER, 1950, p. 71]

Test free, trochospiral, few chambers in whorl, conical; wall granular calcareous, in 2 layers. *Miss.-Trias.*

Tetrataxis EHRENBERG, 1854, *680, p. 24 [*T. conica; OD (M)] [=*Tetrataxis* EHRENBERG, 1843, *671, p. 106 *(nom. nud.)*; *Ruditaxis* SCHUBERT, 1921; *1694, p. 180 (type, *Valvulina rudis* BRADY, 1876, *193, p. 90); *Artetraxoum* RHUMBLER, 1913, *1572b, p. 391 *(nom. van.)*; *Pseudotetrataxis* MARIE in DELEAU & MARIE, 1961, *580A, p. 91 (type, *Tetrataxis planolocula* LEE & CHEN, 1930, *1121, p. 94); *Falsotetrataxis* MARIE in DELEAU & MARIE, 1961, *580A, p. 95 (type, *Tetrataxis scutella* CUSHMAN & WATERS, 1928, *536, p. 65)]. Test free, trochospirally coiled, with all of numerous broad, low chambers visible on spiral side, and only rather few (commonly 4) of final whorl visible on umbilical side, umbilical cavity broad; wall calcareous, with 2 distinct layers, outer one microgranular and inner fibrous; aperture umbilical. [*Ruditaxis* is based on the type-species *Valvulina rudis* BRADY. His original specimens of this species in the British Museum (Natural History) are crushed internal casts, probably of *Tetrataxis*. The genera are here regarded as synonymous.] *Carb.-Trias.*, N.Am.-Eu.-Japan.——FIG. 253,*1*. *T. conica, Carb., Brit.I.; *1a-c*, spiral, umbilical, and edge views, ×51 (*2117).

Polytaxis CUSHMAN & WATERS, 1928, *535, p. 51 [*P. laheei; OD]. Test low conical, similar to *Tetrataxis* in early stage, later spreading, with numerous small chambers to whorl; aperture on umbilical side, ?several. [The aperture is not clearly distinguishable on the type-specimen, although the genus was described as having several elongate ventral openings. *Polytaxis* sp. of PAYARD (*1432), from the Jurassic belongs to the agglutinated genus *Tritaxis* in the Trochamminidae.] *U.Carb.*, N.Am.-Eu.(Carnic Alps).——FIG. 253,*5*. *P. laheei, Penn., USA(Tex.); *5a-c*, spiral, umbilical, and edge views of holotype, ×19 (*2117).

Valvulinella SCHUBERT, 1907 (separate of 1908, *1687, p. 248, dated 1907) [*Valvulina youngi BRADY, 1876, *193, p. 86; SD SCHUBERT, 1908, *1686, p. 379] [=*Valvulinella* SCHUBERT, 1907, *1684, p. 211 *(nom. nud.)*; *Palaeovalvulina* SCHU-

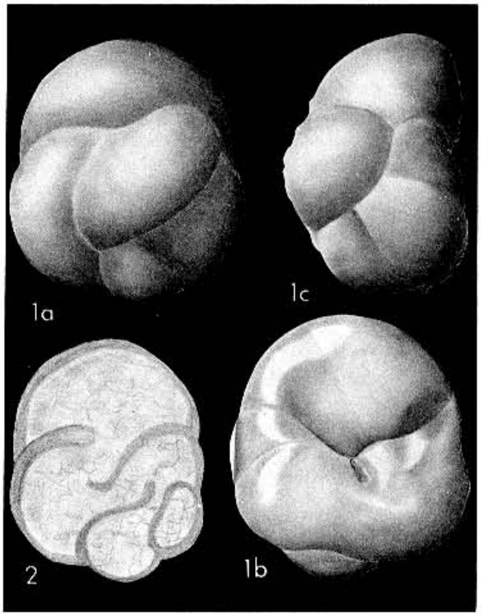


FIG. 255. Biseriamminidae; *1,2, Globivalvulina* (p. *C*338).

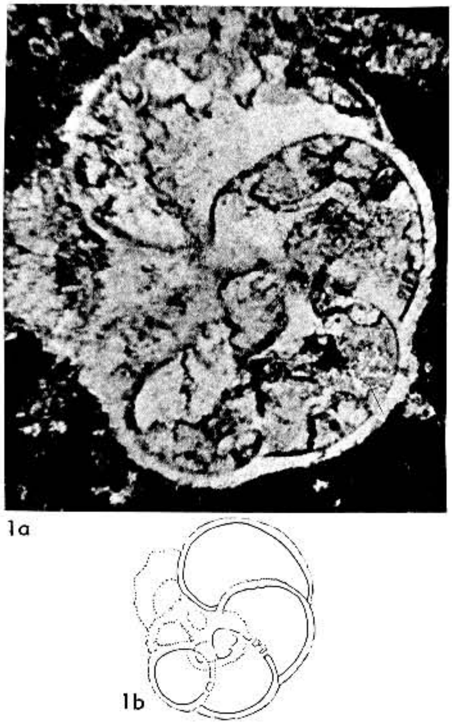


FIG. 256. Biseriamminidae; *1, Olympina* (p. C338).

BERT, 1921, *1694, p. 179 (type, *Valvulina youngi* BRADY, 1876, *193, p. 86, SD LOEBLICH & TAPPAN, herein) (obj.); *Palaeovalvuloria* NEAVE, 1940, *1348c, p. 534 *(nom. null.)*]. Test conical, chambers trochospirally arranged with only 2 or 3 chambers to whorl; interior subdivided by horizontal and vertical partitions, chamberlets slightly visible through outer wall; wall calcareous, microgranular; aperture interiomarginal, on umbilical side. [Differs from *Tetrataxis* in having secondary partitions which form numerous tiny chamberlets. The Jurassic species previously assigned to *Valvulinella* are here placed in *Kurnubia.* The lectotype (BMNH-P41656) and paratypes (BMNH-P35519, P35520, P41655) are from the Carboniferous, Brockley, Lanarkshire, England.] *L.Carb. (Miss.)-U.Carb.(Penn.),* Eu.-N.Am.——FIG. 253, *2-4.* **V. youngi* (BRADY), L.Carb., Eng.; *2,* long. sec. (*193, pl. 4, fig. 8), ×47 (*2117); *3,* transv. sec. (*193, pl. 4, fig. 9), ×47 (*2117); *4a-c,* spiral, umbilical, and edge views, ×65 (*2117).

Family BISERIAMMINIDAE Chernysheva, 1941

[Biseriamminidae CHERNYSHEVA, 1941, p. 70] [=Globivalvulinae REYTLINGER, 1950, p. 75; =Globivalvulininae POKORNÝ, 1958, p. 200]

Test enrolled, biserial, involute; aperture at inner border of septal face. *L.Carb.-Perm.*

Biseriammina CHERNYSHEVA, 1941, *335, p. 69 [**B. uralica*; OD]. Test free, chambers biserially arranged, with axis of biseriality planispirally enrolled; wall calcareous, microgranular; aperture comprising narrow interiomarginal slit where chambers of opposed pair touch at short distance above contact with earlier whorl. *L.Carb.(M. Tournais.),* USSR(S.Urals).——FIG. 254,*1,2*. **B. uralica*; *1a,b,* side, edge views; *2,* cross sec. showing chamber arrangement, dotted lines representing opposed pair of chambers, ×53 (*335).

Globivalvulina SCHUBERT, 1921, *1694, p. 153 [**Valvulina bulloides* BRADY, 1876, *193, p. 89; OD]. Test free, subglobular to hemispherical when somewhat flattened on broad apertural face; chambers biserially arranged with axis of biseriality planispirally to slightly trochospirally coiled; wall calcareous, microgranular, may have inner fibrous or porous layer particularly well developed along septa; aperture interiomarginal against opposite, penultimate chamber, partially covered by valvular projection extending toward opposite chamber near center of apertural face, commonly overlapping aperture of penultimate chamber. [*Globivalvulina* differs from *Biseriammina* in being more advanced, with an apertural valvular projection.] *U.Penn.-Perm.,* N.Am.-Eu.-C.Asia.——FIG. 255,*1,2*. **G. bulloides* (BRADY), U.Penn., USA(Iowa); *1a-c,* opposite sides and edge of syntype, ×93; *2,* sec. of syntype, redrawn (BMNH-P35518, *193, pl. 4, fig. 14), ×79 (*2117).

Olympina REICHEL, 1945, *1517, p. 540 [**O. insolita*; OD]. Test enrolled, chambers inflated, few to whorl; wall calcareous, perforate; aperture in septal face. *Perm.,* Medit.(Cyprus). —— FIG. 256,*1*. **O. insolita; 1a,* holotype, photograph of sec., ×55; *1b,* sketch from photograph showing chambers and septal aperture, ×33 (*1517).

[This genus, described from 2 sections in an algal limestone, is unknown as to mode of coiling, although it was suggested that the umbilical region seemed to show the possibility of a trochospiral arrangement. From comparison of the figures, it seems probable that *Olympina* could also be a biserially enrolled form and it is here transferred to the Biseriamminidae. The strong similarity to sections of *Biseriammina* suggests that further study may even show *Olympina* to be a junior synonym of *Biseriammina.*]

Family TOURNAYELLIDAE Dain, 1953

[Tournayellidae DAIN in DAIN & GROZDILOVA, 1953, p. 16] ——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}family, ^{2}subfamily)] ——[=^{2}Glomospirellinae REYTLINGER, 1950, p. 26 *(nom. nud.)*; =^{2}Tournayellinae DAIN in DAIN & GROZDILOVA, 1953, p. 20; =^{2}Tournauellinae DAIN in DAIN & GROZDILOVA, 1953, p. 21 *(nom. null.)*; =^{2}Forschiinae DAIN in DAIN & GROZDILOVA, 1953, p. 20, 38; =^{1}Forschiidae GROZDILOVA & LEBEDEVA, 1954, p. 36; =^{2}Forshiinae REYTLINGER, 1953, p. 60 *(nom. null.)*; =^{1}Teurnayellidae REYTLINGER, 1958, p. 60 *(nom. null.)*]

Test free, proloculus followed by planispirally enrolled tubular second chamber, subseptate, with slight protuberances or incipient septa forming pseudochambers; wall calcareous, granular, and may have agglutinated inclusions; aperture simple or cribrate. *U.Dev.-U.Perm.*

Tournayella Dain in Dain & Grozdilova, 1953, *550, p. 30 [*T. *discoidea*; OD] [=*Carbonella* Dain in Dain & Grozdilova, 1953, *550, p. 36 (type, *C. spectabilis*); *Septatournayella* Lipina,

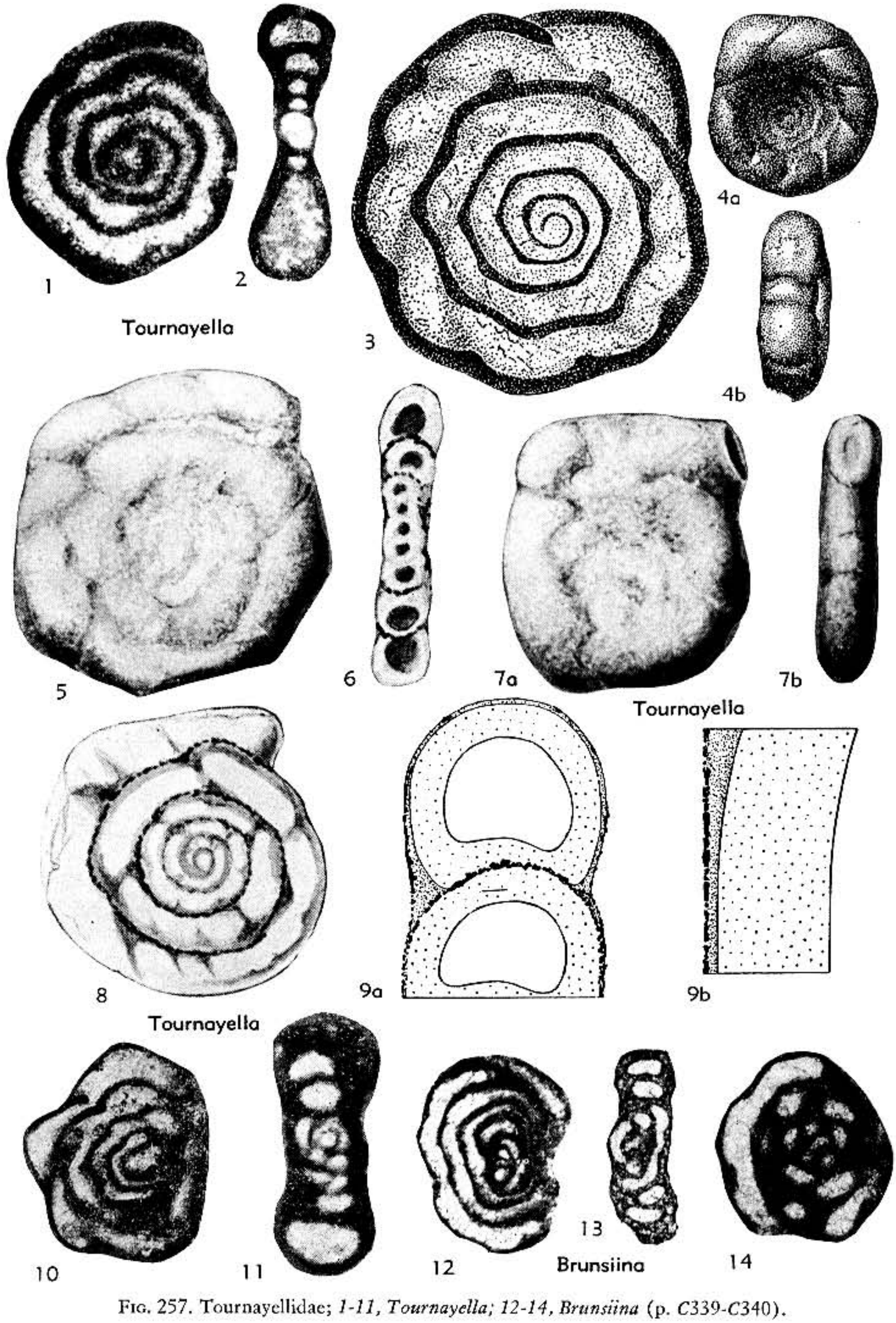


FIG. 257. Tournayellidae; *1-11, Tournayella; 12-14, Brunsiina* (p. C339-C340).

1955, *1143, p. 36 (type, *Tournayella segmentata* Dain in Dain & Grozdilova, 1953, *550, p. 34); *Cepekia* Vašíček & Ružička, 1957, *1985, p. 342 (type, *C. cepeki*)]. Test discoidal, with spherical proloculus and planispirally coiled pseudoseptate later portion, slight apertural constrictions of tubular chamber being preserved as poorly developed septa or slight infoldings of wall; wall thick, calcareous, inner thick translucent layer of microgranular calcite with thin dark opaque layer developed where final whorl overlaps previous coils, and secondary calcareous translucent thickening in sutural depressions; aperture simple rounded or elliptical opening formed by moderate constriction of terminal portion of tubular chambers. *U. Dev. - L. Carb.(Tournais.-Visean) - U. Carb. (Namur.)*, USSR-Czech.——Fig. 257,*1,2*. **T. discoidea*, Tournais., USSR(Donets Basin); *1*, equat. sec. of holotype; *2*, axial sec. of paratype; both ×100 (*550).——Fig. 257,*3,4*. *T. spectabilis* (Dain), Tournais., USSR(Donets Basin); *3*, equat. sec., ×60 (*550); *4a,b*, side, edge views of holotype, ×43 (*550).——Fig. 257,*5-9*. *T. cepeki* (Vašíček & Ružička), Namur., Czech.; *5,7a,b*, side, edge views of paratypes; *6,8*, axial and equat. secs. of paratypes, ×81; *9a,b*, diagrams of wall structure showing part of axial sec. and enlargement of one side of wall with inner granular layer regarded as equivalent to epitheca of fusulinids, dark thin opaque layer resembling fusulinid tectum, and secondary thickening at septal depressions (=protheca) (*1985).——Fig. 257, *10, 11*. *T. segmentata* Dain, Tournais., USSR; *10*, equat. sec., ×70 (*1143); *11*, axial sec., ×81 (*831).

[*Carbonella* was regarded originally as slightly more advanced than *Tournayella*, with better developed "septation," but the slight differences in the holotypes of the 2 type-species suggest that only specific distinction should be made. *Septatournayella*, as based on the type-species, has chambers of more irregular width, slightly inflated, and fewer chambers in each whorl, but these also are here regarded as of specific distinction only. *Cepekia cepeki*, type-species of *Cepekia*, is very similar to *Carbonella spectabilis* Dain, and most probably specifically identical, as well as congeneric.]

Brunsiina Lipina in Dain & Grozdilova, 1953, *550, p. 27 [**B. uralica*; OD] [=*Glomospiranella* Lipina in Dain & Grozdilova, 1953, *550, p. 21 (type, *G. asiatica*)]. Early portion in streptospiral coil, later planispiral and similar to *Tournayella* in poorly developed septation; aperture simple, at slightly constricted open end of tubular chamber. [Differences between *Brunsiina* and *Glomospiranella* largely consist of a shorter period of streptospiral coiling in *Brunsiina*. This is here regarded as of specific importance only.] *U.Dev.-L.Carb.(Tournais.)*, USSR.——Fig. 257, *12,13*. **B. uralica*, Tournais.; *12*, equat. sec. of holotype; *13*, axial sec. of paratype; both ×100 (*550).——Fig. 257,*14*. *B. asiatica* (Lipina), Tournais., Sib.; equat. sec. of holotype, ×76 (*1143).

Forschia Mikhaylov, 1939, *1260, p. 50, 59 [**Spirillina subangulata* von Möller, 1879, *1296, p. 27, 130 (=*S. angulata* von Möller, 1879, *1296, p. 27) *(nom. null.)*; OD]. [=*Forschia* Mikhaylov, 1935, *1259, p. 41 *(nom. nud.)*]. Test free, proloculus followed by planispiral evolutely coiled tubular chamber, without distinct septation; aperture terminal, cribrate where tube flares terminally. *L.Carb.(Visean)*, USSR.——Fig. 258,*1-3*. **F. subangulata* (von Möller); *1*, equat. sec., ×60 (*1509); 2, axial sec., ×20 (*1509); *3*, axial sec., ×75 (*1296).

Forschiella Mikhaylov, 1935, *1259, p. 41 [**F. prisca*; OD]. Early stage similar to *Forschia*, later uncoiling and septate; aperture cribrate. *L.Carb. (Visean)*, USSR.——Fig. 258,*7*. **F. prisca*; paratype showing axial sec. through early coiled stage, ×59 (*769).

Glomospiroides Reytlinger, 1950, *1560, p. 28 [**G. fursenki* (*nom. imperf.*, =*G. fursenkoi*, *nom. correct.* Voloshinova, Dain & Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 184); OD] [=*Glomospirella* Reytlinger, 1950, *1560, p. 27 (type, *G. borealis*) (*non Glomospirella* Plummer, 1945)]. Test with early glomospirine coil, later uncoiling, septate throughout, but septa thin and irregular; wall calcareous, finely granular; aperture terminal, simple. *M.Carb.(Moscov.)*, USSR.——Fig. 258, *4,5*. **G. fursenkoi*; *4*, long. sec. of holotype; *5*, tang. sec., ×76 (*1560).——Fig. 258,*6*. *G. borealis* (Reytlinger), holotype, ×76 (*1560).

[Originally *Glomospirella* Reytlinger, 1950 (*non* Plummer, 1945) included species with early glomospirine coil and later irregular development, whereas *Glomospiroides* became distinctly rectilinear in the later stage. Voloshinova, Dain & Reytlinger in Rauzer-Chernousova & Fursenko (1959, *1509, p. 184) regarded *Glomospirella* Reytlinger as a synonym of *Glomospiroides*.]

Gourisina Reichel, 1945, *1517, p. 539 [**G. broennimanni*; OD]. Status of genus doubtful; known only from a single section, it was described as having a calcareous wall, radially striate, with thin dark granular inner layer, and formed from 2 series of chambers in spire around proloculus. [It could equally well consist of a nonseptate plectogyrally coiled tube, so-called chambers consisting of sections through the tube as it spiraled. Because of the similarity to *Glomospiranella* in sections, it is here placed with the Tournayellidae.] *U.Perm.*, Greece(Attica).——Fig. 258,*10*. **G. broennimanni*; *10a,b*, holotype, photograph of thin sec. and outline of same showing chamber development, ×80 (*1517).

Lituotubella Rauzer-Chernousova, 1948, *1502, p. 161 [**L. glomospiroides*; OD]. Test with long tubular chamber, early stage in unsegmented glomospirine coil, later uncoiling, with regular constrictions of wall indicating chambers; no complete septa; wall granular, calcareous; aperture at open end of tube. *L.Carb.(Visean)*, USSR.——Fig. 258,*8,9*. **L. glomospiroides*; *8*, median sec. of early coil; 9, long. sec. of holotype, ×50 (*1502).

Septabrunsiina Lipina, 1955, *1143, p. 42 [**Endothyra? krainica* Lipina, 1948, *1141, p. 254; OD] [=*Septaglomospiranella* Lipina, 1955, *1143, p. 46 (type, *Endothyra? primaeva* Rauzer-Chernousova, 1948, *1505, p. 5); *Tournayellina* Lipina, 1955, *1143, p. 52 (type, *T. vulgaris*)]. Early

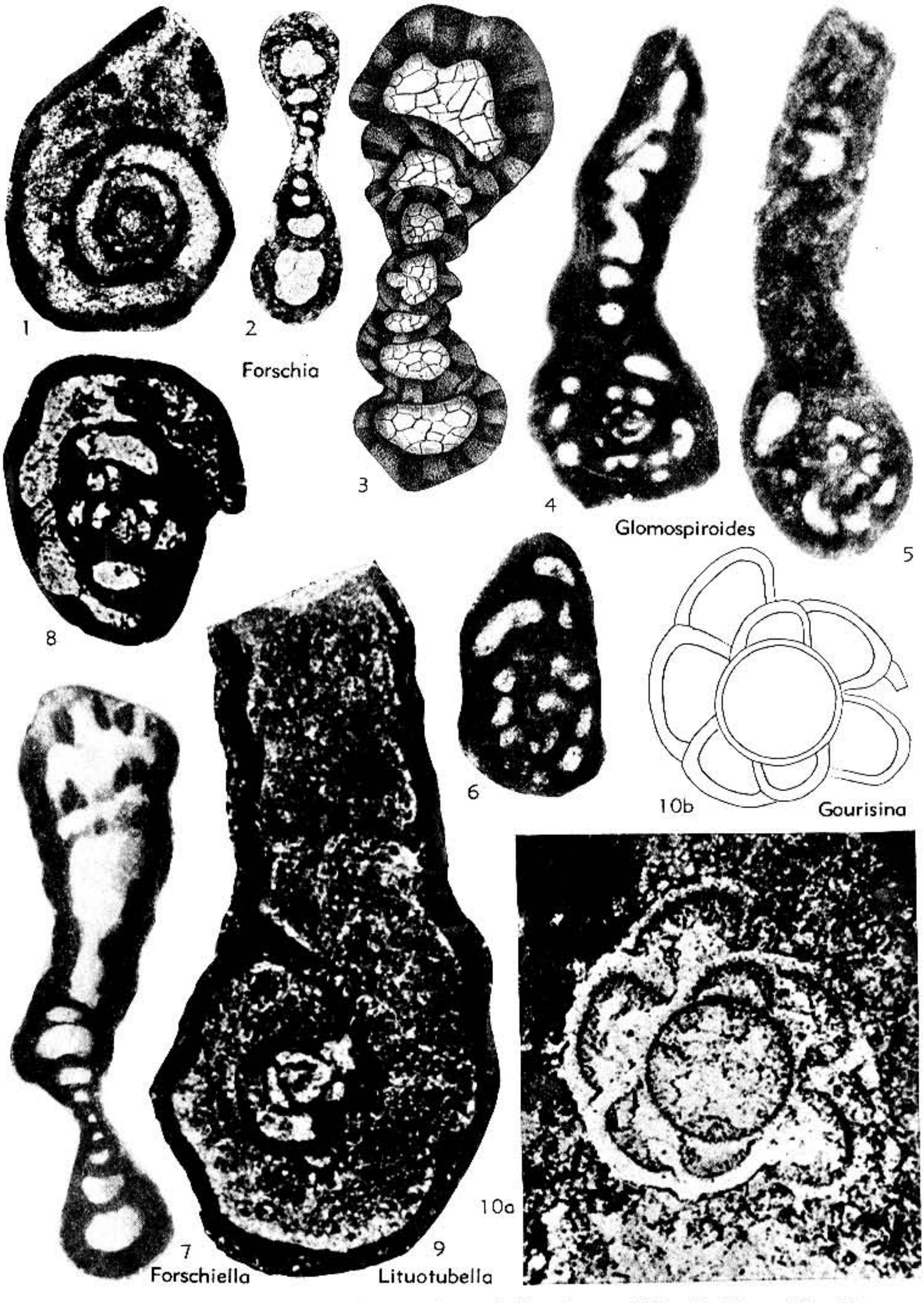


Fig. 258. Tournayellidae; *1-3, Forschia; 4-6, Glomospiroides; 7, Forschiella; 8,9, Lituotubella; 10, Gourisina* (p. *C*340).

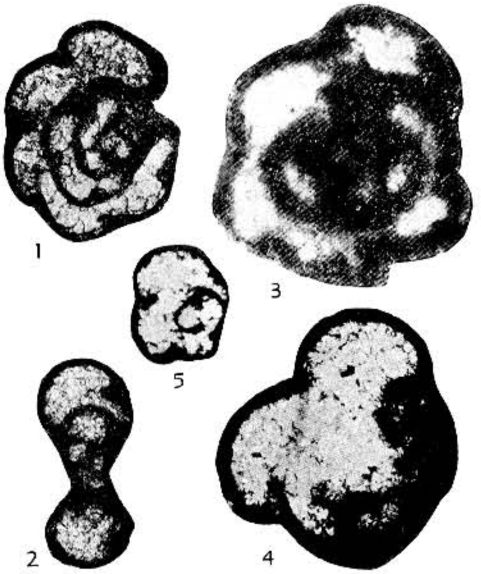


FIG. 259. Tournayellidae; *1-5, Septabrunsiina* (p. C341-C342).

stage streptospiral and poorly or nonseptate, later planispiral as in *Brunsiina,* but with few inflated chambers to whorl, resulting in appearance of better-developed septation in later portion; wall calcareous, microgranular; aperture simple, at open end of tube. *U.Dev.-L.Carb.(Tournais.),* USSR.——FIG. 259,*1,2*. **S. krainica* (LIPINA), Tournais.; *1,* equat. sec.; *2,* axial sec.; both ×70 (*1143).——FIG. 259,*3*. *S. primaeva* (RAUZER-CHERNOUSOVA), Tournais.; ×100 (*550).——FIG. 259,*4,5*. *S. vulgaris* (LIPINA), L.Carb.; *4,* subequat. sec. of paratype (early coil poorly seen); *5,* equat. sec. of smaller paratype showing early spire, ×70 (*1143).

Family ENDOTHYRIDAE Brady, 1884

[*nom. correct.* RHUMBLER, 1895, p. 92 (*pro* family Endothyrina LANKESTER, 1885, p. 847)]——[All names referred to are of family rank]——[=Endothyrinae DELAGE & HÉROUARD, 1896, p. 133; =Cribrospiridae WEDEKIND, 1937, p. 79; =Plectogyridae REYTLINGER MS in POYARKOV, 1957, p. 29; =Bradyinidae REYTLINGER, 1958, p. 57]

Test enrolled, planispiral or plectogyral; aperture simple or multiple. *Dev.-Perm.*

Subfamily LOEBLICHIINAE Cummings, 1955

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 286 (*pro* subfamily Loeblichinae CUMMINGS, 1955, p. 3)] [=Nanicellinae FURSENKO in RAUZER-CHERNOUSOVA & FURSENKO, 1959, p. 252]

Test planispiral, compressed, involute or evolute; chambers numerous; aperture basal. *Dev.-Perm.*

Loeblichia CUMMINGS, 1955, *398, p. 3 [**Endothyra ammonoides* BRADY, 1873, *190, p. 63, 95; OD]. Test free, discoidal, planispiral and evolute, with numerous whorls; chambers small, numerous, appearing rectangular in horizontal section; sutures distinct, radial; wall calcareous, finely granular; aperture low equatorial, interiomarginal arch. [*Loeblichia* differs from *Endothyra* PHILLIPS in being evolute rather than involute and planispiral rather than with changing axis of coiling. It also has a much shorter axis of coiling, resulting in a discoid or complanate test, and far more numerous whorls and chambers in each whorl. It differs from *Nanicella* in being completely evolute, and with more numerous chambers.] *L.Carb.(Visean),* Brit.I.-USSR.——FIG. 260,*1,2*; 261,*1*. **L. ammonoides* (BRADY), Eng.; 260,*1a,b,* side, edge views of lectotype (BMNH-P41650, *193, pl. 5, fig. 5), redrawn; 260,*2,* sec. of paratype (BMNH-P35500, *193, pl. 5, fig. 6), redrawn, ×64 (*2117); 261,*1a,* axial sec. (where septa are cut area appears darker), ×75; 261,*1b,* diagram of wall structure, enlarged (*398).

Eocristellaria K. V. MIKLUKHO-MAKLAY, 1954, *1277, p. 67 [**E. permica*; OD]. Test ovate in outline, with gradually enlarging chambers arranged as in *Astacolus*; wall calcareous, with outer hyaline layer and granular calcareous inner layer; aperture peripheral, ?radiate. *U.Perm.,* USSR(Caucasus).——FIG. 261,*4*. **E. permica,* holotype, ×47 (*1277).

Nanicella HENBEST, 1935, *895, p. 34 [**Endothyra gallowayi* THOMAS, 1931, *1907, p. 40; OD]. Test planispirally coiled and partially evolute; chambers numerous, low; wall calcareous with thin dark outer layer and thicker inner finely granular layer; aperture interiomarginal equatorial slit. *Dev.,* N.Am.-USSR.——FIG. 260,*3,4*; 261,*2,3*. **N. gallowayi* (THOMAS), USA(Iowa); 260,*3a,b,4,* side, edge views of topotypes, ×99 (*2117); 261,*2,3a,* axial and equat. secs. of paratypes; *3b,* portion of *3a* enlarged (*1907).

Rhenothyra H. BECKMANN, 1950, *103, p. 184, 187 [**R. refrathensis*; OD]. Test planispiral, evolute, similar to *Loeblichia,* but with few chambers to whorl; wall with 3 layers; aperture large, rounded, at the base of apertural face. [*Loeblichia* may prove to be a synonym of *Rhenothyra,* but in view of the fewer chambers in each whorl, fewer whorls, different wall structures described, large, round aperture instead of a basal slit, and the different geologic ages, both are tentatively recognized.] *M.Dev.,* Eu.——FIG. 261,*8-10*. **R. refrathensis,* Ger.; *8,9,* equat. and axial secs.; *10,* somewhat abraded exterior of holotype; approx. ×60 (*103).

Robuloides REICHEL, 1945, *1517, p. 531 [**R. lens*; OD] [=*Pararobuloides* K. V. MIKLUKHO-MAKLAY, 1954, *1277, p. 65 (type, *P. orientalis*)]. Test lenticular, nearly planispiral, involute, periphery acute; wall calcareous perforate, radially striate, with lamellar thickening pronounced; septa porous as is outer wall; aperture circular to radiate, areal, in lower part of septal face. [*Robuloides* differs from *Lenticulina* in the wall character, in having

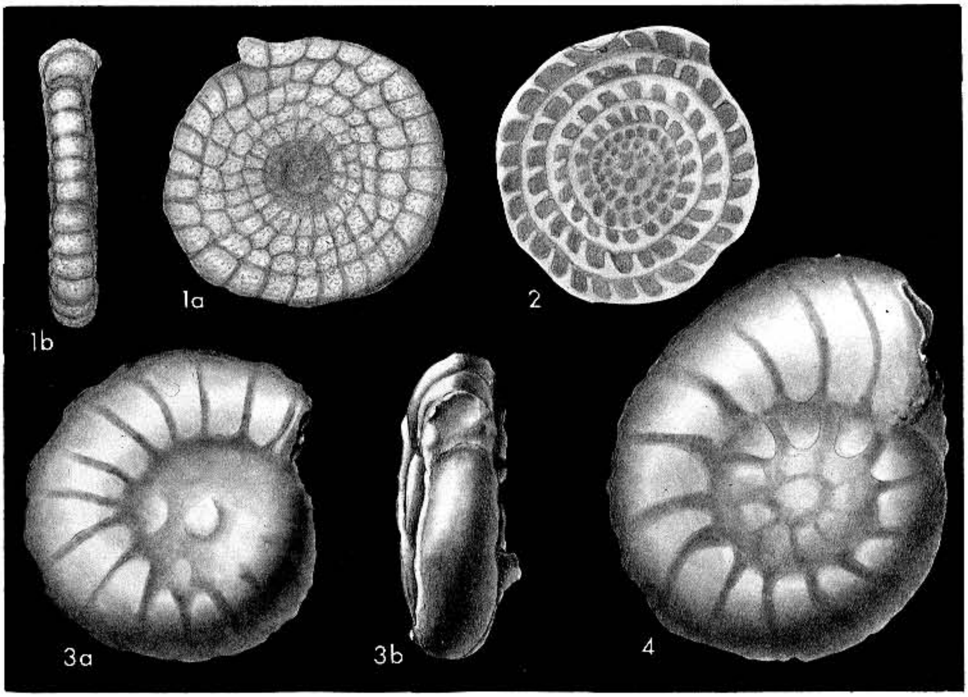


Fig. 260. Endothyridae (Loeblichiinae; *1,2, Loeblichia; 3,4, Nanicella*) (p. *C*342).

perforate septa, and an areal rounded aperture instead of a radial aperture at the dorsal angle.] *U.Perm.*, Eu.(Greece)-USSR(Caucasus). —— Fig. 261,*5,6*. **R. lens,* Greece(Hydra Is.); *5,* holotype nearly equat. sec., tang. to proloculus; *6,* paratype, slightly oblique axial sec.; both ×100 (*1517).——Fig. 261,*7*. *R. orientalis* (K. V. Miklukho-Maklay), USSR(Caucasus), axial sec. of holotype, ×47 (*1277).

Subfamily ENDOTHYRINAE Brady, 1884

[Endothyrinae Brady, 1884, p. 66] [=Plectogyrinae Reytlinger, 1958, p. 57; =Quasiendothyrinae Reytlinger, 1961, p. 53]

Test enrolled, planispiral to streptospiral, possibly uncoiling in later stages; may be incompletely septate; wall of granular calcite, nonporous, with 2 or 3 distinct layers in well-preserved specimens, may have agglutinated material in addition; aperture single, simple, basal or areal. *U.Dev. (Famenn.)-Perm.*

Endothyra Phillips, 1846, *1452B, p. 277 (*nom. conserv.* ICZN (S.) 768, pending) (*non Endothyra* Gude, 1899) [**E. bowmani* (=*Involutina lobata* Brady, 1870, *187A, p. 382); =*Endothyra bradyi* Mikhaylov, 1939, *1260, p. 51 (*nom. conserv.* ICZN (S.) 768, pending); OD (M)] [*Endothyra* Phillips in Brown, 1843, *245, p. 17 (*nom. reject.* ICZN (S.) 768, pending)] [=*Plectogyra* Zeller, 1950, *2103, p. 3 (type, *P. plectogyra*); *Plectogyrina* Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 196 (type, *Endothyra*(?) *fomichaensis* Lebedeva, 1954, *1100, p. 256); *Endostaffella* Rozovskaya, 1961, *1593, p. 20 (type, *Endothyra parva* Möller, 1879, *1296, p. 18)]. Test enrolled, partially involute, plane of coiling changes during growth, turning through 30°-90°, may turn gradually as in plectogyral coiling, or abruptly nearly 90°, few chambers to whorl, whorls few; wall calcareous, with 2 layers, thin dark outer layer (tectum) and thicker, fibrous alveolar, inner layer (diaphanotheca); partial recrystallization may result in granular appearance, secondary deposits in form of nodes, ridges, or forward-directed hooks secreted on chamber floors; external aperture not always evident, but interiomarginal, equatorial to asymmetrical slit may be present, relatively large intercameral foramina in same position. *?U.Dev., L.Carb.-Perm.*, Eu.-N. Am.-Afr.-Japan-S.Am.——Fig. 262,*1,2*. **E. bowmani,* L.Carb., Eng.; *1a,b,* side and apertural views of neotype, here designated, showing "skew"-coiling, ×82; *2,* equat. sec. (Brady's specimen BMNH-P41674 *ex* P35440) showing coiling, ×64 (*2117).——Fig. 262,*3*. *E. plectogyra* (Zeller), U.Miss.(Meramec.), USA(Mo.); equat. sec. of holotype, ×66 (*2103).——Fig. 262,*4,5*. *E.* sp., U.Miss.(Meramec.), USA(Mo.); *4,* axial sec., ×66 (*2103); *5,* equat. sec. showing well-developed hook-shaped secondary deposit in final chamber, ×66 (*2103).——FIG. 262,*6,7*. *E. fomichaensis* LEBEDEVA, L.Carb.(Visean), USSR; *6*, equat. sec. of paratype, ×33 (*1100); *7*, axial sec., ×20 (*1509).——FIG. 263,*8*. *E.* sp., diagram of wall structure (*398).

[The confusion as to the status of *Endothyra* has been

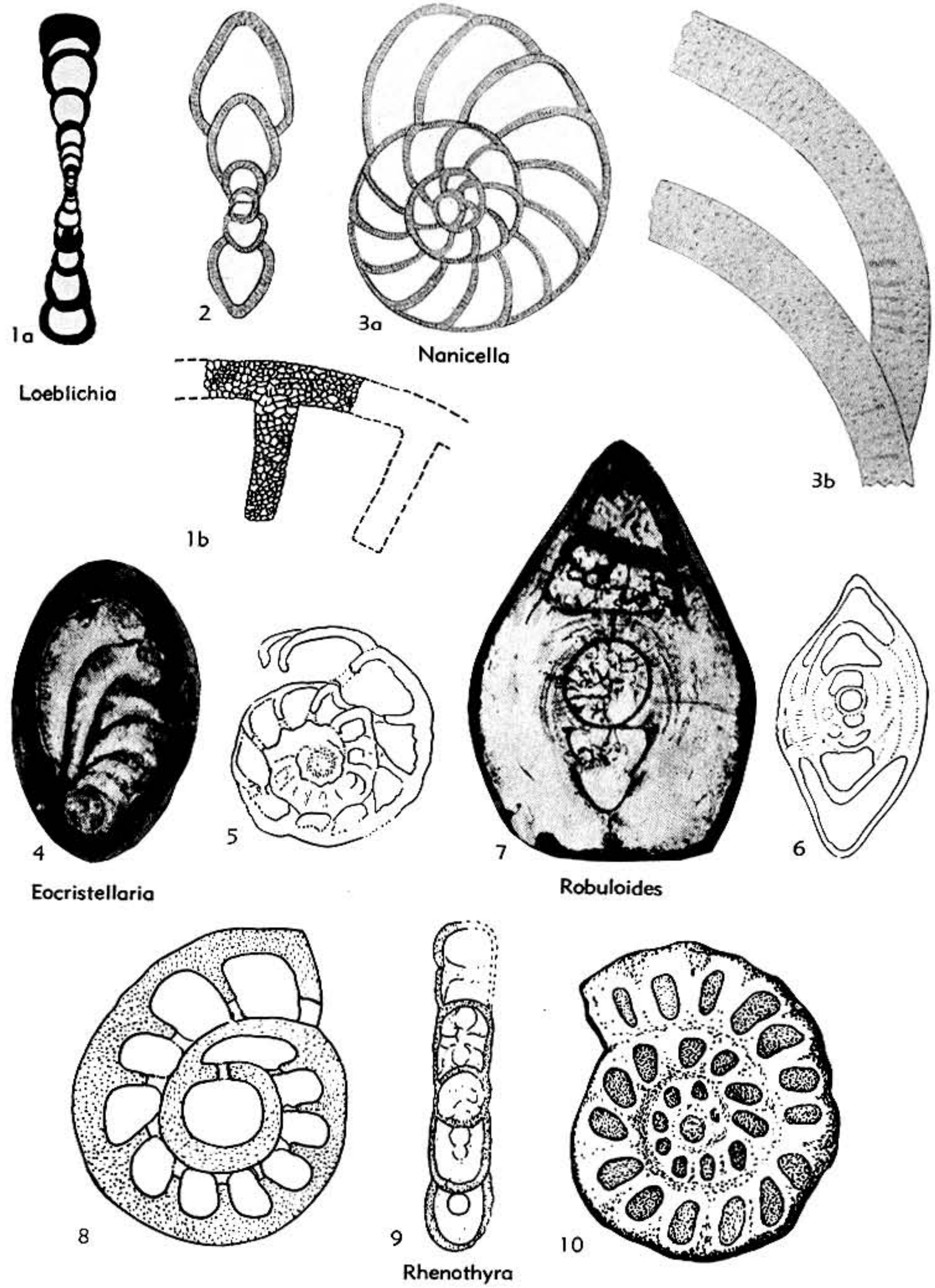


FIG. 261. Endothyridae (Loeblichiinae; *1, Loeblichia; 2,3, Nanicella; 4, Eocristellaria; 5-7, Robuloides; 8-10, Rhenothyra*) (p. *C342-C343*).

discussed in detail by Scott, Zeller & Zeller (1947, *1708), Zeller (1950, *2103), Henbest (1953, *897), and St. Jean (1957, *1619), some authors regarding the plectogyral and planispiral modes of coiling as representing only a dimorphism found within most species. Others have regarded it variously as a generic, subfamily, or family character. According to Henbest (1953, *897, p. 64), about 1 per cent of shells referred to *Endothyra baileyi*

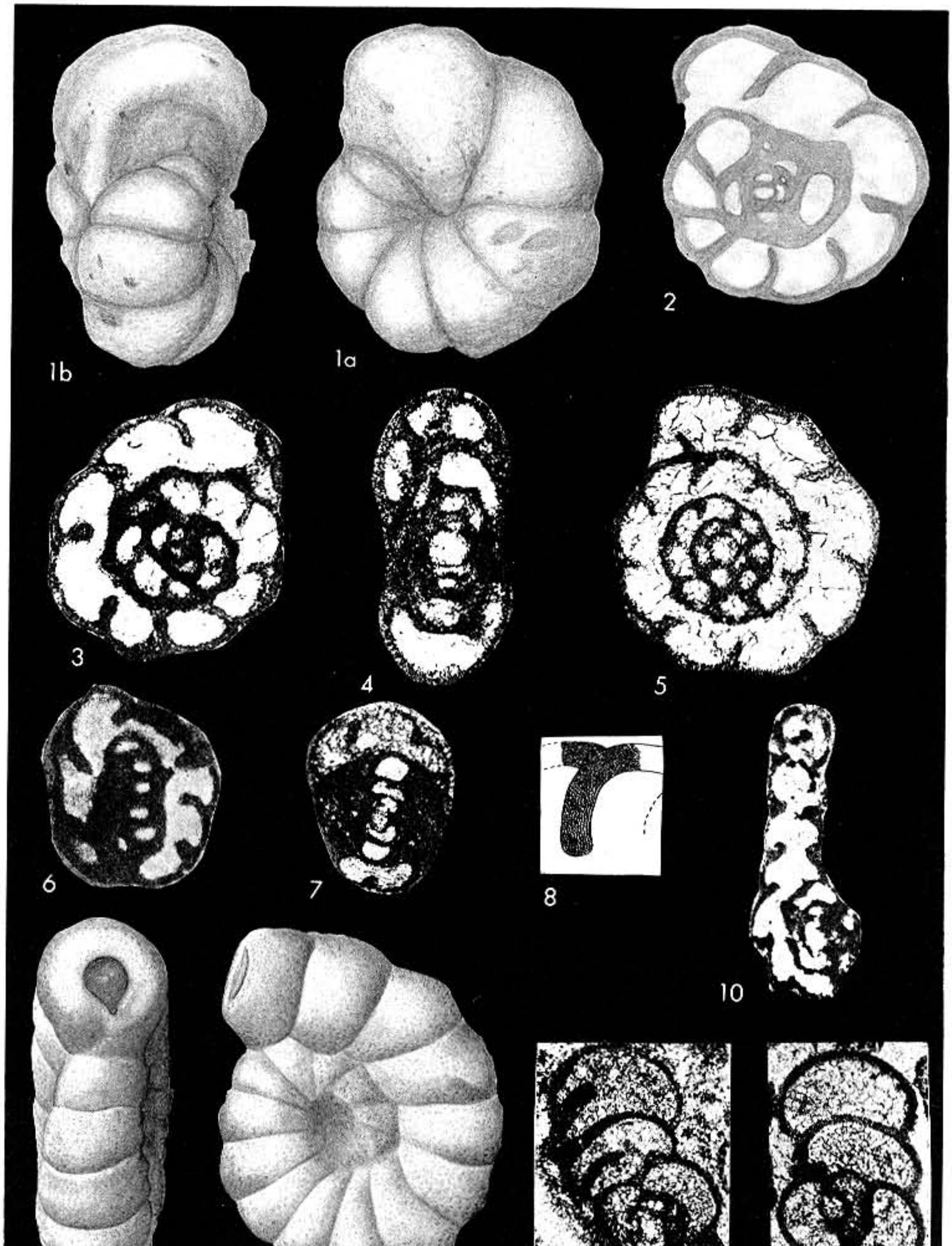


Fig. 262. Endothyridae (Endothyrinae; *1-8, Endothyra; 9-12, Endothyranella*) (p. C343-C346).

(Hall) have an early plectogyral coil and later planispiral growth, the remainder being planispiral throughout. *Endothyra? fomichaensis* has a sharp change of 90° in plane of coiling just before the final whorl is added. Much of the confusion is due to the loss of the type specimens of *Endothyra*. Henbest (1953, *897) stated that a petition was to be submitted to the ICZN validating *Endothyra* Phillips, 1846, as emended by Brady, 1876, and to suppress "*Endothyra* Brown, 1843." This was again referred to by St. Jean (1957, *1619), but apparently such a petition has never been formally acted upon by the ICZN. In the interests of stability of nomenclature and because of loss of the original types of *Endothyra bowmani* Phillips the specimen of Brady in the British Museum (Natural History) (BMNH-P41665, *ex* P35440) here redrawn, is designated as neotype. It is from the Carboniferous, Brankamhall Quarry, Lanarkshire. After the present text had been sent to press, May, 1962, Henbest published the ICZN petition Z.N. (S.) 768, July, 1962, in which *Endothyra bowmani* Phillips, 1846, is to be conserved, in the sense of Brady, 1876, and *Endothyra bowmani* Phillips in Brown, 1843, rejected.]

Dainella Brazhnikova, 1962 (see p. *C*795).

Endothyranella Galloway & Harlton in Galloway & Ryniker, 1930, *765, p. 13 [**Ammobaculites powersi* Harlton, 1927, *879, p. 21; OD] [=*Chernyshinellina* Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 196 (type, *Ammobaculites pygmaeus* Malakhova, 1954, *1207, p. 58); *Rectochernyshinella* Lipina, 1960, *1145, p. 51 (type, *Spiroplectammina mirabilis* Lipina, 1948, *1141, p. 257)]. Test free, early portion enrolled and plectogyral, later nearly planispiral, finally uncoiling and becoming rectilinear; wall calcareous, fibrous, or may be recrystallized and granular, aperture high interiomarginal equatorial arch, later areal and terminal in uncoiled portion. *L.Carb.(U.Miss.)-U.Penn.*, USA-USSR.——Fig. 262,*9*. **E. powersi* (Harlton), Penn., USA(Okla.); *9a,b*, side, edge views of holotype, ×76 (*2117).——Fig. 262,*10*. *E. pygmaea* (Malakhova), L.Carb.(Tournais.), USSR; long. sec., ×66 (*1509).——Fig. 262, *11,12*. *E. mirabilis* (Lipina), L.Carb.(Tournais.), USSR; long. secs. of holotype and paratype, ×50 (*700).

[*Chernyshinellina* was regarded as differing in characters of the septa, which were a gradual extension of the outer chamber wall and not sharply delineated. The angle of septal insertion is here regarded as of specific value only and *Chernyshinellina* is thought to be a synonym of *Endothyranella*. The briefly diagnosed *Rectochernyshinella* was regarded as similar to *Chernyshinellina*, with a biserial later stage. The type-species (original figures here reproduced) is known only from thin sections and shows some irregularities in chamber development, but is not truly biserial. Later references to the type-species (*1143, pl. 13, figs. 10, 11) are equally inconclusive. It is regarded as a synonym of *Endothyranella*.]

Kahlerina Kochansky-Devidé & Ramovs, 1955, *1047A, p. 383, 412 [**K. pachytheca*; OD] [=*Ussuriella* Sosnina in Kiparisova *et al.*, 1956, *1040, p. 21 (type, *U. ussurica*) (*non Ussuriella* Paramonov, 1929)]. Test enrolled, subspherical, umbilici slightly indented; early coiling somewhat plectogyral, that of microspheric form having 1 or 2 abrupt turns of about 90 degrees similar to *Endothyra*, few (4-8) whorls; microspheric proloculus small and globular, megalospheric proloculus up to 0.14 mm., 8-10 chambers per whorl, increasing fairly rapidly in height; septa straight, radial, thick-walled; wall thick, of 2 layers (referred to tectum and keriotheca, although keriothecal structure is indistinct), reduced chomata, as in *Quasiendothyra*, and some very small parachomata rarely present, tunnel low, not continuous, observed rarely; foramina and very fine septal pores present. [Originally *Kahlerina* was regarded as a primitive form placed in the Verbeekininae *1047A), but later it was transferred to the Staffellinae (*1509). It is here considered as simpler than the Fusulinacea and tentatively placed in the Endothyrinae.] *U.Perm.*, Yugoslav.-USSR.——Fig. 262A,*1*. **K. pachytheca*, U.Perm., Yugoslav.; *1a*, axial sec. of microspheric form (holotype), ×40; *1b*, axial sec. of megalospheric form, ×20; *1c,d*, median secs. of microspheric forms, ×20 (*1047A).——Fig. 262A,*2*. *K. ussurica* (Sosnina), U.Perm., USSR; *2a,b*, axial and median secs., ×25; *2c*, portion of wall showing "keriothecal" structure, ×70 (*1040).

Novella Grozdilova & Lebedeva, 1950, *830A, p. 20 [**N. evoluta*; OD]. Test small, discoidal, planispiral and evolute, symmetrical; early chambers small and globular, later ones numerous, relatively broad and low and forming 2.5 to 7 whorls; septa straight, simple; wall thin, undifferentiated, chomata well developed in later whorls; aperture a single crescentic opening. [Originally placed with the staffellids, close to *Eostaffella* and *Millerella*, it was also considered to be related to *Nanicella*. It is here assigned to the Endothyrinae, because of the undifferentiated wall, single aperture, and presence of chomata.] *U.Carb.(Namur.-Moscov.)*, USSR.——Fig. 262A,*3*. **N. evoluta*, *Moscov.*, Ural Mtns.; *3a,b*, axial secs. of paratype and holotype, ×100 (*830A).——Fig. 262A,*4*. *N. primitiva* Rauzer-Chernousova, Vereisk., medial sec., ×80 (*2074).

Paraendothyra Chernysheva, 1940, *334, p. 129, 134 [**P. nalivkini*; OD]. Test free, enrolled, slightly evolute, biumbilicate, early coiling plectogyral, later nearly planispiral; wall dark, coarsely granular; aperture areal, crescentic slit. [*Paraendothyra* is characterized by its areal aperture.] *L. Carb.(Tournais.)*, USSR(Urals).——Fig. 263,*1-3*. **P. nalivkini*; *1a,b*, side, apert. views, ×30; *2*, axial sec., ×40; *3*, equat. sec., ×40 (*1509).

Paraplectogyra Okimura, 1958, *1386, p. 254 [**P. masanae*; OD]. Test similar to *Endothyra*, but wall with 3 distinct layers, corresponding to tectum, diaphanotheca, and lower tectorium of fusulinids. *L.Carb.-Low.U.Carb.*, Japan.——Fig. 263,*6,7*. **P. masanae*, L.Carb.(M.Miss.); *6*, axial sec. of paratype; *7*, equat. sec. of holotype, ×125 (*1386).

Quasiendothyra Rauzer-Chernousova, 1948, *1504, p. 228 [**Endothyra kobeitusana* Rauzer-Chernousova, 1948, *1505, p. 7; OD] [=*Cribroendothyra* Lebedeva, 1956, *1101, p. 46 (type, "*C.* no. 1 sp. et gen. nov.," *nom. nud.*); *Planoendothyra* Reytlinger, 1958, *1564, p. 57 (*nom.*

nud.); *Planoendothyra* REYTLINGER in RAUZER-CHERNOUSOVA & FURSENKO, 1959, *1509, p. 194 (type, *Endothyra aljutovica* REYTLINGER, 1950, *1560, p. 34); *Eoendothyra* MIKLUKHO-MAKLAY, 1960, *1273, p. 140 (type, *Endothyra communis* RAUZER-CHERNOUSOVA, 1948, *1505, p. 6)]. Test

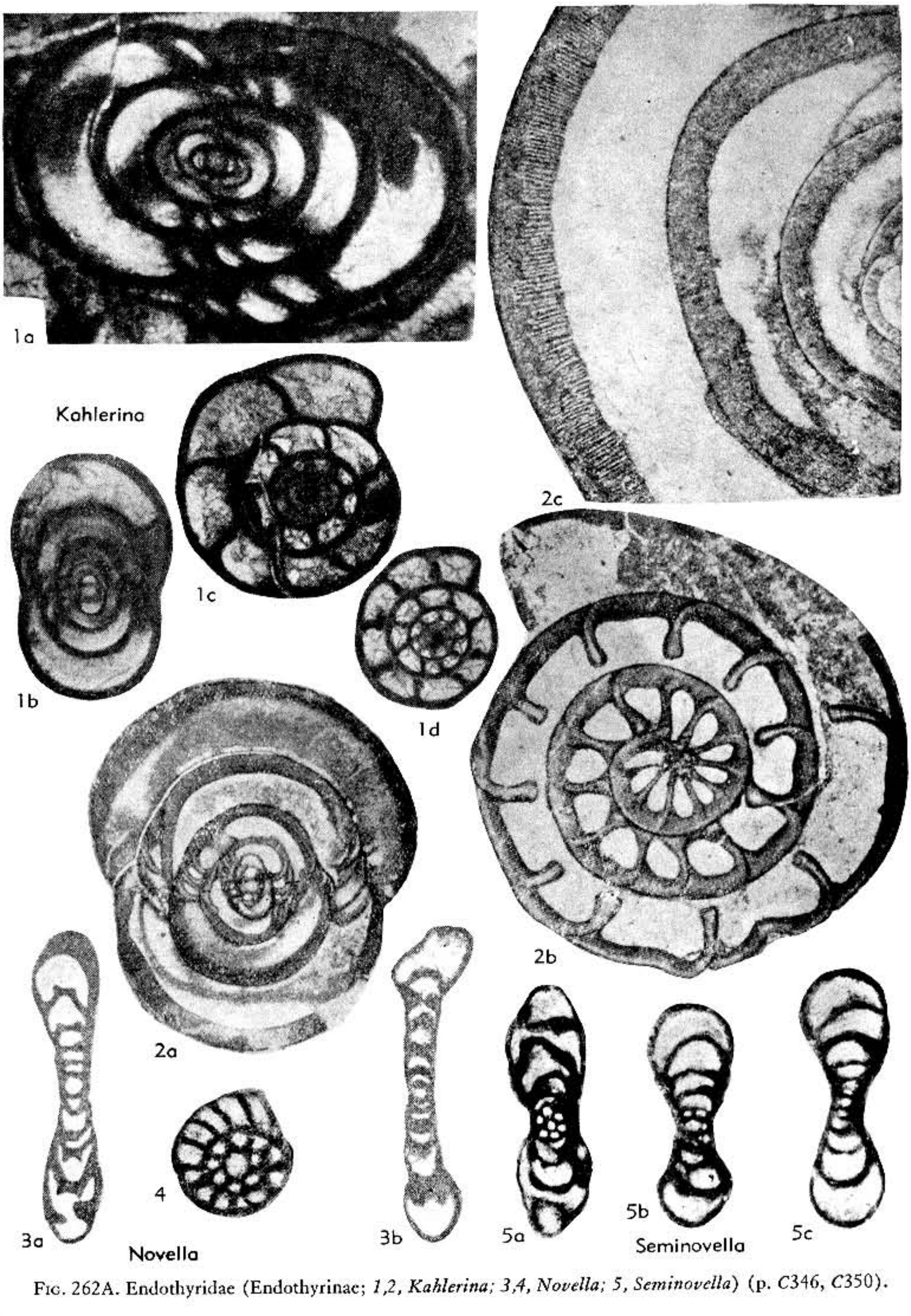


FIG. 262A. Endothyridae (Endothyrinae; *1,2*, *Kahlerina*; *3,4*, *Novella*; *5*, *Seminovella*) (p. C346, C350).

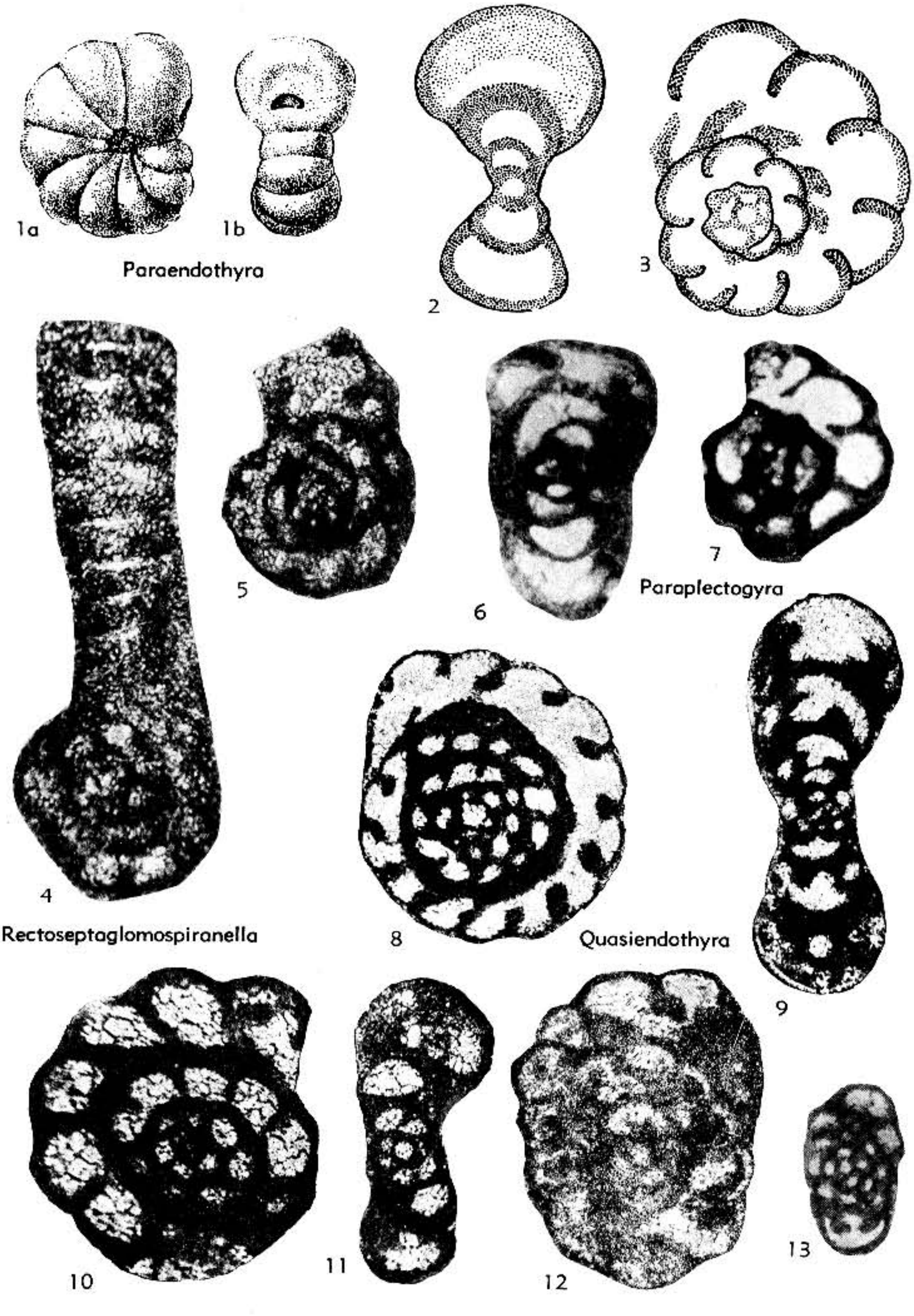


FIG. 263. Endothyridae (Endothyrinae; *1-3*, *Paraendothyra*; *4,5*, *Rectoseptaglomospiranella*; *6,7*, *Paraplectogyra*; *8-13*, *Quasiendothyra*) (p. C346-C350).

enrolled, compressed, early stage plectogyral, later planispiral, evolute; wall homogeneous, with secondary deposits at base of chambers at outer margins, giving appearance of chomata of fusulinids, aperture interiomarginal. *Dev.-Carb.*, USSR.——Fig. 263,*8,9*. *Q. kobeitusana* (Rauzer-Chernousova), Dev.(Famenn.); equat. and axial secs., showing lateral secondary deposits, ×75 (*1509).——Fig. 263,*10,11*. *Q. aljutovica* (Reytlinger), U.Carb.(Moscov.); equat. and axial secs.,

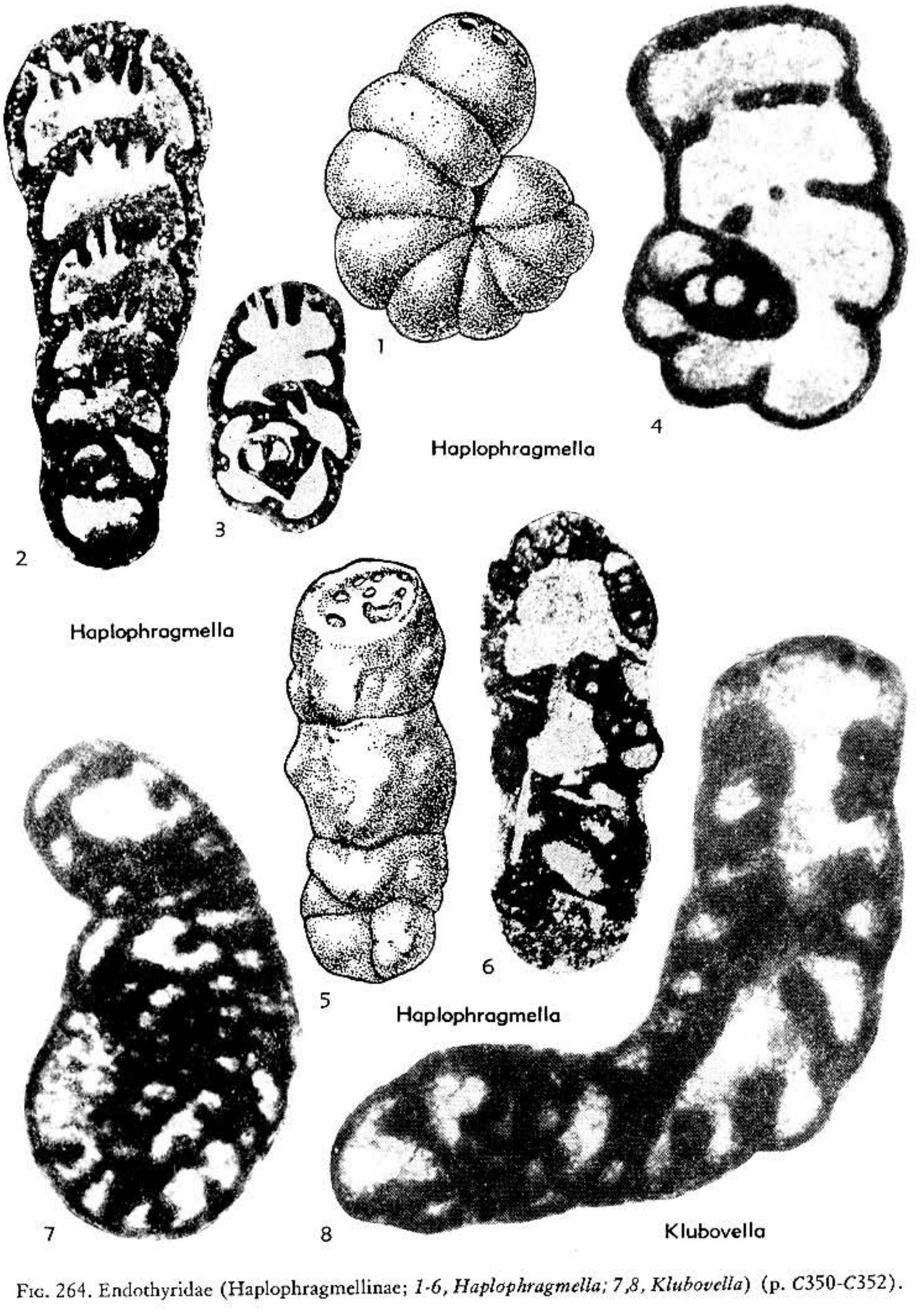


Fig. 264. Endothyridae (Haplophragmellinae; *1-6, Haplophragmella; 7,8, Klubovella*) (p. C350-C352).

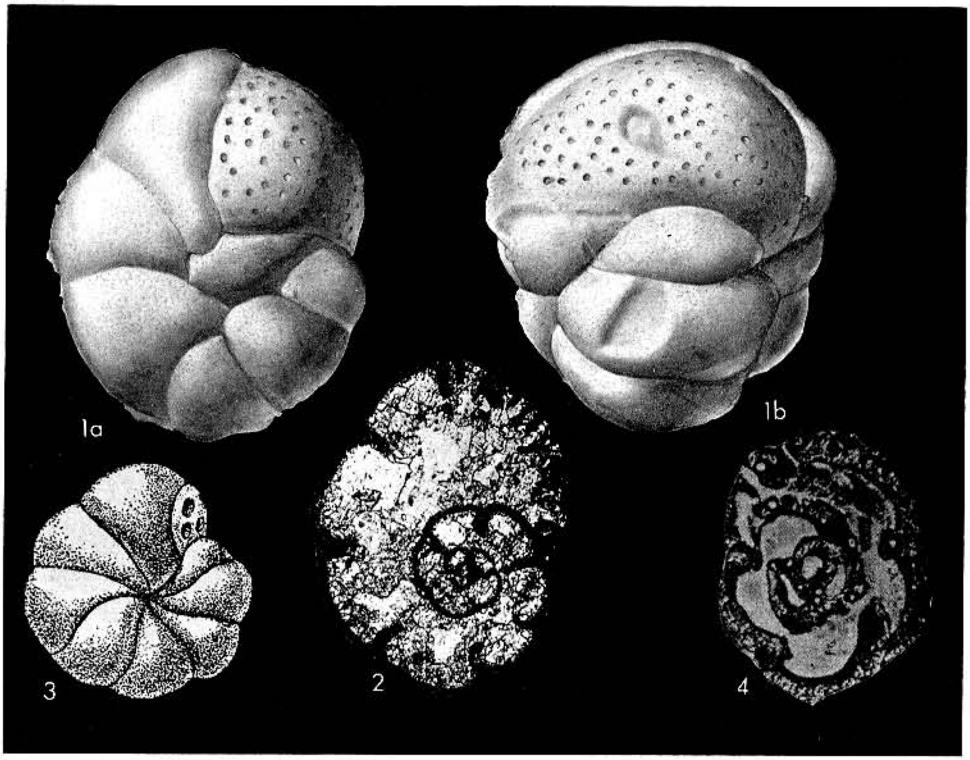


FIG. 265. Endothyridae (Haplophragmellinae; *1-4, Cribrospira*) (p. C352).

×46 (*1509).——FIG. 263,*12,13*. *Q. communis* (RAUZER - CHERNOUSOVA), U. Dev., USSR (C. Kazakh.); *12,* horiz. sec., ×46 (*1505); *13,* axial sec., ×61 (*1101).

Rectoseptaglomospiranella REYTLINGER, 1961, *1566, p. 62 [**Septaglomospiranella (Rectoseptaglomospiranella) asiatica*; OD] [=*Septaglomospiranella (Rectoseptaglomospiranella)* REYTLINGER, 1961, *1566, p. 62 (obj.)]. Test elongate, early portion streptospirally coiled, later becoming planispiral and then uncoiled and rectilinear; incompletely septate in coiled stage, rectilinear stage with broad, low, closely appressed chambers, completely septate; wall calcareous, coarsely granular, thick; aperture simple, at least in early stages. *U.Dev.(Famenn.), ?L.Carb.(L.Tournais.),* USSR(Kazakh.).——FIG. 263,*4,5*. **R. asiatica,* U.Dev.(Famenn.); *4,* long. equat. sec. of holotype; *5,* equat. sec. of juvenile specimen, ×75 (*1566).

[This genus was originally described as a subgenus of *Septaglomospiranella* (here placed in the synonymy of *Septabrunsiina*), which is similar to the early coiled stage of the present form. As *Rectoseptaglomospiranella* differs in the uncoiled later stage, it is here elevated to generic status. It differs from *Haplophragmella* in its low, closely appressed chambers and simple noncribrate aperture of the rectilinear stage.]

Seminovella RAUZER-CHERNOUSOVA, 1951, *2074, p. 64 [**Eostaffella (Seminovella) elegantula*; OD] [=*Eostaffella (Seminovella)* RAUZER-CHERNOUSOVA, 1951, *2074, p. 64 (obj.)]. Test planispiral, discoidal to biconcave, slightly asymmetrical, early 1 or 2 whorls involute, later 2 to 4 whorls becoming evolute, with whorls rapidly increasing in thickness, leaving broad, deep umbilicus; septa simple; wall homogeneous in structure, minor supplementary deposits (pseudochomata); single aperture. [*Seminovella* was originally regarded as transitional between *Millerella* and *Novella,* but because of the simple wall structure and single aperture it is here transferred to the Endothyrinae and elevated to generic status.] *U.Carb.(U.Namur.-Moscov.),* USSR.——FIG. 262A,*5*. **S. elegantula*; *5b,* axial sec. of holotype, ×74; *5a,c,* axial secs. of paratypes, ×74 (*2074).

Subfamily HAPLOPHRAGMELLINAE
Reytlinger, 1959

[Haplophragmellinae REYTLINGER in RAUZER-CHERNOUSOVA & FURSENKO, 1959, p. 185]

Test free, early stage enrolled as in the Endothyrinae, later may be uncoiled; aperture simple in early stage, areal and cribrate in adult. *L.Carb.(Tournais.) - M.Carb. (Moscov.).*

Haplophragmella RAUZER-CHERNOUSOVA & REYTLINGER in RAUZER-CHERNOUSOVA, BELYAEV, & REYTLINGER, 1936, *1507, p. 215, 228 [**Endothyra panderi* VON MÖLLER, 1879, *1296, p. 17; OD] [=*Endothyrina* MIKHAYLOV, 1935, *1259,

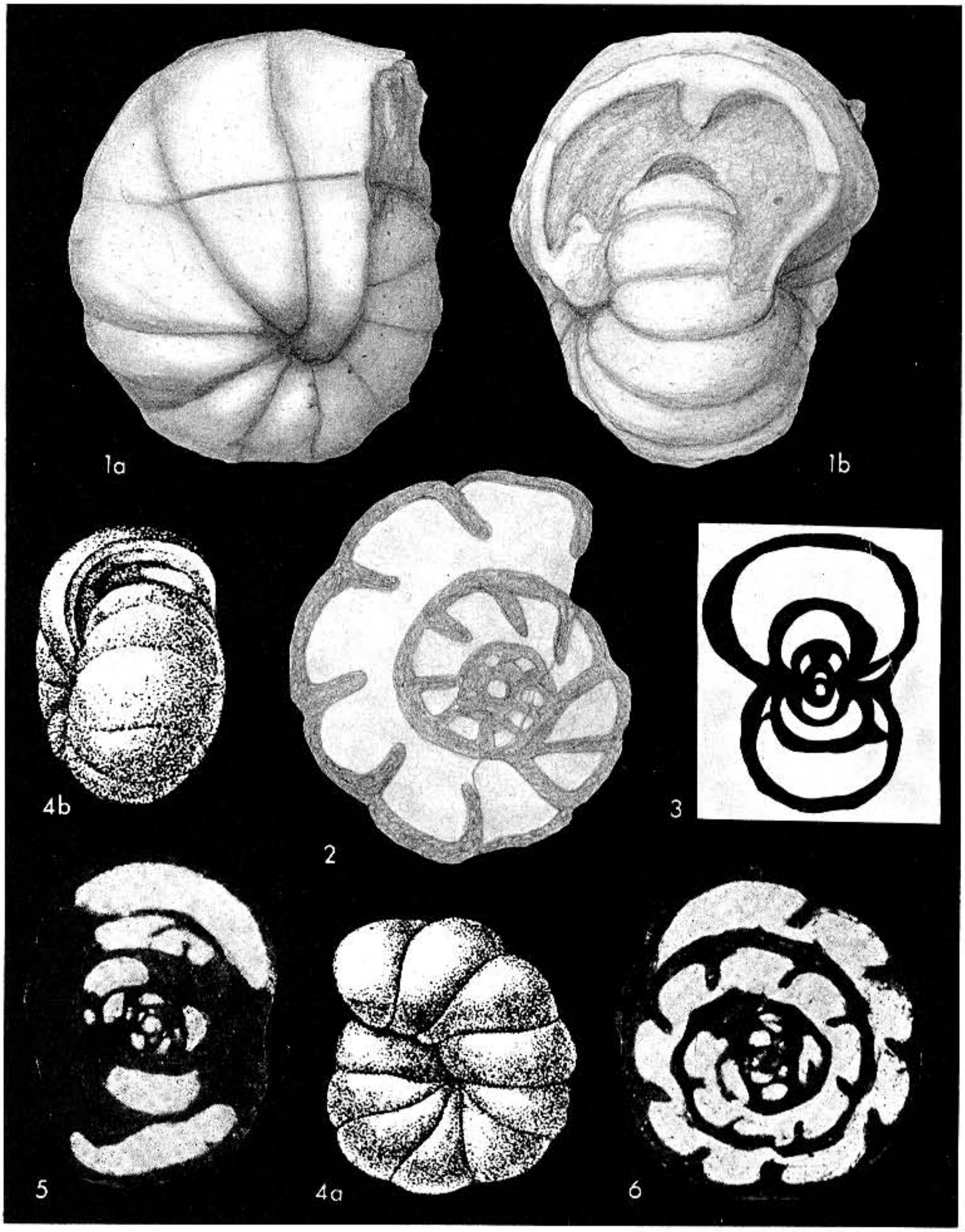


FIG. 266. Endothyridae (Endothyranopsinae; *1-6, Endothyranopsis*) (p. *C*352).

p. 40 (type, *E. typica, nom. nud.*); *Haplophragmina* REYTLINGER, 1950, *1560, p. 28 (type, *H. kashirica*); *Mikhailovella* GANELINA, 1956, *769, p. 100 (type, *Endothyrina? gracilis* RAUZER-CHERNOUSOVA, 1948, *1502, p. 163)]. Test free, early portion enrolled as in *Endothyra*, later uncoiling and rectilinear; wall calcareous but may include some adventitious material; aperture simple and interiomarginal in early coiled stage, later becoming terminal and cribrate. *L.Carb.(Tournais.) - U.Carb.(Moscov.)*, USSR.——FIG. 264,*1*. **E. panderi* (VON MÖLLER), Visean; side view, ×44 (*1509).——FIG. 264,*2,3*. *E. irregularis* (RAUZER-CHERNOUSOVA), Visean, long. secs., ×20 (*1509).——FIG. 264,*4*. *E. gracilis* RAUZER-CHERNOUSOVA, L.Carb.; long. sec., ×72 (*769).

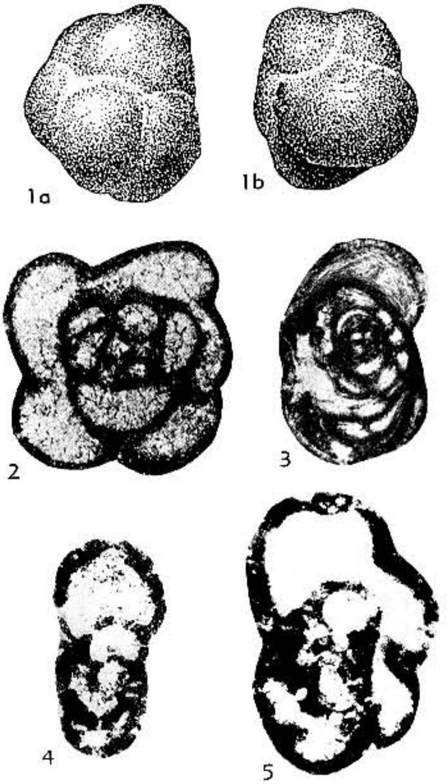


Fig. 267. Endothyridae (Endothyranopsinae; *1-5, Chernyshinella*) (p. C352-C353).

——Fig. 264,*5,6*. *E. kashirica* (Reytlinger), Moscov.; *5*, side view, ×55; *6*, long. sec., ×46 (*1509).

Cribrospira von Möller, 1878, *1295, p. 86 [**C. panderi*; OD (M)] [=*Mstinia* Mikhaylov, 1939, *1260, p. 59 (type, *M. bulloides*)]. Test free, enrolled, with somewhat irregular coiling, probably plectogyral, nearly involute, chambers increasing rapidly in size, whorls few; septa short, final septal face probably resorbed as new chambers are added; wall calcareous, granular; aperture cribrate, consisting of large pores on apertural face, intercameral openings large, interiomarginal, possibly by resorption of apertural face. [*Mstinia* was defined as differing from *Cribrospira* in having the final septal face equivalent to the septa. These differences seem to be rather a matter of shape and proportions, however.] *L.Carb.(Visean)*, USSR.——Fig. 265,*1,2*. **C. panderi*; *1a,b*, side, apert. views, ×44 (*2117); *2*, equat. sec., approx. ×28 (*1503).——Fig. 265,*3,4*. *C. bulloides* (Mikhaylov); *3*, side view; *4*, equat. sec., ×28 (*1509).

Klubovella Lebedeva, 1956, *1101, p. 52 [**K. konensis*; OD]. Test with early plectogyral enrolled portion, later uncoiled, with "biserially arranged" chambers; wall calcareous, with 2 layers; aperture simple, basal in early stage, later terminal, multiple. *L.Carb.*, USSR(Kazakh.).——Fig. 264,*7,8*. **K. konensis*; *7,8*, syntypes, long. secs., ×83 (*1101).

[This genus is provisionally recognized on the basis of the original description, but the "biserial" character seems questionable. No other biserial forms are known in this group and the original illustrations (here copied) do not show any clear biseriality. Both of the original figured specimens were labeled "holotype" on the plate description.]

Subfamily ENDOTHYRANOPSINAE
Reytlinger, 1958

[Endothyranopsinae Reytlinger, 1958, p. 57] [=Chernyshinellinae Reytlinger, 1958, p. 60]

Test planispiral, involute, not compressed, distinctly septate; wall a single layer of thick granular calcite with some adventitious material, perforate; aperture simple, basal. *L.Carb.*

Endothyranopsis Cummings, 1955, *398, p. 1 [**Involutina crassa* Brady in Moore, 1870, *1306, p. 379, 382; OD] [=*Globoendothyra* Reytlinger, 1958, *1564, p. 57 *(nom. nud)*; *Globoendothyra* Reytlinger in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 196 (type, *G. pseudoglobulus*)]. Test free, subglobular to nautiloid, biumbilicate, planispiral and involute but with slight axial rotation resulting in somewhat asymmetrical test; chambers broad, low; sutures somewhat depressed, radial; wall finely granular, perforate, may have some adventitious material, surface smoothly finished; aperture low, interiomarginal, equatorial arch. *L.Carb.*, Eu.-Asia(USSR, Bashkiri).——Fig. 266,*1,2*. **E. crassa* (Brady), Wales; *1a,b*, side, apert. views of lectotype; *2*, equat. sec., ×41 (*2117).——Fig. 266,*3*. *E.* sp.; axial sec., ×35 (*398). —— Fig. 266,*4-6*. *E. pseudoglobulus* (Reytlinger), Visean, USSR(Bashkiri); *4a,b*, side, apert. views, ×22 (*1509); *5,6*, axial equat. secs., approx. ×40 (*2008).

[Differs from *Bradyina* in its slight axial rotation and in having a simple arched aperture, rather than one or more rows of pores across the apertural face. It differs from *Endothyra* in its included adventitious matter and wall perforations, whereas *Endothyra* has a 2-layered, imperforate wall.]

Chernyshinella Lipina, 1955, *1143, p. 47 [**Endothyra glomiformis* Lipina, 1948, *1141, p. 254; OD] [=*Granuliferella* E. J. Zeller, 1957, *2104, p. 694 (type, *G. granulosa*)]. Test enrolled, slightly asymmetrical, coiling plectogyral, few volutions, umbilicate; chambers few to whorl and relatively large; septa oblique, continuing chamber curvature and not sharply delineated from outer chamber wall, which is single-layered, relatively thick, and granular; aperture low, narrow, equatorial interiomarginal slit. [Differs from *Endothyra* in having a single-layered wall, and

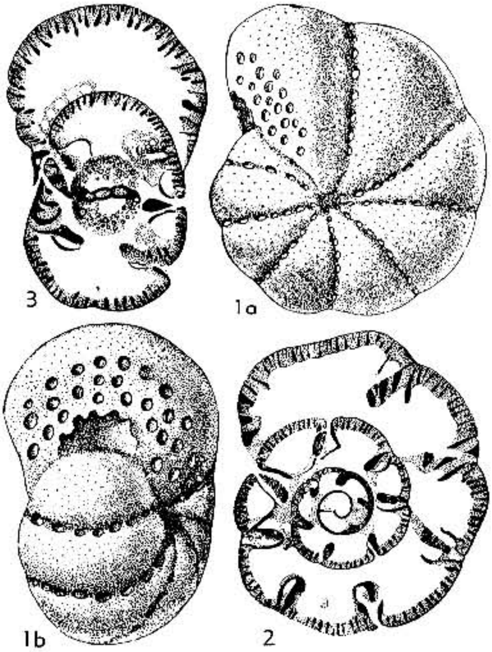


FIG. 268. Endothyridae (Bradyininae; *1-3, Bradyina*) (p. *C*353).

from *Endothyranopsis* in its fewer, more inflated chambers in each whorl, and plectogyral coiling.] *L.Carb.(Tournais.)*, USSR-N.Am.-Japan. —— FIG. 267,*1-3*. **C. glomiformis* (LIPINA), USSR; *1a,b*, ext. views, ×72 (*1509); *2*, equat. sec., ×70 (*1143); *3*, axial sec., ×35 (*649).——FIG. 267, *4,5*. *C. granulosa* (ZELLER), L.Miss., USA(Utah); axial and equat. secs., ×100 (*2104).

Subfamily BRADYININAE Reytlinger, 1950

[Bradyininae REYTLINGER, 1950, p. 38]

Test planispiral, involute; wall of granular calcite, complex interior; chambers alternating, with small chamberlets visible externally by row of openings along sutures; aperture multiple, areal, and interiomarginal. *Carb.*

Bradyina VON MÖLLER, 1878, *1295, p. 78 [**B. nautiliformis* (=*Nonionina rotula* EICHWALD, 1860, *691, p. 349); SD CUSHMAN, 1927, *433, p. 189]. Test free, robust, planispiral, involute, few chambers and whorls; chamberlets or canals formed by converging septal lamellae or infolding of outer wall to form septa, chamberlets extending into umbilical region; wall calcareous, microgranular, perforate, with distinct radial lamellae; primary interiomarginal aperture, with additional large areal pores forming cribrate aperture, and supplementary septal pores opening into septal chamberlets. *L.Carb.(Miss.)-U.Carb.(Penn.)*, Eu.-N.Am.——FIG. 268,*1-3*. **B. rotula* (EICHWALD), L.Carb.(Visean), USSR; *1a,b*, side, apert. views; *2,3*, equat., axial secs., ×14 (*1509).

Glyphostomella CUSHMAN & WATERS, 1928, *535, p. 53 [**Ammochilostoma? triloculina* CUSHMAN & WATERS, 1927, *534, p. 152 (=*Bradyina holdenvillensis* HARLTON, 1927, *879, p. 18); OD] [=*Pseudobradyina* REYTLINGER, 1950, *1560, p. 45 (type, *P. pulchra*)]. Test planispiral, involute, few (usually 3) chambers to whorl, in-

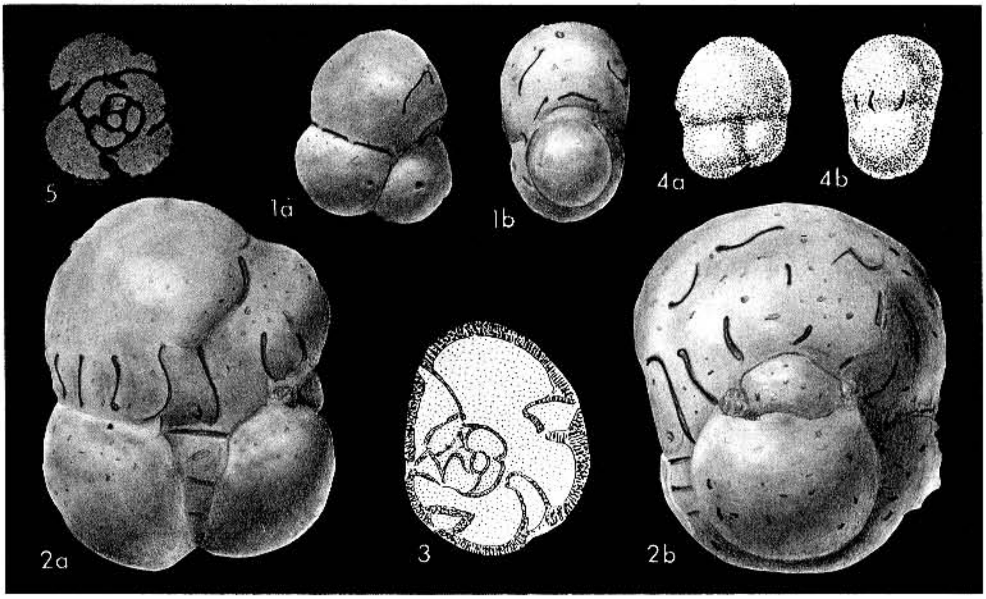


FIG. 269. Endothyridae (Bradyininae; *1-5, Glyphostomella*) (p. *C*353-*C*354).

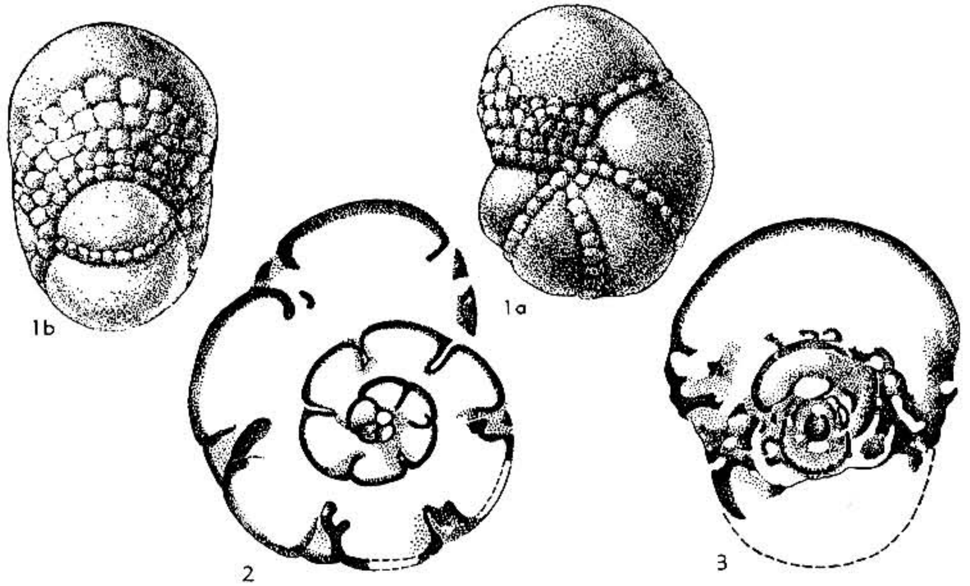


FIG. 270. Endothyridae (Bradyininae; *1-3, Janischewskina*) (p. C354).

creasing rapidly in size; septal chamberlets similar to those of *Bradyina*; wall calcareous, alveolar, granular, perforate; aperture consists of one to many straight or curved narrow slits at base and in face of final chamber, and supplementary sutural slits opening into septal chamberlets. [The synonymy of *Ammochilostoma? triloculina* Cushman & Waters, 1927 (Sept.) with *Bradyina holdenvillensis* Harlton, 1927 (July) was noted by Warthin (1930, *2040, p. 23).] *U.Carb.(Penn.)*, USA-USSR.——Fig. 269,*1,2*. **G. holdenvillensis* (Harlton), Penn., USA(Tex.); *1a,b*, side, apert. views of holotype of *Ammochilostoma? triloculina* Cushman & Waters, ×50; *2a,b*, large paratype of *A.? triloculina*, ×50 (*2117).——Fig. 269,*3*, *G.* sp., equat. sec., ×24 (*535).——Fig. 269,*4,5*. *G. pulchra* (Reytlinger), U.Carb., USSR; *4a,b*, side, apert. views, ×28; *5*, equat. sec., ×36 (*1509).

Janischewskina Mikhaylov, 1935, *1259, p. 40 [**J. typica*; OD] [=*Yanischewskina* Mikhaylov, 1939, *1260, p. 59 *(nom. null.)*; *Samarina* Rauzer-Chernousova & Reytlinger in Rauzer-Chernousova, Belyaev & Reytlinger, 1940, *1508, p. 53 (type, *S. operculata*)]. Test free, planispiral, involute; septal chamberlets formed by infolding of outer wall as in *Bradyina*; wall calcareous, fibrous, but without radial lamellae of *Bradyina*; aperture cribrate, in apertural "shield" and with secondary sutural openings. [*Janischewskina* differs from *Bradyina* in its less complex wall and cribrate aperture in a "shield," but without a definite interiomarginal opening.] *L.Carb. (Visean)*, USSR.——Fig. 270,*1-3*. **J. typica*; *1a,b*, side, apert. views, ×14; *2,3*, equat., axial secs., ×25 (*1509).

Family ARCHAEDISCIDAE Cushman, 1928

[*nom. transl.* Chernysheva, 1948, p. 151 (*ex* subfamily Archaediscinae Cushman, 1928, p. 209)] [=Asteroarchaediscinae Miklukho-Maklay, 1957, p. 37]

Proloculus followed by tubular second chamber, involute in early stage, later streptospirally or planispirally coiled; outer wall layer of radial calcite, inner layer finely granular; aperture at end of spiral chamber. *L.Carb.-Perm.*

Archaediscus Brady, 1873, *189, p. 286 [**A. karreri*; OD (M)] [=*Archaediscoum* Rhumbler, 1913, *1572b, p. 389 (obj.) *(nom. van.)*; *Neodiscus* A. D. Miklukho-Maklay, 1953, *1262, p. 129 (type, *N. milliloides*); *Propermodiscus* A. D. Miklukho-Maklay, 1953, *1262, p. 128 (type, *Hemigordius ulmeri* Mikhaylov, 1939, *1260, p. 61); *Paraarchaediscus* Orlova, 1955, *1399, p. 621 (type, *P. dubitabilis*); *Asteroarchaediscus* A. D. Miklukho-Maklay in Kiparisova, *et al.*, 1956, *1040, p. 10 (type, *Archaediscus baschkiricus* Krestovnikov & Teodorovitch, 1936, *1055, p. 87); *Rugosoarchaediscus* A. D. Miklukho-Maklay, 1957, *1266, p. 37 (type, *Archaediscus akchimensis* Grozdilova & Lebedeva, 1954, *831, p. 53)]. Test free, lenticular; proloculus followed by streptospirally coiled, long, undivided tubular second chamber, evolute, tending to become more

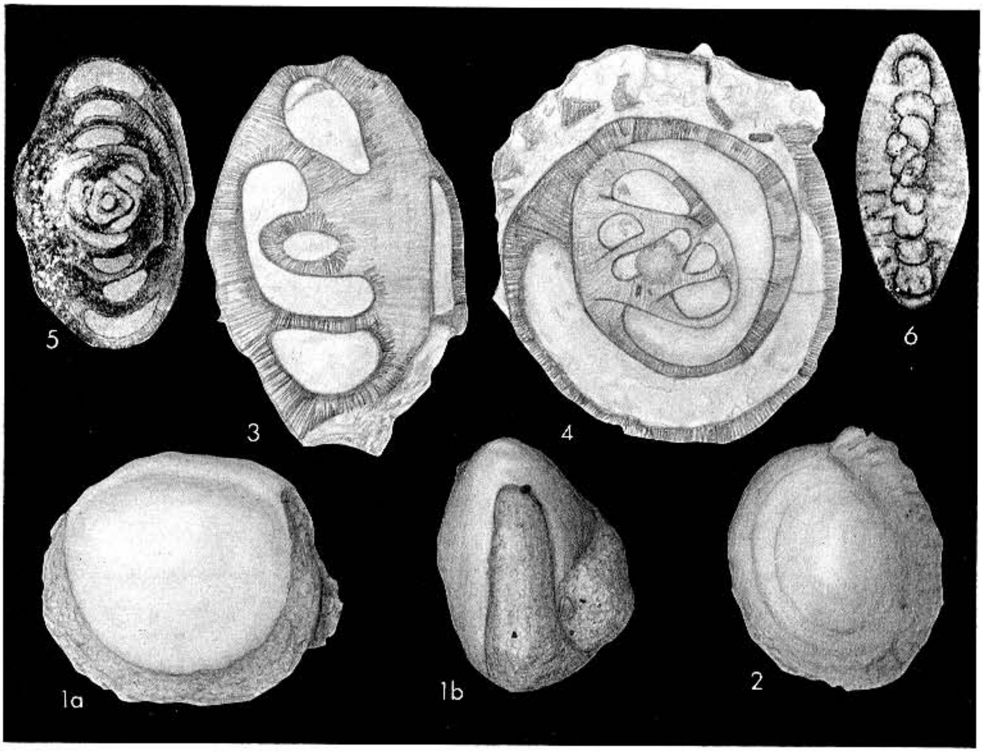


Fig. 271. Archaediscidae; *1-6*, *Archaediscus* (p. C354-C355).

nearly planispiral with growth; wall calcareous, finely fibrous, with noticeable thickenings at sides of test, no outer imperforate layer observed; aperture at open end of tube. [Different generic names have been given to forms with varying degrees of symmetry of test thickening and relative amount of planispiral development. These are here regarded as specific distinctions only.] *L.Carb.-Perm.*, Eu.——Fig. 271,*1-4*. **A. karreri*, Carb., Eng.; *1a,b*, side, edge views of syntype; *2*, syntype in which later planispiral development can be distinguished; *3*, axial sec. of syntype; *4*, equat. sec. of syntype; all ×64 (*2117).——Fig. 271,*5*. *A. milliloides* (Miklukho-Maklay), U.Perm., Caucasus; axial sec. of holotype, ×17 (*1262).——Fig. 271,*6*. *A. ulmeri* (Mikhaylov), L.Carb. (Visean), USSR; ×80 (*1262).——Fig. 272,*1,2*. *A. dubitabilis* (Orlova), U.Tournais., Saratov; *1*, ext., ×40; *2*, axial sec. of holotype, ×100 (*1399).——Fig. 272,*3*. *A. baschkiricus* Krestovnikov & Teodorovitch, M.Carb.(Bashkir.), USSR(Kolva); axial sec., ×100 (*1509).——Fig. 272,*4*. *A. akchimensis* Grozdilova & Lebedeva, L.Carb.(L.Bashkir.), USSR; axial sec., ×100 (*831).

Brunsia Mikhaylov, 1939, *1260, p. 58 [**Spirillina irregularis* von Möller, 1879, *1295, p. 41; OD] [=*Neoarchaediscus* A. D. Miklukho-Maklay in Kiparisova, *et al.*, 1956, *1040, p. 11 (type, *Archaediscus incertus* Grozdilova & Lebedeva, 1954, *831, p. 60); *Planoarchaediscus* A. D. Miklukho-Maklay in Kiparisova, Markovskii & Radchenko, 1956, *1040, p. 10 (type, *Archaediscus spirillinoides* Rauzer-Chernousova, 1948, *1505, p. 12); *Hemiarchaediscus* A. D. Miklukho-Maklay, 1957, *1266, p. 36 (type, *H. planus*); *Quasiarchaediscus* A. D. Miklukho-Maklay, 1960, *1274, p. 150 (type *Q. pamirensis*)]. Test discoidal, consisting of proloculus followed by coiled nonseptate tubular chamber, which in early stage is plectogyral as in *Archaediscus* and in later stage is planispiral; wall calcareous, perforate, without lateral thickening; aperture at open end of tubular chamber. *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.(USSR)-Asia(USSR).——Fig. 272,*5*. *B. plana* (Miklukho-Maklay), Pamir region; axial sec. of holotype, ×100 (*1266).——Fig. 272,*6*. *B. incerta* (Grozdilova & Lebedeva), Baskir region; holotype, ×100 (*1509).——Fig. 272,*7,8*. *B. pulchra* Mikhaylov, Ukraine; equat. and axial secs., ×100 (*1509).——Fig. 272,*9*. **B. irregularis* (von Möller), holotype, ×135 (*700).——Fig. 272,*10,11*. *B. spirillinoides* (Rauzer-Chernousova), Kazakh.; *10*, axial sec. of holotype; *11*, equat. sec. of paratype, ×75 (*1505).——Fig. 272,*12*. *B. pamirensis* (A. D. Miklukho-Maklay), Visean, Pamir region; holotype, horiz. sec., ×180 (*1274).

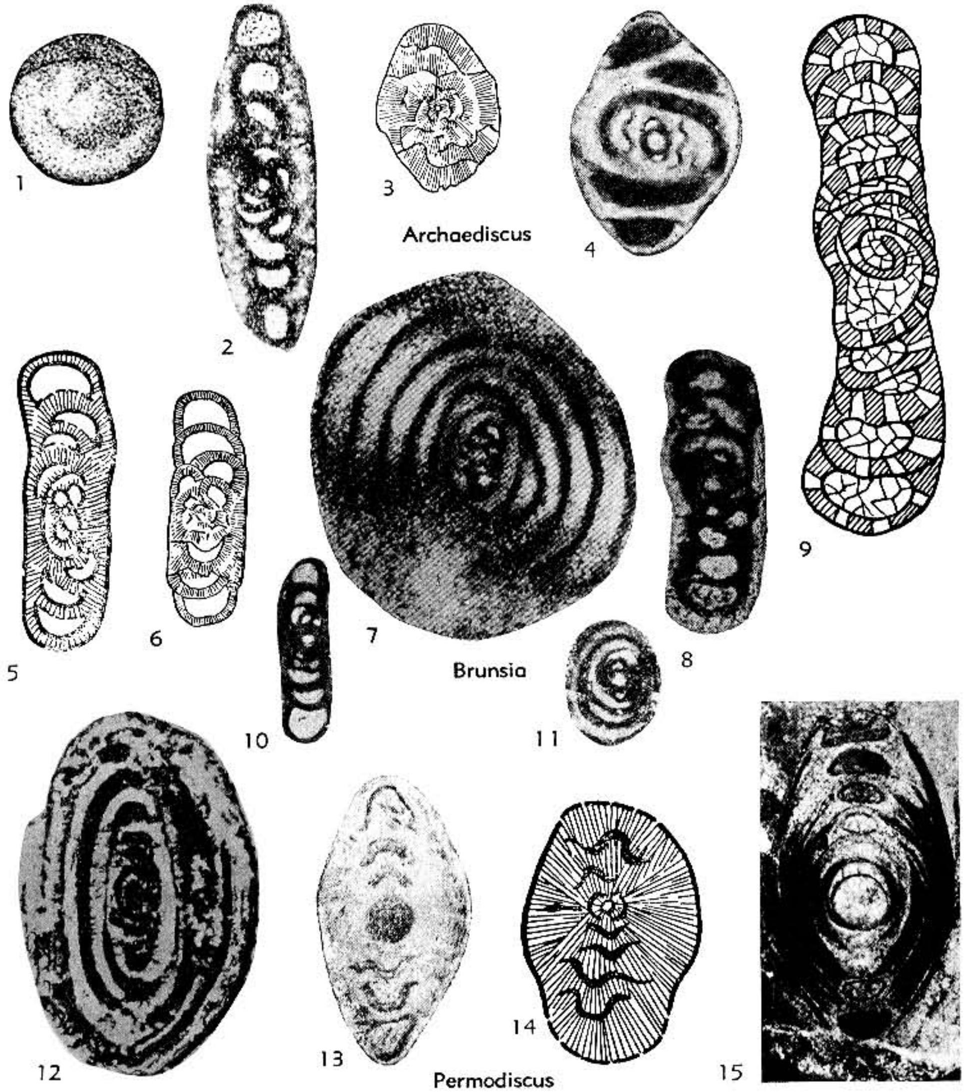


FIG. 272. Archaediscidae; *1-4, Archaediscus; 5-12, Brunsia; 13-15, Permodiscus* (p. *C355-C358*).

[*Brunsia* differs from *Archaediscus* in being plectogyral only in the early stage, and planispiral in the later stage, and in lacking the pronounced lateral thickening of the wall. *Brunsia* was originally described as being agglutinated calcareous, with a cribrate aperture. The type-species is *Spirillina irregularis* von Möller, by original designation. Later Myatlyuk (*1332, p. 26) stated that *Spirillina? irregularis* was calcareous, with a very thin perforate wall and not agglutinated, hence she did not regard it as belonging to *Brunsia*, as that genus had been described. In a later publication, Grozdilova & Lebedeva (1954, *831, p. 29) cited *Brunsia pulchra* Mikhaylov as genotype species. As the type-species can never be changed once it has been fixed, the genus *Brunsia* must include *S. irregularis* von Möller, whose specimens were described from thin sections which show an early irregular coil and later planispiral one, with distinctly fibrous or porous wall (the original figures being similar to those of *S. subangulata* von Möller, type-species of *Forschia*). Both undoubtedly have the granular calcareous fibrous or radially striate walls of the majority of the Endothyracea which are also characteristic of the Tournayellidae and Archaediscidae. True *Spirillina* does not appear in the Carboniferous. The cribrate aperture described by Mikhaylov apparently refers to the coarse perforations seen in the walls of *S. irregularis*, and does not represent a true aperture in these nonseptate forms. We regard *B. irregularis* and *B. pulchra* as congeneric. In addition, *Neoarchaediscus, Planoarchaediscus*, and *Hemiarchaediscus* are regarded as synonymous, their differences being regarded as of specific importance only.]

Permodiscus Dutkevich in Chernysheva, 1948, *336, p. 154 [**P. vetustus*; OD] [=*Permodiscus* Mikhaylov, 1939, *1260, p. 49 *(nom. nud.)*; *Multidiscus* A. D. Miklukho-Maklay, 1953, *1262,

p. 130 (type, *Nummulostegina padangensis* Lange, 1925, *1091, p. 271); *Lensarchaediscus* Porchnjakova in A. D. Miklukho-Maklay, 1957, *1266, p. 37 (type, *L. ovalis*)]. Similar to *Archaediscus*, with massive lateral thickening of wall, but planispiral throughout. *L.Carb.-U.Perm.*, USSR-

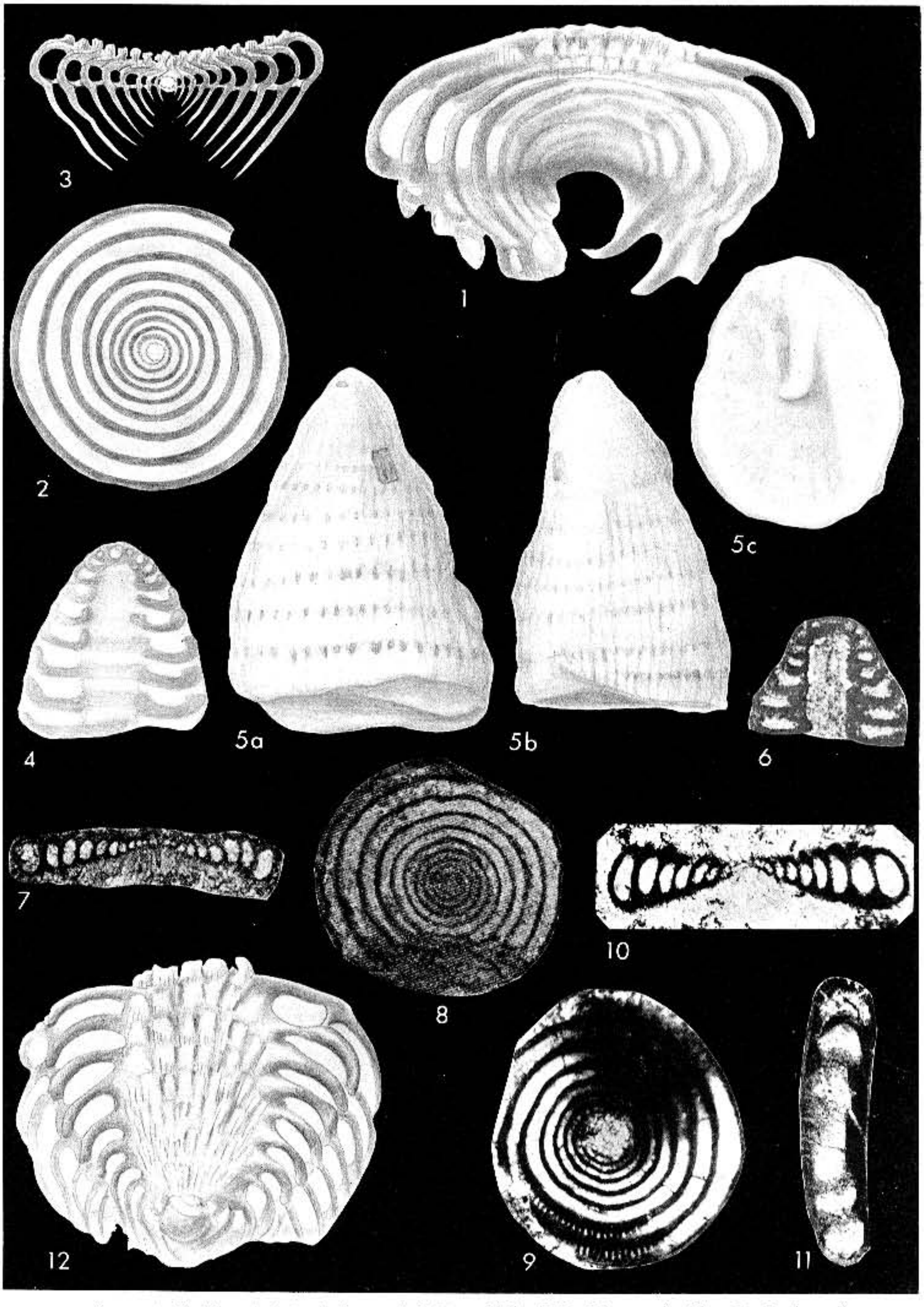


Fig. 273. Lasiodiscidae; *1-3, Lasiodiscus; 4-6, Howchinia; 7-11, Monotaxinoides; 12, Lasiotrochus* (p. C358).

