PART C
PROTISTA 2

SARCODINA
CHIEFLY "THECAMOEBIANS" AND FORAMINIFERIDA

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with some systematic descriptions of Foraminiferida by R. WRIGHT BARKER, W. STORRS COLE, R. C. DOUGLASS, MANFRED REICHEL, and M. L. THOMPSON as recorded

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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.

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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.

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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}Plasmodromat† 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

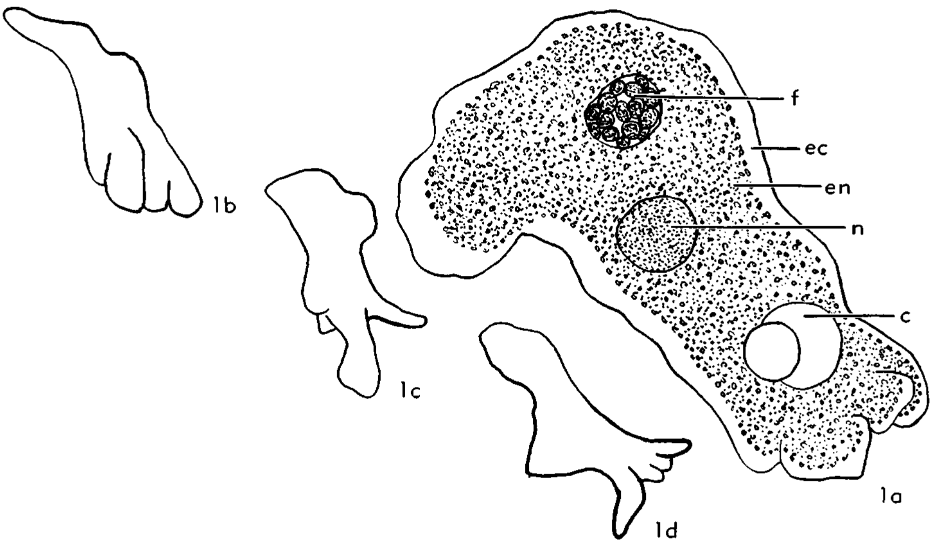

FIG. 1. Pelomyxidae; *1, Chaos diffluens* MÜLLER, a representative pelomyxid protistan; *1a,* living specimen enlarged to show ectoplasm *(ec),* endoplasm *(en),* nucleus *(n),* food vacuole *(f),* and contractile vacuole *(c)*; *1b-d,* outline views showing successive positions of pseudopodia during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

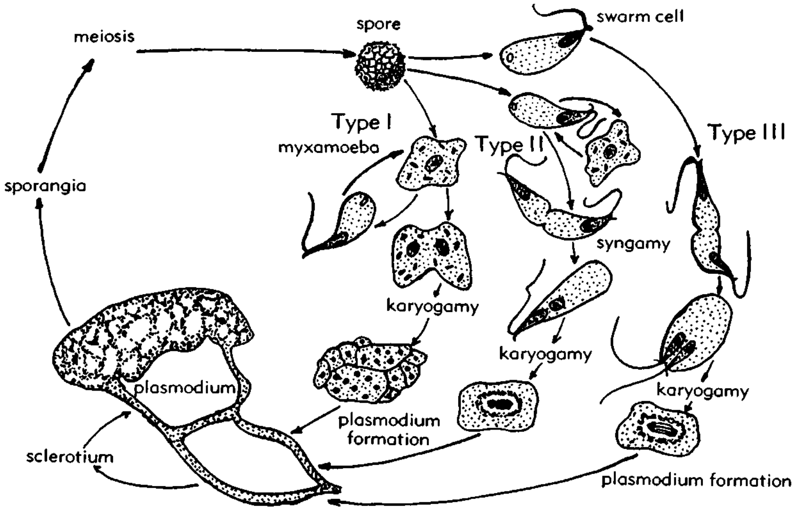

FIG. 2. Life cycle of Mycetozoida (diagrammatic) (*1585).

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 (*eigentliehe* 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; =^{5}Mycetozoidea Doflein, 1901, p. 47; =^{4}Mycetozoen (Schleimtiere) Hertwig, 1919, p. 188 (*nom. neg.*); =Micetozoos Fernández Galiano, 1921, p. 39 (*nom. neg.*)]——[=^{4}Phytomyxini Schröter, 1886, p. 133; =^{4}Phytomyxinae MacBride, 1892, p. 111; =Phytomyxinae Schröter, 1897, p. iii, 5; =^{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; =^{6}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; =^{16}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;

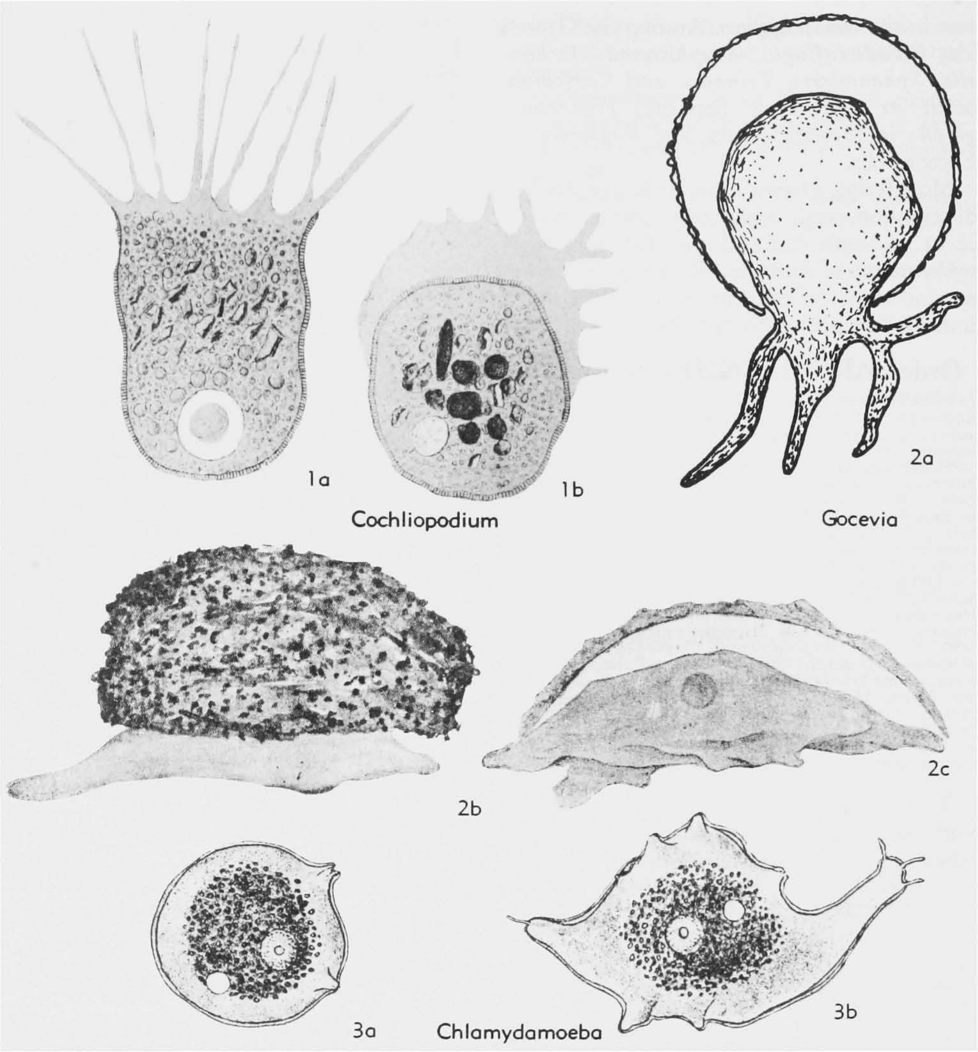

FIG. 3. Cochliopodiidae; *1, Cochliopodium; 2, Gocevia; 3, Chlamydamoeba* (p. C19).

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.*

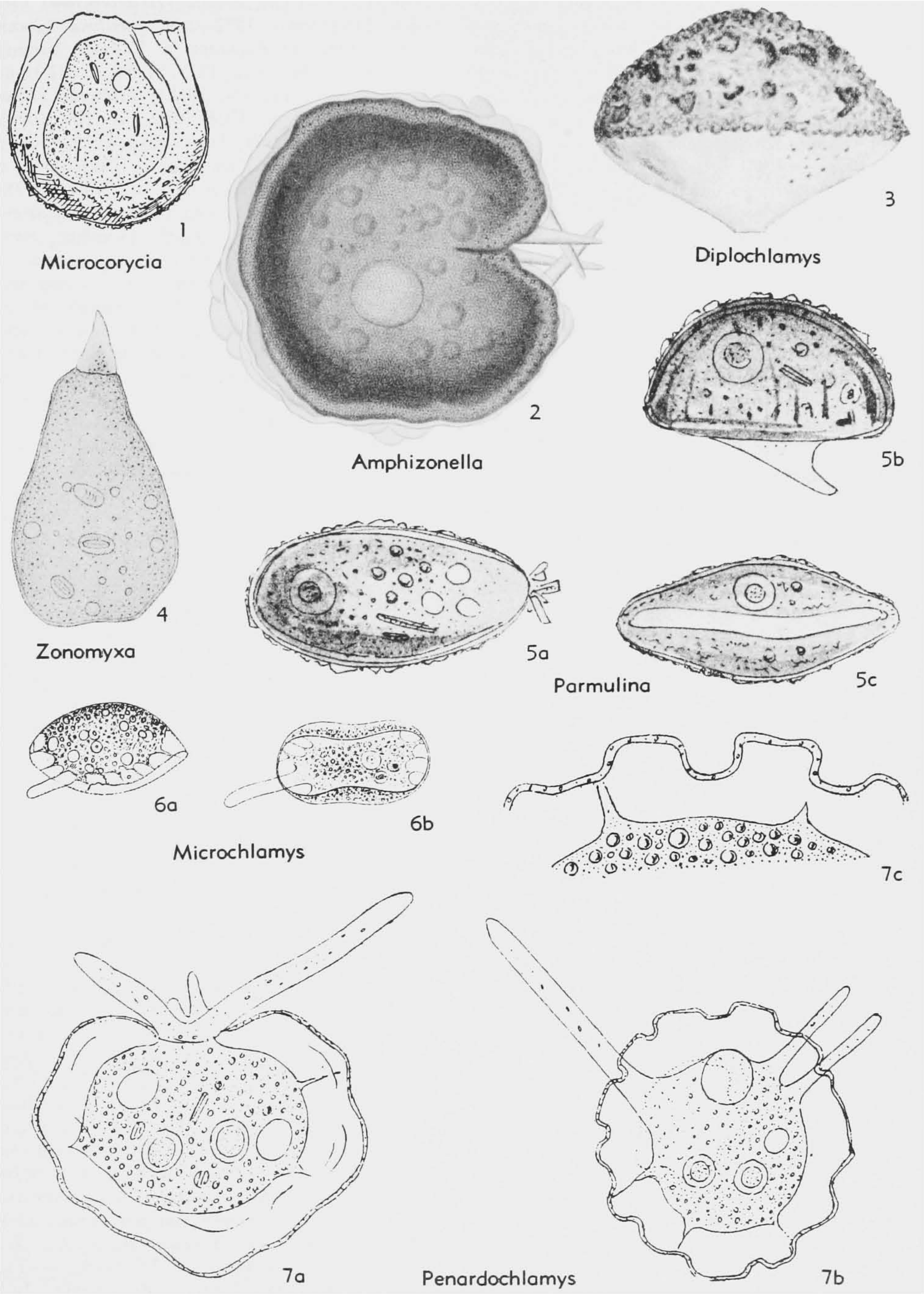

FIG. 4. Microcoryciidae; *1, Microcorycia; 2, Amphizonella; 3, Diplochlamys; 4, Zonomyxa; 5, Parmulina; 6, Microchlamys; 7, Penardochlamys* (p. C19-C22).

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).

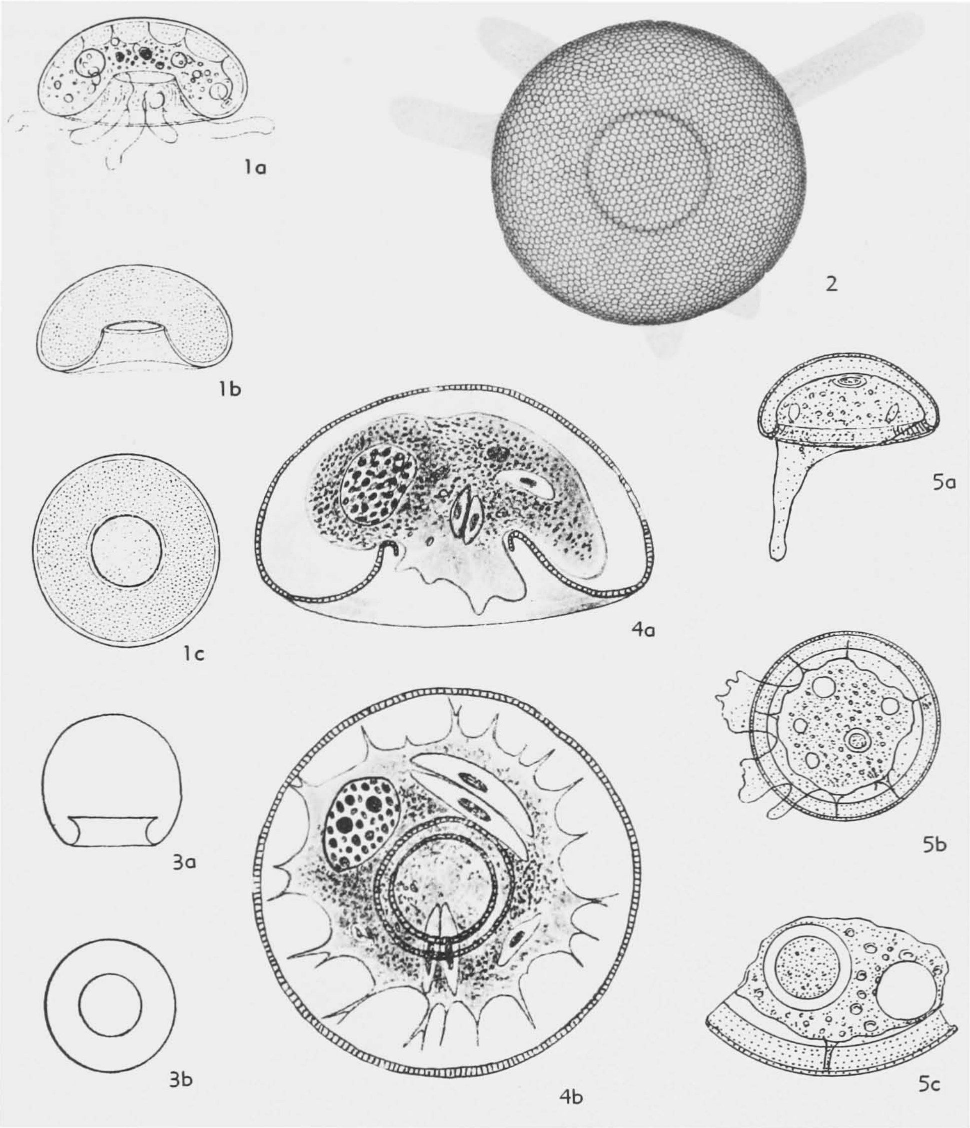

FIG. 5. Arcellidae; *1-5, Arcella* (p. *C*22).

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

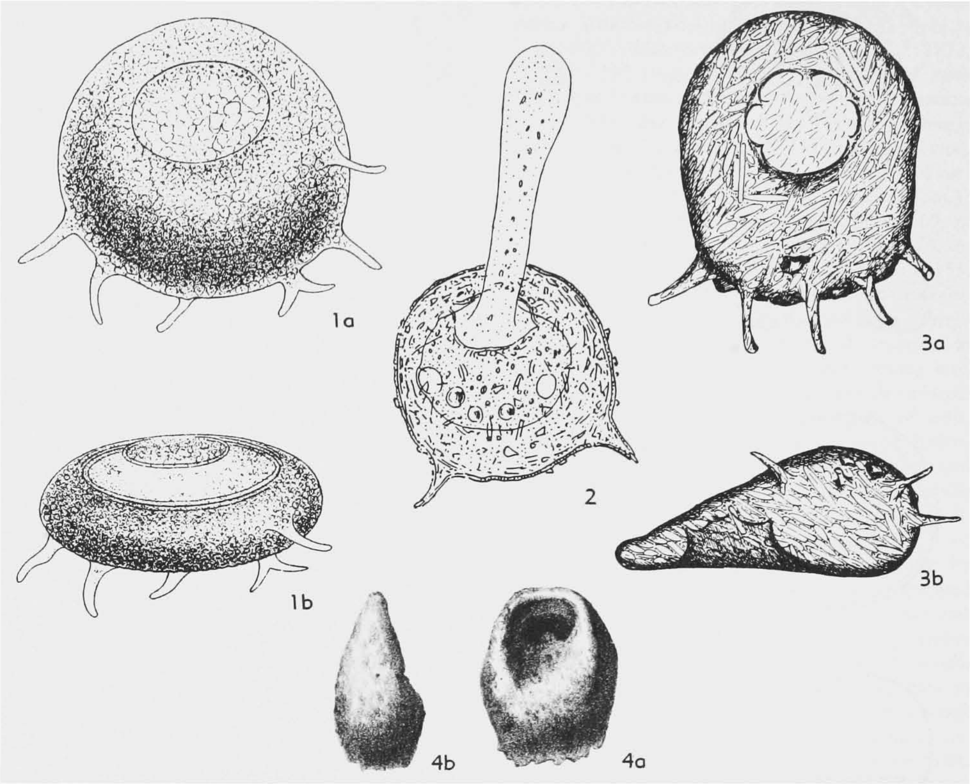

FIG. 6. Centropyxidae; *1-4, Centropyxis* (p. C23-C24).

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

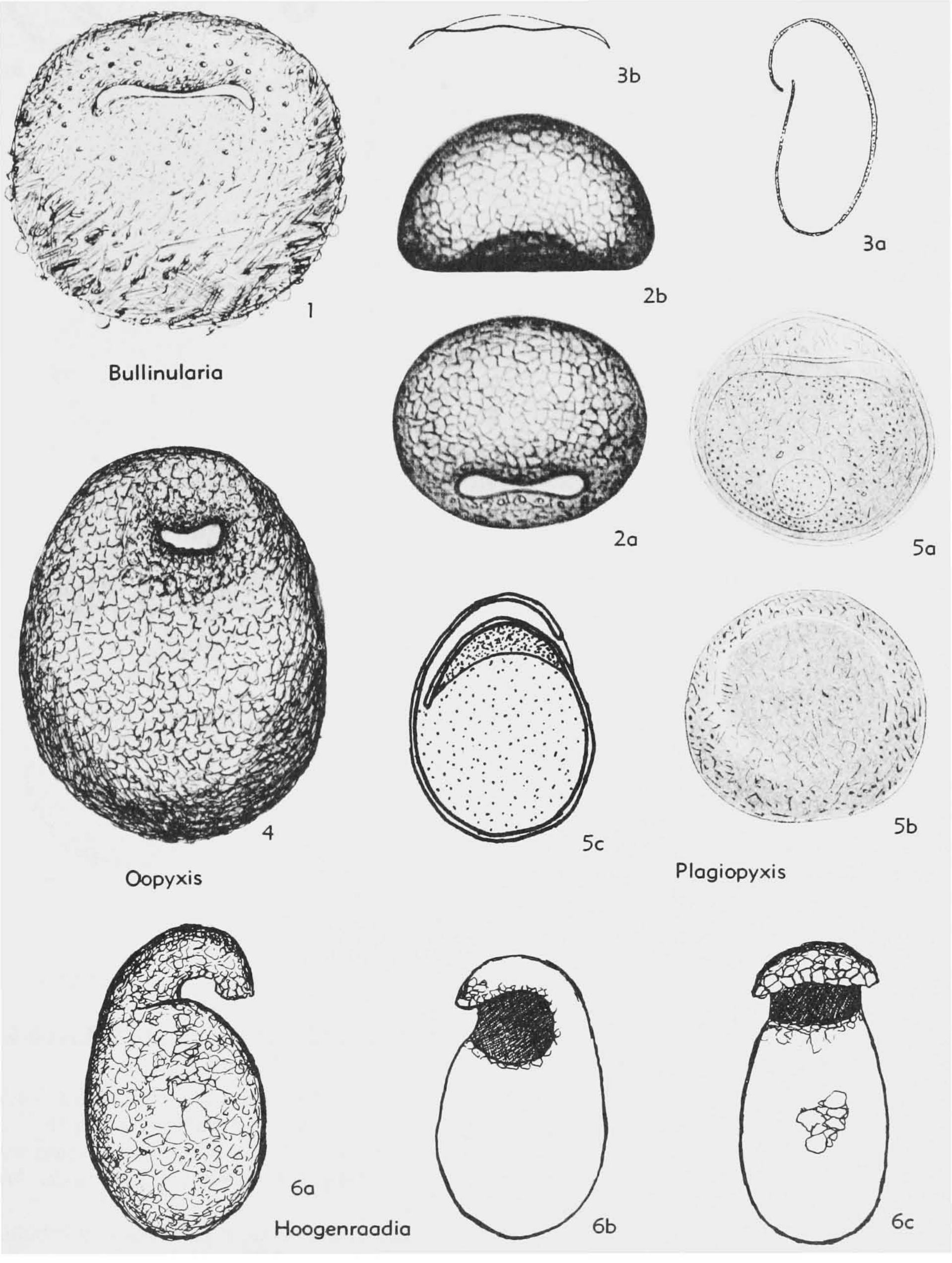

FIG. 7. Plagiopyxidae; *1-3, Bullinularia; 4, Oopyxis; 5, Plagiopyxis; 6, Hoogenraadia* (p. C24-C26).

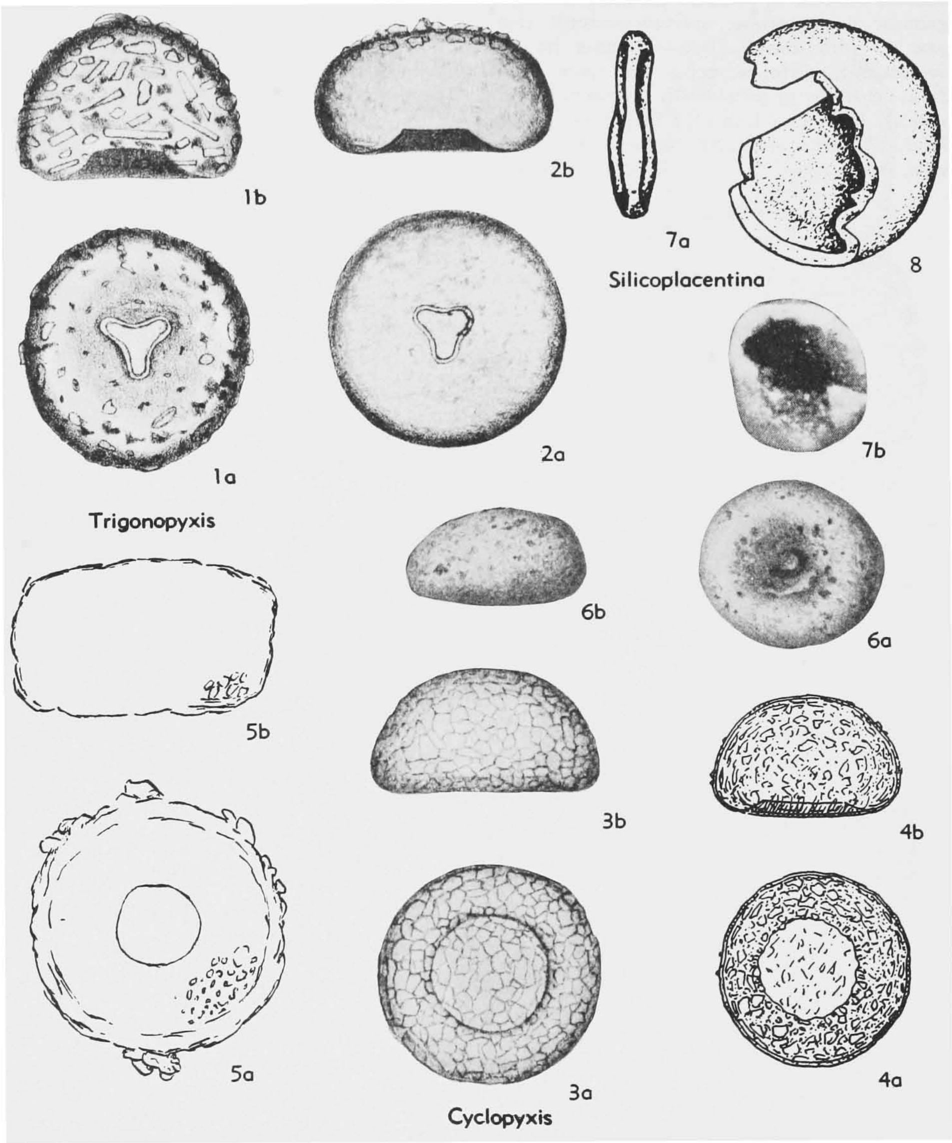

FIG. 8 Trigonopyxidae; _1,2, Trigonopyxis; 3-6, Cyclopyxis; 7,8, Silicoplacentina_ (p. C26-C27).

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]

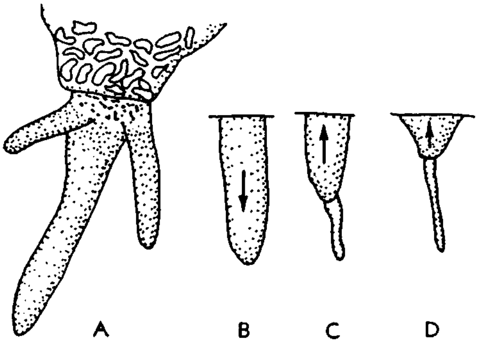

FIG. 9. Hyalospheniidae; *A-D,* successive stages in pseudopodial movement of *Lesquereusia spiralis* (p. *C*30-*C*31).

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-

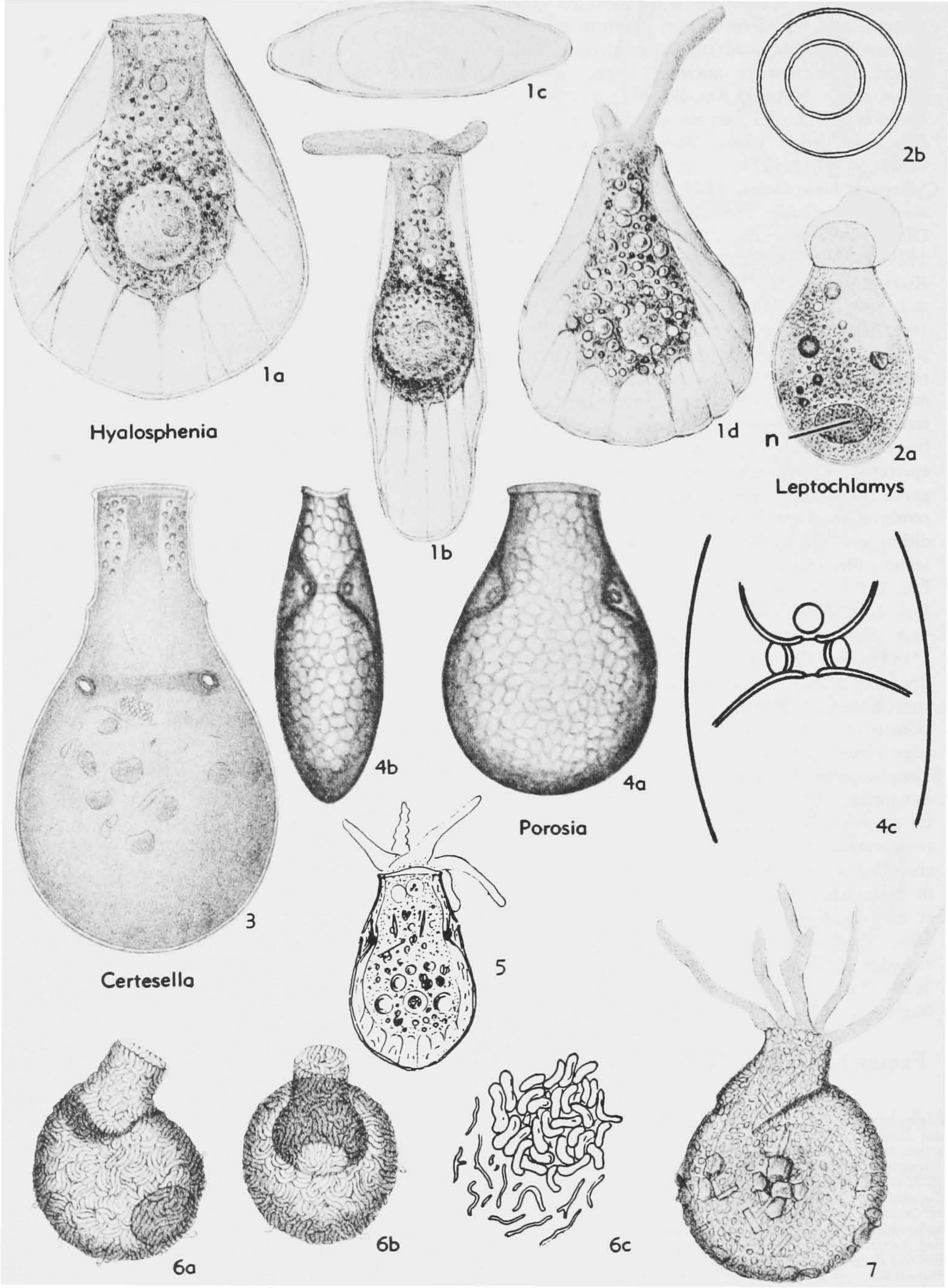

FIG. 10. Hyalospheniidae; *1, Hyalosphenia; 2, Leptochlamys; 3, Certesella; 4,5, Porosia; 6,7, Lesquereusia* (p. *C27-C32*).

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).

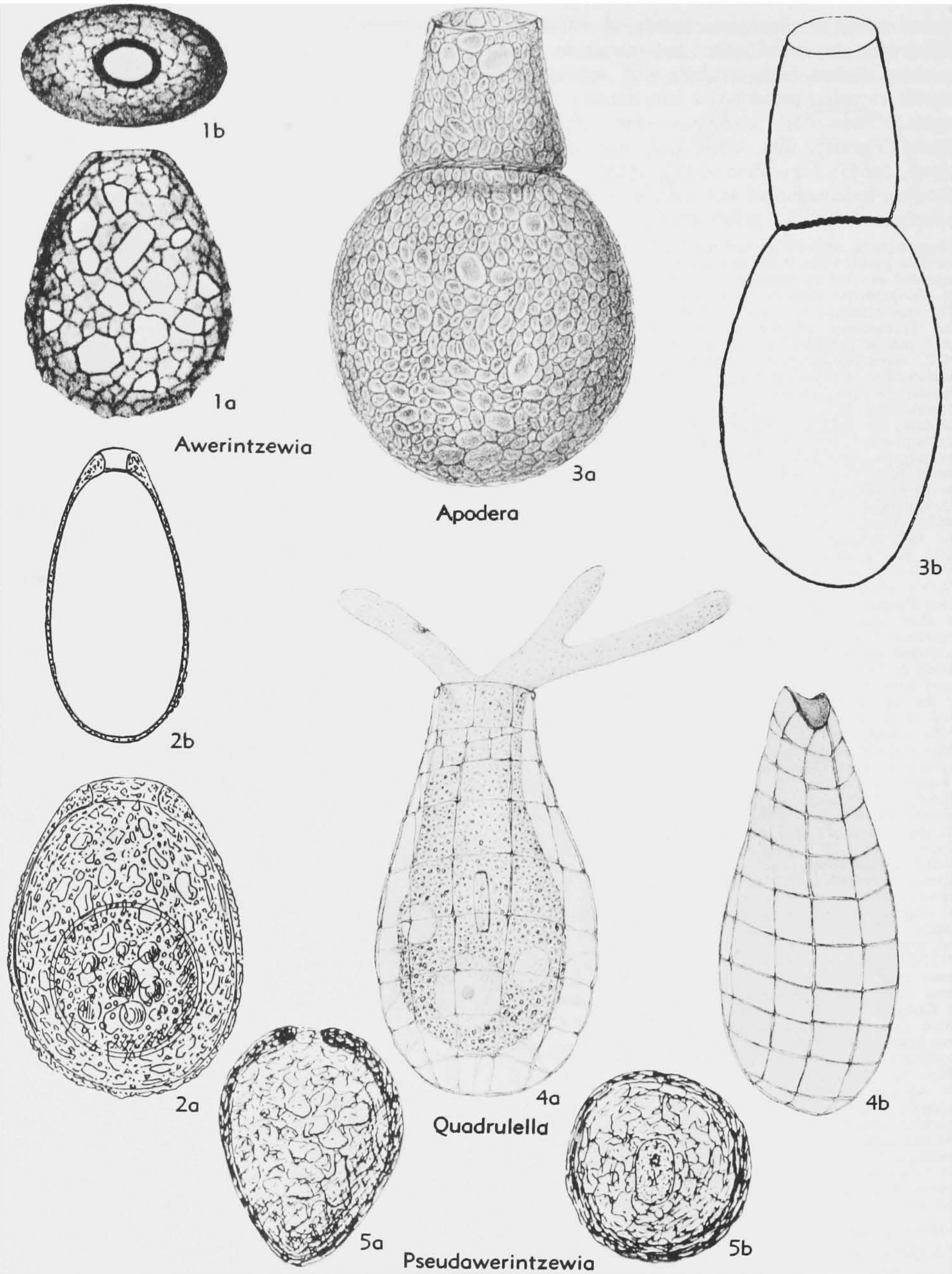

FIG. 11. Hyalospheniidae; *1,2, Awerintzewia; 3, Apodera; 4, Quadrulella; 5, Pseudawerintzewia* (p. *C*29, *C*32).

