## Treatise on Invertebrate Paleontology

# Part E **PORIFERA**

## Revised

Volume 3: Porifera (Demospongea, Hexactinellida, Heteractinida, Calcarea)

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## PART E, Revised PORIFERA

## VOLUME 3: PORIFERA (Demospongea, Hexactinellida, Heteractinida, Calcarea)

R. M. FINKS, R. E. H. REID, and J. K. RIGBY

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## INFORMATION ON *TREATISE* VOLUMES

Parts of the *Treatise* are distinguished by assigned letters with a view to indicating their systematic sequence while allowing publication of units in whatever order each is made ready for the press. Copies can be obtained from the Publication Sales Department, The Geological Society of America, 3300 Penrose Place, P.O. Box 9140, Boulder, Colorado 80301, www.geosociety.org.

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Part A. INTRODUCTION: Fossilization (Taphonomy), Biogeography, and Biostratigraphy, xxiii + 569 p., 169 fig., 1979.

Part C. PROTISTA 2 (Sarcodina, Chiefly "Thecamoebians" and Foraminiferida), Volumes 1 and 2, xxxi + 900 p., 653 fig., 1964.

- Part D. PROTISTA 3 (Protozoa: Chiefly Radiolaria, Tintinnina), xii + 195 p., 92 fig., 1954.
- Part E. Archaeocyatha and Porifera, xviii + 122 p., 89 fig., 1955.
- Part E, Revised. ARCHAEOCYATHA, Volume 1, xxx + 158 p., 107 fig., 1972.
- Part E, Revised. PORIFERA, Volume 2 (Introduction to the Porifera), xxvii + 349 p., 135 fig., 10 tables, 2003.
- Part F. COELENTERATA, xx + 498 p., 358 fig., 1956.
- Part F. COELENTERATA, Supplement 1 (Rugosa and Tabulata), Volumes 1 and 2, xl + 762 p., 462 fig., 1981.
- Part G. BRYOZOA, xiii + 253 p., 175 fig., 1953.
- Part G, Revised. BRYOZOA, Volume 1 (Introduction, Order Cystoporata, Order Cryptostomata), xxvi + 625 p., 295 fig., 1983.
- Part H. BRACHIOPODA, Volumes 1 and 2, xxxii + 927 p., 746 fig., 1965.
- Part H, Revised. BRACHIOPODA, Volume 1 (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.
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- Part K. MOLLUSCA 3 (Cephalopoda General Features, Endoceratoidea, Actinoceratoidea, Nautiloidea, Bactritoidea), xxviii + 519 p., 361 fig., 1964.
- Part L. MOLLUSCA 4 (Cephalopoda: Ammonoidea), xxii + 490 p., 558 fig., 1957.
- Part L, Revised. MOLLUSCA 4, Volume 4 (Cretaceous Ammonoidea), xx + 362 p., 216 fig., 1996.
- Part N. MOLLUSCA 6 (Bivalvia), Volumes 1 and 2 (of 3), xxxvii + 952 p., 613 fig., 1969.
- Part N. MOLLUSCA 6 (Bivalvia), Volume 3, iv + 272 p., 153 fig., 1971.
- Part O. ARTHROPODA 1 (Arthropoda General Features, Protarthropoda, Euarthropoda General Features, Trilobitomorpha), xix + 560 p., 415 fig., 1959.

- Part O, Revised. ARTHROPODA 1 (Trilobita: Introduction, Order Agnostida, Order Redlichiida), xxiv + 530 p., 309 fig., 1997.
- Part P. ARTHROPODA 2 (Chelicerata, Pycnogonida, Palaeoisopus), xvii + 181 p., 123 fig., 1955 [1956].
- Part Q. ARTHROPODA 3 (Crustacea, Ostracoda), xxiii + 442 p., 334 fig., 1961.
- Part R. ARTHROPODA 4, Volumes 1 and 2 (Crustacea Exclusive of Ostracoda, Myriapoda, Hexapoda), xxxvi + 651 p., 397 fig., 1969.
- Part R. ARTHROPODA 4, Volumes 3 and 4 (Hexapoda), xxii + 655 p., 265 fig., 1992.
- Part S. ECHINODERMATA 1 (Echinodermata General Features, Homalozoa, Crinozoa, exclusive of Crinoidea), Volumes 1 and 2, xxx + 650 p., 400 fig., 1968 [1967].
- Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1-3, xxxviii + 1,027 p., 619 fig., 1978.
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- Part V. GRAPTOLITHINA, xvii + 101 p., 72 fig., 1955.
- Part V, Revised. GRAPTOLITHINA, xxxii + 163 p., 109 fig., 1970.
- Part W. MISCELLANEA (Conodonts, Conoidal Shells of Uncertain Affinities, Worms, Trace Fossils, Problematica), xxv + 259 p., 153 fig., 1962.
- Part W, Revised. MISCELLANEA, Supplement 1 (Trace Fossils and Problematica), xxi + 269 p., 110 fig., 1975.
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#### THIS VOLUME

Part E, Revised. PORIFERA, Volume 3 (Demospongea, Hexactinellida, Heteractinida, Calcarea), xxxi + 872 p., 506 fig., 1 table, 2004.

#### VOLUMES IN PREPARATION

- Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Charophyta, Diatomacea, Pyrrhophyta, etc.).
- Part E, Revised. PORIFERA (additional volumes).
- Part F, Revised. CNIDARIA (Scleractinia).
- Part G, Revised. BRYOZOA (additional volumes).
- Part H, Revised. BRACHIOPODA (additional volumes).

Part K, Revised. MOLLUSCA 3 (Nautiloidea).

- Part L, Revised. MOLLUSCA 4 (Ammonoidea) (additional volumes).
- Part M. MOLLUSCA 5 (Coleoidea).
- Part O, Revised. ARTHROPODA 1 (Trilobita) (additional volumes).
- Part Q, Revised. ARTHROPODA 3 (Ostracoda).
- Part R, Revised. ARTHROPODA 4 (Crustacea Exclusive of Ostracoda).
- Part T, Revised. ECHINODERMATA 2 (Crinoidea).
- Part V, Revised. GRAPTOLITHINA.
- Part W, Revised. TRACE FOSSILS.

## EDITORIAL PREFACE

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From the outset the aim of the Treatise on Invertebrate Paleontology has been to present a comprehensive and authoritative yet compact statement of knowledge concerning groups of invertebrate fossils. Typically, preparation of early Treatise volumes was undertaken by a small group with a synoptic view of the taxa being monographed. Two or perhaps three specialists worked together, sometimes co-opting others for coverage of highly specialized taxa. Recently, however, both new Treatise volumes and revisions of existing ones have been undertaken increasingly by teams of specialists led by a coordinating author. This volume, Part E Revised, Porifera, Volume 2, has been prepared by such a team. In the early stages of the work, R. M. Finks and R. E. H. Reid worked together on the volume. Final preparation of this volume was coordinated by J. K. Rigby, working with manuscript that was submitted previously by both Finks and Reid. Editorial matters specific to this volume are discussed near the end of this editorial preface.

#### ZOOLOGICAL NAMES

Questions about the proper use of zoological names arise continually, especially questions regarding both the acceptability of names and alterations of names that are allowed or even required. Regulations prepared by the International Commission on Zoological Nomenclature (ICZN) and published in 1999 in the International Code of Zoological Nomenclature, hereinafter referred to as the Code, provide procedures for answering such questions. The prime objective of the Code is to promote stability and universality in the use of the scientific names of animals, ensuring also that each generic name is distinct and unique, while avoiding unwarranted restrictions on freedom of

thought and action of systematists. Priority of names is a basic principle of the *Code;* but, under specified conditions and by following prescribed procedures, priority may be set aside by the Commission. These procedures apply especially where slavish adherence to the principle of priority would hamper or even disrupt zoological nomenclature and the information it conveys.

The Commission, ever aware of the changing needs of systematists, revised the Code in 1999 to enhance further nomenclatorial stability, specifying that the revised Code should take effect at the start of 2000. In spite of the revisions, the nomenclatorial tasks that confront zoological taxonomists are formidable and have often justified the complaint that the study of zoology and paleontology is too often merely the study of names rather than the study of animals. It is incumbent upon all systematists, therefore, at the outset of their work to pay careful attention to the Code to enhance stability by minimizing the number of subsequent changes of names, too many of which are necessitated by insufficient attention to detail. To that end, several pages here are devoted to aspects of zoological nomenclature that are judged to have chief importance in relation to procedures adopted in the Treatise, especially in this volume. Terminology is explained, and examples are given of the style employed in the nomenclatorial parts of the systematic descriptions.

## GROUPS OF TAXONOMIC CATEGORIES

Each taxon belongs to a category in the Linnaean hierarchical classification. The *Code* recognizes three groups of categories, a species-group, a genus-group, and a familygroup. Taxa of lower rank than subspecies are excluded from the rules of zoological nomenclature, and those of higher rank than superfamily are not regulated by the *Code*. It is both natural and convenient to discuss nomenclatorial matters in general terms first and then to consider each of these three recognized groups separately. Especially important is the provision that within each group the categories are coordinate, that is, equal in rank, whereas categories of different groups are not coordinate.

#### FORMS OF NAMES

All zoological names can be considered on the basis of their spelling. The first form of a name to be published is defined as the original spelling (*Code*, Article 32), and any form of the same name that is published later and is different from the original spelling is designated a subsequent spelling (*Code*, Article 33). Not every original or subsequent spelling is correct.

#### **ORIGINAL SPELLINGS**

If the first form of a name to be published is consistent and unambiguous, the original is defined as correct unless it contravenes some stipulation of the *Code* (Articles 11, 27 to 31, and 34) or unless the original publication contains clear evidence of an inadvertent error in the sense of the *Code*, or, among names belonging to the family-group, unless correction of the termination or the stem of the type genus is required. An original spelling that fails to meet these requirements is defined as incorrect.

If a name is spelled in more than one way in the original publication, the form adopted by the first reviser is accepted as the correct original spelling, provided that it complies with mandatory stipulations of the *Code* (Articles 11 and 24 to 34).

Incorrect original spellings are any that fail to satisfy requirements of the *Code*, represent an inadvertent error, or are one of multiple original spellings not adopted by a first reviser. These have no separate status in zoological nomenclature and, therefore, cannot enter into homonymy or be used as replacement names. They call for correction. For example, a name originally published with a diacritical mark, apostrophe, dieresis, or hyphen requires correction by deleting such features and uniting parts of the name originally separated by them, except that deletion of an umlaut from a vowel in a name derived from a German word or personal name unfortunately requires the insertion of *e* after the vowel. Where original spelling is judged to be incorrect solely because of inadequacies of the Greek or Latin scholarship of the author, nomenclatorial changes conflict with the primary purpose of zoological nomenclature as an information retrieval system. One looks forward with hope to further revisions of the Code wherein rules are emplaced that enhance stability rather than classical scholarship, thereby facilitating access to information.

#### SUBSEQUENT SPELLINGS

If a subsequent spelling differs from an original spelling in any way, even by the omission, addition, or alteration of a single letter, the subsequent spelling must be defined as a different name. Exceptions include such changes as an altered termination of adjectival specific names to agree in gender with associated generic names (an unfortunate impediment to stability and retrieval of information); changes of family-group names to denote assigned taxonomic rank; and corrections that eliminate originally used diacritical marks, hyphens, and the like. Such changes are not regarded as spelling changes conceived to produce a different name. In some instances, however, speciesgroup names having variable spellings are regarded as homonyms as specified in the Code (Article 58).

Altered subsequent spellings other than the exceptions noted may be either intentional or unintentional. If "demonstrably intentional" (*Code*, Article 33), the change is designated as an emendation. Emendations may be either justifiable or unjustifiable. Justifiable emendations are corrections of incorrect original spellings, and these take the authorship and date of the original spellings. Unjustifiable emendations are names having their own status in nomenclature, with author and date of their publication. They are junior, objective synonyms of the name in its original form.

Subsequent spellings, if unintentional, are defined as incorrect subsequent spellings. They have no status in nomenclature, do not enter into homonymy, and cannot be used as replacement names.

## AVAILABLE AND UNAVAILABLE NAMES

Editorial prefaces of some previous volumes of the Treatise have discussed in appreciable detail the availability of the many kinds of zoological names that have been proposed under a variety of circumstances. Much of that information, while important, does not pertain to the present volume, in which authors have used fewer terms for such names. The reader is referred to the Code (Articles 10 to 20) for further details on availability of names. Here, suffice it to say that an available zoological name is any that conforms to all mandatory provisions of the Code. All zoological names that fail to comply with mandatory provisions of the Code are unavailable and have no status in zoological nomenclature. Both available and unavailable names are classifiable into groups that have been recognized in previous volumes of the Treatise, although not explicitly differentiated in the Code. Among names that are available, these groups include inviolate names, perfect names, imperfect names, vain names, transferred names, improved or corrected names, substitute names, and conserved names. Kinds of unavailable names include naked names (see nomina nuda below), denied names, impermissible names, null names, and forgotten names.

Nomina nuda include all names that fail to satisfy provisions stipulated in Article 11 of the Code, which states general requirements of availability. In addition, they include names published before 1931 that were unaccompanied by a description, definition, or indication (*Code*, Article 12) and names published after 1930 that (1) lacked an accompanying statement of characters that differentiate the taxon, (2) were without a definite bibliographic reference to such a statement, (3) were not proposed expressly as a replacement (*nomen novum*) of a preexisting available name (*Code*, Article 13.1), or (4) for genus-group names, were unaccompanied by definite fixation of a type species by original designation or indication (*Code*, Article 13.2). *Nomina nuda* have no status in nomenclature, and they are not correctable to establish original authorship and date.

## VALID AND INVALID NAMES

Important considerations distinguish valid from available names on the one hand and invalid from unavailable names on the other. Whereas determination of availability is based entirely on objective considerations guided by articles of the Code, conclusions as to validity of zoological names may be partly subjective. A valid name is the correct one for a given taxon, which may have two or more available names but only a single correct, hence valid, name, which is also generally the oldest name that it has been given. Obviously, no valid name can also be an unavailable name, but invalid names may be either available or unavailable. It follows that any name for a given taxon other than the valid name, whether available or unavailable, is an invalid name.

One encounters a sort of nomenclatorial no-man's land in considering the status of such zoological names as *nomina dubia* (doubtful names), which may include both available and unavailable names. The unavailable ones can well be ignored, but names considered to be available contribute to uncertainty and instability in the systematic literature. These can ordinarily be removed only by appeal to the ICZN for special action. Because few systematists care to seek such remedy, such invalid but available names persist in the literature.

## NAME CHANGES IN RELATION TO GROUPS OF TAXONOMIC CATEGORIES SPECIES-GROUP NAMES

Detailed consideration of valid emendation of specific and subspecific names is unnecessary here, both because the topic is well understood and relatively inconsequential and because the Treatise deals with genusgroup names and higher categories. When the form of adjectival specific names is changed to agree with the gender of a generic name in transferring a species from one genus to another, one need never label the changed name as nomen correctum. Similarly, transliteration of a letter accompanied by a diacritical mark in the manner now called for by the *Code*, as in changing originally bröggeri to broeggeri, or eliminating a hyphen, as in changing originally published cornu-oryx to cornuoryx, does not require the designation nomen correctum. Of course, in this age of computers and electronic databases, such changes of name, which are perfectly valid for the purposes of scholarship, run counter to the requirements of nomenclatorial stability upon which the preparation of massive, electronic databases is predicated.

#### **GENUS-GROUP NAMES**

Conditions warranting change of the originally published, valid form of generic and subgeneric names are sufficiently rare that lengthy discussion is unnecessary. Only elimination of diacritical marks and hyphens in some names in this category and replacement of homonyms seem to furnish basis for valid emendation. Many names that formerly were regarded as homonyms are no longer so regarded, because two names that differ only by a single letter or in original publication by the presence of a diacritical mark in one are now construed to be entirely distinct (but see *Code*, Article 58).

As has been pointed out above, difficulty typically arises when one tries to decide whether a change of spelling of a name by a subsequent author was intentional or unintentional, and the decision has to be made often arbitrarily.

## FAMILY-GROUP NAMES Family-Group Names: Authorship and Date

All family-group taxa having names based on the same type genus are attributed to the author who first published the name of any of these groups, whether tribe, subfamily, or family (superfamily being almost inevitably a later-conceived taxon). Accordingly, if a family is divided into subfamilies or a subfamily into tribes, the name of no such subfamily or tribe can antedate the family name. Moreover, every family containing differentiated subfamilies must have a nominate subfamily (sensu stricto), which is based on the same type genus as the family. Finally, the author and date set down for the nominate subfamily invariably are identical with those of the family, irrespective of whether the author of the family or some subsequent author introduced subdivisions.

Corrections in the form of family-group names do not affect authorship and date of the taxon concerned, but in the *Treatise* recording the authorship and date of the correction is desirable because it provides a pathway to follow the thinking of the systematists involved.

#### Family-Group Names: Use of *nomen translatum*

The *Code* (Article 29.2) specifies the suffixes for tribe (-ini), subfamily (-inae), family (-idae) and superfamily (-oidea), the formerly widely used ending (-acea) for superfamily having been disallowed. All these family-group categories are defined as coordinate (*Code*, Article 36.1): "A name established for a taxon at any rank in the family group is deemed to have been simultaneously established for nominal taxa at other ranks in the family group; all these taxa have the same type genus, and their names are

formed from the stem of the name of the type genus [Art. 29.3] with appropriate change of suffix [Art. 34.1]. The name has the same authorship and date at every rank." Such changes of rank and concomitant changes of endings as elevation of a subfamily to family rank or of a family to superfamily rank, if introduced subsequent to designation of the original taxon or based on the same nominotypical genus, are nomina translata. In the Treatise it is desirable to distinguish the valid alteration in the changed ending of each transferred family-group name by the term nomen translatum, abbreviated to nom. transl. Similarly for clarity, authors should record the author, date, and page of the alteration, as in the following example.

#### Family HEXAGENITIDAE Lameere, 1917

[nom. transl. DEMOULIN, 1954, p. 566, ex Hexagenitinae LAMEERE, 1917, p. 74]

This is especially important for superfamilies, for the information of interest is the author who initially introduced a taxon rather than the author of the superfamily as defined by the *Code*. For example:

## Superfamily AGNOSTOIDEA M'Coy, 1849

[nom. transl. SHERGOLD, LAURIE, & SUN, 1990, p. 32, ex Agnostinae M'Coy, 1849, p. 402]

The latter is merely the individual who first defined some lower-ranked, family-group taxon that contains the nominotypical genus of the superfamily. On the other hand, the publication that introduces the superfamily by *nomen translatum* is likely to furnish the information on taxonomic considerations that support definition of the taxon.

#### Family-Group Names: Use of *nomen correctum*

Valid name changes classed as *nomina correcta* do not depend on transfer from one category of the family group to another but most commonly involve correction of the stem of the nominotypical genus. In addition, they include somewhat arbitrarily chosen modifications of endings for names of tribes or superfamilies. Examples of the use of *nomen correctum* are the following.

#### Family STREPTELASMATIDAE Nicholson, 1889

[nom. correct. WEDEKIND, 1927, p. 7, pro Streptelasmidae NICHOLSON in NICHOLSON & LYDEKKER, 1889, p. 297]

#### Family PALAEOSCORPIDAE Lehmann, 1944

[nom. correct. Petrunkevitch, 1955, p. 73, pro Palaeoscorpionidae Lehmann, 1944, p. 177]

#### Family-Group Names: Replacements

Family-group names are formed by adding combinations of letters, which are prescribed for all family-group categories, to the stem of the name belonging to the nominotypical genus first chosen as type of the assemblage. The type genus need not be the first genus in the family to have been named and defined, but among all those included it must be the first published as name giver to a family-group taxon. Once fixed, the family-group name remains tied to the nominotypical genus even if the generic name is changed by reason of status as a junior homonym or junior synonym, either objective or subjective. Seemingly, the Code requires replacement of a family-group name only if the nominotypical genus is found to have been a junior homonym when it was proposed (Code, Article 39), in which case . . . it must be replaced either by the next oldest available name from among its synonyms [Art. 23.3.5], including the names of its subordinate family-group taxa, or, if there is no such synonym, by a new name based on the valid name . . . of the former type genus." Authorship and date attributed to the replacement family-group name are determined by first publication of the changed family-group name. Recommendation 40A of the Code, however, specifies that for subsequent application of the rule of priority, the family-group name ". . . should be cited

with its original author and date (see Recommendation 22A.2.2), followed by the date of its priority as determined by this Article; the date of priority should be enclosed in parentheses." Many family-group names that have been in use for a long time are *nomina nuda*, since they fail to satisfy criteria of availability (*Code*, Article 11.7). These demand replacement by valid names.

The aim of family-group nomenclature is to yield the greatest possible stability and uniformity, just as in other zoological names. Both taxonomic experience and the Code (Article 40) indicate the wisdom of sustaining family-group names based on junior subjective synonyms if they have priority of publication, for opinions of the same worker may change from time to time. The retention of first-published, family-group names that are found to be based on junior objective synonyms, however, is less clearly desirable, especially if a replacement name derived from the senior objective synonym has been recognized very long and widely. Moreover, to displace a widely used, family-group name based on the senior objective synonym by disinterring a forgotten and virtually unused family-group name based on a junior objective synonym because the latter happens to have priority of publication is unsettling.

A family-group name may need to be replaced if the nominotypical genus is transferred to another family group. If so, the first-published of the generic names remaining in the family-group taxon is to be recognized in forming a replacement name.

#### SUPRAFAMILIAL TAXA: TAXA ABOVE FAMILY-GROUP

International rules of zoological nomenclature as given in the *Code* affect only lowerrank categories: subspecies to superfamily. Suprafamilial categories (suborder to kingdom) are either not mentioned or explicitly placed outside of the application of zoological rules. The *Copenhagen Decisions on Zoo*- logical Nomenclature (1953, Articles 59 to 69) proposed adopting rules for naming suborders and higher taxa up to and including phylum, with provision for designating a type genus for each, in such manner as not to interfere with the taxonomic freedom of workers. Procedures were outlined for applying the rule of priority and rule of homonymy to suprafamilial taxa and for dealing with the names of such taxa and their authorship, with assigned dates, if they should be transferred on taxonomic grounds from one rank to another. The adoption of terminations of names, different for each category but uniform within each, was recommended.

The Colloquium on Zoological Nomenclature, which met in London during the week just before the 15th International Congress of Zoology convened in 1958, discussed thoroughly the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new Code or recommended for exclusion from it. A decision that was supported by a wide majority of the participants in the colloquium was against the establishment of rules for naming taxa above family-group rank, mainly because it was judged that such regulation would unwisely tie the hands of taxonomists. For example, a class or order defined by an author at a given date, using chosen morphologic characters (e.g., gills of bivalves), should not be allowed to freeze nomenclature, taking precedence over another class or order that is proposed later and distinguished by different characters (e.g., hinge teeth of bivalves). Even the fixing of type genera for suprafamilial taxa would have little, if any, value, hindering taxonomic work rather than aiding it. Beyond mere tidying up, no basis for establishing such types and for naming these taxa has yet been provided.

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

1. The name of any suprafamilial taxon must be a Latin or Latinized, uninominal noun of plural form or treated as such, with a capital initial letter and without diacritical mark, apostrophe, diaeresis, or hyphen. If a component consists of a numeral, numerical adjective, or adverb, this must be written in full.

2. Names of suprafamilial taxa may be constructed in almost any manner. A name may indicate morphological attributes (e.g., Lamellibranchiata, Cyclostomata, Toxoglossa) or be based on the stem of an included genus (e.g., Bellerophontina, Nautilida, Fungiina) or on arbitrary combinations of letters (e.g., Yuania); none of these, however, can end in -idae or -inae, which terminations are reserved for family-group taxa. No suprafamilial name identical in form to that of a genus or to another published suprafamilial name should be employed (e.g., order Decapoda LATREILLE, 1803, crustaceans, and order Decapoda LEACH, 1818, cephalopods; suborder Chonetoidea MUIR-WOOD, 1955, and genus Chonetoidea JONES, 1928). Worthy of notice is the classificatory and nomenclatorial distinction between suprafamilial and family-group taxa that are named from the same type genus, since one is not considered to be transferable to the other (e.g., suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontoidea McCoy,

1851 or family Bellerophontidae McCoy, 1851).

3. The rules of priority and homonymy lack any force of international agreement as applied to suprafamilial names, yet in the interest of nomenclatorial stability and to avoid confusion these rules are widely applied by zoologists to taxa above the familygroup level wherever they do not infringe on taxonomic freedom and long-established usage.

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

## Order CORYNEXOCHIDA Kobayashi, 1935

#### [nom. transl. MOORE, 1959, p. 217, ex suborder Corynexochida Ковачазні, 1935, p. 81]

A name revised from its previously published form merely by adoption of a different termination without changing taxonomic rank is a *nomen correctum*.

## Order DISPARIDA Moore & Laudon, 1943

[nom. correct. MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, pro order Disparata MOORE & LAUDON, 1943, p. 24]

A suprafamilial name revised from its previously published rank with accompanying change of termination, which signals the change of rank, is recorded as a *nomen translatum et correctum*.

## Order HYBOCRINIDA Jaekel, 1918

[nom. transl. et correct. MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 613, ex suborder Hybocrinites JAEKEL, 1918, p. 90]

5. The authorship and date of nominate subordinate and supraordinate taxa among

suprafamilial taxa are considered in the *Treatise* to be identical since each actually or potentially has the same type. Examples are given below.

## Subclass ENDOCERATOIDEA Teichert, 1933

[nom. transl. TEICHERT in TEICHERT & others, 1964, p. 128, ex order Endoceroidea TEICHERT, 1933, p. 214]

## Order ENDOCERIDA Teichert, 1933

[nom. correct. TEICHERT in TEICHERT & others, 1964, p. 165, pro order Endoceroidea TEICHERT, 1933, p. 214]

#### TAXONOMIC EMENDATION

Emendation has two distinct meanings as regards zoological nomenclature. These are alteration of a name itself in various ways for various reasons, as has been reviewed, and alteration of the taxonomic scope or concept for which a name is used. The *Code* (Article 33.1 and Glossary) concerns itself only with the first type of emendation, applying the term to intentional, either justified or unjustified changes of the original spelling of a name. The second type of emendation primarily concerns classification and inherently is not associated with change of name. Little attention generally has been paid to this distinction in spite of its significance.

Most zoologists, including paleontologists, who have emended zoological names refer to what they consider a material change in application of the name such as may be expressed by an importantly altered diagnosis of the assemblage covered by the name. The abbreviation emend, then must accompany the name with statement of the author and date of the emendation. On the other hand, many systematists think that publication of *emend*. with a zoological name is valueless because alteration of a taxonomic concept is introduced whenever a subspecies, species, genus, or other taxon is incorporated into or removed from a higher zoological taxon. Inevitably associated with such classificatory expansions and restrictions is

some degree of emendation affecting diagnosis. Granting this, still it is true that now and then somewhat more extensive revisions are put forward, generally with a published statement of the reasons for changing the application of a name. To erect a signpost at such points of most significant change is worthwhile, both as an aid to subsequent workers in taking account of the altered nomenclatorial usage and to indicate where in the literature cogent discussion may be found. Authors of contributions to the Treatise are encouraged to include records of all especially noteworthy emendations of this nature, using the abbreviation emend. with the name to which it refers and citing the author, date, and page of the emendation. Examples from *Treatise* volumes follow.

## Order ORTHIDA Schuchert & Cooper, 1932

[nom. transl. et correct. MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 220, ex suborder Orthoidea SCHUCHERT & COOPER, 1932, p. 43; emend., WILLIAMS & WRIGHT, 1965, p. 299]

#### Subfamily ROVEACRININAE Peck, 1943

[Roveacrininae Реск, 1943, р. 465; *emend.*, Реск in Moore & Teichert, 1978, р. 921]

## STYLE IN GENERIC DESCRIPTIONS CITATION OF TYPE SPECIES

In the *Treatise* the name of the type species of each genus and subgenus is given immediately following the generic name with its accompanying author, date, and page reference or after entries needed for definition of the name if it is involved in homonymy. The originally published combination of generic and trivial names of this species is cited, accompanied by an asterisk (\*), with notation of the author, date, and page of original publication, except if the species was first published in the same paper and by the same author as that containing definition of the genus of which it is the type. In this instance, the initial letter of the generic name followed by the trivial name is given without repeating the name of the author and date. Examples of these two sorts of citations follow.

- **Orionastraea** SMITH, 1917, p. 294 [\**Sarcinula phillipsi* McCoy, 1849, p. 125; OD].
- Schoenophyllum SIMPSON, 1900, p. 214 [\*S. aggregatum; OD].

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

Actinocyathus D'ORBIGNY, 1849, p. 12 [\**Cyathophyllum crenulate* PHILLIPS, 1836, p. 202; M; =*Lons-daleia floriformis* (MARTIN), 1809, pl. 43; validated by ICZN Opinion 419].

In some instances the type species is a junior homonym. If so, it is cited as shown in the following example.

Prionocyclus MEEK, 1871b, p. 298 [\*Ammonites serratocarinatus MEEK, 1871a, p. 429, non STOLICZKA, 1864, p. 57; =Prionocyclus wyomingensis MEEK, 1876, p. 452].

In the *Treatise* the name of the type species is always given in the exact form it had in the original publication. Where mandatory changes are required, such as removal of diacritical marks or hyphens, these are introduced later in the text, typically in the description of a figure.

#### Fixation of Type Species Originally

It is desirable to record the manner of establishing the type species, whether by original designation (OD) or by subsequent designation (SD). The type species of a genus or subgenus, according to provisions of the *Code*, may be fixed in various ways in the original publication; or it may be fixed subsequently in ways specified by the Code (Article 68) and described in the next section. Type species fixed in the original publication include (1) original designation (in the Treatise indicated by OD) when the type species is explicitly stated or (before 1931) indicated by n. gen., n. sp. (or its equivalent) applied to a single species included in a new genus, (2) defined by use of *typus* or *typicus* for one of the species included in a new genus (adequately indicated in the Treatise by the

specific name), (3) established by *monotypy* if a new genus or subgenus has only one originally included species (in the *Treatise* indicated as M), and (4) fixed by *tautonymy* if the genus-group name is identical to an included species name not indicated as the type.

#### Fixation of Type Species Subsequently

The type species of many genera are not determinable from the publication in which the generic name was introduced. Therefore, such genera can acquire a type species only by some manner of subsequent designation. Most commonly this is established by publishing a statement naming as type species one of the species originally included in the genus. In the Treatise such fixation of the type species by subsequent designation in this manner is indicated by the letters SD accompanied by the name of the subsequent author (who may be the same person as the original author) and the publication date and page number of the subsequent designation. Some genera, as first described and named, included no mentioned species (for such genera established after 1930, see below); these necessarily lack a type species until a date subsequent to that of the original publication when one or more species is assigned to such a genus. If only a single species is thus assigned, it becomes automatically the type species. Of course, the first publication containing assignment of species to the genus that originally lacked any included species is the one concerned in fixation of the type species, and if this publication names two or more species as belonging to the genus but did not designate a type species, then a later SD designation is necessary. Examples of the use of SD as employed in the Treatise follow.

- Hexagonaria GURICH, 1896, p. 171 [\**Cyathophyllum hexagonum* GOLDFUSS, 1826, p. 61; SD LANG, SMITH, & THOMAS, 1940, p. 69].
- Mesephemera Handlirsch, 1906, p. 600 [\**Tineites lithophilus* Germar, 1842, p. 88; SD Carpenter, herein].

Another mode of fixing the type species of a genus is through action of the International

Commission of Zoological Nomenclature using its plenary powers. Definition in this way may set aside application of the *Code* so as to arrive at a decision considered to be in the best interest of continuity and stability of zoological nomenclature. When made, it is binding and commonly is cited in the *Treatise* by the letters ICZN, accompanied by the date of announced decision and reference to the appropriate numbered opinion.

Subsequent designation of a type species is admissible only for genera established prior to 1931. A new genus-group name established after 1930 and not accompanied by fixation of a type species through original designation or original indication is invalid (*Code*, Article 13.3). Effort of a subsequent author to validate such a name by subsequent designation of a type species constitutes an original publication making the name available under authorship and date of the subsequent author.

#### HOMONYMS

Most generic names are distinct from all others and are indicated without ambiguity by citing their originally published spelling accompanied by name of the author and date of first publication. If the same generic name has been applied to two or more distinct taxonomic units, however, it is necessary to differentiate such homonyms. This calls for distinction between junior homonyms and senior homonyms. Because a junior homonym is invalid, it must be replaced by some other name. For example, Callophora HALL, 1852, introduced for Paleozoic trepostomate bryozoans, is invalid because Gray in 1848 published the same name for Cretaceous-Holocene cheilostomate bryozoans. Bassler in 1911 introduced the new name Hallophora to replace Hall's homonym. The Treatise style of entry is given below.

Hallophora Bassler, 1911, p. 325, nom. nov. pro Callophora Hall, 1852, p. 144, non Gray, 1848.

In like manner, a replacement generic name that is needed may be introduced in the *Treatise* (even though first publication of generic names otherwise in this work is generally avoided). An exact bibliographic reference must be given for the replaced name as in the following example.

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

#### Synonymous Homonyms

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

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

A rare but special case of homonymy exists when identical family names are formed from generic names having the same stem but differing in their endings. An example is the family name Scutellidae RICHTER & RICHTER, 1925, based on *Scutellum* PUSCH, 1833, a trilobite. This name is a junior homonym of Scutellidae GRAY, 1825, based on the echinoid genus *Scutella* LAMARCK, 1816.

Mysterium De LAUBENFELS, herein, nom. nov. pro Mystrium SCHRAMMEN, 1936, p. 183, non ROGER, 1862 [\*Mystrium porosum SCHRAMMEN, 1936, p. 183; OD].

The name of the trilobite family was later changed to Scutelluidae (ICZN, Opinion 1004, 1974).

#### SYNONYMS

In the *Treatise*, citation of synonyms is given immediately after the record of the type species. If two or more synonyms of differing date are recognized, these are arranged in chronological order. Objective synonyms are indicated by accompanying designation *obj.*, others being understood to constitute subjective synonyms, of which the types are also indicated. Examples showing *Treatise* style in listing synonyms follow.

- Mackenziephyllum Pedder, 1971, p. 48 [\*M. insolitum; OD] [=Zonastraea Tsyganko in Spasskiy, KRAVTSOV, & Tsyganko, 1971, p. 85, nom. nud.; Zonastraea Tsyganko, 1972, p. 21 (type, Z. graciosa, OD)].
- Kodonophyllum WEDEKIND, 1927, p. 34 [\*Streptelasma Milne-Edwardsi DyBowski, 1873, p. 409; OD; =Madrepora truncata LINNE, 1758, p. 795, see SMITH & TREMBERTH, 1929, p. 368] [=Patrophontes LANG & SMITH, 1927, p. 456 (type, Madrepora truncata LINNE, 1758, p. 795, OD); Codonophyllum LANG, SMITH, & THOMAS, 1940, p. 39, obj.].

Some junior synonyms of either the objective or the subjective sort may be preferred over senior synonyms whenever uniformity and continuity of nomenclature are served by retaining a widely used but technically rejectable name for a genus. This requires action of the ICZN, which may use its plenary powers to set aside the unwanted name, validate the wanted one, and place the concerned names on appropriate official lists.

## OTHER EDITORIAL MATTERS BIOGEOGRAPHY

Purists, *Treatise* editors among them, would like nothing better than a stable world with a stable geography that makes possible a stable biogeographical classification. Global events of the past few years have shown how rapidly geography can change, and in all likelihood we have not seen the last of such change as new, so-called republics continue to spring up all over the globe. One expects confusion among readers in the future as they try to decipher such geographical terms as U.S.S.R., Yugoslavia, or Ceylon. Such confusion is unavoidable, as books must be completed and published at some real time. Libraries would be limited indeed if publication were always to be delayed until the political world had settled down. In addition, such terms as central Europe and western Europe are likely to mean different things to different people. Some imprecision is introduced by the use of all such terms, of course, but it is probably no greater than the imprecision that stems from the fact that the work of paleontology is not yet finished, and the geographical ranges of many genera are imperfectly known.

Other geographic terms can also have varying degrees of formality. In general, *Treatise* policy is to use adjectives rather than nouns to refer to directions. Thus we have used *southern* and *western* in place of *South* and *West* unless a term has been formally defined as a geographic entity (e.g., South America or West Virginia). Note that we have referred to western Texas rather than West Texas, which is said to be not a state but a state of mind.

#### NAMES OF AUTHORS: TRANSLATION AND TRANSLITERATION

Chinese scientists have become increasingly active in systematic paleontology in the past two decades. Chinese names cause anguish among English-language bibliographers for two reasons. First, no scheme exists for one-to-one transliteration of Chinese characters into roman letters. Thus, a Chinese author may change the roman-letter spelling of his name from one publication to another. For example, the name Chang, the most common family name in the world reportedly held by some one billion people, has been spelled more recently Zhang. The principal purpose of a bibliography is to provide the reader with entry into the literature. Quite arbitrarily, therefore, in the interest of information retrieval, the Treatise editorial staff has decided to retain the roman spelling

that a Chinese author has used in each of his publications rather than attempting to adopt a common spelling of an author's name to be used in all citations of his work. It is entirely possible, therefore, that the publications of a Chinese author may be listed in more than one place under more than one name in the bibliography.

Second, most but by no means all Chinese list their family name first followed by given names. People with Chinese names who study in the West, however, often reverse the order, putting the family name last as is the Western custom. Thus, for example, Dr. Yi-Maw Chang, formerly of the staff of the Paleontological Institute, was Chang Yi-Maw when he lived in Taiwan. When he came to America, he became Yi-Maw Chang. In the *Treatise*, authors' names are used in the text and listed in the references as they appear in the source being cited.

Several systems exist for transliterating the Cyrillic alphabet into the roman alphabet. On the recommendation of skilled bibliographic librarians, we have adopted the American Library Association/Library of Congress romanization table for Russian and other languages using the Cyrillic alphabet.

## MATTERS SPECIFIC TO THIS VOLUME

Some languages, in this volume most notably the Polish and Czech languages, are enriched with the use of diacritical marks that provide enhanced alphabetical diversity. While celebrating diversity, we have nevertheless elected to omit such marks from Polish and Czech geographical terms used in the Treatise. We continue to insert diacritical marks into authors' names. Two factors have led us to this editorial decision. First, we in the Treatise editorial office typeset electronically all the pages, and such diacritical marks must be inserted by hand into the final computer-prepared pages. This is a costly and time-consuming operation that is fraught with the possibility of introducing errors. Second, in the burgeoning information age of the new millennium, databases and schemes for information retrieval will be of critical importance in managing paleontological information. Stability and uniformity of terminology are requisites of databasemanagement systems, and the use of diacritical marks and computer technology are likely to remain incompatible for some time to come. We hope that linguistic purists will be tolerant of this transgression, which we have undertaken solely in the interest of expediency, consistency, and information retrieval.

In this volume we have taken special pains to acknowledge authorship of chapters and subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a chapter or subsection.

While editor of the Treatise, the late Professor Curt Teichert once remarked that a published Treatise volume is a progress report and should be considered by no means as the last word on the systematics and paleontology of the organisms it discusses. Differences of opinion occur naturally among Treatise authors of good will, who may see things differently or give different weights to morphological characters. In this volume the careful reader will find some taxa, especially higher taxa, included in more than one place in the classification. This has occurred because the authors of the sections on Paleozoic sponges have a different idea of the proper classificatory scheme from the authors of Mesozoic and Cenozoic sponges. We in the editorial office, unwilling to impose our less well-informed views on the specialists, have accommodated this lack of tidiness in the interest of getting the ideas out where all can see them. The next generation of paleontologists will have to address these discrepancies as, in the final analysis, there can be only one phylogeny and should be but one classification expressing it.

Stratigraphic ranges of taxa have been compiled from the ranges of lower taxa. In all instances, we have used the *range-through* method of describing ranges. In instances, therefore, where the work of paleontology is not yet finished, some ranges of higher taxa will not show gaps between the ranges of their subtaxa and may seem to be more complete than the data warrant.

#### ACKNOWLEDGMENTS

The Paleontological Institute's Assistant Editor for Text, Jill Hardesty, and the Assistant Editor for Illustrations, Jane Kerns, have faced admirably the formidable task of moving this volume through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team including Mike Cormack with his outstanding computer skills, Mary Huyck with her work on illustrations, and Denise Mayse with general support. Jill Krebs, the remaining member of the Paleontological Institute editorial staff, is involved with preparation of PaleoBank, the paleontological database for future Treatise volumes, and has not been closely involved with this volume.

Many of the illustrations in this volume were prepared a number of years ago by the late Roger B. Williams, who served the Paleontological Institute as assistant editor for illustrations until shortly before his death. We remain indebted to him for his dedication to the *Treatise* project, his very high standards, and his synoptic view of the *Treatise*.

This editorial preface and other, recent ones are extensive revisions of the prefaces prepared for previous *Treatise* volumes by former editors, including the late Raymond C. Moore, the late Curt Teichert, and Richard A. Robison. I am indebted to them for preparing earlier prefaces and for the leadership they have provided in bringing the *Treatise* project to its present status.

Finally, on behalf of the members of the staff of the Paleontological Institute and the other authors of this volume, I am pleased to have the opportunity to extend our sincere thanks to Professor J. Keith Rigby for helping us bring this volume to publication. Throughout his career, his work has been marked by scrupulous scholarship, complete dedication to the task, and unwavering attention to detail. He has brought the same approach to this project, and we are grateful to him for all he has done.

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- Robison, R. A., and C. Teichert. 1979. Treatise on Invertebrate Paleontology. Part A, Introduction. The Geological Society of America and The University of Kansas. Boulder & Lawrence. 569 p.

Roger L. Kaesler Lawrence, Kansas May 5, 2004

## STRATIGRAPHIC DIVISIONS

The major divisions of the geological time scale are reasonably well-established throughout the world, but minor divisions (e.g., subseries, stages, and substages) are more likely to be provincial in application. The stratigraphic units listed here represent an authoritative version of the stratigraphic column for all taxonomic work relating to the revision of Part E. They are adapted from the International Stratigraphic Chart, and units are approved by the International Commission on Stratigraphy (ICS) and ratified by the International Union of Geological Sciences (IUGS). A copy of the comple chart can be obtained at the following website: http://www.iugs.org/iugs/pubs/intstratchart.htm.

**Cenozoic Erathem** Neogene System Holocene Series Pleistocene Series **Pliocene Series** Miocene Series Paleogene System Oligocene Series **Eocene Series** Paleocene Series Mesozoic Erathem Cretaceous System Upper Cretaceous Series Lower Cretaceous Series **Jurassic System** Upper Jurassic Series Middle Jurassic Series Lower Jurassic Series **Triassic System** Upper Triassic Series Middle Triassic Series Lower Triassic Series

Paleozoic Erathem Permian System Lopingian Series Guadalupian Series Cisuralian Series Carboniferous System Pennsylvanian Subsystem Mississippian Subsystem Devonian System Upper Devonian Series Middle Devonian Series Lower Devonian Series Silurian System Pridoli Series Ludlow Series Wenlock Series Llandovery Series Ordovician System Upper Ordovician Series Middle Ordovician Series Lower Ordovician Series Cambrian System Furongian Series Middle Cambrian Series Lower Cambrian Series Neoproterozoic Erathem Ediacaran System Cryogenian System **Tonian System** 

## **COORDINATING AUTHOR'S PREFACE**

J. KEITH RIGBY [Brigham Young University]

Volumes 2 and 3 of the current revision are the first to revise and update the Porifera section of the 1955 pioneer volume of *The Treatise of Invertebrate Paleontology, Part E,* by M. W. de Laubenfels. That significant work helped initiate renewed interest in the sponges among the next generation of researchers, an interest also prompted, in part, by the focused studies of N. D. Newell and G. A. Cooper and their students and coworkers on the faunas and facies of the Permian reefs of Texas and New Mexico.

The current revision includes this systematic volume concerned largely with those forms that have been traditionally included in the Porifera. This volume was preceded by an introductory volume, published in December 2003. An additional volume is in preparation documenting those groups relatively newly included in the phylum, such as the stromatoporoids, chaetetids, and sclerosponges. Some minor overlap of these two efforts is inevitable, particularly where taxonomic limits are blurred in the gray area established between categories.

Sponges are relatively simple animals with a long and incomplete geologic record, for many taxa likely left no readable record of their organic skeleton or skeletons of easily disassembled elements, although they contributed to cherty units and spiculites throughout the geologic record. Sponges are common animals in modern seas, yet relatively few paleontologists have focused research efforts on fossil sponges and their geologic record, possibly because of their perceived limited value as time-stratigraphic index fossils and also because their selective preservation of biologic information has made use of classifications of living forms difficult for fossils in some instances because of limitation of what can be seen in the fossils. As a result, records of sponges with solid skeletons, such as the lithistid demosponges

or groups of calcareous sponges, have been overplayed because of their ease of preservation compared to the probably large and diverse populations of sponges with easily disarticulated or organic skeletons that are undocumented. Nonetheless more than 1,200 genera of fossil sponges have been described and illustrated here, representing numerous families and orders in each of the traditional classes of the Porifera.

Investigations of fossil Porifera have had cycles of interest when numbers of investigators and, as a consequence, numbers of publications increased and decreased, as documented in the extensive bibliography compiled for the volumes. Peaks of activity were recorded in the 1870–1890s and 1960– 1990s, but comparatively few papers were published in the mid-1800s, the 1900– 1920s, and during the immediate past few years.

This revision of the Porifera volume is largely the result of three specialists: Robin E. H. Reid, Robert M. Finks, and J. Keith Rigby. Reid and Finks began their compilations and manuscript preparation in the 1970s at the invitation of R. C. Moore, with Reid focusing on Mesozoic and Cenozoic hexactinellid and demosponge taxa and Finks on Paleozoic taxa and the heteractinid and calcareous sponges. Both of them completed manuscripts on several chapters of the introduction and made preliminary compilations on some systematic sections. Reid completed manuscripts on Mesozoic and Cenozoic demospongiid and hexactinellid taxa by the late 1970s but shifted his research interests some time later to work on vertebrate fossils. I became officially involved in 1987 after it became apparent that preparation of manuscripts and illustrations for the fossil sponges needed renewed efforts to complete and update earlier compilations and descriptions and to include descriptions

and illustrations of the various taxa added to the geologic record since the period of active involvement of the first two authors. Numerous colleagues have contributed much and willingly helped with literature and locality and distribution data. They have assisted in helping to settle many problems satisfactorily.

Appreciation is expressed to colleagues for their assistance in preparation of the manuscript and illustrations for this volume of the Treatise of Invertebrate Paleontology. In particular I would like to thank Baba Senowbari-Daryan, Institute für Paläontologie, Universität Erlangen-Nürnberg; Andrzej Pisera, Polska Akademia Nauk, Warsaw; Diego Garcia-Bellido Capdevila, Universidad Complutense, Madrid; Loren Babcock, Ohio State University; Dorte Mehl-Janussen, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main; Fan Jiasong, Institute of Geology, Beijing; Wu Xichun, Chengdu Institute of Geology, China; Rachel Wood, University of Cambridge; Andrey Yu. Zhuravlev, Palaeontological Institute, Russian Academy of Sciences, Moscow; V. J. Goryansky, Leningrad; Barry D. Webby, University of Sidney; and John Pickett, Geological Survey of New South Wales. Appreciation is also extended to Robert B. Blodgett, Oregon State University; Robert E. Sloan and Penny Krosch, University of Minnesota; Wilbert R. Danner, University of British Columbia; Karl W. Flessa, University of Arizona; Fred D. Bosworth, Johns Hopkins University; Carl W. Stock, University of Alabama; Colin W. Stearn, McGill University; Robert J. Elias, University of Manitoba; Françoise Debrenne, Laboratoire de Paléontologie, Paris; Björn E. E. Neuman, University of Bergen; Tomasz Wrzolek, Silesian University,

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I thank the faculty and staff of the Department of Geology, Brigham Young University, for their support and continuing interest, and thank personnel of the Interlibrary Loan Office of the Harold B. Lee Library, also at Brigham Young University, for their invaluable assistance. I also express gratitude for secretarial help in preparation of final verisons of manuscripts at Brigham Young University, some of which was partially funded by a grant from The Paleontological Institute, University of Kansas, which also funded translation by Dmitri Slinkov of critical Russian literature for the compilation. The continued interest and support of editors and the staff of The Paleontological Institute, University of Kansas, through the long process of preparation and production of the manuscript and illustrations, editing the compilations, and, finally, publication of the volumes is also much appreciated.

## **REPOSITORIES AND THEIR ABBREVIATIONS**

Abbreviations and locations of museums and institutions holding type material, which are used throughout the volume, are listed below.

- AGE: Archiv für Geschiebekunde, Geologisch-Paläontologisches Institut, Hamburg, Germany
- AI: Institute of Geological Sciences, Polish Academy of Sciences, Kraków, Poland
- AMNH: American Museum of Natural History, New York City, New York, USA
- AM or AMu: Australian Museum, Sydney, Australia
- BM: Berlin Museum, Berlin, Germany
- BMNH: British Museum (Natural History), London, United Kingdom
- BMS: Buffalo Museum of Science, Buffalo, New York, USA
- **BSPGM:** Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany
- BYU: Geology Department, Brigham Young University, Provo, Utah, USA
- CCG: Chengdu College of Geology (now Chengdu University of Technology), Chengdu, Sichuan, China
- CEGH-UNC: Cátedra de Estratigrafía y Geología Histórica, Universidad Nacional de Córdoba, Córdoba, Argentina
- CSGM: Central Siberian Geological Museum, United Institute of Geology, Geophysics, & Mineralogy, Siberian Branch of the Russian Academy of Sciences, Novosibirsk, Russia
- CU: University of Cincinnati, Cincinnati, Ohio, USA
- CUG: Colgate University, Geology Department Collections, Hamilton, New York, USA
- CPC: Bureau of Mineral Resources, Canberra, Australia
- CRICYT: Centro Regional de Investigaciones Científicas y Tecnológicas, Mendoza, Argentina
- FEGI: Far East Geological Institute, Russian Academy of Sciences, Vladivostok, Russia
- FM: Field Museum (Natural History), Chicago, Illinois, USA
- GII: Institut für Geologie und Paläontologie der Universität Innsbruck, Innsbruck, Austria
- GIK: Geologisch-Paläontologisches Institut, Universität zu Köln, Köln, Germany
- GPIMH: Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Hamburg, Germany
- GSC: Geological Survey of Canada, Ottawa, Canada
- GSM: British Geological Survey (formerly Geological Survey Museum; Institute of Geological Sciences, London), Keyworth, Nottinghamshire, United Kingdom
- GSS: Geological Survey of Scotland, Edinburgh, United Kingdom
- **GSWA:** Geological Survey of Western Australia, East Perth, Australia
- HM: Hunterian Museum, University of Glasgow, Glasgow, United Kingdom

- IGASB: Institute of Geology, Academia Sinica, Beijing, China
- IGPTU: Institut und Museum für Geologie und Paläontologie, Tübingen Universität, Tübingen, Germany
- IPFUB: Institut für Paläontologie, Freie Universität, Berlin, Germany
- IPPAS: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland
- IPM: Institut de Paléontologie du Muséum national d'Histoire naturelle de Paris, Paris, France
- IPUB: Institüt für Paläontologie, Universität Bonn, Bonn, Germany
- IPUM: Instituto di Paleontologia, Università di Modena, Modena, Italy
- IRSNB: Institut Royal des Sciences naturelles de Belgique, Brussels, Belgium
- ISM: Illinois State Geological Survey, Urbana, Illinois, USA, formerly at Illinois State Museum, Springfield, Illinois, USA
- IU: Îndiana University, Bloomington, Indiana, USA
- JPI: Jianghan Petroleum Institute, Jingsha, Hubei, China
- KUMIP: University of Kansas, Lawrence, Kansas, USA
- LGI: Leningrad Mining Institute, Leningrad, Russia
- MCCA: Museo Comunale in Cortina d'Ampezzo, Cortina d'Ampezzo, Italy
- MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA
- MFGI: Museum Far Eastern Geological Institute, Vladivostok, Russia
- MHGI: Museum of the Hungarian Geologic Institute, Budapest, Hungary
- MIGT: Museum, Institute of Geology, Dushambe, Tajikistan
- MMMN: Manitoba Museum of Man and Nature, Winnipeg, Canada
- MMF: Geological and Mining Museum, Sydney, Australia
- MNCN: Museo Nacional de Ciencias Naturales, Madrid, Spain
- MNHN: Muséum National d'Histoire Naturelle de Paris, Paris, France
- MUZ IG: Museum of the State Geological Institute, Warsaw, Poland
- NIGPAS: Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, China
- NIUPGAS: Nanjing Institute of Geology and Paleontology, Academia Sinica, Nanjing, China
- NMV: National Museum of Victoria, Melbourne, Australia
- NRM: Naturhistoriska Riksmuseet (Swedish Museum of Natural History), Stockholm, Sweden
- NYSM: New York State Museum, Albany, New York, USA

- **ODM:** Old Dominion College, Norfolk, Virginia, USA
- OSU: Ohio State University, Department of Geology, Columbus, Ohio, USA
- OUZC: Ohio University Zoological Collections, Athens, Ohio, USA
- PDMNH-P: Paleontological Department of the National Museum, Museum of Natural History, Prague, Czech Republic
- **PIUB:** Paleontological Institute of the University of Bonn, Bonn, Germany
- PIUFB: Paläontologisches Institut, Freie Universität Berlin, Berlin, Germany
- PIUW: Paläontologichen Instituts, Universität Wien, Vienna, Austria
- PIUZ: Paleontological Institute, University of Zürich, Zürich, Switzerland
- PIW: Institut für Paläontologie der Universität Würzburg, Würzburg, Germany
- P-MD: Provincial Museum of Danzig, Danzig, Germany
- PRM: Peter Redpath Museum, Montreal, Canada
- PU: Princeton University, Princeton, New Jersey, USA
- ROM: Royal Ontario Museum, Toronto, Canada
- SAM: South Australian Museum, Adelaide, Australia
- SGIP: Sammlung des Geologisch-Paläontologichen Institutes der Universität Palermo, Palermo, Italy
- SMF: Natur-Museum und Forschungs-Institut, Senckenberg, Germany
- SPIE: Sammlung des Institut für Paläontologie, Universität Erlangen-Nürnberg, Erlangen, Germany
- SPIML: Sammlung des Paläontologischen Institutes der Universität Marburg, Lahn, Germany
- SPIT: Sammlung des Paläontologischen Institutes der Universität Tübingen, Tübingen, Germany
- SSPHG: Staatliches Sammlung für Paläontologie und historische Geologie, München, Germany
- SSSBGF: Stratigraphische Sammlung der Sektion Geowissenschaften der Bergakademia Freiberg, Freiberg, Germany
- SUP: Sydney University, Department of Geology, Sydney, Australia

- TMM: Texas Memorial Museum, University of Texas, Austin, Texas, USA
- TsNIGER: Ts NIGER Museum, Russia
- UA: University of Alberta, Edmonton, Alberta, Canada
- UAF: University of Alaska, Fairbanks, Alaska, USA
- UC: University of Cincinnati, Cincinnati, Ohio, USA
- UCC: Chicago Natural History Museum, formerly in Walker Museum, Chicago, Illinois (see also FM), USA
- UCM: Universidad Complutense de Madrid, Madrid, Spain
- UG: University of Göttingen, Göttingen, Germany
- UL: Lodz University, Institute of Geography, Lodz, Poland
- UM: University of Minnesota, Minneapolis, Minnesota, USA
- UMG: University of Montana, Department of Geology, Missoula, Montana, USA
- UNE: University of New England, Armidale, New South Wales, Australia
- **UPLGS:** Université de Paris, Laboratoire de Géologie de la Sorbonne, Paris, France
- U-SK: Universitäts-Sammlung zu Kiel, Germany
- UTBEG: University of Texas, Bureau of Economic Geology, Austin, Texas, USA
- VK: Theo Van Kemper Collection, Amsterdam, The Netherlands
- WAGS: Western Australia Geological Survey, Perth, Australia
- WAM: Western Australia Museum, Perth, Australia
- WIF: Wadi Institute of Himalayan Geology, Dehra Dun, India
- WMC: Woodwardian Museum, University of Cambridge, Cambridge, United Kingdom
- WMNM: Wesfälisches Museum für Naturkunde, Münster, Germany
- YaFAN: Institute of Geology, Yakut Branch, Siberian Division AN SSR, Yakutsk, Russia
- YPM: Yale Peabody Museum, New Haven, Connecticut, USA
- ZPAL: Institute of Paleobiology, Warsaw, Poland

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## CLASSIFICATION

### J. K. Rigby

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The outline classification presented below is principally of fossil sponges treated in this volume. It summarizes taxonomic relationships and presents stratigraphic ranges of the various taxa. Numbers in parentheses indicate the number of recognized fossil genera in each suprageneric group, from family to class, with the number of subgenera included being the second number, listed after the semicolon. Because some differences in taxonomic approaches exist between sections in this volume, particularly in dealing with the Demospongea, the classification below should be considered as a work in progress. It does not necessarily reflect systematic concepts presented in chapters written by R. E. H. Reid or R. M. Finks.

The order of taxa in the outline represents taxonomic relationships and may be different from the order presented in the systematic sections because taxa in those sections are generally separated into Paleozoic and Mesozoic-Cenozoic occurrences. As a result, some major categories may be represented in two or three systematic sections. For example, the section treating hypercalcified sponges documents sponges strictly included in the class Calcarea and also some demosponges (noted by the symbol \*\* after the stratigraphic ranges) that have calcareous skeletons. In other sections, a family with a long stratigraphic range may be represented in both Paleozoic and Mesozoic sections or chapters where those demosponges or hexactinellid sponges are treated (marked by the symbol <sup>†</sup>). Question marks on some geologic ages indicate questionable occurrences of that taxon in rocks of that age.

Phylum Porifera Grant, 1836 (1,183;30). Cryogenian-Holocene.

Class Demospongea Sollas, 1875 (615;11). Cryogenian-Holocene.

Subclass Clavaxinellida Lévi, 1956 (54). Cryogenian-Holocene.

Order Protomonaxonida Finks & Rigby, herein (39). Cryogenian-Holocene.

- Family Leptomitidae de Laubenfels, 1955 (4). Cambrian-Silurian.
- Family Sinospongiidae Finks & Rigby, herein (1). Cryogenian-Ediacaran.
- Family Hamptoniidae de Laubenfels, 1955 (4). Middle Cambrian-Middle Ordovician.
- Family Ulospongiellidae Rigby & Collins, 2003 (2). Middle Cambrian.
- Family Choiidae de Laubenfels, 1955 (4). Lower Cambrian-Middle Cambrian.
- Family Wapkiidae de Laubenfels, 1955 (1). Middle Cambrian.
- Family Halichondritidae Rigby, 1986 (2). ?Middle Cambrian, Upper Cambrian–Carboniferous (Serpukhovian).
- Family Piraniidae de Laubenfels, 1955 (2). Middle Cambrian.
- Family Sollasellidae von Lendenfeld, 1887 (7). Devonian (Lochkovian)-Holocene.
- Family Tethyidae Gray, 1867 (1). ?Paleogene, Holocene.
- Family Hazeliidae de Laubenfels, 1955 (4). Middle Cambrian-Lower Devonian.
- Family Takakkawiidae de Laubenfels, 1955 (1). Middle Cambrian.
- Family Mahalospongiidae Rigby & Stuart, 1988 (1). Silurian-Devonian.

Family Heliospongiidae Finks, 1960 (5). Carboniferous (Middle Pennsylvanian)–Permian (Changhsingian).

Order Clavulina Vosmaer, 1887 (15). Ordovician–Holocene.

- Family Clionaidae Gray, 1867 (9). Ordovician-Holocene.
- Family Adociidae de Laubenfels, 1936 (1). Triassic (Carnian)-Holocene.
- Family Spirastrellidae Hentschel, 1909 (2). Paleogene-Holocene.

Family Suberitidae Ridley & Dendy, 1886 (3). Cretaceous-Holocene.

Subclass Choristida Sollas, 1880 (52;2). Ordovician-Holocene.

Order Plakinida Reid, 1968 (5). ?Upper Jurassic, Lower Cretaceous (?Albian), Upper Cretaceous (?Cenomanian-?Santonian, Campanian)–Holocene.

Family Plakinidae Schulze, 1880 (3). Lower Cretaceous (?Albian), Paleogene (upper Eocene)– Holocene.

Family Thrombidae Sollas, 1887 (1). ?Upper Cretaceous, Paleogene (upper Eocene)–Holocene.

Family Acanthastrellidae Schrammen, 1924 (1). ?Upper Jurassic, Upper Cretaceous (Campanian).

## Porifera

Order Pachastrellida Reid, herein (13). Carboniferous-Holocene. Family Pachastrellidae Carter, 1875 (10). Carboniferous (Mississippian)-Holocene. Subfamily Pachastrellinae Carter, 1875 (2). Carboniferous (?Mississippian), ?Jurassic, ?Cretaceous, Paleogene (?upper Eocene), Holocene. Subfamily Calthropellinae von Lendenfeld, 1907 (1). ?Cretaceous, Holocene. Subfamily Halininae de Laubenfels, 1934 (2). Lower Cretaceous (?Albian), Paleogene (upper Eocene-Holocene. Subfamily Uncertain (5). Family Costamorphiidae Mostler, 1986 (1). Upper Triassic. Family Theneidae Gray, 1872 (2). Upper Cretaceous (?Turonian, Coniacian)-Holocene. Order Ancorinida Reid, 1968 (19;2). Carboniferous (Mississippian)-Holocene. Family Ancorinidae Schmidt, 1870 (6). Jurassic-Holocene. Subfamily Ancorininae Schmidt, 1870 (3). Jurassic-Holocene. Subfamily Stellettinae Carter, 1875 (3). ?lower Lower Jurassic, Cretaceous (?Albian, Turonian)-Holocene. Family Geodiidae Gray, 1867 (11;2). Carboniferous (Mississippian)-Holocene. Subfamily Geodiinae Gray, 1867 (9). Carboniferous (Mississippian)-Holocene. Subfamily Erylinae Sollas, 1888 (2;2). Upper Jurassic-Holocene. Family Paelospongiidae Mostler, 1986 (2). Upper Triassic. Order Craniellida Reid, 1968 (2). Upper Cretaceous (Campanian)-Holocene. Family Tetillidae Sollas, 1886 (2). Upper Cretaceous (Campanian)-Holocene. Order Uncertain (13). Family Cephaloraphiditidae Reid, 1968 (7). Jurassic-Neogene. Family Helminthophyllidae Schrammen, 1936 (1). Upper Jurassic (Kimmeridgian). Family Scolioraphididae Zittel, 1879 (2). Cretaceous. Family Uncertain (3). Subclass Tetractinomorpha Lévi, 1953 (30). Ordovician-Holocene. Order Streptosclerophorida Dendy, 1924 (13). Middle Ordovician-Permian (Lopingian). Suborder Eutaxicladina Rauff, 1894 (13). Middle Ordovician-Permian (Lopingian). Family Hindiidae Rauff, 1893 (13). Middle Ordovician-Permian (Changhsingian). Order Hadromerida Topsent, 1898\*\* (17). Permian-Triassic. Family Celyphiidae de Laubenfels, 1955\*\* (13). Permian (Guadalupian)-Cretaceous. Family Ceotinellidae Senowbari-Daryan, 1978\*\* (1). Triassic (Ladinian-Carnian). Family Polysiphonidae Girty, 1909\*\* (3). Permian-Triassic. Subclass Ceractinomorpha Lévi, 1953 (479;9). Cambrian-Holocene. Order Dictyoceratida Minchin, 1900 (5). Lower Jurassic-Holocene. Family Spongiidae Gray, 1867 (1). Holocene. Family Dysideidae Gray, 1867 (3). Lower Jurassic-Holocene. Family Uncertain (1). Order Dendroceratida Minchin, 1900 (0). Holocene. Order Verongida Bergquist, 1978 (3). Middle Cambrian-Holocene. Family Verongiidae de Laubenfels, 1936 (2). Middle Carboniferous-Holocene. Family Vauxiidae Walcott, 1920 (1). Middle Cambrian. Order Halichondrida Topsent, 1898 (2). Paleogene (Oligocene)-Holocene. Family Halichondriidae Gray, 1867 (1). Holocene. Family ?Hymeniacidonidae de Laubenfels, 1936 (1). Paleogene (Oligocene)-Neogene (Miocene). Order Poecilosclerida Topsent, 1928 (16). Cretaceous-Holocene. Family Myxillidae Hentschel, 1923 (3). Paleogene-Holocene. Family Tedaniidae Ridley & Dendy, 1886 (4). Paleogene-Holocene. Family Cladorhizidae de Laubenfels, 1936 (2). Paleogene-Holocene. Family Amphilectidae de Laubenfels, 1936 (2). Paleogene-Holocene. Family Latrunculiidae Topsent, 1922 (1). Paleogene-Holocene. Family Acarniidae de Laubenfels, 1936 (2). Cretaceous-Holocene. Family Uncertain (2). Order Haplosclerida Topsent, 1898 (18). Jurassic-Holocene. Family Spongillidae Gray, 1867 (10). Jurassic-Holocene. Family Haliclonidae de Laubenfels, 1932 (2). Paleogene (?Eocene), Holocene. Family Petrosiidae Van Soest, 1980 (2). Paleogene (Eocene)-Holocene. Family Desmacidonidae Gray, 1867 (2). Paleogene-Holocene. Family Uncertain (2).

- Order Agelasida Verrill, 1907\*\* (145). Ordovician–Triassic.
  - Family Catenispongiidae Finks, 1995\*\* (4). Permian (Artinskian)-Triassic.
  - Family Virgolidae Termier, Termier, & Vachard, 1977\*\* (14). Permian-Triassic.
    - Subfamily Virgolinae Termier & Termier, 1977\*\* (6). Permian (Kungurian)–Triassic.
    - Subfamily Preeudinae Senowbari-Daryan, 1996\*\* (6). Permian (Kungurian-Changhsingian).
    - Subfamily Pseudohimatellinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian.
  - Subfamily Parahimatellinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Lopingian).
  - Family Sphaeropontiidae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Lopingian).
  - Family Exotubispongiidae Rigby & Senowbari-Daryan, 1996 (1). Permian (Lopingian).
  - Family Sestrostomellidae de Laubenfels, 1955\*\* (8). Triassic-Lower Cretaceous.
  - Family Pharetrospongiidae de Laubenfels, 1955\*\* (9). Permian (Guadalupian)–Cretaceous. Subfamily Pharetrospongiinae de Laubenfels, 1955\*\* (2). Triassic (Carnian)–Cretaceous. Subfamily Leiofungiinae Finks & Rigby, herein\*\* (7). Permian (Guadalupian)–Cretaceous.
  - Family Auriculospongiidae Termier & Termier, 1977\*\* (9). Permian (Asselian–Changhsingian).
    Subfamily Auriculospongiinae Termier & Termier, 1977\*\* (3). Permian (Asselian–Changhsingian).
    Subfamily Daharellinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Changhsingian).
    Subfamily Gigantospongiinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Guadalupian).
    Subfamily Spinospongiinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Changhsingian).
    Subfamily Acceliinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Changhsingian).
    Subfamily Acceliinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Changhsingian).
  - Family Stellispongiellidae Wu, 1991\*\* (3). Permian (Guadalupian)–Triassic (Norian).
     Subfamily Stellispongiellinae Wu, 1991\*\* (1). Permian (Guadalupian)–Triassic (Norian).
     Subfamily Prestellispongiinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Lopingian).
     Subfamily Estrellospongiinae Rigby & Senowbari-Daryan, 1996\*\* (1). Permian (Lopingian).
  - Family Preperonidellidae Finks & Rigby, herein\*\* (14). Upper Ordovician–Upper Triassic. Subfamily Preperonidellinae Finks & Rigby, herein\*\* (3). Permian (Guadalupian)–Upper Triassic. Subfamily Permocorynellinae Rigby & Senowbari-Daryan, 1996\*\* (3). Permian (Lopingian)– Upper Triassic.
  - Subfamily Precorynellinae Termier & Termier, 1977\*\* (6). Upper Ordovician–Upper Triassic. Subfamily Heptatubispongiinae Rigby & Senowbari-Daryan, 1996\*\* (2). Permian (Lopingian)– Upper Triassic.
  - Family Fissispongiidae Finks & Rigby, herein\*\* (2). Devonian (Eifelian)-Permian.
  - Family Maeandrostiidae Finks, 1971\*\* (6). Carboniferous (Middle Pennsylvanian)–Triassic. Family Angullongiidae Webby & Rigby, 1985\*\* (5). upper Lower Ordovician–upper Upper
  - Ordovician.
  - Family Phragmocoeliidae Ott, 1974\*\* (2). Devonian (Lochkovian)-Triassic (Carnian).
  - Family Intrasporeocoeliidae Finks & Rigby, herein\*\* (4). Permian (Guadalupian–Lopingian).
  - Family Cryptocoeliidae Steinmann, 1882\*\* (5). Silurian (Ludlow)–Upper Triassic.
  - Family Palermocoeliidae Senowbari-Daryan, 1990\*\* (1). Upper Triassic.
  - Family Girtyocoeliidae Finks & Rigby, herein\*\* (9). Ordovician-Triassic.
  - Family Thaumastocoeliidae Ott, 1967\*\* (7). Middle Ordovician–Triassic.
  - Family Aphrosalpingidae Myagkova, 1955\*\* (10). upper Upper Ordovician–Triassic.
  - Subfamily Fistulospongininae Termier & Termier, 1977\*\* (5). upper Upper Ordovician–Permian (Lopingian).
  - Subfamily Vesicocauliinae Senowbari-Daryan, 1990\*\* (4). Triassic.
  - Subfamily Palaeoschadinae Myagkova, 1955\*\* (1). Silurian (Ludlow).
  - Family Glomocystospongiidae Rigby, Fan, & Zhang, 1989\*\* (2). Permian (Lopingian).
  - Family Sebargasiidae de Laubenfels, 1955\*\* (13). ?Ordovician, Carboniferous-Triassic.
  - Family Olangocoeliidae Bechstädt & Brandner, 1970\*\* (1). Middle Triassic.
  - Family Cliefdenellidae Webby, 1969\*\* (3). Middle Ordovician-Upper Ordovician.
  - Family Girtycoeliidae Finks & Rigby, herein\*\* (2). Carboniferous (Upper Pennsylvanian)-Triassic.
  - Family Guadalupiidae Girty, 1909\*\* (7). Carboniferous-Triassic (Norian).
  - Family Uncertain\*\* (3).

## Porifera

Order Vaceletida Finks & Rigby, herein\*\* (51). Lower Cambrian-Holocene.

Family Solenolmiidae Engesser, 1986\*\* (13). Lower Cambrian-Triassic, ?Jurassic.

Subfamily Solenolmiinae Senowbari-Daryan, 1990\*\* (12). Lower Cambrian–Triassic, ?Jurassic. Subfamily Battagliinae Senowbari-Daryan, 1990\*\* (1). Triassic (Norian–Rhaetian).

Family Colospongiidae Senowbari-Daryan, 1990\*\* (13). Lower Cambrian-Triassic.

Subfamily Colospongiinae Senowbari-Daryan, 1990\*\* (6). Lower Cambrian-Triassic.

Subfamily Corymbospongiinae Senowbari-Daryan, 1990\*\* (7). ?Lower Ordovician-?Middle Ordovician, upper Upper Ordovician-Triassic (Rhaetian).

Family Gigantothalamiidae Senowbari-Daryan, 1990\*\* (2). Upper Triassic.

Family Tebagathalamiidae Senowbari-Daryan & Rigby, 1988\*\* (3). Permian-Triassic.

Family Cheilosporitiidae Fischer, 1962\*\* (1). Triassic (Carnian-Rhaetian).

Family Salzburgiidae Senowbari-Daryan & Schäfer, 1979\*\* (1). Permian-Triassic (Rhaetian).

- Family Cribrothalamiidae Senowbari-Daryan, 1990\*\* (1). Triassic (Norian-Rhaetian).
- Family Verticillitidae Steinmann, 1882\*\* (16). Permian (Guadalupian)–Holocene.

Subfamily Verticillitinae Steinmann, 1882\*\* (9). Permian (Guadalupian)–Holocene.

Subfamily Polytholosiinae Seilacher, 1962\*\* (4). Permian (?Lopingian), Triassic.

Subfamily Fanthalamiinae Senowbari-Daryan, 1990\*\* (2). Triassic (Carnian–Norian, ?Rhaetian). Subfamily Polysiphospongiinae Senowbari-Daryan, 1990\*\* (1). Triassic (Norian–Rhaetian). Family Uncertain\*\* (1).

Order Sigmatosclerophorida Burton, 1956 (4). Lower Ordovician–Upper Ordovician. Family Dystactospongiidae Miller, 1889 (4). Lower Ordovician–Upper Ordovician.

Subclass Lithistida Schmidt, 1870 (114). Cambrian-Permian (Lopingian).

Order Orchocladina Rauff, 1895 (114). Middle Cambrian–Permian (Lopingian).
Family Anthaspidellidae Miller, 1889 (63). Middle Cambrian–Permian (Lopingian).
Family Streptosolenidae Johns, 1994 (17). Upper Cambrian–Silurian.
Family Chiastoclonellidae Rauff, 1895 (8). Silurian (Wenlock)–Permian (Lopingian).
Family Anthracosyconidae Finks, 1960 (5). Lower Devonian–Permian (Capitanian).
Family Astylospongiidae Zittel, 1877 (21). Upper Ordovician–Permian (Roadian).

- Order Tetralithistida Lagneau-Hérenger, 1962 (93;9). Upper Triassic (Norian)-Holocene.
  - Suborder Tetracladina Zittel, 1878 (70;9). Upper Triassic (Norian)–Holocene.
    - Family Radiocelliidae Senowbari-Daryan and Wurm, 1994 (1). Upper Triassic (Norian).
    - Family Protetraclisidae Schrammen, 1924 (3). Jurassic (Kimmeridgian).

Family Siphoniidae d'Orbigny, 1849 (27;4). Jurassic-Holocene.

Subfamily Siphoniinae d'Orbigny, 1849 (10;4). Jurassic-Holocene.

Subfamily Phymatellinae Schrammen, 1910 (14). Upper Jurassic–Cretaceous.

Subfamily Lerouxiinae Moret, 1926 (3). Upper Cretaceous (Cenomanian–Campanian).

- Family Astrocladiidae Schrammen, 1901 (2). Upper Cretaceous (Cenomanian-Maastrichtian).
- Family Phymaraphiniidae Schrammen, 1910 (7;3). Lower Cretaceous (Aptian)–Upper Cretaceous. Family Theonellidae von Lendenfeld, 1904 (21;2). Cretaceous–Holocene.
- Subfamily Theonellinae von Lendenfeld, 1904 (8). Lower Cretaceous (Aptian)–Holocene. Subfamily Acrochordoniinae Schrammen, 1910 (7;2). Cretaceous–Neogene (Miocene). Subfamily Phymaplectiinae Reid, herein (2). Upper Cretaceous (Coniacian)–Paleogene (Eocene). Subfamily Uncertain (4).
- Family Plinthosellidae Schrammen, 1910 (3). Cretaceous (Albian-Campanian).
- Family Chenendoporidae F. A. Roemer, 1864 (4). Cretaceous (Aptian–Maastrichtian), Paleogene (?Eocene).
- Family Uncertain (2).
- Suborder Dicranocladina Schrammen, 1924 (16). Upper Jurassic (upper Oxfordian)–Holocene.
  Family Corallistidae Sollas, 1888 (15). Upper Jurassic (upper Oxfordian)–Holocene.
  Subfamily Corallistinae Sollas, 1888 (6). Upper Jurassic (upper Oxfordian)–Holocene.
  Subfamily Gignouxiinae de Laubenfels, 1955 (8). Cretaceous (Aptian)–Neogene (Miocene).
  Subfamily Pachinioninae Schrammen, 1924 (1). Cretaceous (Aptian–Campanian).
  Family Pseudoverruculinidae de Laubenfels, 1955 (1). Cretaceous (Aptian–Santonian).
- Suborder Pseudorhizomorina Schrammen, 1901 (2). Cretaceous-Holocene. Family Macandrewiidae Gray, 1859 (1). ?Upper Cretaceous, Holocene.
  - Family Neopeltidae Sollas, 1888 (1). Cretaceous- Holocene.
- Suborder Didymmorina Rauff, 1893 (5). Middle Jurassic–Upper Jurassic (Kimmeridgian). Family Cylindrophymatidae Schrammen, 1924 (5). Middle Jurassic–Upper Jurassic (Kimmeridgian).

Order Megalithistida Reid, herein (28). Lower Ordovician–Holocene.

Suborder Helomorina Schrammen, 1924 (6). Upper Jurassic (Kimmeridgian)–Cretaceous (Maastrichtian).

Family Carterellidae Schrammen, 1901 (6). Upper Jurassic (Kimmeridgian)–Cretaceous (Maastrichtian).

Subfamily Carterellinae Schrammen, 1901 (3). Cretaceous (Albian-Maastrichtian).

Subfamily Isoraphiniinae Schrammen, 1924 (3). Upper Jurassic (Kimmeridgian)–Cretaceous (Maastrichtian).

Suborder Megamorina Zittel, 1878 (22). Lower Ordovician-Holocene.

Family Archaeodorydermatidae Reid, 1968 (1). Carboniferous (Visean).

Family Saccospongiidae Rigby & Dixon, 1979 (6). Lower Ordovician–Silurian (Ludlow, ?Pridoli). Family Nexospongiidae Carrera, 1996 (1). Lower Ordovician.

Family Pleromatidae Sollas, 1888 (14). Carboniferous (?Mississippian), Upper Jurassic (Kimmeridgian)-Holocene.

Subfamily Pleromatinae Sollas, 1888 (7). Carboniferous (?Mississippian), Cretaceous (Albian)– Holocene.

Subfamily Heterostiniinae Schrammen, 1924 (7). Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian).

Order Axinellida Bergquist, 1967 (1). Permian-Holocene.

Family Axinellidae Verrill, 1907 (0). Holocene.

Family Agelasidae Verrill, 1907 (1). Permian.

Order Monalithistida Lagneau-Hérenger, 1955 (18). Lower Jurassic (Pliensbachian)–Holocene. Suborder Megarhizomorina Schrammen, 1924 (2). Upper Cretaceous (Cenomanian–Campanian).

Family Megarhizidae Schrammen, 1901 (2). Upper Cretaceous (Cenomanian–Campanian).
Suborder Sphaerocladina Schrammen, 1910 (16). Lower Jurassic (Pliensbachian)–Holocene.
Family Vetulinidae von Lendenfeld, 1904 (11). Middle Jurassic (Bathonian)–Holocene.
Subfamily Vetulininae von Lendenfeld, 1904 (9). Middle Jurassic (Bathonian)–Holocene.
Subfamily Macrobrochinae Reid, herein (2). Upper Cretaceous (Santonian–Campanian).
Family Lecanellidae Schrammen, 1924 (4). Upper Jurassic (Oxfordian)–Upper Cretaceous.
Family Uncertain (1).

Order Uncertain (7).

Family Criccospongiidae Mostler, 1986 (1). Triassic.

Family Uncertain (6).

Order Spirosclerophorida Reid, 1963 (114;9). Middle Cambrian-Holocene.

Suborder Rhizomorina Zittel, 1895 (88;9). Middle Cambrian-Holocene.

Family Haplistiidae de Laubenfels, 1955 (18). Lower Ordovician–Permian. Family Uncertain (1).

Superfamily Azoricoidea Sollas, 1888 (29;2). Upper Jurassic-Holocene.

Family Azoricidae Sollas, 1888 (25). Upper Jurassic-Holocene.

Subfamily Azoricinae Sollas, 1888 (7). Cretaceous (Aptian)-Holocene.

Subfamily Cytoraciinae Schrammen, 1924 (3). Upper Jurassic-Neogene (Miocene).

Subfamily Aulosominae Schrammen, 1924 (6). Upper Jurassic-Upper Cretaceous (Campanian).

Subfamily Leiochoniinae Schrammen, 1924 (3). Cretaceous (Aptian-Campanian).

Subfamily Astroboliinae de Laubenfels, 1955 (5). Upper Jurassic–Upper Cretaceous (Maastrichtian).

Subfamily Siphonidiinae von Lendenfeld, 1904 (1). Cretaceous (Campanian).

Family Cnemidiastridae Schrammen, 1924 (4;2). Upper Jurassic (Oxfordian)–Neogene (Miocene).

Superfamily Platychonioidea Schrammen, 1924 (12;2). Jurassic-Holocene.

Family Platychoniidae Schrammen, 1924 (5). Jurassic–Holocene.

Family Discostromatidae Schrammen, 1924 (6;2). Jurassic.

Subfamily Discostromatinae Schrammen, 1924 (4). Upper Jurassic (Oxfordian–Kimmeridgian). Subfamily Pyrgochoniinae Schrammen, 1924 (2;2). Upper Jurassic.

Family Aretotragosidae Malecki, 1966 (1). Jurassic.

Superfamily Scleritodermatoidea Sollas, 1888 (28;5). Upper Jurassic (Callovian)-Holocene.

Family Scleritodermatidae Sollas, 1888 (8;5). Upper Jurassic (Oxfordian)-Holocene.

Subfamily Scleritodermatinae Sollas, 1888 (1). ?Cretaceous, Holocene.

Subfamily Leiodorellinae Schrammen, 1924 (2). Upper Jurassic (Oxfordian–Kimmeridgian). Subfamily Amphithelioninae Schrammen, 1924 (4;5). Cretaceous–Neogene (Miocene).

Subfamily Uncertain (1).

Family Jereicidae Schrammen, 1924 (5). Upper Jurassic (Callovian)-Holocene.

Family Seliscothonidae Schrammen, 1924 (9). Cretaceous (Aptian)-Holocene.

Family Uncertain (6).

Suborder Uncertain (26).

## Porifera

Class Hexactinellida Schmidt, 1870 (432;19). Lower Cambrian-Holocene.

Subclass Amphidiscophora Schulze, 1887 (160). Lower Cambrian-Holocene.

- Order Amphidiscosa Schrammen, 1924 (41). Lower Cambrian-Holocene.
  - Family Hyalonematidae Gray, 1857 (1). Cretaceous (Turonian)-Holocene.
  - Family Pattersoniidae Miller, 1889 (3). Middle Ordovician-Upper Ordovician.
  - Family Pelicaspongiidae Rigby, 1970 (24). Lower Ordovician (Tremadocian)-Triassic (Carnian).
  - Family Stiodermatidae Finks, 1960 (13). Lower Cambrian-Permian.
- Order Reticulosa Reid, 1958 (118). Ediacaran-Holocene.

Superfamily Protospongioidea Hinde, 1887 (20). Lower Cambrian-Jurassic.

- Family Protospongiidae Hinde, 1887 (20). Lower Cambrian-Jurassic.
- Superfamily Dierespongioidea Rigby & Gutschick, 1976 (24). Middle Cambrian-Holocene.
- Family Dierespongiidae Rigby and Gutschick, 1976 (6). Middle Ordovician-Permian (Artinskian).
- Family Hydnodictyidae Rigby, 1971 (2). Middle Cambrian-Upper Ordovician.
- Family Amphispongiidae Rauff, 1894 (1). upper Silurian.
- Family Multivasculatidae de Laubenfels, 1955 (1). Upper Cambrian.
- Family Titusvillidae Caster, 1939 (6). Upper Devonian–Holocene.
- Family Aglithodictyidae Hall & Clarke, 1899 (8). Upper Devonian–Carboniferous (Visean).
- Superfamily Dictyospongioidea Hall & Clarke, 1899 (62). Ediacaran–Upper Triassic (Carnian).
- Family Dictyospongiidae Hall & Clarke, 1899 (55). Ediacaran–Permian (Roadian). Subfamily Dictyospongiinae Hall & Clarke, 1899 (17). Ediacaran–Permian (Roadian).
  - Subfamily Prismodictyinae de Laubenfels, 1955 (8). Upper Ordovician–Carboniferous (Serpukhovian).
  - Subfamily Hydnoceratinae Finks, herein (10). Middle Cambrian–Carboniferous (Lower Mississippian).
  - Subfamily Calathospongiinae Hall & Clarke, 1899 (9). Upper Devonian–Carboniferous (Serpukhovian).
  - Subfamily Physospongiinae Hall & Clarke, 1899 (4). Middle Devonian–Carboniferous (Lower Mississippian).
  - Subfamily Thysanodictyinae Hall & Clarke, 1899 (7). Devonian (Frasnian)–Carboniferous (Serpukhovian).
- Family Docodermatidae Finks, 1960 (5). Silurian (Ludlow)–Permian (Roadian, ?Wordian– ?Capitanian).
- Family Stereodictyidae Finks, 1960 (2). Carboniferous (Visean)–Upper Triassic (Carnian).
- Superfamily Hintzespongioidea Finks, 1983 (12). Lower Cambrian–Carboniferous (Upper Mississippian).
  - Family Hintzespongiidae Finks, 1983 (5). Lower Cambrian-Devonian (Givetian).
  - Family Teganiidae de Laubenfels, 1955 (7). Cambrian (Furongian)–Carboniferous (Upper Mississippian).
- Order Hemidiscosa Schrammen, 1924 (1). Carboniferous (Upper Pennsylvanian).
- Family Microhemidisciidae Finks & Rigby, herein (1). Carboniferous (Upper Pennsylvanian).
- Subclass Hexasterophora Schulze, 1887 (272;19). Ordovician-Holocene.
  - Order Lyssacinosa Zittel, 1877 (36). Ordovician–Holocene.
    - Family Pheronematidae Gray (2). ?Upper Jurassic, Cretaceous-Holocene.
    - Family Euplectellidae Gray, 1867 (11). Lower Triassic-Holocene.
      - Subfamily Euplectellinae Ijima, 1903 (1). Holocene.
      - Subfamily Taegerinae Schulze, 1887 (8). Lower Triassic-Holocene.
      - Subfamily Uncertain (2).
    - Family Asemematidae Schulze, 1887 (1). Paleogene (?middle Eocene), Holocene. Subfamily Asemematinae Schulze, 1887 (0). Holocene.
    - Subfamily Caulophacinae Schulze, 1887 (1). Paleogene (?middle Eocene), Holocene.
    - Family Rossellidae Schulze, 1887 (1). ?Paleogene-?Neogene, Holocene.
    - Subfamily Rossellinae Schulze 1887 (1). ?Paleogene-?Neogene, Holocene.
    - Family Stauractinellidae de Laubenfels, 1955 (1). Jurassic (Oxfordian)-Neogene.
    - Family Leucopsacidae Ijima, 1903 (1). Paleogene (Eocene).
    - Family Uncertain (6).
    - Superfamily Crepospongioidea Finks and Rigby, herein (1). Triassic (Carnian).
    - Family Crepospongiidae Finks and Rigby, herein (1). Triassic (Carnian).
    - Superfamily Brachiospongioidea Beecher, 1889 (11). Upper Ordovician-Permian (Guadalupian).
      - Family Brachiospongiidae Beecher, 1889 (4). Upper Ordovician–Silurian (Ludlow).
      - Family Pyruspongiidae Rigby, 1971 (1). Upper Ordovician.
      - Family Malumispongiidae Rigby, 1967 (5). Upper Ordovician–Carboniferous (lower Tournaisian). Family Toomeyospongiidae Finks, herein (1). Permian (Guadalupian).
    - Superfamily Lumectospongioidea Rigby & Chatterton, 1989 (1). Silurian (Ludlow).
      - Family Lumectospongiidae Rigby & Chatterton, 1989 (1). Silurian (Ludlow).

	tinosa Schrammen, 1903 (134;8). Upper Ordovician–Holocene.
	Euryplegmatidae de Laubenfels, 1955 (1). ?Cretaceous, Holocene.
	Farreidae Schulze, 1885 (4;1). Cretaceous (Turonian)–Holocene.
	Euretidae <sup>†</sup> Zittel, 1877 (38;2). Triassic (Carnian)–Holocene.
	mily Euretinae Zittel, 1877 (23;2). Triassic (Carnian)–Holocene.
Subfa	mily Polythyridinae Schrammen, 1912 (2). ?Lower Cretaceous, Upper Cretaceous–Holocene. mily Pseudobecksiinae Reid, herein (1). Cretaceous (Coniacian–Maastrichtian).
	mily Chonelasmatinae Schrammen, 1912 (9). Jurassic (Oxfordian)–Holocene.
	mily Uncertain (1).
	Craticulariidae <sup>†</sup> Rauff, 1893 (30). Triassic (Carnian)–Holocene.
	mily Craticulariinae Rauff, 1893 (8). Triassic–Paleogene (Thanetian).
Subfa	mily Laocoetidinae de Laubenfels, 1955 (6). Triassic (Carnian)–Neogene (Miocene,
	ocene).
	mily Leptophragmatinae Schrammen, 1912 (7). ?Jurassic, Cretaceous (?Berriasian–?Aptian,
	ian)-Holocene.
	mily Caseariinae Schrammen, 1936 (5). Triassic (Carnian)–Upper Jurassic.
	mily Uncertain (4). Cribrospongiidae F. A. Roemer, 1864 (15;3). Middle Triassic–Holocene.
	Staurodermatidae Zittel, 1877 (6). Jurassic–Neogene.
	Aphrocallistidae Gray, 1867 (1). Lower Cretaceous–Holocene.
	Tretodictyidae Schulze, 1887 (9;2). Upper Jurassic–Holocene.
	mily Tretodictyinae Schulze, 1887 (7;2). Upper Jurassic–Holocene.
	mily Placotrematinae Reid, herein (2). Cretaceous (Turonian).
Family	Cystispongiidae Reid, herein (1). Upper Cretaceous (Coniacian)–Neogene.
	Aulocalycidae Ijima, 1927 (1). Upper Jurassic.
	Emplocidae de Laubenfels, 1955 (1). Middle Jurassic.
	Uncertain (16).
1	ily Pillaraspongioidea Rigby, 1986 (1). Devonian (Frasnian–Famennian). Pillaraspongiidae Rigby, 1986 (1). Devonian (Frasnian–Famennian).
	ily Pileolitoidea Finks, 1960 (9;1). Upper Ordovician–Holocene.
1	Pileolitidae Finks, 1960 (2). Permian (?Asselian-?Sakmarian, Artinskian)–Middle Triassic.
Family	Wareembaiidae Finks & Rigby, herein (2). Upper Ordovician.
	Euretidae <sup>†</sup> Zittel, 1877 (2). Upper Devonian (Frasnian).
Family	Craticulariidae <sup>†</sup> Rauff, 1893 (5). Upper Devonian.
Family	Pileospongiidae Rigby, Keyes, & Horowitz, 1979 (1). Carboniferous (Serpukhovian).
	iscosa Schrammen, 1903 (81;11). Jurassic–Holocene.
	Calyptrellidae Schrammen, 1912 (1). Cretaceous (Coniacian–Maastrichtian).
	Callodictyonidae Zittel, 1877 (23;4). Upper Jurassic–Holocene.
	mily Callodictyoninae Zittel, 1877 (9). Upper Jurassic–Upper Cretaceous. mily Microblastidinae Schrammen, 1912 (2). Cretaceous.
	mily Becksinae Schrammen, 1912 (6;2). Cretaceous–Paleogene (Oligocene).
	mily Callicylicinae Reid, herein (6;2). Jurassic–Holocene.
	Coeloptychidae F. A. Roemer, 1864 (4;3). Lower Cretaceous–Upper Cretaceous.
	mily Coeloptychinae F. A. Roemer, 1864 (2;3). Lower Cretaceous–Upper Cretaceous.
	mily Cameroptychinae Reid, herein (2). Upper Cretaceous.
	Ventriculitidae Smith, 1848 (21). Jurassic–Upper Cretaceous.
	mily Ventriculitinae Smith, 1848 (17). Jurassic–Upper Cretaceous.
	mily Bolitesiinae Schrammen, 1912 (1). Cretaceous (Coniacian–Maastrichtian).
	mily Stauronematinae Sollas, 1877 (1). Lower Cretaceous (Albian)–Upper Cretaceous ronian).
	mily Lychniscaulinae Reid, herein (2). Upper Jurassic.
	Camerospongiidae Schrammen, 1912 (4;2). Lower Cretaceous (Valanginian)–Upper
	ceous.
Family	Polyblastidiidae Schrammen, 1912 (2). Upper Jurassic–Cretaceous (Coniacian).
	Dactylocalycidae Gray, 1867 (10;2). Jurassic (Bajocian)–Holocene.
	mily Dactylocalycinae Gray, 1867 (5;2). Jurassic (Bajocian)–Cretaceous (Maastrichtian).
	mily Ophrystomatinae Schrammen, 1912 (1). Cretaceous (Albian–Cenomanian).
	mily Uncertain (4).
	Sporadopylidae Schrammen, 1936 (3). Upper Jurassic–Cretaceous (Cenomanian).
	Pachyteichismatidae Schrammen, 1936 (3). Upper Jurassic–Lower Cretaceous. Cypelliidae Schrammen, 1936 (5). Jurassic.
	Uncertain (5).
Order Uncer	

## Porifera

Class Heteractinida de Laubenfels, 1955 (32). Lower Cambrian-Permian (Cisuralian).

Order Octactinellida Hinde, 1887 (26). Lower Cambrian–Permian (Cisuralian). Family Astraeospongiidae Miller, 1889 (10). upper Lower Cambrian–Devonian. Family Eiffeliidae Rigby, 1986 (8). Lower Cambrian–Carboniferous (Middle Pennsylvanian). Family Wewokellidae King, 1943 (5). Carboniferous (Mississippian)–Permian (Cisuralian).

Family Nuchidae Pickett, 2002 (3). Lower Cambrian-Middle Cambrian.

?Order Hetairacyathida Bedford & Bedford, 1937 (4). Lower Cambrian.

Family Hetairacyathidae Bedford & Bedford, 1934 (4). Lower Cambrian. Order Uncertain (2).

Class Calcarea Bowerbank, 1864\*\* (57). Lower Cambrian-Holocene.

- Subclass Calcinea Bidder, 1898 (3). Holocene.
  - Order Murrayonida Vacelet, 1981 (3). Holocene. Family Murrayonidae Kirkpatrick, 1910 (1). Holocene.

Family Paramurrayonidae Vacelet, 1967 (2). Holocene.

Order Clathrinida Hartman, 1958 (0). Holocene.

Family Clathrinidae Minchin, 1900 (0). Holocene.

Family Soleneiscidae Borojevic & others, 2002 (0). Holocene.

Family Levinellidae Borojevic & Boury-Esnault, 1986 (0). Holocene.

Family Leucaltidae Dendy & Row, 1913 (0). Holocene.

Family Leucascidae Dendy, 1893 (0). Holocene.

Family Leucettidae Borojevic, 1968 (0). Holocene.

Subclass Calcaronea Bidder, 1898 (54). Lower Cambrian-Holocene.

Order Leucosolenida Hartman, 1958 (0). Holocene.

Family Leucosoleniidae Minchin, 1900 (0). Holocene.

Order Sycettida Bidder, 1898 (4). Carboniferous-Holocene.

Family Sycettidae Dendy, 1893 (0). Holocene.

Family Grantiidae Dendy, 1893 (3). Carboniferous-Holocene.

Family Leuconiidae Vosmaer, 1887 (1). Lower Jurassic-Holocene.

Family Heteropiidae Dendy, 1893 (0). Holocene.

Family Amphoriscidae Dendy, 1893 (0). Holocene.

Order Stellispongiida Finks & Rigby, herein (32). Permian-Holocene.

Family Stellispongiidae de Laubenfels, 1955 (28). Permian-Neogene (Miocene). Subfamily Stellispongiinae de Laubenfels, 1955 (19). Permian-Paleogene (Eocene).

Subfamily Holcospongiinae Finks, herein (9). Permian-Neogene (Miocene).

Family Endostomatidae Finks, herein (2). ?Lower Triassic-?Middle Triassic, Upper Triassic (Norian)–Paleogene (Eocene).

Family Lelapiidae Dendy & Row, 1913 (2). Holocene.

Order Sphaerocoeliida Vacelet, 1979 (5). Permian-Cretaceous (Cenomanian).

Family Sphaerocoeliidae Steinmann, 1882 (5). Permian–Cretaceous (Cenomanian).

Order Lithonida Doederlein, 1892 (12). Jurassic-Holocene.

Family Lepidoleuconiidae Vacelet, 1967 (1). Holocene.

Family Minchinellidae Dendy & Row, 1913 (10). Jurassic-Holocene.

Family Petrobionidae Borojevic, 1979 (1). Holocene.

Order Uncertain (1).

Class and Order Uncertain (46)

Family Polyactinellidae Mostler, 1985 (9). Lower Cambrian-Permian.

Family Stromatidiidae Finks, 1960 (1). Permian (Guadalupian).

Family Tadassiidae Zhuravleva & Pyanovskaya (1). Middle Cambrian–Upper Cambrian.

Family Uncertain (35).

Unrecognizable Genera (235).

# PALEOZOIC DEMOSPONGES

ROBERT M. FINKS and J. KEITH RIGBY

[Department of Geology, Queens College (CUNY); Department of Geology, Brigham Young University]

# Class DEMOSPONGEA Sollas, 1885

[nom. correct. DE LAUBENFELS, 1955, p. 36, pro class Demospongiae MINCHIN, 1900, p. 145, nom. transl. ex order Demospongiae SOLLAS, 1885a, p. 395]

Spicules of opaline silica are monaxonic or tetraxonic with axial canal of triangular cross section; spongin and mesoglea commonly abundant; architecture of aquiferous system of rhagon type, with small choanocyte chambers and small choanocytes (see Fig. 92). [The Demospongea was apparently first proposed as a taxonomic unit by SOLLAS in a short article in 1885, although SOLLAS's (1887) extensive article on sponges in the ninth edition of Encyclopaedia Britannica has been commonly cited as the publication where the Demospongea was proposed. The article has been commonly dated as 1875, but that volume of the encyclopedia was actually published in 1887, although publication dates for various volumes of the series do range from 1875 to 1889.] Cryogenian-Holocene.

## Subclass CLAVAXINELLIDA Lévi, 1956

[Clavaxinellida LÉVI, 1956, p. 167; emend., FINKS & RIGBY, herein]

Skeleton typically fibrous with abundant spicules; fibers typically of plumose or subparallel sheaves of oxeas (most primitive), or styles, or tylostyles (most advanced); microscleres absent, or microrhabds or spinispires (most advanced); oviparous in living forms, larva typically a parenchymella. *Cryogenian–Holocene*.

## Order PROTOMONAXONIDA new order

[Protomonaxonida FINKS & RIGBY, herein]

Fibrous skeleton composed of oxeas alone. *Cryogenian–Holocene.* 

## Family LEPTOMITIDAE de Laubenfels, 1955

[Leptomitidae DE LAUBENFELS, 1955, p. 69]

Thin-walled, tubular to fan-shaped sponges whose skeleton is composed of monaxons arranged in two layers, outer layer of vertically oriented, small spicules (possible oxeas). With moderately widely spaced, coarse, vertical, parallel rods composed of en echelon oxeas; and inner layer of horizontal, irregularly spaced to bundled, small oxeas. [The family was considered within the lyssacinosid sponges by DE LAUBENFELS (1955, p. 69-70) but was moved to the monaxonid demosponges by RIGBY (1986a, p. 22), following reinterpretation of the skeleton as a two-layered structure rather than a single, reticulate, layered structure like that in the protosponge hexactinellids.] Cambrian-Silurian.

Leptomitus WALCOTT, 1886, p. 89 [\*L. zitteli; OD] [= Tuponia WALCOTT, 1920, p. 271, partim (type, T. lineata WALCOTT, 1920, p. 272), non REUTER, 1875]. Elongate, tubular, very thin-walled sponges with double-layered skeleton; coarse, moderately widely spaced, en echelon oxeas are dominant elements that combine to produce parallel rods that extend virtually entire length of sponge; space between rods filled with thatch of smaller, vertical oxeas that combine with coarse rods to produce striped-appearing, outer, skeletal layer; inner layer a thatch of tiny, horizontal, monaxial spicules; neither vertical nor horizontal, small spicules occur in bundles; walls without parietal gaps and major ostia or canals. Lower Cambrian-Middle Cambrian: Canada (British Columbia), Greenland, USA (Georgia, Vermont, Virginia, Pennsylvania, Utah), China (Yunnan).-FIG. 1a-c. L. lineata (WAL-COTT), Stephen Formation, Burgess Shale, Albertan, Burgess quarry, Mount Field, British Columbia; a, generalized restoration, ×1; b, idealized segment of wall showing outer layer of monaxial thatch subdivided by coarse oxeas and inner, horizontal thatch of irregularly spaced, small oxeas, not to scale (Rigby, 1986c); c, lower part of lectotype showing general shape and skeletal structure, USNM 66448, ×2 (Walcott, 1920).

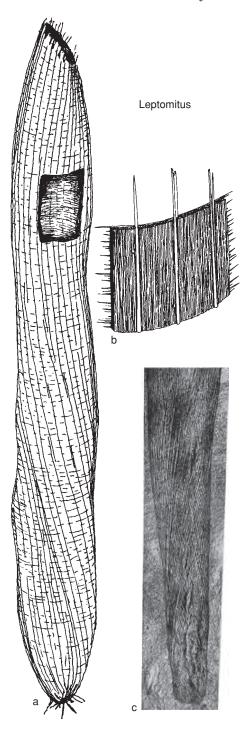


FIG. 1. Leptomitidae (p. 9).

- Leptomitella RIGBY, 1986a, p. 24 [\*Leptomitus metta RIGBY, 1983a, p. 243; OD]. Cylindrical to steeply conical, thin-walled, smooth with walls of monaxons in two layers, outer layer of fine, vertical thatch with inserted, vertical rods of en echelon oxeas; inner layer of horizontal monaxons in bundles that spiral; two layers produce reticulatedappearing wall. Lower Cambrian-Middle Cambrian: China (Yunnan), Lower Cambrian; USA (Utah), Middle Cambrian:-FIG. 2a-d. \*L. metta (RIGBY), Marjum Formation, Albertan, House Range, Utah; a, holotype showing prominent, pigmented, horizontal bands of monaxons that are interior to long, vertical spicules of outer layer preserved in bas-relief, ×1; b, photomicrograph of skeletal net showing both spicules in horizontal bands and vertical structure of outer layer in holotype, BYU 1564, ×10 (Rigby, 1983a); c, generalized restoration showing form and nature of skeletal structure, ×1; d, idealized segment of wall showing outer, monaxial thatch and inner, distinct bundles of monaxons, not to scale (Rigby, 1986a).
- Paraleptomitella CHEN, HOU, & LU, 1989, p. 23 [29] [\*P. dictyodroma; OD]. Tubular to globose, thinwalled sponges with double-layered skeleton of monaxons; outer layer of coarse, slightly curved oxeas that are interlocked with one another to form vertically elongate net in which openings are filled with smaller, vertically arranged, fine monaxons; inner layer of monaxons in horizontal bundles. [Leptomitella is similar in having a double-layered skeleton with an inner layer of bundled spicules, but it has an outer layer of straight, coarse and fine, vertical spicules.] Lower Cambrian: China (Yunnan).-FIG. 3,1a-c. \*P. dictyodroma, Chiungchussu Formation, Chengjiang; a, holotype, generalized form, 1108492, ×1.2; b, photomicrograph of skeletal structure of holotype showing curved, subvertical spicules, and less distinct, irregular, inner, horizontal spicule bundles, ×4; c, generalized restoration of skeletal segment showing relationships between coarse and fine, outer spicules and inner spicule bundles, ×20 (Chen, Hou, & Lu, 1989).
- Wareiella RIGBY & HARRIS, 1979, p. 977 [\*W. typicala RIGBY & HARRIS, 1979, p. 978; OD]. Small, conicocylindrical to subcylindrical sponge with deep, simple spongocoel; thin walled with simple, skeletal net principally a thin thatch of vertical, short diactines with minor, horizontal or diagonal diactines, or perhaps more complex spicules; osculum armored with prostalia; marginalia absent; base rounded to round-pointed with root tuft of a few long spicules. Silurian (Llandovery-Wenlock): Canada (British Columbia).-Fig. 3,2. W. typicala, unnamed Silurian siltstone, north-central British Columbia; iron-oxide-stained, argillaceous impression of holotype with vertical prostalia showing at oscular margin, GSC 60643, ×2 (Rigby & Harris, 1979).

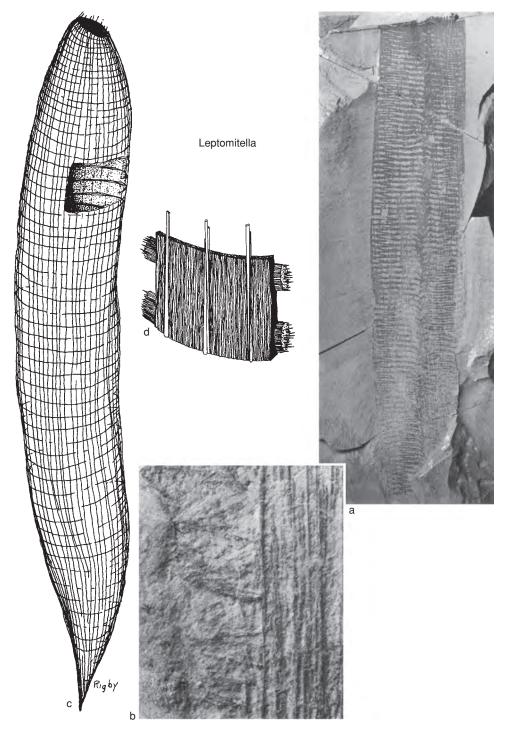


FIG. 2. Leptomitidae (p. 10).

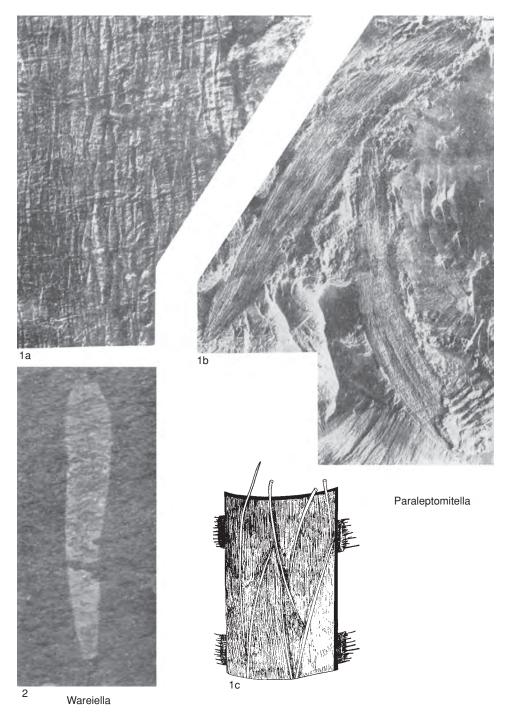


FIG. 3. Leptomitidae (p. 10).

#### Family SINOSPONGIIDAE new family

#### [Sinospongiidae FINKS & RIGBY, herein] [type genus, Sinospongia CHEN in CHEN & XIAO, 1992, p. 518]

Supposed sponges with thin walls characterized by coarse, curved, monaxial spicules that are more or less horizontal; smaller monaxial spicules may be present. *Cryogenian–Ediacaran.* 

Sinospongia CHEN in CHEN & XIAO, 1992, p. 518 [526] [\*S. chenjunyuani; OD] [=Niuganmafeia CHEN in CHEN & XIAO, 1992, p. 520, nom. nud. (type, N. obesa, OD); Xilinxiaella LI in DING & others, 1996, p. 106 (type, X. bella, OD]. Supposed sponge, tall and sausage shaped, skeleton a single layer of rods or spicules curved and more or less horizontal tangential to surface, sometimes forming rounded, rhombic openings, or elsewhere with only a few scattered elements; small spicules may occur between larger elements. [Although the sponge origin of the fossils is not certain (XIAO & others, 2002), they appear similar to Cambrian protomonaxonids and are tentatively placed here.] Cryogenian-Ediacaran: China (Hubei).-—Fig. 4a-b. \*S. chenjunyuani, Doushantuo Formation, Ediacaran, Miaohe Village, Zigui County; a, general view of holotype showing form and skeletal structure,  $\times 2$ ; *b*, photomicrograph of part of skeletal net showing curved, mainly horizontal spicules, ×10 (Chen & Xiao, 1992).

#### Family HAMPTONIIDAE de Laubenfels, 1955

[Hamptoniidae DE LAUBENFELS, 1955, p. 39]

Massive, globose, or frondescent sponges with skeletons of two series of spicules; large, moderately smooth monaxons, either isolated or clumped, separated by tracts of smooth, smaller, monaxial spicules; generally lacking cross-bracing, horizontal elements; larger spicules do not develop coronal fringe. *Middle Cambrian–Middle Ordovician.* 

Hamptonia WALCOTT, 1920, p. 296 [\*H. bowerbanki WALCOTT, 1920, p. 297; M]. Globose, bladderlike, or frondescent sponges, subparallel, large monaxons either singly or in small bundles or bands are separated by tracts of small, thatched, possibly monaxial spicules radiating from center or central axis of sponge to meet periphery at right angles; bundles may be crossed at high angles or by inosculation in outer part of sponge. *Middle Cambrian:* Canada (British Columbia).——FIG. 5a-b. \*H. bowerbanki, Stephen Shale, Burgess Shale, Mount Field; a, flattened lectotype showing generally circular sponge with radiating, skeletal structure,  $\times 0.5$ ; *b*, enlarged part of upper skeleton showing monaxial structure and coarse, principal oxeas grouped into crude tufts, USNM 66493,  $\times 5$  (Walcott, 1920).

- Hamptoniella RIGBY & COLLINS, 2004, p. 35 [\*H. foliata; OD]. Obconical to turbinate or goblet shaped with three-dimensional skeleton; largely without a spongocoel but with axial region with moderately coarse, subvertical canals and a marginal region of endosome where canals diverge upwardly and outwardly from axial zone; skeleton of clustered to unclustered, long oxeas, arranged generally parallel to canals in interior but somewhat less clustered in exterior. Locally spicules may diverge to produce echinating-appearing tracts that may inosculate or have some cross bracing; oxeas generally straight. Middle Cambrian: Canada (British Columbia).---FIG. 6,1a-b. \*H. foliata, Burgess Shale, Albertan, Mount Stephen; a, side view of holotype with moderately compact, endosomal skeleton of upwardly and outwardly expanding tracts and with central, open canal zone obscured behind dense skeleton, ROM 43816, ×2; b, vertically flattened paratype with radiating skeleton of oxeas in anastomosing tracts that grade outwardly to straight tracts, ROM 44283, ×4 (Rigby & Collins, 2004).-FIG. 6,1c. H. hirsuta RIGBY & COLLINS; side view of holotype showing somewhat annulate, obconical form with coarse canals between ragged, coarse tracts of echinated, long oxeas, ROM 44285, ×2 (Rigby & Collins, 2004).
- Lasiothrix HINDE in DAWSON & HINDE, 1889, p. 50 [\*L. curvicostata HINDE in DAWSON & HINDE, 1889, p. 51; OD]. Small, cup-shaped sponge with root tuft; meridional bundles of diactines (oxeas or rhabdodiactines) are underlain by transverse diactines or stauractines; fringe of crowded diactines surrounding upper edge of cup. [L. flabellata DAWSON & HINDE, 1889, comprises plumose masses of diactines diverging from a root tuft; it may not be congeneric with the type species.] Upper Cambrian: Canada (Quebec) .--Fig. 6,2a-b. \*L. curvicostata, Metis shale, Metis Bay; a, drawing of holotype, side view of lower part, ×1; b, enlarged, upper part showing curved spicules and cross-connecting, transverse spicules in main net with prostalia above, PRM, approximately ×15 (Dawson & Hinde, 1889).
- Offela ROGERS, JACKSON, & MCKINNEY, 1964, p. 135 [\*O. spondeum; M]. Small, ovoid, vasiform sponge with thin body wall and somewhat collared osculum smaller than cloacal diameter; root tuft present at base; spicules long and short diactines (oxeas or rhabdodiactines) crossing one another (possibly at low angles); longer spicules more abundant on exterior, near osculum, and near and in root tuft. *Middle Ordovician:* USA (Virginia, Alabama).——FIG. 6,3a-b. \*O. spondeum, Lenoir Limestone, Chazyan, Cahaba Valley, Alabama; a, side view of small holotype showing globose form and osculum of shallow spongocoel, ODC 2511;

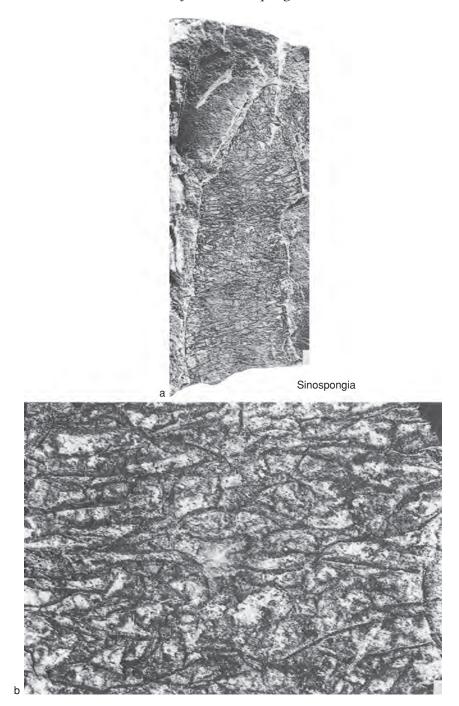
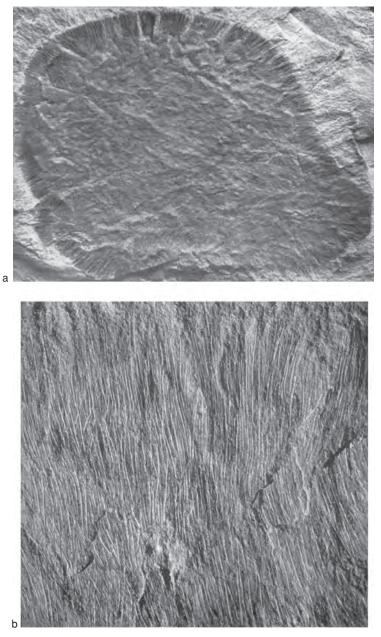


FIG. 4. Sinospongiidae (p. 13).



Hamptonia

FIG. 5. Hamptoniidae (p. 13).

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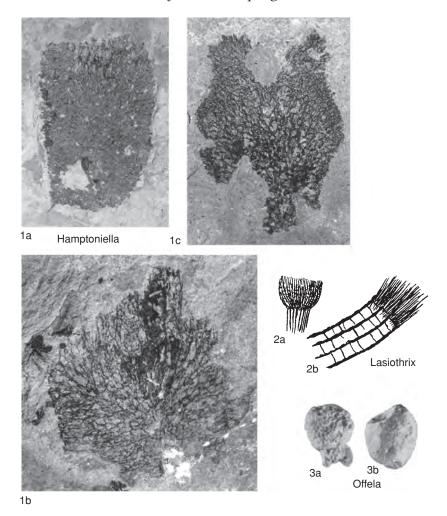


FIG. 6. Hamptoniidae (p. 13-16).

*b*, side view of globose paratype with a prominent root tuft, ODC 2512, ×1.5 (Rogers, Jackson, & McKinney, 1964).

## Family ULOSPONGIELLIDAE Rigby & Collins, 2004

[Ulospongiellidae RIGBY & COLLINS, 2004, p. 38] [type genus, Ulospongiella RIGBY & COLLINS, 2004, p. 39]

Sponges whose skeletons are made of strongly curved to sigmoidal or gently serpentine oxeas or strongyles arranged in irregular felt or in upwardly echinating tracts, at least in interior of sponge; tracts, when present, parallel to large, subvertical to upwardly and outwardly directed canals. *Middle Cambrian.*  Ulospongiella RIGBY & COLLINS, 2004, p. 39 [\*U. ancyla; OD]. Moderately small, conicocylindrical, obconical, or subcylindrical sponges whose relatively massive, felted-appearing skeleton is made of moderately large, curved oxeas or strongyles that are commonly sigmoidal, undulating, curved or hooked to locally straight; moderately open-textured skeleton not in tracts; canals ill defined; coarse marginalia may include oxeas or strongyles as isolated spicules; spongocoel not developed. Middle Cambrian: Canada (British Columbia).----FIG. 7,1a-b. \*U. ancyla, Burgess Shale; a, side view of holotype showing generalized growth form, with felted skeleton that includes upwardly and outwardly radiating, coarse marginalia, ROM 43830, ×3; b, photomicrograph of upper left part of holotype with endosomal skeleton of curved spicules and coarse tylostyle and oxea marginalia, ×5 (Rigby & Collins, 2004).

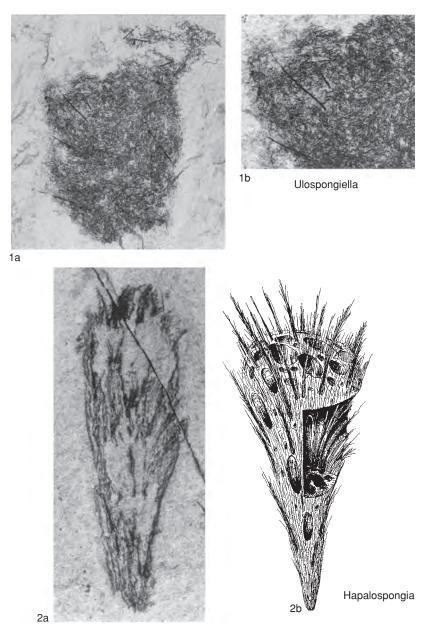


FIG. 7. Ulospongiellidae (p. 16-18).

Hapalospongia RIGBY & COLLINS, 2004, p. 41 [\**H. flexuosa*; OD]. Steeply obconical to flaring sponges without spongocoel; interior perforated by large, subvertical canals that branch upwardly and outwardly and are paralleled by smaller canals; skeleton delicate, made of fine tracts or unclustered, aligned, small, curved oxeas or strongyles that range from straight to sigmoidal or gently serpen-

tine; spicules echinating in tracts. *Middle Cambrian*: Canada (British Columbia).——FIG. 7,2*a*– *b.* \**H. flexuosa*, Middle Cambrian trilobite beds, Mount Stephen; *a*, side view of steeply obconical holotype with loose-textured skeleton of curved to straight oxeas or strongyles, in tracts between upwardly divergent, coarse canals, ROM 43819, X4; *b*, restoration showing general relationships of spicule tracts to canals of various size in upwardly divergent skeletal structure of steeply obconical sponge, ×2.5 (Rigby & Collins, 2004).

#### Family CHOIIDAE de Laubenfels, 1955

#### [Choiidae DE LAUBENFELS, 1955, p. 42]

Unattached forms consisting of a thin, circular to elliptical, central disc from which radiate long, coronal spicules that are inserted at various levels within thatch of central disc; both small spicules and large coronal spicules are probably oxeas. *Lower Cambrian–Middle Cambrian.* 

- Choia WALCOTT, 1920, p. 291 [\*C. carteri WALCOTT, 1920, p. 292; OD]. Small to medium-sized, low, conical, oval to elliptical sponges with thatched, central disc surrounded by corona with relatively large diameter, long spicules that extend beyond and radiate from central disc; central disc composed of fine, radiating monaxial spicules (probably oxeas) with interspersed, large, monaxial, coronal spicules, which may be oxeas or styles. Lower Cambrian-Middle Cambrian: China (Anhui), Lower Cambrian; Canada (British Columbia, Quebec), USA (Utah), Wales, Middle Cambrian.-FIG. 8,1. \*C. carteri, Stephen Formation, Burgess Shale, Albertan, Mount Field, British Columbia; flattened lectotype showing compact, circular, central disc and longer, radiating, coronal oxeas or styles, USNM 66482, ×2 (Walcott, 1920).
- Allantospongia RIGBY & HOU, 1995, p. 1015 [\*A. mica; OD]. Small, elongate, ovate to sausagelike sponges with skeleton of small, monaxial, radiating to somewhat irregular monaxons, with longer, coarser spicules in distinct tufts that extend beyond central, thatched part of skeleton. Lower Cambrian: China (Yunnan).——FIG. 8,3a-b. \*A. mica, Chungchussu Formation, Xiaolantian, Chengjiang County; a, small, sausagelike holotype with skeleton a radiating thatch of possible oxeas, NIGPAS 115322, x2; b, enlarged lower part of holotype showing dense, outer, radiating fringe and irregularly oriented spicules in skeletal interior, ×10 (Rigby & Hou, 1995).
- Choiaella RIGBY & HOU, 1995, p. 1,014 [\*C. radiata; OD]. Small, discoidal to broad obconical sponges with skeleton of radiating thatch of small monaxons of one size that may be locally bundled but do not extend beyond margin of disc, other than as limited fringe; coarse coronal spicules absent. [These small sponges do not have the coronal spicules of Choia and the distinctly bundled skeleton of Belemnospongia.] Lower Cambrian: China (Yunnan).-FIG. 8,2a-b. \*C. radiata, Chiungchussu Formation, Xiaolantian, Chenjiang County; a, small, discoidal holotype with radiate skeleton of oxeas, ×4; b, enlargement of part of disc showing radiating oxeas but without large, coronal spicules, NIGPAS 115325, ×10 (Rigby & Hou, 1995).

Lenica GORYANSKY, 1977, p. 275 [\*L. unica; OD]. Wide, funnel- or fan-shaped sponges with radiating skeleton of long, thin bundles of diactine spicules, perhaps joined by spongin during life; large spicules up to 70 mm long, with broad, axial canals and very thin walls covered with spiraled wrinkles; smaller spicules up to 35 mm long. [Corralia WALCOTT, 1920, to which Lenica was considered to be related by GORYANSKY, was placed in the new genus Capsospongia by RIGBY (1986a) and included in the Anthaspidellidae because it has a skeleton of dendroclones. Lenica is included here in the family Choiidae because of its radiate structure and relatively simple skeleton.] Lower Cambrian: Russia (eastern Siberia).-FIG. 9. \*L. unica, Lena layer, Lena River; flattened holotype with radiate, fanlike skeletal structure, Ts NIGRM 12/10833, ×1 (Goryansky, 1977).

#### Family WAPKIIDAE de Laubenfels, 1995

#### [Wapkiidae DE LAUBENFELS, 1955, p. 37]

Elongate, oval or flattened sponges whose endodermal skeleton is principally of oxeas arranged in upwardly plumose tracts that outline cellular canals that are particularly pronounced in exterior; rows of canals produce uniformly wrinkled pattern in exterior skeleton; dermal layer as a thin sheet of differentiated coarse and fine spicules, as in *Leptomitus*, may be present. *Middle Cambrian:* Canada (British Columbia).

Wapkia WALCOTT, 1920, p. 279 [\* W. grandis; M]. Elongate oval or flattened fronds; slender, parallel spiculofibers have a plumose pattern centered on longitudinal axis of sponge; they are crossed by outer layer of parallel, long, vertical oxeas; fibers made of parallel, elongate oxeas and possible styles and outline outer layer with cellular canals in upwardly and outwardly flaring pattern. Middle Cambrian: Canada (British Columbia).---FIG. 10a-b. \*W. grandis, Stephen Formation, Burgess Shale, Mount Field; a, flattened, elongate holotype with radiating to plumose, clumped, spicule structure, ×1 (Walcott, 1920); b, generalized three-dimensional restoration of wall showing bundled spicules separated by canals in outer part of sponge and outer layer of vertical oxeas, not to scale (Rigby, 1986a).---FIG. 11. \*W. grandis; Stephen Formation, Burgess Shale, Mount Field; enlarged upper left part of holotype showing upward divergence of spicules in flattened skeleton, USNM 66458, ×4 (Walcott, 1920);

#### Family HALICHONDRITIDAE Rigby, 1986

[Halichondritidae RIGBY, 1986a, p. 30]

Conicotubular to steeply obconical sponges in which principal skeleton is made

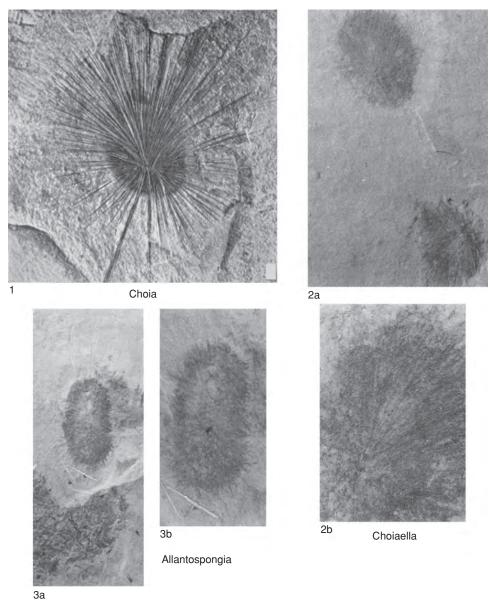


FIG. 8. Choiidae (p. 18).

of long, upwardly plumescent, monaxial spicules; main endosomal net is coarse thatch of generally vertically oriented oxeas; with prominent, coarse marginalia and prostalia. *?Middle Cambrian, Upper Cambrian–Carboniferous (Serpukhovian).* 

Halichondrites DAWSON in DAWSON & HINDE, 1889, p. 52 [\*H. confusus; M]. Oval or irregular masses of oxeas (or possible rhabdodiactines) organized in two parallel series crossing one another at low angle; very much smaller spicules may have formed a dermal layer. [*H. elissa* WALCOTT, 1920, may be a hexactinellid, with rectangular crossings of spicules (possible stauractines) and may not belong to this genus. WALCOTT's action in designating it as the type was invalid.] ?*Middle Cambrian, Upper Cambrian:* Canada (Quebec, ?British Columbia).— FIG. 12.a. \**H. confusus,* Metis shale, Upper Cambrian, Metis, Quebec; irregular cluster of enlarged spicules from oval or irregular masses in drawing by

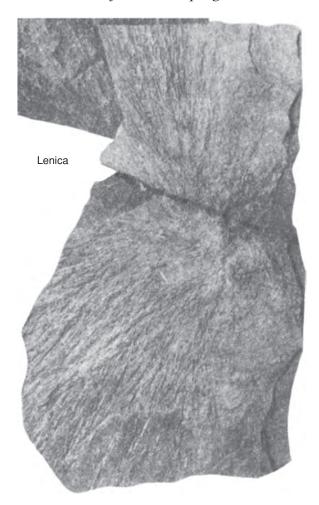


FIG. 9. Choiidae (p. 18).

DAWSON, scale unknown (Dawson & Hinde, 1889).——FIG. 12*b. H. elissa* WALCOTT, Stephen Formation, Burgess Shale, Albertan, Mount Field, British Columbia; generalized restoration showing general form of species and its coarse spiculature, not to scale (Rigby, 1986a).——FIG. 13. *H. elissa* WALCOTT, Stephen Formation, Burgess Shale, Albertan, Mount Field, British Columbia; flattened holotype showing steep, obconical form and coarse, vertical oxeas of skeletal thatch and as pronounced prostalia, USNM 66447, ×1 (Walcott, 1920).

Arborispongia RIGBY, 1986c, p. 446 [\**A. delicatula;* OD]. Tall, arborescent sponge with dichotomous branches, without spongocoel or dermal layer; skeleton composed of bundles of long, upwardly divergent monaxons, which produce a bristly, dermal surface to relatively smooth branches, and spinose, frayed-appearing terminations to branches; circular canals parallel skeletal bundles in upwardly and outwardly divergent pattern and produce elongate-oval ostia where they emerge dermally. [This genus is placed in the family with some question.] *Carboniferous (Serpukhovian):* USA (Montana).——FIG. 14*a*–*b.* \**A. delicatula,* Heath Formation, Fergus County; *a*, photomicrograph of brushlike termination of branch with long, monaxial spicules, ×10; *b*, holotype with 5 or 6 dichotomous branches with smooth exteriors, UMG 5716, ×0.5 (Rigby, 1986c).

# Family PIRANIIDAE de Laubenfels, 1955

[Piraniidae DE LAUBENFELS, 1955, p. 40]

Subcylindrical to obconical, branching sponges with deep spongocoel; marginalia consisting principally of tylostyles with points directed upwardly and outwardly; with principal skeleton composed of upwardly and outwardly radiating, subparallel tufts of oxeas, tufts with hexagonal placement; walls pierced by circular canals parallel to tufts. *Middle Cambrian*.

- Pirania WALCOTT, 1920, p. 298 [\*P. muricata; OD]. Steeply obconical to conicocylindrical, small, moderately thick-walled, branching to complexly branching sponges with pronounced marginalia; wall composed of tufts of oxeas; individual tufts may be cored by large tylostyles that are the marginalia and prostalia; small canals parallel tufts. Middle Cambrian: Canada (British Columbia).-FIG. 15a-c. \*P. muricata, Stephen Formation, Burgess Shale, Mount Field; a, branching growth form of lectotype with steep, obconical branches and prominent marginalia, USNM 66549, ×2; b, enlargement of part of paralectotype showing small, spicule tufts of main wall and coarse, large, tylostyle marginalia, USNM 66497, ×10; c, restoration showing growth form of sponge and its walls composed of tufts of monaxons into which are inserted large, tylostyle marginalia, not to scale (Rigby, 1986a).
- Moleculospina RIGBY, 1986a, p. 34 [\*Hazelia mammillata WALCOTT, 1920, p. 286; OD]. Moderately thick-walled sponges with skeleton of radial tufts of monaxons that converge toward tuft axis and produce low, mounded, nodes cored by one or several moderately large, possible oxeas; radial tufts cross braced by smaller tufts of similar but fewer monaxons; surface marked by elevated, mamelon-like nodes perforated by circular, excurrent ostia; general shape of genus unknown. Middle Cambrian: Canada (British Columbia). FIG. 16a-b. \*M. mammillata (WALCOTT), Stephen Formation, Burgess Shale, Mount Field; a, holotype showing four prominent, possible, excurrent openings on mamelon-like mounds, ×1; b, enlargement showing moderately coarsely tufted skeleton with large-diameter monaxons now largely molds, USNM 66780, ×25 (Rigby, 1986a).

#### Family SOLLASELLIDAE von Lendenfeld, 1887

[Sollasellidae VON LENDENFELD, 1887, p. 584]

Epipolasid sponges with radiate architecture, with dermal cortex; principal spicules oxeas and strongyles that may have swollen shafts, skeleton lacking tetraxons and spongin; microscleres absent. *Devonian (Lochkovian)–Holocene.* 

Sollasella VON LENDENFELD, 1888, p. 56 (VON LENDENFELD, 1887, p. 584, nom. nud.) [\*S. digitata; OD]. Ramose sponges with spicules including oxeas and strongyles in plumose arrangement. [There are no fossils in this genus; included here because it is type genus of family.] *Holocene:* southwestern Pacific Ocean.

- Coniculospongia RIGBY & CLEMENT, 1995, p. 215 [\*C. radiata; OD]. Broadly flaring, funnel-like to discoidal or basinlike sponges with or without small stalks, skeletons composed of radiating, smooth oxeas, unclustered and generally parallel or subparallel, may be somewhat more loosely spaced on upper, gastral surface; coronal spicules absent; spicules not interwoven but radially subparallel. Devonian (Lochkovian): USA (Tennessee).-FIG. 17,2a-b. \*C. radiata, Ross Formation, Bird Song Shale Member, western Tennessee; a, funnel-shaped holotype seen from above showing fine, radial skeleton, Benton Quarry, southwestern Benton County, USNM 463591, ×2; b, paratype skeleton of upwardly and outwardly divergent oxeas, Road cut b on Tennessee Route 69, northwestern Perry County, USNM 463592, ×5 (Rigby & Clement, 1995).
- Ginkgoopongia RIGBY & CLEMENT, 1995, p. 212 [\*G. foliata RIGBY & CLEMENT, 1995, p. 213; OD].
  Stalked, thin-walled, lobate or crenulate palmate to funnel-like sponge, expanding upwardly from stalk as lobes, each with upwardly expanding, fibrous, brushlike arrangement of monaxons, probably oxeas, to produce leaflike, flattened form. Devonian (Lochkovian): USA (Tennessee).——FIG. 17,1a-b. \*G. foliata, Ross Formation, Birdsong Shale Member, Parsons Quarry, northwestern Perry County; a, leaflike, stalked, lobate to palmate holotype, ×2; b, photomicrograph of fine, dense, brushlike skeleton of small oxeas, USNM 463590, ×20 (Rigby & Clement, 1995).
- **Opetionella** ZITTEL, 1878b, p. 4 (94) [\*O. radians; OD]. Globular tuberous to irregularly crustose appearing; neither oscula, pores, nor canals observed; skeleton a thick layer of closely spaced, parallel oxeas. Jurassic: Germany.—FIG. 17,3a-b. \*O. radians, Cuvieri Pläner, Upper Jurassic, Salzgitter; a, side view of small, irregular sponge, ×1; b, skeletal fabric of oxeas, ×10 (Zittel, 1878b).
- Rhizopsis SCHRAMMEN, 1910, p. 132 [\*R. horrida; OD]. Elongate, rootlike or ramose, composed of thick filaments of united amphioxea and amphistrongyles. Upper Cretaceous: Germany.— FIG. 18,1. \*R. horrida, Scaphitenplaner, Turonian, Nettlingen; side view of irregular sponge with upwardly divergent spicules in filaments on right, ×0.5 (Schrammen, 1910).
- Sphaeriella RIGBY & POLLARD BRYANT, 1979, p. 1,005 [\*S. radiata; OD]. Spherical or subspherical to ovoid, small sponges with radiating skeleton of unbundled, thin monaxons, principally oxeas; canals straight and radiating from center, may increase in diameter radially; microscleres and cortex unknown. [Belemnospongia (MILLER, 1889) has a radiate architecture but is a discoidal sponge, as is Choia WALCOTT, 1920. Tethya LAMARCK, 1815, is spheroidal but has a strongly corticate surface.

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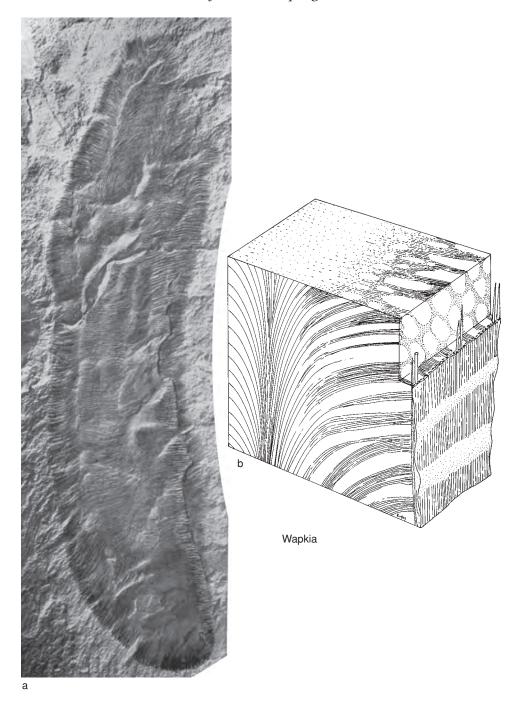


FIG. 10. Wapkiidae (p. 18).



Fig. 11. Wapkiidae (p. 18).

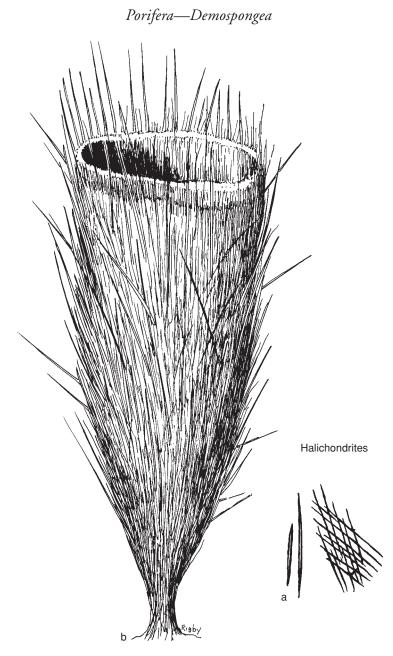


FIG. 12. Halichondritidae (p. 19-20).

This genus is placed in the family with some question.] *Carboniferous (Lower Mississippian):* USA (Alabama).—FIG. 18.2*a-b. \*S. radiata,* Fort Payne Chert, Aurora, northwestern Etowah County; *a*, spherical holotype with fine, radiating skeleton, BYU 1534, ×2; *b*, photomicrograph of paratype showing fine, hairlike, radiating spicules

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in interior and radial canals in outer part of vertical section, BYU 1536, ×5 (Rigby & Pollard Bryant, 1979).

Trichospongia BILLINGS, 1865, p. 357 [\*T. sericea; OD]. Hemispherical sponge with obscure, concentric structure and radiate, diactinal spicules; common branching canals occur throughout. [No



Halichondrites

FIG. 13. Halichondritidae (p. 19–20).

# Porifera—Demospongea

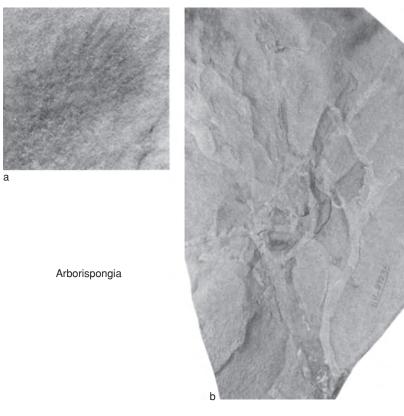


FIG. 14. Halichondritidae (p. 20).

known suitable figures.] Ordovician (Champlainian): Canada (Mingan Islands, Quebec).

#### Family TETHYIDAE Gray, 1848

[Tethyidae GRAY, 1848, p. 1] [=Donatiadae GRAY, 1872a, p. 460; Xenospongina CARTER, 1882, p. 357; Tethyidae VOSMAER, 1887, p. 326; Donatiidae BAER, 1906, p. 26]

Spheroidal sponges with strongly radiate, skeletal structure of bundles of monaxons; dermal layer prominent; microscleres include sphaerasters and euasters. [The family is commonly attributed to GRAY (1867, p. 540), but the name was used earlier by GRAY (1848).] *?Paleogene, Holocene.* 

Tethya LAMARCK, 1815, p. 69, non GRAY, 1840, p. 148 [\*Alcyonium aurantium PALLAS, 1766, p. 357; SD TOPSENT, 1920b, p. 641]. Spherical to subspherical with two well-marked, concentric zones, an inner choanosome and an outer ectosome with strong, nodose, dermal layer; pronounced, radiate, skeletal structure produced by bundles of styles and megaster megascleres; microscleres include sphaerasters and euasters. ?Paleogene, Holocene: Atlantic Ocean, Mediterranean Sea.—FIG. 19*a.* \*T. *aurantium* (PALLAS), Holocene; drawing of outer part of skeleton showing bundles of megascleres, common microscleres, and canal patterns (Sarà & Manara, 1991; courtesy of Springer-Verlag GmbH & Co.).——FIG. 19*b–c. T. cranium* LAMARCK, Holocene, Atlantic Ocean off British Isles; *b*, ovoid, complete sponge, ×1; *c*, transverse section showing radiate, skeletal structure with embedded gemmules and distinct, dermal layer, ×1 (Bowerbank, 1874a).

# Family HAZELIIDAE de Laubenfels, 1955

#### [Hazeliidae DE LAUBENFELS, 1955, p. 37]

Fibrous skeleton; fibers composed of oxeas in either plumose or parallel arrangement; fibers anastomosing or sub-isodictyal; canals, where present, parallel fibers; dermal layer of tangential oxeas may be present. *Middle Cambrian–Lower Devonian*.

Hazelia WALCOTT, 1920, p. 281, *non* TAYLOR, 1920 [\**H. palmata* WALCOTT, 1920, p. 282; OD]. Flabellate, conical, frondescent, branching or tubular, expanding upwardly from narrow base; composed

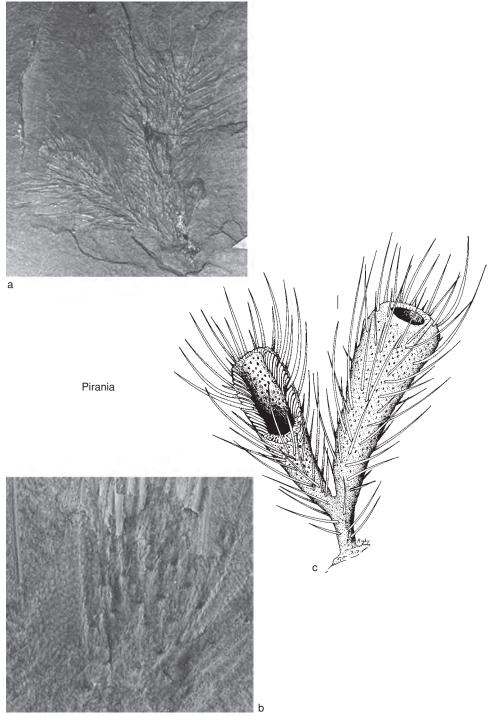


FIG. 15. Piraniidae (p. 21).

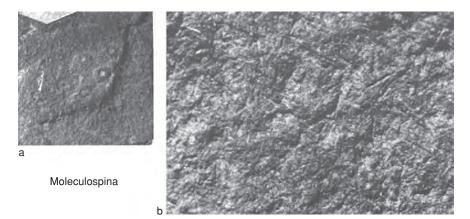


FIG. 16. Piraniidae (p. 21).

of branching and anastomosing, subparallel spiculofibers; fibers composed of plumosely arranged, smooth oxeas; canals small and parallel to fibers; a dermal layer of tangential oxeas may be present. [H. delicatula WALCOTT, which is tubular and branching and has a more nearly isodictyal net of bundles of parallel oxeas, perhaps should be placed in a separate, new genus.] Middle Cambrian: Canada (British Columbia), USA (Utah).-—Fig. 20,1a-f. \*H. palmata, Stephen Formation, Burgess Shale, Mount Field, British Columbia; a, lectotype, fragment of disc with ragged, tufted margin and radiating bundles of coarse oxeas, USNM 66463, ×1; b, paralectotype with coarse tufts of bundled oxeas, USNM 66492, ×2; c, enlarged upper of paralectotype showing two diagonally oriented series of tufts of oxeas, USNM 66492, ×5; d-f, growth forms of various species of Hazelia, not to uniform scale (Rigby, 1986a).

- Crumillospongia RIGBY, 1986a, p. 44 [\*Morania (?) frondosa WALCOTT, 1919, p. 231; OD]. Sackshaped to globular or globose with thin walls of principally vertical, subparallel, monaxial spicules that form tracts around circular canals of at least two sizes; gastral layer a vertical, monaxial thatch that is less perforate; skeleton with weakly developed tufts; marginalia or prostalia absent. Middle Cambrian: Canada (British Columbia).----FIG. 21,1a-c. \*C. frondosa (WALCOTT), Stephen Formation, Burgess Shale, Mount Field; a, saclike holotype with rounded base and irregular, oscular margin, USNM 66779, ×2; b, enlargement of part of counterpart wall showing open, porous nature and two sizes of canals that interrupt vertically oriented, spicule net, USNM 66778, ×5; c, photomicrograph of holotype exterior showing vertical thatch of spicules interrupted by matrix clumps that fill irregular canals, USNM 66779, ×20 (Rigby, 1986a).
- Falospongia RIGBY, 1986a, p. 44 [\**F. falata;* OD]. Frondescent to thin-walled, obconical; composed

of isolated, somewhat anastomosing, radiating tracts cross connected by abundant, horizontal or concentric tracts that produce three-dimensional, gridlike wall, tracts of clustered oxeas and possibly other monaxons. *Middle Cambrian:* Canada (Brit-ish Columbia).——FIG. 20,2. \**F falata,* Stephen Formation, Burgess Shale, Mount Field; holotype, upper part of thin-walled, funnel-shaped sponge with anastomosing, skeletal tracts cross braced at irregular intervals by smaller tracts, both composed of oxeas, ROM 40317a, ×5 (Rigby, 1986a).

Lasiocladia HINDE, 1884a, p. 19 [\*L. compressa; OD]. Cylindrical; composed of oxeas arranged in plumose fashion about longitudinal axis of sponge; known from a single fragment. Lower Devonian: Belgium.——FIG. 21,2. \*L. compressa, Jemelle; holotype, flattened, plumose, spicule cluster, BMNH, ×1 (Hinde, 1884a).

### Family TAKAKKAWIIDAE de Laubenfels, 1955

[Takakkawiidae DE LAUBENFELS, 1955, p. 38]

Slender, thin walled, conicocylindrical sponges in which dermal skeleton is made of vertically elongate, tiny oxeas; internally skeleton includes eight twisted, ribbonlike tracts that extend from base to differentiated, oscular fringe; exterior marked by vertical fins that reach from base to oscular margin where they produce a cockscomblike, oscular apparatus; entire skeleton made of clustered, monaxial spicules, except perhaps rare, triaxial spicules in twisted strands in interior (RIGBY, 1986a, p. 46). *Middle Cambrian.* 

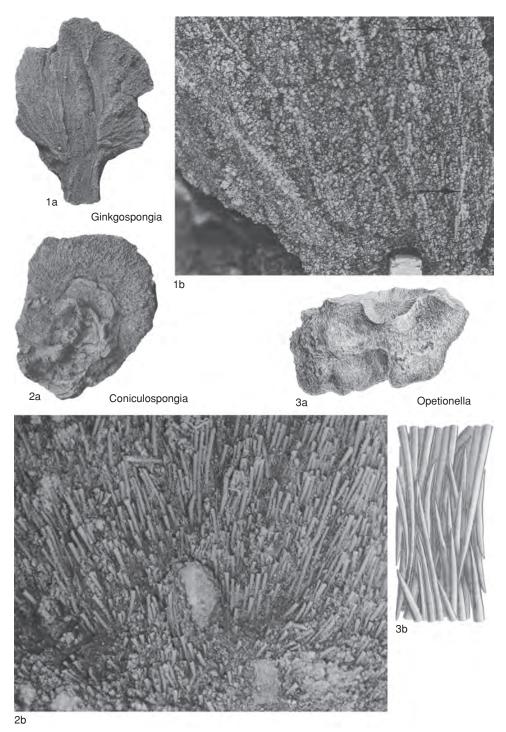


FIG. 17. Sollasellidae (p. 21).

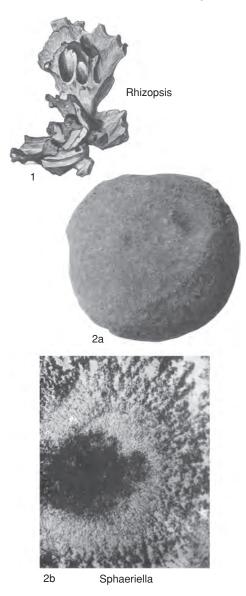


FIG. 18. Sollasellidae (p. 21-24).

Takakkawia WALCOTT, 1920, p. 277 [\* *T. lineata*; OD]. Conical-fusiform, with pointed base, widest part near mid-height, and slightly contracted toward broad osculum; prismatic, eight-sided, with narrow, radial, external fins at interfacial angles; vertical bundles of spicules at interfacial angles; vertical ly twisted structure (RIGBY, 1986a, p. 47–48) and splay out at oscular end (oscular apparatus of RIGBY, 1986a); spicules possibly rhabdodiactines, tauactines, or stauractines; horizontal spicule rays extend across space between bundles; there is a suggestion of a finer quadrate mesh of possible stauractines between bundles. Middle Cambrian: Canada (British Columbia).-FIG. 22a-c. \*T. lineata, Stephen Formation, Burgess Shale, Field, British Columbia; a, flattened lectotype showing general form, oscular apparatus, and twisted, spiral strands characteristic of genus, ×2 (Walcott, 1920); b, photomicrograph of upper part of lectotype showing twisted, ribbonlike strands and their upper, frayed ends associated with radiating fins of oscular apparatus, horizontal elements cross connect between spiral tracts in main part of sponge, ×10; c, lower part of lectotype showing traces of eight spiral tracts and associated radial fins; rates of spiraling are relatively constant within a tract, but vary between tracts, USNM 66539, ×5 (Rigby, 1986a).-FIG. 23. \*T. lineata, Stephen Formation, Burgess Shale, Field, British Columbia; restoration showing relationships between spiral tracts, radiating fins, and their rounded tips in oscular apparatus, ×4 (Rigby, 1986a).

### Family MAHALOSPONGIIDAE Rigby & Stuart, 1988

[Mahalospongiidae RIGBY & STUART, 1988, p. 130]

Small, simple, monaxonid sponges with thin walls composed mainly of tangential, diagonal to horizontal, curved to serpentine ophirhabds; prostalia may form dense, oscular fringe. *Silurian–Devonian*.

Mahalospongia RIGBY & STUART, 1988, p. 130 [\*M. floweri; OD]. Small, conicocylindrical to subcylindrical sponges with thin wall and deep, simple spongocoel; walls smooth and unornamented; skeletal net composed principally of irregularly subhorizontal to diagonal, curved to sinuous monaxons, mainly ophirhabds; oscular fringe a dense prostalia of diactines, principally oxeas, of several sizes; skeletal structure becoming more nearly vertical near base; root tuft unknown. Silurian-Devonian: USA (Nevada).-FIG. 24a-b. \*M. floweri, Roberts Mountains Formation, Silurian, Independence Mountains; a, flattened holotype and associated paratypes, with sharp, pointed base and distinct, oscular fringe, USNM 415777, ×2; b, enlargement of central part of paratype showing dominantly subhorizontal monaxons (possible ophirhabds) in moderately loose, open, skeletal net, USNM 415778, ×10 (Rigby & Stuart, 1988).

### Family HELIOSPONGIIDAE Finks, 1960

[Heliospongiidae FINKS, 1960, p. 40]

Skeletal net a radial-reticulate mesh of spiculofibers composed of thick bundles of smooth, slightly curved oxeas closely packed parallel to length of fiber; dense, dermal

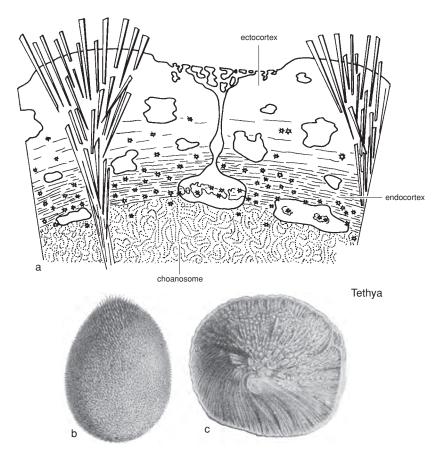


FIG. 19. Tethyidae (p. 26).

layer may be present, composed of similar oxeas closely packed, tangential to surface and arranged concentrically about pores; vertical fibers perpendicular to growing surface, horizontal fibers parallel to it. *Carboniferous (Middle Pennsylvanian)–Permian (Changhsingian).* 

Heliospongia GIRTY, 1908, p. 288 [\*H. ramosa GIRTY, 1908, p. 289; OD] [=Corynospongia DENG, 1990, p. 317 (type, C. tubuliforma DENG, 1990, p. 319, OD)]. Tubular and branching with deep cloaca, or flabellate and solid with shallow, lateral, multiple, cloacal depressions; horizontal spiculofibers form upwardly arched layers parallel to top surface of sponge; vertical spiculofibers at right angles to these, diverging upwardly and outwardly from axial region or cloaca of sponge; larger, exhalant canals parallel to horizontal spiculofibers and open as circular pores on cloacal surface, arranged in vertical and horizontal rows and forming surface grooves about osculum on sponge exterior; somewhat smaller, circular to stellate, inhalant pores on outer surface lead into inhalant canals that follow vertical fibers inwardly and downwardly; lower part of cloaca filled in secondarily with less regular mass of spiculofibers pierced by vertical, exhalant canals; juvenile stage solid, hemispherical, and encrusting. Upper Carboniferous-Permian (Sakmarian): southwestern North America, USA (Kansas, Ohio, Texas), Tunisia, Spain, China (Ziangsu, Guizhou, Sichuan).-FIG. 25a-b. \*H. ramosa, Plattsburg (Allen) Limestone, Missourian, Chanute, Kansas; a, holotype block, ×0.25, and b, part showing branching habit, axial spongocoel, and regular arrangement of spicules in skeleton, USNM 53472, ×1 (Girty, 1908).-FIG. 25c. H. excavata KING, 1933, Graford Formation, Missourian, Lake Bridgeport Dam, Texas; median section of topotype showing general pattern of skeleton, USNM 127582f, ×1 (Finks, 1960).—FIG. 25d. H. vokesi KING, Leonard Formation, Leonardian, Glass Mountains, Texas; weathered longitudinal section showing thick walls around axial spongocoel and

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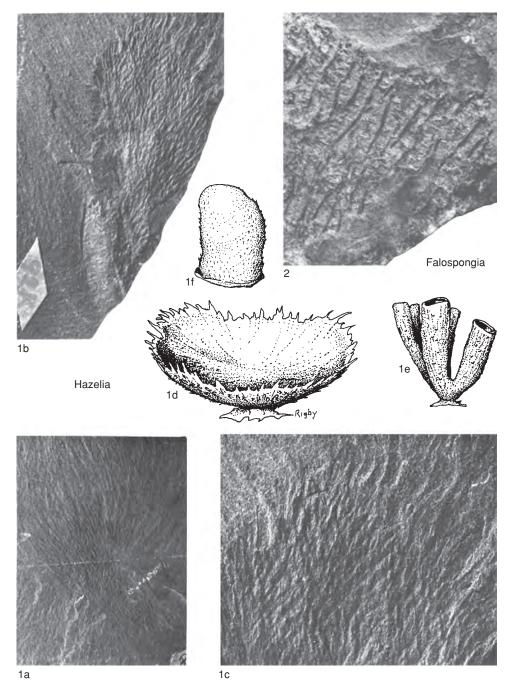


FIG. 20. Hazeliidae (p. 26-28).

upwardly arched, skeletal structure pierced by aligned apochetes, USNM 127588d, ×1 (Finks, 1960; courtesy of The American Museum of Natural History). **Coelocladia** GIRTY, 1908, p. 287 [\**C. spinosa* GIRTY, 1908, p. 288; OD]. Tubular and branching with deep cloaca (not continuous between branches), or funnel shaped and frondose; sponge smaller,

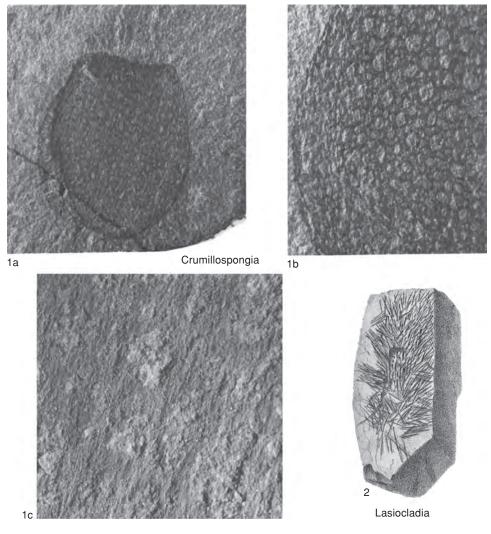


FIG. 21. Hazeliidae (p. 28).

spiculofibers thinner and more closely spaced, and somewhat less regularly arranged than in *Heliospongia*; horizontal fibers forming convex-up layers parallel to top of sponge or growing edge of frond; vertical fibers subparallel to exhalant (cloacal) surface and diverging upwardly and outwardly to inhalant (exterior) surface; exhalant surface bearing rows of irregular, exhalant pores parallel to growing edge; inhalant surface covered with a dense, imperforate layer that forms collars about circular, evenly distributed, inhalant pores; adjacent collars may unite to form meandriform ridges; exhalant canals parallel to vertical fibers. *Carboniferous (Middle Pennsylvanian–Upper Pennsylvanian)*: North America, Spain.——FIG. 26,1*a–e.* \**C. spinosa,* Plattsburg Limestone, Chanute, Kansas, USA; *a*, lectotype, cylindrical fragment with no-dose prosopores and osculum of axial spongocoel at summit, USNM 53469a, ×1 (Girty, 1908); *b*, longitudinal section of paratype showing upwardly divergent, trabecular, skeletal net in thick walls around axial spongocoel, USNM 53469c, ×5; *c*, transverse section of same paratype showing radial, excurrent, canal system in trabecular, skeletal net, USNM 53469c, ×5; *d*, side view of figured specimen showing lower stem and upper, funnel-shaped parts with nodose or lipped prosopores in dermal layer, USNM 127591a, ×1; *e*, opposite side view showing thin walls and broad

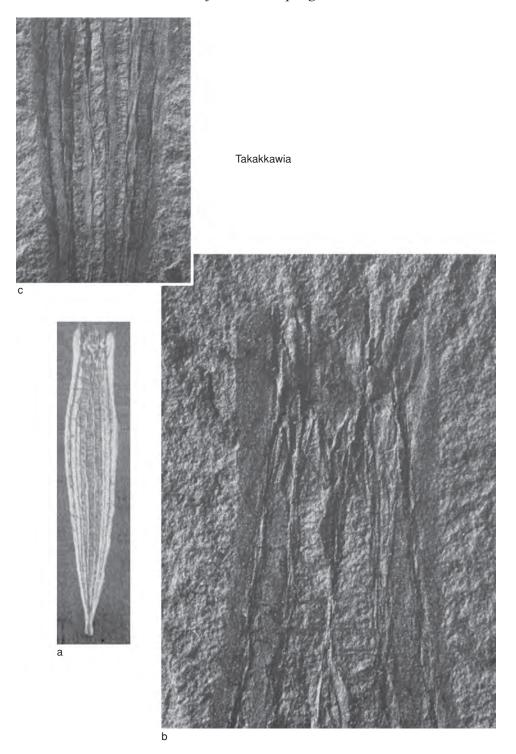


FIG. 22. Takakkawiidae (p. 30).

spongocoel with apopores, USNM 127591a, ×1 (Finks, 1960; courtesy of The American Museum of Natural History).

- Coelocladiella FINKS, 1960, p. 52 [\*C. lissa FINKS, 1960, p. 53; OD]. Tubular and thin walled with broad cloaca; resembles Coelocladia but differs in that dense, external layer, with collars about inhalant pores, is absent, and skeletal net less regular and more open; no spicules have been observed. Upper Carboniferous-Permian (Lopingian): USA (Texas, ?Missouri), Upper Carboniferous-Permian (Sakmarian); China (Guangxi), Permian (Lopingian).-FIG. 26,2a-c. \*Č. lissa, Gaptank Formation, Missourian-Wolfcampian, Brewster County, Texas; a, holotype from side, ×1; b, vertical section showing upwardly divergent, skeletal structure, USNM 127595, ×5; c, side view of silicified specimen showing deep, simple spongocoel and pores of canal system, USNM 127594, ×1 (Finks, 1960; courtesy of The American Museum of Natural History).
- Neoheliospongia DENG, 1981, p. 426 [\*N. typica; OD]. Branching, cylindrical sponge lacking axial spongocoel, with relatively dense skeleton of thick, upwardly divergent, ascending tracts interconnected by convex layers of thick, concentric horizontal tracts that turn down sharply around periphery; spicule structure unknown; canal system well developed with canals partially parallel to ascending tracts and to horizontal tracts with ascending canals connecting to horizontal ones; surface with irregular to distinctly aligned pores. [Neoheliospongia is structurally similar to Heliospongia GIRTY, 1908, but without characteristic large, axial spongocoel of the latter. Heliospongia has skeletal tracts composed of bundled, smooth oxeas and until skeletal details of Neoheliospongia can be obtained, comparisons depend on larger, structural relationships.] Permian (Changhsingian): China (Guangxi).-FIG. 27,2a-b. \*N. typica, Changhsing Formation; a, longitudinal section of holotype showing upwardly divergent, vertical tracts connected by arched, horizontal tracts in regular skeletal structure, NIGPAS 59971, ×2.5; b, transverse section of cylindrical holotype showing uniform skeletal structure and lacking spongocoel, NIGPAS 59972, ×2.5 (Deng, 1981).
- Spitsbergenia HURCEWICZ, 1983, p. 90 [\*S. patella; OD]. Plate- or bowl-shaped sponges without differentiated canal system within skeleton; reticulate skeleton of numerous smooth, straight to slightly bent, sharply terminated diactines. Permian: Spitzbergen.-FIG. 27, 1a-c. \*S. patella, Kapp Starostin Formation, Hornsund, Treskellen; a, holotype, transverse section showing dense, skeletal structure and absence of major canals, IPPAS AI-69-66, ×3; b, transverse section of reference specimen with laterally divergent, skeletal structure, below, overgrown by coarser Haplistion skinneri (KING, 1943), IPPAS AI-69-31, ×2; c, drawings of diactine spicules from reference thin section, IPPAS AI-69/66, ×50 (Hurcewicz, 1983; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).

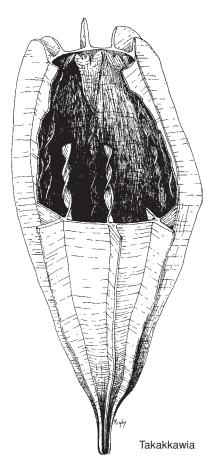


FIG. 23. Takakkawiidae (p. 30).

# Order CLAVULINA Vosmaer, 1887

[nom. transl. FINKS & RIGBY, herein, ex tribus Clavulina VOSMAER, 1887, p. 328] [=suborder Hadromerina TOPSENT, 1898, p. 93]

Diagnostic microscleres are spinispires; megascleres characteristically tylostyles that may be accompanied by oxeas and styles. *Ordovician–Holocene*.

#### Family CLIONAIDAE d'Orbigny, 1851

[nom. correct. BOUCHET & RUTZLER, 2003, p. 99, pro Clionidae D'ORBIGNY, 1851, p. 209; emend., BOUCHET & RUTZLER, 2003, p. 99] [=Clioniadae GRAY, 1867, p. 524, non RAFINESQUE, 1815, gastropod]

Clavulinid sponges that excavate ramifying and usually anastomosing galleries in calcareous shells; numerous openings to surface occur along length of galleries, diameter being about same as that

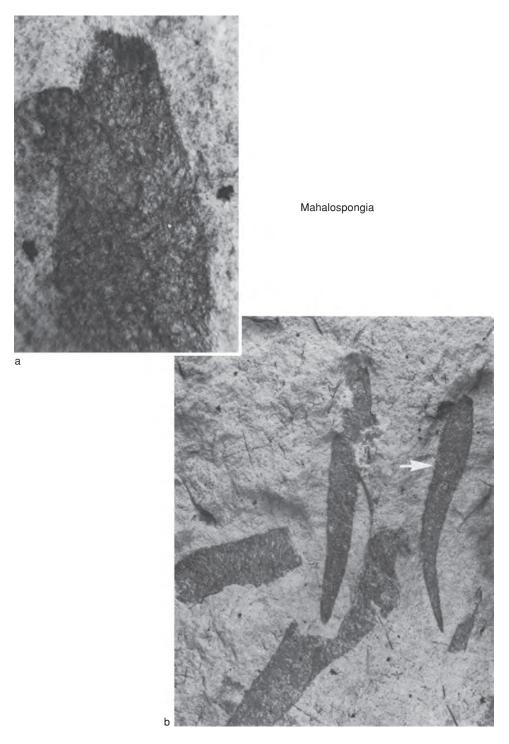


FIG. 24. Mahalospongiidae (p. 30).

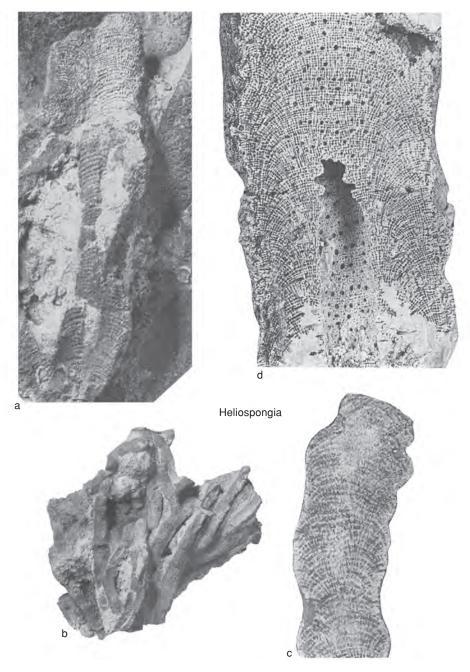


FIG. 25. Heliospongiidae (p. 31-32).

of galleries; abundant tylostyles may remain in well-preserved borings, but are unknown from Paleozoic forms. *Ordovician– Holocene.*  Cliona GRANT, 1826a, p. 79 [\*C. celata; OD]. Shallow, sponge borings as meandering impressions in calcareous shells or other substrates; spicules mainly tylostyles but may include spirasters and less commonly oxeas. *Devonian–Holocene:* cosmopolitan.

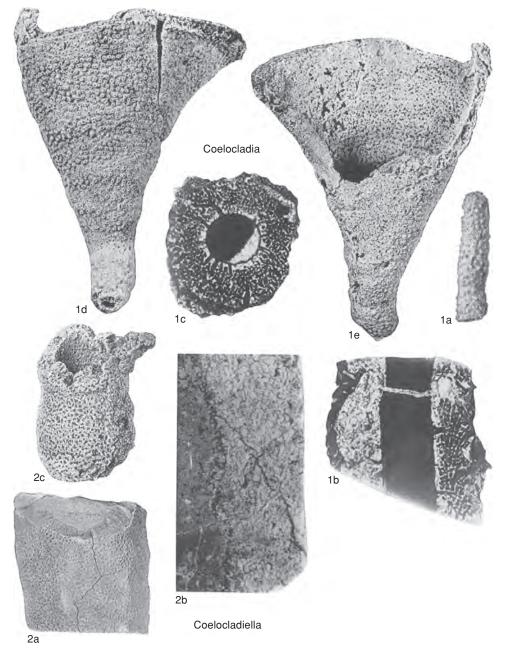


FIG. 26. Heliospongiidae (p. 32-35).

——FIG. 28,4*a*–*b*. *C. cretacica* FENTON & FENTON, Navesink Formation, Upper Cretaceous, New Egypt, New Jersey, USA; *a*, shell of *Exogyra* with perforations of boring sponge, ×0.5; *b*, etched shell of *Gryphaea* showing casts of sponge borings, ×1 (Fenton & Fenton, 1932b). Alectona CARTER, 1879, p. 497 [\*A. millari; SD DE LAUBENFELS, 1936, p. 156]. Membranous like Thoosa, but not certainly burrowing, and larva seem to be choristid; some megascleres peculiarly lumpy. Paleogene–Holocene: New Zealand, Paleogene–Neogene; cosmopolitan, Holocene.——FIG.

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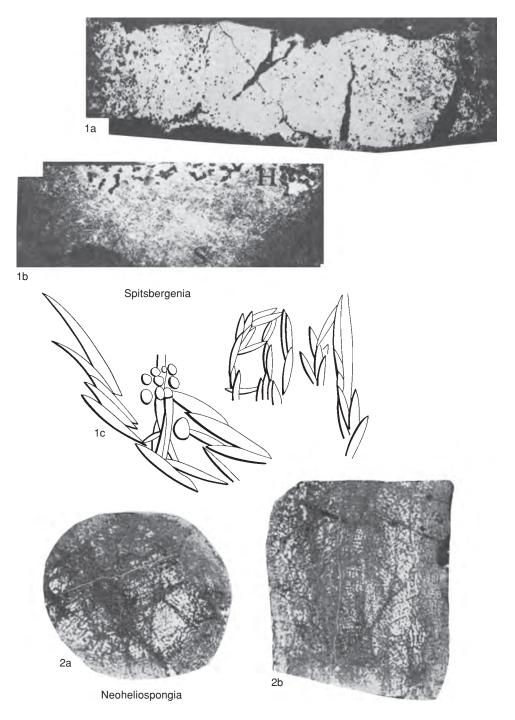


FIG. 27. Heliospongiidae (p. 35).

29,1*a-c.* \**A. millari*, Holocene, North Atlantic Ocean; *a-b*, microscleres, ×400 (de Laubenfels, 1955); *c*, nodose megascleres, ×100 (Carter, 1879).

- Clionoides FENTON & FENTON, 1932a, p. 47 [\*C. thomasi FENTON & FENTON, 1932a, p. 48; OD]. Borings in shells consist of long, rather straight tubes that may branch once or twice; they communicate to exterior by series of closely spaced openings along length of each tube. [This last characteristic makes an assignment to the sponges more likely than is the case with the other borings described here, although it must still be considered doubtful. See also HANTSCHEL, 1962, p. 230.] *Middle Devonian:* North America.—FIG. 28,2. \*C. thomasi, Cedar Valley Limestone, Waterloo, Iowa, USA; holotype boring in brachiopod valve, USNM 184641a, ×1 (Fenton & Fenton, 1932a).
- Clionolithes CLARKE, 1908, p. 168 [\*C. radicans; SD FENTON & FENTON, 1932a, p. 43] [=Olkenbachia SOLLE, 1938, p. 156 (type, O. hirsuta SOLLE, 1938, p. 157, OD)]. Borings in shells; from central cavity, opening to exterior, and radiating in one plane with numerous branching tubes that each taper to point. [This may not be a sponge. See also HANTZ-SCHEL, 1962, p. 230.] Ordovician–Carboniferous: Europe, Ordovician; Europe, USA, China, Devonian–Carboniferous.—FIG. 28,3. C. irregularis FENTON & FENTON, Cedar Valley Limestone, Upper Devonian, Blackhawk County, Iowa, USA; holotype as ramifying borings in an Atrypa shell, USNM 84693, ×1 (Fenton & Fenton, 1932a).
- Entobia BRÖNN, 1838 in 1837-1838, p. 691 [\*E. cretacea PORTLOCK, 1843, p. 360; SD HÄNTZSCHEL, 1962, p. 230]. Borings in calcareous substrates as small, chambered impressions with short aporhyses that widen at base; chambers not spherical but irregularly nodular and commonly occurring in closely adjacent rows; apertures variable but up to several millimeters wide; large canals connecting with these apertures and may have half chambers on their sides. ?Silurian, Upper Cretaceous-Holocene: Ireland, ?Silurian; England, Ireland, Upper Cretaceous; Greece, Pliocene; Italy, Ho--FIG. 28, 1a-b. E. goniodes BROMLEY & locene.— ASGAARD, upper Pliocene occupation of Jurassic Elaphokampos Cherty Limestone, Tsampika Bay, Island of Rhodes, Greece; a, counterpart to holotype pebble with entobian borings in interior, MGUH 20743b, ×1; b, enlarged view of holotype with chambers and aporhyses, ×5 (Bromley & Asgaard, 1993; courtesy of Gordon and Breach Publishers).
- ?Filuroda SOLLE, 1938, p. 158 [\*Clionolithes reptans CLARKE, 1908, p. 168; OD]. Threadlike, serpentine, irregularly branching borings in shells, ramifying just beneath surface. [This may not be a sponge. See also HÄNTZSCHEL, 1962, p. 230.] Lower Devonian-Carboniferous (Pennsylvanian): North America, Europe, Lower Devonian-Middle Devonian; North America, Pennsylvanian......FIG. 28,5. \*F. reptans (CLARKE), Oriskany Sandstone, Lower Devonian, Becraft Mountain, New York, USA; holotype, threadlike boring, ×30 (Solle,

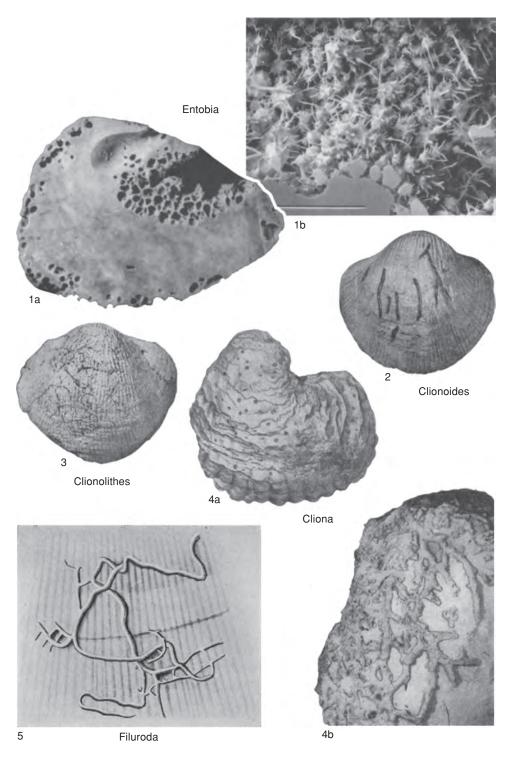
1938; courtesy of Senckenberg Naturforschende Gesellschaft).

- ?Palaeosabella CLARKE, 1921, p. 91, nom. nov. pro Vioa M'Coy, 1855, p. 260, non Nardo, 1833 [\*Vioa prisca M'Coy, 1855, p. 260; OD] [=Palaeosabella CLARKE, 1921, p. 91, nom. null.; Paläosabella SOLLE, 1938, p. 157, nom. null.; Topsentopsis DE LAUBENFELS, 1955, p. 41, nom. nov. pro Topsentia CLARKE, 1921, p. 88, non BERG, 1899]. Borings in shells and stromatoporoids, consisting of straight, occasionally branching tubes, often enlarged at end, that may radiate from central cavity or open directly to shell surface. [This may not be a sponge, but it shows some resemblance to Clionoides FENTON & FENTON, 1932a, with which it occurs.] ?Silurian, Devonian: England, ?Silurian; North America, ?Silurian, Devonian.-FIG. 29,2. \*P. prisca (M'COY), upper Silurian, Malverns, England; central cavities from which radiate relatively straight tubes, all as fillings, ×1 (Fenton & Fenton, 1932a).
- Runia MAREK, 1984, p. 402 [\*R. runica; OD]. Horizontal series of borings, each of which consists of short, vertical, almost straight, nodular to cylindrical, narrow tunnels that have circular cross sections and appear like short, dotted line in early stages; later stages have two or three branches in forklike structure, and later stages may have secondary branches; tunnels in single series more or less alike, but may differ from those above and below in branched development; series of borings follow growth lines in host shells. Silurian (Ludlow): Czech Republic, Slovakia.---FIG. 29,4a-b. \*R. runica, Kopanina Formation, central Bohemia, Barrandian area; a, holotype series of borings in Orthoceras shell, Lejskov hill, near Zdice, PDMNH-P NM L 20273, ×1; b, enlargement of one series of borings from holotype showing beaded form of borings, ×8 (Marek, 1984).
- Thoosa HANCOCK, 1849, p. 345 [\*T. cactoides; SD DE LAUBENFELS, 1936, p. 156]. Sponges branched or lobed, buried in calcareous bodies; interior with anastomosing tubes without spicules; surficial megascleres typically conjoined spheres with one or more radiating shafts; microscleres commonly with verticillate spines as in Ditriaenella. Paleogene-Holocene: New Zealand, Paleogene-Neogene; cosmopolitan, Holocene.-FIG. 29,3a-b. \*T. cactoides, Holocene, Indo-Pacific Ocean; a, part of branched individual with terminal, twiglike tips, ×1; b, highly enlarged spicule from surface of same specimen as in *a*, approximately  $\times 2,000$ (Hancock, 1849).-FIG. 29,3c. T. bulbosa HANCOCK, Holocene, Indo-Pacific Ocean; triradiate, surficial megascleres, approximately ×200 (Hancock, 1849).

# Family ADOCIIDAE de Laubenfels, 1936

[Adociidae DE LAUBENFELS, 1936, p. 65]

Boring sponges with oxeas in bundles or brushes; spicules of inner sponge with





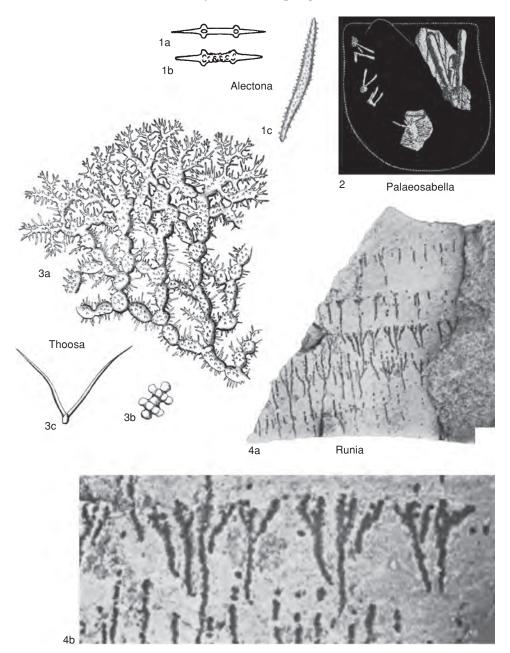


FIG. 29. Clionaidae (p. 38-40).

cortical, spicule tracts perpendicular to central, spicule bundles; prominent chimneys with apertures protruding from burrowed surfaces. *Triassic (Carnian)–Holocene*.

Aka de Laubenfels, 1936, p. 155, nom. nov. pro Acca Johnson, 1899, p. 461, non Huebner, [1819], p. 49, Lepidoptera [\**Acca insidiosa* JOHNSON, 1899, p. 461; OD] [=*Siphonodictyon* BERGQUIST, 1965, p. 158 (type, *S. mucosa*, OD)]. Excavating sponges with elongate to sack-shaped borings in calcareous substrates, spicules are oxeas in bundles or brushes, with cortical, spicule tracts perpendicular to more central spicule tracts; prominent chimneys with apertures protruding from burrowed surfaces.

[Specimen for type species lost.] Triassic (Carnian)– Holocene: Italy, Carnian; Germany, Spain, Jurassic; Spain, Cretaceous; Spain, Eocene; Mediterranean and Caribbean Seas, Holocene.——FIG. 30,1a. A. muelleri REITNER & KEUPP, Kimmeridge sponge mounds, Upper Jurassic, Rossbach, Germany; holotype, photomicrograph of spicule tracts including coarse oxeas, in burrow, IPFUB, JR6/89, ×10 (Reitner & Keupp, 1991).——FIG. 30,1b. A. coralliphaga (RUTZLER), Holocene, Playa Kalki, Curacao, Caribbean Sea; spicule bundle of central part of exterior chimney, scale bar indicates magnification (Reitner & Keupp, 1991).

### Family SPIRASTRELLIDAE Ridley & Dendy, 1886

[Spirastrellidae RIDLEY & DENDY, 1886, p. 490] [=Choanitidae de LAUBENFELS, 1936, p. 140]

Sponges having astrose microscleres, not boring. *Paleogene–Holocene*.

- Spirastrella SCHMIDT, 1868, p. 17 [\*S. cunctatrix; OD]. Megascleres comprise tylostyles only and microscleres spirasters only. *Holocene:* cosmopolitan.——FIG. 30,3. \*S. cunctatrix, Cyprus; tylostyle megasclere and associated spiraster microscleres, approximately ×500 (Schmidt, 1868).
- Dirriaenella HINDE & HOLMES, 1892, p. 232 [\*D. oamaruensis; OD] [=Ditraenella DE LAUBENFELS, 1955, p. 40, nom. null.]. Verticillate spined microrhabds, similar to some in Latrunculia, which seem to be immature chessman spicules. Paleogene–Neogene: New Zealand.—FIG. 30,5. \*D. oamaruensis; spined microsclere, ×400 (de Laubenfels, 1955).

### Family SUBERITIDAE Ridley & Dendy, 1886

[Suberitidae RIDLEY & DENDY, 1886, p. 484]

Similar to Spirastrellidae but lacking microscleres other than microrhabds, spicules commonly styles or tylostyles, not boring. *Cretaceous–Holocene*.

- Suberites NARDO, 1833, p. 523 [\*Alcyonium domunculum OLIVI, 1792, p. 241; OD]. Architecture radiate with small tylostyles in cortex and large ones in endosome; microscleres absent. ?Paleogene-?Neogene, Holocene.—FIG. 30,6. S. sp.; isolated tylostyle, ×50 (de Laubenfels, 1955).
- Calcisuberites REITNER & SCHLAGINTWEIT, 1990, p. 249 [\*C. stromatoporoides; OD]. Coralline, hadromerid sponge with a magnesium-calcite, basal skeleton in stromatoporoid organization; spicular skeleton consisting of typical hadromerid tylostyles, in dermal layer arranged in plumose, bushlike patterns. Lower Cretaceous (Coniacian): Germany.—FIG. 30,2a-b.\*C. stromatoporoides, Gosau Formation, Chiemgau; a, drawing of spi-

cule development in vertical section of outer part of wall, vertical scale, 200  $\mu$ m long, approximately ×50; *b*, photomicrograph showing tylostyles in outer part of wall and calcareous, basal skeleton below, with horizontal tabulae indicated by *arrow points*, IPFUB/ JR 90, ×100 (Reitner & Schlagintweit, 1990).

Rhopaloconus SOLLAS, 1880d, p. 392 [\**R. tuberculatus;* OD]. Tylostyles extremely thick, with heads covered with many small, tentlike tubercles. *Cretaceous:* England.—FIG. 30,4. \**R. tuberculatus,* Trimmingham Chalk, Maastrichtian, Norfolk; isolated, type tylostyle with conical tubercules on rounded head, scale uncertain (Sollas, 1880d).

# Subclass CERACTINOMORPHA Lévi, 1953

[nom. correct. BERGQUIST, 1967, p. 167, pro Céractinomorphes LEVI, 1953, p. 855]

Spicules when present are exclusively monaxonic, without triaenes; megascleres generally sigmoid or chelate, never astrose; microscleres when present are usually sigmas or derivatives thereof or microrhabds and never astrose; spongin usually abundant and may form entire skeleton with or without foreign particles; living sponges viviparous with parenchymella larva. *Cambrian– Holocene.* 

# Order DICTYOCERATIDA Minchin, 1900

[nom. correct. BERGQUIST, 1978, p. 176, pro Dictyoceratina MINCHIN, 1900, p. 153]

Ceractinomorph sponges without mineralized, spicule skeleton, but with skeleton of spongin fibers, often of great complexity, constructed in anastomosing patterns involving differentiated, primary and secondary fibers. *Jurassic–Holocene*.

## Family SPONGIIDAE Gray, 1867

[nom. correct. de Laubenfels, 1936, p. 7, pro Spongiadae Gray, 1867, p. 508]

Dictyoceratid sponges with small, flagellated chambers, not preserved as fossils, and fibers uniform in cross section and without diffuse, central pith. *Holocene*.

Spongia LINNÉ, 1759, p. 1,348 [\*S. officinalis; SD BOWERBANK, 1862, p. 1119]. Sponges with fibers spongy, even when dry; chiefly clear, but a few

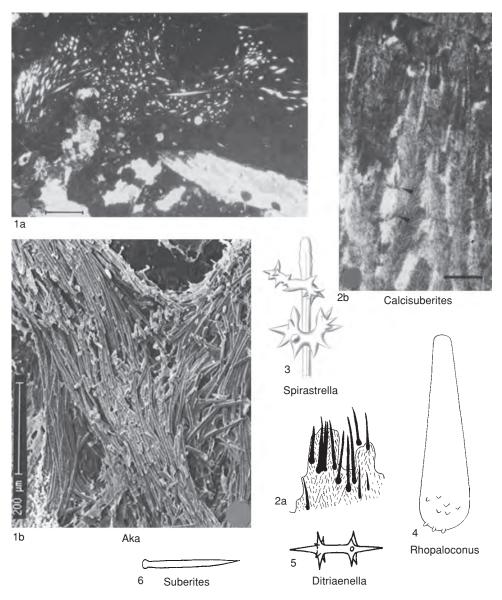


FIG. 30. Adociidae, Spirastrellidae, and Suberitidae (p. 42-43).

ascending fibers that may contain debris. *Holocene:* cosmopolitan.

#### Family DYSIDEIDAE Gray, 1867

#### [Dysideidae GRAY, 1867, p. 511]

Large, sac-shaped (eurypylous), flagellate chambers (not visible in fossils) with skeleton of fibers usually containing much foreign debris. *Lower Jurassic-Holocene*. Dysidea JOHNSTON, 1842, p. 251 [\*Spongia fragilis MONTAGU, 1818, p. 114; SD DE LAUBENFELS, 1936, p. 27] [=Spongelia NARDO, 1847, p. 3 (type, S. elegans, M]. Fragile sponges with all fibers cored with foreign debris and many appearing rugose, as though covered by sand. Paleogene (Eocene)– Holocene: Belgium, Eocene; cosmopolitan, Holocene, —FIG. 31, I. \*D. fragilis (MONTAGU), Holocene, Devon coast, United Kingdom; side view of small, coarsely reticulated sponge, ×1 (Montagu, 1818).

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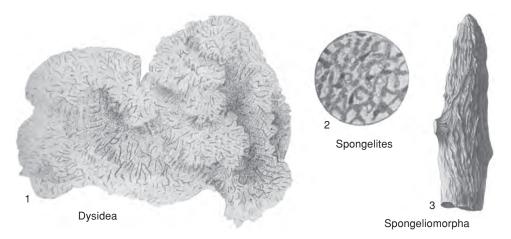


FIG. 31. Dysideidae (p. 44-45).

- Spongelites ROTHPLETZ, 1900, p. 154 [\*S. fellenbergi; OD]. Bladelike sponges with anastomosing, not sharply defined, brown strings that are reticulate to anastomosing, sand-filled fibers that form dark network with light, mesh spaces. Lower Jurassic: Switzerland.——FIG. 31,2. \*S. fellenbergi, upper Lias, Bern; photomicrograph of thin section with dark fibers and light, matrix-filled meshes, ×40 (Rothpletz, 1900).
- Spongeliomorpha DE SAPORTA, 1887, p. 298 [\*S. iberica DE SAPORTA, 1887, p. 299; OD]. Resembles Spongelites with skeleton of more or less sinuous, interconnected, anastomosing, longitudinal tracts with long, ridgelike impressions of spicules; lateral oscules occurring on low nodes that may have been small branches on side of generally cylindrical-appearing sponge. Neogene (Miocene): Spain.——FIG. 31,3. \*S. iberica, Alocoy; broken, cylindrical fragment showing skeletal structure and lateral nodes in natural mold, ×0.5 (De Saporta, 1887).

#### Family UNCERTAIN

Felixium DE LAUBENFELS, 1955, p. 36 [\**Rhizo-corallium glaseli* FELIX, 1913, p. 19; OD]. Elaborately sculptured cylinder 5 cm in diameter and 29 cm high. [No suitable figures available for illustration.] *Cretaceous:* Germany.

# Order VERONGIDA Bergquist, 1978

[Verongida BERGQUIST, 1978, p. 178]

Ceractinomorpha without mineralized skeleton and with reduced, spongin, fibrous skeleton; fibers with pith, and in some forms pith alone where outer bark lost. *Middle Cambrian–Holocene*.

## Family VERONGIIDAE de Laubenfels, 1936

[nom. transl. FINKS & RIGBY, herein, ex Verongiinae DE LAUBENFELS, 1936, p. 21]

Fibers not homogenous throughout, but with laminated, concentric, cylindrical layers, and divided into a peripheral, semitransparent region and a more or less opaque pith within. *Middle Carboniferous–Holocene*.

- Verongia BOWERBANK, 1845, p. 403 [\*Spongia fistularis PALLAS, 1766, p. 385; OD]. Fibers peculiarly pithed. *Holocene:* cosmopolitan.——FIG. 32, *1.* \*V. fistularis (PALLAS), Hamilton Harbor, Bermuda Islands; skeletal fiber cored with pith, ×100 (de Laubenfels, 1955).
- Aplysinofibria BOLKHOVITINOVA, 1923, p. 69 [\*A. carbonicola; OD]. Looped, interlaced, slender, secondary calcareous fibers that sometimes spread out fanwise; fibroid structures similar to those of Verongia, for such have often been called aplysinoid fibers where several species of Verongia have been incorrectly identified as Aplysina. Middle Carboniferous: Russia.——FIG. 32,2. \*A. carbonicola, Moscow region; fibrous skeletal structure of holotype, ×1 (Rezvoi, Zhuravleva, & Koltun, 1962).

### Family VAUXIIDAE Walcott, 1920

[nom. transl. DE LAUBENFELS, 1955, p. 77, ex Vauxininae WALCOTT, 1920, p. 316]

Thin-walled, tubular, keratose sponges, branched or unbranched, with doublelayered skeleton; inner layer of fused, cored fibers united in single-layered, open net with cellular, hexagonal or polygonal openings;

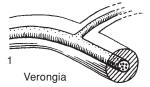




FIG. 32. Verongiidae (p. 45).

## outer or dermal layer thin and generally irregular, supported by radial fibers. *Middle Cambrian*.

Vauxia WALCOTT, 1920, p. 317 [\*V. gracilenta; OD]. Low, obconical, conicocylindrical to branched, keratose sponges with entire double-layered skeleton a continuously fused framework without spicules; outer layer ranging from irregularly anastomosing or arborescent to moderately regular and delicate (see Fig. 33). Middle Cambrian: Canada (British Columbia), USA (Utah).-FIG. 34a-f. \* V. gracilenta, Stephen Formation, Burgess Shale, Mount Field, British Columbia; a, small, branching form with secondary branches, USNM 66511, ×1; b, small form with long branches, USNM 66510, ×1 (Walcott, 1920); c, photomicrograph of upper end of branch on holotype showing regular, fused, endosomal layer of skeleton below, flattened, irregular, dermal layer in upper part of impression, and laterally flattened, outer layer along complete edges of stem, USNM 66515, ×10; d, camera lucida drawing of part of endosomal layer of holotype showing rectangular net of fibers with irregularly flattened, radial rays extending into cells, ×25; e, camera lucida drawing of laterally flattened margin of holotype showing arborescent, radial fibers extending out from endosomal layer and supporting fine-textured, irregular, outer layer, above, ×25; f, camera lucida drawing of inner part of dermal layer of holotype where primary and secondary fibers form moderately uniform ostia, ×25 (Rigby, 1986a).—FIG. 34g. V. bellula WALCOTT, Stephen Formation, Burgess Shale, Albertan, Mount Field, British Columbia; camera lucida drawing of part of endosomal net of lectotype showing nonspiculate fibers of skeleton cored by what is interpreted to be pithy elements inside a cortex, somewhat similar to living Verongia, USNM 66508, ×25 (Rigby, 1986a).

# Order HALICHONDRIDA Topsent, 1898

#### [Halichondrida TOPSENT, 1898, p. 93]

Ceractinomorph sponges in which megascleres are oxeas, styles, or strongyles in many combinations, and microscleres absent; skeleton lacking organization except for dermal layer of tangential spicules; sometimes supported by brushes of endosomal spicules; endosomal spicules commonly in confused arrangement. *Paleogene* (Oligocene)–Holocene.

## Family HALICHONDRIIDAE Gray, 1867

 [nom. transl. DE LAUBENFELS, 1936, p. 133, ex Halichondriadae GRAY, 1867, p. 518] [=Halichondridae VOSMAER, 1887, p. 335; Stylotellinae LENDENFELD, 1888, p. 185; Ciocalyptidae HENTSCHEL, 1923 in 1923– 1924, p. 408; Spongosoritidae TOPSENT, 1928b, p. 35; ?Hymeniacidonidae DE LAUBENFELS, 1936, p. 136]

Principal megascleres diactines, principally oxeas, although minor styles may be present; marked system of subdermal spaces developed and separating dermal layer from endosomal part of sponge. *Holocene*.

Halichondria FLEMING, 1828, p. 520 [\*Spongia panicea PALLAS, 1766, p. 388; OD]. Sponges of great variety of forms from tubular to irregular nodular with numerous oscular tubes; spicules only oxeas with great range in size and scattered throughout sponge; definite dermal layer of tangential spicules over large, subdermal spaces, without microscleres. Holocene: cosmopolitan.—FIG. 35,2a-b. \*H. panicea (PALLAS), Atlantic Ocean around British Isles; a,

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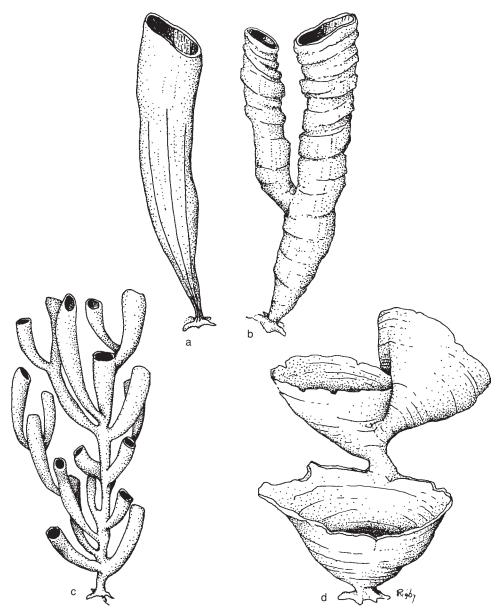


FIG. 33a-d. Growth forms of species of Vauxia; a, V. bellula WALCOTT, 1920; b, V. densa WALCOTT, 1920; c, V. gracilenta WALCOTT, 1920; d, V. venata WALCOTT, 1920 (Rigby, 1986b).

tubular form of species,  $\times 0.25$ ; *b*, fistulose form with numerous oscular tubes,  $\times 1$  (Bowerbank, 1874a).

### Family ?HYMENIACIDONIDAE de Laubenfels, 1936

[?Hymeniacidonidae DE LAUBENFELS, 1936, p. 136]

Fleshy ectosome not profusely echinated with erect spicules; endosomal structure

varying from plumose to confused, and often more or less gelatinous; dermalia skinlike, often with few, if any, spicules and those present, commonly styles, are tangential; microscleres largely absent. *Paleogene* (*Oligocene*)–*Holocene*.

Roepella VAN KEMPEN, 1977, p. 114 [\*R. solanensis; OD]. Cylindrical, unbranched sponge with deep

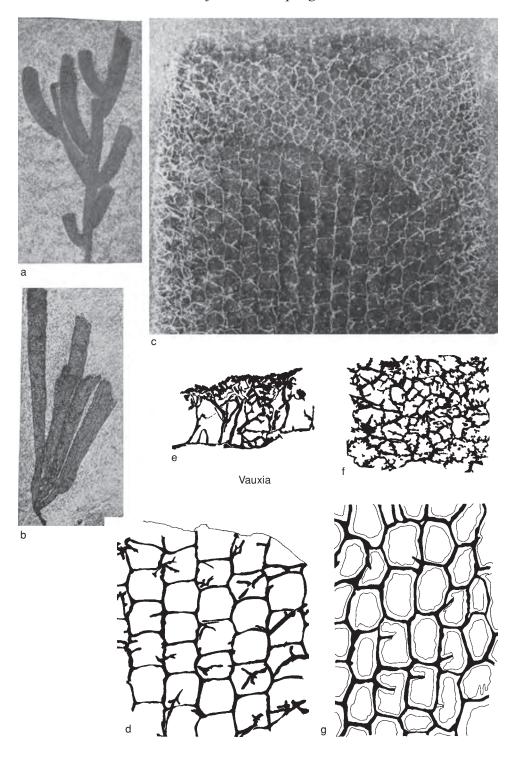


FIG. 34. Vauxiidae (p. 46).

spongocoel with walls of varying thickness and more or less horizontally folded to form irregular, horizontal, annular swellings and constrictions; walls without parietal openings; canal system obscure, apparently fine textured with oscules at summit of tubules; skeleton nonreticulate, confused feltwork of irregularly strewn but loosely vertical, monaxial spicules in vaguely defined tracts with overall tendency to diverge upwardly; skeleton without defined ectosomal or endosomal specialization; megascleres smooth, monactinal and diactinal monaxons including styles, oxeas, subtylostyles, and strongyles; microscleres unknown. Paleogene (Oligocene)-Neogene (Miocene): Spain.-FIG. 35, 1a-e. \*R. solanensis, Solana Formation, Velez Rubio area, southeastern Spain; a, side view of small, tubular sponge with irregular annulations, PA 8677,  $\times 2$ ; *b*, transverse section showing irregular spicule orientation, PA 8684, ×30; c, part of transverse section showing irregular, loose bundles of monaxial spicules, PA 8684 (II), ×100; d, cluster of tylostyles, PA 8684, approximately ×100; e, style, PA 8684, approximately ×100 (van Kempen, 1977).

# Order POECILOSCLERIDA Topsent, 1928

[nom. correct. DE LAUBENFELS, 1955, p. 38, pro Poecilosclerina TOPSENT, 1928b, p. 41] [=Poeciloscleridae TOPSENT, 1894, p. 5]

Demosponges with dermal specialization or other complexities of spicules but no radiate structure or astrose microscleres; spiny spicules, spongin, or both commonly present. *Cretaceous–Holocene*.

#### Family MYXILLIDAE Hentschel, 1923

[Myxillidae HENTSCHEL, 1923 in 1923–1924, p. 406]

Megascleres diactinal, smooth in ectosome, and monactinal, chiefly spined, in endosome. *Paleogene–Holocene*.

- Myxilla SCHMIDT, 1862, p. 71 [\*Halichondria rosacea LIEBERKÜHN, 1859, p. 520; SD DE LAUBENFELS, 1936, p. 85]. Sponges fragile with nodes or spinose projections; megascleres including tylotes and acanthostyles; microscleres consisting of sigmas and anchorate isochelas. *Paleogene–?Neogene, Holocene:* New Zealand; *Holocene:* Adriatic Sea.——FIG. 36,2*a–f.* \**M. rosacea* (LIEBERKÜHN), ?Paleogene– ?Neogene, New Zealand; *a–b*, monaxon megascleres including tylote and acanthostyle, ×100; *c–f*, microscleres including sigmas and anchorate isochela in two views, ×500 (de Laubenfels, 1955).
- Iophon GRAY, 1867, p. 534 [\*Halichondria scandens BOWERBANK, 1866, p. 259; SD DENDY, 1924a, p. 347]. Sponges soft and crumbling, with main skeleton a reticulation of loose, spicule fibers or single spicules, usually acanthostyles but sometimes

smooth. Microscleres usually palmate anisochelae and bipocilla, including deformed isochelas. *Paleogene–Holocene:* New Zealand, *Paleogene–Neogene;* cosmopolitan, *Holocene.*—FIG. 36,3*a-c.* \**I. scandens* (BOWERBANK), Paleogene–Neogene, New Zealand; deformed isochelas, ×500 (de Laubenfels, 1955).

Iophonopsis DENDY, 1924a, p. 348 [\*Halichondria nigricans BOWERBANK, 1866, p. 266; SD DENDY, 1924a, p. 348]. Soft sponge, perhaps lobose, with rounded margin that has rows of oscula of cylindrical tubes; main skeleton a reticulation of loose fibers or single spicules, usually acanthostyles but sometimes smooth styles; not echinated by accessory acanthostyles; weak, dermal skeleton of secondary diacts, including tylotes; microscleres palmate isochelae in which small end is spurred, and bipocilla. Holocene: New Zealand (Spirits Bay near North Cape), British Isles. FIG. 36, 1a-c. \*I. nigricans (BOWERBANK), British Isles; a, strongyle with spinose terminations, from dermal layer; b, larger, endosomal, spinose acanthostyle, ×250; c, anisochela microsclere from dermal layer, ×500 (Bowerbank, 1874b).

## Family TEDANIIDAE Ridley & Dendy, 1886

[nom. transl. et correct. DE LAUBENFELS, 1955, p. 38, ex subfamily Tedaniina RIDLEY & DENDY, 1886, p. 335]

Megascleres chiefly smooth monaxons in endosome; without chelae or sigmas. *Paleogene–Holocene*.

