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

Second Printing 1973
Third Printing 1978
Fourth Printing 1980
Fifth Printing 1985*

Library of Congress Catalogue Card Number 53-12913

ISBN 0-8137-3003-1

* Distributed by the Geological Society of America, Inc., P.O. Box 9140, Boulder, Colorado 80301, from which current price lists of Parts in print may be obtained and to which all orders and related correspondence should be directed. Editorial office for the *Treatise*: Paleontological Institute, 121 Lindley Hall, The University of Kansas, Lawrence, Kansas 66045.

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

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Part A. INTRODUCTION.
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Part U. ECHINODERMATA 3 (Echinozoa, Asterozoa).
Part X. ADDENDA, INDEX.

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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 věd 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.

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[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.
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SOURCES OF ILLUSTRATIONS

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 Previously unpublished illustrations are marked by the letter "n" (signifying "new") with the name of the author.

STRATIGRAPHIC DIVISIONS

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

Generally Recognized Divisions of Geologic Column

EUROPE	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)
Ashgill Series	Richmondian Stage Maysvillian Stage Edenian Stage
Caradoc Series	**Champlainian Series (Middle Ordovician)** Mohawkian Stage Trentonian Substage Blackriveran Substage
Llandeilo Series **Llanvirn Series**	Chazyan Stage
Arenig Series **Tremadoc Series**	**Canadian Series (Lower Ordovician)**
CAMBRIAN SYSTEM	**CAMBRIAN SYSTEM**
Upper Cambrian Series	**Croixian Series (Upper Cambrian)** Trempealeauan Stage Franconian Stage Dresbachian Stage
Middle Cambrian Series	**Albertan Series (Middle Cambrian)**
Lower Cambrian Series	**Waucoban Series (Lower Cambrian)**
EOCAMBRIAN SYSTEM	**EOCAMBRIAN SYSTEM**
ROCKS OF PRECAMBRIAN AGE	**ROCKS OF PRECAMBRIAN AGE**

RAYMOND C. MOORE

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

[2] Classed as division of Senonian Subseries.

[3] Classed as division of Neocomian Subseries.

[4] Includes Purbeckian deposits.

[5] Interpreted as lowermost Jurassic in some areas.

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

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

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

[9] Classed as uppermost Cambrian by some geologists.

PART 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]

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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

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[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

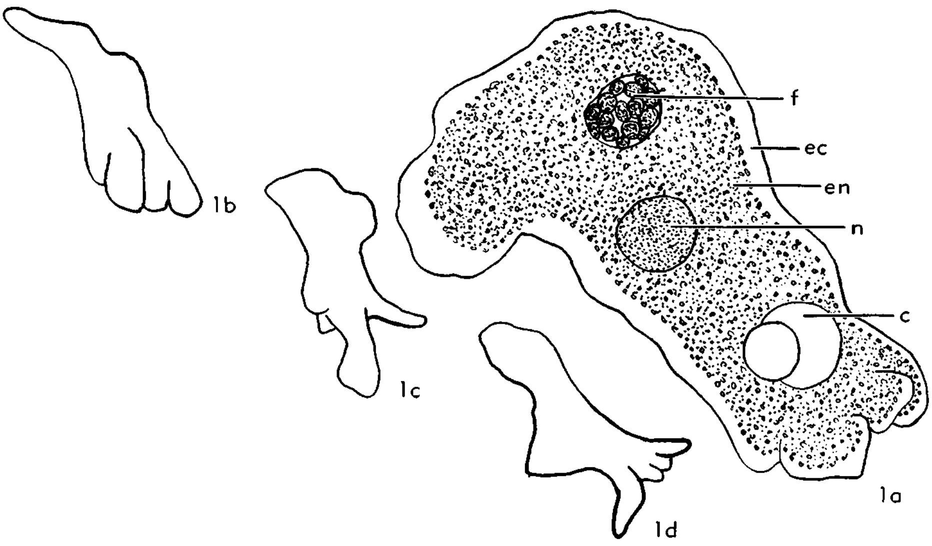

FIG. 1. Pelomyxidae; *1, Chaos diffluens* Müller, a representative pelomyxid protistan; *1a,* living specimen enlarged to show ectoplasm *(ec)*, endoplasm *(en)*, nucleus *(n)*, food vacuole *(f)*, and contractile vacuole *(c)*; *1b-d,* outline views showing successive positions of pseudopodia during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

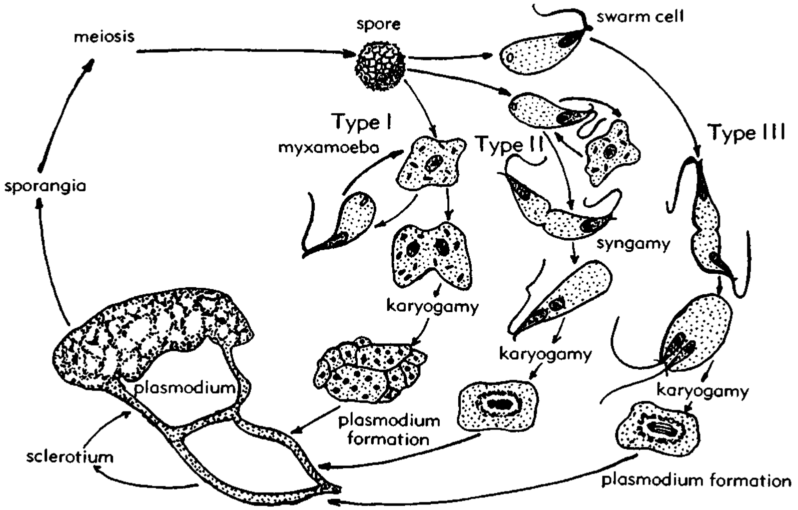

FIG. 2. Life cycle of Mycetozoida (diagrammatic) (*1585).

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*)]——[=^{5}Myxogastres Fries, 1829, p. 3, 67; =^{4}Myxogasteres Schröter, 1886, p. 91, 98; =^{2}Myxogasteres (*eigentliche* Myxomyceten) Schröter, 1897, p. iii, 8; =^{3}Myxogastres MacBride, 1899, p. 20; =^{5}Myxogastres Morgan, 1900, p. 119; =^{5}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.*); =^{5}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; =^{6}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; =^{3}Phytomyxinae MacBride, 1899, p. 16; =^{5}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.*); =^{2}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; =^{5}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.)*]——[=^{3}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}Stereonemeen 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; =^{8}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; =Atrichae† 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;

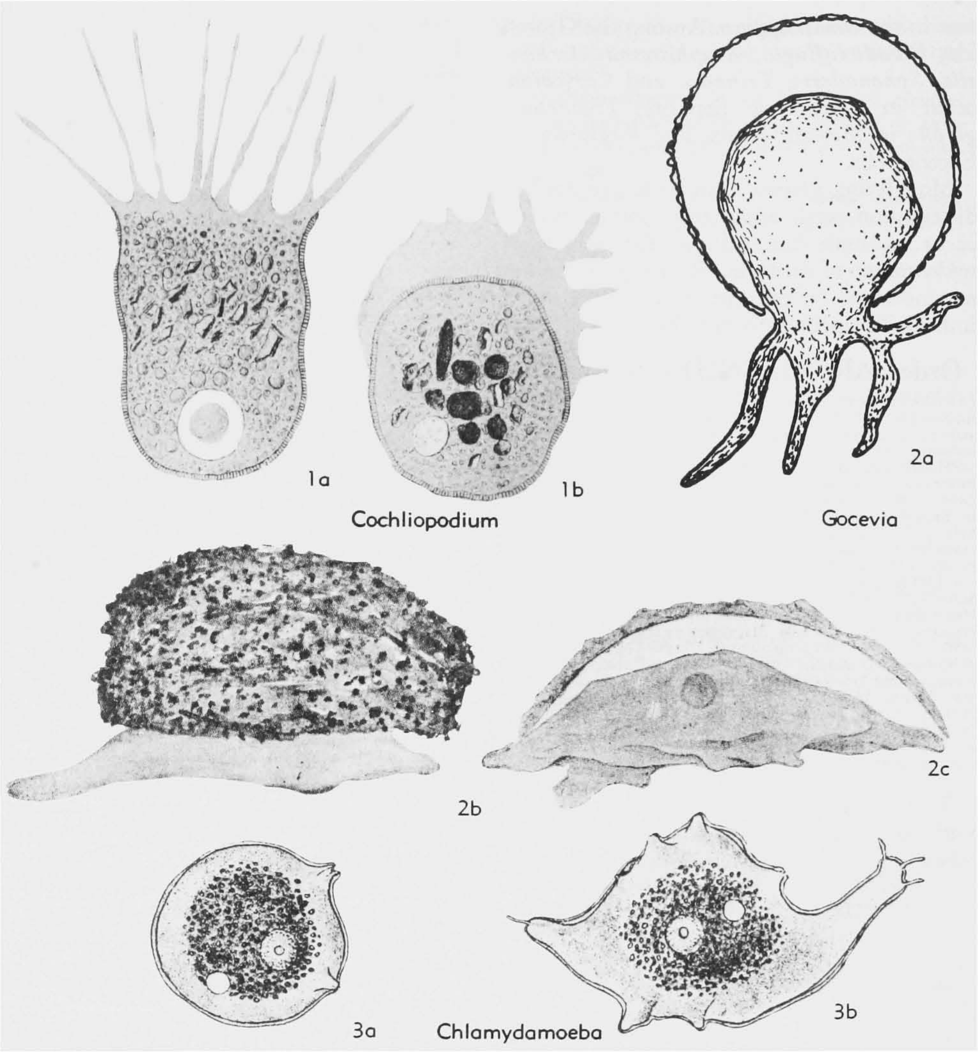

FIG. 3. Cochliopodiidae; *1, Cochliopodium; 2, Gocevia; 3, Chlamydamoeba* (p. C19).

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.*

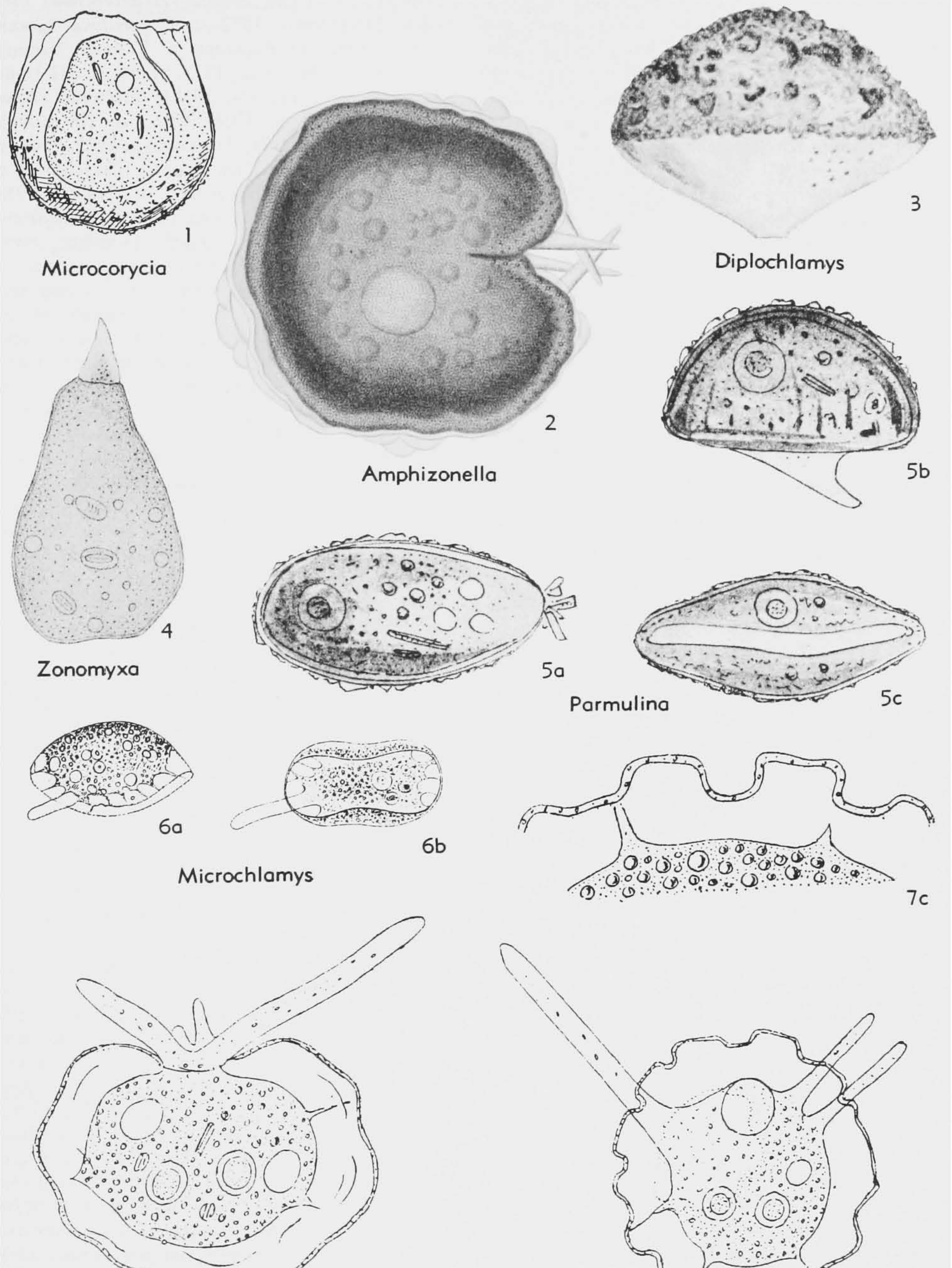

FIG. 4. Microcoryciidae; *1, Microcorycia; 2, Amphizonella; 3, Diplochlamys; 4, Zonomyxa; 5, Parmulina; 6, Microchlamys; 7, Penardochlamys* (p. C19-C22).

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 by 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).

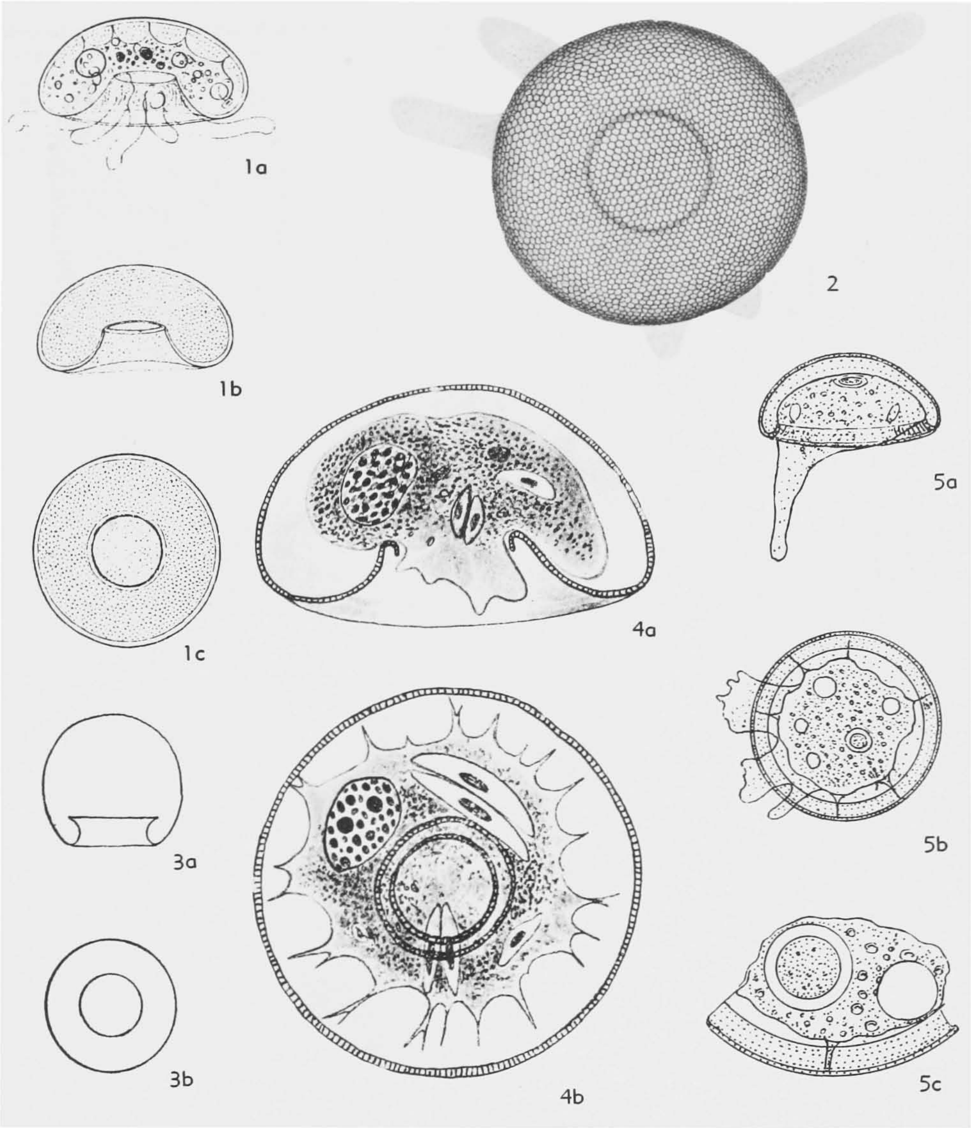

FIG. 5. Arcellidae; *1-5, Arcella* (p. *C*22).

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

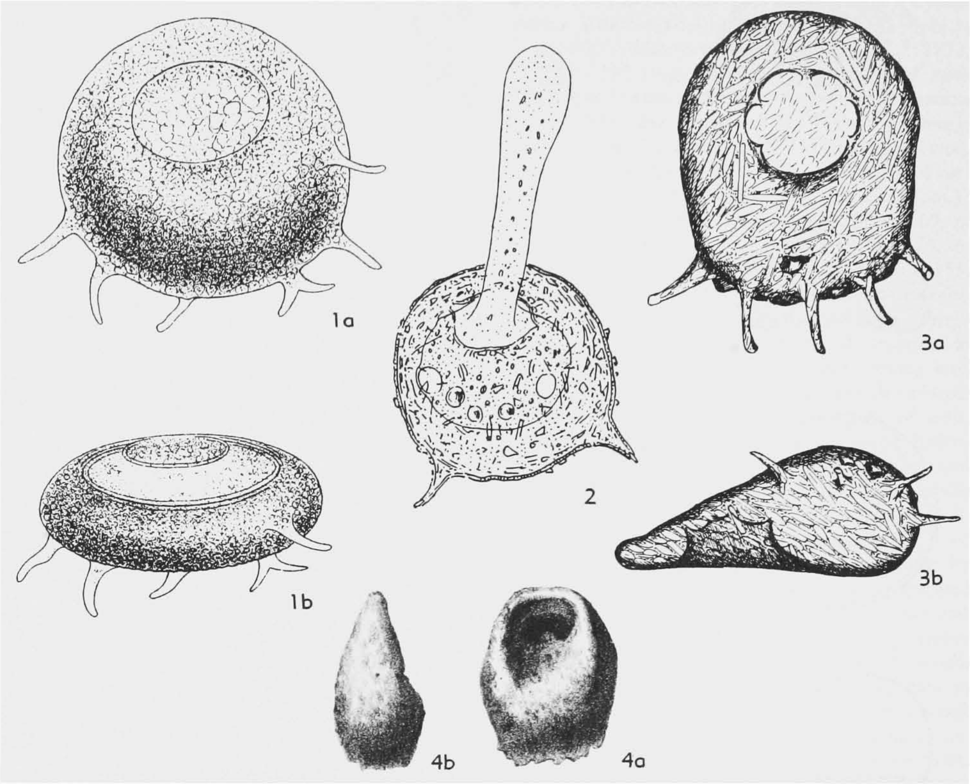

FIG. 6. Centropyxidae; *1-4, Centropyxis* (p. C23-C24).

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

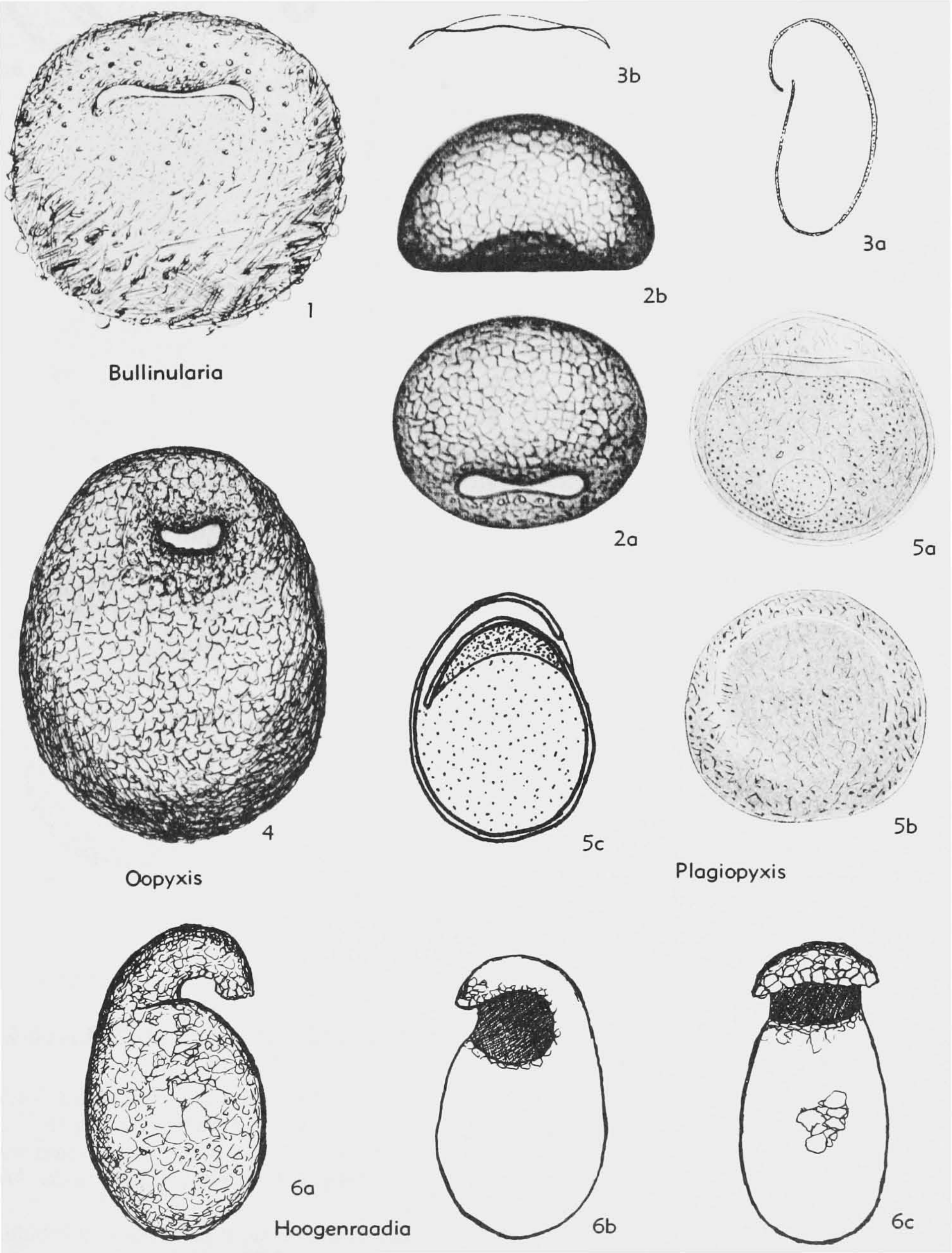

FIG. 7. Plagiopyxidae; *1-3*, *Bullinularia; 4*, *Oopyxis; 5*, *Plagiopyxis; 6*, *Hoogenraadia* (p. C24-C26).

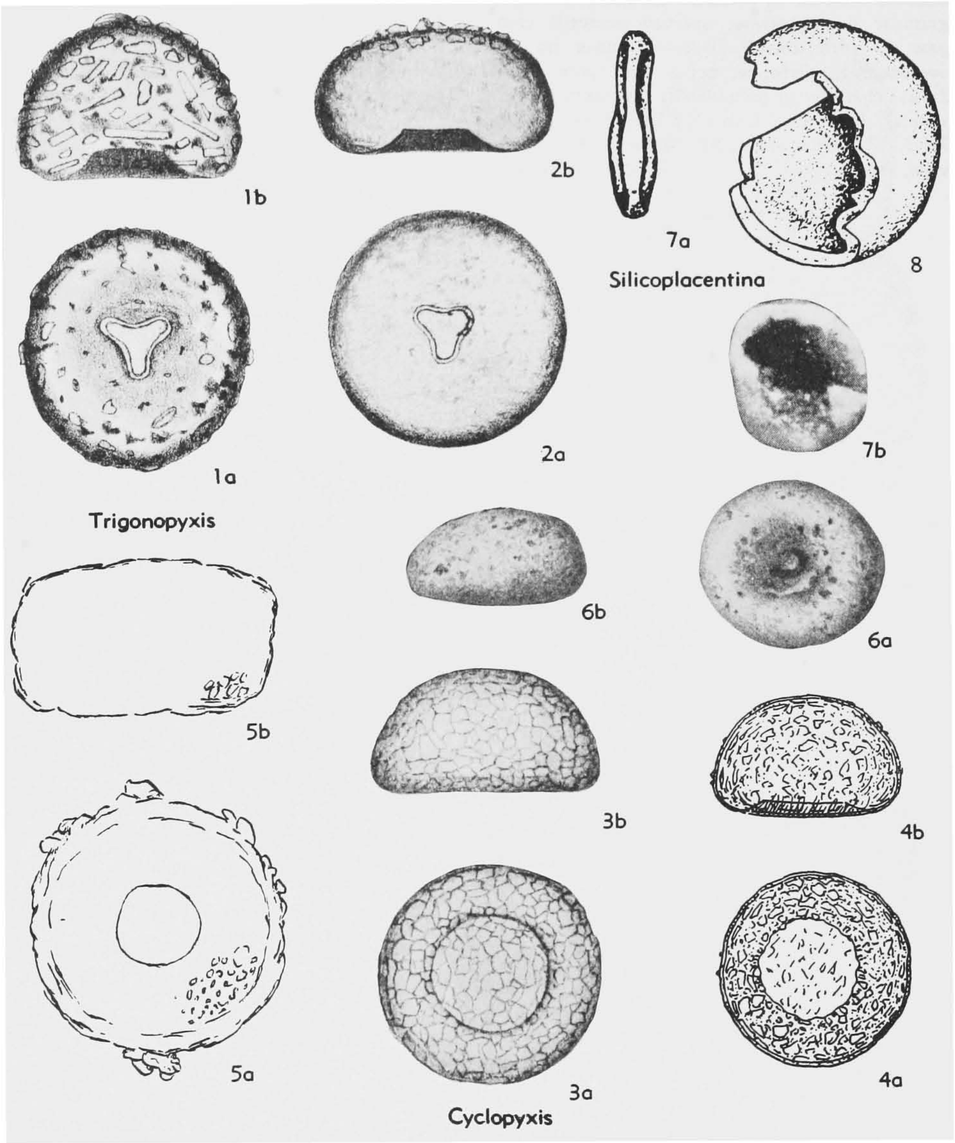

FIG. 8 Trigonopyxidae; *1,2, Trigonopyxis; 3-6, Cyclopyxis; 7,8, Silicoplacentina* (p. C26-C27).

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 KÖVÁRY, 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 TARÁNEK, 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]

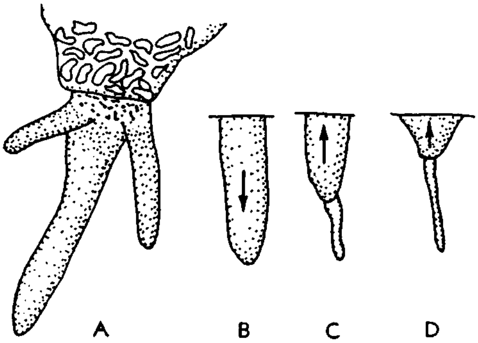

FIG. 9. Hyalospheniidae; *A-D,* successive stages in pseudopodial movement of *Lesquereusia spiralis* (p. *C*30-*C*31).

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-

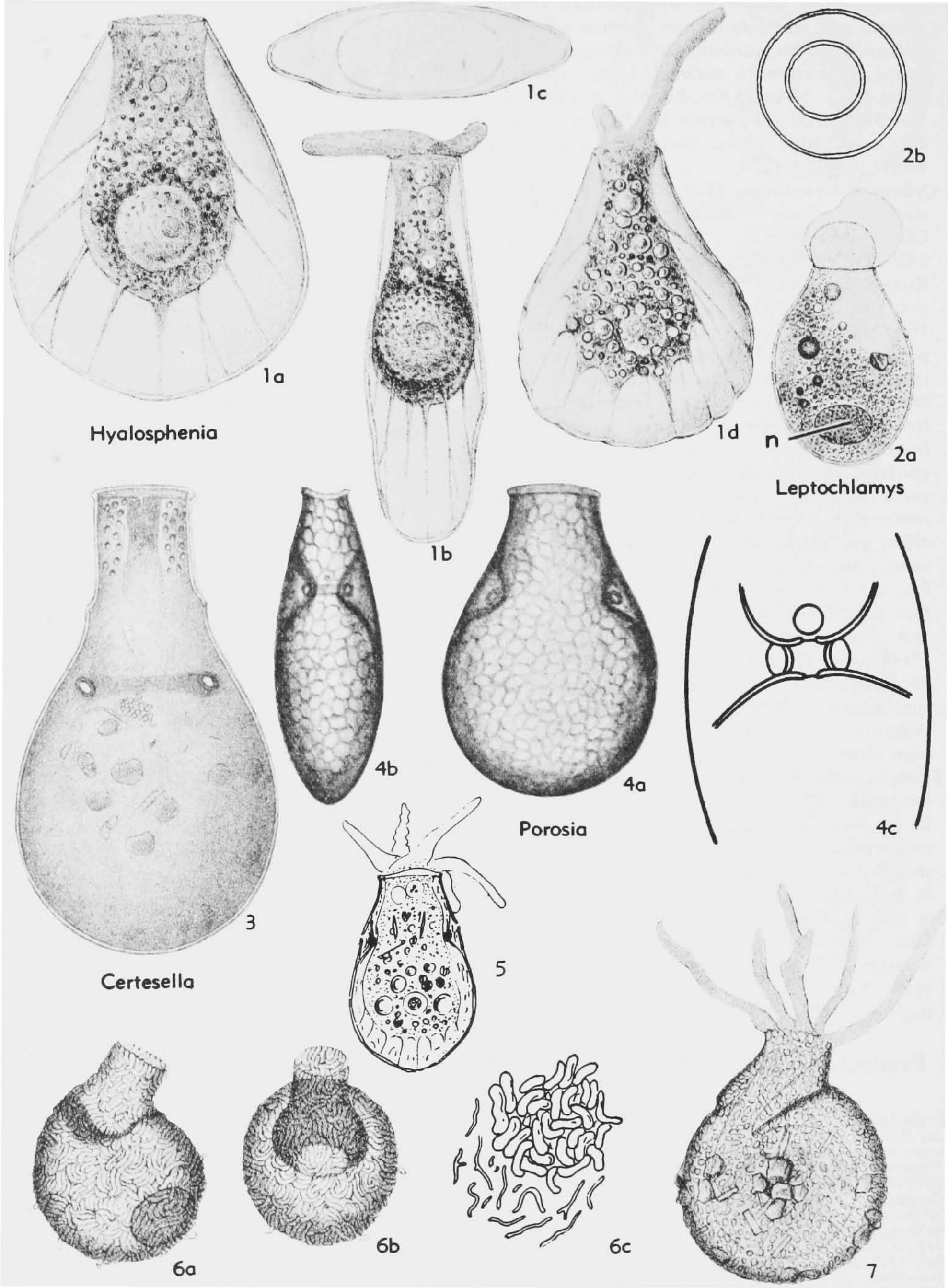

FIG. 10. Hyalospheniidae; *1, Hyalosphenia; 2, Leptochlamys; 3, Certesella; 4,5, Porosia; 6,7, Lesquereusia* (p. C27-C32).

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).

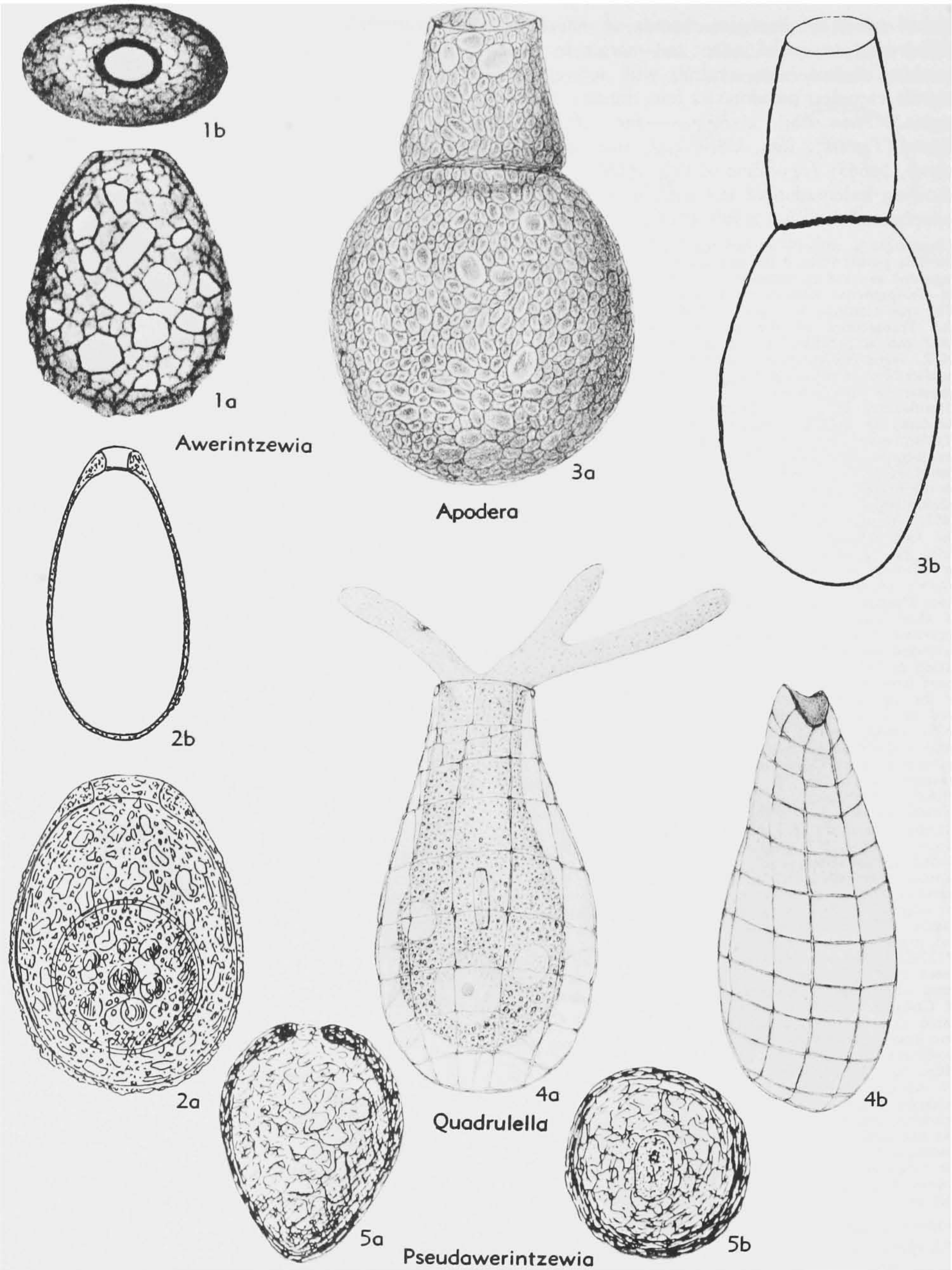

FIG. 11. Hyalospheniidae; *1,2, Awerintzewia; 3, Apodera; 4, Quadrulella; 5, Pseudawerintzewia* (p. *C*29, *C*32).

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

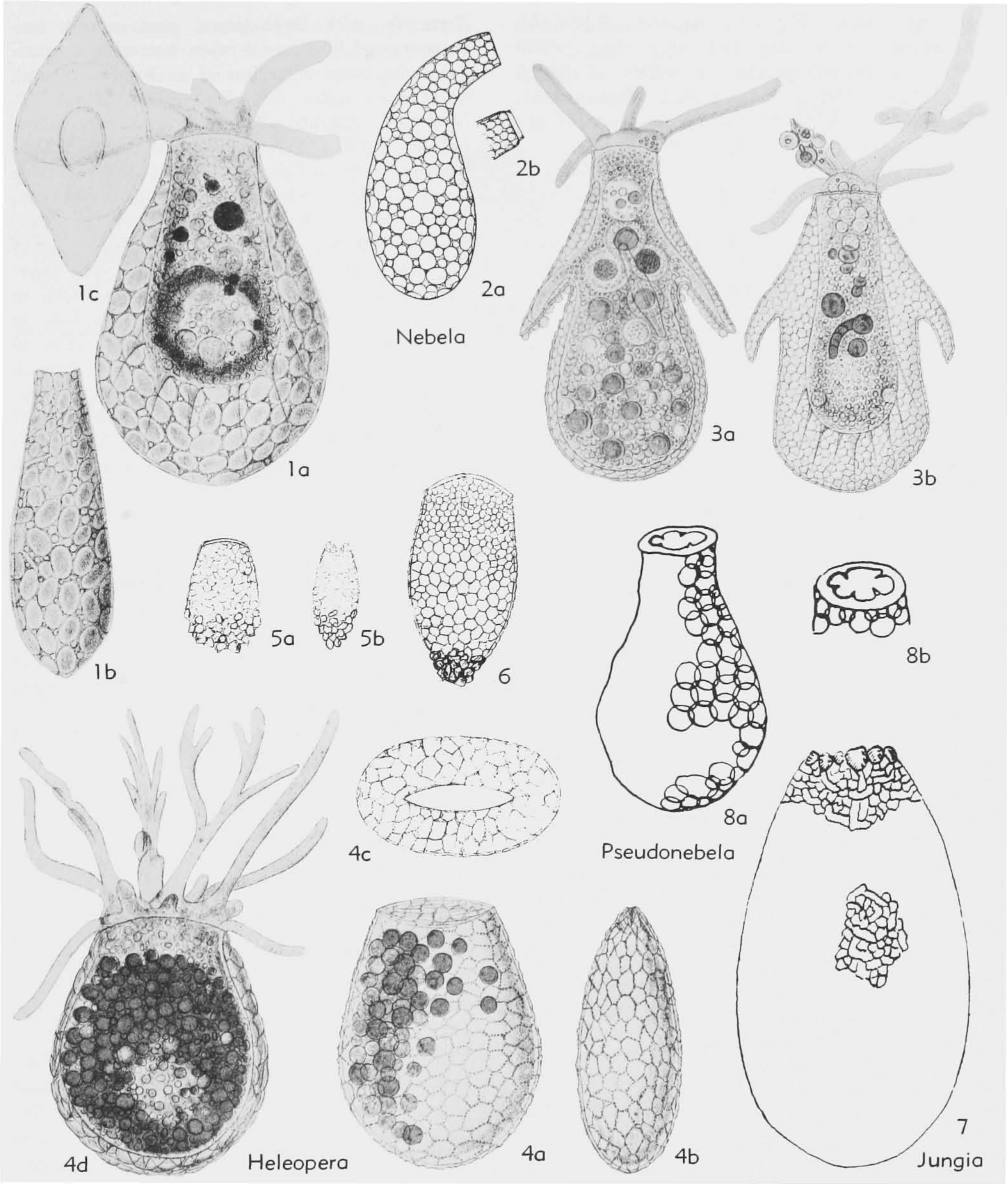

FIG. 12. Hyalospheniidae; *1-3, Nebela; 4-6, Heleopera; 7, Jungia; 8, Pseudonebela* (p. *C*29, *C*32).

[**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,

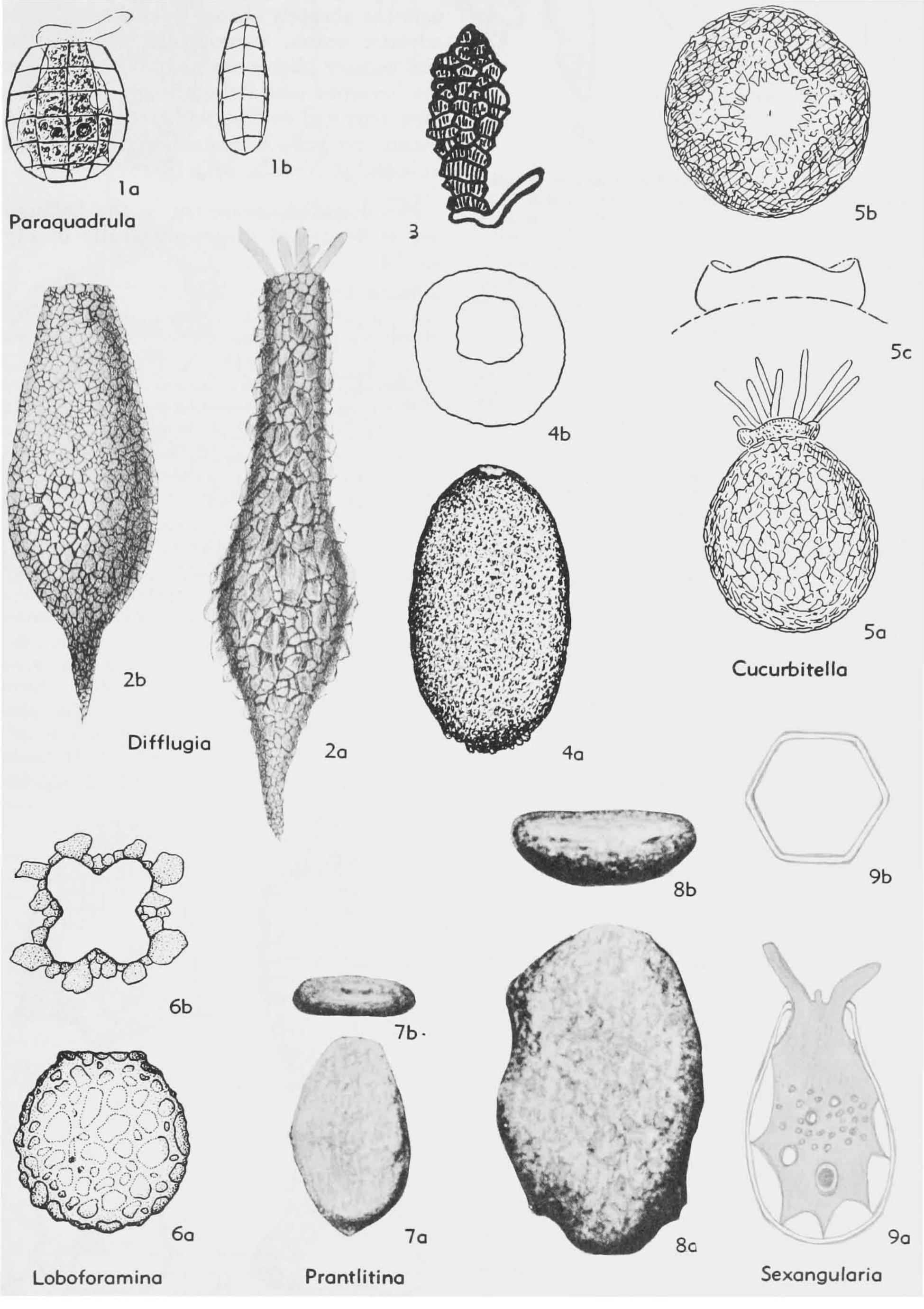

FIG. 13. Paraquadrulidae; *1, Paraquadrula;* Difflugiidae; *2-4, Difflugia; 5, Cucurbitella; 6, Loboforamina; 7,8, Prantlitina; 9, Sexangularia* (p. C34-C37).

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

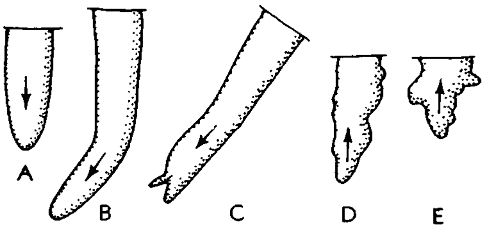

Fig. 14. Diagrams indicating the nature of pseudopodial movement in *Difflugia oviformis,* Rec. (entire animal not shown, arrows marking direction of movement); *A,B,* advance of lobose pseudopodium; *C,* bifurcating pseudopodium; *D,E,* retraction of pseudopodium showing undulatory margin, loss of rigidity,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

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}Difflugınae 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*

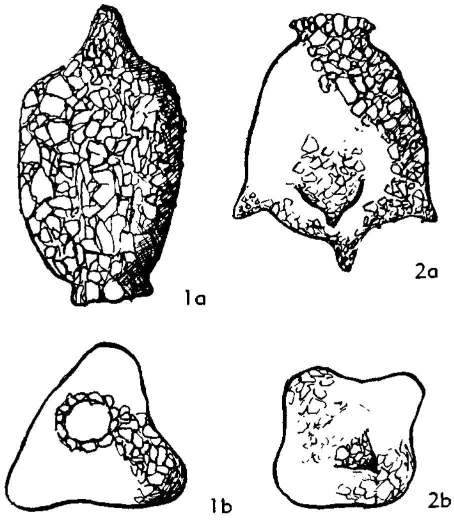

Fig. 15. Difflugiidae; *1,2, Difflugia* (p. C34-C35).

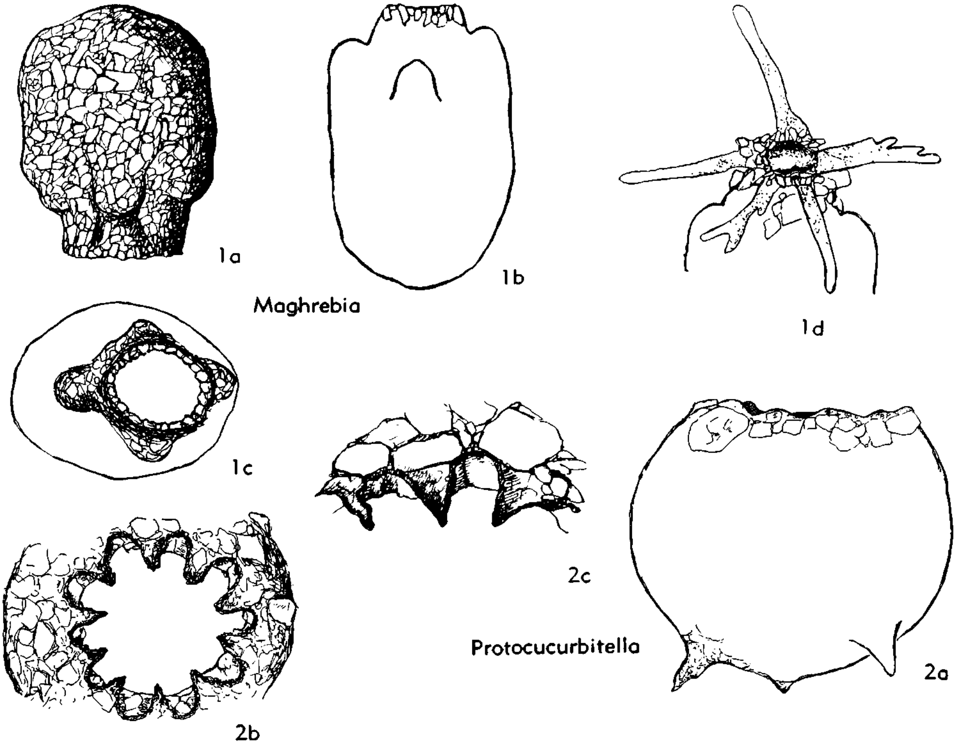

FIG. 16. Difflugiidae; *1, Maghrebia; 2, Protocucurbitella* (p. *C*36).

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*

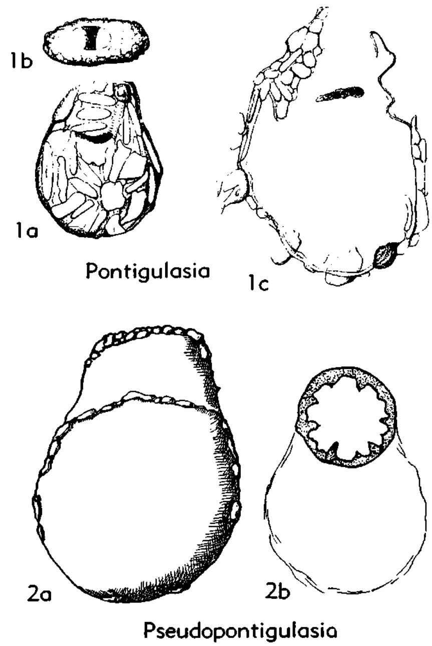

Fig. 17. Difflugiidae; *1, Pontigulasia; 2, Pseudopontigulasia* (p. C36).

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).

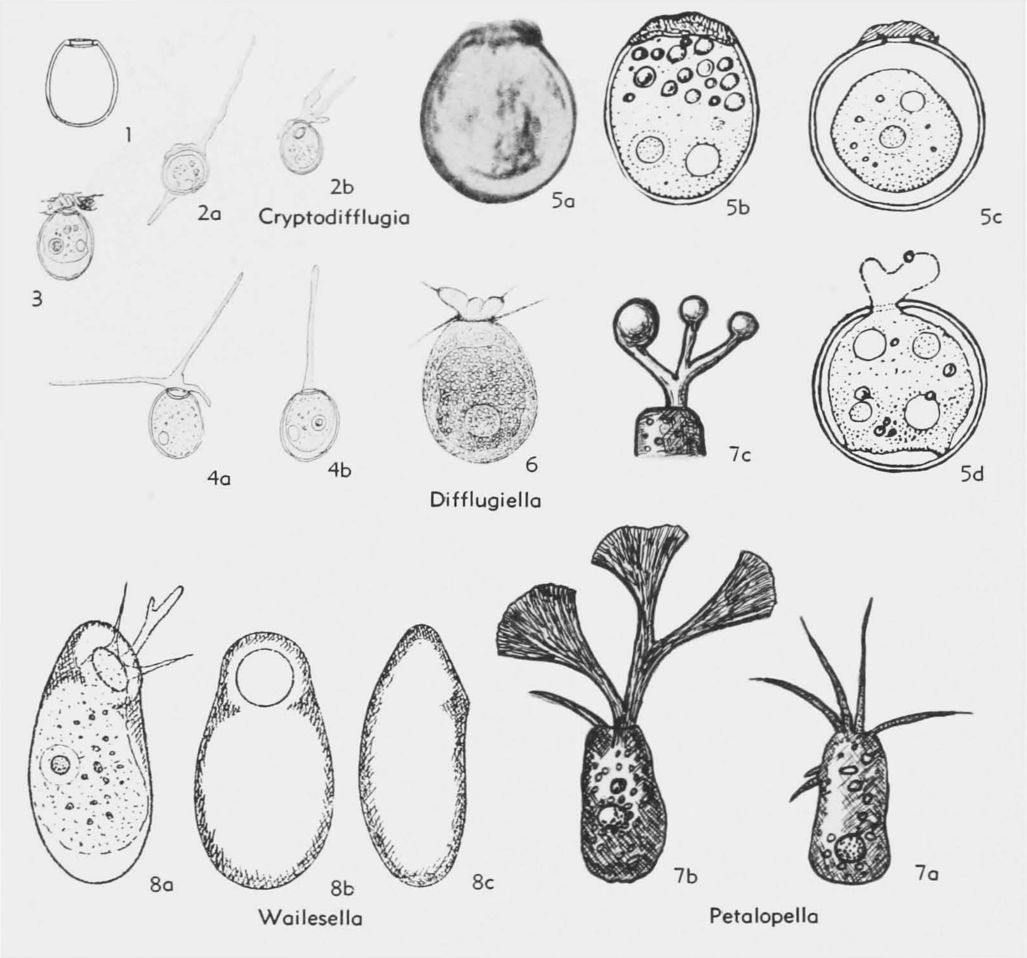

FIG. 18. Cryptodifflugiidae; *1-5, Cryptodifflugia; 6, Difflugiella; 7, Petalopella; 8, Wailesella* (p. *C37-C38*).

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,*

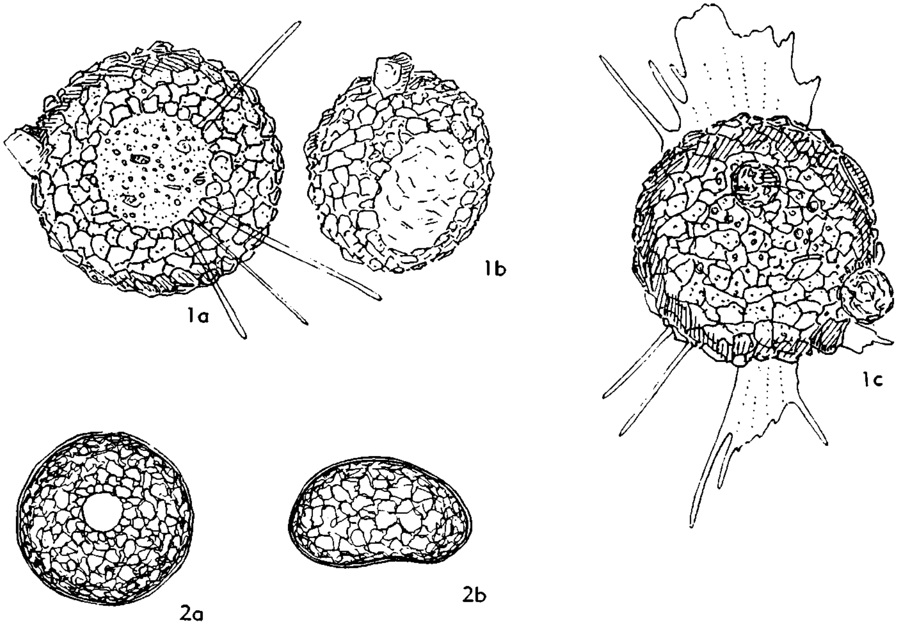

Fig. 19. Phryganellidae; *1,2, Phryganella* (p. C38-C39).

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-

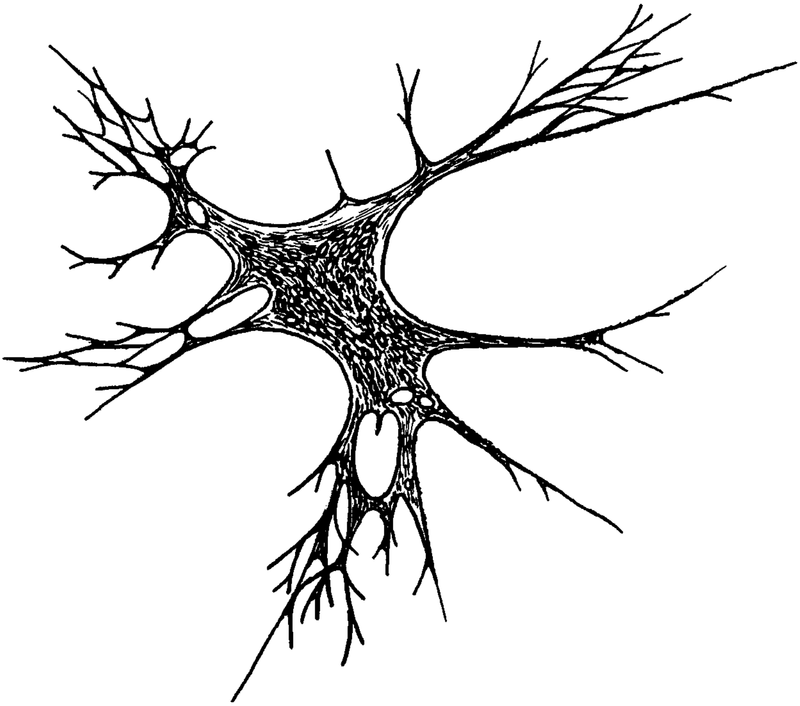

FIG. 20. Penardiidae; *Penardia* (p. *C*40).

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

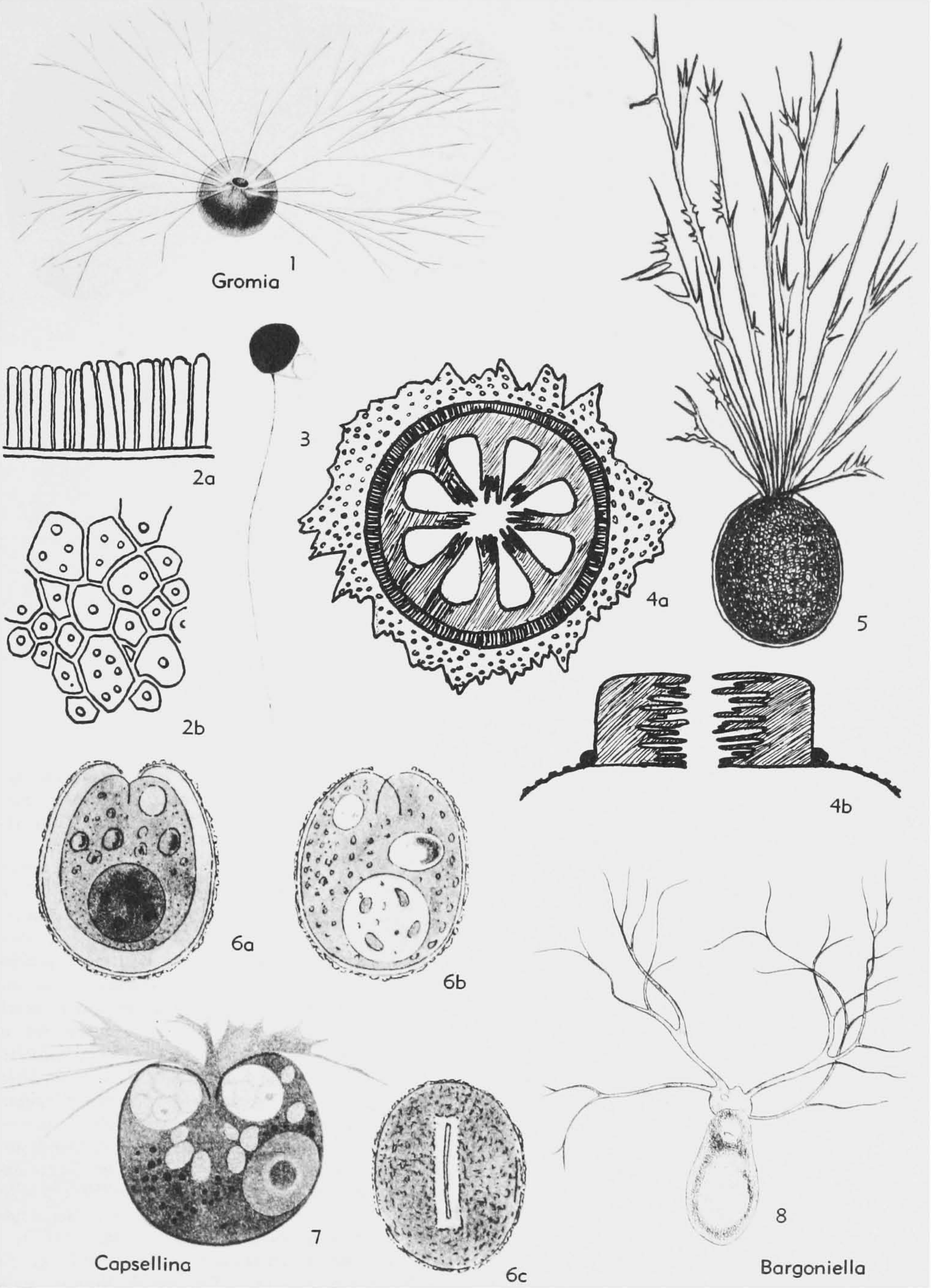

Fig. 21. Gromiidae; *1-5, Gromia; 6,7, Capsellina; 8, Bargoniella* (p. C40-C42).

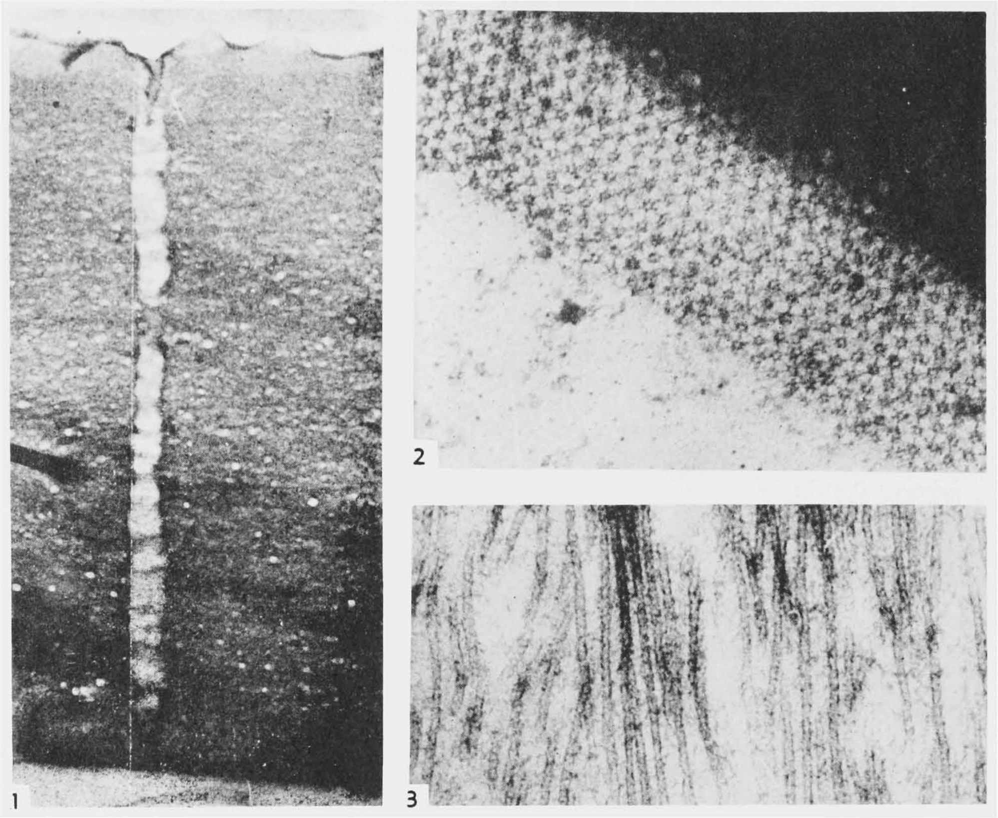

FIG. 22. Gromiidae; *1-3, Gromia oviformis,* electron micrographs (p. *C*40).

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

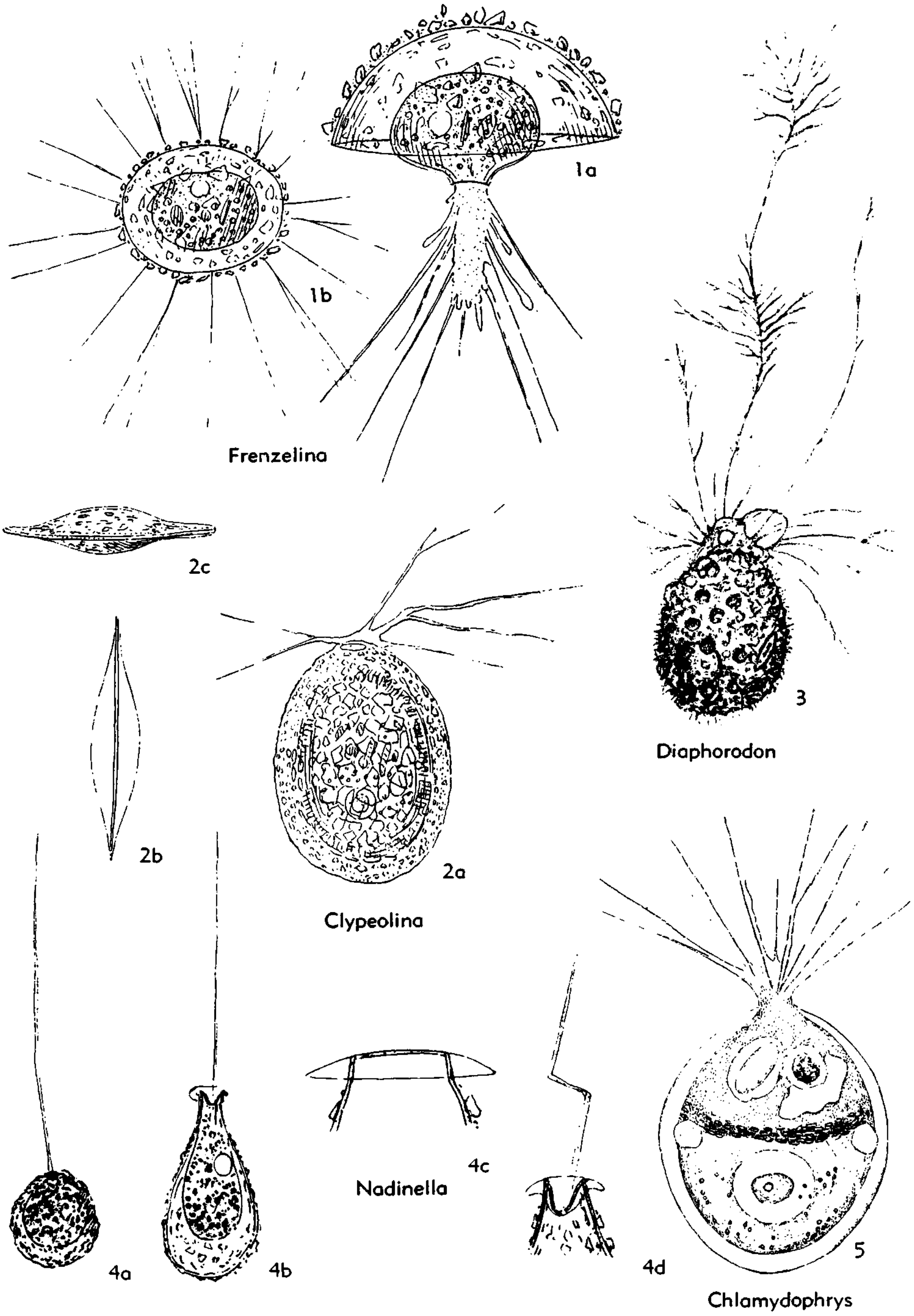

FIG. 23. Gromiidae; *1, Frenzelina; 2, Clypeolina; 3, Diaphorodon; 4, Nadinella; 5, Chlamydophrys* (p. C42-C46).

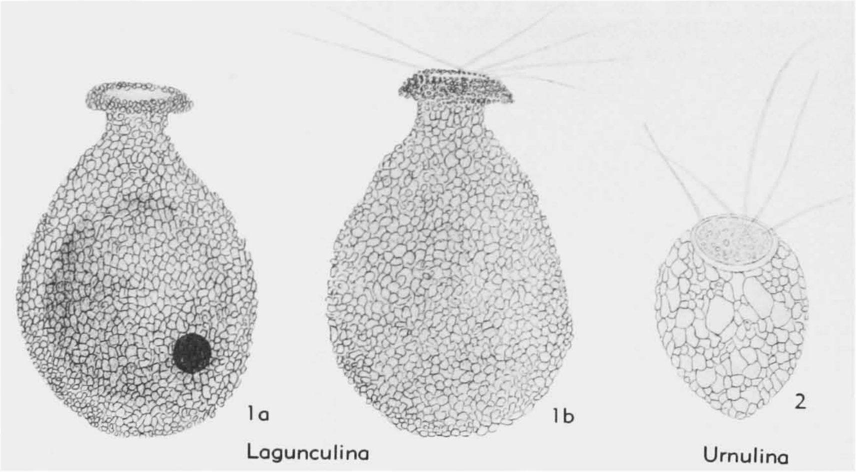

FIG. 24. Gromiidae; *1, Lagunculina; 2, Urnulina* (p. C44, C46-C47).

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-

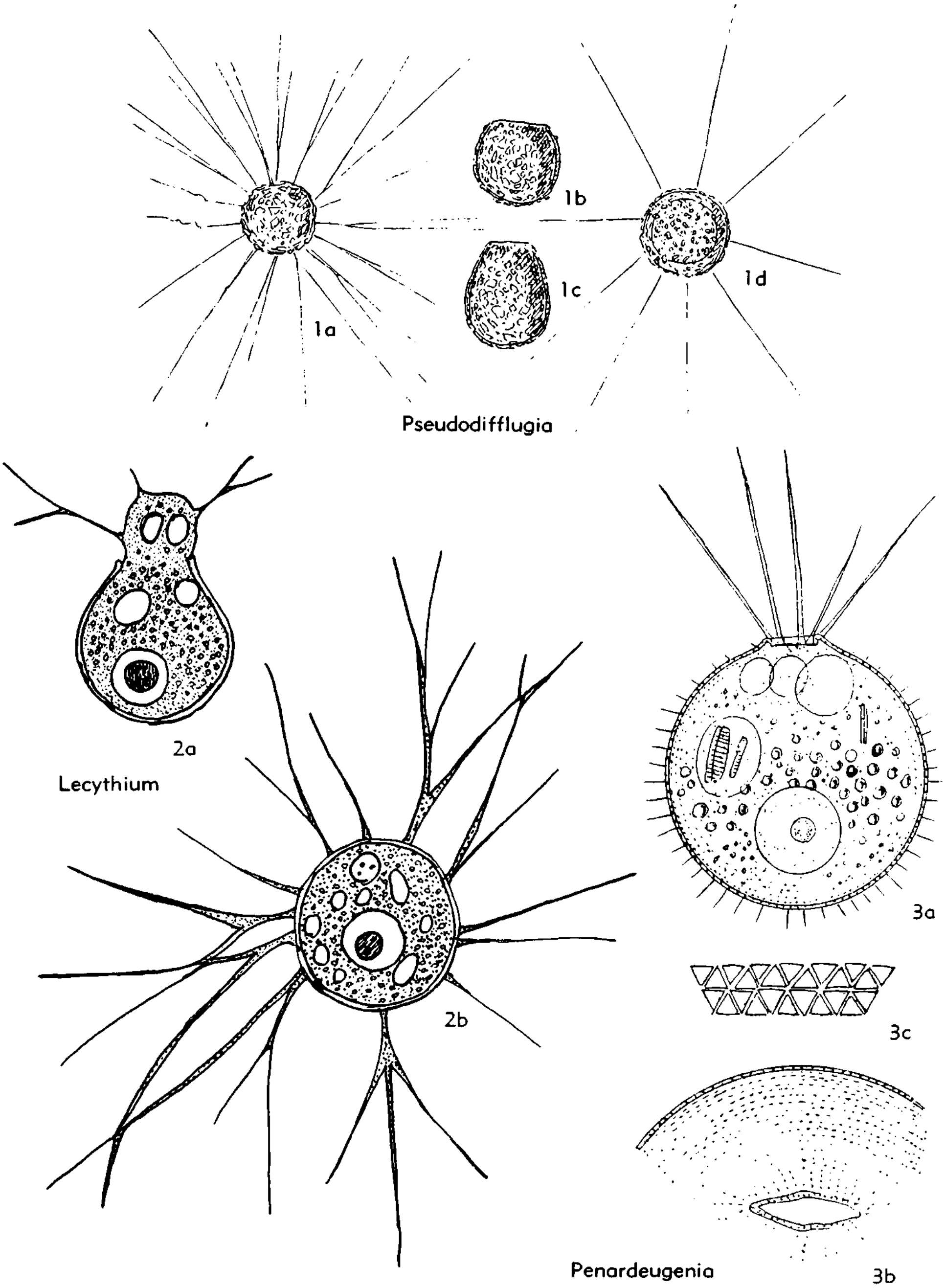

Fig. 25. Gromiidae; *1, Pseudodifflugia; 2, Lecythium; 3, Penardeugenia* (p. C44-C46).

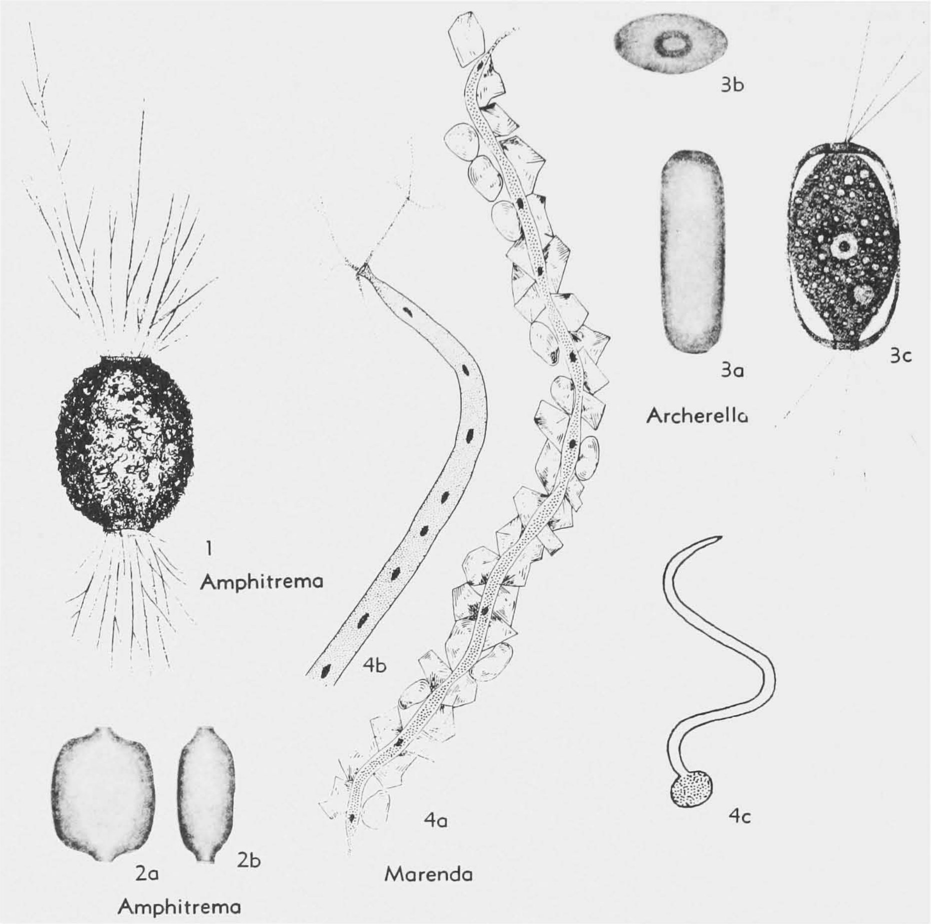

FIG. 26. Amphitrematidae; *1, 2, Amphitrema; 3, Archerella; 4, Marenda* (p. C47).

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.)*; =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.

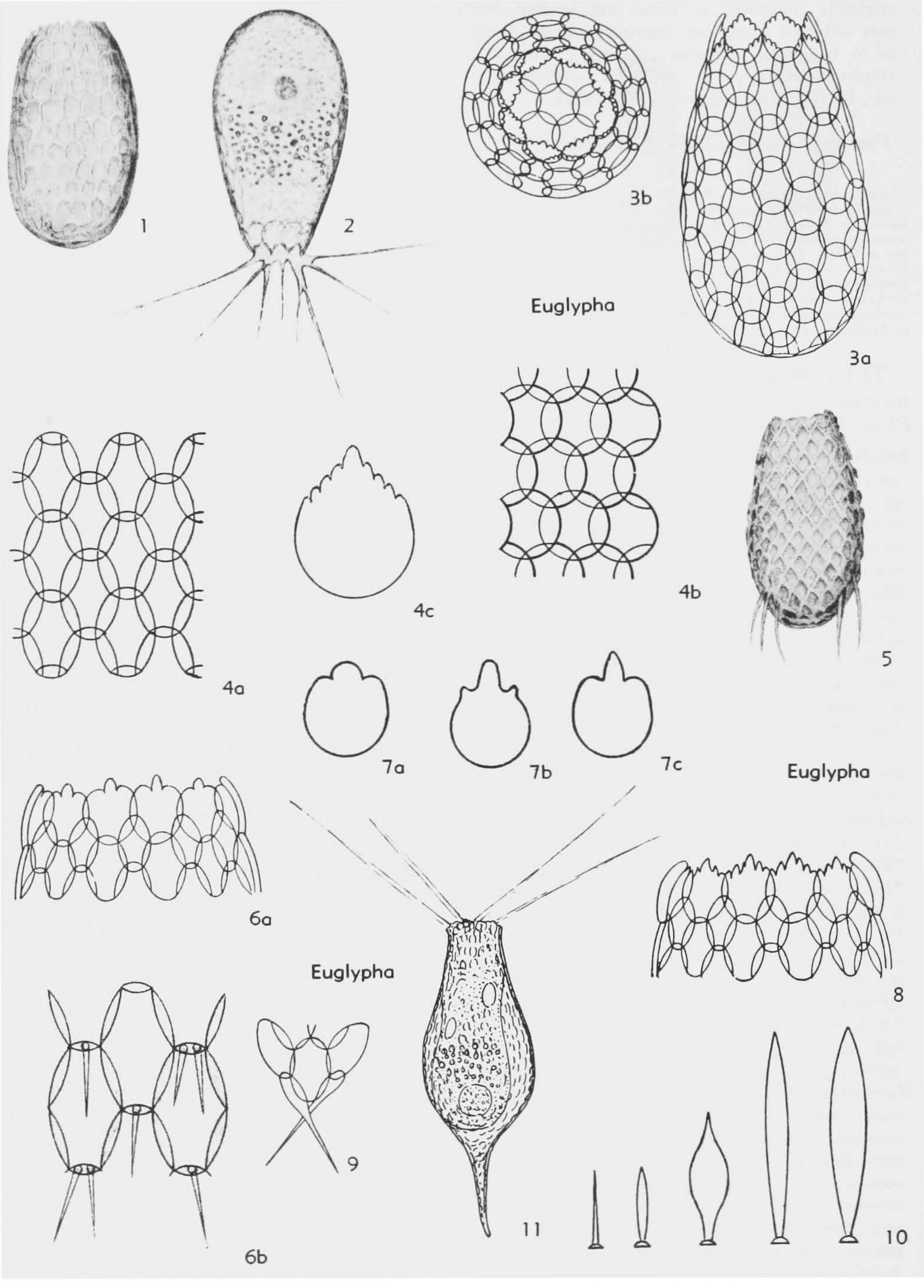

FIG. 27. Euglyphidae (Euglyphinae; *1-10, Euglypha*) (p. C47-C49).

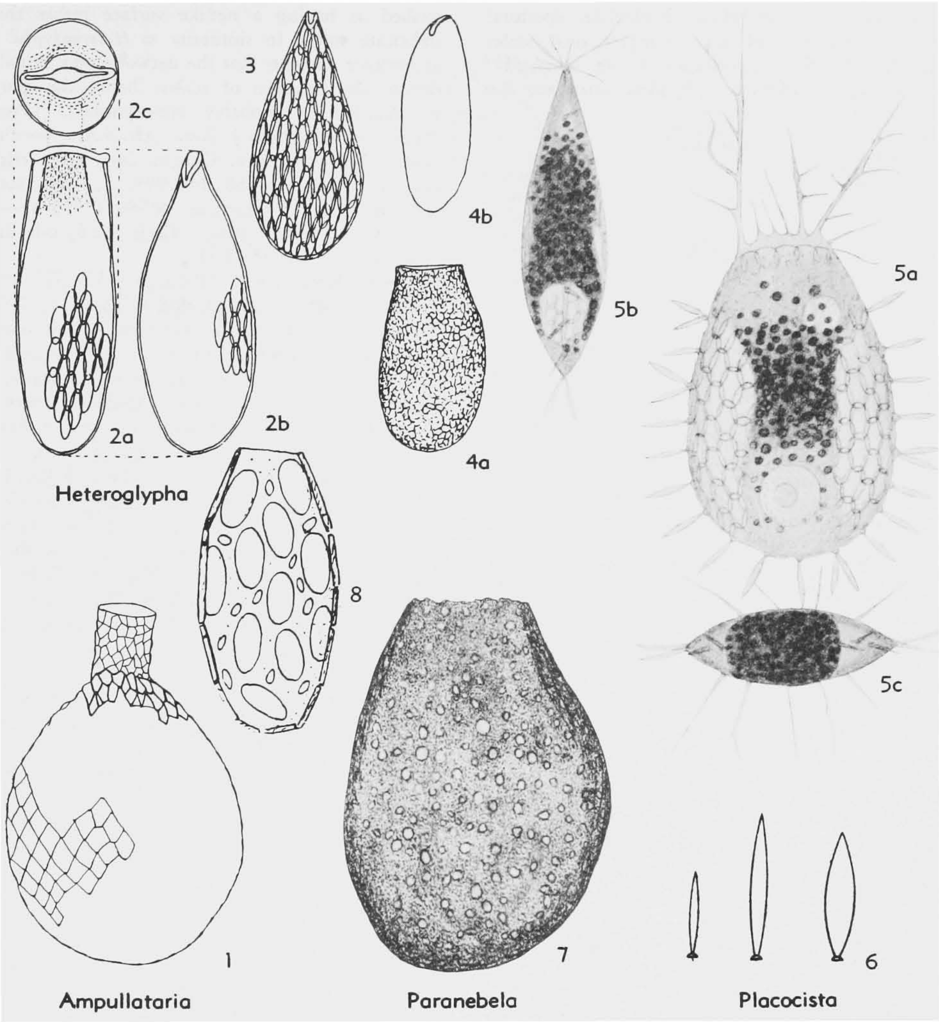

FIG. 28. Euglyphidae (Euglyphinae; *1, Ampullataria; 2-4, Heteroglypha; 5, 6, Placocista; 7, 8, Paranebela*) (p. *C*49-*C*50).

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).