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

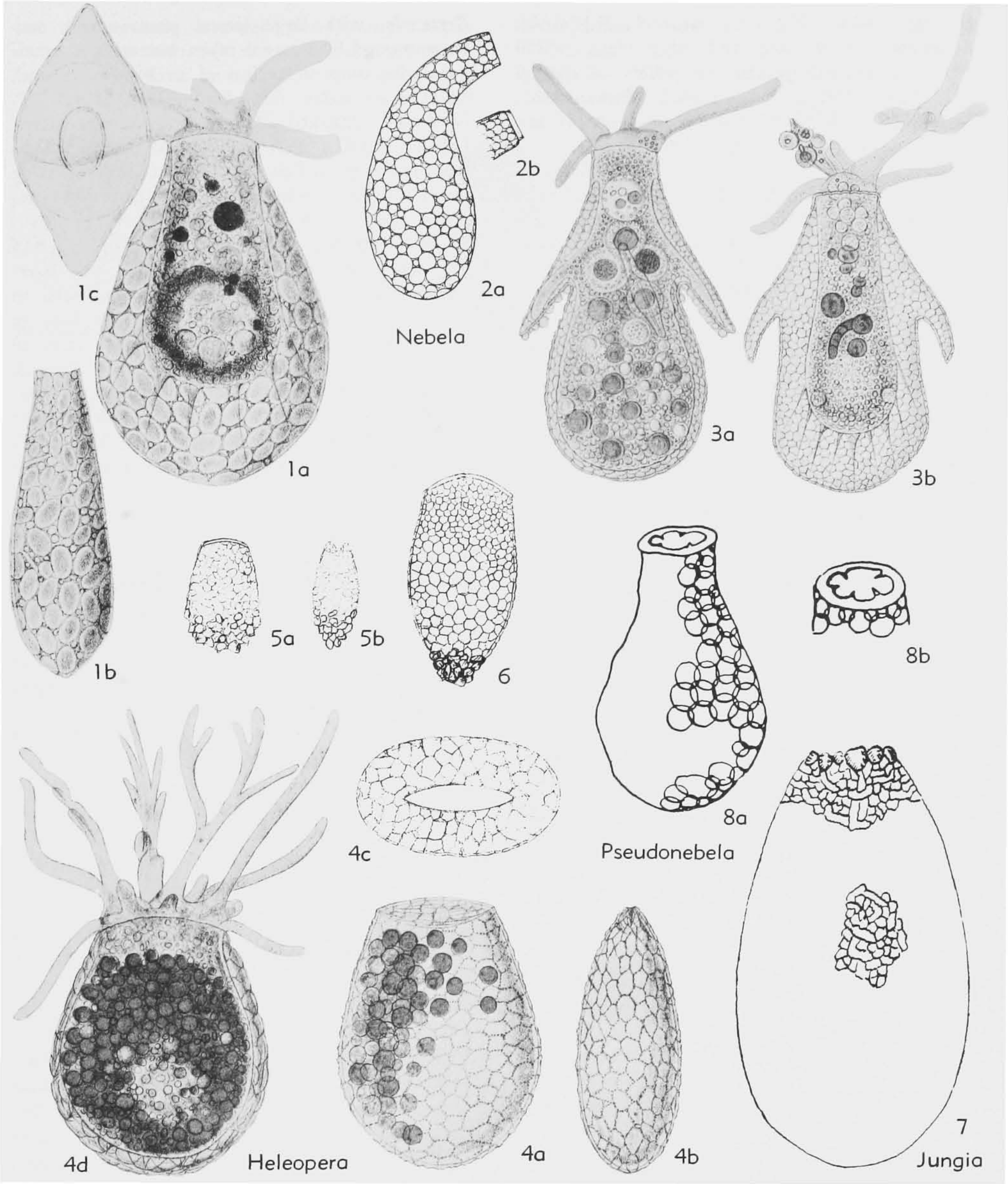

FIG. 12. Hyalospheniidae; *1-3, Nebela; 4-6, Heleopera; 7, Jungia; 8, Pseudonebela* (p. *C*29, *C*32).

[**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,

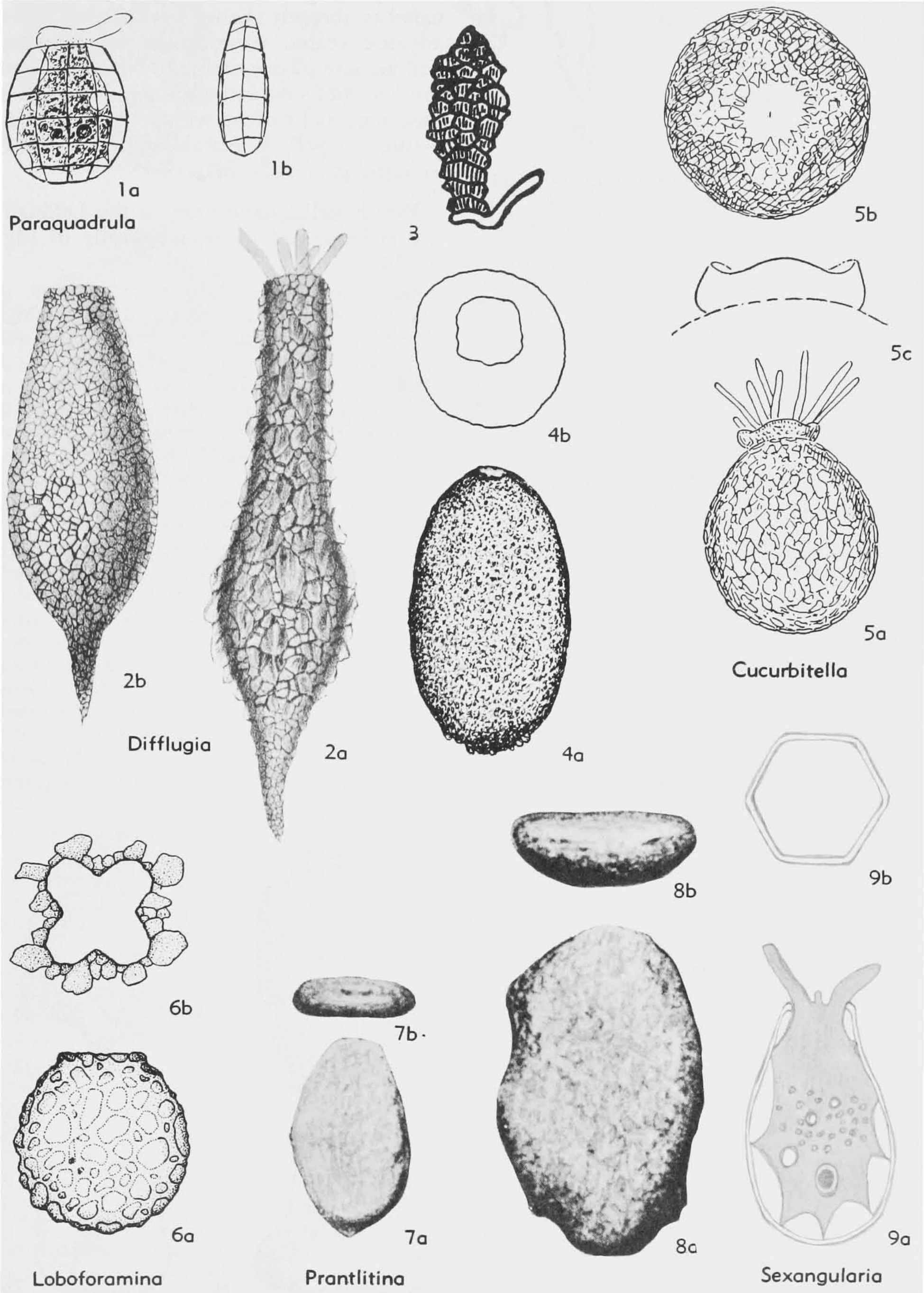

FIG. 13. Paraquadrulidae; *1, Paraquadrula;* Difflugiidae; *2-4, Difflugia; 5, Cucurbitella; 6, Loboforamina; 7,8, Prantlitina; 9, Sexangularia* (p. C34-C37).

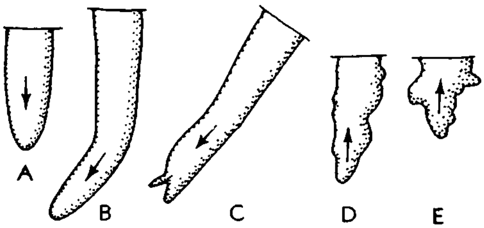

FIG. 14. Diagrams indicating the nature of pseudopodial movement in *Difflugia oviformis*, Rec. (entire animal not shown, arrows marking direction of movement); *A,B*, advance of lobose pseudopodium; *C*, bifurcating pseudopodium; *D,E*, retraction of pseudopodium showing undulatory margin, loss of rigidity,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

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

Family PARAQUADRULIDAE Deflandre, 1953

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

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

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

Family DIFFLUGIIDAE Wallich, 1864

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

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

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

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

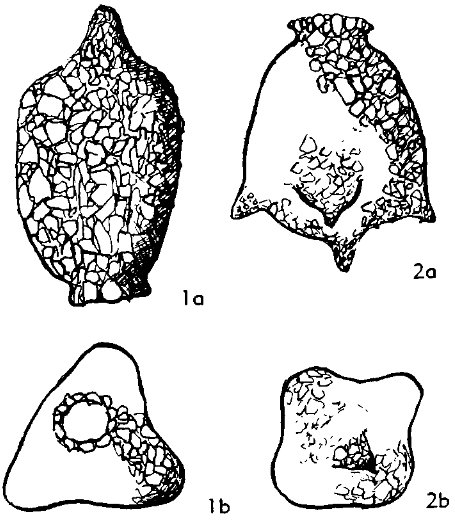

FIG. 15. Difflugiidae; *1,2, Difflugia* (p. C34-C35).

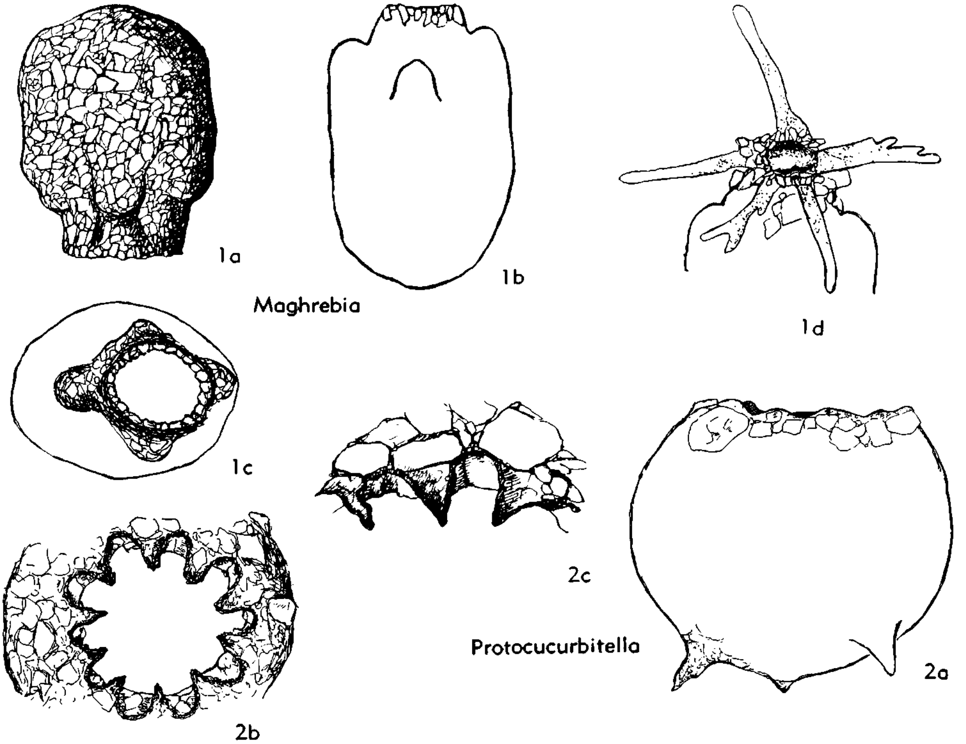

FIG. 16. Difflugiidae; *1, Maghrebia; 2, Protocucurbitella* (p. *C36*).

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*

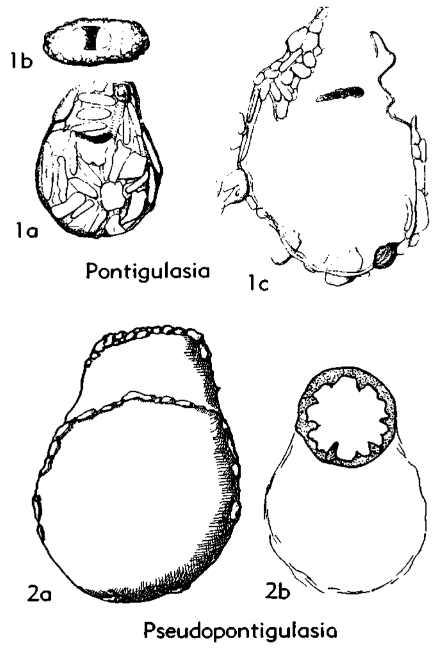

Fig. 17. Difflugiidae; *1, Pontigulasia; 2, Pseudopontigulasia* (p. C36).

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).

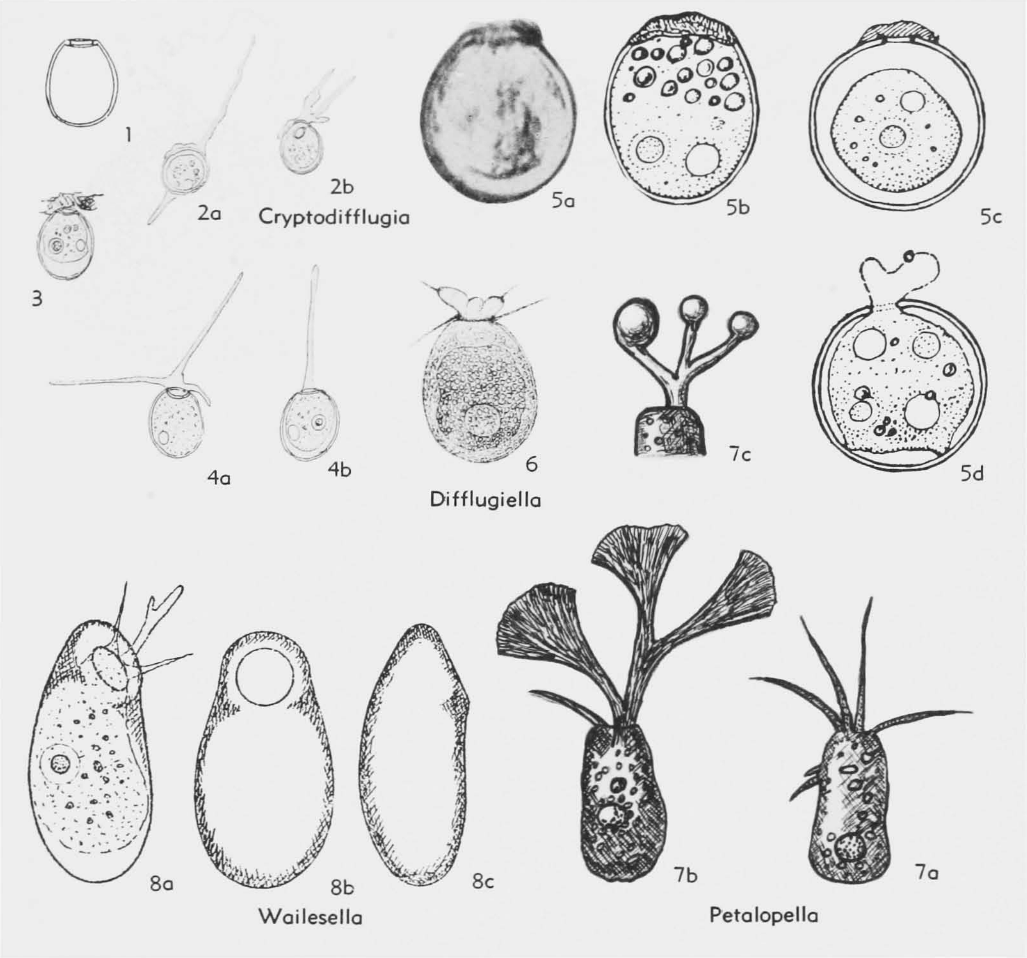

FIG. 18. Cryptodifflugiidae; *1-5, Cryptodifflugia; 6, Difflugiella; 7, Petalopella; 8, Wailesella* (p. C37-C38).

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,*

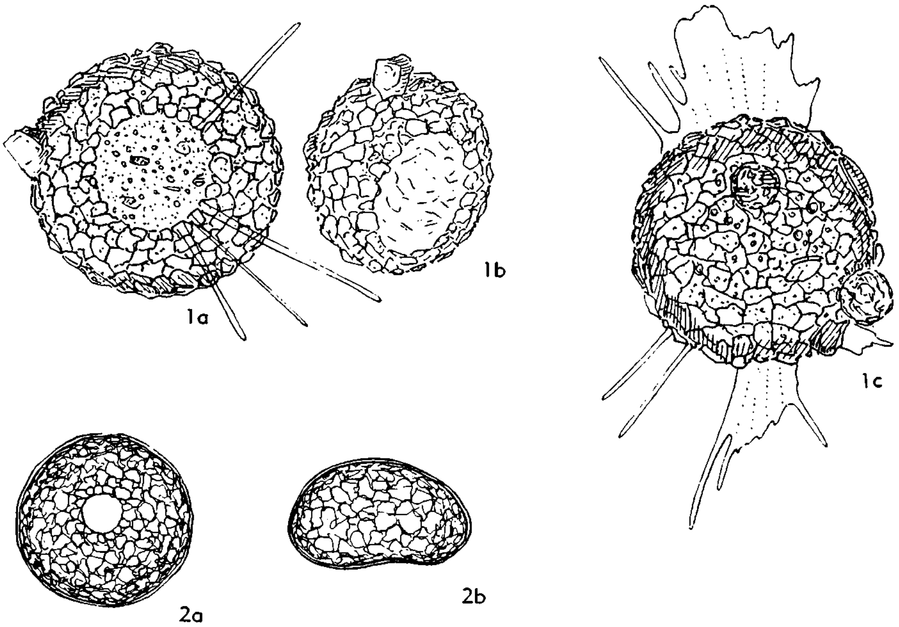

FIG. 19. Phryganellidae; *1,2, Phryganella* (p. C38-C39).

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-

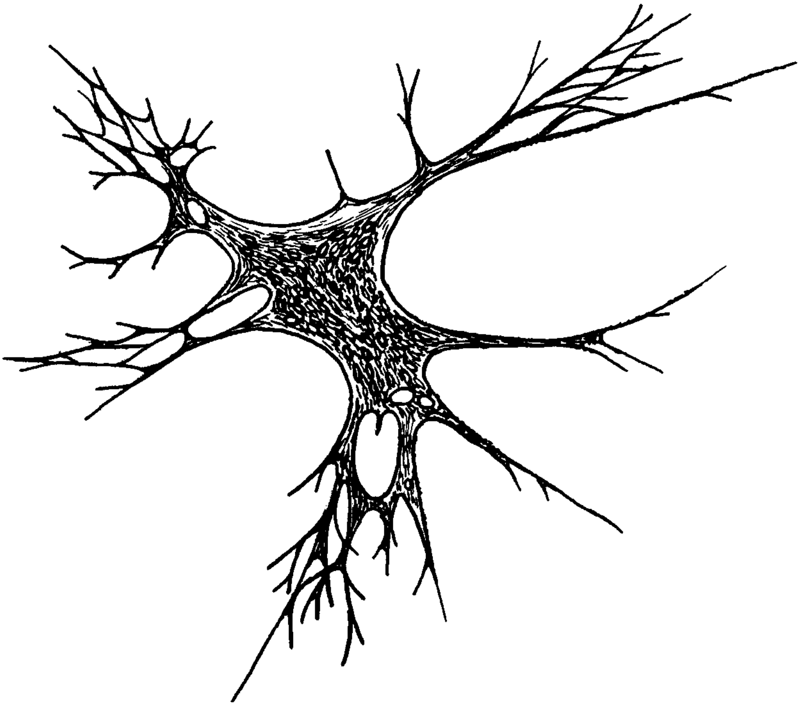

FIG. 20. Penardiidae; *Penardia* (p. *C*40).

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

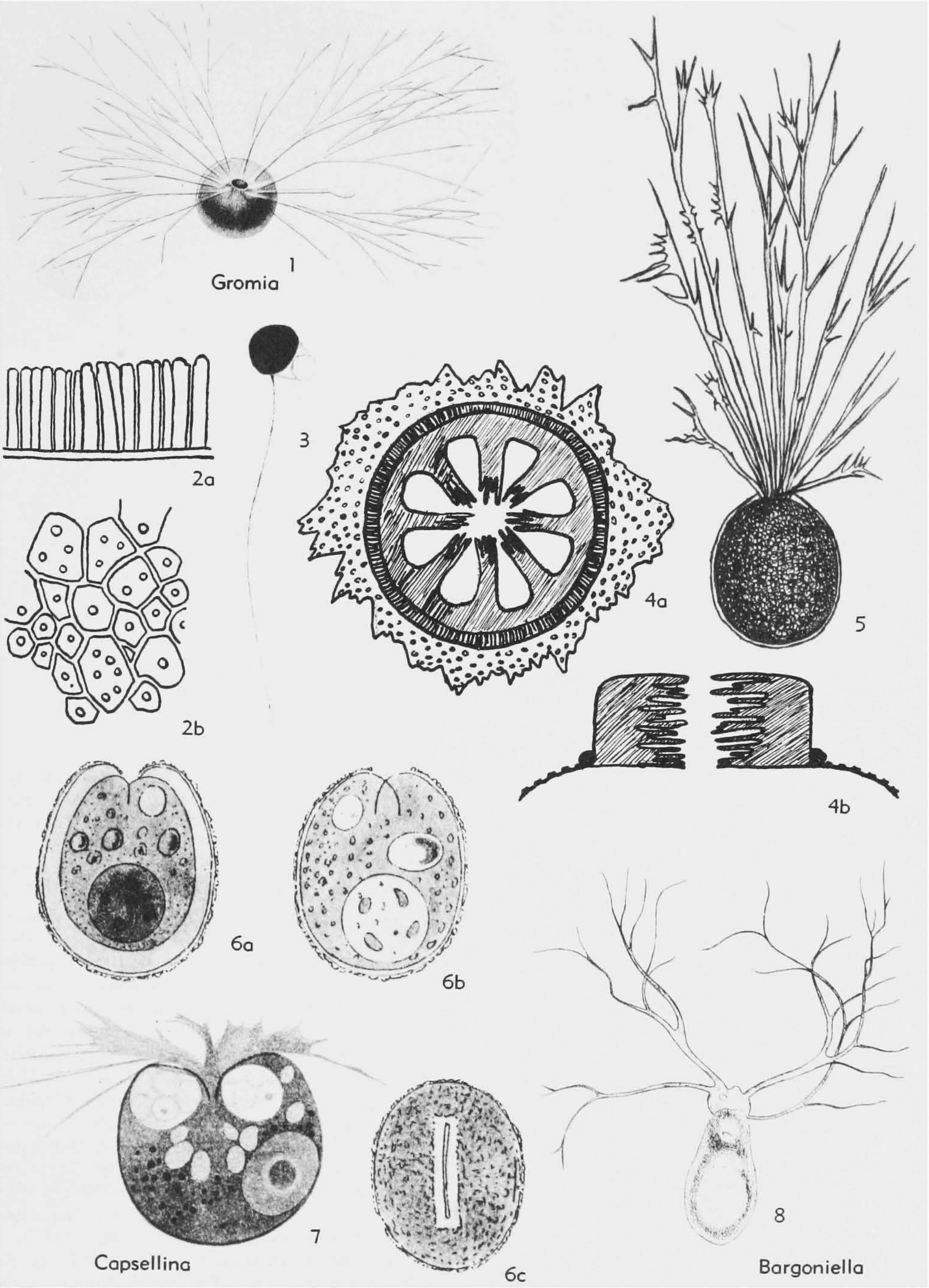

Fig. 21. Gromiidae; *1-5, Gromia; 6,7, Capsellina; 8, Bargoniella* (p. *C*40-*C*42).

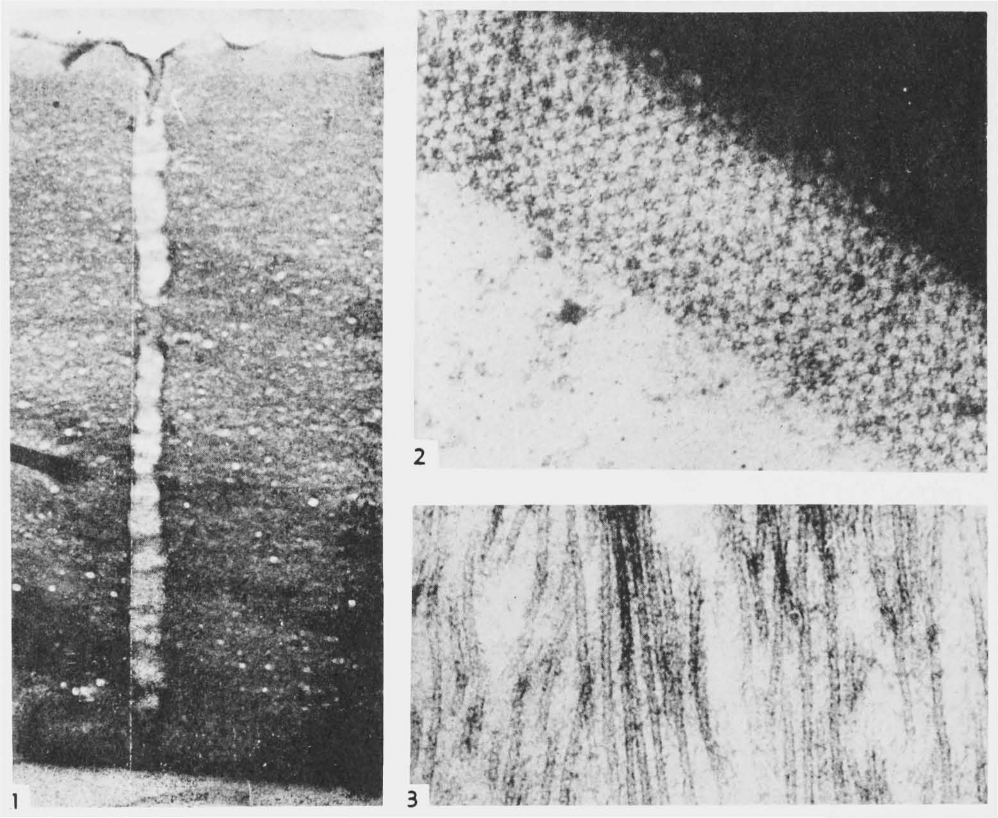

FIG. 22. Gromiidae; *1-3, Gromia oviformis,* electron micrographs (p. *C*40).

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

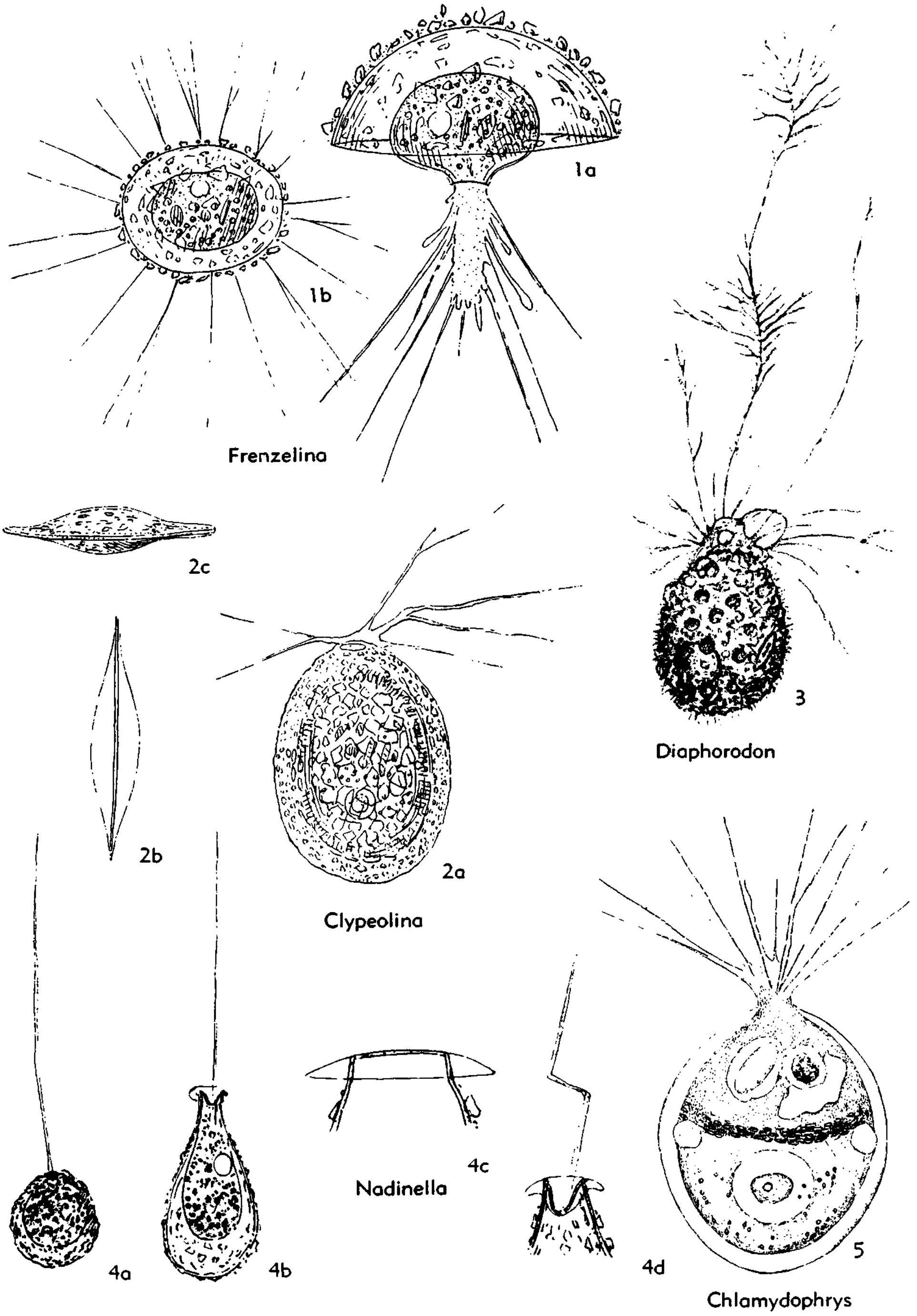

FIG. 23. Gromiidae; *1, Frenzelina; 2, Clypeolina; 3, Diaphorodon; 4, Nadinella; 5, Chlamydophrys* (p. C42-C46).

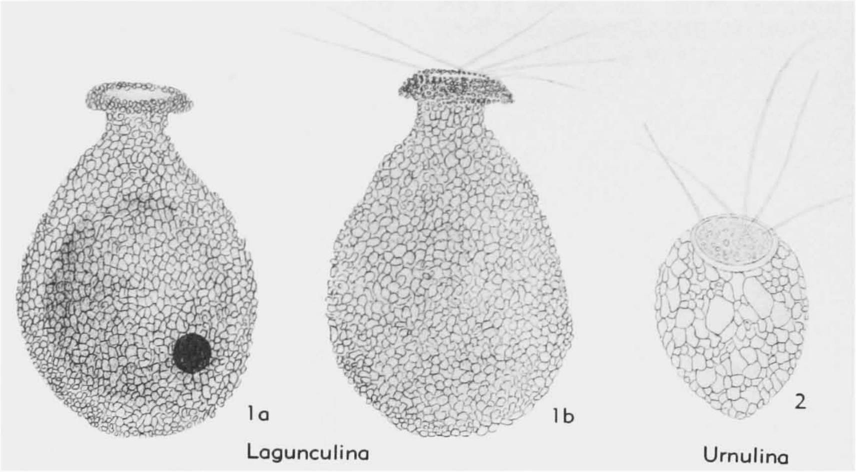

FIG. 24. Gromiidae; *1, Lagunculina; 2, Urnulina* (p. *C*44, *C*46-*C*47).

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-

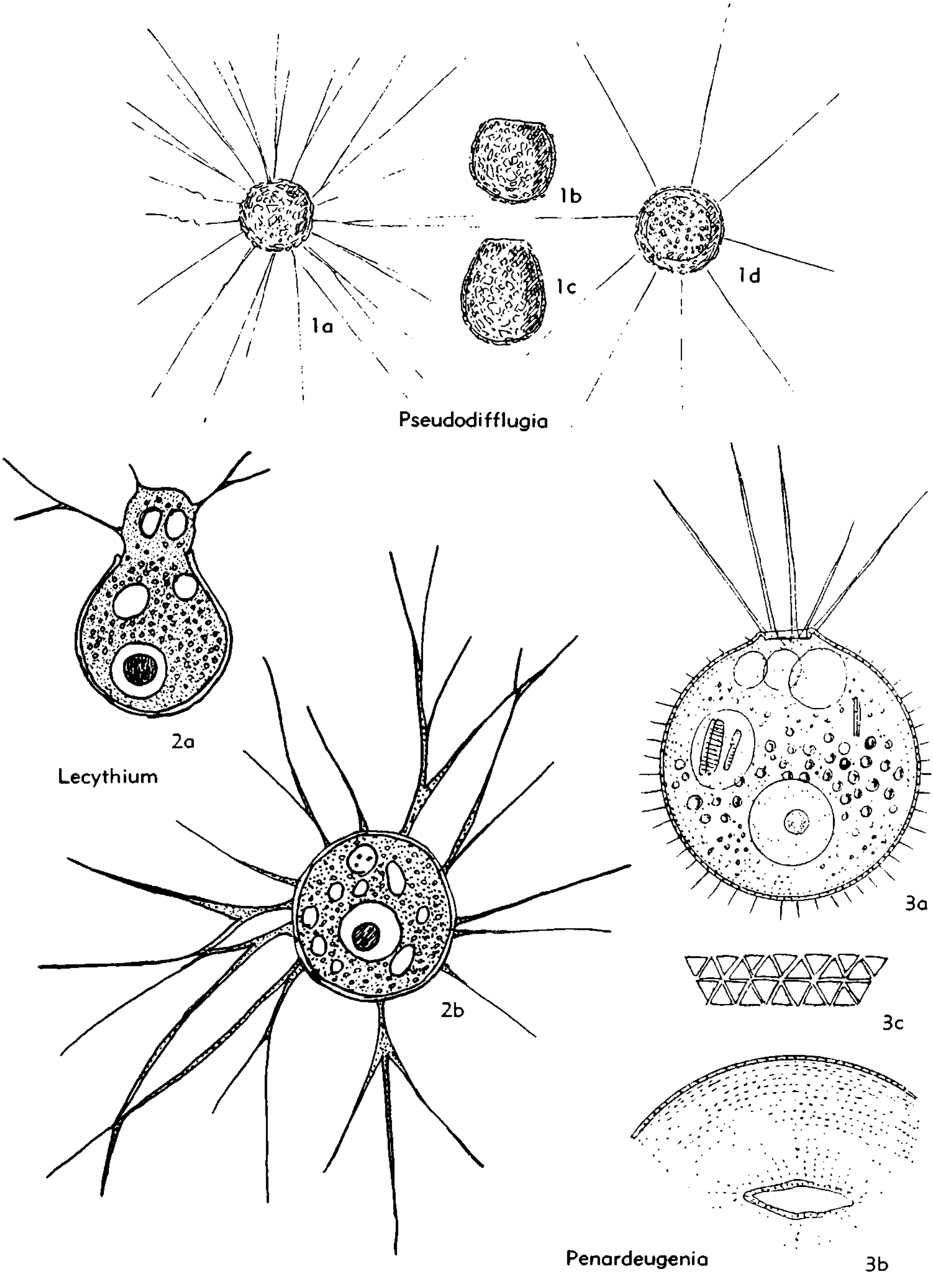

Fig. 25. Gromiidae; *1, Pseudodifflugia; 2, Lecythium; 3, Penardeugenia* (p. C44-C46).