Malay Arch.(Sumatra).——Fig. 272,*13*. **P. vetustus,* L.Carb.(Visean), USSR; ×100 (*1262).——Fig. 272,*14*. *P. ovalis* (Porchnjakova), U.Carb. (Namur.), USSR(Fergana); axial sec. of holotype, ×100 (*1266).——Fig. 272,*15*. *P. padangensis* (Lange), M.Perm., Sumatra; ×12 (*1091).

Family LASIODISCIDAE Reytlinger, 1956

[Lasiodiscidae Reytlinger, 1956, p. 74]

Test planispiral to conical, proloculus followed by unsegmented tubular chamber; wall calcareous, with microgranular layer and radially built vitreous layer, latter concentrated as umbilical fillings perforated by canal-like fissures in advanced forms but consisting only of bridges across spiral suture in simple forms; aperture at open end of tubular chamber, with supplementary sutural openings. *L.Carb.-U.Perm.*

Lasiodiscus Reichel, 1945, *1517, p. 525 [**L. granifer*; OD]. Test free, consisting of proloculus, followed by planispirally enrolled tubular second chamber, one of surfaces ornamented by hyaline tubercles of radially fibrous thickening, and opposite side with tubular chamberlets, opening into main enrolled chamber by apertures along spiral suture; test calcareous, imperforate, finely granular, dark in transmitted light, tubercles vitreous. [Magnification of the illustrations has been computed from the size of the specimens, as a discrepancy is found in the stated magnifications of the photographs and text figures with the stated size in the original publication.] *M.Carb.-U. Perm.,* Eu. (Greece - Cyprus - USSR). ——Fig. 273,*1-3*. **L. granifer,* U.Perm., Cyprus; *1,* holotype, oblique sec. passing near proloculus, ×145; *2,3,* reconstr. equat. and axial secs., ×85 (*1517).

Howchinia Cushman, 1927, *431, p. 42 [**Patellina bradyana* Howchin, 1888, *965, p. 544; OD] [=*Monotaxis* Vissarionova, 1948, *2009, p. 190 (type, *Tetrataxis conica* var. *gibba* von Möller, 1879, *1296, p. 71) (*non Monotaxis* Bennett, 1830; *nec* Hulst, 1898; *nec* Hampson, 1900)]. Test free, conical, consisting of nonseptate tube coiled in high spire around slightly depressed umbilical region filled with microcrystalline calcite; spiral suture depressed, bridged by many small extensions of shell matter, leaving spiraling series of small pits between them; wall calcareous, minutely granular; aperture extending from umbilicus to periphery. *L.Carb.(Visean),* Eu.(Eng.-USSR).——Fig. 273,*4,5*. **H. bradyana* (Howchin), Eng.; *4,* sectioned hypotype, ×105; *5a-c,* side, edge and apert. views of neotype, ×105 (*2117).——Fig. 273,*6*. *H. gibba* (von Möller), USSR; ×80 (*2009).

[The specimen of *Howchinia bradyana* here figured is that designated by Davis (1951, *564) as lectotype (BMNH-P40403) from the Carboniferous limestone, Tipalt, D Zone, Old High Shd., Tipalt, Northumberland, England, lat. 54°59′53″ N., long. 2°30′46″W. However, as it is not from the original type lot it must be considered as a neotype.]

Lasiotrochus Reichel, 1946, *1517, p. 531 [**L. tatoiensis*; OD]. Test free, small, similar in structure to *Lasiodiscus,* but with conical form due to high trochospiral enrollment of tubular chamber; tubular chamberlets from outer margin recurving toward proloculus, umbilical region filled by hyaline tubercles which have developed into distinct pillars of transparent calcite; wall calcareous, finely granular, umbilical pillars vitreous. [The genus was originally described from a single section of the type-species. Possibly additional material may show this to be a synonym of *Lasiodiscus.*] *L. Perm. - U. Perm.,* Eu. (Greece) - USSR (Azerbaidzhan).——Fig. 273,*12*. **L. tatoiensis,* U.Perm., Greece; long. sec. of holotype, ×140 (*1517).

Monotaxinoides Brazhnikova & Yartseva, 1956, *205, p. 65 [**M. transitorius*; OD] [=*Eolasiodiscus* Reytlinger, 1956, *1562, p. 75 (type, *E. donbassicus*)]. Test discoidal, concave on one side with proloculus followed by planispirally coiled nonseptate tubular second chamber; wall calcareous, with finely granular dark inner layer and clear, radiate vitreous outer layer that becomes thickened on concave side; aperture at open end of tube. [*Eolasiodiscus* was described as having supplementary fissure-like openings along the spiral suture, as seen in the figured equatorial section. It seems probable that this appearance is due to cutting of the radiate layer by the section. *Eolasiodiscus* is here regarded as synonymous with *Monotaxinoides.* It is apparently transitional between *Howchinia* and *Lasiodiscus.*] *L. Carb.-U.Carb.,* Eu.(USSR).——Fig. 273,*7,8*. **M. transitorius,* L.Carb., Donets Basin; *7,* axial sec. of holotype; *8,* equat. sec. of paratype; both ×100 (*205).——Fig. 273,*9-11*. *M. donbassicus* (Reytlinger), M.Carb., Donets Basin; *9,* equat. sec. of holotype; *10,* axial sec.; *11,* tang. axial sec., all ×174 (*1562).

FUSULINACEA

By M. L. Thompson

[Illinois State Geological Survey, Urbana]

INTRODUCTION

Foraminifers of the superfamily Fusulinacea are mostly robust representatives of the order characterized by distinctive complex internal structure of their spindle-shaped, spheroidal, or discoid calcareous tests (Fig. 274). Extraordinarily profuse in many rock formations, they are an exclusively late Paleozoic group of fossils. In the century

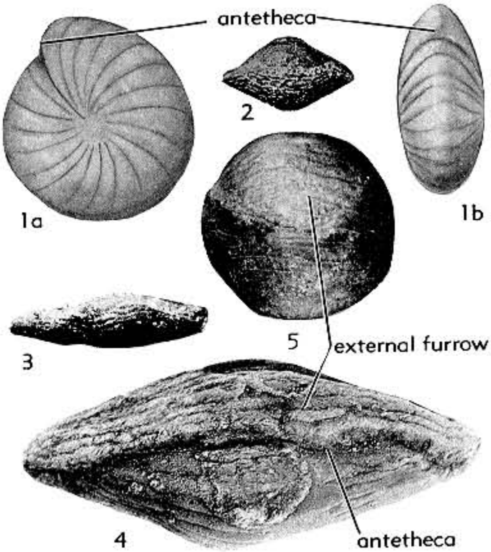


FIG. 274. Exterior views of fusulinaceans showing typical shapes of shells.——*1.* Discoid; **Nummulostegina velebitana* SCHUBERT, Perm., Yugo., *1a,b,* side and edge views of holotype, ×20 (*2120B).——*2-4.* Fusiform: *2, Fusulina girtyi* (DUNBAR & CONDRA), M.Penn., USA(Ill.), holotype, ×3.3 (*1922); *3,* **Waeringella spiveyi* THOMPSON, U. Penn., USA(Tex.), paratype, ×6.7 (*1922); *4, Triticites ventricosus* (MEEK & HAYDEN), L.Perm., USA(Kans.), holotype, ×6.7 (*1926).——*5.* Spheroidal: **Verbeekina verbeeki* (GEINITZ), U. Perm., Sumatra, topotype, ×6.7 (*1922).

and a half during which they have been under study by paleontologists, several dozen workers have contributed to our knowledge of their shell morphology, taxonomy, stratigraphic distribution, and evolution.

The fusulinaceans had their beginning in late Mississippian time, and the last members did not survive to the close of Permian time. Within this relatively short span of their collective existence, they developed into many biologic branches.

For classification of the whole assemblage, different students have proposed that the fusulinaceans should be ranked as an independent order, treated as a suborder, grouped in three rather disparate superfamilies, divided into seven families and 21 subfamilies, and recognized as containing more than 150 genera and subgenera with many hundreds of species. Many of these taxonomic units are not considered in the *Treatise* to be valid, since numerous nominal genera of fusulinaceans undoubtedly are synonymous with others. It is evident that these foraminifers became very highly diversified, yet as a whole seem to be classifiable appropriately as a superfamily. Because members of various major fusulinacean groups are found associated in certain deposits of a given age, it is judged that several lines of evolution developed simultaneously within the superfamily.

In terms of well-preserved entire specimens, fusulinaceans far outnumber the representatives of any other single invertebrate group in Pennsylvanian and Permian strata of many areas. In some of these, well-preserved entire fusulinaceans probably exceed in number, and possibly in volume, the combined remains of all other types of invertebrates in this part of the upper Paleozoic.

The fusulinaceans were sensitive to their physical environment and mostly are closely restricted to certain lithologic units of the Pennsylvanian and Permian. Although exceedingly abundant in various stratigraphic units, in some of which fusulinaceans may compose more than half the bulk of the rock, they are found in many places associated with very few other types of fossils. At numerous stratigraphic levels in the Pennsylvanian and Permian, the same general types of invertebrate faunas immediately precede and immediately follow the units in which prolific fusulinaceans are found. This order of faunal arrangement and association is especially noticeable in the central United States.

Fusulinaceans have been recognized in more than 80 distinct stratigraphic units of Pennsylvanian age in New Mexico. Many of the fusulinacean-bearing rock divisions occur over areas hundreds of square miles in extent. About an equal number of fusulinacean-bearing units have been found in the Pennsylvanian of the northern mid-continent region and in Texas. In the mid-continent region, some fusulinacean-rich strata are distributed over even larger geographic areas than those in New Mexico, and some seem to be continuous with New Mexico units that extend outward from the edges of Pennsylvanian land areas in the Rocky Mountain region.

Although fusulinaceans are abundant and occur in many widespread zones in the Permian of the United States, most fusulinacean faunas of this system are more restricted in geographic distribution than are those of the Pennsylvanian, presumably owing largely to the physical nature of the Permian seas.

ACKNOWLEDGMENTS

Thanks are extended to the many individuals who contributed to this section of the *Treatise.* A part of the years 1960-61 was spent by me in Fukuoka, Japan, working with RYUZO TORIYAMA and other members of the staff of Kyushu University on fusulinacean genera recently proposed in the Asiatic area. Many other individuals in Japan and in the United States contributed information and material. SUSUMU HONJO, of Hokkaido University, worked briefly with me in Urbana. KENJI KONISHI, of Kanazawa University, went with me on trips to Akasaka with Prof. TORIYAMA and HISAYOSHI IGO, of the Tokyo University of Education. Dr. IGO later spent a year with me in Urbana. YASUO NOGAMI, of Kyoto University, furnished thin sections and information concerning some Japanese fusulinaceans. J. W. SKINNER and G. L. WILDE, of the Humble Oil & Refining Company, Midland, Texas, furnished illustrations and information. Use has been made of all published reports. W. D. FARRIS and BEULAH UNFER of the Illinois State Geological Survey prepared photographs and copies. P. X. SARAPUKA, of the Survey, prepared numerous translations from the Russian. Special thanks are given to FRANCES ALSTERLUND, of the Survey, who contributed greatly to the final organization of the transcript.

Numerous data bearing on fusulinacean systematics and the literature were kindly furnished by A. R. LOEBLICH, JR. and HELEN TAPPAN.

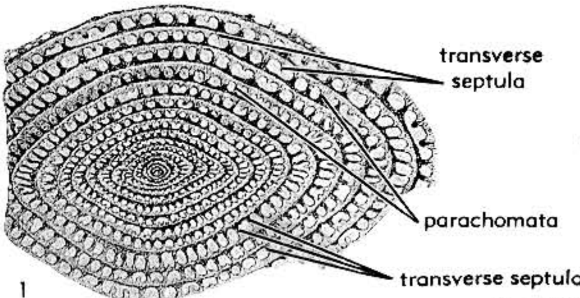
MORPHOLOGY

GENERAL DESCRIPTION OF SHELL

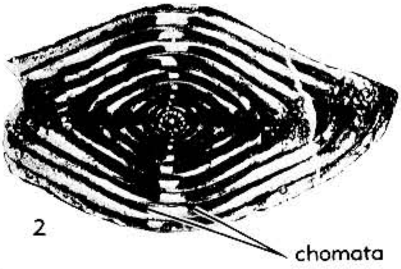
The fusulinaceans are referred to the order Foraminiferida and are therefore assumed to have been one-celled animals. As with many of the foraminifers, the individual shells of fusulinacean species are remarkably similar in almost all respects. Externally, the shells of many species closely resemble each other. Internally, however, structures may be markedly different in different forms. The shells of primitive species are relatively simple, but those of some more advanced forms are among the most complex of all foraminifers. The fusulinaceans occur geologically only a short time after the earliest foraminifers having unquestionably calcareous shells, and they died out considerably before development of the prolific Mesozoic foraminiferal faunas dominated by groups having calcareous shells. Most of the calcareous, as well as arenaceous types of other foraminifers, are classified on the basis of external shell structures, but classification of the fusulinaceans is based largely on internal shell features that generally can be determined only from thin or polished sections. The few other groups of Foraminiferida that are classified largely on the basis of internal shell structures, such as nummulitids and orbitoidids, occur in the upper part of the geologic section, and the terminology applied to their shell structures is mostly not applicable to shell features of the fusulinaceans, and conversely. Although some terms applied to fusulinacean shell structures are also used for other foraminifers, much of the terminology used in describing fusulinacean shells is restricted to this superfamily. The terms are included in the glossary given in the general description of foraminiferal morphology (p. C58).

Some of the structural features of fusulinacean shells can be interpreted from external observations, but many are completely internal. Two sections cut through the beginning chamber reveal most internal features of the shell. One of these is cut along the axis of coiling and is called an **axial section** (Fig. 275,*1-3a, 4,5,6b*). The

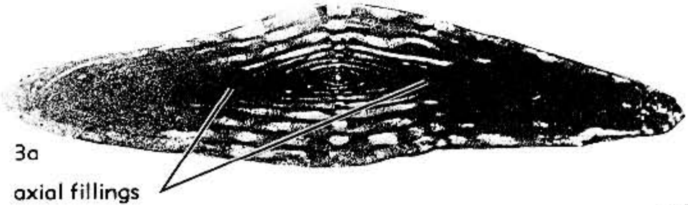
FIG. 275. *(Facing page.)* Axial, sagittal, and parallel sections of fusulinaceans.——*1. *Neoschwagerina craticulifera* (SCHWAGER), U.Perm., China; slightly oblique axial sec. of holotype, ×16.3 (*1922).——*2. Yangchienia tobleri* THOMPSON, U. Perm., Sicily; axial sec., ×16.3 (*1922).——*3. *Wedekindellina euthysepta* (HENBEST), M.Penn., USA(Ill.); *3a,* axial sec. of holotype; *3b,* sagittal sec. of paratype; both ×20 (*1922).——*4. Triticites ventricosus* (MEEK & HAYDEN), L.Perm., USA (Kans.); axial sec., topotype, ×8 (*1926).——*5. Lepidolina elongata* (GUBLER), U.Perm., Cambodia; axial sec. of submature specimen, ×8 (*838).——*6a. Parafusulina nosonensis* THOMPSON & WHEELER, L.Perm., USA(Calif.); parallel sec. of paratype showing cuniculi, ×8 (*1922).——*6b. Parafusulina wanneri* (SCHUBERT), Perm., Timor; axial sec. of holotype, ×8 (*1923).



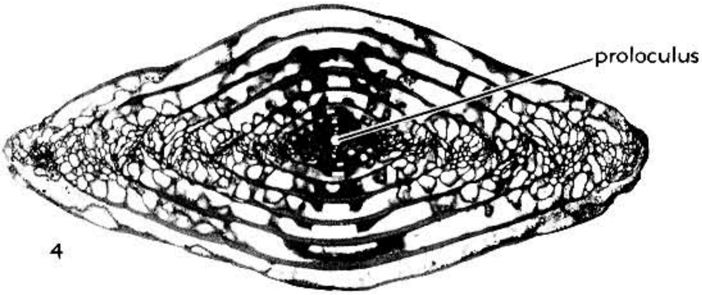
1



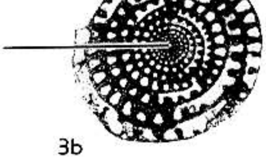
2



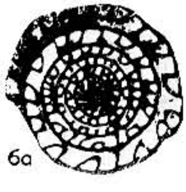
3a



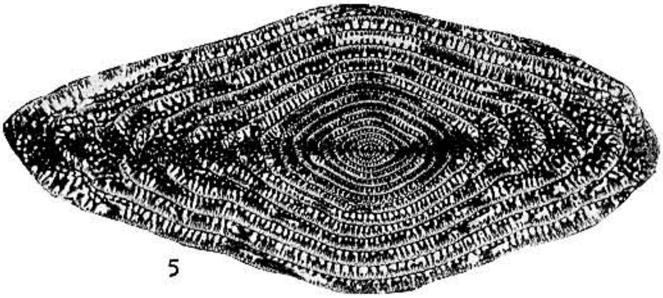
4



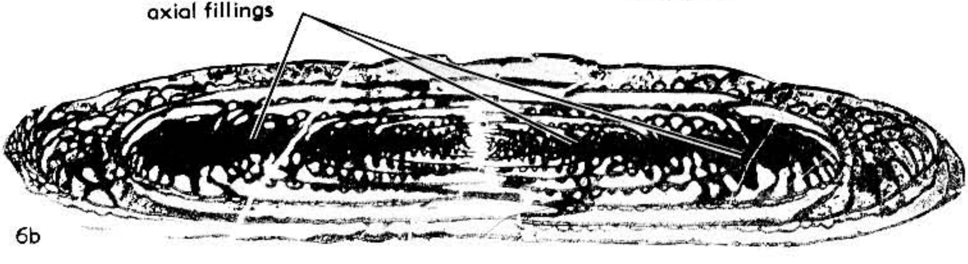
3b



6a



5



6b

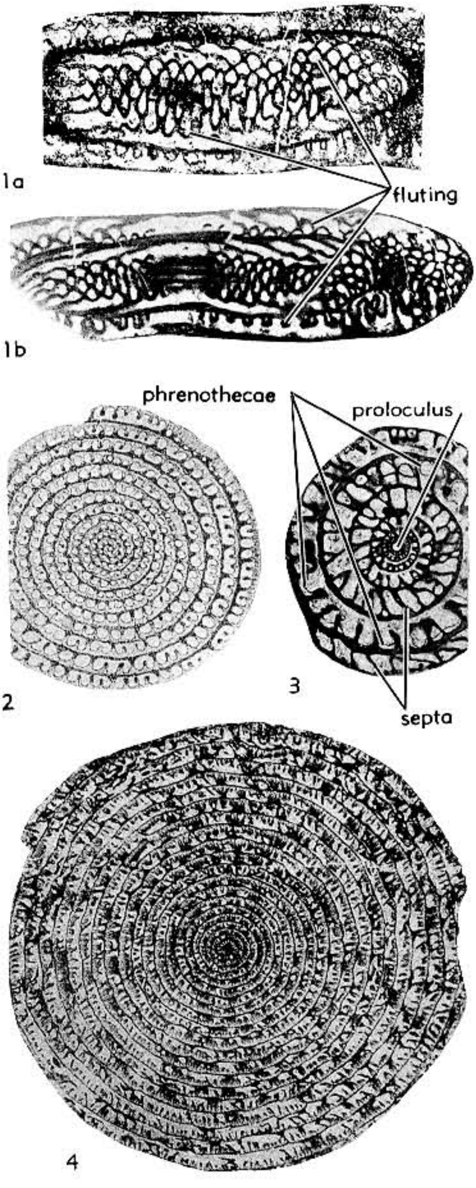


FIG. 276. Sagittal, tangential, and parallel sections of fusulinaceans.——*1a. Parafusulina nosonensis* THOMPSON & WHEELER, L.Perm., USA (Calif.); tang. sec. of paratype showing septal fluting, ×8 (*1922); *1b. Parafusulina gracilis* (MEEK), L.Perm., USA (Calif.); tang. sec. showing septal fluting and cuniculi, ×8 (*1934).——*2. *Neoschwagerina craticulifera* (SCHWAGER), U.Perm., China; parallel sec. of paratype, ×16 (*1922).——*3. Schwagerina fax* THOMPSON & WHEELER, L.Perm., USA (Calif.); sagittal sec. of syntype, ×8 (*1922).——*4. Lepidolina elongata* (GUBLER), U.Perm., Cambodia; parallel sec., ×12 (*838).

other, cut at right angles to the axis of coiling, is called a **sagittal section** (Fig. 275,*3b*, 276,*3*). The terminology applied to sections cut through areas other than these two depends on directions of their orientation and position. A section cut normal to the axis of coiling but not through the beginning chamber is termed a **parallel section.** One cut parallel to the axis of coiling but not through the beginning chamber is termed a **tangential section** (Fig. 276,*1*). Sections cut in directions not parallel to the axis of coiling or normal to it are referred to as **oblique sections.** For thorough observation of all structural features of a species, it is necessary to study numerous axial and sagittal sections and numerous parallel, tangential, and oblique sections cut through different parts of the shell and at various angles. It is also desirable to observe the external nature of the shell.

An external view of the fusulinacean shell shows a relatively smooth surface broken by shallow, closely spaced **external furrows** (Fig. 274). These furrows extend from end to end of the shell and mark the tops of the partitions between the chambers, termed **septa** (Fig. 276,*3*). Adjacent external furrows come together as they reach the axial poles. The surface is interrupted by an abrupt wall, termed the **antetheca** (Fig. 274), which forms the front wall of the last chamber and is punctured by numerous small openings, called **septal pores** (Fig. 277,*2,3a*). In many fusulinaceans the antetheca is arcuate anteriorly, or is plane. In others it is folded or corrugated into somewhat irregular to uniformly spaced waves, termed **fluting** (Fig. 275,*4*; 276,*1*; 278). The fluting is more pronounced in the lower part of the antetheca than in its upper portion.

Thin sections of the fusulinacean shell reveal highly complicated internal structures, all of which are considered in the classification and identification of species. The beginning chamber, termed the **proloculus** (Fig. 275, 276, 282), of most forms is spherical to subspherical in shape, and several coils or volutions of chambers are developed about it. The antetheca does not possess an aperture, and accordingly the cell depended on the septal pores for communication with the exterior of the shell.

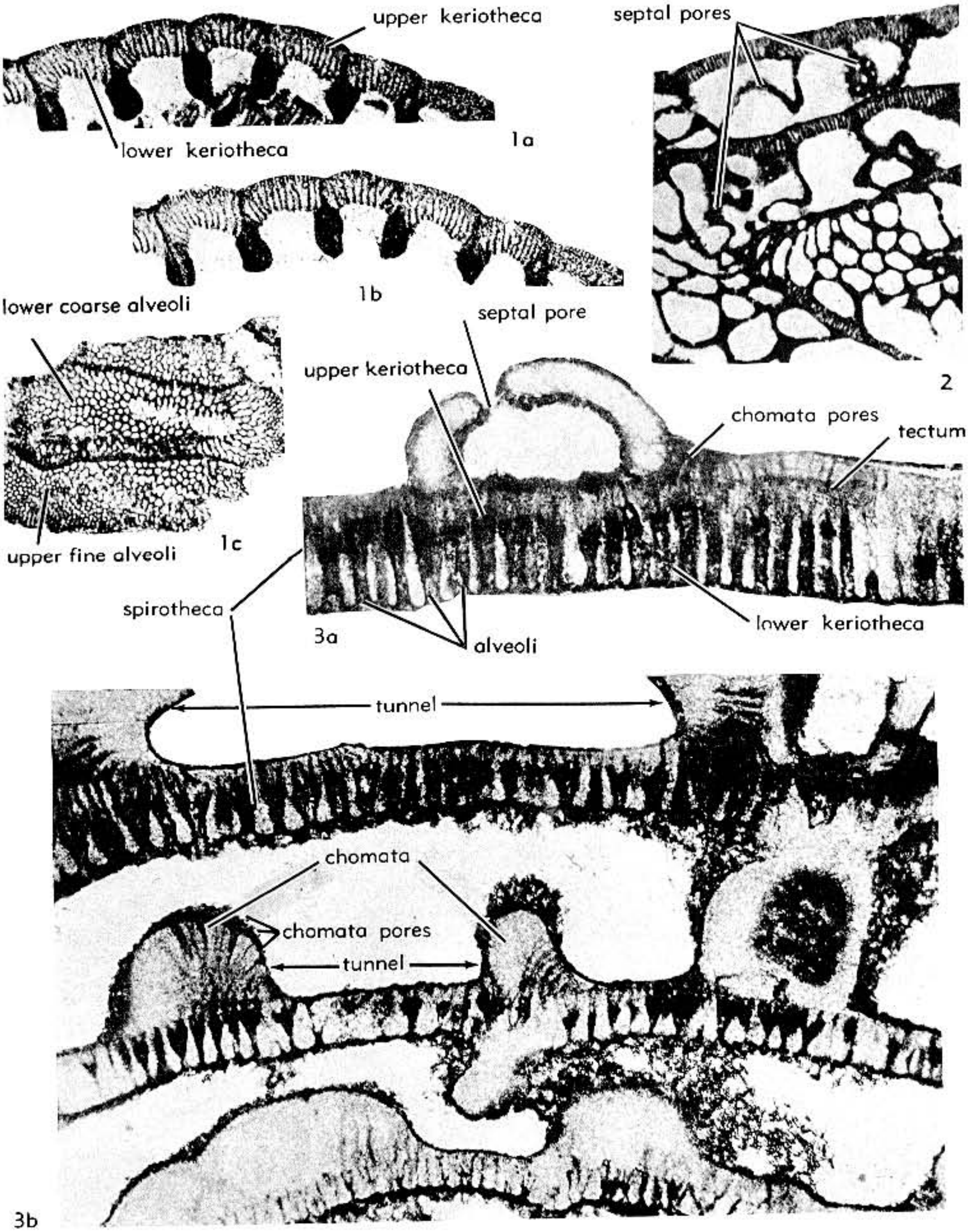


FIG. 277. Spirothecal and septal structures of fusulinaceans.——*1. Schwagerina rutschi* THOMPSON, L. Perm., Sumatra; *1a,* part of sagittal sec. showing lower and upper keriotheca of spirotheca; *1b,* part of sagittal sec. showing coarse and fine alveoli in lower and upper keriothecal layers of spirotheca; *1c,* tang. sec. of spirotheca showing cross sections of coarse and fine alveoli of lower and upper keriothecal layers, respectively; all ×40 (*1915).——*2. Triticites ventricosus* (MEEK & HAYDEN), L.Perm., USA(Kans.); part of axial sec. showing numerous closely spaced septal pores in outer volution, ×30 (*1922).——*3. Schwagerina campensis* THOMPSON, L.Perm.(Camp Cr. Sh.), USA(Tex.); *3a,* part of sagittal sec. of spirotheca showing septal and chomatal pores, alveoli, lower and upper keriothecae, and tectum; *3b,* part of axial sec. showing tunnel, chomata, and chomata pores; both ×200 (*1924).

FIG. 278. *Parafusulina wordensis* DUNBAR & SKINNER, L.Perm.(Word F.), USA(Tex.); acid-etched silicified specimens showing prominent septal fluting which produces regularly arranged chamberlets, ×5 (*1922).

Communication between adjacent chambers inside the shell was aided by resorption of a **tunnel** (Fig. 277,*3b*) at the base of septa in the central part of the shell of many fusulinaceans, and by resorption of several tunnels or small circular **foramina** (sing., foramen) at the base of septa throughout the length of the shell in others. Ridges of dense calcite, termed **chomata** (sing., choma) (Fig. 275,*2*; 277,*3b*), were built along the margins of the single tunnel in most fusulinaceans, and ridges of dense calcite **(parachomata)** were developed between adjacent foramina in forms having multiple foramina. Seemingly simultaneous formation of the chomata or parachomata, excavation of the tunnel or foramina, and deposition of dense calcite **(axial fillings)** (Fig. 279) in the axial regions occurred in some fusulinaceans. The internal surfaces of the chamber of many fusulinaceans, particularly in the subfamily Fusulininae, are lined with a layer of dense calcite formed at or near the same time as that in which the tunnel was excavated, and near the time the chomata and axial fillings were deposited. This lining of the chambers comprises layers designated as **tectoria** (sing., tectorium) (Fig. 280).

The wall above the chamber is referred to as the **spirotheca** (Fig. 277) because of its spiral arrangement. In primitive forms it consists of a thin, dense, primary layer **(tectum)** (Fig. 280, 281) that is later covered above and below by layers of tectoria. In more advanced forms, the tectum is supplemented by various other layers, including a transparent layer **(diaphanotheca)** or a thick layer of honeycomb-like structure **(keriotheca)** (Fig. 277, 280, 281). Each chamber has only a front and top wall of its own, for it uses the front wall of the preceding chamber as its posterior wall, and the tops of the chambers in the preceding volution as its floor. The structure of the spirotheca plays an important part in classification and differentiation of fusulinaceans. Ridges, termed **septula** (sing., septulum) (Fig. 275,*1*; 276,*2*, 290), extend

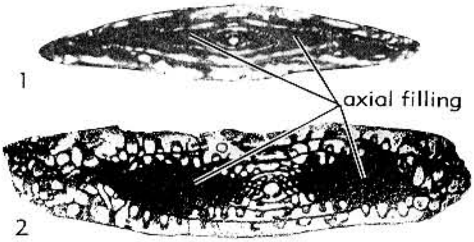


FIG. 279. Axial fillings in fusulinacean shells.——*1.* **Pseudowedekindellina prolixa* SHENG, M.Penn. (Penchi Ser.), China; axial sec. showing dense axial filling, ×14 (*1729).——*2.* **Quasifusulina longissima* (VON MÖLLER), U.Carb.(C_3), USSR(Tsarev Kurgan); axial sec. showing solid axial filling, ×10.5 (*1922).

down from the lower surface of the spirotheca in the subfamily Neoschwagerininae so as partly to subdivide the chambers.

Numerous specimens of *Schwagerina campensis* obtained from the Camp Creek Shale of Texas were gray in color when collected. Of the many specimens sectioned, all were found to be filled with calcite. On heating to temperatures just short of calcining, the specimens became red to brown. The structural features of the shell became greatly accentuated, and the septa, septal pores, keriotheca, and surface of the spirotheca became well defined. In most of them, the fibrous-like structures of the spirotheca were seen to penetrate the tectum and pass on through the chomata deposits. Both surfaces of the septa and walls of the septal pores are covered by thin layers of reddish oxides. It seems evident that these surfaces were coated by iron-bearing deposits before the chambers were filled with crystalline calcite. Similarly, it can be observed that thin layers of oxidized deposits cover surfaces of the spirotheca and completely line insides of the clear cell-like structures **(alveoli)** (Fig. 277,*3*), continuing around the lower surfaces of their bordering walls. Although these films of iron oxide completely line the alveoli, they do not occur over their lower ends, indicating that the alveoli were open spaces when the films were deposited. Furthermore, thin films of oxide line the inside or completely fill the continuations of alveoli as they pass through the tectum and overlying chomata. It might be argued that these films formed on parts of the outer area of secreted calcite crystals. However, if the clear areas were calcite pillars, the oxide films lining the alveoli should also be found over the lower ends of the prisms. Other evidence that the spirotheca was perforate is observed in continuity of the oxide films in the alveoli with those that occur as coatings on the septa, linings of the septal pores, and coatings on top of the chomata, all of which almost certainly were open spaces shortly after death of the animal.

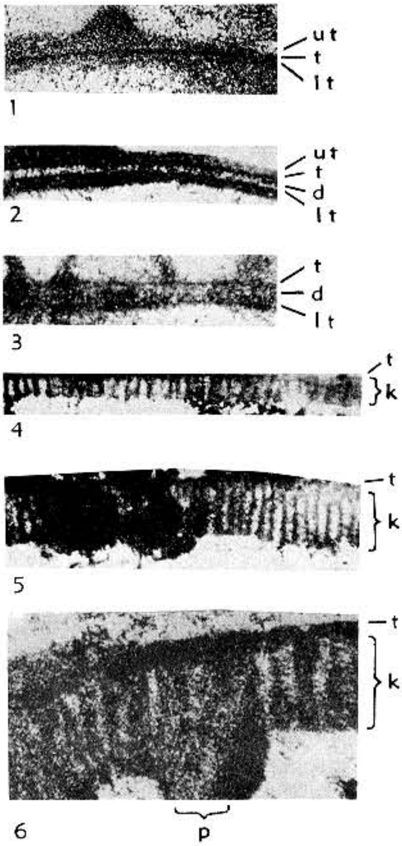


FIG. 280. Spirothecal structures of fusulinaceans, all ×100 (*1922).——*1. Profusulinella regia* THOMPSON, M.Penn., USA(Tex.); three-layered spirotheca.——*2. Fusulina* sp., M.Penn.(Garcia F.), USA(N. Mex.); four-layered spirotheca.——*3. *Fusulina cylindrica* FISCHER DE WALDHEIM, Low.U.Carb. (Myatschkovo, USSR; spirotheca composed of tectum, diaphanotheca, and discontinuous lower tectorium.——*4. Triticites irregularis* (STAFF), U. Penn.(Winterset Ls.), USA(Iowa); spirotheca composed of tectum and alveolar keriotheca.——*5. T. moorei* DUNBAR & CONDRA, U.Penn.(Graham F.), USA(Tex.); like fig. *4*.——*6. Schwagerina furoni* THOMPSON, U.Perm.(Bamian Ls.), Afghan.; thick spirotheca composed of tectum and keriotheca, with inserted pycnotheca continuous above septa. [Explanation: *d*, diaphanotheca; *k*, keriotheca; *lt*, lower tectorium; *t*, tectum; *ut*, upper tectorium; and *p*, pycnotheca.]

Similar oxidized coatings within the wall of the fusulinacean shell have been observed and photographed by HENBEST (*896). He did not state whether these specimens were dissolved by weathering and replacement, however, or whether they contained solid calcite fillings. DUNBAR (*639) has observed that specimens of *Parafusulina alaskensis* contain fillings of iron oxides in alveoli of the spirotheca, but the degree of replacement of associated fossils by oxides was not discussed. SKINNER & WILDE (*1796) have observed similar features in *Fusulina*

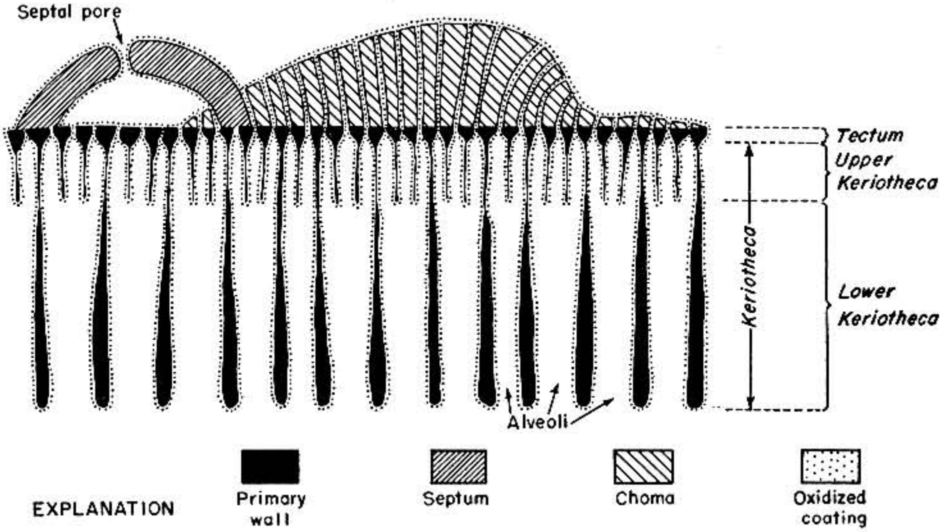


FIG. 281. Diagram of spirotheca showing pendant-like walls of alveoli, choma with chomatal pores, and septal pore, based on exceptionally well-preserved specimens of *Schwagerina campensis* THOMPSON, L.Perm. (Camp Cr. Sh.), USA(Tex.) (*1924).

from Desmoinesian rocks of Texas. These authors also observed and photographed porosity in the wall of *Millerella.*

The tectum has been interpreted by some to be a rindlike layer of the shell above the keriotheca, and the alveoli have been considered to end at the tectum. Since the alveoli and their bordering walls are almost perfectly displayed in specimens of *Schwagerina campensis* which I have studied, it is possible to demonstrate the cause for the seemingly solid nature of the dense tectum. I have been unable to show by photographs the structures of the tectum because its pores are very minute and partly filled with red oxides. An accompanying diagrammatic sketch is given from a highly magnified tectum, however (Fig. 281). It is evident that even though the tectum is not a solid layer, its density is due to a sharp reduction in size of pores of the keriotheca and a simultaneous and comparable sharp increase in thickness of the pore walls. Perhaps most important for study of thin sections, pores of the tectum are considerably smaller in diameter than thickness of the sections, and therefore observation is nearly always through several of the pore walls.

It has been noted by several students of fusulinaceans that structure of the keriotheca is more evident in the lower area of the spirotheca than in its upper part. In the lower area, the alveoli walls are thick and widely spaced, whereas in the upper part they are thin and closely spaced. Many specimens show a faint line of demarcation between the lower, coarser part of the keriotheca and its upper, finer part. Oxidized specimens demonstrate that the line of demarcation parallel to the tectum and located slightly below the keriothecal top is a line that marks the lower ends of the tubelike fine alveoli at the point where they open into the larger alveoli below.

The terminology here employed for different parts of the fusulinacean spirotheca is the same, in general, as that commonly used in recent years by most students of the superfamily. Although the tectum (roof) is not a complete covering as it was thought to be when proposed, and the keriotheca (honeycomb wall) lacks a truly honeycomb-like nature, the alveoli being tubes instead of pits or cavities, these terms have become well established in the literature, and most of them are reasonably descriptive of the spirothecal structures.

The pendant shape of the walls of the alveoli, as displayed in some thin sections, is due to their downward thickening as they approach the lower surface of the spirotheca. Correspondingly, the alveoli become constricted downward as their walls increase in thickness. Some of the abnormal downward thickening of the alveoli walls observed in thin sections is due partly to their oblique intersection with the thin sections. Growth of the fusulinacean wall after its inception does not seem difficult to understand, accepting the general concept that the wall was porous (*1924) (Fig. 277,*1b, 3a,b*). The spirotheca of *Schwagerina campensis* is divisible into three parts that are distinguishable largely because of variation in size of the alveoli and thickness of their surrounding walls. The terms applied to them are, from top to bottom, tectum, **upper keriotheca** composed of small alveoli with thin walls, and **lower keriotheca,** composed of large alveoli with thick walls (Fig. 281). It seems probable that the walls of all fusulinaceans have the same three layers. The alveoli of many fusulinaceans are too small for observation, and in others it seems possible that the upper and lower keriotheca appear in thin sections as a single layer because the upper one is too thin to be distinguished from the lower.

The differences between details of structures of the diaphanotheca and those of the keriotheca are not clearly understood. Furthermore, it seems possible that the central single layer of *Profusulinella* may be comparable in structure to the diaphanotheca and tectum of the Fusulininae and to the tectum and keriotheca of the Schwagerininae (Fig. 281).

PROLOCULUS

All fusulinaceans are multichambered. The chambers can be divided into first chamber (proloculus) and chambers of the coiled part of the shell (Fig. 282). In most fusulinaceans the proloculus is spherical to subspherical in shape, and proloculi of conspecific specimens generally are closely similar in size. Some forms have a proloculus only a few microns in diameter, whereas in others, it is more than 1 mm. in diameter. Although the proloculus of most forms is spherical, or nearly so, in some it is irregularly subspherical or even irregularly rectangular in shape. Almost all forms possessing irregular proloculi are large and have large proloculi. Although the irregular proloculi are much larger than the average size of those for the entire superfamily, some specimens of a given species characterized by large proloculi may have a spherical proloculus or one that is ellipsoidal, rectangular, or somewhat irregular.

Dunbar & Henbest (*643) and others have discussed the shape of the proloculus of fusulinaceans and have proposed several hypotheses as to the cause for its spherical

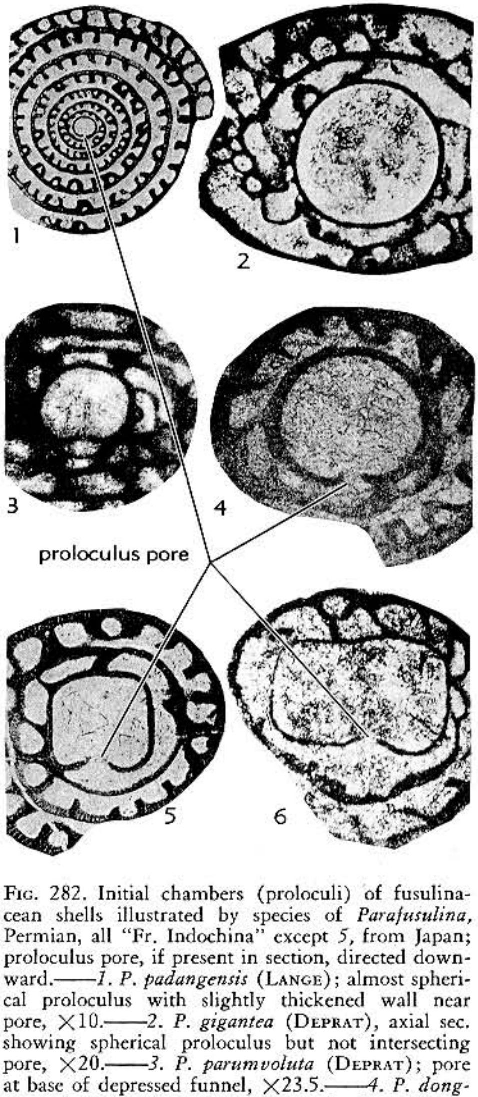


Fig. 282. Initial chambers (proloculi) of fusulinacean shells illustrated by species of *Parafusulina,* Permian, all "Fr. Indochina" except *5,* from Japan; proloculus pore, if present in section, directed downward.——*1. P. padangensis* (Lange); almost spherical proloculus with slightly thickened wall near pore, ×10.——*2. P. gigantea* (Deprat), axial sec. showing spherical proloculus but not intersecting pore, ×20.——*3. P. parumvoluta* (Deprat); pore at base of depressed funnel, ×23.5.——*4. P. dongvanensis* (Colani); subspherical proloculus with depressed area around pore, ×27.——*5. P. japonica* (Gümbel); subquadrate proloculus with depressed area around pore, ×30.——*6. P. gigantea* (Deprat); rectangular proloculus with cone around pore, ×20 (*1922).

to subspherical shape. One of these suggests that the cell around which the proloculus was formed may have had a different surface tension than fluids outside the area of the proloculus, which would tend to give the cell a globular form and produce a spherical proloculus. The smaller the fluid globule, the more nearly spherical should be its shape, and this accords with the more nearly spherical shape of small proloculi as compared with larger ones. It should be pointed out, however, that specimens of several forms having abnormally large proloculi may possess almost perfectly spherical proloculi. It cannot be demonstrated that the proloculus of fusulinaceans enclosed the entire embryonic cell, the nucleus, or an area of multiple nuclei. MYERS (*1336, *1337) has observed formation of the proloculus in several living foraminifers. In some, the proloculus surrounded the embryonic cell but in others only the nucleus of the cell, and in still others it surrounded a budlike protrusion on a side of the cell. The beginning chamber or beginning part of the shell of many other animals is spherical to subspherical. The cause of the spherical shape of this initial chamber or beginning stage of the shell in multicellular animals is not known, but it may be similar to that which developed the spherical proloculus of most fusulinaceans.

The wall of the proloculus is dense and uniform throughout its thickness, and in general structure it resembles closely that of the dense wedge-shaped layer of the septa of some forms. Its structure does not resemble that of the walls of immediately following chambers, except in forms having walls composed of a single thin layer, and the proloculus with a wall composed of a single thin layer. The proloculus wall in most fusulinaceans is thicker than that of the beginning chamber of the coiled part of the shell.

The proloculus wall is broken by a single circular opening, called **proloculus pore** (Fig. 282), that opens into the first chamber of the coiled part of the shell. The aperture of the proloculus in some specimens has a simple unmodified margin that is continuous with the surface of the proloculus wall. In some specimens the margin of the aperture is bordered by a short tubelike structure that extends into the proloculus. In many others the aperture is not bordered by a tubelike structure, but the surface of the wall immediately surrounding the aperture is depressed and the aperture is at the base of a shallow funnel. Various shapes and configurations of proloculi of fusulinaceans are shown on Figure 282.

Scattered specimens of many species of fusulinaceans contain two proloculi, around each of which one or more volutions of normal-appearing chambers are developed, and around both of which a normal set of spirally arranged chambers is seen. Rare specimens contain three proloculi. The full size of these specimens is not noticeably different from that of other conspecific associated specimens having a single proloculus. Specimens provided with double proloculi have been illustrated by many workers since those illustrated by STAFF in 1909 (*1830). Double or triple proloculi seem not to be confined to any particular group of fusulinaceans, though observed most commonly among Fusulininae and Schwagerininae.

Several hypotheses as to why some shells contain two or three proloculi have been suggested. The most generally accepted idea is that young individuals became joined to continue as a single individual, though the cause for such union is not known. It may have been for mutual benefit under conditions of adverse food supply, or union may have been merely an accident caused by close crowding of embryonic forms, such as may occur during encystation.

Characters of the proloculus have a bearing on the subject of dimorphism in fusulinaceans. Dimorphic reproduction in this group has been postulated by many workers, and attempts often have been made to demonstrate the presence of microspheric forms (representing sexual generation) and megalospheric forms (asexual generation). In many cases cited all gradations in size of proloculi have been found in a single suite of specimens, and the range of volume of the proloculus is no greater than the range in size of other features in specimens having equal-sized proloculi. Some most convincing evidence of dimorphism among fusulinaceans has been presented by DUN-

BAR, SKINNER, & KING (*647), based on studies of *Parafusulina.* Giant individuals with minute proloculi and highly asymmetrical early volutions occur in association with smaller individuals which bear large proloculi and differing internal shell structures. The giant specimens are rare among relatively abundant smaller specimens. Giant specimens of *Parafusulina* possessing minute proloculi do not show a distinct single tunnel, but associated smaller specimens provided with large proloculi have a well-developed tunnel. DUNBAR & SKINNER (*646) described giant specimens of several forms of *Polydiexodina* that contain minute proloculi and asymmetrical early volutions, and these are associated with more abundant, smaller specimens with large proloculi and symmetrical volutions. The smaller specimens possess multiple tunnels, whereas the giant specimens lack tunnels. These giant individuals have tunnel-like paths, however, that penetrate the septal walls and provide for internal communication. Rare specimens having minute proloculi and highly asymmetrical early volutions have been found in association with abundant normal-appearing specimens of species of *Fusulina* and of *Triticites.* The outer parts of shells of these two types seem identical in other respects. It is supposed by some that the specimens characterized by minute proloculi represent the microspheric generation and that the more abundant specimens with large proloculi represent the megalospheric generation. The preponderance of specimens considered to represent the asexual generation is noticeable. Only one type of shell has been identified for most species of fusulinaceans. It is not certain that the fusulinaceans display dimorphism.

CHAMBERS

The proloculus aperture opens into the first chamber of the coiled part of the shell. The first coiled chamber of most specimens is smaller in cross section than the proloculus, but in most specimens it is distinctly elongate in the direction of the axis of coiling of the outer volutions. In some specimens having an unusually large proloculus, the aperture opens into a somewhat irregular chamber that almost completely surrounds the proloculus. This large irregular chamber generally does not contain as large a volume as that of the proloculus, and its walls conform in structure more closely to the walls of the succeeding chambers (Fig. 283). In some specimens, the first chamber

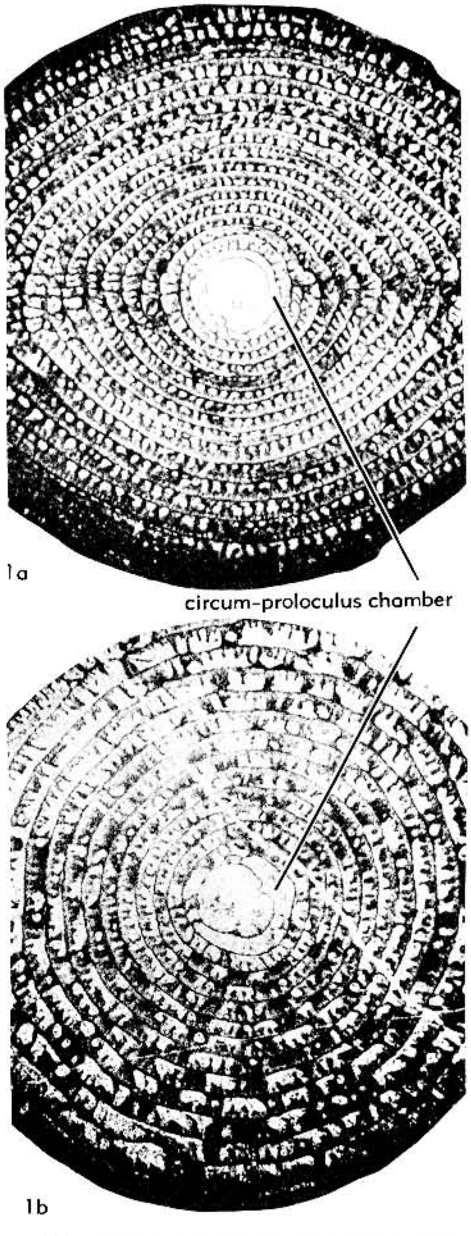


FIG. 283. Irregular circum-proloculus chamber observed in some fusulinaceans.——*1.* **Lepidolina multiseptata* (DEPRAT), U.Perm., Cambodia; *1a,b,* axial sec. of holotype, sagittal sec. of paratype, ×10 (*1922).

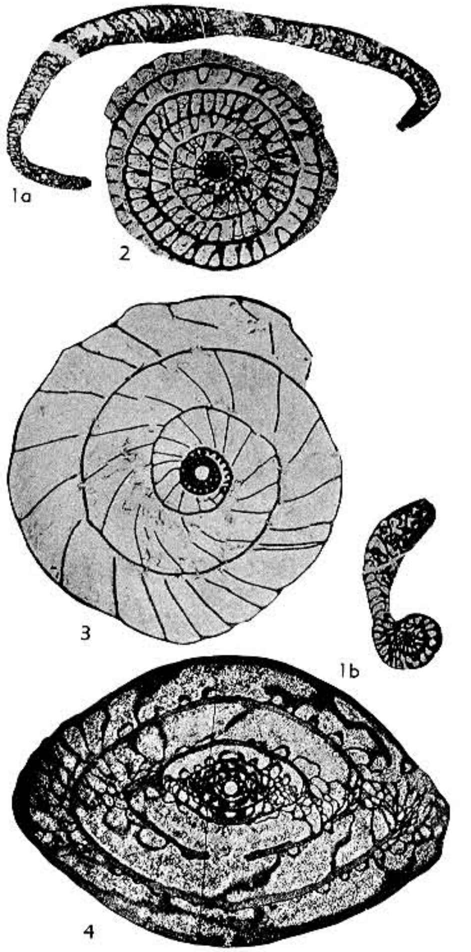


FIG. 284. Variation in chamber height and coiling in ontogeny of fusulinaceans.——*1. Nipponitella* HANZAWA, Perm.(Maiya Gr.), Japan; *1a, N. auricula* HANZAWA, axial sec. of syntype showing extreme uncoiling, ×6 (*1922); *1b, *N. explicata* HANZAWA, parallel sec. of paratype, ×6 (*1922).——*2. *Paraschwagerina gigantea* (WHITE), L. Perm.(Wolfcamp.), USA(Tex.), sagittal sec. of paratype showing contrast between juvenile and mature parts of shell, ×6 (*1922).——*3. *Robustoschwagerina tumida* (LIKHAREV), Perm.(Darvaz Ser.), USSR(Darvaz); sagittal sec. of paratype showing relatively large proloculus surrounded by two or three volutions with very low height of chambers followed by greatly increased height in mature parts of the shell, ×6 (*1276).——*4. Pseudoschwagerina muongthensis* (DEPRAT), L. Perm., N.Vietnam(Tonkin); axial sec. showing abrupt increase in chamber height beginning in fourth whorl, ×9 (*587A).

of the coiled part of the shell is much larger than that of the immediately succeeding chamber.

Beyond the proloculus, the fusulinacean shell is composed of numerous chambers coiled about the proloculus in such a fashion that the axis of coiling in most forms coincides with the greatest diameter of the shell, commonly defined as length of the shell. Similarly, the greatest diameter at right angles to the axis of coiling is commonly defined as width of the shell. In some, length of the shell in the axis of coiling is about equal to the width, and in others the axis of coiling is the shortest diameter. Almost all chambers of the coiled part of the shell are much shorter in the direction of coiling than their width measured parallel to the axis of coiling. The chambers are widest in the center of the shell and are reduced to near-zero width at the poles. Starting with the first few chambers of the first volution, the chambers gradually increase in height. This increase is almost uniform throughout most of the shell in many fusulinaceans, but chambers of the last one or two volutions of gerontic individuals in many forms are lower than those of the immediately preceding volutions. In forms of some genera, particularly of *Pseudoschwagerina* and *Paraschwagerina,* the chambers of the first few volutions are low; in the following one or two volutions their heights increase rapidly, and the outer volutions are highly inflated (Fig. 284,*2-4*). However, the last one or two volutions of gerontic individuals of these genera decrease in height slightly. In a few aberrant genera (e.g., *Codonofusiella, Nipponitella*), the inner volutions increase in height gradually, but the outer volutions are uncoiled and highly flared or subrectilinear (Fig. 284,*1*).

Most specimens of all genera of Schubertellinae have minute proloculi and the first one to three volutions are tightly coiled, their axis of coiling being at large angles to the axis of coiling of the outer volutions. The first part of this asymmetrically coiled part of the shell is slightly evolute, and it does not attain a form ratio of unit value. Early members of the Fusulininae also have highly asymmetrical early volutions, particularly species of *Pseudostaffella* and early species of *Profusulinella*. The cause of this asymmetrically coiled nature of the juvenile shell is not known. The asymmetrical coiling of the juvenile part of giant specimens associated with *Parafusulina* and *Polydiexodina,* discussed by DUNBAR, SKINNER & KING (*647), is seemingly similar to that in more primitive forms of *Profusulinella* and some of the Schubertellinae (Fig. 299,*1a-d*). However, specimens of Schubertellinae distinguished by asymmetrical coiling are not large, and many such forms are not associated with specimens having symmetrical early volutions and markedly larger proloculi. No evidence is found that these primitive fusulinaceans exhibiting minute proloculi and asymmetrical early volutions represent the microspheric generation of dimorphic forms. The proloculus is unevenly ellipsoidal in some forms (Fig. 285).

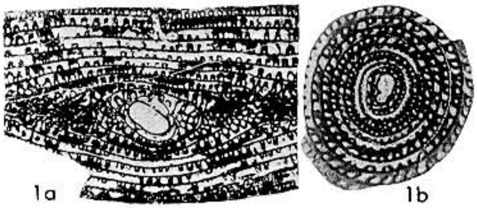


FIG. 285. Axial and sagittal sections of fusulinacean shells.——*1. Polydiexodina* DUNBAR & SKINNER, U. Perm.; *1a, P. afghanensis* THOMPSON, Bamian Ls., Afghan., axial sec. of holotype showing ellipsoidal proloculus and adjacent volutions, ×6.7 (*1922); *1b, *P. capitanensis* DUNBAR & SKINNER, Capitan Ls., USA(Tex.), sagittal sec. of paratype, ×6.7 (*1922).

ANTETHECA AND SEPTA

The anterior wall of the last chamber (antetheca) becomes the septum between the last two chambers when an additional chamber is developed. In primitive forms of *Millerella* the antetheca is curved anteriorly immediately below its top and is curved posteriorly near its base, resulting in septa that are strongly arcuate. In most of the more highly developed forms of the family Ozawainellidae, the antetheca is plane and perpendicular to the outer wall of the chamber. Also, members of the family Verbeekinidae have plane perpendicular antetheca and septa.

Except in *Pseudostaffella* and very primitive forms of *Profusulinella*, the septa of members of the subfamily Fusulininae are corrugated or fluted to some extent. The fluting in primitive forms is confined to broad undulations in the extreme polar regions and to the basal part of the septa. In more highly developed forms, the plication of the septal walls progressively moves from the poles toward the center of the shell and progressively moves up toward the tops of the septa. The salient of the fold in the antetheca corresponds in position to the reentrant in the fold of the preceding septum. In forms with closely spaced septa or sufficiently strong septal fluting, adjacent septa are brought into contact at these points, resulting in enclosed areas **(chamberlets)** at base of the chambers that open upward (Fig. 278). In primitive forms of Fusulininae the fluting is sufficiently intense to bring adjacent septa into contact only at their lower margins and only in the extreme polar regions where the chambers are shortest. Primitive forms of Schwagerininae (e.g., *Triticites*), also have septal fluting developed only in the extreme polar regions (Fig. 275,*4*). Highly developed forms of the Fusulininae and Schwagerininae have closely and highly fluted septa throughout the length of the shell, and the fluting brings the septa into contact at opposing folds even above the tunnel. In some members of the Schwagerininae (e.g., many forms of *Paraschwagerina* and most forms of *Pseudofusulina*) the septa are plicated to the top of the septa. In many species of these genera the fluting forms chamberlets that extend more than half the height of the chambers. In highly developed forms of *Schwagerina* and all species of *Parafusulina* and *Polydiexodina,* the salient fold of the fluting extends forward a great distance and the antetheca or septum of the following chamber bends downward near to or even behind the greatest forward projection of this salient (Fig. 276, 278). Therefore, the re-entrant of the later antetheca or septum is impounded against the salient of the preceding septum, as illustrated in the accompanying diagram (Fig. 286). In the polar regions of many forms of *Parafusulina* the salient extends forward as much as the combined length of the following two chambers.

In species of *Parafusulina* and *Polydiexodina* the extended salients, combined with

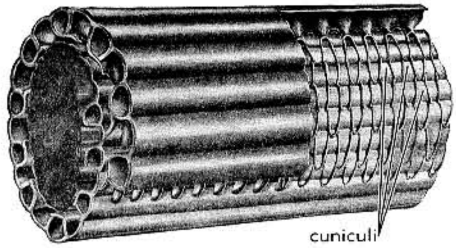


FIG. 286. Diagram illustrating inferred development of cuniculi in *Parafusulina* and *Polydiexodina* (*1922).

impounded re-entrants of the following septum, produce a tunnel-like structure running transverse to the axis of coiling at each crest and trough of the fluting in the antetheca. Interruptions formed by the downturned edge of septal salients in the earlier volutions are resorbed or excavated so as to form a continuous tunnel-like path throughout the earlier part of the shell; this path has been termed **cuniculus** by DUNBAR & SKINNER (*646) (Fig. 286). The cuniculi are bordered by edges of opposing salients and re-entrants to give the appearance of septa running transverse to the axis of coiling. The bordering walls of the cuniculi are highly sinuous in primitive forms that have only moderately fluted septa. They are almost straight in forms having intensely fluted septa (Fig. 287).

DUNBAR & SKINNER (*644) were the first to observe cuniculi in *Parafusulina* and *Polydiexodina*. The structure of the cuniculus has been discussed further by DUNBAR & HENBEST (*643). It was suggested by these workers, and later by THOMPSON (*1921), that foramina are developed by the upturned edges of the salients in the antetheca. Further observations seem to demonstrate that salients in the antetheca do not form foramina but turn downward to the top surface of the preceding volution. The lower margins of the salients are later resorbed to develop the continuous tunnel-like cuniculus. In the earlier parts of the shell of *Parafusulina*, only the margins of the salients remain along the borders of the cuniculi (Fig. 287). It is evident that excavation of the cuniculi developed into the auxiliary tunnels of *Polydiexodina* by coalescence of several cuniculi. The necessity of widening passageways seemingly was due to the extreme length of the shells of *Polydiexodina*.

The antetheca of the shell contains numerous septal pores (Fig. 277,*2*).

So far as can be determined, none of the fusulinaceans had an aperture or foramina in the antetheca; they depended largely or entirely on the septal pores and wall pores for external communication. The antetheca of many fusulinaceans is fluted, and it has seemed quite impossible to determine the total number of septal pores in the antetheca. The relative abundance of septal pores is judged to have no connection with the stage of evolution of the individual (Fig. 303, *3a,c*). Whether the number of septal pores is constant among individuals of a species is not known, but the more highly fluted types of fusulinaceans seem to have more abundant septal pores than those with less fluting.

Primitive fusulinaceans characterized by a *Profusulinella*-type spirothecal structure have a septal structure almost identical to that of the spirotheca. All evidence indicates that the spirotheca and antetheca were deposited simultaneously, for none of the many thousand fusulinacean sections examined by me reveals an incompletely built last chamber. The antetheca of the last chamber of primitive Ozawainellidae, Schubertellinae, and Fusulininae is composed only of tectum that seemingly is identical in structure to the tectum of the spirotheca except for the presence of septal pores. Both the anterior and posterior surfaces of the septa are later covered by tectoria which appear to be simultaneously developed with

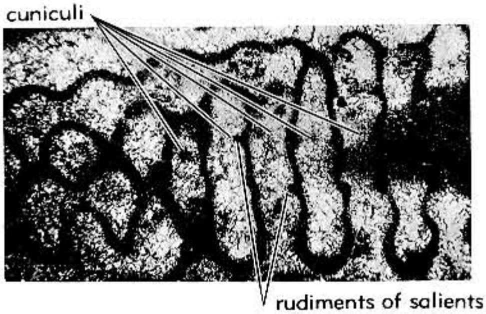


FIG. 287. Rudiments of salients of septa left after excavation of cuniculi in the test of *Parafusulina nosonensis* THOMPSON & WHEELER, L.Perm.(Nosoni F.), USA(Calif.), shown in part of tang. sec. of paratype, ×30 (*1922).

the tectorial lining of the chamber, with the chomata, and with the axial fillings if they are present.

In highly developed genera of the Fusulininae (e.g., *Fusulinella, Fusulina, Wedekindellina*) the tectum and diaphanotheca of the spirotheca are deflected downward to form the septum, but the diaphanotheca decreases in thickness rapidly downward from the top of the septum. Also, the diaphanotheca of the spirotheca of the following chamber extends a short distance down the anterior side of the septum. The development of tectoria on the septa of these genera is similar to that of the more primitive genera discussed above. However, the tectoria of the more highly developed forms of *Fusulina* are thin and discontinuous or they may be entirely absent.

The tectum of the spirotheca of Schwagerininae is deflected downward to the base of the antetheca. The keriotheca of the spirotheca of members of this subfamily extends only a short way down the septa. At the point of downward deflection of the tectum at the top of the antetheca, a dense layer is developed on the posterior side of the tectum in most forms. This layer, designated **pycnotheca** by DUNBAR & HENBEST (*643), seems to wedge in between the anterior edge of the keriotheca and the tectum (Fig. 280,*6*). It extends to the base of the antetheca, gradually decreasing in thickness. The structure of the pycnotheca is similar to that of the wall of the proloculus in being dense and uniform. The uniformity of the pycnotheca is broken only by the septal pores. The keriotheca does not resemble the pycnotheca closely and a sharp line of demarcation appears where they come in contact. The pycnotheca is thickest immediately above the tunnel and thins toward the poles. In many forms of Schwagerininae that have thin septa, the pycnotheca is so tenuous that it cannot be distinguished from the thin tectum, or it is absent. In other Schwagerininae, the pycnotheca is distinctly thick just below its upper surface but cannot be distinguished from the tectum in the lower part of the septum. It has been suggested that the pycnotheca developed from the keriotheca, but its structure strongly suggests that it was formed by thickening of the tectum.

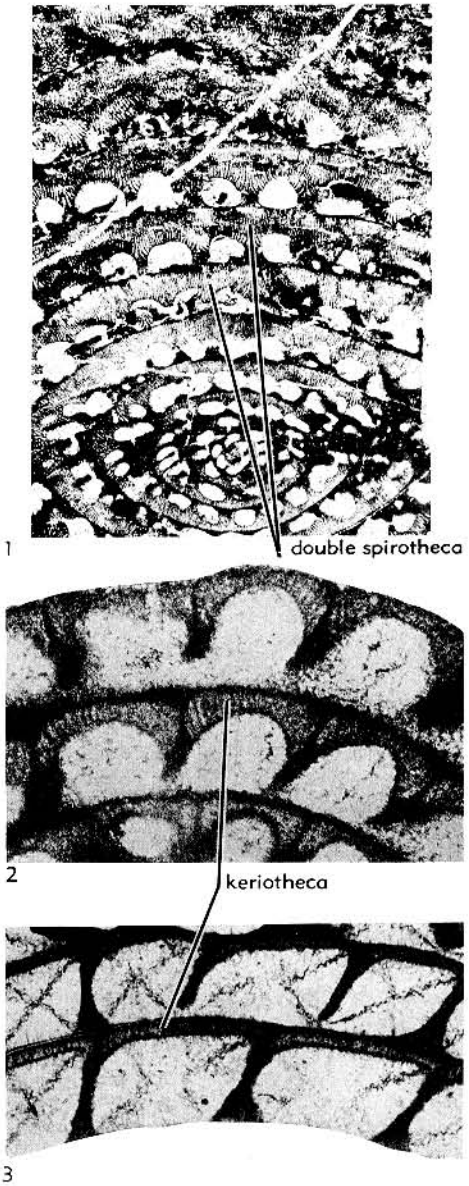


FIG. 288. Structural features of fusulinacean spirotheca and septa illustrated by *Neoschwagerina* YABE, U.Perm., and *Cancellina* HAYDEN, U.Perm., with thick spirotheca, and *Verbeekina* STAFF, U.Perm., with thin spirotheca.——*1. N. ovalis* (MINATO & HONJO), Akasaka Ls., Japan(Gifu Pref.); slightly tang. axial sec. showing radially diverging alveoli of keriotheca in basal parts of septa, ×40 (*1287).——*2. *C. primigena* (HAYDEN), Iran; part of sagittal sec. showing keriothecal layers on both sides of septa, ×100 (*1922).——*3. *V. verbeeki* (GEINITZ), Sumatra; part of sagittal sec. showing structure of spirotheca, ×40 (*1922).

The antetheca of members of the Verbeekininae and Neoschwagerininae is formed by the downward deflection of the tectum of the spirotheca. In forms with thick spirotheca, the keriotheca of the spirotheca extends down both sides of septa almost to their base, and keriothecal structures can be observed almost to the base of the septa (Fig. 288,*2*). In genera having a thin keriotheca (e.g., *Verbeekina*) this layer extends only a short distance down both sides of a septum (Fig. 288,*3*).

The lower margins of the septa of many fusulinaceans, as seen above the tunnel or above the foramina in sagittal sections, are distinctly thicker than the upper part of the septa, resulting in a pendant-shaped cross section. Their cross section, however, is not pendant-shaped in the outer few chambers. The thickening of the lower margins of the septa is due largely, if not entirely, to deposits similar to the chomata, parachomata, and tectoria that are laid down during or shortly after excavation of the tunnel or foramina.

SPIROTHECA

The structure of the spirotheca, which furnishes one of the most reliable criteria for differentiation and classification of many fusulinaceans, is highly complicated, and its evolution has been determined within many branches of the group (Fig. 277, 280). The anterior-posterior profile of the top of the spirotheca of most forms turns downward sharply immediately adjacent to the septa, resulting in distinct external septal furrows. The upper surface across the central part of the chamber of most tests conforms closely with the curvature of the volution.

The spirotheca of the most primitive genus, *Millerella,* is composed of a central thin dense layer, the tectum, and adjoining less dense but thicker structureless layers, the **upper tectorium** above and the **lower tectorium** below. The spirothecal structure of most early Middle Pennsylvanian genera is similar to that of *Millerella.* This type of structure is best developed in *Profusulinella* and is referred to as a *Profusulinella*-type of wall (Fig. 280,*1*). A transparent layer, the diaphanotheca, is developed below the tectum in forms more highly advanced biologically than *Profusulinella,* resulting in a four-layered spirotheca. This sort of spirotheca is referred to as a *Fusulinella*-type of wall (Fig. 280,*2*). The spirotheca in the outer part of the last volution of mature and submature specimens of *Millerella, Profusulinella,* and other primitive forms is composed of a single thin layer. It is evident that the tectoria are deposited later, and that the primary spirothecal structure is composed of a single layer, the tectum. In forms of *Fusulinella, Fusulina,* and other genera having a *Fusulinella*-type of spirothecal structure, the last few chambers of both mature and immature individuals have a spirotheca composed of tectum and diaphanotheca. Seemingly, the primary structure of the spirotheca of these forms is composed of a tectum and diaphanotheca (Fig. 280,*3*). The tectoria are of later or secondary origin, developed contemporaneously with the chomata and axial fillings and with excavation of the tunnel.

The spirotheca of the Schwagerininae is composed of a tectum and a lower, thicker layer, the keriotheca. Such spirothecal structure is referred to as a *Triticites*-type of spirotheca (Fig. 280,*4-6*).

Although it seems that the entire spirotheca of a chamber was deposited simultaneously with deposition of its antetheca, all evidence indicates that the spirotheca continued to grow in thickness after completion of its original form. The keriotheca of the last chamber is thinner in most shells than in immediately preceding chambers. In submature specimens the keriotheca of the last chamber seems to be thinner than that of the same part of the shell in mature specimens. Thus, the keriotheca of any chamber seemingly continued to increase in thickness with later growth of the individual.

Thin sections of the keriotheca show numerous dark lines normal to its surfaces, and these are separated by larger transparent areas. Sections cut tangent to the surface of the spirotheca show that the transparent areas (alveoli) are columnar in cross section, somewhat irregular to circular in outline, and are surrounded by the darker thin areas (Fig. 277,*1c*). Most students have interpreted the alveoli as cell-like openings in the keriotheca, and the darker thin zones as the enclosing walls of the openings. The keriotheca of many Schwagerininae is divisible into a lower layer with coarse alveoli (lower keriotheca) and an upper layer of smaller alveoli (upper keriotheca) (Fig. 277,*1a,c*). Several smaller alveoli of the upper area are replaced by a single large alveolus below, into which they grade.

GUBLER (*837, *838) has interpreted the keriotheca as a masonry-like structure, in which the alveoli are coarse crystals of calcite cemented with a more fine-grained calcite impregnated with organic material, the latter less transparent material serving as "mortar." The tectum was interpreted by GUBLER as composed of fine-grained calcite and included organic material.

The spirotheca has been judged by most other workers to be porous. The alveoli decrease in size upward and at least part of them in some forms seem to pass through the tectum. Many thin sections of specimens show fine clear areas that pass through the upper surface of the spirotheca, as indicated in figures published by HAYDEN (*885), THOMPSON (*1915, *1921, *1924), DUNBAR & SKINNER (*646), and DUNBAR & HENBEST (*643). Some illustrations published by DUNBAR & SKINNER (*646) and DUNBAR & HENBEST (*643) indicate that fine, rodlike transparent structures penetrate the entire wall and even continue through the chomata.

HENBEST (*896) has stained numerous types of fusulinaceans and has observed structures of the spirotheca that suggest porosity. Stained specimens of Fusulininae reveal porelike structures that pass through all layers of the spirotheca and the chomata (Fig. 277,*3*; 281). As the tunnel is well developed immediately adjacent to the chomata, a necessity for such openings is not obvious. Also, the tunnel is developed when the tectoria are deposited.

The diaphanotheca of some highly developed forms of Fusulininae shows a finely striated structure that seems comparable to the alveoli of the Schwagerininae. Most Fusulininae do not show a porous structure, but the pores may be too small to observe. Pores have not been noted in the tectum of fusulinaceans having a *Profusulinella*-type of spirotheca, even in species represented by abnormally large mature shells. It seems important that in large specimens of *Sumatrina* the spirotheca is composed of a single thin layer, but pores have not been observed even in the outer part of the shell (Fig. 289).

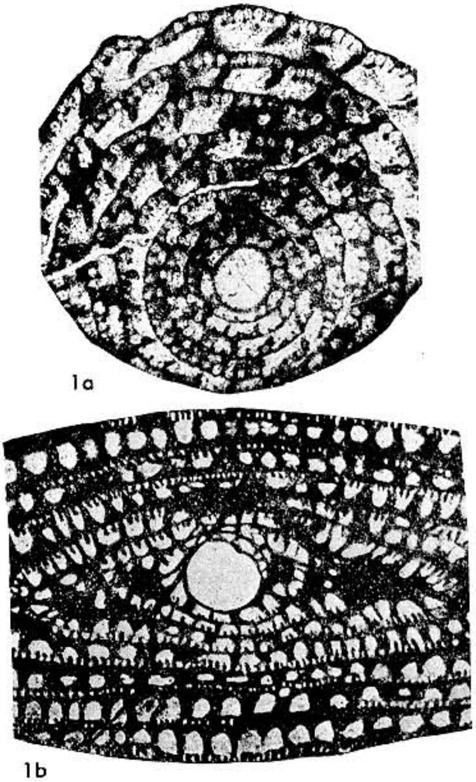


FIG. 289. Thin spirotheca of *Sumatrina* VOLZ, U. Perm., consisting of a single dense layer.——*1a. S. longissima* (DEPRAT), Cambodia (type-sp. of *Pseudolepidolina*), part of sagittal sec., ×45; *1b*, **S. annae* VOLZ, Sumatra, part of axial sec. of holotype, ×30 (*1922).

The porosity of the spirotheca has been especially stressed in recent years by WHITE (*2056), DUNBAR & SKINNER (*646), and DUNBAR & HENBEST (*643). The imperforate nature of the spirotheca was especially stressed by GUBLER (*837, *838). DUNBAR & SKINNER presented the following three points to refute GUBLER's postulate that the alveoli represent clear calcite cemented with finer-grained calcite-bearing organic material: (1) The crystallographic orientation of the calcite in several adjacent alveoli of at least some specimens corresponds to the orientation of the calcite immediately on the inside of the chamber, indicating that the alveoli were filled with

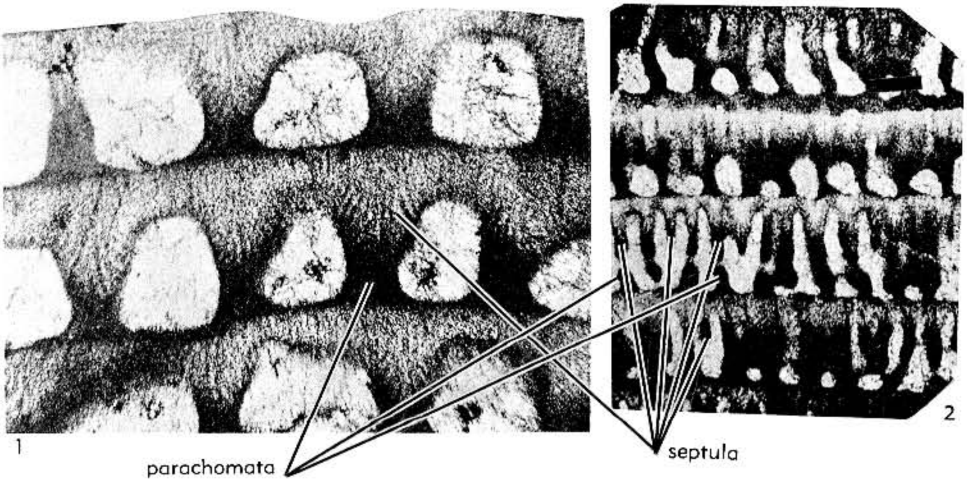


FIG. 290. Alveolar structure of spirotheca and septula in *Neoschwagerina* YABE, U.Perm., and *Yabeina* DEPRAT, U.Perm.——*1. N. haydeni* DUTKEVICH & KHABAKOV, Bamian Ls., Afghan.; part of axial sec. showing divergent alveoli extending through spirotheca into basal part of septula, ×100 (*1922).——*2.* *Y. inouyei* (DEPRAT), Japan(Akasaka Ls.); part of axial sec., enlarged (*1922).

calcite at the same time as the inside of the chamber was filled during fossilization. Therefore, the alveoli seemingly were open spaces during the life of the animal, and they were filled with calcite coincidently with filling of the inside of the chamber; (2) the tectum shows dark and light bands, indicating that its structure somewhat resembles keriothecal structure and that the tectum is not a homogeneous layer on which the calcite prisms of the keriotheca were formed, as postulated by GUBLER; (3) DUNBAR & SKINNER observed in deformed specimens from Nevada that at points of compression of the keriotheca, dark lines of the keriotheca are close together and at points of tension the dark lines are much farther apart. This suggests that the alveoli were compressible in the compressed areas, and they were points of weakness in areas of tensional stresses. Therefore, the alveoli seemingly were hollow spaces during this early period of deformation and before complete fossilization.

As pointed out by DUNBAR & SKINNER, the alveoli of all fusulinaceans are smaller in diameter than the thickness of most thin sections, and consequently it is difficult to observe the crystallographic structure of the materials in a single alveolus. Some fusulinacean shells collected from surface samples have hollow chambers, but shells have not been observed that also have hollow alveoli. Many fusulinacean shells have been studied in which the inside of the chambers are filled with chalcedony, but alveoli in the shells seem to be filled with calcite and lack chalcedony.

The more primitive members of both Neoschwagerininae and Verbeekininae have a spirotheca in which the lower layer contains alternating dark and less dense areas that resemble closely the structure of the keriotheca of the Schwagerininae. The less dense tubelike features are referred to as alveoli. In the Verbeekininae, the alveoli are about normal to the surfaces of the spirotheca but are more easily identified near the lower surface. In primitive members of the Neoschwagerininae, the keriotheca is thicker than in the Verbeekininae, and the alveoli are slightly broader. Also, in Neoschwagerininae the keriothecal structure extends to the base of the septula. In forms of *Neoschwagerina* having a thick keriotheca, the alveoli diverge as the base of the septula is approached. In some forms this divergence seemingly occurs without the introduction of additional alveoli, and both the alveoli and intervening dark areas merely increase in width.

The structure of the septula has been diagrammatically illustrated by many workers, including SCHWAGER (*1706), STAFF

(*1831), Deprat (*584, *586, *587), Lee (*1120), and Gubler (*838). The addition of alveoli in the lower part of the septula has not been indicated in any of these illustrations. Axial sections of *Yabeina katoi* from Akasaka, Japan, indicate that the transverse septula in some parts of the shell, especially near the poles in outer volutions, contain four or five alveoli in this upper area and may have three or four short alveoli added in their lower areas where the alveoli fan out to the edges of the septula (Fig. 290). This does not prove that alveoli are added in the lower part of the septula, for those extending down from the tectum may intersect the plane on the thin section near their lower ends and merely seem to pinch out between the alveoli that follow the plane of the section down from the tectum.

Thin, dense, diaphragm-like partitions that extend across the chambers of *Pseudofusulina* at various angles and in various parts of the chambers are termed **phrenothecae.** The structure of the phrenothecae resembles that of the tectum and seemingly is broken at irregular intervals by small openings similar to the septal pores. The phrenothecae are concave upward in some parts of the chambers and are concave downward in other parts. Most commonly, their edges are attached to the septa, but they may be attached to the floor or roof of the chamber. In forms such as *Pseudofusulina huecoensis* Dunbar & Skinner, having less well-developed phrenothecae, they are confined to the lower part of the chambers and are best developed in the region of the tunnel (Fig. 291). That they are primary parts of the shell structure is indicated by their occurrence in all specimens of some species collected from widely separated localities. Phrenothecae occur in most, if not all, species of *Pseudofusulina,* but are found only rarely in species of *Schwagerina,* as defined in the *Treatise.* At some localities, shells of *Pseudofusulina* contain abundant phrenothecae, but numerous

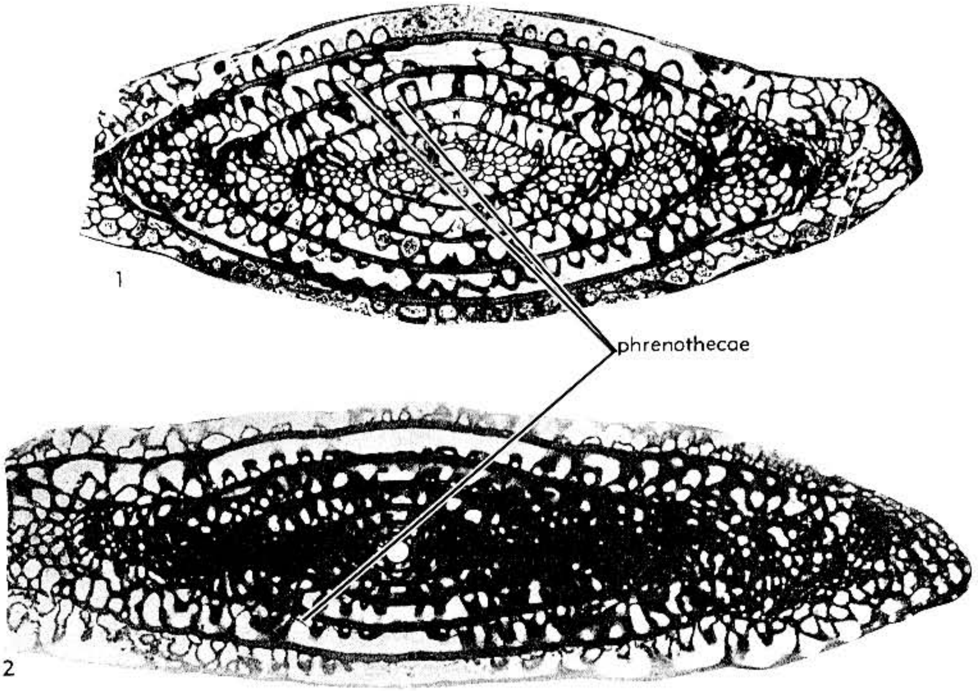


Fig. 291. Phrenothecae of fusulinaceans illustrated by *Pseudofusulina* Dunbar & Skinner, L.Perm.——*1. P. nelsoni* (Dunbar & Skinner), Hueco Ls., USA(Tex.); axial sec. with phrenothecae chiefly adjacent to tunnel, ×10 (*1922).——*2. *P. huecoensis* Dunbar & Skinner, Hueco Ls., USA(Tex.); axial sec. of holotype, ×10 (*1922).

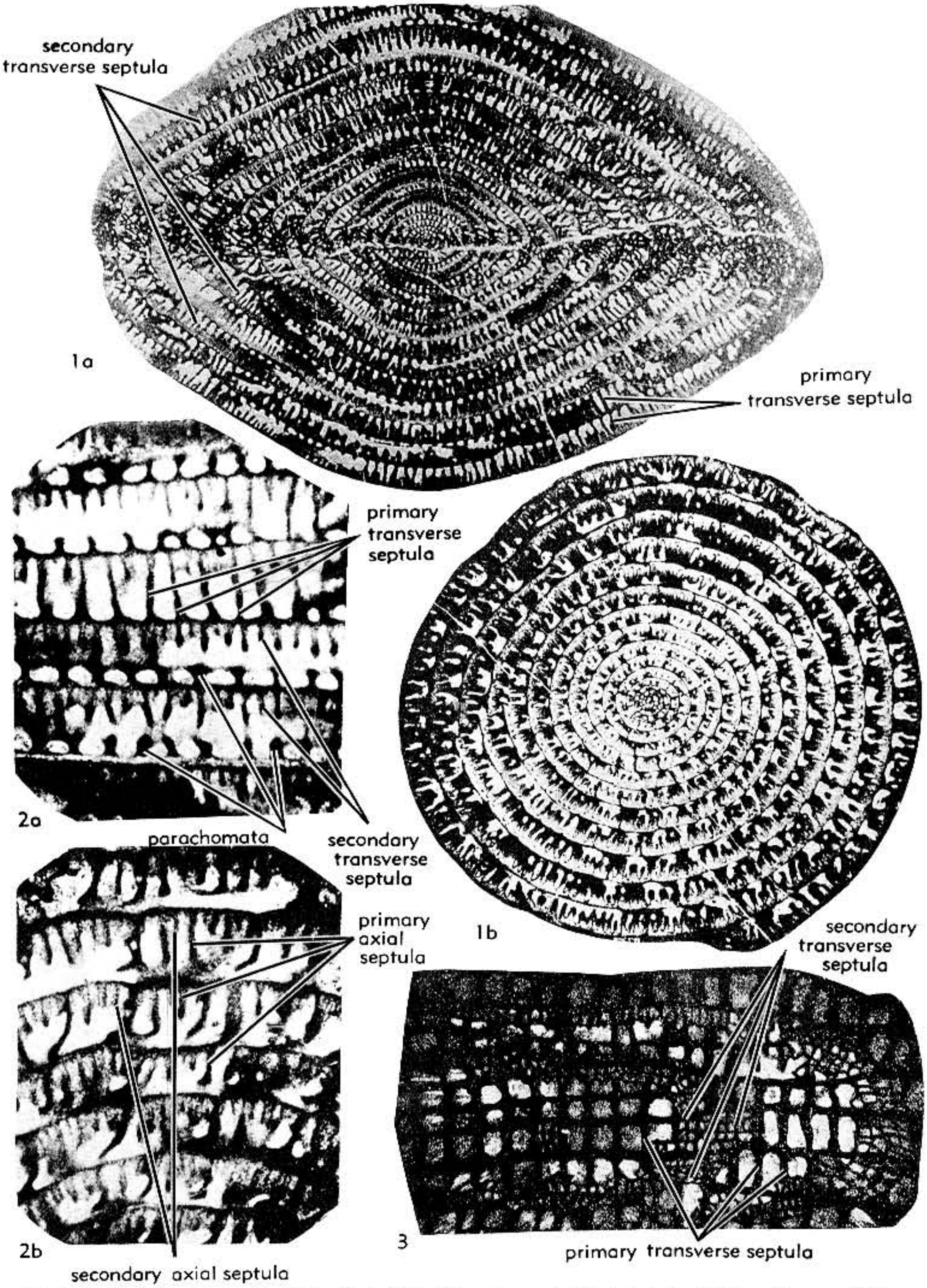


FIG. 292. Septula and parachomata of specialized fusulinaceans illustrated by *Yabeina* DEPRAT, U.Perm., *Lepidolina* LEE, U.Perm., and *Sumatrina* VOLZ, U.Perm.——*1*. **Y. inouyei* (DEPRAT), Akasaka Ls., Japan; *1a,* axial sec. of holotype showing primary and secondary transverse septula, especially in outer volutions, ×10; *1b,* sagittal sec. of paratype showing primary and secondary axial septula, ×10 (*1922).——*2*. **L. multiseptata* (DEPRAT), Cambodia *(2a)*, Akasaka Ls., Japan *(2b)*; *2a,* part of axial sec. showing transverse septula and parachomata, ×45; *2b,* part of sagittal sec. showing long primary septula with short secondary ones between them, ×45 (*1922).——*3*. **S. annae* VOLZ, Sumatra; tang. sec. showing transverse and axial septula, ×30 (*1922).

associated shells belonging to other genera (e.g., *Pseudoschwagerina, Schwagerina*) lack them. The function and origin of phrenothecae are not known.

SEPTULA

The lower surface of the spirotheca of members of the Neoschwagerininae contains ridges (septula) that hang down into the chambers. The septula of primitive members are transverse to the axis of coiling, but highly developed members have two sets of septula, one of which is transverse and the other parallel to the axis of coiling. Septula transverse to the axis of coiling are termed **transverse septula,** and those parallel to the axis are termed **axial septula** (Fig. 292).

The septula of *Cancellina* are represented by broad, short, downward protrusions of the keriotheca that correspond in position with the parachomata on the base of the chamber. The alveoli of the keriotheca of this genus extend to the base of the septula without obvious divergence (Fig. 293). The parachomata are in contact with the septula immediately adjacent to the septa, where the parachomata are highest and septula are longest. The septula are very broad and short in the center of the chamber, and the parachomata are low. The transverse septula of other Neoschwagerininae are long enough to reach the tops of the parachomata completely across the chambers, except for a small circular opening in the center of the chamber above the parachomata. The alveoli of the keriotheca continue to the base of the transverse septula in *Neoschwagerina* and *Yabeina,* and the alveoli diverge outward as they approach the base of the septula. In many sections it seems that alveoli may have been added in the lower part of the septula between the diverging alveoli that extend from the tectum of the keriotheca (Fig. 290,*1*). Short transverse septula, termed **secondary transverse septula,** occur above the foramina in the outer volutions of *Yabeina* and throughout the shell of higher forms. These secondary transverse septula resemble the **primary transverse septula** in all respects except that they are shorter and narrower (Fig. 292). As septula are added, the individual primary septulum, as well as secondary septula, become narrower. The transverse septula of highly developed Neoschwagerininae (e.g., *Lepidolina, Sumatrina*) are very thin and do not contain recognizable alveoli.

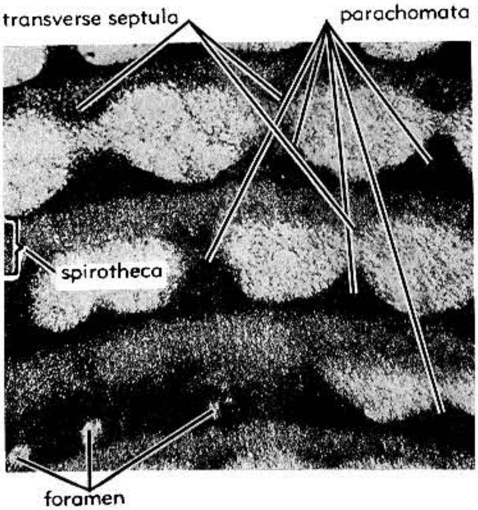


FIG. 293. Spirotheca, rudimentary transverse septula, and parachomata shown in axial sec. of **Cancellina primigena* (HAYDEN), U.Perm., Iran; septula comprise pendant extensions of keriotheca from roofs of chambers opposite parachomata (dark) on floors of chambers, ×100 (*1922)

Axial septula are lacking in *Cancellina;* they first appear in the outer volutions of *Neoschwagerina.* In *Afghanella, Sumatrina, Yabeina,* and *Lepidolina,* several axial septula are introduced between the septa. The axial septula of *Yabeina* and *Lepidolina* are irregular in length, and their lower margins do not reach the tops of the chambers of the preceding volutions. The axial septula of *Afghanella* and *Sumatrina* are short and uniform in length. The upper part of the chambers is divided by the transverse and axial septula into numerous rectangular cubicles.

The structure of the septula of more primitive forms of the Neoschwagerininae (e.g., *Cancellina, Neoschwagerina*) resembles closely that of the keriotheca between the septula (Fig. 293). In *Yabeina,* the width of the septula corresponds closely to the thickness of the keriotheca. The spirotheca of *Lepidolina* consists of a single dense layer, and the septula are composed of a single dense layer without any recognizable alveoli. Also, the spirotheca of *Sumatrina* is composed of a very thin, dense layer and the alveoli are very thin (Fig. 289).

Some paleontologists have suggested that the thin, dense septula of highly developed Neoschwagerininae are formed by isolation of the walls of alveoli, and that the cubicles between opposing pairs of septula are comparable in structure to the alveoli of more primitive forms. The evolutionary trend of the Neoschwagerininae indicates that reduction in thickness of the septula corresponds to reduction in thickness of the spirotheca and that the septula are not the bounding walls of enlarged alveoli.

Both the structure and shape of the septula differ considerably among the Neoschwagerininae. The septula of *Yabeina* and *Lepidolina* are variable in length and are sinuous to irregular in shape, but the sinuosity is not regular or uniform (Fig. 292). Both the transverse and axial septula of *Sumatrina* are uniform in length and they are spaced regularly in both directions. The septula of the inner volutions of *Afghanella, Sumatrina,* and *Lepidolina* are thicker in their lower margins than near their upper margins. However, the septula in the outer few chambers of these genera are about the same in thickness throughout their heights, and it seems evident that the thick lower margins of the septula of earlier volutions are developed by secondary deposits.

The biologic cause or purpose of the septula is problematical. It has been suggested that they serve as strengthening supports for the shell. However, the first Neoschwagerininae to develop septula have a ratio of shell material to open chamber space that is far in excess of most other fusulinaceans, as well as of many other shell-bearing animals. Furthermore, the fusulinacean shell seemingly was filled with cell substance of the animal throughout its development, and there is no evident source of stresses on the shell. Also, the spirotheca of *Sumatrina* is exceedingly thin and fragile, but the septula are shorter and do not seem capable of giving as much support for the shell as those found in more primitive forms having much thicker and stronger walls (Fig. 289, 292,*3*).

TUNNEL AND FORAMINA

So far as has been demonstrated, the only communication between the inside of the fusulinacean shell and the exterior is by means of the numerous septal pores in the antetheca. After the shell developed a few chambers beyond the antetheca of a given chamber, communication with earlier parts of the shell was facilitated by resorption of the lower surface of the septum so as to form a single opening, the tunnel, several widely spaced openings, **multiple tunnels,** or a series of small, closely spaced elliptical openings, foramina. About the same time as the development of these openings at the base of the septa, the fusulinacean laid down dense deposits of calcite in several parts of the shell. In forms having a single tunnel, ridges of dense calcite, the chomata, were deposited at the sides of the tunnel. Dense deposits similar in structure to the chomata completely lined the inside of the chambers of members of Fusulininae and of primitive members of the Ozawainellidae and Schubertellinae. These linings form the tectoria of the spirotheca and septa in forms having *Profusulinella-* and *Fusulinella*-type of wall structure. Dense deposits (axial fillings) completely fill the chambers in the polar regions of *Wedekindellina,* highly developed forms of *Fusulina,* and all forms of *Quasifusulina* (Fig. 275,*3a*; 279).

Primitive members of the Schwagerininae have a single tunnel and massive chomata but no other type of secondary deposits. Highly developed members of this subfamily have small or indistinct chomata and heavy axial fillings. The most highly developed genus of the subfamily, *Polydiexodina,* has multiple tunnels that lack bordering chomata, and axial fillings are well developed (Fig. 275,*3a,6b*).

Foramina occur in all members of the Verbeekininae, and all members have parachomata developed to some extent between adjacent foramina. The parachomata of *Eoverbeekina* are poorly developed and extend only a short distance from the septa in the outermost volutions of mature specimens. The parachomata are discontinuous in the earlier volutions of *Verbeekina* but extend completely across the chambers in outer volutions of mature specimens. All species of more advanced genera have parachomata developed completely across the chambers. Axial fillings occur in some advanced forms of both subfamilies. Also, secondary deposits cover the septa and some parts of the surfaces of the spirotheca of many forms.

The secondary deposits are best developed in chambers having a tunnel or foramina, which seems to mean that these structures are related in origin. The excavated shell material may have been used to form the secondary deposits. Many specimens have secondary deposits that are too massive to have been obtained entirely from the excavated tunnel or foramina, and, accordingly, part of the deposits must have come from other sources. The upper tectorium of many shells occurs on the floor of the tunnel, and it must have been partly formed after excavation of the tunnel. This theory is supported by the absence of secondary deposits in chambers into which the tunnel does not extend.

With few exceptions, most secondary deposits resemble one another closely in structure. In *Yangchienia,* a clear layer occurs above the tectum of the spirotheca and is overlain by a thick layer of dense calcite similar to the tectoria of other fusulinaceans. Neither of these upper layers occurs on the floor of the last chamber; obviously, they are deposited as secondary layers on the floor of the chambers. The chomata of many fusulinaceans are stratified in structure, indicating that they were laid down in stages.

The tunnel and foramina of fusulinacean shells were developed by resorption of the lower parts of the septa, for they do not occur in the antetheca at any stage of growth of the individual. The only logical explanation of their development is that they furnished means of communication between earlier chambers, which may have been more needed after the septal pores were partly sealed by secondary deposits on the septa. The purpose served by the secondary deposits is not known.

EVOLUTIONARY TRENDS

GENERAL CONSIDERATIONS

Fusulinacean shells seem to have changed in structural features more rapidly than has been recognized in most other large groups of fossils. That the shell structures of these foraminifers changed both rapidly and markedly is made evident by comparing *Millerella* from basal Pennsylvanian beds with complex forms from the Permian, such as *Yabeina* and *Polydiexodina.* At first glance these extreme members of the fusulinaceans bear little resemblance, but most of the changes that took place in the shells of forms intermediate between the simple and complex can be identified in the geologic order of their occurrence. During their relatively short geologic history, several larger divisions and about 72 genera represented by more than 1,000 species developed.

Many evolutionary trends of the fusulinaceans can be distinguished with assurance, but it should be stressed that much is yet unknown concerning details of the development within the group. The fusulinaceans had their beginning near the end of the Mississippian, and only two genera are recognized in oldest Pennsylvanian rocks. Very shortly after the beginning of Pennsylvanian time, however, several major divisions of the fusulinaceans evolved and these are recognizable in both the Eastern and Western Hemispheres. Therefore, the fusulinaceans developed along several lines of evolution rather early in their history.

In many provinces that contain abundant fusulinacean faunas distributed throughout great thicknesses of rocks, the fusulinaceans are so closely spaced in stratigraphic sequence that one may observe almost continuous changes which took place within certain groups. Among many large assemblages, changes in shell structure are not only of identical nature, but are found to appear in the same relative geologic order in widely separated areas throughout both hemispheres. Some branches reached ultimate stages of development along certain lines in early Pennsylvanian time, others reached similar stages in early Permian time, and still others did not reach similar stages until the latter half of the Permian. Therefore, it seems evident that many of these changes were due to evolutionary trends inherent within the division.

Gradual changes in shell structure of fusulinaceans in some areas may have been due largely to introduction of more favorable environmental conditions; other changes originating in other areas may represent adaptation to gradually developing adverse conditions. Whatever may have been the causes of some changes in shell structures, certain types of progressive alteration took place in almost all groups, regardless of locality or geologic time. Some of these major changes are summarized below.

(1) Shells became larger. The most primitive fusulinaceans are minute, measuring only a fraction of a millimeter in maximum diameter. Almost all highly developed fusulinaceans are relatively large; indeed, the volume of some advanced forms exceeds that of the most primitive fusulinaceans by several thousand times.

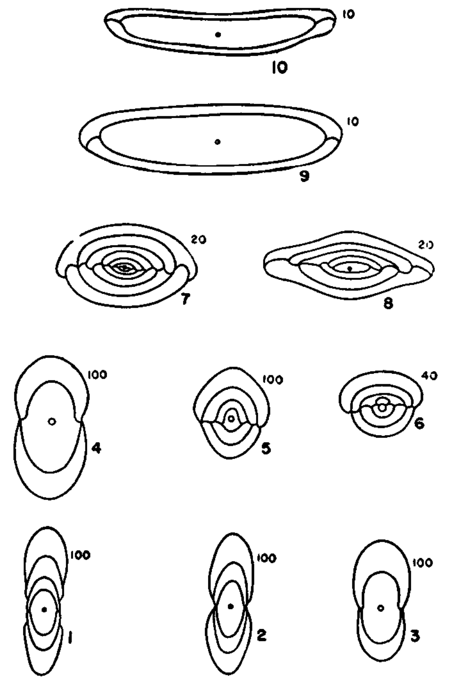


FIG. 294. Development of shell shape and size of fusulinaceans belonging to the Ozawainellidae and Fusulinidae (Fusulininae), numbers at upper right of each figure denoting relative (not actual) magnifications.——*1. *Millerella marblensis,* M.Penn. (Marble Falls Ls.), USA(Tex.).——*2. M. pressa,* L.Penn.(Kearny F.), USA(Kans.).——*3. Paramillerella pinguis,* L.Penn.(Bloyd Sh.), USA(Ark.). ——*4. P. circuli,* L.Penn.(Belden F.), USA(Utah). ——*5. P.* sp., L.Penn.(Amsden F.), USA(Wyo.). ——*6. Eoschubertella gallowayi,* M.Penn.(Boggy F.), USA(Okla.).——*7. Profusulinella regia,* M. Penn., USA(W.Tex., Powow Canyon).——*8. Fusulinella acuminata,* M.Penn.(Fra Cristobal F.), USA (N.Mex.).——*9. Fusulina mysticensis,* M.Penn. (Worland Ls.), USA(Iowa).——*10. F. eximia,* M. Penn.(Cooper Cr. Ls.), USA(Iowa) (*1922).

(2) Shells changed in shape from discoidal to spherical, fusiform, or elongate-subcylindrical. The most primitive genus of the fusulinaceans is discoidal; the axis of coiling of its slightly evolute shell is the shortest diameter through the proloculus. Except for a few aberrant genera, most fusulinaceans have involute shells. The length of the axis of coiling of most of them increased more rapidly than other diameters of the shell, and most groups developed the greatest shell dimension along the axis of coiling.

(3) Shell walls became more complex. The most primitive genus has a thin wall of simple structure. Later fusulinaceans have thicker walls of more complex structure (except in several later aberrant genera that contain thin structureless walls).

(4) The antetheca and septa tended to become fluted. Those of primitive fusulinaceans are straight, but many highly developed fusulinaceans have antetheca and septa that progressively become more irregular or highly fluted.

These general trends are common to most fusulinaceans. Many other progressive developments of shell structure were restricted to parts of the group. Some of the more important of these are (1) development of septula in the Neoschwagerininae; (2) reduction of the chomata in the Fusulininae and later in the Schwagerininae; (3) development of parachomata both in the Verbeekininae and Neoschwagerininae; and (4) development of axial fillings in the Fusulininae, later in the Schwagerininae, and still later in the Verbeekininae and Neoschwagerininae. Some of these changes seem to mark definite evolutionary trends; others probably reflect a combination of factors which may not be related to evolutionary trends.

SIZE AND SHAPE OF TEST

The primitive members of all subfamilies and nearly all genera are smaller than most of the highly developed members. The size of individuals of most types of animals is partly dependent on local environmental conditions, such as food supply, and the average size of mature specimens in one locality may be somewhat different from the average size of mature specimens in another. Therefore, a small difference in size alone is not considered a basis for specific differentiation. Pronounced increase in shell size is recognized within most groups of the fusulinaceans. Primitive Schubertellinae were minute (0.4 to 1.3 mm. maximum diameter) and so were later Permian members (1.3 to 3.0 mm. maximum diameter).

Primitive fusulinaceans are minute (with maximum diameter as small as 0.4 to 0.9 mm.), but most late forms are relatively large (up to 16 mm. in maximum diameter). Marked increase in length is especially noticeable among the Schwagerininae, from early *Triticites* (2 to 3 mm.) to very large *Polydiexodina* and *Parafusulina* (as large as 60 mm.); the relative size increase in this group, however, is no greater than that of the fusulinaceans in general. Early Neoschwagerininae (e.g., *Cancellina*) are small (about 3 mm.), but late members (e.g., *Yabeina*) are large (at least 16 mm.). Figure 294 illustrates the ranges in size of some Ozawainellidae and some Fusulinidae (Fusulininae).

Although the general trend of fusulinaceans was toward increase in size of the shell, some forms seemingly developed from slightly larger ancestors.

The classification of fusulinaceans is based partly on shape of the shell, even though external form, taken alone, is not sufficient for recognition of many genera. The most primitive fusulinaceans are discoidal in shape, and the general trend of most later groups is toward a longer axis of coiling. The general shell profile of *Millerella* to advanced members of *Fusulina* exhibits progressive change from discoidal, slightly evolute ozawainellids (e.g., *Millerella*) to spherical or irregular-elongate members of this family (e.g., *Rauserella*) and Staffellidae (e.g., *Sphaerulina*). Schubertellinae evolved from an ellipsoidal shell (e.g., *Eoschubertella*) to very elongate-fusiform or irregular shapes. Fusulininae developed from subspherical tests (e.g., *Pseudostaffella*) to highly elongate-fusiform or irregular forms (e.g., *Fusulina, Quasifusulina*). Out of fusiform shells of primitive *Triticites,* the Schwagerininae produced the highly elongate-subcylindrical shells of *Parafusulina* and *Polydiexodina.* Most early Verbeekininae are subspherical in shape, but very advanced forms (e.g., *Pseudodoliolina*) are elongate-ellipsoidal in shape. The genus *Brevaxina* has a subspherical shell and strongly umbilicate axial regions, its development and shape being inharmonious with the general trend among fusulinaceans. The most primitive form of the Neoschwagerininae is inflated-ellipsoidal in shape; advanced forms are elongate-subcylindrical to strongly inflated-fusiform in shape. Some subfamilies, particularly the Verbeekininae and Neoschwagerininae, possibly are biphyletic, and the similarity of internal structures, as well as shape of the shell, may indicate parallel development.

Although a general tendency among fusulinaceans was toward development of an elongate shell, possible reversals can be pointed out. A few forms of Schwagerininae, particularly *Triticites* in the Pennsylvanian and *Pseudoschwagerina* in the Permian, have subspherical mature shells. The inner volutions of *Pseudoschwagerina* have far greater length along the axis of coiling, and it is solely the outermost volutions that control the subspherical shape of the mature shell. The subspherical or inflated forms of *Triticites* occur stratigraphically above elongate forms, but it cannot be demonstrated that the former were derived from the latter.

Brevaxina has a short axis of coiling and umbilicate axial regions. Other members of the Verbeekininae are spherical or elongate in the direction of the axis of coiling. Evolutionary trends within this subfamily are obscure; probably the assemblage is biphyletic, *Eoverbeekina* and *Verbeekina* having come from one ancestral form and *Brevaxina, Misellina,* and *Pseudodoliolina* having descended from another.