- Tedania GRAY, 1867, p. 520 [\*Halichondria anhelans LIEBERKUHN, 1859, p. 521; SD DE LAUBENFELS, 1936, p. 90]. Sponge lobed, crested, with lateral tube ending in osculum, spicules needle shaped clavate or slender fusiform to cylindrical with blunt ends; microscleres solely faintly spined raphids. *Holocene:* cosmopolitan.—FIG. 37, *1.* \**T. anhelans* (LIEBERKUHN), Adriatic Sea, near Trieste; gently curved, smooth, needle-shaped style with crepidal canal, ×250 (Lieberkühn, 1859).
- Acarnus GRAY, 1867, p. 544 [\*A. innominatus; OD]. Sponge reticulate, spicules including cylindrical, fasciculated monaxons forming radiating group and peculiar anatetraenes with four short, recurved rays. [No suitable figures available for illustration.] ?Paleogene-?Neogene, Holocene: New Zealand, ?Paleogene-?Neogene; cosmopolitan, Holocene.——FIG. 37,6. \*A. innominatus; idealized reconstruction of skeleton (Hooper, 2002).
- Forcepia CARTER, 1874, p. 248 [\**F. colonensis*; OD]. Microscleres including forceps. *Paleogene–Holocene*: New Zealand, *Paleogene–Neogene*; cosmopolitan, *Holocene*.——FIG. 37,5. \**F. colonensis*, Holocene, Atlantic Ocean, off Colon, Panama; typical, spinose, forceps microsclere, with spines not shown on one side, ×100 (Carter, 1874).
- Melonanchora CARTER, 1874, p. 212 [\**M. elliptica;* OD]. General form globular to corrugated with projecting tubercules in upper two-thirds, lower

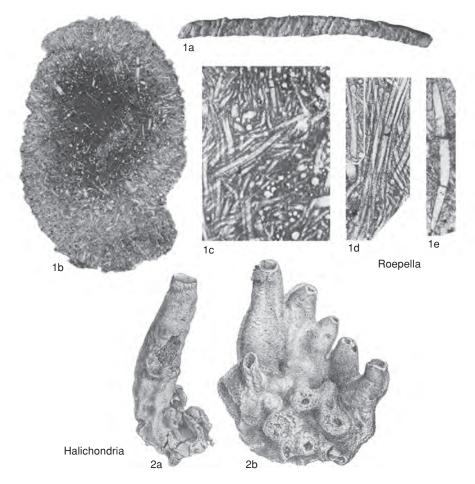


FIG. 35. Halichondriidae and Hymeniacidonidae (p. 46-49).

part smooth; megascleres styles and oxeas; microscleres including equianchorate clavidiscs. ?Paleogene-?Neogene, Holocene: New Zealand, ?Paleogene-?Neogene; cosmopolitan, Holocene. FIG. 37,11a-b. \*M. elliptica, Holocene, North Atlantic Ocean; clavidiscs, ×400 (de Laubenfels, 1955).

#### Family CLADORHIZIDAE Dendy, 1922

[nom. correct. DE LAUBENFELS, 1936, p. 122, pro Cladorhizeae DENDY, 1922, p. 58]

Bizarre-shaped, commonly small, deepsea sponges with axial skeleton of monoactinal and diactinal megascleres, from which tracts diverge to ectosome; microscleres including peculiar chelas, sigmas, forceps, and spear-shaped microstyles. *Paleogene–Holocene*.

- Cladorhiza SARS, 1872, p. 65 [\*C. abyssicola; OD]. Branched sponge with main growth form appearing like a rooted conifer branch, axes of branches formed by long oxeas and with isochelas of several types in outer, organic layer; microscleres swollen anisochelas. Paleogene–Holocene: New Zealand, Paleogene–Neogene; cosmopolitan, Holocene, — FIG. 37,2a-g. \*C. abyssicola, Holocene, Lofoten, Norway; a, branched form of genus, slightly magnified; b, isochela megasclere, ×200; c, anisochela megasclere, ×250; d-g, anisochela microscleres, ×300 (Sars, 1872).
- Chondrocladia C. W. THOMSON, 1873a, p. 188 [\*C. virgata; OD]. General form long, narrow, rarely branching stem; megascleres long styles; microscleres peculiar, anchorate isochelas. Paleogene– Holocene: New Zealand, Paleogene–Neogene; cosmopolitan, Holocene.—FIG. 37,8a-b. \*C. virgata, Holocene, Atlantic Ocean between Scotland and Faroe Islands, anchorate isochela; lateral and dorsal view, ×480 (Carter, 1874).

#### Family AMPHILECTIDAE de Laubenfels, 1936

[Amphilectidae DE LAUBENFELS, 1936, p. 123]

Monactinal spicules throughout in both ectosome and endosome, none spinose. *Paleogene–Holocene*.

- Amphilectus VOSMAER, 1880, p. 109 [\*Isodictya gracilis BOWERBANK, 1866, p. 331; SD DENDY, 1922, p. 58]. Ramose with slender branches dichotomous or trichotomous, terminations attenuated; oscula inconspicuous; microscleres all palmate isochelas.
  ?Paleogene-?Neogene, Holocene: New Zealand, ?Paleogene-?Neogene; cosmopolitan, Holocene.
  FIG. 37,10a-b. \*A. gracilis (BOWERBANK), Holocene, North Atlantic Ocean; a, front side of palmate isochela; b, reverse side of same, ×500 (de Laubenfels, 1955).
- Hamacantha GRAY, 1867, p. 538 [\*Hymedesmia johnsoni BOWERBANK, 1864, p. 35; M]. Microscleres include diancistras. Paleogene-Holocene: New Zealand, Paleogene-Neogene; cosmopolitan, Holocene.—FIG. 37,4. \*H. johnsoni (BOWER-BANK), Holocene; diancistra, ×500 (de Laubenfels, 1955).

## Family LATRUNCULIIDAE Topsent, 1922

[Latrunculiidae TOPSENT, 1922, p. 1]

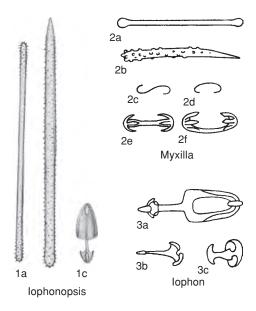
Sponges with wide-meshed, reticulate, choanosomal skeletons of anisostyles or strongyles that are closely spaced in ectosomal skeleton; microscleres acanthodiscorhabds or chessman spicules forming outer layer on ectosome. *Paleogene– Holocene.* 

Latrunculia BARBOZA DU BOCAGE, 1869, p. 161 [\*L. cratera; OD]. Form of sponge is irregular, attached, with low mounds, most of which have distinct oscules; megascleres smooth, greatly curved oxeas, microscleres peculiar, spinose, chessman elements. Paleogene–Holocene: New Zealand, Paleogene– Neogene; Atlantic Ocean, Holocene.—Fig. 37,3a– c. \*L. cratera, Holocene, North Atlantic Ocean; a, side view of attached sponge with low mounds and oscules, ×1; b, tissue of interior with coarse oxeas and associated, small, chessman microscleres, ×200; c, chessman microsclere, ×400 (Barboza du Bocage, 1869).

# Family ACARNIIDAE de Laubenfels, 1936

[Acarniidae DE LAUBENFELS, 1936, p. 79]

Spicules all spinose, mostly with confused arrangements. *Cretaceous–Holocene*.





- Acarnia GRAY, 1867, p. 515 [\*Hymeniacidon cliftoni BOWERBANK, 1864, p. 276; OD]. Sponges epizoic, membranous, with clavate, spinose spicules, ends blunt, covered with spines; acanthostrongyles and acanthotylotes present. *Holocene:* southwestern Pacific Ocean.——FIG. 37,7a-b. \*A. cliftoni (BOWERBANK), Freemantle, Australia; a, fragment of epizoic sponge overgrowing branches of a *Fucus* and having numerous irregularly oriented and spaced acanthostrongyles, ×108; b, isolated, spinose acanthostrongyle from interior part of sponge, ×260 (Bowerbank, 1864).
- Acanthoraphis HINDE, 1884a, p. 20 [\**A. intertextus;* OD]. All spicules are similar spinose oxeas. *Cretaceous:* England.——FIG. 37,9. \**A. intertextus,* Upper Chalk, Upper Cretaceous, Kent; spinose oxeas and their distribution in fragment of dermal layer of sponge, ×10 (Hinde, 1884a).

#### Family UNCERTAIN

- Makiyama DE LAUBENFELS, 1955, p. 39, nom. nov. pro Sagarites MAKIYAMA, 1931, p. 5, non ASHMEAD, 1900 [\*Sagarites chitanii MAKIYAMA, 1931, p. 5; OD]. Tubular, rarely branching with echinated spicules that may have been reticulated on exterior; spicules mainly bent oxeas and strongyles. Paleogene-Neogene: Japan.—FIG. 37,12a-b. \*M. chitanii (MAKIYAMA), Sagara Mudstone, Pliocene, Tôtômi Province; a, restoration of several sponges, each with small osculum at summit and spiculated, dermal surface, attached to plant fragment, ×1; b, oxeas from skeleton, ×200 (Makiyama, 1931).
- Oppligera DE LAUBENFELS, 1955, p. 39, nom. nov. pro Subularia Oppliger, 1921a, p. 205, non

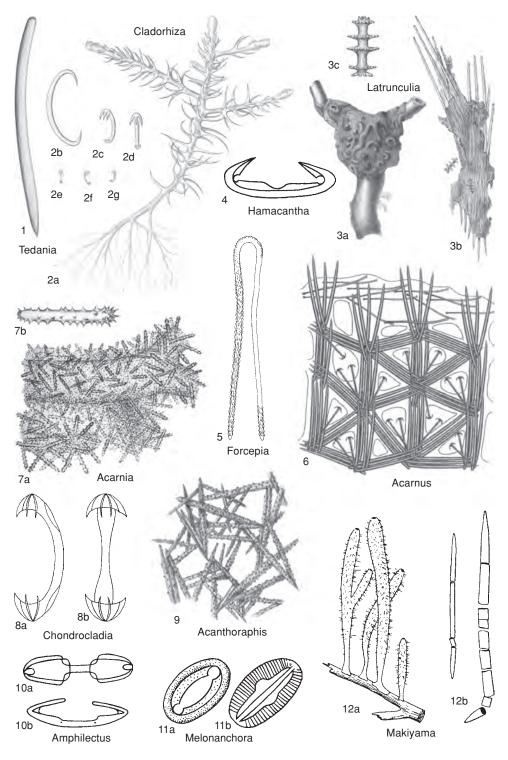


FIG. 37. Tedaniidae, Cladorhizidae, Amphilectidae, Latrunculiidae, Acarniidae, and Uncertain (p. 49–51).

MONTEROSATO, 1884 [\**Subularia clavaeformis* OPPLIGER, 1921a, p. 205; OD]. Small, club-shaped sponge with spongocoel; spicules are styles to 2 mm long. [No known suitable figures.] *Jurassic:* Europe.

# Order HAPLOSCLERIDA Topsent, 1898

[nom. correct. DE LAUBENFELS, 1955, p. 37, pro Haplosclerina TOPSENT, 1898, p. 93]

Sponges with almost no dermal specialization and megascleres generally of one simple type, normally oxeas or strongyles of uniform length within species; skeleton generally reticulate with much spongin and isodictyal with rectangular or triangular meshes; microscleres sigmas and toxas, when present. Jurassic-Holocene.

## Family SPONGILLIDAE Gray, 1867

#### [Spongillidae GRAY, 1867, p. 550]

Freshwater sponges (a few ranging into brackish water) with gemmules; some genera with microscleres as in many hyalosponges. *Jurassic–Holocene*.

- Spongilla LAMARCK, 1816b, p. 98 [\*Spongia lacustris LINNE, 1759, p. 1348; SD POTTS, 1881, p. 388]. Megascleres simple, invariably slender to stout amphioxea; microscleres present in dermal membrane, usually slender amphioxea and generally spined throughout; gemmules also contain spiny oxeas (acanthoxeas). Jurassic-Holocene: cosmopolitan.—FIG. 38,5a-b. \*S. lacustris (LINNE), Holocene; a, spinose microsclere, ×100; b, gemmosclere, ×125 (Penny & Racek, 1968).—FIG. 38,5c. S. alba CARTER, Holocene, Australia or South America; smooth megasclere, ×125 (Penny & Racek, 1968).
- Eospongilla DUNAGAN, 1999, p. 390 [\**E. morrison*ensis; OD]. Small, low, domical to cylindrical sponges; megascleres diactinal, monaxon strongyles and oxeas, spicules straight or slightly curved, without ornamentation; microscleres unknown or absent. [Fossil sponges occur in freshwater lacustrine carbonates.] Upper Jurassic: USA (Colorado).—FIG. 39,1*a-b.* \**E. morrisonensis,* Morrison Formation, possibly uppermost Oxfordian to Kimmeridgian, Fort Collins, USNM 496326; *a*, circular mass of megascleres outlined by small, black arrows, ×20; *b*, cluster of straight oxeas and slightly curved strongyles, ×50 (Dunagan, 1999).
- Ephydatia LAMOUROUX, 1816, p. 2 [\*Spongia fluviatilis LINNÉ, 1759, p. 1348, SD PENNY & RACEK, 1968, p. 82] [=Ephidatia LAMOUROUX, 1816, p. 6, obj.]. Gemmoscleres amphidiscs, smooth to spinose; cylindrical shaft with serrated

discs at both ends; megascleres fusiform, amphioxea, smooth or spinose but all smooth at tips; microscleres absent. *Neogene (Miocene)– Holocene:* cosmopolitan.——FIG. 38,3*a–b. E. mülleri* (LIEBERKÜHN), Katata Formation, Pleistocene, Otsu City, Japan; isolated, smooth and spinose, amphioxea megascleres, ×1,000 (Matsuoka, 1983).

- Eunapius GRAY, 1867, p. 552 [\*A. carteri BOWERBANK, 1858, p. 315; SD ANNANDALE, 1911, p. 97]. Gemmoscleres amphistrongyles or amphioxea, stout and nearly straight to curved, spines sparse but usually more common at spicule tips; megascleres slender, fusiform, smooth amphioxea straight to gently curved; microscleres absent. Neogene (Miocene)-Holocene: cosmopolitan.——FIG. 38,2a-d. E. fragilis (LEIDY), Katata Formation, Pleistocene, Otsu City, Japan; a-b, megascleres including thick and thin types; c-d, gemmoscleres including turved and straight forms, ×1,000 (Matsuoka, 1983).
- Heteromeyenia POTTS, 1881, p. 150 [\*A. baileyi BOWERBANK, 1863, p. 451; SD DE LAUBENFELS, 1936, p. 36; =S. repens POTTS, 1880, p. 357].
  Similar to Myenia, with megascleres usually slender and fusiform amphioxea covered with minute, irregular spines; microscleres long, thin, sharply pointed, fusiform amphioxea, with amphidiscs of two distinct types. Neogene (Pleistocene)–Holocene: cosmopolitan.——FIG. 38,4a-b. \*H. baileyi (BOWERBANK), Holocene, USA; a, characteristic, irregularly spined megasclere, ×150; b, spined, amphioxea microsclere, ×250 (Penny & Racek, 1968).——FIG. 38,4c-d. H. repens POTTS, Holocene, USA; two amphidisc gemmoscleres, ×250 (Penny & Racek, 1968).
- Lutetia RICHTER & WUTTKE, 1999, p. 184 [\*L. heili; OD]. Sponges possibly relatively thin with megascleres as thin, straight to weakly curved, smooth amphioxeas, or with fine spines evenly developed over entire surface of spicules; microscleres unknown; gemmoscleres of two types: larger ones amphistrongyles of unusually variable size and shape and may be straight or slightly bent, their outer surfaces strongly spinose and most spinose on swollen, club-shaped ends; smaller ones short, thin to stocky amphistrongyles or pseudoamphioxeas of very irregular appearance with club-shaped to discoidal ends. Paleogene (Eocene): Germany.-FIG. 38,1a-c. \*L. heili, Lutetian, Messel; a, holotype fragment with cluster of gemmules, SMF ME 1 5143a, ×10; b, wall of gemmule from holotype with irregularly arranged, tangential megascleres, ×100; c, wall of gemmule with large and fine gemmoscleres, ×200 (Richter & Wuttke, 1999).
- Meyenia CARTER, 1881a, p. 90 [\**M. fluviatilis*; SD DE LAUBENFELS, 1936, p. 36]. Gemmules containing amphidisc microscleres; commonly reported erroneously as *Ephidatia* (=*Tupha*). Neogene (Pleistocene)-Holocene: cosmopolitan.——FIG. 38,7*a*-*b*. \**M. fluviatilis*, Holocene; birotulate spicule seen from side and end, ×500 (Cartet, 1881a).

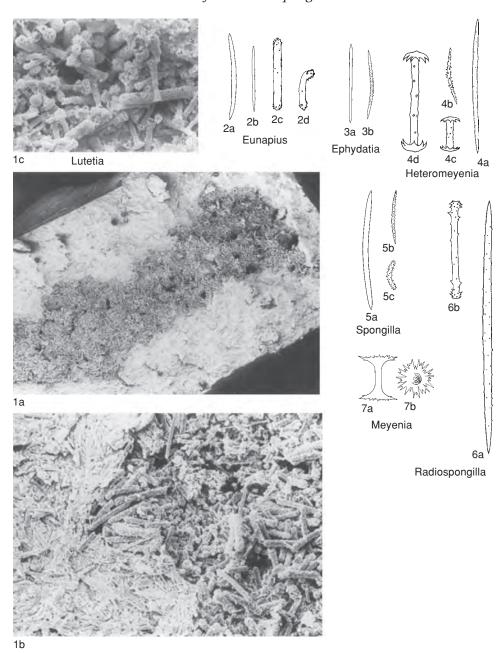


FIG. 38. Spongillidae (p. 53-56).

Oncosclera VOLKMER-RIBEIRO, 1970, p. 435 [\*Spongilla jewelli VOLKMER, 1963, p. 271; OD]. Megascleres amphioxeas to amphistrongyles that are slightly curved, robust, and may have small spines; microscleres not present; gemnoscleres variable amphistrongyles and amphioxeas that are short, robust, commonly curved, and expanded at midlength, usually with spines, which are more common on swollen spicule tips. [Taxonomic position of the genus is in question. It was originally included in the family Spongillidae by VOLKMER-RIBEIRO (1970) but has been included later by others in the family Potamolepidae of BRIEN (1967).] *Neogene (Miocene)–Holocene:* Japan, South

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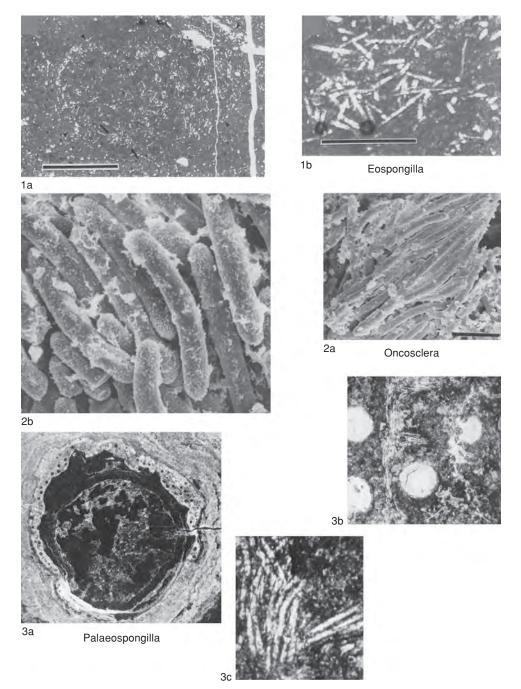


FIG. 39. Spongillidae (p. 53-56).

America, Africa, Asia.——FIG. 39,2a-b. *O. kaniensis* MATSUOKA & MASUDA, Miocene, Nakamura Formation, central Japan; *a*, amphioxea megascleres with minutely spinose, rounded or sharp, ray tips, ×250; *b*, curved gemnoscleres with

spinose, rounded tips, ×100 (Matsuoka & Masuda, 2000).

Palaeospongilla OTT & VOLKHEIMER, 1972, p. 53 [\*P. chubutensis; OD]. Skeleton composed of bundles of smooth, monaxial megascleres that descend steeply at various angles; cavities within framework containing spherical gemmules with small, spinose, needlelike microscleres. [This is one of only a few known gemmule-bearing, fossil, freshwater sponges. J Cretaceous (Coniacian-Maastrichtian): Argentina. FIG. 39, 3a-c. \*P. chubutensis, Chabut Group, lacustrine, freshwater, tuffaceous sandstone and marl, Rio Chabut, Patagonia; a, transverse section of gemmule-bearing, encrusting sponge as thin, basal layer on plant stem, which is in turn overgrown by algal crusts, ×2; b, photomicrograph of spicule bundles around spherical gemmules, ×25; c, photomicrograph of tangential section with bundles of megascleres, ×100 (Ott & Volkheimer, 1972; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen).

Radiospongilla PENNY & RACEK, 1968, p. 61 [\*Spongilla sceptroides HASWELL, 1882, p. 209; OD]. Flat crusts or cushion-shaped sponges that may have rare, small branches; megascleres moderately stout to slender amphioxeas and, rarely, amphistrongyles commonly covered with variable, minute to conspicuous spines, but rarely may be smooth; microscleres absent; gemmules with gemnoscleres slender amphioxeas or amphistrongyles invariable, strongly spinose and may be curved to straight and range to very long elements; spines often aggregated and larger on tips of spicules, forming clublike terminations. Neogene (?Pleistocene), Holocene: widespread in tropical to subtropical, freshwater environments.----FIG. 38,6a-b. \*R. sceptroides (HASWELL), Holocene; a, amphioxea megasclere with widespread, small spines; b, amphistrongyle gemnoscleres with small spines, most concentrated on rounded, clublike tips, ×280 (Penny & Racek, 1968).

## Family HALICLONIDAE de Laubenfels, 1932

[Haliclonidae DE LAUBENFELS, 1932a, p. 111]

Extremely simple skeletons without dermal or ectosomal specialization; spicules almost exclusively simple diactines; microscleres absent; most typical family of order. *Paleogene (?Eocene), Holocene.* 

- Haliclona GRANT, 1841 in 1835–1841, p. 6 [\*Spongia oculata LINNÉ, 1759, p. 1348; OD] [=Chalina BOWERBANK, 1864, p. 209, nom. nud. (type, C. occulata, OD), non GRANT, 1861, p. 76]. Incrusting to ramose sponges. Paleogene (?Eocene), Holocene: cosmopolitan.——FIG. 40,3a-b. \*H. oculata (LINNÉ), Holocene; branched sponge, suspended from digitate base, with lines at pores showing inhalant flow at a, and exhalant flow at b, at pores within fibrous skeleton, scale unknown (Grant, 1835–1841).
- Reniera Nardo, 1847b, p. 3, nom. nov. pro Rayneria Nardo, 1833, p. 519, non Girard, 1848 [\*R. aqueductus Schmidt, 1862, p. 73; SD Schmidt,

1862, p. 73]. Similar to *Haliclona* but a hollow cylinder to weakly branched sponge with small, inhalant ostia and terminal osculum; spicules simple oxeas. [Many Ordovician to Eocene fossils erroneously assigned to this genus based on presence of oxeas.] *Holocene.*—FIG. 40, Ia-c. \*R. aqueductus (SCHMIDT), Sebenico, Adriatic Sea; a, side view of small sponge showing general growth form,  $\times 1$ ; b-c, oxeas of skeleton,  $\times 100$  (Schmidt, 1862).

#### Family PETROSIIDAE van Soest, 1980

#### [Petrosiidae VAN SOEST, 1980, p. 66]

Sponges with multispicular tracts in reticulate pattern with rounded mesh spaces in choanosomal skeleton and mostly tangential, multilayered crust of spicules in irregular to circular patterns in ectosomal skeleton; several kinds of monaxial spicules. *Paleogene–Holocene*.

- Petrosia VOSMAER, 1887, p. 338 [\*Reniera dura SCHMIDT, 1862, p. 76; SD DE LAUBENFELS, 1932a, p. 116]. Sponges hard and stony with numerous well-defined, large ostia; skeleton more or less confused mass of oxeas and strongyles that are usually short and closely packed in tracts. Differs from *Haliclona* in having four kinds of monaxons. ?Paleogene-?Neogene, Holocene: cosmopolitan. FIG. 40,7a-f. \*P. dura (SCHMIDT), Holocene, Zara and Quarnero, Adriatic Sea; a, side view of sponge with ostia on several node summits, ×0.5; b-f, oxeas of various sizes and large strongyle from type specimen, ×125 (Schmidt, 1862).
- Propetrosia PISERA & BUSQUETS, 2002, p. 343 [\*P. pristina; OD]. Petrosiid sponge with only one size of oxea in thick, tangential, multispicular ectosome, and in choanosomal skeleton that is a more or less regular reticulation of multispicular fibers of oxeas of one general size. [This is the first reported, undoubted body fossil of a petrosiid sponge in the geologic record. Other problematic references are to isolated spicules.] Paleogene-Neogene: Spain.—FIG. 40,2a-b. \*P. pristina, Eocene, Bartonia, Catalonia; a, etched holotype fragment showing spicule fibers of ectosome, ×1; b, photomicrograph of skeletal fiber in holotype composed largely of subparallel oxeas, ZPAL Pf.X/ 52, ×50 (Pisera & Busquets, 2002).

## Family DESMACIDONIDAE Gray, 1867

[Desmacidonidae GRAY, 1867, p. 536; non Desmacidonidae DENDY, 1924a, p. 334] [=Desmacidontidae GRAY, 1967, p. 536, non. correct. DE LAUBENFELS, 1955, p. 37 pro Desmacidonidae GRAY, 1867, p. 536; Desmacididae SCHMIDT, 1870, p. 52, partim, non. correct. WIEDENMEYER, 1977a, p. 79, pro Desmacidinae SCHMIDT, 1870, p. 52]

Similar to Haliclonidae but having microscleres; flesh commonly slimy. *Paleogene-Holocene*.

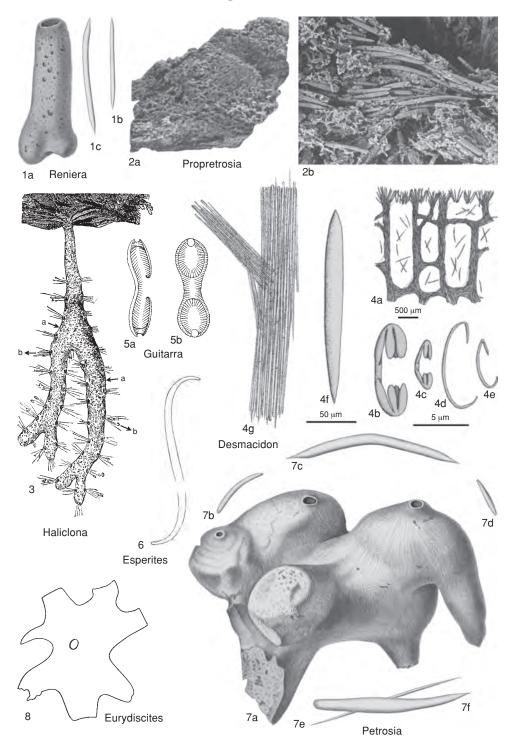


FIG. 40. Haliclonidae, Petrosiidae, Desmacidonidae, and Uncertain (p. 56-58).

- Desmacidon BOWERBANK, 1861, p. 372 [\*Spongia fruticosa MONTAGU, 1818, p. 112; SD DE LAUBEN-FELS, 1936, p. 53]. Skeleton fibrous and irregularly reticulated, with fibers composed entirely of parallel spicules that are cemented together and coated with spongin; megascleres all oxeas; microscleres sigmas and arcuate isochelas; flesh very slimy. ?Paleogene-?Neogene, Holocene: Europe.—FIG. 40,4a-f. \*D. fruticosa (MONTAGU), HOLOCENE, ROSCOFF, FRANCE; drawing of skeleton and spicules made from a slide of specimen (Van Soest, 2002).—FIG. 40,4g. D. aegagropila (JOHNSTON), Holocene, United Kingdom; keratose fiber fragment showing its spiculate nature, ×100 (Bowerbank, 1862).
- Guitarra CARTER, 1874, p. 210 [\*G. fimbriata; SD DE LAUBENFELS, 1932a, p. 63]. Sponge form generally conical, surface with fingerlike to hairlike villi; megascleres oxeas; microscleres include placochelas. Paleogene-Holocene: New Zealand, Paleogene-Neogene; cosmopolitan, Holocene.——FIG. 40,5a-b. \*G. fimbriata, Atlantic Ocean, off northwestern coast of British Isles; characteristic placochela microscleres, lateral and anterior view, ×500 (Carter, 1874).

#### Family UNCERTAIN

- Eurydiscites SOLLAS, 1880d, p. 387 [\*E. irregularis; OD]. Only a few loose spicules distinguished by their large size and coalescence of arms to produce an irregular, lobate disc. Cretaceous: England.— FIG. 40,8. \*E. irregularis, Trimmingham Chalk, Maastrichtian, Norfolk; isolated, large, lobate, irregular, discoidal spicule, scale uncertain (Sollas, 1880d).
- Esperites CARTER, 1871, p. 131 [\**E. giganteus;* OD]. Isolated sigma. *Lower Cretaceous:* Europe.——FIG. 40,6. \**E. giganteus,* Upper Greensand, Haldon Hill, Exeter, England; large, isolated, sigmoidal spicule, ×30 (Carter, 1871).

# Order SIGMATOSCLEROPHORIDA Burton, 1956

[nom. correct. FINKS & RIGBY, herein, pro Sigmatosclerophora Burton, 1956, p. 114]

Microscleres, when present, include sigmas, chelae, or their derivatives; asters absent, but microrhabds may be present; megascleres are styles, strongyles, oxeas, or any combination of these; tylostyles, if present, accompanied by styles; tetraxons absent; skeleton often composed of spiculofibers; different types of megascleres often localized in different parts of skeleton; sublithistid forms occur, but not lithistids. *Lower Ordovician–Holocene.* 

### Family DYSTACTOSPONGIIDAE Miller, 1889

#### [Dystactospongiidae MILLER, 1889, p. 153]

Sublithistid; fibrous skeleton; principal fibers subparallel, connected by smaller fibers and by anastomosis; spicules styles, possible oxeas, and heloclonid desmoids that form spiculofibers either together or separately; when together desmoids forming coating on surface of spiculofiber; styles arranged in fibers either plumosely (axinellid structure) or as coring and echinating elements (ectyonine structure), oxeas arranged tangent to fiber surface. *Lower Ordovician– Upper Ordovician.* 

- Dystactospongia MILLER, 1882, p. 42 [\*D. insolens MILLER, 1882, p. 43; OD]. Massive, tuberose or subdigitate; no cloaca; sponge surface variably hispid and covered with circular, polygonal, or submeandriform pores of varying size; larger, osculelike pores with tributary canals may be present; spiculofibers porous; principal spiculofibers subparallel, radiating from base and perpendicular to outer surface; connected by thin, tangential spicule; spiculofibers seemingly composed solely of subparallel, heloclonid desmoids. [Heterospongia ULRICH, 1889, is very similar, if not identical to this genus. Dystactospongia radicosa RUEDEMANN appears to be the burrow Rauffella ULRICH, 1889.] Upper Ordovician: USA (Illinois, Ohio, Indiana).---FIG. 41a. \*D. insolens, Fairview Formation, Maysvillian, Cincinnati, Ohio; holotype fragment with radial canals around several oscula on gastral surface, ×1 (Miller, 1882).—FIG. 41b-d. D. madisonense FOERSTE, Saluda Formation, Upper Ordovician, Versailles, Indiana; b, side view of reference specimen with two sizes of canal openings, ×1; c, transverse section of fragment base with dark matrix in canals and beaded-appearing, skeletal tracts, ×5; d, photomicrograph of spicules, mainly irregular heloclones in dense structure, OSU 14618, ×250 (Rigby, 1966b).
- Heterospongia ULRICH, 1889, p. 239 [\*H. subramosa ULRICH, 1889, p. 240; OD]. Ramose to lobate, without cloaca; surface smooth or hispid, covered by circular to polygonal or elongate, skeletal pores of variable size and distribution; larger, osculelike pores with tributary surface grooves present in one species (H. knotti) that is not type; spiculofibers porous; principal spiculofibers longitudinal in axial region but curving perpendicular to outer surface, connected by tangential spiculofibers; fibers seemingly coated with, and probably composed of, heloclonid desmoids and smooth monaxons, parallel to fiber surface. [It is not clear whether the monaxons are oxeas or styles. Their presence is the only significant difference between this genus and the senior Dystactospongia MILLER,

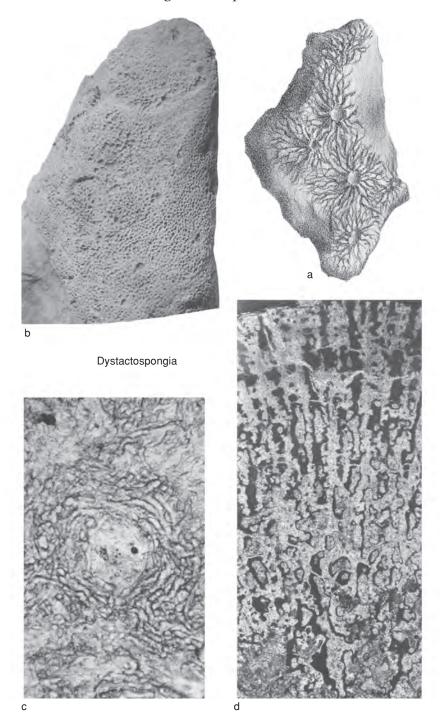


FIG. 41. Dystactospongiidae (p. 58).

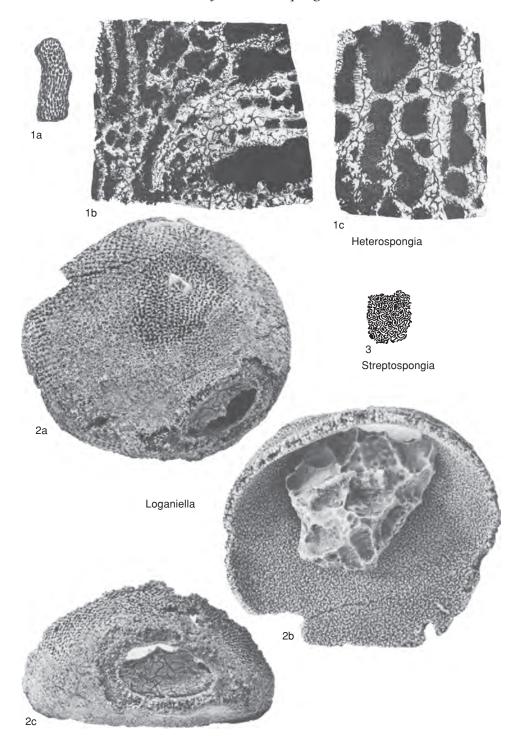


FIG. 42. Dystactospongiidae (p. 58-61).

1882.] Upper Ordovician: USA (Kentucky, Ohio, Minnesota).——FIG. 42, 1a-c. \*H. subramosa, Hudson River Group, Upper Ordovician, Spring Valley, Minnesota; a, side view of small, subcylindrical sponge with ostia of small canals, ×1; b, vertical section of recrystallized, upwardly and outwardly diverging, skeletal tracts, with dark matrix in canals, ×10; c, tangential section with vertically aligned, matrix-filled canals and light, skeletal tracts, specimens in collections of E. O. Ulrich, ×10 (Winchell & Schuchert, 1893).

- Loganiella RIGBY & GILLAND, 1977, p. 476 [\*L. johnsoni; OD]. Cylindrical to subcylindrical or bowl-shaped sponges with flat base; broad spongocoel surrounded by relatively thin walls through which four sizes of generally radial canals penetrate into spongocoel; canals may have regular, quadrangular spacing or occur in linear series; skeletal net composed of curved, possible oxeas combined into relatively thick tracts or spiculofibers in reticulate pattern on sponge surfaces, but radial orientation in wall interiors. [The sponges are associated with conodonts of trilobite zones J-L, so they may have come from upper Lower or lower Middle Ordovician beds. The spicules are known only as impressions on the silicified tract surfaces, so placement in the family is questioned, but the sponge appears similar to Dystactospongia.] Lower Ordovician: USA (Idaho).——FIG. 42,2a-c. \*L. johnsoni, Garden City Limestone, Logan River; a, flat base of holotype with rectangularly arranged, spicule tracts; b, view into spongocoel to flat bottom, partially obscured by matrix, with thin wall in section above; c, side view of preserved, partial, lower wall showing moderately regular canal spacing on upper part of wall, above flat base, BYU 1091, ×0.85 (Rigby & Gilland, 1977).
- Streptospongia ULRICH, 1889, p. 244 [\*S. laby-rinthica; OD]. Fragment with anastomosed, subparallel trabeculae that may be coated with heloclonid desmoids. [This may be a coarsely silicified fragment of Saccospongia or Dystacto-spongia.] ?Upper Ordovician: USA (Kentucky).
   —FIG. 42,3. \*S. labyrinthica, float from Arnheim Formation, Richmondian, Lebanon; drawing of small part of transverse fracture on holotype showing labyrinthic, skeletal structure, ×1 (Ulrich, 1889).

# Subclass LITHISTIDA Schmidt, 1870

[nom. transl. ZITTEL, 1878a, p. 96, ex group Lithistida SOLLAS, 1887, p. 421, nom. correct. pro group Lithistina CARTER, 1875, p. 185, nom. correct. pro group Lithistidae SCHMIDT, 1870, p. 21]

Demospongea whose principal megascleres are desmas that are normally united by articulation (zygosis) to form coherent, skeletal framework; some also with types of megascleres that may be monaxons (e.g., oxeas), triaenes, or both, or with accessory

(supplemental) desmas in addition to main ones; principal desmas tetraxial, tripodal, monaxial, or anaxial in those whose character is known; some with tetraxial desmas intergrading with triodal or monaxial forms; articulatory features (zygomes) sometimes simple facets only, but typically twig, root, or clawlike, or forming tongue, cup, or handlike expansions; few forms with zygosis only weakly developed or absent; skeletal framework uncanalized, or with ostia, postica, or both, or with additional epirhyses, aporhyses, or both, or with skeletal pores or canals of unknown character; triaenes arranged typically at surfaces when present, with shafts running inwardly into meshes of internal framework when long enough, and their cladi in ectosome in living forms; shafts of triaenes never normally incorporated into primary, skeletal meshwork, although sometimes imbedded in secondary meshwork formed by supplemental desmas; supplemental monaxons usually loose in skeletal meshes or lying tangentially at surfaces, but sometimes grasped by zygomes of desmas or incorporated into composite, skeletal fibers; supplemental desmas usually small, rhizoclone-like bodies found in internal meshes, at surface or both, and sometimes intergrading with primary desmas; examples found at surface may form a supplemental cortex that coats skeletal framework, and may then cover ostia or postica, or be pierced by intracortical pores or canals; microscleres present or absent in life in living examples, in which they may be microrhabds, streptoscleres (intergrading plesiasters, metasters, and spirasters), unidentified spirasters or amphiasters, or sigmaspires when present; soft parts as in normal Demospongea, with the ectosome usually a dermis. Cambrian-Holocene.

# Order ORCHOCLADINA Rauff, 1895

[nom. transl. REID, 1963e, p. 93, ex subtribe Orchocladinae RAUFF, 1895, p. 242]

Principal spicules are dendroclones organized parallel to one another in rows or chiastoclones with less regular arrangement; principal skeletal canals radial and paratangential. *Middle Cambrian-Permian* (Lopingian).

### Family ANTHASPIDELLIDAE Miller, 1889

[Anthaspidellidae MILLER, 1889, p. 153] [=Anthaspidellidae ULRICH, 1890a, p. 221; Archaeoscyphiidae RAUFF, 1894, p. 238; Aulocopiidae RAUFF, 1895, p. 247; Eospongiidae DE LAUBENFELS, 1955, p. 64, *partim*]

Dendroclones arranged with long axes paratangential to upper or outer growing surface of sponge, forming an isodictyal net with mainly triangular interspaces; ladderlike rows of dendroclones radiating upwardly and outwardly approximately perpendicular to growing surface; interlocking zygoses of contratangent rows of spicules often forming conspicuous, columnlike structures or trabs that may be cored by smooth monaxons; principal skeletal canals both parallel to dendroclone rows and to dendroclone layers, in latter instance they tend to persist in same place at successive levels to form vertical rows of pores, or frequently by coalescence, vertical, slitlike passages; sponges vasiform, fungiform, or massive; apparently attached to substrate basally but not by root tuft; imperforate, concentrically wrinkled, basal layer common. [MILLER (1889) had seen ULRICH's proofs (1890a) or ms and used ULRICH's new family name without giving him credit, although he did use ULRICH's name for the new type genus.] Middle Cambrian–Permian (Changhsingian).

Anthaspidella ULRICH & EVERETT in MILLER, 1889, p. 153 [\*A. mammulata; OD]. Broadly funnel or saucer shaped, attached to substrate by short, central stalk; upper surface covered by numerous oscules more or less evenly distributed; each oscule with radially arranged, exhalant canals converging upon it; dendroclone rows arranged radially with respect to center of sponge and diverging upwardly and downwardly toward upper and lower surfaces. Lower Ordovician-Devonian (Frasnian): USA (Texas, New Mexico), Argentina, China (Hubei), Ibexian; widespread Canada and USA, and northern Europe, Middle Ordovician; Western Australia, Frasnian. FIG. 43a-b. \*A. mammulata, Platteville Limestone, Chazyan, Dixon, Illinois, USA; a, vertical view of holotype with shallow, gastral depression marked by multiple, low, mounded, exhalant oscula, ×1; *b*, vertical section showing trabs and cross-connecting dendroclones, ISM, ×18 (Ulrich & Everett, 1890).——FIG. 43*c. A. amplia* RIGBY & DESROCHERS, Mingan Formation, Chazyan, Mingan Islands, Canada; view from above of paratype showing numerous moderately coarse clusters of exhalant canals in shallow depression, surrounded by convergent, essentially horizontal, exhalant canals, GSC 111098, ×1 (Rigby & Desrochers, 1995).

- Amplaspongia RIGBY & WEBBY, 1988, p. 41 [\*A. bulba; OD]. Large, hemispherical to globular sponges lacking a spongocoel; anthaspidellid skeleton of uniform, upwardly and outwardly radiating trabs; two major canal series with two different diameters are parallel trabs, canals may be crudely clustered; minor, subhorizontal canals moderately rare and discontinuous; trabs dense, coring spicules largely absent, and dendroclones simple with long shafts; dense, basal dermal layer may be present, pores absent. Upper Ordovician: Australia (New South Wales).——FIG. 44a-b. \*A. bulba, Malongulli Formation, Cliefden Caves area; a, vertical view of gastral, upper surface of holotype showing separated clusters of coarse, excurrent canals in otherwise uniform skeleton pierced by smaller, isolated canals, ×0.5; b, photomicrograph of broken surface of paratype showing ladderlike skeleton including vertical trabs produced by union of ray tips of horizontal, runglike dendroclones, small canals parallel trabs, AMu. F66820, ×8 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).-FIG. 45a-b. \*A. bulba, Malongulli Formation, Cliefden Caves area; a, enlargement of gastral surface of holotype showing a prominent cluster of excurrent canals, on left, and abundant, smaller, circular canals in surrounding uniform skeleton where tiny, rodlike, horizontal dendroclones connect between vertical, rodlike trabs, seen here in transverse sections as small dots, AMu. F66819, ×2; b, side view of paratype where upwardly expanding skeleton of vertical trabs and horizontal dendroclone spicules interrupted locally by vertical canals, ×1 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Annulospongia LIU, RIGBY, & ZHU, 2003, p. 438 [\*A. tarimensis; OD]. Ringlike or tirelike, short, large sponge with broad, deep spongocoel extending upwardly from near base; skeleton anthaspidellid with vertical trabs of dendroclones in double rows nearly parallel to each other so surface of pinnation weak or present only near base; horizontal canals radial, straight to slightly curved and vertically stacked. Ordovician (Darriwilian): China (Xinjiang).—FIG. 46, 1a-b. \*A. tarimensis, Yijianfang Formation, Bachu County; a, tirelike holotype from above with large spongocoel largely filled with matrix,  $\times 0.4$ ; b, transverse, horizontal section with radial canals between ladderlike, double rows of trabs of dendroclone, ×2 (Liu, Rigby, & Zhu, 2003).

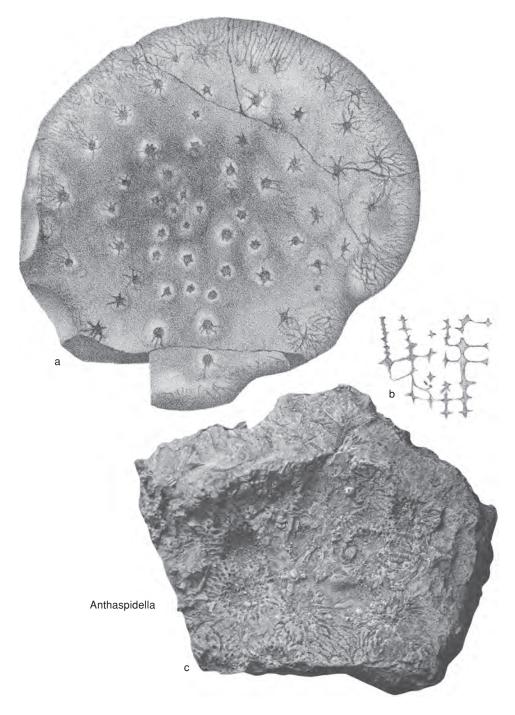


FIG. 43. Anthaspidellidae (p. 62).

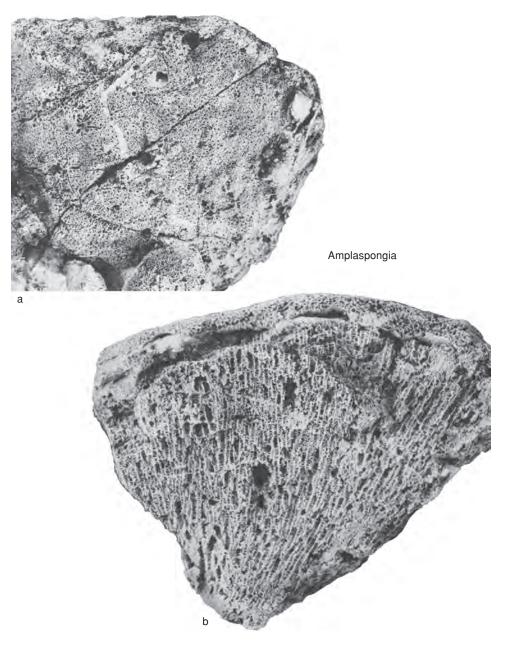


FIG. 44. Anthaspidellidae (p. 62).

Archaeoscyphia HINDE, 1889b, p. 141 [\*Petraia minganensis BILLINGS, 1859, p. 346; OD] [=Costaspongia BARTHOLOMAUS & LANGE, 1998, p. 398 (type, C. nansoedi, OD)]. Conical with flangelike, horizontal, annular outgrowths encircling exterior at regular intervals; cloaca relatively broad, smooth walled; body wall relatively thin, containing closely spaced, vertically stacked, radi-

ally arranged, upwardly arched to horizontal canals that extend from exterior to cloacal surface; spicules principally dendroclones with a minority of rhizoclones and tetraclone-like desmas; may have thin, dermal layer of flattened, dendroclone tips. [Synonym *Costaspongia* BARTHOLOMAUS & LANGE, 1998, p. 398 is differentiated because of its laterally flattened form that is probably a diage-

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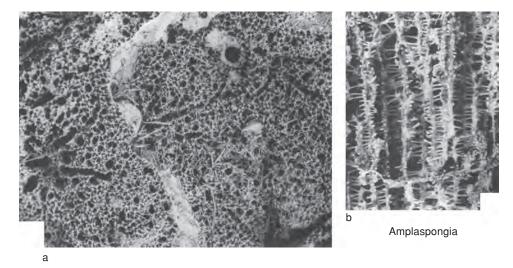


FIG. 45. Anthaspidellidae (p. 62).

netic effect.] *Lower Ordovician–Silurian:* cosmopolitan.——FIG. 47,*1.\*A. minganensis* (BILLINGS), Romaine Formation, Canadian, La Grosse Romaine Island, Mingan Islands, Quebec, Canada; side view of characteristic, steeply obconical sponge, GSC 111103, ×1 (Rigby & Desrochers, 1995).

- Aulacospongia GERTH, 1927, p. 117 [\*A. hanieli GERTH, 1927, p. 118; OD]. Ellipsoid with major axis vertical; surface grooves running vertically up sides and converging on top of sponge; interior with scattered, vertical canals corresponding to such surface grooves at earlier stages of growth; dendroclone rows perpendicular to outer surface and radiating from attachment point within base of sponge. Permian (Lopingian): Timor.-FIG. 46,2a-b. \*A. hanieli, Permian Limestone, Besleo; a, side view of type specimen showing growth form with prominent canals converging from sides to summit, ×1; b, transverse section showing radial, skeletal and canal structure in dense skeleton, ×1.5 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Aulocopina BILLINGS, 1875, p. 230 [\*A. granti BILL-INGS, 1875, p. 231; OD]. Ovoid or pyriform, with deep, central cloaca; principal canals parallel to upper and outer surface, branched to sinuous and converging on cloaca; canals forming surface grooves that cover entire, outer surface; dendroclone rows presumably perpendicular to surface. *Silurian (Wenlock-Ludlow):* Canada.——FIG. 47,3*a-b.* \*A. granti, Niagara Formation, Hamilton, Ontario; *a*, side view of lectotype, with osculum of axial spongocoel on summit and grooves of canals on osculum and exterior; *b*, summit view of larger specimen with radial canals and small spongocoel, ×1 (Billings, 1875).
- Australospongia HOWELL, 1952, p. 1 [\**A. turbinata;* OD]. Small, cylindrical to conical with deep

spongocoel and thin walls perforated by two radial, small, canal series regularly spaced although not uniform; ill-defined trabs radiating upwardly and possibly outwardly from gastral surface, skeletal details unknown but dermal layer evident. [May be a poorly preserved Playfordiella RIGBY, 1986b, and if so then *Playfordiella* is a junior synonym.] Devonian (Famennian): Western Australia.----FIG. 48,1a. \*A. turbinata, Virgin Hills Formation, Mount Pierre; side view of small, steeply obconical sponges, PU 57873, ×1 (Rigby, 1986b).-FIG. 48,1b-c. A. cylindrica HOWELL, Virgin Hills Formation, Mount Pierre; b, side view of cylindrical, small sponge, ×1; c, oscular view showing tubular form with round spongocoel and thin walls, PU 57872, ×2 (Rigby, 1986b).

- Brianispongia PICKETT & RIGBY, 1983, p. 727 [\*B. quadratipora; OD]. Slender, branching, without spongocoel or axial excurrent canals but with scattered ostia and numerous inhalant pores on smooth surface; skeleton of dendroclones and trabs, which arch upwardly and outwardly from axial region. Lower Devonian: Australia (New South Wales).-FIG. 46,3a-c. \*B. quadratipora, Garra Formation, Lochkovian-Pragian, Wellington; a, transverse, weathered surface showing canal pattern and absence of spongocoel in holotype,  $\times$ 4; *b*, side view of subcylindrical holotype with four-sided, inhalant ostia and small, skeletal pores, ×4; c, photomicrograph showing trabs and crossconnecting dendroclones of anthaspidellid, skeletal net, MMF 22570, ×20 (Pickett & Rigby, 1983).
- Calycocoelia BASSLER, 1927, p. 392 [\**C. typicalis;* OD]. Conical and tubular to somewhat club shaped with smoothly convex, upper surface descending into narrow, central cloaca; exterior surface smooth; small (possibly inhalant) pores arranged on outer surface in vertical rows and on

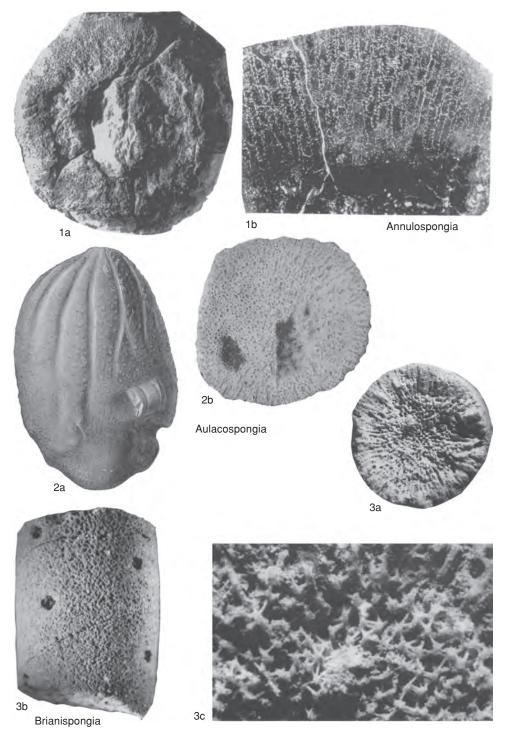


FIG. 46. Anthaspidellidae (p. 62–65).

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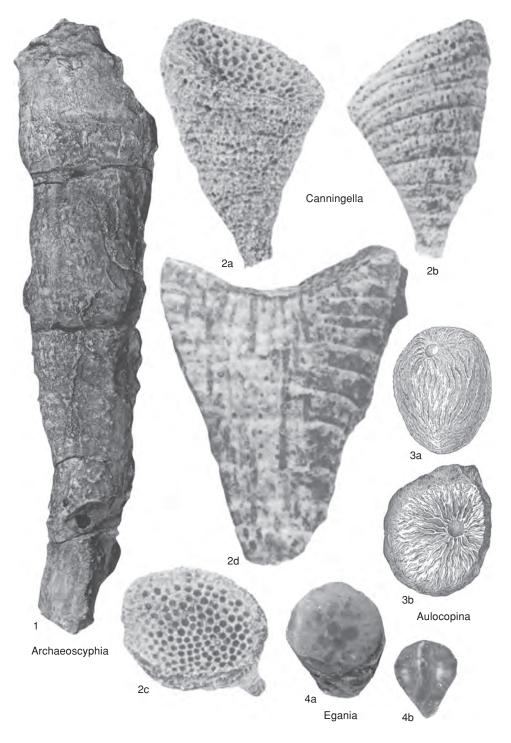


FIG. 47. Anthaspidellidae (p. 64–73).

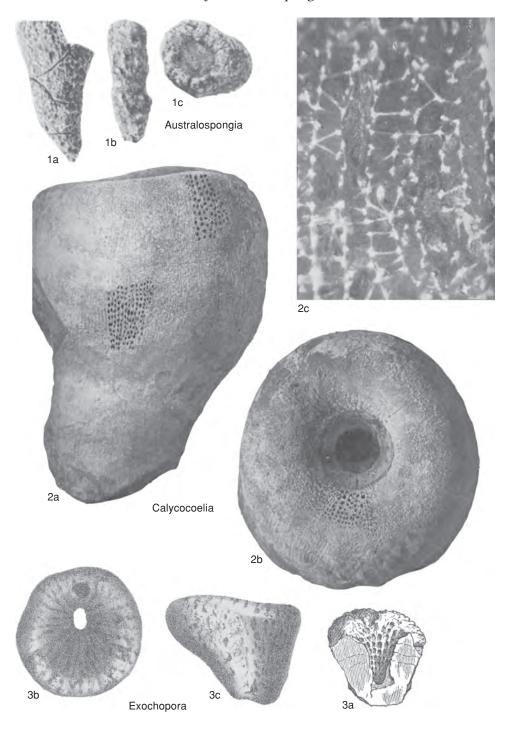


FIG. 48. Anthaspidellidae (p. 65-76).

upper surface in radial rows; dendroclones relatively long for family and arranged in usual, upwardly diverging rows. Lower Ordovician-Silurian: USA (Texas, Colorado), Argentina, China (Xinjiang), Ibexian; USA (Nevada, California), (Quebec, Northwest Territories, Canada Cornwallis Island), China (Sichuan), Germany (Island of Sylt and at other localities across northern Europe, as glacial erratics, presumably from Baltic region), Middle Ordovician-Silurian.-FIG. 48,2a-c. \*C. typicalis, Antelope Valley Formation, Whiterockian, Ikes Canyon, Toquima Range, Nevada; a, side view of goblet-shaped holotype with several inhalant ostia darkened to emphasize their distribution,  $\times 1$ ; b, view from above of rounded, oscular margin, marked by radial series of canals, and central, deep spongocoel, USNM 79637, ×1; c, photomicrograph of transverse section showing radial canals and parallel series of trabs interconnected with runglike dendroclones, ×9 (Bassler, 1941).

- Canningella RIGBY, 1986b, p. 22 [\*C. obconica RIGBY, 1986b, p. 23; OD]. Small to medium-sized, cylindrical-conical or funnel-shaped sponges with major, deep spongocoel or numerous large, excurrent canals; skeletal net with alternating open and dense layers, latter with swollen spicules marking former dermal surfaces of sponge; skeleton anthaspidellid with trabs composed of dendroclones and possible other spicules, but well organized and generally upwardly plumose or expanding. Devonian (Frasnian-Famennian): Australia (Western Australia).-FIG. 47,2a-d. \*C. obconica, Virgin Hills Formation, Lawford Range; a, side view of weathered holotype with numerous exhalant ostia in shallow spongocoel at top,  $\times 1$ ; b, opposite side view showing alternating layers of dense and open skeleton, both with abundant, inhalant canals, ×1; c, view into shallow spongocoel showing numerous uniformly spaced, exhalant ostia, GSWA F7198, ×1; d, natural vertical section through paratype showing alternating, skeletal layers, particularly in outer part, and vertical, exhalant canals in interior, GSWA F7199, ×1 (Rigby, 1986b).
- Capsospongia RIGBY, 1986a, p. 51 [\*Corralia undulata WALCOTT, 1920, p. 288; OD]. Annulate, conicocylindrical, thin walled; skeleton with irregular, vertical trabs formed by combined tips of horizontal dendroclones to produce septate-appearing wall; major canals parallel upwardly divergent skeleton. Middle Cambrian: Canada (British -FIG. 49,2a-b. \*C undulata (WAL-Columbia).-COTT), Stephen Formation, Burgess Shale, Mount Field; *a*, annulate holotype with vertical, skeletal tracts moderately well preserved in calcareous replacement; USNM 66479, ×1; b, detail of tip of small lectotype showing small trabs of skeleton near filled fracture, USNM 66480, ×20 (Rigby, 1986a).
- Cauliculospongia RIGBY & CHATTERTON, 1989, p. 20 [\* *C. solida;* OD]. Small, twiglike, branched or

unbranched without spongocoel; ladderlike series of dendroclones and trabs arching upwardly and outwardly from axis to meet dermal surface at high angles; may have discontinuous, vertical canals irregularly throughout. Silurian (Ludlow): Canada (Northwest Territories, Cornwallis Island).--FIG. 49,1a-b. \*C. solida, Cape Phillips Formation, Baillie-Hamilton Island; a, side view of holotype showing small, ramose form,  $\times 1$ ; b, photomicrograph showing center of stem of sponge lacking spongocoel and with upwardly pinnate trabs in uniform skeleton, with canals essentially normal to trabs, UA 7706, ×10 (Rigby & Chatterton, 1989; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

- Climacospongia HINDE, 1884a, p. 18 [\*C. radiata; OD]. Spheroidal; dendroclone rows radiating from base and perpendicular to surface; columns of interlocking zygoses cored by smooth oxeas; principal skeletal canals radial. Silurian (Wenlock-Ludlow): USA (Tennessee), Wenlock-Ludlow; Canada (Cornwallis Island), Ludlow.—FIG. 50, 1a-b. \*C. radiata, Brownsport Formation, Niagaran, Perry County, Tennessee; a, upwardly divergent skeletal and canal structure in vertical section of type sponge, ×1; b, enlarged view of part of fractured surface showing radiating monaxons and transverse dendroclones in skeleton, BMNH, ×10 (Hinde, 1884b).
- Cockbainia RIGBY, 1986b, p. 15 [\*C. palmata; OD]. Upright, bladed to palmate, anthaspidellid sponges with distal, fingerlike digitations; spongocoel absent but with moderately developed, radiating canals in centers of digitations; trabs originating near base of sponge or near basal parts of digitations and then diverging upwardly and outwardly; trabs composed of fused tips of smooth-shafted dendroclones and cored by one or two monaxons in any section. Devonian (Frasnian): Australia (Western Australia).----FIG. 50, 3a-d. \*C. palmata, Sadler Formation, Sadler Ridge; *a*, side view of holotype showing wrinkled, palmate growth form and partial, dermal layer, ×1; b, view from above showing radiating canals in each of branches, ×1; c, photomicrograph of skeletal structure from above, with dendroclones radiating from rodlike trabs, WAGS F7192, ×25; d, camera lucida drawing of spicule relationships in fragment with coring oxeas of trabs and attached, dendroclone spicules, ×30 (Rigby, 1986b).
- Colinispongia JOHNS, 1994, p. 60 [\*C. regularis JOHNS, 1994, p. 61; OD]. Palmate with relatively thin wall, surface smooth to slightly undulose; straight, radial canals vertically stacked and commonly discontinuous with one to three trabs between canals; exhalant openings quadrate and regular, producing checkerboard pattern; skeletal net ladderlike, of amphiarborescent dendroclones with surface of pinnation one-third to one-half wall thickness from gastral surface; ectosomal layers well developed over exterior, but open textured

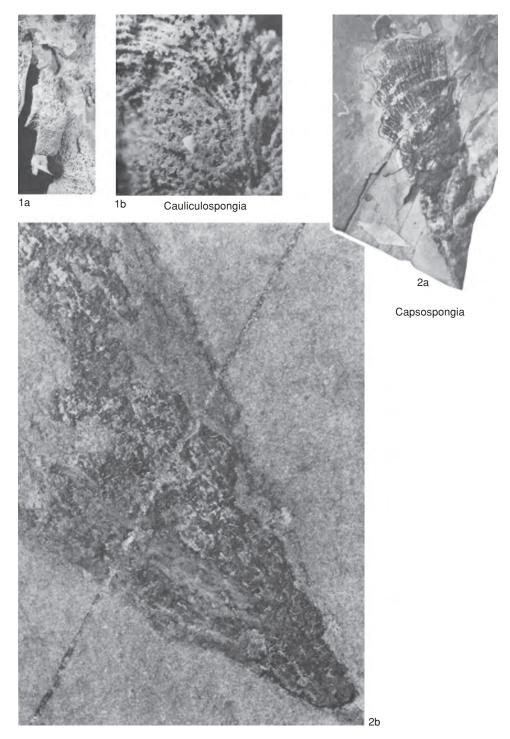


FIG. 49. Anthaspidellidae (p. 69).

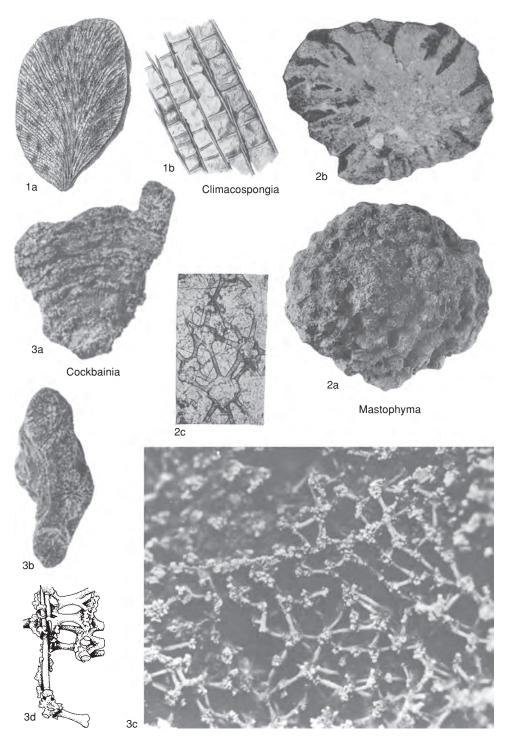


FIG. 50. Anthaspidellidae (p. 69-85).

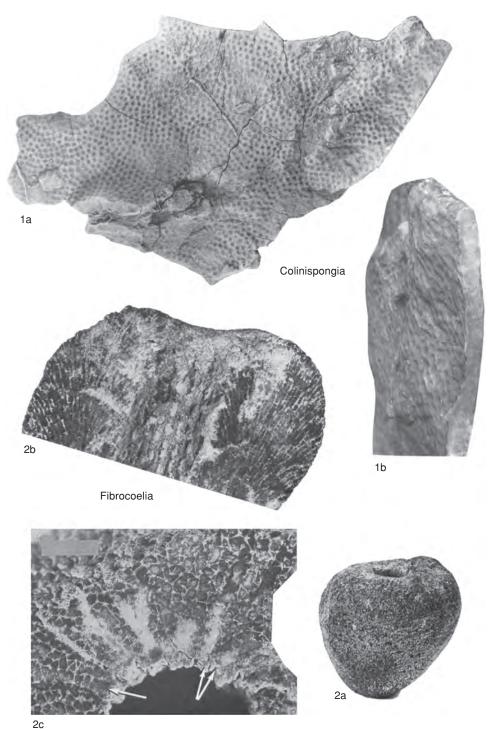


FIG. 51. Anthaspidellidae (p. 69-76).

and thin. Lower Ordovician: USA (western states).——FIG. 51, Ia-b. \*C. regularis, Shingle Limestone, Ibexian, Egan Range, Nevada; *a*, gastral view of holotype with regular dimensions and spacing of exhalant ostia; *b*, vertical section showing horizontal, radial canals and pinnation of skeletal trabs, UT 1787TX1, ×0.8 (Johns, 1994; courtesy of Nevada Bureau of Mines and Geology).

- Diotricheum van KEMPEN, 1989, p. 133 [\*D. vonhachti; OD]. Medium-sized, thick-walled, obconical sponges with narrow, pointed base, upper part probably subhemispherical; lateral walls smooth, dense, and differentiated from inner skeleton, marked with upwardly fanning folds or ribs and rhythmic, concentric growth increments; spongocoel moderately deep and narrow; subhorizontal, radial canals merging into clustered, vertical, axial, exhalant canals; irregularly disposed ostia on summit from upwardly divergent canals that originate near base; skeleton anthaspidellid with less regularly arranged, ladderlike spicule series with trabs cored by small monaxons; principal, runglike spicules are branched dendroclones. [The sponges are glacial erratics, presumably derived from the Baltic region to the northeast of Sylt. The genus is similar to several anthaspidellids but is differentiated by its external appearance with smooth, dense outer walls that are marked by vertical creases and horizontal growth rings and by conspicuous ostia randomly distributed over entire summit. These canals are separable into those of coarse, axial, exhalant cluster and those more peripheral ones that may be inhalant canals and are separate from the exhalant system.] Upper Ordovician: Germany (Island of Sylt), across northern Europe.-FIG. 52,2a-f. \*D. vonhachti, glacial erratic, Island of Sylt; a, holotype, side view with smooth surface and growth marks,  $\times 0.9$ ; *b*, side view of holotype with fractured surface showing growth increments and inner structure, GPIMH/S1, ×0.9; c, vertical section of paratype showing canal pattern and spongocoel with stacked apopores, GPIMH/S27,  $\times 1$ ; d, transverse section of paratype showing distribution of coarse, exhalant canals with converging, smaller canals, GPIMH/S2, ×2; e, photomicrograph of vertical section of paratype showing dendroclones of endosomal skeleton, GPIMH/S3, ×25; f, photomicrograph of cortical spicules in paratype, dermal layer, VK/S30, ×44 (van Kempen, 1989).
- Dunhillia RIGBY & WEBBY, 1988, p. 47 [\*D. tubula RIGBY & WEBBY, 1988, p. 48; OD]. Minute, tubular to conicocylindrical anthaspidellids with cylindrical spongocoel; trabs vertical and only slightly divergent, without surface of pinnation; principal spicules dendroclones; incurrent canals with outer, short tubes or rims, connecting to discontinuous, horizontal, ringlike canals at midwall that connect to horizontal, radial, excurrent canals and to axial spongocoel; dermal layer of small, tilelike, flat-

tened rhizoclones. Upper Ordovician-Silurian (Ludlow): Australia (New South Wales), Upper Ordovician; Canada (Northwest Territories, Baillie-Hamilton and Cornwallis Islands), -FIG. 53,1a-d. \*D. tubula, Malongulli Ludlow.-Formation, Caradoc-Ashgill, Cleifden Caves area, New South Wales; a, side view of holotype showing cylindrical form with separated, incurrent canals, each with a low, labropore rim or short, exaulos-like tube, ×4; b, enlarged side view showing small, rectangular, tilelike rhizoclones of dermal layer in regular rows that deflect around bases of incurrent openings, ×15; c, diagonal view of upper, oscular end with an axial spongocoel and uniform, spicular structure of skeleton, AMu. F66824, ×15; d, vertical section of paratype showing marked regularity of endosomal skeleton of parallel trabs and runglike dendroclones, shelflike rings on gastral surface composed largely of rhizoclones, horizontal ring canals occurring at midwall, AMu. F66825, ×15 (Rigby & Webby, 1988).-FIG. 53, 1e. D. cribrata RIGBY & WEBBY, Malongulli Formation, Caradoc-Ashgill, Cliefden Caves area, New South Wales; side view of holotype showing dense, dermal wall and clustered, incurrent canals, AMu. F66845, ×4 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca) .- FIG. 53, 1f. D. multiporata RIGBY & WEBBY, Malongulli Formation, Caradoc-Ashgill, Cliefden Caves area, New South Wales; side view of holotype showing numerous fairly uniformly spread, incurrent ostia, each with a minor rim, in dense, dermal layer, AMu. F66850, ×5 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- Egania JOHNS, 1994, p. 63 [\*E. typicalis; OD]. Obconical to massive, usually with hemispherical, upper surface commonly without spongocoel; exterior unornamented and smooth; several large, vertical, excurrent canals loosely clustered around axis; radial canals subhorizontal and moderately straight, in more-or-less vertical series; skeletal net with surface of trab pinnation midway between exterior surface and axis of sponge; spicules dominantly polyclonid and less commonly amphiarborescent dendroclones, often not in horizontal orientation. Lower Ordovician: USA (western -FIG. 47, 4a-b. \*E. typicalis, Shingle states).-Limestone, Ibexian, Egan Range, Nevada; a, transverse section of holotype with scattered, vertical, exhalant canals, UT 1784TX38, ×1; b, vertical section of paratype with fine, radial, inhalant canals and coarse, vertical, exhalant canals, UT 1784TX41, ×1 (Johns, 1994; courtesy of Nevada Bureau of Mines and Geology).
- Exochopora RAYMOND & OKULITCH, 1940, p. 208 [\*Calathium canadense BILLINGS, 1865, p. 377; OD]. Conical, thick walled, with deep, central cloaca into which radial, exhalant canals open, their openings being superposed so as to form vertical rows on cloacal wall; exhalant canals parallel

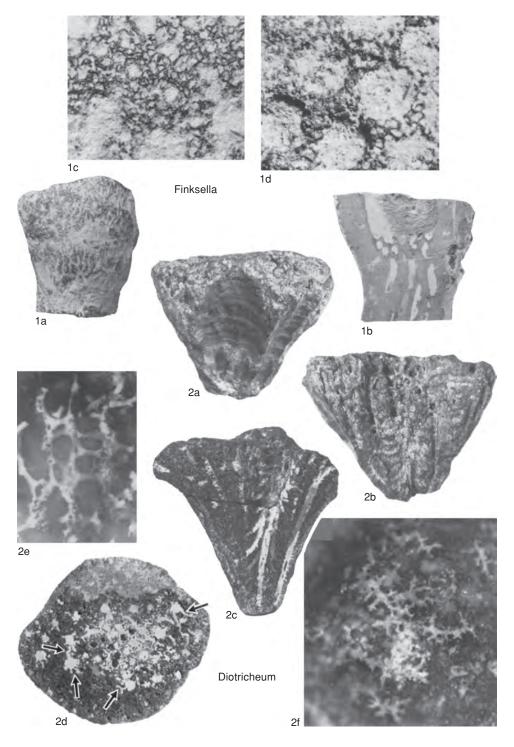
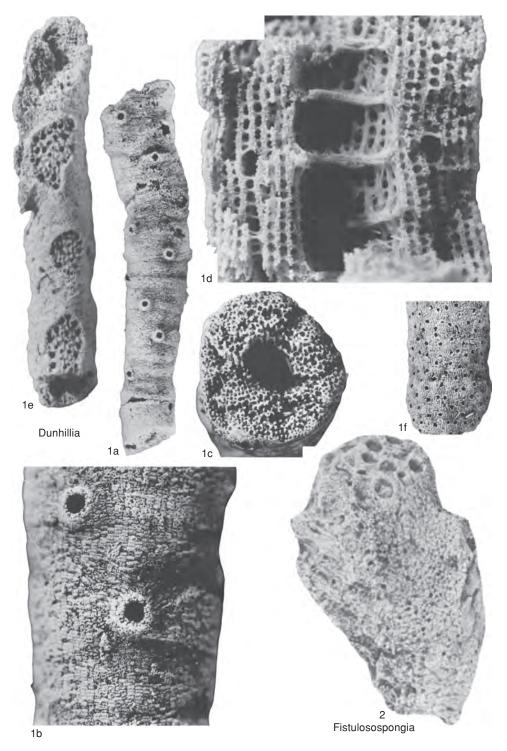


FIG. 52. Anthaspidellidae (p. 73-76).





to upper surface that is broadly convex; internal rows of dendroclones perpendicular to this surface thus radiating upwardly and outwardly. [Genus is similar to Eospongia.] Middle Ordovician: North America.--FIG. 48, 3a. \*E. canadense (BILLINGS), Mingan Formation, Chazyan, Mingan Islands, Canada; vertical section of small holotype showing interior of sponge and coarse, aligned, exhalant ostia in walls of spongocoel, ×1 (Billings, -FIG. 48,3b-c. E. infelix (ULRICH & 1965).-EVERETT), Platteville Limestone, Chazyan, Dixon, Illinois, USA; b, view down into spongocoel of abraded holotype; c, holotype, side view, ISM, ×1 (Ulrich & Everett, 1890).

- Fibrocoelia VAN KEMPEN, 1978, p. 321 [\*F. tubantiensis; OD]. Rounded, steeply obconical sponge with tubular, deep spongocoel; walls thick, with smooth, dermal surface; main canals radial, arched upwardly, and in regular, ascending series; canals may bifurcate laterally, opening into spongocoel in conspicuous, vertical rows; skeleton anthaspidellid and radially or plumosely reticulate with trabs; spicules dendroclones, irregular, moncrepid desmas, rhizoclones, and smooth styles; a few oxeas may be present; trabs formed by union of dendroclone tips and cored with overlapping styles, with discontinuous coating of generally elongated, branchlike, monocrepid desmas; rhizoclones generally occurring in conjunction with dendroclones rather than with trabs; no dermal nor gastral specialization apparent. Upper Ordovician: Netherlands (glacial erratics, presumably derived from the Baltic region).-FIG. 51,2a-c. \*F. tubantiensis, glacial erratic from Baltic region, Westerhaar; a, side view of holotype with deep, cylindrical spongocoel in thick-walled, obconical sponge,  $\times 1$ ; *b*, median section with exhalant ostia in gastral margin of cylindrical spongocoel and upwardly divergent trabs in thick walls,  $\times 1$ ; c, transverse section with light gray, radial canals to black spongocoel and thin dendroclones and rodlike trabs of skeletal net, arrows indicate canals filled by chalcedony, GIA PA 86980, ×4 (van Kempen, 1978; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen).
- Fieldospongia RIGBY, 1986a, p. 50 [\* Tuponia bellilineata WALCOTT, 1920, p. 274; OD]. Moderately thin walled, conical to cylindrical with deep spongocoel; smooth walls of ladderlike, anthaspidellid, skeletal structure of possible dendroclones that cross connect vertical strands; walls without canals; strands may be arranged in bladelike elements. Middle Cambrian: Canada (British Columbia).—FIG. 54,1a-b. \* E. bellilineata (WALCOTT), Mount Whyte Formation, Mount Stephen; a, thick-walled, steeply obconical holotype,  $\times 1$ ; b, photomicrograph of vertical, trablike structures cross connected with short, horizontal elements (possible dendroclones) in moderately preserved skeleton, USNM 66454, ×5 (Rigby, 1986a).
- Finksella RIGBY & DIXON, 1979, p. 620 [\*F. turbinata; OD]. Turbinate to low, conical sponges

with a broad, simple, open spongocoel at crest, into which empty numerous large, circular, excurrent canals from stalked base; circular canals separated by skeleton, so without prismatic packing; wall pierced by canals that rise from exterior toward spongocoel; skeletal net of dendroclones united in characteristic anthaspidellid net with trabs upwardly pinnate from close to dermal margins; well-differentiated dermal layer with considerably less regularity than internal skeleton, but with spicules of similar size and shape. Silurian (Ludlow-Pridoli): Canada (District of Franklin, Arctic Islands).—FIG. 52, 1a-d. \*F. turbinata, Read Bay Formation, Somerset Island; a, holotype, side view with irregular, surficial canals,  $\times 1$ ; b, vertical section showing coarse, exhalant canals in lower part and matrix-filled spongocoel with thick walls in upper part, ×1; c, photomicrograph of irregular spiculation in dermal layer that contrasts with regular structure of interior, ×40; d, photomicrograph of skeletal net and large, exhalant canals in floor of spongocoel, GSC 54843, ×10 (Rigby & Dixon, 1979).

- Fistulosospongia RIGBY, 1986b, p. 17 [\*F. parallela; OD]. Massive to conical sponge; without spongocoel but with several widely separated, vertical, coarse, excurrent canals; incurrent openings subhorizontal and locally in crudely stacked series; skeletal net anthaspidellid, trabs radiating upwardly and outwardly from near base without prominent zone of pinnation; skeleton more or less uniformly textured, without alternation of open and dense layers, except for denser, dermal layer. Devonian (Frasnian-Famennian): Australia (Western Australia).-FIG. 53,2. \*F. parallela, Virgin Hills Formation, Lawford Range; holotype, side view showing irregular, obconical form and large, exhalant oscula on summit, GSWA Fl7248, ×1 (Rigby, 1986b).
- Gleesonia RIGBY & WEBBY, 1988, p. 57 [\*G. porosa RIGBY & WEBBY, 1988, p. 58; OD]. Obconical, coarse-textured anthaspidellid composed of upwardly and outwardly radiating, webbed beams in interior that become simple trabs in outer part; webbed, compound beams of several trabs characteristic of interior, separated by large, axial, excurrent canals and by upwardly and inwardly convergent canals approximately normal to trabs. Upper Ordovician: Australia (New South Wales).----FIG. 55, 1a-e. \*G. porosa, Malongulli Formation, Cliefden Caves area; a, vertical view into oscular pit showing axial canals and general, radiate structure of skeleton composed of compound elements of dendroclones and associated rhizoclones,  $\times 2$ ; b, diagonal view showing upwardly and outwardly divergent beams of endosomal part of skeleton with coarse dendroclones and dense, outer, dermal layer, shallow spongocoel pit showing in upper left, ×2; c, photomicrograph of skeletal elements of rhizoclone spicules around large, central, axial canals, AMu. F66858, ×6; d, photomicrograph of vertical section of paratype showing upwardly and outwardly radiating, compound beams composed

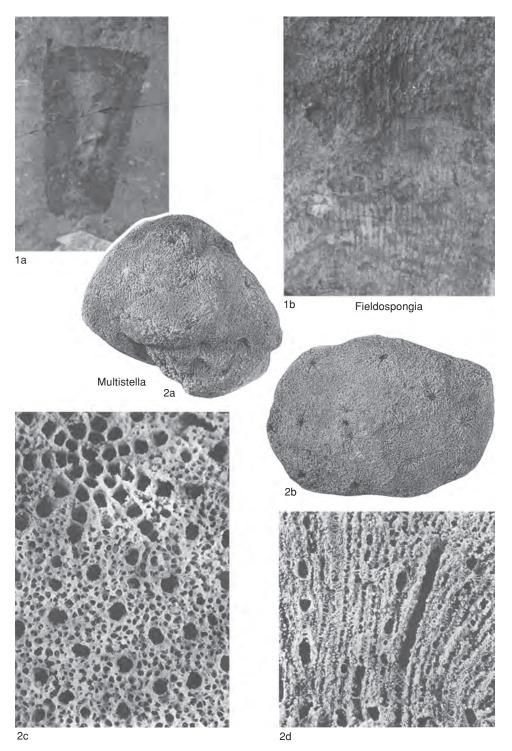


FIG. 54. Anthaspidellidae (p. 76-85).

of clusters of trabs formed by cross webbing and ray tips of large, H-shaped dendroclones, beams separated by parallel, coarse canals, AMu. F66859, ×6; e, photomicrograph of nodose, dermal layer, made of laterally fused ray tips of dendroclones, perforated by tiny, circular ostia and small pores, AMu. F66860, ×15 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- Incrassospongia RIGBY, 1977a, p. 122 [\*I. rhipidos; OD]. Subcylindrical, club shaped to distinctly fan shaped, without spongocoel, spicules dendroclones in upwardly fanning, ladderlike pattern cross connected by less continuous, horizontal fibers; only openings are parallel to skeletal structure; such structures enlarged in older parts where horizontal fibers, cored by spicule shafts, and vertical trabs, composed of united, spicule tips, are of nearly equal diameter. Ordovician: Canada (District of Franklin, Arctic Islands); Argentina, Lower Ordovician .---- FIG. 56, 2a-b. \*I. rhipidos, unnamed formation, Middle Ordovician, Amadjuak Lake, Baffin Island, District of Franklin, Canada; a, holotype, side view, steeply obconical to fan shaped with vertically and horizontally concentric fibers, GSC 43570, ×1; b, paratype, photomicrograph of upper part showing simple dendroclones in upper, outer part of skeleton and increasing in diameter of fibers in older, interior part of sponge, GSC 43576b, ×10 (Rigby, 1977a).
- Incrustospongiella RIGBY & BOYD, 2004, p. 73 [\*I. superficiala; OD]. Thin, sheetlike incrusting sponge with skeleton of unbundled, X-shaped dendroclones, and rarely I-shaped dendroclones, all fused at mutual contacts of digitate ray tips to produce indistinctly layered skeleton; isolated monaxial spicules locally common as erect armoring elements; larger exhalant canals extending through approximately half of sponge thickness to end on dermal surface as isolated openings or small clusters of exopores; smaller inhalant canals occurring between rays of dendroclones and also extending irregularly inward from dermal surface to midthickness. Permian (Wordian): USA (Wyoming) .--—FIG. 57,2a c. \*I. superficiala, Park City Formation, Bull Lake area, eastern Wind River Mountains; a, view of thin film of sponge holotype (arrow) encrusting concave surface of productid brachiopod, on right, and part of hinge area and outer surface of valve on left, UW4026, ×2; b, SEM photomicrograph of dermal surface of holotype showing dominance of Xshaped dendroclones in uniform skeletal structure, with small inhalant ostia and somewhat larger, more rare, exhalant ostia, scale bar, 200 µm; c, SEM image of paratype with uniform dendroclones of encrusting sponge (S) coating central brachiopod spine (B), with prominent, armoring, monaxial spicules radiating from dermal surface, UW4027, scale bar, 500 µm (Rigby & Boyd, 2004).
- Isispongia PICKETT, 1969, p. 16 [\**I. paradoxa*; OD]. Massive, rounded to irregular; surface bearing large to small, more or less evenly distributed

pores; some adjacent pores may be laterally confluent; principal canals and dendroclone rows radial, perpendicular to surface, with connecting canals parallel to surface; similar to *Phacellopegma* but without well-developed grooves. *Middle Devonian:* Australia (New South Wales).——FIG. 58. \**I. paradoxa*, Timor Limestone, ?Eifelian, County Brisbane; side view of weathered holotype with prominent, aligned ostia of canals in uniform skeleton, AM F12903, ×1 (Pickett, 1969).

- Jereina FINKS, 1960, p. 74 [\*J. cylindrica; OD]. Cylindrical, with or without branching; large, exhalant canals occupying axial region, parallel to its length, and opening on end or sides of sponge; inhalant canals radial, perpendicular to sides; spicules chiastoclones and dendroclones without regular arrangement, and meeting in noticeably inflated junctions. Middle Devonian-Permian (Artinskian): Australia (New South Wales), Middle Devonian; USA (Texas), Artinskian.-FIG. 59,2a-d. \*J. cylindrica, Bone Spring Formation, Sierra Diablo; a, holotype, side view, steeply obconical with dense, outer skeleton,  $\times 0.5$ ; b, holotype, cross section showing coarse, axial apochetes and smaller, nearly horizontal, crossconnecting canals, PU 78875, ×1; c, paratype, longitudinal section showing axial apochetes and dense, outer layer of sponge, ×1; d, horizontal section of same specimen showing porous interior of sponge and dense, outer layer with smaller, horizontal prosochetes, PU 78876, ×1 (Finks, 1960; courtesy of The American Museum of Natural History).
- Jianghania LIU & others, 1997, p. 198 [\*]. vichangensis; OD]. Moderately large, annulate, conicocylindrical sponges with deep, annulate spongocoel; thick walls composed of upwardly and outwardly diverging, radially arranged trabs of ladderlike series of dendroclones; pinnation surface one-fourth wall thickness in from gastral margin; outer trabs arching strongly to meet dermal surface at right angles between annulations, but rising to meet upper edges of annulations at 60 to 70 degrees and lower edges less steeply; coarse, horizontal, radial canals arranged in distinct, separated layers around spongocoel at level of middle of annular ridges; individual, horizontal canals may arch upwardly distally. [Jianghania is similar to Archaeoscyphia in its annulate form, but differs from the latter in having the principal, horizontal canals concentrated at one distinct level in the middle of each annular ridge.] Lower Ordovician: China (Hubei).-FIG. 60a-d. \*J. yichangensis, Honghuayuan Formation, Tremadocian-Arenig, Yichang; a, transverse section through wall and spongocoel between annular ridges on holotype, JPI YH-1-a, ×2; b, longitudinal section of annulate walls with trabs diverging upwardly and outwardly from gastral surface of subcylindrical spongocoel, JPI YH-1-d, ×2; c, transverse section through annular ridge with prominent, convergent, horizontal, excurrent canals, JPI YH-1b, ×2;

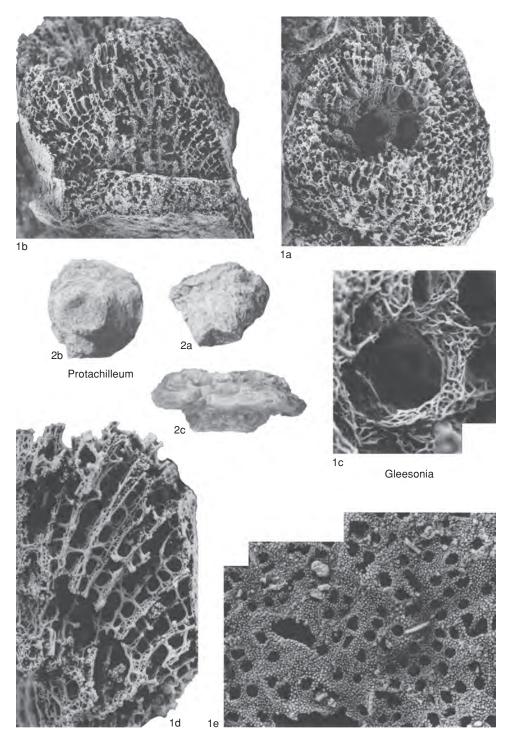


FIG. 55. Anthaspidellidae (p. 76-89).

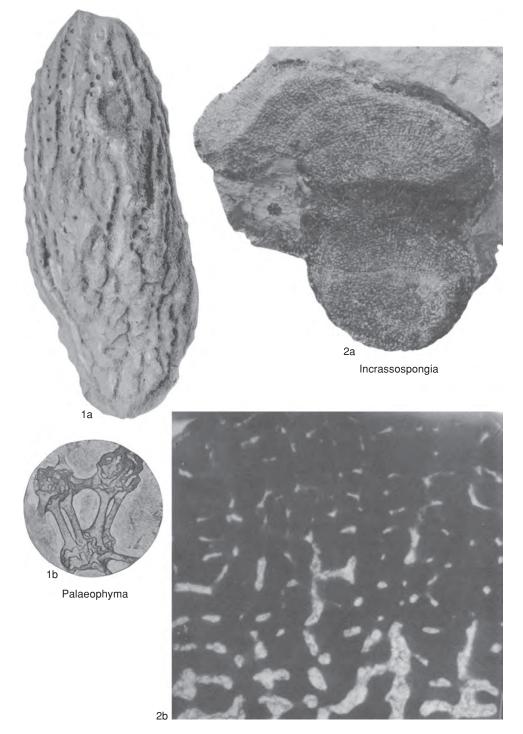


FIG. 56. Anthaspidellidae (p. 78-88).

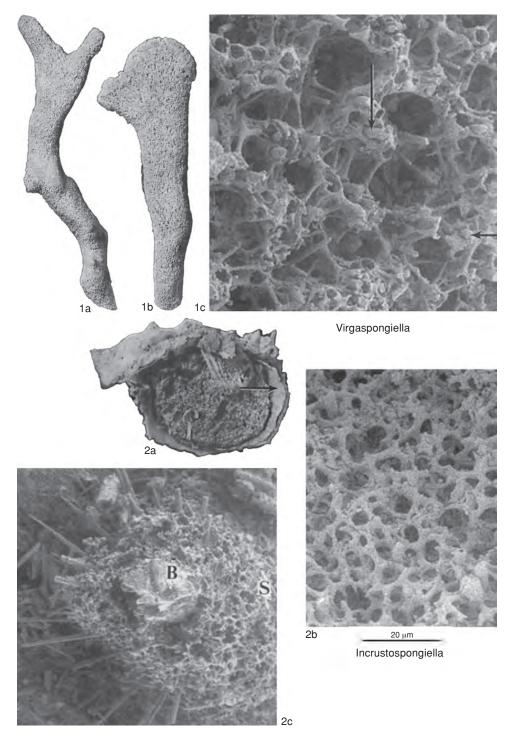


FIG. 57. Anthaspidellidae (p. 78-104).



FIG. 58. Anthaspidellidae (p. 78).

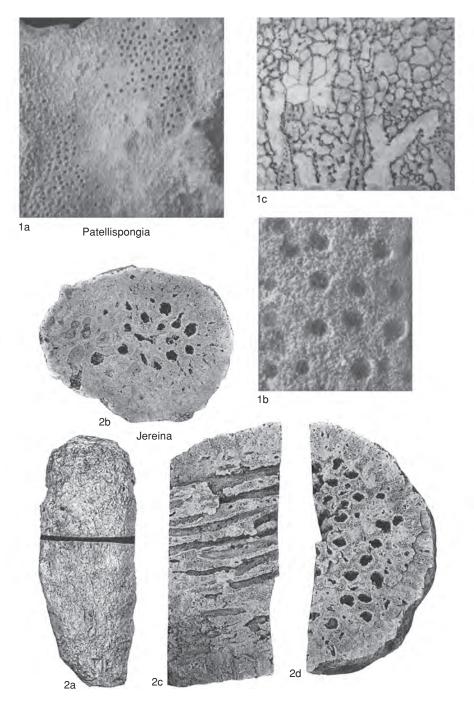


FIG. 59. Anthaspidellidae (p. 78-88).

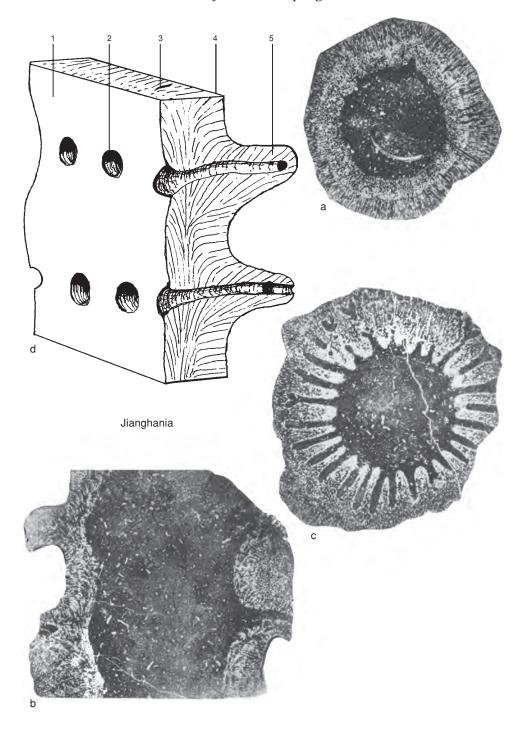


FIG. 60. Anthaspidellidae (p. 78-85).

*d*, diagram of skeletal and canal structure of genus; *1*, gastral surface; *2*, ostium of horizontal canal; *3*, section of trab; *4*, dermal surface; *5*, annulation in outer wall, not to scale (Liu & others, 1997).

- Malongullospongia RIGBY & WEBBY, 1988, p. 44 [\*M. delicatula; OD]. Massive to subhemispherical anthaspidellid without spongocoel but with large, subhorizontal canals in stacks and parallel to gastral surfaces, normal to trabs, which radiate from center of sponge; vertical canals in tracts between stacked canals producing rectangular, interconnected system of canals; skeleton of delicate, longraved dendroclones combined with numerous oxeas to produce thin trabs; dendroclones may be vertical, from dendroclone shaft to shaft, rather than horizontal in normal, ladderlike pattern. Upper Ordovician: Australia (New South Wales). -FIG. 61a-e. \*M. delicatula, Malongulli Formation, Cliefden Caves area; a, side view of holotype showing dense, dermal layer on left, over more open, canalled skeleton of interior,  $\times 1$ ; b, view down onto gastral surface, which is marked with irregular, horizontal canals with vertical ostia of vertical canals on ridges between, ×1; c, vertical section through porous interior showing coarse, horizontal canals that interrupt upwardly expanding, skeletal system, ×1; d, photomicrograph of vertical section through interior of holotype showing curved trabs and ladderlike series of dendroclones curving around some horizontal canals, but interrupted by others, ×5; e, SEM photomicrograph showing prominent, vertical trabs cored by oxeas, and horizontal X- and Y-shaped dendroclones whose branching ray tips grasp oxeas, AMu. F66822, ×200 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Mastophyma GERTH, 1927, p. 109 [\*M. jonkeri GERTH, 1927, p. 110; OD]. Spheroidal; surface covered with conical protuberances alternating with deep depressions into which radially arranged, exhalant canals open; dendroclone rows or trabs are perpendicular to outer surface, radiating from central, presumed initial, attachment point. Permian (Lopingian): Timor.—FIG. 50,2a-c. \*M. jonkeri, Upper Permian Limestone, Nifoetassi; a, side view of nodose, hemispherical, type specimen with large ostia of radial canals; b, transverse section with coarse, radial canals filled with dark matrix, ×1; c, photomicrograph of skeletal structure showing coarse trabs connected by runglike dendroclones, ×30 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Multistella FINKS, 1960, p. 61 [\**M. porosa* FINKS, 1960, p. 62; OD]. Spheroidal to fungiform, with concentrically wrinkled, conical base covered with dense, dermal layer and upper surface strongly convex and smooth; upper surface bearing numerous stellate clusters of exhalant pores; dendroclone rows perpendicular to upper surface, radiating from attachment point within basal region; canals

are dominantly perpendicular to surface. Permian (Guadalupian): USA (Texas).—FIG. 54,2a-d. \*M. porosa, Cherry Canyon Formation, Guadalupe Mountains; a, side view of silicified holotype showing multiple clusters of apopores in upper part of hemispherical, stalked sponge, ×1; b, top view of holotype showing widespread, apopore clusters surrounded by short, convergent canals, ×1; c, photomicrograph of part of upper surface including stellate cluster of apopores and isolated pores in skeleton where dendroclones form spokes around rodlike trabs, ×10; d, vertical section of side of sponge showing dark, vertical and horizontal canals interrupting upwardly divergent, skeletal structure of rodlike trabs and runglike dendroclones, USNM 12760, ×10 (Finks, 1960; courtesy of The American Museum of Natural History).

- Nevadocoelia BASSLER, 1927, p. 392 [\*N. wistae; OD]. Conical to conicocylindrical with deep cloaca; exterior with irregular, horizontal ridges that do not encircle sponge (N. wistae), or evenly spaced, conical protuberances (M. traini), or broad, flangelike annulations (N. pulchra); large ostia of horizontal canals tend to form vertical rows on exterior, canals cross connected by ascending one parallel to rows of dendroclones. [Similar to Archaeoscyphia but differs in having a thicker body wall; in lack of regular, vertical, slitlike spaces in body wall; and in having generally more subdued, external outgrowths (except for N. pulchra). It also resembles the slightly later and still less regular Rhopalocoelia.] Middle Ordovician-Upper Ordovician: USA (Nevada, California, Alabama), Middle Ordovician; northern Europe, Upper Ordovician.——FIG. 62, 1a-b. \*N. wistae, Antelope Valley Formation, Whiterockian, Ikes Canyon, Toquima Range, Nevada; a, side view of obconical holotype with transverse, ridged, dermal surface, USNM 79632, ×1; b, photomicrograph of vertical section showing outwardly curving trabs of skeleton interrupted by a dark, matrix-filled canal, ×9 (Bassler, 1941).
- Okulitchina WILSON, 1948, p. 21 [\*O. magna WIL-SON, 1948, p. 22; OD]. Broadly conical or discoidal sponge with convex, upper surface; central cloaca present into which empty radial, exhalant passages in form of vertical slits, some of which branch; vertical canals of circular cross section also present, arranged in radial rows as in Psarodictyum. Upper Ordovician: Canada (Ontario).-FIG. 62,3a-c. \*O. magna, ?Cobourg beds, Ottawa; a, side view of paratype with faint, upper depression, GSC 9307d,  $\times$ 1; *b*, transverse section of holotype showing large, radial canals and spongocoel, GSC 9307b, ×1; c, photomicrograph of holotype showing skeleton composed of dendroclones cross-connecting rodlike trabs, GSC 9307b, ×8 (Wilson, 1948; courtesy of Minister of Public Works and Government Services Canada, 2002, and Geological Survey of Canada).

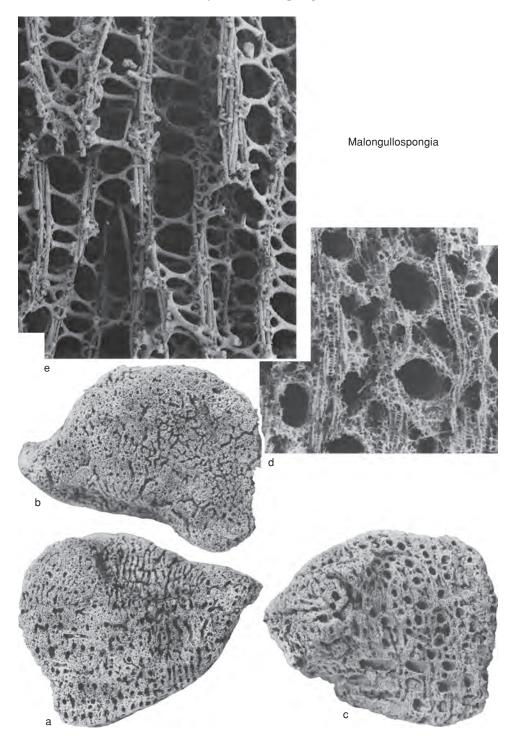


FIG. 61. Anthaspidellidae (p. 85).

## Orchocladina

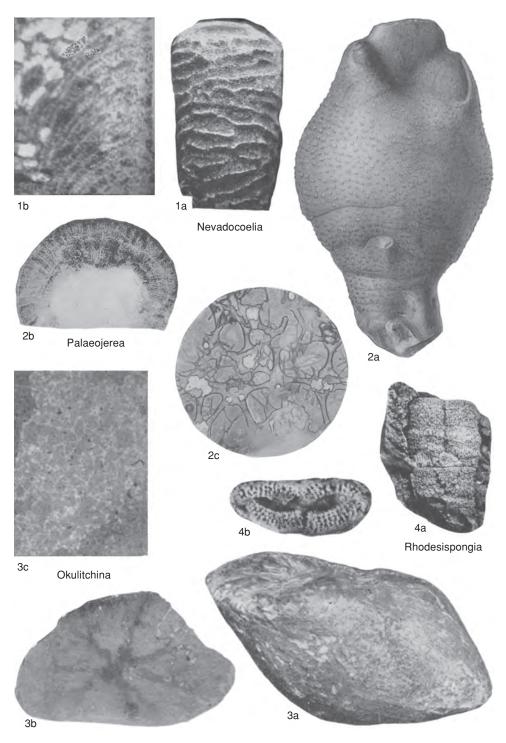


FIG. 62. Anthaspidellidae (p. 85-96).

- Palaeojerea GERTH, 1927, p. 111 [\*P. molengraaffi GERTH, 1927, p. 112; OD] [=Gerthiella ZHURAV-LEVA in REZVOI, ZHURAVLEVA, & KOLTUN, 1962, p. 54, obj.]. Ficiform, stipitate; surface hispid or papillose owing to projecting ends of trabs produced by dendroclone zygoses; entire surface covered with dense, dermal layer; dendroclone rows and skeletal canals perpendicular to outer surface; structures of axial region (including top surface) obliterated by silicification according to author so his assumption of vertical canals here would appear entirely putative. [The name is not a homonyn of Palaeoierea LAUBE, 1864, so nom. subst. Gerthiella ZHURAVLEVA, 1962, is not necessary. The GERTH, 1927, paper was essentially reprinted in 1929 as part of a volume on the paleontology of Timor.] Permian (Lopingian): Timor.—FIG. 62,2a-c. \*P. molengraaffi, Upper Permian limestone, Besleo; a, side view of holotype with micronodose, dermal surface,  $\times 1$ ; b, transverse section showing radial, skeletal structure in outer part, but with structure destroyed in central, silicified region, ×1; c, photomicrograph showing X- and I-shaped dendroclones of skeleton, ×25 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Palaeophyma GERTH, 1927, p. 106 [\*P. cucumeriformis; OD]. Cucumeriform, with anastomosing, vertical, surface grooves on sides convergent on summit; dendroclone rows and principal canals perpendicular to surface, canals opening into bottoms of surface grooves; smooth monaxons scattered in mesh spaces are also reported. Permian (Lopingian): Timor.—FIG. 56,1a-b. \* P. cucumeriformis, Upper Permian limestone, Nifoetassi; a, side view of type specimen with grooves of surficial canals,  $\times 1$ ; *b*, photomicrograph showing trabs, normal to section, interconnected by I-shaped dendroclones whose ray tips interdigitate to produce trabs, ×50 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Patellispongia BASSLER, 1927, p. 393 [\*P. oculata; OD]. Explanate fronds, possibly originally saucershaped as in Anthaspidella; upper surface bearing numerous radial rows of small, closely spaced, exhalant pores without conspicuous, exhalant canals convergent on them, thus differing from Anthaspidella; lower surface with dense, dermal layer; internal spicular net well organized in regular, radial rows of dendroclones, may include some rhizoclones. Lower Ordovician-Silurian (Wenlock): USA (Texas, Colorado), Argentina, Lower Ordovician; USA (Nevada, California), Middle Ordovician; Australia (New South Wales), northern Europe, Upper Ordovician; Canada (Northwest Territories, Baillie-Hamilton Island, District of Mackenzie), Wenlock.-FIG. 59, 1a-c. \*P. oculata, Antelope Valley Limestone, Whiterockian, Ikes Canyon, Toquima Range, Nevada; a, dermal surface of holotype with regularly spaced, exhalant ostia,  $\times 1$ ; b, enlarged, dermal surface with pores and dense, dermal layer, USNM 79638, ×5; c,

photomicrograph of vertical section with distinct, lined canals in open, skeletal net of long dendroclones, ×9 (Bassler, 1941).

- Phacellopegma GERTH, 1927, p. 103 [\*P. campana GERTH, 1927, p. 104; OD]. Massive without cloaca; surface covered with anastomosing grooves into which open principal canals from interior of sponge; dendroclone rows and principal canals perpendicular to surface of sponge. Carboniferous (Middle Pennsylvanian)–Permian (Lopingian): North America, Timor. FIG. 63, 2a-d. \*P. campana, Upper Permian limestone, Lopingian, Besleo, Timor; a, side view of holotype,  $\times 0.5$ ; b, enlarged dermal surface with tips of rodlike trabs and cross-connecting dendroclones shown on ridges between surficial grooves of canals,  $\times 3$ ; c, photomicrograph of section transverse to trabs that are cross connected with dendroclones, best shown on left, surrounded by dark matrix,  $\times 9$ ; d, cross section showing radial rows of dendroclones and parallel canals filled with dark matrix, ×1.2 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Playfordiella RIGBY, 1986b, p. 10 [\*P. cylindrata RIGBY, 1986b, p. 11; OD]. Obconical to conicocylindrical, moderately thin-walled, weakly annulate, anthaspidellid sponges with deep simple spongocoel; canals in vertically stacked series and roughly horizontal; surface of pinnation of trabs at midwall to outer one-third; trabs composed of normal and triclonid dendroclones and cored with smooth monaxons; thin dermal and gastral layers dense, of thickened dendroclones, and more chiastoclones than in main skeleton. Devonian (Frasnian-Famennian): Australia (Western Australia).----FIG. 63, 1a-c. \*P. cylindrata, Sadler Limestone, Sadler Ridge; a, side view of holotype, GSWA F7186, ×1; b, diagonal view of paratype showing open spongocoel, wall thickness, and wrinkled, dermal layer, GSWA F7190, ×1; c, camera lucida drawing of skeletal fragment showing trabs with coring, monaxial spicules and associated dendroclones, GSWA F7191, ×25 (Rigby, 1986b).
- Protachilleum ZITTEL, 1877c, p. 22 [\*P. kayseri; OD]. Mushroom-shaped sponge with broad, short stalk and overhanging, flat to arched, platterlike, upper part, lacking spongocoel; basal part smooth to weakly annulate; dermal ostia prominent, inhalant canals rising sharply upward to produce porous, lower stalk and scattered, vertical canals throughout central part of sponge; skeleton anthaspidellid with trabs diverging from near-basal radiante; surface of pinnation nearly horizontal in thin, upper plate, spicules mainly Y- and X-shaped dendroclones in fine-textured skeleton. Lower Ordovician: Argentina (San Juan Province).-FIG. 55,2a-c. \*P. kayseri, San Juan Formation, Arenig, Precordillera Oriental; a, side view of steeply obconical, reference specimen showing flaring upper part, ×1; b, view from below showing circular base but without spongocoel in lower part of sponge; CRICYT H-43, ×1; c, side view of more

stalked, flaring sponge, CRICYT H-42, ×1 (Beresi & Rigby, 1993).

- Psarodictyum RAYMOND & OKULITCH, 1940, p. 212 [\*P. magnificum; OD]. Large, open, saucer or funnel shaped, with sublobate outline; principal, skeletal canals parallel to outer, growing edge and thus perpendicular to upper and lower surfaces; canals open on both upper and lower surfaces in radial rows. [This genus may be thought of an as everted Exochopora in which the cloacal surface has become the upper surface.] Lower Ordovician-Silurian (Ludlow): Argentina, Lower Ordovician; USA (New York), Canada (Quebec), Middle Ordovician; Canada (Northwest Territories, Baillie-Hamilton Island), Ludlow.-FIG. 64a-d. \*P. magnificum, Chazyan; a, vertical view of lobate holotype with shallow, central depression, Chazy Formation, Valcour Island, New York, MCZ 9330, ×0.125; b, photomicrograph of thin section showing radial and concentric, skeletal elements, Chazy Formation, Valcour Island, New York, MCZ ?9555, ×10 (Raymond & Okulitch, 1940); c, dermal view of weathered, funnel-like sponge showing radial, skeletal structure, Mingan Formation, Mingan Islands, Canada, GSC 111161, ×1; d, vertical section near outer, rounded margin showing divergent, rodlike trabs and runglike, small dendroclones of skeleton interrupted by dark, matrix-filled canals, Mingan Formation, Mingan Islands, Canada, GSC 111158, ×10 (Rigby & Desrochers, 1995).
- Pseudomultistella DENG, 1981, p. 422 [425] [\*S. decipiens; OD]. Ramose sponges without spongocoel, but with canals diverging upwardly toward surface, connected by horizontal canals; skeleton of horizontal dendroclones superposed in ladderlike series either vertically or radially arranged in spokelike groups around common, axial area; surface porous but lacking astrorhizae. [Pseudomultistella has an internal structure like Multistella but is a polelike sponge without astrorhizae on the exterior.] Permian (Changhsingian): China (Guangxi) .---- FIG. 65, 1a-c. \*P. decipiens, Heshan Formation; a, longitudinal section of holotype showing upwardly radial canals piercing anthaspidellid skeleton of upwardly divergent trabs, NIGPAS 59983, ×4; b, transverse section showing radially arranged canals and skeleton, NIGPAS 59984, ×4; c, transverse section of paratype showing lack of central spongocoel in dense skeleton with radiating, tract structure and canals, NIGPAS 59985, ×2.5 (Deng, 1981).
- Pseudopalmatohindia RIGBY & WEBBY, 1988, p. 46 [\*P. digitata; OD]. Large, undulating, vertically palmate to buttressed or anastomosing, digitate anthaspidellids with coarse, parallel, excurrent canals in linear series at midblade or midwall; trabs formed of dendroclones tips and cored by monaxons, trabs diverging upwardly and outwardly from general, mid-wall canal area. Lower Ordovician–Upper Ordovician: China (Xinjiang), Lower Ordovician; Australia (New South Wales), Upper Ordovician.——FIG. 66a–d. \*P. digitata,

Malongulli Formation, Caradoc-Ashgill, Cliefden Caves area, New South Wales; a, irregular, broken surface of digitate holotype showing large, excurrent canals along axes of digitation of palmate blades, direction of growth toward bottom as indicated by downwardly expanding, trab-based skeleton, fragments of other demosponges showing above dark, V-shaped matrix fill between digitations, ×1; b, tip of digitation showing relatively dense, dermal layer on right and more open, endosomal skeleton in interior, with thin, dense, gastral layer around axial canals, ×3.5; c, enlargement of upper part of view b showing three layers of skeleton where dendroclones and trabs show in more open, intermediate layer, ×9; d, photomicrograph showing relatively coarse but smooth dendroclones and trabs that arch outwardly toward left, AMu. F66823, ×10 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- Pycnospongia GERTH, 1927, p. 113 [\*P. timorensis; OD]. Somewhat fungiform with pointed top and horizontal, overhanging bulges on sides; surface reported to be covered with finely perforate, dermal layer without larger pores; principal canals perpendicular to surface but do not penetrate outer layer; dendroclone rows also perpendicular to surface, spicules may include anomoclones and didymoclones. Permian (Lopingian): Timor.— FIG. 67, 1a-b. \*P. timorensis, Upper Permian limestone, Nifoetassi; a, side view of holotype showing dense, lobate, dermal layer with ostia of exhalant canals and pear shape, ×1; b, enlarged, dermal surface showing dense, skeletal net, poorly preserved, cut by arcuate, calcite veinlets, ×3 (Gerth, 1929).
- Rankenella KRUSE, 1983, p. 51, nom. nov. pro Arborella GATEHOUSE, 1968, p. 61, non OSBORN, 1914 [\*Arborella mors GATEHOUSE, 1968, p. 61; OD]. Smooth-walled, explanate or conicocylindrical, digitate sponges with deep, cylindrical spongocoel; skeletal structure anthaspidellid with dendroclones forming trabs that are parallel to gastral surface and diverge upwardly and outwardly toward dermal surface; differentiated canal system not developed; some spicules modified in dermal layer. [The lack of a differentiated canal system separates Rankenella from related genera.] Middle Cambrian: Australia (Northern Terri--FIG. 67, 3a-b. \*R. mors (GATEHOUSE), tory).-Ranken Limestone, Ordian, Soudan; a, longitudinal section of conicocylindrical, possibly branched, reference specimen with longitudinal and transverse sections of axial spongocoel, trabs diverging from gastral to dermal surface, CPC 21238, ×5; b, dendroclones and rhizoclones from associated limestone, SUP 78108, ×50 (Kruse, 1983).
- Rhodesispongia DE FREITAS, 1991, p. 2056 [\*R. simplex; OD]. Obconical to subcylindrical, thinwalled sponge with deep, broad spongocoel; skeleton simple with thick, vertical trabs that parallel dermal and gastral surfaces and are formed by regular union of ray tips of slender, runglike,

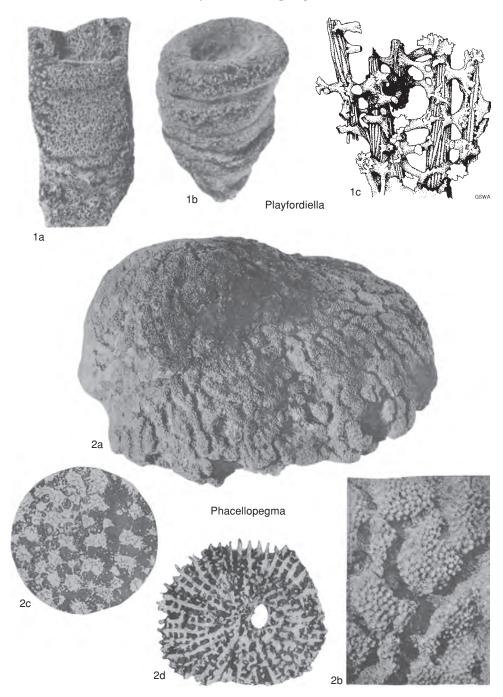


FIG. 63. Anthaspidellidae (p. 88).

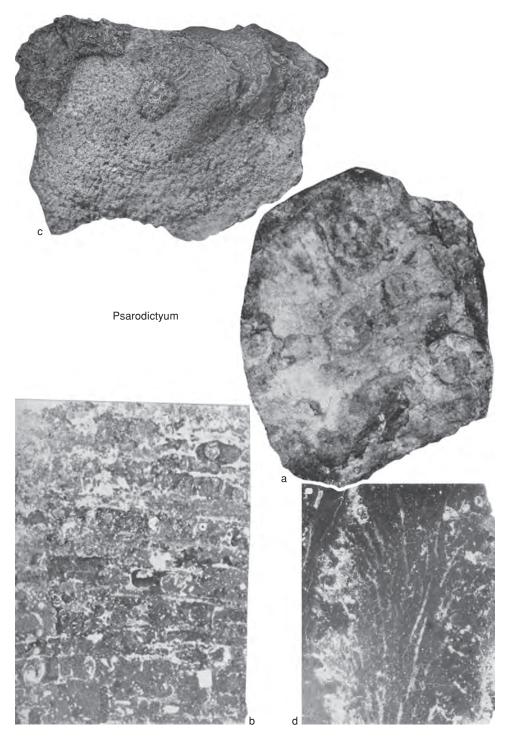


FIG. 64. Anthaspidellidae (p. 89).

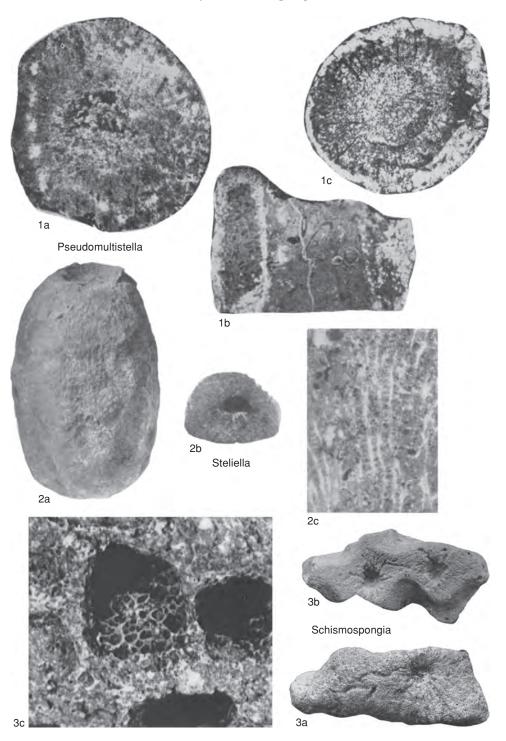


FIG. 65. Anthaspidellidae (p. 89–98).

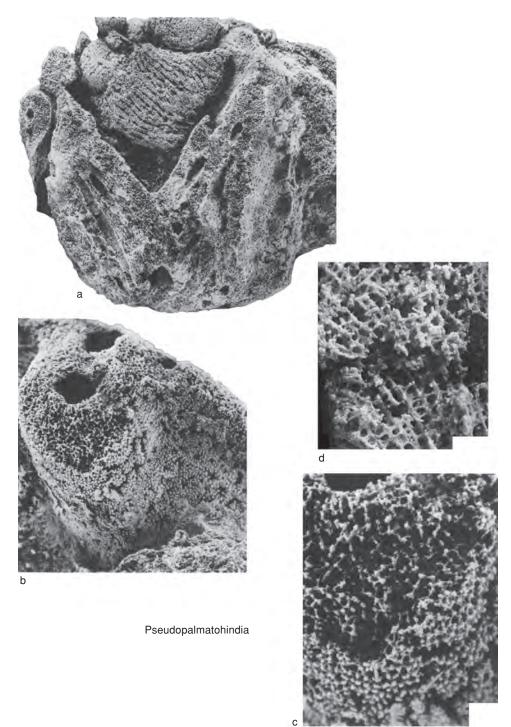


FIG. 66. Anthaspidellidae (p. 89).

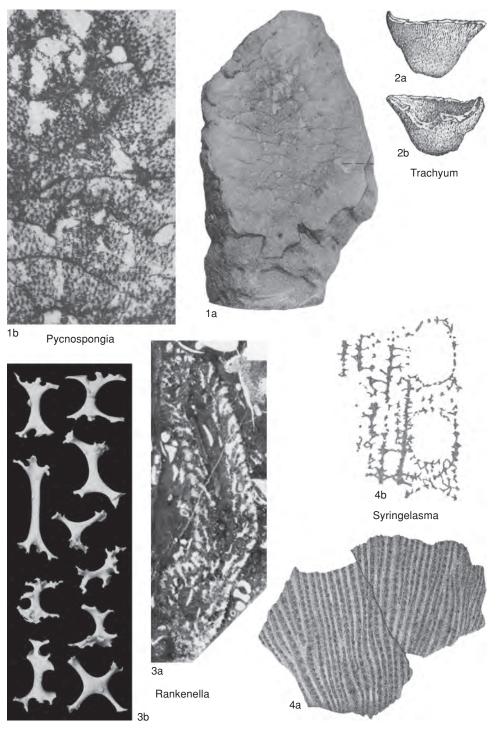


FIG. 67. Anthaspidellidae (p. 89–98).

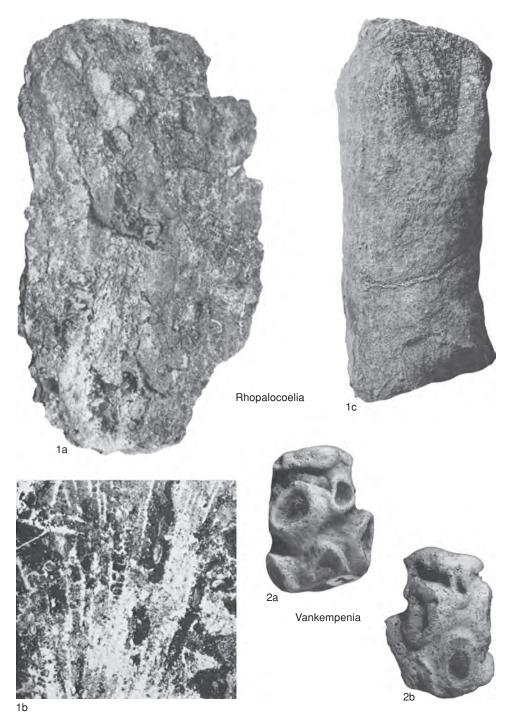


FIG. 68. Anthaspidellidae (p. 96–102).

I-shaped dendroclones; skeletal structure open and coarse; differentiated canals not developed. *Silurian (Ludlow):* Canada (Northwest Territories, Cornwallis Island).——FIG. 62,4*a*–*b.* \**R. simplex*, Cape Phillips Formation, Cornwallis Island; *a*, side view of thin-walled holotype with fine-textured, dermal surface,  $\times 1$ ; *b*, cross section of laterally flattened holotype with a central spongocoel and thin walls with coarse trabs cross connected by I-shaped dendroclones, GSC 102174,  $\times 2.5$  (de Freitas, 1991; courtesy of *Canadian Journal of Earth Sciences*).

- Rhopalocoelia RAYMOND & OKULITCH, 1940, p. 210 [\*R. clarkii; OD]. Cylindrical with deep cloaca into which radial, subhorizontal, branching, exhalant canals open; exterior with broad, irregular swellings; dendroclone rows radiating upwardly and outwardly from base, apparently perpendicular to upper surface. [Similar to the contemporaneous Exochopora and Eospongia, as well as to the earlier Nevadocoelia.] Lower Ordovician-Middle Ordovician: Argentina, China (Hubei, Xinjiang), Ibexian; USA (New York), Canada (Quebec), Middle Ordovician.—FIG. 68, 1a-c. \*R. clarkii, Chazyan; a, side view of holotype showing large, central spongocoel in cylindrical sponge, Chazy Limestone, Valcour Island, New York, MCZ 9352, ×0.66; b, longitudinal section of paratype showing upwardly divergent, rodlike trabs and cross-connecting dendroclones, Chazy Limestone, Valcour Island, New York, MCZ 9354, ×8 (Raymond & Okulitch, 1940); c, upper end of cylindrical sponge showing thin walls and large, matrix-filled spongocoel, Mingan Formation, Mingan Islands, Canada, GSC 111127, ×1 (Rigby & Desrochers, 1995).
- Rugocoelia JOHNS, 1994, p. 84 [\*R. eganensis; OD]. Lamellate to funnel-shaped with regular, concentric ribbing; radial canals straight, normal to exterior, and vertically stacked; vertical canals rare; surface of pinnation of trabs along gastral margin; ladderlike, skeletal net of small, amphiarborescent dendroclones; dermal layer well developed, particularly on rib crests; gastral layer may be present. Lower Ordovician: USA (Nevada).-FIG. 69,2ab. \*R. eganensis, Shingle Limestone, Ibexian, Egan Range; a, regularly wrinkled, dermal surface of holotype,  $\times 1$ ; b, enlargement of dermal surface showing anthaspidellid, skeletal structure and ectosomal thickening along ridge, UT 1784TX1, ×2 (Johns, 1994; courtesy of Nevada Bureau of Mines and Geology).
- Schismospongia RHEBERGEN & VON HACHT, 2000, p. 798 [\*S. syltensis; OD]. Relatively small but massive sponges with triangular to irregularly rectangular, transverse sections and one or two shallow spongocoels on upper surface; distal, exhalant canals curved, but converging toward walls of upper part of spongocoel as straight, nearly parallel, stacked canals 0.7 to 1.5 mm in diameter; inhalant canals 0.4 to 1.2 mm in diameter in outer walls, with obscure ostia in lower half of dermal surface. Spicules are dendroclones typical of fam-

ily, but not well preserved in type material. [Schismospongia was interpreted to have been a natural cleft or small, cavern dweller. Archaeoscyphia attenuata DE FREITAS, 1989 is a small, bladed form with spongocoels located on the edge of the frond. Hesperocoelia BASSLER, 1927 is also bladelike with numerous elliptical oscula on the upper edge. Known only as Plio-Pleistocene glacial erratics recovered from the Island of Sylt.] Middle Ordovician-Upper Ordovician: northwestern Germany (Island of Sylt).-FIG. 65,3a-c. \*S. syltensis, glacial erratic; a, view of holotype from above with shallow spongocoel on right and curved canals in more massive part of skeleton on left, collection U. von Hacht S3, ×1; b, view from above of paratype 2 with two small spongocoels surrounded by convergent, exhalant canals, collection U. von Hacht S1, ×1; c, dendroclone spicules exposed in section of exhalant canal in silicified paratype 4, collection U. von Hacht, S4, ×15 (Rhebergen & von Hacht, 2000).

- Somersetella RIGBY & DIXON, 1979, p. 614 [\*S. conicula RIGBY & DIXON, 1979, p. 615; OD]. High obconical to digitate, smooth-walled to weakly and irregularly annulate sponges with deep, simple spongocoel; vertically stacked, relatively small, straight, radial canals piercing walls; skeleton anthaspidellid with trabs of dendroclones that are cored by oxeas; surface of pinnation near gastral surface; coarse, vertical cluster of short, exhalant canals in base above radiante of skeleton; thin, dermal layer of irregularly oriented dendroclones, with irregular openings of ostia smaller than canals of walls. Silurian (?Wenlock, Ludlow, ?Pridoli): Canada (Northwest Territories, Baillie-Hamilton Island), ?Wenlock; Canada (Northwest Territories, Somerset Island), Ludlow, ?Pridoli. -FIG. 70,2a-b. \*S. conicula, Read Bay Formation, Ludlow, ?Pridoli, Somerset Island; a, annulate, obconical holotype, GSC 54836, ×1; b, photomicrograph of cellulose peel of paratype showing vertical trabs and cross-connecting shafts of dendroclones, GSC 54837, ×20 (Rigby & Dixon, 1979).--FIG. 70,2c. S. digitata RIGBY & DIXON, Read Bay Formation, Somerset Island, Canada; side view of digitate holotype with faint ribbing produced by stacked canals exposed where thin, dermal layer removed, GSC 54828, ×1 (Rigby & Dixon, 1979).
- Steliella HINDE, 1889a, p. 395 [\*S. billingsi HINDE, 1889a, p. 396; SD de Laubenfels, 1955, p. 61]. Club shaped with deep cloaca; principal, skeletal canals arching across from exterior to cloacal surface to form vertical rows of ostia on exterior and probably on cloacal wall, and appear as radial rows of canal intersections in horizontal, cross sections of sponge. [This is poorly known but may be a synonym of Exochopora (possibly a decorticated Upper Ordovician: specimen).] Canada —FIG. 65,2a-c. \*S. billingsi, (Ontario).-Cobourg Formation, Ottawa; a, side view of ribbed, subcylindrical holotype with rounded, oscular margin to spongocoel, GSC 982, ×1; b,

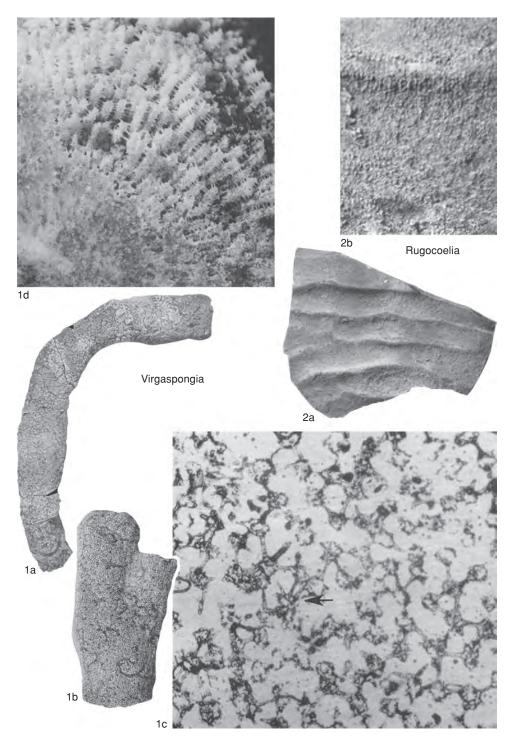


FIG. 69. Anthaspidellidae (p. 96-102).

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transverse section of cotype with central spongocoel and radial, canal pattern, GSC 982e, ×1; *c*, photomicrograph of vertical section with vertical trabs and runglike dendroclones, GSC 982d, ×8 (Wilson, 1948; courtesy of the Minister of Public Works and Government Services Canada, 2002, and Geological Survey of Canada).

- Strotospongia ULRICH & EVERETT in MILLER, 1889, p. 166 [\*S. maculosa; OD]. Externally identical to Anthaspidella, with which it is sympatric, but internal canals irregularly anastomosing and spicular arrangement obscure. [This may be an aberrant or poorly preserved Anthaspidella; MILLER (1889) used proofs of ULRICH and EVERETT (1890) and cited the genus and species as in press in his book.] Upper Ordovician: USA (Illinois).---FIG. 71,1ac. \*S. maculosa, Platteville Limestone, Chazyan, Dixon; a, side view of holotype showing funnellike form with aligned, inhalant ostia in dermal layer, ×1; b, view from above of shallow, gastral depression and several oscula surrounded by radial, exhalant canals, ×1; c, vertical section showing general skeletal and canal patterns in endosome of holotype, ISM, ×1 (Ulrich & Everett, 1890).
- Syringelasma ULRICH, 1890b, pl. 8, nom. nov. pro Syringophyllum ULRICH in MILLER, 1889, p. 166, non MILNE-EDWARDS & HAIME, 1850, p. 242 [\*Syringophyllum wortheni ULRICH, 1890b, p. 250; M]. Flabellate fronds, possibly broken portions of a saucer-shaped sponge, bearing subparallel channels radiating from base of sponge on both flat surfaces; canals perpendicular to surfaces completely penetrate sponge and open into bottoms of radial channels; dendroclone rows radiate from base of sponge and diverge toward both upper and lower surfaces as in Anthaspidella. Middle Devonian: USA (Michigan).-FIG. 67,4a-b. \*S. wortheni (ULRICH), Hamilton Group, Hamiltonian, Thunder Bay; a, surface of platelike fragment with prominent, radial series of ostia separated by ridges of trabs,  $\times 1$ ; *b*, photomicrograph of thin section showing rodlike trabs with runglike dendroclones between, large ostia are openings on right, ×18 (Ulrich, 1890b).
- Talacastonia BERESI & RIGBY, 1993, p. 56 [\*T. chela; OD]. Cylindrical to conicocylindrical sponges with coarse, dendroclone-based skeleton; coarse trabs anastomose or wander and with irregular, almost spinose-appearing surfaces; trab structure complex and cored by oxeas grasped by complex cladomes and other dendroclone, ray tips; skeleton also includes other irregular, vertical elements; canals moderately coarse and essentially horizontal through walls into spongocoel, dermal ostia in crude, vertical rows. Lower Ordovician: Argentina.----FIG. 70, 1a-c. \*T. chela, San Juan Formation, Precordillera Central; a, horizontal section through elliptical holotype with thin walls around spongocoel(s), ×1; b, side view showing relatively robust, medium-gray trabs with light gray matrix in canals in smooth walls,  $\times 1$ ; *c*, photomicrograph

of transverse section of holotype showing coarse canals separated by compound trabs cored by oxeas and cross connected by I-shaped dendroclones (d), CRICYT T-53, ×20 (Beresi & Rigby, 1993).

- Timidella DE LAUBENFELS, 1955, p. 65, nom. nov. pro Timorella GERTH, 1909, p. 695, non BERGH, 1905 [\*Timorella permica GERTH, 1909, p. 695; OD]. Spheroidal; upper part of sponge surface bearing conical protuberances and surface grooves that converge on a small, shallow depression at summit; dendroclone rows and principal canals perpendicular to surface and radiating from a point well in interior of sponge. [The genus is similar to Mastophyma.] Permian: Timor.--FIG. 72,1*a*-c. \*T. permica (GERTH), Permian limestone; a, side view of type specimen showing globose form and complex canal pattern radiating out from small, oscular depression on summit, ×0.5; b, transverse section through sponge with thin, convergent, inhalant canals and thick, irregular, exhalant canals shown in black, ×1; c, drawing of skeletal structure with vertical, coarse trabs cross connected by horizontal dendroclones, all recrystallized, ×20 (Gerth, 1909).
- Trachyum BILLINGS, 1865, p. 211 [\*T. cyathiforme; OD]. Broad, open, thin-walled cup with obtusely rounded base; closely spaced, parallel, slitlike openings running vertically up both surfaces of cup; skeleton of thin, parallel fibers radial from base, spicules not known but probably dendroclones. [This genus is known poorly, but the structure of the wall is like that of *Patellispongia.*] Lower Ordovician: Canada (Newfoundland), USA (?Alabama).——FIG. 67,2*a*-*b.* \*T. cyathiforme, Unit G, Canadian, Cape Norman, Newfoundland; side views of holotype showing broad, funnel-like form, approximately ×1 (Billings, 1865).
- Trochospongia ROEMER, 1887, p. 174 [\*T. cyathophylloides ROEMER, 1887, p. 176; OD]. Conical with concave, upper surface; fine, subparallel, radial canals converging upon axial region of upper surface from its periphery; corresponding, horizontal, radial canals in interior, axial region of sponge occupied by large, vertical canals so closely packed as to have a polygonal outline; dendroclone rows probably perpendicular to upper surface and seemingly outlining radial canals. [This may be a senior synonym of Zittelella.] ?Silurian: Germany (glacial drift).-FIG. 72,2a-c. \*T. cyathophylloides, Pleistocene glacial drift; a, side view of obconical sponge with vertically aligned, skeletal structure suggested by sections of trabs, ×1; b, view into spongocoel from above showing thick walls with radial canals between dotted rows of trabs, ×1; c, enlarged skeletal structure showing rodlike dendroclones connecting trabs that are aligned dots of transverse sections, approximately ×10 (Roemer, 1887).
- Tschernyschevostuckenbergia ZHURAVLEVA, 1962, p. 63, nom. nov. pro Stuckenbergia TSCHERNYSCHEV, 1898, p. 24, non TSERVINSKII, 1898 [\*Kazania

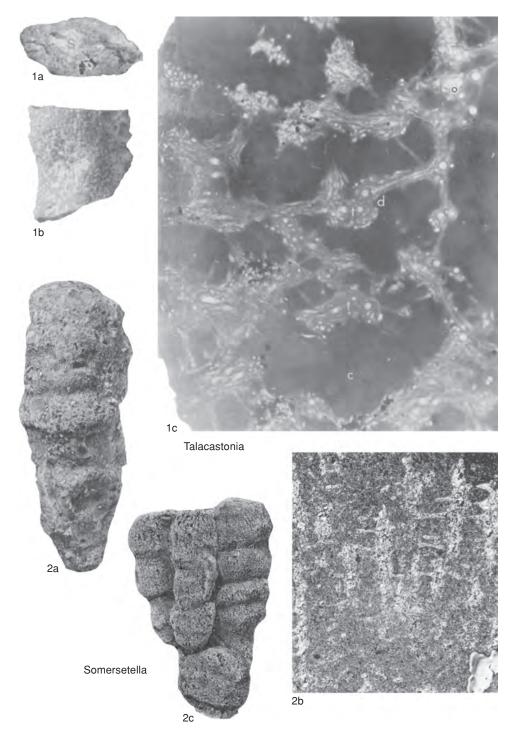


FIG. 70. Anthaspidellidae (p. 96–98).

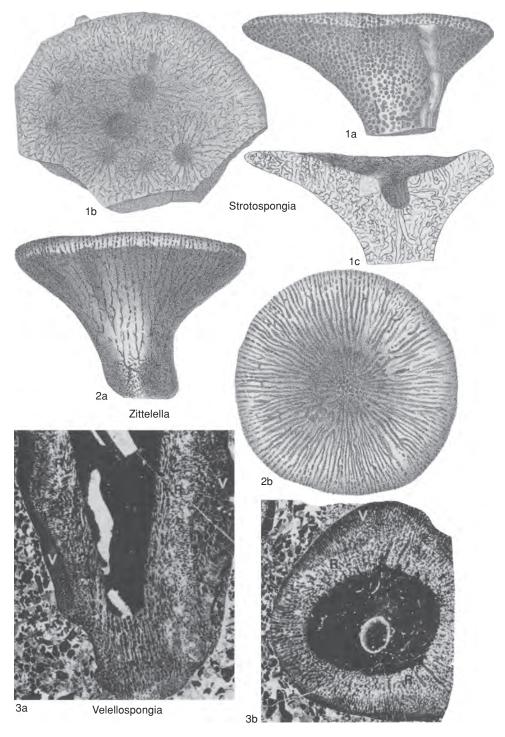


FIG. 71. Anthaspidellidae (p. 98-104).

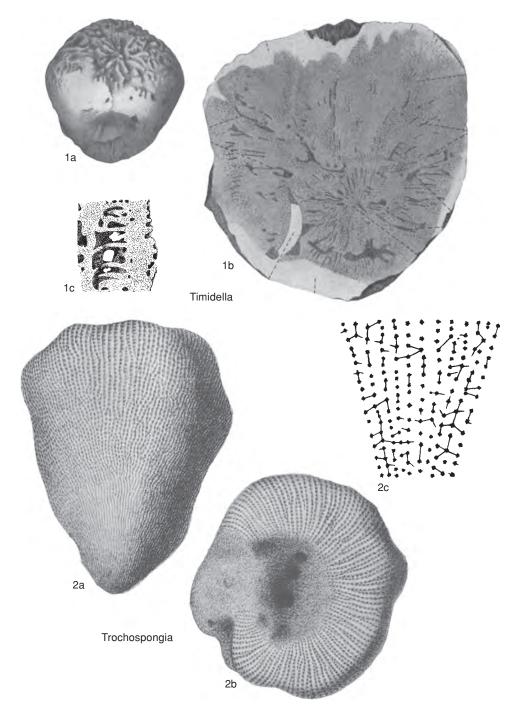


FIG. 72. Anthaspidellidae (p. 98).

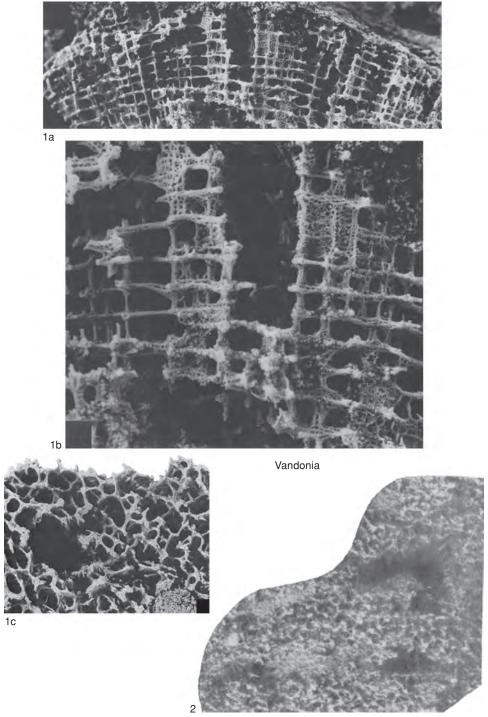
ufimiana STUCKENBERG, 1895, p. 22; OD]. Massive; dendroclone rows and principal canals perpendicular to outer surface and radiating from a point at or near base; no pore clusters or surface grooves; spicules resemble those of *Pemmatites*, but smaller. *Permian*: Russia (South Ural Mountains).—FIG. 73,2. \**T. ufimiana* (STUCKENBERG), Artinskian beds; part of exposed surface showing canals and skeletal structure, ×5 (Rezvoi, Zhuravleva, & Koltun, 1962; courtesy of Russian Academy of Science).

- Vandonia RIGBY & WEBBY, 1988, p. 59 [\*V. clathrata RIGBY & WEBBY, 1988, p. 60; OD]. Cavernous, obconical to massive, subhemispherical sponges with very regular, coarse trabs produced by unusually large dendroclones spaced uniformly to produce almost laminate, stromatoporoid-looking, regular skeleton; canal system of large, medial, excurrent, and smaller, nearly vertical canals subparallel to upwardly and outwardly radiating trabs; vertical webs of cladome origin may connect trabs but do not produce compound beams; dendroclones large for family. Upper Ordovician: Australia (New South Wales).----FIG. 73, 1a-c. \*V. clathrata, Malongulli Formation, Cliefden Caves area; a, vertical section of holotype showing regular, coarse skeleton with trabs produced by large dendroclones and finer webs, with dendroclones spaced uniformly to produce reticulate structure, large canals radiating upwardly, parallel to skeletal elements, ×4; b, photomicrograph of vertical section showing coarse dendroclones in rectangular structure and whose extended ray tips produce principal, discontinuous, webbed, vertical elements,  $\times 8$ ; c, vertical view of upper surface of holotype showing weblike, skeletal elements cross connected by coarse dendroclones, and pierced by vertical canals of several sizes, AMu. F66861, ×4 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Vankempenia VON HACHT, 1994, p. 76 [\*V. erratica; OD]. Sponge cylindrical with broad, central spongocoel and irregularly spaced, thick-walled, craterlike, lateral oscula, or tubular branched with thickened walls; moderately large, more or less horizontal and winding canals pierce principal walls; other canals parallel ladderlike trabs of skeletal system that diverge upwardly and outwardly from near gastral surface to terminate at dermal surface; trabs formed by union of dendroclone tips and cored by long monaxons; upper surfaces of some craterlike oscula may be covered with closely spaced monaxons. Ordovician: Germany and northern Europe.—FIG. 68,2a-b. \*V. erratica, Ordovician glacial erratics, Braderup, Island of Sylt, Germany; a, side view of holotype with several craterlike oscula,  $\times 1$ ; *b*, opposite side of same showing more tubular, basic form, ×1 (von Hacht, 1994; courtesy of Nederlandse Geologische Vereniging).
- Velellospongia LIU & others, 1997, p. 205 [\*V. adnata; OD]. Encrusting, sheetlike anthaspidellid, assuming general contours of substrate but with

separated, low shield, volcano-like mounds; internal, horizontal-radial, exhalant canals converging toward mounds and arching upwardly or outwardly to produce exhalant clusters with dense walls; inhalant canals also walled but perforate and downwardly divergent into lower part of skeleton, either as isolated openings or limited clusters on flanks of mounds; skeleton of I-shaped dendroclones that form trabs generally parallel to encrusting base, but may arch upwardly to meet dermal surface approximately at right angles in mounds and intervening areas; trabs apparently radiate out from mound areas into thin, sheetlike, intervening areas, where skeleton interrupted by convergent, exhalant canals. [Velellospongia is the only distinctly encrusting sponge known in the family.] Lower Ordovician: China (Hubei) .---- FIG. 71,3ab. \*V. adnata, Honghuayuan Formation, Xintan; a, oblique, longitudinal section of holotype of Velellospongia (V) overgrowing cylindrical Rhopalocoelia (R) and separated from it by an abrupt discontinuity between trab-based skeletons, with cluster of convergent, exhalant canals in mound on right, JPI XLOH-3-c, ×2; b, transverse section of holotype showing encrusting habit of genus, JPI XLOH-3-a, ×2 (Liu & others, 1997).

- Virgaspongia RIGBY & MANGER, 1994, p. 735 [\*V. ichnata RIGBY & MANGER, 1994, p. 736; OD]. Irregularly curved, subcylindrical to conicocylindrical, branched to unbranched sponges without spongocoel; skeleton typically anthaspidellid, made of dendroclones whose united ray tips form trabs that diverge upwardly and outwardly from sponge axis, with steeply ascending trabs in axial area that become horizontal in outer two-thirds of stem; most observable spicules I-shaped dendroclones, although Y-shaped dendroclones also occur; canals subparallel to trabs. Carboniferous (Lower Pennsylvanian): USA (Arkansas).--Fig. 69, 1a-d. \*V. ichnata, Bloyd Formation, Ozark Mountains; a, side view of large, cylindrical holotype with tips of outwardly divergent trabs forming minute, stippled surface, USNM 463444,  $\times 0.5$ ; b, side view of branched paratype with minute, stippled exterior produced by trab tips, USNM 4673449, ×1; c, photomicrograph of transverse section of paratype showing cross sections of cylindrical trabs (arrow) formed by union of tips of cross-connecting, rodlike dendroclones, USNM 463454, ×20; d, diagonal photomicrograph of paratype showing silicified, skeletal structure with rodlike trabs and runglike dendroclones, USNM 46342, ×5 (Rigby & Manger, 1994).
- Virgaspongiella RIGBY & BOYD, 2004, p. 72 [\* V. ramosa; OD]. Small, branching, twig-like to palmate sponges without a distinct spongocoel, although axial exhalant canals may be developed; skeleton of ladderlike elements that diverge upwardly and composed of prominent trabs cross connected by runglike, I- and X-shaped dendroclones whose branching tips unite to form trabs; trabs may be cored with one or more axial oxeas at any level and those spicules project outwardly as spines

Orchocladina



Tschernyschevostuckenbergia

FIG. 73. Anthaspidellidae (p. 98-102).

beyond trab tips on dermal surfaces. Permian (Wordian): USA (Wyoming).——FIG. 57, Ia-c. \*V. ramosa, Park City Formation, Bull Lake area, eastern Wind River Mountains; a, side view of twiglike, branching holotype, UW4022, ×2; b, side view of twiggy to palmate paratype with exhalant ostia more prominent in upper part, UW4024, ×2; c, SEM photomicrograph of holotype showing prominent, large exhalant pores and smaller inhalant pores, between I-shaped dendroclones with terminal rays combining to form subcylindrical trabs that are cored by larger monaxons (arrow), now commonly broken, UW4022, scale bar, 200 μm (Rigby & Boyd, 2004).

- Yarrowigahia RIGBY & WEBBY, 1988, p. 56 [\*Y. brassicata; OD]. Laminated, globose to massive anthaspidellid in which smooth to wrinkled laminae curve downwardly from a central core but then sweep upwardly to become subparallel, like leaves of a cabbage, in upper part; main canals concentrated in layers between laminar sets and generally parallel to trabs; trabs of long-shafted dendroclones radiate upwardly and outwardly, generally parallel to curving laminae, although skeletal structure irregular and ladderlike dendroclone series not as clearly defined as in related sponges; trabs cored by oxeas. Upper Ordovician: Australia (New South Wales).—FIG. 74*a–b.* \*Y. brassicata, Malongulli Formation, Cliefden Caves area; a, natural, vertical section through interior showing uparched laminae of central core in lower part and curved laminae in outer, lower part, that sweep up like cabbage leaves to produce upper part of sponge, where they are separated by canals; arrow indicates top of sponge to right, ×1; b, photomicrograph of prominent trabs produced by coring oxeas and fused ray tips of widely spaced, Xand Y-shaped dendroclones, AMu. F66857, ×20 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Zittelella Ulrich & Everett in Miller, 1889, p. 167 [\*Cnemidium? trentonense WORTHEN, 1875, p. 491; M]. Broadly conical to pedunculate and ficiform with broadly concave to deeply cloacate, upper surface; cluster of vertical, exhalant canals along axis; numerous, radially disposed, exhalant canals converging upon axial cluster and cloaca from periphery of sponge; upper surface marked by grooves of convergent, horizontal canals; radial incurrent-excurrent canals of interior tend to be superposed and may coalesce to form vertical, radial slits; dendroclone rows nearly vertical above surface of pinnation, which is near outer, lower margin; imperforate outer layer may be present on base. Lower Ordovician-Middle Ordovician: USA (?Texas, ?Colorado), China (Xinjiang), Ibexian; North America, Middle Ordovician.-FIG. 71,2a-b. \*Z. trentonense (WORTHEN), Platteville Limestone, Chazyan, Dixon, Illinois, USA; a, side view of funnel-shaped holotype with stalk marked by aligned, inhalant ostia,  $\times 1$ ; *b*, view from above of regular radial skeletal and canal structure, with

several vertical, exhalant canals in center, ISM, ×1 (Ulrich & Everett, 1890).

## Family STREPTOSOLENIDAE Johns, 1994

[Streptosolenidae JOHNS, 1994, p. 87]

Sponges ranging from discoidal or palmate to funnel shaped and branched; skeleton of irregularly oriented dendroclones fused at ends to form trabs that may be cored by oxeas, spicules of endosome and ectosome of comparable size; dermal and gastral layers variably developed; canal systems commonly complex and intertwining; exhalant canals may empty into spongocoel or as individual openings in clustered oscula; surface usually smooth but surficial ridges and nodes may be present. Upper Cambrian–Silurian.

- Streptosolen ULRICH & EVERETT in MILLER, 1889, p. 165 [\*S. obconicus; OD]. Broadly conical with shallowly concave upper surface; skeleton of irregularly oriented, small dendroclones that produce only short, discontinuous, and irregular trabs; axial cluster of vertical, exhalant canals joined by sinuous and branching, subhorizontal tributary canals, some of which are subradial, branched, and visible on upper surface, irregularly convergent on central cluster of exhalant openings; outer surface is covered with similar sinuous, branching canals without clear orientation. [This genus differs from Zittelella in the irregular skeleton and pattern of the canal system. MILLER (1889) used proofs of ULRICH and EVERETT (1890) and cited the genus and species as in press in his book.] Middle Ordovician-Upper Ordovician: USA (Illinois, California); northern Europe, Upper Ordovician. ——FIG. 75, 1a-c. \*S. obconicus, Platteville Limestone, Chazyan, Illinois; a, side view of steeply obconical holotype marked by irregular canals on dermal surface, ×1; b, view from above into shallow spongocoel with irregular canals around cluster of vertical, exhalant canals near center, ×1; c, vertical, medial section with central cluster of vertical, exhalant canals and other, more irregular, lateral canals, ISM, ×1 (Ulrich & Everett, 1890).
- Allosaccus RAYMOND & OKULITCH, 1940, p. 208 [\*A. prolixus RAYMOND & OKULITCH, 1940, p. 209; OD]. Discoidal to irregularly hemispherical, with convex, upper surface and concave, lower surface; lower surface covered by imperforate layer; central depression on upper surface containing openings of exhalant canals, and branching, sinuous, radial canals converging upon it across upper surface; skeleton irregular. Lower Ordovician–Middle Ordovician: Argentina (Precordillera), Lower Ordovi cian; USA (?California, Virginia, Tennessee),

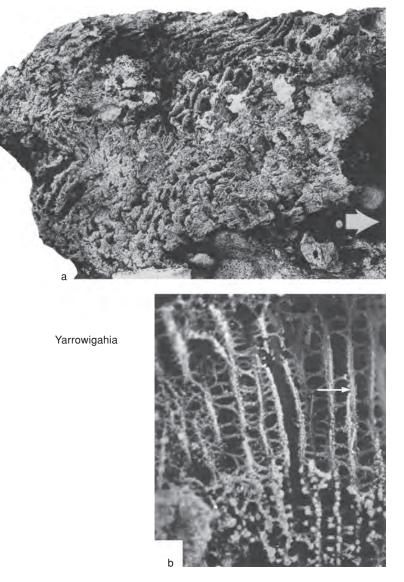


FIG. 74. Anthaspidellidae (p. 104).

Middle Ordovician.——FIG. 75,2*a*–*b*. \**A. prolixus,* Lenoir Limestone, Arenig–Llanvirn, Knoxville, Tennessee; *a*, view of holotype from above showing coarse, exhalant ostia in center and radiating canals on surface, MCZ 9351, ×1; *b,* paratype from above with convergent canals to shallow, exhalant depression, MCZ 9352, ×1 (Raymond & Okulitch, 1940).

Antrospongia RIGBY & CHATTERTON, 1989, p. 15 [\**A. aberrans* RIGBY & CHATTERTON, 1989, p. 16; OD]. Thin-walled, obconical with deep, simple spongocoel, gastral surface with large, conical pits into which exhalant canals empty; inhalant system with large, conical openings bridged with irregular screen in dermal area; skeleton in midwall with moderately well-oriented trabs, but outer and inner part of wall irregular; trabs commonly connected by clusters of subparallel dendroclones that produce irregular dermal and gastral layers. *Silurian (Ludlow):* Canada (Northwest Territories, Baillie-Hamilton Island).—FIG. 76, *1a–c. \*A. aberrans*, Cape Phillips Formation, Baillie-

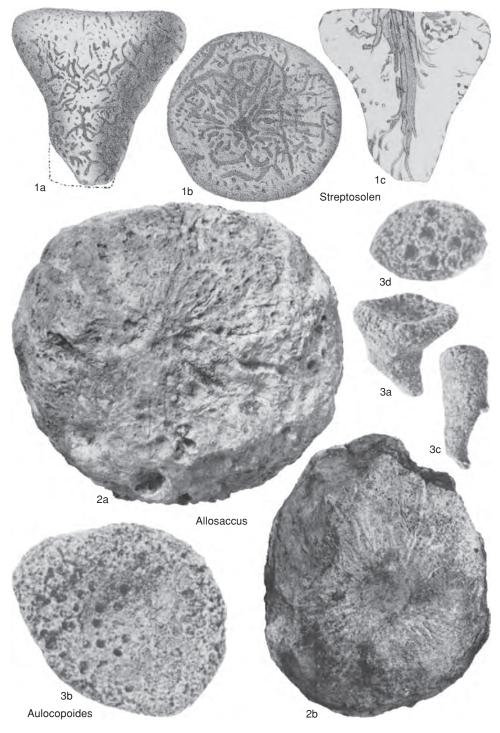


FIG. 75. Streptosolenidae (p. 104–108).

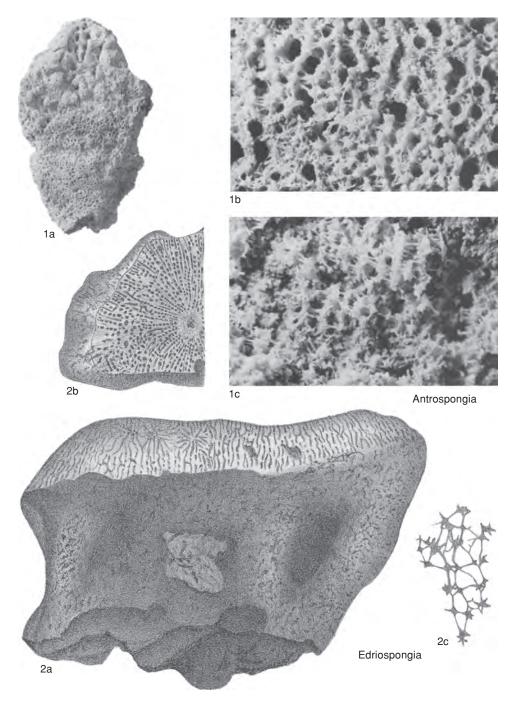


FIG. 76. Streptosolenidae (p. 105–108).

Hamilton Island; *a*, side view of flattened, thinwalled holotype showing dense, dermal layer in lower part and into gastral surface of spongocoel, with coarse, exhalant ostia in crude, vertical rows in upper part,  $\times 1$ ; *b*, photomicrograph of part of irregular dermal net,  $\times 10$ ; *c*, photomicrograph of natural cross section through middle part of wall showing regular, short trabs cross connected with other trabs and dendroclones, UA 7703,  $\times 10$ (Rigby & Chatterton, 1989; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

- Aulocopella RAUFF, 1895, p. 268 [\*A. winnipegensis RAUFF, 1895, p. 269; OD]. Depressed spheroidal, radially lobate, with deep, central cloaca; principal canals strongly arched parallel to upper and outer surface, in stacked series, opening into cloaca; dendroclone rows perpendicular to outer surface and radiating from a point within basal part of sponge, beneath cloaca. Ordovician: North America, Europe.-FIG. 77, 1a-c. \*A. winnipegensis, Red River Formation, Cat Head Member, Caradoc-Ashgill, Lake Winnipeg, Manitoba, Canada; a, holotype from above showing central, matrix-filled spongocoel and radiating, gearlike fins with prominent, exhalant canals, GSC 6863, ×0.6 (Rauff, 1895); b, nearly complete specimen of species from above showing bladed form and open spongocoel with aligned, exhalant ostia in gastral surface,  $\times 0.67$ ; *c*, side view of upper, lateral slope of fin with aligned, outwardly divergent trabs interrupted by upwardly and inwardly arched, exhalant canals, MMMN I-7986, ×0.67 (Rigby & Leith, 1989).
- Aulocopium Oswald, 1847, p. 58 [\*A. aurantium Oswald, 1850, p. 83; SD RAUFF, 1895, p. 257]. Pyriform; base conical and covered by concentrically wrinkled, imperforate layer; central cloaca present and of variable depth; principal canals entering cloaca vertically from below and horizontally from sides, latter being parallel to upper and outer surfaces of sponge; dendroclone rows perpendicular to upper and outer surfaces. [Genus is similar to Eospongia.] Ordovician-Silurian: world--FIG. 78, 1a-c. \*A. aurantium Oswald; a, wide.side view of typical specimen with wrinkled, dermal layer below and canalled, upper part around spongocoel, Silurian strata, near Berlin, Germany, Berlin Museum, ×1; b, vertical, median section with deep spongocoel and upwardly converging, exhalant canals with ostia in gastral surface, crossed by upwardly diverging, skeletal tracts and downwardly converging, smaller, exhalant, skeletal tracts, Silurian strata, Gaarden by Kiel, Germany, Kiel Museum, ×2; c, silicified sponge, photomicrograph of skeletal structure of small, typical specimen with tips of runglike dendroclones forming trabs, Silurian, Gotland, Bonner Museum, ×35 (Rauff, 1895).
- Aulocopoides HOWELL, 1952, p. 2 [\*A. patulum; OD]. Funnel-like to conicocylindrical, unbranched with or without spongocoel into which

empty several large, widely spaced, vertical, cylindrical, excurrent canals but with convergent lower parts; numerous inhalant canals approximately radial and at right angles to dermal surface; skeleton irregular with moderately regular trabs approximately parallel to dermal surface in upper, funnel-like part but irregular below; surface of pinnation near dermal margin. Devonian (Famennian): Australia (Western Australia).-FIG. 75, 3a-b. \*A. patulum, Virgin Hills Formation, Mount Pierre; a, side view of funnel-shaped sponge with shallow spongocoel and minor, exhalant ostia, ×1; b, view from above with minor, exhalant ostia in saucer-shaped spongocoel, PU 57875, ×2 (Rigby, 1986b).——FIG. 75,3c-d. A. teicherti HOWELL, Virgin Hills Formation, Mount Pierre, Western Australia; c, side view showing steeply obconical form of small sponge,  $\times 1$ ; d, view from above of rounded summit with separated, exhalant ostia, PU 57877, ×2 (Rigby, 1986b).

- Dendroclonella RAUFF, 1895, p. 252 [\*D. rugosa; OD]. Cushion-shaped or low, biconical sponge without cloaca or dermal layer; principal canals and dendroclone rows perpendicular to surface. Silurian (Wenlock-Ludlow): USA (Tennessee).— FIG. 79,2a-c. \*D. rugosa, Brownsport Formation, Perry County; a side view of holotype with wrinkled exterior without coarse ostia or canals, ×1; b, vertical section of holotype showing upwardly diverging trabs of skeletal structure and absence of coarse, internal canals, Munich Museum, ×1; c, photomicrograph of coarse trabs and dendroclones in silicified holotype, ×25 (Rauff, 1895).
- Edriospongia ULRICH & EVERETT in MILLER, 1889, p. 159 [\**E. basalis;* OD]. Massive, irregular; skeletal canals partly radial, following dendroclone rows, partly irregular; poorly known and probably an aberrant *Anthaspidella* or *Streptosolen*. *Middle Ordovician–Upper Ordovician:* USA (Illinois).— FIG. 76,2*a–c.* \**E. basalis,* Platteville Limestone, Chazyan, Dixon; *a*, side view of irregularly massive, columnar-appearing holotype, below overgrowing *Anthaspidella*, ×1; *b*, polished surface through smaller specimen showing its radial skeleton made of thin dendroclones that unite to form coarser, rodlike trabs, ×18 (Ulrich & Everett, 1890).
- Eospongia BILLINGS, 1861, p. 18 [\**E. roemeri* BILL-INGS, 1861, p. 19; SD S. A. MILLER, 1889, p. 159]. Pear- or club-shaped sponge; upper surface convex with central depression about one-third diameter of sponge into which vertical, exhalant canals open; inhalant canals regular to irregular for family, connecting to axial, exhalant cluster or emptying horizontally into cloaca; *E. varians*, second of two original species, broadly conical with sinuous, branching, horizontal, exhalant canals convergent upon central depression. [Differs from *Exochopora*, if at all, in the absence of a deep cloaca, it being

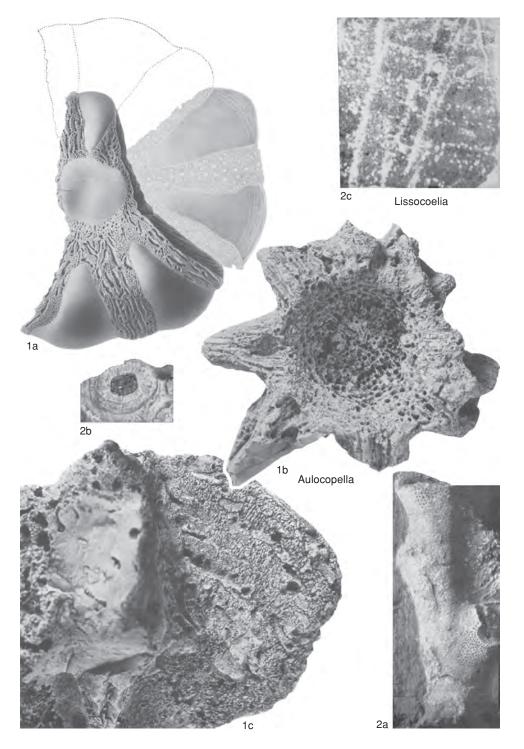


FIG. 77. Streptosolenidae (p. 108–112).

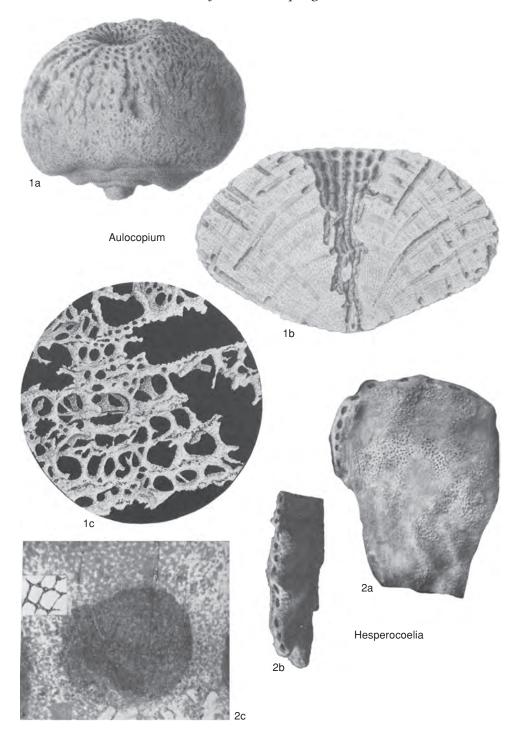


FIG. 78. Streptosolenidae (p. 108–112).

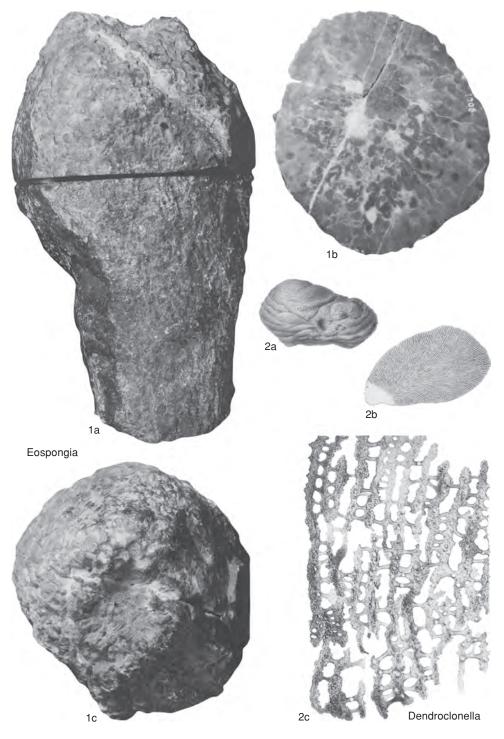


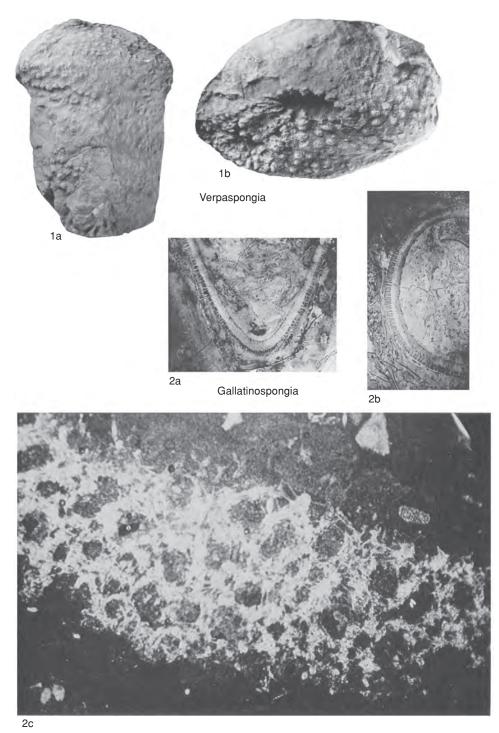
FIG. 79. Streptosolenidae (p. 108–112).

replaced by closely packed, vertical canals in the lower part of the sponge, and in absence of vertical superposition of radial canals.] Lower Ordovician-Middle Ordovician: Argentina, Lower Ordovician; North America, northern Europe, Middle Ordovician.— -FIG. 79, 1a-c. \*E. roemeri, Mingan Formation, Chazyan, Mingan Islands, Canada; a, side view of steeply obconical to clubshaped holotype in which canals show as dark, matrix fillings on side and rounded summit,  $\times 1$ ; *b*, polished, transverse section showing coarsely tubular, vertical, exhalant canals as dark matrix fills that interrupt medium gray skeletal net in calcareous replacement,  $\times 1$ ; *c*, view of rounded summit with irregular, central depression surrounded by coarse ostia of vertical, exhalant canals, GSC 11008a, b, ×1 (Rigby & Desrochers, 1995).

- Gallatinospongia OKULITCH & BELL, 1955, p. 460 [\*G. conica OKULITCH & BELL, 1955, p. 461; OD]. Broad, thin-walled, open cone or cup; outer half of body wall filled with closely packed, radial canals perpendicular to outer surface, inner half of wall packed with canals of similar size that appear to bend upwardly and inwardly to cloacal surface; spicules poorly preserved but appear to be dendroclones organized into ladderlike rows that form walls of skeletal canals. [Genus is similar to Trachyum in gross morphology; it resembles both Trachyum and Archaeoscyphia in the thinness of the wall and in the fineness and subparallel nature of the canals but without the vertical slitlike coalescence of canals. Orlinocyathus KRASNOPEEVA in VOLOGDIN, 1962, p. 126, may be a poorly known synonym.] Upper Cambrian: USA (Wyoming, ?California).-FIG. 80,2a-c. \*G. conica, Gallatin Formation, Franconian, Wind River Mountains, Wyoming; a, longitudinal, polished section of holotype showing obconical form and canals and structure of thin walls,  $\times 1$ ; b, polished transverse section of holotype with large spongocoel and thin walls with radial canals in outer part,  $\times 1$ ; c, photomicrograph of inner part of wall of holotype with coarse, rodlike trabs connected by thin, runglike dendroclones, UBC C108, ×18 (Okulitch & Bell, 1955).
- Hesperocoelia BASSLER, 1927, p. 393 [\*H. typicalis; OD]. Flabellate to frondose; both sides bearing numerous small pores; larger, presumably exhalant, medial, longitudinal canals parallel flat sides open on upper edge in row of elliptical oscula. Middle Ordovician: USA (Nevada, California).
  ——FIG. 78,2a-c. \*H. typicalis, Antelope Valley Limestone, Whiterockian, Ikes Canyon, Toquima Range, Nevada; a, bladelike holotype with ostia of several coarse, exhalant, longitudinal canals visible along margin, ×1; b, view down on upper end of thin sponge showing exhalant costia, ×1; c, transverse section through exhalant canal and associated skeletal net (enlarged to ×30 in small sketch), ×9 (Bassler, 1941).
- Hudsonospongia RAYMOND & OKULITCH, 1940, p. 203 [\*H. cyclostoma RAYMOND & OKULITCH, 1940,

p. 204; OD]. Pyriform to broadly obconical, and unbranched; upper surface with a central, cloacal depression of varying depth and common, axial cluster of vertical, exhalant canals toward which converge other exhalant canals from outer part of sponge in radial structure, although regular radial partitions of Zittelella are absent; less common upwardly and outwardly divergent canals are parallel to divergent trabs of anthaspidellid skeleton in which I-shaped dendroclones are dominant. Lower Ordovician-Upper Ordovician: Argentina, China (Xinjiang), Lower Ordovician; North America, Middle Ordovician; Australia, northern Europe, USA (Tennessee, ?Utah), Upper Ordovician.--FIG. 81a-b. \*H. cyclostoma, Lenoir Limestone, Caradoc, Knoxville, Tennessee, USA; a, side view of steeply obconical holotype with microsculpture of vertical tracts of trabs separated by vertical stacks of inhalant ostia, MCZ 9339, ×1; b, transverse section showing radial canals and dendroclone-based skeleton in thick walls around central spongocoel, ×5 (Raymond & Okulitch, 1940; courtesy of Harvard University and Museum of Comparative Zoology) .---- FIG. 81c. H. minganensis RAYMOND & OKULITCH, Mingan Formation, Chazyan, Mingan Islands, Canada; side view of obconical sponge with thick walls, marked by irregular canals and shallow spongocoel, GSC 11148, ×1 (Rigby & Desrochers, 1995).—FIG. 81d. H. irregularis RAYMOND & OKULITCH, Mingan Formation, Chazyan, Mingan Islands, Canada; vertical view of lobate reference specimen with small, shallow spongocoel and numerous radial canals on oscular margins, GSC 11117, ×1 (Rigby & Desrochers, 1995).

- Lissocoelia BASSLER, 1927, p. 392 [\*L. ramosa; OD] [?=Ozarkocoelia CULLISON, 1944, p. 47 (type, O. irregularis, OD)]. Cylindrical and branching, central cloaca extending full length of branches; outer surface smooth or with low, transverse elevations; major skeletal pores and associated radial canals relatively small, skeleton of irregularly arranged dendroclones. Lower Ordovician-Middle Ordovician: North America, Argentina, Netherlands (from glacial drift, presumably derived from the Baltic region).-FIG. 77, 2a-c. \*L. ramosa, Antelope Valley Limestone, Whiterockian, Ikes Canyon, Toquima Range, Nevada, USA; a, side view of branched holotype with some small, inhalant ostia emphasized to show their distribution,  $\times 1$ ; *b*, view of upper, fractured end showing radial canals and skeletal structure in thin walls around central spongocoel, USNM 79636, ×1; c, photomicrograph of vertical section showing diverging, rodlike trabs cross connected by runglike dendroclones, ×20 (Bassler, 1941).
- ?Orlinocyathus KRASNOPEEVA in VOLOGDIN, 1962, p. 131 (KRASNOPEEVA in VOLOGDIN, 1956, p. 878, nom. nud.) [\*O. olgae; OD]. Thin-walled, steeply obconical, small form with broad spongocoel; skeletal elements rodlike bundles of fibers that are approximately 0.05 mm thick, bundles rising





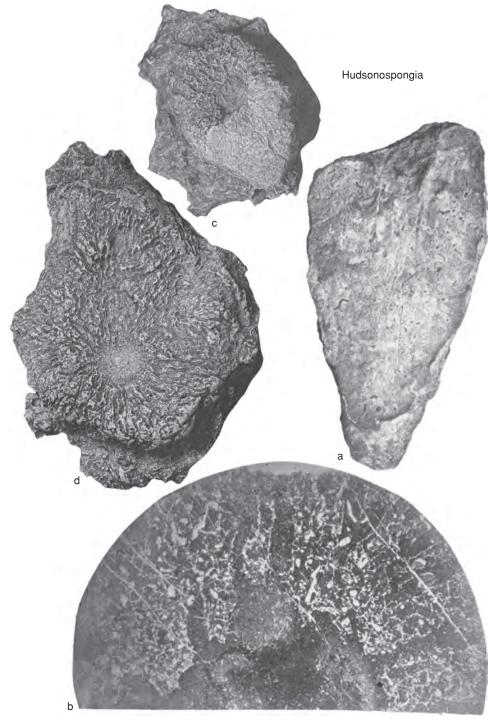


FIG. 81. Streptosolenidae (p. 112).

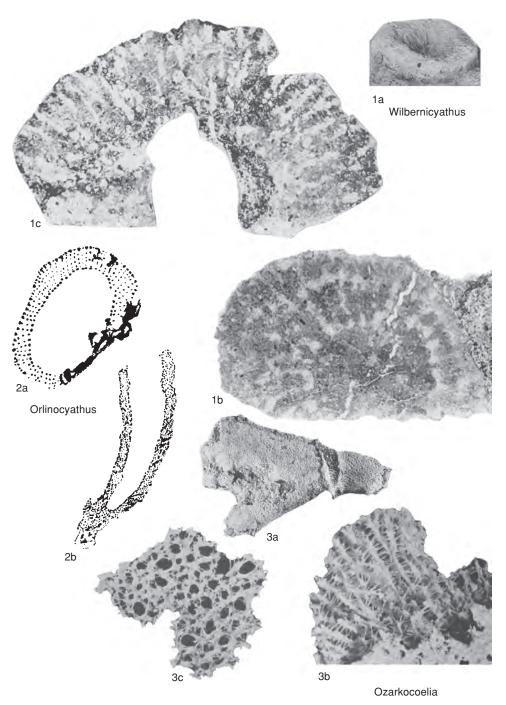


FIG. 82. Streptosolenidae (p. 112–118).

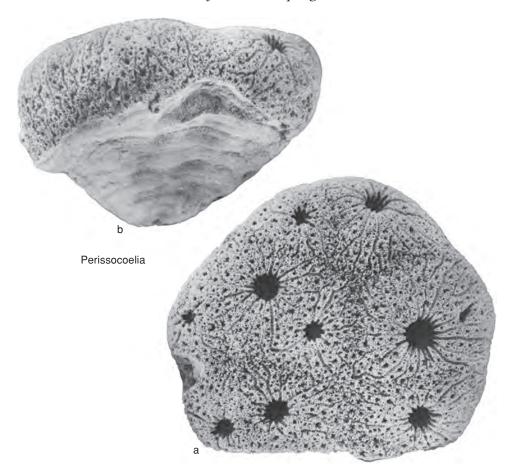


FIG. 83. Streptosolenidae (p. 116-117).

steeply in gastral part of wall and curving outwardly to become radial in dermal part of wall; walls apparently include large, reticulate pores or canals. [Classification of the genus and inclusion in the family are questionable because the skeleteal structure of the type species is uncertain, although HILL (1972, p. 142) considered it to be a probable sponge of the Archaeoscyphidae RAUFF. The genus may be a junior synonym of Gallatinospongia OKULITCH & BELL, 1955.] Upper Cambrian: Russia (Siberia, Salair).-----FIG. 82,2a-b. \*O. olgae, Orlinaya Gora horizon, Salair, Siberia; a, longitudinal section showing thin walls and broad spongocoel, approximately  $\times 2$ ; b, transverse section showing radial structure of pores or canals in thin wall, ×5 (Vologdin, 1962).

?Ozarkocoelia CULLISON, 1944, p. 47 [\*O. irregularis; OD]. Differs from typical Lissocoelia in nondichotomous branching, in presence of small, irregularly shaped, transverse prominences on outer surface, in somewhat larger, less uniform, and less regularly distributed, skeletal pores on exterior, and in a strongly divergent, skeletal structure more regular than in smaller, related *Lissocoelia*. [These differences are questionably of generic rank.] *Lower Ordovician*: USA (Missouri, Texas, ?Colorado).——FIG. 82, 3a-c. \*O. *irregularis*, Rich Fountain Formation, Phelps County, Missouri; *a*, side view of branched holotype with fine-textured, dermal layer, ×1; *b*, radiate trabs and cross-connecting dendroclones, lower right of holotype, ×10; *c*, photomicrograph of outer wall of fragment from holotype, rodlike trabs connected by thin, I-shaped dendroclones, YPM 17136, ×10 (Cullison, 1944).

Perissocoelia RIGBY & WEBBY, 1988, p. 32 [\**P. habra;* OD]. Stalked to irregularly massive with numerous conical, oscular depressions on convex crest, with associated, convergent, astrorhiza-like canals on upper surface and as stacked, arcuate canals in interior, canals rising upwardly and inwardly in lower part of sponge; base of each oscular pit with

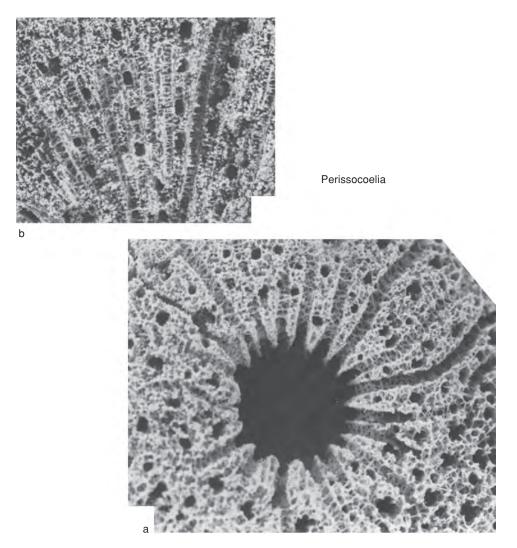


FIG. 84. Streptosolenidae (p. 116-117).

cluster of excurrent canals; discontinuous trabs radiating upwardly from near base, spicules mainly dendroclones but small rhizoclones may occur irregularly throughout; dense, basal, dermal layer. Upper Ordovician-Silurian (Wenlock-Ludlow): Australia (New South Wales), northern Europe, Upper Ordovician; Canada (Northwest Territories, Baillie-Hamilton and Cornwallis Islands), Wenlock-Ludlow.-FIG. 83a-b. \*P. habra, Malongulli Formation, Caradoc-Ashgill, Belubula River area, New South Wales, Australia; a, summit of hemispherical holotype with numerous deep, oscular depressions surrounded by convergent, subtangential, radial canals, smaller oscula are subvertical, inhalant canals that are parallel trabs of skeleton,  $\times 2$ ; b, side view of holotype with dense, dermal layer in lower part, ×2 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca). FIG. 84a-b. \*P. habra, Malongulli Formation, Caradoc-Ashgill, Belubula River area, New South Wales, Australia; a, photomicrograph of deep, oscular depression with almost septate-appearing margin, and surrounding convergent, tangential, exhalant canals, dendroclones of skeletal net show in some of canals and intervening skeletal tracts, which are also perforated by small, inhalant canals, ×8; b, photomicrograph of endosomal skeleton showing prominent, rodlike trabs and runglike dendroclones with long, smooth shafts, AMu F66808, ×6 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

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- Verpaspongia JOHNS, 1994, p. 110 [\* V. nodosa; OD]. Cylindrical with nodose exterior, vertical, excurrent canals emptying into shallow spongocoel, radial canals absent but large, concentric canals irregularly present throughout; skeletal net complex with polyclonid spicules, net becoming more dense toward dermal surface. Middle Ordovician: USA (Nevada).——FIG. 80,1a-b. \* V. nodosa, Antelope Valley Limestone, Ikes Canyon, Toquima Range, holotype; a, side view showing subcylindrical form and nodose, dermal layer, ×1; b, summit with small spongocoel and nodes on oscular margins, UT 1767TX7, ×2 (Johns, 1994; courtesy of Nevada Bureau of Mines and Geology).
- Wilbernicyathus WILSON, 1950, p. 591 [\*W. donegani; OD]. Possibly an open cup, small, perhaps with a concave base, wall may or may not be relatively thick (originally described as a volcanolike mound but may have been upside down), and seeming thickness of wall may have resulted from curvature of wall across plane of section); possible rows of dendroclones radial with respect to axis of sponge. [Poorly known, but may be related to Gallatinospongia and Trachyum.] Upper Cambrian: USA (Texas). — FIG. 82, 1a-c. \*W. donegoni, Wilberns Formation, McCulloch County; a, side view of plaster cast of holotype,  $\times 2$ ; *b*, transverse thin section of holotype with prominent, radiating trabs cross connected by runglike dendroclones, CW-350, ×10; c, thin section of reference specimen showing radiating trabs connected by dendroclones, CW-351, ×5 (Wilson, 1950).

## Family CHIASTOCLONELLIDAE Rauff, 1895

[Chiastoclonellidae RAUFF, 1895, p. 243]

Principal spicules chiastoclones; major skeletal canals radial; sponge massive; attached to substrate basally by overgrowth; imperforate, concentrically wrinkled, basal layer often present. *Silurian (Wenlock)– Permian (Changhsingian).* 

Chiastoclonella RAUFF, 1894, pl. 17 [\*C. headi; OD; RAUFF, 1895, p. 244] [=Anomoclonella RAUFF, 1895, p. 226 (type, A. zittelli, SD DE LAUBENFELS, 1955, p. 64); Pycnopegma RAUFF, 1895, p. 232 (type, P. pileum RAUFF, 1895, p. 233, SD DE LAUBENFELS, 1955, p. 64)]. Spheroidal to fungiform, with convex, upper surface overhanging lower; surface relatively smooth, without cloaca, exhalant grooves, or notably differentiated exhalant openings; skeletal canals and obscure spicule rows radiating from a point within base of sponge and perpendicular to sponge surface; spicules chiastoclones, often quite irregular, with a minority of dendroclones. [May be related to Dendroclonella RAUFF. Type species is figured in RAUFF, 1894, but described and figured in RAUFF, 1895.] Upper Ordovician–Silurian (Ludlow): Germany (Island of Sylt, and elsewhere in northern Europe as glacial drift, presumably from the Baltic region), Upper Ordovician; USA (Tennessee), Wenlock–Ludlow.—FIG. 85,1*a–c.* \*C. headi, Brownsport Limestone, middle Silurian, Decatur County, Tennessee; *a*, side view of characteristic specimen with wrinkled exterior, ×1; *b*, median, vertical section of smaller sponge showing radiate architecture of canals and skeleton, ×1; *c*, drawing of chiastoclones and their relationships, ×100 (Rauff, 1895).

- Actinocoelia FINKS, 1960, p. 70 [\*A. maeandrina; OD]. Spheroidal to flabellate or cylindroidal; large, radial canals and deep, anastomosing clefts perpendicular to surface penetrating sponge interior and reducing skeleton to narrow trabeculae between radial spaces; spicules are dendroclones to chiastoclones without clear orientation; radially oriented, smooth monaxons also present in one species. [Appears to be more closely related to Defordia than to other genera.] Permian (Artinskian-Changhsingian): USA (western states), Artinskian-Capitanian; China (Guangxi), Changhsingian.—FIG. 85,2a-e. \*A. maeandrina, San Andreas Formation, Leonardian-Guadalupian, Guadalupe Mountains, New Mexico; a, side view of holotype with coarse, skeletal tracts or trabeculae separated by coarse, divergent, anastomosing canals and less obvious, concentric, cross-connecting canals, ×1; b-d, outline drawings of spicules from holotype, USNM 127611, ×40; e, side view of smaller, cylindrical paratype showing outer terminations of both skeletal trabeculae and intervening canals, PU 78882, ×1 (Finks, 1960; courtesy of The American Museum of Natural History).
- Allassospongia RIGBY, 1986b, p. 26 [\*A. polystromne RIGBY, 1986b, p. 27; OD]. Small, cylindrical sponges without spongocoel, but with generally axial cluster of discontinuous to continuous, excurrent canals; skeletal net of alternating, dense layers of individually thickened spicules and open layers of thin spicules; dominant spicules chiastoclones with less common dendroclones and rhizoclones; skeleton not strongly organized and without distinct linear or radiating patterns; dermal layer as dense layers of interior, where elements of individual spicules two or three times diameter of those on smaller, interior spicules. Devonian (Frasnian): Australia (Western Australia, Canning basin).----FIG. 86,1a-f. \*A. polystromne, Sadler Limestone, Sadler Ridge, Western Australia; a, side view of cylindrical holotype with layers of alternating density of spiculation,  $\times 2$ ; *b*, holotype from above with layered skeleton and small, exhalant canals in lower left; ×2; c-f, camera lucida drawings of isolated spicules from holotype including robust oxea, knobby strongyle, and more common chiastoclones with smooth shafts and branched terminations, GSWA F7197, ×50 (Rigby, 1986b).

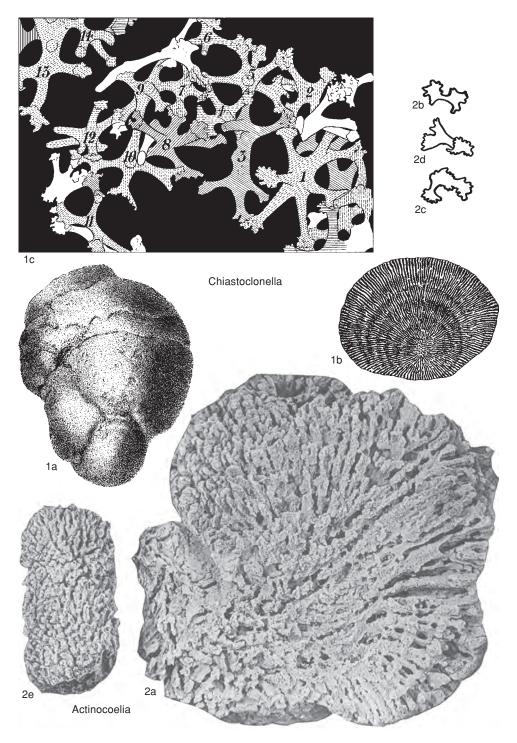


FIG. 85. Chiastoclonellidae (p. 118).

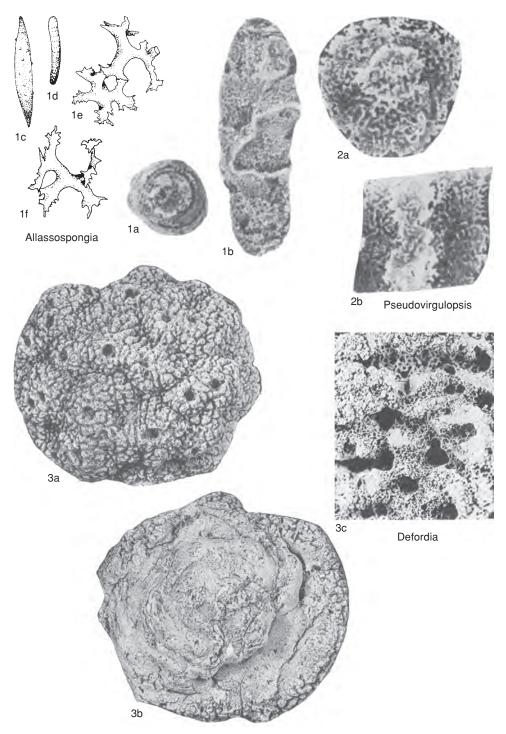


FIG. 86. Chiastoclonellidae (p. 118-123).

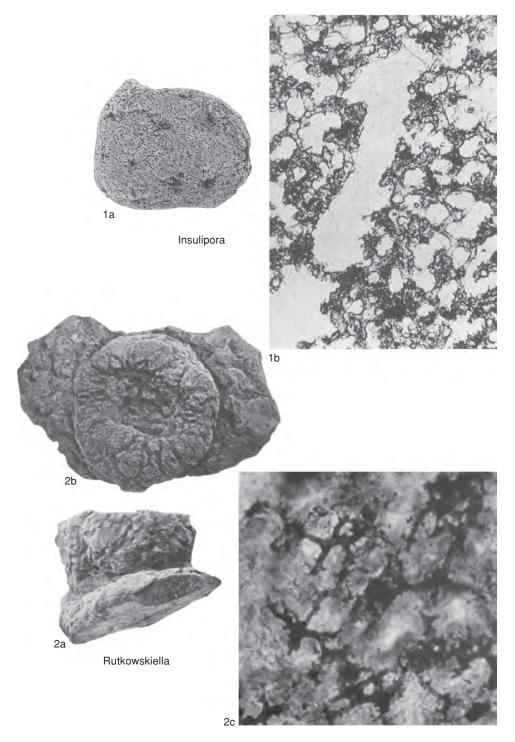


FIG. 87. Chiastoclonellidae (p. 122–124).



FIG. 88. Chiastoclonellidae (p. 124).

Defordia KING, 1943, p. 16 [\*D. defuncta KING, 1943, p. 17; OD]. Massive, spheroidal to lobate or fungiform, with convex, upper surface overhanging concentrically wrinkled, imperforate, basal surface; upper surface bearing large oscules and evenly spaced, smaller ostia, with anastomosing, sometimes deep grooves that connect ostia and concentric; spicules ranging from dendroclones to chiastoclones and are not clearly organized into rows. Permian (?Asselian-?Sakmarian, Artinskian): USA (Texas).—FIG. 86,3a-c. \*D. defuncta, Leonard and Hess Formation, Leonardian, Glass Mountains; a, top of topotype specimen with oscula on summits of mammilose nodes and with

smaller ostia in deep grooves between, USNM 127604h,  $\times 1$ , *b*, base of same sponge with wrinkled, imperforate, basal, dermal layer,  $\times 1$ ; *c*, enlarged, upper surface of topotype showing coarse, anastomosing tracts of chiastoclones and dendroclones, USNM 127604f,  $\times 5$  (Finks, 1960; courtesy of The American Museum of Natural History).

**Insulipora** FINKS, 1960, p. 64 [\**I. elegans;* OD]. Spheroidal with convex, upper surface overhanging lower; upper surface bearing depressed oscules, evenly spaced, smaller ostia, and meandriform, anastomosing grooves that surround and isolate ostia; principal canals and obscure rows of chiastoclones perpendicular to surface. [Related to

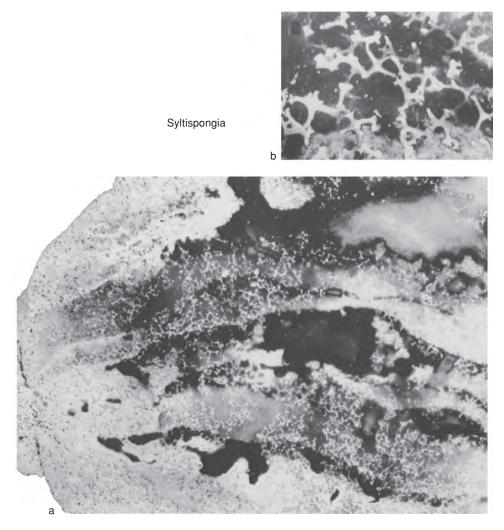


FIG. 89. Chiastoclonellidae (p. 124).

Defordia.] Permian (Artinskian): USA (Texas). ——FIG. 87, *1a–b.* \* *I. elegans*, Leonard Formation, Glass Mountains; *a*, top view of holotype showing distribution of oscula, radial canals, pores, and surface grooves, USNM 127601, ×1; *b*, photomicrograph of paratype showing skeletal net composed of chiastoclones, USNM 127602a, ×50 (Finks, 1960; courtesy of The American Museum of Natural History).

Pseudovirgulopsis DENG, 1981, p. 423 [426] [\*P. solus; OD]. Sponge branching subcylindrical with skeleton of upwardly diverging, thick tracts cross connected by transverse tracts of possible chiastoclones; canal system well defined with ascending canals commonly connected by transverse ones; skeleton of axial region more dense than in peripheral regions. Permian (Changhsingian): China.—FiG. 86,2a-b. \*P. solus, Heshan Forma-

tion, Guangxi; *a*, vertical, axial section of cylindrical holotype showing dense, axial part of skeleton, upwardly arched, skeletal tracts and small, inhalant ostia in dermal area, NIGPAS 59969,  $\times$ 4; *b*, transverse sections showing differentiated, skeletal structure of axial and lateral regions, both with radially arranged, small canals, NIGPAS 59970,  $\times$ 4 (Deng, 1981).

Rutkowskiella RIGBY, 1977d, p. 1,215 [\**R. tumula* RIGBY, 1977d, p. 1,217; OD]. Low, conical to subcylindrical with shallow, broad spongocoel and smooth, dimpled or low-nodose exterior; intermediate-sized, radial canals subhorizontal, particularly in outer third of sponge, and connecting to larger, subvertical, excurrent canals in central part; skeleton of irregularly oriented chiastoclones, with minor rhizoclones and tetraclones; architecture only indistinctly radiating. *Devonian (Givetian):*  USA (Michigan).—FIG. 87,2*a*-*c*. \**R. tumula*, Alpena Limestone, Alpena County; *a*, side view of holotype overgrowing tabulate coral fragment; *b*, view down into spongocoel showing large, radial canals in upper, sponge walls, ×1; *c*, photomicrograph showing irregular chiastoclones of skeletal net as limonite-stained ghosts of massive chalcedony, BYU 1480, ×50 (Rigby, 1977d).

Syltispongia VAN KEMPEN, 1990, p. 155 [\*S. ingemariae; OD]. Massive, hemispherical sponges with flattened, subcylindrical base; smooth, outer surface with a layered appearance produced by irregular layering of skeleton internally; spongocoel absent but with concentration of oscula on summit; principal canals in interior loosely organized into discontinuous, irregularly ascending canals and concentric canals; skeleton of irregularly oriented chiastoclones that in some places have a linear tendency that produces simple, discontinuous, upwardly flaring strands; monaxons occurring as minor component and form cores of sections of more complex strands; sponge without differentiated dermal layer. [The unique layering of internal skeleton and development of anthaspidellid-like, skeletal strands cored by monaxons distinguish the genus from other chiastoclonellid sponges.] Upper Ordovician: Germany (Island of Sylt, from glacial erratic, presumably from the Baltic region).-FIG. 88a-b. \*S. ingemariae, glacial erratic, ?Ordovician, Island of Sylt, the Netherlands; a, side view of holotype with ostia of canals between layers, AGH G 50; b, holotype from above without major, coarse canals and spongocoel, ×1 (van Kempen, 1990).—FIG. 89a-b. \*S. ingemariae, glacial erratic, ?Ordovician, Island of Sylt, the Netherlands; a, photomicrograph of part of polished, vertical section showing layered skeleton of irregular chiastoclones and some irregular canals, ×4; b, photomicrograph of light chiastoclones embedded in transparent chalcedony, ×10 (van Kempen, 1990).

## Family ANTHRACOSYCONIDAE Finks, 1960

#### [Anthracosyconidae FINKS, 1960, p. 76]

Dendroclones arranged with their long axes perpendicular to upper or outer surface of sponge so skeleton is built of concentric or superposed layers of such spicules; in some species spicules within a layer grouped in bundles and bearing lateral zygoses; curved, rhizoclonar spicules may outline pores and canals; sponge massive, fungiform, or digitate; attached to substrate basally by encrusting or overgrowth. *Lower Devonian–Permian (Capitanian)*.

Anthracosycon Girty, 1909, p. 72 [\**A. ficus* Girty, 1909, p. 73; OD] [=*Laubenfelsia* King, 1943, p. 9

(type, L. regularis KING, 1943, p. 10, OD)]. Conical or fungiform; relatively flat, upper surface bearing large oscules; spicule layers parallel to upper surface, their edges exposed on sides of sponge; ostia covering entire surface and most numerous on sides; surface canals most abundant at edge of upper surface; interior canals both perpendicular and parallel to spicule layers. Permian (Artinskian-Capitanian): USA (Texas), Australia (Western Australia).---FIG. 90,2a-d. \*A. ficus, Bone Spring Limestone, Leonardian, Guadalupe Mountains, Texas; a, enlarged side view of holotype showing prosopores and more compact skeleton of upper surface; b, view of summit showing large oscules and surface canals,  $\times 2$ ; *c*, photomicrograph of lower side of holotype with arched layers of unbundled tetraclones where skeletal pores are separated by single spicule,  $\times 10$ ; *d*, photomicrograph of skeletal net near top of holotype, with bundling of some rhabdomes, USNM 118127, ×10 (Finks, 1960; courtesy of The American Museum of Natural History).

- Collatipora FINKS, 1960, p. 81 [\*C. discreta; OD]. Spheroidal to hemispherical and encrusting; pores grouped in one or more sievelike clusters; remainder of surface covered with deep, anastomosing, cleftlike grooves; large oscules may also be present; spicule layers concentric and parallel to surface; interior canals both perpendicular and parallel to Permian (?Asselian-?Sakmarian, surface. Artinskian-Capitanian): USA (Texas).---FIG. 90,1a-b. \*C. discreta, Bell Canyon Formation, Guadalupian, Guadalupe Mountains; a, ellipsoidal holotype with two pore clusters in middle and osculum toward left, ×1; b, enlargement of section normal to surface, showing horizontal, spicule layers in skeleton, AMNH 28094, ×5 (Finks, 1960; courtesy of The American Museum of Natural History).
- Dactylites FINKS, 1960, p. 84 [\*D. micropora; OD]. Digitate with terminal oscules; ostia uniformly distributed over entire surface; few surface grooves; spicule layers parallel to outer surface. Permian (Artinskian): USA (Texas).——FIG. 91,2a-e. \*D. micropora, Bone Spring Limestone, Sierra Diablo; a, side view of holotype showing digitate form, terminal osculum on one branch, and small ostia uniformly distributed over surface, x2; b-e, sketches of isolated spicules from holotype, PU 78881, ×40 (Finks, 1960; courtesy of The American Museum of Natural History).
- Devonospongia HOWELL, 1957c, p. 14 [\*Archaeocyathus? clarkei DE KONINCK, 1877, p. 86; OD]. Branching, cylindrical or vase-shaped, conical sponge with deep cloaca; cloaca not connected between branch and parent stock; principal canals radial and vertically superposed, forming subparallel slits by their vertical coalescence; vertical slits and rows of pores prominent on both exterior and cloacal surfaces; spicules showing knots of fusion of possible chiastoclones in type species and well-defined chiastoclones and dendroclones in *D. garrae* PICKETT & RIGBY (1983, p.

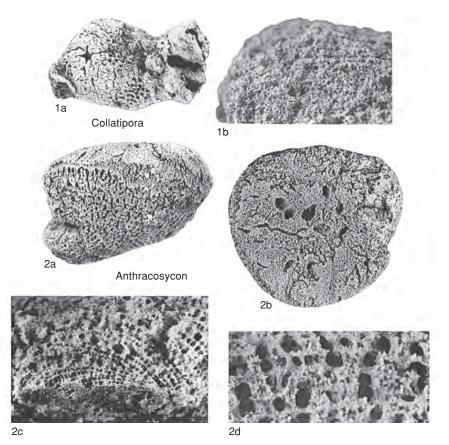


FIG. 90. Anthracosyconidae (p. 124).

726). Lower Devonian, Middle Devonian (?Eifelian): Australia (Western Australia, New South Wales).-FIG. 91,1a-b. \*D. clarkei (DE KONINCK), Sponge Limestone, ?Eifelian, Yass District, New South Wales; a, transverse section of lectotype showing flattened spongocoel and thin walls in dark matrix, PU 80424a, ×1 (Howell, 1957c); b, side view of weathered, branched, reference specimen with vertically aligned series of canals, AMu F13023, ×1 (Pickett, 1969).—FIG. 91,1c. D. garraea (PICKETT & RIGBY), Garra Formation, Lochkovian-Pragian, Wellington, New South Wales; electron photomicrograph of skeletal fragment in which dendroclones and a chiastoclone form knots in skeleton, MMF 25055, approximately ×100 (Pickett & Rigby, 1983).

?Laubenfelsia KING, 1943, p. 9 [\*L. regularis KING, 1943, p. 10; OD]. Differs from type of Anthracosycon only in absence of grouping of spicules in bundles, in larger size, and in more numerous oscules, which are no more than specific differences; here considered a junior synonym of Anthracosycon, and for that reason the genus is not illustrated herein. *Permian (Artinskian–Capitanian):* USA (Texas).