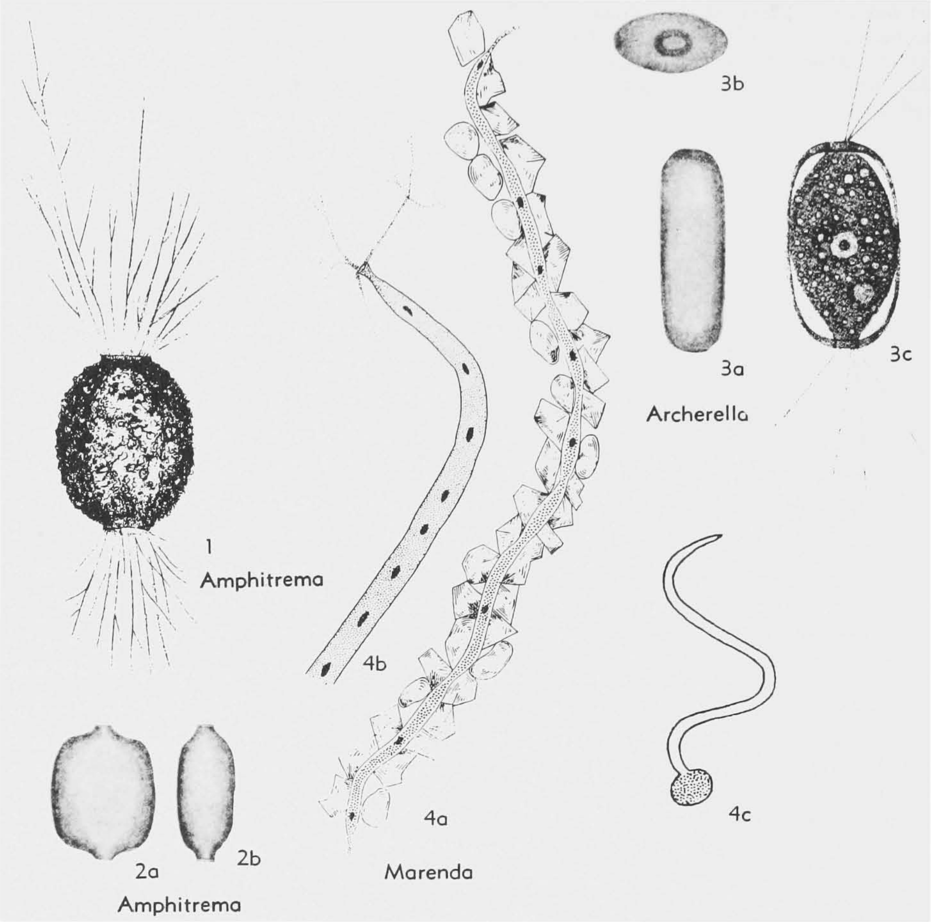

FIG. 26. Amphitrematidae; *1, 2, Amphitrema; 3, Archerella; 4, Marenda* (p. C47).

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}Amphistomina† 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}Amphistomini† 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.

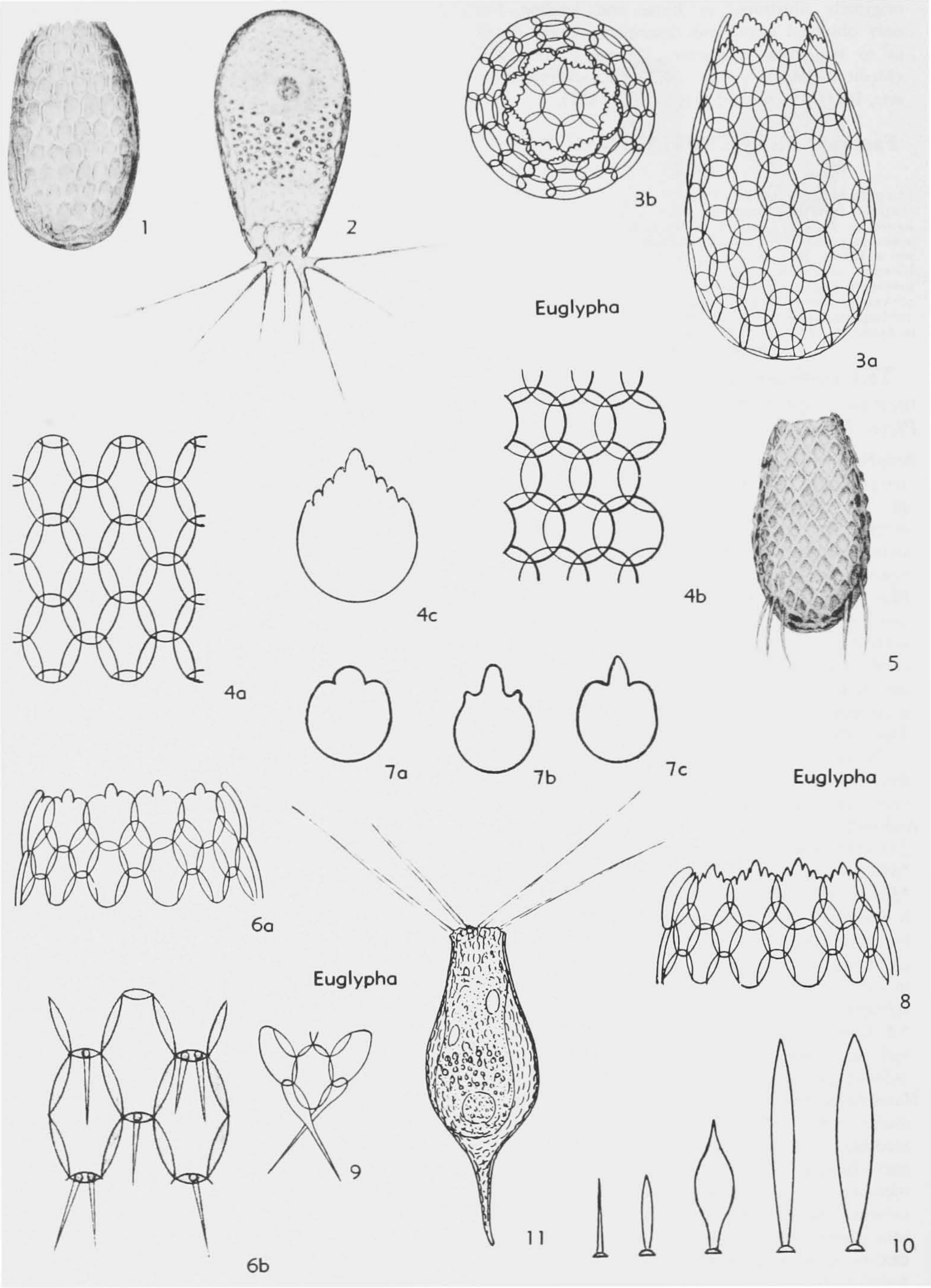

Fig. 27. Euglyphidae (Euglyphinae; *1-10, Euglypha*) (p. C47-C49).

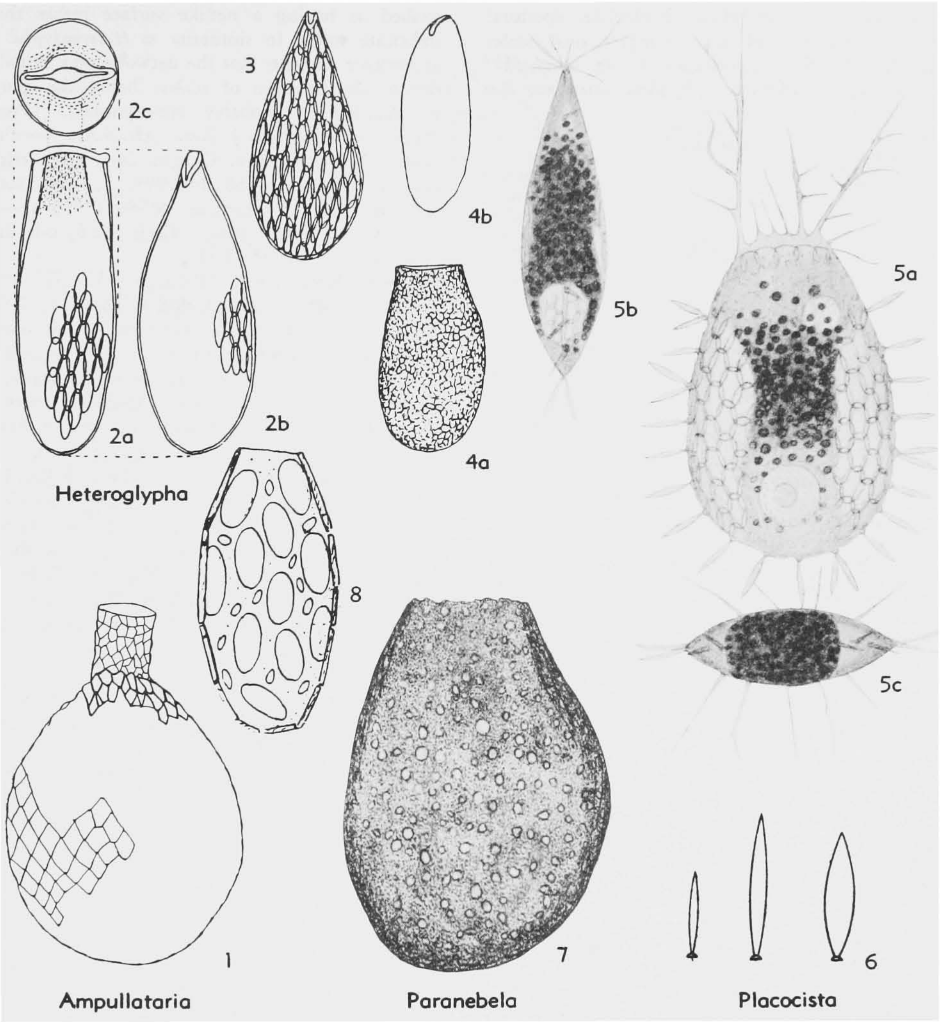

FIG. 28. Euglyphidae (Euglyphinae; *1, Ampullataria; 2-4, Heteroglypha; 5, 6, Placocista; 7, 8, Paranebela*) (p. *C*49-*C*50).

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).

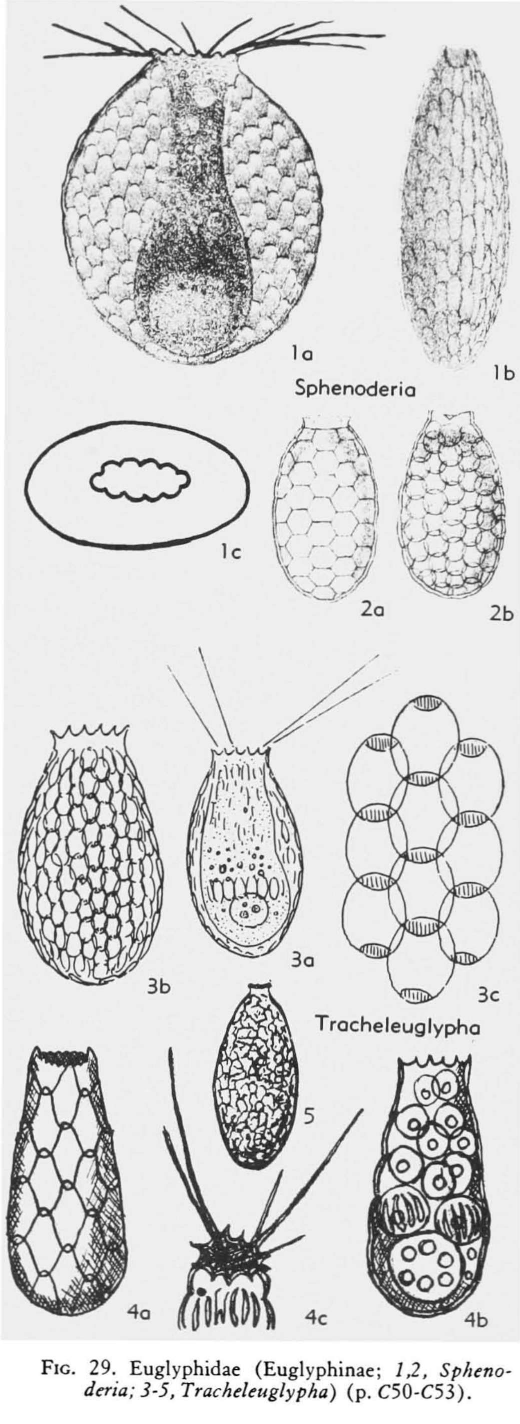

FIG. 29. Euglyphidae (Euglyphinae; *1,2, Sphenoderia; 3-5, Tracheleuglypha*) (p. C50-C53).

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

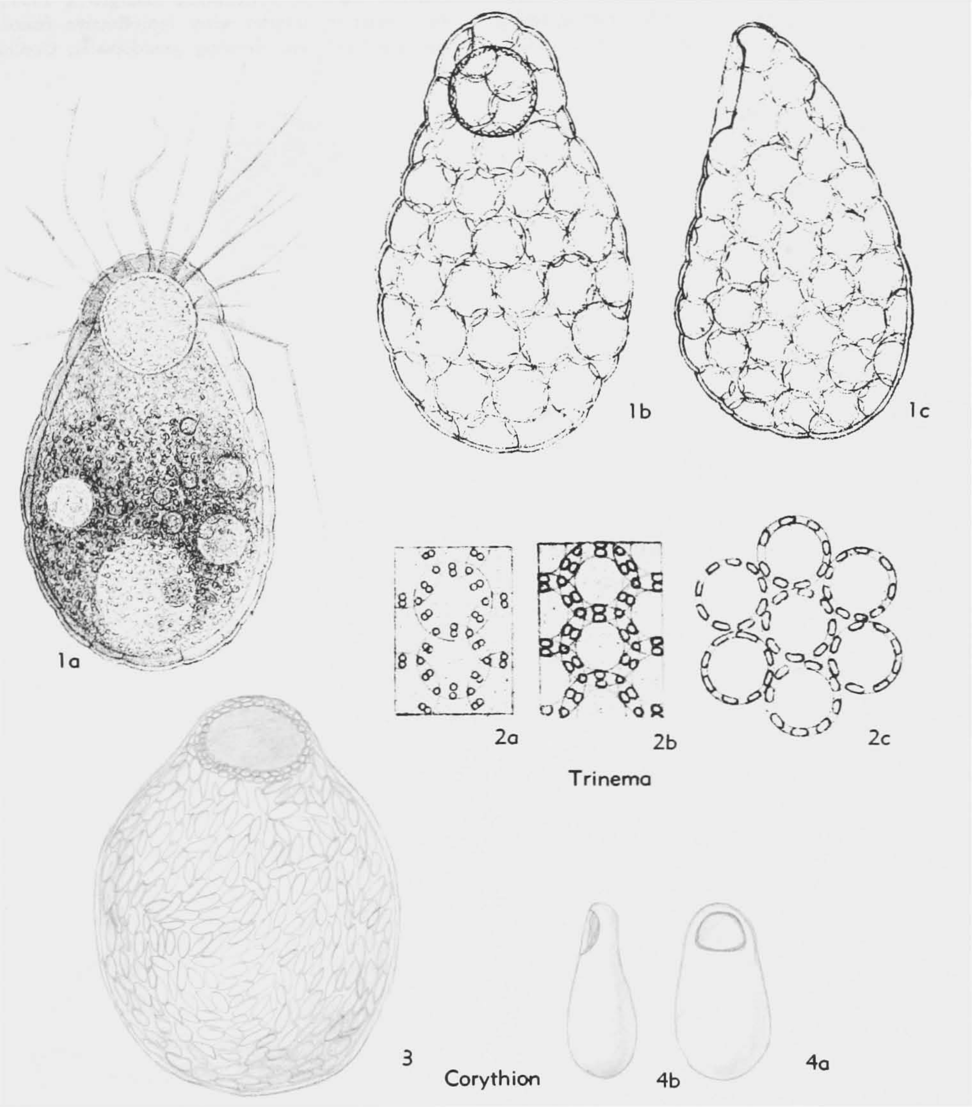

FIG. 30. Euglyphidae (Trinematinae; *1,2, Trinema; 3,4, Corythion*) (p. *C*53).

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.,

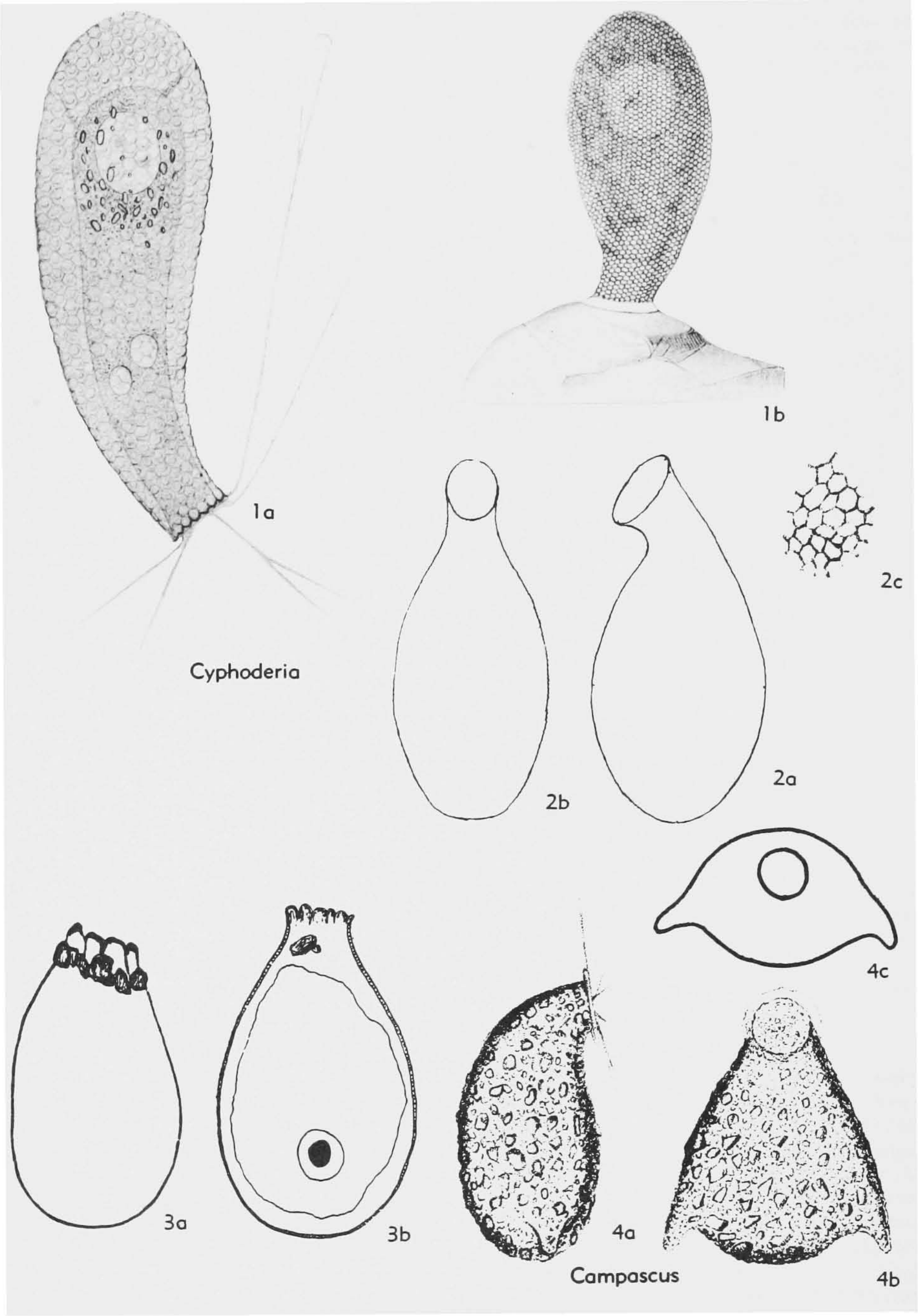

Fig. 31. Cyphoderiidae; *1-3, Cyphoderia; 4, Campascus* (p. C53-C54).

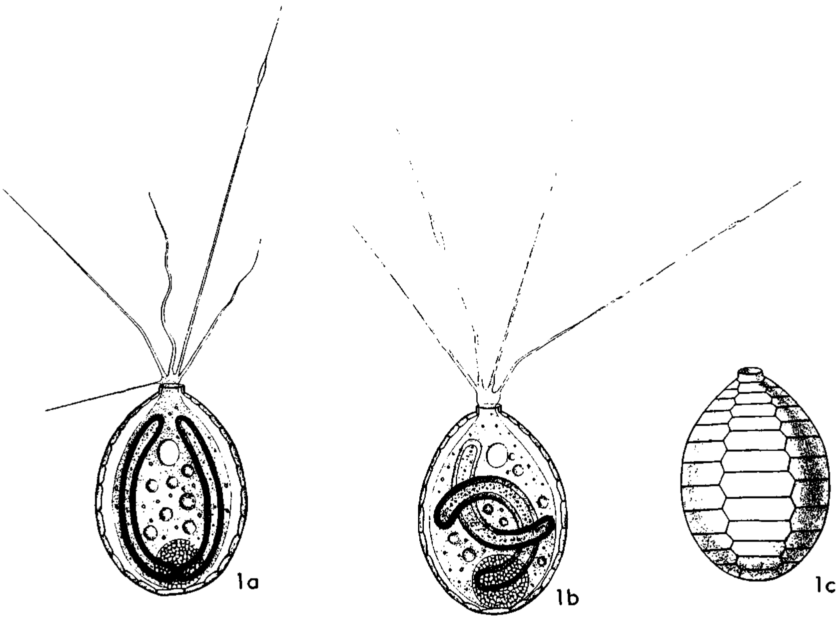

FIG. 32. Paulinellidae; *1, Paulinella* (p. C54).

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,

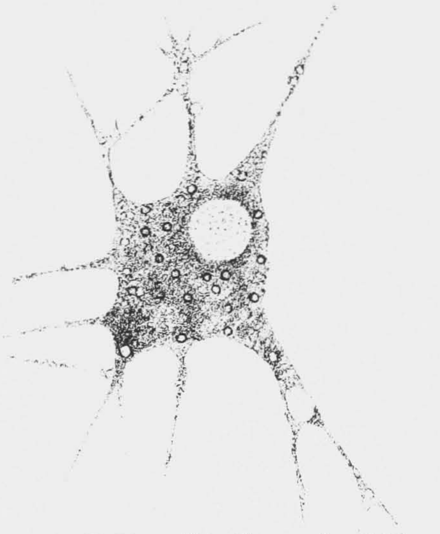

FIG. 33. Biomyxidae; *Biomyxa* (p. C54).

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

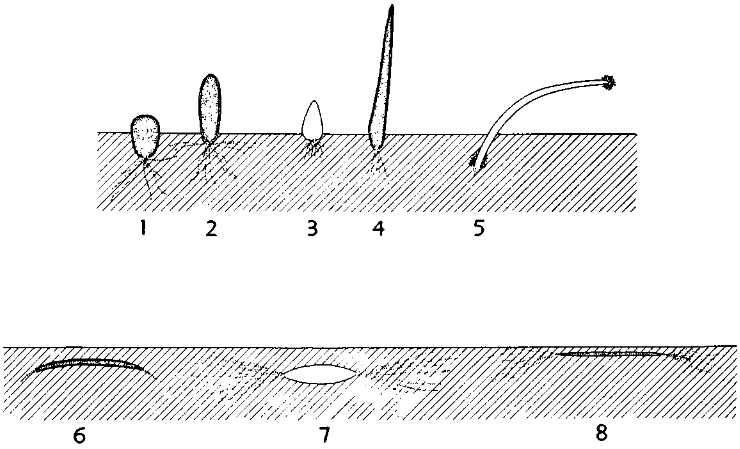

FIG. 34. Pseudopodial function in Foraminiferida.——*1-5.* Erect, rigid pseudopodia; *1,2,* Allogromiidae; *3, Hippocrepina; 4, Micrometula; 5, Bathysiphon.*——*6-8,* Prostrate, fragile, anastomosing pseudopodia; *6, Shepheardella; 7, Phainogullmia; 8, Nemogullmia* (*1379).

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.

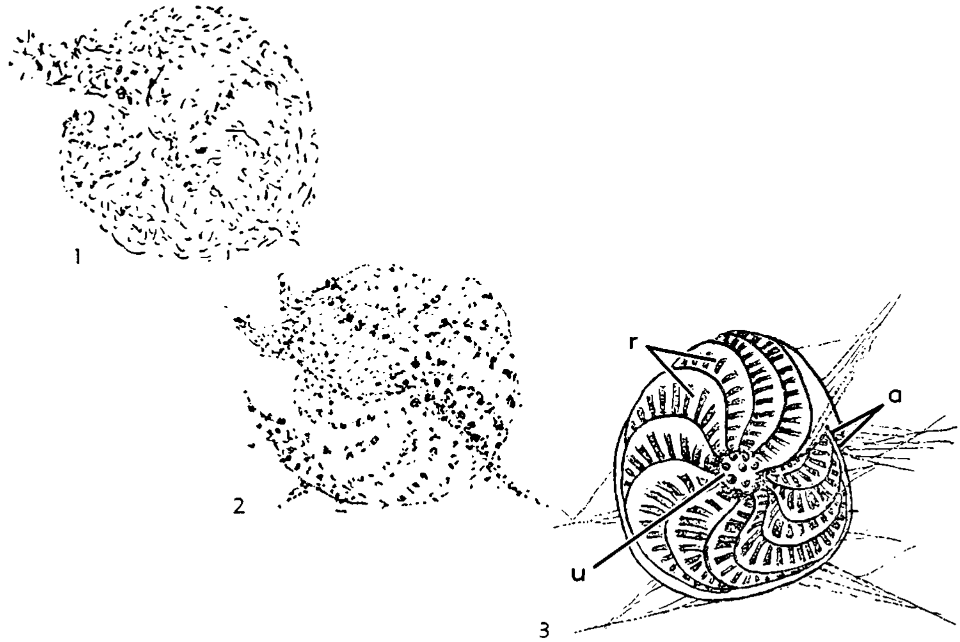

Fig. 35. Feeding cysts in *Elphidium*. Two successive feeding cysts *(1,2)* are shown with *Elphidium (3)* moving to a new location. The cysts are composed of empty diatom frustrules and xanthosomes deposited outside canal openings and along pseudopodial tracks (aperture, *a*; umbo with openings of spiral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

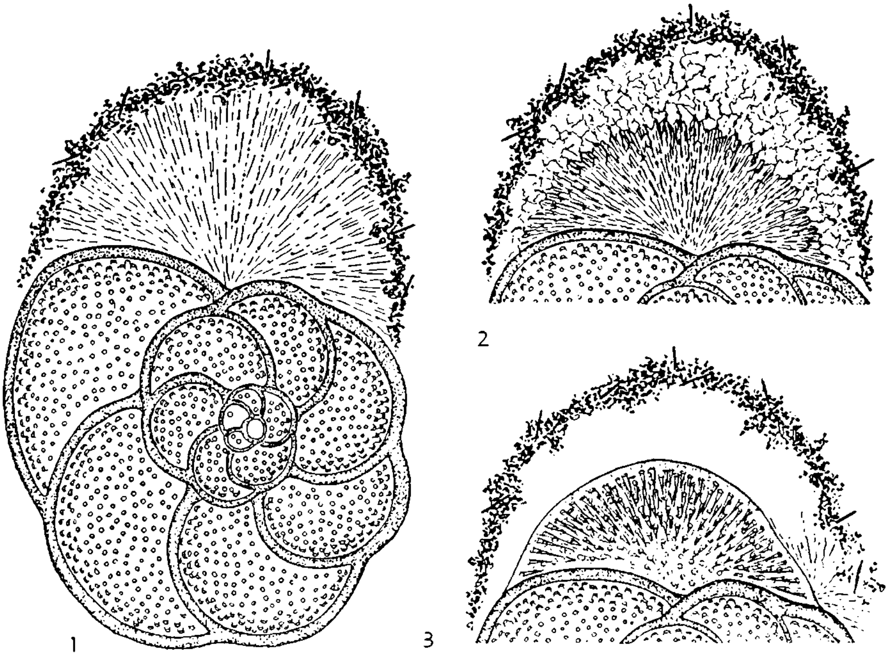

FIG. 36. Chamber formation in *Discorbinella bertheloti*; *1*, pseudopodia forming protective cyst; *2*, main pseudopodia retracted to position of future wall; *3*, formation of pseudochitinous pellicle with perforations, before calcification; all ×60 (*1109).

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

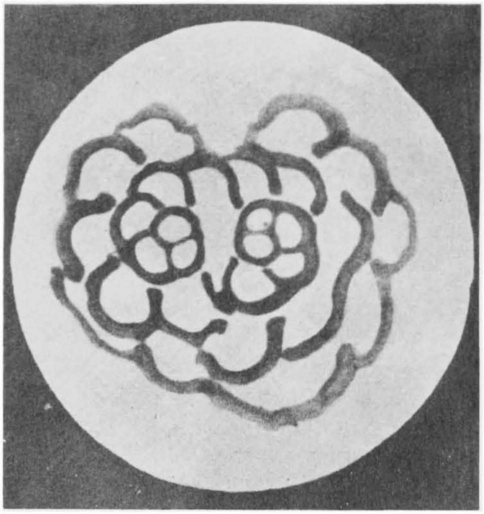

FIG. 37. Polyvalence in juvenile *Planorbulina mediterranensis,* enlarged (*1109).

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.

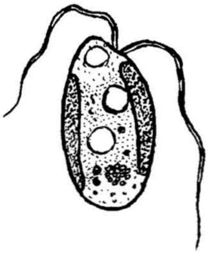

FIG. 38. *Cryptomonas schaudinni* WINTER, symbiotic zooxanthella found in *Peneroplis,* ×2,250 (*2068).

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).

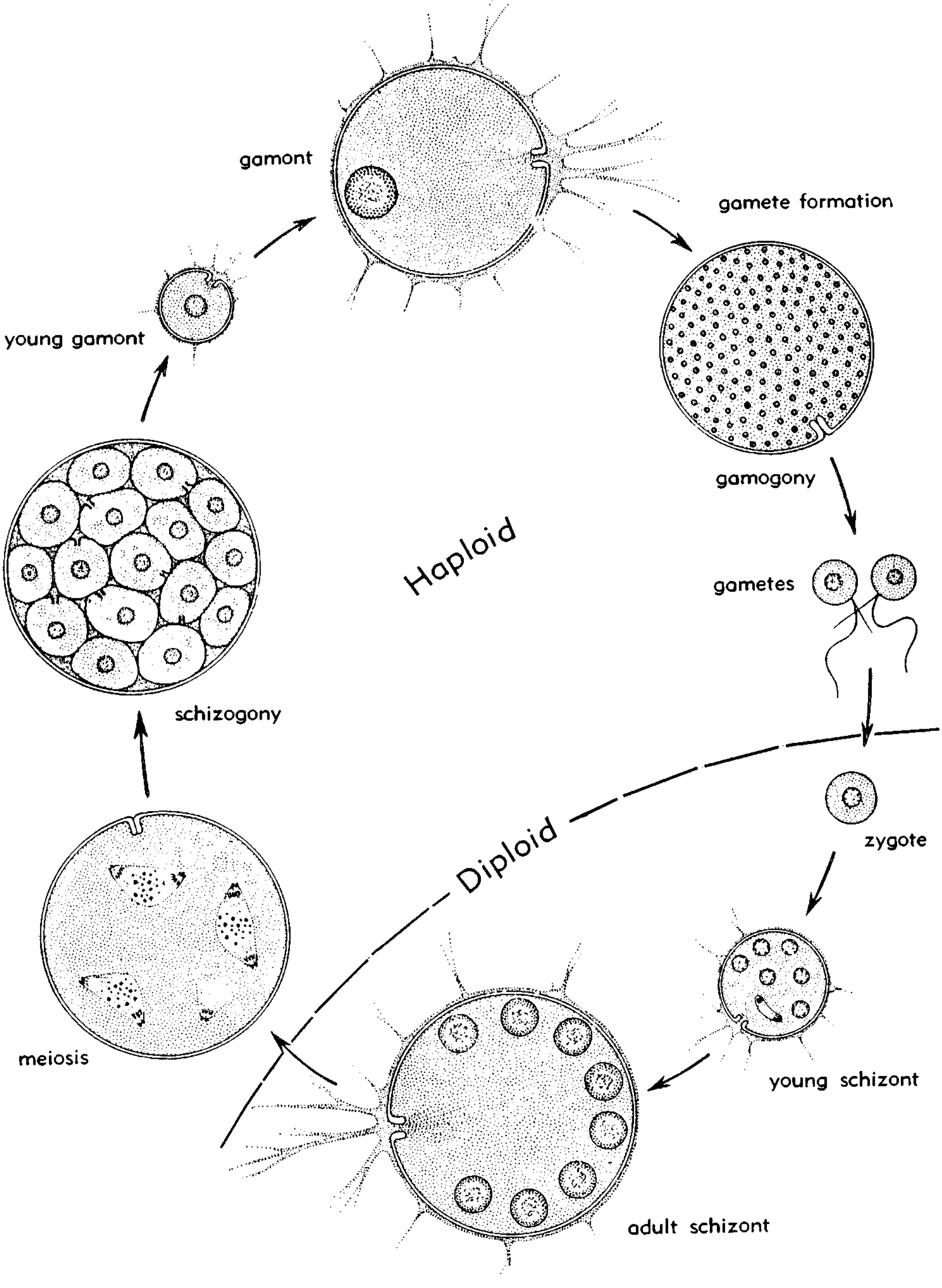

FIG. 39. Life cycle of *Myxotheca arenilega* (*821).