SPIROTHECA

Rather definite trends in evolutionary development of the spirotheca are seen among fusulinaceans. These trends took slightly different paths and rates of change in different divisions of the superfamily. The spirotheca of the more primitive fusulinaceans, such as *Millerella,* was originally

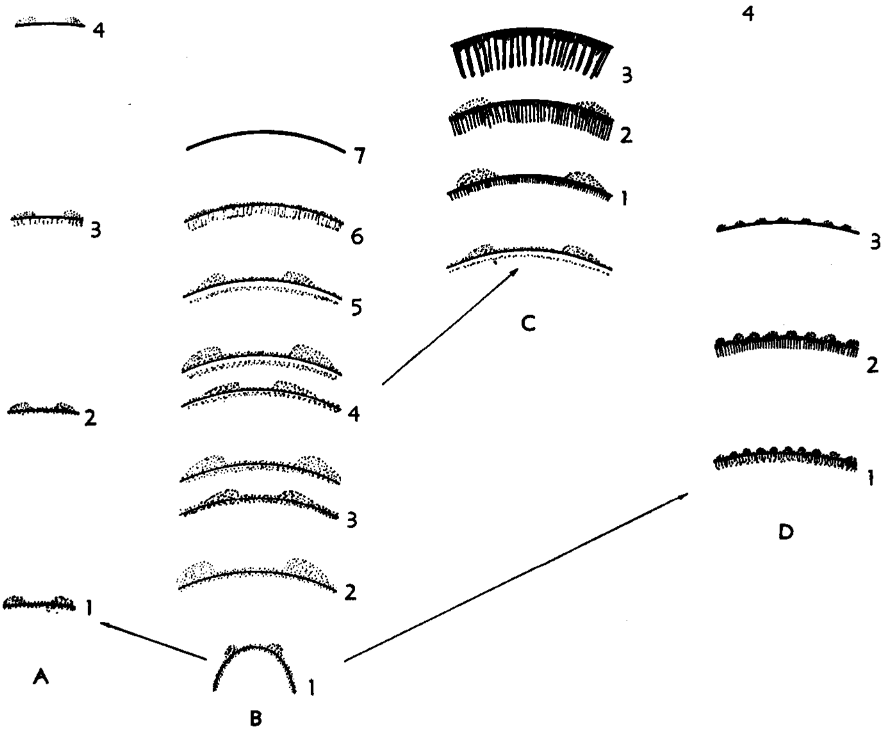


FIG. 295. Evolution of the spirotheca in the Fusulinidae.——*A1-4*. Schubertellinae; *1*, primitive *Eoschubertella; 2*, highly developed *Eoschubertella*; *3*, typical *Schubertella*; *4*, highly developed *Schubertella.*——*B1-7*. Fusulininae; *1, Pseudostaffella*; *2, Profusulinella regia*; *3, Fusulinella? primaeva*; *4, Fusulinella juncea*; *5, Fusulina* n. sp. (intermediate); *6, Fusulina cylindrica*; *7, Gallowayinella* (idealized).——*C1-3*. Schwagerininae; *1. Triticites irregularis*; *2, T. moorei*; *3, Schwagerina furoni.*——*D1-3*, Verbeekininae; *1, Verbeekina verbeeki*; *2, Misellina*; *3*, highly developed *Pseudodoliolina* (*1922).

formed above the last chamber as a single thin dense layer. With growth of additional chambers in an individual, this thin layer was covered above and below by secondary layers of tectoria. The evolutionary trend of most fusulinaceans was to develop a thicker primary wall. Secondary deposits are lacking in many specialized forms.

Among Ozawainellidae, the spirotheca developed from a simple wall structure like that of *Millerella* to a wall composed of a thin indistinct upper primary layer (tectum), a lower, less dense primary layer (diaphanotheca), and secondary layers of upper and lower tectoria. Some advanced forms of the group seem to have a spirotheca composed of a tectum and a less dense structureless lower layer.

Primitive Schubertellinae have a spirotheca like that of *Paramillerella* or *Millerella.* Highly developed forms have a spirotheca composed of a tectum and a relatively thick lower clear layer, but late Permian members of the group have a spirotheca throughout the shell that is composed of only a thin dense layer. The evolution of the wall of the Schubertellinae is diagrammatically shown in Figure 295 (A1 to A4).

Evolution of the spirotheca of the Fusulininae seems to be similar to that of the Schubertellinae, but changes took place geologically much more rapidly than in the Schubertellinae. The three-layered spirotheca of *Pseudostaffella* and *Profusulinella* (Fig. 295,B*1,2*) developed into the four-layered spirotheca of *Fusulinella* (Fig. 295, B*4*). This type of spirothecal structure characterizes all forms of *Fusulina,* with gradually increasing thickness of the diaphanotheca and decreasing thickness of the upper and lower layers. In advanced forms of *Fusulina* (e.g., *F. cylindrica,* Fig. 280,*3*; 295, B6), the diaphanotheca is thick and has a structure somewhat like that of the keriotheca of higher forms, the upper tectorium being absent or thin and the lower tectorium discontinuous. Later forms of Fusulininae (e.g., *Quasifusulina, Gallowayinella*) have a thin spirotheca (Fig. 295,B7). *Gallowayinella* has a spirotheca seemingly composed of a single dense thin layer. The general trend of fusulinaceans characterized by this wall structure (Fig. 280,*3;* 295,B1-B7) reached a peak of development in Pennsylvanian (Desmoinesian) time, but advanced genera range into the Permian period.

Schwagerininae were introduced in rocks of early Missourian age (Pennsylvanian) in North America by *Triticites.* Although the ancestral form of *Triticites* is not definitely known, seemingly it was closely allied to *Fusulinella.* The spirotheca of *Triticites* is composed of a tectum and thick keriotheca having clearly visible alveoli. The structure of the spirotheca remained the same in later members, but the keriotheca increased in thickness and the alveoli became coarser (Fig. 280,*4-6*; 295,C1-C3).

The evolution of the spirothecal structure of the Verbeekininae and Neoschwagerininae was somewhat similar to that of the Schwagerininae, except that late genera of both groups possess a spirotheca composed of only a single dense layer (Fig. 295,D1-D3).

It seems evident that evolutionary development of the spirotheca of the fusulinaceans was toward a thickening of the lower primary layer, the diaphanotheca or keriotheca. All major groups followed the same general pattern of evolution of the spirotheca independently and at different times, and this trend seems to have been inherent within the entire superfamily.

ANTETHECA AND SEPTA

The antetheca and septa of the most primitive fusulinaceans are unfluted from end to end. They are also unfluted throughout the shell in all members of the Ozawainellidae, Verbeekininae, and Neoschwagerininae. Septal fluting developed at different rates in the Schubertellinae, Fusulininae, and Schwagerininae.

The septa of primitive Schubertellinae are unfluted. A few highly developed Permian forms of Schubertellinae have septal fluting developed throughout the length of the shell. The septa of Schubertellinae remained unfluted for a long time and never reached a high stage of development, even in the upper Permian.

The septa of the most primitive Fusulininae *(Pseudostaffella)* are unfluted throughout the length of the shell. *Profusulinella* has septa fluted only in the extreme polar regions. Septal fluting developed rather rapidly and uniformly in the Fusulininae, from *Pseudostaffella,* without septal fluting, to upper Desmoinesian *Fusulina,* with highly fluted septa throughout the length of the shell, and still further to *Quasifusulina* with closely fluted septa.

The development of septal fluting in Schwagerininae was rapid. In North America, the Schwagerininae were first developed in early late Pennsylvanian time and are represented by *Triticites,* having septa fluted only in the polar regions. Before middle late Pennsylvanian time the septa of some forms were fluted throughout the length of the shell. *Triticites* is first known in the mid-continent region in the basal part of the Missourian Series, but the forms there probably are not the most primitive of the genus. More primitive forms of *Triticites* are known from the middle Oquirrh Formation of the Wasatch Mountains of Utah and from the lower part of the Upper Carboniferous as designated by RAUZER-CHERNOUSOVA, BELYAEV & REYTLINGER (*1508) in the Samara Bend area of Russia. Highly evolved Permian members of the group (e.g., *Parafusulina, Polydiexodina*) have intensely fluted septa throughout the length of the shell.

Evolution of septal fluting closely parallels that of shape of the shell. Septal fluting is not developed in some groups having discoidal or spherical shells, such as the Staffellidae and Verbeekinidae. It first began to form in other groups after the shell assumed a fusiform shape, and reached its highest development in subcylindrical shells. In genera that acquired a fusiform shell only after the shell structures had become very complex, as in *Sumatrina,* septal fluting was never developed.

OTHER TRENDS

SEPTULA

The appearance and progressive modification of septula in the Neoschwagerininae comprise one of the most definite evolutionary developments among the fusulinaceans, but septula are restricted to this group (Fig. 292, 293). Their development can be traced from the short, broad, transverse septula of *Cancellina* to the elongate set of broad transverse septula and simple axial septula of *Neoschwagerina,* and still further to the complex sets of transverse and axial septula of *Yabeina* and *Lepidolina.* Complicated sets of transverse and axial septula are found in *Afghanella* and *Sumatrina,* but the position of these genera within the division is not definitely known. The complexity of their septula does not accord with their geologic occurrence associated with primitive forms of the group, such as *Cancellina* and *Neoschwagerina.* Their ancestral forms are unknown.

CHOMATA

The chomata of fusulinaceans with a single tunnel changed with their progressive development, but it is not certain that the changes took definite trends. The chomata of many primitive forms of Fusulininae are massive and large, and the tectoria are correspondingly thick. As the group became more advanced, the chomata became less massive and the tectoria became thinner. In late members of the group the chomata are feebly developed in the innermost volutions and are absent or indistinct in the outer part of the shell. The subfamily Schwagerininae experienced a similar reduction in the chomata. This general reduction in the massiveness of the chomata in late Fusulininae and late Schwagerininae is in reality a reversal of their development in early members of the group, which had small chomata; the chomata gradually became more massive as the early fusulinaceans evolved.

PARACHOMATA

Structural features that are progressively developed in the Verbeekininae and well defined in all members of the Neoschwagerininae are the parachomata (Fig. 292, 293). These are feeble in the outer volutions of *Eoverbeekina* and occur only adjacent to the septa of inner volutions of *Verbeekina* but extend across the chambers of outer volutions. Advanced forms of Verbeekininae have distinct parachomata throughout the shell.

AXIAL FILLINGS

Dense deposits of calcite occur in the axial regions to some extent in all major divisions of the Fusulinacea except the Ozawainellidae (Fig. 279). They are best defined in late members of these divisions. Heavy axial fillings occur in *Wedekindellina* near the middle of the stratigraphic range of the Fusulininae, but it seems probable that *Wedekindellina* is a specialized member of an early branch of the group. The appearance of heavy axial fillings in late forms of Fusulininae and Schwagerininae coincides with reduction of the chomata. Both of these features are of secondary origin, and when one is well developed the other is absent or feeble. Axial fillings are inconspicuous in late forms of the Verbeekininae and Neoschwagerininae.

Some investigators of the fusulinaceans have concluded that development of axial fillings is not constant even among conspecific specimens. Observations do not bear out these statements. It is difficult to cut axial sections exactly along the axis of coiling, and in forms having thin zones of axial fillings many axial sections fail to intersect these fillings. Accordingly, one may not realize the presence of axial fillings in such specimens unless they are seen during the sectioning procedure. Critical observations of many forms indicate that axial fillings are about equally massive in all conspecific specimens.

PHYLOGENY

The phylogeny of the fusulinaceans is interpreted from a combined view of their stratigraphic occurrence and progressive changes of their shell structures. Many fusulinaceans are so closely spaced stratigraphically that it is possible to observe details of progressive development, and their phylogeny can be interpreted with considerable assurance. Some other groups are most common in relatively isolated localities, and their exact stratigraphic relationships to fusulinaceans of other areas are not yet determined. In such cases it is necessary to rely largely on degree of similarity of shell structures. The genus *Misellina,* for example, which represents the early part of one branch of the subfamily Verbeekininae, lacks a recognized closely similar ancestor and its relationship to other members of the Verbeekininae is doubtful. The ancestry of *Afghanella* and *Sumatrina* is likewise open to question. Both resemble other members of the Neoschwagerininae in many respects, but obviously they have reached a stage of evolution far in advance of associated primitive members of the major group (e.g., *Cancellina, Neoschwagerina*).

ECOLOGY

Considerable evidence is available to indicate that fusulinaceans were uncommonly sensitive to their physical surroundings. They seem to have been restricted to offshore open-water environments, and their shells occur as fossils most commonly in limestones or highly calcareous shales, and less commonly in sandstones. Also, fusulinaceans are not considered to be indigenous in coarse clastics or in close association with evaporites. In the Permian of the Texas-New Mexico area, certain limestones can be traced laterally from areas in which fusulinacean faunas are prolific to areas characterized by brackish-water types of faunas, and likewise to areas where the limestones grade into dolomites and evaporites. The fusulinaceans disappear laterally in the section long before the approach to regions of evaporites. Also, fusulinaceans are not found in direct association with fossil forms of invertebrates of the types that live today in brackish-water or nearshore environments.

Fusulinaceans occur abundantly in sandstones at some localities. Several such occurrences are in upper Desmoinesian sandstones of southern Oklahoma and northern Texas. Fusulinacean shells have been found at a few places in these sandstones concentrated in the troughs of undulating structures interpreted as ripple marks, but it is not certain that they were indigenous to the ripple-mark surfaces. Also, fusulinacean shells have been observed with their elongated axes arranged in spiral patterns that make them appear to have been affected upon final settling to the bottom by turbulent currents and swirling eddies or whirlpools. At some outcrops thick limestones contain abundant fusulinaceans with highly elongate shells, most of them oriented in the same direction. Such occurrences have been observed in the Permian of Timor (*1923) and in the Permian of the Island of Letti (*1693), where oriented shells of fusulinaceans compose more than 50 per cent of great thicknesses of limestones. Similar occurrences of oriented fusulinacean shells are found in some Pennsylvanian and Permian limestones of North America and in the Tethyan Permian reef-like limestones of western United States and western Canada. This orientation of the shells of fusulinaceans suggests the presence of submarine currents in these places at the time when the shells were deposited. In no case has it been possible to determine whether the fusulinaceans were dead or alive when their tests became thus oriented.

The most convincing evidence of the normal offshore, open-water habitat of the fusulinaceans is furnished by studies of the sedimentary cycles in the Pennsylvanian rock column of the northern mid-continent region. Moore (*1307, p. 25) divided the complete Pennsylvanian sedimentary cyclothem into ten units, the lower two and uppermost one of which are of continental origin. The intervening seven units are marine, and fusulinaceans occur most abundantly in the middle unit of the marine part of the cyclothem. The fusulinaceans seem to have lived offshore in open seas and they penetrated continental basins farthest when the seas reached their greatest advancement. A fusulinacean-bearing unit at any given place typically is underlain by rocks formed by the advancing sea and overlain by sediments of the retreating sea. The sedimentary cycle in the Lower Permian (Wolfcampian) of Kansas, Oklahoma, and Nebraska differs somewhat from that in the Pennsylvanian (*1308), but, as in Pennsylvanian cyclothems, the fusulinaceans occur in and near the central part of the marine phase of the sedimentary cycle.

OCCURRENCE

GEOGRAPHIC DISTRIBUTION

Fusulinaceans are almost world-wide in geographic distribution, for they have been found on all continents except Australia and Antarctica. The most northerly known occurrence is on Ward Hunt Island north of Ellesmere Island, Canada (*1928). They also have been found in northeastern Greenland (*878, *1949, *647A) and at several places on Spitzbergen (Svalbard) (*1832, *1918). The most southerly recorded occurrence of fusulinaceans in the Western Hemisphere is in Patagonia of southern Chile (*306), and the most southerly occurrence in the Eastern Hemisphere is on North Island of New Zealand (*958). Some of the thicker marine sequences of upper Paleozoic rocks from which fusulinaceans have not been found are the Permian deposits of Australia, Tasmania, and Madagascar.

The accompanying outline map (Fig. 296) shows some of the principal localities from which fusulinacean faunas of Pennsylvanian and Permian ages have been described or reported. This shows that fusulinaceans are more widely known in the Northern than in the Southern Hemisphere. It should be pointed out, however, that other types of upper Paleozoic faunas are about equally more widely known in the Northern Hemisphere than in the Southern Hemisphere. Furthermore, large parts of the land areas of the Southern Hemisphere are covered by permanent ice and snow and are practically unknown geologically.

Fusulinaceans occur in Pennsylvanian and Permian rocks on many of the Arctic islands of Europe and throughout most of the north-south distance across European Russia and Siberia, in the Viséan of Germany, in the Pennsylvanian of Spain, and in the Permian of the Carnic Alps, Velebit Mountains of Yugoslavia, Sicily, Aegean Islands of Greece, and Crimea.

Fusulinaceans have been described from Tunisia in Africa where they occur in Upper Permian rocks.

Fusulinaceans are widespread in Asia and in islands of the Indian and Pacific Oceans. They occur in the Pennsylvanian of Mongolia, China, Japan, and possibly Vietnam. They are present in the Permian at numerous places in the western part of the Eastern Hemisphere, including Pamir, Armenia, Iran, Turkey, Syria, Afghanistan, Karakorum region, northern India, Malaya, Thailand, Vietnam, western, southern, and northern China, northeastern, southeastern, north-central, and extreme western Siberia, Japan, and many of the islands of the Indian Ocean area, including Sumatra, Timor, Letti, and North Borneo. They also have been found in several localities in the Salt Range of West Pakistan.

In the Western Hemisphere, fusulinaceans occur in rocks of Pennsylvanian age in large areas of the United States from Pennsylvania on the east to California on the west. Pennsylvanian fusulinaceans of similar age are known from Peru, Brazil, Bolivia, and southern Chile.

Permian fusulinaceans are widespread in North America, being known throughout much of the far western United States, Rocky Mountain area, south-central United States, and the mid-continent region. Outside of the United States, Permian fusulinaceans occur in western and northern Canada, Greenland, Alaska, across much of Mexico, Central America, Venezuela, Colombia, Peru, Bolivia, and Patagonia of southern Chile (*639A).

It is evident that fusulinaceans occur over a large part of the present land areas of the globe. Because they seem to have been unusually sensitive to their physical surroundings, their widespread occurrence suggests that climates of the world during Pennsylvanian and Permian times may have been more uniform than they are today. It is fully realized, however, that the fusulinaceans were bottom-dwellers beyond shallow waters where they probably lived at depths that were moderately uniform in temperature and other physical conditions at almost all latitudes.

This may account for the same general nature of the Middle Pennsylvanian fusulinacean faunas found in southern South America, extreme northern Canada, and southern United States, without having even to consider the present extremes of climatic conditions in nearby land areas of these different regions.

STRATIGRAPHIC DISTRIBUTION

Comparison of fusulinacean faunas from many localities in North America, Europe, and Asia indicates that most larger groups developed along closely similar biological trends and in about the same stratigraphic order in all areas (Fig. 297). Species have been found very useful as index fossils for stratigraphic correlations in local areas. The ranges of genera are applicable for interregional and intercontinental correlations. Many primitive generic groups have long stratigraphic ranges in both hemispheres and are not recognized to be of much value for correlation. The stratigraphic ranges of some more highly specialized genera seem to be closely similar in all areas where studied in the Americas, and their stratigraphic limits seem to be approximately the same in the Eastern Hemisphere. At least it can be demonstrated that the stratigraphic ranges of these genera in Europe and Asia are in the same order as in North America and South America.

Fusulinacean faunal zones are defined by the predominance of generic groups or restriction of their stratigraphic range. The recognized zones are designated by the names of genera chosen as indices, in upward order: (1) *Millerella,* (2) *Profusulinella,* (3) *Fusulinella,* (4) *Fusulina,* (5) *Triticites,* (6) *Pseudoschwagerina,* (7) *Parafusulina,* (8) *Polydiexodina,* (9) *Verbeekina,* and (10) *Yabeina.*

ZONE OF MILLERELLA

Millerella is the most common genus of fusulinaceans found in Lower Pennsylvanian rocks of North America, and this part of the section is referred to as the fusulinacean Zone of *Millerella.* The genus had its beginning at an earlier time and it ranges into post-Lower Pennsylvanian deposits of North America, which are excluded from the Zone of *Millerella* because they also carry more advanced forms of fusulinaceans. *Millerella* occurs in Europe and probably in Asia, but its range there is not known.

ZONE OF PROFUSULINELLA

The genus *Profusulinella* is restricted in North America to rocks of early Middle Pennsylvanian age, and this part of the rock column is referred to as the Zone of *Profusulinella.* In sections of the northwestern Urals and Samara Bend of the Volga in USSR, *Profusulinella* is associated with fusulinaceans similar to those found in the Pennsylvanian beds of North America. Also, the *Profusulinella*-bearing part of the column in Europe is overlain by rocks containing a fusulinacean fauna that in broader aspects resembles the fusulinacean assemblage occurring immediately above the Zone of *Profusulinella* in North America. A similar occurrence of *Profusulinella* is found in upper Carboniferous rocks of China. It is therefore evident that the Zone of *Profusulinella* is represented in both hemispheres.

ZONE OF FUSULINELLA

The upper part of the lower Middle Pennsylvanian succession in North America is dominated by faunas of *Fusulinella* and is termed the Zone of *Fusulinella.* Although *Fusulinella* has a stratigraphic range higher in the section, the higher fusulinacean faunas that contain *Fusulinella* are dominated by the genus *Fusulina,* and the top of the Zone of *Fusulinella* is placed in North America just below the lowest occurrence of *Fusulina. Fusulinella* is widespread in Europe and Asia, and it occurs in rocks stratigraphically above the Zone of *Profusulinella,* at least in areas where *Profusulinella* has also been recognized.

ZONE OF FUSULINA

The genus *Fusulina* occurs throughout upper Middle Pennsylvanian rocks of North America above the Zone of *Fusulinella,* and this part of the section is referred to as the Zone of *Fusulina.* The lower boundary of the zone coincides with the top of the Zone of *Fusulinella.* The range of *Fusulinella* overlaps into the Zone of *Fusulina* in Europe, as it does in North America. The upper stratigraphic limit of *Fusulina* in Europe seems higher than west of the Atlantic, for *Fusulina* is reported to be associated with *Triticites* in the USSR

(Samara Bend and Moscow regions). Furthermore, the highest forms of *Fusulina* in Russia are more advanced biologically than the highest forms of *Fusulina* in North America. Therefore, the range of *Fusulina* in Europe probably includes more of the stratigraphic column than in North America. *Fusulina* is widespread geographically in China, and its upper and lower limits in both North and South China seem to be equivalent to late Middle Pensylvanian in age.

ZONE OF TRITICITES

The genus *Triticites* dominates fusulinacean faunas of the Upper Pennsylvanian Series in North America, and this part of the section accordingly is referred to as the

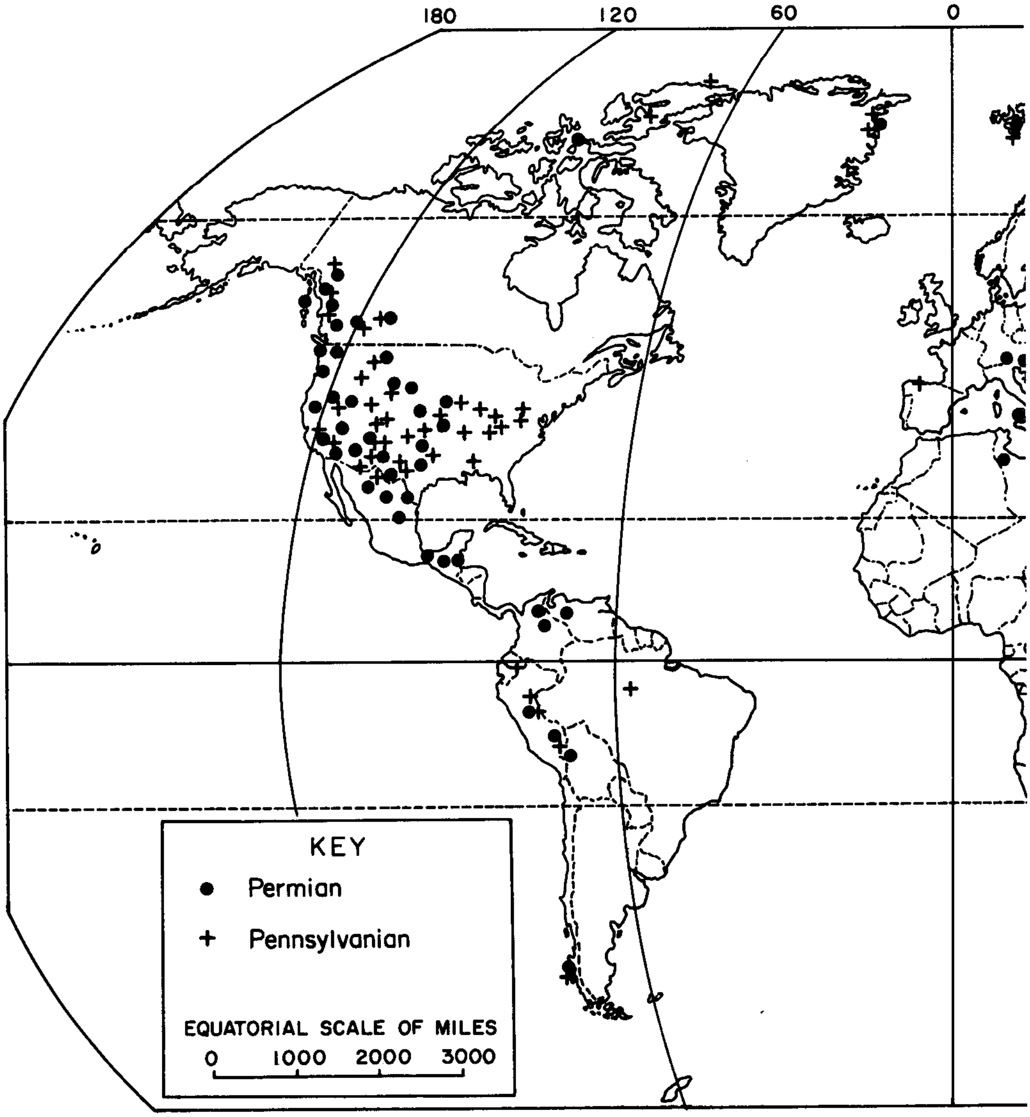


FIG. 296. Distribution of Pennsylvanian (Upper Carboniferous) and Permian fusulinaceans indicated by general localities from which they have been described or reported (*2120B).

Zone of *Triticites*. The zone is distributed from Nevada in the west to Ohio in the east and contains some of the most prolific fusulinacean faunas of North America. Rocks referable to the Zone of *Triticites* have not been recognized in Central or South America or with certainty in Asia but are widespread in the central part of European USSR, where they may be equivalent in age only to the lower part of the Zone of *Triticites* in North America. All evidence indicates that *Triticites* reached its greatest development in North America and its extreme limits as well as intermediate forms are best known here. The upper limit of the Zone of *Triticites* corresponds to the base of the Permian, as defined in North America, but the range of

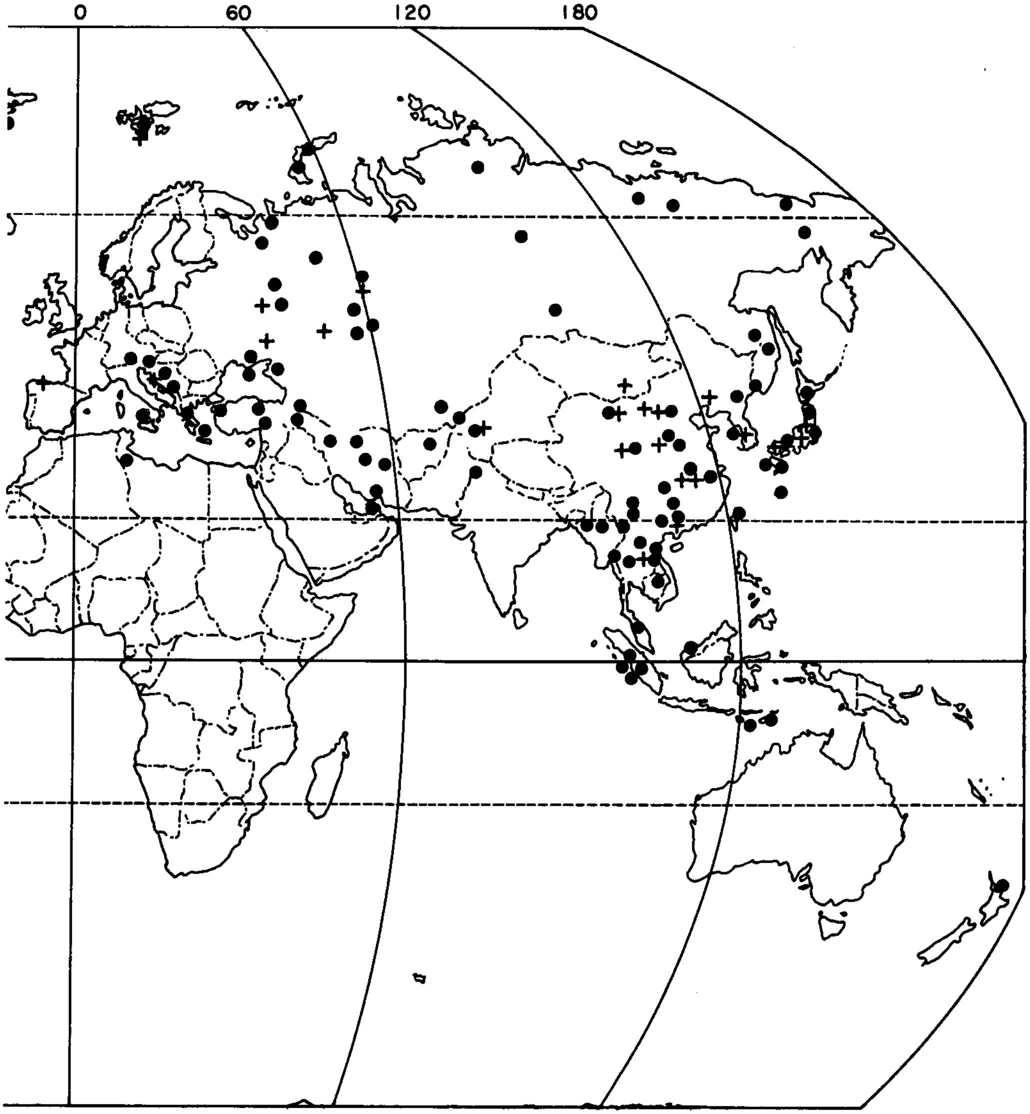


FIG. 296. *(continued from facing page)*.

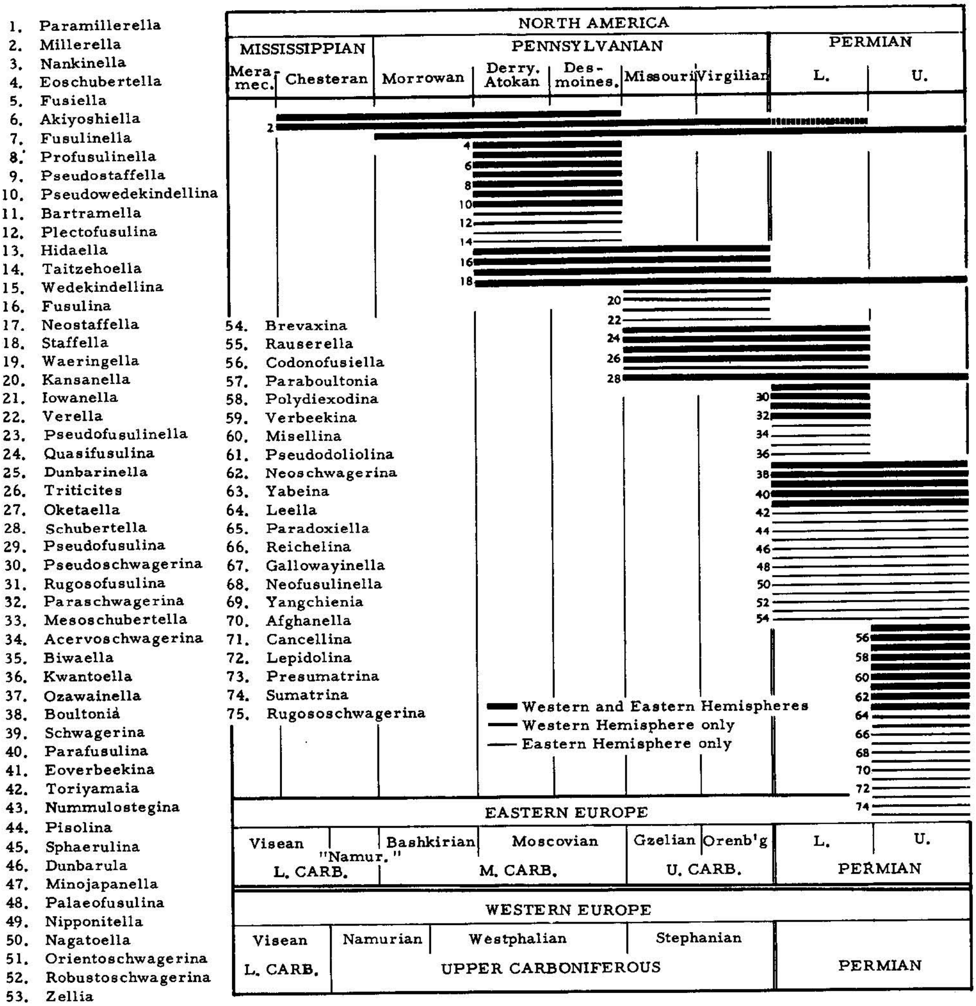


FIG. 297. Stratigraphic distribution of fusulinacean genera as recorded in *Treatise* text devoted to systematic descriptions. Attention is drawn to the fact that many ranges are plotted as spanning all of one or more stratigraphic divisions, whereas the actual ranges, if precisely known, may be appreciably shorter (Moore, n). An alphabetically arranged list of genera follows.

Acervoschwagerina—34
Afghanella—70
Akiyoshiella—6
Bartramella—11
Biwaella—35
Boultonia—38
Brevaxina—54
Cancellina—71
Codonofusiella—56
Dunbarinella—25
Dunbarula—46
Eoschubertella—4
Eoverbeekina—41
Fusiella—5
Fusulina—16
Fusulinella—7
Gallowayinella—67
Hidaella—13
Iowanella—21
Kansanella—20
Kwantoella—36
Leella—64
Lepidolina—72
Mesoschubertella—33
Millerella—2
Minojapanella—47
Misellina—60
Nagatoella—50
Nankinella—3
Neofusulinella—68
Neoschwagerina—62
Neostaffella—17
Nipponitella—49
Nummulostegina—43
Oketaella—27
Orientoschwagerina—51
Ozawainella—37
Palaeofusulina—48
Paraboultonia—57
Paradoxiella—65
Parafusulina—40
Paramillerella—1
Paraschwagerina—32
Pisolina—44
Plectofusulina—12
Polydiexodina—58
Presumatrina—73
Profusulinella—8
Pseudodoliolina—61
Pseudofusulina—29
Pseudofusulinella—23
Pseudoschwagerina—30
Pseudostaffella—9
Pseudowedekindellina—10
Quasifusulina—24
Rauserella—55
Reichelina—66
Robustoschwagerina—52
Rugosofusulina—31
Rugososchwagerina—75
Schubertella—28
Schwagerina—39
Sphaerulina—45
Staffella—18
Sumatrina—74
Taitzehoella—14
Toriyamaia—42
Triticites—26
Verbeekina—59
Verella—22
Waeringella—19
Wedekindellina—15
Yabeina—63
Yangchienia—69
Zellia—53

Triticites extends into Lower Permian rocks.

ZONE OF PSEUDOSCHWAGERINA

The genus *Pseudoschwagerina* (*Schwagerina* of authors prior to 1936) is considered by most paleontologists as an index to the Lower Permian. The genus ranges throughout most of the Wolfcampian in North America, and accordingly these rocks are designated as the Zone of *Pseudoschwagerina.* Until recently, the lowest known occurrence of *Pseudoschwagerina* in the Wolfcampian of the mid-continent region was in the Grenola Formation, about 300 feet above the base of rocks considered Permian. Undescribed specimens of *Pseudoschwagerina* now have been obtained in the Americus Limestone of Kansas (about 200 feet above the base of Wolfcampian strata in this region). *Pseudoschwagerina* is common in uppermost Wolfcampian rocks in the Hueco Mountains of Texas.

The so-called *Schwagerina* limestones of reports on Asia, Europe, and North America are really *Pseudoschwagerina* limestones; the use of fossil names for rock units is not good practice, as demonstrated by the erroneous stratigraphic use of *Schwagerina* for so many years.

Rocks of the Zone of *Pseudoschwagerina* occur in many widely separated areas, including Arctic Islands of the Eastern Hemisphere, European USSR, Austria, Sumatra, China, Japan, southeastern Asia, much of central and western USA, Peru, Bolivia, and possibly Greenland.

ZONE OF PARAFUSULINA

Stratigraphic limits of the genus *Parafusulina* overlap slightly those of *Pseudoschwagerina,* but in North America *Parafusulina* dominates the fusulinacean faunas of Leonardian and lower Guadalupian strata. This part of the American Permian, classed as Lower Permian, is referred to as the Zone of *Parafusulina.* In the Western Hemisphere, rocks referable to the Zone of *Parafusulina* occur in Colombia, Venezuela, Guatemala, southern and northern Mexico, western Texas, southern New Mexico, Washington, California, Oregon, British Columbia, and Alaska. The distribution of *Parafusulina* in the Eastern Hemisphere is not well known, largely owing to the lack of illustrations in early reports of thin sections that are necessary to recognize the genus. Many species of *Parafusulina* may have been described, but from available information they cannot be referred to that genus with certainty. However, *Parafusulina* has been recognized in the Carnic Alps, Salt Range of West Pakistan, southern China, Japan, Karakorum region, and the western edge of the Ural Mountains.

ZONE OF POLYDIEXODINA

The genus *Polydiexodina* is restricted in North America to rocks of late Guadalupian age which are referred to as the fusulinacean Zone of *Polydiexodina.* This zone immediately overlies the Zone of *Parafusulina* in many places in North America. However, *Polydiexodina* has not been found in the Eastern Hemisphere at all localities immediately above rocks containing *Parafusulina.* In southern China, rocks bearing typical faunas of the Zone of *Parafusulina* are overlain by beds that carry a Tethys Sea type of fauna, including *Verbeekina* and *Neoschwagerina.* In Afghanistan, southern Turkey, and northern Iraq, *Polydiexodina* occurs associated with *Verbeekina* and several early members of Neoschwagerininae, including *Neoschwagerina.* Therefore, it seems possible that the Zone of *Polydiexodina* in North America is equivalent in age to at least part of the Tethyan Zone of *Verbeekina. Polydiexodina* occurs both in Asia(Darvaz region of USSR, Burma, Turkey, Iraq, Syria, Iran) and Europe (Aegean Islands of Greece). In the Aegean Islands, a questionable form of *Polydiexodina* is associated with a typical fauna of the Zone of *Verbeekina.*

ZONE OF VERBEEKINA

The lower part of the Tethys Sea fusulinacean faunas of the Eastern Hemisphere is typified by the genus *Verbeekina,* and this part of the stratigraphic section is referred to as the Zone of *Verbeekina.* Rocks referable to this zone are widespread in a relatively narrow belt extending from the Mediterranean area of southern Europe across Asia to Japan. Rocks that contain a lower Tethyan fusulinacean fauna have been discovered at many outcrops in this area, including localities in Sicily, Greece, Turkey, Iraq, Iran, Arabia, Afghanistan, Thailand, Laos, western and southern China, Sumatra, and Japan.

The stratigraphic relationship between this faunal zone in the Eastern Hemisphere and the Zone of *Polydiexodina* in North America is not known. The association of *Polydiexodina* with *Verbeekina* in Afghanistan, in southern Turkey, and northern Iraq, and possibly in Greece, and the occurrence of *Verbeekina* faunas stratigraphically above typical *Parafusulina* faunas in southern China, strongly suggest that the Zone of *Polydiexodina* in North America is at least partly equivalent in age to the Zone of *Verbeekina.*

Ammonoids indicate that the Sosio Beds of Sicily are early Guadalupian (Wordian) in age (*1280). The Sosio Beds contain several fusulinacean genera that occur in other areas in the Zone of *Verbeekina,* and therefore it seems probable that this Tethys Sea faunal zone is in part slightly older than the Zone of *Polydiexodina* in North America.

ZONE OF YABEINA

The genus *Yabeina* occurs in some of the highest fusulinacean-bearing Permian rocks in the Eastern Hemisphere and has been found in British Columbia, Washington, and Oregon in the Western Hemisphere. *Yabeina* has been identified at numerous localities in the Eastern Hemisphere, including Tunisia, Crimea, South China, Cambodia, Thailand, and Japan. At several places *Yabeina* is known to occur stratigraphically above faunas of *Verbeekina.* Furthermore, the biologic stage of development of *Yabeina* and *Lepidolina* suggests that they are younger than early *Neoschwagerina.* Rocks of Late Permian age that contain faunas of *Yabeina* and *Lepidolina* are referred to the Zone of *Yabeina.* It seems probable that the Zone of *Yabeina* represents the youngest fusulinacean-bearing rocks in the Eastern Hemisphere, and that the fusulinaceans became extinct in the narrow belt of Tethys that extended from Oregon in North America, westward across the northern Pacific region to southern Asia, and farther west at least to Tunisia in the Mediterranean area.

SYSTEMATIC DESCRIPTIONS

Superfamily FUSULINACEA
von Möller, 1878

[*nom. correct.* Loeblich & Tappan, 1961, p. 287 (*pro* superfamily Fusulinoidea Ciry in Piveteau, 1952, p. 179)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}superfamily, ^{2}family group); dagger(†) indicates *partim*]——[^{1}=Orthoklinostegia† Eimer & Fickert, 1899, p. 685 (*nom. nud.*); =^{2}Rotaliaridia† Rhumbler in Kükenthal & Krumbach, 1923, p. 88; =^{1}Fusulinaceae Miklukho-Maklay, 1957, p. 96; =^{1}Neoschwagerinaceae Miklukho-Maklay, 1957, p. 109; =^{1}Fusulinidea Pokorný, 1958, p. 220; =^{1}Verbeekinacea Miklukho-Maklay, 1958, p. 7; =Verbeekinidea Miklukho-Maklay, Rauzer-Chernousova & Rosovskaya, 1958, p. 17]

Shell discoidal, spherical, fusiform, or subcylindrical in shape, most commonly irregularly fusiform, calcareous, perforate; planispiral except for aberrant members and for early volutions of some primitive members. Axis of coiling mostly coincident with maximum diameter of test. Proloculus small and spherical, with single proloculus pore located flush with surface or at base of conical depression. Spirotheca composed of one or several layers. Antetheca composed of single layer or of several layers, vertical in attitude, anteriorly arcuate and plane, or plicated to fluted at base in end zones, throughout length of shell, or throughout height and along entire length, fluting less intense at top of antetheca and in center of shell; antethecal pores (septal pores) abundant in most but seemingly irregularly distributed. Chambers numerous and short. Tunnel, tunnels, or foramina resorbed at center and at base of septa or as multiple tunnels throughout length of shell. Secondary deposits in form of chomata, parachomata, tectoria, or axial fillings (*1295). *U.Miss.-U.Perm.*

Family OZAWAINELLIDAE
Thompson & Foster, 1937

[*nom. transl.* A. D. Miklukho-Maklay, 1958, p. 13 (*ex* subfamily Ozawainellinae Thompson & Foster, 1937, p. 132)] [=Reichelininae A. D. Miklukho-Maklay, 1959, p. 630]

Shell umbilicate to spherical or elongate, evolute in early forms, involute or irregularly uncoiled in later ones, axis of coiling short or long, first few volutions discoidal, others spherical to unevenly elongate; spirotheca composed of tectum with upper and lower tectoria in early forms but diaphanotheca occurring below tectum and above lower tectorium in later ones; septa plane; shell generally planispiral but may be asym-

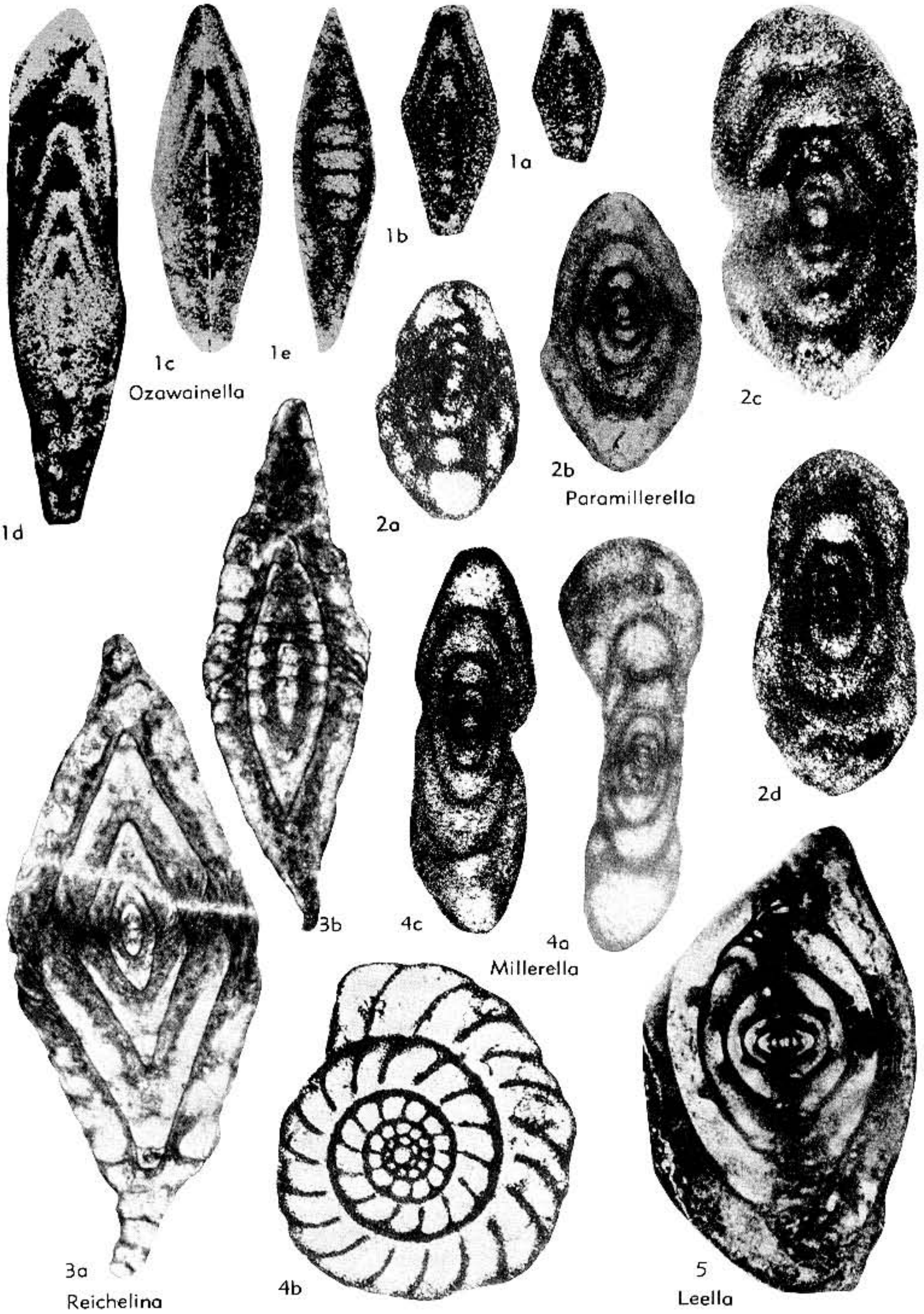


Fig. 298. Ozawainellidae; *1, Ozawainella; 2, Paramillerella; 3, Reichelina; 4, Millerella; 5, Leella* (p. C396-C397).

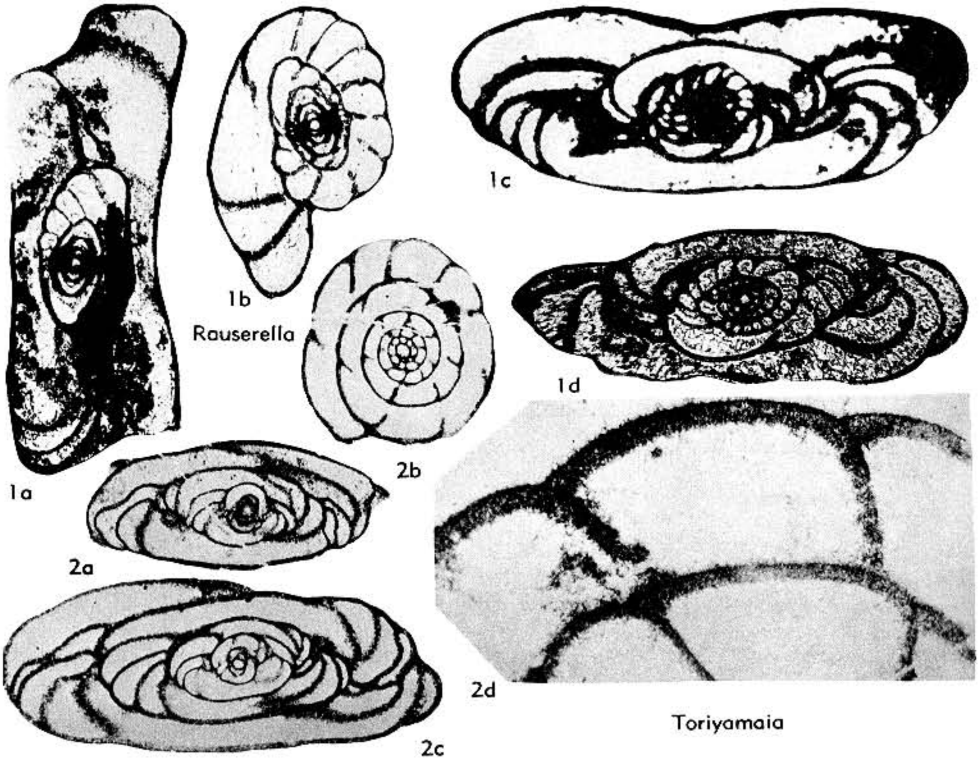


FIG. 299. Ozawainellidae; _1, Rauserella; 2, Toriyamaia_ (p. C397).

metrical, discoidal in at least part of shell with coiling axis in shortest diameter; tunnel singular (*1929). _U.Miss-U.Perm._

Ozawainella Thompson, 1935, *1912, p. 114 [*_Fusulinella angulata_ Colani, 1924, *354, p. 74; OD]. Test discoidal, involute, with angular periphery; wall as in _Millerella_; chomata moderate to massive (*1913, *1929). _L.Perm.-U.Perm._, Arctic Is.-Asia-Eu.-N. Am.——Fig. 298,_1_. *_O. angulata_ (Colani), L.Perm., N.Vietnam; _1a-c_, axial secs. of holotype, ×45; _1d_, axial sec. of paratype, ×45; _1e_, tang. sec. of paratype, ×50 (*1922).

Leella Dunbar & Skinner, 1937, *646, p. 603 [*_L. bellula_; OD]. Shell symmetrical throughout growth, discoidal in early volutions, becoming inflated-fusiform at maturity; spirotheca of tectum, diaphanotheca, and upper and lower tectoria; septa plane; chomata asymmetrical, high, and narrow (*646). _U.Perm._, N.Am.——Fig. 298,_5_. *_L. bellula_, Capitan Ls., USA(Tex.); axial sec. of holotype, ×25 (*1922).

Millerella Thompson, 1942, *1919, p. 404 [*_M. marblensis_; OD]. Shell minute, involute to partly evolute, axis in smallest diameter through proloculus; spirotheca of tectum with upper and lower tectoria; septa arcuate forward; chomata indistinct to massive, their periphery narrowly rounded (*1919, *1922, *1925). _U.Miss.-U.Penn., ?L.Perm. (Millerella Z.),_ N.Am.-Eu.-Asia.——Fig. 298,_4a,b_. *_M. marblensis,_ M.Penn.(Marble Falls Ls.), USA(Tex.); _4a,_ axial sec. of holotype, ×100 (*1922); _4b,_ sagittal sec., ×100 (*1926).——Fig. 298,_4c_. _M. pressa_ Thompson, L.Penn. (Kearny F.), USA (Kans.); axial sec. of holotype, ×100 (*1922). [See also Fig. 294,_1,2_.]

Paramillerella Thompson, 1951, *1925, p. 115 [*_Millerella? advena_ Thompson, 1944, *1920, p. 427; OD] [=?_Staffella (Eostaffella)_ Rauzer-Chernousova, 1948, *1505, p. 14 (type, _S. (E.) parastruvei_; OD); ?_Mediocris_ Rozovskaya, 1961, *1593, p. 20 (type, _Eostaffella mediocris_ Vissarionova, 1948, *2009A, p. 222; OD)]. Shell discoidal, minute, slightly evolute to involute; polar ends slightly umbilicate to rounded; spirotheca of tectum with upper and lower tectoria; chomata massive (*1920, *1925). _U.Miss.-M.Penn._, N. Am.-Asia-Eu.——Fig. 298,_2a_. *_P. advena_ (Thompson), L.Penn.(Morrowan), USA(NW. Ark.); axial sec. of holotype, ×100 (*1926).——Fig. 298,_2b_. _P. ampla_ (Thompson), L.Penn. Kearny F.), USA(Kans.); axial sec. of holotype,

×75 (*1922).——Fig. 298,*2c*. *P. circuli* (Thompson), L.Penn.(Belden F.), USA(Utah); axial sec. of holotype, ×100 (*1926).——Fig. 298,*2d*. *P. pinguis* (Thompson), L.Penn.(Bloyd Sh., USA(Ark.); axial sec. of holotype, ×75 (*1920). [See also Fig. 294,*3-5*.]

Rauserella Dunbar, 1944, *638, p. 37 [**R. erratica*; OD]. Early volutions discoidal, later ones irregularly subcylindrical and coiled at large angle to early volutions; mature shell small; septa plane; wall of tectum with upper and lower tectoria in inner volutions, of tectum and diaphanotheca in outer volutions (*638, *1012, *1047). *U.Perm.*, N.Am.(Tex.-Mex.)-Japan.——Fig. 299,*1*. **R. erratica*, Delaware F., Mex.(La Difunta); *1a*, axial sec. through proloculus, ×25; *1b*, sagittal sec. through proloculus, ×25; *1c*, parallel sec., ×25; *1d*, axial sec. through proloculus showing erratic coiling, ×25 (*1922).

Reichelina Erk, 1941[1942], *709, p. 249 [**R. cribroseptata*; OD]. Shell small, discoidal, divisible into 3 parts, first 1 or 2 volutions evolute, next 3 involute, with narrowly rounded periphery, outer part of last volution somewhat uncoiled; spirotheca composed of tectum and diaphanotheca; tunnel triangular in cross section, with flat bottom tangent to sharp edge of preceding volution; chomata broad, extending from tunnel to polar area, seemingly becoming thicker toward umbilicus (*709). *U.Perm.*, SW.Asia(Turkey)-Japan-China-USSR.——Fig. 298,*3*. **R. cribroseptata*, Turkey; *3a*, axial sec. of holotype, ×70 (*1926); *3b*, tang. sec. of paratype, ×70 (*1926).

Toriyamaia Kanmera, 1956, *1013, p. 251 [**T. laxiseptata*; OD]. Shell small, elongate-fusiform to subcylindrical, with bluntly to broadly rounded polar ends; first 1 or 2 volutions discoidal, evolute, and coiled at right angles to outer cylindrical volutions; mature shape of shell reached in about first 4 volutions; proloculus minute, spherical; spirotheca thin, composed of tectum and less dense, structureless lower layer; septa very broadly spaced, unfluted, only 7 to each volution in outer part of shell (*1013). *Perm.*, Japan.——Fig. 299,*2*. **T. laxiseptata*, Kozaki F., Kyushu; *2a*, axial sec. of holotype, ×25; *2b*, sagittal sec. of paratype, ×25; *2c*, axial sec. of paratype, ×25; *2d*, part of sagittal sec. showing structure of spirotheca, ×100 (*1013).

Family STAFFELLIDAE
Miklukho-Maklay, 1949

[*nom. transl.* A. D. Miklukho-Maklay, 1957, p. 96 (*ex* subfamily Staffellininae A. D. Miklukho-Maklay, 1949, p. 46, *nom. imperf.*)] [=Staffellinidae A. D. Miklukho-Maklay, 1957, p. 96 (*nom. imperf.*); =Staffellidae A. D. Miklukho-Maklay, 1958, p. 11; =Staffellinae Rozovskaya, 1950, p. 378; =Staffelininae Pokorný, 1958, p. 233 (*nom. van.*)]

Shell small, spherical to discoidal, with umbilicate or flush axial ends; septa strongly arched forward, closely spaced, and totally unfluted from end to end; tunnel singular, bordered by distinctly asymmetrical chomata except in terminal part of last volution; walls composed of upper and lower layers that are in turn underlain and overlain by secondary deposits in most forms, except for outer part of last volution (*1261). [The shells of most fossil forms have been replaced by silica and other mineral matter.] *L.Penn.-Perm.*

Staffella Ozawa, 1925, *1401, p. 24 ["**Staffella sphaerica* von Möller" (="*Fusulinella sphaerica* Abich" von Möller, 1878, *1295, p. 114, =**Fusulina sphaerica* Abich, 1859, *1A, p. 439, 528); OD]. Test subspherical at maturity, discoidal in early volutions; wall as in *Nankinella*; septa plane (*1912, *1922). *U.Carb.(M.Penn.)-Perm.*, Eu.-Asia-E.Indies-S.Am.-C.Am.-N.Am. —— Fig. 300,*2a,b*. *S. moellerana* Thompson, U.Perm. (Djulfa Beds), Armenia; *2a*, ext. view, ×10; *2b*, axial sec., ×15 (*1922).——Fig. 300,*2c*. *S. expansa* Thompson, M.Penn.(Marble Falls Ls.), USA(Tex.); axial sec. of holotype, ×50 (*1922).

[The fact that Ozawa (*1401, p. 24) in designating *Staffella sphaerica* as the type-species of *Staffella* erroneously cited von Möller as the author of this species cannot be construed under stipulations of the Zoological Code (1961) to refer to fossils in the hands of von Möller (1878, *1295, p. 114) which he designated as *Fusulinella sphaerica* Abich (1858) [1859], =*Fusulina sphaerica* Abich, 1858 [1859]. Dunbar (1933, *637A, p. 131; 1940, *637B, p. 138) and subsequently Thompson (1935, *1912, p. 113) were mistaken in judging that specimens described and illustrated by von Möller, rather than Abich's *Fusulina sphaerica*, must be recognized in defining characters of *Staffella*. In the first place, it is a named species, whatever its authorship and date, not specimens identified by some later worker as belonging to this species, that governs fixation of the type-species of a nominal genus. Ozawa's (1928, *1401C, p. 131) citation of the type-species of *Staffella* as "genoholotype, *Fusulina sphaerica* Abich" is germane only as an indication of his intent, because the original publication containing an explicit type-species designation is sole authority and evidence for distinguishing it (Zool. Code, 67, f). Thompson (1935, *1912, p. 113) concluded that von Möller's *Fusulinella sphaerica* and Abich's *Fusulina sphaerica* are congeneric, both belonging to *Staffella*, but in his opinion they are not at all conspecific; therefore, in order to avoid homonymy of specific names he published *Staffella moellerana* as designation for von Möller's specimens. *S. moellerana* Thompson is not the type-species of *Staffella*, despite Ozawa's admission, quoted by Dunbar (1940, *637B, p. 138), that he based his choice of type-species on a spheroidal form treated in von Möller's paper; it is Ozawa's action (1925) in designating *Staffella sphaerica* (=*Fusulina sphaerica* Abich, 1859) as the type-species that governs. This is not subsequently alterable by him or anyone else.]

Nankinella Lee, 1933[1934], *1120, p. 14 [**Staffella discoides* Lee, 1931, *1119A, p. 286; OD] [=*Hayasakaina* Fujimoto & Kawada, 1953, *756, p. 119 (type, *H. kotakiensis*; OD)]. Test discoidal, with umbilicate axial areas, periphery angular to rounded in early part, angular at maturity; wall of tectum and diaphanotheca mineralized in all known forms, their original construction unknown; septa plane; chomata distinct (*756, *1120, *1922). *L.Penn.-U.Perm.*, N. Am.-Eu.-Asia.——Fig. 300,*1a*. *N.* sp., M.Penn. (Green Canyon Ls), USA(Tex., Powwow Canyon); outline drawing, ×40 (*1922).——Fig. 300,*1b,c*. *N. plummeri* Thompson, M.Penn. (Marble Falls Ls.), USA(Tex.); *1b*, axial sec. of holotype, ×50 (*1922); *1c*, tang. sec. of paratype, ×50 (*1922).——Fig. 300,*1d*. **N. discoides* (Lee), Perm.(Chihsia Ls.), China(Nan-

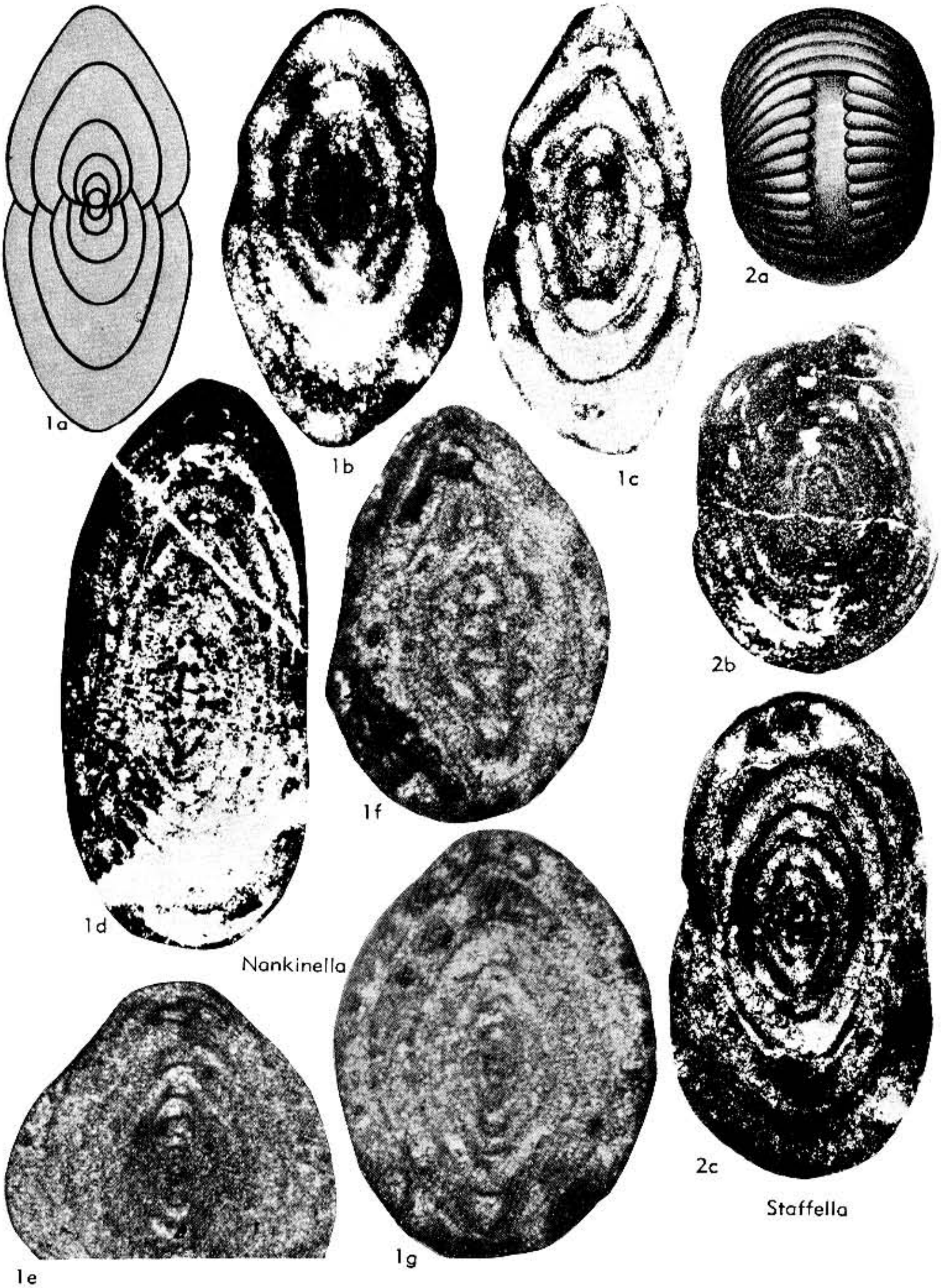


Fig. 300. Staffellidae; *1, Nankinella; 2, Staffella* (p. C397-C399).

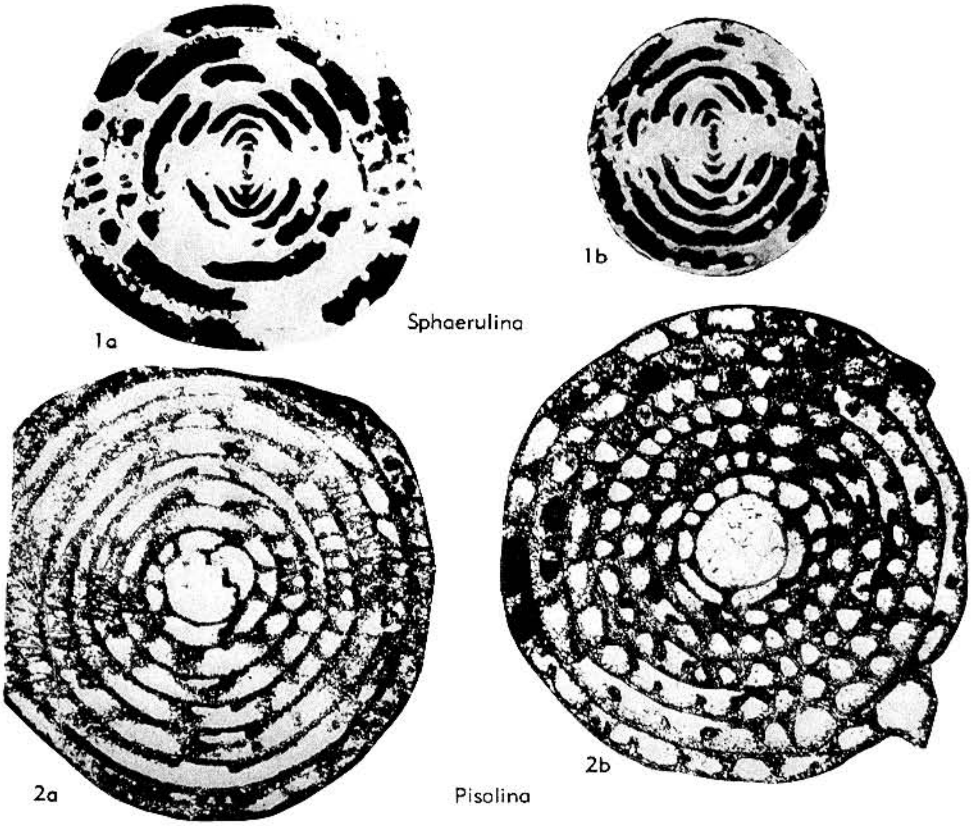


FIG. 301. Staffellidae; *1, Sphaerulina; 2, Pisolina* (p. C399).

king); tang. sec. of holotype, ×15 (*1922).——FIG. 300,*1e-g*. *N. kotakiensis* (FUJIMOTO & KAWADA), L.Perm.(Omi Ls.), Japan(Niigata Pref.); *1e,* near-centered axial sec., ×40; *1f,* eccentric axial sec., ×40; *1g,* axial sec., ×40 (*756).

Nummulostegina SCHUBERT, 1907, *1685, p. 212 [**N. velebitana* SCHUBERT, 1908, *1686, p. 377; SD]. Test subdiscoidal, planispiral, periphery narrowly rounded; septa plane but other internal features poorly known (*1008, *1685). *Perm.,* Eu.——FIG. 274,*1a,b*. **N. velebitana,* Yugo.; *1a,b,* lateral and apert. views of holotype, ×20 (*1922).

Pisolina LEE, 1933[1934], *1120, p. 19 [**P. excessa*; OD]. Shell small, spherical throughout; spirotheca composed of tectum and ?keriotheca, possibly as in *Staffella*; septa widely spaced, plane; tunnel singular, chomata distinct; proloculus large (*1120). *Perm.,* Asia(China-Armenia).——FIG. 301,*2*. **P. excessa,* Wushan Ls., China (Mitsang Gorge); *2a,* axial sec. of holotype, ×15; *2b,* sagittal sec. of paratype, ×15 (*1922).

Sphaerulina LEE, 1933[1934], *1120, p. 16 [**S. crassispira*; OD]. Minute, mature shell spherical and slightly umbilicate, composed of about 10 volutions, planispiral throughout, first 3 or 4 volutions discoidal; spirotheca composed of tectum and alveolar ?keriotheca; septa plane (*1120). *Perm.,* Asia(China).——FIG. 301,1. **S. crassispira,* Kweichow; *1a,* axial sec. of holotype, ×30; *1b,* axial sec. of paratype, ×30 (*1922).

Family FUSULINIDAE von Möller, 1878

[Fusulinidae VON MÖLLER, 1878, p. 133]——[All names cited are of family rank]——[=Fusulinina LANKESTER, 1885, p. 848; =Fusulininae DELAGE & HÉROUARD, 1896, p. 148; =Fusilinidae CALKINS, 1926, p. 356 *(nom. null.)*; =Fusulinida HAECKEL, 1894, p. 185 *(nom. van.)*]——[=Nautiloida SCHULTZE, 1854, p. 53 *(partim) (nom. nud.)*; =Schwagerinidae DUNBAR & HENBEST, 1930, p. 363; =Schubertellidae A. D. MIKLUKHO-MAKLAY, RAUZER-CHERNOUSOVA & ROZOVSKAYA, 1958, p. 17; =Schubertellinidae A. D. MIKLUKHO-MAKLAY, RAUZER-CHERNOUSOVA, & ROZOVSKAYA, 1958, fig. 2 on p. 7 *(nom. null.)*]

Shell spherical, fusiform or subcylindrical, most commonly irregularly fusiform; calcareous, perforate, planispiral, except for aberrant genera, and early stages of a few genera. Spirothecal structure of several sorts, including (1) tectum with upper and lower tectorium (2) tectum and diaphanotheca with upper and lower tectorium; (3) tectum and diaphanotheca, with discontinu-

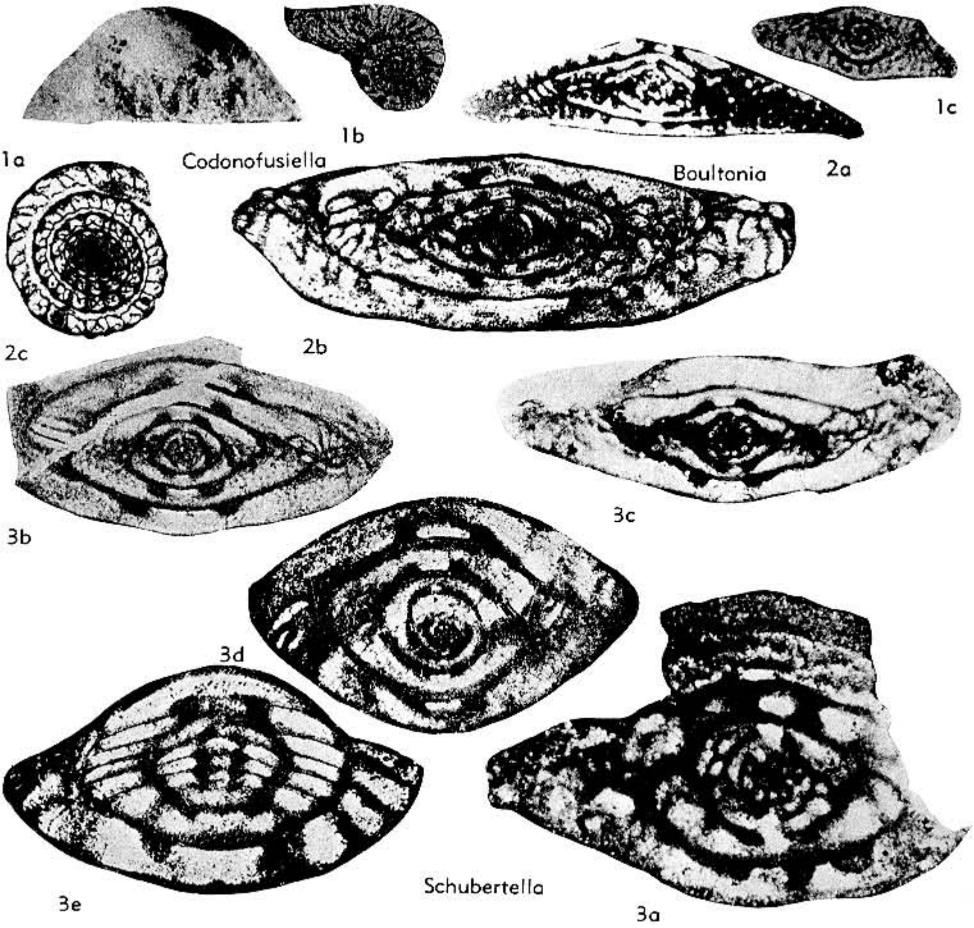


FIG. 302. Fusulinidae (Schubertellinae; *1, Codonofusiella; 2, Boultonia; 3, Schubertella*) (p. *C*400-*C*401).

ous upper or lower tectorium; (4) tectum and structureless lower layer; and (5) tectum with alveolar keriotheca. Axis of coiling generally coincident with maximum diameter of shell. Antetheca composed of single layer that is plicated or fluted in various degrees ranging from unfluted to intensely fluted throughout length of septa. Septal pores found in all forms. Tunnel singular in most, with chomata along borders of tunnel, multiple tunnels in some. Secondary deposits commonly present, including chomata, axial fillings, and tectoria (*1295). *U.Carb.(M.Penn.)-U.Perm.*

Subfamily SCHUBERTELLINAE Skinner, 1931

[Schubertellinae SKINNER, 1931, p. 257 (Although introduced conditionally, this name with authorship and date given is valid; Zoological Code, 1961, Art. 17,8)] [All names cited are of subfamily rank]——[=Boultoniinae SKINNER & WILDE, 1954, p. 437; =Schubertellininae ROZOVSKAYA, 1950, p. 376 (*nom. van.*)]

Shell minute, elongate-fusiform, ellipsoidal or irregular in shape, first few volutions coiled at large angle to outer ones; spirotheca composed of (1) tectum with upper and lower tectoria or (2) tectum with diaphanotheca and tectoria, or (3) tectum with lower layer only, or (4) consisting of single thin layer; septa plane in primitive forms, fluted in end zones of more advanced forms, and fluted throughout length of shell in some advanced members; tunnel singular; chomata small or distinct (*1295, *1929). *U.Carb.(M.Penn.)-U.Perm.*

Schubertella STAFF & WEDEKIND, 1910, *1832, p.

112, 121 [**S. transitoria*; OD] [=*Depratella* Ozawa, 1928, *1402, p. 9 (type, *Neofusulinella giraudi* Deprat, 1915, *587A, p. 11; OD)]. Shell fusiform, first 1 to 3 volutions discoidal, coiled at large angle to outer volutions; spirotheca of tectum with lower layer or of single thin layer only; septa unfluted; chomata large, highly asymmetrical (*1402, *1918, *1922). *U.Penn-U.Perm.*, N. Am.-S. Am.-Eu.-Asia-Arctic Is.-E. Indies. ——Fig. 302,*3a*. **S. transitoria*, L.Perm., Spitz. (Tempel Bay); axial sec. of topotype, ×83 (*1922).——Fig. 302,*3b*. *S. mulleriedi* Thompson & Miller, L.Perm.(Paso Hondo F.), Mex. (Chiapas); axial sec. of syntype, ×20 (*1922).——Fig. 302,*3c*. *S. kingi* Dunbar & Skinner, L. Perm.(Hueco Ls.), USA(Tex.); axial sec. of syntype, ×50 (*1922).——Fig. 302,*3d,e*. *S. giraudi* (Deprat), L.Perm., Laos(Cammon); *3d*, axial sec. of holotype, ×45 (*1922); *3e*, tang. sec. of paratype showing lack of septal fluting, ×45 (*1922).

Boultonia Lee, 1927, *1119, p. 10 [**B. willsi*; OD]. Shell minute, elongate-fusiform, first 1 or 2 volutions discoidal, coiled at large angle to outer fusiform volutions; spirotheca of tectum and faintly porous lower layer; septa fluted throughout; chomata asymmetrical throughout fusiform part of shell (*1119, *1795). *Perm.*, Asia (China-Cambodia)-Eu.(Aus.)-USA (Wash.-Nev.-Tex.).——Fig. 302,*2a*. **B. willsi*, L.Perm. (Taiyuan Ser.), N.China; axial sec. of holotype, ×53 (*1922).——Fig. 302,*2b,c*. *B. guadalupensis* Skinner & Wilde, L.Perm.(Parafusulina Z., Bone Spring Ls.), USA(Tex.); *2b*, axial sec. of holotype, ×40; *2c*, sagittal sec. of paratype, ×40 (*1795).

Codonofusiella Dunbar & Skinner, 1937, *646, p. 606 [**C. paradoxica*; OD]. Shell minute, first 4 volutions tightly coiled, outer ones irregularly uncoiled to rectilinear, first 1 or 2 volutions planispiral around minute proloculus with short axis of coiling and coiled at large angle to next 2 or 3 fusiform-elongate volutions; spirotheca thin; septa also thin, intensely fluted throughout fusiform and later rectilinear uncoiled part of shell; chomata distinct but not massive (*646). *U.Perm.*, USA(Tex.)-Can.(B.C.)-Japan-Asia(Turkey-Cambodia-Crimea).——Fig. 302,*1*. **C. paradoxica*, Capitan Ls., Tex.; *1a*, external view of paratype; *1b*, sagittal sec. of holotype; *1c*, axial sec. of paratype; all ×22 (*1922).

Dunbarula Ciry, 1948, *342, p. 108 [**D. mathieui*; OD]. Shell ellipsoidal to subcylindrical, with rounded polar ends; spirotheca composed of tectum and thin, finely porous diaphanotheca; septa fluted throughout length of shell and to tops of chambers, septal pores closely spaced and arranged in diagonal pattern (*342, *1926). [Shell structure like that of *Rauserella* except for fluted septa.] *Perm.*, N.Afr.——Fig. 303,*3*. **D. mathieui*, S. Tunisia; *3a*, axial sec. of topotype showing diagonal arrangement of septal pores, ×40; *3b*, part of sagittal sec. showing structure of spirotheca, ×150; *3c*, part of axial sec. of *3a* showing diagonal arrangement of septal pores, ×130 (*1926).

Eoschubertella Thompson, 1937, *1918, p. 123 [**Schubertella lata* Lee & Chen in Lee, Chen & Chu, 1930, *1121, p. 111; OD]. Shell small, inflated-ellipsoidal to fusiform; first 1 or 2 volutions coiled at large angle to outer ones; spirotheca composed of tectum with upper and lower tectoria; septa plane; tunnel broad for shell size, bordered by low chomata (*1121, *1918). *U. Carb. (M.Penn.)*, N.Am.-Asia-Eu.-S.Am.——Fig. 303,*4*. **E. lata* (Lee & Chen), Huanglung Ls., China(Lungtan); axial sec. of holotype, ×30 (*1922). [See also Fig. 294,6.]

Fusiella Lee & Chen, in Lee, Chen & Chu, 1930, *1121, p. 107 [**F. typica*; OD]. Shell small, elongate-fusiform; first 1 or 2 volutions discoidal, coiled at large angle to outer fusiform volutions, axial fillings distinct; spirotheca composed of tectum with upper and lower tectoria (*1121, *1922). *U. Carb. (M. Penn.)*, N.Am.-USSR-Asia (China)-Japan.——Fig. 303,*1*. **F. typica*, Huanglung Ls., China(Lungtan); *1a*, axial sec. of holotype, ×30; *1b*, sagittal sec. of paratype, ×30 (*1922).

Mesoschubertella Kanuma & Sakagami, 1957, *1014, p. 42 [**M. thompsoni* Sakagami in Kanuma & Sakagami, 1957; OD]. Shell minute, inflated-fusiform, with form ratio of about 1:1.5, lateral slopes distinctly convex, mature shells of 4 or 5 volutions 1-2 mm. long and 1 mm. wide, inner 2 or 3 volutions evolute and coiled at large angle to outer ones; spirotheca composed of tectum and alveolar keriotheca, seemingly with coating on its lower surface; septa unfluted; chomata asymmetrical and distinct, tunnel singular (*1014). *L.Perm.*, Japan.——Fig. 303,*2*. **M. thompsoni* Sakagami, Amanouchi Ls., Yagooki; *2a,b*, axial secs. of paratype and holotype, ×30; *2c*, tang. sec. of paratype, ×30; *2d*, part of axial sec. of holotype showing structure of spirotheca, ×100 (*1014).

Minojapanella Fujimoto & Kanuma, 1953, *755, p. 150 [**M. elongata*; OD]. Shell minute, highly elongate-fusiform, first 1 or 2 volutions discoidal around large, spherical proloculus and coiled at large angle to outer 5 or 6 greatly elongated, fusiform volutions; spirotheca thin, indistinct; septa closely spaced, intensely fluted throughout fusiform part of shell, axial fillings in at least outer 5 volutions but not massive; tunnel singular but not clearly defined (*755, *1926). [Shell of only known species not well preserved and poorly understood.] *Perm.*, Japan.——Fig. 304,*2*. **M. elongata*, Chichibu Ser.; *2a,c*, axial secs. of holotype and topotype, ×30, ×40; *2b*, sagittal sec. of topotype, ×40; *2d*, tang. sec. of paratype showing septal fluting, ×150 (*1926).

Paraboultonia Skinner & Wilde, 1954, *1795, p.

441 [**P. splendens*; OD] [=*?Tavajzites* Tumanskaya, 1953, *1955, p. 22 (type, *Fusulina ?pseudo-prisca* var. *delicata* Colani, 1924, *354, p. 180; OD)]. Shell small, elongate-subcylindrical at maturity, with blunt polar ends and uncoiled to rectilinear at gerontic stage, first 1 or 1.5 volutions discoidal and coiled at right angle to outer fusiform volutions; spirotheca thin, composed of tectum and diaphanotheca; septa thin, intensely fluted throughout length, cuniculi at base of septa developed in outer part of shell; tunnel singular, narrow, with erratic path, not observed

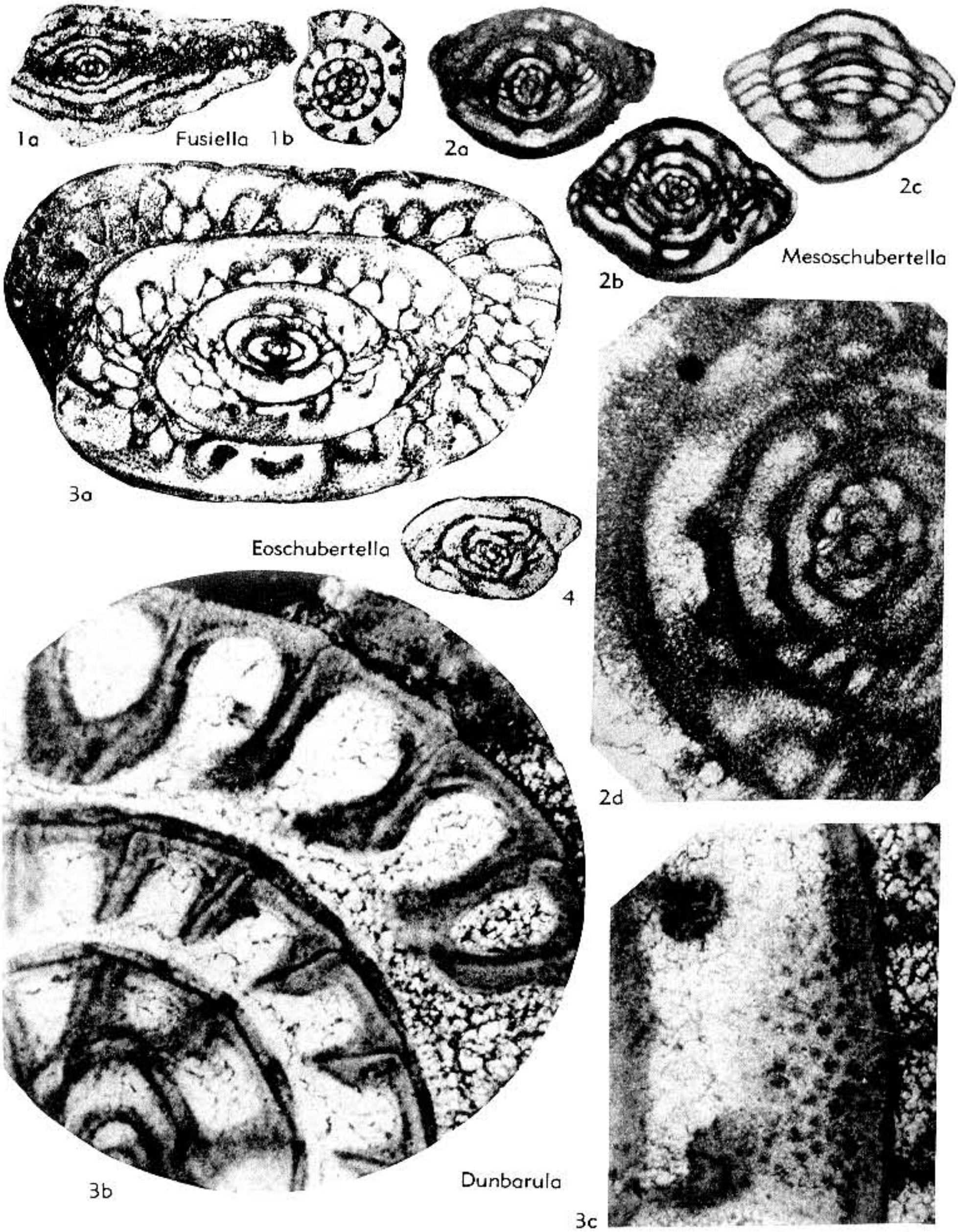


Fig. 303. Fusulinidae (Schubertellinae; *1, Fusiella; 2, Mesoschubertella; 3, Dunbarula; 4, Eoschubertella*) (p. *C*401).

in outer part of shell (*1795, *1946). [Presence of axial fillings is strongly suggested in several of SKINNER & WILDE's type-specimens of this genus (Fig. 304,*1b*; *1795, pl. 44, fig. 2,3).] *U.Perm.*, N.Am.-Asia(China).——FIG. 304,*1a-c*. **P. splendens*, Bell Canyon F., USA(Tex.); *1a*, sagittal sec. of paratype, ×40; *1b*, axial sec. of holotype, ×40; *1c*, tang. sec. of paratype showing cuniculi, ×100 (*1795).——FIG. 304,*1d*. *P. delicata* (COLANI), type-sp. of *Tavajzites*, China(Yunnan); slightly oblique axial sec., ×100 (*354).

Paradoxiella SKINNER & WILDE, 1955, *1797, p. 934 [**P. pratti*; OD]. Shell minute, composed of several planispirally coiled volutions followed

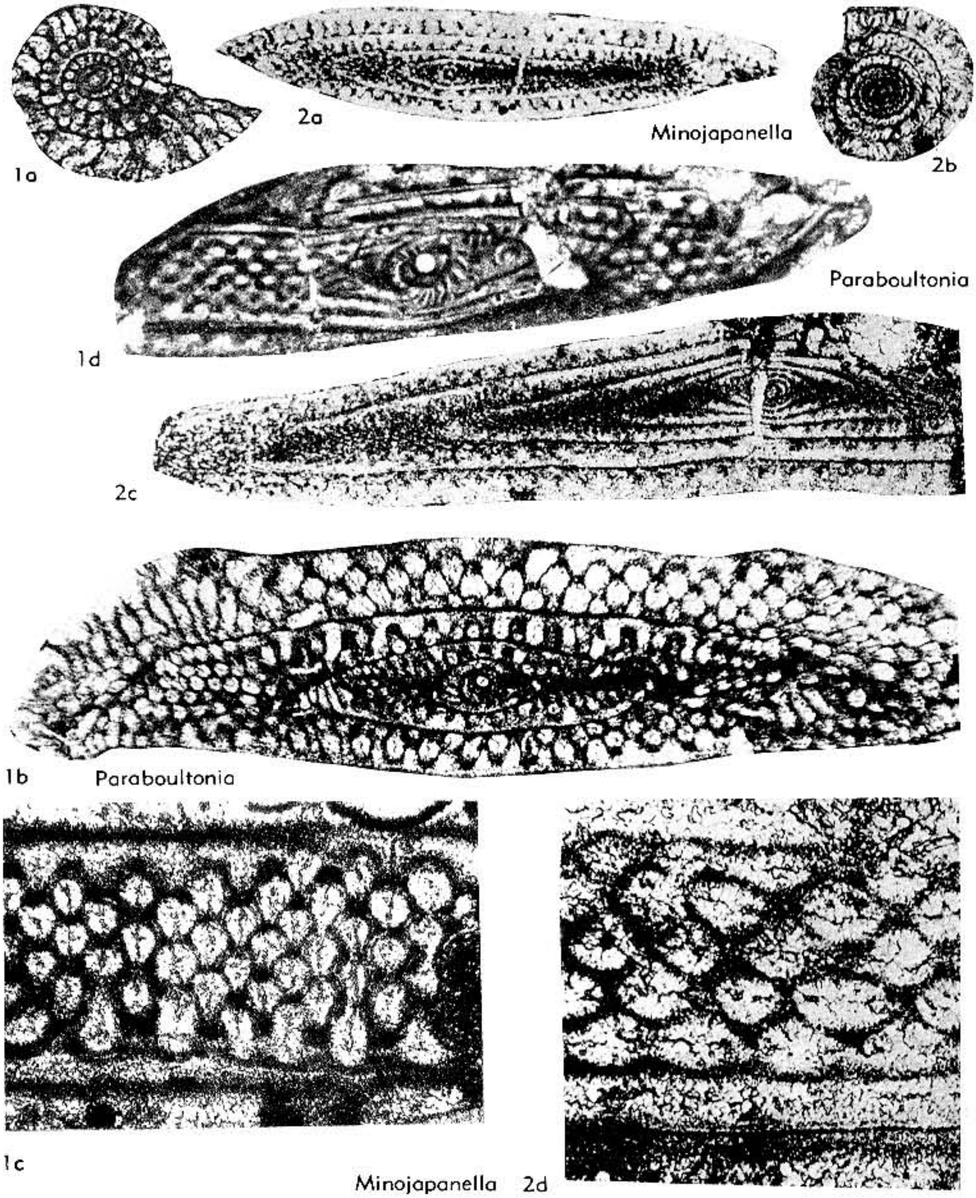


FIG. 304. Fusulinidae (Schubertellinae; *1, Paraboultonia; 2, Minojapanella*) (p. C401-C403).

FIG. 305. Fusulinidae (Schubertellinae; *1, Paradoxiella*) (p. *C*403-*C*404).

by uncoiled, rapidly expanding flared portion that is virtually tangential to final coil of shell; spirotheca thin, consisting of tectum and diaphanotheca; septa composed of same elements as spirotheca, but with thick epithecal layer on anterior and posterior surfaces near center of shell, septa intensely fluted throughout, developing what seem to be cuniculi, septal pores numerous (*1797). [Descriptive terms have been proposed for orientation of shells belonging to this genus (e.g., sagittal view, dorsal view, vertical axial section, inclined axial section, horizontal axial section, and many other possible directional sections). Such terms are not generally applicable to fusulinids but are employed for many other foraminifers (see Glossary).] *U.Perm.*, USA(Tex.).——FIG. 305,*1*. **P. pratti*, Bell Canyon F.(Lamar Ls.); *1a,b,* sagittal and vert. axial secs. of paratypes, ×30; *1c,d,* horiz. axial secs. of paratype and holotype, ×30 (*1797).

Subfamily FUSULININAE von Möller, 1878

[Subfamily Fusulinidae *(sic)* BÜTSCHLI in BRONN, 1880, p. 213 (*nom. transl. ex* family Fusulinidae VON MÖLLER, 1878)] ——[All names cited are of subfamily rank]——[=Fusulininae BRADY, 1884, p. 74; =Fusulinellinae STAFF & WEDEKIND, 1910, p. 112; =Pseudotriticitinae PUTRYA, 1948, p. 112; =Quasifusulininae PUTRYA, 1956, p. 467; =Pseudostaffellinae PUTRYA, 1956, p. 395; =Hemifusulininae PUTRYA, 1956, p. 467; =Eofusulininae RAUZER-CHERNOUSOVA & ROZOVSKAYA in MIKLUKHO-MAKLAY, RAUZER-CHERNOUSOVA & ROZOVSKAYA, 1958, p. 17]

Shell spherical to elongate-fusiform or irregularly subcylindrical, early volutions coiled at large angle to outer ones in primitive genera, planispiral throughout in others; spirotheca generally composed of tectum with upper and lower tectoria, but many genera with diaphanotheca below tectum, and few having spirotheca of single dense, thin layer; septa plane in most primitive genera, first becoming fluted in polar regions and later becoming fluted completely across shell and to top of antetheca; tunnel singular, chomata massive to slight (*1295). *U.Carb.(M.Penn.)-U.Perm.*

Fusulina FISCHER DE WALDHEIM, 1829, *720A, p. 330 [**F. cylindrica* FISCHER DE WALDHEIM, 1837, *720B, p. 126; SD MEEK & HAYDEN, 1865, *1252, p. 13] [=*Hemifusulina* VON MÖLLER, 1877, *1294, p. 146 (type, *H. bocki* VON MÖLLER, 1878, *1295, p. 76; SD); *Hemifusina* VON MÖLLER, 1877, *1294, p. 144 *(nom. null.)*; *Schellwienia* STAFF & WEDEKIND, 1910, *1832, p. 109,

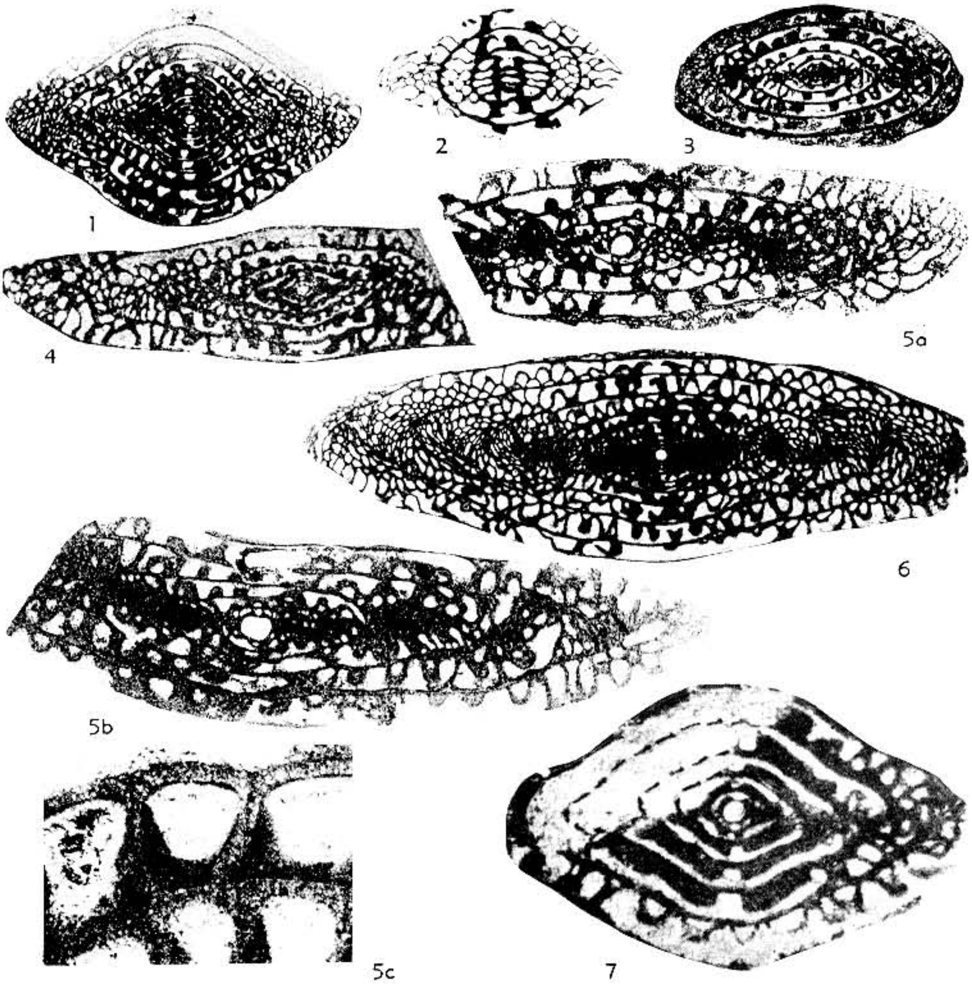


FIG. 306. Fusulinidae (Fusulininae; *1-7, Fusulina*) (p. *C*404-*C*406).

113 (obj.); *Beedeina* GALLOWAY, 1933, *762, p. 401 (type, *Fusulinella girtyi* DUNBAR & CONDRA, 1927[1928], *640, p. 76; OD); *Pseudotriticites* PUTRYA, 1940, *1491, p. 62 (type, *Fusulina? donbassica* PUTRYA, 1939, *1490B, p. 139; OD); ?*Eofusulina* RAUZER-CHERNOUSOVA, 1951, *1507, p. 268 (type, *Fusulina triangula* RAUZER-CHERNOUSOVA & BELYAEV, 1936, in RAUZER-CHERNOUSOVA, BELYAEV & REYTLINGER, 1936, *1507, p. 185; OD); *Dagmarella* SOLOVIEVA, 1955, *1812, p. 945 (type, *D. prima*; OD); *Dutkevichella* PUTRYA, 1956, *1494, p. 460 (type, *Fusulina dutkevichi* PUTRYA, 1937, *1490A, p. 68; OD); ?*Eofusulina (Paraeofusulina)* PUTRYA, 1956, *1494, p. 458 (type, *E. (P.) trianguliformis*; OD)]. Shell fusiform to subcylindrical, planispiral in all volutions; spirotheca of tectum and diaphanotheca with upper and lower tectoria; septa fluted throughout but more intense and higher near polar ends, axial filling in late forms; chomata massive to weak (*762, *1294, *1491, *1812, *1832, *1917, *2083). *U.Carb.(M.Penn.-U.Penn.) (Fusulina Z.)*, N.Am.(USA-Can.-Greenl.)-S.Am. (Peru - Brazil - Chile) - Asia (China-Japan)-USSR-Eu.(Spain).——FIG. 306,*1*. *F. girtyi* (DUNBAR & CONDRA), M.Penn.(Brereton Ls.), USA(Ill.); axial sec., ×10 (*1922).——FIG. 306,*2*. *F.* sp., M. Penn.(Garcia F.), USA(N.Mex.); tang. sec., ×10 (*1922).——FIG. 306,*3*. *F. minima* SCHELLWIEN (=*Hemifusulina bocki* VON MÖLLER, 1878), Moscov., USSR(Tver); axial sec. of holotype, ×15 (*1922).——FIG. 306,*4*. *F. donbassica* (PUTRYA),

Moscov., USSR(Donets Basin); axial sec. of syntype, ×12 (*1491).——Fig. 306,*5*. ****F. cylindrica*** Fischer de Waldheim, Moscov.(Myachkovo Ls.), USSR(Myachkovo Quarry); *5a,b,* axial secs. of topotypes, ×15, ×20; *5c,* part of sagittal sec. of topotype, ×100 (*1922) (see also Fig. 280,*3*).——Fig. 306,*6*. ***F. mysticensis*** Thompson, M.Penn.(Worland Ls.), USA(Iowa); axial sec. of syntype, ×10 (*1922) (see also Fig. 294, *9*).——Fig. 306,*7*. ***F. prima*** (Solovieva), Moscov. (Kachir Horizon), USSR (Noura-Taou); axial sec. of holotype, ×35 (*1812).——Fig. 328A,2. ***F. triangula*** Rauzer-Chernousova & Belyaev, Moscov. (Podolsk Horizon), USSR(Skar-Yu River, Sib.); axial sec. of holotype, ×10 (*1507). [See also Fig. 274,2. *F. girtyi;* 280,*2*; 294,*10*.]

[*Eofusulina,* according to illustrations and authors' description, has an elongate-fusiform to irregular shell, loosely coiled throughout, composed of large proloculus and 3 or 4 inflated volutions; septa fluted throughout length, fluting extending to tops of chambers; septal spacing unknown; spirotheca thin, composed of tectum, discontinuous middle layer and discontinuous lower layer; axial fillings throughout all parts of shell except terminal part of last volution; tunnel wide in 2nd and 3rd volutions; chomata absent, except in 1st and possibly 2nd volution. The characters indicated are essentially those of *Fusulina* as shown by its type-species, *F. cylindrica*. Accordingly, *Eofusulina* is here considered to be a probable synonym of *Fusulina*.]

Akiyoshiella Toriyama, 1953, *1941, p. 251 [**A. ozawai*; OD]. Shell small, elongate-fusiform, planispiral except for highly asymmetrical end regions of some gerontic individuals, loosely coiled throughout; spirotheca like *Fusulina*; septa numerous, highly and narrowly fluted throughout length of shell so as almost to form cuniculi; chomata heavy and spreading to massive axial fillings that spread onto septa and spirotheca (*1930, *1941). *U.Carb.(M.Penn.),* Japan-N.Am. (Can.).——Fig. 307,*3*. ****A. ozawai,*** Akiyoshi Ls., Japan (SW. Honshu); *3a,* axial sec. of holotype, ×20; *3b,* tang. sec. of paratype showing asymmetry of outer volutions, ×20 (*1926).

Bartramella Verville, Thompson & Lokke, 1956, *2004, p. 1278 [**B. bartrami,* OD]. Shell small, elongate-subcylindrical to fusiform, planispiral and symmetrical throughout; spirotheca composed of tectum and lower porous layer; septa thin, narrowly and highly fluted throughout shell length and to tops of chambers, axial fillings massive in all volutions; chomata high asymmetrical, with steep slope on tunnel sides, extending to join with axial fillings toward polar areas (*2004). *M.Penn.,* USA(Nev.-N.Mex.-Idaho).——Fig. 307, *1*. ****B. bartrami,*** Ely Ls., Nev.; axial sec. of holotype, ×20 (*2004).

Fusulinella von Möller, 1877, *1294, p. 144 [**F. bocki* von Möller, 1878, *1295, p. 104; SD Douvillé, 1906, *617, p. 584] [=*Atetsuella* Okimura, 1958, *1386, p. 251 (type, *A. imamurai*; OD]. Shell small, planispiral, and fusiform; spirotheca composed of tectum and diaphanotheca with upper and lower tectoria; septa fluted only in polar regions; chomata massive (*1294, *1386, *1922). *U.Carb.(M.Penn.),* N.Am. (USA-Can.-Mex.)- S.Am.(Peru-Chile)-Asia(China Japan)-USSR-Spitzb.-Greenl.——Fig. 307,*2a*. ***F. juncea*** Thompson, Cuchillo Negro F., USA(N. Mex.); axial sec. of paratype, ×20 (*1922).——Fig. 307,*2b*. ***F. imamurai*** (Okimura), Atetu Ls., Japan(Okayama Pref.); part of axial sec., ×250 (*1386).——Fig. 307,*2c*. ****F. bocki*** von Möller, USSR(Tver, Kresty); axial sec. of topotype, ×40 (*1922).——Fig. 307,*2d*. ***F. iowensis*** Thompson, Cherokee equiv., USA(Iowa); axial sec. of holotype, ×20 (*1910).——Fig. 307,*2e*. ***F. famula*** Thompson, Cuchillo Negro F., USA(N. Mex.); part of sagittal sec. of paratype showing 4-layered spirotheca, ×100 (*1922). [See also Fig. 294,*8*.]

Gallowayinella Chen in Dunbar & Skinner, 1937, *333, p. 571 [*nom. correct.* Thompson, herein (*pro Gallowaiinella* Chen, 1937, *nom. subst. pro Gallowaiina* Chen, 1934, *331, p. 237, =*Gallowayina* Chen, 1934, *nom. correct., non Gallowayina* Ellis, 1932, *699, p. 1)] [**Gallowaiina meitienensis* Chen, 1934, *331, p. 237; OD]. Shell elongate-subcylindrical to inflated-fusiform; spirotheca consisting of single dense layer; axial fillings massive, confined to axial zone; septa narrowly and highly fluted throughout (*331, *333). *U.Perm.,* Asia (S.China).——Fig. 308,*4*. ****G. meitienensis,*** Meitien Ls., Hunan; *4a,b,* axial secs. of holotype, ×15, ×40 (*1922).

[Decision as to the correct name of this genus depends on determination of the status of the original spelling in relation to regulations contained in Art. 32,a,ii, of the Code. The spelling *Gallowaiina,* in which the terminal letter of the name Galloway (referring to Professor J. J. Galloway) is changed to "i," may be construed as an inadvertent error in spelling this surname as a base for the generic name. If this is agreed to, as seems most reasonable, then *Gallowaiina* Chen, 1934, is an incorrect original spelling which has neither separate status in nomenclature nor enters into homonymy (Art. 32,c). It is automatically correctable to *Gallowayina,* in which form it is a junior homonym of *Gallowayina* Ellis, 1932, and a substitute name is called for. *Gallowaiinella* Chen in Dunbar & Skinner, 1937, is such a name, but it is defective in the same ways as *Gallowaiina,* since it contains the same, presumably inadvertent, error in changed spelling of the surname. This may be emended to *Gallowayinella* and this form seems to be most acceptable. Otherwise, it would be necessary to recognize the validity of *Gallowaiina,* since it differs by a single letter from *Gallowayina* (Art. 56,a).]

Hidaella Fujimoto & Igo, 1955, *754, p. 45 [**H. kameii*; OD]. Shell small, elongate-fusiform to subcylindrical, with 5 to 7 volutions, central portions slightly inflated, axial length approx. 3 mm. and axial width approx. 1.3 mm., first 2 or 3 volutions tightly coiled, outer ones inflated; spirotheca composed of thin, dense tectum, diaphanotheca, and less dense upper and lower tectoria, surface of spirotheca undulating throughout length; tunnel singular, chomata massive and high (*754). *U.Carb.,* Central Japan.——Fig. 308,*1*. ****H. kameii,*** Ichinotani F., Hida Mountainland; *1a,* parallel sec. of paratype; *1b,* axial sec. of holotype; *1c,* tang. sec. of paratype; all ×20 (*754).

Neofusulinella Deprat, 1912, *585, p. 1549 [**N.