## Family ASTYLOSPONGIIDAE Zittel, 1877

[nom. correct. FINKS & RIGBY, herein, pro Astylospongidae ZITTEL, 1877b, p. 35] [=Attungaiidae PICKETT, 1969, p. 19, partim; Raanespongiidae RIGBY & TERRELL, 1973, p. 1,437]

Skeleton composed of fused sphaeroclones (possible dendroclones) forming an isodictyal net with mostly triangular interspaces in all directions (ZITTEL, 1884) or by the more usual interpretation (RAUFF, 1894) of concentric layers of six-armed, anapodal spicules (dichotriders); dendroclones, or spicule arms, thin and smooth with terminal expansions for zygosis; large, smooth oxeas may lie in and parallel to radial canals; sponge shapes range from

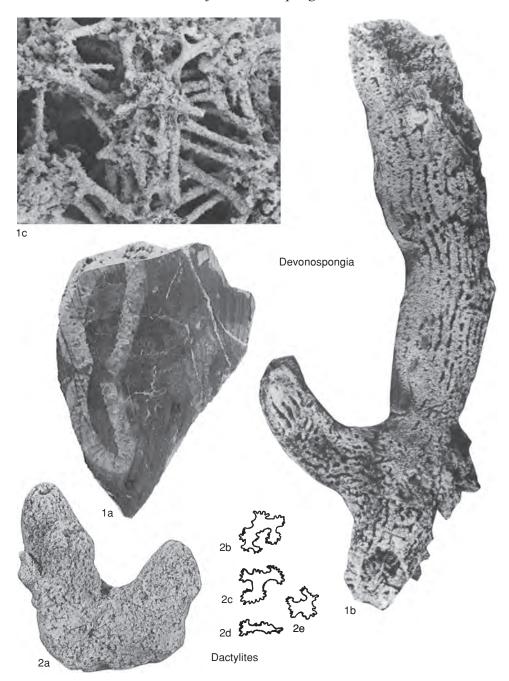


FIG. 91. Anthracosyconidae (p. 124-125).

spherical to tubular and branching. Upper Ordovician–Permian (Roadian).

Separation of the astylospongiids into genera was based by RAUFF (1894) on the ar-

rangement of the canals, and the siting of the exhalant pores. This basic premise has been accepted here. The various external forms are generated by vectors of growth (see Fig. 92). Disposition of the canals results from interaction of growth with the sites of exhalant openings. Internal exhalant canals arise, in general, from the roofing over of surface grooves tributary to the exhalant pores. Thus their form is determined by the position of the surface at a given time, together with the location of their termini, the exhalant pores.

The family Attungiidae was established by PICKETT (1969) for cylindrical forms with sphaeroclones. The new Devonian genera from Australia that he included in the family have spicules and a skeletal net identical to the earlier astylospongiids; and the cylindrical, tubular, or vasiform shape does not, by itself, warrant familial separation, especially as such shapes are either present or approached in many other astylospongiid genera.

Dominance of tubular forms in the Devonian seems to be a genuine phenomenon. One is also tempted to see lineages such as the Ordovician *Phialaspongia* and *Caryospongia* with their exhalant pores concentrated in meridional grooves and their strong vertical canals leading into the Devonian genus *Inglispongia*. Likewise the vasiform or cylindrical Ordovician genera *Caliculospongia* and *Camellaspongia*, with their meandriform surface grooves, may be ancestral to the Devonian *Attungaia* and *Devonoscyphia* with similar features.

The skeletal net of the astylospongiids, when viewed in transverse section, is nearly indistinguishable from that of the anthaspidellids, and indeed genera have been misassigned on the basis of single sections. The difference is that anthaspidellids have triangular interspaces only in tangential or horizontal sections, while in longitudinal and radial sections they are seen to have a ladderlike structure. The astylospongiids have triangular interspaces in all orientations. It is tempting to interpret the astylospongiid skeleton as made of separate dendroclones, as in the anthaspidellids, but attempts to demonstrate this have not been successful. Nevertheless the seemingly anapodal sphaeroclones could be the result

of fusion of separate dendroclones following the deposition of each concentric, spicule layer. It would be natural for such fusion to take place about a particular center of junction of dendroclones, and the newly formed dendroclones would of necessity be on the proximal side of their junctions, assuming the underlying layer to be already fused. Thus each layer would seem to consist of anapodal spicules whose arms would be the once-separate dendroclones. It is significant that ZITTEL (1884) made such an interpretation of the astylospongiid skeleton, although HINDE, in discussing ZITTEL's view (HINDE, 1888, p. 113), believed the spicules to be polyactinal desmas, as did RAUFF (1894, p. 280 ff.), who established the current interpretation of the spicule as a dichotrider or six-armed anapodal desma.

- Astylospongia ROEMER, 1860, p. 7 [\*Siphonia praemorsa GOLDFUSS, 1826, p. 17; OD]. Spheroidal with concave, exhalant depression at upper pole that meets sides of sponge in sharp rim; center of growth near center of sponge; maximum growth over entire lateral surface, which bears meridional, dendritic grooves that end at rim of exhalant depression; internal, exhalant canals are concentric and stacked in radial series, produced by roofing of surface grooves, arcuate parallel to side surface of sponge; canals open as pores in radial rows on upper, exhalant surface; internal, inhalant canals straight and radial with respect to center of growth and nearly perpendicular to outer surface; they may contain oxeas parallel their length; basal attachment absent. Upper Ordovician-Silurian (Wenlock-Ludlow or Wenlock): North America, Europe; Lower Devonian: Australia (New South Wales).----FIG. 93,1a-c. \*A. praemorsa (GOLDFUSS), Silurian limestone, Neustadt, Germany; a, side view of globular, silicified specimen with shallow spongocoel whose walls have regular, exhalant ostia of concentric canals similar to those on exterior,  $\times 1$ ; b, same specimen from above with shallow spongocoel, P-MD, ×1; c, vertical medial section showing concentric, exhalant canals and finer, radial, inhalant canals in alternating positions, laterally, U-SK, ×1 (Rauff, 1893).
- Astyloscyphia RIGBY & PISERA in RIGBY & others, 2001, p. 463 [\*A. irregularia; OD]. Small, obconical to cup-shaped astylospongiids with deep spongocoel, dermal surface pierced by irregularly placed to diagonally packed canals, exhalant openings aligned in horizontal rows in diplorhysal canal pattern. Dermal and gastral layers formed of swollen sphaeroclones and interior skeleton with gentle, upward expansion; interior centra essentially same size throughout skeleton. Upper Devonian (Frasnian): Poland.—FIG. 93,3a-b.

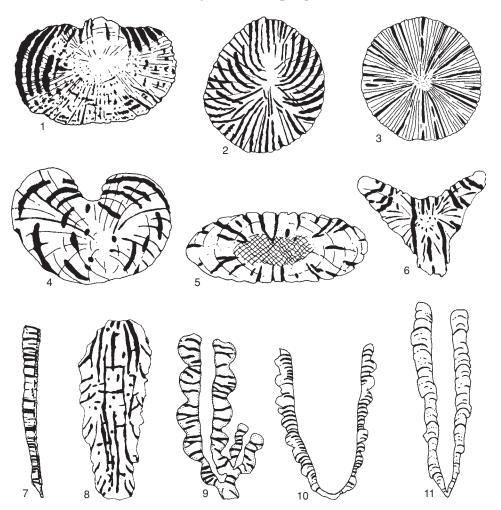


FIG. 92. Outline drawings of genera included in Astylospongiidae, showing relationships of growth forms, dermalgastral layers, and canals; all drawings generalized; I, Astylospongia; major, subconcentric, large canals stacked and cross connected by radiating, intermediate, small series, ×1; 2, Caryospongia; large canals radiating out from center but sweeping to almost vertical in stacked series; minor secondary series of radiating straight canals, ×1; 3, Carpospongia; radiating canals of two sizes probably differentiated incurrent and excurrent openings, ×1; 4, Astylospongiella; large, irregularly spaced canals not in vertically stacked series, nor are smaller, almost plumose ones, ×1; 5, Ellesmerespongia; centeral area filled with matrix; branching, more or less subradial canals are large series and connected by irregularly spaced, subconcentric, intermediate canals, ×0.5; 6, Phialaspongia; large, central canals vertical and connected by radiating, intermediate-sized ones, ×1; 7, Garraspongia; bladed, flabellate form with differentiated dermal surface and more or less straight canals through blade; small, nearly vertical canal series occurring just below dermal surface, ×1; 8, Inglispongia; large, vertically continuous, cylindrical canals piercing more or less through central part of body; cross connected by moderately large, subhorizontal canals and still smaller, irregular series, ×0.5; 9, Devonoscyphia; small, sometimes branching form with irregular radial canals and differentiated dermalgastral layer, ×3; 10, Camellaspongia; deep, obconical sponge with regularly stacked, arcuate canals that lead directly through thin walls; stacking shows best on interior, ×1; 11, Attungaia; conical-cyclindrical sponge with upwardly arcuate canals that lead more or less directly through walls; canals irregularly placed in outer wall but may be more regular in inner wall, ×1 (Rigby, 1986b).

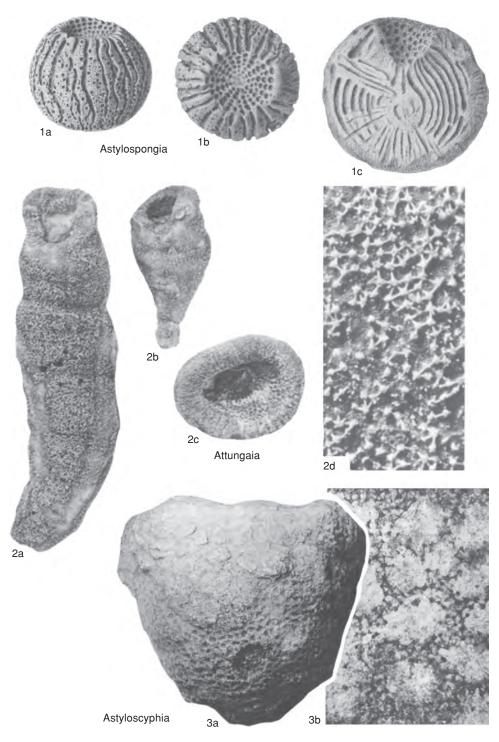


FIG. 93. Astylospongiidae (p. 127-130).

\*A. irregularia, Holy Cross Mountains; a, side view of holotype showing general form of sponge and irregular distribution of closely spaced canals, ×1; b, details of ostia organization and skeletal net of sphaeroclones on dermal surface, ×10 (Rigby & others, 2001).

- Astylospongiella RIGBY & LENZ, 1978, p. 158 [\*A. megale RIGBY & LENZ, 1978, p. 159; OD]. Robust, subspherical with obconical to rounded spongocoel; largest canals with ostia on lower surface arching upwardly and inwardly, irregularly spaced and not stacked; small, cross-connecting canals radiating upwardly and outwardly, approximately normal to larger canals; sphaeroclones uniform size throughout sponge. Silurian (Wenlock-Ludlow): Canada (Northwest Territories, Baillie Hamilton and Cornwallis Islands).-FIG. 94,1a-c. \*A. megale, Cape Phillips Formation, Ludlow, Baillie-Hamilton Island; a, side view of holotype showing globular form and small spongocoel at summit, with shallow, convergent canals on upper slope and summit, small, circular ostia to inhalant canals showing on side,  $\times 1$ ; b, view from above into spongocoel and onto rounded, oscular summit with radial canals and small, inhalant ostia between, ×1; c, photomicrograph showing characteristic sphaeroclone spicules in regular, skeletal net interrupted by circular canals, GSC 54152, ×25 (Rigby & Lenz, 1978; courtesy of Canadian Journal of Earth Sciences).
- Astylostroma RIGBY & WEBBY, 1988, p. 76 [\*A. micra; OD]. Massive, laminate astylospongiid with skeleton of minute sphaeroclones, generally of uniform size throughout massive structure; laminated appearance produced by layers of dense, skeletal structure alternating with layers where up to fifty percent of space is subtangential canals; small, radial canals oriented normal to laminated layers. [Astylostroma is the only known genus of the family that has a massive, laminate skeleton.] Upper Ordovician: Australia (New South Wales). -FIG. 95,1a-b. \*A. micra, Malongulli Formation, Cliefden Caves area; a, side view of massive, although laminated holotype, AMu. F66891, ×0.75; b, SEM photomicrograph of small sphaeroclones in silicified paratype, with centrum well exposed in center of figure and others uniformly distributed in fabric, tips of radiating ray fusing to adjacent centra to produce cross-braced skeleton, AMu. F66894, ×200 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Astylotuba RIGBY & PISERA in RIGBY & others, 2001, p. 466 [\*A. modica RIGBY & PISERA in RIGBY & others, 2001, p. 467; OD]. Large, tubular astylospongiids with diplorhizal, canal system in craticulariid pattern; sphaeroclones in skeleton of uniform size throughout; skeletal structure generally upwardly and outwardly divergent, pierced by coarse, inhalant and exhalant canals that end blindly within sponge wall. Upper Devonian (Frasnian): Poland.—FIG. 96, 1a-b. \*A. modica,

Holy Cross Mountains; a, longitudinal section of holotype showing wall thickness and canal distribution; b, detail of ostia on dermal surface, ×1 (Rigby & others, 2001).

- Attungaia PICKETT, 1969, p. 19 [\*A. cloacata PICKETT, 1969, p. 20; OD]. Tubular and branching, thin walled with deep cloaca; cloaca of branches not connected with that of parent branch; exhalant pores somewhat aligned in vertical rows on cloacal surface; inhalant pores in meandriform, anastomosing, surface grooves on exterior of sponge; internal canals radial, exhalant canals in stacked, vertical series, sloping gently inwardly and downwardly to meet cloaca, spicules essentially same size throughout sponge. Lower Devonian (Lochkovian)-Upper Devonian (Frasnian): Australia (New South Wales), Lochkovian, ?Givetian; Australia (Western Australia), Frasnian.-FIG. 93,2a-d. \*A. cloacata, Sadler Limestone, Frasnian, Sadler Ridge, Western Australia; a, side view of subcylindrical sponge with matrix-filled osculum to a deep spongocoel at top, GSWA F2221; b, side view of smaller, obconical sponge, GSWA F7223; c, view down into spongocoel with ostia of exhalant canals aligned on gastral surface and radial canals in sections of rounded wall, GSWA F7250, ×1; d, photomicrograph of sphaeroclone skeleton with swollen centra connected by radiating rays, circular gaps are ostia of canals, GSWA 7237, ×10 (Rigby, 1986b).
- Caliculospongia FOERSTE, 1916, p. 340 [\*C. pauper; M]. Cylindrical with shallow, cloacal depression at upper end surrounded by a flattish rim; cloacal surface bearing exhalant pores in more or less radial rows; internal canals meandriform and anastomosing, open on exterior of sponge and on upper edge of cloaca, as circular pores to meandriform slits (surface possibly decorticated); sponge surface between pores smooth and composed of apparently normal astylospongiid net (judging from coarsely silicified sole specimen) with no other skeletal pores than interspicular spaces; basally attached to shell fragments. Upper Ordovician: USA —Fig. 94,2a-b. \*C. pauper, Cynthi-(Kentucky) .-ana Formation, Lexington; a, side view with osculum toward top in small, globular sponge; b, opposite side showing irregular canals and ostia at surface, ×2 (Foerste, 1916).
- Camellaspongia RIGBY & BAYER, 1971, p. 619 [\*C. tumula; OD]. Conical with deep, exhalant depression or cloaca surrounded by a relatively thin body wall above pedunculate, lower portion; center of growth not known; growing surface just below rim on upper surface of cloaca, with maximum growth at outside edge; meridional surface grooves confined to this surface, and by upward growth of sponge around them forming canals running inwardly and downwardly toward cloaca, where they open as exhalant pores in vertical rows; inhalant canals perpendicular to outer surface more irregularly placed, their larger openings concentrated in depressions between irregular protuberances that

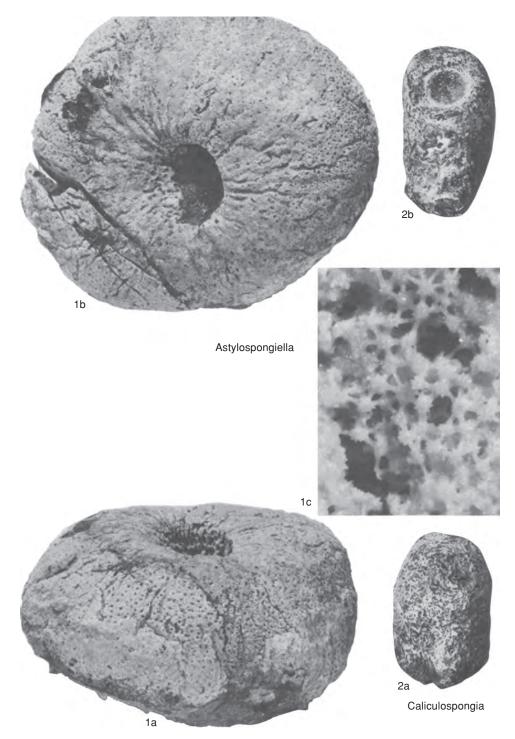


FIG. 94. Astylospongiidae (p. 130).

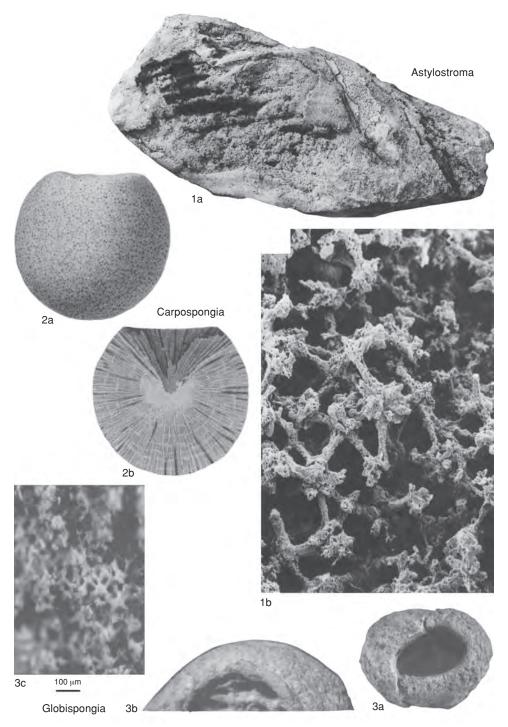


FIG. 95. Astylospongiidae (p. 130-138).

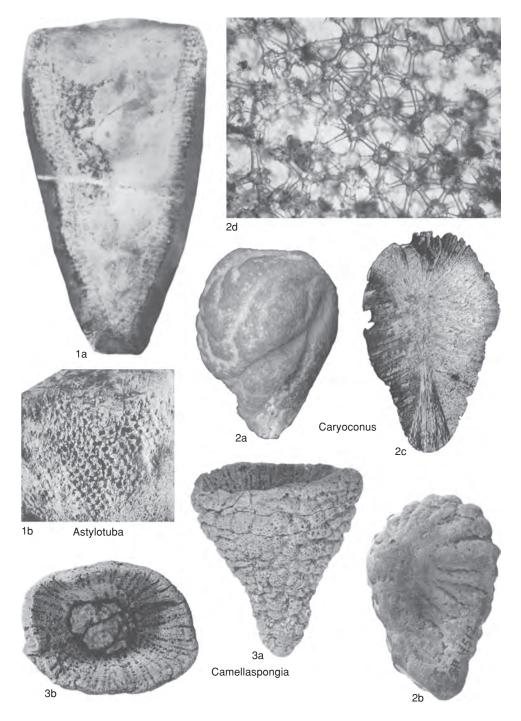


FIG. 96. Astylospongiidae (p. 130-134).

cover exterior surface; spicules increasing upwardly in size. Upper Ordovician: USA (Minnesota).— FIG. 96,3a-b. \*C. tumula, Maquoketa Formation, Granger; a, side view of holotype with nodose, dermal surface perforated by inhalant canal; b, view down into spongocoel showing thin walls and rows of exhalant ostia, UM 12039, ×1 (Rigby & Bayer, 1971).

- Carpospongia RAUFF, 1894, p. 304 [\*Manon globosum EICHWALD, 1860, p. 188; SD REZVOI, ZHURAVLEVA, & KOLTUN, 1962, p. 56] [= Carpomanon RAUFF, 1894, p. 313, obj.]. Spheroidal, without cloaca, growing uniformly in all directions from center of growth; exhalant pores scattered over entire surface, as are stellate or anastomosing, surface grooves, when present; principal inhalant and exhalant, internal canals radial, straight, and may contain large oxeas parallel their length; no basal attachment; spicule size increasing radially from center of sponge in radiating skeleton. Middle Ordovician-Silurian: Europe, North America.—FIG. 95,2a-b. \*C. globosum (EICH-WALD), Silurian limestone, Ostrowitt, West Prussia, Germany; a, exterior of globose sponge with smooth, dermal layer perforated by small ostia of both inhalant and exhalant canals; b, vertical, median section showing strongly radiate, spicule series and both inhalant and exhalant canals, P-MD, ×1 (Rauff, 1893).
- Caryoconus Rhebergen & van Kempen, 2002, p. 188 [\*Astylospongia gothlandica SCHLÜTER, 1884, p. 79; OD]. Irregularly stalked, subspherical to subglobular to obconical or cylindrical astylospongiids without an osculum; subspherical and stalked parts generally smooth, but with irregular, anastomosing or branched, surficial furrows that radiate from lateral bulge in some specimens; lateral knob is at maximum diameter; furrows commonly extending along one side of stalk; no close connection between internal canals and surficial grooves; numerous small prosopores and fewer larger apopores are irregularly distributed over entire dermal area; more or less straight canals radiating from center of subspherical, upper part of sponge, and straight, parallel canals extending from sides of lower cone toward dermal surface; concentric canals absent; principal, choanosomal skeleton composed of interconnected, regular sphaeroclones, but sphaeroclones in conical part of sponge often irregular, with longitudinally elongate rays forming strands that diverge downwardly and outwardly toward base. Silurian (Llandoveryupper Wenlock): Sweden (Gotland, erratics). FIG. 96,2a-d. \*C. gothlandicus (SCHLÜTER), probably Upper Högklint Formation, Wenlock, erratic on beach south of Högklint; a, holotype, side view showing growth form, PIUB Schlüter 134, ×1; b, side view of reference specimen showing lateral bulge with apical knob, NRM Sp. 4512, ×1; c, paratype, vertical section showing skeletal and canal structure, NRM Sp. 147, ×1; d, paratype, in-

terconnected sphaeroclones of choanosomal skeleton, NRM Sp. 129, ×20 (Rhebergen & van Kempen, 2002).

- Caryospongia RAUFF, 1894, p. 296 [\*Siphonia juglans QUENSTEDT, 1878 in 1877-1878, p. 555; SD DE LAUBENFELS, 1955, p. 61] [= Caryomanon RAUFF, 1894, p. 313, obj.]. Spheroidal, without cloaca; meridional surface grooves and maximum growth on upper hemisphere; center of growth below center of sponge; grooves may be deeply incised, rendering sponge meridionally lobate, exhalant pores concentrated in these surface grooves; internal, exhalant canals bending outwardly and upwardly from center of growth, arcuate convex toward exterior; internal, inhalant canals straight and radial with respect to center of growth; basal attachment absent; spicule size increasing radially from center of sponge in regularly radiating skeleton. Middle Ordovician-Silurian: Europe, North America.-FIG. 97, 1a-c. \*C. juglans (QUENSTEDT), Magdeburg, Germany; a, side view of large specimen with exhalant ostia on summit and sides marked by canal segments, BM, ×1; b, vertical median section of large sponge showing small, straight, inhalant canals and upswept, larger, exhalant canals, defined by shaded, skeletal areas, BM, ×1; c, smaller sponge with clustered, exhalant ostia on summit and slopes with grooves of concentric canal series, glacial erratic, Island of Sylt, U-SK, ×1 (Rauff, 1893).
- Devonoscyphia RIETSCHEL, 1968b, p. 99 [\*D. sandbergeri; OD]. Cylindrical to spheroidal with deep cloaca; principal, exhalant canals radial and branching peripherally; disposition of exhalant pores on cloacal surface not known; small, inhalant pores scattered over exterior surface that is otherwise dense and bearing only interspicular spaces; there is some suggestion of meandriform, surface grooves connecting inhalant pores; skeleton of uniform sphaeroclones. [Genus is similar to Attungaia PICKETT, 1969.] Devonian (Givetian): Germany, Belgium, Poland.——FIG. 98,1a-b. \*D. sandbergeri, Lahnmulde, Rheinische Schiefergebirge, Germany; a, etched, upper surface of silicified holotype with central, spicule-free osculum,  $\times$ 4; *b*, silicified sphaeroclones from holotype, SMF XXVI 201, ×30 (Rietschel, 1968b)
- Ellesmerespongia RIGBY, 1970b, p. 1,143 [\**E. feildeni* RIGBY, 1970b, p. 1,145; OD]. Massive, obloid to biscuit-shaped astylospongiid without spongocoel, surface marked with impressed, round, radiating grooves; canals of three sizes: small, intraray, polygonal openings; intermediate-sized, radial and concentric canals; and large, straight canals that radiate pinnately from nearly horizontal, open-textured zone in center of sponge, latter canals opening into surficial grooves and onto surficial ridges; spicules sphaeroclones typical of family. *Permian* (*Cisuralian*): Canada (northern Ellesmere Island).——FIG. 99*a–c. \*E. feildeni*, unnamed limestone, Feilden Peninsula, Baffin Island; *a*, side

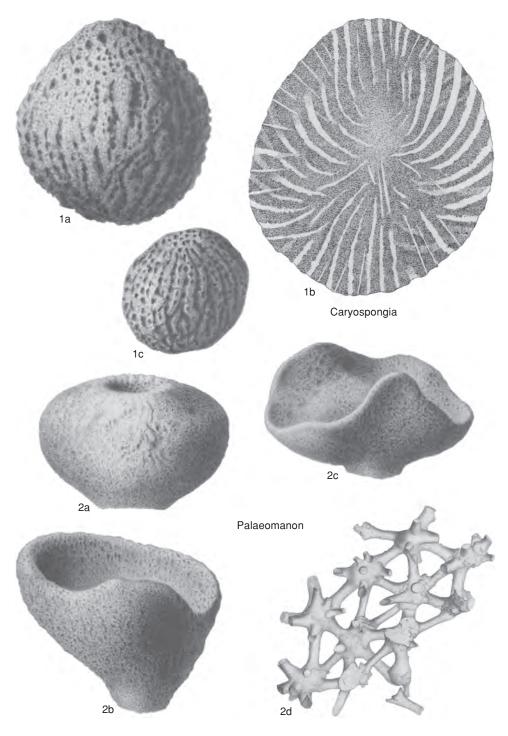


FIG. 97. Astylospongiidae (p. 134–141).

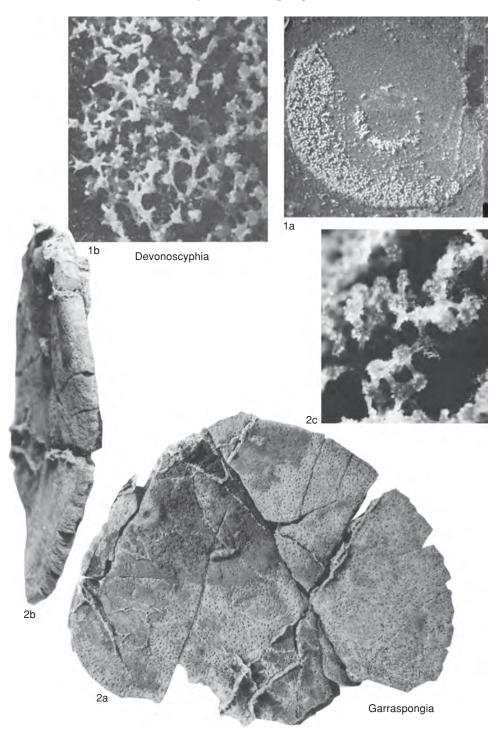


FIG. 98. Astylospongiidae (p. 134–138).

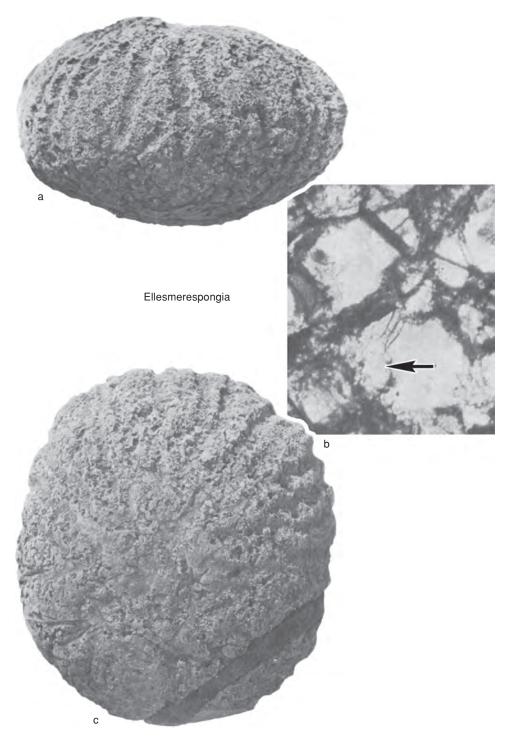


FIG. 99. Astylospongiidae (p. 134–138).

view of globose holotype with tangential grooves on margin,  $\times 1$ ; *b*, rounded outline from above, with broad grooves along flanks,  $\times 1$ ; *c*, photomicrograph showing parts of six centra and associated thin, radiating rays, GSC 81005,  $\times 75$  (Rigby, 1970b).

- Garraspongia PICKETT & RIGBY, 1983, p. 733 [\*G. vannus; OD]. Flabellate with differentiated, incurrent and excurrent surfaces, canals normal to surfaces except upwardly plumose canals parallel to excurrent surface immediately beneath differentiated, dermal layer; skeleton of sphaeroclones with occasional, possible, accessory oxeas. Devonian (Lochkovian-Pragian): Australia (New South Wales).—FIG. 98,2a-c. \*G. vannus, Garra Formation, Wellington; a, side view of inhalant surface of fanlike holotype with numerous inhalant ostia, ×1; b, upper end of thin, bladelike holotype, MMF 23743, ×1; c, photomicrograph of paratype showing sphaeroclones of endosomal skeleton, MMF 23746, ×30 (Pickett & Rigby, 1983).
- Globispongia Jux, 1992, p. 308 [\*G. paffrathi; OD]. Hemispherical to ovate, tuberlike sponges with flat, lower surface and deep, upper spongocoel, with irregularly arranged, inhalant ostia on mostly smooth, dermal surface, large, polygonal to horizontally elliptical apopores arranged in rings on spongocoel wall; spicules sphaeroclones as in family. Devonian (Givetian): Germany .---- FIG. 95,3a-c. \*G. paffrathi, Hornstein beds, upper Givetian, Bergisches Land; a, view from above of paratype with ovate outline and large spongocoel and inhalant ostia in dermal surface, GIK, ×1; b, diagonal view of part of holotype showing oscular margin and gastral surface with large, elliptical, exhalant ostia, GIK 998, ×1; c, photomicrograph showing swollen centra of sphaeroclones of skeleton (Jux, 1992; courtesy of Senckenberg Naturforschende Gesellschaft).
- Inglispongia PICKETT, 1969, p. 22 [\*I. scriveni; OD]. Large, cylindrical, flabellate, or irregular massive; no cloaca; large, parallel, vertical, exhalant canals in axial region opening on upper surface; inhalant canals radial. Devonian (?Givetian): Australia (New South Wales) .---- FIG. 100, 1a-c. \*I. scriveni; a, transverse section with large, vertical canals near axis but absent in outer parts, Moore Creek Limestone, County Inglis, AM F12864, ×1; b, weathered, vertical section of reference specimen with large, vertical canals and horizontal canals in dense, skeletal net, Timor Limestone, County Brisbane, AM 13296, ×1; c, photomicrograph of sphaeroclone spicules in reference specimen, Moore Creek Limestone, County Inglis, AM 12862, ×12 (Pickett, 1969).
- Jazwicella RIGBY & PISERA in RIGBY & others, 2001, p. 458 [\*J. media RIGBY & PISERA in RIGBY & others, 2001, p. 460; OD]. Small, obconical astylospongiids with craticulariid canal pattern where canals regularly spaced in uniform rows; inhalant canals end short of gastral margin and exhalant canals do not appear in dermal layer; centra of sphaeroclone spicules of uniform size

throughout skeleton. Upper Devonian (Frasnian): Poland.——FIG. 101,2*a*-*b*. \*J. media, Holy Cross Mountains; *a*, side view of holotype showing regular placement of inhalant ostia, ZPAL PfXI/24, ×2; *b*, detail of skeletal and canal pattern showing uniform size of centra of interconnected sphaeroclones around aligned ostia in holotype, ×10 (Rigby & others, 2001).

- Malinowskiella HURCEWICZ, 1985, p. 277 [\*M. actinosum; OD]. Cylindrical to conical, gobletshaped sponges with deep spongocoel and broad osculum, walls moderately thick and with smooth, gastral surface, dermal skeleton, and surface rarely preserved; inhalant ostia round and in depressed, vertical rows separated by elevated, skeletal areas; principal, interior skeleton of regularly spaced and oriented sphaeroclones without layering; sphaeroclones with swollen, spinose, centrum where spines directed dermally; spicules with 3 to 4 rays oriented toward interior; ray tips fused to centra of adjacent spicules; traces of spicules in outer or dermal part of wall suggesting dichotrienes with long rays present. [Review of the original material by other workers suggests that some reported skeletal details are not easily visible.] Devonian (Frasnian): Poland.—FIG. 101,3a-g. \*M. actinosum, Kowala Formation, upper Frasnian, Holy Cross Mountains; a, side view of obconical holotype with broad osculum and impressed, irregular, vertical rows of inhalant ostia, MUZ IG 1501.II/3, ×1.5; b, transverse cross section through a cluster of individuals with open spongocoel cavities and moderately thick walls, MUZ IG 1501.II/72, ×1; c-g, drawings of monaxon and sphaeroclones of interior part of skeleton, ×35 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).
- Palaeomanon ROEMER, 1860, p. 12 [\*Siphonia cratera ROEMER, 1848, p. 685; OD] [=Astylomanon RAUFF, 1894, p. 313, obj.]. Bowl shaped and pedunculate to conical; concave, exhalant surface with sharp rim at top of sponge; center of growth below center of sponge; meridional, surface grooves and site of maximum growth on outside just below rim of exhalant depression; internal, exhalant canals parallel to these grooves and formed from them by upward and outward growth of sponge around them, opening onto exhalant surface; internal, inhalant canals possibly radial, leading in from outer surface. Spicules uniform size throughout skeleton. [This genus differs from Astylospongia ROEMER in development of a peduncle and in the concentration of growth about the upper part of the exterior, producing the bowl-like shape; the spicules and mesh spaces are also larger relative to the size of the sponge than in Astylospongia.] Silurian (Wenlock-Ludlow): USA (Tennessee), Canada (Northwest Territories).-FIG. 97,2a-d. \*P. cratera (ROEMER), Brownsport Limestone, Niagaran, Decatur County, Tennessee; a, globose form of type species with small spongocoel in summit, Münchener Museum; b, broad, bowlshaped representative of type species, Münchener

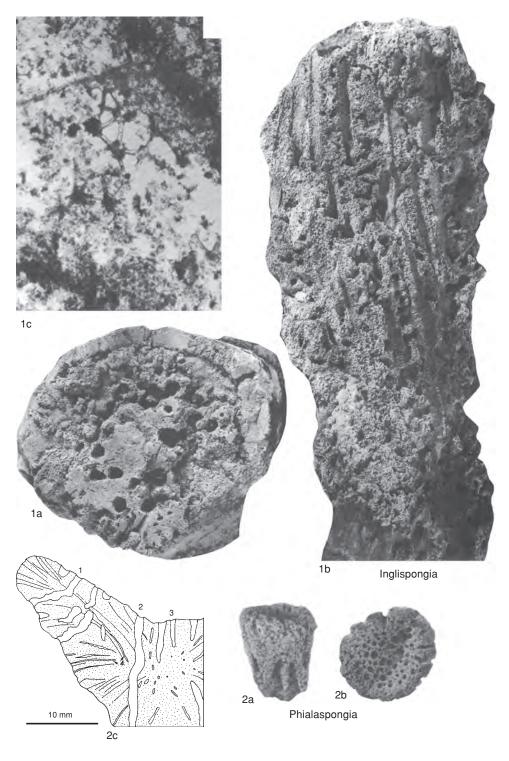


FIG. 100. Astylospongiidae (p. 138-141).

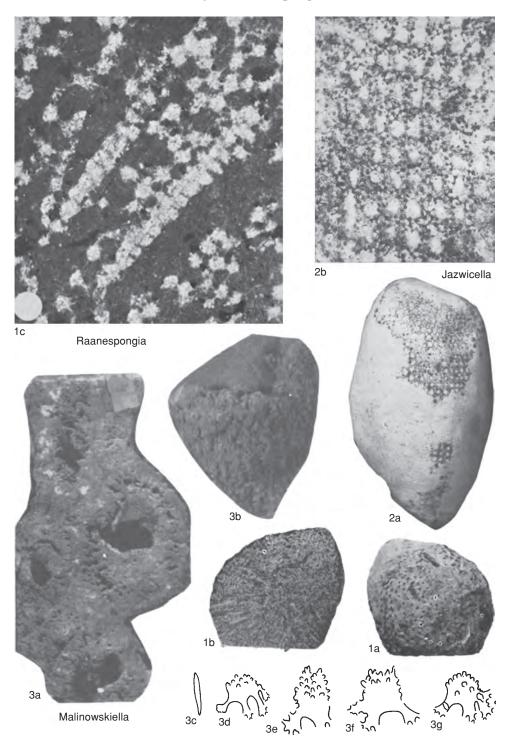


FIG. 101. Astylospongiidae (p. 138-141).

Museum; c, undulate, bowl-shaped representative of type species, Münchener Museum, ×1; d, drawing of skeletal details showing mutually attached sphaeroclones in silicified sponge, Königlich Museum für Naturkunde, Berlin, ×50 (Rauff, 1893).

- Phialaspongia RIGBY & BAYER, 1971, p. 622 [\*P. fossa RIGBY & BAYER, 1971, p. 623; OD]. Conical with concave depression at top with rounded rim; maximum upward growth at center of this rim; prominent, meridional, surface grooves run up exterior surface, across rim, and onto upper surface; internal, exhalant canals approximately perpendicular to both exhalant and outer surfaces, being vertical at center of sponge where continuation of stalk canals arcuate and concave upward in upper part of sponge, opening into meridional grooves; internal, inhalant canals radial with respect to center of growth at center of sponge, forming pinnate pattern in upper, bowl-like part of sponge; spicule size may increase upwardly. Upper Ordovician: USA (Minnesota).---FIG. 100,2a-c. \*P. fossa, Maquoketa Formation, Fillmore County; a, side view of holotype showing coarse, vertical canals in lower part,  $\times 1$ ; b, vertical view showing coarse, exhalant ostia in shallow spongocoel, UM 9149, ×1; c, sketch of vertical section through paratype showing distribution of canals in skeleton from large ones that pierce upper walls (1) to larger (2) and smaller (3) ones that empty into spongocoel floor, (4) possible fine inhalant canals, ×15 (Rigby & Bayer, 1971).
- Raanespongia RIGBY & TERRELL, 1973, p. 1,438 [\*R. monilis; OD]. Small to medium-sized, subspherical or oblate to spindle-shaped sponges with radiating, skeletal structure of separate to beaded or stringlike clusters of sphaeroclones with many rays; large and intermediate-sized, radial canals nearly straight, cross connected with irregularly developed, intermediate-sized, concentric canals and with small, radial canals; surface weakly hispid, marked by extended tips of beadlike rods of spicules. Permian (Artinskian-Roadian): Canada (Ellesmere Island).-FIG. 101, 1a-c. \*R. monilis, Assistance Formation; a, side view of holotype with nodose, dermal surface produced by dark, radiating, spicule tracts,  $\times 1$ ; b, vertical section showing radial structure of skeleton as light gray separated by radial canals filled with dark matrix, ×1; c, photomicrograph of thin section of beaded strands of sphaeroclones, along with isolated sphaeroclones, in areas between canals filled with dark matrix, GSC 32716, ×10 (Rigby & Terrell, 1973; courtesy of Canadian Journal of Earth Sciences).

# Order SPIROSCLEROPHORIDA Reid, 1963

[nom. correct. FINKS & RIGBY, herein, pro Spirosclerophora REID, 1963d, p. 199; emend., FINKS & RIGBY, herein]

Microscleres sigmaspires or microrhabds. Middle Cambrian–Holocene.

# Suborder RHIZOMORINA Zittel, 1895

### [Rhizomorina ZITTEL, 1895, p. 52]

Lithistid sponges whose principal desmas are rhizoclones and whose spicules are entirely monaxonic; microscleres, when present, are sigmaspires or microrhabds. *Middle Cambrian–Holocene.* 

## Family HAPLISTIIDAE de Laubenfels, 1955

#### [Haplistiidae DE LAUBENFELS, 1955, p. 37] [=Columellaespongiidae PICKETT, 1969, p. 11]

Principal skeleton of rhizoclones, which may be accompanied by dendroclones, chiastoclones, oxeas, and strongyles; dermal skeleton of tangential oxeas and possibly strongyles; principal skeleton made of radial spiculofibers connected by lateral or concentric fibers that are generally thinner; form of sponge spheroidal, discoidal, tubular, foliate, massive, or encrusting. *Lower Ordovician–Permian*.

Haplistion YOUNG & YOUNG, 1877, p. 428 [\*H. armstrongi; OD] [=?Rhaphidhistia CARTER, 1878, p. 140 (type, R. vermiculata, OD); ?Pemmatites DUNIKOWSKI, 1884, p. 13 (type, P. verrucosa, SD DE LAUBENFELS, 1955, p. 49); ?Pseudopemmatites KING, 1943, p. 12 (type, P. skinneri KING, 1943, p. 16, OD), ?non FRAIPONT, 1911; ?Monarchopemmatites DE LAUBENFELS, 1947, p. 187 (type, Pseudopemmatites skinneri KING, 1943, p. 16, OD); ?Radiatospongia WOLFENDEN, 1959, p. 567 (type, R. carbonaria, OD)]. Spheroidal, ovoid, discoid, lobate, or irregular; no cloaca; cylindroid spiculofibers radiating from an eccentric center of growth and end as hispid projections at surface (new fibers being added by intercalation); they are connected by usually thinner fibers at right angles, forming a quadrate mesh in longitudinal section and a polygonal, mainly quadrate, mesh in surface view; rhizoclones are mainly stout and straight with warty, lateral protuberances, often on one side only, but curved forms occurring around pores and at fiber junctions; dendroclones also present in horizontal connecting fibers; abundance of smooth, curved oxeas and strongyles adherent to surfaces of many specimens suggests that these were part of sponge, probably connected with a dermal layer; larger, circular, oscule-like openings may also be present; fibers composed of rhizoclones and smooth oxeas oriented roughly parallel length of fibers. [Because of poor preservation, there is some doubt as to the presence of rhizoclones in the type specimens of Haplistion; originally both Haplistion and

Pemmatites were described as having only oxeas.] (Capitanian, Middle Ordovician–Permian ?Changhsingian): Australia, North America, Spitzbergen, Europe (Ural Mountains, Spain), -FIG. 102, 1a-b. \*H. armstrongi, lower Timor.limestone series, Visean, Ayrshire, Scotland; a, small, spheroidal holotype (center) with tracts of rhizoclones,  $\times 2$ ; b, skeletal tracts enlarged to show rhizoclone spicules, ×40 (Finks, 1960; courtesy of The American Museum of Natural History). FIG. 102, 1c-d. H. sphaericum FINKS, Magdalena Formation, Desmoinesian, Otero County, New Mexico; c, section of spheroidal holotype with radiating trabeculae,  $\times 1$ ; *d*, enlarged part of skeletal net showing tracts of subparallel rhizoclones, USNM 127632, ×10 (Finks, 1960; courtesy of The American Museum of Natural History).

- Boonderooia RIGBY & WEBBY, 1988, p. 25 [\*B. spiculata; OD]. Bladelike, flabellate or open obconical sponge with three-dimensional network of tracts made of clustered rhizoclones cored by monaxial oxeas, which project through tracts as spines at tract junctions; skeletal net irregular, without major linear structure but with tract segments mainly surrounding irregularly rectangular openings; well-defined dermal and more obscure gastral layers composed of bladelike, clustered tracts that are somewhat larger than interior ones; walls perforated by large, generally radial, discontinuous canals that commonly interconnect to illdefined, vertical series in middle walls. Upper Ordovician: Australia (New South Wales).----FIG. 103,2a-d. \*B. spiculata, Malongulli Formation, Cliefden Caves area; a, gastral surface of holotype with open skeleton and larger, excurrent canals more or less uniformly distributed, ×2; b, side view showing ladderlike, skeletal tracts diverging upwardly toward gastral surface and outwardly toward lateral, dermal surface, ×2; c, dermal surface with relatively uniform, textured skeleton and absence of clearly differentiated, large canals in network of tracts,  $\times 2$ ; *d*, photomicrograph of dermal, skeletal structure with irregular, ropy tracts of dendroclones with tips of coring oxeas exposed at intersections and elsewhere, AMu. F66802, ×8 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Chaunactis FINKS, 1960, p. 93 [\*C. foliata FINKS, 1960, p. 94; OD]. Foliate to flabellate, skeletal net organized in porous partitions perpendicular to flat sides, originating from center of growth on attached edge and radiating toward opposite free edge; partitions connected at right angles by thinner partitions that together outline cylindrical canals that are perpendicular to flat sides and are parallel to and convex toward beveled edge; canals open as radial rows of oval pores on both flat sides; skeletal net composed of possible rhizoclones; long, smooth monaxons, parallel to flat sides locally imbedded in radial, skeletal partitions; exterior surface may bear fine, radial and concentric, rectangular, dermal mesh of bundles of parallel,

smooth, small monaxons (possible oxeas); one species (not the type) showing polygonal pores on one flat side. [Genus is similar to Mortiera DE KONINCK, but principal spicules may be rhizoclones rather than possible dendroclones of Mortiera, in that the dermal mesh is composed of reticulately arranged, rather than parallel and densely crowded oxeas and in that the growth is from a lateral center of origin.] Carboniferous (Middle Pennsylvanian)-Permian (Wordian): USA (Colorado, Oklahoma, Texas), Mexico (Coahuila), Spitzbergen.-FIG. 104a-c. \*C. foliata, Gaptank Formation, Missourian, Glass Mountains, Texas; a, convex surface of holotype showing fine, dermal mesh in upper part and coarse, internal mesh below, USNM 127640, ×2; b, side view of nearly complete paratype without fine, dermal mesh but showing coarse, aligned, canal series, ×2; c, photomicrograph perpendicular to growing edge, at left, with monaxons parallel to radial, skeletal fibers showing in lower part of paratype, USNM 127641, ×5 (Finks, 1960; courtesy of The American Museum of Natural History).

- Columellaespongia PICKETT, 1969, p. 11 [\*C. woolomolensis PICKETT, 1969, p. 12; OD]. Tubular and branching with deep cloaca; principal spiculofibers cylindroid, extending upwardly and outwardly to external surface from specialized cloacal lining; fibers connected laterally by thinner spiculofibers so as to outline polygonal to rounded, external pores and corresponding canals between principal fibers, presumably associated with inhalant canals; cloaca lined by denser net in which principal fibers are horizontal and outline horizontal, exhalant canals that open as large, round pores on cloacal surface and extend back into main net where they subdivide and branch; fibers composed of straight or somewhat curved rhizoclones parallel length of fiber. Devonian (Eifelian-Givetian): Australia (New South -FIG. 105a-d. \*C. woolomolensis; a, ex-Wales).terior of holotype, fragment of large, cylindrical sponge showing skeletal pores and dimensions of dermal, skeletal net, Timor Limestone, County Brisbane,  $\times 1$ ; *b*, vertical section through holotype showing large, cylindrical spongocoel and thick walls with skeletal tracts that diverge upwardly and outwardly, Timor Limestone, County Brisbane, AM F13723, ×1; c, reference specimen, drawing of transverse section showing differentiated, dermal and gastral parts of skeleton, with radial canals interrupting endosomal structure, Moore Creek Limestone, County Inglis, AM F1064, ×1; d, reference specimen, vertical section showing gastral layer and upwardly divergent, endosomal, skeletal tracts, Moore Creek Limestone, County Inglis, AM F10508, ×1 (Pickett, 1969).
- Crawneya PICKETT, 1969, p. 13 [\*C. massiva; OD]. Massive, irregular, possibly encrusting; spiculofibers radial and normal to outer, upper surface; connected by thinner, lateral fibers; outer surface bearing polygonal, rounded to irregular,

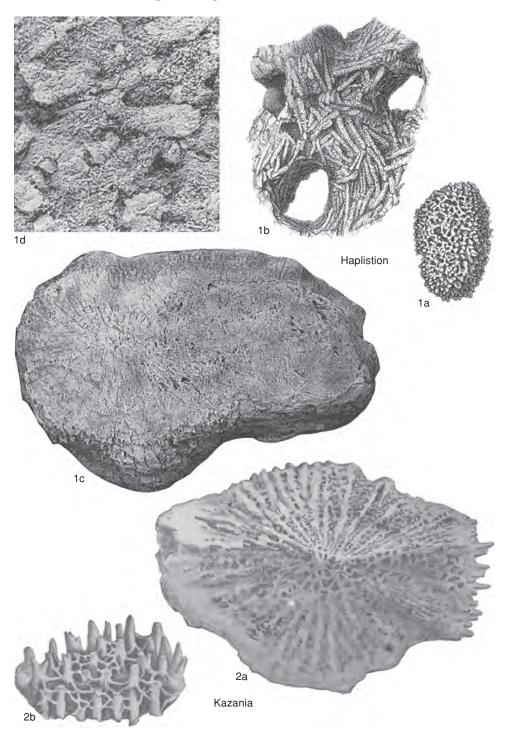


FIG. 102. Haplistiidae (p. 141–145).

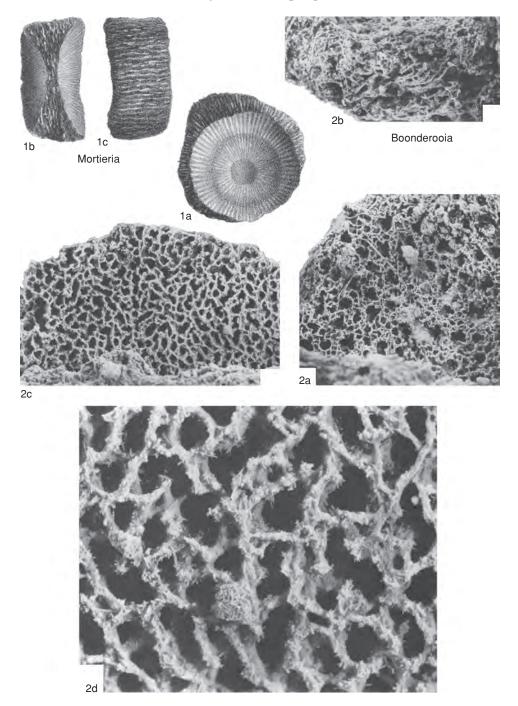


FIG. 103. Haplistiidae (p. 142-148).

submeandriform pores; large, radial canals of interior do not emerge at surface but are covered by skeletal net; fibers composed of straight to curved rhizoclones. *Devonian (?Eifelian):* Australia (New South Wales).——FIG. 106, 1a-b. \**C. massiva*, Timor Limestone, County Brisbane; *a*, fractured end of holotype showing radiate, skeletal, and canal structure in massive sponge, ×0.8; *b*, side view

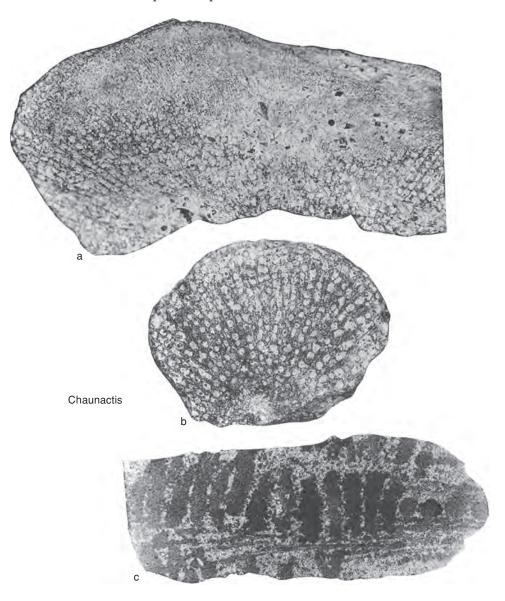


FIG. 104. Haplistiidae (p. 142).

of holotype showing variation in ostia of canals and radiate, skeletal tracts in fractured areas, AM F4896, ×0.8 (Pickett, 1969).

Kazania STUCKENBERG, 1895, p. 183 [\*K. elegantissima; SD TSCHERNYSCHEV, 1898, p. 14]. Resembles Haplistion but differs in that spiculofibers are cored by long, smooth oxeas, and in that tangential, connecting fibers are frequently branched or anastomosing. Permian (Artinskian): Russia (Ural Mountains).—FIG. 102,2a-b. \*K. elegantissima, upper Kohlenkalksteine; a, radial section of ellipsoidal holotype, ×0.5; b, section of skeleton showing rodlike trabeculae and cross-connecting fibers, ×1 (Stuckenberg, 1895).

Lewinia RIGBY & WEBBY, 1988, p. 22 [\*L. cavernosa; OD]. Obconical to open disclike, cavernous with skeleton dominantly of vertical rods and weblike blades in regular, upwardly and outwardly expanded, radiating pattern pierced by large, vertical canals; tracts with coring monaxons, vertical tracts cross braced by horizontal tracts or single spicules that may radiate in pincushion-like patterns; dense, dermal layer over base and sides. Upper Ordovician: Australia (New South Wales).—FIG.



FIG. 105. Haplistiidae (p. 142).

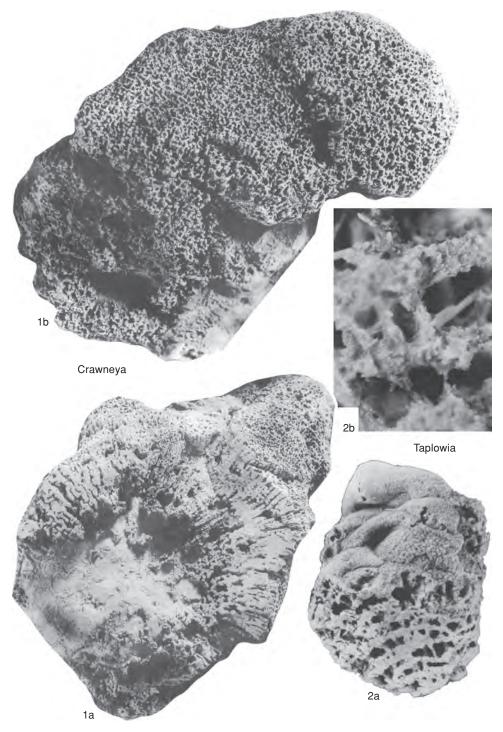


FIG. 106. Haplistiidae (p. 142–152).

107,1*a–b.* \**L. cavernosa*, Malongulli Formation, Cliefden Caves area; *a*, broken base of holotype showing major canals parallel to and normal to vertical, skeletal tracts of rhizoclones interior to dense, dermal layer, AMu. F66797, ×2; *b*, photomicrograph of skeletal structure of paratype showing vertical tracts cross connected by ropy tracts or by single rhizoclones that produce weblike texture of skeleton; large, vertical canals cross connected by smaller, horizontal openings, AMu. F66798, ×10 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- ?Monarchopemmatites DE LAUBENFELS, 1947, p. 187, nom. nov. pro Pseudopemmatites KING, 1943, p. 12, non FRAIPONT, 1911 [\*Pseudopemmatites skinneri KING, 1943, p. 16; OD]. Identical in external form, skeletal net, and rhizoclone spiculation to Pemmatites DUNIKOWSKI, 1884, p. 13, and Haplistion YOUNG & YOUNG, 1877, p. 428. The type species was included in Hapliston by FINKS (1960). [That placement is followed here, and for that reason the genus is not illustrated herein.] Permian (Artinskian): USA (Texas).
- Mortieria DE KONINCK, 1842 in 1842-1844, p. 12 [\*M. vertebralis; OD]. Biconcave discs or short cylinders, thickening from center to maximum at cylindrical, outer edge (possibly originally growing about a now-disappeared algal stalk or similar object); vertical edge a sharp rim; outer surfaces may bear closely spaced, long, smooth oxeas, arranged radially on upper and lower surfaces and vertically on outer edge; similar spicules may be present in interior; upper and lower surfaces bearing radial rows of circular to oval pores of vertical canals subparallel to (convex toward) outer edge where canals are represented by vertical, surface grooves; internal skeleton an open meshwork of desmas organized into continuous, radial, vertical lamella between rows of canals, connected by concentric, vertical lamella that outline canals; desmas appear to be dendroclones (or dendroclone-shaped spiculofibers), chiastoclones (or chiastocloneshaped spiculofibers), and possible rhizoclones; the so-called dendroclones may have their axes horizontal and connect radial fibers. [Genus is similar to Chaunactis FINKS.] Carboniferous (Tournaisian)-Permian (Kungurian): North America, Europe, Timor.--FIG. 103, 1a-c. \*M. vertebralis, Europe, a, view from above of discoidal sponge with broad, depressed, gastral surface; b, vertical section showing thinned, medial part and thicker, marginal parts of specimen; c, side view showing vertical ribbing of dermal margin, ×1 (de Koninck, 1842).
- Nipterella HINDE, 1889b, p. 144 [\**Calathium paradoxicum* BILLINGS, 1865, p. 358; OD]. Cylindrical, expanded basally, upper surface shallowly concave, canals perpendicular to surface; spicules largely rhizoclones (or possibly chiastoclones); poorly known. *Lower Ordovician*: Canada.— FIG. 108,2*a*-*b*. \**N. paradoxicum* (BILLINGS), Romaine Formation, Mingan Islands, Quebec; *a*, side view of holotype, ×1 (Billings, 1865); *b*, isolated

rhizoclone spicules from holotype, ×50 (Hinde, 1889b).

- Oremo PICKETT, 1969, p. 14 [\*O. fibrosus; OD]. Spheroidal to irregular; no cloaca; principal spiculofibers radial, connected by thinner, lateral fibers composed of straight or curved rhizoclones parallel to length of fibers; exterior with numerous fine, irregular pores. [Genus differs from Crawneya PICKETT, 1969, chiefly in absence of large, internal canals and in somewhat less regular spiculofibers. Haplistion robustum PICKETT, 1969, is here considered an Oremo, a possibility suggested by its author.] Devonian (?Eifelian-?Givetian): Australia (New South Wales) .---- FIG. 109a-c. \*O. fibrosus, Moore Creek Limestone, ?Eifelian, County Inglis; a, holotype showing dimensions of columella-like, skeletal tracts and their orientations, AM F12833,  $\times 1$ ; b, reference specimen showing lower range of dimensions of skeletal tracts in divergent, skeletal structure, AM F, ×1; c, photomicrograph of skeletal tracts composed of numerous rhizoclones in holotype, AM F12833, ×30 (Pickett, 1969).
- Parodospongia RIGBY & CHATTERTON, 1989, p. 13 [\*P. euhydra; OD]. Thin-walled, cuplike or bowl shaped with deep spongocoel; skeleton of rhizoclone tracts, bladelike in middle and gastral parts of wall, anastomosed and upwardly oriented around canals that enter horizontally, but rise steeply to gastral margin; tracts of loosely spaced, small rhizoclones subparallel to axes, with ragged surfaces. Silurian (Ludlow): Canada (Northwest Territories, Baillie-Hamilton Island).-FIG. 108, 1a-c. \*P. euhydra, Cape Phillips Formation, Baillie-Hamilton Island; a, side view of gastral surface of holotype with moderately coarse, irregular canals bounded by ragged tracts of rhizoclones in upwardly expanding skeleton, ×1; b, photomicrograph of gastral surface with ragged tracts of closely packed rhizoclones, ×10; c, photomicrograph of dermal surface with tracts of rhizoclones around inhalant ostia, UA 7699, ×10 (Rigby & Chatterton, 1989; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).
- ?Pemmatites DUNIKOWSKI, 1884, p. 13 [\*P. verrucosa; SD DE LAUBENFELS, 1955, p. 49]. Spheroidal, discoidal, or lobate; no cloaca; spiculofibers cylindroid and radial with tangential connections forming a polygonal, mainly quadrate mesh; fibers composed of subparallel rhizoclones and smooth oxeas. [Genus is identical to Haplistion YOUNG & YOUNG, unless that genus lacks rhizoclones; Pemmatites is here considered a junior synonym of Haplistion, and is therefore not illustrated herein.] Permian: Spitzbergen.
- ?Radiatospongia WOLFENDEN, 1959, p. 567 [\*R. carbonaria; OD]. Skeletal net identical in form and proportions to that of *Haplistion* YOUNG & YOUNG and *Pemmatites* DUNIKOWSKI. [In the original description the skeletal fibers were interpreted as canals. No spicules were reported, and none have been discovered in subsequent investigation

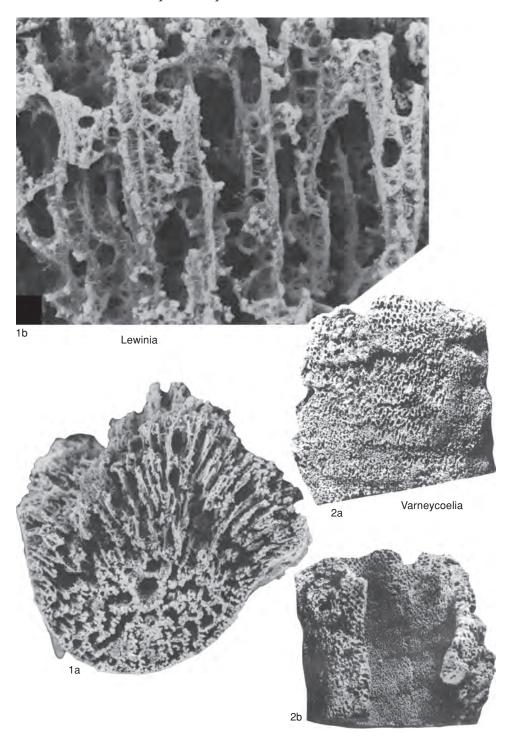


FIG. 107. Haplistiidae (p. 145–152).

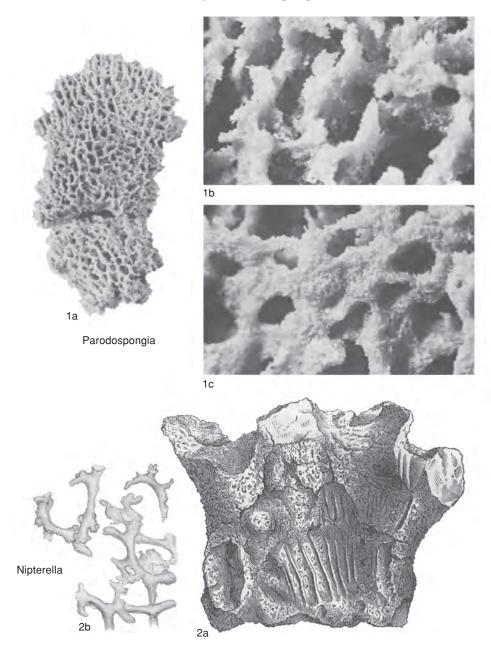


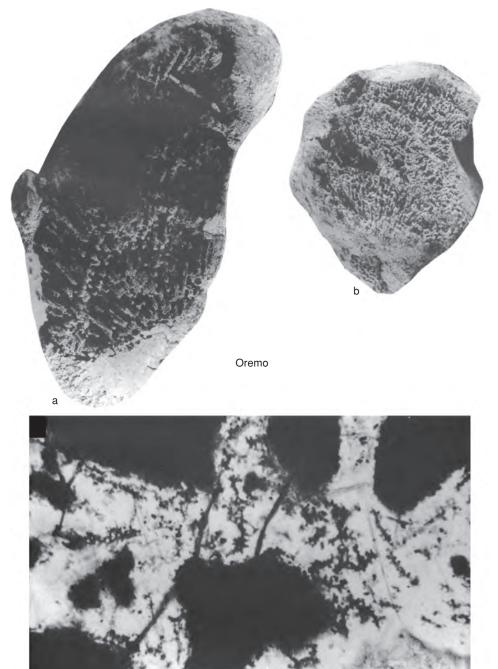
FIG. 108. Haplistiidae (p. 148).

of original material, nor in additional topotype specimens. It is herein considered a junior synonym of Haplistion on assumption that should spicules be found they will prove to be rhizoclones. For that reason it is not illustrated herein.] Carboniferous (Visean): England. ?Rhaphidhistia CARTER, 1878, p. 140 [\*R.

vermiculata; OD]. The sole specimen, a small

hemisphere, comes from the type locality of Haplistion YOUNG & YOUNG; it appears identical to Haplistion (see HINDE, 1887b, pl. 5,1-2) and, thus, is not illustrated herein. Carboniferous (Visean): Scotland.

**Taplowia** RIGBY & WEBBY, 1988, p. 21 [\**T. ordinata;* OD]. Strongly obconical, regular stromatoporoidlike with pillarlike and lamina-like vertical and



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FIG. 109. Haplistiidae (p. 148).

horizontal elements of tracts of rhizoclones, tracts dividing sponge into chambers; pillarlike tracts limited between chamber floors; horizontal tracts at uniform levels; dense, dermal net of fused, tilelike, small rhizoclones. Upper Ordovician: Australia (New South Wales).——FIG. 106,2*a*-*b*. \**T. ordinata*, Malongulli Formation, Cliefden Caves area; *a*, side view of holotype with irregular,

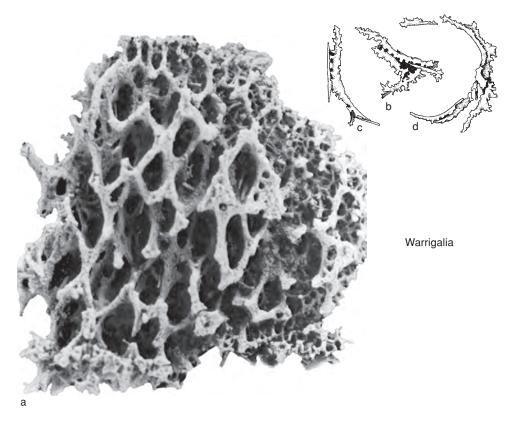


FIG. 110. Haplistiidae (p. 152).

bulbous upper part and tangential view of inner part with pillars and floors all composed of bundled rhizoclones, ×4; *b*, photomicrograph of tracts composed of small, bundled rhizoclones, AMu. F66796, ×20 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- Varneycoelia PICKETT, 1969, p. 10 [\*V. favosa; OD]. Cylindrical, thin-walled, with deep, broad cloaca; exterior and cloacal surfaces bearing subdued, horizontal swellings and contractions; spicular net of straight, subparallel rhizoclones forming thin, porous walls between closely packed, radial, horizontal canals of polygonal to rounded outline; wall resembles a honeycomb in tangential section; canals open as rounded pores of somewhat smaller diameter on both cloacal and exterior surfaces. Lower Devonian: Australia (New South Wales). -FIG. 107, 2a-b. \* V. favosa, Gara beds, Wellington Caves; a, side view of cylindrical holotype with aligned ostia of canals in uniform, skeletal mesh,  $\times 1$ ; b, vertical section of holotype with thick walls around axial spongocoel, AM F19973, ×1 (Pickett, 1969).
- Warrigalia RIGBY & WEBBY, 1988, p. 18 [\*W. elliptica; OD]. Thin-walled, flabellate to massive sheetlike or obconical to bladed sponges, interior, skeletal

tracts undulating or anastomosing, irregular ribbons beneath differentiated, dermal layer; tracts of long, tightly packed rhizoclones without coring monaxons, tracts locally cross braced with isolated dendroclones. Upper Ordovician: Australia (New South Wales).—FIG. 110a-d. \*W. elliptica, Malongulli Formation, Cliefden Caves area; a, fragment of holotype showing elliptical canals limited by tracts of bundled rhizoclones in interior and finer textured, dermal layer around right margin, AMu. F66792, ×10; b-d, camera lucida drawings of silicified spicules of holotype; b, irregular cluster of rhizoclones of several sizes; c, curved rhizoclone attached with zygomes to small, coring oxeas; d, curved rhizoclones with smooth surfaces around a pore and articulations on opposite side in interior of skeletal tract, ×50 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

#### Family UNCERTAIN

Sentinelia WALCOTT, 1920, p. 289 [\*S. draco WALCOTT, 1920, p. 290; OD]. Flat to gently lobate or rounded, frondescent sponges marked by low, rounded tubercules to elongate mounds a few

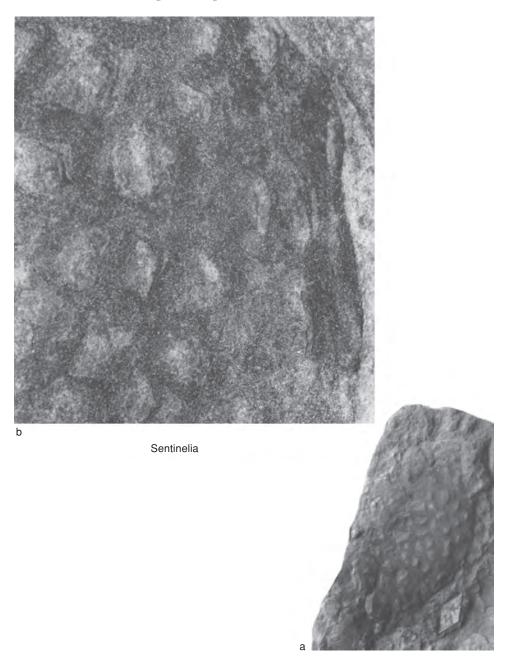


FIG. 111. Uncertain (p. 152-153).

millimeters in diameter, rising less than 1 mm above the general surface; small openings piercing tubercules and entire openings may have been parietal gaps; skeleton of irregular, monaxial spicules, perhaps with a dermal layer of even smaller, monaxial spicules. *Middle Cambrian:* USA (Utah).——FIG. 111*a–b. \*S. draco,* Wheeler Formation, House Range; *a*, nodose, holotype fragment of bun-shaped sponge, ×1; *b*, enlargement showing linear fabric of elongate, possible monaxons in tracts between canal openings, USNM 66478, ×5 (Rigby, 1986a).

## Subclass TETRACTINOMORPHA Lévi, 1953

#### [nom. correct. BERGQUIST, 1967, p. 166, pro subclass Tétractinomorphes LEVI, 1953, p. 855]

Principal spicules typically tetraxons, which may be accompanied by oxeas or styes; microscleres are euasters or streptoscleres, which may be accompanied by microrhabds; sigmas are not present. Ordovician-Holocene.

# Order STREPTOSCLEROPHORIDA Dendy, 1924

[nom. correct. FINKS & RIGBY, herein, pro Streptosclerophora DENDY, 1924b, p. 249; emend., FINKS & RIGBY, herein]

Living forms with streptosclere microscleres; lithistid forms built of layers of anapodal spicules, which may be accompanied by other types of desma (rhizoclones, tetraclones); dermal spicules consisting of radial dichotriaenes and derivatives in Mesozoic and later forms, radial oxeas in Paleozoic forms, and also include tangential, dermal monaxons (oxeas, strongyles) and derivatives (plates, discostrongyles). Upper Ordovician–Permian (Changhsingian).

## Suborder EUTAXICLADINA Rauff, 1894

[nom. transl. ZITTEL, 1895, p. 49, ex tribus Eutaxicladinidae RAUFF, 1894, p. 280; emend., FINKS & RIGBY, herein] [=Tricranocladina REID, 1968a, p. 24]

Principal spicules tricranoclones, which may be accompanied by megarhizoclones; dermal spicules radial, large oxeas (and possibly strongyles) and tangential, small oxeas and strongyles. *Upper Ordovician–Permian* (Lopingian).

### Family HINDIIDAE Rauff, 1893

[nom. correct. FINKS, 1960, p. 97, pro Hindiadae RAUFF, 1894, p. 327] [=Microspongiidae MILLER, 1889, p. 153]

Skeleton of concentric or parallel layers of anapodal tricranoclones with approximation of hexagonal packing in each layer; spicules occupying corresponding positions in each layer so as to form radial stacks that outline radial, skeletal canals between them, opening as pores on outer surface; each tricranoclone has a short, distal arm in most early Paleozoic forms that is absent in late Paleozoic forms, and three distally convex, proximal arms (occasionally four) whose ends are terminally expanded into concave, articular facets and whose distal surfaces are generally covered with spheroidal tubercles; each proximal arm bearing articular facets of overlying tricranoclones on its distal surface near centrum; in Scheiella megarhizoclones occupying spaces between tricranoclones; possible dermal skeleton of radial and tangential oxeas present in some genera, with radial oxeas occupying radial canals. [MILLER (1889, p. 153) included in his family Microspongiidae both Microspongia and Hindia, which he considered to be separate genera. Because the identity of the nominal genus is doubtful (see below) and is here considered unrecognizable, the later family name Hindiidae is used instead for this taxon.] Upper Ordovician-Permian (Changhsingian).

Hindia DUNCAN, 1879, p. 91, nom. conserv., proposed RIGBY, 2004, ICZN pending, application 3316 [\*H. sphaeroidalis; OD] [=Sphaerolites HINDE, 1875, p. 88 (type, S. nicholsoni, OD); ?Microspongia MILLER & DYER, 1878, p. 37 (type, M. gregaria, OD)]. Spheroidal; three-armed tricranoclones in radially stacked series; spicules with short, crownlike brachyome and with tubercles or projections on distal surface of thin-armed cladome and on brachyome; cladi articulate at base of brachyome; radial canals and pores of two sizes (smaller inhalant and larger exhalant), but large oscules absent; radial and tangential oxeas present. [Sphaerolites HINDE, 1875 has priority, for it was based on the same specimens as Hindia DUNCAN, 1879 (fide HINDE, 1888, p. 115). The original description of Microspongia Miller & Dyer, 1878 does not correspond to that of Hindia DUNCAN (neither does that of Sphaerolites) and the types are lost (fide ULRICH, 1890a, p. 228-229). Retention of the more widely used name Hindia is recommended here (ICZN ruling pending, application 3316).] Upper Ordovician-Lower Devonian: North America, Europe, Australia.——FIG. 112,2a-c. \*H. sphaeroidalis; a, silicified, spherical sponge with flattened base, Silurian, Gotland, Sweden, ×1; b, median section showing radiate, canal pattern defined by radial series of stacked spicules, Silurian, near St.

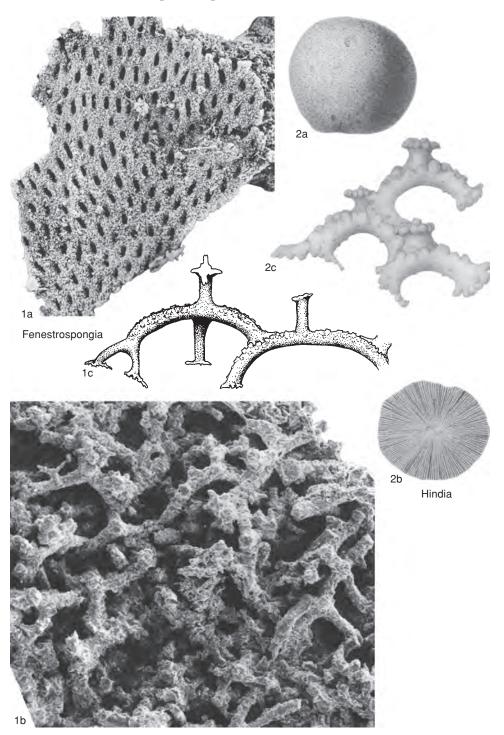


FIG. 112. Hindiidae (p. 154–158).

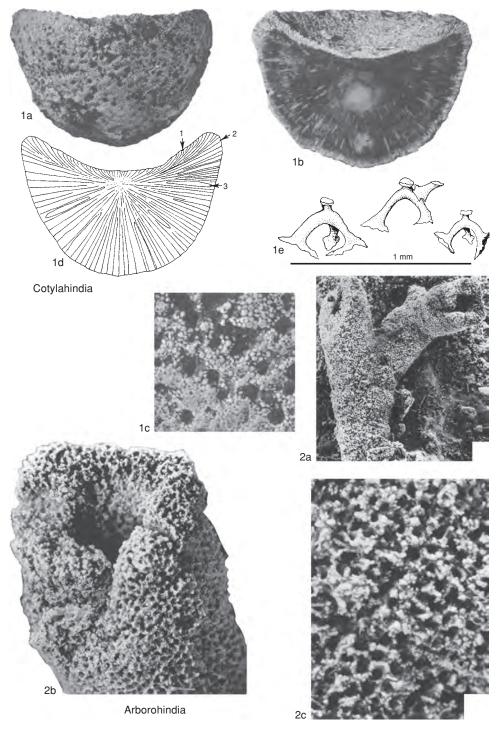


FIG. 113. Hindiidae (p. 157–158).

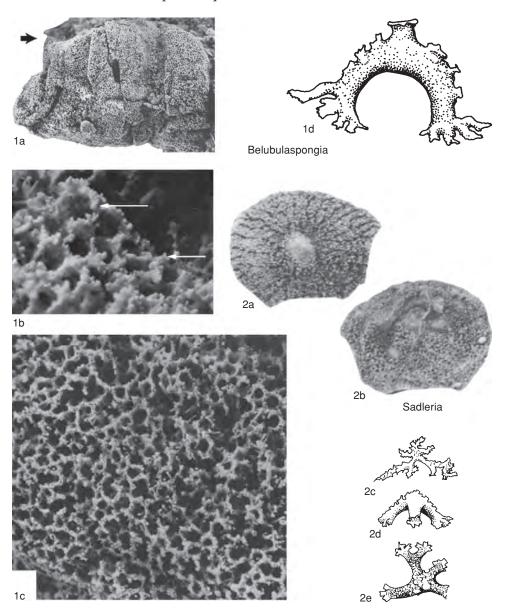


FIG. 114. Hindiidae (p. 158-164).

Petersburg, Russia, ×1; *c*, drawing of relationships of tricranoclone spicules characteristic of genus and family, Silurian, Gotland, ×120 (Rauff, 1893).

Arborohindia RIGBY & WEBBY, 1988, p. 70 [\*A. uniforma; OD]. Small, branching, subcylindrical hindiids with deep spongocoel; walls generally without canals other than uniformly spaced, skeletal pores between spicules; skeleton of normal tricranoclones with pronounced brachyomes and three sculptured, cladome rays, arranged in layers parallel to upwardly convex, growing margin of wall. [Belubulaspongia RIGBY & WEBBY, 1988, is a related larger, unbranched sponge, but with a similar skeletal structure.] Upper Ordovician: Australia (New South Wales).—FIG. 113,2a-c. \*A. uniforma, Malongulli Formation, Cliefden Caves area; a, side view of branching holotype showing upper end of tubular, axial spongocoel and uniform, skeletal structure,  $\times 2$ ; *b*, enlarged oscular end of branch with rounded, oscular margin and walls generally without canals other than interconnecting pores between normal tricranoclones,  $\times 8$ ; *c*, photomicrograph of dermal layer with dermal tricranoclones that have nodose, distal structure on cladome rays that surround circular pores, AMu. F66882,  $\times 18$  (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

- Belubulaspongia RIGBY & WEBBY, 1988, p. 63 [\*B. gigantea; OD]. Tubular, unbranched, relatively large, hindiid sponges with deep, central spongocoel; skeleton of stacked tricranoclones with prominent brachyome; spicules added parallel to rounded, upper edge of wall, but do not produce lamination in skeleton; canal system ill defined as crude, upwardly and outwardly radiating, skeletal pores. Upper Ordovician: Australia (New South Wales).----FIG. 114, 1a-d. \*B. gigantea, Malongulli Formation, Cliefden Caves area; a, side view of nearly complete, conicocylindrical holotype, ×1; b, photomicrograph of weathered, silicified surface showing sculptured, distal surfaces of cladomes of spicules and bifid brachyomes that project distally (arrows), ×18; c, photomicrograph of dermal layer of uniform skeleton with undifferentiated tricranoclones with three cladomes tangentially around circular ostia, ×8; d, sketch of side view of isolated tricranoclone showing distal ornamentation on cladomes that have digitate tips and are approximately 0.5 mm long with prominent brachyome on top, AMu. F66869 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Cotylahindia RIGBY & BAYER, 1971, p. 617 [\*C. panaca RIGBY & BAYER, 1971, p. 618; OD]. Open, thick-walled, bowl-shaped sponge with massive base and shallow, broad spongocoel; base pierced by canals of three sizes that radiate from point within base, except in upper few millimeters where they curve abruptly upwardly into spongocoel; spicules moderately smooth tricranoclones in which clonomes weakly curved to straight and in which brachyome short but distinct. upper Upper Ordovician: USA (Minnesota).-—FIG. 113,1*a–e.* \*C. panaca, Richmondian, Maquoketa Formation, Fillmore County; a, side view of exterior of holotype with dark matrix filling inhalant canals; b, vertical section showing radiating canals below base of broad spongocoel, ×1; c, photomicrograph of dermal surface showing canals and skeletal pores defined by rays of adjacent tricranoclones,  $\times$ 3; d, sketch of vertical section showing orientation of canals that flex up into floor of spongocoel and radiate upwardly and downwardly in outer parts of skeleton, approximately ×1; e, camera lucida drawings of isolated tricranoclones from silicified holotype, UM 9150, ×47 (Rigby & Bayer, 1971).

- Fenestrospongia RIGBY & WEBBY, 1988, p. 74 [\*F. explanata; OD]. Fenestrate appearing, thin, saucerlike sponges with principal, round, skeletal tracts composed of compactly spaced, tiny tricranoclones, on which a prominent brachyome rises above long, thin, arcuate clonomes; two series of strong tracts cross diagonally to produce elliptical openings. Upper Ordovician: Australia (New South Wales).----FIG. 112, 1a-c. \*F. explanata, Malongulli Formation, Cliefden Caves area; a, concave, gastral surface of holotype showing regular, round, spicule tracts and fenestrate form of sponge, ×2; b, SEM photomicrograph showing narrow-rayed tricranoclones in felted structure with three long, cladome rays tangential to surface and vertical, brachyome rays, ×100; c, sketch of articulated spicules from side showing weakly sculptured, long, cladome rays and prominent, vertical brachyomes, AMu. F66890, spicules 0.3 to 0.4 mm across (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- Mamelohindia RIGBY & WEBBY, 1988, p. 72 [\*M. planata RIGBY & WEBBY, 1988, p. 73; OD]. Saucer-shaped to stalked, explanate hindiid in which upper, gastral surface marked with low, mamelon-like nodes, particularly above stalk; canals moderately well defined and pinnately arranged about midwall axis; skeleton of tricranoclones without brachyomes but ray junction marked with small hemisphere, nodes, and cylinders; dermal layer of thickened tricranoclones. [Cotylahindia RIGBY & BAYER, 1971, is also a bowl-shaped hindiid, but it has a prominent, radiate skeleton and different canal pattern; Scheiella FINKS, 1971b, and Sadleria RIGBY, 1986b, lack the mamelon-like nodes on the gastral surface and have more complex skeletons.] Upper Ordovician: Australia (New South Wales).-FIG. 115a-d. \*M. planata, Malongulli Formation, Cliefden Caves area; a, vertical view of upper gastral surface of holotype with distinctive mounds in central part where spicules are particularly swollen, dark, excurrent ostia scattered across surface,  $\times 2$ ; b, lower surface of holotype showing uniform skeleton interrupted by coarse, incurrent ostia and broken stalk, ×2; c, side view of holotype with weakly stalked base and complete, rounded, growing margin, ×2; d, photomicrograph of dermal skeleton showing triangular-appearing tricranoclones with strongly nodose centra and distal parts of cladomes, largest openings are incurrent ostia, AMu. F66885, ×20 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
- ?Microspongia MILLER & DYER, 1878, p. 37 [\*M. gregaria; OD]. Originally described as a spheroidal, calcareous sponge with fibrous or finely porous texture, without large canals or openings on surface and with minute, needle-shaped spicules. [Genus may be the same as *Hindia* DUNCAN, 1879 (MILLER, 1889, p. 160, expressed doubt as to such

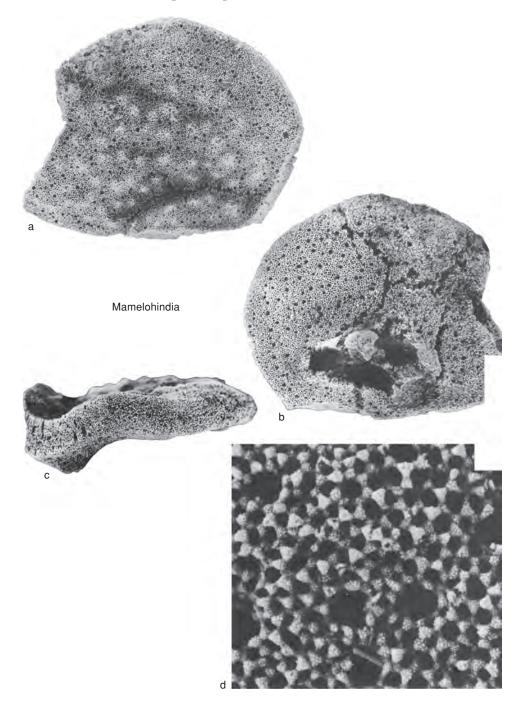


FIG. 115. Hindiidae (p. 158).

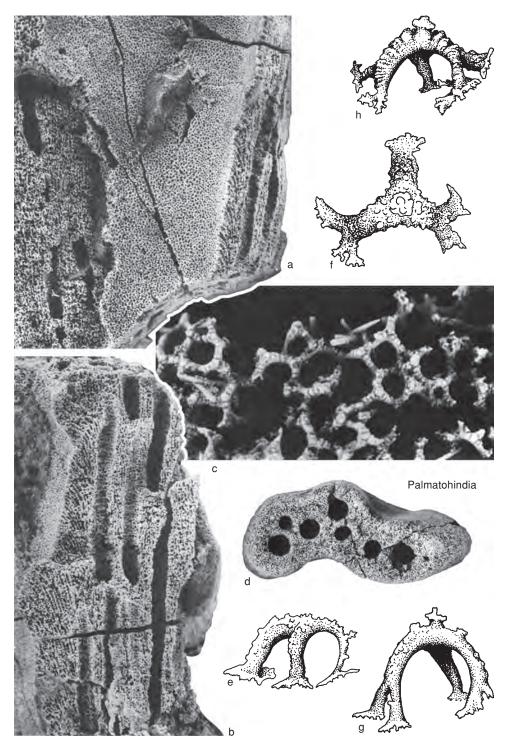


FIG. 116. Hindiidae (p. 162–163).

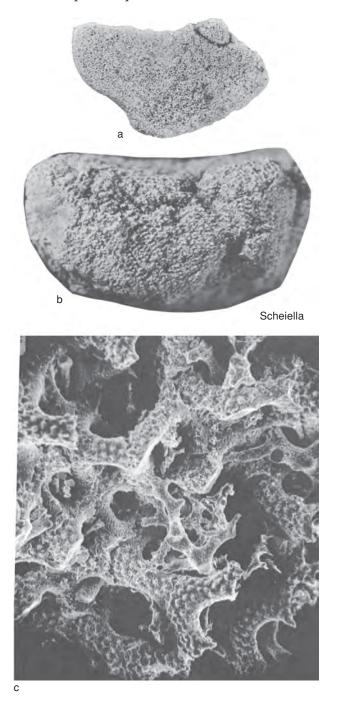


FIG. 117. Hindiidae (p. 164).

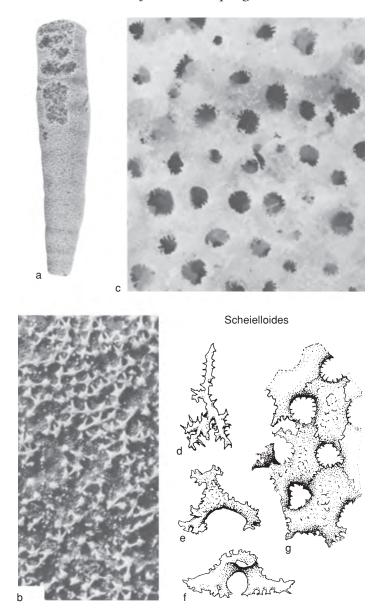


FIG. 118. Hindiidae (p. 164).

a synonymy); the types are lost (see *Hindia* above), and it must be considered unrecognizable.] *Upper Ordovician:* USA (Ohio).

Palmatohindia RIGBY & WEBBY, 1988, p. 65 [\*P. multipora; OD]. Vertically palmate to bladed hindiids with blades perforated along blade axis by numerous vertical, excurrent canals; skeleton of normal tricranoclones oriented with brachyomes vertical or normal to arcuate, growing surface; dermal layer of thickened tricranoclones. Upper Ordovician: Australia (New South Wales).——FIG. 116*a*–*h*. \**P. multipora*, Malongulli Formation, Cliefden Caves area; *a*, diagonal side view of holotype showing uniform ostia in dense, dermal layer and upwardly divergent stacks of tricranoclones on broken end where two large, subparallel, excurrent canals also show, ×2; *b*, broken end showing multiple vertical, excurrent canals and upwardly diver-

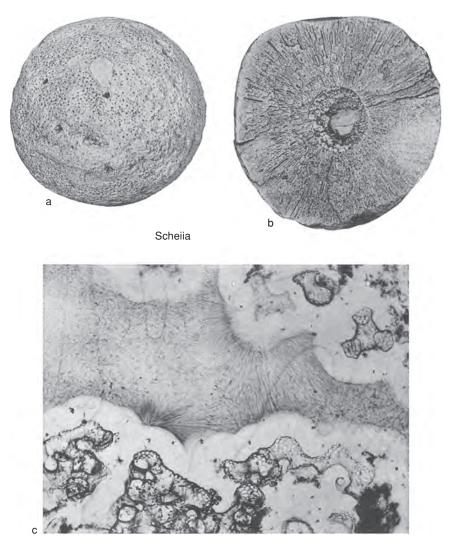


FIG. 119. Hindiidae (p. 164).

gent stacks of spicules terminating at dense, dermal layer, AMu. F66871,  $\times 2$ ; *c*, photomicrograph of tricranoclones with sculptured, distal surfaces of cladome rays and nodose or swollen, central brachyomes, shown in profile in upper, central part of figure, paratype, AMu. F66877,  $\times 20$ ; *d*, horizontal section of relatively small, undulating, bladed paratype and size and spacing of excurrent canals along midline of blade, AMu. F66873,  $\times 2$ ; *e*-*h*, camera lucida drawings of spicules from holotype, cladome rays 0.3 to 0.4 mm long (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

Sadleria RIGBY, 1986b, p. 31 [\*S. pansa RIGBY, 1986b, p. 32; OD]. Small, funnel-shaped hindiid sponge in which major, irregular canals interrupt somewhat irregular skeleton composed predominantly of nodose, tripodal tricranoclones and less common, tetrapodal tricranoclones, megarhizoclones, and small, spinose rhizoclones; rare, monaxonid spicules occurring in canals; dense, dermal and gastral layers both composed of swollen spicules. *Devonian (Frasnian):* Australia (Western Australia).——FIG. 114,2*a–e.* \**S. pansa,* Sadler Formation, Sadler Ridge; *a*, view from below of holotype showing prominent, tangential canals in thin walls above rounded base, ×2; *b*, view into broad, shallow spongocoel showing numerous small, exhalant ostia and thin walls, ×2; *c–e*, camera lucida drawings of isolated spicules from holotype, including a megarhizoclone and more common, sculptured tricranoclones with three and four clonomes, GSWA F7220, ×50 (Rigby, 1986b).

- Scheiella FINKS, 1971b, p. 978 [\*S. thesaurium FINKS, 1971b, p. 979; OD]. Flattened and cake shaped; tricranoclones as in Scheiia but with a substantial minority four armed; combined in principal net with megarhizoclones, which are especially abundant on basal surface; net more open and somewhat less regular than in Scheiia; radial and tangential oxeas present. Permian (Capitanian): USA (Texas).—FIG. 117a-c. \*S. thesaurium, Bell Canyon Formation, Guadalupe Mountains; a, upper surface of cakelike holotype, coarse canals absent,  $\times 2$ ; *b*, broken side of holotype with vertical rows of superposed tricranoclones but no coarse canals, ×6; c, scanning electron photomicrograph of holotype fragment with nodose tricranoclones and smaller megarhizoclones, USNM 170273, ×100 (Finks, 1971b).
- Scheielloides RIGBY, 1986b, p. 28 [\*S. conica RIGBY, 1986b, p. 29; OD]. Conicocylindrical to obconical with deep spongocoel; skeleton moderately regular, dominantly of tricranoclones but with some tetrapodal and bipodal spicules, generally arranged with clonomes toward base and knobby surfaces distally; spicules without brachyome but in armourlike, dermal layer with swollen, hemispherical knob in place of brachyome; small, spinose rhizoclones throughout; rare, radial monaxons; differentiated canals absent. Devonian (Frasnian): Western Australia. ——FIG. 118a-q. \*S. conica, Sadler Limestone, Sadler Ridge; a, side view of small, subcylindrical holotype, GSWA F7215,  $\times 2$ ; *b*, vertical section through paratype showing cylindrical spongocoel, gastral surface, and nature of skeleton in walls, ×5; c, photomicrograph of gastral layer showing thickened tricranoclones around spinose, circular, exhalant ostia, GSWA F7217, ×50; d-g, camera lucida drawings of isolated spicules, including irregular megarhizoclones, more characteristic tricranoclones, and thickened tricranoclones of gastral layer, GSWA F7217, ×48 (Rigby, 1986b).
- Scheiia TSCHERNYSCHEV & STEPANOV, 1916, p. 14 [\*S. tuberosa; OD]. Spheroidal, tuberose or bun shaped; three-armed tricranoclones without brachyome, with broad, triangular centrum; tricranoclones with four cladi may be present; distal surface of centrum and cladi covered by uniformly spaced, spheroidal tubercles; articulation on surface of centrum and adjacent cladi; larger oscules may be present in addition to pores of two or more sizes; radial and tangential oxeas present. Carboniferous (Visean)-Permian (Changhsingian): North America, USSR (Ural Mountains), Timor.—FIG. 119a-c. \*S. tuberosa, Leonard Formation, Leonardian, Glass Mountains, Texas, USA; a, spherical sponge with small, inhalant and exhalant pores and isolated, larger, exhalant oscula, USNM 127643b, ×1; b, median section with rows of spicules and canals radiating from central hollow, AMNH 28072, ×1; c,

photomicrograph of tricranoclone spicules with swollen centra, rather than distal brachyomes, and with spherical tubercules on distal ray surfaces, USNM 127643c,  $\times$ 50 (Finks, 1960; courtesy of The American Museum of Natural History).

Sphaerolites HINDE, 1875, p. 88 [\*S. nicholsoni; M]. Based on the same specimens as *Hindia* DUNCAN, 1879 (fide HINDE, 1888, p. 115) although described as a favositid coral, this is a senior objective synonym of *Hindia* DUNCAN. Retention of the more widely used name *Hindia* is recommended here (Rigby, 2004, ICZN ruling pending, application 3316). Upper Ordovician–Lower Devonian: North America, Europe, Australia.

# Order MEGALITHISTIDA new order

[Megalithistida Reid, herein] [=Megamorina Zittel, 1878a, p. 99; sensu Zittel, 1878a, p. 99, non Schrammen, 1924a, p. 61]

Lithistids that typically have dermal dichotriaenes and monaxial desmas in form of heloclones or megaclones; dermalia sometimes simple triaenes only or absent, but never phyllotriaenes, discotriaenes, or related types; rarely with additional small rhizoclonids; microscleres of modern examples microrhabds, spirasters, and amphiasters. [Definition and discussion of the order is given by REID (herein, p. 254) in treatment of Mesozoic sponges.] *Lower Ordovician–Holocene.* 

## Suborder MEGAMORINA Zittel, 1878

[nom. transl. SCHRAMMEN, 1924a, p. 38, ex tribus Megamorina ZITTEL, 1878a, p. 99; emend., REID 1968a, p. 23] [=family Megamorinidae SCHRAMMEN, 1910, p. 32]

Principal spicules megaclones, heloclones, or ophirhabds. *Lower Ordovician–Holocene*.

### Family ARCHAEODORYDERMATIDAE Reid, 1968

[Archaeodorydermatidae REID, 1968b, p. 1,253]

### Presumptively sublithistid Megamorina. Carboniferous (Visean).

Archaeodoryderma REID, 1968b, p. 1,253 [\*Doryderma dalryense HINDE, 1884a, p. 210; M]. Isolated spicules grade from ophirhabds through heloclones to simple megaclones; presumed to be from a sublithistid sponge, although a true lithistid, some loose desmoids cannot be ruled out; form of sponge unknown. Carboniferous (Visean): Scot-

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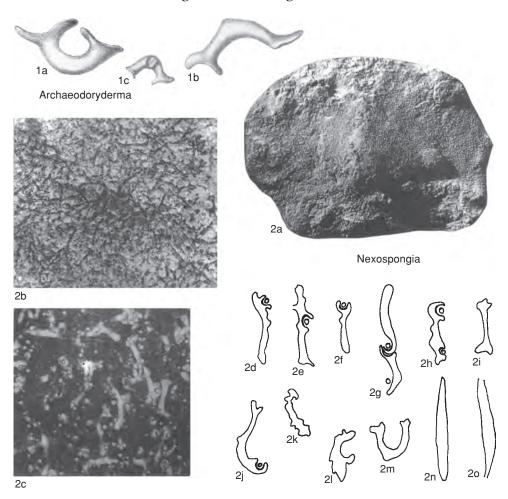


FIG. 120. Archaeodorydermatidae and Nexospongiidae (p. 164-169).

land.——FIG. 120, *Ia–c.* \**A. dalryense* (HINDE), Law Quarry, Dalry, Ayrshire; type suite of isolated spicules, ×28 (Hinde, 1884a).

### Family SACCOSPONGIIDAE Rigby & Dixon, 1979

#### [Saccospongiidae RIGBY & DIXON, 1979, p. 603]

Sponges with skeletal nets of simple, radiating to branching or complexly crossconnected tracts composed dominantly of heloclones with intermixed styles and oxeas or of tracts cored with styles and blanketed with heloclones; megaclones wanting or minor; triaenes unknown. *Lower Ordovician–Silurian (Ludlow, ?Pridoli).* 

- Saccospongia ULRICH, 1889, p. 242 [\*S. rudis; OD]. Ramose, with well-developed, central spongocoel in each branch; sponge surface hispid with subparallel ridges and grooves; principal spiculofibers subparallel to axis of branch, intersecting outer surface obliquely; fibers composed of styles arranged both plumosely and in coring and echinating positions; fibers covered to a variable extent with a layer of heloclonid desmoids. Upper Ordovician: USA (Kentucky, Tennessee, Alabama).——FIG. 121,3. \*S. rudis, Cynthiana Formation, Lexington, Kentucky; side view of subovate holotype showing skeletal fibers and part of impervious basal layer, USNM 465781, ×1 (Ulrich, 1889).
- Cliefdenospongia RIGBY & WEBBY, 1988, p. 27 [\*C. lamina RIGBY & WEBBY, 1998, p. 28; OD]. Curved, thin-walled, possibly tubular; skeleton of tracts of heloclones as principal spicules around coring oxeas, latter particularly evident in dermal

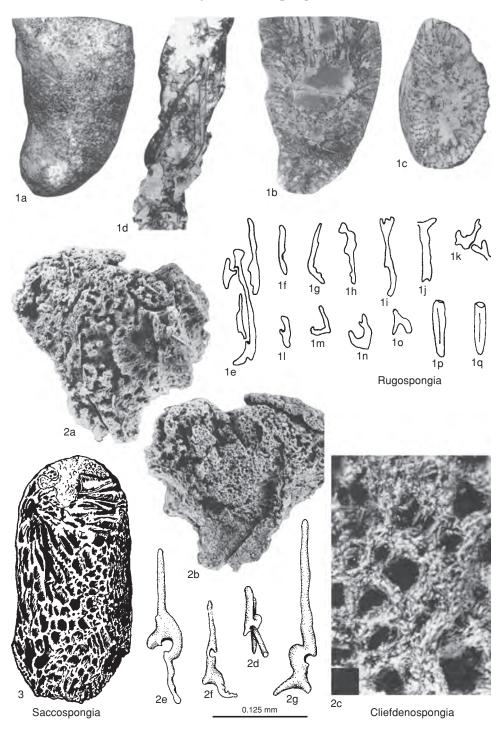


FIG. 121. Saccospongiidae (p. 165-168).

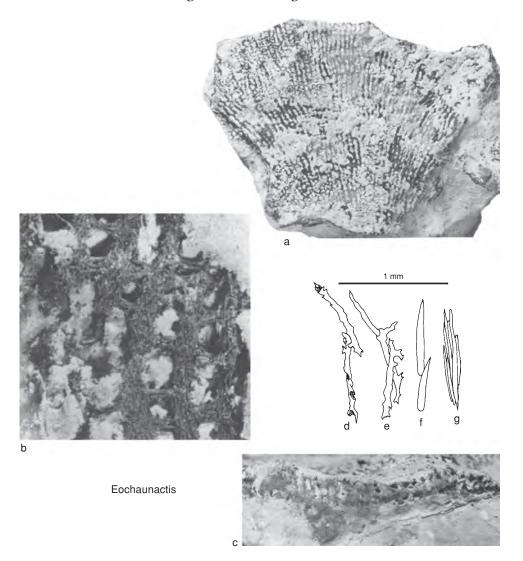


FIG. 122. Saccospongiidae (p. 167-168).

and gastral layers that are moderately thick; may include rhizoclones; tracts generally normal to dermal and gastral layers. *Upper Ordovician*: Australia (New South Wales).——FIG. 121,2*a*-*g*. \**C*. *lamina*, Malongulli Formation, Cliefden Caves area; *a*, holotype from above showing coarse tracts and open canals; *b*, dermal surface of holotype from below showing thick, dermal layer, ×2; *c*, photomicrograph of stout skeletal tracts of short, robust, rhizoclones and heloclones as seen on lower surface, ×25; *d*-*g*, holotype, isolated heloclones with circular, grasping facets, one with an associated oxea, AMu. F66803, ×200 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca). Eochaunactis RIGBY & DIXON, 1979, p. 604 [\**E. radiata* RIGBY & DIXON, 1979, p. 605; OD]. Flabellate, bladed to low, obconical sponges with moderately large canals normal to blade surfaces between uniformly spaced, vertical, finlike tracts of strongly radiating skeleton, radial tracts cross connected at irregular intervals by tracts of smaller diameter; spicules dominantly irregular heloclones, with less common, possible rhizoclones and possible dendroclones; moderately common styles and oxeas concentrated in central parts of strands, although all types occur throughout skeletal net; dermal and gastral layers well differentiated and with less regular, radial structure. *Silurian* (*Ludlou, ?Pridoli*): Canada (Northwest Territories, District of Franklin, Somerset Island).——FIG. 122*a*–*g.* \**E. radiata*, Read Bay Formation, Somerset Island; *a*, upper surface of flabellate holotype with upwardly radiating tracts with partial, undulating dermal layer in upper part, ×1; *b*, photomicrograph of skeletal tracts composed mainly of pyritized heloclones cross connected by smaller, simpler tracts, ×10; *c*, cross section of base showing I-beam shaped tracts, with gastral surface toward top, ×2; *d*–*g*, camera lucida drawings of spicules; *d*–*e*, heloclones; *f*, styles with one hemispherical base; *g*, cluster of oxeas. ×29 (Rigby & Dixon, 1979).

- Epiplastospongia RIGBY, 1977c, p. 2,663 [\*E. coactilis; OD]. Massive sponges with threedimensional, skeletal net of diactines as cores of both ascending and concentric or horizontal fibers; central spicule core of each fiber overgrown and thickened by layered to laminated, smooth, unsculptured, monaxial spicules; canals radiatingascending with horizontal cross connections. [Taxonomic position of the sponge is uncertain but it appears to be related to Saccospongia, and hence is included here with some question.] Middle Ordovician: Canada (Newfoundland) .-FIG. 123a-c. \*E. coactilis, Lourdes Formation, western Newfoundland; a, side view of holotype with base toward lower left and with section through skeleton with ascending, spicular columns and reticulate, outer surface on right, ×1; b, photomicrograph of horizontal section through holotype showing canal characteristics and skeletal net near periphery of sponge; canals markedly restricted by secondary overgrowth of coring skeletal net by laminated, concentric spicules,  $\times 10$ ; c, horizontal section across a clustered series of coring spicules (arrow), blanketed by laminated to concentrically arranged spicules in lower center, GSC 53763, ×100 (Rigby, 1977c).
- Haplistionella RIGBY & DIXON, 1979, p. 608 [\*H. garnieri RIGBY & DIXON, 1979, p. 609; OD]. Low, obconical to flabellate sponge with skeleton of robust, irregularly branching, radiating tracts cross connected by irregular mesh of considerably finer, textured tracts; major canals parallel large, radiating elements but connected laterally by numerous short canals; tracts cored by plumosely arranged, smooth monaxons and heloclones associated with moderately smooth, rare, possible rhizoclones and coated by heloclones; no well-defined dermal layer. Silurian (Ludlow, ?Pridoli): Canada (Northwest Territories, Somerset Island).-FIG. 124af. \*H. garnieri, Read Bay Formation, Somerset Island; a, vertical cross section through central part of holotype showing low, obconical form, broad, saucerlike spongocoel, and irregular base, ×1; b, vertical view of base showing radiating, branching, skeletal tracts in light gray matrix, ×1; c, photomicrograph of pyritized, radial, skeletal tract and branching, lateral tracts, both made dominantly of heloclones, ×20; d-f, camera lucida drawings of spicules etched from holotype, d-e, heloclones, and f, curved style with rounded,

proximal base, GSC 54834, ×36 (Rigby & Dixon, 1979).

Rugospongia CARRERA, 1996, p. 644 [\*R. viejoensis; OD]. Obconical to steeply obconical sponges with a moderately deep spongocoel; skeleton of vertical and web tracts of heloclones and monaxons as principal spicules that parallel main axes of tracts, monaxons irregularly distributed along tracts; tracts may include megaclones and rhizoclones; skeletal structure expanding upwardly and outwardly and is roughly paralleled by large, vertical and horizontal canals; exterior with moderately thick, dermal layer. Lower Ordovician: Argentina (Precordillera).—FIG. 121, 1a-q. \*R. viejoensis, San Juan Formation, Jáchal area; a, side view of obconical holotype, ×0.9; b, vertical, medial section of holotype with deep, broad spongocoel and upwardly arching canals in walls, ×0.9; c, transverse section of upper end of holotype showing irregular spongocoel and radial canals in thick walls, ×1.1; d, photomicrograph of vertical, spicule tract showing long heloclones,  $\times 30$ ; e-q, drawings of isolated, heloclone spicules from holotype, CEGH-UNC 9252, ×25 (Carrera, 1996; courtesy of Geobios).

## Family NEXOSPONGIIDAE Carrera, 1996

[Nexospongiidae CARRERA, 1996, p. 648]

Low, conical, top-bladed, or laminated sponges without spongocoel; skeletal net irregular and homogenous mass of heloclones and monaxons as major spicules; rare megaclones and dendroclones may be present; spicules articulate with circular, clasping facets in heloclones or simply attaching axis to axis or zygome to zygome; some spicules appear loose or isolated in skeleton; differentiated canals absent but openings developed between spicules. *Lower Ordovician.* 

Nexospongia CARRERA, 1996, p. 648 [\*N. sillaensis; OD]. Low, obconical to laminated and discoidal sponges without spongocoel or canals; skeletal net irregular, homogenous mass of heloclones and monaxons with rare megaclones and dendroclones; heloclones ranging from short-shafted, smooth spicules to ones with numerous protuberances and zygomes throughout their length; most heloclones horizontal and articulate with vertical monaxons. Lower Ordovician: Argentina (Precordillera).-FIG. 120,2a-o. \*N. sillaensis, San Juan Formation, Jáchal area; a, upper surface of low conical to discoidal holotype, ×1.4; b, detail of upper surface of holotype showing irregular net and skeletal pores, CEGH-UNC 3613, ×8; c, photomicrograph of thin section of paratype showing characteristic heloclones, CEGH-UNC 3602?, ×18; d-o, draw-

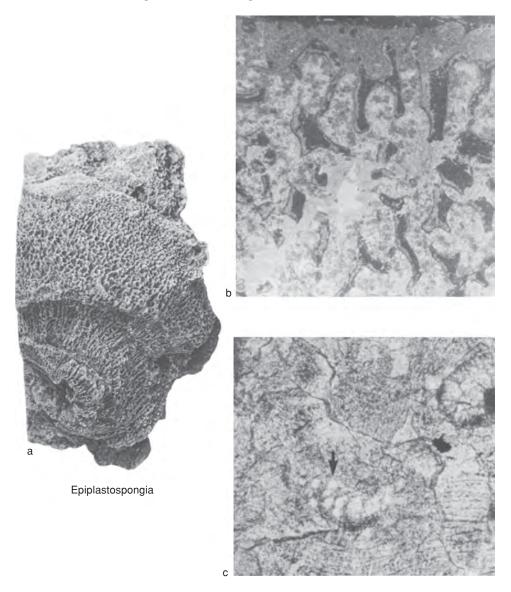


FIG. 123. Saccospongiidae (p. 168).

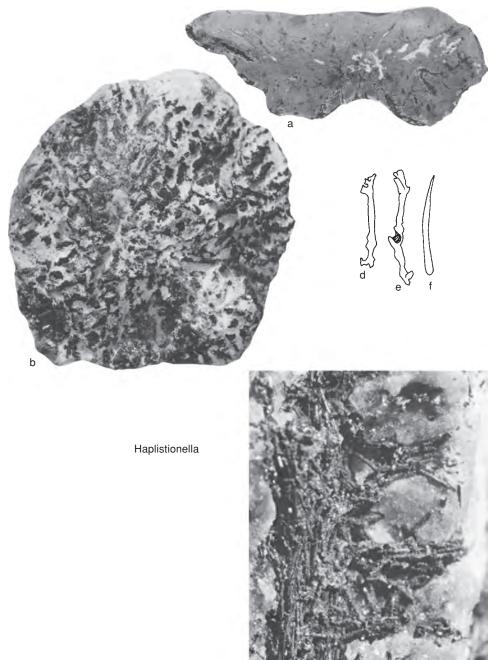
ing of spicules from type specimens, ×25 (Carrera, 1996; courtesy of *Geobios*).

# Order AXINELLIDA Bergquist, 1967

[Axinellida Bergquist, 1967, p. 166]

Tetractinomorpha with a skeleton of spicules and fibers condensed into an axial region from which diverge plumose or plumoreticulate, extra-axial skeleton that may be reinforced by spongin fibers. Megascleres are monaxons, oxeas, styles, or strongyles in all combinations and often sinuous, curved, or irregular at one end. Microscleres commonly absent, but raphides and microoxeas are most common, asterose and sigmoid forms also occur; specific microscleres characterize some families. *Permian– Holocene.* 

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с

FIG. 124. Saccospongiidae (p. 168).

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#### Family AXINELLIDAE Carter, 1875

#### [Axinellidae CARTER, 1875, p. 133]

Usually branched sponges with distinct, axial fibers that are plumosely branched and filled with styles, strongyles, or oxeas; spirasters or asters may be present as flesh spicules, but not chelae; microscleres usually absent. [This family, containing only recent forms, is included herein due to origin of order name.] *Holocene*.

#### Family AGELASIDAE Verrill, 1907

#### [Agelasidae VERRILL, 1907, p. 333]

Sponges with reticulate, fibrous skeleton with spongin fibers lacking primary, coring spicules, but echinated by distinctive acanthostyles with verticillate spines, or rarely smooth styles or strongyles of similar size. *Permian*.

Ropalospongia MOSTLER, 1994, p. 344 [\*R. fluegeli; OD]. Demosponges with acanthostyles ornamented with 12 to 36 horizontal rings of spines, and with an enlarged, ornamented, head end. Permian: USA (Texas).——FIG. 125. \*R. fluegeli, Road Canyon Formation, Roadian, Glass Mountains; holotype spicule showing characteristic spinose ornamentation, ×150 (Mostler, 1994).

## Order UNCERTAIN Family CRICCOSPONGIIDAE Mostler, 1986

#### [Criccospongiidae MOSTLER, 1986, p. 347]

Demosponges whose spicules have a criccomorph structure, including sponges with criccostyles and criccotriaenes. [As proposed by MOSTLER, the family included the new genera *Criccospongia* and *Criccophorina*. No species was named or described for *Criccospongia*, however, and hence it is unrecognizable. Thus, *Criccophorina* is here designated as the type genus. The family is included in the Tetractinomorpha with some question.] *Triassic*.

Criccophorina MOSTLER, 1986, p. 348 [\**C. praelonga;* OD]. Sponges with very long, monactine spicules that have many pronounced, separated, surficial rings, which have granular, outer surfaces. *Triassic:* 



FIG. 125. Agelasidae (p. 171).

Austria.——FIG. 126, *I.* \**C. praelonga*, Zlambachschichten, lower Rhaetian, St. Agatha; holotype, criccostyle spicule with clearly developed rings that have granulated, outer surfaces, and with a hemispherical upper end that has coarser, surficial granules, ×75 (Mostler, 1986).

## Order and Family UNCERTAIN

- Atractosella HINDE, 1888, p. 123 [\*A. siluriensis; M]. Isolated, small, fusiform oxeas in which the maximum thickness is nearer one end of the spicule than to other. [It is recommended that this taxon not be used.] Silurian (Wenlock): England.
- Belemnospongia ULRICH in MILLER, 1889, p. 155 [\*B. fascicularis; M]. Discoidal, consisting of long oxeas radiating from single center and more or less grouped in fascicles. [Although it is possible that this is a root tuft; its consistently circular outline and apparent lack of attachment to another part of a sponge suggest that it represents the entire sponge. The lateral connections between spicules described by ULRICH may be diagenetic silica.] Silurian (Wenlock)-Permian: Canada (Northwest Territories), Wenlock; USA, Britain, Carboniferous; New South Wales, Permian.-FIG. 126, c. \*B. fascicularis, Burlington Limestone, Osagian, Burlington, Iowa, USA; a, discoidal holotype with radiate, skeletal structure, ×1; b, bundle of spicules as exposed on surface; c, edge of holotype

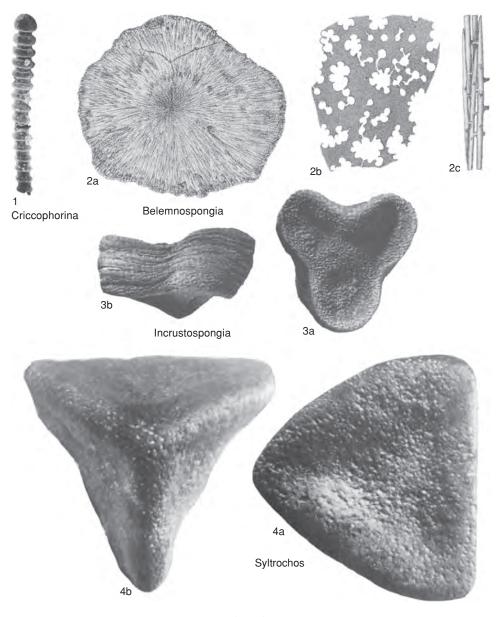


FIG. 126. Criccospongiidae and Uncertain (p. 171-173).

showing transverse sections of spicule bundles and lateral connections, ×10 (Ulrich & Everett, 1890). Incrustospongia MOLINEAUX, 1994, p. 980 [\*1. meandrica; OD]. Small, encrusting, coralline sponges, probably originally aragonitic, currently aspiculate because too few spicule pseudomorphs show diagnostic features; surface with meandroid processes, also seen in internal layers; host organism determines initial shape, but later growth adopts unconstrained, meandroid pattern. Carboniferous (Middle Pennsylvanian-Upper Pennsylvanian): USA (Texas).—FIG. 126,3a-b. \*I. meandrica, Bluff Creek Shale, Upper Pennsylvanian, Coleman County; a, top view of holotype showing nodose, lobate structure, TMM 1785TX1, ×1; b, side view showing distinct, layered structure of holotype, ×1 (Molineaux, 1994).

Petrosites HOWELL & LANDES, 1936, p. 58 [\*P. humilis; OD]. Isolated small, slightly curved oxeas

in which ends are terminated somewhat abruptly by truncation on concave side. [It is recommended that this taxon not be used.] *Ordovician:* North America.

Syltrochos VON HACHT, 1981, p. 154 [\*S. pyramidoidalis; OD]. Platter- to bowl-shaped sponge that develops a pointed, lower stem in mature stages; upper surface of complete sponge showing closely spaced, canal ostia of one to a few centers of water flow that occur under platter upper surface; canal walls are formed of and braced by closely spaced monaxons; skeletal system of sponge body is so built that a three-sided pyramid developed; open form reflecting structure system again. [Because details of the nature and relationships of the spicules are uncertain, assignment to higher taxa is questionable. Consequently the genus is listed here as of uncertain taxonomic affinity.] Upper Ordovician: The Netherlands (Island of Sylt, glacial erratic presumably from Baltic region).— FIG. 126,4*a*-*b*. \*S. pyramidoidalis, glacial debris, ?Caradoc, Ashgill, Sylt; *a*, view from above with triangular outline and small ostia on gastral surface; *b*, view from below with dense, dermal surface pierced by small, inhalant canals, ×1.02 (von Hacht, 1981).

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# MESOZOIC AND CENOZOIC CHORISTID DEMOSPONGES

## R. E. H. Reid

[formerly of Department of Geology, The Queens University of Belfast]

# Subclass CHORISTIDA Sollas, 1880

[nom. transl. REID, herein, ex order Choristida SOLLAS, 1886, p. 177, nom. transl. et correct. ex suborder Choristidae SOLLAS, 1880d, p. 386] [=Tetractinellidae MARSHALL, 1876, p. 134, sensu ZITTEL, 1878b, p. 96]

Demospongea with triactinal, tetractinal, or pentactinal megascleres but without any spicules developed as desmas, and similar sublithistid, monaxonid, microspiculate, and askeletose sponges. Megascleres usually including both tetractines and monaxons; the latter oxeas in most genera, but other diactines (e.g., strongyles) or monactines (e.g., styles) in some; tetractinal megascleres calthrops, triaenes, or both, intergrading or not; either calthrops or triaenes accompanied in some genera by variants with more or fewer rays; a few genera with triactinal or pentactinal (centrotriaene) megascleres but no tetractines; triaenes typically arranged radially. Choanosomal megascleres of forms with triaenes may be mainly or all monaxons, which are felted without order or arranged radially; spicules of microspiculate genera diactinal to polyactinal, with triactines or tetractines always present and tetractines predominant in most genera; principal microscleres of forms with megascleres may be streptoscleres, euasters, or sigmaspires, which are not found together, except that simple euasters may accompany streptoscleres; additional microrhabds or spiny variants in some genera; a few genera with these microscleres only, or no microscleres although megascleres are present. Canal systems of modern forms eurypylous, aphodal, or diplodal; their ectosome a dermis or a cortex. Cortex sometimes packed with microscleres to form an external armor. Reproduction mainly unknown and then presumably oviparous or asexual, but a few with incubated amphiblastulae or parenchymelloid embryos. Spongin typically absent,

but reportedly rarely present and then cementing megascleres. Included monaxonid genera agree closely with various choristid genera except for having only monaxon megascleres. *Ordovician–Holocene*.

This taxon, here ranked as a subclass, is used *sensu* SOLLAS (1880d, 1888) as including all nonlithistid genera with tetractinal megascleres, irrespective of whether these are calthrops or triaenes, and comparably microspiculate sponges in which typical megascleres are absent. It is not used *sensu* DE LAUBENFELS (1936, p. 166), as restricted to forms in which tetractines are longshafted triaenes, or in the further restricted sense of BERGQUIST and HOGG (1969, p. 217), which excludes Choristida *sensu* DE LAUBENFELS in which the microscleres are sigmaspires.

The division by DE LAUBENFELS (1936, p. 166, 177; 1955, p. 42-43) of SOLLAS's order Choristida into orders Choristida sensu DE LAUBENFELS and Carnosa CARTER sensu DE LAUBENFELS (not sensu CARTER), with the latter comprising forms that typically lack long-shafted triaenes, was effectively a reversion to SOLLAS's (1886) provisional distinction between the suborders Triaenina SOLLAS and Tetradina SOLLAS. This arrangement was rejected by SOLLAS (1888) after study of the microscleres, which he used for his final distinctions between the suborders Sigmatophora SOLLAS, Astrophora SOLLAS, and Microsclerophora Sollas. DE LAUBENFEL'S use of the megascleres is here rejected as inconsistent with probable relationships among the Choristida, which were more correctly understood by SOLLAS (1888), and with both the intergradation of megascleric calthrops and short-shafted and longshafted triaenes and the presence of longshafted triaenes in some Carnosa sensu DE LAUBENFELS. The name Choristida SOLLAS is

also preferred for the subclass to the alternative Tetractinellida MARSHALL *sensu* ZITTEL (1878b), because the latter taxon has been used by various authors, including MARSHALL (1876) and SOLLAS (1888), as including the Lithistida.

Division of the subclass into orders is based mainly on the methods used by SOLLAS (1888) to distinguish suborders of his order Choristida with the following differences: (a) suborders are raised in rank to orders; (b) names based on spicular characters are replaced by names based on type genera; and (c) a division (Demus, SOLLAS) of SOLLAS's suborder Astrophora is made a separate order. Equivalents are as follows: suborder Microsclerophora SOLLAS: order Plakinida REID, herein; suborder Sigmatophora SOLLAS: order Craniellida REID, herein; suborder Astrophora SOLLAS in part (Demus Euastrosa SOLLAS, Demus Sterrastrosa Sollas): order Ancorinida Reid herein; and suborder Astrophora SOLLAS in part (Demus Streptastrosa SOLLAS): order Pachastrellida REID, herein.

A few modern monaxonids are so similar to various sponges with tetractinal megascleres that their inclusion in this subclass seems well justified; but their treatment as Choristida depends on soft parts and microscleres, not available for study in the fossils. These forms are mentioned in diagnoses of the subclass and orders, but no attempt is made here to identify fossil examples. The most likely fossil examples are monaxonids placed here in the family Ophiraphiditidae SCHRAMMEN of the order Epipolasida SOLLAS, subclass Monaxonida, which agree with the choristid Cephaloraphiditidae REID except for absence of tetractines.

## Order PLAKINIDA Reid, 1968

[Plakinida Reid, 1968a, p. 22] [=Microsclerophora Sollas, 1887, p. 423; Megasclerophora von Lendenfeld, 1903, p. 28; Homosclerophora Dendy, 1905, p. 64]

Microspiculate sponges with tetractinal or triactinal spicules, to which diactines or forms with more than four rays may be added, and askeletose sponges with amphiblastular embryos like those seen in some forms with spicules; tetractine spicules simple, partly or all lophose, or developed as candelabras; triactine spicules typically triodal, often linked with diactine spicules morphologically by intermediates with one short ray and two larger ones more or less straightened into line; some with diactines and triactines only, with either predominant; triaenes absent in most but some with short-shafted triaenes, which may be varied as diaenes or tetraenes; one modern species with triaenes and very small amphiasters. ?Upper Jurassic, Lower Cretaceous (?Albian), Upper Cretaceous (?Cenomanian, ?Santonian, Campanian)–Holocene.

This order includes forms regarded as similar to *Plakina* SCHULZE (Plakinidae) and others (Thrombidae, Acanthastrellidae) having spicules of similar size, although genera are not certainly allied to *Plakina*. The latter applies specially to *Thrombus* SOLLAS (Thrombidae; Eocene, Holocene), in which shafts of small triaenes may have a swelling suggesting a spicular center that does not correspond with the center from which the rays radiate.

Because of the small size of the spicules, the fossils ascribed to this order are rare and mainly from deposits yielding microscleres. The oldest are small, isolated calthrops and lophose calthrops from the Carboniferous (Visean) of Ireland, not ascribed to any genus but similar to those of some living Plakinidae. Spicules like those of *Acanthastrella* SCHRAMMEN occur in the Upper Jurassic (Kimmeridgian) of Germany, and this genus occurs in the Upper Cretaceous of Germany. Spicules like those of modern species of *Plakina* and *Thrombus* occur in the Eocene of New Zealand, and some other loose Cretaceous spicules may be plakinid.

The family Helobrachiidae SCHRAMMEN, 1910, which was included in this order (as Homosclerophora DENDY, 1905) by REZVOI, ZHURAVLEVA, and KOLTUN (1962), comprises one genus with large megascleres and is here referred to the order Pachastrellida.

#### Family PLAKINIDAE Schulze, 1880

[Plakinidae Schulze, 1880, p. 441] [=Corticiolae Vosmaer, 1885, p. 323]

Microspiculate sponges, without triaenes unless a subtriaene occurs as a variant of a calthrops; spicules typically including tetractines, which are often predominant, although diactines, triactines, pentactines, or forms with more rays may occur; some genera with triactines and diactines only, with either predominant. Diactines commonly irregular, intergrading with triactines. Tetractines all simple or some lophose, then sometimes candelabras (s.s.). One modern genus viviparous, with amphiblastula embryos. [Monolophose and trilophose tetractines have triaenose symmetry but are not classed as triaenes, being simply two forms in a series from monolophose to tetralophose; this type of variation does not occur in triaenes s.s. The doubtful records above are based on isolated spicules, not identified generically. The Carboniferous (Mississippian) record is acceptable as genuine, since spicules concerned include small, lophose calthrops.] Lower Cretaceous (?Albian), Paleogene (upper Eocene)-Holocene.

- Plakina SCHULZE, 1880, p. 448 [\*P. monolopha; SD DE LAUBENFELS, 1955, p. 44]. Simple, encrusting sponges with thin dermis or no ectosome; eurypylous; spicules simple diactines, triactines, and tetractines, and monolophose to tetralophose tetractines; embryos incubated amphiblastulae. Lower Cretaceous (?Albian), Paleogene (upper Eocene)-Holocene: England, ?Albian; New Zealand, upper Eocene; cosmopolitan, Holocene.-FIG. 127, 1a-i. \*P. monolopha, Holocene, Mediterranean Sea; *a–e*, various diactine to tetractine megascleres; f-i, monolophous tetractines, ×400 (Schulze, 1880).—FIG. 127, 1j-l. P. trilopha SCHULZE, Holocene, Mediterranean Sea; trilophose tetractines, ×400 (Schulze, 1880).-FIG. 127, 1m-p. P. australis HINDE & HOLMES, Oamaru Formation, upper Eocene, New Zealand; *m*, monolophose calthrops; n, dilophose calthrops; o-p, trilophose calthrops, last placed with this species by HINDE and HOLMES, 1892, ×600 (Hinde & Holmes, 1892).
- Acanthoplakina BURTON, 1959, p. 156 [\*Plakinolopha spinosa KIRKPATRICK, 1900, p. 350; OD]. Spicules diactines, triactines, and calthrops, with strong, lateral spines, repeatedly branched (polycladose) tips, or both; successive divisions of tips in planes rotating at right angles; rays of

calthrops often with whorl of large spines near their origins; diactines may be larger than other spicules. *Paleogene (upper Eocene)–Holocene:* New Zealand, *upper Eocene;* Indian Ocean, Western Pacific, *Holocene.*—FIG. 127,4. A. sp., upper Eocene, Otago, New Zealand; characteristic spiny calthrops, ×600 (Hinde & Holmes, 1892).

Corticium SCHMIDT, 1862, p. 42 [\**C. candelabra;* OD]. Aphodal to diplodal; spicules simple calthrops and subtriaenes, lophose calthrops and candelabras (tetralophose calthrops, with one branching ray distinct from others, and its branches often spiny). *Paleogene (upper Eocene)– Holocene:* New Zealand, *upper Eocene;* cosmopolitan, *Holocene.*—FIG. 127,2*a*-*c. C.* spp., upper Eocene, Otago, New Zealand; candelabra spicules, ×600 (Hinde & Holmes, 1892).

#### Family THROMBIDAE Sollas, 1887

#### [Thrombidae SOLLAS, 1887, p. 428]

Microspiculate sponges whose characteristic spicules are short-shafted, spiny triaenes, sometimes having a central or subcentral enlargement of axial filament of rhabdome; sometimes also with monaene, diaene, tetraene, or mesotriaene variants of characteristic triaenes; one modern species with very small, additional amphiasters (possible amphitetraenes). [The group is sometimes included with Plakinidae, but axial enlargement in rhabdomes suggests a spicular center; if this is correct, the seeming triaenes are trichodiactines, not tetractines. This feature does not occur in Plakinidae s.s.] ?Upper Cretaceous, Paleogene (upper Eocene)–Holocene.

Thrombus SOLLAS, 1886, p. 179 [\*T. challengeri; OD]. Encrusting to nodular; spicules sometimes trichotriaenes or mesotriaene variants of this type (mesotrichotriaenes), to which other variants (e.g., monaenes, diaenes) or very small amphiasters (possible amphitetraenes) may be added; sometimes partly or all sigmatriaenes (short-shafted protriaenes with cladal tips flexed outwardly) and monaene to tetraene variants; central enlargement of rhabdal axis sometimes marked by external annulation; second rhabdal ray of mesotriaenes up to about half length of primary one. ?Upper Cretaceous, Paleogene (upper Eocene)-Holocene: northern Germany, ?Upper Cretaceous; New Zealand, upper Eocene; Indian Ocean, Western Pacific, Caribbean, Atlantic, Holocene.—FIG. 127,3a. T. sp.? SCHRAMMEN, Mukronatenkreide, Campanian, Misburg, Germany; trichotriaene, lacking characteristic spines, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).--Fig.

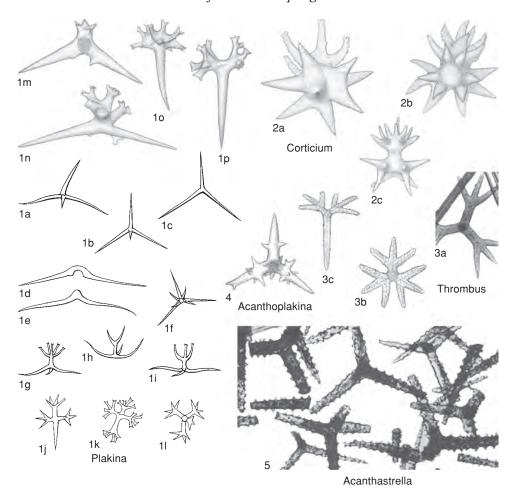


FIG. 127. Plakinidae, Thrombidae, and Acanthastrellidae (p. 177-178).

127,3b-c. *T.* sp., upper Eocene, Otago, New Zealand; cladome of trichotriaene and trichodiaene,  $\times 200$  (Hinde & Holmes, 1892).

#### Family ACANTHASTRELLIDAE Schrammen, 1924

#### [Acanthastrellidae SCHRAMMEN, 1924a, p. 37]

Spicules small, spiny, grading from calthrops into short-shafted triaenes, some approaching size of true megascleres; other characters unknown. [The relationships of this group are doubtful, possibly with recent families Plakinidae, Pachastrellidae, or Plakinastrellidae (no known fossils). The axial enlargement seen in triaenes of Thrombidae is not developed. Similarly shaped calthrops to triaenes from Carboniferous (Mississippian, Ireland) are of megascleric size and occur with apparently related pentactines (tetraenes) and hexactines.] ?Upper Jurassic, Upper Cretaceous (Campanian).

Acanthastrella SCHRAMMEN, 1924a, p. 44 [\*A. panniculosa; OD]. Encrusting or nodular; rays of spicules unbranched; spines without order or locally with more or less annular or spiral arrangement. ?Upper Jurassic, Upper Cretaceous (Campanian): southern Germany [loose spicules only], ?Upper Jurassic; northern Germany, Campanian.—FiG. 127,5. \*A. panniculosa, Mucronatenkreide, Campanian, Misburg; isolated triaenes with spinose rays, ×50 (Schrammen, 1924; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

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# Order PACHASTRELLIDA new order

# [Pachastrellida REID, herein] [=Demus Streptastrosa SOLLAS, 1888, p. cxxvii]

Choristid sponges whose characteristic microscleres are streptoscleres (plesiasters, metasters, and related forms of spirasters and amphiasters), having triaenes, calthrops, or both among their megascleres, and similar sponges having euasters or diactinal microscleres but no typical triaenes; streptoscleres often accompanied by microrhabds and in some forms by simple oxyasters having 4 to 6 rays. *Carboniferous–Holocene*.

Due to absence of microscleres in fossils, recognition of genera referred to this order is based on comparison of their megascleres with those of modern examples and especially on occurrence of megascleric calthrops or comparable spicules (triactines, centrotriaenes). These calthrops and comparable spicules are confined to this order in the modern Choristida; the same is here assumed to be true of the fossils, although without direct knowledge of their microscleres.

Genera with streptoscleres were formerly placed by REID (1968a) in an order Poecillastrida REID, equivalent to DENDY's (1924a) Streptosclerophora. Because of the absence of microscleres in fossils, it is here more convenient to follow SOLLAS in including forms with calthrops, with euasters or diactinal microscleres, in the family Pachastrellidae CARTER. This also seems consistent with their probable relationships. The order name is changed to allow for this difference in concept, and because (a) the name Poecillastrida can be criticized as resembling Poecillosclerida TOPSENT, which refers to the Desmacidontida of this classification, and (b) Poecillastra SOLLAS is not the type genus of a family and is also regarded by some authors as a synonym of Pachastrella SCHMIDT.

The order appears to be first represented by loose calthrops or subtriaenes from the Upper Ordovician of Sweden (REIF, 1968), assuming that these did not belong to other unknown forms. Branching calthrops like those of some modern *Pachastrella* species (e.g., *P. abyssi* SCHMIDT) occur from the Carboniferous (Visean) of Ireland.

### Family PACHASTRELLIDAE Carter, 1875

[*nom. transl.* SOLLAS, 1886, p. 177, ex "group" (subfamily) Pachastrellina CARTER, 1875, p. 185] [=Calthropellidae VON LENDENFELD, 1907, p. 301; Halinidae DE LAUBENFELS, 1934, p. 1]

Megascleres typically include calthrops, replaced sometimes by subtriaenes or centrotriaenes; some genera with both calthrops and typical triaenes, intergrading or not; monaxon megascleres present or absent; microscleres of modern examples include either streptoscleres or euasters, to which microrhabds or variants may be added, or microrhabds only. Subtriaenes may be nearly triactinal, with one ray represented by a rudiment. [This family includes the zoological families Pachastrellidae CARTER and Calthropellidae VON LENDEN-FELD, united for convenience. Because these families cannot be distinguished without reference to microscleres, the reference of fossils without microscleres to living genera is always doubtful.] Carboniferous-Holocene.

Halinidae DE LAUBENFELS, as used in the previous *Treatise Part E* (DE LAUBENFELS, 1955), is a junior synonym of five older family names based on included genera: Pachastrellidae CARTER, 1875; Plakinidae SCHULZE, 1880; Corticidae VOSMAER, 1885; Calthropellidae VON LENDENFELD, 1907; and Acanthastrellidae SCHRAMMEN, 1924a. Here *Plakina* SCHULZE and *Corticium* SCHMIDT are in the Plakinidae and *Acanthastrella* SCHRAMMEN in the Acanthastrellidae.

The following key shows pachastrellid genera suggested by a number of types of megascleric skeletons, including some not recorded below.

A. With calthrops or subtriaene variants, or both intergrading; sometimes also with other variants having more or fewer rays.

A<sub>1</sub>. Oxea megascleres absent.

a. No distinct category of dichotriaene megascleres; branching rays uncommon or absent in calthrops etc.; *Halina* BOWERBANK (Halininae) or *Calthropella* SOLLAS (Calthropellinae).

b. With no subordinate dichotriaenes, which may form an ectosomal skeleton; main megascleres simple and branching calthrops, the branches of the latter sometimes resembling zygomes of desmas: *Propachastrella* SCHRAMMEN (subfamily unknown).

A<sub>2</sub>. Oxea megascleres present.

c. No triaenes, unless calthrops are varied as subtriaenes; *Pachastrella* SCHMIDT (Pachastrellinae).

d. With calthrops or subtriaenes accompanied by short-shafted orthotriaenes or plagiotriaenes, intergrading or not: *Poecillastra* SOLLAS (Pachastrellinae).

e. With calthrops and dichotriaenes: *Chelotropella* VON LENDENFELD (Calthropellinae).

f. With calthrops and centrotriaenes: *Yodomia* LEBWOHL (Pachastrellinae).

B. No calthrops or comparable subtriaenes; oxeas present.

 $B_1$ . Megascleres other than oxeas are triactines or subtriactines, the latter spicules with a fourth ray represented by a rudiment or an internal axial rudiment.

a. Rays of triactinal spicules straight or branching, not curved nor terminally hooked: *Nethca* SOLLAS (Pachastrellinae) or *Pachastrissa* VON LENDENFELD (Calthropellinae).

b. Rays of triactinal spicules unbranched, markedly curved, or hooked terminally: *Helobrachium* SCHRAMMEN (subfamily unknown).

 $B_{2.}$  With centrotriaenes, whose cladi branch repeatedly: *Triptolemma* DE LAUBEN-FELS (Halininae).

### Subfamily PACHASTRELLINAE Carter, 1875

[*nom. correct.* REID, herein, *pro* "group" (subfamily) Pachastrellina CARTER, 1875, p. 185]

Characteristic microscleres of modern species are streptoscleres, often accompanied by microrhabds or variants; euasters (unless triactinal or tetractinal plesiasters are consid-

## ered as such). Carboniferous (?Mississippian), ?Jurassic, ?Cretaceous, Paleogene (?upper Eocene), Holocene.

- Pachastrella SCHMIDT, 1868, p. 15 [\*P. monilifer; OD]. Encrusting to massive, funnel-like or lamellar; megascleres typically oxeas and calthrops or equiradiate subtriaenes, calthrops and subtriaenes intergrade if both are present; triactines or pentactines may occur as tetractine variants; calthrops sometimes simple, but often with one to all four rays branching; irregularly branching form common; subtriaenes with three rays bent toward or away from the fourth; no distinct category of triaenes; no radial arrangement of megascleres; all modern species with streptoscleres; microrhabds often also present, commonly stout microstrongyles, sometimes also including slender, rough to finely spinulate spicules, which may be straight, bent, or spirally twisted so as to resemble spinispiras. [Supposed fossil records all doubtful, based on isolated calthrops or on material lacking oxeas. Fossil spicules ascribed to Pachastrella SCHMIDT, with termination -ites; invalid under Code Article 20 (ICZN, 1999).] Carboniferous (?Mississippian), ?Jurassic, ?Cretaceous, Paleogene (?upper Eocene), Holocene: Ireland, Scotland, ?Mississippian; England, Germany, ?Jurassic; Czech Republic, Slovakia, England, Germany, Poland, ?Cretaceous; New Zealand, ?upper Eocene; cosmopolitan, Holocene.-FIG. 128,4a-g. P. abyssi SCHMIDT, Holocene, South Atlantic; a, calthrops, ×25; b, calthrops with branching rays, ×50; *c*–*f*, streptoscleres; *g*, microstrongyle, ×540 (Sollas, 1888).
- Nethea SOLLAS, 1888, p. 103 [\* Tisiphonia nana CARTER, 1880b, p. 138; OD]. Encrusting, massive, lamellar, or other shapes; megascleres oxeas and triactines or subtriactines, the last with three main rays fully developed, simple or branched, and a fourth represented by a rudiment, or an internal axial rudiment; microscleres microoxeas and spirasters. Upper Cretaceous (?Coniacian-?Maastrichtian), Holocene: northern England, ?Coniacian-?Maastrichtian; cosmopolitan, Holocene.—FIG. 128,5a-b. N. ? plana (HINDE), Upper Chalk, ?Senonian, Upware, northern England; a, sponge, ×1; b, triactine megascleres, similar to those of living N. amygdaloides (CARTER), ×10 (Hinde, 1884a).

### Subfamily CALTHROPELLINAE von Lendenfeld, 1907

[nom. transl. REID, herein, ex Calthropellidae von LENDENFELD, 1907, p. 301]

Characteristic microscleres of modern species are euasters; streptoscleres absent. ?Cretaceous, Holocene.

Calthropella SOLLAS, 1888, p. 107 [\*C. simplex; SD VON LENDENFELD, 1903, p. 83] [=Corticellopsis BERGQUIST, 1968, p. 62 (type, Corticella Pachastrellida

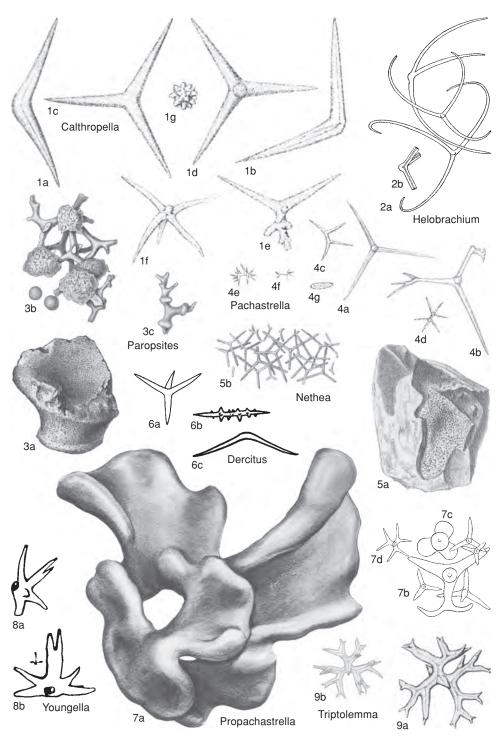


FIG. 128. Pachastrellidae (p. 180-183).

novaezealandiae Bergquist, 1961, p. 45)]. Encrusting to massive; megascleres calthrops and subordinate variants; the latter monactines (rare), diactines, triactines, pentactines, or hexactines, sometimes mainly triactines or all pentactines or hexactines; rays of megascleres all unbranched or dichotomous in occasional examples; no oxeas; microscleres spherasters or strongylasters plus oxyasters, the latter distinct or developmental stages of the others. [Possible identification of supposed fossil Pachastrella species lacking oxeas: but see also Halina BOWERBANK.] ? Cretaceous (fide DE LAUBEN-FELS, 1955, untraced), Holocene: cosmopolitan.-FIG. 128, 1a-g. \*C. simplex, Holocene, Cape Verde Islands, eastern Atlantic; *a–b*, calthrops reduced to diactinate; c, triod; d-e, calthrops, the latter with stunted cladi, making it appear like a lithistid spicule; f, triode with three adventitious rays,  $\times 25$ ; g, microsclere or young spheraster, ×225 (Sollas, 1888).

### Subfamily HALININAE de Laubenfels, 1934

[nom. transl. REID, herein, ex Halinidae DE LAUBENFELS, 1934, p. 1]

Characteristic microscleres of modern species are spiny microrhabds or variants; sometimes also with euasters or toxas. [Originally invalid (junior) substitute for family name Pachastrellidae CARTER, 1875, based on the idea that family type should be oldest genus included; here adopted in new sense for Pachastrellidae grouped with *Halina* BOWERBANK.] Lower Cretaceous (?Albian), Paleogene (upper Eocene)– Holocene.

Dercitus GRAY, 1867, p. 542 [\*Hymeniacidon bucklandi BOWERBANK, 1858, p. 288; SD DE LAUBENFELS, 1936, p. 43] [=Halina BOWERBANK, 1858, p. 288, non DE BLAINVILLE, 1830 (type, H. bucklandi BOWERBANK, 1858, p. 288); Battersbya BOWERBANK, 1874b, p. 343 (type, Hymeniacidon bucklandi BOWERBANK, 1864, p. 234)]. Encrusting to nodular, with a cortex; megascleres typically regular calthrops or slightly subtriaenose variants, with unbranched rays, not accompanied by monaxons; other variants unusual; microscleres toxas and spiny microrhabds, which may pass into sanidasters or amphiasters. [ENGESER and MEHL (1993) considered Dercites and Dercitus as the same genus. They have different type species and probably should be kept separate, with Dercites as the unidentifiable form as treated by DE LAUBENFELS (1955, p. 105).] Lower Cretaceous (?Albian), Holocene: southern England, ?Albian; cosmopolitan, Holocene.--Fig. 128,6a-c. \*D. bucklandi (BOWERBANK), Holocene, Europe; a, calthrops, ×50; b, spiny microxea; c, toxa, ×300 (de Laubenfels, 1955).

Triptolemma DE LAUBENFELS, 1955, p. 43, nom. nov. pro Triptolemus SOLLAS, 1888, p. 93, obj., non PECKHAM, 1885 [\* Triptolemus cladosus Sollas, 1888, p. 93; OD]. Characteristic megascleres centrotriaenes, with rhabdal rays short, equal, conical, and cladi irregularly polycladose; sometimes also with oxeas, but no calthrops or other tetractines; microscleres spiny microrhabds, spinispira-like strongylospires, or amphiasters. [Diagnosis by DE LAUBENFELS, 1955, in which he cited calthrops as megascleres, does not fit characters of type or any species.] Paleogene (upper Eocene)-Holocene: New Zealand, upper Eocene; eastern Atlantic, Indonesia, Holocene.--Fig. 128,9a. \*T. cladosa (SOLLAS), Holocene, Indonesia; centrotriaene, ×150 (Sollas, 1888).--Fig. 128,9b. T. australis (HINDE & HOLMES), upper Eocene, Otago, New Zealand; characteristic centrotriaene, showing one of rhabdal rays only, ×40 (Hinde & Holmes, 1892).

### Subfamily UNCERTAIN

Fossil Pachastrellidae *s.l.* with megascleres comparable to those of living species or more than one subfamily above, or with no living species.

- Acanthophora SOLLAS, 1873, p. 79 [\**A. hartogii;* OD]. Massive, lobose with oxea megascleres and tornote, triradiate to hexiradiate microscleres, but poorly known. [No known suitable figures.] *Lower Cretaceous:* Europe.
- Helobrachium SCHRAMMEN, 1910, p. 128 [\*H. consecatum; OD]. Encrusting to irregularly lobate; principal megascleres subtriactines with three long, curved to terminally hooked rays, and a fourth ray represented by a buttonlike rudiment; hooked ends may intermesh so that skeleton is loosely coherent without zygosis; oxeas also present; microspiculation unknown (no exact modern couterpart, but comparable subtriactines occur in Nethea SOLLAS of Pachastrellinae and Pachastrissa von Lendenfeld of Calthropellinae). [The genus was placed in the lithistid suborder Megamorina by DE LAUBENFELS (1955, p. 50-51) and said to have "typical megaclone desmas," with additional triactines; but spiculation as given by SCHRAMMEN (1910) and above are to the present author's knowledge.] Upper Cretaceous (Coniacian-Maastrichtian): northern Germany.-FIG. 128,2a-b. \*H. consecatum, Quadratenkreide, Senonian, Oberg; a, triactine spicules with long, curved rays that have axial canals; b, part of small spicule with node that has short canal suggesting rudimentary fourth ray, ×10 (Schrammen, 1910).
- Paropsites POČTA, 1884, p. 40 [\*P. hindei; OD]. Sponge basin shaped with a thick, basal stalk, thick walled with well-developed, radial, canal system; gastral surface with round, exhalant ostia; spicules are oxeas with associated, small spheres, and calthrops with tips of rays finely branched. *Creta*-

*ceous:* Europe.——FIG. 128, 3a-c. \**P. hindei*, Malnitzer Schichten, Bohemia; *a*, side view of typical sponge, ×0.5; *b*, skeletal fragment with small spheres and calthrops; *c*, isolated, small spicule with ringlike structures on rays, ×50 (Počta, 1884).

- Propachastrella SCHRAMMEN, 1910, p. 71 [\*Pachastrella primaeva VON ZITTEL, 1878b, p. 9; OD]. Lamellar, leaf or ear shaped to irregularly lobate or nodular; principal megascleres simple and branching calthrops; distinct dichotriaenes also present, sometimes forming an ectosomal skeleton; terminal branches of branched calthrops may resemble zygomes of desmas, although not articulated; some examples also with calthrops in which unbranched rays are shortened and swollen, or with pentactinal to polyactinal calthrops variants; no oxea megascleres, microspiculation unknown (no exact counterpart in living sponges, and calthrops and dichotriaenes found together in both Pachastrellinae and Calthropellinae). [Comparable modern forms include Pachastrella chuni von LENDENFELD, 1907 (Pachastrellinae), Chelotropella sphaerica VON LENDENFELD, 1907 (Calthropellinae), calthrops and dichotriaenes in both, although oxeas also present.] Cretaceous (Turonian-Maastrichtian): France, Germany, Poland.-FIG. 128,7a-d. \*P. primaeva (VON ZITTEL), Mucronatenkreide, Senonian, Misburg, Germany; a, leaflike, irregularly lobate sponge,  $\times 0.5$ ; *b-c*, spicules of type species, calthrops, latter with swollen rays, Quadratenkreide, Oberg, Germany; d, dermal dichotriaene, Quadratenkreide, Oberg, Germany, ×10 (Schrammen, 1910).
- Youngella DE LAUBENFELS, 1955, p. 44, nom. nov. pro Chlamys YOUNG & YOUNG, 1877, p. 429, non KNOCH, 1801 [\*Chlamys magna YOUNG & YOUNG, 1877, p. 429; OD]. Resembles Corticium but poorly known. Carboniferous: Scotland.——FIG. 128,8a-b. \*Y. magna (YOUNG & YOUNG), Carboni fierous limestone, Cunning Baidland, Ayrshire; isolated bitornote spicules of type suite, ×6 (Young & Young, 1877).

### Family COSTAMORPHIIDAE Mostler, 1986

#### [Costamorphiidae MOSTLER, 1986, p. 343]

Sponges whose megascleres are composed of diverse calthrops, asterlike triaenes or of calthrops-derived needles and diverse triders, all showing outer sculpture of riblike halfrings with irregular margins; known only from isolated spicules. *Upper Triassic*.

Costamorpha MOSTLER, 1986, p. 343 [\*C. zlambachensis; OD]. Sponges whose skeleton is composed of calthrops and associated mesotriaenes with characteristic outer sculpture of irregular half rings. Upper Triassic: Austria.—FIG. 129, Ia-b. \*C. zlambachensis, Zlambach Formation, Rhaetian, St. Agatha; a, holotype calthrop; b, drawing of characteristic calthrop, scale not given but approximately ×100 (Mostler, 1986).

#### Family THENEIDAE Gray, 1872

[nom. correct. SOLLAS, 1886, p. 178, pro Theneadae GRAY, 1872a, p. 460]

Sponges with triaene and oxea megascleres and streptosclere microscleres; no megascleric calthrops, triactines, or centrotriaenes; triaenes usually long shafted; architecture radiate or not; some anchored by protruded anatriaenes, or rarely by distally knobbed pseudotylostyles, in which terminal knob may contain axial rudiments of anatriaene cladi; modern examples eurypylous and noncorticate. [Diagnoses were sometimes based on soft parts and microscleres (e.g., SOLLAS, 1888), which then would include some genera with calthrops, which here are included in the family Pachastrellidae (subfamily Pachastrellinae). MALDONADO (2002, p. 141) included the Theneidae in the Pachastrellidae, but they are retained here as separate families. Sponges considered here as within the Theneidae were included with Ancorinidae by DE LAUBENFELS (1936, 1955) through identification of streptoscleres with ancorinid sanidasters.] Upper Cretaceous (?Turonian, Coniacian)–Holocene.

Thenea GRAY, 1867, p. 541 [\* Tethea muricata BOWERBANK, 1858, p. 308; OD]. Typically symmetrical, usually globular, hemispherical, or mushroomlike, and attached by a diffuse root tuft or by a group of more compact, rootlike processes; often hispid or with a prominent equatorial fringe of hisapidating spicules; pores mainly in special lateral areas; internal skeleton radiate; triaenes typically including dichotriaenes, with short, primary cladi and long branches, additional protriaenes, and small anatriaenes; radical megascleres usually large anatriaenes, to which a few pseudotylostyles may be added, but occasionally all pseudotylostyles; with streptoscleres only, or with plesiaster-variant oxyasters having four or one to several more rays (supposed records based on isolated megascleres). Cretaceous (?Turonian, Coniacian-Maastrichtian), Paleogene (?upper Eocene), Holocene: Czech Republic, Slovakia, England, ?Turonian, Coniacian-Maastrichtian; New Zealand, ?upper Eocene; cosmopolitan, Holocene.-FIG. 129,2a-e. T. wyvillii SOLLAS, Holocene, Philippine Islands; a, side view of sponge showing roots,  $\times 0.5$ ; b, dichotriaene, ×10; c, internal anatriaene, ×100; d, metaster, ×300; e, calthrops-like oxyaster (plesiaster), ×49

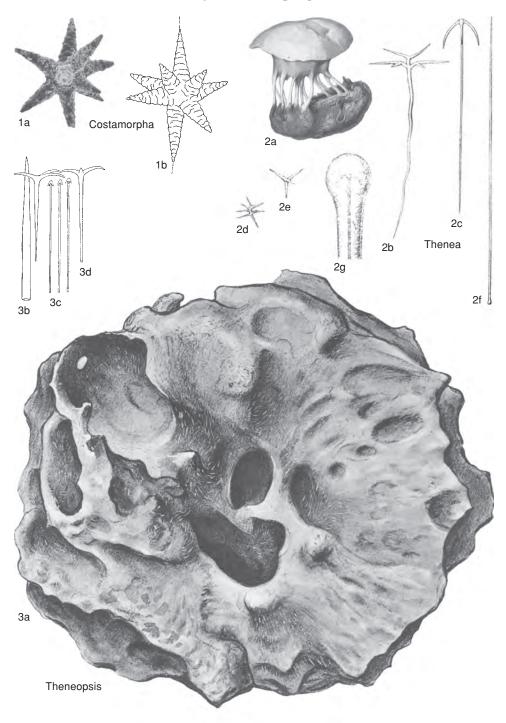


FIG. 129. Costamorphiidae and Theneidae (p. 183-185).

(Sollas, 1888).—FIG. 129,2*f-g. T. delicata* SOLLAS, Holocene, South Indian Ocean; *f*, radical pseudotylostyle, ×15; *g*, terminal knob (tylus) of same, showing axial rudiments, ×180 (Sollas, 1888).

?Theneopsis SCHRAMMEN, 1910, p. 54 [\* Tethyopsis steinmanni von ZITTEL, 1878b, p. 9, OD] [=Tethyopsis VON ZITTEL, 1878b, p. 9, obj., non STEWART, 1870, p. 281]. Nodular or tuberlike, some examples lacunar internally; megascleres large oxeas, smaller orthotriaenes and delicate, but long-shafted anatriaenes arranged perpendicular to external surface or to surfaces of internal lacunae; microscleres unknown. [Name suggests relationship to Thenea, but compared with Sphincterella DE LAUBENFELS (as Sphinctrella SCHMIDT, non SCHMARDA) by original author; could equally be ancorinid or geodiid.] Cretaceous (upper Campanian): northern Germany.—FIG. 129,3ad. \* T. steinmanni (VON ZITTEL), Quadratenkreide, Misburg; a, irregular, tuberlike sponge with internal lacunae,  $\times 1$ ; *b*-*d*, spicules including orthotriaenes, anatriaenes, incomplete, and oxea, incomplete, ×10 (Schrammen, 1910).

# Order ANCORINIDA Reid, 1968

[Ancorinida REID, 1968a, p. 22; emend., REID, herein]

Choristid sponges with triaenes and euaster microscleres, or with additional spinulated microrhabds or sanidasters or these types of microscleres only, and similar monaxonids that differ only in absence of triaenes; some with sterrasters or aspidastera in addition to normal euasters; most choristids with oxea megascleres in addition to triaenes, and some with strongyles or styles. *Carboniferous (Mississippian)– Holocene.* 

Recognition of fossils referred to this order may be based on comparison of megascleres with those of modern examples or recognition of sterraster or aspidaster microscleres, which occur in some sediments. The oldest apparent sterrasters are Carboniferous (Mississippian), and occur with dichotriaene megascleres like those of various modern Geodiidae, of which these microscleres are characteristic. Since this family is the most specialized of the order, both the family and the order are likely to be older than the known record.

The order Ancorinida was originally taken as including all choristids with

microscleres of the above types and all monaxonids with true euasters (i.e. not pseudoeuasters; REID, 1968a). The choristid Calthropellidae von Lendenfeld and Halinidae DE LAUBENFELS are now included in the order Pachastrellida (family Pachastrellidae) following SOLLAS (1888), and most of the monaxonids are placed in the order Epipolasida DE LAUBENFELS. This change is partly for convenience in paleontology; but it also seems clear that the monaxonids have varied affinities and that some, at least, are allied to the Spirastrellida, although the latter have spinispira microscleres when any distinctive forms are present. Tethya LAMARCK in particular agrees closely with the typical Spirastrellida biochemically (BERGQUIST & HOGG, 1969), although the microscleres are euasters like those of typical Ancorinida. Biochemical agreement is thought here to be probably more significant than occurrence of similar microscleres, which should be seen as representing parallel developments.

Some modern monaxonids do, however, seem likely to belong with the order Ancorinida, and DENDY (1916) claimed a series of pairs of similar choristid and monaxonid species within the genus *Aurora* SOLLAS. Some fossils placed here in the artificial order Epipolasida could be monaxonid Ancorinida; but there is no way by which they can be recognized as such.

### Family ANCORINIDAE Schmidt, 1870

[Ancorinidae SCHMIDT, 1870, p. 64] [=Stellettidae SOLLAS, 1888, p. cxxxiv, nom. transl. et correct. SOLLAS, 1888, p. cxxxiv, ex group (=subfamily) Stellettina CARTER, 1875, p. 184]

Sponges with triaene and oxea megascleres and with euaster microscleres that do not include sterrasters or aspidasters; no megascleric calthrops or triactines; some genera with typical microscleres accompanied by microrhabds or sanidasters; may also have diaenes or monaenes as subordinate variants of triaenes, or diaenes as typical megascleres of special oscular outgrowths; styles or strongyles sometimes present as oxea variants; whole skeleton commonly

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radiate; but some have choanosomal oxeas irregularly felted and only triaenes radial; modern examples typically aphodal, with cortex or not; euasters in forms from oxyaster to sterrospheraster, alone or in various combinations; few with dermal armor formed by cortex packed with spherasters or sterrospherasters; triaenes sometimes inconspicuous or vestigial, so that sponge may at first seem monaxonid (some purely monaxonid sponges included in zoology, on basis of detailed resemblance in soft parts and microscleres, not available in paleontology). *Jurassic–Holocene*.

## Subfamily ANCORININAE Schmidt, 1870

[nom. transl. DE LAUBENFELS, 1936, p. 167, ex Ancorinidae SCHMIDT, 1870, p. 64; emend., REID, herein]

Euaster microscleres of modern examples typically accompanied by differentiated microrhabds that are rough, finely spined, or developed as sanidasters; these microrhabds often intergrading with diactinal, euaster variants, from which they are only distinguished by slightly further modification (e.g., thickening, shortening), or with a typical, radiate euaster through irregular intermediates. [The subfamily is emended by removal of genera with microscleres identified as streptoscleres, that are here placed in Pachastrellidae (Pachastrellinae) or Theneidae, because identification of streptoscleres with ancorinid sanidasters (DE LAUBENFELS, 1936) is rejected. Microscleres taken as typical of Ancorininae are occasionally present in species or genera referred to the subfamily Stellettinae; but, broadly, Ancorinidae either have or do not have these microscleres. Subfamilies employed by DE LAUBENFELS (1936) are retained here accordingly.

A few Ancorinidae have simple microxeas that are microrhabds that seem to be allied to oxea megascleres homologically; these genera are here placed in the Stellettinae.] *Jurassic–Holocene.* 

Ancorina SCHMIDT, 1862, p. 51 [\*A. cerebrum; SD DE LAUBENFELS, 1936, p. 167]. Sponges spherical, of moderate size with skeleton containing oxeas, anatriaenes, dichotriaenes, and three kinds of asters; dermal layer consisting of bundles of anchorate spicules and main web of fibers including those and other kinds of spicules. *Holocene:* cosmopolitan. ——FIG. 130,2*a*-*f.* \**A. cerebrum,* Zara and Quarnero, Adriatic Sea; various spicules from fibrous skeleton of type sponge, including large anatriaenes and dichotriaenes, *b,e,f,* ×60; *a,c,d,* ×125 (Schmidt, 1862).

- Discispongia KOLB, 1910 in 1910–1911, p. 251 [\*D. unica; OD]. Discoidal to cup-shaped form with skeleton of oxeas and various triaenes; canal system not developed. Jurassic: Europe.——FIG. 130,6a-d. \*D. unica, Weiss Jura, Kimmeridgian, Sontheim, Germany; a, discoidal holotype from above with marginal ring, ×0.5; b, protriaene; c, dichotriaene, ×25; d, anatriaene, ×50 (Kolb, 1910–1911).
- Ecionemia BOWERBANK, 1862, p. 1,101 [\*E. acervus; OD] [=Ecionema SOLLAS, 1886, p. 192, nom. null.]. Massive, lobate, pyriform, cup-shaped, or related shapes; megascleres oxeas and orthotriaenes, plagiotriaenes, or protriaenes, or with additional anatriaenes; radiate architecture; euasters are tylasters, spherasters, or both; microrhabds smooth, finely spined, or developed as sanidasters; cortex typically absent. [Separation from Ancorina SCHMIDT controversial, here based chiefly on absence of dichotriaenes, oxyasters, cortex.] Paleogene (Eocene)-Holocene: Western Australia, Eocene, Miocene; cosmopolitan, Holocene.-FIG. 130, 1. E. glauteri CHAPMAN & CRESPIN, Miocene, Western Australia; rodlike specimen with expanded base, possibly a stalk, preserving oxeas, protriaenes and spherasters, sanidasters, WAGS, ×1 (Chapman & Crespin, 1934, courtesy of The Royal Society of Western Australia).

### Subfamily STELLETTINAE Carter, 1875

[nom. transl. VON LENDENFELD, 1907, p. 253, ex Stellettidae SOLLAS, 1886, p. 187, nom. transl. et correct. ex group Stellettina CARTER, 1875, p. 184; sensu DE LAUBENFELS, 1936, p. 167; emend., REID, herein]

Microscleres of modern examples are typically euasters only, without microrhabds except as otherwise unmodified, diactinal, euaster variants; rarely, also with smooth microxeas. [The Stellettinae sensu VON LENDENFELD comprises the Ancorinidae without special oscular tubes, seen in forms grouped as Tethyopsidinae VON LENDENFELD (1907, p. 253), without reference to microscleres. Emendation of Stellettinae sensu DE LAUBENFELS allows inclusion of *Penares* GRAY, in which microxeas are thought to be related to oxea megascleres, not to microrhabds typical of the Ancorininae.] ?lower Lower Jurassic, Cretaceous (?Albian, Turonian)-Holocene.

Ancorinida

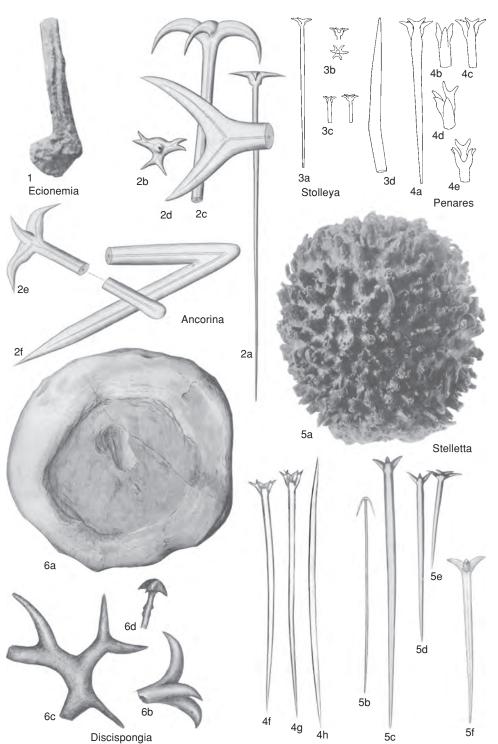


FIG. 130. Ancorinidae (p. 186–188).

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- Stelletta SCHMIDT, 1862, p. 46 [\*S. boglicii; SD SOLLAS, 1888, p. cxxxix, not S. grubii SCHMIDT, 1862, p. 46, SD DE LAUBENFELS, 1955, p. 42]. Massive, spherical, cylindrical, cuplike, or related shapes; surface hispid in some species or rarely conulose; megascleres radially arranged oxeas and plagiotriaenes, orthotriaenes, or dichotriaenes, or also including anatriaenes; euasters typically oxyasters and tylasters (chiasters), found mainly in choanosome and ectosome respectively, but sometimes lacking oxyasters or with tylasters replaced by strongylasters or spherasters; strongly corticate, with cortex two layered, the inner layer fibrous (supposed fossil records based on isolated megascleres). ?lower Lower Jurassic, Cretaceous (?Coniacian-?Maastrichtian), Cretaceous (?Albian), Paleogene (?Eocene), Holocene: Austria, ?lower Lower Jurassic; southern England, ?Albian; Czech Republic, Slovakia, England, Germany, ?Coniacian-?Maastrichtian; New Zealand, Western Australia, ¿Eocene; cosmopolitan, Holocene.-FIG. 130,5ae. S. arghulana von Lendenfeld, Holocene, Arghulas Bank, South Africa; a, side view of whole sponge, ×0.5; b, anatriaene, ×100; c-d, plagiotriaenes; e, dichotriaene, ×25 (von Lendenfeld, 1907).—FIG. 130,5f. S. sp., upper Eocene, Otago, New Zealand; triaene ascribed to S. sp., ×40 (Hinde & Holmes, 1892).
- Penares GRAY, 1867, p. 542 [\*Stelletta helleri SCHMIDT, 1864, p. 32; OD]. Nodular or massive; megascleres oxeas and dichotriaenes, arranged more or less radially or also with styles or subtylostyles; microscleres oxyasters and smooth microxeas, the latter centrotylote or not; ectosome thin, packed with tangentially arranged microxeas (doubtful record based on megascleres). Cretaceous (?Campanian), Holocene: northern Germany, ?Campanian; South Africa, Holocene.-FIG. 130, 4a-e. P. sp.?, Quadratenkreide, Oberg; triaene spicules of genus, ×10 (Schrammen, 1910).-FIG. 130,4f-h. P. obtusus von Lendenfeld, Holocene, Arghulas Bank, South Africa, megascleres; f-g, dichotriaenes; h, oxea; ×20 (von Lendenfeld, 1907).
- Stolleya SCHRAMMEN, 1899, p. 7 [\*S. microtulipa; SD DE LAUBENFELS, 1955, p. 42]. Form of body uncertain; collapsed examples nodular or crustlike, or with traces of rounded elevations with osculum-like pits at their summits; megascleres large oxeas and smaller, long-shafted dichotriaenes with small cladomes, or also with subordinate plagiotriaenes or protriaenes as variants of typical dichotriaenes; cladal branches of most dichotriaenes more or less in one plane; microscleres unknown. [Compared with Anthastra SOLLAS of Stellettinae by original author but could represent several other genera: e.g., see Penares GRAY.] Cretaceous (Turonian-Maastrichtian): England, northern Germany.-FIG. 130, 3a-d. \*S. microtulipa, Quadratenkreide, upper Campanian, Oberg, northern Germany, spicules of type species; a, dichotriaene; b, cladome of dichotriaene; c, cladal ends of further dichotriaenes; d, oxea, incomplete, ×10 (Schrammen, 1910).

### Family GEODIIDAE Gray, 1867

[nom. correct. SOLLAS, 1888, p. cxliii, pro Geodiadae GRAY, 1867, p. 504] [=Sterrastrosa SOLLAS, 1888, p. 209; Erylidae VON LENDENFELD, 1910, p. 11]

Sponges similar to Ancorinidae but distinguished by having a cortex that is densely packed with sterrasters or aspidasters to form a stony, dermal armor. Most with other euasters in choanosome, their forms ranging as in Ancorinidae; some also with microrhabds or spheres, or with spheres as sole choanosomal microscleres. [Dermal sterrasters and aspidasters are formed in the choanosome, but moved outwardly and accumulated in the cortex. Sterrasters originate from highly polyactinal oxyasters, whose rays grow in all directions equally; aspidasters from similar prototypes with rays all in one plane. The Carboniferous (Mississippian) record from loose triaenes and sterrasters is not determinable at the generic level.] Carboniferous (Mississippian)-Holocene.

### Subfamily GEODIINAE Gray, 1867

[nom. correct. REID, herein, pro Geodina SOLLAS, 1888, p. cxlviii, nom. transl. ex Geodiadae Gray, 1867, p. 504]

### With sterrasters but not aspidasters. Carboniferous (Mississippian)–Holocene.

Geodia LAMARCK, 1815, p. 333 [\*G. gibberosa; OD] [=*Cydonium* FLEMING, 1828, p. 516 (type, *C*. mulleri, OD); Silicosphaera HUGHES, 1985, p. 603 (type, S. asteroderma, OD), described from isolated sterraster microscleres]. Massive, globose, lobate, forming thick-walled cups or related shapes; intracortical canals (chones) cribiporal or with exhalant chones opening through single apertures (uniporal); exhalant, pore sieves or other apertures usually localized, in a small, central cavity in some uniporal forms, mainly on inner face if body is cup shaped, or in special lateral areas; typical megascleres oxeas and orthotriaenes or dichotriaenes, to which anatriaenes, protriaenes, or both may be added; sometimes with subordinate, triaene variants (e.g., diaenes) or oxea variants (e.g., strongyles; some with additional small oxeas (e.g., 0.10 as large as main ones), distributed generally or localized in cortex; microscleres other than sterrasters are smaller euasters in range of oxyaster to spheraster, of one sort only or more than one; no microrhabds; some species with spherasters of choanosome entering cortex in walls of chones, or with protruded megascleres (supposed fossil records based chiefly on loose megascleres). ?Lower Jurassic, Cretaceous (?Aptian, Albian)-Holocene: Austria, ?Lower Jurassic;

southern England, ?*Aptian, Albian;* England, Germany, Poland, ?*Upper Chalk;* USA (Alabama), *Paleocene;* New Zealand, ?*upper Eocene;* Western Australia, Spain, *Miocene;* cosmopolitan, *Holocene.*—FIG. 131, *Ia–g. G. stellata* VON LENDENFELD, Holocene, Arghulas Bank, South Africa; *a*, vertical or axial section through sponge with radiate structure,  $\times 0.5$ ; *b–c*, small diaene and triaene, with short, extra, rhabdal ray, pointing upwardly,  $\times 50$ ; *d*, dichotriaene,  $\times 33$ ; *e–f*, small anatriaenes (shown with rhabdome incomplete),  $\times 50$ ; *g*, group of elliptical sterrasters,  $\times 150$  (von Lendenfeld, 1907).

- Caminus SCHMIDT, 1862, p. 48 [\*C. vulcani; OD]. Globular to massive or lobate; inhalant chones as in Geodia, but exhalant water leaving through oscula of a few local, paragastral cavities; typical megascleres strongyles and orthotriaenes, but latter may be varied as dichotriaenes and strongyles may grade into oxea or amphitylote (=tylostrongyle) variants; no anatriaenes; accessory microscleres euasters and spheres or spheres only. Upper Cretaceous (?Turonian-?Maastrichtian), Paleogene (Eocene)-Holocene: Czech Republic, Slovakia, England (supposed records based on loose megascleres), ?Turonian-?Maastrichtian; Western Australia, Eocene; cosmopolitan, Holocene.——FIG. 131,2a-d. C. sphaeroconia SOLLAS, Holocene, Brazil, South Atlantic; a, side view of complete sponge,  $\times 0.5$ ; b, vertical section showing exhalant canals and paragastral cavity, ×1; c, exceptionally large, somal sphere; d, compounded spheres, ×400 (Sollas, 1888).
- Conciliaspongia ROBINSON & HASLETT, 1995, p. 199 [\*C. rarus; OD]. Sponge characterized by oblong to oval, siliceous microscleres whose surfaces are covered with pentameral pores except for single small, barren patch that has an X standing out in relief, which is interpreted as hilum; two larger pores occur in areas between greatest angles of X. [Taxonomic placement of these isolated microscleres is uncertain, but they are grouped here with apparently related forms such as Geodia.] Paleogene (middle lower Miocene:) Ecuador.-FIG. 131,5. \*C. rarus, Dos Bocas Formation, 3 km south of San Pedro; holotype microsclere with characteristic surface sculpture, Slide JW 199, BMNH, ×200 (Robinson & Haslett, 1995; courtesy of Journal of South American Earth Sciences).
- Cydonium FLEMING, 1828, p. 516 [\**C. mulleri;* OD]. Distinguished from *Geodia* LAMARCK in usage of SOLLAS (1888), restricting *Geodia* to forms with a distinct, paragastral cavity when young, sometimes also when adult, and with sphinctrate, uniporal, exhalant chones; this usage now generally rejected since characters relied upon are not constant. [There is one record under SOLLAs's usage.] *Paleogene (Eocene):* Western Australia.
- ?Geodiopsis SCHRAMMEN, 1910, p. 117 [\*Geodia cretacea SCHRAMMEN, 1899, p. 8; SD DE LAUBENFELS, 1955, p. 42]. Form unknown; megascleres stout oxeas and protriaenes, slender anatriaenes, and variants, the last with a short, sec-

ond, rhabdal ray or developed as pseudotylostyles; only microscleres known are smooth, spherical bodies. [The genus is a geodiid if microscleres are sterrasters, but closest resemblance is to Tetillidae (spp. of *Tetilla* SCHMIDT, *Cinachyra* SOLLAS) if they are spheres.] *Cretaceous* (*Coniacian– Maastrichtian*): northern Germany.——FIG. 131, *3a–f.* \*G. cretacea (SCHRAMMEN), Quadratenkreide, Campanian, Oberg; spicules of type species including stout protriaene, oxea, anatriaene, 2 below, and variants, above, ×10 (Schrammen, 1910).

- 'Geoditesia Zhuravleva in Rezvoi, Zhuravleva, & KOLTUN, 1962, p. 51, nom. nov. pro Geodites CARTER, 1871, p. 129, obj., non RAFINESQUE, 1832 [\*Geodites haldonensis CARTER, 1871, p. 129; OD]. Sponge and microscleres unknown; type species based on stout triaenes, dichotriaenes, and diaenes, loose in sediment, like those of various modern ancorinids and geodiids; some also like or more like dermalia of contemporaneous megamorine lithistids. [Used by ZHURAVLEVA as equivalent to Geodites CARTER s.l., with records from the Carboniferous-Quaternary. Geodites used for loose trianes, dichotriaenes, and a diaene ascribed to Geodia LAMARCK, 1815, with termination -ites; invalid under Code Article 20 (ICZN, 1999). Also used as a generic name for supposedly geodiid spicules, not identified as Geodia.] Carboniferous (Mississippian)-Paleogene (upper Eocene): southern England.—FIG. 131,4a-e. \*G. haldonensis (CARTER), Upper Greensand, Upper Cretaceous, Exeter, England; a, spheroidal, siliceous spicule, lateral view, ×75; b, triaene; c, diaene; d, anatriaene; e, dichotriaene, ×25 (Carter, 1871).
- Pachymatisma BOWERBANK, 1842, p. 244 [\*Halichondria johnstonia BOWERBANK, 1842, p. 198; OD]. Nodular to massive; inhalant chones as in Geodia; exhalant chones with single apertures, conspicuous or not, distributed generally or in lines that follow ridges of surface; megascleres orthotriaenes and strongyles, to which subordinate variants may be added, or with additional cortical oxeas; no anatriaenes; accessory microscleres euasters and microrhabds, of which latter are numerous in external layer of cortex; microrhabds typically rough or finely spined, but not developed as sanidasters (supposed record based on loose megascleres). Cretaceous (?Albian), Holocene: southern England, ?Albian; cosmopolitan, Ho--FIG. 132,2a. \*P. johnstonia (BOWERlocene.-BANK), Holocene, littoral specimens, British Isles; holotype, ×1 (Bowerbank, 1874b).-FIG. 132,2b-c. P. ? virga HINDE, ?Albian, southern England; b, strongyle, ×40; c, strongyle, ×30 (Hinde, 1885).
- Rhaxella HINDE, 1890, p. 59 [\*R. perforata; OD]. Sponges palmate, flabellate, or funnel shaped with thin walls composed entirely of aggregated masses of globular or spheroidal, sterraster spicules; plates of wall interweave to form labyrinthine interspaces; sterrasters ranging ellipsoidal to nearly spherical with prominent hilum or depression on one side. Upper Jurassic: England.—FIG.

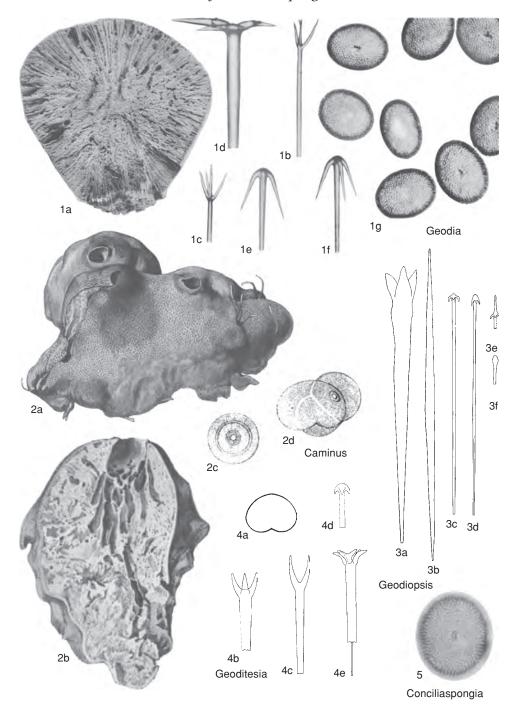


FIG. 131. Geodiidae (p. 188–189).

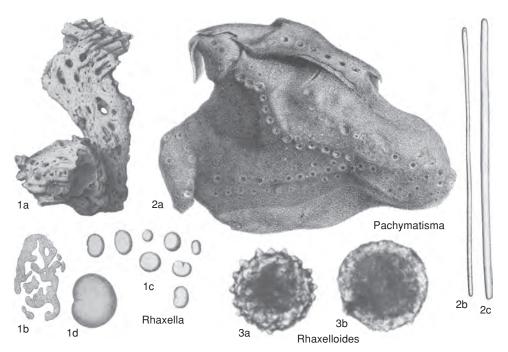


FIG. 132. Geodiidae (p. 189–191).

132,1*a–d.* \**R. perforata*, Lower Calcareous Grit, Oxfordian, Scarborough, Yorkshire; *a*, side view of subpalmate sponge with labyrinthine upper end,  $\times 0.5$ ; *b*, transverse section showing complex, canal pattern of interior,  $\times 1$ ; *c*, drawings of several sterrasters showing range of size and shape,  $\times 40$ ; *d*, globose sterraster with minute points of surface produced by tips of radial fibers,  $\times 100$  (Hinde, 1890).

Rhaxelloides TREJO, 1967, p. 37 [\*R. sphaerica; OD]. Isolated microscleres star shaped, spherical to cylindrical; spherical forms 80 to 170 microns in diameter and of two types: hollow with small and irregularly distributed protuberances, and solid with large, conical, regularly distributed protuberances. Upper Cretaceous: Mexico.—FIG. 132,3ab. \*R. sphaerica, Malpaso, Chiapas; a, typical solid, spherical spicule with large protuberances; b, typical hollow, spherical spicule with small, surficial protuberances, ×205 (Trejo, 1967).

### Subfamily ERYLINAE Sollas, 1888

[nom. correct. REID, herein, pro Erylina SOLLAS, 1888, p. cxlvii]

### With aspidasters. Upper Jurassic– Holocene.

Erylus GRAY, 1867, p. 549 [\**Stelletta mammillaria* SCHMIDT, 1862, p. 48; OD]. Encrusting to massive, lobate, spheroidal or cylindrical; inhalant chones with single apertures only (uniporal); exhalant apertures oscula or pores of single chones; megascleres oxeas, strongyles, or both, and orthotriaenes or dichotriaenes; no anatriaenes; internal architecture not radiate except near cortex; accessory microscleres microrhabds and euasters, latter of a single sort or more in range from oxyaster to spheraster; microrhabds centrotylote or not, sometimes forming a layer at surface of cortex; aspidasters range from thin discs with radial canals or ridges to thicker, tuberculate bodies, like flattened sterrasters. *Paleogene (upper Eocene)–Holocene:* New Zealand, *upper Eocene;* Western Australia, *?Miocene;* cosmopolitan, *Holocene.* 

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- E. (Erylus). Adult aspidaster resembles a flattened sterraster, with tuberculate surfaces; tubercles without order or in groups, sometimes stellate in form; opposite sides may be ornamented differently. Paleogene (?upper Eocene), Neogene (?Miocene), Holocene: New Zealand, ?upper Eocene; Western Australia, ?Miocene; cosmopolitan, Holocene.——FIG. 133,3a-f. E. (E.) lendenfeldi SOLLAS, Holocene, Indian Ocean, aspidasters; a-b, adult examples with opposite sides differently ornamented, x200; c-e, developmental stages, x200; f, stellate tuberculation, x770 (Dendy, 1916; courtesy of Academic Press Ltd.).
- E. (Triate) GRAY, 1867, p. 549 [\**Stelletta discophora* SCHMIDT, 1862, p. 47; OD]. Adult aspidaster a very thin disc or elliptical plate,

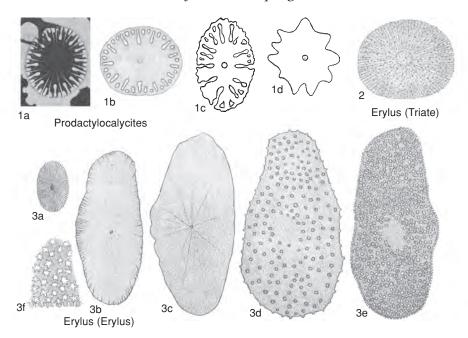


FIG. 133. Geodiidae (p. 191-192).

finely granulate or smooth; may be radially ridged along tracks of original rays (resembles young stages of *E. (Erylus)* aspidasters). *Paleogene (upper Eocene)–Holocene:* New Zealand, *upper Eocene*; East Atlantic, Mediterranean, Indian Ocean, *Holocene.*—FIG. 133,2. \**E. (T.)* sp., upper Eocene, Otago, New Zealand; aspidaster, ×200 (Hinde & Holmes, 1892).

Prodactylocalycites REID, nom. nov. herein, nom. nov. pro Dactylocalycites CARTER, 1871, p. 123 (invalid, Code Art. 20, ICZN, 1999), sensu DE LAUBENFELS, 1955, p. 58 [\*Dactylocalycites callodiscus CARTER, 1871, p. 123; OD]. Sponge unknown; represented by spicules called pinakids, in form of thin discs with marginal notches or submarginal perforations, located between fine, tubular canals that radiate from center. [Spicules sometimes thought to be dermalia of a lithistid, by comparison with phyllotriaenes and discotriaenes, but distinguished from known lithistid dermalia by the multiple radial canals; here compared with aspidasters of Triate GRAY. The invalid name Dactylocalycites CARTER (1871, p. 123) was proposed to refer to spicules, not entire sponges; phyllotrianes, discotrianes, and pinakids were referred to Dactylocalyx STUTCHBURY, 1842, p. 87.] Upper Jurassic-Holocene: southern Germany, Upper Jurassic; southern England, Germany, Albian-Campanian; New Zealand, upper Eocene; West Atlantic (Barbados), Paleogene-Neogene; Indian Ocean, Holocene.—FIG. 133, 1a. \*P. callodiscus (CARTER), Quadratenkreide, Campanian, Oberg, Germany; pinakid disc showing canals, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).——FIG. 133,*1b. P.* sp., upper Eocene, Otago, New Zealand; dermal disc (pinakid) with submarginal perforations, ×200 (Hinde & Holmes, 1892).——FIG. 133,*1c-d. P. ellipticus* (CARTER), Upper Greensand, Upper Cretaceous, Exeter, England; modified pinakids, ×75 (Carter, 1871).

### Family PAELOSPONGIIDAE Mostler, 1986

[Paelospongiidae MOSTLER, 1986, p. 337]

Family known only from isolated megascleres that are characteristically complexly developed triaenes, including mesotriaenes, and dichotriaenes with missing rhabds; their cladi have characteristic spinose development and each of many spines has its own canal. *Upper Triassic*.

Paelospongia MOSTLER, 1986, p. 337 [\*P. longiradiata; OD]. Spicules are mesotriaenes with rhabds of variable length and strong, spinose cladi. Upper Triassic: Italy, Austria.——FIG. 134, Ia-b. \*P. longiradiata, Zlambach Formation, Rhaetian, St. Agatha, Austria; a, photomicrograph of holotype mesotriaene, ×100; b, drawing of spinose mesotriaene characteristic of genus, scale not given but approximately ×50 (Mostler, 1986). Actinospongiella REID, herein, nom. nov. pro Actinospongia MOSTLER, 1986, p. 342, non D'ORBIGNY, 1849 [\*Actinospongia hexagona MOSTLER, 1986, p. 342; OD]. Spicules are strongly spinose dichotriaenes with rhabd missing or reduced to button. Upper Triassic: Austria.— FIG. 134,2. \*A. hexagona (MOSTLER), Zlambach Formation, Rhaetian, St. Agatha; photomicrograph of characteristic dichotriaene, scale not given but approximately ×100 (Mostler, 1986).

# Order CRANIELLIDA Reid, 1968

[Craniellida REID, 1968a, p. 22] [=suborder Sigmatophora SOLLAS, 1887, p. 423; suborder Spirosclerina REID, 1963d, p. 199; "Spirophorides" (no rank given) BOROJEVIC, CABIOCH, & LÉVI, 1968, p. 4]

Choristid sponges that typically have sigmaspire microscleres, although a few have only microrhabds or no microscleres, and monaxonids that resemble choristids except for absence of tetraxial megascleres (triaenes); some choristids with sigmaspires accompanied by microrhabds, spheres, or cheloids, or rarely replaced by toxaspires; most choristids with long-shafted triaenes, which are typically protriaenes and anatriaenes; protriaenes of some with unequal cladi and varied as diaenes and monaenes; single genera with additional subtriaene or amphitriaene megascleres and one with amphitriaenes only; dichotrianes absent in most, and may be polycladose when present; additional oxea megascleres in most choristids, and oxeas only in monaxonids; megascleric calthrops unknown; euasters and streptoscleres absent. Upper Cretaceous (Campanian)–Holocene.

Recognition of possible fossil examples of this order is based entirely on occurrences of megascleres like those of modern species. Slender protriaenes and mesotriaene variants, like those of various living Tetillidae, first appear in the Carboniferous (Visean) of Ireland. Polycladose dichotriaenes, like those of *Tetilla infrequens* (HENTSCHEL), occur in the lower Cenomanian of southern England.

This order has no obvious relationship to the other Choristida, although it shares possession of tetraxial megascleres. Modern examples can commonly be recognized by the general aspect of their megascleres, of which

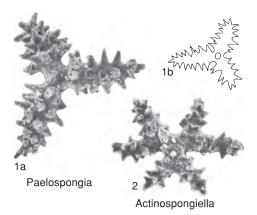


FIG. 134. Paelospongiidae (p. 192-193).

asymmetrical (anisocladose) protriaenes are peculiar to this order. They are also unusual in the rarity of dichotriaenes that, when present, are prodichotriaenes whose cladi may branch more than once. The latter forms do not occur in Pachastrellida or Anocorinida, although similar branching occurs in the spicules of some Plakinida.

Two modern monaxonids, *Trachygellius* TOPSENT and *Raphidotethya* BURTON, are so much like the typical choristids, apart from lacking triaenes, that their inclusion in the order seems appropriate; but no fossils of this type can be recognized in the absence of microscleres and soft parts.

### Family TETILLIDAE Sollas, 1886

[Tetillidae SOLLAS, 1886, p. 178; sensu DE LAUBENFELS, 1936, p. 170] [=Craniellidae DE LAUBENFELS, 1936, p. 173]

Sponges with triaene and oxea megascleres and, typically, with sigmaspire microscleres, no megascleric calthrops; some with typical microscleres accompanied by microrhabds or spheres or with microrhabds only or no microscleres; triaenes typically long-shafted protriaenes and anatriaenes, although either may be absent; often including hairlike (trichodal) protriaenes with unequal cladi (commonly one long, two short), which are distinctive in absence of sigmaspires; all types sometimes vary as diaenes or monaenes, which predominate in some species; a few with additional orthotriaenes, subtriaenes, amphitriaenes, or

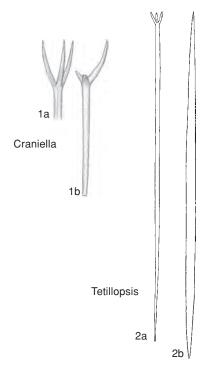


FIG. 135. Tetillidae (p. 194).

vestigial triaenes only; no typical dichotriaenes, although rarely a triaene may have cladi branching once or more often; main skeleton typically radiate, rarely plumose; some with special, cortical oxeas, arranged radially or tangentially; most anchored by protruded anatriaenes, replaced rarely by distally knobbed pseudotylostyles; modern examples eurypylous, with ectosome varying from minimal dermis to two-layered cortex; some viviparous, with parenchymella-like embryos. [The group was divided by DE LAUBENFELS (1936, 1955) into the Craniellidae, with sigmaspires, and Tetillidae, without microscleres, on the basis of absence of microscleres in type species of Tetilla SCHMIDT, T. euplocamos SCHMIDT. (see DE LAUBENFELS (1955, p. 42) for remarks on Tetillopsis SCHRAMMEN). This division is not followed here because the species has trichodal triaenes like those of many species with sigmaspires, and because various species of Craniellidae also lack microscleres.

The Carboniferous record is based on loose protriaenes like those of living tetillids, from the Visean of Fermanagh, Ireland.] *Upper Cretaceous (Campanian)–Holocene.* 

- ?Tetillopsis SCHRAMMEN, 1910, p. 49 [\*T. doeringi; SD DE LAUBENFELS, 1955, p. 42, as T. dorinzi, nom. null., here accepted as a typographical mistake intended to refer to T. doeringi SCHRAMMEN]. Form unknown; megascleres oxeas and slender protriaenes; no anatriaenes; microscleres unknown. [Position uncertain, but megascleres are comparable with those of living Tetilla sandalina SOLLAS, for example, that lacks anatriaenes.] Upper Cretaceous (Campanian): Germany.—FIG. 135,2a-b. T. longitridens SCHRAMMEN, Quadratenkreide, Oberg; oxea and protriaene, ×10 (Schrammen, 1910).
- Craniella SCHMIDT, 1870, p. 66 [\*C. tethyoides; SD DE LAUBENFELS, 1936, p. 175; not Alcyonium cranium Müller, 1776, p. 255, as cited in DE LAUBENFELS, 1955, p. 42]. Megascleres typical of family; main skeleton radiate; ectosome developed as a cortex with radial, cortical oxeas in an inner, fibrous layer and a cavernous, outer layer; sigmaspires present and rarely accompanied by chelalike variants. [The genus was also treated by DE LAUBENFELS (1936) as including noncorticate sponges, here regarded as species of Tetilla SCHMIDT, 1868, by restriction of that genus to forms lacking sigmaspires. Doubtful Eocene records (HINDE & HOLMES, 1892, p. 235; CHAPMAN & CRESPIN, 1934, p. 110) are based on loose triaenes only. MÜLLER's article cited by DE LAUBENFELS, as listed above, was published in 1776.] Paleogene (?Eocene), Holocene: Australia, New Zealand, ?Eocene; cosmopolitan, Holocene. -FIG. 135, 1a-b. C. cranium; loose protriaenes similar to those of living Craniella cranium (MÜLLER), ×50, ×40 (Hinde & Holmes, 1892).

# Order UNCERTAIN

Choristid and sublithistid sponges with modern counterparts, but possessing tetraxial megascleres; no microscleres known.

## Family CEPHALORAPHIDITIDAE Reid, 1968

### [Cephaloraphiditidae REID, 1968c, p. 1,252]

Megascleres include sinuous monaxons (ophirhabds), to which oxeas, strongyles, amphitylotes, or styles may be added, and short-shafted triaenes or subtriaenes with unbranched cladi; ophirhabds typically intertwined to form a loosely coherent, skeletal framework, without formation of zygomes; tetraxial megascleres arranged ra-

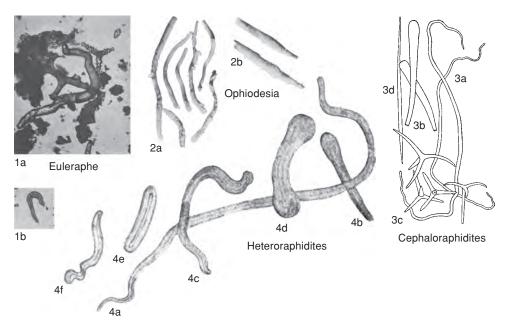


FIG. 136. Cephaloraphiditidae (p. 195-197).

dially with their cladi at surface of skeleton or scattered among ophirhabds; no microscleres known. [Members of this family were placed by SCHRAMMEN (1903, p. 17) in the family Ophiraphiditidae SCHRAMMEN; but the type genus, Ophiraphidites CARTER, 1876, is known only from fragmentary material, in which tetraxial megascleres are absent. ZITTEL (1878b) had previously identified Ophiraphidites with Cretaceous forms possessing triaenes, and was followed by SCHRAMMEN in this usage; but the most nearly similar modern sponge, "Jaspis" serpentina WILSON, has no tetraxial megascleres in life. It seems better to place the forms with monaxons only in the order Epipolasida of the subclass Monaxonida, therefore, which is also appropriate because the microscleres of *J. serpentina* are euasters. If that species is a so-called epipolasid derivative of a form with tetraxons, its euasters should place the Cephaloraphiditidae in the order Ancorinida.

The combination of ophirhabds and triaenes are also appropriate in a source stock of the lithistid order Megalithistida; but the known cephaloraphiditids occur too late in time, and the microscleres of living megalithistids are microrhabds and spirasters.] *Jurassic–Neogene.* 

- Cephaloraphidites SCHRAMMEN, 1899, p. 6 [\*C. cavernous; SD DE LAUBENFELS, 1955, p. 43]. Thickwalled cup with shallow, paragastral cavity; external and paragastral surfaces with numerous small, skeletal pores (ostia, postica), from which radiate skeletal canals; principal megascleres ophirhabds and clublike styles (rhopalostyles); additional oxeas and short-shafted triaenes in meshes of skeletal framework; microscleres unknown. [The type species was based on a fragment; but the habit is known from C. milleporatus SCRHAMMEN, 1899, which has similar spicules.] Cretaceous (Campanian): Germany. FIG. 136, 3a-d. C. milleporatus SCHRAMMEN, Quadratenkreide, Oberg; spicule suite including a, ophirhabds; b, rhopalostyles; c, triaenes; and d, an oxea, ×10 (Schrammen, 1910).
- Euleraphe SCHRAMMEN, 1937, p. 82 (SCHRAMMEN, 1936, p. 184, nom. nud.) [\*E. incrustans; OD]. Thin crusts on other sponges; canal system barely developed in inner part; spicules short and sinuous, termed eulerhabds, forming thick blanket. Jurassic: Germany.——FIG. 136,1a-b. \*E. incrustans, Weiss Jura, Gerstetten; a, sinuous eulerhabd with associated acanthotriaene; b, strongly curved eulerhabd, ×50 (Schrammen, 1937).
- Heteroraphidites SCHRAMMEN, 1901, p. 17 [\*H. spongiosus SCHRAMMEN, 1901, p. 18; OD]. Globose or tuberose, attached sponges with skeleton largely of strongyles and tylostyles, with large

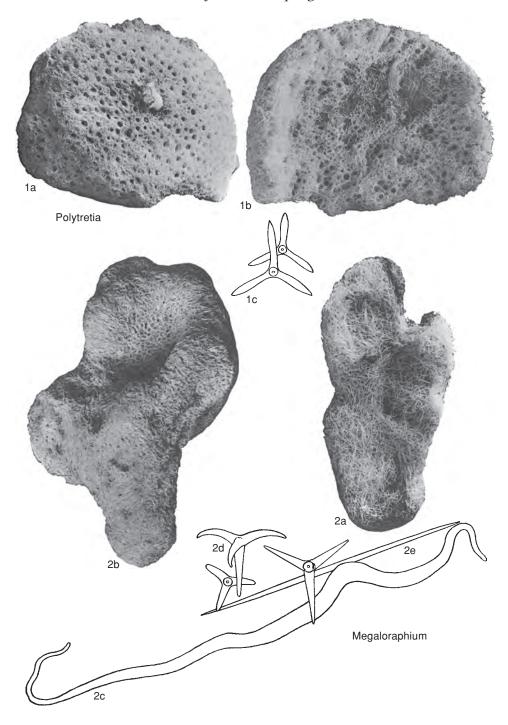


FIG. 137. Cephaloraphiditidae (p. 197).

amphioxeas; tetractine spicules rare; microscleres unknown. *Upper Cretaceous–Neogene:* cosmopolitan.——FIG. 136,4*a–f.* \**H. spongiosus,* Quadratenkreide, Campanian, Oberg, Germany; representative spicules (Schrammen, 1901).

- Megaloraphium SCHRAMMEN, 1910, p. 127 [\*M. auriforme; OD]. Irregularly ear shaped; skeletal pores typically absent although a few small examples may occur; no skeletal canals; main megascleres very large ophirhabds (e.g., 10 mm long); oxeas and small triaenes in skeletal meshes; microscleres unknown. Cretaceous (Campanian): Germany.—\_\_\_FIG. 137,2a-e. \*M. auriforme, Quadratenkreide, Oberg; a, young individual without skeletal pores but with well-preserved, spicular structure; b, example with a few small pores in parts, ×1; c-e, spicule suite including ophirhabd, triaenes, oxea, ×16 (Schrammen, 1910).
- Ophiodesia SCHRAMMEN, 1937, p. 70 (SCHRAMMEN, 1936, p. 183, nom. nud.) [\*O. solivaga; OD]. Flat, ear-shaped sponges with moderately thick wall; megascleres are sinuous ophirabds and lumpy styles. Upper Jurassic: Germany.—FIG. 136,2ab. \*O. solivaga, Weiss Jura, Streitberg; a, ophirhabds; b, nodular styles, ×10 (Schrammen, 1937).
- Polytretia SCHRAMMEN, 1910, p. 126 [\**P. seriatopora;* OD]. Ear shaped; convex side more or less smooth with large, skeletal pores from which short canals run inwardly; concave side irregularly sculptured with large postica in depressed parts, typically in groups of 5 to 10; main megascleres ophirhabds; oxeas and triaenes in skeletal meshes; microscleres unknown. *Cretaceous (Campanian):* Germany. ——FIG. 137, *Ia-c. \*P. seriatopora,* Quadratenkreide, Oberg; *a*, convex surface with large, skeletal pores; *b*, concave surface with large, skalant postica, ×1; *c*, triaenes as seen from below, ×16 (Schrammen, 1910).
- Rhabdospongia SOLLAS, 1873, p. 79 [\**R. cummunis;* OD]. Sponges more or less rodlike, megascleres are sinuous oxeas. [No known suitable figures.] *Lower Cretaceous:* Europe.

### Family HELMINTHOPHYLLIDAE Schrammen, 1937

#### [Helminthophyllidae SCHRAMMEN, 1937, p. 69]

Sublithistid sponges whose principal megascleres are short, curved monaxons (kyphorhabds), with successive, semiannular swellings interrupted on concave sides, and with weakly developed, zygomelike expansions at ends in some examples; dichotriaenes occur as dermalia; no other spicules known. [The kyphorhabds are arranged so that their ends abut on other examples and are loosely coherent when zygomelike ends are developed. The sublithistid character of the single known genus was recognized by SCHRAMMEN (1937, p. 70).] *Upper Jurassic (Kimmeridgian).* 

Helminthophyllum SCHRAMMEN, 1937, p. 69 (SCHRAMMEN, 1924a, p. 150, nom. nud.; SCHRAM-MEN, 1936, p. 183, nom. nud.) [\*H. feifeli; OD]. Earlike or platelike; no skeletal pores or canals; main megascleres kyphorhabds; dermalia shortshafted dichotriaenes; no other spicules known. Upper Jurassic (Kimmeridgian): Germany.——FIG. 138,2. \*H. feifeli, Weiss Jura; kyphorhabds, ×20 (Schrammen, 1937).