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

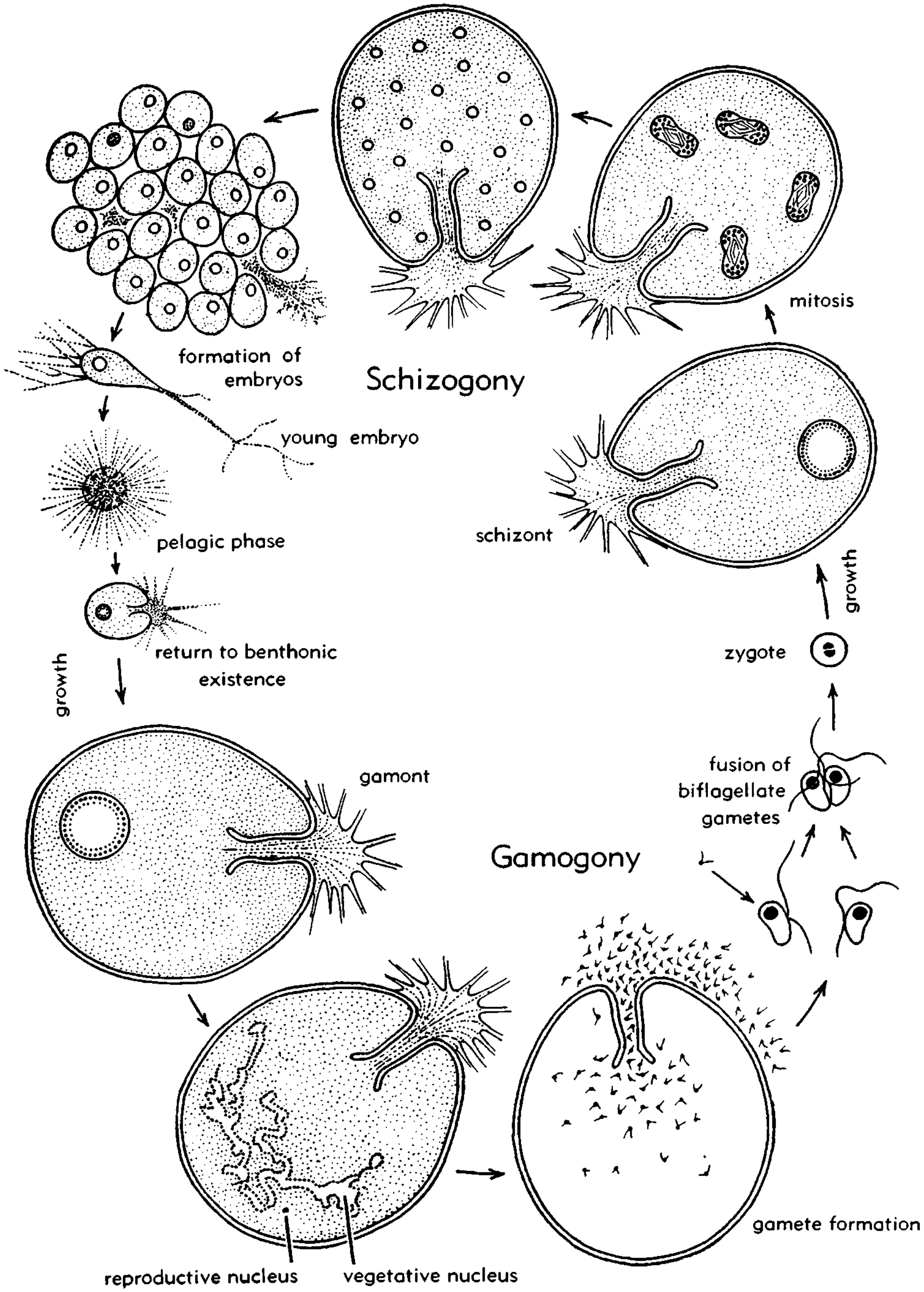

FIG. 40. Life cycle of *Iridia lucida* (*810).

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 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

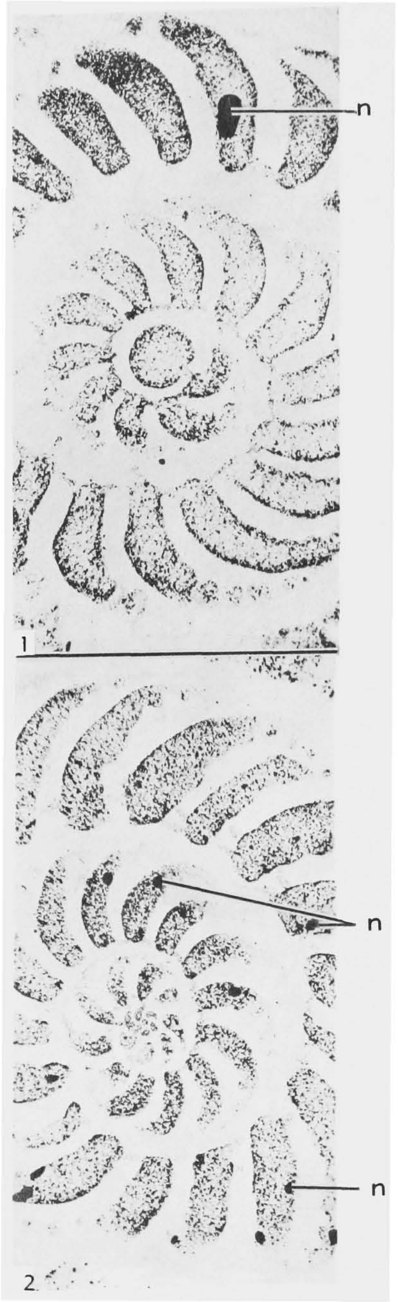

FIG. 41. Horizontal sections of *Elphidium crispum,* enlarged (*1340).——*1.* Megalospheric gamont, with large proloculus and single large nucleus (*n*).——*2.* Microspheric schizont, with minute proloculus and many nuclei (*n*).

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

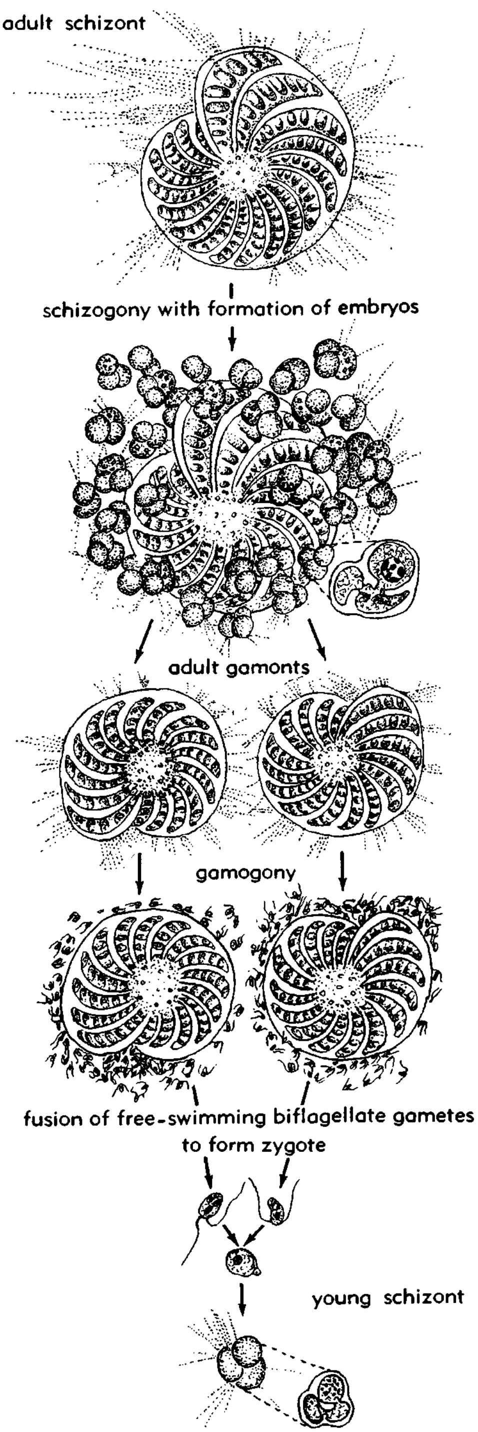

Fig. 42. Life cycle of *Elphidium crispum* (*1338).

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

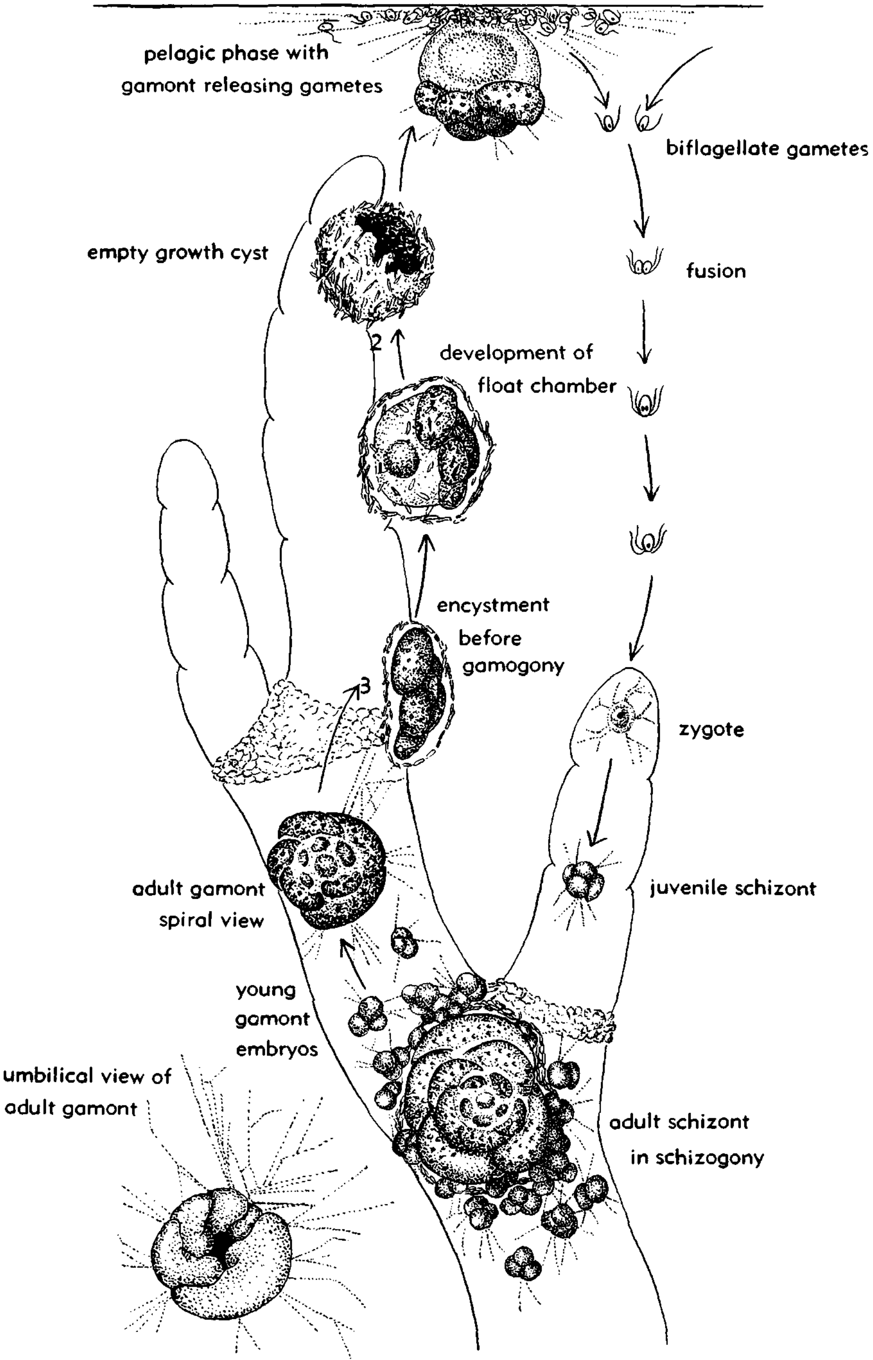

FIG. 43. Life cycle of *Tretomphalus bulloides* (*1341).

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

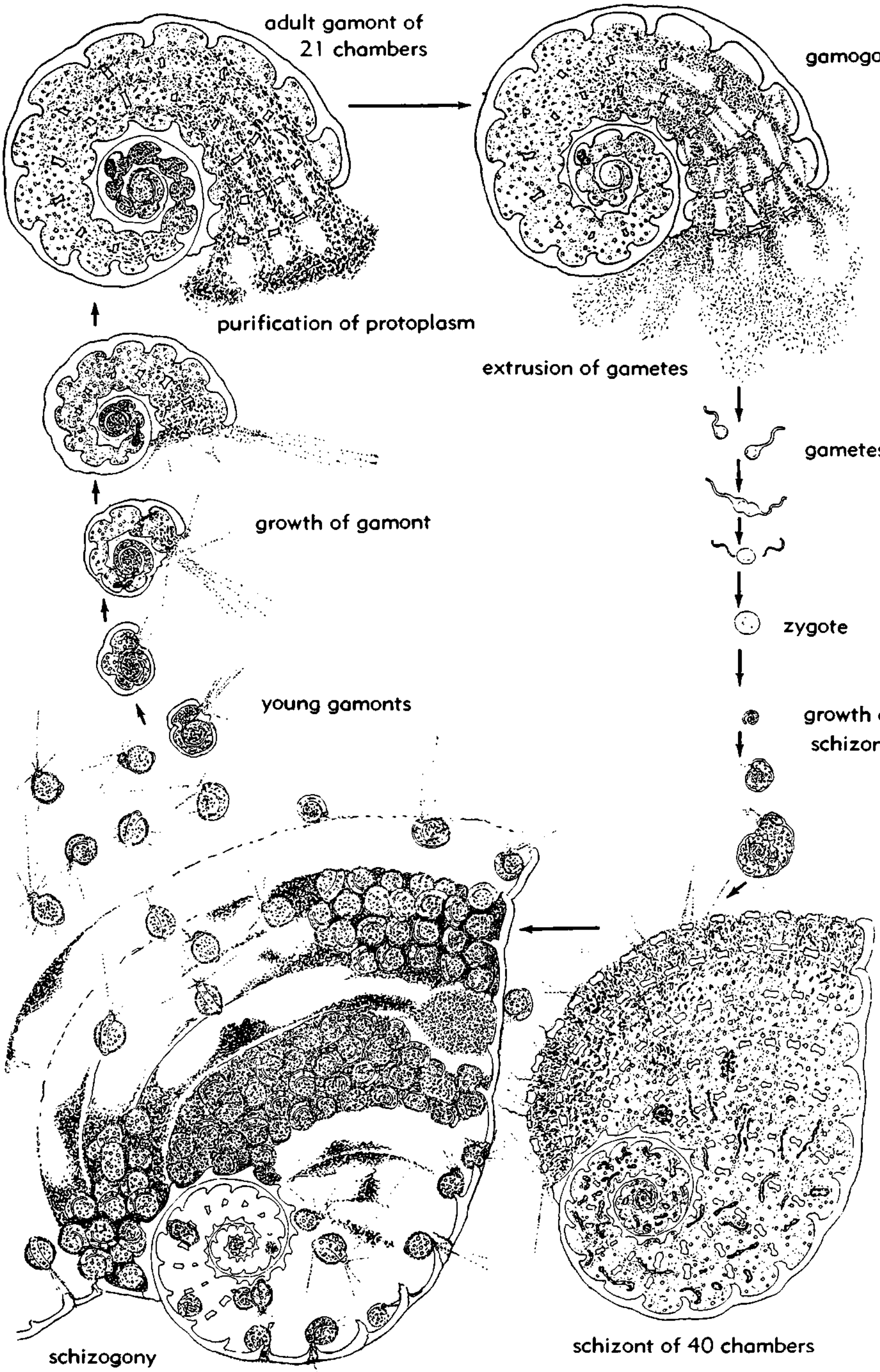

Fig. 44. Life cycle of *Peneroplis pertusus* (*2068).

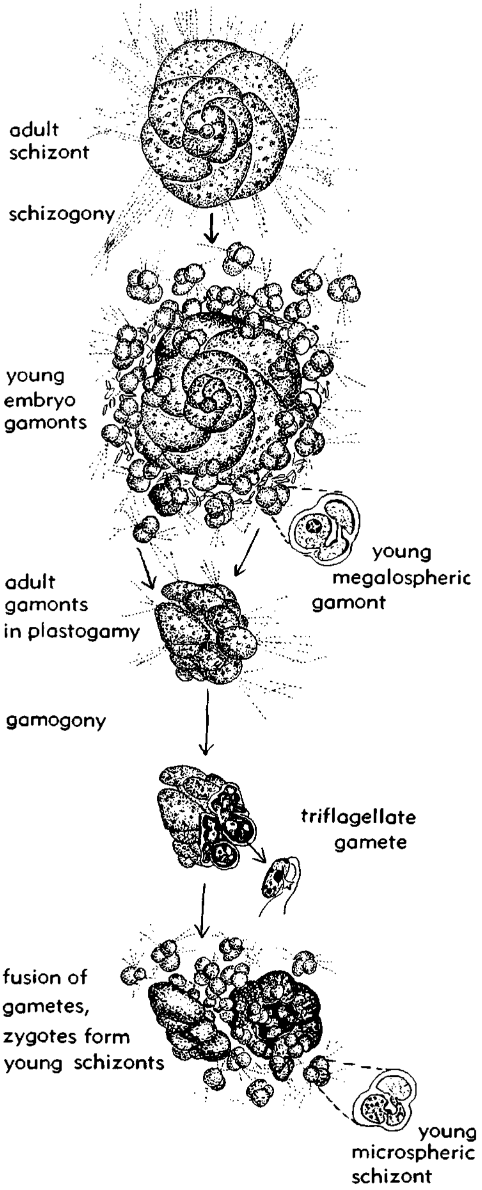

Fig. 45. Life cycle of *Glabratella patelliformis* (*1338).

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).

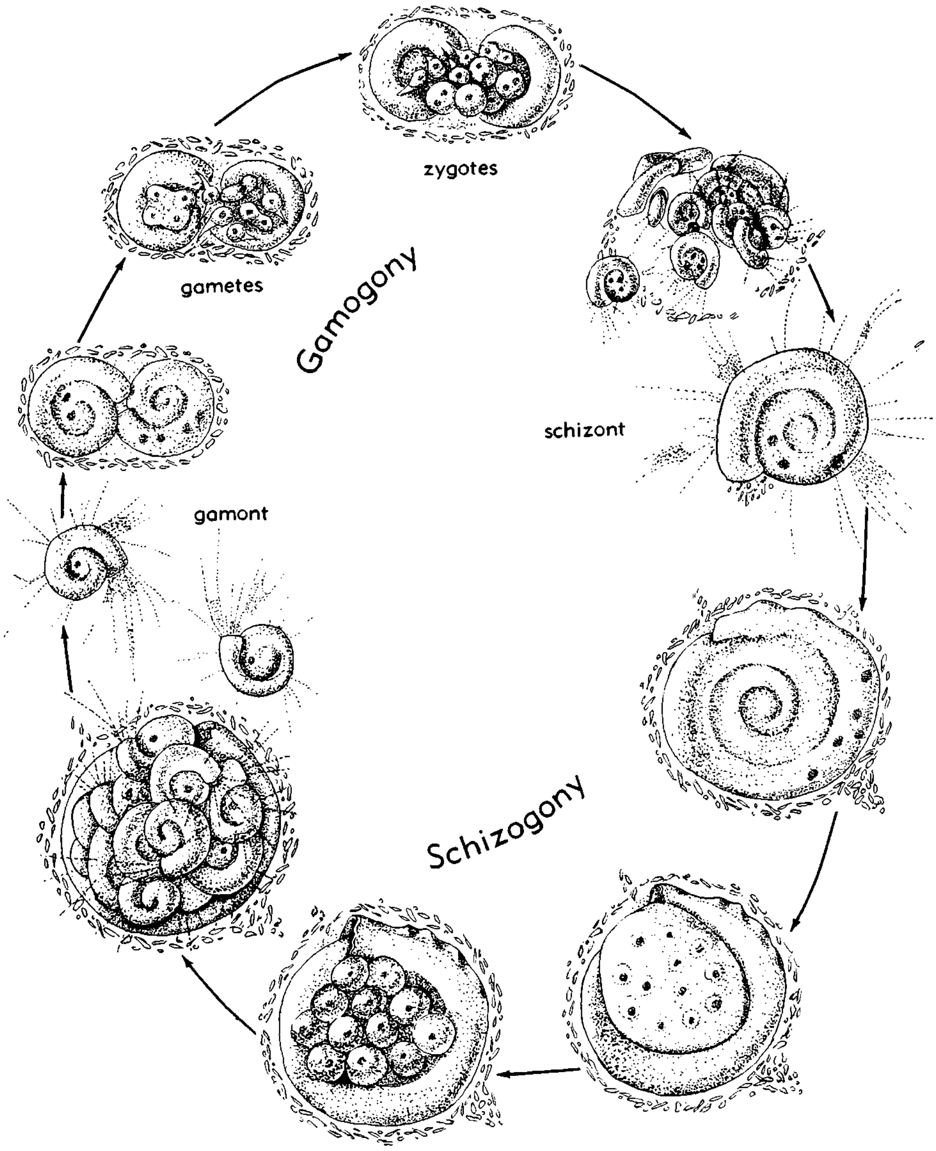

FIG. 46. Life cycle of *Spirillina vivipara* (*1337).

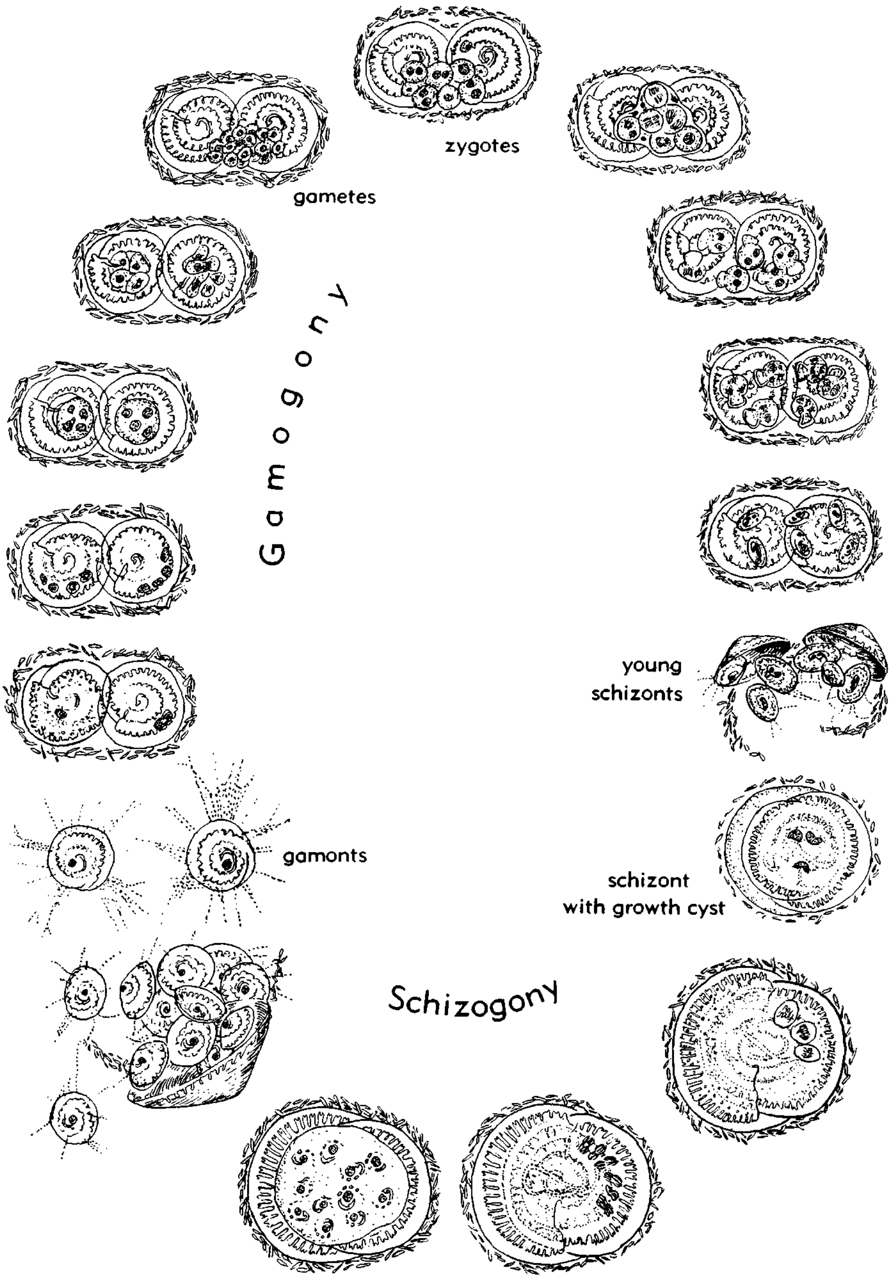

FIG. 47. Life cycle of *Patellina corrugata* (*1336).

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

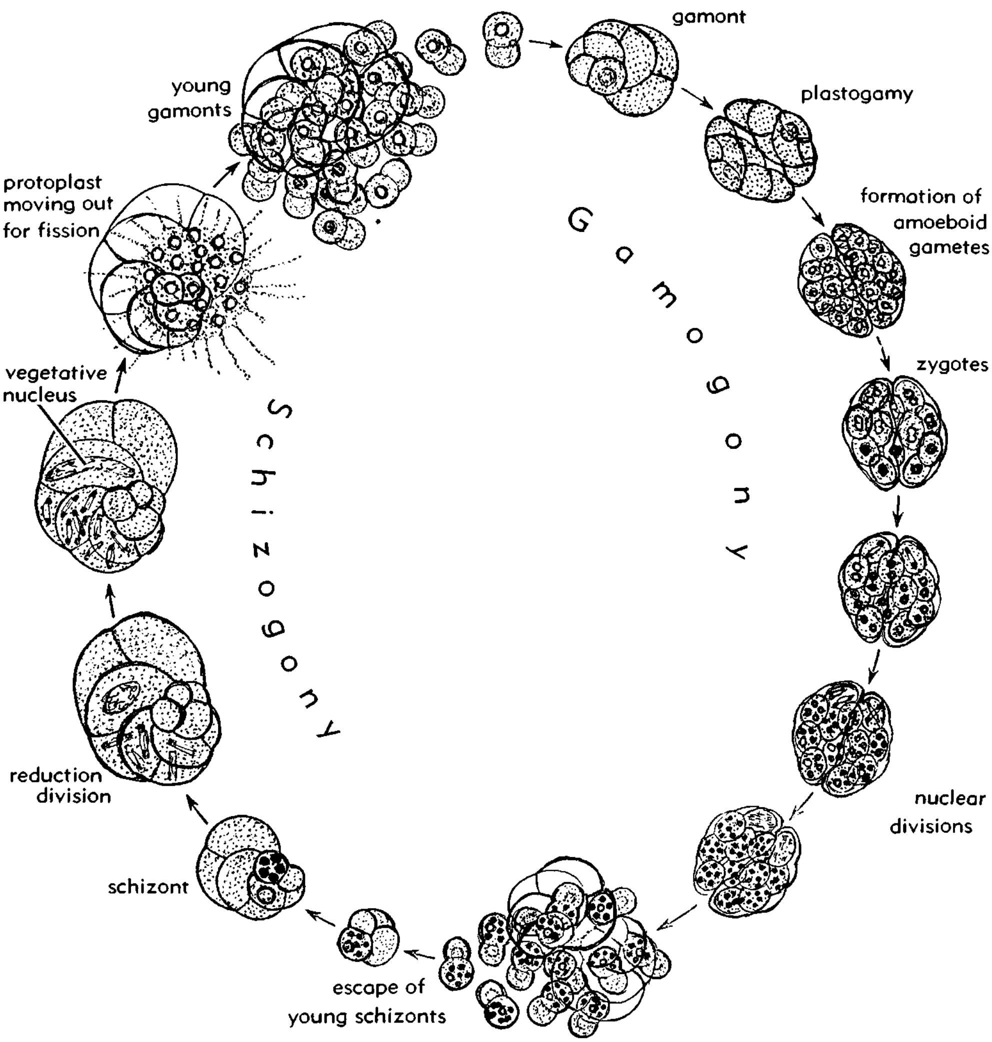

FIG. 48. Life cycle of *Rubratella intermedia* (*821).

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.

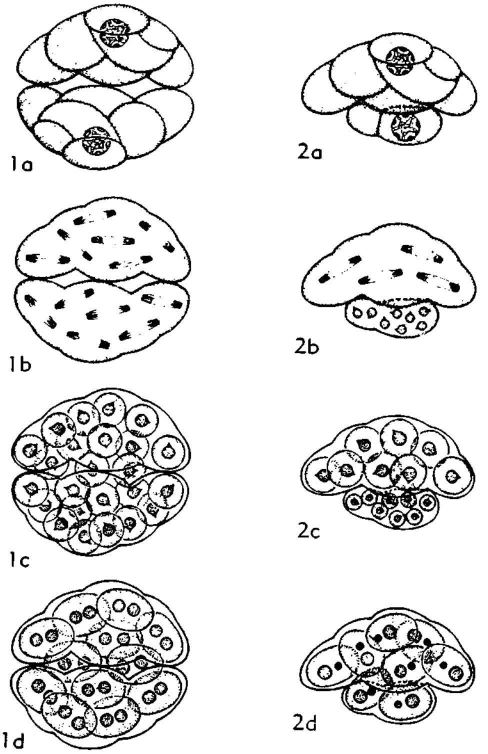

FIG. 49. Plastogamy in *Rubratella intermedia*; *1*, gamonts of similar size; *2*, gamonts of dissimilar size (*1a,2a*, pairing of gamonts; *1b,2b*, nuclear division; *1c,2c*, formation of gametes, those of unequal-sized gamonts being also dissimilar in size and with differing size of nuclei; *1d,2d*, zygotes resulting from pairing of gametes, unequal sizes of fusing nuclei demonstrating that only gametes from different tests fuse) (*821).

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.

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

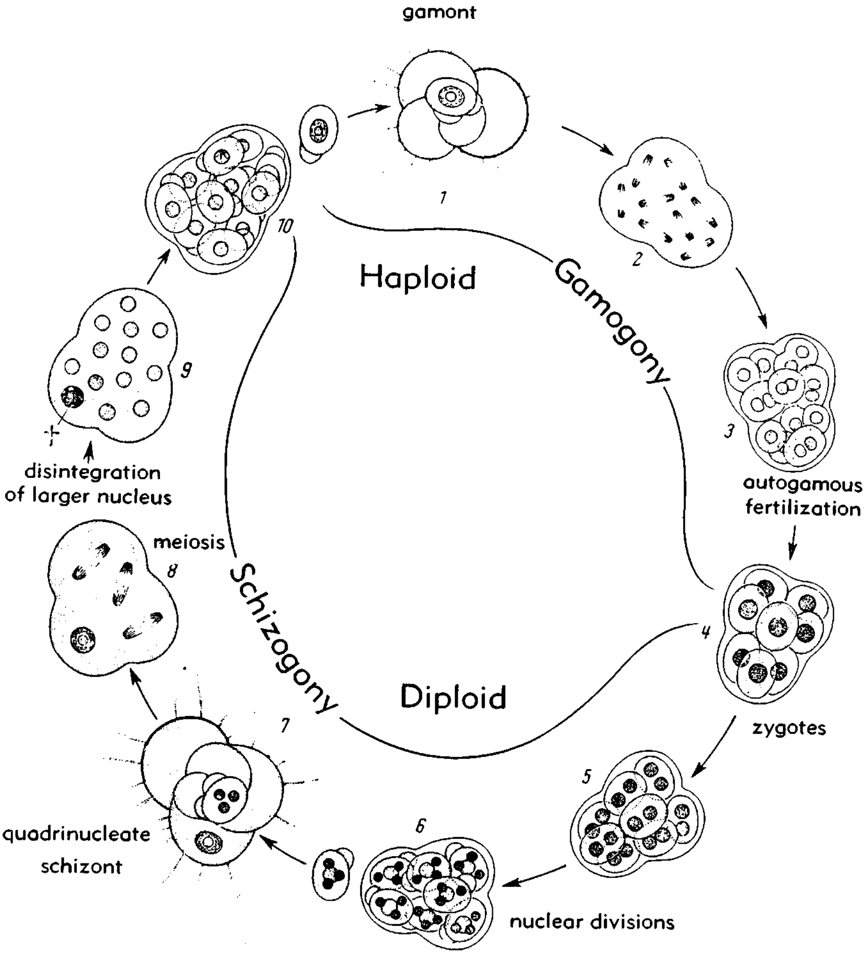

FIG. 50. Life cycle of *Rotaliella heterocaryotica* (*821).

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*).

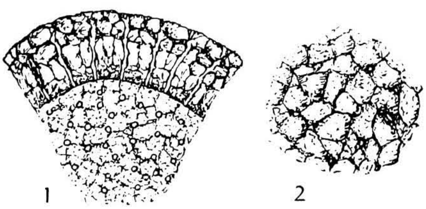

FIG. 52. Wall structure of *Textularia agglutinans* (*1075).——*1.* Fragment of wall showing internal surface of chamber with perforations at bottom and section through wall with irregular perforations, ×100.——*2.* Exterior surface of fragment showing tiny pores between sand grains, ×500.