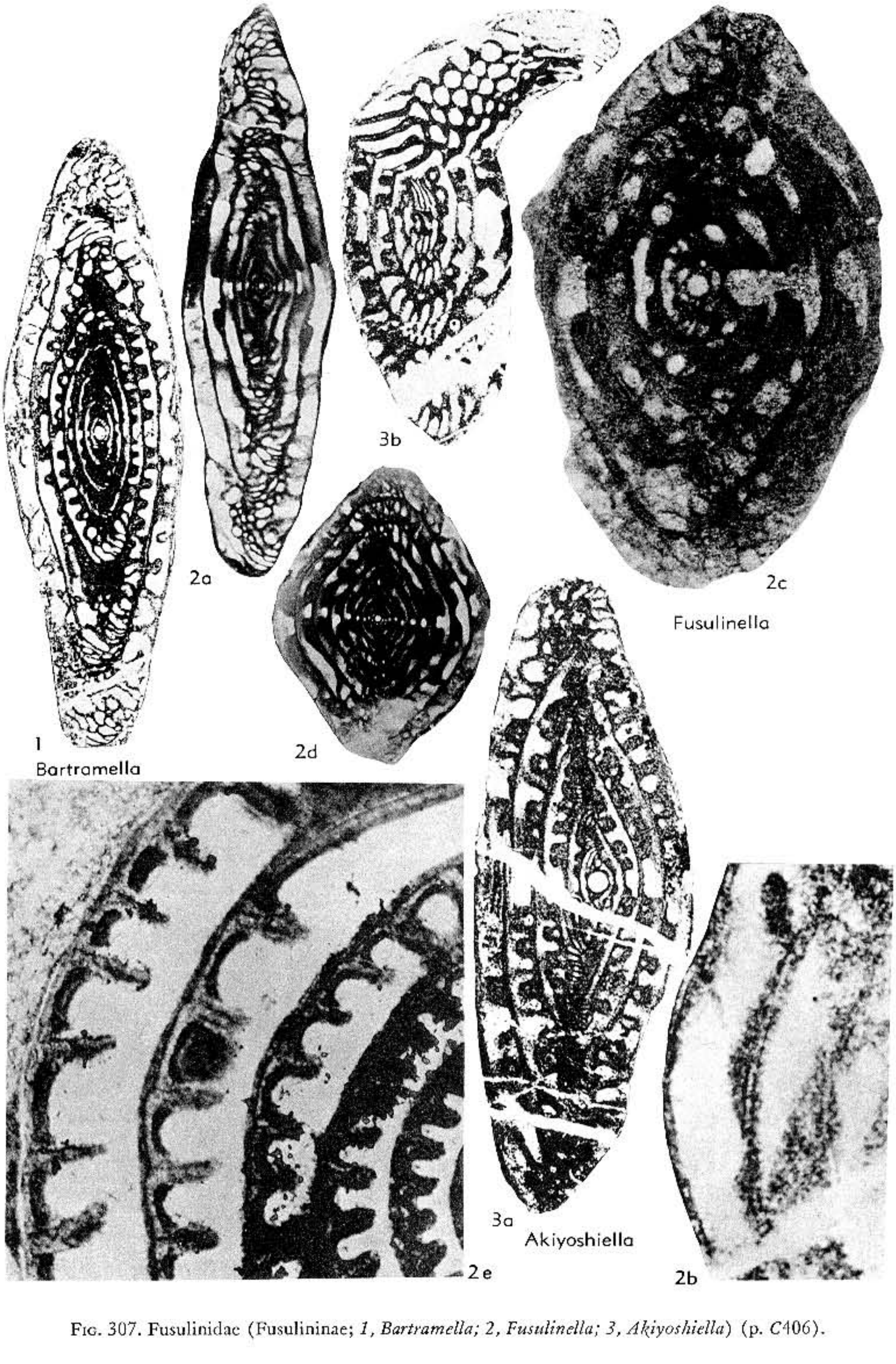


Fig. 307. Fusulinidae (Fusulininae; *1, Bartramella; 2, Fusulinella; 3, Akiyoshiella*) (p. C406).

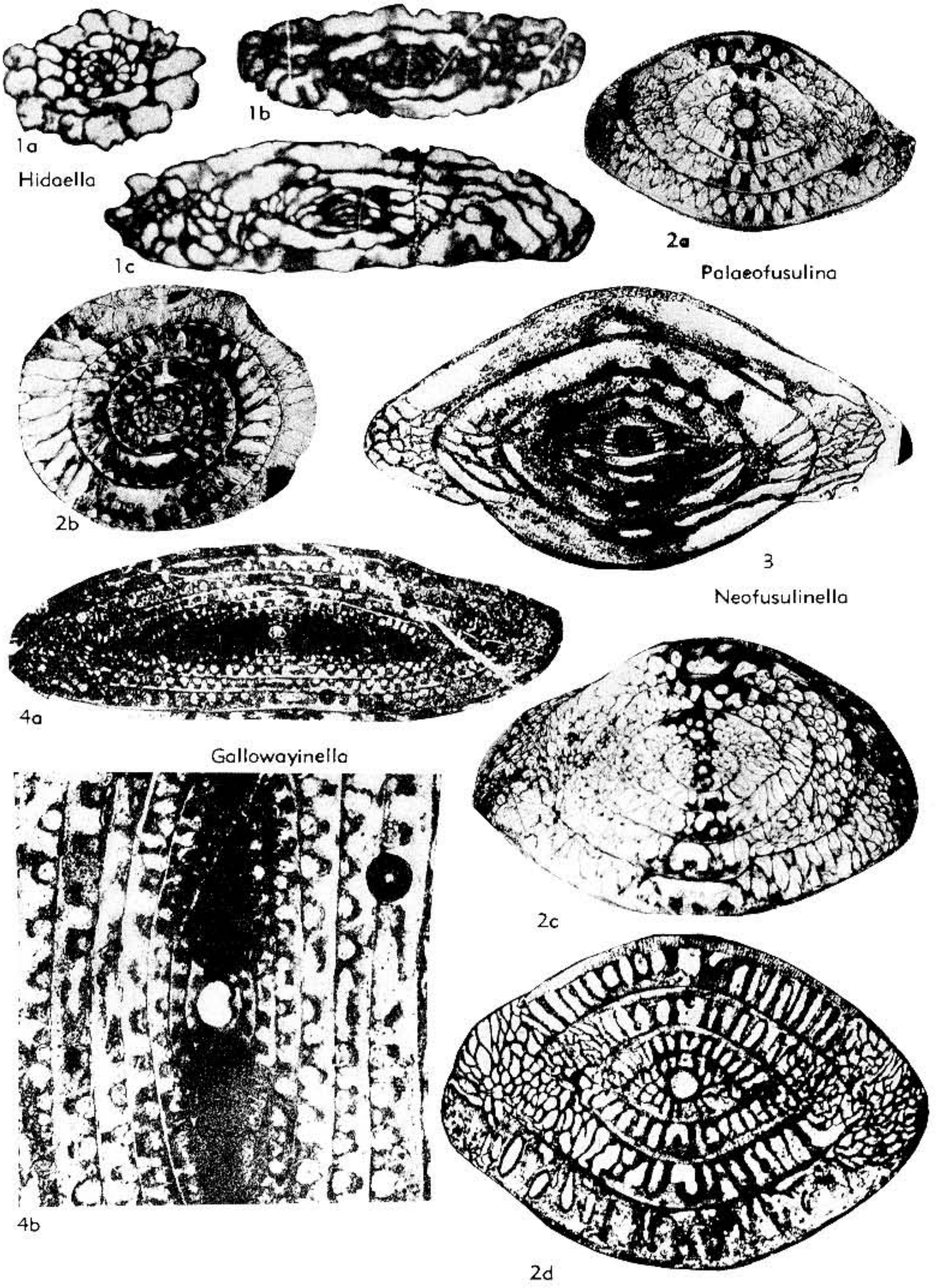


Fig. 308. Fusulinidae (Fusulininae; *1, Hidaella; 2, Palaeofusulina; 3, Neofusulinella; 4, Gallowayinella* (p. *C*406-*C*409).

lantenoisi Deprat, 1913, *586, p. 90); OD (M)] [*non N. praecursor* Deprat, 1913 (SD Galloway & Ryniker, 1930, *765, p. 23)]. Shell small, planispiral throughout, inflated-fusiform, early volutions discoidal; spirotheca composed of tectum and lower transparent layer without obvious alveoli; septa fluted in end zones; chomata narrow to massive (*765, *1910, *1922, *1929, *1934). *U.Perm.*, "Fr. Indochina"-China-Japan.——Fig. 308,*3*. *N. lantenoisi* Deprat, Laos; tang. sec. of holotype, ×20 (1922).

[When Deprat (1912, *585, p. 1549) proposed the name *Neofusulinella* he stated that it was for a form from the Permian limestones at Bam-Na-Mat, between Sam-Neua and Luang-Prabang, writing as follows: "*Neofusulinella.* J'ai trouvé dans les calcaires rapportés de Bam-Na-Mat (entre Sam-Neua et Luang-Prabang), par M. Mansuy, un autre Fusulinidé constituant indiscutablement un genre nouveau. . . . Malgré le grande nombre de caractères génériques qui la rapprochent de *Fusulinella,* l'allongement oblige à faire de cette forme un genre nouveau auquel convient l'appellation de *Neofusulinella.* . . ."——¶Thus it is clear that *Neofusulinella* was proposed for a described but unnamed form from the Permian limestones of Laos. It then became our problem to decide what this form was called when given a formal specific name. No mention was made by Deprat in 1912 of specimens from Indochina which he described in 1913 (*586, p. 40-44) as *Neofusulinella praecursor* and *N. schwagerinoides.* Deprat's 1913 paper contains the following: "*Neofusulinella* nov. gen. J'ai signalé il y a quelque temps un nouveau genre de Fusulinidée dans les calcaires rapportés de Ban-Na-Mat, entre Sam-neua et Luang-Prabang (Laos) par mon ami et collègue M. Mansuy. Depuis j'ai découvert deux autres espèces, l'une dans les calcaires rapportés du Tran-ninh, au N. de Xieng-khouang, par notre collaborateur le lieutenant Roux, l'autre des calcaires du Cammon, recueillis par le Commandant Dussault dans des conditions très bonnes au point de vue de la situation stratigraphique. . . . Je décrirai maintenant les trois espèces de mon nouveau genre. . . . *Neofusulinella praecursor* n. sp. se trouve à la base du Moscovien. . . . *Neofusulinella lantenoisi* n. sp. . . . se trouve dans un calcaire clair de Ban-Na-Mat (Laos) recueilli par M. Mansuy. . . . *Neofusulinella schwagerinoides* n. sp. est la seule espèce représentée dans un niveau moscovien des calcaires du Cammon. . . ."——The selection of the type-species of *Neofusulinella* must be governed by the International Rules of Zoological Nomenclature in effect in 1912. Article 30,I of these Rules reads: "Cases in which the generic type is accepted *solely* upon the basis of the original publication." Case c, Article 30,I states "A genus proposed with a single original species takes that species as its type. (Monotypical genera.)" The Rules do not state that the form must be a nominal species. The species for which Deprat proposed *Neofusulinella* was redescribed and named in 1913 as *N. lantenoisi* Deprat (*586, p. 90). Galloway & Ryniker in 1930 (*765, p. 23) designated *Neofusulinella praecursor* as the type-species of *Neofusulinella.* In order for *Neofusulinella praecursor* to be designated as a substitute for *N. lantenoisi,* plenary action would be required by the ICZN, and no such action has been requested.] [Note by R. C. Moore.—One cannot disagree with Thompson's statement of the record concerning *Neofusulinella* as just given or with his conclusion that Deprat actually based his recognition and initial description of this genus on the species later named *N. lantenoisi.* Even so, all this is irrelevant in applying the explicit stipulations given in Article 69(a)(ii)(3) of the Zoological Code (1961): Prior to 1931, "If an author established a nominal genus but did not designate or indicate its type-species, any zoologist may subsequently designate as the type-species one of the originally included nominal species, or, if there were no original nominal species, one of those first subsequently referred to the genus. . . . If no nominal species were included at the time the genus was established, the nominal species-group taxa that were first subsequently and expressly referred to it are to be treated as the only originally included species. . . . If two or more nominal species were simultaneously referred to a nominal genus, all are equally eligible for subsequent type-designation." Thus, in the case of *Neofusulinella* "the only originally included species" are *N. praecursor, N. lantenoisi,* and *N. schwagerinoides* and each of them is equally eligible for designation as the type-species by a first subsequent reviser. It happens that Galloway & Ryniker in 1930 (*765, p. 23) selected *N. praecursor,* thereby fixing the type-species in manner that is alterable only by ICZN using its plenary powers. Thompson has declined to accept advice that the Rules must be followed in this way, holding the view (quite untenable in my opinion) that *Neofusulinella* is a monotypic genus based on a species unnamed in Deprat's original publication but found to be one of three species described and named by this author in 1913. It is unnecessary to challenge Thompson's curious interpretation of Article 30 of old rules because the XV International Congress of Zoology (London, 1958) abrogated all such old rules when, in adopting the new Code, it included the regulation "This Code comes into force on the day of its publication (6 November 1961) and all previous editions of the International Rules of Zoological Nomenclature are thereby superseded" (Art. 84). Accordingly, the type-species of *Neofusulinella* and the mode of its fixation are incorrectly given by Thompson as printed above; the correct citation should read "*N. praecursor* Deprat, 1913, *586, p. 40; SD Galloway & Ryniker, 1930, *765, p. 23."]

Neostaffella A. D. Miklukho-Maklay, 1959, *1270, p. 630 [**Melonia (Borelis) sphaeroidea* Ehrenberg, 1842, *669A, p. 274; OD]. Shell spherical to subspherical, polar areas flush to deeply umbilicate; chomata distinct, septa totally unfluted, axis of coiling of most volutions almost parallel (*1270). [Miklukho-Maklay in the original diagnosis pointed out that all known species of *Neostaffella* were approximately twice as large as most forms of *Pseudostaffella,* some of which we now recognize as belonging to *Neostaffella.* The chief feature of *Neostaffella* is its 4-layered spirotheca, which has a diaphanotheca below the tectum from the 3rd volution to maturity.] *U.Carb.(M.Penn.-U.Penn.),* Eu.-Asia-N. Am.——Fig. 311,*2a*. *N. paradoxa* (Dutkevitch), Myachkovo Horizon, USSR(Polazna); axial sec., ×20 (*1509A).——Fig. 311,*2b*. *N. ozawai compacta* (Manukalova), Podolsk Horizon, USSR (Nytva); axial sec., ×20 (*1509A).——Fig. 311,*2c*. **N. sphaeroidea* (Ehrenberg), Podolsk Horizon, USSR(Andreyev Gorge); axial sec., ×20 (*1509A).

Palaeofusulina Deprat, 1912, *585, p. 1548 [**P. prisca* Deprat, 1913, *586, p. 37 (=*Fusulina pseudo-prisca* Colani, 1924, *354, p. 79); SD (SM)]. Shell small, inflated-subcylindrical to fusiform; spirotheca consisting of single dense layer; septa narrowly and highly fluted throughout (*354, *585, *586, *1137, *1728, *1922). *Perm.,* Asia(Caucasia-"French Indochina"-China)-Japan-Malay Arch. (Timor).——Fig. 308,*2*. **P. pseudo-prisca* (Colani), "French Indochina"(Lang-nac); *2a,* centered axial sec., ×20; *2b,* sagittal sec., ×20; *2c,* axial sec. tangent to proloculus, ×20 (*354); *2d,* axial sec. of holotype of *P. pseudo-prisca* (Colani), seemingly retouched, ×25 (*1922).

Plectofusulina Stewart, 1958, *1839, p. 1056 [**P. franklinensis*; OD]. Shell minute, short, ellipsoidal, inflated, mature shell with about 4 volutions; spirotheca composed of tectum and diaphanotheca with upper and lower tectoria; proloculus large; septa strongly sinuous, chambers inflated; chomata massive (*1839). *M.Penn.,* N. Am.(USA).——Fig. 309,*1*. **P. franklinensis,* Bishops Cap Ls., Tex.; *1a,* axial sec. of holotype, ×70; *1b,* sagittal sec. of paratype, ×70; *1c,* part of sagittal sec. showing structure of spirotheca, ×600 (*1839).

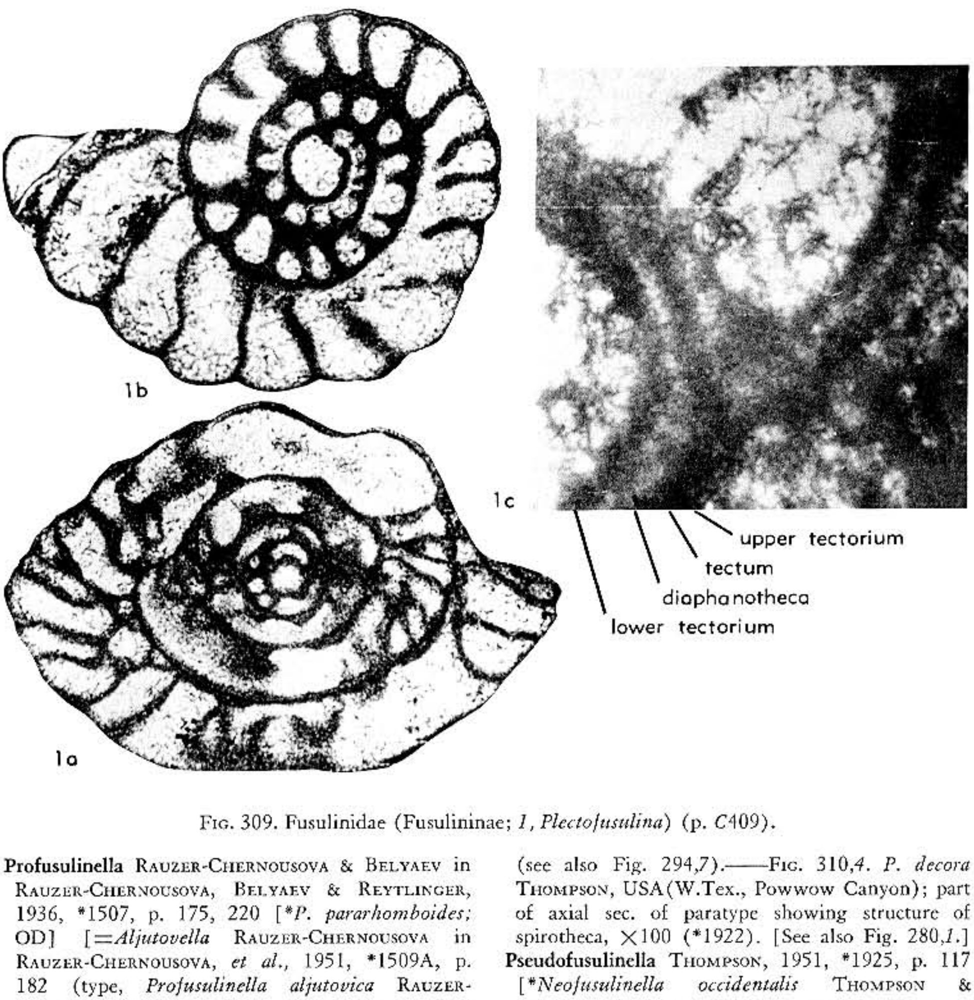


FIG. 309. Fusulinidae (Fusulininae; *1, Plectofusulina*) (p. C409).

Profusulinella Rauzer-Chernousova & Belyaev in Rauzer-Chernousova, Belyaev & Reytlinger, 1936, *1507, p. 175, 220 [_*P. pararhomboides;_ OD] [=_Aljutovella_ Rauzer-Chernousova in Rauzer-Chernousova, *et al.*, 1951, *1509A, p. 182 (type, *Profusulinella aljutovica* Rauzer-Chernousova, 1938, *1501, p. 97; OD]. Shell fusiform or ellipsoidal, early volutions asymmetrical in some, symmetrical throughout in most; spirotheca composed of tectum with upper and lower tectoria; septa fluted in polar regions (*1501, *1507, *1922). *U.Carb.(M.Penn.),* N. Am.-S. Am. (Peru)-USSR-China-Japan. —— FIG. 310,*1. P. aljutovica* Rauzer-Chernousova, Vereia Horizon, USSR(Samara Bend, Volga River); *1a,b,* axial secs. of paratype and holotype, ×30 (*1501); *1c,* part of axial sec. showing structure of spirotheca, ×100; *1d,* thin section of limestone containing several sections of *P. aljutovica* associated with forms of *Pseudostaffella* and *Millerella* (not shown), depth of 515.9-518.65 meters, well no. 402, Samara Bend, USSR, ×20 (*1922).—FIG. 310,2. _*P. pararhomboides,_ Moscov., USSR(N. Urals); axial sec. of holotype, ×50 (*1922).—— FIG. 310,*3. P. regia* Thompson, USA(W.Tex., Powwow Canyon); part of sagittal sec. of paratype showing spirothecal structure, ×100 (*1922) (see also Fig. 294,*7*).——FIG. 310,*4. P. decora* Thompson, USA(W.Tex., Powwow Canyon); part of axial sec. of paratype showing structure of spirotheca, ×100 (*1922). [See also Fig. 280,*1*.]

Pseudofusulinella Thompson, 1951, *1925, p. 117 [_*Neofusulinella occidentalis_ Thompson & Wheeler in Thompson, Wheeler & Hazzard, 1946, *1934, p. 25; OD]. Shell inflated-fusiform, volutions expanding uniformly from small proloculus; spirotheca composed of upper layer, tectum, and thin lower porous layer; septa closely spaced and fluted in polar ends of shell; axial fillings throughout shell, becoming thin in last few volutions; chomata massive, asymmetrical, with steep tunnel sides and low lateral slopes (*1925). *U. Carb.(U. Penn.)-L. Perm.,* N.Am.-Japan.——FIG. 311,*4a-c.* _*P. occidentalis_ (Thompson & Wheeler), L.Perm.(McCloud Ls.), USA (Calif.); *4a,* axial sec. of holotype, ×20; *4b,* sagittal sec. of paratype, ×20; *4c,* tang. sec. of paratype with fluted septa in polar regions, ×20 (*1926).——FIG. 311,*4d. P. utahensis* Thompson & Bissell, L.Perm.(Oquirrh F.), USA(Utah); axial sec. of holotype, ×20 (*1926).

Pseudostaffella Thompson, 1942, *1919, p. 407 [_*P. needhami;_ OD]. Shell spherical, umbilicate, early volutions of most species asymmetrical to

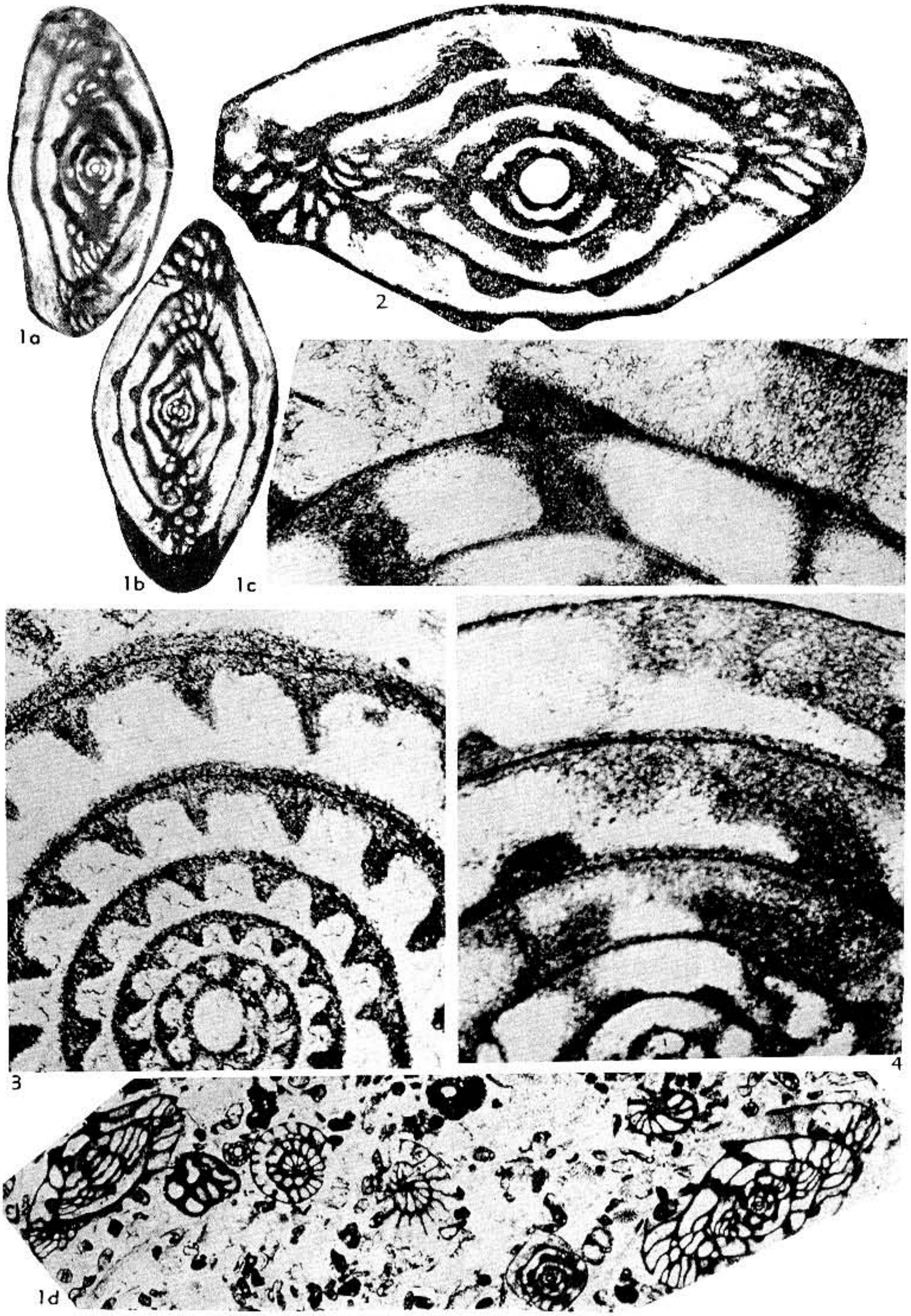


Fig. 310. Fusulinidae (Fusulininae; *1-4, Profusulinella*) (p. *C*409-*C*410).

outer ones but symmetrical in some forms; spirotheca composed of tectum with upper and lower tectoria, or, in advanced forms, of tectum and diaphanotheca with upper and lower tectoria; septa unfluted; chomata massive, large (*1919, *1928). _U.Carb.(M.Penn.),_ N.Am.-S.Am.-Eu.-Asia.——Fig. 311,_3a-c_. *_P. needhami,_ Cuchillo Negro F., USA(N.Mex.); _3a,b,_ axial secs. of paratypes, ×50; _3c,_ axial sec. of holotype, ×50 (*1922).

Pseudowedekindellina Sheng, 1958, *1729, p. 87 [*_P. prolixa_; OD] [=_Frumentella_ Stewart, 1958, *1839, p. 1055 (type, _F. exampla_; OD)]. Shell small, highly elongate-fusiform, composed of 4 or 5 volutions at maturity with form ratio of shell up to 5.0; with slightly convex lateral slopes, sharply pointed polar ends, and straight to slightly irregular axis of coiling; spirotheca composed of 3 layers comprising tectum with upper and lower tectoria; septa closely fluted at very base, plane in middle and upper part; axial fillings rather heavy throughout length of shell; chomata prominent, highly asymmetrical, broad (*1729, *1839). _U.Carb.(M.Penn.),_ Asia(China)-USA.——Fig. 311,_1a,b_. _P. exampla_ (Stewart), Bishops Cap Ls., USA(Tex.); _1a,b,_ axial secs. of holotype and paratype, ×70 (*1839).——Fig. 311,_1c,d_. *_P. prolixa,_ Penchi Ser.(Hsiaoshih Ls.), China; _1c,d,_ axial sec. of holotype and enlarged part, ×20, ×100 (*1729) (see also Fig 279,_1_).

Quasifusulina Chen, 1934, *332, p. 91 [*_Fusulina longissima_ von Möller, 1878, *1295, p. 59; OD] [=_Epifusulina_ Chen, 1936 (_fide_ Grabau, 1936, *809A, p. 21, footnote) (obj.)]. Shell elongate, irregularly subcylindrical; wall composed of tectum and diaphanotheca; septa intensely fluted throughout length, axial fillings heavy, cuniculi possibly present in some forms (*332). _U.Carb.(U.Penn.)-L.Perm.,_ Eu.-Asia-Can.(B.C.).——Fig. 279,_2_. *_Q. longissima_ (von Möller), U.Carb. (C_3), USSR(Tsarev Kurgan); axial sec. of holotype, ×10.5 (*1922).

Taitzehoella Sheng, 1951, *1727, p. 79 [*_T. taitzehoensis_; OD]. Shell small, caltrop-like in shape at maturity, median part highly inflated, lateral slopes concave, poles sharp to bluntly pointed, coiling divisible into early stage with short axis and endothyroid arrangement, and later stage with straight axis of coiling oriented differently from early stage; spirotheca thin, composed of 2 layers of tectum and lower less dense layer; septa straight, axial fillings slight but present throughout entire shell; tunnel quadrate in cross section, chomata asymmetrical, high (*1727). _U.Carb.(Moscov.),_ China-Greenl.——Fig 312,_3_. *_T. taitzehoensis,_ Penchi Ser.; _3a,_ axial sec. of holotype, ×25; _3b,_ oblique sec. of paratype, ×35 (*1727).

Verella Dalmatskaya, 1951, *551, p. 194 [*_V. warsanofievie;_ OD]. Shell minute, highly elongate-fusiform, axis of coiling arcuate to straight with as many as 4 volutions; proloculus large; spirotheca thin, composed of tectum and distinct protheca, layers poorly differentiated; septa fluted at base in outer volutions, axial fillings distinct in all volutions except in outer part of last volution; tunnel singular, chomata asymmetrical and distinct (*551). _U.Carb.,_ USSR.——Fig. 312,_4a_. *_V. warsanofievie,_ Kaial Stage, Penza Oblast (Kikina); axial sec. of holotype showing fluting at base of septa, ×30 (*551).——Fig. 312,_4b_. _V. spicata_ Dalmatskaya, Kaial Stage, Penza Oblast(Kikina); axial sec. of holotype, ×30 (*551).

Waeringella Thompson, 1942, *1919, p. 413 [*_W. spiveyi_; OD]. Shell minute, elongate-fusiform, with inflated central area; spirotheca composed of tectum with upper and lower layers; septa fluted in polar regions, axial fillings heavy (*1919, *1931). _U.Penn.,_ USA(Tex.-Utah).——Fig. 312, _1_. *_W. spiveyi,_ Salem School Ls., Tex.; _1a,_ ext. view of paratype, ×10; _1b,_ sagittal sec. of paratype, ×20; _1c,d,_ axial sec. of holotype and part enlarged to show 3 layers of spirotheca, ×20, ×100 (*1922) (see also Fig. 274,_3_).

Wedekindellina Dunbar & Henbest in Cushman, 1933, *461, p. 134 [_nom. subst. pro Wedekindia_ Dunbar & Henbest, 1931 (_non_ Schindewolf, 1925)] [*_Fusulinella euthysepta_ Henbest, 1928, *893A, p. 80; OD] [=_Wedekindella_ Dunbar & Henbest, 1930, *641, p. 362 (obj.) (_non_ Schindewolf, 1928); _Wedekindia_ Dunbar & Henbest, 1931, *642, p. 458 (_nom. subst. pro Wedekindella_ Dunbar & Henbest, 1930) (obj.) (_non_ Schindewolf, 1928); _Parawedekindellina_ Safonova in Rauzer-Chernousova _et al._, 1951, *1509A, p. 240 (type, _P. kamensis_; OD)]. Shell highly elongate-fusiform, axis of coiling straight, polar ends sharply pointed; spirotheca composed of tectum and diaphanotheca with upper and lower tectoria; septa unfluted, axial fillings massive throughout shell except for last part of last volution; chomata massive and broad (*641, *642, *643, *1610, *1922). _U.Carb.(M.Penn.-U.Penn.),_ N.Am(USA-Can.-Greenl.) - USSR - Japan-?China.——Fig. 312,_2a,b_. _W. kamensis_ (Safonova), Podolsk Horizon, USSR(Polazna); _2a,_ axial sec. of holotype, ×20; _2b,_ typical specimen from Myachkovo beds at Levshino, ×20 (*1509A).——Fig. 312,_2c_. _W. matura_ Thompson, M.Penn. Youghall F.), USA(Utah); axial sec. of holotype, ×20 (*1922).——Fig. 312,_2d,e_. *_W. euthysepta_ (Henbest), M.Penn.(Stonefort Ls.), USA(Ill.); _2d,e,_ axial sec. of holotype and part showing wall pore at _p,_ ×40, ×250 (*1922) (see also Fig. 275,_3_).

Yangchienia Lee, 1933[1934], *1120, p. 14 [*_Y. iniqua_; OD] [=_Jangchienia_ A. D. Miklukho-Maklay, 1953, *1263, p. 21 (_nom. van._)]. Shell small, inflated-fusiform, inner 3 or 4 volutions discoidal, with asymmetrical to fusiform outer volutions; spirotheca consisting of tectum and diaphanotheca with thick lower and upper tec-

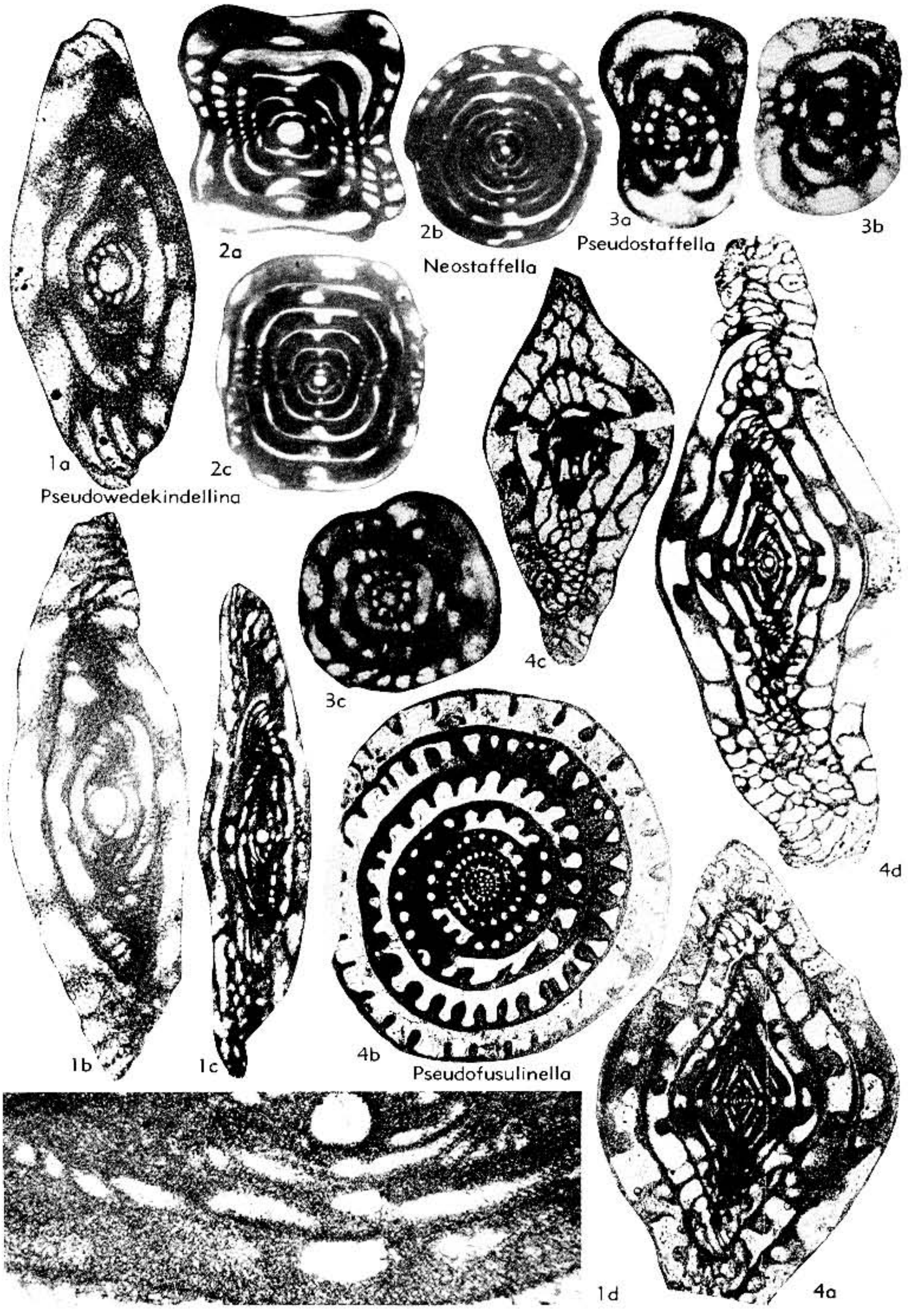


Fig. 311. Fusulinidae (Fusulininae; *1, Pseudowedekindellina, 2, Neostaffella, 3, Pseudostaffella; 4, Pseudofusulinella*) (p. C409-C412).

toria; septa unfluted; chomata massive, extending almost to polar ends (*1269, *1911, *1922). *U.Perm.(Verbeekina Z.)*, Eu.(Sicily-Greece) - Asia (China-AsiaM.-Afghan.).——FIG. 313,*1*. **Y. iniqua*, Chihsia Ls., China(E. of Chusanshan); *1a*, axial sec. of holotype, ×40; *1b*, tang. sec. of paratype, ×40 (*1922).——FIG. 313,*2*. *Y. haydeni* THOMPSON, U.Perm.(Bamian Ls.), Afghan.; *2a*, axial sec. of holotype, ×20; *2b*, enlargement of *2a* showing chomata structure, ×100 (*1922).

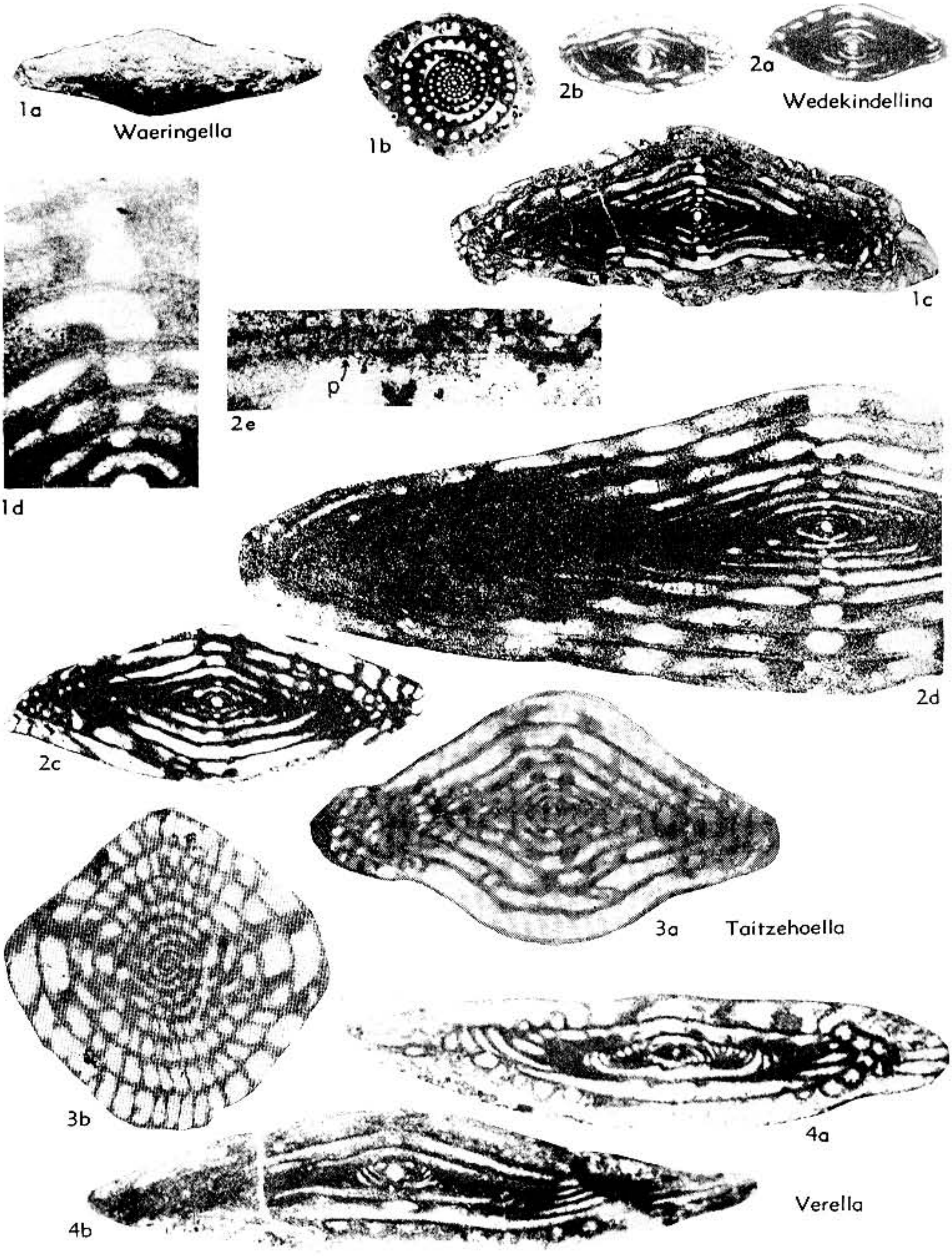


FIG. 312. Fusulinidae (Fusulininae; *1, Waeringella; 2, Wedekindellina; 3, Taitzehoella; 4, Verella*) (p. *C*412).

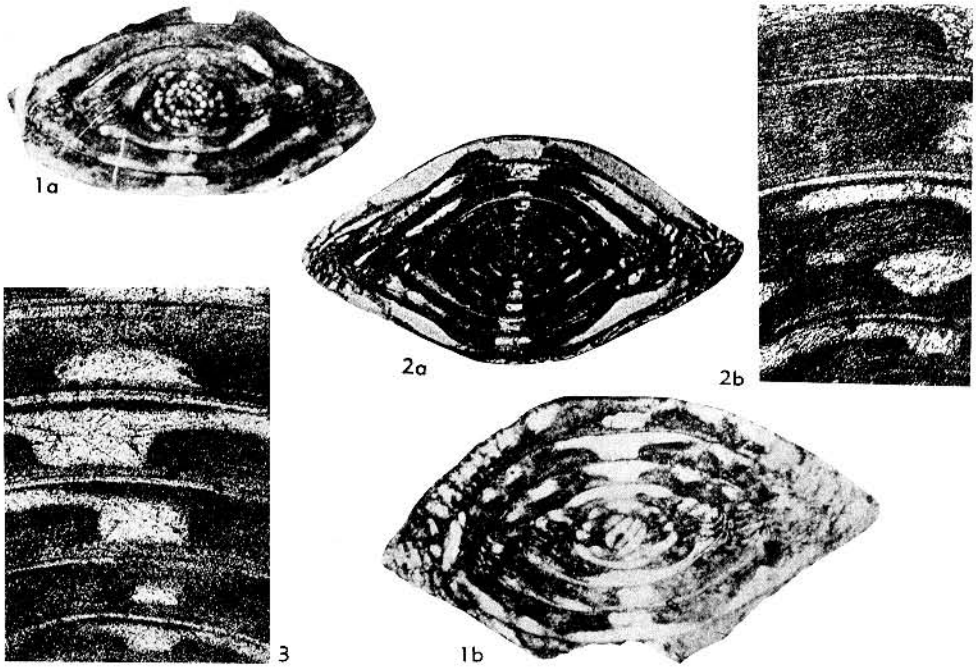


Fig. 313. Fusulinidae (Fusulininae; *1-3, Yangchienia*) (p. *C*412-*C*414).

——Fig. 313,*3*. *Y. tobleri* Thompson, U.Perm. (Sosio Beds), Sicily (Castellamare del Golpo); part of axial sec. showing structure of spirotheca, ×100 (*1922) (see also Fig. 275,*2*).

Subfamily SCHWAGERININAE
Dunbar & Henbest, 1930

[*nom. transl.* Yabe & Hanzawa, 1932, p. 42 (*ex* family Schwagerinidae Dunbar & Henbest, 1930)] [=Pseudofusulininae Dutkevich, 1934, p. 53; =Polydiexodininae A. D. Miklukho-Maklay, 1953, p. 21]

Shell large, fusiform to irregularly cylindrical, planispiral, involute in most, irregularly uncoiled in some; spirotheca thick, composed of tectum and alveolar keriotheca; septa fluted in end zones of primitive genera, fluted completely across shell and to tops of chambers of more advanced genera; tunnel singular in most forms or multiple in one genus, axial fillings absent to massive; chomata massive to slight (*641, *1295). *U.Carb.(M.Penn.)-U.Perm.*

Schwagerina von Möller, 1877, *1294, p. 143 [**Borelis princeps* Ehrenberg, 1842, *669A, p. 274; OD (M)] [=*Chusenella* Lee, 1942, *1120A, p. 171 *(nom. nud.)*; *Chusenella* Hsu, 1942, *973, p. 175 (type, *C. ishanensis*); *Triticites (Jigulites)* Rozovskaya, 1948, *1590, p. 1638 (type, *Triticites jigulensis* Rauzer-Chernousova, 1938, *1501, p. 120, 157; OD); *Daixina* Rozovskaya, 1949, *1591, p. 252 (type, *D. ruzhencevi*; OD); *Triticites (Rauserites)* Rozovskaya, 1948, *1590, p. 1637 *(nom. nud.)*; *T. (Rauserites)* Rozovskaya, 1950, *1591A, p. 30 (type, *Triticites stuckenbergi* Rauzer-Chernousova, 1938, *1501, p. 110, 155); *Codonoschwagerina* Viên, 1959, *2005A, p. 111 (type, *C. thuanae*; OD)]. Shell fusiform to subcylindrical; spirotheca thick and composed of tectum and alveolar keriotheca; septa fluted throughout length of shell, fluting intense to tops of septa in some, only in lower parts of septa of others, axial fillings highly variable; chomata distinct or thin and discontinuous (*645, *973, *1294, *1591). *Perm.*, Eu. - Asia - N. Afr.-N.Am.-C.Am.-S.Am.——Fig. 314,*1*. *S. fax* Thompson & Wheeler, L.Perm. (McCloud Ls.), USA (Calif.); *1a*, tang. sec. of syntype showing septal fluting, ×10; *1b*, centered axial sec. of syntype, ×10 (*1922) (see also Fig. 276,*3*).——Fig. 314,*2*. **S. princeps* (Ehrenberg), L.Perm. (Mountain Ls.), USSR (Pinega Archangel); *2a*, sagittal sec. of paratype, ×10; *2b*, axial sec. of holotype, ×10; *2c*, etched surface of paratype showing fluting of septa across specimen, ×10 (*1922).——Fig. 314,*3*. *S. jigulensis* (Rauzer-Chernousova), L.Perm., USSR (Samara Bend); axial sec. of holotype, ×15 (*1926).——Fig. 314,*4*. *S. ruzhencevi* (Rozovskaya), C_3^{1-e} Horizon, USSR (Ural River); axial sec. of holotype, ×9 (*1926).——Fig. 314,*5*. *S. gruperaensis* Thomp-

SON & MILLER, L.Perm.(Grupera F.), Mex. (Chiapas); axial sec. of syntype, ×10 (*1922).——FIG. 314,*6*. *S. ishanensis* (HSU), Chungkuh Ls., China(Kuangsi); axial sec. of holotype, ×10 (*1922).——FIG. 328A,*3*. *S. stuckenbergi* (RAUZER-CHERNOUSOVA), Horizon I_1, U.Carb., USSR (Shiryayevo, Samara Bend) (type-sp. of *Rauserites*); axial sec. of holotype, ×15 (*1501).——

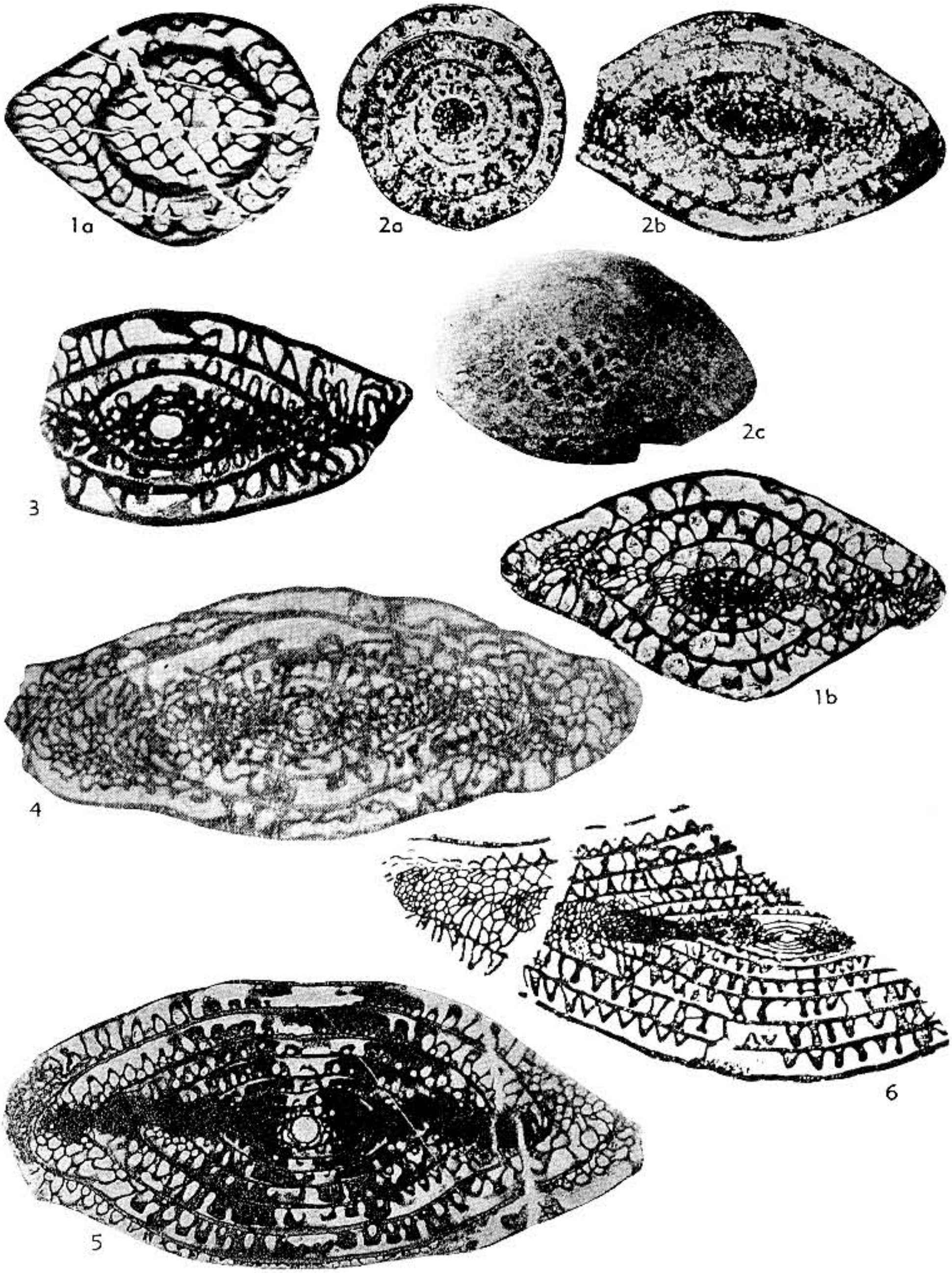


FIG. 314. Fusulinidae (Schwagerininae; *1-6, Schwagerina*) (p. C415-C416).

FIG. 328A,*4*. *S. thuanae* (VIÊN), Perm., Asia(S. Vietnam) (type-sp. of *Codonoschwagerina*); sec. cut through proloculus, ×5 (*2005A). [See also Fig. 277,*1,3*; 280,*6*; 281.]

Acervoschwagerina HANZAWA, 1949, *871, p. 207 [**Paraschwagerina (Acervoschwagerina) endoi*; OD]. Shell large, elongate-fusiform, surface broadly irregular, with 5 or 6 volutions, first 2 or 3 tightly coiled with elongate axis, outer volutions greatly inflated; spirotheca thin, with structure as in *Schwagerina*; septa broadly and irregularly fluted throughout length and height, flut-

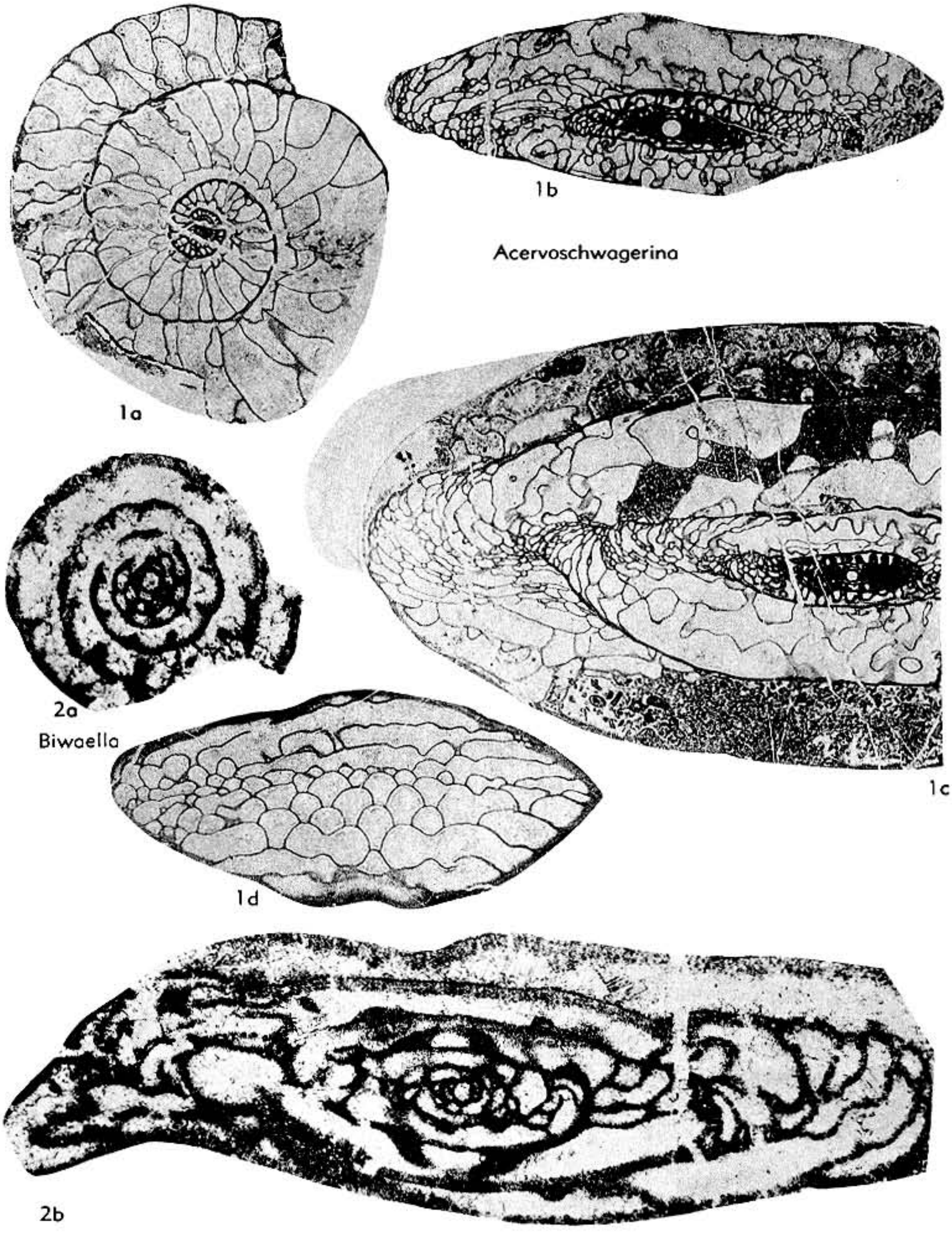


FIG. 315. Fusulinidae (Schwagerininae; *1, Acervoschwagerina; 2, Biwaella*) (p. C417-C418).

ing in broad irregular contortions, with irregular spacing and without uniform patterns; tunnel singular, enclosed in irregular phrenotheca, bordered by asymmetrical chomata in tightly coiled early part of shell (*871, *1926). *L.Perm.*, Japan.——Fig. 315,*1*. **A.* *endoi* (Hanzawa), Gombo Ls., Gifu Pref.; *1a*, sagittal sec. of topotype showing phrenotheca over tunnel, ×10; *1b*, axial sec. of submature topotype, ×10; *1c*, axial sec. of mature topotype, ×10; *1d*, tang. sec. of topotype showing irregular fluting of septa, ×10 (*1926).

Biwaella Morikawa & Isomi, 1960, *1313, p. 301 [**B. omiensis*, OD]. Shell minute, elongate-fusiform, lateral slopes broadly convex, external furrows distinct, more broadly spaced than in most other fusulinids of similar size; axis of coiling straight to irregularly arcuate, first 1 or 2 volutions evolute and coiled at right angles to outer fusiform volutions, shell becoming ellipsoidal at second to third volution and then fusiform, rapidly attaining mature shape; spirotheca thick, composed of tectum and thicker porous lower layer (?keriotheca); septa widely spaced, slightly fluted in polar regions; chomata distinct throughout fusiform part of shell, overhanging along sides of tunnel (*1313). *L.Perm.*, Japan.——Fig. 315, *2*. **B. omiensis*, Honshu Is.; *2a,b*, sagittal and axial secs. of paratype and holotype, ×50 (*1313).

Dunbarinella Thompson, 1942, *1919, p. 416 [**D. ervinensis*; OD]. Shell moderately large, fusiform, with pointed polar ends; spirotheca composed of tectum and keriotheca; septa highly fluted throughout length, higher in end zones than central region, axial fillings thick in all except last 1 or 2 volutions (*1919, *1926). *U.Carb. (U.Penn.)-L.Perm.*, N.Am.-S.Am. (Peru)-Asia (China-Karakorum)-Japan-Eu.——Fig. 316,*3a-c*. **D. ervinensis*, U.Penn.(Ervine Creek Sh.), USA (Okla.); *3a*, external view of paratype; *3b*, sagittal sec. of paratype; *3c*, axial sec. of holotype; all ×10 (*1922).——Fig. 316,*3d*. *D. eoextenta* Thompson, L.Perm.(Waldrip No. 1 Ls.), USA (Tex.); axial sec. of paratype, ×10 (*1926).——Fig. 316,*3e,f*. *D. tumida* (Skinner), L.Perm. (Neva Ls.), USA(Kans.); *3e,f*, axial and sagittal secs., ×10 (*1926).

Kansanella Thompson, 1957, *1927, p. 299 [**K. (Kansanella) joensis*; OD]. Shell large, inflated-fusiform to elongate-fusiform; wall of tectum and keriotheca; septa irregularly fluted throughout length and height, axial fillings throughout shell in elongate-fusiform species; chomata prominent in all species, massive throughout shell in inflated forms (*1927). *U.Penn.*, N.Am.

K. (Kansanella) Thompson, 1957, *1927, p. 303. Shell elongate, irregularly fusiform, axis of coiling irregular and shifting; spirotheca thin, composed of tectum and keriotheca; septa thin, closely spaced, fluted throughout their length and height, fluting irregularly spaced both vertically and horizontally, axial fillings throughout most of shell; chomata distinct, broad (*1927). *U.Penn.*, N.Am.——Fig. 316,*1*. **K. (K.) joensis*, Iatan Ls., USA (Mo.); *1a*, tang. sec. of paratype showing septal fluting, ×10; *1b*, axial sec. of holotype, ×20 (*1927).

K. (Iowanella) Thompson, 1957, *1927, p. 301 [**Triticites winterensis* Thompson, Verville & Lokke, 1956, *1932, p. 807; OD]. Shell large, inflated-fusiform; wall structure as in *Triticites*, except thin for shell size; septa irregularly fluted throughout length and to top of chamber; chomata massive, extending to poles in first 5 or 6 volutions (*1927, *1932). *U.Penn.*, N.Am.——Fig. 316,*2*. **K. (I.) winterensis* (Thompson, Verville & Lokke), Winterset Ls., USA (Iowa); *2a*, tang. sec. of paratype, ×10; *2b*, axial sec. of holotype, ×20 (*1927).

Kwantoella Sakagami & Omata, 1957, *1621, p. 251 [**K. fujimotoi*; OD]. Shell minute, elongate-subcylindrical to fusiform; coiling planispiral about large proloculus; composed of 5 or 6 volutions; spirotheca composed of tectum and keriotheca; septa plane in most of shell, fluting confined to end regions and base of septa, axial fillings thickest in extreme ends but more massive in 2nd to 5th volutions; chomata distinct (*1621). *L. Perm.*, Japan.——Fig. 317,*4*. **K. fujimotoi*, Shiraiwa Ls., Ome, Tokyo Pref.; *4a,c*, axial sec. of holotype and enlarged part, ×30, ×100; *4b*, sagittal sec. of paratype, ×30 (*1621).

Nagatoella Thompson, 1936, *1916, p. 196 [**Fusulina (Schellwienia) ellipsoidalis* var. *orientis* Ozawa, 1925; *1401A, p. 22; OD]. Shell ellipsoidal, polar ends rounded; spirotheca composed of tectum and thick keriotheca; septa fluted at base, axial fillings thick, widespread (*1013, *1916). *Perm.*, Japan.——Fig. 317,*3a*. **N. orientis* (Ozawa), Akiyoshi Ls., Yamaguchi Pref.; *3a*, axial sec. of holotype, ×10 (*1922).——Fig. 317,*3b,c*. *N. kobayashii* Thompson, Akiyoshi Ls., Yamaguchi Pref.; *3b*, tang. sec. of holotype, ×10 (*1916); *3c*, axial sec., ×10 (*1013).

Nipponitella Hanzawa, 1938, *868, p. 256 [**N. explicata*; OD]. Early shell fusiform, coiled like *Triticites*, gerontic stage irregularly and loosely uncoiled; spirothecal structure like that in *Triticites*; septa fluted at base across fusiform part, irregularly and highly fluted in uncoiled part, giving forward arcuate attitude in uncoiled part (*868). *Perm.*, NE.Japan.——Fig. 317,*1*. **N. explicata*, Maiya Gr., Rikuzen Prov.; *1a*, axial sec. of paratype; *1b,c*, tang. secs. of paratype and holotype; all ×10 (*1922) (see also Fig. 284,*1b*). [See Fig. 284,*1a*, *N. auricula*.]

Oketaella Thompson, 1951, *1925, p. 116 [**O. fryei*; OD]. Shell minute, inflated-ellipsoidal to fusiform; proloculus large, shell loosely coiled; spirotheca composed of tectum and alveolar keriotheca; tunnel singular, chomata distinct (*1925, *1926). *U.Penn.-L.Perm.*, N.Am.——Fig. 317,*2*. **O. fryei*, L.Perm.(Oketo Sh.), USA(Kans.); *2a*, axial sec. of holotype, ×50; *2b*, sagittal sec. of topotype, ×50 (*1926).

Orientoschwagerina A. D. MIKLUKHO-MAKLAY, 1955, *1264, p. 573 [*O. *abichi*; OD]. Shell large, inflated-fusiform, first few volutions tightly coiled, highly elongate, outer ones greatly inflated, last volution slightly more tightly coiled than those preceding; wall composed of three layers?,

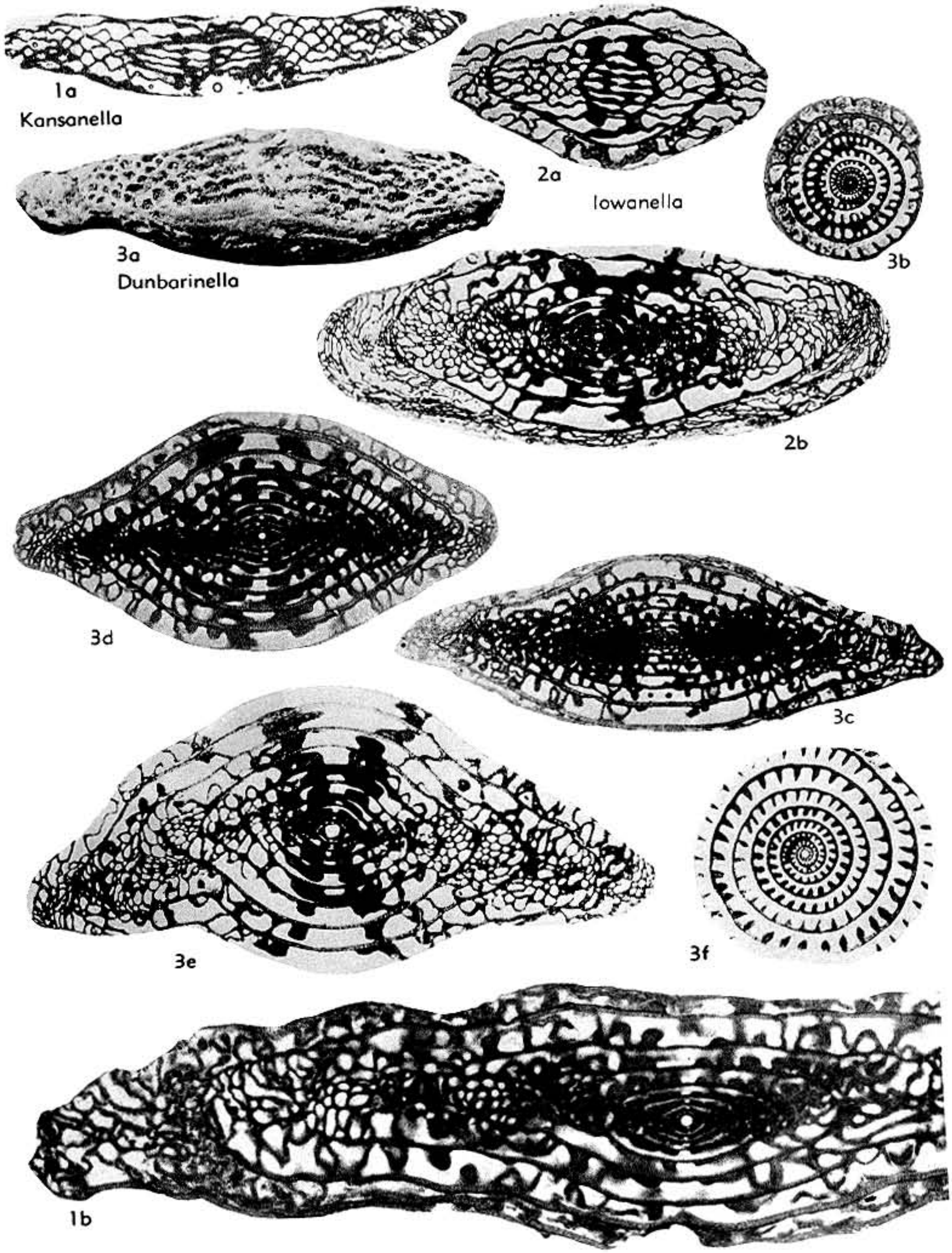


FIG. 316. Fusulinidae [Schwagerininae; *1, Kansanella (Kansanella); 2, K. (Iowanella); 3, Dunbarinella*] (p. C418).

spirotheca increasing in thickness only slightly during early, tightly coiled part of shell, becoming thinner in next 2 or 3 volutions, and then distinctly thicker in outer part of shell, keriotheca composed of upper and lower layers; septa closely spaced in tightly coiled inner part of shell, more widely spaced in outer volutions; chomata distinct in early part of shell, very faint and indistinct in outer inflated volutions (*1264). *Perm.*, USSR. ——FIG. 317,*5*. **O.* abichi*, Transcaucasia; *5a,b*, axial sec. of holotype and enlargement of internal part, X15, X40 (*1264).

Parafusulina DUNBAR & SKINNER, 1931, *644, p. 258 [**P. wordensis*; OD] [=*Monodiexodina* SOSNINA in KIPARISOVA *et al.*, 1956, *1040, p. 24 (type, *Schwagerina wanneri sutschanica* DUTKEVITCH in LIKHAREV, *et al.*, 1939, *1138, p. 39; OD); *P. (Eoparafusulina)* COOGAN, 1960, *381, p. 262 (type, *Fusulina gracilis* MEEK, 1862, *1257A, p. 4; OD); *P. (Skinnerella)* COOGAN, 1960, *381, p. 262 (type, *P. schucherti* DUNBAR & SKINNER, 1937, *646, p. 672; OD)]. Shell elongate, cylindrical to irregular in shape; spirotheca composed of tectum and alveolar keriotheca, abnormally thin for size of shell; septa intensely fluted, forming cuniculi; axial fillings heavy (*381, *644, *1816, *1922). *Perm.*, S.Am. (Peru-Colombia-Venez.)-C.Am.(Guatemala)-Mex.-USA-N.Can.-W.Can.-Malay Arch. (Indonesia- Malaya)-Japan-Asia(N.India-China).——FIG. 318,*1a*. *P. sutschanica* (DUTKEVITCH), Perm.(Doliolinovaya F.), USSR(Ussuriy Region); axial sec., approx. X6.8 (*1816).——FIG. 318,*1b*. *P. gracilis* (MEEK), L.Perm.(McCloud Ls.), USA(Calif.); axial sec., X10 (*1934) (see also Fig. 276,*1b*).——FIG. 318, *1c-e*. *P. nosonensis* THOMPSON & WHEELER, L. Perm.(Nosoni F.), USA(Calif.); *1c*, axial sec. of holotype; *1d*, sagittal sec. of paratype; *1e*, tang. sec. of paratype showing development of cuniculi; all X10 (*1922) (see also Fig. 275,*6a*, 276,*1a*, 287).——FIG. 318,*1f*. *P. schucherti* DUNBAR & SKINNER, L.Perm.(Bone Spring F.), USA(Tex.); axial sec. of lectotype, X10 (*646). [See also Fig. 275,*6b*, *P. wanneri*; 278, **P. wordensis*; 282,*1-6*.]

Paraschwagerina DUNBAR & SKINNER, 1936, *645, p. 89 [**Schwagerina gigantea* WHITE, 1932, *2056, p. 82; OD]. Shell inflated, fusiform, first 2 or 3 volutions tightly coiled and elongate-fusiform, outer volutions distinctly inflated-fusiform; spirothecal structure as in *Schwagerina*; septa highly fluted throughout (*645, *1926). *L.Perm.*, N.Am.-C.Am.-Asia.——FIG. 318,*2*. **P. gigantea* (WHITE), Wolfcamp. F., USA(Tex.); *2a*, axial sec. of holotype, X10 (*1922); *2b*, tang. sec., X10 (*1926) (see also Fig. 284,*2*).

Polydiexodina DUNBAR & SKINNER, 1931, *644, p. 263 [**P. capitanensis*; OD]. Shell highly elongate-subcylindrical; spirothecal structure as in *Parafusulina*; cuniculi throughout shell; multiple tunnels; axial fillings heavy (*644, *1921). *U. Perm.*, USA(Tex.-N.Mex.)-Mex.-Eu.(Greece-Turkey-Yugo.-Crimea)-Asia(Afghan.-Iran-Iraq-India)-USSR(Darvaz).——FIG. 319,*2a,b*. *P. afghanensis* THOMPSON, Bamian Ls., Afghan.; *2a*, tang. sec. of paratype showing numerous auxiliary tunnels, X10; *2b*, enlarged part of axial sec. showing structure of spirotheca, X100 (*1922) (see also Fig. 285,*1a*).——FIG. 319,*2c*. **P. capitanensis*, Capitan Ls., USA(Tex.); axial sec. of holotype, X10 (*1922) (see also Fig. 285,*1b*).

Pseudofusulina DUNBAR & SKINNER, 1931, *644, p. 252 [**P. huecoensis*; OD] [=*Grabauina* LEE, 1924, *1118, p. 51 (type, *G. disca*; OD); *Leeina* GALLOWAY, 1933, *762, p. 406 (type, *Fusulina vulgaris fusiformis* SCHELLWIEN in DYHRENFURTH, 1909, *650A, p. 165; OD)]. Shell fusiform, large, loosely coiled throughout; spirotheca thick, with structure like *Schwagerina*; septa broadly but highly fluted, axial fillings light in some, absent in most, phrenothecae abundant (*644, *762, *1118, *1922). *L.Perm.*, N.Am.-S.Am.-C.Am.-Eu.-Asia-Japan-Asia Minor.——FIG. 319,*1a*. **P. huecoensis*, Hueco Ls., USA(Tex.); tang. sec. of paratype, approx. X10 (*1922) (see also Fig. 291,*2*, holotype).——FIG. 319,*1b*. *P.? disca* (LEE), Taiyuan Ser., China; axial sec. of holotype, X30 (*1922).——FIG. 319,*1c*. *P. vulgaris fusiformis* (SCHELLWIEN), USSR(Darvaz Ser.); axial sec. of holotype, X15 (*1922). [See also Fig. 291,*1*, *P. nelsoni*.]

Pseudoschwagerina DUNBAR & SKINNER, 1936, *645, p. 89 [**Schwagerina uddeni* BEEDE & KNIKER, 1924, *105, p. 27; OD] [=*Occidentoschwagerina* A. D. MIKLUKHO-MAKLAY, 1959, *1271, p. 166 (type *Schwagerina fusulinoides* SCHELLWIEN, 1898, *1644, p. 259; OD); *Parazellia* RAUZER-CHERNOUSOVA, 1961, *1506, p. 9 (type, *Fusulina muongthensis* DEPRAT, 1915, *587A, p. 5; OD)]. Shell inflated-fusiform, first 2 or 3 volutions tightly coiled, outer ones inflated; spirotheca as in *Schwagerina*; septa fluted at base, closely spaced at first, widely spaced later (*645, *1271, *1506, *1926). *L.Perm.*, N.Am.-S.Am.-Eu.-Asia-Malay Arch.-Japan-Arct. Is.——FIG. 320,*1a*. *P. roeseleri* THOMPSON & HAZZARD, Bird Spring F., USA (Calif.); axial sec. of holotype, X8.3 (*1922). ——FIG. 320,*1b*. *P. fusulinoides* (SCHELLWIEN), Uggowitzer Breccie, Aus.(Carnic Alps); polished axial sec., X8.3 (*1644).——FIG. 320,*1c*. **P. uddeni* (BEEDE & KNIKER), Hueco Ls., USA (Tex.); axial sec. of holotype, X8.3 (*1922). [See also Fig. 284,*4*, *P. muongthensis*.]

Robustoschwagerina A. D. MIKLUKHO-MAKLAY, 1959, *1271, p. 160 [**Pseudoschwagerina tumida* LIKHAREV, 1939, *1138, p. 41; OD] [=*Robustoschwagerina* A. D. MIKLUKHO-MAKLAY, 1956, *1265, p. 1154 *(nom. nud.)*]. Shell large, deeply umbilicate, highly inflated, first 2 or 3 volutions distinctly fusiform in shape, moderately tightly coiled, and containing prominent chomata, next 3 volutions greatly inflated, deeply umbili-

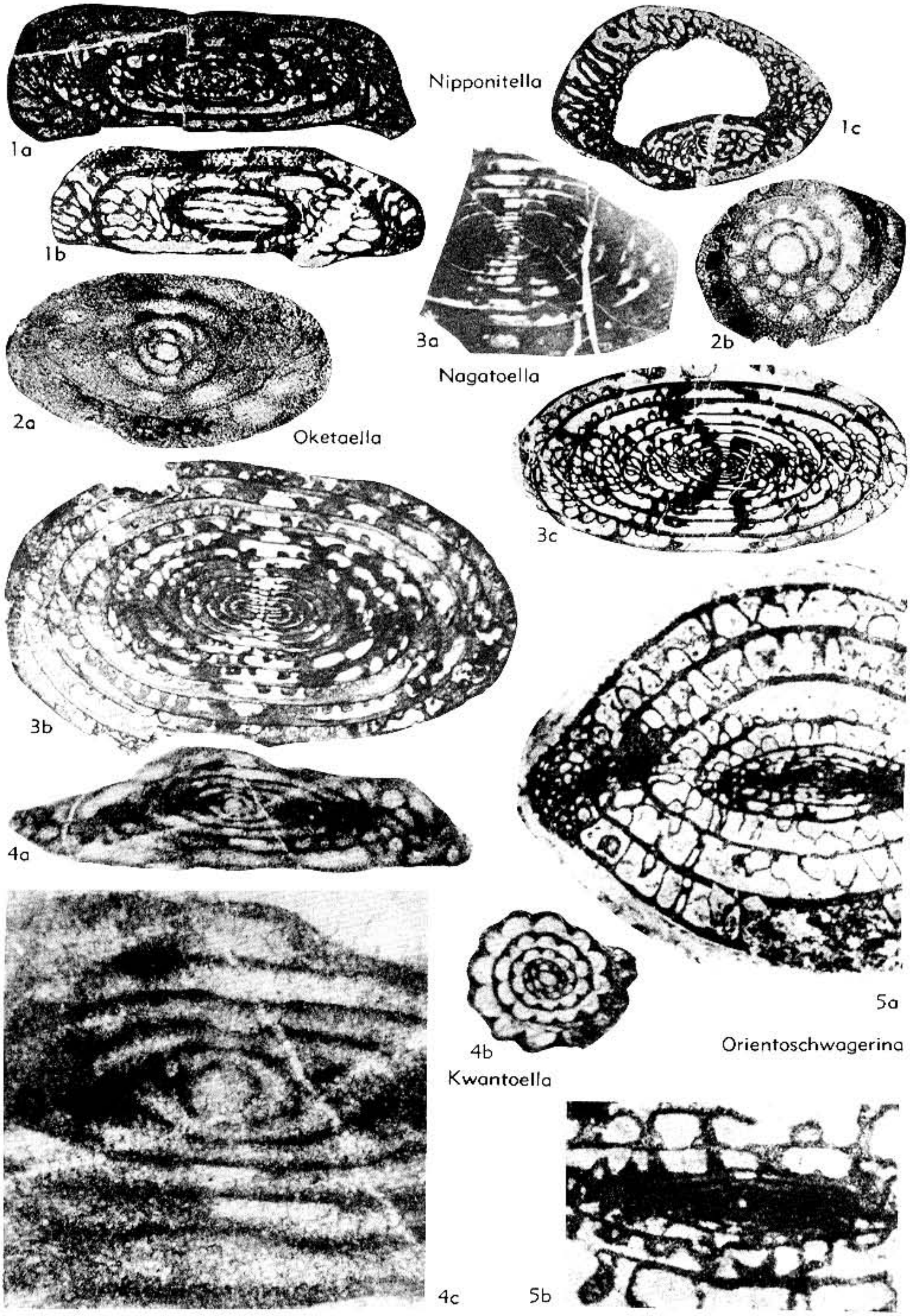


FIG. 317. Fusulinidae (Schwagerininae; *1, Nipponitella; 2, Oketaella; 3, Nagatoella; 4, Kwantoella; 5, Orientoschwagerina*) (p. *C*418-*C*420).

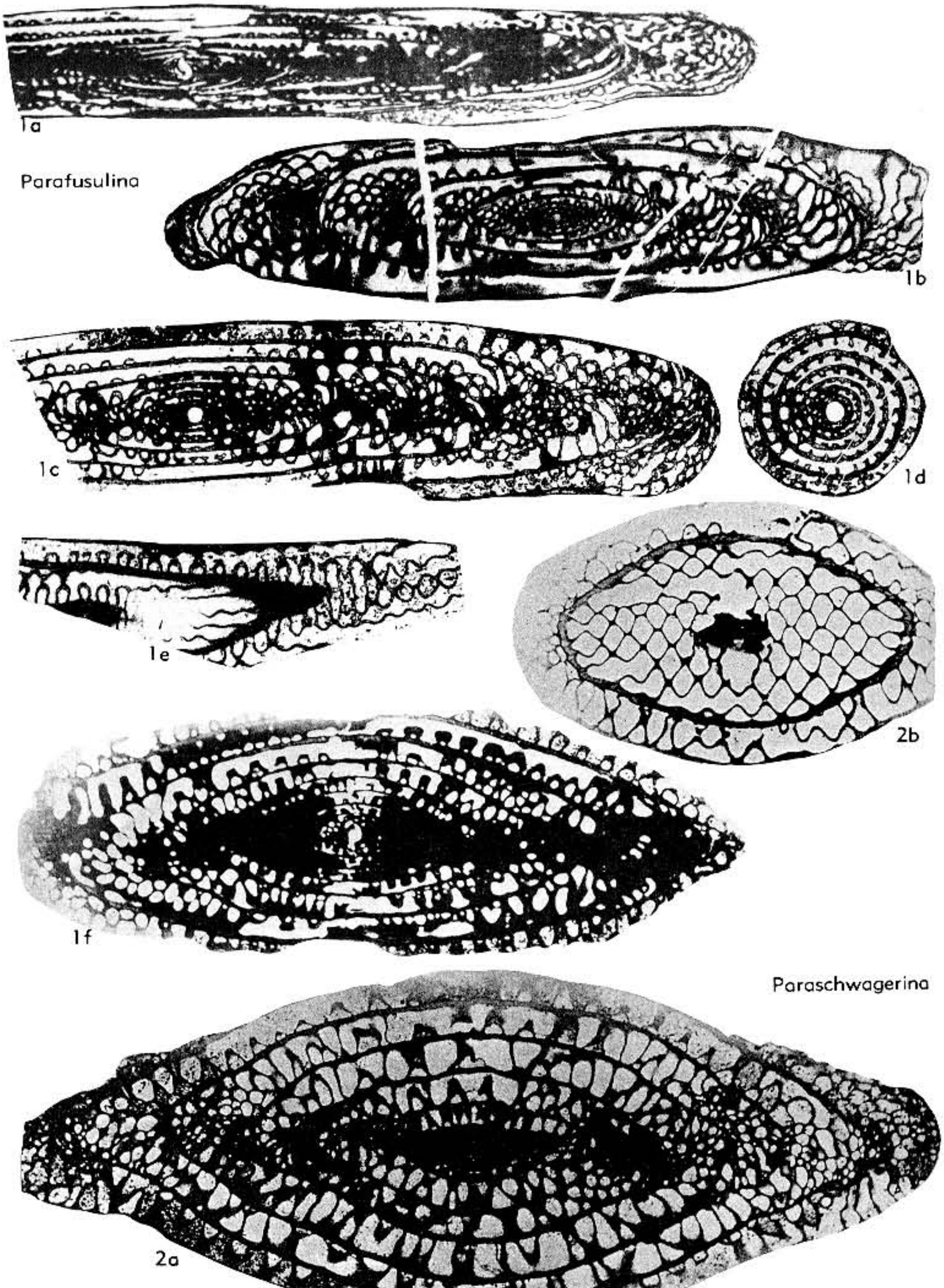


FIG. 318. Fusulinidae (Schwagerininae; *1, Parafusulina; 2, Paraschwagerina*) (p. *C*420).

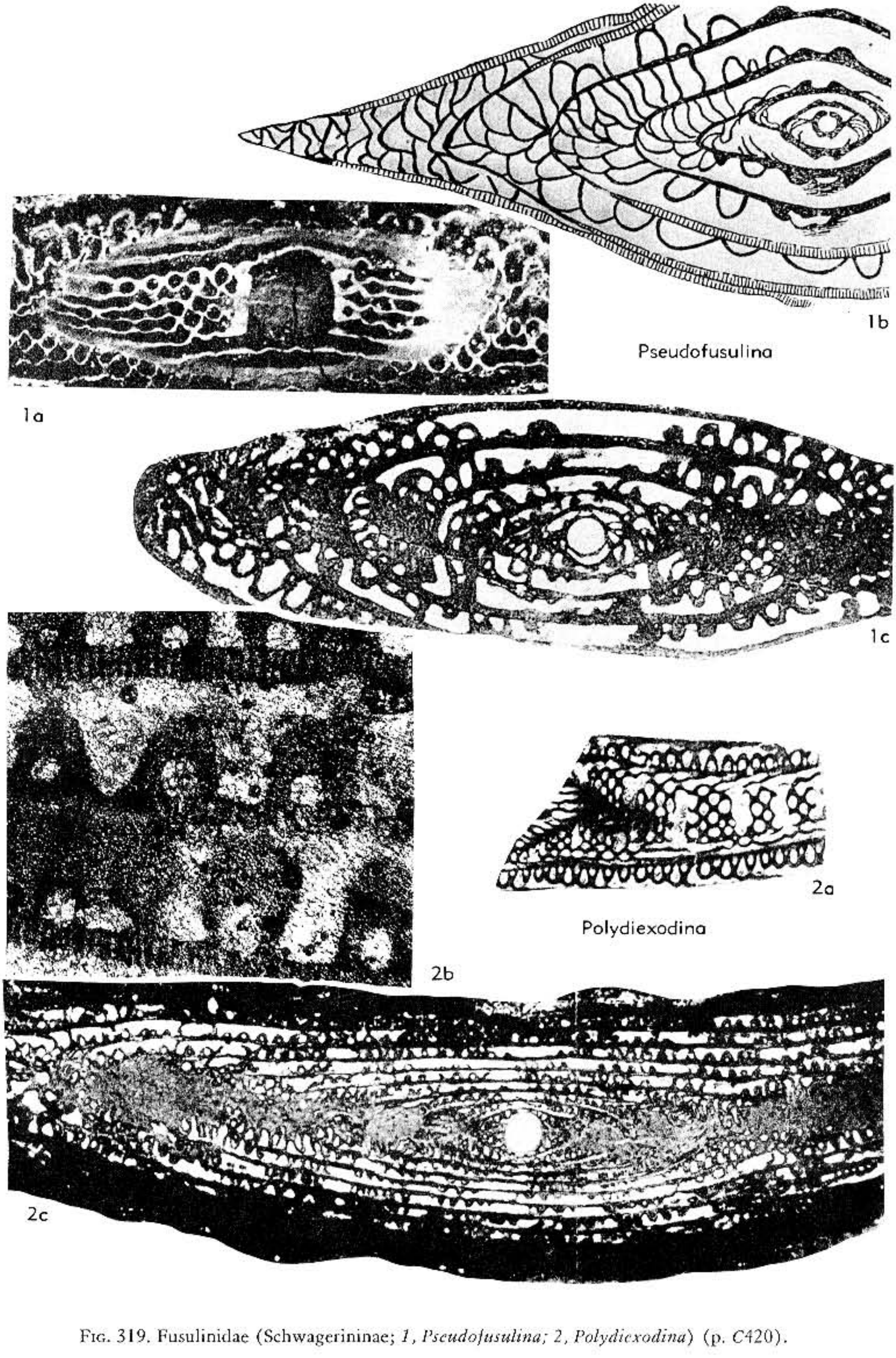


FIG. 319. Fusulinidae (Schwagerininae; *1, Pseudofusulina; 2, Polydiexodina*) (p. C420).

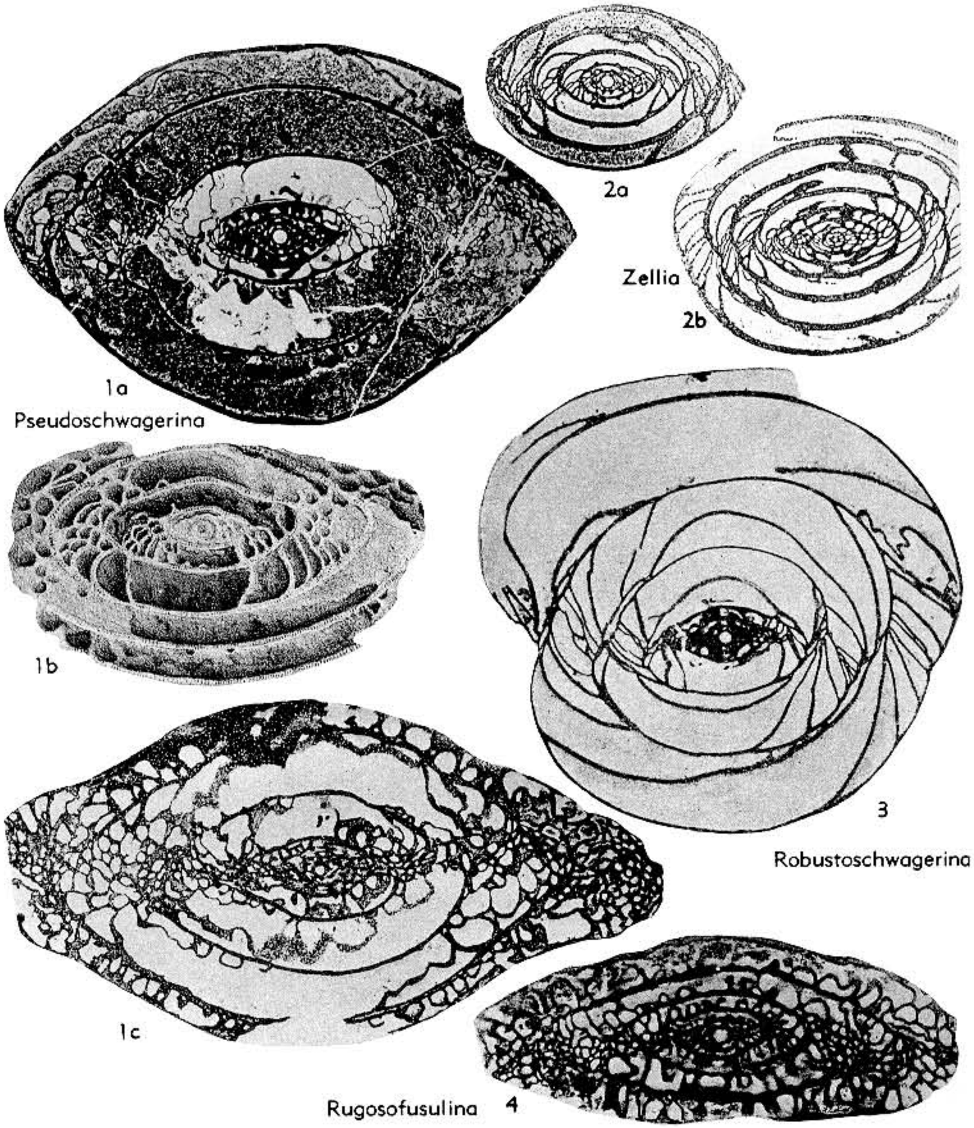


Fig. 320. Fusulinidae (Schwagerininae; *1, Pseudoschwagerina; 2, Zellia; 3, Robustoschwagerina; 4, Rugosofusulina*) (p. C420-C424, C426).

cate, with very faint chomata against widely spaced septa, outer part of last volution more tightly coiled and with moderately thick spirotheca (*1138, *1265). *Perm.*, USSR.——Fig. 320, *3*. **R. tumida* (Likharev), Darvaz Ser., Darvaz; axial sec. of holotype, ×8.3 (*1138) (see also Fig. 284,*3*).

Rugosofusulina Rauzer-Chernousova, 1937, *1500, p. 11 [**Alveolina prisca* Ehrenberg, 1842, *669A, p. 274; OD] [=*Rugofusulina* Dunbar in Cushman, 1940, *637B, p. 146 *(nom. null.)*]. Shell irregularly fusiform; spirotheca thick, composed of tectum and alveolar keriotheca, surface of spirotheca undulating in somewhat uniformly spaced rugae; septa moderately highly and irregularly fluted throughout length of shell; chomata slight to heavy (*1500). *L.Perm.*, Eu.-Asia-N.Am.——Fig. 320,*4*. **R. prisca* (Ehrenberg), USSR (Tsarev Kurgan); axial sec. of one of von Möller's specimens used in defining genus, ×12.5 (*1922).

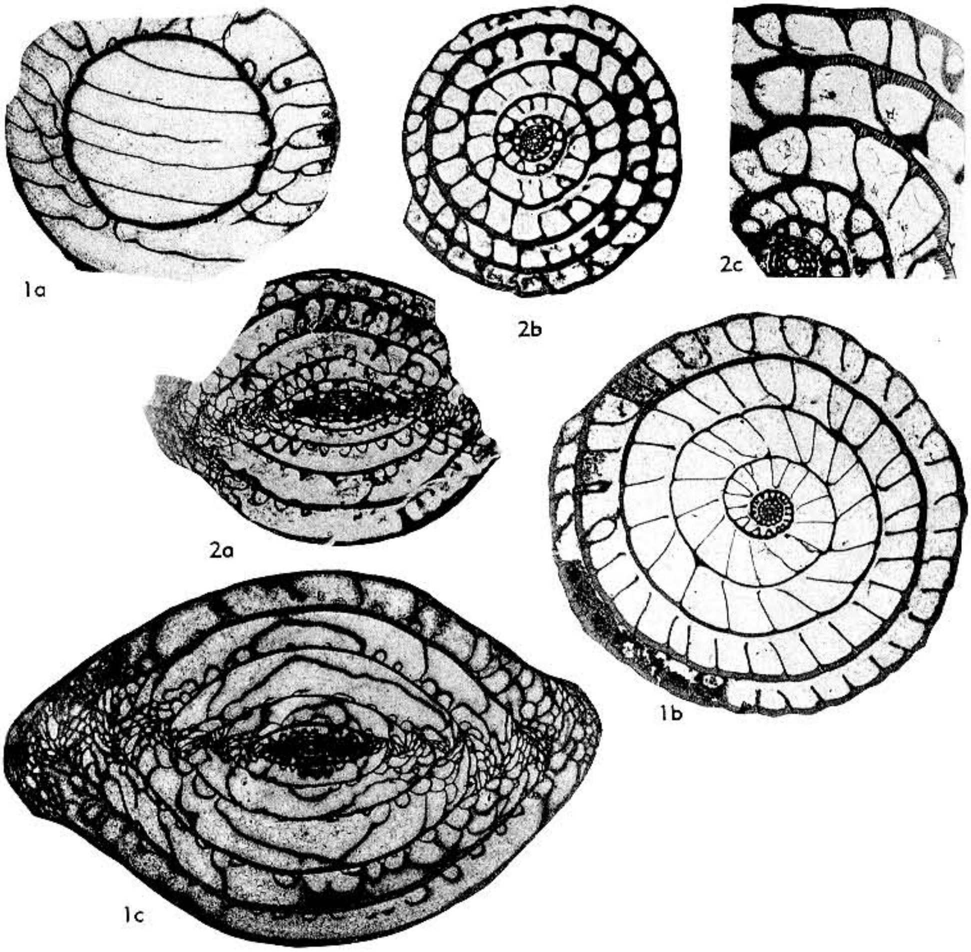


FIG. 321. Fusulinidae (Schwagerininae; *1,2, Rugososchwagerina*) (p. C425).

Rugososchwagerina A. D. Miklukho-Maklay, 1959, *1271, p. 160 [**Schwagerina yabei* Staff, 1909, *1830, p. 463; OD] [=*Rugososchwagerina* A. D. Miklukho-Maklay, 1956, *1265, p. 1154 *(nom. nud.)*]. Shell inflated-fusiform, first 3 or 4 volutions tightly coiled, elongate-fusiform, outer volutions greatly inflated; spirotheca with structure as in *Schwagerina*, moderately thin in early, tightly coiled part of shell and next 1 or 2 volutions, becoming rather thick and more coarsely alveolar in outer 2 or 3 volutions; septa closely spaced in first 3 or 4 volutions, more widely spaced in next 2 or 3 and then more closely spaced again in outer 1 or 2; chomata moderately well developed but somewhat discontinuous throughout most of shell, absent in outer volution (*1271). *U.Perm.(Verbeekina Z.)*, Eu. (Sicily)-Asia (Iran-Iraq-Afghan.-W. China-Asia Minor).——FIG. 321,*1a-c*. **R. yabei* (Staff), Sosio Beds, Sicily; *1a-c,* tang., sagittal, and axial secs., ×8 (*1922).——FIG. 321,*2*. *R. fosteri* (Thompson & Miller), Yanghsin Ls., W.China; *2a,* axial sec. of lectotype, ×8; *2b,c,* sagittal sec. of paratype, ×8, ×16 (*1922).

Triticites Girty, 1904, *789, p. 234 [**Miliolites secalicus* Say in James, 1823, *984A, p. 328; OD] [=*Girtyina* Staff 1909, *1830, p. 490 (type, *Fusulina cylindrica* var. *ventricosa* Meek & Hayden, 1859, *1251B, p. 261; OD); *Triticites (Montiparus)* Rozovskaya, 1948, *1590, p. 1637 (type, *Alveolina montipara* Ehrenberg, 1854, *680, p. xxxviii; OD); *Protriticites* Putrya, 1948, *1492, p. 91 (type *P. globulus*; OD); *?Obsoletes* Kireeva, 1950, *1040B, p. 201 (type, *Fusulina obsoleta* Schellwien, 1908, *1645A, p. 186; OD); *Ferganites* A. D. Miklukho-Maklay, 1959,

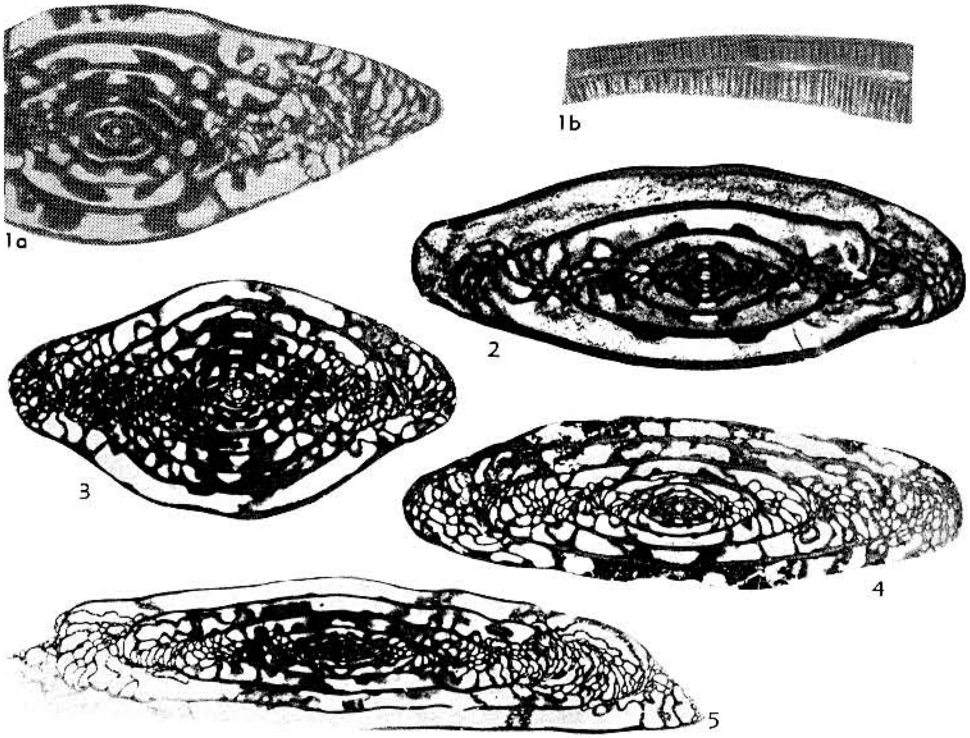


FIG. 322. Fusulinidae (Schwagerininae; *1-5, Triticites*) (p. *C*425-*C*426).

*1270A, p. 16 (type, *Triticites ferganensis* A. D. MIKLUKHO-MAKLAY, 1950, *1261A, p. 61,68; OD]. Shell fusiform to subcylindrical, planispiral throughout; spirotheca composed of tectum and alveolar keriotheca; septa fluted in end zones but less highly fluted in center of shell; chomata distinct (*789, *1270A, *1492, *1590, *1830). *U. Carb.(U.Penn.) - L. Perm.,* N.Am.(USA-Can.)-?China-Japan-USSR-S. Am.(Chile-Peru). —— FIG. 322,*1*. *T. globulus* (PUTRYA), C_3^{n}F., USSR(European); *1a,* axial sec. of holotype, ×15; *1b,* apparent double wall of *"Protriticites" globulus,* approx. ×80 (*1492).——FIG. 322,*2*. *T. milleri* THOMPSON, U.Penn.(Hartville Ls.), USA(Wyo.); axial sec. of syntype, ×20 (*1922).——FIG. 322, *3*. *T. beedei* DUNBAR & CONDRA, U.Penn.(Ervine Creek Ls.), USA(Kans.); axial sec. of syntype, ×10 (*1922).——FIG. 322,*4*. **T. secalicus* (SAY), U.Penn.(Plattsmouth Ls.), USA(Neb.); axial sec., ×10 (*1922).——FIG. 322,*5*. *T. ohioensis* THOMPSON, U.Penn.(Cambridge Ls.), USA(Ohio); axial sec. of syntype, ×10 (*1922). [See also Fig. 274,*4*, 275,*4*, 277,*2*, *T. ventricosus*; 280, *4,5*.]

Zellia KAHLER & KAHLER, 1937, *1009, p. 20 [**Pseudoschwagerina (Zellia) heritschi* var. *heritschi*; OD]. Shell inflated-subspherical, slightly umbilicate; proloculus large, chambers expanding uniformly in first 2 or 3 volutions, then remaining inflated to maturity; spirotheca thick, with coarsely alveolar keriotheca; septa widely spaced, plane except for slight fluting at base with numerous septal pores; chomata faint (*1009). *Perm.,* Eu. (Aus. - Yugo.) - USSR (Darvaz)-Japan-Asia(Vietnam-China).——FIG. 320,*2*. **Z. heritschi* (KAHLER & KAHLER), L.Perm., Aus.(Carnic Alps); *2a,* axial sec. of paratype, ×8.3; *2b,* tang. sec. of holotype, ×7.5 (*1922).

Family VERBEEKINIDAE
Staff & Wedekind, 1910

[*nom. transl.* A. D. MIKLUKHO-MAKLAY, 1957, p. 110 (*ex* subfamily Verbeekininae STAFF & WEDEKIND, 1910)] [=Neoschwagerinidae DUNBAR in CUSHMAN, 1948, p. 164]

Shell of medium size, spherical, ellipsoidal to elongate-ellipsoidal, or distinctly fusiform. Closely spaced foramina through the bases of all septa. Parachomata discontinuous in early forms, becoming extended completely across chambers in later forms. Axial and transverse septula hang from spirotheca of some later genera. Axial fillings present in most forms, becoming prominent in some. Spirotheca composed of tectum and keriotheca in early members of family but in later genera may be composed of single homogeneous layer (*1832). *Perm.*

Subfamily VERBEEKININAE
von Staff & Wedekind, 1910

[Verbeekininae STAFF & WEDEKIND, 1910, p. 114] [=Doliolininae GUBLER, 1935, p. 9; =Misellininae A. D. MIKLUKHO-MAKLAY, 1958, p. 9]

Shell large, subspherical to elongate-ellipsoidal, completely involute, planispiral; early genera with tunnel in first few volutions, later ones with multiple tunnels, and last-formed ones with foramina, but advanced genera have foramina bordered by parachomata throughout length of shell; spirotheca composed of tectum and alveolar keriotheca or of single thin layer (*1832). *Perm.*

Verbeekina STAFF, 1909, *1830, p. 468, 476 [**Fusulina verbeeki* GEINITZ in GEINITZ & VON DER MARCK, 1876, *776A, p. 400; OD] [=*Paraverbeekina* A. D. MIKLUKHO-MAKLAY, 1955, *1264, p. 574 (type, *P. pontica*); *Armenina* A. D. MIKLUKHO-MAKLAY, 1955, *1264, p. 576 (type, *A. karinae*)]. Shell spherical to slightly ellipsoidal; symmetrical in all volutions; foramina throughout length of septa, parachomata discontinuous in inner volutions and continuous across chambers in outer volutions; spirotheca composed of tectum and finely alveolar keriotheca (*1264, *1401, *1865, *1914, *1922). *U.Perm. (Verbeekina Z.),* Eu.(Sicily-Greece-Yugo.)-Asia (Asia Minor-S., SE. Asia-Indonesia)-Japan-N.Am. (Can., B.C.-USA, Wash.).——FIG. 323,*1a-d.* **V. verbeeki* (GEINITZ), Sumatra(Boekit Besi); *1a,* broken topotype showing parachomata developed only adjacent to septa in 10th volution, ×8; *1b,* etched surface of the same topotype *(1a)* showing development of parachomata in outer volution, ×8; *1c,* central part of axial sec. of topotype, ×32; *1d,* axial sec. of topotype, ×8 (*1922) (see also Fig. 274,*5*, 288,*3*).——FIG. 323,*1e. V. grabaui* THOMPSON & FOSTER, Yanghsin Ls., China (Szechuan); axial sec. of syntype, ×8 (*1922).——FIG. 323,*1f. V. karinae* (A. D. MIKLUKHO-MAKLAY), USSR(Transcaucasia); axial sec., ×12 (*1264).——FIG. 323,*1g. V. pontica* (A. D. MIKLUKHO-MAKLAY), USSR(Crimea); axial sec. of holotype, ×12 (*1264).

Brevaxina SCHENCK & THOMPSON, 1940, *1646, p. 587 [**Doliolina compressa* DEPRAT, 1915, *587A, p. 14; OD]. Shell small, subspherical, axis of coiling in shortest diameter through proloculus, polar ends deeply umbilicate; spirotheca thick, with structure as in *Misellina*; parachomata high, extending more than half height of chambers; foramina circular in section, located near lower part of chamber, numerous (as many as 24) in last volution (*1646). *Perm.,* Asia(Laos-USSR).——FIG. 323,*2.* **B. compressa* (DEPRAT), Laos (Cammon); *2a,* sagittal sec. of paratype, ×12; *2b,* axial sec. of holotype, ×12 (*1922).

Eoverbeekina LEE, 1933[1934], *1120, p. 18 [**E. intermedia*; OD]. Shell subspherical; tunnel singular in early volutions, dividing into 2 at 5th volution, foramina throughout length of shell in outer volutions; narrow chomata in inner volutions, rudimentary parachomata in outer volutions; spirotheca composed of tectum and keriotheca (*1120). *Perm.,* C.Am.-Asia(China)-Japan.——FIG. 323,*3.* **E. intermedia,* Chihsia Ls., China; axial sec. of holotype, ×12 (*1922).

Misellina SCHENCK & THOMPSON, 1940, *1646, p. 587 [**Doliolina ovalis* DEPRAT, 1915, *587A, p. 15; OD] [=*Moellerina* SCHELLWIEN, 1898, *1644, p. 238, 257, 281 (type, *Schwagerina lepida* SCHWAGER, 1883, *1706, p. 138) (*non Moellerina* ULRICH, 1886, *nec* EIMER & FICKERT, 1899); *Doliolina* SCHELLWIEN, 1902, *1645, p. 67 (type, *Schwagerina lepida* (*nom. subst. pro Moellerina* SCHELLWIEN, 1898) (*non Doliolina* BORGERT, 1894)]. Shell ellipsoidal, axis of coiling in greatest diameter; spirotheca thick, composed of tectum and thick keriotheca; foramina throughout shell; parachomata high, extending across chamber (*1644, *1645, *1646). *U.Perm.,* SE.Eu.-SE. Asia (Laos-China)-Japan-Malay Arch. (Sumatra)-?NW.N.Am.——FIG. 324,*1.* **M. ovalis* (DEPRAT), Laos(Cammon); *1a,b,* tang. and parallel secs. of paratype, ×15; *1c,* axial sec. of holotype, ×15 (*1922).