### Family SCOLIORAPHIDIDAE Zittel, 1879

[nom. correct. DE LAUBENFELS, 1955, p. 42, pro Scolioraphidae ZITTEL, 1879, p. 2]

Some spicules strikingly annulate; microscleres unknown. *Cretaceous*.

- Scolioraphis ZITTEL, 1878b, p. 4 [\*S. cerebriformis; SD DE LAUBENFELS, 1955, p. 42]. Meandriform leaves or irregular shapes containing dense masses of annulate, lumpy spicules. Upper Cretaceous: Europe. ——FIG. 138,4. \*S. cerebriformis, Quadratenkreide, Campanian, Sutmerberges, Germany; characteristic spicules, ×25 (de Laubenfels, 1955).
- Condylacanthus FISCHER, 1867, p. 237 [\*C. gaudryi; OD]. Spicules elongate, needlelike with regular, prominent annulations; head with three short branches, each of which is trilobed and tuberculose. Cretaceous: France.——FIG. 138,5. \*C. gaudryi, sandstone of Chalk, Pontavesnes by Beauvais, Oise; isolated spicule, ×40 (Fischer, 1867).

### Family UNCERTAIN

Arthaberia SIEMIRADZKI, 1913, p. 190 [\*A. balinensis; OD]. Semilithistid, top-shaped sponge with thick walls and numerous oval ostia on upper surface; lower surface finely porous; skeleton of very long but thin, rodlike spicules that have curved nodes scattered here and there on their sides; these are sometimes associated with same size rhizomorines in upper layer, but latter were not observed in interior where rodlike spicules form closely packed fibers that are radially arranged; outer, dermal layer formed by growth of nodose, triaene, anchorlike spicules whose epirhabd follows fiber trend, but whose zygomes occur singly or generally form three-rayed structures. Jurassic: Poland.-FIG. 138,6a-b. \*A. balinensis, Krakau; a, side view,  $\times 1$ ; b, section through outer part of wall with radially oriented, monaxial spicules in interior and three-rayed spicules in outer wall, ×3 (Siemiradzki, 1913).

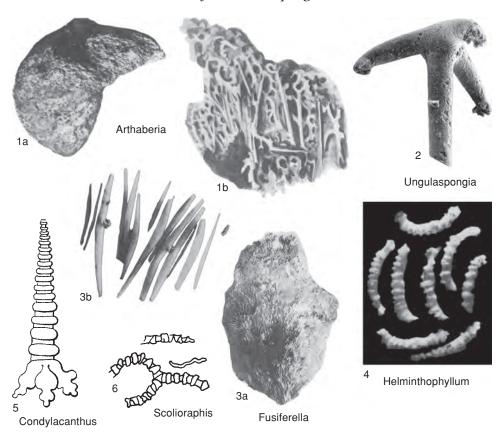


FIG. 138. Helminthophyllidae, Scolioraphididae, and Uncertain (p. 197-198).

Fusiferella DE LAUBENFELS, 1955, p. 43, nom. nov. pro Atractophora SCHRAMMEN, 1924a, p. 76, non STALL, 1853 [\*Atractophora armata SCHRAMMEN, 1924a, p. 76; OD]. Sponge elongate, with skeleton composed of spindle-shaped, straight to curved amphioxeas that form thick bundles that are radially arranged in wall and form a fur of slanting spicules on surface. Upper Cretaceous: Germany. ——FIG. 138, Ia-b. \*F. armata (SCHRAMMEN), Mukronatenkreide, Campanian, Misburg; a, holotype with skeletal bundles, ×0.5; b, amphi-

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oxeas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Ungulaspongia MOSTLER, 1996c, p. 157 [\*U. permica; OD]. Isolated, anatriaene spicules whose three reflexed clads have expanded radially spinose or nodose, pawlike tips. Permian (Roadian): USA (Texas).—FIG. 138,3. \*U. permica, Road Canyon Formation, Glass Mountains; isolated, holotype anatriaene with clads having characteristic, pawlike tips, ×150 (Mostler, 1996c).

# MESOZOIC AND CENOZOIC LITHISTID DEMOSPONGES: TETRACLADINA

# R. E. H. Reid

[formerly of Department of Geology, The Queens University of Belfast]

# Subclass LITHISTIDA Schmidt, 1870

[nom. transl. REID, herein, ex order Lithistida ZITTEL, 1878a, p. 96, nom. transl. pro group Lithistida SOLLAS, 1887, p. 421, nom. transl. ex group Lithistina CARTER, 1875, p. 185, nom. correct. pro group Lithistidae SCHMIDT, 1870, p. 21]

Demospongea whose principal megascleres are desmas that are normally united by articulation (zygosis) to form coherent, skeletal framework; some also with types of megascleres that may be monaxons (e.g., oxeas), triaenes, or both, or with accessory (supplemental) desmas in addition to main ones; principal desmas tetraxial, triodal, monaxial, or anaxial in those whose character is known: some with tetraxial desmas intergrading with triodal or monaxial forms; articulatory features (zygomes) sometimes simple facets only, but typically twig-, root-, or clawlike, or forming tongue-, cup-, or handlike expansions; few forms with zygosis only weakly developed or absent; skeletal framework uncanalized, or with ostia, postica, or both, or with additional epirhyses, aporhyses, or both, or with skeletal pores or canals of unknown character; triaenes arranged typically at surfaces when present, with shafts running inwardly into meshes of internal framework when long enough, and their cladi in ectosome in living forms; shafts of triaenes never normally incorporated into primary, skeletal meshwork, although sometimes imbedded in secondary meshwork formed by supplemental desmas; supplemental monaxons usually loose in skeletal meshes or lying tangentially at surfaces, but sometimes grasped by zygomes of desmas or incorporated into composite, skeletal fibers; supplemental desmas usually small, rhizoclone-like bodies, found in internal meshes, at surface, or both, and sometimes intergrading with primary desmas; examples found at surface may form a supplemental cortex that coats skeletal framework, and may then cover ostia or postica, or be pierced by intracortical pores or canals; microscleres present or absent in living examples, in which they may be microrhabds, streptoscleres (intergrading plesiasters, metasters, and spirasters), unidentified spirasters or amphiasters, or sigmaspires when present; soft parts as in normal Demospongea, with the ectosome usually a dermis. *Cambrian–Holocene*.

The lithistid sponges were interpreted as monophyletic by ZITTEL (1878a) and SOLLAS (1887) but are here considered polyphyletic following Schrammen (1903), Hentschel (1923-1924), BURTON (1929), and DE LAUBENFELS (1936). They appear to comprise forms produced by repetitive (or iterative) evolution of lithistid characters in sponges that were sometimes originally choristids but sometimes monaxonids. On this basis, SCHRAMMEN, HENTSCHEL, BURTON, and DE LAUBENFELS, of the above dates, each attempted to classify lithistids in taxa that also included their nearest supposed nonlithistid relatives and did not use the single group Lithistida. In practice, however, relationships of lithistid and nonlithistid sponges are mainly uncertain, and sometimes probably unknowable. Hence DE LAUBENFELS (1955) reverted to use of order Lithistida in the previous Treatise, Part E and his usage is followed here except that the taxon is treated as a subclass. Orders Tetralithistida LAGNEAU-HÉRENGER (sensu nov.), Megalithistida nov., and Monalithistida LAGNEAU-HÉRENGER (sensu nov.) are thought to comprise forms that probably have had separate origins. The three orders may also include groups having more than one origin, although this is less certain. In addition to genera that fall in the

recognized orders and suborders, there are various isolated modern forms (e.g., *Lophacanthus* HENTSCHEL) for which no attempt is made to classify here.

In further classification, division of orders into suborders is based on methods developed by ZITTEL (1878a), RAUFF (1893, 1894), and SCHRAMMEN (1924b), whose traditional taxa (e.g., Tetracladine ZITTEL, Dicranocladine SCHRAMMEN) are employed at this taxonomic level. Division of suborders into families is based chiefly on the methods of SCHRAMMEN but also on various other sources.

Treatment of genera is based on paleontological methods of ZITTEL (1877a, 1877b, 1878a, 1878b) and later writers, treatments that differ from those of many zoologists. In paleontology, generic diagnoses have been generally based on combinations of details of habitus, internal or external canalization, various characters of the skeletal framework or individual desmas, and such further features as the presence and extent or absence of a supplemental cortex, or presence or absence of intracortical pores when a cortex is present. Reference to loose spicules is almost entirely restricted to the form of dermal triaenes, when these are present. On the other hand, zoological diagnoses given often omit many or all of these characters and may depend entirely on features of the soft parts, on loose megascleres or on microscleres, which are not seen in the fossils.

Some characters used for generic separations in paleontology can certainly be doubted sometimes. For example, the living *Macandrewia azorica* CARTER is irregularly funnel-like or fan shaped with small apopores (or oscules) on the inner surface; but *M. clavatella* (SCHMIDT) is club shaped or toplike, with a few small apopores at the summit. *M. ramosa* TOPSENT is initially similar to *M. azorica* but divides at the top into short branches, which may then divide again into smaller ones. A paleontologist finding such forms as fossils would probably place them into two or three genera on the basis of habitus; yet the habitus of *M. clavatella* is that of the young forms of *M. azorica*. As another instance, otherwise similar sponges would usually be placed in separate genera if they differed in that postica were (a) in groups on an unfurrowed skeletal surface; (b) in groups at the centers of radiating patterns of superficial furrows; or (c) arranged as in (b) but within the furrows roofed over by a skeletal cortex, with separate intracortical postica. On the other hand, a modern form (e.g., M. azorica, or species of Corallistes SCHMIDT) may have skeletal characters as in (a), but also have radiating, subdermal canals around groups of exhalant canals that emerge through the postica and a dermis with separate, osculelike apopores. This suggests that the skeletal differences cited might depend only on how far development of rigid skeletal meshwork extended outside the choanosome in sponges with identical soft parts. Such differences might represent closely allied species, local subspecies, individual variation, or simply individuals that died at different stages of life.

On the other hand, the paleontologist normally has characters of only the skeletal framework, to which characters of triaenes may be added when these spicules are present, as a basis for generic diagnoses. Distinctions based on presence or absence of microscleres, or on their character or arrangement when present, cannot be used. In addition, greater morphological diversity than is shown by modern forms is often confronted. For example, most modern species of the suborder Tetracladina ZITTEL have been referred to two genera only, Theonella Gray and Discodermia DU BOCAGE, whose type species are also so similar that their treatment as subgenera could be justified. The same group, however, has the greatest known diversity among Cretaceous Lithistida, with 55 nominal genera, although this total is inflated to some extent by the nontypological practice of proposing new genera for any species with features not mentioned in a previously published, generic diagnosis. The total cannot be substantially reduced without rejection of some major

category of observable characters, with results that would differ according to which characters are ignored.

Further, examples exist in which paleontological methods seem clearly the more realistic. For example, Azorica pfeifferae CARTER, type species of Azorica CARTER of the suborder Rhizomorina ZITTEL, is a typically flabellate or convoluted sponge with the following characteristics: (a) a nonfibrous skeletal framework; (b) well-developed internal epirhyses and aporhyses; (c) strong, superficial furrowing occuring on both surfaces of the skeletal framework, related to subdermal channels of the soft parts, with primary ostia and postica in floors of furrows, and with furrows mainly longitudinal on the inhalant side of the framework, but tending to form radiating patterns on the exhalant (paragastral) side; (d) on the inhalant side, the furrows are roofed over by a thin, dense, skeletal cortex, with numerous closely spaced, small, intracortical ostia; (e) on the other side, a more or less discontinuous, skeletal cortex is developed mainly around apertures of larger, widely spaced, osculelike, intracortical postica. In contrast, "Seliscothon" chonelloides DOEDERLEIN, described as a supposed living species of the fossil Seliscothon ZITTEL, 1878a, has a fibrous skeletal framework, no epirhyses, aporhyses, or primary ostia, and no superficial furrowing, skeletal cortex, or intracortical pores on either surface. Yet this species was referred to Azorica by SOLLAS (1888), apparently on the basis of its having a flabellate habitus and no microscleres, as in Azorica. These forms seem clearly too different to be placed into one genus; and, if compared with others that have fibrous and nonfibrous structures, it is difficult to justify placing them even into the same family.

# Order TETRALITHISTIDA Lagneau-Hérenger, 1962

### [nom. transl. REID, herein, ex suborder Tetralithistida LAGNEAU-HERENGER, 1962, p. 35; emend., REID, herein]

Lithistida that typically have triaenes or related types of megascleres as dermalia, and desmas whose zygomes are branching twig-, root-, or clawlike structures; desmas all or mainly tetraxial, triodal, or monaxial, with two of these types sometimes present as intergrading variants but with one subordinate, and smooth, spined, or with zygomes tuberculate, or tuberculate on other parts; tetraxial forms typically tetraclones but sometimes developed as triders; triodal forms triders or two-armed variants; monaxial forms sometimes developed as elongate variants of tetraclones, restricted to stalks or root processes, but found chiefly as principal desmas that may be rhizoclones, dicranoclones s.l. or didymoclones; zygosis by zygomes interlocking from desma to desma to form syzygial nodes, or by zygomes grasping arms, central parts, or tubercles of other desmas; one or the other of these two main styles commonly predominant, but with some forms having both styles together; crepides (i.e., initial bodies from which desmas develop), small calthrops, triods, triaenes, or strongyles; dermalia usually dichotriaenes or forms grading from phyllotriaene to discotriaene, but sometimes trichotriaenes, monaxial, discotriaene-like bodies, or anaxial plates; supplemental oxeas in some; many with small, rhizoclone-like bodies (rhizoclonids) as supplemental desmas that may form a dense, supplemental cortex at skeletal surfaces; rhizoclonids often with no obvious axial system but sometimes demonstrably intergrading with principal desmas; microscleres of modern examples microrhabds, amphiasters, plesiasters, metasters, or spirasters. Upper Triassic (Norian)-Holocene.

This taxon was proposed by LAGNEAU-HÉRENGER (1962) to comprise all Lithistida with tetraxial megascleres as desmas or dermalia, called lithistid Tetraxonia by SCHRAMMEN (1910, 1912). Although tetraclone desmas of the suborder Tetracladina appear to have been derived from a calthrops from which they develop in ontogeny, the heloclones of the Helomorina and the megaclones of Megamorina are probably monaxon derivatives. The heloclone, especially, develops from an ophirhabd (sinuous oxea) that is almost as large as the fully formed desma and is, in effect, simply a modified ophirhabd in which zygosis is produced in the simplest manner possible (by means of articulatory notches without formation of typical zygomes). The two latter groups are considered here to have arisen independently of the Tetracladina and, as a result, are placed into the new order Megalithistida.

In addition to the Tetracladina, the other forms referred here to the Tetralithistida have desmas that are normally monaxial but have triaenes or related types of megascleres as dermalia and zygomes like those of Tetracladine. Three suborders are distinguished. The Dicranocladina SCHRAMMEN have desmas that are typically tuberculate. Desmas are dicranoclones s.l. in the family Corallistidae SOLLAS, and dicranoclone-like forms with the tubercles in transverse rows in the Pseudoverruculinidae DE LAUBENFELS. The Pseudorhizomorina SCHRAMMEN have rhizoclonar desmas, which are sometimes tuberculate on the zygomes but typically not on the central parts, and phyllotriaenes or similar monaxial dermalia in the Macandrewiidae GRAY. With these is grouped Neopelta SOLLAS, the only genus of Neopeltidae SOLLAS, whose dermalia are monaxial discs. The Didymmorina RAUFF comprises only the Cylindrophymatidae SCHRAMMEN, in which the desmas are typically didymoclones and the dermalia are dichotriaenes, in the only example in which they are known [in Cylindrophyma milleporata (GOLDFUSS)]. The Pseudorhizomorina were included by SCHRAMMEN (1924a) in his Dicranocladina (although the former name is older), but are thought here to be probably of independent origin. He also regarded the Didymmorina as lithistid Monaxonia, i.e., forms without tetraxons and of monaxonid origin; but triaene dermalia, which do not appear to be extrinsic, are now known from a specimen of C. milleporata identified by SCHRAMMEN himself.

The relationship of forms with monaxial desmas to the Tetracladina is unproven but is

suggested by (a) the similar character of the zygomes; (b) the striking resemblance of desmas of the Corallistidae (Dicranocladina) to those of plinthosellid and many theonellid Tetraclina; (c) the presence of tetraxial desmas, as intergrading subordinates of the main, monaxial ones, in Macandrewia GRAY of the Pseudorhizomorina; and (d) the presence of similar special microscleres (plesiasters, metasters, spirasters) in some of the living Tetracladina (e.g., Racodiscula ZITTEL), Dicranocladina (Corallistes SCHMIDT), and Pseudorhizomorina (Daedalopelta SOLLAS). In broader terms, the microscleres cited suggest that these groups are related to the choristid Poecillastrida (families Pachastrellidae SOLLAS and Theneidae GRAY).

The small Upper Jurassic family Protetraclisidae SCHRAMMEN is worth mention as a possible link between the Tetracladina, in which it is included, and other Tetralithistida. The two included genera (Protetraclis STEINMANN and Rhizotetraclis KOLB) have more or less irregular tetraclones with strongly branching arms that grade into rhizoclone-like desmas. Rhizotetraclis has some desmas that resemble tetrapodal dicranoclones and are comparable with desmas of the contemporaneous dicranocladine Kyphoclonella KOLB. In Protetraclis the dermalia are dichotriaenes. While the known species of this family are contemporaries (not precursors) of the earliest Dicranocladina and the Didymmorina, they have features appropriate to a tetracladine root stock of the groups with monaxial desmas.

If this view of relationships is rejected, alternative comparisons can be made with various Paleozoic lithistids in which triaenes are absent: (a) the Tetracladina and Pseudorhizomorina with the anthaspidellid Orchocladina; (b) the Dicranocladina with the hindiid Tricranocladina (=Eutaxicladina *sensu* SCHRAMMEN); and (c) the Didymmorina with the anomoclonellid Orchocladina, in which some desmas resemble didymoclones. Derivation of the Tetralithistida from these sources, however, presumably involves the *de novo* evolution of triaenes at some point of phylogeny (from monaxons). It is here thought more likely that the triaenes were inherited from choristid ancestors and that resemblances to Paleozoic Lithistida are due to convergence, not relationships.

# Suborder TETRACLADINA Zittel, 1878

[*nom transl.* SOLLAS, 1887, p. 423, *ex* family Tetracladina ZITTEL, 1878a, p. 100]

Desmas typically tetraxial and usually developed as tetraclones although sometimes as triders (brachytriders); some also with elongate, diaxial or monaxial desmas in stalks or root processes, or with triodal, diaxial, or monaxial forms as subordinate variants of normal tetraclones; ultimate syzygial processes spinelike or thickened into tubercles, arms of desmas smooth, spined, or tuberculate; smooth and tuberculate forms found mainly in different genera but sometimes together and intergrading; zygosis by zygomes that interlock to form syzygial fibers or nodes, or that clasp arms, centers, or tubercles of other desmas; dermalia usually dichotriaenes, phyllotriaenes, or discotriaenes, but sometimes trichotriaenes, monaxial variants of discotriaenes, or apparently anaxial plates; supplemental oxeas in some; many with small, supplemental rhizoclonids that may form a skeletal cortex when present; modern species mainly with microrhabds as microscleres but some with spirasters that may grade into metasters or plesiasters. Upper Triassic (Norian)-Holocene.

The name Tetracladina was originally designated at the family level by ZITTEL (1878a) but cannot be treated as a family name, having no generic basis. It was technically first published as the name of a suborder by SOLLAS (1878) but is here ascribed to ZITTEL in accordance with reality and the practice of all later authors, including SOLLAS.

The suborder Tetracladina is envisaged here as characterized, especially in the fossils, by the combined occurrence of tetraclonar desmas and dermal triaenes and in modern forms additionally by occurrence of the microscleres cited. It is not regarded as including forms without dermal triaenes, unless these spicules are thought to have been lost in phylogeny or before burial and fossilization and does not include forms with desmas of outwardly tetraxial shapes that are either monaxial or anaxial, or are regarded as derived from monaxons. With these restrictions, the suborder seems acceptable as probably a natural assemblage. The oldest known genera with both tetraclones and triaenes are Upper Jurassic, although these forms are sufficiently diverse to imply that the group must be older.

The most important exclusion that results from this concept of the taxon is that of the Anthaspidellidae Paleozoic Ulrich (=Archaeoscyphiidae RAUFF and Aulocopiidae RAUFF in DE LAUBENFELS, 1955), which were formerly included because some of the desmas have the form of tetraclones. Some examples of the characteristic desmas (dendroclones) of this family are similar to tetracladine amphitriders (tetraclones with a large, trifid zygome at the end of the primary arm). On the other hand, the simplest of these desmas are in effect bipolar rhizoclones with unspecialized zygomes at both ends of a smooth, central shaft. Some such spicules are demonstrably monaxial. Intergradations in various genera imply that the tetraclonelike desmas are four-armed chiastoclones homologically and hence probably either monaxial or anaxial (REID, 1963d). In addition, no triaenes are known from any Anthaspidellidae. The resemblance of some anthaspidellids to Tetracladina is, hence, interpreted here as convergent; and the family is referred to the suborder Orchocladina RAUFF (=Orchocladinidae RAUFF, 1895, nom. correct. REID, 1963d) of the order Monalithistida LAGNEAU-HÉRENGER.

Jereina FINKS of the Permian is here thought to be an anthaspidellid despite its prevalence of tetraclone-like desmas and resemblance to the tetracladine Jerea LAMOUROUX. Both of these genera are cylindriform sponges with a bundle of axial aporhyses and no paragaster; but this resemblance need not have any implication of relationship, because the same type of organization is present for example in *Carterella* ZITTEL of the Helomorina, *Doryderma* ZITTEL of the Megamorina, and *Jereica* ZITTEL of the Rhizomorina.

From the presence of triaenes and of desmas that develop from a calthrops in ontogeny, it seems likely that the Tetracladina are of choristid origin. The occurrence in some species [e.g., Racodiscula polydiscus (SCHMIDT)] of spirasters, metasters, and plesiasters points to an origin from the same source as the family Pachastrellidae SOLLAS of the order Poecillastrida (=Streptastrosa SOLLAS or Streptosclerophora DENDY), in which choanosomal megascleres may be calthrops. The occurrence of microrhabds only in many others (mainly species of the two main modern genera, Theonella GRAY and Discodermia DU BOCAGE) is not opposed to this conclusion because similar bacilliform microrhabds are abundant in some species of Pachastrella SCHMIDT and allied genera (e.g., Yodomia LEBWOHL).

A possible prototype of the tetraclone is the type of calthrops in which the rays divide terminally into more or less irregular branches as in Pachastrella abyssi SCHMIDT. Such a prototype can be pictured as giving rise to a tetraclone with anaxial zygomes by reduction of the terminal branches of the axial filaments. This process is not demonstrable stratigraphically, for the first forms appear cryptogenically; but some modern species have only weak development of zygomes, and one is recorded as having both tetraclones and calthrops together. In addition, a similar development is represented apparently in the isolated genus Brachiaster WILSON, which has centrotrider desmas and seems probably to be a lithistid version of the choristid Triptolemma DE LAUBENFELS (= Triptolemus Sollas, 1888, non Peckham, 1885). As pointed out by SCHRAMMEN (1910, p. 30), the type of spiculation expected in an ancestor of the Tetracladina (choanosomal calthrops, dermal dichotriaenes) occurs in Propachastrella SCHRAM-MEN, although recorded occurrences of this genus are too late stratigraphically (Late Cretaceous).

After sparse representation in the Upper Jurassic, the Tetracladina have their greatest known development from the Aptian to the Campanian. Tertiary examples are few, and many modern species are referred by zoologists to two genera (*Theonella* and *Discodermia*), although some of these should probably be distinguished generically.

Many Aptian genera fall into two major series, characterized by desmas that are either smooth or strongly tuberculate. Most forms with smooth tetraclones are referred here to the family Siphoniidae D'ORBIGNY, in which dermalia are typically dichotriaenes. Those with tuberculate desmas comprise most of the family Theonellidae VON LENDENFELD (=Discodermiidae SCHRAMMEN), in which dermalia are rarely dichotriaenes but typically phyllotriaenes or discotriaenes, plus the family Plinthosellidae SCHRAMMEN, which differ in that desmas are triders and dermalia sometimes anaxial plates. These two groups presumably mark divergent evolutionary series with the siphoniids, in theory, most similar to the primitive type.

A third distinctive stock, first known from loose desmas in the Upper Jurassic, is the mainly Cretaceous family Phymaraphiniidae SCHRAMMEN, in which dermalia are phyllotriaenes and in which smooth-armed desmas have prominent annulations at the base of each arm. If the phymaraphiniids are regarded as derived from a siphoniid origin, phyllotriaenes of this family presumably evolved independently of those seen in theonellids.

Two Jerea-like Cretaceous genera (Lerouxia MORET and Jereomorpha MORET) have desmas of siphoniid type but phyllotriaene dermalia, which suggests a similar development in siphoniids. If these views are correct, evolution of phyllotriaenes has been iterative in Tetracladina. Some caution is needed, however, because some theonellids have both smooth and tuberculate desmas or smooth desmas only in some species (many species of the modern Theonella).

Among theonellids, evolution of phyllotriaenes from dichotrianes appears to have followed two patterns. One pattern resulted by simple broadening of cladi, with the spicule retaining a dichotriaene shape, for example as in *Thamnospongia* HINDE. The other pattern developed through forms that resemble an irregular dichotriaene in which cladi bear spinelike, lateral processes, as in Cladodermia SCHRAMMEN. The typical irregularly shaped phyllotriaenes intergrade with discotrianes, which in turn may grade into monaxial variants, with an axis in the rhabdal shaft only, through forms with minute, cladal axes. Since both true discotriaenes and monaxial variants may intergrade in one specimen, they are clearly homologous. Assuming that this sequence has reduction of spicular axes, its end term appears to be development of apparently anaxial scales, seen as probably independent developments in the otherwise dissimilar genera Placoscytus SCHRAMMEN (Theonellidae) and Plinthosella ZITTEL (Plinthosellidae).

A further development that seems to be iterative is replacement of tetraclones by triders with one arm reduced to a rudiment and typically bearing no zygome. This is seen in (a) the isolated Jurassic Sontheimia KOLB; (b) various Phymaraphiniidae; (c) a few theonellids, for example, Pseudojerea MORET, as a minor development; and (d) as a characteristic feature of the family Plinthosellidae. Those of the plinthosellid *Plinthosella* ZITTEL are also typically accompanied by two-armed variants that are triodal or diaxial and strikingly similar to dipodal dicranoclones in appearance. In plinthosellid triders, the axis of the aborted arm (brachyome) is often rudimentary; but in Phymaraphiniidae the corresponding ray of the crepis is typically developed fully and may project as a ray beyond the basal annulation.

In some Siphoniidae (e.g., *Siphonia* GOLDFUSS, *Callopegma* ZITTEL), the zygomes are mainly united to form syzygial fibers or nodes. The latter may have spherical enlargement. In contrast, when desmas are triders the zygomes are typically applied to arms, centers, or tubercles of other desmas, without terminal zygosis. In other forms, a mixture of both styles is usual, and terminal, lat-

eral, and central zygoses may be shown by different arms of one desma. Hence modes of zygosis do not seem to have any major bearing on tetracladine evolution, although two extreme patterns can be recognized (mainly terminal, in some siphoniids; mainly by zygomes applied to central parts, in plinthosellids).

If zygomes were evolved from the terminal branches of a calthrops, the smooth-armed type of tetraclone should be primitive, although sometimes it could be reversional (e.g., in the living *Theonella*). Because the finest branches of siphoniid zygomes may thicken into tubercles and tubercles and zygomelike spines are interchangeable in the living *Theonella* and *Discodermia*, the tuberculate type of desma suggests a secondary spread of zygomelike outgrowths to the rest of the desma. This process seems to be present in the Upper Jurassic *Sontheimia*, in which both zygomes and spines on the arms are more or less thickened into tubercles.

Classification here is based mainly on the character of desmas and dermalia, following SCHRAMMEN (1910) but with some of his families merged or called by senior names (e.g., Siphoniidae D'ORBIGNY for Phymatellidae; Theonellidae von LENDENFELD for Discodermiidae SCHRAMMEN). Some of the families that include only one or two genera (Sontheimiidae SCHRAMMEN, Astrocladiidae SCHRAMMEN, Chenendoporidae SCHRAM-MEN) are essentially for isolated genera whose relationships to others are not evident. This classification differs markedly from that of DE LAUBENFELS (1955).

## Family RADIOCELLIIDAE Senowbari-Daryan & Wurm, 1994

### [Radiocelliidae SENOWBARI-DARYAN & WURM, 1994, p. 448]

Thalamid demosponges with a skeleton of tetraclones in a chambered sphinctozoan structure but without a rigid, calcareous skeleton. [Treated as sphinctozoan demosponges by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002, p. 1,533).] *Upper Triassic (Norian).* 

Radiocella SENOWBARI-DARYAN & WURM, 1994, p. 449 [\**R. prima;* OD]. Thalamid sponges with clearly defined, inner segmentation, which is less well defined on exterior; spicular skeleton consisting of tetraclones; basal skeleton not developed; chambers radiating and arranged in whorl or spiral; spongocoel retrosiphonate and extending through entire sponge; interwalls thick. Upper Triassic (Norian): Austria.-FIG. 139, 1a-c. \*R. prima, Dachstein reef limestone, northern Calcareous Alps; a, longitudinal section of holotype showing chambers in thick walls, around axial spongocoel, and upwardly divergent, skeletal structure, ×1; b, transverse section of holotype with axial spongocoel and radiating chambers in uniform, skeletal structure pierced by small, inhalant canals,  $\times 1$ ; c, photomicrograph of tetracladine, spicule arrangement in holotype, BSPGM Senowbari-Daryan 1992, G1-G5, ×30 (Senowbari-Daryan & Wurm, 1994).

### Family PROTETRACLISIDAE Schrammen, 1924

[Protetraclisidae Schrammen, 1924b, p. 148] [=Sontheimiidae Schrammen, 1924b, p. 148]

Early Tetracladina with tetraclones or triders and irregular, rhizoclone-like desmas, with dichotriaenes when any dermalia are known; arms of desmas sometimes simple but often more or less irregularly branching and smooth, spinose, or finely tuberculate; phyllotriaenes possible in one species; other spicules unknown. [The family comprises early forms difficult to relate to later families and is possibly most similar to Theonellidae. Family name was initially proposed without diagnosis but taken here as validly established because a recognizable type genus (*Protetraclis* KOLB) was cited.] *Jurassic* (*Kimmeridgian*).

- Protetraclis STEINMANN, 1881, p. 154 [\**P. linki*; OD]. Cylindrical or top shaped, thick walled, with a deep, tubular, paragastral cavity; paragastral surface with postica of branching aporhyses whose branches also open through small pores in external surface; desmas strongly branching tetraclones that grade into rhizoclone-like variants; dermalia dichotriaenes; other spicules unknown. *Jurassic* (*Kimmeridgian*): Germany.—FIG. 139,3. \**P. linki*, Weiss Jura, Heukchstetten; desmas, ×20 (Schrammen, 1937).
- Rhizotetraclis KOLB, 1910 in 1910–1911, p. 208 [\*R. plana; OD]. Platelike with rounded margin; both surfaces with small, skeletal pores; no internal canals; desmas strongly branched tetraclones, rhizoclone-like variants, and some that resemble dicranoclones or didymoclones; no other spicules known. Jurassic (Kimmeridgian): Germany.——FIG. 139,2a-d. \*R. plana, Weiss Jura, Sontheim; a, side

view with irregular, radiate structure, SSPHG,  $\times 1$ ; *b*-*d*, branched tetraclone and rhizoclone-like spicules,  $\times 40$  (Kolb, 1910–1911).

Sontheimia KOLB, 1910 in 1910-1911, p. 206 [\*S. parasitica; SD DE LAUBENFELS, 1955, p. 56]. Habit variable; sometimes encrusting; globular or forming a group of small, tuberous growths; sometimes cylindrical or toplike with a deep, narrow, paragastral cavity; aporhyses opening through small, stellate groups of postica when a paragastral cavity is absent; extending from postica in paragastral wall to small pores in external surface when a paragastral cavity is present; desmas include some tetraclones but are typically triders with rudimentary brachyome, some more or less irregularly branched and grading into rhizoclone-like bodies; arms of desmas finely spined or tuberculate; dermalia dichotriaenes when known (sometimes possible phyllotriaenes); other spicules unknown. [May include more than one genus if dermalia of S. parasitica were phyllotriaenes as thought by SCHRAMMEN, 1937.] Jurassic (Kimmeridgian): Germany.-FIG. 139,4. \*S. parasitica, Weiss Jura, Gerstetten; characteristic triders and other desmas, ×20 (Schrammen, 1937).

### Family SIPHONIIDAE d'Orbigny, 1851

[nom. correct. REID, herein, pro Siphonidae D'ORBIGNY, 1851, p. 211] [=Phymatellinae ScHRAMMEN, 1910, p. 33; Hallirhoidae DE LAUBENFELS, 1955, p. 56; Aulaxinidae DE LAUBENFELS, 1955, p. 57; Jereidae DE LAUBENFELS, 1955, p. 57]

Typically with smooth-armed tetraclones as desmas and dichotriaenes as dermalia, but sometimes with more or less strongly tuberculate tetraclones, or with dermal trichotriaenes or phyllotriaenes; some with irregular forms of tetraclones, but triders normally absent; some genera with zygomes united to form regular, syzygial nodes, which may have spherical enlargement, but others with no regular style of zygosis; forms with stalks or root processes may have elongate, monaxial, radical desmas that intergrade with normal tetraclones through irregular intermediates; may have supplemental rhizoclonids that may form a dense supplemental cortex in which dermalia are imbedded; microscleres unknown in most genera, but short spirasters in one modern genus. Upper Jurassic-Holocene.

This family is understood in essentially the sense of SCHRAMMEN'S (1910) Phymatellinae (=Phymatellidae SCHRAMMEN, 1924a), except for inclusion of two genera

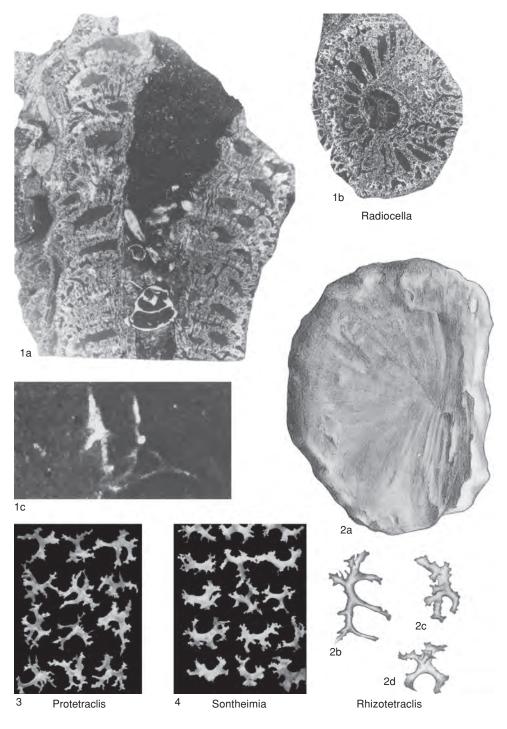


FIG. 139. Radiocelliidae and Protetraclisidae (p. 205–206).

with phyllotriaene dermalia that seem better placed here than in the family Theonellidae. Inclusion of some forms with tuberculate desmas is to allow for *Hallirhoa* LAMOUROUX, 1821, in which desmas are strongly tuberculate in some species not studied by SCHRAMMEN.

DE LAUBENFELS (1955) divided these sponges mainly between three families: Hallirhoidae DE LAUBENFELS, Aulaxiniidae DE LAUBENFELS, and Jereidae DE LAUBENFELS. Of the relevant type genera, Hallirhoa is only distinguished from Siphonia GOLDFUSS by a lobate outline and has been considered only a subgenus by some authors. Jerea LAMOUROUX is difficult to separate from Siphonia, generically and is either intergrading or overlapping in characters, according to whether it is distinguished sensu ZITTEL (1878a; presence or absence of a paragastral cavity) or sensu SCHRAMMEN (1910; size of skeletal meshwork). The types of canal system cited by DE LAUBENFELS are variants of a single type, depending chiefly on different styles of growth, which is mainly terminal in Jerea but mainly lateral in the adult Siphonia. Aulaxinia ZITTEL, made the type of the family Aulaxiniidae, is a form in which strong, external furrowing is present in adults; but similar furrowing is present in young examples of Siphonia and the regular furrowing shown by DE LAUBENFELS (1955, fig. 39,3a) is not always present in Aulaxinia. It is, therefore, not considered appropriate to base separate families on these genera. Several further genera placed by DE LAUBENFELS as Chenendoporidae also have the desmas and dermalia of Siphoniidae, and one (Pachycalymma SCHRAMMEN, 1901) was based on young specimens of Jerea (Schrammen, 1910).

# Subfamily SIPHONIINAE d'Orbigny, 1851

[nom. transl. REID, herein, ex Siphoniidae D'ORBIGNY, 1851, p. 211]

Solitary or compound Siphoniidae with no paragastral cavity, in which aporhyses are longitudinal (vertical) and epirhyses are radial or absent, and similar forms with a paragastral cavity, in which aporhyses run vertically in axial parts but arch outward progressively outside it; dermalia dichotriaenes or rarely trichotriaenes. [A single living genus, *Neosiphonia* SOLLAS (=*Jereopsis* SCHMIDT, 1880, *non Jereopsis* POMEL, 1872; =*Jereica* VON ZITTEL, 1878a), has spiraster microscleres and trichotriaene dermalia.] *Upper Jurassic–Holocene.* 

- Siphonia GOLDFUSS, 1826, p. 16 [\*S. pyriformis; SD HINDE, 1884a, p. 63; not Choanites konigii MANTELL, 1822, p. 178, listed by DE LAUBENFELS, 1955, p. 56 as designated by HINDE, 1887b] [=Siphoneudea DE FROMENTEL, 1860a, p. 29 (type, Siphonia ficus GOLDFUSS, 1833, pl. 65,14, OD)]. Typically stalked-pyriform, tuliplike, or intermediate or other related shapes, with stalk up to several times height of body, and usually divided into lobes or root processes at base; sometimes sessile, stalkless; paragastral cavity usually present, and ranging from shallow depression to deep, narrow, tubular space that extends to near root of stalk but not into it; outer surface with small ostia of radial epirhyses that often slope downwardly in upper parts; paragastral surface with postica of larger aporhyses, often opening in vertical series when paragaster is well developed; aporhyses run vertically downward and into stalk in axial parts, but otherwise arch outwardly and downwardly around it, with those in highest parts following general contour of surface; stalk sometimes with sinuous, longitudinal furrows in which small ostia may open; similar furrows sometimes on other parts; summit sometimes with radiating furrows representing incompletely enclosed aporhyses; desmas typical tetraclones in body, but passing into elongate, fiberlike variants in long stalks; dermalia dichotriaenes; rhizoclonids sometimes present but not usually forming a supplemental cortex; microscleres unknown. [See HINDE, 1883 for discussion of authorship of Siphonia.] Cretaceous (Aptian-Maastrichtian), Neogene (?Miocene): Britain, Czech Republic, Slovakia, France, Germany, Poland, Russia, Brazil, Aptian-Maastrichtian; Italy, ?Miocene.
  - S. (Siphonia) GOLDFUSS, 1826, p. 16 [\*S. pyriformis; OD]. Skeletal framework typically fine meshed and sometimes especially dense at surface, which then has smooth appearance; no regular development of spherical, syzygial nodes, which are usually absent; stalk normally present, often long. Cretaceous (Aptian-Maastrichtian): Britain, Czech Republic, Slovakia, France, Germany, Poland, Russia, Brazil.-FIG. 140,4a. S. (S.) tulipa ZITTEL, Upper Greensand, Warminster, Wiltshire, England; skeletal meshwork, ×20 (Hinde, 1884a).—FIG. 140,4b-c. S. (S.) tuberosa (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; characteristic spicules including desmas, rhizoclonids, and dichotriaenes, ×30 (Schrammen, 1910).

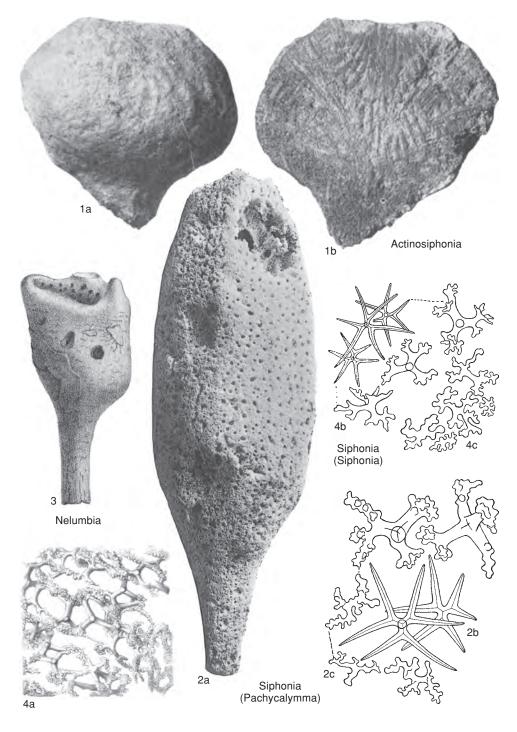


FIG. 140. Siphoniidae (p. 208-212).

- S. (Pachycalymma) SCHRAMMEN, 1901, p. 9 [\*Pachycalymma subglobosa SCHRAMMEN, 1901, p. 10; OD; not SD DE LAUBENFELS, 1955, p. 55; =Jerea quenstedti ZITTEL, SCHRAMMEN, 1910, p. 89; ?Jerea quenstedti ZITTEL, 1878a, p. 145; Siphonia ficus GOLDFUSS, 1831, p. 221]. Skeletal framework wider meshed than in typical Siphonia s.s., due to larger size of desmas, and not being especially dense at surface; regular syzygial nodes may be conspicuous; stalk long, short, or replaced by a number of separate outgrowths, a well-developed, supplemental cortex may coat lowest parts or much of body in small, globular specimens that have died without forming a paragastral cavity. [Type species recognized by SCHRAMMEN (1910, p. 89-90) as based on young forms of J. quenstedti, as identified by SCHRAMMEN, comprised of forms with wide, skeletal meshwork and a deep paragastral cavity, as in Siphonia, sensu VON ZITTEL. SCHRAMMEN'S distinction between Jerea, sensu SCHRAMMEN, and Siphonia s.s., here transferred to Pachycalymma SCHRAMMEN as a subgenus of Siphonia; diagnosis also based partly on characters of P. ("Choanites") koenigi (MANTELL) regarded as a further species.] Cretaceous (Turonian-Campanian): England, Germany.-FIG. 140, 2a-c. \*S. (P.) globosa (SCHRAMMEN), Quadratenkreide, Campanian, Oberg, Germany; a, side view of stalked, subcylindrical form with irregular inhalant ostia,  $\times 1$ ; *b*-*c*, characteristic spicule assemblage, including desmas, rhizoclonids, and dermalia, ×30 (Schrammen, 1910).
- Actinosiphonia SINTZOVA, 1878, p. 34 [\*Siphonia radiata FISCHER DE WALDHEIM, 1837 in 1830–1837, p. 179; OD; non QUENSTEDT, 1877]. Type species a typical, stalked, globular Jerea, except that dermalia are unknown. Openings of excurrent canals in upper part, less often on lateral surface; principal spicules large and smooth with numerous branches. Upper Cretaceous: Russia.——FIG. 140,1a-b. A. radiata (FISCHER DE WALDHEIM), Santonian, Saratov, Volga region; a, side view of exterior; b, vertical section showing distribution of major canals in globose sponge, ×1 (Rezvoi, Zhuravleva, & Koltun, 1962).
- Aulaxinia ZITTEL, 1878a, p. 138 [\*Siphonocoelia sulcifera F. A. ROEMER, 1864, p. 30; OD]. Apple shaped to elongate ovoid or cylindrical, with stalk at base and sometimes branched in cylindrical examples; paragaster a shallow depression or conical or tubular cavity; external surface with conspicuous, longitudinal furrows that begin at paragastral margin and typically run downwardly as far as start of stalk; intervening surface with ostia of radial epithyses; similar pores sometimes also present in furrows; furrows sometimes regular and unbranched, with intervening ridges along which are vertical series of ostia; in other examples furrows less regular, narrower and branching, with interven

ing ostia then showing no regular order; paragaster with postica of large aporhyses, which run downwardly through body, but not usually into stalk; desmas regular tetraclones in body, with zygomes sometimes forming regular syzygial nodes, but irregular in stalk and grade down into fiberlike variants with a single axial canal; supplemental cortex absent; microscleres unknown. Lower Cretaceous (Aptian)-Upper Cretaceous: Spain, Aptian; Spain, England, Albian; England, France, Germany, Poland, Upper Cretaceous .----FIG. 141,2a-c. \*A. sulcifera (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; a, side view of subcylindrical, ovoid form with vertical, dermal furrows; b, smaller, branched sponge with parallel, dermal furrows on one branch, ×1 (Schrammen, 1910); c, skeletal fragment showing spicule relationships, ×40 (Zittel, 1878a).

- Bathotheca OPPLIGER, 1915, pl. 9-10 [\*Batotheca ovata OPPLIGER, 1915, p. 60, pl. 9,4; SD DE LAUBENFELS, 1955, p. 56] [=Batotheca OPPLIGER, 1915, p. 59, nom. null., obj., non ENDERLEIN, 1905, p. 227]. Sponge globose with short, thin, basal stalk, without central spongocoel or osculum; dermal surface with prominent nodes or projections and larger, exhalant ostia and finer, inhalant pores that connect to complicated canal system of large openings throughout; skeleton may be composed of ennomoclones or didymoclones, most with four or five rays that diverge in various directions and range from bent to straight, simple or branched, and thin to thick; knotlike brachyomes are swollen and commonly occur at corners of quadrate openings, but also may be flattened and spread out. [OPPLIGER (1915) proposed both Batotheca (in the text) and Bathotheca (in the figure explanations).] Jurassic: Switzerland.—FIG. 141,1a-b. \*B. ovata (OPPLIGER), Birmensdorferschichten, Solothurn; a, side view of nodular, globose sponge with prominent ostia and pores, ×0.5; b, photomicrograph of calcified, skeletal elements, magnification not evident on copy, probably ×40 (Oppliger, 1915; courtesy of Komission der Schweizerischen Paläontologischen Abhandlungen, Basel)
- Callopegma ZITTEL, 1878a, p. 139 [\*C. acaule; SD DE LAUBENFELS, 1955, p. 56]. Pyriform, depressed globular with small, central cone, hemispherical, discoidal, or basin or funnel-like and thick walled; short stalked or sessile; lower surfaces with distinct, skeletal pores (ostia) or with open, skeletal meshes only; center of upper or inner surface with conspicuous group of postica from which large aporhyses run downwardly in central parts but obliquely outward around them; unenclosed branches of outermost aporhyses forming radiating furrows, which may continue to undersurface; desmas regular tetraclones that are mostly united to form regular, syzygial nodes; these nodes often spherically swollen and give external surface a granulated aspect; dermalia dichotriaenes; rhizoclonids not recorded; microscleres unknown. Cretaceous (Aptian-

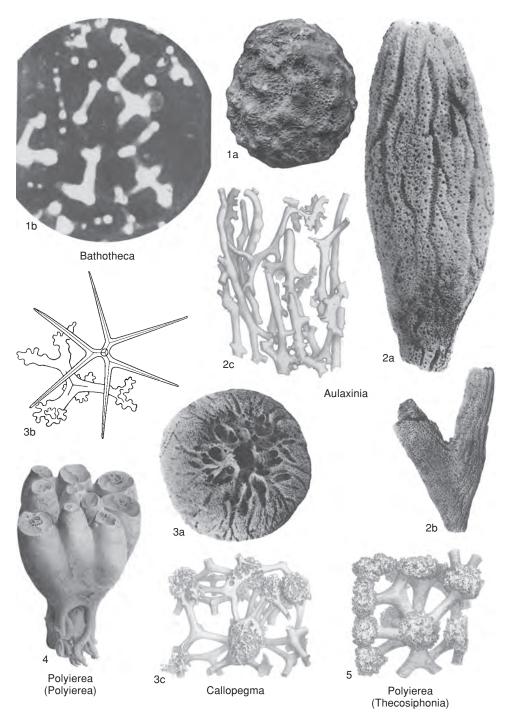


FIG. 141. Siphoniidae (p. 210-214).

*Campanian):* Spain, *Aptian;* England, Germany, Poland, Puerto Rico, *Campanian.*——FIG. 141,*3a–c.* \**C. acaule,* Quadratenkreide, Campanian, Oberg, Germany; *a*, upper surface showing postica and radiating furrows, ×1; *b*, representative spicules including tetraclone and dermal dichotriaene, ×30 (Schrammen, 1910); *c*, skeletal fragment of inner wall with tetraclones united to form syzygial nodes, ×25 (Zittel, 1878a).

- Hallirhoa LAMOUROUX, 1821, p. 72 [\*H. costata; OD]. Body apple shaped in profile but radially lobate, with usually four to seven lobes; long stalked, with branching, basal, root processes; paragastral cavity variable, from deep and narrow to almost obsolete; outside of body with small ostia from which radial epirhyses run inwardly; aporhyses larger, vertical in axial parts, but arching outwardly around it; some of axial aporhyses continue down stalk; outermost aporhyses subparallel with external surface and forming radial grooves around paragastral opening or depression in abraded specimens; skeletal framework dense, formed from typical and irregular tetraclones; long, fiberlike desmas in stalk; desmas more or less strongly tuberculate in some species; rhizoclonids not recorded; large oxeas may occur in internal meshes; microscleres unknown. [This genus is similar to Siphonia GOLDFUSS and sometimes treated as a subgenus only; but it should be treated as senior synonym if that practice is followed. The definition was extended by HINDE (1884a) to include depressed, lobate forms with phyllotriaene dermalia, here referred to Phyllodermia SCHRAMMEN of the Theonellidae.] Lower Cretaceous (Albian)-Upper Cretaceous: England, Albian; England, France, Cenomanian; France, Santonian-Campanian; Germany, Campanian; Russia, Upper —FIG. 142, 1a-c. \*H. costata, Upper Cretaceous.— Greensand, Warminster, Wiltshire, England; a, side view of five-lobed example with stem and rootlike terminations; b, transverse section from below level of spongocoel showing larger, arched and vertical, exhalant canals, ×0.5; c, part of interior skeletal structure of tetraclones that unite at tuberose, ray terminations, ×50 (Hinde, 1884a).
- Jerea LAMOUROUX, 1821, p. 79 [\* J. pyriformis; OD]. Stalked-globular or pyriform to cylindrical, with apex truncated or having a shallow depression but no distinct paragastral cavity; stalk long or short and simply expanded, lobate, or dividing into root processes at base; outer surface of body with ostia of small, radial epirhyses; apex or apical depression with postica of larger, tubular aporhyses that run vertically downward, or in part slope somewhat outwardly outside axial parts; desmas simple tetraclones or with one to four arms branching dichotomously before emitting zygomes; when simple, sometimes united to form regular, syzygial nodes that may be spherically swollen; dermalia dichotriaenes; rhizoclonids sometimes present, but not usually forming a cortex. [The genus is here understood sensu VON ZITTEL, 1878a. An alternative definition by SCHRAMMEN (1910), based on size of skeletal elements, was not based on comparison of

the two relevant type species. On comparison of *J. pyriformis* with a specimen identified by SCHRAMMEN as *Siphonia tubulosa* F. A. ROEMER, MORET (1926b, p. 159) concluded he could not see "la moindre difference appreciable dans la taille des desmes."] *Jurassic (?Oxfordian), Cretaceous (Aptian-Campanian):* Poland, *?Oxfordian, Spain, Aptian;* England, *Albian;* England, France, Germany, Czech Republic, Slovakia, Poland, Russia, *Cenomanian-Campanian.*——FIG. 142,2. \**J. pyriformis,* Holocene, Mediterranean Sea, near Caen, France; type specimen from side showing gobletlike form with truncated apex and numerous exhalant ostia and grooves of canals along margin, ×0.5 (Lamouroux, 1821).

- Nelumbia POMEL, 1872, p. 194 [\*Polystoma cupula COURTILLER, 1861, p. 126; SD DE LAUBENFELS, 1955, p. 58]. Elongate, club-shaped with apex truncated or slightly hollowed, and number of small, lateral depressions that are sometimes on nodular prominences; stalk and root processes at base; sides with ostia of small epirhyses; central parts with longitudinal aporhyses that open at summit; further short canals, suggesting accessory aporhyses, may open in lateral depressions; desmas tetraclones; dermalia dichotriaenes; rhizoclonids unknown; microscleres unknown. [Poorly known; in effect a Jerea with accessory pseudogastral cavities at the sides, although a "delicate siliceous skin" occurring on some examples by COURTILLER (1861, p. 126) may represent a cortex.] Upper Cretaceous: England, France.——FIG. 140,3. \*N. cupula (COURTILLER); side view of stalked form with lateral ostia, scale not given, approximately ×1 (Courtiller, 1861).
- Polyierea DE FROMENTEL, 1860a, p. 33 [\* Jerea gregarea MICHELIN, 1847 in 1840-1847, p. 134; OD] [=Polyjerea POMEL, 1872, p. 173, nom. null.]. Sometimes solitary but usually compound, with a group of Jerea- or Siphonia-like sponges arising from a common base or from branches of a common stalk; apices rounded, truncated, or with distinct, paragastral depressions; base simple or with root processes; exterior of skeletal framework coated more or less extensively by dense, epitheca-like, supplemental cortex, which is usually continuous between sponge individuals and may coat whole surface except where aporhyses open; desmas normal tetraclones; dermalia dichotriaenes when known; additional large oxeas in cortex of one species; microscleres unknown. [Dermalia not recognized by ZITTEL (1878a) or SCHRAMMEN (1910) but recorded by HINDE (1884a, subgenus P. (Polyierea), proposed herein) and MORET (1926b, subgenus P. (Thecosiphonia) ZITTEL, proposed herein.] Upper Cretaceous-Neogene: Spain, Aptian; England, France, Cenomanian; Germany, Turonian-Campanian.
  - P. (Polyierea) DE FROMENTEL, 1860a, p. 33, nom. transl. REID, herein, ex Polyierea DE FROMENTEL, 1860a, p. 33. Branched or lobate body of tubules in distinct center typically covered by supplemental cortex, except in terminal parts where aporhyses open. Cretaceous (Coniacian-

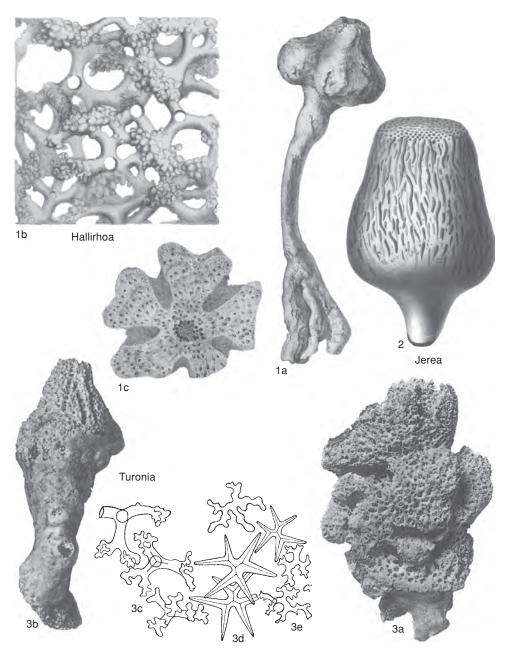


FIG. 142. Siphoniidae (p. 212-214).

*Maastrichtian):* France.——FIG. 141,4. \**P. (P.)* gregarea (MICHELIN), Chloritic chalk; side view of large sponge showing branched, tubular structure and shallow, terminal depressions that contain large aporhyses, ×0.25 (Michelin, 1840– 1847). P. (Thecosiphonia) ZITTEL, 1878a, p. 148, nom. transl. REID, herein, ex Polyierea DE FROMENTEL, 1860a, p. 33 [\*Lymnorea nobilis F. A. ROEMER, 1864, p. 37; SD DE LAUBENFELS, 1955, p. 56] [=Orecyta DE LAUBENFELS, 1955, p. 49, obj., nom. nov. pro Cytorea POMEL, 1872, p. 225, non LAPORTE, 1849]. Cortex usually absent from higher parts of body where skeletal surface has ostia and irregular, superficial furrows; epirhyses sometimes more conspicuous than in *Polyierea s.s.*; one species with large oxeas in cortex. [Proposed as a separate genus by ZITTEL (1878a), but differs from *Polyierea s.s.* only in having cortex less extensively developed.] *Upper Cretaceous– Neogene:* Europe.——FIG. 141, *5. P. (T.) grandis* (ROEMER), Cuvier Pläner, Turonian, Ost Haringen, Germany; drawing of skeletal fragment showing nodes produced by union of ray tips of tetraclones, ×30 (Zittel, 1878a).

Turonia MICHELIN, 1844 in 1840–1847, p. 125 [\*T. variabilis; OD]. Shape very varied, often irregular; lower part of body obconical with small, central stalk and typically coated by dense and transversely corrugated cortex, from which short, accessory root processes may grow downwardly; upper part flattened, conical, subcylindrical, cerebriform, or irregularly lobate or nodular, with central, paragaster-like cavity or none; upper surfaces usually not coated by cortex and have ostia, from which straight epirhyses run inwardly; some forms also with conspicuous, simple or branching furrows that radiate from center of body or from more than one center, at which points there may be either a prominence or a shallow depression; in these forms, vertical canals (aporhyses) open into furrows; in others, network of internal canals or larger spaces originating as ramifications of a paragaster-like cavity and may perforate walls in various places; desmas typical tetraclones, which may unite to form regular, syzygial nodes; cortex formed of rhizoclonids; dermalia dichotriaenes; microscleres unknown. Lower Cretaceous (Aptian)-Upper Cretaceous: Spain, Aptian; France, Cenomanian-Campanian; England, Upper Cretaceous; Germany, Poland, Campanian.-FIG. 142,3a-b. \*T. variabilis, Quadratenkreide, Campanian, Oberg, Germany; a, side view of example with conical summit, above lumpy base covered with dense dermal layer,  $\times 1$ ; b, side view of example with irregularly lobate summit largely lacking dermal layer, ×2 (Schrammen, 1910).—FIG. 142,3c-e. T. cerebriformis SCHRAMMEN, Quadratenkreide, Campanian, Oberg, Germany; spicules including tetraclones, dichotriaenes, and rhizoclonids, ×30 (Schrammen, 1910).

## Subfamily PHYMATELLINAE Schrammen, 1910

[Phymatellinae SCHRAMMEN, 1910, p. 33]

Mainly solitary Siphoniidae without vertical aporhyses, except sometimes in stalks; epirhyses and aporhyses radial and more or less similar, or developed in various other ways, and sometimes absent; dermalia dichotriaenes. [This subfamily comprises Phymatellinae *sensu* SCHRAMMEN, 1910, minus

# forms placed here under the subfamily Siphoniinae D'ORBIGNY.] *Upper Jurassic– Cretaceous.*

- Phymatella ZITTEL, 1878a, p. 137 [\*Eudea intumescens F. A. ROEMER, 1864, p. 26; SD DE LAUBENFELS, 1955, p. 56] [=Pseudoplocoscyphia SCHRAMMEN, 1901, p. 4 (type, P. maeandrina, M)]. Stalked or sessile; body roughly globular, pyriform, elongateovate, or cylindrical, with lower parts or sides having flattened or bulbous swellings or nipplelike to fingerlike outgrowths; paragastral cavity deep, extending nearly to stalk when a cavity is present; often of irregular width and with diverticula extending into lateral prominences; outside surface with ostia of varying sizes from which radial epirhyses run inwardly; paragastral surface with postica of similar aporhyses; desmas tetraclones in body, pass downwardly into monaxial, fiberlike variants in stalks; rhizoclonids often inconspicuous or absent but sometimes forming a supplemental cortex; microscleres unknown. Cretaceous (Aptian-Campanian): Spain, Aptian; England, France, Germany, Poland, Czech Republic, Slovakia, Cenomanian-Campanian. FIG. 143, 5a-e. P. bulbosa ZITTEL, Quadratenkreide, Campanian, Oberg, Germany; a, side view of young, globular, pyriform sponge with irregular, coarse, exhalant ostia and fine, inhalant pores, ×1; b-e, characteristic spicules including tetraclone, young tetraclone, dichotriaene, and rhizoclonids, ×30 (Schrammen, 1910).
- Asterocalyx MORET, 1926b, p. 150 [\**A. beaussetense;* OD]. Cup or funnel shaped, stalked; outside with ostia of radial epirhyses that run inwardly; inside with postica of smaller aporhyses, arranged in groups at centers of clusters of short, radiating furrows; desmas tetraclones; dermalia dichotriaenes; rhizoclonids forming supplemental cortex in lower parts; microscleres unknown. *Cretaceous (Santonian):* France.——FIG. 143, *1a–d. \*A. beaussetense,* Saint-Cyr; *a.* side view of obconical type specimen with ostia of radial epirhyses, slightly reduced; *b–d,* tetraclones and dichotriaene, magnification not stated (Moret, 1926b; courtesy of Société Géologique de France).
- Astrolemma SCHRAMMEN, 1924a, p. 59 [\*A. semiglobosa; OD]. Hemispherical with undersurface concentrically wrinkled; upper surface with scattered apertures presumed to be postica and numerous smaller, skeletal pores (possibly ostia); internal canals apparently absent; undersurface covered by dense, epitheca-like, supplemental cortex of small rhizoclonids; dermalia dichotriaenes; microscleres unknown. [Cited illustrations are poor; no other suitable illustrations are known.] Cretaceous (Campanian): Germany.—FIG. 143,3. \*A. semiglobosa, Emscher, Sudmerberges; side view of hemispheroidal type with scattered oscula or postica, x0.5 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Bolojerea RAUFF, 1933, p. 63 [\*B. glebuta; OD]. Irregularly globular with no paragastral cavity;

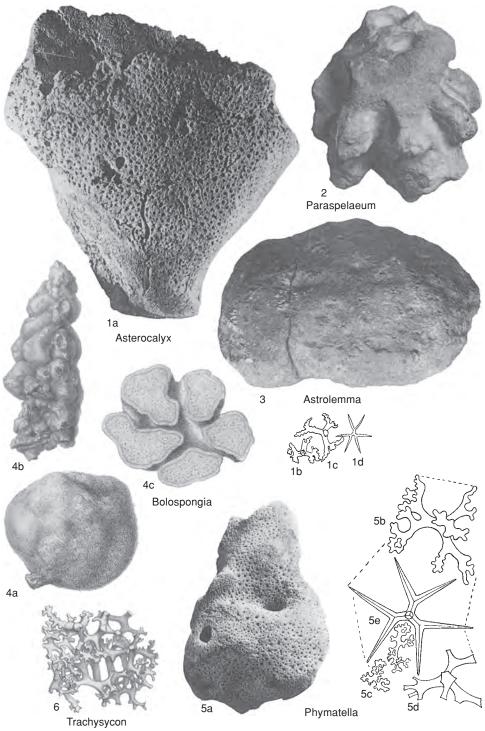


FIG. 143. Siphoniidae (p. 214–218).

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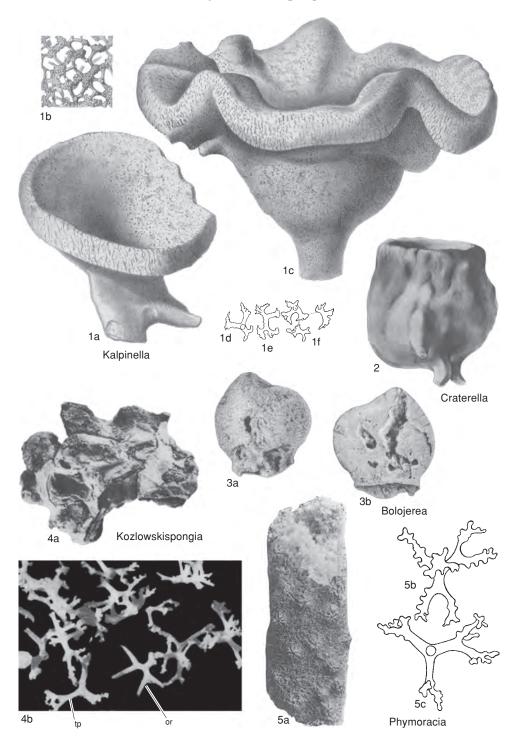


FIG. 144. Siphoniidae (p. 214–218).

exterior with scattered ostia; interior with fine, radial canals, epirhyses and aporhyses not distinguishable; desmas tetraclones, united mainly to form swollen, syzygial nodes; oxeas and microstrongyles recorded; dermalia and rhizoclonids unknown. [Possibly identical with *Bolospongia* HINDE.] *Cretaceous (Turonian):* Germany.——FIG. 144,3*a*–*b.* \**B. glebuta*, Greensand, upper Turonian, Ruhr Valley; *a*, side view of small, globular sponge; *b*, vertical, median section showing small, inhalant, radial canals, larger openings are secondary borings, ×1 (Rauff, 1933).

- **Bolospongia** HINDE, 1884a, p. 73 [\*B. globata; SD DE LAUBENFELS, 1955, p. 56]. Stalked, globular and small or columnar and irregularly lobate; irregularly hollowed internally with internal spaces opening through osculum-like apertures or between adjacent lobes; no skeletal pores or canals apparent although fine, external furrows may radiate from apertures of internal cavities; desmas smooth tetraclones; dense, cortical layer of unknown composition present; dermal triaenes and microscleres unknown. [Position uncertain but clearly a tetracladine and possibly allied to Phymatella ZITTEL.] Upper Cretaceous (?Campanian): England.—FIG. 143,4a. \*B. globata, Upper Chalk; side view of globose sponge, ×1 (Hinde, 1884b).—FIG. 143,4b-c. B. constricta HINDE, Upper Chalk, Campanian, Flamborough, Yorkshire; b, side view showing nodular exterior,  $\times 0.5$ ; c, transverse section showing internal cavities and cortex, ×1 (Hinde, 1884b).
- Calymmatina ZITTEL, 1878a, p. 149 [\*C. rimosa; SD DE LAUBENFELS, 1955, p. 54; =Scyphia dichotoma MICHELIN, 1847 in 1840-1847, p. 5, non BENETT, 1831, teste ZITTEL, 1878a, p. 129]. Compound or solitary, in former example with individual sponges united at base or side by side; individuals nodular, top, club shaped, or cylindrical, with deep, narrow, paragastral cavities; base massive or stalked; external surface of skeletal framework with short, irregular, longitudinal, and transverse furrows, in which are ostia of short, radial epirhyses; paragastral wall with postica of similar aporhyses; most of external surface typically covered by smooth or transversely wrinkled, supplemental cortex that covers furrows and ostia; dermalia dichotriaenes; microscleres unknown. Cretaceous (Coniacian-Maastrichtian): England, France, Germany.——FIG. 145,2a-d. \*C. rimosa, Mucronatenkreide, Campanian, Misburg, Germany; characteristic spicules including desmas, rhizoclonids, dermal dichotriaene, and calthropslike, young tetraclone, ×30 (Schrammen, 1910).
- Craterella SCHRAMMEN, 1901, p. 4 [\*C. tuberosa; OD] [=Carterella DE LAUBENFELS, 1955, p. 56, nom. null., non ZITTEL, 1878a]. Cup, funnel, or ear shaped, thick walled; sessile or with a few short, root processes; exterior with small ostia of short, radial epirhyses; paragastral surface with similar postica or with additional, larger apertures of canals that anastomose internally; desmas large tetraclones; dermalia dichotriaenes; rhizoclonids and microscleres unknown. [Carterella DE LAUBENFELS, 1955 appears to be a misprint, since the cited type species

C. tuberosa can only be the type of the present genus. Forms identified by MORET (1926b) and LAGNEAU-HÉRENGER (1962) as Craterella SCHRAM-MEN should probably be described as a new genus.] Upper Cretaceous (Campanian): Germany.——FIG. 144,2. \*C. tuberosa, Quadratenkreide, Misburg; side view of type specimen,  $\times 0.5$  (Schrammen, 1901).

- Kalpinella HINDE, 1884a, p. 76 [\*K. pateraeformis; SD DE LAUBENFELS, 1955, p. 55]. Cup or bowl shaped, thick walled, with margin folded up and down in some examples; stalk and root processes at base; external surface with numerous small ostia; paragastral surface with similar postica; epirhyses and aporhyses in wall similar and radial, oblique, or sinuous; skeletal margin rounded or truncated, with open furrows representing incompletely enclosed canals; a few long, vertical aporhyses in stalk; desmas tetraclones or variants with some arms aborted and tending to be tuberculate on zygomes; dermalia, rhizoclonids, and microscleres unknown. Cretaceous (Aptian-Cenomanian): Spain, Aptian; England, Albian-Cenomanian; France, Santonian.-FIG. 144, 1a-b. \*K. pateraeformis, Albian, Upper Greensand, Warminster, England; a, side view of stalked, open, funnel-shaped form, ×0.5; b, skeletal meshwork showing nodular zygomes, ×25 (Hinde, 1884b).—FIG. 144, 1c. K. rugosa HINDE, Upper Greensand, Albian, Warminster, Yorkshire, England; side view of funnel-shaped form with crenulate margin, ×0.5 (Hinde, 1884b).-FIG. 144,1d-f. K. pateraeformis, Santonian, Saint-Cyr, France; desmas, approximately ×25 (Moret, 1926b; courtesy of Société Géologique de France).
- Kozlowskispongia HURCEWICZ, 1966, p. 44 [\*K. bulbosa Hurcewicz, 1966, p. 45; OD]. Sponges with hollow, irregularly bulbous, hemispherical protuberances on platelike form; canal system poorly defined but apparently piercing plate; exhalant postica well defined and uniformly developed over entire dermal surface; inhalant ostia smaller and indistinctly outlined; dermal skeleton continuous with fairly large orthodichotriaenes; parenchymal tetraclones somewhat variable in size but smooth with branched zygomes. Upper Cretaceous (Cam--FIG. 144,4a-b. \*K. bulbosa, panian): Poland .--Miechów; a, lateral view of holotype with bulbous, dermal protuberances, ×0.5; b, isolated megascleres from holotype; or, dermal orthodichotriaenes; tp, parenchymal tetraclones, ×30; Z. Pal. UL Sp. II/93 (Hurcewicz, 1966).
- Marginospongia D'ORBIGNY, 1849, p. 549 [\*Alcyonium infundibulum DE FRANCE, 1816, p. 107; OD] [=Marginoierea FROMENTEL, 1860a, p. 33, obj.]. Similar to Kalpinella but pores minute. [LAMOUROUX (1822, p. 131) was cited as the author of the type species by DE LAUBENFELS (1955, p. 55), but SHERBORN (1922 in 1922–1932, p. 3,887) indicated that DE FRANCE (1816) was probably author of the species.] Cretaceous: Europe.
- Paraspelaeum SCHRAMMEN, 1924a, p. 60 [\**P. obductum;* OD]. Nodular sponge with deep, narrow, paragastral cavity and radially lobate walls;

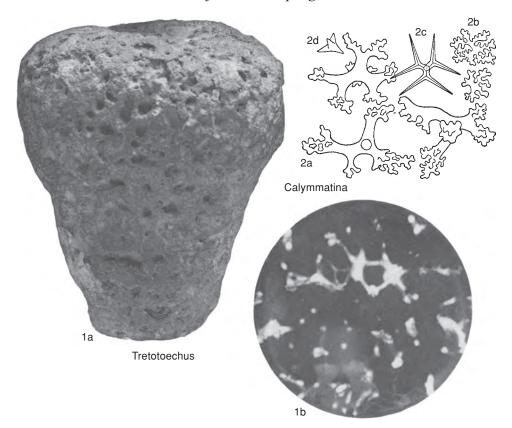


FIG. 145. Siphoniidae (p. 217-219).

ostia and postica very small; skeletal canals apparently absent; desmas tetraclones; dermalia dichotriaenes; rhizoclonids form supplemental cortex; microscleres unknown. [This genus shows little difference from *Phymatella ZITTEL*, except for weaker canalization.] *Cretaceous (Campanian):* Germany. ——FIG. 143,2. \**P. obductum*, Mukronatenkreide, Misburg; side view of nodular sponge with small ostia in dermal layer, ×0.75 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Phymoracia POMEL, 1872, p. 227 [\*Stellispongia verrucosa F. A. ROEMER, 1864, p. 50; OD] [=Myrmeciophytum SCHRAMMEN, 1910, p. 80, obj.]. Cylindrical (possibly branched cylindrical) with no paragastral cavity; sides with groups of postica surrounded by radiating furrows, postica groups on short, conical prominences in some examples; desmas large, smooth tetraclones; dermalia, rhizoclonids, and microscleres unknown. [The type species was regarded as a form of Astrocladia ZITTEL by ZITTEL, 1878a, but was distinguished by the character of the desmas by SCHRAMMEN, 1910. It is here regarded as probably allied to Trachysycon ZITTEL, with the paragastral cavity suppressed and replaced functionally by lateral aporhyses and oscula.] *Cretaceous (Campanian):* Germany, Poland. ——FIG. 144,*5a–c.* \**P. verrucosa* (F. A. ROEMER), Quadratenkreide, Oberg, Germany; *a*, cylindrical fragment with clusters of exhalant ostia and radial canals on low nodes, ×1; *b–c*, characteristic tetraclones, ×30 (Schrammen, 1910).

Trachysycon ZITTEL, 1878a, p. 140 [\*Plocoscyphia muricata F. A. ROEMER, 1864, p. 28; OD]. Stalkedpyriform to elongate ovoid, with exterior showing conical prominences with fine furrows radiating from their tops; intervening surface with small ostia; paragastral cavity deep, with postica of radial aporhyses; desmas normal tetraclones; rhizoclonids may form a supplemental cortex on stalk or lower parts of body; dermalia and microscleres unknown. [Lateral features suggest presence of secondary, lateral oscula, with radiating, exhalant canals in the subdermal region.] Cretaceous (Cenomanian-Campanian): England (Upper Chalk), Cenomanian; Germany, Campanian.-FIG. 143,6. \*T. muricatum (ROEMER), Quadratenkreide, Campanian, Sutmerberg, Germany; camera lucida drawing of skeletal structure of tetraclone desmas, with minor rhizoclones, ×30 (Zittel, 1878a).

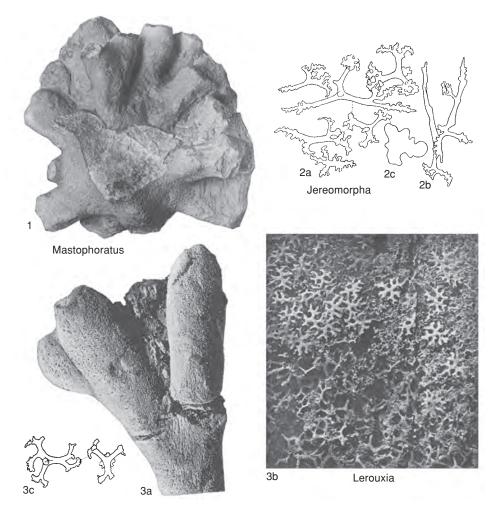


FIG. 146. Siphoniidae (p. 220).

?Tretotoechus Oppliger, 1915, p. 56 [\*T. coniformis; OD]. Narrow, top-shaped sponge with tubular, paragastral cavity; outside with large apertures, apparently of radial canals (epirhyses); aporhyses and postica not known, but summit with radiating furrows that may be incipient aporhyses; desmas smooth-armed tetraclones; no other spicules known. [Known only from poor material but apparently an early siphoniid with unusually large epirhyses, unless the lateral features are pseudogasters.] Upper Jurassic: Switzerland.—FIG. 145,1a-b. \*T. coniformis, Weiss Jura, Kimmeridgian, Aarau; a, side view of top-shaped holotype with distinct oscula on summit and ostia probably of large, radial canals on sides, ×1; b, photomicrograph of skeletal structure with tetraclones, ×50 (Oppliger, 1915).

### Subfamily LEROUXIINAE Moret, 1926

[nom. transl. et correct. REID, herein, ex Le Rouxides MORET, 1926b, p. 172]

Jerea-like sponges with phyllotriaene dermalia; distinct epirhyses present or absent; long, tubular aporhyses in axial bundle; desmas smooth, regular tetraclones, or partly irregular and grading into elongate, monaxial variants; rhizoclonids present or absent; microscleres unknown. [This subfamily could be placed into the family Theonellidae VON LENDENFELD from the form of the dermalia, as they were by PISERA

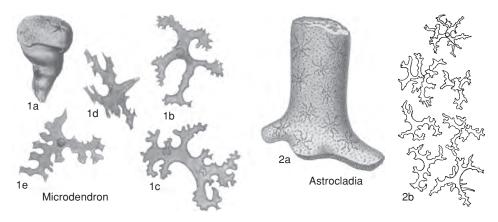


FIG. 147. Astrocladiidae (p. 221).

# (2002, p. 402), but are here regarded as siphoniids from the character of the desmas.] *Upper Cretaceous (Cenomanian–Campanian).*

- Lerouxia MORET, 1926b, p. 173 [\*L. galloprovincalis; OD]. Branched cylindrical with no paragastral cavity; sides with small, scattered ostia and locally with intersecting furrows in which additional ostia may occur at points of intersection; ends of branches with postica of long, tubular aporhyses that traverse axial parts in bundles; desmas mainly tetraclones, to which monaxial variants are added, and usually smooth armed but sometimes tuberculate; dermalia phyllotriaenes; rhizoclonids forming supplemental cortex; microscleres unknown. [In 1955 DE LAUBENFELS (p. 58) corrected the name from Le Rouxia MORET, 1926b.] Cretaceous (Santonian): France.—FIG. 146, 3a-c. \*L. galloprovincalis, Saint-Cyr; a, side view of branched fragment showing ends of branches, ×1; b, surface showing phyllotriaenes, supplemental cortex, and some desmas of underlying framework, ×15; c, spicules including tetraclone and variant, phyllotriaenes, and rhizoclonid, magnification not stated, approximately ×45 (Moret, 1926b; courtesy of Société Géologique de France).
- Jereomorpha MORET, 1926b, p. 174 [\*J. cenomanense; OD]. Club shaped or pyriform, stalked; summit rather flattened and with no paragastral depression; sides with numerous small ostia of radial epirhyses that curve downwardly toward interior; summit with postica of axial bundle of tubular aporhyses; some desmas regular tetraclones but others with arms of varying lengths, grading into elongate forms similar to those found in stalks of various other siphoniids; dermalia broadly trilobed phyllotriaenes; some rather large rhizoclonids present but not forming a cortex; microscleres unknown. Cretaceous (Cenomanian): France.-FIG. 146,2a-c. \*J. cenomanense, Sablons; characteristic spicules including tetraclones, irregular variants, and phyllotriaene, magnification not stated, ap-

proximately ×45 (Moret, 1926b; courtesy of Société Géologique de France).

?Mastophoratus REID, herein, nom. nov. pro Mastophorus SCHRAMMEN, 1924a, p. 54, non DIESING, 1853 [\*Mastophorus arborescens SCHRAMMEN, 1924a, p. 54; OD]. Radiating mass of more or less fused cylindrical branches; no paragaster, epirhyses, or ostia; each branch traversed by bundle of tubular aporhyses; desmas large, smooth tetraclones; dermalia unknown, but thought by SCHRAMMEN to be probably phyllotriaenes. [The genus is questionably included in the subfamily because the nature of dermalia is uncertain.] Cretaceous (Campanian): Germany.—FIG. 146,1. \*M. arborescens (SCHRAMMEN, MEN), Mukronatenkreide, Misburg; diagonal view of radiating, branched sponge, ×0.5 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

# Family ASTROCLADIIDAE Schrammen, 1901

[nom. correct. Schrammen, 1924a, p. 38, pro Astrocladidae Schrammen, 1901, p. 10]

Sponges with small, smooth-armed tetraclones as desmas and phyllotriaenes as dermal triaenes, when any are present; paragastral cavity absent; postica in stellate groups from which radiate short furrows; branched cylindrical in habit, with postica in lateral positions, or pyriform to cylindrical, simple or compound, with postica terminal; zygomes of desmas strongly branched, spiny; rhizoclonids forming supplemental cortex; microscleres unknown. [This is a small group of uncertain relationship, perhaps derived from a genus closely related to *Trachysycon* ZITTEL and Myrmeciophytum SCHRAMMEN of the Siphoniidae (Phymatellinae). They were placed in the Theonellidae LENDENFELD, 1903, by PISERA (2002, p. 401).] Upper Cretaceous (Cenomanian–Maastrichtian).

- Astrocladia ZITTEL, 1878a, p. 147 [\*Asterospongia laevis F. A. ROEMER, 1864, p. 54; SD DE LAUBEN-FELS, 1955, p. 57]. Narrow, cylindrical growths with no paragastral cavity, often branched dichotomously; exterior of skeletal framework with conspicuous, stellate features formed by small groups of skeletal pores presumed to be postica, and short, radiating furrows; intervening surface with ostia of short epirhyses; a few longitudinal aporhyses may be present in axial parts; desmas small tetraclones with very short, smooth, primary arms and strongly branched, spiny zygomes, passing into irregular, rhizoclone-like variants; rhizoclonids forming supplemental cortex, which may cover ostia and other lateral features when well developed; no dermal triaenes or microscleres known. [Asterospongia ROEMER, 1864, was listed by DE LAUBENFELS (1955, p. 65) as a separate genus, with the same type species. It is recommended that Asterospongia sensu DE LAUBENFELS not be used.] Cretaceous (Cenomanian-Maastrichtian): England, Germany, Poland, Cenomanian-Turonian; France, Germany, Coniacian-Maastrichtian.-Fig. 147,2a. \*A. laevis (F. A. ROEMER), Coniacian, Germany; side view of holotype, basal parts with stellate features and ostia, but without cortex, ×1 (Roemer, 1864).—FIG. 147,2b. A. subramosa (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; tetraclones and irregular, rhizoclone-like variants, ×30 (Schrammen, 1910).
- Microdendron SCHRAMMEN, 1901, p. 10 [\*M. ramulosum; OD]. Solitary or compound; individuals pyriform to cylindrical, joined basally in compound examples; sides of skeletal framework with small ostia; stellate groups of postica and furrows on terminal parts, which may be rounded or flattened; desmas small tetraclones and rhizoclone-like variants, similar to those of Astrocladia ZITTEL; dermalia small phyllotriaenes with irregularly sculptured cladi; basal parts and sides covered by dense, supplemental cortex formed from small rhizoclonids that conceal ostia; microscleres unknown. Upper Cretaceous (Campanian): Germany.----FIG. 147, 1a-e. \*M. ramulosum, Mucronatenkreide, Misburg; *a*, side view of club-shaped sponge, ×1; b-e, characteristic spicules including desmas and phyllotriaenes, ×50 (Schrammen, 1901).

#### Family PHYMARAPHINIIDAE Schrammen, 1910

[nom. transl. et correct. SCHRAMMEN, 1924a, p. 38, ex Phymaraphininae SCHRAMMEN, 1910, p. 34] [=Kaliapsidae DE LAUBENFELS, 1936, p. 175, partim]

Sponges with desmas in which base of each arm typically surrounded by annular

swelling, and with dermal phyllotriaenes or discotriaenes; principal desmas tetraclones, triders, or both; arms of desmas typically smooth beyond basal annulation but sometimes tuberculate or with further annulations; reduced arms (brachyomes) of triders retain annular swelling and may either form buttonlike feature or have crepidal ray protruding through it; some forms with variant desmas in which two or three arms are aborted in this manner, or with elongate, radical desmas with diactinal or monaxial crepides; rhizoclonids frequent, sometimes forming supplemental cortex in which shafts of dermalia are imbedded; microscleres unknown. [This is a small, compact group presumably divergent from the same source as the Siphoniidae but distinguished by the annulated desmas and modified dermalia. The Upper Jurassic record is based on isolated desmas that have the characteristic annulation. The family is regarded here as not including the living Calliopsis BURBANK, in which annulation of arms is restricted to special basal triders.] Lower Cretaceous (Aptian)-Upper Cretaceous.

- Phymaraphinia SCHRAMMEN, 1901, p. 8 [\*P. infundibuliformis; OD]. Funnel-like or flabellate with short stalk sometimes present at base; both surfaces of skeletal framework strongly sculptured by narrow, closely spaced furrows in which ostia or postica are located; furrows short, sinuous, and irregularly reticulating to elongate and subparallel, then typically radiating from base, but sometimes also changing direction abruptly in upper parts; desmas mainly tetraclones, in which arms are smooth beyond annulations, but including variant forms in which one to three arms are represented by buttonlike rudiments; dermalia phyllotriaenes; rhizoclonids present at both surfaces, sometimes forming dense, supplemental cortex that covers superficial furrows; microscleres unknown. Cretaceous (Aptian-Maastrichtian): Spain, Aptian-Albian; England, Germany, Coniacian-Maastrichtian .-FIG. 148,2a-b. \*P. infundibuliformis, Mucronatenkreide, Campanian, Misburg, Germany; a, side view of medium-sized, obconical type specimen, ×1; b, large fragment showing variation in form of superficial furrows, ×0.5 (Schrammen, 1910).
- Compsapsis SOLLAS, 1880d, p. 387 [\*C. cretacea; OD]. Name based on isolated tetraclones with characteristic phymeraphiniid annulations. Upper Cretaceous (Maastrichtian): England.—FIG. 148,3a-b. \*C. cretacea, Trimmingham Chalk, Norfolk; type tetraclone spicules, scale uncertain (Sollas, 1880d).

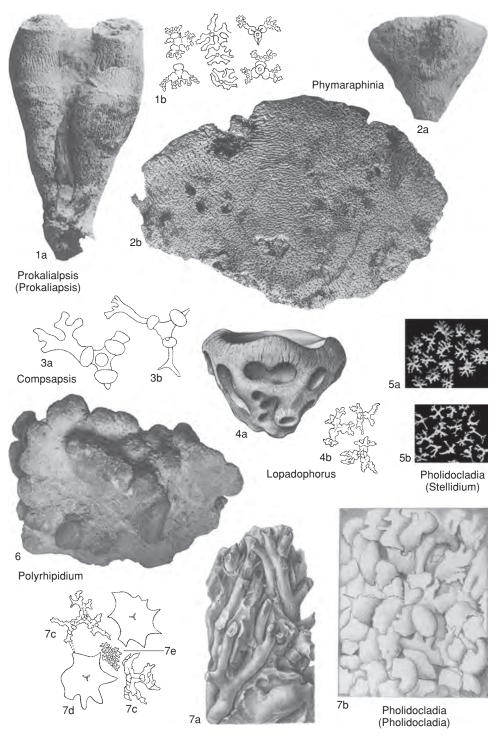


FIG. 148. Phymaraphiniidae (p. 221-224).

- Cycloclema SCHRAMMEN, 1910, p. 105 [\*Rhagadinia compressa HINDE, 1884a, p. 82; OD]. Funnel-like, wide or narrow, sometimes laterally compressed, with short, basal stalk; expanded, encrusting base sometimes present; skeletal surfaces with apertures (ostia, postica) of tubular epirhyses and aporhyses that enter wall obliquely upward, often at upper ends of short, longitudinal furrows; desmas tetraclones with arms smooth beyond basal annulations and variants with one to three arms aborted; latter with suppressed arms represented by buttonlike rudiments; those near surface may be mainly triders, with buttonlike, short arm (brachyome) facing outwardly; rhizoclonids not recorded; dermalia phyllotriaenes; microscleres unknown. Cretaceous (Campanian): England, France, Germany, Poland.—FIG. 149a-d. C. compressa (HINDE), Quadratenkreide, Oberg, Germany; a, outside or lower surface with elongate ostia of canals that enter wall obliquely upward; b, inside or upper surface with circular, exhalant ostia in shallow grooves,  $\times 0.5$ ; *c*-*d*, characteristic spicules including desmas (tetraclone and trider) and dermal phyllotriaene, ×20 (Schrammen, 1910).
- Lopadophorus SCHRAMMEN, 1910, p. 109 [\*Oculispongia janus F. A. ROEMER, 1864, p. 48; SD DE LAUBENFELS, 1955, p. 59]. Shape variable, for example, irregularly nodular, roughly globular, hemispherical, or top shaped with summit flat or concave, cup shaped, or related shapes; sides have more or less numerous large, hemispherical depressions, sometimes on prominences; base encrusting; fine, radiating furrows around some or all of lateral depressions and on paragastral margin when body is cuplike; summit or central cavity with pores presumed to be postica, from which short canals (aporhyses) run inwardly; sides with similar or smaller ostia; desmas tetraclones and triders, rather small; dermalia phyllotriaenes; rhizoclonids and cortex not recorded; microscleres unknown. Cretaceous (Aptian-Maastrichtian): Spain, Aptian; England, Germany, Coniacian-Maastrichtian.-FIG. 148,4a. \*L. janus (F. A. ROEMER), Santonian, Sudmerberges near Goslar, Germany; side view with broad, upper osculum and irregular depressions on sides, ×0.5 (Schrammen, 1910).--Fig. 148,4b. L. lacunosus SCHRAMMEN, Quadratenkreide, Campanian, Oberg, Germany; representative triders, ×20 (Schrammen, 1910).
- Pholidocladia HINDE, 1884a, p. 80 [\**P. dichotoma*; SD DE LAUBENFELS, 1955, p. 59]. Small, repeatedly branching growths with cylindrical or vermiform branches; no distinct epirhyses or ostia; ends of branches with one to several postica of tubular aporhyses that traverse branches, or without these features; desmas mainly triders with a buttonlike brachyome or with a crepidal ray projecting through basal annulation; skeletal meshwork usually very dense; dermalia phyllotriaenes or discotriaenes; rhizoclonids that may or may not form supplemental cortex; microscleres unknown. *Upper Cretaceous (Turonian–Campanian):* Europe.

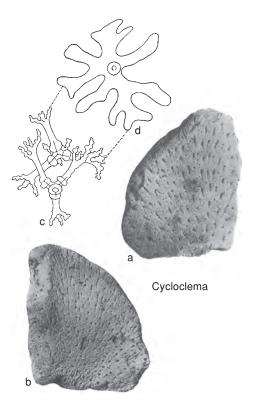


FIG. 149. Phymaraphiniidae (p. 223).

- P. (Pholidocladia). Desmas tuberculate beyond their basal annulations; dermalia discotriaenes that range from marginally scalloped discs to irregularly ovate plates; rhizoclonids sometimes present. Cretaceous (Turonian-Campanian): Germany, England; France, Santonian-Campanian.—FIG. 148,7a-e. \*P. (P.) dichotoma; a, repeatedly branched specimen preserved in flint, Upper Chalk, Wiltshire, England, ×0.5; b, dermal skeleton showing overlapping discotriaenes, Upper Chalk, Wiltshire, England, ×50 (Hinde, 1884b); c-e, typical spicules including desmas, discotriaenes, and rhizoclonids, Quadratenkreide, Campanian, Oberg, Germany, ×20 (Schrammen, 1910).
- P. (Stelidium) SCHRAMMEN, 1924a, p. 55 [\*S. vermiculare; OD]. Arms of desmas smooth beyond basal annulations; dermalia phyllotriaenes, rhizoclonids unknown. Cretaceous (Campanian): Germany.—\_\_\_\_FIG. 148,5a-b. \*P. (S.) vermiculare, Mukronatenkreide, Misburg; a, phyllotriaenes; b, desmas, triders, and irregular variants, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- **Polyrhipidium** SCHRAMMEN, 1924a, p. 54 [\**P. cristagalli;* OD]. Clump of intergrown, subcylindrical stems or lateral branches; crest of cluster with

numerous round postica; ostia on margins are scarce; supporting skeleton made of small tetraclones, each with a ring or bulge near center of ray divergence; dermalia unknown. *Cretaceous (Santonian):* Germany.—FIG. 148,6. \*P. cristagalli, Emscher beds, Sudmerberges; side view of clumped sponge, ×1 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

- Prokaliapsis SCHRAMMEN, 1901, p. 7 [\*P. cylindrica; SD DE LAUBENFELS, 1955, p. 59; = Rhagadinia clavata HINDE, 1884a, p. 84, subj.] [=Procaliapsis SCHRAM-MEN, 1910, p. 108, nom. null.]. Globular, club shaped, cylindrical, or branched cylindrical, with unbranched forms sometimes in groups; no paragastral cavity; sides finely furrowed, with furrows of various directions but often subparallel locally and with widely scattered ostia from which short epirhyses run inwardly; summit(s) with postica of bundle of longitudinal aporhyses that traverse axial parts; desmas tetraclones and variants without one or more arms in interior, but as triders near surface, with buttonlike rudiment facing outwardly; dermalia phyllotriaenes; supplemental cortex over parts of surface; microscleres unknown. Lower Cretaceous (Aptian)-Upper Cretaceous: Europe.
  - P. (Prokaliapsis). Comprises species that are typically solitary, although individuals sometimes grow in groups. Lower Cretaceous (Aptian)–Upper Cretaceous: Spain, Aptian; France, Santonian–Campanian; Germany, Campanian; England, Upper Cretaceous.—FIG. 148, Ia-b. \*P. (P.) clavata (HINDE), Quadratenkreide, Campanian, Oberg, Germany; a, example of two steeply obconical individuals that have arisen from common base, ×1; b, characteristic spicules including triders and phyllotriaenes, ×20 (Schrammen, 1910).

# Family THEONELLIDAE von Lendenfeld, 1904

[Theonellidae von Lendenfeld, 1904c, p. 126] [=Discodermiidae Schrammen, 1924a, p. 37, nom. correct. pro Discoderminae Schrammen, 1910, p. 97]

Sponges typically with desmas that are strongly tuberculate tetraclones and with dermal phyllotriaenes or discotriaenes; but including apparently related forms showing different conditions in which desmas are mainly or all smooth or spinose, or are partly forms with less than four arms, or the normal dermalia are replaced by dichotriaenes or siliceous discs; desmas never exclusively triders; rhizoclonids present or absent, where present sometimes comprising a supplemental cortex; microscleres of modern forms all microrhabds, or including plesiasters, metasters, spirasters, or amphiasters; spirasters in one fossil genus. [The modern family type *Theonella* GRAY comprises species in which the desmas are typically nontuberculate; but the holotype of the type species, *T. swinhoei* GRAY, has strongly tuberculate desmas in the lower parts. The type species of *Discodermia* DU BOCAGE, *D. polydiscus* DU BOCAGE, is also not a sponge of the type called *Discodermia* by SCHRAMMEN (1910) and MORET (1926b) but a form here thought similar to *Theonella* and separable perhaps only subgenerically. The Acrochordoniidae, as proposed by *Schrammen* (1924a), is included in the Theonellidae as a subfamily.] *Lower Cretaceous–Holocene.* 

#### Subfamily THEONELLINAE von Lendenfeld, 1904

[nom. transl. Reid, herein, pro Theonellinae von Lendenfeld, 1904c, p. 126]

Modern Theonellidae in which rhizoclonids are absent, and similar fossils in which they appear to be absent; microscleres of modern forms microrhabds only, or including plesiasters, metasters, spirasters, or amphiasters. [The subfamily should possibly include forms placed here in the family Protetraclisidae SCHRAMMEN (Upper Jurassic).] Lower Cretaceous-Holocene.

- Theonella GRAY, 1868b, p. 565 [\*T. swinhoei GRAY, 1868b, p. 566; OD]. Cup- or funnel-like, thick walled, or clublike, with a tubular, central cavity that extends to base; outside smooth or with irregular, nodular or shelflike projections; external surface of skeletal framework with scattered ostia, from which tubular epirhyses run in radially or obliquely; paragastral surface with similar or larger postica of aporhyses that usually branch within wall; desmas typically long-armed tetraclones, with zygomes sometimes slightly developed and usually smooth, but sometimes more or less strongly tuberculate in basal parts; dermalia typically slender phyllotriaenes with distinct protocladi and curving branches, arranged to enclose rounded, porelike interspaces; some also with zygomelike articulations on cladi but not on rhabdal shafts; rhizoclonids absent; microscleres microrhabds only. [Doubtful Eocene record based on isolated phyllotriaenes (HINDE & HOLMES, 1892).] Paleogene (?Eocene), Holocene: New Zealand, ?Eocene; cosmopolitan, Holocene. -FIG. 150, 1. isolated phyllotriaene ascribed to Theonella GRAY, ×40 (Hinde & Holmes, 1892).
- Colossolacis SCHRAMMEN, 1910, p. 103 [\*C. plicata; OD]. Basically funnel shaped but with wall irregularly plicated, and with folds anastomosing, base

with rootlike processes; outside with numerous small ostia; gastral surfaces with similar postica and larger apertures of pitlike cavities; desmas mainly smooth-armed tetraclones, to which amphitrider-like variants may be added; rhizoclonids apparently absent; microscleres unknown. *Cretaceous (Campanian):* Germany.—FIG. 151, *1a-d.* \**C. plicata*, Quadratenkreide, Oberg; *a*, lower surface of plicated to digitate sponge; *b*, upper surface of same, ×0.25; *c*, fragment in spicular preservation with postica and other apertures of paragastral surface, ×0.5; *d*, typical tetraclone desmas, ×20 (Schrammen, 1910).

- Discodermia DU BOCAGE, 1869, p. 160 [\*D. polydiscus; OD] [?=Rhoptrum SCHRAMMEN, 1910, p. 104 (type, R. scytaliforme, OD); ?Leiophyllum SCHRAMMEN, 1924a, p. 52 (type, L. panniculosum, OD); ?Nedlandsia DE LAUBENFELS, 1953b, p. 113 (type, N. clarkei, OD)]. Typically cuplike or funnel-like, sometimes in groups, but may be flabellate or pass into other shapes; outside with small ostia, from which simple or branching epirhyses run into skeletal framework; paragastral surface with larger postica of similar aporhyses with more or less prominent rims in some species; desmas mainly or all tetraclones, to which irregular variants may be added, and typically tuberculate but sometimes smooth armed or more or less spinose; irregular tetraclone variants sometimes triodal or diaxial; dermalia phyllotrianes, discotriaenes, or both, and intermediates; discotriaenes typically arranged to form overlapping pavement, overlapped spicules may have marginally notched discs grown around shafts of other spicules; no rhizoclonids; microscleres microrhabds only. [Other supposed records based on form are referred here to other genera.] ? Upper Cretaceous, Paleogene (? Eocene), Neogene (Miocene)-Holocene: Germany, ?Upper Cretaceous; Australia, New Zealand, ?Eocene; Spain, ?Northern Africa, Miocene; cosmopolitan, Ho--FIG. 150, 3a-b. \*D. polydiscus, Holocene, locene.— Atlantic Ocean, Portugal; a, side view of small sponge with irregular nodes, ×1; *b*, dermal spicules, ×100 (du Bocage, 1869).—FIG. 150,3c. D. sp., Eocene, Otago, New Zealand; discotriaene ascribed to Discodermia sp., ×100 (Hinde & Holmes, -FIG. 150,3d. D. sinuosa CARTER, Eocene, 1892).-Otago, New Zealand; phyllotriaene ascribed to modern species, ×100 (Hinde & Holmes, 1892).
- Leiophyllum SCHRAMMEN, 1924a, p. 52 [\*L. panniculosum; OD]. Flabellate, forming irregularly lobate plate; surfaces with anastomosing furrows and irregular, skeletal pores; desmas tuberculate tetraclones; dermalia phyllotriaenes; rhizoclonids apparently absent; microscleres unknown. [Acceptable as a true Discodermia if rhizoclonids were absent and microscleres were microrhabds.] Cretaceous (Campanian): Germany.—FIG. 150,2. \*L. panniculosum, Quadratenkreide, Höver; irregularly lobate sponge, ×0.50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Placoscytus Schrammen, 1910, p. 101, nom. nov. pro Sollasella Schrammen, 1901, p. 6, non von

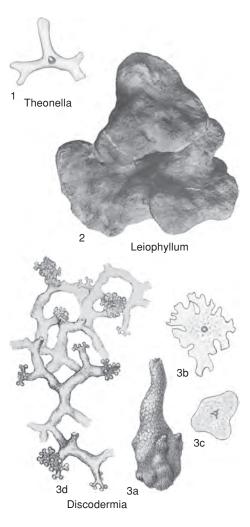


FIG. 150. Theonellidae (p. 224-225).

LENDENFELD, 1887 [\*Sollasella jereaeformis SCHRAMMEN, 1901, p. 6; OD]. Simple or compound, stalked; individuals top shaped to cylindrical, with summit rounded, truncated, or slightly hollowed; sides with shallow, sinuous, anastomosing furrows and small ostia, which occur both within furrows and between them; summit(s) with postica of tubular aporhyses, which run downwardly through body; desmas smooth and slightly tuberculate tetraclones; dermalia siliceous plates with denticulated margins; rhizoclonids apparently absent; microscleres unknown. [Dermalia interpreted as discotriaenes by SCHRAMMEN, 1910, but axial canals not certainly present.] Cretaceous (Campanian): Germany.——FIG. 151,5a-d. \*P. jereaeformis (SCHRAMMEN), Quadratenkreide, Misburg; a, stalked, compound example with

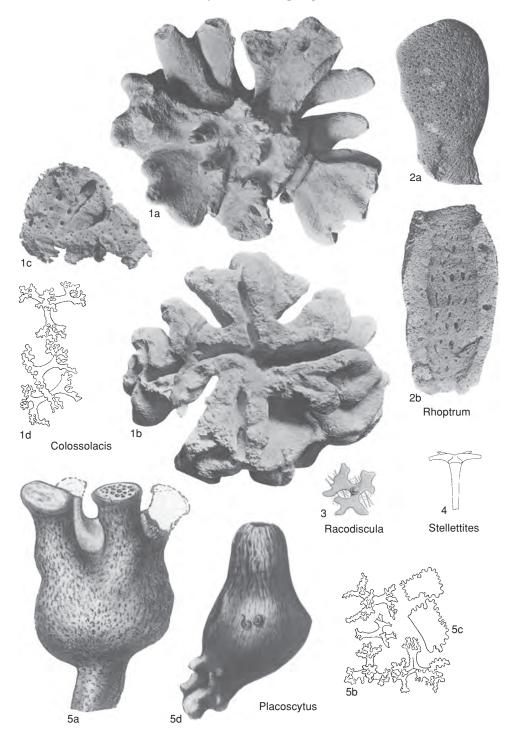


FIG. 151. Theonellidae (p. 224–227).

cylindrical, upper branches,  $\times 1$ ; *b–c*, characteristic spicules including tetraclones and dermal plates  $\times 20$  (Schrammen, 1910); *d*, solitary example,  $\times 1$  (Schrammen, 1901).

- Racodiscula ZITTEL, 1878a, p. 151 [\*Corallistes polydiscus SCHMIDT, 1870, p. 24; =R. asteroides ZITTEL, 1878a, p. 151 (ascribed to CARTER, 1873, p. 441); SD DE LAUBENFELS, 1955, p. 58, as C. asteroides CARTER]. Nodular, club shaped or cylindrical, with no paragastral cavity; summit with postica of vertical, tubular aporhyses; ostia apparently absent; dermalia discotriaenes with simple, lobate, or denticulated margins; desmas irregular tetraclones, not markedly tuberculate; rhizoclonids absent; microscleres microrhabds, plesiasters, metasters, spirasters, or amphiasters. [Supposed Cretaceous record by ZITTEL, 1878a, based on isolated dermalia, also claimed by SOLLAS (1880d) to represent dicranocladine Macandrewia GRAY. The name asteroides ascribed to CARTER by ZITTEL and DE LAUBENFELS was not proposed as the name of a species but mentioned as an alternative MS name on a slide of C. polydiscus supplied by SCHMIDT (see CARTER, 1873, p. 442).] ?Cretaceous; Holocene: cosmopolitan.-FIG. 151,3. R. sp., Holocene, Philippine Islands; isolated, lobate, dermal discotriaene, ×30 (Zittel, 1878a).
- Rhoptrum SCHRAMMEN, 1910, p. 104 [\*R. scytaliforme; OD]. Pyriform, club shaped or cylindrical, with paragastral cavity extending to base; exterior with small, rounded ostia; no epirhyses; paragastral surface with larger postica of short aporhyses, which enter wall obliquely upward; desmas more or less irregular tetraclones, smooth or tuberculate; dermalia phyllotriaenes; rhizoclonids unknown; microscleres unknown. [Acceptable as Discodermia sensu DU BOCAGE if rhizoclonids were absent and microscleres were microrhabds.] Cretaceous (Aptian-Campanian): Spain, Aptian; Germany, Cam-panian.—FIG. 151,2a-b. \*R. scytaliforme, Quadratenkreide, Campanian, Oberg, Germany; a, side view of club-shaped specimen; b, longitudinal section of subcylindrical specimen showing relatively thin walls and coarse, exhalant ostia in gastral surface of broad spongocoel, ×1 (Schrammen, 1910).
- Stellettites CARTER, 1871, p. 129 [\*S. haldonensis; OD]. Spicules resembling those of Dactylocalycites but with rays spread horizontally or laterally and branches somewhat recurved. Lower Cretaceous: Europe.——FIG. 151,4. \*S. haldonensis, Upper Greensand, Exeter; isolated spicule, ×25 (Carter, 1871).

#### Subfamily ACROCHORDONIINAE Schrammen, 1910

[nom. correct. REID, herein, pro Acrochordoninae SCHRAMMEN, 1910, p. 33; emend., REID, herein] [=Acrochordoniidae SCHRAMMEN, 1924a, p. 38]

Theonellidae with rhizoclonids that often form a supplemental cortex and with

dermalia that are sometimes dichotriaenes, but typically phyllotriaenes or discotriaenes; canal systems commonly like those of Siphonia or Jerea of family Siphoniidae, but sometimes of other types; microscleres unknown. [The subfamily was proposed by SCHRAMMEN, 1910 for Acrochordonia only, in which dermalia are dichotriaenes. This genus is here regarded as similar to Phyllodermia SCHRAMMEN, in which dermalia are slightly modified dichotriaenes in the subgenus Cladodermia SCHRAMMEN. The type genus was placed into the suborder Dicranocladina by LAGNEAU-HÉRENGER (1962) but is a true tetracladine.] Lower Cretaceous (Aptian)–Neogene (Miocene).

- Acrochordonia SCHRAMMEN, 1901, p. 6 [\*A. ramosa; OD]. Branched cylindrical, irregularly nodular, funnel-like, or flabellate with lobate margins, or in intermediate shapes; postica open in a number of shallow depressions, usually on upper surface when one is apparent; ostia scattered over other parts of surface; tubular aporhyses radiating from groups of postica, with outermost imperfectly enclosed and forming radiating furrows; desmas strongly tuberculate tetraclones; rhizoclonids sometimes possibly present; dermalia dichotriaenes; microscleres unknown. [Rhizoclonids claimed by MORET (1926b, p. 175) in generic diagnosis, but not described in any species.] Cretaceous (Aptian-Campanian): Spain, Aptian; France, Santonian; Germany, Poland, Campanian.—FIG. 152,4a-c. \*A. ramosa, Quadratenkreide, Campanian, Oberg, Germany; a, example with three nodular lobes radiating from common stalk, ×0.5; b-c, representative spicules including desmas and dichotriaenes, ×20 (Schrammen, 1910).
- Achrochordiella RIGBY, 1981, p. 129 [\*A. vokesi RIGBY, 1981, p. 130; OD]. Massive, lobate to anastomosing or branched, fingerlike sponges; principal skeleton of small to medium-sized, warty tetraclones; dermalia characteristic dichotriaenes or modifications of dichotriaenes that may have lost one or two primary or secondary branches; phyllotriaenes rare; surfaces marked by moderately indented, strong, somewhat anastomosing but generally nearly vertical canals; individual branches without spongocoel and relatively dense. Paleogene (Eocene): USA (North Carolina).—FIG. 152,3a-l. \*A. vokesi, Castle Hayne Limestone, Wayne County; a, side view of branched holotype, USNM 252489, ×0.5; b, photomicrograph of principle, skeletal net with nodes formed by junctions of tetraclone, ray tips, ×10; c, dichotriaenes of dermal net, ×20; dl, characteristic spicules including d-f, dichotriaenes of dermal net, g-h, simple orthotriaenes, i-j, knobby tetraclones, and k-l, bladed phyllotriaenes,

Porifera—Demospongea

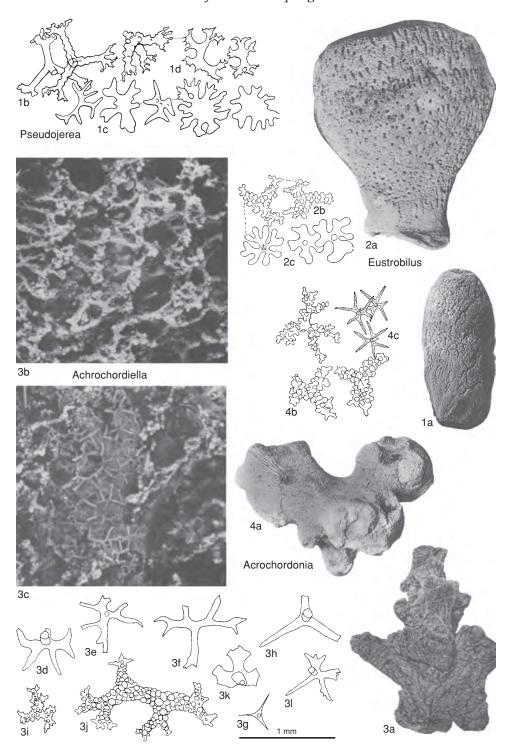


FIG. 152. Theonellidae (p. 227-230).

×25 (Rigby, 1981; courtesy of *Tulane Studies in Geology and Paleontology*).

- Eustrobilus SCHRAMMEN, 1910, p. 102 [\*E. callosus; OD]. Top shaped or cylindrical with the summit truncated, short stalked; base encrusting or dividing into processes; paragastral cavity deep, narrow; outside with numerous rounded ostia from which short furrows commonly run downwardly; paragastral wall with simple postica; epirhyses and aporhyses deep and overlapping within wall; inceptional examples of both form radiating furrows around paragastral margin; desmas tuberculate tetraclones; dermalia phyllotriaenes; rhizoclonids apparently absent. [Absence of rhizoclonids is queried because a cortex appears to be present in SCHRAMMEN's (1910) figured material.] Cretaceous (Aptian-Campanian): Spain, Aptian; France, Santonian; Germany, Poland, Campanian.-FIG. 152,2a-c. \*E. callosus, Quadratenkreide, Campanian, Oberg, Germany; a, side view of club-shaped example with circular ostia above grooves,  $\times 1$ ; b-c, characteristic spicules including desmas and phyllotriaenes, ×20 (Schrammen, 1910).
- Phyllodermia SCHRAMMEN, 1924a, p. 48 [\*Discodermia antiqua SCHRAMMEN, 1901, p. 5; OD; not Phyllodermia spinosa SCHRAMMEN, 1924a, p. 50, SD DE LAUBENFELS, 1955, p. 58]. Solitary in normal individuals but sometimes in groups; individuals pyriform to cylindrical, top shaped, discoidal, or other related shapes; paragaster varies from shallow depression to deep, central cavity; encrusting base, multiple root processes, or no evident attachment; external surfaces of skeletal framework with small ostia or open meshes only and sometimes furrowed in varying directions; paragastral surface with postica of aporhyses, unless these veiled by superficial accretion of desmas; aporhyses vertical in axial parts but arch outwardly away from them with highest ones sometimes horizontal or sloping upwardly according to body form; incompletely enclosed aporhyses may form conspicuous furrows around paragastral margin; desmas tetraclones, all tuberculate or including smooth examples; usually with supplemental cortex formed from flattened rhizoclonids; microscleres unknown. [For SCHRAM-MEN's original designation of the type species, see the paragraph before his (1924a) formal diagnosis. Diagnosis combines characters of Phyllodermia sensu SCHRAMMEN and Cladodermia SCHRAMMEN, here regarded as subgenera.] Cretaceous (Aptian-Santonian), Paleogene (?Eocene):
  - P. (Phyllodermia). Dermalia normal phyllotriaenes; paragastral cavity typically shallow, sometimes obsolete; with encrusting base, multiple root processes, or no evident attachment. *Cretaceous* (Aptian-Campanian): Spain, Aptian; France, Santonian; Germany, Campanian.——FIG. 153,1a-d. \*P. (P.) antiqua (SCHRAMMEN), Quadratenkreide, Campanian, Oberg, Germany; a, vertically sectioned example showing spongocoel with aporhyses and postica veiled by accretion of desmas of gastral layer, ×1; b-d, spicules including b, smooth-armed tetraclones and

a triodal variant, *c*, tuberculate tetraclone, and *d*, a dermal phyllotriaene, ×20 (Schrammen, 1910).——FiG. 153, *le. P. (P.) stellata* (MORET), Santonian, Saint-Cyr, France; obconical sponge with shallow, paragastral cavity and prominent, radial structure and canals, ×1 (Moret, 1926b; courtesy of Société Géologique de France).

- P. (Cladodermia) SCHRAMMEN, 1924a, p. 51 [\*Discodermia colossea SCHRAMMEN, 1910, p. 98; OD]. Dermalia finely branched phyllotriaenes in which cladi are not markedly flattened and terminal branches are pointed; paragastral cavity deep, tubular; base encrusting. Cretaceous (Aptian-Campanian), Paleogene (?Eocene): Spain, Aptian; England, ?Albian; Germany, Campanian; New Zealand, ?Eocene. FIG. 153,4a. \*P. (C.) colossea (SCHRAMMEN), Mukronatenkreide, Campanian, Misburg, Germany; dermal phyllotriaene, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).—FIG. 153,4b-c. P. (C.) type, ?Eocene, Otago, New Zealand; phyllotriaenes, ×40 (Hinde & Holmes, 1892).
- Pliegatella BRIMAUD & VACHARD, 1986, p. 305 [\*P. genovefae; OD]. Sponges with branched, stalked, or asymmetric and irregular growth; both short and long ranches have rounded or flattened ends, never depressed or ending in apochetes; exhalant system is often indistinct; inhalant canals have little bifurcation; surface is rough on a small scale because of warty swellings of exposed desmas that are large tetraclones, which may be locally smooth, and some very typical dicranoclones; cortical skeleton not observed. [Pliegatella differs from Achrochordiella in growth form, rarity of radial canals, and the large size of its tetraclones and their close packing.] Neogene (Miocene): Spain.-FIG. 153,3a-b. \*P. genovefae, Tortonian strata, upper Miocene, Pliego, southern Spain; a, side view of irregularly branched sponge with large tetraclones in upper right, IPM R6941, ×0.5; b, photomicrograph of typical tetraclones with nodular sculpture, IPM R6948, ×50 (Brimaud & Vachard, 1986; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
- Pseudojerea MORET, 1926b, p. 181 [\*P. massiliensis; SD DE LAUBENFELS, 1955, p. 58]. Pyriform to club shaped, or cylindrical with irregular, radial lobes; paragastral cavity deep to shallow or absent; sides with ostia and sometimes reticulating furrows; some with vertical aporhyses only, which open at conical apex or in shallow depression; others with additional lateral aporhyses that open in vertical series in walls of distinct paragaster; size of ostia and postica similar; desmas smooth and tuberculated tetraclones and tuberculate triders; dermalia phyllotriaenes and forming gradational to discotriaenes; lower parts covered by supplemental cortex, formed from large rhizoclonids; microscleres unknown. Cretaceous (Santonian): France.—FIG. 152, 1a-d. \*P. massiliensis, Saint-Cyr; a, pyriform sponge with shallow, apical (paragastral) depression and reticulated furrows on flanks with scattered ostia in upper

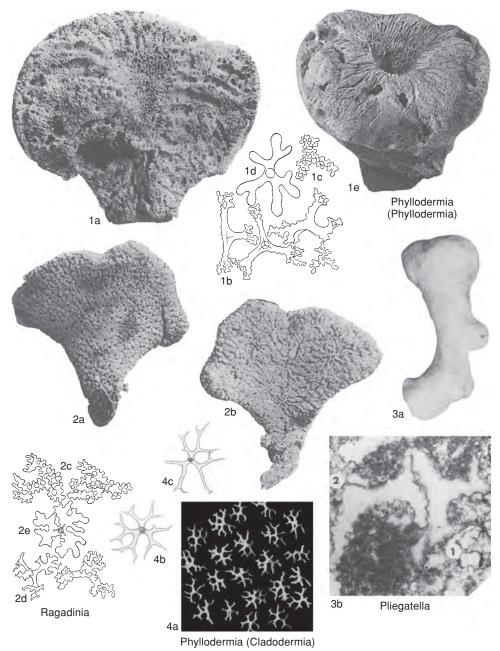


FIG. 153. Theonellidae (p. 229–231).

parts, slightly reduced; *b–d*, characteristic spicules including tetraclones, trider, and cortical rhizoclonids, magnification not stated but approximately ×40 (Moret, 1926b; courtesy of Société Géologique de France).

Ragadinia ŽITTEL, 1878a, p. 152 [\**Cupulospongia* rimosa F. A. ROEMER, 1864, p. 51; OD] [=*Rhaga*- dinia SCHRAMMEN, 1910, p. 100, obj., nom. null.]. Funnel or bowl-like, or in flabellate shapes; stalked or sessile; exterior of skeletal framework with radiating network of fine, irregular furrows in which ostia are located, or with closely spaced and irregularly interconnected ostia; paragastral surface sometimes similar, but typically with postica in groups

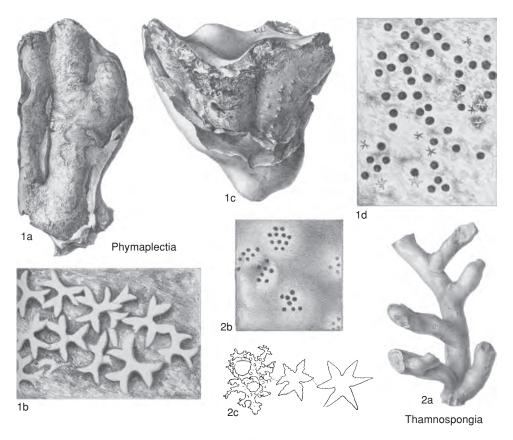


FIG. 154. Theonellidae (p. 231-232).

from which some furrows radiate; epirhyses and aporhyses short; postica groups sometimes in shallow depressions; without postica and external furrows in some variants, although paragastral furrows still present; desmas tuberculate tetraclones and smooth or partly smooth variants; dermalia phyllotriaenes; rhizoclonids forming supplemental cortex on both sides of skeletal framework, whose surfaces are concealed unless cortex is lost; supplemental cortex of gastral side sometimes forming small, conical elevations over groups of postica; microscleres unknown. [Ragadinia spp. of HINDE (1884a, Upper Chalk, England) are Phymaraphiniidae: cf. SCHRAMMEN, 1910.] Cretaceous (Cenomanian-Campanian): Czech Republic, Slovakia, Cenomanian; France, Santonian; Germany, Poland, Campanian.—FIG. 153, 2a-e. \*R. rimosa (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; a, inhalant surface of flabellate example with evenly distributed, inhalant ostia,  $\times 1$ ; *b*, exhalant surface of same specimen with grooves radiating from several centers, ×1; *c*-*e*, characteristic spicules including tuberculate desmas, smooth and partly smooth variants, one of which is probably a young form, and phyllotriaene, ×20 (Schrammen, 1910).

#### Subfamily PHYMAPLECTIINAE new subfamily

[Phymaplectiinae REID, herein] [type genus, *Phymaplectia* HINDE, 1884a, p. 87]

Dermalia dichotriaenes with slightly flattened cladi or dichotriaene-like phyllotriaenes; rhizoclonids present, sometimes forming a supplemental cortex that may be pierced by conspicuous, intracortical pores; spiraster microscleres in one fossil (Eocene) species. [This is a small group distinguished chiefly by distinctive dermalia.] Upper Cretaceous–Paleogene (Eocene).

Phymaplectia HINDE, 1884a, p. 87 [\*P. irregularis; SD DE LAUBENFELS, 1955, p. 56]. Flabellate and leaf shaped to digitate, or irregularly convoluted, or assuming secondary funnel shape through union of infolded margins; thin walled; skeletal pores and canals absent or sparsely developed; surfaces sometimes with irregular furrows that may radiate from small, conical prominences on one surface; desmas more or less irregular, tuberculate tetraclones and triders; dermalia sometimes simple dichotriaenes, but typically phyllodichotriaenes with flattened cladi; supplemental cortex formed by small rhizoclonids; cortex sometimes pierced by intracortical pores; microscleres unknown. Upper Cretaceous, Paleogene (?Eocene): England; France, Santonian; Western Australia, ?Eocene.-FIG. 154, 1a-b. \*P. irregularis, Upper Chalk, Santonian, Wiltshire, England; a, side view of specimen in flint, ×0.5; b, dermal surface showing phyllodichotriaenes, ×25 (Hinde, 1884a).—FIG. 154, 1c. P. spinosa HINDE, Upper Chalk, Santonian, Wiltshire, England; surface of skeletal framework, ×25 (Hinde, 1884a). -FIG. 154, 1d. P. cribrata HINDE, Upper Chalk, Santonian, Wiltshire, England; surface showing cortex, intracortical ostia, and small dichotriaenes, ×25 (Hinde, 1884a).

Thamnospongia HINDE, 1884a, p. 78 [\*T. glabra; SD DE LAUBENFELS, 1955, p. 59]. Branched cylindrical, with single, upright stem and lateral branches, or forming bushlike group of cylindrical branches, some of which may more or less coalesce; lateral branches sometimes rudimentary or represented only by conical prominences; ends of branches with one or more postica of tubular, longitudinal aporhyses that traverse axial parts; no other skeletal pores; desmas small tetraclones and irregular variants, strongly tuberculate; dermalia dichotriaenes with slightly flattened cladi, or well-developed dichophyllotriaenes; sometimes with supplemental cortex formed from small rhizoclonids and pierced by intracortical pores, which may be in groups; spiraster microscleres in one Eocene species. Upper Cretaceous-Paleogene (Eocene): England, Upper Cretaceous; France, Santonian; Germany, Campanian; Western Australia, Eocene.-FIG. 154,2a-c. \*T. glabra, Santonian; a, branched holotype, Upper Chalk, Berkhampton, England, ×0.5; b, enlarged surface of specimen showing groups of intracortical pores, Upper Chalk, Berkhampton, England, ×32 (Hinde, 1884b); c, characteristic spicules including tetraclones and dermal phyllodichotriaenes, Saint-Cyr, France, magnification not stated but about ×25 (Moret, 1926b; courtesy of Société Géologique de France).

#### Subfamily UNCERTAIN

Genera whose only known spicules are tuberculate desmas of theonellid type, unless oxeas are also present.

Pachycorynea Počta, 1907, p. 171 [\**P. erecta*; OD]. Cylindrical initially with ovoid, terminal swelling and lateral, paragastral opening; shallow furrows around this opening but no other canalar features; desmas large, regular tetraclones with spined to tuberculate arms; supplemental oxeas at surface; no other spicules known. [One specimen known.] Cretaceous (Santonian): France.—FiG. 155,3a–b. \*P. *erecta*, Nice; characteristic spicules include various tetraclones, magnification not stated (Moret, 1926b; courtesy of Société Géologique de France).

- Rhopalospongia HINDE, 1884a, p. 89 [\*Polypothecia gregaria BENETT, 1831, p. 9; SD DE LAUBENFELS, 1955, p. 57]. Elongate, club-shaped, stalked sponges, growing singly, in groups united side by side, or with two or more individuals on one stalk; root processes at base; no paragastral cavity; external surface smooth or with small, pustular elevations, and with ostia of skeletal canals (possible epirhyses) that curve downwardly toward axis of body; no apparent aporhyses if these canals are regarded as epirhyses; stalk sometimes with vertical furrows; desmas strongly tuberculate and regular tetraclones in interior, but more or less irregular at surface; no other spicules known. Cretaceous (Albian): England.—FIG. 155, 1a-b. \*R. gregaria (BENETT), Upper Greensand, Warminster; a, group of individuals, ×0.5; b, spicular meshwork of tubercular desmas of interior, ×50 (Hinde, 1884a).
- Verrucodesma REID, nom. nov. herein (LAGNEAU-HÉRENGER, 1962, p. 141, nom. nud.) [\* V. subconica LAGNEAU-HÉRENGER, 1962, p. 141; OD]. Cylindroconical or cylindrical with tubular, paragastral cavity; outside of skeletal framework with numerous small ostia; fine furrows around paragastral opening; no other canalar features; desmas smooth and tuberculate tetraclones in which arms may be tuberculate and unbranched, or smooth and branched more or less strongly; no other spicules known. Cretaceous (Aptian): Spain. -FIG. 155,2a-b. \*V. subconica, Can Casanyas Castellet, Catalogne; a, side view of conicocylindrical sponge with osculum at top and minor canals around its margin, with numerous inhalant ostia in dermal surface, ×1; b, tuberculate tetraclones from main skeleton, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Zitteleus DE LAUBENFELS, 1955, p. 56, nom. nov. pro Spongodiscus ZITTEL, 1878a, p. 153, non EHREN-BURG, 1854 [\* Turonia radiata COURTILLER, 1861, p. 142; OD]. Discoidal, lenticular, or hemispherical; one surface, presumed to be upper, with radial ridges and furrows; other side, presumed lower, ribbed radially nodular, or concentrically corrugated, and sometimes with a few central outgrowths that appear to be root processes; no skeletal pores or canals; main part of skeletal framework formed from regular, tuberculate tetraclones with weakly developed zygomes, but supposed lower surface with skeletal cortex in which desmas are irregular and more or less elongate; large supplemental strongyles sometimes present; no other spicules known. Cretaceous (Santonian): France .---–Fig. 155,4a-b. \*Z. radiata (COURTILLER); a, view of discoidal form from above with radial ridges or furrows, approximately ×1; b, vertical section showing distribution of canals in interior, ×1 (Courtiller, 1861).

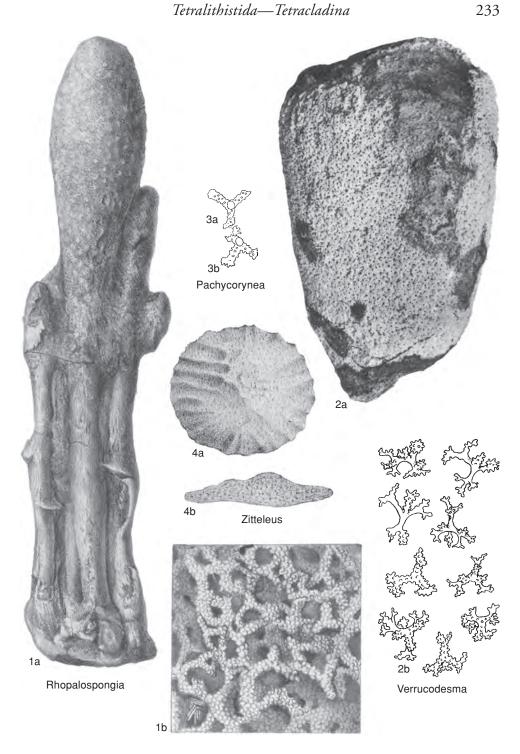


FIG. 155. Theonellidae (p. 232).

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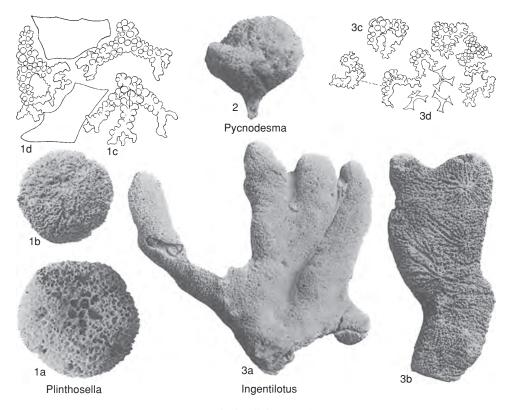


FIG. 156. Plinthosellidae (p. 234-235).

#### Family PLINTHOSELLIDAE Schrammen, 1910

[nom. transl. et correct. SCHRAMMEN, 1924a, p. 38, ex Plinthosellinae SCHRAMMEN, 1910, p. 34]

Sponges with strongly tuberculate desmas that are typically triders, to which variants with only two arms may be added, and with phyllotriaenes, discotriaenes, or irregular siliceous plates as dermalia; four-armed tetraclones absent; axial systems of desmas sometimes tetraxial, sometimes triodal or diaxial; supplemental rhizoclonids sometimes present; microscleres unknown. [The family is here used sensu SCHRAMMEN, 1910 (not sensu SCHRAMMEN, 1924a) because passage from phyllotriaenes like those of Ingentilotus DE LAUBENFELS (=Dactylotus SCHRAMMEN, 1910, non SCHOENHERR, 1844) to irregular plates like those of *Plinthosella* ZITTEL occurs in *Plinthosellopsis*. The family is probably from the same stock as the Theonellidae but distinguished by desmas being triders or two-armed variants, perhaps representing descendants of Jurassic *Sontheimia* KOLB (see family Protetraclisidae), in which desmas are triders.] *Lower Cretaceous (Albian)–Upper Cretaceous.* 

Plinthosella ZITTEL, 1878a, p. 153 [\*P. squamosa; OD]. Typically small, globular, with basal stalk or none; top rounded, flattened, or with shallow depression or distinct, cuplike, paragastral cavity; lateral surfaces of skeletal framework with small ostia, irregular furrows, or both or neither; top or central cavity with group of postica, from which aporhyses run downwardly; desmas large, tuberculate triders and two-armed variants, with distinct, short brachyome or none, that sometimes have adventitious zygomes on outwardly facing sides; triders tetraxial or triodal, with axis corresponding with brachyome that may be rudimentary or absent; two-armed forms correspondingly triodal or diaxial; dermalia scalelike, anaxial plates of irregularly variable shapes; some examples with small rhizoclonids that form supplemental cortex in lower parts; microscleres unknown. Cretaceous (Albian-Maastrichtian): England; France, CenomanianCampanian; Czech Republic, Slovakia, Turonian; Germany, Poland, Campanian.—FIG. 156, 1a-d. \*P. squamosa, Quadratenkreide, Campanian, Oberg, Germany; a, spheroidal sponge seen from above showing postica, ×2; b, view of same specimen from below showing inhalant ostia and limited surficial grooves, ×1; c-d, characteristic spicules including trider and two-armed variants and dermal plates, ×20 (Schrammen, 1910).

- Ingentilotus DE LAUBENFELS, 1955, p. 57, nom. nov. pro Dactylotus SCHRAMMEN, 1910, p. 115, non SCHOENHERR, 1884 [\*Dactylotus micropelta SCHRAMMEN, 1910, p. 115; OD]. Flattened branching to handlike or leaflike growths; both surfaces with small, skeletal pores, one side (supposedly gastral) may be furrowed with locally radiating arrangement; no distinct internal canals; desmas mainly tuberculate triders with brachyome strongly tuberculate, centrumlike swelling, but including two-armed variants in some examples; triders usually tetraxial but two-armed forms triodal; rhizoclonids and microscleres unknown. Upper Cretaceous: Europe.—FIG. 156,3a-d. \*I. micropelta (SCHRAMMEN), Mucronatenkreide, Campanian, Misburg, Germany; a, handlike example, from presumed dermal side,  $\times 1$ ; *b*, branch fragment, from furrowed (possibly gastral) side, ×2; c-d, characteristic desmas including triders and two-armed variants and young desmas, ×20 (Schrammen, 1910).
- Pycnodesma SCHRAMMEN, 1910, p. 115 [\*P. globosa; OD]. Small, globular or nodular, with or without rootlike stalk; no paragastral depression; exterior with small ostia a little larger than normal skeletal meshes and a few irregular furrows; no distinct postica; desmas small, tuberculate triders; meshwork, hence, denser in appearance than Plinthosella species; no other spicules known. [This genus is included here on the basis of the form of the desmas; it is similar to Plinthosella ZITTEL, but the genus lacks the central group of aporhyses that the denser meshwork should have outlined if corresponding canals were present.] Cretaceous (Santonian-Campanian): France, Santonian; Germany, Campanian.-FIG. 156,2. \*P. globosa, Quadratenkreide, Oberg; side view of small, globular, stalked sponge, ×1 (Schrammen, 1910).

#### Family CHENENDOPORIDAE F. A. Roemer, 1864

[nom. correct. SCHRAMMEN, 1924a, p. 38, pro Chenendoporinae SCHRAMMEN, 1910, p. 34, nom. transl. ex Chenendoporidea F. A. ROEMER, 1864, p. 2]

Sponges with small, smooth-armed or tuberculate tetraclones that grade into rhizoclone-like variants toward skeletal surfaces; no other spicules known (dermalia possible dichotriaenes). [The name was described as new by SCHRAMMEN (1910) and ascribed to him by other authors, but in fact it was proposed first by ROEMER (1864). The type genus, *Chenendopora* LAMOUROUX, was placed in the Rhizomorina by ZITTEL (1878a), but the tetraxial character of the desmas was detected by SCHRAMMEN (1910). Dermalia are unknown in material from England, France, Germany, Czech Republic, and Slovakia but were said to be dichotriaenes in REZVOI, ZHURAVLEVA, and KOLTUN (1962, p. 55). The family is listed here because *Chenendopora* must be placed into ROEMER's family, but relationship to other Tetracladina is uncertain.] *Cretaceous (Aptian–Maastrichtian), Paleogene (?Eocene).* 

- Chenendopora LAMOUROUX, 1821, p. 77 [\*C. fungiformis; OD] [=Bicupula COURTILLER, 1861, pl. 35-37 (type, B. gratiosa COURTILLER, 1861, pl. 35,1, SD DE LAUBENFELS, 1955, p. 104); ?Dimorphina REID, nom. nov. herein, p. 235 (type, Dimorpha cornuta COURTILLER, 1861, p. 124, OD); ?Tragalimus POMEL, 1872, p. 202 (type, Dimorpha balanus Courtiller, 1861, p. 123, SD DE LAUBENFELS, 1955, p. 49)]. Sometimes earlike or cuplike but typically funnel shaped, more or less long stalked, with simple, basal expansion or rootlike processes; wall thick; margin rounded or abruptly truncated; exterior sometimes with small ostia and short, irregular furrows, but usually with these features obliterated by skeletal accretion; surface then smooth or irregularly corrugated; no epirhyses; inner surface with postica of more or less sinuous aporhyses that enter wall obliquely downward, with inclination of these canals increasing toward stalk, and lowermost ones continuing down it; margin often with furrows that represent incompletely enclosed aporhyses; desmas tetraclones in interior, but grade outwardly into flattened and rhizoclone-like variants that form secondary, cortical meshwork of exterior; stalk sometimes furrowed longitudinally and with more or less elongate desmas; supplemental strongyles sometimes present; no dermalia or microscleres known. [Dichotriaenes are reported as dermalia according to REZVOI, ZHURAVLEVA, and KOLTUN, 1962, but these spicules are not known from other material.] Lower Cretaceous (Albian)-Upper Cretaceous: England, Spain, Albian; Czech Republic, Slovakia, Cenomanian; France, Cenomanian, Campanian; Germany, Campanian; Russia, Upper Cretaceous.-FIG. 157,1a. \*C. fungiformis, Mucronatenkreide, Campanian, Misburg, Germany; characteristic tetraclones, ×20 (Schrammen, 1910).--Fig. 157,1b. C. gratiosa COURTILLER, Senonian, Touraine, France; longitudinally sectioned example showing internal surface, shallow spongocoel, and aporhyses, ×0.5 (Moret, 1926b; courtesy of Société Géologique de France).
- ?Dimorphina REID, herein, nom. nov. pro Dimorpha COURTILLER, 1861, p. 123, non JURINE, 1807, nec HUEBNER, 1822, nec GRAY, 1840, nec HODGSON,

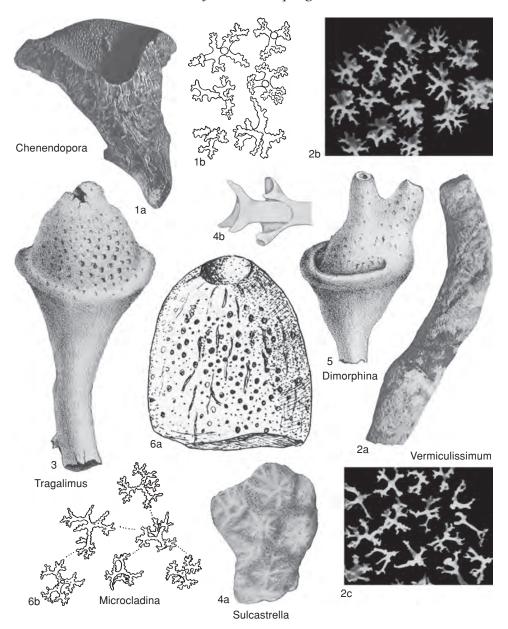


FIG. 157. Chenendoporidae and Uncertain (p. 235-237).

1841 [\*Dimorpha cornuta COURTILLER, 1861, p. 124; OD]. Character uncertain, but possibly based on gerontic *Chenendopora* in which secondary growths have arisen from paragastral surface; skeletal structure unknown. *Cretaceous (Coniacian-Maastrichtian):* France.——FIG. 157,5. \*D. cornuta

(COURTILLER); side view of obconical form with secondary branched growth in upper part,  $\times 0.5$  (Courtiller, 1861).

Microcladina LAGNEAU-HÉRENGER, 1962, p. 146 [\*M. aptiensis; OD]. Cylindrical with rounded summit, sometimes growing in groups, and with deep, narrow, paragastral cavity that extends to base; exterior with pores of two sizes, larger are ostia of radial epirhyses, and with irregular, longitudinal furrows that radiate from paragastral margin; aporhyses longitudinal, some beginning as furrows around paragastral margin or opening into other furrows; character of paragastral surface not stated; desmas small, regular tetraclones with granular ornament in interior, becoming small and passing into rhizoclonelike bodies toward outside; no other spicules known. [Placed in Discodermiidae (=Theonellidae) by LAGNEAU-HÉRENGER (1962) but here thought probably similar to Chenendopora.] Cretaceous (Aptian): Spain.—FIG. 157,6a-b. \*M. aptiensis, Mas de Artis, Catalogne; a, side view of terminal part of sponge with many inhalant ostia and minor, surficial grooves, ×1; b, small, regular tetraclones with fine granulations, ×25 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

?Tragalimus POMEL, 1872, p. 202 [\*Dimorpha balanus COURTILLER, 1861, p. 123; SD DE LAUBENFELS, 1955, p. 49]. Character uncertain but possibly a gerontic Chenendopora with a hollow, ovate, secondary growth arising from paragastral surface; skeletal characters unknown. Cretaceous (Coniacian-Maastrichtian), Paleogene (?Eocene): France, Coniacian-Maastrichtian; Western Australia, ?Eocene.—FIG. 157,3. \*T. balanus (COUR-TILLER), Senonian, France; side view of obconical sponge with hollow, secondary mound and osculum above, ×0.5 (Courtiller, 1861).

#### Family UNCERTAIN

- Sulcastrella SCHMIDT, 1879, p. 27 [\*S. clausa; OD]. Has the outward appearance of Astrobolia ZITTEL, but its stellate grooves lead into large oscula. Cretaceous-Holocene: Europe, Gulf of Mexico.— FIG. 157,4a-b. \*S. clausa, Holocene, Gulf of Mexico; a, side view of small sponge with stellate grooves and fine pores, ×1; b, tips of isolated spicules showing three-rayed tips to coarse axes, magnification unknown (Schmidt, 1879).
- Vermiculissimum DE LAUBENFELS, 1955, p. 59, nom. nov. pro Stelidium SCHRAMMEN, 1924a, p. 55, non ROBERTSON, 1903 [\*Stelidium vermiculare SCHRAM-MEN, 1924a, p. 55; OD]. Small finger- to wormlike, with very small pores; upper end more or less covered with dermal layer with short-rayed and branched phyllotriaenes; principal skeleton fine meshed and composed of small tetraclones. Cretaceous (Cenomanian): Germany.——FIG. 157,2a-c. \*V. vermiculare (SCHRAMMEN), Mukronatenkreide, Misburg: a, side view of cylindrical sponge with small pores, ×1; b, photomicrograph of dermal phyllotriaenes; c, tetraclones of interior skeleton, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

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## MESOZOIC AND CENOZOIC LITHISTID SPONGES: DICRANOCLADINA, PSEUDORHIZOMORINA, DIDYMMORINA, HELOMORINA, MEGAMORINA, MEGARHIZOMORINA, SPHAEROCLADINA, AND ORDER AND SUBORDER UNCERTAIN

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## Suborder DICRANOCLADINA Schrammen, 1924

[nom. transl. Reid, 1963d, p. 199, ex tribus Dicranocladina Schrammen, 1924a, p. 39]

Desmas monaxial, when axial system is known, and typically strongly tuberculate; most genera with desmas of dipodal to polypodal shapes, which may be dicranoclones s.s., with an erect, crepidal axis in a brachyome-like prominence (the basaltheil of SCHRAMMEN, 1910), or similarly shaped forms with axis in line with two of the arms, or no known axial system; other desmas of irregular shapes, with this type sometimes predominant or only type present; zygomes twiglike, rootlike, or clawlike and typically applied to arms, tubercles, or central parts of other desmas; dermalia dichotriaenes, modified dichotriaenes with spines or zygomelike cladi or monaxial, discotriaenelike spicules; supplemental oxeas sometimes present; some with large, rhizoclone-like spicules (megarhizoclonids), small rhizoclonids, or both as supplemental desmas, with either sometimes forming a supplemental, skeletal cortex; microscleres of modern examples amphiasters or spirasters and latter may be varied as metasters or plesiasters. Upper Jurassic (upper Oxfordian)–Holocene.

The designation tribus used by SCHRAM-MEN (1924a) for his Dicranocladina was directly equivalent to suborder, since the taxon formed a primary division of the order Tetraxonia VOSMAER (ascribed to SCHULZE by SCHRAMMEN).

The Dicranocladina have been treated formerly as characterized by the occurrence of dicranoclones, but this is misleading. Dicranoclones s.s. (i.e., as described by SCHRAMMEN, 1910, p. 65), with the crepidal axis in a basaltheil are in fact known from only one species of Schrammeniella BREISTROFFER (= Phalangium SCHRAMMEN, non LINNÉ; = Iouea DE LAUBENFELS), although probably also present in Procorallistes SCHRAMMEN, whose characteristic desmas have an elongate, basaltheil-like structure. In modern Corallistidae (=Coscinospongiidae VON LENDENFELD, 1903, of SCHRAMMEN, 1910, p. 28), however, desmas have arms or less regular outgrowths at both ends of an epirhabd (the part enclosing the crepidal axis). Other arms grow out from sides of the epirhabd in three- or four-armed examples. In most fossils, however, the position of the axis is unknown. SCHRAMMEN (1924a) and others have assumed that the desmas are dicranoclones s.s. if a centrumlike feature or a large, central tubercle is present. Some of these desmas, however, pass gradually into more or less irregular forms (in e.g., Leiocarenus SCHRAMMEN) like those prevalent in the living Corallistes SCHMIDT or are all irregular types (in Leiohyphe SCHRAMMEN). Further, modern examples show that a large, central tubercle need not represent a basaltheil. Some fossil desmas with a centrum may grade into variants showing arms at both ends of a distinct, central shaft (in e.g., Pycnoclonella Lagneau-Hérenger). Hence this suborder is not defined here in terms of dicranoclones. The two types of desmas comprising dicranoclones s.l. are accepted as homologous, however, because forms bearing arms at both ends of an epirhabd are also present in Schrammeniella, in addition to dicranoclones s.s.

Scope of the taxon is also modified by exclusion of the family Macandrewiidae GRAY, which was included by SCHRAMMEN (1924a). Some of the genera have desmas that are tuberculate on zygomes but central parts that are typically smooth. Desmas of the type genus Macandrewia GRAY are smooth rhizoclones. Macandrewia also has (a) an anthaspidellid-like structure, not matched in any typical Dicranocladina, and (b) some additional tetraxial desmas that intergrade with the main ones. No tripodal or similar desmas are known. Although desmas in these sponges are comparable with supplemental megarhizoclonids of the Dicranocladina, their homology seems doubtful. This family is therefore removed to a separate suborder, using SCHRAMMEN's old name Pseudorhizomorina (SCHRAMMEN, 1901).

The Dicranocladina appear cryptogenically in the Upper Jurassic, represented by genera (Kyphonella KOLB, Leiocarenus SCHRAMMEN, *Dicranoclonella* SCHRAMMEN) that already had strongly tuberculate desmas. Some of the desmas have dicranoclone (i.e., dipodal to polypodal) shapes; but none has a typical basaltheil; and others are of more or less irregular shapes as in the living Corallistidae. Some Lower Cretaceous forms (e.g., Pycnoclonella LAGNEAU-HÉRENGER) have desmas with a prominent, swollen, central tubercle; but examples with a typical basaltheil or a comparable armlike outgrowth are known only from the Upper Cretaceous. This suggests that dicranoclones s.s. are a secondary development, produced from desmas like those of the Jurassic and modern forms by restriction of arms to one end of the epirhabd.

No dicranoclones *s.s.* are known from modern forms. Desmas of *Corallistes* SCHMIDT may be weakly tuberculate with more or less transition into rhizoclones, but those of *Paracorallistes nolitangere* (SCHMIDT) are as stout as in any of the fossils and may be accompanied by typical megarhizoclonids. In various fossils, megarhizoclonids intergrade with the principal desmas, and they seem to be essentially late-formed variants. In *Pseudoverruculina* MORET, there is more or less continuous transition from typical desmas through smaller variants (megarhizoclonids) to small rhizoclonids that form a cortex.

The tuberculate desmas of Dicranocladina are strikingly similar to those of Plinthosellidae and many Theonellidae of the Tetracladina. Dipodal to polypodal forms, especially, are similar to tetracladine triders from these families and two-armed (or dipodal) variants seen in Plinthosellidae. While these resemblances could be simply convergent, they may also mark iterative developments in forms that have shared a common origin. First, some kind of relationship is suggested by occurrence of streptosclere-like microscleres in both Corallistes species and the theonellid Racodiscula ZITTEL. Second, tubercles and zygomelike spines are interchangeable in corallistids and some modern theonellids. Third, tetraclones of the theonellid Discodermia DU BOCAGE are sometimes partly replaced by triodal or diaxial variants, and some of the desmas are triders in the fossil Pseudojerea MORET. Plinthosellid desmas are typically triders, and those of Plinthosella ZITTEL are in part two-armed variants that are triodal. These forms and the Dicranocladina could then represent three stocks of common origin. The three shared (a) a trend to production of tuberculate desmas, and (b) a trend to reduction of the crepis from tetraxial to triodal, diaxial, or monaxial. The crepis (i) remained incipient only in the typical Theonellidae, and (ii) proceeded to a stage in which desmas became typically triders, to which triodal, twoarmed variants may be added in the family Plinthosellidae, first known from the Aptian. Evolution (c) proceeded rapidly to completion in a third stock that became the Dicranocladina before their Upper Jurassic first appearance.

If this is correct, the original root stock may be the family Protetraclisidae SCHRAMMEN of the Tetracladina, although recorded examples of this family are contemporaries of early Dicranocladina. Protetraclisidae have branching tetraclones that grade into rhizoclone-like variants; and *Rhizotetraclis* KOLB also has some desmas that resemble a four-armed dicranoclone. Sontheimia KOLB of this family has desmas developed as triders, although tetraclones occur also, and has thickening of both zygomes and spines on the arms into incipient tubercles. While this is not conclusive evidence, the occurrence of forms that have features that might be expected in a rootstock (passage of tetraclones into triders and rhizoclone-like spicules; thickening of lateral spines into incipient tubercles) at nearly the right period may not be coincidence.

FINKS (1971b) has suggested derivation of the Dicranocladina from the Paleozoic family Hindiidae RAUFF (suborder Tricranocladina REID, =Eutaxicladina RAUFF *sensu* SCHRAMMEN). The Hindiidae are forms with desmas of triderlike shapes in which the axial system is unknown, but the desmas are markedly tuberculate in the two latest genera (*Scheiia* TSCHERNYCHEV & STEPANOV; *Scheiella* FINKS). Such a derivation is also possible but is open to a number of objections.

(1) No triaenes are known from hindiids, although ectosomal microrhabds are sometimes preserved at the surfaces.

(2) The desmas of the oldest forms (*Hindia* DUNCAN) are constantly tetraxial in shape and were regarded as tetraxons by SCHRAMMEN (1937, p. 77). If this is correct and dicranocladine triaenes are claimed to be derived from monaxons, desmas and dermalia must be pictured as evolving in opposite directions.

(3) If Dicranocladina were hindiid derivatives, one would expect the most constantly tripodal desmas in the oldest forms. In practice, the desmas of Jurassic forms are irregularly variable, and the form in which desmas are most constantly tripodal is Santonian (*Gignouxia* MORET).

(4) No dicranocladine sponge approaches the special radiate structure of hindiids. The oldest Dicranocladina have more or less irregular structures, and the greatest regularity is again seen in *Gignouxia*. In addition, the diagram of its structure shown by DE LAUBENFELS (1955, fig. 46,5), is diagrammatic, not factual, and has a structure more like that of hindiids than exists in his material.

(5) Zygomes of hindiid desmas are typically simple terminal expansions, with a single distal facet; but those of dicranocladine desmas are like the zygomes of tetraclones, unless more or less aborted.

(6) Megarhizoclonids of Dicranocladina sometimes clearly intergrade with the principal desmas, with which they are presumably homologous. Supplemental desmas of *Scheiella* do not have this relationship and may be derived from small, supplemental oxeas that sometimes have irregular outgrowths. On these grounds, resemblances between Dicranocladina and Hindiidae are here thought to be convergent, although neither view can currently be verified.

Absence of an obvious axial canal in most fossil dicranocladine desmas is presumed herein to be due to its loss during fossilization. This is not surely always correct; but the crepis is typically minute in the modern Corallistidae where it is sometimes destroyed by internal solution and replacement that reduced central parts of the desmas to a granular marrow.

#### Family CORALLISTIDAE Sollas, 1888

[Corallistidae SOLLAS, 1888, p. cliv] [=Coscinospongiidae von LENDENFELD, 1903, p. 135; Pachinionidae SCHRAMMEN, 1924a, p. 39; Gignouxiidae DE LAUBENFELS, 1955, p. 61; Phrisosopongiidae LAGNEAU-HERENGER, 1962, p. 168]

Desmas more or less strongly tuberculate and of dipodal to polypodal, irregular, or intermediate shapes, that may occur in various combinations and with any type predominant; dicranoclones *s.s.* in one species; tubercles buttonlike or capstanlike, not in regular, transverse rows, and sometimes more or less replaced by conical or branching spinules; dermalia simple dichotriaenes or variants with spinose or polycladose cladi; large, rhizoclone-like desmas (megarhizoclonids) sometimes accompany tuberculate forms; some with small rhizoclonids that may form a supplemental cortex at surface of skeletal framework; microscleres of modern forms include plesiasters, metasters, spirasters, or amphiasters, and sometimes additional microrhabds. [Desmas of this family are not described generally as dicranoclones: (a) dicranoclones in the strict sense of SCHRAMMEN (1910, p. 65), in which arms are produced from one end of an epirhabd (basaltheil of SCHRAMMEN), are known only from one species, Schrammeniella scytaliforme (SCHRAMMEN); (b) outwardly comparable desmas of the living Corallistes SCHMIDT, for example, have arms arising from both ends of the epirhabd and sometimes also from its sides; (c) most fossil examples have no axial system and could be of either type; (d) transition from tripodal or tetrapodal desmas, for example, into forms with arms arising from the ends of a short, central shaft (e.g., in Pycnoclonella Lagneau-Hérenger), or into more or less irregular spicules like some Corallistes desmas (in e.g., Dicranoclonella SCHRAMMEN), suggests that desmas of such genera are not dicranoclones s.s.] Upper Jurassic (upper Oxfordian)-Holocene.

#### Subfamily CORALLISTINAE Sollas, 1888

[nom. transl. REID, herein, ex Corallistidae SOLLAS, 1888, p. cliv]

Desmas mainly or all of more or less irregular shapes, although dipodal to polypodal desmas may also be present, and sometimes grading into rhizoclone-like variants in which spines replace tubercles; dicranoclones *s.s.* unknown; plesiasters, metasters, spirasters, amphiasters, or microrhabds in modern examples. [Includes recent Corallistidae and similar fossils.] *Upper Jurassic (upper Oxfordian)–Holocene.* 

**Corallistes** SCHMIDT, 1870, p. 22 [\**C. typus;* OD] [=*Zosterospongia* DE LAUBENFELS, 1953b, p. 109 (type, *Z. thaumasta*, OD)]. Funnel to bowl-like or flabellate, then sometimes irregularly convolute or forming a secondary funnel with exhalant side external; inhalant side of skeletal framework with small ostia or open, skeletal meshes only; exhalant side with larger postica, which sometimes have slightly raised margins; epirhyses and aporhyses vague to distinct, simple or branching; desmas mainly irregular in shape, often weakly tuberculate, but usually including some dipodal and polypodal variants; usually no distinct megarhizoclonids; small, ectosomal rhizoclonids absent; dermalia simple dichotriaenes; microscleres plesiasters, metasters, spirasters, or amphiasters. [Supposed Upper Cretaceous (SOLLAS, 1880c) and Eocene (HINDE & HOLMES, 1892) records are based on isolated dermalia with no diagnostic value, although similar to those of some modern species.] ?Upper Cretaceous; Paleogene (Eocene)-Holocene: England, ?Upper Cretaceous; Australia, New Zealand, Eocene; cosmopolitan, Holocene.——FIG. 158,4. C. sp., Eocene, Otago, New Zealand; dichotriaene ascribed to Corallistes, ×200 (Hinde & Holmes, 1892).

- Dicranoclonella REID, nom. nov. herein (SCHRAMMEN, 1937, p. 79, nom. nud.) [\*D. praecursor SCHRAMMEN, 1937, p. 79; OD]. Irregularly funnellike or flabellate; both surfaces of skeletal framework with small, skeletal pores (ostia, postica), from which branching canals (epirhyses, aporhyses) run inwardly; desmas mainly of irregular shapes; dermalia dichotriaenes; small, flattened rhizoclonids may form supplemental cortex; microscleres unknown. [DE LAUBENFELS (1955, p. 62) subsequently designated the type species for Dicranoclonella, but according to Code Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xxiii, herein).] Jurassic (upper Oxfordian-Kimmeridgian): Germany.-FIG. 158, 1a. \*D. praecursor, Weiss Jura, upper Oxfordian, Streitburg; dicranoclone desmas, ×20 (Schrammen, 1937).—FIG. 158,1b. D. schmidti SCHRAMMEN, Weiss Jura, Kimmeridgian, Gerstetten; rhizoclonids from supplemental cortex, ×20 (Schrammen, 1937).
- Heterophymia POMEL, 1872, p. 143 [\*Dactylocalyx heteroformis BOWERBANK, 1869, p. 86, ="Conscinospongia heteroformis" VALENCIENNES ms, nom. nud., =Heterophymia valenciennesii POMEL, 1872, p. 144; OD] [= Coscinospongia von Lendenfeld, 1903, p. 135, obj.]. Similar to Corallistes SCHMIDT in forms with distinct margins to postica, but with dermal dichotriaenes restricted to inhalant surface; exhalant surface with supplemental cortex formed from flattened rhizoclonids. [Cretaceous to Holocene record in DE LAUBENFELS, 1955, p. 62, as Coscinospongia BOWERBANK refers possibly to SCHRAMMEN's record of Coscinospongia (Campanian, Germany), based on dermalia of Paracorallistes type.] Holocene: China.-FIG. 158,5a-b. \*H. heteroformis (BOWERBANK), Shanghai; a, irregular spicule structure of dermal membrane, magnification uncertain; b, oval, inhalant pore with projecting spicule tips from dermal layer, apparently for defense against incursions of other animals, magnification uncertain (Bowerbank, 1869).
- Kyphoclonella KOLB, 1910 in 1910–1911, p. 212 [\*K. multiformis; OD]. Cylindrical or top shaped, sometimes laterally compressed, with deep, narrow, paragastral cavity; outside with numerous very small ostia from which fine epirhyses run inwardly; paragastral side with larger postica of tubular

dicranoclones: trict sense of which arms are f an epirhabd re known only lated dermalia wid similar to those of *Cretaceous, Paleoge ?Upper Cretaceous;* cosmopolitan, *Ho* Eocene, Otago, Ner to *Corallistes*, ×200 Dicranoclonella REID, 1937, p. 79, m

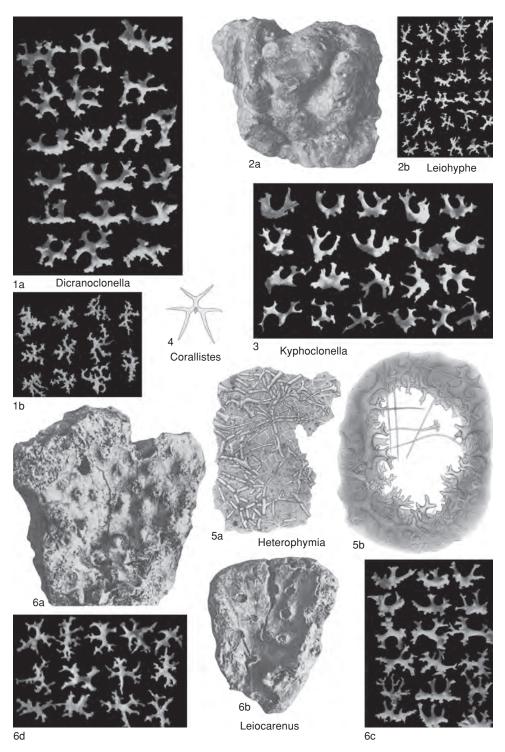


FIG. 158. Corallistidae (p. 242–244).

aporhyses that curve downwardly through wall; desmas partly irregular, partly dipodal to polypodal; dermal triaenes unknown; cortical covering of rhizoclone-like spicules in lower parts of some examples; microscleres unknown. *Jurassic (Kimmeridgian):* Germany.——FIG. 158,3. \**K. multiformis,* Weiss Jura, Sontheim; dicranoclone desmas, ×20 (Schrammen, 1937).

- Leiocarenus REID, nom. nov. herein (SCHRAMMEN, 1937, p. 78, nom. nud.) [\*L. papillosus SCHRAMMEN, 1937, p. 78; OD]. Irregularly funnel-like or flabellate; external (inhalant) surface of skeletal framework with very small ostia; paragastral surface with groups of postica in shallow depressions with distinct margins, or at tops of small papillae; desmas mainly irregular, some tuberculate but others developed as smooth rhizoclones; supplemental cortex formed from flattened rhizoclonids on paragastral surface; dermalia dichotriaenes; microscleres unknown. [Very similar to existing Heterophymia POMEL (1872, p. 143), possibly identical. De LAUBENFELS (1955, p. 62) subsequently designated the type species for Leiocarenus, but according to Code Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xxiii, herein).] Jurassic (Kimmeridgian): Germany.—FIG. 158,6a-d. \*L. papillosus, Weiss Jura, Sirchingen; ab, two specimens have papillae and smooth cortex of paragastral surface,  $\times 1$ ; *c*, tuberculate desmas; *d*, rhizoclones, ×20 (Schrammen, 1937).
- Leiohyphe SCHRAMMEN, 1924a, p. 67 [\*L. solitaria; M]. Incompletely known; nodular mass with lower parts covered by dense, skeletal cortex; upper parts bare with numerous round, osculelike apertures; desmas irregular, strongly branched in cortical meshwork; supplemental oxeas; no other spicules known. *Cretaceous (Campanian):* Germany.— FIG. 158,2a-b. \*L. solitaria, Emscher, Sudmerberges; a, side view of nodular holotype, ×0.50; b, desmas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

#### Subfamily GIGNOUXIINAE de Laubenfels, 1955

[nom. transl. REID, herein, ex Gignouxiidae DE LAUBENFELS, 1955, p. 61]

Desmas mainly tripodal to polypodal, although dipodal or irregular forms may occur also and include sometimes true dicranoclones *s.s.* or desmas of similar shape; megarhizoclonids usually more or less distinct from typical desmas; small rhizoclonids sometimes also present; microscleres unknown. *Cretaceous (Aptian)–Neogene (Miocene).* 

Gignouxia MORET, 1926b, p. 107 [\*G. niciensis; SD DE LAUBENFELS, 1955, p. 61]. Cup or funnel-like and marginally lobate to flabellate or leaflike; sides sometimes with irregular outgrowths, with osculelike pore at top; exterior of skeletal framework with narrow furrows that contain ostia of epirhyses that run obliquely downward; paragastral side with larger postica having more or less prominent margins, or groups of postica from which shallow furrows radiate; desmas dipodal to polypodal with up to six arms but commonly three; arms of surficial desmas directed inwardly and applied to centra of desmas underlying them; cortical layer of megarhizoclonids; dermalia dichotriaenes with laterally spinulated cladi; microscleres unknown. Cretaceous (Santonian-Campanian): France.---FIG. 159, 3a-d. \*G. niciensis, Campanian, Nice, characteristic spicules; a, desmas with two, three, and four arms; b, dicranoclones; c, dermal dichotriaene; d, megarhizoclonid; magnification not stated, but about ×50 (Moret, 1926b; courtesy of Société Géologique de France).

- Gelasinophorus SCHRAMMEN, 1924a, p. 66 [\*G. reitemeyeri; M]. Incompletely known; flabellate to earlike or platelike; surfaces of skeletal framework with small pores, or covered by cortical layer of unknown character (composed of possible rhizoclonids); desmas small; dermalia and microscleres unknown. Cretaceous (Coniacian): Germany.— FIG. 159,2. \*G. reitemeyeri, Emscher, Sudmerberges; dicranoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Gilletia LAGNEAU-HÉRENGER, 1962, p. 170 [\*G. catalaunica; OD]. Form not surely known, but apparently flabellate; one surface of skeletal framework with large pores with raised margins, resembling postica of various other genera; desmas stout, tripodal, or tetrapodal, with short arms, very strong, buttonlike tubercles on central part with one in polar position; megarhizoclonids also present; other spicules unknown. Cretaceous (Aptian): Spain.——FIG. 159,4a-c. \*G. catalaunica, Can Casanyas Castellet, Catalogne, characteristic spicules; a, isolated desmas; b, megarhizoclonids; c, fragment of skeletal meshwork showing their relationships, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Phrissospongia MORET, 1926b, p. 112 [\*P. glandiformis; OD]. Solitary, elongate ovoid with deep, narrow, paragastral cavity, or compound with more than one such sponge arising from common base; exterior of skeletal framework with small ostia; no epirhyses or exhalant features (aporhyses, postica) known; desmas tripodal to polypodal in interior, grading into megarhizoclonids that form cortical layer; dermalia dichotriaenes in which cladi bear sharp, outwardly pointing spines; microscleres unknown. Cretaceous (Santonian): France.-FIG. 160, 3a-e. \*P. glandiformis, Saint-Cyr; a-b, small, unbranched, normal and twinned individuals, slightly reduced; c-e, characteristic spicules including c, desmas, d, dermal dichotriaenes showing spines, and e, megarhizoclonids, magnification not stated, but approximately ×50 (Moret, 1926b; courtesy of Société Géologique de France).

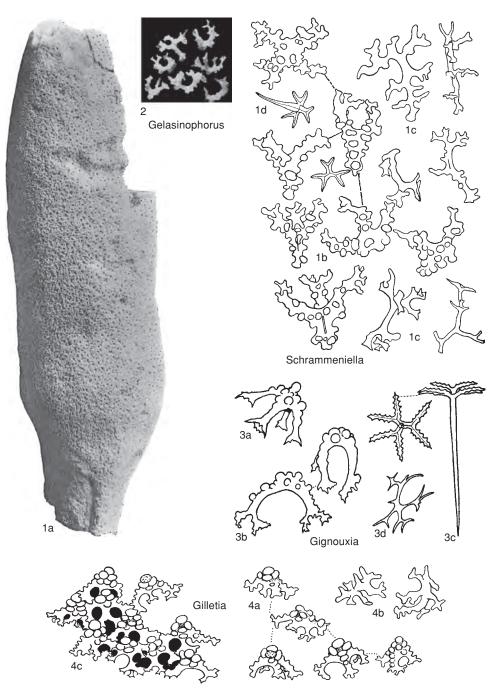


FIG. 159. Corallistidae (p. 244-247).

Procorallistes SCHRAMMEN, 1901, p. 14 [\*P. polymorphus; SD DE LAUBENFELS, 1955, p. 45]. Irregularly funnel-like or flabellate, stalked or not; both sides of skeletal framework with small, skeletal pores (ostia or postica), from which short, radial canals (epirhyses, aporhyses) run inwardly; many desmas dipodal or tripodal and typically with conical or armlike, central outgrowth that bears no

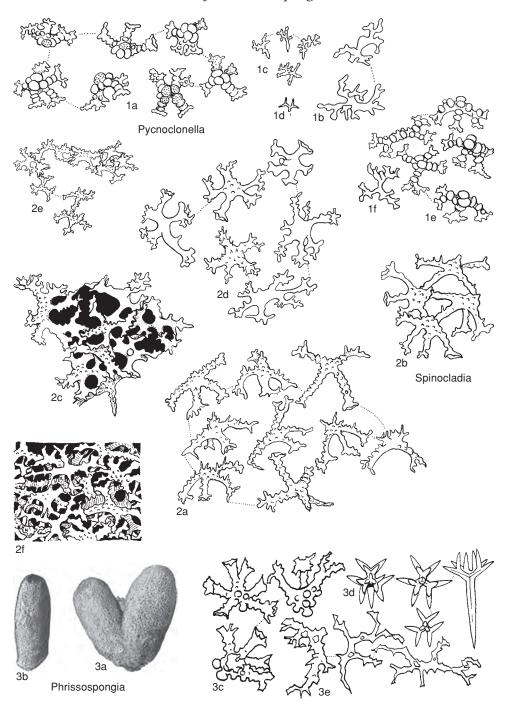


FIG. 160. Corallistidae (p. 244-248).

zygome but may be longer than zygome-bearing arms; these desmas probably dicranoclones s.s., although axial canals are unrecorded; other desmas of irregular shapes and grade into megarhizoclonids; dermalia dichotriaenes; microscleres and small rhizoclonids unknown. Cretaceous (Albian)-Neogene (Miocene): Spain, Albian; France, Santonian-Campanian; Germany, Turonian-Campanian; Northern Africa, Miocene.-FIG. 161a-d. \*P. polymorphus, Mucronatenkreide, Maastrichtian, Misberg, Germany; a, side view of irregular, earshaped variety of species with long stem, ×1 (Schrammen, 1901); b, characteristic spicules, desmas with and without the characteristic long, central growth (or basaltheil), one showing a large, solution cavity that does not represent an axial system; c, megarhizoclonids; d, dermal dichotriaenes, ×20 (Schrammen, 1910).

- Pycnoclonella Lagneau-Hérenger, 1962, p. 168 [\*P. dactyliformis; OD]. Cylindroid with deep, narrow, paragastral cavity and encrusting base, sometimes also with small, hollow outgrowths near base; external surface of skeletal framework with small ostia; no evident epirhyses, aporhyses, or postica; desmas stout, with two to four arms; their central parts bearing large tubercles, one of which may have a polar position; some also grade into forms with two arms at each end of short, central shaft; smooth megarhizoclonids also present; parts of surface with supplemental cortex formed from small rhizoclonids; dermalia not certainly known but apparently dichotriaenes; microscleres unknown. [Dermalia only known from a single, fragmentary dichotriaene, not certainly intrinsic.] Cretaceous (Aptian): Spain.—FIG. 160, 1a-d. \*P. dactyliformis, Can Casanyas Castellet, Catalogne, characteristic spicules; a, typical desmas; b, megarhizoclonids; c, rhizoclonids of cortex; d, fragmentary dichotriaene, not certainly intrinsic, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de -FIG. 160, Ie-f. P. ramosa LAGNEAU-France).-HÉRENGER, Can Casanyas Castellet, Catalogne; desmas, including one with distinct, central shaft, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Schrammeniella BREISTROFFER, 1949, p. 103 [\*Phalangium scytaliforme SCHRAMMEN, 1910, p. 70; OD] [=Iouea DE LAUBENFELS, 1955, p. 61 (type, Phalangium cylindratum SCHRAMMEN, 1910, p. 70, OD)]. Cylindrical or branched cylindrical, with deep, narrow, paragastral cavity, or cup-shaped or flabellate; outside of skeletal framework with small ostia or short epirhyses; exhalant features (aporhyses, postica) absent; desmas typically dipodal to tetrapodal and mainly dicranoclones s.s., with axial canal sometimes seen in short, projecting basaltheil; spicules of exterior arranged with arms directed inwardly and applied to central parts of underlying desmas; other irregular desmas and megarhizoclonids also present; small rhizoclonids sometimes forming supplemental cortex; dermalia dicho-

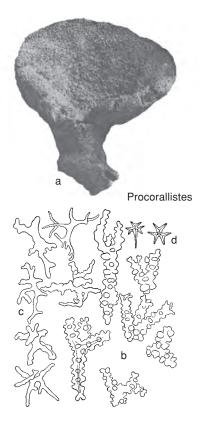


FIG. 161. Corallistidae (p. 245-247).

triaenes; microscleres unknown. [Schrammeniella BREISTROFFER, 1949, and Iouea DE LAUBENFELS, 1955, were both proposed as nom. nov. pro Phalangium Schrammen, 1910, non LINNÉ, 1758, and type species are almost identical ("Allgemeine Form, Oberflache und Kanalsystem wie bei Phalangium scytaliforme, wovon sich die Spezies aber durch gracileren Bau gut unterscheidet.' SCHRAMMEN, 1910, p. 70).] Cretaceous (Turonian-Campanian): France, Santonian; Germany, Poland, Turonian-Campanian.—FIG. 159, 1a-d. \*S. scytaliforme (SCHRAMMEN), Mucronatenkreide, Campanian, Misburg, Germany; a, side view of typical cylindrical form with numerous irregular, inhalant ostia, ×1; b-d, characteristic spicules including principal desmas, some showing axial canal in basaltheil, megarhizoclonids, one showing axial canal and dermal dichotriaene, ×30 (Schrammen, 1910).

Spinocladia LAGNEAU-HÉRENGER, 1962, p. 171 [\*S. tubulata; OD]. Initially cylindrical, with encrusting base and narrow, paragastral cavity, then sometimes laterally branching or expanding upwardly; small

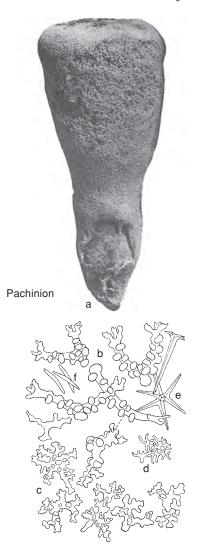


FIG. 162. Corallistidae (p. 248).

ostia at skeletal surface; no epirhyses, aporhyses, or postica; desmas with spines instead of tubercles, mainly tripodal and tetrapodal in interior but less regular and with five or six arms near surface; becoming flattened at surface and passing into megarhizoclonids; some zygomes more or less cupular; supplemental cortex formed by small rhizoclonids; no other spicules known. [Included in the family with some question.] *Cretaceous (Aptian):* Spain.——FIG. 160,2*a–f.* \**S. tubulata,* Can Casanyas Castellet, Catalogne, desmas; *a,* dicranoclones of interior; *b,* fragment of interior skeleton; *c,* fragment of outer skeleton; *d–f.* irregular dicranoclones and megarhizoclones from outer part of skeleton, ×20 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

#### Subfamily PACHINIONINAE Schrammen, 1924

[nom. transl. REID, herein, ex Pachinionidae SCHRAMMEN, 1924a, p. 39; emend., REID, herein]

Desmas mainly dipodal, with one- or three-armed variants subordinate, and arranged to form more or less distinct skeletal fibers; megarhizoclonids and small rhizoclonids present; dermalia dichotriaenes; microscleres unknown. [The group was originally distinguished from Coscinospongiidae LENDENFELD (=Corallistidae SOLLAS) by supposed absence of megarhizoclonids and *deckschicht* (supplemental cortex formed from small rhizoclonids) in the latter; this distinction is here rejected because megarhizoclonids occur in living corallistids; and a cortex formed from small rhizoclonids occurs in living Heterophymia POMEL, 1872, p. 143, both of which are herein placed into the subfamily Corallistinae. The subfamily Pachinioninae is here redefined in terms of the skeletal structure of Pachinion ZITTEL, 1878a.] Cretaceous (Aptian-Campanian).

Pachinion ZITTEL, 1878a, p. 130 [\*Jerea scripta F. A. ROEMER, 1864, p. 34; OD] [=Pachynion DE LAUBENFELS, 1955, p. 62, nom. null.; Neohindia SCHRAMMEN, 1901, p. 11 (type, N. cylindrica, OD)]. Cylindrical to club shaped, with short, basal stalk, or sometimes growing in groups with individuals united at base; paragastral cavity deep, wide, or narrow; no skeletal pores or canals, except at base of paragastral cavity from which a few tubular aporhyses may run down stalk; desmas mainly dipodal but also including tripodal and irregular variants and united to form network of skeletal fibers; no distinct basaltheil in most, although prominent, central tubercle may occur; megarhizoclonids also present; dermalia dichotriaenes, supplemental cortex formed by small, finely branched rhizoclonids in basal parts, or more extensive; small, tangentially arranged oxystrongyles may also occur; microscleres unknown. Cretaceous (Aptian-Campanian): Spain, Aptian-Albian; France, Turonian; England, Campanian; Germany, Poland, Turonian-Campanian.-FIG. 162a-f. \*P. scriptum (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; a, small, steeply obconical example, ×1; b-f, typical spicules, including characteristic desma, megarhizoclonids, cortical rhizoclonid, dermal dichotriaenes, small, cortical oxeas, ×20 (Schrammen, 1910).

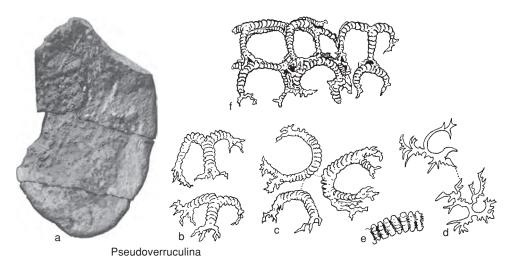


FIG. 163. Pseudoverruculinidae (p. 249).

#### Family PSEUDOVERRUCULINIDAE de Laubenfels, 1955

[Pseudoverruculinidae DE LAUBENFELS, 1955, p. 63]

Desmas with small tubercles arranged mainly in transverse rows along more or less prominent, semiannular swellings; desmas mainly dipodal, tripodal, or anchor shaped with tuberculated ridges on their convex sides; no brachyome or centrumlike features (i.e., no basaltheil); megarhizoclonids also present; sometimes with small, cortical variants of principal desmas; dermalia and microscleres unknown. [The family is comprised of a single, isolated genus with desmas of distinctive appearance that cannot be dicranoclones s.s. because a basaltheil is absent. The family is placed in the suborder Dicranocladina, following MORET (1926b), who included the genus in the family Corallistidae Sollas, and LAGNEAU-HÉRENGER, 1962, who placed the genus under the family Pachinionidae SCHRAMMEN. Its desmas could also be compared with the kyphorhabds of Helminthophyllum SCHRAM-MEN (subclass Choristida; family Helminthophyllidae), and may possibly be of independent origin.] Cretaceous (Aptian-Santonian).

Pseudoverruculina MORET, 1926b, p. 105 [\*P. niciensis; OD]. Flabellate lamellar or leaflike; one

surface of skeletal framework, presumed inhalant, with small, skeletal pores (ostia); other with larger pores, presumed to be postica, at tops of papillar outgrowths; desmas mainly bow shaped, tripodal, or anchor shaped, and arranged to form skeletal fibers; megarhizoclonids also present; some examples with small, cortical rhizoclonids, and forms intermediate between these and principal desmas; no other spicules known. Cretaceous (Aptian-Santonian): Spain, Aptian; France, Santonian .-FIG. 163a-f. \*P. niciensis, Santonian, Saint-Cyr, France; *a*, upper surface, ×0.5; *b-f*, characteristic spicules include: b-c, isolated desmas; d, megarhizoclonids; e, detail of ornament; f, skeletal meshwork, approximately ×20 (Moret, 1926b; courtesy of Société Géologique de France).

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## Suborder PSEUDORHIZOMORINA Schrammen, 1901

[nom. transl. et correct. REID, herein, ex tribus Pseudorhizomorinidae SCHRAMMEN, 1901, p. 14; emend., REID, herein]

Desmas typically monaxial and developed as simple rhizoclones, or as more or less tuberculate forms that do not include dicranoclones; some also with subordinate, tetraxial desmas, in which crepis has form of triaene, intergrading with main ones; zygomes spiny, twiglike, or rootlike, forming more or less random zygoses, or united to form radiating, syzygial fibers like those of some Orchocladina; dermalia phyllotriaenes, monaxial, phyllotriaene-like spicules, or monaxial plates; supplemental rhizoclonids unknown; modern forms with microrhabds, amphiasters, and spirasters that may pass into metasters or plesiasters, or no microscleres. *Cretaceous–Holocene*.

This taxon is revived because of considerable differences between *Macandrewia* GRAY and the typical Dicranocladina, with which it has been included formerly.

SCHRAMMEN's taxon Pseudorhizomorina (as Pseudorhizomorinidae) was proposed originally for the family Corallistidae sensu SOLLAS, in which SOLLAS (1888) included Macandrewia, plus the fossils Pachinion ZITTEL and Procorallistes SCHRAMMEN that SCHRAMMEN took to be fossil Corallistidae. These had been treated as Rhizomorinidae by ZITTEL (1878a) and RAUFF (1893, 1894) but were interpreted by SCHRAMMEN (1901) as distinct from true Rhizomorina, in which tetraxial spicules are absent, because these genera have triaene (i.e., tetraxial) dermalia. The name was then dropped in his next classification (1910) and replaced by Dicranocladina in his final one (1937, p. 77).

SCHRAMMEN then distinguished three families of Dicranocladina: (a) Pachinionidae SCHRAMMEN for fossils with dicranoclones s.l. and megarhizoclonids; (b) Coscinospongiidae von Lendenfeld for the modern corallistids, supposed to lack megarhizoclonids; and (c) Macandrewiidae GRAY (ascribed by SCHRAMMEN to himself), for Macandrewia and other genera with monaxial, phyllotriaene-like dermalia. Genera that fall in the first and second of these families are essentially similar, except that dicranoclones (or dipodal to polypodal desmas) occur chiefly in the first (Pachinionidae). Macandrewia is a sponge in which the desmas are irregular or bipolar rhizoclones that are arranged to form radiating, syzgial fibers similar to those of anthaspidellid Orchocladina. The skeleton is so different from that of any fossil placed by SCHRAMMEN in his Dicranocladina that his familiarity with specimens of the genus may be doubted. Macandrewia is also distinguished by occurrence of tetraxial desmas, with the crepidal axes of a triaene, as subordinate variants of the main ones. These are not mentioned in SCHRAMMEN's papers, and he thought that dicranocladine desmas were of monaxon origin. A second genus, *Daedalopelta* SOLLAS, does not have an anthaspidellid-like structure, but its desmas, again, are not like forms called dicranoclones by SCHRAMMEN in the fossils.

In theory, desmas of these sponges might be thought to correspond with megarhizoclonids of typical Dicranocladina, which in turn might represent an unspecialized prototype of typical dicranocladine desmas. In practice, how the desmas are related is entirely unknown; and the group would still need to be pictured as having descended independently since a time before dicranocladine desmas assumed their characteristic aspect. In this light, it seems best to remove them from the Dicranocladina, and the older taxon Pseudorhizomorina is revived to comprise them. This usage seems appropriate because the desmas are of rhizoclonar type, while Dicranocladina is based on the desma name dicranoclone.

#### Family MACANDREWIIDAE Gray, 1859

[nom. correct. SCHRAMMEN, 1924a, p. 39, pro Macandrewiadae GRAY, 1859, p. 440]

Desmas large, smooth rhizoclones or tuberculate variants in which the tubercles are typically restricted to zygomes or branches; no tripodal or comparable desmas (i.e., dicranoclones s.l.); sometimes with tetraxial variants of normal, rhizoclonar desmas; dermalia phyllotriaenes or discotriaenes, with finely sculptured margins; no rhizoclonids; microscleres microrhabds, amphiasters, or spirasters. [The name was described as new by SCHRAMMEN (1924a) but was first proposed by GRAY in discussion of the type genus, Macandrewia GRAY. Dermalia were described as monaxial by SCHRAMMEN (1924a, p. 39), but this is not their character in the two modern genera now included (Macandrewia GRAY, Daedalopelta SOLLAS) but may refer to Callipelta SOLLAS, here excluded because its desmas are of dicranocladine type (strongly tuberculate, sometimes dipodal, and with a strong, central tubercle).] *?Upper Cretaceous, Holocene.* 

Macandrewia GRAY, 1859, p. 438 [\*M. azorica; OD]. Irregularly funnel-like, flabellate, club shaped or with short branches arising from clublike stock; usually stalked with encrusting base; lateral surfaces with small pores from which radial epirhyses run inwardly; inside of funnel-like or flabellate examples have small, marginated oscules; beneath these, surface of skeletal framework showing stellate groups of postica from which aporhyses run into skeleton, and shallow furrows radiate on its surface; other forms with aporhyses that open at summit or ends of short branches, with corresponding, exhalant canals opening through small oscules in these positions; desmas mainly smooth, of irregular to bipolar shapes, and mainly arranged so that zygomes unite to form radiating, skeletal fibers that spread out longitudinally and end at skeletal surface; dermalia phyllotriaenes to discotriaenes, with finely sculptured margins and granulated, external surfaces; microscleres microrhabds. ?Upper Cretaceous, Holocene: Germany, ?Upper Cretaceous; Northern Atlantic, West Indies, East Indies, Holocene.-FIG. 164,4. \*M. azorica, Holocene, West Indies, Barbados; side view of holotype showing lobed, stalked, obconical form, and scattered, exhalant ostia on gastral surface, ×0.3 (Gray, 1859).

#### Family NEOPELTIDAE Sollas, 1888

[Neopeltidae Sollas, 1888, p. 344] [=Daedalopeltidae de Laubenfels, 1936, p. 184]

Sponges with dermal armor of discotriaenes present and with rhizomorine, principal spicules. *Cretaceous–Holocene*.

Neopelta SCHMIDT, 1880, p. 88 [\**N. imperfecta;* OD]. Sponge body irregularly nodose to irregularly obconical; upper end with ostia of open canals; endosomal skeleton of rhizomorine desmas and some smooth oxeas and amphiasters; dermal surface armored with discotriaenes. *Cretaceous–Holocene:* cosmopolitan.——FIG. 164,*6a–b.* \**N. imperfecta,* Holocene, North Atlantic; *a*, isolated dermal discotriaene, ×50; *b*, spinose amphiaster, ×500 (de Laubenfels, 1955).

## Suborder DIDYMMORINA Rauff, 1893

[nom. transl. REID, 1963d, p. 200, ex tribus Didymmorina SCHRAMMEN, 1937, p. 102, nom. correct. pro unter-tribus Didymmorinidae RAUFF, 1893, p. 195]

Desmas monaxial and typically developed as didymoclones, although some may be bipolar or more or less irregular rhizoclones; zygomes twiglike, rootlike, or handlike, and in didymoclones typically applied to swollen pseudocentra of other desmas; dermalia dichotriaenes or apparently absent; small rhizoclonids unknown, but some with skeletal cortex formed by rhizoclones that intergrade with typical didymoclones; no microscleres known. *Middle Jurassic–Upper Jurassic (Kimmeridgian).* 

The Didymmorina have formerly been listed as "lithistid Monaxonia" by SCHRAM-MEN (1937, p. 102) and as Monalithistida by LAGNEAU-HÉRENGER (1962, p. 40), because tetraxial spicules were unknown. They are placed here in the Tetralithistida because a specimen of Cylindrophyma milleporata (GOLDFUSS), identified by SCHRAMMEN himself, shows dichotriaenes that do not appear to be intrusive and because of the character of the zygomes, which are like those of tetraclones and dicranoclones. Relationships are strictly unknown, but the group may be similar to the Dicranocladina because the dermal dichotriaenes of C. milleporata are like those of the fossil and modern Corallistidae and some dicranocladine desmas have didymoclone-like shapes, as do some of those of the Jurassic Leiocarenus SCHRAMMEN, for example.

In ZITTEL's first classification (1878a, p. 100), the didymmorine genera Melonella ZITTEL and Cylindrophyma ZITTEL were united with Lecanella ZITTEL and Mastosia ZITTEL as Anomocladina. The two latter genera have astroclone and sphaeroclone desmas, respectively, and are here placed in the Sphaerocladina SCHRAMMEN. The taxon was defined as though all desmas were sphaeroclones. SOLLAS (1885b) also treated the desmas as sphaeroclones but cited only genera not included by ZITTEL. SOLLAS included the living Vetulina SCHMIDT, which SOLLAS had specially investigated, and the Paleozoic Astylospongiidae ZITTEL, which ZITTEL (1877b, p. 44) had mistaken for dictyonine Hexactinellida. RAUFF (1893, p. 159) coined the term didymoclone and proposed a distinction between the Didymmorinidae RAUFF, with didymoclones, and the Anomocladinidae ZITTEL, with desmas termed ennomoclones. The latter spicules

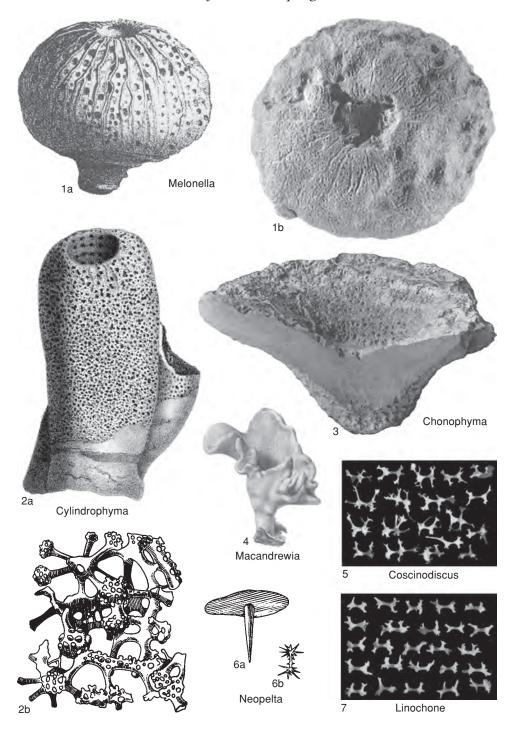


FIG. 164. Macandrewiidae, Neopeltidae, and Cylindrophymatidae (p. 251–252).

include the sphaeroclones of Astylospongiidae and later genera (e.g., Mastosia, Vetulina) and the triderlike desmas of the Paleozoic Hindia Duncan. Hindia had not been established when ZITTEL's first system was published. The Hindia desma and the sphaeroclone were supposed to be allied types with simple and branching arms, respectively, which RAUFF termed triders and dichotriders. ZITTEL (1878a), however, preferred to use Anomocladina for RAUFF's Didymmorinidae, despite its being contrary to his first diagnosis, and was followed by RAUFF (1893), who proposed the name Eutaxicladinidae for his former Anomocladinidae.

At this stage, the name Anomocladina, thus, had been used in four different senses, in terms of the desmas of the forms that were included. There are two more, due to SCHRAMMEN (1937, p. 108) and DE LAUBEN-FELS (1955). SCHRAMMEN identified the desmas of Lecanella as anomoclones and used Anomocladina as a suborder name (tribus, SCHRAMMEN) for his family Lecanellidae SCHRAMMEN, in accordance with his general use of taxa whose names correspond with those of desmas. DE LAUBENFELS (1955, p. 64) used the name Anomocladina but took the desmas as sphaeroclones in his diagnosis. Only one genus included, however, has sphaeroclone desmas (Mastosia); the others have didymoclones (e.g., Cylindrophyma), dendroclones (e.g., Anthaspidella MILLER), anomoclones (Anomoclonella RAUFF), do not have desmas of any sort (e.g., Heliospongia GIRTY), or have unknown affinities (e.g., Calathium BILLINGS). All other genera with sphaeroclones were placed in the Eutaxicladina RAUFF, together with others in which desmas are tricranoclones (Hindia, identified with Microspongia MILLER), dicranoclones (e.g., Pachinion ZITTEL, Gignouxia MORET), astroclones (Regnardia MORET), dendroclones (e.g., Phacellopegma GERTH), or chiastoclones (Chiastoclonella RAUFF). RAUFF's (1893, p. 157-158) term ennomoclone was replaced by SCHRAMMEN's dicranoclone, although desmas called dicranoclones by SCHRAMMEN (1910, p. 65) were called rhizoclones by RAUFF (1893, p. 161), not ennomoclones.

Because of this confusion in usage of the name Anomocladina and because the alternative Didymmorina is related to the name of the characteristic desmas, the latter name is here considered preferable. In addition, because first designation of Anomocladina as a suborder was by SOLLAS—not by ZITTEL, who termed his taxon family—the taxon should strictly be treated as equivalent to Sphaerocladina SCHRAMMEN.

The confusion in ZITTEL's original publication was probably due partly to the resemblance of the two pseudocentra of didymoclones to the centra of sphaeroclones and to the similar mode of zygosis (zygomes applied to centra or pseudocentra) of these sponges. SCHRAMMEN at first interpreted didymoclones as monaxial but later suggested (1910, p. 169) that they might be composed of two linked sphaeroclones. This idea was dropped in his final work (1937) and is shown to be mistaken by the gradation of didymoclones into simple rhizoclones and their observable young stages, which are monaxons with incipient outgrowths at the ends.

#### Family CYLINDROPHYMATIDAE Schrammen, 1936

[nom. correct. DE LAUBENFELS, 1955, p. 64, pro Cylindrophymidae SCHRAMMEN, 1937, p. 102] [=Coscinodiscidae SCHRAMMEN, 1937, p. 105]

With didymoclones and usually other desmas, having intergradation from didymoclones to rhizoclones; desmas of rhizoclonar type sometimes forming skeletal cortex; dermalia dichotriaenes when present. *Middle Jurassic–Upper Jurassic (Kimmeridgian):* 

Cylindrophyma ZITTEL, 1878a, p. 134 [\*Scyphia milleporata GOLDFUSS, 1826, p. 8; SD DE LAUBENFELS, 1955, p. 64] [=Didymosphaera LINCK, 1883, p. 59 (type, D. steinmanni, OD)]. Cylindrical or pyriform with paragastral cavity extending to base; exterior of skeletal framework with numerous small ostia of fine, radial epirhyses; paragastral surface with larger postica of radial or branching aporhyses; desmas didymoclones and rhizoclonar variants; latter sometimes forming skeletal cortex in lower parts, then covering ostia of main skeletal framework; dermalia dichotriaenes; other spicules unknown. Jurassic (Oxfordian–Kimmeridgian): Germany, Poland, Oxfordian–Kimmeridgian; Switzerland, Kimmeridgian.—FIG. 164,2a–b. \*C. milleporata (GOLDFUSS), Germany; a, cylindrical specimen with inhalant ostia in porous dermal surface and coarse exhalant ostia in gastral surface of open paragastral cavity at top; a second attached specimen shows behind, ×0.5 (Quenstedt, 1878– 1879); b, drawing of part of skeleton, ×30 (de Laubenfels, 1955).

- Chonophyma OPPLIGER, 1921a, p. 204 [\*C. perforata; OD]. Funnel or bowl shaped, thick walled; outside with small, closely spaced ostia of fine, radial epirhyses; paragastral side with rather larger postica of arching aporhyses and other smaller pores that perforate smooth, cortical layer; desmas small didymoclones; other details unknown. [All known material calcified.] *Jurassic (Kimmeridgian):* Switzerland.——FiG. 164,3. \*C. perforata, Malm, Randen; side view of thick-walled, funnel-shaped type specimen, ×0.5 (Oppliger, 1926).
- Coscinodiscus SCHRAMMEN, 1937, p. 105 (SCHRAMMEN, 1936, p. 186, nom. nud.) [\*C. suevicus; OD]. Funnel to bowl shaped to platelike or flabellate, thick walled; exterior of skeletal framework with small ostia of short epirhyses and large, irregular apertures of uncertain character; paragastral surface with large, rounded postica; desmas didymoclones and some irregular variants; other spicules unknown. Jurassic (Kimmeridgian): Germany.——FIG. 164,5. \*C. suevicus; desmas, ×20 (Schrammen, 1937).
- Linochone SCHRAMMEN, 1937, p. 103 (SCHRAMMEN, 1936, p. 186, nom. nud.) [\*L. rimosa; OD]. Compressed, funnel shaped, thick walled; outside with closely spaced, rounded to cleftlike ostia; inside with more widely spaced postica; form of internal canals unknown; desmas small didymoclones and variants that are bipolar rhizoclones; other details unknown. Jurassic (Kimmeridgian): Germany.— FIG. 164, 7. \*L. rimosa, Weiss Jura, Gerstetten; desmas, didymoclones and rhizoclonar variants, ×20 (Schrammen, 1937).
- Melonella ZITTEL, 1878a, p. 134 [\*Siphonia radiata QUENSTEDT, 1858, p. 679; OD] [= Emploca SOLLAS, 1883, p. 541 (type, E. ovata SOLLAS, 1883, p. 542, M)]. Globular, apple shaped, pyriform, or hemispherical, with short stalk or none, and narrow, conical, paragastral cavity usually extending to base; outside with small ostia of radial epirhyses and sometimes with furrows that radiate from paragastral margin and represent inceptional aporhyses; paragastral wall with postica of arched aporhyses that curve downwardly in general conformity with external form; desmas didymoclones and rhizoclonar variants, latter may form dense, wrinkled, skeletal cortex on under surface; dermal triaenes and microscleres unknown. Middle Jurassic (Bajocian)-Upper Jurassic: England; Germany, Poland, Oxfordian-Kimmeridgian; Switzerland, Kimmeridgian.—FIG. 164, 1a-b. \*M. radiata

(QUENSTEDT), Kimmeridgian, Germany; *a*, side view of stalked, globose sponge with relatively small osculum at summit of spongocoel, ×1 (Quenstedt, 1858); *b*, oscular view with central osculum and radially arranged, exhalant canals, ZPAL Pf. VIII/119, ×1 (Pisera, 1997; courtesy of *Palaeontologica Polonica*).

## Order MEGALITHISTIDA new order

[Megalithistida REID, herein] [=Megamorina ZITTEL, 1878a, p. 156, sensu ZITTEL, 1878a, p. 99, non SCHRAMMEN, 1924a, p. 61]

Lithistids that typically have dermal dichotriaenes and monaxial desmas in form of heloclones or megaclones; dermalia sometimes simple triaenes only or absent, but never phyllotriaenes, discotriaenes, or related types; rarely with additional small rhizoclonids; microscleres of modern examples microrhabds, spirasters, and amphiasters. *Carboniferous (?Mississippian), Upper Jurassic–Holocene.* 

This order comprises triaene-bearing lithistids whose desmas appear to be derivatives of ophirhabds, from which they develop in ontogeny in the instance of heloclones. Those of the suborder Helomorina (heloclones) are barely lithistid in character, the zygomes being terminal and lateral notches. A megaclone seems to be simply a more completely lithistid form of the same type of desma, with a much reduced crepis, true anaxial arms, and sometimes prominent, expanded zygomes.

If triaenes are supposed to point to origin from choristids, the occurrence of spirasters in the two living genera (Costifer WILSON, Pleroma SOLLAS) suggests a source in the order Pachastrellida; although these spirasters do not pass into plesiasters and, hence, are not surely streptoscleres. The expected spiculation of an ancestral stock (ophirhabds, simple triaenes) is seen in the Cretaceous Cephaloraphiditidae (=Ophiraphiditidae SCHRAMMEN), which MORET (1926b) included as Megamorina s.l. (i.e., Megalithistida herein); but these forms are too late stratigraphically. A possible true ancestor is Archaeodoryderma REID, in which bluntended ophirhabds grade into heloclones and these in turn grade into forms that agree with the simplest typical megaclones. This genus is, however, only known from loose spicules and is not surely known to have had triaenes, although examples occur with its spicules.

A further problem is occurrence of similar desmas in some probably unrelated sponges and in some sponges of uncertain status. These include (a) small, heloclone-like desmas in the axinellid Saccospongia BASSLER (Ordovician; FINKS, 1967a); (b) more or less megaclone-like desmas in the living Desmatiderma TOPSENT and Helophloeina TOPSENT, which are sublithistid Desmacidontida; and (c) megaclone-like desmas in one species of the fossil Megarhiza SCHRAMMEN (M. colungensis MORET) that intergrade with typical megarhizoclones. The living Lyidium SCHMIDT also has desmas that are megaclones, morphologically but no other megascleres except oxeas. Genera with desmas of these types are not referred here to the order Megalithistida unless the skeleton in general is of megalithistid type. Taxa are certainly not referred to the order if triaenes are absent.

## Suborder HELOMORINA Schrammen, 1924

[nom. transl. Reid, 1963d, p. 199, ex tribus Helomorina Schrammen, 1924a, p. 38]

Desmas typically heloclones but some genera with additional branching variants; dermalia sometimes simple plagiotriaenes but usually dichotriaenes; supplemental oxeas in some; small rhizoclonids in one genus; microscleres of a modern example short spirasters and granulated microrhabds. [The original designation tribus was directly equivalent to suborder as a primary division of an order (Tetraxonia VOSMAER, ascribed to SCHULZE). Includes one living genus, *Costifer* WILSON.] *Upper Jurassic (Kimmeridgian)– Holocene.* 

#### Family CARTERELLIDAE Schrammen, 1901

[Carterellidae Schrammen, 1901, p. 11] [=Isoraphiniidae Schrammen, 1924a, p. 38]

Diagnosis as for suborder. [The name Isoraphiniidae used in the previous *Treatise*, *Part E* (DE LAUBENFELS, 1955, p. 51) is here replaced by Carterellidae on grounds of seniority, but is retained as a subfamily designation in the translated form, Isoraphiniinae SCHRAMMEN, 1924a.] *Upper Jurassic* (*Kimmeridgian*)–*Holocene*.