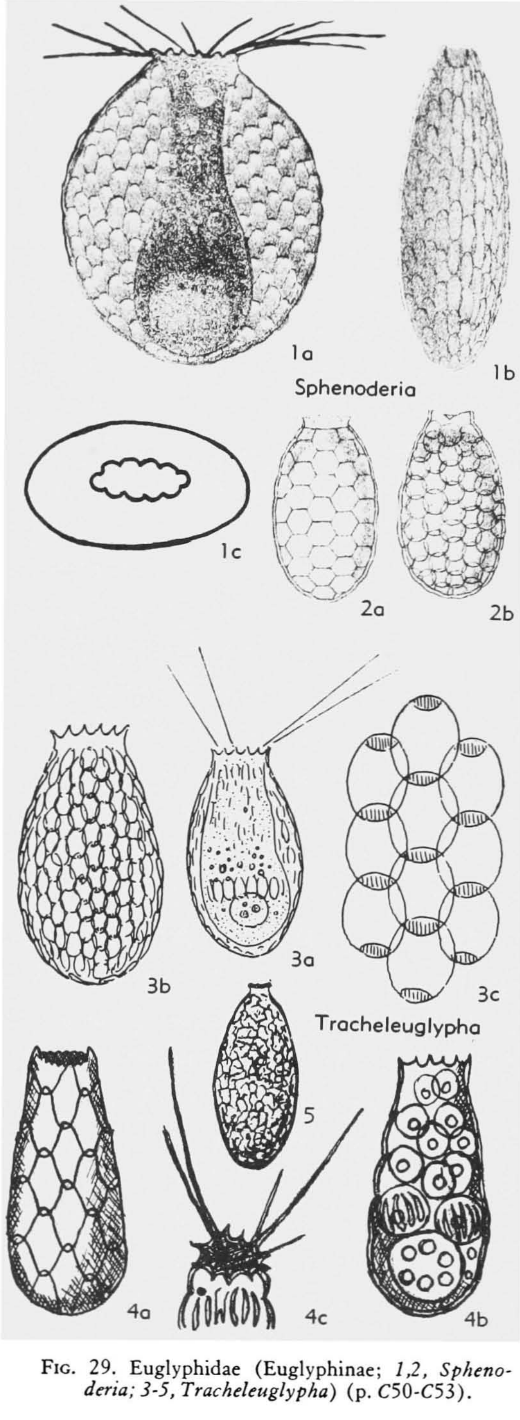

Fig. 29. Euglyphidae (Euglyphinae; *1,2, Sphenoderia; 3-5, Tracheleuglypha*) (p. C50-C53).

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

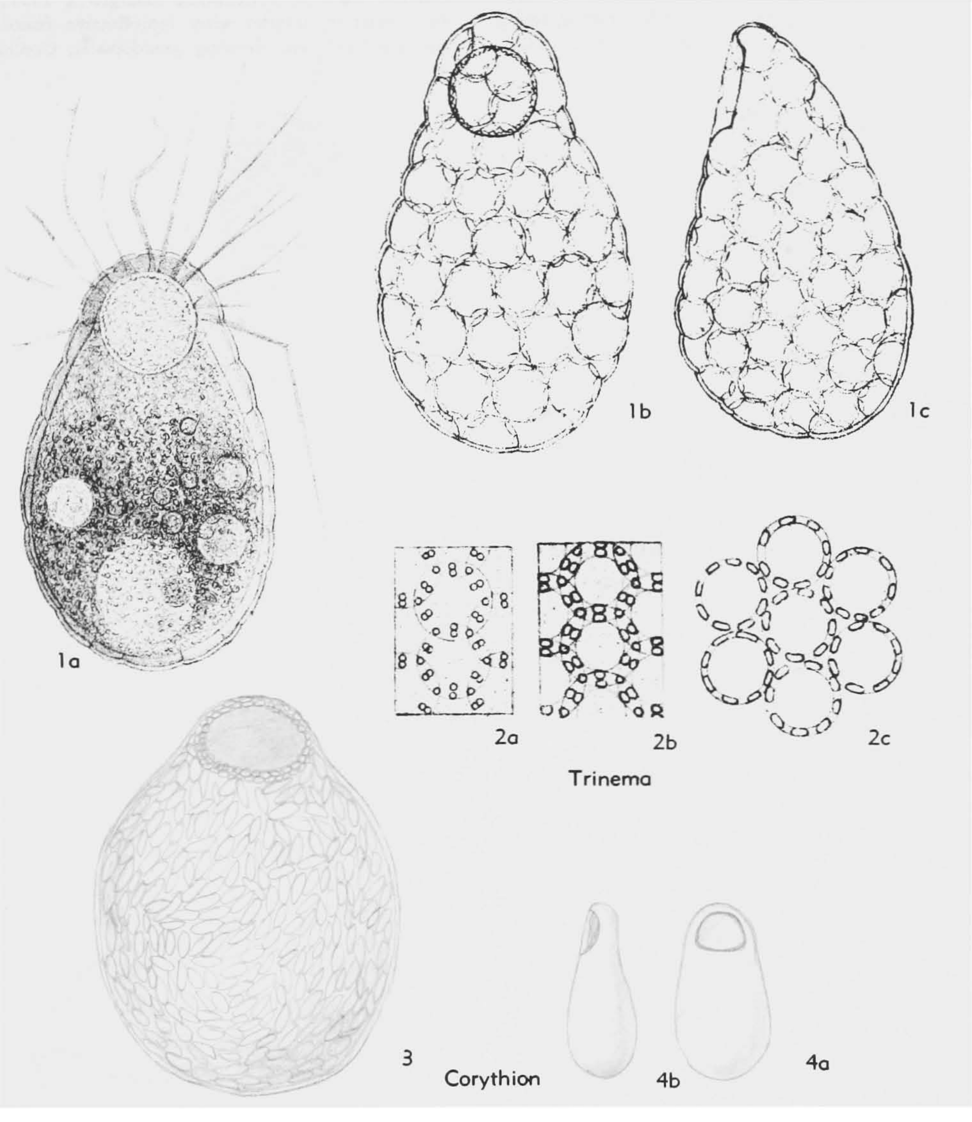

FIG. 30. Euglyphidae (Trinematinae; *1,2, Trinema; 3,4, Corythion*) (p. C53).

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.,

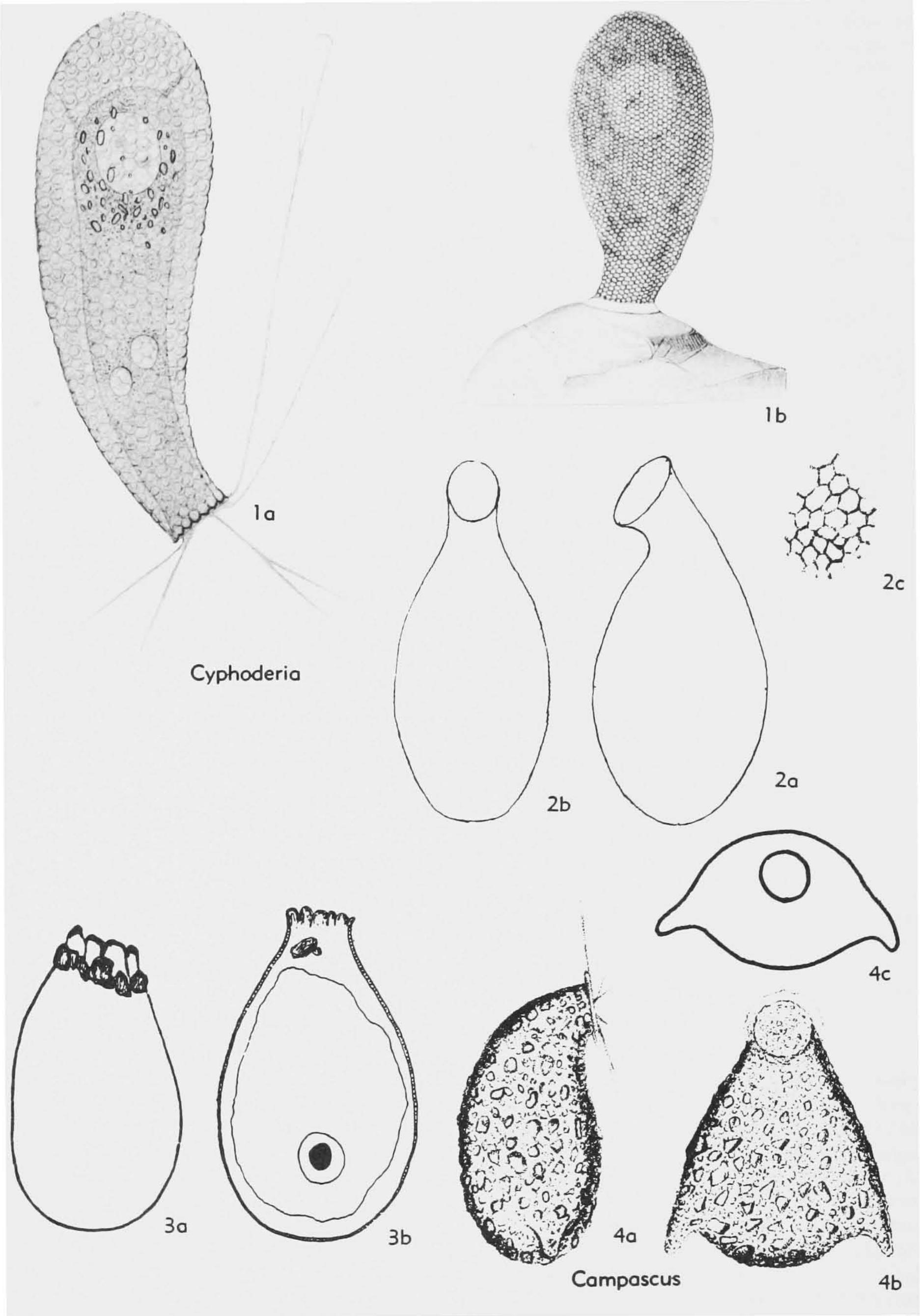

Fig. 31. Cyphoderiidae; *1-3, Cyphoderia; 4, Campascus* (p. C53-C54).

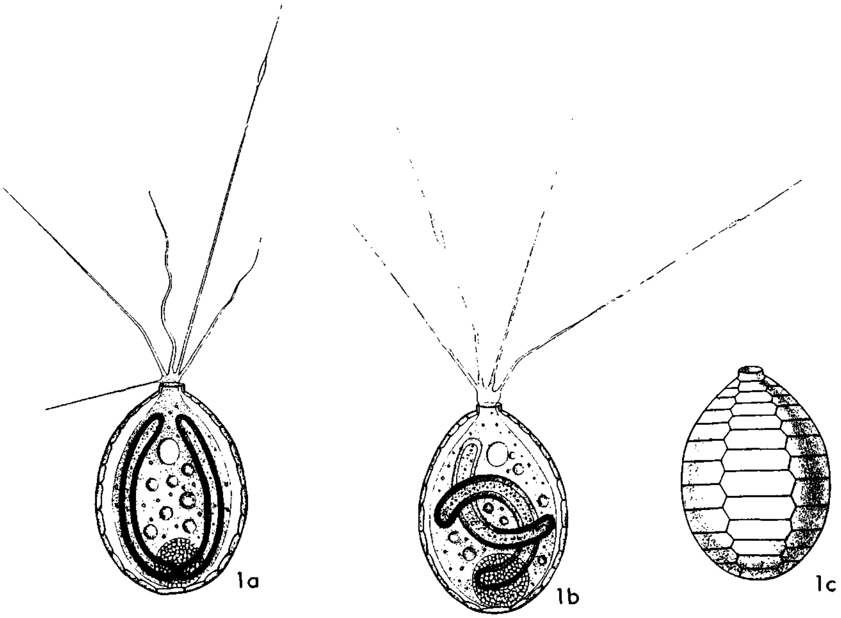

Fig. 32. Paulinellidae; *1, Paulinella* (p. C54).

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,

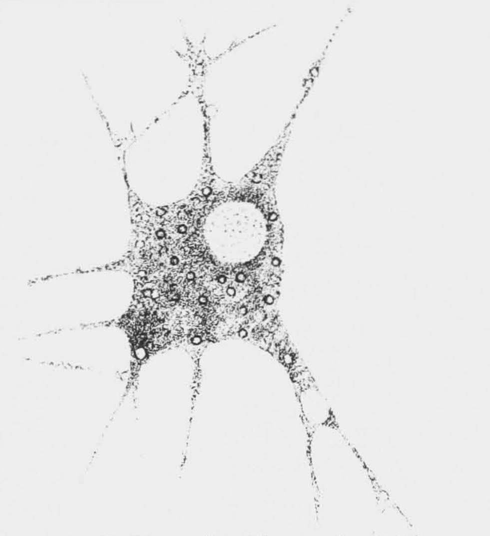

FIG. 33. Biomyxidae; *Biomyxa* (p. C54).

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

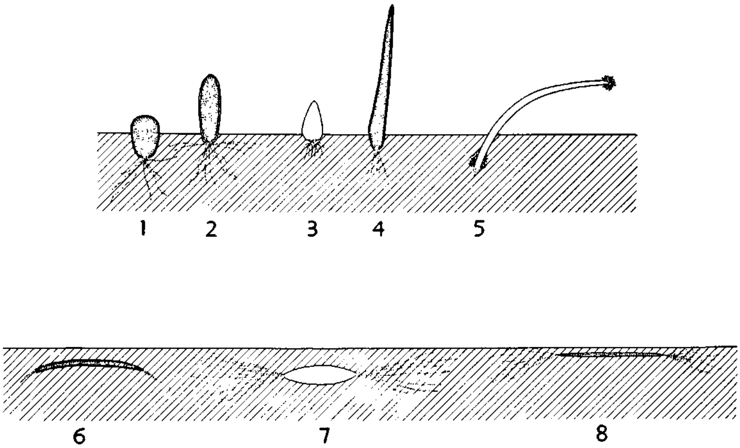

FIG. 34. Pseudopodial function in Foraminiferida.——*1-5.* Erect, rigid pseudopodia; *1,2,* Allogromiidae; *3, Hippocrepina; 4, Micrometula; 5, Bathysiphon.*——*6-8,* Prostrate, fragile, anastomosing pseudopodia; *6, Shepheardella; 7, Phainogullmia; 8, Nemogullmia* (*1379).

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.

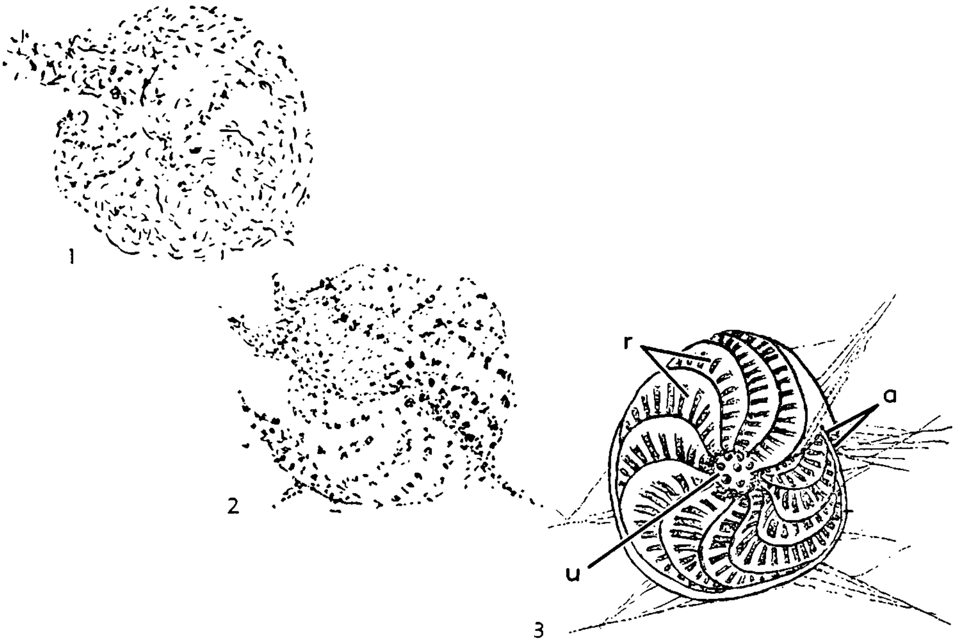

Fig. 35. Feeding cysts in *Elphidium.* Two successive feeding cysts *(1,2)* are shown with *Elphidium (3)* moving to a new location. The cysts are composed of empty diatom frustrules and xanthosomes deposited outside canal openings and along pseudopodial tracks (aperture, *a*; umbo with openings of spiral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

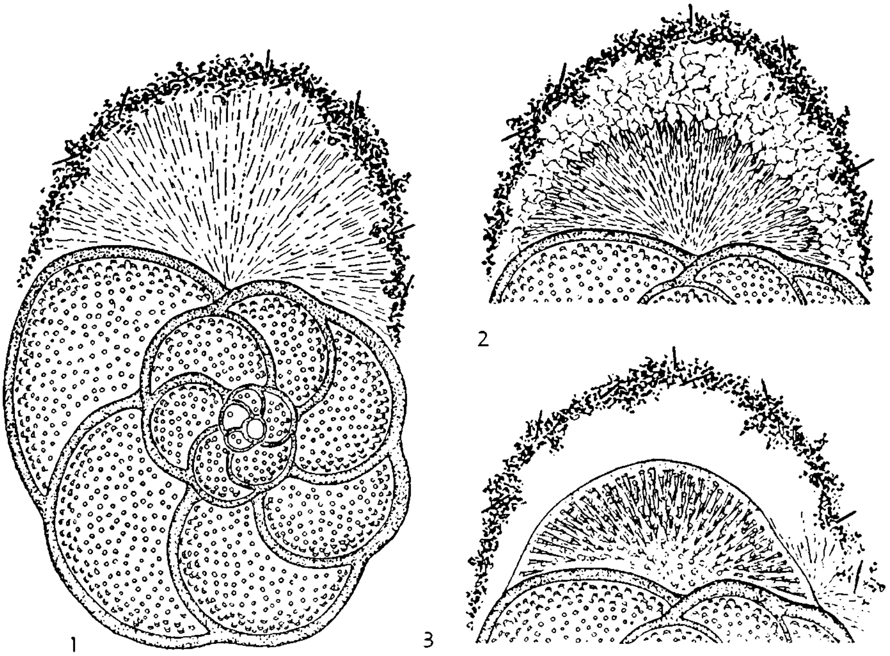

FIG. 36. Chamber formation in *Discorbinella bertheloti*; *1*, pseudopodia forming protective cyst; *2*, main pseudopodia retracted to position of future wall; *3*, formation of pseudochitinous pellicle with perforations, before calcification; all ×60 (*1109).

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

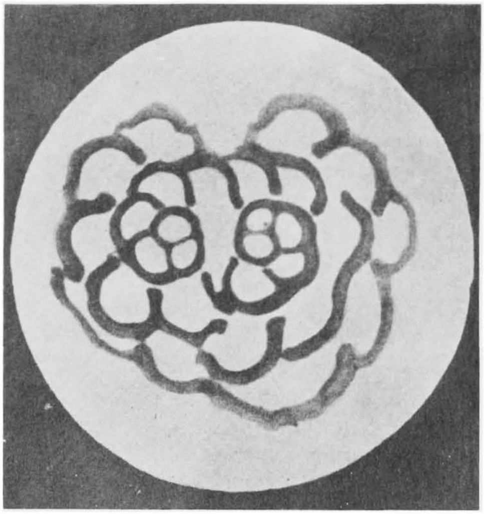

FIG. 37. Polyvalence in juvenile *Planorbulina mediterranensis*, enlarged (*1109).

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.

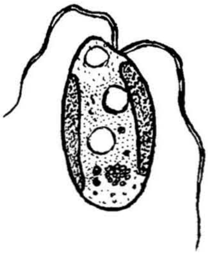

FIG. 38. *Cryptomonas schaudinni* WINTER, symbiotic zooxanthella found in *Peneroplis*, ×2,250 (*2068).

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).

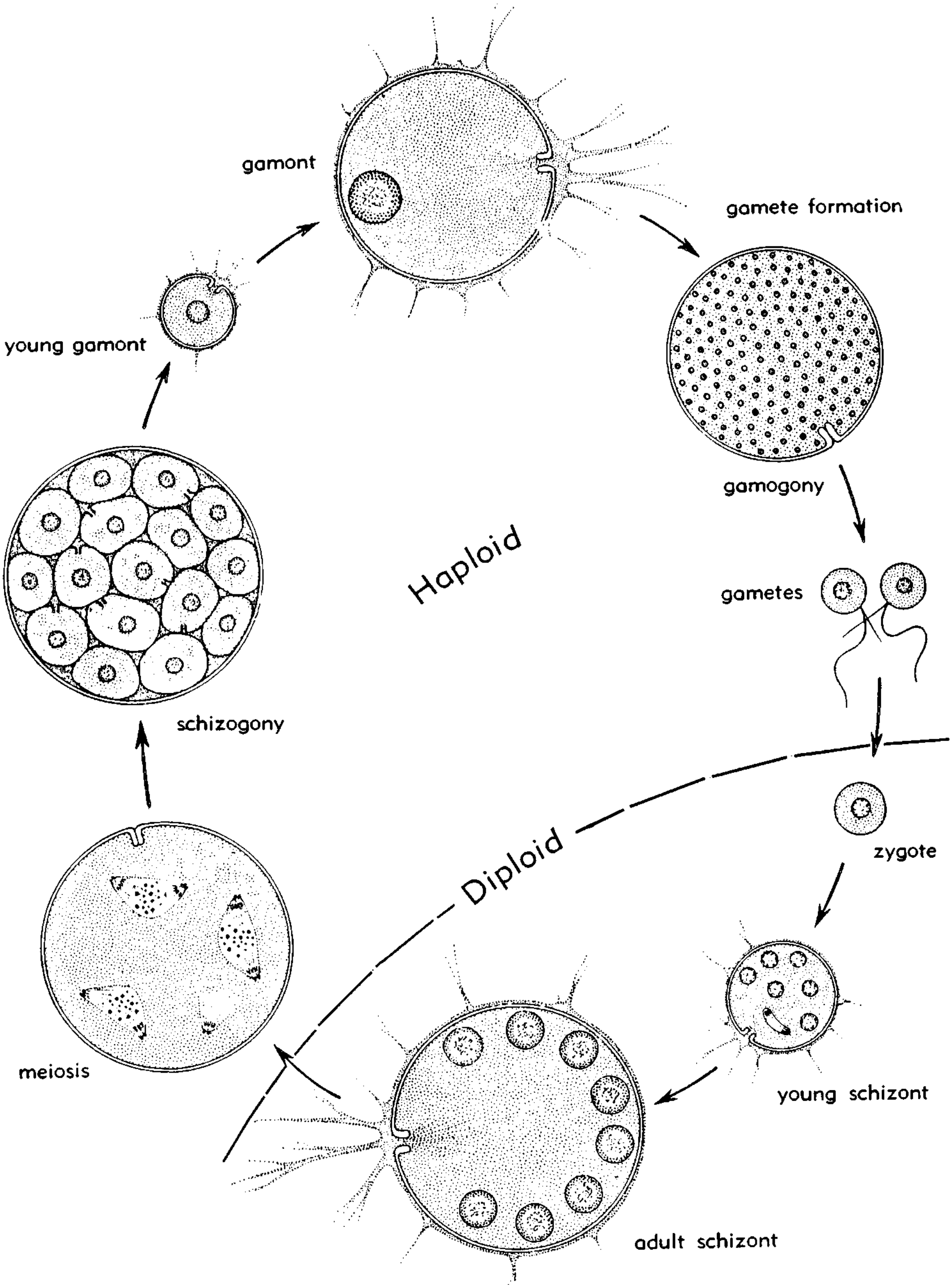

Fig. 39. Life cycle of *Myxotheca arenilega* (*821).

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

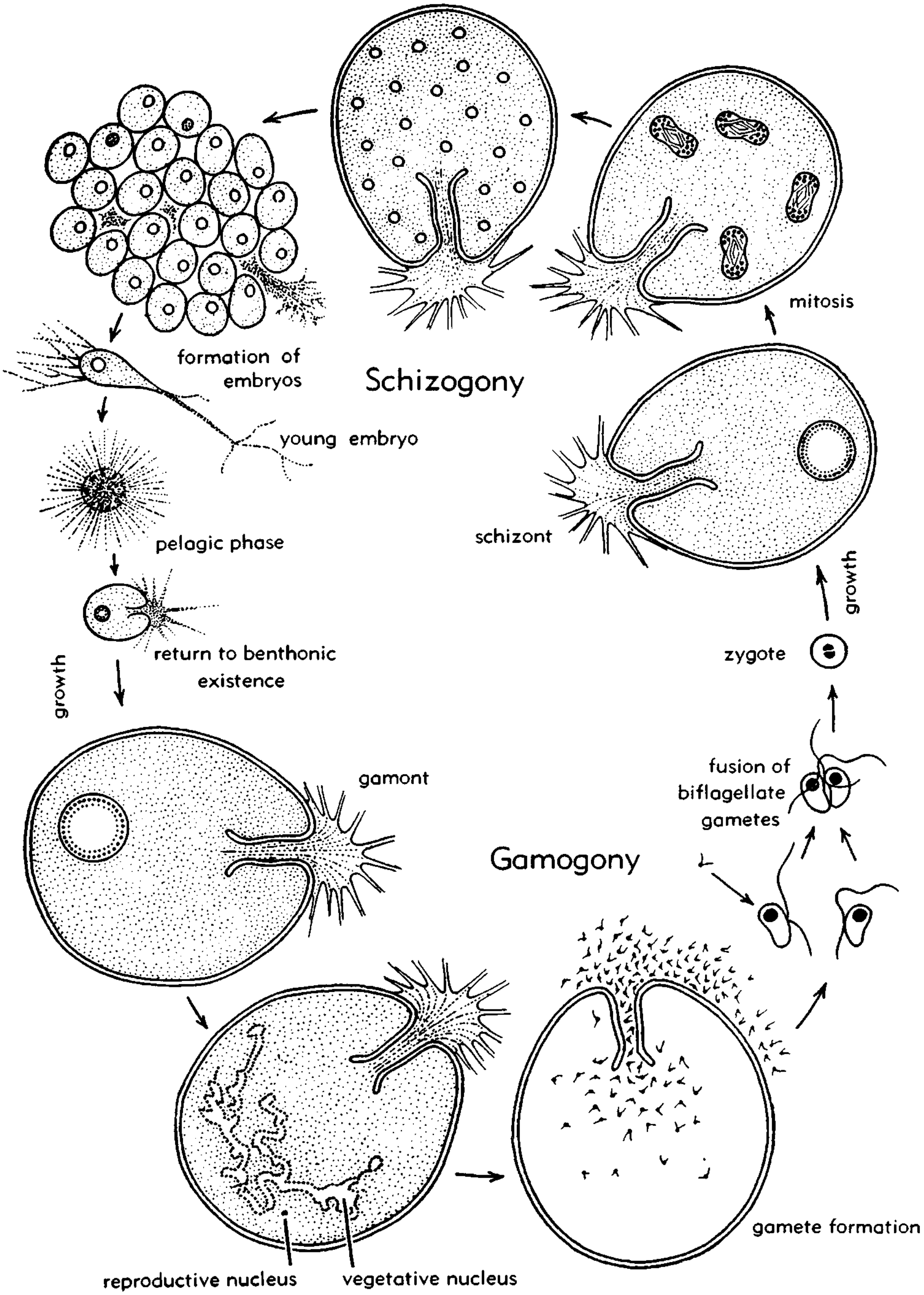

FIG. 40. Life cycle of *Iridia lucida* (*810).

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

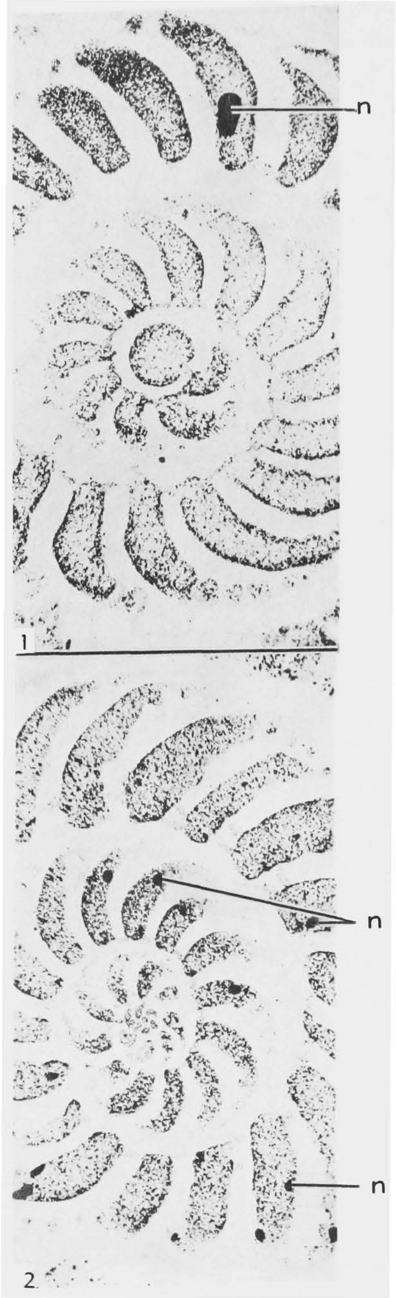

FIG. 41. Horizontal sections of *Elphidium crispum*, enlarged (*1340).——*1.* Megalospheric gamont, with large proloculus and single large nucleus (*n*).——*2.* Microspheric schizont, with minute proloculus and many nuclei (*n*).

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

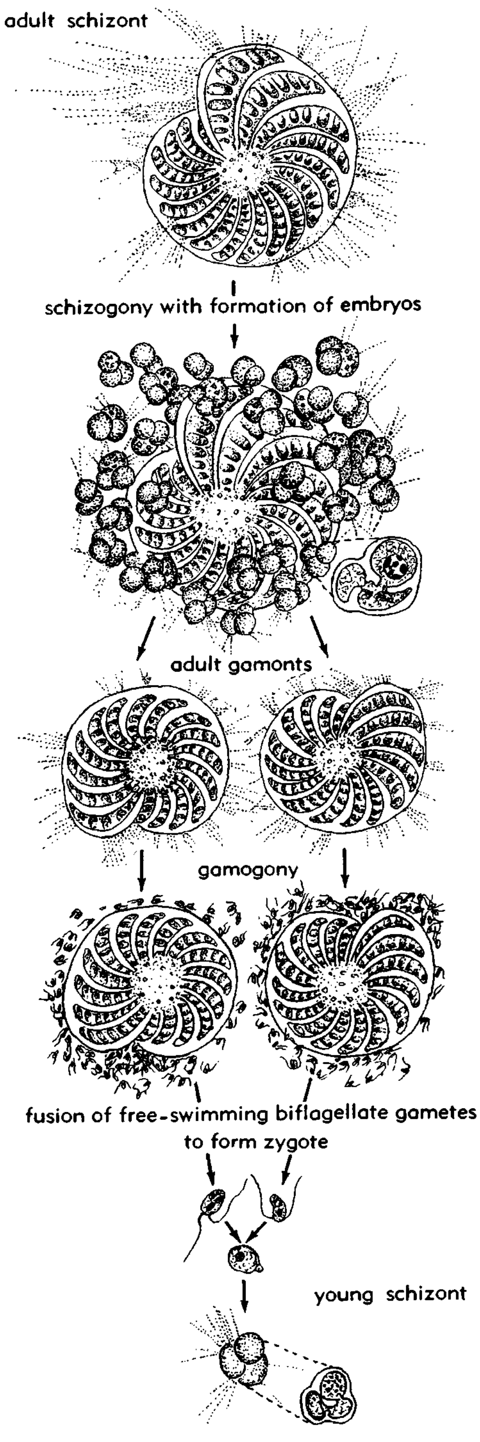

Fig. 42. Life cycle of *Elphidium crispum* (*1338).

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

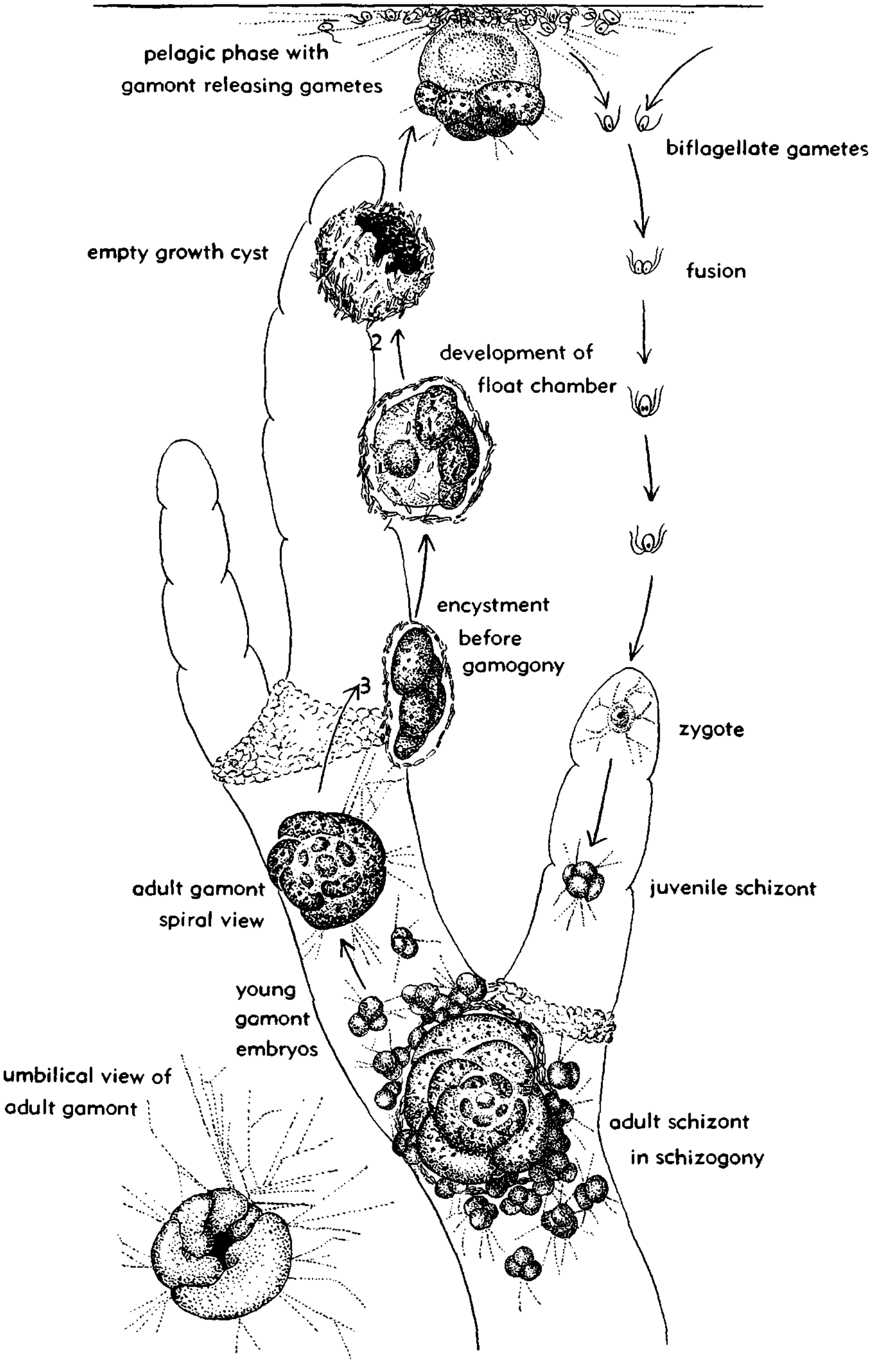

FIG. 43. Life cycle of *Tretomphalus bulloides* (*1341).

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

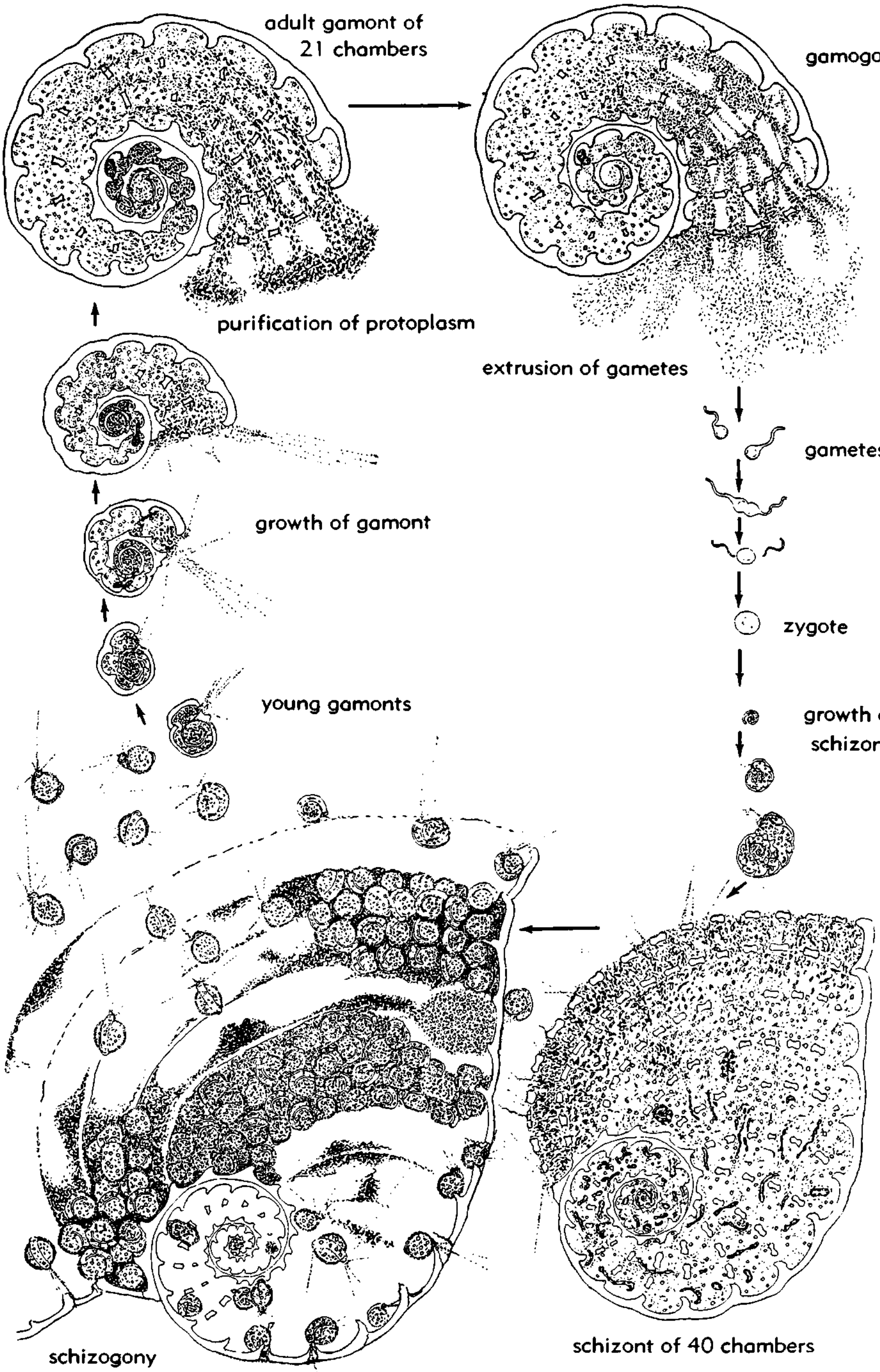

FIG. 44. Life cycle of *Peneroplis pertusus* (*2068).

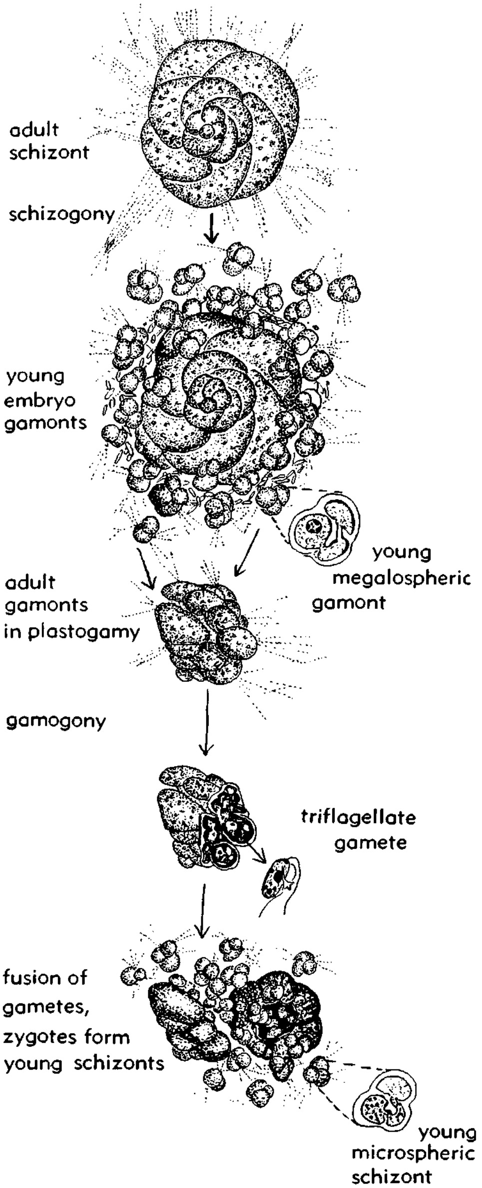

FIG. 45. Life cycle of *Glabratella patelliformis* (*1338).

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).

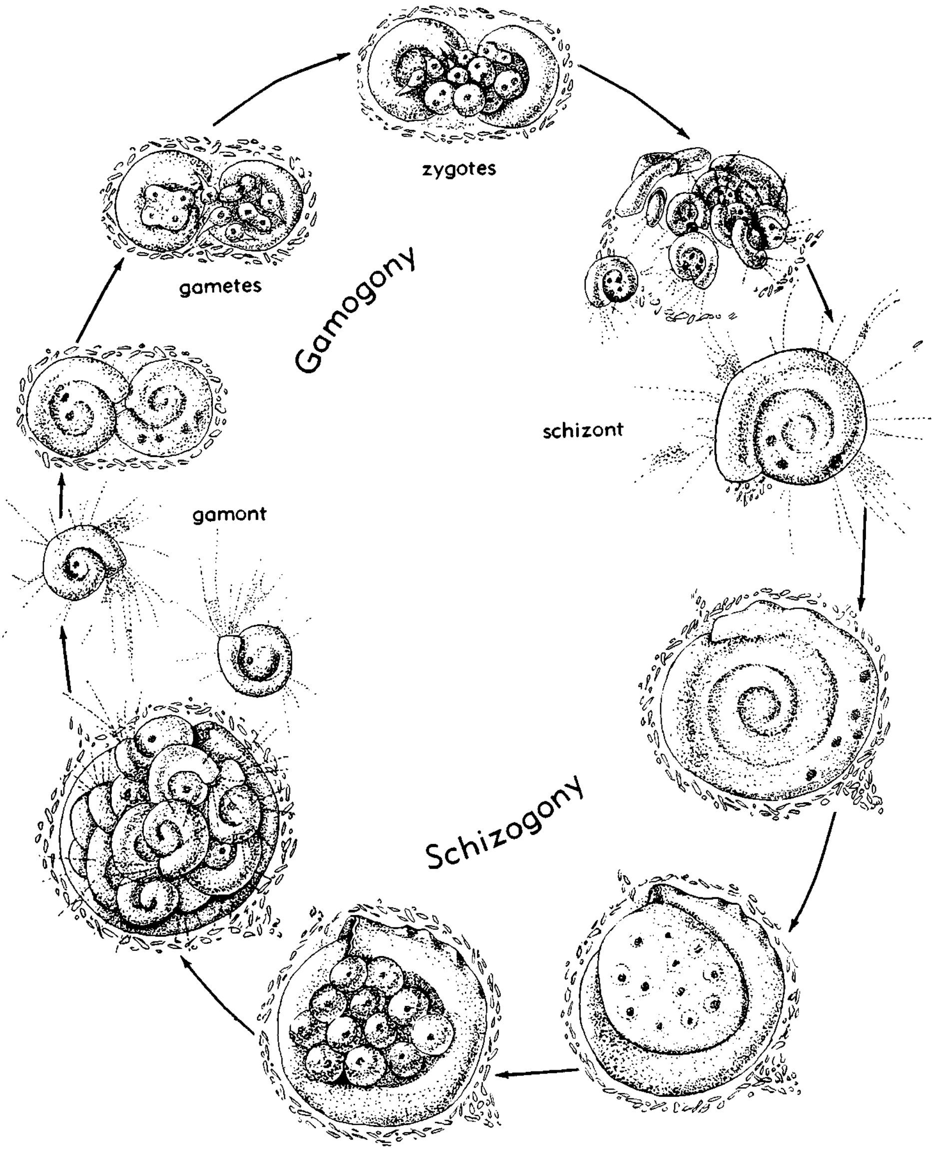

Fig. 46. Life cycle of *Spirillina vivipara* (*1337).

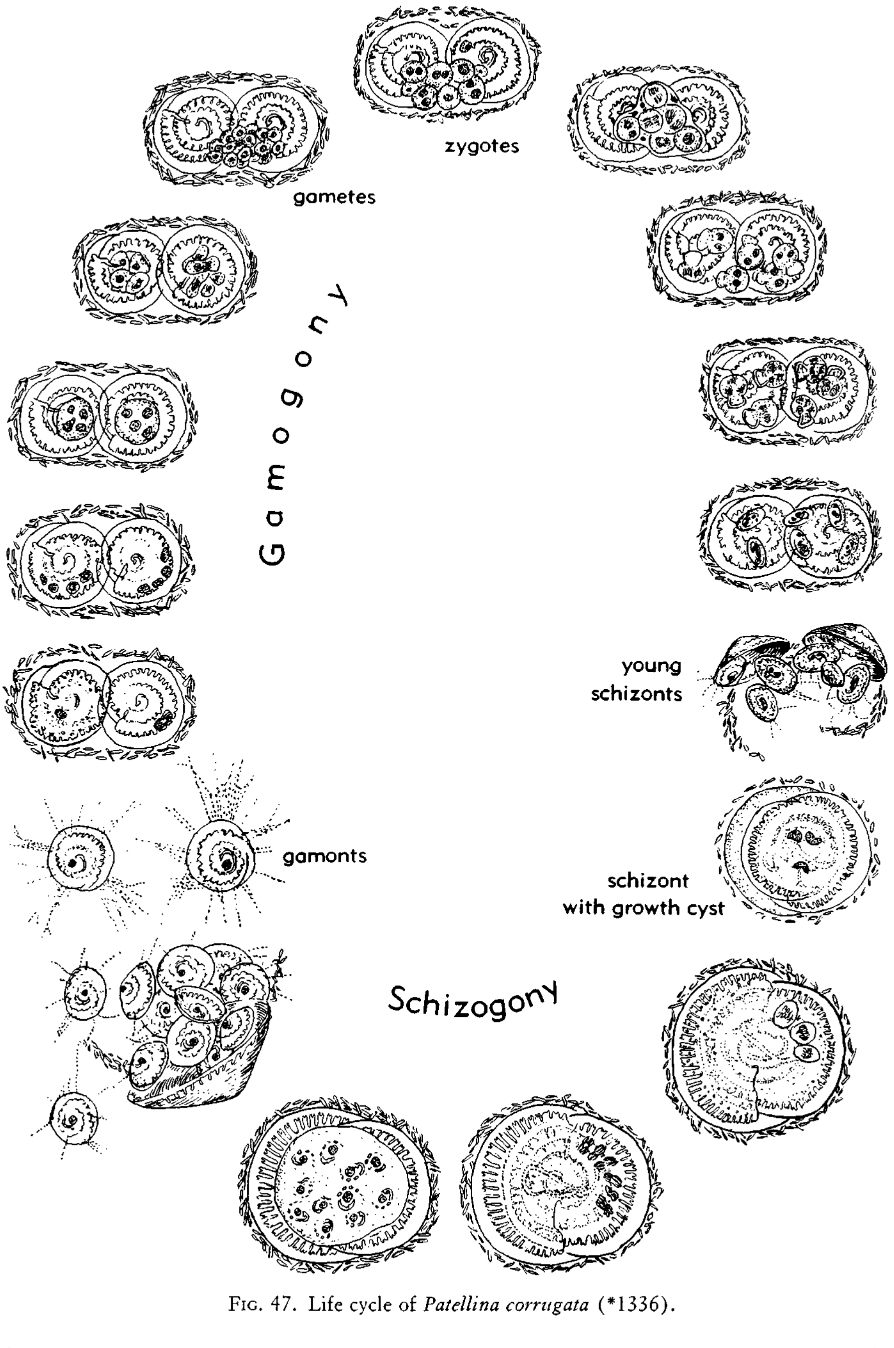

FIG. 47. Life cycle of *Patellina corrugata* (*1336).

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

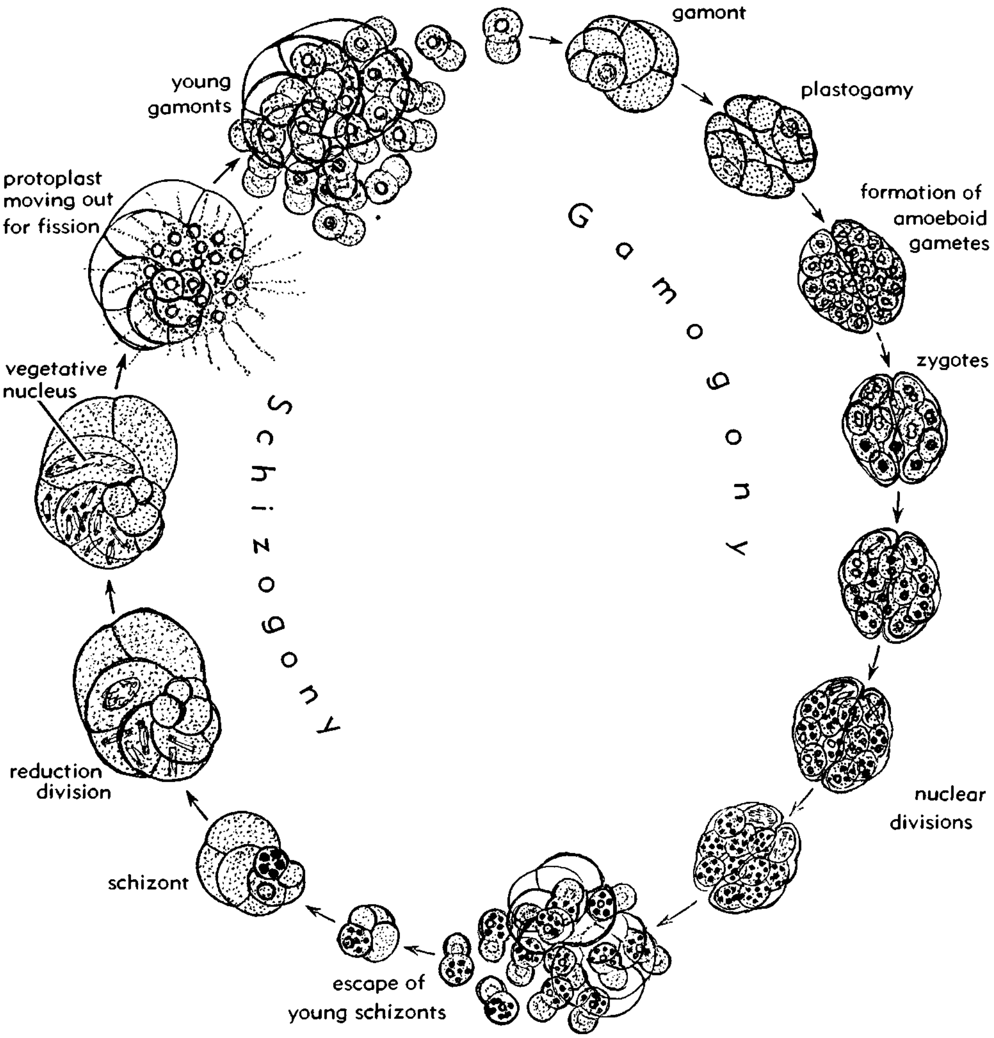

FIG. 48. Life cycle of *Rubratella intermedia* (*821).

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.

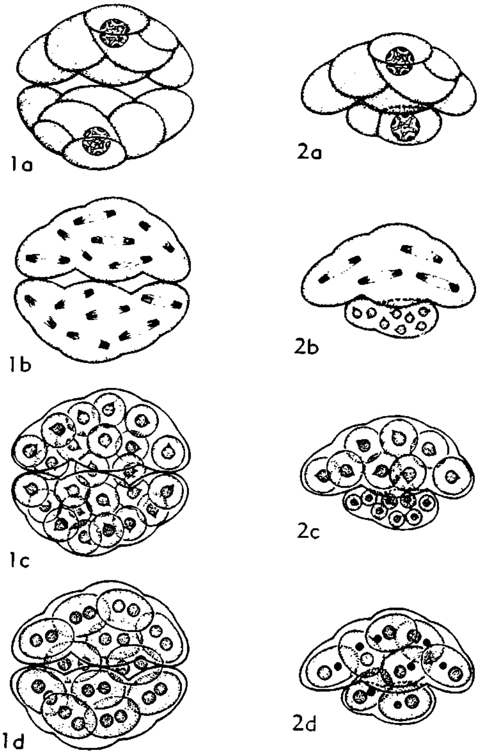

Fig. 49. Plastogamy in *Rubratella intermedia*; *1*, gamonts of similar size; *2*, gamonts of dissimilar size (*1a,2a*, pairing of gamonts; *1b,2b*, nuclear division; *1c,2c*, formation of gametes, those of unequal-sized gamonts being also dissimilar in size and with differing size of nuclei; *1d,2d*, 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

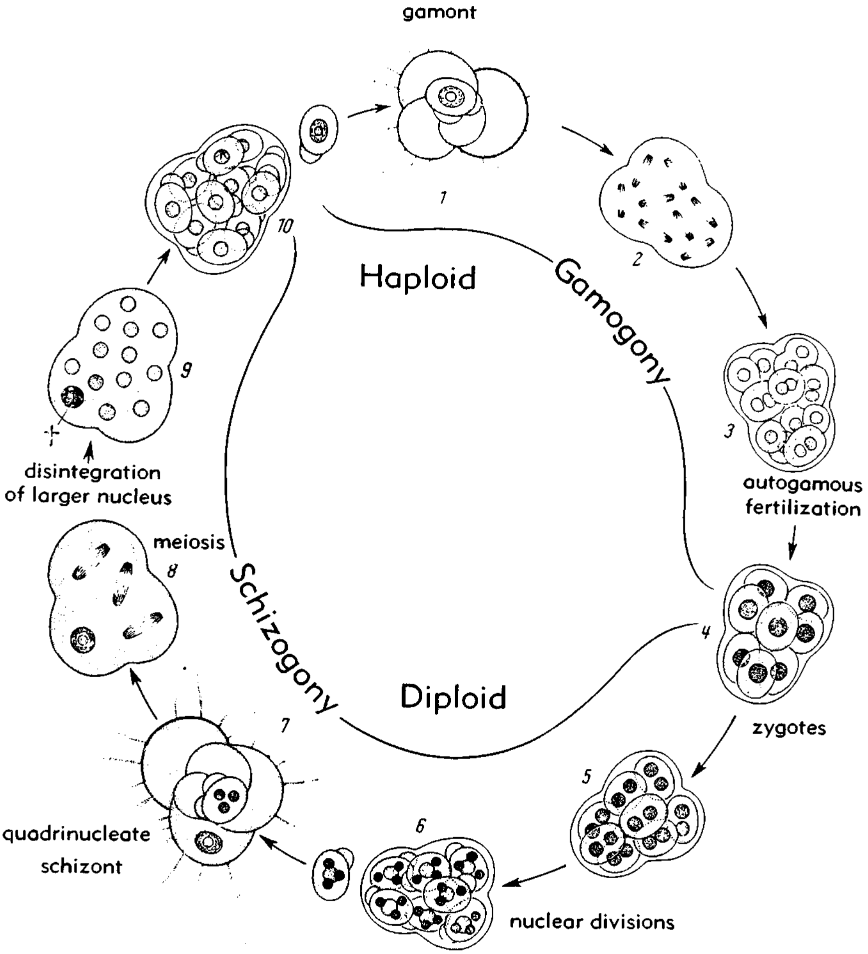

FIG. 50. Life cycle of *Rotaliella heterocaryotica* (*821).

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*).

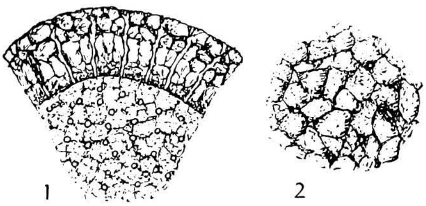

FIG. 52. Wall structure of *Textularia agglutinans* (*1075).——*1.* Fragment of wall showing internal surface of chamber with perforations at bottom and section through wall with irregular perforations, ×100.——*2.* Exterior surface of fragment showing tiny pores between sand grains, ×500.

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.

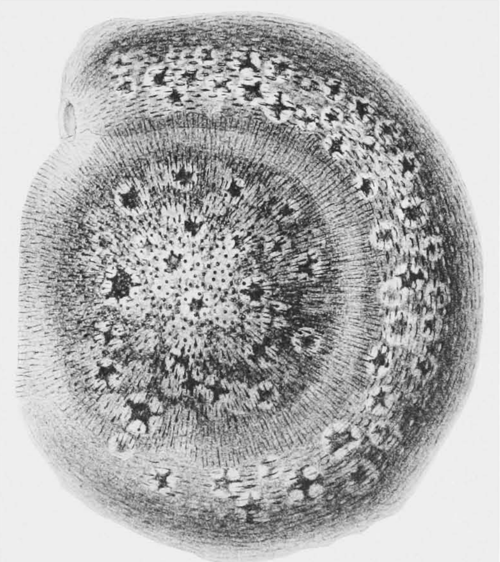

FIG. 53. Juvenile specimen of *Peneroplis pertusus* with globular, finely perforate proloculus and enrolled spiral passage, ×850 (*2068).

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, Ceratobuliminninae, 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

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[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 (=Rotaliacea) 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.

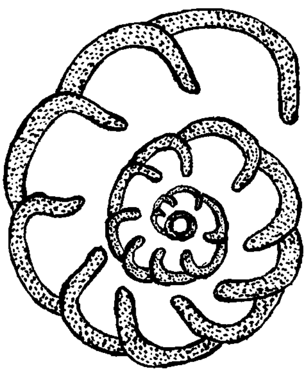

FIG. 54. Diagrammatic section of nonlamellar test (*2117).

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-

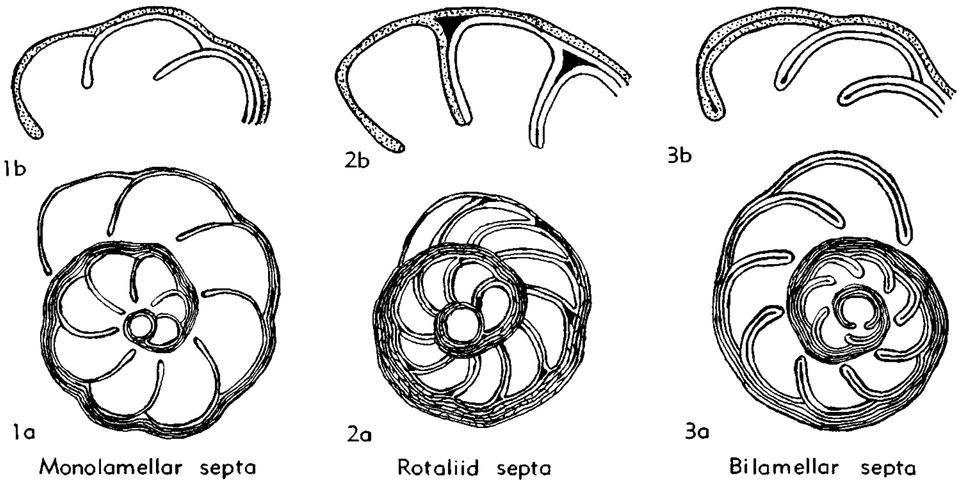

FIG. 55. Diagrammatic sections of lamellar tests.——*1a,2a,3a.* Equatorial sections showing lamellar development.——*1b,2b,3b.* Final three chambers showing their lamellar character (last added chamber and lamella indicated by stippled pattern) (*2117).

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

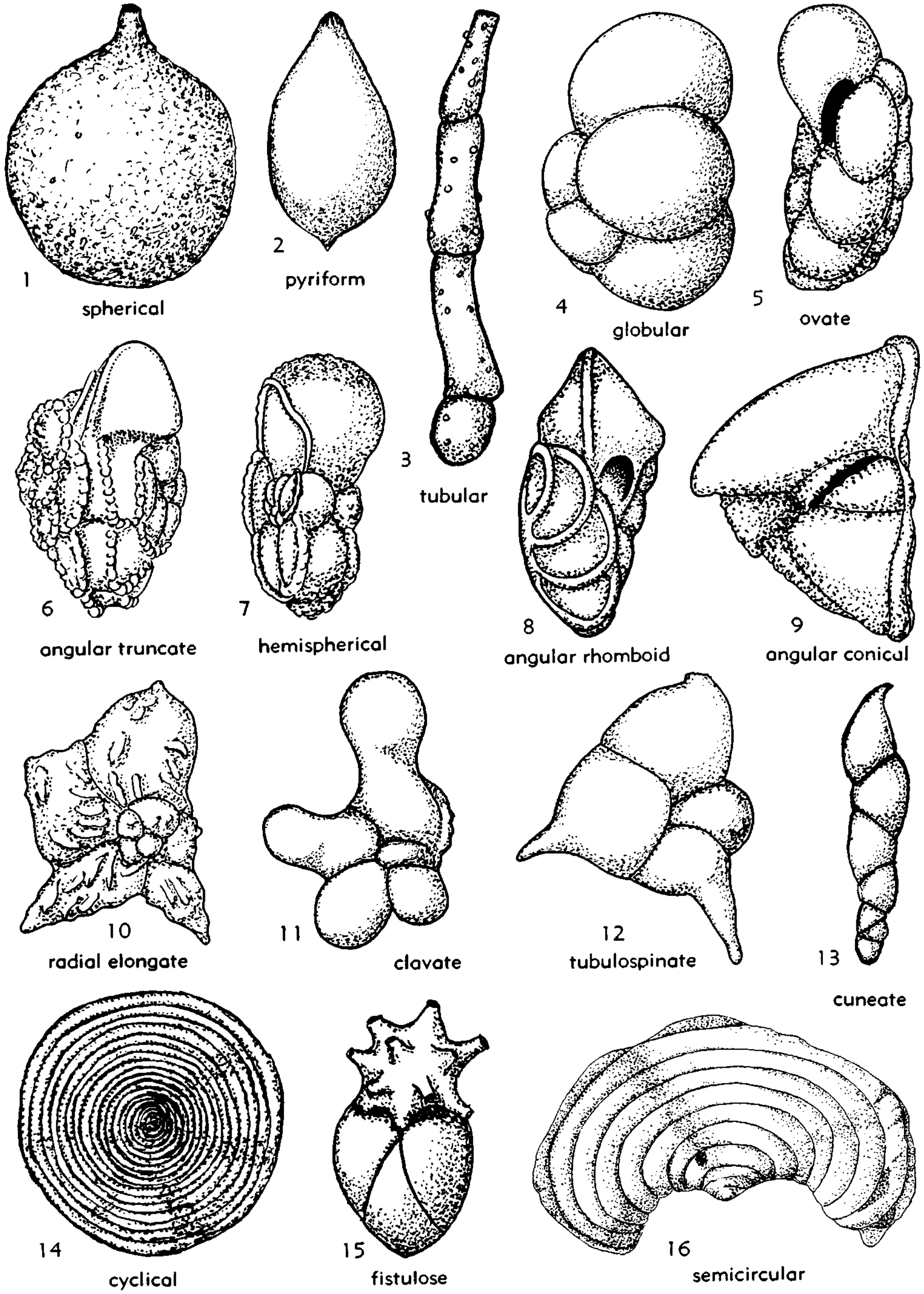

Fig. 56, *1-16*. Shapes of chambers in foraminiferal tests (*2117).

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-

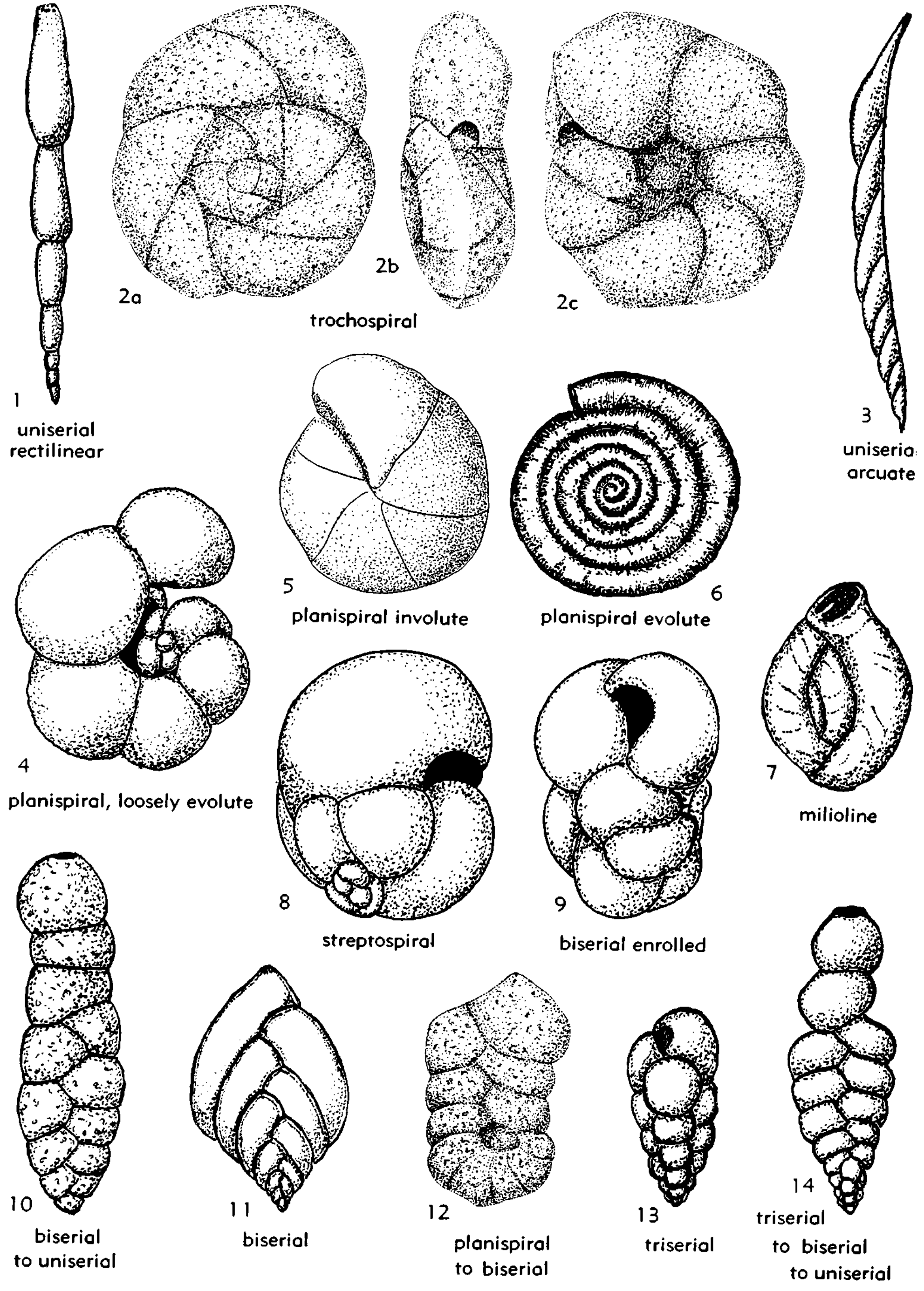

FIG. 57, *1-14*. Arrangement of chambers in foraminiferal tests (*2117).

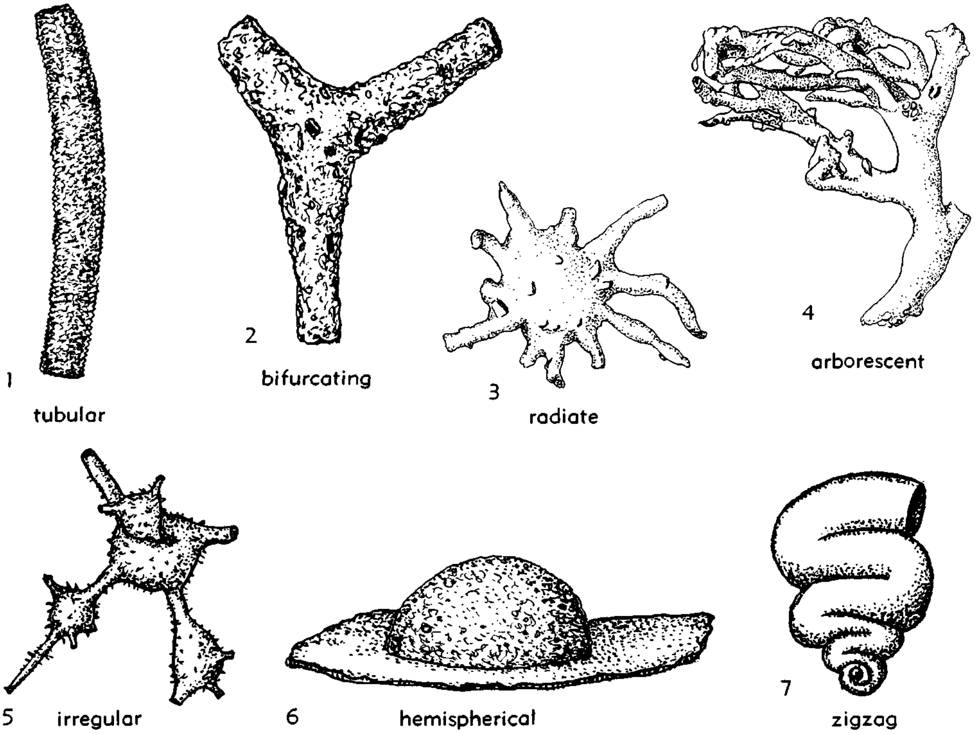

Fig. 58, *1-7*. Shapes of foraminiferal tests (*2117).

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

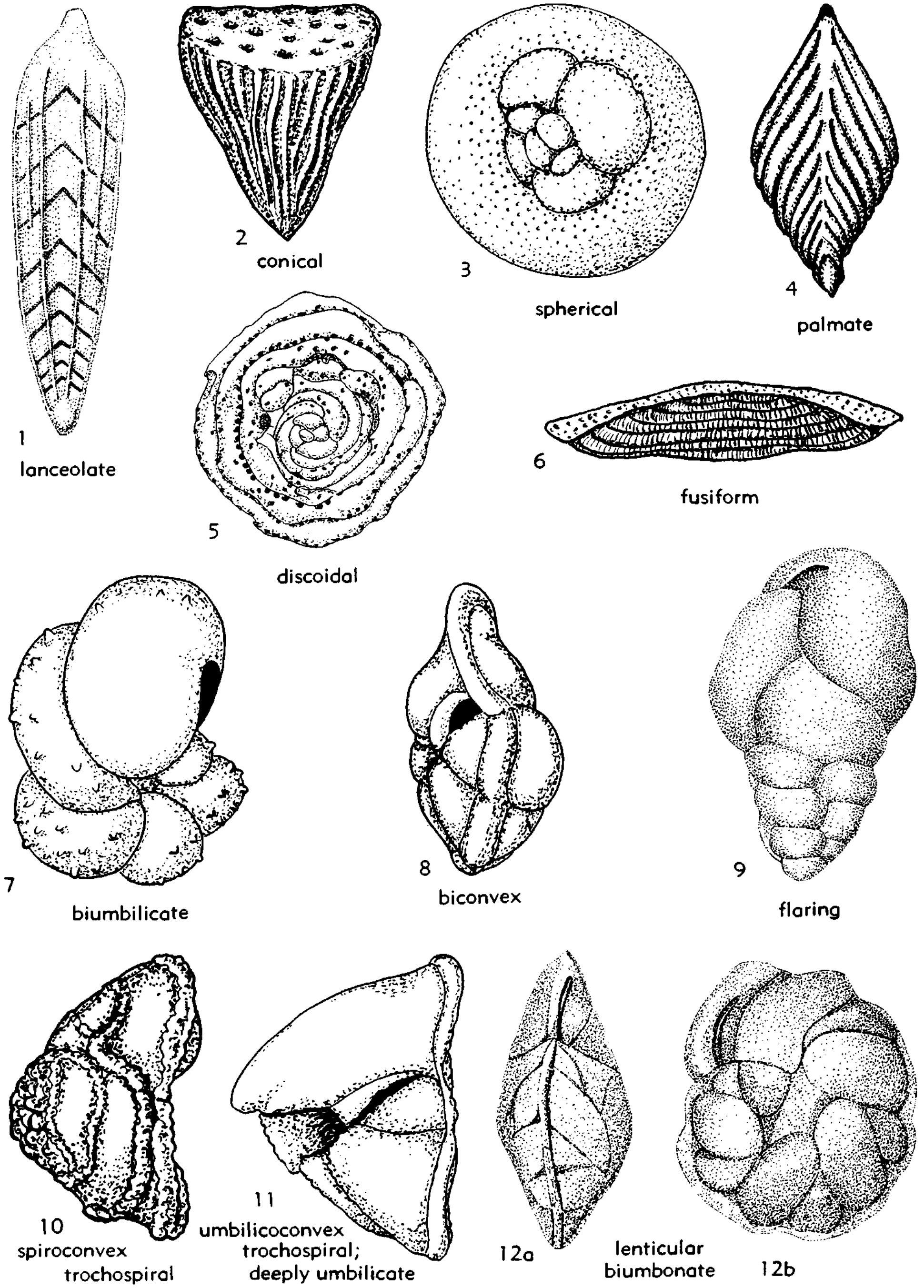

Fig. 59, *1-12*. Shapes of foraminiferal tests (*2117).

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

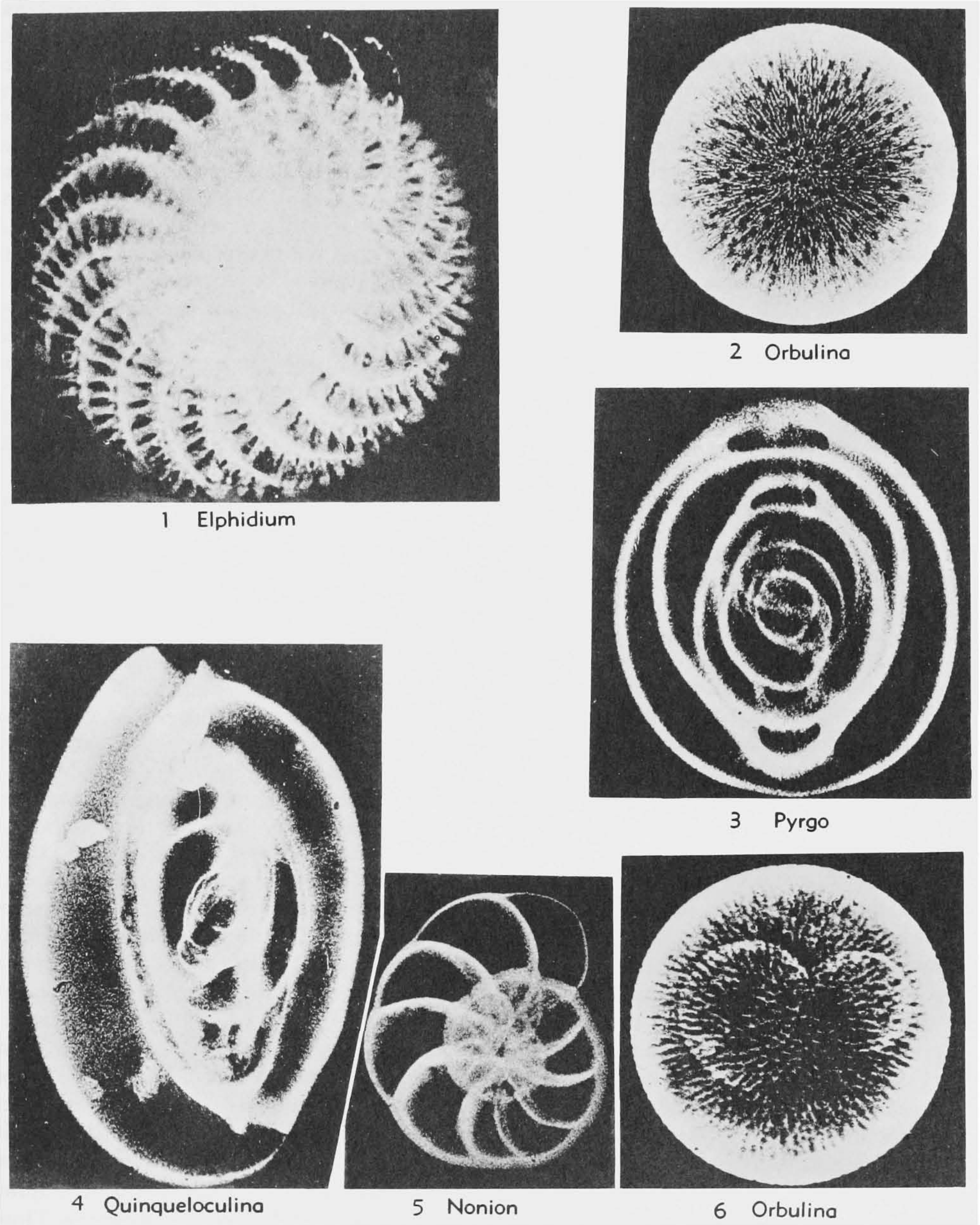
1 Elphidium
2 Orbulina
3 Pyrgo
4 Quinqueloculina
5 Nonion
6 Orbulina

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

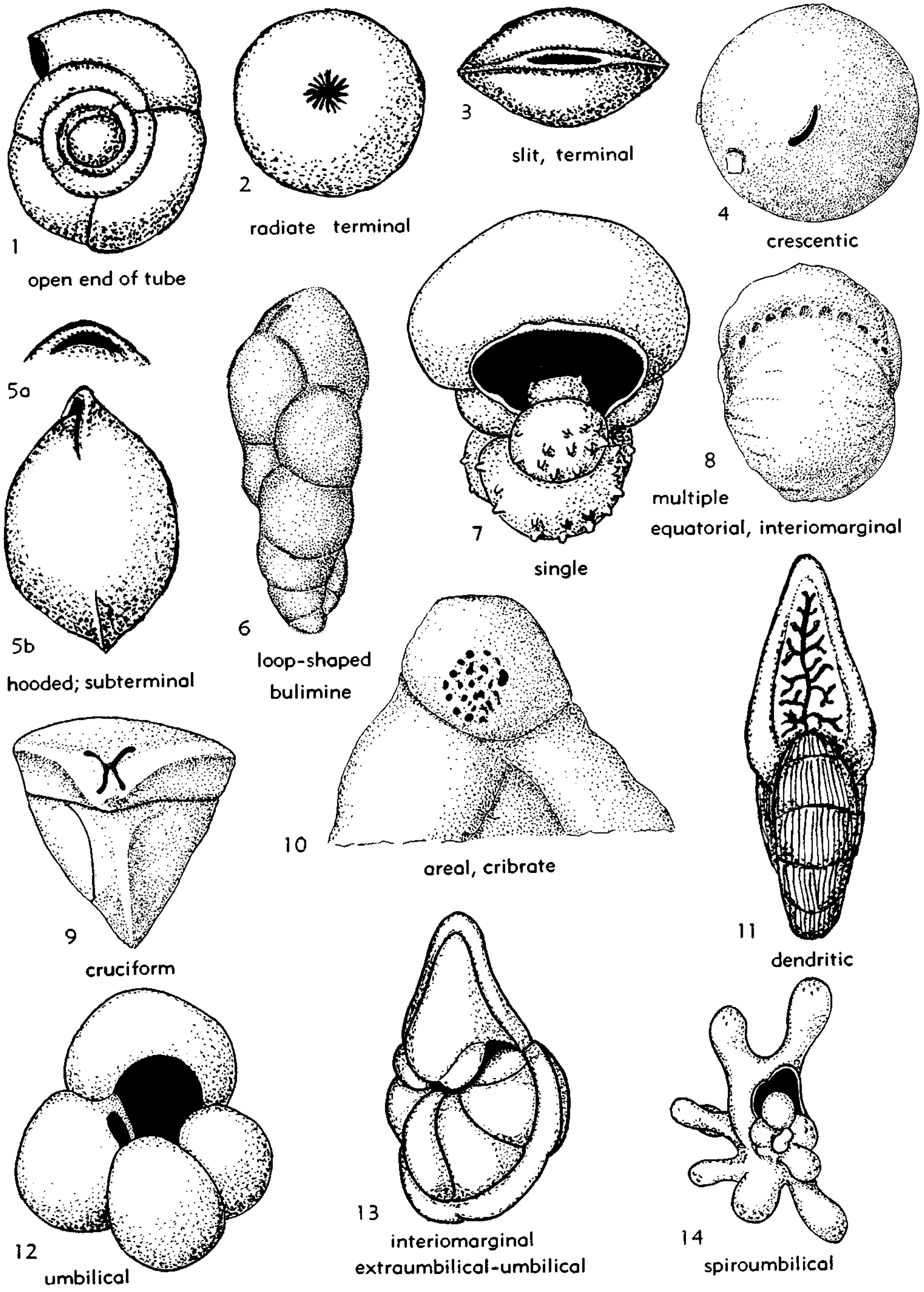

Fig. 61, *1-14.* Location and form of primary apertures in foraminiferal tests (*2117).