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.

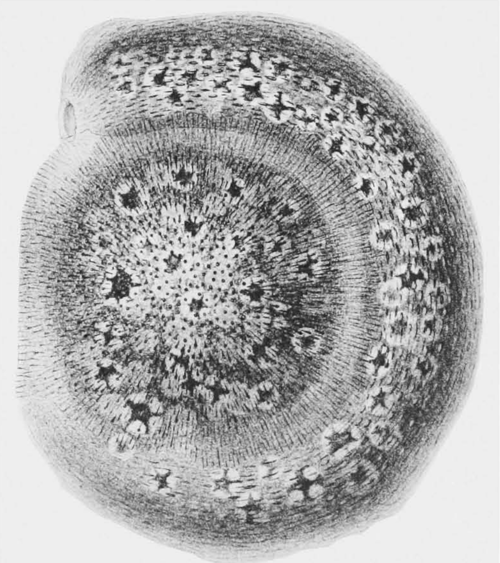

FIG. 53. Juvenile specimen of *Peneroplis pertusus* with globular, finely perforate proloculus and enrolled spiral passage, ×850 (*2068).

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, Ceratobulimininae, 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.

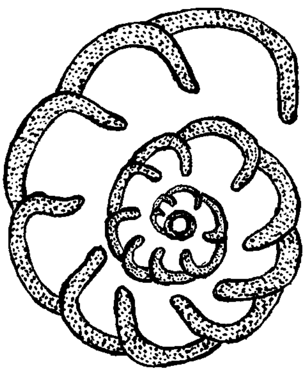

FIG. 54. Diagrammatic section of nonlamellar test (*2117).

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-

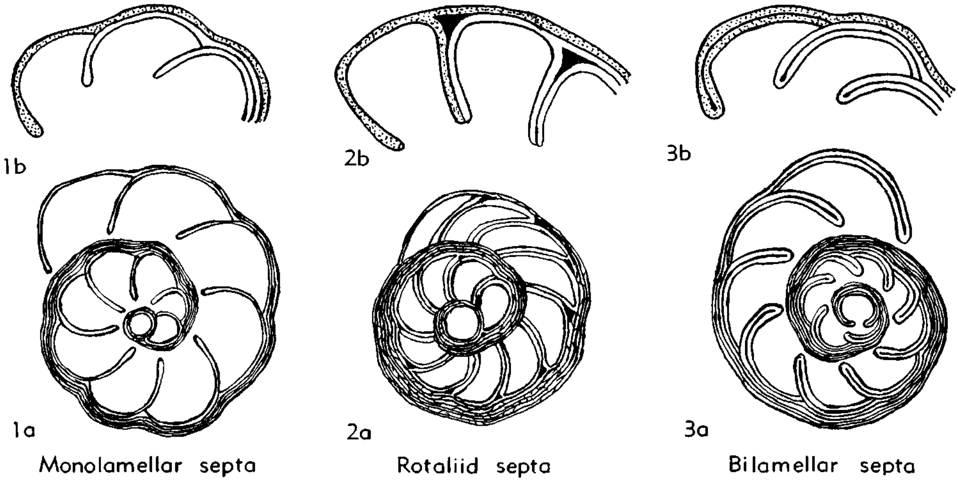

Fig. 55. Diagrammatic sections of lamellar tests.——*1a,2a,3a.* Equatorial sections showing lamellar development.——*1b,2b,3b.* Final three chambers showing their lamellar character (last added chamber and lamella indicated by stippled pattern) (*2117).

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

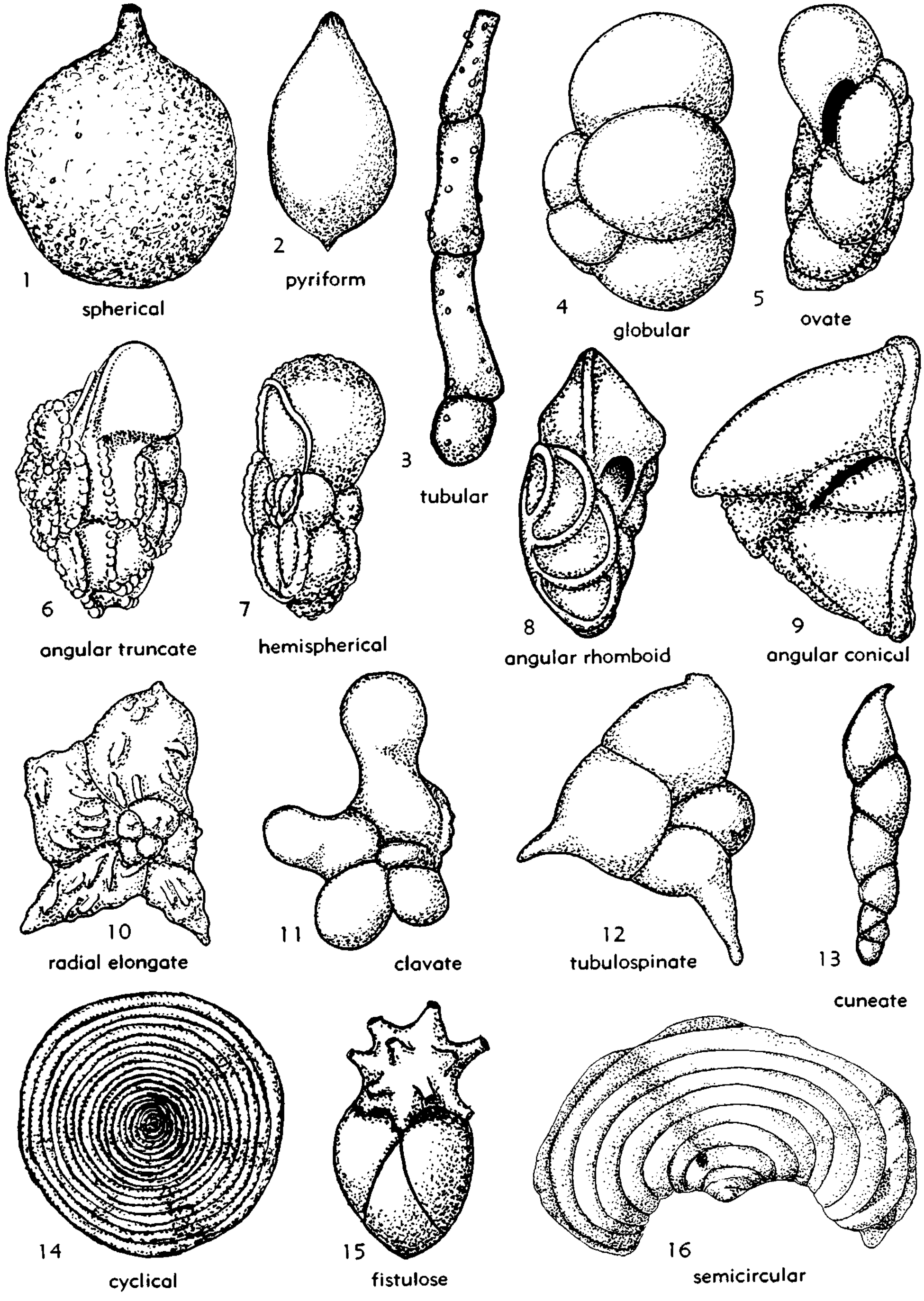

Fig. 56, *1-16*. Shapes of chambers in foraminiferal tests (*2117).

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-

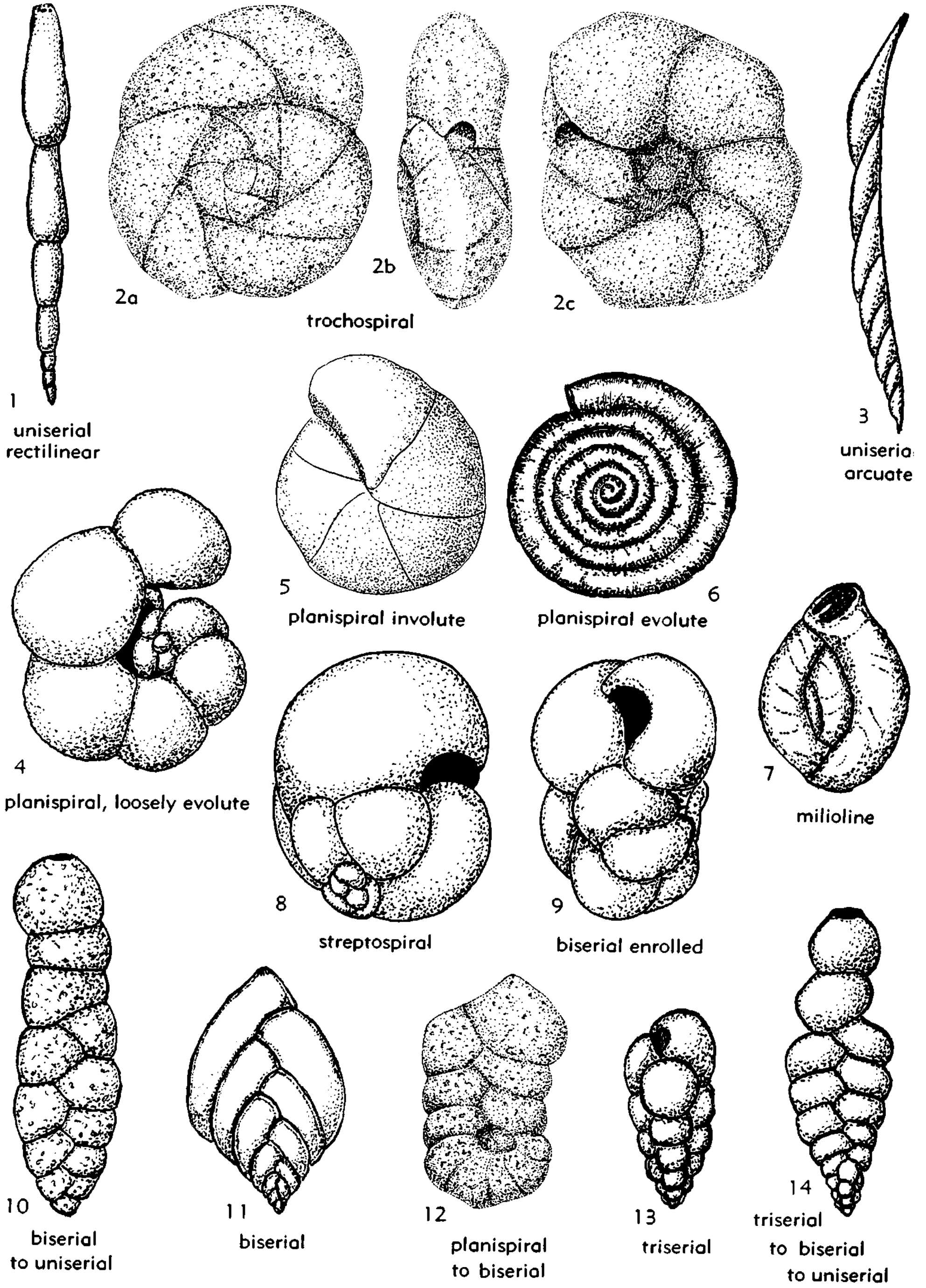

FIG. 57, *1-14*. Arrangement of chambers in foraminiferal tests (*2117).

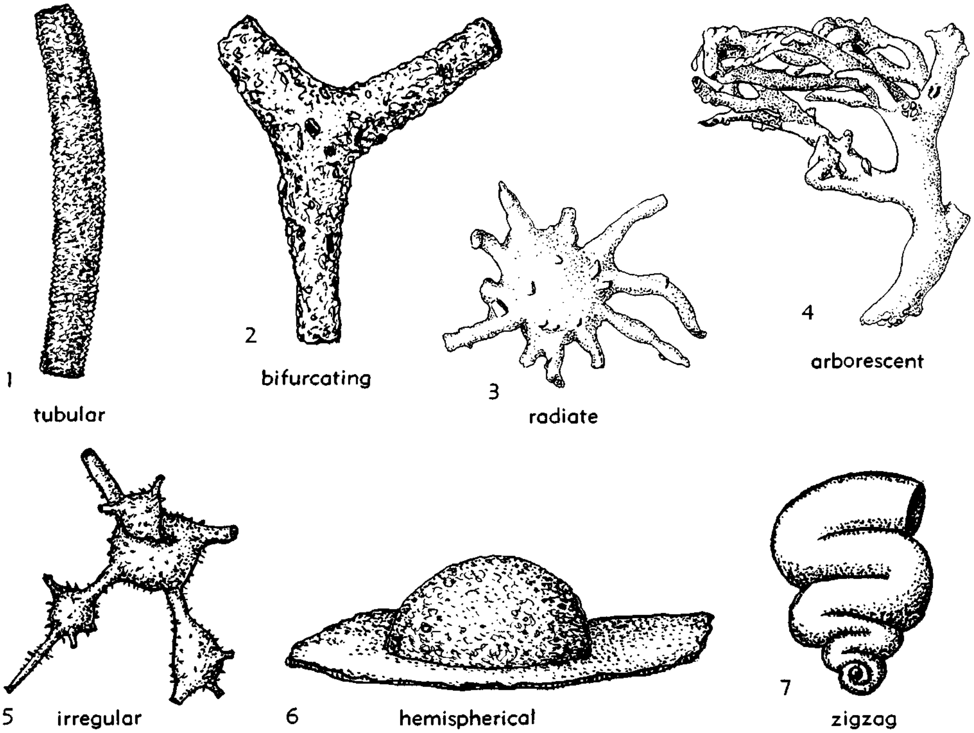

FIG. 58, *1-7*. Shapes of foraminiferal tests (*2117).

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

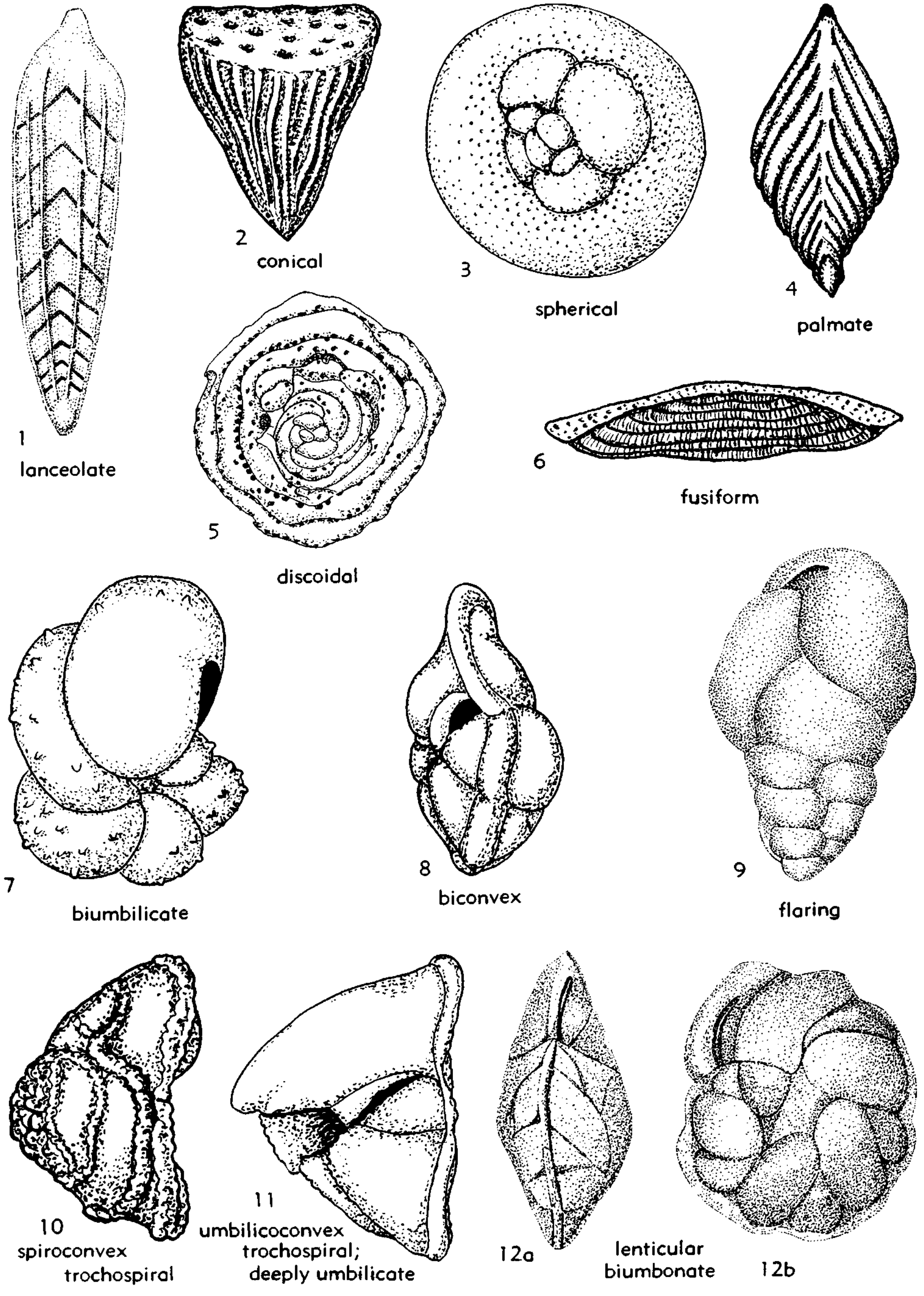

FIG. 59, *1-12.* Shapes of foraminiferal tests (*2117).

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

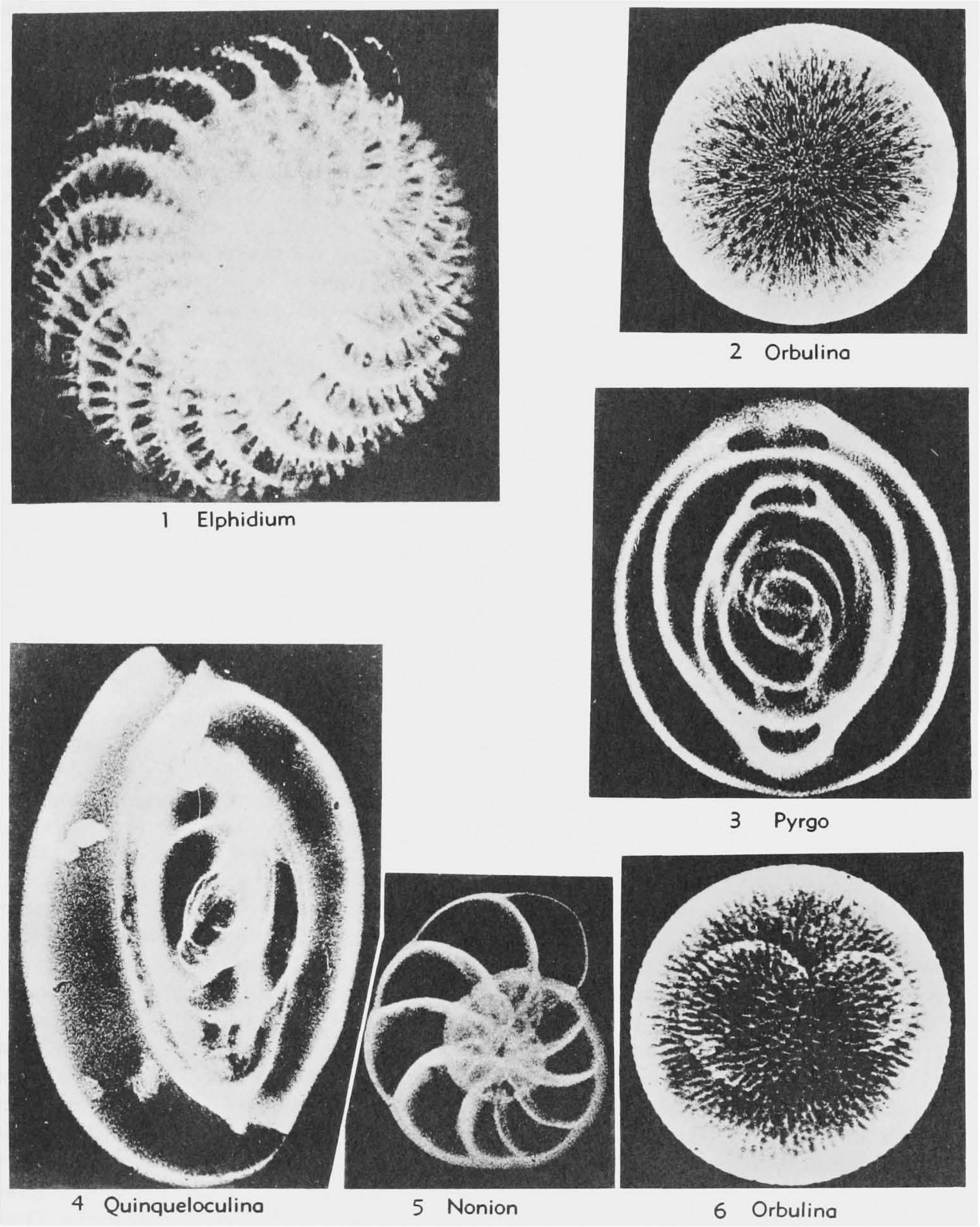
1 Elphidium
2 Orbulina
3 Pyrgo
4 Quinqueloculina
5 Nonion
6 Orbulina

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

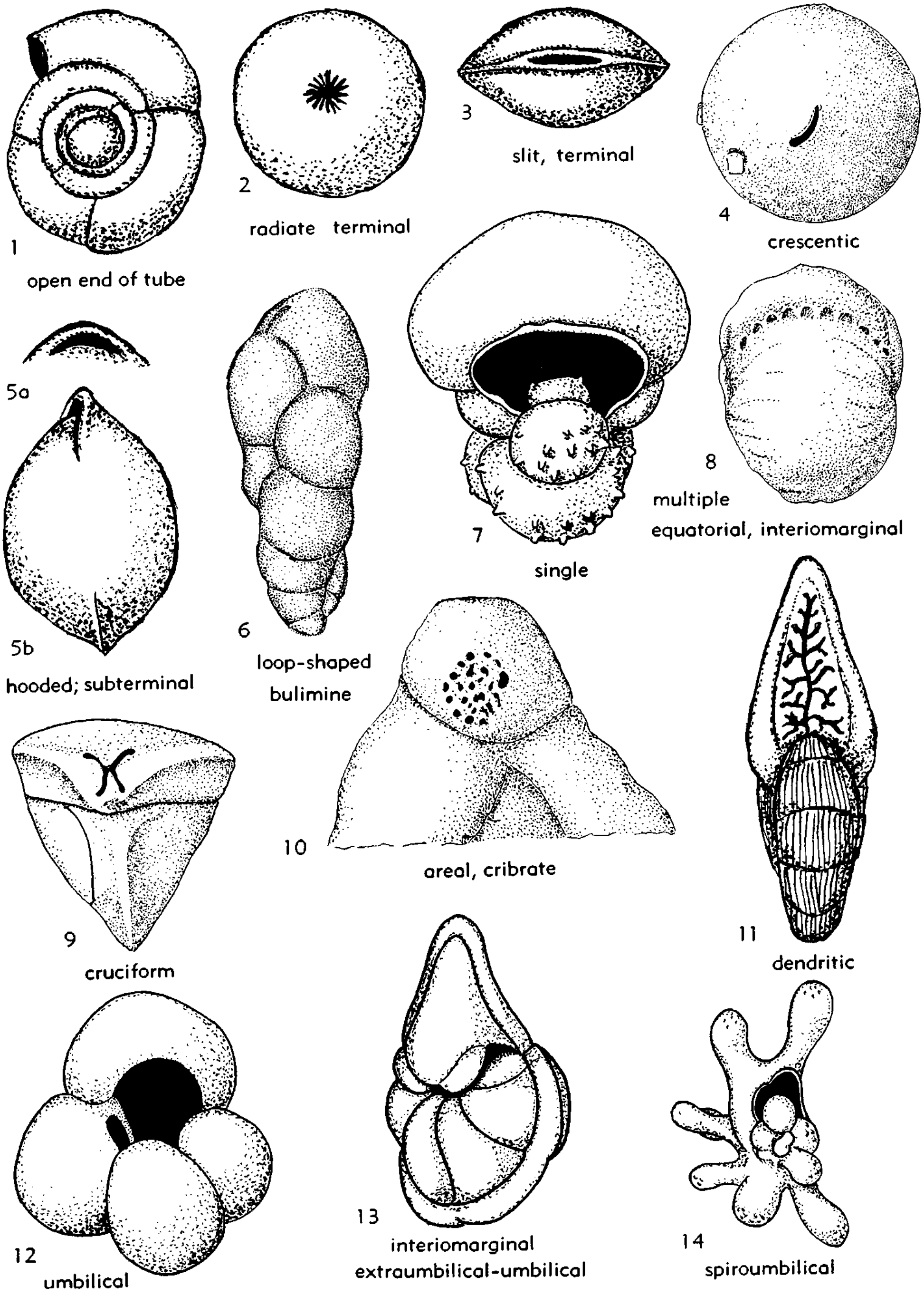

Fig. 61, *1-14*. Location and form of primary apertures in foraminiferal tests (*2117).

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.,

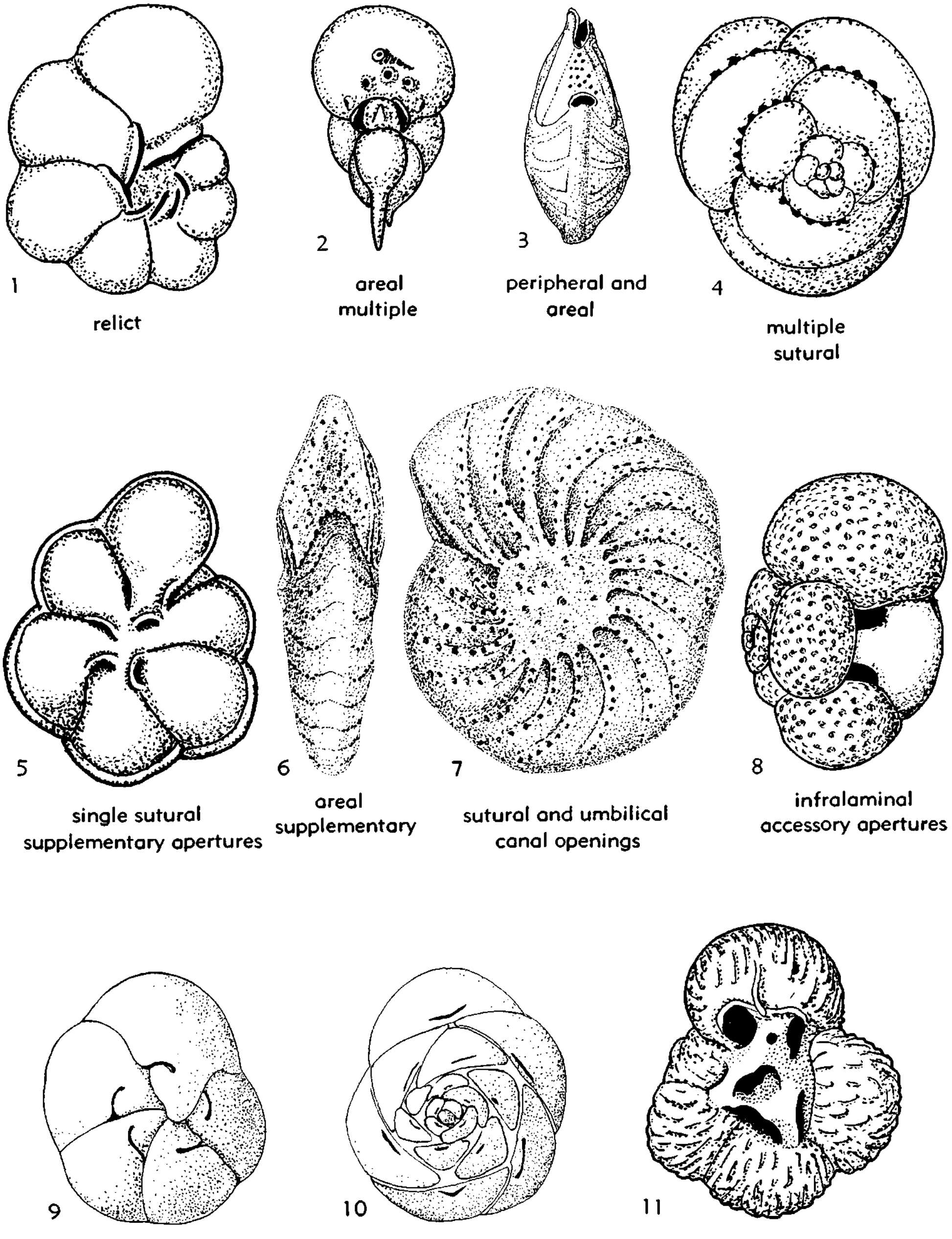

FIG. 62. Type of supplementary apertures *(1-6)* and accessory apertures *(7-11)* in foraminiferal tests (*2117).

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

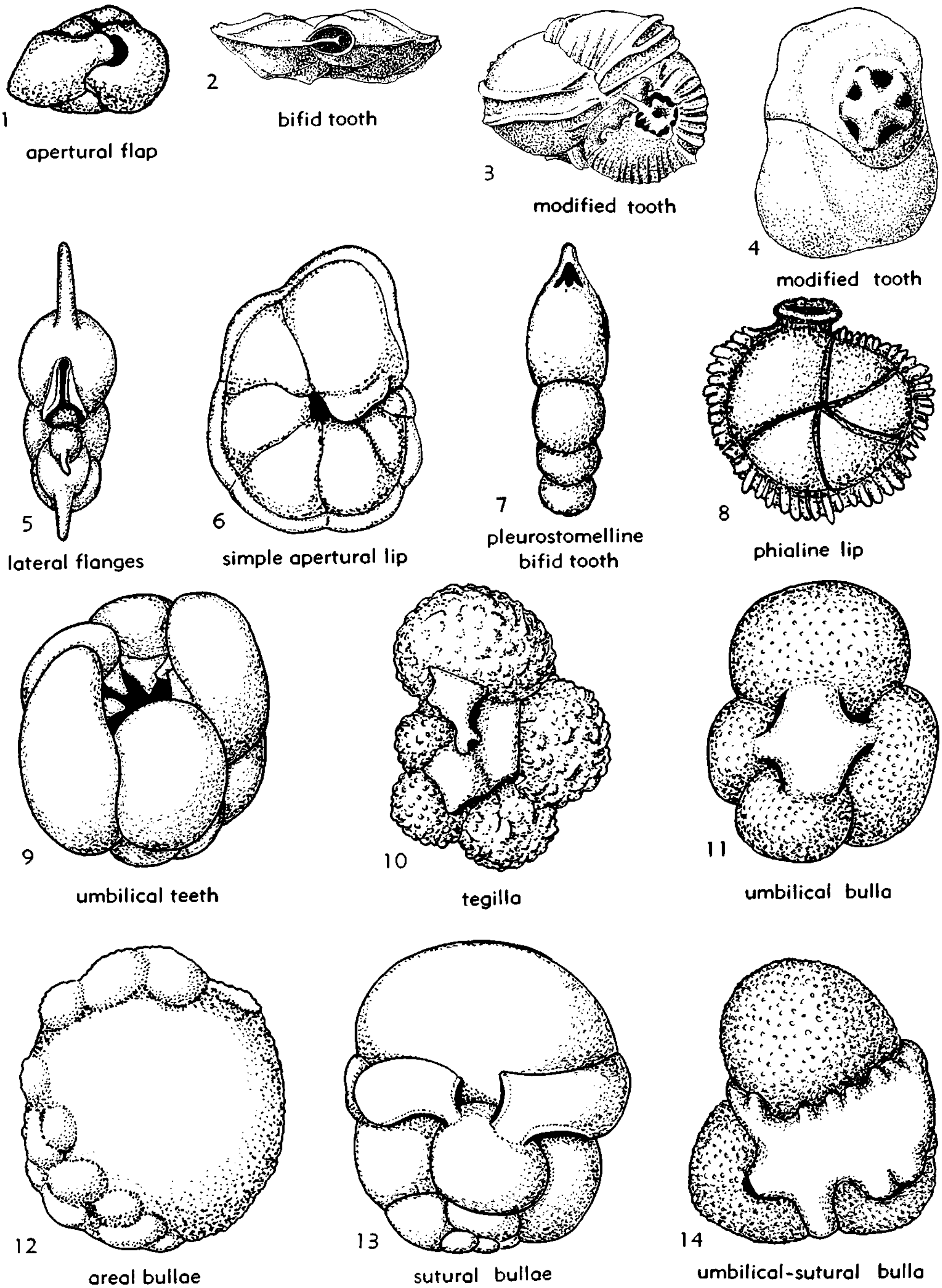

FIG. 63, *1-14*. Modifications of apertures in foraminiferal tests (*2117).

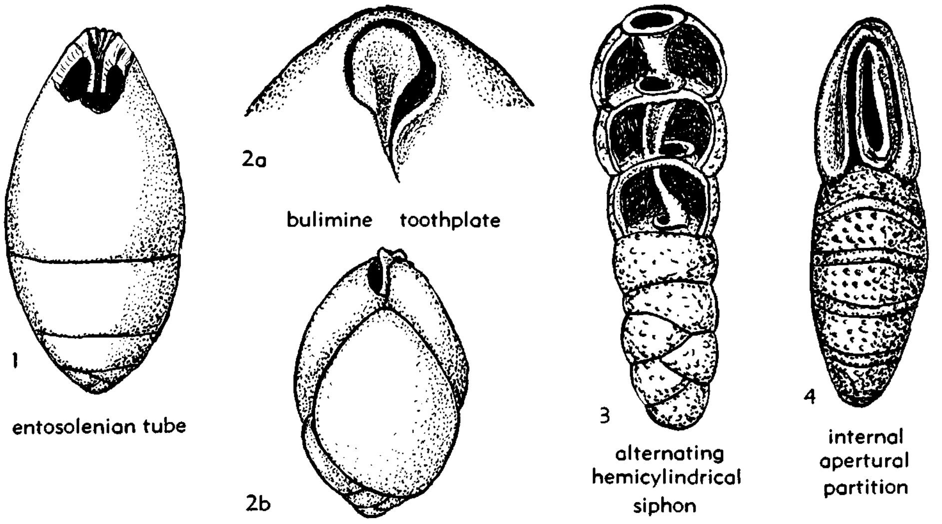

FIG. 64, *1-4*. Internal apertural modifications in foraminiferal tests (*2117).