Pseudodoliolina YABE & HANZAWA, 1932, *2094, p. 41 [**P. ozawai*; OD] [=*Metadoliolina* ISHII & NOGAMI, 1961, *978A, p. 162 (type, *Pseudodoliolina pseudolepida gravitesta* KANMERA, 1954, *1012, p. 12]. Shell elongate-cylindrical, uniformly expanding, with bluntly rounded polar ends; spirotheca thin in inner 10 volutions where it seems composed of single thin layer, from 12th volution to maturity spirotheca thin but can be recognized in some specimens as composed of tectum, thin inner layer, and middle layer with dark lines normal to its surfaces that may be comparable to alveoli of other fusulinids; septa plane, composed of single, dense layer; foramina closely spaced; parachomata narrow, high, with circular lateral openings (*1929, *2094). *U.Perm. (Verbeekina Z.),* N.Am.(W.Can.-NW.USA)-E.Indies-Japan-Asia(Afghan.-S., E. China-Asia Minor)-Eu.(Yugo.-Crimea).——FIG. 324,*2a,b. P. pseudolepida* (DEPRAT), China(Szechuan); *2a,b,* sagittal and axial secs., ×10 (*1922).——FIG. 324,*2c,d.* **P. ozawai,* Akasaka Ls., Japan(Mino Prov.); *2c,d,* axial and sagittal secs. of topotypes, ×20 (*1922).

Subfamily NEOSCHWAGERININAE
Dunbar & Condra, 1928

[Neoschwagerininae DUNBAR & CONDRA, 1927[1928], p. 74] [=Sumatrininae KAHLER & KAHLER, 1946, p. 170; =Lepidolininae A. D. MIKLUKHO-MAKLAY, 1958, p. 10]

Shell planispiral, fusiform to ellipsoidal; spirotheca composed of tectum and alveolar keriotheca or of a single dense layer; foramina throughout length of shell; parachomata high, extending across chambers; transverse septula in all members, axial septula and transverse septula in later members, secondary transverse septula in latest members (*640, *1832). *U.Perm.*

Neoschwagerina YABE, 1903, *2083, p. 3 [*Schwag-

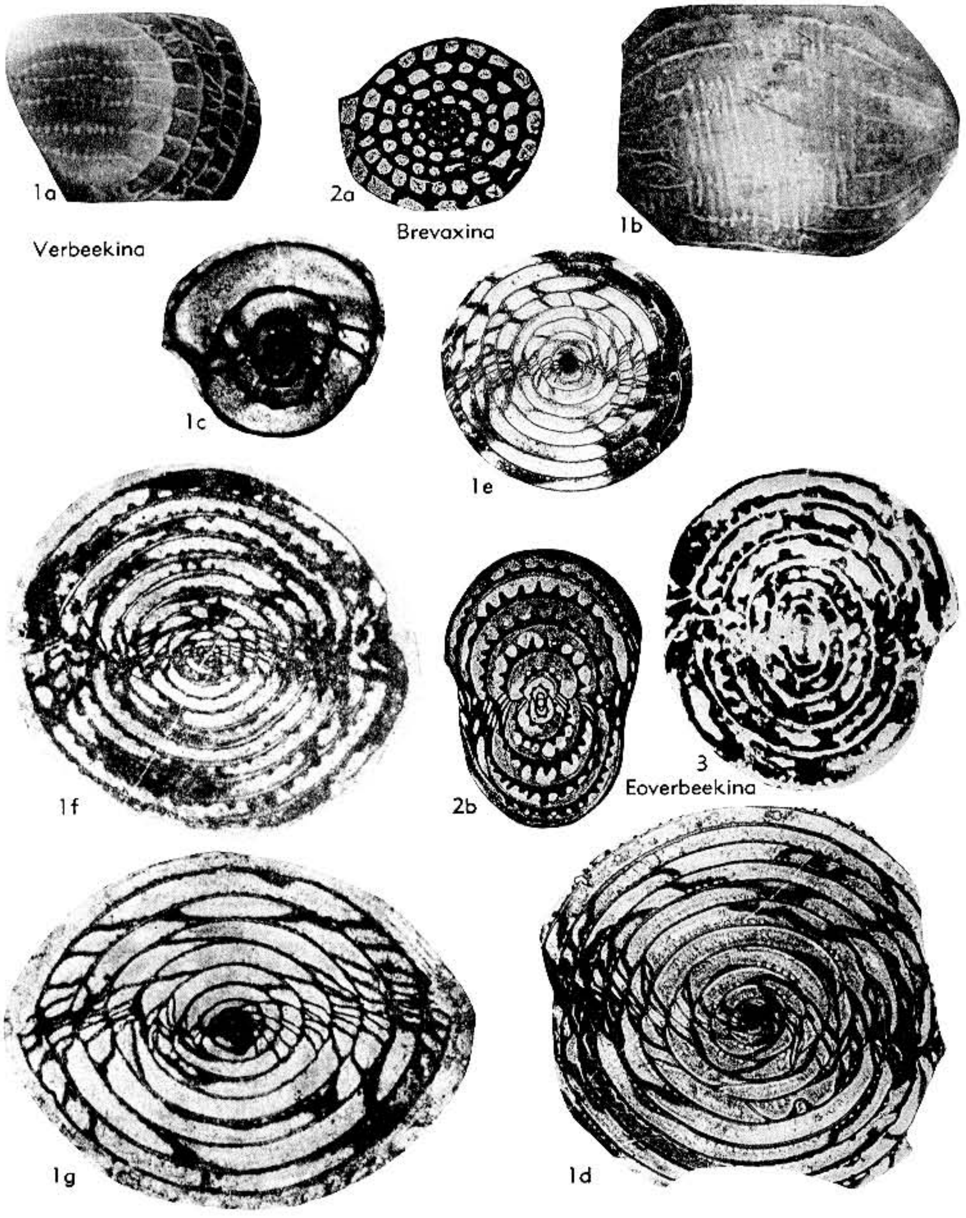


FIG. 323. Verbeekinidae (Verbeekininae; *1, Verbeekina; 2, Brevaxina; 3, Eoverbeekina*) (p. C427).

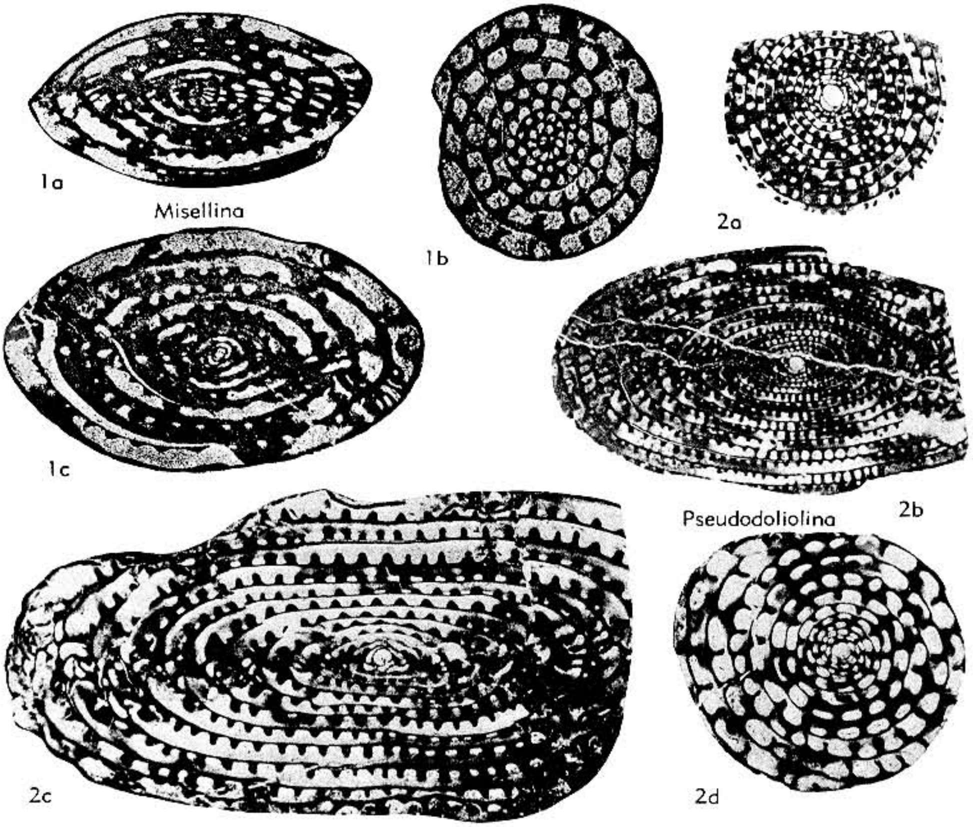


FIG. 324. Verbeekinidae (Verbeekininae; *1, Misellina; 2, Pseudodoliolina*) (p. C427).

erina craticulifera Schwager, 1883, *1706, p. 140; OD] [=*Crimellina* Tumanskaya, 1953, *1955, p. 4 (type *C. verae*); *Metaschwagerina* Minato & Honjo, 1958, *1287, frontispiece (type, *M. ovalis* Minato & Honjo); *Minoella* Honjo, 1959, *954, p. 124 (type, *Neoschwagerina (Cancellina) nipponica* Ozawa, 1927, *1401B, p. 160); *Gifuella* Honjo, 1959, *954, p. 131 (type, *G. gifuensis*)]. Shell large, inflated-fusiform to ellipsoidal; wall thick, composed of tectum and alveolar keriotheca, alveoli to base of septula; one transverse septulum to each foramen, reaching parachomata adjacent to septa, as many as 3 axial septula between septa (*954, *1287, *1922, *1955). *U. Perm.(Verbeekina Z.)*, Eurasia(Tethys)-S.Eu.-N. Afr.-S., SE. Asia-N. Am.(NW. USA-W. Can.).——Fig. 325,*1a,b*. *N. nipponica* (Ozawa), Akasaka Ls., Japan, Gifu Pref.; *1a*, sagittal sec. of paratype, ×10; *1b*, oblique sec. of holotype, ×10 (*1401B).——Fig. 325,*1c,d*. *N. gifuensis* (Honjo), Akasaka Ls., Japan, Gifu Pref.; *1c*, axial sec. of holotype, ×15; *1d*, sagittal sec. of paratype, ×15 (*954).——Fig. 325,*1e*. *N. haydeni* Dutkevich & Khabakov, Bamian Ls., Afghan.; axial sec. of holotype, ×20 (*1922) (see also Fig. 290,*1*).——Fig. 325,*1f*. *N. verae* (Tumanskaya), USSR (Crimea); axial sec. of holotype, ×15 (*1955). [See also Fig. 275,*1*, 276,*2*, **N. craticulifera*, holotype, paratype; 288,*1*, *N. ovalis*.]

Afghanella Thompson, 1946, *1921 p. 152 [**A. schencki*; OD] [=*Pseudosumatrina* Tumanskaya, 1950, *1954A, p. 91 (type, *Neoschwagerina sumatrinaeformis* Gubler, 1935, *838, p. 123); *Avganella* A. D. Miklukho-Maklay, 1953, *1263, p. 21 *(nom. van.)*]. Shell of medium size, inflated-fusiform; spirotheca thin, finely alveolar; parachomata high; septula thin, secondary transverse septula from 4th or 5th volution to maturity, axial septula uniform in length from 3rd volution to maturity, and as many as 4 between septa in outer volutions (*838, *1921, *1945). *U.Perm. (Verbeekina Z. —Polydiexodina Z.)*, Eu.(Greece-

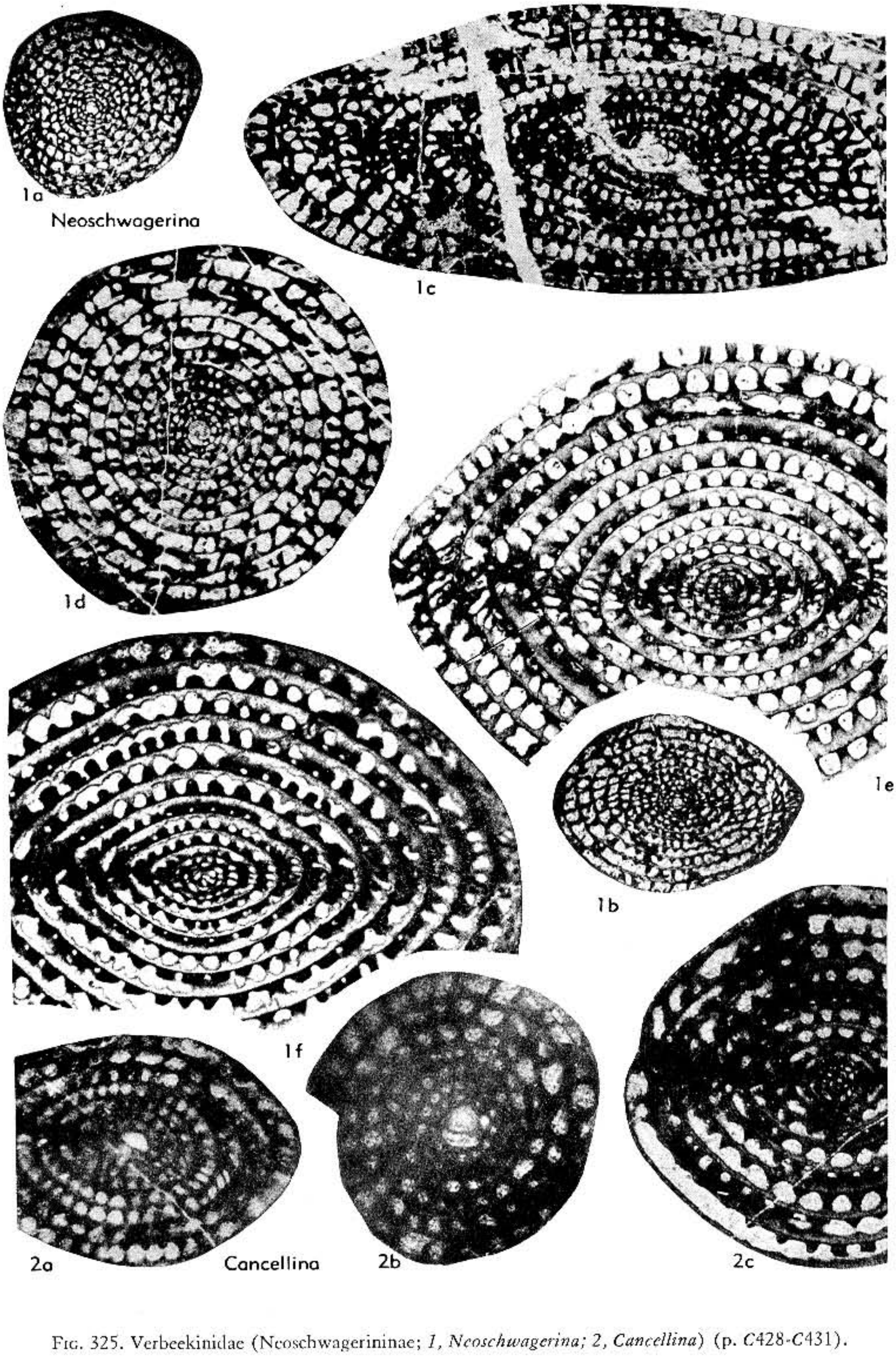


FIG. 325. Verbeekinidae (Neoschwagerininae; *1, Neoschwagerina; 2, Cancellina*) (p. *C*428-*C*431).

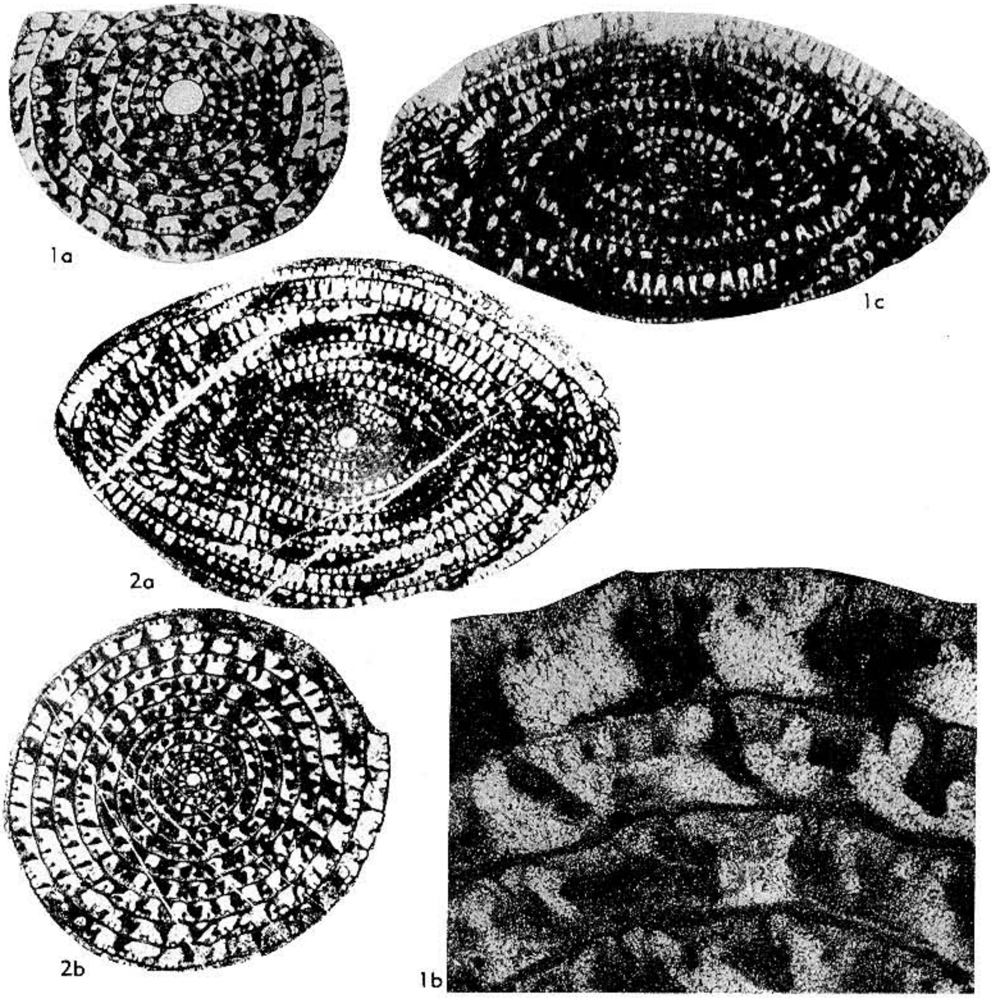


FIG. 326. Verbeekinidae (Neoschwagerininae; *1,2, Afghanella*) (p. *C*429-*C*431).

Crimea-Yugo.)-Asia (Afghan.-Turkey-Pamir-Laos)-Japan.——FIG. 326,*1*. **A. schencki*, Bamian Ls., Afghan.; *1a,b*, sagittal sec. of paratype and enlarged part, ×20, ×100; *1c*, axial sec. of holotype, ×20 (*1922).——FIG. 326,*2*. *A. sumatrinaeformis* (GUBLER), Laos(Pong Oua); *2a,b*, axial and sagittal secs., ×15 (*838).

Cancellina HAYDEN, 1909, *885, p. 244 [**Neoschwagerina primigena* HAYDEN, 1909; SD OZAWA, 1925, *1401, p. 26]. Shell small, inflated-ellipsoidal; spirotheca thick, coarsely alveolar, alveoli extending to base of septula; parachomata high, continuing to tops of chambers adjacent to septa; transverse septula short and broad, one above each parachomata, as many as 20 foramina and parachomata in last volution; secondary deposits filling extreme polar ends of chambers (*885, *1922). *U.Perm.*, Asia(Iran-Afghan.)-Japan.——FIG. 325, *2*. **C. primigena* (HAYDEN), Bamian Ls., Afghan. *(2a,b)*, Iran *(2c)*; *2a*, oblique axial sec. of holotype, ×17; *2b*, sagittal sec. of paratype, ×20; *2c*, axial sec., ×20 (*1922) (see also Fig. 288,*2*, 293).

Lepidolina LEE, 1933[1934], *1120, p. 21 [**Neoschwagerina (Sumatrina) multiseptata* DEPRAT, 1912, *584, p. 53; OD] [=*Colania* LEE, 1933 [1934], *1120, p. 20 (type, *C. kwangsiana*); *Gublerina* MINATO & HONJO, 1959, *1288, p. 331

non Kikoïne, 1948) (type, *Neoschwagerina elongata* Gubler, 1935, *838, p. 108)]. Shell large, inflated-fusiform; spirotheca thin, dense; septula thin, irregular in length and shape, thickest at their lower margins, secondary transverse septula first appearing in inner 1st to 3rd volution, as many as 2 between transverse septula of outer volutions, as many as 7 axial septula in outer volutions (*584, *1120, *1288, *1922). *U.Perm. (Yabeina Z.)*, Japan-SE. Asia-Eu. (Crimea).——Fig. 327,*1*. *L. kwangsiana* (Lee), China(Chienkiang, Kwangsi); axial sec. of holotype, ×15 (*1922).——Fig. 327,*2*. **L. multiseptata* (Deprat), Akasaka Ls., Japan, Gifu Pref. *(2a,b)*, Cambodia *(2c)*; *2a*, sagittal sec. of paratype, ×15; *2b*, axial sec., ×15; *2c*, tang. sec., ×10 (*1922) (see also Fig. 283,*1*, holotype, paratype; 292,*2*). [See also Fig. 275,*5*, 276,*4*. *L. elongata*.]

Presumatrina Tumanskaya, 1950, *1954A, p. 77 [**Doliolina schellwieni* Deprat, 1913, *586, p. 51; OD] [=*Praesumatrina* A. D. Miklukho-Maklay, Rauzer-Chernousova & Rozovskaya in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 206 *(nom. van.)*]. Shell small, elongate-ellipsoidal, with convex lateral slopes; spirotheca thin, seemingly composed of single thin layer, with extensions wedged down surfaces of septa and down septula; septula system composed of 1 transverse septulum alternating with foramina, and axial septula system composed of 1 or possibly 2 secondary axial septula alternating with septa; transverse septula extending down to join with tops of parachomata (*586, *1954A). *U.Perm.*, Asia (Vietnam-S.China)-Eu.(Crimea).——Fig. 328A,*1*. **P. schellwieni* (Deprat), Dong-Hoi Prov.; axial sec., ×20 (*586).

[The "correct original spelling" of this nominal genus unquestionably is *Presumatrina*, for the name in this form appears in three places and no other spelling was given. Subsequent alteration to *Praesumatrina* (e.g., A. D. Miklukho-Maklay *et al.*, 1958, *1275) constitutes an "incorrect subsequent spelling."]

Sumatrina Volz, 1904, *2024, p. 182 [**S. annae*; OD] [=*Pseudolepidolina* Tumanskaya, 1953, *1955, p. 14 (type, *Neoschwagerina (Sumatrina) longissima* Deprat, 1914, *587, p. 36)]. Shell elongate-subcylindrical, most volutions loosely coiled; spirotheca consisting of single dense layer; proloculus large; secondary transverse and axial septula uniform in length, pendant-shaped, present throughout shell, as many as 4 secondary transverse septula between primary septula, and as many as 7 axial septula to each chamber; some axial fillings in all except last part of last volution (*587, *838, *1921, *1954A). *U.Perm.(Verbeekina Z.)*, S.Eu.-Asia Minor-S.Asia-Japan-Malay Arch. (Sumatra).——Fig. 328,*2*. *S. longissima* Deprat, Cambodia (type-sp. of *Pseudolepidolina*); axial sec., ×15 (*1922) (see also Fig. 289,*1a*). [See Fig. 289, *1b*, 292,*3*, **S. annae*, holotype, paratype.]

Yabeina Deprat, 1914, *587, p. 30 [**Neoschwagerina (Yabeina) inouyei* Deprat; OD (M)] [=*Jabeina* A. D. Miklukho-Maklay, 1953, *1263, p. 21 *(nom. van.)*]. Shell large, inflated-fusiform; spirotheca thin, alveolar; secondary transverse septula between some primary transverse septula, as many as 3 between primary transverse septula in outer volutions of late forms, as many as 9 axial septula between septa in outer volutions of later forms (*587, *1921, *1933). *U.Perm. (Yabeina Z.)*, Japan-SE.Asia(China)-Malay Arch. Eu. (Crimea)-Africa (Tunisia)-USSR (SE.Siberia)-Can.(B.C.) - USA(Wash., Ore., Tex.) - N.Z.——Fig. 328,*1*. *Y. texana* Skinner & Wilde, Bell Canyon F., USA (Tex.); *1a,b*, axial and sagittal secs. of paratypes, ×20 (*1797). [See also Fig. 290,*2*, 292,*1*, **Y. inouyei*, paratype, holotype.]

NOMINAL FUSULINACEAN GENERA OF UNCERTAIN STATUS

The following alphabetically arranged nominal genera of fusulinacean foraminifers are those for which I have insufficient information for analysis or thorough understanding. For such completeness as is possible now, I record what I know about them. These names were brought together by M. L. Thompson and R. Toriyama in Japan, and by A. R. Loeblich, Jr., and Helen Tappan. Special thanks are extended to the Loeblichs for their help in assembling and discussing this group.

Chenella A. D. Miklukho-Maklay, 1959, *1270, p. 628 [**Orobias kueichihensis* Chen, 1934, *332, p. 15; OD]. "The chenella shell is just like that of *Eostaffelloides*, but the height of its volution is abruptly higher, and the wall of the body whorls has a diaphanotheca." [The quoted statement was given in a footnote. The genus was stated to belong in the Ozawainellinae.] *Carb.*, S.China.

Codonofusiella (Lantschichites) Tumanskaya, 1953, *1955, p. 20 [**C. (L.) maslennikovi*; OD]. *Lantschichites* was elevated to generic status by Rauzer-Chernousova & Fursenko (1959, *1509, p. 212), where it was also regarded as including *Paraboultonia* Skinner & Wilde, 1954, in synonymy. Tumanskaya gave the following diagnosis: "The new subgenus *Lantschichtes* differs from the genus *Codonofusiella* by the different form of its shell: by its elongated, almost cylindrical form and broadly rounded sides at the poles. The septal folding is considerably more developed and septa occupy almost all of a volution. Similar features are: the small size of the shell, the endothyroid structure of the early volutions, the small

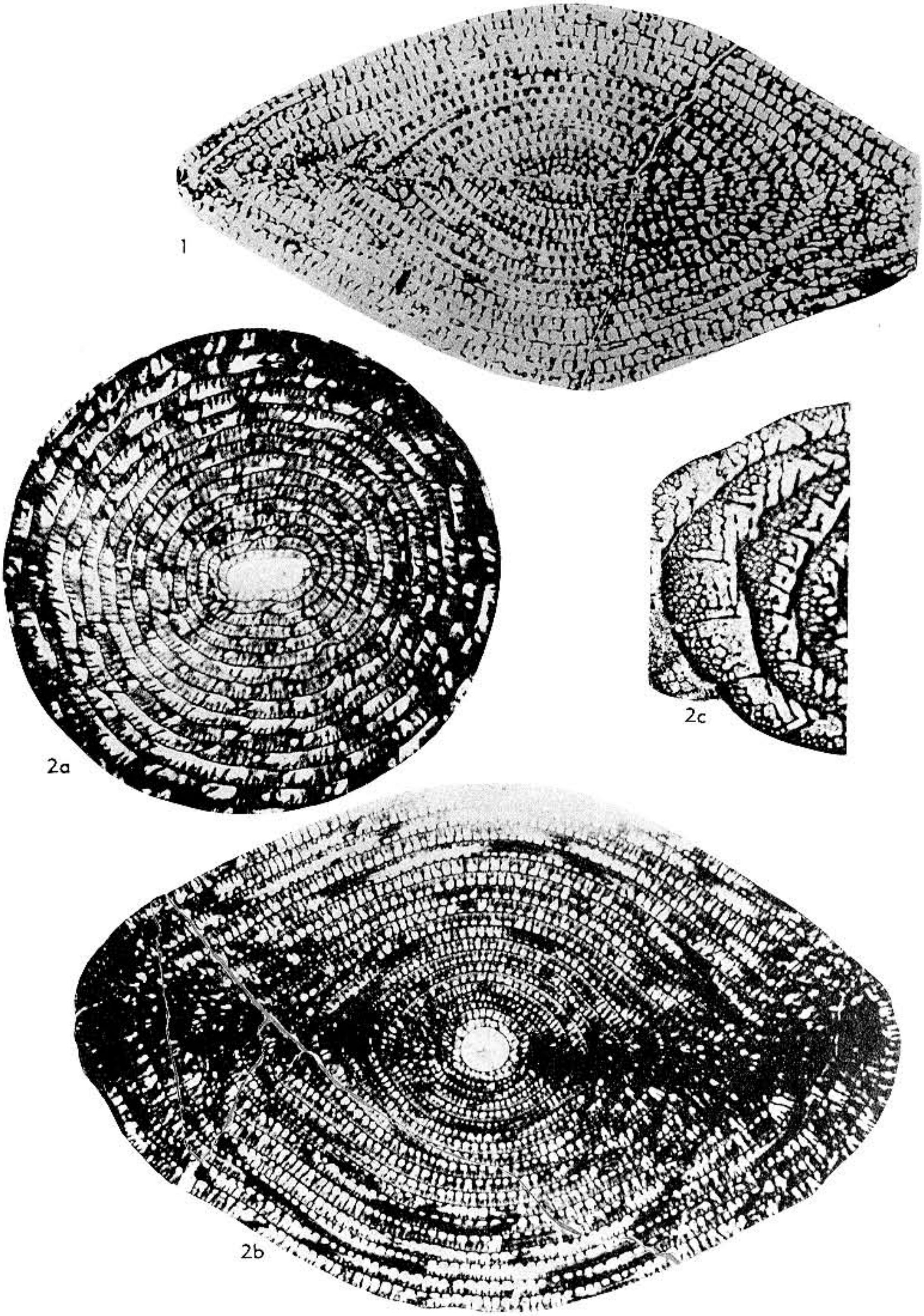


FIG. 327. Verbeekinidae (Neoschwagerininae; *1,2, Lepidolina*) (p. C431-C432).

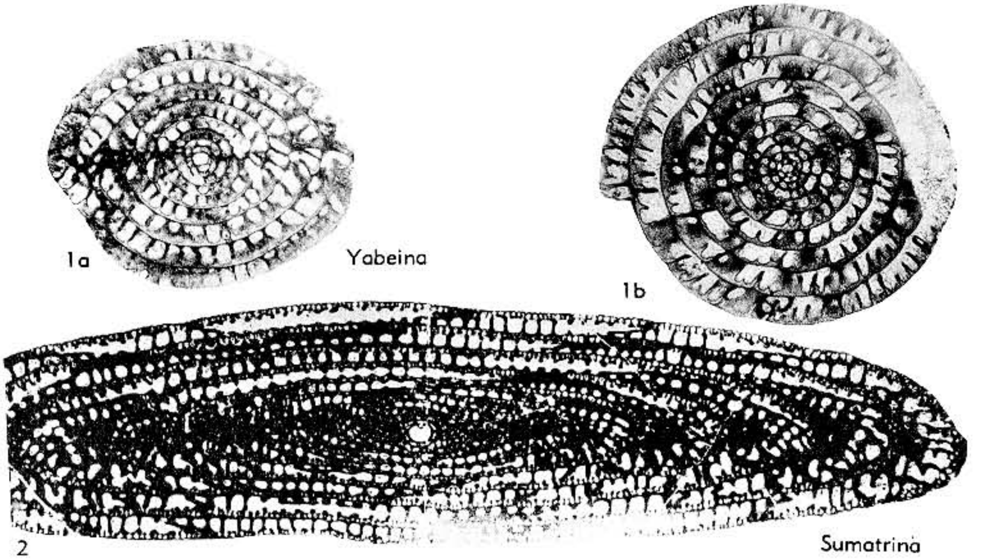


Fig. 328. Verbeekinidae (Neoschwagerininae; *1, Yabeina; 2, Sumatrina*) (p. *C*432).

dimensions of the embryonic chamber and, principally, the same kind of straightening and expansion of the terminal volution as in the genus *Codonofusiella*. Age. Upper Permian." She compares the subgenus to forms described by Schubert (1915, *1693A, p. 78) from Timor as *Fusulina weberi*, which were referred by Thompson (1949, *1923, p. 186) to *Palaeofusulina* Deprat, 1912. I cannot determine all of the morphological features of *Lantschichites* significant for generic determination from Tumanskaya's illustrations of the type-species. *U.Perm.*, USSR.

Darvasites A. D. Miklukho-Maklay, 1959, *1270A, p. 12,13,16 [**Triticites ordinatus* var. *daroni* A. D. Miklukho-Maklay, 1949, *1261, p. 70; OD] [=*Darvasites* A. D. Miklukho-Maklay, 1957, *1267, p. 108 (obj.) (*nom. nud.*, name and type-species cited but no diagnosis given)]. Originally placed in Schwagerinidae. [I have seen Chen's (1934) illustrations of *Triticites ordinatus* but not of *T. ordinatus daroni*, though Helen Tappan has kindly furnished me with a translation of the description of this subspecies by A. D. Miklukho-Maklay (1949). From this it is strongly suggested that the genus *Darvasites* may be referable to *Schwagerina* von Möller, 1877. The main feature in the original description which would indicate some difference from the type of *Schwagerina* is the occurrence of massive chomata in all whorls of *Darvasites daroni*.] *L.Perm.*, Darvaz, Asia (USSR).

Eostaffelloides A. D. Miklukho-Maklay, 1959, *1270, p. 629 [**E. orientalis*; OD]. *Eostaffelloides* resembles *Chenella* in most respects except that *Eostaffelloides* does not have an abrupt increase in height of the last volution and the wall of the body whorls does not contain a diaphanotheca. The shell is lens-shaped and measures about 0.4 mm. in axial length and 0.7 mm. in width. The diameter of the proloculus of one specimen was given as 0.03 mm. and heights of succeeding volutions as 0.06 (1st), 0.11 (2nd), 0.20 (3rd), 0.37 (4th), and 0.70 (5th). The chomata are triangular in outline. The genus originally was placed in the Ozawainellinae. *U.Perm.*, Asia (USSR).

Fujimotoella Morikawa, 1952, *1312A, p. 36 [**F. umblicata*; OD]. The type-specimens of *F. umblicata* are badly crushed. They are large and have large proloculi. The shell is loosely coiled throughout. The septa are closely spaced and seem to be entirely unfluted. Considerable evidence is shown on many of the illustrations that the axial areas are highly filled with dense calcite which is closely similar to axial fillings in specimens of *Wedekindellina* Dunbar & Henbest, 1933. The author described *Fujimotoella* as being like *Triticites* Girty, 1904, but the types seem to be too poorly preserved for comparison or for generic definition. *Perm.*, Japan.

Moscoviella K. V. Miklukho-Maklay, 1952, *1276, p. 991 [**Ozawainella mosquensis* Rauzer-Chernousova in Rauzer-Chernousova *et al.*, 1951, *1509A, p. 136; OD] [=*Moscovella* Thompson, 1954, *1926, p. 12 (*nom. van.*)]. The designation of type-species was somewhat ambiguous, as an error in typesetting placed the line "Tip roda *Reichelina cribroseptata* Erk, 1941" [1942] in two places (p. 991, line 25 and line 37) erroneously indicating it as type of both

Moscoviella and *Reichelina* Erk, 1941[1942], although most of the article consisted of distinguishing the two genera. Nevertheless, lines 16-20 (p. 991, preceding the above-mentioned error) stated definitely that the new name *Moscoviella* was there proposed for the group of Carboniferous foraminifers, for which the type is *Ozawainella mosquensis*. According to Rauzer-Chernousova & Fursenko (1959, *1509, p. 208) *Moscoviella* is a junior synonym of *Ozawainella* Thompson, 1935. Therefore, in view of the fact that most Russian paleontologists have not accepted *Moscoviella* as an established genus, I concur in their decision. *U.Carb.*, Eu.-Asia.

Parareichelina K. V. Miklukho-Maklay in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 208 [**P. reticulata*; OD] [=*Parareichelina* K. V. Miklukho-Maklay in A. D. Miklukho-Maklay, Rauzer-Chernousova & Rozovskaya, 1958, *1275, p. 17 *(nom. nud.)*]. *Paraeichelina* differs from *Reichelina* Erk, 1941[1942], principally in the last stages of the uncoiled part of the shell. The detailed differences here mainly concern attitude of the septa. The genus originally was placed in the Ozawainellinae. *U.Perm.*, USSR (N. Caucasus-Ussuriy).

Praeparafusulina Tumanskaya, 1962, *1955A, p. 1397 [**Parafusulina pseudojaponica* Dutkevitch in Gorsky, 1939, *809, p. 43; OD].

Pseudoendothyra Mikhaylov, 1939, *1260, p. 54,60 [**Fusulinella struvii* von Möller, 1879, *1296, p. 22; OD] [=*Parastaffella* Rauzer-Chernousova, 1948, *1505, p. 14 (obj.)]. It is found that in the original publication on *Fusulinella struvii* illustrations were given of external views and drawings of thin sections. The wall structures are shown in part to be identical to those in *Millerella* Thompson, 1942, and *Paramillerella* Thompson, 1951. However, no chomata are seen in the figures of *F. struvii* and, indeed, no secondary deposits of any kind. Furthermore, some of the illustrations given by Mikhaylov (1939) are copies of those published by von Möller. One thin section figured by Mikhaylov (*1260, pl. 4, fig. 4) shows a foraminifer resembling an ozawainellid, but the section is not well centered. The other illustrations do not seem to be of fusulinaceans. *Carb.-L.Perm.*, USSR-W.Eu.-Asia-N.Am.

Putrella Rauzer-Chernousova, 1951, *1509A, p. 319 [**Pseudotriticites brazhnikovae* Putrya, 1948, *1493, p. 98; OD]. *Putrella* was proposed to include specimens that Rauzer-Chernousova described from the upper part of the Moscovian stage, base of Podolsk Horizon, and uppermost part of the Kashir Horizon. The type-species is reported to have features like those of some variants of highly advanced *Fusulina* Fischer de Waldheim, 1829, and the genus was classed in the Fusulininae. It is my judgment that the type-

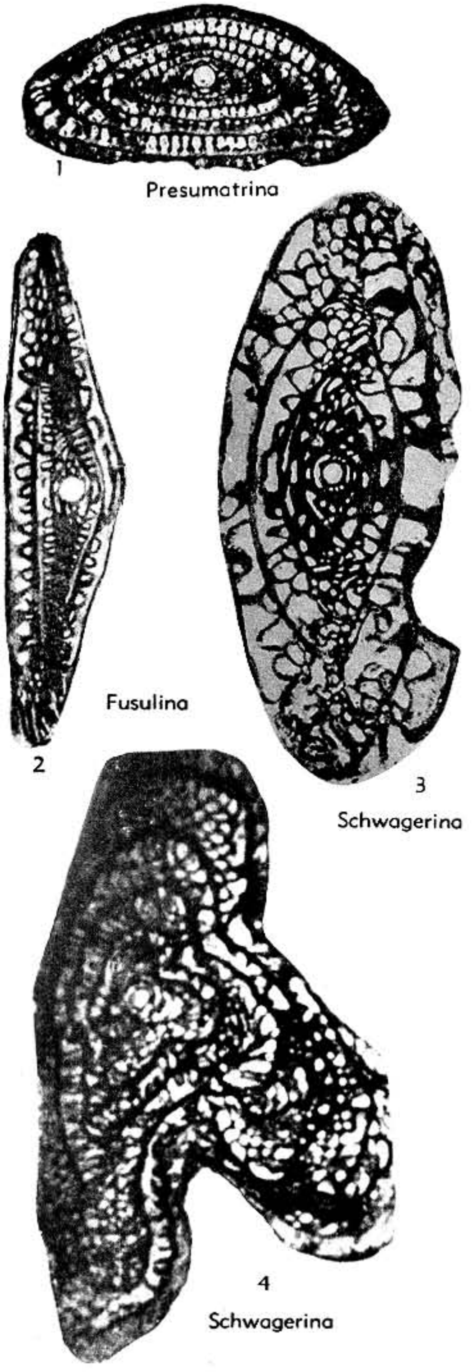


Fig. 328A. Verbeekinidae (Neoschwagerininae; *1, Presumatrina*); Fusulinidae (Fusulininae; *2, Fusulina*); Fusulinidae (Schwagerininae; *3,4, Schwagerina*) (p. C404, C415, C432).

species of *Putrella* may properly be included in a broad understanding of *Fusulina*. However, it may possibly be somewhat like some of the forms that have been referred to *Quasifusulina* Chen, 1934.

Quasifusulinoides Rauzer-Chernousova & Rozovskaya in Rauzer-Chernousova & Fursenko, 1959, *1509, p. 210 [**Pseudotriticites fusiformis* Rozovskaya, 1952, *1592A, p. 29; OD] [=*Quasifusulinoides* Rauzer-Chernousova & Rozovskaya in A. D. Miklukho-Maklay, Rauzer-Chernousova & Rozovskaya, 1958, *1275, p. 17 *(nom. nud.)*]. An enlargement of the wall structure illustrated by Rauzer-Chernousova & Fursenko (1959, *1509, pl. 7, fig 15B), shows it to be rather typical of the Fusulininae group of forms that occur from the upper part of the Myachkovo Horizon to the bottom of the Upper Carboniferous, southern Urals, Russian Platform. No axial fillings are visible in the axial section (*loc. cit.*, pl. 7, fig. 15A) and the septa are intensely fluted. The details by which this genus differs from *Quasifusulina* Chen, 1934, are not understood by me.

Russiella A. D. Miklukho-Maklay, 1957, *1267, p. 98 [**R. pulchra*; OD]. The illustrations of *R. pulchra* show a highly elongate shell with intensely fluted septa and rather massive axial fillings. The holotype has about 5 volutions. The minute size of the shell and rather indistinct details of its internal structure suggest that it may be related to *Minojapanella* Fujimoto & Kanuma, 1953. *Russiella* originally was placed in the "Boultoniinae." *U.Perm.*, USSR(Crimea).

Sichotenella Tumanskaya, 1953, *1955, p. 22 [**S. sutschanica*; OD]. Shells of *Sichotenella* are small, discoidal forms with an angular periphery. The last part of the shell, according to the author, becomes straightened out or uncoiled, the uncoiled part of the last volution being greater in volume than the entire coiled stages. Originally referred to the Fusulininae. *U.Perm.*, USSR (Yuzhno-Ussuriy region).

Sphaeroschwagerina A. D. Miklukho-Maklay, 1959, *1271, p. 157 ["**Schwagerina princeps* (Ehrenberg)" Schellwien, 1898, *1644, p. 258 (*non Borelis princeps* Ehrenberg, 1842, *669A, p. 274) (=*Schwagerina sphaerica* Shcherbovich var. *karnica* Shcherbovich in Rauzer-Chernousova & Shcherbovich, 1949, *1509B, p. 102); OD] [=*Sphaeroschwagerina* A. D. Miklukho-Maklay, 1956, *1265, p. 1154 (*nom. nud.*, type designated but no generic description) (obj.)]. An outline sketch of a typical specimen of *Sphaeroschwagerina* 1959, *1271, p. 159, suggests relationship to *Robustoschwagerina tumida* (Likharev), 1939. Originally placed in the Schwagerinidae. *L.Perm.(U.Karachatyr Horizon* P_1^e*)*.

NOMINA NUDA (FUSULINACEANS)

Armeniella A. D. Miklukho-Maklay, 1953 (*1263, p. 20).

Carina A. D. Miklukho-Maklay, 1953 (*1263, p. 18).

Eozawainella A. D. Miklukho-Maklay, 1953 (*1263, p. 18).

Orientella A. D. Miklukho-Maklay, 1953 (*1263, p. 21).

Pseudoyabeina Tumanskaya, 1955 (cited in A. D. Miklukho-Maklay, 1958, *1268, p. 6,10).

NOMEN INQUIRENDUM (FUSULINACEANS)

Eoparastaffella Vdovenko, 1954 [*fide* Rauzer-Chernousova & Fursenko, 1959, *1509, p. 207, a synonym of *Pseudoendothyra* Mikhaylov, 1939].

Suborder MILIOLINA Delage & Hérouard, 1896

[*nom. correct.* Loeblich & Tappan, 1961, p. 219 (*pro* suborder Miliolidae Delage & Hérouard, 1896, p. 117)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}order, ^{2}suborder, ^{3}group, ^{4}division, ^{5}subclass); dagger(†) indicates *partim*]——[=^{2}Monosomatia† Ehrenberg, 1839; table opp. p. 120; =Monothalamia† Schultze, 1854, p. 52; =Foraminifera Monomera† Reuss, 1862, p. 362; =^{4}Monothalamia† Marriott, 1878, p. 30; =^{1}Monothalamia† Haeckel, 1894, p. 164]——[=^{1}Agathistègues d'Orbigny in de la Sagra, 1839, p. xxxix, 153 *(nom. neg.)*; =^{1}Éntomostègues d'Orbigny in de la Sagra, 1839, p. xxxix, 113 *(nom. neg.)*; =^{1}Cyclostègues† d'Orbigny, 1851, p. 192 *(nom. neg.)*; =^{3}Helicoidea Schultze, 1854, p. 53; =Nautiloidea† Reuss, 1860, p. 151]——[=^{2}Imperforata Carpenter, 1861, p. 469; =^{3}Imperforata Claus, 1872, p. 108; =^{5}Imperforata† Lankester, 1885, p. 845; =^{1}Imperforida Delage & Hérouard, 1896, p. 107; =^{2}Imperforina† Calkins, 1901, p. 106]——[=Foraminifera Polymera† Reuss, 1862, p. 365; =^{1}Polystegia† Haeckel, 1894, p. 164; =^{2}Biloculinidea† Sigal in Piveteau, 1952, p. 157; =Pluriloculinidea† Sigal in Piveteau, 1952, p. 160]——[=Porcellanea Carpenter, 1879, p. 375, 376; =^{1}Flexostylidia† Calkins, 1926, p. 355; =^{1}Flexostili (Imperforata) Silvestri, 1937, p. 77]——[=^{1}Miliolidea Lankester, 1885, p. 846; =^{1}Miliolidaceae Hartog in Harmer & Shipley, 1906, p. 59; =^{1}Miliolida Calkins, 1909, p. 39]——[^{1}Hellenoidea† Wedekind, 1937, p. 79; =Cornuspiroidea Wedekind, 1937, p. 87; =^{2}Cristellariacea† Wedekind, 1937, p. 93; =^{2}Orbitolitacea Wedekind, 1937, p. 120; =^{2}Cornuspiridea Jírovec, 1953, p. 335]

Test calcareous, porcelaneous, commonly with pseudochitinous lining, may also include some adventitious material in wall, imperforate in post-embryonic stages. *Carb.-Rec.*

Superfamily MILIOLACEA Ehrenberg, 1839

[*nom. correct.* Loeblich & Tappan, 1961, p. 289 (*pro* superfamily Miliolidea Glaessner, 1945, p. 116, and Miliolicae Easton, 1960, p. 65, 76)]——[In synonymic citations superscript numbers indicate taxonomic rank assigned by authors (^{1}tribu, ^{2}superfamily, ^{3}family group); dagger(†) indicates *partim*]——[=^{1}Milleporita† Latreille, 1825, p. 166; =^{1}Orthocerata† Latreille, 1825, p. 162; =^{1}Polycyclica† Latreille, 1825, p. 164]——[=^{2}Orthoklinostegia† Eimer & Fickert, 1899, p. 185; =^{3}Archi-Monothalamidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 85; =^{3}Flexostylidia† Rhumbler in Kükenthal & Krumbach, 1923, p. 87; =^{2}Alveolinidea Voloshinova in Rauzer-Chernousova & Fursenko, 1959, p. 244]

Wall porcelaneous, commonly with pseudochitinous inner lining, and may have adventitious material on exterior, imperforate at least in postembryonic stages; proloculus with spiral passage followed by numerous chambers which may be planispirally coiled or arranged in definite planes; aperture terminal, single or cribrate and may be variously modified. *Carb.-Rec.*

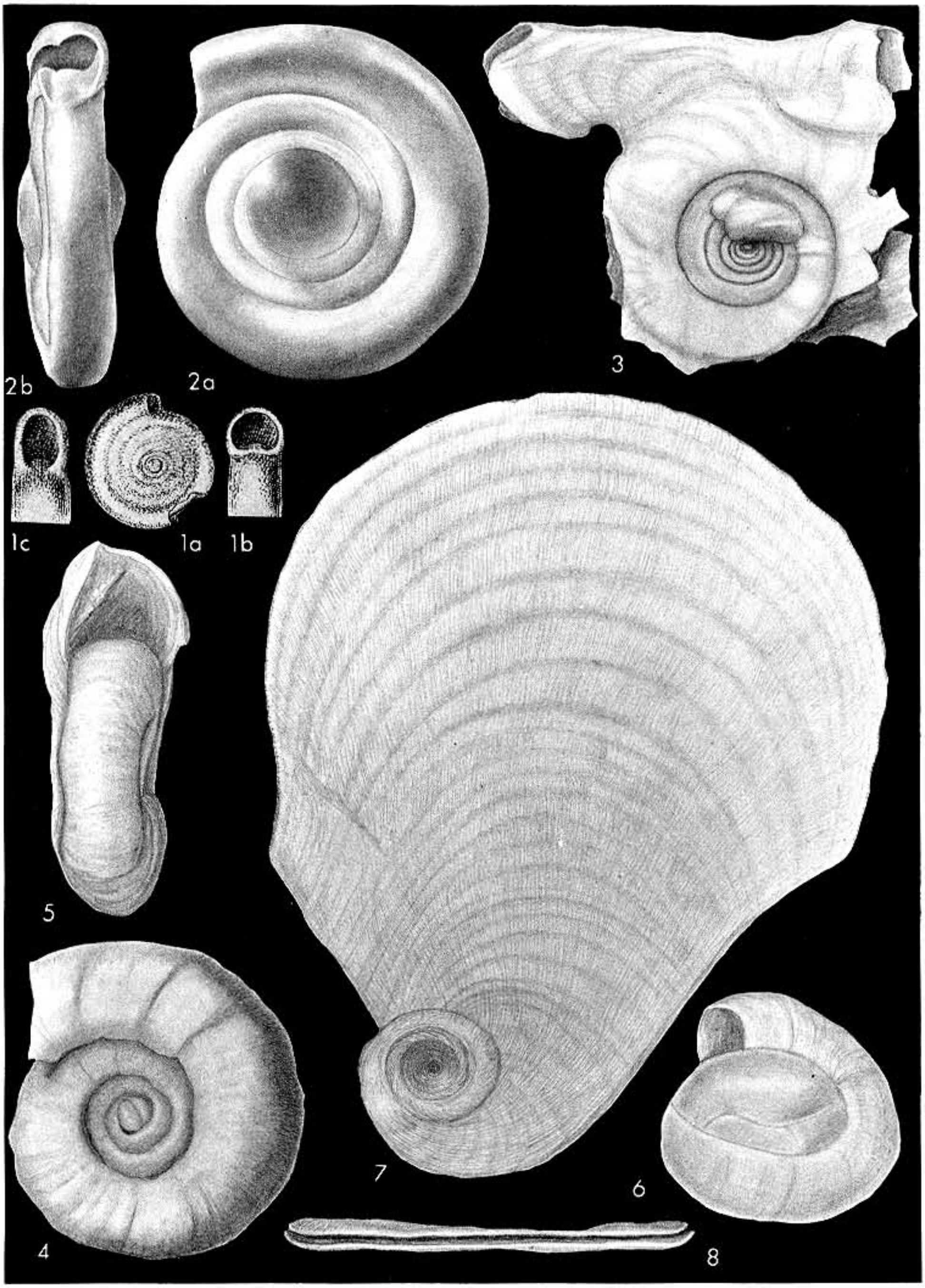


FIG. 329. Fischerinidae (Cyclogyrinae; *1,2, Cyclogyra; 3, Cornuspirella; 4-6, Gordiospira; 7,8, Cornuspiroides*) (p. C438-C439).

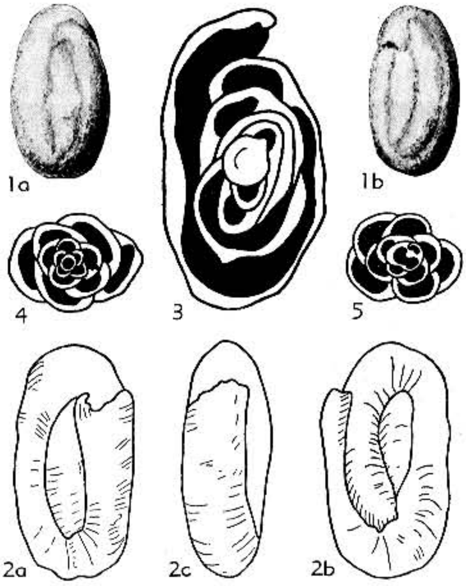


FIG. 330. Fischerinidae (Cyclogyrinae; *1-5, Agathammina*) (p. *C*438).

Family FISCHERINIDAE Millett, 1898

[*nom. transl.* Cushman, 1927, p. 40 (*ex* subfamily Fischerininae Millett, 1898, p. 611)]——[All names referred to are of family rank]——[=Cornuspirida Schultze, 1854, p. 52; =Cornuspiridae Reuss, 1860, p. 177; =Cornuspiridea Reuss, 1862, p. 364, 394; =Cornuspirideae Gümbel, 1870, p. 26; =Cornuspirida Haeckel, 1894, p. 185]

Test free or attached, proloculus followed by undivided tubular or spreading second chamber; wall calcareous, porcelaneous; aperture terminal, rounded or slitlike. [As redefined herein the Fischerinidae includes the subfamilies Cyclogyrinae, Fischerininae, and Calcivertellinae and differs from the Nubeculariidae in lacking development of separate chambers after the early cyclogyrine development.] *Carb.-Rec.*

Subfamily CYCLOGYRINAE Loeblich & Tappan, 1961

[Cyclogyrinae Loeblich & Tappan, 1961, p. 290 (*nom. subst. pro* subfamily Cornuspirinae Rhumbler, 1904, p. 284)]——[=Arcornuspirinia Rhumbler, 1913, p. 387 *(nom. van.)*; =Cornuspirininae Cushman, 1919, p. 633 *(nom. van.)*]

Proloculus followed by undivided second chamber; generally tubular and coiled, but adult variable; free or attached. *Carb.-Rec.*

Cyclogyra Wood, 1842, *2077, p. 458 [**C. multiplex*; OD (M)] [=*Cornuspira* Schultze, 1854, *1695, p. 40 (type, *Orbis foliaceus* Philippi, 1844, *1452A, p. 147); SD Cushman, 1917, *404f, p. 24; *Arcornuspirum* Rhumbler, 1913, *1572b, p. 387 *(nom. van.)*; *Conicocornuspira* Marie in Deleau & Marie, 1961, *580A, p. 74 (type, *C. conica* Marie, 1961)]. Test free, discoidal, consisting of globular proloculus and long undivided planispirally wound tubular second chamber, partly or wholly evolute; wall calcareous, imperforate, porcelaneous; aperture at the open end of the tube. *Carb.-Rec.*, cosmop.——Fig. 329,*1*. **C. multiplex*, Plio., Eng.; *1a*, side view of holotype, ×5.5; *1b,c*, apert. views, enlarged (*2077).——Fig. 329,*2*. *C. planorbis* (Schultze), Rec., Gulf Mex.; *2a,b*, side and apert. views of hypotype, ×224 (*2117).

[The synonymy of *Cornuspira* with *Cyclogyra* was noted by Loeblich & Tappan (1961, *1177, p. 290), and had been indicated questionably by Galloway (1933, *762, p. 109). *Orbis foliaceus* Philippi, 1844, was designated by Cushman, 1917 as type-species of *Cornuspira*, but in 1927, Cushman (*433, p. 188) changed the type designation to *Cornuspira planorbis* Schultze, 1854, stating that the previous designation was in error, as *C. foliacea* was not one of the names used by Schultze. However, as Schultze, 1854, p. 41 (footnote) definitely included *Orbis foliaceus* in the genus, the original designation of Cushman must stand. The two species are not conspecific.]

Agathammina Neumayr, 1887, *1354, p. 171 [**Serpula pusilla* Geinitz in Geinitz & Gutbier, 1848, *776, p. 6; SD Cushman, 1927, *433, p. 188]. Test ovate; globular proloculus followed by enrolled, nonseptate tubular second chamber, which coils in quinqueloculine manner; wall calcareous, imperforate with growth lines on surface but no internal subdivisions; aperture simple, terminal, may have thickened rim. [Commonly placed in the Miliolidae because of its quinqueloculine appearance, *Agathammina* has been shown to be nonseptate and is here transferred to the *Cyclogyrinae*. Agglutinated species placed herein by various authors should be reallocated, in the Ammodiscidae.] *Carb.-Perm., ?Trias., ?Jur.*, C.Eu.——Fig. 330,*1-5*. **A. pusilla* (Geinitz), U.Carb.(Namur.), Czech.; *1a,b*, opposite sides, ×117 (*1985); *2a-c*, opposite sides and edge view showing nonseptate character, ×25; *3*, long. sec. of megalospheric form, ×55; *4,5*, transv. secs. of microspheric and megalospheric forms, ×25 (*2070).

Cornuspirella Cushman, 1928, *436, p. 4 [**Cornuspira diffusa* Heron-Allen & Earland, 1913, *908, p. 272; OD]. Early portion as in *Cyclogyra*, planispiral and evolute, later rectilinear, spreading and branching in various directions but in plane of original coiling; aperture elongate, narrow, at ends of flattened branches. *Rec.*, N.Atl. ——Fig. 329,*3*. **C. diffusa* (Heron-Allen & Earland); lectotype (BMNH-ZF3578) from Goldseeker Station 41A, Haul 8265 at lat. 56°48′N., long. 1°19′E., at 94 m., showing branches in 2 directions and broken areas where other branches had formerly occurred, ×48 (*2117).

Cornuspiroides Cushman, 1928, *436, p. 3 [**Cornuspira striolata* Brady in Tizard & Murray, 1882, *1936, p. 713; OD]. Test free, large, flabelliform, early portion planispiral with coils increasing very gradually in diameter, later portion

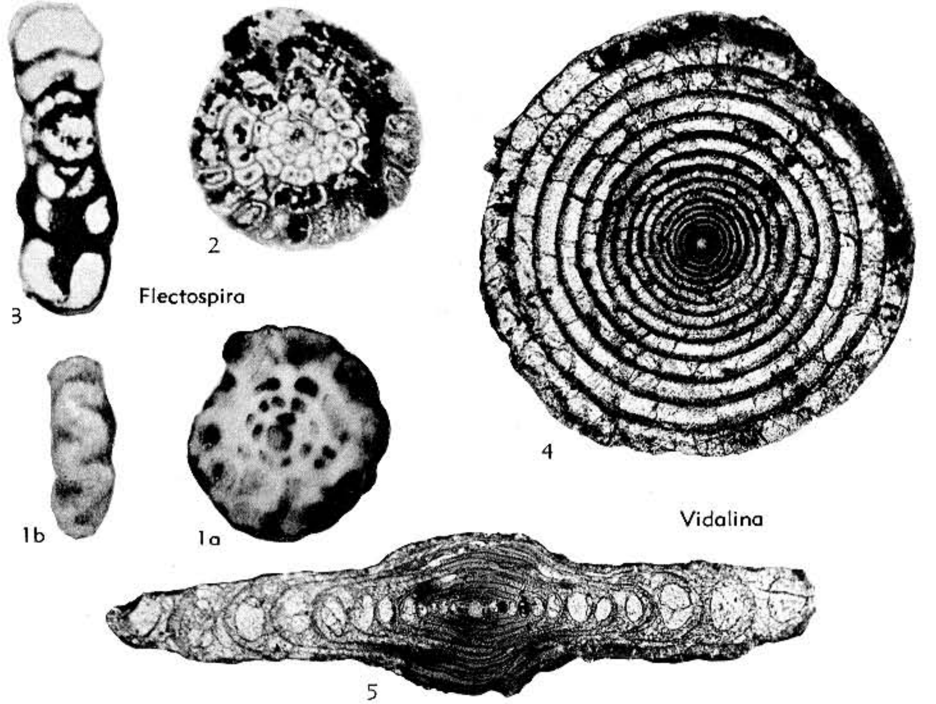


FIG. 331. Fischerinidae (Cyclogyrinae; *1-3, Flectospira; 4,5, Vidalina*) (p. C439-C441).

of coil increasing very rapidly in height and spreading out into an uncoiled, flattened and flabelliform portion, nonseptate but with distinct transverse growth lines and in type-species with fine vertical striae on surface; wall calcareous, milky white, imperforate; aperture narrow elongate slit at open end of expanded, flattened test. [*Cornuspiroides* differs from *Cyclogyra* in its later uncoiled, flabelliform development and from *Cornuspirella* Cushman in being unbranched in the later portion.] *Rec.*, Atl.——FIG. 329,*7,8*. **C. striolata* (Brady); *7*, side view of hypotype, ×5; *8*, apert. view of hypotype, ×5.5 (*2117).

Flectospira Crespin & Belford, 1957, *395, p. 76 [**F. prima*; OD]. Test discoidal, similar to *Meandrospira* in development but evolutely coiled, so that earlier whorls of zigzagging tubular second chamber are visible; aperture large, rounded, at open end of tube. *L.Perm.(Artinsk.)*, W. Australia.——FIG. 331,*1-3*. **F. prima; 1a,b*, side, edge views of holotype; *2*, equat. sec.; *3*, axial sec.; all ×77 (*395).

Gordiospira Heron-Allen & Earland, 1932, *914d, p. 254 [**G. fragilis*; OD (M)]. Test free, consisting of proloculus and long undivided second chamber, early portion coiling about proloculus in varying planes, becoming planispiral and partially involute in later portion; wall calcareous, imperforate, with numerous transverse wrinkles; aperture comprising broad arch at open end of tube. *Rec.*, Antarctic-Arctic.——FIG. 329, *4-6*. **G. fragilis*, S. Georgia Is.; *4*, large microspheric paratype, ×64; *5*, edge view (*914d, pl. 6, fig. 13), redrawn, showing crushing of test in the apertural region simulating a triangular aperture, ×64; *6*, small megalospheric paratype showing early irregular coiling and arched aperture, ×146 (*2117).

[*Gordiospira* differs from *Hemigordius* Schubert in possessing a thin, delicate test wall and in lacking lateral secondary thickening. It differs from *Cyclogyra* in the glomospiroid early coiling. Cushman (1948, *486, p. 193) stated that the aperture is "somewhat triangular." This was shown by the original figures and also by the edge view of the figure herein given of the same specimen, but it is due to the broken, slightly collapsed wall, which gives a pseudotriangular appearance. On uncrushed specimens the aperture is merely a broadly arched opening. The original specimens figured in side view are broken in the British Museum slides. Those here illustrated are from the same slide, however (BMNH-ZF3284).]

Hemigordiopsis Reichel, 1945, *1516, p. 528 [**H. renzi*; OD]. Test globular, consisting of globular proloculus followed by nonseptate second chamber, coiling streptospiral in early portion and later planispiral, involute, so that only final whorl is

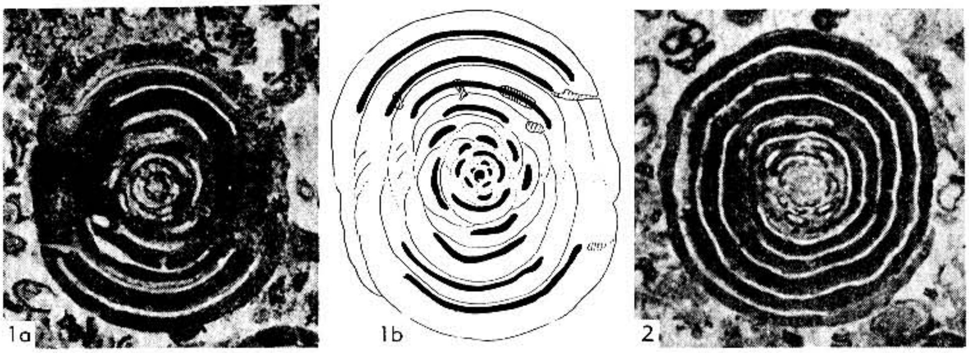


FIG. 332. Fischerinidae (Cyclogyrinae; *1,2, Hemigordiopsis*) (p. *C*439-*C*440).

visible externally; wall calcareous, porcelaneous, thick, chamber cavity much reduced. [*Hemigordiopsis* is similar to *Vidalina* and *Hemigordius* in its involute, later planispiral development, but differs from *Vidalina* in early streptospiral coiling, and differs from *Vidalina* and *Hemigordius* in its globular test resulting from very broad and low chambers.] *Perm.*, E.Medit.(Cyprus).——FIG. 332,*1,2*. **H. renzi*; *1a*, axial sec. of holotype (wall appears dark and chamber cavity light); *1b*, holotype, diagrammatic to show early streptospiral development and later planispiral coiling, ×20; *2*, equat. sec. of paratype showing nonseptate tube, ×20 (*1516).

Hemigordius Schubert, 1908, *1686, p. 381 [**Cornuspira schlumbergeri* Howchin, 1895, *967, p. 195] [=*Hemigordiella* Marie in Deleau & Marie, 1961, *580A, p. 75 (type, *Hemigordius calcarea* Cushman & Waters, 1928, *535, p. 44); *Ondogordius* Marie in Deleau & Marie, 1961, *580A, p. 78 (type, *O. campanula* Marie, 1961); *Neoangulodiscus* Kristan - Tollmann, 1962, *1059A, p. 230 (type, *N. leischneri*)]. Test similar to *Gordiospira*, with early whorls glomospiroid, later planispiral, but whorls involute, resulting in umbonal thickening. *Carb.-L.Jur.(Lias.)*, Australia-N.Am.-Eu.-USSR.——FIG. 333,*1*. **H. schlumbergeri* (Howchin), Carb., Australia; *1a-c*, opposite sides and edge of topotype, ×62 (*2117).

Meandrospira Loeblich & Tappan, 1946, *1154, p. 248 [**M. washitensis*; OD] [=*Streblospira* Crespin & Belford, 1957, *395, p. 74 (type, *S. meandrina*)]. Test free, small, composed of proloculus followed by tubular second chamber, which spirals streptospirally and involutely about proloculus in short zigzag bends, so that side view shows numerous loops reaching toward umbilicus, loops being formed by tubular chamber swinging back upon itself and only those of final whorl visible externally; wall calcareous, imperforate; aperture simple, terminal. *L.Perm.(Artinsk.)-Rec.*, N.Am.-Eu.-N.Afr.-Australia.——FIG. 333,*3*. **M. washitensis*, L.Cret.(Alb.), USA (Tex.); *3a-c*, holotype, opposite sides and edge views, ×211 (*2117).——FIG. 333,*4-6*. *M. meandrina* (Crespin & Belford). U.Perm., Australia; *4a-c*, opposite sides and edge views of holotype (in glycerine), ×53; *5*, equat. sec., ×90; *6*, axial sec., ×95 (*395).

[*Meandrospira* differs from *Calcitornella* and *Calcivertella*, both of which have a zigzag tubular second chamber, in being free living and enrolled, rather than attached to a flat substratum. *Streblospira* (L.Perm.) is a synonym and *Glomospira glomerata* Höglund (Rec., Sweden) also belongs to *Meandrospira*.]

Orthovertella Cushman & Waters, 1928, *535, p. 45 [**O. protea*; OD]. Proloculus followed by undivided tubular second chamber, streptospirally coiled in early portion, later becoming uncoiled; aperture at open end of tube. [Reytlinger (1950, *1560, p. 22) regarded *Orthovertella* as a synonym of *Lituotuba*, but *Orthovertella* has a porcelaneous rather than agglutinated wall.] *Penn.-Perm.*, N. Am.——FIG. 333,*2*. **O. protea*, Penn., USA (Tex.); *2a,b*, side, edge views of holotype, ×122 (*2117).

Rectocornuspira Warthin, 1930, *2040, p. 15 [**R. lituiformis*; OD]. Test differing from *Orthovertella* in being completely planispiral, rather than streptospiral in early stage, later portion uncoiled; wall porcelaneous; aperture rounded at open end of tube. *Penn.*, N.Am.——FIG. 333,*7*. **R. lituiformis*, USA(Okla.); *7a,b*, side, edge views, ×63 (*2117).

Vidalina Schlumberger, 1900, *1660, p. 459, 460 [**V. hispanica*; OD (M)] [=*Arvidaloum* Rhumbler, 1913, *1572b, p. 388 (obj.) (*nom. van.*)]. Test large, to 1.5 mm. in diam., with proloculus followed by planispirally enrolled, involute, nonseptate, tubular second chamber, involute whorls resulting in umbonal thickening; wall calcareous, imperforate; aperture at open end of tube. *U.Cret.*, Eu.——FIG. 331,*4,5*; 333, *8,9*. **V. hispanica*, Santon., Spain; 331,*4*, equat.

sec., ×45; 331,*5*, axial sec., ×85 (*1660); 333, *8a,b*, side, edge views of large paratype, ×23 (*2117); 333,*9a,b*, side, edge views of small hypotype, ×55 (*2117).

Subfamily FISCHERININAE Millett, 1899

[Fischerininae Millett, 1899, p. 611]

Few tubular chambers to whorl, planispiral or in conical spire; aperture at open end of final chamber. *Jur.-Rec.*

Fischerina Terquem, 1878, *1889, p. 80 (*non* Stuckenberg, 1904) [**F. rhodiensis*; OD (M)] [=*Planispirina* Seguenza, 1880, *1713, p. 310 (type, *P. communis*); *Trisegmentina* Wiesner, 1920, *2061, p. 18 (type, *T. compressa* Wiesner, 1931, *2063, p. 70, =*Hauerina compressa* Sidebottom, 1904, *non H. compressa* d'Orbigny, 1846, =*T. sidebottomi* Cushman, 1933)]. Test free, globular proloculus followed by enrolled nonseptate tubular chamber of nearly full coil in

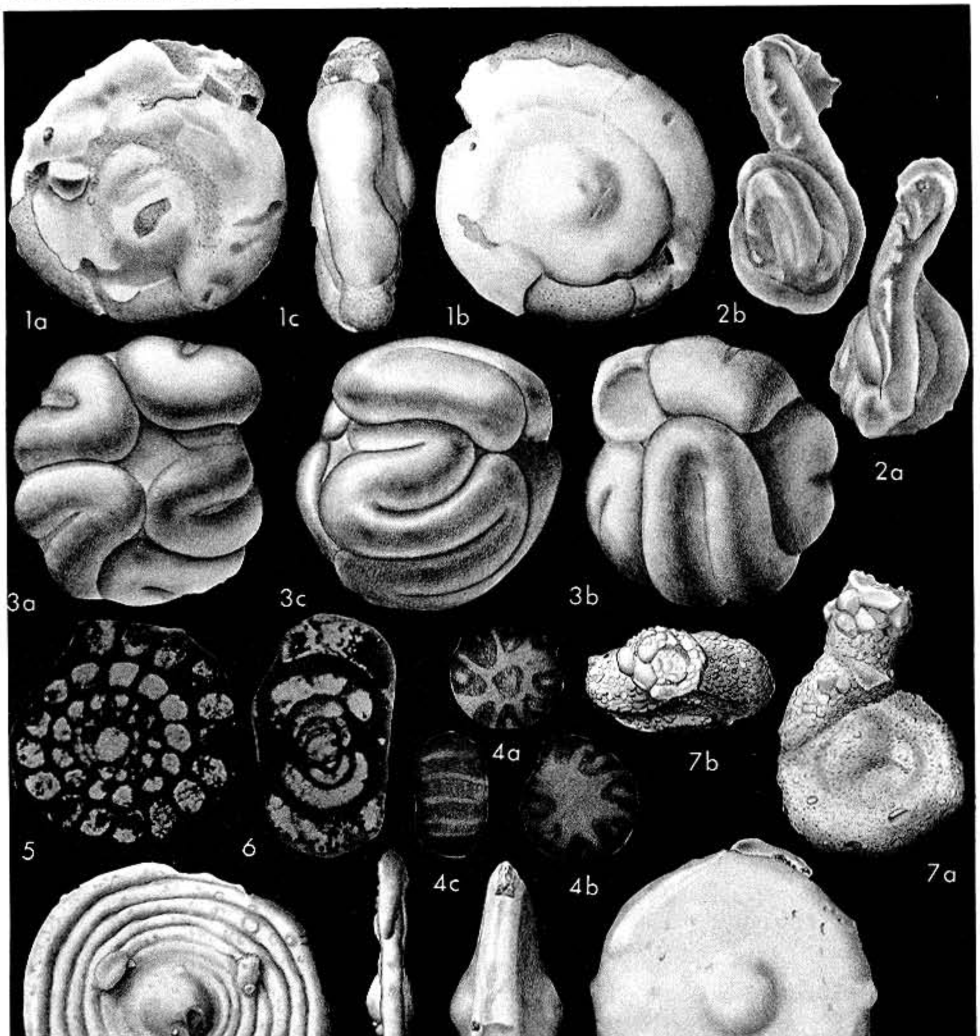


Fig. 333. Fischerinidae (Cyclogyrinae; *1, Hemigordius; 2, Orthovertella; 3-6, Meandrospira; 7, Rectocornuspira; 8,9, Vidalina*) (p. C440-C441).

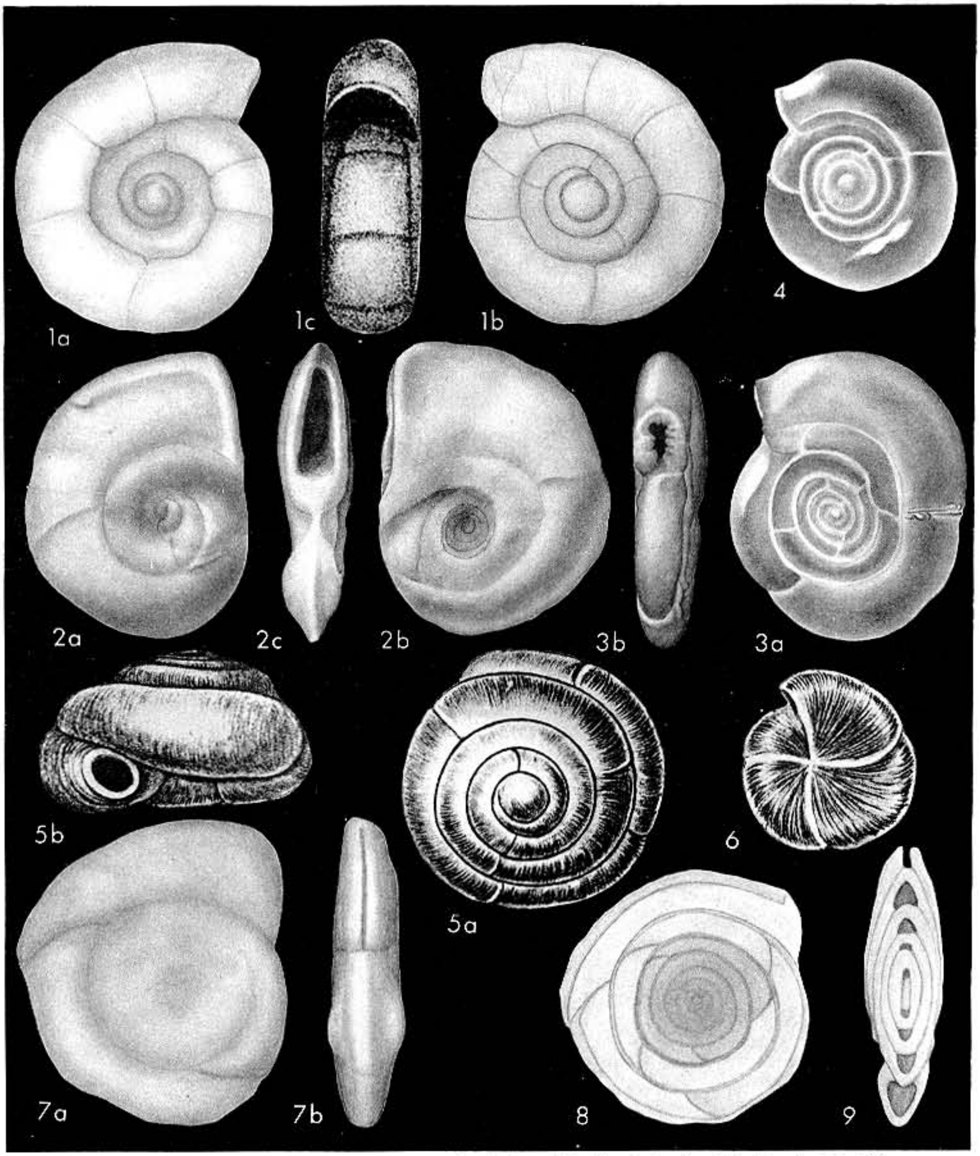


FIG. 334. Fischerinidae (Fischerininae; *1-4, Fischerina; 5,6, Fischerinella; 7-9, Planispirinella*) (p. *C*441-*C*443).

length, later chambers continuing about proloculus in planispiral coil; wall calcareous, thin, imperforate; aperture at open end of tube. *?Paleoc., Oligo.-Rec.*, cosmop.——FIG. 334,*1*. **F. rhodiensis*, Rec., Medit.; *1a,b*, opposite sides of holotype, ×79 (*2117); *1c*, edge view, ×79 (*1889).——FIG. 334,2. *F. communis* (SEGUENZA), Pleist., USA (Calif.); *2a-c*, opposite sides and edge views, ×115 (*2117).——FIG. 334,*3,4*. *F. compressa* (WIESNER), Rec., Medit.; *3a,b*, side, edge views of microspheric topotype; *4*, side view of megalospheric topotype; all ×111 (*2117).

[Although *Fischerina* is commonly described as trochospiral, with involute umbilical side, the holotype of the type-species, preserved in the Museum National d'Histoire Naturelle, Paris, is completely planispiral. *Fischerina* is therefore similar to *Cyclogyra*, but septate. *Trisegmentina* WIESNER was previously shown to be a junior synonym of *Planispirina* by LOEBLICH & TAPPAN (1955, *1166, p. 15), but with the redefinition of *Fischerina* TERQUEM to conform to the type-species, both *Trisegmentina* and *Planispirina* become synonyms of *Fischerina*. The original type of *Fischerina* was from the Pliocene, Isle of Rhodes, that of *Planispirina communis* from the Pliocene (Astian) of Sicily, and that of *Trisegmentina compressa* Wiesner from Recent of the Mediterranean. The nomenclature of this last species is discussed by Loeblich & Tappan (1955, *1166, p. 16). *P. communis* differs only in having somewhat more rapidly enlarging chambers and thus a higher arched opening, but the relative proportions are regarded as of specific importance only.]

Fischerinella Loeblich & Tappan, 1962, *1185, p. 108 [**Fischerina helix* Heron-Allen & Earland, 1915, *910b, p. 591; OD]. Test similar to *Fischerina* but with trochospiral coiling and involute umbilical side. *Rec.*, E.Afr.(Kerimba Arch.).——Fig. 334,*5,6*. **F. helix* (Heron-Allen & Earland); *5a,b,* spiral and edge views of large specimen; *6,* umbilical view of smaller form, all ×49 (*910b).

Nautiloculina Mohler, 1938, *1297, p. 18 [**N. oolithica*; OD]. Test free, planispirally enrolled, with numerous chambers in each whorl, completely involute and bilaterally symmetrical; wall calcareous, imperforate; aperture crescentic equatorial interiomarginal slit. [*Nautiloculina* differs from *Planispirinella* in its robust rather than flattened form and basal slitlike aperture, instead of a high vertical slit in the apertural face.] *Jur.*, Eu.(Switz.).——Fig. 335,*1-3*. **N. oolithica,* Raurac. *(1,2),* Sequan. *(3)*; *1,* equat. sec., ×75; *2,* equat. sec., central portion enlarged to show planispiral development, ×230; *3,* axial secs., ×75 (*1297).

Planispirinella Wiesner, 1931, *2063, p. 69 [**Hauerina exigua* Brady, 1879, *196b, p. 267; OD]. Test free, discoidal, planispiral and involute; proloculus followed by low, broad spiraling chambers, about 3 to whorl; sutures obscure, internal septa very thin and oblique; wall calcareous, imperforate, porcelaneous, composed of successive laminae developed with addition of each chamber, laminae each covering entire test, obscuring early chamber divisions externally; aperture high, elongate, subtriangular or slitlike opening extending up face of final chamber. *Tert.-Rec.*, Pac.O.——Fig. 334,*7-9*. **P. exigua* (Brady), Rec., *Challenger* Station 187-A, off Booby Island at 8 fathoms; *7a,b,* side, apert. views of lectotype, here designated and redrawn (BMNH-ZF3616 ex ZF2107); *8,* equat. sec. (BMNH-ZF2110); *9,* axial sec. (BMNH-ZF2108), ×79 (*2117).

Subfamily CALCIVERTELLINAE
Loeblich & Tappan, n. subfam.

Test attached, proloculus followed by nonseptate tubular second chamber. *Penn.-Jur.*

Calcivertella Cushman & Waters, 1928, *535, p. 48 [**C. adherens*; OD]. Test attached, with proloculus partially encircled by nonseptate tubular second chamber, which then has rectilinear development in closely appressed zigzag across attachment, and finally tends to spread; wall calcareous, porcelaneous; aperture at open end of tube. [*Calcivertella* differs from *Plummerinella* in having a rectilinear, rather than enrolled, zigzag development of chamber.] *Penn.-Perm.*, N.Am. ——Fig. 336,*1*. **C. adherens,* Penn., USA(Tex.); holotype, ×47 (*2117).

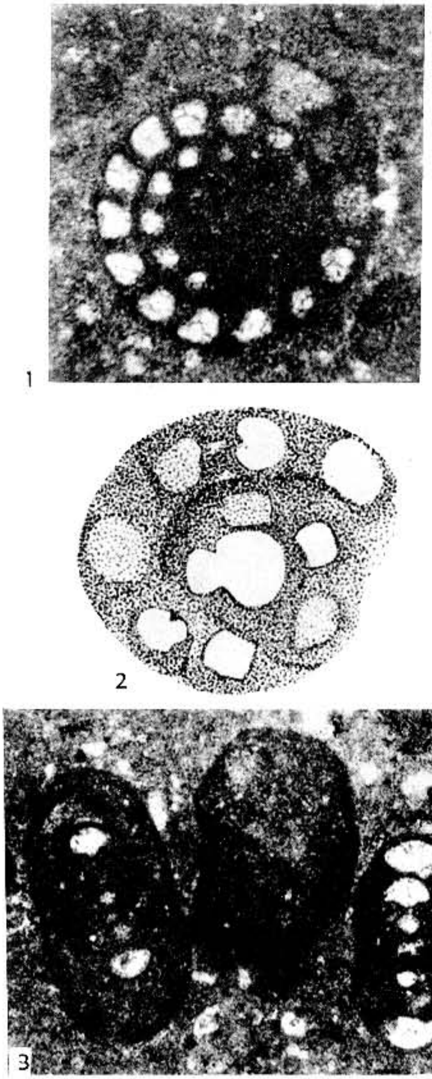


Fig. 335. Fischerinidae (Fischerininae; *1-3, Nautiloculina*) (p. C443).

Calcitornella Cushman & Waters, 1928, *535, p. 45 [**C. elongata*; OD] [=*Apterrinella* Cushman & Waters, 1928, *536, p. 64 (type, *Tolypammina grahamensis* Harlton, 1928, *880, p. 305)]. Test attached, proloculus followed by nonseptate enrolled portion, later uncoiling and winding irregularly across attachment; wall calcareous, porcelaneous; aperture terminal. [The attached side of the holotype of *Calcitornella elongata* shows irregularly spaced transverse thickenings which give the appearance of septa in the early portion,

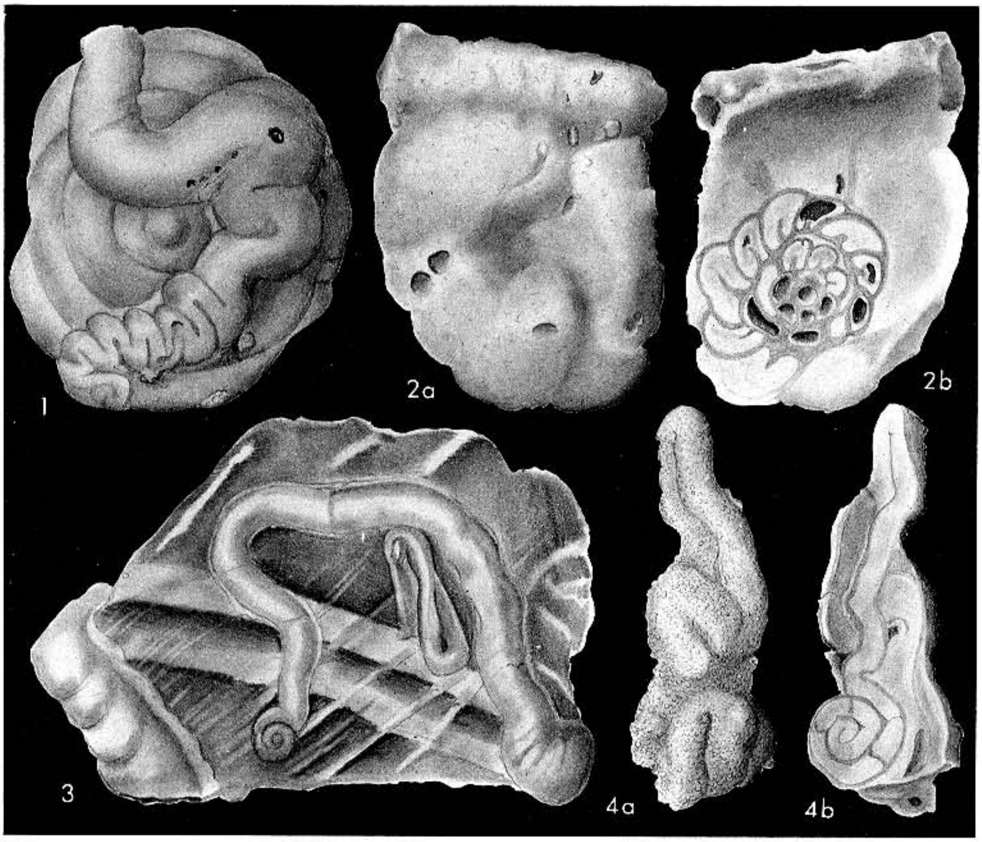


FIG. 336. Fischerinidae (Calcivertellinae; *1, Calcivertella; 2, Plummerinella; 3,4, Calcitornella*) (p. C443-C444).

but apparently are only thickenings of the attached wall and not true septa. The later portion is definitely nonseptate. *Apterrinella* is here regarded as a synonym of *Calcitornella,* as the two are similar in all respects. The actual form of the test depends largely on the area of the attachment and both type-species grow back upon themselves to some extent.] *Penn.-Jur.,* N.Am.-Eu.——FIG. 336,*3*. *C. grahamensis* (Harlton), Penn., USA(Tex.); holotype, ×35 (*2117).——FIG. 336,*4*. **C. elongata,* Penn., USA(Tex.); *4a,b,* free and attached sides of holotype, ×53 (*2117).

Carixia Macfadyen, 1941, *1200, p. 27 [**C. langi*; OD]. Test attached, consisting of unsegmented tubes radiating from central point and anastomosing over surface of substratum; wall calcareous, imperforate, with attachment of calcareous cement; apertures formed by simple open ends of tubes. *Jur.,* G.Brit.(Eng.).——FIG. 337,*1*. **C. langi*, Lias., hypotype, ×80 (*2117).

Planiinvoluta Leischner, 1961, *1128, p. 11 [**P. carinata*; OD]. Test flattened, discoidal, probably originally attached; with globular proloculus and nonseptate planispirally enrolled second chamber, evolute on one side, involute on opposite side, which as a result is centrally inflated. [Described from thin sections, the genus is not completely known. As the flattened side suggests an attached condition, the genus is here placed in the Calcivertellinae.] *U.Trias.(Rhaet.),* Eu.(Aus.).——FIG. 337,*3-5*. **P. carinata; 3,* axial sec. of holotype; *4,5,* equat. secs., ×100 (*1128).

Plummerinella Cushman & Waters, 1928, *535, p. 49 [**P. complexa*; OD]. Test attached, development otherwise similar to *Meandrospira* in early stage, with tubular nonseptate second chamber enrolled about proloculus in zigzag pattern, later spreading and tending to uncoil; wall calcareous, porcelaneous; aperture at open end of tube. *Penn.,* N.Am.——FIG. 336,*2*. **P. complexa,* USA(Tex.); *2a,b,* opposite sides of holotype, ×73 (*2117).

Family SQUAMULINIDAE Reuss, 1862

[*nom. correct.* Loeblich & Tappan, herein (*pro* family Squamulinidea Reuss, 1862, p. 364, and Squamulinida Haeckel, 1894, p. 190)]

Test single-chambered, attached. *Rec.*

Squamulina Schultze, 1854, *1695, p. 56 [**S.*

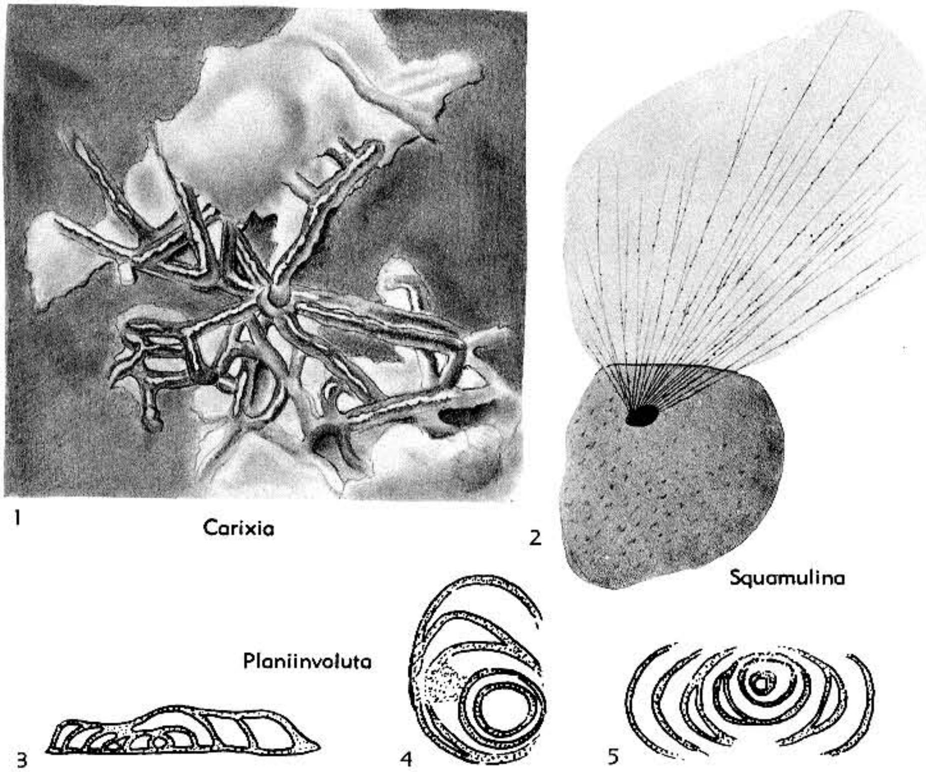


FIG. 337. Fischerinidae (Calcivertellinae; *1, Carixia; 3-5, Planiinvoluta*); Squamulinidae; *2, Squamulina* (p.*C*444-*C*445).

laevis; OD(M)] [=*Arsquamulum* Rhumbler, 1913, *1572b, p. 346 (obj.) *(nom. van.)*]. Test attached, consisting of single inflated chamber with calcareous imperforate wall; aperture rounded on upper surface. *Rec.*, Eu.(Baltic Sea).——FIG. 337,2. **S. laevis*; ×72 (*1695).

Family NUBECULARIIDAE Jones, 1875

[*nom. correct.* Avnimelech & Reiss in Avnimelech, Parness & Reiss, 1954, p. 838 (*pro* family Nubecularida Jones in Griffith & Henfrey, 1875, p. 319, and Nubecularidae Lister in Lankester, 1903, p. 143)]——[All names referred to are of family rank]——[=Inequilateralidae d'Orbigny in de la Sagra, 1839, p. 26 *(nom. nud.)*; =Inaequilateralidae d'Orbigny, 1846, p. 73 *(nom. nud.)*; =Ovulinetta Haeckel, 1894, p. 164 *(nom. nud.)*]——[=Nubecularina Lankester, 1885, p. 846; =Nubecularinae Delage & Hérouard, 1896, p. 122]——[=Opthalmidiidae Cushman, 1927, p. 36; *(nom. imperf.)*; =Ophthalmidiidae Cushman, 1928, p. 159; =Ophtalmidiidae Le Calvez, 1935, p. 96 *(nom. van.)*; =Ophthalmididae Dogel, 1951, p. 464 *(nom. van.)*; =Vertebralinidae Pokorný, 1958, p. 251; =Calcitubida Haeckel, 1894, p. 185]

Test free or attached, planispiral or irregularly coiled, at least in early stages, later spreading or branched; aperture simple, rounded or slitlike or more rarely cribrate. *M.Carb.-Rec.*

Subfamily NUBECULARIINAE Jones, 1875

[*nom. correct.* Chapman, 1901, p. 169 (*pro* subfamily Nubecularinae Brady, 1884, p. 61, *nom. transl. ex* family Nubecularida Jones, 1875)] [=Nubeculinellinae Avnimelech & Reiss in Avnimelech, Parness & Reiss, 1954, p. 838]

Test attached, early stage coiled, later may be irregular. *Jur.-Rec.*

Nubecularia Defrance, 1825, *579f, p. 210 [**N. lucifuga*; OD (M)]. Test attached, early portion in cornuspirine coil, later stage chambered, may continue coiling or become linear but varies considerably in shape according to substratum, terminal portion may grow away from substratum as tubular projection; wall calcareous, imperforate, commonly incorporates small grains of sand; aperture elongate slit at attachment when specimen is attached, but becoming rounded with lateral toothlike infoldings of walls when growing free. *Jur.-Rec.*, cosmop.——FIG. 338,*1-3*. **N. lucifuga*, M.Eoc.(Lutet.), Fr.; *1*, specimen showing attached side; *2*, specimen with free-growing final portion and infolded apertural margin; *3*, top view of specimen showing restricted aperture, ×25 (*2117).

[Galloway (1933, *762, p. 116) stated that the genus does not have a lower wall. However, specimens of the type-species show a complete lower wall, others show various stages between this and an absence of a lower wall, so that it seems that this character may be due to nature of the substratum. Apparently, infolding of the apertural wall has not been previously noted for this species, although it is shown on approximately half of the specimens from the Lutetian at Grignon, France. The original illustrations of DEFRANCE were at very low magnification and did not show this feature. Most other references to the species have been to Recent specimens, which probably belong to a distinct species, as some show much closer coiling, with more numerous chambers, and others are coarsely agglutinated. The original types were from the *Calcaire coquillier grossier* (Lutetian) at *la falunière de Hauteville, Dept. de la Manche,* France.]

Calcituba VON ROBOZ, 1884, *1580, p. 420 [**C. polymorpha*; OD]. Test attached to algae, con-

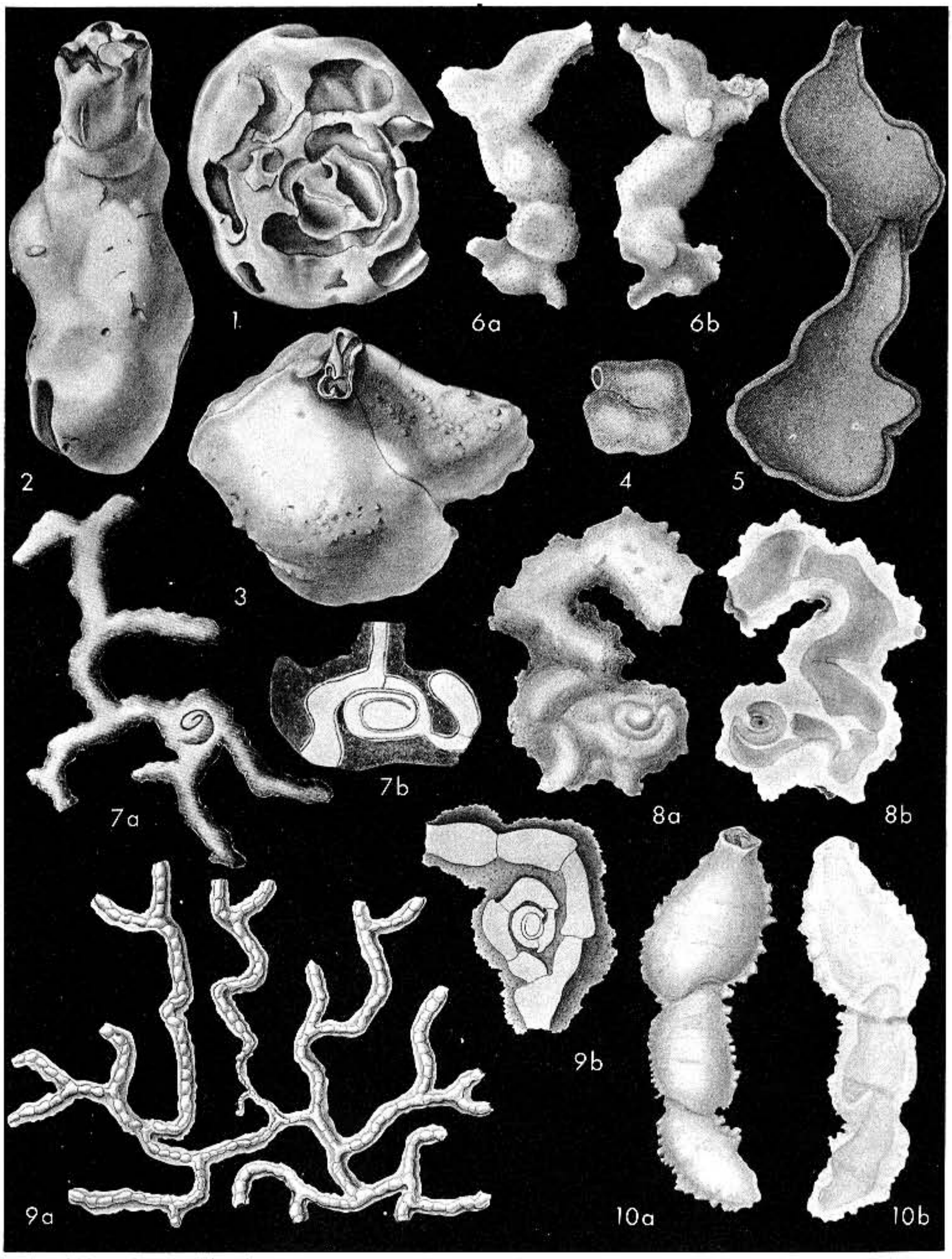


FIG. 338. Nubeculariidae (Nubeculariinae; *1-3, Nubecularia; 4-6, Calcituba; 7-9, Cornuspiramia; 10, Webbina*) (p. C445-C448).

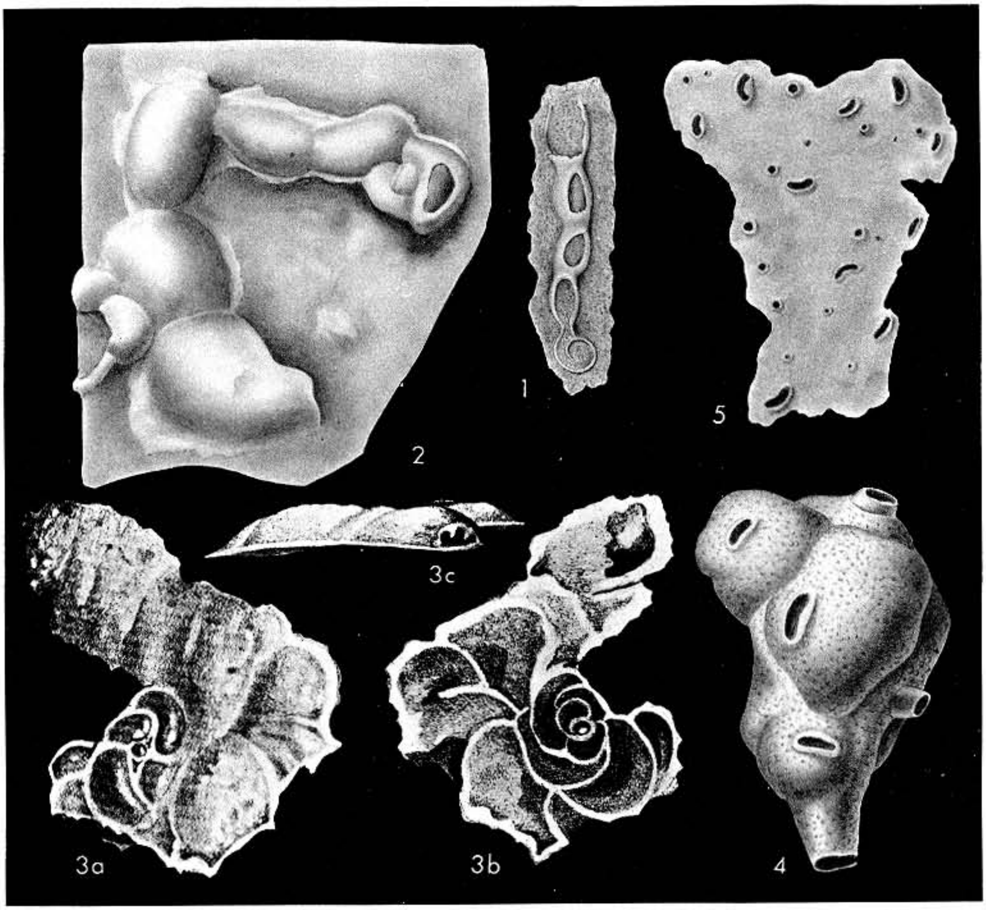


FIG. 339. Nubeculariidae (Nubeculariinae; *1,2, Nubeculinella; 3, Nubeculopsis; 4,5, Sinzowella*) (p. *C*447-*C*448).

sisting of irregular elongate chambers, uniserial or branching; wall calcareous, porcelaneous; aperture rounded, terminal, on one or more chambers. *Rec.*, Adriatic Sea-Gulf Mex.——FIG. 338, *4-6*. *_C. polymorpha_, Adriatic *(4,5)*, Gulf Mex. *(6)*; *4*, young form showing spiral appearance, ×50; *5*, optical sec. of 2-chambered form, ×150 (*1580); *6a,b*, opposite sides of larger specimen, ×56 (*2117).

Cornuspiramia CUSHMAN, 1928, *436, p. 4 [*_Nubecularia antillarum_ CUSHMAN, 1922, *416, p. 58; OD] [=_Rhizonubecula_ J. LE CALVEZ, 1935, *1102, p. 96 (type, *R. adherens*)]. Test attached, proloculus followed by enrolled tubular second chamber of nearly 1 complete volution in length, and later subpyriform chambers in irregularly rectilinear series, later dichotomously branching over substrate. [*Cornuspiramia* was originally described as a nonchambered, tubular, attached form, as the chambers are difficult to distinguish externally on attached specimens. On specimens which have broken free of attachment the chamber development can be seen.] *Rec.*, Gulf Mex.-Carib.-Medit.——FIG. 338,*7,8*. *_C. antillarum_ (CUSHMAN), Gulf Mex. *(7)*, Carib. *(8)*; *7a,b*, ext. and attached side, enlarged (*436); *8a,b*, dorsal and attached surfaces showing chamber development, ×73 (*2117).——FIG. 338,9. *C. adherens* (J. LE CALVEZ), Medit.; *9a*, entire specimen, ×7; *9b*, early portion enlarged to show chamber development, ×50 (*1102).

Nubeculinella CUSHMAN, 1930, *446, p. 133 [*_N. bigoti_; OD]. Test attached, consisting of proloculus followed by second chamber coiling around first, varying from half coil to one and one-half coils in length, forms with smaller proloculus followed by longer and more enrolled second chamber, later chambers elongate-ovate to irregular in outline, uniserially arranged but winding somewhat upon shell fragments to which they attach; wall calcareous, imperforate, milky white; aperture semi-circular opening against substratum. [Differs from *Nubecularia* in its more regular chamber development, with early coil followed by uncoiled portion.] *U.Jur.*, Eu.——Fig. 339,*1,2*. **N. bigoti*, Oxford., Fr.; *1*, holotype (*446); *2*, paratype, ×65 (*2117).

Nubeculopsis Collins, 1958, *375, p. 375 [**N. queenslandica*; OD]. Test attached, similar to *Nubeculinella* but early portion with arcuate chambers forming early coil, instead of nonseptate tube coiling around proloculus, later chambers tending to uncoil; aperture terminal arch against attachment, with infolded teeth, similar to those in *Nubeculina*. *Rec.*, Australia.——Fig. 339,*3*. **N. queenslandica*; *3a*, upper surface of holotype; *3b*, surface of attachment; *3c*, top view showing apert. teeth; all ×66 (*375).

Sinzowella Cushman, 1933, *458, p. 33 [**Nubecularia novorossica* var. *deformis* Karrer & Sinzow, 1877, *1024, p. 283; OD]. Test to 10 mm. in length, attached, early stage planispiral as in *Cyclogyra*, later with globular chambers forming irregular mass; wall calcareous, porcelaneous, thick; elongate reniform aperture with bordering lip on each of globular chambers. *Mio.*, Eu.——Fig. 339,*4,5*. **S. deformis* (Karrer & Sinzow), Sarmat., Rumania; *4*, ext. showing globular chambers and apertures; *5*, long. sec. showing thick walls, enlarged (*1024).

Webbina d'Orbigny in de la Sagra, 1839, *1611, p. 26 [**W. rugosa* d'Orbigny in Barker-Webb & Berthelot, 1839, *86, p. 126; SD (SM)] [=*Webbum* Rhumbler, 1913, *1572b, p. 444 (type, *Webbina rugosa* d'Orbigny, SD Loeblich & Tappan, herein); *Arwebbum* Rhumbler, 1913, *1572b, p. 445 *(nom. van.)*]. Test attached by entire lower surface, chambers few in number, inflated, surface marked by faint transverse "growth lines," margins of chambers bordered by fimbriate "keel"; wall thin, calcareous, appearing milky white and imperforate, surface smooth except for transverse wrinkles; aperture terminal, with bordering lip. *Rec.*, Atl.-Timor Sea. ——Fig. 338,*10*. **W. rugosa*, Atl.; *10a,b*, holotype, showing convex chambers on free side and opposite side flattened against attachment, ×58 (*2117).