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.,

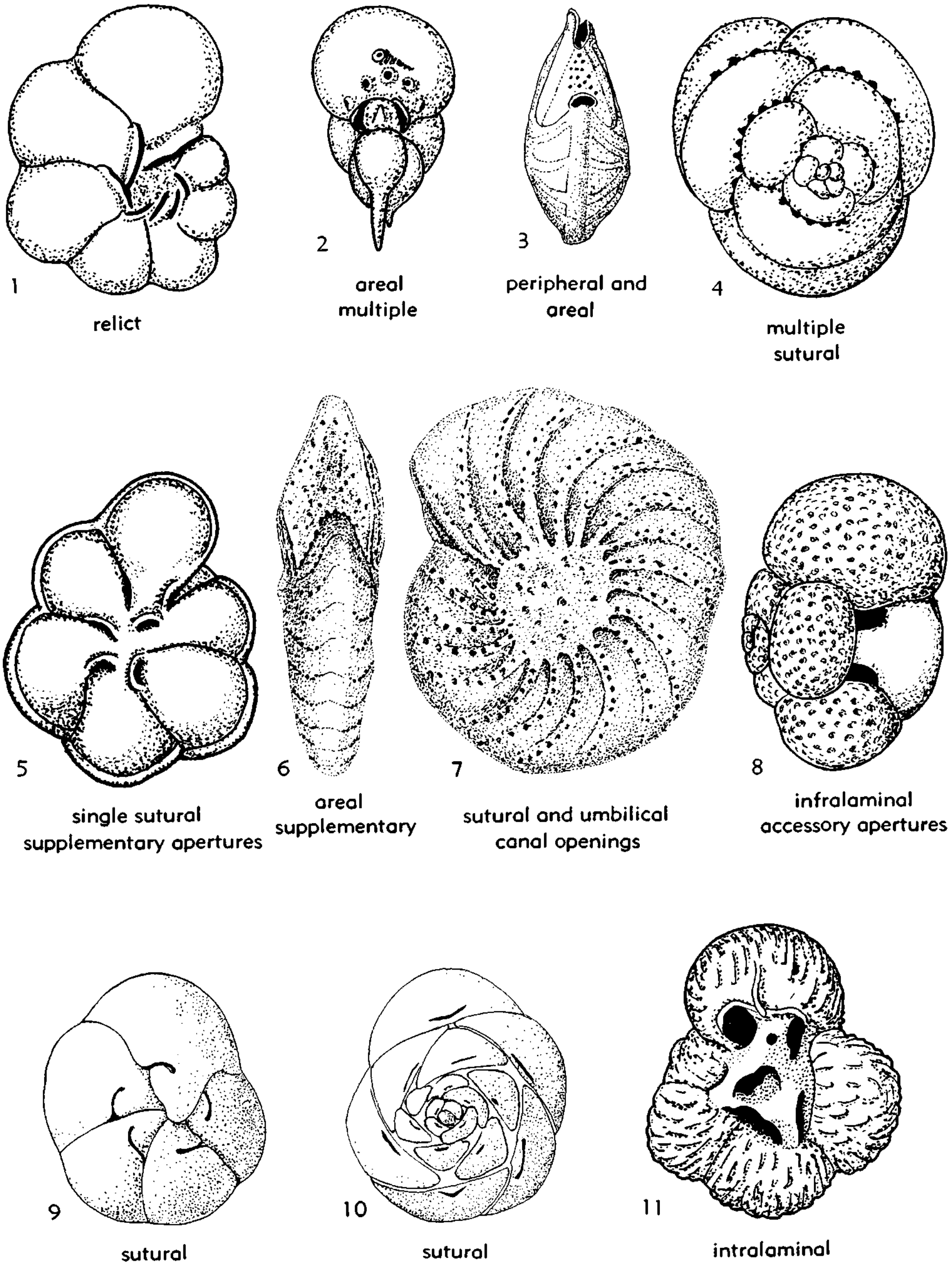

Fig. 62. Type of supplementary apertures *(1-6)* and accessory apertures *(7-11)* in foraminiferal tests (*2117).

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

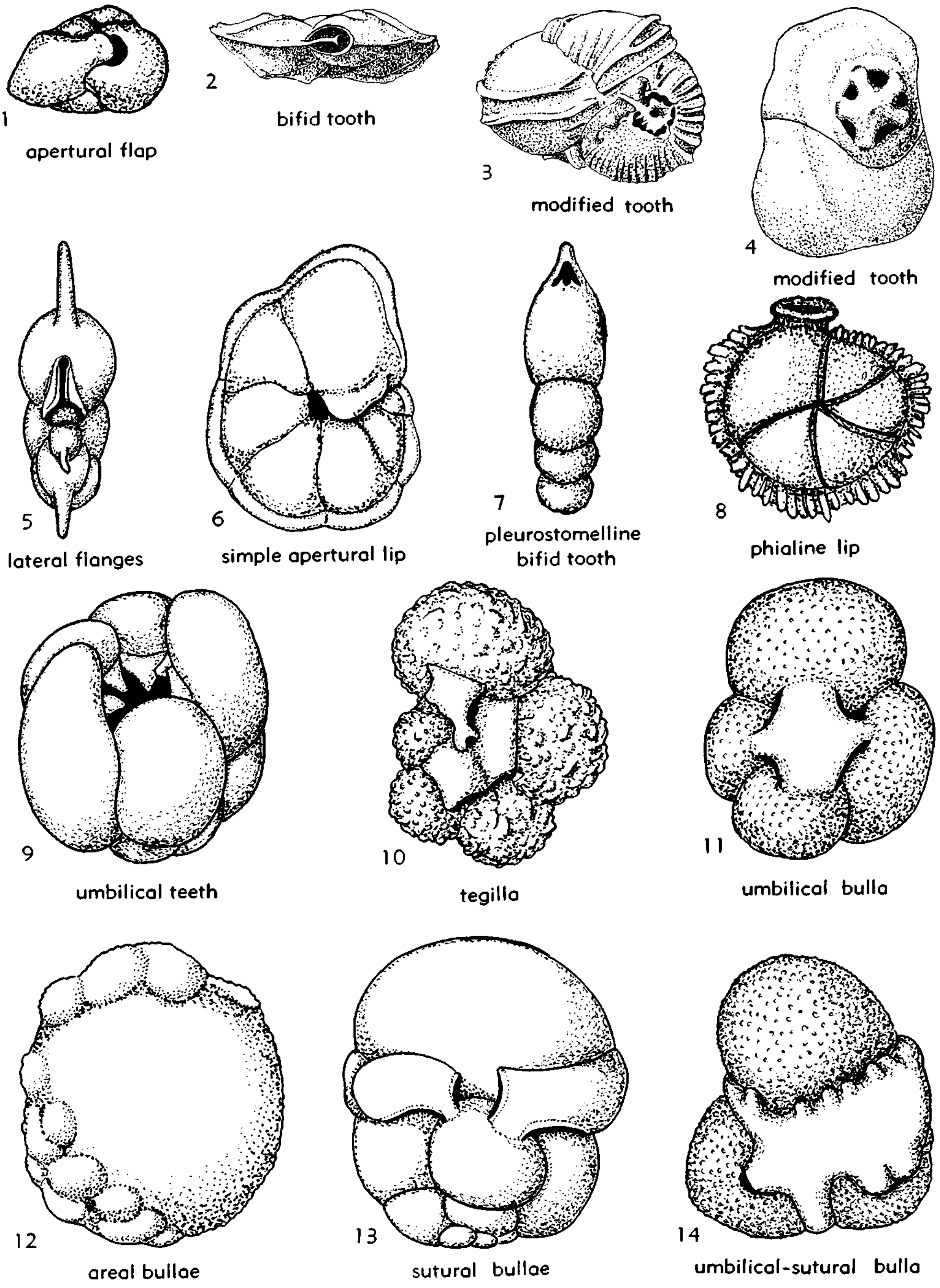

FIG. 63, *1-14*. Modifications of apertures in foraminiferal tests (*2117).

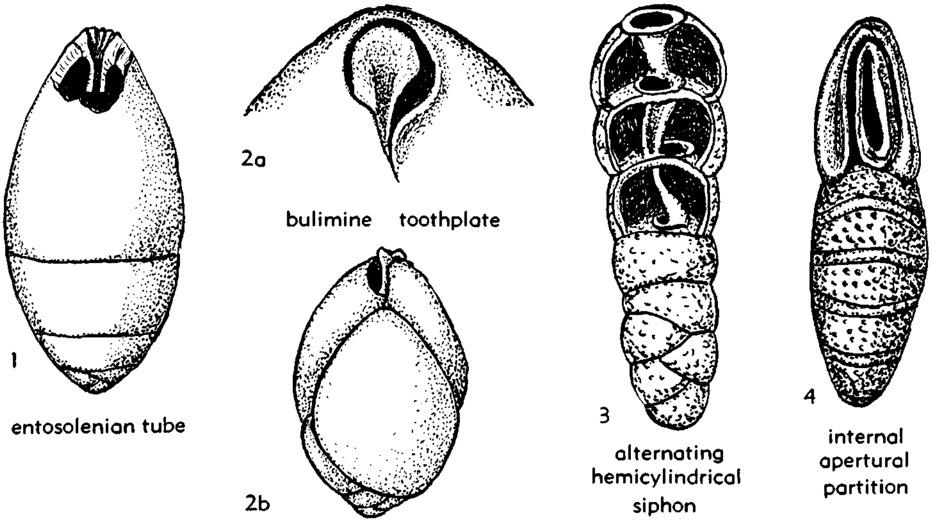

Fig. 64, *1-4*. Internal apertural modifications in foraminiferal tests (*2117).

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

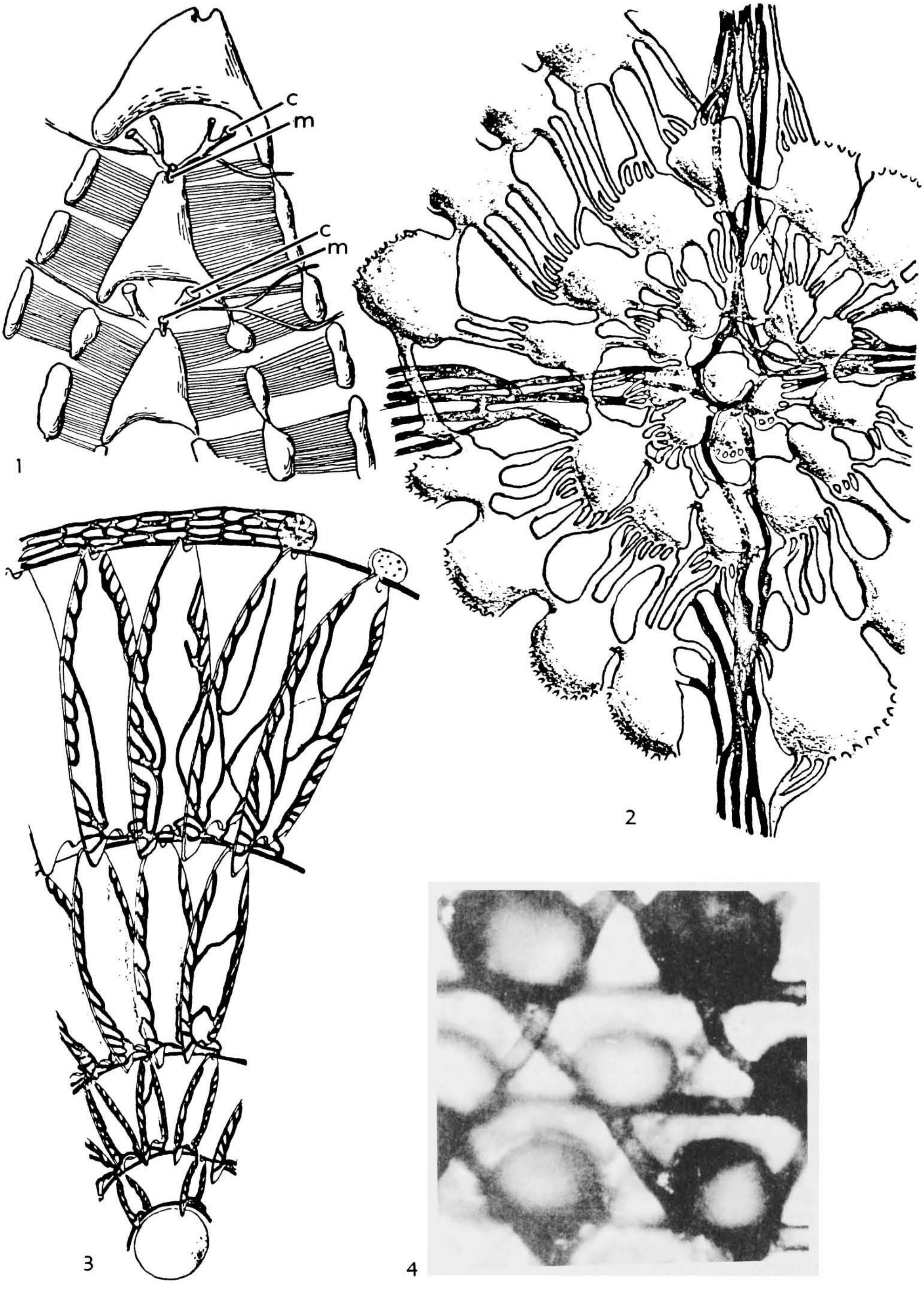

FIG. 65. Canal systems and stolons in foraminifers.——*1.* Portion of axial section of *Nummulites laevigatus* showing marginal cord *(m)* and spiral canal *(c)*, enlarged (*928a).——*2.* Equatorial section of decalcified *Calcarina spengleri*, canal system shown dark, located in region of spines, ×95 (*928a).——*3.* Canal system of *Nummulites complanatus*, diagrammatic (*928a).——*4.* Decalcified section of *Lepidocyclina favosa* showing diagonal and annular stolons, enlarged (*1998).

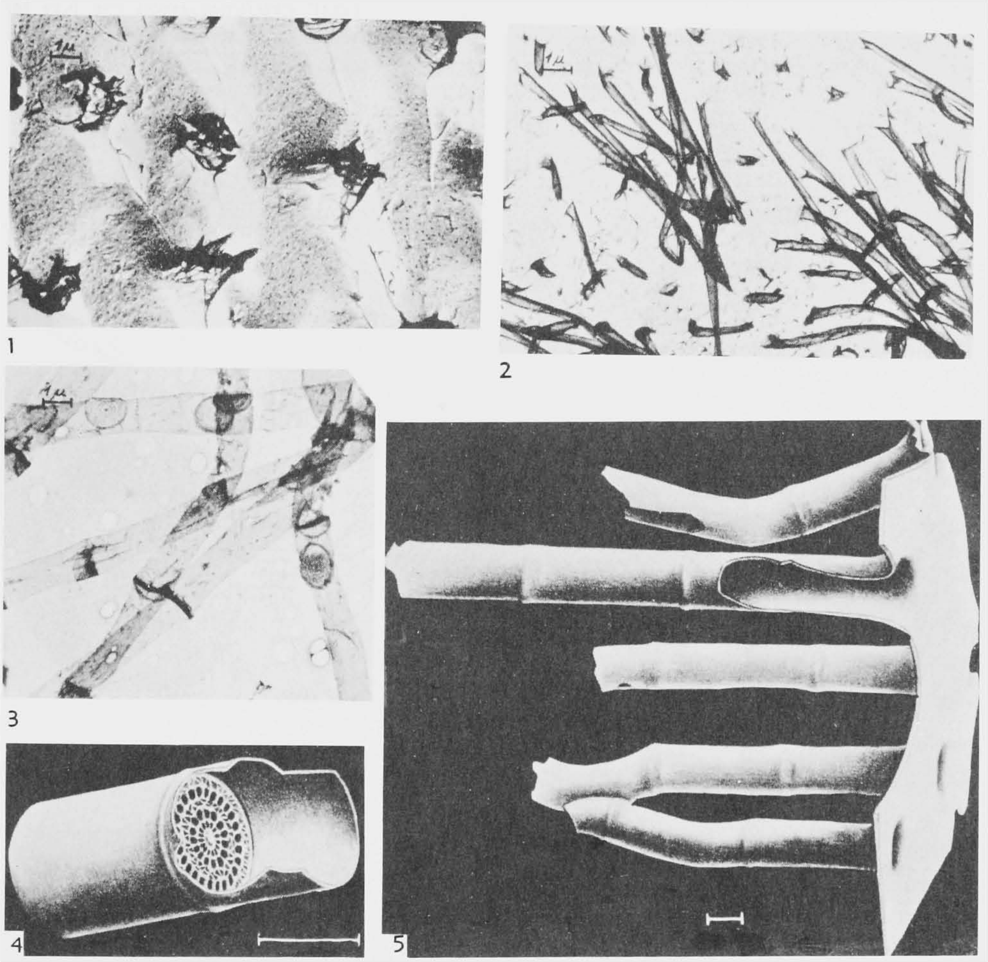

Fig. 66. Electron micrographs of decalcified foraminiferal tests and reconstruction of pore canals and sieve plates.——*1*. Organic wall layer.——*2*. Organic canals.——*3*. Decalcified specimen showing pseudochitinous lining of pores and regularly spaced sieve plates, all ×4,000.——*4*. Reconstruction of 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.

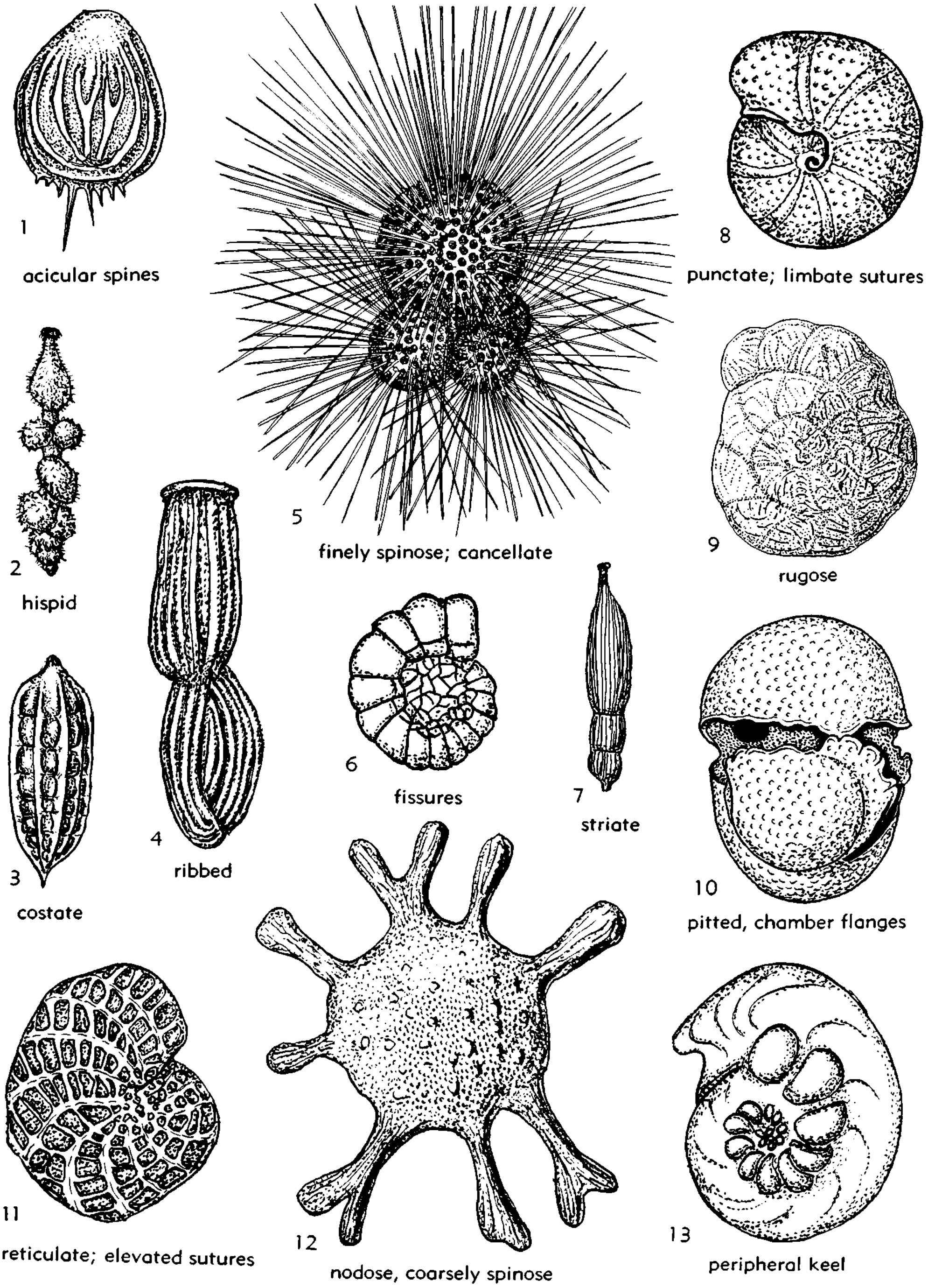

FIG. 67, *1-13*. Ornamentation of foraminiferal tests (*2117).

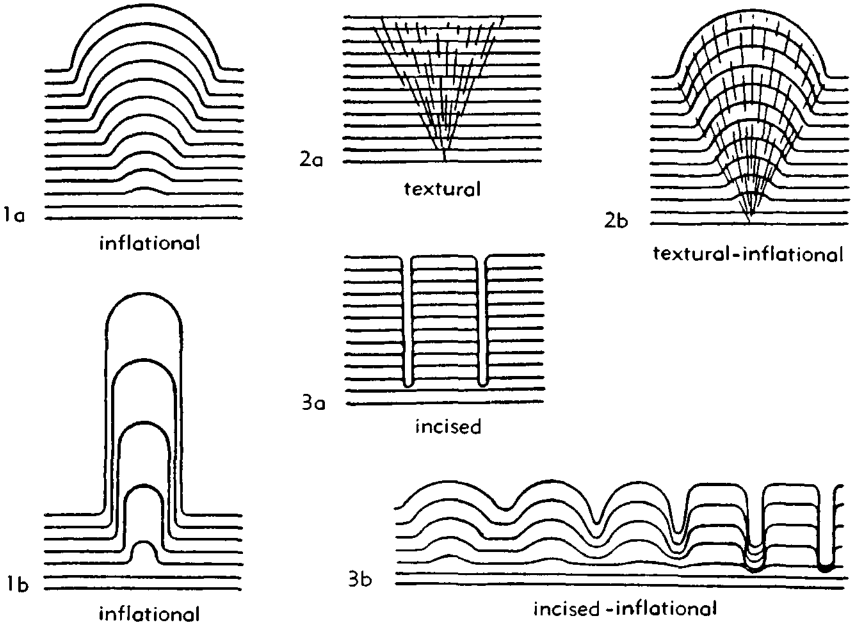

FIG. 68. Development of pillars in foraminiferal tests.——*1a,b.* Inflational pillars.——*2a,b.* Textural pillars.——*3a,b.* Incised pillars (*1803).

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.

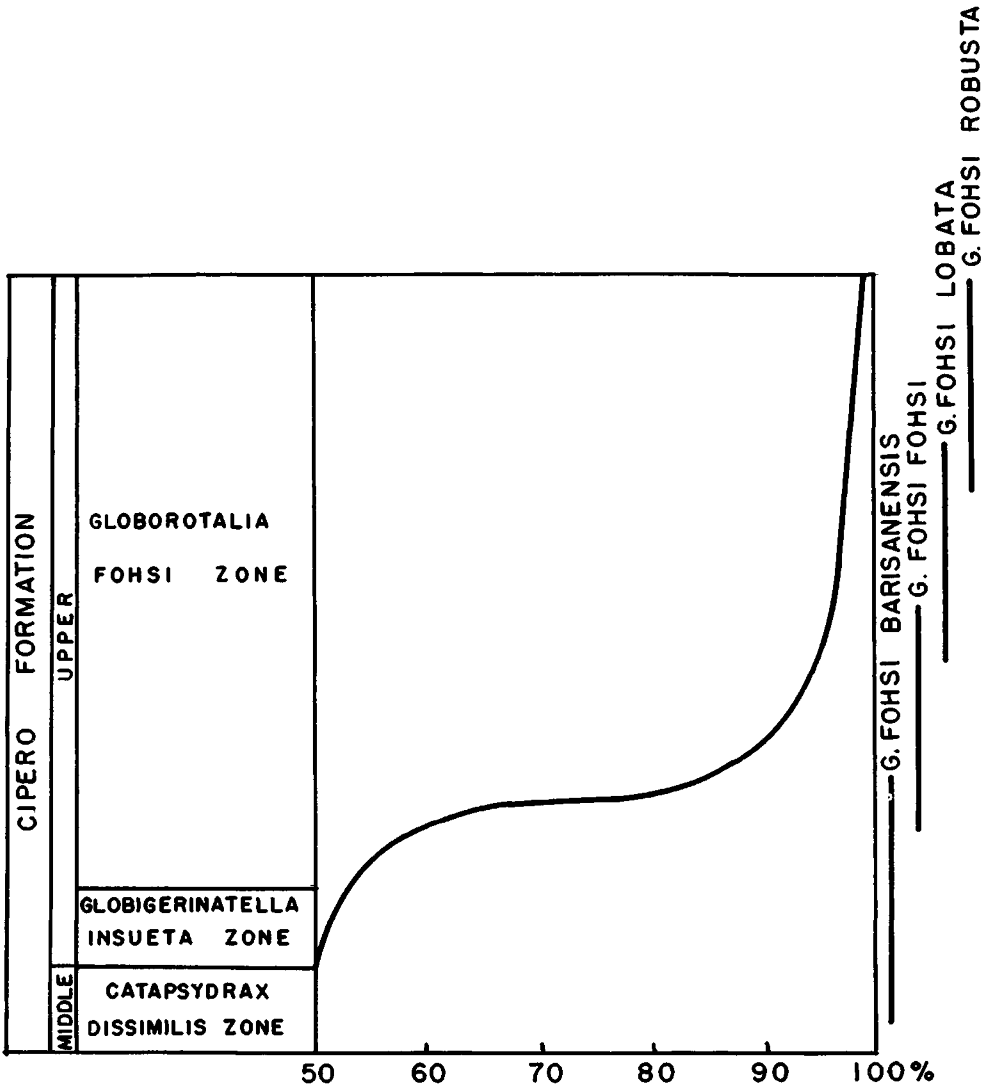

Fig. 69. Percentages of sinistrally coiled *Globorotalis fohsi* in the Miocene of Trinidad, showing change from random to dominantly sinistral tests with lapse of geologic time (*164).

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

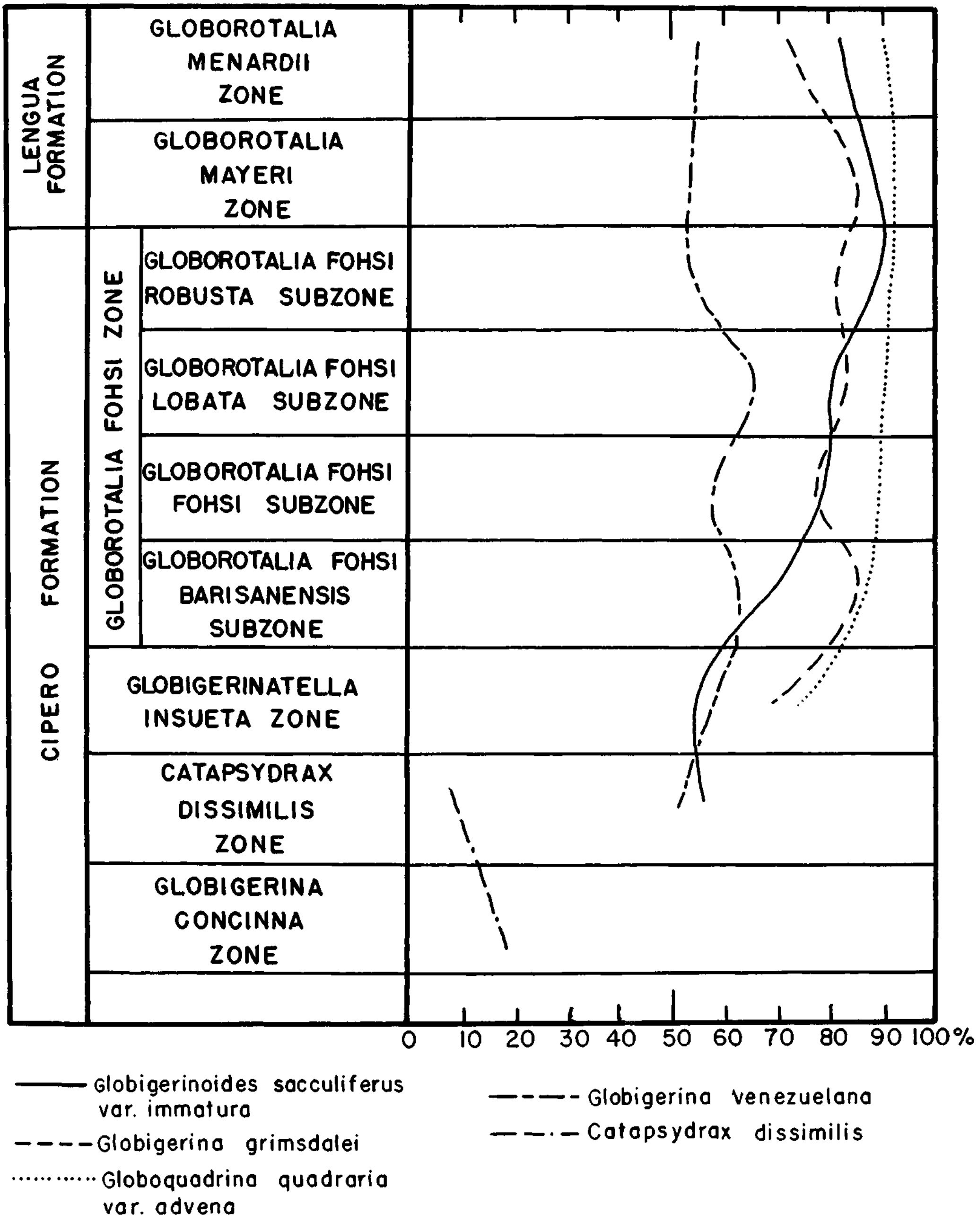

Fig. 70. Percentage of sinistrally coiled globigerinid tests in Oligocene-Miocene deposits (*164).

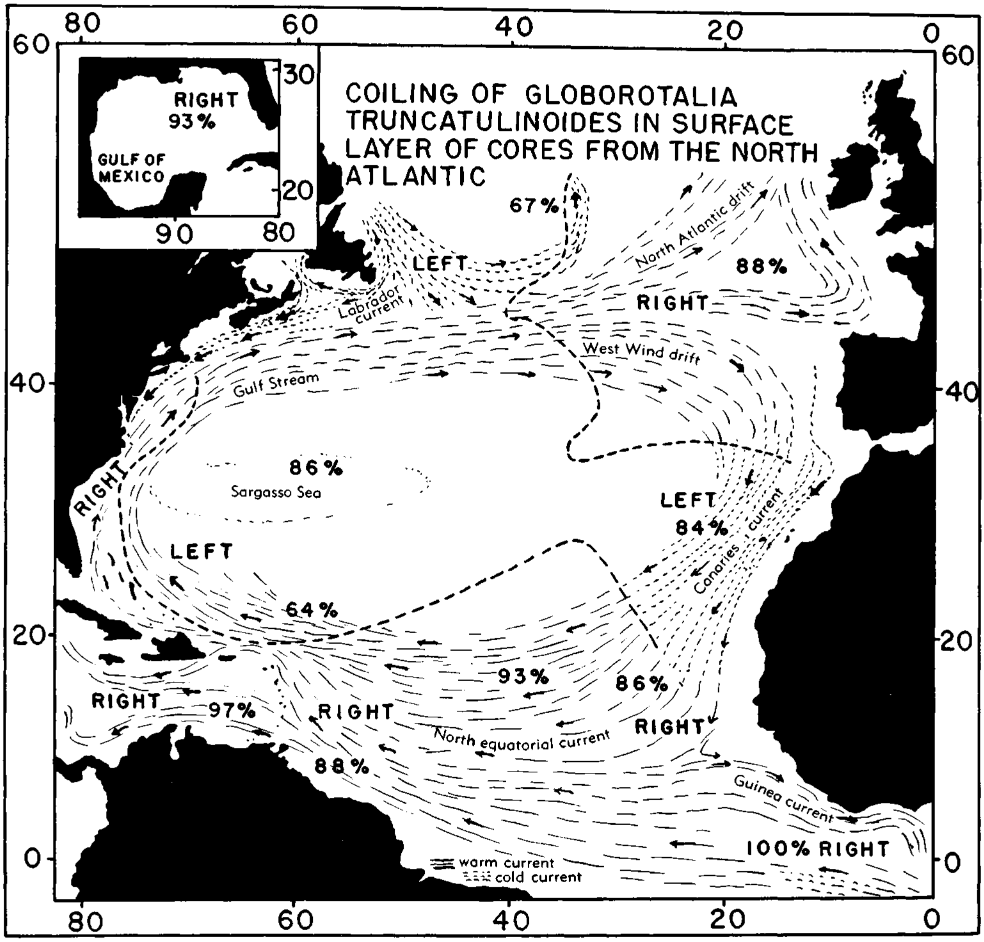

FIG. 71. Provinces of living *Globorotalia truncatulinoides* defined by distribution of dominantly sinistral- and dextral-coiled tests, respectively. Warm currents (solid lines) and cold currents (dotted lines) have been added to indicate possible influencing factors (*708, modified).

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-

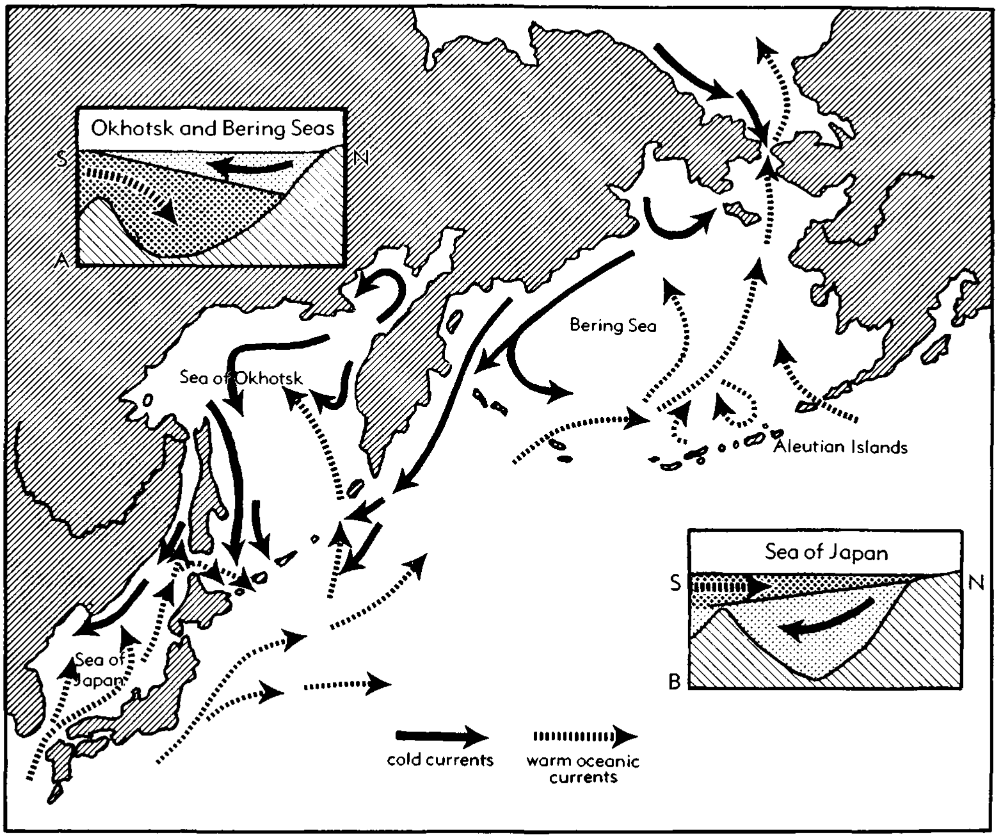

FIG. 72. Distribution of warm and cold waters in Sea of Okhotsk and Bering Sea, with inset figures indicating vertical interchange of warm-water (heavy stippled pattern) and cold-water (light stippled pattern) masses in the Okhotsk-Bering Sea areas *(A)* and Sea of Japan area *(B)* (P. V. Ushakov in *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.

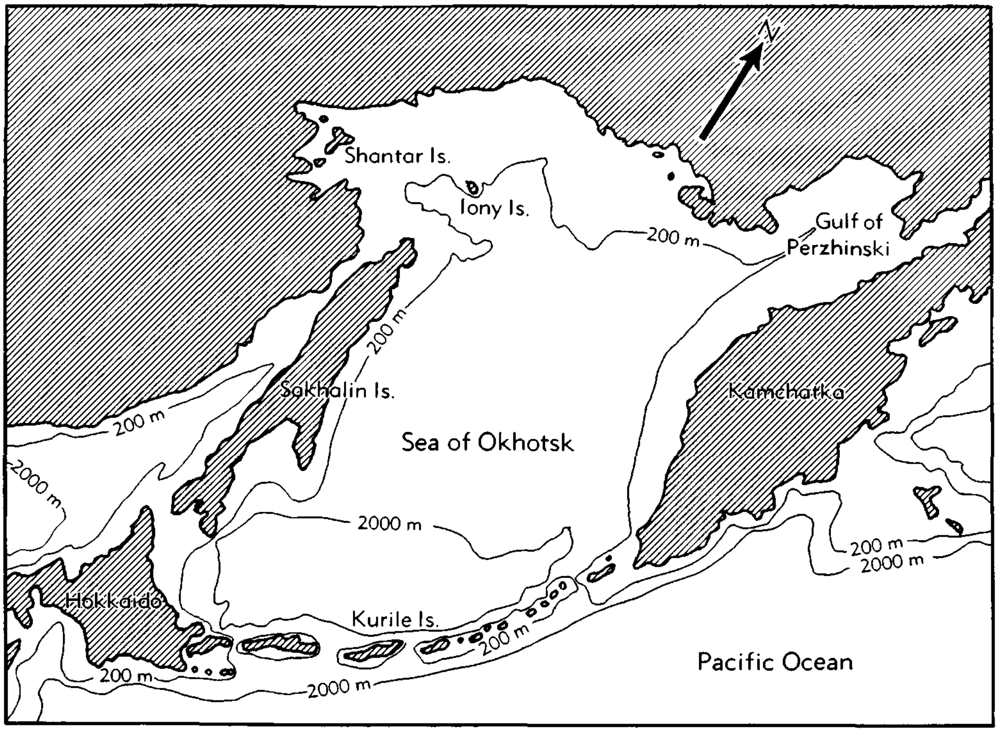

Fig. 73. Generalized water depths in Sea of Okhotsk, for comparison with distribution of faunal zones (Fig. 74) (*2117).

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.

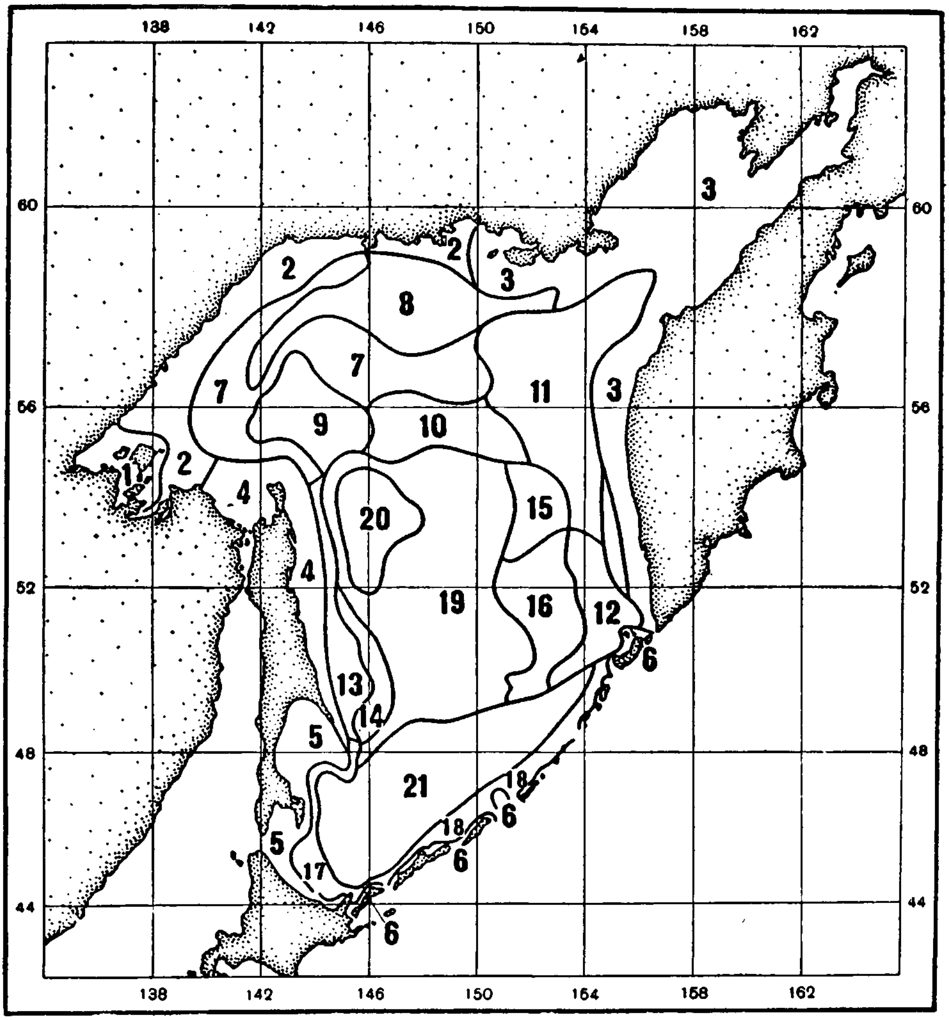

FIG. 74. Distribution of faunal assemblages in Sea of Okhotsk (*1617).

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

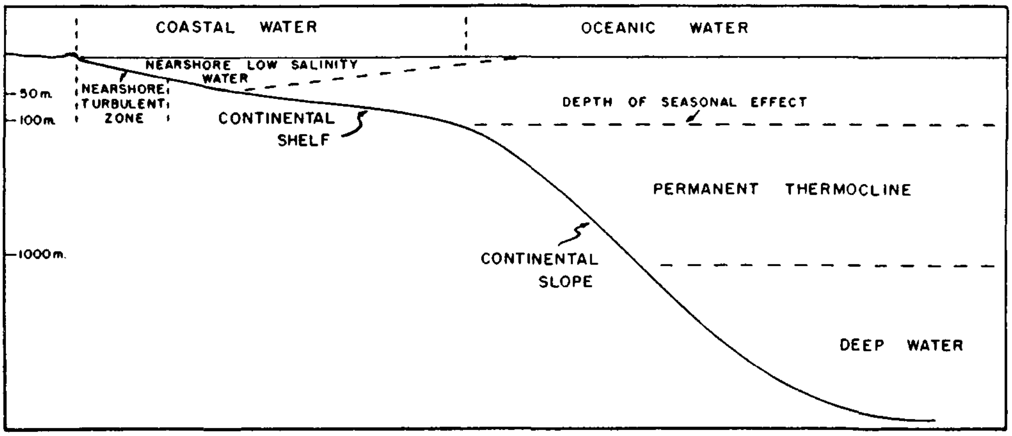

Fig. 75. Classification and distribution of coastal and oceanic waters near area of high runoff from land (*1454).

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

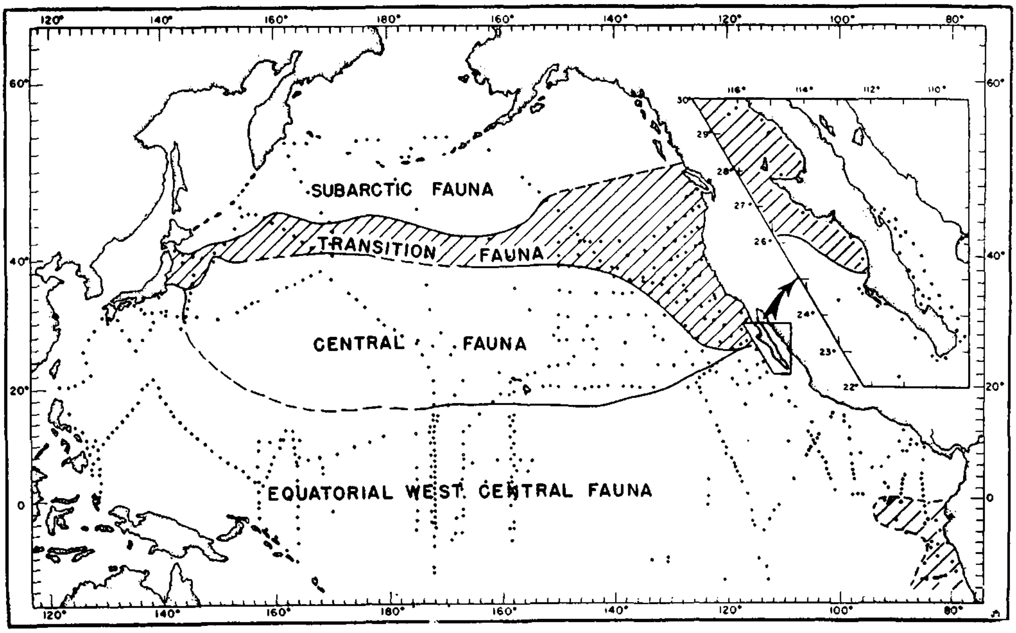

FIG. 76. Generalized distribution of planktonic assemblages of organisms in central and northern Pacific region (extent of sampling indicated by dots) (*185).

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.

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.

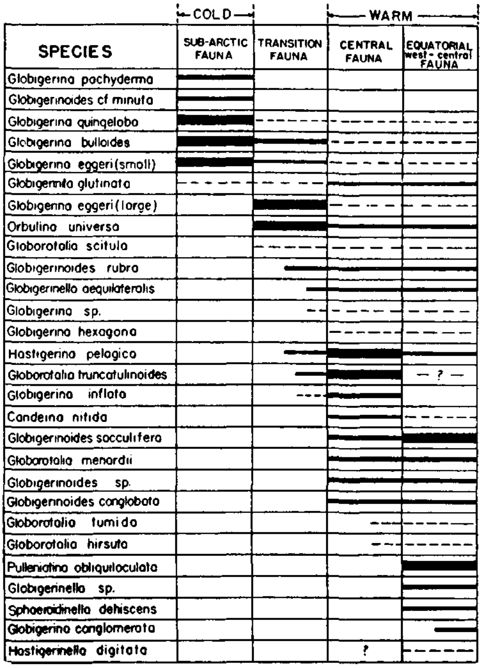

Fig. 77. Generalized distribution of planktonic foraminifers showing composition of assemblages in warm, transitional, and cold environments (*185).

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

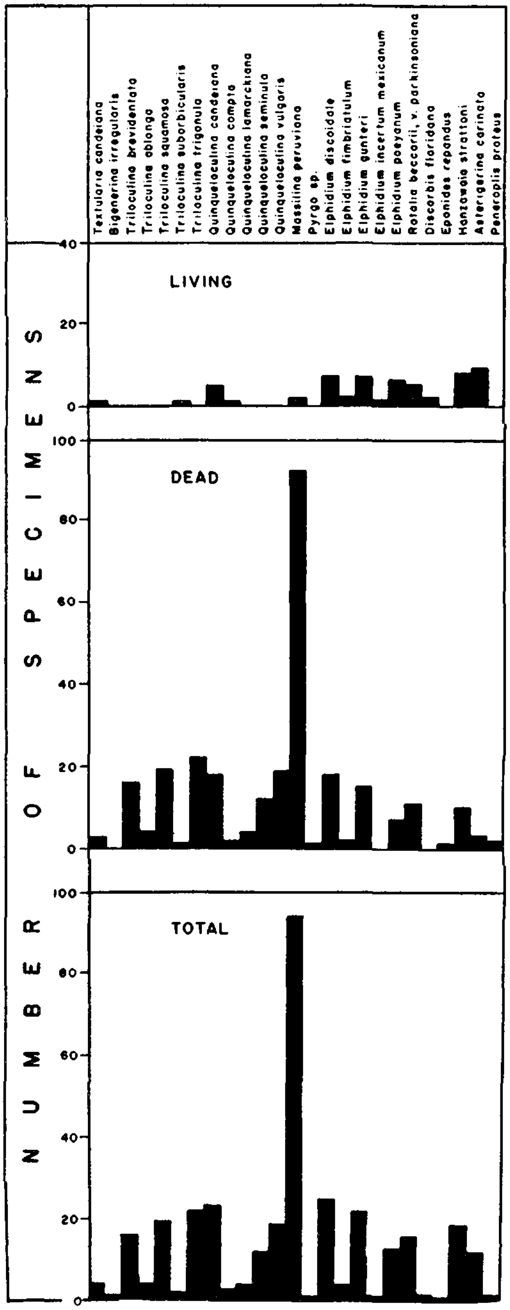

FIG. 78. Histograms showing foraminiferal populations on sandy shell bank in northwestern Gulf of Mexico. The large numbers of dead *Massilina peruviana* and other miliolids suggest post-mortem transportation of tests (*1733).

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

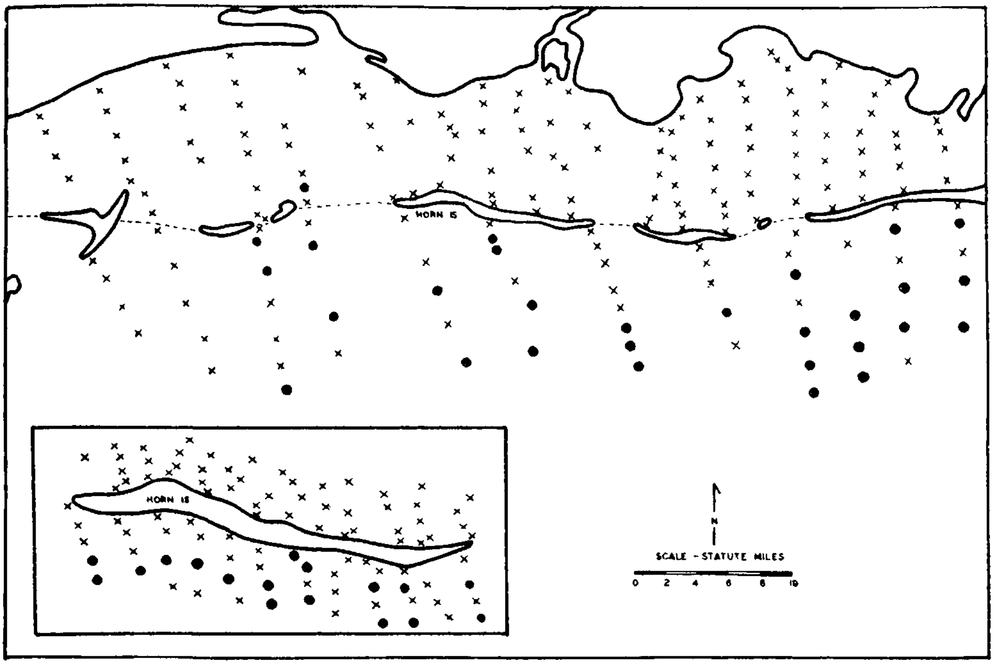

Fig. 79. Occurrence of planktonic and benthonic foraminifers in Mississippi Sound (blackened circles indicating samples that contain planktonic species and crosses those that contain only benthonic species). Planktonic forms are restricted to open Gulf areas, since the barrier islands effectively prevent 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

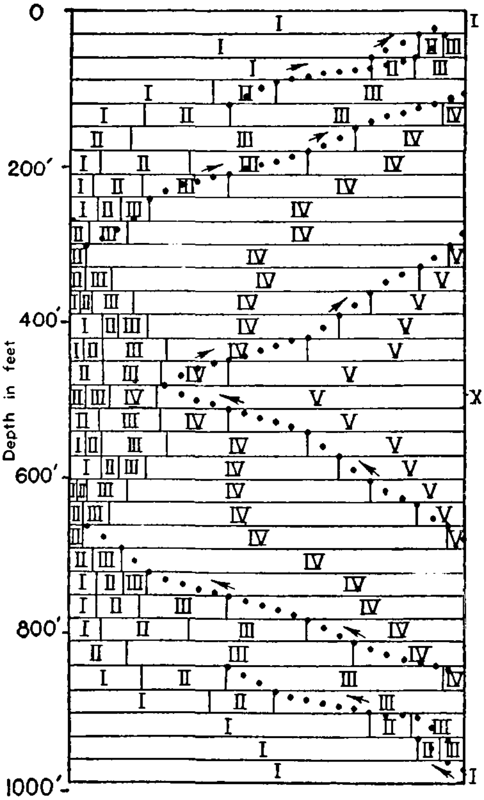

FIG. 80. Hypothetical marine cycle shown by depth oscillation chart. [Explanation: I, brackish-water assemblage; II, beach assemblage; III, seaweed-zone assemblage; IV, V, successively deeper water assemblages. Leftward shift of numbers in upward succession and left-pointing arrows indicates deepening 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

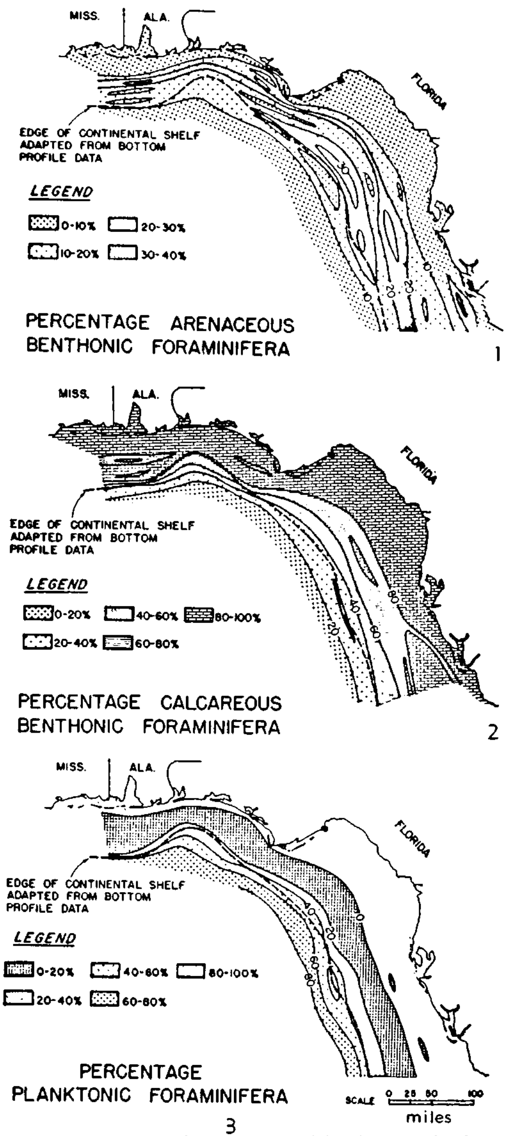

FIG. 81. Marine biofacies indicated by foraminiferal assemblages in northeastern Gulf of Mexico.——*1.* Biofacies defined by percentages of arenaceous benthonic foraminifers.——*2.* Biofacies defined by percentages of calcareous benthonic foraminifers.——*3.* Biofacies defined by percentages of planktonic foraminifers in total assemblage, decrease indicating direction toward shore (*1971).

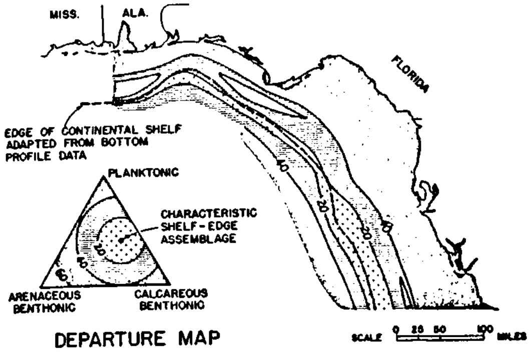

Fig. 82. "Departure map" based on shelf-edge foraminiferal assemblages, showing optimum assemblage for a selected environment and distances both shoreward and seaward from its location (*1971).

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

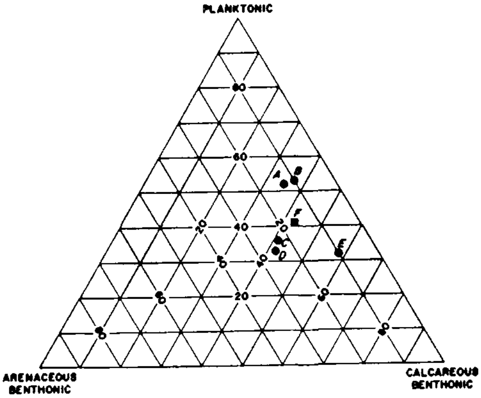

Fig. 83. Triangular graph showing selected target environment and its optimum point, based on analysis of foraminiferal assemblages. [Solid dots indicate percentages of different assemblages found along different traverses; solid square *(F)* represents average of these and the optimum point] (*1971).

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 micrograular *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——Nubecularidae——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; Buliminae; 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; Buliminae; Virgulininae; Reussiinae; Uvigerininae) —— Ellipsoidinidae——Rotaliidae (Spirillininae; Turrispirillininae; Discorbisinae; Rotaliinae; Bagginae)—— 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; Buliminnae 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; Heterostegininae 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; Buliminnae; Virgulininae; Reussellinae; Uvigerininae)——Cassidulinidae —— Pleurostomellidae——Heterohelicidae (Heterohelicinae; Gümbelininae; Bolivinitinae; Plectofrondiculariinae; Eouvigerininae)——Rotaliidae (Discorbinae; Cymbaloporinae; Rotaliinae; Pegidiinae; Siphonininae; Bagginінae; Cibicidinae; Planorbulininae; Rupertiinae; Homotreminae; Amphistegininae; 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; Sphaeramminninae)——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; Buliminae; Reussellinae; Uvigerininae; Plectofrondiculariinae; Bolivininae) —— Cassidulinidae —— Ellipsoidinidae ——Chilostomellidae

Superfamily Rotaliidea

Spirillinidae (Spirillininae; Patellininae) —— Discorbidae (Discorbinae; Siphonininae; Anomalininae) —— Globigerinidae (Globigerininae; Hantkennininae)——Globorotaliidae —— Gümbelinidae——Planorbulinidae (Planorbulininae; Rupertiinae)——Cymbaloporidae——Nonionidae Ceratobuliminidae —— Amphisteginidae —— Rotaliidae —— Calcarinidae——Miogypsinidae Orbitoididae (Omphalocyclinae; Orbitoidinae; Helicolepidininae) —— Discocyclinidae —— Camerinidae (Camerininae; Heterosteginninae)

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; *Sphaeramminninae) —— 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; Buliminae; Virgulininae; *Reussellinae; [Reussiinae]; Uvigerininae) —— Rotaliidae (Spirillininae; Turrispirillininae; *Discorbinae;

[Discorbisinae]; Rotaliinae; *Siphonininae; Bagginae) —— **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 nonperforate 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; Bulimininae; 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; Heterostegininae) —— 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; Bagginae; Anomalininae)——Planorbulinidae —— Rupertiidae (Rupertiinae; Homotrematinae)—— Pegidiidae——Cymbaloporidae —— Ceratobuliminidae——Epistominidae——Robertinidae—— Orbulinidae —— Hantkeninidae —— Globorotaliidae —— Heterohelicidae —— Amphisteginidae —— Elphidiidae —— Rotaliidae —— Baculogypsinidae —— Miscellaneidae——Nummulitidae (Nummulitinae; Heterostegininae) —— 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)

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[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; Bagginінae 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; Heterosteginae 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)
Hemisphaerammininae (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)
Sphaerammininae (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)
Pfenderininae (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)
      - Buliminінae (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)
      - Bagginінae (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)

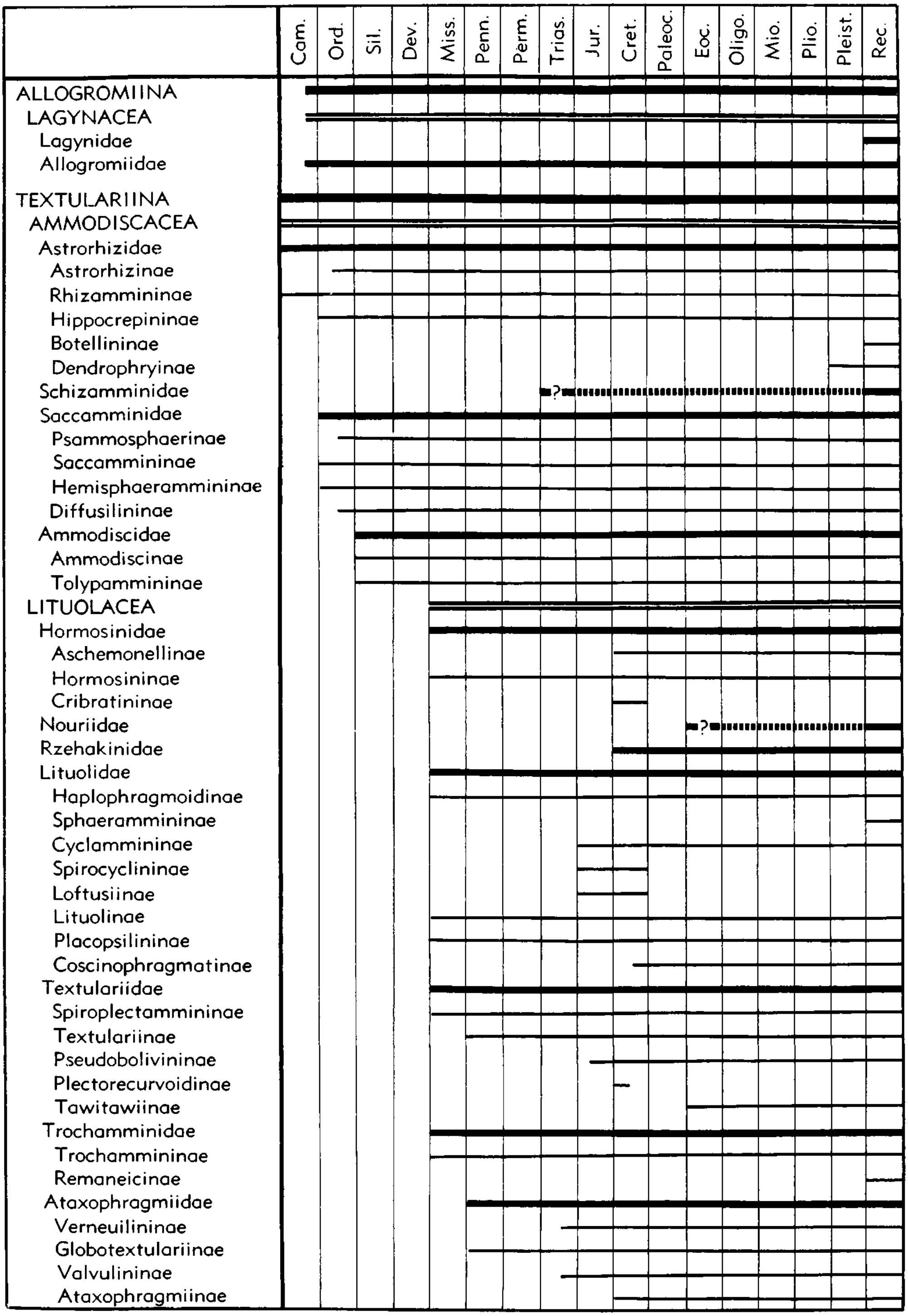

FIG. 83A. Stratigraphic distribution of suprageneric taxa of Foraminiferida (*2117).

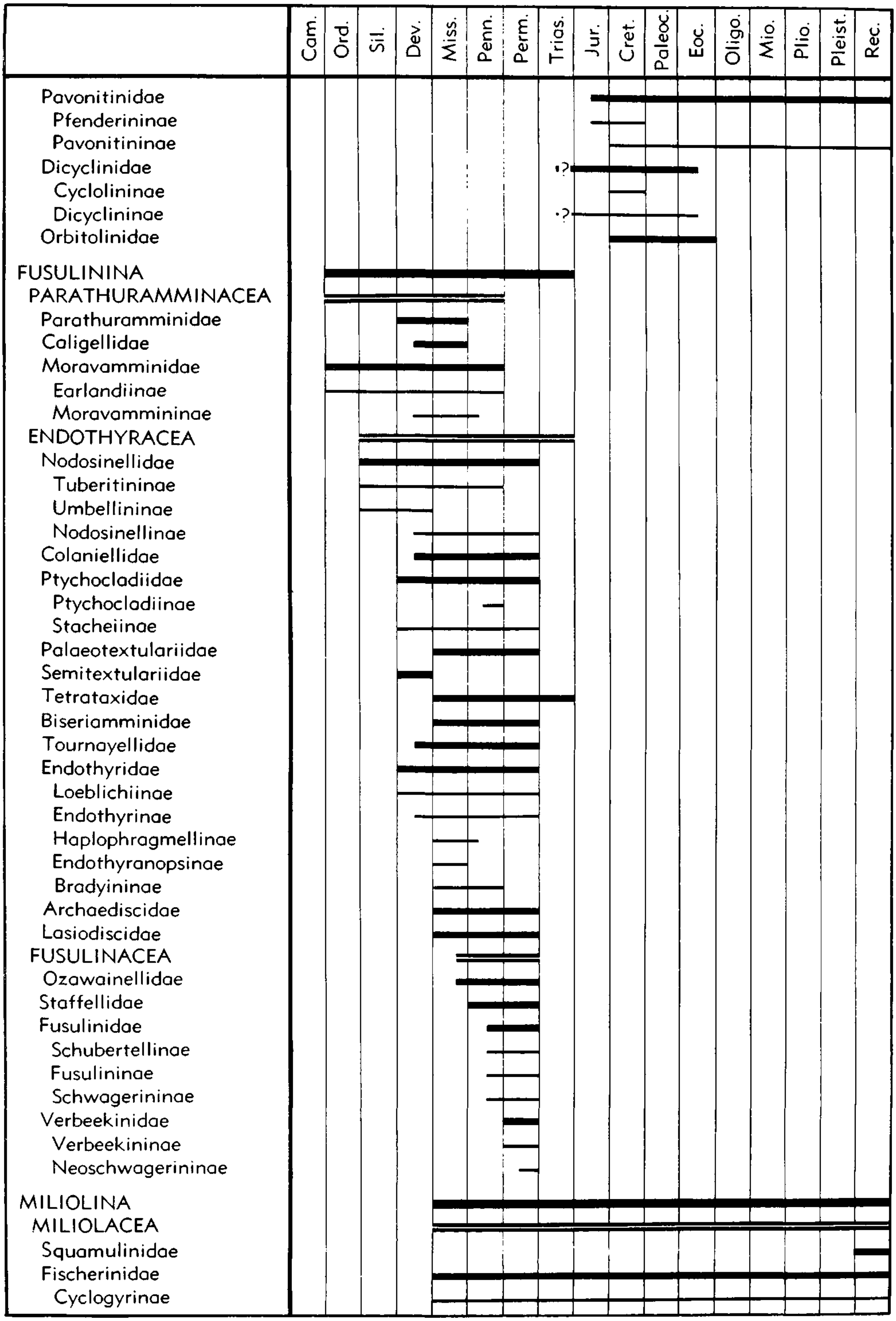

FIG. 83A *(continued)*.

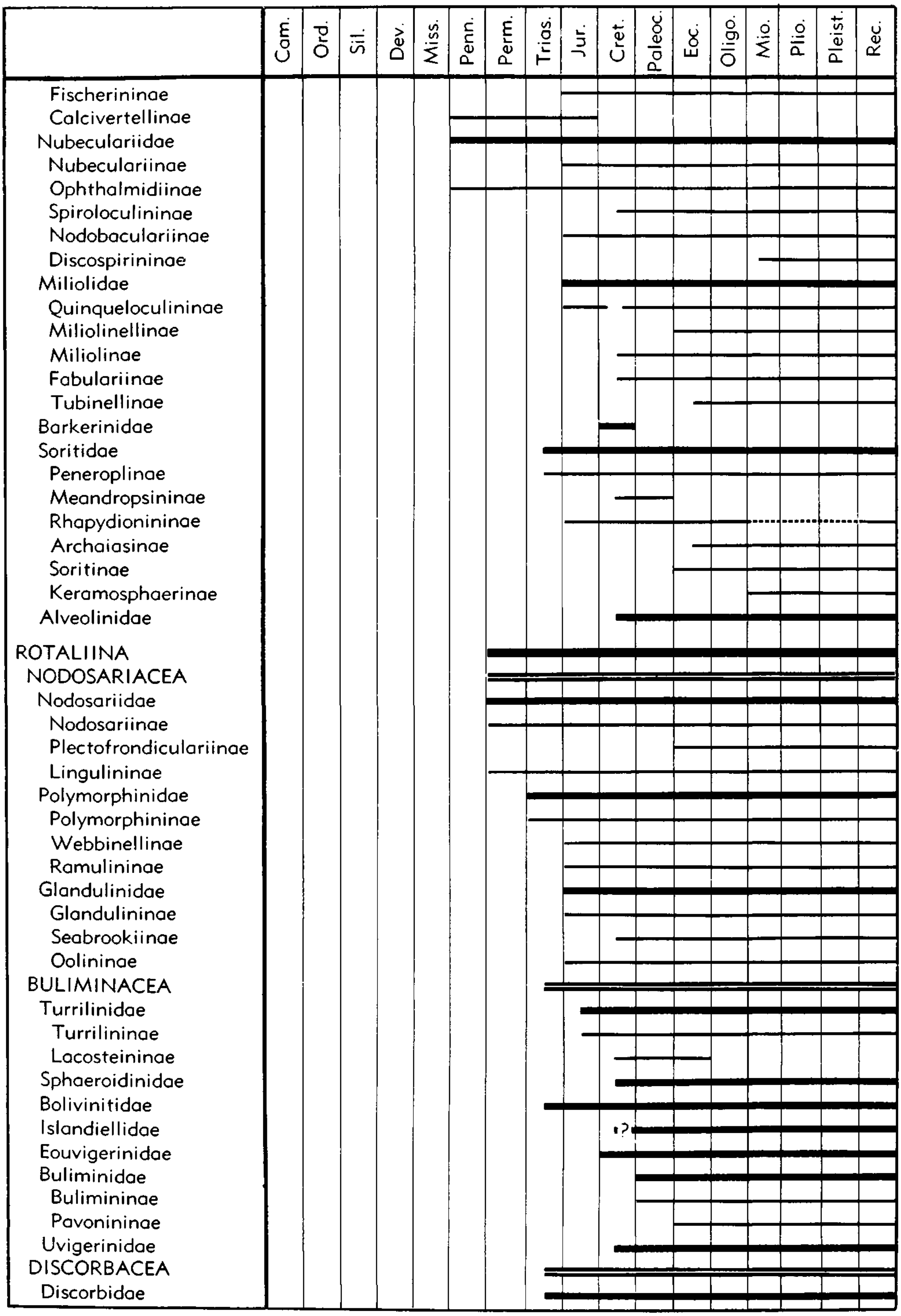

Fig. 83A *(continued)*.

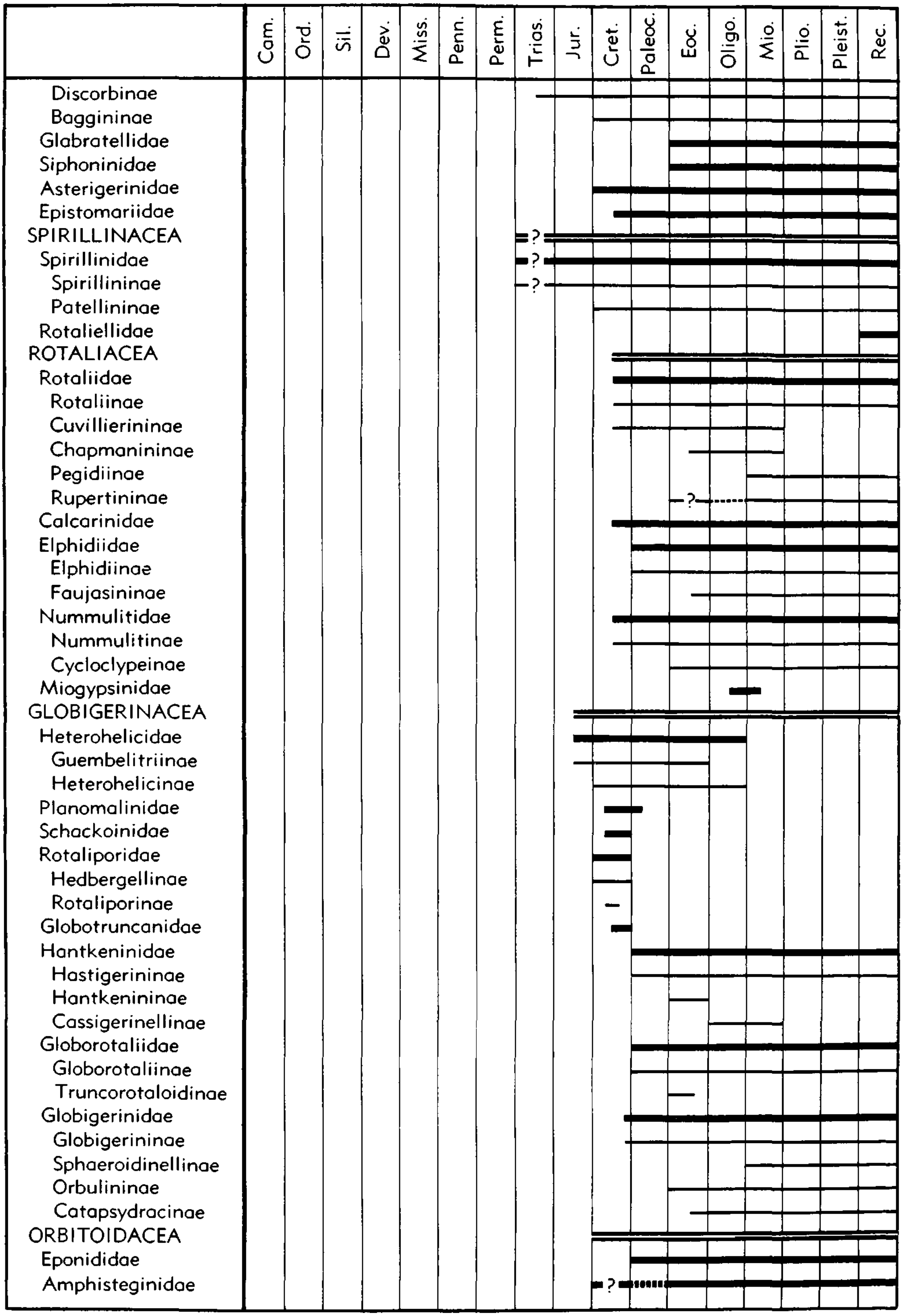

FIG. 83A *(continued)*.

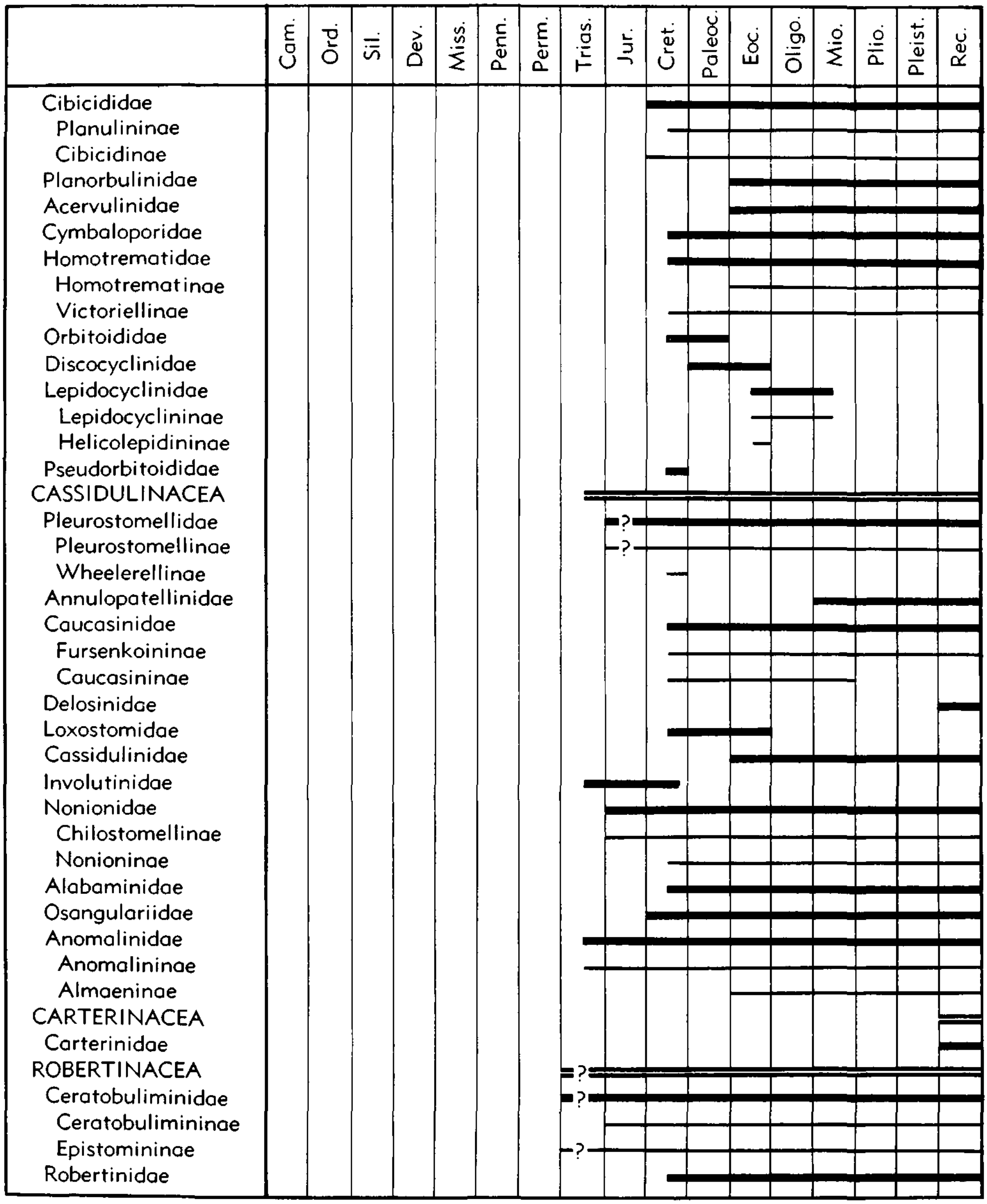

FIG. 83A *(continued)*.

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)

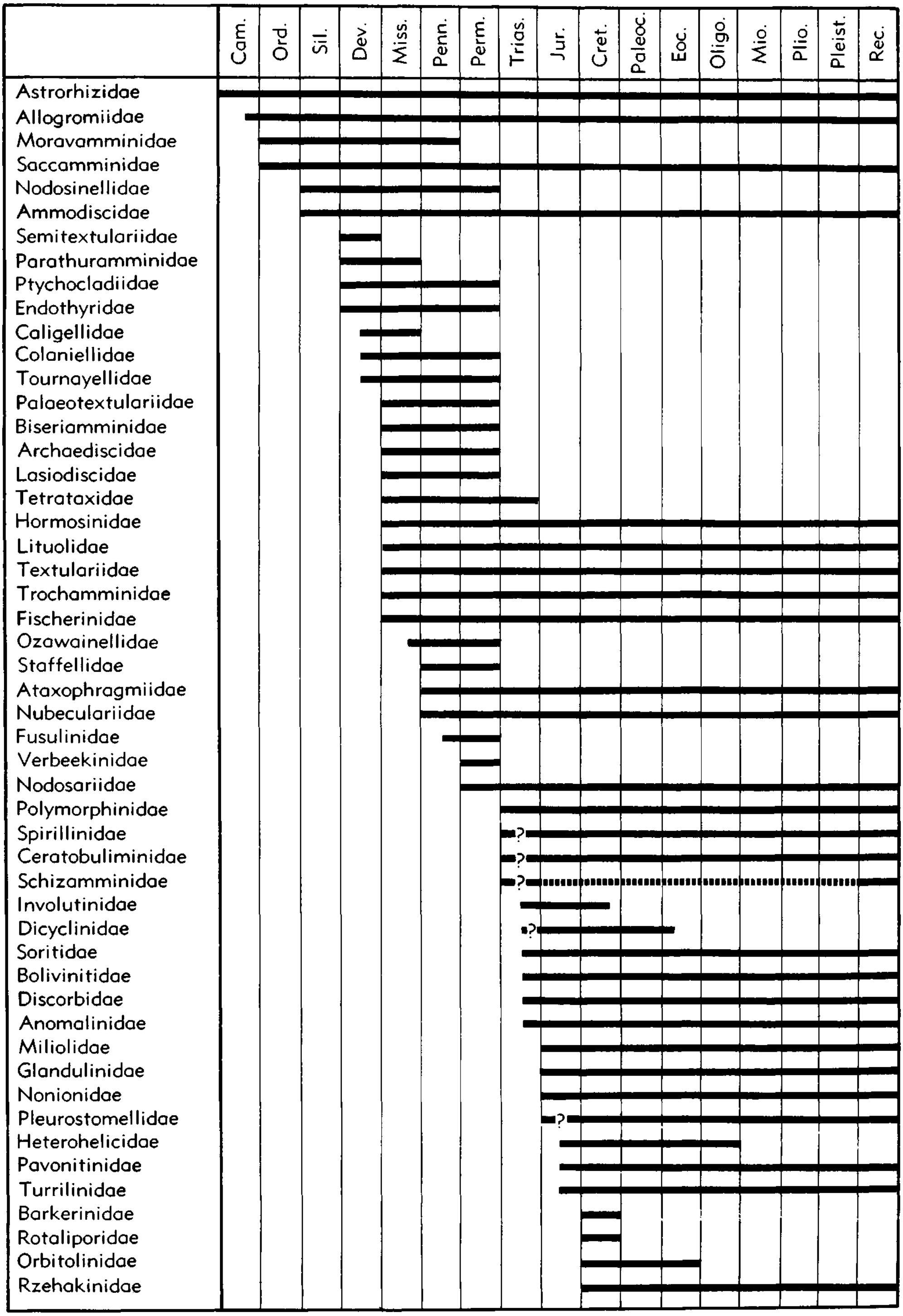

FIG. 83B. Graph showing stratigraphic distribution of families of Foraminiferida plotted according to relative time values (*2117).