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

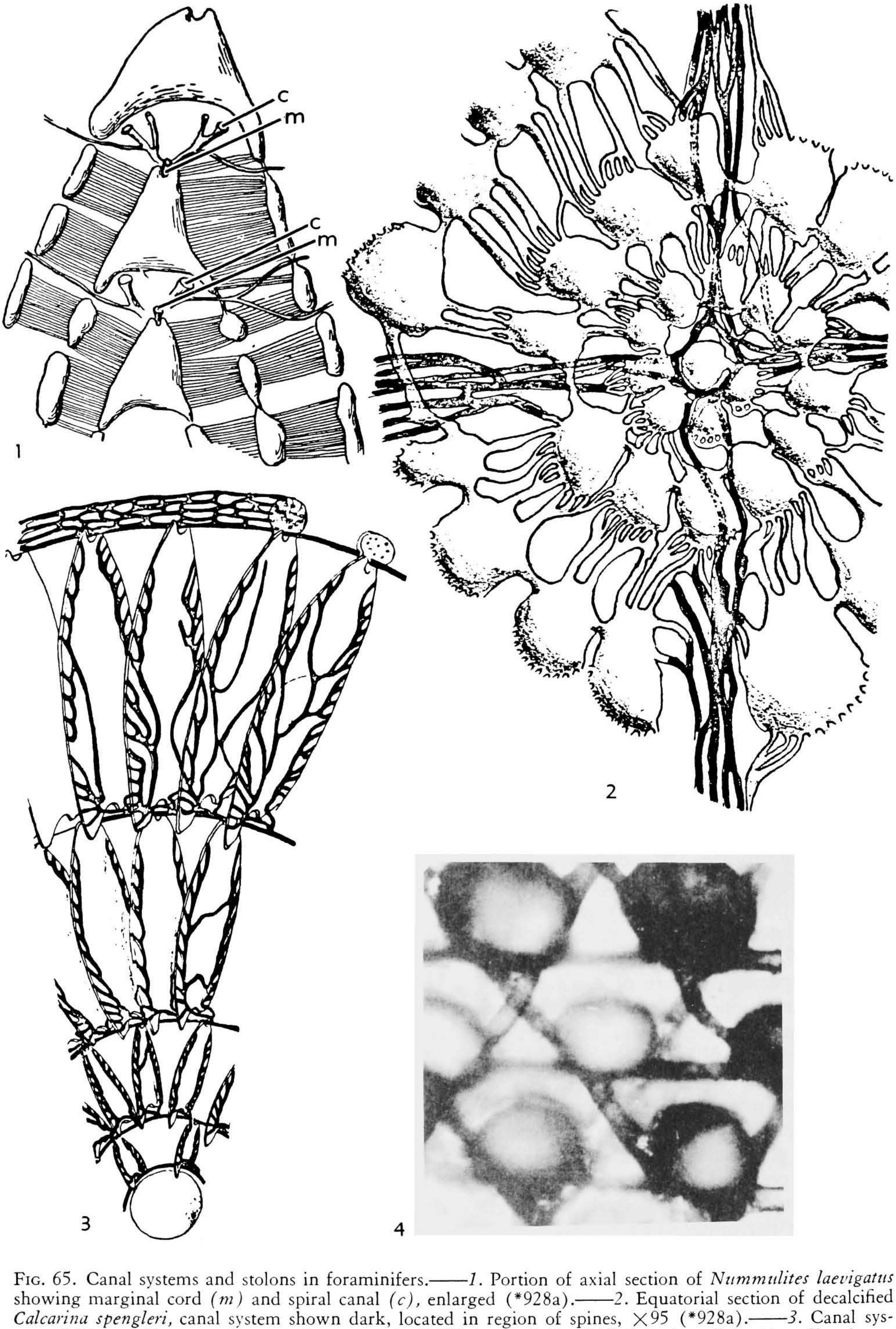

FIG. 65. Canal systems and stolons in foraminifers.——*1.* Portion of axial section of *Nummulites laevigatus* showing marginal cord *(m)* and spiral canal *(c)*, enlarged (*928a).——*2.* Equatorial section of decalcified *Calcarina spengleri*, canal system shown dark, located in region of spines, ×95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

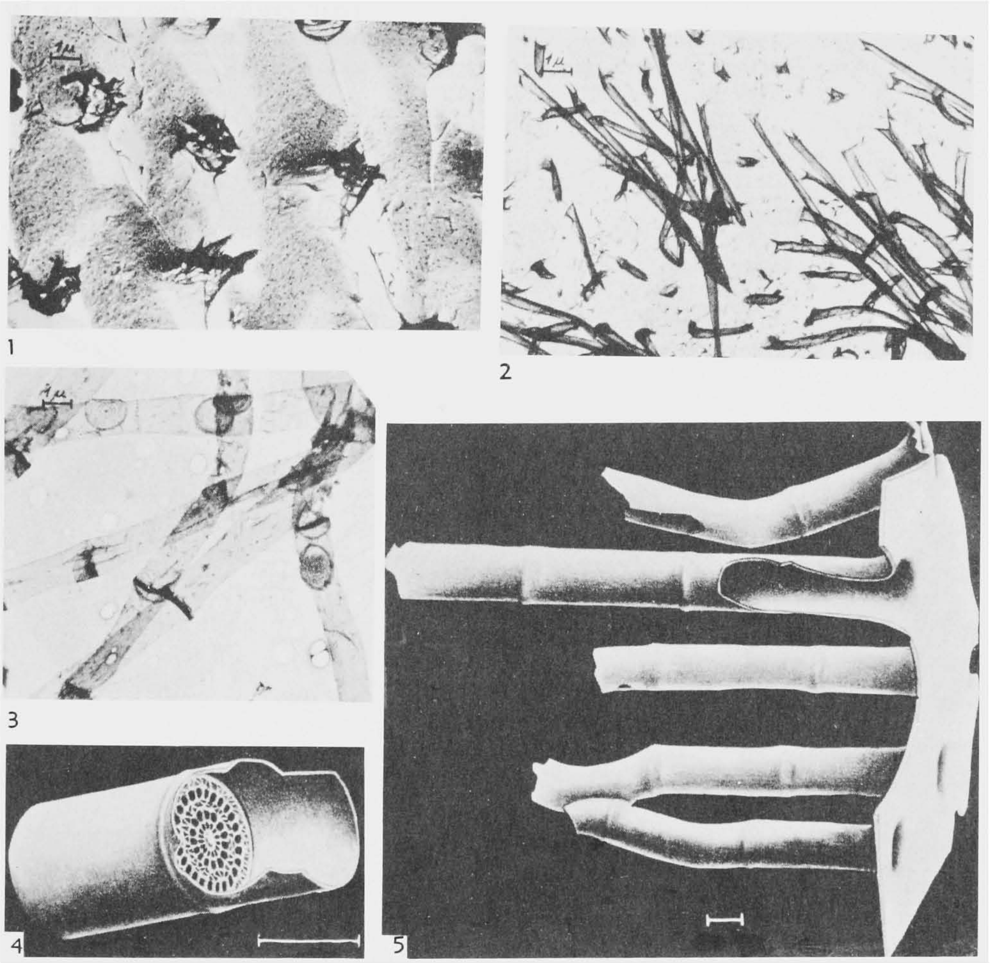

FIG. 66. Electron micrographs of decalcified foraminiferal tests and reconstruction of pore canals and sieve plates.——*1.* Organic wall layer.——*2.* Organic canals.——*3.* Decalcified specimen showing pseudochitinous lining of pores and regularly spaced sieve plates, all ×4,000.——*4.* Reconstruction of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

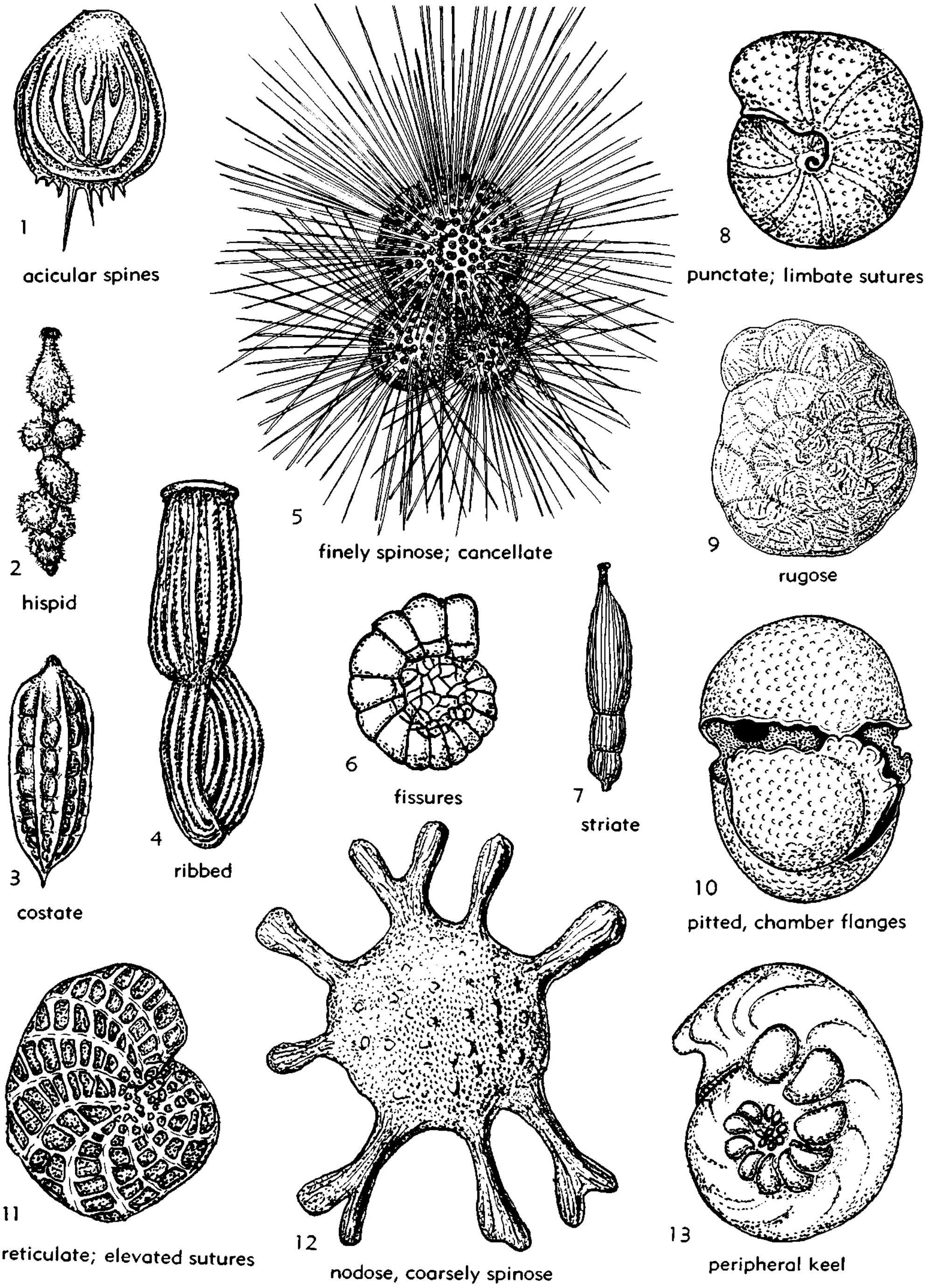

FIG. 67, *1-13*. Ornamentation of foraminiferal tests (*2117).

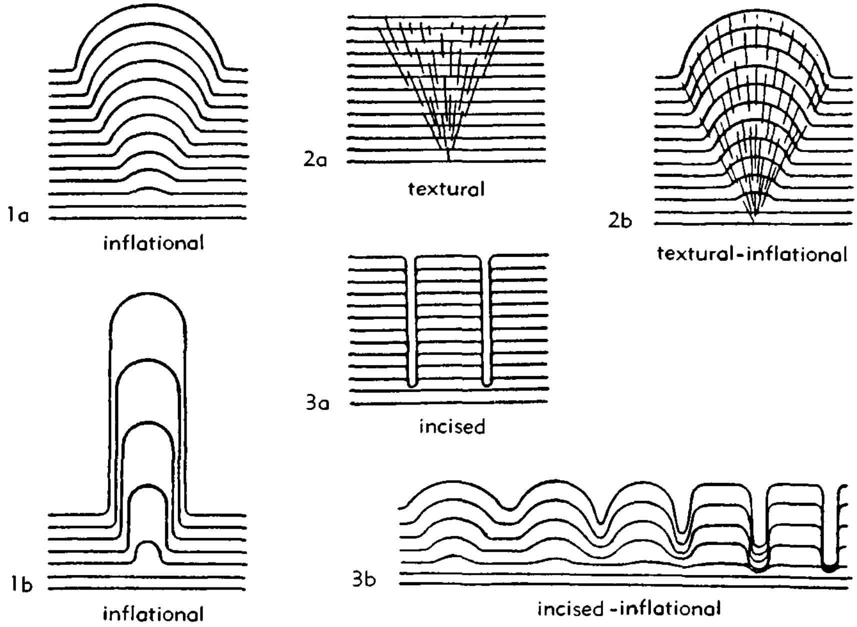

Fig. 68. Development of pillars in foraminiferal tests.——*1a,b*. Inflational pillars.——*2a,b*. Textural pillars.——*3a,b*. Incised pillars (*1803).

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.

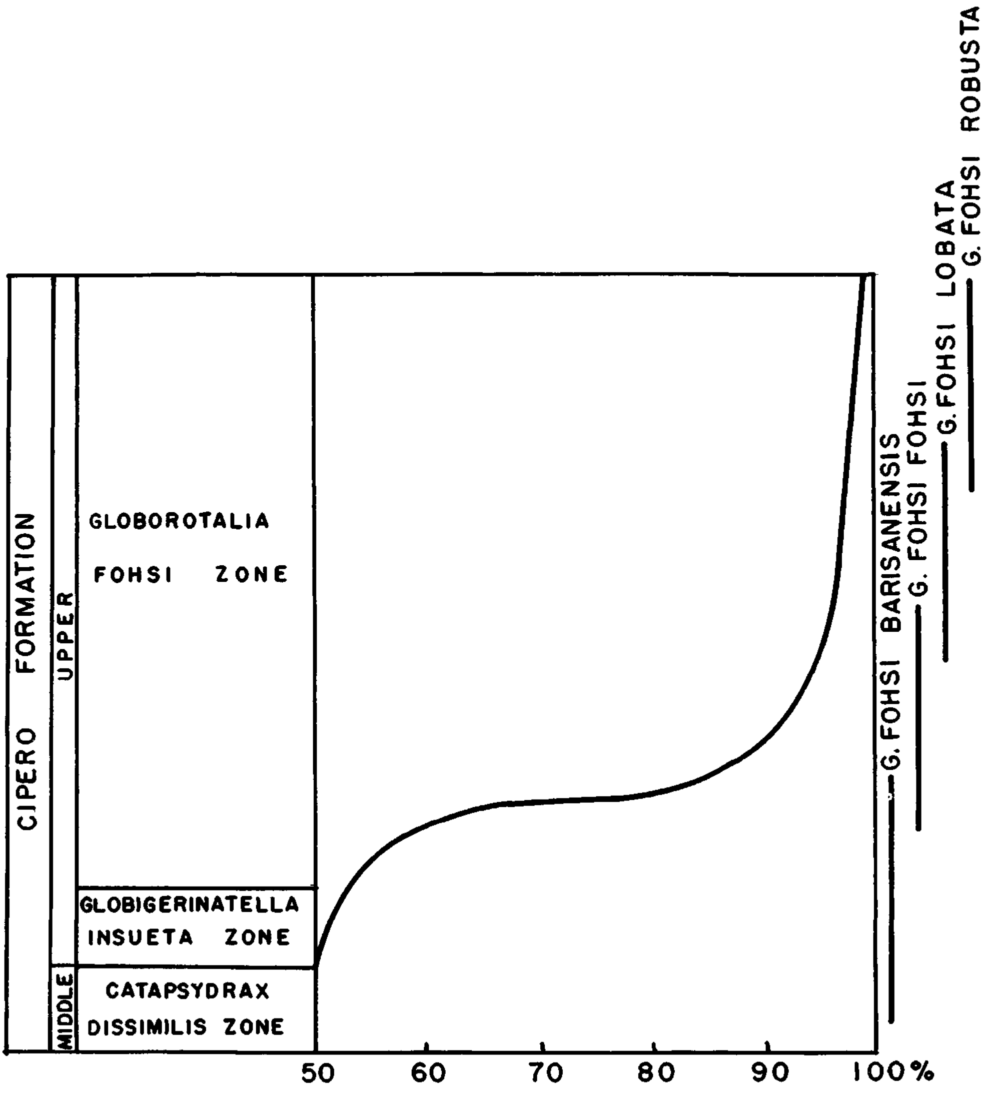

FIG. 69. Percentages of sinistrally coiled *Globorotalis fohsi* in the Miocene of Trinidad, showing change from random to dominantly sinistral tests with lapse of geologic time (*164).

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

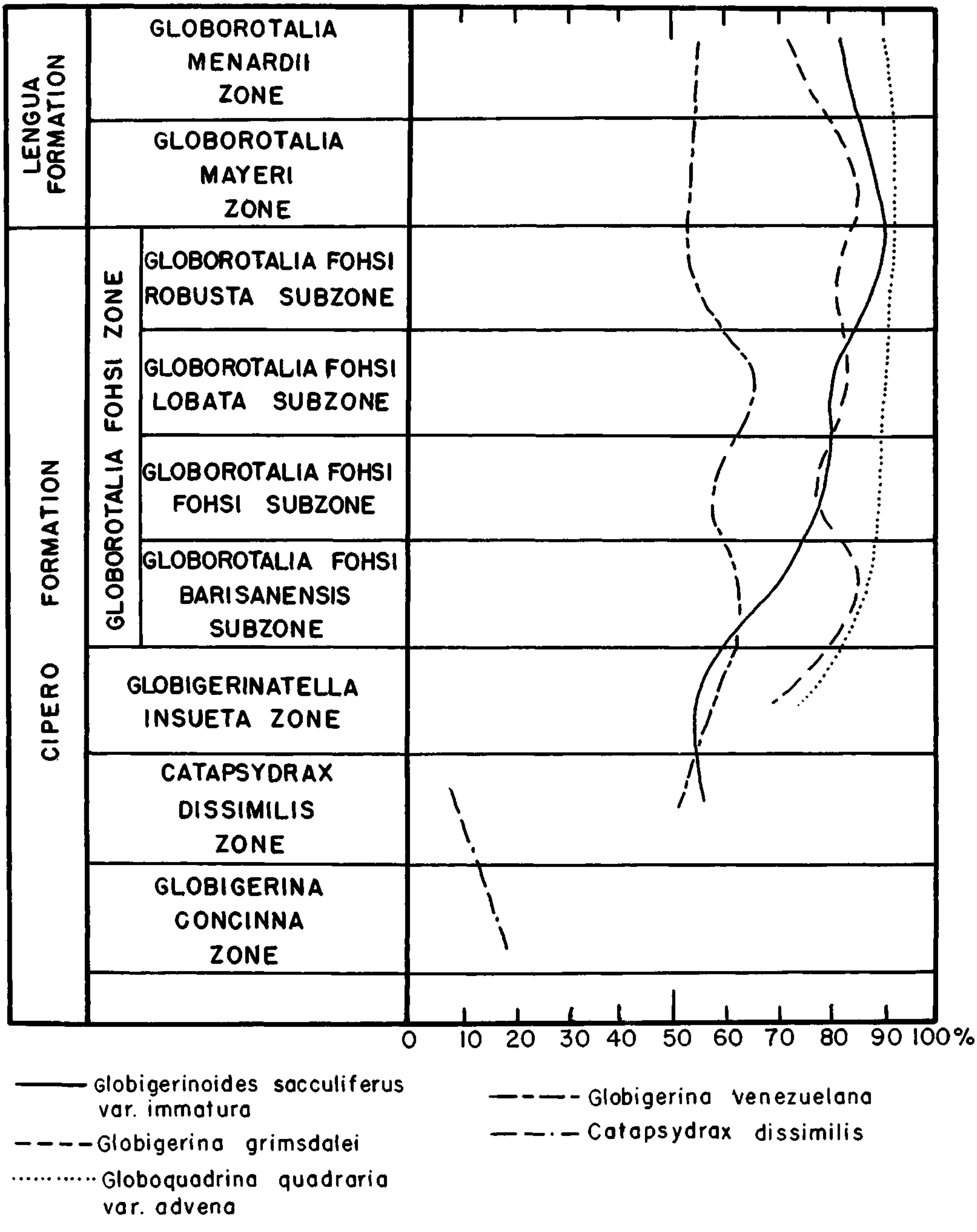

FIG. 70. Percentage of sinistrally coiled globigerinid tests in Oligocene-Miocene deposits (*164).

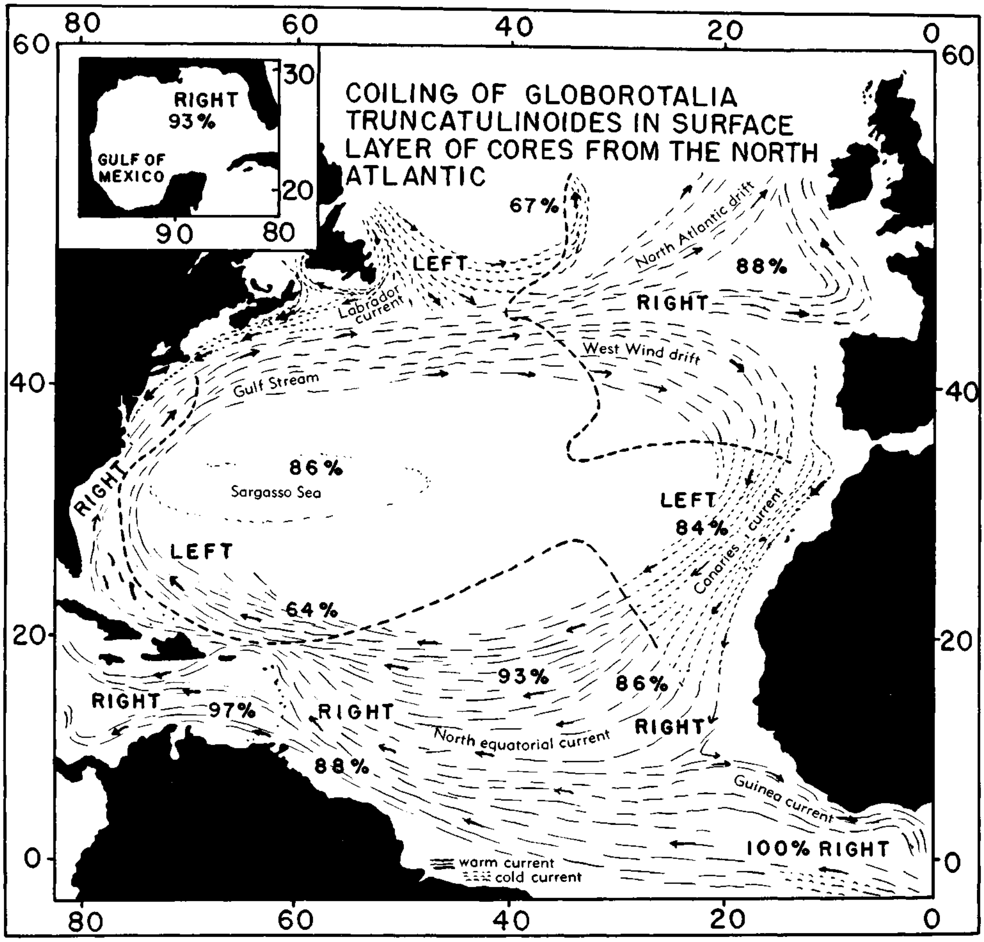

Fig. 71. Provinces of living *Globorotalia truncatulinoides* defined by distribution of dominantly sinistral- and dextral-coiled tests, respectively. Warm currents (solid lines) and cold currents (dotted lines) have been added to indicate possible influencing factors (*708, modified).

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-

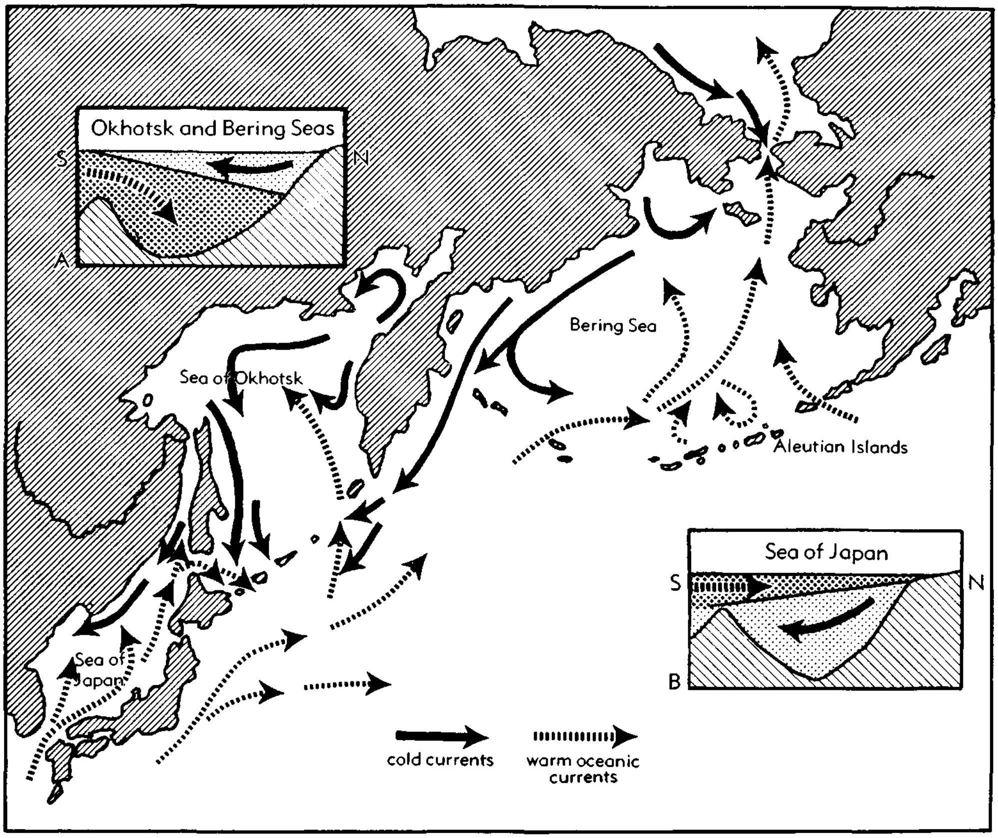

FIG. 72. Distribution of warm and cold waters in Sea of Okhotsk and Bering Sea, with inset figures indicating vertical interchange of warm-water (heavy stippled pattern) and cold-water (light stippled pattern) masses in the Okhotsk-Bering Sea areas *(A)* and Sea of Japan area *(B)* (P. V. Ushakov in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

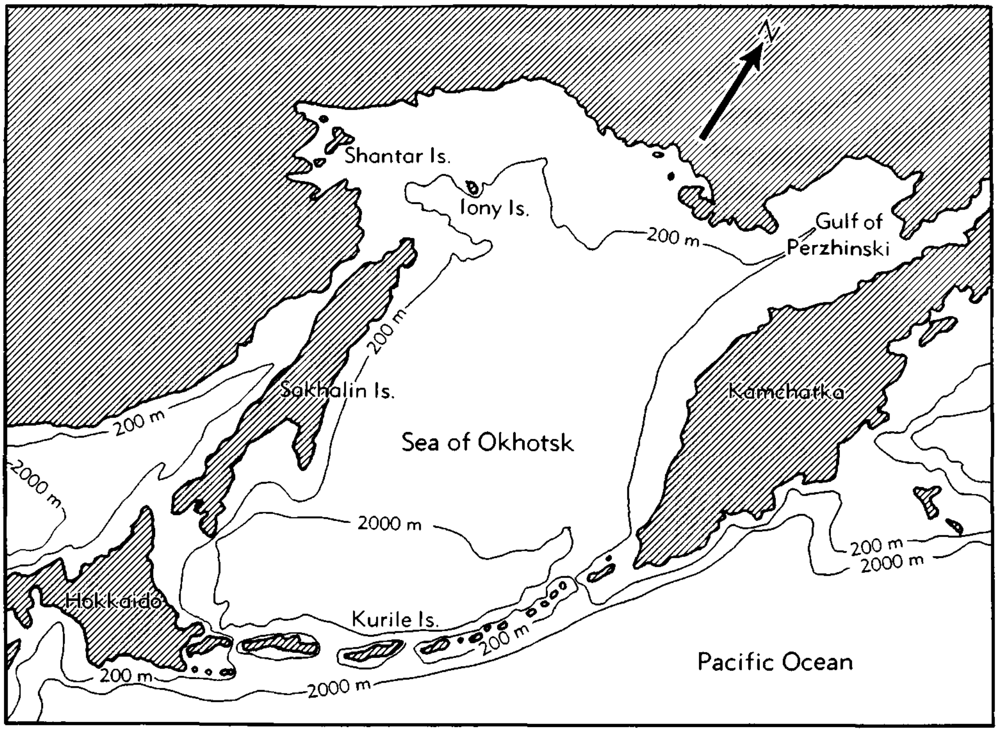

FIG. 73. Generalized water depths in Sea of Okhotsk, for comparison with distribution of faunal zones (Fig. 74) (*2117).

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.

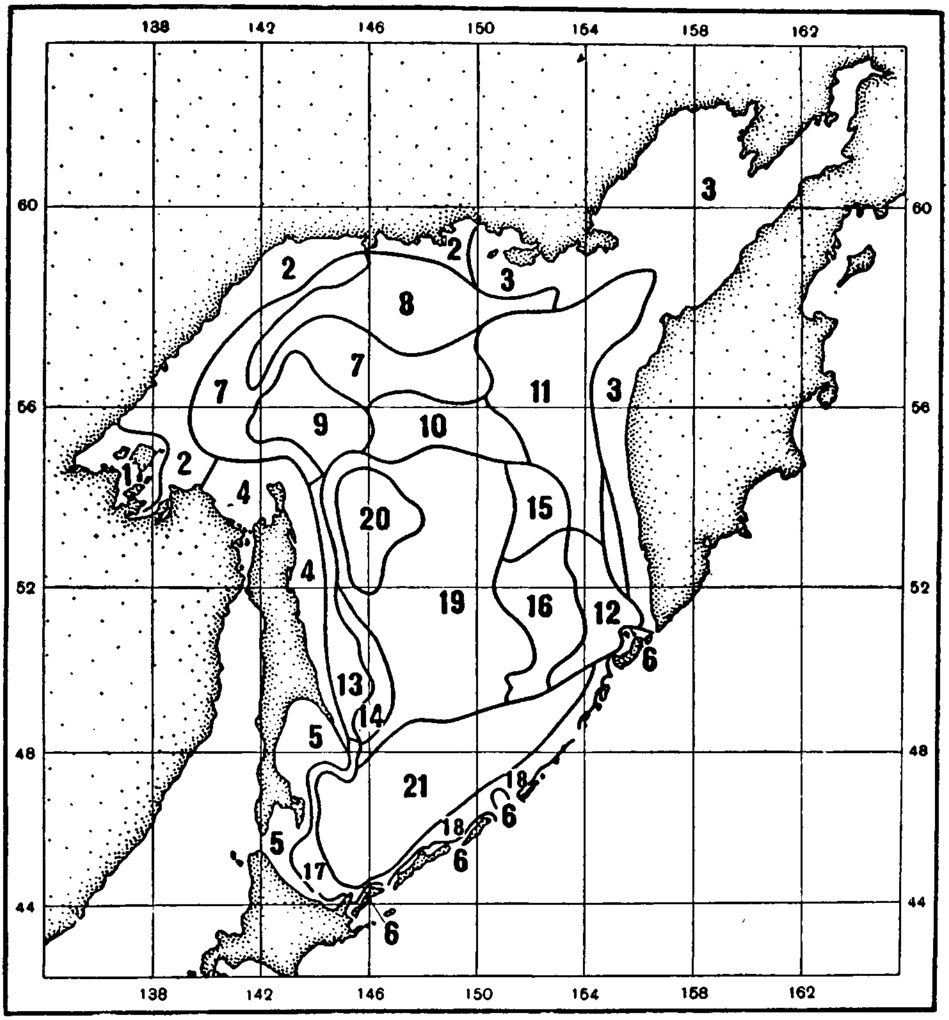

FIG. 74. Distribution of faunal assemblages in Sea of Okhotsk (*1617).

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

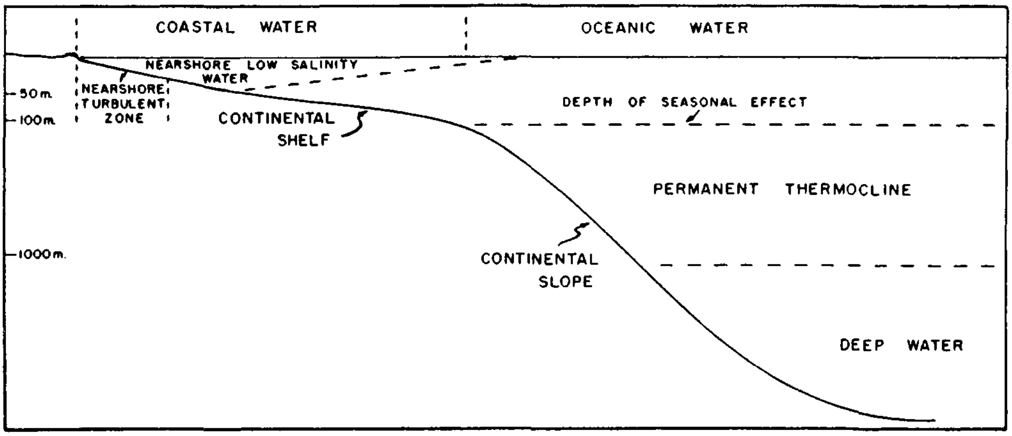

FIG. 75. Classification and distribution of coastal and oceanic waters near area of high runoff from land (*1454).