[Although commonly placed with the perforate calcareous genera, in the Cibicidinae (*762, p. 296; *486, p. 339; *1509, p. 287), the holotype, in the Museum National d'Histoire Naturelle, Paris, has a porcelaneous and imperforate wall, the "rugose" appearance being due merely to surface wrinkles. The genus was redefined by Loeblich & Tappan (*1166, p. 23) and is here transferred to the Nubeculariinae. Specimens of *Webbina* recently have been obtained from the Sahul Shelf, northern Australia, at a depth of 72 fathoms.]

Subfamily OPHTHALMIDIINAE Wiesner, 1920

[Ophthalmidiinae Wiesner, 1920, p. 17]——[All names of subfamily rank]——[=Trisegmentininae Wiesner, 1920, p. 17, 18; =Miliolidae holostreptae Eimer & Fickert, 1899, p. 688 *(nom. nud.)*; =Opthalmidiinae Cushman, 1927, p. 37 *(nom. van.)*; =Planispirinellinae Wiesner, 1931, p. 58, 60, 69, 110]

Test free, proloculus and undivided planispirally coiled chamber followed by irregular later chambers. *M.Carb.-Rec.*

Ophthalmidium Kübler & Zwingli, 1870, *1061, p. 46 [*pro Oculina* Kübler & Zwingli, 1866, *1060, p. 11 (*non* Lamarck, 1816)] [**Oculina liasica* Kübler & Zwingli, 1866, *1060, p. 11; OD] [=*Spiropthalmidium* Cushman, 1927, *431, p. 37 *(nom. imperf.)* (type, *Spiroloculina acutimargo* Brady, 1884, *200, p. 154); *Spirophthalmidium* Galloway, 1933, *762, p. 112 *(nom. correct.*, obj.)]. Test free, ovate to fusiform in outline, flattened, consisting of globular proloculus followed by spirally wound second chamber of one-half to complete whorl in length, later chambers one-half coil in length and regularly added, chambers may taper slightly from early portion to oral end, and may be loosely coiled with flattened plate between whorls; wall calcareous, imperforate, porcelaneous; aperture rounded to ovate, at end of final chamber. *U. Trias.-Rec.*, cosmop.——Fig. 340,*1*. **O. liasica* (Kübler & Zwingli), U.Lias., Eu.(Switz.); holotype (small megalospheric specimen), ×14 (*2071).——Fig. 340,*2*. *O. acutimargo* (Brady), Rec., S.Atl.O.; *2a,b*, side and top views of topotype, ×48 (*2117).

Cornuloculina Burbach, 1886, *253b, p. 497 [**Hauerina inconstans* Brady, 1879, *196b, p. 268; SD Loeblich & Tappan, herein] [=*Hauerinella* Schubert, 1921, *1694, p. 162 (obj.)]. Test free, planispirally coiled and evolute, globular proloculus followed by planispirally wound tubular second chamber of up to 3 whorls, followed by chambers of approximately one-half coil in length, or slightly less, resulting in 2.5 to 3 chambers to whorl in later stages, chambers somewhat loosely coiled, those of adjacent whorls being separated by thin plate; wall calcareous, imperforate; aperture at open end of final chamber. [*Cornuloculina* is separated from *Ophthalmidium* in the less regular coiling with more than 2 chambers in each whorl.] *Jur.-Rec.*, S.Atl.O.-S. Pac.O.-Eu.——Fig. 340,*3-7*. **C. inconstans* (Brady), off Brazil *(3-6)*, S.Pac. *(7)*; *3-5*, topotypes, showing various stages of development from early planispiral tubular chamber to 2 or more chambers to whorl, ×31 (*2117); *6*, microspheric topotype in transmitted light, ×30; *7*, megalospheric hypotype in transmitted light, ×50 (*2074).

Edentostomina Collins, 1958, *375, p. 370 [**Miliolina cultrata* Brady, 1879, *196c, p. 45; OD]. Test compressed, ovate, apparently planispiral, with chambers one-half coil in length; wall porcelaneous, surface smooth, longitudinally striate or pitted; aperture terminal, commonly somewhat produced, with thickened rim, without apertural teeth, but may be ovate, slitlike, or cruciform. *Rec.*, Indo-Pac.O.——Fig. 341,*1*. **E. cultrata* (Brady), Malay Arch.; *1a-c*, opposite sides and apert. view showing planispiral development, ×40 (*1284a).——Fig. 341,*2*. *E. milletti* (Cushman); specimen mounted in balsam and viewed in transmitted light to show chamber arrangement, exterior suture lines omitted, ×40 (*1284a).

[The original description stated in part, "Test triloculine or biloculine . . . last two chambers added at approximately 180°, . . . aperture oval with a thickened rim and no tooth." In addition to the type-species, *Miliolina durrandii* MILLETT, *Miliolina rupertiana* BRADY, and *Biloculina milletti* CUSHMAN were transferred to *Edentostomina.*

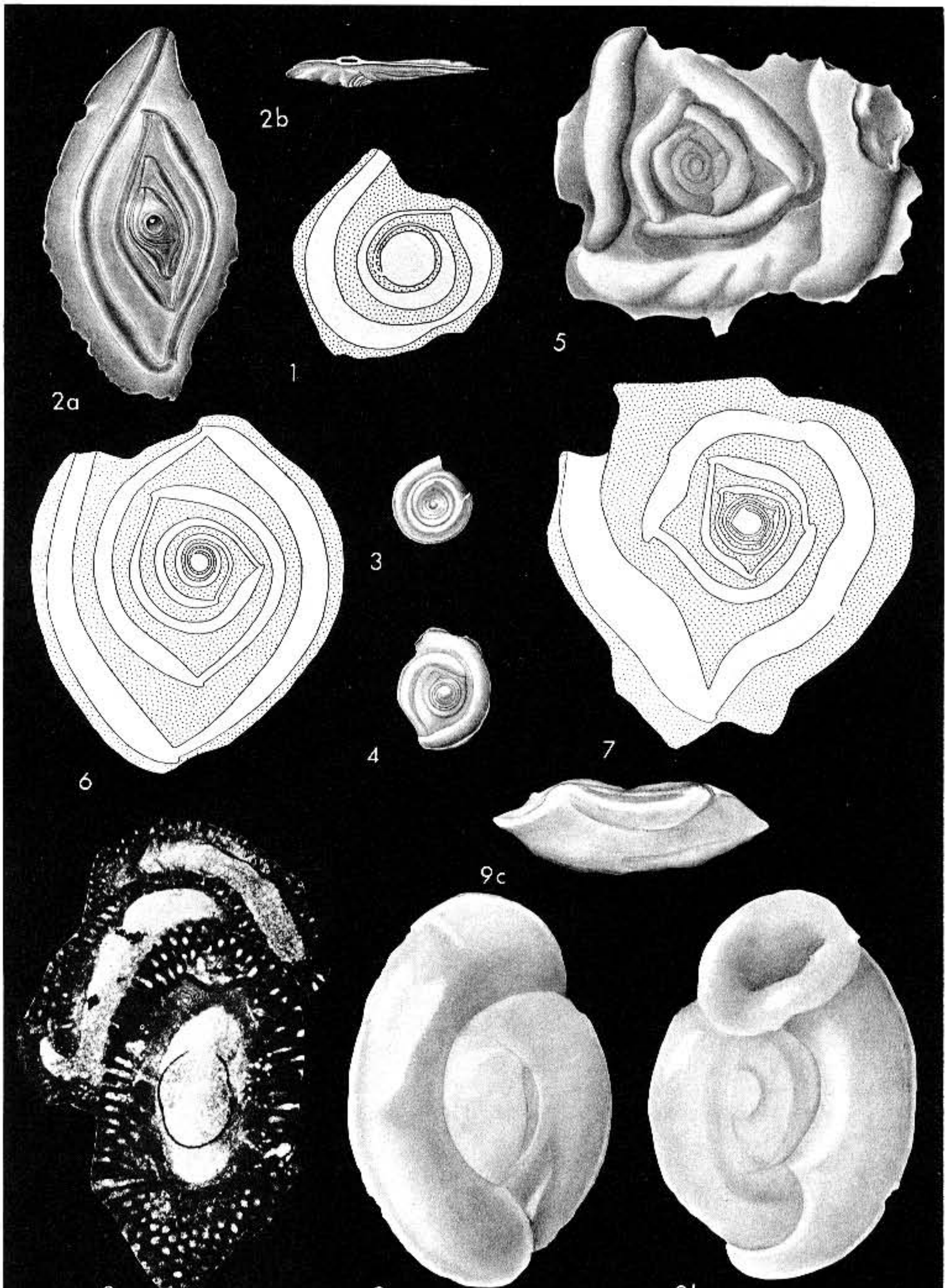


FIG. 340. Nubeculariidae (Ophthalmidiinae; *1,2, Ophthalmidium; 3-7, Cornuloculina; 8, Pseudovermiporella; 9, Wiesnerella*) (p. C448, C450-C452).

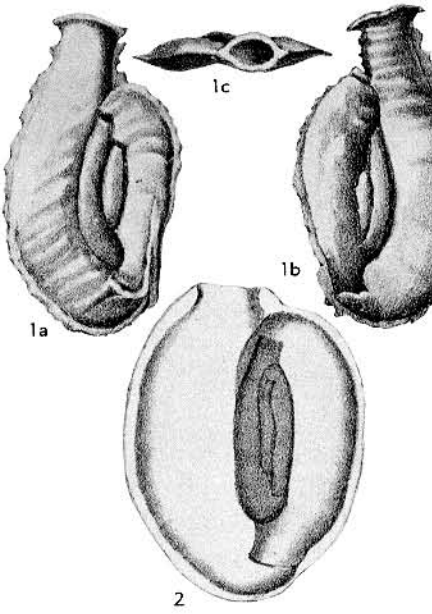


Fig. 341. Nubeculariidae (Ophthalmidiinae; *1,2, Edentostomina*) (p. *C*448-*C*450).

None of these species shows a typical triloculine development or is typically miliolid, since in most species the same number of chambers is visible on both sides (4 on each side in *E. durrandii*, and in Millett's specimens of *E. cultrata* whereas Brady figured one side only of 2 different specimens, and 2 on each side in *E. milletti*). Only in *Miliolina rupertiana* does a suggestion of asymmetry appear, although no figures have been published showing both sides of a single specimen. The views of *E. milletti* in transmitted light given by Millett (Fig. 341,*2*) also appear to show a planispiral development. For this reason, and because of the absence of an apertural tooth, *Edentostomina* is here transferred to the Ophthalmidiinae.]

Eosigmoilina Ganelina in Kiparisova, *et al.*, 1956, *1040, p. 17 [**E. explicata*; OD]. Test compressed-ovate, globular proloculus followed by nonseptate tubular second chamber in glomospirine coil, later portion with 2 chambers to whorl and development as in *Sigmoilina*, with plane of coiling gradually changing to form sigmoid curve as seen in transverse section; septa very thin; wall calcareous, imperforate, thin, aperture simple rounded opening at end of final chamber. [Originally placed in the Miliolidae, this genus is here transferred to the Ophthalmidiinae, family Nubeculariidae, because of its nonseptate enrolled second chamber and later milioline development, and the simple apertural opening.] *M.Carb.*, USSR(Dnieper-Donets Basin)-Eu. (Czech.).——Fig. 342,*1,2*. **E. explicata,* USSR; *1a-c,* opposite sides and edge views of paratype, ×100; *2,* long. sec. showing change in axis of coiling, ×150 (*1040).

Galeanella Kristan, 1958, *1058, p. 114 [*pro Galea* Kristan, 1957, *1057, p. 291 (*non* Meuschen, 1787; *nec* Meyen, 1833; *nec* Moerch, 1852)] [**Galea tollmanni* Kristan, 1957, *1057, p. 291; OD]. Test consisting of globular proloculus and enrolled close-coiled later chambers, which taper distally as in *Ophthalmidium,* whorls or chambers scarcely perceptible from exterior; wall calcareous, porcelaneous and thick, leaving only small chamber cavities, may form thickened rim or keel of test; in thin section few large pore canals seen to pierce thickened wall; aperture rounded opening with radial grooves radiating from it across depressed apertural face. *U.Trias.(Rhaet.),* Eu. (Aus.).——Fig. 342,*6-8*. **G. tollmanni* (Kristan); *6a-d,* opposite sides and opposite edge views of holotype; *7a,* tang. sec. showing pore canals leading from proloculus; *7b,* parallel but deeper section, showing numerous tapering chambers, thick walls and pore canals; *8,* vert. long. sec.; all ×35 (*1057).

Glomulina Rhumbler, 1936, *1575, p. 198 [**G. fistulescens*; OD]. Test free, globular, proloculus followed by cyclogyrine tubular second chamber, later streptospirally coiled with chambers half coil in length; wall calcareous, imperforate; aperture rounded, terminal. *Rec.,* Baltic Sea.——Fig. 342,*3*. **G. fistulescens; 3a,b,* opposite sides; 3c, specimen viewed as in *3a* but in transmitted light to show chamber arrangement, ×45 (*1575).

[The genus was described as having secondary apertures on fistulose projections along the final chamber, as can be seen in the figure. It is uncertain, however, whether this is a characteristic of the foraminifer, or due to a parasite or other abnormal growth.]

Ophthalmina Rhumbler, 1936, *1575, p. 217 [**O. kilianensis*; OD]. Test compressed, planispiral, proloculus followed by nonseptate cyclogyrine stage and later with 2 chambers to whorl; wall calcareous, imperforate; aperture at open end of final chamber. [*Ophthalmina* superficially resembles *Wellmanella* and *Pseudomassilina* but differs in having an early planispiral stage instead of early milioline one, and differs from *Pseudomassilina* in the simple, nonpitted or canaliculate wall. It differs from *Hauerinella* and *Zoyaella* in having only 2 chambers to each whorl.] *Rec.,* Eu.(N.Ger.).——Fig. 342,*9-11*. **O. kilianensis; 9a,b,* opposite sides, ×50; *10,* ext., ×70; *11,* axial sec., ×70 (*1575).

Pseudovermiporella Elliott, 1958, *698, p. 419 [**P. sodalica*; OD]. Test large, irregular, consisting of meandriform tubes, to 1.4 mm. diam., which may be free-growing and circular in section or closely appressed or attached and hemispherical in form; wall of finely crystalline calcite, pierced by numerous, closely set perforations, about 50 visible in single transverse section, in tangential section coarse pores appear to form round-pored mesh, inner continuous solid dark calcareous layer occurring within outer radially perforated layer, probably of secondary origin. [Originally regarded as questionably a primitive dasyclad alga, although also compared to foraminifers and bryozoans, this genus was later regarded as a true foraminifer (Henbest, 1960, *898, p. B387).] *Perm.,*SW.Asia(Arabia)-N.Afr.(?Tunisia)-

?Japan.——Fig. 340,*8*. **P. sodalica,* Arabia; holotype showing meandriform tubes and coarse perforations appearing as mesh in tang. section, ×28 (*698).

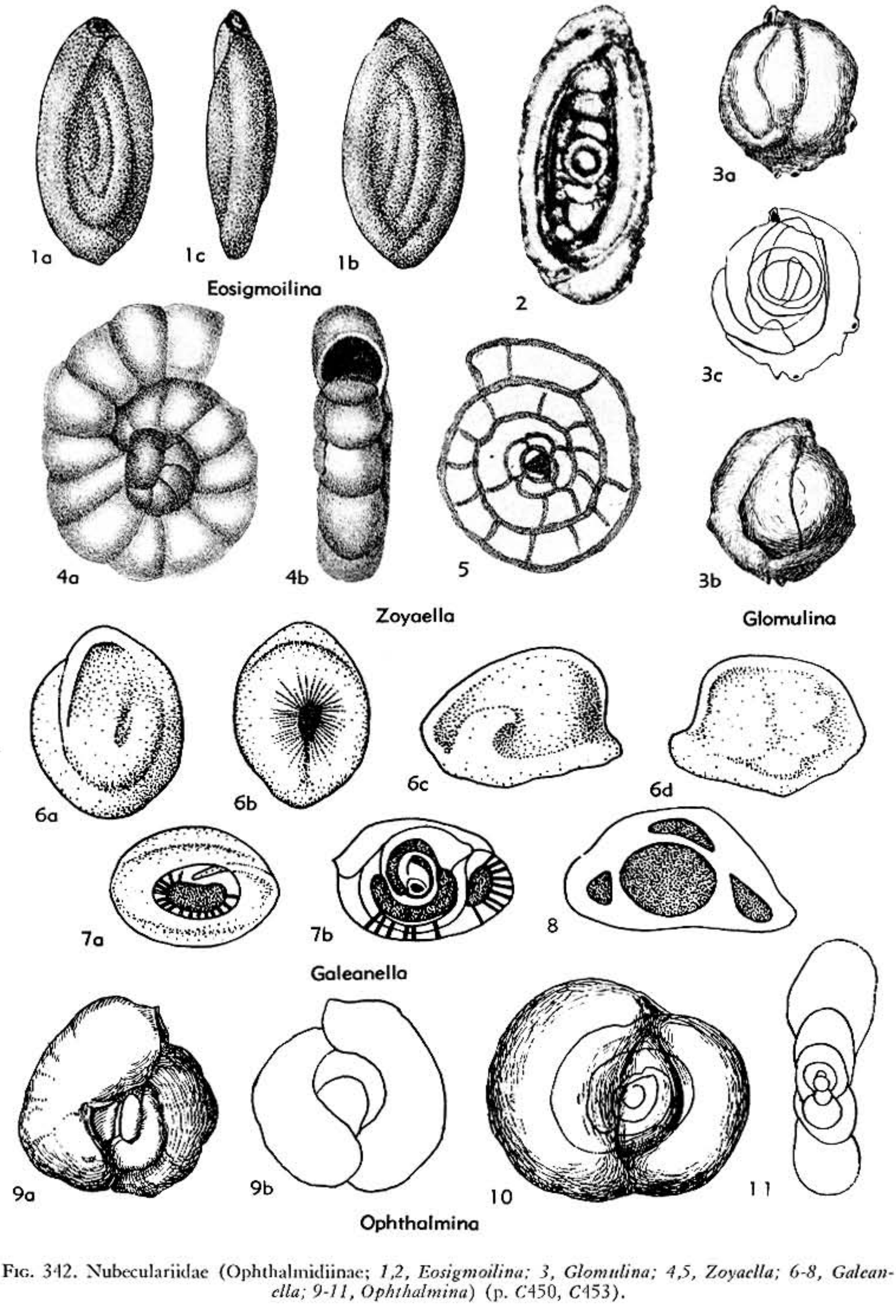


Fig. 342. Nubeculariidae (Ophthalmidiinae; *1,2, Eosigmoilina; 3, Glomulina; 4,5, Zoyaella; 6-8, Galeanella; 9-11, Ophthalmina*) (p. C450, C453).

Wiesnerella CUSHMAN, 1933, *458, p. 33 [**Planispirina auriculata* EGGER, 1893, *658, p. 245; OD]. Test planispiral in early stage, later chambers somewhat embracing, each one-half coil in length; wall thin, porcelaneous; aperture large, rounded, with everted lip. *Rec.*, Atl.O.-Gulf Mex.

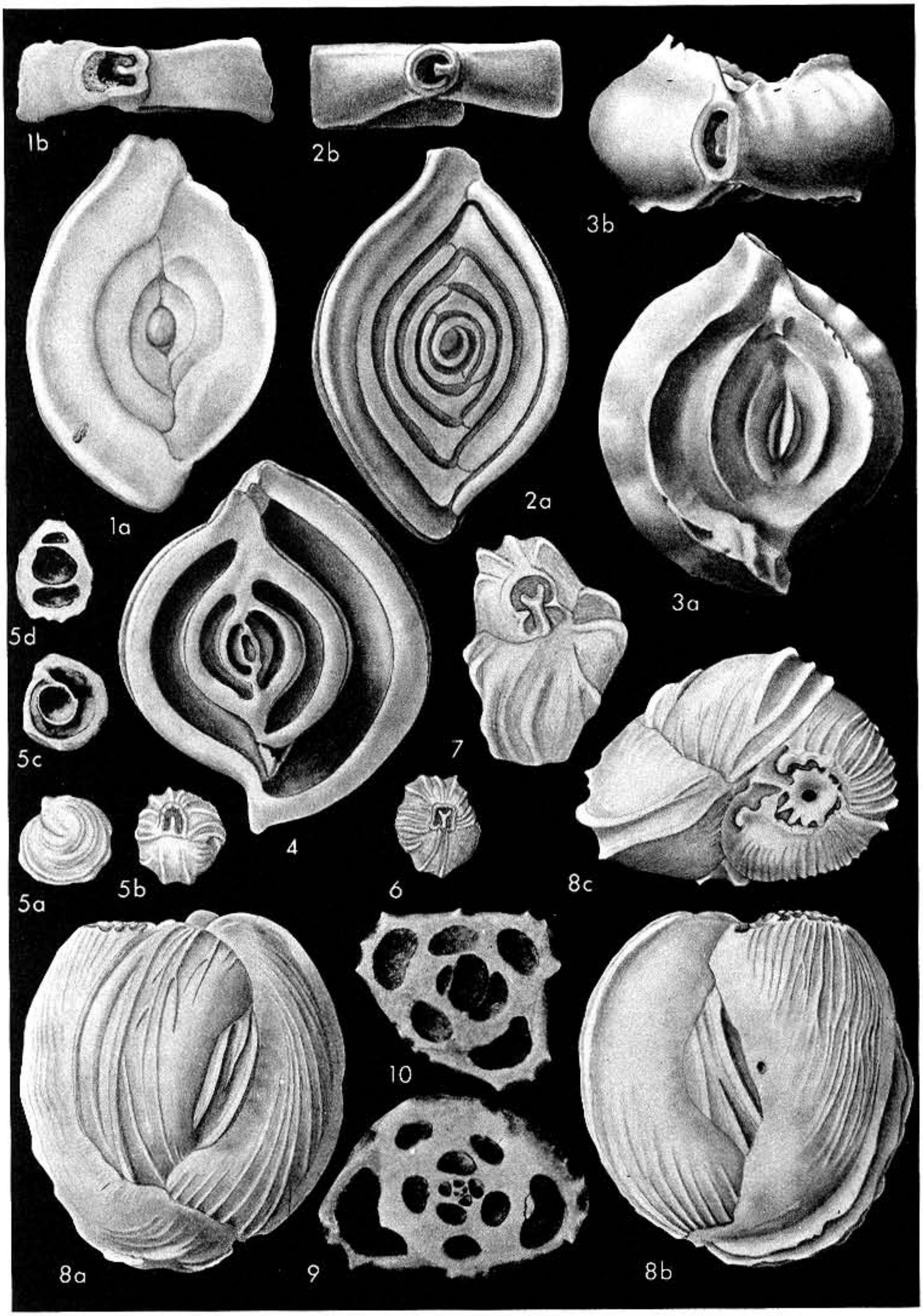


FIG. 343. Nubeculariidae (Spiroloculininae; *1-4, Spiroloculina; 5-10, Cribrolinoides*) (p. C453).

——Fig. 340,9. **W. auriculata* (Egger), Gulf Mex.; *9a-c,* opposite sides, top view, ×174 (*2117).

Zoyaella Loeblich & Tappan, 1962, *1185, p. 109 [*pro Ceratina* Goës, 1894, *804, p. 122 (*non* Latreille, 1802; *nec* Menge, 1868)] [**Ceratina trochamminoides* Goës, 1894, *804, p. 122; OD]. Test free, discoidal, proloculus followed by tubular second chamber, then streptospirally enrolled as in *Glomulina,* and finally planispiral, involute, with numerous chambers to whorl; wall calcareous, porcelaneous; aperture high arch at open end of final chamber. [*Zoyaella* differs from *Fischerina* in its early streptospiral stage, and from *Glomulina* in its later planispiral stage.] *Rec.,* N.Atl.O.(Azores).——Fig. 342,*4,5.* **Z. trochamminoides* (Goës); *4a,b,* side, edge views of holotype, ×21; *5,* equat. sec. showing chamber arrangement, ×37 (*804).

Subfamily SPIROLOCULININAE Wiesner, 1920

[Spiroloculininae Wiesner, 1920, p. 17, 18]

Proloculus followed by cornuspirine coil, adult chambers one-half coil in length; aperture commonly with phialine lip and with simple or bifid tooth. *U.Cret.-Rec.*

Spiroloculina d'Orbigny, 1826, *1391, p. 298 [**S. depressa*; SD Cushman, 1917, *404f, p. 29] [=*Spirolocunina, Spiroculina* Stöhr, 1877, *1840, p. 640 (*nom. null.*); *Flintia* Schubert, 1911, *1689b, p. 124 (type, *Spiroloculina robusta* Brady, 1884, *200, p. 150)]. Test free, commonly with flattened sides and lanceolate or fusiform outline, earliest stage may consist of single chamber completely encircling proloculus, later chambers (or all chambers in megalospheric forms) being added 2 to whorl on alternate sides and in single plane; wall calcareous, imperforate, porcelaneous; aperture at open end of final chamber, with simple or bifid tooth. *U.Cret.-Rec.,* cosmop.——Fig. 343, *1,2.* **S. depressa,* Plio., Eu.(Italy); *1a,b,* side, top views of megalospheric topotype, ×41; *2a,b,* side, top views of microspheric hypotype showing early cyclogyrine coil, ×105 (*2117).——Fig. 343,*3,4.* *S. robusta* Brady; *Rec.,* Carib. *(3),* Gulf Mex. *(4)*; *3a,b,* side and top views of topotype, ×25; *4,* sectioned hypotype showing early stage, ×31 (*2117).

[Differs from *Massilina* in having a planispiral early stage, as can be seen in the figures, and all chambers are added in a single plane, whereas *Massilina* is quinqueloculine in the early stage. *Flintia* was described as differing from *Massilina* in being biloculine throughout, rather than having an early quinqueloculine stage. Galloway (1933, *762) regarded *Flintia* as a synonym of *Massilina,* but because of the absence of an early milioline stage in the type-species of *Flintia,* it is here regarded as a synonym of *Spiroloculina.*]

Cribrolinoides Cushman & LeRoy, 1939, *510, p. 15 [**Quinqueloculina disparilis* d'Orbigny var. *curta* Cushman, 1917, *404f, p. 49; OD]. Test quinqueloculine in adult, but early stage with planispirally wound second chamber forming complete volution around proloculus; aperture terminal, with simple linear tooth in earliest stages, later bifid and then with bifid tips elongating and fusing in ring, toothlike projections from ring then attaching first to opposite side of opening and then in various places, resulting in complex cribrate aperture. [Because of the early cyclogyrine coil, *Cribrolinoides* is here transferred from the Miliolidae to the Nubeculariidae, subfamily Spiroloculininae.] *Plio.-Rec.,* Indo-Pac.O. ——Fig. 343,*5-10.* **C. curta* (Cushman), Plio., Java; *5-8,* specimens showing changes in apert. development from 2-chambered stage with simple tooth to quinqueloculine stage developing apert. ring; *5a-d,* side and apert. views, long. and axial secs. of 2-chambered stage, ×15 (*510); *6,7,* intermediate stages showing aperture, ×15 (*510); *8a-c,* opposite sides and apert. view of adult specimen, ×15 (*2117); *9,10,* axial secs. of microspheric and megalospheric adults; all ×15 (*510).

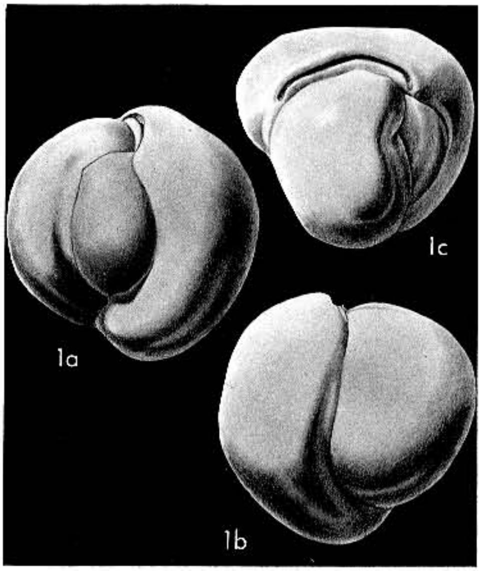


Fig. 344. Nubeculariidae (Spiroloculininae; *1, Planispirinoides*) (p. C453-C455).

Planispirinoides Parr, 1950, *1429, p. 287 [**Miliolina bucculenta* Brady, 1884, *200, p. 170; OD]. Test free, early stage planispirally coiled as in *Cyclogyra,* later chambers coiled in plane perpendicular to original plane of coiling and final chambers triloculine in same plane; wall calcareous, porcelaneous, imperforate; aperture an elongate slit, with a broad flaplike lip. [*Planispirinoides* differs from *Planispirina* in having the chambers of later stages coiled in a different plane and in development of a broad flaplike tooth. It differs from *Miliolinella* in possessing an early *Cyclogyra* stage.] *Rec.,* Atl.O.-Antarctic-Australia-

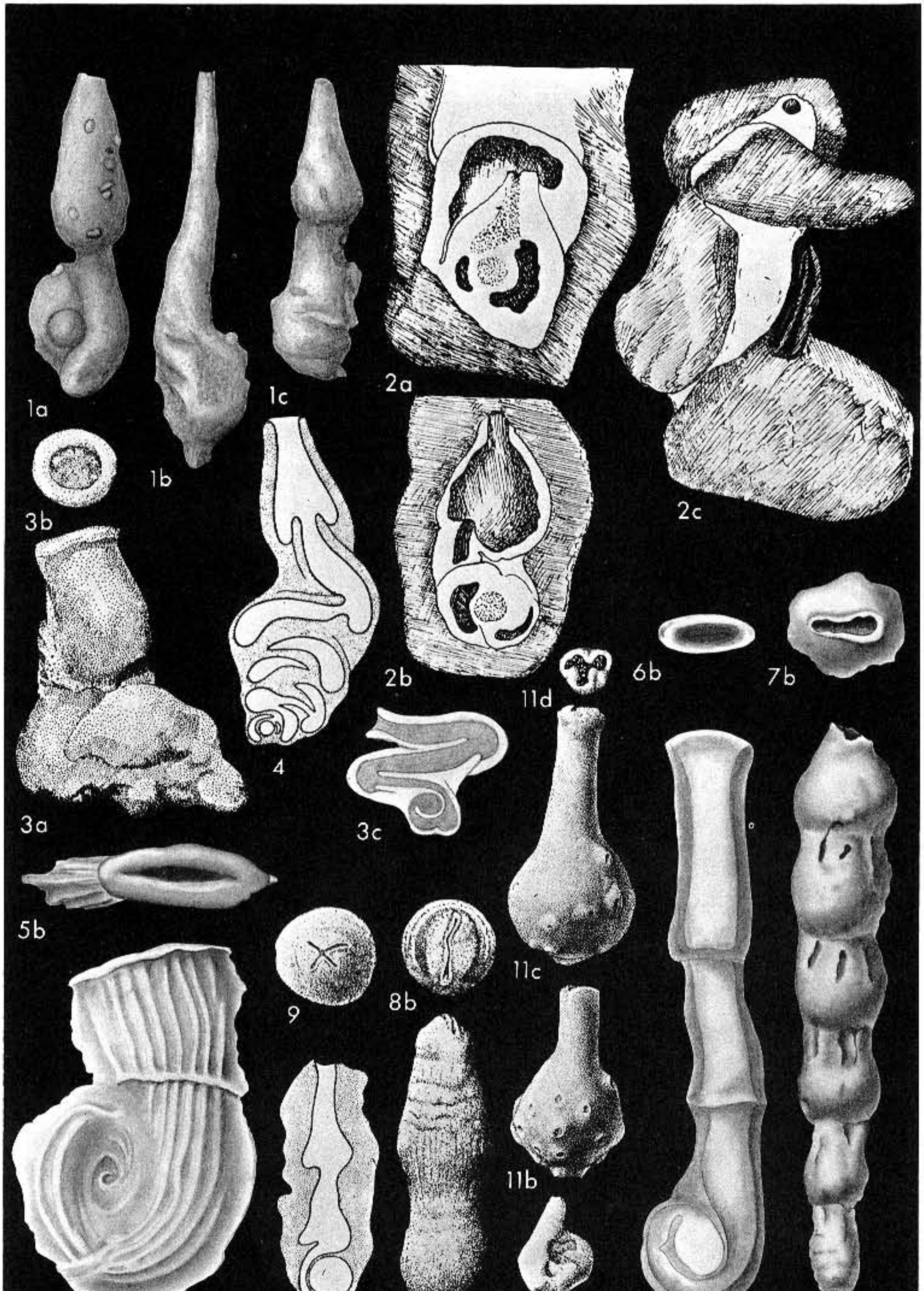


FIG. 345. Nubeculariidae (Nodobaculariinae; *1,2, Nodobacularia; 3,4, Meandroloculina; 5, Nodobaculariella; 6-11, Nodophthalmidium*) (p. C455-C456).

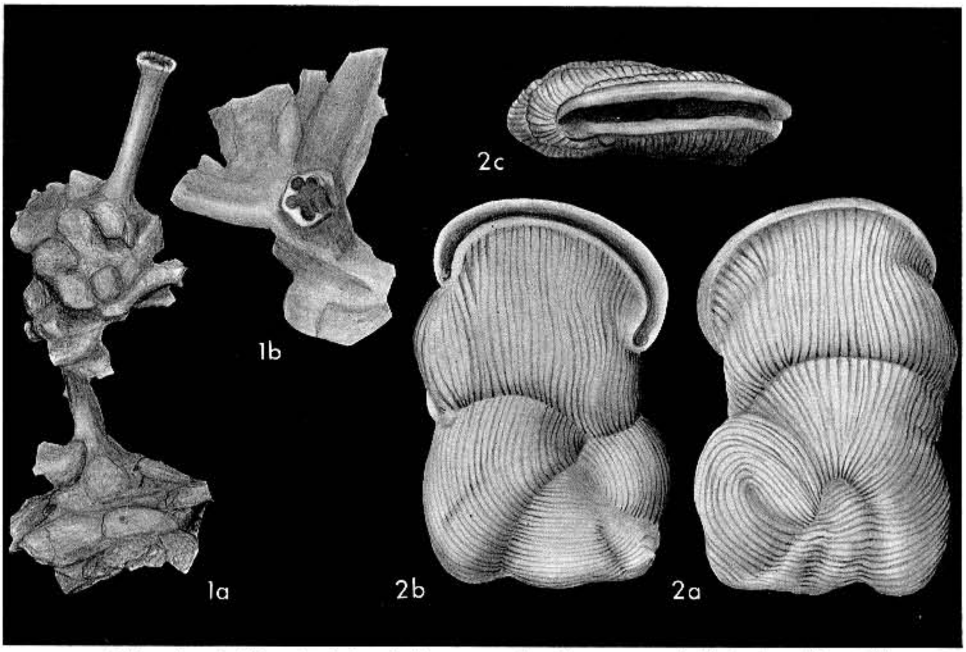


FIG. 346. Nubeculariidae (Nodobaculariinae; *1, Nubeculina; 2, Vertebralina*) (p. *C*456-*C*457).

Kerguelen Is.——FIG. 344,*1*. **P. bucculenta* (BRADY), Atl.; *1a-c,* opposite sides, top view, ×10 (*2117).

Subfamily NODOBACULARIINAE Cushman, 1927

[Nodobaculariinae CUSHMAN, 1927, p. 36] [=Nodophthalmidiinae CUSHMAN, 1940, p. 179]

Early portion planispiral, later chambers uncoiling. *Jur.-Rec.*

Nodobacularia RHUMBLER, 1895, *1568A, p. 87 [**Nubecularia tibia* JONES & PARKER, 1860, *999, p. 455; OD (M)] [=*Pseudonubeculina* BARTENSTEIN & BRAND, 1949, *94, p. 670 (type, *Nubecularia nodulosa* CHAPMAN, 1891, *308, p. 573); *Gymnesina* COLOM, 1959, *377, p. 16 (type, *G. glomerosa*)]. Test attached, consisting of globular proloculus surrounded by single coil of 2 or rarely 3 chambers which may not be discernible except in section, later portion uniserial, with chambers or chamber cavity pyriform in outline; wall calcareous and imperforate, and incorporating occasional sand grains; aperture at open tubular end of final chamber. *Jur.-Rec.*, cosmop.——FIG. 345,*1*. **N. tibia* (JONES & PARKER), L.Jur.(Lias.), Eng.; *1a,* lectotype (*999, fig. 51) showing early coil and pyriform later rectilinear chambers; *1b,c,* paratypes (*999, fig. 48, 49) showing generally obscure appearance of early coil, ×146 (*2117).——FIG. 345,*2*. *N. glomerosa* (COLOM), Rec., Medit. Sea; *2a,* holotype showing early chamber arrangement, ×30; *2b,* paratype showing early development, ×30; *2c,* paratype showing coarsely agglutinated test, ×17 (*377).

[MACFADYEN (1939, *1199, p. 167) considered *Nubecularia tibia* as identical with *Bullopora rostrata* QUENSTEDT, basing his opinion on English Jurassic specimens, which he thought to be identical with QUENSTEDT'S species. Topotypes of QUENSTEDT'S species have perforate calcareous walls, however, and never include agglutinated material, and are thus generically distinct from the imperforate to agglutinated *Nodobacularia* with early coil and typically pyriform later uniserial chambers. *Pseudonubeculina* was described as completely uniserial, although no early stages were described, all tests being broken in the European Lower Cretaceous material studied. Early coiled stages were found in *Lagenammina pyriformis* TAPPAN, later transferred to *Nodophthalmidium*, from the Albian of Texas (*1154), a species which is probably conspecific with *Nubecularia nodulosa*. The thin connecting necks commonly result in broken tests. *Gymnesina glomerosa* differs from typical *Nodobacularia* only in coarseness of the agglutinated fragments and is therefore here regarded as congeneric. *Nodobacularia* differs from *Nubeculina* in lacking the phialine apertural lip and teeth, and from *Nodophthalmidium* in its simple aperture and agglutinated covering. The types of *Nubecularia tibia* JONES & PARKER are in the PARKER collection of the British Museum (Natural History). The lectotype, here designated (BMNH-P41672), and paratypes (BMNH-P41671) were isolated and mounted by us in 1953 from the original material of JONES & PARKER in the British Museum. Originally described as from the Triassic at Chellaston near Derby, this material was actually from the Lias of Leicestershire, England, according to the Catalogue of Foraminifera of the Parker Collection (Index to Boxes I-XLV, by T. RUPERT JONES). Three of the original specimens are here illustrated.]

Meandroloculina BOGDANOVICH, 1935, *151, p. 695 [**M. bogatschovi*; OD]. Proloculus followed by cyclogyrine second chamber, later chambers elongate and alternating in uncoiled zigzag, pseudobiserial manner, finally becoming rectilinear, with subpyriform chambers; wall calcareous, imperforate, thick; aperture terminal, rounded or irregular, with thick bordering lip. *Mio.(L.Sarmat.)*, USSR (Trans. - Caucasus).——FIG. 345,*3*. **M. bogatschovi*; *3a,b,* side, top views of holotype, ×33 (*152); *3c,* long. sec. showing early cham-

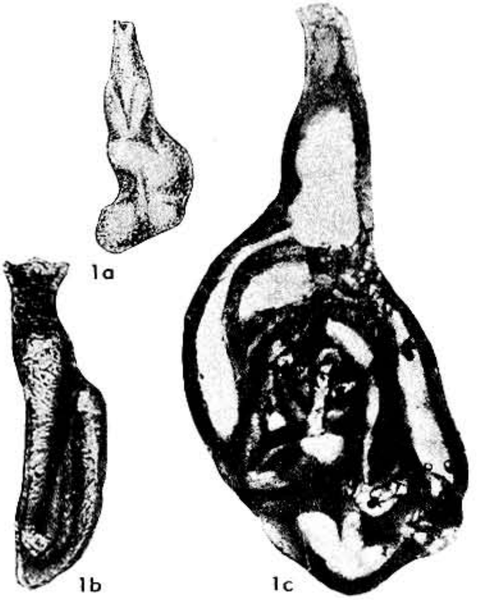


FIG. 347. Nubeculariidae (Nodobaculariinae; *1, Orthella*) (p. *C*456).

ber development, ×60 (*151).——FIG. 345,*4*. *M. litoralis* Bogdanovich; long. sec. showing early zigzag chambers and later tendency to become rectilinear, enlarged (*152).

Nodobaculariella Cushman & Hanzawa, 1937, *505, p. 41 [**N. japonica*; OD]. Test similar to *Vertebralina*, but early coil completely planispiral and terminal aperture symmetrically placed. [The holotype was originally stated to be in the Institute of Geology and Paleontology, Tohoku Imperial University, Sendai, Japan, but the specimen figured as holotype (*505, pl. 5) is in the Cushman collection, U.S. National Museum.] *Plio.-Pleist.*, Japan(Ryukyu Is.).——FIG. 345,*5*. **N. japonica*; *5a,b*, side and apert. views of holotype, ×44 (*2117).

Nodophthalmidium Macfadyen, 1939, *1199, p. 167 [**Nodobacularia compressa* Rhumbler, 1906; *1571, p. 38; OD] [=*Sarmatiella* Bogdanovich, 1952, *152, p. 217 (type, *S. costata*); *Foraminella* Bogdanovich, 1960, *153, p. 19 (type, *F. obscura*) (*non Foraminella* Sowerby, 1835; *nec* Levinsen, 1909]. Test free, proloculus rounded or ovate, followed by planispiral second chamber approximately half coil in length, adult chambers uniserial in development; wall calcareous, imperforate; aperture terminal, rounded or slitlike with lip, triradiate or cruciform. *Paleog.-Rec.*, Adriatic Sea-Medit. Sea-USSR.——FIG. 345,*6*. **N. compressum* (Rhumbler), Rec., Adriatic Sea; *6a,b*, side, top views of holotype, ×200 (*1571).——FIG. 345,*7*. *N. costatum* (Bogdanovich), Mio. (M.Sarmat.), USSR(Caucasus); *7a*, side view; *7b*, top view of different specimen; both ×70 (*152).——FIG. 345,*8-10*. *N. primum* (Bogdanovich), Mio.(M.Sarmat.), USSR(pre-Caucasus); *8a,b, 9*, side view and apert. views of 2 specimens, originally described as *Sarmatiella*, showing variation from slit to cruciform aperture, ×53; *10*, sec. showing early chamber arrangement, ×100 (*152).——FIG. 345,*11*. *N. obscurum* (Bogdanovich), Paleog., USSR(Kuban); *11a*, holotype showing early coil; *11b-d*, side and apert. views of final chamber of holotype showing parasitic borings, ×55 (*153).

[*Nodophthalmidium* differs from *Articulina* d'Orbigny in having a planispiral rather than milioline early stage. *Sarmatiella* differs only in surface ornamentation from the type of *Nodophthalmidium*, although in addition, some species of *Sarmatiella* develop a triradiate or cruciform aperture. *Foraminella* was described as having an early planispiral coil around the globular proloculus, followed by rectilinear chambers, the distinguishing character being the additional openings on the nipple-like protuberances occurring over the chambers and said to connect with the chamber interior by means of canals. As these openings seem obviously the result of a boring predator or parasite and are found in specimens of many species and genera, they are not considered a valid basis for generic separation, and the species *Foraminella obscura* is here placed in *Nodophthalmidium*. *Foraminella* is also a homonym of *Foraminella* Sowerby, 1835, and of Levinsen, 1909.]

Nubeculina Cushman, 1924, *418, p. 52 [**Sagrina divaricata* Brady, 1879, *196b, p. 276; OD]. Test free, or possibly attached in early portion; second chamber coiling around globular proloculus, later chambers inflated and in rectilinear or slightly arcuate uniserial arrangement, may be separated by slender stolon-like necks; wall calcareous, imperforate, milky white, with much coarse agglutinated material on exterior of chambers; aperture terminal on tubular neck, with phialine lip and few inwardly directed teeth. *Rec.*, Pac.O.——FIG. 346,*1*. **N. divaricata* (Brady); *1a*, lectotype, showing agglutinated wall and stolon-like apert. necks, ×105; *1b*, top view of another specimen (broken chamber) showing apert. teeth, ×146 (*2117).

[*Nubeculina* differs from *Nodobacularia* in having an aperture with phialine lip and inwardly pointing teeth. The original syntypes of *Sagrina divaricata* Brady are in the British Museum (Natural History), and a lectotype is here designated (BMNH-ZF3615, *ex* ZF2004, Brady, 1884, *200, pl. 76, fig. 13) with paratypes (BMNH-ZF2004 and ZF2005), all from *Challenger* station 217A, Humboldt Bay, Papua, at 37 fathoms.]

Orthella E. V. Bykova in Kiparisova, *et al.*, 1956, *1040, p. 19 [**O. paalzowi*; OD]. Test with globular proloculus followed by streptospirally wound tubular chambers, coiling partially to entirely involute, whorl divisions obscure externally, final portion becoming uncoiled, with no distinct internal septa but chambers thickened basally and tapering distally into elongate necklike extension, thus separating chambers; wall calcareous, imperforate; aperture simple, rounded opening. *U. Jur.(U.Oxford.)*, USSR.——FIG. 347,*1*. **O. paalzowi*; *1a,b*, ext. views of paratypes, ×80, ×100; *1c*, long. sec. approx. ×200 (*1040).

Vertebralina d'Orbigny, 1826, *1391, p. 282 [**V. striata*; OD (M)]. Test free, flattened, early

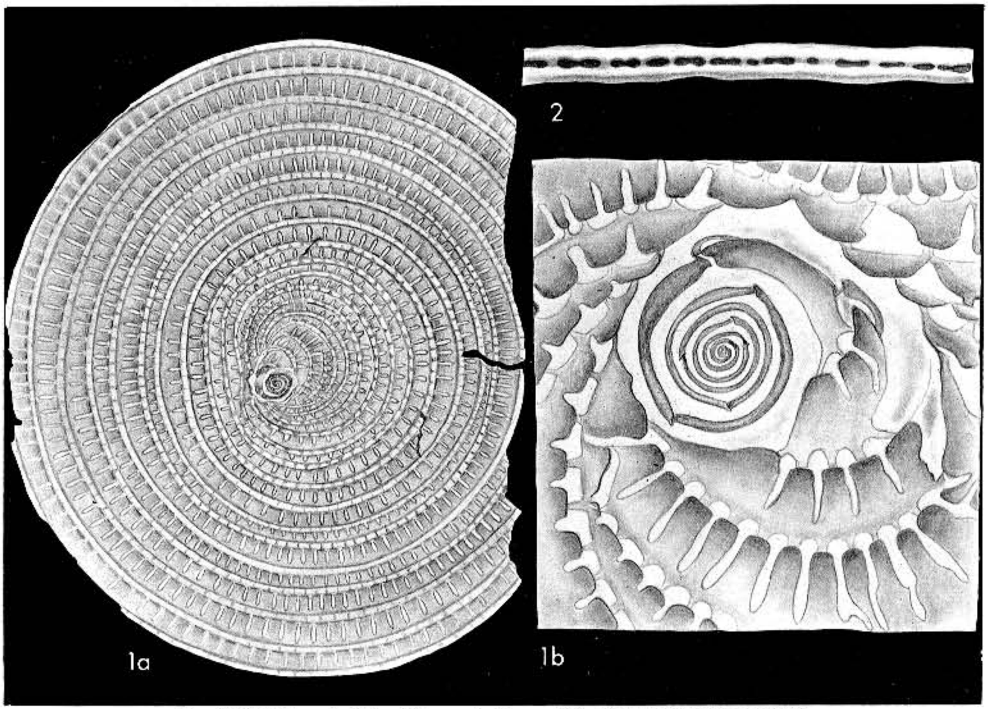


FIG. 348. Nubeculariidae (Discospirininae; *1,2, Discospirina*) (p. C457).

portion trochospiral, later uncoiling; wall calcareous, porcelaneous, surface may have longitudinal ribs or striae; aperture terminal, narrow, elongate slit with bordering lip, aperture most evident from umbilical side of coil. *Rec.*, Atl.O.-Pac.O.-Medit. Sea.——FIG. 346,*2*. **V. striata*, Delos Is., Grecian Arch.; *2a,b*, opposite sides showing trochospiral coil and aperture turned toward umbilical side; *2c*, top view showing simple slitlike aperture, ×64 (*2117).

Subfamily DISCOSPIRININAE Wiesner, 1931

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 291 (*pro* subfamily Discospiriniinae WIESNER, 1931, p. 60, 73)] [=Krumbachininae WIESNER, 1920, p. 17]

Test discoidal, thin, proloculus followed by cornuspirine coil of several volutions, later chambers one-half coil in length and finally annular, may be incompletely divided into chamberlets; aperture comprising row of pores at margin of final chamber. *M.Mio.-Rec.*

Discospirina MUNIER-CHALMAS, 1902, *1328, p. 353 [**Orbitolites tenuissimus* CARPENTER in CARPENTER & JEFFREYS, 1870 (*279, p. 155, name and reference to description), CARPENTER in CARPENTER, JEFFREYS & THOMSON, 1870 (*280, p. 421, description only) =*Pavonina italica* COSTA, 1856 (*392, p. 178); OD] [=*Cyclophthalmidium* LISTER in LANKESTER, 1903 (*1094, p. 108) (obj.); *Krumbachina* WIESNER, 1920 (*2061, p. 14) (obj.); *Discospirinia* CUSHMAN, 1927 (*431, p. 37) *(nom. null.)*]. Test free, discoidal; globular proloculus followed by undivided coil of about 1.5 whorls and series of elongate tubular chambers, which at first comprise nearly complete coil in length, becoming progressively shorter to about one-half coil in length, this early nucleoconch projecting somewhat above general surface, chambers then abruptly becoming higher, flaring and flabelliform, and subdivided by few vertical partitions, at first only 3 or 4 partitions, which arise from basal wall, then chambers becoming more enveloping and finally annular, with increasingly numerous partitions that extend only partially toward chamber roof, leaving continuous open area just below roof for chamberlet intercommunication, chamberlets also connected with previous annular chambers and with exterior by slitlike apertural pores; sutures nearly flush to slightly limbate, best visible when specimen is dampened; wall calcareous, imperforate; aperture single row of slits around entire periphery. *M.Mio.-Rec.*, Eu.-Medit. Sea(Cyprus)-Atl.O.——FIG. 348,*1,2*. **D. italica* (COSTA), Rec., Atl.; *1a*, sectioned specimen showing chamber development, ×11; *1b*, central portion, ×58; *2*, edge view of portion of hypotype showing apertures, ×44 (*2117).

[*Discospirina* is similar to *Cornuspiroides* in its early cyclogyrine portion and later flabelliform development but differs in being chambered, in having secondary septa, and in its multiple aperture of peripheral slits, *Cornuspiroides* being nonseptate in the flabelliform stage and having a single elongate, terminal slitlike aperture.]

Family MILIOLIDAE Ehrenberg, 1839

[*nom. correct.* d'Orbigny in de la Sagra, 1839, p. xxxix, 160 (*pro* family Miliolina Ehrenberg, 1839, table opp. p. 120)]——[All names referred to are of family rank; dagger (†) indicates *partim*]——[=Polythalamat† Latreille, 1825, p. 161; (*nom. nud.*); =Agathistègues d'Orbigny, 1826, p. 297 (*nom. nud.; nom. neg.*); =Enthomostègues† d'Orbigny, 1826, p. 304 (*nom. nud.; nom. neg.*); =Plicatilia Ehrenberg, 1839, table opp. p. 120 (*nom. nud.*); =Fabularina Ehrenberg, 1839, table opp. p. 120; =Helicosorinat† Ehrenberg, 1839, table opp. p. 120; =Multiloculidae d'Orbigny in de la Sagra, 1839, p. xxxix, 169 (*nom. nud.*); =Rhizopodes† Dujardin, 1841, p. 126, 240 (*nom. neg.*; *nom. nud.*); =Tubularina Agassiz, 1844, p. 10 (*nom. nud.*); =Nautiloidat† Schultze, 1854, p. 53 (*nom. nud.*); =Multiloculidaeen Abich, 1859, p. 106 (*nom. neg.*); =Multoloculidaeen Abich, 1859, p. 105 (*nom. null.*)]——[=Spherulaceat†, Sphérulacés† de Blainville, 1825, p. 369; =Sphaerulatat† Crouch, 1827, p. 40 (*nom. nud.*); =Spherulidae† Broderip, 1839, p. 321 (*nom. nud.*)]——[=Miliolida Schultze, 1854, p. 52; =Miliolitidae Parker, 1858, p. 53; =Miliolidea Reuss, 1862, p. 374; Miliolidee Schwager, 1876, p. 476, 483; =Miliolidina Bütschli in Bronn, 1880, p. 189; =Milioletta Haeckel, 1894, p. 164; =Miliolinidae Rhumbler, 1895, p. 86; =Miliolinae Delage & Hérouard, 1896, p. 122; =Armiliolidia Rhumbler, 1913, p. 341 (*nom. van.*)]——[=Hauerinidee Schwager, 1876, p. 483; =Hauerinidae Steinmann, 1881, p. 41; =Hauerinina Lankester, 1885, p. 846; =Hauerinae Delage & Hérouard, 1896, p. 124]

Test free, septate, typically with 2 chambers to whorl arranged in varying planes about longitudinal axis, may become rectilinear or involute, or may be subdivided into chamberlets; aperture terminal, simple, or with spatulate or bifid tooth, or cribrate. *Jur.-Rec.*

Subfamily QUINQUELOCULININAE Cushman, 1917

[Quinqueloculininae Cushman, 1917, p. 41]——[All names cited of subfamily rank]——[=Miliolidea genuina Reuss, 1862, p. 374 (*nom. nud.*); =Miliolidae opisthostreptae Eimer & Fickert, 1899, p. 687 (*nom. nud.*); =Massilininées Lacroix, p. 1 (*nom. neg.*); =Massillininae Thalmann, 1941, p. 682; =Sigmoilopsinae Vella, 1957, p. 18]

Wall simple; aperture with bifid tooth or modification of such. *Jur.-Rec.*

Quinqueloculina d'Orbigny, 1826, *1391, p. 301 [*nom. conserv.* proposed Loeblich & Tappan, 1962, *1184, p. 123 (ICZN pend.)] [**Serpula seminulum* Linné, 1758, *1140, p. 786; SD Parker & Jones, 1859, *1417a, p. 480] [=*Retorta* Walker & Boys, 1784, *2033, p. 3 (*nom. reject.* ICZN Op. 558); *Frumentarium* Fichtel & Moll, 1798, *716, p. 16 (obj.) (*nom. reject.*, proposed Loeblich & Tappan, 1962, *1184, p. 123, ICZN pend.); *Pollontes* de Montfort, 1808, *1305, p. 247 (type, *P. vesicularis*) (*nom. reject.*, proposed Loeblich & Tappan, 1962, *1184, p. 123, ICZN pend.); *Adelosina* d'Orbigny, 1826, *1391, p. 303 (type, *A. laevigata, non Quinqueloculina laevigata* d'Orbigny, 1826, =*Q. longirostra* d'Orbigny, 1826, *1391, p. 303); *Uniloculina* d'Orbigny in de la Sagra, 1839, *1611, p. 161 (type, *U. indica*); *Multiloculina* Abich, 1859, *1, p. 105, 150 (type, *Serpula seminulum* Linné, SD Loeblich & Tappan, herein); *Pollonites* Brady, 1884, *200, p. 156 (*nom. van. pro Pollontes* de Montfort, 1808); *Quinqueloculina (Lachlanella)* Vella, 1957, *2001, p. 24 (type, *Q. (L.) cooki*)]. Test coiled, with chambers one-half coil in length and alternating regularly in 5 planes of coiling 72° apart, but with successive chambers in planes 144° apart, so that 3 chambers are visible from exterior on one side of test and 4 visible from opposite side; wall calcareous, porcelaneous, imperforate, with inner pseudochitinous layer, rarely with some agglutinated grains added to exterior; aperture terminal, rounded, with simple or bifid tooth. *Jur.-Rec.*, cosmop.——Fig. 349,*1*. **Q. seminulum* (Linné), Rec., shore sands at Rimini, Italy; *1a-c,* opposite sides and apert. views of neotype (USNM), ×35 (*2117).——Fig. 349,*2,3*. *Q. longirostra* d'Orbigny, Plio., Italy; *2a-c,* opposite sides and top view of lectotype (MNHN) of *Adelosina laevigata* d'Orbigny; *3,* paratype consisting of proloculus only of *A. laevigata,* ×36 (*2117).——Fig. 349,*4*. *Q. cooki* Vella, Rec., N.Z.; *4a-c,* opposite sides and apert. view of holotype, ×30 (*2001).

[A proposal was submitted to ICZN by Loeblich & Tappan (1962, *1184) to suppress the generic names *Frumentarium* Fichtel & Moll, 1798, and *Pollontes* de Montfort, 1808, which would otherwise have priority over the more widely used *Quinqueloculina*. Because of the wide variety of forms included in *Q. seminulum* by various authors, the inadequate original description and figures, and loss of the original type, a neotype was designated from the original type locality and is here figured. The young megalospheric forms of *Quinqueloculina* were given the generic name *Adelosina* by d'Orbigny, 1826. The original types of *A. laevigata* d'Orbigny are in the Museum National d'Histoire Naturelle, Paris. A lectotype is here designated (*1395, pl. 20, figs. 22-24) and redrawn. The original figures show a distinct apertural tooth, but this was apparently broken away since the time of the original description; the tooth does not appear in the present figures. The 2-chambered lectotype and figured paratype, consisting of proloculus only, are from the Pliocene (Piacenzan) at Castell'Arquato, Italy. *A. laevigata* is the megalospheric generation of *Q. longirostra* d'Orbigny, 1826, also described from Castell'Arquato. *Lachlanella* was proposed as a subgenus of *Quinqueloculina* for species with subquadrate chambers, and a high, narrow aperture with elongate, narrow tooth. As these distinctions consist solely of relative dimensions, *Lachlanella* is here regarded as synonymous with *Quinqueloculina*.]

Cruciloculina d'Orbigny in de la Sagra, 1839, *1611, p. 182 [**C. triangularis* d'Orbigny, 1839, *1393, p. 72; SD (SM) d'Orbigny, 1839, *1393, p. 72]. Test free, chambers one-half coil in length, with longitudinal planes of successive chambers added 120° apart as in *Triloculina,* test rounded to triangular in section; sutures distinct, depressed; wall calcareous, imperforate, smooth or faintly striate; aperture complex, varying in shape from triradiate in young to cruciform or dendritic in adult, bordered by narrow lip, but without distinct tooth. [Differs from *Triloculina* in lacking the distinct tooth and developing a cruciform or dendritic aperture in the adult.] *Plio.-Rec.*, N.Atl.-S.Atl.O.-Japan.——Fig. 349,*5,6*. **C. triangularis,* Rec., Falk Is. *(5)*, S. Georgia Is. *(6)*; *5a,b,* side, top views of lectotype, ×26 (*1173); *6a-c,* opposite sides and top view of another specimen, ×20 (*1173).

Dentostomina Carman, 1933, *270, p. 31 [**D. bermudiana*; OD]. Test free, quinqueloculine in plan; wall with imperforate calcareous porcelaneous inner layer, external agglutinated layer of grains embedded in calcareous cement; aperture terminal, circular, with crenulate margin and bifid tooth. *Rec.*, N.Atl.O.(Bermuda Is.)-W. Indies(Cuba).——FIG. 350,*1*. **D. bermudiana,*

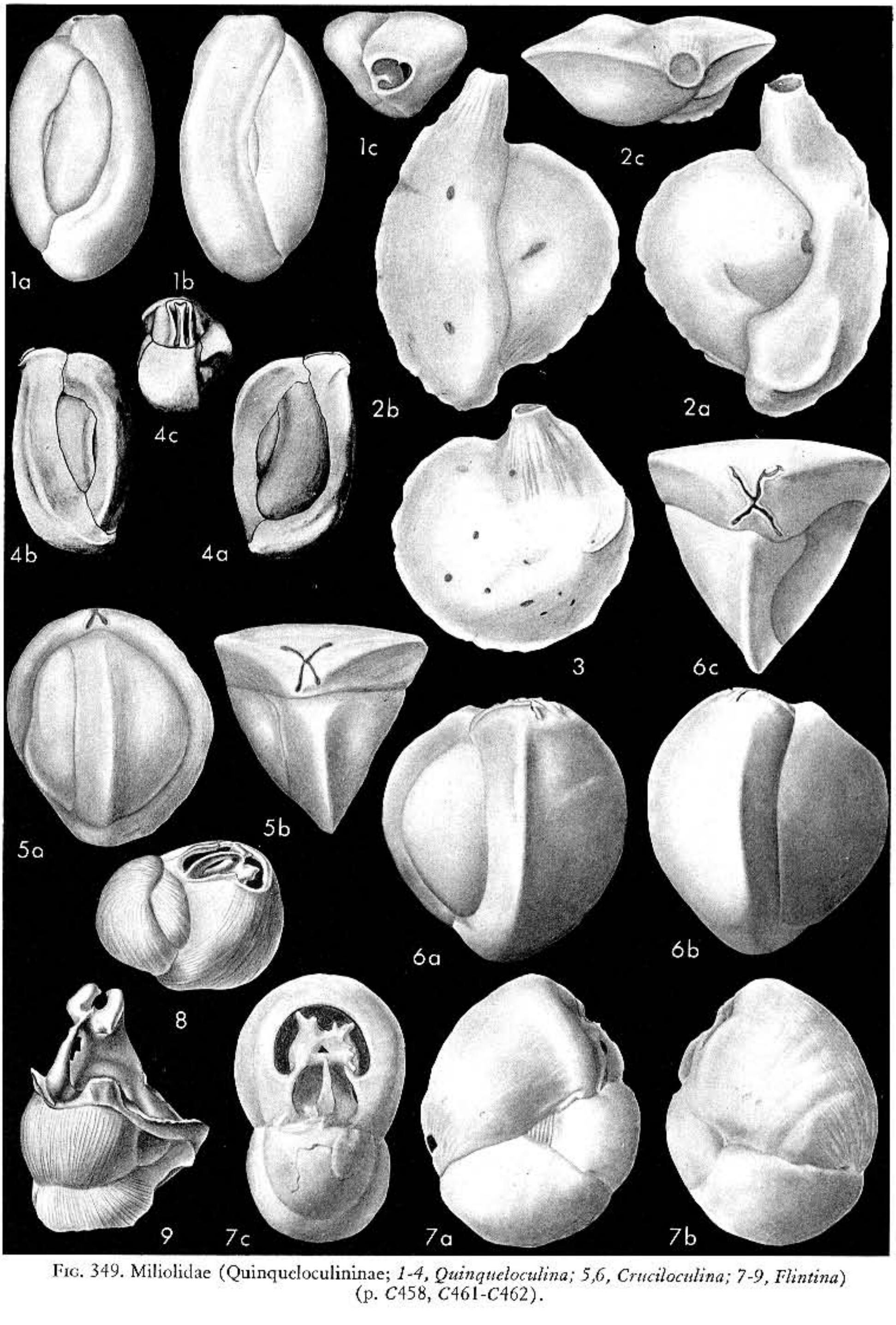


FIG. 349. Miliolidae (Quinqueloculininae; *1-4, Quinqueloculina; 5,6, Cruciloculina; 7-9, Flintina*) (p. C458, C461-C462).

off Bermuda; *1a-c*, opposite sides and top views of holotype, ×20 (*2117).

[Differs from *Quinqueloculina* in having a denticulate or crenulate apertural border and in its external agglutinated layer of the wall, which is less common in *Quinqueloculina*. In the original figures (*270, pl. 3, fig. 6c) the apertural view is shown as a mirror image of the true appearance,

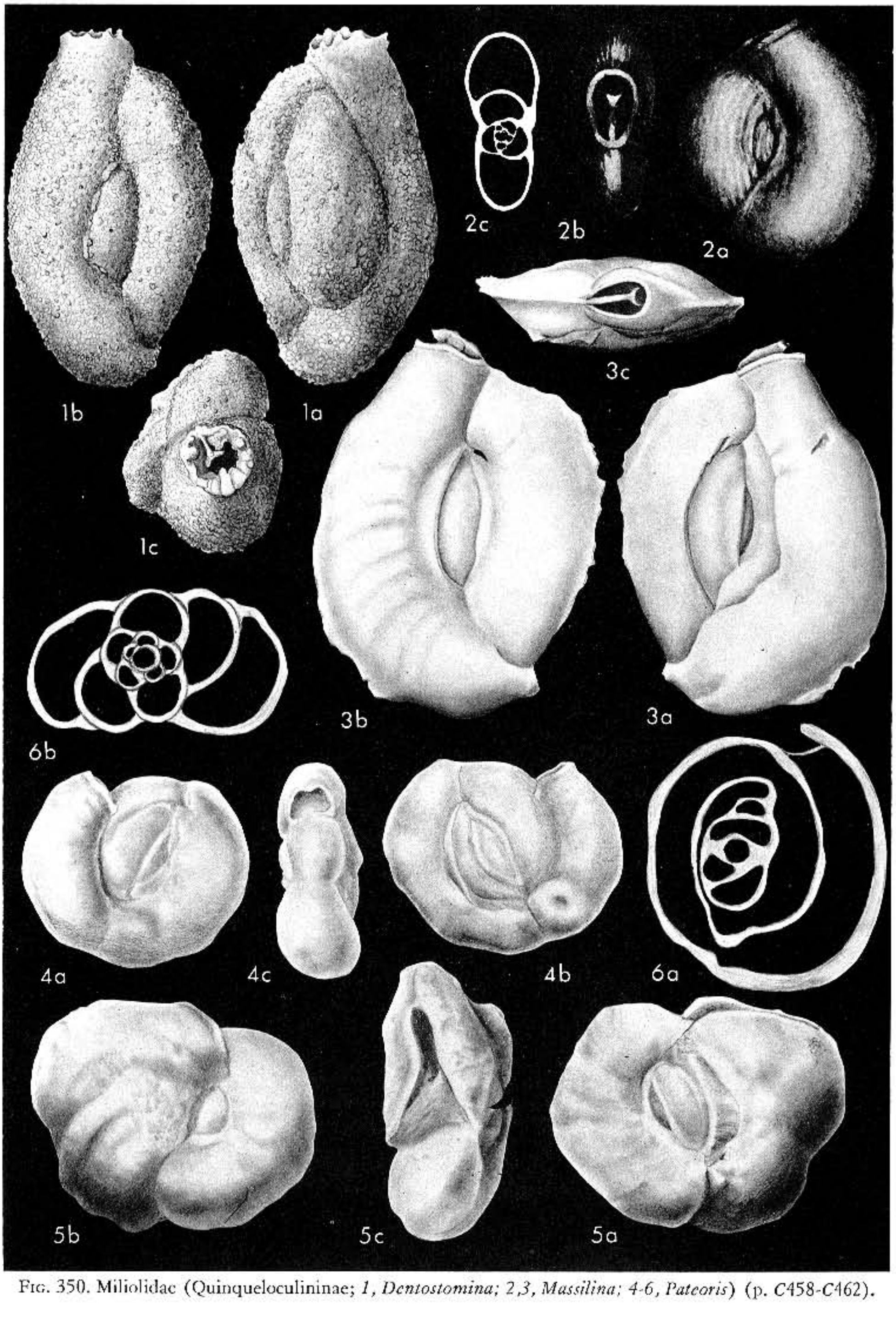


Fig. 350. Miliolidae (Quinqueloculininae; *1, Dentostomina; 2,3, Massilina; 4-6, Pateoris*) (p. C458-C462).

as can be seen by comparing figures 6b and 6c, for the final chamber (and aperture) of the holotype is at the right when viewed from the side where 4 chambers are visible. Therefore, in apertural view, the final chamber is at the left when the flatter side is at the bottom of the illustration.]

Flintina Cushman, 1921, *415, p. 465 [**F. bradyana*=*Miliolina fichteliana* Brady, 1884, *200, p. 169 (*non* d'Orbigny, 1839); OD]. Test free, ovate to rounded in outline, early portion with 2

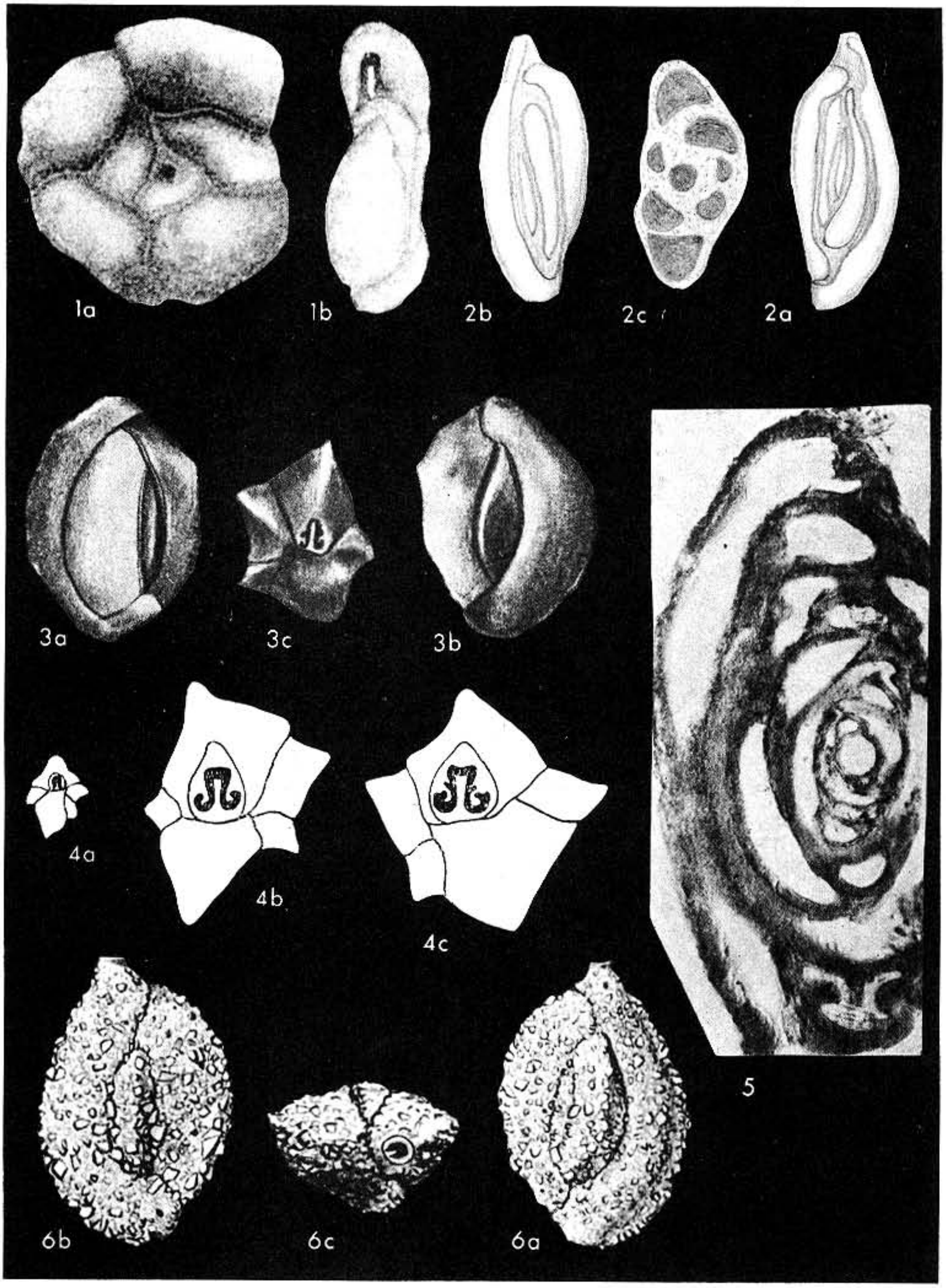


Fig. 351. Miliolidae (Quinqueloculininae; *1, Flintinella; 2, Palaeomiliolina; 3-5, Podolia; 6, Siphonaperta*) (p. *C*462, *C*466).

chambers to whorl in triloculine arrangement, later increasing to 3 in each whorl and tending to become planispiral, as in *Hauerina*; wall calcareous, imperforate, porcelaneous; aperture large, high, ovate opening partially filled by bifid tooth in young stage, later becoming keyhole-shaped, somewhat narrower against earlier chambers and expanding abruptly about one-third of distance up face, outer margin of aperture at this point acutely angled and acuminate, tooth in adult of type-species becoming very complex, 2 modified branches of early bifid tooth being much enlarged, many-pronged, curving up and around to rejoin above, with arched plate extending back within chamber from beginning of bifurcation to attach to interior of chamber, lower portion of tooth remaining bladelike at surface in lower portion of opening, but also expanding basally within final chamber to form broad, triangular attachment occupying almost one-third of chamber, only central area of this tooth being free. *Rec.*, Pac.O.——FIG. 349,*7-9*. **F. bradyana*, Philip. (Cebu Is.); *7a-c*, opposite sides and apert. view of holotype, ×15; *8*, oblique apert. view showing arched plate connecting bifid tooth to test wall; *9*, partially dissected specimen, outer wall of final chamber removed to show complex apert. tooth within, ×16 (*2117).

[Differs from *Triloculina* in its later subplanispiral development with three chambers per whorl, and in the more complex aperture and apertural tooth. It resembles *Hauerina* in the early milioline stage and later planispiral development but differs in being more involute and in having an open aperture and complex tooth, whereas *Hauerina* has a trematophore or sieve plate completely filling the apertural region. *Involvohauerina* differs in having a multiple cribrate aperture rather than an open aperture and complex tooth.]

Flintinella DIDKOVSKIY, 1960, *595, p. 1433 [**F. volhynica*; OD]. Test free, compressed, early stage similar to *Quinqueloculina*, with 2 chambers to whorl, later increasing to 3, resembling *Wellmanella* and *Pateoris*, with up to 6 chambers in final whorl, coiling partially involute, up to 5 whorls may be present, periphery rounded; sutures depressed, curved, nearly radial; wall calcareous, porcelaneous, smooth; aperture elongate opening at open end of final chamber, with lateral margins somewhat thickened and infolded, elongate, simple tooth occupying more than 0.75 length of apertural opening. [*Flintinella* differs from *Pateoris* in having an elongate simple apertural tooth.] *Mio.(M.Sarmat.)*, USSR(Ukraine). ——FIG. 351,*1*. **F. volhynica*; *1a,b*, side, edge views of holotype, ×40 (*595).

Massilina SCHLUMBERGER, 1893, *1655, p. 76 [**Quinqueloculina secans* D'ORBIGNY, 1826, *1391, p. 303; SD CUSHMAN, 1917, *404f, p. 56] [=*Proemassilina* LACROIX, 1938, *1079, p. 3 (type, *Massilina rugosa* SIDEBOTTOM, 1904, *1738, p. 18)]. Test free, ovate in outline, somewhat flattened, proloculus followed by chambers one-half coil in length, early ones in quinqueloculine arrangement, later chambers added in single plane, on alternate sides, as in *Spiroloculina*; wall calcareous, porcelaneous, imperforate; aperture at open end of final chamber, with bifid tooth. *L. Cret.-Rec.*, cosmop.——FIG. 350,*2*. *M. rugosa* SIDEBOTTOM, Rec., Delos Is.; *2a,b*, side, apert. views of holotype; *2c*, sec. showing chamber arrangement, ×33 (*1738).——FIG. 350,*3*. **M. secans* (D'ORBIGNY), Rec., Greece(Delos Is.); *3a-c*, opposite sides, apert. views, ×24 (*2117).

Palaeomiliolina LOEBLICH & TAPPAN, n. gen. (Proposed by BOGDANOVICH, 1952 (*152, p. 41, 77, 86) without description or citation of included species and described by ANTONOVA, 1958 (*23, p. 915) with 3 included species, but without citation of type-species, hence a *nomen nudum* requiring type designation for validation.) [**Spirophthalmidium occultum* ANTONOVA, 1958, *24, p. 52; designated herein] [=*Palaeomiliolina* BOGDANOVICH, 1952, *152, p. 41, 77, 86 *(nom. nud)*; *Palaeomiliolina* ANTONOVA, 1958, *23, p. 915 *(nom. nud.)*]. Test similar to *Massilina*, but aperture lacking apertural tooth. *Jur. (Bajoc.-Oxford.)*, Eu.——FIG. 351,*2*. **P. occulta* (ANTONOVA), Bajoc., USSR(C.Caucasus); *2a,b*, opposite sides, ×160; *2c*, transv. sec., ×320 (*24).

Pateoris LOEBLICH & TAPPAN, 1953, *1162, p. 42 [**Quinqueloculina subrotunda* (MONTAGU) forma *hauerinoides* RHUMBLER, 1936, *1575, p. 206, 217, 226; OD]. Test quinqueloculine in early stage, with chambers one-half coil in length, later planispiral, with gradually shortened chambers so that slightly more than 2 chambers to coil may occur; wall porcelaneous; aperture at open end of chamber, varying from low arch to high, narrow slit with lateral margins somewhat infolded. *Rec.*, N.Sea-Pac.O.(Alaska).——FIG. 350, *4-6*. **P. hauerinoides* (RHUMBLER), Rec., Alaska; *4a-c*, *5a-c*, opposite sides and edge views of hypotypes showing variation in chamber length and height of aperture, ×44; *6a,b*, long. and axial secs. showing early quinqueloculine development and later planispiral stage, ×66 (*1162).

[*Pateoris* differs from *Pseudomassilina* in its smooth, rather than punctate or canaliculate, wall. It is very similar to *Wellmanella* in the adult stage but quinqueloculine in the early stage, whereas *Wellmanella* was described as triloculine in the early stage without a quinqueloculine stage. No sections have been published for *Wellmanella*, and if a restudy of the type-species of *Wellmanella* shows a quinqueloculine stage to be present, *Pateoris* would become a junior synonym.]

Podolia SEROVA, 1961, *1720, p. 56 [**Hauerina lyra* SEROVA, 1955, *1719, p. 329 (=*Hauerina lyra* SEROVA, 1953, *1718, p. 63 *(nom. nud.)*; OD]. Test similar to *Quinqueloculina* in form and chamber arrangement, aperture lyre-shaped, wtih narrow, straight normal tooth and 2 lateral supplementary teeth projecting into opening. *Mio.(U.Torton.)*, USSR (Ukraine).——FIG. 351,*3-5*. **P. lyra* (SEROVA); *3a-c*, opposite sides and apert. view of holotype, ×40; *4a-c*, outline views of ontogenetic stages, showing development of complex aperture in adult (*1720); *5*, long. sec., ×250 (*1721).

Pseudomassilina LACROIX, 1938, *1079, p. 3 [**Massilina australis* CUSHMAN, 1932, *455, p. 32; OD]. Test broad and compressed, early chambers quinqueloculine, with 2 chambers to whorl, later planispiral, as in *Pateoris*, with gradually shortening chambers; wall porcelaneous, with interior network of fine canals opening into tiny pores in small pits at surface, but not opening into cham-

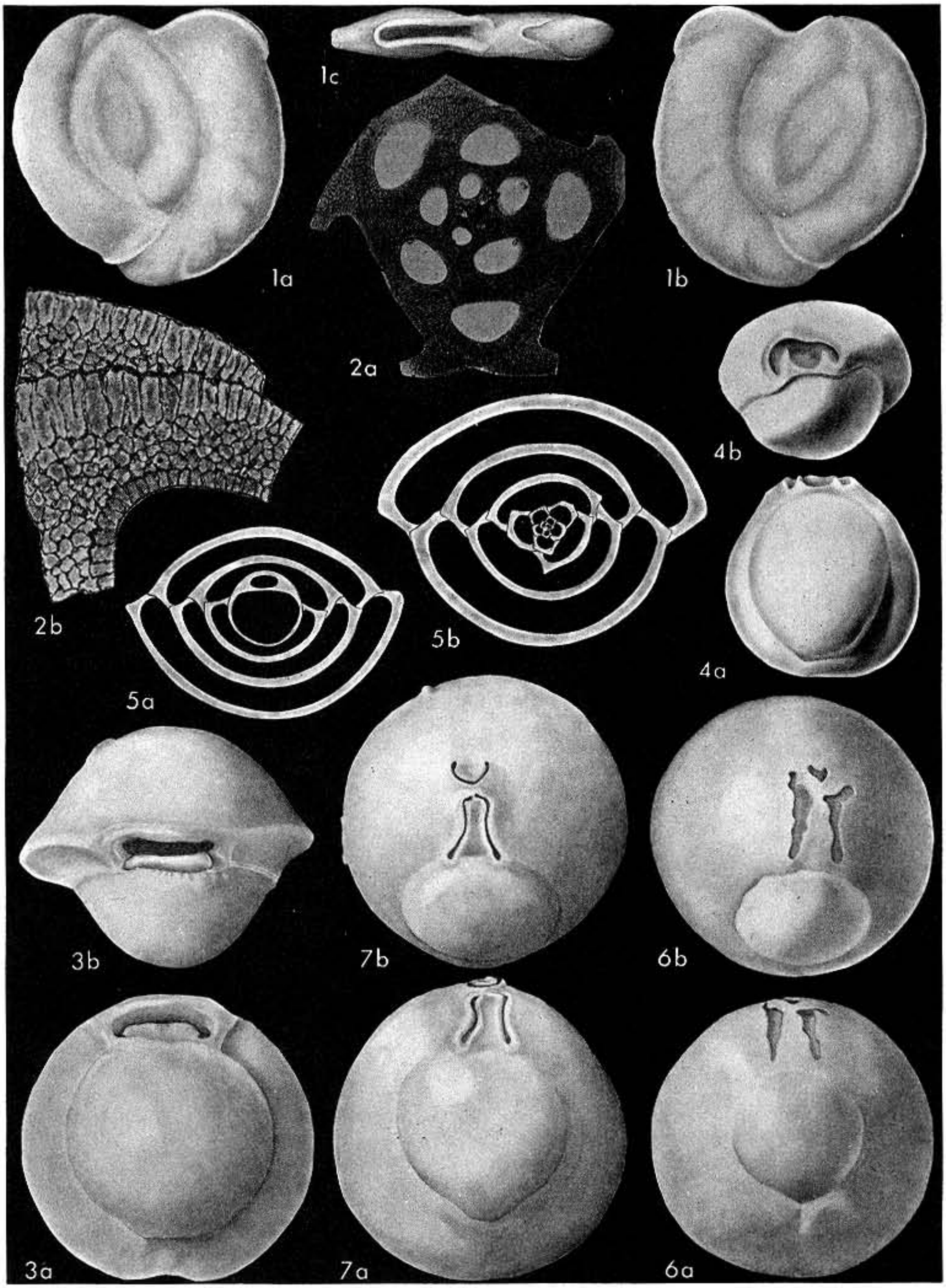


FIG. 352. Miliolidae (Quinqueloculininae; *1,2*, *Pseudomassilina; 3-5*, *Pyrgo; 6,7*, *Pyrgoella*) (p. *C*463-*C*465).

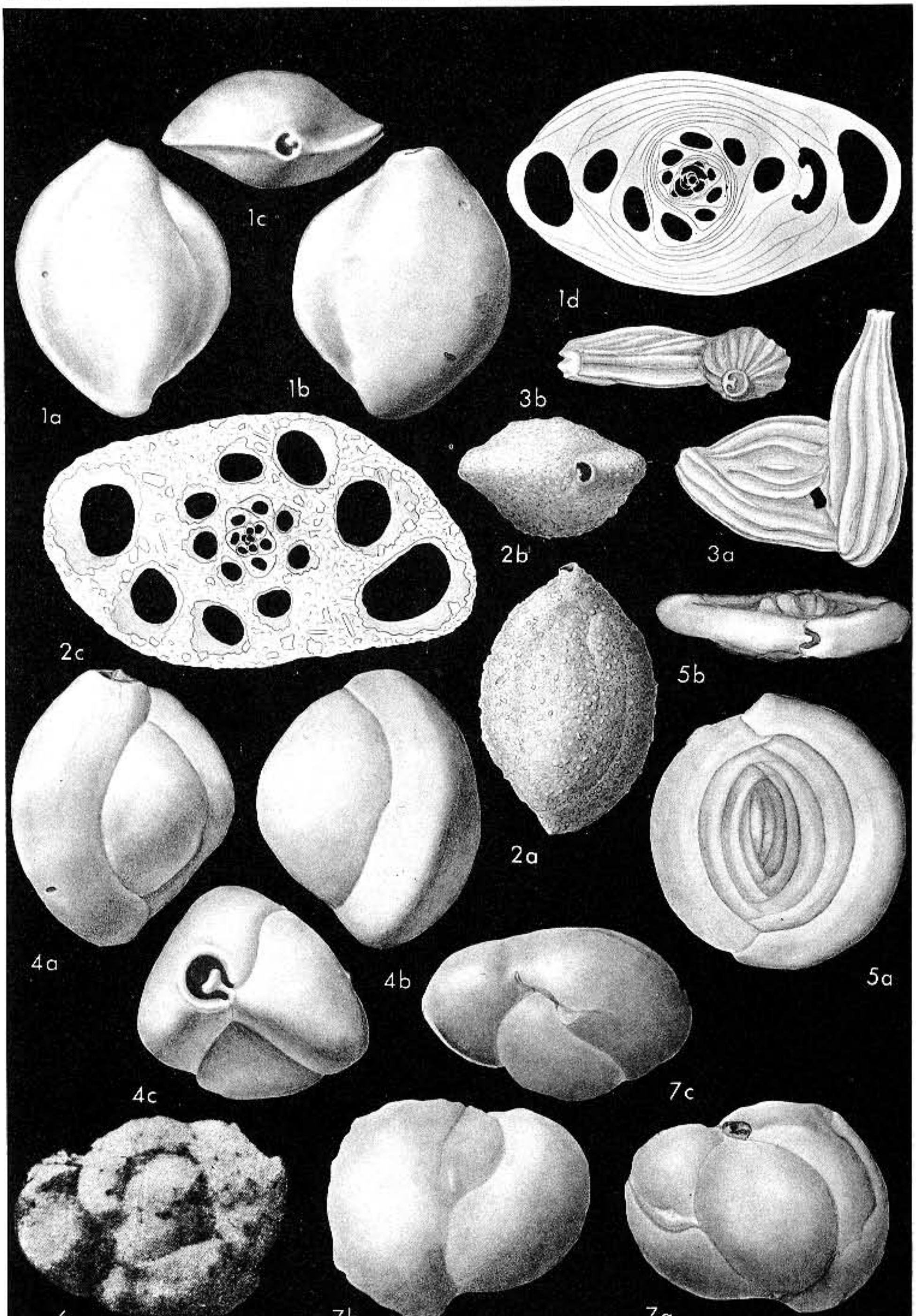


Fig. 353. Miliolidae (Quinqueloculininae; *1, Sigmoilina; 2, Sigmoilopsis; 3, Ptychomiliola; 4, Triloculina; 5, Spirosigmoilina; 6,7, Wellmanella*) (p. C465-C466).

ber cavity, being separated from it by imperforate pseudochitinous layer; aperture high slit with bordering lip, similar to that of *Pateoris,* without tooth. [Differs from *Pateoris* in its characteristic wall texture.] *Rec.,* Australia-Asia(Indochina)-Pac.O.-Red Sea(Gulf Aqaba)-E.Afr.(Kerimba Arch.).——Fig. 352,*1,2*. **P. australis* (Cushman), Rec., Cook Is.; *1a-c,* opposite sides and apert. views of holotype, ×50 (*2117); *2a,* enlarged photograph of central portion of axial sec. showing wall structure; *2b,* portion of wall enlarged, diagram showing crystalline pseudofibrous outer layer with vertical canals and inner layer with irregularly granular appearance (*1078).

Ptychomiliola Eimer & Fickert, 1899, *692, p. 687 [**Miliolina separans* Brady, 1881, *196c, p. 45; SD Cushman, 1928, *439, p. 154]. Test free, early chambers milioline in arrangement, later ones planispiral and evolute, about 3 to whorl, some rare specimens uniserial; wall calcareous, porcelaneous, imperforate, may be longitudinally costate; aperture terminal, rounded, produced on neck, with lip and distinct bifid tooth. [Differs from *Hauerina* in being more evolute, and in having apertural tooth instead of apertural pore plate or trematophore.] *Rec.,* S.Pac.O.——Fig. 353,*3*. **P. separans* (Brady), lectotype (here designated, BMNH-ZF 1902) from Storm Bay, Tasm.; *3a,b,* side, apert. views, ×16 (*2117).

Pyrgo Defrance, 1824, *597e, p. 273 [**P. laevis*; OD (M)] [=*Biloculina* d'Orbigny, 1826, *1391, p. 297 (type, *B. bulloides*); *Praelacazina* Hofker, 1959, *952, p. 372 (type, *Biloculina fragilis* Hofker, 1927, *927, p. 173)]. Test free, inflated, discoidal to ovate, proloculus followed by chambers one-half coil in length; in microspheric form early chambers arranged in quinqueloculine pattern, later triloculine, and finally biloculine; megalospheric forms may be biloculine throughout development, with successive discoidal to hemispherical chambers opposing each other; wall calcareous, imperforate, porcelaneous; aperture terminal, near junction of 2 last chambers, rounded to elongate, with distinct and commonly bifid tooth. [*Pyrgo* differs from *Biloculinella* in having a bifid tooth instead of a broad apertural flap nearly filling the aperture. No locality or horizon was given in the original description of *Pyrgo laevis.*] *Jur.-Rec.,* cosmop.——Fig. 352,*3*. **P. laevis,* Plio.(Piacenz.), Eu.(Italy); *3a,b,* side and apert. views showing relatively broad tooth of this species, ×38 (*2117).——Fig. 352,*4*. *P. williamsoni* (Silvestri), Rec., N.Am.(Alaska); *4a,b,* side and apert. views of species with distinctly bifid tooth, ×33 (*1162).——Fig. 352,*5*. *P. sarsi* (Schlumberger), Rec., Eu.(N.Sea); *5a,b,* secs. of megalospheric and microspheric forms showing chamber arrangement, ×20 (*1654).

Pyrgoella Cushman & E. M. White, 1936, *540, p. 90 [**Biloculina sphaera* d'Orbigny, 1839, *1393, p. 66; OD]. Test free, subglobular, with strongly overlapping chambers in biloculine arrangement, as in *Pyrgo*; wall calcareous, imperforate, porcelaneous; aperture in young with large triangular tooth, in adult V-shaped opening may be divided into 2 elongate openings with original tooth attached at both ends, with one or more supplementary sinuate, straight, or chevron-shaped openings also present. [*Pyrgoella* resembles *Pyrgo* and *Biloculinella* in chamber development but differs in having a more complex aperture, like that of *Cruciloculina. Cribropyrgo* is like the present genus, but has a regularly cribrate aperture with numerous small openings in place of the cruciform or chevron-like openings of *Pyrgoella.*] *Pleist.-Rec.,* S.Atl.O.-USA (Calif.)-Gulf Mex.——Fig. 352,*6,7*. **P. sphaera* (d'Orbigny), Pleist., USA(Calif.)*(6),* Rec., Gulf Mex. *(7)*; *6a,b,* side and apert. views, ×48; *7a,b,* side and apert. views of hypotype, ×48 (*2117).

Fig. 354. Miliolidae (Quinqueloculininae; *Triloculina*) (p. C466).

Sigmoilina Schlumberger, 1887, *1651, p. 118 [**Planispirina sigmoidea* Brady, 1884, *200, p. 197; SD Cushman, 1917, *404f, p. 60]. Test free, ovate in outline, in microspheric generation with earliest chambers opposite, then with plane of chamber addition changing so that it forms sigmoid curve, successive chambers at first in planes about 120° apart but angle gradually enlarging to 180° in adult stage, chambers with broad lateral extensions which obscure all preceding chambers except penultimate one, giving external biloculine appearance; wall calcareous, thick, imperforate, porcelaneous; aperture terminal, rounded, with tooth. [Differs from *Pyrgo* in having a gradual change from a pseudoquinqueloculine stage to one with chambers added 180° apart, so that the changing plane of coiling forms a sigmoid curve.] *M.Eoc.-Rec.,* cosmop. ——Fig. 353,*1*. **S. sigmoidea* (Brady), Rec., Carib.; *1a-c,* opposite sides and top view of hypotype, ×46 (*2117); *1d,* sec. showing chamber arrangement, ×55 (*1651).

Sigmoilopsis Finlay, 1947, *717e, p. 270 [**Sigmoilina schlumbergeri* Silvestri, 1904, *1760, p. 267; OD]. Test free, ovate, with chambers one-half coil in length, at first quinqueloculine in arrangement, then with increasing angle between planes of coiling of successive chambers, so that chambers are nearly opposing, but changing plane of coils results in early sigmoid curve, extremities of curve spiraling outward, much as in *Sigmoilina*; wall agglutinated with calcareous cement enclosing sand, calcareous shell fragments and sponge spicules; aperture terminal, rounded, with small tooth. *Mio.-Rec.,* Eu.-Atl.O.-Carib.-Australia-N.Z.——Fig. 353,*2*. **S. schlumbergeri* (Silvestri), Rec., Atl.; *2a,b,* side and apert. views of hypotype showing small bifid tooth, ×48 (*2117); *2c,* horiz. sec. showing chamber arrangement, originally referred to *Sigmoilina celata* (Costa), ×42 (*1651).

[Differs from *Sigmoilina* in having an agglutinated wall and less enveloping chambers so that more than the final pair are visible externally and the interior does not have the laminated appearance of *Sigmoilina*. Originally it was described (*717e, p. 270) as differing further in its possession of an apertural tooth, but one is also here shown to be present in *Sigmoilina*. Thalmann (1961, *1905, p. 321) cited the reference to *Sigmoilina schlumbergeri* Silvestri, 1904, and commented "Probably a nomen nudum." *Sigmoilina schlumbergeri* Silvestri, 1904, was defined as a *nom. nov.,* but actually was a new species including *Miliolina celata* (Costa) of Brady in Tizard & Murray, 1882, and *Planispirina celata* of Brady, 1884, Silvestri, 1893, and Flint, 1899, and *Sigmoilina (Planispirina) celata* Schlumberger, 1887 (*non Spiroloculina celata* Costa, 1856). Although no illustrations were published by Silvestri (1904) for this new species, a description was given and a reference was made to illustrations by Brady, 1884, Flint, 1899, and Schlumberger, 1887 (including that here refigured). Hence, this is a valid species and not a *nomen nudum*. No type-specimen was selected for the present species, although Finlay, 1947, defined *Sigmoilopsis* for *S. schlumbergeri* as interpreted and figured by Cushman, 1946, and Brady, 1884. A lectotype is here designated as the specimen figured by Brady, 1884 *200, pl. 8, figs. 1a,b) from *Porcupine* station 23, west of Ireland at 630 fathoms, and in the BMNH.]

Siphonaperta Vella, 1957, *2001, p. 19 [**S. macbeathi*; OD]. Test with chamber arrangements as in *Quinqueloculina,* but wall agglutinated as in *Sigmoilopsis* and with simple ridgelike tooth and porcelaneous phialine lip. *Pleist.-Rec.,* Australia-N.Z.——Fig. 351,*6*. **S. macbeathi,* L.Pleist., N.Z.; *6a-c,* opposite sides and apert. views of holotype, ×36 (*2001).

Spirosigmoilina Parr, 1942, *1426, p. 361 [**Spiroloculina tateana* Howchin, 1889, *966, p. 3; OD]. Test with early chambers in sigmoid arrangement as in *Sigmoilina,* later chambers 180° apart, as in *Massilina*; wall porcelaneous; aperture terminal, with short tooth. *Mio.,* Australia.——Fig. 353,*5*. **S. tateana* (Howchin); side, apert. views of topotype, ×115 (*2117).

Triloculina d'Orbigny, 1826, *1391, p. 299 [**Miliolites trigonula* Lamarck, 1804, *1085c, p. 351; SD Cushman, 1917, *404f, p. 65] [=*Renoidea* Brown, 1827, *244, p. 1 (type, *R. glabra*); *Spidestomella* Costa, 1856, *392, p. 370 (type, *S. globulifera*); *Miliolina* Williamson, 1858, *2065, p. 83 (type, *Triloculina laevigata* d'Orbigny, 1826, *1391, p. 300); *Trillina* Munier-Chalmas, 1882, *1322, p. 424 (type, *Triloculina strigillata* d'Orbigny, 1850, *1397b, p. 409)]. Test free, with chambers each one-half coil in length, early chambers at least in microspheric generation in quinqueloculine arrangement, later triloculine, with successive chambers added in planes 120° apart, only final 3 chambers visible externally; wall calcareous, imperforate, porcelaneous, or rarely with surficial agglutinated layer; aperture terminal, typically wtih bifid tooth; gametes biflagellate, with axostyle. [*Triloculina* differs from *Quinqueloculina* in its later triloculine development, from *Miliolinella* in having a bifid tooth instead of a broad apertural flap, and from *Cruciloculina* in having a simple, rounded aperture with a bifid tooth.] *Jur.-Rec.,* cosmop.——Fig. 353,*4*. **T. trigonula* (Lamarck), Eoc. (Lutet.), Eu.(Hauteville, Fr.); *4a-c,* opposite sides, apert. view, ×31 (*2117).——Fig. 354. *T. rotunda* d'Orbigny, Rec., Atl.O.; biflagellate gamete with axostyle, ×6,000 (*820a).

Wellmanella Finlay, 1947, *717e, p. 270 [**W. kaiata*; OD] [=*Hechtina* Bartenstein & Brand, 1949, *94, p. 669 (type, *H. praeantiqua*)]. Test similar to *Pateoris* but with triloculine, rather than quinqueloculine, early stage, and later stage with 3 or 4 chambers to whorl, aperture at open end of final chamber, varying from low arch to slit with infolded margins, as in *Pateoris*. [No sections showing early growth stages have been published, hence it is possible that an early quinqueloculine stage may be present and that *Pateoris* thus is a junior synonym of *Wellmanella*.] *L.Cret.(M.Valangin.)-U.Eoc.,* N. Z.-Ger. —— Fig. 353,*6*. **W. kaiata,* U.Eoc., N.Z.; holotype, ×35 (*717e).——Fig. 353,*7*. *W. praeantiqua* (Bartenstein & Brand), L.Cret.(U.Valangin.), Ger.; *7a-c,* opposite sides and edge of topotypes, ×111 (*2117).

Subfamily MILIOLINELLINAE Vella, 1957

[Miliolinellinae Vella, 1957, p. 20]

Wall simple, with broad, flat tooth or flap partially closing aperture. *Eoc.-Rec.*

Miliolinella Wiesner, 1931, *2063, p. 63, 65, 107 [**Vermiculum subrotundum* Montagu, 1803, *1298, p. 521; OD] [=*Triloculinella* Riccio, 1950, *1577, p. 90 (type, *T. obliquinodus*)]. Test free, triloculine in chamber arrangement; sutures distinct; wall calcareous, porcelaneous, imperforate; aperture at open end of chamber, partially covered by broad, low flap which leaves only crescentic opening. [Differs from *Triloculina* in possessing a large broad, flaplike tooth constricting the aperture rather than a simple or bifid tooth.] *Oligo.-Rec.,* Eu.-N.Am.-Pac.O.-Antarctic.——Fig. 355,*1,2*. **M. subrotunda* (Montagu); Rec., Ire. *(1),* Delos Is., Greece *(2)*; *1a-c,* opposite sides

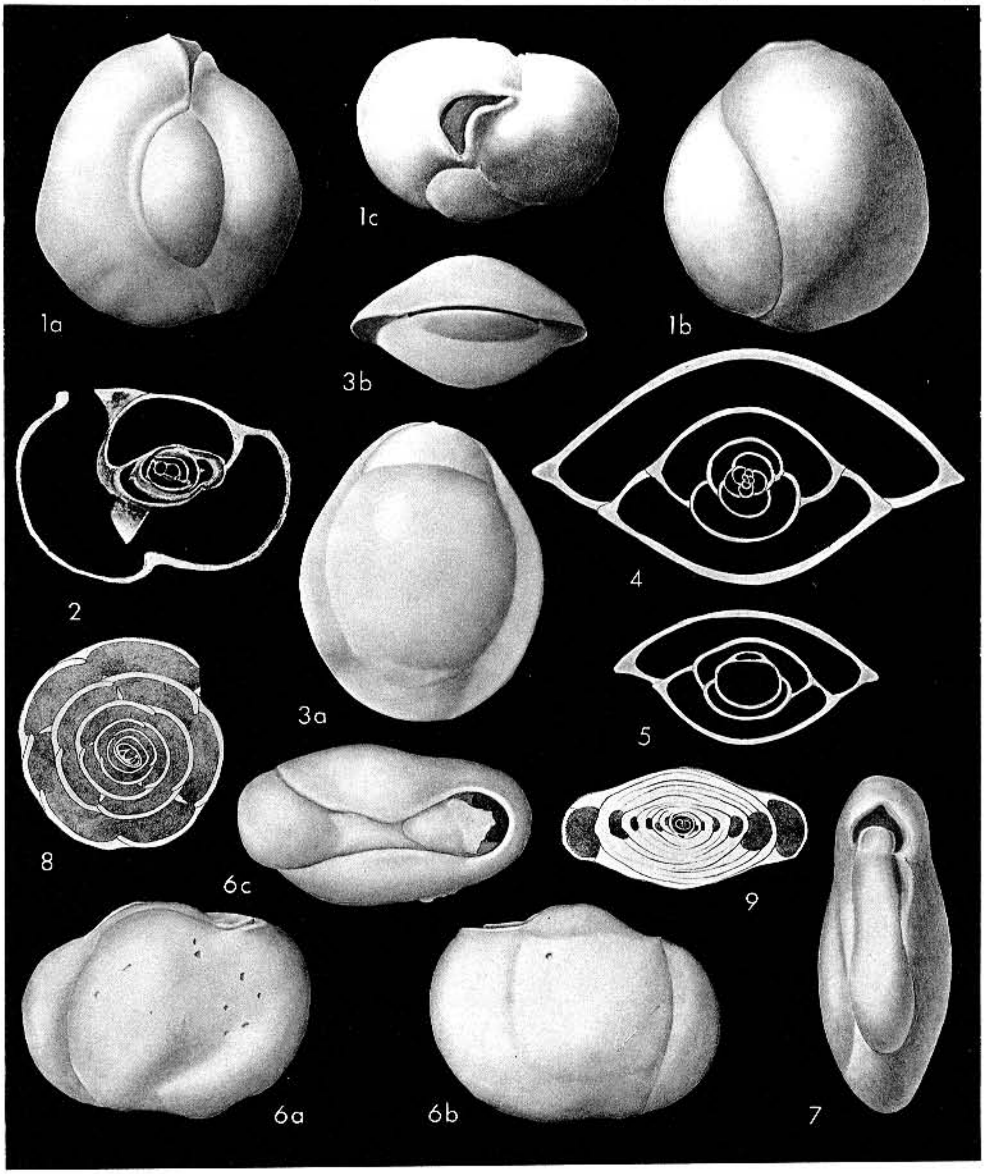


FIG. 355. Miliolidae (Miliolinellinae; *1,2, Miliolinella; 3-5, Biloculinella; 6-9, Nummoloculina*) (p. C466-C468).

and top view showing apert. flap, ×73 (*2117); *2*, horiz. sec., ×56 (*1738).

Biloculinella WIESNER, 1931, *2063, p. 69 [*Biloculina labiata SCHLUMBERGER, 1891, *1654, p. 556; OD]. Test free, discoidal to ovate, proloculus followed by chambers one-half coil in length, early chambers in microspheric form arranged in quinqueloculine pattern, later chambers in triloculine arrangement and finally biloculine, with involute coiling, leaving only final pair of chambers visible, megalospheric form may be biloculine throughout development; wall calcareous, imperforate, porcelaneous; aperture terminal, nearly covered by broad flap, so that only narrow crescentic opening remains. [*Biloculinella* differs from *Pyrgo* in having a broad, flaplike lip, instead of a bifid apertural tooth. The lectotype and paratypes of *Biloculina labiata* SCHLUMBERGER are in the collections of the Sorbonne, University of Paris.] *Eoc.-Rec.*, Medit. Sea-Antarctic-N. Am.——FIG. 355,*3-5*. *B. labiata (SCHLUMBERGER), Rec., Medit.; *3a,b*, side, top views of paratype,

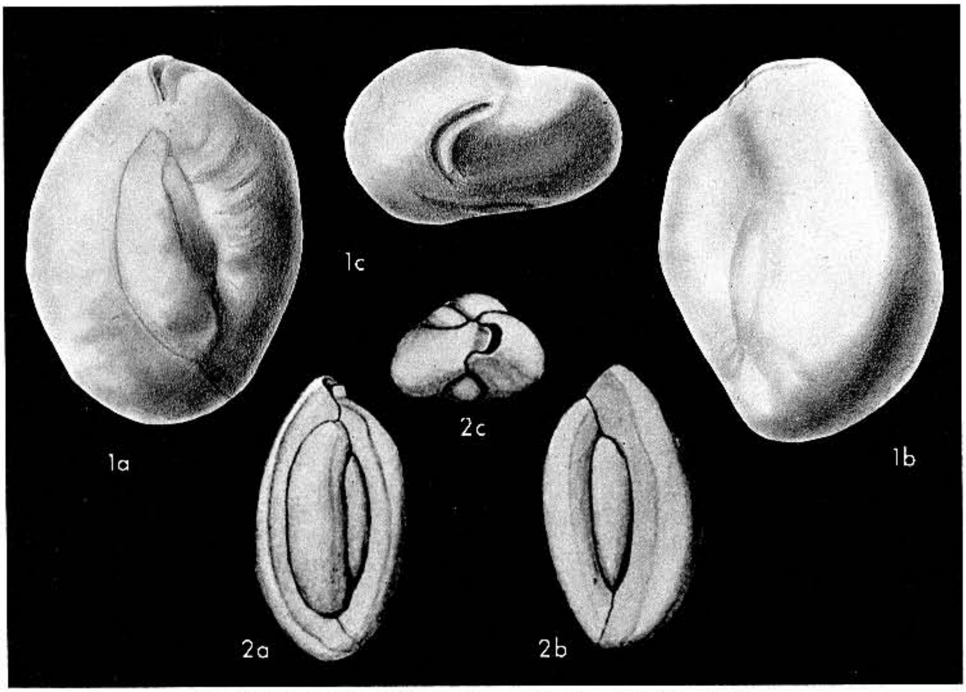


FIG. 356. Miliolidae (Miliolinellinae; *1,2, Scutuloris*) (p. C468).

×70 (*2117); *4,* microspheric test sectioned to show early quinqueloculine stage, ×87 (*1654); *5,* megalospheric test, sectioned to show biloculine development throughout, ×85 (*1654).