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)

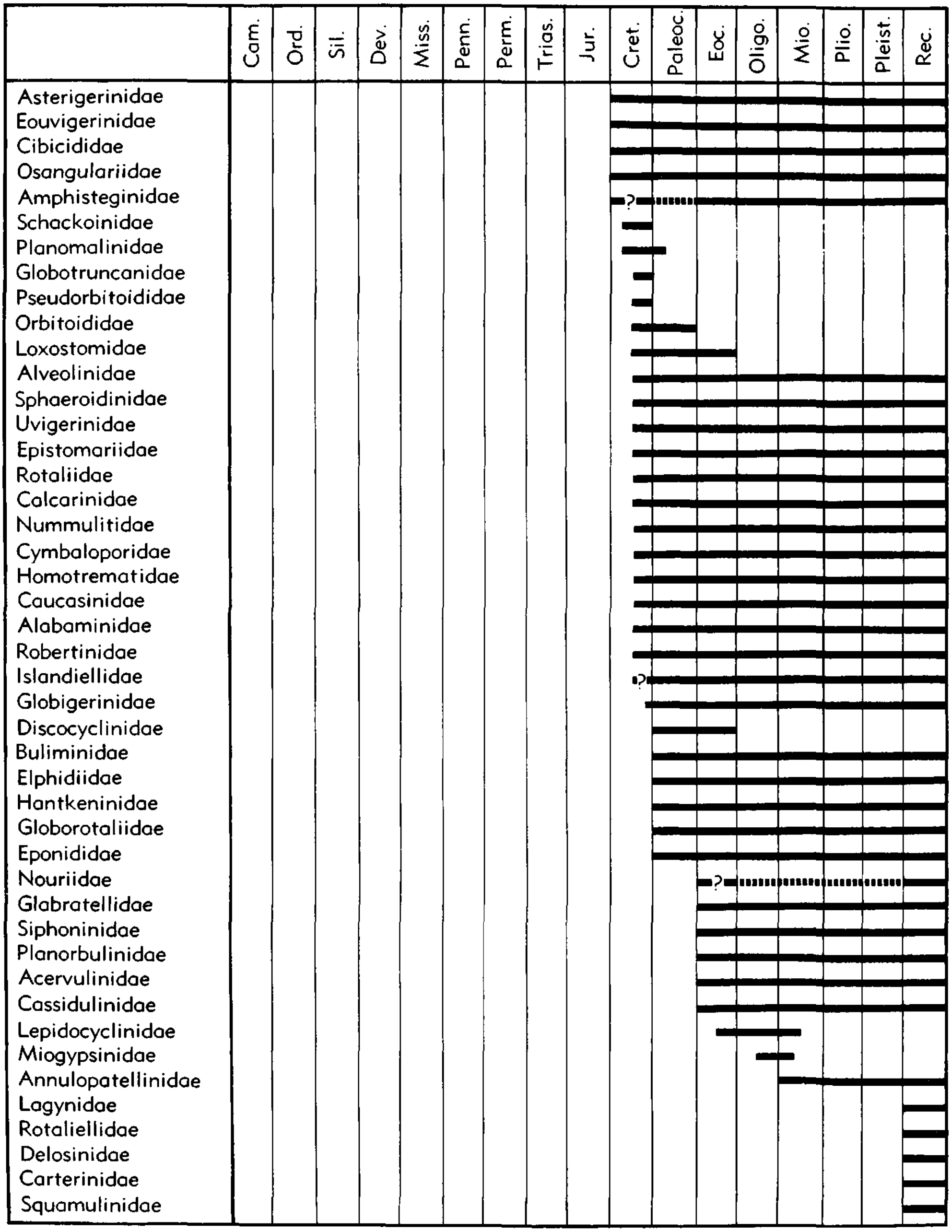

Fig. 83B *(continued)*.

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; =^{5}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; =^{3}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; =^{2}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

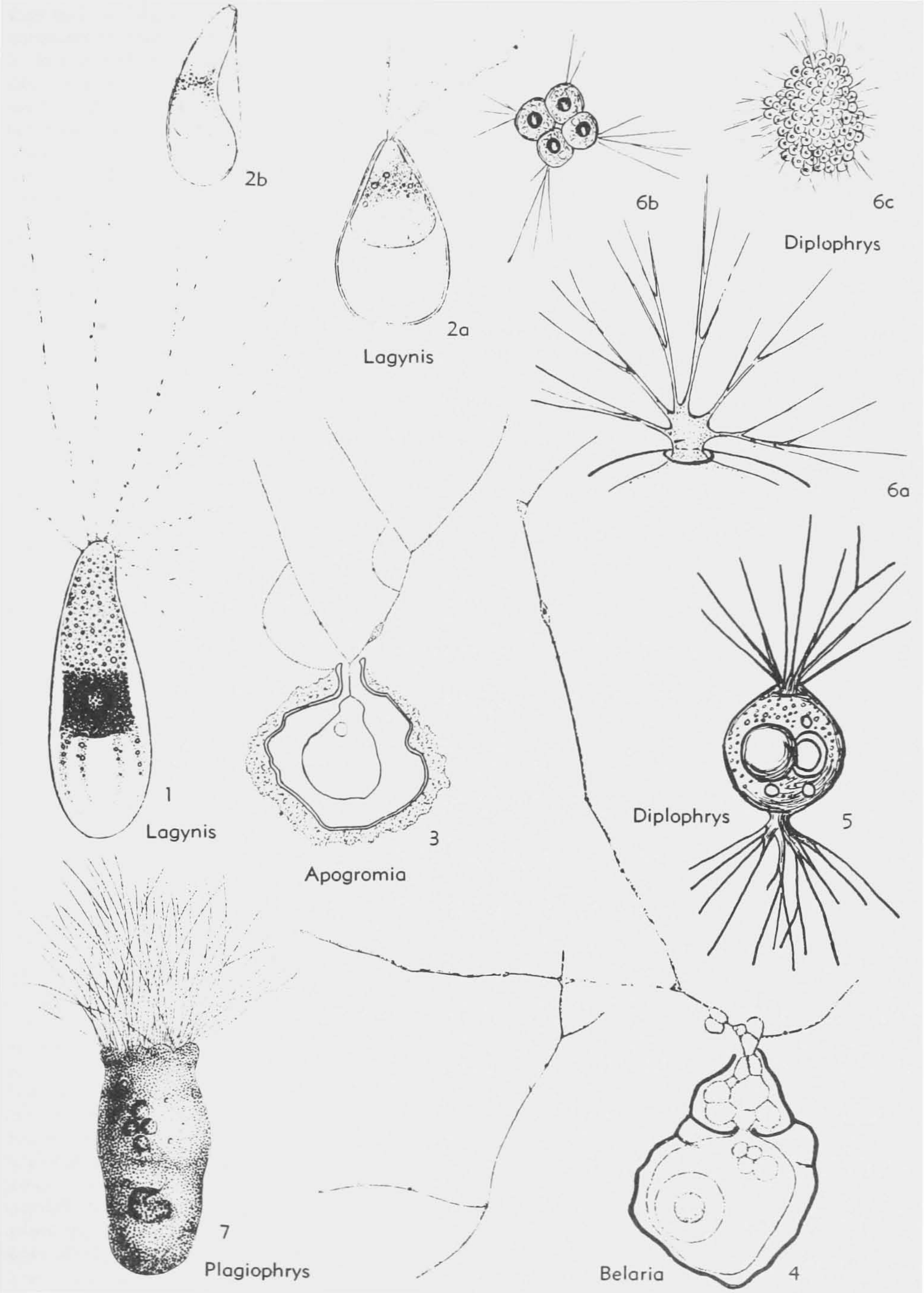

FIG. 84. Lagynidae; *1, 2, Lagynis; 3, Apogromia; 4, Belaria; 5, 6, Diplophrys; 7, Plagiophrys* (p. C166, C170).

(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-

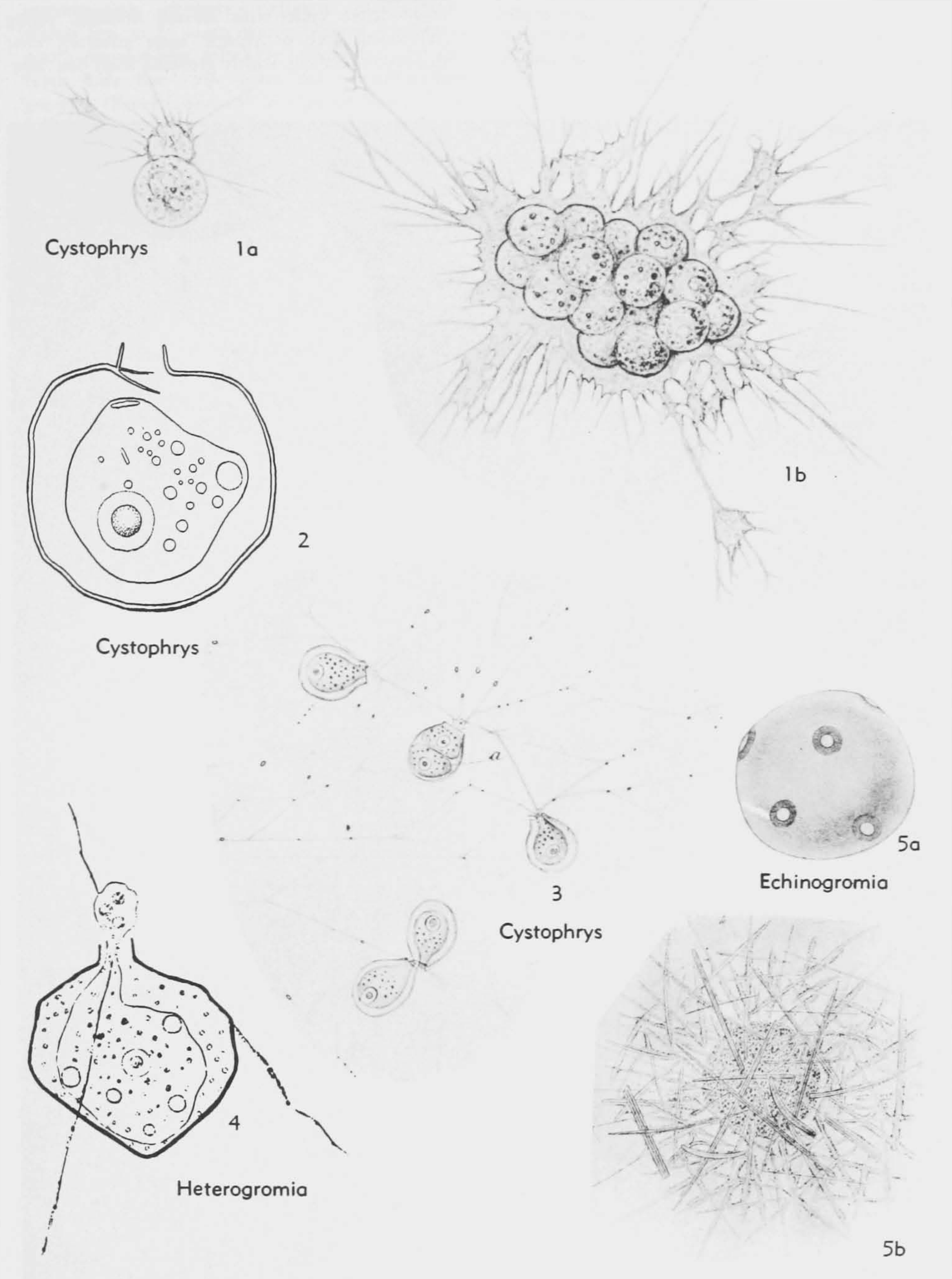

FIG. 85. Lagynidae; *1-3, Cystophrys; 4, Heterogromia; 5, Echinogromia* (p. *C*166-*C*167).

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-

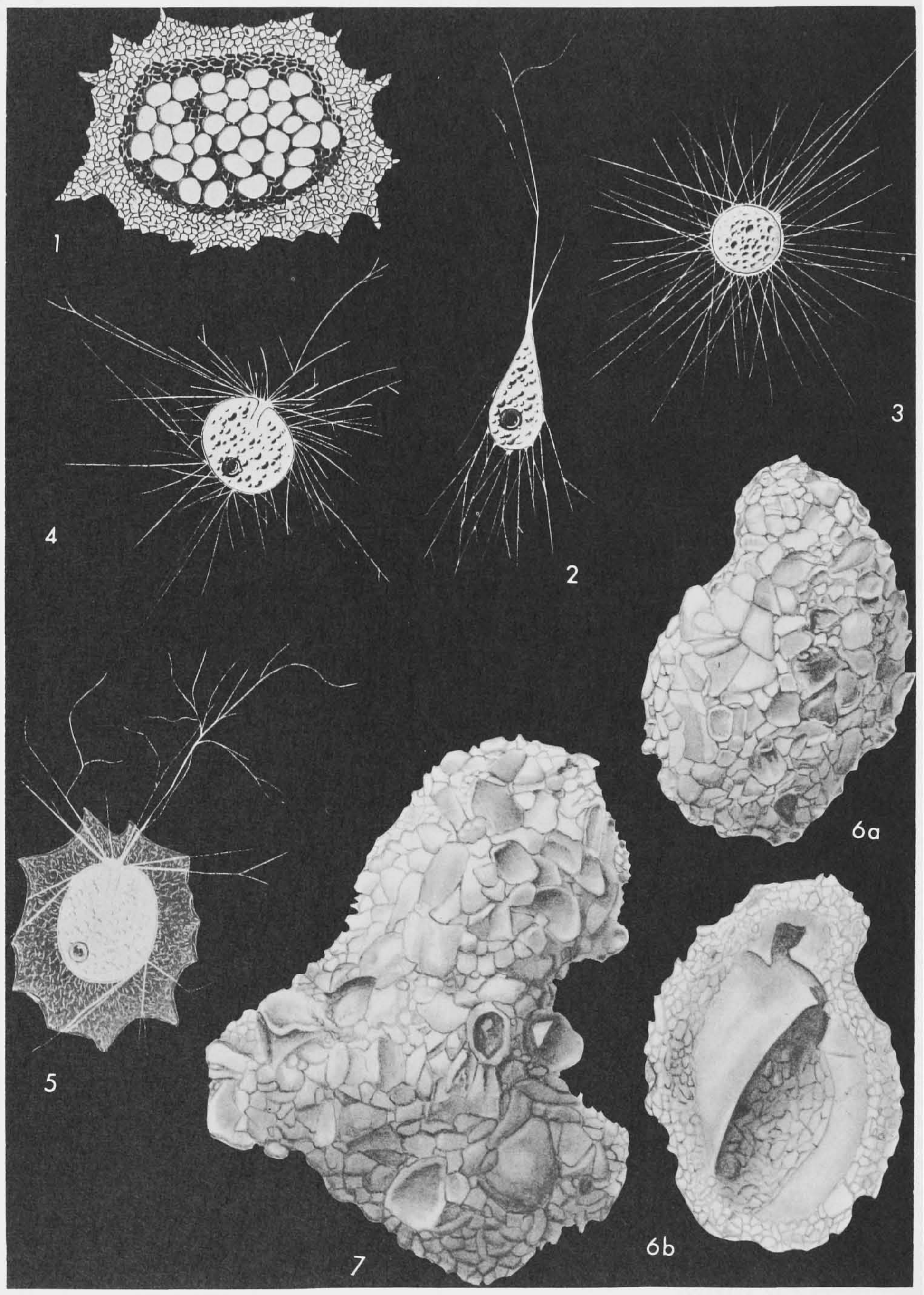

FIG. 86. Lagynidae; *1-7, Iridia* (p. C167-C169).

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).

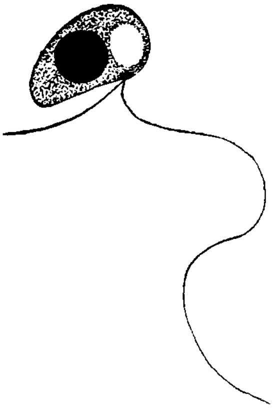

Fig. 87. Lagynidae; *Iridia* (p. C167-C169).

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,

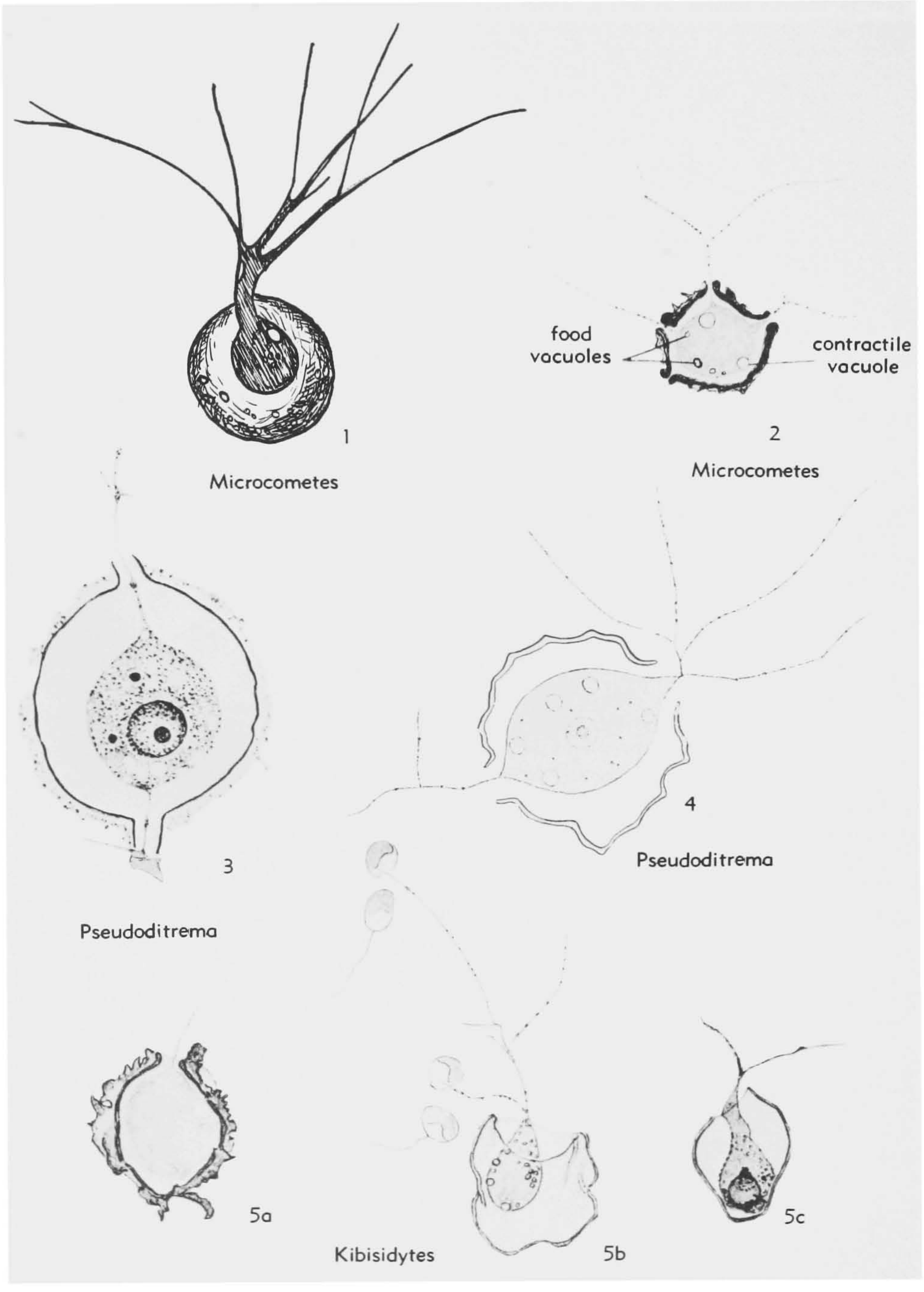

Fig. 88. Lagynidae; *1,2, Microcometes; 3-4, Pseudoditrema; 5, Kibisidytes* (p. C169, C172).

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. sphaerica*. 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. sphaerica* was identical to *Pamphagus hyalinus* (=*Lecythium*), but de-

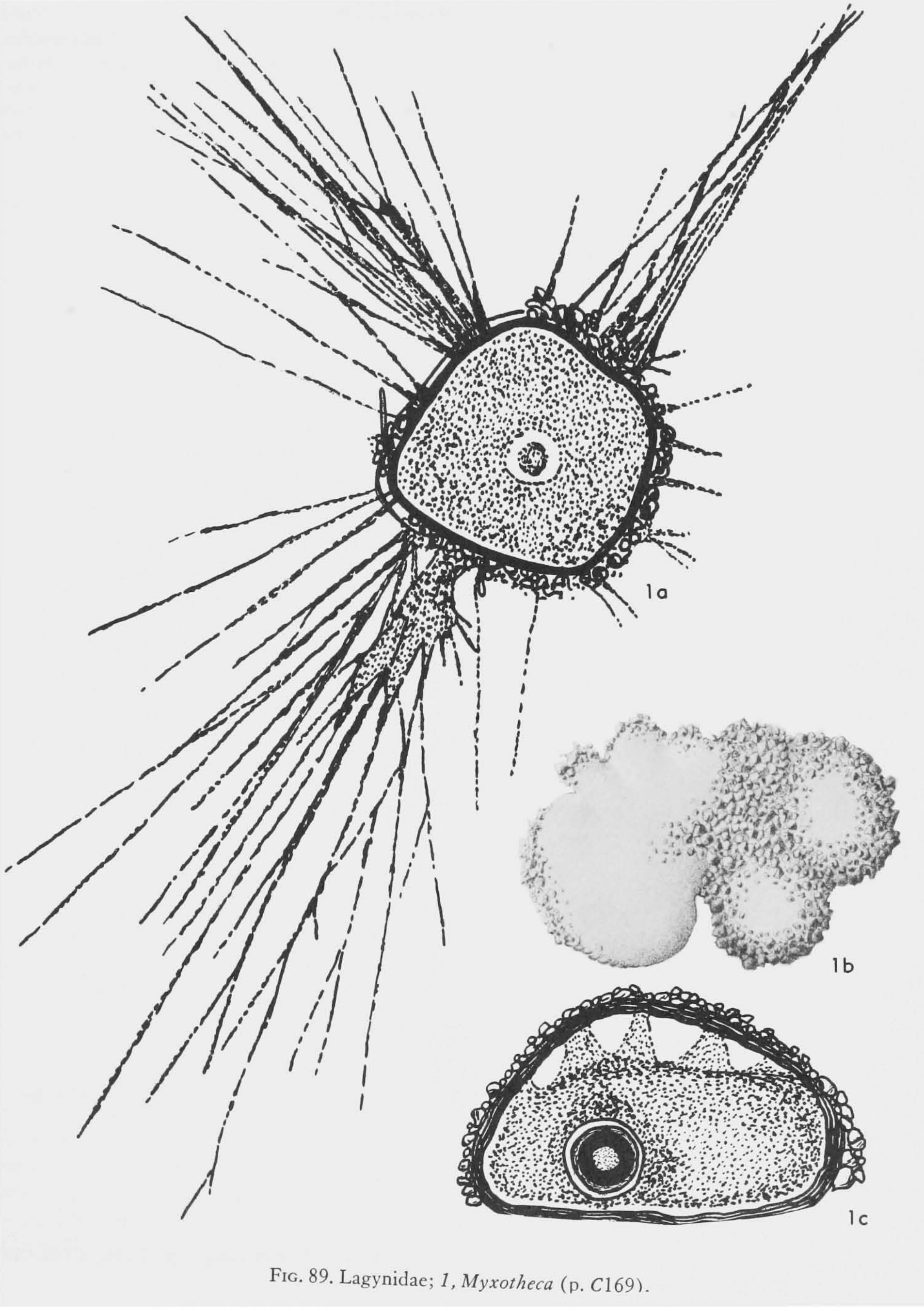

FIG. 89. Lagynidae; *1, Myxotheca* (p. C169).

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

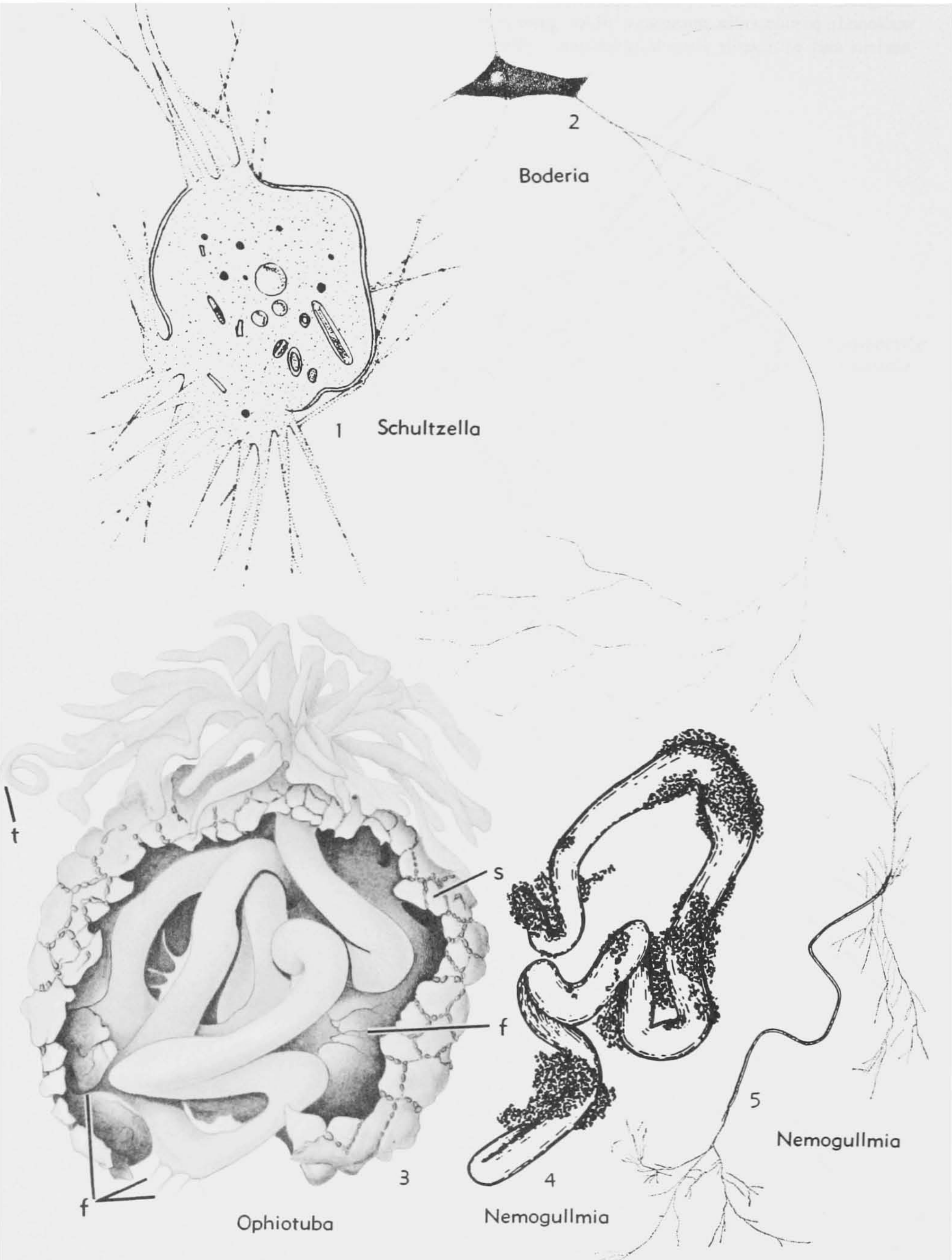

FIG. 90. Lagynidae; *1, Schultzella; 2, Boderia; 3, Ophiotuba; 4,5, Nemogullmia* (p. C166, C169-C170, C173).

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}Cratermininae 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.*

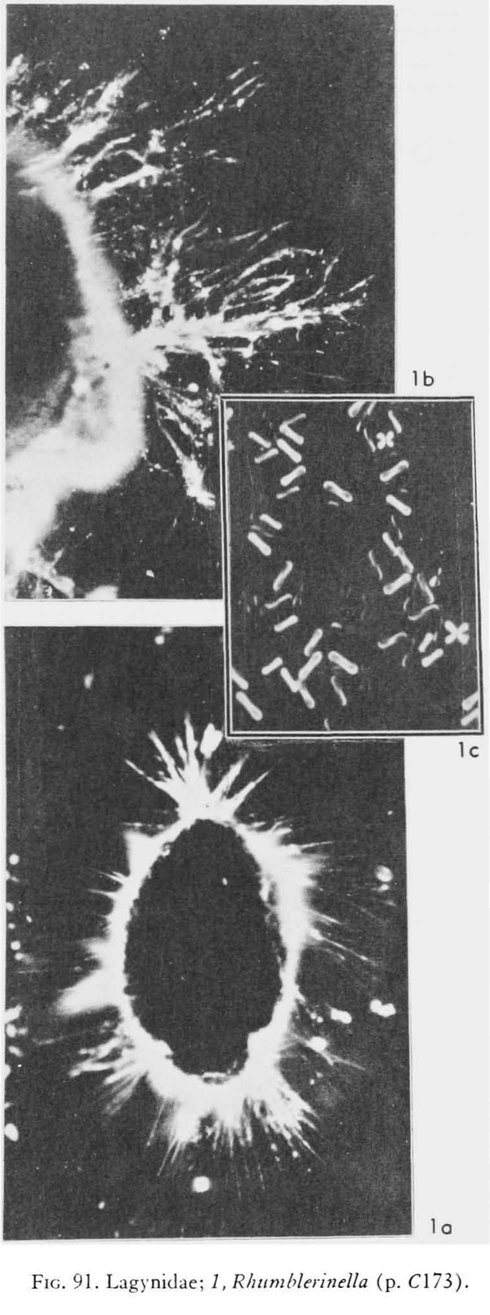

FIG. 91. Lagynidae; *1, Rhumblerinella* (p. C173).

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

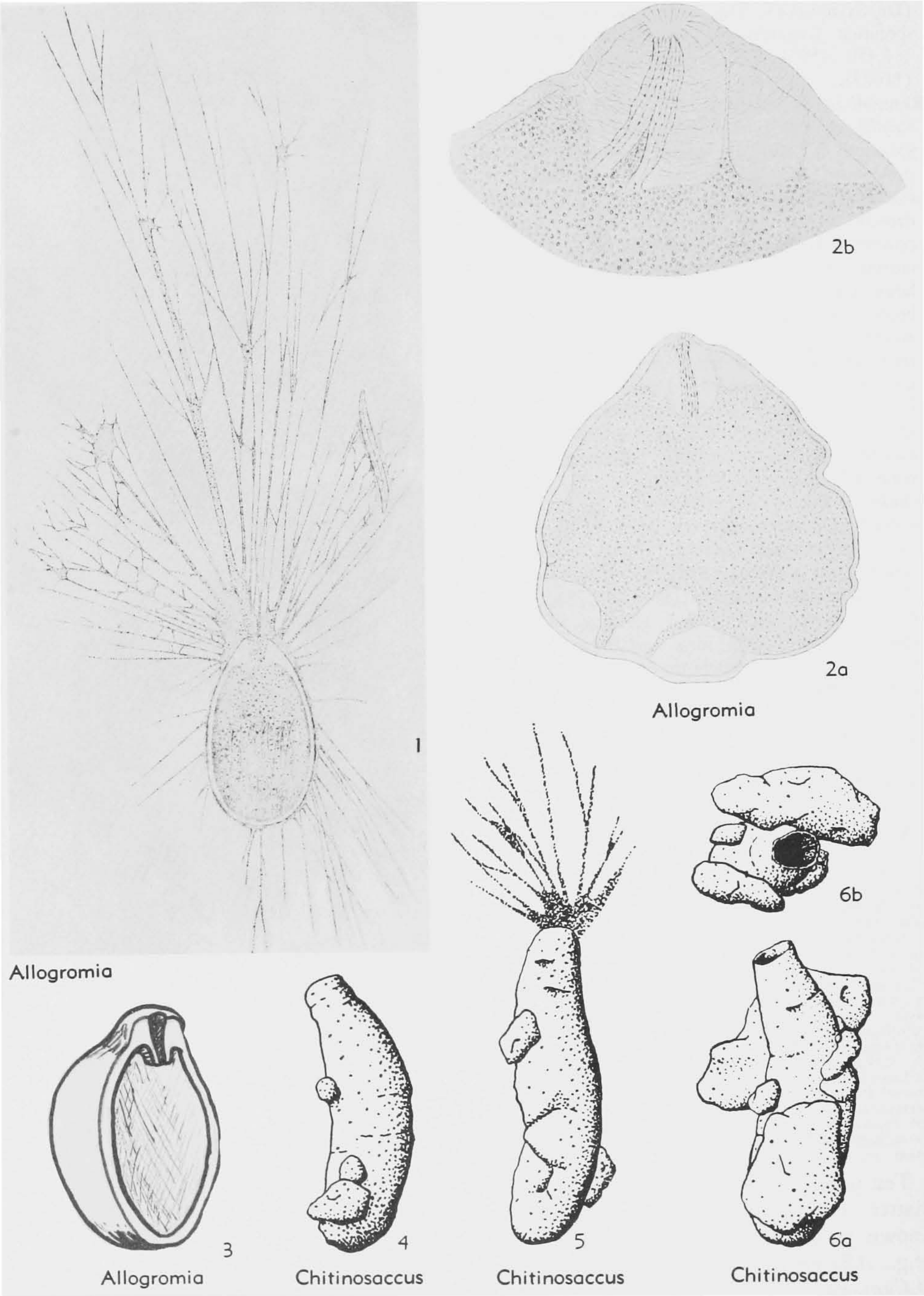

FIG. 92. Allogromiidae; *1-3, Allogromia; 4-6, Chitinosaccus* (p. C173-C176).

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).

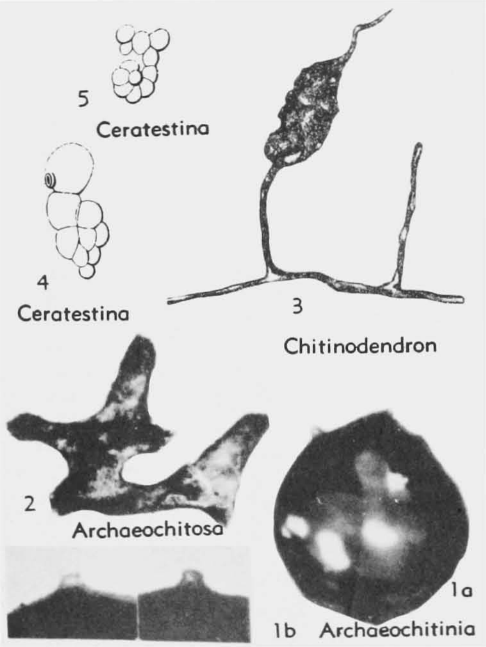

FIG. 93. Allogromiidae; *1, Archaeochitinia; 2, Archaeochitosa; 3, Chitinodendron; 4, 5, Ceratestina* (p. C175).

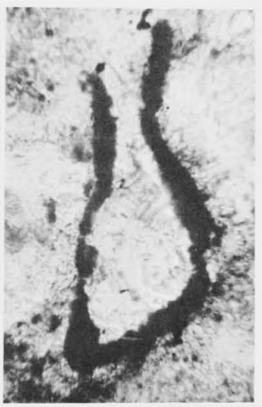

FIG. 94. Allogromiidae; *Chitinolagena* (p. C175).

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

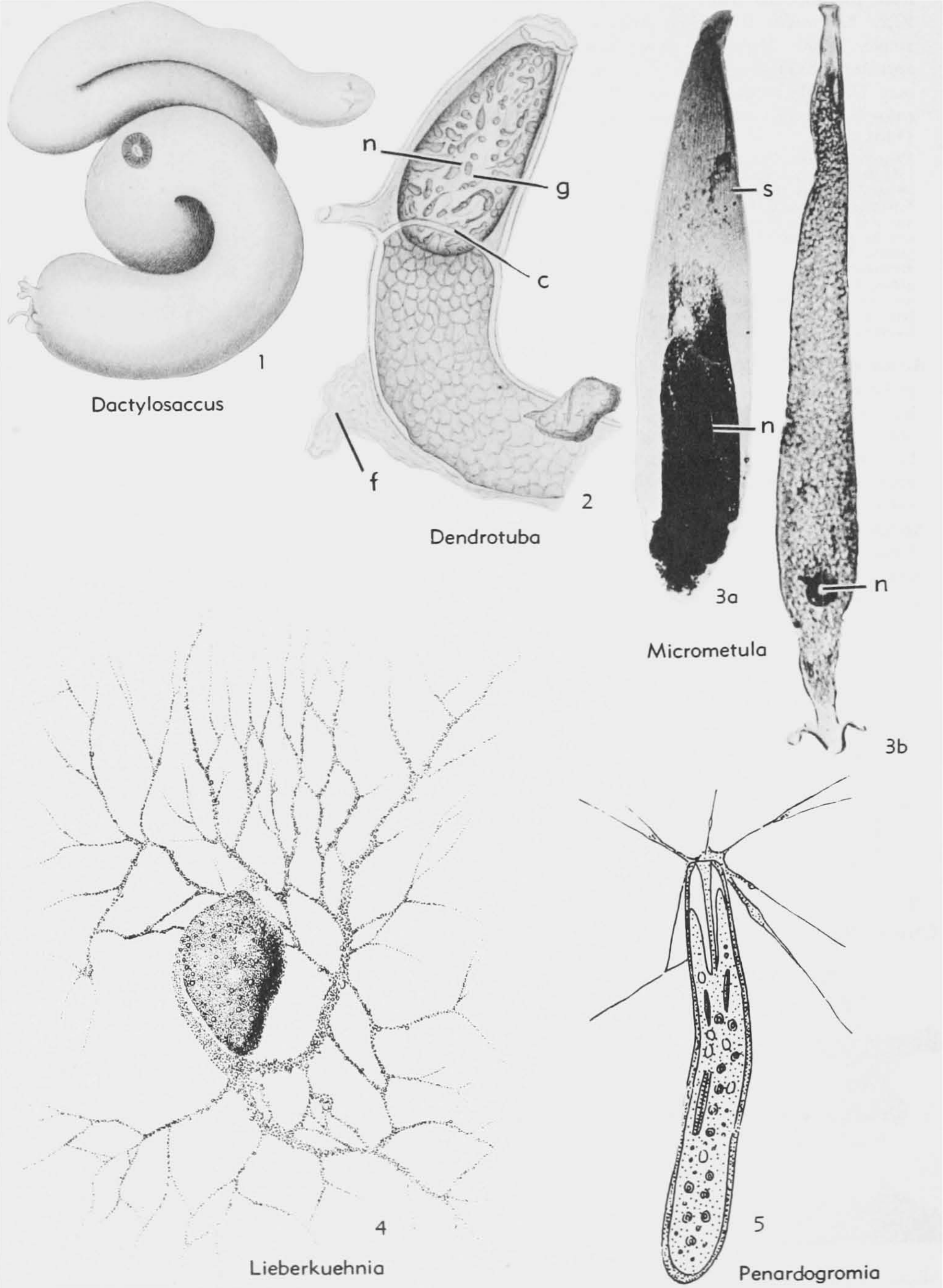

FIG. 95. Allogromiidae; *1, Dactylosaccus; 2, Dendrotuba; 3, Micrometula; 4, Lieberkuehnia; 5, Penardogromia* (p. C176-C177, C179, C181).

[**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).

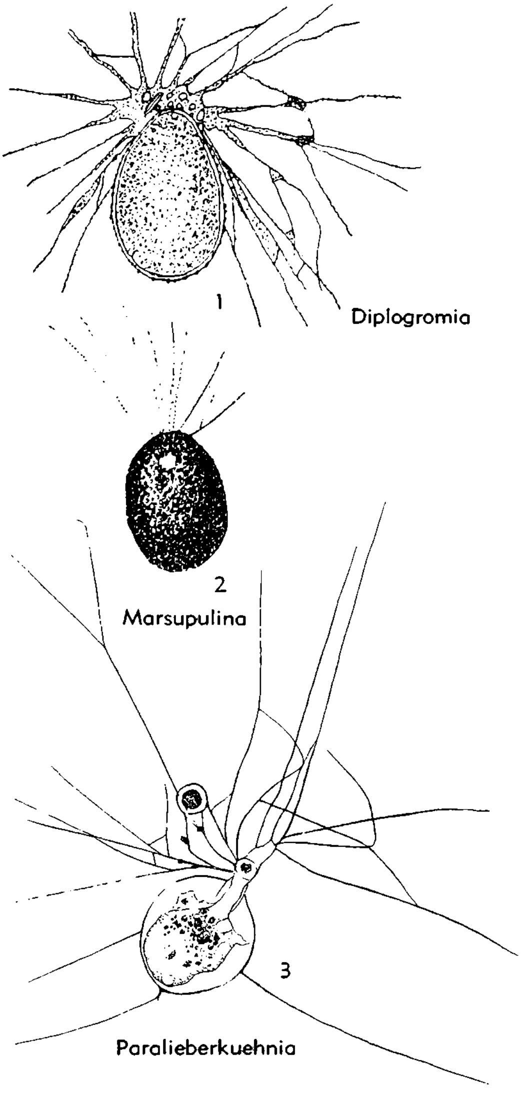

Fig. 96. Allogromiidae; *1, Diplogromia; 2, Marsupulina; 3, Paralieberkuehnia* (p. C177, C179, C181).

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. *tastikoliensis; 1,* holotype, *2*, paratype, ×330 (*2112).

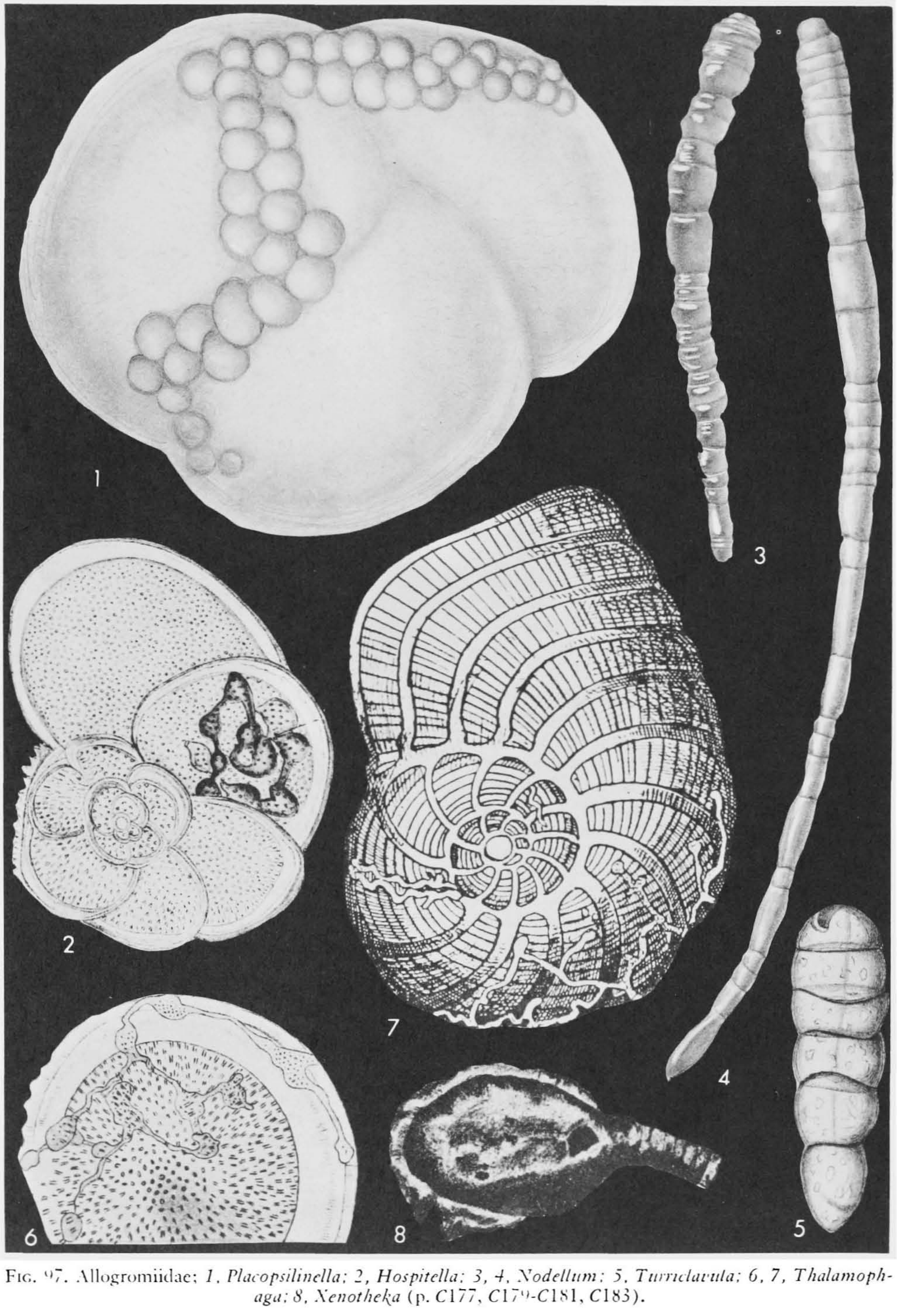

FIG. 97. Allogromiidae; *1, Placopsilinella; 2, Hospitella; 3, 4, Nodellum; 5, Turriclavula; 6, 7, Thalamophaga; 8, Xenotheka* (p. C177, C179-C181, C183).

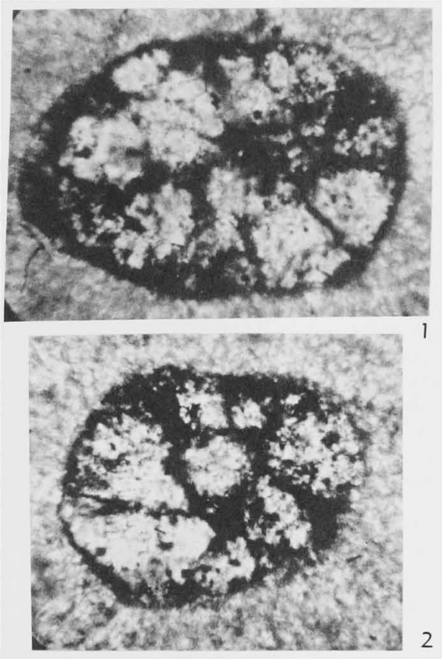

FIG. 98. Allogromiidae; *1,2, Labyrinthochitinia* (p. *C*177-*C*178).

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 ribbon-like 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.*,

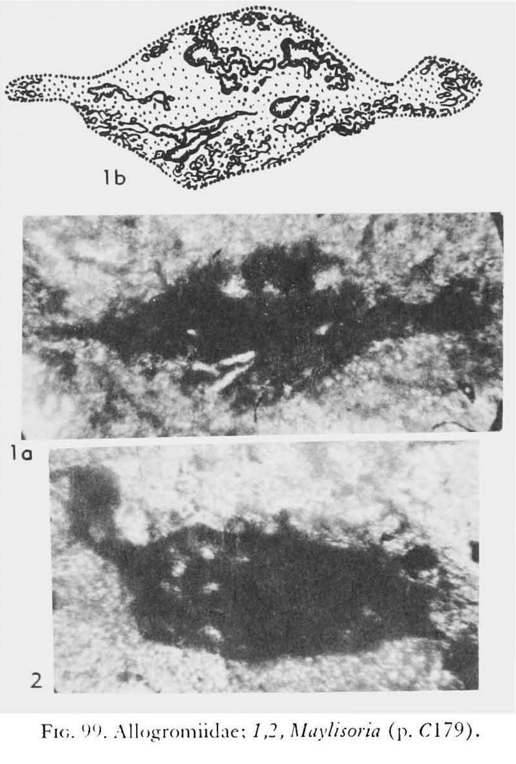

FIG. 99. Allogromiidae; *1,2, Maylisoria* (p. *C*179).

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-

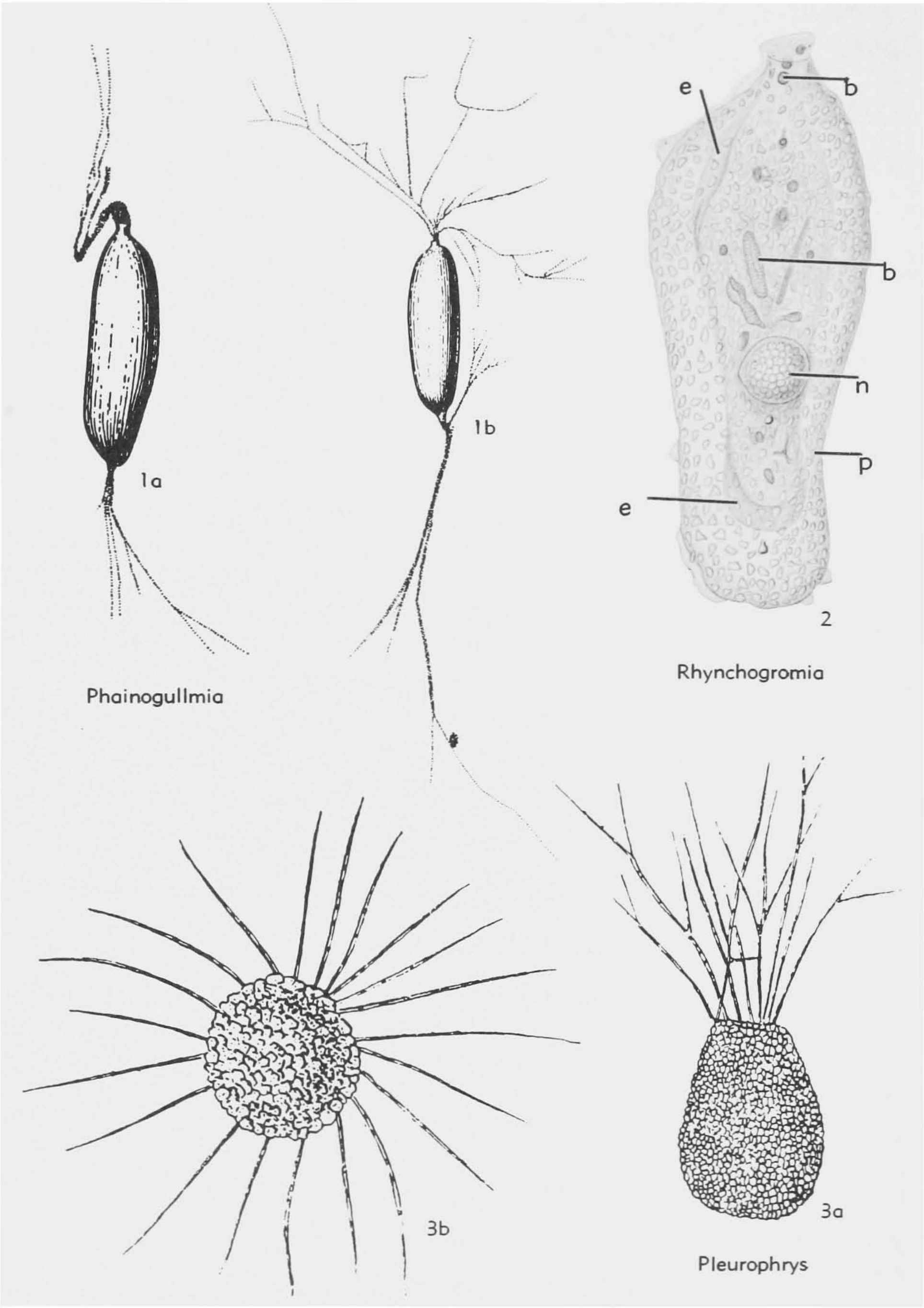

Fig. 100. Allogromiidae; *1, Phainogullmia; 2, Rhynchogromia; 3, Pleurophrys* (p. C181).

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-

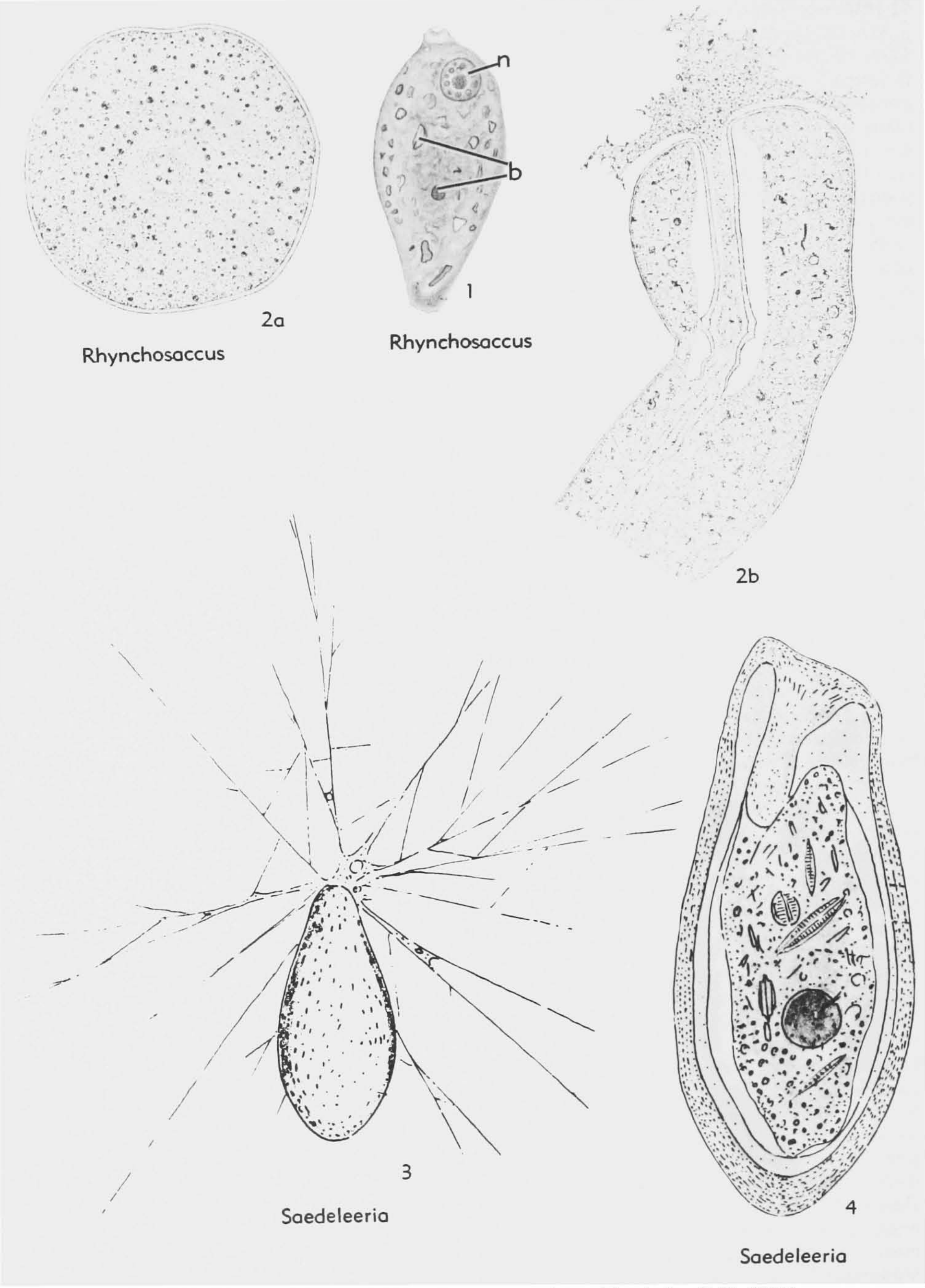

FIG. 101. Allogromiidae; *1, 2, Rhynchosaccus; 3, 4, Saedeleeria* (p. C181-C182).

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. ḳlinostoma;* 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 *Xenotheḳa* it is here recognized as belonging to the Allogromiidae.] *Sil.*, Eu.——Fig. 97,*8*. **X. ḳlinostoma,* E. Prussia [Poland]; paratype, ×60 (*700).

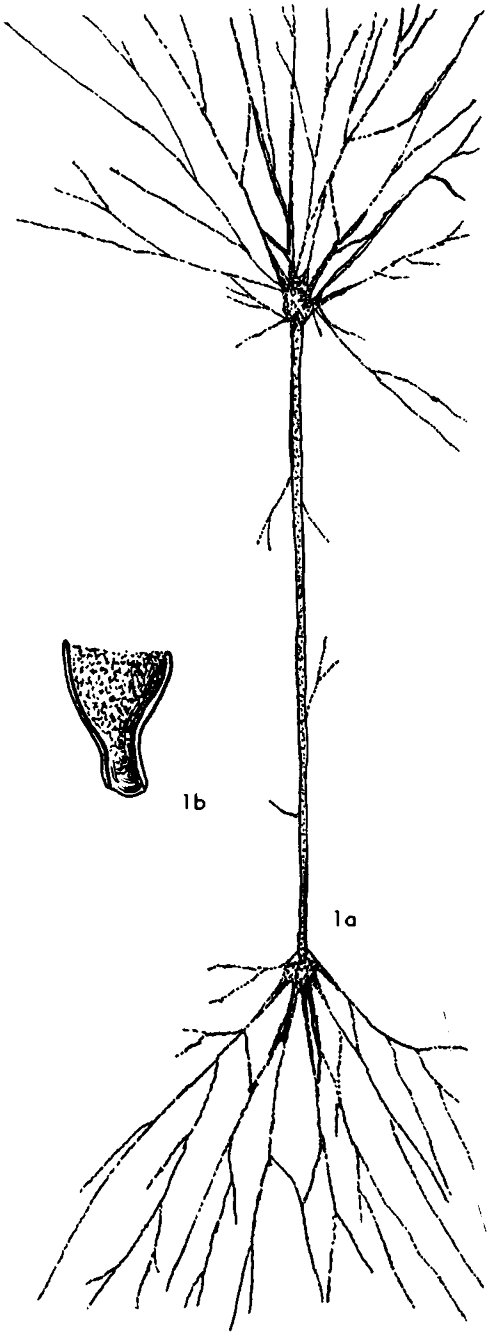

Fig. 102. Allogromiidae; *1, Shepheardella* (p. C182-C183).

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,

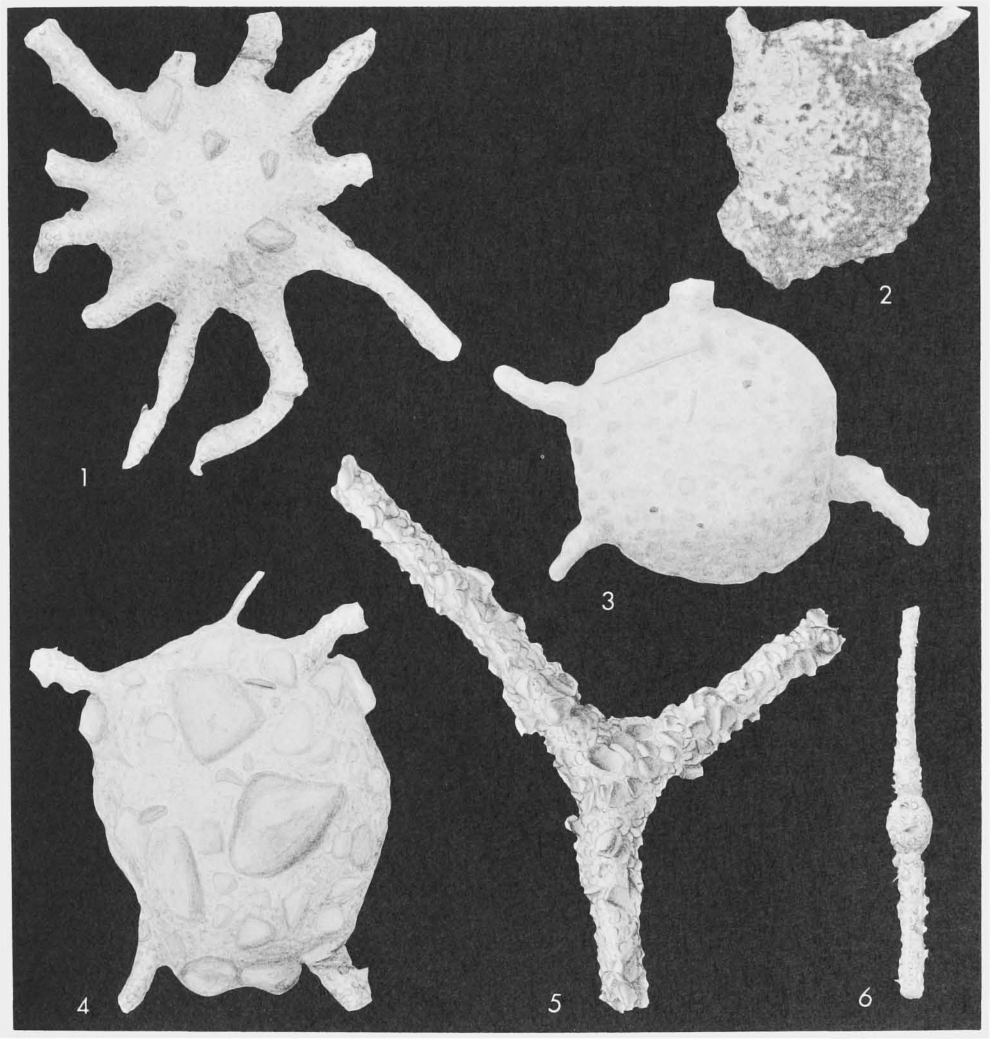

Fig. 103. Astrorhizidae (Astrorhizinae; *1, Astrorhiza; 2-4, Astrammina; 5,6, Rhabdammina*) (p. C184-C186).

*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

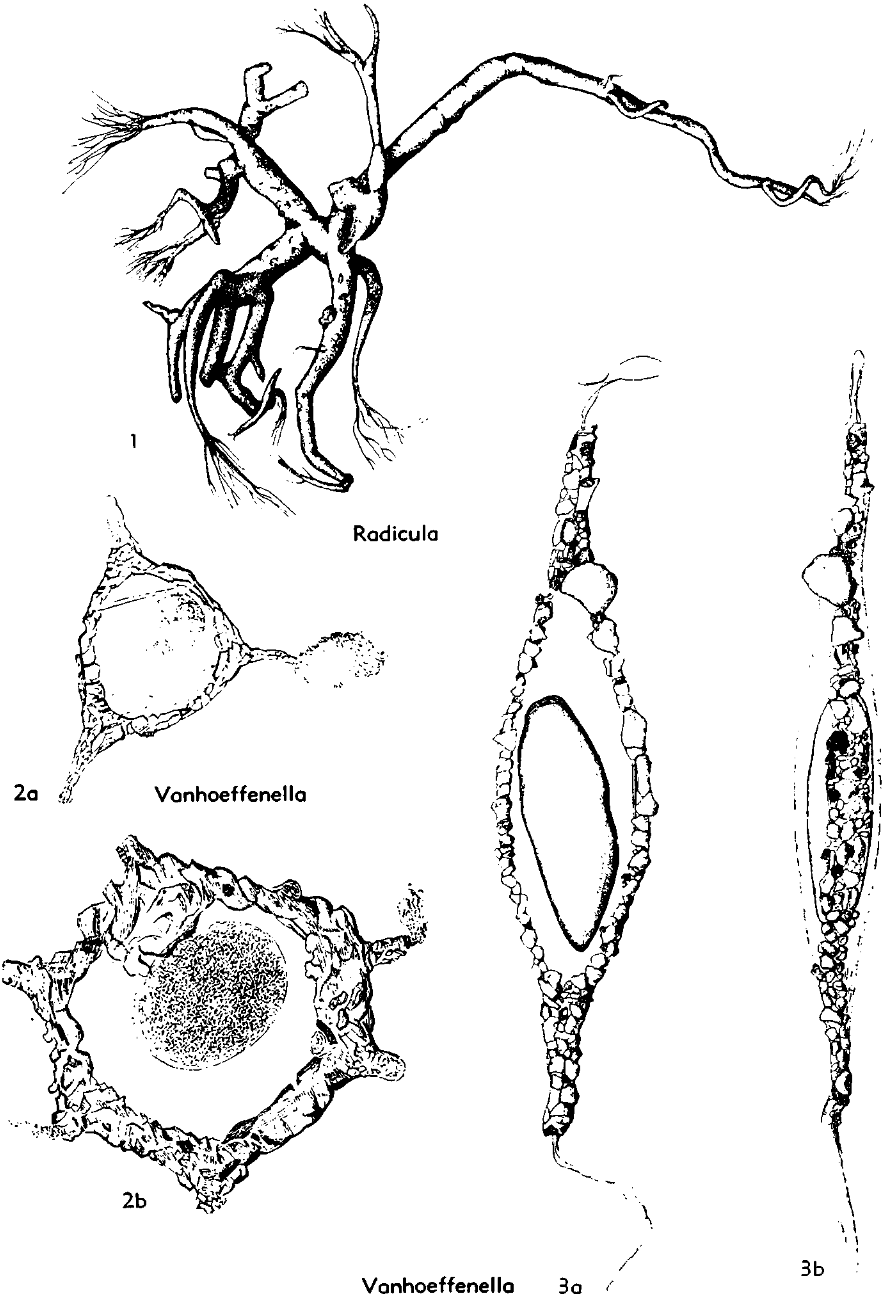

FIG. 104. Astrorhizidae (Astrorhizinae; *1*, *Radicula*; *2*,*3*, *Vanhoeffenella*) (p. C185-C186).

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-

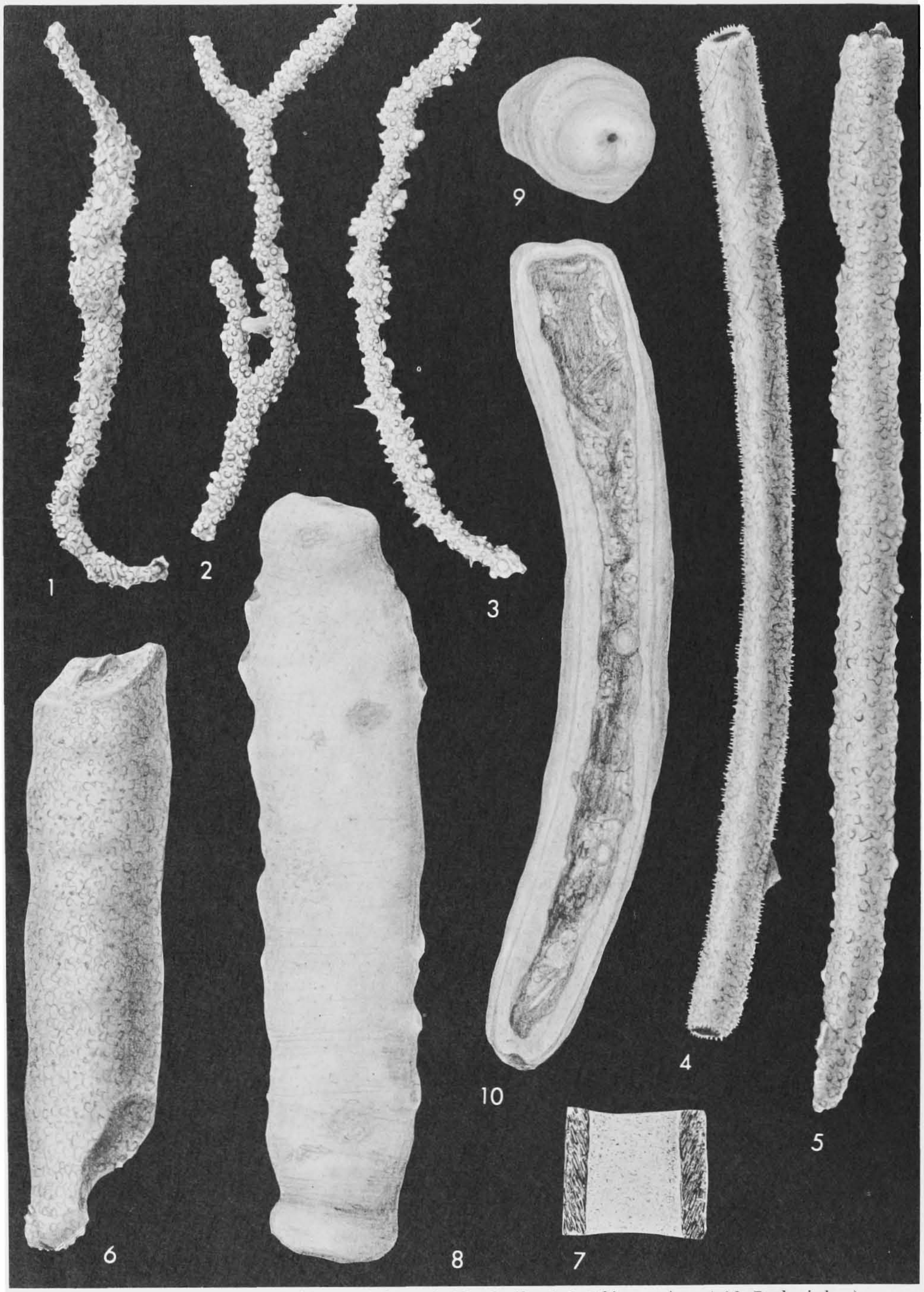

Fig. 105. Astrorhizidae (Rhizammininae; *1, Marsipella; 2, 3, Rhizammina; 4-10, Bathysiphon*) (p. *C*186-*C*187).

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-

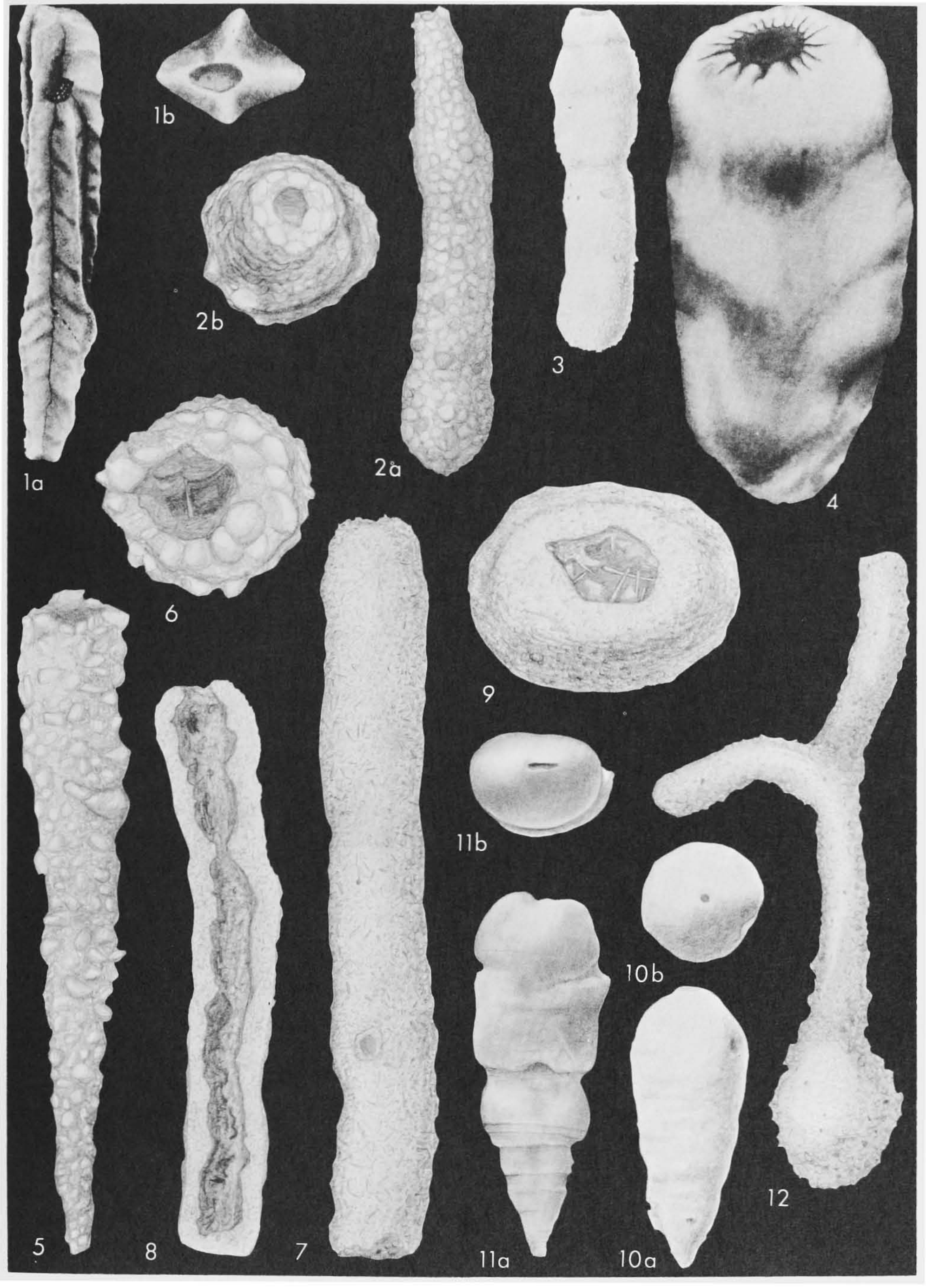

FIG. 106. Astrorhizidae (Hippocrepininae; *1, Giraliarella; 2, 3, Hyperammina; 4, Pseudohyperammina; 5, 6, Jaculella; 7-9, Protobotellina; 10, 11, Hippocrepina; 12, Saccorhiza*) (p. C188-C190).

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-

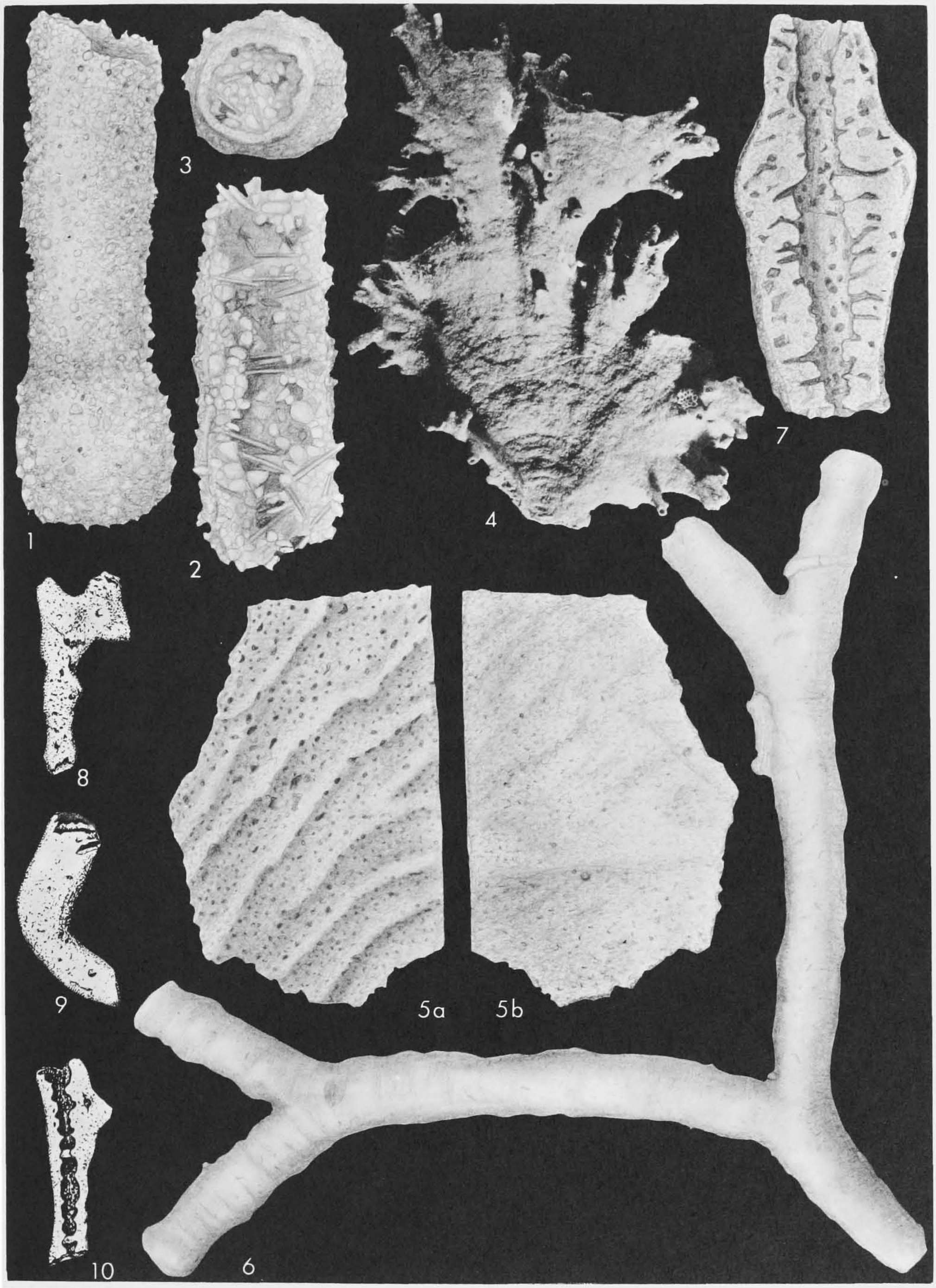

Fig. 107. Astrorhizidae (Botellininae; *1-3, Botellina*); Schizamminidae; *4, 5, Jullienella; 6-10, Schizammina* (p. C190-C194).

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.*

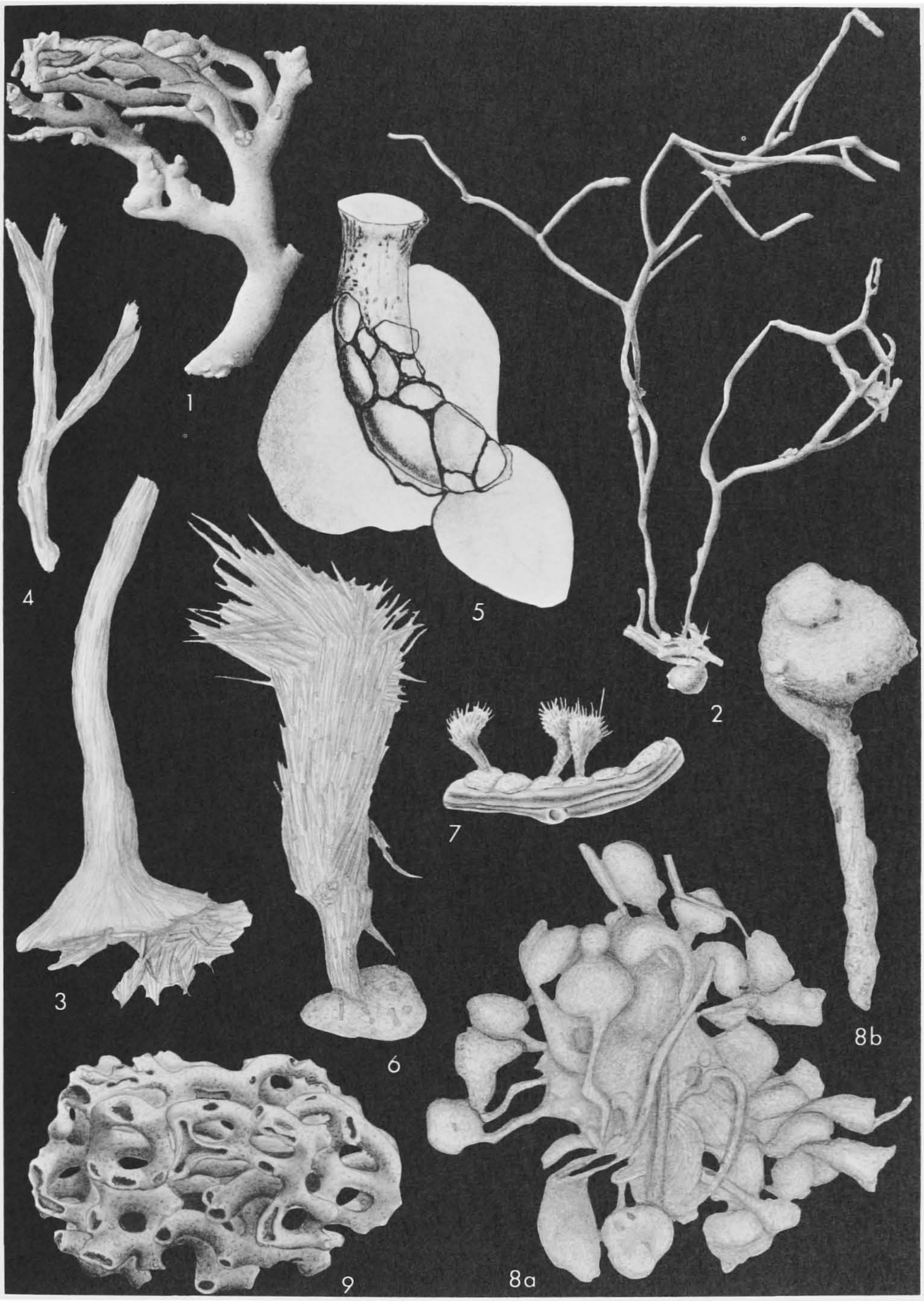

FIG. 108. Astrorhizidae (Dendrophryinae; *1,2, Dendrophrya; 3,4, Dendronina; 5, Nubeculariella; 6,7, Halyphysema; 8, Normanina; 9, Syringammina*) (p. C192).

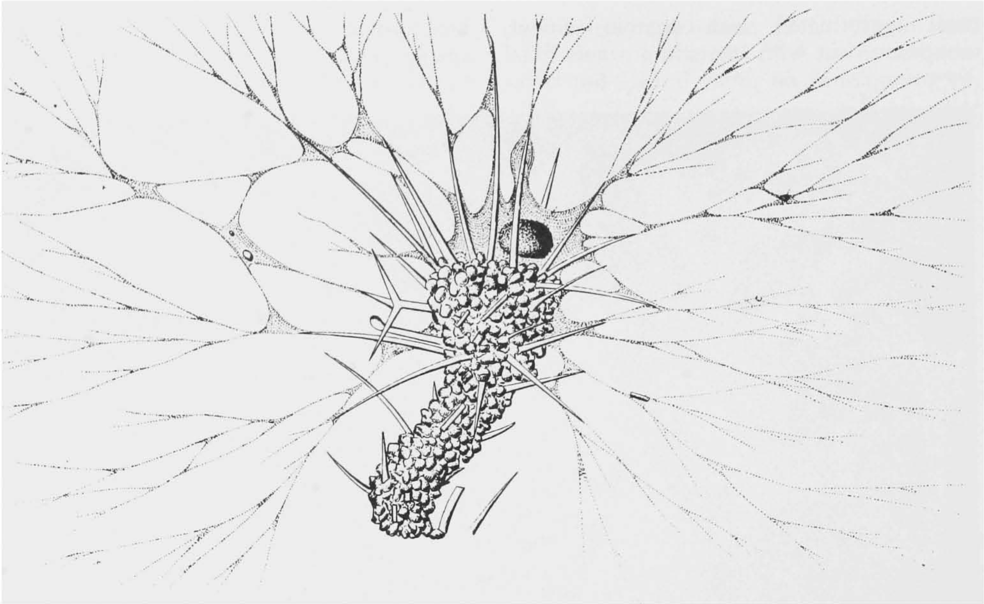

Fig. 109. Astrorhizidae (Dendrophryinae; *Halyphysema*) (p. C192).

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).

Jullienella 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*.