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

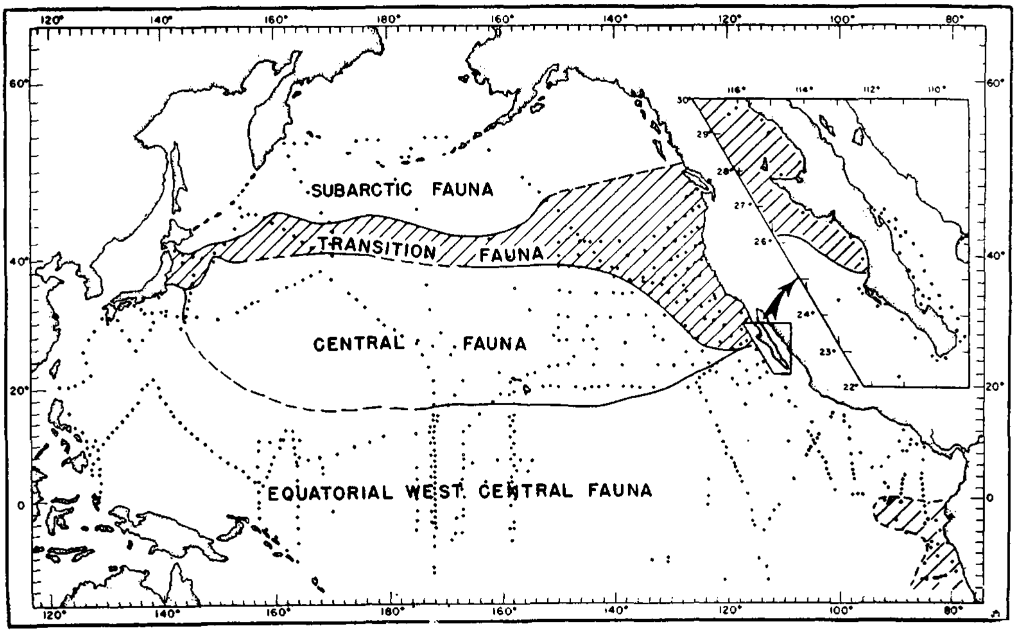

FIG. 76. Generalized distribution of planktonic assemblages of organisms in central and northern Pacific region (extent of sampling indicated by dots) (*185).

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.

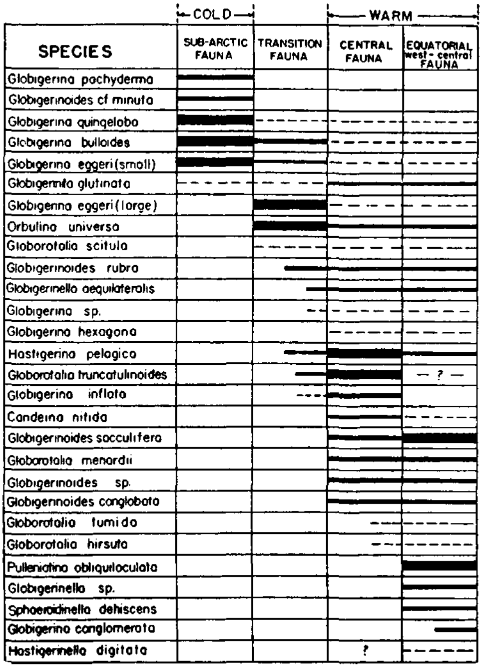

Fig. 77. Generalized distribution of planktonic foraminifers showing composition of assemblages in warm, transitional, and cold environments (*185).

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

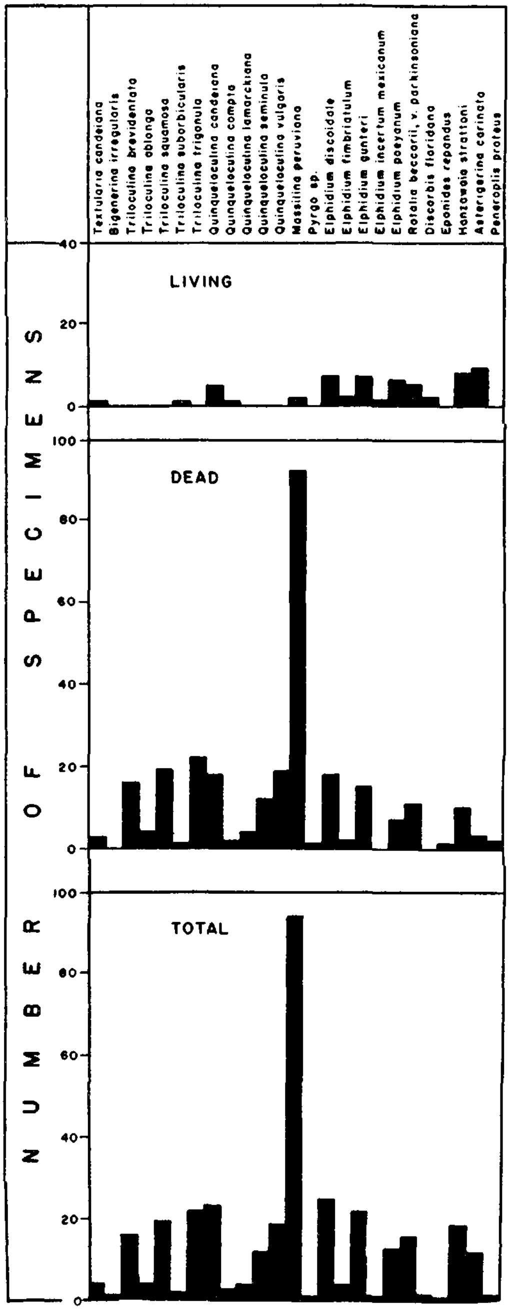

FIG. 78. Histograms showing foraminiferal populations on sandy shell bank in northwestern Gulf of Mexico. The large numbers of dead *Massilina peruviana* and other miliolids suggest post-mortem transportation of tests (*1733).

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

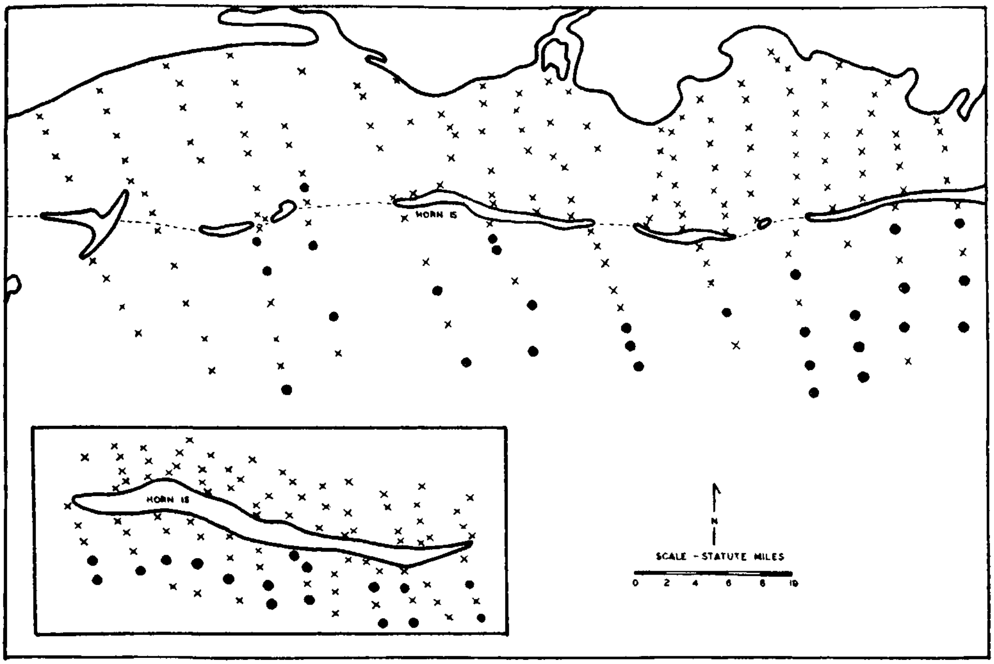

Fig. 79. Occurrence of planktonic and benthonic foraminifers in Mississippi Sound (blackened circles indicating samples that contain planktonic species and crosses those that contain only benthonic species). Planktonic forms are restricted to open Gulf areas, since the barrier islands effectively prevent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

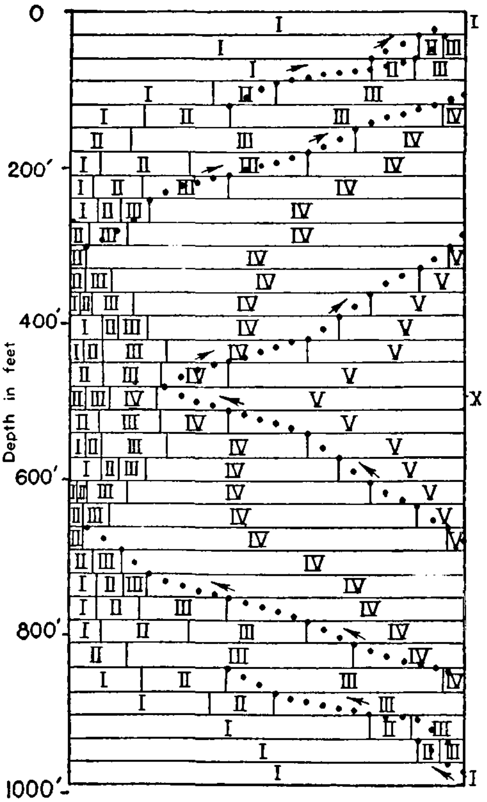

Fig. 80. Hypothetical marine cycle shown by depth oscillation chart. [Explanation: I, brackish-water assemblage; II, beach assemblage; III, seaweed-zone assemblage; IV, V, successively deeper water assemblages. Leftward shift of numbers in upward succession and left-pointing arrows indicates deepening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

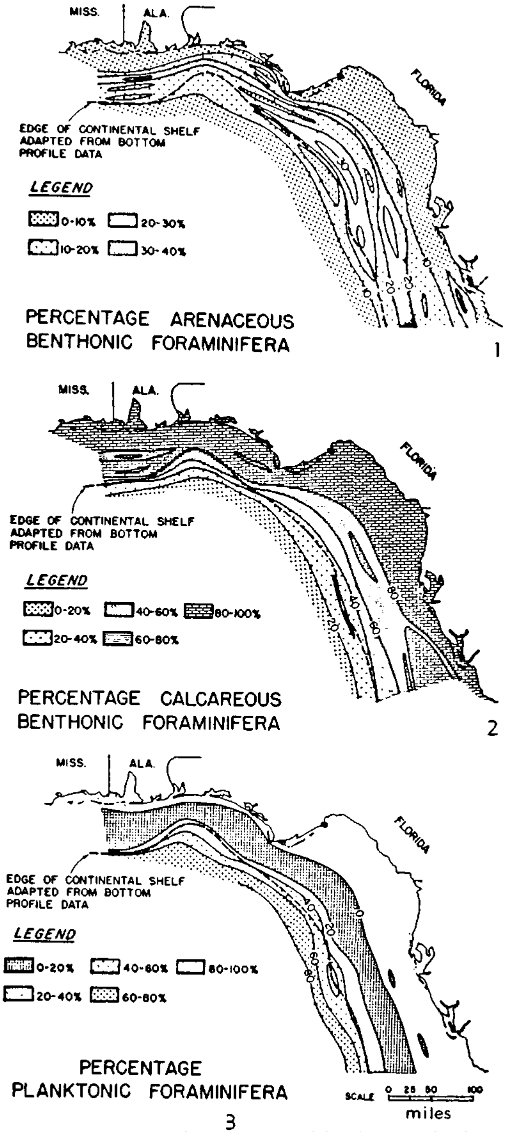

Fig. 81. Marine biofacies indicated by foraminiferal assemblages in northeastern Gulf of Mexico.——*1.* Biofacies defined by percentages of arenaceous benthonic foraminifers.——*2.* Biofacies defined by percentages of calcareous benthonic foraminifers. ——*3.* Biofacies defined by percentages of planktonic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

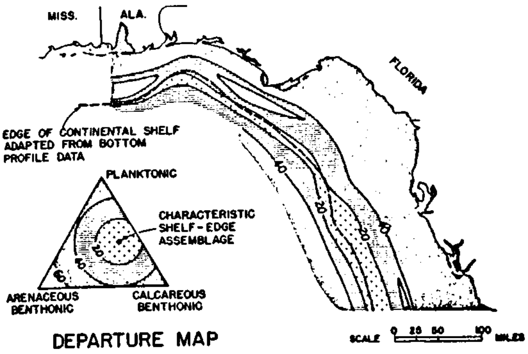

Fig. 82. "Departure map" based on shelf-edge foraminiferal assemblages, showing optimum assemblage for a selected environment and distances both shoreward and seaward from its location (*1971).

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

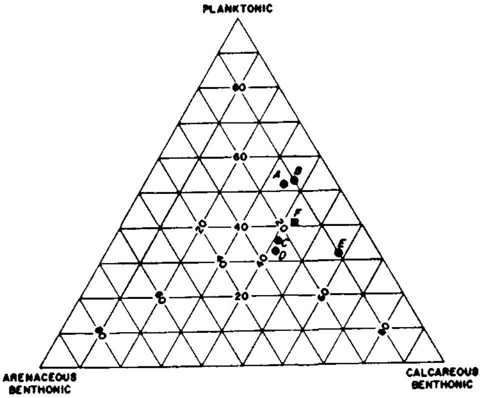

Fig. 83. Triangular graph showing selected target environment and its optimum point, based on analysis of foraminiferal assemblages. [Solid dots indicate percentages of different assemblages found along different traverses; solid square *(F)* represents average of these and the optimum point] (*1971).

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 microgranular *Colaniella* (Colaniellidae), *Pachyphloia* (Nodosinellidae), and *Lasiotrochus* (Lasiodiscidae). The porcelaneous genera with enrolled zigzag chambers *(Flectospira, Meandrospira)* and others with complex interior *(Pseudovermiporella)* appeared in the Permian. The final expansion of the Fusulinacea occurred, many developing long, attenuated tests and highly fluted septa. All became extinct at the close of the Permian.

A minor but important constituent of the Permian foraminiferal fauna comprise forerunners of the perforate hyaline groups, which are earliest representatives of the Nodosariidae *(Nodosaria, Astacolus, Dentalina, Frondicularia, Pseudonodosaria, Pseudotristix, Lingulina, Lingulonodosaria)*.

TRIASSIC

The known Triassic faunas are mostly from latest Triassic rocks, very little being known of the earlier Triassic. The oldest representatives of the arenaceous Schizamminidae *(Schizammina)*, Verneuilininae *(Gaudryina)* and Valvulininae *(Valvulina)*, the first porcelaneous Soritidae *(Triasina)*, and last of the microgranular forms *(Tetrataxis)* occur in the Triassic. The faunas known are dominated by the Nodosariidae, mostly the same genera that began in the Permian but in the Triassic represented by more ornamented forms, as well as the additional genera *Lenticulina, Marginulina, Vaginulina,* and *Vaginulinopsis.*

The earliest representatives of several families were Triassic species of Polymorphinidae *(Pyrulinoides, Sagoplecta)*, Bolivinitidae *(Brizalina)*, Involutinidae *(Involutina, Aulotortus, Paalzowella, Semiinvoluta, Trocholina)*, and questionably Spirillinidae *(Spirillina)* and Ceratobuliminidae *(Epistomina)*. In addition, a peculiar mid-Triassic fauna from Austria has been reported to contain the oldest Discorbidae *(Diplotremina, Duostomina, Variostoma)* and Anomalinidae *(Asymmetrina, Involvina, Plagiostomella)*, although nothing is known of the microstructure or lamellar character of these genera. If additional study upholds these reported occurrences, we may say that by Triassic time most of the superfamilies of calcareous foraminifers had been introduced (but not the Rotaliacea, Globigerinacea, and Orbitoidacea).

JURASSIC

During the Jurassic Period dominant members of the faunas were the Nodosariacea, represented by many genera, many with ornately ribbed surfaces, but with such great intraspecific variation that generic limits are difficult to delineate. The earliest attached Polymorphinidae also are found in the Jurassic, as are the first Glandulinidae.

In some areas a great expansion of the Lituolidae, Pavonitinidae, and Dicyclinidae occurred, with first appearance of many forms having a complex interior. Among porcelaneous forms were the earliest Nubeculariinae, Nodobaculariinae, Miliolidae *(Quinqueloculina)*, and Rhapydionininae. The Turrilinidae began in the Jurassic *(Praebulimina)*, as did the first of many genera of the Spirillinidae *(Spirillina, Conicospirillina, Miliospirella, Planispirillina, Terebralina, Turrispirillina)*.

The earliest planktonic foraminifers apparently were Jurassic forms representing the Guembelitriinae *(Gubkinella)*. The first Nonionidae *(Allomorphina)* and Ceratobuliminae *(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——Nubeculariidae——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; Bulimininae; Cassidulininae)——Lagenidae (Lageninae; Nodosariinae; Polymorphininae; Uvigerininae; Ramulininae)——Chilostomellidae——Globigerinidae——Rotaliidae (Spirillininae; Rotalinae)——Nummulitidae (Fusulininae; Polystomellinae; Cycloclypeinae)——Miliolidae (Cornuspirininae; Quinqueloculininae)

CUSHMAN, 1927

In 1927 Cushman replaced the Gromidae by the Allogromiidae, and elevated various subfamilies to family status, with the result that 15 arenaceous families (instead of three), and six porcelaneous families (instead of one) were distinguished. The calcareous and agglutinated subfamilies of the Textulariidae were separated, with recognition of the Heterohelicidae, Buliminidae, and Cassidulinidae, and trochospiral hyaline forms were divided into a number of families and subfamilies. The previously recognized ten families were increased to 45. Cushman's 1927 classification is summarized in Table 21.

Table 21. *Classification of Foraminiferida by Cushman, 1927 (*431)*

Order Foraminifera

Families Allogromiidae (Myxothecinae; Allogromiinae)——Astrorhizidae——Rhizamminidae——Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae)——Hyperamminidae (Hyperammininae; Dendrophryinae)——Reophacidae (Aschemonellinae; Reophacinae)——Ammodiscidae——Lituolidae (Haplophragmiinae; Lituolinae) —— Textulariidae (Spiroplectammininae; Textulariinae)——Verneuilinidae —— Valvulinidae—Fusulinidae (Fusulininae; Verbeekininae) Loftusiidae——Neusinidae —— Silicinidae——Miliolidae——Opthalmidiidae (Cornuspirinae; Nodobaculariinae; Opthalmidiinae; Nubeculariinae) —— Fischerinidae —— Trochamminidae (Trochammininae; Globotextularinae; Ammosphaeroidininae)——Placopsilinidae (Placopsilininae; Polyphragminae) —— Orbitolinidae——Lagenidae (Nodosariinae; Lageninae)——Polymorphinidae (Polymorphininae; Ramulininae) ——Nonionidae——Nummulitidae ——Peneroplidae (Spirolininae; Archaisinae [*sic*]; Orbitolitinae)——Alveolinellidae —— Keramosphaeridae——Heterohelicidae (Heterohelicinae; Pavonininae; Guembelininae; Bolivinitinae; Spiroplectininae; Plectofrondicularinae; Eouvigerininae) ——Hantkeninidae——Buliminidae (Terebralininae; Turrilininae; Bulimininae; Virgulininae; Reussiinae; Uvigerininae) —— Ellipsoidinidae——Rotaliidae (Spirillininae; Turrispirillininae; Discorbisinae; Rotaliinae; Baggininae)——Amphisteginidae——Calcarinidae——Cymbaloporidae —— Cassidulinidae (Ceratobuliminae; Cassidulininae; Ehrenberginae) —— Chilostomellidae (Allomorphininae; Chilostomellinae; Seabrookiinae; Allomorphinellinae; Sphaeroidininae)——Globigerinidae (Globigerininae; Orbulininae; Pulleniatininae; Candeininae)——Globorotaliidae —— Anomalinidae (Anomalininae; Cibicidinae) —— Planorbulinidae——Rupertiidae——Homotremidae——Orbitoididae

GALLOWAY, 1933

The classification of Galloway (1933, *762) recognized 35 families and his was the first attempt to cite authors and dates for the family categories, as well as to recognize priority in suprageneric classification. Thus, some family names differed from the previous classifications even when included genera were the same. Many features were similar to the classification of Rhumbler (1895), which recognized the Spirillinidae, Endothyridae, and Nodosinellidae as separate families. Greater subdivision of the hyaline calcareous families was made although with somewhat different grouping as compared with Cushman's classification. Galloway's arrangement is outlined in Table 22.

Table 22. *Classification of Foraminiferida by Galloway, 1933 (*762)*

Order Foraminifera d'Orbigny, 1826

Families Lagynidae Schultze, 1854 (Subfamilies Lagyninae Galloway, n. subfam.; Amphitreminae Galloway, n. subfam.; Myxothecinae Rhumbler, 1895; Allogromiinae Rhumbler, 1904; Rhynchogromiinae Galloway, n. subfam.)——Astrorhizidae Brady, 1881 (Saccammininae Brady, 1884; Proteonininae Galloway, n. subfam.; Astrorhizinae

Brady, 1884; Hyperammininae Cushman, 1910)——Spirillinidae Reuss, 1861 (Spirillininae Brady, 1884; Problematininae Rhumbler, 1913; Patellininae Rhumbler, 1906)——Ammodiscidae Rhumbler, 1895——Miliolidae d'Orbigny, 1839 (Cornuspirinae Reuss, 1861; Nubeculariinae Brady, 1884; Miliolinae Reuss, 1861; Hauerininae Brady, 1884)——Soritidae Ehrenberg, 1840 (Peneroplinae Schultze, 1854; Orbitolitinae Brady, 1881)——Alveolinellidae Cushman, 1928 (Alveolinellinae Galloway, n. name; Keramosphaerinae Brady, 1884)——Endothyridae Rhumbler, 1895 (Endothyrinae Brady, 1884; Tetrataxinae Galloway, n. subfam.) —— Nodosinellidae Rhumbler, 1895——Reophacidae Cushman, 1927——Trochamminidae Schwager, 1877 (Trochammininae Brady, 1884; Placopsilininae Cushman, 1927)——Lituolidae Reuss, 1861 (Lituolinae Brady, 1884; Neusininae Cushman, 1910)——Orbitolinidae Martin, 1890 —— Ataxophragmiidae Schwager, 1877 (Ataxophragmiinae Galloway, n. subfam.; Verneuilininae Cushman, 1911)——Textulariidae d'Orbigny, 1846 (Palaeotextulariinae Galloway, n. subfam.; Textulariinae Schultze, 1854)——Nodosariidae Schultze, 1854 (Frondiculariinae Reuss, 1861; Nodosariinae Reuss, 1861; Robulinae Galloway, n. subfam.)——Polymorphinidae d'Orbigny, 1846 (Polymorphininae Brady, 1881; Ramulininae Brady, 1884)——Nonionidae Reuss, 1860 (Nonioninae Schultze, 1854; Elphidiinae Galloway, n. subfam.)——Rotaliidae Reuss, 1860 (Rotaliinae Schultze, 1854; Discorbinae Cushman, 1927; Cibicidinae Galloway, n. subfam.; Planorbulininae Galloway, n. subfam.)——Acervulinidae Schultze, 1854 (Rupertiinae Galloway, n. subfam.; Acervulininae Galloway, n. subfam.)——Tinoporidae Schwager, 1877—Asterigerinidae d'Orbigny, 1839——Chapmaniidae Galloway, n. fam.——Chilostomellidae Brady, 1881——Orbulinidae Schultze, 1854——Pegidiidae Heron-Allen & Earland, 1928——Heterohelicidae Cushman, 1927 (Heterohelicinae Cushman, 1927; Gümbelininae Cushman, 1927; Bolivinitinae Cushman, 1927)——Buliminidae Jones, 1876 (Turrilininae Cushman, 1927; Bulimininae Brady, 1884)——Cassidulinidae d'Orbigny, 1839——Uvigerinidae Galloway & Wissler, 1927 (Uvigerininae Cushman, 1913; Angulogerininae Galloway, n. subfam.)——Pleurostomellidae Reuss, 1860——Fusulinidae Möller, 1878 (Fusulininae Rhumbler, 1895; Schwagerininae Dunbar & Henbest, 1930; Verbeekininae Staff & Wedekind, 1910)——Camerinidae Meek & Hayden, 1865 (Camerininae Galloway, n. name; 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; Bulimininae; Virgulininae; Reussellinae; Uvigerininae)——Cassidulinidae —— Pleurostomellidae——Heterohelicidae (Heterohelicinae; Gümbelininae; Bolivinitinae; Plectofrondiculariinae; Eouvigerininae)——Rotaliidae (Discorbinae; Cymbaloporinae; Rotaliinae; Pegidiinae; Siphonininae; Bagginineae; 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; Sphaeramminae)——Textulariidae —— Trochamminidae (Trochammininae; Globotextulariinae; Ammosphaeroidininae; Nouriinae) —— Valvulinidae (Tetrataxinae; Valvulininae; Orbitolininae)——Verneuilinidae ——Fusulinidae (Fusulininae; Schwagerininae; Verbeekininae; Neoschwagerininae)

GLAESSNER, 1945

Glaessner (1945, *796) recognized 37 families, grouped into seven superfamilies. Two arenaceous superfamilies were distinguished, one of unilocular and the other of multilocular families. Another superfamily included the Endothyridae and Fusulinidae and still another included porcelaneous forms; the hyaline families were divided into three superfamilies, one for the Lagenidae and Polymorphinidae, one for most biserial and elongate genera, and a third for all spirally enrolled and discoidal forms. Most families were similar to those of Cushman's 1927 classification except that the Spirillinidae and Discorbidae were recognized as distinct families and the Hantkeninidae, Anomalinidae, Rupertiidae, and Homotremidae were included in other families. Glaessner's arrangement of foraminifer suprageneric taxa is shown in Table 24.

Table 24. *Classification of Foraminiferida by Glaessner, 1945 (*796)*

Superfamily Astrorhizidea
Astrorhizidae (Astrorhizinae; Rhizammininae; Hyperammininae)——Saccamminidae (Psammosphaerinae; Saccammininae)——Ammodiscidae
Superfamily Lituolidea
Reophacidae——Lituolidae (Haplophragmiinae; Lituolinae; Loftusiinae)——Orbitolinidae—— Textulariidae——Trochamminidae (Trochammininae; Tetrataxinae)——Verneuilinidae (Verneuilininae; Eggerellinae; Ataxophragmiinae; Valvulininae)
Superfamily Endothyridea
Endothyridae —— Fusulinidae (Fusulininae; Schwagerininae; Verbeekininae; Neoschwagerininae)
Superfamily Miliolidea
Miliolidae——Ophthalmidiidae——Peneroplidae——Alveolinidae
Superfamily Lagenidea
Lagenidae——Polymorphinidae
Superfamily Buliminidea
Buliminidae (Turrilininae; Bulimininae; Reussellinae; Uvigerininae; Plectofrondiculariinae; Bolivininae) —— Cassidulinidae —— Ellipsoidinidae ——Chilostomellidae
Superfamily Rotaliidea
Spirillinidae (Spirillininae; Patellininae) —— Discorbidae (Discorbinae; Siphonininae; Anomalininae) —— Globigerinidae (Globigerininae; Hantkenininae)——Globorotaliidae —— Gümbelinidae——Planorbulinidae (Planorbulininae; Rupertiinae)——Cymbaloporidae——Nonionidae Ceratobuliminidae —— Amphisteginidae —— Rotaliidae —— Calcarinidae——Miogypsinidae Orbitoididae (Omphalocyclinae; Orbitoidinae; Helicolepidininae) —— Discocyclinidae —— Camerinidae (Camerininae; Heterosteginae)

CUSHMAN, 1948

In the last edition of his text, Cushman (1948, *486) recognized 50 families, adding five to the 45 families of his 1927 classification. Changes in subfamilies were made. Table 25 lists only families in which additional subfamilies were recognized (marked by an asterisk) or subfamilies were omitted (indicated by enclosure within square brackets), together with the five added families (marked by two asterisks).

Table 25. *Family-group Taxa of Foraminiferida added by Cushman (1948, *486) to his 1927 Classification*

Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae; *Webbinellinae)——Reophacidae (Aschemonellinae; Reophacinae; *Sphaeramminae) —— Ammodiscidae (*Ammodiscinae; *Tolypammininae)——Lituolidae (Haplophragmiinae; *Endothyrinae; Lituolinae)——Valvulinidae (*Valvulininae; *Eggerellinae)—— Fusulinidae Möller, 1878 (Fusulininae Rhumbler, 1895 [Verbeekininae]; *Schwagerininae Dunbar & Henbest, 1930)——**Neoschwagerinidae Dunbar, nov. (Verbeekininae Staff & Wedekind, 1910; *Neoschwagerininae Dunbar & Condra, 1927)——Silicinidae (*Involutininae; *Rzehakininae)——Ophthalmidiidae (Cornuspirinae; [Nodobaculariinae]; *Nodophthalmidiinae; Ophthalmidiinae; Nubeculariinae) —— Trochamminidae (Trochammininae; Globotextularinae; Ammosphaeroidininae; *Tetrataxinae)——**Camerinidae [Nummulitidae] (*Archaediscinae; *Camerininae) —— Heterohelicidae (Heterohelicinae; [Pavonininae]; Gümbelininae; Bolivinitinae; [Spiroplectininae]; Plectofrondiculariinae; Eouvigerininae)——Buliminidae (Terebralininae; Turrilininae; Bulimininae; Virgulininae; *Reussellinae; [Reussiinae]; Uvigerininae) —— Rotaliidae (Spirillininae; Turrispirillininae; *Discorbinae;

[Discorbisinae]; Rotaliinae; *Siphonininae; Bagginninae) —— **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; Buliminae; Reus-

sellinae; Bolivininae; Uvigerininae; Robertininae; Lacosteininae)——Cassidulinidae——Ellipsoidinidae——Chilostomellidae——Nonionidae——Heterohelicidae
Superfamily ROTALIIDEA
Discorbidae (Patellininae; Discorbinae; Cancrininae; Discorbinellinae; Chapmanininae)——Anomalinidae——Epistominidae—Ceratobuliminidae——Globigerinidae (Globigerininae; Orbulininae; Pulleniatininae; Candeininae)——Hantkeninidae——Globorotaliidae——Gümbelinidae——Elphidiidae——Planorbulinidae——Rupertiidae——Victoriellidae—Homotremidae——Pegidiidae——Cymbaloporidae——Rotaliidae——Calcarinidae——Miscellaneidae——Nummulitidae (Nummulitinae; Siderolitinae; Heterosteginae)——Miogypsinidae——Orbitoididae (Omphalocyclinae; Orbitoidinae; Pseudorbitoidinae; Clypeorbinae; Lepidorbitoidinae)——Discocyclinidae (Discocyclininae; Orbitoclypeinae)——Amphisteginidae——Helicolepidinidae——Lepidocyclinidae

POKORNÝ, 1958

POKORNÝ (1958, *1478) recognized nine superfamilies, adding to those of SIGAL the Spirillinidea, distinguished as a separate superfamily. Among his 60 families were included the Semitextulariidae, Tournayellidae, Lasiodiscidae, Archaediscidae, and Loftusiidae. His classification is summarized in Table 28.

TABLE 28. *Classification of Foraminiferida by Pokorný (1958, *1478)*

Class GRANULORETICULOSA de Saedeleer, 1934
Order FORAMINIFERA d'Orbigny, 1826
Superfamily ALLOGROMIIDEA
Superfamily ASTRORHIZIDEA
Families Saccamminidae (Psammosphaerinae; Saccammininae; Pelosininae)——Astrorhizidae——Rhizamminidae——Hyperamminidae (Hyperammininae; Earlandiinae; Dendrophyrinae; Moravammininae)——Reophacidae——Ammodiscidae (Ammodiscinae; Rzehakininae)——Tournayellidae——Lasiodiscidae——Archaediscidae
Superfamily LITUOLIDEA
Lituolidae——Loftusiidae——Textulariidae——Semitextulariidae——Trochamminidae——Tetrataxidae (Tetrataxinae; Globivalvulininae)——Verneuilinidae (Verneuilininae; Valvulininae; Ataxophragmiinae)——Orbitolinidae——Endothyridae (Endothyrinae; Bradyininae)
Superfamily FUSULINIDEA
Fusulinidae (Schubertellinae; Staffelininae [*sic*]; Boultoniinae; Fusulininae; Schwagerininae)——Neoschwagerinidae (Verbeekininae; Neoschwagerininae)
Superfamily MILIOLIDEA
Ophthalmidiidae (Cornuspirinae; Ophthalmidiinae; Nubeculariinae)——Miliolidae——Peneroplididae——Alveolinidae——Keramosphaeridae
Superfamily NODOSARIIDEA
Nodosariidae——Polymorphinidae——Enantiomorphinidae
Superfamily BULIMINIDEA
Buliminidae (Turrilininae; Buliminae; 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; Heterosteginae)——Orbitoididae——Pseudorbitoididae——Lepidorbitoididae——Discocyclinidae——Orbitoclypeidae——Helicolepidinidae——Lepidocyclinidae——Miogypsinidae

REISS, 1958

REISS (1958, *1530) published a revised classification of perforate hyaline foraminifers based on the lamellar character of the walls and septa. In addition to five superfamilies with nonlamellar tests (these groups not being subdivided or discussed), he recognized five superfamilies of lamellar-shelled foraminifers, although the Monolamellidea and Bilamellidea (and Biloculinidea) were invalid according to rules of nomenclature since they were not based on the name of an included genus. In part, families were those proposed by HOFKER, but some invalid families were indicated (e.g., Hyalovirgulinidae) and others were placed conflictingly in two superfamilies (i.e., Orbitoididae, "Pulvinulinidae"). In spite of these defects, REISS's studies re-emphasized the importance of wall structures in many of the smaller foraminifers as well as in the so-called "larger foraminifera." The classification is recorded in Table 29.