#### Subfamily CARTERELLINAE Schrammen, 1901

[nom. transl. REID, herein, ex Carterellidae SCHRAMMEN, 1901, p. 11]

Cylindrical sponges with bundle of vertical, tubular aporhyses in axial parts and their postica at summit of body; some desmas may be branched irregularly or more or less triradiate; dermalia dichotriaenes when known; microscleres unknown. *Cretaceous (Albian– Maastrichtian).* 

- Carterella ZITTEL, 1878a, p. 132 [\*Jerea cylindrica GÜMBEL, 1868, p. 761; SD DE LAUBENFELS, 1955, p. 50]. Cylindrical, branched cylindrical, or elongate club shaped; exterior of skeletal framework with numerous irregularly shaped ostia of fine, radial epirhyses; summit with postica of bundle of tubular, radial aporhyses that run mainly down axial parts of body but in some instances nearer to surface; lower parts often with irregular, longitudinal furrows; skeletal framework with densely packed heloclones forming longitudinal fibers in parts; some desmas irregularly branched at ends; small rhizoclonids in interspaces locally; dermalia unknown; microscleres unknown. Cretaceous (Cenomanian-Maastrichtian): Germany, Poland. FIG. 165, 4a-c. \*C. cylindrica (GUMBEL), Greensand, Cenomanian, Regensberg, Germany; a, side view of cylindrical sponge, ×0.5; b, sketch of part of dermal surface showing irregular ostia between fibers, somewhat enlarged; c, transverse section showing radial epirhyses and sectioned aporhyses, ×1 (Zittel, 1878a).
- Inodia MORET, 1925, p. 487 [\*I. elisabethae; OD]. Known incompletely from cylindrical fragments only; surface with small ostia; axial parts with bundle of tubular aporhyses; desmas resemble heloclones but have irregular, ramified outgrowths, similar to elongate, basal desmas of some Tetracladina (Siphoniidae); zygosis loose or absent; no other spicules known. Cretaceous (Cenomanian): France, Poland.——FIG. 165,3a-b. \*I. elisabethae, Sablons, France; characteristic, large desmas, magnification not stated, about ×10 (Moret, 1926b; courtesy of Société Géologique de France).
- Nematinion HINDE, 1884a, p. 54 [\*N. calyculum; OD]. Elongate cylindrical, with small, cuplike expansion at top and stalk that ends bluntly or divides into root processes; sides with ostia of radial epirhyses; summit with postica of tubular, vertical aporhyses that traverse axial parts; desmas of interior normal heloclones; those of exterior branching,

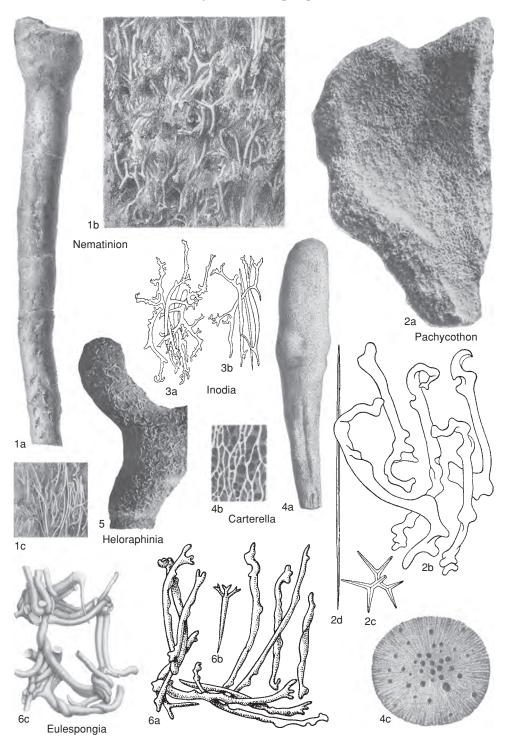


FIG. 165. Carterellidae (p. 255–257).

sometimes triradiate in form; other spicules unknown. *Cretaceous (Albian):* England.——FIG. 165, *Ia-c.* \**N. calyculum*, Upper Greensand, Warminster, Wiltshire; *a*, side view of cylindrical holotype with cuplike, upper end, ×0.5; *b*, external meshwork with apparently triradiate desmas, ×8; *c*, elongate heloclones of internal meshwork, ×10 (Hinde, 1884a).

### Subfamily ISORAPHINIINAE Schrammen, 1924

[nom. transl. REID, herein, ex Isoraphiniidae SCHRAMMEN, 1924a, p. 38]

Hollow cylindrical, bowl to funnel-like, flabellate, or branched cylindrical sponges that have no canalar features (ostia, postica, epirhyses, aporhyses) in skeletal framework, or with ostia or postica only; desmas all typical heloclones; dermalia plagiotriaenes or dichotriaenes; supplemental oxeas in some, but rhizoclonids unknown; microscleres short spirasters and granulated microrhabds in living example. [The subfamily includes the single living carterellid, *Costifer* WILSON, which is also the only genus with plagiotriaene dermalia.] *Upper Jurassic (Kimmeridgian)–Holocene.* 

- Eulespongia QUENSTEDT, 1877 in 1877-1878, p. 105 [\*Siphonocoelia texta F. A. ROEMER, 1864, p. 29; SD DE LAUBENFELS, 1955, p. 51; note: listed as OD by DE LAUBENFELS (1955, p. 51), but ZITTEL (1878a, p. 133) listed Siphonocoelia hirta F. A. ROEMER, 1864, p. 30, as a possible second species] [=Isoraphinia ZITTEL, 1878a, p. 133, obj.]. Body cylindrical or club shaped, passing downwardly into stalk, with truncated summit and a deep, narrow, paragastral cavity; no skeletal pores or canals; heloclones united in irregular fibers and radiating clusters; dermalia dichotriaenes; no rhizoclonids; some examples with cortical layer of small, tangentially oriented oxeas that underlie heads of dermalia; no microscleres known. Cretaceous (Cenomanian-Maastrichtian): England, France, Germany, Czech Republic, Slovakia. FIG. 165, 6a-c. \*E. texta (F. A. ROEMER), Cenomanian, France; a, characteristic, heloclone desmas; b, dermal dichotriaene, ×30 (de Laubenfels, 1955); c, part of inner wall showing relationships of spicules, ×10 (Zittel, 1878a).
- Heloraphinia SCHRAMMEN, 1937, p. 76 (SCHRAMMEN, 1936, p. 184, nom. nud.) [\*H. arborescens; OD]. Only known from branched, cylindrical fragments; skeletal framework wide meshed with no paragastral cavity or canalar features; no other spicules known. Jurassic (Kimmeridgian), Cretaceous (?Aptian, Cenomanian): Germany, Kimmeridgian; Spain, ?Aptian; Poland, Cenomanian.—FiG. 165,5. \*H. arborescens, Weiss Jura, Kimmeridgian, Schwabtal,

Germany; side view of branched holotype with heloclones in dermal layer, ×2 (Schrammen, 1937).

Pachycothon SCHRAMMEN, 1901, p. 11 [\*P. giganteum; OD; = Cupulospongia gigantea F. A. ROEMER, 1864, p. 51, according to SCHRAMMEN, 1910, p. 130]. Funnel- to platelike or flabellate, stalked or not, fairly thick walled; skeletal surfaces with open, skeletal meshes only, or with distinct ostia and postica; no epirhyses or aporhyses; skeletal framework a network of large, terminally connected heloclones; dermalia dichotriaenes; supplemental oxeas may occur; no other spicules known. Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian): Germany, Kimmeridgian; France, Santonian; Germany, Poland, Turonian-Campanian.-FIG. 165,2a-d. \*P. giganteum, Campanian, Germany; a, fragment of flabellate example, ×1 (Schrammen, 1901); b-d, characteristic spicules including heloclones, dermal dichotriaene, and supplemental oxea, ×5 (Schrammen, 1910).

# Suborder MEGAMORINA Zittel, 1878

[nom. transl. SCHRAMMEN, 1924a, p. 38, ex family Megamorina ZITTEL, 1878a, p. 99; emend, REID, 1968a, p. 23] [tribus Megamorina ZITTEL; here accepted as equivalent to suborder, as a primary division of order Tetraxonida VOSMAER (ascribed to SCHULZE by SCHRAMMEN), emended by REID, 1968a, p. 23]

Desmas megaclones; dermalia dichotriaenes except for occasional variants with some cladi unbranched; large or small rhizoclonids sometimes present; supplemental oxeas may occur; microscleres spirasters and microrhabds in a living example. *Carboniferous (?Mississippian), Upper Jurassic (Kimmeridgian)–Holocene.* 

One certain living genus, *Pleroma* SOLLAS, is included in the suborder. A possible second genus, *Lyidium* SCHMIDT, has megaclone desmas but is not known to have either triaenes or spirasters.

Members of this group have been placed into four nominal families (Pleromatidae SOLLAS, 1888; Dorydermatidae SCHRAMMEN, 1901; Heterostiniidae SCHRAMMEN, 1924a; Megalithistidae SCHRAMMEN, 1924a), but the differences relied on for separation are tenuous. The characteristic desmas of *Pleroma* SOLLAS have unusually elongate shafts, with arms along one side but are otherwise like those of other forms. There are also unusual branched variants of this type, but other variants resemble some forms of *Doryderma* ZITTEL. Passage of typical megaclones into branched, sometimes rhizoclone-like variants occurs also in the Jurassic Megalithista ZITTEL and the allied *Anomorphites* KOLB. *Doryderma* has desmas in which the zygomes are mainly longitudinal facets, instead of cup- or hand-shaped or tonguelike expansions as in most other forms; but Pachypoterion HINDE may have desmas of Doryderma type in the lower parts and desmas with expanded zygomes in upper ones. Heterostinia ZITTEL has accessory rhizoclonids, which were emphasized by LAGNEAU-HÉRENGER (1962); and MORET (1926b) found that small rhizoclonids may occur in Doryderma. Desmas of Megalithista are mainly forms with branching zygomes at ends of an arched or straight shaft; and similar forms also occur in Heterostinia. Thus, none of the types of these nominal families has a specially distinctive spiculation.

An alternative grouping can be based on the pattern of canalization: (a) the names Pleromatidae and Dorydermatidae are based on sponges with tubular, axial aporhyses traversing a top-shaped to cylindrical, branched cylindrical or fan-shaped body; (b) the names Heterostiniidae and Megalithistidae are based on sponges that typically have distinct, paragastral and external surfaces, in which canals are usually radial, when present, and in which vertical aporhyses are seen only in stalks, if at all. This distinction is taken here as distinguishing subfamilies Pleromatinae SOLLAS and Heterostiniinae SCHRAMMEN.

Division of these sponges between Pleromatidae and Dorydermatidae by DE LAUBENFELS (1955, p. 50), based on occurrence of branching in the latter, is rejected because this places forms with and without axial aporhyses in both groups and places species of *Doryderma* ZITTEL in both groups (e.g., *D. benetti* HINDE, unbranched; *D. roemeri* HINDE, branching). The additional family Helobrachiidae SCHRAMMEN, described as having megaclones by DE LAUBENFELS (1955, p. 51), comprises a single choristid genus (*Helobrachium* SCHRAMMEN) with no spicules other than large, hooked tripods (helotriaenes, SCHRAMMEN).

### Family PLEROMATIDAE Sollas, 1888

[nom. correct. VON LENDENFELD, 1903, p. 140, pro Pleromidae SOLLAS, 1888, p. 312] [=Dorydermatidae SCHRAMMEN, 1901, p. 12, nom. correct. DE LAUBENFELS, 1955, p. 50, pro Dorydermidae SCHRAMMEN, 1901, p. 12 (ascribed to MORET, 1926b); Heterostiniidae SCHRAMMEN, 1924a, p. 39; Megalithistidae SCHRAMMEN, 1924a, p. 148]

Diagnosis as for suborder. Carboniferous (?Mississippian), Upper Jurassic (Kimmeridgian)–Holocene.

# Subfamily PLEROMATINAE Sollas, 1888

[nom. transl. et correct. REID, herein, ex Pleromidae SOLLAS, 1888, p. 312]

Top- to club-shaped, cylindrical, branched cylindrical, or leaf- or fan-shaped sponges with long, tubular, longitudinal aporhyses and normally no paragastral cavity; epirhyses radial when present; dermalia dichotriaenes; rhizoclonids occasionally present; microscleres microrhabds and spirasters in single living example. [The microscleres are known in the living type genus, *Pleroma* SOLLAS, 1888.] *Carboniferous* (?Mississippian), Cretaceous (Albian)– Holocene.

- Pleroma Sollas, 1888, p. 312, non Smith, 1891, p. 113 [\*P. turbinatum; OD] [?=Propleroma MORET, 1925, p. 486 (type, P. regnardi, OD)]. Small, topshaped sponge with shallow depression at top; base encrusting; no ostia or epirhyses; summit with postica of vertical aporhyses that form axial bundle; desmas with more or less elongate axis in typical examples but grading into short forms and spicules approaching megarhizoclones; normal forms typically arranged so that zygomes grasp outer surfaces of shafts of desmas below them in skeleton; dermalia dichotriaenes, supplemental oxeas present; microscleres microxeas and elongate spirasters that may pass into amphiasters. [Fossil examples cited as the new genus Propleroma by MORET, 1925, p. 486, may represent Pleroma in the Cretaceous record.] ?Upper Cretaceous, Paleogene (Eocene)–Holocene: France, ?Upper Cretaceous; Western Australia, Eocene; Spain, Miocene; East Indies, Holocene.-FIG. 166, 1a-f. \*P. turbinatum, Holocene, East Indies; *a-b*, side view of characteristic rhabdocrepid desmas; c-d, short and elongate desmas, from below; e, megarhizoclone-like desma; f, two desmas showing mode of zygosis, ×50 (Sollas, 1888).
- Doryderma ZITTEL, 1878a, p. 131 [\*Polyjerea dichotoma F. A. ROEMER, 1864, p. 36; SD DE LAUBENFELS, 1955, p. 50; =Doryderma roemeri HINDE, 1884a, p. 49, obj.] [=Dichojerea POMEL, 1872, p. 176, obj.; Brochodora SCHRAMMEN, 1910, p. 58, obj.]. Typically branched cylindrical but sometimes simply cylindrical or pyriform; no paragastral cavity; external surface of skeletal

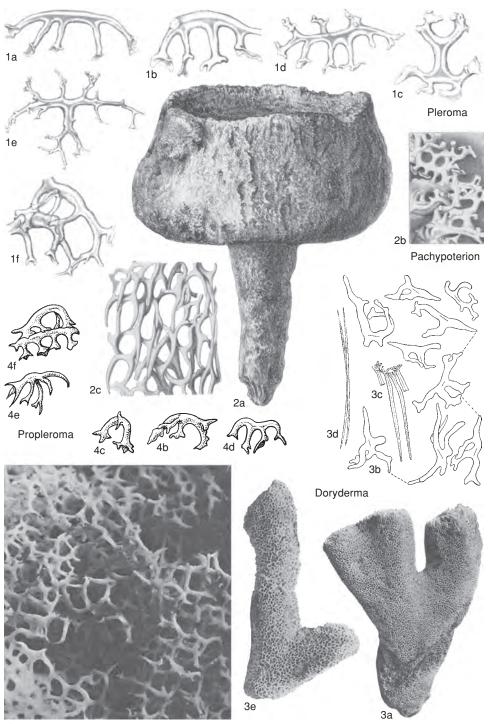




FIG. 166. Pleromatidae (p. 258–262).

framework with large, open meshes only (i.e., no distinct ostia); a short, radial canal (epirhysis) usually runs inwardly from each external meshwork opening; axial parts with bundle of tubular, longitudinal aporhyses, with postica at ends of branches or at summit in unbranched examples; desmas large, irregular megaclones, with zygomes typically as oblique, longitudinal facets at ends of arms or absent on some arms; in outer parts of skeleton, desmas mostly branched irregularly at ends of epirhabd and arranged so that epirhabds lie in partitions between epirhyses, with ends interlocked between groups of epirhyses; in axial parts, desmas more elongate and aligned longitudinally; dermalia dichotriaenes; supplemental oxeas common, often arranged radially when present; rhizoclonids typically absent, but rarely present at skeletal surface; microscleres unknown. [Dichojerea is an objective synonym of Doryderma ZITTEL, 1878a, due to subsequent designation of Polyjerea dichotoma F. A. ROEMER, 1864, as type species of both nominal genera by DE LAUBENFELS (1955): of Doryderma ZITTEL as Doryderma roemeri HINDE, 1884a, pro Polyjerea dichotoma ROEMER, "1861" [sic., 1864 is correct date]; DE LAUBENFELS, 1955, p. 50); and of Dichojerea POMEL (1872, p. 176), as Polyjerea dichotoma ROEMER, 1864 (DE LAUBENFELS, 1955, p. 57). These nominal genera were not treated as synonyms by DE LAUBENFELS. He referred Doryderma ZITTEL to the family Dorydermatidae SCHRAMMEN, 1901 (MORET, 1926b; DE LAUBENFELS, 1955, p. 50) of the suborder Megamorina ZITTEL and referred Dichojerea POMEL to the family Jereidae DE LAUBENFELS (1955, p. 57) of the suborder Tetracladina ZITTEL. Dichojerea is here suppressed under Code Art. 23.2 (ICZN, 1999) as not used as a senior synonym within the required period.

Brochodora SCHRAMMEN (1910, p. 58) was proposed as a subgenus of Doryderma ZITTEL, 1878a, with the species B. roemeri (HINDE) [=Doryderma roemeri HINDE, 1884a, p. 49, nom. nov. pro Polyjerea dichotoma F. A. ROEMER, 1864, non Doryderma dichotoma (BENETT) HINDE, 1884a, p. 47, =Polypothecia dichotoma BENETT, 1831, pl. 13] and B. ramusculus SCHRAMMEN, 1910. The type species is distinguished from D. dichotoma (F. A. ROEMER) only by dimensions ("Korperform, Kanalsystem und Skelett wie bie Brochodora roemeri, von der sich Brachodora ramusculus aber durch gracileren Bau und viel geringere Dimensionen unterscheidet," SCHRAMMEN, 1910, p. 59). In this writer's opinion, the species was based simply on small forms of D. dichotoma.] Carboniferous (?Mississippian), Cretaceous (Albian-Campanian): Russia, ?Mississippian; England, France, Germany, Spain, Czech Republic, Slovakia, Poland, Russia, Albian-Campanian. FIG. 166, 3a-d. \*D. dichotoma (F. A. ROEMER) (=D. roemeri HINDE), Quadratenkreide, Campanian, Oberg, Germany; a, side view of branched sponge with widely spaced, inhalant ostia and coarse, skeletal pores, ×0.5; *b–d*, characteristic spicules including desmas, dermal dichotriaenes, and oxeas, ×10 (Schrammen, 1910).—FIG. 166,*3e. B. ramusculus* SCHRAMMEN, Quadratenkreide, Campanian, Oberg, Germany; side view of small, branched fragment, ×1 (Schrammen, 1910).

- Homalodoriana REID, herein, nom. nov. pro Homolodora Schrammen, 1910, p. 59, non MOTSCHOULSKY, 1860 [\*Spongia ramosa MANTELL, 1822, p. 162; OD] [= Trachycinclis POMEL, 1872, p. 110, obj., nom. oblit.]. Branched cylindrical, stalked pyriform, globular, and related shapes, sometimes strongly compressed; lateral surfaces of skeletal framework fine meshed between widely spaced, rounded ostia of short epirhyses, which run in radially or curve obliquely downward; other mesh spaces not canaliform (as in Doryderma ZITTEL); outer skeletal meshwork correspondingly not showing Doryderma structure; longitudinal aporhyses in central parts open terminally in branching examples, and in corresponding positions in others; desmas similar to those of Doryderma; dermalia dichotriaenes where known; no other spicules known. Cretaceous (Albian-Campanian): England, France, Germany, Poland.-FIG. 167,1a. \*H. ramosa (MANTELL), Quadratenkreide, Campanian, Oberg, Germany; side view of multibranched sponge with terminal osculum in each branch and inhalant ostia in dermal mesh, ×0.5 (Schrammen, -FIG. 167, 1b. H. plana SCHRAMMEN, 1910).---Quadratenkreide, Campanian, Oberg, Germany; side view of compressed, leaf-shaped example, ×0.5 (Schrammen, 1910).-FIG. 167, 1c. H. dichotoma (BENETT), Upper Greensand, Albian, Wiltshire, England; part of external surface showing ostia and small, skeletal meshes, ×8 (Hinde, 1884a).
- Pachypoterion HINDE, 1884a, p. 51 [\*P. robustum; SD DE LAUBENFELS, 1955, p. 50]. Stalked, cup or gobletlike sponges with upper part mainly solid, but with shallow depression or paragastral cavity at top, and similar forms in which upper part forms thick-walled, open funnel; exterior with vague ostia, from which radial epirhyses extend inwardly; axial parts with bundle of vertical, tubular aporhyses and other aporhyses around them sloping obliquely outward; postica of aporhyses occur in floor of summit depression or in walls of paragastral cavity, if present; desmas irregularly branching with short epirhabd and well-developed zygomes in main part of body, but elongate and articulated by longitudinal facets in stalk; supplemental oxeas may occur; dermalia, rhizoclonids, and microscleres unknown. [Dichotriaenes were incorrectly cited as dermalia of the genus by SCHRAMMEN (1910, p. 63) but this record was based on spicules of P. auritum SCHRAMMEN, 1910, p. 64, which was later designated as the type species of Gigantodesma SCHRAMMEN, 1924a and removed from Pachypoterion. See p. 263 herein.] Cretaceous (Albian-Cenomanian): England, Spain, Albian;

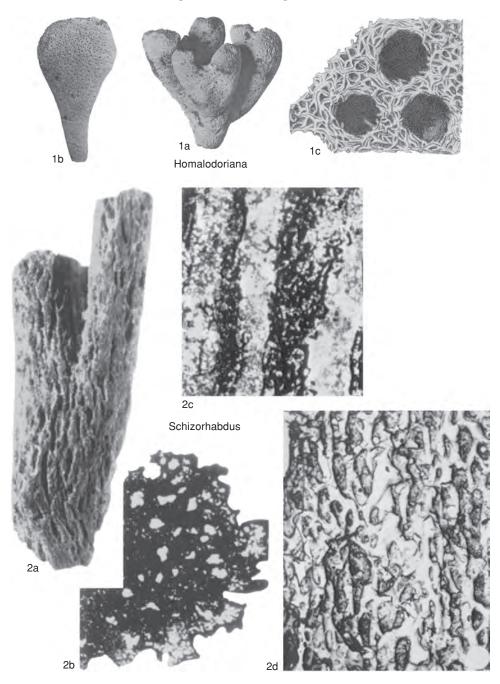


FIG. 167. Pleromatidae (p. 260–262).

France, Poland, *Cenomanian.*—FIG. 166,2*a–c.* \**P. robustum*, Upper Greensand, Albian, Pewsey, England; *a*, side view of goblet-shaped, figured syntype, herein designated lectotype,  $\times 0.5$ ; *b*, skeletal meshwork with desmas of main body, as shown in thin section; *c*, desmas at surface of stalk with absence of expanded zygomes,  $\times 10$  (Hinde, 1884a).

- Propleroma MORET, 1925, p. 486 [\*P. regnardi; OD]. Cylindrical with small, lateral outgrowths; a few surface meshes rounded to form ostia, from which radial epirhyses run inwardly; axial part with group of longitudinal aporhyses; characteristic desmas have arched to elongate shaft with short, zygomebearing arms on one side, which is convex in arched examples; arms arranged facing inwardly and applied to shafts of other desmas, as in Pleroma SOLLAS; some also of tripodal or irregular shapes; supplemental oxeas present; no other spicules known. [Fossil examples from the Cretaceous of France with skeletal structure and spicules similar to those of Pleroma were placed in the new genus Propleroma by MORET (1925), but they might be included in the Holocene genus.] Cretaceous (Cenomanian-Maastrichtian): France, Poland .--FIG. 166,4a-f. \*P. regnardi, Cenomanian, Coulonges-les-Sablons, France; a, skeletal meshwork, ×20 (Moret, 1926b); b-f, desmas, ×40 (Hill, 1972).
- Schizorhabdus ZITTEL, 1877b, p. 51 [\*S. libycus; OD]. Cylindrical to steeply obconical sponges, occasionally branched, exterior somewhat grooved or longitudinally fluted with bifurcated and braided elements; commonly with vertical, axial cluster of exhalant canals, but may have limited, central spongocoel and additional isolated, coarse, vertical, exhalant canals; radially convergent, inhalant canals much smaller and more difficult to trace; skeleton of irregularly branched, megaclone desmas that interlock to form a rigid framework. Cretaceous (Maastrichtian)-Paleogene (Paleocene): Libya, Egypt.—FIG. 167,2a-d. \*S. libycus, Sudr Formation, Maastrichtian, Wadi Natila, Sinai Peninsula, Egypt; a, side view of branched sponge showing characteristic exterior, GIK 1007, ×1; b, transverse section with dark skeleton and light canals, GIK 1012, ×5; c, longitudinal section with light, vertical, exhalant canals and darker, skeletal tracts between, GIK 1913, ×10; d, electron photomicrograph of vertical section showing variously sized, intergrown megaclones, ×15 (Jux, 1994; courtesy of Senckenberg Naturforschende Gesellschaft).
- Trachycinclis POMEL, 1872, p. 110 [\*Spongia ramosa MANTELL, 1822, p. 162; OD]. Listed with same type species as *Homalodora* SCHRAMMEN, 1910, by DE LAUBENFELS, 1955, p. 66; but not recognized as synonym of *Homalodora*, and placed into suborder Uncertain, herein treated as *nomen oblitum* under *Code* Article 23.2 (ICZN, 1999). *Upper Cretaceous:* England.

# Subfamily HETEROSTINIINAE Schrammen, 1924

[nom. transl. REID, herein, ex Heterostiniidae SCHRAMMEN, 1924a, p. 39]

Hollow, cylindrical to cup-shaped or platelike sponges in which epirhyses and aporhyses are typically similar when any are developed; without vertical, tubular aporhyses, except sometimes in stalks; dermalia dichotriaenes; rhizoclonids present; microscleres unknown. [A possible living genus, *Lyidium* SCHMIDT, has desmas of megaclone type but apparently lacks both triaenes and spirasters and cannot be referred certainly to this suborder.] *Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian).* 

- Heterostinia ZITTEL, 1878a, p. 133 [\*H. cyathiformis; OD] [=Valhalla DE LAUBENFELS, 1955, p. 50 (type, Asteroderma expansa SCHRAMMEN, 1901, p. 14, OD), nom. nov. pro Asteroderma SCHRAMMEN, 1901, p. 13, non PERRIER, 1888]. Body cup shaped or funnel-like, flabellate, or forming a convoluted plate, sometimes stalked; both surfaces of skeletal framework with more or less distinct, skeletal pores (ostia, postica), from which simple canals (epirhyses, aporhyses) may extend inwardly; a few vertical aporhyses may traverse stalk if one is present; megaclones usually stout with short epirhabds, in part branched irregularly and in part simply arched or tripodal examples; rhizoclonids usually present, sometimes forming supplemental cortex at surfaces, but may be only sparsely represented in other specimens; supplemental oxeas may occur; dermalia dichotriaenes; microscleres unknown. Cretaceous (Aptian-Campanian): Spain, Aptian; France, England, Cenomanian-Santonian; Germany, Poland, Campanian.—Fig. 168,2a-c. H. obliqua (BENETT), Mucronatenkreide, Campanian, Misburg, Germany; a, fan-shaped example showing paragastral surface,  $\times 0.5$ ; *b–c*, characteristic spicules including arched and tripodal desmas with granular ornament on convex sides and dermal dichotriaenes, ×16 (Schrammen, 1910).
- Amphiplectella SCHRAMMEN, 1901, p. 13 [\*A. piriformis; OD]. Stalked pyriform and variant shapes with deep, narrow, paragastral cavity; outside with ostia of epirhyses that run into wall obliquely downward; interior with postica of aporthyses, which cross with epirhyses within wall; desmas mainly arched forms with fairly simple ends; dermalia dichotriaenes; no other spicules known. Cretaceous (Campanian): Germany.—FIG. 169, 1a-c. \*A. piriformis, Quadratenkreide, Oberg; a, side view of stalked, pyriform sponge with irregularly distributed, inhalant ostia in moderately coarse, dermal mesh, ×0.5; b-c, characteristic spicules includeing desmas and dichotriaenes, ×10 (Schrammen, 1910).

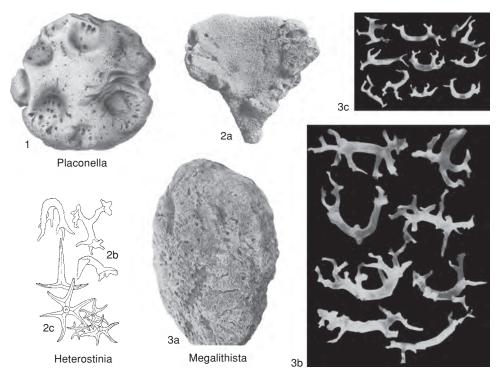


FIG. 168. Pleromatidae (p. 262-265).

- Anomorphites KOLB, 1910 in 1910–1911, p. 249 [\*A. plicatus; SD DE LAUBENFELS, 1955, p. 50]. Convoluted cup or plate, fairly thick walled, small; no apparent canalization; desmas like those of Megalithista ZITTEL; no other spicules known. [Character uncertain due to poor material.] Jurassic (Kimmeridgian): Germany, Switzerland.——FIG. 169,2a-d. \*A. plicatus, Weiss Jura, Kimmeridgian, Sontheim; a, side view of cup-shaped sponge, SSPHG, ×1; b-d, representative spicules, ×40 (Kolb, 1910–1911).
- Gigantodesma SCHRAMMEN, 1924a, p. 62 [\*Pachypoterion auritum SCHRAMMEN, 1910, p. 64; OD]. Cup- or earlike, sometimes marginally lobate, thick walled; exterior with ostia in openings of skeletal mesh, as in Doryderma ZITTEL; other canals and postica not developed; desmas with well-developed zygomes; dermalia dichotriaenes; no other spicules known. [See also Pachypoterion, p. 260 herein.] Cretaceous (Campanian): Germany.-FIG. 169,3a-c. \*G. auritum (SCHRAMMEN), Mucronatenkreide, Misburg; a, cup-shaped example with lobate margins showing ostia in form of open meshes,  $\times 0.5$ ; b, views of a dermal dichotriaene, ×10 (Schrammen, 1910); c, megaclone desmas, ×10 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Holodictyon HINDE, 1884a, p. 50 [\*H. capitatum; OD]. Body inverted conical or nodular, with short, massive stalk and root processes; top rounded or flattened with central depression or cavity; no skeletal pores or canals; desmas similar to those of *Doryderma* ZITTEL, with articulation mainly by oblique, longitudinal facets; no other spicules known. *Cretaceous (Albian):* England.——FIG. 169,4a-c. \*H. capitatum, Upper Greensand, Warminster, Yorkshire; a, side view of obconical holotype with massive stalk, ×0.5; b, upper part of sponge in vertical section, ×1; c, desmas of surface, ×25 (Hinde, 1884a).
- Megalithista ZITTEL, 1878a, p. 130 [\**M. foraminosa;* OD] [?=*Placonella* HINDE, 1884a, p. 47 (type, *P. perforata,* M)]. Pyriform, cylindrical, or top-shaped with deep, narrow, paragastral cavity, or cuplike and thick walled; exterior sometimes transversely wrinkled or with irregular swellings; exterior with ostia of short epirhyses; sometimes locally also with short, irregular furrows in which some ostia are located; interior with postica of similar or larger postica or aporhyses that are vertical in central part of body and arch outwardly around central cavity; desmas typically with arched, central shaft and simple or branching ends, sometimes passing into forms that resemble megarhizoclones; dermalia

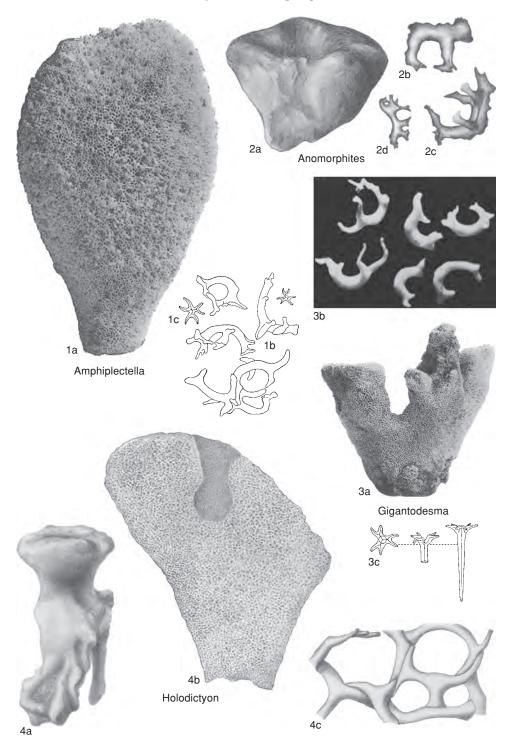


FIG. 169. Pleromatidae (p. 262–263).

possible dichotriaenes; other spicules unknown. [Dermalia unknown according to SCHRAMMEN, 1937, but recorded by ZITTEL, 1878a.] *Jurassic* (*Kimmeridgian*): Germany, Switzerland.——FIG. 168,3*a*-*c*. \**M. foraminosa*, Weiss Jura, Gerstetten, Germany; *a*, side view of medium-sized, top-shaped sponge with irregular, short furrows and scattered, inhalant ostia, ×0.5; *b*, desmas, mainly branching examples, ×5; *c*, desmas, but mainly simpler examples, ×5 (Schrammen, 1937).

Placonella HINDE, 1884a, p. 47 [\*P. perforata; OD]. Flattened, cake-shaped mass with several shallow depressions in convex, upper surface; apertures of skeletal canals (possible aporhyses) in depressions, and of smaller ones (possible epirhyses) scattered on surface between them; desmas like those of Megalithista ZITTEL; dermalia unknown. [Based on a single specimen, regarded by SCHRAMMEN (1937, p. 75) as part of a specimen of Megalithista foraminosa ZITTEL.] Jurassic (Kimmeridgian): Germany.——FIG. 168, 1. \*P. perforata, upper Jura, Würtemberg; upper surface of holotype, possibly base of specimen of M. foraminosa ZITTEL, ×0.5 (Hinde, 1884a).

# Order MONALITHISTIDA Lagneau-Hérenger, 1955

[Monalithistida LAGNEAU-HÉRENGER, 1955, p. 1,564]

Lithistida in which desmas are monaxial or anaxial and developed as rhizoclones, megarhizoclones, sphaeroclones, or variants of these types, but without tetraxial megascleres as either desmas or dermalia; some forms with supplemental monaxons (oxeas etc.) in addition to desmas; a few with supplemental rhizoclonids when desmas are anaxial; modern examples with or without microscleres that may be microrhabds or sigmaspires when present.

[The original Monalithistida of LAGNEAU-HÉRENGER, proposed as a suborder of the order Tetraxonia VOSMAER (ascribed to SCHULZE), comprised the lithistid Monaxonia of SCHRAMMEN that here fall into the suborders Didymmorina, Rhizomorina ZITTEL, and Megarhizomorina SCHRAMMEN. The Didymmorina are here removed to the order Tetralithistida because of discovery of tetraxial dermalia in *Cylindrophyma* ZITTEL of that suborder. The suborder Orchocladina RAUFF, included formerly with the Tetracladina, is added herein because the desmas are thought to be monaxial, not tetraxial, and the Sphaerocladina are regarded as probably derived from the Orchocladina. The order is regarded as probably polyphyletic, and this seems likely also to be true of the Rhizomorina.

For further comments, see suborder descriptions.] Lower Jurassic (Pliensbachian)– Holocene.

# Suborder MEGARHIZOMORINA Schrammen, 1924

# [nom. transl. REID, herein, ex tribus Megarhizomorina SCHRAMMEN, 1924a, p. 69]

Principal megascleres are large, monaxial, rhizoclone-like spicules (megarhizoclones) with firm or loose zygosis or are partly or all unconnected; zygomes more or less like those of megaclones when distinctly developed; supplemental oxeas or other monaxons sometimes present; some with smaller, flattened, rhizoclone-like bodies as ectosomal spicules; no microscleres known. [The original designation tribus is here regarded as equivalent to suborder, as applied to a primary division of the order Monaxonia SCHULZE. The single family, Megarhizidae SCHRAMMEN, was created for fossil genera, Megarhiza SCHRAMMEN and Chalaropegma SCHRAMMEN, but the living Monanthus KIRKPATRICK and Petromica TOPSENT have comparable desmas. Although these modern genera are of uncertain affinities, some features suggest evolution from an ancestor in the order Axinellida.] Upper Cretaceous (Cenomanian–Campanian).

### Family MEGARHIZIDAE Schrammen, 1901

[Megarhizidae SCHRAMMEN, 1901, p. 15]

Diagnosis as for suborder. Upper Cretaceous (Cenomanian–Campanian).

Megarhiza SCHRAMMEN, 1901, p. 15 [\**M. dubia;* OD; not SD DE LAUBENFELS, 1955, p. 52]. Body nodular, truncated conical or cylindrical, built in succession of thin, superimposed layers; outside covered by skeletal cortex, below which are ostia of fine epirhyses that run inward horizontally; axial parts with bundle of vertical, tubular aporhyses that open through postica at summit; desmas large megarhizoclones, to which megaclone-like variants sometimes added; cortex formed from smaller, flattened, rhizoclone-like desmas; oxeas and strongyles

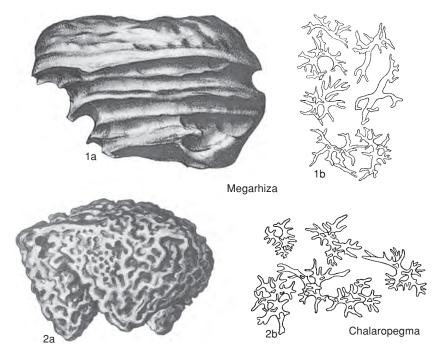


FIG. 170. Megarhizidae (p. 265–266).

also present in interior; microscleres unknown. Cretaceous (Cenomanian-Campanian): France, Cenomanian; Germany, Campanian.——FIG. 170,1a-b. \*M. dubia, Campanian, Germany; side view showing superimposed layers of body, ×1; b, characteristic megarhizoclones, ×10 (Schrammen, 1910).

Chalaropegma SCHRAMMEN, 1910, p. 168 [\*C. cerebriformis; OD]. Body nodular mass with surface covered with sinuous, anastomosing ridges similar to surface convolutions of brain; no apparent canalar features; desmas typical megarhizoclones, loosely coherent, smaller than in Megarhiza SCHRAMMEN; no other spicules known. [Placed into suborder Tetracladina, family Uncertain, by DE LAUBENFELS (1955, p. 59) but contains no tetraclones or triaenes, and was placed into family Megarhizidae by SCHRAMMEN when first proposed.] Cretaceous (Campanian): Germany.--Fig. 170,2a-b. \*C. cerebriformis, Mucronatenkreide, Misburg; a, nodular holotype with coarse, anastomosing ridges, ×0.5; b, characteristic megarhizoclones, ×16 (Schrammen, 1910).

# Suborder SPHAEROCLADINA Schrammen, 1924

[nom. transl. REID, 1968a, p. 23, ex tribus Sphaerocladina (=primary subdivision of order Cryptaxonia SCHRAMMEN) SCHRAMMEN, 1924a, p. 130; sensu REID, 1968a, p. 23]

Desmas anaxial where their character is known, and developed as sphaeroclones,

astroclones, or intermediates, to which irregular variants may be added; centrum of sphaeroclone desmas may contain a granular nucleus that develops by enclosure of a hilumlike depression in ontogeny, or a sinuous canal of unknown origin, which does not represent a crepidal body or axis; some with anaxial, phyllotriaene-like spicules as dermalia; supplemental monaxons may occur; no microscleres in Vetulina, the single living genus. [SCHRAMMEN named the new tribus Sphaerocladina in 1924a, p. 78 in a list to include the family he had named the Sphaerocladinidae in 1910, p. 37. REID in 1968 raised the Sphaerocladina (sensu SCHRAMMEN, 1924a) to suborder rank within the order Cryptaxonia as that name was used by SCHRAMMEN, 1924a, p. 130. The Sphaerocladina are now included in the order Monalithistida Lagneau-Herenger, 1955.] Lower Jurassic (Pliensbachian)-Holocene.

Post-Paleozoic Sphaerocladina comprise two contrasting groups of sponges with comparable desmas but possibly of different origins. These are (a) forms grouped here as Vetulinidae VON LENDENFELD, in which typical desmas are small sphaeroclones that may have a nucleus or a sinuous canal in the centrum and a centrum that is often finely spined; and (b) forms grouped as Lecanellidae SCHRAMMEN, which have large, smooth desmas that are sphaeroclones, astroclones, or intermediates.

In the first group, desma size compares with that of Paleozoic Astylospongiidae, and some genera (Macrobrochus SCHRAMMEN, Ozotrachelus DE LAUBENFELS) resemble astylospongiids in their general morphology. In the second group, size of desmas is more like that of megaclones; and their shapes and zygomes suggest comparison with desmas of the sublithistids Desmatiderma TOPSENT and Crambe VOSMAER, although those of the former are monaxial, not anaxial. Hence these families could have different origins and relationships, although this is not demonstrable. The relationship of forms with small desmas (Vetulinidae) to the Astylospongiidae is also not demonstrable, because of the gap between the latest Paleozoic astylospongiids and the later forms. Grouping is, hence, based here on morphological resemblance of the desmas, without certainty that all forms included are related, although they may be.

# Family VETULINIDAE von Lendenfeld, 1904

[Vetulinidae VON LENDENFELD, 1904c, p. 149] [=Anomocladina SOLLAS, 1885b, p. 492, partim; Anomocladidae sensu SOLLAS, 1888, p. 354, partim; Mastosiidae SCHRAMMEN, 1924a, p. 154]

Desmas small; typically sphaeroclones to which subordinate astroclones may be added, but sometimes with astroclones predominant; centra of sphaeroclones sometimes with granular nucleus, or with sinuous, internal canal, and often with simple or branching spines; zygomes root-, hand-, or cuplike; supplemental monaxons in some; phyllotriaene-like dermalia may occur; no microscleres in single living genus. [The family comprises forms that could be grouped with the middle Paleozoic Astylospongiidae based on the size of their desmas, but these Jurassic to Holocene sponges are mainly of different habits and occur much later in time. There is a living genus, *Vetulina* SCHMIDT, 1880.] *Middle Jurassic* (*Bathonian*)–*Holocene*.

### Subfamily VETULININAE von Lendenfeld, 1904

[Vetulininae VON LENDENFELD, 1904c, p. 149]

Vetulinidae of varying habits, not resembling Astylospongiidae except in character of desmas. *Middle Jurassic (Bathonian)– Holocene.* 

- Vetulina SCHMIDT, 1879, p. 19 [\*V. stalactites; OD]. Irregular, convoluted plates attached by encrusting structures and with more or less marked, concentric growth lines on one surface; both skeletal surfaces with small pores (ostia, postica) from which canals (epirhyses, aporhyses) run radially inward; desmas mainly sphaeroclones whose centra bear branching, rootlike spines that may take part in zygosis when zygomes of other desmas are applied to them; sphaeroclones also grading into astroclones or irregular variants, which may locally be more abundant; supplemental strongyles present; no dermalia; no microscleres in life. ?Upper Cretaceous, Holocene: France, ?Upper Cretaceous; West Indies, Holocene. -FIG. 171, 1a-e. \*V. stalactites, Holocene, West Indies; a-d, characteristic desmas including astroclone, sphaeroclone, irregular desma, and inceptional body, showing nucleus, ×30 (de Laubenfels, 1955); e, side view of type sponge composed of convoluted plates, ×0.5 (Schmidt, 1879).
- Cladodia MORET, 1926b, p. 137 [\*C. kiliani; OD]. Incompletely known from cylindrical fragments; surface with small, skeletal pores; other canalar features unknown; desmas typical sphaeroclones internally, passing outwardly into astroclones; phyllotriaene-like dermalia present; no other spicules known. [Skeleton much like that of *Multipocula* DE LAUBENFELS; possibly based on a stalk of that genus.] *Cretaceous (Santonian):* France.—FIG. 171,2a-c. \*C. kiliani, Nice, characteristic spicules; a, fragment of meshwork; b, sphaeroclone; c, astroclones of outer parts, ×50 (Moret, 1926b; courtesy of Société Géologique de France).
- Cryptodesma SCHRAMMEN, 1924a, p. 132 [\*Asterospongia globosa F. A. ROEMER, 1864, p. 54; OD] [=Asterospagia POMEL, 1872, p. 245, nom. oblit. (type, Asterospongia globosa F. A. ROEMER, 1864, p. 54, SD DE LAUBENFELS, 1955, p. 104), use of name not traceable since first proposed]. Hemispherical, base encrusting; surface with small ostia and stellate groups of larger postica from which short furrows radiate; desmas sphaeroclones; no other spicules known. Cretaceous (Coniacian-Maastrichtian): Germany.——F1G. 171,3a-b. \*C. globosa (F. A. ROEMER); side view showing radiating patterns of furrows that presumably mark positions of subdermal, exhalant canals, Campanian, ×1 (Roemer, 1864); b, sphaeroclone desmas, Emscher,

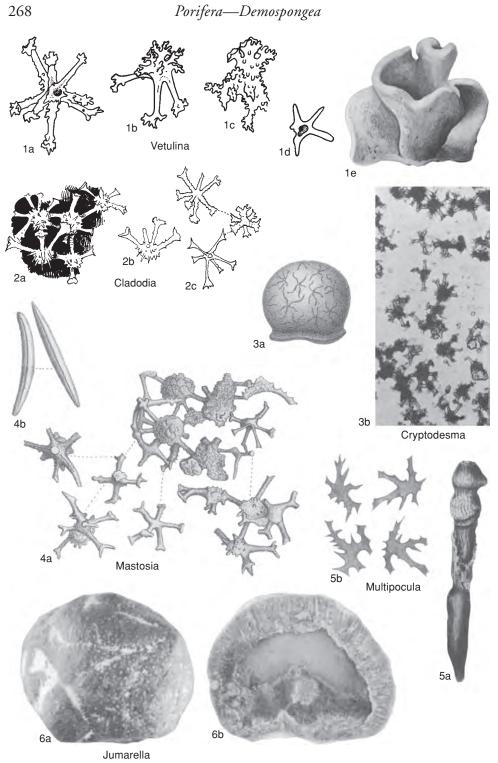


FIG. 171. Vetulinidae (p. 267–269).

Coniacian, Sudmerberges, Germany, ×50 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

- Exodictydia MORET, 1926b, p. 138 [\*E. canalifera; SD DE LAUBENFELS, 1955, p. 63]. Club or cup shaped; surface of club-shaped forms and both surfaces of cup-shaped ones with numerous small, skeletal pores, supposedly ostia, between which there is network of very fine, superficial furrows; small canals, supposedly epirhyses, run inwardly from these pores; aporhyses in axial bundle open through postica at summit in clublike examples, or open in groups into irregular or roughly stellate clefts in internal surface of cuplike sponges; desmas sphaeroclones, in which a sinuous canal may be present; other spicules unknown. Cretaceous (Santonian): France. FIG. 172, 1a-b. \*E. canalifera, Saint-Cyr; a, club-shaped example with numerous inhalant ostia,  $\times 0.5$ ; b, isolated and associated sphaeroclones, about ×50 (Moret, 1926b; courtesy of Société Géologique de France).----FIG. 172,1cd. E. cyathiformis MORET, Saint-Cyr; c, incomplete, cuplike example from above showing interior and wall section,  $\times 0.5$ ; *d*, external surface showing skeleton, ×35 (Moret, 1926b; courtesy of Société Géologique de France).
- Jumarella MEHL & FÜRSICH, 1997, p. 26 [\*J. astrorhiza; OD]. Hemispherical sponge with broad, flat base, without spongocoel but with deep astrorhizae that radiate from several elevated centers distributed over entire upper surface; prominent, radial, narrow canals correspond with small, circular pores; spicules are small sphaeroclones. Jurassic (Bathonian): India.—FIG. 171,6a-b. \*J. astrorhiza, Patcham Formation, Jumara Dome, Kachchh, western India; a, side view of exterior of holotype with astrorhizae, ×1; b, polished, vertical section showing prominent, radial canals in outer part of geodelike preservation, PIW1997I 77, ×1 (Mehl & Fürsich, 1997).
- Mastosia ZITTEL, 1878a, p. 136 [\*M. wetzleri; OD]. Nodular or crustose, some forms hollowed below with nipplelike or fingerlike outgrowths above; upper surface with numerous small, skeletal pores, all of similar size; no skeletal canals, paragastral cavity, or oscula; desma sphaeroclones and some astroclones; centra of sphaeroclones with conical spines in some examples; no other spicules known. [Other spicules noted by ZITTEL, here regarded as extrinsic; cf. ZITTEL, 1878a, p. 136 and SCHRAMMEN, 1937, p. 106.] Jurassic (Kimmeridgian): Germany.-FIG. 171,4a-b. \*M. wetzleri, Weiss Jura, Günzburg; a, isolated, characteristic desmas and fragments of skeletal meshwork, ×64; b, monaxons from surface, here regarded as extrinsic, because similar spicules have a general distribution in sediment (cf. Schrammen, 1937, p. 106), ×64 (Zittel, 1878a).
- Multipocula DE LAUBENFELS, 1955, p. 49, nom. nov. pro Polypora SCHRAMMEN, 1901, p. 16, non M'COY, 1842 [\*Polypora reticulata SCHRAMMEN, 1901, p. 16; OD]. Elongate, irregularly cylindrical, with narrow, tubular, paragastral cavity; exterior with ostia, some of which are in narrow, longitudinal furrows;

desmas small, spiny sphaeroclones and rhizoclonelike variants; further details and other spicules unknown. [Poorly known from one specimen with skeleton preserved as limonite only; possibly a form of *Ozotrachelus* DE LAUBENFELS, to which this name would be senior, since the type species was referred to *Pachytrachelus* SCHRAMMEN (=*Ozotrachelus*) by SCHRAMMEN, 1910, p. 171.] *Cretaceous (Campanian):* Germany.—FIG. 171,5*a*–*b.* \**M. reticulata* (SCHRAMMEN), Quadratenkreide, Misburg; *a*, side view of only known example, ×0.5; *b*, desmas, ×50 (Schrammen, 1901).

- Rhytidoderma SCHRAMMEN, 1937, p. 107 (SCHRAMMEN, 1924b, p. 154, nom. nud.) [\*R. berckhemeri; OD]. Nodular; surface irregularly sculptured, with skeletal pores in interspaces of network of narrow, anastomosing ridges; tubular skeletal canals run inwardly from these pores; desmas small sphaeroclones, similar to those of Mastosia ZITTEL; no other spicules known. [Canals epirhyses teste SCHRAMMEN, 1937, p. 107, but function unknown. Original publication was without diagnosis. First formal diagnosis was by SCHRAMMEN, 1937, p. 107.] Jurassic (Kimmeridgian): Germany.---FIG. 172, 3a-b. \*R. berckhemeri, Weiss Jura, Gerstetten; a, irregular surface with anastomosing ridges and circular pores, ×0.5; b, typical sphaeroclones, ×20 (Schrammen, 1937).
- Tetraspongia TERMIER & TERMIER in MASSA, TERMIER, & TERMIER, 1989, p. 828 [\*T. balmensis; OD]. Figshaped sponges with isolated dichotriaenes with long, bifurcated rays as dermalia, over principalia of alternating layers of sphaeroclones, locally bordered by spongin frameworks in outer part, and frameworks of dicranoclones with aligned, small spines; subcircular pores occurring in latter layers. Cretaceous (Albian): France.-FIG. 172,2a-b. \*T. balmensis, Cretaceous beds, Sainte-Baume, Provence; a, sketch showing disposition of various types of spicules and skeletal elements in layers; 1, framework of spongin; 2, dermal layer of dichotriaenes; 3, layer of sphaeroclones; 4, internal framework of dicranoclones, not to scale; b, drawing of quadrangular distribution of spongin (black) around subjacent, circular, spinose nodes of sphaeroclones, approximately ×40 (Massa, Termier, & Termier, 1989; courtesy of Geobios).

### Subfamily MACROBROCHINAE new subfamily

[Macrobrochinae REID, herein] [type genus, *Macrobrochus* SCHRAMMEN, 1910, p. 174]

Vetulinidae with canal systems like those of typical Astylospongiidae, but much later in time. Upper Cretaceous (Santonian– Campanian).

Macrobrochus SCHRAMMEN, 1910, p. 174 [\*M. emscherensis; SD de LAUBENFELS, 1955, p. 50]. Hemispherical to conical, with small, paragastral depression at summit, or none; sides with

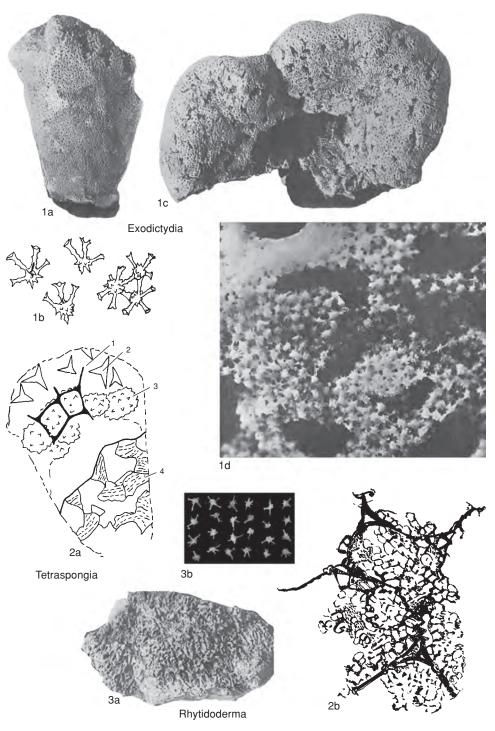


FIG. 172. Vetulinidae (p. 269).

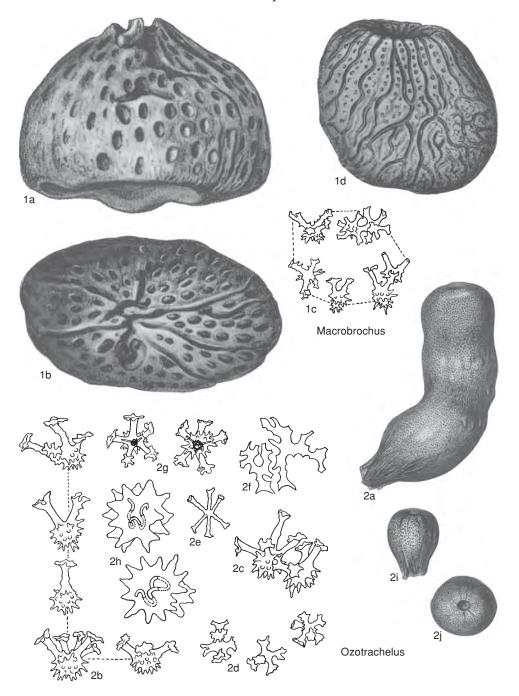


FIG. 173. Vetulinidae (p. 269–272).

conspicuous furrows that radiate from summit and may branch and anastomose downwardly, here regarded as subdermal, aporhytic channels; between these are ostia of radial epirhyses; internal aporhyses not known; desmas small sphaeroclones with spiny centra; other spicules unknown. Cretaceous (Santonian-Campanian): Germany.-FIG. 173, 1a-c. \*M. emscherensis, Westphalicuskreide, Santonian, Ilsede; a, side view showing large ostia on flanks of coarse, hemispherical sponge; b, view of same from above showing ostia and radiating furrows, but no paragastral cavity, ×1; c, characteristic desmas, ×50 (Schrammen, 1910).-—Fig. 173,1d. M. rimosus SCHRAMMEN, Mucronatenkreide, Campanian, Misburg; side view showing ostia, external furrows, and osculum to shallow, paragastral cavity, ×1 (Schrammen, 1910).

Ozotrachelus DE LAUBENFELS, 1955, p. 61, nom. nov. pro Pachytrachelus SCHRAMMEN, 1910, p. 170, non CHAUDOIR, 1852 [\*Pachytrachelus exspectatus SCHRAMMEN, 1910, p. 174; OD as P. expectatus DE LAUBENFELS, 1955, p. 61, nom. null., here accepted as intended to designate P. exspectatus]. Pyriform to cylindrical with rounded top; stalked or with short, root processes; paragastral cavity narrow, deep or shallow; external surface with numerous small, closely spaced ostia, from which simple epirhyses run horizontally or obliquely downward; paragastral surface with postica of aporhyses that curve down toward external surface; incipient aporhyses at summit may form narrow, radiating furrows around paragastral margin; desmas mainly sphaeroclones with spiny centra but including some astroclones; a sinuous canal may occur in centra of sphaeroclones; phyllotriaene-like siliceous plates may occur as dermalia; no other spicules known. Cretaceous (Campanian): Germany.—FIG. 173,2a-h. \*O. exspectatus (SCHRAMMEN), Mucronatenkreide, Misburg; a, side view of subcylindrical sponge with rounded top and distinct osculum,  $\times 0.5$ ; *b*-*h*, characteristic spicules including: b, sphaeroclones with 1 to 5 arms,  $\times$  50; *c*, two connected sphaeroclones,  $\times 50$ ; *d-e*, six-armed astroclones,  $\times 50$ ; *f*, phyllotriaene-like dermalia, ×60; g, sphaeroclone with an internal canal, from above and below,  $\times 50$ ; h, centra showing sinuous canals, ×100 (Schrammen, 1910).-FIG. 173,2i-j. O. conica (F. A. ROEMER), Sudmerberges; i, summit showing ostia, paragastral opening, and radiating furrows; j, side view of top-shaped sponge, ×1 (Schrammen, 1910).

# Family LECANELLIDAE Schrammen, 1924

#### [Lecanellidae SCHRAMMEN, 1924b, p. 154]

Desmas large, developed as astroclones (=anomoclones *sensu* SCHRAMMEN, 1937, *non* RAUFF, 1895), as forms between this type and sphaeroclones, or partly as modified (e.g., elongate, flattened, irregular) variants of astroclones or sphaeroclones; zygomes sometimes scarcely developed; internal canals unknown, although a granular nucleus or marrow is present in some forms; no other spicules known. [Desmas of this family were called anomoclones by SCHRAMMEN (1937) but do not correspond with the anomoclones of the Anomoclonellidae (suborder Orchocladina). SCHRAMMEN's usage seems to have depended on RAUFF's (1895) description of anomoclones as irregular ennomoclones (i.e., sphaeroclones); but anomoclones are here thought to be related to chiastoclones and dendroclones. The large size of the desmas suggests that this group may have had a different origin from the Vetulinidae, although this is not demonstrable. Original publication was without diagnosis but in new combination with type genus. First formal diagnosis was by SCHRAMMEN, 1937, p. 108.] Upper Jurassic (Oxfordian)–Upper Cretaceous.

- Lecanella ZITTEL, 1878a, p. 135 [\*L. pateraeformis; OD]. Funnel- to basinlike or ear shaped, thin or thick walled; both surfaces with small, skeletal pores when well preserved; skeletal canals (epirhyses, aporhyses) simple and radial or absent; desmas typical astroclones and flattened variants, latter with discoidal or arcuate centers in some examples, and then sometimes with a nucleus; zygosis often more or less loose; no other spicules known. Jurassic (Oxfordian-Kimmeridgian): Poland, Oxfordian; Germany, Switzerland, Kimmeridgian.-FIG. 174, 3a-b. \*L. pateraeformis, Weiss Jura, Kimmeridgian, Sontheim, Germany; a, camera lucida drawing of part of inner wall showing relationships of spicules, ×50 (Zittel, 1878a); b, astroclone desmas, ×20 (Schrammen, 1937).
- Poterionella PočTA, 1903a, p. 8 [\**P. trunciformis;* OD]. Sponge, similar to *Lecanella* in exterior form and skeletal structure, thin walled and globose with short-necked osculum and large stalk or stem; walls without distinct ostia so water must have flowed through irregular, interstitial openings; spicules without regular arrangement are large and approach tetraclones in appearance but individual elements difficult to distinguish. *Upper Cretaceous: Czech* Republic, Slovakia.——FIG. 174,5*a*–*b.* \**P. trunciformis,* Beds of Korycany, upper Cenomanian, Kutná Hora; *a*, side view of upper part of globose sponge with a necked osculum, ×0.5; *b*, skeletal fragment of coarse, fused elements, ×40 (Počta, 1903a).
- Regnardia MORET, 1925, p. 487 [\**R. lapparenti;* OD]. Known incompletely from cylindrical fragments, which are traversed by longitudinal, skeletal canals (presumed to be aporhyses) in axial parts; principal

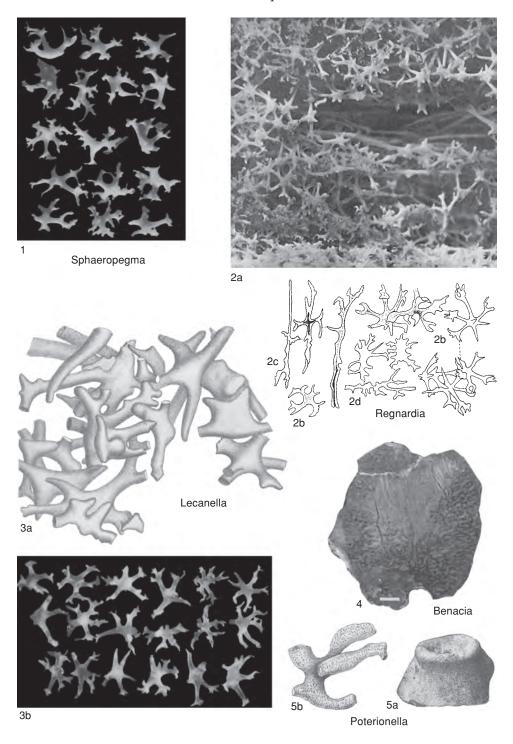


FIG. 174. Lecanellidae and Uncertain (p. 272-274).

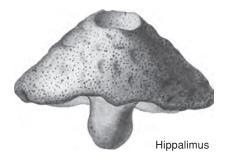


FIG. 175. Uncertain (p. 274).

desmas between typical astroclones and sphaeroclones, with arms well developed and ending in zygomes on one side of center; these forms grade into flattened and irregular variants and into elongate desmas suggesting irregular megaclones in axial parts; some desmas with granular marrow; no other spicules known. *Cretaceous (Cenomanian):* France.——FIG. 174,2*a*–*d.* \**R. lapparenti*, Sablons; *a*, skeleton showing normal desmas and elongate variants, ×20; *b*–*d*, characteristic spicules including normal desmas, elongate desma variants, and irregular variants, magnification not given but approximately ×25 (Moret, 1926b; courtesy of Société Géologique de France).

Sphaeropegma SCHRAMMEN, 1937, p. 109 (SCHRAMMEN, 1924b, p. 154, nom. nud.; SCHRAMMEN, 1936, p. 186, nom. nud.) [\*S. nuda; OD]. Globular with central cavity, thick walled; outside with small, skeletal pores (ostia); paragastral surface with postica of tubular aporhyses that are vertical in axial parts but

arch outwardly following form of growth layers around them; desmas like those of *Lecanella* ZITTEL; no other spicules known. [Original publication was without diagnosis. First formal diagnosis was by SCHRAMMEN, 1937, p. 109.] *Jurassic (Kimmeridgian):* Germany.——FIG. 174, *I.* \**S. nuda*, Weiss Jura, Streitberg; astroclone desmas, ×20 (Schrammen, 1937).

### Family UNCERTAIN

Benacia KRAUTTER, 1996, p. 308 [\*B. princeps; OD]. Nodular sponge, without spongocoel, irregularly radial, inhalant canals in walls converging to axial cluster of vertical, exhalant canals; skeleton of very small, four-rayed anomoclones. Lower Jurassic (Pliensbachian): Italy.—174,4. \*B. princeps, Misonekalk, southern Alps; vertical section of holotype showing axial cluster of exhalant canals and surrounding irregularly convergent, inhalant canals in outer part of skeleton, S 758, ×0.5 (Krautter, 1996).

# Order and Suborder UNCERTAIN

Hippalimus LAMOUROUX, 1821, p. 77 [\*H. fungoides; OD]. Mushroom-shaped sponge with dense, dermal layer on flat base around stalk; summit with broad, deep spongocoel and numerous moderately distinct, inhalant ostia in surrounding upper dermal layer; spicule structure unknown. Upper Cretaceous: Europe.——FIG. 175. \*H. fungoides, Upper Cretaceous blue marl or clay, Calvados, Normandy, France; side view of sponge with stalked base and conical, upper part with distinct spongocoel, ×0.5 (Lamouroux, 1822).

# MESOZOIC AND CENOZOIC DEMOSPONGES: RHIZOMORINA AND SUBORDER UNCERTAIN

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# Suborder RHIZOMORINA Zittel, 1895

#### [Rhizomorina ZITTEL, 1895, p. 52]

Desmas monaxial and all developed as rhizoclones, and never as typical amphitrider-like dendroclones or chiastoclones, although some may resemble simple dendroclones; tetraxial dermalia always absent; some with special ectosomal desmas, in the form of flattened and strongly branched rhizoclones; skeletal framework compact, semifibrous, or with well-developed, composite, skeletal fibers; supplemental oxeas in some; modern examples with microrhabds, sigmaspires, or no microscleres. [In 1895 ZITTEL subdivided the Lithistidae into 5 suborders (tribus) based on so-called defining families (Tetracladina, Eutaxicladina, Anomocladina, Megamorina, and Rhizomorina).] Cambrian-Middle Holocene.

This suborder is understood in SCHRAM-MEN's (1901, 1910) restricted sense to exclude all genera with tetraxial dermalia that were included by ZITTEL (1878a) and RAUFF (1893, 1894, 1895) and that are now referred to the suborders Dicranocladina SCHRAMMEN (Corallistes SCHMIDT, Pachinion ZITTEL) and Pseudorhizomorina SCHRAMMEN (Macandrewia GRAY) of the order Tetralithistida LAGNEAU-HÉRENGER. Rhizoclones are understood as comprising all the four types of desmas (linear, irregular, bipolar, radiate) shown in RAUFF's original figure (1893, fig. 26), which was copied mainly from ZITTEL's (1878a, pl. 3,4) figure of desmas of Hyalotragos patella (GOLDFUSS), in which all these types are present together. Absence of typical amphitrider-like dendroclones and chiastoclones is mentioned in diagnosis because of correspondence between bipolar rhizoclones and the simplest types of dendroclones. Rhizoclones alone are not regarded as distinctive of any suborder, because rhizoclones occur also as supplementary desmas in various Dicranocladina, Didymmorina, and Orchocladina and as the principal desmas of the Pseudorhizomorina and Megarhizomorina.

Family classification of fossil Rhizomorina presents several problems, which need brief explanation.

(a) SOLLAS (1888) distinguished four families in dealing with modern forms: (i) Azoricidae SOLLAS, without microscleres or special dermalia; (ii) Cladopeltidae SOLLAS (no generic type; now Siphonidiidae von LENDENFELD), without microscleres but with dermalia in the form of flattened, strongly branching rhizoclones; (iii) Neopeltidae SOLLAS, with monaxial plates as dermalia and with amphiaster microscleres; and (iv) Scleritodermatidae SOLLAS, without special dermal megascleres but with sigmaspire microscleres. Most of the fossils are azoricid in the sense of lacking microscleres and special dermalia; but it cannot be said whether these conditions are original, or due to loss of the spicules of concern after death.

(b) In SCHRAMMEN's later classifications (1924a, 1937), fossil Rhizomorina were referred to 18 families with fossil type genera based on various details of habit, wall thickness, canalization, and the form of the desmas, to which occurrence of special dermal desmas is added in some instances. Each consists of a few genera only or a single genus only. While forms grouped together are usually acceptable as related, the grounds for distinguishing some genera and families are tenuous. The most extreme example is seen in treatment of forms placed by ZITTEL (1878a) into his genera *Verruculina* ZITTEL

and Amphithelion ZITTEL, the latter regarded by ZITTEL (1878a, p. 123) as possibly a subgenus only. Amphithelion was treated as a synonym of Verruculina by HINDE (1884a), MORET (1926b), and initially by SCHRAMMEN (1910); but species at first referred by SCHRAMMEN to Verruculina sensu HINDE were divided between eight genera and five families in his later work (SCHRAMMEN, 1924a, 1937; see Scleritodermatidae below, p. 300). All species referred to these taxa are essentially similar in (a) habitus (funnel-like, flabellate, or variant habits); (b) general skeletal structure (framework fibrous internally with more or less compact, surface layers), and the form of skeletal pores (pustular to papilliform on the exhalant surface, and usually on both surfaces). Some criteria relied on by SCHRAMMEN (wall thickness, relative size of ostia and postica) are of doubtful value even at subgeneric level. Other criteria cited included presence (Verruculinidae SCHRAM-MEN) or absence (other families) of special dermal desmas and occurrence of distinct, internal canals in some genera (Heterothelionidae SCHRAMMEN) but not others. Of these, the first may be simply dependent on accidents of preservation or on whether the special dermal desmas were united by zygosis in life, the second, simply on the relative size of the skeletal meshes and the canals of the soft parts. SCHRAMMEN's methods are also hard to apply to species apart from those he cited or to imperfectly known species or genera.

(c) MORET (1926b) made a general distinction between Rhizomorina with fibrous and nonfibrous skeletons, also used by LAGNEAU-HÉRENGER (1962) to group various families of SCHRAMMEN's system. This distinction was not made by SCHRAMMEN (1924a) and was rejected by DE LAUBENFELS (1955), who noted the occurrence of intermediate structures. Zoologists since SOLLAS (1888) have placed fibrous and nonfibrous species into the single genus *Azorica* CARTER, and MORET himself accepted treatment of *Azorica* in this manner.

Classification here is based partly on compromise between these divergent opinions and partly on the writer's observations in work preparatory to this volume. First, four types of skeletal structure are distinguished.

(1) In compact, skeletal structures, there are typically no mesh spaces larger than those formed by the union of individual desmas. The desmas may unite without order, or some may have more or less marked, longitudinal and transverse alignments. When alignment of desmas is pronounced, longitudinal sections have strandlike trains of desmas that spread out toward one or both surfaces of the skeletal framework or from the axial parts to the surface in for example, solid pyriform sponges.

(2) In semifibrous structures, as in only a few Jurassic genera, the skeletal framework is internally lacunar, as in fibrous types, but true, composite, skeletal fibers are absent. The internal lacunae may extend in all directions or have a general, longitudinal alignment and may then resemble fine, longitudinal canals or form spaces between radial, septalike lamellae. The desmas forming interlacunar trabeculae or lamellae have corresponding irregular or longitudinal alignments. Irregular and strongly lacunar skeletal structures of this type may locally approach true, fibrous structure.

(3) In truly fibrous skeletons, the skeletal framework is lacunar and consists of a threedimensional network of stout, composite skeletal fibers, in which individual rhizoclones are densely matted together. The fibers may have no directional alignment, or some may be aligned longitudinally and spread out toward skeletal surfaces or from an axial region to the surface. Longitudinal fibers may lack any special arrangement or be arranged and united to form perforated, septalike, radial lamellae.

(4) Pseudofibrous structure is produced by strong canalization of compact, skeletal meshwork, which may assume a fibrous aspect if skeletal canals (usually epirhyses) are close together, and their lumina are wider than the intervening skeletal partitions. A similar development may occur at skeletal surfaces if external meshwork is formed between subdermal spaces on the soft parts.

The first three types of skeletal structures are then used as the principal basis for arranging the post-Paleozoic Rhizomorina into three superfamilies, here called Azoricoidea, Platychonioidea, and Scleritodermatoidea. These are ascribed nominally to the authors of the corresponding families Azoricidae SOLLAS, Platychoniidae SCHRAMMEN, and Scleritodermatidae SOLLAS, as required by the Code (ICZN, 1999), although comprising new assemblages. It is not claimed that the three types of skeletal structure are completely distinct or completely distinctive or that all forms with the same type of structure must always be closely related; but their use in this manner is convenient, has at least some further justification, and does not appear contrary to any more evident relationships. Further details are as follows.

(1) The families Azoricidae SOLLAS and Cnemidiastridae SCHRAMMEN, in which skeletal structure is compact, comprise the superfamily Azoricoidea. The family Azoricidae is taken as comprising the living azoricids, plus all fossils with compact, skeletal structure in which skeletal canalization is either absent, or of normal types when present. The Cnemidiastridae are distinguished by special canalization, which in one form resembles that of some Orchocladina (e.g., *Archaeoscyphia* HINDE).

(2) Jurassic forms with compact to semifibrous skeletal structure, which appear to be all closely related, are placed in the Platychonioidea, with families Discostromatidae SCHRAMMEN (1924a; =Hyalotragosidae SCHRAMMEN, 1937) and Platychoniidae SCHRAMMEN distinguished by differences in habit and canalization. An additional feature of this group is that rhizoclones are often larger than in most later genera.

(3) Genera with truly fibrous structures and a few that appear to be relatives but lack fibrous structure are grouped as Scleritodermatoidea because fibrous, skeletal structure occurs in the living scleritodermatids *Scleritoderma* SCHMIDT, *Microscleroderma* KIRKPATRICK, and *Taprobane* DENDY. Fossils that resemble these genera in having fibrous structure (but without conspicuous longitudinal fibers) and general habit (mainly funnel-like or flabellate, with pustulelike oscules) are included as members of the family Scleritodermatidae SOLLAS. Those with longitudinal fibers are placed into families Jereicidae SCHRAMMEN, comprising jereiform sponges, and Seliscothonidae SCHRAMMEN, resembling some Discostromatidae.

Treatment of Azorica CARTER as type of an assemblage that is characterized by compact, skeletal structure conflicts with MORET's (1926b) description of this genus as fibrous. Investigation of the holotype of A. pfeifferae CARTER, type species of *Azorica*, showed it to have compact, skeletal meshwork, with no trace of fibrous structure except in pseudofibrous, external meshwork related to subdermal spaces. This sponge is closely similar to Coscinostoma SCHRAMMEN, accepted as nonfibrous by MORET (1926b), except for occurrence of an external cortex, which this canalized meshwork underlies. The structure of "A." chonelloides (DOEDERLEIN), which MORET (1926b, p. 70) cited in ascribing fibrous structure to Azorica, is instead like that of scleritodermatids, and the treatment of this sponge as an Azorica is herein thought to be clearly mistaken.

Last, DE LAUBENFELS (1955, p. 45) also remarked that "... various genera (as *Scytalia, Chonella,* and others) have been interpreted divergently by different authors ..." in regard to whether skeletal structure is fibrous or nonfibrous. In *Scytalia* ZITTEL, as pointed out by MORET (1926b, p. 97), the skeleton is essentially compact but may be locally pseudofibrous due to canalization. *Cytoracia* POMEL (1872, p. 228) was described as fibrous by LAGNEAU-HÉRENGER (1962) but is considered herein to be similar to *Aulosoma* SCHRAMMEN (=*Scytalia sensu* ZITTEL in part).

*Chonella* ZITTEL was regarded as fibrous by ZITTEL (1878a) and as differing chiefly from the fibrous *Seliscothon* ZITTEL in lacking a radial arrangement of fibers to form septumlike lamellae. MORET (1926b, p. 95) treated *Chonella* as nonfibrous and thought that fibrous structure occurs only exceptionally in young specimens, disappearing in adults. SCHRAMMEN (1924a), in contrast, divided Chonella sensu ZITTEL between two genera, Chonella s.s., placed in the family Chonellidae SCHRAMMEN (=Azoricidae SOLLAS herein), and Pachyselis SCHRAMMEN, placed in the family Seliscothonidae SCHRAMMEN. C. tenuis (F. A. ROEMER), type species of *Chonella*, as known to the writer, is clearly nonfibrous; but Pachyselis auriformis (F. A. ROEMER) (=C. auriformis, ZITTEL, 1878a) has a fibrous skeletal structure, described by ROEMER (1864, p. 51) and figured by SCHRAMMEN (1910, pl. 19,3-4). On the other hand, some specimens identified by SCHRAMMEN before 1910 as C. auriformis (e.g., BMNH P7436) are true, nonfibrous Chonella. Hence divergent descriptions in this instance seem to be due to confusion of the two different genera (Chonella s.s. and Pachyselis) as Chonella, and two different species as C. auriformis.

# **ORIGIN AND RELATIONSHIPS**

Comment on these topics seems desirable because of the importance of this group among Mesozoic fossils, but the available evidence, frankly, is inadequate for more than speculation.

How the Rhizomorina are related to other Demospongea is hard to assess because of two contrasting indications and lack of other evidence. First, bipolar rhizoclones are not distinguishable from the simplest type of orchocladine dendroclone, and linear rhizoclones accompany dendroclones in various Orchocladina. This suggests origin of the Rhizomorina from the Orchocladina by rhizoclones becoming predominant, although none of the Rhizomorina contains typical dendroclones or chiastoclones. Cnemidiastrum ZITTEL of the Azoricoidea, family Cnemidiastridae, has canalization similar to that of Archaeoscyphia HINDE of the Orchocladina, for example. Supposed Carboniferous records of Cnemidiastrum, however, are based on isolated desmas without diagnostic value, and the skeleton is compact with no suggestion of orchocladine

fibers. In contrast, living Scleritodermatidae Scleritoderma SCHMIDT) have (e.g., sigmaspire microscleres, apparently identical with those of the choristid Craniellida and a few monaxonid sponges (e.g., Tentorina BUR-TON, order Spirastrellida). Unless the Orchocladina were allied to modern forms with sigmaspires, this could indicate that Rhizomorina have had more than one origin. The microscleres of scleritodermatids suggest relationship to nonlithistid sponges with sigmaspires, but their fibrous skeletal structure suggests a connection with the Carboniferous Haplistion YOUNG & YOUNG, which occurs in Ireland and Texas with anthaspidellid Orchocladina and seems likely to be derived from them.

It is also possible in theory for a seemingly rhizomorine sponge to have evolved from the Pseudorhizomorina by loss of tetraxial dermalia in either phylogeny or fossilization. *Neopelta* SOLLAS, with amphiaster microscleres and monaxial discs as dermalia, is here placed with the Pseudorhizomorina; but a fossil example, in which these loose spicules were absent, would appear rhizomorine. Monaxial discs similar to *Neopelta* dermalia have been found loose in Cretaceous sediments (SCHRAMMEN, 1924a, pl. 5,6).

Stratigraphic evidence is also not helpful. Most post-Paleozoic Rhizomorina are from the Upper Jurassic or Cretaceous, and most are from Europe. Jurassic and later faunas are also largely different. The predominant Jurassic forms represented by few genera but by numerous individuals in the main outcrops are the cnemidiastrid Azoricoidea and the Platychonioidea, although a few Azoricidae and Scleritodermatoidea are also known. In contrast, nearly all later genera are Azoricidae or Scleritodermatoidea. Hence there seems to have been a post-Late Jurassic extinction of the characteristically Jurassic forms and a burst of new evolution before the Aptian when the characteristic Cretaceous fauna made its first-known, major appearance (LAGNEAU-HÉRENGER, 1962). On the other hand, presence in the Upper Jurassic of the specialized azoricid Cytoracia POMEL and a fully evolved jereicid, Moretispongia BREISTROFFER, suggests that genera now known first from the Cretaceous may already have existed elsewhere.

Comparing all Mesozoic genera, it is tempting to postulate evolution from compact through semifibrous to true, fibrous skeletons. On the other hand, origin of these genera from the fibrous Carboniferous Haplistiidae would require the opposite. Different authors might prefer either picture.

The Upper Jurassic forms seem to show that at least five main lines of descent had already been established, long enough to be well differentiated (Cnemidiastridae, Azoricidae, Platychonioidea, Jereicidae, Scleritodermatidae). Whether Cnemidiastridae and Azoricidae, which share compact skeletal structure, had a common origin is uncertain; but resemblance of some Cnemidiastridae to some Orchocladina in their skeletal canalization seems fairly likely to be convergent. Of the Platychonioidea, Platychonia ZITTEL is structurally a possible ancestor of the fibrous Scleritodermatidae and is also known earlier than most other Jurassic genera (middle Lias, upper Pliensbachian, England). Jereicidae and Seliscothonidae could then be interpreted as representing divergent side lines from this line of descent; but jereicids might also be pictured as derived from a pseudofibrous prototype by acquiring a condition that is fibrous morphologically in relation to canalization. The lamellofibrous structure of some species of Seliscothon ZITTEL, type genus of Seliscothonidae, might be thought to point to origin of Platychonioidea from Hyalotragos ZITTEL, for example, by way of *Proseliscothon* SIEMIRADZKI in which this type of structure is partially anticipated, although this mode of origin seems less likely than that these genera are convergent.

# Superfamily AZORICOIDEA Sollas, 1888

[nom. transl. REID, herein, ex family Azoricidae SOLLAS, 1888, p. clviii] [=Cladopeltidae SOLLAS, 1888, p. clvii]

Meshwork of the skeletal framework compact, unless disrupted by canalization and then pseudofibrous in some genera; most

without special dermalia, but some with flattened, strongly branching, ectosomal rhizoclones, which may not be articulated; supplemental oxeas in some; modern examples without microscleres in life. [The family name Cladopeltidae SOLLAS (1888, p. clvii) is senior to Azoricidae SOLLAS by page priority but is invalid due to not being based on the name of a genus. The type genus Azorica CARTER is interpreted in terms of its type species A. pfeifferae CARTER, in which internal, skeletal meshwork is compact in CARTER's holotype, and is not considered to include the fibrous "A." chonelloides (DOEDERLEIN) of zoologists (e.g., SOLLAS, 1888) and MORET (1926b), which is a scleritodermatid. The fossils thought nearest to Azorica are Chonella ZITTEL, Coscinostoma SCHRAMMEN, and Pliobolia POMEL (Azoricidae, Azoricinae herein).] Upper Jurassic-Holocene.

#### Family AZORICIDAE Sollas, 1888

[Azoricidae Sollas, 1888, p. clviii] [=Leiodermatiidae von Lendenfeld, 1904c, p. 145]

Sponges of various habits in which skeletal canalization of normal types, when present, and never of special types distinctive of Cnemidiastridae; internal meshwork of skeletal framework compact unless strongly canalized, when pseudofibrous structure may occur, and entirely confused or having traces of longitudinal and transverse alignment of desmas; skeletal cortex present or absent, in some instances covering lacunar, subdermal stratum when present; a few with special flattened and strongly branched, ectosomal desmas, which may not be articulated; supplemental monaxons may occur; modern examples with microrhabds or no microscleres. [Rhizomorina grouped here were placed into nine separate families by SCHRAMMEN (1924a, 1937; Azoricidae SOLLAS, Aulosomidae SCHRAMMEN, Chonellidae SCHRAMMEN, "Cladopeltidae" SOLLAS (=Siphonidiidae von Lendenfeld), Cytoraciidae SCHRAMMEN, Leiochoniidae SCHRAMMEN, Lophiophoridae SCHRAMMEN, Oncophoridae SCHRAMMEN, Trachynotidae SCHRAMMEN), but all have compact skeletal

structure and normal types of canalization when any is present. All are, hence, included in one family here; but various former families based on genera included are adopted as subfamilies for convenience.] Upper Jurassic-Holocene.

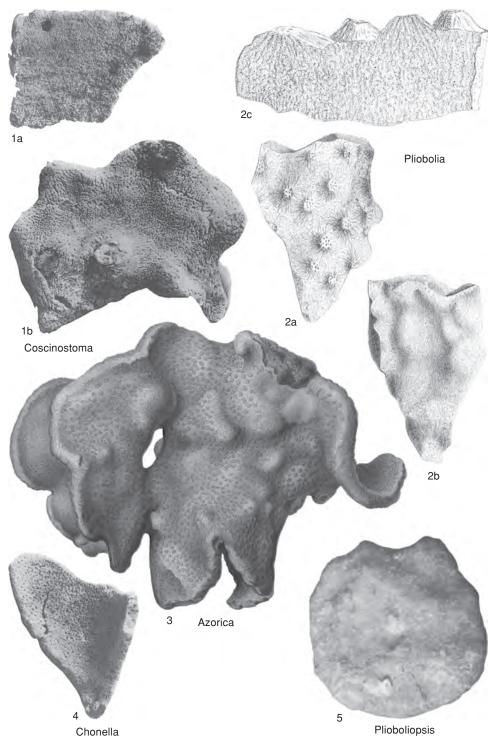
#### Subfamily AZORICINAE Sollas, 1888

[nom. transl. REID, herein, ex Azoricidae SOLLAS, 1888, p. clviii] [=Chonellidae SCHRAMMEN, 1924a, p. 83; Trachynotidae SCHRAMMEN, 1924a, p. 82; Plinthodermatiidae DE LAUBENFELS, 1955, p. 49]

Funnel-like and flabellate sponges that usually have distinct and similar epirhyses and aporhyses; surfaces of skeletal framework smooth or with superficial furrows, which may form radiating patterns on paragastral surface; some with additional external, cortical meshwork, pierced by small, intracortical ostia that open into underlying, passages; supplemental subcortical monaxons may occur; no microscleres in living examples. [Some fossil genera (Cnemaulax POMEL, 1872, Coscinostoma SCHRAMMEN, 1910, and Pliobolia POMEL, 1872) are similar to Azorica CARTER but are treated as distinct because their loose spiculation is unknown.] Cretaceous (Aptian)-Holocene.

Azorica CARTER, 1873, p. 439 [\*A. pfeifferae; OD] [=Cisselia POMEL, 1872, p. 119, nom. oblit.]. Funnel-like in some examples but usually flabellate, gently or strongly convoluted, or with convoluted walls anastomosed to form cluster of secondary funnels; inhalant surface of soft parts with fine pores only, but exhalant surface with scattered, more or less prominent, small oscules; inhalant side of skeletal framework with thin, external, skeletal cortex and small, intracortical pores, which open into closely spaced, subcortical canals that have more or less regular alignment toward skeletal margin, or with open, longitudinal furrows if cortical layer absent; ostia of epirhyses in floors of subcortical canals or open furrows; epirhyses and aporhyses more or less sinuous; postica of aporhyses in furrows or subcortical canals that radiate from oscules of paragastral surface; oscules outlined by dense, nonporous, external, cortical layer, which may not be continuous between them; supplemental oxeas but no microscleres in living species. [Skeletal structure described here from CARTER's type material of A. pfeifferae.] Cretaceous (?Santonian), Holocene: France, ?Santonian; cosmopolitan, Holocene .-FIG. 176,3. \*A. pfeifferae, Atlantic Ocean, Holocene; side view of moderately complex specimen, with convoluted walls and prominent, inhalant pores, ×0.85 (Topsent, 1892).

- Chonella ZITTEL, 1878a, p. 116 [\* Cupulospongia tenuis F. A. ROEMER, 1864, p. 51; OD] [=Pumicia POMEL, 1872, p. 118, nom. oblit.]. Funnel-, cuplike, or flabellate, some examples being irregularly convoluted or with infolded margins united to form secondary funnels; stalked or not; when rigid skeleton completely developed, both surfaces with thin, external, cortical layer with numerous small, intracortical ostia or postica, underlain by labyrinthine, subcortical canals from which sinuous epirhyses or aporhyses run into internal framework; surfaces with irregular furrowing and exposed ostia or postica when cortical meshwork absent; supplemental oxeas may occur; microscleres unknown. Cretaceous (Aptian)-Holocene: Spain, Aptian; Czech Republic, Slovakia, Cenomanian; France, Santonian; Germany, Cenomanian-Campanian; Algeria, Miocene; Mediterranean Sea, Holocene.-FIG. 176,4. \*C. tenuis (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; small, flabellate example showing paragastral surface that is mostly noncorticate, ×1 (Schrammen, 1910).
- Cnemaulax POMEL, 1872, p. 213 [\*C. verrucosus; OD]. Bowl shaped, attached eccentrically, not stalked; lower (inhalant) surface with finely furrowed, irregular ridges and bosses, between which rest of surface forms depressed, poriferous areas; skeletal canals more or less radial; paragastral surface with postica of aporhyses at centers of groups of radiating, superficial furrows, which may reticulate from one group to another; loose spicules unknown. [Skeleton incompletely known, but the genus was compared by POMEL (1872) with Azorica CARTER (as Cisselia POMEL, 1872). The same species of POMEL (1872) was transferred to Chonella ZITTEL by MORET (1924, p. 14), but the paragastral surface of type species agrees with Coscinostoma SCHRAMMEN; and the external surface is unique, unless poriferous areas mark indentations by foreign bodies.] Neogene (Miocene): Algeria, Spain.—FIG. 177, 1a-b. \*C. verrucosus, Djebel Djambeida, Algeria; a, broad, upper or paragastral surface with numerous exhalant postica at centers of radiating canals; b, lobate to ridged, lower or inhalant surface, ×0.5 (Pomel, 1872).
- Coscinostoma SCHRAMMEN, 1910, p. 162 [\*C. fragilis; SD SCHRAMMEN, 1924a, p. 113]. Irregularly funnellike or flabellate, stalked or not; inhalant side of skeleton with finely porous, external cortex, under which labyrinthine, subcortical canals have locally longitudinal alignment; ostia of internal epirhyses in floors of these canals, exposed in furrows when cortex absent; paragastral surface with small pores in furrows that radiate from numerous centers, at which small, pitlike depressions may be present; no loose spicules known. [Subcortical canals of the inhalant side were not recognized by SCHRAMMEN but are present in material that he identified; soft parts were probably similar to those of Azorica CARTER, but genus apparently lacks paragastral skeletal cortex and oscules.] Cretaceous (Aptian-Campanian): Spain, Aptian; France, Santonian; Germany, Poland, Campanian.—FIG. 176,1a. \*C. fragilis,





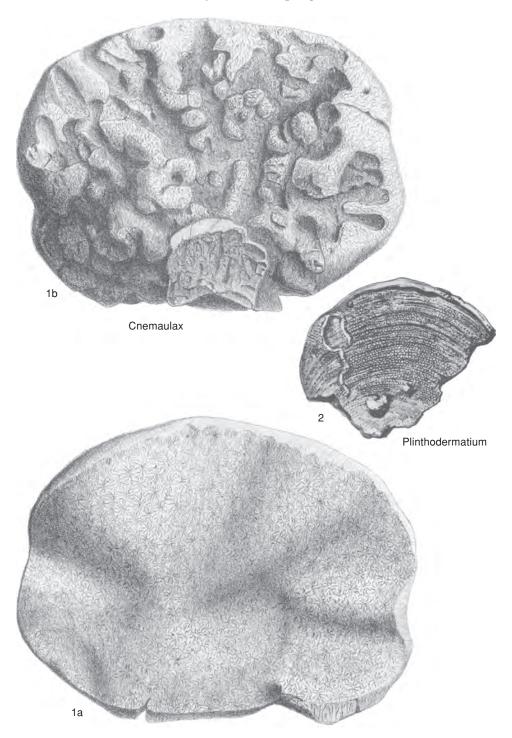


FIG. 177. Azoricidae (p. 280–283).

Quadratenkreide, Campanian, Oberg, Germany; paragastral surface with pitlike depressions and canals that radiate from them, ×1 (Schrammen, 1910).——FIG. 176,*1b. C. auricula* SCHRAMMEN, Mucronatenkreide, Campanian–Maastrichtian, Misburg, Germany; outer or lower surface showing skeletal pores in irregular growth form, ×1 (Schrammen, 1910).

- Plinthodermatium SCHRAMMEN, 1910, p. 158 [\*P. exile; OD]. Flabellate, earlike or fanlike, or forming an incomplete funnel; one surface of skeletal framework, presumed to be external, with conspicuous, transverse corrugations linked by short, oblique or longitudinal furrows, surface has scaly appearance; closely spaced, small, skeletal pores, presumed to be ostia, in floors of these furrows; opposite surface coated by smooth, skeletal cortex; skeletal surface beneath this has apertures of skeletal canals in longitudinal furrows, which radiate from base to skeletal margin; no loose spicules known. Cretaceous (Campanian): Germany.-FIG. 177,2. \*P. exile, Mucronatenkreide, Misburg; external view with transverse corrugations linking short, oblique or longitudinal furrows, ×0.5 (Schrammen, 1910).
- Pliobolia POMEL, 1872, p. 212 [\*P. vermiculata; OD] [=Trachynoton DE LAUBENFELS, 1955, p. 49, nom. nov. pro Trachynotus SCHRAMMEN, 1924a, p. 112 (type, Coscinostoma auricula SCHRAMMEN, 1910, p. 163, OD), non LATREILLE, 1829]. Flabellate, earlike or platelike, stalked or not; external, skeletal surface finely porous; canals more or less sinuous; paragastral surface with postica in elevated groups or in hollows at tops of conical prominences, and with anastomosing, superficial furrows that radiate from groups of postica; surfaces may be coated by layer of flattened and strongly branching, ectosomal desmas. [Pliobolia was equated with Coscinostoma SCHRAMMEN by DE LAUBENFELS (1955, p. 47) and is probably similar to that genus, but is here equated with Trachynoton following BREISTROFFER (1949, p. 103).] Cretaceous (Campanian)-Neogene (Miocene): Germany, Poland, Campanian; Algeria, Spain, Miocene.--FIG. 176,2a-c. \*P. vermiculata, Miocene, Djebel Djambeida, Algeria; a, older specimen with postica at tops of conical prominences, as seen from paragastral surface, with postica and radiating furrows; b, irregularly nodose undersurface of same,  $\times 0.5$ ; c, vertical section,  $\times 1$  (Pomel, 1872).
- Plioboliopsis BRIMAUD & VACHARD, 1986, p. 310 [\*P. hispanica BRIMAUD, 1984, p. 421, nom. nud.; OD]. Sponge a flattened, thick-walled, stalked cup; inhalant pores small, simple, and numerous on lower face; exhalant pores on upper face a little larger and surrounded by short, radial furrows. [Species was proposed in BRIMAUD's unpublished thesis.] Neogene (Miocene): Spain.—FIG. 176,5. \*P. hispanica (BRIMAUD), Tortonien strata, upper Miocenee, Almeria, southern Spain; upper surface with faint, exhalant openings and canals, IPM R6951, ×1 (Brimaud & Vachard, 1986; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

### Subfamily CYTORACIINAE Schrammen, 1924

# [nom. transl. et correct. REID, herein, ex Cytoraceidae Schrammen, 1924a, p. 81]

Pyriform or globular to irregularly nodular sponges, simple or compound, in which ostia are restricted to depressed poriferous areas, between which skeletal surface is more or less conspicuously furrowed. Upper Jurassic-Neogene (Miocene).

- Cytoracia POMEL, 1872, p. 228 [\*Stellispongia impressa F. A. ROEMER, 1864, p. 49; SD SCHRAMMEN, 1910, p. 153; not Stellispongia grandis F. A. ROEMER, 1864, p. 49, SD DE LAUBENFELS, 1955, p. 47 [=Cytoracea ZITTEL, 1878a, p. 115, nom. null.; Cnemispongia QUENSTEDT, 1877 in 1877-1878, p. 258 (type, C. goldfussii, SD DE LAUBENFELS, 1955, p. 47); Coelocorypha ZITTEL, 1878a, p. 128 (type, Siphonocoelia nidulifera ROEMER, 1864, p. 29, SD DE LAUBENFELS, 1955, p. 45)]. Solitary or compound sponges of pyriform or globular to irregularly nodular shapes, with narrow, tubular, paragastral cavities, and with ostia restricted to broad or pitlike, depressed, poriferous areas, between which surface forms more or less prominent ridges; external surface typically strongly furrowed between poriferous areas, with some furrows radiating from margins of paragastral oscula, others crossing ridges between poriferous areas transversely; paragastral surface with postica of fine aporhyses that are sometimes in vertical series; parts of surface may be coated by external cortex; no loose spicules known. [Coelocorypha was regarded as distinct from Cytoracia POMEL by DE LAUBENFELS (1955, p. 45, 47), who placed the two nominal genera in different families; but the type designated by DE LAUBENFELS (1955, p. 45) was identified previously by Schrammen (1924a, p. 105) as Cytoracia nidulifera.] Upper Jurassic (Kimmeridgian)–Upper Cretaceous (Campanian), Neogene (?Miocene): Germany, Switzerland, Upper Jurassic (Kimmeridgian)-Upper Cretaceous; Spain, Aptian; France, Santonian-Campanian; Germany, Poland, Turonian-Campanian; North Africa, ?Miocene.-FIG. 178, 3a-b. C. variabilis (KOLB), Weiss Jura, Kimmeridgian, Gestalten, Germany; a, nodular, compound example showing multiple, paragastral openings surrounded by radial canals,  $\times 0.5$ ; b, rhizoclone desmas, ×20 (Schrammen, 1937).-FIG. 178,3c-d. C. turbinate SCHRAMMEN, Mucronatenkreide, Campanian, Misburg, Germany; c, oblique view showing terminal osculum, with poriferous area at right; d, lateral view showing depressed, poriferous area and furrowing of surrounding surface, ×0.5 (Schrammen, 1910).
- ?Allomera POMEL, 1872, p. 194 [\*A. obovata POMEL, 1872, p. 195; SD DE LAUBENFELS, 1955, p. 9] [=Pleuromera POMEL, 1872, p. 199 (type, P. inaequalis, OD)]. Small, bilaterally compressed

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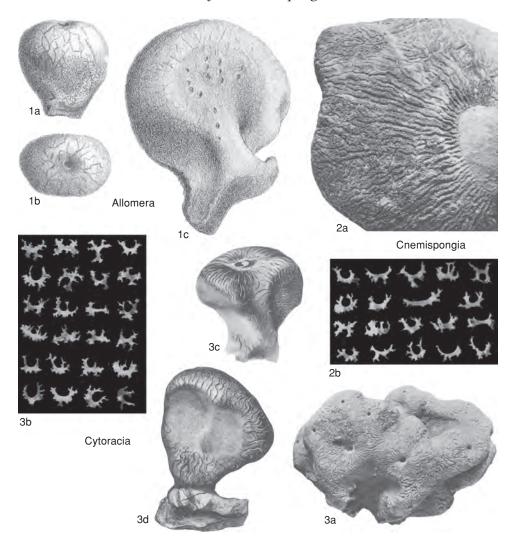


FIG. 178. Azoricidae (p. 283-285).

pyriform, with one side poriferous and opposite side and summit poreless but with fine furrows that radiate from small, terminal osculum; larger examples with number of impressed, poriferous areas, areas between poreless but furrowed ridges, and in some with number of osculeike apertures in terminal or lateral positions; skeletal structure unknown. [Position strictly unknown, but considered rhizomorine by ZITTEL (1878a, p. 125); habitus only matched in *Cytoracia* POMEL, and not distinguishable from that genus except by multiple oscula if the skeleton was compact.] *Neogene (Miocene):* Algeria.——FIG. 178, *Ia–b. \*A. obovata*, Djebel Djambeida; *a*, side view of top-shaped sponge; *b*, view from above showing small, radial canals around osculum, ×1 (Pomel, 1872).——FIG. 178,*1c. A. inaequalis* (POMEL), Djebel Djambeida; larger example with poriferous areas on one side, multiple oscules on other, ×1 (Pomel, 1872).

Cnemispongia QUENSTEDT, 1877 in 1877–1878, p. 258 [\*C. goldfussi; SD DE LAUBENFELS, 1955, p. 47]. Described by DE LAUBENFELS (1955, p. 47) as, "Externally like Cnemidiastrum but skeleton unknown;" type species identified previously as Cytoracia goldfussi by SCHRAMMEN, who also figured the desmas (1937, p. 90, pl. 23,6); this species depressed, top shaped, with strong, radiating furrows on summit and poriferous areas near base, but not otherwise distinctive. Jurassic (Oxfordian-Kimmeridgian): Germany.—FIG. 178,2a-b. \*C.

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*goldfussi*, Weiss Jura; *a*, view of summit with radial canals and matrix-filled spongocoel, Kimmeridgian, Hossingen, ×1; *b*, rhizoclone desmas, upper Oxfordian, Streitberg, ×20 (Schrammen, 1937).

# Subfamily AULOSOMINAE Schrammen, 1924

[nom. transl. REID, herein, ex Aulosomidae SCHRAMMEN, 1924a, p. 82]

Typically solitary sponges of globular to cylindrical or branched, cylindrical shapes without special poriferous areas and usually have deep, narrow, paragastral cavity; skeletal framework uncanalized, or with skeletal pores but no canals, or with distinct epirhyses or aporhyses; aporhyses do not perforate external surface when present; some with pseudofibrous structure due to interruption of meshwork by numerous closely spaced epirhyses; distinct, skeletal cortex present or absent; no special ectosomal desmas; no loose spicules known. [Possibly represented at present by Gastrophanella SCHMIDT, but desmas figured by some authors are not typical rhizoclones.] Upper Jurassic-Upper Cretaceous (Campanian).

- Aulosoma SCHRAMMEN, 1924a, p. 106 [\*Spongia radiciformis PHILLIPS, 1835 in 1829-1836, p. 90; OD]. Body elongate, often swollen and constricted alternately but not transversely wrinkled, with a conical summit and a stalk that may divide into root processes; paragastral cavity narrow, extending through most of body but not into stalk; sides finely porous and more or less irregularly furrowed, with larger pores as ostia of tubular epirhyses, which arch downwardly toward paragastral wall; aporhyses rather wider, sloping downwardly toward exterior around paragastral cavity, and with basal group running down stalk; postica covered by superficial network of composite skeletal fibers in some examples, presumably through formation of cortical meshwork in endosomal stratum of soft parts; no loose spicules known. [Diagnosis based on topotype material that has epirhyses and the paragastral cortex not mentioned by SCHRAMMEN.] Cretaceous (Aptian-Campanian): Spain, Aptian; France, Germany, Turonian-England, Campanian.—FIG. 179,2a-b. \*A. radiciformis (PHILLIPS); a, small example, with constrictions moderately developed, Quadratenkreide, upper Campanian, Oberg, Germany, ×1 (Phillips, 1875); b, side view of typical sponge with transverse section showing general interior structure, Chalk, Sowerby, Yorkshire, England, ×0.25 (Phillips, 1829-1836).
- Coelosphaeroma SCHRAMMEN, 1910, p. 159 [\*C. appendiculata; OD]. Obliquely distorted ovoid,

with eccentric, oscular opening facing upwardly near one end and small root processes at other; paragastral cavity cylindrical near osculum, but expanded irregularly to occupy most of interior of lower parts; outside with fine furrows that radiate from paragastral margin and small ostia of short, radial epirhyses; paragastral surface locally with postica of arching aporhyses, which more or less follow form of external surface; no loose spicules known. [Skeletal meshwork said to be fibrous by LAGNEAU-HÉRENGER, 1962, p. 175, but not so in material identified by SCHRAMMEN, 1910.] Cretaceous (Aptian-Campanian): Spain, Aptian; Germany, Campanian.-FIG. 179,5a-b. \*C. appendiculata, Mukronatenkreide, Campanian, Misburg, Germany; a, sectioned example showing canals (epirhyses, aporhyses) and form of paragastral cavity; b, external view, osculum at right, root processes at left, ×0.5 (Schrammen, 1910).

- Oncodona DE LAUBENFELS, 1955, p. 49, nom. nov. pro Oncophora SCHRAMMEN, 1924a, p. 112, non DIESLING, 1851 [\*Oncophora meandrina SCHRAM-MEN, 1924a, p. 112; OD]. Cylindrical or pyriform, with tubular, paragastral cavity, outside wrinkled transversely; no distinct skeletal pores or canals; no cortical meshwork; loose spicules reported to be rhizoclones by SCHRAMMEN (1924a). Cretaceous (Campanian): Germany.—FIG. 179,1. \*O. meandrina (SCHRAMMEN), Emscher, Sudmerberges; rhizoclones, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Polyrhizophora LINCK, 1883, p. 61 [\*P. jurassica; OD]. Hollow-cylindrical to funnel-like; canal system poorly known, but apparently consisting of small, external pores (ostia) and downwardly arched aporhyses; no cortical meshwork; no loose spicules known. Upper Jurassic: Germany.—FIG. 179,3ab. \*P. jurassica, Malm, Sontheim; a, drawing of longitudinal section showing radial canal system and central spongocoel; b, drawing of transverse section showing radial inhalant canals and central exhalant canals, ×1 (Linck, 1883).
- Stachyspongia ZITTEL, 1878a, p. 129 [\*Siphonocoelia spica F. A. ROEMER, 1864, p. 30; SD DE LAUBENFELS, 1955, p. 45]. Typically elongate cylindrical with conical summit, deep, tubular, paragastral cavity, and conical, lateral outgrowths; the latter few to numerous and spirally arranged in some specimens, produce resemblance to fir cone; one species branched-cylindrical, with a few fingerlike, lateral outgrowths; outside with fine, reticulating furrows and small ostia; aporhyses branched, more or less radial; cortex usually absent, but may be present in some specimens; no loose spicules known. Cretaceous (Aptian-Campanian): Spain, Aptian; England, Cenomanian, Campanian; Germany, Poland, Turonian-Campanian.-FIG. 180a-b. \*S. spica (F. A. ROEMER), Grey Chalk, Cenomanian, Dover, England; a, side view of part of large specimen showing resemblance to a fir cone where lateral outgrowths are numerous,  $\times 0.5$ ; b, transverse section of another example from same locality showing

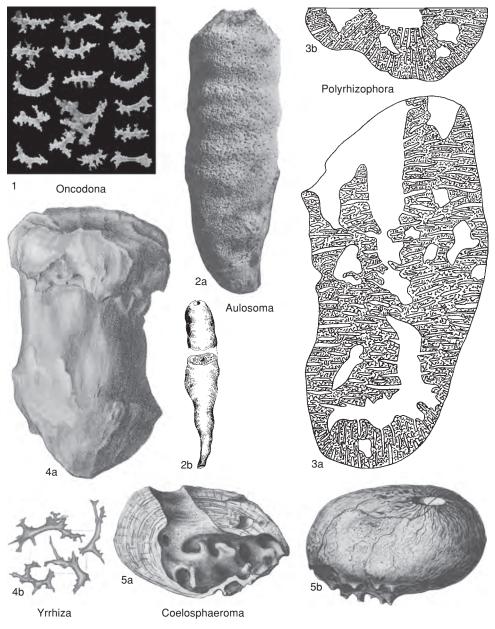


FIG. 179. Azoricidae (p. 285-286).

central spongocoel and parts of radial, horizontal canals,  $\times 1$  (Hinde, 1884a).

Yrrhiza DE LAUBENFELS, 1955, p. 45, nom. nov. pro Rhizinia KOLB, 1910 in 1910–1911, p. 242, non HAMMER SCHMIDT, 1838 [\*Rhizinia amanita KOLB, 1910 in 1910–1911, p. 242; M]. Cylindrical, tapered to base; summit with shallow, paragastral depression from which a few aporhyses may run downwardly; no external pores or epirhyses; rhizoclone spicules reported. *Jurassic (Kimmeridgian):* Germany.——FIG. 179,4*a*–*b.* \*Y. *amanita* (KOLB), Weiss Jura, Sontheim; *a*, cylindrical, side view, paragastral cavity on summit, SSPHG, ×1; *b*, characteristic rhizoclone spicules, ×40 (Kolb, 1910–1911).

# Subfamily LEIOCHONIINAE Schrammen, 1924

#### [nom. transl. REID, herein, ex Leiochoniidae SCHRAMMEN, 1924a, p. 82] [=Scytaliidae DE LAUBENFELS, 1955, p. 45].

Hollow-cylindrical, top-shaped, and funnel-like or flabellate sponges, with skeletal canals opening through both surfaces of skeletal framework, and apertures typically becoming covered by secondary, cortical meshwork on one or both surfaces; external surface often with more or less conspicuous transverse growth lines; no loose spicules known. [Perforation of the skeletal framework by canals suggests comparison with Cnemidiastridae, but external apertures are never arranged in series, and canals have no tendency to merge to form linear fissures. The subfamily is here interpreted as similar to Aulosomatinae but with aporhyses open subdermally.] Cretaceous (Aptian-Campanian).

- Leiochonia SCHRAMMEN, 1901, p. 16 [\*L. cryptoporosa; OD]. Funnel-, bowl- or platelike, or flabellate, stalked or not; surfaces of primary, skeletal framework with conspicuous, transverse, growth lines and numerous skeletal pores, mainly of irregular shapes; interior with branched and anastomosing, radial canals, some of which open through both skeletal surfaces; margin more or less abruptly truncated and strongly furrowed by incompletely enclosed canals; external and paragastral surfaces may be coated by dense but finely porous, cortical meshwork that conceals underlying skeletal pores of internal framework; no loose spicules known. Cretaceous (Coniacian-Campanian): France, Coniacian-Santonian; Germany, Poland, Coniacian-Campanian.—FIG. 181,4a-b. \*L. cryptoporosa, Quadratenkreide, Campanian, Oberg, Germany; a, ear-shaped example showing furrowed margin and paragastral surfaces coated with cortical meshwork,  $\times 0.5$ ; b, external view of specimen in which cortical meshwork is absent, showing growth lines and external, skeletal pores, ×0.5 (Schrammen, 1910).
- Pseudocytoracea LAGNEAU-HÉRENGER, 1962, p. 184 [\*P plicata; OD]. Irregularly top shaped with conical summit, small, bowl-shaped, paragastral cavity, and sides vertically ridged between broad, concave indentations; outside of skeletal framework with rounded or irregularly shaped, skeletal pores that may be in reticulating furrows in lower parts; skeletal canals radiating outwardly and downwardly from postica in paragastral surface; summit radially furrowed by incompletely formed canals; lower parts may be coated by dense, transversely wrinkled, skeletal cortex; no losse spicules known. [Placed

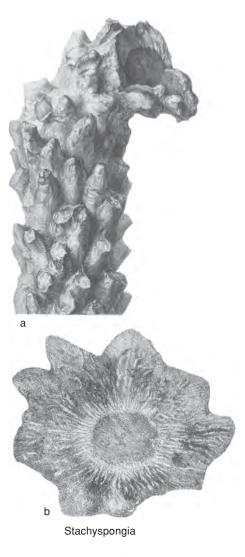


FIG. 180. Azoricidae (p. 285-286).

into Cnemidiastridae by LAGNEAU-HÉRENGER, 1962, but here interpreted as similar to *Scytalia* ZITTEL.] *Cretaceous (Aptian):* Spain.—FIG. 181,3*a-c.* \**P. plicata*, Can Casanyas Castellet, Catalogne; *a*, side view with small osculum at summit, which is also marked by convergent, radial furrows, lower sides with vertical ridges, ×0.5; *b-c*, characteristic spicules including desmas of interior and cortical desmas that are more strongly branched, ×25 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).

Scytalia Zittel, 1878a, p. 128 [\**Jerea turbinata* F. A. ROEMER, 1864, p. 32; SD SCHRAMMEN, 1924a, p.

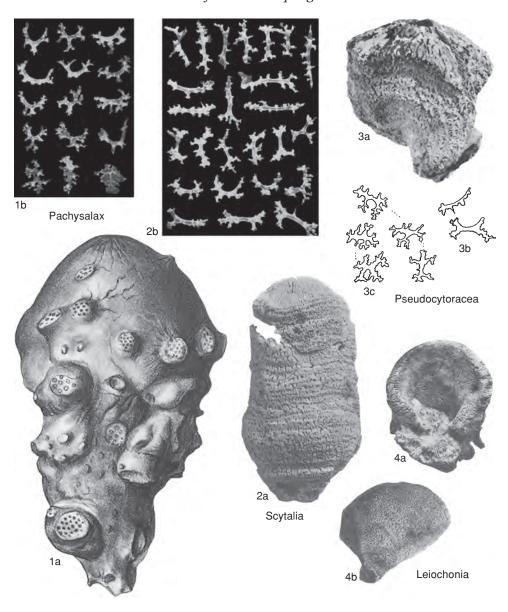


FIG. 181. Azoricidae (p. 287-291).

106; *=Spongia terebrata* PHILLIPS, 1835 in 1829– 1836, p. 90, subj., according to SCHRAMMEN, 1910, p. 150] [*=Pseudoscytalia* SCHRAMMEN, 1924a, p. 109 (type, *Spongia terebrata* PHILLIPS, 1835 in 1829– 1836, p. 90, OD)]. Top to club shaped or cylindrical with tapered, basal part, usually stalked, and may also have transverse, external constrictions or corrugations; summit flattened, conical, or rounded; paragastral cavity tubular, deep, and may extend into stalk when present; external surface of skeletal framework with transverse growth lines and small, rounded or irregularly shaped, skeletal pores, some of which may be in short, vertical furrows or reticulating furrows; skeletal canals numerous, radial, branching, and horizontal to arched or sloped downwardly in conformity with form of summit; some branches may unite before opening through external surface; paragastral surface with numerous closely spaced, small postica, arranged without order or in furrows between vertical ridges; external

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surface may be coated by thin, finely porous, cortical layer pierced by numerous minute, intracortical ostia, that covers skeletal pores of primary framework; summit with radiating furrows representing incompletely formed canals, or with these concealed by extension of cortex to oscular margin; no loose spicules known. [Cortex and paragastral furrows were not recognized by SCHRAMMEN (1924a, p. 98), but both are shown in ROEMER's original figure of S. turbinata (1864). Cortex is also mentioned in his description (ROEMER, 1864, pl. 12, 1 and p. 32-33); hence presence of a cortex is not regarded as distinctive of Pseudoscytalia.] Cretaceous (Aptian-Campanian): Spain, Aptian; Czech Republic, Slovakia, Cenomanian; England, Campanian; France, Turonian-Santonian; Germany, Poland, Turonian-Campanian.—FIG. 181,2a. \*S. turbinata (ROEMER), Mucronatenkreide, Campanian, Misburg, Germany; rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).----FIG. 181,2b. S. (Pseudoscytalia) terebrata (PHILLIPS), Quadratenkreide, Campanian, Oberg, Germany; cylindrical example showing outside of skeletal framework as exposed when cortex is absent,  $\times 0.5$  (Schrammen, 1910).

### Subfamily ASTROBOLIINAE de Laubenfels, 1955

#### [nom. transl. REID, herein, ex Astroboliidae DE LAUBENFELS, 1955, p. 47]

Globular to nodular or branchedcylindrical sponges without depressed, poriferous areas, distinct paragastral cavities, or special oscular outgrowths, and in which skeletal framework has no skeletal pores or canals, or surface showing small pores, not divisible into ostia and postica, or showing numerous small ostia arranged without order and few larger postica, arranged in groups from which short furrows radiate; some with additional skeletal cortex composed of small, finely branching desmas that coat surface of skeletal framework and conceal small pores and furrows; no loose spicules known. *Upper Jurassic–Upper Cretaceous (Maastrichtian).* 

Astrobolia ZITTEL, 1878a, p. 115 [\* Cnemidium conglobatum REUSS, 1846 in 1845–1846, p. 72; SD DE LAUBENFELS, 1955, p. 47] [=Rhagosphecion POMEL, 1872, p. 223, obj., nom. oblit., SD DE LAUBENFELS, 1955, p. 65]. Hemispherical to nodular; surface of skeletal framework with postica in small, depressed groups from which shallow, superficial furrows radiate; intervening parts of surface with small ostia; no special cortex; no losse spicules known. Cretaceous (Cenomanian–Campanian): Czech Republic, Slovakia, Cenomanian; Germany, Cenomanian–Campanian.—F1G. 182,4. \*A.

*conglobatum* (REUSS), Cenomanian, Czech Republic, Slovakia; view from above of broadly conical sponge with several postica surrounded by convergent canals, ×1 (Reuss, 1845–1846).

- Bolidium ZITTEL, 1878a, p. 114 [\*Amorphospongia palmata F. A. ROEMER, 1864, p. 55; OD]. Nodular to branched cylindrical; surface of skeletal framework with small, skeletal pores, all of similar size (not divisible into ostia and postica); lower parts coated by skeletal cortex formed from small, finely branching desmas; no loose spicules known. Cretaceous (Coniacian–Maastrichtian): Germany, Coniacian–Maastrichtian; Poland, Campanian.— FIG. 182,1a–b. \*B. palmatum (ROEMER), Quadratenkreide, Campanian, Sutmerberges, Germany; a, side view of nodose, lobate holotype, ×50 (Zittel, 1878a).
- Microrhizophora KOLB, 1910 in 1910–1911, p. 241
  [\**M. pentagona*; SD DE LAUBENFELS, 1955, p. 49]. Discoidal or cylindrical with pentagonal outline or cross section; no apparent canalization or cortex; no loose spicules known. [Name based on small size of rhizoclones compared with those of contemporary genera.] *Upper Jurassic*: Germany.—FIG. 182,2*a*–*b*. \**M. pentagona*, Weiss Jura, Kimmeridgian, Sontheim; *a*, side view of obconical sponge, SSPHG, ×1; *b*, representative desmas, ×50 (Kolb, 1910–1911).
- Oncocladia KOLB, 1910 in 1910–1911, p. 244 [\*O. sulcata; OD]. Nodular, with broad, encrusting base and number of rounded elevations above; tops of elevated parts with network of anastomosing furrows; other parts with numerous small pores; no distinct postica or cortex; spicules rhizoclone desmas. Jurassic (Kimmeridgian): Germany.——FIG. 182,3a-e. \*O. sulcata, Weiss Jura, Sontheim; a, side view of irregularly nodular sponge, SSPHG, ×0.5; b-e, characteristic desmoid spicules, ×40 (Kolb, 1910–1911).
- Urnacristata DE LAUBENFELS, 1955, p. 49, nom. nov. pro Lophiophora SCHRAMMEN, 1924a, p. 101, non BRYK, 1915 [\*Lophiophora sulcata SCHRAMMEN, 1924a, p. 101; OD]. Encrusting or unattached, nodular, with broadly rounded to nipplelike elevations; skeletal framework with postica at summits of elevated parts, and with very small ostia and network of superficial furrows on its intervening parts; surface of skeletal framework may be coated by skeletal cortex, formed from small, finely branched and flattened desmas; no loose spicules known. [The genus resembles Oncocladia KOLB, 1910 in 1910-1911, but is distinguished apparently by the occurrence of a cortex and special cortical desmas.] Cretaceous (Campanian): Germany.——FIG. 182,5a-b. \*U. sulcata (SCHRAMMEN), Mukronatenkreide, upper Campanian, Misburg; a, unattached example, ×0.75; b, rhizoclone and dermalia desmas, top row probably from cortex, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung) .----- FIG. 182, 5c. U. incrustans (SCHRAM-MEN), Mukronatenkreide, upper Campanian, Misburg; irregular sponge showing superficial

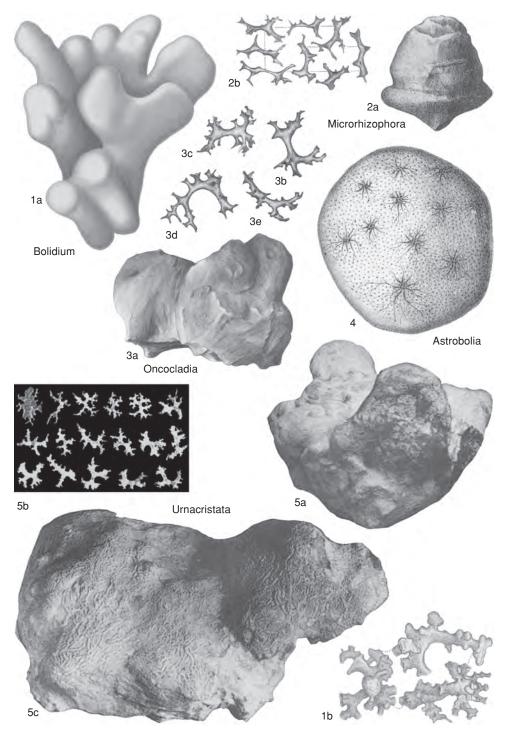


FIG. 182. Azoricidae (p. 289-291).

furrows as seen when cortex is absent, ×0.75 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

# Subfamily SIPHONIDIINAE von Lendenfeld, 1904

[*nom. transl.* REID, herein, *ex* Siphonidiidae VON LENDENFELD, 1904c, p. 140] [=Cladopeltidae SOLLAS, 1888, p. clvii; invalid, not based on a genus name]

Sponges with nodular to tuberose or trunklike body bearing stump or branchlike, oscular outgrowths, and also with strongly branching, flattened ectosomal (cortical) desmas that may not be articulated; supplemental monaxons but no microscleres in single modern genus. [The living type genus, *Siphonidium* SCHMIDT, has a short to elongate, tree-trunklike body that bears thin, branchlike, oscular outgrowths, with an oscule at end of each, through which an exhalant canal discharges.] *Cretaceous (Campanian.* 

Pachysalax SCHRAMMEN, 1910, p. 157 [\*P. processifera; OD]. Encrusting, nodular, or tuberlike, erect or not, with postica of aporhyses in groups at flattened ends of tree-stumplike outgrowths; intervening surface of skeletal framework with fine, superficial furrows and small ostia, which may be covered by layer of finely branched, flattened, cortical desmas; no loose spicules known. Cretaceous (Campanian): Ger--FIG. 181, 1a. \*P. processifera, Mucromany.natenkreide, Misburg; holotype with nodes that contain ostia of aporhyses on ends, ×0.5 (Schrammen, 1910).-FIG. 181, 1b. P. sinuosa SCHRAM-MEN, Mukronatenkreide, Misburg; desmas with cortical desmas in bottom row, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

# Family CNEMIDIASTRIDAE Schrammen, 1924

#### [Cnemidiastridae SCHRAMMEN, 1924a, p. 151]

Typically symmetrical, from top shaped with narrow, central cavity to funnel-, bowllike, or discoidal, in which skeletal wall is traversed radially by regular, longitudinal series of closely spaced, tubular canals, which open through both skeletal surfaces, or by a network of branching and anastomosing, longitudinal fissures, or by some intermediate condition; meshwork of skeletal framework compact, except between closely spaced canals, and typically with more or less conspicuous, longitudinal and transverse alignment of many of the desmas; distinct, cortical meshwork present or absent; loose spiculation unknown. [Publication of this family name without diagnosis (SCHRAMMEN, 1924a, p. 151) is accepted as valid because Cnemidiastrum ZITTEL and three other recognizable genera were listed. Cnemidiastrum ZITTEL is understood here sensu DE LAUBENFELS as identical with *Lithostrobilus* SCHRAMMEN. This is contrary to previous practice but is required by DE LAUBENFELS'S choice of Cnemidium stellatum GOLDFUSS as the type species. Cnemidiastrum sensu SCHRAMMEN (1924a, 1936) becomes Cnemopeltia POMEL.

When developed in the form of regular series of closely spaced canals, the canalization of this family is strikingly similar to that of *Archaeoscyphia* HINDE of the Orchocladina; but the desmas are all rhizoclones and the skeleton is not fibrous. Description of the skeleton as fibrous by LAGNEAU-HÉRENGER (1962) is mistaken and may refer to the regular alignment of many desmas.] *Upper Jurassic (Oxfordian)–Neogene* (*Miocene*).

Cnemidiastrum ZITTEL, 1878a, p. 109 [\*Cnemidium stellatum GOLDFUSS, 1826, p. 15; SD DE LAUBENFELS, 1955, p. 47] [?=Bembixastrum SCHRAMMEN, 1924b, p. 129 (type, Cnemidium granulosum MUNSTER in GOLDFUSS, 1833; see p. 765 herein); Lithostrobilus SCHRAMMEN, 1937, p. 87, obj.]. Top to carrot shaped, with narrow, central cavity and flattened or conical summit, or funnel, bowl, or mushroom shaped; some elongate examples with conspicuous, external constrictions; skeletal framework traversed by more or less regularly longitudinal series of closely spaced, tubular canals, which open through both skeletal surfaces, and may merge locally to form continuous clefts; canals all simple, or some branching toward exterior, and then anastomosing or crossing one another; both surfaces with regular, longitudinal series of small, skeletal pores as apertures of internal canals; these pores in regular, longitudinal series, typically not reticulating, and sometimes in longitudinal furrows; summit or margin with conspicuous, radiating furrows, representing incompletely formed canals, which may produce markedly corallike appearance in poor material; lower parts of some examples may have secondary cortical

meshwork obscuring skeletal pores; no loose spicules known. [Lithostrobilus was originally published without a diagnosis (SCHRAMMEN, 1924b, p. 130), but is based on an identifiable species. It was distinguished by SCHRAMMEN (1937, p. 87) from Cnemidiastrum ZITTEL sensu SCHRAMMEN as comprising forms here referred to Cnemopeltia POMEL. Lithostrobilus is now an objective synonym of Cnemidiastrum ZITTEL because of designation of Cnemidium stellatum GOLDFUSS as the type species of that genus by DE LAUBENFELS (1955, p. 47); the record from Italy is based on dubious material, thought to be "scarcely convincing" by MORET (1924, p. 7).] Upper Jurassic (Oxfordian)-Neogene (Miocene): France, Germany, Poland, Switzerland, Oxfordian-Kimmeridgian; Spain, Aptian; Spain, ?Italy, Miocene. FIG. 183, 1a-c. \*C. stellatum (GOLDFUSS), Weiss Jura, Kimmeridgian, Streitberg, Germany; a, camera lucida drawings of various rhizoclones, ×50 (Zittel, 1878a); b, part of elongate example having vertical rows of skeletal pores; ×1; c, upper surface of funnel-like example, ×0.25 (Quenstedt, 1877-1878).-FIG. 183,1d. C. hoheneggeri ZITTEL, Weiss Jura, Upper Jurassic, Krakau, Poland; side view of subcylindrial sponge with numerous inhalant ostia in generally longitudinal canals, ×1 (Zittel, 1878a).

- Cnemopeltia POMEL, 1872, p. 82 [\*Cnemidium rimulosum GOLDFUSS, 1826, p. 15; OD] [=Cnemidiastrum ZITTEL, 1878b, p. 45 (type, C. pluristellum ZITTEL, 1878a, p. 26[10]) as understood by Schrammen, 1937, p. 84; not Cnemidiastrum sensu DE LAUBENFELS, 1955, p. 47]. Funnel or bowl shaped, or depressed, top shaped with shallow, central cavity or none, or discoidal, or asymmetrical; radial canals distinct locally, but replaced mainly by continuous branching and anastomosing clefts; outer (lower) surface of skeletal framework with open clefts, which radiate upwardly from base, or with corresponding series of closely spaced, small, simple or pustular skeletal pores, which open into clefts below surface; paragastral (upper) surface similar, with clefts or pore series radiating from center, or from number of points from which canal-like, tubular cavities may run down toward base; no loose spicules known. Jurassic (Oxfordian-Kimmeridgian): Germany, Switzerland.
  - C. (Cnemopeltia). Clefts or pore series of paragastral (upper) surface radiating from center. *Jurassic (Oxfordian-Kimmeridgian)*: Germany, Switzerland.——FIG. 183,2*a-c.* \**C. (C.) rimulosum* (GOLDFUSS), Weiss Jura, Kimmeridgian, Heuberg, Germany; *a*, segment of upper surface; *b*, lower surface, ×1 (Quenstedt, 1877–1878); *c*, desmas, ×20 (Schrammen, 1937).
  - C. (Tremastrum) SCHRAMMEN, 1924b, p. 129 [\*Cnemidiastrum pluristellatum ZITTEL, 1878a, p. 110; OD]. Paragastral (upper) surface with clefts radiating from a number of points, one of which is usually central, from which tubular, canal-like cavities run downwardly. [Original publication was without diagnosis but in new

combination with type species. First formal diagnosis was by SCHRAMMEN, 1937, p. 84–85.] *Jurassic (Oxfordian–Kimmeridgian):* Germany, Switzerland.——FIG. 183,3*a–b.* \**C. (T.) pluristellatum* (ZITTEL), Weiss Jura, Kimmeridgian, Heuberg, Germany; *a*, upper surface with clefts convergent to several oscula; *b*, lower surface with radially aligned series of inhalant ostia, ×1 (Quenstedt, 1877–1878).

- Corallidium ZITTEL, 1878a, p. 110 [\**Cnemidium diceratinum* QUENSTEDT, 1852, p. 675; OD]. Top to carrot shaped, with small, central cavity at summit; skeletal framework traversed vertically by numerous fine, radial fissures, between which skeleton forms thin, vertical plates that resemble septa of coral; internal structure exposed at summit, but covered on sides or under surface by dense, cortical layer resembling epitheca; no loose spicules known. *Jurassic (Kimmeridgian):* Germany.——FIG. 184,2*a*–*b.* \**C. diceratinum* (QUENSTEDT), Weiss Jura, Aue; *a*, small, top-shaped example, seen from above; *b*, same sponge seen from side, ×1 (Quenstedt, 1877–1878).
- Cucumaltina BRIMAUD & VACHARD, 1986, p. 315 [\*C. placocephalus; OD]. Elongate, stalked sponge with numerous irregular constrictions throughout its length; surface finely porous and smooth; spongocoel long and narrow with surface weakly and irregularly enlarged from base to summit, without particular relationships to exterior; inhalant canals bifurcate and arranged oblique to dermal exterior and surface of spongocoel; apex flat; osculum round and neither depressed nor jutting out, surrounded by ramified, superficial, radial canals; skeletal structure of dense, radial fibers composed uniquely of rhizoclones, which are not particularly differentiated in cortical skeleton. Neogene (Miocene): Spain. FIG. 184, 1a-c. \*C. placocephalus, Tortonian strata, upper Miocene, Pliego, southern Spain; a, stalked, constricted sponge with central osculum of deep spongocoel on upper face, IPM R6960, ×0.48; b, longitudinal section of paratype with light matrix in central spongocoel and lateral, canal system, IPM R6961, ×0.5; c, photomicrograph of rhizoclones in skeletal structure, IPM R6962, ×50 (Brimaud & Vachard, 1986; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

# Superfamily PLATYCHONIODEA Schrammen, 1924

[nom. transl. Reid, herein, ex Platychoniidae Schrammen, 1924b, p. 152]

Meshwork of skeletal framework typically semifibrous and commonly with some desmas united to form strandlike, longitudinal trains; some with internal meshwork constructed to produce an appearance of

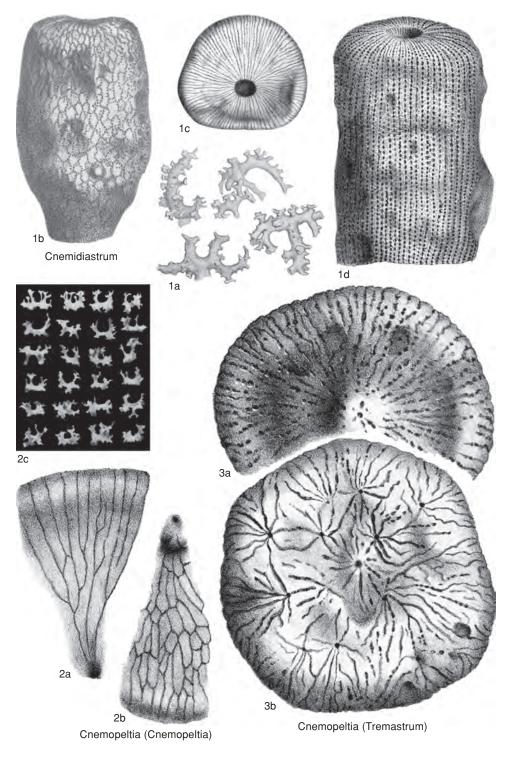


FIG. 183. Cnemidiastridae (p. 291–292).

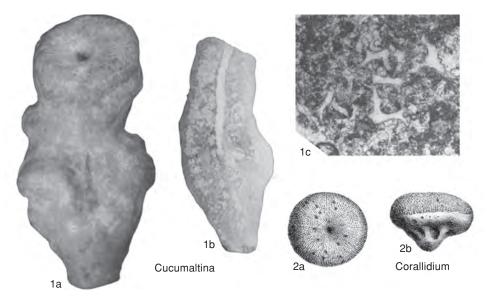


FIG. 184. Cnemidiastridae (p. 292).

fine, longitudinal canals or of radial septa; less commonly with semifibrous structure indistinctly developed or with local development of true, composite, skeletal fibers; outermost meshwork of framework may be similar to that of interior, or form a compact, skeletal cortex on either surface or both; no special ectosomal desmas; loose spicules unknown. [The superfamily comprises Rhizomorina, whose structure approached that of the typical fibrous Scleritodermatoidea (Scleritodermatidae, Seliscothonidae) but which normally lack true, composite, skeletal fibers.] *Jurassic–Holocene.* 

# Family PLATYCHONIIDAE Schrammen, 1924

#### [Platychoniidae SCHRAMMEN, 1924b, p. 152]

Plate- to funnel-like, flabellate, encrusting, or nodular sponges without distinct skeletal canals (epirhyses, aporhyses), in which surfaces of skeletal framework have numerous small, closely spaced, skeletal pores, to which larger, osculelike apertures may be added, or may be coated by dense, external, cortical meshwork without distinct skeletal pores; internal meshwork typically semifibrous, but sometimes tending to become distinctly fibrous, and with or without longitudinal, strandlike trains of desmas, between which fine, canal-like spaces may be seen, when such strands are developed; no loose spicules known. [Original publication of the family name Platychoniidae SCHRAM-MEN was without diagnosis, but the type *Platychonia* ZITTEL and another recognizable genus (*Bothrolemma* SCHRAMMEN) were listed. A supposed Eocene record of *Platychonia* (CHAPMAN & CRESPIN, 1934, p. 117) is thought to be based on a sphaerocladine genus because the desmas have "4 to 7 or more radiating arms."] *Jurassic–Holocene.* 

Platychonia ZITTEL, 1878a, p. 114 [\*Spongites vagans QUENSTEDT, 1877 in 1877-1878, p. 328; SD HINDE, 1893b, p. 203; =Scyphia schlotheimi GOLDFUSS, 1829, p. 90, according to SCHRAMMEN, 1937, p. 95]. Plate or bowl-like, irregularly funnellike, or flabellate, earlike to irregularly convolute; both surfaces of skeletal framework with small, closely spaced, skeletal pores that are arranged without order; internal meshwork semifibrous with distinct, longitudinal strands, between which canallike spaces may be present, or irregularly reticulate and tending to become distinctly fibrous; no loose spicules known. Jurassic (Sinemurian– Kimmeridgian): England, Sinemurian, upper Pliensbachian; England, Bajocian; Germany, Switzerland, Poland, Oxfordian-Kimmeridgian.---FIG.

185, 3a-b. \*P. vagans (QUENSTEDT), Weiss Jura, Oxfordian, Streitberg and Bosler, Germany; a, rhizoclone desmas, ×20 (Schrammen, 1937); b, side view of large, subcylindrical specimen with convolute structure, ×0.33 (Quenstedt, 1877-1878).

- Amphibleptula SCHMIDT, 1879, p. 28 [\*A. madrepora; OD]. Platelike, rhizomorine sponges with thick, dermal layer composed of long oxeas and ectosomal desmas with more branches than in interior. Jurassic-Holocene: Germany, Jurassic; Barbados, Atlantic Ocean, Holocene.-FIG. 185,2a-b. A. jurassica PISERA, Kimmeridgian marls, Upper Jurassic, Genkingen, Germany; a, upper or gastral surface of platelike sponge, ZPAL Pf.VIII/133, ×0.75; b, transverse section through margin of holotype showing choanosomal skeleton and bundles of protruding oxeas, ZPAL Pf.VIII552, ×5 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Bothrolemma SCHRAMMEN, 1924b, p. 133 [\*Platychonia osculifera KOLB, 1910 in 1910-1911, p. 240; OD]. Platelike, nodular, or forming crusts on other sponges; surfaces or unattached surface of skeletal framework with small pores and larger, osculelike apertures; internal meshwork as in Platychonia ZITTEL; no loose spicules known. [Original publication was without diagnosis but in new combination with established species *Platychonia osculifera* KOLB; first formal diagnosis was by SCHRAMMEN, 1937, p. 99.] Jurassic (Oxfordian-Kimmeridgian): Poland, Oxfordian; Germany, Kimmeridgian.-FIG. 185,5. \*B. osculifera (KOLB), Weiss Jura, Kimmeridgian, Heuchstetten, Germany; rhizoclone desmas, ×20 (Schrammen, 1937).
- Chonellopsis Reid, nom. nov. herein (Schrammen, 1924b, p. 128, nom. nud.; SCHRAMMEN, 1936, p. 185, nom. nud.) [\*C. striata SCHRAMMEN, 1936, p. 185; OD]. Platelike, flabellate, or leaflike to earlike, or irregularly convolute; surfaces of skeletal framework with very small, skeletal pores, arranged without order on one surface, but in longitudinal series that radiate from base to margin on other surface; internal meshwork denser than in Platychonia species; no loose spicules known. [DE LAUBENFELS (1955, p. 46) subsequently designated the type species for Chonellopsis, but according to Code Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xxiii, herein).] Jurassic (Oxfordian-Kimmeridgian): Germany.-FIG. 185, 1a-b. \*C. striata, Weiss Jura, Gerstetten; a, irregularly convolute example,  $\times 1$ ; b, rhizoclone desmas,  $\times 20$ (Schrammen, 1937).
- Hyaloderma OPPLIGER, 1921a, p. 204 [\*H. porata; M; SD DE LAUBENFELS, 1955, p. 65]. Plate- to earlike, with central or marginal attachment; both surfaces of skeletal framework densely coated by smooth, external cortex, without distinct skeletal pores; some desmas of internal framework showing longitudinal and transverse alignments; no loose spicules known. Jurassic (Kimmeridgian): Switzerland.-FIG. 185,4. \*H. porata, Badenerschichten, Kimmeridgian, Rümikon; view from above into funnel-

shaped gastral surface of thin-walled sponge, ×1 (Oppliger, 1926).

# Family DISCOSTROMATIDAE Schrammen, 1924

[nom. correct. REID, herein, pro Discostromidae SCHRAMMEN, 1924b, p. 151] [=Pyrgochoniidae SCHRAMMEN, 1924a, p. 153; Hyalotragosidae SCHRAMMEN, 1937, p. 91]

Discoidal or mushroomlike to funnel- or toplike sponges with distinct aporhyses or other skeletal canals; internal meshwork of skeletal framework compact to distinctly semifibrous, or forming radial, septalike lamellae, meshwork at surfaces compact, usually forming more or less distinct, skeletal cortex in which small, finely branched desmas may be added to others similar to those of interior; no loose spicules known. [Original publication of the family name Discostromatidae was without diagnosis, but the type genus *Discostroma* ZITTEL was listed. This genus is based on a species D. intricata (QUENSTEDT) whose structure is obscure in its author's original material, but is accepted as similar to Hyalotragos ZITTEL, type of Hyalotragosidae SCHRAMMEN, on ZITTEL's (1878a) authority.] Upper Jurassic.

# Subfamily DISCOSTROMATINAE Schrammen, 1924

[nom. transl. et correct. REID, herein, ex Discostromidae SCHRAMMEN, 1924a, p. 151]

Outer or lower (inhalant) skeletal surface without conspicuous pores or osculelike apertures, although small, intracortical pores may be seen under magnification; aporhyses well developed, numerous. Upper Jurassic (Oxfordian–Kimmeridgian).

Discostroma ZITTEL, 1878a, p. 112 [\* Tragos intricatum QUENSTEDT, 1877 in 1877-1878, p. 295; OD]. Discoidal or initially funnel-like, then expanding horizontally, with small, basal stalk and with upper surface convex around small, central cavity; lower surface with compact and concentrically wrinkled, surface meshwork; upper surface irregularly ridged and pitted; skeleton and canal system otherwise as in Hyalotragos ZITTEL, according to ZITTEL (1878a, p. 112). [Skeletal structure is obscure in QUEN-STEDT's material and in topotypes obtained by SCHRAMMEN (1937, p. 94). The type species is possibly identical with Hyalotragos patella (GOLDFUSS), the type species of Hyalotragos, in which the upper, skeletal surface may have irregular pitting or furrowing.] Jurassic (Kimmeridgian): Germany.-

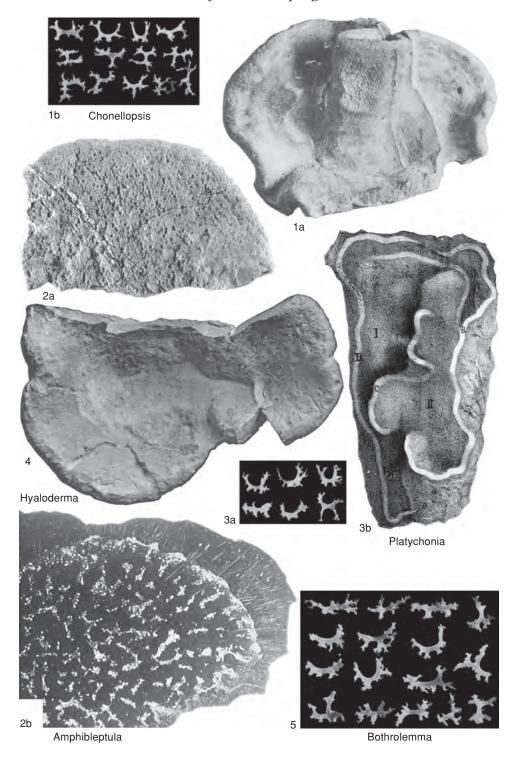




FIG. 186,2*a*-*b*. \**D*. *intricatum* (QUENSTEDT), Kimmeridgian marls, Upper Jurassic, Genkingen; *a*, upper surface of funnel-shaped sponge with irregular pits, ZPAL Pf.VIII/263; *b*, side view of same specimen with lower stalk to broadly obconical form, ×1 (Pisera, 1997; courtesy of *Palaeontologica Polonica*).

- Hyalospongia SIEMIRADZKI, 1913, p. 181 [\* Tragos infrajugosum QUENSTEDT, 1878 in 1877-1878, p. 292; OD; ?= Tragos rugosum GOLDFUSS, 1829, p. 96, according to SCHRAMMEN (1937, p. 93), which was used as the type species of Diacyparia by POMEL, 1872, although SIEMIRADZKI (1913, p. 181) considered the two species as different and used T. infrajugosum as the type species of Hyalospongia]. Funnel- to mushroomlike, stalked, with or without shallow, central depression; meshwork of lower skeletal surface more or less compact, with or without distinct, skeletal pores; internal meshwork semifibrous, with or without distinct, longitudinal strands; upper surface with shallow, round pits, in which are postica of groups of aporhyses, and surface between which formed by dense, smooth, cortical layer; or similar but with marginated, osculelike apertures, through which aporhyses open in groups or individually; no loose spicules known. Jurassic (Oxfordian-Kimmeridgian): Germany, Poland, Switzerland.—FIG. 186,3a-b. \*H. infrajugosum (QUENSTEDT), Weiss Jura, Ulm, Germany; a, upper surface with round, rimmed pits of postica in smooth, cortical layer; b, folded lower surface with dense, dermal layer, ×0.5 (Quenstedt, 1877-1878).
- Hyalotragos ZITTEL, 1878a, p. 111 [\* Tragos patella GOLDFUSS, 1826, p. 14; SD DE LAUBENFELS, 1955, p. 48] [=Saccotragos OPPLIGER, 1926, p. 67 (type, S. acuminata Oppliger, 1926, p. 66, SD DE LAUBENFELS, 1955, p. 107)]. Discoidal to mushroom, funnel or top shaped, with lower surface smooth or concentrically wrinkled and sometimes with wall plicated radially; meshwork of lower, skeletal surface compact, dense, with small ostia or none; internal meshwork compact to semifibrous, with longitudinal, strandlike trains of desmas spreading out toward both skeletal surfaces, or apparently traversed by fine, longitudinal canals; aporhyses well developed, vertical in axial parts, sloped or arched outwardly around them; upper surface more or less compact, smooth or irregularly furrowed with central group of postica through which axial aporhyses open, and other scattered postica around them; no loose spicules known. [Diagnosis here based on H. patella and similar species, not including forms of Hyalospongia SIEMI-RADZKI and Proseliscothon SIEMIRADZKI as in ZITTEL's (1878a) and SCHRAMMEN's (1937) diagnoses.] Jurassic (Oxfordian-Kimmeridgian): Germany, Poland, Switzerland.-FIG. 186,4a-b. \*H. patella (GOLDFUSS), Weiss Jura, Heuberg, Germany; a, side view of stalked, broad sponge; b, view of lower, dermal surface, ×1 (Quenstedt, 1877-1878).-FIG. 186,4c. H. patella SCHRAMMEN, Weiss Jura, Oxfordian, Streitberg, Germany; rhizoclone

desmas, ×20 (Schrammen, 1937).——FIG. 186,4*d. H. (Saccotragos) acuminata* (OPPLIGER), Badenerschichten, Kimmeridgian, Rümikon, Switzerland; side view of funnel-shaped sponge, ×0.5 (Oppliger, 1926).

Proseliscothon SIEMIRADZKI, 1913, p. 186 [\*P. cracoviense; OD]. Funnel to top shaped; lower surface of skeletal framework with small, closely spaced, skeletal pores arranged without order; internal meshwork forming thin, closely spaced, septalike, radial lamellae; upper surface coated by dense, external, cortical layer, with small, intracortical pores arranged along fine, radial ridges, corresponding with internal septa, and additional larger apertures as postica of aporhyses; internal meshes containing small, accessory desmas, which become more numerous toward upper surface and form cortical meshwork; no loose spicules known. Jurassic (Oxfordian): Poland.—FIG. 186, 1a-c. \*P. cracoviense; a, upper surface; b, lower surface, ×1; c, vertical section of upper part of wall, ×30 (Siemiradzki, 1913).

## Subfamily PYRGOCHONIINAE Schrammen, 1924

[nom. transl. REID, herein, ex Pyrgochoniidae Schrammen, 1924a, p. 153]

Outer or lower skeletal surface with conspicuous pores or osculelike apertures, from which shallow pits or distinct, tubular canals extend into skeletal framework; normal aporhyses well developed or absent. [Original publication of the name Pyrgochoniidae SCHRAMMEN was without diagnosis, but the type genus *Pyrgochonia* ZITTEL was listed. The subfamily is separated from the Discostromatinae because the form of the external apertures suggests development of secondary, exhalant vents on the normally inhalant surface; thus, the associated skeletal canals should then be secondary aporhyses, not epirhyses.] *Upper Jurassic.* 

Pyrgochonia ZITTEL, 1878a, p. 112 [\**Tragos acetabulum* GOLDFUSS, 1826, p. 13; OD] [=*Forospongia* D'ORBIGNY, 1849, p. 549, obj., *nom. oblit.*]. Bowl or funnel-like, more or less thick walled to toplike with shallow, central depression; usually stalked; outer (or lower) skeletal surface with numerous rounded, simple or marginate, osculelike apertures arranged without order, in rough, longitudinal series, or along longitudinal furrows; intervening surface formed by thin, compact, skeletal cortex, with or without distinct, small, intracortical ostia; paragastral surface similar, or with smaller and more numerous apertures; internal meshwork semi-fibrous; axial parts or stalk with tubular, vertical aporthyses that open at center of paragastral surface;

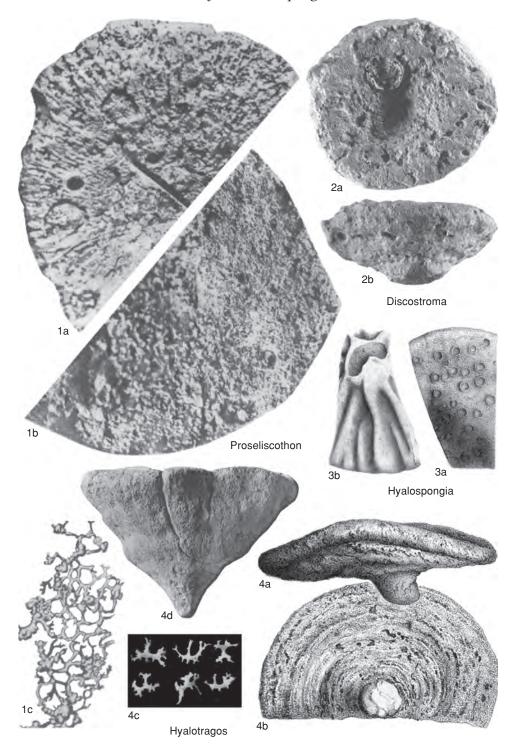


FIG. 186. Discostromatidae (p. 295–297).

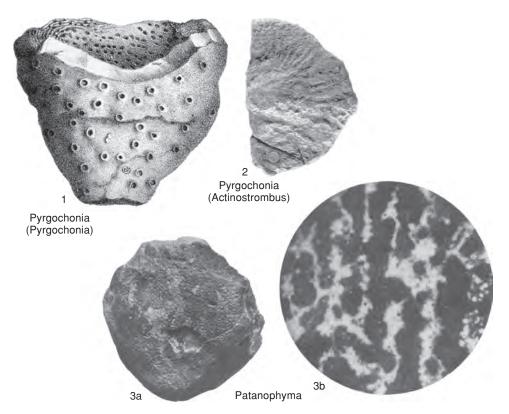


FIG. 187. Discostromatidae (p. 299).

lateral parts with oblique or meandering canals that may open through apertures of either surface; no loose spicules known. *Upper Jurassic*.

- P. (Pyrgochonia). External apertures marginated, not in longitudinal series or furrows, and may be larger than those of interior. Upper Jurassic: Europe.—FIG. 187, I. \*P. (P.) acetabulum (GOLD-FUSS), Weiss Jura, Kimmeridgian, Heuberg; side view of bowl-shaped sponge with rimmed, inhalant ostia on dermal surface and unrimmed, exhalant ostia on gastral surface, ×1 (Quenstedt, 1877–1878).
- P. (Actinostrombus) SCHRAMMEN, 1924b, p. 129 [\*Tragos radiatum GOLDFUSS, 1829, p. 96; OD]. External apertures not marginated, arranged in longitudinal series or along longitudinal furrows on lower surface. [Original publication was without diagnosis but in new combination with type species. First formal diagnosis was by SCHRAMMEN, 1937, p. 98.] Jurassic (Kimmeridgian): Germany.—FIG. 187,2. \*P. (A.) radiata (GOLDFUSS), Kimmeridgian marl, Bärenthal; dermal or lower surface with radial furrows, ZPAL Pf. VIII/212, ×0.5 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Patanophyma OPPLIGER, 1915, p. 74 [\*P. polypora; OD]. Bowl shaped, stalked; lower skeletal surface with dense, external cortex, pierced by apertures of canals that may extend to near upper, skeletal sur-

face; internal meshwork semifibrous, with some desmas in strandlike, longitudinal trains; upper surface finely porous, without apertures of canals; no loose spicules known. [Allocation of the genus to this family is uncertain, and it could belong with the Platychoniidae; external apertures here are assumed to correspond with those of *Pyrgochonia* ZITTEL.] *Jurassic (Kimmeridgian):* Switzerland.— FIG. 187, 3a-b. \**P. polypora*, Birmensdorfer beds, Olten; *a*, side view with coarse ostia in dermal layers,  $\times 0.5$ ; *b*, photomicrograph showing small, rhizoclone spicules and aligned, skeletal pores, scale not given, approximately  $\times 30$  (Oppliger, 1915).

## Family ARETOTRAGOSIDAE Malecki, 1996

#### [Aretotragosidae MALECKI, 1996, p. 4]

Moderately thick-walled, funnel- or topshaped, rhizomorine sponges with moderately closely spaced, small ostia and irregularly arranged postica groups on gastral surface; postica clusters may form rosettes on summits of papillae or in shallow or deep grooves; dermal skeleton made of more or less branched rhizoclones. *Jurassic:* Poland.

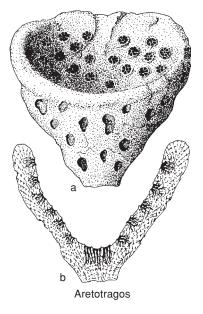


FIG. 188. Aretotragosidae (p. 300).

Aretotragos MALECKI, 1996, p. 4 [\*A. jaraczi; OD]. Sponges funnel, broad basin, or top shaped, with thick walls marked on curved, dermal surface with very small prosopores in shallow depressions; gastral surface with clusters of postica that form rosettes 1 to 4 mm across and irregularly 1 to 8 mm apart; main skeleton of rhizoclones with upwardly and outwardly divergent structure. Jurassic: Poland.— FIG. 188a-b. \*A. jaraczi, Transversarius beds, Weiss Jura, Krakow; a, side view of funnel-like sponge with prosopores in small, dermal depressions and exhalant ostia in rosettes on gastral surface; b, vertical section showing skeletal structure and nature of exhalant, canal clusters, ×0.5 (Malecki, 1996).

# Superfamily SCLERITODERMATOIDEA Sollas, 1888

[nom. transl. et correct. REID, herein, ex Scleritodermidae SOLLAS, 1888, p. clvii]

Skeletal framework typically composed of three-dimensional network of composite, skeletal fibers, in which desmas are matted together side by side; with or without compact, cortical meshwork, which masks fibrous interior but outlines skeletal pores or oscules when present; some with special cortical desmas that are smaller and more finely branched than those forming internal framework; a few with fibrous structure indistinctly developed or absent, or with fibers constructed from zygomes of bipolar rhizoclones, arranged transversely between adjacent fibers; modern forms with sigmaspires, additional microrhabds, or no microscleres. *Jurassic (Callovian)–Holocene.* 

Scleritodermatidae in SOLLAS's original sense (1888) are distinguished by possession of sigmaspire microscleres, without reference to skeletal structure. Sigmaspires occur in the three living genera Scleritoderma SCHMIDT, Microscleroderma KIRKPATRICK, and Taprobane DENDY, of which only Scleritoderma was known to SOLLAS (1888). Use of the translated name Scleritodermatoidea for forms distinguished by fibrous, skeletal structure is based on the writer's observation of this type of structure in a specimen of S. paccardi SCHMIDT, type species of Scleritoderma, and in the holotypes of *M. hirsuta* KIRKPATRICK and T. herdmanni DENDY, sole species of these genera. A condition in which fibrous structure is not distinctly developed was seen in S. flabelliforme SOLLAS, in which sigmaspires are present. Fibrous structure also occurs in the living "Seliscothon" chonelloides DOEDERLEIN, here regarded as a scleritodermatid without sigmaspires (Neoseliscothon REID).

Fossil genera, in which nothing is known of the microscleres, are identified as Scleritodermatidae if similar to the cited living genera in skeletal structure and habit. Others are placed in families Seliscothonidae SCHRAM-MEN (if similar but with conspicuous longitudinal skeletal fibers) and Jereicidae SCHRAMMEN (if jereiform in habit).

# Family SCLERITODERMATIDAE Sollas, 1888

[nom. correct. VON LENDENFELD, 1904c, p. 141, pro Scleritodermidae SOLLAS, 1888, p. clvii] [=Amphichondriidae SCHRAMMEN, 1924a, p. 83; Heterothelionidae SCHRAMMEN, 1924a, p. 83; Verruculinidae SCHRAMMEN, 1924a, p. 83; Taprobancidae De LAUBENFELS, 1936, p. 74, partim; Amphibleptulidae DE LAUBENFELS, 1936, p. 102, partim]

Typically cup- to funnel-like, flabellate, or irregularly convolute sponges in which paragastral surface has conspicuous, marginated oscules, or similar features present on both surfaces; skeletal framework usually clearly fibrous internally, but without conspicuous, longitudinal fibers; internal fibrous structure exposed at skeletal surfaces, or masked by dense, external cortex with perforating, skeletal pores on paragastral surface or both surfaces; desmas of cortical meshwork similar to those of interior or smaller and more finely branched; skeletal pores minute, punctiform and large and pustular or papilliform; some with distinct, internal aporhyses; supplemental oxeas or styles in some species; modern examples with sigmaspire microscleres only, additional microrhabds, or no microscleres. Jurassic (Oxfordian)-Holocene.

This family is interpreted as including the three living scleritodermatids *Scleritoderma* SCHMIDT, *Microscleroderma* KIRKPATRICK, and *Taprobane* DENDY, in which sigmaspires are present, and all fossil and modern Rhizomorina that resemble them in general habit and skeletal structure.

Systematic treatment by SCHRAMMEN (1924a) of some forms included here requires comment. The nominal genera Verruculina ZITTEL, 1878a and Amphithelion ZITTEL, 1878a were regarded by ZITTEL (1878b) as perhaps only distinct subgenerically, but were united by HINDE (1884a) as a single genus Verruculina. This practice was followed initially by SCHRAMMEN (1910), but he later (1924a) divided forms referable to this genus s.l. into eight genera (Verruculina ZITTEL, Amphithelion ZITTEL; Amphichondrium SCHRAMMEN, Heterothelion SCHRAMMEN, Sporadothelion SCHRAMMEN, Amphistomium SCHRAMMEN, Seliscothon SCHRAMMEN, Cryptothelion SCHRAMMEN), which were placed in five families (Leidorellidae SCHRAMMEN, Amphichondriidae SCHRAMMEN, Amphithelionidae SCHRAM-MEN, Heterothelionidae SCHRAMMEN, Verruculinidae Schrammen). DE LAUBENFELS (1955) listed all eight genera, but recognized only the Leiodorellidae of SCHRAMMEN's families and treated three genera (Cryptothelion, Heterothelion, Sporadothelion) as family Uncertain (DE LAUBENFELS, 1955, p. 4850). LAGNEAU-HÉRENGER (1962) recognized only *Verruculina*, placed in SCHRAMMEN's Verruculinidae, in part because criteria used by SCHRAMMEN are difficult to apply to poor material.

The genera distinguished by SCHRAMMEN (1924a) seem to have no characters that justify their reference to more than one family, and most are not separable except as subgenera. The principal difference among them is occurrence of two main types of desmas; these are used herein to distinguish ZITTEL's genera, although not in his original sense. SCHRAMMEN's Leiodorellidae and Amphithelionidae are adopted as subfamilies for various reasons.

# Subfamily SCLERITODERMATINAE Sollas, 1888

# [nom. transl. et correct. REID, herein, ex Scleritodermidae SOLLAS, 1888, p. clvii]

Cup- to funnel-like, flabellate, or irregularly convolute sponges, with more or less prominent oscules on paragastral surface; sigmaspire microscleres, to which normal or irregular microrhabds may be added; skeletal framework vaguely or clearly fibrous with layer of dense, cortical meshwork at paragastral surface, or no cortical meshwork; supplemental oxeas may occur within interfibrous meshes or project from skeletal surfaces. [There is no certain fossil record of the subfamily. Diagnosis above is based on limited material, but cortical meshwork is restricted to the paragastral surface in type material of Scleritoderma flabelliforme SOLLAS and absent in types of Microscleroderma hirsuta KIRKPATRICK and Taprobane herdmanni DENDY.] ?Cretaceous, Holocene.

Scleritoderma SCHMIDT, 1879, p. 28 [\*S. paccardi; OD]. Cuplike or flabellate, with prominent oscules on paragastral surface but no corresponding, external features; skeletal framework vaguely or clearly fibrous, with paragastral cortex or none; supplemental oxeas may occur; microscleres sigmaspires and simple, crooked or irregular microrhabds, latter packing ectosome and lining internal canals. [The range was given as Cretaceous–Holocene by DE LAUBENFELS (1955, p. 49), but no fossil record has been traced; possibly represented by *Pleurophymia* POMEL (Miocene, Northern Africa), herein listed under the subfamily Uncertain.]

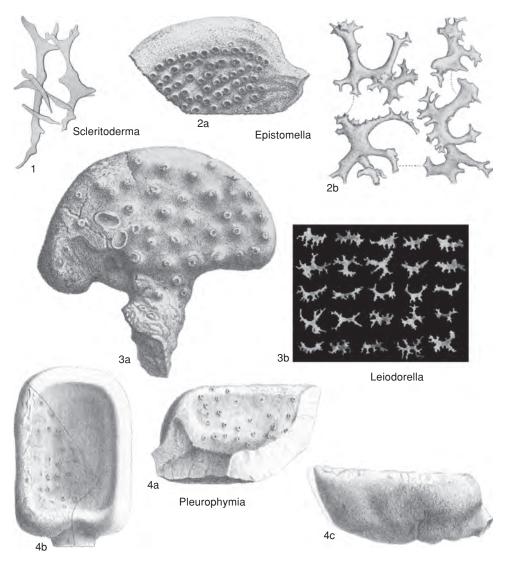


FIG. 189. Scleritodermatidae (p. 301-307).

*Cretaceous, Holocene:* West Indies, East Indies.— FIG. 189,*1. \*S. paccardi,* Holocene, West Indies; isolated, monaxial desmas showing ranges in size and irregular form, ×100 (Schmidt, 1879).

# Subfamily LEIODORELLINAE Schrammen, 1924

[nom. transl. REID, herein, ex Leiodorellidae SCHRAMMEN, 1924a, p. 82]

Flabellate sponges with dense, skeletal cortex and large, osculelike, skeletal pores on one or both surfaces of skeletal framework; internal meshwork more or less compact; no loose spicules known. [The subfamily comprises two isolated genera, resembling later (Cretaceous–Holocene) Scleritodermatidae but not related clearly to them. These sponges may belong with the Platychoniidae but are placed here because desmas are more similar to those of the Cretaceous Amphithelioninae, and the genus *Epistomella* ZITTEL resembles living *Scleritoderma flabelliforme* SOLLAS.] *Upper Jurassic (Oxfordian– Kimmeridgian).* 

- Leiodorella ZITTEL, 1878a, p. 113 [\*L. expansa; SD DE LAUBENFELS, 1955, p. 48] [=Amphisyringium SCHRAMMEN, 1924a, p. 114, obj.; ?Amphihamma SCHRAMMEN, 1924b, p. 128, nom. nud. (type, A. pustulosa, ?=Leiodorella pustulosa SCHRAMMEN, 1937, p. 100)]. Flabellate, flat or concavoconvex; both skeletal surfaces with dense, skeletal cortex and large, marginated or pustular, osculelike pores; internal meshwork more or less compact; no loose spicules known. Jurassic (Oxfordian-Kimmeridgian): Germany, Switzerland, Poland.-FIG. 189, 3a. \*L. expansa, Krakau, Poland; side view of flabellate form with dermal surface marked by oscular-like, rimmed pore, ×1 (Zittel, 1878a).——FIG. 189,3b. L. tubata (QUENSTEDT), Weiss Jura, Kimmeridgian, Sontheim, Germany; rhizoclone desmas, ×20 (Schrammen, 1937).
- Epistomella ZITTEL, 1878a, p. 113 [\*Spongites clivosus QUENSTEDT, 1877 in 1877–1878, p. 321; OD] [?=Verruculinopsis SCHRAMMEN, 1924a, p. 132, nom. nud. (type, V. aurita SCHRAMMEN, 1924a, p. 132, nom. nud., ?=Epistomella aurita SCHRAMMEN, 1937, p. 101)]. Similar to Leiodorella ZITTEL, but with skeletal cortex and large, pustular, skeletal pores on one surface only; other skeletal surface finely porous. Jurassic (Kimmeridgian): Germany.——FIG. 189,2a-b. \*E. clivosa (QUENSTEDT), Weiss Jura, Sozenhausen; a, small fragment with pustular, skeletal pores on one surface, ×1; b, desmas identified with species by ZITTEL (1878a), ×50 (Zittel, 1878a).

### Subfamily AMPHITHELIONINAE Schrammen, 1924

[nom. transl. REID, herein, ex Amphithelionidae SCHRAMMEN, 1924a, p. 82]

Mainly funnel-like, flabellate, or irregularly convolute sponges with internally fibrous, skeletal frameworks that typically have more or less dense, skeletal cortex on both sides of skeletal framework, and commonly with marginated, pustular, or papilliform skeletal pores on both surfaces; some examples with variant habits irregularly lobate, roughly toplike, forming secondary funnels through union of enrolled and apposed, skeletal margins, or forming composite growths; skeletal pores (postica) of paragastral surface small, marginated to large, elongate papilliform; pores of external surface minute punctiform to large pustular and commonly smaller and more numerous than postica; internal framework frequently uncanalized, but some with distinct aporhyses or with canals that run inwardly from pores of external surface; cortical meshwork

formed from desmas similar to those of interior or partly from smaller, flattened and strongly branching desmas; supplemental oxeas may occur; no microscleres known. [Skeletal pores of the external surface are not called ostia here because their commonly pustular form suggests an exhalant function. Amphithelioninae resemble *Leiodorella* ZITTEL (Upper Jurassic) when pustular pores are present on both surfaces; but the commonly small size of external pores and their punctiform character in some species suggest an independent, parallel development.] *Cretaceous–Neogene (Miocene)*.

- Amphithelion ZITTEL, 1878a, p. 123 [\*Verrucospongia macrommata F. A. ROEMER, 1864, p. 45; SD SCHRAMMEN, 1924a, p. 117; ?=A. reussi (MCCOY), cf. SCHRAMMEN, 1910, p. 140, synonymy] [=Cladostelgis POMEL, 1872, p. 150 (type, Verrucospongia damaecornis F. A. ROEMER, 1864, p. 45, OD); Pleurostelgis POMEL, 1872, p. 150, nom. oblit.; Heterothelion SCHRAMMEN, 1924a, p. 118 (type, Verruculina cupula SCHRAMMEN, 1910, p. 142); Sporadothelion SCHRAMMEN, 1924a, p. 120 (type, S. dissipatum SCHRAMMEN, 1924a, p. 122)]. Usually flabellate, stalked or not, taking leaf-, ear-, fan-, or bladelike shapes, or forming an incomplete funnel or secondary funnel; but may also be regularly plate-, bowl-, or funnel-like, or roughly top shaped; external, skeletal pores punctiform to pustular, usually small, closely spaced, and always more numerous and smaller than postica; postica marginated to elongate, papilliform, often large; distinct aporhyses present or absent; desmas typically stout, arched, or branching, with arched forms often predominant; special, cortical desmas unknown; some with supplemental oxeas; microscleres unknown. [Distinction from Verruculina ZITTEL is here based on the form of the desmas and absence of special, cortical desmas, not on the form of the external pores, as suggested by ZITTEL, 1878a. Pleurostelgis (POMEL, 1872, p. 150) was equated by DE LAUBENFELS (1955, p. 107) with Stelgis POMEL (=Ventriculites MANTELL, 1822, p. 167, class Hexactinellida), but the type species is Amphithelion miliare of ZITTEL, 1878a, and Sporadothelion miliare of SCHRAMMEN, 1924a (=A. miliare herein). Upper Cretaceous (Cenomanian-Campanian): Europe.
  - A. (Amphithelion). Aporhyses present or absent and radial or branching but not longitudinal when present. Cretaceous (Cenomanian-Santonian): Czech Republic, Slovakia, Cenomanian; England, Germany, Turonian-Campanian; France, Coniacian-Santonian.— FIG. 190,2a. \*A. (A.) macrommata (F. A. ROEMER), Mukronatenkreide, Campanian, Misburg, Germany; characteristic rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E.

Schweizerbart'sche Verlagsbuchhandlung).-FIG. 190,2b-c. A. (A.) reussi (McCoy), Upper Chalk, ?Campanian, Flamborough, Yorkshire, England; b, complete example with elongate, papilliform postica on paragastral surface,  $\times 0.5$ ; c, part of external surface showing smaller external pores, ×1 (Hinde, 1884b).---Fig. 190,2d. A. (A.) cupula (SCHRAMMEN), Mukronatenkreide, Campanian, Misburg, Germany; rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung). FIG. 190, 2e. A. (A.) dissipatum (SCHRAMMEN), Quadratenkreide, Campanian, Höver, Germany; rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung) .---- FIG. 190, 2f-g. A. (A.) miliare (REUSS), Upper Chalk, Upper Cretaceous, Flamborough, Yorkshire, England; f, general view showing paragastral surface and stump of broken stalk, long in this species; g, part of external surface showing small, external pores, sole Amphithelion species for which ZITTEL (1878a) studied another author's original material, ×1 (Hinde, 1884b).

- A. (Amphistomium) SCHRAMMEN, 1924a, p. 114 [\*A. aequibile SCHRAMMEN, 1924a, p. 115; OD]. Funnel-like or flabellate; both skeletal surfaces with numerous large, pustular, skeletal pores; external pores similar in size to those of paragastral surface, although rather more numerous; desmas slender, mainly linear in interior, finely branching in cortical layers; no loose spicules known. [Here thought to be similar to Verruculina ZITTEL; the relationship to Leiodorella ZITTEL of Upper Jurassic, claimed by SCHRAMMEN (1924a, p. 114), is uncertain.] Cretaceous (Campanian): Germany.-—Fig. 190, 1a-b. \*A. (A.) aequibile; a, external surface seen from below, ×0.75; b, characteristic rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- A. (Cryptothelion) SCHRAMMEN, 1924a, p. 122 [\*C. geminum; OD]. Aporhyses present, usually simple, and traversing skeletal framework longitudinally from postica toward basal parts; may form composite, flabellate growths by lateral budding. Cretaceous (Campanian): England, ?Campanian; Germany, Campanian.--Fig. 191, 2a. \*A. (C.) geminum, Quadratenkreide, Campanian, Höver, Germany; rhizoclone desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).-FIG. 191,2b-c. A. (C.) papillata (HINDE), Upper Chalk, Campanian, Flamborough, Yorkshire, England; b, incomplete example with margin broken in part, showing paragastral surface and postica, where skeletal cortex is broken away near base, and internal meshwork is locally not preserved, aporhyses are seen in section; c, part of external surface, ×1 (Hinde, 1884a).

- Cladostelgis POMEL, 1872, p. 150, nom. oblit. [\*Verrucospongia damaecornis F. A. ROEMER, 1864, p. 45; OD]. Flabellate, of distinctive, digitate, staghorn shaped, but without other special features. [Equated incorrectly by DE LAUBENFELS (1955, p. 107) with Stelgis POMEL (1872, p. 149, type, Ventriculites radiatus MANTELL, 1822, p. 168), =Ventriculites MANTELL (1822, p. 168) of class Hexactinellida, order Lychniscosa.] Cretaceous: Europe.——FiG. 191, J. \*C. damaecornis (F. A. ROEMER), Cuvieri beds, Turonian, Windmuhlenberges near Salzgitter, Germany; side view of staghorn-shaped sponge with pronounced but small, exhalant ostia, ×1 (Roemer, 1864).
- Scythophymia POMEL, 1872, p. 131 [\*S. crassa POMEL, 1872, p. 132; SD DE LAUBENFELS, 1955, p. 48] [=Scytophymia MORET, 1924, p. 15, nom. null.]. Cup to mushroomlike, thick walled; both surfaces of skeletal framework with smooth, dense, skeletal cortex; paragastral surface with large, widely spaced, punctiform or marginated postica; external (or lower) surface apparently without skeletal pores; further details unknown. [Position strictly unknown, but interpreted by MORET (1924, p. 15) as based on forms of Verruculina ZITTEL (s.l.); absence of external pores is distinctive, if genuine.] Neogene (Miocene): Algeria.—FIG. 191, 3a-b. \*S. crassa, Djebel Djambeida; a, side view of thick-walled, mushroomlike sponge with prominent, broad, upper depression; b, view from above into summit area with marginated postica on gastral surface, ×0.5 (Pomel, 1872).
- Verruculina ZITTEL, 1878a, p. 122 [\*Chenendopora aurita F. A. ROEMER, 1864, p. 43; SD SCHRAMMEN, 1924a, p. 124; not Manon micrommata F. A. ROEMER, 1840 in 1840-1841, p. 3, des. DE LAUBENFELS, 1955, p. 48] [=Chondriophyllum SCHRAMMEN, 1924a, p. 126 (type, Manon tenue ROEMER, 1840 in 1840-1841, p. 3)]. Bowl- to funnel-like or flabellate, stalked or not, some flabellate examples enrolled to form secondary funnels or irregularly convolute; external, skeletal pores punctiform, minute, to pustular, small, always numerous; postica nearly always pustular, and usually larger but less numerous than external pores; size and spacing of postica greatest in thick-walled and least in thin-walled species; desmas of interior typically slender and predominantly branching, although simple, arched forms also occur; most species with special, flattened, and finely branching desmas in cortical meshwork; supplemental oxeas in some; no microscleres known. [Chondriophyllum SCHRAMMEN (type, Manon tenue F. A. ROEMER, 1841 in 1840-1841, p. 3) includes species in which thickness of the skeletal wall is typically not more than about 0.5 cm, and special cortical desmas are present.] Cretaceous (Aptian)-Neogene (Miocene).
  - V. (Verruculina). Special cortical desmas present; wall thick or thin; size of postica varied correspondingly. *Cretaceous (Aptian)–Neogene (Mi*ocene): Spain, *Aptian;* Czech Republic, Slovakia,

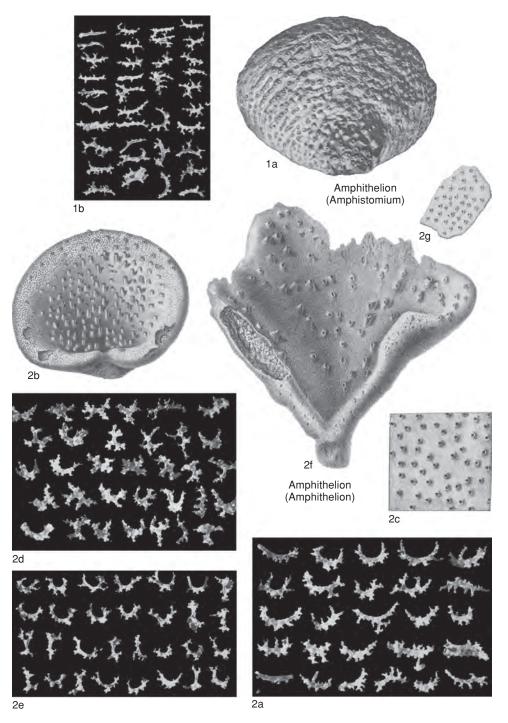


FIG. 190. Scleritodermatidae (p. 303-304).

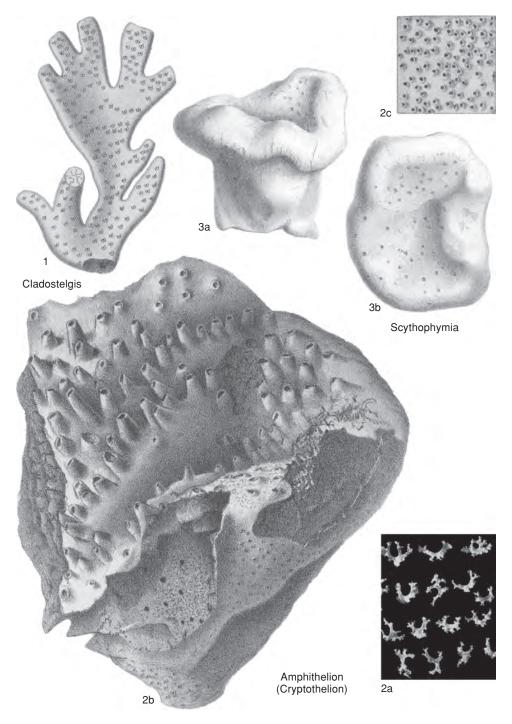


FIG. 191. Scleritodermatidae (p. 304).

Cenomanian; England, Santonian-Campanian; France, Santonian; Germany, Turonian-Campanian; Western Australia, Eocene; Algeria, Miocene.—FIG. 192a-b.\*V. (V.) aurita (ROEMER), Mukronatenkreide, Campanian, Misburg, Germany; a, side view of funnelshaped holotype, ×1 (Roemer, 1864); b, characteristic desmas, ×22 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung) .---- FIG. 192c. V. (V.) seriatopora (F. A. ROEMER), Quadratenkreide, Campanian, Oberg, Germany; paragastral surface of flabellate specimen showing postica. [This species is identical with V. aurita according to SCHRAMMEN, 1910, p. 141, but not 1924a, p. 124; may be same species, but with cortex incompletely developed], ×1 (Schrammen, 1910).-FIG. 192d-e. V. (V.) tenuis (F. A. ROEMER), Upper Chalk, ?Campanian, Flamborough, Yorkshire, England, type species of Chondriophyllum SCHRAMMEN, 1924a, figured by HINDE, 1884a as V. pustulosa HINDE; d, general view showing paragastral surface and thin wall of funnelshaped sponge; e, part of external surface, ×1 (Hinde, 1884a).

V. (Amphichondrium) SCHRAMMEN, 1924a, p. 127 [\*Spongia convoluta QUENSTEDT, 1877 in 1877-1878, p. 368; OD]. Special cortical desmas (said to be) absent; wall typically thin; external pores and postica both minute, about equally numerous, punctiform to pustular. Cretaceous (upper Turonian-Campanian): Germany, upper Turonian-Campanian; England, Campanian. -FIG. 193a-d. \*V. (A.) convoluta (QUEN-STEDT), Campanian; a, funnel-shaped sponge, Upper Chalk, Flamborough, Yorkshire, England,  $\times 0.5$ ; *b*-*c*, paragastral surface with small, exhalant pores, external surface with minute, inhalant pores, Upper Chalk, Flamborough, Yorkshire, England, ×4 (Hinde, 1884a); d, characteristic rhizoclone desmas, Mukronatenkreide, Misburg, Germany, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

### Subfamily UNCERTAIN

Pleurophymia POMEL, 1872, p. 135 [\*P. cotyle; SD DE LAUBENFELS, 1955, p. 48; =P. sessilis POMEL, 1872, p. 138]. Irregularly cuplike or flabellate, thick walled, may be stalked; paragastral surface of skeletal framework with skeletal cortex and large, widely spaced, marginated to papilliform postica; external surface finely rugose, with small pores along irregular furrows, and apparently no cortex; interior with branching, skeletal canals that begin from postica and run to pores of external surface; further details unknown. [Spicular structure of type species unknown, but all nominal species are probably identical, and one (P. ambigua POMEL, 1872, p. 137) referred by MORET (1924, p. 15) to Verruculina ZITTEL (s.l.); herein thought likely to be more similar to living Scleritodermatinae because of seeming absence of an external cortex, if POMEL's descriptions are correct.] *Neogene (Miocene):* Algeria.— FIG. 189, 4a-c. \**P. cotyle*, Djebel Djambeida; *a*, incomplete specimen from above, showing postica; *b*, same from below, restored where detail absent; *c*, lateral view showing lateral point of attachment, with internal canals exposed along fracture, ×0.5 (Pomel, 1872).

### Family JEREICIDAE Schrammen, 1924

#### [Jereicidae Schrammen, 1924a, p. 81] [=Jereopsidae de Laubenfels, 1955, p. 48]

Globular to club-shaped or cylindrical sponges without distinct, paragastral cavities, although terminal depression may be present, but with axial group of vertical aporhyses whose apertures (postica) are at summit; additional epirhyses present or absent; skeletal framework vaguely to distinctly fibrous internally, and with or without distinct, longitudinal, skeletal fibers that radiate upwardly from axial parts when present; surface meshwork usually forming compact, skeletal cortex, with perforating ostia outside area where aporhyses open; supplemental monaxons in some; no microscleres known. [Change of the family name from Jereicidae to Jereopsidae, if Jereica ZITTEL is regarded as a synonym of Jereopsis POMEL, as by DE LAUBENFELS (1955, p. 48), is not required nor permitted by the Code (ICZN, 1999).] Jurassic (Callovian)–Holocene.

Jereica ZITTEL, 1878a, p. 126 [\*Jerea polystoma F. A. ROEMER, 1864, p. 34; SD MORET, 1926b, p. 87]. Globular, pyriform, top to club shaped or cylindrical, often stalked, with or without shallow, terminal depression; skeletal surface typically formed by dense, external cortex with numerous small, closely spaced, perforating ostia, except in terminal area where aporhyses open; skeletal framework clearly fibrous internally, with axial part traversed by bundle of vertical, tubular aporhyses that extend to near base, and with radiating, skeletal fibers and fine, radial epirhyses in lateral parts around them; no radial aporhyses in lateral parts; postica several to many times larger than ostia, simple or slightly marginated, and located in terminal depression when present; cortical desmas may be smaller than those of internal fibers; supplemental oxeas may occur; no microscleres known. Jurassic (Oxfordian)-Upper Cretaceous: Poland, Oxfordian; Europe, Upper Cretaceous; England, Cenomanian, Campanian; France, Turonian-Santonian; Germany, Santonian-Campanian.—FIG. 194, 3a-b. \*J. polystoma (F. A. ROEMER), Coniacian, Paris basin, France; a-b,

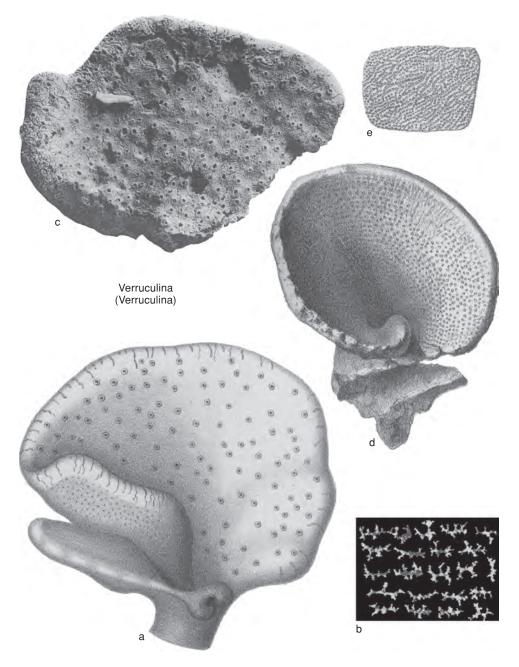
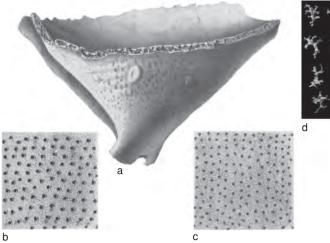
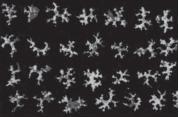


FIG. 192. Scleritodermatidae (p. 304-307).

diagrams showing structure: *a*, external appearance and *b*, vertical section; *ip*, inhalant pores (ostia); *c*, cortex, removed in part; *ep*, exhalant pores (postica); *f*, fibers of interior, seen where cortex is removed (view *a*); *f*, fibrous lateral part of skeletal framework (view b); ic, supposed inhalant canals (spaces between radial fibers); ec, exhalant canals (aporhyses) (Moret, 1926b).——FIG. 194,3c. J. punctata (GOLDFUSS), Santonian, Saint-Cyr, France; skeletal surface with cortex and pores present at





Verruculina (Amphichondrium)

FIG. 193. Scleritodermatidae (p. 307).

right and fibrous interior exposed at left, ×20 (Moret, 1926b; courtesy of Société Géologique de France).

- Jereopsis POMEL, 1872, p. 177 [\*J. inaequalis; SD DE LAUBENFELS, 1955, p. 48; =Jerea clavaeformis POMEL, 1872, p. 162, non SCHMIDT, 1879; for synonymy of J. clavaeformis see MORET, 1924, p. 12-13] [=Jereopsidea POMEL, 1872, p. 188 (type, Jereopsis aberrans POMEL, 1872, p. 187, SD DE LAUBENFELS, 1955, p. 48)]. Globular to short-cylindrical or elongate pyriform, or forms compound growths in which two or more sponges are united; individuals always with shallow, bowl-like, terminal depression, in which aporhyses open, and some with depression surrounded by flattened and radially furrowed surface; sides with ostia that perforate dense, external cortex; underlying surface of internal, skeletal framework with sinuous, anastomosing furrows that run downwardly from summit; interior fibrous but without distinct, radial fibers, traversed vertically by bundle of axial aporhyses and with additional radial aporhyses that arch outwardly and downwardly in lateral parts, and in some instances open into furrows at external surface of framework; postica little larger than ostia; no loose spicules known. Neogene (Miocene): Algeria, Spain.—FIG. 194,2a-c. \*J. inaequalis, Djebel Djambeida, Algeria; a, side view of subcylindrical form, ×0.5; b, view from above of shallow spongocoel depression with exhalant ostia and surrounding, radial canals, ×1; c, side view of compound example (=Jerea sobolifera POMEL), ×1 (Pomel, 1872).
- Moretispongia BREISTROFFER, 1949, p. 103 [\*Epeudea praegnans DUMORTIER, 1871, p. 53; OD; type genus is not Meta pyriformis POMEL, as cited in LAGNEAU-HÉRENGER, 1962, p. 182] [=Marisca POMEL, 1872, p. 192 (type, M. pyriformis, M), non GRAY, 1840]. Pyriform to irregularly cylindrical with shallow, ter-

minal depression in which aporhyses open; sides with skeletal cortex pierced by widely spaced, marginated ostia that are similar to postica in size or larger; underlying surface of internal framework may be furrowed; internal meshwork fibrous; some desmas may resemble spiny tetraclones or sphaeroclones; no loose spicules known. Middle Jurassic (Callovian)-Neogene (Miocene): France, Callovian; Europe, Upper Jurassic-Lower Cretaceous; Spain, Aptian; Northern Africa, Miocene.-—Fig. 194, 1a. M. pyriformis (POMEL), Miocene, Benibou Mileuk, Algeria; side view showing cylindrical form with nodose, inhalant ostia on sides and furrows of small, exhalant ostia on summit, slightly reduced (Moret, 1924; courtesy of Société Géologique de France).—FIG. 194, 1b-c. M. micropora LAGNEAU-HÉRENGER, Aptian, Can Casanyas Castellet, Catalogne, Spain; characteristic spicules including desmas of interior, some resembling spiny sphaeroclones, and normal rhizoclones, ×25 (Lagneau-Hérenger, 1962).

- Pomelia ZITTEL, 1878a, p. 126 [\*P. schmidti; OD]. Club shaped to subcylindrical with arched summit marked by shallow grooves around summit cluster of small oscula of deep, exhalant canals; dermal surface with regular, fine, inhalant ostia; endosomal skeleton of rhizoclones united with short, thick, ray tips and dermal rhizoclones more nodose. [Included in the family with some question.] Neogene (?Miocene), Holocene: North Africa, ?Miocene; USA (Florida), Holocene.—FiG. 195,2a-b. \*P. schmidti, Holocene, Florida; a, side view of small, clubshaped sponge with short stalk and oscular cluster at summit, ×1; b, spicule relationships in endosomal skeleton, ×40 (Zittel, 1878a).
- Stichophyma POMEL, 1872, p. 188 [\*Manon turbinatum F. A. ROEMER, 1840 in 1840–1841, p. 3; SD de LAUBENFELS, 1955, p. 48; M. turbinatum

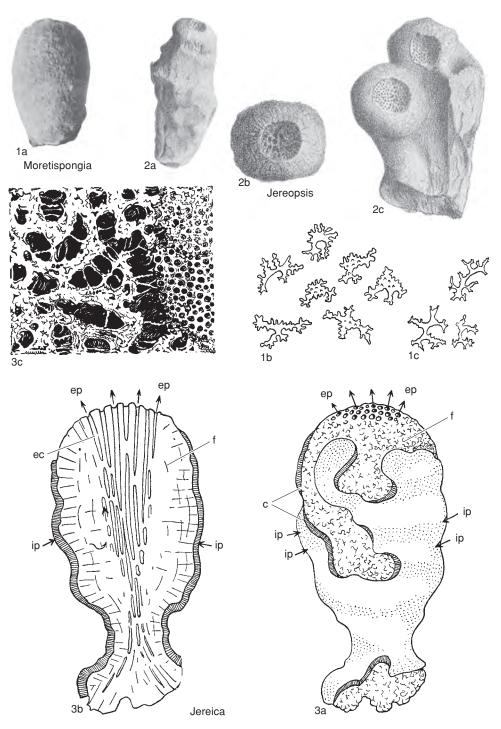


FIG. 194. Jereicidae (p. 307–309).

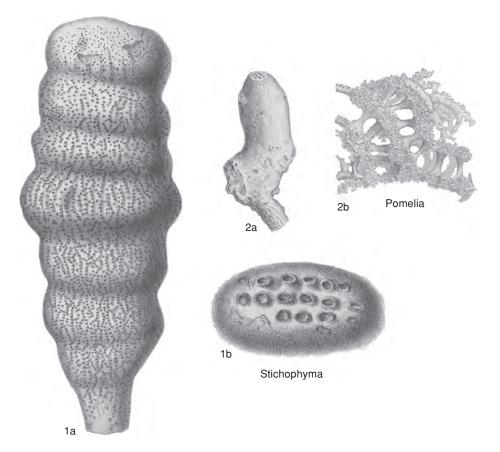


FIG. 195. Jereicidae (p. 309-311).

only mentioned, not designated, by RAUFF, 1893, p. 96, to whom DE LAUBENFELS (1955) ascribed designation] [=Stychophyma VOSMAER, 1885, p. 291, nom. null.; Sticophyma MORET, 1924, p. 13, nom. null.; Meta POMEL, 1872, p. 188, obj., non KOCH, 1835]. Pyriform to top or club shaped, cylindrical, or irregularly nodular, with rounded or flattened summit but no terminal depression; some elongate examples also branched or with transverse constrictions; skeletal surface formed by dense, external cortex pierced at summit by group of large, simple or marginated postica, and on sides by numerous smaller pores that are typically pustular; internal framework fibrous with an axial group of vertical aporhyses that extend to base, and with radiating fibers and fine, radial epirhyses in lateral parts but no radial aporhyses; no loose spicules known. Upper Cretaceous-Neogene (Miocene): Europe, Upper Cretaceous; Czech Republic, Slovakia, Cenomanian; France, Santonian; England, Campanian; Germany, Poland, Turonian-Campanian; Algeria, Miocene. -FIG. 195, 1a-b. S. tumida HINDE, Upper Chalk, Campanian, Flamborough, England; a, large, clubshaped example with transverse constrictions and numerous pustular, inhalant pores in dense, dermal layer,  $\times 0.5$ ; *b*, summit of another specimen from above showing large, marginated postica,  $\times 1$ (Hinde, 1884a).

# Family SELISCOTHONIDAE Schrammen, 1924

[Seliscothonidae SCHRAMMEN, 1924a, p. 81]

Hollow, cylindrical, funnel- to mushroomlike or flabellate sponges with fibrous, skeletal frameworks, in which radially spreading, longitudinal, skeletal fibers are conspicuous; skeletal canalization typically either absent or restricted to development of ostia or postica; some also with vertical aporhyses in axial parts only; longitudinal fibers arranged without special order, or so as to form more or less regular, radial lamellae; skeletal surfaces may expose internal structure or be formed by skeletal cortex in which desmas are similar to those of interior or smaller and more finely branched; supplemental oxeas may occur within internal meshes, at surfaces, or enclosed within longitudinal fibers; microscleres unknown. [Living "Seliscothon" chonelloides DOEDERLEIN is not referred to this family because longitudinal skeletal fibers appear to be absent.] Cretaceous (Aptian)–Holocene.

- Seliscothon ZITTEL, 1878a, p. 117 [\*Spongia plana PHILLIPS, 1835 in 1828-1836, p. 177; SD DE LAUBENFELS, 1955, p. 45] [=Trachydictya POMEL, 1872, p. 107, nom. oblit.]. Usually funnel- or mushroomlike, but may be hollow cylindrical or flabellate; interior of skeletal framework with radial lamellae or not, or with more or less regular lamellae in parts but not others; external (lower) surface of framework with thin, fibrous, skeletal cortex, in which branching and anastomosing fibers are aligned longitudinally, and may be finer than those of interior; this surface commonly striated longitudinally, striations corresponding with skeletal fibers, but in some with fibrous cortex coated by very thin, dense, external cortex, formed by small, finely branching, flattened desmas, and without skeletal pores; paragastral (upper) surface usually with more or less compact, skeletal cortex and closely spaced postica, but exposing internal structure if cortex is developed incompletely or absent; interior usually not canalized, but mushroomlike specimens may have central group of vertical aporhyses that extend into stalk; supplemental oxeas may occur in interfibrous meshes, at surfaces, or incorporated into longitudinal fibers; microscleres unknown. [Lamellar internal structure is often treated as extensively developed in this genus, but it occurs only locally or is absent in the type species S. plana, in which fine, longitudinal striation of the external surface does not represent internal structure.] Cretaceous (Aptian)-Neogene (Miocene): Spain, Aptian; Czech Republic, Slovakia, Cenomanian; France, Cenomanian-Campanian; Germany, Poland, Santonian-Campanian; England, Santonian-Maastrichtian; Spain, Algeria, Miocene.-FIG. 196,2a-c. \*S. planum (PHILLIPS); a, small example with funnel-like shape seen from above, Upper Chalk, ?Campanian, Flamborough, Yorkshire, England; b, same seen from side, inverted, Upper Chalk, ?Campanian, Flamborough, Yorkshire, England, ×1 (Hinde, 1884a); c, rhizoclone desmas and oxeas, Mukronatenkreide, Campanian, Misburg, Germany, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Histiodia POMEL, 1872, p. 144 [\**H. undulata;* SD DE LAUBENFELS, 1955, p. 45] [=*Histodia* MORET, 1924, p. 16, *nom. null.*]. Only known from fragments but

apparently flabellate, forming thin-walled, undulating plates; both surfaces of skeletal framework with fine, closely spaced, and more or less sinuous, longitudinal furrows, along which are regular series of skeletal pores; when complete, furrows roofed by thin, smooth, external cortex, pierced by skeletal pores corresponding with those of underlying framework, and with roofed furrows forming longitudinal, subcortical channels; interior fibrous but not lamellar; further details unknown. [The genus is regarded as being essentially identical with Seliscothon ZITTEL and MORET (1924, p. 16), but distinguished by characters of the skeletal surfaces.] Neogene (Miocene): Algeria.-FIG. 196,3a-b. \*H. undulata; a, fragment of skeletal framework, showing external furrows, Beni bou Mileuk, slightly reduced (Moret, 1924; courtesy of Société Géologique de France); b, skeletal surface as seen with cortex present (right) and absent (left), Djebel Djambeida, slightly enlarged (Pomel, 1872).

- Kaliapsis BOWERBANK, 1869, p. 337 [\*K. cidaris; OD]. Sponges a thin coating, parasitic, spicules phyllotriaenes, rhizoclad desmas, and acanthostyles. Holocene: Indian and Pacific Oceans.——FIG. 196,4a-b. \*K. cidaris, South Seas; a, section normal to surface, showing vertical shift from fibers with canals at base, to those strongly branched at surface, ×150; b, associated small phyllotriaene, ×175 (Bowerbank, 1869).
- ?Laosciadia POMEL, 1872, p. 148 [\*L. fungiformis; OD]. Class uncertain; equated with Seliscothon ZITTEL by DE LAUBENFELS (1955, p. 45) but not MORET (1924, 1926b) or LAGNEAU-HÉRENGER (1962); type species resembles a Seliscothon from POMEL's description, but not figured; skeleton thought to be calcareous by POMEL; and no specimens known; belongs with order Pharetronida, class Calcarea, if the skeleton were calcareous. Upper Cretaceous: England.
- Pachyselis SCHRAMMEN, 1924a, p. 93 [\*Achilleum auriforme F. A. ROEMER, 1840 in 1840-1841, p. 2; OD]. Flabellate, ear- or leaflike, or irregularly lobate to convolute; skeletal framework fibrous internally but not lamellar; one surface with fine, longitudinal striations or small, skeletal pores; the other coated by dense, external cortex with small, round pores; cortical meshwork formed from small, flattened, strongly branching desmas; loose oxeas may occur; microscleres unknown. [The type species was formerly known as Chonella auriformis (see ZITTEL, 1878a; SCHRAMMEN, 1910; MORET, 1926b) and regarded as nonfibrous by MORET; some specimens identified under this name by SCHRAMMEN also nonfibrous and clearly azoricids; but fibrous structure present in others and mentioned by ROEMER (1864, p. 51); the name C. auriformis hence thought herein to have been used for two different species.] Cretaceous (Turonian-Campanian): Germany.—FIG. 196,1a-b. \*P. auriformis (F. A. ROEMER); a, small example with surface meshwork poorly developed, showing fibrous structure of interior, Scaphiten-Planer, upper Turonian, Nettlingen, ×1 (Schrammen, 1910);

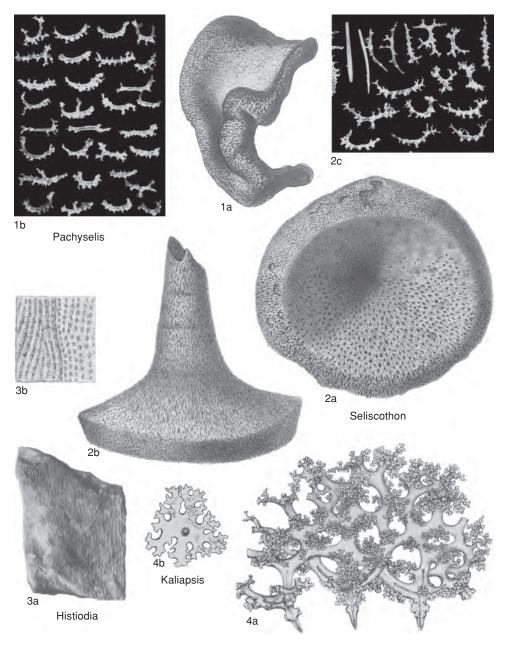
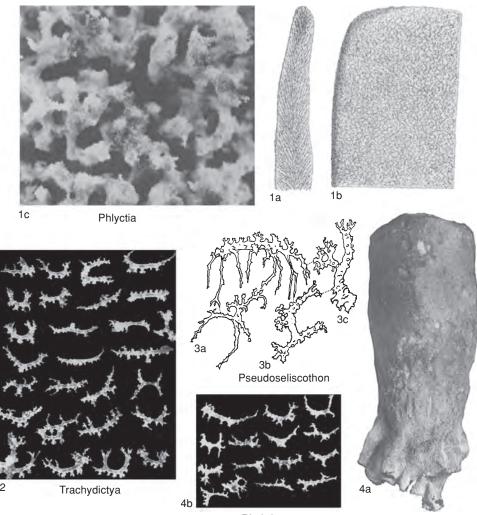


FIG. 196. Seliscothonidae (p. 312-313).

*b*, rhizoclone desmas of internal meshwork, Mukronatenkreide, Campanian, Misburg, Germany, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

Phlyctia POMEL, 1872, p. 235 [\*P. expansa; SD DE LAUBENFELS, 1955, p. 47]. Initially funnel-like, becoming flabellate or expanding horizontally; skeletal framework fibrous but not lamellar, with longitudinal fibers spreading out toward both surfaces; external (or lower) surface with no cortex, exposing internal structure; paragastral surface similar or locally with round postica; no loose spicules known. *Neogene (Miocene):* Algeria.——FIG. 197, *Ia-c. \*P. expansa,* Djebel Djambeida; *a*, dermal surface; *b*,



Rhabdotum

FIG. 197. Seliscothonidae (p. 313-315).

section through bladelike fragment showing divergent, skeletal structure, ×1 (Pomel, 1872); c, photomicrograph of skeletal surface, ×10 (Moret, 1924; courtesy of Société Géologique de France).

Pseudoseliscothon MORET, 1926b, p. 81 [\*P. cazioti; OD]. Hollow, cylindrical or trumpetlike, thick walled; external surface of skeletal framework formed by skeletal cortex with numerous minute, closely spaced, intracortical ostia; interior fibrous, but not lamellar; character of paragastral surface unknown; desmas large, some finely tuberculate, others with very long spines that give desmas spiderlike appearance; no other spicules known. *Cretaceous (Santonian):* France.—FIG. 197,3a-c. \*P. cazioti, Saint-Cyr; characteristic desmas including tuberculate desmas from internal fibers, cortical desma, and spiderlike desma from interior, ×25 (Moret, 1926b; courtesy of Société Géologique de France).

Rhabdotum SCHRAMMEN, 1924a, p. 95 [\*R. columna; OD]. Cylindrical or club shaped, short stalked, with deep, tubular, paragastral cavity; external surface of skeletal framework with fibrous structure, or coated locally by very thin, dense, external cortex with round ostia; distinct postica absent; external cortex formed from small, finely branching, flattened desmas; no other spicules known. Cretaceous (Campanian): Germany.——FIG. 197,4a-b. \*R. columna, Quadratenkreide, Höver; a, cylindrical sponge with lower root tufts, ×0.75; b,

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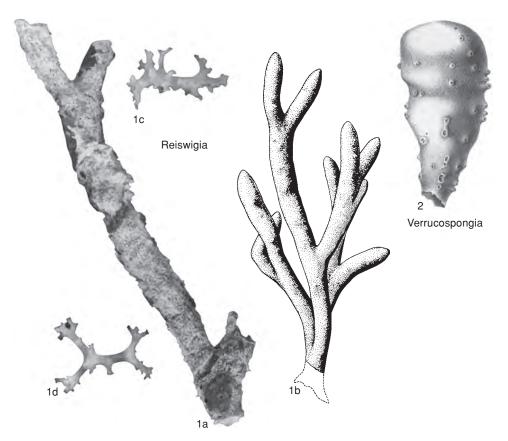


FIG. 198. Uncertain (p. 315-316).

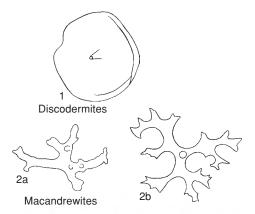
rhizoclone desmas,  $\times 20$  (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

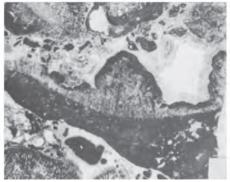
Trachydictya POMEL, 1872, p. 107 [\*Scyphia mantelli GOLDFUSS, 1831, p. 219; OD]. Based on a funnellike species with finely lamellar structure and smaller postica than S. plana, but not otherwise distinctive. Cretaceous (Campanian): Germany.— FIG. 197,2. \*T. mantelli (GOLDFUSS), Mukronatenkreide, Misburg; desmas, ×20 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).