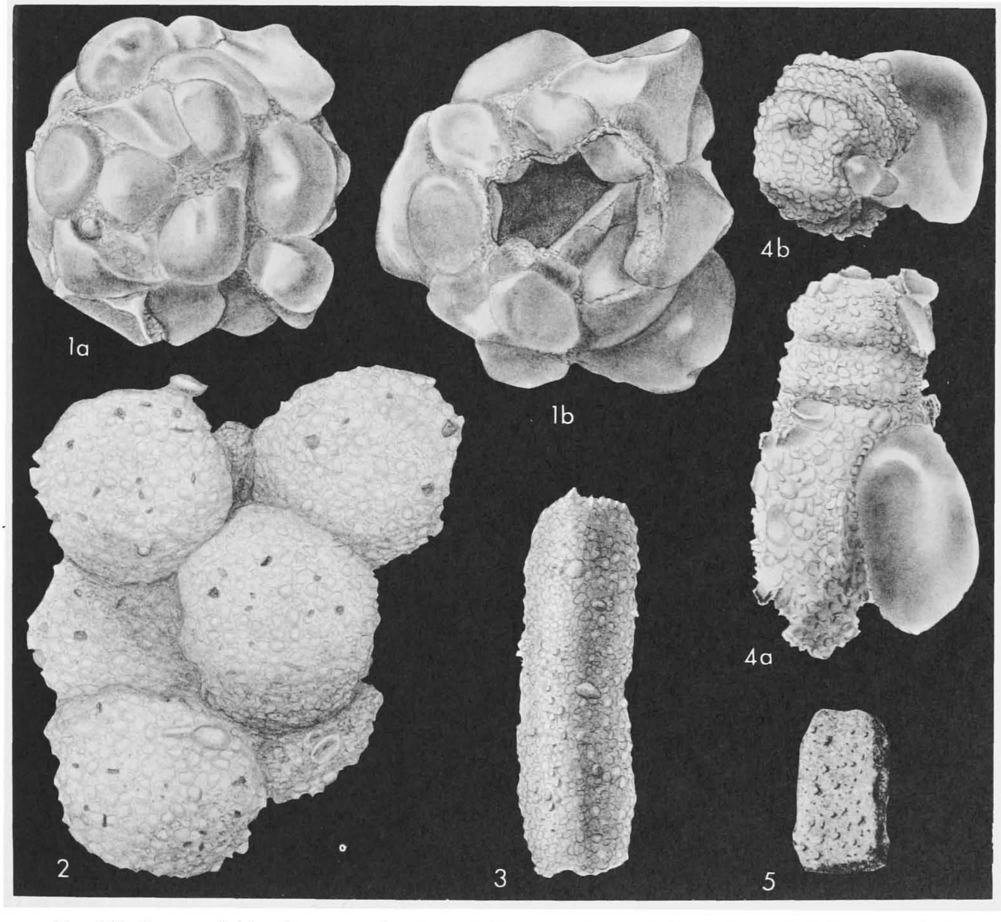

Fig. 110. Saccamminidae (Psammosphaerinae; *1, Psammosphaera; 2, Sorosphaera; 3-5, Stegnammina*) (p. C195-C196).

**B. polymorpha,* Sweden(Gotl.); *5,* neotype, ×67 (*694); *6,* hemispherical form, ×58 (*693a); *7,* irregularly grooved, ×40 (*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.); ×40 (*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, ×50 (*694).——Fig. 111,*10.* *P. hospitalis* (Wetzel), Paleoc. (Dan.), Ger., ×115 (*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.; ×22 (*2117).——Fig. 111,*11.* *S. consociata* (Rhumbler), Rec., Antarctic; ×23.5 (*2063).——Fig. 111,*12.* *S. gracilis* (Frentzen), Jur., Ger.; approx. ×30 (*747).——Fig. 111,*13.* *S. robusta* (Frentzen), Jur., Ger.; holotype, approx. ×20 (*747).——Fig. 111,*14.* *S. perforata* (Shchedrina), Rec., USSR(Kara Sea); *14a,* 3-chambered specimen with last one broken; *14b,* portion of test wall, ×40 (*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), ×62 (*2117).——Fig. 110,*4.* *S. mica* (Moreman), Ord., USA(Okla.); *4a,b,* side and end view, ×83 (*2117).——Fig. 110,*5.* *S. quadrangularis* (Dunn), Sil., USA(Ill.); ×24 (*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, ×20; *17,* sectioned specimen showing wall thickness, ×20 (*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.; ×47 (*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.,

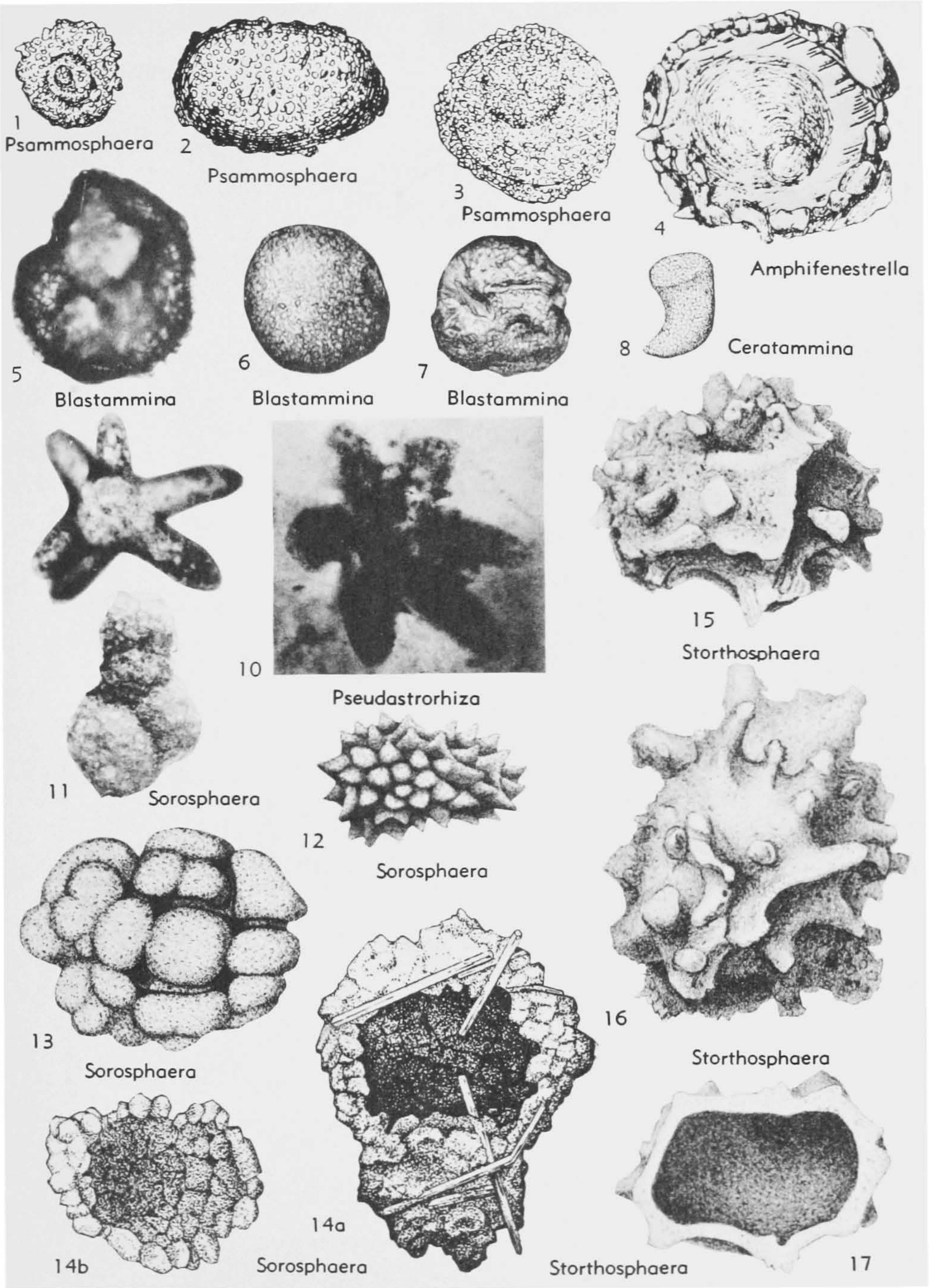

FIG. 111. Saccamminidae (Psammosphaerinae; *1-3*, *Psammosphaera; 4*, *Amphifenestrella; 5-7*, *Blastammina; 8*, *Ceratammina; 9,10*, *Pseudastrorhiza; 11-14*, *Sorosphaera; 15-17*, *Storthosphaera*) (p. C195-C196).

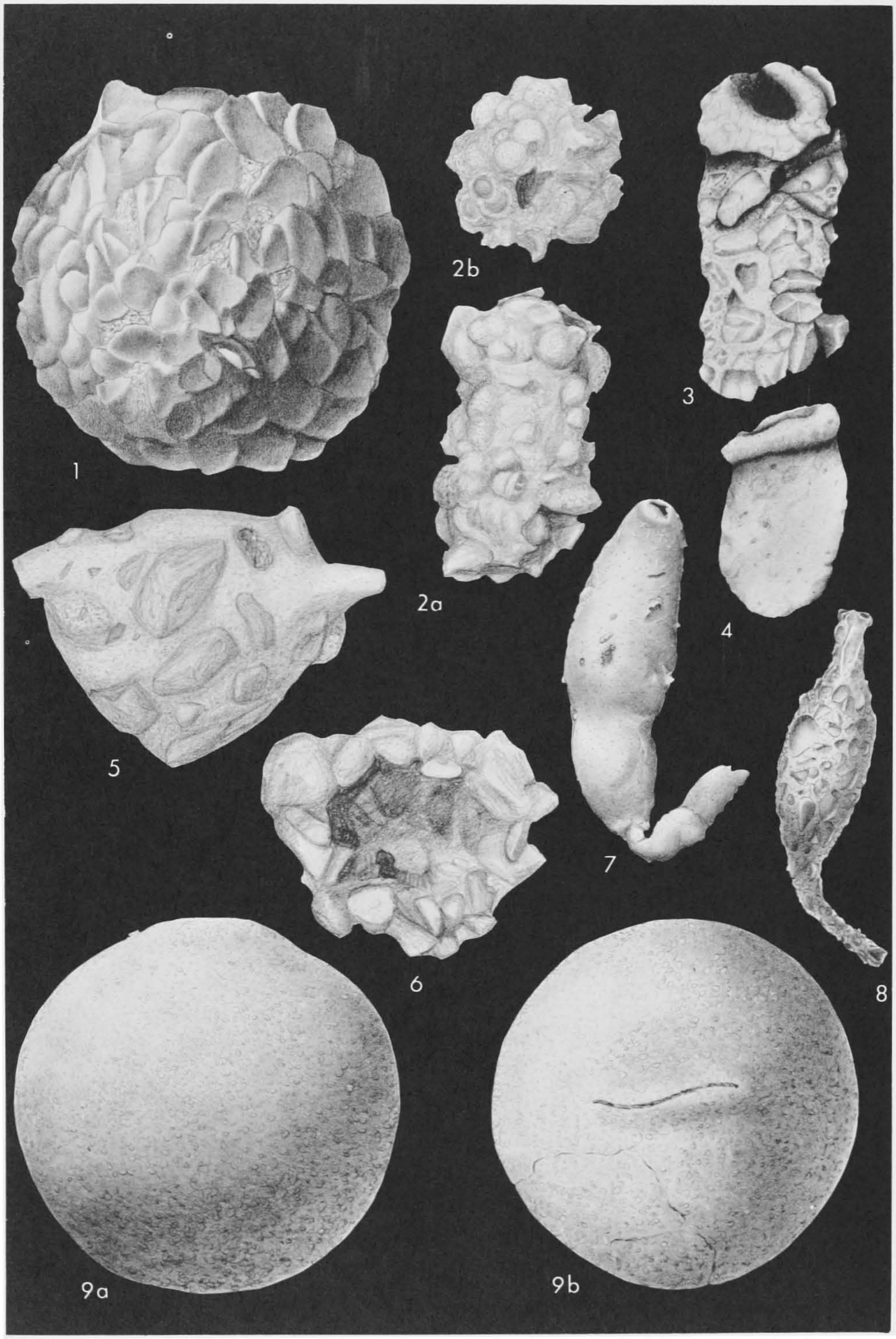

FIG. 112. Saccamminidae (Saccammininae; *1, Saccammina; 2-4, Brachysiphon; 5,6, Pelosphaera; 7,8, Pelosina; 9, Pilulina*) (p. C196-C201).

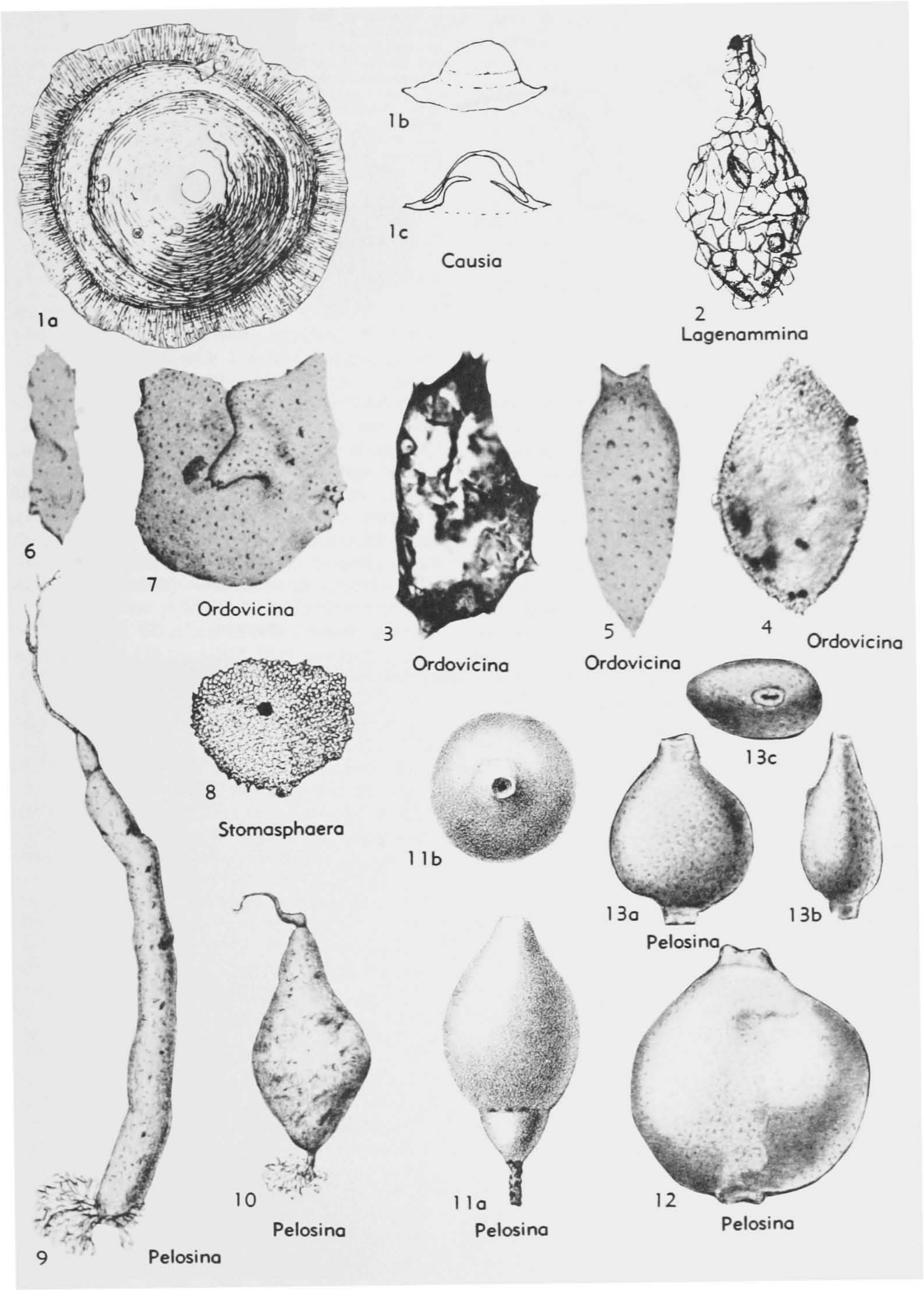

FIG. 113. Saccamminidae (Saccammininae; *1, Causia; 2, Lagenammina; 3-7, Ordovicina; 8, Stomasphaera; 9-13, Pelosina*) (p. C200-C202).

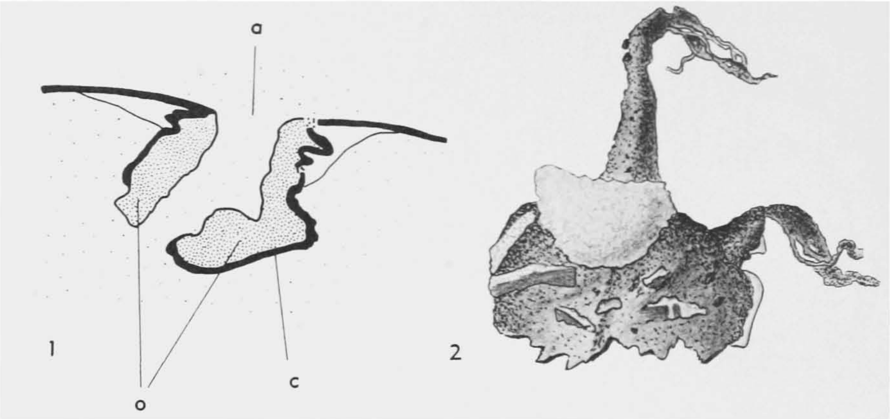

Fig. 114. Saccamminidae (Saccammininae; *1,2, Pelosphaera*) (p. *C*201).

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

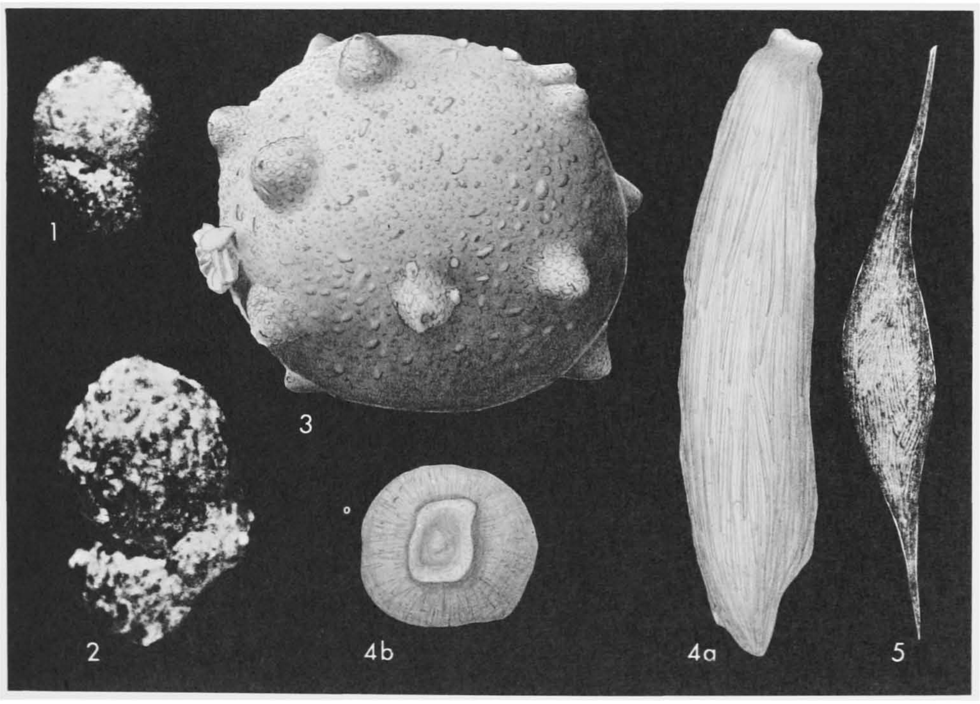

FIG. 115. Saccamminidae (Saccammininae; *1,2, Saccamminoides; 3, Thurammina; 4,5, Technitella*) (p. C201-C202).

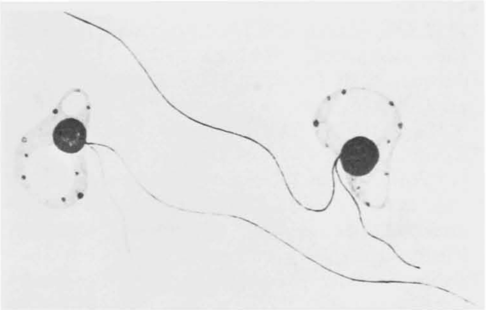

FIG. 116. Saccamminidae (Hemisphaeramminінae; *Hemisphaerammina*) (p. C202).

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

[Hemisphaeramminінae 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

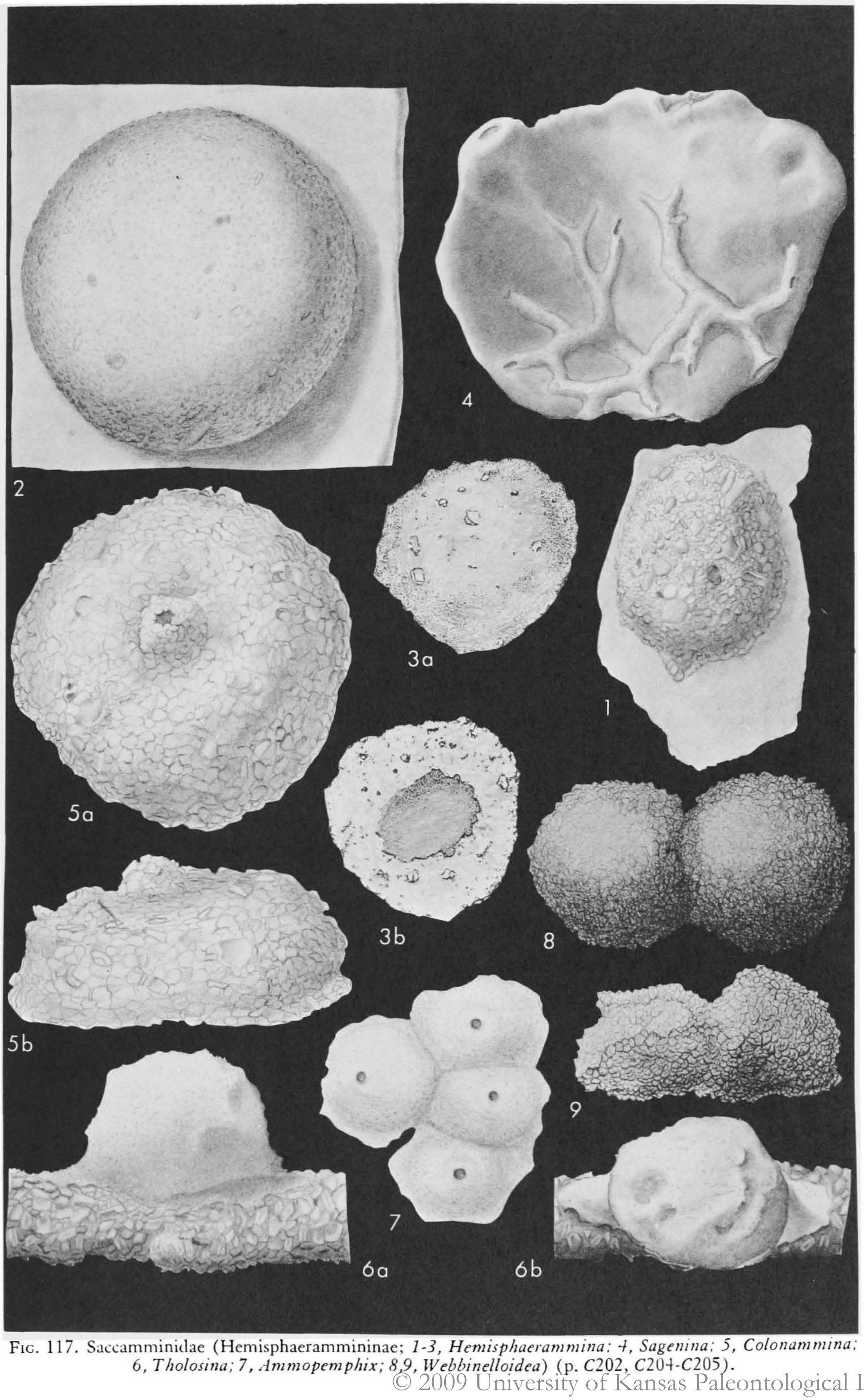

FIG. 117. Saccamminidae (Hemisphaeramminae; *1-3, Hemisphaerammina; 4, Sagenina; 5, Colonammina; 6, Tholosina; 7, Ammopemphix; 8,9, Webbinelloidea*) (p. C202, C204-C205).

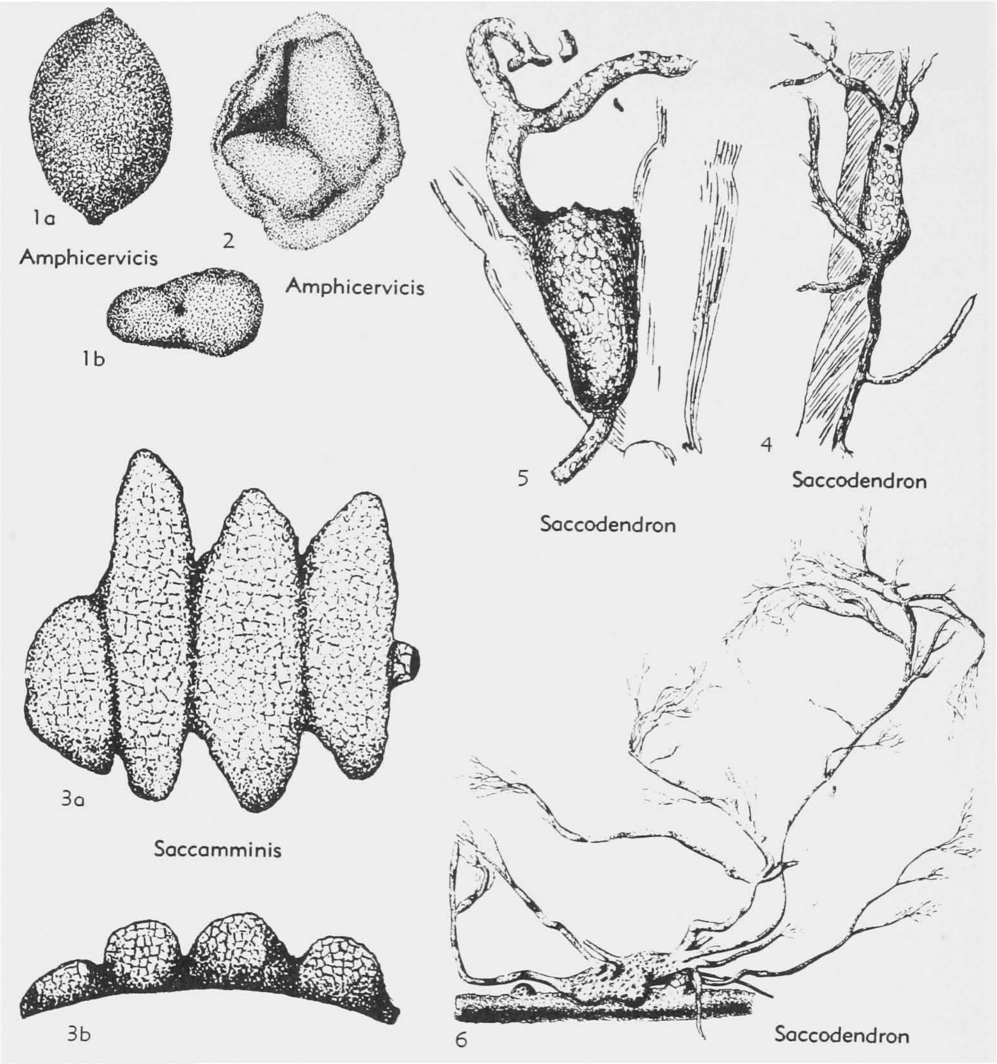

FIG. 118. Saccamminidae (Hemisphaeramminiae; *1,2, Amphicervicis; 3, Saccamminis; 4-6, Saccodendron*) (*C*202-*C*205).

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

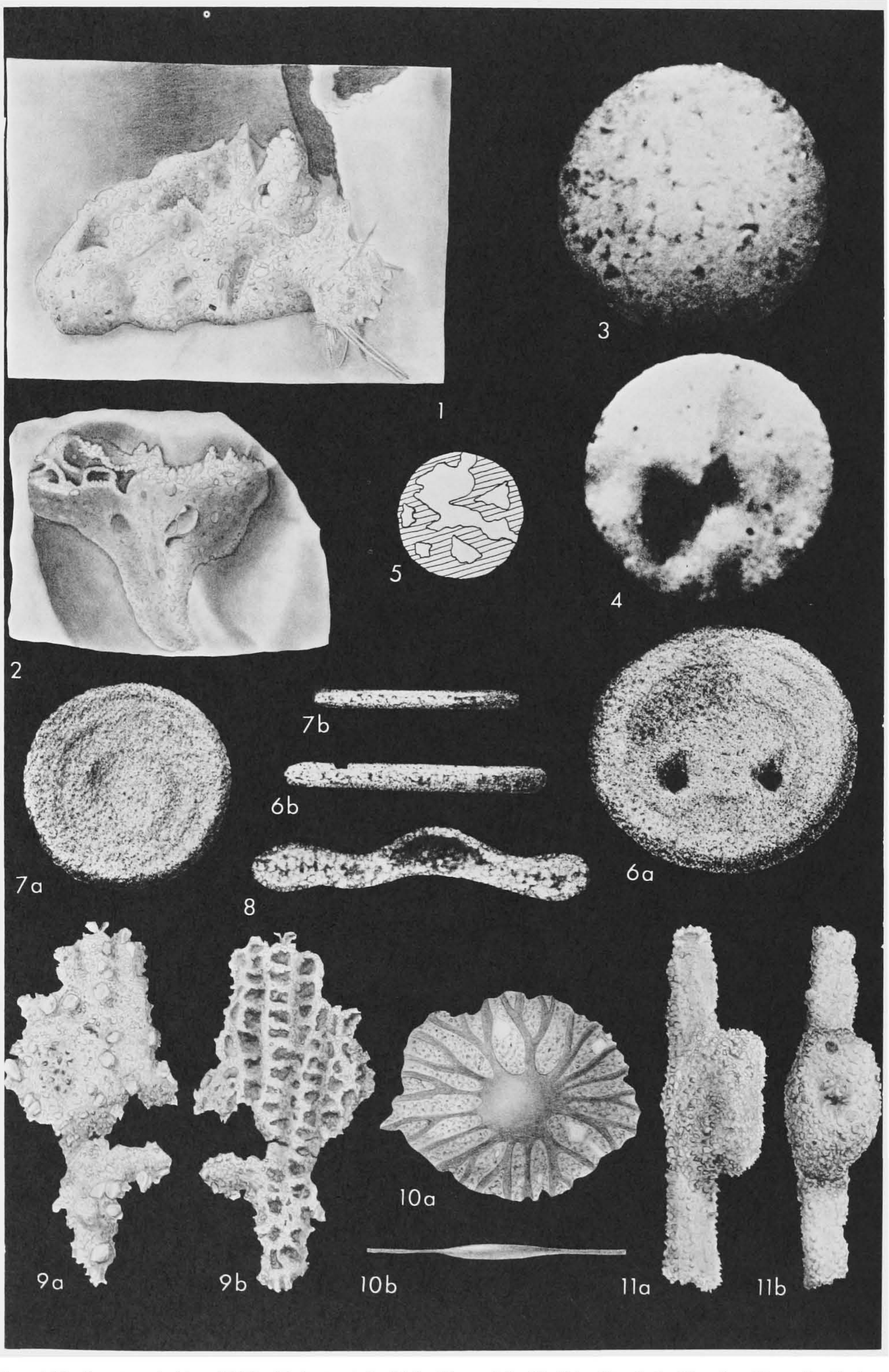

FIG. 119. Saccamminidae (Diffusilininae; *1,2, Diffusilina; 3-5, Weikkoella; 6-8, Discobotellina; 9, Kerionammina; 10, Masonella; 11, Verrucina*) (p. C205-C210).

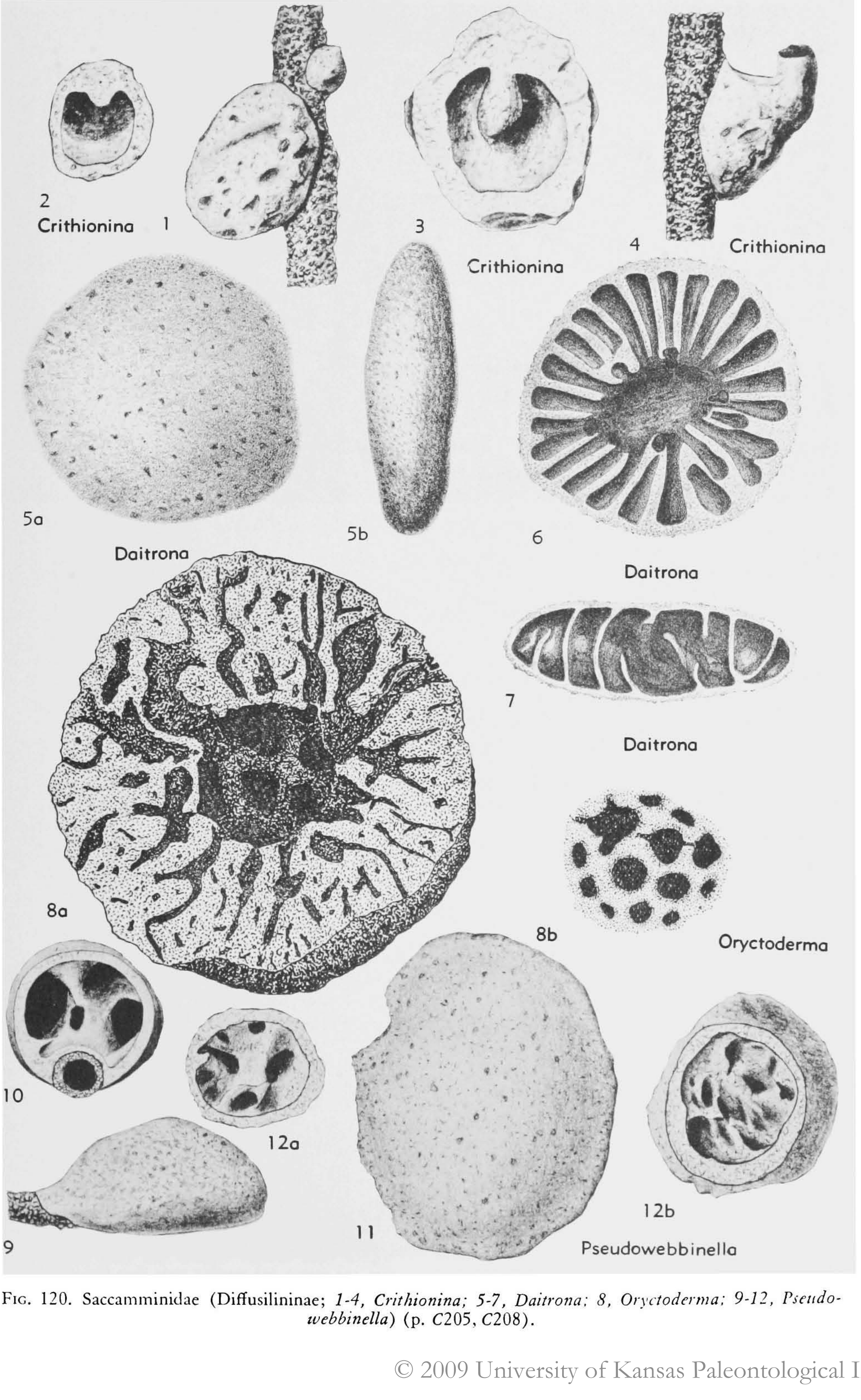

FIG. 120. Saccamminidae (Diffusilininae; *1-4, Crithionina; 5-7, Daitrona; 8, Oryctoderma; 9-12, Pseudowebbinella*) (p. *C*205, *C*208).

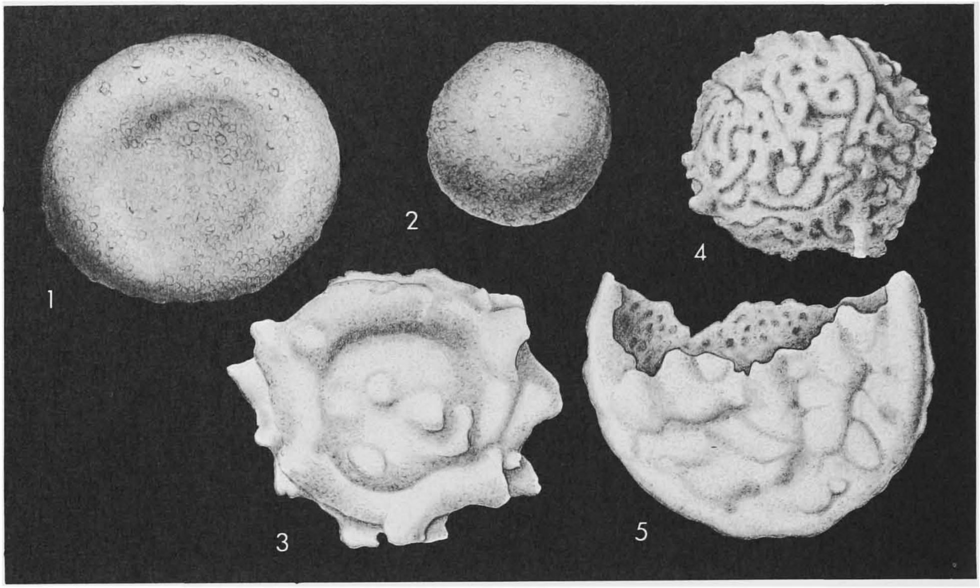

FIG. 121. Saccamminidae (Diffusilininae; *1-5, Thuramminoides*) (p. C208-C210).

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.

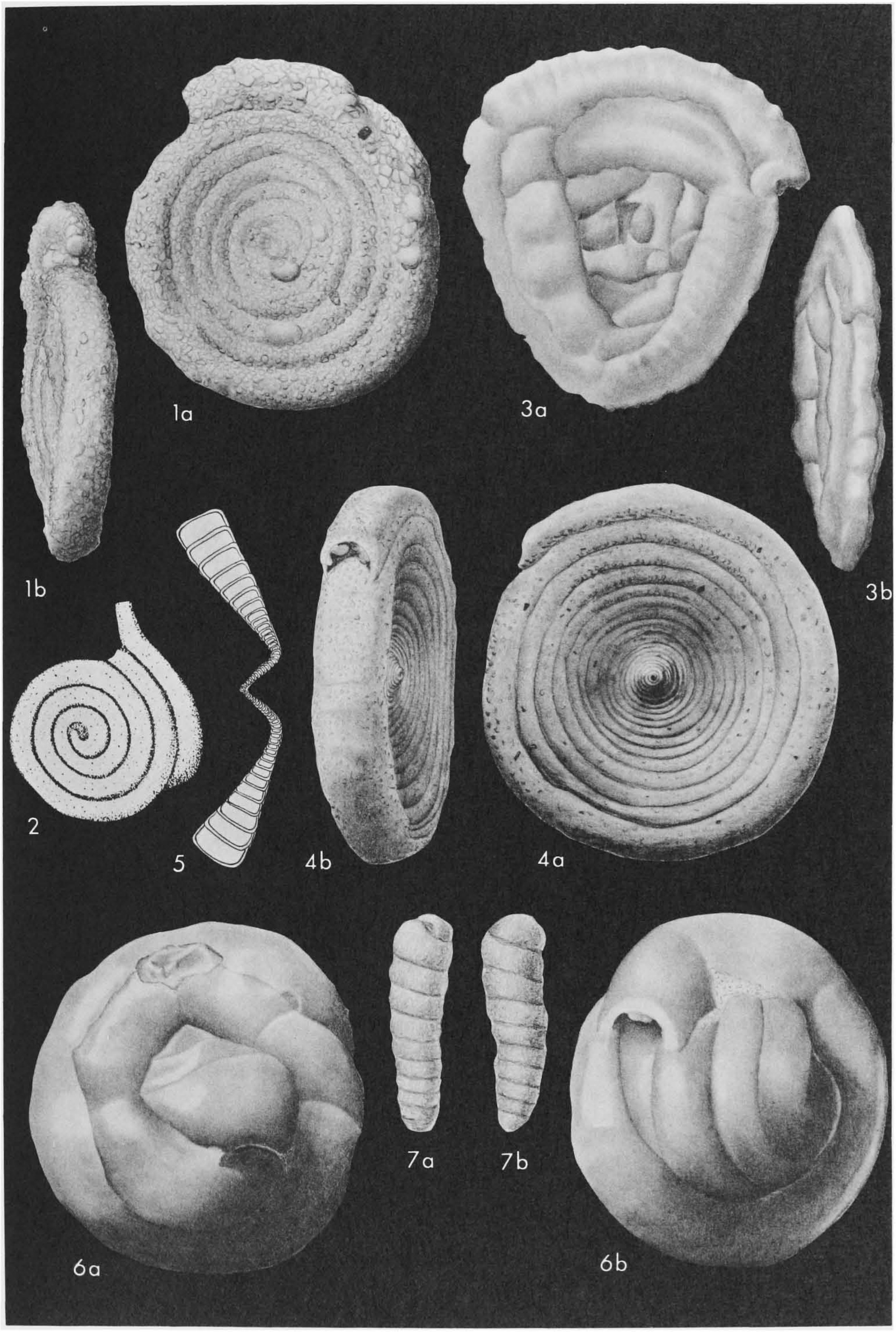

Fig. 122. Ammodiscidae (Ammodiscinae; *1,2, Ammodiscus; 3, Glomospirella; 4,5, Ammodiscoides; 6, Glomospira; 7, Turritellella*) (p. C210, C212).

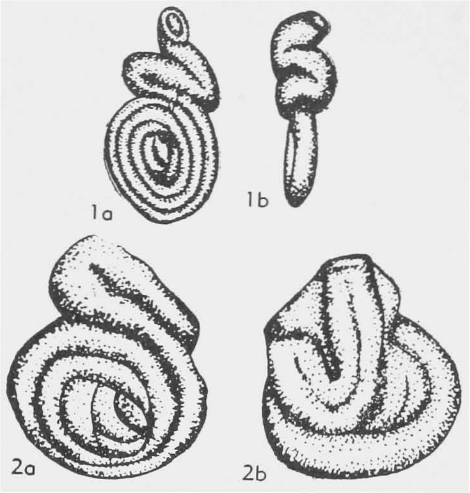

FIG. 123. Ammodiscidae (Ammodiscinae; *1,2, Ammovertellina*) (p. *C*210).

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,

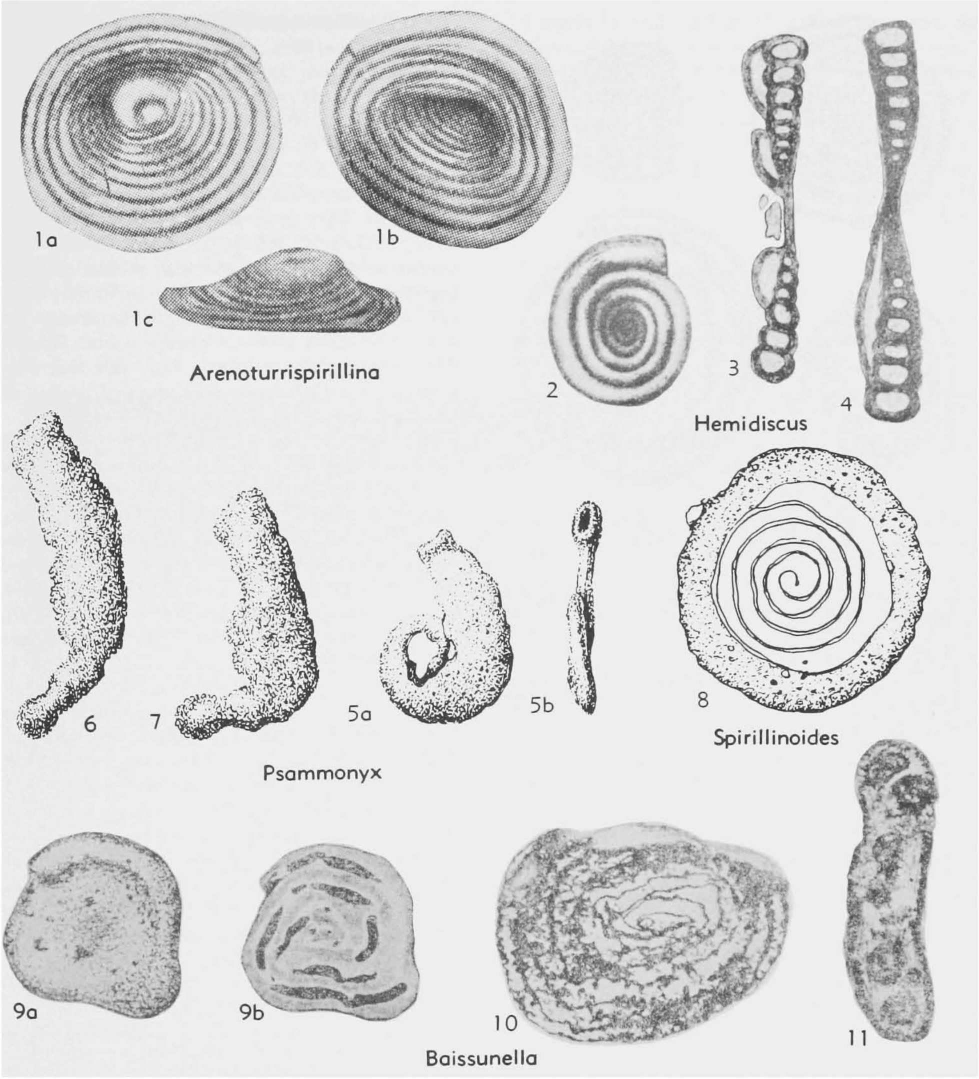

FIG. 124. Ammodiscidae (Ammodiscinae; *1, Arenoturrispirillina; 2-4, Hemidiscus; 5-7, Psammonyx; 8, Spirillinoides; 9-11, Baissunella*) (p. C210-C212).

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-

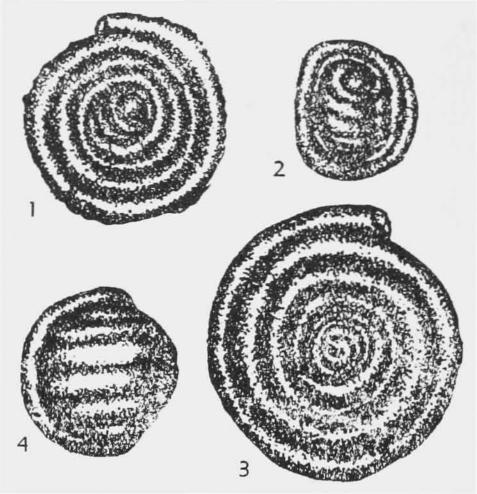

FIG. 125. Ammodiscidae (Ammodiscinae; *1-4, Usbekistania*) (p. C212).

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).

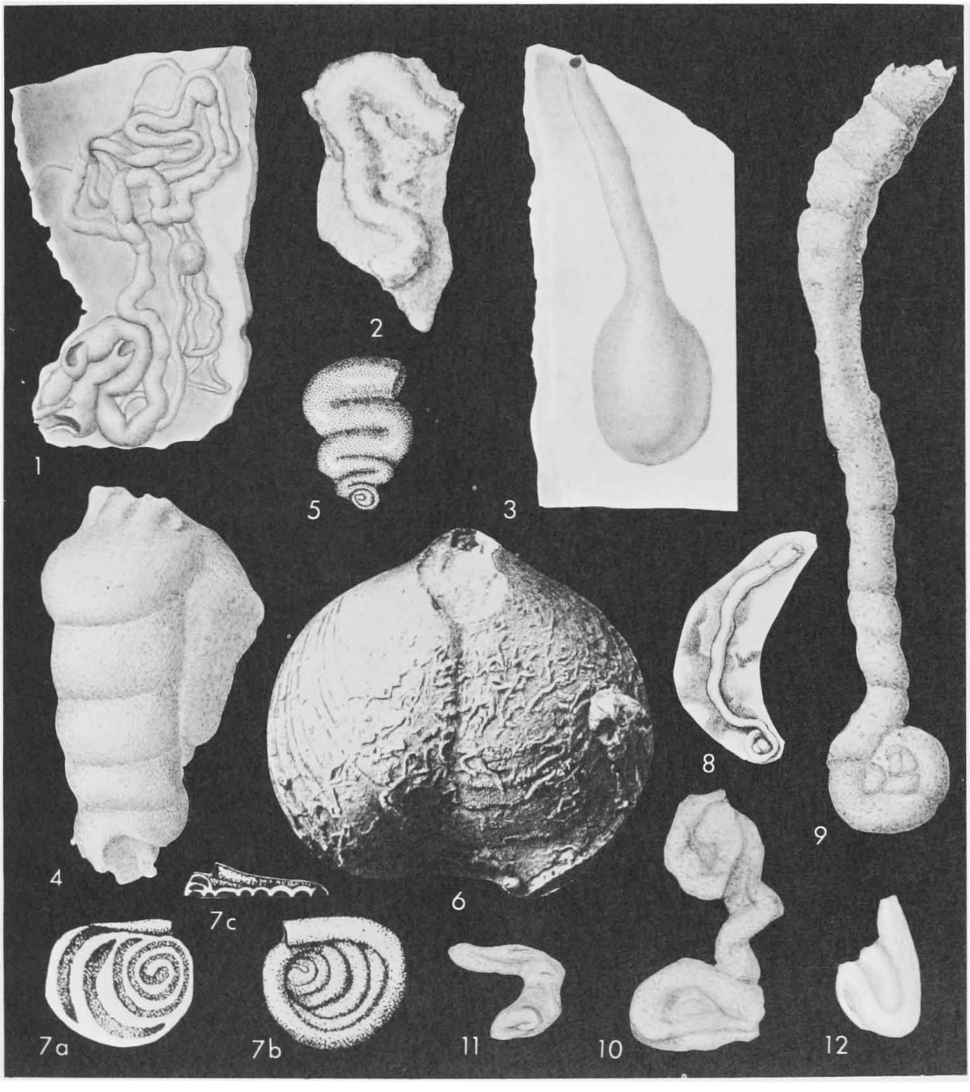

Fig. 126. Ammodiscidae (Tolypammininae; *1,2*, *Tolypammina*; *3*, *Ammolagena*; *4*, *Trepeilopsis*; *5*, *Ammovertella*; *6*, *Serpulopsis*; *7*, *Ammodiscella*; *8-12*, *Lituotuba*) (p. *C*213-*C*214).

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 Psamniophis* 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-

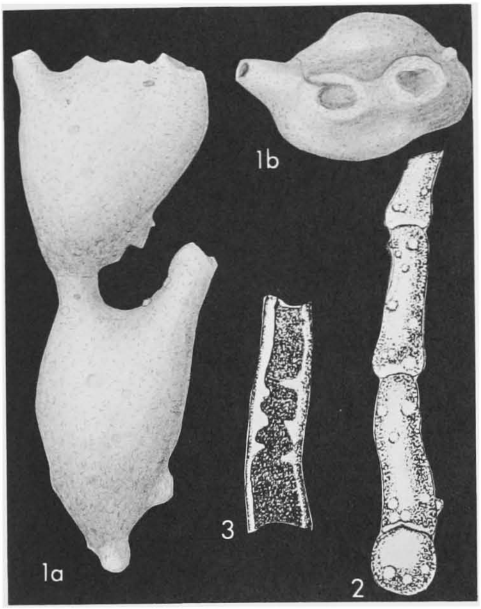

FIG. 127. Hormosinidae (Aschemonellinae; *1, Aschemonella; 2,3, Kalamopsis*) (p. C214-C215).

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).

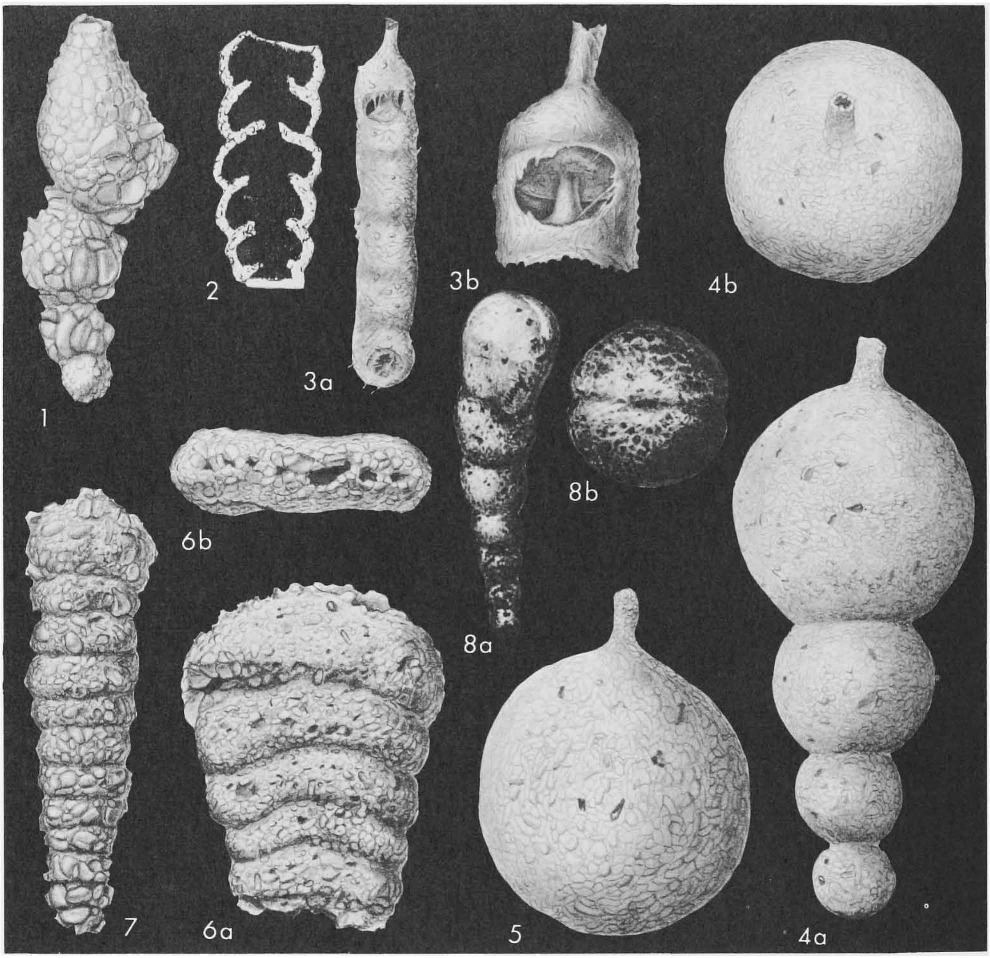

Fig. 128. Hormosinidae (Hormosininae; *1-3, Reophax; 4,5, Hormosina; 6,7, Polychasmina; 8, Sulcophax*) (p. *C*215-*C*217).

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

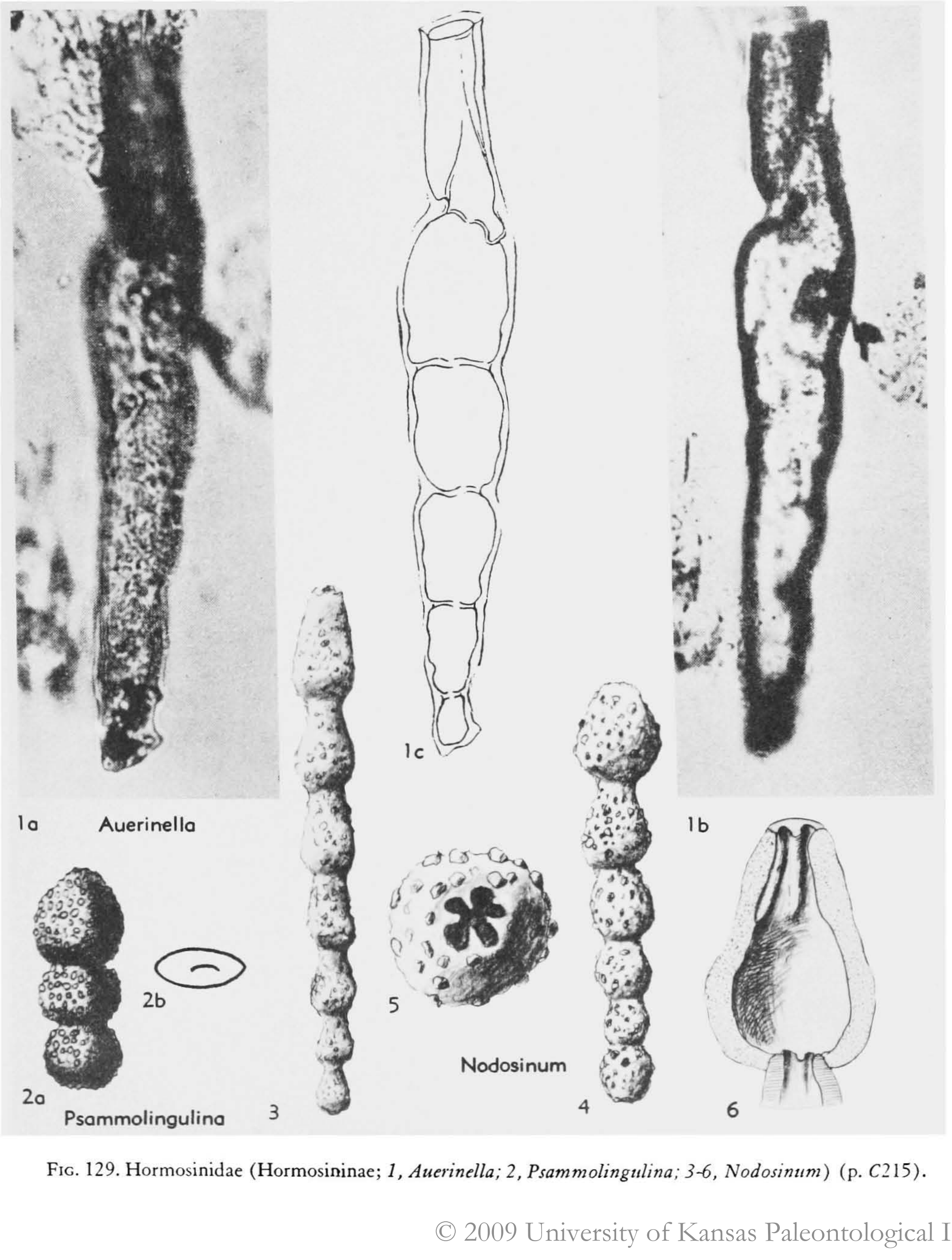

FIG. 129. Hormosinidae (Hormosininae; *1, Auerinella; 2, Psammolingulina; 3-6, Nodosinum*) (p. *C*215).

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

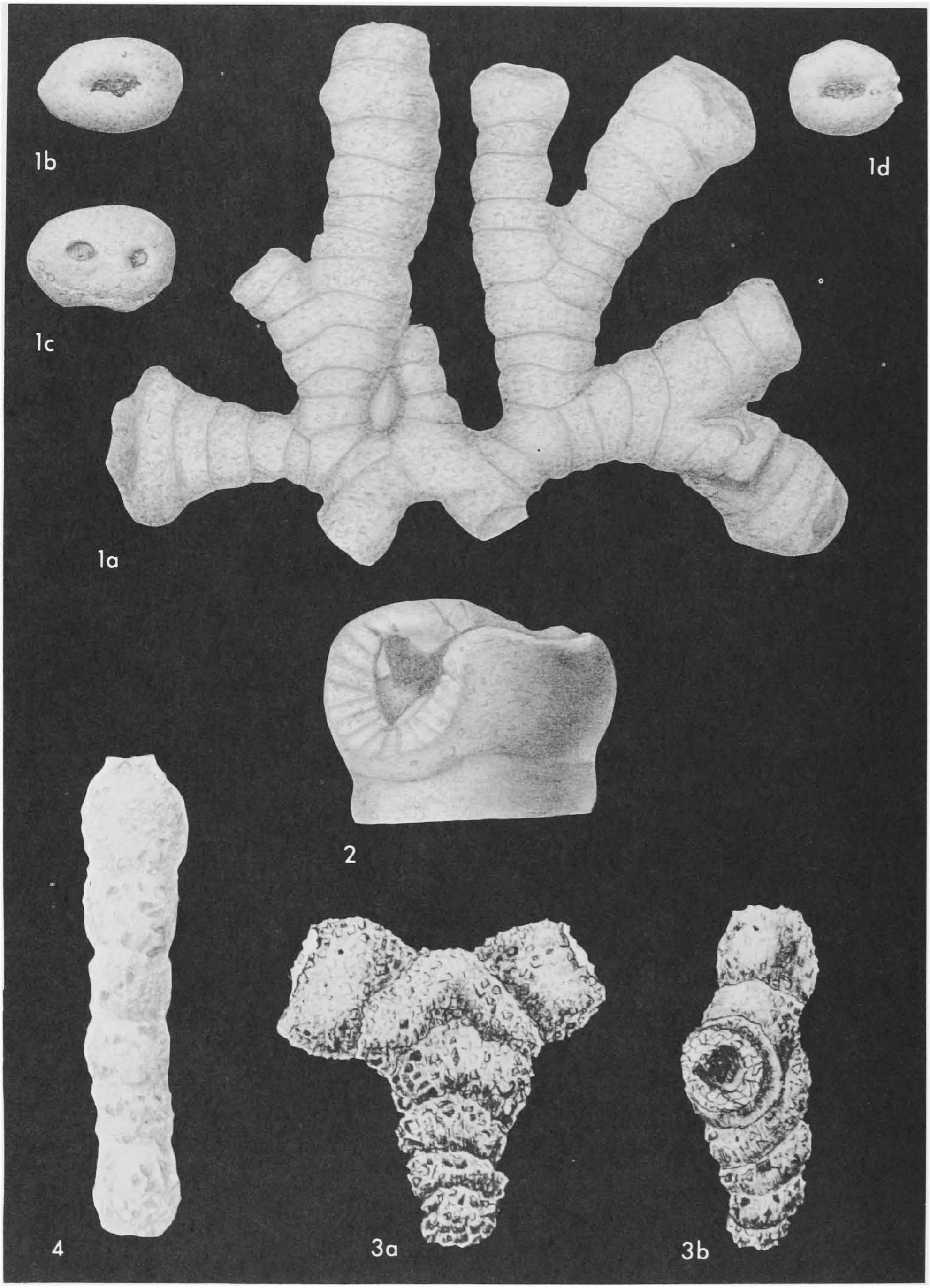

FIG. 130. Hormosinidae (Hormosininae; *1-3, Thomasinella; 4, Protoschista*) (p. C215, C217-C219).

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 Maync)," 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.]

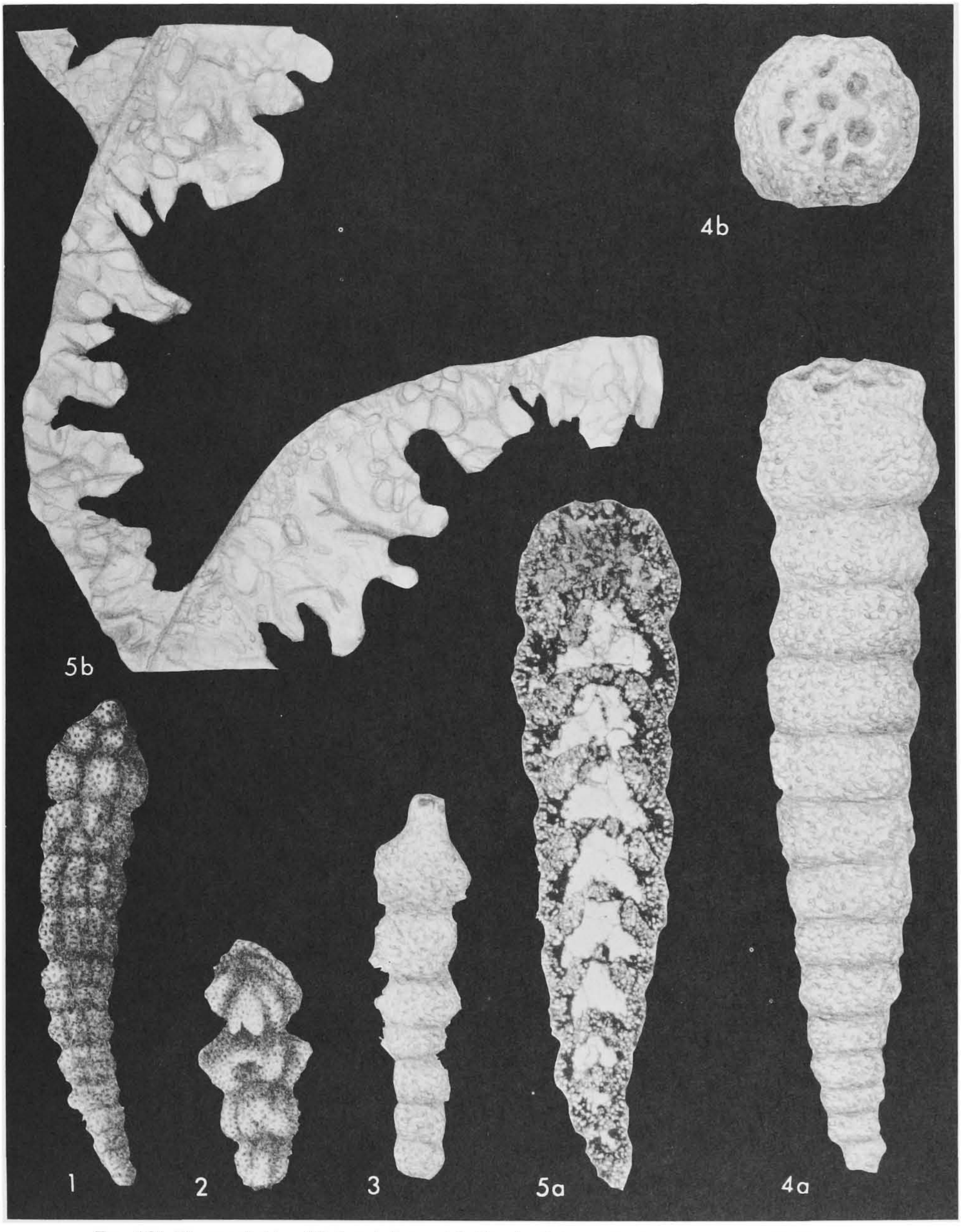

FIG. 131. Hormosinidae (Cribratininae; *1,2*, *Haplostiche*; *3-5*, *Cribratina*) (p. C220).

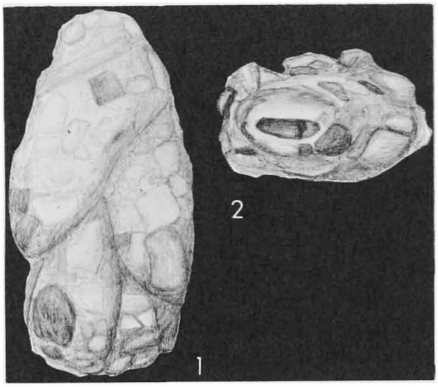

FIG. 132. Nouriidae; *Nouria* (p. C220).

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.*

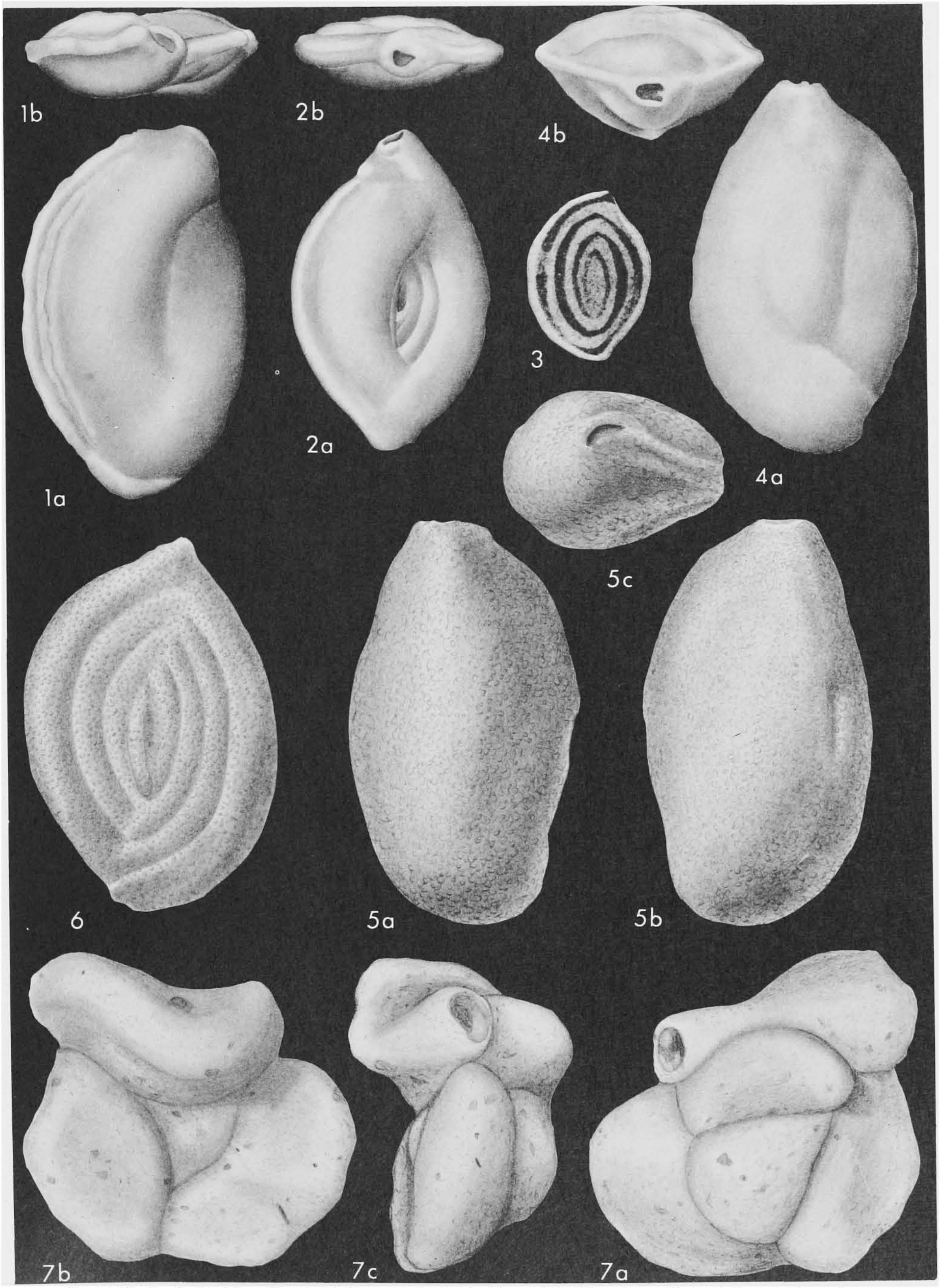

FIG. 133. Rzehakinidae (Rzehakininae; *1-3, Rzehakina; 4,5, Silicosigmoilina; 6, Psamminopelta; 7, Ammoflintina*) (p. C220-C222).

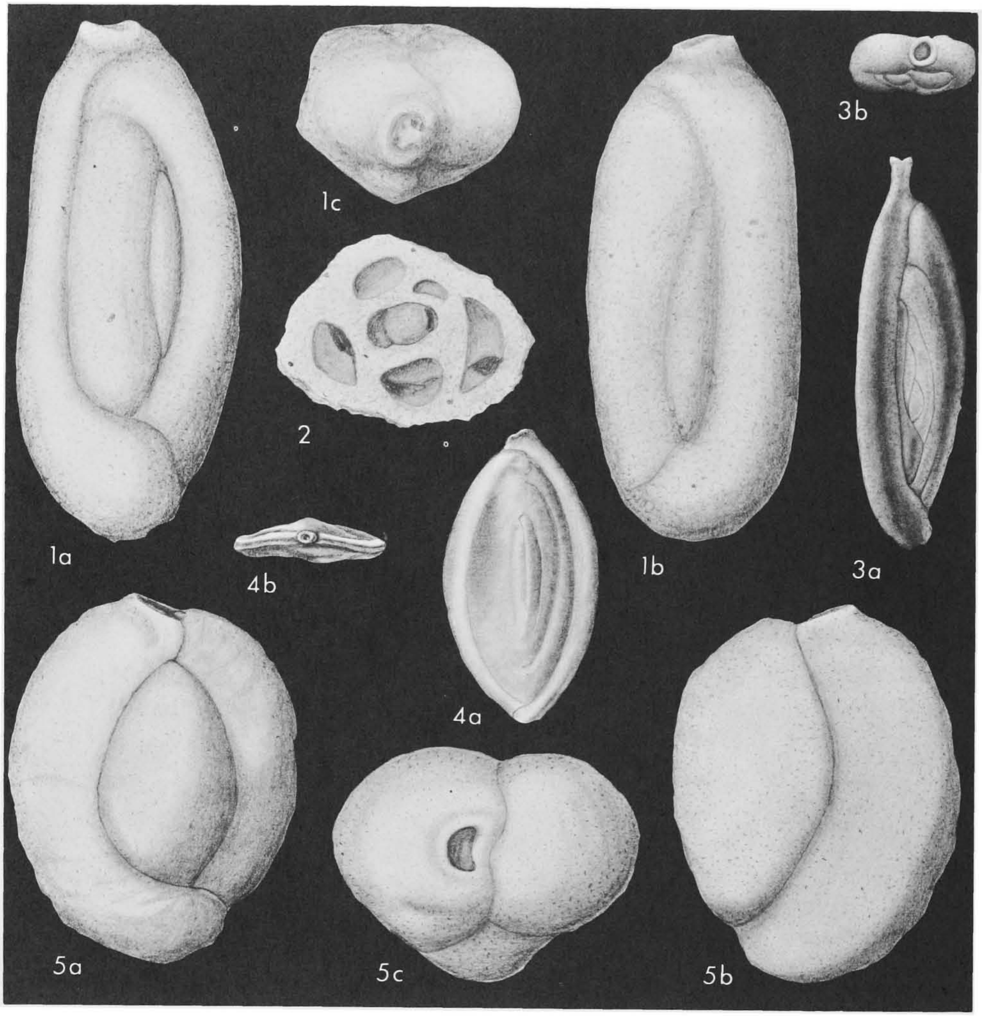

Fig. 134. Rzehakinidae (Rzehakininae; *1,2, Miliammina; 3, Spirolocammina; 4, Spirosigmoilinella; 5, Trilocularena*) (p. *C220-C224*).

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).

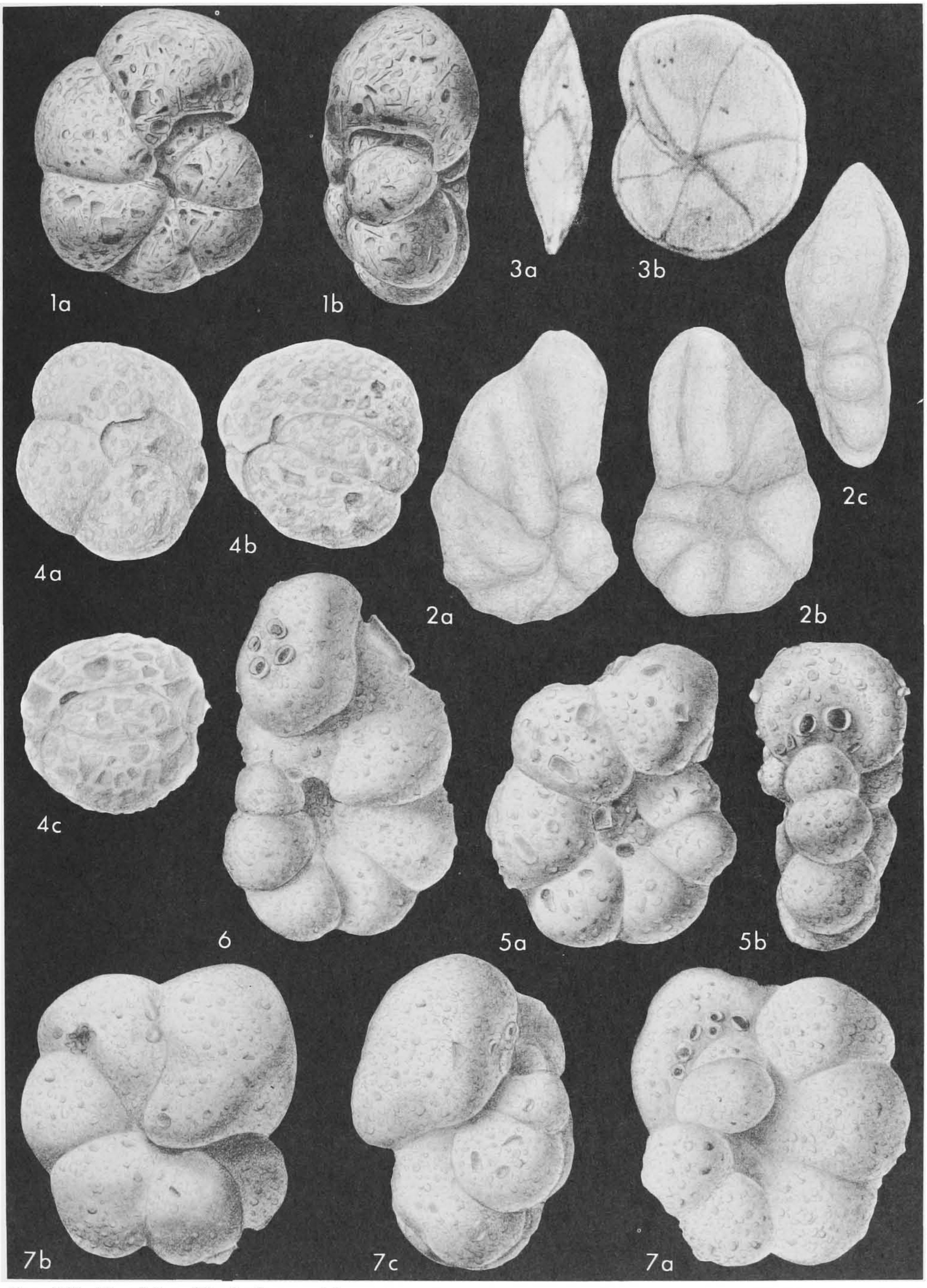

FIG. 135. Lituolidae (Haplophragmoidina *1-3, Haplophragmoides; 4, Adercotryma; 5-7, Trochamminita*) (p. *C*225-*C*227).

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*

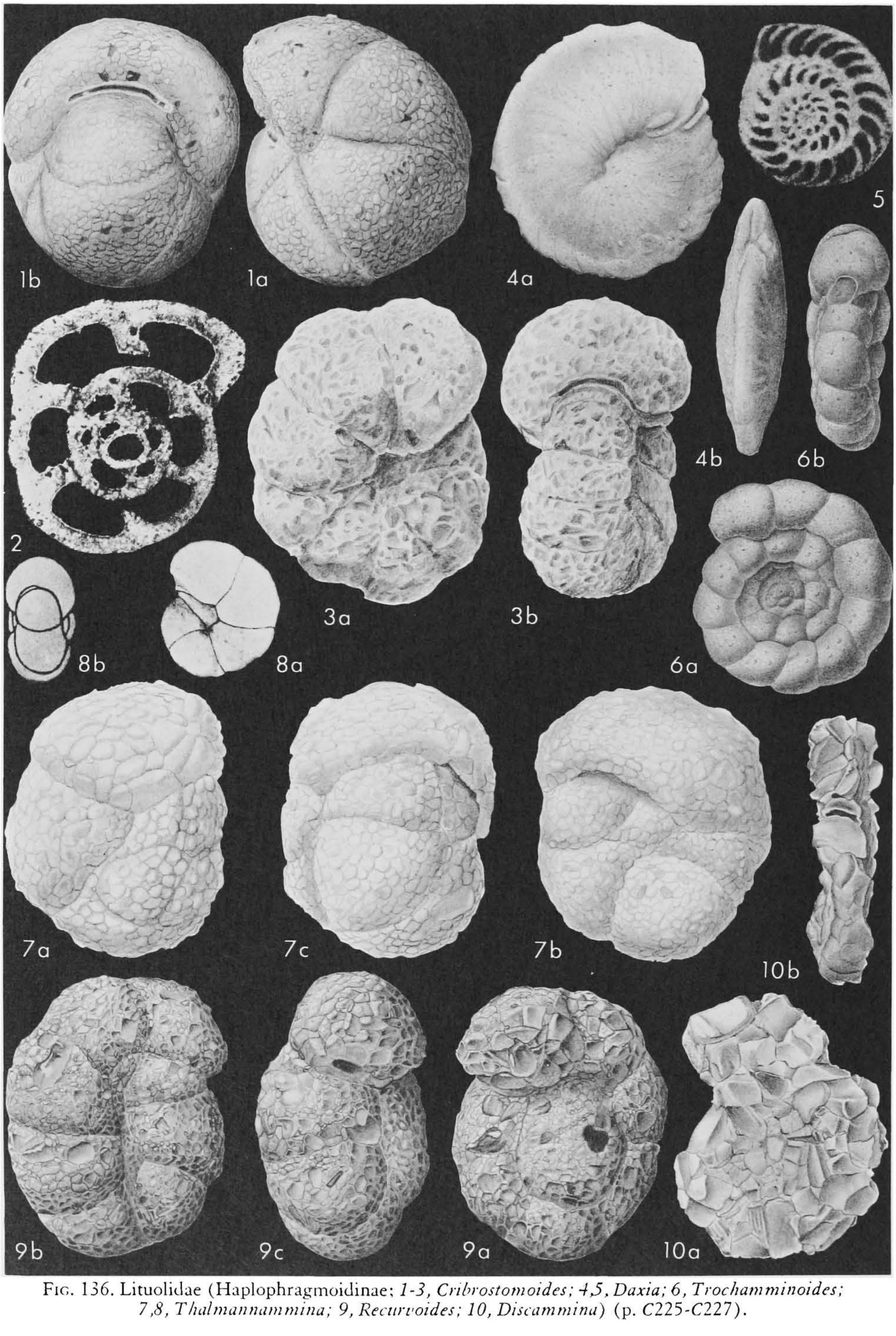

Fig. 136. Lituolidae (Haplophragmoidinae; *1-3, Cribrostomoides; 4,5, Daxia; 6, Trochamminoides; 7,8, Thalmannammina; 9, Recurvoides; 10, Discammina*) (p. C225-C227).

(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]——[=Polythalamat† 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.*

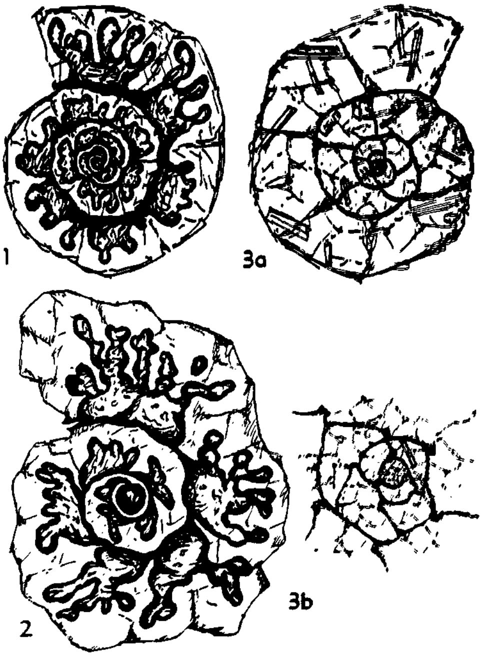

Fig. 137. Lituolidae (Haplophragmoidinae; *1-3, Discammina*) (p. C226).