TABLE 29. *Classification of Foraminiferida by Reiss (1958, *1530)*

NONLAMELLAR TESTS
- Superfamily ASTRORHIZIDEA (agglut., pseudochitin.)
- Superfamily ENDOTHYRIDEA (calc. complex)
- Superfamily LITUOLIDEA (pseudochitin., agglut., "fibrous," microgran.)
- Superfamily MILIOLIDEA (cryptocrystalline, "porcelan.")
- Superfamily BILOCULINIDEA (agglut., porcelan., radiate)

LAMELLAR, CALCAREOUS PERFORATE TESTS
- Superfamily LAGENIDEA (radiate microstructure)
  - Families Lagenidae——Polymorphinidae——Enantiomorphinidae
- Superfamily BULIMINIDEA (PROTOFORAMINATA) (radiate and granular microstructure)
  - Buliminidae —— Buliminellidae —— Virgulinidae —— Hyalovirgulinidae —— Uvigerinidae ——Bolivinidae —— Cassidulinidae —— Chilostomellidae
- Superfamily MONOLAMELLIDEA (radiate and granular microstruct.)
  - (A) BIFORAMINATE
    - Ceratobuliminidae[1] —— Epistominidae[1] —— Robertinidae[1] —— Nonionidae —— Alabaminidae —— Eponididae —— Parrelloididae —— Siphoninidae
  - (B) DEUTEROFORAMINATE
    - Conorbidae —— "Pulvinulinidae" *(pars)* —— Valvulineriidae —— Asterigerinidae —— Planorbulinidae
- Superfamily ROTALIIDEA (bi- and deuteroforaminata, radiate)
  - Rotaliidae — Rupertiidae —— Miscellaneidae ——Nummulitidae —— Baculogypsinidae —— Elphidiidae —— Miogypsinidae —— Orbitoididae
- Superfamily BILAMELLIDEA (deuteroforaminata, radiate and granular)
  - Gavelinellidae —— "Pulvinulinidae" *(pars)*—— Anomalinidae —— Globigerinidae —— Hantkeninidae —— Gümbelinidae —— Globorotaliidae —— Cymbaloporettidae —— Amphisteginidae —— Helicolepidinidae —— Discocyclinidae ——Orbitoididae *(pars)*

RAUZER-CHERNOUSOVA & FURSENKO, 1959

In 1959 a classification of foraminifers directed by RAUZER-CHERNOUSOVA & FURSENKO (*1509) and including the work of many Soviet micropaleontologists was published in *Osnovy Paleontologii.* This classification utilized 13 orders, 14 superfamilies, and 72 families. Major differences from other published arrangements consisted in the addition of numerous families and some superfamilies (Parathuramminidea, Tournayellidea, Endothyridea) for Paleozoic genera which had been studied in detail. The ten families of BRADY were elevated to the rank of orders in this classification, as they had been by LISTER in LANKESTER (1903, *1094), except that the Chilostomellidae remained a family and the Globigerinidae was raised only to superfamily rank. Five additional orders were introduced—Ammodiscida, Endothyrida, Fusulinida, Ataxophragmida, and Heterohelicida.

The Soviet publication also cited authors and dates for family-group names, although the Lagynidae of SCHULTZE, 1854 (based on *Lagynis,* a pseudochitinous form) was mistaken for the Lagenidae (=Nodosariidae). Many new genera were included, although coverage at this level was limited largely to genera known from the USSR. Because of the relative inaccessibility of many of the original publications, it is an excellent record for other genera published in the Soviet Union prior to 1956, when this volume apparently went to press. The classification is outlined in Table 30.

TABLE 30. *Classification of Foraminiferida in Osnovy Paleontologii (1959, *1509)*

Subclass FORAMINIFERA
- Order ALLOGROMIIDA
- Order ASTRORHIZIDA
  - Superfamily ASTRORHIZIDEA H. B. Brady, 1881
    - Families Astrorhizidae H. B. Brady, 1881—— Rhizamminidae H. B. Brady, 1879——Saccamminidae H. B. Brady, 1884 (Psammosphaerinae Cushman, 1927; Saccammininae H. B. Brady, 1884; Webbinellinae Cushman, 1927)——Hyperamminidae Eimer & Fickert, 1899 (Hyperammininae Eimer & Fickert, 1899; Dendrophryinae Cushman, 1927)——Reophacidae Cushman, 1927
  - Superfamily PARATHURAMMINIDEA E. V. Bykova, 1955
    - Parathuramminidae E. V. Bykova, 1955—— ——Caligellidae Reytlinger, fam. nov.
  - ASTRORHIZIDA incertae sedis
    - Neusinidae Cushman, 1927——Familiae incertae
- Order AMMODISCIDA
  - Superfamily AMMODISCIDEA Rhumbler, 1895
    - Ammodiscidae Rhumbler, 1895 (Ammodiscinae Rhumbler, 1895; Tolypammininae Cushman, 1929)
  - Superfamily TOURNAYELLIDEA Daïn, 1953
    - Tournayellidae Daïn, 1953 (Tournayellinae Daïn, 1953; Forschiinae Daïn, 1953)

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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; Bagginae Cushman, 1927; Eponidinae Hofker, 1951)——Siphoninidae Cushman, 1928 (Siphonininae Cushman, 1927; Almaeninae Myatlyuk, subfam. nov.)——Pseudoparrellidae Voloshinova, 1952——Chapmaniidae Galloway, 1933

Superfamily CERATOBULIMINIDEA Glaessner, 1937

Epistominidae Brotzen, 1942——Ceratobuliminidae Glaessner, 1937——Robertinidae Sigal, 1952——Asterigerinidae d'Orbigny, 1839

Superfamily NONIONIDEA Schultze, 1854

Anomalinidae Cushman, 1927 (Anomalininae Cushman, 1927; Cibicidinae Cushman, 1927)——Nonionidae Schultze, 1854 (Nonioninae Schultze, 1854; Nonionellinae Voloshinova, 1958; Melonisinae Voloshinova, 1958)——Planorbulinidae Cushman, 1927——Rupertiidae Cushman, 1927——Victoriellidae Chapman & Crespin, 1930——Homotremidae Cushman, 1927——Cymbaloporettidae Cushman, 1927

Superfamily GLOBIGERINIDEA Carpenter, 1862

Globigerinidae Carpenter, 1862 (Globigerininae Carpenter, 1862; Orbulininae Schultze, 1854; Pulleniatininae Cushman, 1927; Candeininae Cushman, 1927)——Hantkeninidae Cushman, 1924——Globorotaliidae Cushman, 1927 (Globotruncaninae Brotzen, 1942; Globorotaliinae Cushman, 1927; Rugoglobigerininae Subbotina, subfam. nov.)

Superfamily ROTALIIDEA Reuss, 1860

Rotaliidae Reuss, 1860——Elphidiidae Galloway, 1933 (Elphidiinae Galloway, 1933; Cribroelphidiinae Voloshinova, 1958)

Order NUMMULITIDA

Nummulitidae Carpenter, 1859 (Nummulitinae Carpenter, 1859; Miscellaneinae Sigal, 1952; Siderolitinae Sigal, 1952; Heterostegininae Galloway, 1933)——Miogypsinidae Tan Sin Hok, 1936——Orbitoididae Prever, 1904 (Omphalocyclininae Vaughan, 1920; Orbitoidinae Prever, 1904; Pseudorbitoidinae Rutten, 1935; Lepidorbitoidinae Silvestri, 1907)——Discocyclinidae Vaughan & Cole, 1940 (Discocyclininae Vaughan & Cole, 1940; Orbitoclypeinae Brönnimann, 1946)——Lepidocyclinidae Scheffen, 1932 (Helicolepidininae Tan Sin Hok, 1936; Lepidocyclininae Tan Sin Hok, 1936)

Order BULIMINIDA

Buliminidae Jones, 1876 (Buliminellinae N. K. Bykova, subfam. nov.; Virgulininae Cushman, 1927; Baggatellinae N. K. Bykova, subfam. nov.; Buliminae 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)
      - Hemisphaeramminінae (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)
      - Sphaeramminіnae (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)

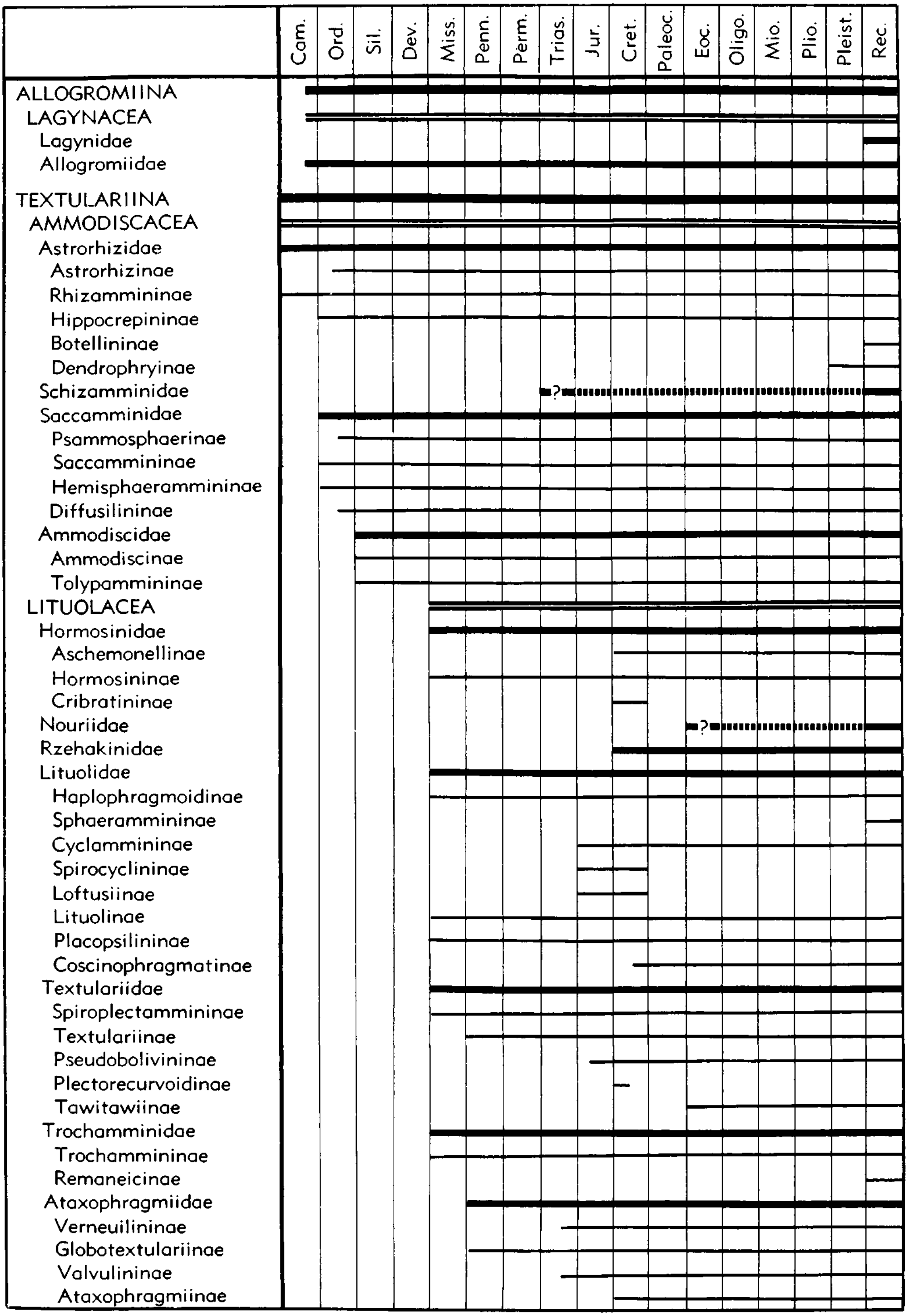

FIG. 83A. Stratigraphic distribution of suprageneric taxa of Foraminiferida (*2117).

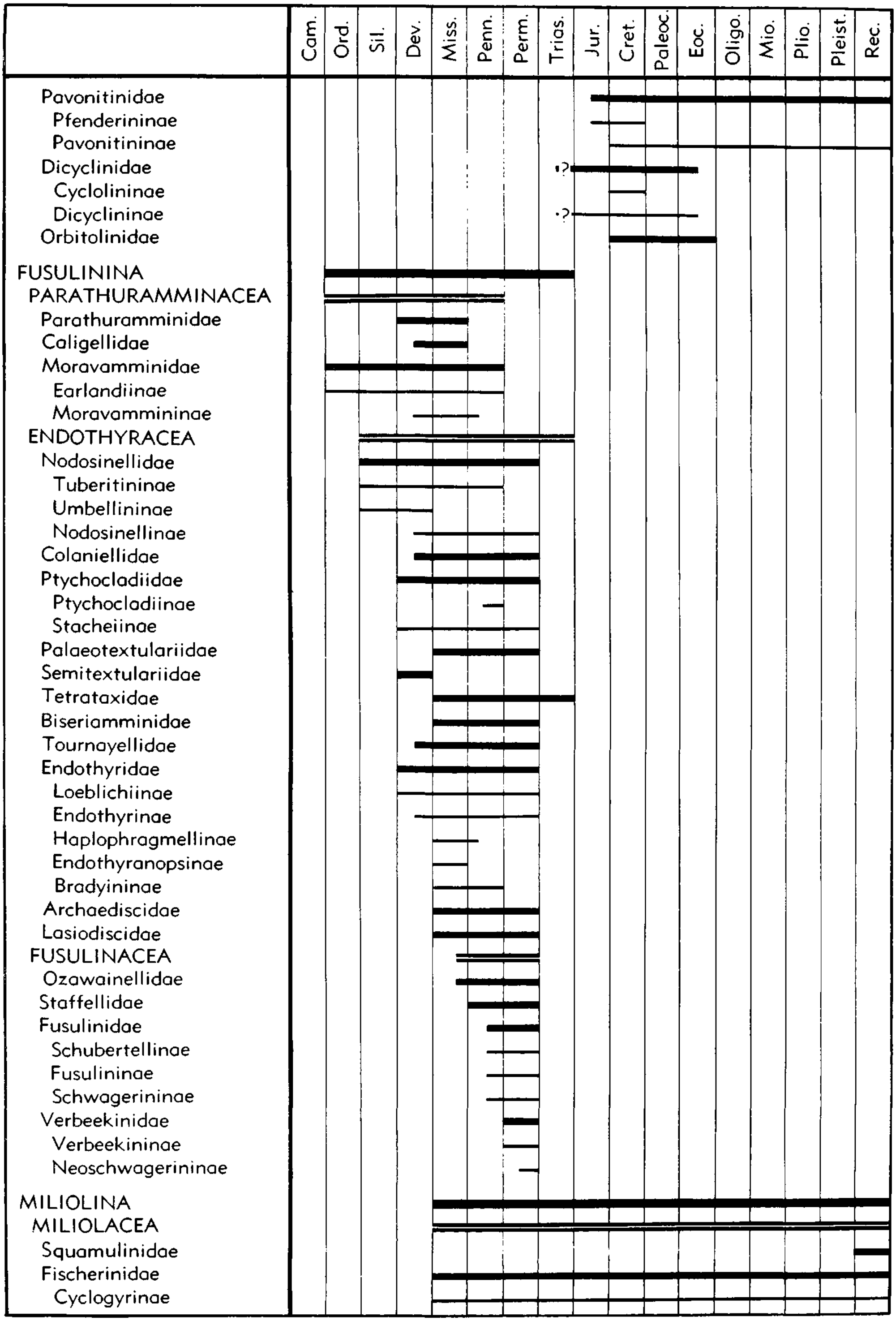

FIG. 83A *(continued)*.

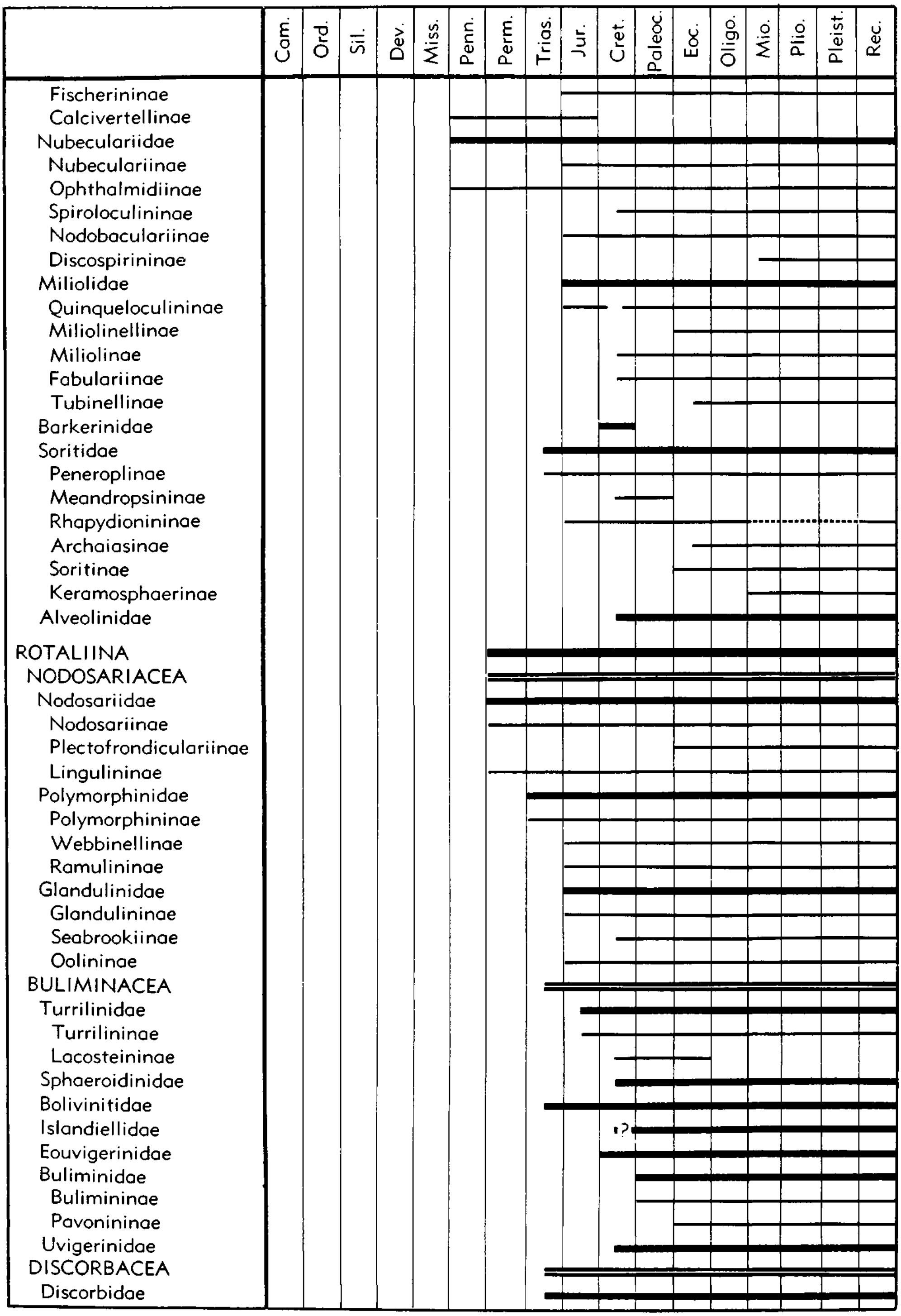

FIG. 83A *(continued)*.

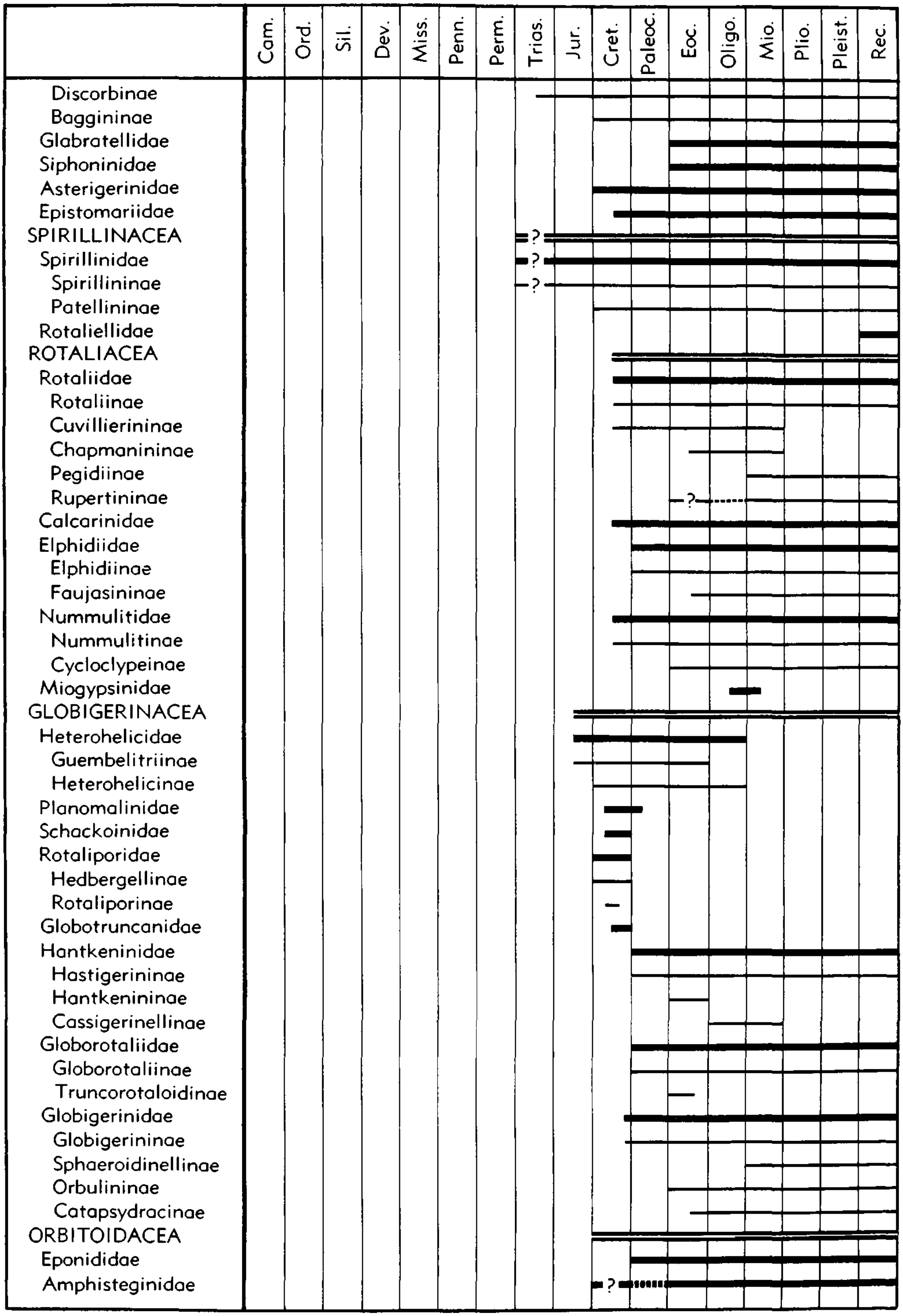

FIG. 83A *(continued)*.

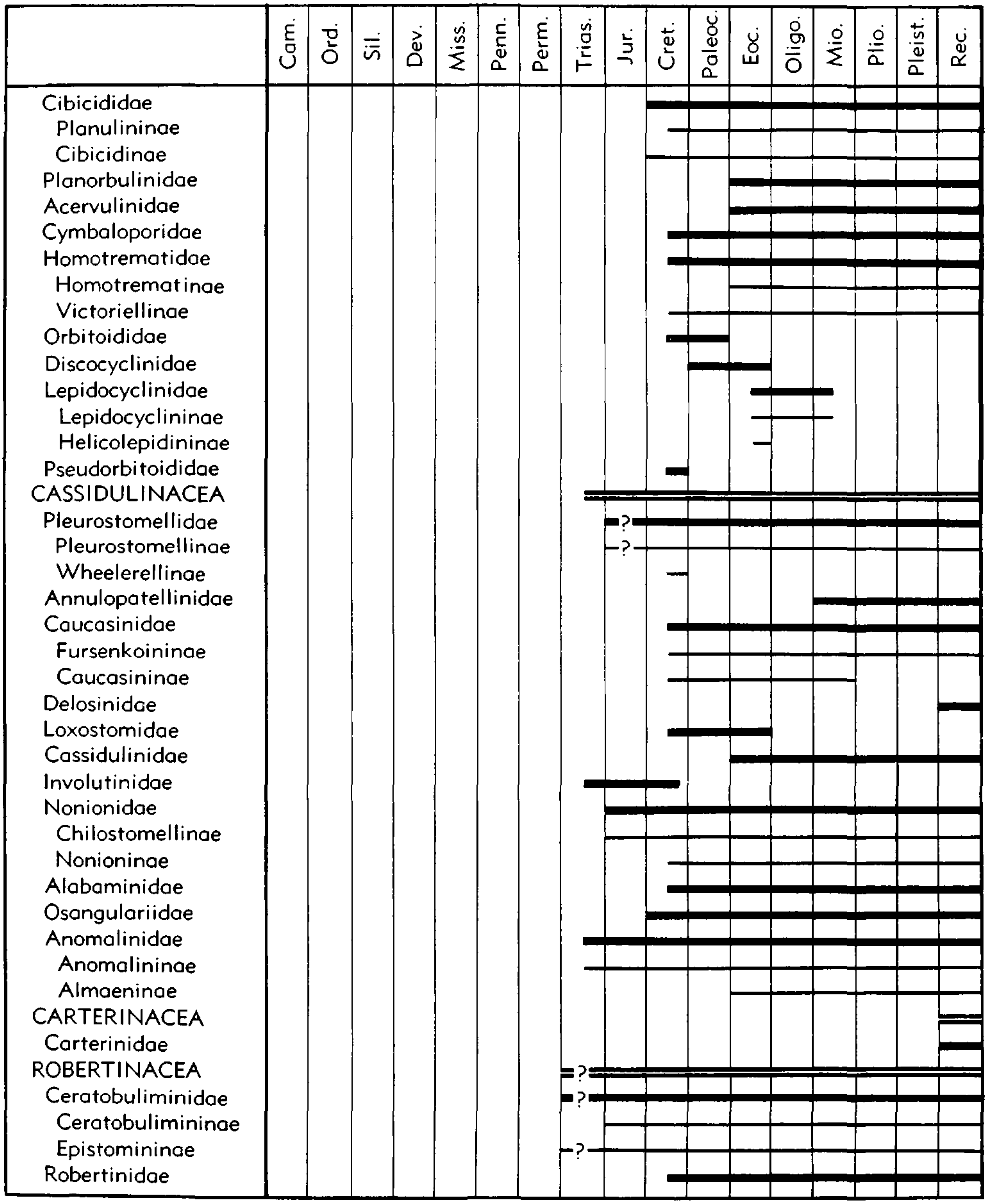

FIG. 83A *(continued)*.

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)

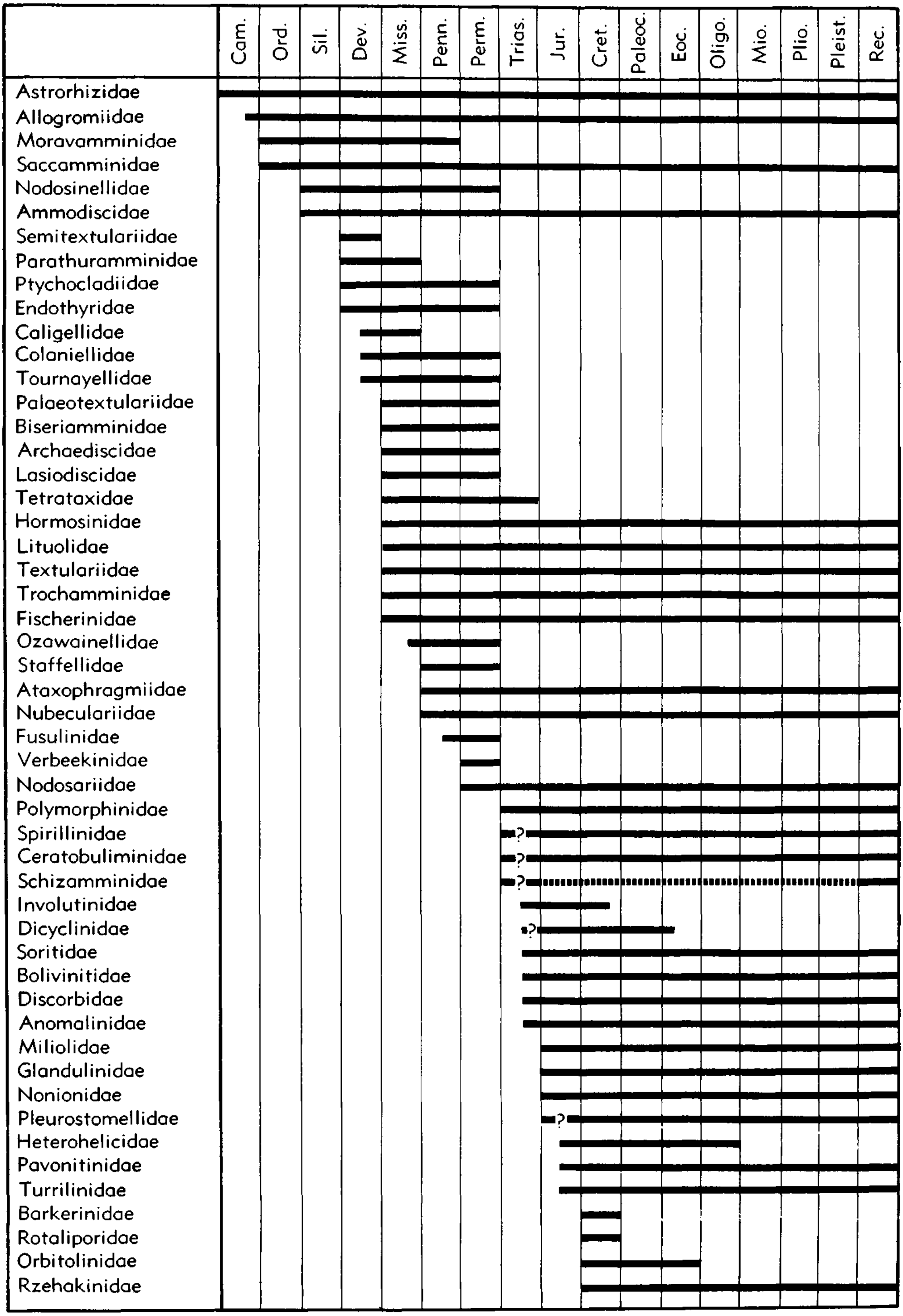

FIG. 83B. Graph showing stratigraphic distribution of families of Foraminiferida plotted according to relative time values (*2117).

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)

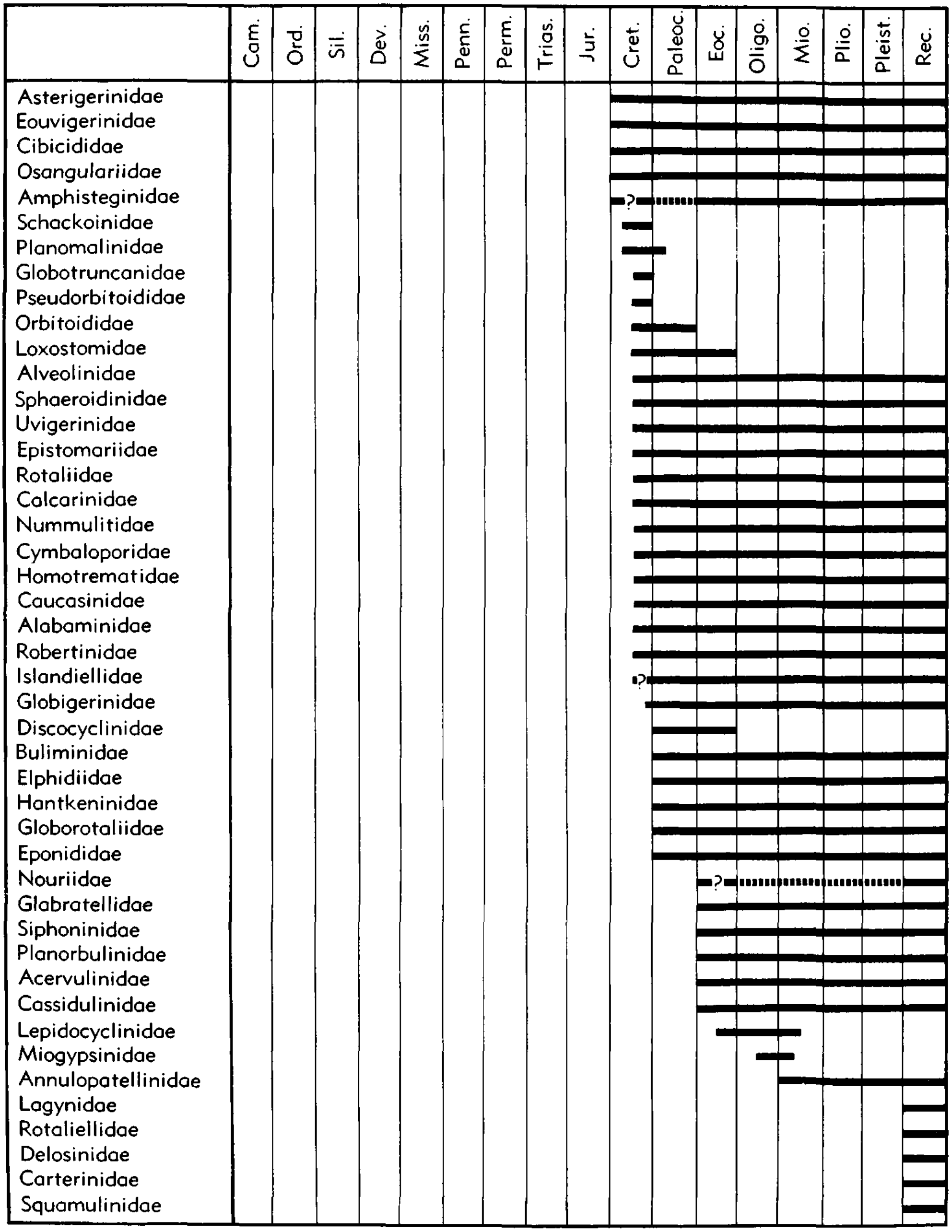

FIG. 83B *(continued)*.