#### Family UNCERTAIN

- Orecyta DE LAUBENFELS, 1955, p. 49, nom. nov. pro Cytorea POMEL, 1872, p. 225, non LAPORTE, 1849 [\*Limnorea nobilis ROEMER, 1864, p. 37; OD]. Cretaceous: Europe.
- Perimera POMEL, 1872, p. 200 [\*Polystoma boletiformis COURTILLER, 1861, p. 127; OD]. Cretaceous: Europe.
- Plococonia POMEL, 1872, p. 248 [\*Spongia contortilobata MICHELIN, 1847 in 1840–1847, p. 144; OD]. Cretaceous: Europe.

- Pocillospongia COURTILLER, 1861, p. 125 [\*P. pyriformis; SD DE LAUBENFELS, 1955, p. 49] [=Poecilospongia POMEL, 1872, p. 117, nom. null.]. Cretaceous: Europe.
- Reiswigia TRAMMER, 1979, p. 40 [\*R. ramosa TRAMMER, 1979, p. 41; OD]. Branching sponge without a spongocoel and distinct canal system but with small pores scattered over dermal surface; skeleton of rhizoclones covered with sharp-ended processes. *Jurassic (Oxfordian):* Poland.—FIG. 198, *1a-d.* \*R. *ramosa,* Lower Oxfordian deposits, Polish Jura Chain; a, holotype fragment, ×1; b, restoration showing branched habit, ×0.5; *c-d,* isolated rhizoclones, ×50 (Trammer, 1979).
- Verrucospongia D'ORBIGNY, 1849, p. 549 [\*Manon sparsum REUSS, 1844, p. 170; SD DE LAUBENFELS, 1955, p. 49]. Subcylindrical or steeply to irregularly obconical sponge with rounder upper end; numerous variously sized, perforated, wartlike projections around possible inhalant ostia irregularly distributed over polymorphic dermal surface; dermal layer a thick web of anastomosing fibers. Upper Cretaceous: Europe.—FIG. 198,2. \*V sparsa (REUS), Lower Plänerkalk, near Bilin, Germany; side view





3

Mastostroma



of steeply obconical, slightly annulate sponge with wartlike projections around possible inhalant ostia irregularly distributed over dermal surface,  $\times 1$  (Reuss, 1845–1846).

## Suborder UNCERTAIN

- Bothrochlaenia POMEL, 1872, p. 72 [\*B. pavonia; OD]. Upper Jurassic: ?Europe.
- Chlaenia POMEL, 1872, p. 72 [\*Chenendopora complanata D'ORBIGNY, 1850, vol. 1, p. 391; SD ENGESER & MEHL, 1993, p. 186] [=Cymbochlaenia POMEL, 1872, p. 72, obj.]. Cretaceous: Europe.
- Cladilithosia POMEL, 1872, p. 252 [no species]. Cretaceous: Europe.
- Cupulina COURTILLER, 1861, pl. 20, 39 [\**C. pocillum;* SD DE LAUBENFELS, 1955, p. 65]. *Upper Cretaceous:* France.
- Diacyparia POMEL, 1872, p. 90 [\* *Tragos rugosum* GOLDFUSS, 1829, p. 96 (*teste* SCHRAMMEN, 1937, p. 93); =*Chenendopora rugosa* D'ORBIGNY, 1850, vol. 1, p. 391, SD DE LAUBENFELS, 1955, p. 65]. *Cretaceous:* Europe.

- Discodermites SOLLAS, 1880d, p. 386 [\*D. cretaceus; OD]. Isolated spicule with circular, discoidal head and conical shaft with smooth, cylindrical arms and botryoidal apophyses. Cretaceous: Europe.——FIG. 199,1. \*D. cretaceus, Trimmingham Chalk, Maastrichtian, Norfolk, England; isolated type spicule with discoidal head and conical shaft, scale unknown (Sollas, 1880d).
- Elasmalimus POMEL, 1872, p. 203 [\*Dimorpha prolifera COURTILLER, 1861, p. 124; SD DE LAUBENFELS, 1955, p. 65] [=Elasmolimus DE LAUBENFELS, 1955, p. 65, nom. null.]. Cretaceous: Europe.
- Hypothyra POMEL, 1872, p. 116 [\**Scyphia trilobata* MICHELIN, 1847 in 1840–1847, p. 141; OD]. *Cretaceous*: Europe.
- Ishadia POMEL, 1872, p. 210 [\**I. typica;* OD]. *Paleogene–Neogene:* North Africa.
- Macandrewites SOLLAS, 1880d, p. 389
   [\*Dactylocalycites vicaryi CARTER, 1871, p. 123;
   OD]. Cretaceous: Europe.——FIG. 199,2a-b. \*M. vicaryi (CARTER), Trimmingham Chalk, Maastrichtian, Norfolk, England; type with tetraclone spicules (Sollas, 1880d).
- Mastostroma WU, 1991, p. 93 [\*M. punctiformis; OD]. Sheetlike with mounds on upper surface, pierced by larger, horizontal tubes and smaller, vertical ones; lithistid skeleton of so-called knots and shafts where spherical knots formed by fusion of ray tips. Permian (Guadalupian): China.——FIG. 199,3. \*M. punctiformis, Reef of Xiangbo, Maokou Stage, Longlin, Guangxi; vertical section of holotype showing form with mounds and horizontal and vertical canals, IGC xb36-1-2, ×2 (Wu, 1991).
- Ocellaria RAMOND DE CARBONNIÈRE, 1801, p. 177 [\*O. nuda; SD POMEL, 1872, p. 87]. [=Ocellarioscyphia FROMENTEL, 1860, p. 40 (intended but unjustified emendation of genus; subsequent designation of Ventriculites radiatus MANTELL, 1822, by DE LAUBENFELS (1955, p. 106) as the type species is therefore invalid).] Upper Cretaceous: Europe.
- Orosphecion POMEL, 1872, p. 222 [\*Manon pulvinarium GOLDFUSS, 1826, p. 2; OD]. Cretaceous: Europe.
- Ortmannispongia DE LAUBENFELS, 1955, p. 65, nom. nov. pro Ortmannia SCHRAMMEN, 1924a, p. 74, non RATHRUN, 1902 [\*Ortmannia colligens SCHRAMMEN, 1924a, p. 74; OD]. [DE LAUBENFELS (1955, p. 65) cited the genus as renamed by SCHRAMMEN (1936), but the reference where that change was made has not been found.] Cretaceous: Europe.
- Pachypsechia POMEL, 1872, p. 154 [\**P. subannulata;* OD]. *Jurassic:* North Africa.
- Physocalpia POMEL, 1872, p. 117 [\**Scyphia mamillata* COURTILLER, 1861, p. 122; OD]. *Cretaceous:* France.
- Placojerea POMEL, 1872, p. 193 [\*Jerea desnoyersii MICHELIN, 1847 in 1840–1847, p. 135; OD]. Cretaceous: France.
- Platispongia Courtiller, 1861, p. 139 [\**P. speculum;* SD de LAUBENFELS, 1955, p. 65]. *Upper Cretaceous:* France.

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- Plethosiphonia POMEL, 1872, p. 127 [\**P. oroides;* OD] [=*Pliobunia* POMEL, 1872, p. 206 (type, *P. oroides,* OD)]. *Paleogene–Neogene:* North Africa.
- **Podapsis** SOLLAS, 1880d, p. 388 [\**P. cretacea*; SD DE LAUBENFELS, 1955, p. 65]. Spicules relatively small but with curious, footlike shape of articular surface at end of unbranched rays. *Cretaceous:* Europe.
- Polysiphoneudea FROMENTEL, 1860a, p. 30 [\**Siphonia* arbuscula MICHELIN, 1847 in 1840–1847, p. 139; OD] [=*Polysiphonia* POMEL, 1872, p. 127, obj.]. *Upper Cretaceous:* Europe.
- Polystomiella REID, herein, nom. nov. pro Polystoma COURTILLER, 1861, p. 126, non ZEDER, 1800, nec ZEDER, 1803, nec DE LAROCHE, 1811, nec KUHL & HASSELT, 1822, nec STEPHENS, 1835 [\*Polystoma

*irregulare* COURTILLER, 1861, p. 126; OD] [?=*Perimera* POMEL, 1872, p. 200 (type, *Polystoma boletiformis* COURTILLER, 1861, p. 126, OD]. *Upper Cretaceous:* France.

- Polythyra POMEL, 1872, p. 116 [\**Scyphia perforata* COURTILLER, 1861, p. 121; OD]. *Cretaceous:* Europe.
- Pterocalpia POMEL, 1872, p. 117 [\**Scyphia alata* COURTILLER, 1861, p. 123; OD] [=*Petrocalpia* RAUFF, 1893, p. 68, *nom. null*.]. *Cretaceous:* Europe.
- Rhizostele POMEL, 1872, p. 158 [\**Rhizospongia clavata* COURTILLER, 1861, p. 119; OD]. *Cretaceous:* Europe.
- Siphonocoelia FROMENTEL, 1860a, p. 31 [\*Scyphia elegans GOLDFUSS, 1826, p. 5; OD]. Upper Jurassic (Oxfordian): Europe.

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# PALEOZOIC HEXACTINELLID SPONGES

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# Class HEXACTINELLIDA Schmidt, 1870

[nom. transl. MINCHIN, 1900, p. 111, ex order Hexactinellida CARTER, 1875, p. 131, nom. correct. pro "Gruppe" Hexactinellidae SCHMIDT, 1870, p. 13]

Sponges with siliceous spicules that are orthotriaxial hexactines or related forms with fewer than six rays, and with soft parts of adults comprising an internal, choanocytal membrane suspended within networks of syncytial filaments (trabeculae) with waterfilled interspaces. Diverticula of choanocytal membrane form flagellated chambers, which may either face a paragastral surface directly (as in sycons or rhagons) or have leuconoid arrangements to folding of primary chamber layer. Circulation wholly intertrabecular, or in part through subdermal or subgastral lacunae, or inhalant or exhalant canals that arise by special local enlargement of intertrabecular spaces. Outermost trabeculae modified on both sides of wall to form finely porous surface membranes that cover subdermal or subgastral ends of canals unless secondary perforations develop. Megascleres typically with a three-fold division into dermal and gastral series (dermalia, gastralia) that support surface membranes, and a parenchymal skeleton that supports choanosome; some also with further hypodermal or hypogastral megascleres (hypodermalia, hypogastralia) that may have a relationship to those of parenchymal skeleton; or, with special protruded megascleres (prostalia) of hypodermal or parenchymal origin. Parenchymal skeleton one of two types: (a) lyssacine, with megascleres in forms from hexactine to rhabdodiactine, of a single type or two or more different types, and all loose unless rigidly united by a secondary development of fusion; or (b) dictyonine, with megascleres (dictyonalia) that are typically all hexactines, and are united to form a rigid

framework as part of their normal development. Attachment by encrusting basal parts or by imbedded prostalia. Common microscleres of two living subclasses are microholactines and amphidiscs in Amphidiscophora, hexasters without amphidiscs in Hexasterophora; additional sceptrules in one order of Hexasterophora (Hexactinosa); hemidiscs in fossil (Carboniferous, Cretaceous) Amphidiscophora; paraclavules in some Paleozoic forms (Dictyospongiidae) of uncertain subclass. [Taxon initially termed "Gruppe" (group) (SCHMIDT, 1870, p. 13) but subsequently ranked as an order in the same publication (1870, p. 83) and in the same year by KENT (1870). Initial form "Hexactinellidae" has been used as a family name, attributed to SCHMIDT by DE LAUBENFELS (1936, 1955), but had no generic basis and no possible connection with Hexactinella CARTER, 1885, published 15 years later. Translation from order to subclass was by TOPSENT (1892, p. 24).

The taxon Hexactinellida SCHMIDT is preferred to the alternative Hyalospongiae CLAUS used by DE LAUBENFELS (ascribed to VOSMAER; 1882, 1883, 1885, 1887) because (a) SCHMIDT's diagnosis states the character of the spicules correctly; whereas (b) characters cited by CLAUS (euplectellid type of skeletal framework, beardlike roots, nonexistent siliceo-fibrous skeleton) define no group of sponges at any level. The Hyalospongiae of CLAUS also included lithistid Demospongea, supposed with dictyonine Hexactinellida to have skeletons composed of siliceous fibers. The Hyalospongea of DE LAUBENFELS (1955, not 1936) included the Heteractinellida (as Heteractinida), herein regarded as a separate class of sponges, in which spicules are of unknown composition and were possibly calcareous.] Lower Cambrian-Holocene.

# Subclass AMPHIDISCOPHORA Schulze, 1887

# [nom. transl. REID, 1958a, p. xliii, ex Amphidiscophora SCHULZE, 1887a, p. 178; emend., SCHRAMMEN, 1924a, p. 18]

Hexactinellida with microholactine and amphidisc or hemidisc microscleres, to which other birotulates (staurodiscs, hexadiscs) may be added, but without any form of hexaster. All known genera lyssacine and having no fusion of spicules in any part of body; modern genera all with large, pentactinal hypodermalia and with monactinal basalia.

[This taxon was originally (SCHULZE, 1887a) a tribe Amphidiscophora of the suborder Lyssacina ZITTEL, with the class Hexactinellida treated as an order of Porifera. It was then raised to suborder status when SCHULZE (1899, p. 93) abandoned ZITTEL's taxa. Subclass status here corresponds with class status of the Hexactinellida. The subclass is known chiefly from modern examples of one order (Amphidiscosa SCHRAMMEN), in which birotulates are typically amphidiscs and never hemidiscs. The latter were first known as loose microscleres of Late Cretaceous age (SCHRAMMEN, 1924a, p. 21), but have been found with associated megascleres in a Carboniferous genus, Microhemidiscia KLING & RIEF. The first certain genus (Uralonema LIBROVICH) is Carboniferous (Mississippian); but the subclass may be older, because patterns of megaspiculation that approach those of modern pheronematids occur in unplaced forms back to the Ordovician (Brachiospongia MARSH). The Reticulosa (=Protospongioidea FINKS; Cambrian-Permian) may belong here if their paraclavule microscleres are related to amphidiscs and hemidiscs.] Lower Cambrian–Holocene.

# Order AMPHIDISCOSA Schrammen, 1924

[nom. transl. et corr. REID, 1958a, p. xliii, ex tribus Amphidiscaria SCHRAMMEN, 1924a, p. 18]

Birotulate microscleres are characteristically amphidiscs with equal umbels and never hemidiscs; modern forms always with pentactinal hypodermalia and monactinal basalia, and usually with pentactinal autodermalia and autogastralia in which unpaired ray is distal and pinular; some with staurodiscs or hexadiscs as rare variants of normal amphidiscs.

[Common features of the megaspiculation of modern forms point to an origin from a source with these features already developed. Three largely modern families (Pheronematidae, Monoraphididae, Hyalonematidae) are distinguished mainly by differences in their parenchymal megascleres. The oldest known amphidiscs are early Pennsylvanian, occurring in Uralonema LIBROVICH, 1929, which is possibly an early hyalonematid, even though it lacks some of the characteristic megascleres. Still earlier genera are included here, however, because they resemble Uralonema in having differentiated hypodermalia, a thick, parenchymal layer of nonparallel hexactines organized around skeletal canals, and a stout root tuft with some spicules having quadridentate, anchorate terminations, where preserved.] Lower Cambrian-Holocene.

#### Family HYALONEMATIDAE Gray, 1857

[*nom. correct.* SCHULZE, 1887a, p. 178, *pro* Hyalonemadae GRAY, 1857, p. 278]

Parenchymal principalia mainly or all rhabdodiactines, although pentactines or hexactines may also occur; basalia typically with four or more terminal teeth and arranged to form an anchor rope (hence vernacular name glass-rope sponges), often spirally twisted in adults, with proximal, imbedded part forming axial columella through body; some with prostal rhabdodiactines, with distal ray smooth or pinular; acanthophores in basal parts; sceptres absent. *Cretaceous (Turonian)–Holocene.* 

Hyalonema GRAY, 1832, p. 59 [\**H. sieboldi;* M]. Some species thick-walled cup with columellar prominence in paragaster floor; osculum covered by sieve plate; other species without a spongocoel and may have mushroomlike shape; anchor rope typically compact and spirally twisted; no prostalia. [The Cretaceous occurrence in northwestern Germany (MEHL & HAUSCHKE, 1995) is the only Mesozoic record of the genus. A doubtful Tertiary record is

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### Family PATTERSONIIDAE Miller, 1889

#### [Pattersoniidae MILLER, November 1889, p. 153]

Sponges without cloaca or osculum but with skeletal canals of two sizes (epirhyses and possible aporhyses) and a stout, root tuft in which some spicules end in quadridentate anchors; parenchymal spicules hexactines in nonparallel orientation with differentiated, hypodermal pentactines or hexactines. [Oldest whole sponges are Trentonian, but earlier, isolated, massive root tufts are included in stratigraphic range.] *Middle Ordovician– Upper Ordovician.* 

Pattersonia MILLER, 1882, p. 42 [\*P. difficilis MILLER, 1882, p. 43; OD] [=? Strobilospongia BEECHER, April 1889, p. 14 (type, S. tuberosa BEECHER, April 1889, p. 26, OD); ? Chirospongia MILLER, November 1889, p. 156 (type, C. wenti MILLER, November 1889, p. 157, OD)]. Sponge body a conical, lobate mass, narrowest at top with lobes pendent so resembles a fir or spruce tree (or a pine cone); very thick root tuft emerging at base and extending a considerable distance below body; in many individuals lobate body diverging basally to reveal root tuft in axial region for a considerable distance toward apex; some individuals have two root tufts and seemingly represent two bodies fused side by side; root tuft consisting of parallel, smooth, spicule rays (possible rhabdodiactines) of unknown but great length; root tuft occupying much of interior and may have gentle twisting or curvature; surfaces of lobes bearing pores of two sizes, larger ones continuing into body wall as radial tubes of same diameter and may be epirhyses or diarhyses. [No body spicules are visible on the calcified cotypes of Pattersonia difficilis or on the silicified holotype of Chirospongia wenti. BEECHER (1889, p. 26) stated that cruciform ends of large, hexactinellid spicules can be seen on some parts of the surface of Strebilospongia tuberosa, and resemble those of Brachiospongia. He further said, "Smaller dermal spicules and traces of a spicular mesh can likewise be detected." Examination of the types leave little doubt that the three genera are identical; furthermore, the silicified types of Strobilospongia and Chirospongia are from the same locality. Chirospongia faberi is not congeneric with the type of its genus, and has spicular structures reminiscent of the receptaculitid Leptopoterion. Near-topotype root tufts, probably of Pattersonia,

that have been prepared out with acid are composed of fine rhabdodiactines with a minority of clemes that have quadrianchorate ends.] *Middle Ordovician–Upper Ordovician:* USA (Kentucky, Ohio).——FIG. 200, *Ia.* \**P. difficilis*, Corryville Formation, Maysvillian, Cincinnati, Ohio; side view of holotype showing lobate form, USNM 46565, ×1 (Rauff, 1893).——FIG. 200, *Ib–c. P. ulrichi* RAUFF, Corryville Formation, Maysvillian, Cincinnati, Ohio; *b*, side view of lobate to digitate holotype, ×1; *c*, photomicrograph of skeletal net of irregularly oriented hexactines, USNM 46566, ×71 (Rauff, 1893).

- Chirospongia MILLER, November 1889, p. 156 [\*C. wenti; OD]. From same locality and having same preservation as senior Strobilospongia BEECHER, 1889 (April). The calcified, Cincinnatian, senior genus Pattersonia MILLER, 1882, is identical in all other respects. The Cincinnatian C. faberi is not congeneric. Upper Ordovician: USA (Kentucky).
- Strobilospongia BEECHER, 1889 (April), p. 14 [\*S. tuberosa BEECHER, 1889, p. 26; OD]. Sole genus in family for which body spicules have been described. [In external form, pores, parietal gaps, and root tuft, it is identical to the senior calcified Pattersonia MILLER, 1882, and to the junior, topotypic, and likewise silicified Chirospongia MILLER, 1889 (November).] Upper Ordovician: USA (Kentucky).

# Family PELICASPONGIIDAE Rigby, 1970

[Pelicaspongiidae RIGBY, 1970a, p. 11] [=Keriogastrospongiidae WU, 1989, p. 767]

Thick-walled, vasiform sponges with circular, parietal openings or well-defined canal system; skeleton with specialized gastral or dermal layer, or both, of large simple hypodermal and hypogastral hexactines whose gastral or tangential rays appear unoriented with reference to one another but whose proximal and distal rays are arranged approximately normal to surface; interior spicules unoriented, smaller hexactines and related forms. *Lower Ordovician* (*Tremadocian*)–*Triassic (Carnian*).

Pelicaspongia RIGBY, 1970a, p. 12 [\**P. sterea*; OD]. Thick-walled and bowl-shaped with flat base and rounded sides; hypogastralia are hexactines of larger size than interior spicules and have a variably shortened, distal ray; on one isolated near-pentactine the proximal ray very stout and contracts abruptly short of crossing; hypodermalia seem to be similar but poorly preserved; paratangential rays of both in nonparallel orientation; parenchymalia simple hexactines in nonparallel orientation and somewhat larger and more closely spaced about numerous, large, cylindrical skeletal canals that open on both dermal and gastral surfaces, and unclear whether

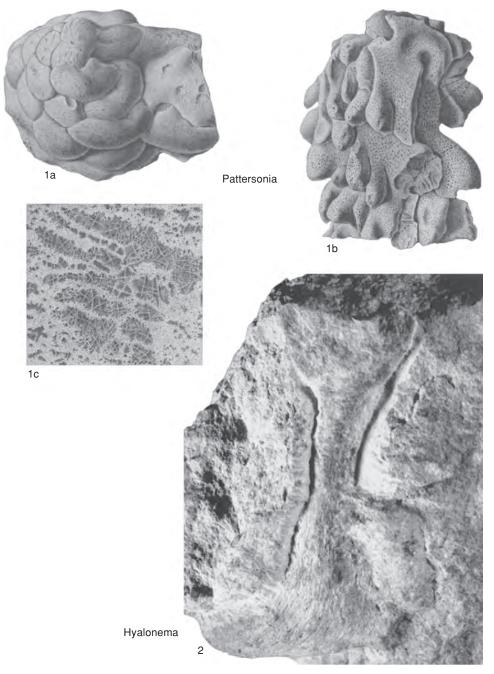


FIG. 200. Hyalonematidae and Pattersoniidae (p. 320-321).

they are epirhyses and aporhyses or parietal gaps; long, coarse spicule fragments, adherent to base of sponge, may represent root-tuft rhabdodiactines. *Devonian (Frasnian):* Canada (Alberta).——FIG. 201,2*a*-*c*. \**P sterea*, Mount Hawk Formation, Front Range; *a*, view down into broad, bowl-shaped spongocoel with prominent parietal gaps and smaller canals filled with light gray matrix in surrounding thick walls; *b*, side view of bowl-shaped holotype with light gray matrix filling parietal gaps,  $\times 0.5$ ; *c*, etched surface of spongocoel with irregularly oriented, siliceous hexactines of various sizes, GSC 24501,  $\times 3$  (Rigby, 1970a).

- Arakespongia RIGBY, CHAMBERLAIN, & BLACK, 1970, p. 827 [\*A. mega RIGBY, CHAMBERLAIN, & BLACK, 1970, p. 828; OD]. Thick-walled bowl to goblet shaped, with flat-bottomed to short, stalklike base; numerous large, radial, cylindrical epirhyses and aporhyses (or possible parietal gaps); smaller, more irregular and anastomosing, skeletal canals connecting with them, canals mainly radial near gastral surface but mainly concentric near dermal surface; hypodermalia are larger pentactines with reflexed, paratangential rays bearing a few tubercles on their distal surfaces; apparently no hypogastralia; parenchymal spicules including hexactines of several sizes, irregularly curved or bent rhabdodiactines, some of which are strongylelike and outline skeletal canals; relatively large oxyhexasters (with fourbranched rays) occurring near dermal surface, rays bearing an ornament of spiral ridges resembling spicules of Spiractinella HINDE; all parenchymal and hypodermal spicules have nonparallel orientation; long rhabdodiactines with quadrianchorate terminations occurring in basal part of sponge and may be basalia. Carboniferous (Lower Pennsylvanian): USA (Oklahoma).-FIG. 202a-c. \*A. mega, Wapanuka Limestone, Ouachita Mountains; a, side view of holotype with stalked base and smooth, bow-shaped profile; b, vertical cut and etched section with light and dark gray matrix filling parietal gaps in both basal area and walls; c, view down into spongocoel of large, bowl-shaped holotype, BYU 1596, ×0.5 (Rigby, Chamberlain, & Black, 1970).
- Ascospongiella García-Bellido Capdevila & Rigby, 2004, p. 445 [\*A. capdevila; OD]. Sack-shaped, moderately thick-walled pelicaspongiid with broad and deep spongocoel; walls perforated by straight, radial, closely spaced, parietal gaps or coarse canals that are cross connected by smaller canals with relatively uniform diameters; all canals separated by thin walls composed of irregularly oriented hexactines of several sizes; distinct, gastral layer of enlarged and irregularly oriented hexactines locally developed but not uniformly present; differentiated dermal layer absent. Carboniferous (upper Bashkirian): Spain.-FIG. 203a-c. \*A. capdevila, San Emiliano Formation, Villafeliz Léon, northwestern Spain; *a*, longitudinal section of large holotype with wide, open spongocoel and thick walls; arched light lines, saw marks, ×0.5; b, dermal surface of paratype with oscular area and round ostia filled with light matrix,  $\times 0.4$ ; c, detail of various sizes of hexactines in dermal layer, ×8 (García-Bellido Capdevila & Rigby, 2004).
- Asturiaspongia GARCÍA-BELLIDO CAPDEVILA & RIGBY, 2004, p. 441 [\**A. aqualiforma*; OD]. Bowl-shaped, thin-walled pelicaspongiid with walls perforated by common, interconnected, tubular canals of at least three sizes, all irregularly distributed, separated by

relatively thin, skeletal tracts of small, irregularly oriented hexactines of several sizes; distinct dermal layer of small hexactines with four rays tangential to dermal surface. *Lower Devonian (Emsian):* Spain. ——FIG. 204,3*a*–*b.* \**A. aqualiforma*, Aguión Formation, Arno, Asturias, northern Spain; *a*, side view of bowl-shaped holotype with large inhalant ostia in dermal layer, MNCN-I-3565a, ×1; *b*, tangential section of wall of paratype, on left, showing canals in wall, and transverse section of bowl-shaped paratype, on right, with large spongocoel filled with light matrix, MNCN-I-3565b, ×1 (García-Bellido Capdevila & Rigby, 2004).

- Bayviewia REIMANN, 1945b, p. 48 [\*B. echinata; OD]. Subglobular with osculum; surface bearing tufts of prostalia (possible rhabdodiactines); body spicules hexactines but poorly known. [This genus is included here with considerable doubt, mainly because of its resemblance to the sympatric *Calicispongia.*] Middle Devonian: USA (New York).—FIG. 204,4. \*B. echinata, Wanakah Shale, Bayview; side view of holotype with rows of small clumps of prostalia, BMS E16566, ×1 (Reimann, 1945b; courtesy of Buffalo Museum of Science).
- Calicispongia REIMANN, 1945b, p. 48 [\*C. airiness; OD]. Bowl shaped with rounded rim; hypogastral hexactines (those on upper surface) larger than rest; several layers of parenchymal hexactines; all spicules in nonparallel orientation; the paratype (REIMANN, 1945b, pl. 9,3) appearing to bear circular openings of possible aporhyses on gastral surface. [This genus resembles Pelicaspongia.] Middle Devonian: USA (New York) .--FIG. 201, 3a-c. \*C. airiness, Wanakah Shale, Bayview; a, view of holotype from above showing broad, shallow spongocoel and thick walls with low nodes on saucer-shaped sponge; ×1; b, view of rounded base of holotype, BMS E14107, ×1; c, view from above showing exhalant ostia in gastral surface of broad, saucer-shaped paratype, BMS E16565, ×2 (Reimann, 1945b).
- Cavospongiella RIGBY, 1986b, p. 38 [\*C. confossa; OD]. Moderately thin-walled, cup- to bowl-shaped brachiosponges with gently convex sides curving inwardly toward osculum; two sizes of circular to polygonal, parietal gaps make up over two-thirds of wall; skeleton of irregularly oriented, smooth hexactines of various sizes; dermal layer present but not thick nor well defined, composed of enlarged hexactines. Devonian (Famennian): Western Austra--FIG. 205,2a-b. \*C. confossa, Virgin Hills lia.-Formation, Lawford Range; a, view of flattened holotype from above showing thin walls and large, parietal gaps filled with dark matrix,  $\times 1$ ; b, side view with rounded profile showing large, parietal gaps and ostia of smaller canals, in intervening areas, filled with dark matrix, GSWA F7226, ×1 (Rigby, 1986b).
- Estrellaspongia GARCÍA-BELLIDO CAPDEVILA & RIGBY, 2004, p. 443 [\**E. irregulara;* OD]. Globose pelicaspongiid with small, shallow spongocoel; thick walls perforated by irregular, branched,

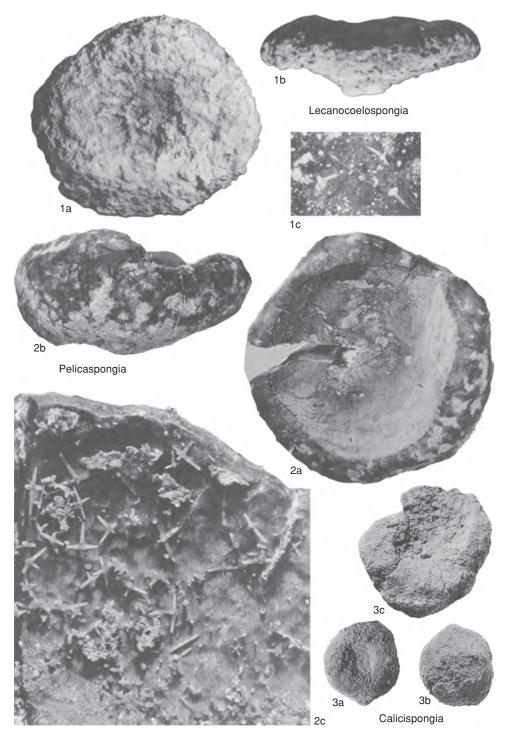


FIG. 201. Pelicaspongiidae (p. 321-329).

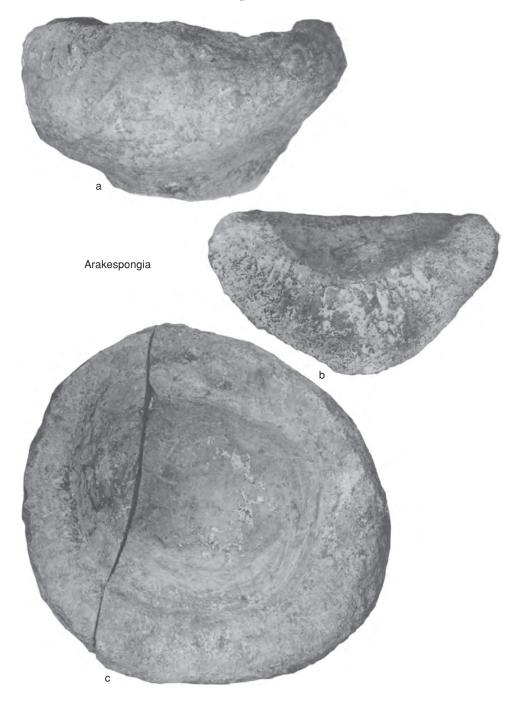


FIG. 202. Pelicaspongiidae (p. 323).

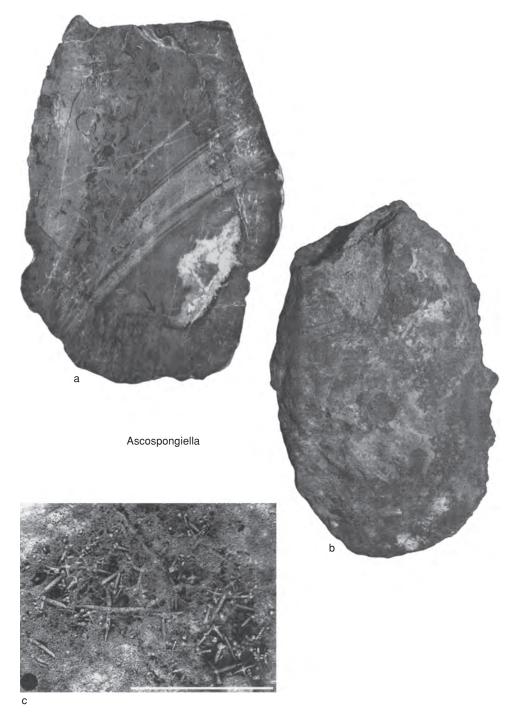


FIG. 203. Pelicaspongiidae (p. 323).

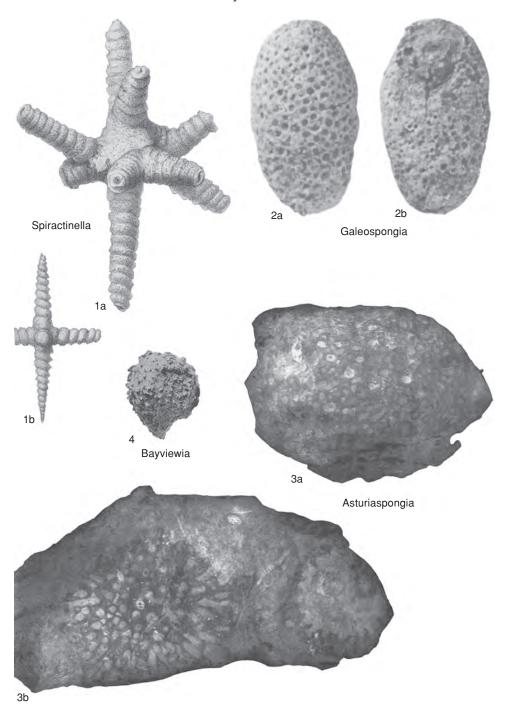


FIG. 204. Pelicaspongiidae (p. 323-336).

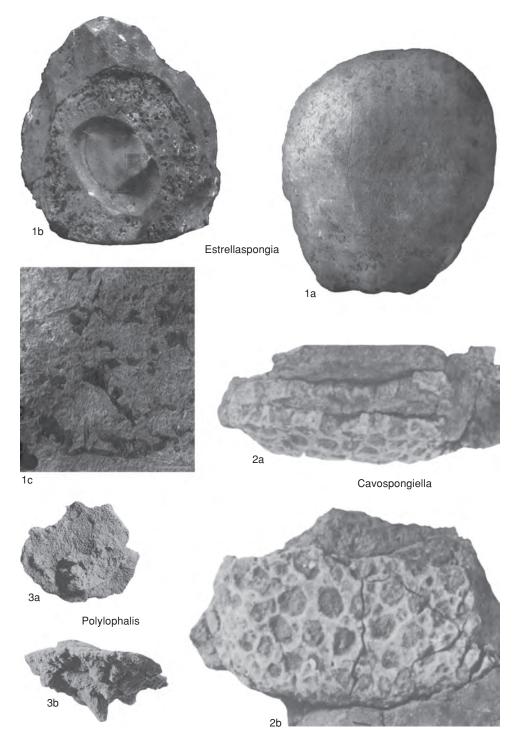


FIG. 205. Pelicaspongiidae (p. 323-333).

moderately coarse, inhalant canals that converge to coarse, irregular, exhalant canals in wall interior; endosomal skeleton of irregularly oriented and spaced, small hexactines; distinct, dermal layer composed of irregularly spaced, enlarged hexactines whose dermal rays are irregularly oriented. Carboniferous (Visean): Spain.-FIG. 205, 1a-c. \*E. irregulara, Sierra del Castillo Unit, Asbian-Brigantian, upper Visean, Sierra de la Estrella, Córdoba, southern Spain; a, side view of globose holotype with osculum at top, 98SSEC-1,  $\times 0.5$ ; b, weathered transverse section through paratype with sinuous canal system, spongocoel partially filled with matrix, 98SSEC-2,  $\times 0.5$ ; *c*, obliquely eroded, irregularly oriented, large, dark hexactines in dermal layer of holotype, 98SSEC-1, ×2 (García-Bellido Capdevila & Rigby, 2004).

- Galeospongia RIGBY, 1986b, p. 39 [\*G. pleraducta; OD]. Conicocylindrical or prolate spheroidal to sack-shaped sponges with contracted, oscular margin and rounded base, with thin walls and deep, simple spongocoel; circular, parietal gaps make up most of wall, spaced less than their diameter apart and notably larger on one side than other; skeletal net poorly preserved of irregularly oriented, small hexactines and possibly other spicules. Devonian (Frasnian–Famennian): Western Australia.——FIG. 204,2a–b. \*G. pleraducta, Virgin Hills Formation, Lawford Range; a, side view showing elliptical shape and coarse, inhalant ostia; b, opposite side view showing matrix-filled osculum at top, GSWA F7239, ×1 (Rigby, 1986b).
- Hadrophragmos GARCÍA-BELLIDO CAPDEVILA & RIGBY, 2004, p. 443 [\*H. soleniscus; OD]. Bowl-shaped to globose pelicaspongiid with thick walls perforated by coarse, parietal gaps that are normal to dermal and gastral surfaces of wall; skeleton composed of small hexactines that are irregularly spaced and oriented; walls without differentiated dermal and gastral layers of enlarged spicules. Carboniferous (upper Bashkirian): Spain.—FIG. 206,1a-c. soleniscus, San Emiliano Formation, Villafeliz, Léon, northeastern Spain; a, polished vertical section of holotype, with shallow upper spongocoel and coarse parietal gaps filled with matrix, 99VI4-9B, ×2.0; b, detail of polished section of holotype showing wide parietal gaps cross connected by small, irregular canals,  $\times 3.0$ ; c, thin section with irregularly oriented hexactines and with long-rayed hexactines in upper right, associated with dark, rimmed microborings, ×9 (García-Bellido Capdevila & Rigby, 2004).
- Keriogastrospongia WU, 1989, p. 767 [\*K. phialoides; OD]. Bowl-shaped lyssacine sponges with shallow spongocoel marked by concentric rings of coarse ostia of subradial, exhalant canals; walls thick and composed of irregularly oriented and spaced hexactines and hexactine-based spicules of several sizes in generally fine-textured skeleton, except for dermal layer of somewhat coarser, more consistently oriented, hexactines of general brachiospongiid appearance. *Triassic (Carnian):* China (Sichuan).— FIG. 207,2a-b. \*K. phialoides, Hanwang Formation,

Hanwang; *a*, view from above of broad spongocoel in figured specimen with thick walls and coarse, exhalant ostia, S-1096,  $\times$ 1; *b*, photomicrograph of longitudinal section with coarse, irregularly oriented hexactines, light matrix on right filling exhalant canal and dark rings in upper left are sections through *Terebella*-like worms that occupy some canals, IGASB R6-23(073),  $\times$ 10 (Rigby, Wu, & Fan, 1998).

- Larispongia CARRERA, 1998, p. 206 [\*L. magdalenae CARRERA, 1998, p. 207; OD]. Bowl-shaped, thickwalled hexactinellid with broad, simple spongocoel and closely spaced, parietal openings; gaps separated by thin parietes; dermal and gastral layers of enlarged (first-order), irregularly oriented hexactines; interior of skeleton of smaller, second- and third-order, irregularly oriented hexactines; dermal and gastral hexactines with four rays parallel to surface and proximal and distal rays at right angles to surface; most spicules with regular form and finetextured appearance. [Twenhofelella lacks a differentiated gastral layer and the dermal layer is of pentactines; and Vaurealispongia lacks a differentiated dermal layer. Pelicaspongia has both dermal and gastral layers of enlarged hexactines, but it has thick parietes with spicules that have considerable variety in morphology and dimensions, in contrast to more uniform hexactines in Larispongia.] Ordovician (Tremadocian): Argentina.—FIG. 207,3a-b. \*L. magdalenae, Las Vicuñas Formation, Puna region of Salta Province; a, vertical view of entire specimen showing open spongocoel and part of exterior, ×1.7; b, photomicrograph of exterior of holotype with enlarged, dermal hexactines around parietal openings with spongocoel at bottom, Cegh-Unc 17365, ×5 (Carrera, 1998).
- Lecanocoelospongia WU, 1989, p. 769 [\*L. brachystypos; OD]. Broadly obconical to open, mushroom-shaped sponges with short stalk; slightly concave to flat, upper gastral surface of thick wall with honeycomb-like spacing of coarse oscula; nodose, lower, dermal surface with smaller, inhalant ostia; skeleton mainly of stout, irregularly oriented and spaced hexactines and long monactines, with occasional small, secondary oxeas. [Genus tentatively included in family for development of coarsely spiculed dermal or gastral layers unknown.] Triassic (Carnian): China (Sichuan) .--—Fig. 201, 1a-c. \*L. brachystypos, Hanwang Formation, upper member, Jiangyou County; a, view onto upper, gastral surface with shallow spongocoel and irregular, coarse, exhalant ostia of holotype; b, side view showing general form and short, lower stalk of holotype,  $\times 1$ ; c, photomicrograph showing ray junctions of robust hexactines and transverse sections of other rays in skeleton of holotype, ×10 (Wu, 1989).
- Liscombispongia RIGBY & WEBBY, 1988, p. 84 [\*L. nodosa; OD]. Thin walled, cuplike, with distinctly knobby exterior; canal system diplorhysal with both incurrent and excurrent canals ending blindly in midwall; skeleton of three layers: outer, dermal layer knobby of small to large, irregularly oriented,

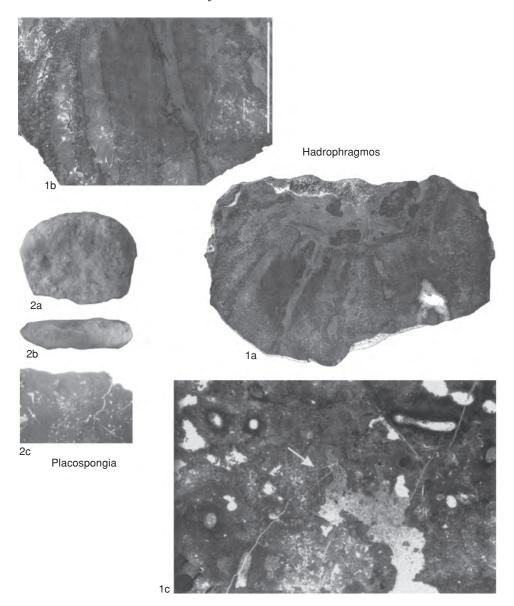


FIG. 206. Pelicaspongiidae (p. 329-333).

normal hexactines; middle layer of straps of subparallel, long, monaxial or rhabdodiactine spicules that occur between tracts of irregular hexactines; gastral layer of ropy tracts of long-rayed rhabdodiactines or other reduced derivatives of hexactines. *Upper Ordovician:* Australia (New South Wales).——FIG. 208*a*-*e.* \**L. nodosa*, Malongulli Formation, Cliefden Caves area; *a*, view from above of thick-walled, somewhat collapsed, cup-shaped holotype with irregular, nodose exterior and interior; *b*, side view of exterior with widely spaced, incurrent ostia in nodose, dermal layer,  $\times 1$ ; *c*, photomicrograph of coarse, outer part of dermal layer, with finer spicules that line canals and occur in bottoms of grooves, between nodes; *d*, photomicrograph of gastral surface with characteristic, somewhat bundled, long-rayed, fine spicules; *e*, photomicrograph of part of endosomal layer where dermal layer has been removed, with straps of bundled, long-rayed, possible rhabdodiactines associated with normal, small hexactines, tracts of spicules lining incurrent canals in outer part of wall,

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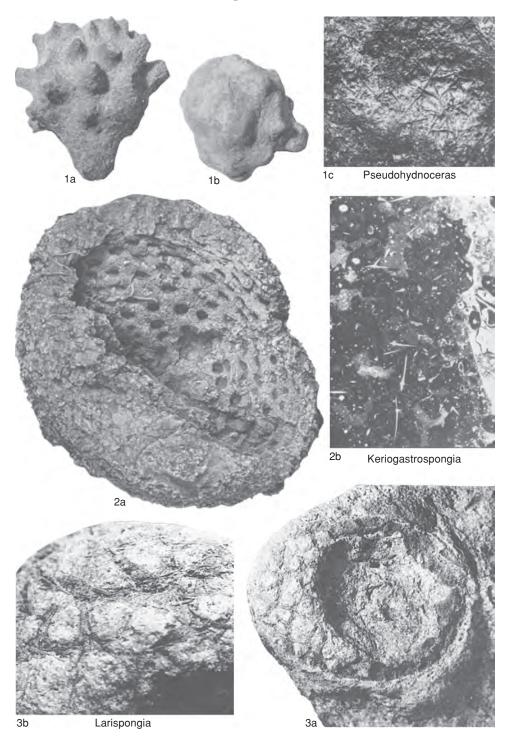


FIG. 207. Pelicaspongiidae (p. 329-333).

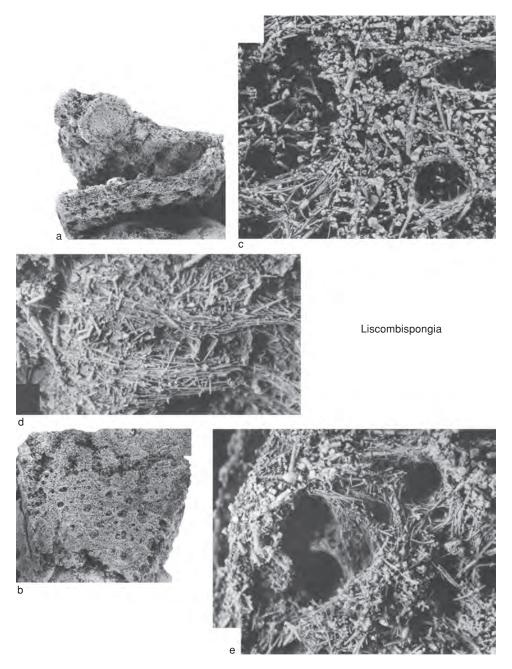


FIG. 208. Pelicaspongiidae (p. 329-332).

AMu. F66904, ×8 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).
Lysactinella GIRTY, 1895, p. 267 [\*L. gebhardi GIRTY, 1895, p. 269; SD DE LAUBENFELS, 1955, p. 94].
Small, spheroidal sponge without cloaca, canals, or

root tuft; interior filled with closely packed, separate, nonaligned, smooth, possible hexactines and derivatives, with larger, dermal spicules near periphery having a suppressed distal ray; inter-ray angles, seen only in section on single, complete sponge;

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frequently nonrectangular, and sometimes with five rays in one plane. [Such spicules suggest, together with the lack of a cloaca, that it might be a heteractinid, although such irregularities are also common in lyssacines. Isolated irregular, smooth hexactines, pentactines, and stauractines of somewhat smaller size, however, occur in the associated sediment, as do larger ones that are distinctively strongly spinose and were assigned to a second species, L. perelegans GIRTY, 1895, p. 270. It is possible that the whole specimen is a juvenile and the larger, spinose spicules are from adults of the same species (smaller spicules have some nonspinose rays). If the genus is to be recognized it must be based on the whole specimen, which is here designated the lectotype. The genus is assigned here with considerable doubt; however, the larger dermalia are characteristic of the family.] Devonian (Lochkovian): USA (New York).-FIG. 209, 3a-d. \*L. gebhardi, shaly limestone, Gedinnian, Lower Helderberg Group, Indian Ladder, Albany County; a-c, various hexactine-based spicules from type specimen; d, representative spicule from type specimen with five rays in one plane, ×25 (Girty, 1895).

- Placospongia WU, 1989, p. 770 [\*P. annulicarina; OD]. Round to elliptical or rectangular or fanshaped, flat plates, in which margin may turn up slightly and plate may be slightly concave; upper, gastral surface may be marked by low, radiate ridges and with exhalant ostia that range from obscure and shallow to prominent and deep; lower, dermal surface with small tubercles and shallow, inhalant ostia; megascleres of skeleton mainly coarse monactines and scattered hexactines, with associated small oxeas. [Genus tentatively included in the family for development of coarse, dermal or gastral layer unknown.] Triassic (Carnian): China (Sichuan).-FIG. 206,2a-c. \*P. annulicarina, Hanwang Formation, upper member, Mianzhu County; a, gastral surface of platelike holotype with faint impressions of exhalant ostia; b, side view of holotype with rounded margins,  $\times 1$ ; c, photomicrograph of relatively fine spicules of holotype, including some small hexactines, ×10 (Wu, 1989).
- Polylophalis REIMANN, 1945b, p. 45 [\*P. bayviewensis REIMANN, 1945b, p. 46; OD]. Sponge broadly conical with flat, upper surface bearing a shallow, central depression; lower surface bearing conical tufts of (possible rhabdodiactine) prostalia; upper surface bearing rhabdodiactine prostalia directed toward central depression; internal, skeletal canals present; hexactines not preserved on type species, according to author, but present in P. clivulatus from same locality; numerous micromonaxon impressions said to occur in the adherent matrix of one specimen; microscopic (200 µm) hollow, possibly organic, spheres said to occur in some specimens were interpreted by author as possible gemmules. Middle Devonian: USA (New York).-FIG. 205, 3a-b. \*P. bayviewensis, Wanakah Shale, Bayview; a, view of funnel-like holotype from above with prostalia radiating from central area,  $\times 1$ ; b, view from side

with pointed base and smaller, pointed tufts of basalia below expanded, upper part of sponge, BMS E15576, ×1 (Reimann, 1945b).

- Prenehydnoceras HURCEWICZ & CZARNIECKI, 1986, p. 339 [\*P. trachys; OD]. Small, conical, with narrow, rounded base and somewhat contracted, rounded summit; no osculum; moderately thick-walled with broad cloaca; exterior bearing rounded protuberances in obscure, longitudinal and transverse rows; skeletal net of parallel hexactines in loose, cubic mesh, with pentactines and short rhabdodiactines at surface; sinuous canals interrupting skeletal net and opening as pores (possibly exhalant), being concentrated at summit and also on protuberances. Carboniferous (Visean): Poland.—FIG. 209,2a-i. \*P. trachys, Carboniferous limestone of Galezice, Holy Cross Mountains; a, wider side view of holotype, black line is trace of section; b, vertical section showing broad spongocoel filled with bioclasts, ×1; c, fragment showing skeletal structure, ×100; d-i, spicules of endosomal skeleton drawn from thin section; d, regular hexactines; e, axial hexactines with one or two longer rays; f, large hexactines; g, pentacts; h, oxeas; i, strongyle, scale bars, 0.1 mm, AI-68/19 (Hurcewicz & Czarniecki, 1986; courtesy of Polish Geological Society, Krakow).
- Pseudohydnoceras REIMANN, 1935, p. 13 [\*P. erraticum; OD]. Vasiform with stalklike base and large, rounded nodes on subglobose, upper part; osculum not known in type species; closely spaced, parallel, large, cylindrical epirhyses and aporhyses penetrating thick, sponge wall; possible rhabdodiactine pleuralia and basalia present; only a few hexactines preserved. Middle Devonian-Upper Devonian (Frasnian): USA (New York), Middle Devonian; Poland, Frasnian.-FIG. 207,1a. \*P. erraticum, Ludlowville Shale, Hamiltonian, Erie County, New York; side view of lobate lectotype, NYSM, ×0.8 (Reimann, 1935; courtesy of Buffalo Museum of Science) .---- FIG. 207, 1b-c. P. obscurum REIMANN, Ludlowville Shale, Hamiltonian, Erie County, New York; b, side view of globose holotype with low nodes,  $\times 0.66$ ; c, photomicrograph of surface of holotype with numerous hexactine-based spicules, BMS, ×5 (Reimann, 1935; courtesy of Buffalo Museum of Science).
- Spiractinella HINDE, 1887b, p. 74 [\*Holasterella wrighti CARTER, 1880a, p. 209; OD]. Known only from isolated, smallish hexactines that bear spiral ridges on each of the rays; many rays bifurcate or trifurcate terminally; associated, smaller, smooth spicules have trifurcate (and possibly quadrifurcate) terminations and resemble hexasters. [The genus is included here because of the resemblance to the oxyhexaster spicules of Arakespongia. REID (personal communication, early 1970s) considers these spicules of Spiractinella to be pseudohexasters of demosponge origin. Although the formal description of the genus was published in HINDE, 1888, p. 164, the name was first mentioned in HINDE, 1887b, p. 74, accompanied by a reference to plate 8, figure 1 of the same volume, where the type

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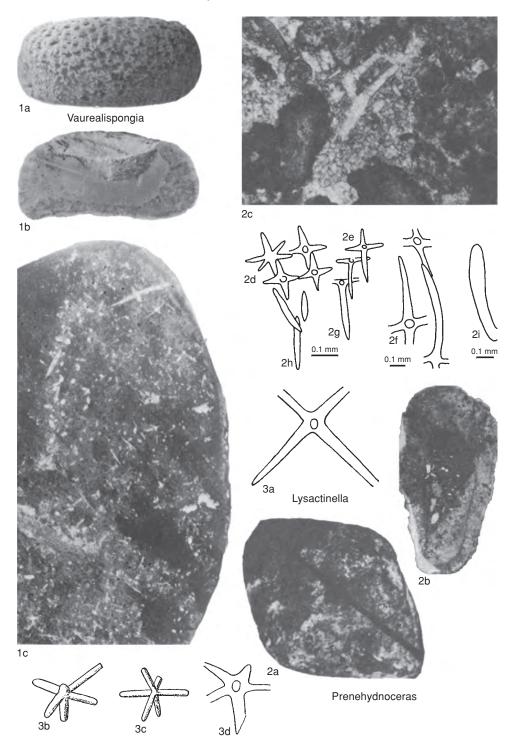


FIG. 209. Pelicaspongiidae (p. 332-338).



FIG. 210. Pelicaspongiidae (p. 336).

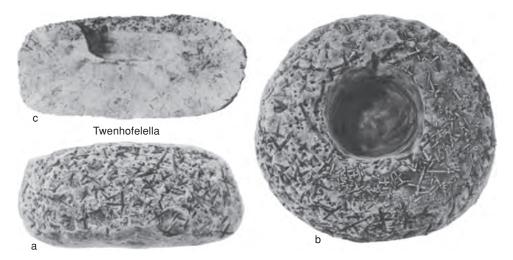


FIG. 211. Pelicaspongiidae (p. 336).

species is named, and the spicules illustrated and briefly described; this constitutes an "indication" as required by the *Code* (ICZN, 1999). *Carboniferous* (*Visean*): Ireland.——FIG. 204, *Ia–b.* \*S. wrightii (CARTER), Lower Carboniferous limestone, Sligo; *a*, large, hexactine spicule with spiral sculpture and bifurcated, transverse rays; *b*, smaller hexactine with typical spiral sculpture, ×40 (Hinde, 1887b).

- Stiodermiella RIGBY & CLEMENT, 1995, p. 224 [\*S. amanita; OD]. Stalked, mushroomlike, or inverted, cup-shaped sponge with stalk, if present, of normalappearing hexactines, but upwardly expanded cap with dense, gastral armor of spicules with expanded ray junctions, or centra, which may be papillose and combine to produce dense cortex; internal spicules in nonparallel arrangement; cortex if present covers canals. Devonian (Lochkovian): USA (Tennessee).--FIG. 210a-c. \*S. amanita, Ross Formation, Benton County; a, arched upper surface of massive, mushroomlike holotype where distal rays of spicules are side by side, USNM 463603; b, base with massive stalk and overhanging upper part of sponge, irregular hexactines developed in center and more regular hexactines in upper left, USNM 464606, ×2; c, photomicrograph of paratype with grossly enlarged spicules typical of upper part of sponge with some regular, smaller hexactines between, USNM 463604, ×20 (Rigby & Clement, 1995).—FIG. 210d. S. tetragona RIGBY & CLEM-ENT, Ross Formation, Benton County; holotype with swollen papillae that are petalloid appearing on terminations of distal rays of dermal hexactines in armored, dermal layer, USNM 463608, ×20 (Rigby & Clement, 1995).
- Twenhofelella RIGBY, 1974, p. 1347 [\*Hyalostelia anticostiana TWENHOFEL, 1928, p. 103; OD]. Bowlshaped, smooth, unribbed, small sponge with large, central spongocoel and thick walls perforated with

radially arranged, circular, parietal gaps curved from outer surface to spongocoel except in basal part where they begin within wall; skeleton of irregularly oriented, variously sized, smooth-rayed hexactines; dermalia enlarged hexactines and possible pentactines with four rays tangential to surface but in nonparallel orientation; gastralia not developed. Silurian (Wenlock)-Devonian (Lockhovian): Canada (Quebec, Anticosti Island), Wenlock-Ludlow; USA (Indiana), Wenlock; USA (Tennessee), Loch--FIG. 211a-c. \*T. anticostiana (TWENkovian.— HOFEL), Jupiter Formation, Niagaran, Anticosti Island, Canada; a, side view of exterior showing irregular arrangement of dermal hexactines in holotype, ×1; b, view down onto oscular margin with enlarged hexactines of dermal layer of wall around cylindrical spongocoel, ×1; c, vertical section showing shallow spongocoel and light gray matrix in parietal gaps and canals of wall, YPM 10404, ×1 (Rigby, 1974; courtesy of Canadian Journal of Earth Sciences).

Vaurealispongia RIGBY, 1974, p. 1343 [\*V. perforata RIGBY, 1974, p. 1346; OD]. Bowl shaped to vasiform with large, central, simple spongocoel and moderately thick walls of irregularly oriented, smooth-rayed hexactines and related spicules, with largest enlarged, interleaved hexactines of gastral layer; wall perforated by numerous, dominantly radially arranged, irregular to circular, tubular, parietal gaps and smaller, circular canals that may bifurcate or anastomose in interior and interconnect with one another. Ordovician-Silurian: Canada (Quebec, Anticosti); USA (Indiana), Wenlock .-FIG. 209, 1a-c. \*V. perforata, Vaureal Formation, Ashgill, Anticosti Island, Canada; a, side view of holotype showing dimpled surface produced by large, parietal gaps; b, vertical section showing thick wall around part of matrix-filled spongocoel, ×1; c,

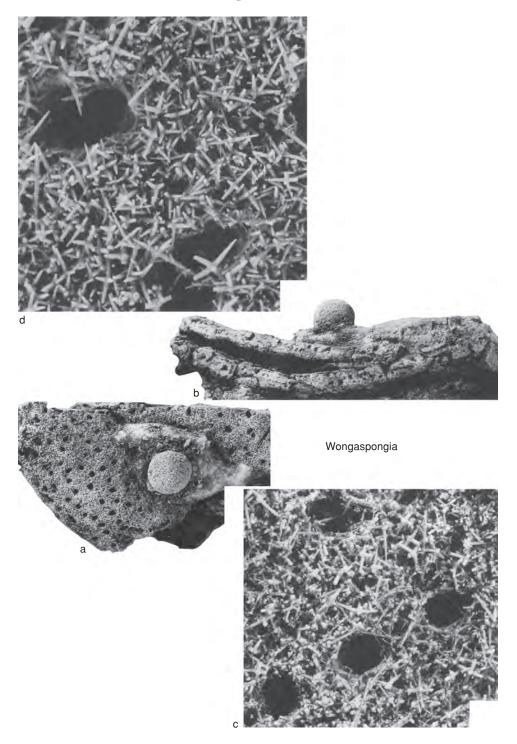


FIG. 212. Pelicaspongiidae (p. 338).

photomicrograph of cellulose, acetate peel of vertical section of upper, oscular rim showing matrixfilled, parietal gaps and skeleton with irregularly oriented and spaced hexactines and with enlarged hexactines as gastral layer on left, GSC 38402, ×10 (Rigby, 1974; courtesy of *Canadian Journal of Earth Sciences*).

Wongaspongia RIGBY & WEBBY, 1988, p. 79 [\*W. minor RIGBY & WEBBY, 1988, p. 80; OD]. Open conical to bowl-shaped sponges with smooth, moderately thin walls with diplorhysal canal system; larger, circular to polygonal, epirhysal openings on exterior spaced irregularly but generally more than their diameter apart; large, subcircular, aporhysal openings on gastral surface spaced less than their diameter apart; epirhyses communicating with vertical canals within body wall, or else end blindly halfway through wall; aporhyses and epirhyses alternating more or less quincuncially; walls of two layers; dermal layer of coarse, armoring, irregularly oriented hexactines and less common pentactines; main skeleton of irregularly oriented hexactines and bundles of thinner rhabdodiactines, or hexactines with two long rays parallel to bundle; bundles mostly parallel to sponge surface and outlining canals. *Upper Ordovician:* Australia (New South Wales).——FIG. 212*a–d. \*W. minor,* Malongulli Formation, Cliefden Caves area; a, side view of collapsed, thin-walled holotype with smooth exterior perforated by incurrent canals that extend through wall, gastral surface showing in upper right, beyond broken margin above small, spherical Hindia, with excurrent openings slightly larger than incurrent ones, ×1; b, view from above of collapsed sponge where dark groove is spongocoel, round, midwall canals showing in both walls below small, spherical Hindia, ×1; c, photomicrograph of dermal surface showing irregularly oriented and spaced, coarse hexactines in outer part of sponge and somewhat finer hexactines in interior in tracts between incurrent openings, AMu. F66897, ×8; d, photomicrograph of dermal layer and outer part of endosome of paratype perforated by incurrent canals and composed of irregularly spaced and oriented hexactines, AMu. F66898, ×10 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

#### Family STIODERMATIDAE Finks, 1960

#### [Stiodermatidae FINKS, 1960, p. 130]

Thin-walled, vasiform sponges with root tuft (at least some spicules of which bear quadridentate, anchorate terminations where preserved); enlarged, hypodermal pentactines or subhexactines, often with swollen, distal and paratangential rays; similar hypogastralia may be present; parenchymal hexactines nonparallel; large, circular parietal gaps or epirhyses and aporhyses; amphidiscs found in or associated with most genera. *Lower Cambrian–Permian.* 

- Stioderma FINKS, 1960, p. 132 [\*S. coscinum FINKS, 1960, p. 133; OD]. Sponge goblet shaped, relatively thin walled, with stalklike base from which emerges a long, stout, root tuft; body wall pierced by numerous large, circular, possible parietal gaps, not covered by preserved skeleton and much broader than longest rays of hypodermalia; hypodermalia and possible autodermalia fused in adult sponge into rigid skeleton that curves over oscular rim and extends a short distance down into cloaca; hypodermalia large hexactines in which distal ray is enlarged into spheroidal knob and paratangential rays are variably swollen and not reflexed; possible autodermalia smaller, similarly knobbed hexactines more or less radially disposed about distal knob of hypodermalia and external to their paratangential rays, which are in nonparallel orientation; parenchymalia simple hexactines, some spinose, in nonparallel orientation; specialized gastralia and hypogastralia apparently not present except for some short, straight, smooth, oxeote rhabdodiactines irregularly oriented parallel to gastral surface; terminations of long, smooth, root-tuft spicules not preserved but a broken spicule with a quadrianchorate termination found in association with isolated, hypodermal spicules. Carboniferous (?Mississippian), Carboniferous (Pennsylvanian)-Permian: USA (Texas, Arkansas, ?Illinois), Spain, ?Scotland, ?Mississippian, Pennsylvanian-Permian; China, Moscovian.——FIG. 213, 1a-b. \*S. coscinum, Victorio Peak Limestone, Leonardian, Sierra Diablo, Texas; a, holotype as natural sagittal section showing upper, cup-shaped part of sponge above stalk and prominent, basal, root tuft, ×0.5; b, photomicrograph of outer surface of holotype with coarse, parietal gaps and fine, skeletal pores between distal knobs of dermalia, USNM 127666, ×5 (Finks, 1960; courtesy of The American Museum of Natural History).
- Acanthactinella HINDE, 1888, p. 167 [\*Holasterella bennei HINDE, 1884a, p. 153; OD]. Isolated hexactines with stout rays that bifurcate or trifurcate terminally or branch irregularly; also pentactines with a stout, tapering, unbranched, possible proximal ray. [They are placed here because of a distinct similarity to Rhakistella WELLER, 1930, but the trifurcate branching of some spicules suggests demosponge affinities, and it is not clear that all these are hexactinellid or from the same genus of sponges.] Carboniferous (Visean): United Kingdom (Scotland).——FIG. 213,4a-c. \*A. bennei (HINDE), Lower Limestone series, Ayrshire; a, isolated hexactine with bifurcated rays in type suite; b, large hexactine with trifurcated rays; c, large spicule with bifurcated rays, ×10 (Hinde, 1887b).
- Astroconia SOLLAS, 1881, p. 254 [\*A. granti; OD]. Large, isolated, hexactine-based spicules include common, normal, smooth-rayed hexiradiates, ones

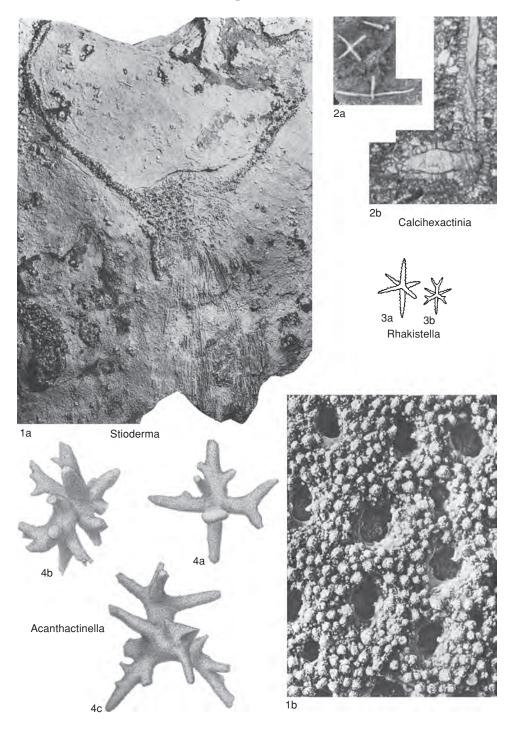


FIG. 213. Stiodermatidae (p. 338-344).

with spinose rays, ones with large, downwardly directed, bifid spines over more normal reflexed rays. [Nature of the complete sponge is unknown and position in the family is tentative.] *Silurian:* Canada, England.——FIG. 214,*3a–d.* \**A. granti*, isolated, large spicules of sponge, Niagara, possibly Lockport, Limestone, lower Silurian, Ontario, Canada; *a*, normal hexactine, ×20; *b*, hexactine with spinose rays, ×50; *c*, hexactine with reflexed rays, ×20 (Sollas, 1881).

- Calcihexactinia SDZUY, 1969, p. 139 [\*C. franconica; OD]. Isolated spicules, preserved as calcium carbonate with wide, axial canals, includes hexactines and pentactines with rays of uneven lengths; some spicules have a very long ray and others have reduced rays; no needles showing signs of overgrowths or fusion together. *Middle Cambrian*: Germany.——FIG. 213,2a-b. \*C. franconica, Wildsteiner Schichten, Frankenwaldes; a, latex cast of three hexactines of type suite, SMF 26174, ×10; b, thin section of hexactine with wide, axial canals characteristic of genus, SMF 26173, ×60 (Sdzuy, 1969).
- Divaricospongia RIGBY & MAHER, 1995, p. 1025 [\*D. dilata; OD]. Cylindrical to cuplike sponges with walls of hexactines and pentactines, spicules arranged in upwardly and outwardly plumose pattern diverging from surface of pinnation at midwall; spicules with swollen, proximal rays, but reduced or aborted distal and transverse rays; spicules of gastral layer with reduced, tangential rays; dermal part of wall with more nearly normal-appearing hexactines; paratangential or transverse rays not regularly oriented; skeletal structure not reticulate. Silurian (Ludlow): USA (Nevada).——FIG. 214, 1a-b. \*D. dilata, Roberts Mountains Formation, Snake Mountains; a, diagonally flattened, tubular to cupshaped holotype with upwardly plumose, hexactinebased skeletal structure, ×2; b, photomicrograph showing upwardly divergent spicules in axial and gastral part of wall with moderately dense, gastral layer on right, USNM 480434, ×10 (Rigby & Maher, 1995).
- Hyalostelia ZITTEL, 1878c, p. 185 [\*Acanthospongia smithii Young & Young, 1876, p. 38; OD]. Form of whole sponge unknown but probably thin walled and vasiform with a root tuft; hypodermalia stout pentactines or subhexactines in which distal ray is reduced to a short, but not strongly swollen knob, and in which paratangential rays are generally reflexed; small hexactines may lie distal to hypodermalia and parenchymal hexactines of varying size lie beneath; gastralia not known, all spicules smooth rayed and in nonparallel orientation; circular openings of about same diameter as length of hypodermal, paratangential rays outlined by skeletal net and may be either parietal gaps or inhalant or exhalant canals; compact groups of root-tuft spicules with quadrianchorate terminations attached to some specimens. [Isolated spicules like hypo-

dermalia of *Stioderma* have been found in association with coherent, skeletal fragments of *Hyalostelia*, but not attached to them. REID (1968b, p. 1,247) noted the occurrence of loose amphidiscs in a deposit (age not given) yielding juvenile *Hyalostelia* sp.] *?Ordovician, Devonian (Frasnian)– Carboniferous (Visean):* Australia (Northern Territory), *?Ordovician;* Poland, *Frasnian;* Scotland, *Visean.*—FIG. 214,2*a*–*c.* \**H. smithii* (YOUNG & YOUNG), Visean, Dalry, Ayrshire, Scotland; isolated spicules including, among others, sexiradiate spicules, ×12, anchoring or root tuft spicules, ×3, and polyactines with eight transverse rays, ×5 (Young & Young, 1877).

- Irpaspongia MEHL & MOSTLER, 1993, p. 10 [\*I. permica; OD]. Known as yet only as isolated, hexactine-based spicules that attach to one another at ray tips by zygoses; middle parts of rays are spinose, but rays become more so on their broadened ends; spaces between spicules may be conspicuously rectangular. [Irpaspongia is the only known hexactinellid to create a skeletal structure by zygosis of ray tips, as in the lithistid demosponges.] Permian (Artinskian): USA (Texas).—FiG. 215, Ia-b. \*I. permica, Bone Spring Limestone, Guadalupe Mountains; isolated hexactines of holotype (syntype) suite, with spinose rays and articulating ray tips, GII ME/MO 730, ×40 (Mehl & Mostler, 1993).
- Itararella KLING & REIF, 1969, p. 1432 [\*I. gracilis; OD]. Sponge probably thin walled, vasiform, with root tuft; skeletal canals unknown; principal skeleton of simple, slender-rayed hexactines and pentactines, the latter at presumed dermal and gastral surfaces; no specialized hypodermalia or hypogastralia known; rhabdodiactines also present, some are smooth and others are clemate, occurring in bundles and bearing at one end an umbel with 9 to 12 teeth; amphidiscs with 7 to 8 (rarely 9) long, slender teeth occurring among spicules and showing bimodal size frequency, smaller including some with unequal-sized ends, larger including some with aborted teeth; spinose microhexactines also occur, as well as hexasters with quadrifurcate ray tips. Carboniferous (Pennsylvanian): Uruguay .--Fig. 216, 1a-c. \*I. gracilis, Itararé Formation, Rio Negro, Tacuarembó-Durazno; a, holotype thin section with anchorate diactines (D) in axial area, near bottom, and with amphidiscs (A) in central part, GPIT Po 1340/1,  $\times 80$ ; b, photomicrograph of amphidiscs at (A); c, anchorate ends of diactines in axial cluster, ×200 (Kling & Reif, 1969).
- Protohyalostella CHAPMAN, 1940, p. 103 [\*P. mawsoni; OD] [=Protohyalostelia CHAPMAN, 1940, p. 104, nom. null.]. Cup- to vase-shaped sponges with double walls, separated approximately 2 mm, and each 3 to 4 mm thick, around a broad and deep spongocoel; spicules largely curved, fusiform microscleres, with scattered, large hexactines. [PICKETT (1983, p. 98) noted that the type locality is probably in the Parara Limestone at Ten Mile

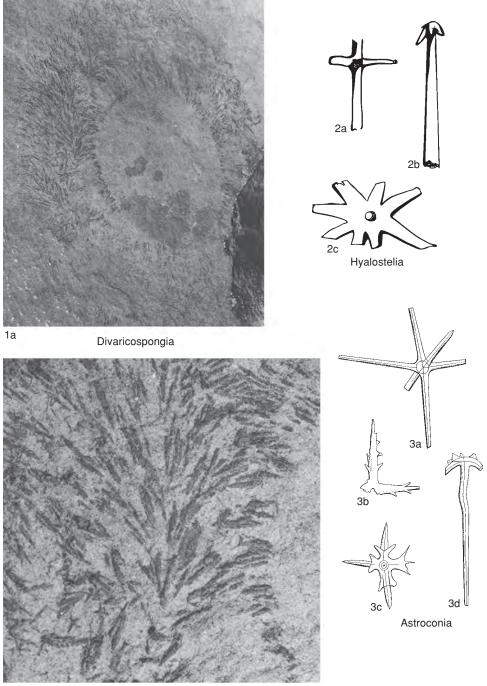




FIG. 214. Stiodermatidae (p. 338-340).

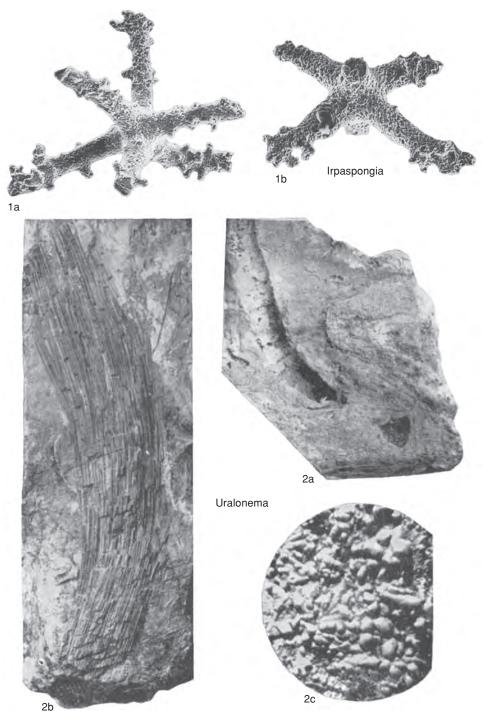


FIG. 215. Stiodermatidae (p. 340-344).

Amphidiscosa

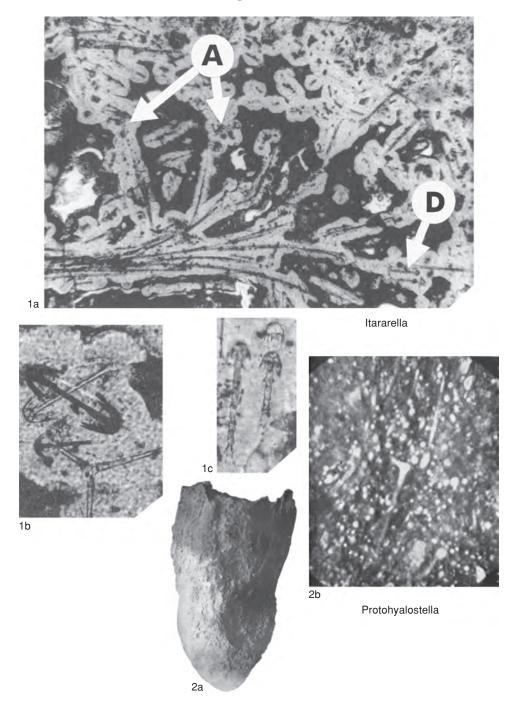


FIG. 216. Stiodermatidae (p. 340-344).

Creek in the Flinders Range. The type material has been lost, perhaps destroyed in a 1953 fire at the Bureau of Mineral Resources. Skeletal details and position in the family remain uncertain.] *Lower Cambrian:* Australia.—FIG. 216,2*a*–*b*. \**P mawsoni*, Flinders Range, South Australia; *a*, side view of vase-shaped holotype with section through double-layered wall on right, ×0.5; *b*, section near base of reference sponge showing part of coarse hexactine and sections through rays of associated spicules, ×25 (Chapman, 1940).

- Rhakistella WELLER, 1930, p. 243 [\*R. alba; OD]. Isolated hexactines with spinose and sometimes bifurcate rays, associated with isolated, spheroidally swollen hexactines like hypodermalia of Stioderma (Hyalostelia diabola WELLER, 1930) and with isolated, quadrianchorate, probable basalia. [Inasmuch as these spinose hexactines resemble some of the parenchymalia of Stioderma coscinum, it is possible that Rhakistella alba and Hyalostelia diabola pertain to a single sponge belonging to Stioderma.] Carboniferous (Pennsylvanian): USA (Illinois, Indiana). FIG. 213, 3a-b. \*R. alba WELLER, Spoon Formation, lower Pennsylvanian, Rock Island County, Illinois; a, isolated hexactine with spinose rays, cotype; b, isolated hexactine with some bifurcated rays, cotype, ×15 (Weller, 1930).
- Rigbyella MOSTLER & MOSLEH-YAZDI, 1976, p. 19 [\*R. ruttneri Mostler & Mosleh-Yazdi, 1976, p. 20; OD]. Isolated hexactines and pentactines with greatly swollen, long, possibly distal rays, with possible proximal and lateral rays commonly of unequal length and development that also may be greatly swollen; minor, short, supernumerary rays also may occur and may bifurcate or terminate as spines. [Spicules on which the type species and genus are based occur in the Mila Formation of Iran. Others that may be included in the genus were earlier reported from the Wilberns Formation of Texas (RIGBY, 1975).] Middle Cambrian–Upper Cambrian: Iran, USA (Texas).——FIG. 217, 1a-h. \*R ruttneri; a, holotype, swollen spicule, Mila Formation, Middle Cambrian, Elburz Mountains, Iran, ×100; *b*–*c*, additional swollen spicules of different shapes, Mila Formation, Middle Cambrian, Elburz Mountains, Iran, ×100 (Mostler & Mosleh-Yazdi, 1976); d-g, drawings of isolated spicules showing various degrees of enlargement of distal rays and development of tangential rays, Wilberns Formation, Upper Cambrian, Llano Uplift, Texas, ×20; h, reconstruction of possible spicule association in dermal pavement, Wilberns Formation, Upper Cambrian, Llano Uplift, Texas, ×20 (Rigby, 1975).
- Thoracospongia MEHL, 1996, p. 34 [\* T. follispiculata; OD]. Hexactinellid sponges known only from isolated, follipinule spicules that have greatly swollen and longitudinally ribbed, distal rays, which probably formed an armored-appearing, outer layer, with more normal-appearing transverse rays tangential to dermal surface. [The genus is placed in the family with some question because of the similarity of the spicules to those in *Stioderma*.] *Middle Cam*-

*brian:* Australia (Queensland).——FIG. 217,2*a*–*c*. \**T. follispiculata*, Georgina Basin; *a*, holotype, isolated follipinule spicule, CPC 33671; *b*, spicule from paratype suite showing hexactine base, CPC 33674; *c*, reconstruction of skeleton of genotype showing possible relationships of various kinds of spicules, scale bar, 200 μm (Mehl, 1996).

Uralonema LIBROVICH, 1929, p. 13 [\*U. karpinskii; OD]. Thin-walled, vasiform with root tuft; hypodermalia hexactines with spheroidally swollen, distal ray and generally swollen remaining rays (sometimes including proximal); paratangential rays may be curved but apparently not reflexed; hypogastralia similar but less strongly swollen; parenchymalia simple, smooth hexactines of varying size down to microscopic, associated with short, smooth, sometimes slightly curved rhabdodiactines; all spicules in nonparallel orientations; numerous eight-toothed amphidiscs found among parenchymalia; microscopic hexactine spicules, described as pinuli in which distal ray is spheroidally swollen and apparently spinose, associated with dermal and gastral layers; isolated fragments of stout, root tuft associated with, but not found attached to, body fragments; isolated fragments of clemes and of rodlike spicules with quadrianchorate terminations also found; no parietal gaps or skeletal canals known from body fragments. Carboniferous (Mississippian, ?Bashkirian): Russia (Ural Mountains, western Qian Shan).-FIG. 215, 2a-c. \*U. karpinskii, Mississippian, Resh River, Ural Mountains, Russia; a, side view of flattened sponge; b, root tuft,  $\times 1$ , c, part of dermal skeleton, ×8 (Rezvoi, Zhuravleva, & Koltun, 1962; courtesy of Russian Academy of Science).

# Order RETICULOSA Reid, 1958

#### [Reticulosa REID, 1958a, p. xlv]

Amphidiscophora in which a dermal skeleton of parallel stauractines, pentactines, or hexactines form a major part of sponge skeleton, and in which microscleres include paraclavules. [The oldest specimens well preserved enough to be referred to a genus date from the Middle Cambrian, but isolated stauractines are known from Lower Cambrian sediments.] *Ediacaran–Holocene.* 

# Superfamily PROTOSPONGIOIDEA Hinde, 1887

[nom. transl. FINKS, 1960, p. 101, ex Protospongiidae HINDE, 1887b, p. 90]

Thin-walled Reticulosa in which a dermal layer, together with prostalia, forms entire skeleton. *Lower Cambrian–Jurassic.* 

Reticulosa

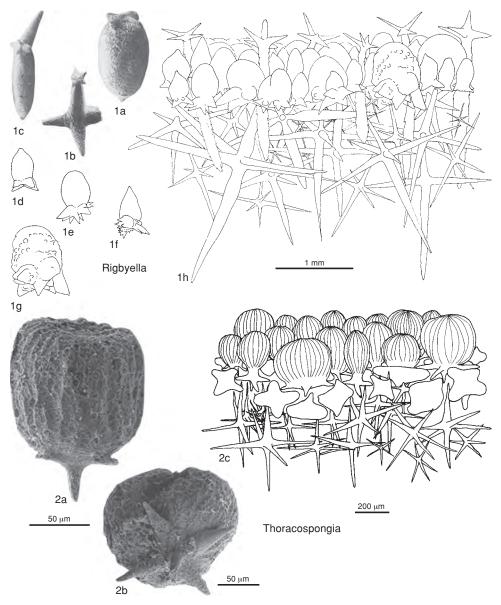


FIG. 217. Stiodermatidae (p. 344).

## Family PROTOSPONGIIDAE Hinde, 1887

[Protospongiidae HINDE, 1887b, p. 90]

Vasiform or spheroidal; skeletal net essentially a single layer or thin, multiple layers of stauractines or pentactines, together with possible rhabdodiactines in some species; spicules typically in parallel arrangement, largest usually in quincuncial arrangement (but sometimes in overlapping, quadrate arrangement), smaller spicules in several orders of size subdividing quadrules thus formed into nonoverlapping, quadrate arrangement; spicules may be irregularly arranged in some genera, however; parietal gaps may be

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present; prostalia (possible rhabdodiactines) may be strongly developed about osculum and may project from entire surface; basalia often developed. *Lower Cambrian– Jurassic.* 

- Protospongia SALTER, 1864, p. 238 [\*P. fenestrata; M] [=?Testiispongia RIGBY, 1983a, p. 262 (type, T. venula, OD)]. Large, ovoid or vasiform sponge with osculum; thin body wall composed of stauractines arranged parallel to principal dimensions of sponge with rays gently reflexed; largest stauractines in quincuncial arrangement overlapping slightly to form primary quadrules that are subdivided into as many as six or more orders of quadrules by smaller stauractines, each about half as large as preceding order, each smaller spicule lying beneath next larger; layer of nonparallel, small rhabdodiactines may underlie all the rest; rhabdodiactine prostalia may be present over entire body and may form a coronal fringe about osculum; small number of elongate, possible rhabdodiactines may form root tuft. Lower Cambrian-Devonian (Givetian): China (Anhui), Lower Cambrian; Wales, Ireland, Russia, USA (Utah, Idaho), Canada (British Columbia, Quebec), Middle Cambrian; Argentina, Australia, Lower Ordovician; Australia (Victoria), Middle Ordovician; Canada (British Columbia), lower Silurian-middle Silurian; Portugal, USA (?Nevada), upper Silurian; USA (Nevada), Givetian.---FIG. 218, 1a-c. \*P. fenestrata, Menevian strata, Middle Cambrian, St. David's, southern Wales, England; a, holotype fragment with spicule impressions,  $\times 1$ ; *b*, enlargement of spicules of type, BMNH, ×4 (Salter, 1864); c, drawing of holotype, ×5 (Hinde, 1884a
- Acanthodictya HINDE in DAWSON & HINDE, 1889, p. 47 [\*A. hispida HINDE in DAWSON & HINDE, 1889, p. 48; M]. Cylindrical, small sponges; stauractines and possibly rhabdodiactines grouped into bundles parallel to longitudinal axis of sponge; bundles connected by single, horizontal spicules or spicule rays to form quadrules; entire lateral surface, as well as oscular rim, covered with densely bristling prostalia that may be greatly elongate, unpaired rays of pentactines; longitudinal strands prolonged to form root tuft. Middle Cambrian: Canada (Quebec). -FIG. 219, 3a-c. \*A. hispida, Metis Shale, Little Metis; a, holotype, flattened fragment of subcylindrical sponge with vertical and horizontal strands and with pronounced marginalia and prostalia; b, restoration of complete sponge based on several fragments, ×1; c, drawing of skeletal relationships of main body skeleton and projecting marginalia, ×5 (Dawson & Hinde, 1889).
- Actinodictya HALL, 1890b, p. 59 [\*A. placenta HALL, 1890b, p. 60; M]. Large, flattened, ovoid sponges with no indication of osculum or root tuft; surface crossed in all directions by interlaced, spicular bands with distinct irregularity but with some indication of rectangular reticulation; large, irregularly

arranged stauractines, some more than half diameter of sponge, together with smaller intervening ones forming apparently single-layered, skeletal net. *Devonian (Givetian–Frasnian):* USA (Nevada), *Givetian;* USA (New York), *Frasnian.*—FIG. 220,1. \*A. placenta, Chemung Group, Senecan, Cohocton, New York; holotype, two essentially complete sponges with rounded outlines showing differences in sizes of spicule elements and their orientations, UCC 13158A, ×0.5 (Hall & Clarke, 1899).

- Ammonella WALTHER, 1904, p. 162 [\*A. quadrata; OD]. Thin-walled, cup- to bowl-shaped sponge without recognizable canal system in regular, quadratic, protospongiid, skeletal meshwork of stauractines of at least four orders, which may have thickened, small nodes at ray junctions; principal quadrate openings approximately 0.5 mm across, but may be larger where some needles are destroyed; curved, spicule fibers defining general shape of expanding sponge; root plate rather than root tuft locally preserved. [Ammonella has the skeletal structure of a protosponiid, but there is a major break in the record of the protosponges from the lower Paleozoic until the Jurassic. KEUPP and MEHL (1994, 1995) concluded that the Jurassic form may be a result of convergent evolution rather than preservation of a Lazarus taxon. Consequently, the genus is included in the family with some question.] Jurassic: Germany, Italy.—FIG. 221,2. \*A. quadrata, Solnhofen Plattenkalk, Pfalzpaint, Bavaria; flattened, thin-walled, bowl-shaped sponge with curved, upwardly divergent, spicule fibers in uniform, quadrate skeleton, ×1 (Keupp & Mehl, 1994).
- Asthenospongia RIGBY, KING, & GUNTHER, 1981, p. 843 [\*A. acantha Rigby, King, & Gunther, 1981, p. 844; OD]. Thin-walled, open conical to conicocylindrical protosponge in which stauractines and hexactines of skeleton moderately to regularly oriented; right-angled rays of hexactine-based spicules mainly vertical and horizontal, although locally irregularly diagonal; crudely ordered spicules of at least four, and possibly six, orders subdividing net into rough quadrules; most distinctive spicules are large hexactines with rays commonly bent to produce variably oriented spicules and oriented with four rays tangential and one ray distal, producing long marginalia; large spicules placed two or three first-order quadrules apart, but in predictable diamond pattern; oscular and basal margins unknown; root tuft uncertain. Lower Ordovician: USA (Idaho) .---- FIG. 220, 2. \*A. acantha, Phi Kappa Formation, Trail Canyon, Rock Roll Canyon quadrangle; holotype with large hexactines near lower margin with rays extending beyond principal net, and with four orders of ranked hexactines somewhat irregularly and diagonally oriented in upper part, BYU 1711, ×4 (Rigby, King, & Gunther, 1981).
- Diagoniella RAUFF, 1894, p. 248 [\*Protospongia coronata DAWSON & HINDE, 1889, p. 41; SD

Reticulosa

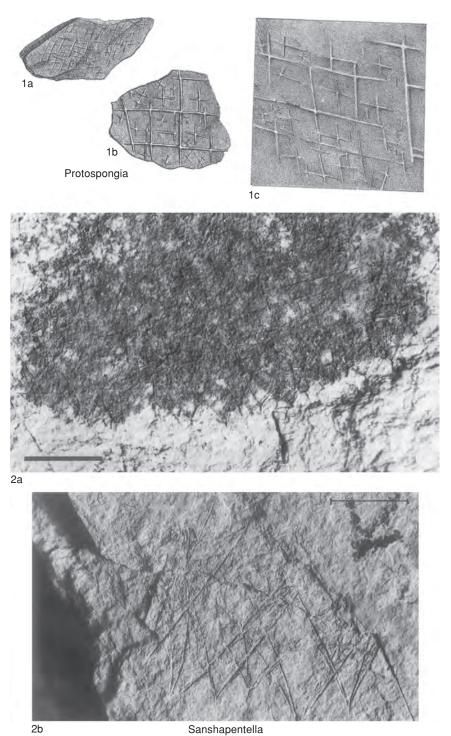


FIG. 218. Protospongiidae (p. 346-356).

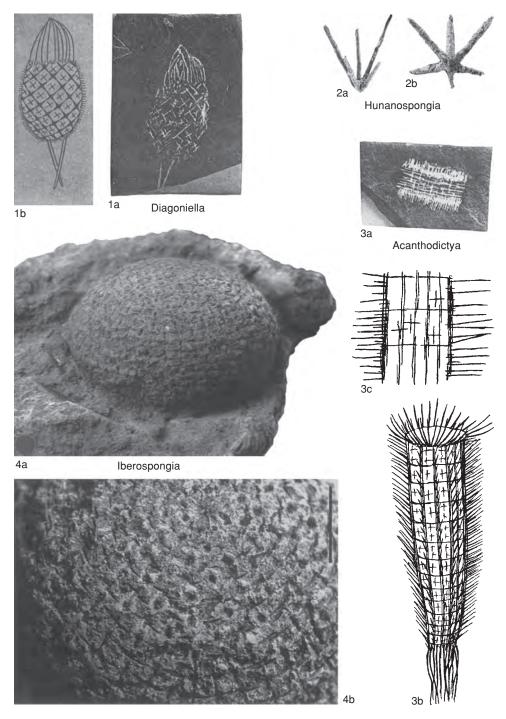
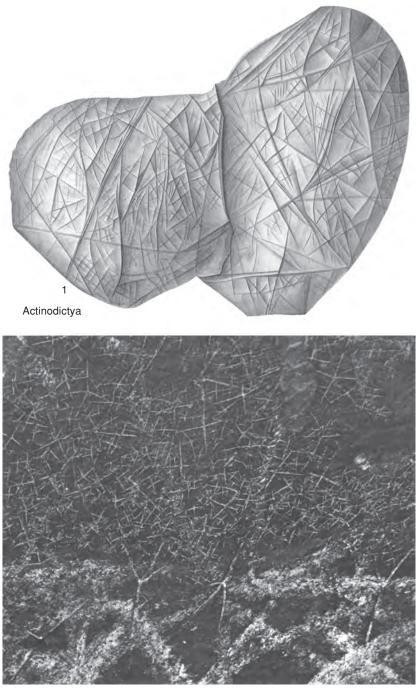
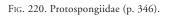


FIG. 219. Protospongiidae (p. 346-351).





Asthenospongia



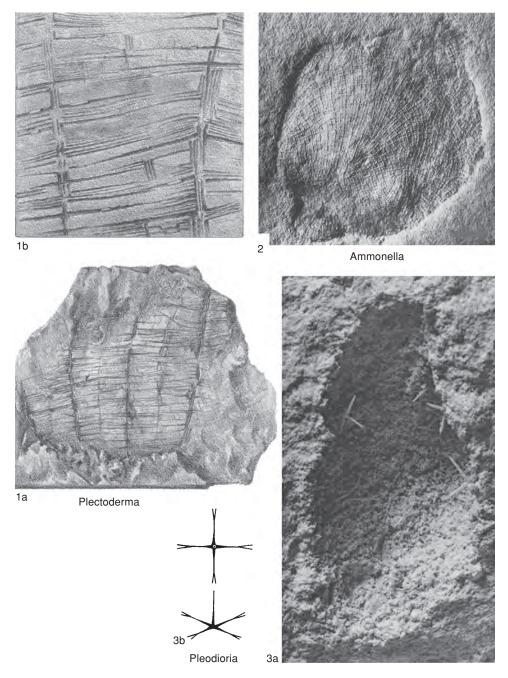


FIG. 221. Protospongiidae (p. 346-355).

WALCOTT, 1920, p. 310]. Ovoid or vasiform with broad osculum with or without strong prostalia (seemingly rhabdodiactines); principal spicules stauractines in parallel arrangement but diagonal to longitudinal axis of sponge; stauractines may be to five orders of size and may form smaller orders of quadrules in inner layer or layers; larger quadrately arranged in quincuncial arrangement; entire surface may be covered with short, rhabdodiactine prostalia perpendicular to surface; a few, long, stout basalia

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present. Lower Cambrian–Silurian (lower Llandovery–Wenlock): China (Anhui), Canada (Quebec, British Columbia), USA (Utah, Nevada), Portugal.——FiG. 219, *Ia–b.* \*D. coronata (DAWSON & HINDE), Metis Shale, Arenig, Little Metis Bay, Quebec, Canada; *a*, flattened holotype with white ink over spicules, including long prostalia and root tuft, PRM xx, ×1 (Dawson & Hinde, 1889); *b*, drawing from holotype showing skeletal relationships and diagonal, principal skeleton, ×1 (Rauff, 1893).

- Gabelia RIGBY & MURPHY, 1983, p. 798 [\*G. pedunculus RIGBY & MURPHY, 1983, p. 799; OD]. Gobletshaped, thin-walled, moderately large protosponge, with cylindrical, stemlike, lower stalk and eggshaped, upper part; stem with hemispherical base; thin, upper, skeletal net of regularly oriented hexactines with essentially equidimensional rays, arranged in crude quadrules and up to five orders of decreasing spicule size; those in lower stalk with vertical rays markedly elongate in comparison to short, lateral rays; oscular margin unknown; walls unsculptured except for prostalia-like, distal rays of hexactines in net; spicules unbundled. ?Lower Cambrian, upper Silurian-Upper Devonian: China (Anhui), ?Lower Cambrian; USA (Nevada), Upper Devonian; Canada (British Columbia), lower Silurian-middle Silurian; USA (Nevada), ?Portugal, upper Silurian.——FIG. 222a-c. \*G. pedunculus, unnamed Devonian shale, Upper Devonian, Roberts Mountains, Nevada; a, flattened holotype showing ovate upper part and cylindrical lower stem, all with skeleton of ranked hexactines, USNM 340059, ×1; b, generalized restoration, approximately natural size; c, photomicrograph of rounded base of stem with several orders of hexactines that have short, lateral rays and elongate, vertical ones, USNM 340059, ×10 (Rigby & Murphy, 1983).
- Hexatractiella MEHL, 1996, p. 35 [\*Diagoniella tubulara RIGBY & HARRIS, 1979, p. 970; OD]. Sponge body branched to subcylindrical, thin walled with deep, open spongocoel above rounded base without root tuft; prominent, uniformly separated, longitudinal bands of skeleton of greatly elongated, vertical tips of diagonally oriented hexactines; uniform skeleton between bands composed of four orders of diagonally oriented hexactines in ranked quadrules. lower Silurianupper Silurian: Canada (British Columbia).-FIG. 223a-b. \*H. tubulara (RIGBY & HARRIS), unnamed Silurian siltstone, Llandovery-Wenlock, near Ware; a, side view of flattened holotype with two tubular branches on right and one on left, all with skeleton of diagonal stauractines and hexactines, ×1.5; b, photomicrograph showing diagonally oriented, larger stauractines and smaller hexactines in two flattened branches, GSC 60633, ×10 (Rigby & Harris, 1979).-FIG. 223c. H. nevadensis (RIGBY & STUART), Roberts Mountains Formation, upper Silurian, Independence Mountains, Nevada; restoration showing extended rays of diagonal hexactines that produce vertical, skeletal

bands between bands of diagonal, smaller spicules, ×1 (Mehl, 1996).

- Hunanospongia QIAN & DING in DING & QIAN, 1988, p. 47 [\*H. delicata; OD]. Shape of sponge body unknown but with small, hexactine-based pentactine to hexactine spicules with sharply to weakly reflexed rays; spicules occurring isolated or joined to form connected framework. [Somewhat similar spicules have been described from the Lower Cambrian of northern Hunan by MEHL and ERDT-MANN (1994) as Sanshapentella, but the spicules described by them are much larger, and most are without the vertical rays that are well developed in Hunanospongia.] Lower Cambrian: China.--Fig. 219,2a-b. \*H. delicata, Yangjiaping Formation, Shimen County, Hunan; a, holotype hexactine with gently reflexed, lateral rays; b, pentactine with sharply reflexed rays, ×50 (Ding & Qian, 1988).
- Iberospongia GARCÍA-BELLIDO CAPDEVILA & RIGBY, 2004, p. 447 [\*I. globulara; OD]. Globular to subspherical, thin-walled sponge with single-layered, lyssacid skeleton of quadrately arranged hexactines that increase in size upwardly from invaginated base to maximum diameter of sponge at approximately midheight; first-order spicules with unfused, overlapping rays; second-order spicules present above midheight; upper part of skeleton converging toward oscular margin; coarse, basal root tuft present. Lower Devonian (Emsian): Spain.—\_\_\_\_FIG. 219,4a-b. \*I. globulara, Abadia Formation, Cortés Member, upper Zlichovian, Polentinos, Palencia, northern Spain; a, holotype, oblique view of base and side showing general ovoid shape of sponge and hexactine-defined skeletal quadrules of skeleton, POL1-1, ×2; b, detail of basal region of holotype showing molds left by dissolved, regular, proximal and tangential rays of hexactines, ×4 (García-Bellido Capdevila & Rigby, 2004).
- Kiwetinokia WALCOTT, 1920, p. 311 [\*K. utahensis WALCOTT, 1920, p. 313; OD]. The type species consists of scattered stauractines, tauactines, and two possible rhabdodiactines twisted together spirally. [K. spiralis WALCOTT and K. metissica (DAWSON, 1889) consist of similar spicules with cablelike rods apparently of a half-dozen or so rhabdodiactines twisted together. HINDE (1893a) considered the cablelike spicules called Hyalostelia metissica by DAWSON (1889) to be possibly the root tufts of co-occurring Palaeosaccus, an opinion subsequently concurred with by DAWSON (1896, p. 108). Kiwetinokia could be considered a junior subjective synonym of Palaeosaccus.] Middle Cambrian: USA (Utah), Canada (Quebec), Argentina.----FIG. 224, 1a-b. \*K. utahensis, Marjum Limestone, House Range, Utah; a, photomicrograph of strew of stauractines in lectotype; b, rod formed of twisted diactine in lectotype fragment, USNM 66542, ×2 (Walcott, 1920).
- Megastylia RUEDEMANN, 1934, p. 71 [\*M. caliciformis; OD]. Vase-shaped, small sponges with straight, upper margin of wide osculum and principal spicules larger than in *Protospongia*, but in a similar

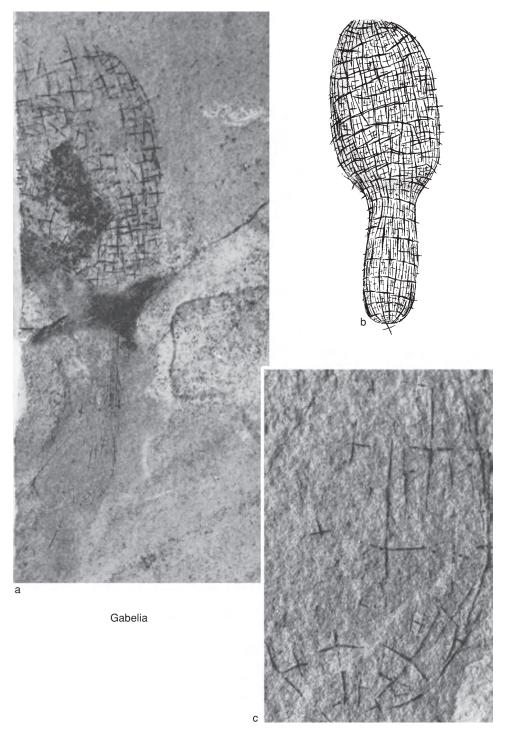


FIG. 222. Protospongiidae (p. 351).

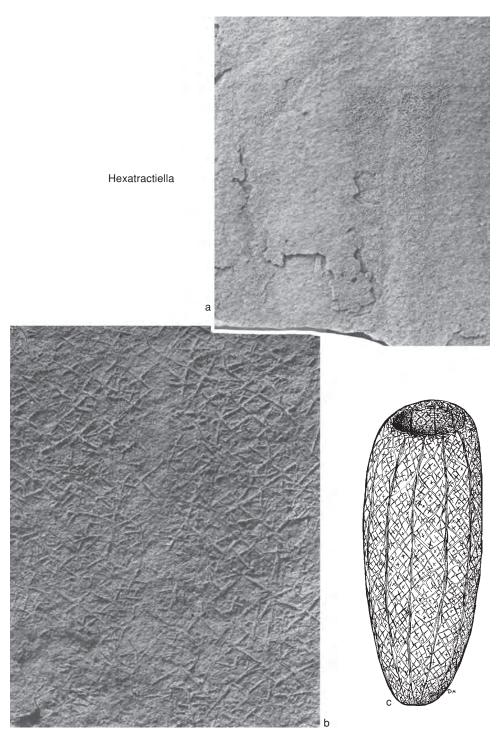


FIG. 223. Protospongiidae (p. 351).

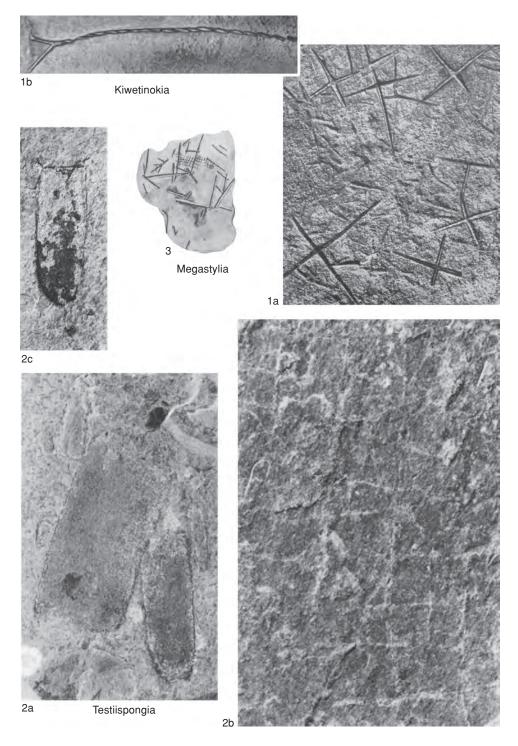


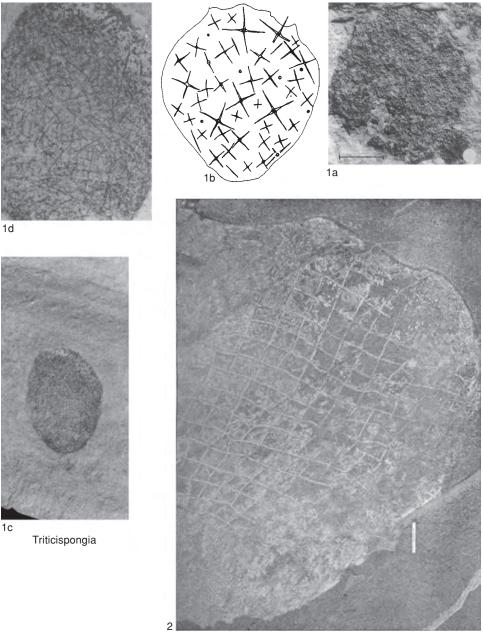
FIG. 224. Protospongiidae (p. 351-357).

quadrate mesh. *Lower Ordovician:* USA (New York).——FIG. 224,3. \**M. caliciformis*, Schaghticoke Shale, Schaghticoke; irregularly preserved, hexactine-based spicules of holotype with some in reticulate arrangement in upper part, NYSM, ×1 (Ruedemann, 1934).

- Palaeosaccus HINDE, 1893a, p. 57 [\*P. dawsoni; M]. Large, presumably vasiform sponges with large quadrules (14-20 mm wide) outlined by bundles of rhabdodiactines supplemented by large stauractines, or pentactines at bundle crossings; quadrule interiors with thin layer of small rhabdodiactines, stauractines, and possibly pentactines; stout spicules having form of ropes of spirally twisted, tuberculate filaments associated with this sponge but not connected to it. [Stout spicules were interpreted as basalia of Palaeosaccus in the original description, having been earlier assigned to Hyalostelia metissica DAWSON & HINDE, 1889. Similar spicules were included in Kiwetinokia WALCOTT, 1920, which embraced H. metissica among other species.] Middle Cambrian: Canada (Quebec).-FIG. 225,2. \*P. dawsoni, Metis Shale, ?Canadian, Little Metis Bay; holotype with coarse, reticulate net of spicule bundles, including stauractines, ×0.33 (Hinde, 1893a).
- Plectoderma HINDE, 1884a, p. 132 [\*P. scitulum; M]. Form unknown but moderately large and probably vasiform; nearly monolayered, spicular net of stauractines or pentactines of at least 3 orders in parallel arrangement; largest spicules may be superposed in groups of two or more at one spot so that primary quadrules are bordered by bundles of parallel, spicule rays; largest spicules may be in overlapping quadrate, rather than quincuncial, arrangement; at least two orders of smaller quadrules may occur in primary quadrules. [Although the original description cites lack of parallelism of smaller spicules as a generic character, examination of topotype material, as well as original illustrations, shows that at least two size orders of smaller, parallel spicules form second- and third-order quadrules.] Silurian (Ludlow): Scotland.--Fig. 221,1a-b. \*P. scitulum, Silurian strata, Edinburgh; a, holotype with reticulate, quadruled skeleton of stauractines or possible pentactines,  $\times 1$ ; b, part of holotype showing some stauractine spicules in tract junctions, GSS, ×5 (Hinde, 1884a).
- Pleodioria ÖPIK, 1961, p. 50 [\**P. tomacis;* M]. Small, conical to vasiform; largest spicules stauractines with reflexed rays, smaller spicules pentactines; paratangential rays of some of both types are terminally bifid. *Middle Cambrian:* Australia (Queensland).——FIG. 221, *3a–b.* \**P. tomacis,* Roaring Siltstone, Selwyn Range; *a*, holotype, largely a mold but with a few siliceous spicules, CPC 3666, ×3; *b,* drawings of pentactines with bifid, ray tips that occur with normal pentactines and stauractines in holotype, ×10 (Öpik, 1961).
- Quadrolaminiella CHEN, HOU, & LI, 1990, p. 404 [411] [\*Q. diagonalis; OD]. Large, cylindrical to steeply obconical sponges with skeleton of

quadrately arranged, hexactine-based spicules and possibly associated monaxons parallel to spicule rays; space between rays filled with finer spicules that appear as oxeas. [The genus was initially interpreted and described as a demosponge with a fourlayered wall. It is interpreted here as a laterally flattened protosponge in which elements of both the lower and upper walls, as flattened and perhaps rotated somewhat, have left impressions of the hexactine-based spicules and possible associated monaxial spicules. Impressions of both walls are possible because there was no infilling of the broad spongocoel before the sponges were flattened. The genus is difficult to distinguish from Protospongia or Diagoniella.] Lower Cambrian: China (Yunnan). FIG. 226a-b. \*Q. diagonalis, Chiungchussu Formation, Chengjiang; a, flattened, quadrate skeleton of steeply obconical holotype, ×0.88; b, enlarged section of holotype showing two quadrate, skeletal layers rotated with reference to one another, probably as flattened, upper and lower walls of thin-walled sponge, NIGPAS 108497, ×8 (Chen, Hou, & Li, 1990).

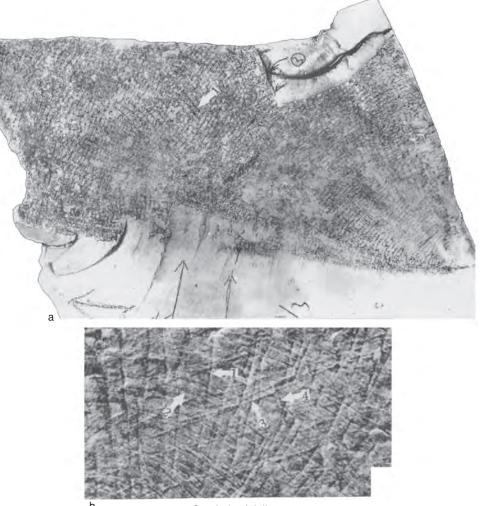
- Saetaspongia MEHL & REITNER in STEINER & others, 1993, p. 310 [\*S. densa; OD]. Moderately small, circular sponges with skeleton a dense accumulation of fine diactines (possible oxeas) arranged in semiparallel, almost plumose-appearing bundles; spicules line but do not protrude from well-defined sponge body; skeleton may include small hexactines in layer beneath bundled spicules. Lower Cambrian: China (Hunan, Yunnan).-FIG. 227a-c. \*S. densa; a, flattened, circular holotype, cluster of diactines dominantly, Niutitang Formation, Yangtze Platform, Hunan, IPFUB San 102-L, ×2 (Steiner & others, 1993); b, small, figured specimen, flattened impression, Yu'anshan Member of Qiongzhusi Formation, Maotianshan, Yunnan, ×4; c, photomicrograph clusters or tufts of long-rayed spicules in upper and lower right, with hexactine in right center, Yu'anshan Member of Qiongzhusi Formation, Atdabanian, Maotianshan, Yunnan, NIGPAS 115321, ×12 (Rigby & Hou, 1995).
- Sanshapentella MEHL & ERDTMANN, 1994, p. 316 [\*S. dapingi; OD]. Hexactinellid sponges in which fanshaped, quadripod-like, dermal pentactines prominent along periphery of sponge; closely spaced spicules with long, slightly curved, paratangential rays in pairs and bent to point in same overall direction into interior of body, but with fifth ray protruding outwardly. [Sanshapentella is similar to Hunanospongia DING & QIAN, 1988, but spicules of the latter have a central, proximal ray, which is not present in spicules of Sanshapentella. It is also similar to Asthenospongia RIGBY, KING, & GUNTHER, 1981, but in the latter, four of the large rays are tangential to the dermal surface in the well-organized protosponge, and the fifth projects distally.] Lower Cambrian: China (Hunan, Anhui).---FIG. 218,2a-b. \*S. dapingi, Niutitang Formation, Tommotian, Sansha, Hunan; a, flattened holotype with prominent, dermal pentactines and interior of



Palaeosaccus

FIG. 225. Protospongiidae (p. 355-359).

hexactine-based spicules arranged in quadrules, IPFUB San 148b,  $\times$ 4 (Mehl & Erdtmann, 1994); *b*, photomicrograph of paratype with prominently oriented, spicule cluster that represents dermal layer, IPFUB San 118-z,  $\times$ 4 (Steiner & others, 1993). **?Testiispongia** RIGBY, 1983a, p. 262 [\**T. venula;* OD] [?=*Protospongia* SALTER, 1864, p. 238 (type, *P. fenestrata*, M)]. Subcylindrical, smooth, test-tubelike, thin-walled protosponge with hemispherical base; stauractine-based skeletal net with main rays principally horizontal and vertical but only in crude

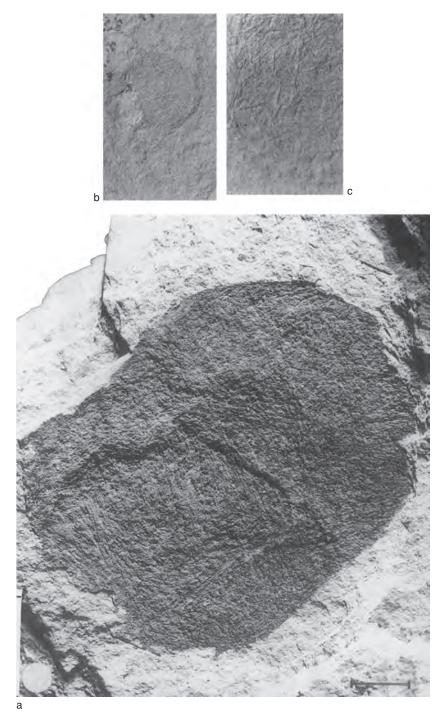


Quadrolaminiella

FIG. 226. Protospongiidae (p. 355).

quadrules, with other spicules oriented parallel to major axes of sponge; possible hexactine-based spicules also oriented at odd angles; skeletal net increasingly better organized in upper, chimneylike part of sponge near osculum; parietal gaps not developed and marginalia and prostalia absent, other than possible short, brushlike, root tuft; principal spicules with striated or weakly ribbed, main rays. Middle Cambrian: USA (Utah).-FIG. 224,2a-b. \*T. venula, Marjum Formation, House Range; a, large holotype and small paratype showing testtubelike form of genus and rectangular, skeletal net in upper part of holotype, with associated, irregular hexactines,  $\times 1$ ; *b*, photomicrograph of somewhat crudely ranked spicules in upper part of holotype, BYU 1747, ×5; c, paratype showing form of sponge in limonite replacement, BYU 1749, ×1 (Rigby, 1983a).

Triticispongia MEHL & REITNER in STEINER & others, 1993, p. 307 [\**T. diagonata;* OD]. Small, oval, thin-walled sponges with goatee-like root tuft, walls of small triaxons, mainly delicate stauractines, with paratangentalia in diagonal, rectangular, quadruled arrangement. *Lower Cambrian:* China (Hunan, Yunnan, Anhui).—FIG. 225, *Ia-d.* \**T. diagonata*, Niutitang Formation, Tommotian, Hunan; *a*, flattened, small holotype with diagonal stauractines and possible hexactines, ×5; *b*, sketch of holotype showing positions and orientations of most obvious spicules, IPFUB San 143-x, ×5 (Steiner & others, 1993); *c*, figured specimen with complete, oval skeleton around a deep spongocoel, with a faint, basal,



Saetaspongia

FIG. 227. Protospongiidae (p. 355).

root tuft and hexactine-based skeleton arranged in quadrules, NIGPAS 115320b,  $\times$ 4; *d*, photomicrograph showing details of hexactine-based skeleton with quadrules most apparent in lower center and right,  $\times$ 10 (Rigby & Hou, 1995).

# Superfamily DIERESPONGIOIDEA Rigby & Gutschick, 1976

[nom. transl. FINKS, 1983b, p. 109, ex Dierespongiidae RIGBY & GUTSCHICK, 1976, p. 79]

Reticulosa in which both dermal and gastral layer of simple, parallel hexactines, or reduced derivatives, form principal skeleton; rhabdodiactines or other prostalia may be developed and, in some groups, additional layers of parallel hexactines may be developed internal to dermal and gastral layers; parietal gaps not present. *Middle Cambrian– Holocene.* 

#### Family DIERESPONGIIDAE Rigby & Gutschick, 1976

[Dierespongiidae RIGBY & GUTSCHICK, 1976, p. 79]

Mostly spheroidal Dierespongioidea in which skeleton consists of dermal and gastral layers plus long, rhabdodiactine prostalia that radiate from interior of sponge and protrude extensively from outer surface. *Middle Ordovician–Permian (Artinskian).* 

- Dierespongia RIGBY & GUTSCHICK, 1976, p. 80 [\*D. palla; OD]. Spheroidal; body wall composed of two layers (dermal and gastral) of hexactines and stauractines separated by a space; at least dermal layer consisting of parallel spicules of three nested orders of size; radially oriented prostalia distributed evenly over whole body but grouped into clusters of a few spicules each, and are chiefly rhabdodiactines but include hexactines of dermal layer with greatly elongated, proximal and distal rays; prostalia extending from gastral layer to well beyond dermal layer (at least one sponge diameter). lower Upper Ordovician: USA (Oklahoma).---FIG. 228,1a-b. \*D. palla, upper Blackriver or lower Trenton, Bromide Formation, Criner Hills, Carter County; a, holotype with central, inner body, outer cortex, and radiating tufts of prostalia, ×1; b, photomicrograph of part showing ranked spicules of cortex and somewhat less well organized net of interior, USNM 188528, ×4 (Rigby & Gutschick, 1976).
- Foerstella RUEDEMANN, 1925, p. 29 [\*F. rotunda RUEDEMANN, 1925, p. 30; OD]. Compressed specimen with rounded, squarish outline; stout bundles of long, possible rhabdodiactines crossing one another in nonparallel arrangement as presently preserved; each bundle interpreted as enclosing an ex-

halant cavity that opened separately to surface by an osculum situated in a depression [this does not seem likely]; bundles may be root tufts or internal bundles as in dictyospongiids; between bundles are small stauractines and rhabdodiactines, presumably forming body wall. *Upper Ordovician*: USA (New York).——FIG. 228,2*a*–*b*. \**F. rotunda*, Upper Utica Shale, Holland Patent; *a*, holotype, compressed specimen with bundles of long, monaxial spicules that end in depression in impression, ×0.5; *b*, enlargement of spicules from area between large, spicule bundles, ×5 (Ruedemann, 1925; courtesy of New York State Museum, Albany).

- Polylophidium FINKS, 1960, p. 111 [\*P. discus; M]. Discoid, perhaps originally globular, with small, root tuft; sponge interior filled with long rhabdodiactines radiating from central point and more or less organized in bundles of one or two dozen spicules, bundles penetrating sponge wall as long tufts regularly spaced over entire sponge body; body wall composed of several layers of simple, slender-rayed hexactines, with an outer layer of similar pentactines and stauractines, possibly of nested sizes but only partly parallel to one another. Permian (Artinskian): USA (Texas) .---- FIG. 229,2a-c. \*P. discus, Word Formation, Glass Mountains; a, holotype lodged in brachiopod shell with regular, small tufts over sponge surface and ring of monaxons that may be root tuft at upper left, AMNH 28076, ×1; b, paratype with part of outer layer removed to show radial bundles of monaxons in interior, AMNH 28067:1, ×1; c, enlarged view of outer surface of paratype showing dermal layer of pentactines and stauractines of various sizes, pierced by radial tufts of monaxons, AMNH 2067:1, ×5 (Finks, 1960; courtesy of The American Museum of Natural History).
- Polyplectella RUEDEMANN, 1925, p. 32 [\*P. mira RUEDEMANN, 1925, p. 35; OD]. Cylindroid to vasiform with terminal osculum; sponge body composed of stauractines, pentactines, or hexactines, and described as having numerous openings in lower part, presumably skeletal canals; long, separate tufts of prostalia (rhabdodiactines or pentactines with elongate, distal ray) distributed over much of sponge body and extending outwardly for at least one sponge diameter; lower part of sponge said to contain a "confused mass of twisted fiberlike" basalia (RUEDEMANN, 1925, p. 34). [The presence of possible skeletal canal openings suggests a closer relationship to Cyathophycus and the Hintzespongiidae, but Polyplectella is here retained in the Dierespongiidae on the basis of the more certain tufts of prostalia. In any event the Dierespongiidae and Hintzespongiidae are quite similar, both morphologically and phylogenetically, despite their seeming distance in the present classification, where the latter have been separated out as a stock possibly leading to the Pattersoniidae and Brachiospongiidae.] Upper Ordovician: USA (New York).-FIG. 229, 3a-c. \*P. mira, Frankfort Shale, Rome; a, holotype, cylindrical sponge with basal root tufts, approximately ×5; b, drawing of sponge body with a large osculum at top and

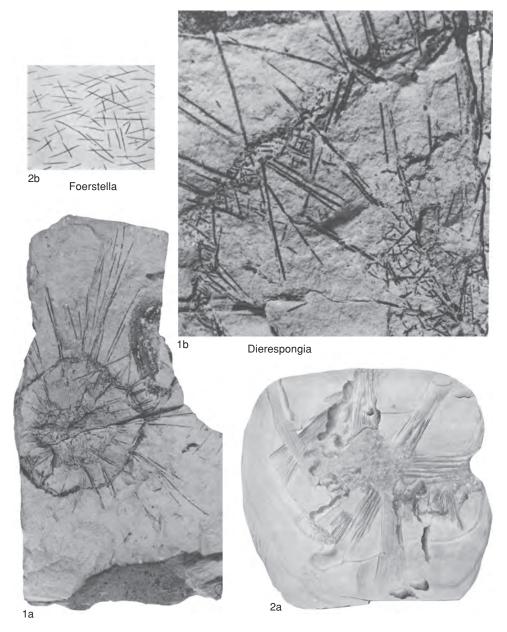


FIG. 228. Dierespongiidae (p. 359).

possible ostia on side, showing cylindrical form of holotype and irregularly distributed tufts of spicules with hexactine-based spicules between, USNM,  $\times 5$ ; *c*, associated specimen with long root tufts,  $\times 1$ (Ruedemann, 1925; courtesy of New York State Museum, Albany).

Stephanella HINDE, 1891, p. 23 [\*S. sancta; OD]. Circular masses of possible rhabdodiactines radiating from a center. *Middle Ordovician–Upper Ordovi-* *cian:* Canada (Ontario), Australia (?Victoria).— FIG. 229,1. \*S. sancta, Utica Shale, Upper Ordovician, Ottawa, Canada; drawing of radial spicule structure of type (Hinde, 1891).

Sycodictya RUEDEMANN, 1925, p. 34 [\*S. rara; OD]. Conicocylindrical, vasiform sponge with a thick wall containing skeletal canals (said not to penetrate either dermal or gastral surface); skeleton said to consist of "monactines (derived from hexactines),"

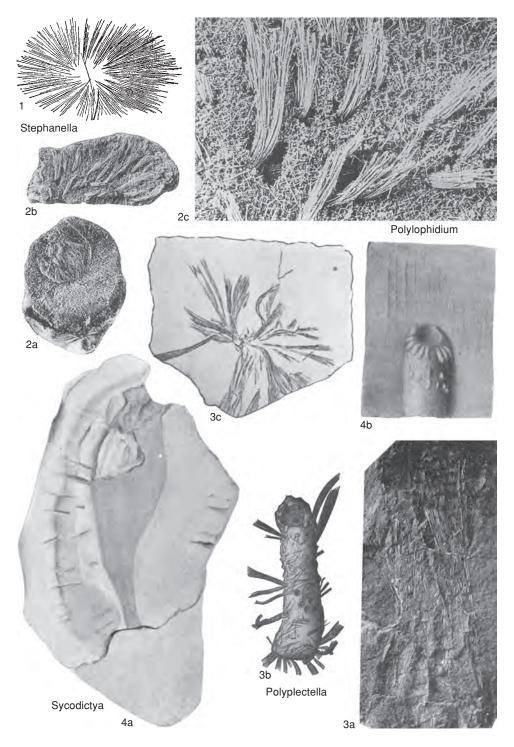


FIG. 229. Dierespongiidae (p. 359-362).

i.e., rhabdodiactines, "arranged in radiating and concentric systems," together with dermalia that are long, thin tetractines (RUEDEMANN, 1925, p. 35). [If the tetractines were tetraxons, which the illustration suggests, this would be a demosponge, but the illustration shows the principal spicules to intersect at right angles, which favors hexactinellid affinities suggested by the author of the genus and an interpretation of the dermalia as modified hexactines. The dubious inclusion of the genus in the present family is mainly for convenience and is based on its co-occurrence with more certain members of the family and on the predominance of rhabdodiactines in the skeleton. An isolated sexiradiate on the same slab as the sole specimen raises the question of heteractinid affinities.] Upper Ordovician: USA (New York).—FIG. 229,4a-b. \*S. rara, Upper Utica Shale, Holland Patent; a, holotype, side view with dark, matrix-filled spongocoel and thick walls with radial canals, ×1; b, regular, spicular structure of wall and extremity of canal, ×10 (Ruedemann, 1925; courtesy of New York State Museum, Albany).

## Family HYDNODICTYIDAE Rigby, 1971

[Hydnodictyidae RIGBY, 1971, p. 52]

Thin-walled but sculptured Dierespongioidea in which orientation of spicules in gastral layer differs from that in dermal layer, although spicules within each layer are parallel to each other; prostalia may be present. *Middle Cambrian–Upper Ordovician.* 

- Hydnodictya RIGBY, 1971, p. 53 [\*H. acantha; OD]. Sponge vasiform, base and osculum unknown; thin walls bearing sharp-crested, ridgelike nodes capped by tufts of prostalia; wall composed of two quadrate layers of stauractines and hexactines; presumed outer layer arranged parallel to longitudinal axis of sponge, presumed inner at about 45° to this axis; irregularly oriented spicules also occur; no parietal gaps or skeletal canals. Upper Ordovician: Canada (Manitoba).—FIG. 230, 1a-b. \*H. acantha, Red River Formation, Caradoc-Ashgill, Lake Winnipeg; a, flattened holotype with prostalia tufts along nodose margins, with generally quadrate skeleton best shown in upper part, ×0.9; b, enlarged section of sponge surface with quadrate skeleton best shown in upper part, GSC 25907, ×4.5 (Rigby, 1971; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).
- Valospongia RIGBY, 1983a, p. 264 [\*V. gigantis; OD]. Large, conicocylindrical to keg-shaped, thin-walled hexactinellid with separated, low, hemispherical protuberances spaced less than their diameter apart that appear to overlie circular, aporhysal gaps in principal net over entire surface; protuberances formed of a finer, more irregular, spicule net that outlines numerous circular pores in fractal-like rep-

etition of larger net on smaller scale; protuberances of two sizes, smaller alternating quincuncially with larger ones; oscular margin without spicule fringe; skeleton hexactines and stauractines and possibly with three layers: inner layer of principal net forming large quadrules parallel to sponge axis with roughly rectangularly arranged, long fibers or rays; intermediate and probably overlying layer composed of diagonally oriented quadrules, each likewise enclosing one of large mounds; third layer, between and connected to both series, includes smaller quadrules, both longitudinal and diagonal; finest are same size as net on protuberances and may represent a continuous layer of autodermalia that covers entire sponge of hexactine-based spicules; some nodes may have short, spinose tips. Middle Cambrian: USA (Utah).-FIG. 230,2a-b. \*V. gigantis, Marjum Formation, House Range; a, flattened holotype showing form of sponge and mounds of skeleton along margins, ×0.5; b, photomicrograph showing impressions of irregularly oriented, hexactine-based spicules and general distribution of flattened mounds as circular interruptions, BYU 1745, ×5 (Rigby, 1983a).

## Family AMPHISPONGIIDAE Rauff, 1894

[Amphispongiidae RAUFF, 1894, p. 275]

Sponges with strongly radiate, coarse spicules in lower part and reticulate skeleton including stauractines, pentactines, and diactines in upper part. *upper Silurian*.

Amphispongia SALTER, 1861, p. 135 [\*A. oblonga; OD]. Tubular to oblong sponges with lower radiate mass of coarse styles radiating from a central point; upper part solid or with a narrow, central spongocoel and skeleton of fine, reticulate stauractines, pentactines, and thin diactines; common spicule Tshaped with bulbous ray junction and arranged transverse to axis. upper Silurian: Scotland.——FIG. 231,2. \*A. oblonga, upper Ludlow beds, Ludlow, Pentland Hills, Scotland; side view of sponge preserved as mold, with coarse, basal spicules and finer, reticulate, upper skeleton, ×1.5 (Rauff, 1893).

### Family MULTIVASCULATIDAE de Laubenfels, 1955

[Multivasculatidae DE LAUBENFELS, 1955, p. 77]

Encrusting Dierespongioidea in which additional layers of parallel hexactines are intercalated between and parallel to dermal and gastral layers. *Upper Cambrian*.

Multivasculatus HOWELL & VAN HOUTEN, 1940, p. 7 [\**M. ovatus;* OD]. Numerous low cups connected by an intervening, encrusting sheet; spicules mostly simple, slender hexactines in parallel orientation, with distal rays aborted on dermal and gastral surfaces; body wall moderately thick with more than

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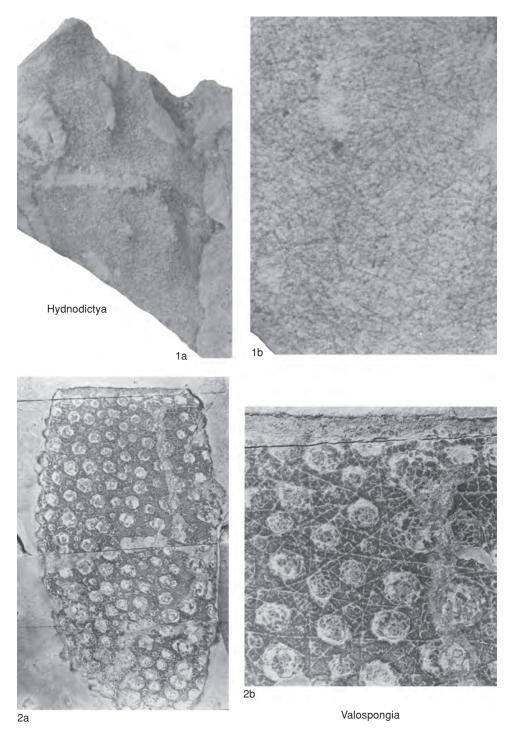


FIG. 230. Hydnodictyidae (p. 362).

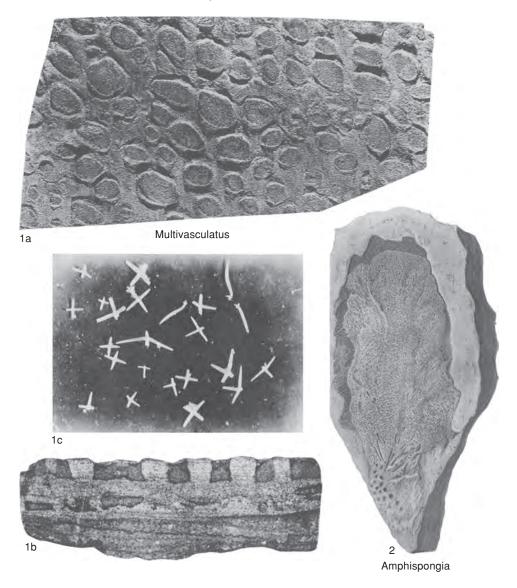


FIG. 231. Amphispongiidae and Multivasculatidae (p. 362-364).

one layer of hexactines between dermal and gastral layers; substauractines also present, as are hexactines in which five rays are reduced and sixth curved at an angle to crossing and papillose; simple rhabdodiactines occurring in matrix and may have been prostalia. *Upper Cambrian:* USA (Wyoming, Nevada).——FIG. 231, *Ia–c.* \**M. ovatus*, Gallatin Formation, Bighorn Mountains, Wyoming; *a*, view from above of holotype colony; *b*, side view of part of holotype colony, PU 5229a, ×1; *c*, hexactinebased spicules from holotype, PU 5229b, ×10 (Howell & van Houten, 1940).

#### Family TITUSVILLIDAE Caster, 1939

#### [Titusvillidae CASTER, 1939, p. 1]

Tubular, branching, segmented Dierespongioidea in which dermal and gastral layers, accompanied by prostalia, may enclose an additional layer, or layers, of spicules. *Upper Devonian–Holocene.* 

Titusvillia CASTER, 1939, p. 1 [\*T. drakei; OD]. Long, slender, somewhat sinuous branches that diverge

initially at angles close to 90°; each branch consisting of a linear series of subequal, nested funnels or cups; in some branches cups opening away from origin of branch, in other branches opening toward it; surface bearing fine, quadrate reticulation parallel to branch axis; peripheral ring of apparent prostalia fringes edges of some cups; longitudinal, paratangential rays of dermalia thinner than horizontal ones and slightly bowed outwardly; distal ray reduced to small knob; continuous, internal cylindrical tube about half maximum diameter of sponge apparently representing a cloaca; it may be eccentrically located and lined by quadrate mesh somewhat finer than dermal one; mesh showing spiral orientation; space between dermal and gastral surfaces apparently contained spicules in less regular orientation, including possible rhabdodiactines and clemes, but said to be too poorly preserved to analyze; a third quadrate mesh lying just under and subparallel to center mesh; rings of tubercles on cloacal, internal mold were interpreted as canals leading from expanded flange of cup where there is evidence in some cups of a circle of perforations just inside cup margin. Carboniferous (Lower Mississippian): USA (Pennsylvania).-FIG. 232,2a-c. \*T. drakei, Tidioute Member of Oil Lake Series, Titusville; *a*, side view of branched holotype,  $\times 0.75$ ; b, enlargement to show growth form with sequence of cups in branch, UCM 22130, ×1; c, restoration of upper part of cup showing canals and possible spiculation of skeleton, approximately ×2 (Caster, 1939).

- Annulispongia RIGBY & MOYLE, 1959, p. 401 [\*A. interrupta; M]. Sponge cylindrical, with sharpedged, upwardly flaring, annular expansions; body wall thick with exhalant canals said to extend inwardly and downwardly to cloaca; spicules small hexactines arranged in concentric layers, more densely spaced in interior of body wall; horizontal rays more pronounced in exterior layers and vertical rays longer within body wall. [The poriferan nature of this genus is in doubt. Spicule impressions may be foreign.] Carboniferous (Lower Mississippian): USA (Utah) .---—Fig. 232,1*a*-*b*. \**A*. interrupta, Manning Canyon Shale, Chesterian, Oquirrh Mountains; a, side view of weathered, annulate-appearing holotype, ×1; b, polished, transverse section showing possible canals and spicule character, BYU 11029-1, ×2 (Rigby & Moyle, 1959).
- Armstrongia CLARKE, 1920, p. 143 [\*Ceratodictya oryx CLARKE, 1918, p. 180; M]. No spicules are preserved, but in external form it shows no difference from *Titusvillia* CASTER, 1939, including the reversed expansion of annulations in some branches (that is, flaring toward point of branching); suggestions of terminal prostalia, as in *Titusvillia*, also noted by author. [This genus could be regarded as a senior synonym of *Titusvillia*.] Upper Devonian: USA (Pennsylvania).——FIG. 233,3. \*A. oryx (CLARKE), Upper Chemung Group, Erie; part of cast of original slab preserved as mold, ×0.5 (Clarke, 1920; courtesy of New York State Museum, Albany).

- Iowaspongia THOMAS, 1922, p. 87 [\*I. annulata; M]. Large, conical to broadly turbinate, but incipiently cylindrical in upper part, with sharp-crested, annular ridges separated by broad, smooth, concave interspaces that are generally asymmetrical, contracting rapidly from crest below, then gradually flaring outwardly and upwardly to next crest. [Personal observation of the holotype by FINKS confirms the original author's statement that a skeletal net is not clearly preserved, except for some locally visible, finely spaced, vertical and horizontal ridges. It is possible that this object is a burrow or cubichnium, with vertical striations representing slickensides, a result of differential movement in a soft, clay matrix, and horizontal ones in the sedimentary laminae.] Upper Devonian: USA (Iowa).---FIG. 233,2. \*I. annulata, Lime Creek Shale, Rockford; side view of regularly annulate, steeply obconical co-type, approximately ×0.5 (Thomas, 1922).
- Protoarmstrongia CASTER, 1941, p. 488 [\*P. ithacensis; OD]. Said to differ from *Titusvillia* and Armstrongia in that annulations are toroidal rather than infundibuliform. Upper Devonian: USA (New York).——FIG. 233,1a-b. \*P. ithacensis, Enfield Shale Member, Portage Formation, Senecan, Ithaca; a, part of holotype slab showing growth form and intertwined structure of branches, ×0.9; b, enlargement of basal part of one colony of holotype slab with limonite crust of spicule felt, ×2 (Caster, 1941).
- Sclerothamnus MARSHALL, 1875, p. 171 [\*S. clausi; OD]. Shape and size much like *Titusvillia* but branching simpler; dictyonine strands spined; microscleres tylohexasters. *Holocene:* East Indies. ——FIG. 234. \*S. clausi, off Timor; branched sponge with most nodes as ceratodictyan double nodes rather than cups, ×0.25 (Caster, 1941).

### Family AGLITHODICTYIDAE Hall & Clarke, 1899

[nom. transl. FINKS & RIGBY, herein, ex Aglithodictyinae Hall & CLARKE, 1899, p. 53]

Thick-walled, conoidal Dierespongioidea, in which several layers of spicules are intercalated between dermal and gastral layers; skeletal canals are present. [All the genera assigned here to the family Aglithodictyiidae are confined to the Late Devonian or Early Carboniferous, have similar thick walls with radial slits, a central cloaca, and a cubic mesh that may be dictyonine. This is probably, therefore, a natural group of worldwide occurrence.] Upper Devonian–Carboniferous (Visean).

Aglithodictya HALL & CLARKE, 1899, p. 145 [\*A. nummulina; OD]. Sponge small, turbinate, but abruptly contracted toward osculum, bearing possible radial canals upon upper slope; peripheral frill may be present about widest part; obscure, quadrate

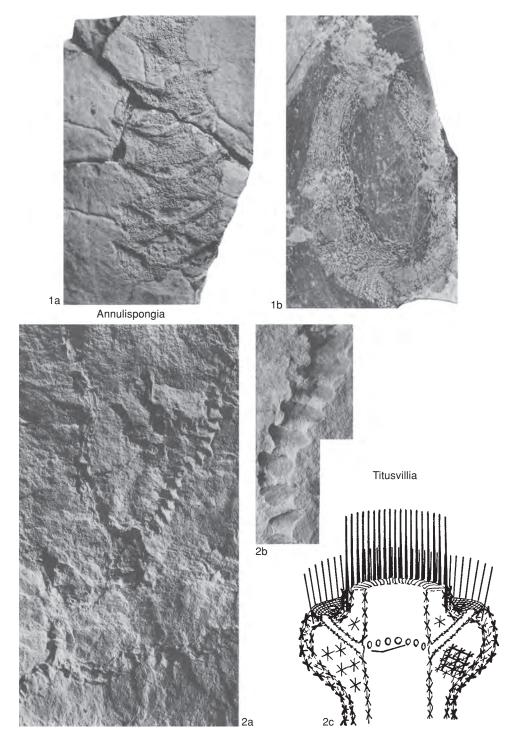


FIG. 232. Titusvillidae (p. 364–365).

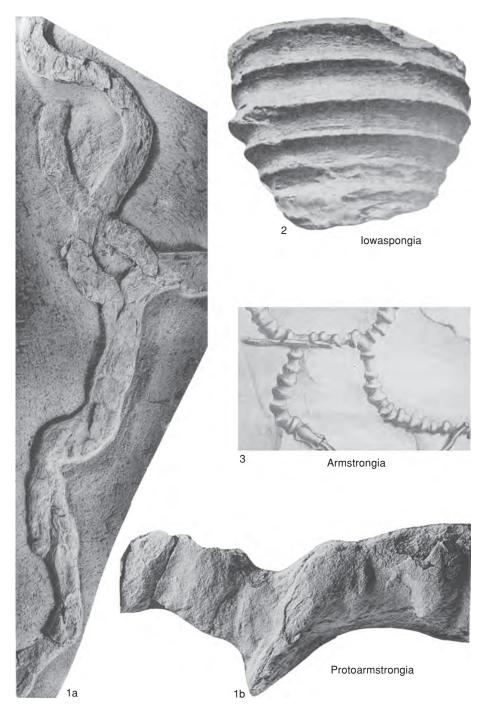


FIG. 233. Titusvillidae (p. 365).



FIG. 234. Titusvillidae (p. 365).

mesh seemingly present. [HALL and CLARKE, whose description of the sole specimen is paraphrased, suggested that the sponge may be thick-walled, presumably corresponding to the width of the canalbearing upper surface, and thus not a true dictyosponge.] *Upper Devonian:* USA (Pennsylvania).——FiG. 235, *1a–c.* \**A. nummulina*, Chemung Group, Lawrenceville, as cited in text but from Cohocton, New York, as cited in plate explanation; *a*, side view of holotype showing steeply obconical form that abruptly tapers in upper part to osculum; *b*, view into osculum from above, ×1; *c*, enlarged view of skeletal net showing reticulate pattern, NYSM, ×4 (Hall & Clarke, 1899).

Asociatella HURCEWICZ, 1985, p. 285 [\*A. fruticum; OD]. Sponge with club-shaped branches; thin walled with deep cloaca; skeleton possibly dictyonine; short canals present. Devonian (Frasnian): Poland.——FIG. 235,2a-c. \*A. fruticum, lower Frasnian limestones, Wietrznia; a, side view of globular sponge, ×1; b, photomicrograph of spicules in skeletal fragment, ×50; c, drawings of skeletal structure in holotype, MUZ IG 1501.II/1, ×19 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).

Czarnockiella Hurcewicz & Czarniecki, 1986, p. 342 [\*C. concinella; OD]. Broadly conical with beveled, upper margin; no cloaca; top surface shallowly concave with numerous circular, closely spaced, exhalant pores that are openings of exhalant canals rising inwardly and upwardly through much of interior; dermal skeleton small hexactines or stauractines in parallel arrangement; principal skeleton of much larger hexactines, pentactines, stauractines, tauactines, and rhabdodiactines, of various sizes, in more or less parallel arrangement. [The external shape of the type species resembles Aglithodictya HALL & CLARKE, 1899.] Carboniferous (Visean): Poland.-FIG. 235, 3a-i. \*C. concinella, Carboniferous limestone, Galezice, Holy Cross Mountains; a, side view of holotype with characteristic shape,  $\times 0.5$ ; b, view of holotype from above, AI-68/34, ×0.5; c, vertical section showing canal and skeletal development, AI-68/25, ×0.5; d, photomicrograph of endosomal, skeletal structure showing axial hexactine, regular hexactines, and stauractines,

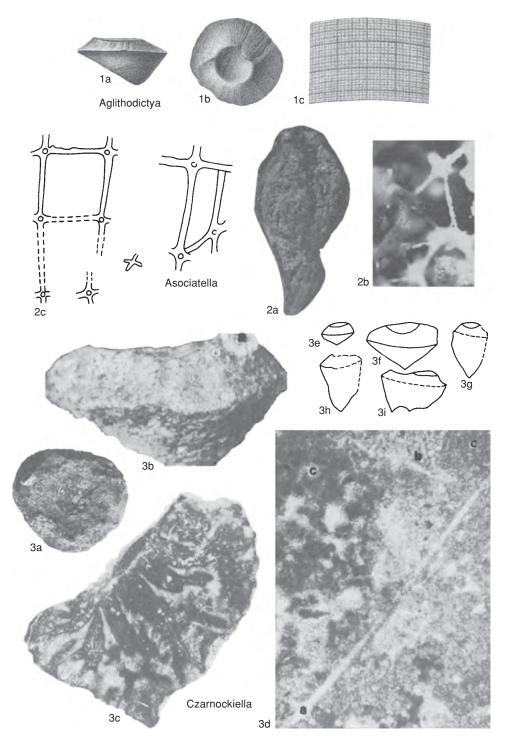


FIG. 235. Aglithodictyidae (p. 365–371).

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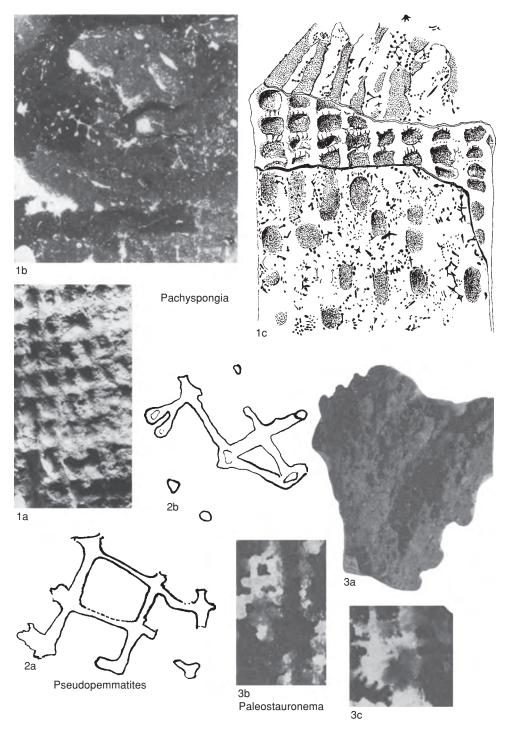


FIG. 236. Aglithodictyidae (p. 371–372).

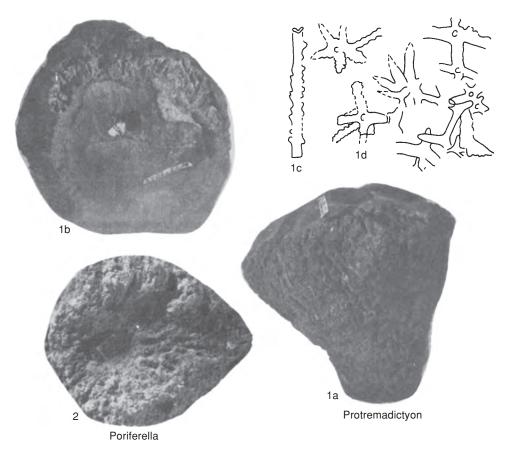


FIG. 237. Aglithodictyidae (p. 371-372).

AI-68/22a, ×100; *e–i*, drawings showing variations in outlines within type species, not to scale (Hurcewicz & Czarniecki, 1986; courtesy of Polish Geological Society, Krakow).

Pachyspongia TERMIER & TERMIER in TERMIER, TERMIER, & TSIEN, 1981, p. 292 [\*P. columbarium; OD]. Thick-walled fragment; exterior bearing quadrules, each outlined by a raised wall or ridge; it is not clear whether ridges are largest hexactines, in overlapping orientation outlining quadrules of one ray length, or whether they are erect lamellae like those of Clathrospongia HALL, 1884; interior containing several layers of smaller hexactines in parallel orientation, forming a cubic mesh, interrupted by somewhat irregular, anastomosing canals wider than mesh spaces; shape of whole sponge not known. Devonian (Frasnian): Belgium.-FIG. 236,1a-c. \*P. columbarium, Neuville Formation, Philippeville; a, exterior surface of holotype fragment with numerous ostia of radial canals,  $\times 5$ ; b, photomicrograph showing dictyonine, skeletal net interrupted by dark, matrix-filled canals, ×8; c, drawing of skeletal and canal relationships showing shaded, radial canals in main net and ostia in cortical layer in front, ×20 (Termier, Termier, & Tsien, 1981).

- Paleostauronema HURCEWICZ, 1985, p. 282 [\*P. transversallos HURCEWICZ, 1985, p. 283; OD]. Conical, thin walled, with deep cloaca; canals or parietal gaps present in walls; spinose hexactines in parallel arrangement forming cubic mesh (possibly dictyonine); synapticulae present. Devonian (Frasnian): Poland.—FIG. 236,3a-c. \*P. transversallos, upper Frasnian limestone, Kowala; a, longitudinal section of syntype with open spongocoel and moderately thick walls, X1; b, photomicrograph showing dictyonal structure; c, photomicrograph of spinose spicules, MUZ IG 1501.II/8, ×50 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).
- Poriferella HURCEWICZ, 1985, p. 283 [\*P. formosum; OD]. Conical, thick-walled, deep, central cloaca; vertical, slitlike aporhyses or possibly epirhyses; skeleton possibly dictyonine with smooth hexactines. Devonian (Frasnian): Poland.——FIG. 237,2. \*P. formosum, upper Frasnian limestone, Kowala; view of holotype from above with central spongocoel and thick walls, with elongate ostia on

gastral surface, MUZ IG 1501.II/65, ×1 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).

- Protremadictyon HURCEWICZ, 1985, p. 284 [\**P. kainos;* OD]. Conical, thick walled with narrow, central cloaca; vertically elongate, radial canals (possible aporhyses) covered by dermal layer; spinose hexactines or stauractines forming irregular net with broad mesh spaces. *Devonian (Frasnian):* Poland.——FIG. 237, *Ia–d. \*P. kainos,* upper Frasnian limestone, Kowala; *a,* side view of holotype with prominent, inhalant ostia; *b,* top view with small, axial spongocoel and canals around margin, ×1; *c– d,* silicified fragments of uncinates (*a*) and parenchymal skeleton with dictyonal structure in part (*b*), MUZ IG 1501.II/1, ×20 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).
- Pseudopemmatites FRAIPONT, 1911, p. 197 [\*F. fourmarieri; OD]. Sponge broadly conical with flat base and volcano-like summit, bearing oscular opening; lateral slopes of upper surface bearing closely spaced, radial slits (possible aporhyses) that do not reach osculum; skeletal net of hexactines in parallel arrangement and forming cubic mesh, but spicules not clearly organized into continuous, dictyonal strands as claimed by FRAIPONT, because there are instances of offsets in spicule series (see his fig. FN 132C-132D). [The upper surface of the sponge resembles that of the contemporaneous Aglithodictya HALL & CLARKE, 1899, and the general canal and skeletal-net structure resembles that of other Frasnian genera in the family, particularly that of Poriferella HURCEWICZ, 1985.] Devonian (Frasnian): Belgium.—FIG. 236,2a-b. \*P. fourmarieri, Frasnian limestone, Villers-en-Fagne; a, drawing of characteristic fragment of skeletal net showing dictyonine structure, scale not given; b, drawing showing some irregularities in skeletal net, scale not given (Fraipont, 1911).

# Superfamily DICTYOSPONGIOIDEA Hall & Clarke, 1899

[nom. transl. FINKS, 1983b, p. 109, ex Dictyospongiidae Hall & Clarke, 1899, p. 52]

Reticulosa in which one or more layers of vertical and horizontal bundles of spicules (rhabdodiactines or other hexactine derivatives) are developed beneath dermal layer; dermal skeleton of hexactine derivatives usually differentiated into an outer (possibly autodermal) quadrate mesh of finer spicules and an inner (possibly hypodermal), quadrate mesh of coarser spicules of nested sizes; similar gastral layer, usually of finer spicules, may be developed; rarely both dermal and gastral layers may be suppressed; sponges almost always vasiform; root tuft with bidentate spicule terminations may or may not be present; comitalia of short, stout, curved strongyles and short-shafted, bidentate anchors frequently present; zigzag clemes may be present in root tufts and internal spicule bundles; tauactines and pinulelike spicules often present. *Ediacaran– Upper Triassic (Carnian).* 

# Family DICTYOSPONGIIDAE Hall & Clarke, 1899

[Dictyospongiidae HALL & CLARKE, 1899, p. 52]

Thin-walled Dictyospongioidea with fine, autodermal and hypodermal, quadrate mesh of nested sizes of simple spicules; internal, vertical and horizontal bundles regularly and widely spaced; root tuft may be absent; dermal armor of closely spaced paraclavules may be developed; tripinuli in some genera. *Ediacaran–Permian (Roadian)*.

#### Subfamily DICTYOSPONGIINAE Hall & Clarke, 1899

[Dictyospongiinae HALL & CLARKE, 1899, p. 52]

Dictyospongiidae that are basically tubular with prism faces sometimes developed at top. *Ediacaran–Permian (Roadian)*.

Dictyospongia HALL & CLARKE, 1899, p. 72 [\*Dictyophyton sceptrum HALL, 1890b, p. 56; OD]. Sponge cylindrical, elongate, with narrow, conical base terminating in a root tuft; contracted slightly about osculum; surface smooth and unornamented except for usual quadrate, skeletal mesh that has relatively subdued differentiation into several orders of quadrule size; paraclavules, curved strongyles, and spinose hexactines reported from Mississippian species, otherwise spicules unknown except for root tuft, possible rhabdodiactines; incipient prism faces reported from upper end of larger specimen. [Pre-Upper Devonian species described by HALL and CLARKE (1899) are not this genus or are not identifiable.] Silurian (?Wenlock), Middle Devonian (?Givetian), Upper Devonian-Carboniferous (Lower Mississippian): Canada (Northwest Territories, Cornwallis Island), ?Wenlock; USA (Nevada), ?Givetian; USA (New York, Indiana, ?Alabama), Upper Devonian-Carboniferous (Lower Mississippian).—FIG. 238,2. \*D. sceptrum (HALL), Chemung Group, New York; side view of slender, nearly complete reference individual with circular, transverse section and characteristic, skeletal grid, UCC 13148B, ×0.5 (Hall & Clarke, 1899).

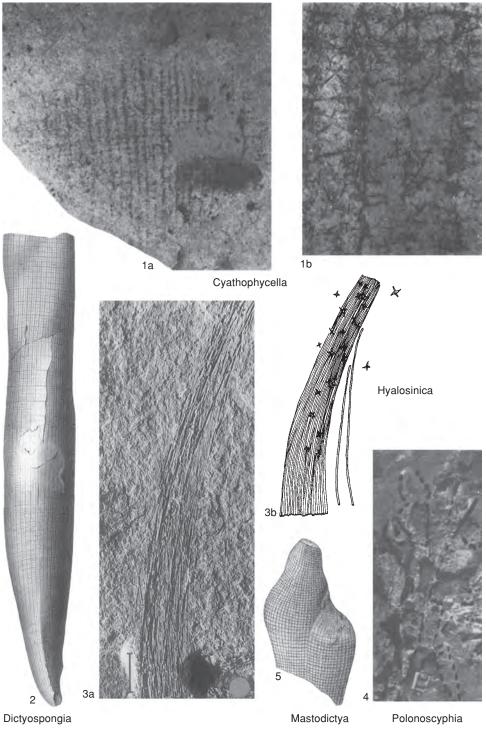


FIG. 238. Dictyospongiidae (p. 372-376).

- Cyathophycella RIGBY & STUART, 1988, p. 135 [\*C. quadrata; OD]. Thin-walled dictyosponge with vertical and horizontal tracts composed of latticelike, rectangularly arranged hexactines and hexactine derivatives in ranked arrangements within individual skeletal tracts. *Silurian–Devonian*: USA (Nevada).——FIG. 238, *1a–b.* \*C. quadrata, Roberts Mountains Formation, Independence Mountains; *a*, flattened holotype with slightly radiating, skeletal tracts cross connected by less continuous, horizontal ones, ×1; *b*, photomicrograph of upper center of holotype with vertical tracts of ranked stauractines and hexactines, USNM 415785, ×10 (Rigby & Stuart, 1988).
- Dialyscyphia HURCEWICZ & CZARNIECKI, 1986, p. 344 [\*D. breviramosa Hurcewicz & Czarniecki, 1986, p. 345; OD]. Cylindrical, branching; no cloaca; exhalant depression at apex of branch; exhalant canals concentrated in axial region and open on both sides and top; skeleton of parallel hexactines (pentactines at surface in nonquincuncial arrangement) such that primary quadrules are two ray lengths on a side and are subdivided by nine smaller hexactines having similar arrangement. Carboniferous (Visean): Poland.-FIG. 239,2a-f. \*D. breviramosa, Carboniferous limestone, Galezice, Holy Cross Mountains; a, side view of holotype,  $\times 1$ ; b, transverse section of lower part showing inhalant canals (a) and axial, exhalant area (b),  $\times 20$ ; c-f, drawing of spicules from holotype and their distribution, c, outline of pores in skeletal network; d, scheme of spicule distribution; e-f, small and large hexactines, bar scale, 0.1 mm, AI-68/28 (Hurcewicz & Czarniecki, 1986; courtesy of Polish Geological Society, Krakow).
- Dictyorhabdus WALCOTT, 1892, p. 165 [\*D. priscus; OD]. Fragments of tubelike sponge with bulbous swellings along one side, with thick walls of latticework skeleton. [Position in the family is uncertain.] Ordovician: USA (Colorado).——FIG. 239,1a-b.
  \*D. priscus, Harding Sandstone, Middle Ordovician, Cañon City; a, side view of fragment with swellings on one side, ×3; b, photomicrograph of reticulate, skeletal structure, ×5 (Walcott, 1892).
- Hyalosinica MEHL & REITNER in STEINER & others, 1993, p. 305 [\**H. archaica;* OD]. Stalk and root tuft of coarse, anisoactine spicules with loosely twisted texture; small hexactines, stauractines, and pentactines are associated; body of sponge unknown except for a few triaxial spicules in proximal end of tuft. *lower Lower Cambrian-middle Lower Cambrian:* China (Anhui, Hunan).—FIG. 238,3*a*-*b.* \**H. archaica,* Niutitang Formation, Tommotian, Hunan; *a*, flattened, holotype stalk and root tuft of coarse, anisoactine, triaxial spicules, ×1 (Steiner & others, 1993); *b*, sketch of tuft and associated, small hexactines, pentactines, and stauractines, IPFUB San 109 A, B, ×1.5 (Mehl, 1996).
- Lobospongia HURCEWICZ, 1985, p. 280 [\*L. varsovia; OD]. Foliose, irregular; no cloaca; hexactines (pentactines in dermal layer) in nonquincuncial ar-

rangement, so that quadrules are formed by two ray lengths; some hexactines have longitudinal rays that are longer than other rays. *Devonian (Frasnian):* Poland.——FIG. 239,5*a*–*d.* \**L. varsovia*, upper Frasnian limestone, Kowala; *a*, irregular, lobate holotype from side, ×1; *b*–*d*, spicules from holotype, including regular hexactines from parenchymal skeleton, pentactines from cortex, and network pattern of axial hexactines, MUZ IG 1501.II/15, ×25 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).

- Mastodictya HALL & CLARKE, 1899, p. 167 [\*Dictyospongia (Mastodictya) osculata; OD]. Sponge small, seemingly fusiform, but incomplete at each end; orientation not clear; examination of specimen suggests that supposed oscula of HALL and CLARKE may be broken parts, that narrowest part may be basal apex, and supposed second protuberance an irregularity partly covered with matrix; skeletal net consisting of very small stauractines or pentactines of at least three orders of size, largest with overlapping rays and possibly accompanied by smaller comitalia (possible rhabdodiactines); a few of larger spicules with knoblike, distal ray; skeletal net locally slightly irregular and curved to follow outlines of body; HALL and CLARKE reported paraclavules and curved strongyles. [This may be a young sponge of another species, but the fusiform shape seems distinctive.] Carboniferous (Lower Mississippian): USA (Indiana).—FIG. 238,5. \*M. osculata (HALL & CLARKE), Keokuk Group, Crawfordsville; side view of small sponge with complete oscular margin, but broken at base, NYSM, ×1 (Hall & Clarke, 1899).
- Microstaura FINKS, 1960, p. 103 [\*M. doliolum; M]. Sponge barrel-shaped to cylindrical and subprismatic; wall thick, composed of cubic mesh of very small hexactines (pentactines at outer and cloacal surfaces) of up to three orders of size, at least at surface, with largest having overlapping rays; possible internal, vertical bundles of rhabdodiactines; root tuft not certainly known; osculum and cloaca broad, but sponge generally contracting toward oscular opening. [This is similar to a short, thickwalled Dictyospongia.] Permian (Artinskian-Roadian): USA (Texas).-FIG. 240,3a-c. \*M. doliolum, ?Word Formation, Leonardian, Glass Mountains; a, side view of holotype showing its general form, with a crushed osculum at top and silicified skeleton on flattened side,  $\times 2$ ; b, magnified view of part of dermal surface with skeleton mainly of pentacts, mostly of one size, with overlapping rays, USNM 127648, ×10; c, silicified, skeletal net fragment of paratype showing cubic arrangement of simple, overlapping hexactines in wall interior, USNM 127649d, ×10 (Finks, 1960; courtesy of The American Museum of Natural History).
- Ozospongia CLARKE, 1918, p. 185 [\*O. johnstoni; OD]. Sponge begins as slender, cylindrical stalk that branches upwardly one or more times, each branch expanding into a fusiform or club-shaped body that contracts toward osculum; surface bearing closely spaced, longitudinal ridges, sometimes

Reticulosa

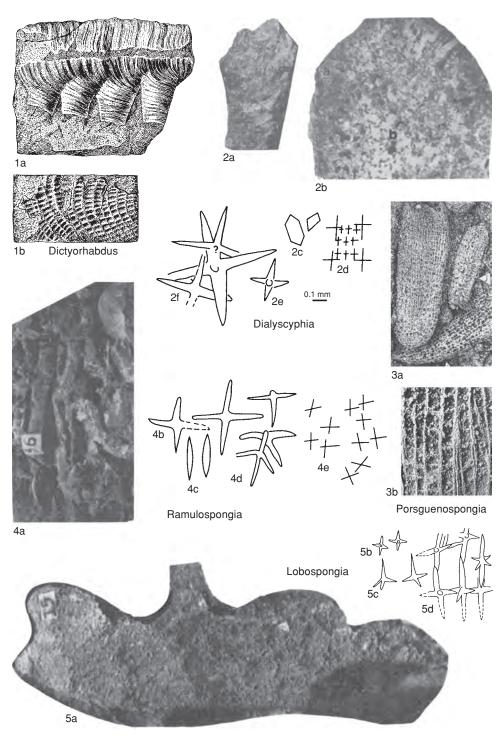


FIG. 239. Dictyospongiidae (p. 374-376).

irregular or discontinuous; they are crossed by less prominent horizontal ridges, producing coarse quadrules reminiscent of *Thysanodictya* or *Clathrospongia*; spicules not known. *Upper Devonian*: USA (New York); ?Poland, *Frasnian*.——FIG. 241. \*O. *johnstoni*, Chemung Sandstone, Upper Devonian, Hinsdale, New York; side view of plaster case of natural mold of branched holotype showing growth form and reticulate skeleton, New York State Museum, ×1 (Clarke, 1918; courtesy of New York State Museum, Albany).

- Palaeophragmodictya GEHLING & RIGBY, 1996, p. 188 [\*P. reticulata; OD]. Convex disc- to hemisphericalshaped sponges with reticulate skeleton where straight, radial tracts and laterally perpendicular, concentric tracts combine to produce rectangular, dictyosponge-appearing, skeletal structure; principal disc surrounded by peripheral frill marked by radial ridges that appear to be extensions of reticulate net of main disc. [The genus is questionably included here because of its gross morphology and reticulate, quadrate, skeletal structure. The fossils, however, consist largely of three-dimensional impressions without clearly identifiable individual spicules. These are the oldest dictyosponges and the oldest body fossils of sponges known.] Ediacaran: South Australia. FIG. 242a-c. \*P. reticulata, Ediacara Member, Rawnsley Quartzite, Chase Range; a, silicone rubber cast of flattened holotype with mesh on right surrounded by frill impression, SAM P32324a, ×0.8; b, flattened paratype with anastomosing ridges and surrounding frill, SAM P32325,  $\times 0.8$ ; c, generalized restorations and flattened impressions, not to scale (Gehling & Rigby, 1996).
- Phormosella HINDE, 1888, p. 125 [\*P. ovata; M]. Small, ovoid sponges without apparent osculum or root tuft; spicules stauractines or pentactines of three size orders, the largest arranged regularly so as to produce quadrules parallel to longitudinal axis of sponge. [The smaller spicules were said to be irregularly arranged, thus distinguishing this from Protospongia, but illustrations show only a slight disarray that does not obscure an arrangement into three size orders of quadrules. The genus is possibly a synonym of Dictyophytra and Prismodictya (q.v.).] Silurian (Ludlow): England.-FIG. 240,2a-b. \*P. ovata, Ludlow strata, Shropshire; a, impressions of nine sponges of species, holotype, ×1; b, enlargement of part of one sponge showing spicule structure of wall, British Geological Survey Museum, ×5 (Hinde, 1887b).
- Polonoscyphia HURCEWICZ, 1985, p. 279 [\**P. delicatula* HURCEWICZ, 1985, p. 280; OD]. Sponge small, obconical, thin walled with deep cloaca; spicules unconnected triactines. *Devonian (Frasnian):* Poland.——FIG. 238,4. \**P. delicatula*, upper Frasnian limestone, Kowala; side view of thinwalled holotype, MUZ IG 1501.II/11, ×1 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).
- Porsguenospongia PICKETT & PLUSQUELLEC, 1998, p. 718 [\*P. lejalnicolae; OD] [=Platyphyllum LEJAL-

NICOL, 1976, p. 341, obj.]. Small, cylindrical to vasiform, thin-walled dictyosponges with rounded base; oscular margin without supplementary spicules; skeletal net with long stauractines and oxeas grouped into prominent, primary, vertical tracts that are cross connected by continuous, less robust horizontal tracts; openings between primary tracts subdivided by smaller, more discontinuous, secondand third-order tracts. Devonian (Famennian): France.—FIG. 239, 3a-b. \*P. lejalnicolae, Famennian II, Schistes de Porsquen, Brest; a, type sponges in latex cast, ×1; b, enlarged part of skeletal net showing long rays in vertical bundles and some shorter horizontal rays of stauractines in spaces between, approximately ×5 (Pickett & Plusquellec, 1998; courtesy of Geobios).

- Ramulospongia HURCEWICZ, 1985, p. 279 [\*R. rasus; OD]. Thin branches without cloaca; spicules hexactines, pentactines, stauractines, tauactines, and rhabdodiactines in parallel orientation. Devonian (Frasnian): Poland.——FIG. 239,4a-e. \*R. rasus, upper Frasnian limestone, Kowala; a, side view of branched holotype, ×1; b-d, outlines of spicules from holotype, parenchymal skeleton, cortex, and associate fusiform diactines; e, sketch of spicule positions in cortex, MUZ IG 1501.II/56, ×25 (Hurcewicz, 1985; courtesy of Panstwowy Instytut Geologiczny, Warsaw).
- Repospongia Hurcewicz & Czarniecki, 1986, p. 347 [\*R. carbonaria Hurcewicz & Czarniecki, 1986, p. 348; OD]. Colonies broadly conical to discoidal with depressed, upper surface, composed of small, hollow, ellipsoidal individuals that branch from one another in spiraling panicles, their hollow interiors being serially connected; spicules small hexactines of two sizes in parallel orientation, with stauractines at surface. Carboniferous (Visean): Poland .-–Fig. 243,1a-c. \*R. carbonaria, Carboniferous limestone, Culm of Orlej, southern Poland; a, top view of holotype showing branched form,  $\times 1$ ; *b*, section through individual branch, ×10; c, drawings of spicules from thin section, showing small and large hexactines, AI-68/47, bar scale, 0.1 mm (Hurcewicz & Czarniecki, 1986; courtesy of Polish Geological Society, Krakow).
- Retifungus RIETSCHEL, 1970, p. 31 [\*R. rudens; M]. Upper portion resembling Prismodictya, fusiform and eight sided; lower portion long and tubular passing into long, twisted root tuft; spicules include rhabdodiactines of various sizes and possibly stauractines, pentactines, and hexactines in quadrules of main body; root tuft strands appear to pass upwardly into body as regularly spaced, vertical, spicule bundles. Devonian (Pragian): Germany.— -FIG. 240, 1a-c. \*R. rudens, Siegenian, Hunsrückshiefer, Hunsrück; a, upper end of holotype stalk with lower end of reticulate sponge, SMF 19992, ×1; b, upper end of paratype showing twisted spicules of long root stalk, ×0.5; c, restoration of long root stalk and upper sponge body, approximately ×0.25 (Rietschel, 1970).
- Sanshadictya MEHL & REITNER in STEINER & others, 1993, p. 304 [\*S. microreticulata; OD]. Sponges

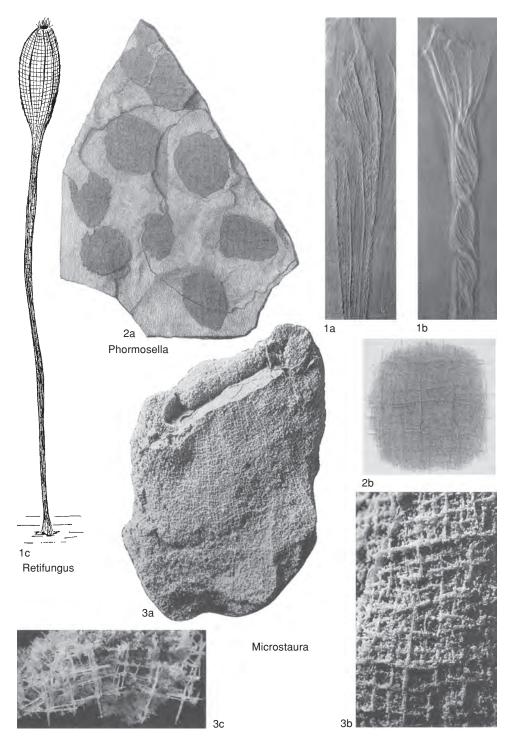


FIG. 240. Dictyospongiidae (p. 374-376).



Ozospongia

FIG. 241. Dictyospongiidae (p. 374-376).

with a skeleton of regular, rectangularly arranged, parallel bundles of thin diactines and stauractines, with at least three orders of very fine quadrules; may have had anchoring spicules. [Fragments of the reticulate sponge document that development of dictyosponge skeletal structure had taken place by the Early Cambrian.] *Lower Cambrian:* China (Hunan).——FIG. 243,2*a*–*b*. \**S. microreticulata*, Niutitang Formation, Tommotian; *a*, flattened holotype fragment of reticulate bundles of diactines and stauractines, ×1.5 (Steiner & others, 1993); *b*, sketch of holotype interpreting bundles and presence of stauractines in upper right, IPFUB San 117, ×5 (Mehl, 1996).

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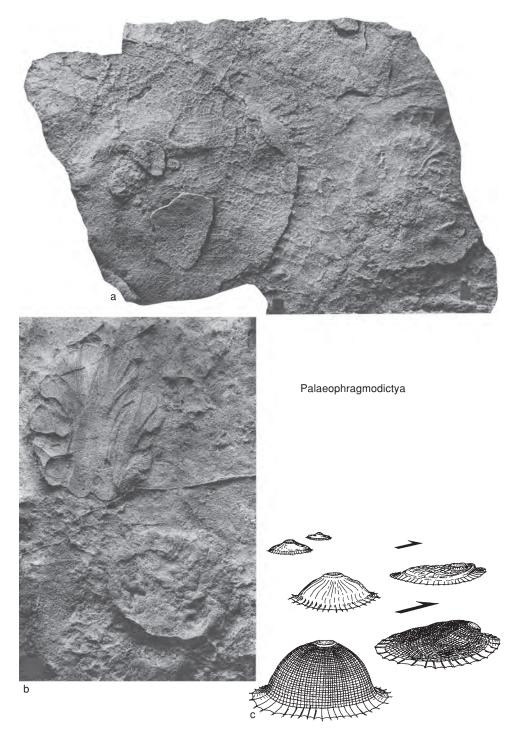


FIG. 242. Dictyospongiidae (p. 376).

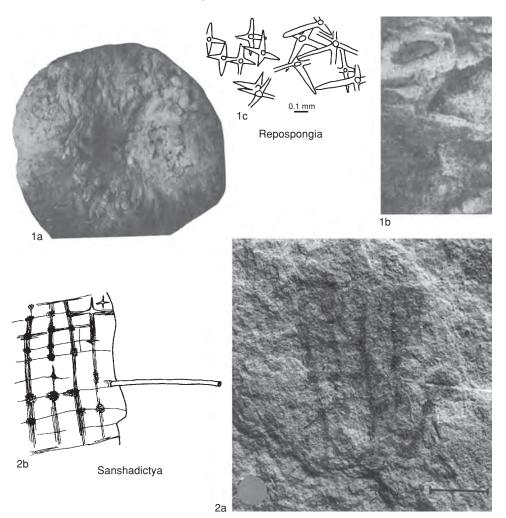


FIG. 243. Dictyospongiidae (p. 376-378).

#### Subfamily PRISMODICTYINAE de Laubenfels, 1955

#### [Prismodictyinae DE LAUBENFELS, 1955, p. 74]

Dictyospongiidae with well-developed prism faces and no protuberances. [These are one of the earliest and presumably most primitive groups of the dictyosponges.] Upper Ordovician–Carboniferous (Serpukhovian).

Prismodictya HALL & CLARKE, 1899, p. 79 [\*Dictyophyton telum HALL, 1884, p. 470; OD] [=?Dictyophyton HALL, 1863, p. 87 (type, D. filitextile HALL, 1863, p. 88, SD MILLER, 1889, p. 158), nom. oblit.; ?Phormosella HINDE, 1887b, pl. 3,2; HINDE, 1888, p. 125 (type, P. ovata, M), nom. oblit.; ?Dictyophytra RAUFF, 1894, p. 249 (type, Tetragonis danbyi M'Coy, 1855, p. 62, M), nom. oblit.; ?Helicodictya HALL & CLARKE, 1899, p. 114 (type, H. trypania, OD); ?Ithacadictya CASTER, 1939, p. 16 (type, I. cornelli, M)]. Sponge prismatically conicocylindrical to strongly fusiform, often contracting toward aperture as well as having a pointed base; generally light prism faces, each often slightly concave with interfacial angles sharp; some individuals with spiral twisting of prism faces about longitudinal axis; Helicodictya here considered to be based on extreme examples of such twisting, and to be, therefore, a junior synonym of Prismodictya. Spicules unknown (traces of simple stauractines or pentactines of the usual orders of size are preserved in somewhat doubtful Mississippian P. polyhedra, as well as in the Silurian Phormosella); net composed of usual quadrules of several orders of size, although differences in widths of outlining ridges not strongly marked; neither root tufts, lateral tufts, nor apertural fringes are known. [The type of Dictyophyton HALL, 1863, appears to be a species of Prismodictya, as does the type of Dictyophytra RAUFF, 1894, and possibly also that of Phormosella HINDE, 1887b. All three genera are senior to the better-known Prismodictya, but they have not, to my knowledge (RMF), been used in this sense during the past fifty years. They are treated here as nomina oblita.] upper Silurian–Upper Devonian, Carboniferous (?Lower Mississippian): England, USA (New York, Pennsylvania, ?Indiana).--Fig. 244,3. \*D. telum (HALL), Chemung Group, Upper Devonian, Wellsville, New York; side view of characteristic specimen with prismatic, transverse section and typical, reticulate, skeletal grid, NYSM, ×1 (Hall & Clarke, 1899).

- ?Dictyophyton HALL, 1863, p. 87 [\*D. filitextile HALL, 1863, p. 88; SD MILLER, 1889, p. 158]. The type specimen, as described and illustrated by HALL and CLARKE (1899, pl. 21,7), appears to be a rather straight-sided Prismodictya with subdued and convex prism faces. [If so, Dictyophyton would then be a senior synonym of Prismodictya HALL & CLARKE, 1899. We believe Dictyophyton should be suppressed as a nomen oblitum under the Code (ICZN, 1999).] Devonian (Frasnian): USA (New York).
- ?Dictyophytra RAUFF, 1894, p. 249 [\* Tetragonis danbyi M'Coy, 1855, p. 62; M]. [Although apparently intended as a so-called correction of the name Dictyophyton HALL, 1863, the only species definitely referred to it by RAUFF was the Silurian Tetragonis danbyi M'Coy, 1855, which thereby becomes the type by monotypy. (Another new species, D. (?) walcotti RAUFF, 1894, Upper Ordovician, was referred to it with a query. That species is not generically assignable.) The name is, thus, available for a genus that includes M'Coy's species. Examination of the type specimens shows that they are indistinguishable from Prismodictya. This species is not Dictyospongia as concluded by HALL and CLARKE (1899). There is a possibility that D. danbyi is also conspecific, or at least congeneric, with the type of Phormosella HINDE, 1887b, which is very nearly contemporaneous and sympatric. Dictyophytra is, thus, a senior subjective synonym of Prismodictya HALL & CLARKE, 1899, and possibly a junior subjective synonym of Phormosella HINDE, 1887b. Dictyophytra qualifies as a nomen oblitum under the Code (ICZN, 1999). See discussion under Prismodictya, above.] Silurian (Ludlow): England. -FIG. 245,2a-b. \*D. danbyi (M'COY), upper Ludlow beds, Kendal; a, side view of cast of small type with reticulate skeleton, ×1; b, enlarged part of surface showing quadruled skeletal structure, WMC, ×5 (Rauff, 1894).
- ?Helicodictya HALL & CLARKE, 1899, p. 114 [\*H. trypania; OD]. Resembles a Prismodictya in which

prism faces have been spirally twisted about longitudinal axis of sponge, with a helical angle of 45° or more to axis. [The genus is here considered to be a possible junior synonym of *Prismodictya*.] *Devonian* (*Frasnian*): USA (New York, Pennsylvania).— FIG. 244,1. \*H. trypania, Chemung Group, Senecan, Wellsville, New York; side view of holotype with helical ridges parallel to one of reticulate, spicule series, ×1 (Hall & Clarke, 1899).

- ?Ithacadictya CASTER, 1939, p. 16 [\*I. cornelli; OD]. The characters cited as distinguishing this genus from Prismodictya, namely, the small size, comparatively weak, secondary reticulation (nevertheless, four orders of quadrule size are recognized), and nearly isotelous shape, are not considered here to be significant at the generic level; genus is, therefore, treated as a possible junior synonym of Prismodictya. Devonian (Frasnian): USA (New York).
- Norfordia RIGBY & HARRIS, 1979, p. 976 [\*N. gabrielsei; OD]. Small, conicocylindrical, thinwalled sponge with pointed base and root tuft, sponge widest at oscular end and with deep, simple spongocoel; skeletal net of irregular tracts and bundles of principally diactine spicules (rhabdodiactines or oxeas) arranged in vertical bundles cross connected by less distinct, horizontal bundles forming rectangular net in which quadrules twice as high as wide; oscular margin unornamented; entire surface blanketed by mainly vertically arranged diactines of thin (possibly dermal) layer. [The genus is placed here because of its rectangular net and thin walls of prominent tracts, even though hexactines have not been clearly identified in the only moderately well-preserved type specimen, where most spicules are broken. A possible placement as a demosponge resembling the heliospongiids is a less likely alternative.] Silurian (Llandovery)-Carboniferous (Serpukhovian): Canada (British Columbia), Llandovery-Wenlock; USA (Montana), Serpukhov--FIG. 244,2a-b. \*N. gabrielsei, unnamed Siian.lurian siliceous siltstone, Llandovery-Wenlock, near Ware, British Columbia, Canada; a, side view of small, flattened, cylindrical holotype with rectangularly arranged, skeletal net of ropy tracts; ×2; b, enlarged view of middle part of sponge showing vertical bundles of diactines cross connected by horizontal bundles, GSC 60644, ×3 (Rigby & Harris, 1979).
- Tiddalickia RIGBY & WEBBY, 1988, p. 77 [\*T. quadrata RIGBY & WEBBY, 1988, p. 78; OD]. Thin-walled skeleton of rectangularly arranged straps principally of monaxons or rhabdodiactines but with moderately large stauracts and rare hexactines at strap junctions; horizontal straps apparently distal; radial straps absent; dermal layer thin, of irregular hexactines; one order of reticulate straps developed, quadrules not subdivided into smaller units. [The genus is placed within the Prismodictyinae with some question because only a fragment is known, and the shape of the sponge or skeletal details of other parts are uncertain.] Upper Ordovician: Australia (New South Wales), Canada (Manitoba).—

Porifera–Hexactinellida

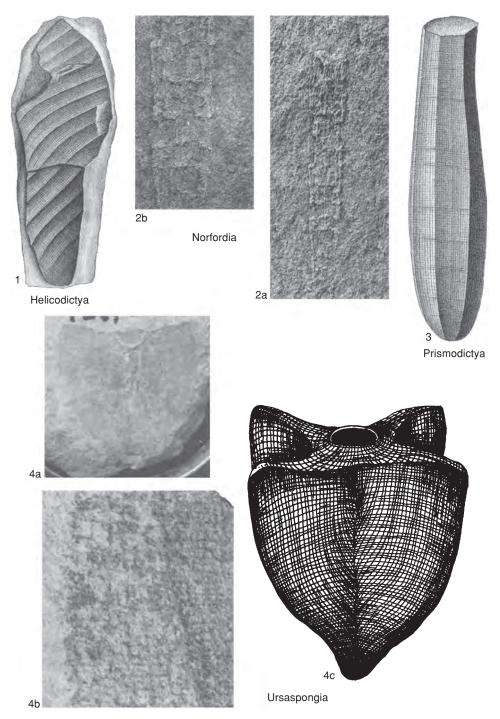


FIG. 244. Dictyospongiidae (p. 380-384).

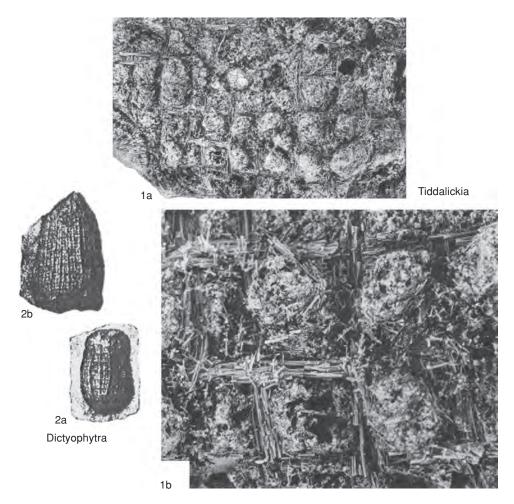


FIG. 245. Dictyospongiidae (p. 381-383).

FIG. 245, *1a–b.* \* *T. quadrata*, Malongulli Formation, Caradoc–Ashgill, Cliefden Caves area, New South Wales; *a*, most of holotype showing rectangularly arranged spicule straps and spiculiferous matrix into which straps are impressed, ×2; *b*, photomicrograph of skeletal net with straps composed of monaxons or rhabdodiactines but with large stauracts at strap junctions; dermal layer, if present, was probably composed of small, irregular hexactines like those in intervening quadrangles, AMu. F66895, ×8 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

Ursaspongia RIGBY, 1986c, p. 451 [\*U. tulipa; OD]. Small to medium size, thin walled, unbranched prismodictyids with upwardly expanding, indented, X-shaped cross section, with rounded base and circular, restricted osculum at top of simple, deep spongocoel; skeletal net of hexactines and hexactine-derived simple spicules, in narrow bundles or tracts arranged horizontally and vertically in rectangular pattern in side walls but radially and concentrically around oscular margin in sharply inwardly flexed top; horizontal tracts straight across in juvenile forms but upwardly arcuate in larger adult forms; irregularly preserved, secondary bundles subdividing primary quadrules into smaller rectangles; much of skeleton may be bundles of monaxons; dermal layer ill defined. Carboniferous (Serpukhovian): USA (Montana).——FIG. 244,4ac. \*U. tulipa, Heath Formation, Fergus County; a, side view of flattened holotype showing smooth walls and rounded base of sponge with regular, skeletal net, UMG 5718, ×1; b, photomicrograph of skeletal net with moderately well defined horizontal and vertical bundles of hexactine-based spicules of paratype, UMG 5720, ×10; c, generalized

restoration showing shape of sponge, rounded osculum and regular skeletal net, approximately ×2 (Rigby, 1986c).

# Subfamily HYDNOCERATINAE new subfamily

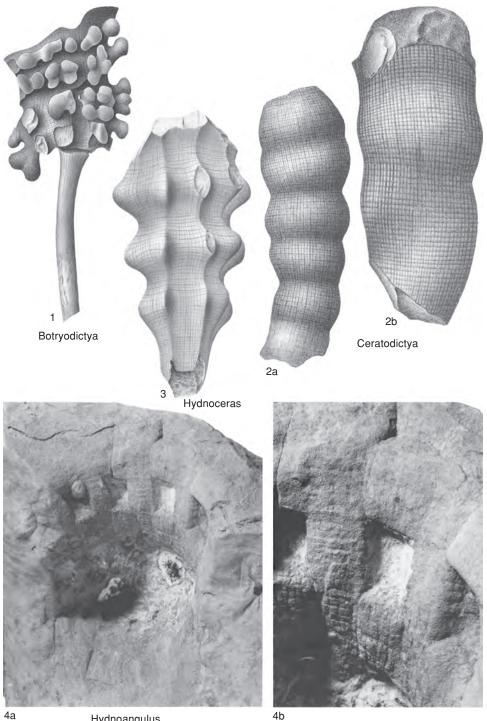
[Hydnoceratinae FINKS & RIGBY, herein] [type genus, *Hydnoceras* CONRAD, 1842, p. 267]

Conicocylindrical Dictyospongiidae with annular expansions that may bear quite large protuberances; if prism faces are present, the protuberances are at interfacial angles. [This group may have arisen from the Prismodictyinae by development of annular expansions and protuberances.] *Middle Cambrian–Carboniferous (Lower Mississippian).* 

- Hydnoceras CONRAD, 1842, p. 267 [\*H. tuberosum; M]. Sponge conicocylindrical with alternating, annular expansions and contractions; each expansion bearing a whorl of generally eight nodes, or four double nodes, of varying degrees of protrusion that range from simple, conical bumps to pendulous, saccular protuberances resembling those of Botryodictya; on forms with low nodes, a conspicuous vertical ridge, which probably corresponds to an internal spicule bundle, connects each vertical series of nodes and causes sponge to resemble a nodose Prismodictya; each node may bear a protruding tuft of spicules; nodes are subdued or missing near apex; skeletal net a quadrate mesh of five orders of size of squares, each smaller size being outlined by progressively smaller sizes of ridges, as in most dictyosponges; largest quadrule about a centimeter wide, each order about half as wide as next larger order; spicules not known, but on basis of other dictyosponges, it is likely that net consisted of parallel stauractines or pentactines, whose ray lengths equaled widths of quadrules, largest quadrule outlined by overlapping rays, the rest not, and with rhabdodiactine bundles underlying each sets of rays; occasional malformations of net show by curving bands that a linear series of spicules was fundamental unit of construction, rather like dictyonines. [Not only does Hydnoceras represent a middle ground between Prismodictya and Botryodictya (=Tylodictya), it could also be considered a nodose Ceratodictya (of which Rhabdosispongia may be an internal, poorly preserved mold) as well as a more regular Hydnocerina or Clepsydrospongia, although these genera differ from Hydnoceras in having a more uniform, fine quadrate mesh. Cleodictya, too, is like a Hydnoceras with one whorl of nodes.] Upper Devonian: USA (New York), France.-FIG. 246,3. \*H. tuberosum, Chemung Group, Senecan, reported to have come from near Cohocton, New York; side view of plaster cast of holotype, ×0.5 (Hall & Clarke, 1899).
- Botryodictya Hall & Clarke, 1899, p. 111 [\*Dictyophyton ramosum Lesquereux, 1884, p.

827; OD] [= Tylodictya HALL & CLARKE, 1899, p. 151 (type, T. warrenensis, OD)]. Sponge composed of smooth, cylindroid stalk surmounted by an abruptly wider cylindroid body whose wall bears horizontal and vertical rows of long, saccular, pendulose protuberances that may bifurcate or quadrifurcate; diaphragm may separate body from stalk; skeletal net fine meshed with small, parallel stauractines or pentactines, and with larger pentactines or horizontal and vertical, spicule bundles outlining slightly larger quadrules; vertical bundles have a radial arrangement on diaphragm; stalk has same kind of skeletal net as body. Devonian (Frasnian)-Carboniferous (Lower Mississippian): USA (Pennsylvania).---FIG. 246,1. \*B. ramosa (Lesquereux), Chemung Group, Upper Devonian, Lawrenceville; side view of nearly complete sponge with cylindrical, basal stalk and nodose, upper cup, NYSM, ×0.5 (Hall & Clarke, 1899).

- Ceratodictya Hall & Clarke, 1899, p. 117 [\*Dictyophyton annulatum HALL, 1863, p. 90; OD]. Sponge conicocylindrical and elongate, bearing transverse annular expansions and contractions; in some species alternate contractions are broader and deeper, causing expansions to be grouped in pairs; surface otherwise smooth and quadrate mesh uniformly fine; spicules not known. Devonian (Frasnian): USA (New York, Pennsylvania).—FIG. 246,2a-b. \*C. annulata (HALL), Senecan, Chemung Group; a, side view of holotype with regular annulations and reticulate skeleton, western New York state, locality lost; b, side view of larger specimen with less pronounced annulations, Upper Devonian, Naples, New York, NYSM, ×1 (Hall & Clarke, 1899).
- Cleodictya HALL, 1884, p. 467 [\*C. gloriosa HALL, 1884, p. 479; OD]. Cylindroid, expanding from possible flat base to an equatorial whorl of low, rounded nodes, thence generally contracting, but expanding again slightly to oscular rim; external, dermal armor of closely packed paraclavules (head ends outwardly) overlying a layer of small stauractines or pentactines that form primary, skeletal mesh; comitalia of fine, possible rhabdodiactines; beneath this outer layer is a layer of vertical bundles over a layer of similar, horizontal bundles of long, possible rhabdodiactines, each spicule paralleled by smaller comitalia of same form; bundles parallel each row of stauractines of outer mesh, but every few bundles are thicker with bigger spicules, and these outline larger quadrules of reticulum. [Spicular structure described herein is based on personal examination (RMF) of the holotype of C. mohri HALL & CLARKE, 1899. In addition to the spicules cited above, HALL and CLARKE (1899, p. 184 ff.) reported from the same species: smooth and spinose hexactines, tripinules, clemes, anadiaenes, various irregular spicules (see their p. 186, fig. 37,14-15), and possible exfoliated spicule rays (their p. 186, fig. 36,4 and 37,17.] Carboniferous (Lower Mississippian): USA (Indiana, Ohio).——FIG. 247a. C. claypolei HALL



Hydnoangulus

4b

FIG. 246. Dictyospongiidae (p. 384-389).

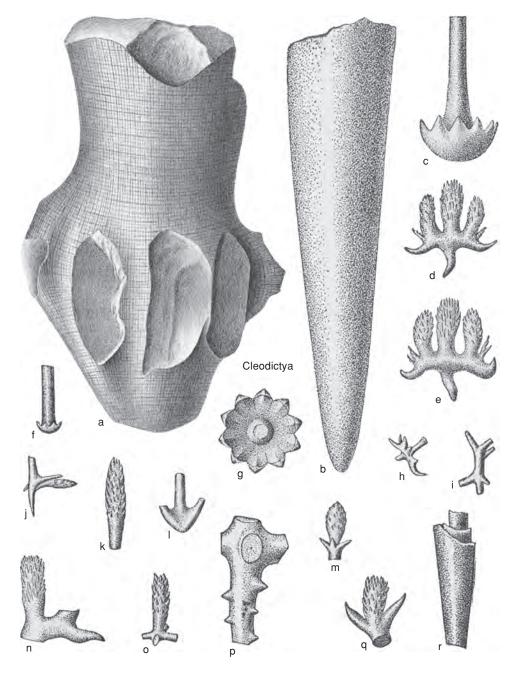


FIG. 247. Dictyospongiidae (p. 384-386).

& CLARKE, Waverly Group, Kinderhookian– Osagean, Akron, Ohio; side view of vase-shaped sponge with lower ring of prominent nodes and expanded oscular area, ×1 (Hall & Clarke, 1899).—FIG. 247*b*–*r*. isolated spicules of *C*. mohri Hall & Clarke,  $\times 400$  (Hall & Clarke, 1899).

?Clepsydrospongia HALL & CLARKE, 1899, p. 71 [\*C. matutina; OD]. Sponge cylindroid, contracted in middle; top and bottom not preserved; contracted

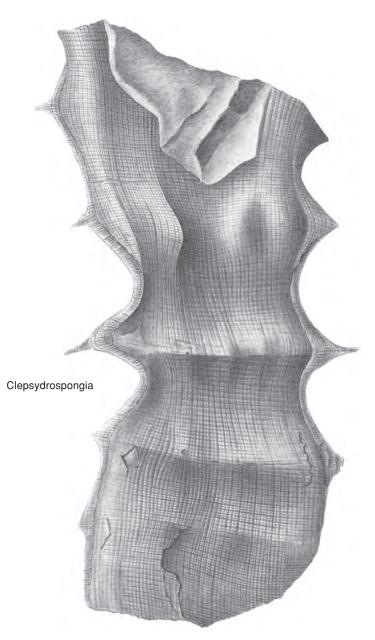


FIG. 248. Dictyospongiidae (p. 386-387).

portion bearing alternate, annular swellings and contractions, with swellings each bearing a single series of low, rounded nodes with a protruding, spicular tuft. Spicular net fine, uniform, quadrate mesh; spicules not known. [This may be an aberrant Hydnoceras or Hydnocerina.] Devonian (Frasnian): USA (New York).——FIG. 248. \*C. matutina, Senecan, Portage Group, Naples; side view of holotype with contracted, median, nodose area and with spicule tufts on nodes, ×1 (Hall & Clarke, 1899).

Hydnoangulus RIGBY & AUSICH, 1981, p. 377 [\*H. quadratus RIGBY & AUSICH, 1981, p. 378; OD]. Thin-walled, lotuslike to upwardly expanding and flaring funnel-shaped or goblet-shaped dictyosponge, with generally smoothly circular cross

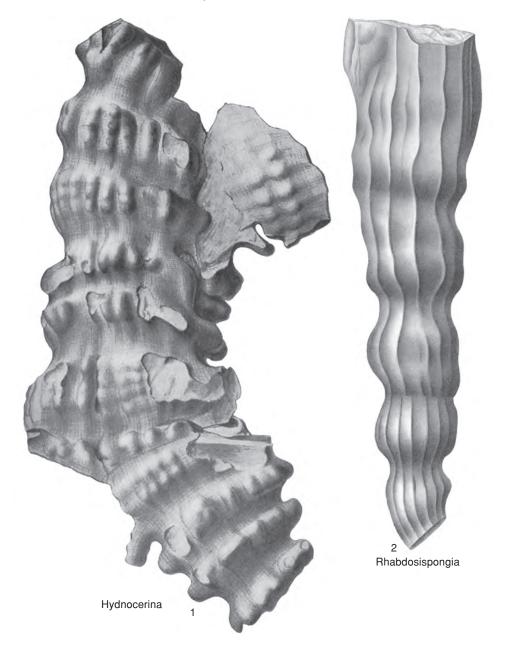


FIG. 249. Dictyospongiidae (p. 389-390).

section marked by sharply defined, rectangular, boxlike nodes, each of which terminates radially in a short, single ridge, like an elongate housetop; skeletal net of moderately uniformly arranged horizontal and vertical straps that outline quadrangles that may be subdivided into secondary and tertiary quadrules by smaller straps or single spicules; oscular margin and base unknown. *Carbon-iferous (Lower Mississippian):* USA (Indiana).— FIG. 246,4*a*–*b.* \**H. quadratus,* Edwardsville Formation, Lower Mississippian, Monroe Reservoir, Monroe County; *a*, partial mold with rectangular nodes, skeletal net as in other dictyosponges, ×0.5; *b*, interior of spongocoel with skeletal net

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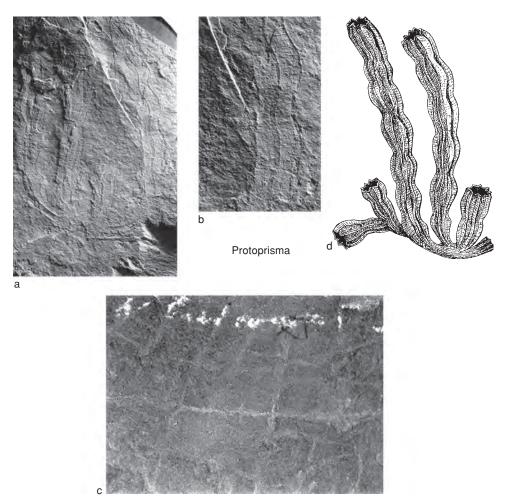


FIG. 250. Dictyospongiidae (p. 389-390).

emphasized by prismatic, outward bulges of nodes, IU 15107-47, ×1 (Rigby & Ausich, 1981).

Hydnocerina CLARKE, 1918, p. 182 [\*H. armstrongi; OD]. Sponge conicocylindrical, bearing more or less regularly spaced, horizontal rows of closely spaced protuberances; each protuberance is low, rounded, and usually elongate vertically, although often broken up vertically into two or three subprotuberances; all protuberances in a horizontal row have same number of sub-protuberances; spicule net a fine, uniform, quadrate mesh without conspicuous ridges or spicule bundles; spicules probably as in other dictyosponges, but not known. [Sponge resembles a Cleodictya with multiple whorls of nodes.] Devonian (Frasnian): USA (Pennsylvania, New York).-FIG. 249,1. \*H. armstrongi, Chemung Group, Senecan, Erie, Pennsylvania; side view of holotype with horizontal annulations capped by multiple series of nodes in upper part, ×1 (Clarke, 1918; courtesy of New York State Museum, Albany).

Protoprisma RIGBY & COLLINS, 2004, p. 81 [\*P. annulata; OD]. Handlike, upwardly digitate, branched sponges with annulate conicocylindrical stems marked by vertical, angular ridges that produce prismatic, polygonal, transverse sections; each annular ridge and trough with spicule strands cross connected by horizontal strands to produce reticulate, skeletal net; intervening walls with thatch of fine, vertical monaxons; hexactines with horizontal and vertical rays regularly oriented in horizontal and vertical strands. Middle Cambrian: Canada (British Columbia).---FIG. 250a-d. \*P. annulata, Stephen Shale, Raymond Quarry, Mount Stephen; a, flattened holotype with lowangle illumination from right to emphasize its branches, their sculpture, and common, curved base, ROM 43557, ×0.5; b, right branch of sponge, illuminated from right, with rectangular-appearing skeletal structure, annulations of branch, and prominent, vertical, angular ridges and troughs of skeleton,  $\times 1$ ; *c*, photomicrograph of sponge surface with rectangular skeletal grid of vertical and horizontal tracts, with moderately preserved hexactines in lower right,  $\times 1$ ; *d*, restoration of the species to show its general skeletal form and sculpture,  $\times 0.5$  (Rigby & Collins, 2004).

- Rhabdosispongia HALL & CLARKE, 1899, p. 116 [\*Dictyophyton amalthea HALL, 1890b, p. 58; OD]. Sponge conicocylindrical with annular contractions alternating with somewhat broader expansions; surface with more or less continuous vertical ridges that are more numerous than the eight seen in Prismodictya, although apical portion in French species commences with eight; these ridges may represent vertical bundles of rhabdodiactines, but no spicules nor any other traces of skeletal net are known in type species; in French species a fine quadrate mesh is present. [Vertical ridges separate this genus from Calathospongia and from the more sharply annulate Ceratodictya, the absence of nodes separates it from Hydnoceras.] Devonian (Frasnian): USA (Pennsylvania), France.—FIG. 249,2. \*R. amalthea (HALL), Senecan, Chemung Group, Susquehanna County, Pennsylvania; side view of tall sponge with broad annulations and sharp, vertical ridges, ×0.5 (Hall & Clarke, 1899).
- ?Tylodictya HALL & CLARKE, 1899, p. 151 [\*T. warrenensis; OD]. The type specimen (HALL & CLARKE, 1899, p. 152, fig. 19–20), which is incomplete, resembles part of the upper portion of a Botryodictya. It is here considered a junior synonym of Botryodictya. Carboniferous (Lower Mississippian): USA (Pennsylvania).

#### Subfamily CALATHOSPONGIINAE Hall & Clarke, 1899

[Calathospongiinae HALL & CLARKE, 1899, p. 53]

Smooth, cylindroid Dictyospongiidae, more or less hourglass shaped, sometimes vertically fluted. [This group may have arisen from the Hydnoceratinae by subduing annulations and protuberances.] Upper Devonian-Carboniferous (Serpukhovian). areas with intervening contractions; surface otherwise smooth and unornamented; quadrate mesh rather uniform with relatively subdued differentiation of quadrule sizes, horizontal bands said to be characteristically more prominent than vertical ones; spicules not known. [DE LAUBENFELS (1955) assigned *Calathospongia* to *Ectenodictya*, but that genus is known from fragments only and is considered unrecognizable.] *Carboniferous (Lower Mississippian):* USA (Ohio, Pennsylvania, Indiana).— FIG. 251. \**C. redfieldi* (HALL), Waverly Group, Akron, Ohio; side view of large, annulate sponge with nearly complete, oscular margin at top with faint, prismatic faces, ×0.9 (Hall & Clarke, 1899).