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.,

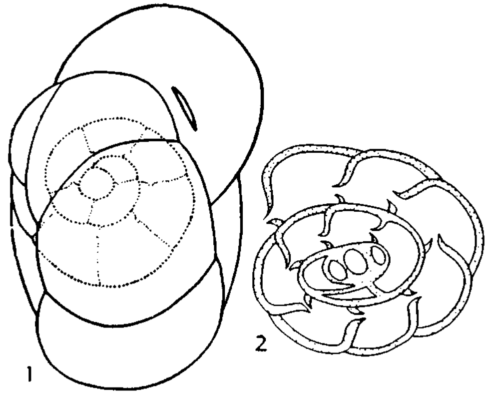

FIG. 138. Lituolidae (Haplophragmoidinae; *1,2, Recurvoides*) (p. C226).

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

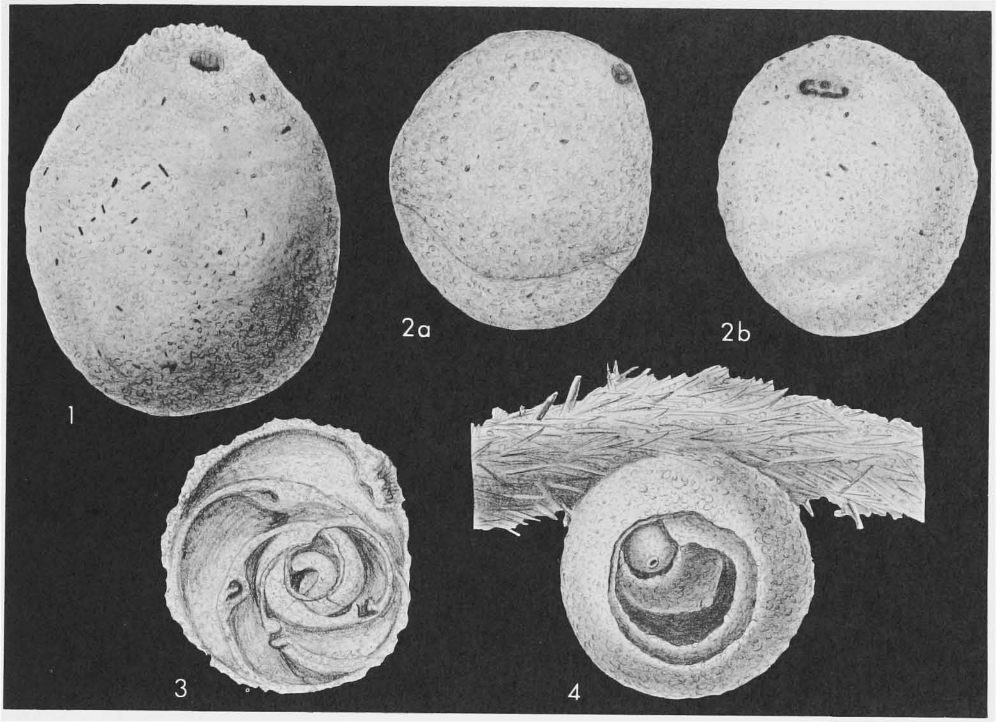

FIG. 139. Lituolidae (Sphaeramminnae; *1-3, Sphaerammina; 4, Ammosphaerulina*) (p. *C*227-*C*228).

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

[Sphaeramminnae 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 (Sphaeramminnae; *1, Sphaerammina*) (p. *C*227).

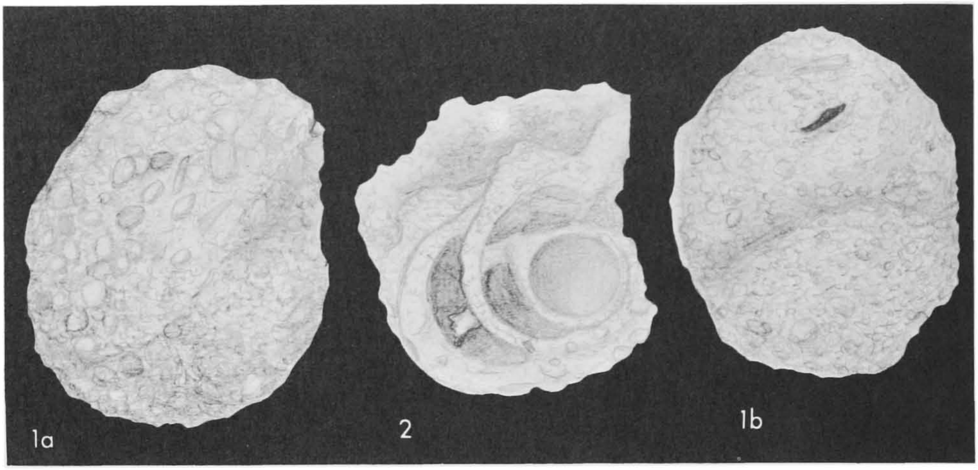

FIG. 141. Lituolidae (Sphaeramminlnae; *1,2, Canepaia*) (p. *C*228).

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

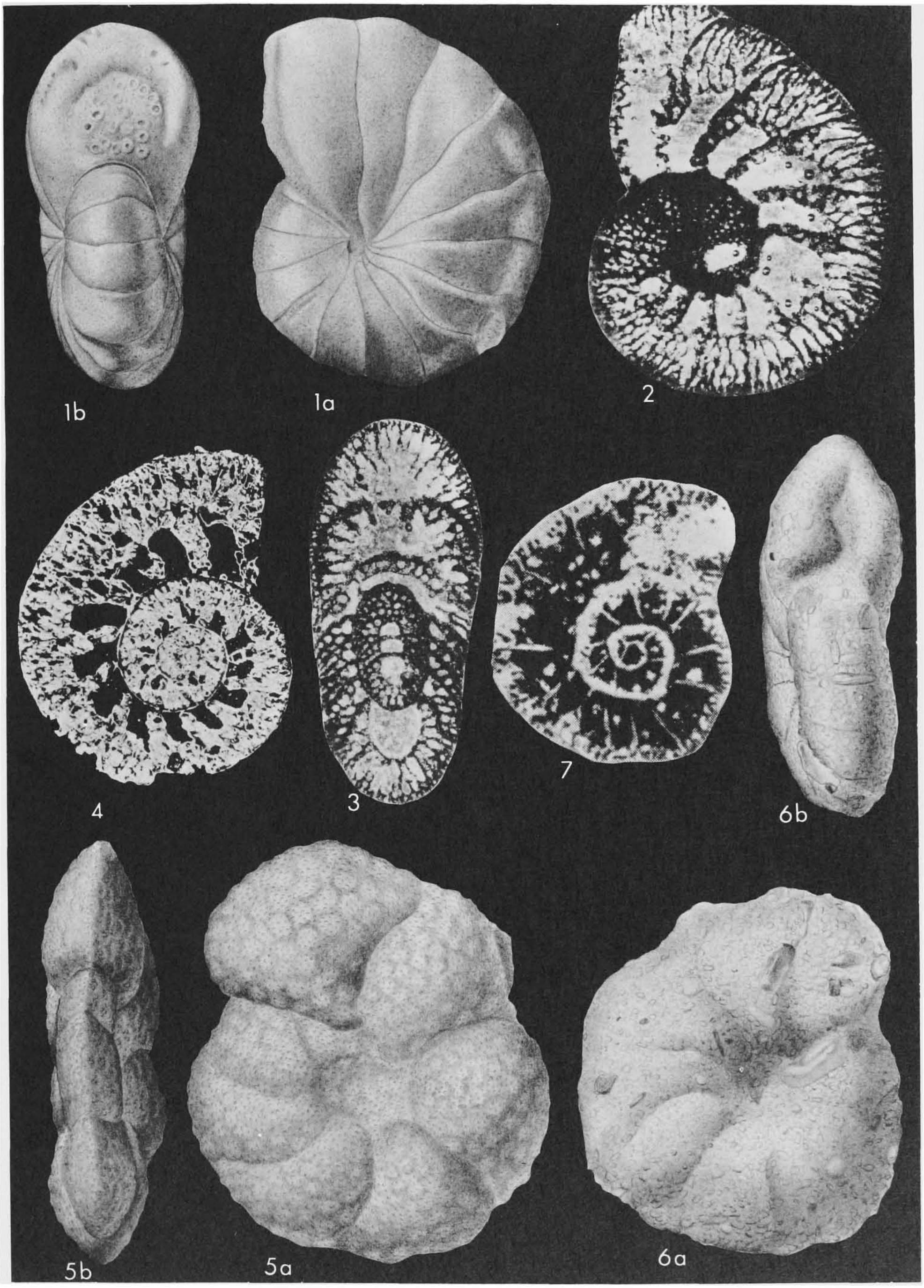

Fig. 142. Lituolidae (Cyclammininae; *1-4, Cyclammina; 5, Reticulophragmium; 6,7, Hemicyclammina*) (p. C228-C231, C233).

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

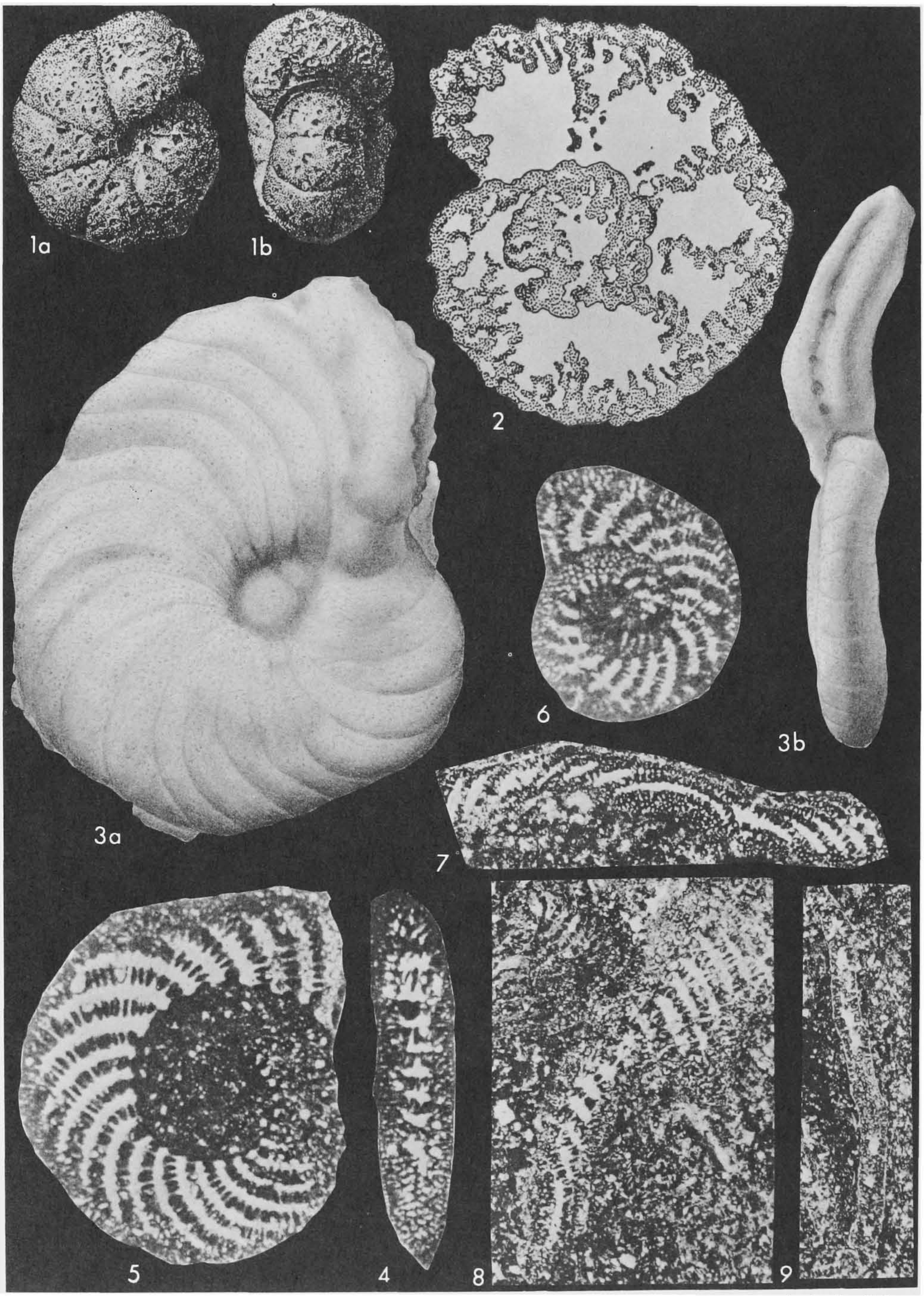

FIG. 143. Lituolidae (Cyclammininae; *1,2, Alveolophragmium; 3-6, Choffatella; 7-9, Pseudochoffatella*) (p. *C*228, *C*233).

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-

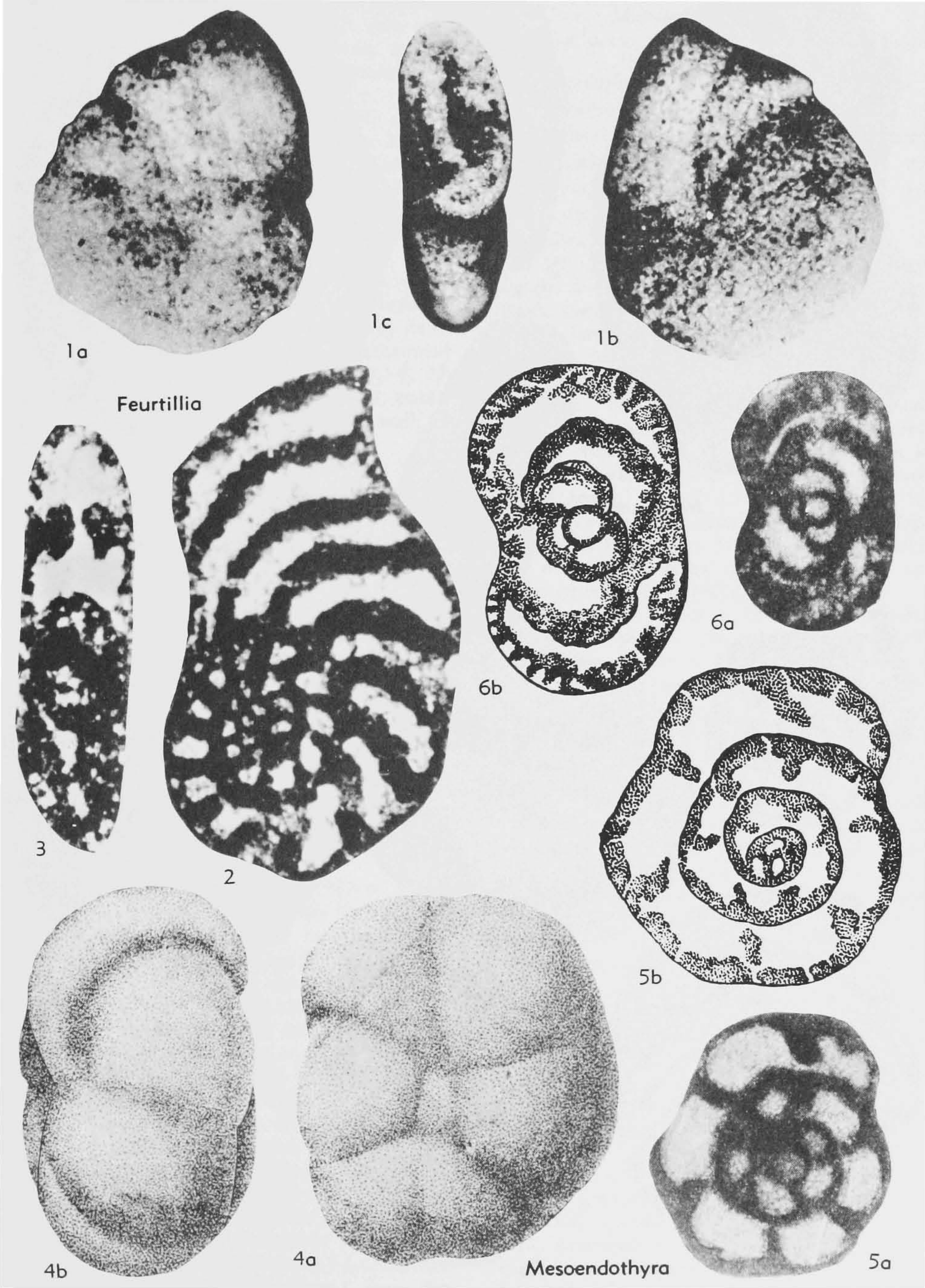

Fig. 144. Lituolidae (Cyclammininae; *1-3, Feurtillia; 4-6, Mesoendothyra*) (p. *C*228-*C*229, *C*232-*C*233).

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-*

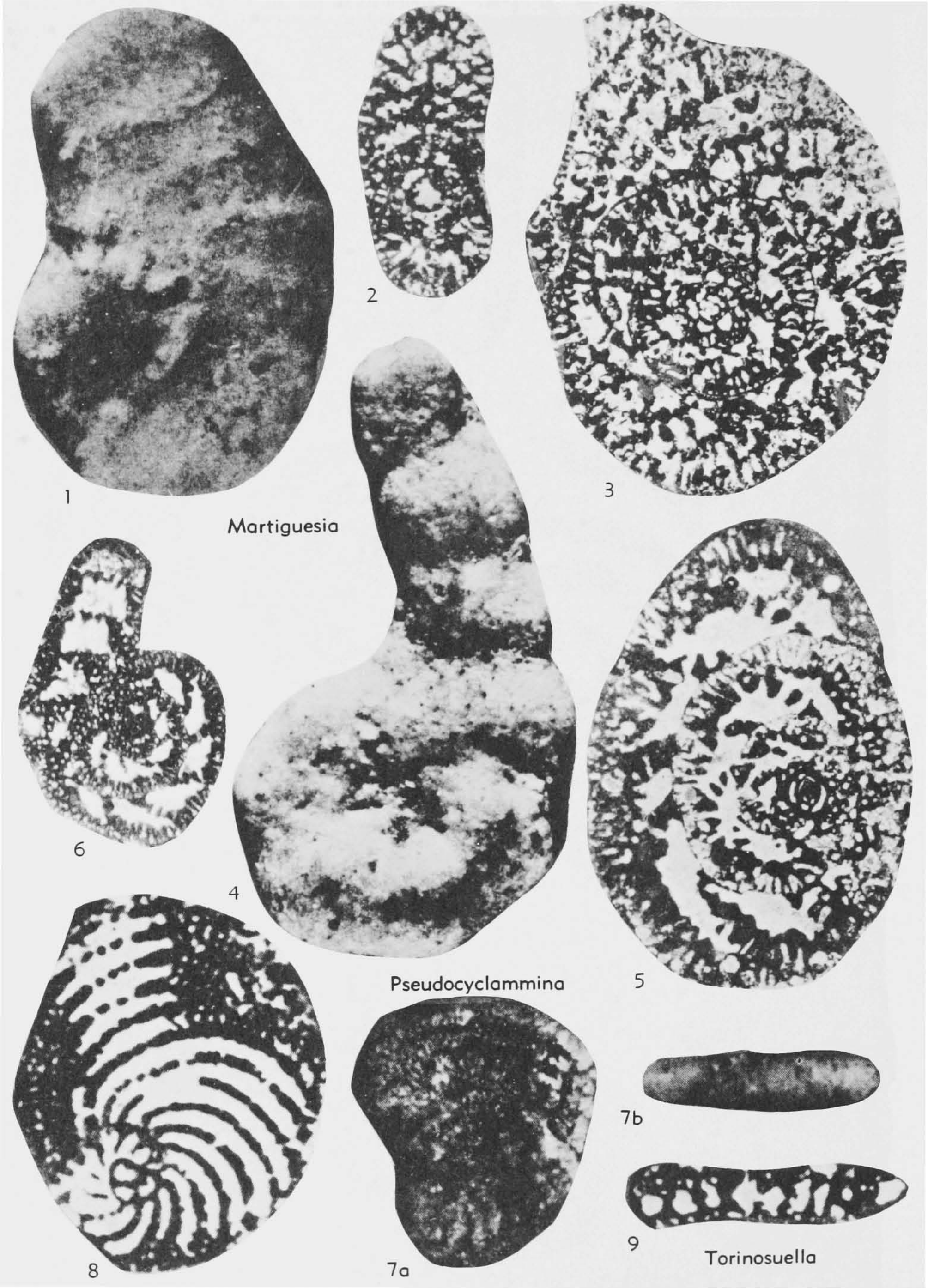

Fig. 145. Lituolidae (Cyclammininae; *1-3, Martiguesia; 4-6, Pseudocyclammina; 7-9, Torinosuella*) (p. *C*231-*C*233).

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),

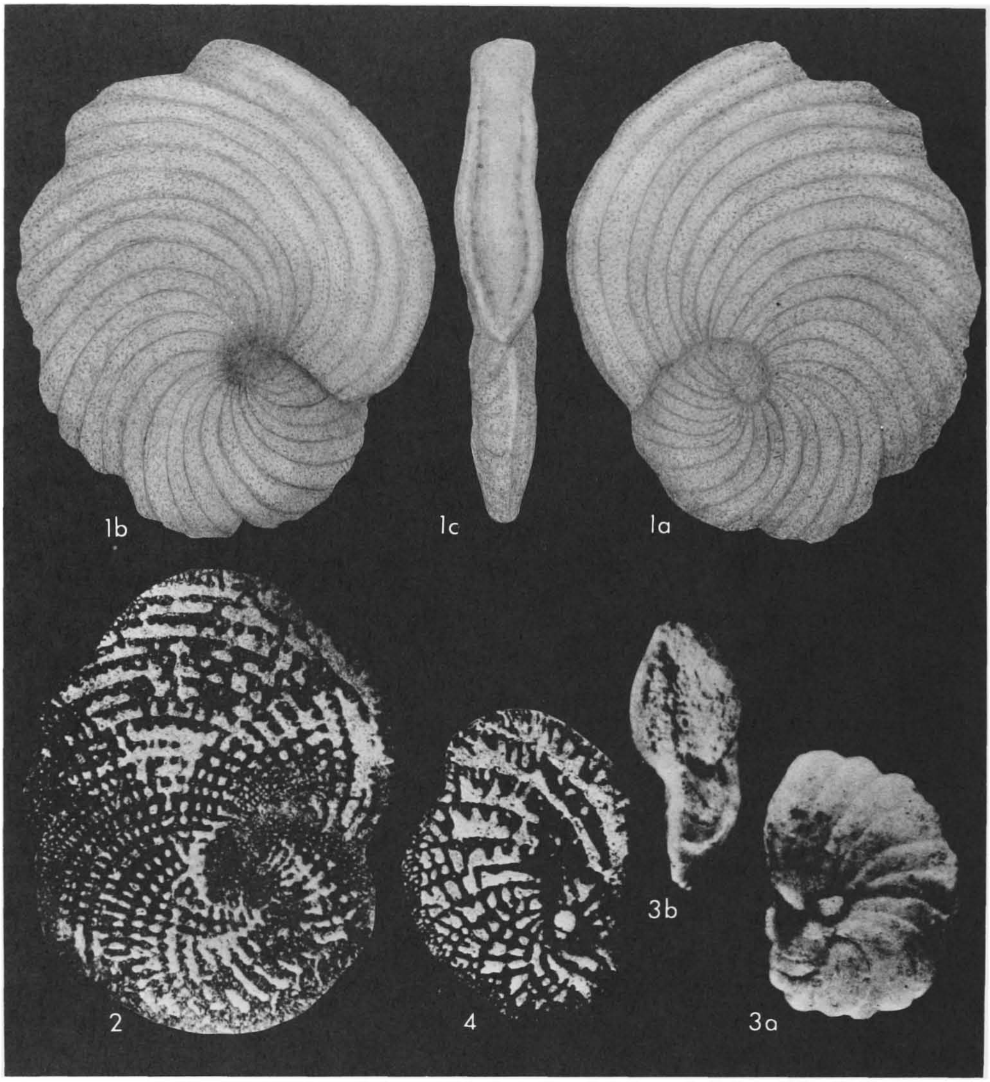

Fig. 146. Lituolidae (Spirocyclininae; *1,2, Spirocyclina; 3,4, Sornayina*) (p. *C*233, *C*236).

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).

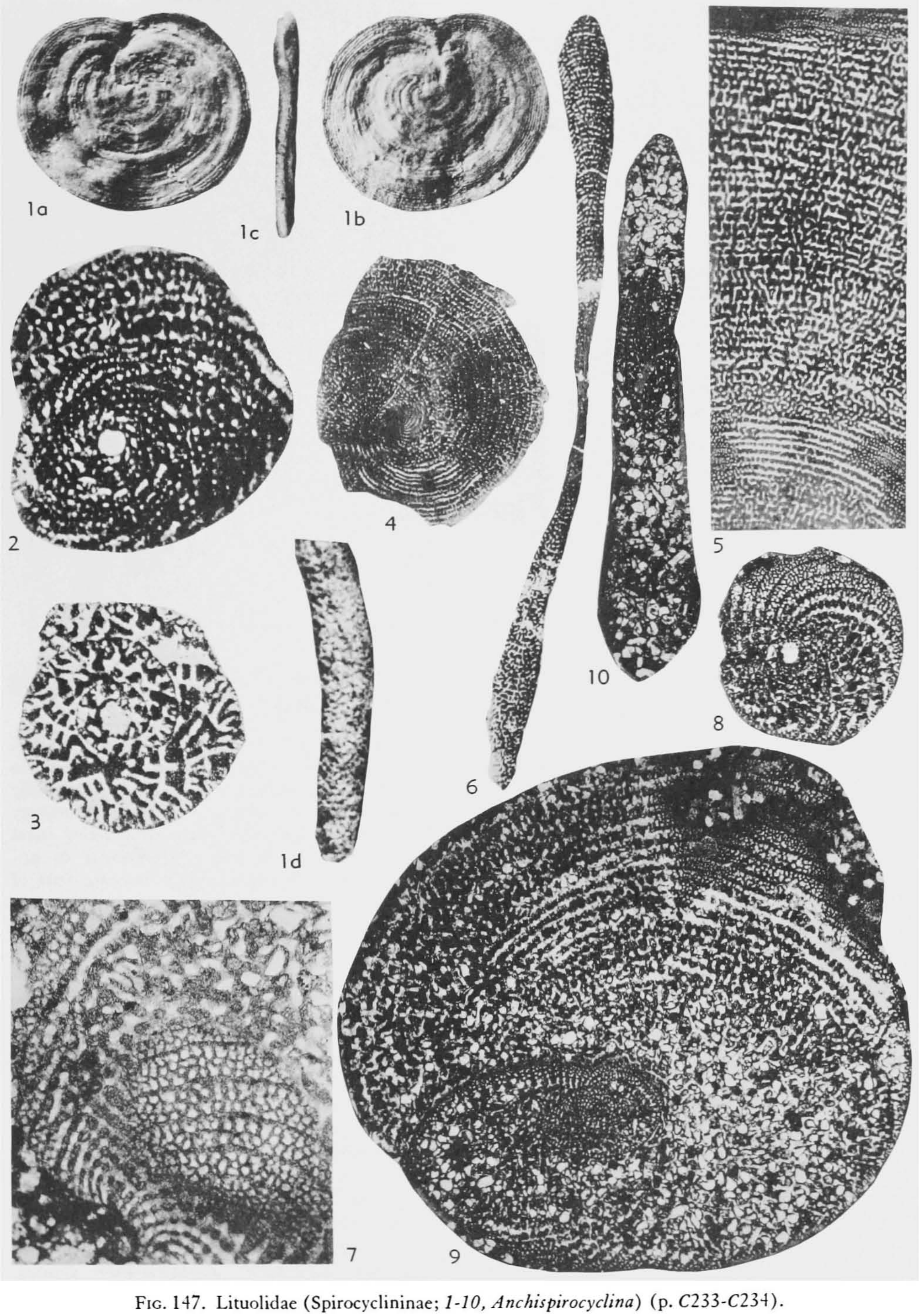

FIG. 147. Lituolidae (Spirocyclininae; *1-10, Anchispirocyclina*) (p. C233-C234).

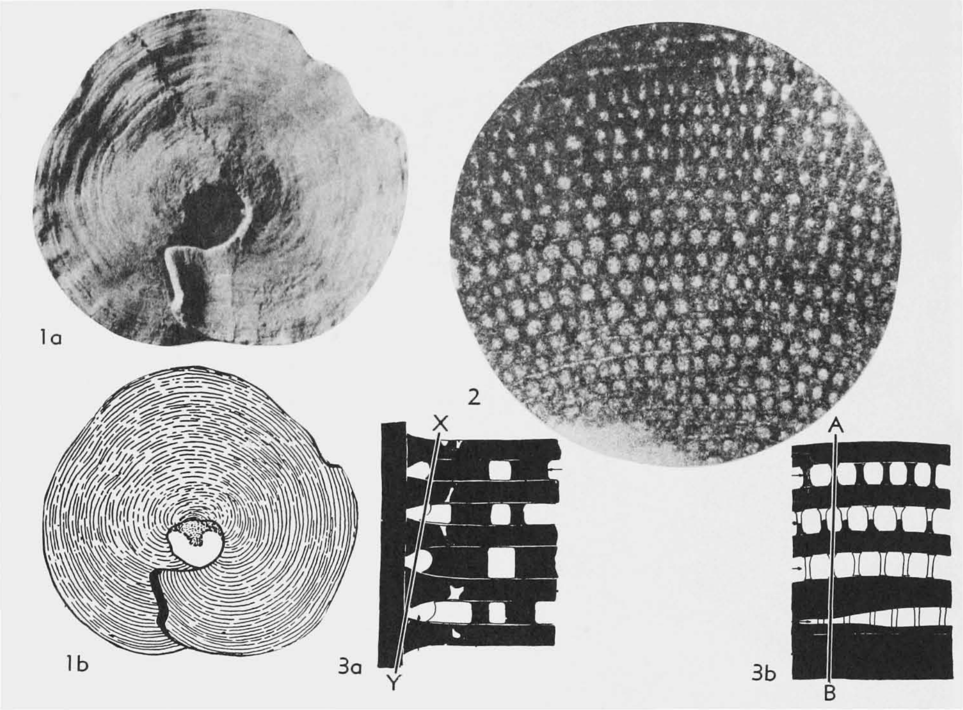

FIG. 148. Lituolidae (Spirocyclininae; *1-3, Orbitammina*) (p. C234-C235).

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*

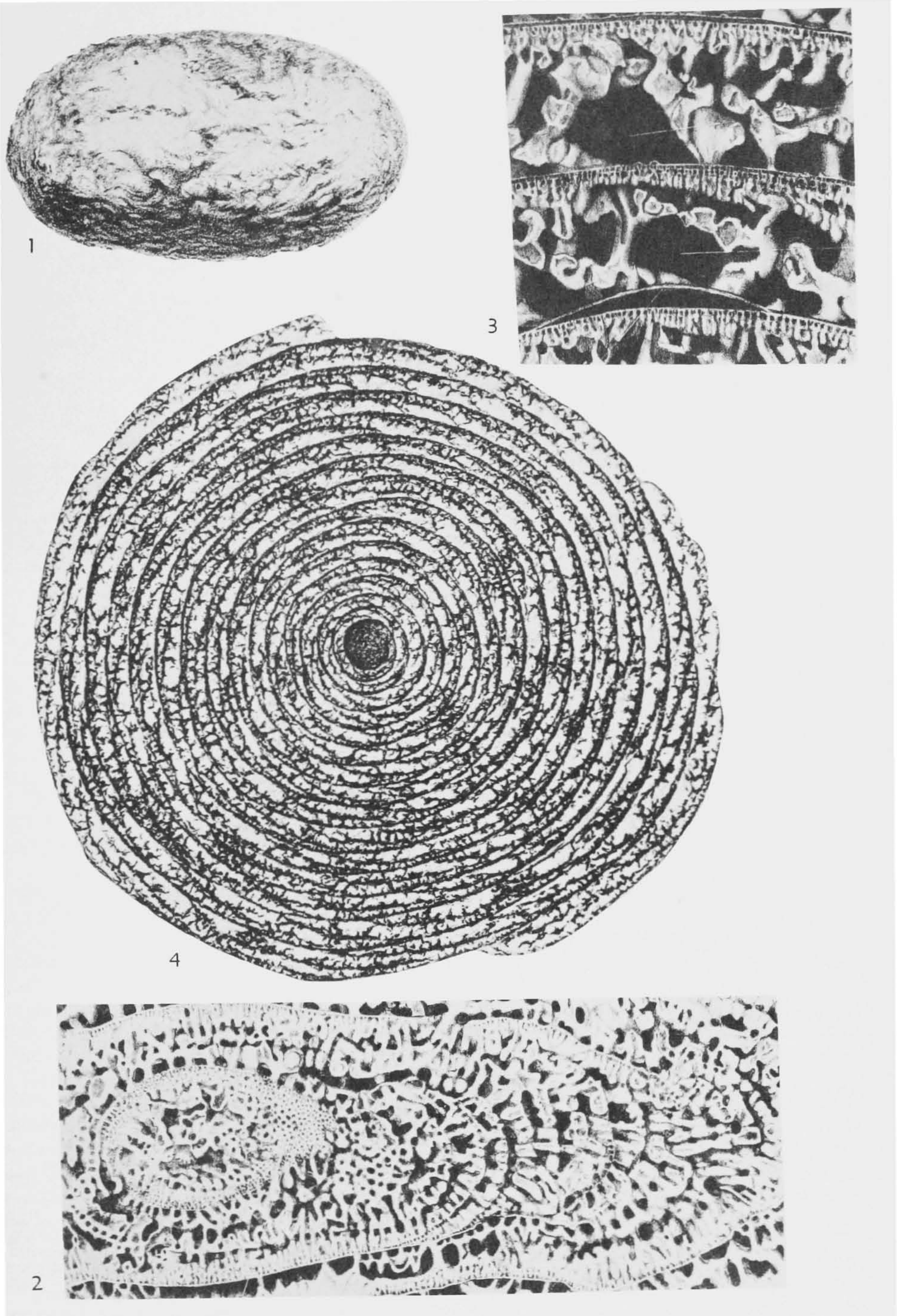

FIG. 149. Lituolidae (Loftusiinae; *1-4, Loftusia*) (p. *C236*).

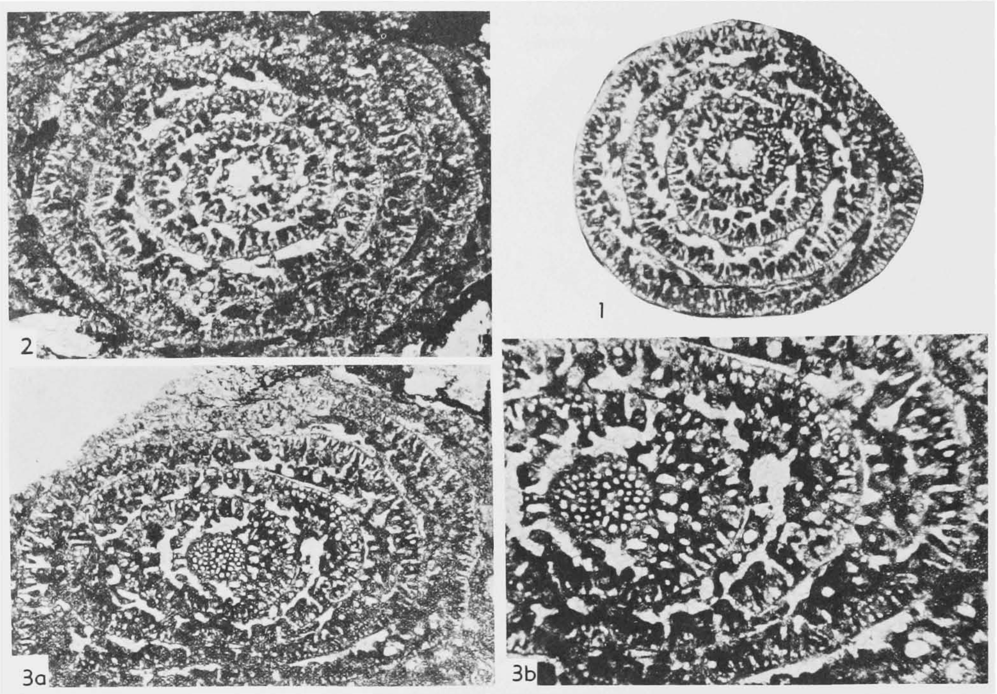

FIG. 150. Lituolidae (Loftusiinae; *1-3, Paracyclammina*) (p. C236-C238).

(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;

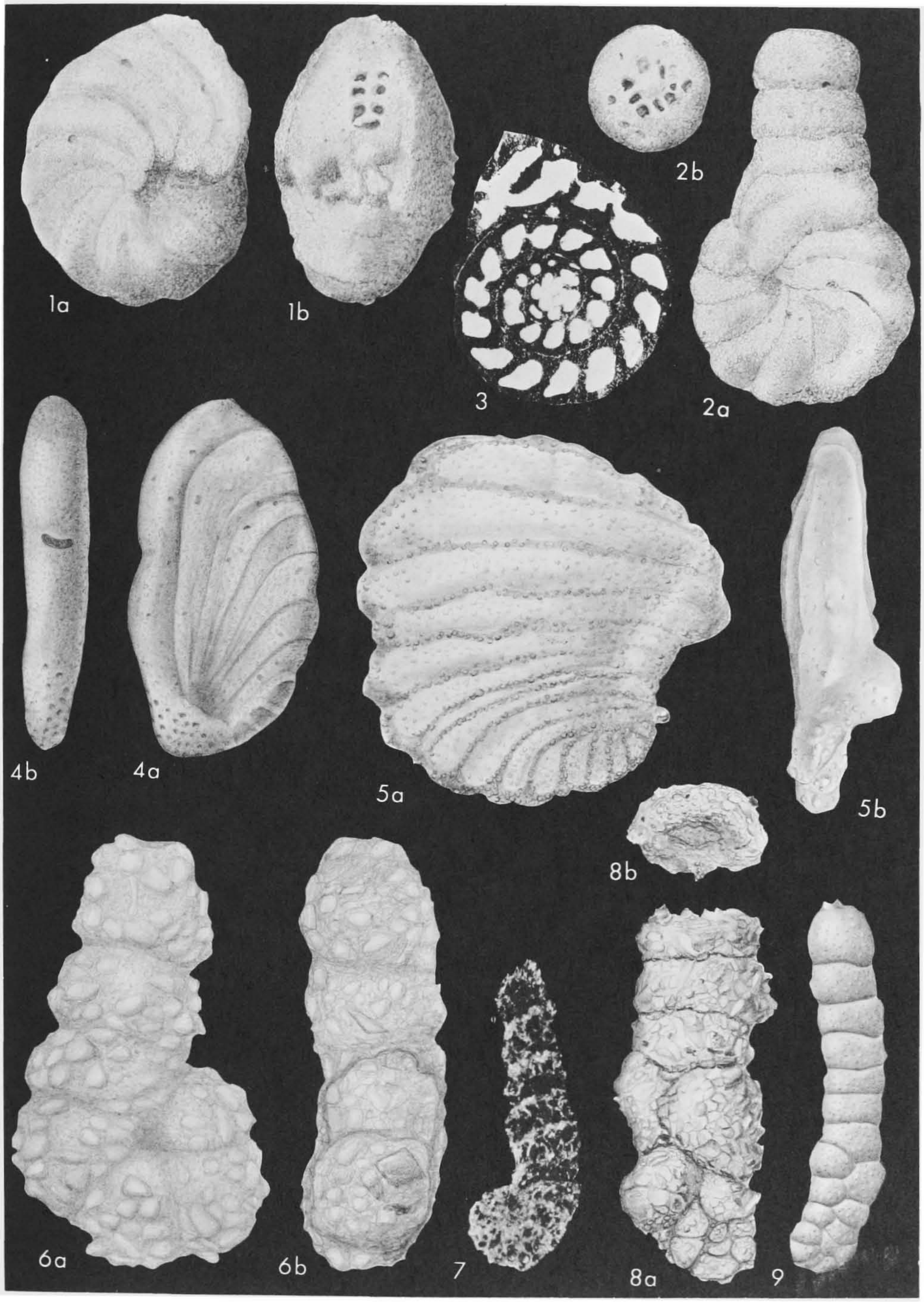

FIG. 151. Lituolidae (Lituolinae; *1-3, Lituola; 4,5, Ammoastuta; 6, Ammobaculites; 7, Ammomarginulina; 8,9, Ammobaculoides*) (p. *C238-C241*).

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

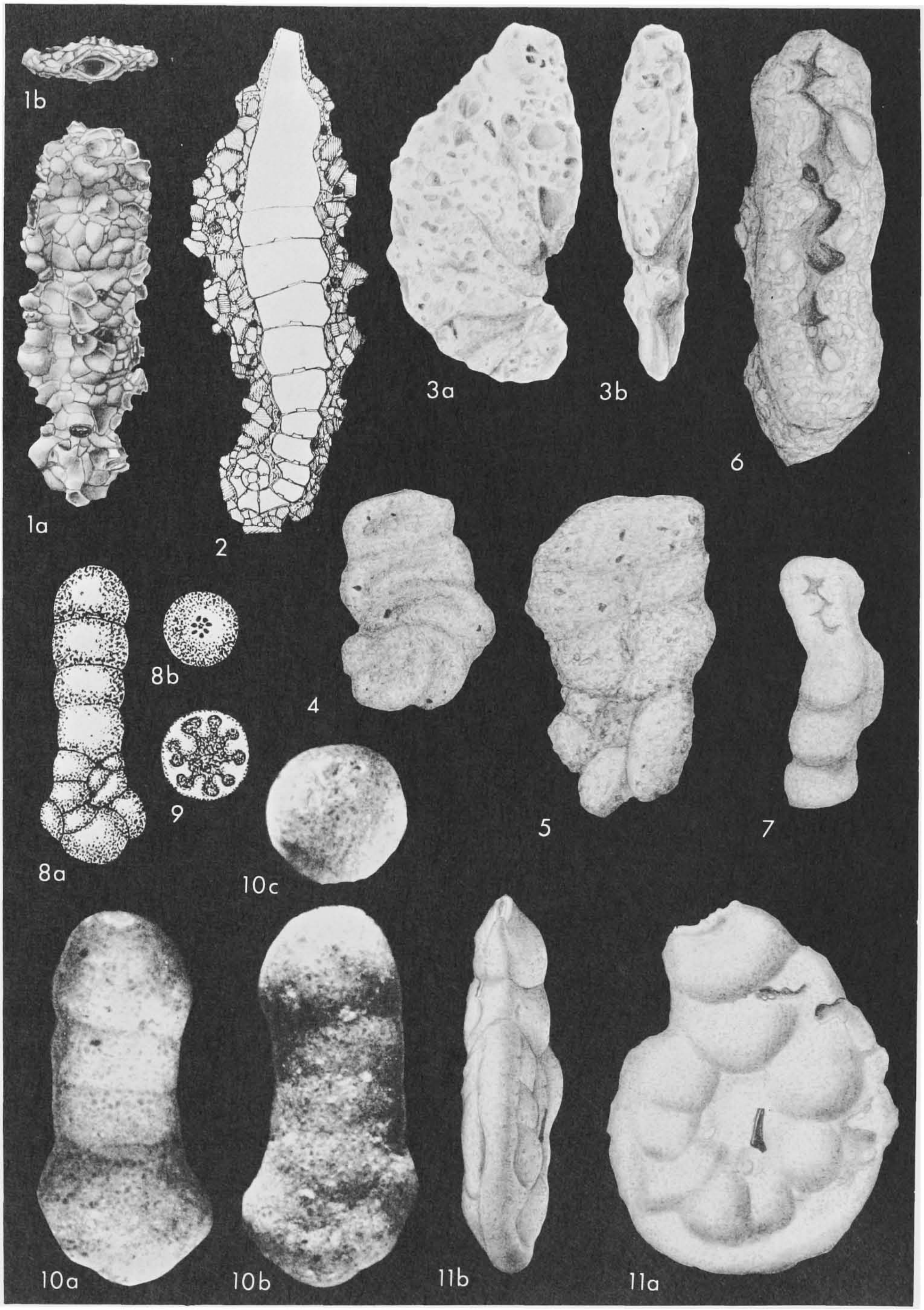

FIG. 152. Lituolidae (Lituolinae; *1,2, Ammoscalaria; 3, Ammotium; 4-7, Buccicrenata; 8-10, Bulbophragmium; 11, Discamminoides*) (p. C241-C244).

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).

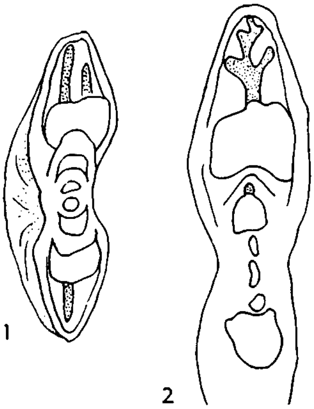

FIG. 153. Lituolidae (Lituolinae; *1,2, Discamminoides*) (p. *C*242-*C*244).

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).

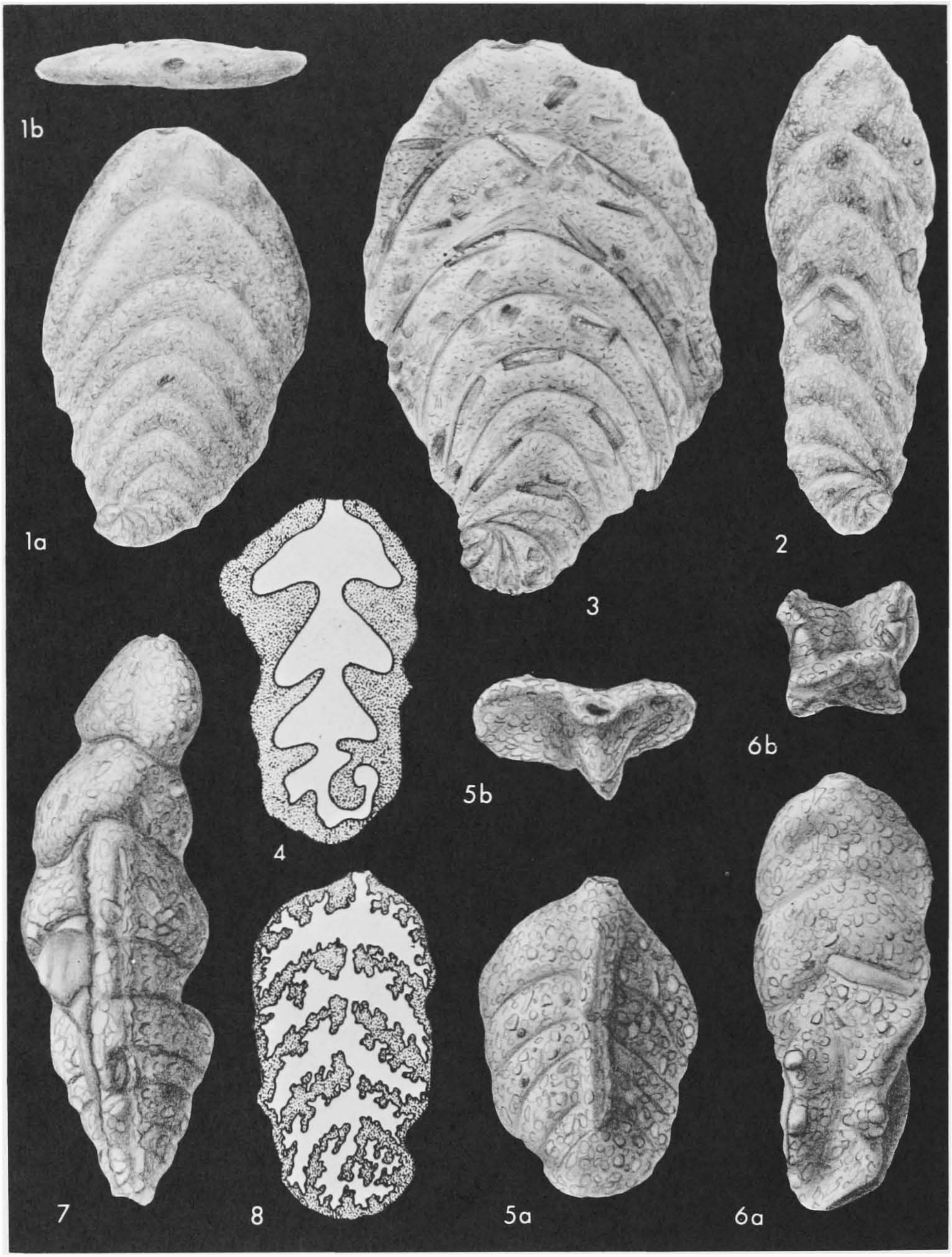

Fig. 154. Lituolidae (Lituolinae; *1-4, Flabellammina; 5-8, Flabellamminopsis*) (p. C244).

[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-

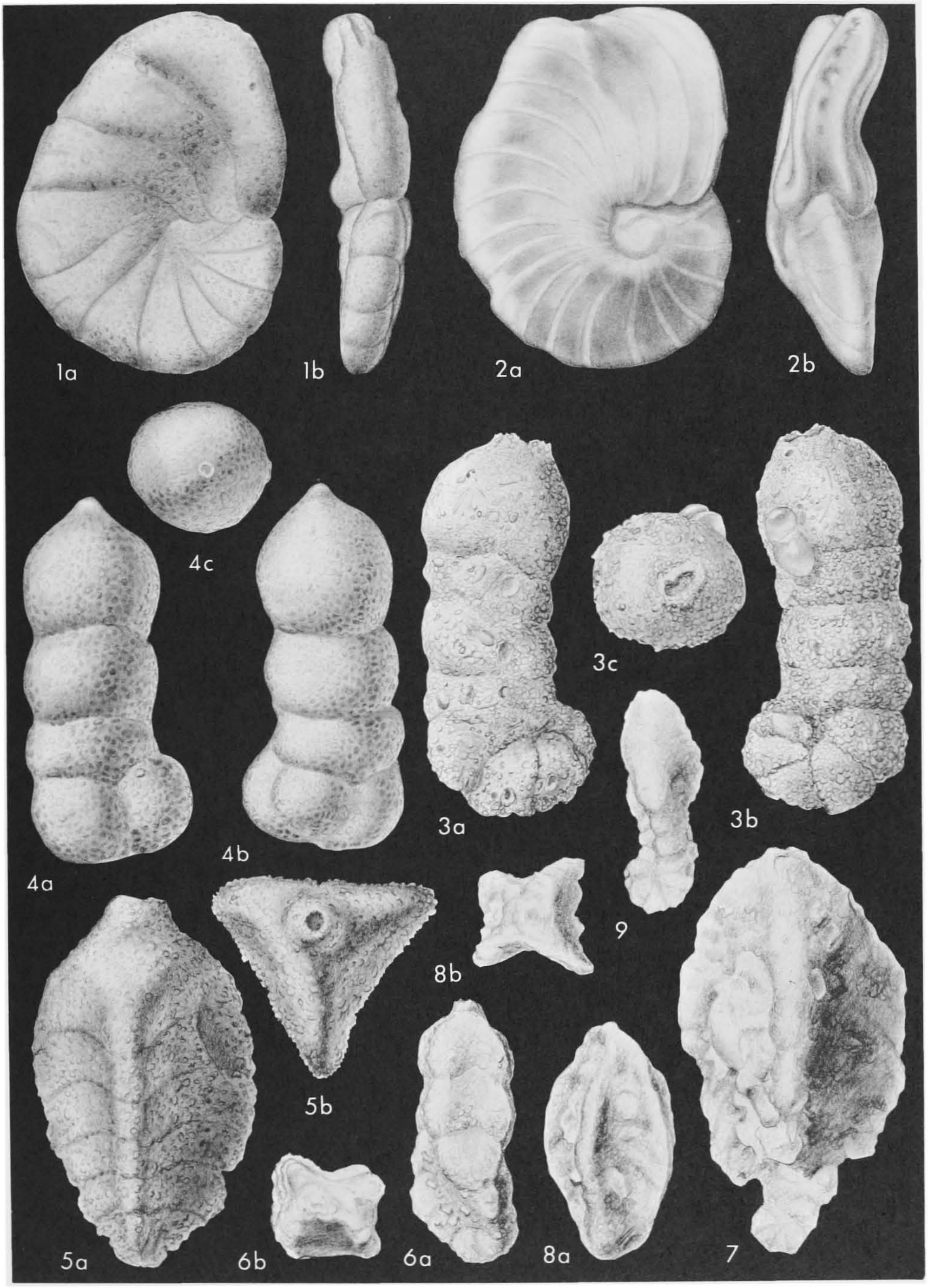

Fig. 155. Lituolidae (Lituolinae; *1, Phenacophragma; 2, Stomatostoecha; 3,4, Haplophragmium; 5-9, Triplasia*) (p. C244-C247).

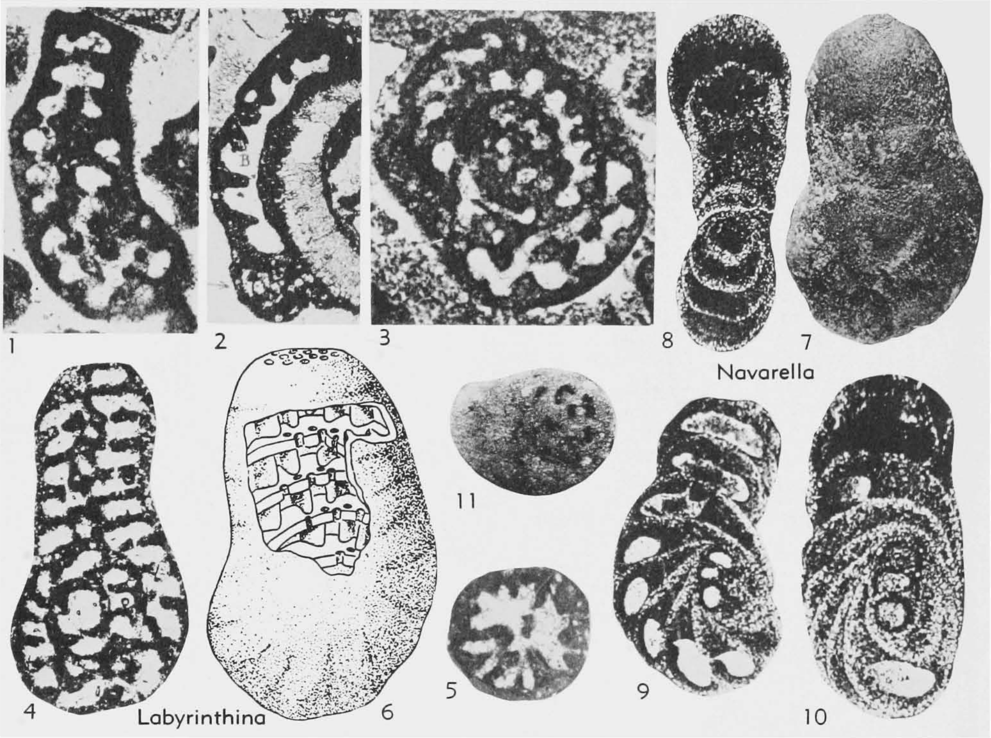

FIG. 156. Lituolidae (Lituolinae; *1-6, Labyrinthina; 7-11, Navarella*) (p. C245).

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).

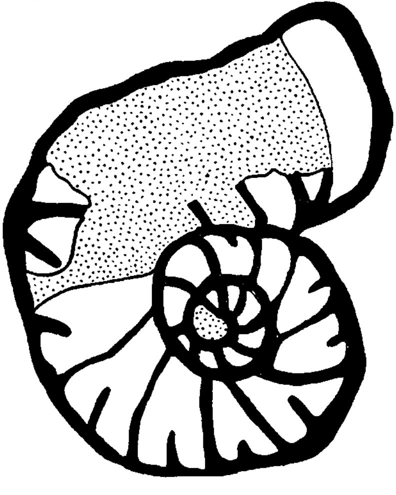

Fig. 157. Lituolidae (Lituolinae; *Phenacophragma*) (p. C245).

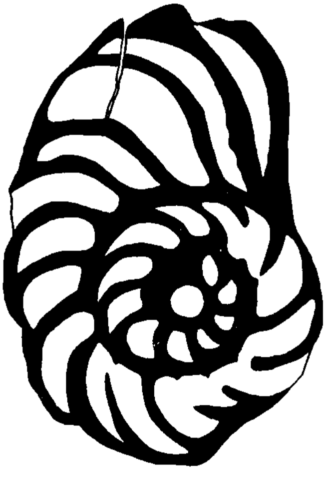

Fig. 158. Lituolidae (Lituolinae; *Stomatostoecha*) (p. C245).

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

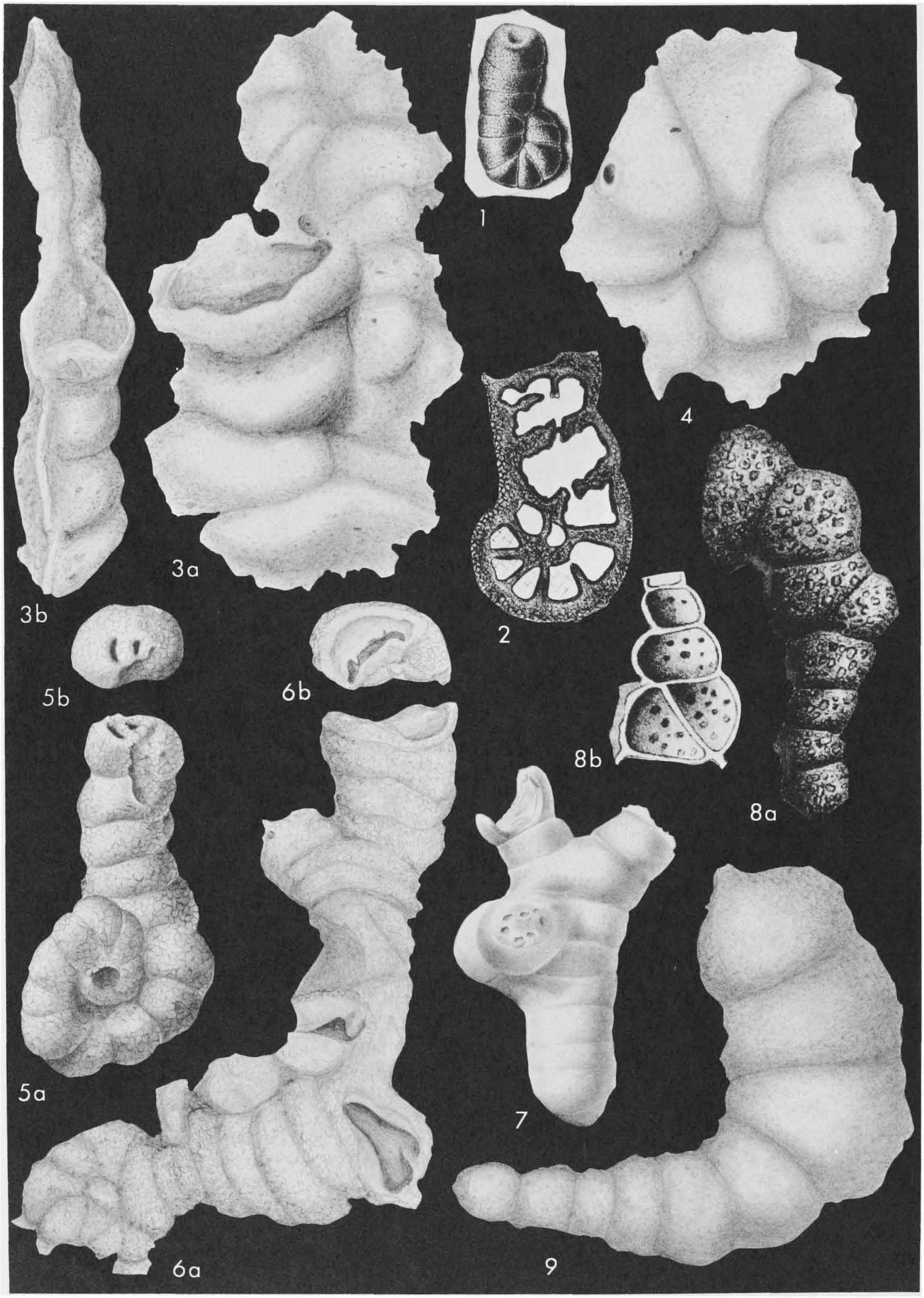

Fig. 159. Lituolidae (Placopsilininae; *1-4, Placopsilina; 5, Acruliammina; 6, Haddonia; 7, Manorella; 8,9, Subbdelloidina*) (p. *C*247-*C*248).

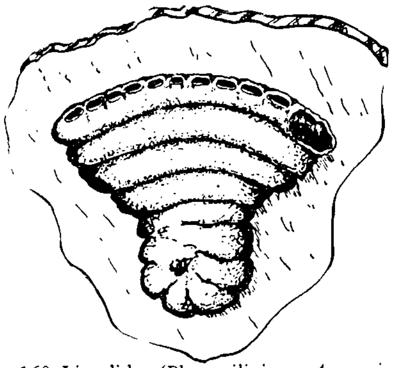

FIG. 160. Lituolidae (Placopsilininae; *Arenonina*) (p. *C*247).

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).

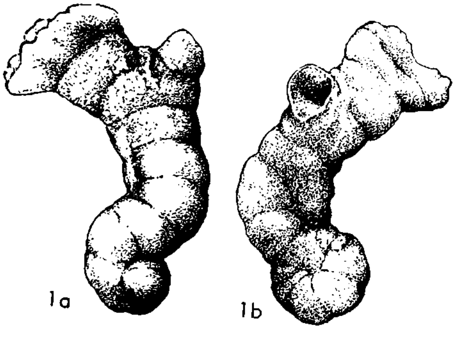

FIG. 161. Lituolidae (Placopsilininae; *1, Manorella*) (p. *C*248).

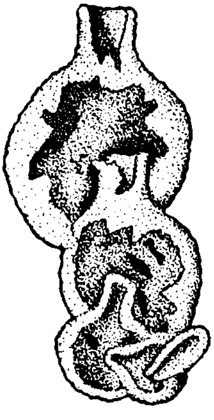

FIG. 161A. Lituolidae (Placopsilininae; *Oxinoxis*) (p. C248).

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

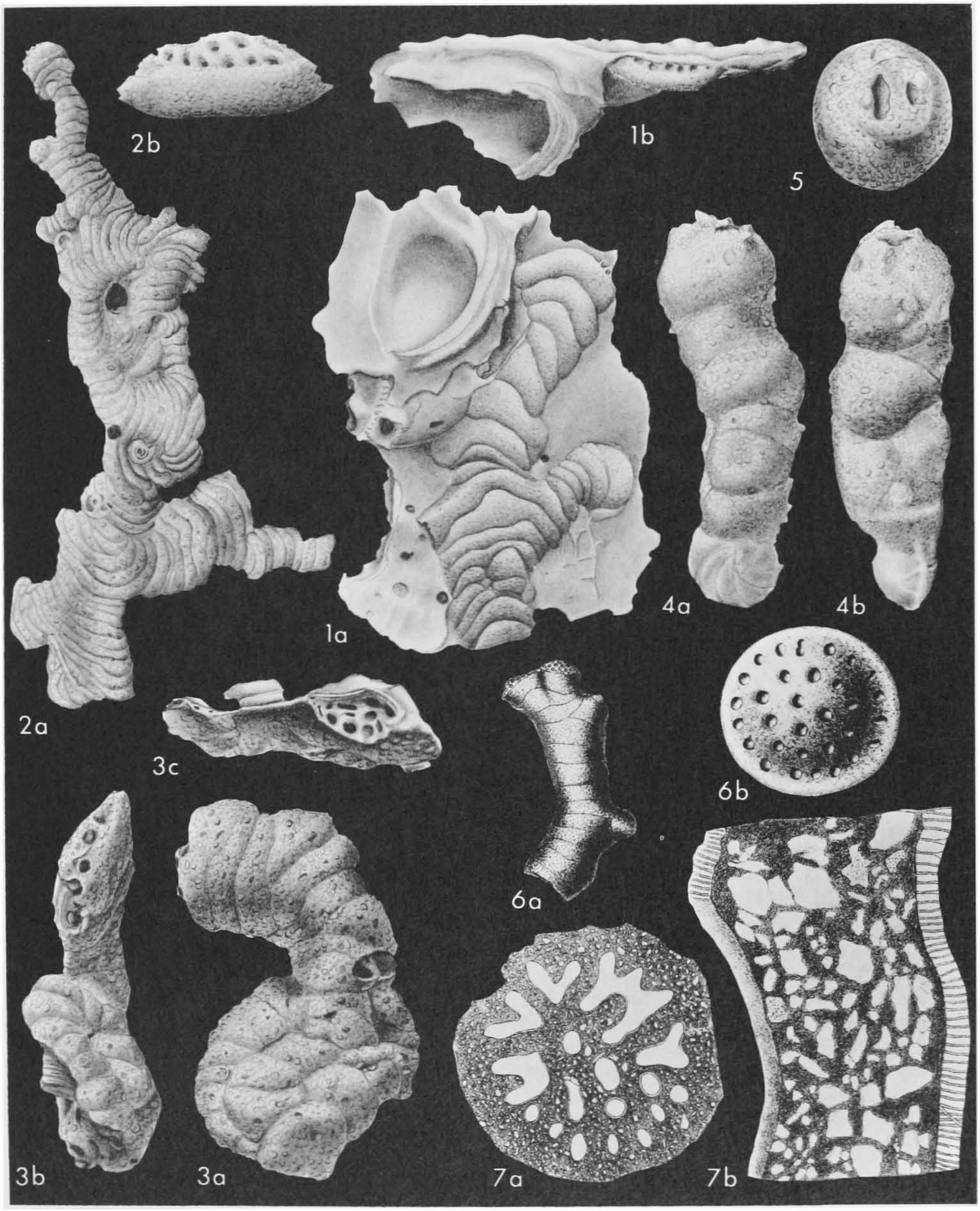

Fig. 162. Lituolidae (Coscinophragminae; *1-3, Bdelloidina; 4,5, Adhaerentia; 6,7, Coscinophragma*) (p. C248-C250).

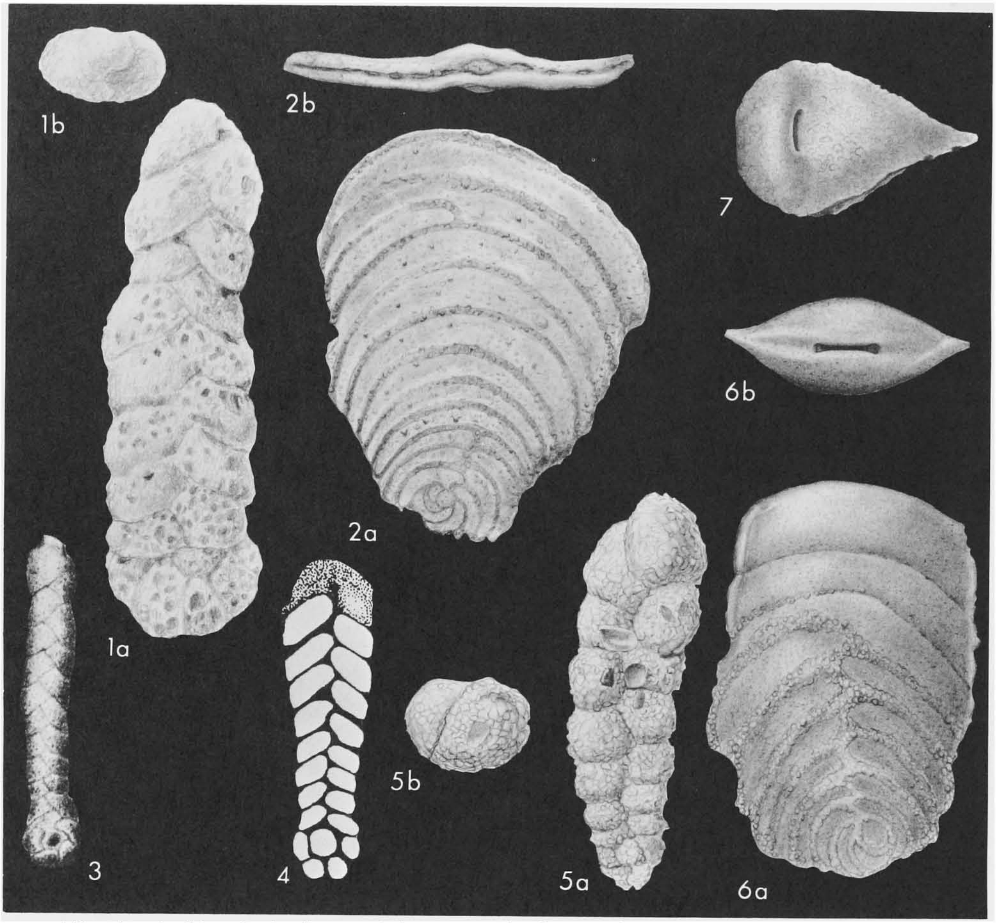

FIG. 163. Textulariidae (Spiroplectammininae; *1, Spiroplectammina; 2, Ammospirata; 3,4, Bolivinopsis; 5, Morulaeplecta; 6,7, Vulvulina*) (p. C251-C253).

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).

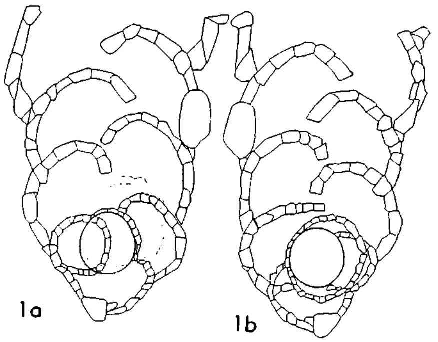

FIG. 164. Textulariidae (Spiroplectammininae; *1, Morulaeplecta*) (p. C251).

[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,*1,a,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

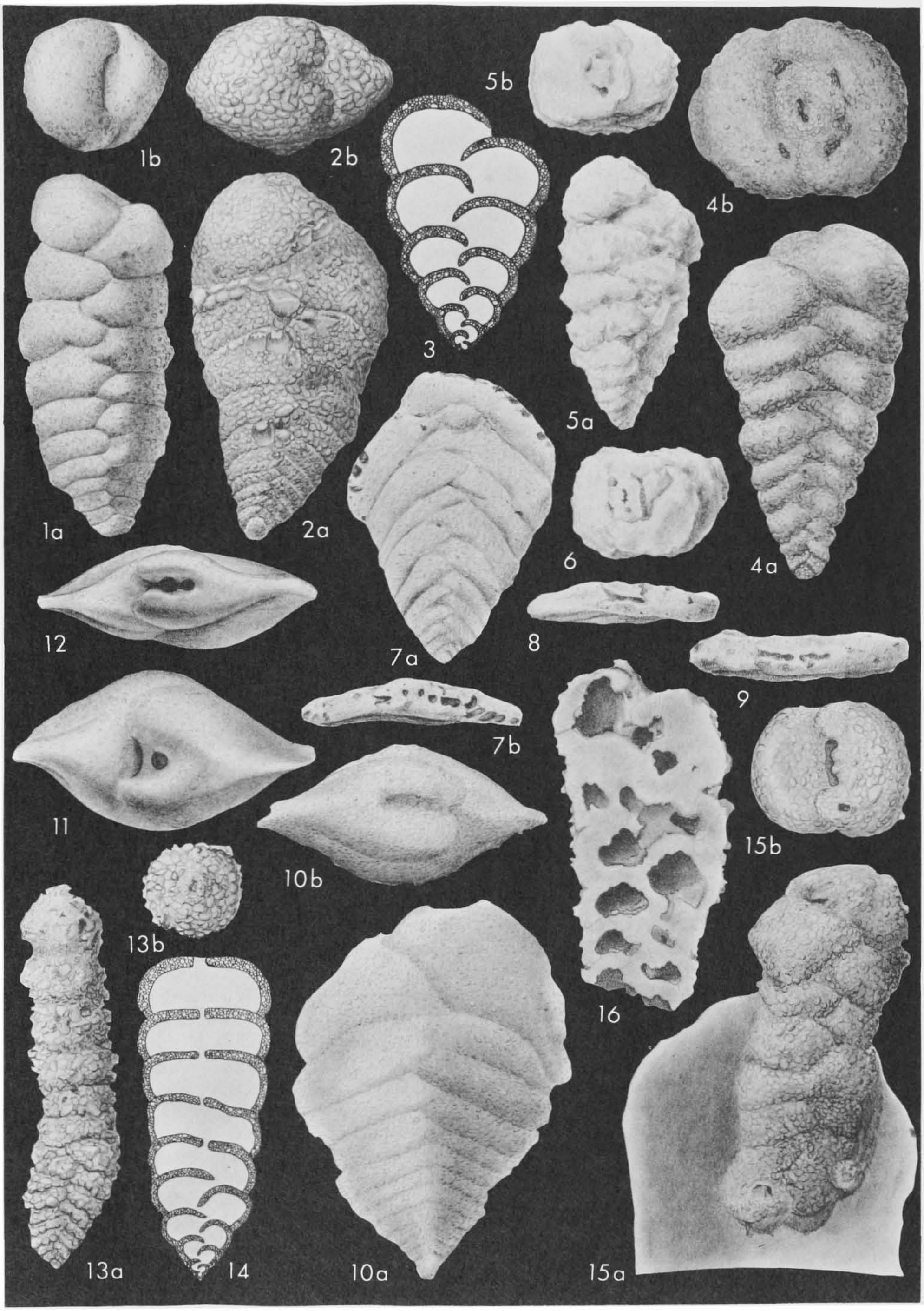

FIG. 165. Textulariidae (Textulariinae; *1-3, Textularia; 4-6, Olssonina; 7-9, Poritextularia; 10-12, Semivulvulina; 13-14, Bigenerina; 15,16, Textularioides*) (p. C253-C255).

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).

[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.*]

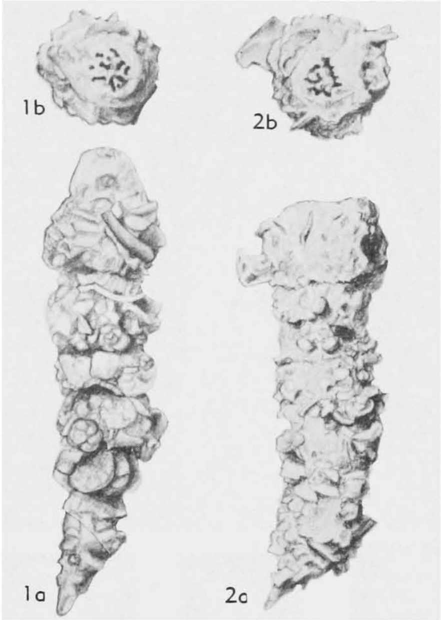

Fig. 166. Textulariidae (Textulariinae; *1,2, Cribrobigenerina*) (p. C254).

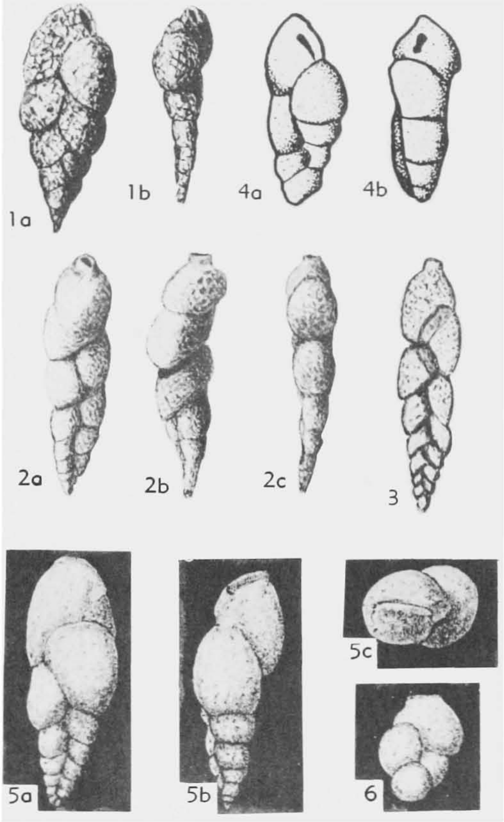

Fig. 167. Textulariidae (Pseudobolivininae; *1-6, Pseudobolivina*) (p. C255).

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

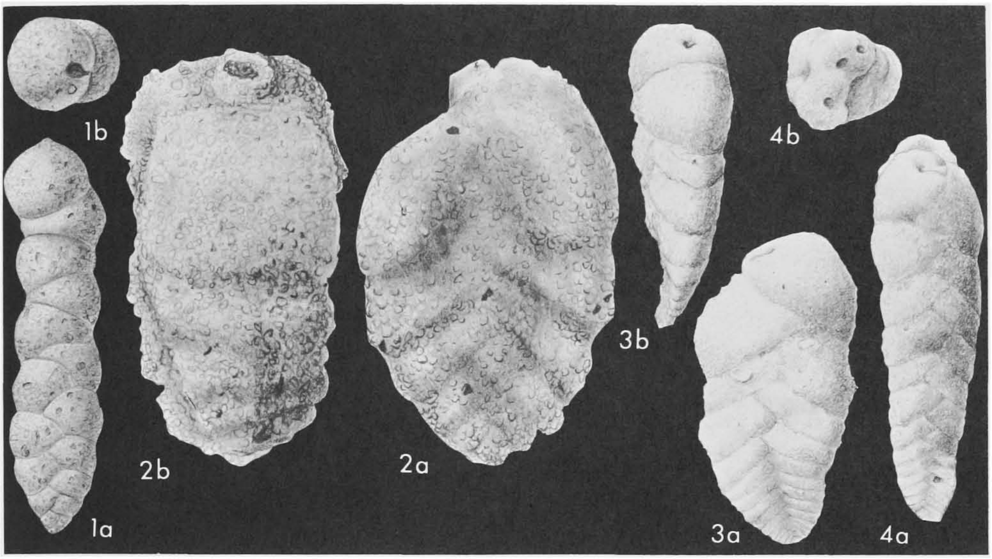

FIG. 168. Textulariidae (Pseudobolivininae; *1, Haeuslerella; 2, Siphotextularia; 3,4, Planctostoma*) (p. *C256-C258*).

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-

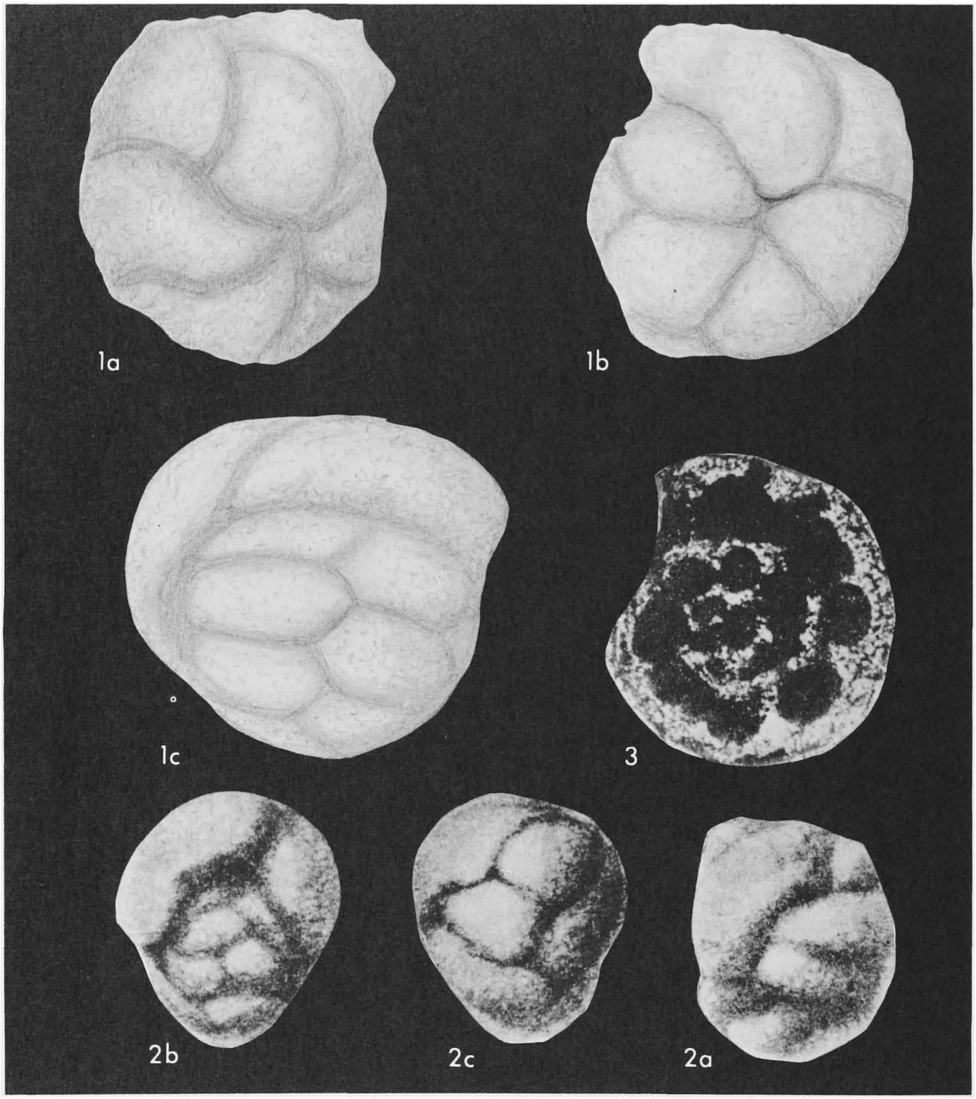

FIG. 169. Textulariidae (Plectorecurvoidinae; *1-3, Plectorecurvoides*) (p. C258).

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).