Nummoloculina STEINMANN, 1881, *1837, p. 31 [**Biloculina contraria* D'ORBIGNY, 1846, *1395, p. 266; OD]. Test free, discoidal to biconvex, early portion in milioline arrangement with 2 chambers to whorl, later planispiral with 3 chambers to whorl, increasing in adult to 5 or 6 low, broad chambers to whorl; sutures obscure; wall calcareous, imperforate, composed of successive laminae added over entire test, thickening wall and obscuring chamber division; aperture at open end of final chamber, semicircular in outline, but largely filled by broad spatulate tooth extending upward from base of opening and leaving open only small crescentic remnant of aperture. [*Nummoloculina* differs from *Fischerina* in having a broad spatulate flap in the aperture, instead of a high open aperture. *Hauerina* has a cribrate trematophore in the aperture, instead of a simple tooth.] *Mio.-Rec.,* Eu.-Atl.O.-Medit.Sea-Indo-Pac. —— FIG. 355,*6-9.* **N. contraria* (D'ORBIGNY), Mio., Aus. *(6),* Rec., Scot. (off Skye) *(7-9)*; *6a-c,* opposite sides and edges of topotype, apert. flap slightly broken, ×48 (*2117); *7,* edge view showing well-preserved apert. flap, ×20 (*200); *8,9,* equat. and axial secs. enlarged (*1837).

Scutuloris LOEBLICH & TAPPAN, 1953, *1162, p. 41 [**S. tegminis*; OD] [=*Quinquinella* VELLA, 1957, *2001, p. 21 (type, *Q. hornibrooki*)]. Test free, chambers in quinqueloculine arrangement; wall calcareous, imperforate; aperture at end of chamber and nearly filled by broad, low flap. [*Scutuloris* differs from *Miliolinella* in having a quinqueloculine chamber arrangement and from *Quinqueloculina* in having a broad flap filling the aperture, in place of the bifid tooth characteristic of the latter.] *Rec.,* Arctic.-Pac.O.——FIG. 356,*1.* **S. tegminis,* Alaska; *1a-c,* opposite sides and top view of holotype, ×66 (*1162).——FIG. 356,*2.* *S. hornibrooki* (VELLA), N.Z.(Cook Strait); *2a-c,* opposite sides and top view of holotype, ×60 (*2001).

Subfamily MILIOLINAE Ehrenberg, 1839

[*nom. transl.* RHUMBLER, 1895, p. 87 (*ex* family Miliolina EHRENBERG, 1839)] [=Miliolininae BRADY, 1881, p. 43; =Haueríninae BRADY, 1884, p. 62; =Trematoforininae SILVESTRI, 1937, p. 80 *(nom. nud.)*]

Wall simple; with cribrate aperture (trematophore). *U.Cret.-Rec.*

Miliola LAMARCK, 1804, *1085c, p. 349 [**Miliolites saxorum* LAMARCK, 1804; SD CUSHMAN, 1927, *432, p. 125 [=*Miliolites* LAMARCK, 1804, *1085c, p. 349 (type, *M. saxorum,* SD LOEBLICH & TAPPAN, herein) (obj.); *Miliolithes* CUVIER, 1817, *542a, p. 376 (*nom. van. pro Miliolites* LAMARCK) (obj.); *Saxicoline* DESHAYES, 1830, *590, p. 231 *(nom. neg.)* (obj.); *Pentellina* MUNIER-CHALMAS, 1882, *1322, p. 424 (obj.); *Saxicolina* SHERBORN, 1896, *1731b, p. 404 (*nom. correct. pro Saxicoline* DESHAYES, 1830) (obj.)]. Test with quinqueloculine chamber arrangement; aperture with trematophore (cribrate). *Eoc.*, Eu.-N.Am.——FIG. 357,*2,3*. **M. saxorum* (LAMARCK), Eoc. (Lutet.), Fr.; *2a-c*, opposite sides and apert. view, ×26 (*2117); *3*, transv. sec. showing chamber arrangement, ×50 (*1664).

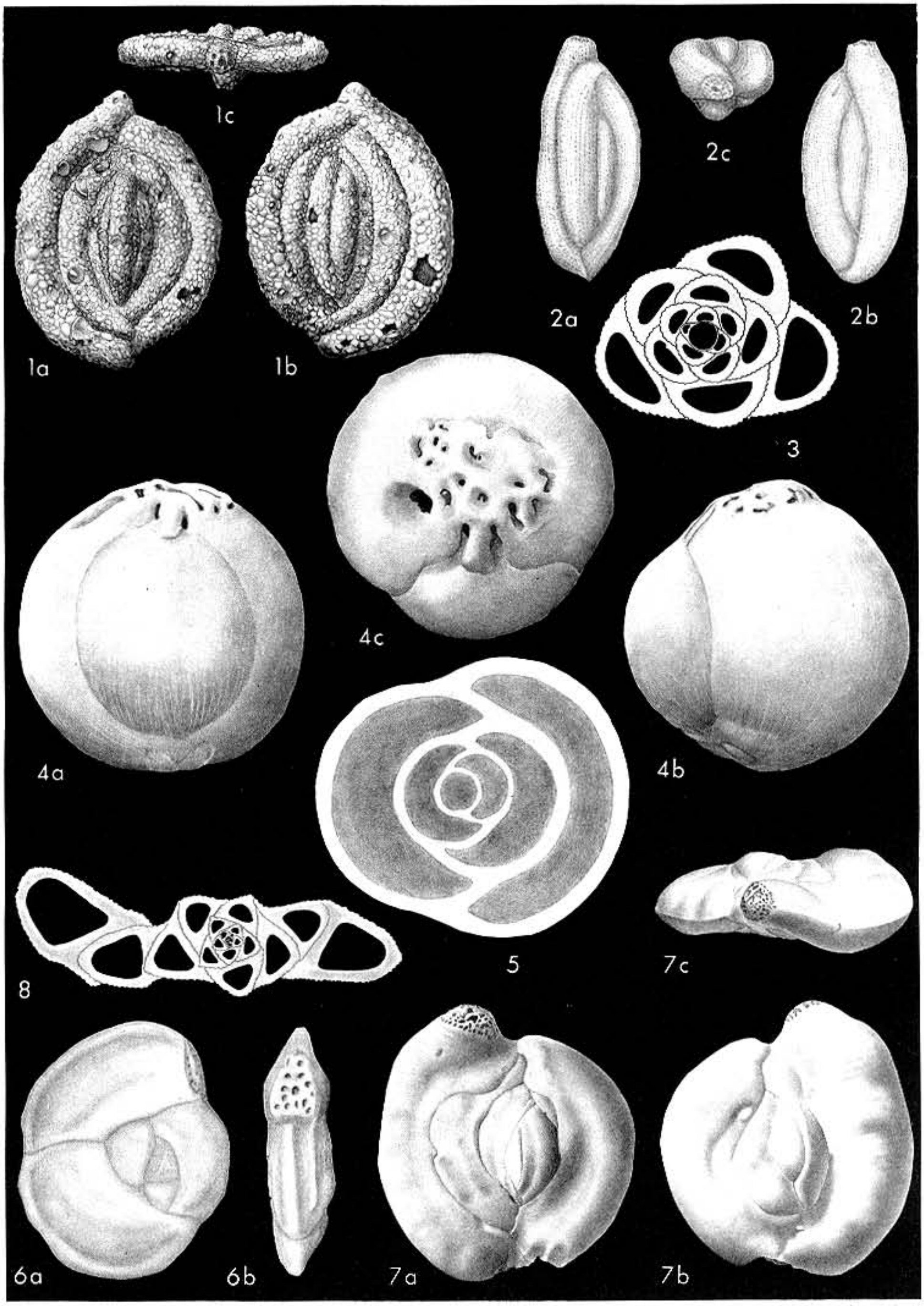


FIG. 357. Miliolidae (Miliolinae; *1*, *Ammomassilina; 2,3, Miliola; 4,5, Cribropyrgo; 6, Hauerina; 7,8, Heterillina*) (p. C468-C470).

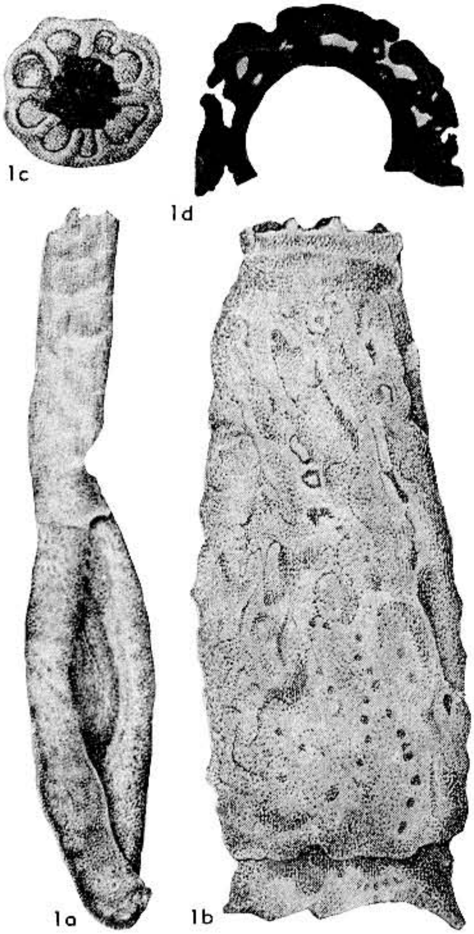


FIG. 358. Miliolidae (Miliolinae; *1, Dogielina*) (p. *C*470).

Ammomassilina CUSHMAN, 1933, *458, p. 32 [**Massilina alveoliniformis* MILLETT, 1898, *1284b, p. 609; OD]. Test free, early chambers milioline in development, later chambers added in single plane; wall agglutinated; aperture with trematophore. [Differs from *Schlumbergerina* in having later chambers added in a single plane.] *Rec.*, Malay Arch.(Malay).——FIG. 357,*1*. **A. alveoliniformis* (MILLETT); *1a-c*, opposite sides and apert. view, ×29 (*2117).

Cribropyrgo CUSHMAN & BERMÚDEZ, 1946, *493, p. 119 [**C. robusta*; OD]. Test free, subglobular, chamber arrangement as in *Pyrgo*; aperture cribrate, consisting of numerous irregular openings scattered over protruding terminal portion of final chamber. [Differs from *Pyrgoella* in having a cribrate, rather than chevron-shaped or cruciform aperture, and from *Fabularia* in having a simple interior.] *Rec.*, Carib.——FIG. 357,*4,5*. **C. robusta*, Cuba; *4a-c*, side, edge, and top views of holotype; *5*, sectioned paratype, all ×17 (*2117).

Dogielina BOGDANOVICH & VOLOSHINOVA, 1949, *154, p. 185 (*non Dogielina* RAABE, 1959) [**D. sarmatica*; OD]. Test with early chambers in milioline arrangement, as in *Quinqueloculina*, later uncoiling, with rectilinear chambers; wall calcareous, spongy in structure, surface with pits and grooves; aperture terminal, with toothlike infoldings from apertural wall giving radiate appearance. *U.Mio.* (*Sarmat.*), Carpath.——FIG. 358,*1*. **D. sarmatica*; *1a*, side view of holotype, ×47; *1b*, surface of uniserial chamber, ×115; *1c*, apert. view showing infolded wall, ×115; *1d*, partial section of wall showing spongy structure, ×150 (*154).

Hauerina D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. xxxviii [**H. compressa* D'ORBIGNY, 1846, *1395, p. 119; SD (SM)]. Test free, lenticular to discoidal, compressed, subcircular in outline, early stages quinqueloculine, later planispiral with 3 or more chambers to whorl; aperture series of pores in the sievelike trematophore. [Differs from *Heterillina* in having 3 or more chambers to whorl in adults, rather than 2.] *Eoc.-Rec.*, cosmop. ——FIG. 357,*6*. **H. compressa*, Mio., Eu.(Aus.); *6a,b*, side, apert. views of holotype, ×57 (*1166).

Heterillina MUNIER-CHALMAS & SCHLUMBERGER in SCHLUMBERGER, 1905, *1664, p. 131 [**H. guespellensis* SCHLUMBERGER, 1905; SD CUSHMAN, 1928, *439, p. 150] [=*Heterillina* MUNIER-CHALMAS & SCHLUMBERGER, 1883, *1329, p. 862 (*nom. nud.*)]. Test free, ovate in outline, flattened, chambers one-half coil in length, at first in quinqueloculine arrangement, later added on opposite sides as in *Spiroloculina*; sutures depressed; aperture terminal, multiple, with trematophore. [*Heterillina* differs from *Massilina* in having an apertural plate with numerous pores, and in lacking a bifid tooth. It differs from *Hauerina* in having all chambers one-half coil in length, whereas in adult *Hauerina* 3 chambers occur in each whorl. The types of *H. guespellensis* are from the middle Eocene at Le Guespelle, France, and are deposited in collections of the Sorbonne, University of Paris, France. Figured paratypes are from this locality.] *M.Eoc.-Oligo.*, Eu.(Fr.).——FIG. 357,*7,8*. **H. guespellensis*, M.Eoc.; *7a-c*, opposite sides and apert. view of paratype, ×27 (*2117); *8*, transv. sec. showing chamber arrangement, ×30 (*1664).

Idalina SCHLUMBERGER & MUNIER-CHALMAS, 1884, *1668, p. 629 (*non* NORMAN, 1890) [**I. antiqua* SCHLUMBERGER & MUNIER-CHALMAS, 1884, =*Biloculina antiqua* D'ORBIGNY, 1850, *1397b, p. 210 (*nom. nud.*), =*Triloculina cretacea* D'ORBIGNY, 1850, *1397b, p. 210 (*nom. nud.*) (*non Biloculina antiqua* KARRER, 1867); OD (M)]. Test free, ovoid, initial stage quinqueloculine followed successively by triloculine and biloculine stages and finally with completely enveloping chambers in adult, one or more of early stages may be lacking in some specimens; aperture in quinqueloculine stage with simple tooth, in triloculine stage with crenulate border in addition to tooth, in biloculine stage with more strongly marked crenulations and adult with raised trematophore pierced by numerous irregular openings. *U.Cret.(Senon.),* Eu. ——Fig. 359,*1-5*. **I. antiqua,* topotypes, Fr.;

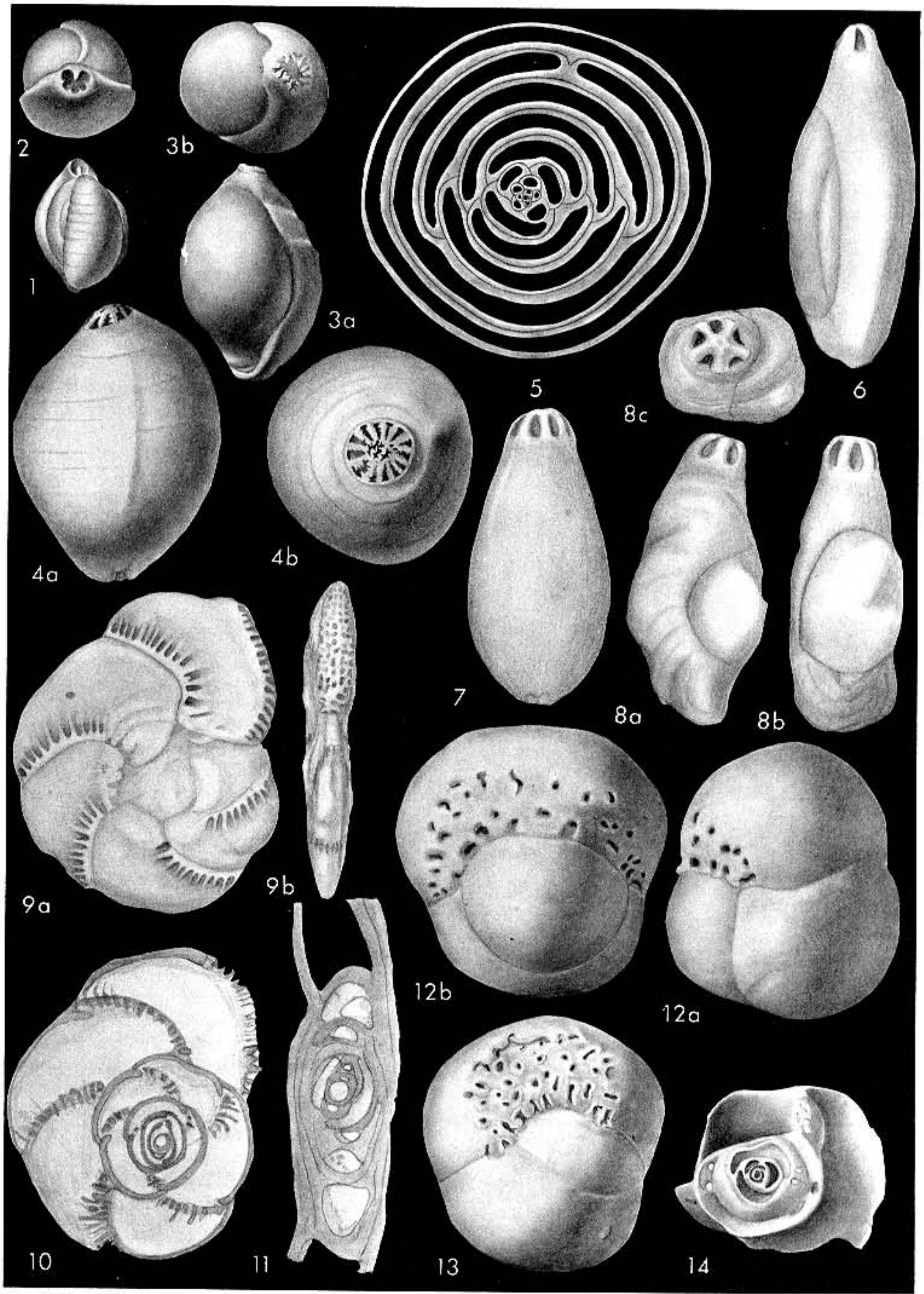


Fig. 359. Miliolidae (Miliolinae; *1-5, Idalina; 6-8, Nevillina; 9-11, Polysegmentina; 12-14, Involvohauerina*) (p. *C*470-*C*472).

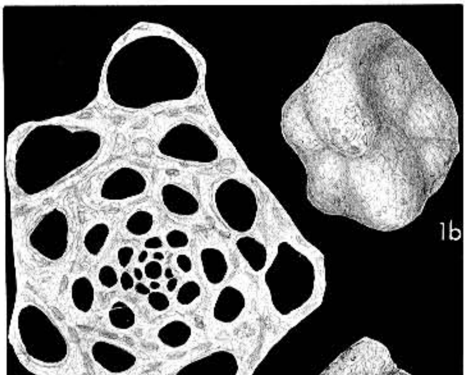


FIG. 360. Miliolidae (Miliolinae; *1-3, Schlumbergerina*) (p. C472-C473).

1, young quinqueloculine specimen with simple tooth, ×17 (*1330); *2,* triloculine specimen with crenulate apertural border, ×11 (*1330); *3a,b,* biloculine specimen, side and top views showing dendritic aperture, ×15 (*2117); *4a,b,* side, top views of adult with completely overlapping chambers and complex apert. trematophore, ×8 (*2117); *5,* horiz. sec. of adult showing chamber development, ×16 (*1330).

[*Idalina* was validly described in 1884 (although not figured) and the type-species by monotypy was referred to as "*Idalina antiqua,* d'Orb." SCHLUMBERGER & MUNIER-CHALMAS stated (*1668, p. 630), "*L'Idalina antiqua,* d'Orb. sp., comprend les deux genres *Biloculina antiqua* et *Triloculina cretacea* mentionnés par D'ORBIGNY dans son Prodrôme (Étage 21^{e}, n^{os} 353 et 359)." The species *Biloculina antiqua* and *Triloculina cretacea* were *nomina nuda,* however, and the species *I. antiqua* correctly should be credited to SCHLUMBERGER & MUNIER-CHALMAS who first described it. *Idalina* differs from *Fabularia* in having a final enveloping stage and in lacking the labyrinthic interior. The holotype was from the Senonian, zone of *Hippurites cornuvaccinum* and *H. organisans,* Étang de Berre, near Martigues, Dept. Bouche du Rhône, France.]

Involvohauerina LOEBLICH & TAPPAN, 1955, *1166, p. 14 [**I. globularis*; OD]. Test free, early portion quinqueloculine, later tending to become planispiral and involute with 3 chambers to whorl and only those chambers of last whorl visible; aperture areal, cribrate, with numerous irregularly shaped pores. [Differs from *Hauerina* in being almost globular, rather than compressed, and in being involutely coiled, rather than evolute.] *Rec.,* Atl.O.-Pac.O.——FIG. 359,*12-14.* **I. globularis,* Atl.; *12a,b,* side, apert. views of holotype; *13,* apert. view of paratype showing more complex aperture; *14,* dissected paratype showing chamber development; all ×20 (*1166).

Nevillina SIDEBOTTOM, 1905, *1739, p. 1 [**Biloculina coronata* MILLETT, 1898, *1284a, p. 263; OD (M)]. Test free, pyriform in outline, early chambers triloculine in plan, later biloculine, adult chambers completely embracing early ones, aperture of each succeeding chamber at opposite ends of test; wall smooth or marked by some transverse wrinkles; aperture terminal, rounded opening surrounded by additional radiating slits, between encurved lamellae which meet in ring around small central opening. [The holotype of *Biloculina coronata* is in the BMNH-ZF3626, from the Malay Archipelago. The original reference states that it occurred at Station 18, but the slide is labeled Station 19.] *Rec.,* Malay Arch. (Malay)-Ind.O.——FIG. 359,*6-8.* **N. coronata* (MILLETT), Malay; *6,* triloculine specimen, ×79; *7,* adult specimen with completely overlapping chambers, ×36; *8a-c,* side, edge and top views of holotype, ×79 (*2117).

Polysegmentina CUSHMAN, 1946, *483, p. 1 [**Hauerina circinata* BRADY, 1881, *196c, p. 47; OD]. Test free, discoidal, early portion milioline in plan, later planispiral and slightly involute, with 3 to 6 chambers in final whorl, later chambers being relatively shorter, so that number per whorl gradually increases; wall thickened, calcareous, imperforate; aperture consisting of numerous irregular pores in trematophore, marginal row of pores being left exposed in earlier chambers and remaining as sutural pores connecting with interior. [Differs from *Hauerina* in its peculiar sutural retral processes bordering the relict lateral pores of previous apertures, which continue to connect with the interior.] *Rec.,* Pac.O.——FIG. 359,*9-11.* **P. circinata* (BRADY); *9a,b,* side, edge views of lectotype, ×47; *10,* horiz. sec. showing chamber arrangement and apertural pores, ×47; *11,* axial sec. of central area showing early chamber arrangement and lamellar wall, ×109 (*1166).

Schlumbergerina MUNIER-CHALMAS, 1882, *1322, p. 424 [**S. areniphora*; OD]. Test free, milioline in development, but with chambers added in more than 5 planes; wall agglutinated; aperture with trematophore, lateral rather than terminal in position. [MUNIER-CHALMAS described this form

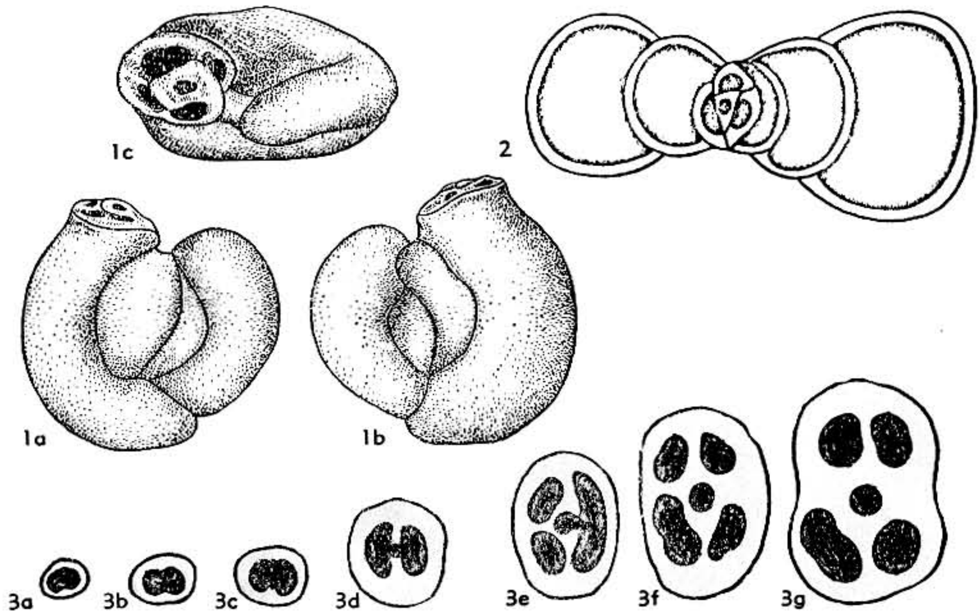


FIG. 361. Miliolidae (Miliolinae; *1-3, Tortonella*) (p. *C*473).

as having 5 chambers externally, but in his figure of the type, 5 chambers are visible from one side of the test. None of the types of MUNIER-CHALMAS preserved in collections of the Sorbonne, Paris, France, show a test with only 5 chambers externally. Even in the early stage no quinqueloculine development is seen. *Schlumbergerina* differs from *Ammomassilina* in having chambers added in many planes, rather than in a single plane in the adult.] *Rec.*, Pac.O.-Gulf Mex.——FIG. 360,*1-3*. **S. areniphora*; Samoa *(1)*, Torres Straits *(2)*, Philip. *(3)*; *1a,b*, side, top views of lectotype, ×28; *2*, apert. region of paratype, ×64; *3*, sectioned specimen showing chambers added in numerous planes, ×64 (*2117).

Tortonella DIDKOVSKIY, 1957, *593, p. 1138 [**T. bondartschuki*; OD]. Test free, flattened, early stage triloculine, later chambers added in single plane, 2 chambers to whorl or more rarely spreading somewhat so that 2 chambers do not quite complete volution; aperture large and rounded, with modified tooth, resulting in central perforation surrounded by 4 additional openings. *Mio.(Torton.)*, USSR(Ukraine).——FIG. 361,*1-3*. **T. bondartschuki*; *1a-c*, opposite sides and apert. view of holotype, ×25; *2*, transv. sec. showing early triloculine stage, followed by planispiral stage, ×48; *3a-g*, diagram. outlines of apertures of progressively larger specimens showing change from simple to bifid tooth to ringlike tooth attached in 4 places to leave 5 openings, ×55 (*593).

[*Tortonella* is close in appearance to *Cribrolinoides*, and apparently has a similar apertural development from simple opening and tooth to ringlike apertural tooth, and finally multiple openings. Although the definition of *Tortonella* stated that the early stage was quinqueloculine (which would make it a synonym of *Cribrolinoides*), the sectioned specimen figured shows only a triloculine early stage; hence both are provisionally recognized.]

Subfamily FABULARIINAE Ehrenberg, 1839

[*nom. correct.* LOEBLICH & TAPPAN, 1961, p. 293 (*pro* subfamily Fabularidea REUSS, 1862, p. 375)]

Interior complex; chambers subdivided into chamberlets; aperture multiple. *U.Cret. (Senon.)-Rec.*

Fabularia DEFRANCE, 1820, *579a, p. 557 [**F. discolites* DEFRANCE in BRONN, 1825, *209, p. 43 (=*Nummulites ovata* DE ROISSY, 1805, *1584, p. 59); SD (SM) DEFRANCE in BRONN, 1825, *209, p. 43]. Test free, large, early stage biloculine in megalospheric form, at first quinqueloculine in microspheric forms, then triloculine, adults biloculine; wall thick, interior subdivided by secondary partitions; surface ornamented by fine striae and punctations; aperture with large trematophore pierced with numerous irregular openings. *M.Eoc.(Lutet.)-Rec.*, Eu.(Fr.)-Afr.-N.Am.——FIG. 362,*1-4*. **F. ovata* (DE ROISSY), M.Eoc. (Lutet.), Fr.; *1a-c*, opposite sides and apert. view of juvenile triloculine specimen, ×10 (*2117); *2a,b*, side, edge views of biloculine specimen, surface abraded to show wall characters, ×10 (*2117); *3*, horiz. sec. of microspheric specimen, ×41; *4*, horiz. sec. of megalospheric specimen, ×35 (*1664).

Austrotrillina Parr, 1942, *1426, p. 361 [**Trillina howchini* Schlumberger, 1893, *1656, p. 119, 123; OD]. Test with chamber arrangement as in *Triloculina,* new chambers adding layers against previous ones as well as new chamber wall; wall thick, new outer portion alveolar, that against

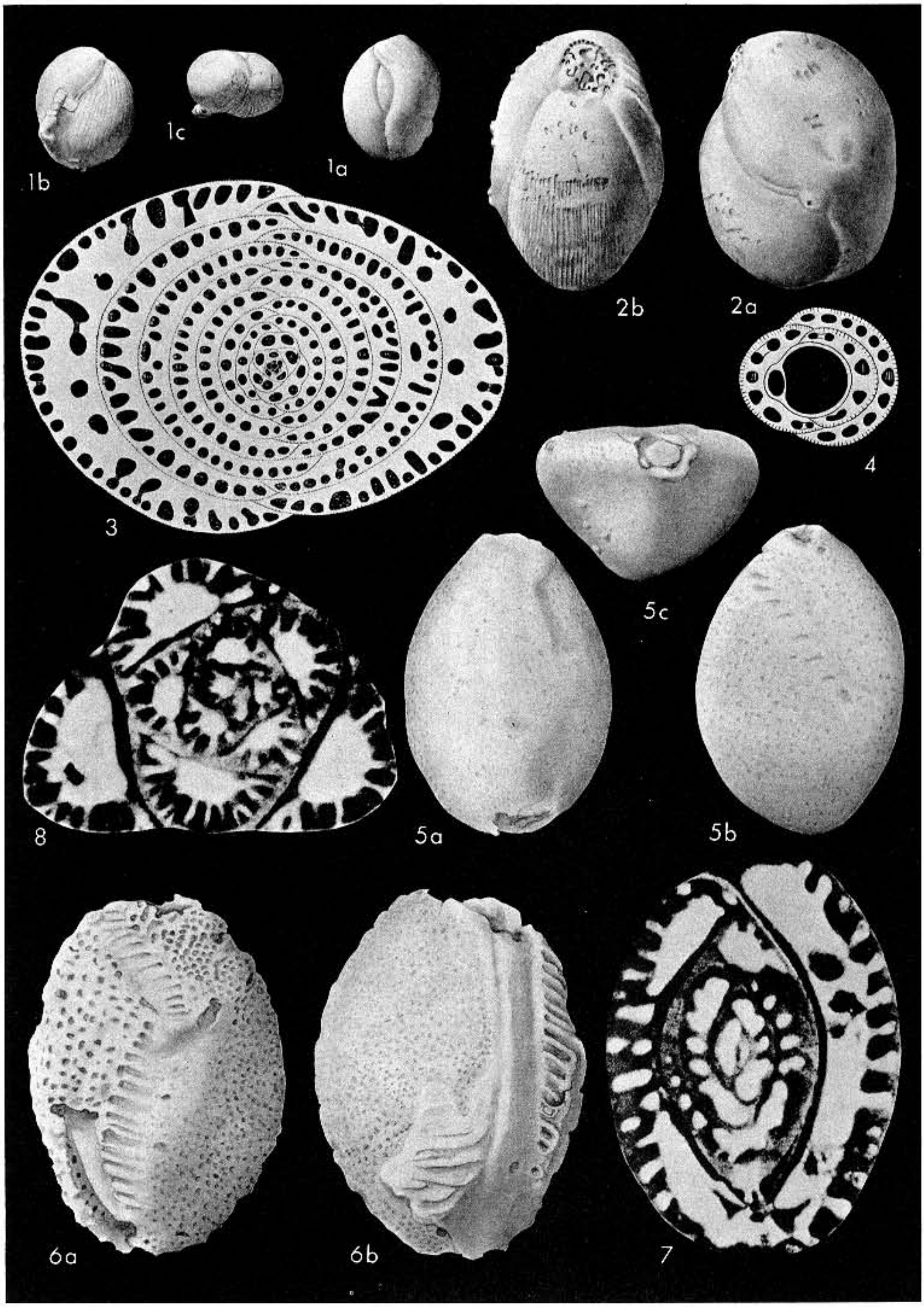


Fig. 362. Miliolidae (Fabulariinae; *1-4, Fabularia; 5-8, Austrotrillina*) (p. C473-C476).

previous chambers thin and simple in structure; chamber cavity undivided; aperture terminal, with trematophore. [*Austrotrillina* was defined to include some of the species placed by SCHLUMBERGER in *Trillina*, the type-species of which (*T. strigillata* D'ORBIGNY) is a true *Triloculina*; hence,

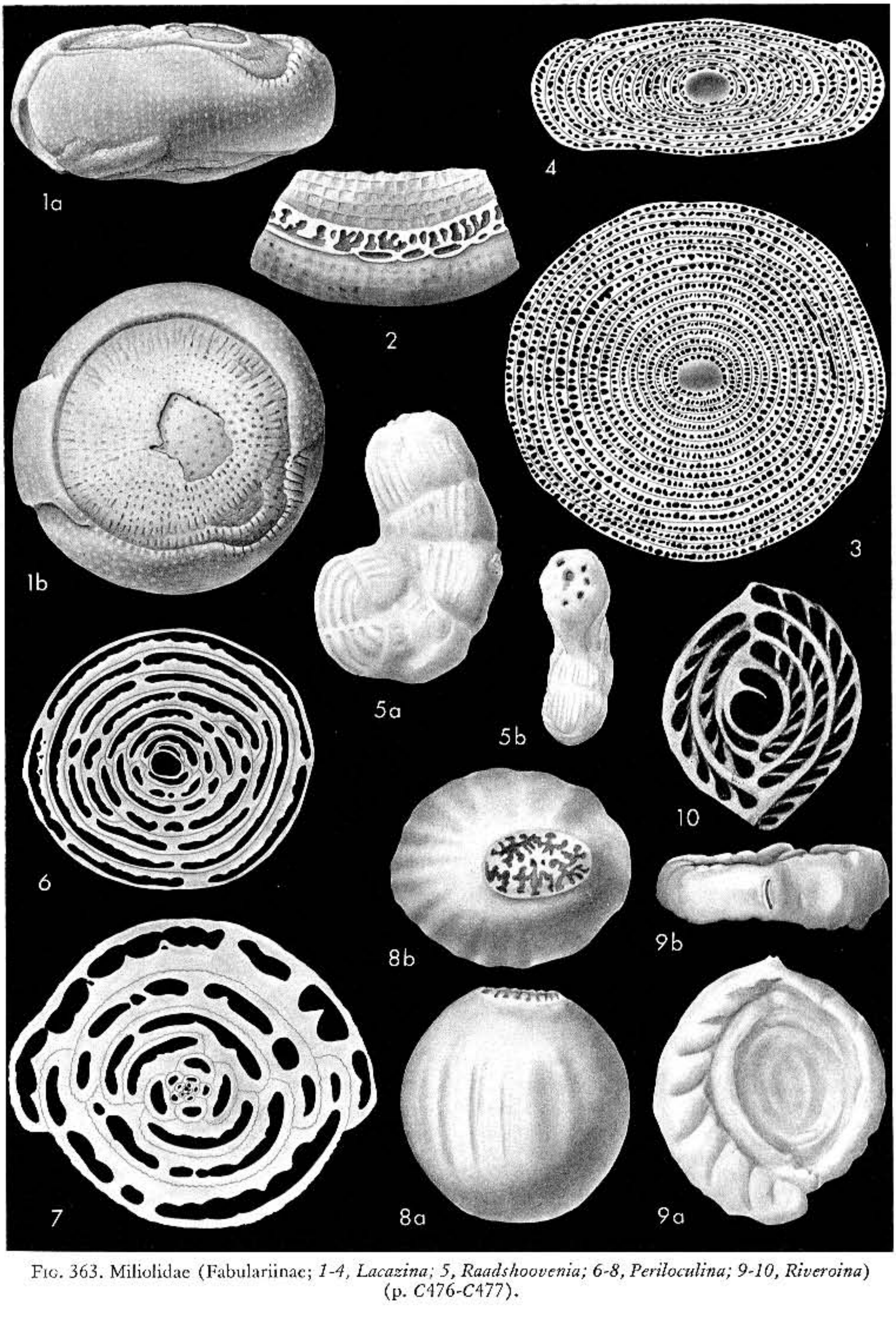


FIG. 363. Miliolidae (Fabulariinae; *1-4, Lacazina; 5, Raadshoovenia; 6-8, Periloculina; 9-10, Riveroina*) (p. C476-C477).

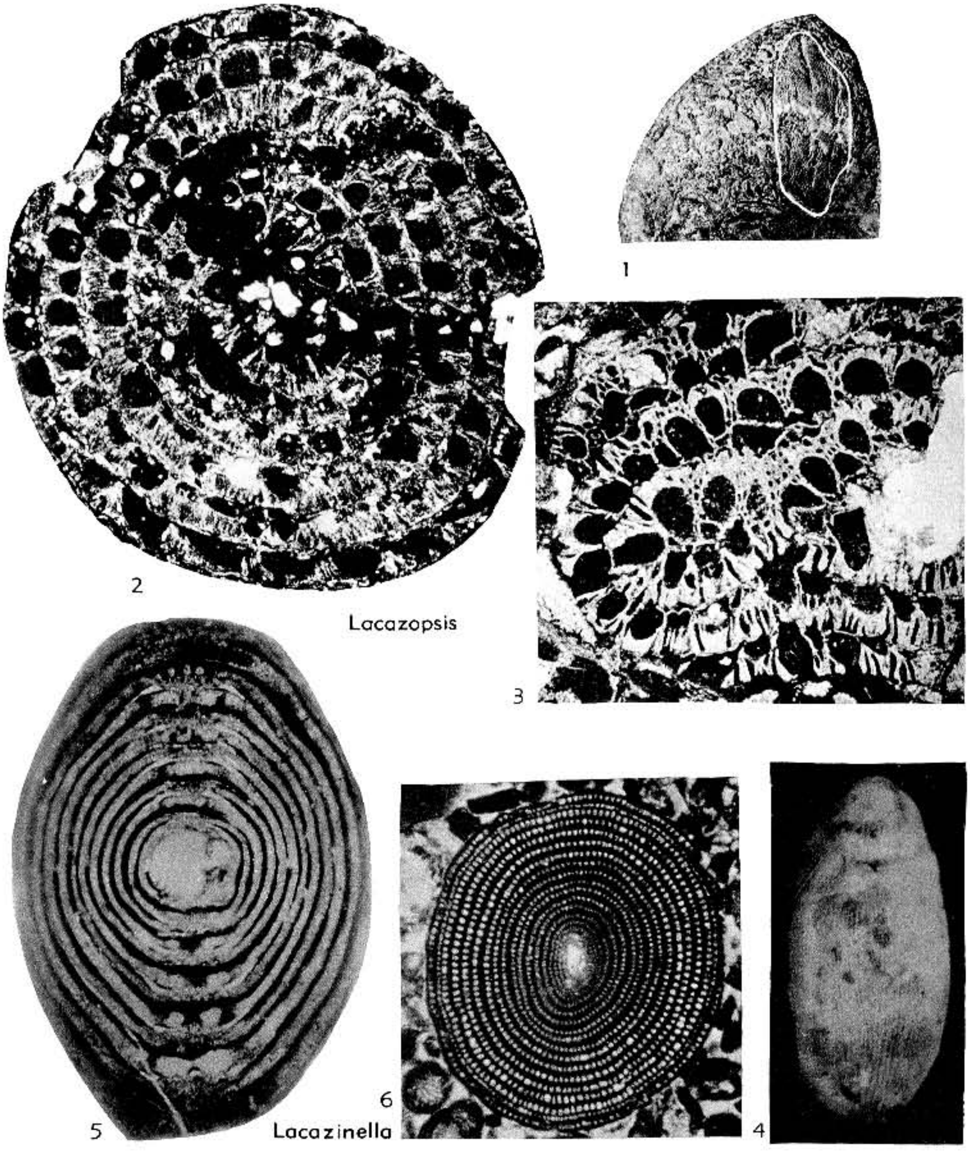


FIG. 364. Miliolidae (Fabulariinae; *1-3, Lacazopsis; 4-6, Lacazinella*) (p. *C477*).

Trillina is a junior synonym of *Triloculina*.] *Eoc.-Mio.*, Pac.O.-Australia-Asia(Iraq.)-E.Afr.(Somaliland).——FIG. 362,*5-8*. **A. howchini* (SCHLUMBERGER), Mio., Australia; *5a-c*, opposite sides and top view of specimen, ×35 (*2117); *6a,b*, opposite sides of eroded specimen in which alveolar wall character is evident, ×35 (*2117); *7,8*, long. and transv. secs., ×53 (*361).

Lacazina MUNIER-CHALMAS, 1882, *1324, p. 472 [**Alveolina compressa* D'ORBIGNY, 1850, *1397b, p. 210; OD]. Test free, discoidal; chambers biloculine, being added alternately on each side of test, subdivided by numerous small longitudinal pillars; aperture large, circular, ringlike, at entire margin of final chamber, covered by similarly ringlike trematophore with irregular openings separated by anastomosing denticulations. [*Lacazina* differs from *Periloculina* in having a ringlike aperture and trematophore instead of a small circular aperture and discoidal trematophore.

D'ORBIGNY's types are from the Senonian, Martigues and La Fare, Dept. Bouche du Rhône, France.] *U.Cret.(Senon.),* Eu.——FIG. 363,*1-4*. **L. compressa* (D'ORBIGNY), Santon., Sp. *(1),* Senon., Fr. *(2-4)*; *1a,b,* edge and apert. views, ×8 (*2117); *2,* part of test showing trematophore, ×15; *3,4,* horiz. and axial secs., enlarged (*1330).

Lacazinella CRESPIN, 1962, *394A, p. 337 [**Lacazina wichmanni* SCHLUMBERGER, 1894, *1656A, p. 295; OD]. Test large, 2-3 mm. in length, elongate-ovate in outline, circular in section, each chamber completely enveloping test, only final chamber visible externally, proloculus subspherical, each successive chamber with aperture at opposite end of test from that of preceding one, chamber interiors partially filled by longitudinal internal perforated ribs which anastomose somewhat below apertural region; wall calcareous, porcelaneous, imperforate, surface smooth or longitudinally grooved; aperture terminal cribrate, consisting of trematophore at one end of long axis. [Differs from *Lacazina* in having completely embracing chambers, elongate axis, and endoskeleton of ribs, rather than pillars, and from *Periloculina* in lacking an early milioline development.] *U.Eoc., ?Oligo.,* W.Pac.O.(New Guinea-Moluccas Is.).——FIG. 364,*4-6*. **L. wichmanni* (SCHLUMBERGER); *4,* side view, ×14; *5,* vert. sec. showing completely enveloping chambers with apertures at alternate ends and sectioned trematophore, ×20; *6,* horiz. sec. showing radiating vert. ribs, ×18 (*394A).

Lacazopsis DOUVILLÉ, 1930, *629, p. 247 [**L. termieri*; OD (M)]. Test free, to 22 mm. in length, irregularly fusiform, with completely enveloping chambers that alternate from pole to pole, subdivided into chamberlets by longitudinal and transverse interseptal partitions; wall calcareous, agglutinated, outer regular layer thin, inner layer with anastomosing pillars that form irregular network, tangential section appearing reticulate, and perpendicular section showing nearly parallel pillars; aperture terminal, cribrate. [*Lacazopsis* has the general form of *Lacazina* but is much larger. The wall was described as finely agglutinated and reticulate, rather than calcareous imperforate. It was originally placed with the trematophorate miliolids, but restudy of the wall character is necessary to determine if it actually is porcelaneous. The Fiche-Type H. DOUVILLÉ 37 (4), Institut Français du Pétrole, stated that the chamber appearance suggested a cheilostome bryozoan.] *U.Cret.(Senon.),* N.Afr.(Morocco).——FIG. 364, *1-3*. **L. termieri*; *1,* specimen (outlined) on pebble, ×2; *2,* transv. sec. showing annular chambers and interseptal partitions, ×20; *3,* oblique sec. showing at left interseptal pillars perpendicular to surface and at right alveolar structure, ×20 (*629).

Periloculina MUNIER-CHALMAS & SCHLUMBERGER, 1885, *1330, p. 308 [**P. zitteli*; OD (M)]. Test free, ovoid, in adult consisting of completely embracing chambers, microspheric form with initial quinqueloculine stage followed by triloculine, biloculine, and finally embracing development, megalospheric form either triloculine or biloculine in young; wall commonly with longitudinal ornamentation, internal wall of chambers with longitudinal ridges which may become sufficiently produced to touch opposite wall and secondarily subdivide chamber; aperture elongate and crescentic with denticulate margin in early stage, with trematophore pierced by irregular anastomosing openings in adults. [Differs from *Idalina* in having the interior of the chambers subdivided by internal longitudinal ribs. It differs from *Lacazina* in having a platelike, instead of ringlike, trematophore and in having internal ribs instead of the radiating pillars characteristic of *Lacazina*.] *U.Cret.(Senon.),* Eu. (Fr.).——FIG. 363,*6-8*. **P. zitteli*; *6,7,* transv. secs. of megalospheric (×18) and microspheric (×42) forms; *8a,b,* side, apert. views, ×12 (*1330).

Raadshoovenia VAN DEN BOLD, 1946, *155, p. 123 [**R. guatemalensis*; OD]. Test free, early chambers in quinqueloculine arrangement, later 4 to 6 chambers to whorl in planispiral coil, adult uncoiling and rectilinear; later chambers with secondary interseptal partitions, visible as ridges at surface of slightly eroded specimens; aperture terminal, multiple. *L.Eoc.,* C.Am.(Guat.).——FIG. 363,*5*. **R. guatemalensis; 5a,b,* side, top views, ×15 (*2117).

Riveroina BERMÚDEZ, 1939, *121b, p. 248 [**R. caribaea*; OD]. Test free, planispiral, with chambers one-half coil in length, as in *Spiroloculina,* but interior of chambers with oblique secondary septa, those of each chamber projecting toward its apertural end; aperture terminal, single, elongate curved slit. *Rec.,* Carib. Sea.——FIG. 363, *9,10*. **R. caribaea; 9a,b,* side, apert. views of paratype, ×76 (*2117); *10,* sectioned paratype, ×50 (*121b).

Subfamily TUBINELLINAE Rhumbler, 1906

[Tubinellinae RHUMBLER, 1906, p. 25] [=Artubinia RHUMBLER, 1913, p. 352 *(nom. van.)*]

Early milioline stage reduced; later portion uniserial, with rudimentary septa; aperture formed by open end of final chamber. *M.Eoc.-Rec.*

Tubinella RHUMBLER, 1906, *1571, p. 25 [**Articulina funalis* var. *inornata* BRADY, 1884, *200, p. 186; SD CUSHMAN, 1928, *439, p. 151] [=*Artubinum* RHUMBLER, 1913, *1572b, p. 352 (obj.) *(nom. van.)*; *Tubinellina* WIESNER, 1931, *2063, p. 67 (type, *Articulina funalis* BRADY, 1884, *200, p. 185)]. Test free, with vestigial early milioline stage consisting of bulbous proloculus and closely appressed second chamber, reversing direction of growth; later chambers

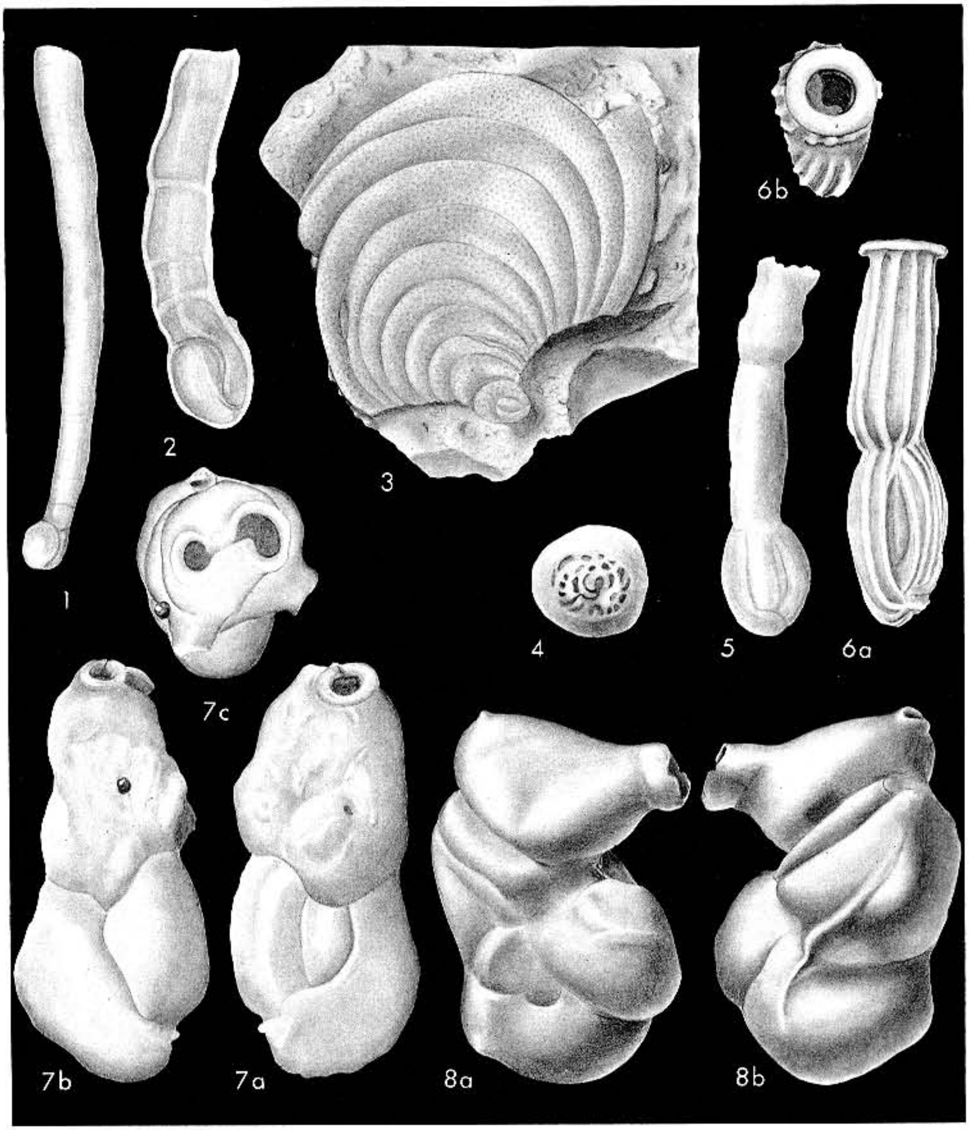


FIG. 365. Miliolidae (Tubinellinae; *1,2, Tubinella; 3, Pavoninoides; 4,5, Poroarticulina; 6, Articulina; 7,8, Parrina*) (p. *C477-C480*).

cylindrical, uniserially arranged; septa vestigial, consisting of slight transverse thickenings of wall, visible in transmitted light; aperture at open end of tube. [*Tubinella* is very close to *Articulina* in possessing a milioline early stage, although much reduced, and is probably derived from *Articulina* by reduction of the septa to mere wall thickenings.] *Rec.*, Pac.O.-Atl.O.——FIG. 365,*1,2*. **T. inornata* (Brady), Rec., Ind.O.(Kerguelen Is.); *1*, side view of lectotype, ×48; *2*, paratype, ×105 (*1166).

Articulina d'Orbigny, 1826, *1391, p. 300 [**A. nitida*; OD (M)] [=*Ceratospirulina* Ehrenberg, 1858, *683, p. 11 (type, *C. spratti*)]. Test in early stage milioline, later rectilinear, ornamentation may consist of longitudinal costae; aperture in adult terminal, rounded, with everted margin. *M.Eoc.-Rec.*, cosmop.——FIG. 365,*6*. **A. nitida*, M.Eoc.(Lutet.), Eu.(Fr.); *6a,b*, side, top views of topotype, ×83 (*2117).

Parrina Cushman, 1931, *448, p. 20 [=*pro Silvestria* Schubert, 1921, *1694, p. 166 (*non* Verhoeff, 1895; *nec* Brian, 1902)] [**Nubecularia bradyi* Millett, 1898, *1284a, p. 261; OD] [=*Erichsenella* Tinoco, 1955, *1935, p. 19 (type, *E. kegeli*)]. Test with early stage milioline, later chambers irregularly uniserial; aperture rounded, without tooth and commonly with more than one aperture on terminal chamber. [*Parrina* was defined by CUSHMAN as "irregularly coiled" in the early stage, but both the type-species of *Parrina* and that of *Erichsenella* have a more or less well-

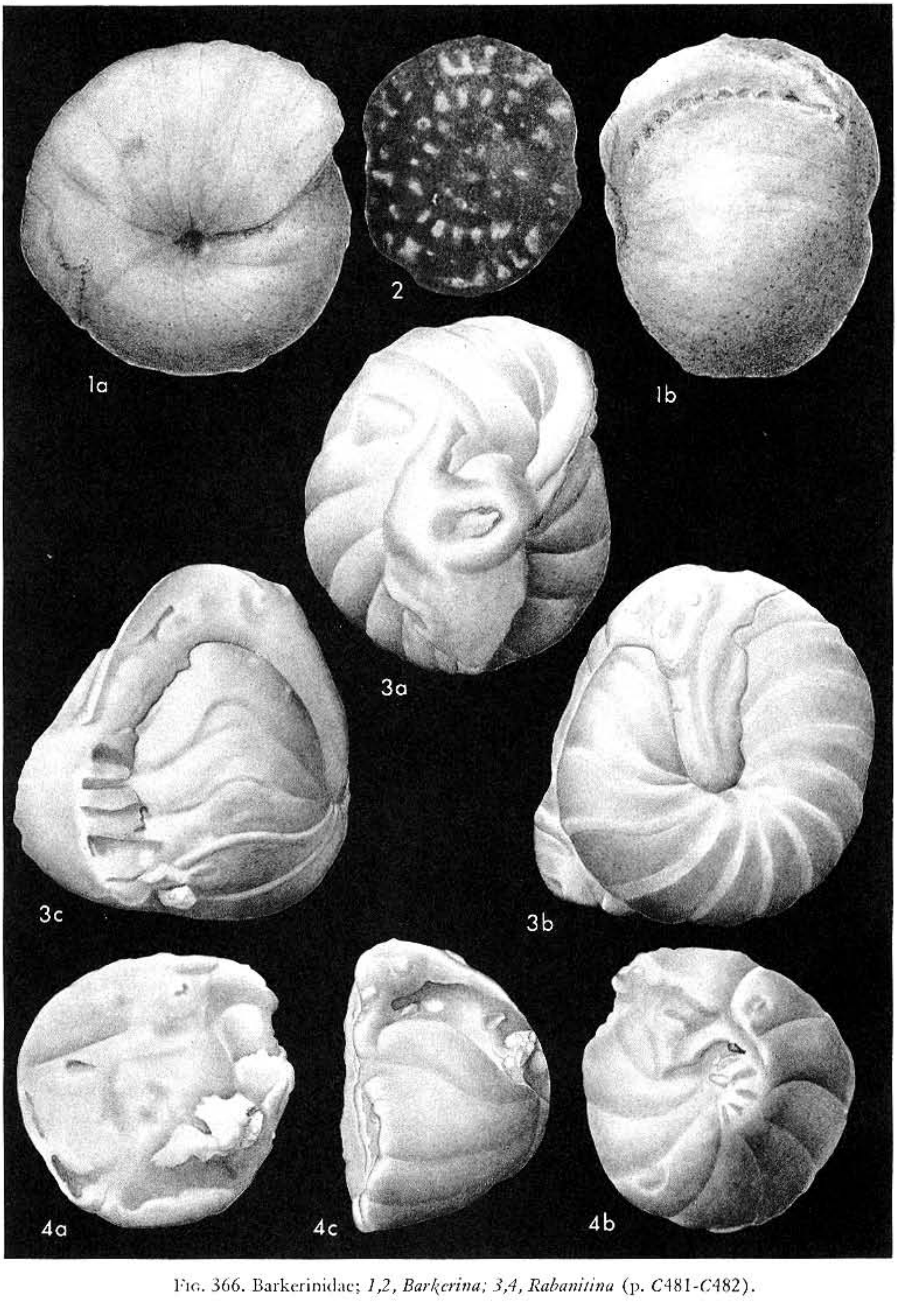


FIG. 366. Barkerinidae; *1,2, Bar*k*erina; 3,4, Rabanitina* (p. C481-C482).

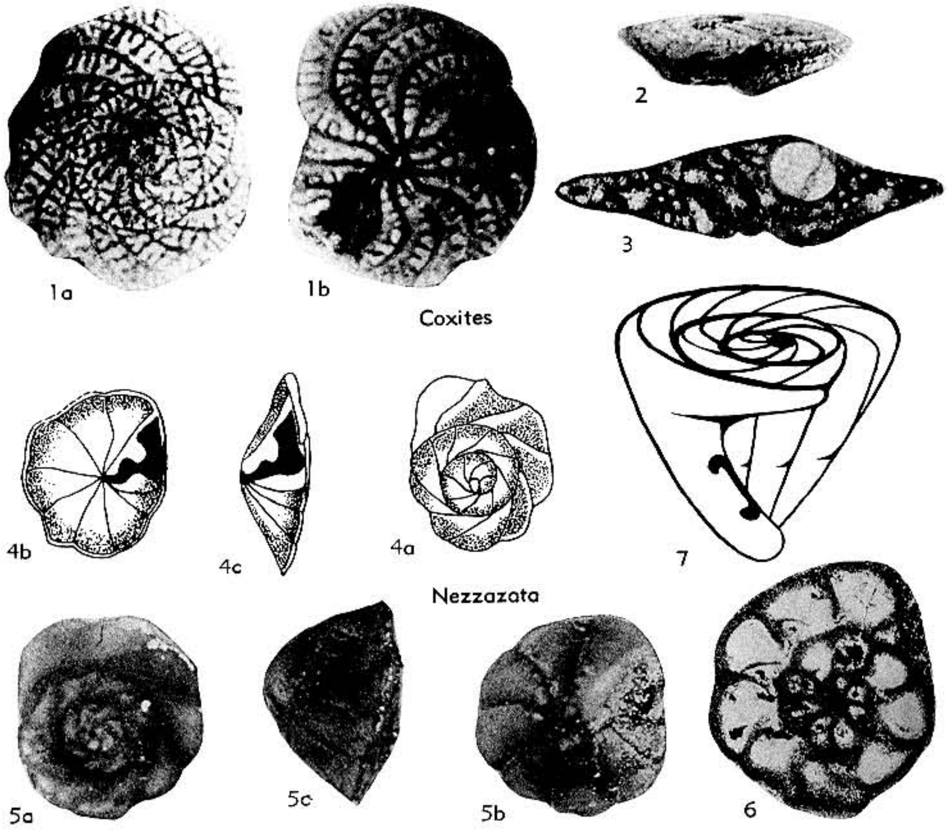


FIG. 367. Barkerinidae; *1-3, Coxites; 4-7, Nezzazata* (p. C481).

developed milioline stage, although this may be somewhat obscured by the irregular later chambers. *Parrina* differs from *Articulina* in being irregular in later development and in having more than one asymmetrically placed aperture.] *Rec.*, W.Pac.O.-Atl.O.——FIG. 365,*7*. **P. bradyi* (MILLETT), Rec., W.Pac.(Fiji Is.); *7a-c*, opposite sides and top view of hypotype, showing milioline early stage and numerous apertures on final chamber, ×89 (*2117).——FIG. 365,*8*. *P. kegeli* (TINOCO), Rec., Atl.O.(Brazil); *8a,b*, opposite sides of topotype, ×99 (*2117).

Pavoninoides BERMÚDEZ, 1949, *123, p. 58 [**P. panamensis*; OD]. Test flabelliform, chambers in early stage in triloculine arrangement, later uniserial, with rapidly increasing breadth; wall calcareous, imperforate, but with surface pitting; aperture multiple, single row of pores on peripheral margin of final chamber. *U.Eoc.*, C.Am.(Panama). ——FIG. 365,*3*. **P. panamensis*; side view of holotype, ×28 (*2117).

Poroarticulina CUSHMAN, 1944, *479, p. 52 [**P. glabra*; OD]. Test with early chambers in quinqueloculine arrangement, later uniserial, rectilinear; aperture in early stage with tooth, in uniserial stage terminal, cribrate. *Mio.*, Eu.(Rumania).——FIG. 365,*4,5*. **P. glabra*; *4*, top view of holotype; *5*, side view of paratype, ×74 (*2117).

Family BARKERINIDAE Smout, 1956

[Barkerinidae SMOUT, 1956, p. 342] [=Barkerininae LOEBLICH & TAPPAN, 1961, p. 280 (*nom. transl. ex* family Barkerinidae SMOUT, 1956)]

Test trochospiral in early stage, later planispiral and involute, or planispiral throughout; chambers subdivided by transverse partitions; wall imperforate, calcareous, microgranular (?recrystallized); aperture single or multiple. *Cret.(Alb.-Turon.)*.

[As defined by SMOUT, the Barkerinidae included only *Barkerina, Coxites,* and *Rabanitina*, all characterized by a complexly folded plate subdividing the chambers. Although this is represented only by a small tooth plate in *Nezzazata*, the similarity in the imperforate granular wall and the *Nezzazata*-like juvenile stage of *Rabanitina* suggests such a relationship. The Barkerinidae are stated not to be agglutinated, the granular, commonly recrystallized imperforate wall suggesting a relationship to the porcelaneous foraminifers, as noted by SMOUT (*1805). The proloculus is not followed by a spiral passage as in the Nubeculariidae nor are the chambers coiled about an elongate axis as in the Miliolidae. The family Barkerinidae is here placed in the Miliolacea. The subdivided cham-

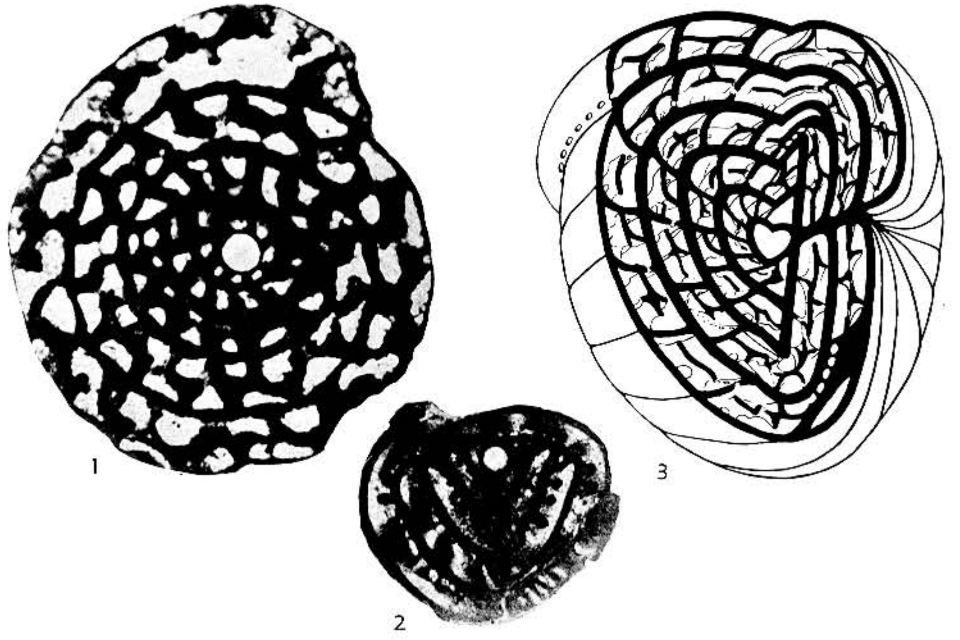


FIG. 368. Barkerinidae; *1-3, Rabanitina* (p. C482).

bers are similar to the Soritidae and Alveolinidae, but the early trochospiral development is distinct.]

Barkerina FRIZZELL & SCHWARTZ, 1950, *753, p. 5 [**B. barkerensis*; OD]. Test planispirally coiled, involute; chambers numerous, low and broad, subdivided internally by transverse partitions, visible on eroded specimens; wall of microgranular calcite; aperture comprising row of arched openings at base of septal face. *L.Cret.(Alb.)*, USA (Tex.).——FIG. 366,*1,2*. **B. barkerensis*; *1a,b*, side, edge views of holotype, ×86 (*2117); *2*, sec. showing subdivided chambers, ×60 (*753).

Coxites SMOUT, 1956, *1805, p. 342 [**C. zubairensis*; OD]. Test trochospiral, unequally biconvex, with all whorls visible on flattened spiral side, only final whorl visible on low conical umbilicate opposite side, periphery acute; chambers numerous, low and curved, with long marginal prolongation as in *Nezzazata*, with incomplete oblique longitudinal plate extending from roof to floor of each chamber, transverse partitions in all chambers, commonly simple, more rarely forked; sutures curved, flush but distinct; wall of thin, imperforate, granular calcite, without arenaceous particles, internal structure visible through thin, almost transparent wall; apertural characters unknown as apertural face is broken in all specimens observed. *U.Cret.(Turon.)*, SW. Asia(Iraq).——FIG. 367,*1-3*. **C. zubairensis*; *1a,b*, opposite sides of holotype; *2*, edge view of paratype; *3*, axial sec., ×40 (*1805).

Nezzazata OMARA, 1956, *1389, p. 887 [**N. simplex*; OD] [=*Begia* SMOUT, 1956, *1805, p. 339 (type, *B. gyra*)]. Test trochospiral, plano-convex to unequally biconvex, all whorls visible from flattened to slightly convex spiral side, only those of final whorl visible around closed umbilical region; chambers with projection at periphery similar to tectum of *Alabamina*; wall calcareous, imperforate (*1805, *1527) or possibly finely perforate (*1389), microgranular in structure, described as nonlamellar, septa single (monolamellar); aperture a narrow interiomarginal opening from near umbilicus to periphery, bending up apertural face parallel to peripheral margin, internal tooth plate extending between adjacent septa may attach to outer chamber wall where it shows as slight indentation of suture. *Cret.(Alb.-Turon.)*, Afr.-Asia(Israel-Iraq).——FIG. 367,*4*. **N. simplex*, U.Cret.(Cenoman.), Egypt; *4a-c*, opposite sides and edge view of holotype, ×38 (*1389).——FIG. 367,*5-7*. *N. gyra* (SMOUT), U. Cret.(Turon.), Iraq; *5a-c*, opposite sides and edge view of holotype, ×40; *6*, horiz. sec., showing tooth plates, ×40; *7*, oblique diagram of exterior, showing tectum, angled aperture and apert. tooth, enlarged (*1805).

[The position of this genus is doubtful. It was placed in the Ceratobuliminidae by SMOUT (*1805), though it lacks an aragonitic wall. It was compared to the "Rotaliidea" by OMARA (*1389) but regarded as differing from that superfamily in its granular wall. REISS (*1527) referred the genus to the Barkerinidae. The photomicrographs given by SMOUT and REISS suggest the recrystallized porcelaneous wall as figured by Wood (*2073, pl. 13, fig. 2) for *Alveolinella,* and the family Barkerinidae is here regarded as having a porcelaneous wall.]

Rabanitina Smout, 1956, *1805, p. 343 [**R. basraensis*; OD]. Test subspherical, early stage trochospiral, plano-convex and umbilicate on elevated umbilical side, then changing abruptly to completely involute, globular form; in all adult chambers, complex longitudinal perforated plate roughly parallels spiral wall, but it is twisted and buttressed to chamber floor and roof; sutures flush or slightly depressed, septa radial; shell calcareous, nonlamellar, microgranular, without arenaceous matter, porcelaneous, imperforate, but shell material altered in described specimens, surface not ornamented; aperture not observed. [*Rabanitina* is similar to *Barkerina* in the adult, but differs in having an early conical trochospiral stage.] *U.Cret.(L.Cenom.)*, Iraq.——Fig. 366,*3,4*; 368,*1-3*. **R. basraensis;* 366,*3a-c,* opposite sides and edge view of involute adult specimen, ×40 (*2117); 366,*4a-c,* opposite sides and edge view of young trochospiral specimen, ×40 (*2117); 368,*1,2,* subequat. and axial secs., ×30; *3,* block diagram showing relationship of axial and equat. secs., enlarged (*1805).

Family SORITIDAE Ehrenberg, 1839

[*nom. correct.* Galloway, 1933, p. 132 (*pro* family Soritina Ehrenberg, 1839, table opposite p. 120)]——[All names cited are of family rank; dagger(†) indicates *partim*]——[=Planulacea and Planulacés de Blainville, 1825, p. 370 *(nom. nud.)*; =Polythalamat† Latreille, 1825, p. 161 *(nom. nud.)*; =Cristata Crouch, 1827, p. 40 *(nom. nud.)*; =Helicostègues† d'Orbigny, 1826, p. 268 *(nom. nud.; nom. neg.)*; =Enthomostègues† d'Orbigny, 1826, p. 304 *(nom. nud.; nom. neg.)*; =Cristacidae Broderip, 1839, p. 321 *(nom. nud.)*; =Helicosorina† Ehrenberg, 1839, table opp. p. 120 *(nom. nud.)*; =Asterodiscina† Ehrenberg, 1839, table opp. p. 120; =Myrioporina Agassiz, 1844, p. 16 *(nom. nud.)*; =Nautiloida† Schultze, 1854, p. 53 *(nom. nud.)*; =Heliostegia† Reuss, 1860, p. 151, 205 *(nom. nud.)*]——[=Orbitolitidae Gray, 1840, *fide* Agassiz, 1844, p. 19 (cited in error as Gray, 1804); =Orbitulitidea Reuss, 1862, p. 376; =Orbitulitideae Gümbel, 1870, p. 27; =Orbiculinida Jones in Griffith & Henfrey, 1875, p. 319; =Orbitulitidee Schwager, 1876, p. 483; =Orbitulita Marriott, 1878, p. 31; =Orbitolitina Bütschli in Bronn, 1880, p. 192; =Familie des Orbitolites Douvillé, 1902, p. 290 *(nom. neg.)*; =Familie des Orbiculines Douvillé, 1902, p. 297 *(nom. neg.)*]——[=Soritida Schultze, 1854, p. 53]——[=Peneroplidae Reuss, 1860, p. 151; =Peneroplideae Reuss, 1860, p. 217; =Peneroplidea Reuss, 1862, p. 379; =Peneroplida Schmarda, 1871, p. 165; =Peneroplidee Schwager, 1876, p. 483; =Peneroplidina Bütschli in Bronn, 1880, p. 190; =Peneroplinae Delage & Hérouard, 1896, p. 124; =Peneroplididae Lister in Lankester, 1903, p. 143]——[=Cristellaridae Reuss, 1860, p. 151, 205; =Cristellaridea Reuss, 1862, p. 307, 335, 368; =Cristellarideae Gümbel, 1870, p. 54; =Cristellarida Schmarda, 1871, p. 165; =Cristellaroidi Schwager, 1876, p. 477; =Cristellarioidea Schwager, 1877, p. 19; =Cristellariidae Wedekind, 1937, p. 98]——[=Poritida Schmarda, 1871, p. 165; =Keramosphaerina Lankester, 1885, p. 847; =Keramosphaerinae Delage & Hérouard, 1896, p. 127; =Keramosphaeridae Lister in Lankester, 1903, p. 143; =Meandropsinidae Henson, 1948, p. 77] [=Soritina Ehrenberg, 1838, p. 200 *(nom. nud.)*; genus invalid until 1840] [Also =Orbitulitida Haeckel, 1894, p. 185]

Wall calcareous, porcelaneous, may be pitted or perforated in early stage; chambers planispiral, later serial, flabelliform or cyclical; interior simple or labyrinthic; aperture single and simple, dendritic, or multiple. [Because of its type-species, *Cristellaria* is a synonym of *Peneroplis,* hence the family and subfamily names based on *Cristellaria* are included here.] *U.Trias.-Rec.*

Subfamily PENEROPLINAE Schultze, 1854

[*nom. correct.* Cushman in Eastman, 1913, p. 39 (*pro* subfamily Peneroplida Schultze, 1854, p. 53)]——[All names cited are of subfamily rank]——[=Cristellarida Schultze, 1854, p. 53; =Cristellarinae Rhumbler, 1895, p. 91; =Peneroplidinae Brady, 1884, p. 62; =Spirolininae Cushman, 1927, p. 54]

Test close-coiled in early stage, later may be uncoiled or annular; chambers simple, not divided into chamberlets; aperture rounded, slitlike, or series of pores on final septal face. *U.Trias.-Rec.*

Peneroplis de Montfort, 1808, *1305, p. 258 [**Nautilus planatus* Fichtel & Moll, 1798, *716, p. 91; OD] [=*Cristellaria* Lamarck, 1816, *1089, p. 14 (type, *Nautilus planatus* Fichtel & Moll, =*C. squammula* Lamarck, 1822, *1090, p. 607 (obj.), SD Children, 1823, *337, p. 117=153); *P. (Peneroplis)* d'Orbigny in de la Sagra, 1839, *1611, p. 59 (obj.); *Archiacina* Munier-Chalmas in Vasseur, 1878, *1987, p. 1049 (type, *Cyclolina armorica* d'Archiac in Tournour, 1868, *1947, p. 376); *Laevipeneroplis* Šulc, 1936, *1850, p. 161 (type, *Peneroplis karreri* Wiesner, 1923, *2062, p. 95, 96); *Puteolus* Hofker, 1950, *933a, p. 394 (type, *Peneroplis protea* d'Orbigny, 1839, *1611, p. 60) (*non Puteolus* Monterosato, 1888); *Puteolina* Hofker, 1952, *933c, p. 450 (*nov. nom. pro Puteolus* Hofker, 1950, *non* Monterosato, 1888)]. Test compressed, planispirally enrolled at least in early stages, later may be uncoiled and flaring, external form variable; chambers broad, low, not subdivided; wall porcelaneous, surface smooth, pitted, or more commonly, longitudinally striate; aperture terminal, row of slits in slight depression along the apertural face. [*Puteolus* (=*Puteolina*) was based on a species with pitted rather than striate surface ornamentation. We do not regard ornamentation as of generic importance.] *?U.Cret., Eoc.-Rec.,* cosmop.——Fig. 369,*1*. **P. planatus* (Fichtel & Moll), Rec., Medit. Sea; *1a,b,* side, edge views, ×45 (*2117).——Fig. 369,*2,3*. *P. proteus* d'Orbigny; Rec., W.Indies *(2),* Bermuda *(3);* side views, ×30 (*200).——Fig. 369,*4,5*. *P. armorica* (d'Archiac), M.Oligo., Eu.(Fr.); topotypes, showing tendency of species to become cyclical, ×37 (*2117).

Dendritina d'Orbigny, 1826, *1391, p. 285 [**D. arbuscula*; SD Cushman, 1927, *433, p. 189] [=*Peneroplis (Dendritina)* d'Orbigny in de la Sagra, 1839, *1611, p. 58 (obj.); *Meneghinia* O. Silvestri, 1889, *1792, p. 53 (*non Meneghinia* Fucini, 1931) (type, *M. nautiliformis*); *Neopeneroplis* Didkovskiy, 1958, *594, p. 1252 (type, *N. sarmaticus*)]. Test free, planispirally enrolled, nearly or completely involute; chambers simple, not subdivided; surface smooth or striate; aperture dendritic, on apertural face. *Eoc.-Rec.*, Eu.-Carib.-Afr.-Atl.O.——FIG. 370,*1*. **D. arbuscula*, Mio., Fr.; *1a,b*, side, apert. views, enlarged (*1391).

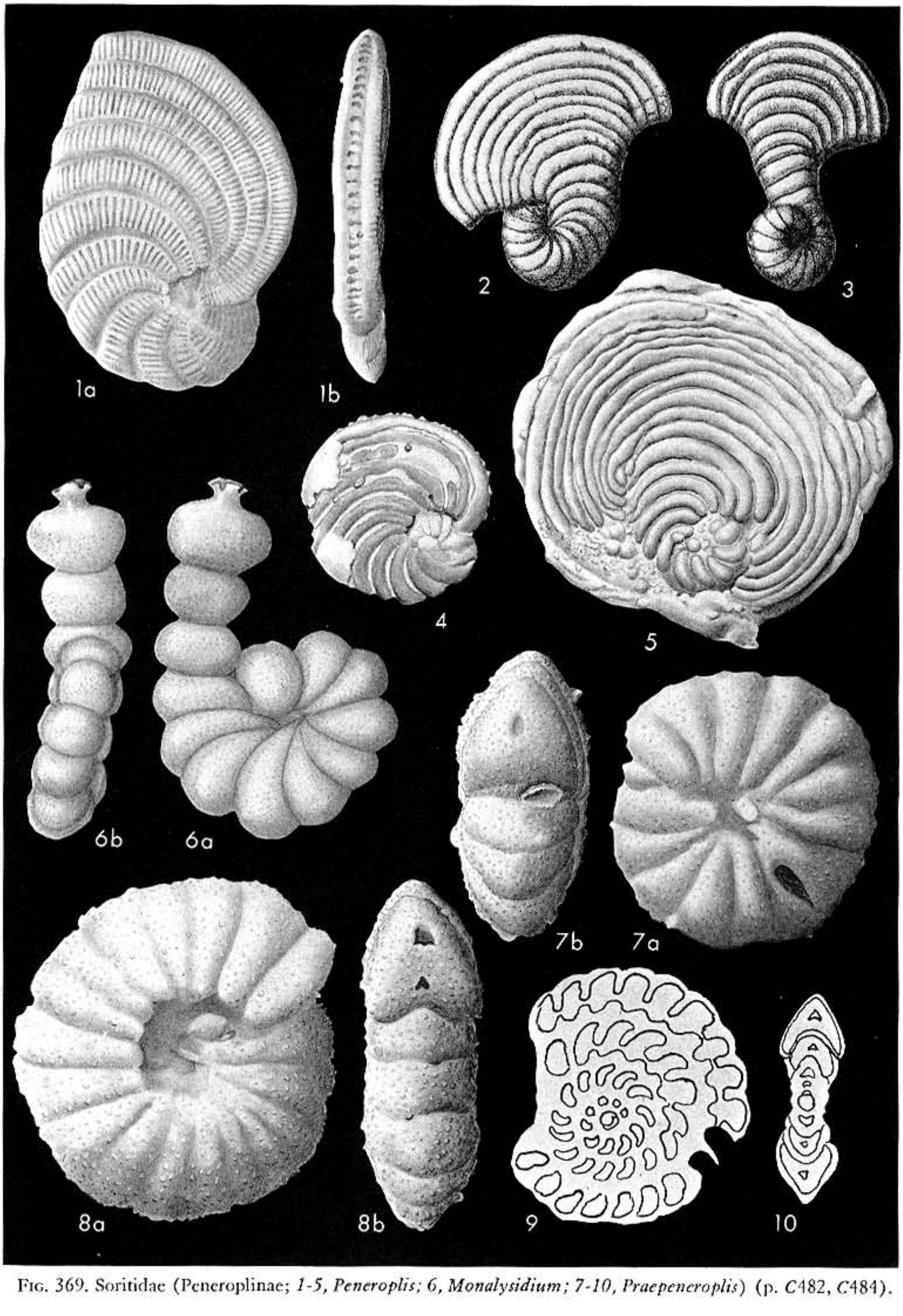


FIG. 369. Soritidae (Peneroplinae; *1-5, Peneroplis; 6, Monalysidium; 7-10, Praepeneroplis*) (p. C482, C484).

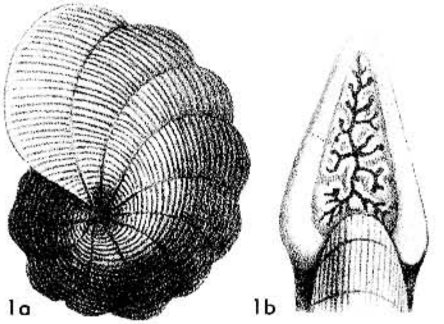


Fig. 370. Soritidae (Peneroplinae; *1, Dendritina*) (p. *C*482-*C*483).

Monalysidium Chapman, 1900, *314, p. 3 [**Peneroplis (Monalysidium) sollasi*; OD] [=*Peneroplis (Monalysidium)* Chapman, 1900, *314, p. 3 (obj.)]. Test free, with early subglobular chambers arranged in evolute planispiral coil, later uncoiled and rectilinear; wall calcareous, distinctly perforate in appearance; aperture terminal, somewhat produced on neck with phialine, fimbriate lip. *Rec.*, Pac.O.——Fig. 369,*6*. **M. sollasi*, Funafuti Atoll; *6a,b*, side, edge view of holotype, ×105 (*1166).

Praepeneroplis Hofker, 1952, *933c, p. 463 [*pro Protopeneroplis* Hofker, 1950, *933a, p. 393 (*non* Weynschenck, 1950)] [**Peneroplis senoniensis* Hofker, 1949, *931, p. 41; OD]. Test free, closely enrolled, planispiral, slightly evolute, with numerous chambers to whorl of triangular transverse section; sutures radial, depressed; wall porcelaneous; aperture areal, simple, ovate, or with a toothlike projection from lower margin resulting in triangular opening. [*Praepeneroplis* is similar to *Dendritina* in its close-coiled planispiral test but differs in the simple areal, rather than dendritic, aperture.] *U.Cret.(Senon.)*, Eu. (Neth.).——Fig. 369,*7-10*. **P. senoniensis* (Hofker); *7a,b, 8a,b*, side and edge views, ×86 (*2117); *9,10*, equat. and axial secs., ×50 (*933b).

Renulina Lamarck, 1804, *1085c, p. 353 (*non* de Blainville, 1825; *nec* Blake, 1876) [**R. opercularia*; OD (M)] [=*Renulites* Lamarck, 1804, *1085c, p. 353 (obj.); *Renulinites* Lamarck, 1804, *1085c, p. 353 *(nom. null.)*]. Test enrolled in early stage, with tubular chambers nearly full whorl in length, later reduced to 2 or 3 to whorl, then expanding in height and rapidly expanding in breadth, resulting in flabelliform test; surface of type-species smooth; aperture single narrow elongate slit extending length of terminal face. [Differs from *Peneroplis* in having a single slitlike aperture rather than a row of pores.] *M.Eoc.(Lutet.)*, Eu. (Fr.).——Fig. 371,*1*. **R. opercularia*; *1a,b*, side, apert. views, ×62 (*2117).

Spirolina Lamarck, 1804, *1085c, p. 244 [**S. cylindracea*; SD Cushman, 1927, *432, p. 125] [=*Spirolinites* Lamarck, 1804, *1085c, p. 245 (obj.); *Coscinospira* Ehrenberg, 1839, *667, p. 110, 131 (type, *C. hemprichii*, SD Loeblich & Tappan, herein); *Spirulina* Ehrenberg, 1843, *670, p. 167 (*nom. van., pro Spirolina* Lamarck, 1804, *non Spirulina* Bory, 1826); *Spiralina* Brown, 1944, *246, p. 145 (*nom. van. pro Spirolina* Lamarck, 1804) (*non Spiralina* Hartmann, 1840; *nec* Chaster, 1898; *nec* Martens, 1899)]. Test planispirally enrolled and biumbilicate in early stage, later uncoiling and cylindrical; chambers short; wall calcareous, porcelaneous, surface smooth or many be longitudinally striate; aperture terminal, rounded, with numerous toothlike projections extending into opening. *Eoc.-Rec.*, Eu.-N.Am.-Medit. Sea-Carib. Sea-Atl.O.-Pac.O. ——Fig. 371,*2*. **S. cylindracea*, M.Eoc.(Lutet.), Fr.; *2a,b*, side, top views of topotype, ×54 (*2117).

Triasina Majzon, 1954, *1205, p. 245 [**T. hantkeni*; OD]. Test free, numerous small chambers planispirally arranged in 7 to 9 whorls; short radial septa; wall calcareous, porcelaneous, imperforate, surface with small nodes; apertural character unknown. *U.Trias.*, Eu.(Hung.).——Fig. 372,*1-3*. **T. hantkeni*; *1,2*, ext., ×138; *3*, equat. sec., ×150 (*1205).

Vandenbroeckia Marie, 1958, *1223, p. 128 (*nom. correct.* Ellis & Messina, 1940, *700, *pro Vandenbroekia* Marie, 1958, *nom. imperf.*) [**V. munieri*; OD]. Test compressed, early stage en-

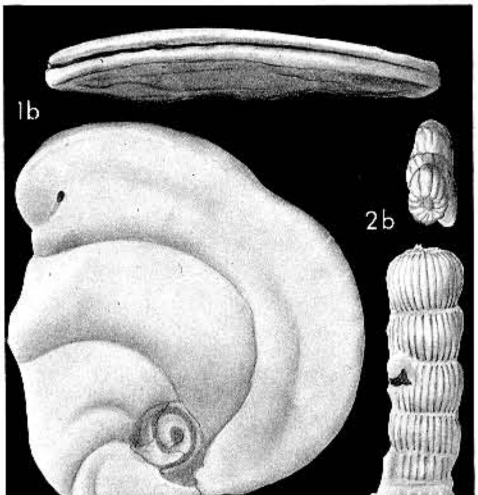


Fig. 371. Soritidae (Peneroplinae; *1, Renulina; 2, Spirolina*) (p. *C*484).

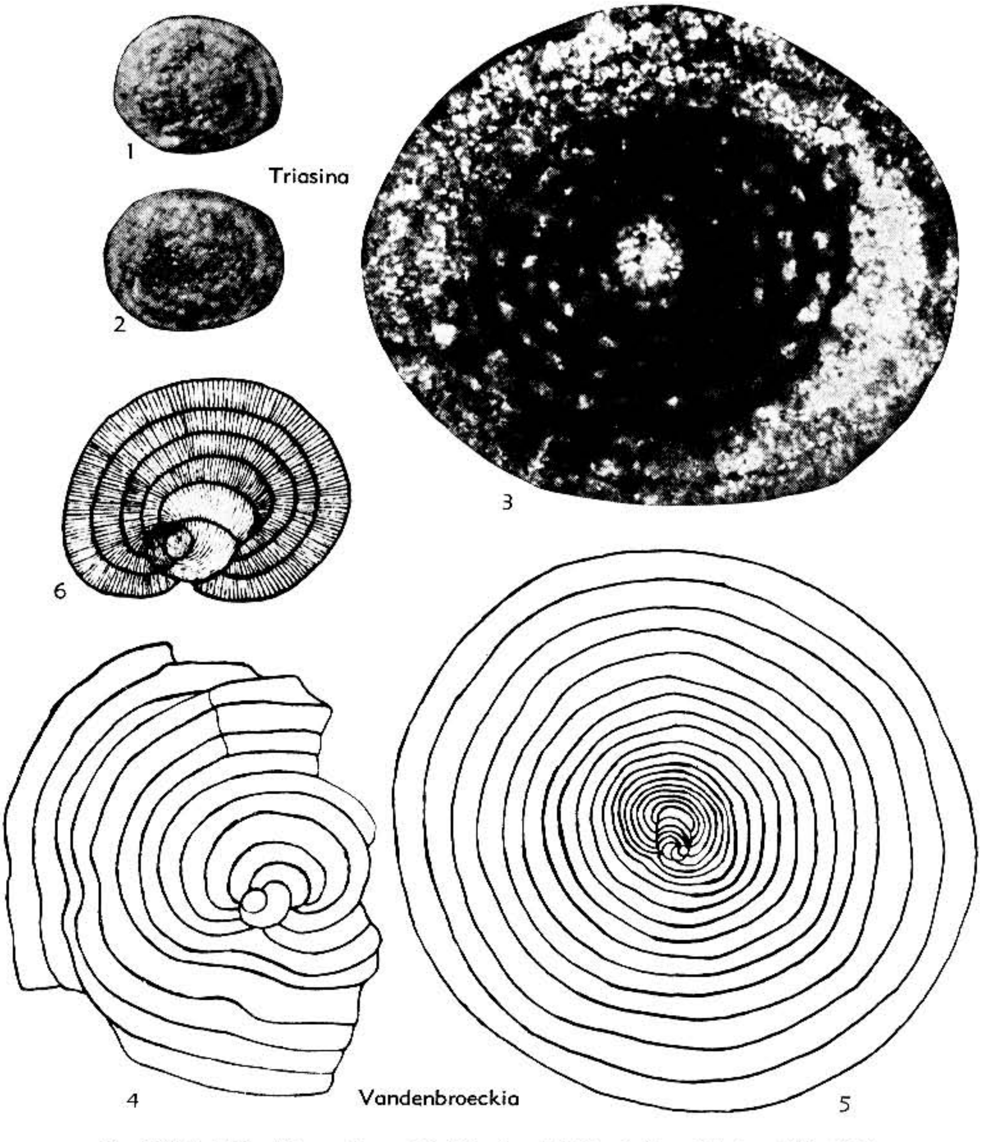


FIG. 372. Soritidae (Peneroplinae; *1-3, Triasina; 4-6, Vandenbroeckia*) (p. *C*484-*C*485).

rolled, later with chambers increasing rapidly in breadth and finally cyclical, interior not subdivided; surface may have longitudinal striae; aperture row of circular perforations on periphery. *U.Cret.(Senon.)*, Eu.(Fr.).——FIG. *372,4-6*. **V. munieri*; *4*, outline of megalospheric holotype, ×13.5; *5*, microspheric test, ×13.5; *6*, early portion of megalospheric test showing ornamentation, ×19 (*1223).

Subfamily MEANDROPSININAE Henson, 1948

[*nom. transl.* SIGAL in PIVETEAU, 1952, p. 202 (*ex* family Meandropsinidae HENSON, 1948)] [=Broekininae MARIE, 1958, p. 128]

Early stage planispirally coiled, later may be discoidal, operculiform, flabelliform, cylindrical or conical in shape; subepidermal chamberlets in marginal zone, with interseptal pillars; aperture commonly cribrate. *U.Cret.-Paleoc.*

Meandropsina MUNIER-CHALMAS in SCHLUMBERGER, 1898, *1658, p. 336 [**M. vidali* SCHLUMBERGER, 1898, *1658, p. 337; SD CUSHMAN, 1928, *439, p. 220] [=*Cyclomeandropsina* HENSON, 1950, *903, p. 5, 18 (*nom. nud.*)]. Test discoidal, enrolled, with very low and numerous chambers containing many incomplete transverse partitions; outer margin of chambers may become meandriform; aperture multiple, in rows on periphery. *U.Cret.(Senon.)*, Eu.-SW.Asia.——Fig. 373,*1-3*. **M. vidali* Schlumberger, Sp.; *1a,b*, ext. and portion showing surface, ×4, ×10; *2*, equat.

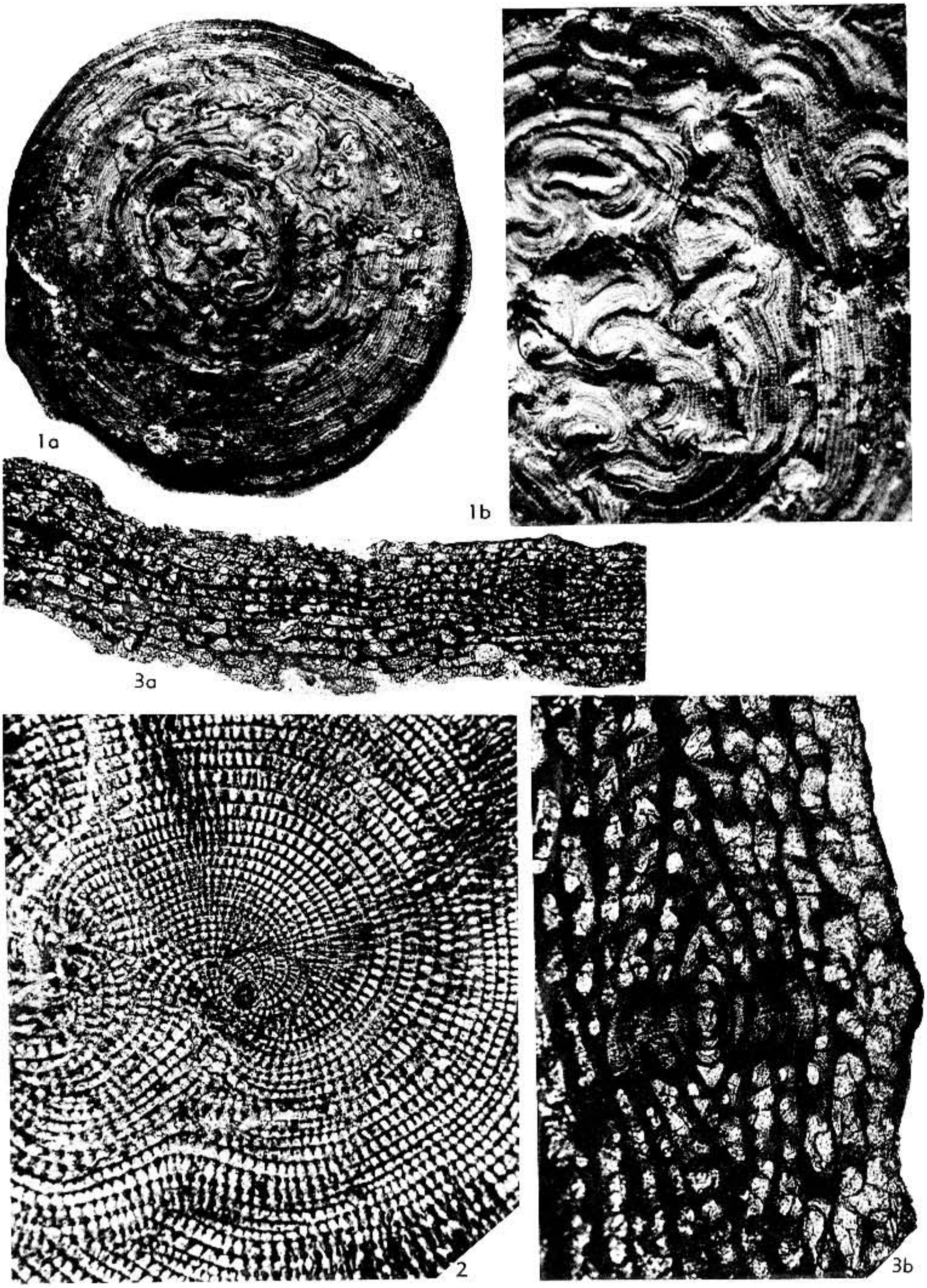


Fig. 373. Soritidae (Meandropsininae; *1-3, Meandropsina*) (p. C485-C487).

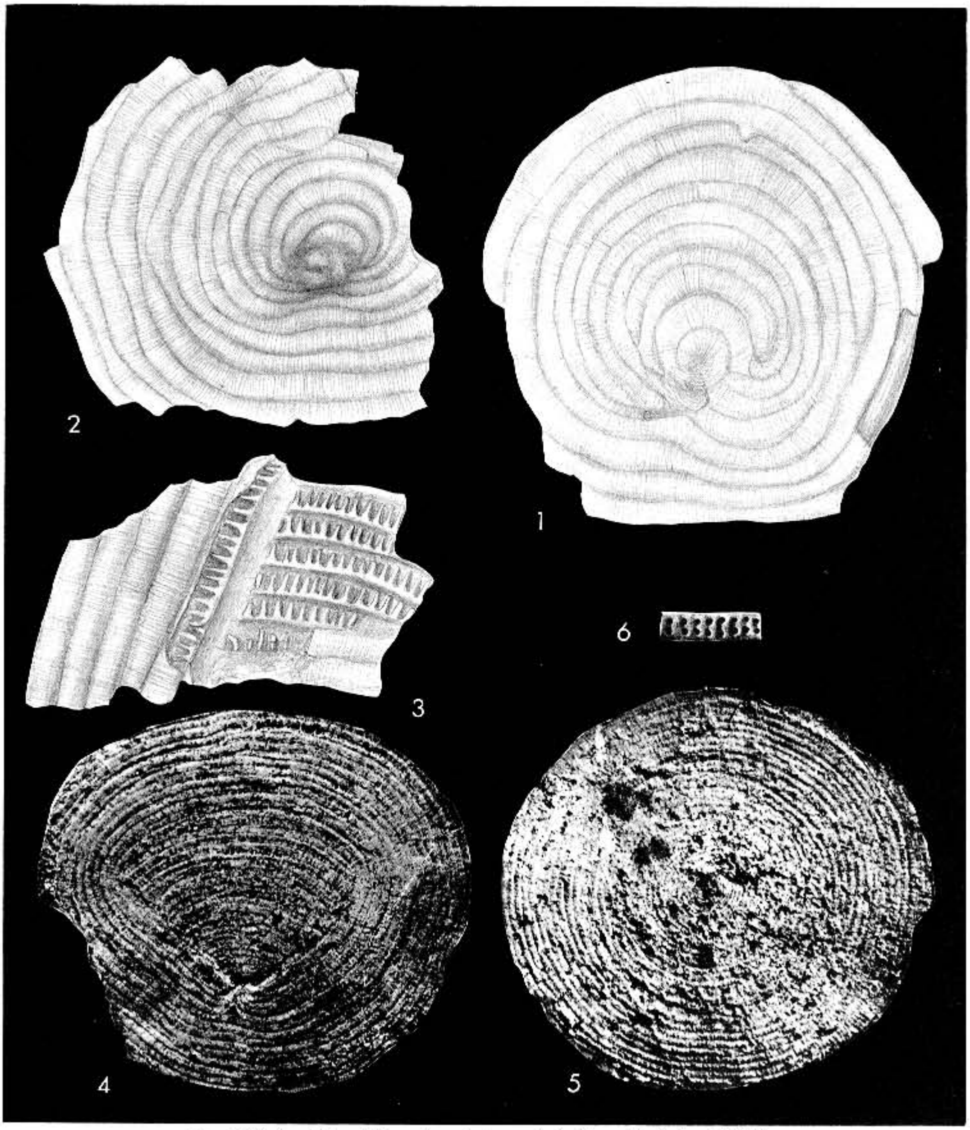


FIG. 374. Soritidae (Meandropsininae; *1-6, Broeckina*) (p. C487).

sec., ×4.5; *3a,b,* axial sec. and portion showing initial coil, ×40, ×185 (*1658).

Broeckina MUNIER-CHALMAS, 1882, *1323, p. 471 [**Cyclolina dufresnoyi* D'ARCHIAC in D'ARCHIAC & HAIME, 1854, *39, p. 205; OD] [=*Praesorites* DOUVILLÉ, 1902, *614, p. 291 (type, *P. moureti*); *Broekina* MARIE, 1958, *1223, p. 125 *(nom. van.)*]. Test discoidal, early stage with more or less well-developed coil of few chambers, which enlarge rapidly in breadth to become cyclical; interior complex, with secondary incomplete transverse partitions; wall porcelaneous; aperture consisting of 2 rows of circular openings on peripheral margin of final chamber. [The synonymy of *Broeckina* and *Praesorites* was noted by MARIE (1958, *1223). *Praesorites* is here suppressed as it is a junior synonym.] *U.Cret.(Senon.)*, Eu.——FIG. 374,*1,2.* **B. dufresnoyi* (D'ARCHIAC), Fr. (side views of specimens of MUNIER-CHALMAS, Paris); *1,* ×17; *2,* ×10 (*2117).——FIG. 374,*3-6.* *B. moureti* (DOUVILLÉ), L.Campan., Fr.; *3,* holotype, fragment with surface partially abraded showing chamberlets, ×12 (*2117); *4,5,* paratype, ×5; *6,* portion of margin showing aperture, ×24 (*614).

Edomia HENSON, 1948, *902, p. 84 [**E. reicheli*; OD]. Test large, flattened; chambers numerous, microspheric form apparently cyclogyrine in early

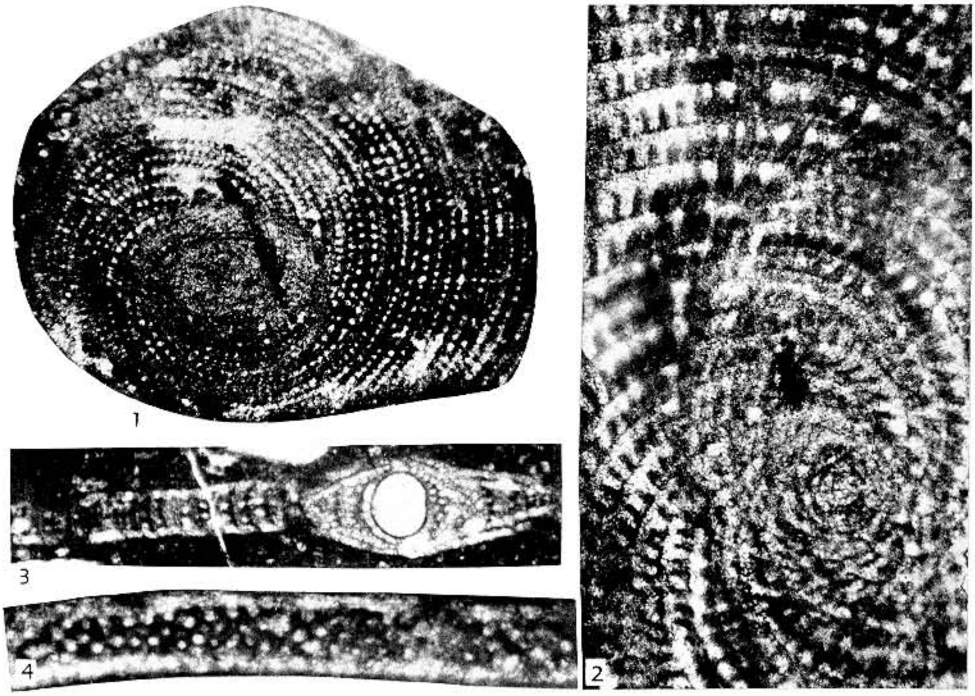


FIG. 375. Soritidae (Meandropsininae; *1-4, Edomia*) (p. C487-C488).

stage, megalospheric form with spherical proloculus and long, tubular second chamber, then numerous planispiral, involute chambers as in *Meandropsina,* with incomplete transverse interseptal partitions projecting inward from both surfaces of test, those of succeeding chambers aligned, irregularly distributed interseptal pillars occurring in central layers of later chambers; large pores pierce septa between pillars. *U.Cret.(Cenom.-Turon.),* SW.Asia(Palest.-Iran).——FIG. 375,*1-4.* **E. reicheli,* Cenom., Palest.; *1,* equat. sec. of paratype, ×26; *2,* slightly oblique equat. sec. showing interseptal partitions, ×70; *3,* axial sec. of megalospheric form, ×36; *4,* tang. sec. parallel to septum showing apert. pores, ×60 (*2115).

Fallotia Douvillé, 1902, *614, p. 298 [**F. jacquoti*; OD] [=*Fascispira* A. Silvestri, 1940, *1789, p. 230 (type, *F. colomi*); *Ayalaina* Seiglie, 1961, *1715, p. 346 (type, *Meandropsina? rutteni* Palmer, 1934, *1408, p. 252]. Test lenticular, planispirally enrolled and involute, chambers low, numerous, and internally subdivided by transverse partitions but not compressed and annular as in *Meandropsina,* although rarely chambers become meandriform, number of whorls numerous; aperture row of pores at basal margin of apertural face. *U.Cret.,* Eu.-W.Indies(Cuba).——FIG. 376,*1-3.* **F. jacquoti,* Fr.; *1,* side view of holotype, ×7.5; *2,* fragment showing marginal meandriform deformation of chambers, ×3; *3a,b,* transv. sec. parallel to axis showing minute chamberlets and portion, enlarged, ×6.3, ×18 (*2117).——FIG. 376,*4.* *F. colomi* (A. Silvestri), Maastricht., Sp.; *4a,b,* side, apert. views of topotype, ×47 (*2117).

Nummofallotia Barrier & Neumann, 1959, *89, p. 228 [**Nonionina cretacea* Schlumberger, 1899, *1660, p. 460 (=*Goupillaudina sanctipetri* Marie, 1957, *1222b, p. 869); OD]. Test planispirally enrolled and involute; chambers numerous, apparently subdivided by secondary, transverse septa; originally type-species described as having calcareous perforate umbilical "button" later shown to be a product of recrystallization, when present resulting in umbilically inflated test; wall calcareous, imperforate; aperture interiomarginal. *U. Cret.(Senon.),* Eu.——FIG. 377,*1-6.* **N. cretacea* (Schlumberger), Sp. *(1,2),* Fr. *(3-6)*; *1,* equat. sec., ×85; *2,* axial sec. showing umbilical "buttons" on both sides of test, ×100 (*1660); *3,* axial sec. showing lenticular original form and very small amount of recrystallization, stated to be ×30 [doubtful]; *4,* axial sec. of specimen with advanced stage of recrystallization (umbilical "button" appearing white) and original internal structure almost completely resorbed, ?×30; *5,* equat. sec. of free specimen, ×50; *6,* detached umbilical "button," ×50 (*89).

[The umbilical "button," due to recrystallization of the test, tends to become detached from the remainder of the shell and has been described as various "species" of different rotaliform genera. The "buttons" have been shown in thin sections to be varied in development, sometimes appearing on only one side of the test, though commonly they are developed to a variable degree on both sides. They are best observed in axial sections. The original internal structure of the test is not well known, no free specimens occurring without the recrystallized central

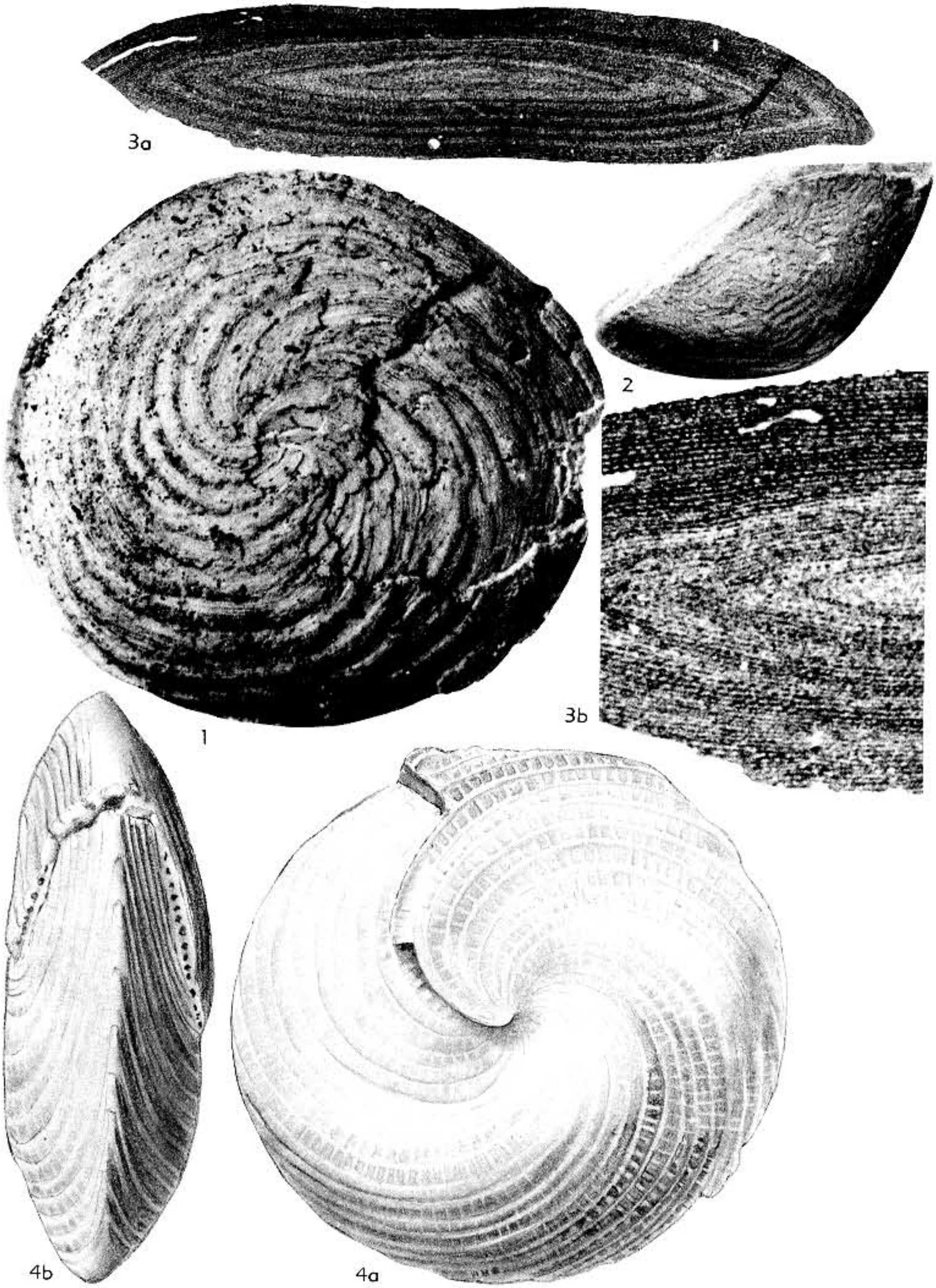


FIG. 376. Soritidae (Meandropsininae; *1-4, Fallotia*) (p. C488).