- Corticospongia CASTER, 1939, p. 14 [\*C. bradfordensis; OD]. Sponge subquadrately cylindroid, being broadly fluted vertically into four lobes; thin walled; lower part unknown; surface covered by horizontal, lenticular swellings resembling lenticels of tree bark, and produced by local crowding of swollen, horizontal rays of surface hexactines that have a knoblike distal ray and horizontal pair of tangential rays more strongly developed than vertical pair; hexactines and possibly pentactines of several orders of size, occasionally not in parallel orientation; discontinuous, vertical bundles of fine, spicule rays locally visible. Upper Devonian (Famennian): USA (Pennsylvania).-FIG. 252, 1a-d. \*C. bradfordensis, Chautauquan, Lewis Run Sandstone Member, Venango Stage, Chautauqua Series, Lewis Run; a, side view of holotype showing part of lobate aperture and barklike exterior, ×1; b, enlargement of part of exterior showing lenticular bundles of spicules and finer, horizontal elements, ×3; c, drawing of holotype fragment showing generalized, reticulate, skeletal structure and general form of genus, approximately ×0.5; d, generalized diagram of spicule relationships adjacent to one of lenticular bundles, approximately ×5 (Caster, 1939).
- Cryptodictya HALL, 1890b, p. 60 [\**C. alleni;* OD]. Flattened, irregular objects (possible concretions) with irregularly distributed bumps; surface smooth, showing no trace of spicules except for supposed spicular impressions in matrix on bedding planes adjacent to bumps. *Upper Devonian:* USA (New York).—FIG. 252,2. \**C. alleni,* Chemung Sandstone, Senecan, Alfred; side view of holotype with irregular, nodose sculpture, UCC 13153A, ×0.5 (Hall & Clarke, 1899).
- ?Ectenodictya HALL, 1884, p. 466 [\*E. implexa HALL, 1884, p. 475; SD HALL & CLARKE, 1899, p. 164]. This genus is unrecognizable, having been based on fragmental material, as HALL and CLARKE (1899, p. 164–165) stated. They suggested that the type species represents fragments of the type species of *Calathospongia*. This is by no means certain, and to make such a synonymy would have the unfortunate, undesirable, and unnecessary effect of making the better-founded genus, *Calathospongia*, a junior synonym of *Ectenodictya*.

Calathospongia HALL & CLARKE, 1899, p. 155 [\*Dictyophyton redfieldi HALL, 1863, p. 88; OD]. Sponge cylindroid with a few broad contractions and expansions; most specimens illustrated by HALL and CLARKE (1899) are shaped somewhat like an hourglass, but they seem incomplete both at top and bottom. Holotype of type species (*ibid.*, pl. 49,2-4) with globose upper end, surmounting more slender, downwardly expanding portion; another specimen (*ibid.*, pl. 48) with three expanded



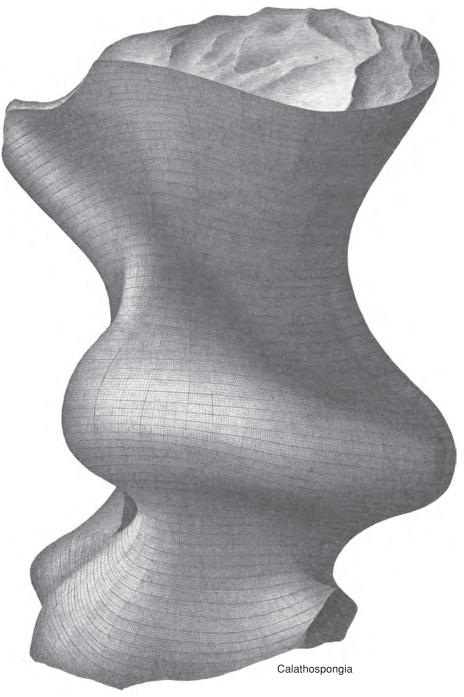


FIG. 251. Dictyospongiidae (p. 390).

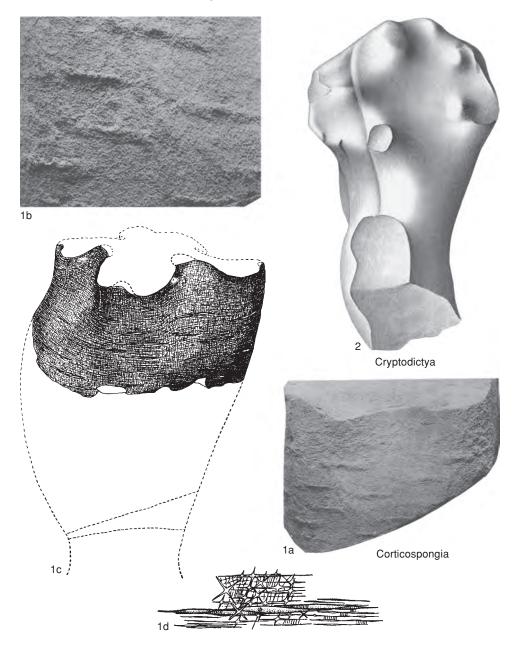


FIG. 252. Dictyospongiidae (p. 390).

Carboniferous (Lower Mississippian): USA (Penn-sylvania, Ohio).

Griphodictya HALL & CLARKE, 1899, p. 179 [\*G. epiphanes HALL & CLARKE, 1899, p. 180; OD]. Sponge cylindroid but contracted in middle, smooth surfaced; lateral surfaces have a continuous layer of closely spaced, possible rhabdodiactines perpendicular to surface; these seem continuous with a solid mass of similar spicules that occupy interior of sponge, and whose orientations follow paths that sweep inwardly and upwardly in upper half of sponge, but inwardly and downwardly in lower half of sponge so that spicules are vertical in axial part of sponge; obscurely defined bundles of similar spicules, perhaps including hexactines, pentactines, or stauractines, locally

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outlining a quadrate mesh of dimensions in other dictyosponges but here composed of bundles rather than a layer of single spicules; in addition, a few larger vertical bundles of stouter spicules (possible rhabdodiactines) seem to extend much of length of sponge. [In addition to above spicules, reported by HALL and CLARKE (1899, p. 180-181, fig. 33), personal examination of holotype and sole specimen (RMF), showed presence of hexasters with three-pronged and four-pronged branches on some rays, paraclavules with seven and eight teeth, and spicule rays with spinose tips.] Carboniferous (Lower Mississippian): USA (Indiana).-FIG. 253,2a-l. \*G. epiphanes, Keokuk Group, Crawfordsville; a, side view of small sponge from which spicules shown in views b-l were taken,  $\times 1$ ; b-l, spicules of genus, UCC 13186, ×200 (Hall & Clarke, 1899).

- Hallodictya HALL & CLARKE, 1899, p. 140 [\**H. sciensis;* OD]. Genus based on an incomplete specimen with broadly undulating surface on which are local, elongate, subparallel depressions of irregular distribution; surface said to bear impression of fine, quadrate mesh of two orders of size. *Upper Devonian:* USA (New York).——FIG. 254. \**H. sciensis,* Chemung Group, Scio; holotype impression of interior of large sponge with irregular growth and node development but regular, reticulate, skeletal grid, ×1 (Hall & Clarke, 1899).
- Hydriodictya HALL & CLARKE, 1899, p. 77 [\*Dictyophyton patulum HALL, 1884, p. 469; OD]. Type species known from a single specimen without top or bottom; broadly flaring cone; spicular net, as described, consisting of vertical and horizontal spicules (possible rhabdodiactine) bundles of equal size, forming broad, quadrate mesh that is subdivided by smaller, vertical and horizontal bundles to form finer quadrules; surface of sponge smooth. Devonian (Frasnian)-Carboniferous (Mississippian): USA (New York), Frasnian; USA (Indiana), Mississippian.-FIG. 255,2. \*H. patulum (HALL), Chemung Group, Senecan, Cohocton, New York; side view of holotype showing flaring form and quadruled, reticulate skeleton, ×1 (Hall & Clarke, 1899).
- Lyrodictya HALL, 1884, p. 466 [\*L. romingeri HALL, 1884, p. 476; OD]. Sponge as illustrated by HALL and CLARKE (1899) broadly conical, base and top unknown; prominent, relatively thick, vertical bundles of possible rhabdodiactines with slightly plumose structure, rather widely spaced, and new ones intercalated in upper (wider) part of sponge; corresponding horizontal bundles not known but traces of finer quadrules present between bundles; large clemes present in these bundles have their barbs pointing downwardly rather than upwardly; other spicules reported include pentactines, larger with coarse spines and curved rays, and paraclavules. Carboniferous (Lower Mississippian): USA (Indiana, ?Iowa).—FIG. 255,1. \*L. romingeri, Keokuk Group, Crawfordsville, Indiana; side view of broadly obconical holotype with prominent, vertical bundles or tracts in reticulate skeleton, ×1 (Hall & Clarke, 1899).

Phragmodictya HALL, 1884, p. 466 [\*Dictyophyton catilliforme WHITFIELD, 1881, p. 18; SD MILLER, 1889, p. 163]. Cylindroid, expanded at base and top; broadly conical basal disk; downwardly directed, basal frill (periloph) at junction of basal disk and sides; rounded vertical ridges on sides, often discontinuous, continue onto basal frill; fine reticulum on smooth, basal disk radial and concentric; fine reticulum on sides outlined by pentactines with comitalia of possible rhabdodiactines; other spicules present include tauactines, psi-shaped stauractines, tylote stauractines, curved, stout strongyles, and spinose fragments, some of which may be parts of pinules. [It is possible that the basal disk and frill were an oscular sieve, as in the living Euplectella, and that the sponge has been restored upside down. Phragmodictya resembles Thysanodictya but without the coarse reticulation, among other things.] Carboniferous (Lower Mississippian, Serpukhovian): USA (Indiana, Alabama).——FIG. 253,1a-c. \*P. catilliforme (WHITFIELD), Keokuk Group, Osagean, Crawfordsville, Indiana; a, small, nearly complete individual with characteristic form and sculpture in reticulate skeleton; b, side view of somewhat fan-shaped, thin specimen with nearly complete, basal disc; c, side view of same specimen showing structure of basal disc, ×0.9 (Hall & Clarke, 1899).

# Subfamily PHYSOSPONGIINAE Hall & Clarke, 1899

[Physospongiinae HALL & CLARKE, 1899, p. 53]

Dictyospongiidae with strongly developed, vertical and horizontal spicule bundles, with bullate protuberances between them. [This group may have arisen from the Prismodictyinae or from early members of the Hydnoceratinae.] *Middle Devonian–Carboniferous (Lower Mississippian).* 

Physospongia HALL, 1884, p. 467 [\*Uphantaenia dawsoni WHITFIELD, 1881, p. 16; SD MILLER, 1889, p. 163]. Sponge conicocylindrical; surface divided into checkerboard of small rectangles usually (but not always) wider than high that are outlined by interpenetrating, horizontal and vertical bundles of possible rhabdodiactines of several sizes; every second vertical bundle twice as wide as others; vertical bundles, in part, external to horizontal ones; each rectangle occupied by either a saccular protuberance (bulla) or a depression, which alternate in quincuncial pattern (local asymmetries may occur); paraclavules present normal to surface with head ends oriented outwardly; they appear to lie, in part, below outermost layer of spicules and are interspersed among spicules of bundles; small rhabdodiactines tangential to surface forming a radial pattern about center of each bulla; principal skeletal net of both bullae and depressions

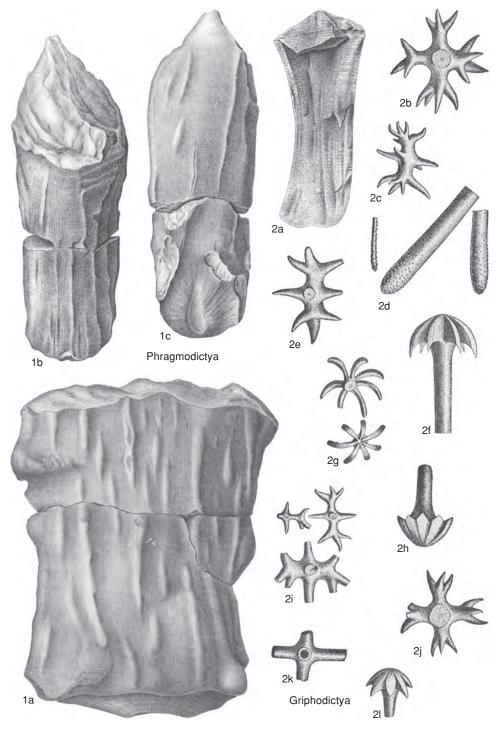


FIG. 253. Dictyospongiidae (p. 392-393).

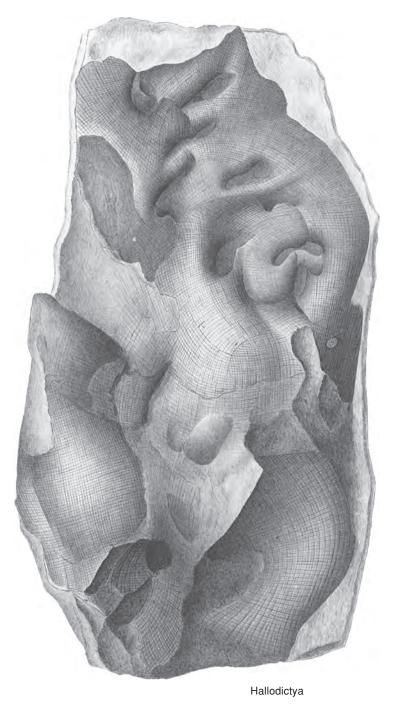


FIG. 254. Dictyospongiidae (p. 393).

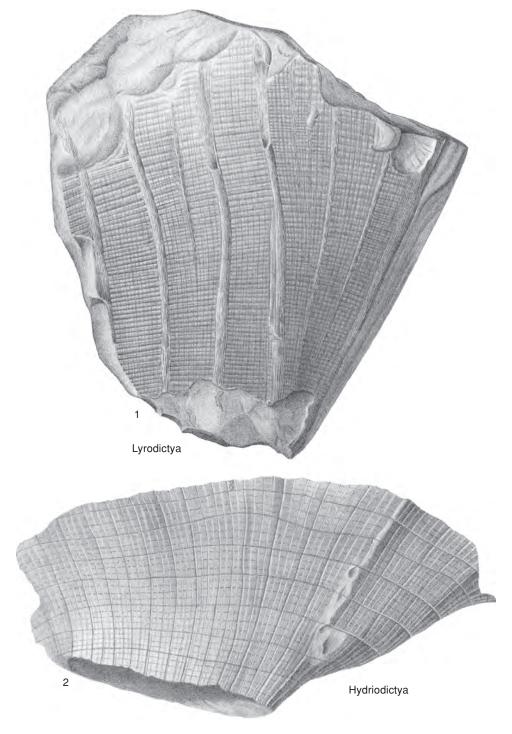


FIG. 255. Dictyospongiidae (p. 393).

Reticulosa

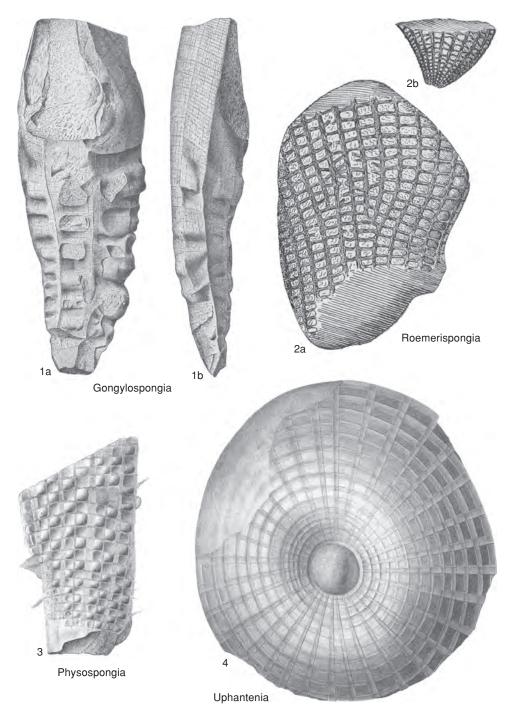


FIG. 256. Dictyospongiidae (p. 393–398).

consisting of fine, quadrate mesh of parallel, uniformly small stauractines (or possible pentactines); anadiaenes and clemes occurring in vertical bundles (pointed ends up), appearing to be concentrated on exterior side of bundle; lateral projections, much longer than bullae, frequently seen in profile opposite horizontal bundles, and unclear whether they are tufts of lateralia or some other structure. Spinose spicule rays and strongyles have been reported from some specimens. *Carboniferous (Lower Mississippian)*: USA (Indiana).— FiG. 256,3. \**P. dawsoni* (WHITFIELD), Keokuk Group, Crawfordsville; side view of small, obconical sponge with typical node and skeletal strap development, UCC 13176B, ×1 (Hall & Clarke, 1899).

- Gongylospongia HALL & CLARKE, 1899, p. 92 [\*G. marshi; OD]. Sponge conicocylindrical and distinctly prismatic; on each prism face is a single, vertical row of low, rounded protuberances alternating with low, rounded depressions, most strongly developed in middle part of sponge; protuberances and depressions wider than high and at approximately same level in adjacent rows; skeletal net a quadrate mesh with at least two orders of size of quadrules; spicules not known, but probably as in other dictyospongiids, with vertical, spicule bundles underlying prism angles. [The prismatic shape and simple, horizontally elongate protuberances distinguish this genus from Hydnocerina, and the nonquincuncial arrangement of protuberances (among other things) differentiate this genus from Physospongia.] Devonian (Frasnian): USA (New York).—FIG. 256, 1a-b. \*G. marshi, Senecan, Chemung Group, Wellsville; a, side view of holotype with characteristic alternation of nodes and depressions on prism faces; b, lateral view of same sponge, ×0.5 (Hall & Clarke, 1899).
- Roemerispongia Hall & CLARKE, 1899, p. 67 [\*Dictyophyton gerolsteinensis C. F. ROEMER, 1883, p. 707; OD]. Steeply obconical to subcylindrical sponge with pointed base; skeleton of relatively robust, subequal, vertical bundles of spicules, crossed by narrower, horizontal, spicule bands in moderately regular, rectangular pattern, to define quadrules that bulge outwardly with convex surfaces such as in Physospongia, but without welldefined, subordinate, spicule bands. Middle Devonian: Germany.-FIG. 256,2a-b. \*R. gerolsteinensis (ROEMER), Gerolstein, Eifel; a, side view of steeply obconical upper part with prominent, rectangularly arranged, skeletal bands, but convex bulges of quadrules not well shown; b, pointed base with convergent, vertical, spicule bands and somewhat more irregular, horizontal tracts, ×1 (Hall & Clarke, 1899).
- Uphantenia VANUXEM, 1842, p. 183 [\*U. chemungensis; M] [=Hyphantaenia HALL & CLARKE, 1899, p. 137, nom. van.]. Sponge large and discoid, similar to a bowl with central, uplifted area in base; concentric (horizontal) and ra-

dial (vertical) spicule bundles outlining rectangular interspaces that form alternately wide and narrow, radial rows; in each wide, radial row, every second interspace occupied by what appears to have been either horizontally elongate, protuberant bulla, or elliptical parietal gap; spicules not preserved but possibly skeletal net was similar to that of *Physospongia*. [This sponge is a bit like a flat, circular *Gongylospongia*.] *Devonian (Frasnian):* USA (New York).——FiG. 256,4. \*U. chemungensis, Senecan, Chemung Group, Tioga County; discoidal sponge with characteristic concentric and radial skeletal bundles around interspaces, ×0.5 (Hall & Clarke, 1899).

### Subfamily THYSANODICTYINAE Hall & Clarke, 1899

#### [Thysanodictyinae HALL & CLARKE, 1899, p. 52]

Dictyospongiidae with coarse, ridgelike, quadrate mesh that may represent radially erect lamellae, spicule bundles, coarse pentactines, or a combination thereof. [This group may have arisen from the Physospongiinae.] Upper Devonian (Frasnian)– Carboniferous (Serpukhovian).

- Thysanodictya Hall & Clarke, 1899, p. 125 [\*?Dictyophyton (Phragmodictya) halli HALL, 1890b, p. 59; OD; = Thysanodictya edwinhalli HALL & CLARKE, 1899, p. 126, nom. van.]. Gross morphology resembles that of Phragmodictya but with coarse ridges, interpreted by HALL and CLARKE as erect lamellae as in Clathrospongia, outlining larger quadrules; reticulum of basal disk is quadrate rather than radial and concentric, although in type species it appears radial (HALL & CLARKE, 1899, pl. 24,2), also vertical fluting, or low, rounded ridges, seen in Phragmodictya, are absent; spicules unknown. [It is possible that the basal disk is an oscular sieve and the sponge is restored upside down. This is especially likely for T. hermenia (HALL & CLARKE, 1899, pl. 40) and T. scyphina (ibid., pl. 42,8), in which the supposed upper end is contracted to an apex. The former species is the only one in which the quadrate mesh of the basal disk is shown. This genus differs from Clathrospongia HALL, 1884, in the presence of the flat base and frill.] Devonian (Frasnian)-Carboniferous (Lower Mississippian): USA (New York, Pennsylvania, Alabama).---FIG. 257,2a-b. \*T. halli (HALL), Chemung Group, Senecan, Wellsville, New York; a, side view of nearly complete, steeply obconical sponge with coarse, reticulate skeleton, ×1; b, side view of lower part of subcylindrical sponge with broad, flaring frill at margin of basal disk, ×1 (Hall & Clarke, 1899).
- Acloeodictya HALL & CLARKE, 1899, p. 177 [\*A. marsipus HALL & CLARKE, 1899, p. 178; OD]. Sponge cylindroid, widest just above base, which

Reticulosa

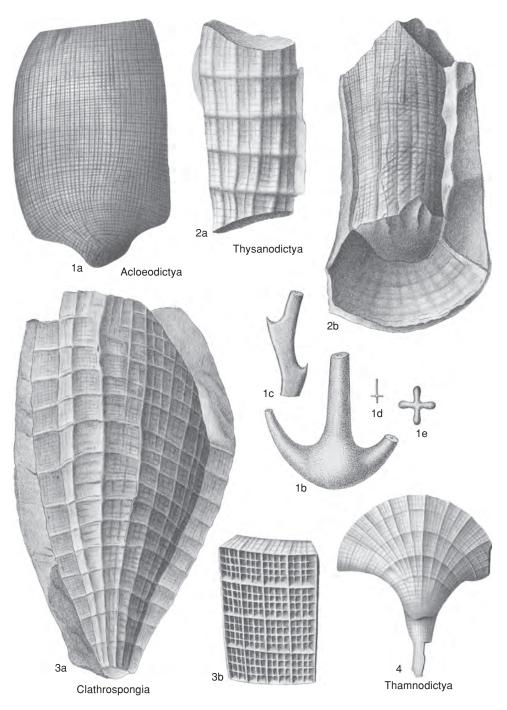


FIG. 257. Dictyospongiidae (p. 398-403).

is broadly conical and ends in pointed apex; quadrate mesh composed of large quadrules subdivided by finer ones; continuations of vertical elements converging to apex on base; if the only syntype that preserves the spicules (HALL & CLARKE, 1899, pl. 55,4, UC 131858) is truly conspecific with those that show external form, then large quadrules are outlined by large stauractines or pentactines, in quadrate arrangement with partly overlapping rays. These spicules accompanied by underlying vertical and horizontal bundles of comitalia that may be rhabdodiactines. HALL and CLARKE (1899, p. 178) mentioned the presence of large anadiaenes, in addition to large pentactines with curved rays. They interpreted the anadiaenes as basalia. Clemes and small, blunt-rayed pentactines or stauractines also occur; finer quadrules on this specimen appear to be composed of thinner bundles of rhabdodiactines. [HALL and CLARKE (1899, p. 178 and pl. 55,4) stated that the vertical and horizontal spicule bundles "were produced into erect reticulating lamellae" as in Clathrospongia (ibid., p. 177). It is not clear from personal examination of the syntype that the structure referred to in the figure caption was an erect or vertical lamella, or that it contained regular, fine quadrules. If it were such, then Acloeodictya would differ from Clathrospongia only in its more abruptly conical base and in the presence of large pentactines.] Carboniferous (Lower Mississippian): USA (Indiana).——FIG. 257, 1a-e. \*A. marsipus, Keokuk Group, Indian Creek; a, side view of nearly complete, robust, subcylindrical sponge,  $\times 0.5$ ; *b-e*, spicules from genus,  $\times 200$  (Hall & Clarke, 1899).

- ?Arystidictya HALL & CLARKE, 1899, p. 136 [\*A. elegans; OD] [=Arystidictyon HALL & CLARKE, 1899, p. 13, per DE LAUBENFELS, 1955, p. 72, nom. null.]. Sponge funnel shaped, flaring upwardly from flat base; broad, quadrate reticulum of vertical and horizontal spicule bundles is all that is preserved; it is probable that finer, quadrate mesh external to it has been lost. [Were such a fine mesh present, all that would distinguish this genus from Thamnodictya would be its flat base; it is possible that Arystidictya is merely a poorly preserved Thamnodictya.] Devonian (Frasnian): USA (New York).-FIG. 258,2. \*A. elegans, Senecan, Lower Chemung Group, Avoca; side view of flaring sponge with reticulate skeleton in base and radiating channels in oscular margin, ×0.5 (Hall & Clarke, 1899).
- Clathrospongia HALL, 1884, p. 121 (as subgenus) [\*Dictyophyton (Clathrospongia) abacus HALL, 1884, p. 474; OD]. Sponge narrowly conical with acute apex; as HALL (1884) and HALL and CLARKE (1899) interpreted structure, largest quadrules (about a centimeter wide as in many other dictyosponges) outlined by lamellae several millimeters high and oriented perpendicular to sponge surface; each lamella bearing secondary and tertiary quadrules, as does sponge wall between them; HALL and CLARKE further infer (1899, p. 153, and

pl. 49,6) that smaller quadrules also produced perpendicular lamellae to form a three-dimensional, open boxwork; presumably each lamella was ultimately built of a layer, or layers, of fine pentactines or stauractines; spicules are unknown. [There is some question about whether the primary lamellae existed; they are preserved in concrete form only at the sides of some specimens, where they are distinguished from the rest of the skeletal net only by the fact that they lie flat on the bedding surface rather than arching over the sediment, filling the sponge. It is possible that they are collapsed parts of the sponge. Elsewhere they are present only as low ridges outlining the quadrules, which could be produced by interior, spicule bundles; evidence for the finer boxwork is even less compelling, for it rests on the low ridges that outline the finer quadrules and their prolongation onto the primary lamellae; this genus differs from Thysanodictya in lacking a flat base and basal frill.] Devonian (Frasnian)-Carboniferous (Serpukhovian): USA (New York, Pennsylvania, Ohio, Alabama).-FIG. 257, 3a-b. \*C. abacus (HALL), Waverly Group, Kinderhookian-Osagean, Warren, Pennsylvania; a, side view of obconical type with what are interpreted to be erect horizontal and vertical lamellae in three-dimensional skeleton, ×1; *b*, interpretation of structure in deep skeleton, ×1 (Hall & Clarke, 1899).

Lebedictya HALL & CLARKE, 1899, p. 169 [\*L. crinita HALL & CLARKE, 1899, p. 170; OD]. Sponge broadly conical but not flaring; base unknown; larger quadrules outlined by what are said to be "erect spicular bands" (HALL & CLARKE, 1899, p. 169) but these could not be seen on the syntype studied (U.C. 13184; HALL & CLARKE, 1899, pl. 61,5), rather quadrate mesh formed from parallel pentactines or stauractines of at least three orders of size, largest seeming mostly to be in quadrate, not quincuncial, arrangement with overlapping rays; resulting quadrules are subdivided by next smaller spicules and those by next; comitalia (possible rhabdodiactines) forming vertical and horizontal bundles under rays of pentactines; long, longitudinal, spicule ray, much larger than largest pentactines, also present; fringe of parallel, vertical, spicule rays (possible rhabdodiactines) crowning upper rim; fringe on possible gastral surface and may have been covered by a fine, quadrate mesh of small pentactines or stauractines on specimen studied; other spicules reported by HALL and CLARKE include paraclavules, tripinules, spinose pentactines, and strongyles. [The shape of this sponge is not as flaring as that of Thamnodictya or Arystidictya.] Carboniferous (Lower Mississippian): USA (Indiana).-FIG. 258, 1a-m. \*L. crinita, Keokuk Group, Crawfordsville; a, side view of broadly obconical holotype with pronounced fringe of prostalia around oscular margin, bundle of vertical spicules in interior, on right, and traces of spicule bundles that form coarse quadrules on exterior,  $\times 0.5$ ; *b*-*m*, spicules from type species, ×400 (Hall & Clarke, 1899).

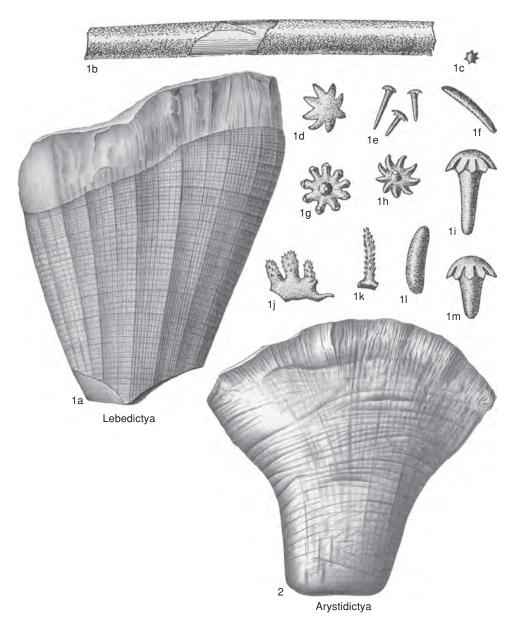


FIG. 258. Dictyospongiidae (p. 400).

Mattaspongia RIGBY, 1970a, p. 8 [\**M. apaches* RIGBY, 1970a, p. 9; OD]. Sponge broadly conical and rapidly expanding, although less so in upper part; thin walled, composed of simple, moderately large, parallel hexactines coated by smaller, rhabdodiactine comitalia that cause quadrule spaces to have circular outline (parietal gaps of original description); large, single, widely spaced, rhabdodiactine prostalia projecting outwardly and upwardly at an acute angle; at least two nested orders of size of hexactines seem to be present, larger perhaps in quadrate, nonquincuncial arrangement with overlapping rays; as sponge expands upwardly, new vertical rows of hexactines intercalated. [Genus is similar to *Lebedictya* and *Acloeodictya*.] *Devonian (Frasnian):* Canada (Alberta).—FIG. 259*a-b. \*M. apaches,* Mount Hawk Formation, Front Range; *a*, holotype

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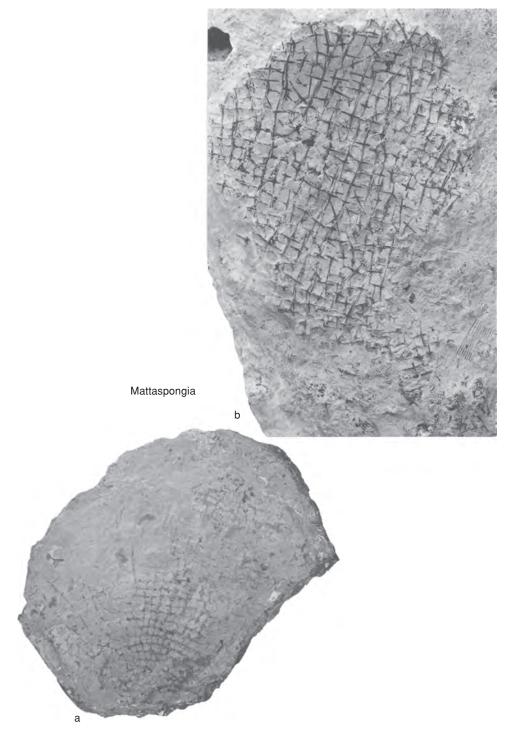


FIG. 259. Dictyospongiidae (p. 401–403).



Mattaspongia

FIG. 260. Dictyospongiidae (p. 401-403).

showing thin-walled fragment with regular, reticulate, hexactine-based skeleton perforated by matrix-filled, parietal gaps, GSC 24500,  $\times 0.5$ ; *b*, paratype, skeletal fragment, GSC 24800,  $\times 2$ (Rigby, 1970a).——FIG. 260. \**M. apaches*, Mount Hawk Formation, Front Range; paratype with hexactines arranged into rough, vertical rows and less continuous horizontal rows in reticulate skeleton, irregular orientation of some spicules apparently normal, their rays interleaving with adjacent spicules,  $\times 4$  (Rigby, 1970a).

Thamnodictya HALL, 1884, p. 466 [\*Dictyophyton newberryi HALL, 1863, p. 87; OD]. Sponge funnel shaped, flaring upwardly from a narrow, tubular, stalklike base; conspicuous vertical and horizontal, spicule bundles outline larger quadrules, which are not rectangular because of upward flaring, within which is a finer quadrate mesh. [This genus is similar to Arystidictya in form.] Carboniferous (Lower Mississippian, ?Serpukhovian): USA (Ohio, ?Alabama, New York).—FIG. 257,4. \*T. newberryi (HALL), Waverly Group, Kinderhookian– Osagean, Cuyahoga Falls, New York; side view of funnel- or frondlike sponge with narrow base and expanding, quadruled skeleton, ×0.5 (Hall & Clarke, 1899).

#### Family DOCODERMATIDAE Finks, 1960

[Docodermatidae FINKS, 1960, p. 118]

Dictyospongioidea with coarse hypodermalia of several sizes, often tuberculate and often with supernumerary, paratangential rays; root tuft usually present; asymmetrical tauactines typically present as comitalia or as constituents of rather coarse, internal, spicule bundles. *Silurian (Ludlow)–Permian* (*Roadian, ?Wordian–?Capitanian*).

**Docoderma** FINKS, 1960, p. 120 [\**D. rigidum* FINKS, 1960, p. 121; OD]. Large, vasiform, thick-walled sponge with root tuft; primary, paratangential rays of hypodermalia strongly reflexed and distally papillose; in type species, additional, nonreflexed, paratangential rays arising from crossing and fusing to form beamlike structures with digitate ends in adult sponge that interlock so that hypodermalia form a rigid net; in D. papillosum additional paratangential rays occur only in special smaller hypodermalia, and beamlike structures are not developed; in both species an autodermal mesh of fine, parallel hexactines or stauractines forming continuous cover over hypodermalia and, in adult sponges, fusing with these and with each other; hypogastralia with similarly papillose, paratangential rays but more slender and without supernumerary rays; parenchymalia include hexactines (those near dermal surface often papillose and with extra rays), tauactines, and rhabdodiactines; parenchymalia, hypodermalia, and hypogastralia in nonparallel orientation; root tuft of rhabdodiactines and clemes; very small, short, curved rhabdodiactines, some blunt ended like strongyles, as well as tauactines (in D. papillosum), coating all larger spicules as comitalia; large aporhyses covered distally by hypodermalia and autodermalia. Carboniferous (Middle Pennsylvanian)-Permian (Roadian, ?Wordian-?Capitanian): USA (Texas, ?New Mexico), Mexico (?Sonora).-FIG. 261a-d. \*D. rigidum, Word Limestone, Leonardian, Glass Mountains, Texas; a, basal end of holotype showing solid, dermal layer of skeleton and root tuft,  $\times 0.5$ ; b, enlarged view of main dermal skeleton in which each star-shaped configuration is formed by fused, outer, supernumerary rays of single spicules, with spherical nodes on beam edges; larger openings are noncircular, parietal gaps, ×5; c, enlarged view of inner surface of dermal layer with reflexed, tangential rays of dermal spicules, which are most of larger rays, and several smaller hexactines of interior of wall, which is interrupted by circular, parietal gaps, USNM 127659, ×5; d, sketch of mature, dermal spicule with beamlike, supernumerary rays above principal rays of spicule, not to scale (Finks, 1960; courtesy of The American Museum of Natural History).

Acanthocoryna FINKS, 1960, p. 128 [\*A. stauroma FINKS, 1960, p. 129; OD]. Sponge thick walled and probably vasiform but known only from fragment; possible hypodermalia hexactines with long, stout, fusiform, proximal ray, slender, paratangential rays and distal ray replaced by a cluster of oblique, branching, conical spikes; possible hypogastralia somewhat smaller pentactines with long, stout, fusiform, proximal ray bearing a ring of six to eight conical spikes just below crossing; above ring ray becomes slender; paratangential rays of hypogastralia short and slender with protuberance on distal surface of each near crossing; paratangential rays of both hypodermalia and hypogastralia are in parallel orientation and in quadrate arrangement; principal parenchymalia are several layers of simple hexactines in subparallel orientation, with pentactines and stauractines nearest dermal and gastral surfaces; accompanying hexactines are bundles of fusiform rhabdodiactines parallel to sponge surface but intersecting at irregular angles and partly outlining skeletal canals and pores; small, subcircular openings of possible epirhyses and aporhyses with openings on presumed dermal surface larger than those on presumed gastral surface, suggesting that original designation of surfaces should perhaps be reversed (which was based on spicule size and supernumerous rays). Permian (Roadian): USA -FIG. 262, 1a-b. \*A. stauroma, Word (Texas).-Limestone, Leonardian, Glass Mountains; a, photomicrograph of holotype fragment showing top of dermal surface with dermalia that have varying development of distal rosettes; spicule at bottom has rosette rays bisecting angles between main rays; b, photomicrograph of gastral spicule associated with smaller hexactines, USNM 127663, ×15 (Finks, 1960; courtesy of The American Museum of Natural History).

- Carphites FINKS, 1960, p. 125 [\*C. plectus; OD]. Thick-walled, probably vasiform sponge, with root tuft but known only from fragments; hypodermalia very large, thick-rayed hexactines with distal ray variably shortened (or, rarely, replaced by cluster of spherical knobs); hypodermalia in subparallel, quincuncial arrangement with rays overlapping and crossing at half length; a much finer, possibly autodermal, quadrate mesh of bundles of small tauactines lies external to hypodermalia; similar tauactines, along with small, short, curved rhabdodiactines (both oxeote and strongylelike) and small hexactines, coating hypodermal spicules as comitalia; parenchymal spicules are tauactines of various sizes organized into bundles; bundles have a rectangular arrangement near hypodermal spicules but more randomly disposed interiorly, curving about large, circular aporhyses; tauactines largest near gastral surface, but other than a single hexactine of comparable ray thickness (much more slender than hypodermalia) there is no sign of hypogastralia or gastralia; gastral surface bearing large, circular openings of aporhyses, which may branch or anastomose within body wall; smaller, subcircular openings on dermal surface may be epirhyses. Permian (Artinskian, Roadian, ?Wordian): USA -FIG. 262, 2a-c. \*C. plectus, Word For-(Texas).mation, Leonardian, Glass Mountains; a, outer surface of holotype showing dermal hexactines and finer, subdermal triactines around circular, parietal gaps; b, broken edge of holotype showing coarse, dermal hexactines at top and finer spicules in interior and on gastral surface, at bottom; c, gastral surface of holotype showing large triactines and circular, parietal gaps, USNM 127661, ×1.5 (Finks, 1960; courtesy of The American Museum of Natural History).
- Corticulospongia RIGBY & CHATTERTON, 1989, p. 41 [\*C. floccosa; OD]. Sheetlike, thin-walled sponge; presumed dermal surface with interlaced bundles of rhabdodiactines in irregular, but dominantly possible longitudinal orientation parallel to surface; gastral surface with similar, but finer and less

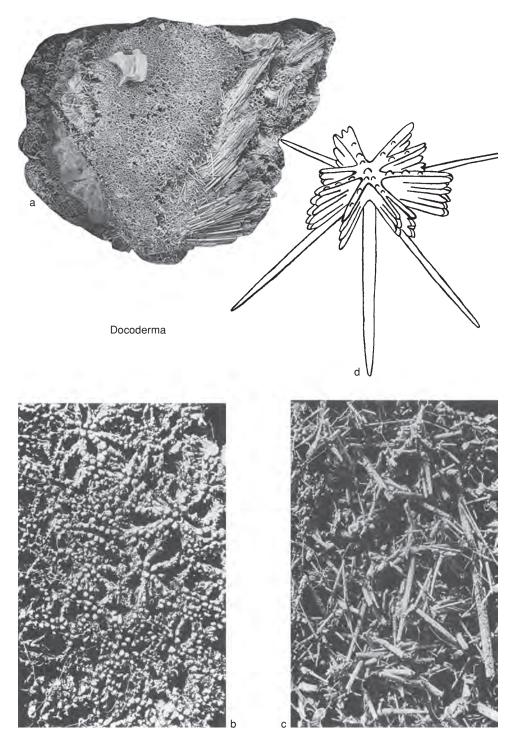


FIG. 261. Docodermatidae (p. 403-404).

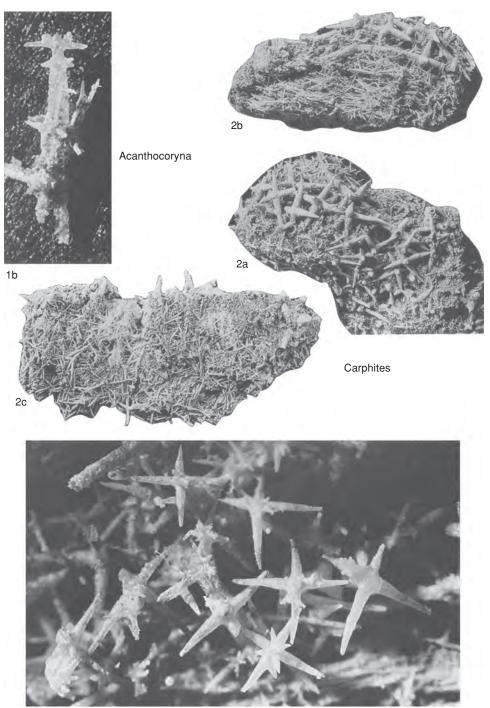




FIG. 262. Docodermatidae (p. 404).

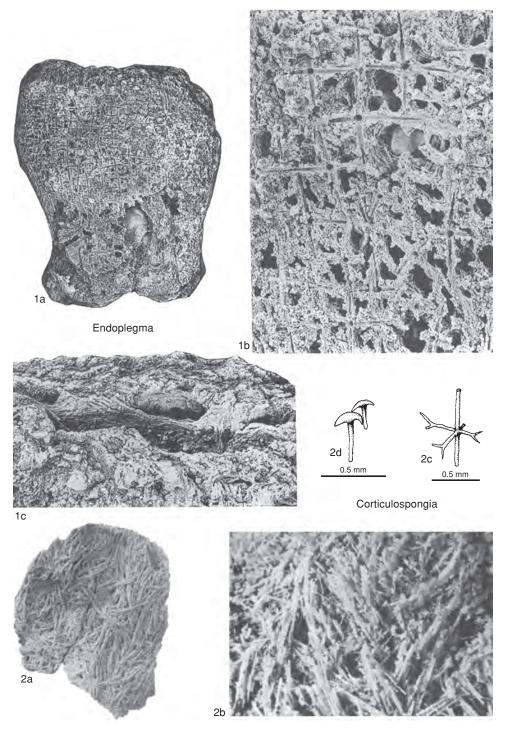


FIG. 263. Docodermatidae (p. 404-408).

well defined bundles; similar bundles in sponge interior diverging upwardly from midplane of wall toward both surfaces, meeting them at an angle; small, closely spaced, polygonal openings between bundles on both surfaces are openings of epirhyses and aporhyses, respectively; small, irregularly oriented hexactines, down to microsclere size, occurring in and beneath gastral layers, along with true oxyhexasters, short-shafted, bidentate anchors occurring rarely in interior. [The genus resembles Endoplegma FINKS, 1960, without the large, dermal pentactines. It is possible that they were present and became detached before burial, for in the holotype of Endoplegma they are preserved only as molds on the interior silicification. It could also be that this is a genus in which such dermalia were not developed. The spicule bundles that make up the wall are here identified as rhabdodiactines. In the holotype of Endoplegma they also look like monaxons, but in better preserved topotype specimens of that genus (personal observation, RMF) are seen to be very long tauactines (FINKS, 1960, p. 128, footnote, there identified as Carphites diabloensis FINKS, 1960). It is possible that they are tauactines here as well. Another feature this genus shares with Endoplegma is the presence of oxyhexasters and bidentate anchors, which occur in Endoplegma diabloense.] Silurian (Ludlow): Canada (Northwest Territories, Baillie-Hamilton Island) .---- FIG. 263, 2a-d. \*C. floccosa, Cape Phillips Formation, Baillie-Hamilton Island; a, dermal surface of holotype showing coarse clusters of subparallel spicules, ×1; b, photomicrograph of gastral surface with range of spicules in irregularly subparallel clusters of mixed rhabdodiactines and oxeas, with delicate hexactines as hairlike spicules between, irregular openings are exhalant ostia, UA 7733, ×10; c-d, camera lucida drawings of spicules from holotype: fragment of oxyhexaster with subdivided, ray tips and clemes with curved, anchor-shaped rays that may have been part of root tuft or wall, scale indicated by bars (Rigby & Chatterton, 1989; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

Endoplegma FINKS, 1960, p. 105 [\*E. calathus FINKS, 1960, p. 106; OD]. Vasiform, subprismatic, rather thick-walled sponge with root tuft; hypodermalia large but slender rayed, pentactines of two orders of size in parallel orientation, larger arranged quincuncially; parenchymalia with several layers of broad, straplike, vertical and horizontal bundles of long-rayed tauactines and possibly rhabdodiactines; gastralia apparently absent; autodermalia not known; comitalia include tauactines, hexactines, and small, curved rhabdodiactines, some of which are strongylelike, and accompany hypodermalia; large, circular aporhyses outlined by parenchymal bundles and covered by hypodermalia; epirhyses may also be present; short, spreading root tuft continuous with parenchymal bundles. A paraclavule and an oxyhexaster have been found in

a specimen of E. diabloense (FINKS, 1960), a species formerly assigned to Carphites. Permian (Artinskian, Roadian): USA (Texas).--Fig. 263, 1a-c. \*E. calathus, Word Formation, Leonardian, Glass Mountains; a, side view of laterally flattened holotype showing molds of dermal pentactines in silicified, outer layer; straplike clusters of monaxons at base may have projected as root tufts, ×0.5; b, enlarged part of dermal layer showing molds of dermal pentactines extending across circular, parietal gaps, which are outlined by interior layer of monactines,  $\times 2$ ; *c*, diagonal view into flattened osculum showing lining of straplike bundles of monaxons in gastral surface of spongocoel, USNM 127651, ×2 (Finks, 1960; courtesy of The American Museum of Natural History).

#### Family STEREODICTYIDAE Finks, 1960

#### [Stereodictyidae FINKS, 1960, p. 107]

Dictyospongioidea with three-dimensional, gridlike skeleton composed of multiple layers of closely spaced, vertical and horizontal bundles made of reduced or whole hexactines; finer quadrate mesh of dermal or gastral hexactines present in one species; possibly no root tuft. [This aberrant group appears to have retained only (or almost only) the inner, parenchymal layer of spicule bundles, which has become greatly expanded by multiplication of layers.] Carboniferous (Visean)–Upper Triassic (Carnian).

Stereodictyum FINKS, 1960, p. 108 [\*S. orthoplectum; OD]. Skeleton composed of several alternating layers of vertical, horizontal, and radial bundles of spicules that appear to be mainly four-rayed, with two rays mutually perpendicular to each other and to remaining two; sponge in form of curving sheets, sometimes thick, that may be encrusting (in this instance radial bundles would be vertical in position). Skeletal canals may be present in larger individuals. [D. F. TOOMEY, J. M. PARKS, and J. L. WIL-SON (personal communications, 1970s) report the sponges in encrusting positions in Virgilian reefs in New Mexico. A specialized dermal layer is not known in the type species but in the lower Pennsylvanian species S. proteron RIGBY & WASHBURN, 1972, a finer mesh of small, parallel hexactines is present on one surface; this species is said to have complete hexactines, as well as reduced ones, forming the main interior mesh, and also to have long, possible rhabdodiactines in some of the superficial spicule bundles.] Carboniferous (Visean)-Permian (Artinskian): Spain, Visean; USA (Texas, New Mexico, Nevada), Upper Pennsylvanian-Artinskian; China, Moscovian.-FIG. 264a-e.

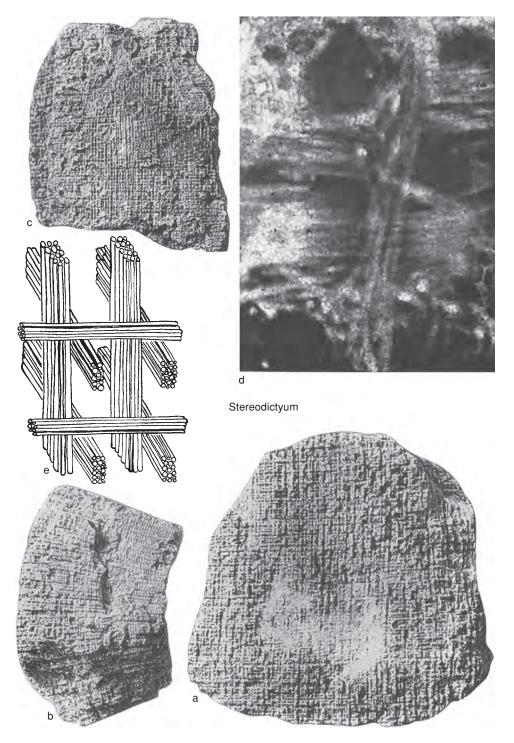


FIG. 264. Stereodictyidae (p. 408-410).

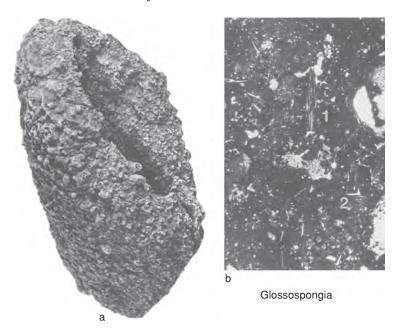


FIG. 265. Stereodictyidae (p. 410).

\*S. orthoplectum, Texas; a, eroded, outer surface of holotype showing reticulate, skeletal structure of thick-walled sponge, Wolfcamp Formation, Wolfcampian, Glass Mountains, ×1; b, horizontal section through wall showing uniform, reticulate, skeletal structure, with gastral surface to right, Wolfcamp Formation, Wolfcampian, Glass Mountains,  $\times 1$ ; *c*, longitudinal section through wall with gastral surface to left, Wolfcamp Formation, Wolfcampian, Glass Mountains, USNM 127654, ×1; d, photomicrograph of longitudinal thin section of paratype showing annular, spicule bundle, top to bottom, and intersecting longitudinal bundles, USNM 127657a, Hueco Formation, Sierra Diablo, Texas, ×25; e, diagram of spicule bundles in three-dimensional relationships, with spongocoel toward left and osculum toward top, not to scale (Finks, 1960; courtesy of The American Museum of Natural History).

Glossospongia WU Xichun, 1989, p. 767 [\*G. angustoscula WU Xichun, 1989, p. 768; OD]. Bellshaped to tongue-shaped sponges with laterally flattened but deep, simple spongocoel with thick walls; skeleton a crude network of upwardly radiating bundles and roughly horizontal bundles of hexactine-based spicules, possibly with additional bundles at right angles, to make a three-dimensional net; areas between bundles not filled by canals, with skeleton formed of irregularly oriented and spaced, small hexactines and hexactine-based spicules around prominent canals that appear radially oriented and normal to dermal-gastral surfaces; most distinctive spicules coarse, hexactinederived forms in which one or two of normal six rays aborted to produce long spicules with fairly short rays normal to bundle trend; gastral margin with coarse, honeycomb-like, exhalant ostia. *Triassic (Carnian):* China (Sichuan).——FIG. 265*a-b.* \**G. angustoscula*, Hanwang Formation, Jushui; *a*, laterally flattened, steeply obconical specimen with nodose exterior and thick walls around deep spongocoel, S-1095, ×1; *b*, photomicrograph showing nearly continuous, vertical spicule bundle (*I*) and less distinct, horizontal bundle of hexactines with irregularly oriented hexactines in spaces between bundles, IGASB R6-11, ×10 (Rigby, Wu, & Fan, 1998).

## Superfamily HINTZESPONGIOIDEA Finks, 1983

#### [Hintzespongioidea FINKS, 1983b, p. 110]

Thin-walled Reticulosa in which an outer dermal layer of parallel, slender-rayed hexactines or derivatives, as in Protospongioidea, is underlain by a layer of slender-rayed hexactines or derivatives in nonparallel orientation that surround closely spaced, circular gaps or aporhyses that are covered by dermal layer; rhabdodiactine prostalia perpendicular to outer surface commonly present. Lower Cambrian– Carboniferous (Upper Mississippian).

#### Family HINTZESPONGIIDAE Finks, 1983

[Hintzespongiidae FINKS, 1983b, p. 110]

Obconical, ovate, or vasiform Hintzespongioidea with defined osculum but major prostalia absent. *Lower Cambrian– Devonian (Givetian).* 

- Hintzespongia RIGBY & GUTSCHICK, 1976, p. 81 [\*H. bilamina RIGBY & GUTSCHICK, 1976, p. 82; OD]. Sponge thin walled, possibly conical to barrel shaped or ovoid, with an outer, dermal layer of parallel, slender-rayed stauractines of at least four orders of size, overlying a layer of slender-rayed stauractines and hexactines in nonparallel orientation, that outline circular, parietal gaps of more or less quincuncial arrangement. [It is possible that the senior genus Ratcliffespongia RIGBY, 1969, is the inner layer of a Hintzespongia.] Middle Cambrian: USA (Utah).-FIG. 266a-b. \*H. bilamina, Marjum Limestone, House Range; a, holotype fragment with prominent, irregular spiculation around parietal gaps of inner, skeletal layer of sponge,  $\times 2$ ; b, photomicrograph of parts of both layers of skeleton, with regular, dermal layer of ranked stauractines and hexactines on left and more irregularly spiculed, gastral layer on right, BYU 1153, ×10 (Rigby & Gutschick, 1976).
- Cyathophycus WALCOTT, 1879, p. 18 [\*C. reticulatus; OD] [=Cyathospongia DAWSON & HINDE, 1889, p. 44, nom. van., non HALL, 1882; Cyathodictya HALL & CLARKE, 1899, p. 200, nom. van.]. Conicocylindrical, slightly contracted about broad osculum; single, outer layer of parallel stauractines or pentactines arranged to form a series of quadrules of three orders of size, parallel to longitudinal axis of sponge; short, root tuft present at base; inner layer not resolvable into spicules but possibly composed of them, bearing circular openings resembling parietal gaps, that have about same diameter and spacing as largest quadrules but which do not coincide regularly with these quadrules. [Cyathospongia quebecensis DAWSON, 1888, from the Middle Cambrian is here considered to belong to Acanthodictya Dawson & HINDE, 1889.] Middle Ordovician-Devonian (Givetian): USA (New York, Nevada), Middle Ordovician-Upper Ordovician; Canada (British Columbia, Northwest Territories), Llandovery-Wenlock; USA (Nevada), Givetian. FIG. 267, 1a-c. \*C. reticulatus, Utica Shale, Trentonian, Holland Patent, New York; a, side view of characteristic specimen with pointed base, rounded osculum, and reticulate, quadruled skeleton, ×1; b, enlarged base showing development of root tuft, ×3; c, enlarged part of quadruled skeleton with ranked stauractines overlying irregularly developed aureoles, ×5 (Hall & Clarke, 1899).
- Ratcliffespongia RIGBY, 1969, p. 126 [\*R. perforata; OD]. Conicocylindrical sponge; thin body wall composed of stauractines of several sizes in non-

parallel arrangement, outlining closely spaced, oval to circular parietal gaps that have a quincuncial arrangement; possible rhabdodiactine prostalia may be present. [It is possible that this is the inner layer of *Hintzespongia* RIGBY & GUTSCHICK, 1976.] *Middle Cambrian*: USA (Utah).——FIG. 268*a*–*b*. \**R. perforata*, Marjum Limestone or Wheeler Shale, House Range; *a*, steeply obconical holotype with prominent, parietal gaps outlined by irregularly oriented, hexactine-based spicules, ×1; *b*, photomicrograph of lower part of holotype showing irregularly oriented spicules with rays tangent to margins of parietal gaps, BYU 1482, ×5 (Rigby, 1969).

Stephenospongia RIGBY, 1986a, p. 55 [\*S. magnipora RIGBY, 1986a, p. 56; OD]. Conicocylindrical, thin-walled reticulosid, walls with numerous large, vertically elliptical, parietal gaps outlined by tracts of irregularly oriented and unclumped, thin rhabdodiactines or fine stauractines of several sizes; base not known. [This resembles the mesh of Sentinelia WALCOTT, 1920, and Valospongia RIGBY, 1983a, but apparently lacks the fine, quadrate mesh over the large openings. However, one of the broader tract areas shown at the left side of figure 7 on plate 18 of RIGBY, 1986a, has a fine quadrate mesh and may, in fact, be the dermal covering of an underlying opening.] Middle Cambrian: Canada (British Columbia).-FIG. 267,2a-b. \*S. magnipora, Stephen Formation, Ogygopsis shale, Mount Stephen, near Field; a, holotype fragment with hairlike, hexactine-based spicules in matte around large, parietal gaps, ×1; b, photomicrograph of part of matte showing irregular, delicate spicules and gaps, ROM 433127, ×5 (Rigby, 1986a).

# Family TEGANIIDAE de Laubenfels, 1955

#### [Teganiidae DE LAUBENFELS, 1955, p. 70]

Spheroidal Hintzespongioidea without osculum and with numerous short, closely spaced prostalia. *Cambrian (Furongian)– Carboniferous (Upper Mississippian).* 

Teganium RAUFF, 1894, p. 256 [\*Cyathophycus subsphaericus WALCOTT, 1879, p. 19; OD] [=Sphaerodictya HALL & CLARKE, 1899, p. 26, obj.]. Spherical; relatively thick, outer layer of rhabdodiactine (or possibly pentactine) prostalia, together with a quadrate mesh of hexactines or derivatives, of nested sizes in parallel orientation; inner layer of hexactines or derivatives in nonparallel orientation, surrounding closely spaced, circular aporhyses; neither osculum nor root tuft known. [The foregoing description is based on HALL and CLARKE's illustrations of topotypes (HALL & CLARKE, 1899, pl. 1,14-22). Personal observation of WALCOTT's holotype and RAUFF's hypotypes confirm HALL and CLARKE's statements (1899, footnotes, p. 24-26) and their quotation of



FIG. 266. Hintzespongiidae (p. 411).

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## Reticulosa

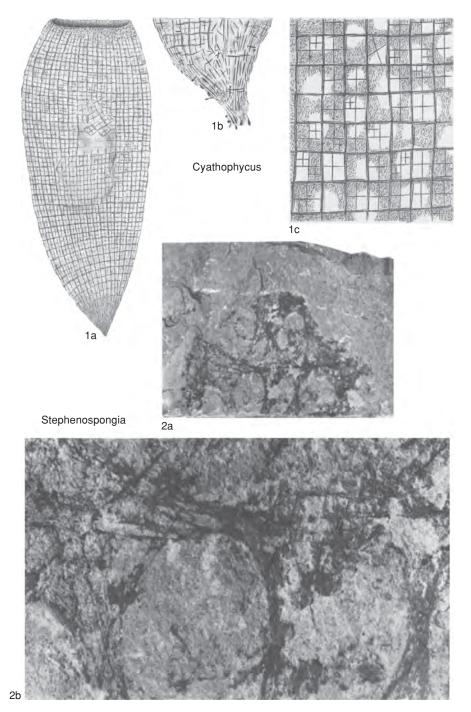
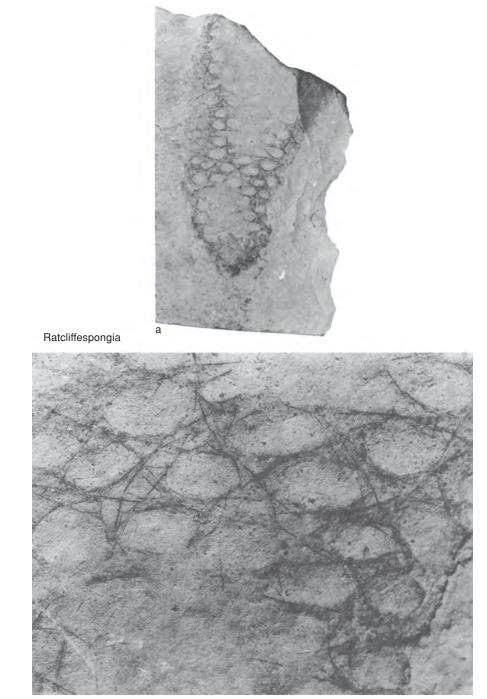


FIG. 267. Hintzespongiidae (p. 411).

## Porifera–Hexactinellida



b

FIG. 268. Hintzespongiidae (p. 411).

Reticulosa

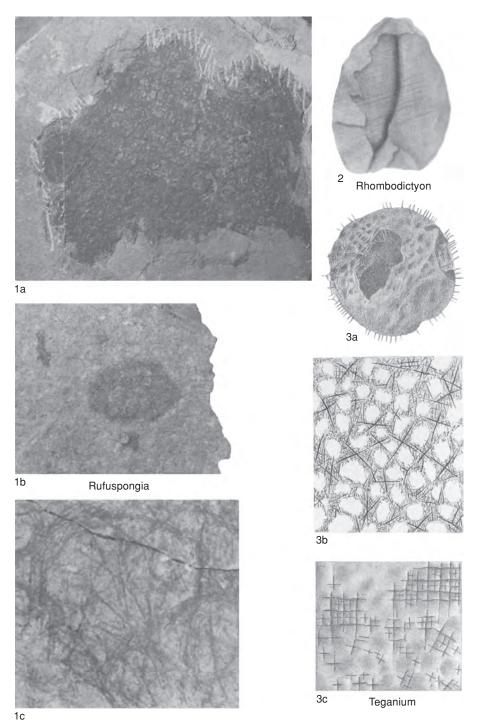


FIG. 269. Teganiidae (p. 411-419).

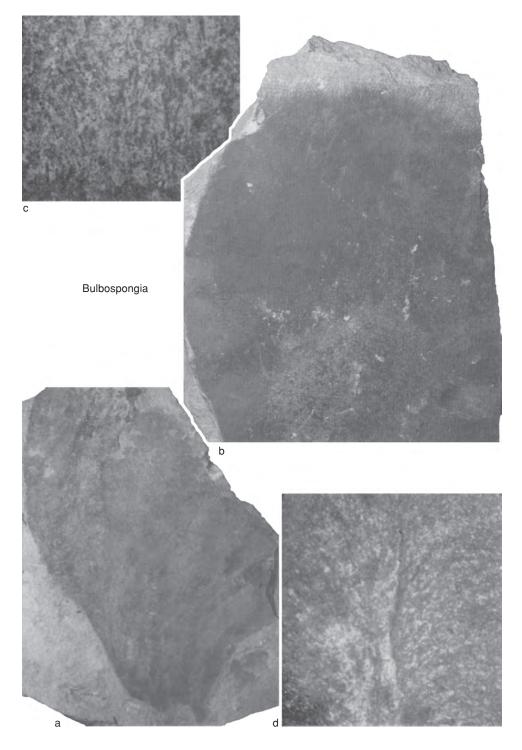
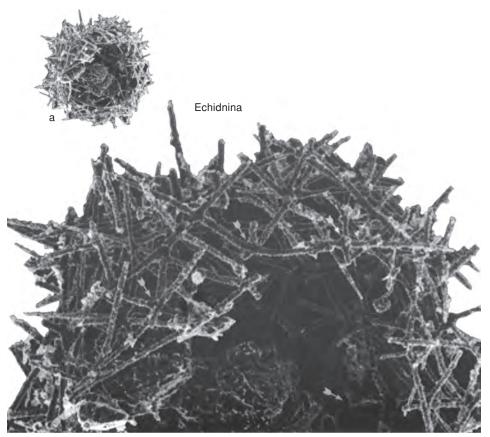


FIG. 270. Teganiidae (p. 417).



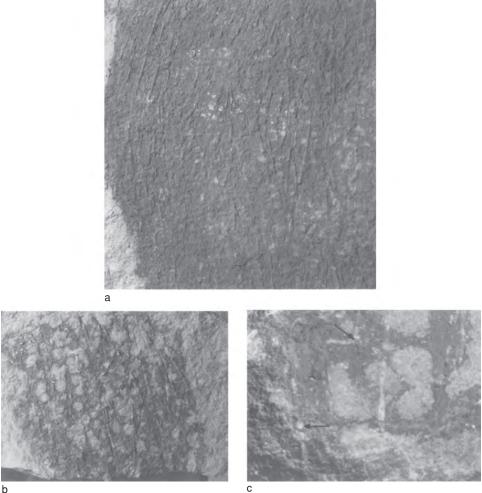
b

FIG. 271. Teganiidae (p. 417-418).

SCHUCHERT's statements (*loc. cit.*) that the spicules are not visible and that the supposed osculum and cup shape reconstructed by RAUFF are not supported by the specimens. RUEDEMANN (1925) designated a new holotype for *Sphaerodictya subsphaerica* (WALCOTT) HALL & CLARKE but this is not valid.] *Upper Ordovician:* USA (New York).——FIG. 269, 3a-c. \*T. subsphaericum (WALCOTT), Utica Shale, Holland Patent; *a*, enlarged type showing general form, cruciform spicules on surface, and radiate, marginal spicules; *b*, enlargement of part of inner wall showing aureoles defined by irregularly oriented, cruciform spicules; *c*, enlargement of part of outer wall showing regular, quadruled, skeletal net, ×3 (Hall & Clarke, 1899).

Bulbospongia RIGBY & MEHL, 1994, p. 141 [\*B. bullata; OD]. Vase- or balloonlike, teganiid sponge with bulbous, upper part above steeply obconical, lower part; thin walls have low, vertical ridges in lower part but are smooth in upper part; fine-textured skeleton upwardly divergent and locally plumose, composed of mixed fine and moderately coarse, long spicules that are mainly diactines, but includes some stauractines; without coarse hexactines or rhabdodiactines, as well as reticulate spicules and prominent pores or gaps; inner part of wall with coarser spicules. Devonian (Givetian): USA (Nevada).—FIG. 270a-d. \*B. bullata, Red Hill beds, northern Simpson Park Range; a, side view of vertically ridged, but now flattened, thin-walled holotype preserved as hematite impression, USNM 463560, ×1; b, hematitereplaced paratype with prostalia forming spiculed, oscular rim at top, USNM 463561, ×1; c, photomicrograph of coarse diactine spicules of paratype with parallel, thatchlike, skeletal structure, USNM 463560; d, upwardly plumose diactines that diverge from one of flattened ridges, USNM 463574, ×5 (Rigby & Mehl, 1994).

Echidnina BENGTSON, 1986, p. 202 [\**E. runnegari;* OD]. Tiny, globular, thin-walled, with broad osculum as opening to cloaca; skeleton of hexactines, pentactines, stauractines, and possibly rhabdodiactines in irregular orientation, so that external



Taleolaspongia

FIG. 272. Teganiidae (p. 419).

surface is spiny because of protruding rays. [These may be juveniles, propagules, or adults.] *Cambrian (Furongian):* Australia (Queensland).——FIG. 271*a–b. \*E. runnegari*, Mindyalian, Mungerebar Limestone, western Queensland; *a*, holotype globular, thin-walled, spicule cluster with broad osculum; ×100; *b*, enlargement of part of holotype showing spicule relationships, UNE F16424, ×450 (Bengtson, 1986).

Rhombodictyon WHITFIELD, 1886, p. 347 [\*R. reniforme; OD]. Subglobular sponge with rhomboidal mesh spaces in primary skeleton formed by diagonally oriented, rodlike elements, probably spicule rays, crossing at angles other than right angles. Devonian: New York.—FIG. 269,2. \*R. reniforme, Normanskill Shale, Chazyan, Kenwood; side view of globular fossil with diagonal, skeletal meshwork, ×1 (Whitfield, 1886).

Rufuspongia RIGBY & MEHL, 1994, p. 133 [\*R. triporata; OD]. Sheetlike to low, funnel-shaped teganiid sponge with two-layered skeleton; gastral layer with coarse pores and dermal layer with smaller pores; skeleton of hairlike diactines or possibly rhabdodiactines and stauractines with associated, small stauractines; spicules grouped in irregular clusters and tangentially around pores or gaps; without regular arrangement of protospongiid or dictyospongiid structure. Devonian (Givetian): USA (Nevada).——Fig. 269, Ia-c. \*R. triporata, Red Hill beds, northern Simpson Park Range; a, holotype with fractured outline of dense, hematitic-replaced, skeletal net with large,

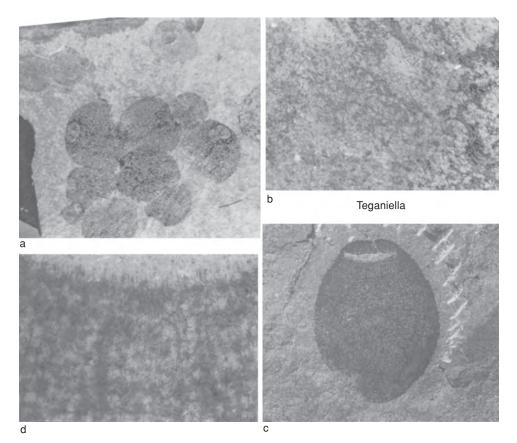


FIG. 273. Teganiidae (p. 419-420).

oval, gastral gaps interrupted by smaller, circular gaps in dermal layer, USNM 463548,  $\times 0.5$ ; *b*, relatively obscurely spiculed, paratype fragment in which layers of spicules obscure larger opening and only intermediate-sized openings are evident, USNM 463572,  $\times 1$ ; *c*, coarse, oval gap outlined by tangential, spicule bundles as seen through finer-textured, more dermal layer with circular, intermediate-sized openings and smaller openings in skeleton of paratype, USNM 463552,  $\times 5$  (Rigby & Mehl, 1994).

Taleolaspongia RIGBY & MEHL, 1994, p. 137 [\*T. modesta; OD]. Broad, open funnel-shaped to palmate, teganiid sponge with thin wall constructed of two major skeletal elements: hexactine and hexactine-derived, small, hairlike spicules that are regularly oriented in irregular thatch, and coarse, upwardly divergent hexactines and rhabdodiactines with elongate, vertical rays generally subparallel, although not in regular, protosponge orientations, in midwall or possibly as separate layer; wall pierced by coarse, circular to oval gaps or ostia with moderately uniform diameters and possibly arranged in crude rows. Devonian (Givetian): USA (Nevada).——FIG. 272*a*-*c*. \* T. modesta, Red Hill beds, northern Simpson Park Range; *a*, dense, dermal net of holotype sculptured by positive impressions of moderately regularly oriented and spaced, coarse hexactines, light gray matrix fills gaps in net, USNM 463554, ×1; *b*, well-preserved paratype with dark, dermal layer interrupted by light gray gaps, light colored hexactines showing through net, USNM 463556, ×1; *c*, photomicrograph with light gray hexactines in dark, skeletal net, interrupted by medium gray matrix in gaps, USNM 463556, ×5 (Rigby & Mehl, 1994).

Teganiella RIGBY, 1986c, p. 449 [\**T. heathi;* OD]. Globular to egg-shaped sponges with rounded base and flattened, upper, oscular rim; thin walls of delicate hexactines of several sizes, with shortened, distal and proximal rays; irregularly arranged in two orientations, either parallel or diagonal to longitudinal axis, but it is not clear whether these represent two distinct layers; meridional bundles of long rays (possible rhabdodiactines) also

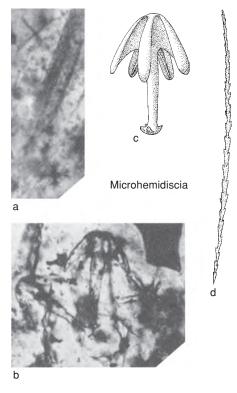


FIG. 274. Microhemidisciidae (p. 420).

present; numerous small, vertically elongate ostia of about quadrule size apparently developed only in dermal layer; marked prostalia absent; basalia unknown. [These could be juveniles of some larger dictyospongid and rather resemble the juveniles of the Permian Microstaura FINKS, 1960, except for the thinner wall and diagonal orientation of some skeletal elements.] Devonian (Givetian)-Carboniferous (Upper Mississippian): USA (Nevada), Givetian; USA (Montana), Upper Mississippian.—Fig. 273a-b. \*T. heathi, Heath Formation, Chesterian, Fergus County, Montana; a, cluster of sponges with holotype, UMG 5723 on right, and paratype, UMG 5724, on left, ×1; b, photomicrograph of skeletal net of holotype with crudely rectangular pattern of hexactine-based spicules with one layer diagonal and other horizontalvertical, ×10 (Rigby, 1986c).—FIG. 273c-d. T. ovata RIGBY & MEHL, Red Hill beds, Givetian, Simpson Park Range, Nevada; c, holotype, side view of globose sponge with skeletal structure parallel to oscular margin in upper part but diagonally in middle and lower part, USNM 463539,  $\times 2$ ; d, photomicrograph of skeletal structure at oscular margin with fringe of short prostalia above regular, reticulate skeleton, USNM 463539, ×10 (Rigby & Mehl, 1994).

### Order HEMIDISCOSA Schrammen, 1924

[nom. transl. REID, 1958, p. xliv, pro Hemidiscaria Schrammen, 1924a, p. 18]

Amphidiscophora whose principal microscleres are hemidiscs. *Carboniferous (Upper Pennsylvanian)*.

#### Family MICROHEMIDISCIIDAE new family

[Microhemidisciidae FINKS & RIGBY, herein] [type genus, Microhemidiscia KLING & REIF, 1969, p. 1433]

Hemidiscs with spatulate teeth on major umbel, occurring together with uncinates. *Carboniferous (Upper Pennsylvanian).* 

Microhemidiscia KLING & REIF, 1969, p. 1,433 [\*M. ortmanni; OD]. External form unknown; principal skeleton of unfused, simple hexactines, pentactines, and rhabdodiactines accompanied by uncinates and hemidiscs; hemidiscs bearing five long, spatulate rays at one end and five (rarely six) short, conical rays at other end. Carboniferous (Upper Pennsylvanian): Uruguay.——FIG. 274a–d. \*M. ortmanni, Itararé Formation, Rio Negro, Tacuarembó-Durazno; a, uncinates from paratype, GPIT Po 1340/6, ×300; b, hemidiscs from holotype, GPIT, Po 1340/5, ×200; c, drawing of hemidisc from holotype, GPIT Po 1340/5, ×250; d, drawing of uncinate from paratype, GPIT Po 1340/6, ×150 (Kling & Reif, 1969).

## Subclass HEXASTEROPHORA Schulze, 1887

[nom. transl. REID, 1958a, p. xliv, ex Hexasterophora SCHULZE, 1887b, p. 36]

Hexactinellida with microscleres that include hexasters but not spicules with umbellate ray terminations (such as paraclavules, hemidiscs, amphidiscs, staurodiscs, or hexadiscs). [The oldest known hexasters are early Carboniferous (Mississippian) and were found within a paraclavule-bearing sponge (Griphodictya HALL & CLARKE, 1899), here included with the Amphidiscophora. Hexasters have also been found in the late Carboniferous (Pennsylvanian) amphidisc-bearing Itararella KLING & REIF, 1969. Although late Paleozoic isolated hexasters are known, none have been found physically within sponges here included with the Hexasterophora. Paleozoic sponges

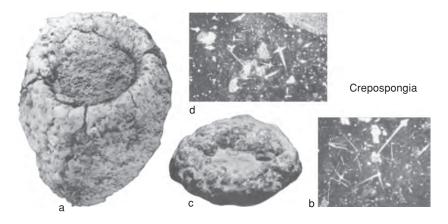


FIG. 275. Crepospongiidae (p. 421-422).

are herein assigned to the Hexasterophora on the strength of a graded, morphologic series extending back from the Permian possible hexactinosan Pileolites FINKS, 1960, in the Ordovician Brachiospongia MARSH, 1867. Other than the paraclavule or amphidisc-bearing genera cited, Arakespongia RIGBY, CHAMBERLAIN, & BLACK, 1970 (Pennsylvanian), the dubious Erythrospongia HUDSON, 1929 (Carboniferous), and a single hexaster occurring with a single paraclavule in the Permian Endoplegma FINKS, 1960, there are no hexaster-bearing, whole, Paleozoic sponge fossils known. It is worth noting, however, that the type specimens of Pileolites were found in association with isolated hexasters in the accompanying sediment.] Ordovician-Holocene.

## Order LYSSACINOSA Zittel, 1877

[nom. transl. REID, 1958a, p. xliv, ex tribus Lyssacinaria SCHRAMMEN, 1924a, p. 18, nom. transl. ex order Lyssakina ZITTEL, 1877b, p. 22; emend., IJIMA, 1927, p. 319]

Hexasterophora without dictyonal strands. [It is possible that many isolated hexactines, as well as isolated hexasters, from Paleozoic sediments were derived from disintegrated lyssacines other than the genera with more coherent skeletons described below.] Ordovician–Holocene.

## Superfamily CREPOSPONGIOIDEA new superfamily

[Crepospongioidea FINKS & RIGBY, herein] [type genus, Crepospongia WU, 1989, p. 768]

Lyssacinosid sponges with skeleton of irregularly oriented and spaced hexactines and related spicules; without bundled spicule tracts or differentiated layers of coarse dermalia or gastralia. *Triassic (Carnian)*.

### Family CREPOSPONGIIDAE new family

[Crepospongiidae FINKS & RIGBY, herein] [type genus, Crepospongia WU, 1989, p. 768]

Lyssacinosan sponges with skeletons of irregularly oriented and spaced hexactines, stauractines, and related spicules of several sizes; differentiated, coarsely spiculed, dermal and gastral layers absent. *Triassic* (*Carnian*).

Crepospongia WU, 1989, p. 768 [\*C. circulana; OD] [=Oospongia WU, 1989, p. 768 (type, O. radiocanalis, OD); Calpidospongia WU, 1989, p. 768 (type, C. rhynchoprocta WU, 1989, p. 769, OD); Pyrenospongia WU, 1989, p. 769 (type, P. omalohemisphaera, OD)]. Spheroidal to ovate or urn- or slipper-shaped sponges with deep, central spongocoel and moderately thick walls; coarse, exhalant oscula irregularly placed and shaped on gastral surface; skeleton mainly of irregularly oriented and spaced stauractines and hexactines of several sizes, and may include small oxeas or rhabdodiactines. *Triassic (Carnian):* China (Sichuan).——FIG. 275*a–b.* \**C. circulana*, Hanwang Formation, Mianzhu County; *a*, side view of slipper-shaped holotype showing moderately thick wall around sediment-filled spongocoel, ×1; *b*, photomicrograph of variously sized hexactines and related spicules in wall of holotype, ×15 (Wu, 1989).— FIG. 275*c–d. C. radiocanalis* (WU), Hanwang Formation, Mianzhu County; *c*, view from above of ovate holotype with nodose, thick walls around sediment-filled spongocoel, ×1; *d*, photomicrograph of characteristic, irregularly spaced and sized hexactines in wall, ×12 (Wu, 1989).

## Superfamily BRACHIOSPONGIOIDEA Beecher, 1889

[nom. transl. FINKS, 1960, p. 115, ex Brachiospongiidae BEECHER, 1889, p. 13]

Vasiform sponges that rest directly on sea floor without root tuft or other attachment structure; enlarged hypodermalia and sometimes hypogastralia that are commonly differentiated from irregularly oriented, parenchymal hexactines that are usually organized around epirhyses and aporhyses; autodermalia and autogastralia may be present. *Upper Ordovician–Permian (Guadalupian).* 

#### Family BRACHIOSPONGIIDAE Beecher, 1889

#### [Brachiospongiidae BEECHER, 1889, p. 13]

Lobate brachiospongioids in which hollow, radial protuberances of body serve as props; larger, hypodermal spicules may bear distal knobs; epirhyses and aporhyses present. Upper Ordovician–Silurian (Ludlow).

Brachiospongia MARSH, 1867, p. 88 [\*Scyphia digitata OWEN, 1858, p. 111; SD BEECHER, 1889, p. 13]. Sponges open, round-bottomed cup bearing subequatorial expansion from which 6 to 12 subequal, hollow, fingerlike precursors curve outwardly and downwardly and terminate in blunt to acute tips at about same level well below base of central cup; protuberances may bifurcate distally in some forms; body wall maintaining constant, moderate thickness throughout all parts so that cloaca constitutes most of internal volume of protuberances and central cup; one species reported as externally tuberculate; small, closely and evenly spaced, circular openings penetrate body wall seemingly as exhalant and inhalant canals but end short of opposite surface; between them are smaller skeletal pores; skeletal net consisting of outer layer of small pentactines in parallel orientation that cover inhalant openings as

well as rest of surface, hypodermal layer consisting of larger, nonparallel hexactines in which distal ray reduced to round knob (surrounded by four similar knobs, one on distal surface of each tangential ray near crossing) and inner, parenchymal spiculation consisting of hexactines, some of which are spinose, in nonparallel orientation; no root tuft. [This is similar to Rhaeaspongia LAMONT, 1935 and Colospongia LAMONT, 1935, but they are not identical.] Upper Ordovician: USA (Kentucky, Ohio, Tennessee), Canada (Ontario, Manitoba).--Fig. 276,1a-c. \*B. digitata (OWEN), Bigby Limestone, Trentonian, Frankfort, Kentucky; a, side view of original specimen showing incomplete, lower, hollow digitations and upper, thin-walled chimney with incomplete, oscular margin; b, view from above showing radial pattern of digitations, YPM, ×0.5; c, enlarged outer surface with dermal, spicular mesh and nodes of rays of large, hypodermal pentacts, ×20 (Beecher, 1889).

- Colpospongia LAMONT, 1935, p. 307 [\*C. lineata LAMONT, 1935, p. 308; OD]. Genus could be interpreted as resembling a small Brachiospongia in which radial protuberances coalesce laterally to form radial flutes; inner surface of cloaca apparently bore grooves confluent toward osculum; no spicules known, nor is it clear from illustration and description whether this was truly built like Brachiospongia or whether it was a simple, open cup, as originally described. upper Upper Ordovician: England.—FIG. 276,2. \*C. lineata, Sholeshook Limestone, Haverfordwest; internal cast of plicate, bowl-shaped holotype viewed from below, BMHN S 735, ×1 (Lamont, 1935).
- Fistellaspongia RIGBY & MAHER, 1995, p. 1,027 [\*F. inclinata; OD]. Small, cylindrical sponges with deep spongocoel, moderately thin walls made of irregularly, although dominantly diagonally arranged hexactines of several sizes; coarsest hexactines with paratangential rays diagonal to sponge axis, but not in regular or quadruled pattern, and with short, proximal and distal rays normal to that surface; coarse spicules separated by smaller, irregularly oriented and spaced spicules; canal system irregularly developed in feltlike, irregular skeleton. Silurian (Ludlow): USA (Nevada).-FIG. 277, 1a-c. \*F. inclinata, Roberts Mountains Formation, Snake Mountains; a, side view of flattened, tubular holotype with skeleton of diagonally arranged, hexactine-based spicules with felted structure, ×2; b, photomicrograph of lower part of holotype showing spicules of various sizes, with most diagonally arranged, USNM 480436, ×10; c, photomicrograph of paratype showing distinct layer of uniformly spaced and oriented, coarse, dermal hexactines along left, USNM 480437, ×10 (Rigby & Maher, 1995).
- Rhaeaspongia LAMONT, 1935, p. 305 [\**R. mactagguarti;* OD]. Genus differs from *Brachiospongia,* insofar as preservation permits comparison, in that radial protuberances are broader and more irregular and expand distally to form branched, wedge-shaped segments that terminate at a common circumference; no spicules known.

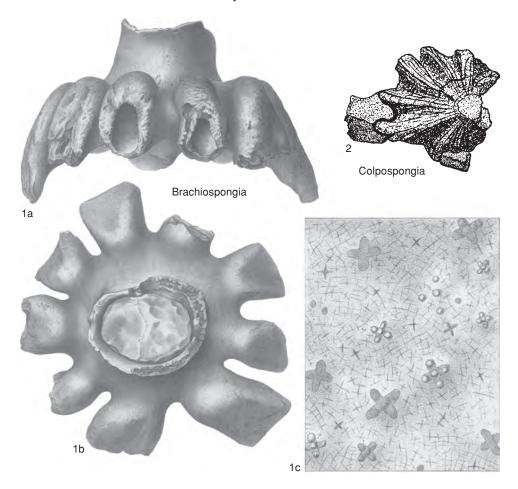


FIG. 276. Brachiospongiidae (p. 422).

[Some Upper Ordovician species assigned to *Brachiospongia* may belong here.] *upper Upper Ordovician:* Scotland, ?North America.——FIG. 277,2*a*-*b.* \**R. mactagguarti*, Lower Drummock Group, Dailly, Scotland; *a*, small holotype, internal cast as viewed from below, with central base of attachment and flared, radial arms, ×1; *b*, drawing of holotype from above showing considerable irregularity in shape and placement of radial arms, HM P 5200, ×1 (Lamont, 1935).

#### Family PYRUSPONGIIDAE Rigby, 1971

#### [Pyruspongiidae RIGBY, 1971, p. 59]

Vasiform brachiospongioids without prominent skeletal canals; skeleton with enlarged, simple, hypodermal pentactines or hexactines over irregularly oriented, parenchymal hexactines. *Upper Ordovician*. Pyruspongia RIGBY, 1971, p. 60 [\*P. ruga; OD]. Sponge moderately thin-walled with flat base and vertically ribbed sides, cylindrical in lower part, globose or bowl-shaped in upper part with broad osculum; parenchymal spicules hexactines in nonparallel, or only locally parallel, arrangement, with outer (possibly hypodermal) layer of larger, stubby pentactines and hexactines; no parietal gaps or large, skeletal canals. [Genus resembles Oncosella in external form but differs in the lack of skeletal canals and in having smooth rather than spiny hexactines.] Upper Ordovician: Canada (Mani--FIG. 278,2a-b. \*P. ruga, Cat Head Memtoba).ber, Red River Formation, Caradoc-Ashgill, Lake Winnipeg; a, side view of ribbed, bulbous holotype preserved as limonite mold, GSC 25410, ×1; b, restoration based upon holotype, approximately ×1 (Rigby, 1971; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

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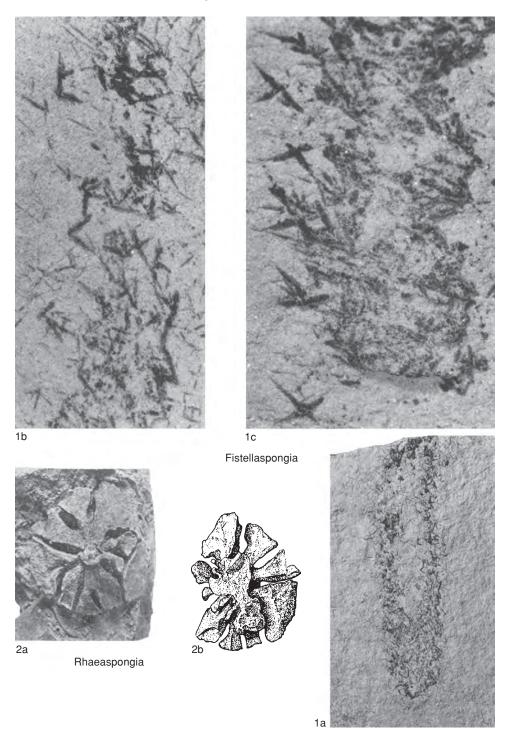


FIG. 277. Brachiospongiidae (p. 422-423).

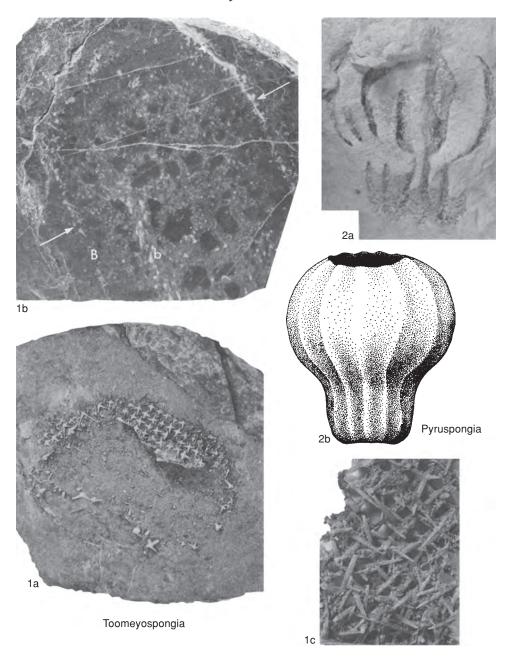


FIG. 278. Pyruspongiidae and Toomeyospongiidae (p. 423-429).

#### Family MALUMISPONGIIDAE Rigby, 1967

#### [Malumispongiidae RIGBY, 1967b, p. 769]

Barrel-shaped to bowl-shaped brachiospongioids with epirhyses and aporhyses well developed; dermalia not differentiated from parenchymalia other than by abortion of distal, and possibly proximal, rays; all spicules irregularly oriented; rhabdodiactines may be present. Upper Ordovician– Carboniferous (lower Tournaisian).

- Malumispongium RIGBY, 1967b, p. 770 [\*Aulocopium hartnageli CLARKE, 1924, p. 10; OD]. Vasiform to cylindroid, uniformly moderately thick walled; widest near flat, centrally concave base, contracting somewhat toward broad osculum; cloaca of same shape as exterior; large, closely spaced, cylindrical, inhalant and exhalant canals, perpendicular to surfaces, almost penetrating body wall and communicating with smaller, skeletal canals within body wall; specialized dermalia and gastralia not preserved, perhaps not developed; parenchymalia simple, smooth hexactines of various sizes in nonparallel orientation; basalia not present. Silurian (Wenlock): Canada (Quebec, Gaspe).----FIG. 279, 1a-b. \*M. hartnageli (CLARKE), La Vieille Formation, Gaspe Peninsula, Quebec; a, vertical section through lectotype showing large, matrix-filled spongocoel and thick walls with light matrix in parietal gaps and canals, NYSM 12562, ×0.5; b, photomicrograph of thin section from syntype showing variation in hexactine size and in orientation, NYSM 12566, ×10 (Rigby, 1967b).
- Carbonella Hurcewicz & Czarniecki, 1986, p. 341 [\*C. rotunda; OD]. Spheroidal to pyriform; thick walled; outer surface with irregularly distributed, low protuberances; no osculum; cloaca narrow and of stellate cross section (because of entering possible canals); canals of circular cross section, closely spaced in more or less quincuncial arrangement, open on exterior; dermal skeleton of small stauractines and rhabdodiactines; principal skeleton of larger hexactines and stauractines, including irregularly distributed, much larger ones; gastral layer containing vertically oriented rhabdodiactines. Carboniferous (Visean): Poland .---Fig. 279,2a-g. \*C. rotunda, Carboniferous limestone of Galezice, Holy Cross Mountains; a, side view of holotype,  $\times 0.5$ ; b, longitudinal section showing cribrate, skeletal structure,  $\times 1$ ; *c*, skeletal fragment with diactine (a), stauractine (b), and larger hexactines with axial rays (c),  $\times 100$ ; d-g, drawing of spicules from thin section, d-e, stauractines and diactines in dermal skeleton; f, hexactines and stauractines in endosomal skeleton; g, diactines,

scale bar, 0.1 mm, AI-68/32 (Hurcewicz & Czarniecki, 1986; courtesy of Polish Geological Society, Krakow).

- Oncosella RAUFF, 1894, p. 264 [\*O. catinum; OD]. Vasiform to cylindroid, somewhat broader than high, and contracting slightly toward osculum from flat, centrally concave base; sides bearing vertical ridges that increase in prominence downwardly and extending a short distance onto basal surface; numerous inhalant and exhalant canals extending nearly through body wall, exhalant canals short and opening onto cloacal surface with uniformly large pores; inhalant pores of larger and smaller sizes; parenchymalia spinose hexactines of various sizes in nonparallel orientation; gastral, canalar, and dermal surfaces may bear paratangential stauractines and pentactines; outer surface also bearing short, slender, slightly spinose rhabdodiactines (but not clearly uncinates); latter paratangential to surface but otherwise nonparallel except on crests of ridges that they parallel; a few similar rhabdodiactines found within body wall; autodermalia possibly present as hexactines or derivatives that cover some inhalant openings; no basalia present. Silurian (Wenlock): England. -FIG. 280, 1a-c. \*O. catinum, Wenlock Limestone, Dudley; a, side exterior view of holotype with broad base, vertical ridges, and rounded, oscular summit, ×1; b, vertical median section showing broad spongocoel and thick walls with radial, inhalant and exhalant canals, ×1; c, spinose, parenchymal hexactines from wall, ×25 (Rauff, 1893).
- Scaphiomanon GUTSCHICK & PERRY, 1959, p. 981 [\*S. nodulosum GUTSCHICK & PERRY, 1959, p. 982; OD]. Thick-walled, bowl-shaped, with more or less flat base and rounded sides curving in toward wide, oscular opening; cloaca of same diameter as osculum; large, exhalant canals with tributaries enter cloaca from below and sides, separated by less than their diameter; exterior bearing ostia smaller than exhalant canals; each ostium is infundibuliform and leads into an inhalant canal; small, meandriform canals occur within wall but internal connections of canal system not clear; spicules poorly preserved, but include hexactines according to RIGBY (1977b, p. 132). [Assessment of the genus is hampered by poor preservation of the skeleton, but it is placed in the family because of its similarity to Malumispongium RIGBY, 1967b.] Carboniferous (lower Tournaisian): USA (Montana).-FIG. 280, 3a-b. \*S. nodulosum, Kinderhookian, Sappington Sandstone, Three Forks; a, oblique view of bowl-shaped holotype with broad osculum; b, median, vertical section showing broad spongocoel and coarse, parietal gaps, filled with light matrix, and thick walls of holotype, USNM 137942, ×0.5 (Gutschick & Perry, 1959).

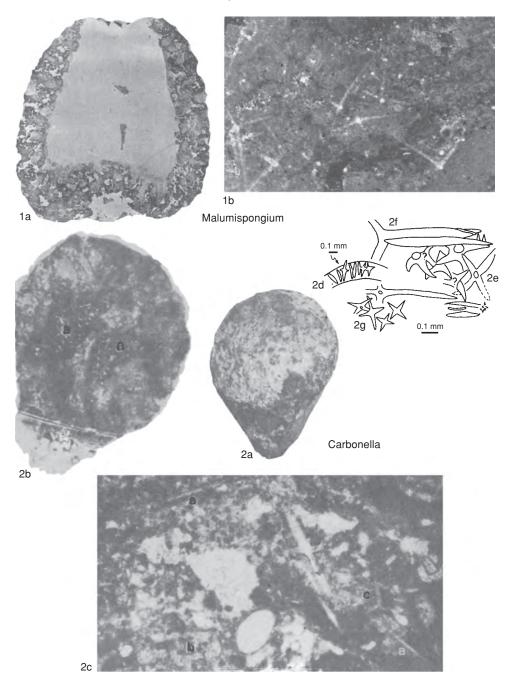


FIG. 279. Malumispongiidae (p. 426).

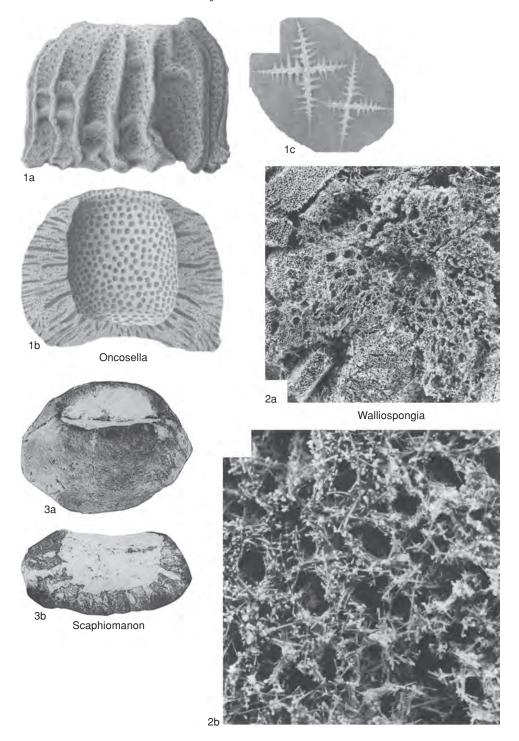


FIG. 280. Malumispongiidae (p. 426-429).

Walliospongia RIGBY & WEBBY, 1988, p. 82 [\* W. gracilis RIGBY & WEBBY, 1988, p. 83; OD]. Saucer shaped to low-conical with delicate, open, porous, skeletal net of fine and uniformly sized hexactines, all irregularly oriented around major, excurrent canals that converge upwardly and inwardly toward spongocoel; incurrent canals in tracts between excurrent series in full diplorhysis; both series end blindly; gastral spicules with four tangential rays; dermal layer ill defined; canals not in rectangular pattern. Upper Ordovician: Australia (New South Wales).—FIG. 280,2a-b. \*W. gracilis, Malongulli Formation, Cliefden Caves area; a, view down into open, saucer-shaped spongocoel showing form of species and its delicate skeleton with moderately uniformly spaced ostia of radial canals on gastral surface,  $\times 2$ ; b, photomicrograph of gastral surface with excurrent openings of radial canals and open-textured skeleton composed of moderately irregularly oriented, small hexactines, AMu. F66903, ×10 (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

# Family TOOMEYOSPONGIIDAE new family

[Toomeyospongiidae FINKS & RIGBY, herein] [type genus, *Toomeyospongia* RIGBY, HORROCKS, & CYS, 1982, p. 317]

Massive hemispherical to bowl-shaped or tubular brachiospongiids with prominent, coarse, exhalant canals but less well defined inhalant openings in thick walls, skeleton of irregularly oriented hexactines and hexactine-derived spicules; prominent, dermal layer of coarse pentactines or hexactines with regular, subparallel orientation of tangential rays. *Permian (Guadalupian).* 

Toomeyospongia RIGBY, HORROCKS, & CYS, 1982, p. 317 [\*T. apachensis RIGBY, HORROCKS, & CYS, 1982, p. 318; OD]. Massive, subhemispherical sponge with coarse stauracts and pentactines as dermalia, which have regular orientation and strongly reflexed tangential rays, but without supernumerary rays or sculpture on distal surface of pentacts, other than single nodes near base of each tangential ray; equalsized dermalia overlap to outline quadrules of one ray length; interior skeleton of variously sized and irregularly oriented hexactines or reduced derivatives, including numerous tauactines (and possible rhabdodiactines) among smaller sizes; interior skeleton perforated by coarse, circular, radial (possible exhalant) canals, which do not penetrate through dermal layer, and by smaller, interconnected, canal series. [Genus differs from Docoderma FINKS, 1960, in the absence of extra, paratangential rays.] Permian (Guadalupian): USA (Texas), Mexico (?Sonora).—FIG. 278, 1a-c. \*T. apachensis, Lamar Limestone of Bell Canyon Formation, Capitanian, Apache Mountains, Texas; *a*, weathered, lateral surface of silicified holotype with large, systematically oriented, dermal pentactines, top of sponge is to upper right, USNM 304046,  $\times 1$ ; *b*, polished surface through holotype showing nonvasiform nature of sponge and large, circular, matrix-filled canals of central part of sponge,  $\times 1$ ; *c*, view up into region directly below dermal layer in paratype showing reflexed tips of dermal pentacts and smaller hexactines that unite in strong skeleton, USNM 303046b,  $\times 2$  (Rigby, Horrocks, & Cys, 1982).

## Superfamily LUMECTOSPONGIOIDEA Rigby & Chatterton, 1989

[nom. transl. FINKS & RIGBY, herein, pro Lumectospongiidae RIGBY & CHATTERTON, 1989, p. 39]

Hexastrophoran sponges with thickwalled skeleton mainly of irregularly felted uncinates, and less commonly, irregularly spaced and oriented, smooth-rayed hexactines. [Certain taxonomic placement of these sponges is impossible because definitive microscleres have not been observed in them. RIGBY and CHATTERTON (1989), however, placed tentatively the then-described single family within the lyssacinosid Hexasterophora because of the common occurrence of uncinates within that subclass. They also observed that these sponges lack dictyonal strands and, thus, were included in the Lyssacinosa ZITTEL, 1877b. That placement is continued here. The Lumectospongioidea RIGBY & CHATTERTON, 1989, lack the enlarged hypodermalia or hypogastralia that characterize the associated Brachiospongioidea BEECHER, 1889.] Silurian (Ludlow).

#### Family LUMECTOSPONGIIDAE Rigby & Chatterton, 1989

[Lumectospongiidae RIGBY & CHATTERTON, 1989, p. 39]

Hexactinellids with skeleton principally an irregular, felted mass of uncinates with less common, irregularly spaced and oriented, smooth-rayed hexactines. *Silurian* (Ludlow).

Lumectospongia RIGBY & CHATTERTON, 1989, p. 39 [\*L. uncinata RIGBY & CHATTERTON, 1989, p. 40; OD]. Thin-walled, obconical to bowl- or cupshaped skeleton of uncinates and less common,

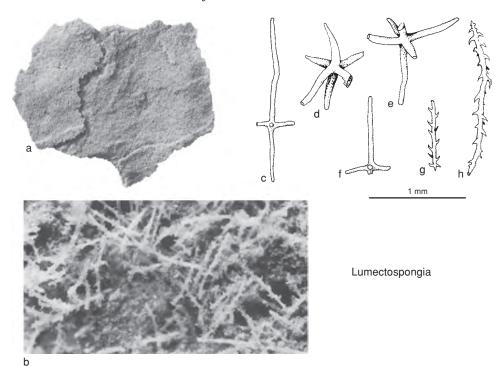


FIG. 281. Lumectospongiidae (p. 429-430).

smooth hexactines of same size in felted mass; hexactines irregularly oriented and spaced; pores widely spaced and ill defined. Silurian (Ludlow): Canada (Northwest Territories, Baillie-Hamilton Island).-FIG. 281a-h. \*L. uncinata, Cape Phillips Formation, Baillie Hamilton Island; a, side view of flattened and folded, thin-walled holotype showing smooth surface and uniform texture of wall composed of felted mass of uncinates,  $\times 1$ ; b, photomicrograph of irregularly oriented uncinates in gastral skeleton, ×50; c-h, camera lucida drawings of spicules of holotype, c-f, more or less uniform hexactines, g-h, spinose uncinates that make up most of skeleton, UA 7732, ×25 (Rigby & Chatterton, 1989; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

## Order HEXACTINOSA Schrammen, 1903

[nom. transl. DE LAUBENFELS, 1936, p. 185, ex Tribus Hexactinosa Schrammen, 1903, p. 4; sensu Schrammen, 1912, p. 190]

Hexasterophora with dictyonal strands that do not bear lychnisc nodes. *Upper Ordovician–Holocene*.

## Superfamily PILLARASPONGIOIDEA Rigby, 1986

[nom. transl. FINKS & RIGBY, herein, pro Pillaraspongiidae RIGBY, 1986b, p. 40]

Hexasterophora with dictyonal, euretoid, thick-walled skeletons and primary canals in full diarhyses. *Devonian (Frasnian– Famennian)*.

#### Family PILLARASPONGIIDAE Rigby, 1986

[Pillaraspongiidae RIGBY, 1986b, p. 40]

Skeleton dictyonal, euretoid, with thick walls and primary canals in full, welldeveloped diarhyses; canals in simple, vertically stacked series. *Devonian (Frasnian– Famennian)*.

Pillaraspongia RIGBY, 1986b, p. 40 [\*P. ellimberia RIGBY, 1986b, p. 41; OD]. Obconical to globular, thick walled, with well-defined spongocoel and coarse, radial diahryses in regular pattern in vertical



FIG. 282. Pillaraspongiidae (p. 430-431).

series; skeletal net euretoid with framework bilateral, nearly symmetrical, strands diverging upwardly and outwardly in outer wall and inwardly in inner part; apparently without differentiated dermalia, gastralia, and cortex. *Devonian (Frasnian– Famennian):* Western Australia.——FIG. 282*a–c. \*P. ellimberia,* Virgin Hills Formation, Lawford Range; *a*, side view of holotype showing inhalant canals filled with dark matrix and an ill-defined osculum filled with matrix at summit, GSWA F7231,  $\times$ 1; *b*, oblique view of paratype with large, radial, parietal gaps in thick walls around matrix-filled spongocoel, GSWA F7232,  $\times$ 1; *c*, photomicrograph showing fused, rectangular, skeletal net in horizontal, thin section of paratype, GSWA F7233,  $\times$ 10 (Rigby, 1986b).

## Superfamily PILEOLITOIDEA Finks, 1960

## [*nom. transl.* FINKS & RIGBY, herein, *pro* Pileolitidae FINKS, 1960, p. 139]

Hexasterophora with layers of dictyonal strands in aulocalycoid organization parallel to layers, together with hexactines and rhabdodiactines connected by synapticulae; layers parallel to gastral surface; sponges grew by adding new layers gastrally and by extending layers peripherally; spicules of dermal surface ornamented with spherical nodes, perhaps at crossings of dictyonal strands; sub-euretoid to euretoid structure may be developed. *Upper Ordovician– Holocene.* 

#### Family PILEOLITIDAE Finks, 1960

#### [Pileolitidae FINKS, 1960, p. 139]

All layers of one kind, and parallel to upper (possibly gastral) surface; dictyonal strands, or hexactines or rhabdodiactines, oriented irregularly within layer; no cloaca; vertical aporhyses perpendicular to layers; rhabdodiactines perpendicular to layers, some bundled, some single, many free in aporhyses; dermal layer on base and sides, with stouter spicules and spherical nodes, is composed of same spicule types as interior layers, but on sides of sponge layer oriented perpendicularly to interior layers; component strands of this lateral, dermal layer mostly oriented irregularly, although occasionally may have parallel, vertical strands; base flat; hexasters present. Permian (?Asselian-?Sakmarian, Artinskian)-Middle Triassic.

Pileolites FINKS, 1960, p. 139 [\**P. baccatus* FINKS, 1960, p. 140; OD]. Small cake, wedge, or thimbleshaped sponges with characteristics of family; tangential, dermal layer fused to inner, dictyonal strands and consisting of coarser spicules or dictyonal strands, in which distal rays are replaced by spherical knobs; internal (parenchymal), dictyonal strands parallel to upper surface and fused to one another by synapticulae and at points of mutual contact; dictyonal strand layers penetrated by perpendicular, cylindrical aporhyses that run from just inside basal, dermal layer to upper surface of sponge; long, fusiform rhabdodiactines oriented vertically in aporhyses and in parenchymal, dictyonal net; oxyhexasters in sediment accompanying type specimens. Permian (?Asselian-?Sakmarian, Artinskian): USA (Texas).-FIG. 283,1a-c. \*P. baccatus, Leonard Formation, Glass Mountains; a, enlarged view of basal (or possibly side) of paratype with well-developed, spherical nodes in place of distal rays on tangential dermalia, USNM 127668f, ×10; b, enlarged view of open-textured, basal surface of paratype with spherical nodes less well developed, but with irregular orientation of long, slender rays and their common cross connection with synapticulae, tangential rays thickened with secondary silica,  $\times 10$ ; c, top surface of paratype showing long, tangential rays of irregularly oriented, choanosome spicules united into a continuous net with synapticulae, particularly in ladderlike clusters, USNM 127668e, ×10 (Finks, 1960; courtesy of The American Museum of Natural History).

Hexactinoderma PISERA & BODZIOCH, 1991, p. 196 [\*H. trammeri PISERA & BODZIOCH, 1991, p. 197; OD]. Thick-walled, tubular or deep, cup-shaped lyssacinosans with distinct, similar, dermal and gastral layers of fused hexactines with rays of various sizes and lengths, distal rays short or aborted but tangential and proximal rays elongate; these layers covering dermal and gastral ends of dominantly radial canals, which may branch; spicules of dermal layer without spherical knobs replacing aborted, distal rays. [Hexactinoderma resembles Cypellospongia RIGBY & GOSNEY, 1983, in having a distinct, dermal layer, but in Cypellospongia that layer is composed of delicate hexactines rather than of robust hexactines. The two genera also differ in general shape. Hexactinoderma differs from *Pileolites* FINKS, 1960, in lacking the coarse, dermal knobs in place of aborted, distal rays on spicules of the dermal layer. Hexactinoderma is placed in the family with some question.] Middle Triassic: Poland.—FIG. 283,2a-c. \*H. trammeri, Muschelkalk, Karchowice beds, Anisian, Strzelce Opolskie; a, holotype interior with gastral layer,  $\times 0.75$ ; b, gastral surface of holotype with specialized hexactines and ostia of canals, ZPAL PfV/20, ×15; c, interior of endosomal skeleton where individual hexactines show in more open structure, ZPAL PfV/5, ×10 (Pisera & Bodzioch, 1991).

#### Family WAREEMBAIIDAE new family

[Wareembaiidae FINKS & RIGBY, herein] [type genus, *Wareembaia* RIGBY & WEBBY, 1988, p. 85]

Layers conoidal, surrounding cloaca; of differing organization within each layer; outermost layer sub-euretoid with dictyonal strands (and possibly rhabdodiactines) parallel to one another, and perpendicular to (upper or outer) growing edge of layer; external, spherical nodes confined to exposed parts of this layer on sides of sponge, but not on base; next interior layer aulocalycoid,

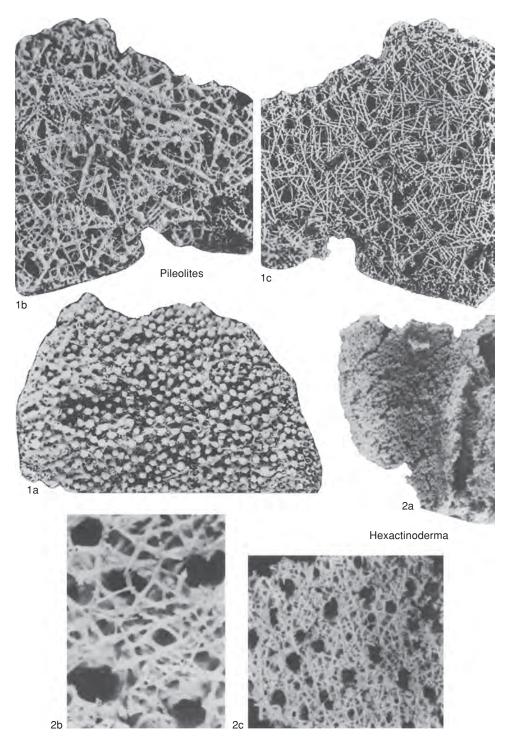


FIG. 283. Pileolitidae (p. 432).

with curved, dictyonal strands mostly subhorizontal; radial, bladelike, inward extensions of this layer separate vertical, exhalant spaces between this layer and next interior layer, which is aulocalycoid with irregularly oriented, curving, dictyonal strands (and possible hexactines or rhabdodiactines) parallel to layers; this sequence of layers may be repeated inwardly and upwardly, cone-in-cone like; transverse sieve of hexactines may cross cloaca at base, and possibly at oscular end. *Upper Ordovician*.

Wareembaia RIGBY & WEBBY, 1988, p. 85 [\* W. concentrica RIGBY & WEBBY, 1988, p. 86; OD]. Subcylindrical, stemlike, with expanded base; specialized, sievelike, gastral layer (or possible oscular sieve) surrounding possible central osculum; cylindrical part consisting of imbricate, conical sheets of spicules (like cone-in-cone, expanding upwardly); each sheet composed of outer layer of parallel, closely spaced, vertically oriented, stout rhabdodiactines or dictyonal strands, next inner layer of finer, paratangential, sinuous, mostly subhorizontal, possible dictyonal strands connected by synapticulae; both these layers produced toward interior as radial, vertical blades that separate parallel, vertical canals; inner ends of these blades connect with innermost layer of paratangential, irregularly oriented, interlaced, stout, curving, very long hexactines or rhabdodiactines, or dictyonal strands; stout vertical elements of outer layer appear to arise from subhorizontal dictyonal strands, curving upwardly like candelabra; where these vertical elements reach exterior surface, their outer surfaces becoming coated with a single series of spherical nodes (possibly corresponding to spicule crossings within dictyonal strands) that become larger upwardly; innermost layer of large curving spicules or strands also repeated cone-in-cone-wise, separated by zones of vertical canals; it is likely that these are the same vertical canals that underlie two outer layers and that each inner layer becomes successively transformed upwardly into next outer layer as expanding cone nears outer surface; very center of cylinder is a shallow, possible spongocoel; in basal expansion, vertical elements of outermost layer are subhorizontal and radial and do not bear spherical nodes, they radiate from a circular area (base of possible spongocoel), which in well-preserved examples contains a grid of parallel, large hexactines, surrounded by a circle of innermost layer of tangential spicules; surrounded by zone of canals separated by radial, bladelike extensions of outer two layers (it is clear that this is beginning of nested series of layers). [Wareembaia somewhat resembles the Permian Pileolites FINKS, 1960, but differs in the arrangement of the parts. The horizontal layers of the main skeleton of *Pileolites* correspond to the obliquely

vertical, innermost layers of Wareembaia. The spherical nodes on the external surfaces of Pileolites are almost identical to those on Wareembaia, but the vertical rhabdodiactines or dictyonal strands on which they occur in the latter are not present in Pileolites, unless the vertical rhabdodiactines in the interior of Pileolites are their homologues. Pileolites is a simpler sponge than Wareembaia. If the two are in fact related, the history of the hexactinosan Hexasterophora goes back to the Ordovician.] Upper Ordovician: Australia (New South Wales) .-FIG. 284a-e. \*W. concentrica, Malongulli Formation, Cliefden Caves area; a, side view of holotype showing relationships of flaring, dermal layer, with dictyonine structure, to canal system that separates it from endosomal part of skeleton that has an irregularly spiculed structure,  $\times 2$ ; b, vertical view down into central spongocoel and showing endosomal skeleton with alternating layers of dense and open texture, ×2; c, vertical view of basal attachment surface showing radiating, irregularly fibrous, crudely dictyonine net and hexactine-based skeleton above, ×5; d, enlarged side view showing nature of spiculation of outer, fused, dictyonine, dermal layer and less regularly oriented, principal, endosomal net made of long-rayed hexactines, AMu. F66905, ×5; e, photomicrograph of fused, dictyonine, dermal layer of paratype showing dermal nodes and taper of vertical rays, with en echelon replacement, that are fused laterally by horizontal elements, layer pierced by small pores, AMu. F66909, ×20 (Rigby & Webby, 1998; courtesy of Paleontological Research Institution, Ithaca).

Kalimnospongia RIGBY & WEBBY, 1988, p. 87 [\*K. pertusa; OD]. Open, conical to frondescent with multi-layered walls; inner layer with large ostia bordered by rays of large hexactines; ostia subdivided by ten finlike, radial blades, each more or less supported by hexactine rays that extend into ostium; principal part of skeleton irregularly oriented hexactines and derivatives, all fused at ray crossings with synapticulae or synapticular webs; gastral layer thin, or fused, bubbly-appearing net not obviously hexactine based; dermal layer of two units: inner part a porous, subdermal layer of delicate, widely spaced and irregularly oriented, hexactine-based spicules with curved rays largely tangential; outer part of dermal layer fused, vertically elongate, dictyonine hexactines in picketfence-like structure with principal rays vertical, secondary proximal and distal rays more limited but thoroughly fused into solid structure, synapticulae also occurring in dermal layer. [Kalimnospongia might be only the upper, broadly expanding, funnel-like part of a more complex sponge, if it and Wareembaia are parts of a single species (RIGBY & WEBBY, 1988, p. 89). They certainly have considerable structural similarity in their distinctive, dermal layers, but they differ in skeletal structure internally. Until additional material is investigated and the two types of structure are found as part of one sponge, they will be treated as

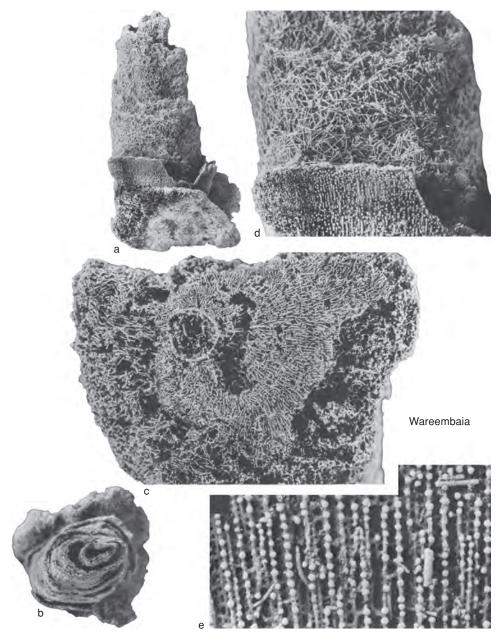


FIG. 284. Wareembaiidae (p. 434).

separate taxa.] Upper Ordovician: Australia (New South Wales).——FIG. 285a-d. \*K. pertusa, Malongulli Formation, Cliefden Caves area; a, holotype (arrow), associated with several other genera of sponges, including coarse-textured, skeletal elements around open-bladed pore (1), as well as dense, thin-walled, frond fragments immedi-

ately below (2),  $\times 1.6$ ; *b*, gastral view of a large pore with bladed partitions and surrounding endosomal and gastral parts of skeleton; coarse hexactine rays are reflexed and supporting blades in pore, beyond which are coarse, endosomal hexactines that are locally united with synapticulae into asolid structure, and overlie irregularly

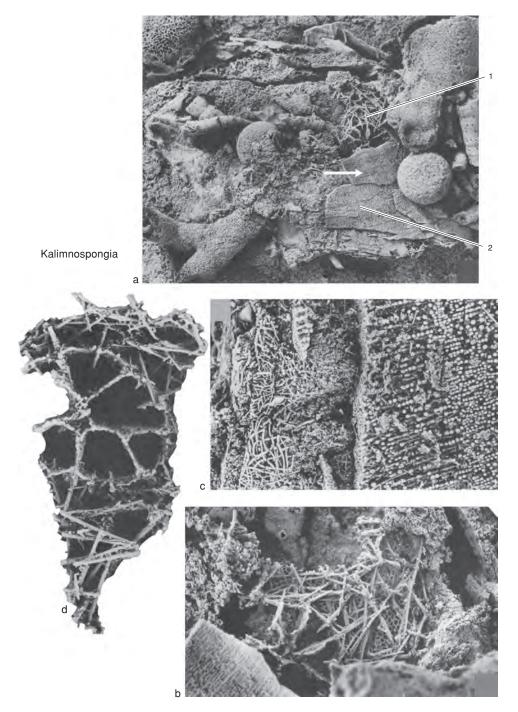


FIG. 285. Wareembaiidae (p. 434-437).

vesicular gastral layer in background,  $\times 3$ ; *c*, photomicrograph of dictyonine, outer layer and underlying, irregular, endosomal layer of thin-walled part of sponge, which are reminiscent of *Wareembaia*, AMu. F66915,  $\times 7.5$ ; *d*, endosomal view of paratype showing bladed pore and irregular, coarse hexactines with synapticulae around pore, AMu. F66916,  $\times 5$  (Rigby & Webby, 1988; courtesy of Paleontological Research Institution, Ithaca).

#### Family EURETIDAE Zittel, 1877

[Euretidae ZITTEL, 1877b, p. 35] [=Monakidae MARSHALL, 1876, p. 121; Coscinoporidae ZITTEL, 1877b, p. 36, partim; Maeandrospongidae ZITTEL, 1877b, p. 38, partim; Chonelasmatidae SCHRAMMEN, 1912, p. 190; Pleurothyrisidae SCHRAMMEN, 1912, p. 192; Myliusiidae DE LAUBENFELS, 1955, p. 82, partim; Wapkiosidae DE LAUBENFELS, 1955, p. 85]

Primary skeletal meshwork three dimensional and not constructed in layers, with subparallel, dictyonal strands in longitudinal or radial orientation ending at dermal surface or some at each surface; some with secondary meshwork in which dictyonal strands are absent, other than in primary meshes; skeletal canalization normally absent or limited to skeletal pores (ostia, postica) or shallow, radial canals (epirhyses, aporhyses) that open into underlying meshes; some with true, radial canals but not in regular series; amararhyses in one genus; modified, primary meshwork or added secondary meshwork may form dictyonal cortex at one or both surfaces. Modern forms normally with scopules, rarely sarules or no sceptrules, never clavules. [Only Paleozoic forms are discussed here. Younger forms are treated in the section on Mesozoic hexactinosans, p. 463 herein.] Upper Devonian (Frasnian).

Paleoramospongia RIGBY & PISERA in RIGBY & others, 2001, p. 470 [\*P. bifurcata; OD]. Branched, medium-sized hexactinosan sponges with deep spongocoel in each branch; canals in possible diplorhysal pattern in dictyonine skeleton with asymmetric, upwardly expanding structure where primary strands are at or near gastral margin. [Genus is questionably included in family Euretidae.] Upper Devonian (Frasnian): Poland.——FIG. 286, Ia-c. \*P. bifurcata, Holy Cross Mountains; a, longitudinal section of holotype, slightly etched, showing branching form and deep spongocoel in each branch, ZPAL Pf.XI/207; b, oscular view of branched reference specimen, ZPAL Pf.XI/51, ×1; c, dictyonine, skeletal structure of holotype in longitudinal thin section, ×10 (Rigby & others, 2001).

Paleoregulara RIGBY & PISERA in RIGBY & others, 2001, p. 468 [\*P. cupula; OD]. Small, steeply obconical to barrel-shaped hexactinosan sponges with regular, three-dimensional, skeletal net uninterrupted by major canals. Upper Devonian (Frasnian): Poland.——FIG. 286,2a-b. \*P. cupula, Holy Cross Mountains; a, side view showing regular, skeletal network in cylindrical paratype, ZPAL Pf.XI /69, ×2; b, regular, skeletal network in polished, longitudinal section of paratype, ZPAL Pf.XI142, ×10 (Rigby & others, 2001).

#### Family CRATICULARIIDAE Rauff, 1893

[Craticulariidae RAUFF, 1893, p. 191] [=Euretidae ZITTEL, 1877b, p. 35, partim; Leptophragmidae SCHRAMMEN, 1912, p. 191; Craticularinae DE LAUBENFELS, 1936, p. 186; Leptophragmatidae DE LAUBENFELS, 1955, p. 80; Laocaetidae MEHL, 1992, p. 71]

Skeletal framework three dimensional initially, constructed as in Euretidae, but normally with fully developed epirhyses and aporhyses; skeletal canals typically radial and blind, arranged with epirhyses and aporhyses in alternating, longitudinal series, and often so that each canal of one sort stands quincuncially between four of others; apertures then arranged in longitudinal and transverse rows; some genera with epirhyses open at both ends or arranged without order, or without aporhyses in some individuals; dictyonal strands spreading subequally to both surfaces from interior, or running mainly or all to dermal surface; beams between ends of strands usually forming cortical meshwork, which secondary accretions may make thicker or denser; superficial meshwork in some genera, formed from dictyonal hexactines, or additionally by ankylosis of dermal or gastral stauractines; scopules in a living example. [Only Upper Devonian forms are treated here. Other genera of the family and their subfamilies are discussed in the section on Mesozoic dictyonine sponges, p. 476 herein.] Upper Devonian.

Conicospongia RIGBY & PISERA in RIGBY & others, 2001, p. 483 [\*C. annulata; OD]. Obconical, weakly annulate, large hexactinosans with deep,

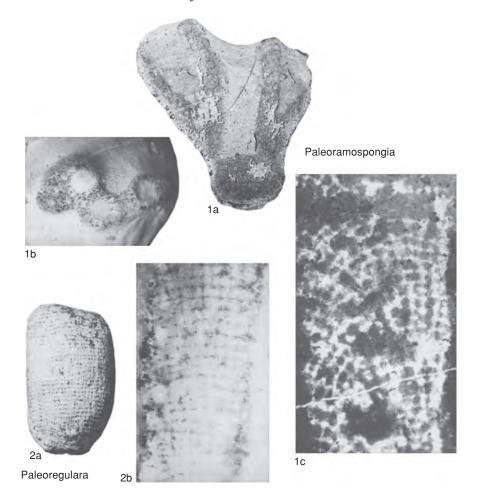


FIG. 286. Euretidae (p. 437).

V-shaped spongocoel and thick walls pierced by densely, but irregularly, spaced canals in diplorhysal pattern; skeleton symmetrical with primary strands in midwall diverging gently toward both dermal and gastral surfaces. *Upper Devonian (Frasnian):* Poland.——FIG. 287*a-c.* \**C. annulata*, Holy Cross Mountains; *a*, side view of holotype, ZPAL Pf.XI/ 321; *b*, longitudinal section of reference specimen showing thick walls and oblique canals, ZPAL Pf.XI/194, ×0.5; *c*, details of dictyonal, skeletal structure in same reference specimen, ×0.75 (Rigby & others, 2001)

**Cordiospongia** RIGBY & PISERA in RIGBY & others, 2001, p. 471 [\**C. conica* RIGBY & PISERA in RIGBY & others, 2001, p. 472; OD]. Broadly obconical, small- to medium-sized, heart-shaped, hexactinosan sponges, with deep, axial spongocoel and irregular, craticulariid, canal system in which both inhalant and exhalant canals flex downwardly into midwall; dictyonine skeleton expanding upwardly and outwardly, with primary strands at or near gastral margin. *Upper Devonian*: Poland.——FIG. 288, *Ia-c.* \**C. conica*, Holy Cross Mountains; *a*, longitudinal section of holotype showing deep spongocoel and nature of walls and canal development, ZPAL Pf./XI/85, ×1; *b*, inhalant ostia and nature of skeletal net as exposed on dermal surface of holotype; *c*, polished, longitudinal section of holotype showing structure of skeletal net, ×10 (Rigby & others, 2001).

Paleocraticularia RIGBY & PISERA in RIGBY & others, 2001, p. 474 [\*P. elongata; OD]. Large or medium-sized, tubular hexactinosan sponges with simple spongocoel and diplorhysal, canal system; canals in distinct, vertical rows producing ribbed exterior; dictyonine skeletal structure diverging



FIG. 287. Craticulariidae (p. 437-438).

gently in symmetrical pattern but meeting dermal surface at moderate angles and gastral surface at low angles. Upper Devonian (Frasnian): Poland. ——FIG. 288,2a-b. \*P. elongata, Holy Cross Mountains; a, weathered holotype showing form of sponge with ribbed exterior produced by vertically aligned, inhalant ostia, ZPAL Pf.XI/20, ×1; b, regular, skeletal net in polished, longitudinal section of holotype, ×10 (Rigby & others, 2001).

Polonospongia RIGBY & PISERA in RIGBY & others, 2001, p. 476 [\**P. devonica* RIGBY & PISERA in RIGBY & others, 2001, p. 478; OD]. Large, cylindrical, hexactinosan sponges with deep spongocoel and coarse, irregular, diplorhysal, canal pattern; skeleton asymmetric with primary strands parallel to gastral margin but divergent toward dermal margins at high angles. *Upper Devonian* (*Frasnian*): Poland.—FIG. 289, *Ia-d.* \**P.*  devonica, Holy Cross Mountains; *a*, side view of cylindrical holotype showing irregular distribution of dermal ostia, ZPAL Pf.XI/212,  $\times 0.37$ ; *b*, transverse section of holotype showing wall thickness and canal pattern,  $\times 0.37$ ; *c*, polished, longitudinal section of paratype, with outer surface to right, showing nature of skeletal net, ZPAL Pf.XI/209,  $\times 7.5$ ; *d*, weathered surface showing skeletal net and distribution of inhalant ostia in paratype, ZPAL Pf.XI/23,  $\times 7.5$  (Rigby & others, 2001).

Urnospongia RIGBY & PISERA in RIGBY & others, 2001, p. 482 [\*U. modica; OD]. Large, broadly obconical, stalked, hexactinosan sponges with shallow spongocoel; canal system irregularly diplorhysal, with vertical, exhalant canals in massive base and parallel strands in upper walls; inhalant canals may empty into these canals rather than into spongocoel; skeleton upwardly divergent from near midwall, primary strands diverging



FIG. 288. Craticulariidae (p. 438-439).

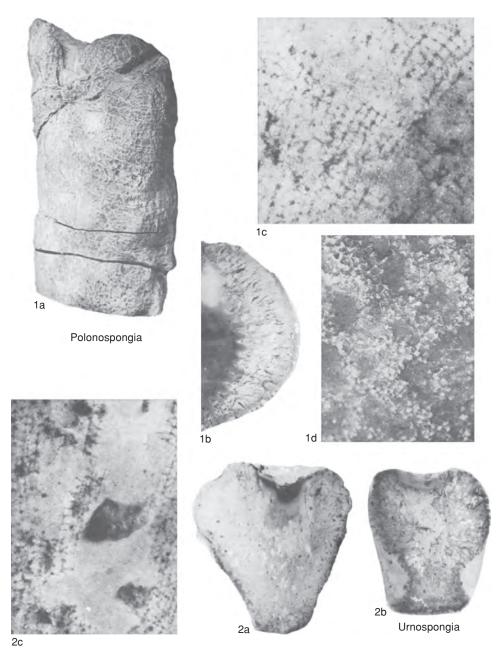


FIG. 289. Craticulariidae (p. 439-441).

abruptly toward dermal surface and gently toward gastral surface. *Upper Devonian (Frasnian):* Poland.——FIG. 289,2*a–c.* \**U. modica,* Holy Cross Mountains; *a*, longitudinal section of holotype showing shallow spongocoel with basal cluster of vertical, exhalant canals and thick walls, ZPAL

Pf.XI/25, ×0.5; *b*, longitudinal, polished section of reference section to show shape, wall thickness, and canal development, ZPAL Pf.XI/201, ×0.50; *c*, photomicrograph of longitudinal section of reference specimen showing skeletal organization and canals, ×7.5 (Rigby & others, 2001).

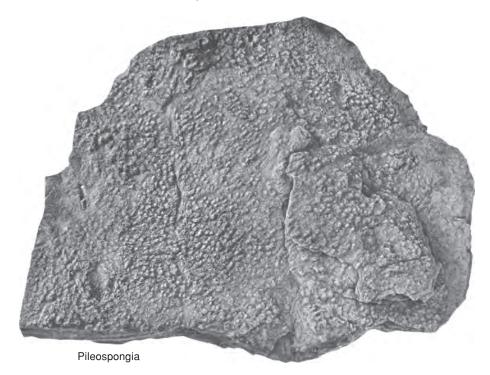


FIG. 290. Pileospongiidae (p. 442).

## Family PILEOSPONGIIDAE Rigby, Keyes, & Horowitz, 1979

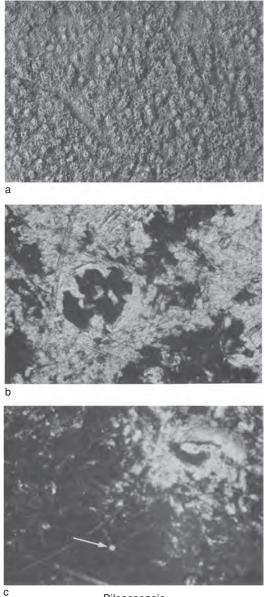
[Pileospongiidae RIGBY, KEYES, & HOROWITZ, 1979, p. 712]

Massive, encrusting sponges with inhalant and exhalant canals opening on same surface; skeletal net built of layers, parallel to surface, composed of irregularly oriented rhabdodiactines, with fewer numbers of hexactines. *Carboniferous (Serpukhovian)*.

Pileospongia RIGBY, KEYES, & HOROWITZ, 1979, p. 713 [\*P. lopados; OD]. Discoidal, thinning toward rounded edges; upper surface covered with small, closely spaced papillae of uniform size, each bearing a terminal pore (osculum); papillae locally basally confluent along ridges that radiate from central area; obscure, dendritic, surface grooves between some of papillae also radiate away from center; large, vertical canals (possibly exhalant) open onto tips of papillae; both papillae and canals may be inclined toward periphery; smaller, vertical canals (possibly inhalant) opening onto surface between papillae; horizontal canals parallel to upper surface (possibly corresponding in part to surface grooves) may connect vertical canals; spicules organized in layers parallel to upper surface; they are nonparallel to one another, are tangent to outlines of vertical canals, radially arranged about each papilla, and parallel to upper surface; most spicules appear to be small, smooth, straight, or slightly curved rhabdodiactines, with fewer numbers of somewhat smaller hexactines; basal surface encrusting upon shell debris; large, vertical canals do not extend to base. Carboniferous (Serpukhovian): USA (Alabama).-FIG. 290. \*P. lopados, Monteagle Limestone, Weeden-Madkin Mountains, Madison County; central part of nodose holotype with craterlike mounds pierced by vertical canals, ×0.45 (Rigby, Keyes, & Horowitz, 1979).-FIG. 291a-c. \*P. lopados, Monteagle Limestone, Weeden-Madkin Mountains, Madison County; a, section of dermal layer with ostia of canals in nodes, USNM 245146, ×2; b, photomicrograph of horizontal section of paratype showing straight to gently curved diactines outlining vertical canal, USNM 245147, ×20; c, photomicrograph of thin section from holotype with hexactines and diactines around canal, in upper part, USNM 245146, ×20 (Rigby, Keyes, & Horowitz, 1979).

## Order and Family UNCERTAIN

Australispongia DONG & KNOLL, 1996, p. 177 [\*A. sinensis; OD]. Sponges known as isolated, pentactine spicules with four lateral rays of varying length in propeller-like structure normal to proximal or central ray; that ray may be straight or



Pileospongia

FIG. 291. Pileospongiidae (p. 442).

curved to moderately twisted, and flaglike or elaborated into three or four longitudinal flanges, edges of which may be serrate or smooth. [Ordovician and Permian occurrences have been reported by KOZUR, MOSTLER, & REPETSKI, 1996.] Lower Cambrian–Permian (Guadalupian): China (Hunan), Lower Cambrian; USA (Nevada), Tremadocian; USA (Texas), Guadalupian.——FIG. 292,4*a*-*c*. \**A. sinensis*, Bitiao Formation, Upper Cambrian, Huayuan, Hunan, China; *a*, holotype spicule of form A showing four lateral rays at top and flanged, central, lower ray, PDS92030, ×25; *b*, type spicule of form B, ×25; *c*, type spicule of form C, ×25 (Dong & Knoll, 1996).

Chelispongia WEBBY & TROTTER, 1993, p. 32 [\*C. prima; OD]. Isolated spicules with elongate,

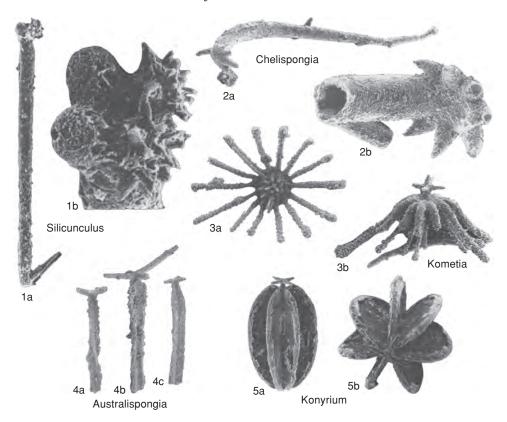


FIG. 292. Uncertain (p. 442-445).

sigmoidal, central ray and small, bulbous, possible proximal tip; opposite end enlarged with recurved, palmate claw with 3 to 11 pointed, tiplike, lateral rays; broken main ray sometimes showing internal axial cavity. Ordovician: Australia (New South Wales).——FIG. 292,2*a–b.* \**C. prima*, Malongulli Formation; *a*, characteristic spicule with swollen tip on one end and clawlike structure on other, SUP 85104, ×20; *b*, spicule fragment showing large, axial cavity and recurved tips of claw, SUP 85105, ×100 (Webby & Trotter, 1993).

Kometia WEBBY & TROTTER, 1993, p. 32 [\*K. cruciformis; OD] [=Flosculus DONG & KNOLL, 1996, p. 175 (type, F. gracilis DONG & KNOLL, 1996, p. 177, OD)]. Modified hexactine spicules with small, propeller-like structure of four pointed, lateral rays diverging at right angles from two central rays; latter comprise small, unmodified, pointed tip toward one pole and a much modified, central ray in opposite direction, with expanded, attachment disc (umbel) extending into an outwardly and backwardly radiating series of long, weakly club-shaped, hispid, accessory rays, with outer ones best developed. Upper Cambrian-Upper Ordovician: China, Upper Cambrian; Australia, Upper Ordovician.—FIG. 292,3a-b. \*K. cruciformis, Malongulli Formation, Upper Ordovician, New South Wales, Australia; a, view of numerous rays of possible proximal part of paratype spicule, SUP 85121; b, side view of holotype spicule with propeller-like structure above and expanded ray cluster below, SUP 85120, ×50 (Webby & Trotter, 1993).

- Konyrium NAZAROV & POPOV, 1976, p. 41 [\*K. varium; OD]. Isolated, distinctly pentactine spicules with prominent propeller at one pole consisting of four lateral rays that diverge essentially at right angles in plane slightly off perpendicular to spicule axis; thin vanes diverging radially from spicule axis and with outer, somewhat thickened, arched margins. Upper Cambrian-Middle Ordovician: Australia (Queensland), Canada (Northwest Territories), Upper Cambrian; Kazakhstan, Canada (Newfoundland), USA (Texas), Middle Ordovi--FIG. 292, 5a-b. K. mariae BENGTSON, cian.— Mungerebar Limestone, Mindyalian, western Queensland, Australia, holotype spicule; a, from side, ×50; *b*, from below, ×200 (Bengtson, 1986).
- Silicosphaera HUGHES, 1985, p. 603 [\*S. asteroderma; OD]. Siliceous, spheroidal bodies with latticelike, outer shell and single aperture and central cavity; prominent hollow, radial rays forming much of

## Uncertain

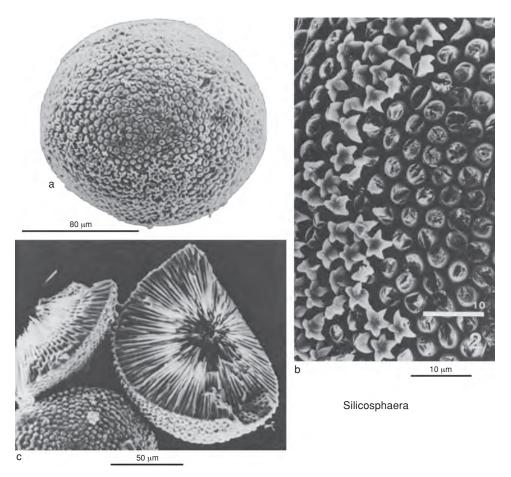


FIG. 293. Uncertain (p. 444-445).

body and with outer, 4- to 5-rayed terminations that are closely spaced so rays may touch but not in growth contact. *Neogene (Miocene)–Holocene:* South China Sea.— FIG. 293*a–c. \*S. asteroderma,* Holocene mud, Sedili River, western Malaysia; *a*, exterior view of spheroidal holotype, scale bar, 80 µm; *b*, detail view of outer surface of holotype with rayed terminations preserved on left, where not abraded, scale bar, 10 µm; *c*, broken holotype showing radial structure, central cavity, and outer layer, Sample Sedili F10, Robertson Research Laboratories, Singapore, scale bar, 50 µm (Hughes, 1985; courtesy of *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*).

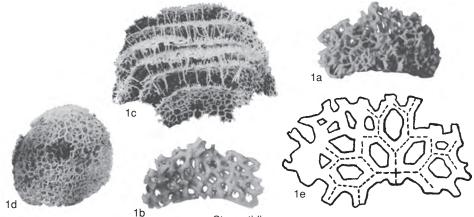
Silicunculus BENGTSON, 1986, p. 200 [\*S. australiensis BENGTSON, 1986, p. 201; OD]. Isolated spicules consisting of a long ray, either straight or slightly curved, bearing a long, slender tip, sharply recurved at acute angle, and at other end, four spinose protuberances resembling aborted, paratangential rays of a pentactine. [This was interpreted as a hexactinellid spicule, but it is so peculiar for a sponge that one wonders whether it is not a scolecodont or other nonporiferan skeletal element.] *Cambrian (Furongian):* Australia (Queensland).——FiG. 292, Ia-b. \*S. australiensis, Mindyalian, Mungerebar Limestone, western Queensland; *a*, holotype spicule with recurved tip and protuberances on upper end, ×50; *b*, enlargement of upper end to show details, UNE F16418, ×250 (Bengtson, 1986).

## Class and Order UNCERTAIN

## Family STROMATIDIIDAE Finks, 1960

#### [Stromatidiidae FINKS, 1960, p. 136]

Skeleton composed of layers of possible pentactines with bifurcated rays, the missing ray being distal. [REID (personal communication) is of the opinion that the spicules are modified demosponge tetraxons rather than



Stromatidium

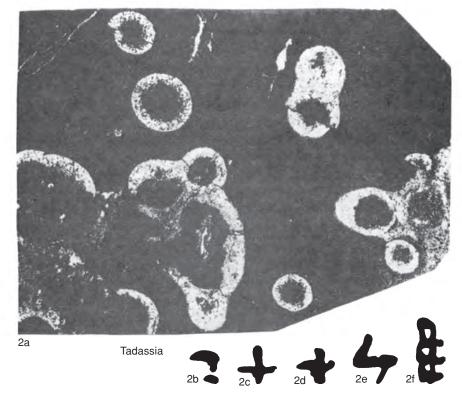
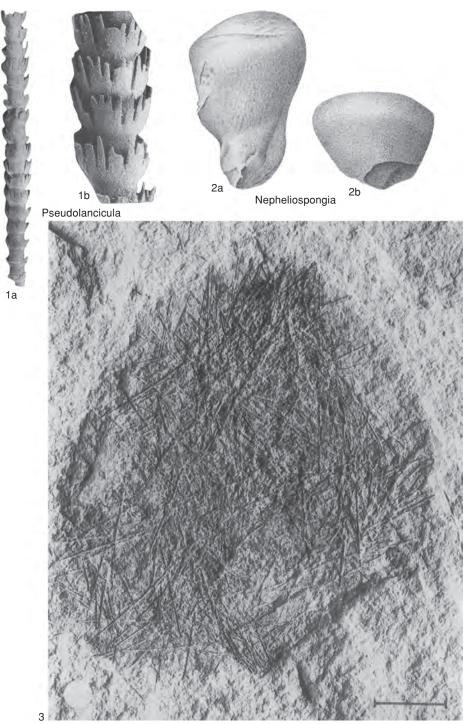


FIG. 294. Stromatidiidae and Tadassiidae (p. 446-448).

hexactinellid pentactines, based on the presence of similar pseudopentactines in some living demosponges. In addition to the Late Permian *Stromatidium typicale*, REID has found similar, but apparently nonfused, spicules in the Carboniferous (Mississippian).] *Carboniferous (Guadalupian)–Permian.*  Stromatidium GIRTY, 1909, p. 77 [\*S. typicale; OD]. Cylindrical sponges with central cloaca; skeleton composed of domical layers, parallel to upper surface, of fused, spinose spicules having form of pentactines with repeatedly bifurcated, paratangential rays; downwardly directed, proximal ray usually terminally bifurcated; upper surface of paratangential rays and sides of proximal rays are densely spinose. *Permian (Guadalupian):* USA



Solactiniella

FIG. 295. Uncertain (p. 448).

(Texas) .---- FIG. 294, 1a-e. \*S. typicale, Bell Canyon Formation, Delaware Mountains; a, lectotype from interior showing complex nature of fused skeleton, ×10; b, dermal view of lectotype showing coarser, fused rays of fragment, USNM 118134a, ×10 (Girty, 1909); c, side view of silicified specimen showing arched layers of silicified, fused pentactines, at bottom right four primary rays of a spicule form a small, rectangular cross, AMNH 28080, ×5; d, view of arched, convex top showing oscule in center surrounded by fused, bifurcated rays, ×5; e, camera lucida drawing of fragment of horizontal spicule layer figured by GIRTY (1909, pl. 27,9), with dashed lines indicating fused branches of a single spicule, whose center is shown by the solid cross, ×18 (Finks, 1960; courtesy of The American Museum of Natural History).

## Family TADASSIIDAE Zhuravleva & Pyanovskaya, 1995

[Tadassiidae ZHURAVLEVA & PYANOVSKAYA, 1995, p. 31]

Chambered colonial and single organisms with one or two walls; chambers nearly spherical to irregularly elongate and may be in shapeless heaps or clusters; chamber walls with irregularly distributed, small pores of rare, radial, curved canals; skeleton of intergrown spicules including stauractines. *Middle Cambrian–Upper Cambrian:* South Tien Shan, Russia.

Tadassia ZHURAVLEVA & PYANOVSKAYA, 1995, p. 31 [\*T. bogambirica; OD]. Chambers spherical to irregularly elongate, may have one or two concentric walls; gastral surface rough and spongy but dermal surface smooth; wall pierced by pores without pattern of distribution; rare, radial canals curved and margins follow endings of spicules; skeleton primarily siliceous of united stauractines of various sizes as macrospicules united in rectangular lattice; smaller spicules present in outer part of external wall. Middle Cambrian-Upper Cambrian: Uzbekistan.——FIG. 294,2a-f. \*T. bogambirica, Koibulak Formation, North Nuratu Range, southern Tien Shan; a, several colonies in thin section.

including holotype in lower center; sponges with open chambers and single walls pierced by pores and canals, CSGM 934/1,  $\times$ 4; *b-e*, drawings of macrospicules as separate elements on left; *f*, united on right, CSGM 934/8,  $\times$ 4 (Zhuravleva & Pyanovaskaya, 1995; courtesy of Geologiya i Geofizikia, Novosibirsk).

## Class, Order, and Family UNCERTAIN

- Nepheliospongia CLARKE, 1900, p. 189 [\*N. typica; OD]. Vase shaped to obconical cup shaped, moderately thick walled, with skeleton of inosculating spicules that form small, irregular polygons, nature of spicules unknown. *Middle Devonian–Upper Devonian*: USA (New York).—FIG. 295,2*a–b.* \*N. typica, Lower Chemung beds, Upper Devonian, Naples; *a*, side view of obconical sponge with reticulate, skeletal pattern, NYSM, ×1; *b*, side view of smaller sponge with ovoid, cross section, and with characteristic reticulation on exterior of moderately thick walls, NYSM, ×1 (Clarke, 1900).
- Pseudolancicula WEBBY & TROTTER, 1993, p. 34 [\*P. exigua; OD]. Siliceous, gently tapering acanthostyle with spines arranged in verticillate pattern, and with an axial filament. Upper Ordovician: Australia (New South Wales).—FIG. 295, 1a-b. \*P. exigua, Malongulli Formation; a, holotype spicule, SUP, ×30; b, holotype spicule, SUP, ×75 (Webby & Trotter, 1993).
- Solactiniella MEHL & REITNER in STEINER & others, 1993, p. 309 [\*S. plumata; OD]. Irregular cluster of mainly, or exclusively, diactine spicules that are organized into bundles that radiate toward margins of sponge body. [The cluster is composed of only one or two types of spicules, and they have a preferred radial orientation that suggests this is part of a sponge. Because of the low order of structural development, taxonomic position of the cluster must remain uncertain.] Lower Cambrian-Middle Cambrian: China (Anhui, Hunan). ——FIG. 295,3. \*S. plumata, Niutitang Formation, Tommotian, Sansha, Hubei; holotype spicule matte with coarse diactines that radiate toward margin, SAN 102, ×3 (Steiner & others, 1993).

# MESOZOIC AND CENOZOIC HEXACTINELLID SPONGES: LYSSACINOSA AND HEXACTINOSA

## R. E. H. Reid

[formerly of Department of Geology, The Queens University of Belfast]

## Subclass HEXASTEROPHORA Schulze, 1887

[nom. transl. REID, 1958a, p. xliv, ex tribe Hexasterophora SCHULZE, 1887b, p. 36]

Hexactinellida with microscleres that include hexasters but not spicules with umbellate ray terminations (such as paraclavules, hemidiscs, amphidiscs, staurodiscs, or hexadiscs); when microscleres are absent, with megascleric features restricted to hexasterbearing sponges among modern forms; parenchymal skeleton of lyssacine or dictyonine types. Parenchymal megascleres of lyssacines range from hexactine to rhabdodiactine, and all loose, or have secondary fusion in parts ranging from only basal part to entire body; dermalia s.s. (autodermalia) supplemented by hypodermalia in some lyssacines, but not in other lyssacines or in dictyonines; lyssacines directly attached with a rigid, basidictyonal skeleton or by prostalia (basalia), which are sometimes pentactines and rhabdodiactines; dictyonines fixed by encrusting base or imbedded root processes, with a rigid, basal skeleton, formed by accretion of dictyonalia or by outgrowth of siliceous filaments from the parenchymal framework; hexasters in all modern genera but one (Cyrtaulon SCHULZE), additional sceptrule and uncinate microscleres in one dictyonine order (Hexactinosa). Ordovician-Holocene.

This taxon was proposed as tribe Hexasterophora of suborder Lyssacina ZITTEL (SCHULZE, 1887b) but was later expanded and raised in rank to include all hexaster-bearing sponges (SCHULZE, 1899).

The three included orders (Lyssacinosa, Hexactinosa, Lychniscosa) are considered here to be of common origin because of their possession of hexasters. Those occurring in lyssacines (Lyssacinosa) and dictyonines (Hexactinosa, Lychniscosa) have essentially the same range of types except in special forms. How the orders are related is unknown, and none is at first represented by especially primitive examples. Some lyssacines resemble Paleozoic Dictyospongiidae, but so-called hexasters of some dictyospongiids are not typical examples of such microscleres and can be compared with acanthophore spicules of some Amphidiscophora. The dictyospongiid paraclavule is also a possible prototype of amphidiscs if these developed via hemidiscs. There is also a fairly marked resemblance between the simplest types of dictyonine skeletons (in e.g., Farrea BOWERBANK, Calyptrella SCHRAMMEN) and the netted patterns seen in some older forms, for example, Microstaura FINKS; but none of these has features that anticipate the production of dictyonal strands of lychniscs.

Most fossils referred to this subclass have been identified as Hexasterophora by possession of dictyonine skeletons, which are not known in Amphidiscophora. Fossils may be considered as lyssacine Hexasterophora (Lyssacinosa) if they have parenchymal frameworks similar to those seen in various modern forms, or either paratropal megascleres or octasters, both confined to the family Rossellidae.

## Order LYSSACINOSA Zittel, 1877

#### [Lyssacinosa Zittel, 1877b, p. 22; *emend.*, Schrammen, 1924a, p. 18; IJIMA, 1927, p. 319]

Hexasterophorans with parenchymal skeleton of megascleres that are typically separate but sometimes secondarily united; spicules range from hexactines to rhabdodiactines,

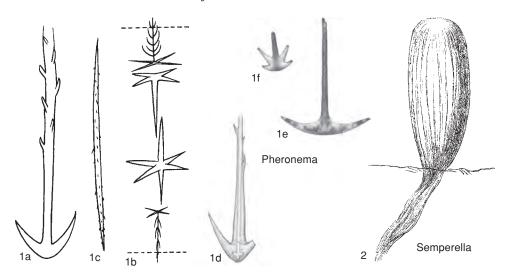


FIG. 296. Pheronematidae (p. 450).

always including latter and sometimes wholly of those spicules. *Ordovician– Holocene*.

450

## Family PHERONEMATIDAE Gray, 1872

[nom. correct. IJIMA, 1927, p. 5, pro Pheronemadae GRAY, 1872a, p. 450]

Characteristic parenchymal megascleres are hexactines or pentactines, not accompanied by rhabdodiactines except as small intermedia; often with uncinates, prostal sceptres, or both; basalia anchorate monactines with two opposite teeth only, and dispersed or in groups but not forming an anchor rope; no acanthophores. [Range based on occurrences of isolated basalia, presumed not to be of Dictyospongiidae, which are not known after Permian.] ?Upper Jurassic, Cretaceous–Holocene.

Pheronema LEIDY, 1868, p. 10 [\*P. annae; M]. Thickwalled cup or bowl, paragaster deep or shallow; basalia long, threadlike, usually in tuft. [Questionable Jurassic and Tertiary records are based on anchorate monactines, which need not be of this genus.] ?Upper Jurassic, Paleogene (?middle Eocene), Holocene: New Zealand, ?Upper Jurassic, ?middle Eocene; cosmopolitan, Holocene.—FIG. 296,1ac.\*P. annae, Holocene, West Indies; a, proximal end of root tuft spicule, ×120; b, spicules of body wall placed as in living sponge, outer surface above and gastral surface below, ×50; c, uncinate spicule, ×120 (de Laubenfels, 1955).—FIG. 296,1d-f. P. sp.; d, anchor spicule ascribed to Pheronema, ?middle Eocene, Otago, New Zealand,  $\times 200$ (Hinde & Holmes, 1892); *e–f,* basal anchor of pheronematid type, left hand spicule, Weiss Jura, Upper Jurassic, Gerstetten, Germany,  $\times 50$ (Schrammen, 1937).

Semperella GRAY, 1868, p. 376 [\*Hyalonema schultzei SEMPER, 1868a, p. 373; OD]. Similar to Pheronema but club shaped, not hollow, with oscules in longitudinal grooves on sides. Cretaceous–Holocene: cosmopolitan (de Laubenfels, 1955).—FIG. 296,2. \*S. schultzei (SEMPER), Holocene, Philippine Islands; side view of tubular sponge with convex lid and long root tuft, skeleton of threadlike, siliceous spicules, scale unknown (Gray, 1868).

#### Family EUPLECTELLIDAE Gray, 1867

[nom. correct. SCHULZE, 1887b, p. 37, pro Euplectelliadae GRAY, 1867, p. 527] [-Hertwigiidae TOPSENT, 1892, p. 25; Alcyoncellidae DE LAUBENFELS, 1936, p. 188; Placoplegmatidae DE LAUBENFELS, 1936, p. 187, partim]

With hexactinal dermalia and no differentiated hypodermalia or hypogastralia; choanosomal megascleres monactines and diactines; lophophytus or basiphytus; lophophytus basalia typically anisodiactinal rhabdodiactines with a terminal umbel, sometimes varied as monactines; basal dictyonalia present; often (if not always) thin-walled sponges with accessory, parietal oscula; some with sieve plates; parenchymal skeleton loose or fused rigidly for varying distance from base or all rigid; dermalia typically swordlike with proximal ray larger than others; gastralia similar or pentactinal. [These sponges have dermalia and gastralia of one category only, consisting of hexactines.] *Lower Triassic–Holocene.* 

### Subfamily EUPLECTELLINAE new subfamily

[Euplectellinae Reid, herein] [type genus, *Euplectella* Owen, 1841, p. 3]

Tubular sponges with terminal sieve plate and with regularly arranged gaps in wall; attached by root tuft; basalia anisodiactinal rhabdodiactines with terminal umbel; shorter of two rays distal or comparable monactines; no basalidictyonalia. *Holocene*.

Euplectella OWEN, 1841, p. 3 [\*E. aspergillian; OD]. Thin-walled, tubular or saccular, with terminal sieve plate and numerous parietal oscula; external surface smooth or ridged transversely; principalia mainly hexactines, pentactines, stauractines, with four rays paratangential and grouped to form longitudinal and transverse bundles; other bundles of spicule rays may take diagonal directions; other megasclere types include tauactines, rhabdodiactines, and others; dermalia swordlike hexactines; gastralia subhexactines or pentactines; hexasters, floricomes, graphicones, and oxyhexasters or oxyasters. Parenchymal skeleton loose or rigid in lower part or throughout, including sieve plate. [Supposed Miocene occurrence was recorded by DE LAUBENFELS, 1955, who provided no evident authority for citation.] Holocene: cosmopolitan .-FIG. 297,2. \*E. aspergillian, Philippine Islands, near Zebu; side view showing upper sieve plate, ridged main body, and root tuft, ×0.5 (Schulze, 1887b).

### Subfamily TAEGERINAE Schulze, 1887

[Taegerinae SCHULZE, 1887a, p. 94] [=Corbitellinae IJIMA, 1902, p. 30]

Root tuft and basalia absent; attached by encrusting basal mass, with basalidictionalia or by rigid, rootlike processes. [Type genus ?Taegeria SCHULZE, 1887b, is probably not separable from *Regadrella* SCHMIDT, but this does not affect the nomenclature.] *Lower Triassic—Holocene.* 

Regadrella SCHMIDT, 1880, p. 61 [\**R. phoenix;* OD] [=?*Taegeria* SCHULZE, 1887b, p. 41 (type, *T. pulchra,* OD)]. Tubular or saccular, with numerous parietal oscula and a sieve plate; principalia rhabdodiactines interwoven diagonally; accessory, parenchymal megascleres smaller diactines and hexactines; parenchymal skeleton rigid in lower part or throughout; outer surface smooth or with irregular ridging or outgrowths; dermalia swordlike hexasters; gastralia pentactines, or with rudimentary distal ray; hexasters, floricomes, graphicomes, and oxyasters, oxyhexasters and oxystaurasters. *Cretaceous* (*Cenomanian*)–*Holocene*: Europe, *Cenomanian*, *Coniacian–Maastrichtian;* southern England, *Cenomanian;* northwestern Germany, *Coniacian–Maastrichtian;* Spain, *Miocene;* cosmopolitan, *Holocene.*—FIG. 298, *Ia–d.* \**R. phoenix,* Holocene, Gulf of Mexico; *a*, side view of upper part of wall and sieve plate, ×1; *b*, swordlike, dermal hexact, ×5; *c*, discohexaster, ×200; *d*, floricome, ×200 (Schulze, 1887a).

- Arhoussia DU DRESNAY, TERMIER, & TERMIER, 1978, p. 277 [\*A. calyx; OD]. Goblet-shaped, rigid sponges with radial canals that are often bifurcated and with their exhalant ostia arranged in longitudinal folds in gastral wall; skeletal net of two parts, lower consolidated base with regular, dictyid structure with horizontal, undulating plates formed by rays of hexactines that limit mesh openings; plates separated and united by vertical rays of hexactines; upper part of sponge with large hexactines regularly spaced in skeleton with little coherence, largest spicules near folds of gastral wall, associated with intermediate-sized hexactines forming spicular network similar to that in adult lyssacid sponges; large diactines occur but rarely in wall interior; canals armored by second-order hexactines that may have reduced rays and appear similar to stauractines. [Placement in the family is uncertain.] Jurassic (Sinemurian): Morocco.—FIG. 298,4a-c. \*A. calyx, reef limestone, Jebel bous Arhous Srhir; a, transverse section through base with regular, dictyonal skeleton, ×4; b, photomicrograph of regular skeletal net, ×20; c, photomicrograph of regular, dictyonal, skeletal net, ×60 (du Dresnay, Termier, & Termier, 1978; courtesy of Geobios).
- Cypellospongia RIGBY & GOSNEY, 1983, p. 790 [\*C. fimbriartis; OD]. Thick walled, goblet shaped, with lower, tubular, somewhat anastomosing, stalklike part; walls pierced by circular, parietal gaps and by at least two additional canal series with full diplorhysis, although with somewhat irregular development; skeleton of hexactine-based spicules solidly fused at contact points and with synapticulae; hexactine-based origin of most spicules obscure due to extensive synapticulae and irregular, noncubic orientation of skeleton; small hexactines in thin dermal layer and hexactine origin of larger, main spicules locally evident where axial canals preserved; microscleres not preserved. Lower Triassic: USA (Utah, Nevada).-FIG. 299, 1a-b. \*C. fimbriartis, Scythian, Thaynes Limestone, Spanish Fork Canyon, Utah; a, side view of goblet-shaped holotype with common, parietal gaps in dermal layer, BYU 1992,  $\times 0.5$ ; *b*, gastral surface with parietal gaps and irregular, hexactine-based, skeletal structure, BYU 1993, ×10 (Rigby & Gosney, 1983).
- Guemeuria DU DRESNAY, TERMIER, & TERMIER, 1978, p. 279 [\*G. elegans; OD]. Conicocylindrical sponges with relatively thin wall around deep spongocoel; walls pierced by numerous radial canals; skeletal structure coherent, formed of regular meshes with spicule rays radial or concentric to wall; details of principal spicules not known, but gastralia or prostalia are parallel monaxons, arranged palisade-like, probably on exterior. Lower Junassic: Morocco.—FIG. 300, La–b. \*G. elegans, red

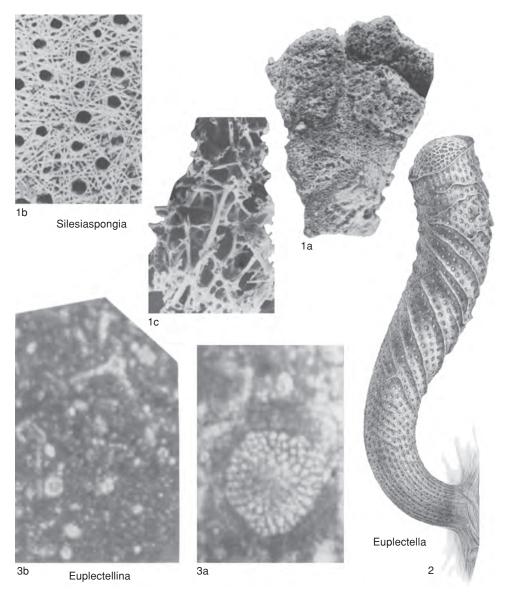


FIG. 297. Euplectellidae (p. 451-456).

ammonitic limestone, Sinemurian, Haut Oued Chouf Guemeur; a, segment through fragment showing dark canals and light skeletal net,  $\times 8$ ; b, photomicrograph of fragment with coherent, dictyonine net,  $\times 25$  (du Dresnay, Termier, & Termier, 1978; courtesy of *Geobios*).

Proeuplectella MORET, 1926b, p. 209 [\*P. fragilis MORET, 1926b, p. 210; M; ?=Prohexactinella cenomanse MORET, 1926b, p. 216, obj.] [?=Prohexactinella MORET, 1926b, p. 216 (type, P. cenomanse, OD)]. Incompletely known; based on fragment with fused reticulation of hexactines and diactines; parietal oscula not recognized, but with pitlike features present on gastral side. [Closest resemblance is to *Regadrella* or to *Prohexactinella*.] *Cretaceous (Cenomanian):* France.——FiG. 298,3*a*– *e.* \**P. fragilis,* Coulonges-les-Sablons; *a*, fragment with fused reticulation of hexactines and diactines, ×10; *b*–*e*, drawing of characteristic spicules including hexactines, spicules with barbs, oxea or diactine, and spicules fused into regular structure, scale not given but approximately ×60 (Moret, 1926b; courtesy of Société Géologique de France).

Purisiphonia BOWERBANK, 1869, p. 342 [\*P. clarkei; OD]. Similar to Regadrella but fairly thick walled with parietal perforations in form of radial canals;

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Lyssacinosa

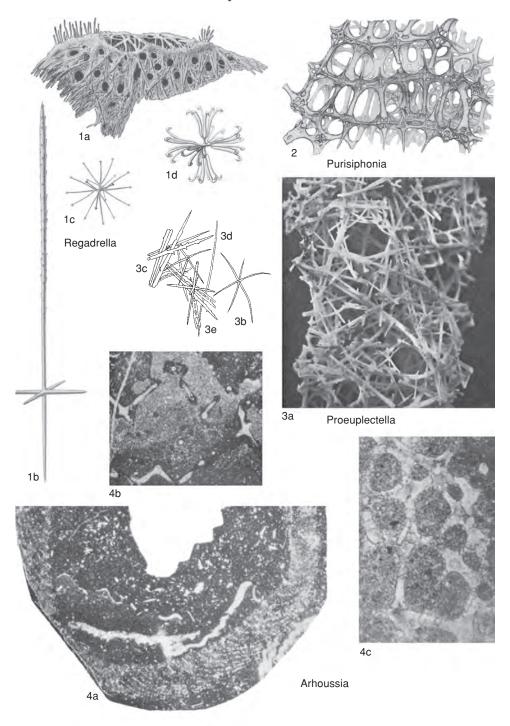


FIG. 298. Euplectellidae (p. 451-455).

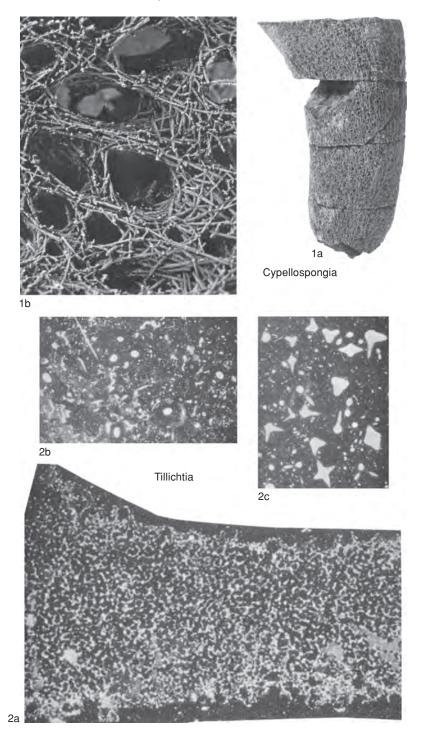


FIG. 299. Euplectellidae (p. 451–456).

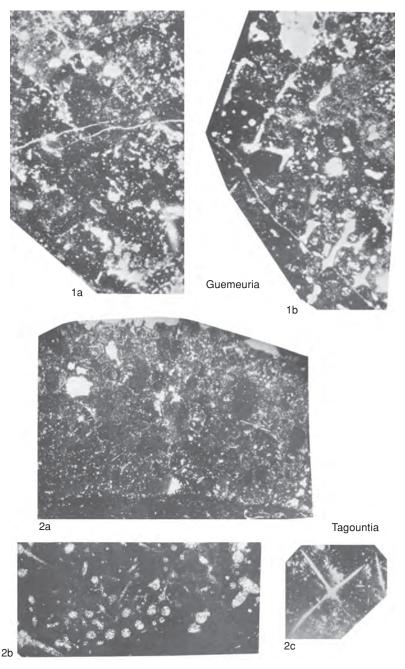


FIG. 300. Euplectellidae (p. 451-456).

sieve plate not known; cup or funnel-like, attached by root processes; other details unknown. *?Lower Cretaceous, Cretaceous (Coniacian–Maastrichtian):* Australia, *?Lower Cretaceous;* northern Germany, *Coniacian–Maastrichtian.*—FIG. 298,2. \*P. *clarkei,* ?Lower Cretaceous, Wollumbilla, Queensland, Australia; part of rigid skeleton showing irregular, siliceous fibers and *in situ*, interstitial hexactine, ×50 (Bowerbank, 1869).

Tagountia DU DRESNAY, TERMIER, & TERMIER, 1978, p. 279 [\*T. flexuosa; OD]. Sponges with thin, flexible walls and coarse, radial canals; relatively rare, large stauractines occurring in irregular skeleton of largely intermediate-sized, hexactine-based spicules not organized into regular mesh; diactines may also occur; spongocoel wall and canal surfaces lined with unfused spicules like hexactines of main wall, but may have one or more rays aborted and appear as pentactines or triactines. *Lower Jurassic*: Morocco.——FIG. 300,2*a*–*c*. \* T. flexuosa, limestone layers, Sinemurian, Petit Tagount; *a*, transverse section through wall with darker, irregular to oval canal sections, and light gray spicules, ×2; *b*, section including more densely spiculed gastral layer; *c*, stauractine and rays of other smaller spicules, ×25 (du Dresnay, Termier, & Termier, 1978; courtesy of *Geobios*).

Tillichtia DU DRESNAY, TERMIER, & TERMIER, 1978, p. 276 [\*T. aedificator; OD]. Cup-shaped sponges with thick walls pierced by numerous radial, branched, parietal canals; principal spicules generally separated from one another in a barely perceptible net with very fine mesh; main spicules robust hexactines with thick centers and elongate, vertical rays; intermediate spicules diactines and stauractines that are more or less parallel to sponge surface and perpendicular to principal spicules; outer net very fine textured and irregular, with openings corresponding to inhalant canals, and ankylosed as in living lyssacid sponges; prostalia of monaxons occur in scattered tufts. [Position in the family is questionable.] Jurassic (Sinemurian): Morocco.-FIG. 299, 2a-c. \*T. aedificator, grayblue limestone, Foum Tillischt; a, uniform, skeletal net with crude layers arcuate toward right, growing direction, scale not given, approximately  $\times 5$ ; *b*, section through parenchymalia net showing regular positions of main spicules, with subcircular sections and smaller spicules, ×5; c, section through hexactines showing spacing and orientation,  $\times 20$  (du Dresnay, Termier, & Termier, 1978; courtesy of Geobios).

#### Subfamily UNCERTAIN

- Euplectellina TERMIER, TERMIER, & THIBIEROZ, 1990, p. 7 [\*E. cevenola; OD]. Sievelike, oscular structure and abundant, isolated diactines and rhabdodiactines derived from triactines, pentactines, and stauractines with two rays reduced; organic axes commonly small, but locally large, microscleres including small hexasters, clavules, and scopules; basalia unknown. [The genus is not well defined and based of fragments from various areas.] Lower Jurassic: France.—FIG. 297, 3a-b. \*E. cevenola, Liassic carbonates, Hetangian-Sinemurian, Cevennes; a, oscular sieve; b, thin section with diverse sections of hexactine-based megascleres, ×35 (Termier, Termier, & Thibieroz, 1990).
- Silesiaspongia PISERA & BODZIOCH, 1991, p. 198 [\*S. rimosa; OD]. Cup-shaped, lyssacinosan sponges with thin walls that are often plicated, and skeleton of irregularly oriented, fused hexactines and hexactine-derived spicules, particularly diactines; distinct, outer layer of long, tangential diactines does not cover openings of numerous radial canals

that pierce the wall; parietal gaps absent. *Middle Triassic*: Poland.——FIG. 297, *Ia–c.* \**S. rimosa*, Karchowice Beds, Anisian, Szymiszów; *a*, side view of steeply obconical holotype with ostia of radial canals, ZPAL PfV/21, ×1; *b*, photomicrograph of outer layer with long, diagonal, tangential diactines and canal openings, ZPAL PfV/1, ×10; *c*, fragment of endosomal skeleton of fused, hexactine-based elements, ZPAL PfV/2, ×25 (Pisera & Bodzioch, 1991).

#### Family ASEMEMATIDAE Schulze, 1887

#### [Asemematidae SCHULZE, 1887a, p. 113]

With pentactine hypodermalia and hypogastralia, and pinnular autodermalia and autogastralia, which may be hexactines or pentactines; principalia mainly rhabdodiactines and hexacts; base encrusting with basidictyonalia; no paratropal hypodermalia or octasters. *Paleogene (?middle Eocene), Holocene.* 

#### Subfamily ASEMEMATINAE Schulze, 1887

[Asemematinae SCHULZE, 1887a, p. 113]

Thin walled, funnel-like to tubular, not stalked. [Not represented as fossils.] *Holocene.* 

### Subfamily CAULOPHACINAE Schulze, 1887

[Caulophacinae SCHULZE, 1887a, p. 124]

Fungiform sponges, with long, tubular stalks; parenchymal megascleres united in varying lengths of stalk. *Paleogene (?middle Eocene)–Holocene.* 

Caulophacus SCHULZE, 1887b, p. 46 [\**C. elegans;* OD]. Fungiform with long stalk; upper convex surface of main body gastral; lower surface dermal and convex to concave; autodermalia pinular hexactines; autogastralia hexactines or pentactines; pinular distal rays short in autodermalia but long in autogastralia; two sorts of discohexasters, to which oxyhexasters may be added. [Supposed Tertiary record based on isolated, pinular hexactines.] *Paleogene (?middle Eocene), Holocene:* New Zealand, *?middle Eocene.*—FIG. 301, *I. C.* sp., ?middle Eocene, Otago, New Zealand; pinular hexactine, ×200 (Hinde & Holmes, 1892).

## Family ROSSELLIDAE Schulze, 1885

[Rossellidae SCHULZE, 1885, p. 447] [=Asconematidae GRAY, 1872a, p. 458; Crateromorphidae GRAY, 1872b, p. 137; Caulophacidae IJMA, 1903, p. 78; Lanuginellidae DE LAUBENFELS, 1955, p. 68, nom. transl. ex Lanuginellinae SCHULZE, 1897, p. 532]

With hexactinal hypodermalia and nonpinular autodermalia and autogastralia;

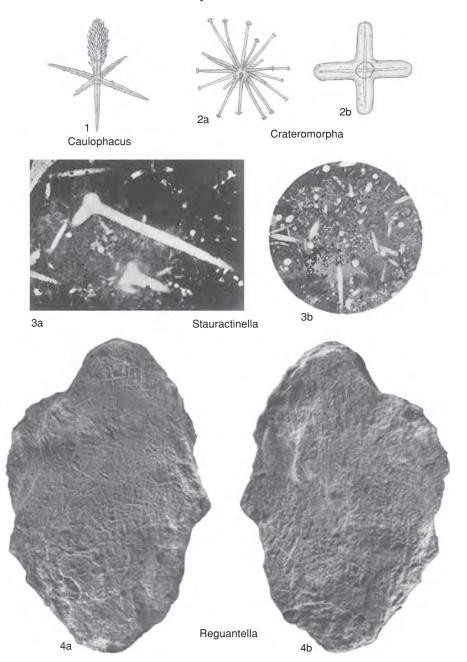


FIG. 301. Asemematidae, Rossellidae, Stauractinellidae, and Leucopsacasidae (p. 456-458).

latter most commonly stauractines or pentactines with (unspecialized) ray proximal; hexactines or rhabdodiactines may also occur; parenchymal megascleres hexactines and rhabdodiactines or latter only; attached by encrusting base or by protruded basalia that are uncinate or anchorate pentactines; hypodermal pentacts may be paratropal, protruded as prostalia, or both. Hexasters, oxyhexasters, additional plumicones, or discohexasters, or both, or with discohexasters replaced or accompanied by octasters. [Cretaceous existence known from loose, paratropal pentactines, exclusive to this family, although no genus is recognized.] ?Paleogene-?Neogene, Holocene.

#### Subfamily ROSSELLINAE Schulze, 1885

[nom. transl. REID, herein, ex Rossellidae SCHULZE, 1885, p. 451]

### Plumocones and octasters absent. ?Paleogene-?Neogene, Holocene.

Crateromorpha GRAY, 1872c, p. 110 [\*C. meyeri; OD]. Cup- or bowl-like with stalk, often large; exterior of main body smooth to strongly perforate with moderate, inhalant ostia; paragastralia in tracts between moderately large, open, exhalant canals; hypodermalia pentactines and may be supplemented by tangential bundles of small rhabdodiactines; hypodermalia not paratropal; autodermalia and autogastralia simple pentacts or stauractines; principalia rhabdodiactines and hexactines, or only former; oxyhexasters and discohexasters; stalk not tubular but with anastomosing, exhalant canals running lengthwise; stalk skeleton rigid. [Doubtful Paleogene records based on hexactines and hexasters similar to those from the stalk.] ?Paleogene-?Neogene, Holocene: New Zealand, ?Paleogene-?Neogene. FIG. 301, 2a-b. C. sp., ?Eocene, Otago, New Zealand; a, spherical discohexasters attributed to Crateromorpha sp., ×200; b, thick-rayed hexactine attributed to Crateromorpha sp., ×100 (Hinde & Holmes, 1892).

### Family STAURACTINELLIDAE de Laubenfels, 1955

[Stauractinellidae DE LAUBENFELS, 1955, p. 68]

Globular sponges in which spicules are a mass of hexacts, but stauracts and other types not present (hence genus and family misnamed). *Jurassic (Oxfordian)–Neogene*.

Stauractinella ZITTEL, 1877b, p. 60 [\*S. jurassica; OD]. Globular with (deep) paragaster; spicules large hexactines with proximal ray that is bigger than the others; other details unknown. [Possible euplectellid because spicules resemble euplectellid dermalia (SCHRAMMEN, 1936); stauractines absent.] Jurassic (Oxfordian), Paleogene–Neogene: Germany, Iran, Oxfordian.——FIG. 301,3a-b. \*S. jurassica, Weiss Jura, Oxfordian, Unterdigisheim, Germany; thin sections with irregularly oriented hexactines with at least one large ray, ×5 (Kolb, 1910–1911).

## Family LEUCOPSACIDAE Ijima, 1903

[Leucopsacidae IJIMA, 1903, p. 29]

Thick-walled, ovoid to cuplike sponges with basal stalks of anchorate spicules;

choanosomal spicules hexactines with rare diactines, outer skeletons with large, dermal pentactines, microsceleres commonly with discoidal, outer ends or sigmatoclones. *Paleogene (Eocene)*.

Reguantella PISERA & BUSQUETS, 2002, p. 326 [\*R. cavernosa; OD]. Ovoid, leucopsacasiid sponges without atrial cavity, with choanosomal skeleton mostly of diactines, locally bundled, supplemented by small pentactines and possible hexactines; interior of sponge cavernous; dermal surface with large, thick pentactines of several sizes with irregular distribution, tangential rays more or less parallel to each other, but not in regular meshwork, with unpaired ray directed inwardly. [This is the first described fossil representative of the family.] Paleogene (Eocene): Spain. FIG. 301, 4a-b. \*R. cavernosa, La Guixa Member of Vic marls Formation, Bartonian, Munter, Catalonia; a, side view of holotype showing prominent dermal pentactines; b, opposite side showing diactines of the choanosomal skeleton, ZPAL Pf.X/22, ×1 (Pisera & Busquets, 2002).

#### Family UNCERTAIN

- Calycomorpha BODZIOCH, 1993, p. 240 [\**C. triasina;* OD]. Small, stalked, gobletlike, thin-walled lyssacinosan with long, diactine spicules that project more or less horizontally into spongocoel from gastral part of wall; principal skeleton of fused hexactines and diactines. *Triassic:* Poland.——FIG. 302,4*a*-*b.* \**C. triasina,* Górazdze beds, lower Muschelkalk, Anisian, eastern upper Silesia; *a,* longitudinal section of small, gobletlike holotype with thick stem, ×2; *b,* upper part of holotype with diactine spicules projecting from gastral surface into matrix-filling spongocoel, ×4 (Bodzioch, 1993).
- Gomphites CARTER, 1871, p. 127 [\*G. parfitte; SD DE LAUBENFELS, 1955, p. 40]. Based on loose pentactines, probably dermalia or gastralia resembling spicules of *Terpios* with heads bearing several lateral protrusions (DE LAUBENFELS, 1955, p. 40). Lower *Cretaceous*: Europe.——FIG. 302, *Ia-b.* \*G. parfitte, Upper Greensand, Exeter, England; *a*, pentactine, dotted lines restored; *b*, pentactine with arched rays, dotted where restored, ×50 (Carter, 1871).
- Krainerella KRAINER & MOSTLER, 1992, p. 137 [\*K. ingridae; OD]. Isolated, delicate, long amphidiscs with a thin, delicate rhabd and similar-sized, umbrella-like umbels at both ends; both umbels have eight recurved rays, but rays of one thinner than those of other; long rhabd distinctly tapered in middle. Middle Triassic: Austria.——FiG. 302,3. \*K. ingridae, Rote Knollenkalke, Ladinian, Kärnter, Karawanken; side view of typical spicule, ×50 (Krainer & Mostler, 1992).
- Opeamorphus DE LAUBENFELS, 1955, p. 78, nom. nov. pro Acestra C. F. ROEMER, 1861, p. 55, non DALLAS, 1852 [\*Acestra subularis C. F. ROEMER, 1861, p. 55; OD]. Awl-shaped spicules, probably in root-tuft clusters. Ordovician–Carboniferous: Europe.
- Pyritonema M'Coy, 1850, p. 273 [\*P fasciculatus; SD DE LAUBENFELS, 1955, p. 78]. Name applied to

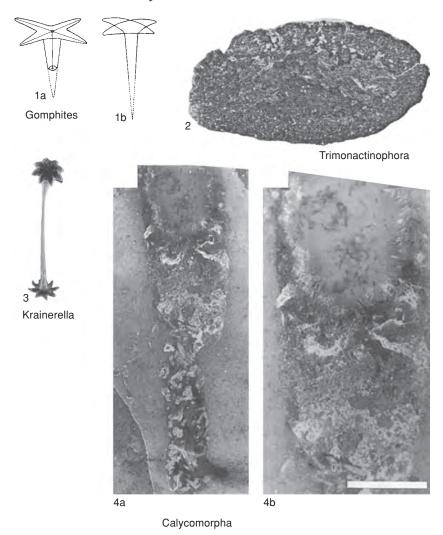


FIG. 302. Uncertain (p. 458-459).

masses of parallel, hairlike spicules that seemingly comprise root tufts of lyssakid sponges; possibly useful but not valid as a distinct genus. [No known suitable figures.] *Silurian:* England.

Trimonactinophora WU & XIAO, 1989, p. 17 [\*T. triassica; OD]. Sponges ranging from short pillars to open conical or tongue shaped; skeleton of hexactines and many monactines and triactines, with some stauractines, two sizes of spicules irregularly distributed, without strands; canals of moderately uniform width but irregularly distributed. Triassic: China.——FIG. 302,2. \*T. triassica, upper member Hanwang Formation, Carnian, Minzhu County, Sichuan; horizontal section of holotype, 256-536 CCG, ×1 (Wu & Xiao, 1989).

## Order HEXACTINOSA Schrammen, 1903

[nom. transl. DE LAUBENFELS, 1936, p. 185, ex tribus Hexactinosa Schrammen, 1903, p. 4, sensu Schrammen, 1912, p. 190]

Dictyonine Hexasterophora without lychniscs at any stage of their ontogeny, and not considered to be derived from any genus with lychniscs; primary skeletal framework composed typically of dictyonal hexactines united to form linear, dictyonal strands, sometimes in single layer only, but usually

spread through three-dimensional meshwork one to many meshes thick without layered arrangement; further dictyonalia, not arranged to form dictyonal strands, may be added as a secondary development; in some forms, doubtfully included (Aulocalycidae), all dictyonalia are united without order; cortical meshwork absent, or present and formed by secondary accretion or by thickening or structural modifications of outermost, primary meshwork; skeletal canalization absent, restricted to secondary meshwork, or intracortical to fully developed in primary meshwork, in the last instance with separate systems of inhalant and exhalant skeletal canals (epirhyses, aporhyses) or with a single system only; superficial meshwork sometimes present, most often formed from adventitious, dictyonal hexactines, but sometimes partly or wholly from connected dermalia or gastralia, or from siliceous filaments that grew out from dictyonalia, dermalia, or gastralia; dermalia and gastralia usually pentactines, less commonly hexactines or stauractines, rarely rhabdodiactines (gastralia only); basal skeleton formed from dictyonal hexactines; most living examples with hexasters, uncinates, and sceptrules. [Usage of SCHRAMMEN, 1912 restricts this taxon to dictyonine genera, excluding lyssacine sponges that were initially (SCHRAMMEN, 1903) included. Order cryptogenic, represented initially by advanced genera (Cribrospongia D'ORBIGNY, Casearia QUENSTEDT); presumably derived from a primitive lyssacine with hexasters, perhaps similar to Microstaura FINKS if the latter had appropriate microscleres.] Upper Ordovician–Holocene.

## Family EURYPLEGMATIDAE de Laubenfels, 1955

[Euryplegmatidae DE LAUBENFELS, 1955, p. 78]

Sponges in which hexactines of main skeleton less intensely fused than in most of order; included here because diactinal spicules, such as characterize lyssakid forms, absent. ?Cretaceous, Holocene. Euryplegma SCHULZE, 1887b, p. 80 [\**E. auriculare;* OD]. Ear-shaped, thin-walled sponges with long, oval-shaped inhalant openings on convex, outer side and small, irregular, round exhalant openings on concave, inner side; skeletal net irregularly dictyonine, of similar thin rays with small, conical spines on their outer surfaces; net without thickened ray junctions or buttresses; parenchymal spicules include small, rough oxyhexactines and discohexasters. *?Cretaceous, Holocene:* cosmopolitan.

#### Family FARREIDAE Gray, 1872

[nom. correct. SCHULZE, 1887b, p. 69, pro Farreadae GRAY, 1872a, p. 457] [=Euretidae ZITTEL, 1877b, p. 35, partim]

Skeletal framework consisting of a single layer of meshwork, in which meshes are typically quadratic, or of a primary layer on which further layered or irregular meshwork is superimposed in older parts or up to growing margins; modern forms also distinguished by occurrence of clavules, sometimes accompanied by sarules or lonchioles but never scopules; thin-walled sponges with a simple chamber system, radial canals absent although small, pitlike, subdermal or subgastral spaces may be present; skeletal pores (ostia, postica) sometimes present if secondary meshwork is developed. [This is a small group of somewhat dissimilar genera, mainly from modern species, with a type of rigid skeleton appropriate in a prototype stock of the order; but they appear after most other families, and with characteristic sceptrules (clavules), which are unknown in the others.] Cretaceous (Turonian)-Holocene.

Farrea BOWERBANK, 1862, p. 1,118, s.l. [\*F. occa; OD]. Branched-tubular or plexiform; habits ranging from erect tubes with short to rudimentary lateral branches, arranged alternately or spirally, to irregular masses of tubes that divide and anastomose repeatedly; free tubes open at ends; base encrusting; sceptrules clavules only (s.-g. Aulodictyon KENT, 1870), clavules and sarules (s.-g. Claviscopulia SCHULZE, 1899) or unknown (Farrea s.s.). [Treated by zoologists as comprising forms referred here to s.-g. Aulodictyon, with Farrea and Claviscopulia as separate genera, but modern type species was based on material without sceptrules; usage here unites that which cannot be distinguished when loose spicules are absent, as in fossils.] Cretaceous (Turonian)-Holocene: southern England, Turonian; Northern Ireland, Santonian; ?Washington, ?Oli-

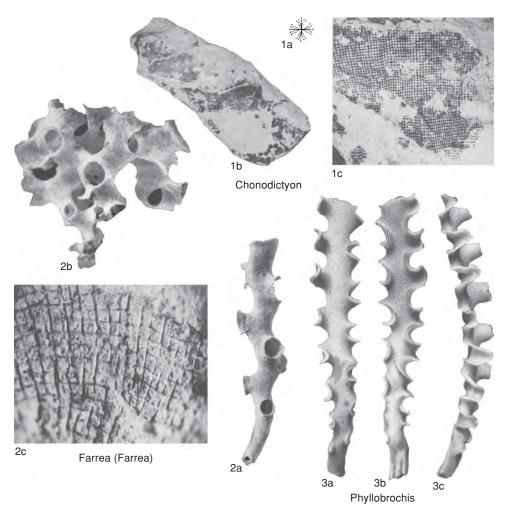


FIG. 303. Farreidae (p. 460-463).

gocene; USA (California), *Miocene*; cosmopolitan, *Holocene*.

F. (Farrea). Name applied here to fossil species, whose loose spicules are unknown. [Not Farrea species of SCHRAMMEN (1912) and MORET (1926b), in which the skeleton is euretid.] Cretaceous (Turonian)–Holocene: southern England, Turonian; Northern Ireland, Santonian; cosmopolitan, Holocene. — FIG. 303,2a-b. \*F. (F.) occa, Holocene, Indian Ocean, off east end of Timor; a, side view with branched, tubular form with thin walls, ×0.5; b, somewhat smaller, more complexly branched specimen showing range of species, ×1 (Ijima, 1927).— FIG. 303,2c. F. (F.) cf. oakleyi REID, chalk, Senonian, Rickmansworth Station, Hertfordhire, England; plan view of dermal skeletal meshwork mold, ×8 (Reid, 1959; courtesy of The Palaeontographical Society, London).

Chonodictyon REID, 1959, p. 9 [\*Farrea infundibuliformis CARTER, 1873, p. 360; OD]. Body funnellike; hexasters floricomes; other loose spiculation unknown. Cretaceous (?Campanian), Holocene: northern England, ?Campanian; Caribbean Sea, Holocene.—FIG. 303,1a. \*C. infundibuliformis (CARTER), Holocene, Caribbean Sea; isolated microsclere floricome spicule, magnification unknown (Reid, 1959; courtesy of Palaeontographical Society, London).—FIG. 303,1b-c. C. ? sowerbyensis REID, Chalk, Senonian, Sewerby, Yorkshire, England; b, side view of chalk nodule with dark, skeletal mesh, GSM Za3575, ×0.5; c, skeleton from same in plan view, ×2 (Reid, 1959; courtesy of Palaeontographical Society, London).

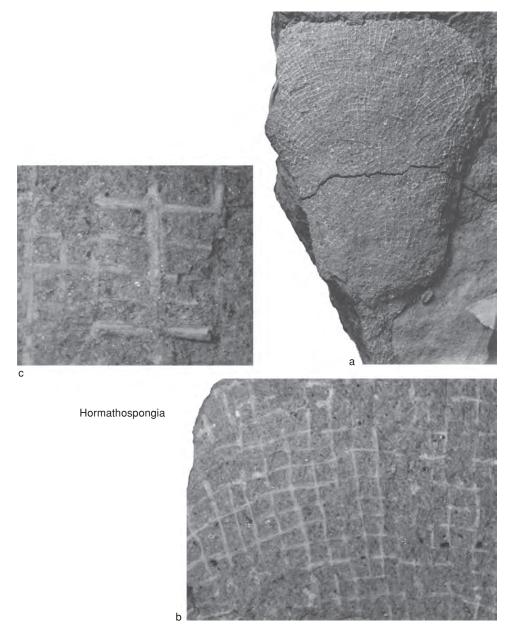


FIG. 304. Farreidae (p. 462-463).

Hormathospongia RIGBY, EMBREE, & MURPHY, 1996, p. 716 [\**H. dictyota;* OD]. Hexactinellid sponges of thin-walled, annulate to beaded-appearing, linear series of attached, upwardly expanding pendant-, bell-, or teardrop-shaped chambers or sections; chamber walls a single layer of rectangularly arranged, reticulate mesh of stauractines fused into dictyonal framework by encasement of overlapping, spicule ray tips. *Cretaceous (Santonian):* USA (California).——FIG. 304*a–c.* \**H. dictyota*, Forbes Formation, Colusa County; *a*, holotype with upwardly arching, dictyonine, skeletal net, ×2; *b*, enlargement of upper left part of overlapping spicule rays (not showing) in center and disappearance of lateral rays toward left in converging net,  $\times 10$ ; *c*, photomicrograph showing spicule rays encased in silica to form beams and smaller spicules in second-order quadrules, USNM 480458,  $\times 20$  (Rigby, Embree, & Murphy, 1996).

Phyllobrochis REID, 1958a, p. iv [\*Farrea laminaris TOPSENT, 1904, p. 43; OD]. Tall, thin, curved, bladelike sponge with sinuously folded, lateral margins where folds on two margins alternate; skeleton dictyonal, with spiculation similar to Farrea. Holocene: Atlantic Ocean.—FIG. 303,3a-c. \*P. laminaris (TOPSENT), Azores; a, side view of convex surface of holotype; b, side view of concave surface; c, side view showing alternating position of folds on sponge margins, ×1 (Topsent, 1904).

#### Family EURETIDAE Zittel, 1877

[Euretidae ZITTEL, 1877b, p. 35, partim] [=Monakidae MARSHALL, 1876, p. 121; Coscinoporidae ZITTEL, 1877b, p. 36, partim; Maeandrospongidae ZITTEL, 1877b, p. 38, partim; Chonelasmatidae SCRAMMEN, 1912, p. 190; Pleurothyrisidae SCHRAMMEN, 1912, p. 192; Myliusiidae DE LAUBENFELS, 1955, p. 82, partim; Wapkiosidae DE LAUBENFELS, 1955, p. 85]

Primary skeletal meshwork three dimensional and not constructed in layers, with subparallel, dictyonal strands in longitudinal or radial orientation ending at dermal surface or some at each surface; some with secondary meshwork in which dictyonal strands are absent, other than in primary meshes; skeletal canalization normally absent or limited to skeletal pores (ostia, postica) or shallow, radial canals (epirhyses, aporhyses) that open into underlying meshes; some with true radial canals but not in regular series; amararhyses in one genus; modified primary meshwork or added secondary meshwork may form dictyonal cortex at one or both surfaces. Modern forms normally with scopules, rarely sarules or no sceptrules, never clavules. [Only Mesozoic and Cenozoic forms are discussed here. Older forms are treated in the section on Paleozoic hexactinosans, p. 437 herein.] Triassic (Carnian)–Holocene.

#### Subfamily EURETINAE Zittel, 1877

[nom. transl. REID, 1958, p. 19, ex Euretidae ZITTEL, 1877b, p. 35] [=Euretidae ZITTEL, 1877b, p. 35, partim; Calycospongiidae WU, 1990, p. 350 (358)]

Typically thin-walled Euretidae of branched-tubular or plexiform habitus, or with a tubular, funnel-, or scabbardlike axis emitting lateral tubes or other appendages; axial funnel not regularly ribbed longitudinally when present; ostia and postica typically without order; no amararhyses; modern examples with scopules in most instances, sarules in one genus, no sceptrules in others; dermalia and gastralia usually pentactines, but sometimes hexactines. [The subfamily includes forms apparently comprising one main line of euretid evolution, not similar to Craticulariidae (*cf.* Chonelasmatinae below); Polythyridinae and Pseudobecksiinae are probably derivatives.] *Triassic (Carnian)– Holocene.* 

- Eurete SEMPER, 1868b, p. 29 [\*E. simplicissimum; OD] [=Botryosella SCHRAMMEN, 1912, p. 259 (type, B. labyrinthica, M); ?Hapalopegma SCHRAMMEN, 1912, p. 258 (type, H. fragilis, SD DE LAUBENFELS, 1955, p. 84); Pararete IJIMA, 1927, p. 193, partim (type, Farreopsis farreopsis CARTER, 1877, p. 122, not SCHULZE, 1887b, p. 70, SD MEHL, 1992, p. 68)]. Branched tube or divided and anastomosed tubes; skeletal framework without canalar features, with skeletal pores only or with shallow canals at either surface; cortex or none at either surface; scopules in living species. ?Middle Jurassic, Upper Jurassic– Holocene: cosmopolitan.
  - E. (Eurete). Habitus variable from an erect tube with lateral branches to complex of divided and anastomosed tubes that do not form regular column; scopules and pentactine dermalia and gastralia in modern examples. [Living E. (Eurete) is distinguished by restriction of hexasters to oxyhexasters.] ?Middle Jurassic; Lower Cretaceous-Holocene: cosmopolitan.—FIG. 305,6a. E. (E.) semperi SCHULZE, Holocene, East Indies; side view of anastomosing tubules with thin walls, ×1 (de Laubenfels, 1955).—FIG. 305,6b. E. (E.) schmidti SCHULZE, Holocene, western Pacific; part of skeleton showing both dictyid megascleres and microscleres, ×40 (de Laubenfels, 1955).
  - E. (Aulodomus) SCHRAMMEN, 1937, p. 54 (SCHRAMMEN, 1936, p. 182, nom. nud.) [\*A. farreides; OD]. Divided and anastomosed tubes forming a columnar growth, with lateral oscula at end of tubes projecting outwardly or in walls of ascending tubes; irregular cortical meshwork and skeletal pores present or absent. Upper Jurassic-Upper Cretaceous: Germany.—FiG. 305,2a. \*E. (A.) farreides, Weiss Jura, Upper Jurassic, Streitberg; surface of exterior with reticulate, skeletal structure, ×10 (Schrammen, 1936). —Fig. 305,2b. E. (A.) prolatum REID, Chalk Marl, Cenomanian, Berkshire, England; holotype showing anastomosed, tubular growth form, GSM 96775, ×0.5 (Reid, 1959;

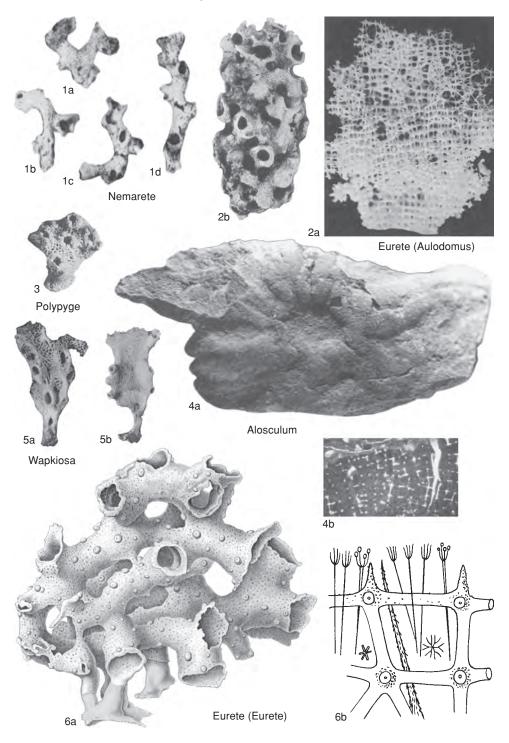


FIG. 305. Euretidae (p. 463-471).

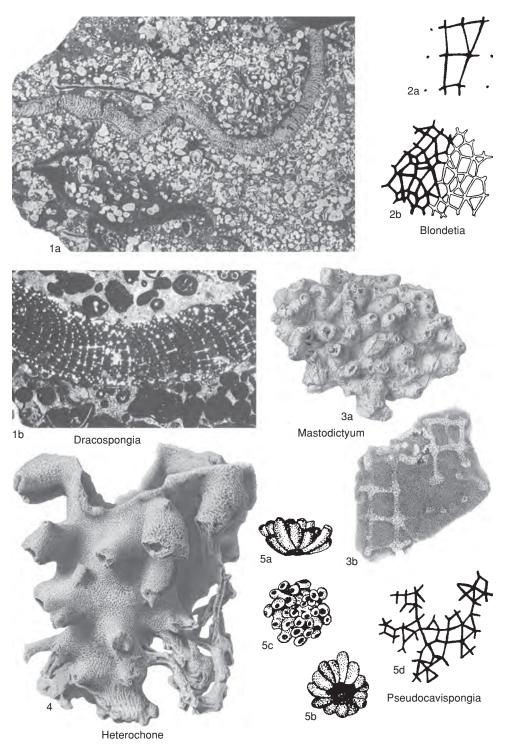


FIG. 306. Euretidae (p. 463–469).

courtesy of The Palaeontographical Society, London).