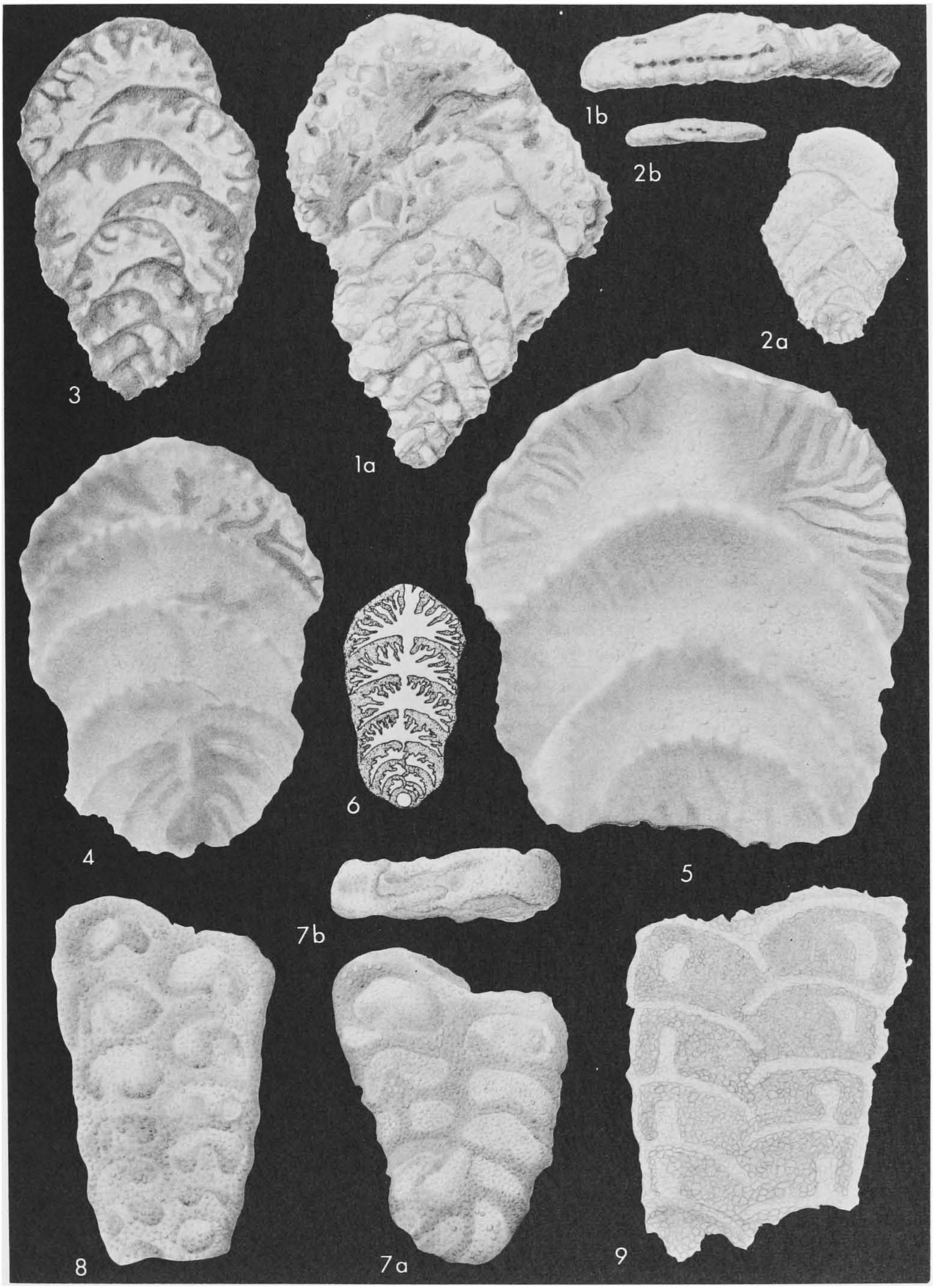

FIG. 170. Textulariidae (Tawitawiinae; *1-3, Tawitawia; 4-6, Phyllopsamia; 7-9, Septigerina*) (p. C258-C259).

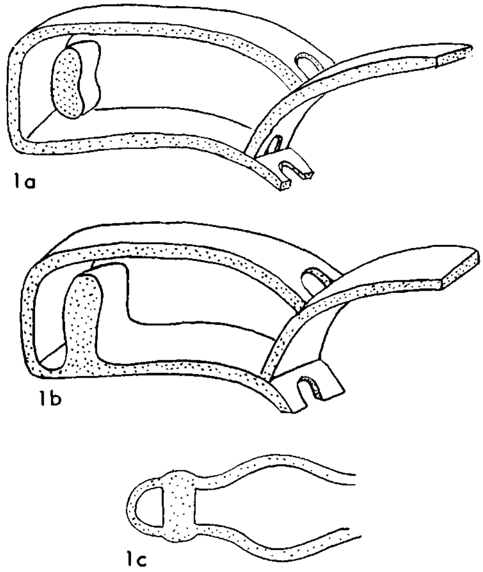

Fig. 171. Textulariidae (Tawitawiinae; *1, Septigerina*) (p. *C*258-*C*259).

[*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,*

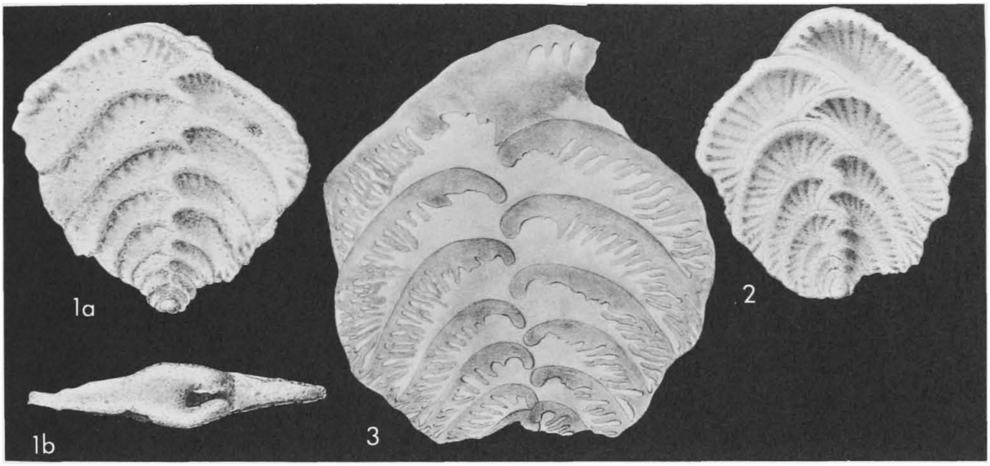

FIG. 172. Textulariidae (Tawitawiinae; *1-3, Zotheculifida*) (p. C259).

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).

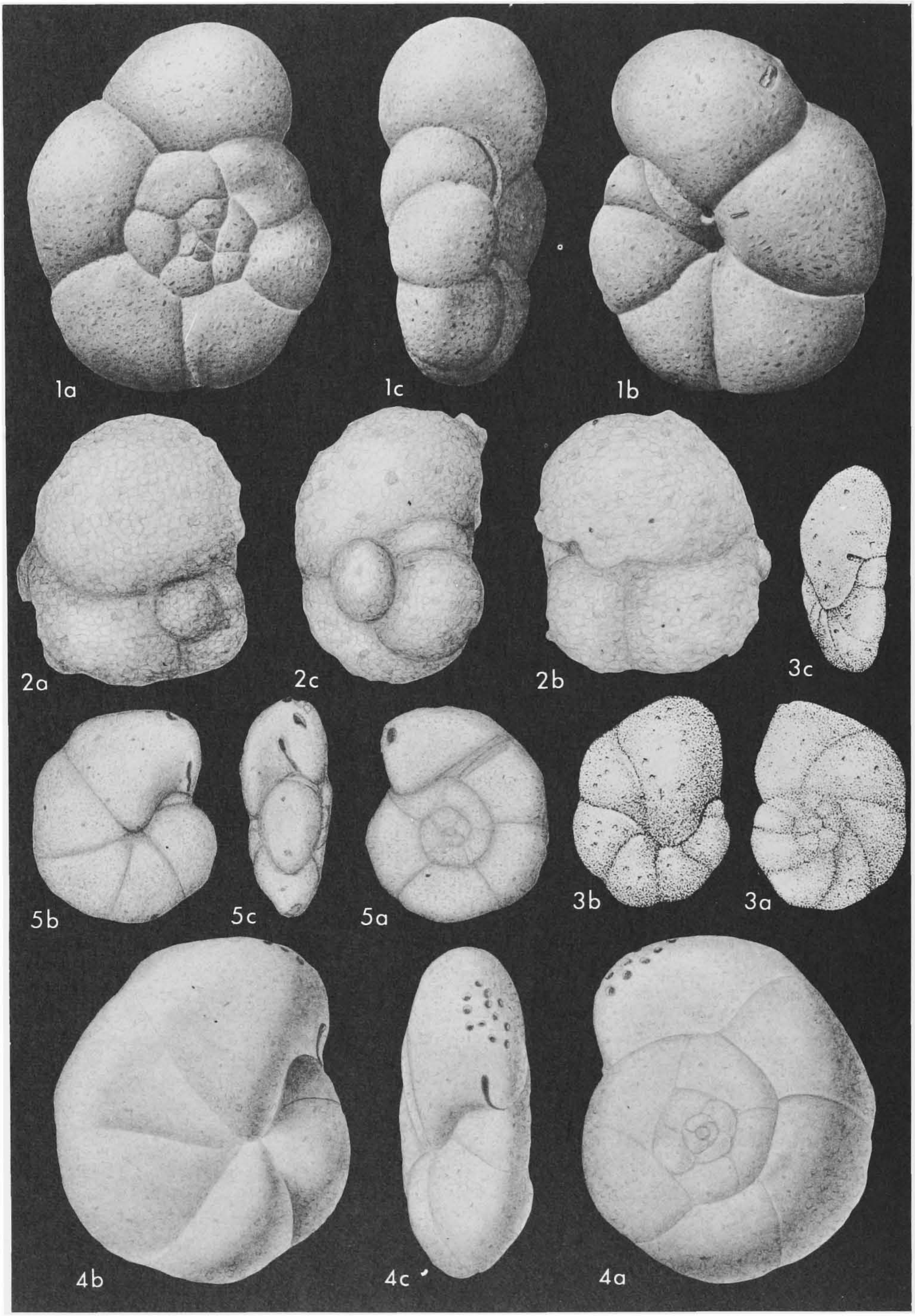

Fig. 173. Trochamminidae (Trochammininae; *1,2, Trochammina; 3, Trochamminula; 4,5, Arenoparrella*) (p. *C*259, *C*262, *C*266).

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

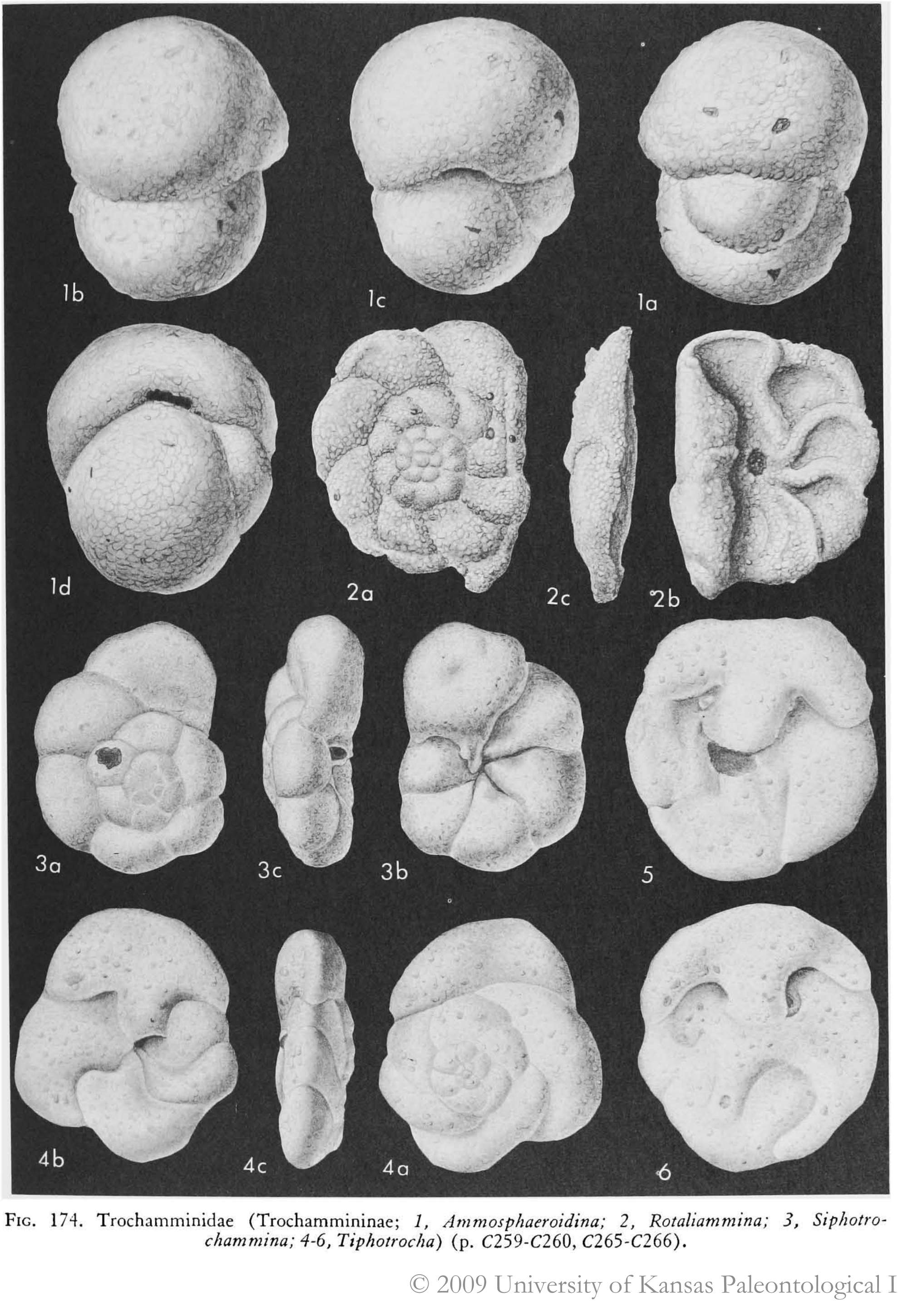

Fig. 174. Trochamminidae (Trochammininae; *1, Ammosphaeroidina; 2, Rotaliammina; 3, Siphotrochammina; 4-6, Tiphotrocha*) (p. C259-C260, C265-C266).

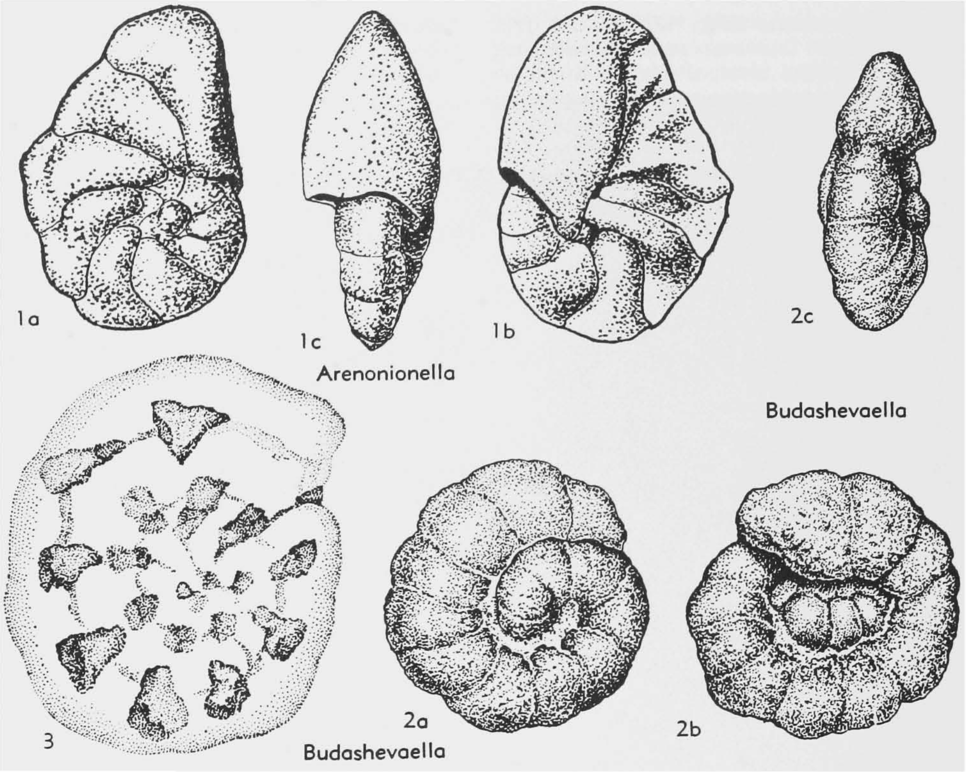

FIG. 175. Trochamminidae (Trochammininae; *1, Arenonionella; 2,3, Budashevaella*) (p. *C*261-*C*262).

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).

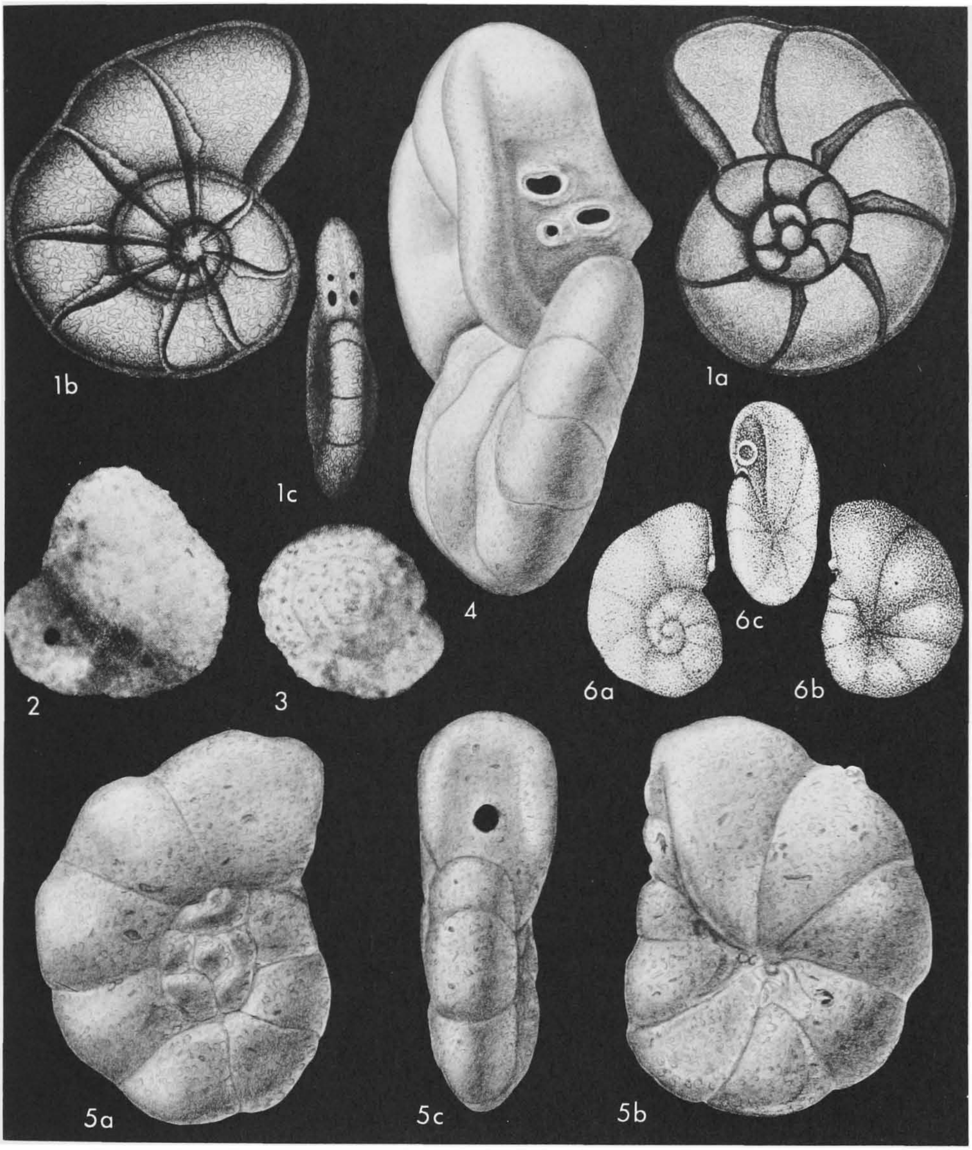

FIG. 176. Trochamminidae (Trochammininae; *1, Entzia; 2,3, Conotrochammina; 4-6, Jadammina*) (p. *C263-C265*).

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

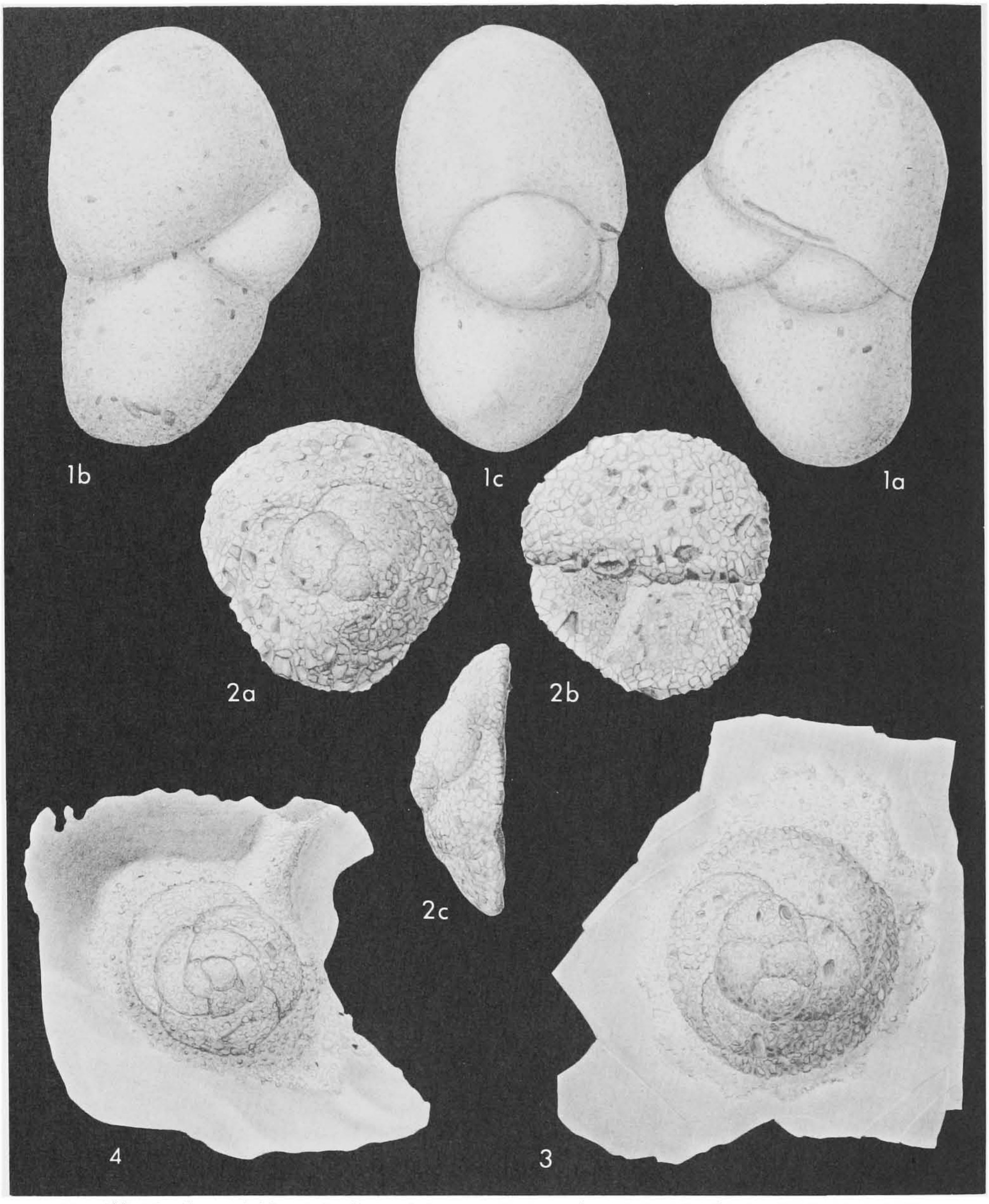

FIG. 177. Trochamminidae (Trochammininae; *1, Cystammina; 2-4, Tritaxis*) (p. C263-C264, C266).

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).

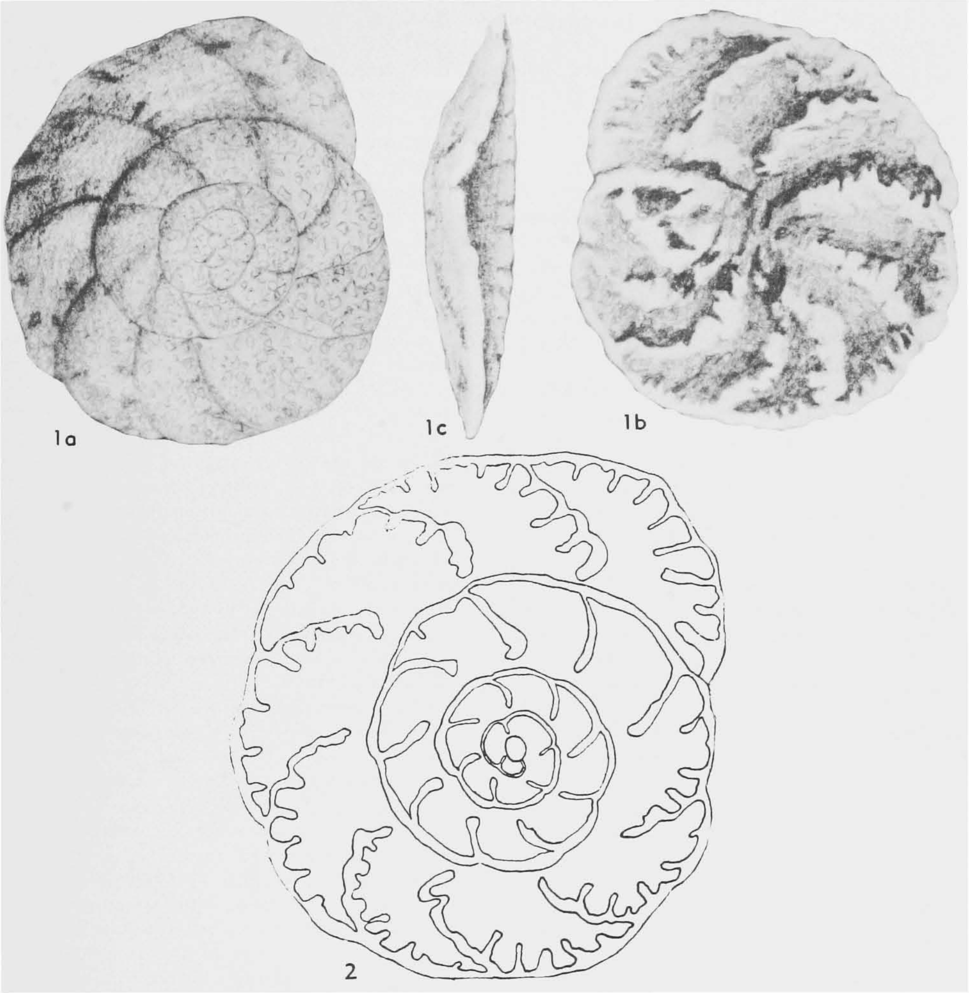

Fig. 178. Trochamminidae (Remaneicinae; *1,2, Remaneica*) (p. *C*266-*C*268).

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 reentrant 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)-

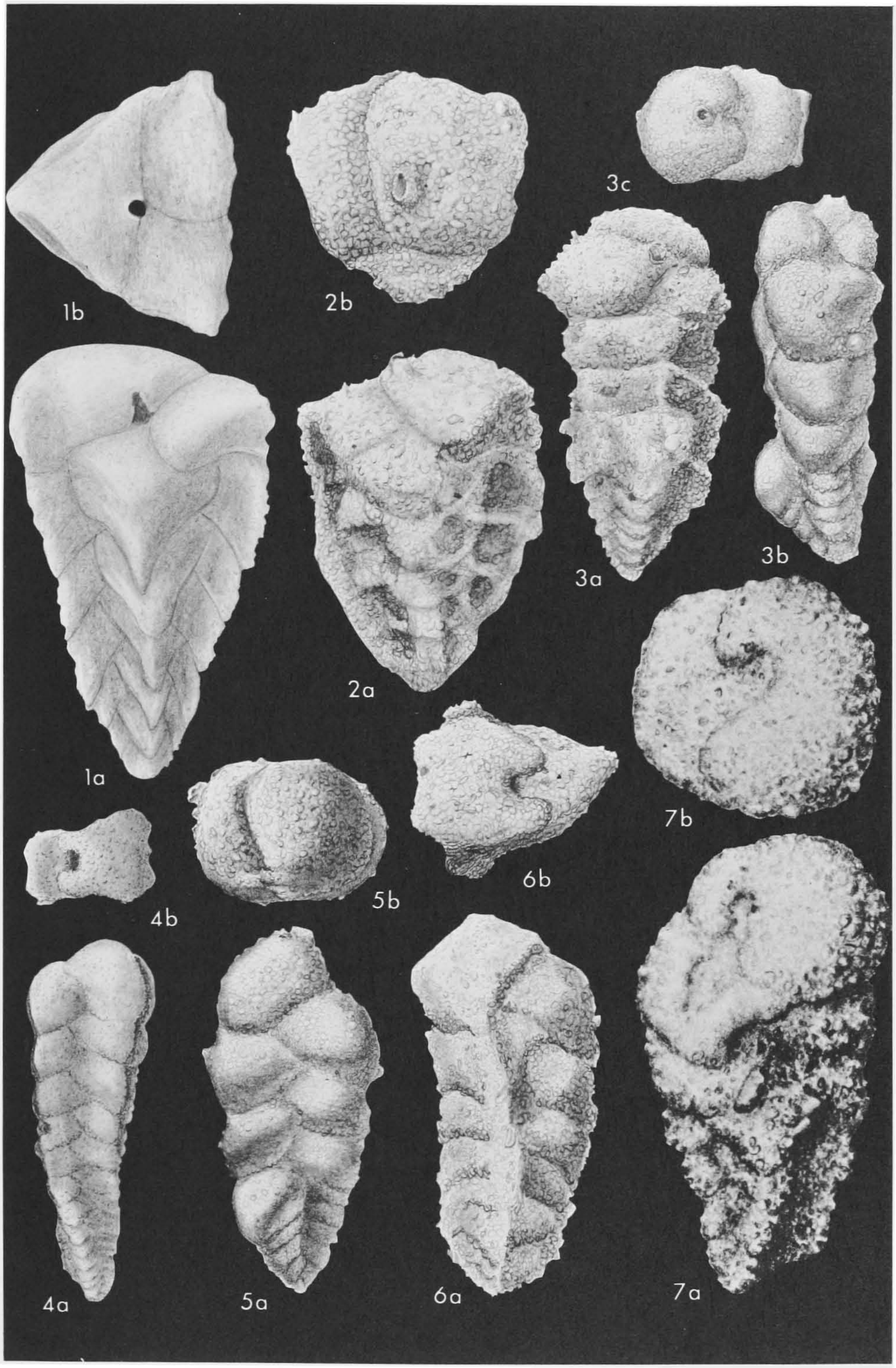

FIG. 179. Ataxophragmiidae (Verneuilininae; *1, Verneuilina; 2, Barbourinella; 3, Bermudezina; 4-7, Gaudryina*) (p. *C*268-*C*269).

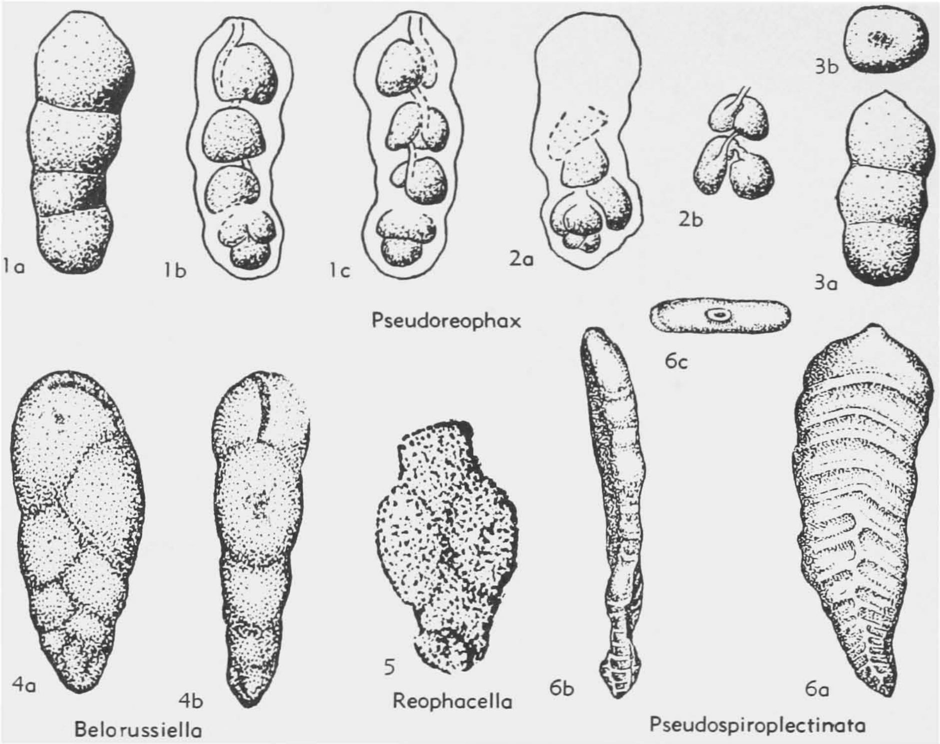

FIG. 180. Ataxophragmiidae (Verneuilininae; *1-3, Pseudoreophax; 4, Belorussiella; 5, Reophacella; 6, Pseudospiroplectinata*) (p. *C*269-*C*272).

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*]——[=Hélicostèguest† 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

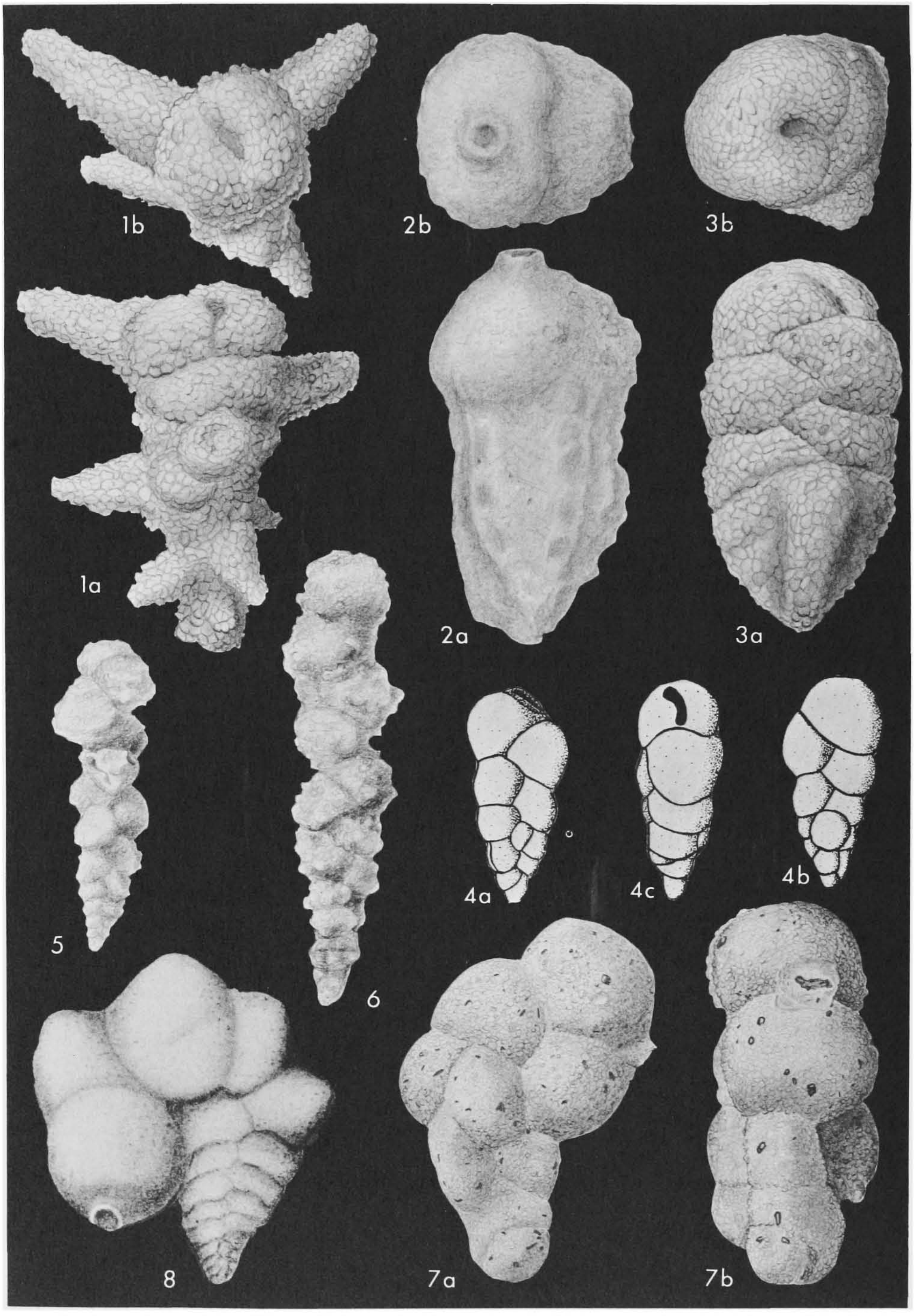

FIG. 181. Ataxophragmiidae (Verneuilininae; *1, Flourensina; 2, Heterostomella; 3,4, Migros; 5,6, Gaudryinella; 7,8, Rudigaudryina*) (p. C269, C272).

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.

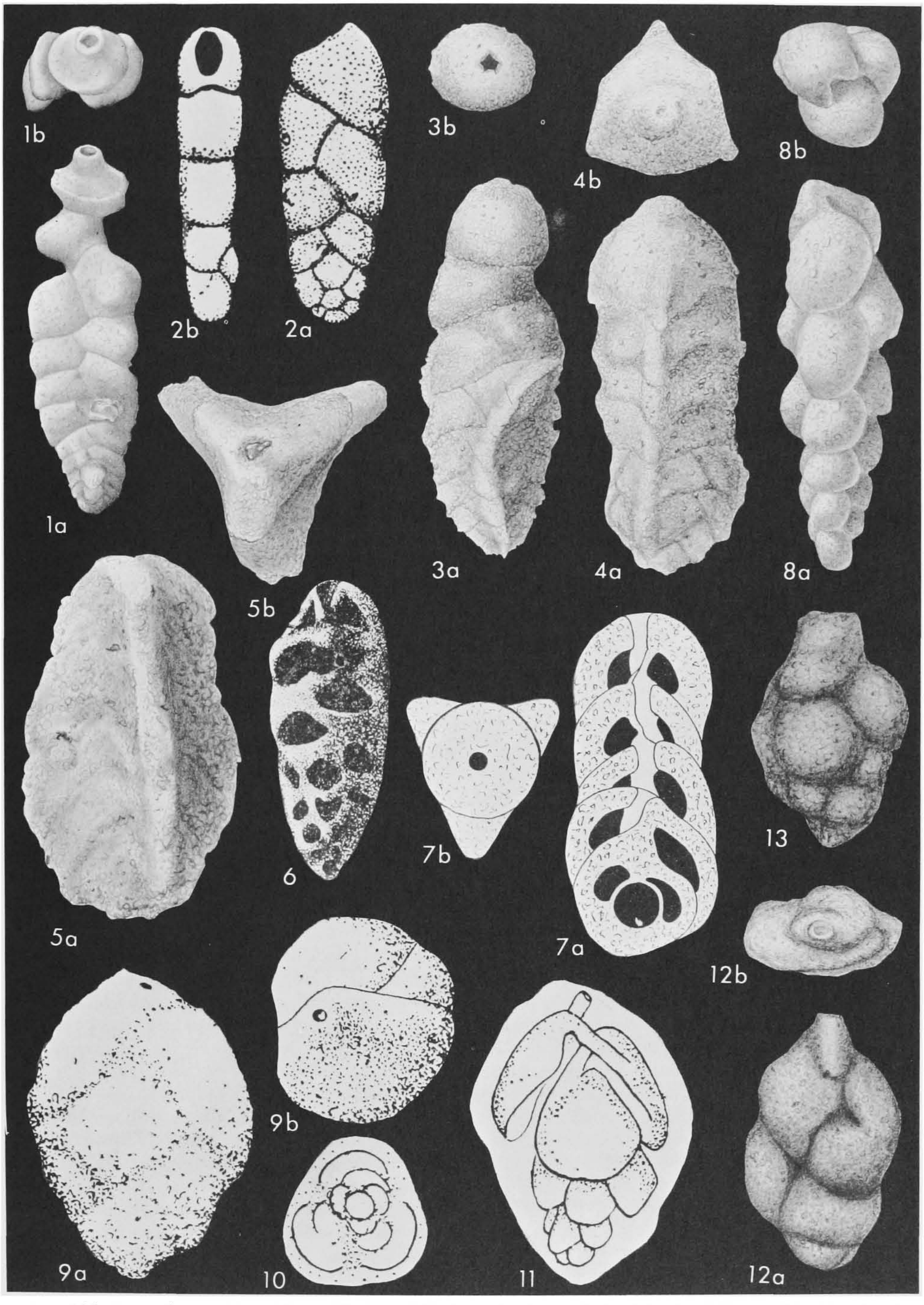

FIG. 182. Ataxophragmiidae (Verneuilininae; *1-2, Spiroplectinata; 3-7, Tritaxia; 8, Verneuilinoides; 9-13, Uvigerinammina*) (p. C272-C273).

(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).

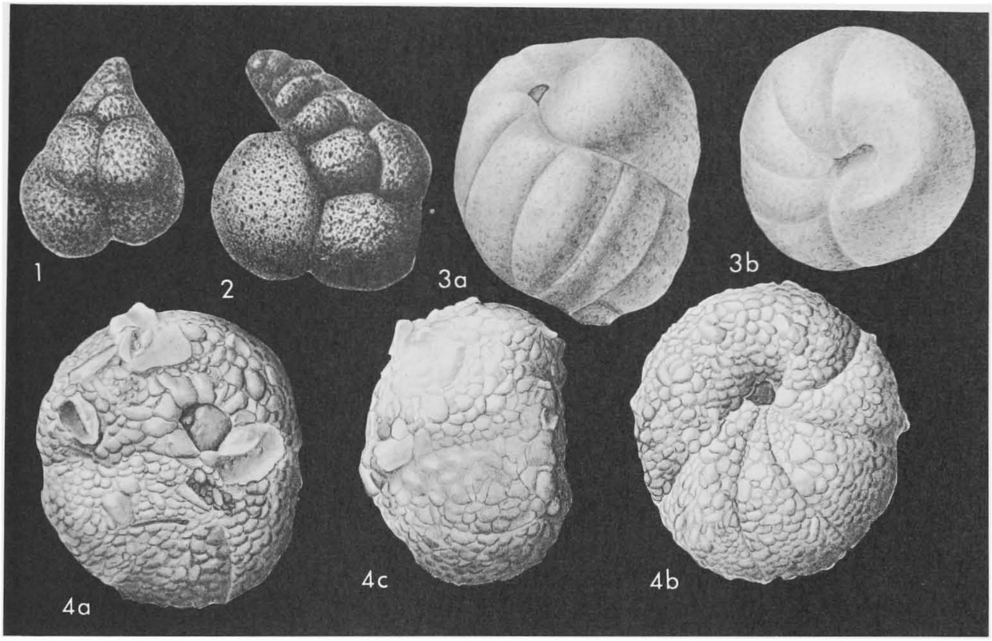

FIG. 183. Ataxophragmiidae (Globotextulariinae; *1,2, Globotextularia; 3,4, Arenobulimina*) (p. C273).

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;

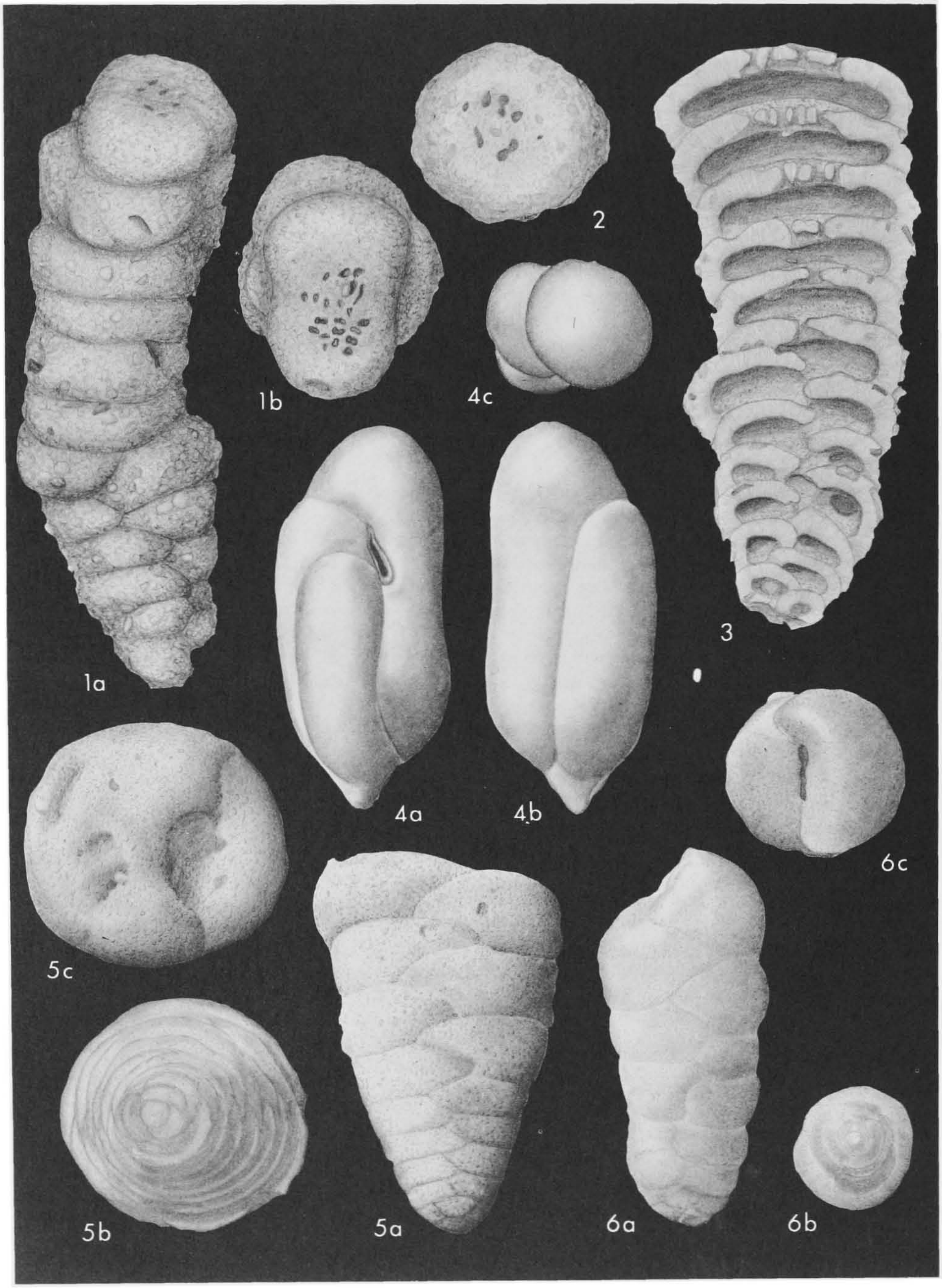

FIG. 184. Ataxophragmiidae (Globotextulariinae; *1-3, Cribrogoesella; 4, Eggerina; 5,6, Dorothia*) (p. C273-C275).

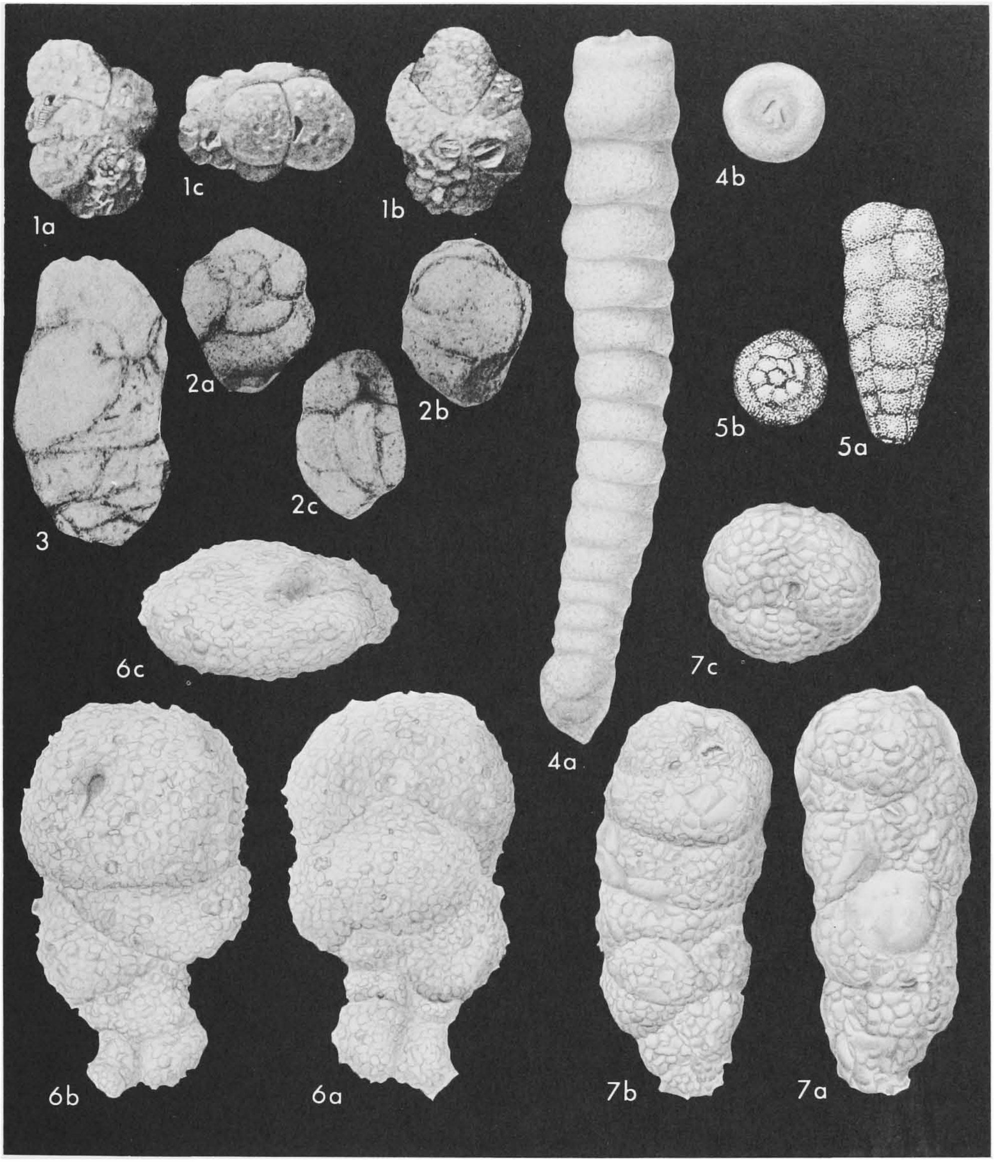

FIG. 185. Ataxophragmiidae (Globotextulariinae; *1-3, Plectotrochammina; 4, Multifidella; 5, Orientalia; 6, Mooreinella; 7, Digitina*) (p. C274, C277-C279).

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).

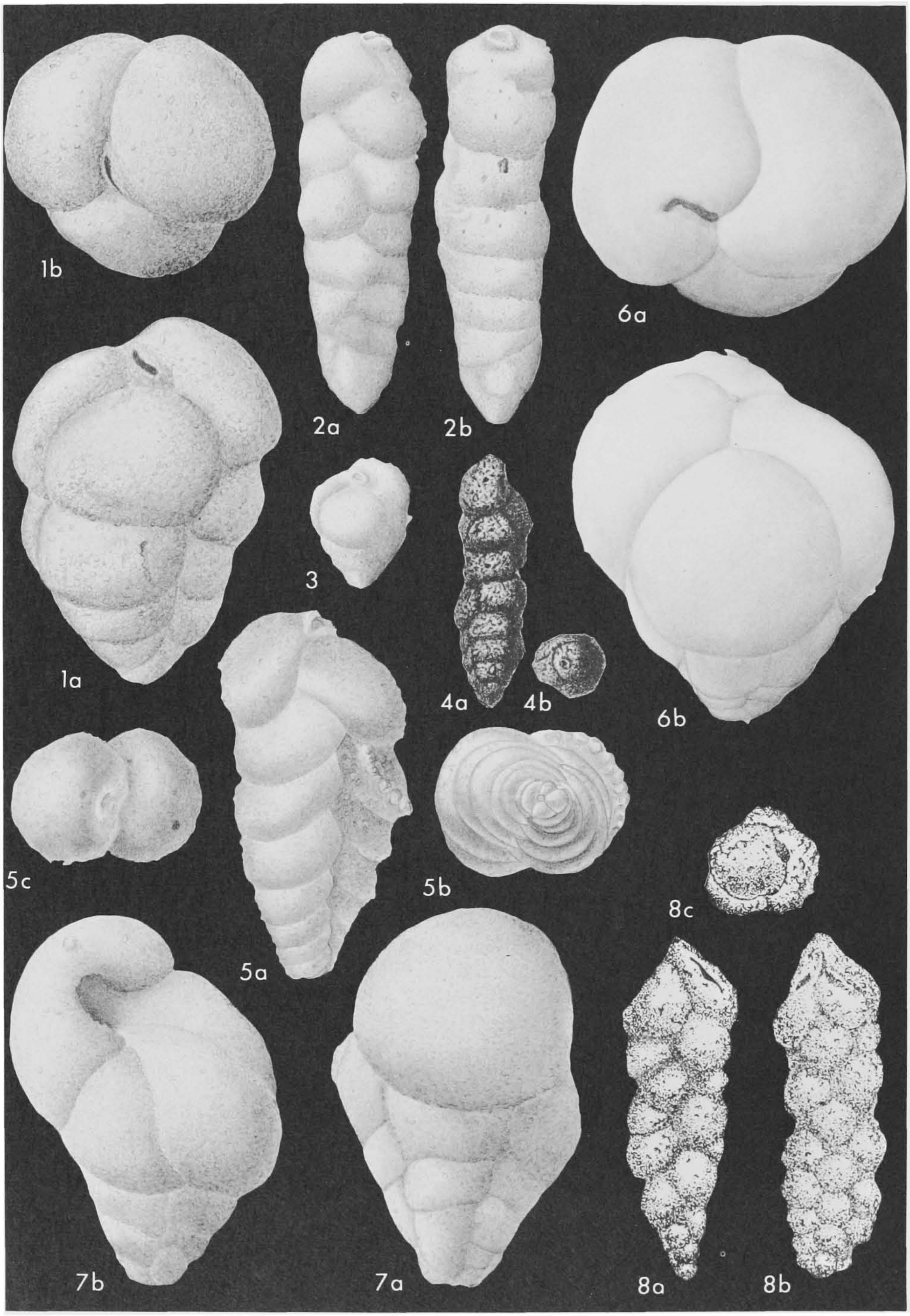

FIG. 186. Ataxophragmiidae (Globotextulariinae; *1, Eggerella; 2-5, Karreriella; 6, Eggerellina; 7,8, Gravellina*) (p. *C275-C277*).

[*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

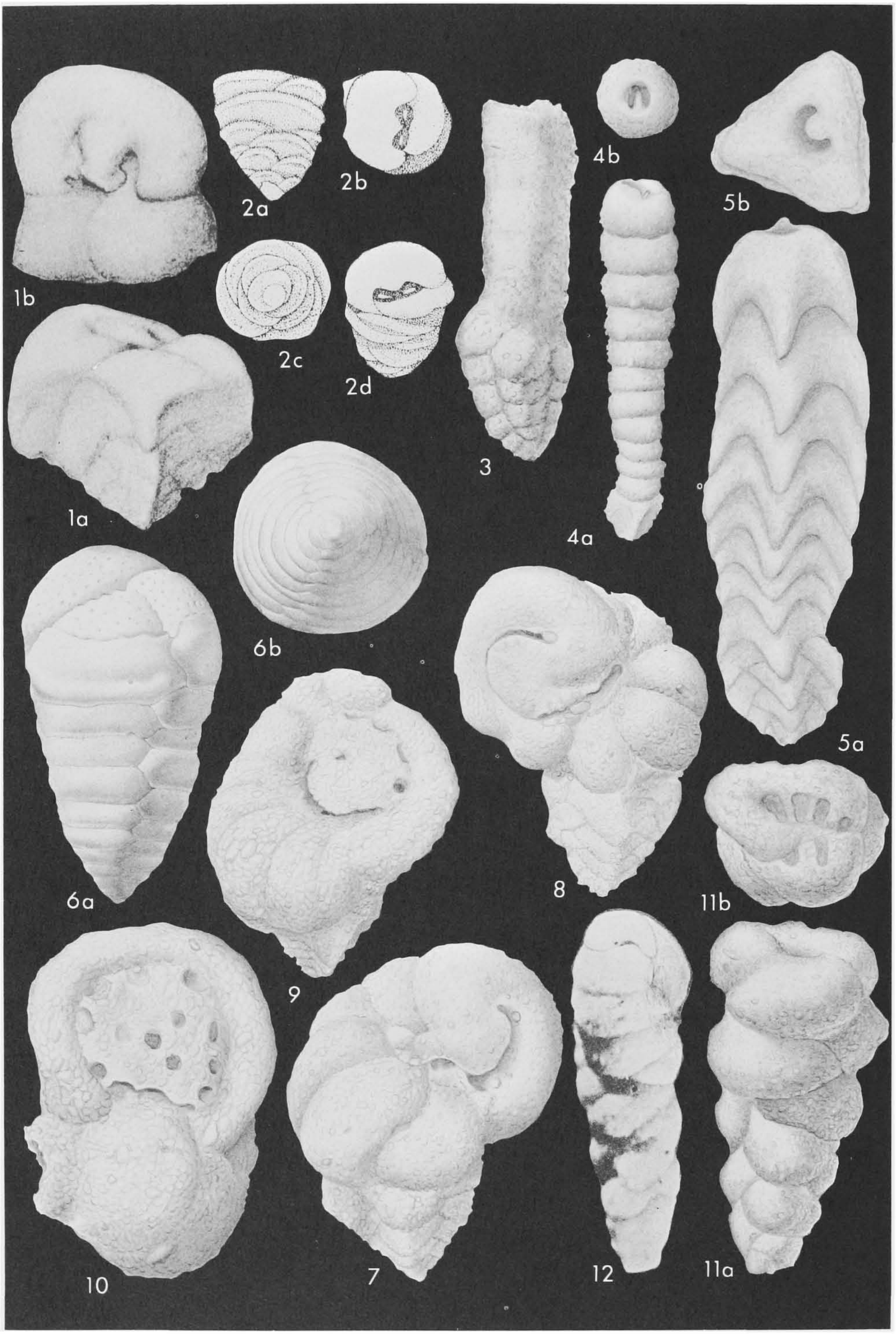

Fig. 187. Ataxophragmiidae (Valvulininae; *1,2, Valvulina; 3-5, Clavulina; 6, Chrysalidina; 7-10, Cribrobulimina; 11,12, Cribroturretoides*) (p. C279-C281).

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 platelike 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,

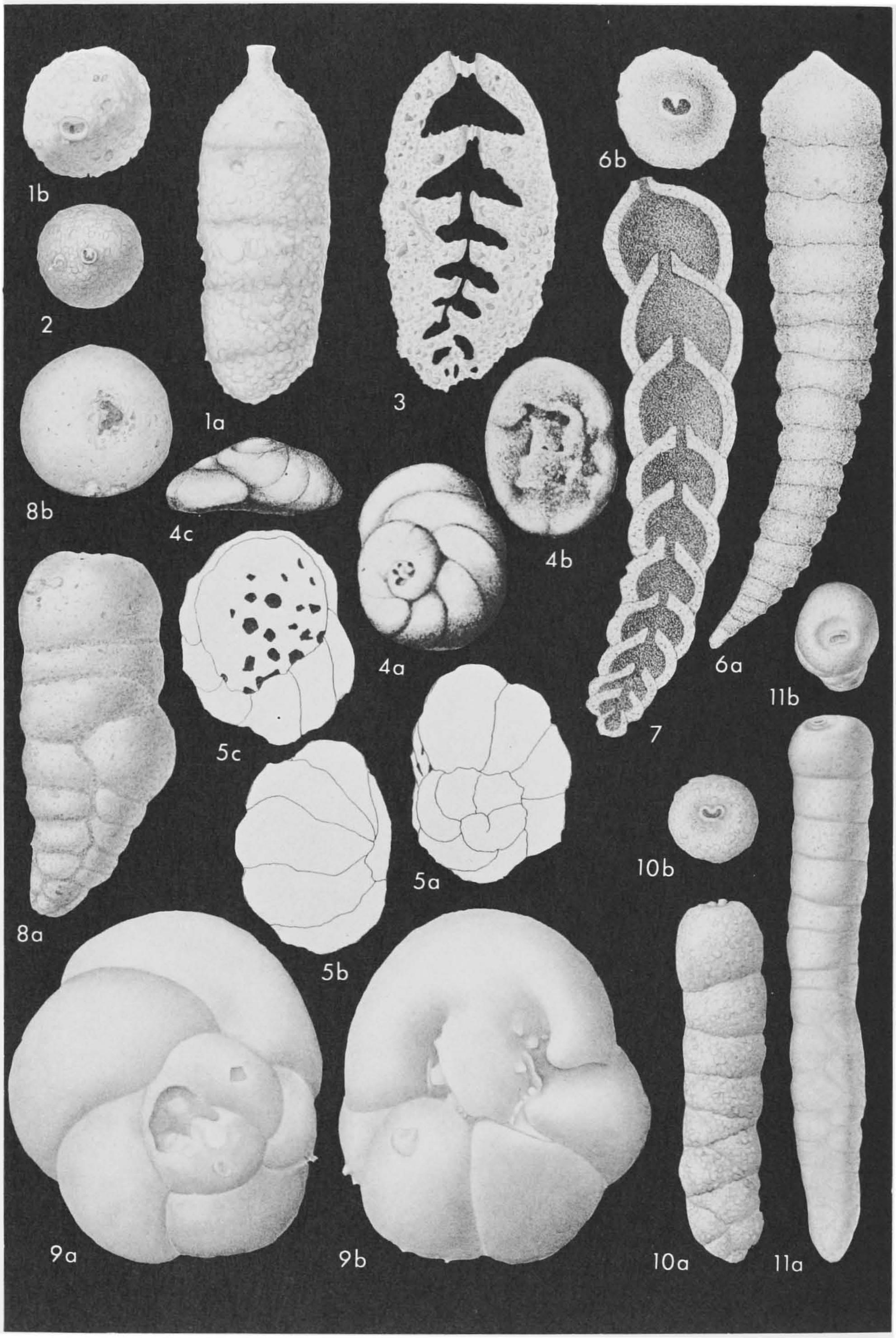

FIG. 188. Ataxophragmiidae (Valvulininae; *1-3, Cylindroclavulina; 4,5, Discorinopsis; 6,7, Dusenburyina; 8, Goesella; 9, Valvulammina; 10,11, Martinottiella*) (p. C281-C283).

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.]

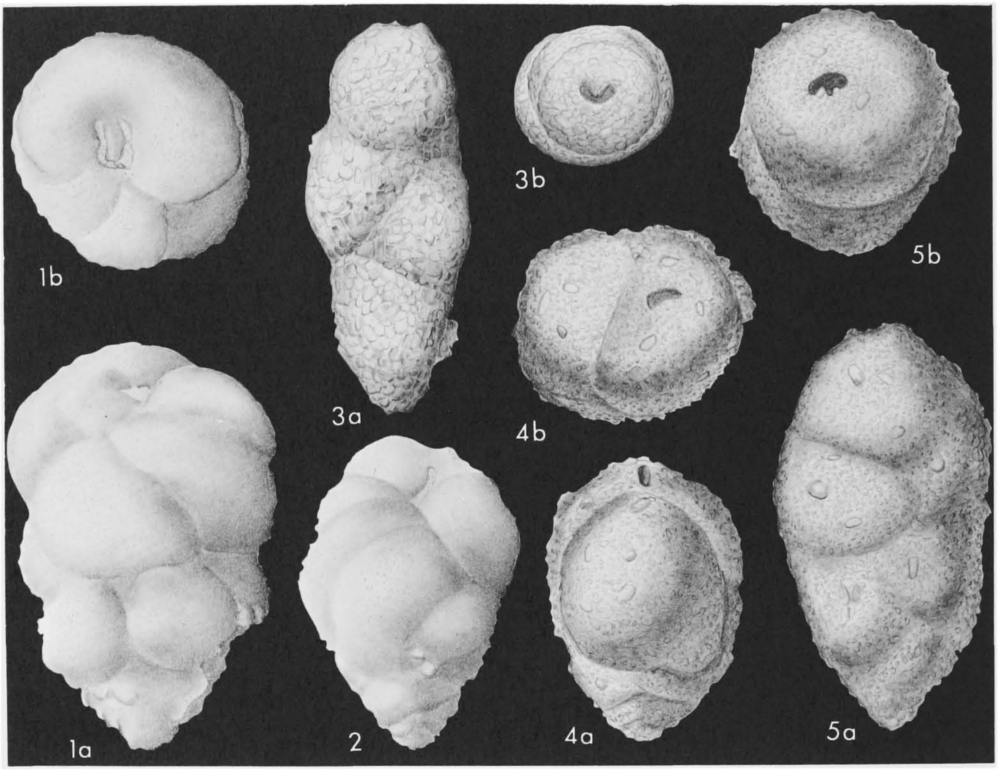

FIG. 189. Ataxophragmiidae (Valvulininae; *1,2, Makarskiana; 3-5, Plectina*) (p. *C*282-*C*283).

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.*

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).

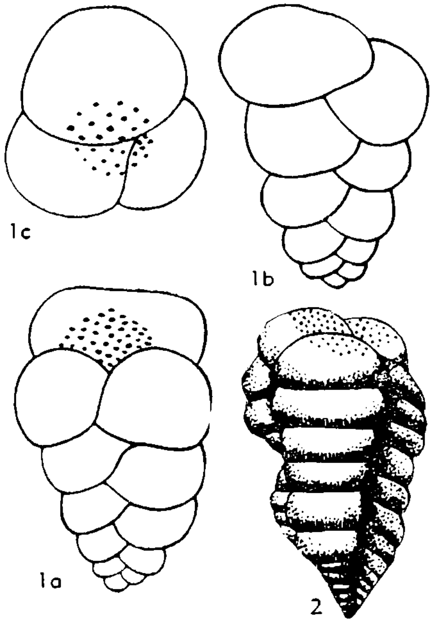

Fig. 190. Ataxophragmiidae (Valvulininae; *1,2, Minouxia*) (p. C282).

[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

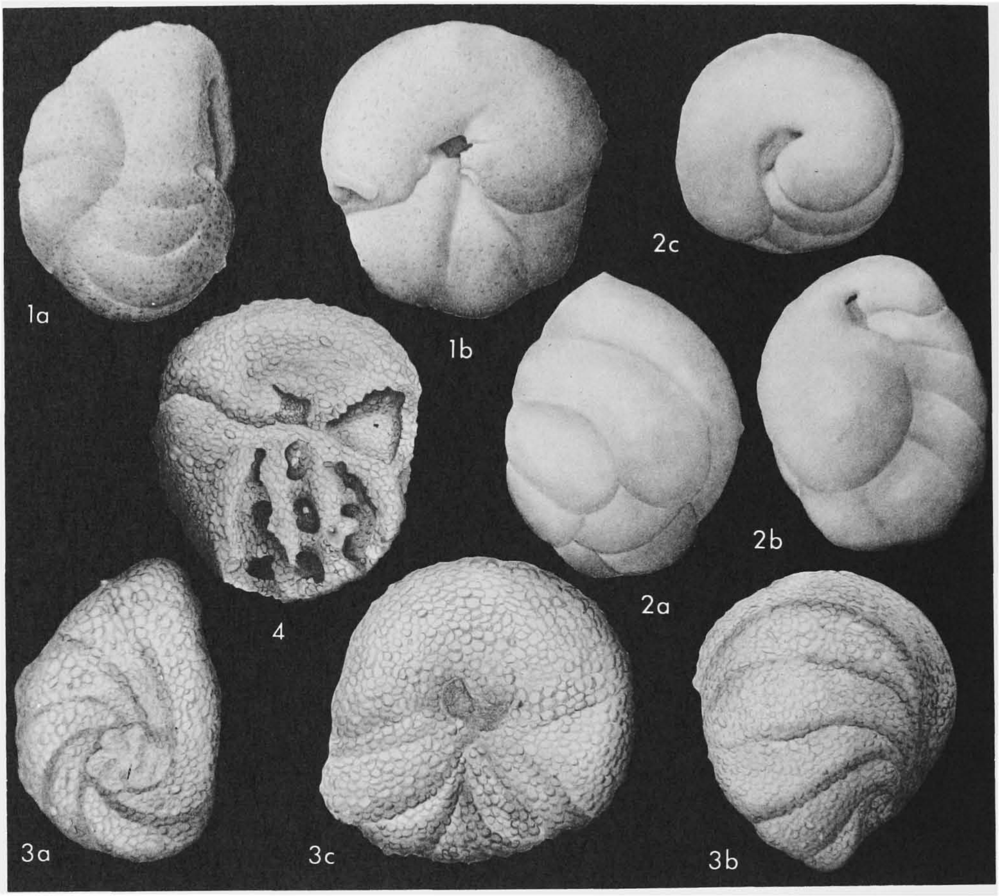

FIG. 191. Ataxophragmiidae (Ataxophragmiinae; *1-4, Ataxophragmium*) (p. C283-C284).

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

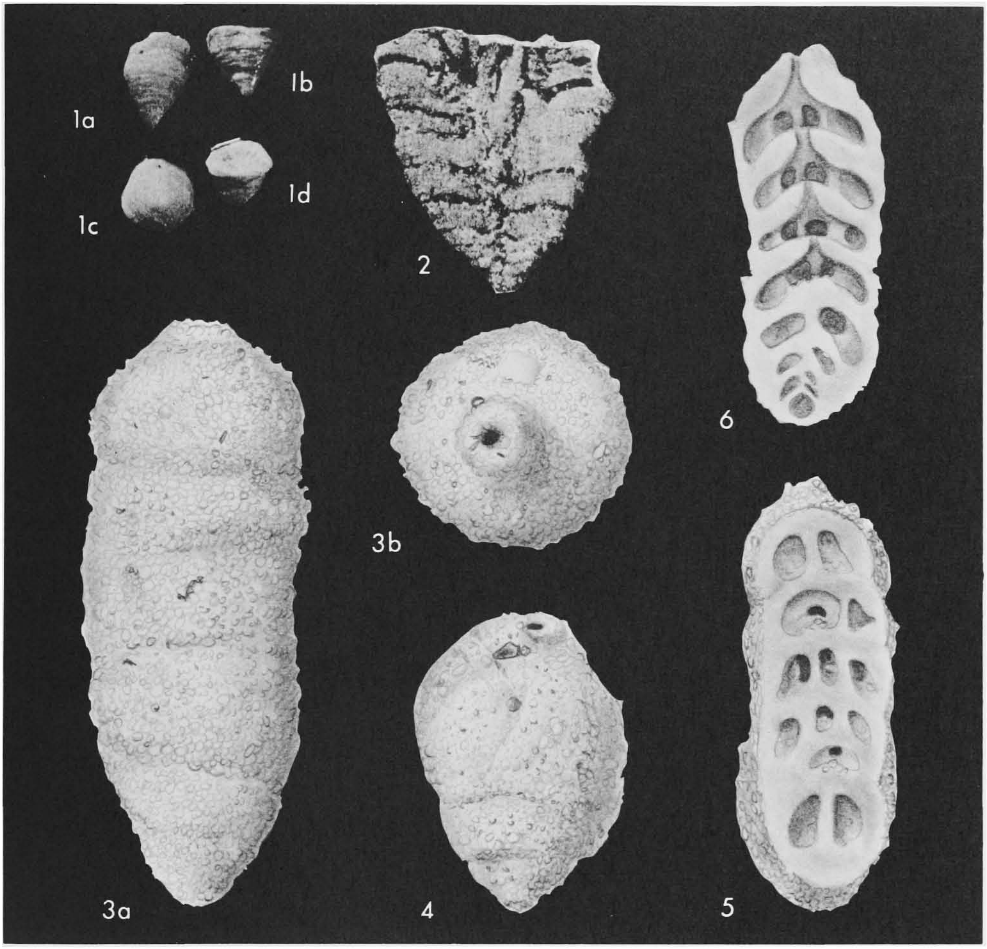

FIG. 192. Ataxophragmiidae (Ataxophragmiinae; *1,2, Camagueyia; 3-6, Cubanina*) (p. *C*284-*C*285).

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

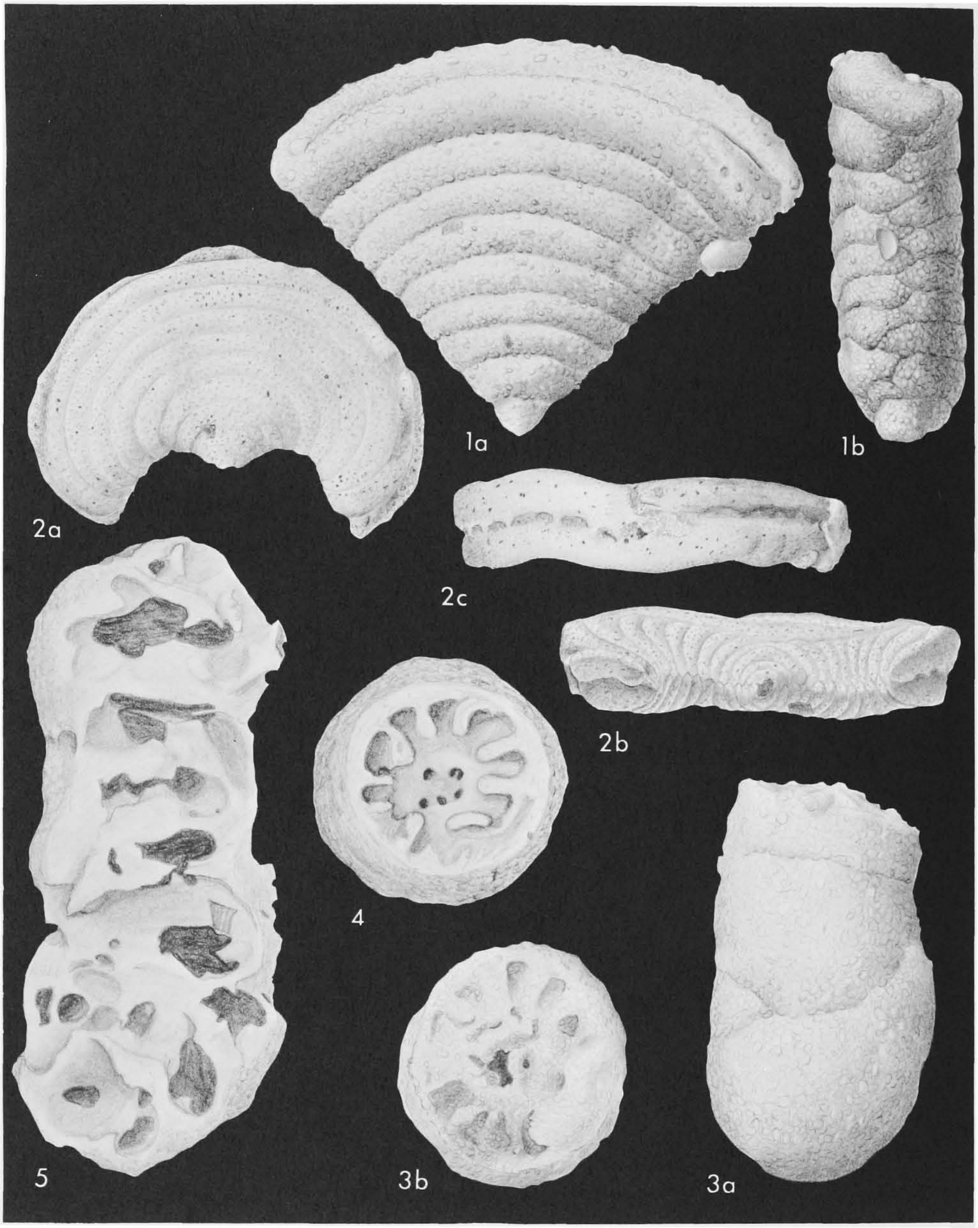

Fig. 193. Ataxophragmiidae (Ataxophragmiinae; *1,2, Cuneolina; 3-5, Coprolithina*) (p. C284-C285).

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,*

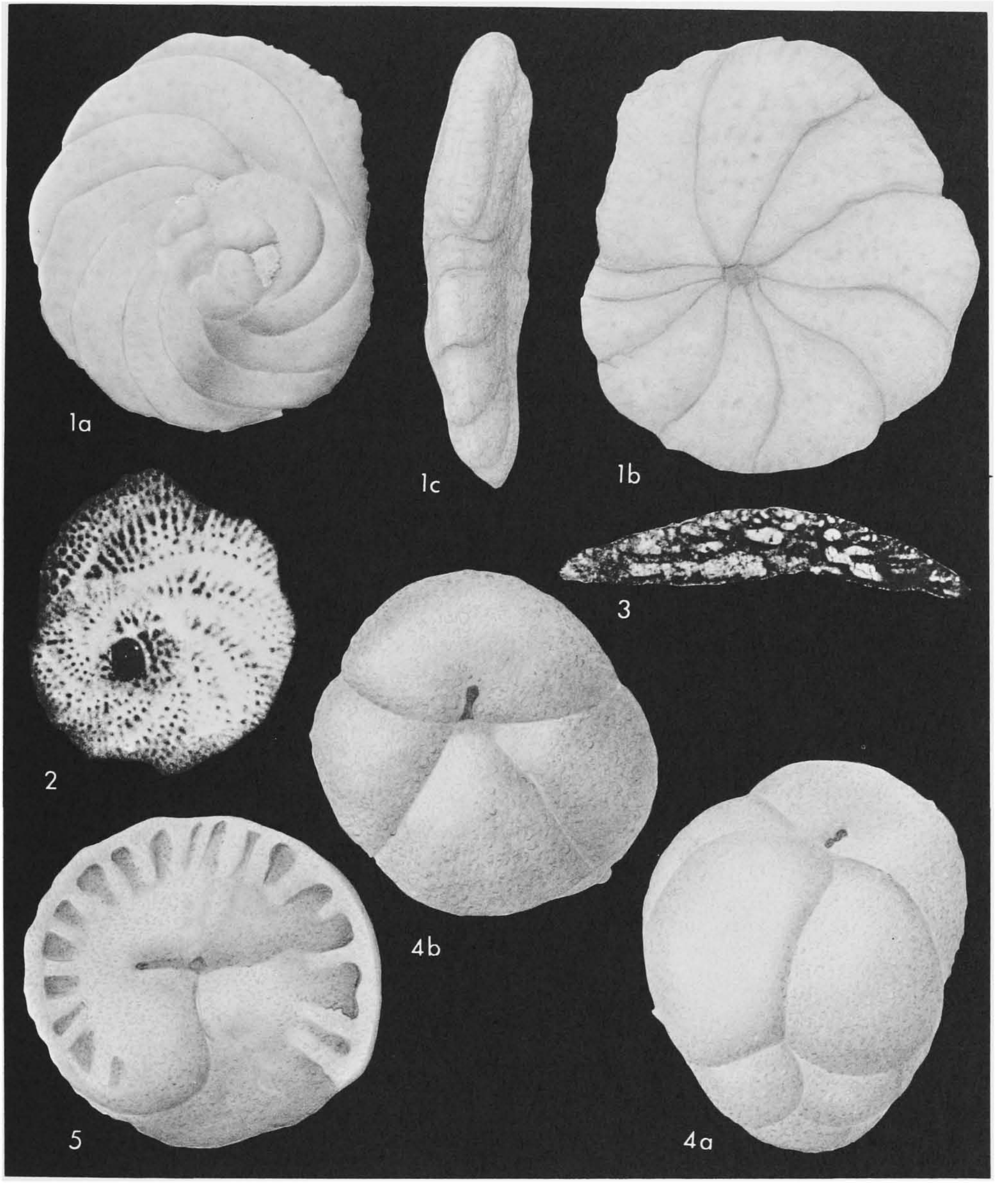

FIG. 194. Ataxophragmiidae (Ataxophragmiinae; *1-3, Dictyopsella; 4,5, Hagenowina*) (p. *C*285-*C*287).