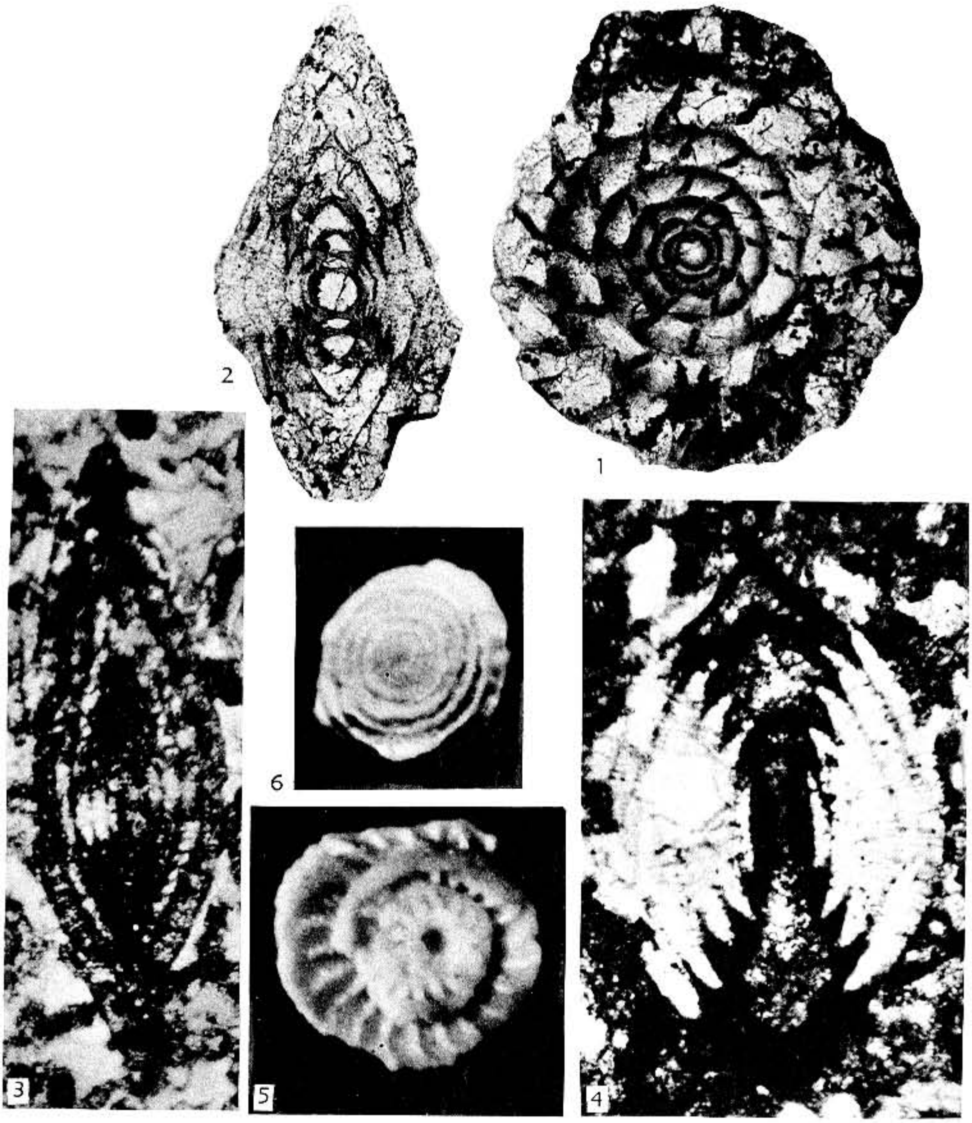


FIG. 377. Soritidae (Meandropsininae; *1-6, Nummofallotia*) (p. C488-C490).

area. Some axial sections indicate the presence of secondary transverse septa, but these are apparently not observable on free specimens. A noticeable similarity of *Nummofallotia* to sections of *Praepeneroplis senoniensis* (HOFKER) from the Senonian of the Netherlands is observed but the recrystallization phenomenon has not been noted in *Praepeneroplis*, which also lacks indications of secondary transverse septa. The exterior of *Nummofallotia* is unknown. Additional study is required in order to determine if *Nummofallotia* is a junior synonym of *Praepeneroplis*. The stated magnification of the accompanying figured sections of the French specimens seems questionable, as the figures of axial sections appear nearly twice the diameter of equatorial sections; the original plate explanation stated them to be half this magnification. No test measurements were given for the French specimens but those from Spain were stated to be approximately 0.8 mm. in diameter, indicating that the axial sections probably are about ×100, not ×30.]

Pseudedomia HENSON, 1948, *902, p. 95 [**P. multistriata*; OD]. Test flattened, early stage planispiral, evolute, bilaterally symmetrical, later flabelliform, with uniserial chambers; numerous transverse secondary partitions project short distance into chambers from outer wall, median region of each chamber with single row of large interseptal pillars; apertures not observed. [Differs from *Edomia* in its evolute early planispiral stage and uniserial later stage. The genus is known only from the holotype of the type-species.] *U. Cret.(Maastricht.)*, Asia(Arabia, Qatar Penin.).

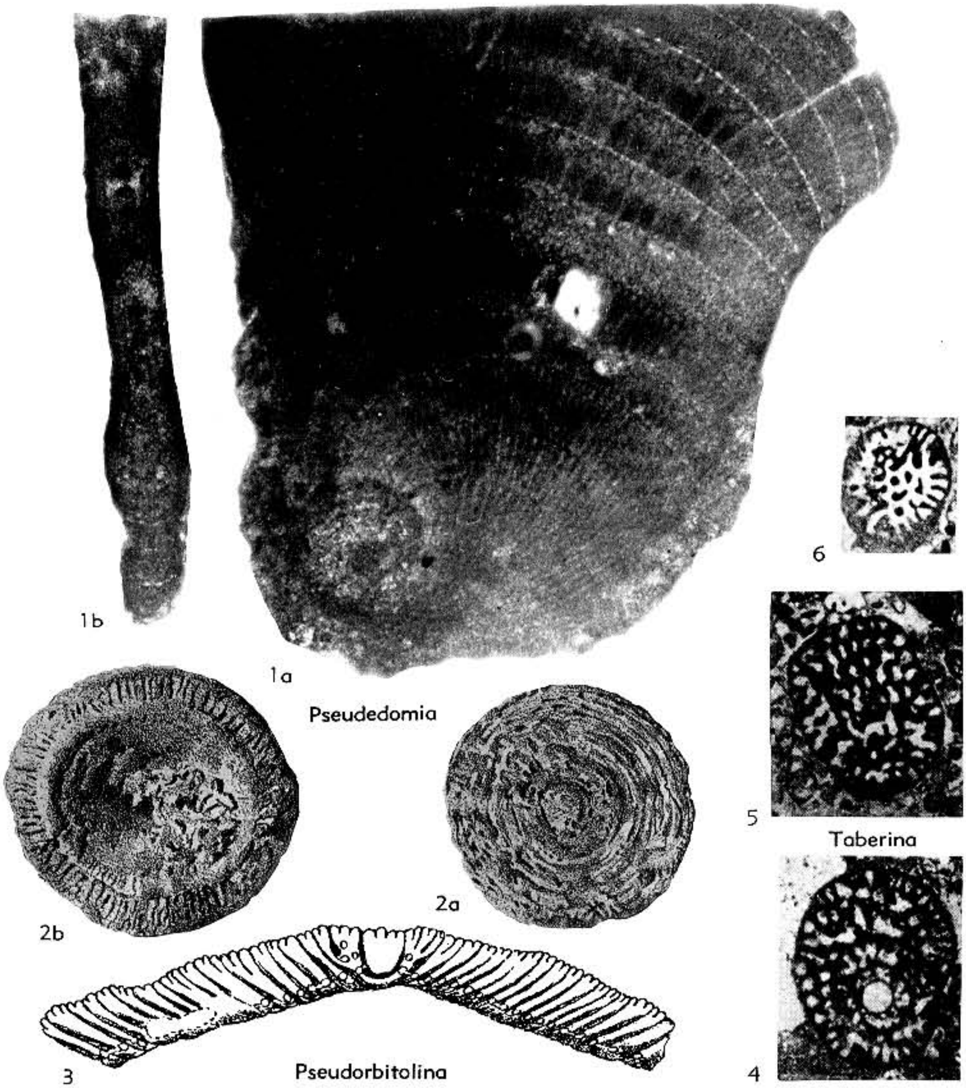


FIG. 378. Soritidae (Meandropsininae; *1, Pseudedomia; 2,3, Pseudorbitolina; 4-6, Taberina*) (p. *C*490-*C*493).

——FIG. 378,*1*. **P. multistriata; 1a,* equat. sec. of holotype, ×41; *1b,* transv. sec. of fragment of holotype cutting through interseptal pillars, ×45 (*2115).

Pseudorbitolina DOUVILLÉ, 1910, *619, p. 57 [**P. marthae*; OD]. Test low conical to concavoconvex; with transverse and parallel subepidermal partitions on one side of test, transverse partitions thickening inward to form chamberlets; wall agglutinated, convex side with concentric growth lines and reticulate surface; aperture consisting of single row of openings near periphery of concave side, which open into annular canal. *U.Cret. (Maastricht.)-Eoc.,* Fr.-Arabia-Carib.——FIG. 378, *2,3.* **P. marthae,* U.Cret.(Dordon.), Fr.; *2a,b,* convex upper and concave lower surfaces showing peripheral row of openings, ×10; *3,* axial sec. showing partitions and canal openings, ×27 (*619).

Taberina KEIJZER, 1945, *1030, p. 200 [**T. cubana*; OD]. Early stage planispiral, later uncoiling and circular in section; coiled stage dominant, with short radial septa, interior with incomplete transverse interseptal partitions and interseptal pillars; aperture multiple, of pores in chamber face. [*Taberina* has both the subepidermal partitions characteristic of *Meandropsina* and the interseptal pillars such as occur in *Archaias.*] *U.Cret.(Cenoman.)-Paleoc.(Dan.)*, Cuba-Iran-Syria-Palest.

——FIG. 378,*4-6*. **T. cubana,* Paleoc.(Dan.), Cuba; *4,* median sec. perpendicular to axis of coiling; *5,* tang. sec. parallel to axis of coiling;

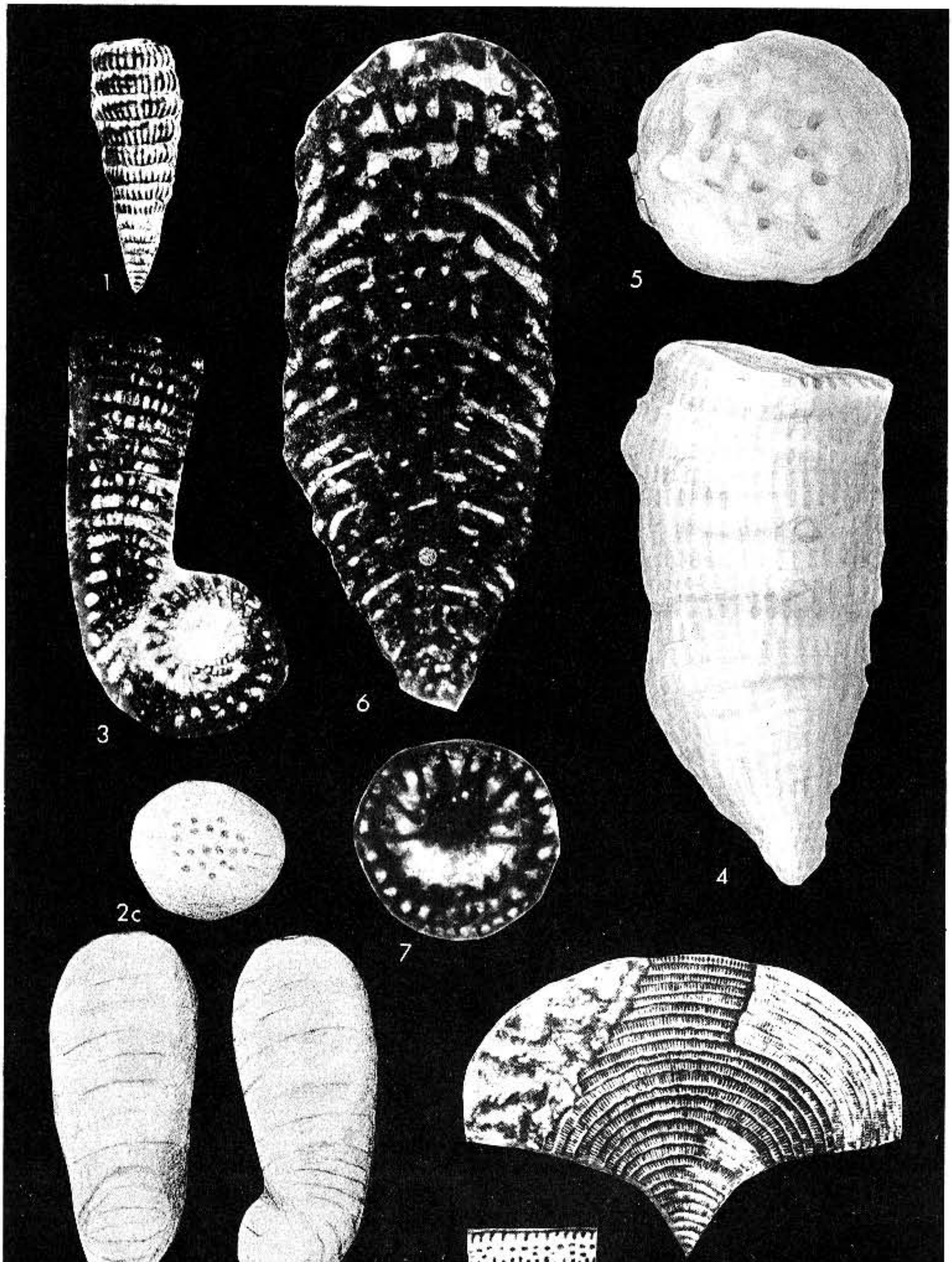


FIG. 379. Soritidae (Rhapydionininae; *1-7, Rhapydionina; 8, Rhipidionina*) (p. C493).

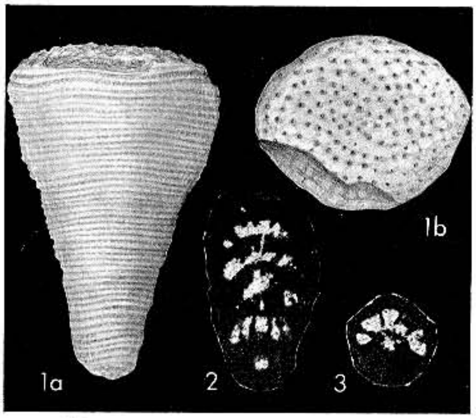


FIG. 380. Soritidae (Rhapydionininae; *1, Ripacubana; 2,3, Praerhapydionina*) (p. C493).

6, transv. sec. through terminal stage, showing apert. pores, pillars and radial partitions, ×25 (*1030).

Subfamily RHAPYDIONININAE Keijzer, 1945

[Rhapydionininae KEIJZER, 1945, p. 200]

Test elongate, conical; chambers in rectilinear series, subdivided into chamberlets; aperture terminal, cribrate. *Jur.-Rec.*

Rhapydionina STACHE, 1913, *1829, p. 661 [**Peneroplis liburnica* STACHE, 1889, *1828, p. 89; OD (M)] [=*Rhapidionina* VAN DEN BOLD, 1946, *155, p. 123 *(nom. van.)*; *Haurania* HENSON, 1948, *902, p. 11 (type, *H. deserta*)]. Test elongate, conical, early stage may have involute planispiral coil, later uniserial; chamber interior subdivided by transverse subepidermal partitions; aperture terminal, cribrate. [*Haurania* was originally included in the Lituolidae, but regarded (*902, p. 11) as "almost an isomorph of *Rhapydionina*." It is here regarded as a synonym.] *Jur.-M.Eoc.*, Istria-Iraq-Cuba-C.Am.——FIG. 379,*1*. **R. liburnica* (STACHE), L.Eoc., Yugosl.(Istria); holotype, enlarged (*700).——FIG. 379,*2,3*. *R. urensis* HENSON, M.Eoc., Iraq; *2a-c,* opposite sides and top view of holotype, ×15; *3,* long. tang. sec. showing subepidermal partitions, ×18 (*902).——FIG. 379,*4-7*. *R. deserta* (HENSON), Jur., Iraq; *4,* side view of holotype, ×41; *5,* apert. view of paratype, ×72 (*2117); *6,* long. sec. of paratype; *7,* transv. sec. of paratype, ×40 (*2115).

Craterites HERON-ALLEN & EARLAND, 1924, *912, p. 611 [**C. rectus*; OD (M)]. Test attached, club-shaped, narrowing slightly just above basal expansion and then gradually enlarging in diameter, upper surface convex, perforated; trunklike portion composed of 10 or 12 superimposed layers of polygonal chamberlets, which increase in number with expanding diameter of test; wall calcareous, nonperforate except for large apertural openings; aperture consisting of numerous large pores on upper surface, which open into chamberlets, and where upper surface has been broken away similar openings may be seen in preceding layer of chamberlets. [This genus is represented by a single known specimen, the holotype of the type-species in the British Museum (Natural History) (BMNH-ZF3613), from between tidemarks as "Middle Beach," lat. 31°31'30"S., long. 159°15'28"E., on the east side of Lord Howe Island, South Pacific. As no additional material was available, sections could not be made for a study of the internal structure.] *Rec.,* S.Pac.——FIG. 381, *1*. **C. rectus*; *1a,b,* side, top views of holotype, ×36 (*2117).

Praerhapydionina VAN WESSEM, 1943, *1980, p. 43 [**P. cubana*; OD]. Test similar to *Rhapydionina* in form and internal structure, differing in having single terminal aperture instead of cribrate one. *U.Cret.-Oligo.*, Cuba-Iraq.——FIG. 380,*2,3*. **P. cubana,* Maastricht., Cuba; *2,* long. deep tang. sec., showing part of subepidermal partitions; *3,* transv. sec. partially cutting septum, showing subepidermal partitions at margins and central aperture, ×22 (*700).

Rhipidionina STACHE, 1913, *1829, p. 661 [**Pavonina liburnica* STACHE, 1889, *1828, p. 85; OD (M)]. Test compressed, flabelliform, early stage with abbreviated and involute planispiral coil followed by numerous uniserially arranged broad, low chambers, with transverse subepidermal partitions; aperture consists of numerous pores in the terminal face. *L.Eoc.-M.Eoc.*, Yugosl.(Istria)-Iraq.——FIG. 379,*8*. **R. liburnica* (STACHE), L.Eoc., Yugosl.; *8a,* ext., ×5; *8b,* apert. surface, enlarged (*700).

Ripacubana LOEBLICH & TAPPAN, *nom. nov.* [*pro Conulina* D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. 24 (*non* BRONN, 1836)] [**Conulina conica* D'ORBIGNY in DE LA SAGRA, 1839, *1611, p. 24, here designated as type-species]. Test free, conical, early stages unknown as only specimen is broken, chambers numerous, low and broad, uniserial in later stage, subdivided by vertical partitions into chamberlets; sutures horizontal, closely appressed;

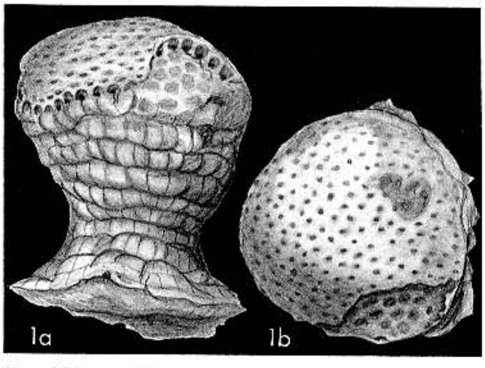


FIG. 381. Soritidae (Rhapydionininae; *1, Craterites*) (p. C493).

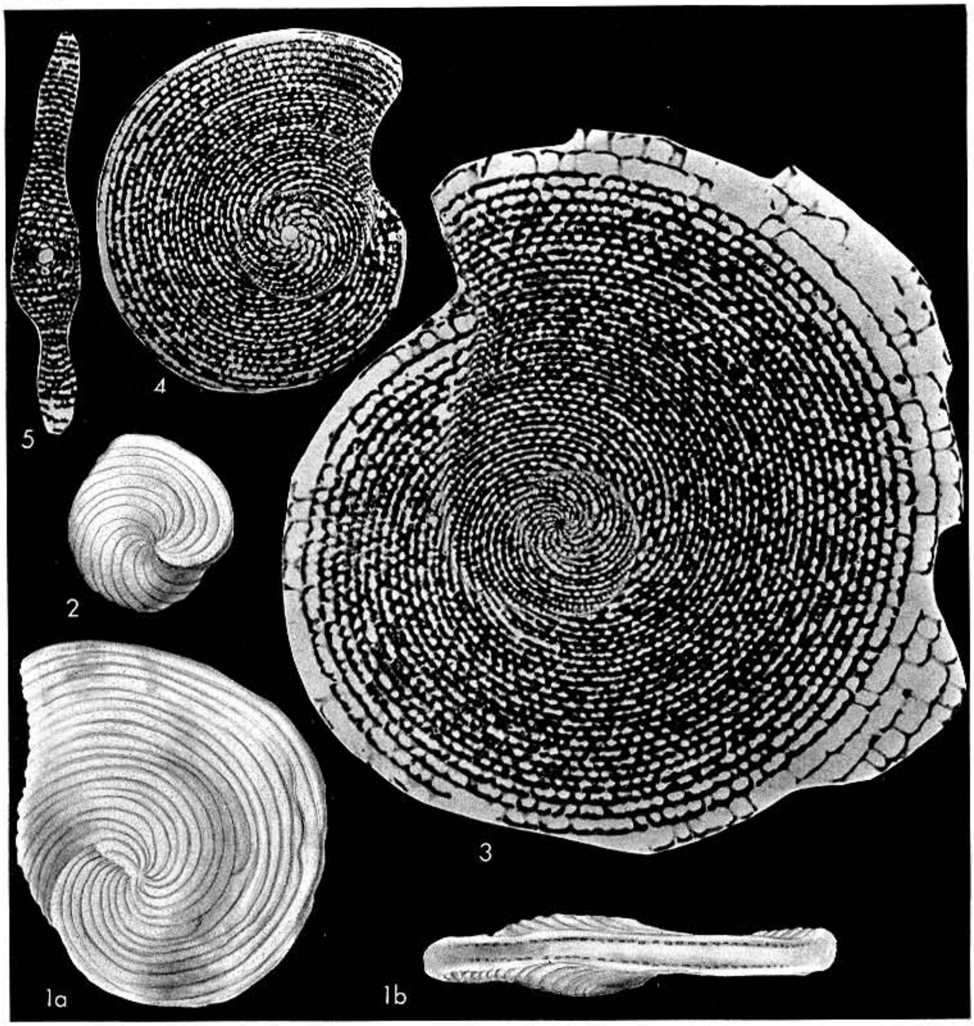


FIG. 382. Soritidae (Archaiasinae; *1-5, Archaias*) (p. *C*494-*C*495).

wall appearing calcareous; aperture terminal, consisting of numerous equally spaced small pores on broad face, opening into chamberlets. [D'ORBIGNY based this genus on the single specimen of his type-species. It has not been recognized since, and as only the holotype is known, no sections are available to determine more exactly its internal characters. Although considered by D'ORBIGNY to be a living species (Rec.), it is probable that the specimen may represent a reworked fossil form. The holotype of *R. conica,* here refigured, is preserved in the Muséum National d'Histoire Naturelle, Paris, and is from Recent sand of Cuba. *Ripacubana* is from *ripa* (Lat., shore or bank)+Cuba, and refers to the only locality from which the genus has been recorded, shore sands of Cuba.] *?Rec.,* Cuba.——FIG. 380,*1*. **R. conica* (D'ORBIGNY); *1a,b,* side, top views of holotype, ×17 (*2117).

Subfamily ARCHAIASINAE Cushman, 1927

[Archaiasinae CUSHMAN, 1927, p. 55] [=Orbiculininae SCHUBERT, 1920, p. 168; WIESNER, 1920, p. 17; Archaiadinae WIESNER, 1931, p. 60, 74, 111]

Test planispiral, later may become annular; chambers divided into rectangular chamberlets which do not alternate regularly with those of adjacent chambers; aperture commonly double row of pores on peripheral face of last chamber. *M.Eoc.-Rec.*

Archaias DE MONTFORT, 1808, *1305, p. 190 [**A. spirans* (=*Nautilus angulatus* FICHTEL & MOLL, 1798, *716, p. 113); OD] [=*Helenis* DE MONTFORT, 1808, *1305, p. 194 (type, *H. spatosus,* =*Nautilus aduncus* FICHTEL & MOLL, 1798, *716, p. 115); *Ilotes* DE MONTFORT, 1808, *1305, p. 198 (type, *I. rotalitatus,* =*Nautilus orbiculus*

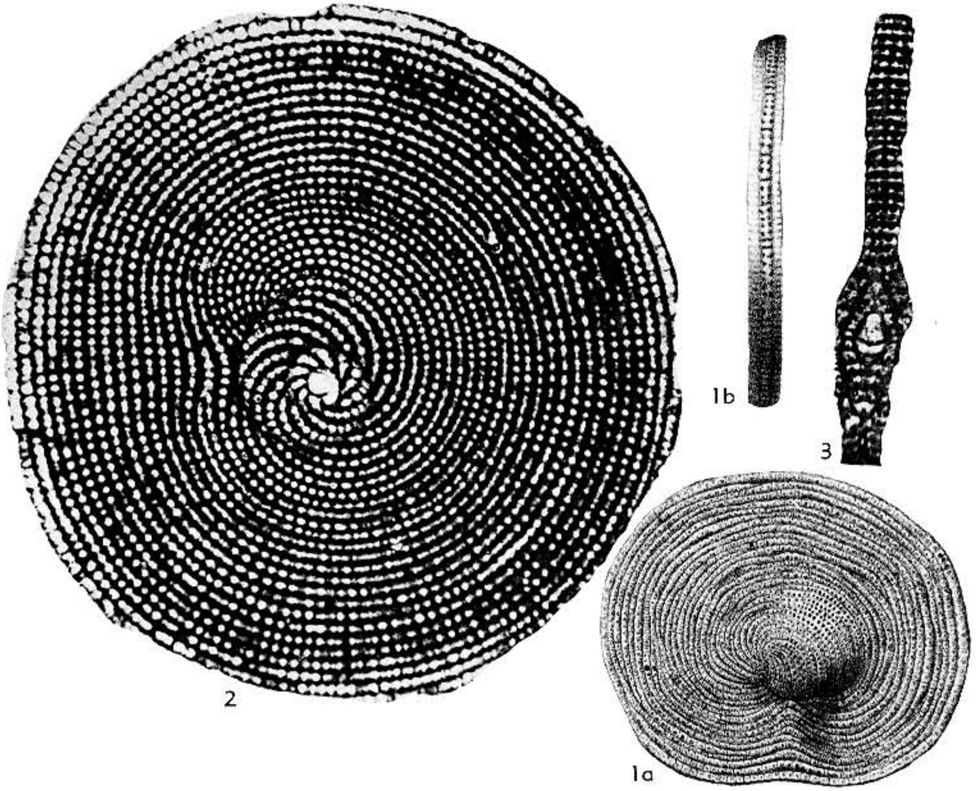


FIG. 383. Soritidae (Archaiasinae; *1-3, Cyclorbiculina*) (p. C495).

Fichtel & Moll, 1798, *716, p. 112); *Archais* Oken, 1815, *1385, p. 322 *(nom. null.)*; *Orbiculina* Lamarck, 1816, *1089, p. 14 (type, *O. nummata*, =*Nautilus orbiculus* Fichtel & Moll, 1798, *716, p. 112) *(non N. orbiculus* Forskål, 1775); *Archaia* Agassiz, 1844, *5, p. 3 *(nom. van.)*; *Elenis* Agassiz, 1844, *5, p. 9 *(nom. van. pro Helenis* de Montfort, 1808); *Nemophora* Conrad, 1865, *380, p. 74 (type, *Nummulites (Assilina) floridanus* Conrad, 1846, *379, p. 399) *(non Nemophora* Illiger, 1798; *nec* Huebner, 1825; *nec* Dahlbom, 1854)]. Test compressed, early stage planispiral, involute, later chambers flaring, becoming evolute to cyclical; interior of chambers with interseptal pillars; aperture multiple, with rows of pores on terminal face of final chamber. *M.Eoc.-Rec.*, cosmop.——Fig. 382,*1-5*. **A. angulatus* (Fichtel & Moll), Rec., Bermuda *(1,2)*, Barbados *(3-5)*; *1a,b,* side, apert. views, ×19 (*2117); *2*, side view of juvenile specimen, ×19; *3*, equat. sec. of microspheric test, ×8; *4*, equat. sec. of megalospheric test, ×13; *5*, axial sec. of megalospheric test, ×13 (*1806).

Cyclorbiculina A. Silvestri, 1937, *1787, p. 88 [**Orbiculina compressa* d'Orbigny in de la Sagra, 1839, *1611, p. 66; OD (M)]. Early stage close-coiled and involute, later chambers evolute, flabelliform, and finally cyclical; interior with distinct subepidermal partitions and with interseptal pillars in central zone; apertures consisting of pores on periphery. [Smout & Eames, 1958 (*1806, p. 222) differentiated *Archaias* with interseptal pillars only from *Cyclorbiculina* with both interseptal pillars and subepidermal partitions.] *U. Oligo.-Rec.,* Carib.-GulfMex.-Atl.-Panama.——Fig. 383,*1-3*. **C. compressa* (d'Orbigny); Rec., Atl.; *1a,b,* side, apert. views of cyclical form, showing transverse partitions, ×13 (*200); *2*, equat. sec., ×13; *3*, axial sec., ×27 (*363).

Fusarchaias Reichel, 1952, *1523, p. 459 [**F. bermudezi*; OD] [=*Fusarchaias* Reichel, 1949, *1520, p. 148 *(nom. nud.)*]. Test elongate, fusiform, planispirally enrolled, elongated axially, externally similar to *Alveolinella;* chambers numerous, with interseptal pillars perpendicular to septa similar to *Archaias*; aperture consisting of circular multiple openings on terminal face, alternating in position between pillars. *Oligo.-Mio.,* Cuba.——Fig. 384,*1-4*. **F. bermudezi*; *1*, holotype, ×13; *2*, axial sec. showing interseptal pil-

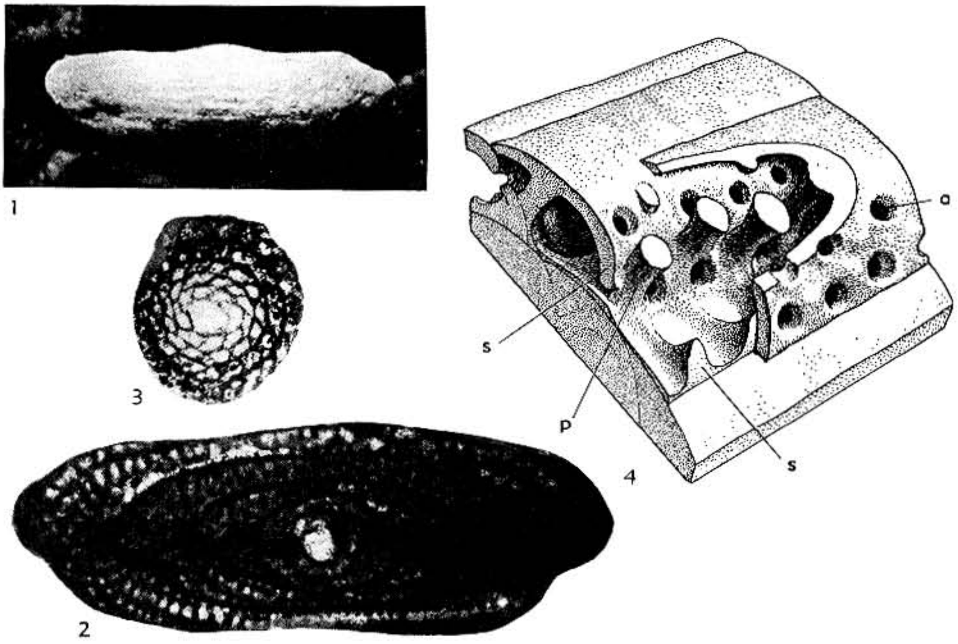


FIG. 384. Soritidae (Archaiasinae; *1-4, Fusarchaias*) (p. C495-C496).

lars; *3*, equat. sec., ×30; *4*, reconstruction showing structure, section of parts of last 3 chambers showing apertures *(a)*, pillars *(p)*, and septa *(s)* (*1523).

Subfamily SORITINAE Ehrenberg, 1839

[*nom. transl.* WIESNER, 1931, p. 60, 74, 111 (*ex* family Soritina EHRENBERG, 1839)]——[All names are of subfamily rank]——[=Orbitulinidea REUSS, 1862, p. 320; =Orbitolitinae BRADY, 1881, p. 43; =Orbitolitidinae WIESNER, 1920, p. 17]

Growth occurs by addition of numerous small chambers in arcuate or annular series, without intercommunications between those of single series, apertures connect adjacent chambers of successive series. *Eoc.-Rec.*

Sorites EHRENBERG, 1839, *667, chart opposite p. 120 [**S. dominicensis* (=*Orbulites marginalis* LAMARCK, 1816, *1088, p. 196); SD CUSHMAN, 1927, *433, p. 190] [=*Taramellina* MUNIER-CHALMAS, 1902, *1328, p. 353 (type, *Sorites dominicensis* EHRENBERG, 1839, *667, p. 134); SD LOEBLICH & TAPPAN, herein (obj.)]. Test discoidal, early stage with proloculus followed by tubular enrolled second chamber of nearly complete coil in length, later chambers added simultaneously in flaring peneropline series and finally in annular series in single layer; adjacent chambers of series interconnected by stolons; apertures connecting each chamber with 2 chambers in preceding and 2 in succeeding series. [Although reported from the Miocene of Venezuela (*1535) the type-species of *Sorites* has not been recorded from Recent deposits of this area, but has undoubtedly been reported as *Sorites marginalis* from the Dominican area (*614), Cuba, and the Atlantic. The types of EHRENBERG were not available for restudy, and were neither figured adequately nor described originally. *Sorites dominicensis* EHRENBERG, 1839 (nominally the type-species) is here regarded as a junior synonym of *S. marginalis* (LAMARCK), 1816, and the generic name is retained on the basis of this latter well-known species.] *Mio.-Rec.*, Carib.-Cyprus-Red Sea-Pac.-Atl.-S.Am.——FIG. 385,*1,2*. **S. marginalis* (LAMARCK), L.Mio., Venez. *(1)*, Rec., N.Pac. *(2)*; *1a,b*, side, edge views, ×33 (*1535); *2*, optical section of early stages of megalospheric form showing chamber development, ×50 (*404f).

Amphisorus EHRENBERG, 1839, *667, chart opposite p. 120 [**A. hemprichii*; OD] [=*Bradyella* MUNIER-CHALMAS, 1902, *1328, p. 353 (type, *Orbitolites duplex* CARPENTER, 1883, *271c, p. 561 (=*A. hemprichii*))]. Test discoidal, biconcave, embryonic region of megalospheric form may be slightly inflated, embryonic apparatus of megalospheric form consisting of globular proloculus, followed by tubular chamber (flexostyle) and then by broadly overlapping chamber with marginal openings that lead into chamberlets of first cyclical series; later chambers cyclical, with 2 layers of chamberlets alternating in position with those of previous cycle and those of same cycle alternating in position when viewed from periphery; a single annular canal in equat. position visible at center of axial sections and in equat. secs. appearing as

undivided area adjacent to previous chamber wall (FIG. 386,*1*); apertures in 2 alternating rows on periphery in small sutural depressions and open-

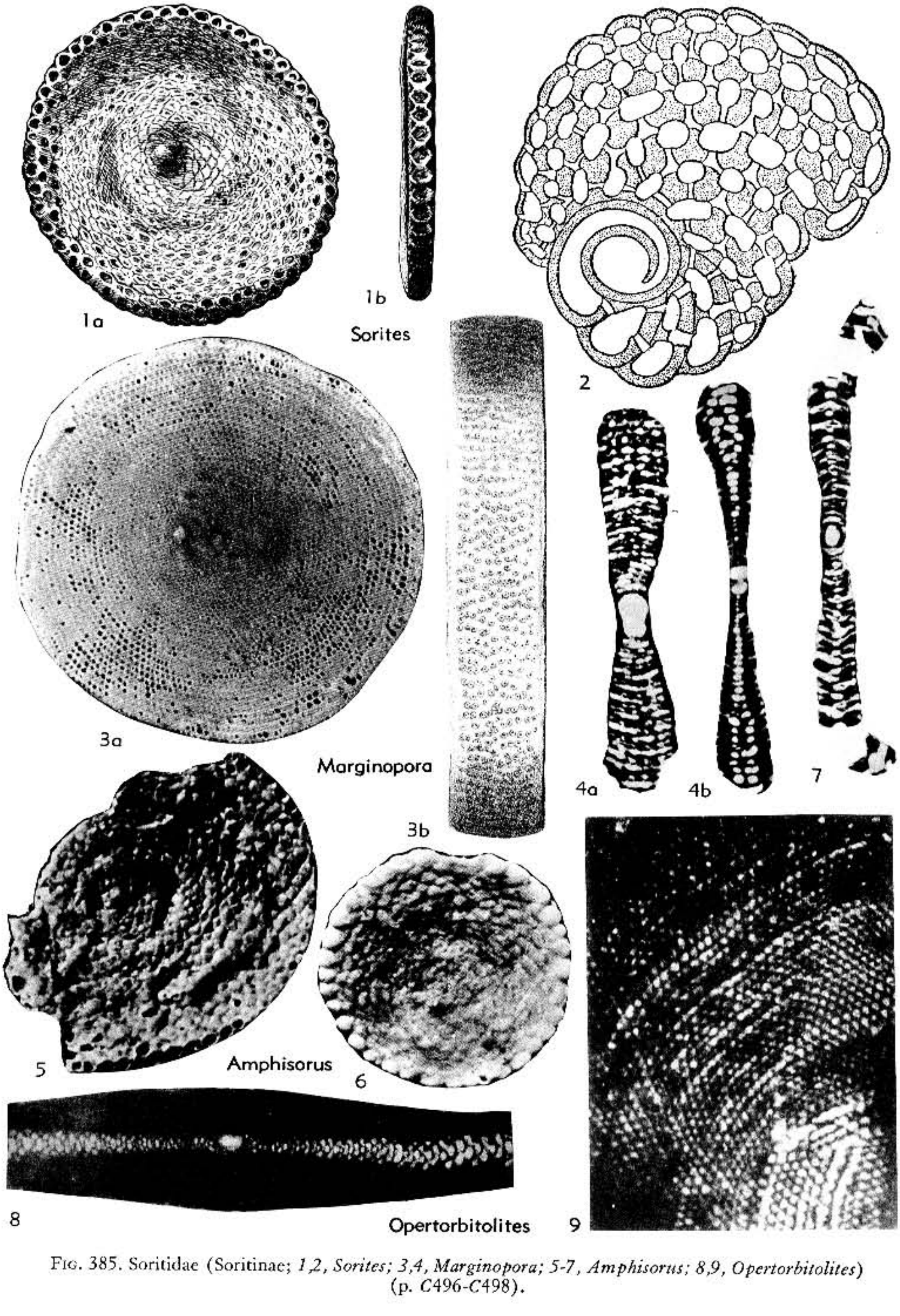


FIG. 385. Soritidae (Soritinae; *1,2, Sorites; 3,4, Marginopora; 5-7, Amphisorus; 8,9, Opertorbitolites*) (p. *C*496-*C*498).

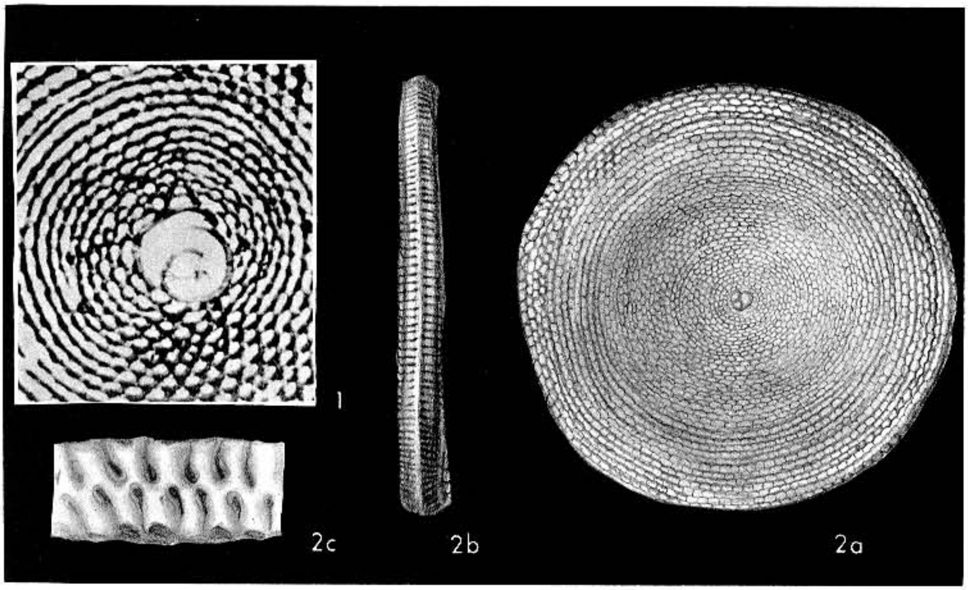


FIG. 386. Soritidae (Soritinae; *1,2, Amphisorus*) (p. *C*496-*C*498).

ing into stolons which lead obliquely into annular canal. *Mio.-Rec.,* Medit.-Pac.-Carib.-N.Am.-S.Am.-Eu.——FIG. *385,5-7; 386,1,2. *A. hemprichii* Rec., Bermuda (*385,5,6*), Bikini Atoll (*385,7*), Kei Is. (*386,1*), Ifaluk Atoll (*386,2*); *385,5,6,* side views, ×20 (*444); *385,7,* axial sec. originally figured as *Marginopora,* but showing equatorial annular canal and alternating intersection of chamber cavity at one side and septum on opposite side, characteristic of alternating chamberlets of *Amphisorus,* ×20 (*361); *386,1,* equat. sec. of megalospheric form, showing embryonic apparatus in center, equatorial annular canal intersected in median part of section, remainder of section slightly tangential to equatorial plane and intersecting chamber walls, ×50 (*1122); *386,2a,b,* side, edge views, ×15 (*2117); *386,2c,* portion of edge view, enlarged to show position of apertures, ×41 (*2117).

Marginopora QUOY & GAIMARD in DE BLAINVILLE, 1830, *141d, p. 377 [**M. vertebralis*; OD (M)]. Test discoidal, biconcave, ovate proloculus followed by cyclic chambers, without distinct flexostyle such as occurs in *Amphisorus* and *Sorites*; chambers similar to *Orbitolites* but less regular, annular canals connecting chamberlets, as in *Amphisorus,* but with one at each side of main chamber in all but first 1 or 2 cyclical chambers, stolons interconnecting primary chamberlets, smaller lateral chamberlets not interconnected, but joined to main chamberlets by stolons; numerous apertural pores in rows in slight depressions on periphery, as in *Orbitolites,* but more irregularly arranged. *Mio.-Rec.,* Atl.-Pac.-Red Sea.——FIG. *385,3,4. *M. vertebralis,* Rec., Fiji *(3a),* Rec., Pac. *(3b),* U.Mio., Bikini Atoll *(4a),* Plio.-Rec., Bikini Atoll *(4b)*; *3a,* side, ×8 (*462); *3b,* edge, ×20 (*200); *4a,b,* axial secs., ×20 (*361).

Opertorbitolites NUTTALL, 1925, *1368, p. 447 [**O. douvillei*; OD]. Test lenticular, with median layer of annular chambers similar to *Orbitolites,* chambers of successive annuli arranged alternately but with thick imperforate laminae on either side of chamber layer, laminae closely adjacent rather than enclosing vacuoles, as in *Somalina. L. Eoc.,* Baluch.——FIG. *385,8,9. *O. douvillei*; *8,* central portion of axial sec. of holotype; *9,* equat. sec. passing through chambers in median plane; both ×16 (*1368).

Orbitolites LAMARCK, 1801, *1084, p. 376 [**O. complanata*; SD DOUVILLÉ, 1902, *614, p. 296] [=*Discolithes* FORTIS, 1801, *735, p. 106 *(nom. neg.)*; *Discolithus* FORTIS, 1802, *735A, p. 97 (obj.); *Discolites* DE MONTFORT, 1808, *1305, p. 186 (type, *D. concentricus,* =*Orbitolites complanata* LAMARCK); *Orbitolithes* OKEN, 1815, *1385, p. 827; *Orbitulites* BRONN in BRONN & ROEMER, 1854, *214b, p. 254 *(nom. van.) (non* BERTHOLD, 1827, *nec* EICHWALD, 1829, *nec* GRIFFITH & PIDGEON, 1834)]. Test discoidal, similar to *Sorites,* megalospheric form with large globular multilocular nucleoconch, surrounded by numerous chambers in annular series, chambers in successive alternate series, each chamber with pores connecting those of preceding and succeeding annulae only, but without stolons interconnecting chambers of single series; annulae poorly defined in later stages and chamberlets separated by thick oblique walls; apertures on periphery in rows perpendicular to median plane. *U.Paleoc.-Eoc.,* Eu.——FIG. *387,1-4. *O. complanata,* M. Eoc.(Lutet.), Fr.; *1a,b,* opposite sides of microspheric topotype, with external wall preserved in center, abraded, showing chamberlets at margins, ×5; *1c*, edge view; *1d*, portion of side showing opened nucleoconch, ×10; *2a,b*, opposite sides of smaller megalospheric topotype, ×5; *2c*, central portion of *2b* showing opened nucleoconch

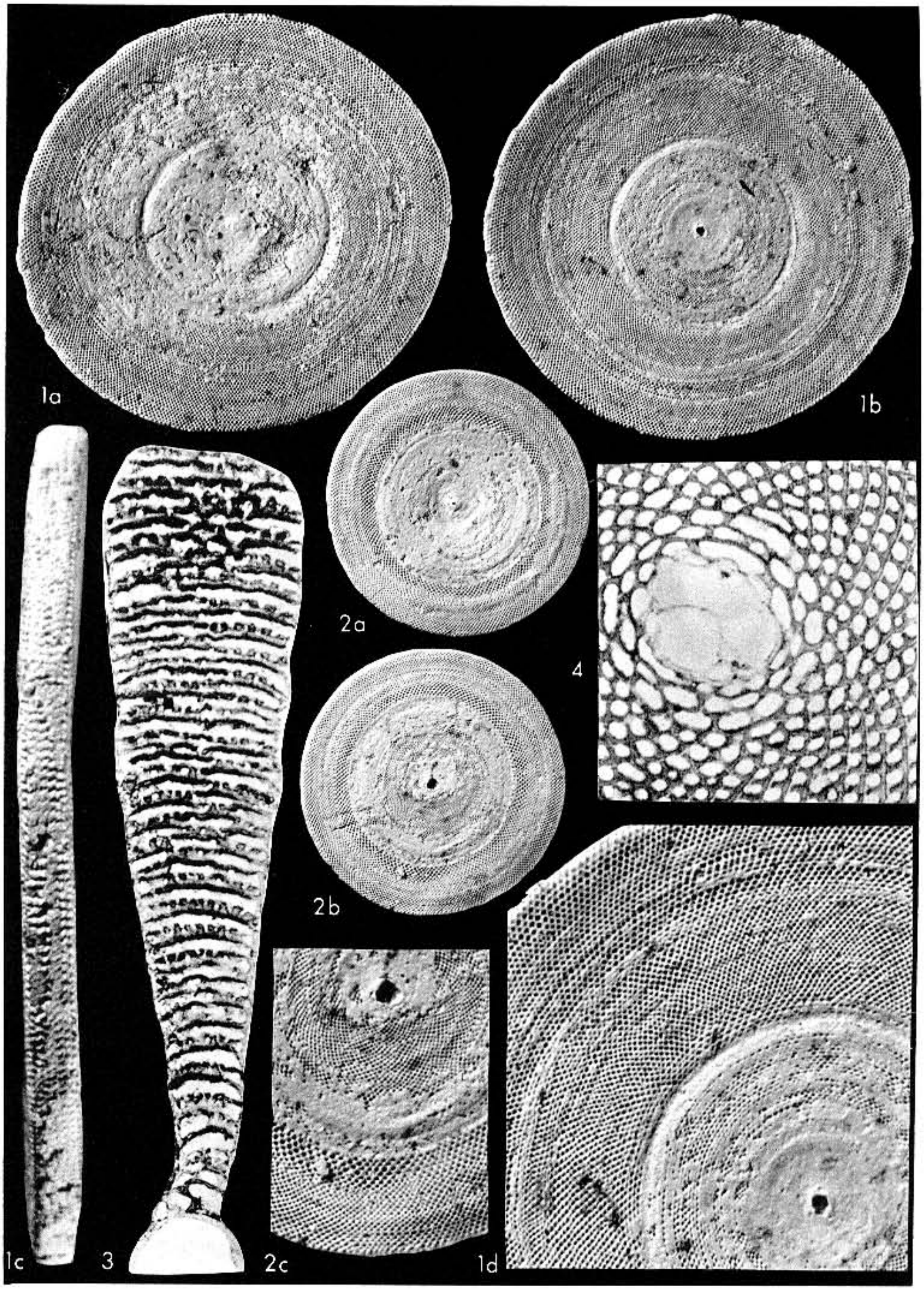


FIG. 387. Soritidae (Soritinae; *1-4*, *Orbitolites*) (p. C498-C500).

and chamberlets where external wall is abraded, ×10 (*1,2*, *2117); *3,4*, portions of axial and horiz. secs., ×50 (*1122).

Somalina A. SILVESTRI, 1939, *1788b, p. 51 [**S. stefaninii*; OD (M)] [=*Somalina* A. SILVESTRI, 1938, *1788a, p. 59, 64 *(nom. nud.)*]. Test dis-

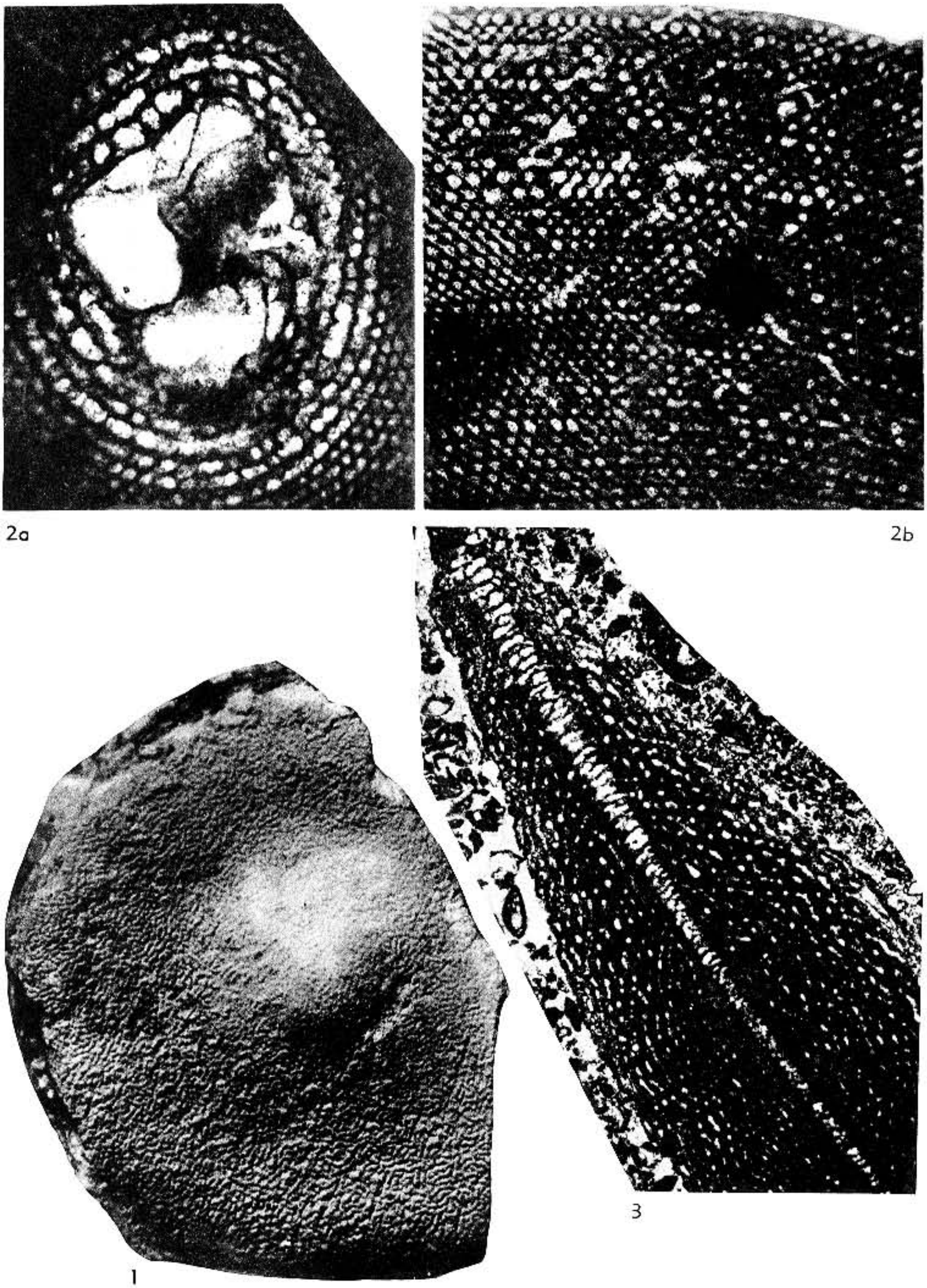


FIG. 388. Soritidae (Soritinae; *1-3, Somalina*) (p. C500-C501).

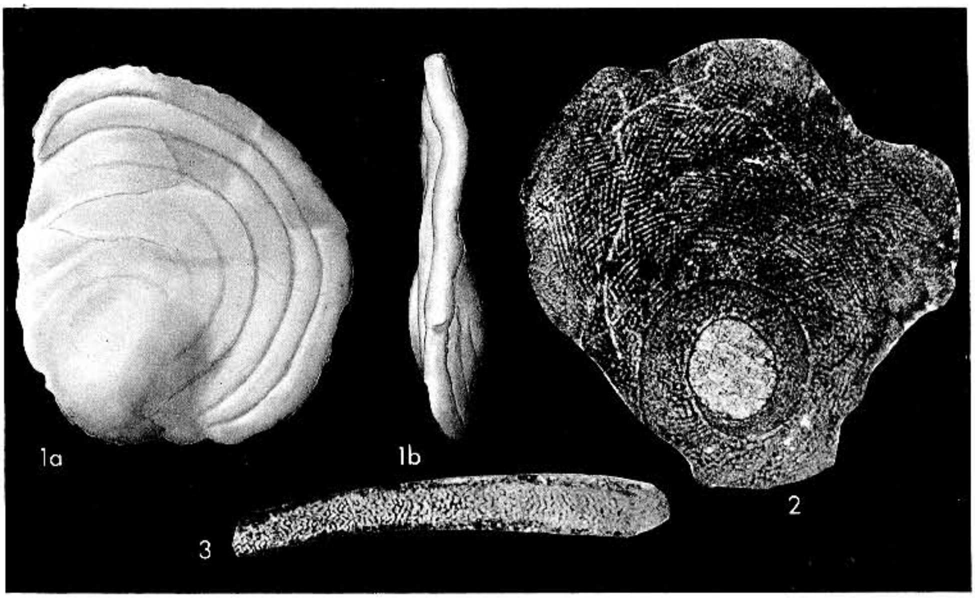


FIG. 389. Soritidae (Soritinae; *1-3, Yaberinella*) (p. C501).

coidal to lenticular, similar to *Orbitolites* in absence of stolons between adjacent chambers of single annular series, chambers forming equatorial layer similar to *Opertorbitolites* but with lateral layers of shell material enclosing vacuoles, superficially resembling chamberlets, but apparently without communication between vacuoles. *Eoc.*, Somali.-Egypt-Iraq.——FIG. 388,*1-3*. **S. stefaninii*, L.Eoc., Somali.; *1*, ext., ×5; *2a,b*, central and marginal parts of equat. sec. of megalospheric test showing "nucleoconch" of large chambers, and small peripheral chambers, ×31 (*1788b); *3*, axial sec., ×20 (*1788a).

Yaberinella VAUGHAN, 1928, *1989, p. 7 [*Y. *jamaicensis*; OD]. Test large, operculine to discoidal in plan, up to 50 mm. diam., early stage peneropline, with very broad, low chambers, which may become cyclical, especially in microspheric form; chambers subdivided into secondary chamberlets; septula numerous, intersecting at low angles to give hachured appearance in section; aperture apparently a series of pores on apertural face, chamberlets communicating through stolons, which occur in 3 planes. *M.Eoc.-U.Eoc.*, Carib. (Jamaica).——FIG. 389,*1-3*. **Y. jamaicensis*, M. Eoc.; *1a,b*, side, edge views of lectotype (here designated, one of VAUGHAN's figured specimens), ×9 (*2117); *2*, horiz. sec. of megalospheric paratype, showing fine radial surface striations at sides, and interwoven appearance of septula in central portion, ×13; *3*, vert. sec. of microspheric specimen, ×7 (*1989).

Subfamily KERAMOSPHAERINAE Brady, 1884

[Keramosphaerinae BRADY, 1884, p. 63]

Test globular, concentric chambers subdivided into chamberlets; pores between chambers of same series and between those of successive series. *Mio.-Rec.*

Keramosphaera BRADY, 1882, *198, p. 242 [**K. murrayi*; OD (M)] [=*Orbulinaria* RHUMBLER, 1906, *1571, p. 23 (type, *O. fallax* RHUMBLER in EGGER, 1909, *662, p. 11); *Arbulinarium* RHUMBLER, 1913, *1572b, p. 347 (*nom. van. pro Orbulinaria* RHUMBLER, 1906)]. Test free, spherical, to 2.5 mm. diam., with numerous somewhat inflated chamberlets of irregular outline added in concentric spherical series, chamberlets of each layer with short lateral stolons for intercommunication, chamberlets of successive layers neither directly superposed nor regularly alternating in position; apertures consisting of pore at margin of each chamberlet, previous apertures serving for intercameral connections between chamberlets of successive layers. *Rec.*, S.Atl.-W.Pac.-N.Sea.——FIG. 390,*1*. **K. murrayi*, SW.Australia; *1a*, ext., holotype, ×25 (*2117); *1b*, part of median sec., ×50 (*198).——FIG. 390,*2*. *K. fallax* (RHUMBLER), S.Atl.; ext., ×218 (*1572a).

[*Orbulinaria* was placed with the agglutinated genera by GALLOWAY (1933, *762) and CUSHMAN (1948, *486) but was originally stated to be entirely calcareous, with scaly meandrine surface and scattered pores according to RHUMBLER. This is identical to *Keramosphaera*, and the type-species of the 2 differ only in size. Although the Cretaceous spheres (=*Oligostegina*) were included in *Orbulinaria* by RHUMBLER, the type is *O. fallax*, a Recent form from the South Atlantic, Ascension Island.]

Kanakaia HANZAWA, 1957, *873, p. 38 [**K. marianensis*; OD]. Test encrusting, to 4 mm. diam., with chambers in layers similar to those of *Keramosphaera*; stolons through septa connecting chambers of same series and oblique stolons connecting chambers with those of preceding and succeeding layers. *Mio.(Aquitan.)*, Saipan-Tinian-Rota.——FIG. 390,*3-5*. **K. marianensis*, Saipan; *3,4*, horiz. and vert. secs., ×20; *5*, vert. sec. through proloculus, ×80 (*873).

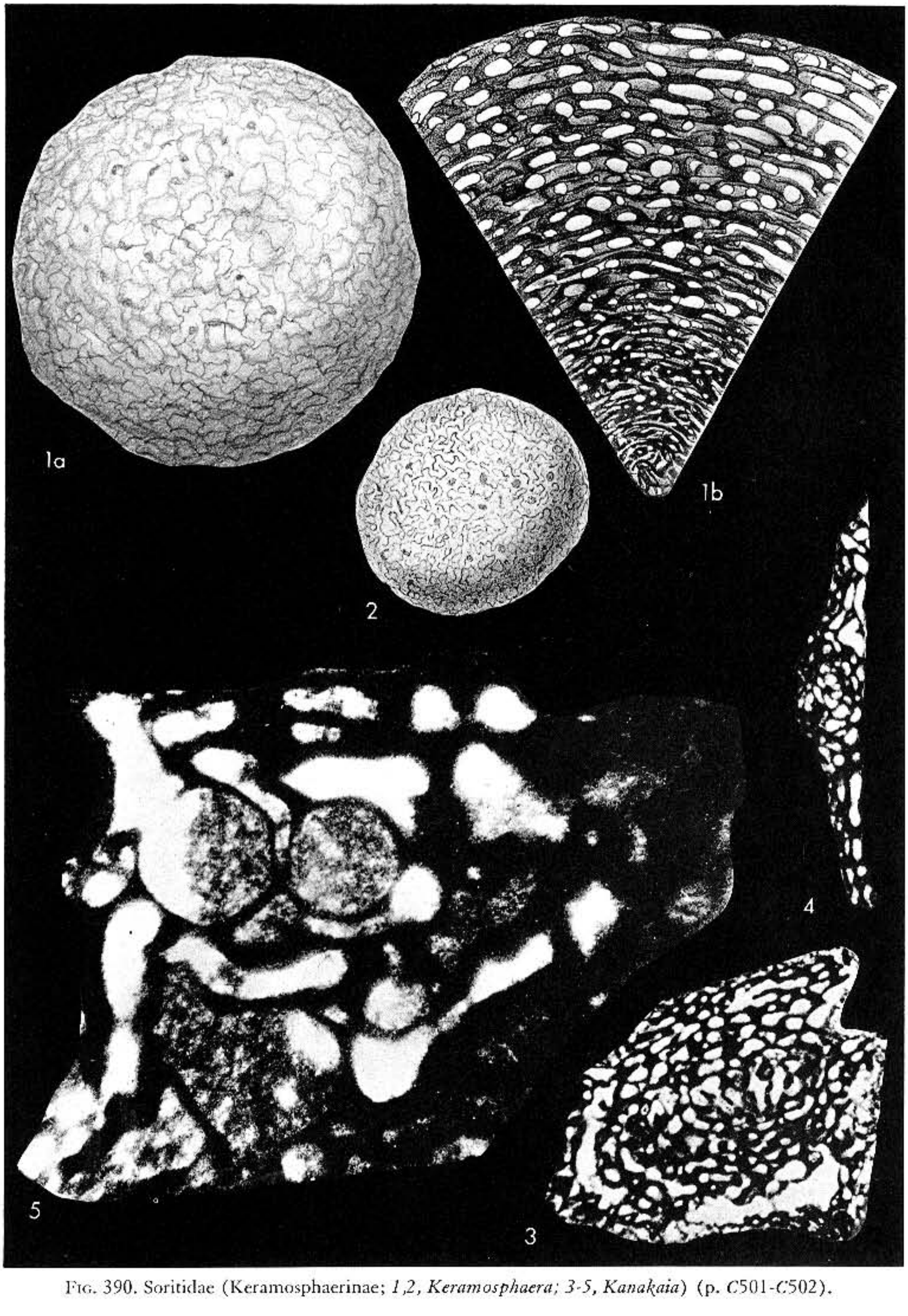


FIG. 390. Soritidae (Keramosphaerinae; *1,2, Keramosphaera; 3-5, Kanakaia*) (p. C501-C502).

ALVEOLINIDAE

By Manfred Reichel

[Bernoullianum, Universität Basel]

Family ALVEOLINIDAE Ehrenberg, 1839

[*nom. correct.* Steinmann, 1881, p. 41 (*pro* Alveolinea Ehrenberg, 1839, table opp. p. 120; type-genus *Alveolina* d'Orbigny, 1826, which is junior objective synonym of *Borelis* de Montfort, 1808)]——[In following citations superscript numbers indicate taxonomic rank assigned by authors as follows: ^{1}family, ^{2}subfamily; dagger(†) indicates *partim*]——[=^{1}Polythalama† Latreille, 1825, p. 161 (*nom. nud.*); =^{1}Enthomostégues† d'Orbigny, 1826, p. 304 (*nom. nud.*); =^{1}Fasciolitidae Bakx, 1932, p. 257]——[=^{1}Alveolinida Schultze, 1854, p. 53; =^{2}Alveolininae Brady, 1884, p. 62; =^{1}Alveolinina Lankester, 1885, p. 847; =^{1}Alveo*lininae* Delage & Hérouard, 1896, p. 127]——[=^{1}Borelida Schmarda, 1871, p. 165; =^{2}Borelidinae Wiesner, 1931, p. 60, 75; =^{1}Borelidae Hanzawa, 1932, p. 36, 102]——[=^{1}Alveolinellidae Cushman, 1927, p. 58; =^{2}Alveolinellinae Galloway, 1933, p. 148]

Wall porcelaneous, imperforate. Test free, usually large, coiled about elongate axis, subcylindrical, fusiform, ellipsoidal or spherical, rarely somewhat nautiloid. Proloculus followed by spiral tube (flexostyle). Juvenile volutions commonly coiled irregularly, at least in microspheric form. Chambers numerous, divided into tubular chamberlets by means of secondary partitions (septula) parallel to direction of coiling; chamberlets may occur in several layers. Apertures numerous, arranged in one or more rows, exceptionally fused into horizontal slit. *L.Cret.-Rec.*

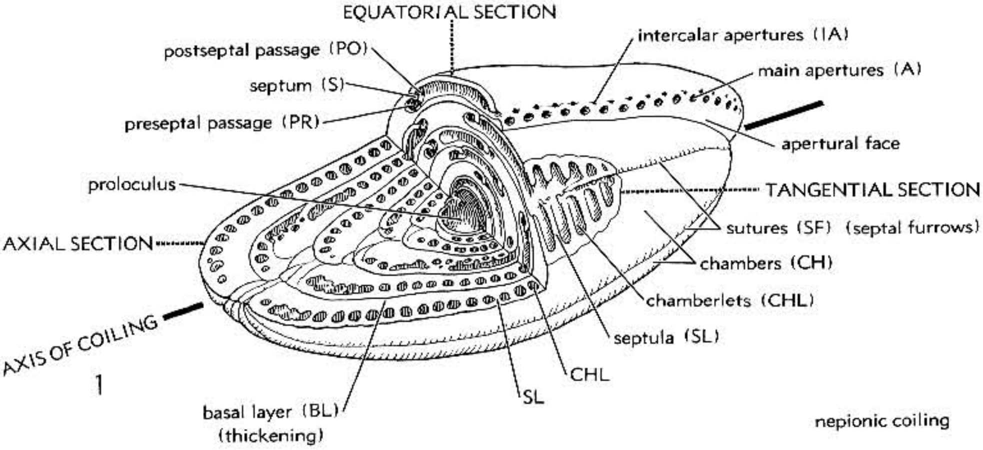
These features make of the Alveolinidae a morphologically well-defined family but probably not a phylogenetic unit. Some of the genera that followed each other in the course of geological epochs surely did not evolve one from another.

In their general shape the alveolinids are somewhat isomorphous with fusulinids but between these families no genetic relations exist. The irregular coiling of the first volutions found in the microspheric forms of nearly all genera and species shows that the Alveolinidae are closely related to the Miliolidae. Their relationship with the Peneroplidae is smaller. Yet in Recent *Alveolinella,* Hofker has observed pores in the wall of the proloculus and peneropline-like coiled first volutions in the microspheric form. It is therefore possible that this genus evolved independently from a peneropline ancestor. Nevertheless, for practical reasons I have placed it in the Alveolinidae. Further study will be needed of the relations between *Alveolinella* which appears in the Miocene, and the structurally very similar Miocene genus *Flosculinella,* the microspheric form of which we still do not know.

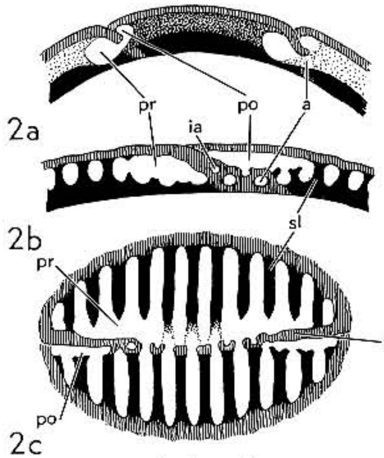
The essential feature of the family—axial elongation of the shell—is extremely variable. As a rule, the axial diameter is greater than equatorial diameter, but very commonly both are of the same length (globular tests) and rarely the equatorial diameter is greatest. The ratio of elongation may reach 9:1 in most elongate shells. The shape of the test also varies greatly. Some genera with only small species (e.g., *Ovalveolina, Bullaveolina, Borelis*) are represented by shells with axial diameter of 1 to 2 mm. Other genera comprise small as well as large forms (e.g., *Praealveolina, Subalveolina, Fasciolites*). The largest tests occur in microspheric specimens of *Fasciolites,* which may attain a length of 100 mm. (e.g., *F. levantina,* from the Mediterranean region).

Internal structure furnishes the most important taxonomic features for distinction of genera (Fig. 391,*1-8*). Almost invariably a definite type of structure is found to characterize the alveolinids of a given time-stratigraphic division. In the endoskeleton we may distinguish: (1) the **basal layer** (basal thickening), usually well developed in the axial region and in some shells enormously thickened (e.g., *"Flosculina"*) (Fig. 391,*6*); (2) the secondary partitions or **septula** which are arranged in the direction of coiling; and (3) the **floors** which divide several layers of chamberlets (e.g., *Praealveolina, Alveolinella*) (Fig. 391,*7,8*).

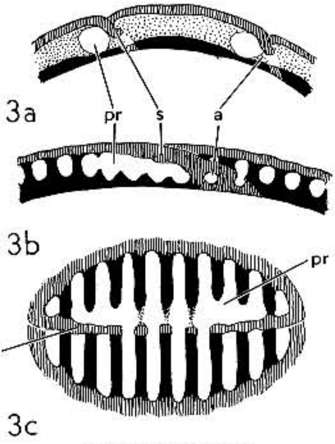
The septula of two adjacent chambers show either an alternating or a continuous arrangement (Fig. 391,*2,3*). A section across the chamberlets is circular or oval. The chamberlets of the uppermost layers in *Flosculinella* and *Alveolinella* are half the size of those of the lower layers and may be compared with the attics (Fr., *mansardes*) of a building. **Alveoli** are blind chamberlets without an opening at their front. At the back, they are connected with the preceding chamber by means of secondary apertures (e.g., *Subalveolina, Bullalveolina*). Irregularly arranged supplementary chamberlets are sometimes seen in the basal layer of certain species of *Fascio-*



1

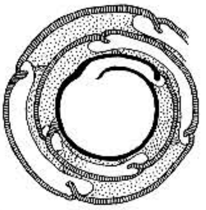


septula alternating

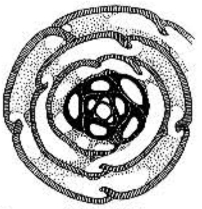


septula in alignment

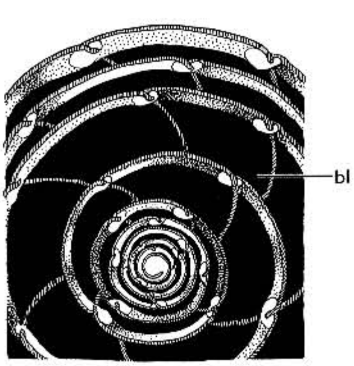
nepionic coiling



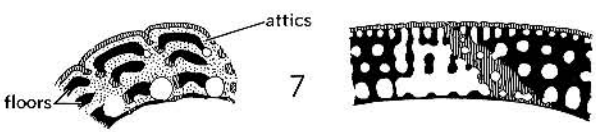
4 regular



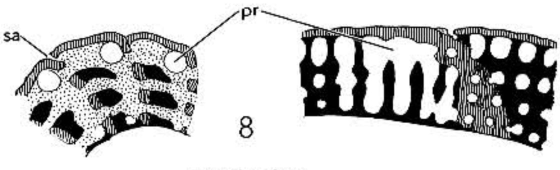
5 irregular



6



equatorial Alveolinella axial



Praealveolina

sa = sutural apertures

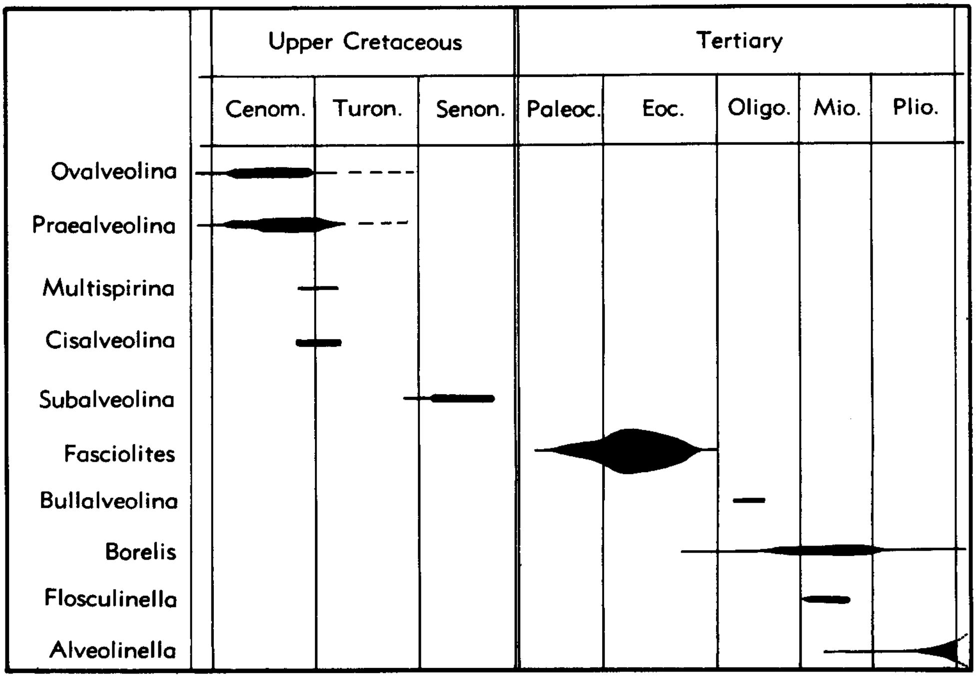


Fig. 392. Stratigraphic distribution of Alveolinidae (*2119A).

lites ("subgenus *Eoalveolinella*"). All chamberlets of the same chamber are connected by a preseptal passage, located in the anterior part of the chamber. A postseptal passage appears in *Fasciolites* in the angle between wall and septum at the back of the chamber. In *Cisalveolina* it occupies the whole posterior part of the chamber and then the preseptal passage is extremely reduced.

In a single genus (*Multispirina*) several spires may be observed. In the megalospheric generation the first spires begin on the proloculus, which possesses several rows of apertures. All species of medium and large size show a clear dimorphism and some exhibit trimorphism.

Fossil alveolinids are only found in neritic sediments where they may be associated with miliolids and calcareous algae. Many large species occur in great abundance and are therefore rock-builders (*Praealveolina*, Cenomanian; *Fasciolites*, Eocene).

Alveolinella lives in tropical seas at depths of 10 to 80 m. *Borelis* has been found to a depth of 411 m.

Stratigraphic distribution of alveolinid genera is indicated in Fig. 392.

Borelis de Montfort, 1808, *1305, p. 170 [**B. melonoides* =**Nautilus melo* var. β Fichtel & Moll, 1798; OD] [*non Borelis* Oken, 1815] [=*Clausulus* de Montfort, 1808, *1305, p. 178 (type, *C. indicator*, =*Nautilus melo* Fichtel & Moll, 1798); *Melonites* Lamarck, 1812, *1087, p. 122 (type, *M. sphaerica* Lamarck, 1816, *1089,

Fig. 391. (*Facing page.*) Morphological features of alveolinid tests and terminology applied to them.——*1*. *Fasciolites* (×32.5), oblique view of partially sectioned test showing morphological nomenclature.——*2,3*. Types of septula illustrated by much-enlarged sections (*2a,3a*, equatorial; *2b,3b*, slightly oblique axial showing septal part; *2c,3c*, tangential); *2*, *Fasciolites*, with alternating septula; *3*, *Borelis*, with continuous, aligned septula [wall and septa, hatched; septula and basal layer, stippled and black].——*4*. Proloculus and regularly coiled first whorls of *Fasciolites* (*Fasciolites*) *schwageri*.——*5*. Proloculus and irregularly coiled first whorls of *Fasciolites* (*Glomalveolina*) *primaeva*.——*6*. Equatorial section of *Fasciolites* (*Fasciolites*) *pasticillatus* showing very thick basal layer of "*Flosculina*" type.——*7,8*. Parts of equatorial and axial sections of *Alveolinella quoyi* (*7*) and *Praealveolina cretacea* (*8*) showing chambers with several rows of chamberlets (*2119A).

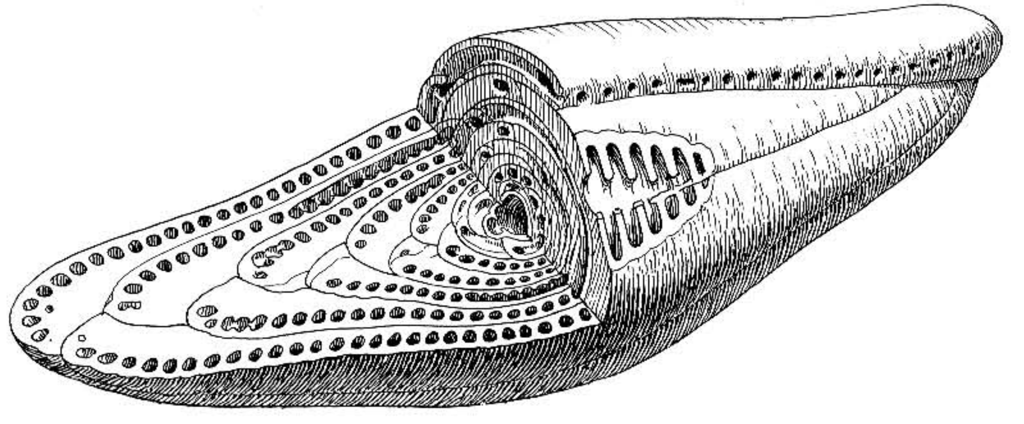


Fig. 393. Alveolinidae; *Borelis* (p. C505-C506).

p. 469, =*Nautilus melo* Fichtel & Moll, 1798, SD Galloway, 1933, *762, p. 150); *Melonia* Lamarck, 1822, *1090, p. 615 (type, *Melonites sphaerica* Lamarck, 1816, =*Nautilus melo* Fichtel & Moll, 1798, SD Galloway, 1933, *762, p. 150); *Alveolina* d'Orbigny, 1826, *1391, p. 306 (type, *Nautilus melo* Fichtel & Moll, 1798, SD Parker & Jones, 1860, *1417c, p. 182); *Borelia* Agassiz, 1844, *5, p. 4 (*nom. van. pro Borelis* de Montfort, 1808); *Neoalveolina* Silvestri, 1928, *1783, p. 35 (type, *Alveolina bradyi* Silvestri, 1927, *1782, p. 227, SD Bakx, 1932, *68, p. 208, =*Nautilus melo* Fichtel & Moll, 1798]. Test minute, spheroidal to fusiform, with septula in continuous arrangement; in some tests, chamberlets of same chamber alternately large and small, with latter displaced toward exterior, septula therefore developing Y-shape; without postseptal passage, first whorls irregularly coiled. *U. Eoc.-Rec.,* Eu.-Asia-Afr.——Fig. 393. *B. schlumbergeri* (Reichel), Rec., Mayotte Is.(NW of Madagascar); ×75 (*2119A).——Fig. 394,*2*. *B. melo curdica* (Reichel), U. Mio., E. Turkey; ×85 (*2119A).

[The nominal genus *Alveolina* d'Orbigny, 1826, from which the family containing *Borelis* has been named and become widely known, is unquestionably a junior objective synonym, since *Nautilus melo* Fichtel & Moll, 1798, according to provisions of the international Rules of Nomenclature, is the type-species of both. For *Borelis* this is fixed by original designation. D'Orbigny did not designate any of the 7 species assigned by him to *Alveolina* as type-species and therefore the first author who selected one of these eligible species to be the type established it unalterably. Such first valid designation was made by Parker & Jones, 1860, when they chose *Nautilus melo,* one of the original 7 species named by d'Orbigny, as type-species of *Alveolina.*—R. C. Moore.]

Alveolinella Douvillé, 1906 [1907] *617, p. 585 [**Alveolina quoii* d'Orbigny, 1826, *1391, p. 307; OD]. Fusiform, very elongate, septa continuously arranged, with several layers of chamberlets, preseptal passages on floor of chambers; last whorls may have small secondary preseptal passages; apertures in several rows, with attics at top of uppermost ones, as in *Flosculinella. Mio.-Rec.,* IndoPac.——Fig. 395,*1*. **A. quoyi* (d'Orbigny), Rec., Torres Str.; ×45 (*2119A).

[D'Orbigny's spelling of the specific name "*quoii,*" referring to the surgeon and student of corals J. R. C. Quoy, is indubitably an inadvertent error in which the last letter of the surname was incorrectly changed from "*y*" to "*i.*" The Code (Art. 32,a,ii) provides for automatic correction to "*quoyi,*" as adopted by Douvillé, Cushman, Galloway, and other authors.—R. C. Moore.]

Bullalveolina Reichel, 1936, *1513, p. 140 [**Alveolina bulloides* d'Orbigny in de la Sagra, 1839, *1611, p. 70 =*A. bulloides* d'Orbigny, 1826, (*1391, p. 306) (*nom. nud.*); OD]. Test minute, subspherical, with several rows of apertures, upper ones opening into alveoli which occupy rear part of chambers; septula alternating, first coils irregular. *Oligo.,* Eu.(S.Fr.-Italy).——Fig. 394,*1*. **B. bulloides* (d'Orbigny), L.Oligo., Fr.(Gaas); ×80 (*2119A).

Cisalveolina Reichel, 1941, *1515, p. 255.[**C. fallax*; OD]. Test ovoid, spherical, or nautiloid, septula alternating, with spacious postseptal passages but preseptal passages greatly reduced; aperture comprising long slit that extends from pole to pole, its upper edge fluted; juvenile coiling of microspheric forms irregular. *U.Cret.(U.Cenoman.-L. Turon.),* M.East.——Fig. 396,*2*. **C. fallax,* Cenoman., Iran; ×35 (*2119A).

Fasciolites Parkinson, 1811, *1420, p. 158 [**Alveolina oblonga* d'Orbigny, 1826, *1391, p. 306, =Parkinson's figured specimen, *1420, pl. 10, figs. 28-31; SD (SM) d'Orbigny, 1826, *1391, p. 306] [=*Miliolites* de Montfort, 1808, *1305, p. 175 (type, *M. sabulosus*) (*non Miliolites* Lamarck, 1804); *Oryzaria* Defrance in Bronn, 1825, *209, p. 30 (type, *O. boscii*); *Alveolina* auctt. *(partim)* (*non* d'Orbigny, 1826 =*Borelis* de Montfort, 1808); *Flosculina* Stache, 1880,

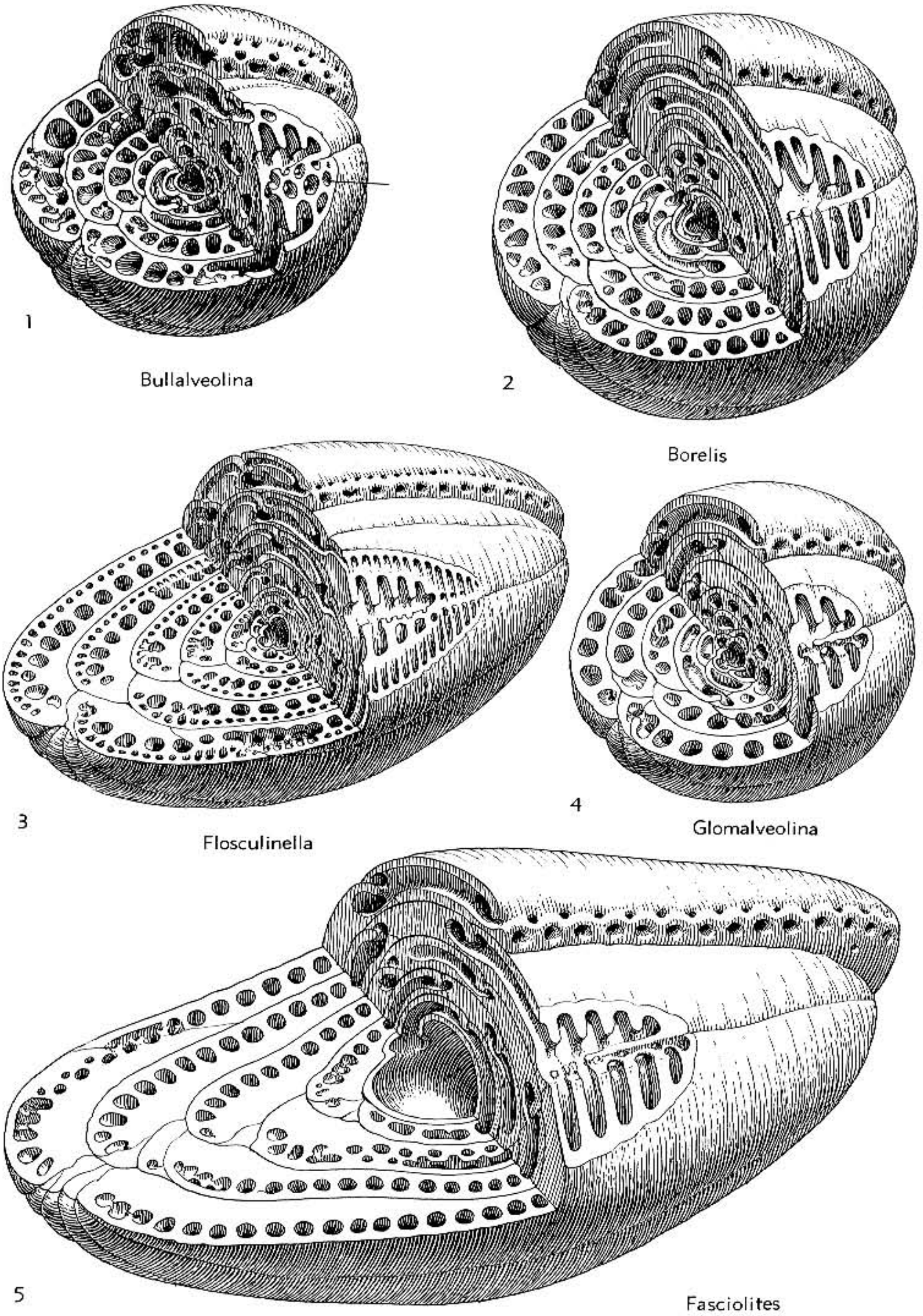


FIG. 394. Alveolinidae; *1, Bullalveolina; 2, Borelis, 3, Flosculinella; 4, Fasciolites (Glomalveolina); 5, F. (Fasciolites)* (p. *C*505-*C*510).

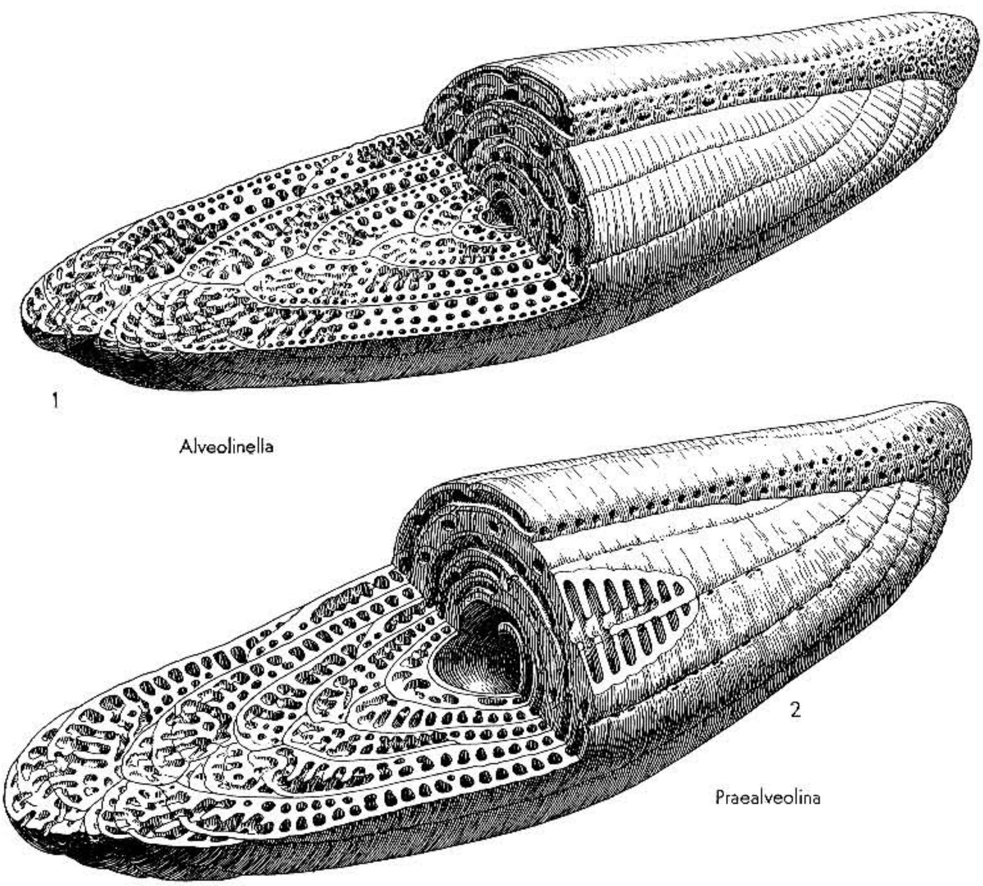


FIG. 395. Alveolinidae; *1, Alveolinella; 2, P. (Praealveolina)* (p. C506, C510).

*1827, p. 199 *(nom. nud.)*; *Flosculina* STACHE in SCHWAGER, 1883, *1707, p. 102 (type, *F. decipiens* SCHWAGER, 1883, SD GALLOWAY, 1933, *762, p. 151); *Flosculina (Semiflosculina)* DONCIEUX, 1905, *608, p. 124, no species named; *Eoalveolinella* SILVESTRI, 1928, *1783, p. 35 (type, *Alveolina violae* CHECCHIA-RISPOLI, 1905, *329, p. 165; *Flosculina (Checchiaites)* SORRENTINO, 1935, *1815, p. 137 (type, *Flosculina daunica* CHECCHIA-RISPOLI, 1912); *Alveolina (Fasciolites)* REICHEL, 1936, *1514, p. 80 (obj.)]. Test spherical, ellipsoidal, fusiform, or cylindrical; septula alternating in adjacent chambers, with pre- and postseptal passages; coiling of first whorls irregular in microspheric form of all species but regular in megalospheric form of most species; 2 rows of apertures alternating in position; may show enormous basal thickening in several internal whorls (e.g., *"Flosculina"*) or secondary apertures and chamberlets irregularly distributed in axial zone and mostly not connected with preseptal passages (e.g., *"Eoalveolinella"*). [Many species are important as rock-builders.] *Paleoc.-Eoc.*, Eu.-Asia-Afr.

[No named species originally were included in *Fasciolites*. *Alveolina oblonga* D'ORBIGNY was based on specimens collected by him from the Eocene (Cuisian) of France, and *Fasciolites* PARKINSON was mentioned by D'ORBIGNY as a synonym of *Alveolina*. GALLOWAY (1933, *762, p. 150) regarded this as constituting subsequent monotypy (ICZN, Art. 2, Op. 46).] [Note by REICHEL.—Because of strong preference, ingrained by many years of usage, especially on the part of European paleontologists, including me, I have endeavored to find ways of conserving the name *Alveolina*, hallowed by tradition. This is because (1) all authors describing Eocene species from Africa and Europe have used it; (2) since adoption of *Alveolina* for recognition in my structural studies (1931, 1936-37) of the tests, the name has become the symbol of a well-defined and characteristic morphological type that is common to all observed Paleocene and Eocene species; (3) deserving respect are the attempts of D'ORBIGNY to establish priority of the name *Alveolina* since "Alvéolite de Bosc" was the oldest name (DESHAYES, 1828, p. 228) without doubt assigned to an Eocene form *(Alvéolite grain de fétusque)* figured 9 years before the *Fasciolites* of PARKINSON; and (4) it has seemed desirable to avoid use of *Fasciolites* as defined by GALLOWAY on the basis solely of test proportions and size of chamberlets. But unfortunately these arguments are insufficient for the Rules of Nomenclature. The term Alvéo-

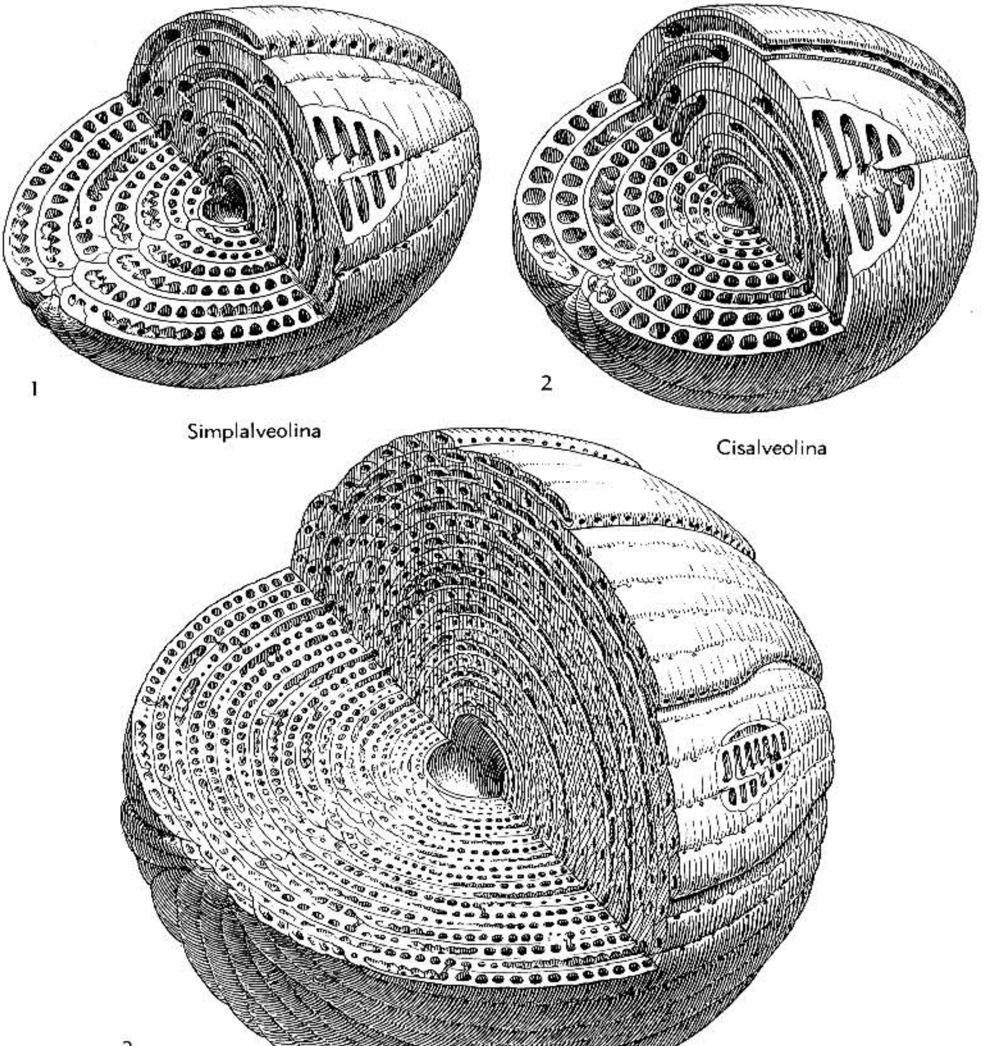


FIG. 396. Alveolinidae; *1, Praealveolina (Simplalveolina); 2, Cisalveolina; 3, Multispirina* (p. C506, C510).

lite of Bosc is a vernacular name; d'Orbigny's figures intended for publication with his 1826 text were not published until much later. Readers should be warned that *Fasciolites* refers only to forms of the structural type of *Alveolina* of Reichel (1931, 1936-37) and *not* to all elongate-ovoid, fusiform, and cylindrical tests with a single layer of chamberlets, as defined by Galloway.]

F. (Fasciolites). Coiling of first whorls regular in megalospheric form; test generally ellipsoidal to fusiform or cylindrical, but may be spherical, *U.Paleoc.-Eoc.,* Eu.-Asia-Afr.——Fig. 397. *F. (F.) boscii* (Defrance), Eoc. (Lutet.), Fr. (Grignon); axial sec. of topotype, ×40 (*2119A).——Fig. 394,*5. F. (F.) schwageri* (Checchia), L.Eoc., N.Italy(Vicentino); first whorls, ×55 (*2119A).

F. (Glomalveolina) Hottinger, 1962, *962, p. 54 [**Alveolina dachelensis* Schwager, 1883, *1707, p. 96; OD] [=*Alveolina (Glomalveolina)* Reichel, 1936, *1514, p. 80 *(nom. nud.)* (type, *Alveolina ovulum* Stache, in Schwager, 1883, p. 95, *nom. nud., =A.* cf. *ovulum* Schwager, 1883, *1707, p. 95, *nom. nud.*)]. Test very small, spherical to ovoid, with irregularly coiled first whorls in both micro- and megalospheric forms. *Paleoc.-Eoc.,* Eu.-Afr.-?Asia.——Fig. 394,*4. F.*

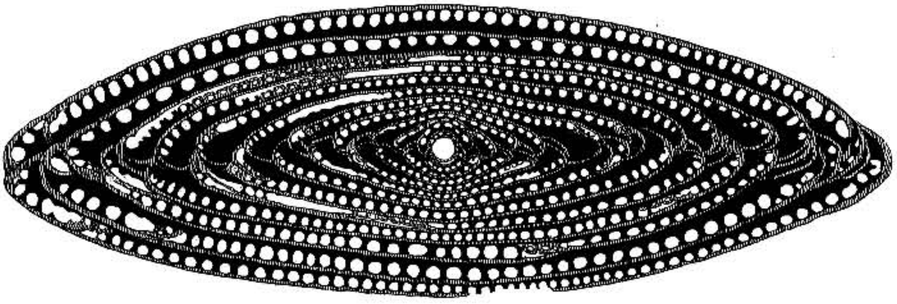


FIG. 397. Alveolinidae; *Fasciolites* (p. C506-C509).

(G.) primaeva (Reichel), Paleoc., S.Fr.; ×55 (*2119A).

[Reichel's (1936) publication of the nominal subgenus *Glomalveolina* failed to comply with requirements of nomenclatural rules (Zool. Code, 1961, Art. 13,b) relating to generic names published after 1930. These must be accompanied by definite fixation of a (valid) type-species. *Glomalveolina* had the status of a *nomen nudum* because its originally designated type-species was (and remains) a *nomen nudum*. This generic name was first validated in 1962 by Hottinger with designation of *Alveolina dachelensis* Schwager as its type-species. The provisional use of *A. dachelensis* by Schwager and attribution of *Glomalveolina* to Reichel by Hottinger have no effect on the validity of *A. dachelensis* and recognition of Hottinger as author of *Glomalveolina*. Also, the date of this nominal subgenus must be given as 1962—not 1936. An unimportant detail is the designation of Schwager, rather than bystander Stache, as the author of *Alveolina* cf. *ovulum*.—R. C. Moore.]

Flosculinella Schubert in Richarz, 1910, *1578, p. 533 [**Alveolinella bontangensis* Rutten, 1913, *1597, p. 221; SD Galloway, 1933, *762, p. 151]. Test globular to fusiform, septula alternating; apertures in 2 rows, upper ones small, leading into narrow chamberlets; first whorls irregularly coiled, *Mio.*, E.Indies-Australia.——Fig. 394,*3*. **F. bontangensis* (Rutten), Burdigal., Borneo; ×60 (*2119A).

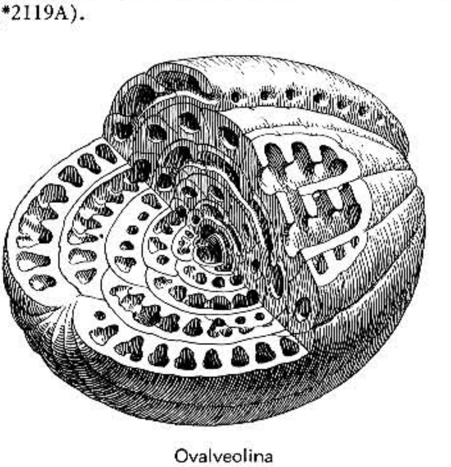


FIG. 398. Alveolinidae; *Ovalveolina* (p. C510).

Multispirina Reichel, 1947, *1518, p. 2 [**M. iranensis*; OD]. Test spherical, with several spires and numerous sutural apertures; internal structure as in *Praealveolina (Simplalveolina)*. *U.Cret.*, Iran.——Fig. 396,*3*. **M. iranensis*, Cenoman.; ×40 (*2119A).

Ovalveolina Reichel, 1936, *1514, p. 69 [**Alveolina ovum* d'Orbigny, 1850, *1397b, p. 185; OD]. Test spherical to ovoid, chambers numerous, septula continuous, short and widely spaced, apertures in single row; coiling regular throughout. *L.Cret.(U.Alb.)-U.Cret.(Cenoman.-Turon.)*, Eu.(Fr.-Sp.-Port.)-N.Afr.——Fig. 398. **O. ovum* (d'Orbigny), U.Cret. (Cenoman.), SW.Fr. (Île Madame); ×50 (*2119A).

Praealveolina Reichel, 1933, *1512, p. 270 [**P. tenuis* (=?*Alveolina cretacea* d'Archiac, 1837, *35, p. 191, unfigured); OD]. Test ovoid, fusiform, or cylindrical; septula of 2 adjacent chambers continuously arranged, with several rows of chamberlets (and apertures) below main row; at least in microspheric form of elongate species, chamberlets of layers belonging to same chamber connected by radial passages which extend downward from preseptal passage; narrow sutural apertures connecting successive whorls, most species regularly coiled throughout (although microspheric form slightly irregular). *L.Cret.(U.Alb.)-U.Cret.(Cenoman.-Turon.)*, N.Afr.-Eu.(Fr.-Spain-Port.)-Asia(M.East-India).

P. (Praealveolina). Microspheric form at least provided with secondary chamberlets. *U.Cret.(Cenoman.)*, Fr.(Beausset).——Fig. 395,*2*. **P. (P.) tenuis*; ×45 (*2119A).

P. (Simplalveolina) Reichel, n.subgen., herein [**P. simplex* Reichel, 1936, *1514, p. 67]. Secondary chamberlets lacking in both micro- and megalospheric generation. *U.Cret.(Cenoman.)*, Eu.(Fr).——Fig. 396,*1*. **P. (S.) simplex*, Île Madame; ×55 (*2119A).

Subalveolina Reichel, 1936, *1514, p. 73 [**S. dordonica*; OD]. Test fusiform in type-species, spherical in smallest ones; septula without definite arrangement, with small alveoli instead of postseptal

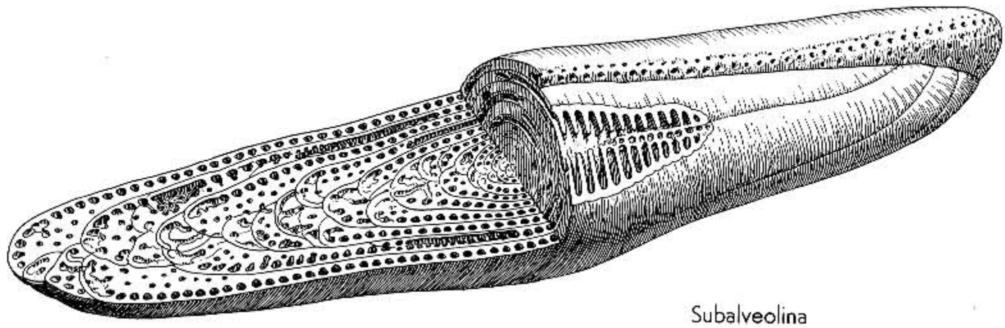


FIG. 399. Alveolinidae; *Subalveolina* (p. *C*510-*C*511).

passage to preceding chamber by upper row of apertures; secondary chamberlets and apertures irregularly arranged in axial zone; dimorphism very pronounced in species with large tests, first whorls irregularly coiled in microspheric form but regular in megalospheric form. *U.Cret.(Campan.)*, Eu.(S.Fr.).——FIG. 399. **S. dordonica*, Belvès; microspheric form, ×30 (*2119A).