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.-

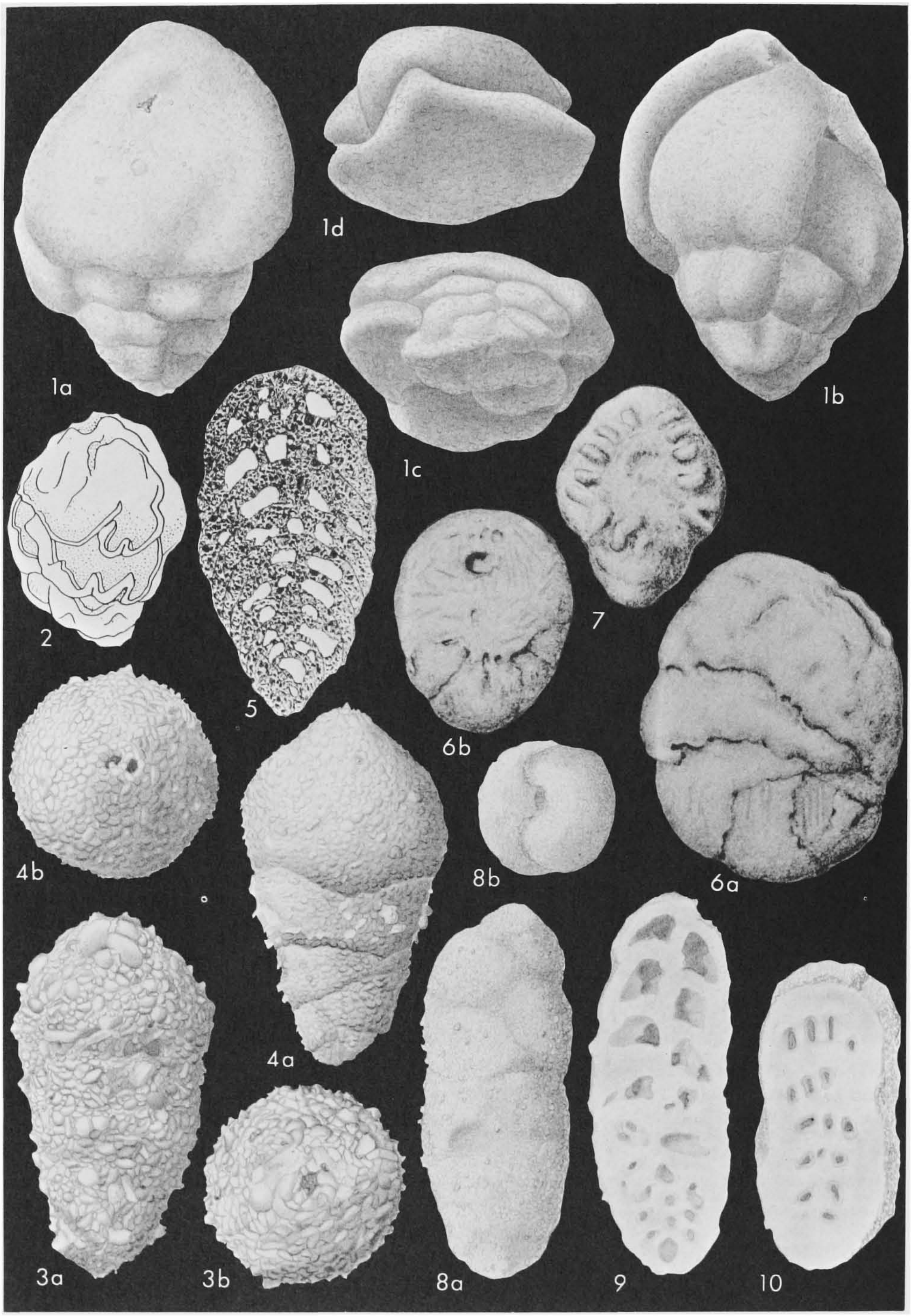

FIG. 195. Ataxophragmiidae (Ataxophragmiinae; *1,2, Jarvisella; 3-5, Liebusella; 6,7, Orbignyna; 8-10, Matanzia*) (p. *C*287-*C*290).

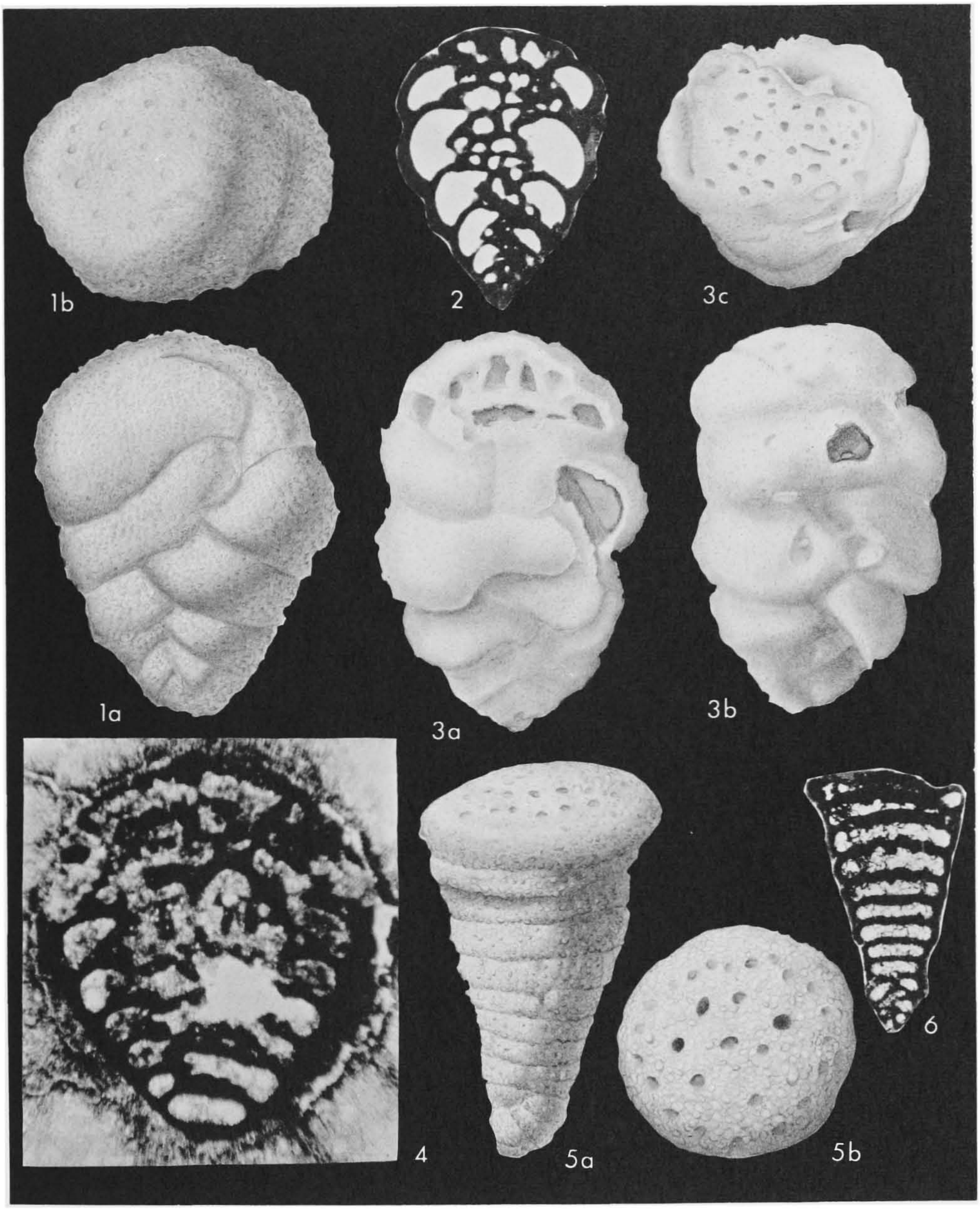

Fig. 196. Ataxophragmiidae (Ataxophragmiinae; *1-4, Pseudochrysalidina; 5,6, Pseudolituonella*) (p. *C*290).

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,

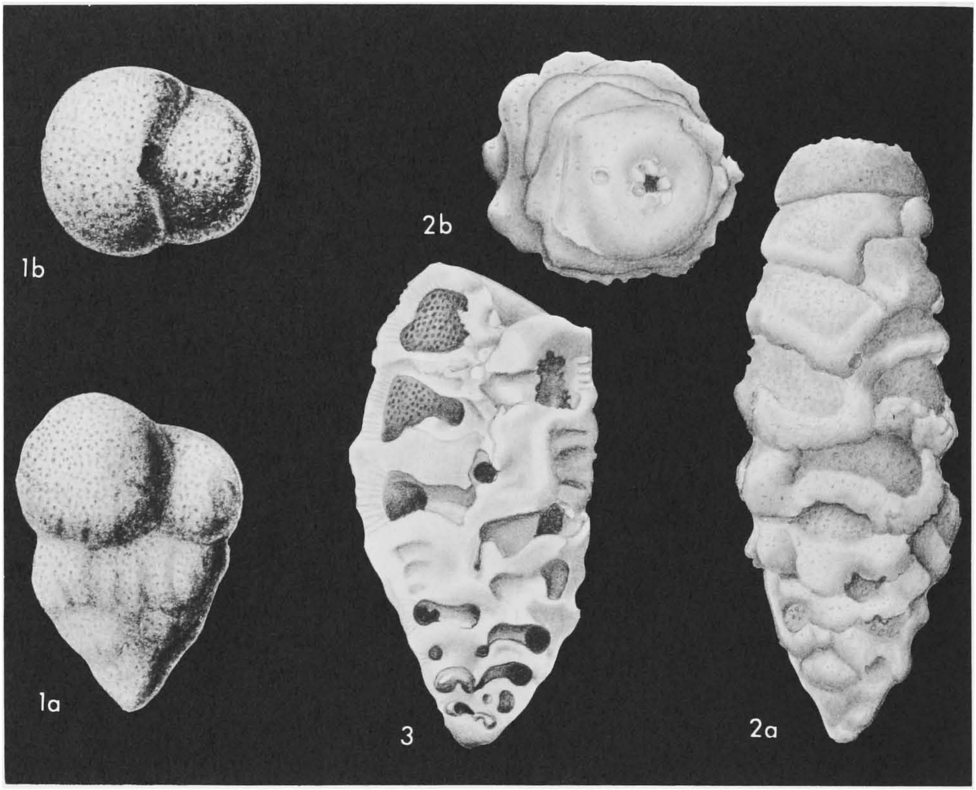

FIG. 197. Ataxophragmiidae (Ataxophragmiinae; *1, Remesella; 2,3, Tritaxilina*) (p. C290-C291).

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-*

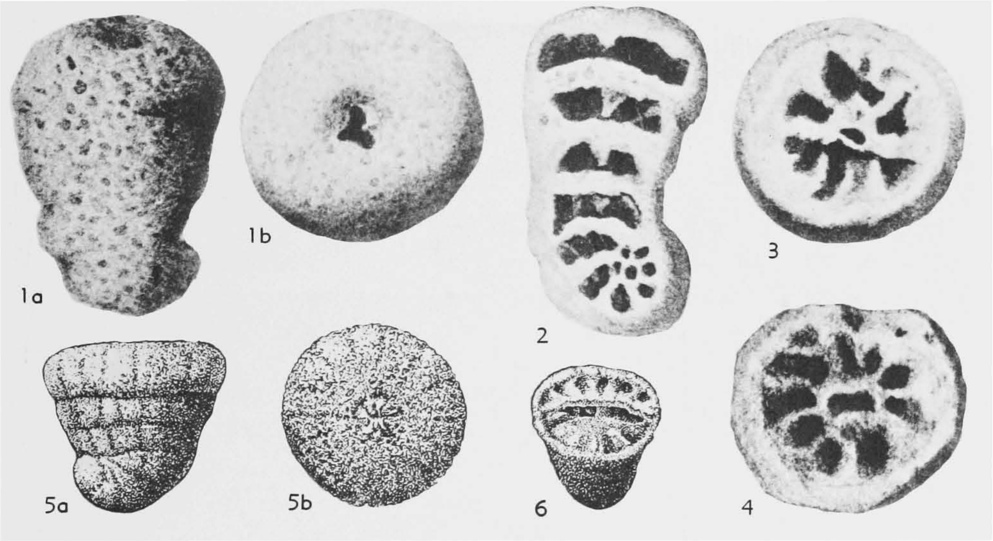

FIG. 198. Ataxophragmiidae (Ataxophragmiinae; *1-6, Voloshinovella*) (p. C291).

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

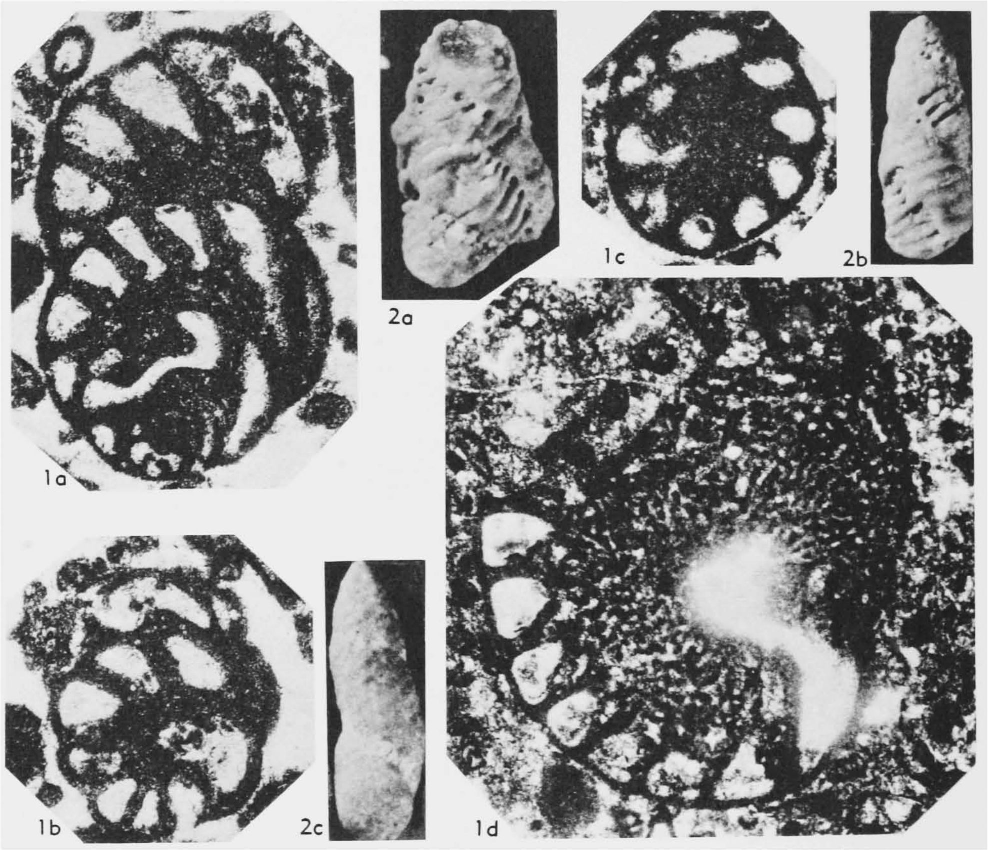

FIG. 199. Pavonitinidae (Pfenderininae; *1,2, Pfenderina*) (p. *C*291-*C*292).

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. *C*795).

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-

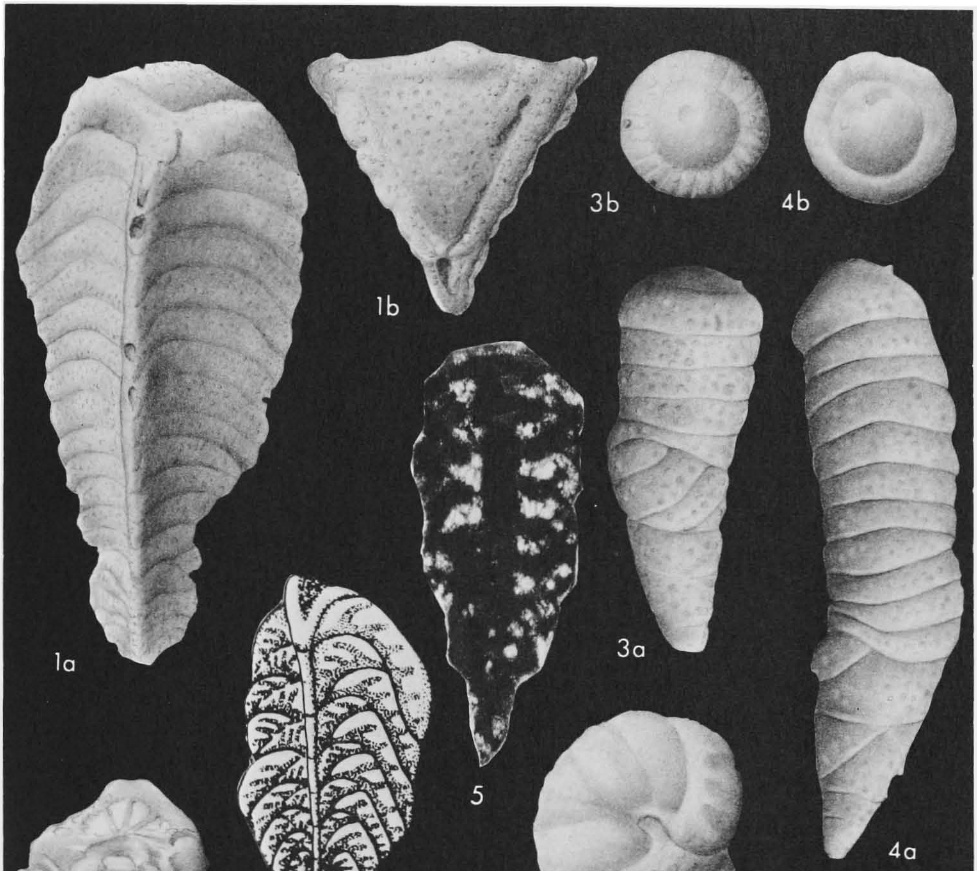

FIG. 200. Pavonitinidae (Pfenderininae; *1, Marieita; 2, Hensonia; 3-9, Kurnubia*) (p. C292-C294).

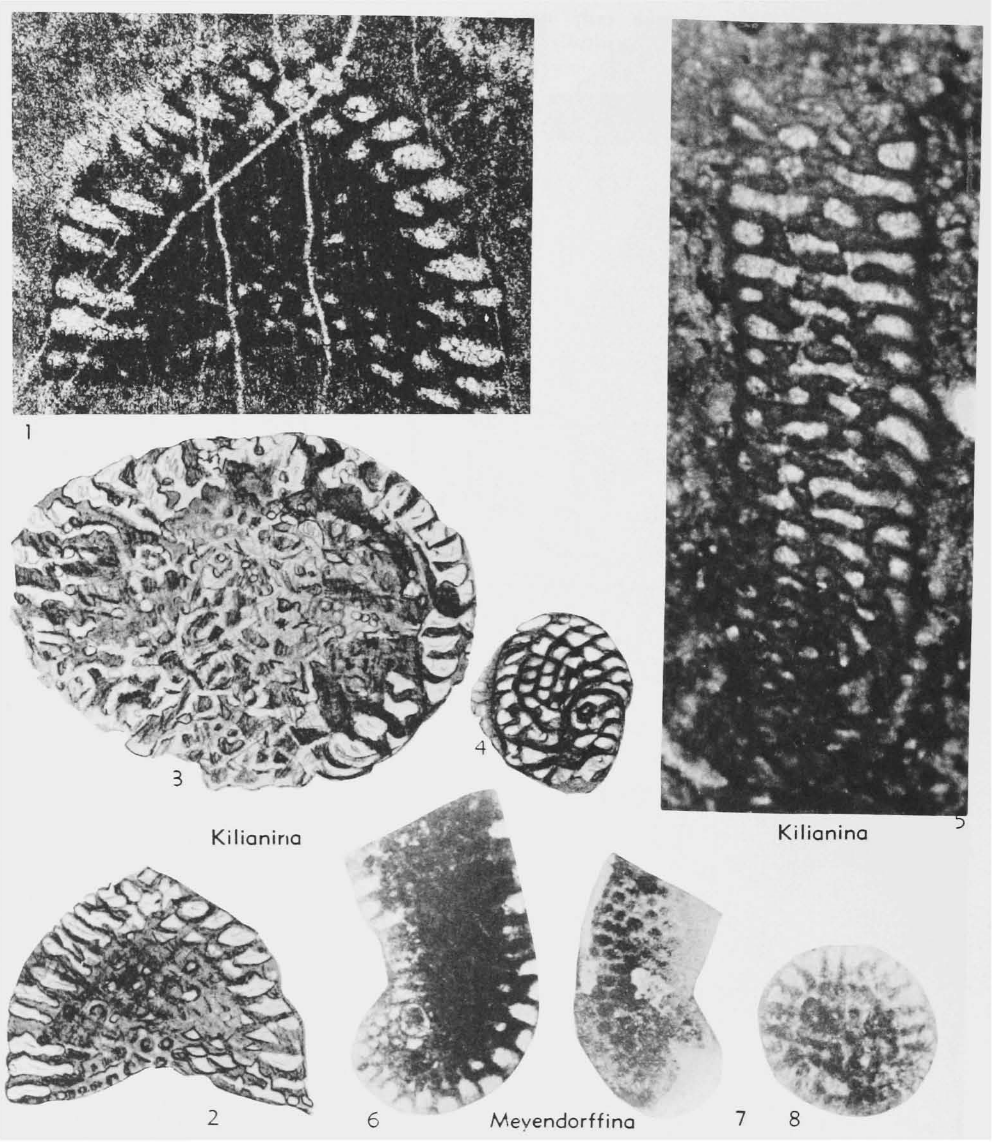

FIG. 201. Pavonitinidae (Pfenderininae; *1-5, Kilianina; 6-8, Meyendorffina*) (p. *C*292, *C*295).

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).

Marieita 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,

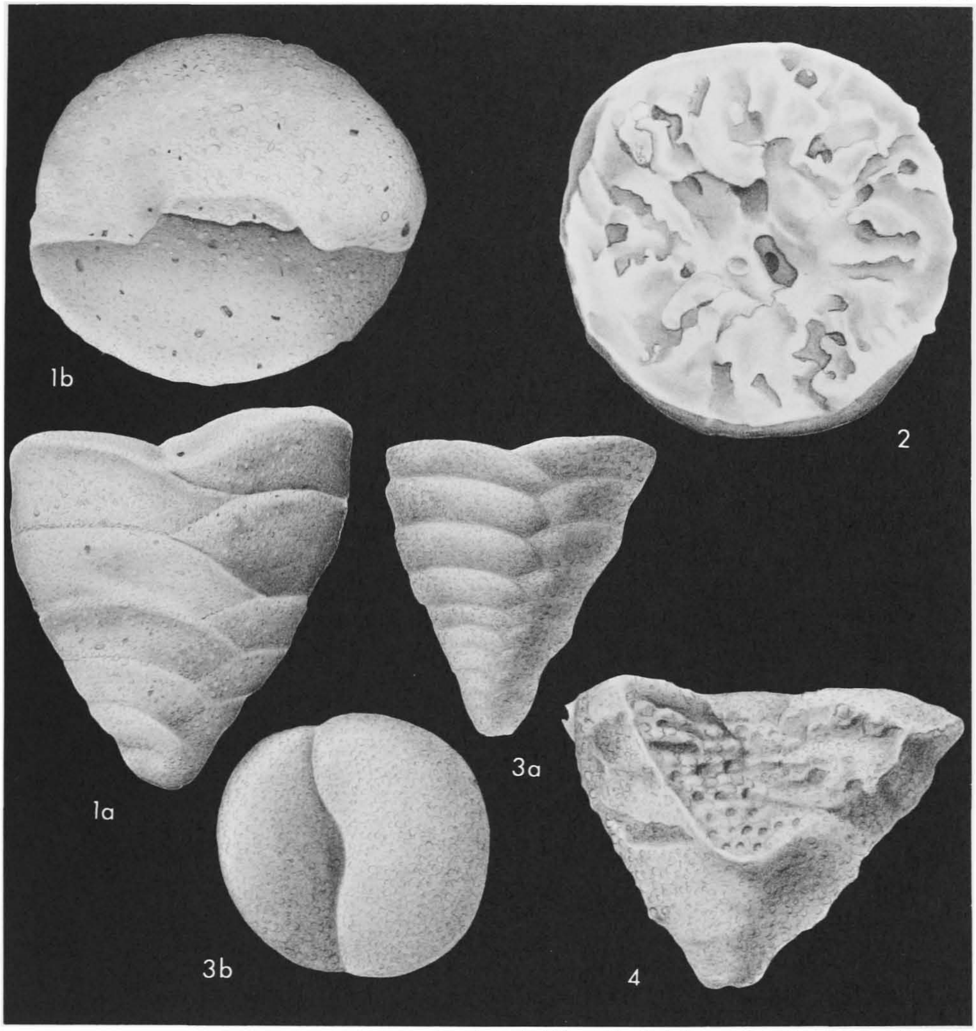

Fig. 202. Pavonitinidae (Pavonitininae; *1,2, Textulariella;* Pfenderininae; *3,4, Pseudotextulariella*) (p. *C*295, *C*299-*C*300).

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

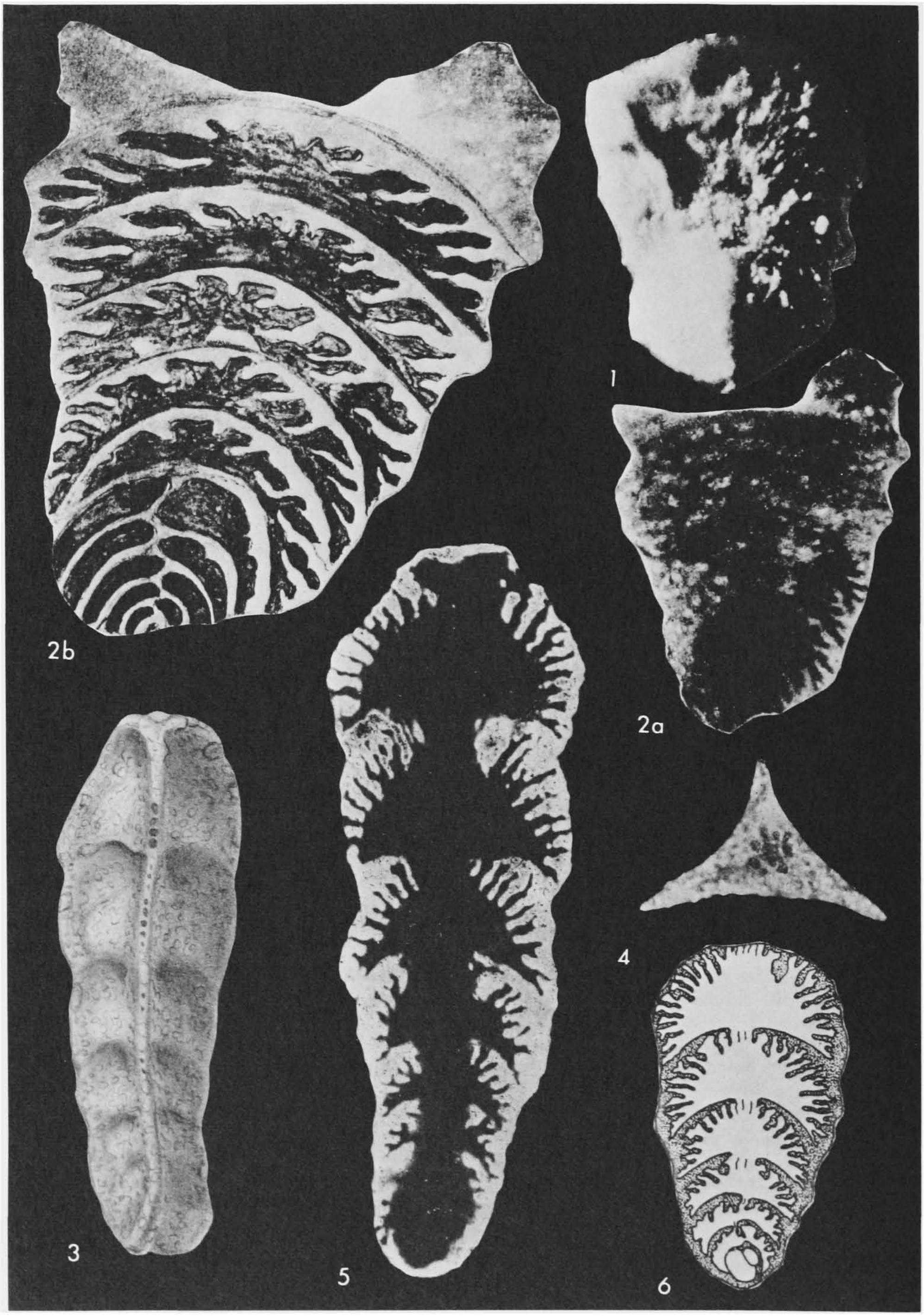

FIG. 203. Pavonitinidae (Pavonitininae; *1-6, Pavonitina*) (p. C296-C298).

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.

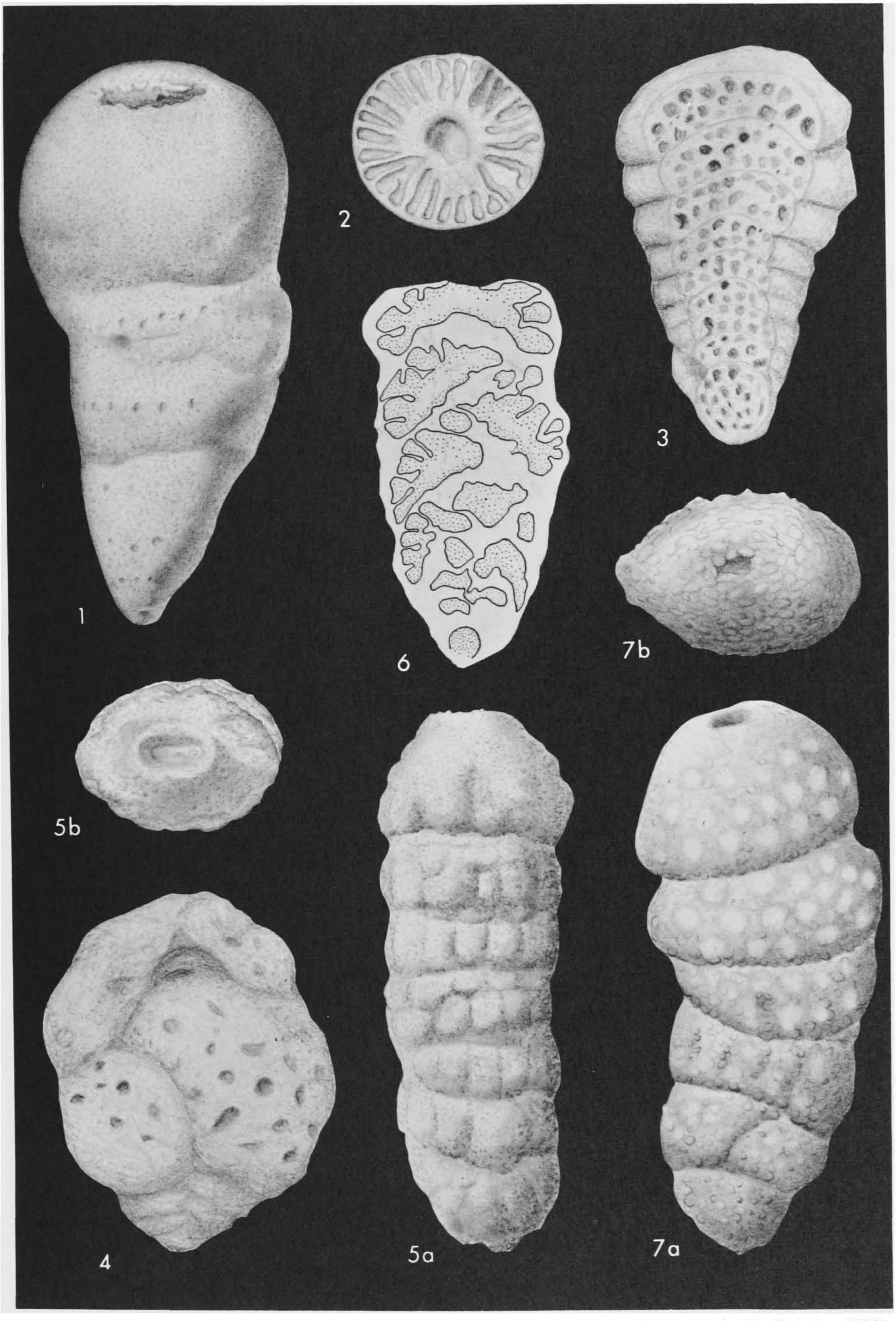

Fig. 204. Pavonitinidae (Pavonitininae; *1-3, Guppyella; 4, Alveovalvulina; 5-7, Alveovalvulinella*) (p. *C*298).

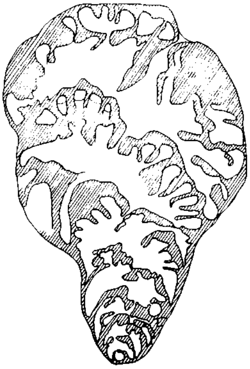

Fig. 205. Pavonitinidae (Pavonitininae; *Alveovalvulina*) (p. C298).

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

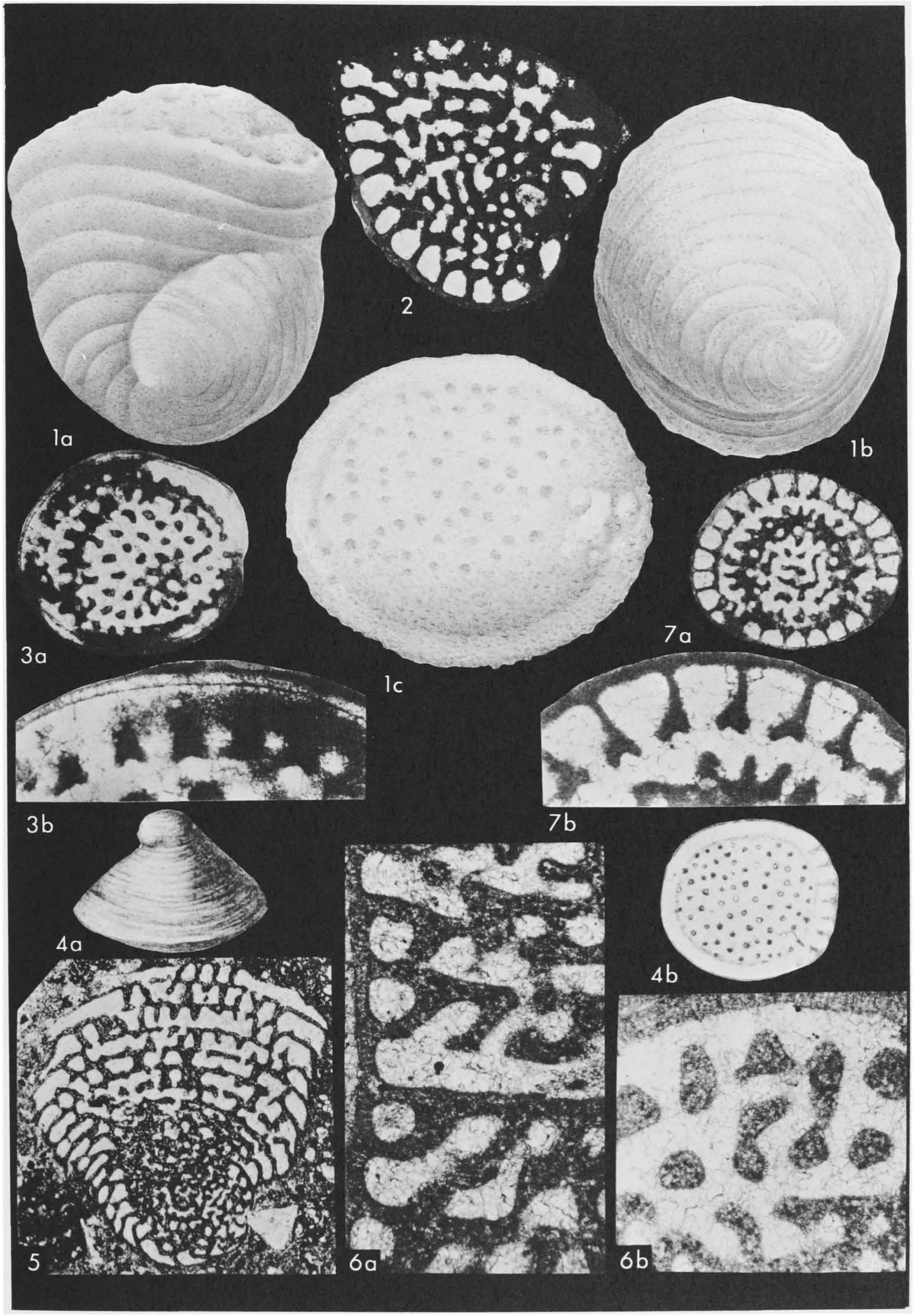

FIG. 206. Pavonitinidae (Pavonitininae; *1-3, Lituonella; 4-7, Coskinolina*) (p. C298).

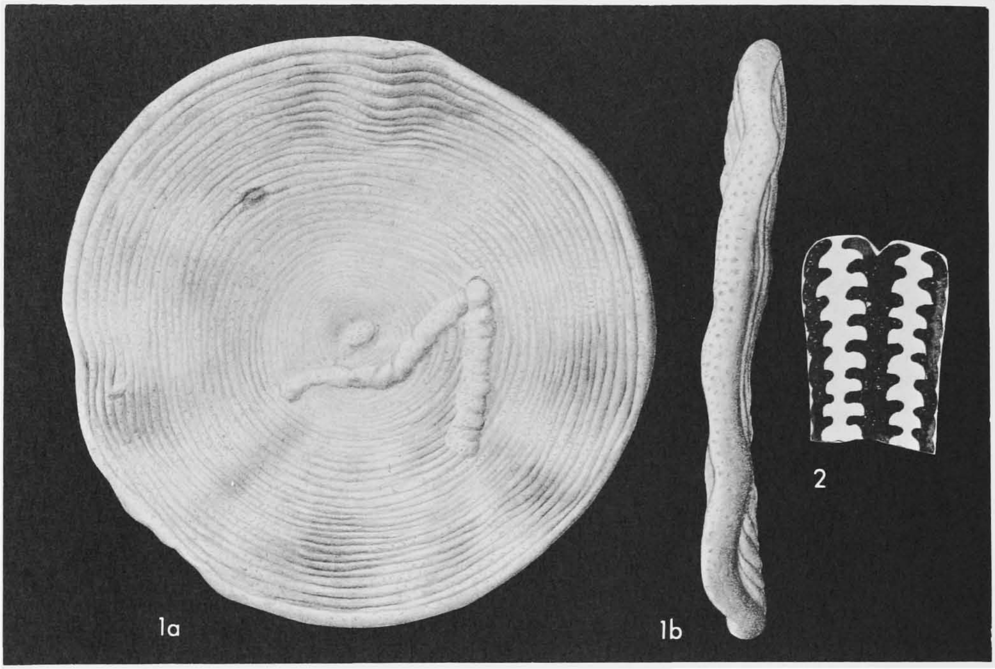

FIG. 207. Dicyclinidae (Cyclolininae; *1, Cyclolina; 2, Cyclopsinella*) (p. C301-C302).

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).

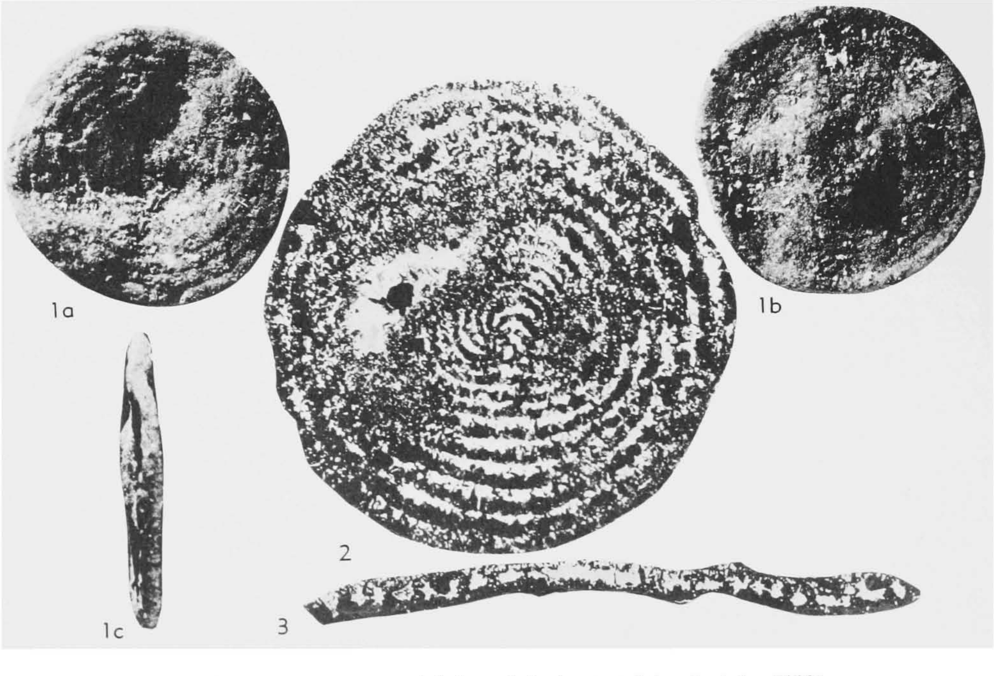

FIG. 208. Dicyclinidae (Cycylolininae; *1-3, Ammocycloloculina*) (p. C302).

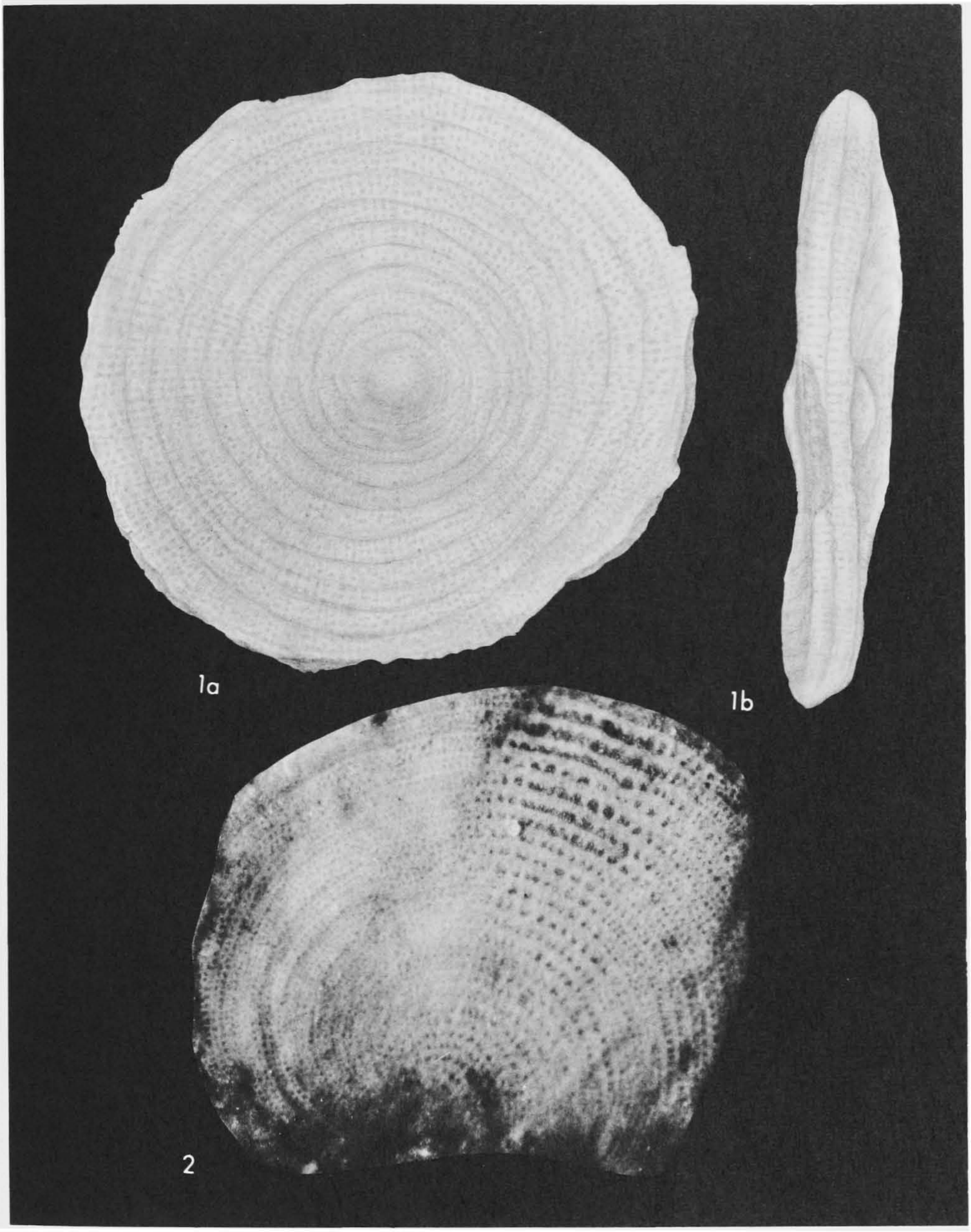

FIG. 209. Dicyclinidae (Dicyclininae; *1, Dicyclina; 2, Broeckinella*) (p. C303-C304).

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-

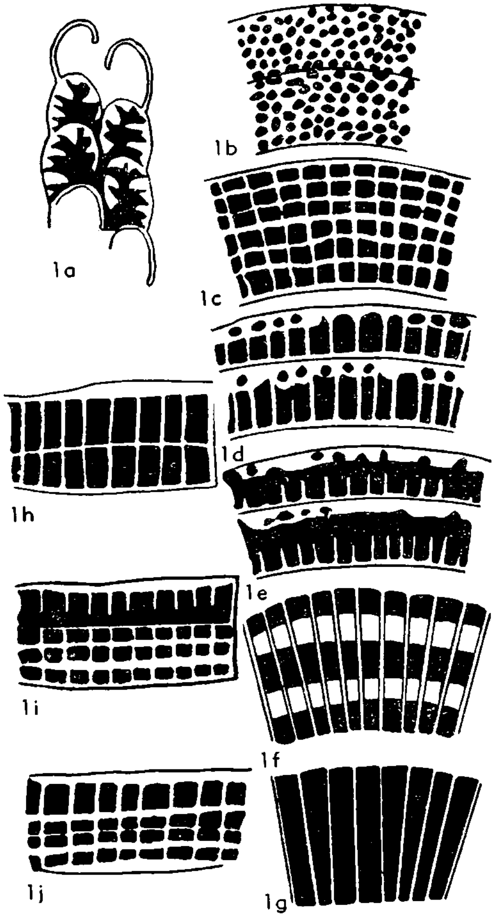

FIG. 210. Dicyclinidae (Dicyclininae; *1, Dicyclina*) (p. C303-C304).

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.*

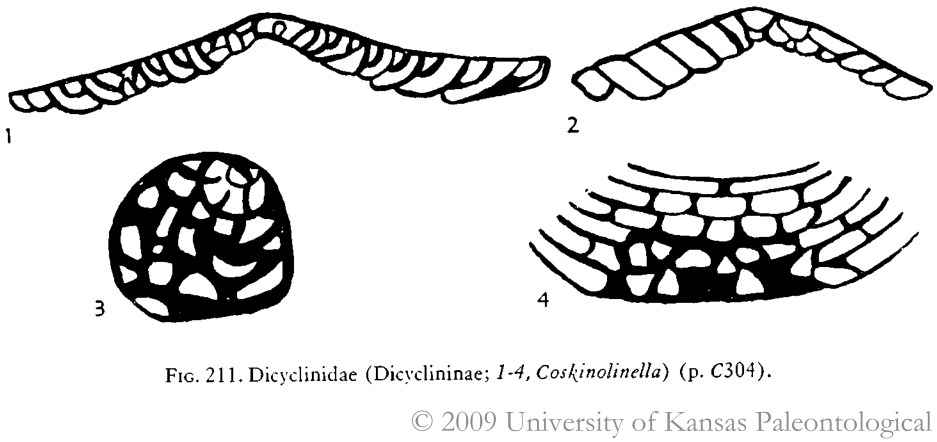

FIG. 211. Dicyclinidae (Dicyclininae; *1-4, Coskinolinella*) (p. C304).

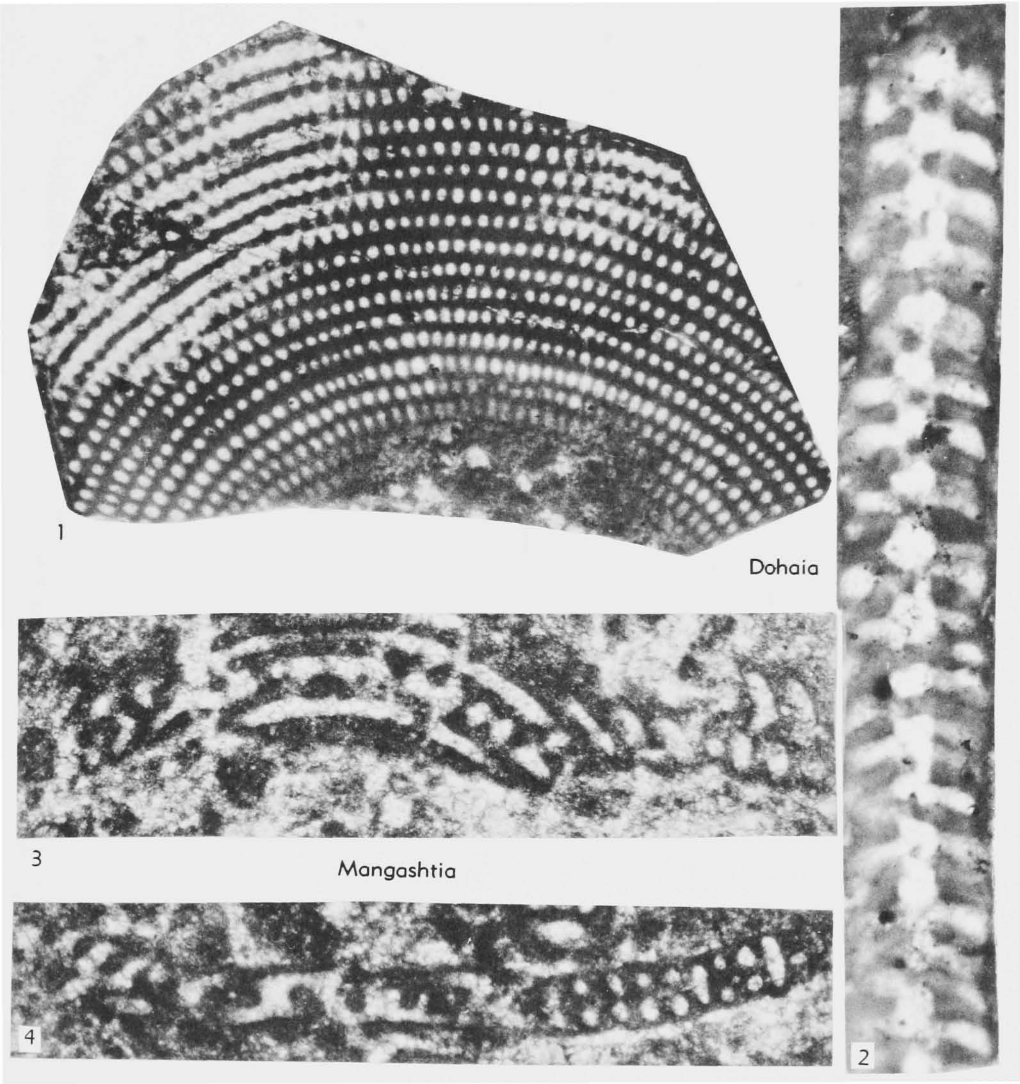

FIG. 212. Dicyclinidae (Dicyclininae; *1,2, Dohaia; 3,4, Mangashtia*) (p. *C*304-*C*307).

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

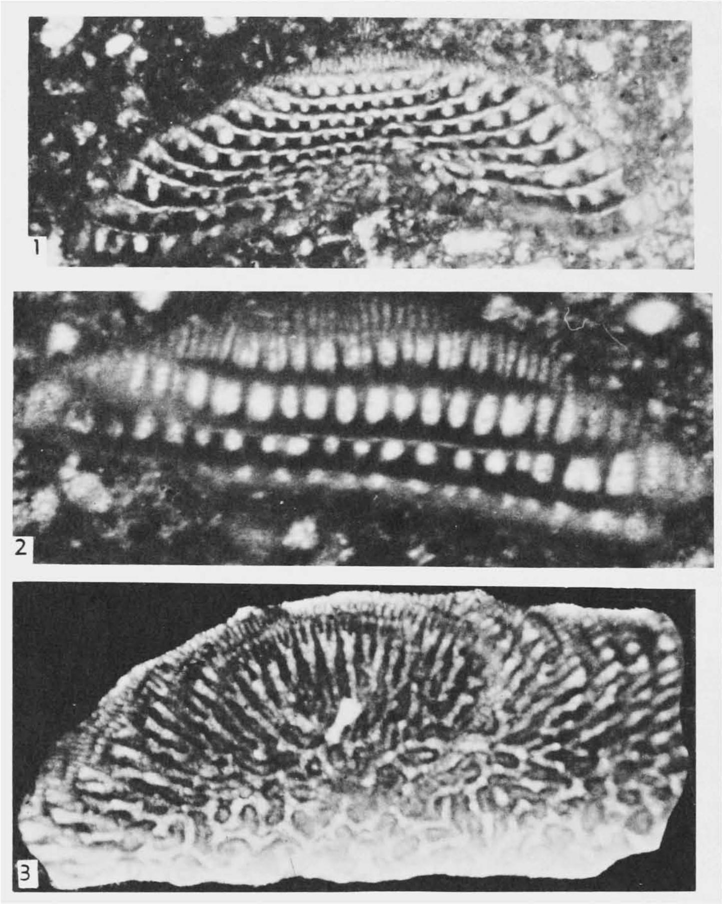

Fig. 213. Dicyclinidae (Dicyclininae; *1-3, Orbitolinella*) (p. C308).

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

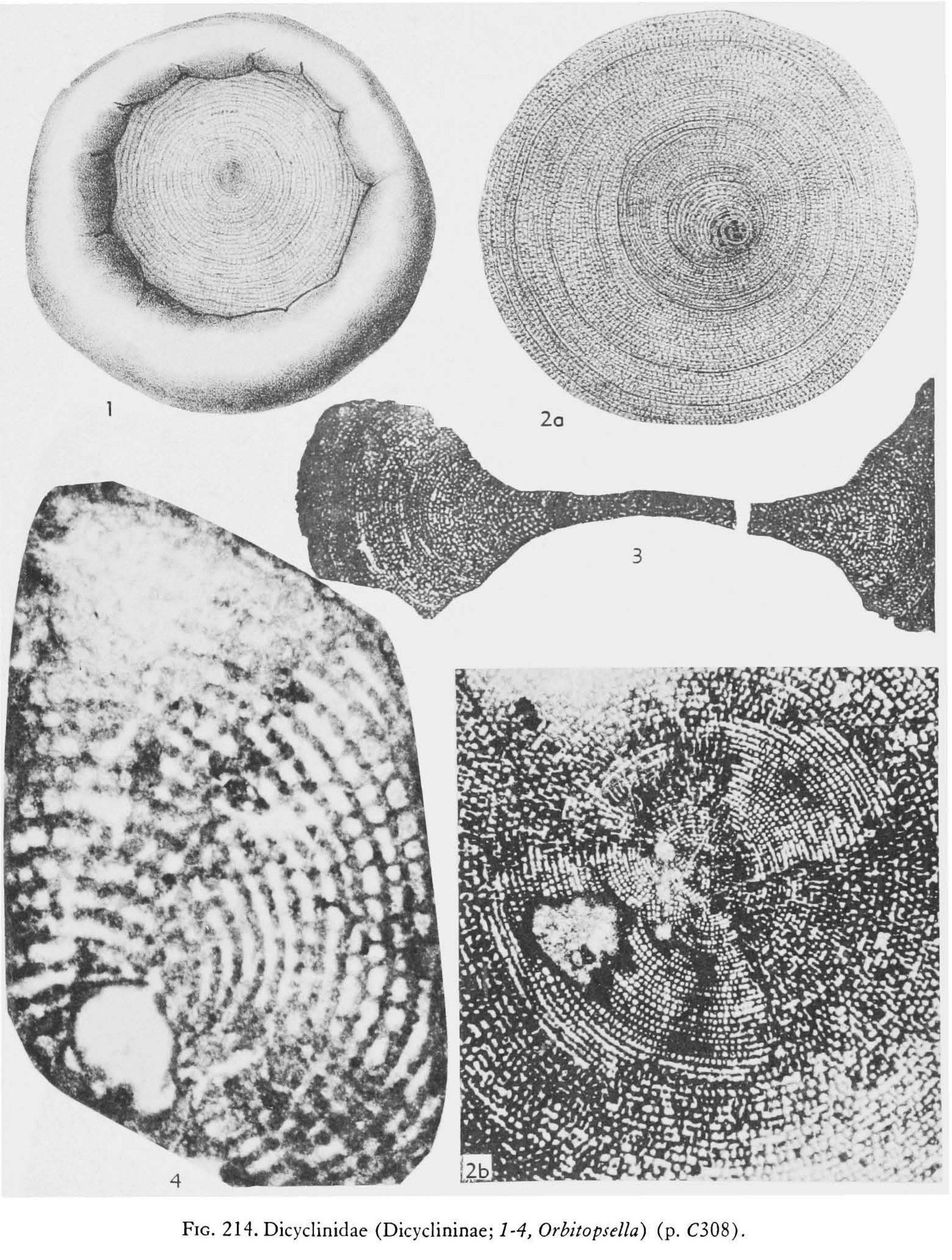

FIG. 214. Dicyclinidae (Dicyclininae; *1-4, Orbitopsella*) (p. C308).

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

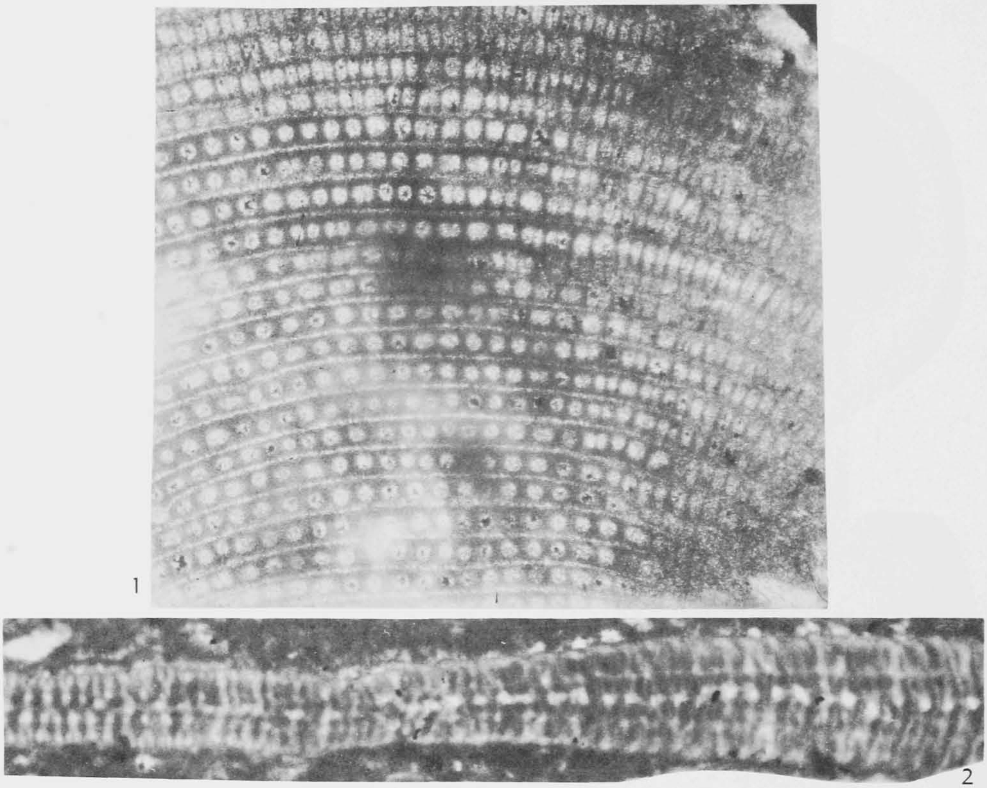

FIG. 215. Dicyclinidae (Dicyclininae; *1,2, Qataria*) (p. *C*308).

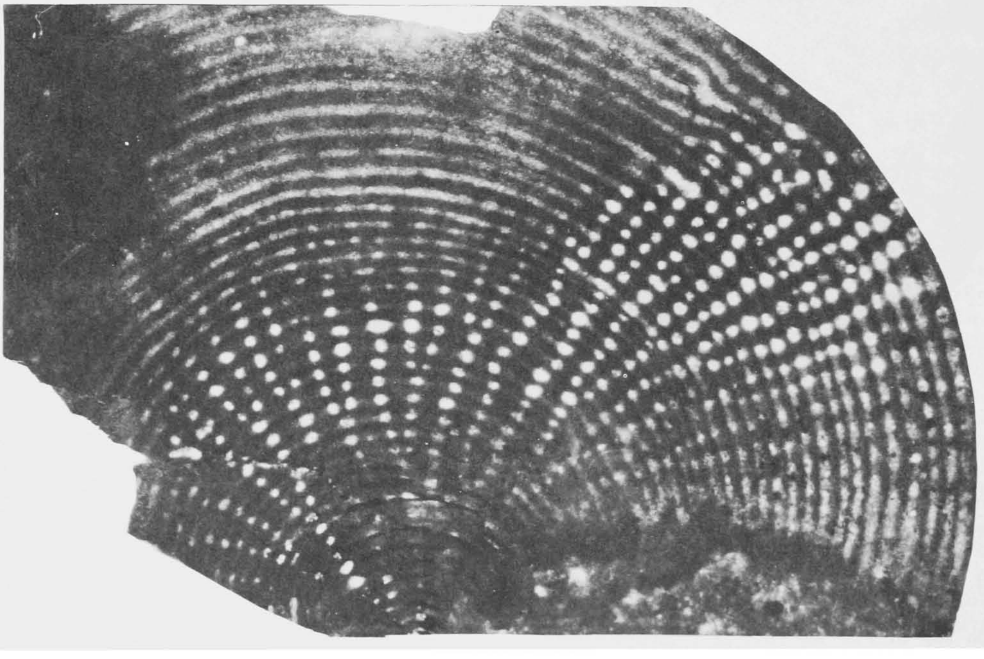

FIG. 216. Dicyclinidae (Dicyclininae; *1, Zekritia*) (p. *C*308).

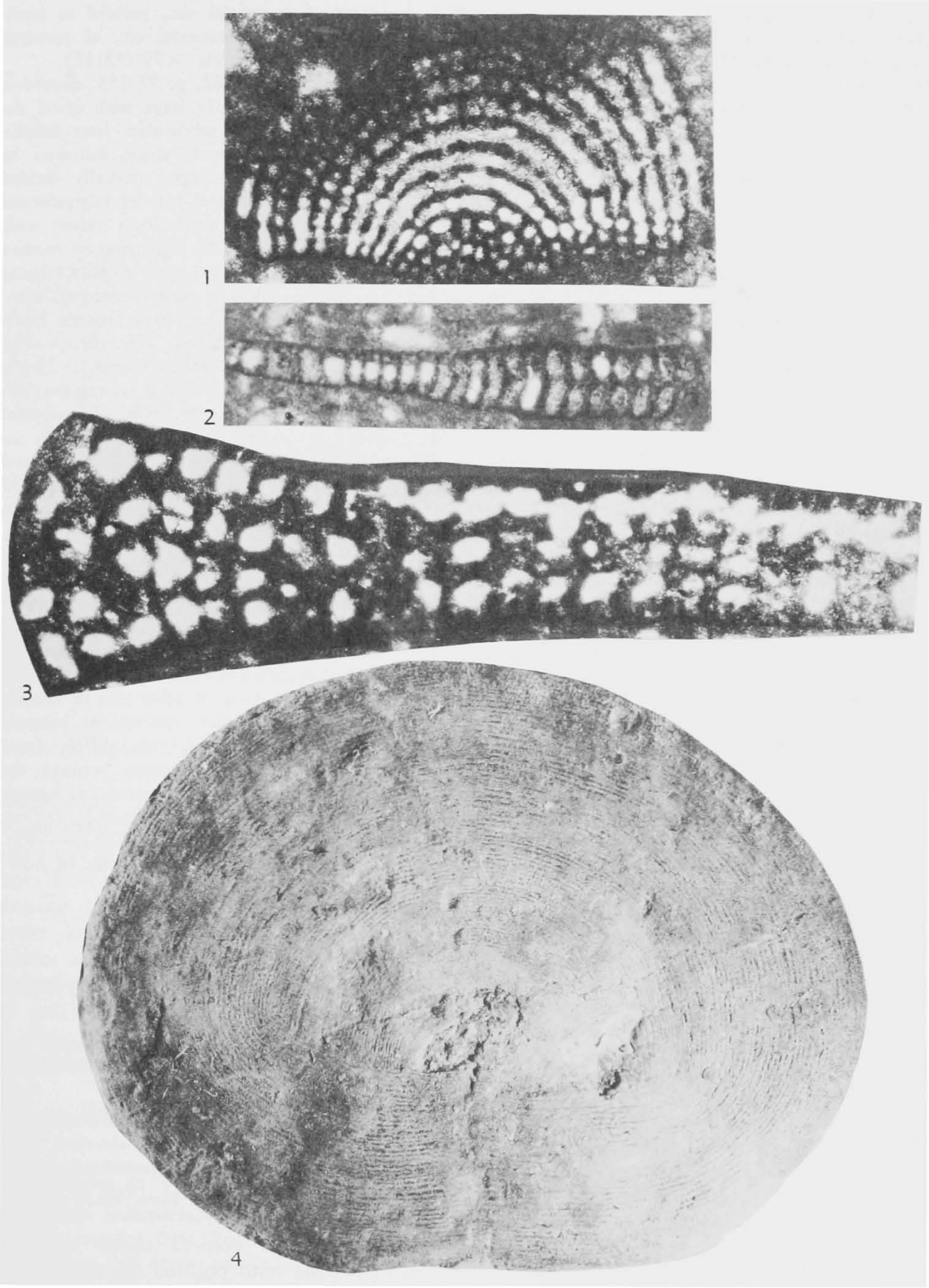

FIG. 217. Dicyclinidae (Dicyclininae; *1-4, Saudia*) (p. C308).

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]

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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,

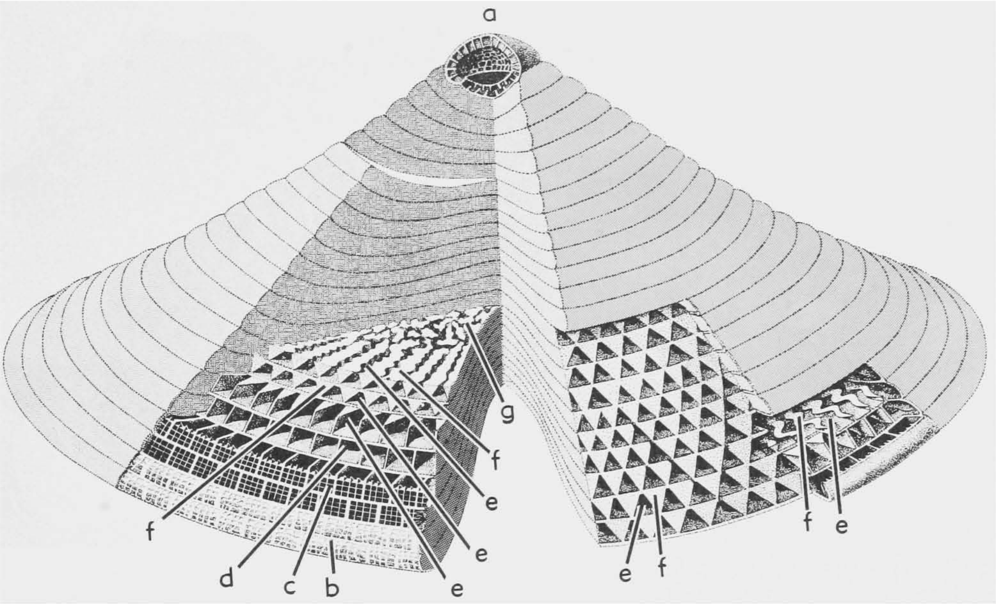

FIG. 218. Orbitolinidae. Reconstruction of *Orbitolina* with parts cut away to show internal structures. [Explanation: *a*, megalospheric embryonic apparatus; *b*, slightly abraded surface showing cellules; *c*, marginal zone beneath cut-away surface; *d*, inframarginal zone exposing chamberlets; *e*, 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, *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,

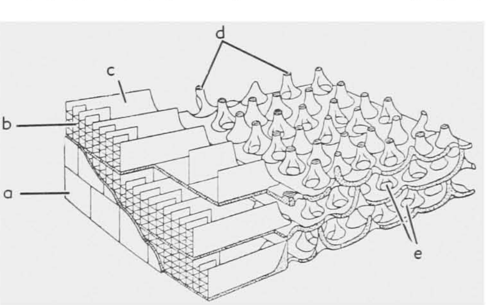

FIG. 219. Orbitolinidae. Reconstruction of a small portion of the test of *Dictyoconus* near its base with parts cut away to show internal structure. [Explanation: *a*, outer surface indicating placement of septa and main partitions; *b*, cellules; *c*, chamberlets; *d*, pillars partially encircling apertural pores; *e*, apertural pores] (*562).

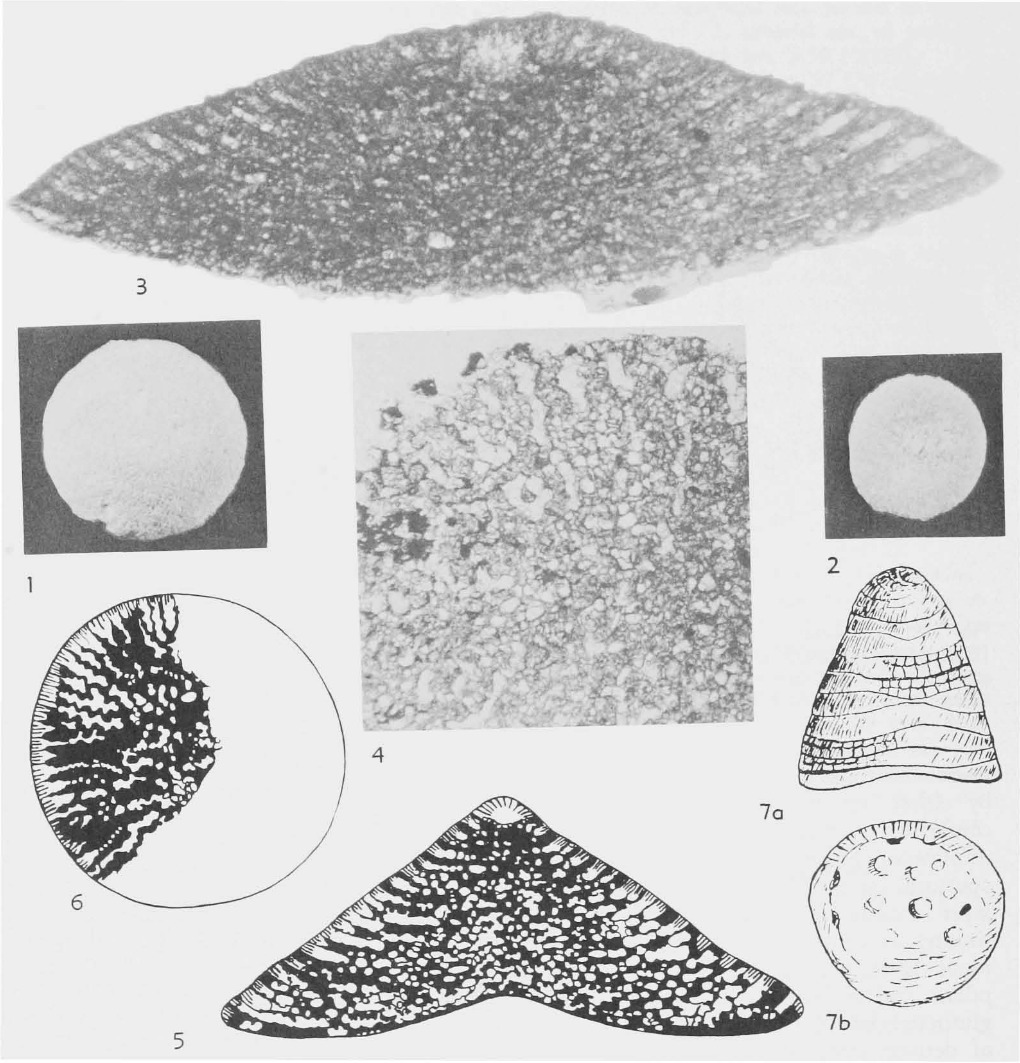

FIG. 220. Orbitolinidae; *1-7*, *Orbitolina* (p. *C*309-*C*310).

×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.*

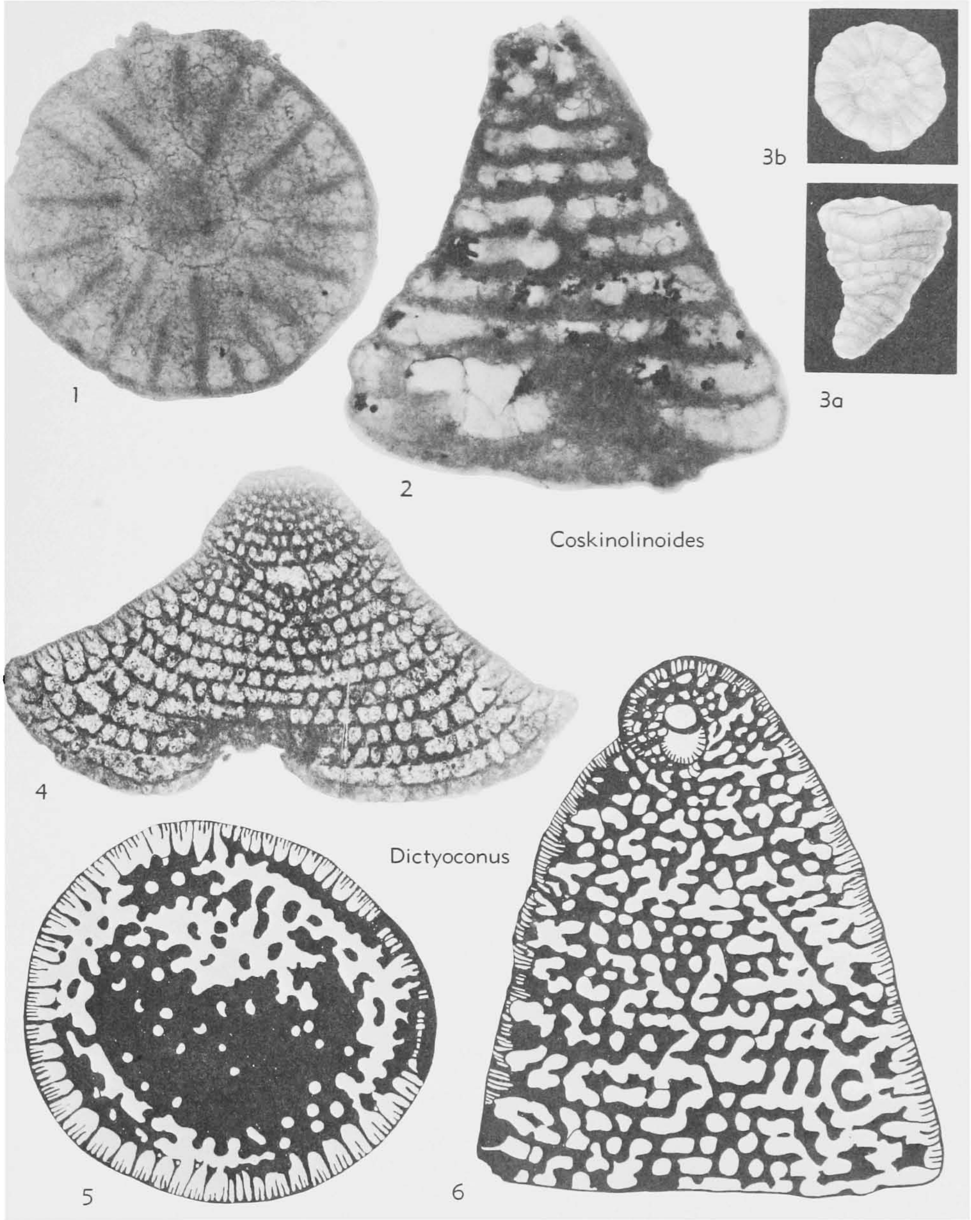

FIG. 221. Orbitolinidae; *1-3, Coskinolinoides; 4-6, Dictyoconus* (p. C310-C311).

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

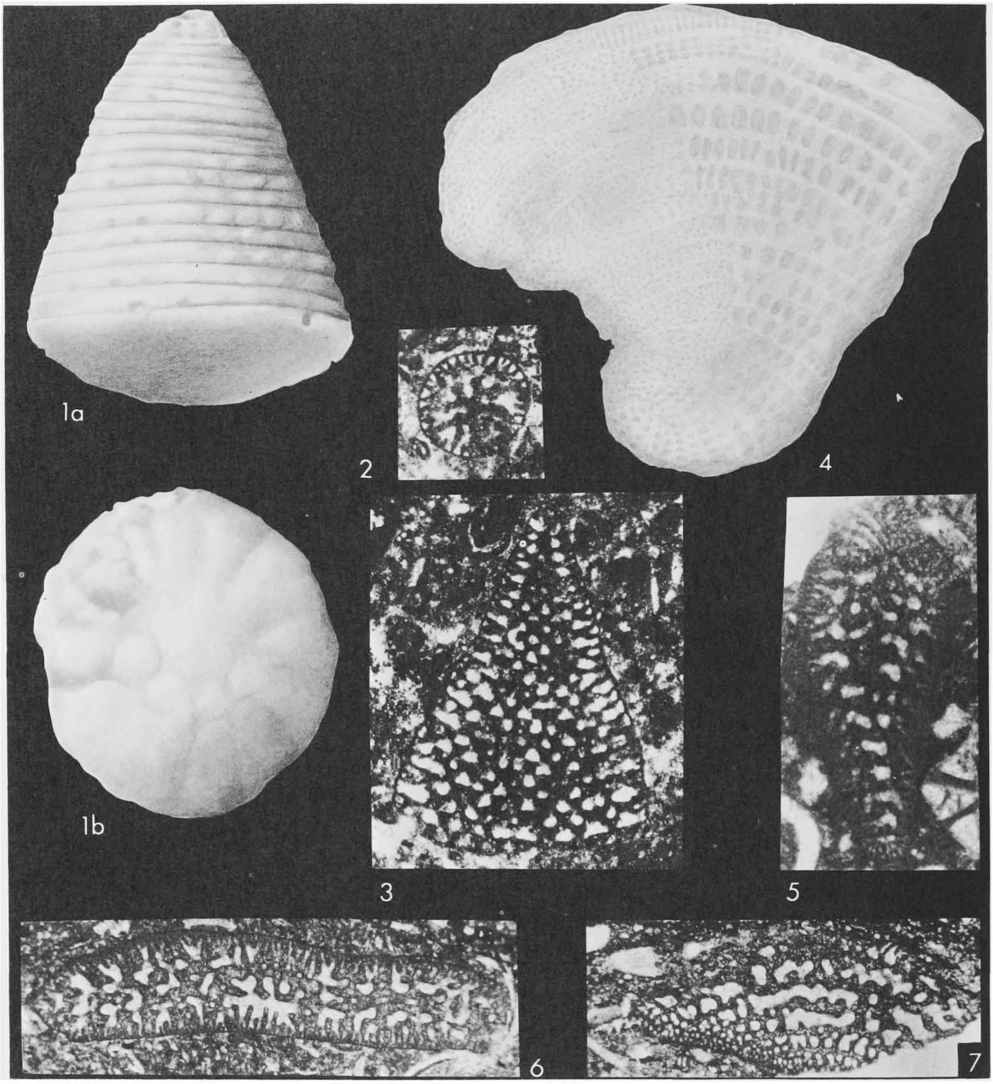

FIG. 222. Orbitolinidae; *1-7*, *Iraqia* (p. *C*311-*C*312).

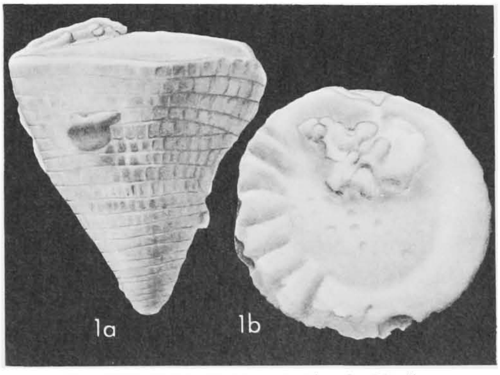

FIG. 223. Orbitolinidae; *1*, *Simplorbitolina* (p. *C*312-*C*313).

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

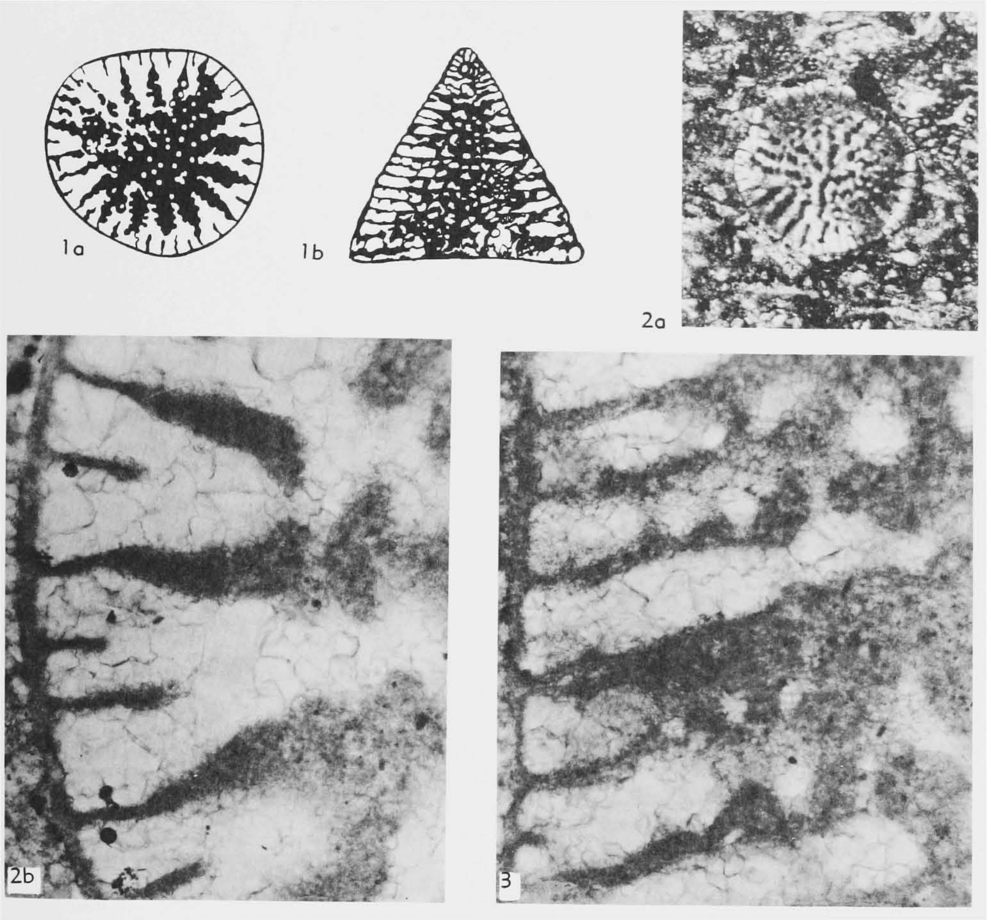

FIG. 224. Orbitolinidae; *1-3, Simplorbitolina* (p. C312-C313).

(*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.*