- Alosculum WU, 1990, p. 351 [359] [\*A. heptapetalum; OD] [?=Radioplica WU, 1990, p. 351 [359] (type, R. stephana, M)]. Trochoid sponge with few large, vertical ridges formed by folded wall; ridges regularly radiating from axial part of sponge; rectangular, dictyonine skeleton evident in both vertical and transverse sections in walls. Upper Triassic (Carnian): China.—FIG. 305,4a-b. \*A. heptapetalum, Hanwang Formation, northwestern Sichuan; a, view from below sponge with prominent, radial ridges in thick walls around indented base, ×1; b, photomicrograph of section showing dictyonine, skeletal structure, ×10 (Wu, 1990).
- Blondetia Hérenger, 1944, p. 105 [\*B. demolyi; OD]. Large, cup-shaped, commonly laterally flattened hexactinosan without visible pores in very thin walls with main dictyonal skeleton of large, regular hexactines in cubic mesh and with a dermal layer of very small hexactines forming an octahedral-based mesh; hexactines of endosomal skeleton with thin, long, vertical rays parallel axis of sponge, and with thicker, lateral rays that produce horizontal, transverse streaks on weathered surface when fine, surficial skeletal net is missing. Upper Cretaceous (Coniacian-Maastrichtian): France.-FIG. 306,2a-b. \*B. demolyi, Gisement de la Chartreuse, Entremont-le-Vieux, southeastern France; a, dictyonine hexactines of main skeleton in basic cubic mesh, with plain nodes and long, vertical rays, approximately  $\times 1$ ; b, segment of finer-textured, dermal skeleton, approximately ×1 (Hérenger, 1944).
- Dracospongia RIGBY, WU, & FAN, 1998, p. 129 [\*D. undulata; OD]. Thin, undulate platelike to broadly obconical sponges with marked regularity in finetextured, advanced, euretoid, skeletal structure; primary strands continuing full length or diameter at midwall or midplate, other strands diverging laterally to both dermal and gastral surfaces; transverse lamellae formed by beams from strands; plates lacking canals; well-defined, dermal and gastral layers of swollen dictyonalia, with additional dictyonalia in dermal layer. Triassic (Carnian): China (Sichuan). -FIG. 306, 1a-b. \*D. undulata, Hanwang Formation, Jushui; a, enlarged vertical section of annulate, platelike holotype in which primary strands diverge laterally and transverse lamellae of horizontal beams form arcuate elements in direction of growth, ×2; b, photomicrograph of holotype section showing undulate nature of sponge with thickened dermal layer, below, and gastral layer, above, with arcuate transverse lamellae curved in direction of growth, IGASB R6-20(064), ×10 (Rigby, Wu, & Fan, 1998).
- Heterochone IJIMA, 1927, p. 284 [\*Chonelasma calyx SCHULZE, 1887a, p. 326; OD]. Axial funnel with

short, lateral tubes that are widely open at ends unless infilled by secondary tissue (or meshwork); exterior of skeletal framework with cortical meshwork and numerous ostia, latter arranged without order; no cortex and few or no postica on gastral side; dictyonal strands begin on gastral side and end in cortical meshwork of dermal side; plan views of latter may have irregular, strandlike series of diagonally interwoven beams; ostia open inwardly into simple meshes under cortex, or into vague epirhyses that may also open on gastral side; gastral surface sometimes with scattered, vague aporhyses that may extend outwardly to cortex; scopules present, dermalia and gastralia pinular hexactines in living examples. [Chonelasma SCHULZE, 1887a, partim; Chonelasma sensu SCHRAMMEN, 1912; not sharply separable from Verrucocoelia ÉTALLON in material lacking dermalia and gastralia.] ?Cretaceous, Holocene: Germany, Atlantic and Pacific Oceans.-FIG. 306,4. \*H. calyx (SCHULZE), Holocene, Enoshima, Japan; side view of dried specimen showing growth form, ×0.5 (Schulze, 1887a).

- Linonema DE LAUBENFELS, 1955, p. 83, nom. nom. pro Linosoma Schrammen, 1937, p. 55, non Eichel-BAUM, 1909 [\*Linosoma calyx SCHRAMMEN, 1937, p. 55; OD]. Narrow, obconical to tubular sponge with deep, open spongocoel and moderately thick walls; dermal surface nodular outgrowths separated by furrows; inhalant ostia vertical, elongate-oval, or slitlike; gastral surface smooth and with similarly shaped, exhalant ostia; curved canals extend into wall from both surfaces but do not pierce it; skeletal net moderately regular dictyonine with rectangular meshes; strands generally parallel gastral surface but curve outward near dermal surface. [Placement in the family is uncertain.] Upper Jurassic: Germany. FIG. 307, 1a-b. \*L. calyx (SCHRAMMEN), Oxfordian, marly limestone and Kimmeridgian marls, Hochwang and Bärenthal; a, side view of steeply obconical sponge with lobate outgrowths, ZPAL Pf.VIII/216, ×0.5; b, vertical section showing broad, deep spongocoel and moderately thick walls with radial canals, ZPAL Pf. VII23, ×0.5 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Lopanella POČTA, 1883, p. 27 [\*L. depressa POČTA, 1883, p. 28; OD]. Thick-walled, basin- or bowl-shaped sponges with thick, short, basal stalk; entire gastral and upper dermal surfaces lacking ostia, al-though small, round to oval pores occur in irregular skeleton, which is composed of small, thick-rayed hexactines in dictyonine skeletal net. [Included in the subfamily with some question.] Upper Cretaceous: Czech Republic, Slovakia.—
   FIG. 308, *Ia-b.* \*L. depressa, Korytzaner Schichten, Kamajk; a, side view of young, thick-walled, obconical sponge, ×1; b, fragment of the thick-rayed, dictyonine, skeletal net, ×40 (Počta, 1883).
- Mastodictyum SOLLAS, 1883, p. 544 [\**M. whidborni;* M]. Imperfectly known, based on specimen in

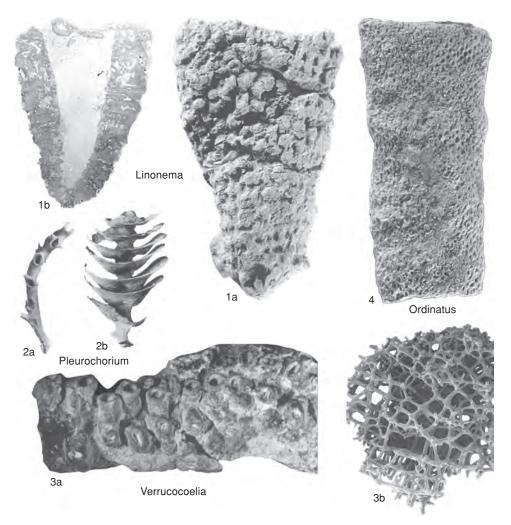


FIG. 307. Euretidae (p. 466-471).

which short, nipplelike outgrowths arise from an allegedly basal plate; ostia present, arranged without order. [Possibly a form of *Verrucocelia* ÉTALLON.] *Middle Jurassic:* England.——FIG. 306,3*a*–*b.* \**M. whidborni*, Inferior Oolite, Burton Bradstock; *a*, upper surface of nearly complete sponge with lobate outgrowths,  $\times 0.5$ ; *b*, part of sponge wall showing skeletal structure,  $\times 50$  (Hinde, 1893b).

Myliusia GRAY, 1859, p. 439 [\*M. callocyathus; OD]. Axial tube or funnel with short, open, lateral outgrowths whose margins become united, producing reticulate, external surface; no cortical or canalar features; skeletal net dictyonine with hexactine, oxyhexaster, and discohexaster microscleres but no sceptrules in living example. Upper Cretaceous– Holocene: Spain, Upper Cretaceous, Miocene; East Indies, West Indies, Holocene.—FIG. 308,3a-c. \*M. callocyathus, Holocene, Little Ki Island, western Pacific Ocean; a, side view of specimen with two oscula, ×1; b, oxyhexaster with S-shaped rays; c, discohexaster with S-shaped, terminal rays, ×150 (Schulze, 1887a).

Nemarete REID, 1961, p. 37 [\*N. mirabilis; OD]. Branched tube or branched and anastomosed tubes; 468

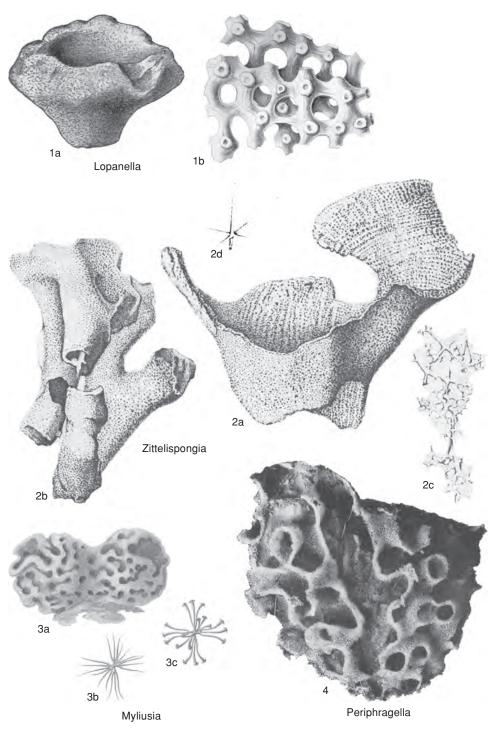


FIG. 308. Euretidae (p. 466-471).

skeletal framework with pores on dermal side; free rays of gastral, skeletal surface emitting siliceous filaments that ramify in plane of surface. *Cretaceous (Cenomanian):* England.——FIG. 305,1*a*–*d.* \**N. mirabilis,* Chalk Marl, Childrey, Berkshire; side view of four fragments of small holotype, GSM 94955, ×1 (Reid, 1961; courtesy of The Palaeontographical Society, London).

- Ordinatus DE LAUBENFELS, 1955, p. 83 nom. nov. pro Eutactus SCHRAMMEN, 1937, p. 38, non GEMMINGER & HAROLD, 1873 [\*Scyphia texturata GOLDFUSS, 1826, p. 6; OD]. Cylindrical to narrow, vaselike with sides full of pores; dermal surface with only slightly thickened, dictyonal skeleton, interior dictyonal skeleton regular with rectangular to square meshes, dictyonal strands diverging toward dermal surface. Jurassic: Germany.——FIG. 307,4. \*O. texturatus (GOLDFUSS), Kimmeridgian marls, Upper Jurassic, Erkenbrectsweiler; side view of fragment with cylindrical form and distribution of ostia, ×1 (Pisera, 1997; courtesy Palaeontologica Polonica).
- Periphragella MARSHALL, 1875, p. 177 [\*P. elisae; OD] [=Proeurete SCHRAMMEN, 1902, p. 21 (type, P. plicata SCHRAMMEN, 1902, p. 22, M, =Periphragella plicata (SCHRAMMEN), SCHRAMMEN, 1912, p. 214)]. Axial funnel emitting divided and anastomosed lateral tubes, similar to those of a plexiform Eurete; framework with pores on dermal side or no canalar features; scopules, pentactinal dermalia, and gastralia in living species. [This genus in not separable sharply from Verrucocoelia ÉTALLON.] Lower Cretaceous-Holocene: cosmopolitan.——FIG. 308,4. P. plicata (SCHRAMMEN), Quadratenkreide, Campanian, Misburg, Germany; side view of plicate sponge, ×1 (Schrammen, 1902).
- Plecteurete HERRMANN-DEGEN, 1980, p. 14 [\*P. megasiphon; OD]. Sponge constructed of very regularly branched and anastomosed tubes that have a zigzag structure in space and spirally overlie one another at each bend at 90 degrees; these branches determine relationships between individual, identical, structured tubes, so that a plexus of unusual regularity develops; skeleton is euretoid and constructed of smooth hexactines; with or without a dictyonal cortex; dermal layer with characteristic, irregularly distributed epirhyses; more extensive canal system not developed. Paleogene (Thanetian): Egypt.--FIG. 309, 1. \*P. megasiphon, Chalk member, Tarawan Formation, Bulaq Oasis, between Kharga and Baris, southwestern Egypt; sponge with characteristic, intertwining, anastomosing, tubular structure, ×1 (Herrmann-Degen, 1980).
- Plectospyris SOLLAS, 1883, p. 545 [\*P. elegans; SD DE LAUBENFELS, 1955, p. 84]. Poorly known, based on incomplete specimens with groups of laterally anastomosing tubes; ostia present, arranged without order; postica apparently in longitudinal grooves. Middle Jurassic: England.——FIG. 309,2a-b. \*P. elegans, Inferior Oolite, Burton Bradstock; a, view from above of branched sponge fragment, with os-

cula in some branches,  $\times 1$ ; *b*, enlarged part of sponge wall with dictyonine structure,  $\times 50$  (Hinde, 1893b).

- Pleurochorium SCHRAMMEN, 1912, p. 251 [\*P. schulzei; OD]. Erect, tubular axis bears leaflike appendages or hat-brim-like flanges, developed above or across parietal oscula; no skeletal pores or cortex; scopules in living species. Cretaceous-Holocene: Germany, East Indies, Indian Ocean.—FIG. 307,2a-b. \*P. schulzei, Quadratenkreide, Cenomanian, Oberg, Germany; a, side view of type with brimlike flanges out from erect axis; b, erect central branch with oscula between bases of flange remnants, ×1 (Schrammen, 1912).
- Polypyge SCHRAMMEN, 1937, p. 61 (SCHRAMMEN, 1936, p. 183, nom. nud.) [\*P. pusilla; OD] [=Polysyge DE LAUBENFELS, 1955, p. 86, nom. null.]. Very small, figlike sponges with flattened summir and base; upper surface with low rims around several oscula of deep spongocoels; smaller, irregularly space ostia of inhalant canals occurring between oscula and on exterior; spongocoel walls with larger, exhalant ostia; dictyonal skeletal network of closely and irregularly space dhexatines; markedly thick-ened spicules producing differentiated dermal layer. Jurassic: Germany.—Fig. 305,3. \*P. pusilla, Weiss Jura, Upper Jurassic, Streitberg; upper surface with rimmed oscula and smaller, inhalant ostia on holotype, ×4 (Schrammen, 1937).
- Pseudocavispongia Hérenger, 1944, p. 86 [\*P. stellata; OD]. Very small sponges formed of several upwardly curved tubes opening as in corolla of a flower, coming from common base that may be concave; tubes with very thin walls whose principal dictyonine skeletons appear composed of small hexactines with plain nodes; young sponge with few tubes, but with additional tubes subsequently inserted around initial, central tube and between earlier formed tubes. Lower Cretaceous (Valanginian): -FIG. 306, 5a-d. \*P. stellata, lower France.-Valanginian, Chateauneuf-de-Chabre by Laragne, southeastern France; a, side view of small sponge with upwardly curved tubes; b, diagonal lower view showing concave base and radially diverging, small, curved tubes; c, view from above of oscular tips of tubular branches, ×1; d, fragment of dictyonal skeleton, ×20 (Hérenger, 1944).
- Radioplica WU, 1990, p. 351 [\*R. stephana WU, 1990, p. 352; OD] [?=Alosculum WU, 1990, p. 351 [359] (type, A. heptapetalum, M)]. Irregular, cuplike sponges with longitudinally fluted or convolute margins that may merge to produce upwardly divergent, tubular projections or subparallel branches; simple, tubelike spongocoels penetrate virtually full length of branches; walls lack major canals in markedly uniform, three-dimensional, dictyonine skeleton where nodes slightly expanded at centers of dictyonalia; neither dermal nor gastral layers differentiated. Triassic (Carnian): China (Sichuan).
  FIG. 309, 4a-b. \*R. stephana, Hanwang Formation, Hanwang-Jushui area; a, section through wall of

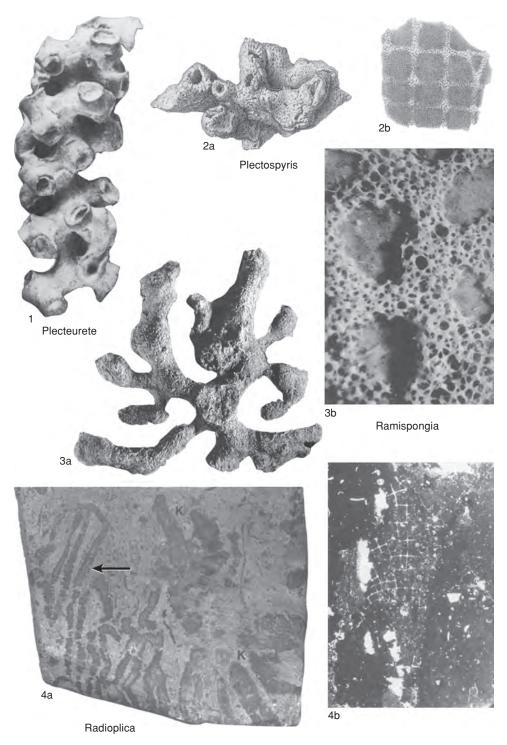


FIG. 309. Euretidae (p. 469–471).

fluted, bowl-shaped, figured sponge (*arrow*), associated with specimens of *Keriogastrospongia* (K) on right,  $\times 1$ ; b, photomicrograph of longitudinal section with upwardly divergent primary strands in thin wall, with gastral margin on right, IGASB T3(3),  $\times 10$  (Rigby, Wu, & Fan, 1998).

- Ramispongia QUENSTEDT, 1877 in 1877-1878, p. 139 [\*R. ramosa; SD DE LAUBENFELS, 1955, p. 83]. Large, sticklike, branched sponges with moderately thick walls to cylindrical to slightly compressed tubular branches, low, ringlike rims surrounding oscula that lie more or less uniformly next to one another on smooth, branch ends; dermal surface with small, round, regularly to irregularly alternating ostia; inner surface with rows of oval to slitlike, exhalant ostia; small, meshed, and somewhat regular, dictyonal skeleton composed of hexactines; dictyonal skeleton somewhat thickened at dermal surface, with specialized, dermal layer of small, fused pentactines. [Included in the family with some question.] Jurassic: Germany, Poland.-FIG. 309, 3a-b. \*R. ramosa, Weiss Jura, Erkenbrechtsweiler and Streitnberg, Germany, a, branched sponge,  $\times 0.5$ ; b, outer surface showing dictyonal dermal net and ostia of canals, ×10 (Schrammen, 1936).
- Verrucocoelia Étallon 1859b, p. 537 [\*Scyphia verrucosa GOLDFUSS, 1829, p. 91; SD HINDE, 1893b, p. 200] [=Mastoscinia POMEL, 1872, p. 106, obj. (type, Scyphia verrucosa GOLDFUSS, 1829, p. 91, M)]. Axial tube or funnel that emits tubular, radial outgrowths that contract at ends, or hoodlike outgrowths with osculum faced obliquely downward; framework with cortex and pores on dermal side or no canalar features. Scopules in living examples, with dermalia and gastralia of pentactines. ?Lower Jurassic, Middle Jurassic-Holocene: Morocco, ?Lower Jurassic; Germany, England, Middle Jurassic-Holocene; India, Eocene. FIG. 307, 3a-b. \*V. verrucosa (GOLDFUSS), Kimmeridgian beds, Upper Jurassic, Geisingen, Germany; a, cluster of radial tubules, each with deep spongocoel, IGPTU, Schrammen's collection, ×0.5; b, fragment of holotype, choanosomal skeleton with dictyonal structure, IPUB Goldfuss'collection, ×50 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Wapkiosa DE LAUBENFELS, 1955, p. 86, nom. nov. pro Pleurothyris SCHRAMMEN, 1912, p. 249, non LOWE, 1843 [\*Pleurothyris tortuosa SCHRAMMEN, 1912, p. 250; OD]. Tubular stalk expanding into scabbardlike growth or radially plicated funnel, with parietal oscula or short, open tubes along margins or outward plications; outermost skeletal meshwork irregular; no skeletal pores. Upper Cretaceous: Germany .- FIG. 305, 5a. \* W. tortuosa (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg; side view of small type with basal stalk and laterally flattened upper part with lateral oscula, ×1 (Schrammen, 1912).-FIG. 305,5b. W. folium SCHRAMMEN, Quadratenkreide, Cenomanian, Oberg; side view of type with lower stalk and flattened, upper part with parietal oscula on short tubes along margin, ×1 (Schrammen, 1912).

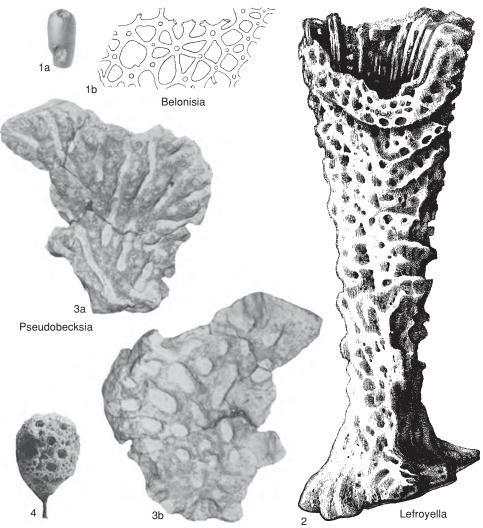
Zittelispongia SINTZOVA, 1879, p. 21 [\*Z. alcyonoides SINTZOVA, 1879, p. 22; OD]. Relatively large, irregularly spherical to angular masses of interconnected tubes and branches; dermal surface with common, irregularly spaced, inhalant ostia and gastral surface with similar exhalant ostia arranged in curved, parallel rows that are evident when thinly covering gastral layer is removed; interior skeleton a latticework of bundles of straight and curved needles and rays of hexactines, with thickened bracing structures at spicule centers; triangular to stretched rectangular spaces occurring between rays throughout skeleton, which is penetrated by large and small pores; gastral layer weblike and composed of hexactines of various sizes. Upper Cretaceous: Russia. FIG. 308, 2a-d. \*Z. alcyonoides, Glauconitic marl, Saratov and Sosnovka areas; a, large type specimen with thin walls showing irregular, inhalant ostia on dermal surface and aligned, exhalant ostia on the gastral surface,  $\times 1$ ; b, figured type specimen showing branched, tubular, growth form, ×0.4; c, fragment of gastral layer of fused skeleton, magnification unknown; d, isolated hexactine from interior part of skeleton, magnification unknown (Sintzova, 1878).

#### Subfamily POLYTHYRIDINAE Schrammen, 1912

[nom. transl. REID, herein, pro Polythyrididae SCHRAMMEN, 1912, p. 194] [=Polythyrididae SCHRAMMEN, 1912, p. 194, partim]

Funnel-shaped sponges in which paragastral surface is regularly ribbed longitudinally, and internal openings of parietal oscula or open lateral outgrowths occur along floors of furrows between paragastral ribs; latter may contain longitudinal clefts, or be pierced below their summits by apertures through which intervening furrows communicate; furrows on gastral side sometimes spanned in life by a secondary membrane, into which dictyonal meshwork may grow to form bridges; outside of funnel not ribbed or furrowed, except locally; modern examples with scopules and with hexactine dermalia and gastralia. [Habitus is a modification of that of Euretinae (e.g., Periphragella MARSHALL) in which an axial funnel bears lateral outgrowths, here complicated by plications of the axial funnel that are fused together externally. Taxon reduced to subfamily status because soft parts and skeleton are typically euretid.] ?Lower Cretaceous, Upper Cretaceous-Holocene.

Polythyris SCHRAMMEN, 1912, p. 261 [\*P. cuneata SCHRAMMEN, 1912, p. 263; M]. Funnel-like with



Polythyris

FIG. 310. Euretidae (p. 471-476).

parietal oscula that open internally in deep, longitudinal furrows on internal surface; no lateral outgrowths; outside with skeletal pores. Upper Cretaceous: Germany.—FIG. 310,4. \*P. cuneata, Quadratenkreide, Cenomanian, Oberg; side view of small type with basal stalk and coarse oscula in upper, funnel-like part of sponge, ×1 (Schrammen, 1912).

Lefroyella THOMSON, 1877, p. 403 [\*L. decora; OD]. Funnel-like with lateral oscula at tops (ends) of stumplike or tubular lateral outgrowths, which may be united in transverse rows; internal longitudinal furrows, along which are internal apertures of lateral outgrowths; internal furrows may also intercommunicate laterally, though perforations in intervening ribs; cortex and skeletal pores on the dermal side; scopules and dermal and gastral hexactines in living example. ?Cretaceous, Neogene (Miocene)– Holocene: Germany, Spain, Algeria, cosmopolitan.——FIG. 310,2. \*L. decora, Holocene, Atlantic Ocean near Bermuda; side view of holotype, ×1 (Thomson, 1877).

## Subfamily PSEUDOBECKSIINAE new subfamily

[Pseudobecksiinae REID, herein] [type genus, *Pseudobecksia* REID, 1964, p. lxv]

Funnel-like sponges in which thin, primary wall is convoluted to enclose two networks of cavaedial spaces, which open on opposite sides of funnel through apertures bounded by anastomosing folds of wall (not marginal surfaces); skeleton as in Euretinae. [Habitus specialized, seen otherwise only in Callodictyonidae (Becksiinae) of order Lychniscosa, in which it appears to be a modification of a simply plicated funnel.] *Cretacous (Coniacian–Maastrichtian).* 

Pseudobecksia REID, 1964, p. lxv [\*P. schmidti; OD]. Funnel-like with thin, primary wall convoluted to enclose two networks of passages that open on opposite sides of funnel; secondary meshwork with ostia on external surface of funnel, loose spicules unknown. Cretaceous (Coniacian–Maastrichtian): England.——FIG. 310,3a-b. \*P. schmidti, Chalk, Rickmansworth, Hertfordshire; a, side view of branching holotype from dermal side; b, side view of same from gastral side showing apertures leading into cavaedial labyrinth, BM S.8631, ×0.5 (Reid, 1964; courtesy of The Palaeontographical Society, London).

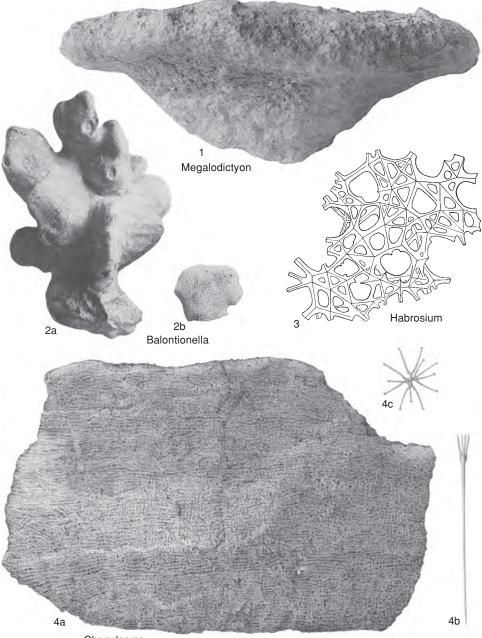
#### Subfamily CHONELASMATINAE Schrammen, 1912

[nom. transl. REID, herein, ex Chonelasmatidae SCHRAMMEN, 1912, p. 190]

Thin- to thick-walled Euretidae of funnellike or flabellate types, and bilaterally compressed or stellate sponges with skeletal characters matched otherwise in funnel-like or flabellate genera; ostia and postica without order or in regular longitudinal series; thickwalled forms often with dictyonal strands showing strong, outward curvature, some with prominent, cortical meshwork; overlapping, tubular, inhalant and exhalant canals in modern examples; living forms with scopules and with pentactine or hexactine dermalia and gastralia. [The subfamily comprises various genera in which skeleton and soft parts are euretid but which do not appear to be allied closely to typical Euretinae. It may include forms close to root stock of Craticulariidae, or Leptophragmatinae of that family that appear to be euretid through loss of canalization.] Jurassic (Oxfordian)-Holocene.

Chonelasma SCHULZE, 1887a, p. 76 [\**C. lamella*; SD IJIMA, 1927, p. 165]. Funnel-like or flabellate, typically thick walled; skeletal framework with thick, cortical strata on both sides of an internal part, and with cortical parts traversed by radial epirhyses or aporhyses that open into meshes of interior; radial canals and apertures (ostia, postica) arranged without order or locally grouped more or less quadrately; dictyonal strands spread from internal part to both surfaces, running steeply to radially outward in cortical meshwork; plan views of latter may have irregular, strandlike series of beams interwoven diagonally; living examples with tubular, radial, inhalant and exhalant canals that overlap in outer part, and with scopules and dermal and gastral pentactines. [Alleged Cretaceous records (SCHRAMMEN, 1912, p. 217) refer to Heterochone IJIMA; original diagnosis based on species of Chonelasma SCHULZE, Heterochone IJIMA, and Leptophragmella REID (see REID, 1964, p. xcviii, footnote).] Holocene: cosmopolitan.-FIG. 311,4a-c. \*C. lamella, near Kermadec Islands, South Pacific Ocean; a, side view of fragment with dictyonine skeletal net, ×1; b, dermal scopule, ×100; c, discohexaster with rough, terminal rays, ×150 (Schulze, 1887a).

- Balantionella SCHRAMMEN, 1902, p. 23 [\*B. elegans SCHRAMMEN, 1902, p. 24; OD]. Sponge composed of thin-walled, small, baglike to leaflike branches that have large, oval openings, dermal surfaces with numerous rows of small, round, inhalant ostia of blind, radial canals; gastral surface without ostia but with regular quadrate meshes in skeleton that has hexatine junctions that lack lychniscoid structure and rays that have small spines; dermal layer not developed. Upper Cretaceous: Germany.——FIG. 311,2a-b. \*B. elegans, Quadratenkreide, Cenomanian, Oberg: a, side view of branched stem; b, small, baglike structures showing regular, skeletal structure, ×1 (Schrammen, 1902).
- Eubrochis SCHRAMMEN, 1902, p. 19 [\*E. senonica; OD] [=Callibrochis SCHRAMMEN, 1912, p. 246, obj.; Oxyrhizium SCHRAMMEN, 1912, p. 249 (type, C. eximium)]. Funnel-like, sometimes stalked; internal, skeletal meshwork with transverse beams forming irregularly meshed, transverse lamellae, through which dictyonal strands run longitudinally; internal structure exposed on gastral side, apart from accretion of small hexactines, or with covering cortex and pores in older parts; masked on dermal side by denser, irregular meshwork, with vague or distinct skeletal pores; loose spicules unknown. Upper Cretaceous: Germany.-FIG. 312,1. \*E. senonica, Quadratenkreide, Campanian, Oberg; side view showing gastral surface on left and sections through wall on right, ×0.5 (Schrammen, 1902).
- Habrosium SCHRAMMEN, 1912, p. 248 [\*H. convolutum; OD]. Irregular, funnel-like sponges with very thin, irregularly indented and folded wall; without obvious ostia, epirhyses, aporhyses, and postica; hexactinosan skeletal structure regular with hexactines fused with additional rays or beams; dermal layer with thickened, tangential rays, gastral surface lacking differentiated layer. [Tentatively included in the family.] Upper Cretaceous: Germany.——FiG. 311,3. \*H. convolutum, Quadratenkreide, Campanian, Oberg; skeletal structure of the interior skeleton, ×45 (Schrammen, 1912).



Chonelasma

FIG. 311. Euretidae (p. 473-475).

Megalodictyon OPPLIGER, 1926, p. 35 [\*M. fretreulensis; OD]. Large, thick-walled funnel; surfaces with large, skeletal pores in irregular, cortical meshwork, with shallow epirhyses on dermal side; internal meshwork wide meshed, not canalized,

with meshes between dictyonal strands predominantly rectangular; loose spicules unknown. [Apparently similar and possibly identical to living *Chonelasma* SCHULZE, 1887a.] *Jurassic (Oxfordian):* Switzerland, Germany.——FIG. 311,1. \**M*.

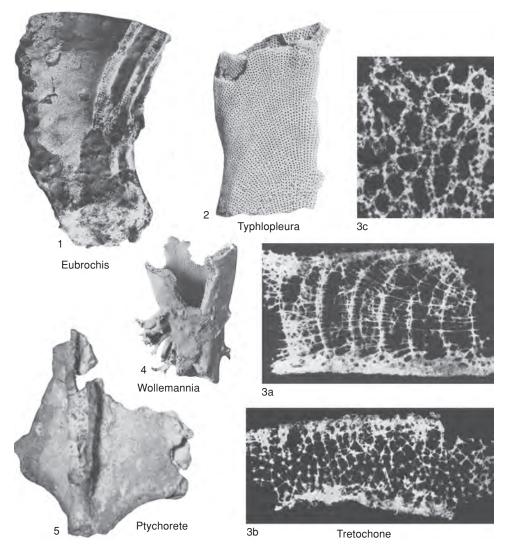


FIG. 312. Euretidae (p. 473-476).

*fretreulensis*, Gorge of l'Areuse, Switzerland; side view of thick-walled, funnel-shaped sponge with large, inhalant ostia, ×0.5 (Oppliger, 1926).

Ptychorete REID, 1964, p. lxiv [\*?: ijimai; OD]. Wall radially folded above tubular stalk to form radiating, bilaterally compressed, hollow flanges, continuous in middle, or with several such growths arising from branching stock; small, parietal oscula along narrow, folded margins; skeleton as in Wollemannia SCHRAMMEN. Cretaceous (Coniacian–Maastrichtan): Northern Ireland.——FIG. 312,5. \*P. ijimai, Glauconitic Chalk, Senonian, County Antrim; side view of incomplete, stellate holotype with two flanges laterally and broken one with flange section toward front, BM S.8619, ×1 (Reid, 1964; courtesy of The Palaeontographical Society, London).

Tretochone REID, 1959, p. 11 [\*Ptychodesia duplicata TOPSENT, 1928c, p. 1; OD]. Flabellate, inversely curved transversely (i.e., gastral side external), sometimes enrolled to form a funnel by union of lateral margins; dermal side with papilliform outgrowths, sometimes replaced locally by transverse, shelflike features; both skeletal surfaces with round, intracortical pores (ostia or postica) arranged in longitudinal series; gastral side with additional slitlike apertures, little wider than pores that open inward into longitudinal tunnels (amarathyses) in internal meshwork; dictyonal strands spreading to both surfaces of skeletal framework, and beams connecting them arranged to form distally convex, transverse lamellae, whose margins unite at both surfaces to form cortical meshwork; branches of amararhyses run to round perforations at tops of outgrowths of dermal side and sometimes also transversely in shelflike features; living example with main canal system as in Chonelasma SCHULZE; pinular hexactines as dermalia and gastralia, and scopules. [Confused by IJIMA (1927, p. 116, 165), TOPSENT (1928c, p. 1), and DE LAUBENFELS (1955, p. 84) with Ptychodesia SCHRAMMEN (1912, p. 252; family Craticulariidae herein), which has no Holocene species.] Holocene: Pacific Ocean (Japan).-FIG. 312,3a-c. \*T. duplicata (TOPSENT), Sugami Bay; a, longitudinal section with transverse lamellae arcuate in direction of growth and emerging bilaterally; b, distal face of transverse lamella with cortical meshwork along top and bottom, ×5; c, tangential view of dermal cortex, all specimens in REID's collection, ×6 (Reid, 1964; courtesy of The Palaeontographical Society, London).

- Typhlopleura SCHRAMMEN, 1902, p. 24 [\*T. dichotoma; OD]. Bilaterally compressed, forms scabbard- or leaflike growths with similar growths arising from their narrow margins, sometimes also reuniting marginally; margins with parietal oscula; exterior with skeletal pores in radiating, longitudinal series piercing fine, cortical meshwork; interior as in *Eubrochis* SCHRAMMEN, or with cortical meshwork and postica on gastral side. *Upper Cretaceous:* Germany.——FiG. 312,2. \*T. dichotoma, Mucronatenkreide, Maastrichtian, Misburg; side view of fragment of scabbardlike sponge with fine, cortical meshwork, ×1 (Schrammen, 1902).
- Wollemannia SCHRAMMEN, 1912, p. 247 [\*W. araneosa; OD]. Similar to Eubrochis but with no skeletal pores; internal framework covered on dermal side or both sides by thin layers of fine, cortical meshwork that is sharply distinct from internal framework; loose spicules unknown. Upper Cretaceous: Germany.—FIG. 312,4. \*W. araneosa, Quadratenkreide, Cenomanian, Oberg; side view of type with steeply funnel-like form and regular, reticulate skeleton and canal pattern, ×1 (Schrammen, 1912).

#### Subfamily UNCERTAIN

Belonisia RAUFF, 1933, p. 26 [\*B. necopinata; M]. Nature uncertain; single example a small budlike sponge, possibly juvenile; exterior with small ostia in form of rounded, skeletal meshes; radial canals possibly internally; loose spiculation unknown. Upper Cretaceous: Germany.—FIG. 310, Ia-b. \*B. necopinata, Greensand, upper Turonian, Ruhr Valley; a, side view of small sponge, ×1; b, drawing showing skeletal structure of outer skeleton, ×50 (Rauff, 1933; courtesy of Preussischen Geologischen Landsanstalt, E. Schweizerbart'sche Verlagsbuchhandlung).

### Family CRATICULARIIDAE Rauff, 1893

[Craticulariidae RAUFF, 1893, p. 191] [=Euretidae ZITTEL, 1877b, p. 35, partim; Leptophragmidae SCHRAMMEN, 1912, p. 191; Craticularinae DE LAUBENFELS, 1936, p. 186; Leptophragmatidae DE LAUBENFELS, 1955, p. 80; Laocaetidae MEHL, 1992, p. 71]

Skeletal framework three dimensional initially, constructed as in Euretidae, but normally with fully developed epirhyses and aporhyses; skeletal canals typically radial and blind, arranged with epirhyses and aporhyses in alternating, longitudinal series, and often so that each canal of one sort stands quincuncially between four of others; apertures then arranged in longitudinal and transverse rows; some genera with epirhyses open at both ends or arranged without order, or without aporhyses in some individuals; dictyonal strands spread subequally to both surfaces from interior, or run mainly or all to dermal surface; beams between ends of strands usually forming cortical meshwork, which secondary accretions may make thicker or denser; superficial meshwork in some genera, formed from dictyonal hexactines, or additionally by ankylosis of dermal or gastral stauractines; scopules in a living example. [Only Mesozoic and Cenozoic forms are discussed here. Older forms are treated in the section on Paleozoic hexactinosans, p. 437 herein.] Triassic (Carnian)–Holocene.

Three subfamilies are included herein, Craticulariinae s.s., Laocoetidinae DE LAUBENFELS, and Leptophragmatinae SCHRAMMEN.

A. Craticulariinae: superficial meshwork formed partly by dictyonal hexactines, partly by fused dermal or gastral stauractines.

B. Laocoetidinae: superficial meshwork formed from dictyonal hexactines only; dermalia, gastralia pentactines where known, sometimes trapped in superficial meshes but not forming distinct tangential networks.

C. Leptophragmatinae: superficial meshwork absent.

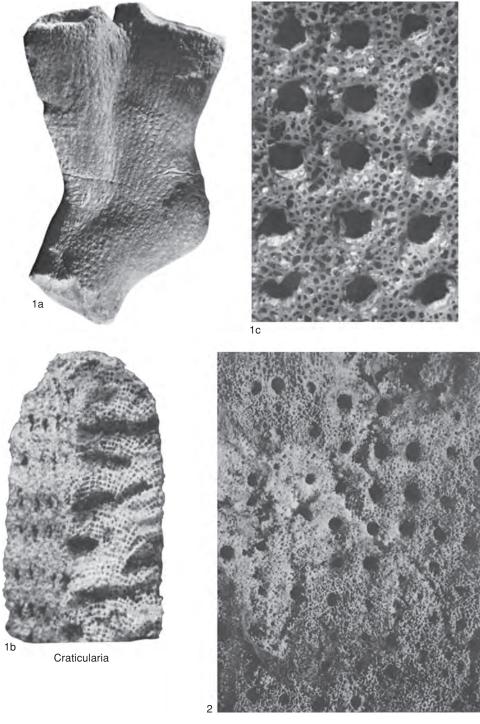
#### Subfamily CRATICULARIINAE Rauff, 1893

#### [*nom. transl.* REID, herein, *pro* Craticulariidae RAUFF, 1893, p. 191] [=Craticulariidae RAUFF, 1893, p. 191, *partim*; Sphenaulacidae SCHRAMMEN, 1937, p. 43]

Craticulariidae in which dermal or gastral stauractines are united to form superficial meshwork in fully developed individuals; tubular to funnel shaped to dishlike, branched tubular, or flabellate sponges, seldom thin walled, with nodular or rootlike, basal masses; ostia and postica grouped quadrately or less regularly, usually round or ovate although sometimes finely denticulated; sometimes in longitudinal furrows; dictyonal strands generally spread equally or subequally to both skeletal surfaces with meshes often mainly rectangular; outermost meshwork usually forming denser cortex on both sides; superficial meshwork of dictyonal origin variably developed, but usually present to some extent, dermal or gastral stauractines simply cemented at points of contact, or additionally connected by siliceous filaments that may form networks in paratangential meshes; connected gastralia in one genus only. [Craticulariinae comprise the Craticulariidae RAUFF sensu SCHRAMMEN, 1937, less Pachyascus SCHRAMMEN, 1937 (herein in Laocoetidinae DE LAUBENFELS), plus the Sphenaulacidae SCHRAMMEN, 1937. Known examples are Jurassic sponges; some genera are recorded from Lower Cretaceous (e.g., LAGNEAU-HÉRENGER, 1962), but characteristic dermal structures have not been verified.] Triassic-Paleogene (Thanetian).

Craticularia ZITTEL, 1877b, p. 46 [\*Scyphia parallela GOLDFUSS, 1826, p. 8; SD HINDE, 1893b, p. 198; not Scyphia paradoxa MÜNSTER, 1883, SD DE LAUBENFELS, 1955, p. 80; =Scyphia procumbens GOLDFUSS, 1826, p. 11 (see ZIEGLER, 1962, p. 575)] [=Paracraticularia SCHRAMMEN, 1937, p. 28 (type, Scyphia procumbens GOLDFUSS, 1826, p. 11, SD DE LAUBENFELS, 1955, p. 80); Desmocinia POMEL, 1872, p. 83 (type, Scyphia procumbens GOLDFUSS, 1826, p. 11, OD), suppressed under Code Art. 23.2 (ICZN, 1999)]. Tubular or branched-tubular, with some branches sometimes ending blindly; skeletal canals in regular series with apertures typically arranged quadrately; apertures (ostia, postica) rounded, quadrate, or finely denticulated by skeletal outgrowths; dictyonal strands spread equally or subequally to both sides of skeletal framework; outermost meshwork of both sides forming a more or less distinct cortex; both sides with superficial outgrowths formed from dictyonal hexactines, and with additional fused dermal stauractines in fully grown examples; basal mass nodular to rootlike. [Records from later systems refer to forms (mainly Laocoetis POMEL, 1872, p. 92) that lack connected dermal stauractines.] Middle Jurassic-Upper Jurassic: Poland, Germany.—FIG. 313, 1a-c. \*C. parallela (GOLDFUSS), Middle Jurassic beds, Callovian, Ardèche, France; a, side view of characteristic specimen with branches and regular series of inhalant ostia, PIUZ E/6, ×1; b, vertical section showing upwardly divergent, skeletal structure interrupted by smaller inhalant and larger exhalant canals, PIUZ E/1, ×5; c, photomicrograph of outer surface showing aligned, inhalant ostia and small, skeletal pores in the fused skeleton, PIUZ E/1, ×10 (Ziegler, 1962; courtesy of Eclogae Geologicae Helvetiae, Birkhäuser Verlag AG).

- Dictyonocoelia ÉTALLON, 1859b, p. 536 [\*Scyphia schweiggeri GOLDFUSS, 1829, p. 91; OD] [= Thyroidium DE LAUBENFELS, 1955, p. 80, obj., nom. nov. pro Thyridium SCHRAMMEN, 1937, p. 31, non DEJEAN, 1833]. Tubular to funnel-like or flabellate, thin or thick walled; skeleton mainly similar to that of Craticularia ZITTEL, but postica open along shallow, longitudinal furrows and dermal stauractines are finely spined. [The type species was written S. schweiggeri by ÉTALLON, 1859b.] Upper Jurassic, ?Lower Cretaceous: Germany, Poland.-FIG. 314, 3a-b. \*D. schweiggeri (GOLDFUSS), Weiss Jura, Upper Jurassic, Hossingen, Germany; a, dictyonal structure of gastral surface of wall, ×5; b, broad, discoidal sponge with regular, radiate, skeletal and canal structure, ×0.5 (Schrammen, 1937).---FIG. 314,3c. D. lineatum (SCHRAMMEN), Weiss Jura, Upper Jurassic, Heuchstetten, Germany; enlarged, outer part of sponge with fine, skeletal structure preserved between circular, inhalant ostia, ×5 (Schrammen, 1936).
- Diphyllospira HERRMANN-DEGEN, 1980, p. 19 [\*D. ectophoios; OD]. Sponges consisting of two non-overlapping, spiralled to occasionally twisted parts; margins of both are distinct and not intergrown with other, so that sponges appear as a double screw, but they may be locally intertwisted along long axis; parenchymal skeleton consisting of smooth hexactines and is euretoid; dictyonal cortex is thicker the dermal surface than on gastral; canal system is craticulariid. Paleogene (Thanetian): Egypt.—FIG. 314,2. \*D. ectophoios, "Chalk member" of Tarawan Formation, Bulaq Oasis, between Kharga and Baris, southwestern Egypt; side view showing double spriralling form of the genus, ×0.5 (Herrmann-Degen, 1980).



Pycnocalyptra



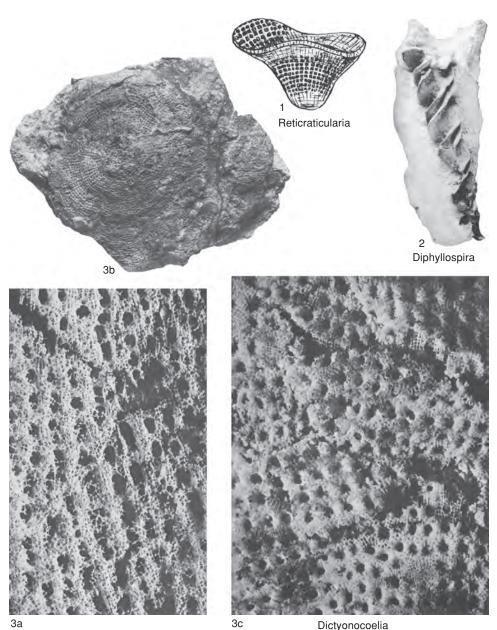
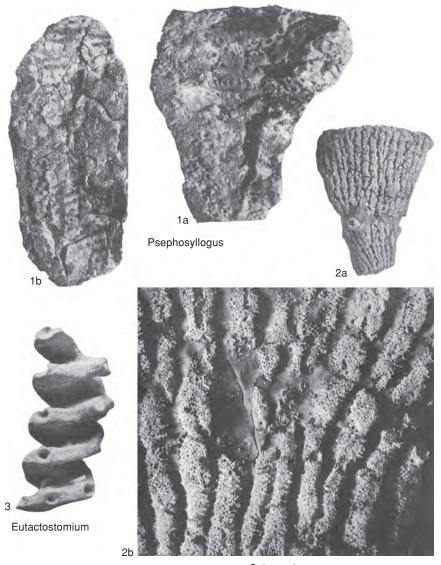


FIG. 314. Craticulariidae (p. 477-481).

Eutactostomium HERRMANN-DEGEN, 1980, p. 17 [\**E. helicosoma* HERRMANN-DEGEN, 1980, p. 18; OD]. Sponges with form of a bilaterally flattened tube that spirals around vertical axis; in spiral structure, regularly crossing, round openings are part of short, tubular, recumbent projections or are reduced, parietal oscula; dictyonine, parenchymal skeleton consisting of smooth, very regular hexactines, which are thickened in both gastral and dermal lay-

ers; small ostia and postica perforate these layers in regular, vertical rows in a quadrunxial pattern; canal system with craticular diplorhysis. *Paleogene (Thanetian):* Egypt.——FiG. 315,3. \**E. helicosoma*, Chalk member, Tarawan Formation, Bulaq Oasis, between Kharga and Baris, southwestern Egypt; frontal view of spiralled sponge showing characteristic growth form, ×1 (Herrmann-Degen, 1980).

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#### Sphenaulax

FIG. 315. Craticulariidae (p. 479-481).

Psephosyllogus SCHRAMMEN, 1937, p. 33 (SCHRAMMEN, 1936, p. 181, nom. nud.) [\*P. diligens; M]. Similar to Pycnocalyptra, but connected stauractines are known from dermal side only, and (some) apopores in transverse corrugations of gastral side; moderately thick walls with inhalant prosopores oval and in vertical rows. [Could be identical with Pycnocalyptra, based on individual differences.] Upper Jurassic: Germany, Poland.——FIG. 315,1ab. \*P. diligens, Weiss Jura, Heuchstetten, Germany; a, gastral view with moderately thick, broken wall and exhalant ostia,  $\times 1$ ; *b*, inner or gastral surface with apopores in transverse corrugations,  $\times 0.5$  (Schrammen, 1937).

Pycnocalyptra REID, nom. nov. herein (SCHRAMMEN, 1937, p. 33, nom. nud.) [\*P. calyx SCHRAMMEN, 1937, p. 34; OD]. Funnel- or dishlike, thick walled with swollen base; ostia and postica widely spaced, puncturelike in flat surfaces; both sides with connected stauractines (dermalia and gastralia), with paratangential meshes filled by networks of siliceous filaments. [DE LAUBENFELS (1955, p. 79) subsequently designated the type species for *Pycnocalyptra*, but according to *Code* Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xix, herein).] *Upper Jurasic:* Germany.——FIG. 313,2. \**P. calyx*, Weiss Jura, Heuchstetten; enlarged outer surface showing dictyonal skeletal area perforated by inhalant ostia, ×5 (Schrammen, 1936).

- Reticraticularia LAGNEAU-HÉRENGER, 1962, p. 54 [\**R. albiensis* LAGNEAU-HÉRENGER, 1962, p. 55; OD]. Small, cup-shaped, pedunculate sponges with thin walls and undulating rims; both dermal and gastral surfaces with similar, moderately large ostia arranged in very regular, quadrangular patterns and gastral layers dictyonine with plain nodes. *Cretaceous (Albian):* France.——FIG. 314, *I. \*R. albiensis,* Andon; side view showing form of thin-walled sponge and regularly distributed, moderately large, inhalant and exhalant ostia of syntype, ×1 (Lagneau-Hérenger, 1962).
- Sphenaulax ZITTEL, 1877b, p. 47 [\*Scyphia costata GOLDFUSS, 1826, p. 6; M] [=Cnemiseudea DU FROMENTEL, 1860a, p. 28, obj., suppressed under Code Art. 23.2 (ICZN, 1999); Rhabdocnemis POMEL, 1872, p. 80, obj. (type, Scyphia costata GOLDFUSS, 1826, p. 6, SD RAUFF, 1893, p. 66), suppressed under Code Art. 23.2 (ICZN, 1999); Calycospongia WU & XIAO, 1989, p. 14 (type, C. pleiopetala, OD)]. Cylindrical or funnel-like; outside with well-marked, longitudinal furrows, along which are ostia of inhalant, skeletal canals (epirhyses); gastral side not furrowed; dermal furrows straight sided, or denticulated by outgrowths that may unite to bridge them; dermal stauractines also fuse to form a tangential network and extend across furrows, but do not line them; wall wrongly said to be radially folded. Triassic (Carnian)-Upper Jurassic: China (Sichuan), Carnian; Germany, Upper Juras--FIG. 315,2a-b. \*S. costata (GOLDFUSS), sic ----Weiss Jura, Streitberg; a, side view of funnel-like sponge with longitudinal grooves, ×0.5; b, enlarged, dermal part of wall with longitudinal grooves and fine-textured skeleton, ×4 (Schrammen, 1937).

#### Subfamily LAOCOETIDINAE de Laubenfels, 1955

[nom. transl. REID, herein, ex Laocoetididae DE LAUBENFELS, 1955, p. 82]

Craticulariidae without superficial meshwork formed by union of dermal or gastral stauractines, although superficial dictyonal meshwork is usually present; thick- or thinwalled sponges, generally similar to Craticulariinae in habitus and skeletal structure. Characteristic arrangement of ostia and postica usually clearly apparent, but obscured in one genus by ostia having very ir-

regular shapes in some examples. [Name Laocoetididae was published (DE LAUBEN-FELS, 1955, p. 82) without diagnosis in definition of family Myliusiidae "DE LAUBENFELS nov." (recte SCHULZE, 1885), apparently as an unadopted alternative to Leptophragmatidae SCHRAMMEN, since Laocoetis POMEL, 1872 (p. 92) (=Laocoetis DE LAUBENFELS, nom. null.) is placed in that family (DE LAUBENFELS, 1955, p. 80). Herein used for Craticulariidae similar to Craticulariinae but lacking connected dermalia or gastralia; comprises all (certain) post-Jurassic genera but those in Leptophragmatinae. Immature Craticulariinae also lack connected dermalia and gastralia (as also may imperfect examples), but their absence in genera herein listed (except, perhaps Pachyascus SCHRAMMEN) is considered due to permanent lack of fusion in life. Occasional dermalia or gastralia trapped in the skeletal framework are also pentactines in cases known to the writer.] Triassic (Carnian)-Neogene (Miocene, ?Pliocene).

Laocoetis POMEL, 1872, p. 92 [\*L. crassipes POMEL, 1872, p. 93; SD DE LAUBENFELS, 1955, p. 80] [=Rhabdocoetis POMEL, 1872, p. 102 (type, Ocellaria cancellata ROEMER, 1864, p. 17, OD), suppressed under Code Art. 23.2 (ICZN, 1999); Laocoetis MORET, 1924, p. 20, nom. null.; Poteridium RAUFF, 1933, p. 22 (type, P. cretaceum, M); Aulacosia RAUFF, 1933, p. 34, obj. (type, Ocellaria cancellata ROEMER, 1864, p. 17, M)]. Funnel-like, tubular or flabelliform, with a massive, tuberous base in some species; skeletal canals in regular series with their apertures in longitudinal and transverse rows or less regularly arranged; beams between ends of dictyonal strands forming cortical meshwork at both skeletal surfaces; dermal or both sides usually with superficial outgrowths or meshwork formed from dictyonal hexactines or partly from siliceous filaments; much of dermal surface sometimes covered by upward extension of basal skeleton, which forms a thick, secondary cortex; no fused stauractines on either side. Middle Jurassic (Bajocian)-Neogene (Miocene, ?Pliocene): Hungary, Bajocian; Germany, Upper Jurassic; Europe, Algeria, Cretaceous-Miocene, ?Pliocene.-FIG. 316,1a. \*L. crassipes, Miocene, Djebel Djambeida, Algeria; side view of large, funnel-shaped sponge with ostia of canals in regular series, ×0.25 (Pomel, 1872).-FIG. 316, 1b-c. L. cancellata (ROEMER), Cuvieri beds, Turonian, Vienenburg, Germany; b, gastral view of small fragment showing radial alignment of ovoid, exhalant ostia in depressed areas,  $\times 1$ ; c,

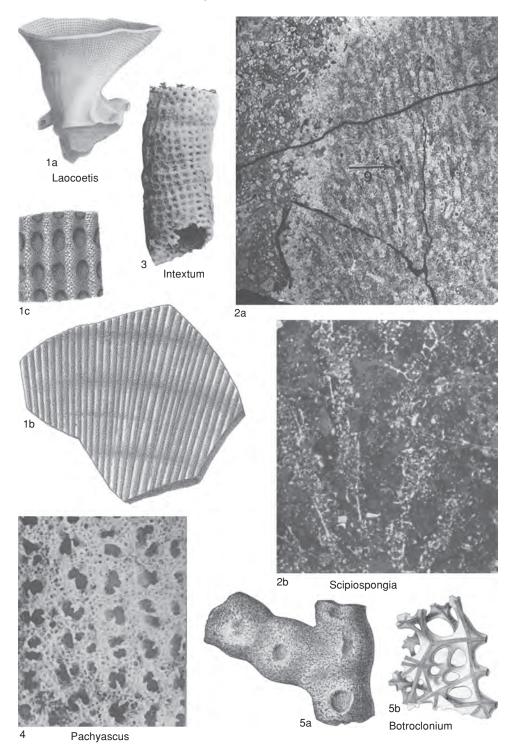
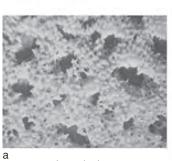


FIG. 316. Craticulariidae (p. 481-483).



Leptolacis

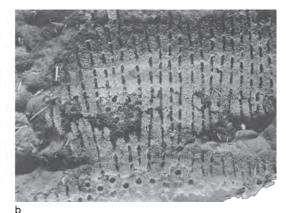


FIG. 317. Craticulariidae (p. 483).

enlarged section showing ostia in radial series, enlarged (Roemer, 1864).

- Botroclonium Počta, 1883, p. 28 [\*B. arborescens Počta, 1883, p. 29; SD DE LAUBENFELS, 1955, p. 84]. Branching growths with oscula of local, gastral cavities along one side; axial paragaster absent or only locally present; ostia of epirhyses arranged quadrately or irregularly; postica crowded in walls of local, gastral cavities; superficial meshwork formed from dictyonal hexactines may bridge or veil ostia. Upper Cretaceous: Czech Republic, Slovakia.—FIG. 316,5a-b. \*B. arborescens, Korytzaner Schichten, Kamajk; a, side view of branched sponge with oscula along one side, ×0.66; b, part of skeletal structure, ×40 (Počta, 1883).
- Intextum DE LAUBENFELS, 1955, p. 84, nom. nov. pro Syringium SCHRAMMEN, 1912, p. 256, non PRINCIPI, 1909 [\*Syringium textum SCHRAMMEN, 1912, p. 256; OD]. Tubular, externally similar to Laocoetis but epirhyses open at both ends; no dictyonal cortex on gastral side; superficial outgrowths on dermal side form veils across ostia. [A pseudogenus, possibly due to preservation.] Upper Cretaceous: Germany.—FIG. 316,3. \*I. textum (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg; side view of tubular type with distinct epirhyses that have minor outgrowths along their margins, ×1 (Schrammen, 1912).
- Leptolacis SCHRAMMEN, 1937, p. 60 (SCHRAMMEN, 1936, p. 183, nom. nud.) [\*L. striata; OD]. Flabelliform, thin walled; apertures of skeletal canals irregularly shaped and arranged without order on possible dermal side, elongate slits arranged in longitudinal series and rough transverse rows on possible gastral side; dictyonal superficial outgrowths or meshwork on the dermal side. Upper Jurassic: Germany.—FIG. 317a-b. \*L. striata, Weiss Jura, Gerstetten; a, enlargement of exterior showing skeletal structure and occurrence of inhalant ostia, ×5 (Schrammen, 1936); b, inner surface of the wall

showing prominent alignment of elongate slits between skeletal tracts, with round ostia in gastral layer at base of figure,  $\times$ 4 (Schrammen, 1937).

- Pachyascus REID, nom. nov. herein (SCHRAMMEN, 1937, p. 35, nom. nud.) [\*P. formosus SCHRAMMEN, 1937, p. 35; OD]. Tubular to funnel-like, fairly thick walled; ostia and postica arranged quadratically or less regularly, sometimes locally evident order; ostia characteristically irregular and variable in shape because outgrowths of skeletal surface may sometimes unite across them. [DE LAUBENFELS (1955, p. 79) subsequently designated the type species for Pachyascus, but according to Code Article 13.3 (ICZN, 1999), subsequent designation is admissable only for genera established prior to 1931 (see also p. xix, herein).] Upper Jurassic-Lower Cretaceous: Germany.-FIG. 316,4. \*P. formosus, Weiss Jura, Upper Jurassic, Oberdigisheim; skeletal tracts with dictyonal structure separated by rows of inhalant ostia, ×5 (Schrammen, 1936).
- Scipiospongia RIGBY, WU, & FAN, 1998, p. 133 [\*S. columnaria; OD]. Steeply obconical, thick-walled dictyonine with vertical rows of inhalant-exhalant canals in possible craticulariid pattern, cross connecting to longitudinal, upwardly divergent canals, separated by distinct skeletal tracts in which thickened, primary strands form vertical rods at canal boundaries and remainder of net of girderlike tracts composed mainly of short beams and synapticulae, producing dominantly triangular, skeletal pores. Triassic (Carnian): China (Sichuan).-FIG. 316,2a-b. \*S. columnaria, Hanwang Formation, Jushui; a, holotype, vertical section with light gray matrix filling canals between darker gray skeletal tracts, radial canals show as circular cross sections in upper part, thick microbial crust coats sponge on left, arrow showing position of b, ×1; b, photomicrograph of characteristic, girderlike tracts in holotype where rodlike, vertical strands are parallel to matrix-filled, vertical canals, IGASB R6-21(065), ×10 (Rigby, Wu, & Fan, 1998).

#### Subfamily LEPTOPHRAGMATINAE Schrammen, 1912

[nom. transl. REID, herein, ex Leptophragmatidae DE LAUBENFELS, 1955, p. 80, nom. correct. pro Leptophragmidae SCHRAMMEN, 1912, p. 191]

Typically thin-walled Craticulariidae of tubular, funnel-like, flabellate, or various special habits; canals small, closely spaced, normally in regular series; apertures (ostia, postica) typically rounded, puncturelike, usually in longitudinal and transverse rows, but sometimes in longitudinal series only; rarely with canalization imperfect in some individuals, then absent internally or seen on dermal side only; dictyonal strands of internal meshwork gradually spread or mainly or all directed toward dermal skeletal surface, which they approach steeply or radially; sometimes radial for most of their length; meshwork seen in tangential sections, hence, often irregular; superficial meshwork absent, except where older parts are coated by basal skeleton or analogous meshwork of gastral side. [A mainly Cretaceous group, centered morphologically on Leptophragma ZITTEL, without superficial specializations of earlier Craticulariinae.] ?Jurassic, Cretaceous (?Berriasian-?Aptian, Albian)-Holocene.

- Leptophragma ZITTEL, 1877b, p. 48 [\*Scyphia murchisoni GOLDFUSS, 1831, p. 219; SD DE LAUBENFELS, 1955, p. 80] [=Polystigmatium SCHRAMMEN, 1912, p. 254 (type, P. striatopunctatum)]. Tubular, scabbardlike, funnel-like, or flabellate; often stalked; sometimes irregularly compressed, convolute, or lobate marginally when funnel-like; dictyonal strands of some species run steeply to radially outward. Dermalia, gastralia pentactines (rarely trapped in meshes). [Distinguished by SCHRAMMEN (1912, p. 254) on the basis of spherical swelling of nodes at skeletal surfaces.] ?Jurassic, ?Lower Cretaceous, Upper Cretaceous: Europe.—FIG. 318,5. L. striatopunctatum (SCHRAM-MEN), Quadratenkreide, Cenomanian, Oberg, Germany; skeletal fragment of dictyonal hexactines, ×45 (Schrammen, 1912).
- Leptophragmella REID, 1963a, p. 226 [\*Chonelasma choanoides SCHULZE & KIRKPATRICK, 1910a, p. 302; OD; =C. lamella choanoides SCHULZE & KIRKPAT-RICK, 1910a, p. 302, non C. lamella F. E. SCHULZE, 1886]. Similar to Leptophragmus in growth form; canalization normal or showing reduction, consisting in ultimate reduction of shallow epirhyses only; aporhyses or corresponding soft structures opening between successive, transverse, skeletal lamellae; no superficial meshwork; loose spicules pentactine dermalia and gastralia, dermal and gastral scopules,

parenchymal uncinates, oxyhexasters and discohexasters. [The only known living craticulariid sponge.] *Holocene:* Antarctic Ocean.——FIG. 318,4*a*-*c*. \**L. choanoides* (SCHULZE & KIRKPATRICK); *a*, side view of funnel-shaped, typical form, ×1; *b*, pentactine dermalia; *c*, parenchymal skeleton with associated scopules and small, spinose hexasters, ×100 (Schulze & Kirkpatrick, 1910a).

- Pleurostoma F. A. ROEMER, 1840 in 1840–1841, p. 5 [\*P. radiatum; SD DE LAUBENFELS, 1955, p. 81]. Bilaterally compressed, scabbardlike, with parietal oscula along narrow margins; or initially of this habitus, expanding above into funnel; postica sometimes in longitudinal furrows. Upper Cretaceous: Europe.—FIG. 318,3. \*P. radiatum, Quadratenkreide, Cenomanian, Oberg, Germany; side view of upper part of scabbardlike sponge with prominent rows of inhalant ostia and oscula along upper, narrow margin, ×1 (Schrammen, 1912).
- Pseudoguettardia MORET, 1926a, p. 16 [\*Guettardia thiolati D'ARCHIAC, 1846, p. 197; OD]. Sponges with folded, thin, finlike walls arranged in a cross or starlike pattern around central axis, similar to in Guettardia; dermal surface marked by irregularly placed, small, cuplike depressions; wall pierced by small, equidistant canals in moderately regular alignment locally; dense hexactinosan skeleton with regular, robust, unperforated nodes. Paleogene (Eocene): Spain.—FIG. 318,7a-c. \*P. thiolata (D'ARCHIAC), Rocher de la Gourêpe, Lutetian, Biarritz; a, side view of double-walled, folded, fin fragment with scattered, small depressions and fine epirhyses in dermal surface, ×1; c, fragments of skeleton, scale unknown (Moret, 1926b; courtesy of Société Géologique de France).
- Ptychocoetis POMEL, 1872, p. 101 [\*Pleurostoma trilobata F. A. ROEMER, 1864, p. 14; OD] [=Pleuroguettardia REID, 1963a, p. 226 (type, Guettardia stumpeli SCHRAMMEN, 1912, p. 240, OD)]. Wall folded longitudinally above the base to form radiating and bilaterally compressed hollow flanges, continuous in the middle; rounded to elongate parietal oscula along outward margins of flanges. Upper Cretaceous: Europe.—FIG. 318,6. \*P. trilobata (ROEMER), Quadratenkreide, Cenomanian, Oberg, Germany; side view of sponge with folded wall and oscula along crests of folds, ×1 (Schrammen, 1912).
- Ptychodesia SCHRAMMEN, 1912, p. 252 [\**P. papillata;* OD]. Ovate plate with papilliform outgrowths on one side, apertures leading into them on the other; additional longitudinal plications may be locally developed, with papillae then rising along them; papillate side probably dermal. *Upper Cretaceous:* Europe.——FIG. 318,2. \**P. papillata,* Quadratenkreide, Cenomanian, Oberg, Germany; papilliform probably dermal surface on plate with ostia on ridge crests, and fine skeletal structure between, ×1 (Schrammen, 1912).
- Strephinia HINDE, 1884a, p. 96 [\*S. convoluta; SD DE LAUBENFELS, 1955, p. 80]. Convoluted funnels or lamella arising from a branched, tubular stock, or latter only; dermal surface of skeletal framework

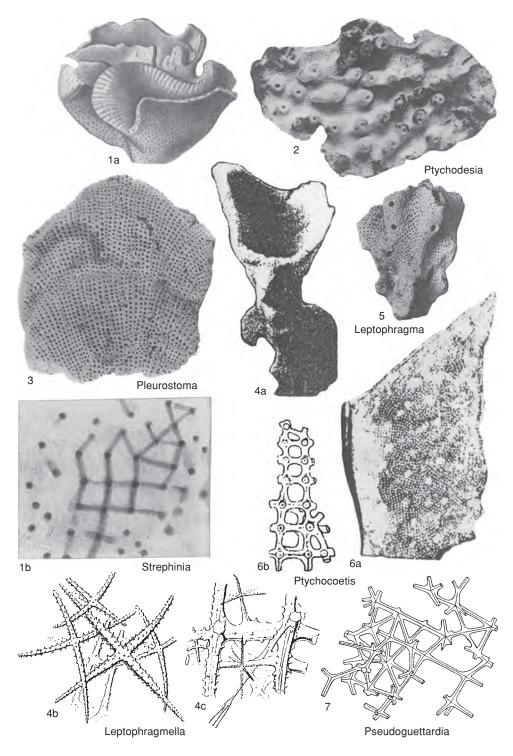


FIG. 318. Craticulariidae (p. 484-486).

with alternating, round or ovate apertures of short, radial canals that open internally in floors of longitudinal or locally reticulate furrows in gastral side of framework; furrows may be absent locally and such parts of surface resemble dermal side; dictyonal strands spread to both surfaces or run all to gastral side when apparent; no special cortical meshwork, although beams may be thickened at external surfaces; internal surfaces with numerous, partly attached, dictyonal hexatines with several free rays; lychniscs unknown. Cretaceous (Albian-Cenomanian): Europe.—FIG. 318, 1a-b. \*S. convoluta, Grey Chalk, Dover; a, side view of convoluted, funnel-like sponge with furrows on gastral surface and ovate ostia of radial canals on dermal surface,  $\times 0.5$ ; *b*, calcite-replaced, hexactine, skeletal structure, gray in light chalk, ×50 (Hinde, 1884a).

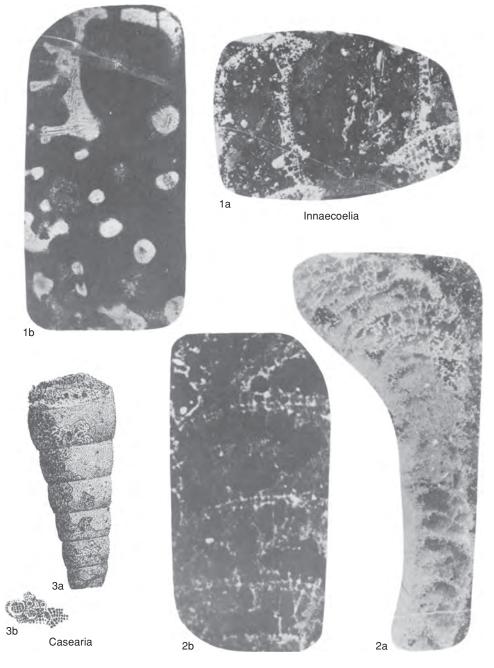
#### Subfamily CASEARIINAE Schrammen, 1937

[nom. transl. REID, herein, ex Caseariidae SCHRAMMEN, 1937, p. 49]
 [=Monilispongiidae WU, 1990, p. 354 [361]; Dracolychnidae WU, 1990,
 p. 352; ?Innaecoelidae BOIKO, 1990, p. 124; ?Tadassiidae
 ZHURAVLEVA & PYANOVSKAY, 1995, p. 31]

Cylindrical to top-shaped or open, funnelshaped possible Craticulariidae in which body consists of a superimposed series of hemispherical to annular or discoidal growths, usually with a common, paragastral cavity; dermal surface may be constricted transversely at segment junctions; skeletal surfaces formed by tangential networks of ankylosed stauractines, interpreted as dermalia and gastralia; stauractine network of outside, continuous to paragastral margin at top of body, and extending through wall to paragastral surface between each segment; ostia and postica of radial canals, arranged quadrately in some examples under surface networks. Triassic (Carnian)–Upper Jurassic.

Casearia QUENSTEDT, 1858, p. 681 [\*Scyphia articulata GOLDFUSS, 1826, p. 8; SD ZITTEL, 1877b, p. 54] [=Arthrocypellia POMEL, 1872, p. 77, obj; Caesaria DE LAUBENFELS, 1955, p. 82, obj; Monilispongia WU & XIAO, 1989, p. 354 [361], obj.; ?Innaecoelia BOIKO, 1990, p. 126, obj.]. Characters same as subfamily. [The genus Casearia ZITTEL is interpreted as a specialized relative of Craticularia ZITTEL, with a mode of growth analogous with that of thalamid Calcarea.] Upper Triassic, Upper Jurassic: Europe, China.—FIG. 319,3a-b. \*C. articulata (GOLD-FUSS), Upper Jurassic, Germany; a, side view of uniserial, chambered-appearing sponge, ×1; b, part of upper end of sponge showing regular, reticulate, skeletal structure, enlarged (Quenstedt, 1858).

- Caucasocoelia BOIKO, 1990, p. 124 [\**C. kunae*; OD]. Cylindrical sponges composed of stacked, cuplike chambers with reticulate skeleton composed of hexactine spicules that are united at their tips to form an open textured, three-dimensional net. *Triassic (Norian-Rhetian):* Russia (northern Caucasus).—FIG. 319,2*a*-*b*. \**C. kunae*, Norian, White River; *a*, cylindrical type specimen showing upwardly arched chamber walls of fused hexactines, MIGACT 15/7, ×4; *b*, photomicrograph showing chamber walls of 2 or 3 layers of fused hexatines, approximately ×10 (Boiko, 1990).
- Dracolychnos WU & XIAO, 1989, p. 13 [\*D. annulirotatus; OD] [=Dracholychnus WU, 1990, p. 352 [360], obj.] Low, funnel-shaped to broadly obconical, thin-walled, platelike sponges composed of annular, ringlike segments that produce somewhat irregular, concentric ridges on both top and bottom surfaces; chambers filled with fine, dictyonine structure, and each with distinct dermal and gastral layer and interwalls between chambers, commonly formed of two thickened, subparallel layers of dictyonalia. Triassic (Carnian): China (Sichuan).-FIG. 320, 1a-d. \*D. annulirotatus, Hanwang Formation, Hanwang-Jushui area; a, side view from below showing annulate, ringlike structure of funnel-shaped, figured specimen, ×1; b, view from above into shallow spongocoel partially encrusted with Terebella-like worm tubes and matrix, S-1059, ×1; c, photomicrograph of longitudinal section of figured specimen with arched, main chamber walls and upwardly radiating, primary strands in coarse skeleton, fine structure obscured by boring worm traces throughout, IGASB T3(a), ×10; d, photomicrograph with thick, distinctive, double-layered interwalls and lack of preservation of fine structure in chamber interiors, IGASB R6-18(058), ×20 (Rigby, Wu, & Fan, 1998).
- Innaecoelia BOIKO, 1990, p. 126 [\*I. pamirica; OD]. Cylindrical sponge with high, spherical-appearing chambers with netlike, hexagonal skeleton in walls; axial spongocoel or canal retrosiphonate; skeletal structure more complex than in *Caucasocoelia* or *Pseudoverticillites. Jurassic (Callovian):* Tadjhikistan.—FIG. 319,1a-b. \*I. pamirica, upper Callovian, southwestern Pamir Mountains; a, section through spherical-appearing chambers showing their complex walls, MIGACT 15/11, ×2; b, photomicrograph showing hexactine spicules in thickened rays of fused skeleton, ×40 (Boiko, 1990).
- Pseudoverticillites BOIKO, 1990, p. 125 [\*P. sahrajensis; OD]. Cylindrical sponges composed of low, empty chambers; chamber walls of six-rayed spicules of uniform size that are fused at their tips to form a relatively simple, rectangular, skeletal net. Triassic (Norian): Russia (northern Caucasus).——FIG. 320,2a-b. \*P. sahrajensis, Upper White River; a, longitudinal section of curved sponge showing low chambers and moderately thick walls of fused hexactines, MIGACT 15/9, approximately ×2; b, photomicrograph of skeletal structure of chamber wall of fused hexactines, ×30 (Boiko, 1990).



Caucasocoelia

FIG. 319. Craticulariidae (p. 486).

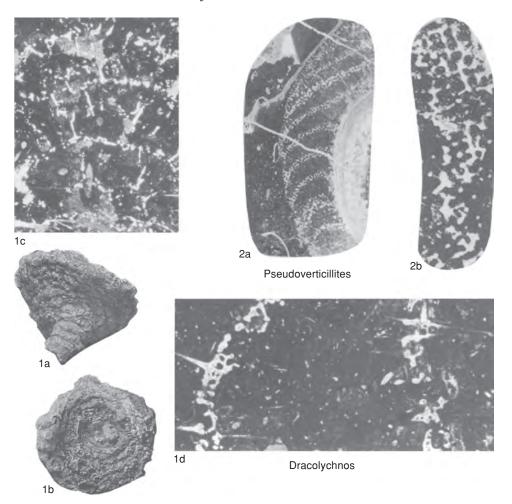


FIG. 320. Craticulariidae (p. 486).

### Subfamily UNCERTAIN

- Ecblastesia RAUFF, 1933, p. 24 [\**E. intrinsecuscostata;* OD]. Nature uncertain; single specimen a group of small, conjoined funnels with separate, paragastral cavities; inside with postica in longitudinal furrows; outside with small, irregularly arranged ostia in parts; canalization obscure, supposedly craticulariid. *Upper Cretaceous:* Europe.—FIG. 321,1. \**E. intrisecuscostata,* Greensand, upper Turonian, Ruhr Valley, Germany; view from above of conjoined funnels where postica occur in grooves on gastral surface, ×1 (Rauff, 1933; courtesy of *Preussischen Geologischen Landsanstalt,* E. Schweizerbart'sche Verlagsbuchhandlung).
- Mimeticosia RAUFF, 1933, p. 36 [\**M. alata;* OD]. Nature uncertain; single specimen massive, cruciate in cross section, with no paragastral cavity; outside with quadratically arranged ostia, like those of

Laocoetis species; interior a solid mass of irregular, skeletal tissue, with large, tubular canals running longitudinally and transversely. Loose spiculation unknown. [Basal part of plicated Laocoetis, with the paragastral cavity filled by possible secondary meshwork.] Upper Cretaceous: Europe.——FIG. 321,4ac. \*M. alata, Greensand, upper Turonian, Ruhr Valley, Germany; a, view from above of small, cross-shaped sponge; b, side view between divergent folds showing moderately large, longitudinal canals, ×1; c, vertical thin section showing skeletal structure and upwardly divergent, coarse canals in the interior, ×4 (Rauff, 1933; courtesy of Preussischen Geologischen Landsanstalt, E. Schweizerbart'sche Verlagsbuchhandlung).

Periplectum RAUFF, 1933, p. 38 [\*P. constrictum; OD]. Nature uncertain; single example fragment of seemingly bowl-like sponge; outside formed by meshwork of basal skeleton with irregularly distributed

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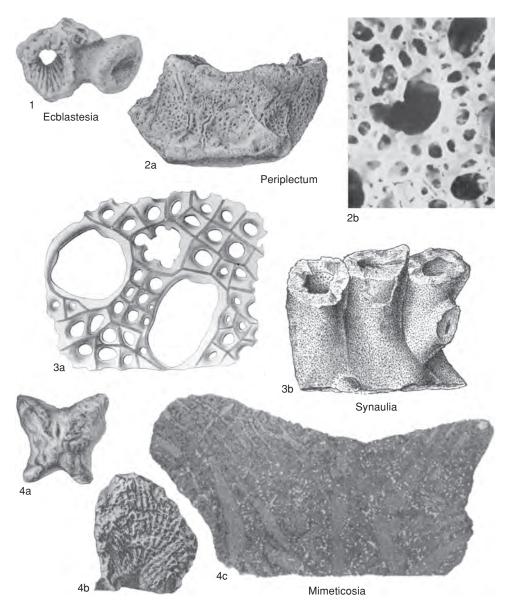


FIG. 321. Craticulariidae (p. 488-490).

ostia and local, sinuous furrows; parts of upper surface with postica of apparently radial aporhyses; loose spiculation unknown. [Basal parts of a possible *Laocoetis.*] *Upper Cretaceous*: Europe.——FIG. 321,2*a*-*b.* \**P. constrictum,* Greensand, upper Turonian, Ruhr Valley, Germany; *a,* side view of bowl-like fragment with irregular furrows and ostia in dermal layer, ×1; *b,* silicified skeletal fragment showing fused nature of secondary thickened elements in skeleton, ×20 (Rauff, 1933; courtesy of *Preussischen Geologischen Landsanstalt,* E. Schweizerbart'sche Verlagsbuchhandlung). Synaulia POČTA, 1883, p. 25 [\*S. germinata POČTA, 1883, p. 26; SD DE LAUBENFELS, 1955, p. 84]. Nature uncertain; type species based on group of three broken, upright tubes fused together side by side, with a common, basal structure; paragastral cavities not continuous; exterior with small skeletal pores in irregular meshwork continuous with basal skeleton; gastral surfaces with postica in rough, longitudinal, and transverse rows; outer part of skeletal meshwork with vertical canals, arranged concentrically around inner part with radial canals. Loose spiculation unknown. [Basal parts of a compound possible Laocoetis.] Upper Cretaceous: Czech Republic, Slovakia.——FIG. 321,3*a–b.* \*S. germinata, Korytzaner Schichten, Zybslav; *a*, side view of upright tubes in holotype with cylindrical spongocoel with exhalant ostia in rows, exterior with fine, inhalant ostia, ×1; *b*, skeletal fragment with canals in dense net, ×40 (Počta, 1883).

#### Family CRIBROSPONGIIDAE F. A. Roemer, 1864

[nom. correct. REID, 1963a, p. 227, pro Cribrospongidea F. A. ROEMER, 1864, p. 10] [=Nelumbifoliidae WU, 1990, p. 356 (361)]

Skeletal framework three dimensional initially, constructed as in Euretidae, but with fully developed epirhyses and aporhyses; skeletal canals radial, blind, arranged in longitudinal series in which epirhyses and aporhyses alternate, often also occuring alternately in adjacent series, or having modifications of this pattern in which canals are open at both ends, intercommunicate, or form labyrinths internally, or lack regular arrangement; arrangement of apertures typically quincuncial when regular; dictyonal strands spread subequally to both surfaces, or run mainly or all to dermal side; beams between ends of strands usually forming cortical meshwork, which secondary accretions may thicken; strand system sometimes extensively disorganized by canalization; superficial meshwork in some genera formed from dictyonal hexactines, from hexactines plus siliceous filaments, or additionally by ankylosis of dermal or gastral stauractines or pentactines; sceptrules unknown. [Family is similar to Craticulariidae, but distinguished from it by a different serial arrangement of epirhyses and aporhyses, implying that chambers bearing structures and inhalant canals were formed alternately in each segment of the growing margin instead of separately in alternate segments.] A single living species, Stereochlamis incerta (IJIMA), is known from washed-out specimens only. Middle Triassic-Holocene.

Cribrospongia D'ORBIGNV, 1849, p. 547 [\**Scyphia* reticulata GOLDFUSS, 1826, p. 11; M] [=*Tremadictyon* ZITTEL, 1877b, p. 46, obj. (type, *S.* reticulata, SD HINDE, 1893b, p. 195)]. Funnel-like or variant shapes; skeletal canals in regular or approximate series, apertures alternating quincuncially or less regularly; apertures round, ovate, or irregularly denticulate; canals simply radial or with lateral branches, which may open into general meshwork or cross connect canals of same kind; internal meshwork with dictyonal strands spreading subequally to both surfaces, and fairly regular to extensively disorganized by minor canal branches; denser cortical meshwork at both surfaces; dermal or both surfaces with superficial outgrowths or meshwork formed from dictyonal hexactines or the latter and siliceous filaments, further external tangential networks formed by ankylosis of dermal or gastral stauractines or pentactines. [SALOMON (1990) and MEHL (1992) discussed the taxonomic history of Porospongia and associated genera and concluded that Cribrospongia and Porospongia were named by D'ORBIGNY in 1849, not in 1847, after an intensive search for documentation of the 1847 paper failed.] Middle Triassic-Cretaceous (Albian): Poland, Middle Triassic; Germany, France, Switzerland, Jurassic; Spain, Albian.—FIG. 322,3a. C. radicatum (QUENSTEDT), Weiss Jura, Upper Jurassic, Heuchstetten, Germany; enlarged part of inner surface with irregular pores and skeletal tracts with dictyonine structure, ×5 (Schrammen, 1936).-FIG. 322,3b. C. elegans (SCHRAMMEN), Weiss Jura, Upper Jurassic, Schwabtal, Germany; enlargement of inner or gastral surface with fine, skeletal tracts and irregular, exhalant ostia, ×5 (Schrammen, 1936).

- Andreaea SCHRAMMEN, 1902, p. 25 [\*A. hexagonalis; OD]. Funnel-like or flabellate; epirhyses blind, arranged irregularly or in hexagonal groups; aporhyses quincuncially alternating and frequently opening at both ends; no superficial meshwork. Cretaceous: Germany.—FIG. 322,4. \*A. hexagonalis, Quadratenkreide, Campanian, Misburg; side view of small, steeply obconical sponge with distinct epirhyses, ×1 (Schrammen, 1902).
- Erineum SCHRAMMEN, 1937, p. 39 (SCHRAMMEN, 1936, p. 181, nom. nud.) [\*E. minutum; OD]. Sponge top shaped and of small size, with thick walls and deep spongocoel; exterior with small, irregularly placed ostia that alternate with those of gastral surface; inhalant and exhalant canals bent and end blindly in wall between exhalant ostia; skeletal structure irregular in interior but regular in the outer part. Upper Jurassic: Germany.—FIG. 322,2a-b. \*E. minutum, Weiss Jura, Streitberg; side views of small sponge with irregular ostia, ×4 (Schrammen, 1937).
- Eubrochus SOLLAS, 1876a, p. 400 [\**E. clausus;* OD]. Club-shaped or vaselike sponges in which walls curve together to cover osculum; reticulate, dermal net preserved as molds of longitudinal and horizontal fibers that diverge upwardly from four centers in looplike fashion and overlap with fibers from other centers to produce three-dimensional, hexactinosid skeleton. [The genus is placed in the family because of its similarity to *Cribrospongia.*] *Cretaceous:* Europe.——FIG. 322, *1a-c. \*E. clausus,* Coprolite bed of Cambridge beds, Cambridge, England; *a,* side view of holotype with reticulate skeleton, ×1; *b,* section of interior hexactinosid skeleton, ×25; *c,*

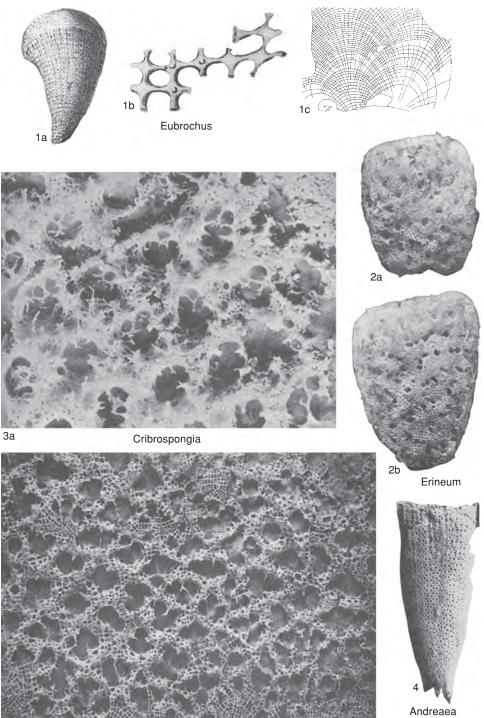




FIG. 322. Cribrospongiidae (p. 490-493).

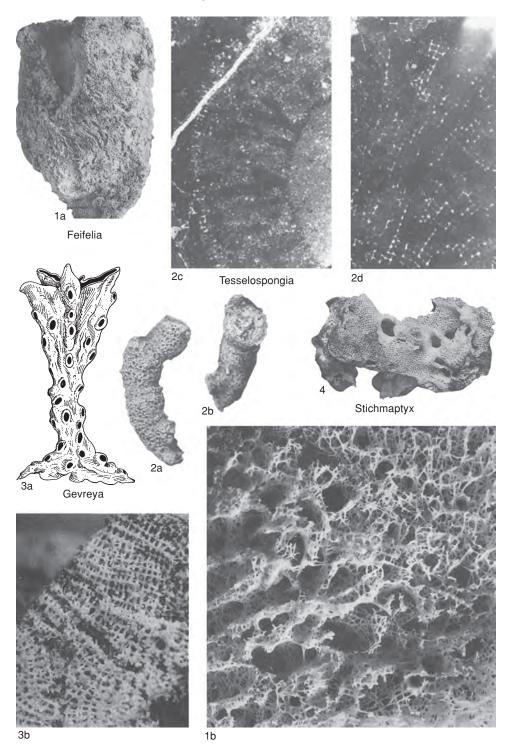


FIG. 323. Cribrospongiidae (p. 493-498).

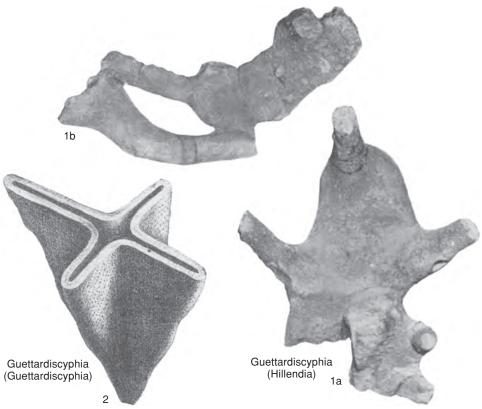


FIG. 324. Cribrospongiidae (p. 494-495).

woodcut showing skeletal fibers and their arcuate interrelationships that produce reticulate net, not to scale (Sollas, 1876a).

- Feifelia SCHRAMMEN, 1937, p. 52 (SCHRAMMEN, 1936, p. 182, nom. nud.) [\*F. gigas; OD]. Large, vase- to pear-shaped, short-stalked, thick-walled sponges with deep spongocoel; exterior with small, closely spaced, irregularly distributed, branched, inhalant ostia; numerous large, exhalant ostia in longitudinal and transverse rows; coarse, dictyonine skeleton irregular to elongate and curving toward both gastral and dermal surfaces; stauractines may occur on both wall surfaces. Jurassic: Germany.——FIG. 323,1a-b. \*F gigas, Weiss Jura, Waldhausen; a, side view of small example of large species, ×0.5; b, section through wall near gastral surface, ×5 (Schrammen, 1937).
- Gevreya MORET, 1927, p. 292 [\*G. synthetica; OD]. Long tube flaring distally in winglike folds as in *Guettardiscyphia*, spongocoel cylindrical but extending radially into lateral folds; large openings (possible oscules) occurring on folds and along sides and perhaps locally on crests of rootlike elements of base; hexactines of skeletal net very regularly arranged, forming cubic meshes, and lack lychniscoid structure; canal system little developed with pores

only a little larger than cubic skeletal openings. [Included in the family with some question.] *Jurassic:* France.—FIG. 323, 3a-b. \*G. synthetica, Callovian, La-Voulte-sur-Rhone, Ardeche; *a*, restoration side view showing form of sponge and lateral oscules, slightly reduced; *b*, skeletal fragment showing robust, dictyonine net with regular, cubic structure, ×10 (Moret, 1928).

Guettardiscyphia DU FROMENTEL, 1860a, p. 39, nom. nov. pro Guettardia MICHELIN, 1847 in 1840-1847, p. 121, non NARDO, 1883 [\*Guettardia stellata MICHELIN, 1847 in 1840-1847, p. 121; OD] Body stellate, bilaterally compressed, or irregularly branched and sometimes partly saccular; parietal oscula along margins of radiating flanges or flattened branches, or variously placed when these are absent; epirhyses and aporhyses in regular, longitudinal series; epirhyses typically open at both ends, unless closed on gastral side by secondary, skeletal accretion; exterior of skeletal framework with ostia of epirhyses only, arranged alternately and often quincuncially; gastral side with twice as many apertures, of which half are true postica, arranged in longitudinal series and often grouped quadrately; dictyonal strands of interior run mainly or to dermal side, usually confined to tracts between

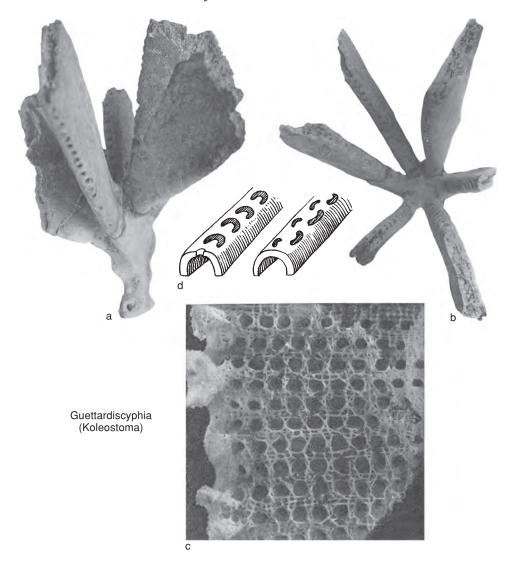


FIG. 325. Cribrospongiidae (p. 495).

series of skeletal canals; dense cortical meshwork on dermal side, and sometimes also superficial meshwork formed from dictyonal hexactines; internal structure exposed on gastral side, or partly obscured by skeletal accretion. *Cretaceous*.

G. (Guettardiscyphia) REID, nom. nov. herein [\*Guettardia stellata MICHELIN, 1847 in 1840– 1847, p. 121; OD]. Wall folded longitudinally above tubular stalk to form radiate and bilaterally compressed, hollow flanges of typically triangular form that remain connected axially; rounded, parietal oscula along narrow margins of flanges; flanges freely open at top, partly closed by transverse bridges of secondary skeletal meshwork, or closed around a single axial osculum. Cretaceous: France.——FIG. 324,2. \*G. (G.) stellata (MICHELIN), Upper Cretaceous, Senonian, Honfleur; diagonal view of hollow, flanged sponge with open, axial spongocoel and relatively thin, folded walls,  $\times 1$  (Fromentel, 1860a).

G. (Hillendia) REID, 1964, p. lxiv [\*H. polymorpha; OD]. Bilaterally compressed to irregularly branched, sometimes partly saccular; parietal oscula rounded, marginal in compressed growths, variously placed in others. Cretaceous (Turonian): Great Britain.—FIG. 324, 1a-b. \*G. (H.) polymorpha, Chalk Rock, Hitchin, Hertfordshire; a, holotype with tubular branches from saccular growth, some with parietal oscula, BM S.8610; *b*, paratype with irregularly branching form, BM S.8611, ×1 (Reid, 1964; courtesy of The Palaeontographical Society, London).

- G. (Koleostoma) REGNARD in MORET, 1926b, p. 220 [\*K. godeti; OD]. Initially similar to Guettardiscyphia s.s., but radial flanges then separate axially, either singly or in pairs, to form bladelike or winglike branches; branches formed from single, radial flanges have parietal oscula along both narrow margins; parietal oscula rounded, or become crescentic through ingrowth of skeletal meshwork. [Koleostoma godeti was described as a new genus and new species by REGNARD (1926, p. 473) in the paper apparently referred to by MORET as "REGNARD, in litt."] Cretaceous: France.—FIG. 325a-d. \*G. (K.) godeti, Cenomanian, Coulonge-les-Sablon; a, side view of plicate form with crescentic oscula along narrow margins; b, view from above showing growth form, ×1 (Regnard, 1926); c, photomicrograph of skeletal net, ×10 (Moret, 1926b; courtesy of Société Géologique de France); d, oblique view of crescentic parietal oscula on crests of folds, ×2 (de Laubenfels, 1955).
- Haynespongia RIGBY, 1981, p. 138 [\*H. vokesae RIGBY, 1981, p. 140; OD]. Irregular, leaflike or anastomosing to thin-walled, tubular cribrospongiid lacking complex sculpture; hexactinosid net euretoid with primary framework at gastral margin from which strands diverge to meet dermal margin at high angles; primary canals show diplorhysis in craticulariid pattern with general alternation of epirhyses and aporhyses; although not in well-defined, linear series; apodiarhysal canals connecting to dermal surface and occurring in skeleton between epirhysal ostia. Paleogene (Eocene): USA (North Carolina). -FIG. 326, 1a-b. \*H. vokesae, Castle Hayne Limestone, Wayne County; a, side view of holotype with oscula along one margin, USNM 252494, ×1; b, photomicrograph of dermal surface of holotype with inhalant ostia and net with expanded nodes at ray junctions, ×20 (Rigby, 1981; courtesy of Tulane Studies in Geology and Paleontology).
- Keuppiella ENGESER & MEHL, 1993, p. 185, nom. nov. pro Rhopalicus SCHRAMMEN, 1937, p. 36, non FOERSTER, 1856 [\*Scyphia pertusa GOLDFUSS, 1826, p. 6; OD] [=Walcottella DE LAUBENFELS, 1955, p. 82, obj., non ULRICH & BASSLER, 1931]. Similar to Cribrospongia D'ORBIGNY, with cribiform, superficial meshwork veiling ostia or postica when fully developed, but without ankylosed dermalia or gastralia. Upper Jurassic: Germany.—FIG. 326,2a-b. \*K. pertusa (GOLDFUSS), Weiss Jura, Schwabtal; a, enlarged view of dermal surface with irregularly spaced, inhalant ostia separating skeletal tracts, ×5 (Schrammen, 1936); b, irregular meshwork over inhalant ostia of dermal surface, ×5 (Schrammen, 1937).
- Nelumbifolium WU, 1990, p. 356 [\**N. pectiniforme;* OD]. Open, funnel-shaped, thin-walled sponges with prominent ostia of exhalant-inhalant system in moderate, concentric, and radial series in rough to nodose, gastral and dermal surfaces; continuous, concentric and radial, midwall canals in coarse,

somewhat open, irregular skeleton where radial strands most prominent, with second- and thirdorder subdividing elements commonly appearing spinose or with free rays, or small hexactines, or with synapticulae near nodes. Triassic (Carnian): China (Sichuan).——FIG. 327,1*a*-b. \*N. pectiniforme, Hanwang Formation, Jushui; a, gastral view of funnel-shaped sponge with characteristic, coarse, aligned, ostia of exhalant canals separated by low nodes in lower part, but upper part encrusted, S-1150, ×1; b, relatively open, dictyonine, skeletal net with large hexactines as primary elements producing first-order quadrules, subdivided by secondand third-order hexactines, some with synapticulae, IGASB R6-2(2), ×10 (Rigby, Wu, & Fan, 1998).

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- Petalope Počta, 1883, p. 24 [\**P. auriformis*; SD DE LAUBENFELS, 1955, p. 82]. Sponge body irregular, with ear-shaped outline above a thick stalk and with thicker central part; radial canals numerous, blind, and curved; upper surface with irregularly distributed, round ostia of shallow canals in gastral layer where spicule rays somewhat thicker than in main skeleton; principal skeleton dictyonine with coarse, six-rayed, irregularly oriented spicules. [Included in the family with some question.] *Upper Cretaceous*: Czech Republic, Slovakia.—FiG. 326,3*a*-*b*. \**P. auriformis*, Korytzaner Schichten, near Zbyslav; *a*, side view of broadly obconical, ear-shaped sponge, ×1; *b*, a fragment of internal, dictyonine skeleton, approximately ×60 (Počta, 1883).
- Polyopesia SCHRAMMEN, 1902, p. 25 [\*P. angustata; SD DE LAUBENFELS, 1955, p. 79]. Tubular to funnellike, flabelliform, or with branches of a tubular stock expanding into convoluted lamellae; dermal skeletal surface with alternating or irregularly arranged apertures of epirhyses, between which are small pores or papillae through which aporhyses open at this surface; gastral surface with alternating apertures of aporhyses only; aporhyses simply radial or intercommunicating, with cross passages sometimes forming diagonal network between epirhyses; no superficial meshwork. [Note: wrongly identified with Hexactinella CARTER (family Tretodictyidae) by SCHRAMMEN (1912, p. 223) and followers]. Upper -FIG. 327,3a. \* P. Cretaceous: Germany.angustata, Quadratenkreide, Cenomanian, Oberg; side view of fragment with irregularly distributed, papillate aporhyses, ×1 (Schrammen, 1912). FIG. 327, 3b-c. P. laevis (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg; b, gastral surface of earshaped variety with coarse apertures of aporhyses irregularly distributed; c, dermal surface of same specimen with papillate pores of aporhyses and intervening pores of epirhyses, ×1 (Schrammen, 1912).
- Stereochlamis SCHRAMMEN, 1912, p. 231 [\*S. praecissa; SD DE LAUBENFELS, 1955, p. 83] [=Tretorete IJIMA, 1927, p. 298 (type, T. incertum, OD)]. Tubular, small; epirhyses and their apertures arranged without order; aporhyses alternating in longitudinal series; dictyonal strands run to dermal side only or largely disorganized; no cortical meshwork; no superficial meshwork. Upper Cretaceous–Holocene:

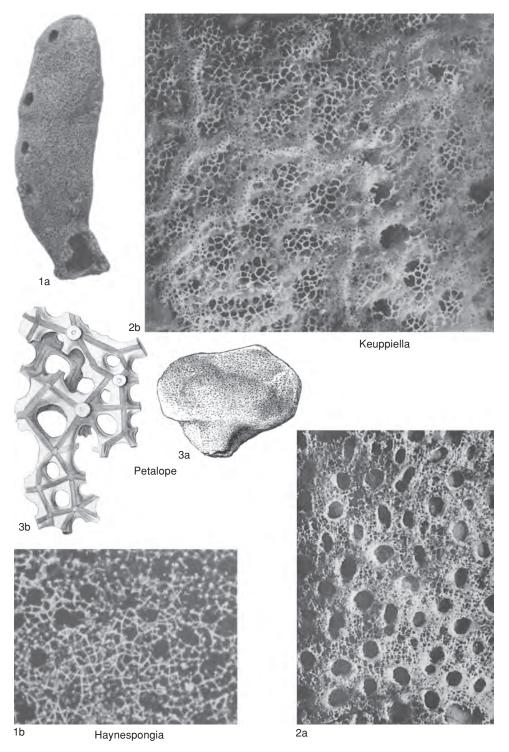


FIG. 326. Cribrospongiidae (p. 495).

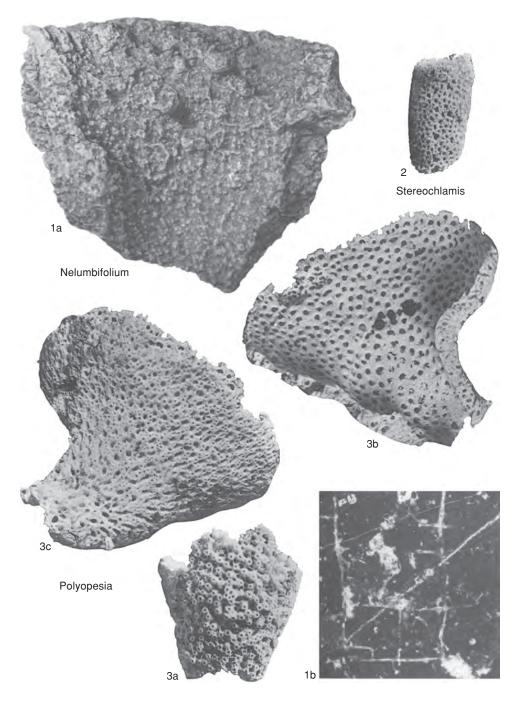


FIG. 327. Cribrospongiidae (p. 495-498).

Germany, Pacific and Indian Oceans.——FIG. 327,2. \*S. praecissa, Quadratenkreide, Cenomanian, Oberg, Germany; side view of tubular to steeply obconical type with irregular skeletal and canal structure, ×2 (Schrammen, 1912).

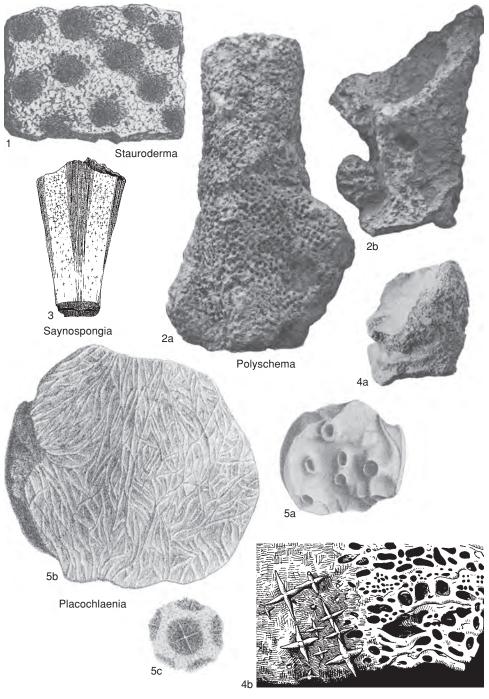
- Stichmaptyx SCHRAMMEN, 1912, p. 255 [\*S. alatus; OD]. Branched and anastomosed tubes, or with branches of tubular stock expanding into sinuously convoluted lamellae; aporhyses or both sets of canals arranged regularly; aporhyses may run obliquely; no superficial meshwork. Cretaceous: Germany.—FIG. 323,4. \*S. alatus, Quadratenkreide, Cenomanian, Oberg: sponge of anastomosed tubes or branches with uniform ostia of canals between oscula, ×0.5 (Schrammen, 1912).
- Tesselospongia RIGBY, WU, & FAN, 1998, p. 138 [\*T. fistulosa; OD]. Small, conicocylindrical sponges with deep, simple spongocoel and smooth walls marked by ostia of cribrospongiid, diplorhysal, canal system; skeleton well organized, uniform, simple, euretoid dictyonine with primary strands near gastral margin; skeletal structure diverging upwardly and outwardly to dermal margin where dermal cortex of swollen elements well defined and thicker than gastral layer. Triassic (Carnian): China (Sichuan).—FIG. 323,2a-d. \*T. fistulosa, Hanwang Formation, Hanwang area; a, side view of subcylindrical holotype with weakly annulate, dermal layer pierced by numerous prominent, inhalant ostia,  $\times 2$ ; *b*, diagonal view from above of broken summit with central spongocoel and traces of radial canals, S-1001, ×2; c, photomicrograph of transverse section showing radial canals in thin wall and dermal layer of thickened spicules, IGASB T3(2), ×10; d, longitudinal section with upwardly divergent, simple, dictyonine, skeletal net interrupted by matrix-filled canals, IGASB T3(4), ×10 (Rigby, Wu, & Fan, 1998).

#### Family STAURODERMATIDAE Zittel, 1877

#### [Staurodermatidae ZITTEL, 1877b, p. 37]

Skeletal framework three dimensional initially, constructed as in Euretidae and with labyrinthine epirhyses and aporhyses; aporhyses open in local depressions in gastral surface of framework and epirhytic labyrinth perforates intervening framework; skeletal surfaces coated by tangential networks of ankylosed, dermal and gastral stauractines or pentactines in mature individuals; sceptrules unknown. [Originally (ZITTEL, 1877b) included a variety of Hexactinosa and Lychniscosa, with conspicuous superficial meshwork formed from dermalia or gastralia. Family herein defined in terms of general characters of the type genus Stauroderma ZITTEL.] Jurassic–Neogene.

- Stauroderma ZITTEL, 1877b, p. 53 [\*Spongites lochensis QUENSTEDT, 1858, p. 669; OD]. Funnel- to platterlike, often large; dermal (outer, lower) surface of skeletal framework with ostia of short, radial epirhyses that divide into branches internally; these branches unite to form a labyrinth of divided and anastomosed, tubular passages; gastral (inner, upper) surface with alternating, rounded depressions in which groups of aporhyses open; intervening parts of surface with numerous small, round apertures and sinuous furrows through which epirhytic labyrinth opens; aporhyses branch and anastomose to form a second labyrinth in interspaces of epirhytic system, but do not perforate dermal surface; internal meshwork much disorganized by canalization, dictyonal strands spread to both sides where detectable; outermost meshwork of dermal side forming a fine-meshed cortex; dermal side also with superficial outgrowths formed from dictyonalia and siliceous filaments, which help define irregular denticulate outlines of ostia; mature individuals with ostia veiled by tangential networks of ankylosed dermal stauractines or pentactines, and gastral side coated continuously by similar network of fused gastralia that line (not span) the aporhytic depressions. Jurassic: Europe.-FIG. 328,1. \*S. lochensis (QUENSTEDT), Weiss Jura, Lochen, Germany; skeletal fragment showing circular ostia in dermal surface of broad, platelike sponge, ×1 (Quenstedt, 1858).
- Placochlaenia POMEL, 1872, p. 73 [\*P. protuberans; OD]. Platelike expansions, somewhat irregular, composed of coarse, irregularly anastomosing, siliceous fibers; upper surface with scattered, elongate or necked oscula of finely porous, gastral layer in which small hexactines show between coarser fibers; lower surface with pronounced, irregular, coarse fibers. Neogene (Miocene): northern Africa.-FIG. 328,5a-c. \*P. protuberans, Terrain cartennien, Djebel Djambeida, Algeria; a, gastral or upper surface of platelike sponge with pronounced, scattered oscula,  $\times 0.5$ ; b, dermal or lower surface of same sponge with irregularly anastomosing, coarse, skeletal fibers, ×1; c, small stauractine in opening between skeletal fibers of upper surface, ×20 (Pomel, 1872).
- Polyschema OPPLIGER, 1915, p. 29 [\**P. hersbergense* OPPLIGER, 1915, p. 30; SD DE LAUBENFELS, 1955, p. 80]. Cylindrical to cup-shaped forms with spongocoel open or covered, dermal surface with inhalant ostia irregularly distributed in short rows; gastral surface with larger, exhalant ostia; skeletal net dictyonine. *Jurassic:* Switzerland.——FIG. 328,2*a*-*b.* \**P. hersbergense*, Birmernsdorfer beds, Hersberge; *a*, side view of cylindrical specimen with irregular, inhalant ostia; *b*, cup-shaped specimen with broad spongocoel and thick walls, ×1 (Oppliger, 1915; courtesy of Komission der Schweizerischen Paläontologischen Abhandlungen, Basel).
- Rhodanospongia MORET, 1927, p. 292 [\**R. robusta;* OD]. Goblet-shaped sponge, robust dictyonine skeletal net with irregularly anastomosing, thick fibers in endosomal net and large pentacts with four



Rhodanospongia

FIG. 328. Staurodermatidae (p. 498-500).

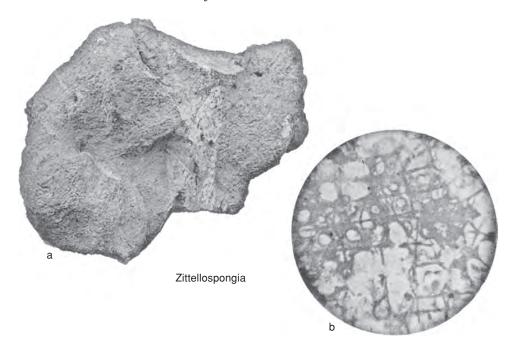


FIG. 329. Staurodermatidae (p. 500).

recurved clads at sponge surface and straight rhabd directed inwardly, in differentiated, dermal cortex. [Included in the family with some question.] *Jurassic:* France.—FIG. 328,4*a*-*b.* \**R. robusta,* Callovian, La Volte-sur Rhone, Ardeche; *a,* side view of lower stem and basal part of upper cup, size reduced; *b,* restoration showing thick, anastomosing rays on endossomal skeleton and large pentacts of dermal cortex, ×10 (Moret, 1928).

- Saynospongia MORET, 1927, p. 292 [\*Elasmoierea palmicea DUMORTIER, 1871, p. 54; OD]. Small sponges shaped like a dagger sheath, with flattened spongocoel and moderately thick wall that has endosomal, dictyonine skeleton of fine, cubical cribwork, but with extended, longitudinal rays, and outer layer with less regularly oriented stauractines. Jurassic: France.—FIG. 328,3. \*S. palmicea (DUMORTIER), Callovian, La Volte-sur-Rhone, Ardeche; side view of restoration showing flattened form of sponge with darker, regular, fine, endosomal skeleton and lighter, dermal layer of more irregularly oriented stauractines, ×1.5 (Moret, 1928).
- Zittellospongia MALFATTI, 1901, p. 288 [\*Z. meandriformis MALFATTI, 1901, p. 289; OD] [=Malfattispongia GREGORIO, 1908, p. 83, obj.; Zittelospongia DE LAUBENFELS, 1955, p. 80, obj.]. Similar to Paracraticularia but more lumpy and crumpled with several shapes from platelike to rugose meandriform, with a shallow, oscular depression; other areas of sponge covered with dermal layer perforated by irregularly placed, small ostia that are openings to small, sinuous canals that ex-

tend throughout sponge; complex skeleton is a quadrate mesh produced by merged, crossing rays of hexactines; fine, axial canals show in spicules of internal parts of sponge. [Placed in the family with some question.] *Paleogene–Neogene:* Europe.— FIG. 329*a–b. \*Z. meandriformis,* middle Miocene, Emilia, Italy; *a*, upper view of irregular type specimen, ×1; *b*, photomicrograph of skeletal structure, ×50 (Malfatti, 1901).

#### Family APHROCALLISTIDAE Gray, 1867

[Aphrocallistidae GRAY, 1867, p. 507] [=Mellitionidae ZITTEL, 1877b, p. 36; Melittionidae SCHULZE, 1887a, p. 74; Aphrocallistidae SCHULZE, 1904, p. 178]

Skeletal framework three dimensional initially, not constructed in layers, with subparallel, dictyonal strands when any are apparent, and with a single system of tubular to prismatic, skeletal canals (diarhyses) that perforate both skeletal surfaces; these canals occupied in living examples by single, lobate, flagellated chambers; dictyonal strands sometimes evident in meshwork between diarhyses, begin on gastral side of framework and run outwardly to dermal side, typically subradial or radial for most or all of their length; diarhyses oriented corre-

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spondingly, open radially on dermal side, radially to obliquely downward on gastral side; other examples with no distinct strand system, although traces of pattern described may be locally present; occasional individual variants have diarhyses incompletely formed, lack apertures on gastral side; no superficial meshwork, although irregular, skeletal accretion may veil apertures of gastral side; scopules in living examples. *Lower Cretaceous–Holocene.* 

Aphrocallistes GRAY, 1858, p. 114 [\*A. beatrix; OD] [=Badinskia POMEL, 1872, p. 84 (type, B. lobata, M, =A. lobatus (POMEL), 1872, p. 85, non A. lobatus SCHRAMMEN, 1912, p. 222; =lobate form of A. cylindrodactylus SCHRAMMEN, 1912, p. 221)]. Branched-tubular, forming funnel-like axes with lobate or radially diverticulated walls, or combining these habits or with intermediates between them; terminal oscula sometimes covered by a perforated sieve plate; skeletal characters of family; diarhyses closely spaced, with intervening skeletal partitions often two dimensional only and from quadrate with regular, dictyonal strands to irregularly triangular, with components distorted so that all six rays lie in one plane; relatively dense, cortical meshwork on dermal side, or none; sieve plate skeleton dictyonal; scopules in living examples; dermalia pentactines or hexactines, but gastralia usually rhabdodiactines. Lower Cretaceous-Holocene: Germany, Poland, Great Britain, Lower Cretaceous-Upper Cretaceous; USA (Washington, Oregon), Algeria, Paleogene-Neogene; Spain, Algeria, Miocene; cosmopolitan, Holocene.——FIG. 330, 1a-b. A. alveolites SCHRAM-MEN, Quadratenkreide, Cenomanian, Oberg, Germany; a, branched lobate form with perforated sieve plate,  $\times 1$ ; *b*, larger, branched form showing regular ostia pattern and thin walls in broken upper end, ×0.5 (Schrammen, 1912).—FIG. 330, 1c-d. A. cylindrodactylus SCHRAMMEN, Quadratenkreide, Cenomanian, Oberg, Germany; c, branched cluster with sieve plates on ends of some branches but others broken, ×0.5; d, lobate form of species, ×1 (Schrammen, 1912).

### Family TRETODICTYIDAE Schulze, 1887

[Tretodictyidae SCHULZE, 1887b, p. 78] [=Sclerothamnidae SCHULZE, 1885, p. 447; Volvulinidae SCHULZE, 1885, p. 447; Tretocalycidae SCHULZE, 1904, p. 179; SCHRAMMEN, 1912, p. 222; Hexactinellidae DE LAUBENFELS, 1936, p. 185 (not SCHMIDT, 1870)]

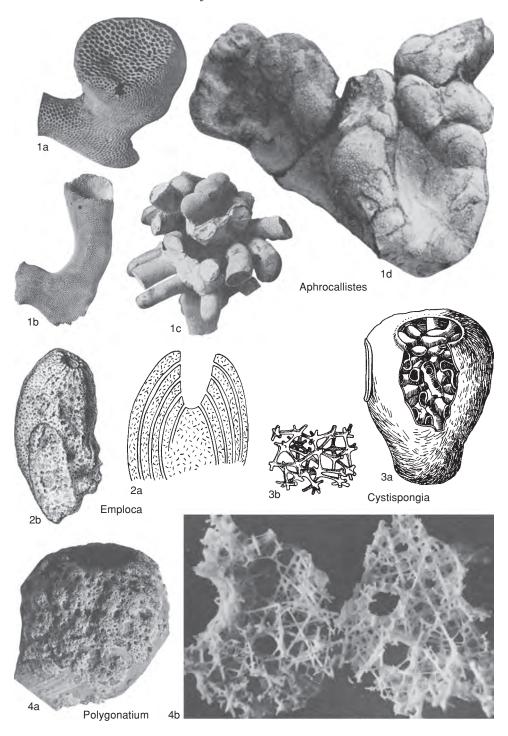
Skeletal framework three dimensional initially, constructed as in Euretidae, with a single system of intercommunicating, cleftlike to labyrinthine, skeletal canals (schizorhyses) that perforate both skeletal surfaces; these skeletal canals occupied in living examples by chamber-lined passages that are open beneath dermal membrane as well as on gastral side; dictyonal strands spread subequally to both surfaces from interior, or run mainly or all to dermal side; cortical modifications usually absent or slightly developed; some with superficial meshwork formed by union of dermal or gastral pentactines connected by direct ankylosis or networks of siliceous filaments. [For more information on the complex name history of Tretodictyidae, see REISWIG, 2002, p. 1,341– 1,342.] Upper Jurassic–Holocene.

#### Subfamily TRETODICTYINAE Schulze, 1887

[nom. transl. REID, herein, pro Tretodictyidae SCHULZE, 1887b, p. 78] [=Tretodictyidae SCHULZE, 1887b, p. 78, partim]

# Without connected dermalia or gastralia. *Upper Jurassic–Holocene.*

- Tretodictyum SCHULZE, 1887b, p. 78 [\*Hexactinella tubulosa SCHULZE, 1887a, p. 328; SD IJIMA, 1927, p. 219]. Irregularly tuberous to shrublike with anastomosed branches; axial, paragastral cavities narrow when present, sometimes continuous in branched growths but more often discontinuous or absent; branches with lateral oscula when an axial paragaster is present, or with lateral, osculum-like apertures developed from canal system and usually all facing one direction; modern examples with scopules, oxyhexasters only, and dermalia pentactines to subpinular hexactines; no superficial meshwork. Cretaceous (Coniacian)-Holocene: Germany, Coniacian-Maastrichtian; cosmopolitan, Holocene.—FIG. 331,2a-c. \*T. tubulosum (SCHULZE), Holocene, Enoshima, Japan, northern Pacific Ocean; a, side view of irregularly branching, dried specimen, ×0.5; b, dermal scopule with four barbed rays, ×100; c, simple oxyhexaster with long principal rays, ×200 (Schulze, 1887a).-FIG. 331,2d. T. pumicosum IJIMA, Holocene, off Great Kei Island, western Pacific Ocean; lateral view of small branched to lobate holotype of species, ×1 (Ijima, 1927).—FIG. 331,2e. T. schrammeni IJIMA, Holocene, off Great Kei Island, western Pacific Ocean; side view of largest branched fragment showing form of sponge, ×1 (Ijima, 1927).
- Auloplax SCHULZE, 1904, p. 148 [\*A. auricularis; OD]. Flabellate, thick walled; schizorhyses longitudinal to irregularly labyrinthic tunnels, separated by typically thin partitions, and have appearance of radiate to divided and anastomosed, thin-walled tubes; surfaces irregularly cavernous where skeletal canals are labyrinthic; skeletal meshwork unusually coarse; dictyonal strands spreading to both surfaces; no distinct cortical meshwork, although meshwork at surfaces may be denser than in interior; single living species with pentactine dermalia and canalaria, hexactinoid discohexasters, and no sceptrules. Cretaceous (?Coniacian-?Maastrichtian), Holocene:





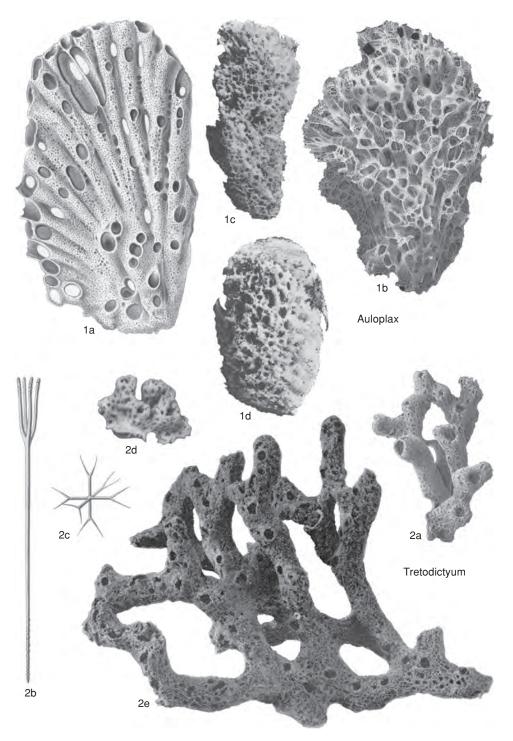


FIG. 331. Tretodictyidae (p. 501–504).

Germany, ?Coniacian-?Maastrichtian; cosmopolitan, Holocene.——FIG. 331, 1a-b. \*A. auricularis, eastern North Atlantic Ocean, southwest of Cape Bojador, Holocene; a, hand sample showing growth form; b, skeleton with soft parts removed, ×1 (Schulze, 1904).——FIG. 331, 1c-d. A. spongiosus SCHRAMMEN, Quadratenkreide, Cenomanian, Oberg, Germany; side views of subcylindrical to globular, thick-walled sponges with irregular, cavernous, skeletal structure and labyrinthic canals, ×1 (Schrammen, 1912).

- Hexactinella CARTER, 1885, p. 397 [\*H. ventilabrum; M]. Funnel-like, flabellate, branched-tubular, or variant conditions; schizorhyses from laterally intercommunicating, longitudinal clefts to irregularly labyrinthine passages; intervening parts of skeleton form radial septa or irregularly anastomosed trabeculae correspondingly; apertures of both surfaces similar, or those of gastral side rounded by secondary constriction; dictyonal strands spreading subequally to both sides, or running mainly or all to dermal side; meshwork denser at surfaces than internally, or not; without true, superficial meshwork, although secondary, dictyonal bridges may grow across schizorhyses at surfaces and internally, or parts of surface may be masked by irregular, secondary masses; living examples with scopules, discohexasters, and with pentactines or nonpinular hexactines as dermalia and gastralia. [Identified wrongly with Polyopesia SCHRAMMEN (family Cribrospongiidae) by SCHRAMMEN (1912, p. 233) and followers.] Cretaceous-Holocene: cosmopolitan.
  - H. (Hexactinella). Funnel-like or flabellate, sometimes irregularly corrugated, or compressed in funnel-like examples; dictyonal strands spreading to both surfaces. ?Cretaceous, Holocene: Germany, ?Cretaceous; Japan, Holocene.——FIG. 332,1. \*H. (H.) ventilabrum, Holocene, Pacific Ocean, Tokyo Bay, Japan; part of skeletal fragment and loose spicules, with dermal surface at top, ×35 (de Laubenfels, 1955).
  - H. (Parahexactinella) REID, 1963a, p. 228 [\*Tretodictyum latum SCHULZE, 1887a, p. 329; OD]. Branched-tubular, branches sometimes expanding into funnels, or with funnel-like or flabellate growths arising from a branched, solid stock; dictyonal strands spreading to both surfaces, or running mainly or all to dermal side. *Cretaceous-Holocene:* Germany, Great Britain, *Cretaceous*; Pacific Ocean, *Holocene.*—FIG. 332,2. H. (P.) loeschmanni (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg, Germany; side view of branched, tubular sponge, ×1 (Schrammen, 1912).
- Prohexactinella MORET, 1926b, p. 216 [\* P. cenomanense; OD; ?=Proeuplectella fragilis MORET, 1926b, p. 210, obj.] [?=Proeuplectella MORET, 1926b, p. 209 (type, P. fragilis MORET, 1926b, p. 210, M)]. Externally globular above a short stalk; paragastral cavity narrow; schizorhyses labyrinthic externally, but open by longitudinally elongate clefts on gastral side; dictyonal skeletal net robust and of large hexactines, no superficial meshwork; loose spicules unknown. [Distinction from

Hexactinella CARTER barely justified; based originally on absence of second-order (aporhytic) pores of Polyopesia SCHRAMMEN, misidentified with Hexactinella following SCHRAMMEN (1912, p. 222).] Upper Cretaceous: France.—FIG. 332,5. \*P. cenomanense, Cenomanian, Mans, Sarthe; side view of globular sponge, ×1 (Moret, 1926b; courtesy of Société Géologique de France).

- Psilocalyx IJIMA, 1927, p. 219 [\*P. wilsoni IJIMA, 1927, p. 265; OD] [=Nitidus DE LAUBENFELS, 1955, p. 86, nom. nov. pro Epaphroditus SCHRAMMEN, 1937, p. 62, non HERMAN, 1912 (type, Epaphroditus nitidus SCHRAMMEN, 1937, p. 62)]. Thick-walled cup or hollow cylinder with a narrow, central cavity; schizorhyses labyrinthic, wide, open externally by rounded apertures in coarsely reticulate surface; living example with scopules, dermal pentactines, and discohexasters. Upper Jurassic, Holocene: Germany, Upper Jurassic; East Indies, Holocene.-FIG. 332,6a-b.\*P. wilsoni, East Indies, Banda Sea, Holocene; a, holotype seen from side; b, holotype seen from above, ×1 (Ijima, 1927).—FIG. 332,6c. P. nitidus (SCHRAMMEN), Weiss Jura, Upper Jurassic, Streitberg, Germany; fragment showing characteristic skeletal structure with coarse ostia, ×4 (Schrammen, 1936).
- Ramalmerina BRIMAUD & VACHARD, 1987, p. 425 [\*R. fischeri; OD]. Hexactinellids with numerous branches that are disposed fanlike, diverging from common base; branches often bear an osculum several millimeters in diameter at point of their bifurcation; skeletal net fine, regular, displaying long hexactines arranged in rectangular mesh. Neogene (Miocene): Spain.——FIG. 332,3a-b. \*R. fischeri, Tortonian strata, upper Miocene, Almeria, southern Spain; a, side view of branched sponge, IPM R6981, ×0.50; b, longitudinal section with preserved, opalline spicules in rectangular mesh, IPM R6981, ×50 (Brimaud & Vachard, 1987; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
- Sclerothamnopsis WILSON, 1904, p. 84 [\*S. compressa; OD]. Branched hexactinellid with oscula situated at extremities or on surface of branches; branches traversed by canals without well-defined patterns; skeleton fine textured with dermalia of hexactines; oxyhexasters present. Neogene (Miocene)–Holocene: Spain, Miocene; eastern Pacific, Holocene.——FIG. 332,4. \*S. compressa, Tortonian strata, upper Miocene, Almeria, Spain; branched tubular form with many small oscula, IPM R6980, ×1 (Brimaud & Vachard, 1987; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

# Subfamily PLACOTREMATINAE new subfamily

[Placotrematinae REID, herein] [type genus, *Placotrema* HINDE, 1884a, p. 127]

With connected dermalia or gastralia, united by ankylosis of paratangential rays or by networks of siliceous filaments in meshes between them. [Contains one living

## Hexactinosa

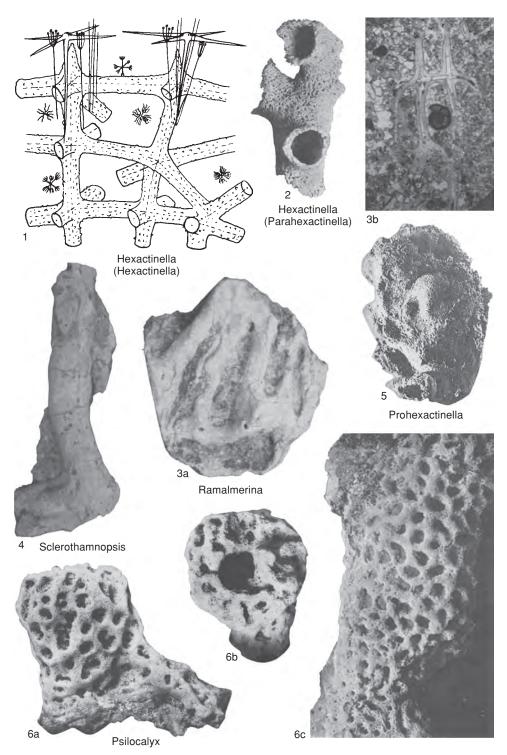


FIG. 332. Tretodictyidae (p. 504).

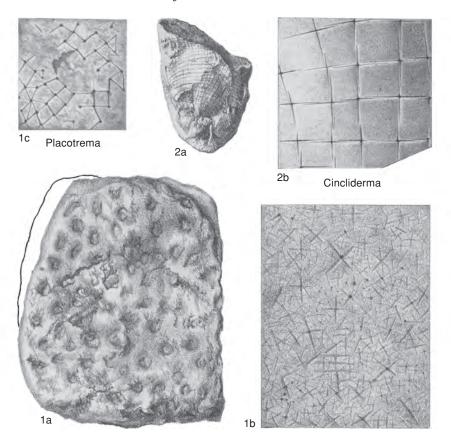


FIG. 333. Tretodictyidae (p. 506).

member, *Fieldingia* KENT, 1870, which has no fossil record.] *Cretaceous (Turonian)*.

Placotrema HINDE, 1884a, p. 127 [\*P. cretaceum; OD]. Usually platterlike or flabellate, sometimes irregularly convoluted, rarely funnel-like; dermal surface of skeletal framework with closely spaced, round or ovate apertures of internally labyrinthic schizorhyses, between which skeletal meshwork forms divided and anastomosed trabeculae; gastral side similar, but coated by dense, tangential layer of superficial meshwork formed from large and small pentactines united mainly by siliceous filaments that form networks between tangential rays; this meshwork perforated at intervals by irregularly alternating, round or ovate, osculum-like openings; dictyonal skeleton fine meshed, with strands spreading to both surfaces; loose spiculation unknown. Cretaceous (Turonian): England.—FIG. 333, 1a-c. \*P. cretaceum, Upper Chalk, Kent; a, upper surface with oscula, ×1; b, drawing of dermal layer where spicules preserved as molds, ×15; c, drawing of internal skeleton from fractured surface where spicules preserved as molds,  $\times 20$  (Hinde, 1884b).

Cincliderma HINDE, 1884a, p. 127 [\*C. quadratum HINDE, 1884a, p. 128; OD]. Nodular or possibly funnel-like; schizorhyses wide, tunnel-like, labyrinthic; skeletal framework coarse meshed, with meshwork between radiating, dictyonal strands often largely irregular; surfaces coated by tangential networks of connected dermal or gastral pentactines, united by ankylosis of their tangential rays only, or with additional smaller pentactines or siliceous filaments in intervening meshes; major meshes of this meshwork typically quadrate and sometimes regularly subdivided if smaller pentactines occur; loose spiculation unknown. Cretaceous (Turonian): England.-FIG. 333, 2a-b. \*C. quadratum, Upper Chalk, southern England; *a*, basal part of funnel-shaped sponge with dermal layer, ×1; b, part of dermal layer with coarse, reticulate skeleton, smaller, intermingled spicules in quadrules not represented, ×10 (Hinde, 1884b).

#### Family CYSTISPONGIIDAE new family

# [Cystispongiidae REID, herein] [type genus, *Cystispongia* F. A. ROEMER, 1864, p. 7]

Tuberlike or pyriform sponges, with dense, external capsule enclosing a labyrinth of thin-walled passages; skeletal meshwork euretoid; loose spicules and nature of internal passages unknown. [Internal passages are comparable with either euretid cavaedia or tretodictyid schizorhyses. The single included genus, *Cystispongia* F. A. ROEMER, is a true hexactinosan, although the name *Cystispongia* has been applied to various Lychniscosa.] *Upper Cretaceous (Coniacian)– Neogene.* 

Cystispongia F. A. ROEMER, 1864, p. 7 [\*Cephalites bursa QUENSTEDT, 1852, p. 670; SD RAUFF, 1893, p. 65] [=Cyrtobolia PočTA, 1883, p. 38 (type, Achilleum formosum REUSS, 1846 in 1845-1846, p. 79, SD DE LAUBENFELS, 1955, p. 83)]. Tuberlike or pyriform, sometimes with a terminal depression but with no axial, paragastral cavity; interior a labyrinth of thin-walled, tubular passages; external surface of mature examples formed by a shell-like capsule, which covers surface completely or has osculumlike, terminal perforation, or terminal and lateral perforations; internal meshwork simple, dictyonal strands spreading from axis when apparent; capsule formed by dictyonal meshwork with triangular meshes and spherically swollen, multiradiate nodes, or possibly with this meshwork covered externally by a thin, siliceous membrane; loose spiculation unknown. Upper Cretaceous (Coniacian)-Neogene: Europe.—FIG. 330, 3a-b. C. bursa (QUENSTEDT), Brogniarti-Planer, Turonian, northern Germany; a, side view of pyriform example with oscule-like openings in dermal layer, ×1; b, fragment of endosomal skeleton, ×12 (de Laubenfels, 1955).

#### Family AULOCALYCIDAE Ijima, 1927

[Aulocalycidae IJIMA, 1927, p. 128]

Skeletal framework three dimensional and constructed so that individual spicular rays or strandlike series of skeletal beams are interwoven diagonally, often also with many anaxial synapticula; canalization absent or limited to occurrence of ostia or shallow epirhyses; sceptrules and uncinates absent in Holocene examples. [Relationship to other Hexactinosa uncertain, but skeletal structure corresponds with the cortical meshwork of several genera (e.g., *Heterochone* IJIMA, *Euryplegma* SCHULZE).] *Upper Jurassic.*  Polygonatium Schrammen, 1937, p. 56 (Schrammen, 1936, p. 182, nom. nud.) [\*P. sphaeroides; OD]. Globular with large osculum and short stalk; exterior with rounded ostia of varying sizes, arranged without order; outer meshwork of framework formed by union of dictyonal hexactines of various sizes with their rays overlapping diagonally, united where they cross one another and also in part by synapticula; meshwork denser at surface, there pierced by ostia; inner part unknown; dermal stauractines may be fused to parts of external surface; other loose spicules unknown. [Skeletal meshwork aulocalycoid as known, but possibly only part of a structure with euretoid meshwork internally (cf. e.g., Heterochone IJIMA, family Euretidae).] Upper Jurassic: Germany.-FIG. 330,4a-b. \*P. sphaeroides, Weiss Jura, Streitberg; a, side view of type specimen with shallow spongocoel on summit of globular sponge, with round ostia of various sizes in dermal surface, ×2; b, fragment of dictyonal, skeletal structure, ×20 (Schrammen, 1937).

# Family EMPLOCIDAE de Laubenfels, 1955

[Emplocidae DE LAUBENFELS, 1955, p. 80]

Hexactinosid sponges with multilayered skeleton in which radially disposed, longitudinal, subdermal canals occur in successive zones separated by layers of regular, rectangular cribwork, so that transverse sections resemble growth rings; skeleton simple, dictyonine network with imperforate nodes; dermal skeleton not preserved. *Middle Jurassic.* 

Emploca SOLLAS, 1883, p. 541 [\*E. ovata SOLLAS, 1883, p. 542; OD] [=Taxoploca SOLLAS, 1888, p. xxviii, obj.]. Cylindrical to ovate sponges with thick walls around deep, cylindrical spongocoel with unobstructed, circular osculum at summit; exhalant canals in ringlike, successive zones approximately parallel to outer margin and open onto gastral surface of spongocoel; inhalant canals, with small, round ostia evenly distributed on dermal surface, continue inwardly obliquely downward toward axis; skeleton simple, hexactinosan network with imperforate nodes; dermal skeleton not preserved. Middle Jurassic: England.-FIG. 330,2a-b. \*E. ovata, Inferior Oolite, Bristol; a, diagrammatic vertical section showing growth form and exhalant canal system, ×2 (de Laubenfels, 1955); b, side view of small sponge, ×1 (Sollas, 1883).

#### Family UNCERTAIN

Carinthiaspongus KRAINER & MOSTLER, 1992, p. 138 [\*C. ramosus; OD]. Isolated, large pentactines with smooth, proximal ray and four irregularly branched rays in a plane; coarse branches longest near spicule center and shorter distally, mainly parallel to four principal rays or directed upwardly and outwardly. *Middle Triassic:* Austria.—FIG. 334,7. \*C. *ramosus*, Rote Knollenkalke, Ladinian, Karawanken, Kärnten; distal view of isolated spicule with smooth, proximal ray and branched, lateral rays, ×75 (Krainer & Mostler, 1992).

- Caseispongia QUENSTEDT, 1877 in 1877-1878, p. 106 [\*C. articulata; OD]. Annulate, chambered sponge with deep, broad spongocoel; thick walls with layered, dictyid skeletal structure; outer dermal layer fine textured, intermediate layer of regular, reticulate, coarser structure, inner or gastral layer of somewhat coarser and more irregular, dictyid structure; coarse, exhalant canals extending from middle of wall into spongocoel. Jurassic: Germany.--Fig. 335,5a-c. \*C. articulata, Weiss Jura, Heuberg; a, side view of moderately complete, annulate, chambered-type sponge with a fine-textured, dermal layer and coarse, exhalant canals in inner part of wall, at spongocoel margin in upper chamber, ×1; b, transverse section of same sponge showing coarse, exhalant canals leading into matrix-filled spongocoel,  $\times 1$ ; *c*, transverse section of fragment showing three layers of dictyid skeleton, with fine, dermal layer at top, approximately ×5 (Quenstedt, 1877-1878)
- Furcicanalis WU & XIAO, 1989, p. 16 [\*F. goniconus; OD]. Obconical sponges with angular, transverse sections, moderately thick walls, and open spongocoel; outer, thin, inhalant canals straight and converging near midwall to form larger, straight, exhalant canals of inner wall; main dictyonine strands of skeleton undulate, and those in thin, dermal and gastral layers and canal walls coarser than in other parts of wall; secondary hexactines constructing rectangular to multiangular meshes. Upper Triassic (Carnian): China.-FIG. 334,6. \*F. goniconus, Upper Member of Hanwang Formation, Shifang County, Sichuan; transverse section of holotype with pentagonal outline and thick walls where thin, inhalant canals converge to form coarser, inner, exhalant canals, CCG 189-129, ×2 (Wu & Xiao, 1989).
- Idiodictyon DE LAUBENFELS, 1955, p. 95, nom. nov. pro Eudictyon BISTRAM, 1903, p. 84, non MARSHALL, 1875b, p. 211 [\*Eudictyon steinmanni BISTRAM, 1903, p. 86; OD]. Cup-shaped sponge with thin walls and broad spongocoel; dictyid skeleton of fused, regular hexactines, gastral layer of regularly arranged and spaced, separate hexactines with coarse, thick rays. Lower Jurassic: Germany.——FIG. 335,1a-c. \*I. steinmanni (BISTRAM), lower Lias, Comasker Alps; a, side view of thin-walled, cupshaped sponge, ×1; b, fragment of hexactinosid, endosomal skeleton, ×25; c, part of gastral layer of skeleton, ×20 (Bistram, 1903).
- Imbricareola WU & XIAO, 1989, p. 15 [\**I. prunivalvaris;* OD]. Steeply obconical, small sponges with deep, open spongocoel surrounded by thin wall composed largely of irregularly distributed, large, thin-walled, hemispherical to

subspherical, hollow nodes that open into spongocoel; wall in transverse sections appears petalloid and perforated by numerous crooked, thin canals; skeleton of irregularly oriented, fused hexactines and associated smaller, second-order hexactines. *Upper Triassic:* China.——FIG. 335,2*a*– *b.* \**I. prunivalvaris,* Upper Member of Hanwang Formation, Carnian, Jiangyou County, Sichuan; *a*, side view of nodose, small holotype, CCG 935-784, ×1; *b.* transverse section of paratype showing petalloid structure and canalled, thin wall, CCG 177-265, ×4 (Wu & Xiao, 1989).

- Misonia KRAUTTER, 1996, p. 306 [\**M. baldensis;* OD]. Cup-shaped hexactinosan with a broad, deep, central spongocoel and a thick wall, with an encrusting base; unbranched epirhyses and aporhyses quadcunxially arranged in longitudinal and horizontal rows and ending deep within sponge wall; dictyonal skeleton very regular and of hexactines arranged in narrow, quadratic meshes; microscleres unknown. *Lower Jurassic (Pliensbachian):* Italy.— FIG. 334,3. \**M. baldensis,* Misone Limestone, Trento platform, southern Alps; transverse section showing thick wall with radial canals and central spongocoel, ×0.5 (Krautter, 1996).
- Multiloqua DE LAUBENFELS, 1955, p. 82, nom. nov. pro Polyphemus SCHRAMMEN, 1937, p. 47, non BERNHAUER, 1914 [\*Polyphemus strombiformis SCHRAMMEN, 1937, p. 48; OD]. Small, spherical, pear- or top-shaped sponge with smooth, outer, cover layer; hemispherical or flat, upper surface with central, round osculum to spongocoel; through folding, thin wall forms a plicate structure with folds separated by deep cavaedia; outer, cavaedial system alternating with an inner one whose openings are in spongocoel surface; porous epirhyses and aporhyses in walls connect outer and inner cavaedia; dictyonalia of principal skeleton hexactines, but outer, cover layer mesh composed of large stauractines and associated, smaller stauractines. Jurassic: Germany.-FIG. 334,2a-b. M. fungulus (QUENSTEDT), Kimmeridgian marls, Upper Jurassic, Bärenthal; a, side view showing characteristic growth form, ZPAL Pf. VIII/304, ×1; b, summit view of same sponge with shallow spongocoel partially filled with matrix, ×1 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Mysterium DE LAUBENFELS, 1955, p. 86, nom. nov. pro Mystrium SCHRAMMEN, 1937, p. 60, non HERMAN, 1912 [\*Mystrium porosum SCHRAMMEN, 1937, p. 60; OD]. Very small, fig or club shaped with massive, thick wall and deep spongocoel; dermal surface with tiny, broadly spaced, irregular ostia of tubular, epirhysal canals that end in interior between exhalant canals; dictyonalia hexactines in close-meshed and only locally regularly meshed skeleton; dermal layer with thickened elements in fused structure. Jurassic: Germany.——FIG. 334,1. \*M. porosum (SCHRAMMEN), Weiss Jura, Upper Jurassic, Streitberg; side view of dermal surface of clubshaped sponge, ×4 (Schrammen, 1937).
- Octobrum DE LAUBENFELS, 1955, p. 86, nom. nov. pro Rhabdium Schrammen, 1937, p. 63, non Schaum,

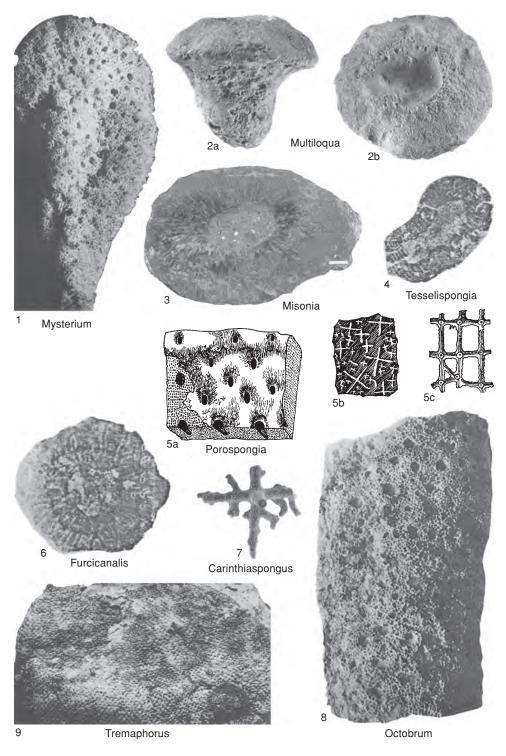


FIG. 334. Uncertain (p. 507-511).

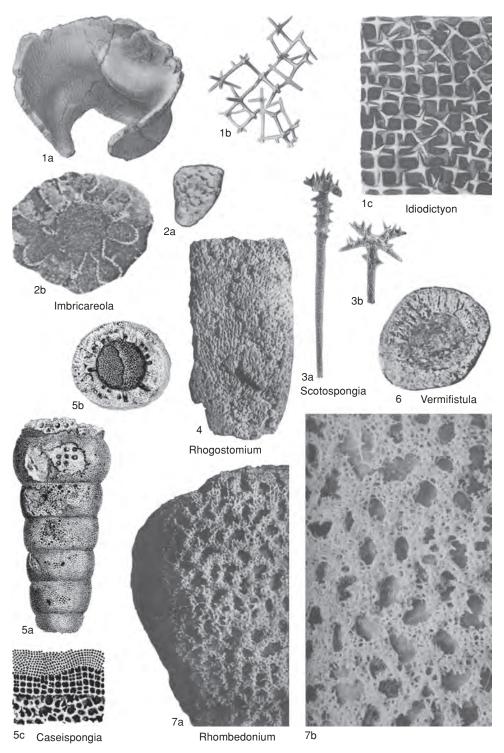


FIG. 335. Uncertain (p. 508-511).

1859 [\**Rhabdium angustatum* SCHRAMMEN, 1937, p. 63; OD]. Sponge rod shaped; outer surface with small, irregularly spaced ostia; dictyonalia hexactines fused into moderately regular framework; dermal layer not differentiated. *Jurassic:* Germany.——FIG. 334,8. \*O. angustatum (SCHRAM-MEN), Weiss Jura, Upper Jurassic, Heuchstetten; side view of cylindrical holotype with irregularly spaced ostia, ×4 (Schrammen, 1937).

- Porospongia D'ORBIGNY, 1849, p. 547 [\*Manon marginatum GOLDFUSS, 1829, p. 94; SD RAUFF, 1893, p. 65] [=Porostoma FROMENTEL, 1860a, p. 43 (type, P. marginata, OD]. Lamellate, upper surface with many large oscules leading from short cloacas; dense dermis with stauractines and hexactines; type species has rim around oscules but others do not. [SALOMON (1990) and MEHL (1992) discussed the taxonomic history of Porospongia and associated genera and concluded that Porospongia and Cribrospongia were named by D'ORBIGNY in 1849, not in 1847, after an intensive search for documentation of the 1847 paper failed.] Upper Jurassic: Europe.—FIG. 334, 5a-c. P. impressa (GOLDFUSS), Germany; a, part of side view of sponge showing common oscules,  $\times 1$ ; *b*, part of dermal layer,  $\times 6$ ; *c*, part of fused, endosomal skeleton, ×12 (de Laubenfels, 1955).
- Rhogostomium SCHRAMMEN, 1937, p. 58 (SCHRAMMEN, 1936, p. 182, nom. nud.) [\*R. corrugatum; OD]. Sponges flat or funnel shaped with massive, thick walls; small, oval to crevicelike, inhalant and exhalant ostia occur in closely spaced, alternating to irregular arrangements in more or less distinct rows; epirhyses and aporhyses end blindly beneath skeletal surface; fused and somewhat irregular, dictyonal skeleton is of hexactines, which are more or less thickened in outer, dermal layer. Jurassic: Germany.——FIG. 335,4. \*R. corrugatum, Weiss Jura, Upper Jurassic, Heuchstetten; side view of exterior of flattened sponge showing nature of ostia, ×0.5 (Schrammen, 1937).
- Rhombedonium Schrammen, 1937, p. 59 (SCHRAMMEN, 1936, p. 182, nom. nud.) [\*R. cypelliaeforme; OD]. Small, top-shaped sponge with thick wall and deep spongocoel; dermal surface with irregularly rounded, inhalant ostia without distinct arrangement, as openings to branched epirhyses that end under skeletal surface as postica; gastral, upper surface with large, round, clearly to obscurely alternating postica of aporhyses that initiate between inhalant canals within skeleton; distinctly irregular and wide-meshed, dictyonal skeleton composed of fused hexactines, more or less thickened in dermal layer. Jurassic: Germany.-FIG. 335,7a-b. \*R. cypelliaeforme, Weiss Jura, Upper Jurassic, Streitberg; a, side view of small sponge with relatively coarse, inhalant ostia, ×4; b, enlarged view of dermal surface showing open,

skeletal net and coarse ostia,  $\times 6$  (Schrammen, 1936).

- Scotospongia KRAINER & MOSTLER, 1992, p. 138 [\*S. aculeata; OD]. Large pentactines with a long, proximal ray that is coarsely spinose in upper part, and four other rays arranged in transverse plane, and all with large spines that are generally directed upwardly. Middle Triassic: Austria.——FIG. 335,3a-b. \*S. aculeata, Rote Knollenkalke, Ladinian, Karawanken, Kärnten; a, side view of typical spicule with long, proximal ray that is spinose near top, and spinose transverse rays, above; b, oblique view from above showing coarse spines on transverse rays and upper part of proximal ray, ×100 (Krainer & Mostler, 1992).
- Tesselispongia WU & XIAO, 1989, p. 17 [\*T. tubifasciculata; OD]. Branched to unbranched, tubular to pillar-shaped sponges with thin, smooth walls and open spongocoels; walls may lack canals or have some radial canals where inhalant and exhalant canals alternate in position; skeleton of very small, regular hexactines that may be coarser in dermal or gastral areas, and may have growth rings where coarser. Upper Triassic (Carnian): China.— FIG. 334,4. \*T. tubifasciculata, upper Member of Hanwang Formation, Mianzhu County, Sichuan; diagonal section through branched sponge showing open spongocoel and moderately thick walls with regular canals, particularly in diagonal section on right, CCG 208-527, ×2 (Wu & Xiao, 1989).
- Tremaphorus SCHRAMMEN, 1937, p. 62 (SCHRAMMEN, 1936, p. 183, nom. nud.) [\*T. punctatus; OD]. Sponge flat, probably funnel or ear shaped, with a proportionally thin wall; dermal surface with closely spaced, pinpoint-sized ostia; epirhyses and aporhyses ending blindly with skeleton between postica; dictyonal skeleton narrow meshed, in inner part of wall regularly meshed, and in outer part strongly thickened in dermal layer. Jurassic: Germany.——FIG. 334,9. \*T. punctatus, Weiss Jura, Upper Jurassic, Erkenbrechtsweiler; dermal surface with regular ostia in thickened, outer part of skeleton, ×1 (Schrammen, 1937).
- Vermifistula WU & XIAO, 1989, p. 16 [\*V. microdictya; OD]. Steeply obconical to pillar-shaped or cylindrical sponges with deep, open spongocoel; moderately thick walls with numerous crooked, inhalant canals that converge irregularly to form somewhat coarser, inner, exhalant canals; skeleton of small, closely spaced hexactines fused at various angles to construct triangular to pentagonal, mesh spaces in wall that shows growth rings. Upper Triassic (Carnian): China.—FIG. 335,6. \*V. microdictya, Upper Member of Hanwang Formation, Shifang County, Sichuan; transverse section showing thick wall around spongocoel and crooked, inhalant and exhalant canals, CCG 179-529, ×2 (Wu & Xiao, 1989).

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### MESOZOIC AND CENOZOIC HEXACTINELLID SPONGES: LYCHNISCOSA AND ORDER UNCERTAIN

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#### Order LYCHNISCOSA Schrammen, 1903

[nom. transl. DE LAUBENFELS, 1936, p. 185, ex tribus Lychniscosa Schrammen, 1903, p. 7]

Dictyonine Hexasterophora with lychniscs at some stage of ontogeny, in either all or some individuals of any given species, or regarded as derived from a genus having lychniscs; primary skeletal framework sometimes composed of dictyonalia united to form a single, netlike layer of dictyonal meshwork, but usually composed of threedimensional meshwork in which dictyonal strands are present and have little or no layered arrangement; secondary components may be added at surfaces or within primary meshes; lychnisc octahedra usually present throughout primary meshwork or absent at surfaces, although present internally; octahedra extensively suppressed in some genera through failure to produce them or to secondary solidification in ontogeny; in latter instances, sometimes only seen in some individual sponges; secondary dictyonal meshwork with nodal octahedra or not; cortical meshwork may be absent, or formed by secondary accretion of dictyonal hexactines at surfaces by modification of outermost, primary meshwork or by outgrowth of anastomosing, siliceous filaments from outermost, dictyonal beams; skeletal canalization absent, intracortical only, or fully developed, with distinct, inhalant and exhalant canals (epirhyses, aporhyses) or a single system only; superficial meshwork sometimes present, formed from dictyonal hexactines, adventitious siliceous filaments, or both, or partly or wholly from connected dermalia or gastralia; latter pentactines in known examples; basal skeleton formed from dictyonal hexactines or from siliceous filaments that grow downwardly from dictyonal skeleton; some genera with peripheral structures, supported by loose spicules only or containing rigid structures; hexasters present in living examples, but uncinates and sceptrules unknown. [The name Lychniscosa SCHRAMMEN, 1903, differs from the earlier Lychniskophora SCHRAM-MEN, 1902 in lacking the root *-phor-* (signifying bearers). Lychniscosa is, therefore, a separate name and not a form of the name Lychniskophora.]

Cryptogenic; presumably derived from an unknown primitive lyssacine with hexaster microscleres. According to IJIMA (1927), origin of lychnisc octahedra before union of the dictyonalia in ontogeny implies origin of Lychniscosa independently of Hexactinosa in phylogeny. Now almost extinct (5 extant genera). Jurassic–Holocene.

#### Family CALYPTRELLIDAE Schrammen, 1912

[Calyptrellidae SCHRAMMEN, 1912, p. 196]

Skeletal framework a single layer of dictyonal meshwork with mainly quadratic meshes; loose spiculation unknown. *Upper Cretaceous.* 

Calyptrella SCHRAMMEN, 1912, p. 306 [\*C. bertae SCHRAMMEN, 1912, p. 307; OD]. Divided and anastomosed tubes; fixation by small, rootlike processes formed from siliceous filaments growing out from dictyonal framework. Cretaceous (Coniacian-Maastrichtian): Germany.——FIG. 336a-b. \*C. bertae, Quadratenkreide, Cenomanian, Oberg; a, characteristic cluster of anastomosed tubes, ×1; b, smaller fragment showing skeletal texture and rootlike attachment processes, ×2 (Schrammen, 1912).

#### Family CALLODICTYONIDAE Zittel, 1877

#### [Callodictyonidae ZITTEL, 1877b, p. 38]

Dictyonal framework three dimensional initially, and uncanalled or with intracortical features only as ostia or postica, or shallow epirhyses or aporhyses; peripheral structures

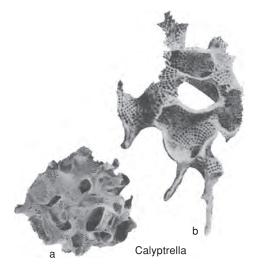


FIG. 336. Calyptrellidae (p. 513).

usually absent (or unknown), but some branched-tubular genera have soft, peripheral capsule or rigid, peripheral meshwork; primary, dictyonal meshwork with gradually diverging, dictyonal strands, without layered arrangement, or locally or mainly arranged so that meshwork shows layered construction; meshes between strands usually regularly quadrate; cortical structures formed by simple thickening of components at surfaces with solidification of lychniscs in some genera; by formation of porous, siliceous membranes from networks of siliceous filaments that cross individual meshes or surface in general; by accretion of secondary dictyonal hexactines, with or without nodal octahedra; by structural modification of outermost meshwork; by anastomosing, siliceous fibers that pass into basal skeleton; or by combinations or two or more of these developments; peripheral meshwork of dictyonal origin when present; basal meshwork formed from secondary hexactines, or from anastomosing siliceous fibers that grow down from surface of dictyonal framework; loose spiculation unknown except in two living genera (with discohexasters; dermal, gastral, and peripheral pentactines). [The scope given to this family is analogous with that given to the family Euretidae of the order Hexactinosa,

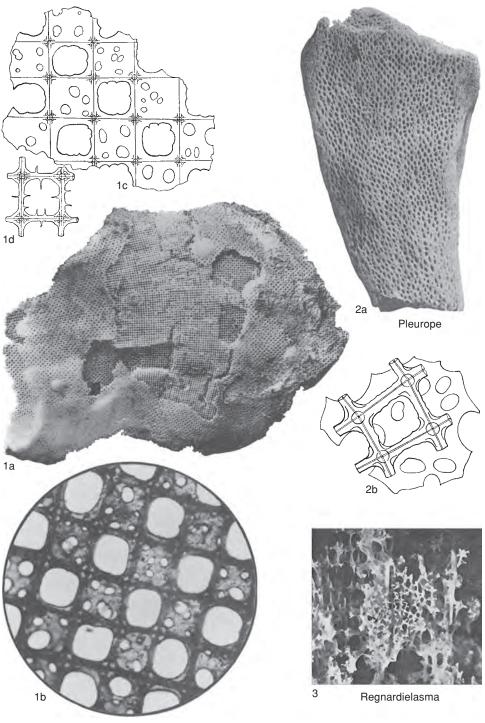
but with genera with peripheral structures (not present in Euretidae) excluded, apart from a few whose inclusion is more convenient.] *Upper Jurassic–Holocene.* 

#### Subfamily CALLODICTYONINAE Zittel, 1877

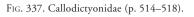
#### [nom. transl. REID, herein, ex Callodictyonidae ZITTEL, 1877b, p. 38]

Tubular to funnel-like, flabellate, or scabbardlike sponges, the latter with parietal oscula along narrow margins; cortical features and basal skeleton formed by outgrowth of siliceous filaments, or by accretion of small, dictyonal hexactines, with or without nodal octahedra; canalization restricted to ostia or postica, or with shallow, radial canals when cortical meshwork is spicular. [Probably includes several main lines of descent. Genera with cortical and basal meshwork formed from siliceous fibers are most similar to Microblastidinae and Becksinae.] *Upper Jurassic–Upper Cretaceous.* 

- Callodictyonella STRAND, 1928, p. 33 [\*Callodictyon infundibulum ZITTEL, 1877b, p. 57; OD] [=Callodictyon ZITTEL, 1877b, p. 57, obj., non SOLLAS, 1877]. Thin-walled cup with very wide spongocoel; wall uniform and composed of layers of united hexactines that form a uniform, quadrate mesh; ray junctions with perforated, octahedral lanterns and with spinose, skeletal beams; dermal layer formed of flattened extensions of rays from outer, skeletal layer; canals and ostia absent. Upper Cretaceous: Germany.-FIG. 337, 1a-d. \*C. infundibulum (ZITTEL), Quadratenkreide, Campanian, Oberg; a, side view showing uniform, skeletal structure lacking large canals, but with remnants of more dense dermal layer left and right, ×2; b, photomicrograph of dermal layer with alternating mesh spaces filled, ×50; c-d, camera lucida drawings of structure of dermal layer and interior net, ×45 (Schrammen, 1912).
- Beaussetia MORET, 1926b, p. 233 [\*B. membraniformis; OD]. Flabellate, with marginal attachments; primary framework regular but masked at both surfaces by fine, irregular meshwork, formed by union of small, secondary hexactines arranged without order; this cortical meshwork pierced by small, skeletal pores, in longitudinal series on one side but without order on other; attachment structures formed by similar meshwork. Upper Cretaceous: France.—FIG. 338,3a-b. \*B. membraniformis, Santonian, Saint-Cyr; a, inner face of flabellate fragment with regular rows of skeletal pores, slightly enlarged, ×1; b, outer surface with skeletal pores less regularly distributed, ×1 (Moret, 1926b; courtesy of Société Géologique de France).



Callodictyonella



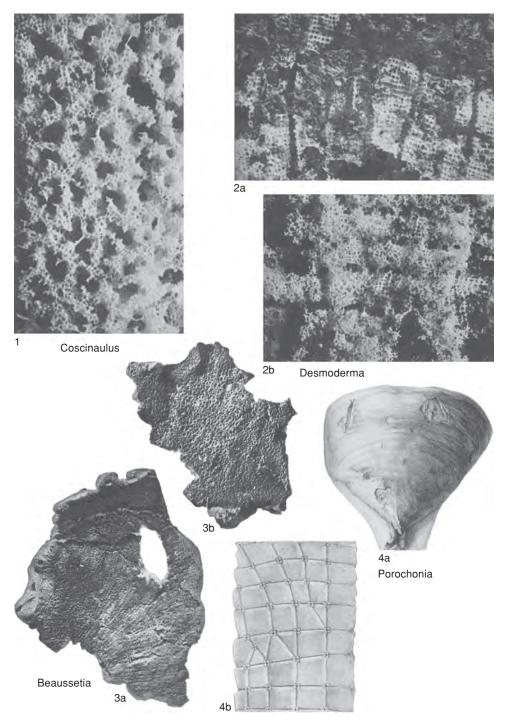


FIG. 338. Callodictyonidae (p. 514-518).

Cinclidella SCHRAMMEN, 1912, p. 334 [\**C. solitaria;* OD]. Narrow funnel with basal root processes; dictyonal framework formed from large and small, dictyonal hexactines, larger forming regular, primary framework and smaller uniting to form irregular meshwork within or outside primary

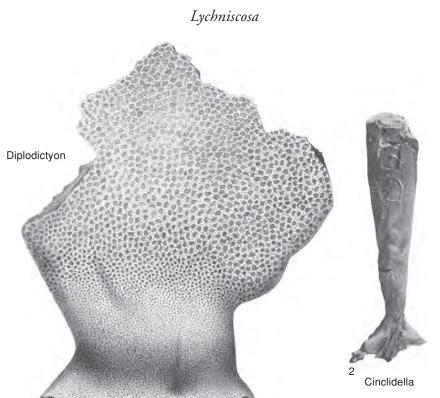


FIG. 339. Callodictyonidae (p. 516-517).

meshes; dermal surface of primary framework coated by fine, secondary meshwork, pierced by ostia or shallow epirhyses that open into underlying, primary meshes; components of cortical meshwork with or without nodal octahedra; ostia arranged without order or in longitudinal series; no similar cortex on gastral side. *Upper Cretaceous:* Germany.——FIG. 339,2. \*C. solitaria, Cuvierplaner, Turonian, Heere; side view of steeply obconical sponge with rootlike base, ×0.5 (Schrammen, 1912).

- Coscinaulus SCHRAMMEN, 1937, p. 20 (SCHRAMMEN, 1936, p. 180, nom. nud.) [\*C. micropora; OD]. Tubular; outside with ostia, some arranged in rough, longitudinal series, along which shallow grooves may occur; meshwork of this surface irregular; internal meshwork regular, not canalized; characters of gastral side not known. Upper Jurassic: Germany, Poland.—FIG. 338,1. \*C. micropora, Weiss Jura, Erkenbrechtsweiler, Germany; enlarged part of outer skeleton showing small, inhalant pores and dimensions of skeletal net, ×5 (Schrammen, 1936).
- Desmoderma SCHRAMMEN, 1937, p. 19 (SCHRAMMEN, 1936, p. 180, nom. nud.) [\*D. evestigata; OD]. Flabellate or possibly funnel-like; both surfaces with irregular, longitudinal furrows, more distinct on one side than other; small, round skeletal pores located along furrows, and locally grouped quadrately; internal meshwork regular, not cana-

lized; cortical meshwork denser and more or less irregular on side with less distinct furrows. [Based on a fragment of doubtful habitus; referred to Ventriculitidae by SCHRAMMEN (1937), but epirhyses and aporhyses absent.] Upper Jurassic: Germany.——FiG. 338,2*a*-*b*. \**D. evestigata*, Weiss Jura, Upper Jurassic, Schwabtal; *a*, enlargement of inner surface showing regular, reticulate, skeletal net with longitudinal furrows; *b*, enlargement of outer surface of wall with less regularity and aligned, inhalant ostia, ×5 (Schrammen, 1937).

- Diplodictyon ZITTEL, 1877b, p. 59 [\*Scyphia heteromorpha REUSS, 1846 in 1845–1846, p. 1; OD].
  Similar to Pleurope ZITTEL, but with external cortex and basal skeleton formed by irregularly united, dictyonal hexactines, without nodal octahedra; gastral surface with simple, open meshes. Upper Cretaceous: Germany.——FIG. 339,1. \*D. heteromorpha (REUSS), Bohemia; side view showing basal stalk and upper, flattened, funnel-like part of sponge with large, inhalant ostia, ×1 (Reuss, 1846).
- Pleurope ZITTEL, 1877b, p. 58 [\*Pleurostoma lacunosa F. A. ROEMER, 1841 in 1840–1841, p. 12; OD]. Bilaterally flattened, scabbard shaped or leaflike, with parietal oscula along two narrow margins; dictyonal framework regular throughout; exterior of framework densely coated with downwardly directed, siliceous fibers, united by transverse synapticula, and continuous with basal skeleton; external surface

with ostia of shallow epirhyses, arranged without order, that perforate this cortical layer to open into meshes of underlying, dictyonal framework; gastral surface with simple, open meshes, or formed by a siliceous membrane pierced by postica arranged without order. Cretaceous (Coniacian– Maastrichtian): Germany.—FIG. 337,2a-b. \*P. lacunosa (F. A. ROEMER), Quadratenkreide, Cenomanian, Oberg; a, side view of laterally flattened, type sponge with uniform epirhyses throughout,  $\times 1$ ; b, fragment of gastral layer with simple, open meshes of lychniscoid structure, ×45 (Schrammen, 1912).

- Porochonia HINDE, 1884a, p. 143 [\* Ventriculites simplex SMITH, 1848, p. 204; OD]. Funnel-like, usually stalked, with basal root processes; dictyonal meshwork regular throughout; exterior of framework coated by finely porous, siliceous membrane with numerous small, round ostia that are arranged without order; gastral side with simple, dictyonal meshes, or with some development of structure seen on dermal side; basal meshwork fibrous. [A further external skeletal membrane claimed by HINDE (1884a, p. 143) does not exist.] Cretaceous (Turonian): England.—FIG. 338,4a-b. \*P. simplex (SMITH), Upper Chalk; a, side view showing smooth, dermal layer of funnel-shaped sponge, ×0.5; b, drawing of spicular structure of interior skeleton preserved as a mold in chalk, ×20 (Hinde, 1884a).
- Regnardielasma ZHURAVLEVA in REZVOI, ZHURAVLEVA, & KOLTUN, 1962, p. 46, nom. nov. pro Elasma REGNARD in MORET, 1926b, p. 233, non JAENNICKE, 1867, nec WRIGHT & STUDER, 1887 [\*Elasma moreti REGNARD, 1926, p. 476; OD]. Sheets planar to wavy and undulating with uniform thickness, with very small pores on one side only; canals not visible; skeletal net of large hexactines forming regular, cubic, lychniscoid net with cortex on both surfaces, but more prominent on one; large pentacts occur on surface at regular distances and regularly oriented with major axis of sponge. [MORET (1926b, p. 233) cited this new genus and species as being described by REGNARD "in litt.," and that publication also has a date of 1926. Apparently that reference was available in proof to MORET.] Upper Cretaceous (Cenomanian): France.—FIG. 337,3. \*R. moreti (REGNARD), Coulonges-les-Sablons; side view of fragment with cubic structure formed by large hexactines in a lychniscoid structure, with part of finer, cortex structure in center and large pentacts on right, ×10 (Moret, 1926b; courtesy of Société Géologique de France).

#### Subfamily MICROBLASTIDINAE Schrammen, 1912

[nom. transl. REID, herein, ex Microblastididae SCHRAMMEN, 1912, p. 195]

Goblet- to mushroom-shaped sponges in which wall is plicated longitudinally above a

tubular stalk; outwardly or downwardly facing folds pierced by parietal oscula, or bearing short, terminally open outgrowths; folds continuous to marginal part of body, or die out submarginally so that unfolded brim is formed; cortical features and basal skeleton formed by outgrowth of siliceous filaments. [Here reduced to subfamily because skeletal characters are not distinguishable from those of some Callodictyoninae (*Callodictyon* ZITTEL, *Porochonia* HINDE). Probably similar to the ancestry of Becksinae and Coeloptychidae.] *Cretaceous*.

- Microblastidium SCHRAMMEN, 1902, p. 15 [\*M. decurrens; OD]. Narrow funnel with wall plicated longitudinally, and with irregular papillae or short, tubular outgrowths along outward plications; dictyonal framework mainly regular throughout; external meshes covered by cribiform lamella or netted, siliceous filaments; round perforations in these structures forming ostia, arranged without order; gastral side of framework mainly with simple meshes only, but coated in parts by superficial network of siliceous filaments that grew out from underlying surface. Cretaceous: Germany, France.-FIG. 340, 1a. \*M. decurrens, Quadratenkreide, Cenomanian, Oberg, Germany; side view of papillose-appearing, funnel-like sponge, ×0.5 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).-FIG. 340,1b. M. gaultinum LAGNEAU-HÉRENGER, Valanginian, Chateauneuf-de-Chabre, France; side view of longitudinally plicated form with ostia, ×1 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Spirolophia POMEL, 1872, p. 106 [\*Pleurostoma tortuosa F. A. ROEMER, 1864, p. 15; OD] [=Marshallia ZITTEL, 1877b, p. 58, obj. (type, Pleurostoma tortuosa ROEMER, 1864, p. 15, SD DE LAUBENFELS, 1955, p. 91)]. Funnel-like or mushroomlike, with wall longitudinally plicated above tubular stalk, but folds die out near top to produce unfolded brim; folds may be spirally twisted; parietal oscula along outwardly facing plications; dictyonal framework regular throughout; outside with cribiform lamella and ostia as in Callodictyon ZITTEL or less regularly developed; simple meshes only on gastral side; root structure fibrous. [Listed by DE LAUBENFELS (1955, p. 91) as Marshallia and Spirolophia (p. 103); latter name used here because genus was regarded as recognizable, although of uncertain position.] Upper Cretaceous: Germany.-FIG. 340,2a-b. \*S. tortuosa (F. A. ROEMER), Quadratenkreide; a, side view of twisted, plicate sponge with unfolded, oscular margin, Hannover, UG, ×0.5 (Roemer, 1864); b, drawing of lychniscoid, skeletal structure with spinose rays or bars, Cenomanian, Oberg, ×45 (Schrammen, 1912).

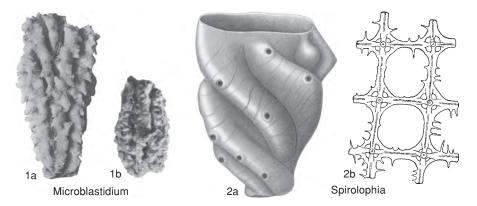


FIG. 340. Callodictyonidae (p. 518).

#### Subfamily BECKSINAE Schrammen, 1912

[nom. transl. REID, herein, ex Becksidae SCHRAMMEN, 1912, p. 196]

Goblet to mushroom-shaped sponges with distinct, central cavity or everted upper surface, in which anastomosing folds of thin wall enclose dermally and gastrally lined networks of cavaedial passages; apertures between divided and anastomosed folds at outer or lower surface of body lead into dermally lined cavaedia, and similar apertures in inner or upper surface lead into gastrally lined cavaedia; folds may continue to top or periphery of body, or die out submarginally so that unfolded rim is produced; root skeleton fibrous. [Reduced here to subfamily status because skeletal characters are not distinguishable from those of Callodictyoninae; and restricted to genera with a habitus similar to that of Becksia SCHLÜTER. For other genera included by SCHRAMMEN (1912), see Callicylicinae.] Cretaceous–Paleogene (Oligocene).

Becksia SCHLUTER, 1868, p. 93 [\**B. soekelandi*; OD]. Cuplike, fixed by spinelike root processes that grow out from external surface; wall mainly folded to enclose two networks of tubular passages that open on opposite sides, folds die out to produce unfolded brim in complete individuals; uppermost, dermally lined tubes sometimes form horizontal ring below unfolded margin, seen in views of interior; skeletal meshwork mainly or all regular; external surfaces with outermost beams thickened, or with some meshes covered by cribiform, siliceous lamella; usually no cortical features on gastral side; root structure fibrous. *Cretaceous*: Germany, France.——FIG. 341, *Ia.* \**B. soekelandi*, upper Quadraten-Schichten, between Lette, Coesfeld, Holtwick and Legden, Germany; part of fused, spinose, lychniscoid skeleton, ×50 (de Laubenfels, 1955).——FIG. 341, *Ib–d. B. augusta* SCHRAMMEN, Quadratenkreide, Cenomanian, Oberg, Germany; *b*, side view of folded wall that encloses tubular passages in type specimen, ×0.5; *c*, exterior with folded wall and small, tubular openings, ×1; *d*, interior surface with tubular openings, ×1 (Schrammen, 1912).

- Discoptycha DEFRETIN-LEFRANC, 1961, p. 96 [\*D. simplex; OD]. Discoidal sponge with slender stalk; lower face with alternating, narrow grooves and broad ribs or folds that may bifurcate; upper surface with inverse, broad grooves and narrow and high ribs that may anastomose or branch in vicinity of center; skeleton with regular, cubic, lychniscoid mesh; canal system absent. Upper Cretaceous (Coniacian): France.—FIG. 342,2a-b. \*D. simplex, Upper Cretaceous beds, Cambrésis à Rumilly; a, upper face of discoidal sponge with radial furrows and ridges, ×0.5; b, drawing of lower face with irregular, lychniscoid, skeletal mesh between small, inhalant pores, ×20 (Defretin-Lefranc, 1961).
- Manzonispongia ENGESER & MEHL, 1993, p. 188, nom. nov. pro Manzonia GIATTINI, 1909, p. 59, non BRUSINA, 1870, nec POMEL, 1883 [\*Manzonia aprutina GIATTINI, 1909, p. 59; OD]. Ovoid to tubular or meandriform sponges without a spongocoel; skeleton resulting from complicated merging of tubes or of sheets of thin walls separated or defined by inhalant and exhalant lacunae (cavaedia); canal system absent; skeletal net regular, a cubic mesh of large lychniscs. Paleogene (Oligocene)-Neogene (Miocene): Spain, Oligocene; Italy, Spain, Miocene.-FIG. 342, 1a-b. M. betica BRIMAUD & VACHARD, Tortonian, Miocene, Betique Region, southern Spain; a, side view of irregular, tubular sponge with large cavaedia, ×5; b, photomicrograph showing lychniscs in skeleton, ×20 (Brimaud & Vachard, 1986; courtesy of

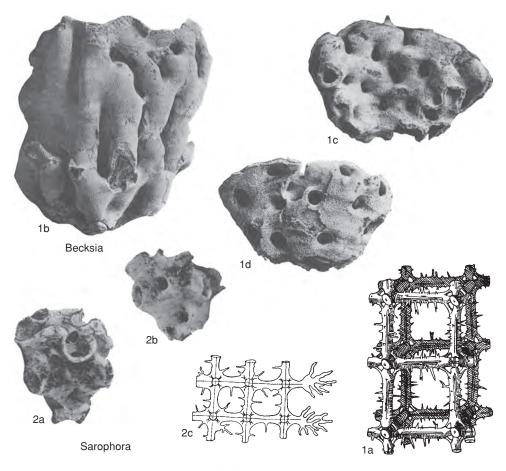


FIG. 341. Callodictyonidae (p. 519-523).

Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

- Oncolpia POMEL, 1872, p. 105 [\*Brachiolites elegans SMITH, 1848, p. 355; OD]. Mushroomlike to globular with tall, oscular chimney, supported by tubular stalk with branching roots at base; wall folded as in *Becksia* SCHLUTER above stalk, and with similar, unfolded brim that forms oscular chimney, if chimney present; dictyonal meshwork mainly regular; external surfaces with irregularly arranged ostia perforating cribiform, siliceous membrane that coats surface of framework; internal and paragastral surfaces with simple meshes only, or with cribiform structure developed locally; root structure fibrous. *Upper Cretaceous*: Europe.
  - O. (Oncolpia). Cavaediate part of body globular to discoidal, sometimes varying in different individuals; unfolded brim growing upwardly to horizontally outward or slightly downwardly, sometimes forming tall, oscular chimney when

body is globular; apertures between divided and anastomosed folds arranged alternately or irregularly; folding not radial on either surface, except sometimes locally on outwardly to downwardly facing surface. *Upper Cretaceous:* Europe.— FIG. 343, *I.* \**O. (O.) elegans* (SMITH), Upper Chalk, England; side view of irregular sponge with folded wall, chimneylike summit, and stalk, approximately ×0.5 (Smith, 1848).

O. (Polyptycha) DEFRETIN-LEFRANC, 1961, p. 98 [\*P. becksioides; OD]. Mushroom shaped, with a narrow, unfolded brim at periphery; anastomosed folds of lower surface forming radiate, locally bifurcated ribs, apertures leading into dermally lined cavaedia in intervening furrows; upper surface as in Oncolpia. [Reduced to subgenus level because structure is identical with Oncolpia except for radial direction of downwardly facing folds.] Cretaceous (Coniacian-Maastrichtian): France.—FIG. 343,2a-b.

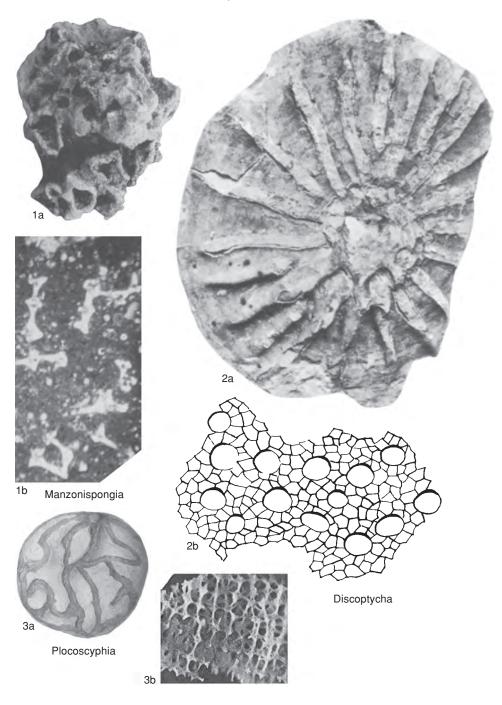


FIG. 342. Callodictyonidae (p. 519-523).

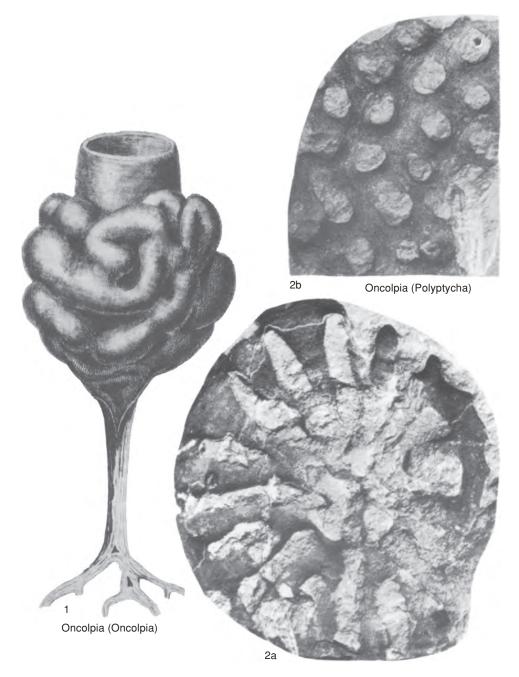


FIG. 343. Callodictyonidae (p. 520-522).

\**O.* (*P.*) *becksioides*, Upper Cretaceous beds, Coniacian, Cambrésis and Lezennes, France; *a*, lower surface of discoidal sponge with branched ridges radiating from stalk area; *b*, impression of upper surface, ×1 (Defretin-Lefranc, 1961). Plocoscyphia REUSS, 1846 in 1845–1846, p. 77 [\*Scyphia labyrinthica REUSS, 1844, p. 173; M; not Spongus labyrinthicus MANTELL, 1822, p. 165, =P. labyrinthica HINDE, 1884a, p. 137, non REUSS, 1846] [=Gyrispongia QUENSTEDT, 1878 in 1877– 1878, p. 478 (type, G. subruta QUENSTEDT, 1878 in 1877-1878, p. 480, SD DE LAUBENFELS, 1955, p. 92, possible weathered specimen]. Character not fully known; based on an incomplete specimen that resembles a globular Oncolpia; possibly identical with that genus. [Name used for various plexiform Lychniscosa, following ZITTEL (1877b); restricted by SCHRAMMEN (1912) and followers to forms with no central cavity, thus excluding the type species P. labyrinthica.] Upper Cretaceous: Europe.-—Fig. 342,3a. \*P. labyrinthica, Upper Chalk, Kent, England; flint nodule with anastomosing folds of sponge wall in surface, ×0.5 (Hinde, 1884a).-FIG. 342,3b. P. communis MORET, Cenomanian, Coulonges, France; typical meandriform skeleton, ×1 (Moret, 1926b; courtesy of Société Géologique de France).

Sarophora SCHRAMMEN, 1912, p. 305 [\*S. armata SCHRAMMEN, 1912, p. 306; OD]. Cuplike; wall folded to enclose two systems of tubes as in Becksia SCHLÜTER, but without unfolded brim, and some gastrally lined tubes also open externally through oscula at ends of stumplike outgrowths; dictyonal framework regular throughout, without distinct, cortical features, but with freely projecting rays of dictyonalia at surfaces that bear spines in pinular manner. [Does not include Sarophora aptiensis LAGNEAU-HÉRENGER, 1962, pl. 16, 6.] Upper Cretaceous: Germany.-FIG. 341,2a-c. \*S. armata, Quadratenkreide, Cenomanian, Oberg; a, cuplike sponge with folded walls to form tubular systems; b, tubular openings in wall of cuplike sponge,  $\times 1$ ; c, drawing of lychniscoid, skeletal structure with projecting, pinnulate rays at sponge surface, ×45 (Schrammen, 1912).

#### Subfamily CALLICYLICINAE new subfamily

[Callicylicinae Reid, herein] [type genus, *Callicylix* SCHRAMMEN, 1912, p. 302]

Body composed entirely of similar, divided and anastomosed tubes, or with additional distinct, axial tube or funnel, or additional small, peripheral tubes; a peripheral capsule in some genera, supported by loose pentactines or stauractines only, or by additional rigid meshwork. *Upper Jurassic– Holocene.* 

Callicylix SCHRAMMEN, 1912, p. 302 [\*C. farreides; OD]. Globular, columnar or shaped irregularly, with similar divided and anastomosed tubes only, or with a distinct axial tube when globose to columnar; soft or rigid capsule sometimes present; surfaces of tubes have open, primary meshes only, with no cortical modification, or modified by secondary accretion of dictyonal hexactines; latter as large as primary components or smaller and with or without nodal octahedra; also scattered sporadically, or sufficiently numerous to produce meshwork enclosing secondary ostia or postica; capsule supported by loose pentactines only, or additionally by dictyonal meshwork growing into it from margins of covered tubes; hexasters and pentactine dermalia and gastralia in living species. [Here includes *Cyclostigma* SCHRAMMEN, 1912, as subgenus, and living species of *Aulocystis* SCHULZE, 1887a, *non* SCHLUTER, 1885, other than *Neoaulocystis grayi* (BOWERBANK).] *Cretaceous (Aptian)–Holocene:* Europe.

- C. (Callicylix). Description as for genus. Cretaceous (Aptian)-Holocene: Europe.—FIG. 344,1. \*C. (C.) farreides, Aptian, Quadratenkreide, Oberg, Germany; side view of globular sponge of anastomosed tubes, ×1 (Schrammen, 1912).
- C. (Cyclostigma) SCHRAMMEN, 1912, p. 303 [\*Plocoscyphia acinosa SCHRAMMEN, 1902, p. 17; SD DE LAUBENFELS, 1955, p. 92]. Tube surfaces typically with ostia on dermal side, sometimes also with postica on gastral side; rigid capsule sometimes present. [Reduced to subgenus level because distinction from Callicylix s.s. depends only on presence of ostia, which may locally occur in Callicylix species]. Cretaceous (Aptian-Maastrichtian): Spain, Germany.-FIG. 344, 3a. \*C. (C.) acinosa (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg, Germany; side view of tubuled sponge, ×1 (Schrammen, 1902).—FIG. 344,3b-c. C. (C.) tubules LAGNEAU-HÉRENGER, Aptian, Can Cabanas Castellet, Catalogne, Spain; b, side view of subcylindrical sponge with osculum at top and tubular surfaces and ostia exposed on side; c, side view of same specimen with ostia and tubes obscured with dermal cortex, ×0.5 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Brachiolites SMITH, 1848, p. 352 [\*B. fenestratus SMITH, 1848, p. 367; SD REID, 1958b, p. 263]. Normally columnar or globular, but sometimes aberrantly branched-tubular without anastomoses; free peripheral tubes widely open or contracted at ends; tube walls sometimes with small parietal perforations; dictyonal framework mainly regular but with irregular meshwork at dermal surface formed by secondary accretion or partly from primary structure; nodal octahedra solidified in meshwork of both surfaces; dermal side with distinct ostia or not; gastral side with meshwork formed by dictyonal strands and connecting beams only, or with meshwork masked locally by secondary accretion, and typically no distinct postica; peripheral meshwork absent. [Limited to type species by REID (1962, p. 34-35), other species placed elsewhere.] Lower Cretaceous (Albian): England.—FIG. 345,2. \*B. fenestratus, Chalk Marl and Upper Greensand, Cretaceous; enlargement of part of dermal surface showing distinctive, peripheral tubes and dictyonal framework of main skeleton, scale uncertain (Smith, 1848).
- Centrosia SCHRAMMEN, 1912, p. 301 [\*C. incrustans SCHRAMMEN, 1912, p. 302; OD]. Nodular or encrusting, with margins of tubes opening at surface joined by smaller, tubular bridges that here perforated walls or possibly also bowl shaped, with

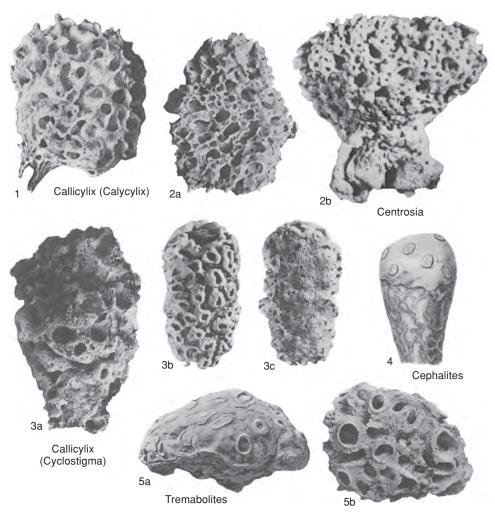


FIG. 344. Callodictyonidae (p. 523-525).

bridges on outside; dictyonal framework mainly regular, but meshwork becoming less regular and more dense at surfaces. *Cretaceous:* Spain, Germany.——FIG. 344,2*a.* \**C. incrustans*, Quadratenkreide, Cenomanian, Oberg, Germany; type sponge with two sizes of tubular openings, smaller of which bridge larger ones, approximately ×1 (Schrammen, 1912).——FIG. 344,2*b. C. regulate* LAGNEAU-HERENGER, Aptian, Can Cabanas Castellet, Catalogne, Spain; side view of bowl-shaped sponge with larger ostia to tubes and smaller pores between, ×1 (Lagneau-Hérenger, 1962).

Cephalites SMITH, 1848, p. 279 [\*C. perforatus SMITH, 1848, p. 294; SD RAUFF, 1893, p. 65]. Similar to *Tremabolites* ZITTEL, but forming narrow, erect column with capsular skeleton restricted to summit; supported by branching root processes that are formed from anastomosed, siliceous filaments. [Name formerly applied to Camerospongiidae here placed under *Stamnia* POMEL, 1872, *Rhytistamnia* POMEL, 1872, and *Toulminia* ZITTEL, that cannot be included in a genus with the type *C. perforatus.*] *Upper Cretaceous:* England.——FIG. 344,4. \**C. perforatus,* Chalk; side view of upper part of sponge with capsular summit, approximately ×0.5 (Smith, 1848).

Ceriodictyon OPPLIGER, 1907, p. 15 [\*C. ceniformis; M]. Conical mass of anastomosed, thin-walled tubes or lamella, whose connected margins form peripheral network; skeletal walls with nodal octahedra internally, solid nodes at surface. [Possibly identical with *Brachiolites* SMITH.] Upper Jurassic: Switzerland.——FIG. 345, *Ia-c.* \*C. ceniformis, Birmenstorfer beds, Mont Rivel; a, view from above of sponge composed of anastomosed, thin-walled tubes, ×0.5; b, side view of obconical sponge, ×1;

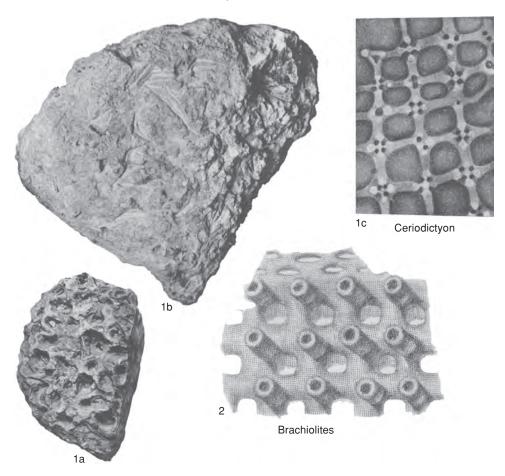


FIG. 345. Callodictyonidae (p. 523-525).

c, photomicrograph of skeleton with distinct, lychniscoid structure, approximately ×40 (Oppliger, 1907).

Tremabolites ZITTEL, 1877b, p. 55 [\*Manon megastoma F. A. ROEMER, 1840 in 1840-1841, p. 3; SD DE LAUBENFELS, 1955, p. 89] [=Pachychlaenia POMEL, 1872, p. 72, obj., senior objective synonym suppressed under Code Art. 23.2 (ICZN, 1999) as nom. oblit.]. Nodular or flattened, sometimes elongate, often convex above and flat below; upper surface covered by dense, rigid capsule that is pierced by oscula of tubes that open through it; each osculum usually with small but prominent rim; lower surface with apertures between divided and anastomosed tubes, and sometimes also parietal oscula in tube walls; these apertures sometimes denticulated by spinose, secondary outgrowths; internal tube walls with unmodified meshwork or accretion of secondary hexactines, which may form meshwork outlining ostia and postica. [Included by SCHRAMMEN (1912) in Camerospongiidae, but developed from sponges indistinguishable from

*Cyclostigma* species until the capsule is fully developed.] *Lower Cretaceous–Upper Cretaceous:* Europe; southern France, *Albian*; northern France, Germany, *Turonian–Maastrichtian.*—FIG. 344, *5a–b.* \**T. megastoma* (F. A. ROEMER), Mukronatenkreide-Quadratenkreide, Cenomanian, Misburg and Oberg, Germany; *a*, side view of flattened, nodular sponge with rigid, outer layer of skeleton pierced by oscula with low rims; *b*, side view of similar form but outer skeletal layer around oscula absent, ×0.5 (Schrammen, 1912).

#### Family COELOPTYCHIDAE F. A. Roemer, 1864

[nom. correct. ZITTEL, 1877b, p. 59, pro family Coeloptychidea F. A. ROEMER, 1864, p. 3]

Radially symmetrical, sometimes stalked Lychniscosa, with three-dimensional, skeletal meshwork and only intracortical canalization, in which an annular to hemispherical, peripheral skeleton truncates longitudinal plications of wall, or radiating tubes that arise from plications of an axial funnel; cortical modification by formation of cribiform lamella across individual meshes, or a continuous, finely porous, cortical membrane; membrane usually more or less restricted to exposed parts of dermal, skeletal surface; peripheral skeleton dense when fully formed, consisting of full-sized dictyonalia, additional smaller hexactines, and anastomosed, siliceous filaments; or skeleton also with seeming stauractines in parts; a sieve plate may cover upwardly facing plications, or line an axial funnel; basal skeleton fibrous. [Separation from Callodictyonidae is essentially arbitrary, based on specialization; possibly derived from forms similar to Spirolophia POMEL and Oncolpia POMEL.] Lower Cretaceous-Upper Cretaceous.

#### Subfamily COELOPTYCHINAE F. A. Roemer, 1864

[nom. transl. REID, herein, ex Coeloptychidae F. A. ROEMER, 1864, p. 3]

Coeloptychidae in which wall is plicated longitudinally, without formation of separate tubes in normal examples; peripheral skeleton annular; upper surface of plications covered by sieve plate formed from anastomosed, siliceous filaments. [Corresponds with family Coeloptychidae as restricted by ZITTEL (1877b, p. 39) and SCHRAMMEN (1912, p. 323).] Lower Cretaceous–Upper Cretaceous.

Coeloptychium GOLDFUSS, 1826, p. 31 [\*C. agaricoides; OD] [=Homoptychium POMEL, 1872, p. 69 (type, Coeloptychium deciminum F. A. ROEMER, 1840 in 1840-1841, p. 10, OD, type species only specifically distinct from *C. agaricoides* GOLDFUSS); Schizoptychium POMEL, 1872, p. 69 (type, Coeloptychium incisum F. A. ROEMER, 1840 in 1840-1841, p. 10, SD REID, herein, type species not generically distinguishable from C. agaricoides GOLDFUSS)]. Funnel or mushroom shaped, with wall plicated longitudinally above a tubular stalk; outwardly or downwardly facing folds forming simple or dichotomized ribs, pierced by series of parietal oscula; similar oscula may occur on stalk; peripheral skeleton continuously annular, or incised between folds from above or below; sieve plate usually continuous across upwardly or inwardly facing folds, but sometimes exposing them locally; with or

without dense, radial bands above covered folds; externally exposed surfaces of stalk and folded wall with finely porous, cortical covering, pierced by alternating or irregularly distributed ostia; cortical meshwork poorly developed or lacking on surfaces between folds and on gastral surface; accessory sieve plates may form transverse diaphragms within stalk. *Lower Cretaceous–Upper Cretaceous:* Germany.

- C. (Coeloptychium). Funnel to mushroom shaped; peripheral skeleton continuously annular except as irregularity. Lower Cretaceous-Upper Cretaceous (Campanian): Germany, Poland, Belgium England, Ireland.——FIG. 346,5. \*C. (C.) agaricoides, Lower Cretaceous, near Peine and Theidessen, Germany; mushroom-shaped sponge with furrowed gastral and lateral surface, prominent stalk, ×1 (Roemer, 1840–1841).
- C. (Lophoptychium) POMEL, 1872, p. 69 [\*Coeloptychium lobatum GOLDFUSS, 1829, p. 94; OD]. Mushroom shaped, but with a conical, central cavity lined by sieve plate; peripheral skeleton deeply incised from below, between downwardly facing folds. [Barely distinct from Coeloptychium s.s., but retained because of distinctive appearance of the type species.] Cretaceous (Coniacian-Maastrichtian): Germany.—FIG. 346, 1. \*C. (L.) lobatum (GOLDFUSS), near Coesfeld; diagonal view of complete, lobate sponge, with broad, funnel-shaped spongocoel, ×1 (Goldfuss, 1833).
- C. (Myrmecioptychium) SCHRAMMEN, 1912, p. 333 [\**M. bodei;* OD]. Similar to *Coeloptychium s.s.*, but with short, open outgrowths along downwardly facing folds instead of simple, parietal oscula. [Separation barely justified; may be based on individuals of a normal *Coeloptychium* species. No known suitable figures.] Upper Cretaceous: Germany, Poland, Russia.
- Troegerella ULBRICH, 1974, p. 69 [\*T. subherzynica; OD]. Sponge body whisklike with thin-walled, slender, funnel-like, axial part and nine radially arranged, bladelike expansions closely spaced under funnel edge; expansions hollow with oval or round parietal oscula on their narrow sides; placement of ostia, postica, epi- and aporhyses corresponding to broad, regular, skeletal meshes; subgastral cavities in lower part of funnel and in radial expansions are separated from spongocoel in upper part of funnel by a sieve plate; skeleton as in Coeloptychium. Cretaceous (Campanian): Germany.-FIG. 346,3a-b. \*T. subherzynica, Ilsenburmergel, Stapelburg; a, side view of holotype showing digitate form and broad spongocoel with coarse, exhalant ostia in gastral surface; b, view of same from above, SSSBGF 210/ 751, ×0.5 (Ulbrich, 1974).

#### Subfamily CAMEROPTYCHINAE new subfamily

[Cameroptychinae REID, herein] [type genus, Cameroptychium LEONHARD, 1897, p. 37]

Coeloptychidae in which radiating, separate or anastomosing tubes arise from

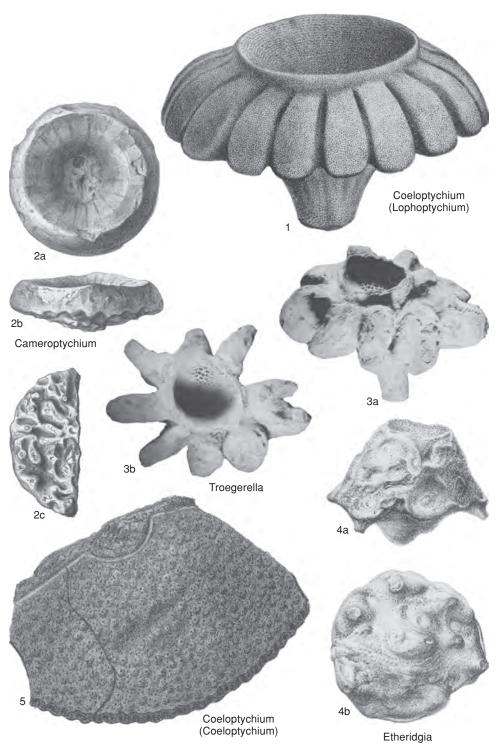


FIG. 346. Coeloptychidae (p. 526–528).

plications of axial funnel; peripheral skeleton annular to hemispherical, truncating tubes, and also attached to margin of axial funnel; underside with exposed surfaces of lowermost tubes, between which are apertures leading into dermally lined cavaedia; sieve plate lining axial funnel or absent. [Includes Coeloptychidae placed by SCHRAMMEN (1912) and others in Camerospongiidae SCHRAMMEN; here regarded as deriving from Callodictyonidae (probably Becksinae) near source of Coeloptychinae, to which Cameroptychinae are basically similar in habitus.] *Upper Cretaceous.* 

- Cameroptychium LEONHARD, 1897, p. 37 [\*C. patella; M] [=?Solenothyia POMEL, 1872, p. 68 (type, Camerospongia schloenbachi F. A. ROEMER, 1864, p. 5, OD); type species seems to be a Cameroptychium; was basis of ZITTEL's (1877b) diagnosis of Camerospongia D'ORBIGNY, with which Cameroptychium was confused; suppressed under Code Art. 23.2 (ICZN, 1999) as nom. oblit.]. Discoidal to hemispherical, with small, central stalk and wide to deep and narrow, central cavity that is lined by sieve plate; exposed tubes of underside simply dichotomise or divide and anastomose, with parietal oscula or none; peripheral skeleton entire, or perforated opposite ends of underlying tubes; stalk and tubes of underside with finely porous, cortical covering, which may close parietal oscula, or form spines that project across spaces between tubes; sieve plate formed from adventitious lychniscs, which unite to form a layer of regularly quadratic meshwork, with beams oriented longitudinally and transversely. Upper Cretaceous: Europe.-FIG. 346,2a-c. \*C. patella, Upper Cretaceous beds, Turonian, Oppeln, Germany; a, view onto gastral surface of broad, central cavity, with regular skeletal net, from above; b, view from side; c, view of dermal surface with exposed, branching tubes, from below, ×0.5 (Leonhard, 1897).
- Etheridgia TATE, 1865, p. 42 [\*E. mirabilis TATE, 1865, p. 43; OD]. Truncated-conical to hemispherical, with narrow, central cavity and no stalk in most individuals; tubes of underside usually broad, once dichotomous, not united except at periphery; peripheral skeleton incomplete, with apertures at opposite ends of underlying tubes, or additional sinuous clefts that extend between them; exposed parts of tubes of underside with finely porous, cortical covering, which grows out locally to form spinelike root processes; no sieve plate. Cretaceous (Coniacian-Maastrichtian): England. -FIG. 346, 4a-b. \*E. mirabilis, Upper Chalk, Island Magee, Whitehead and Woodburn; a, side view of holotype showing osculum to deep spongocoel and rootlike attachments; b, view of base with upper parts of rootlike processes, ×1 (Tate, 1865).

#### Family VENTRICULITIDAE Smith, 1848

## [nom. correct. ZITTEL, 1877b, p. 36, pro Ventriculidae SMITH, 1848, p. 203]

Lychniscosa with initially threedimensional, dictyonal frameworks, not constructed in layers, and with fully developed, intradictyonal epirhyses and aporhyses, unless epirhyses are replaced by superficial furrows; marginal surfaces not covered by a siliceous membrane; epirhyses and aporhyses sometimes separate tubular, radial cavities, arranged alternately in longitudinal series, and in alternate positions in adjacent series; their apertures quincuncially alternate correspondingly; other forms have different conditions, in which similar cavities intercommunicate or form labyrinths, epirhyses lack regular arrangement or occur between series of aporhyses, or surfaces have superficial furrows that may replace epirhyses; dermal surface of dictyonal framework usually formed by finely porous, cortical layer, produced by modification of outermost dictyonalia and usually pierced by small, accessory, intracortical ostia; cortex may be equally developed on gastral side, or less developed, or absent; superficial meshwork often present, formed by siliceous filaments that grew from distal rays of dictyonalia at surface of dictyonal framework, or rarely from adventitious, dictyonal hexactines; basal skeleton constructed in same way as superficial meshwork and forming branching roots where it consists of siliceous fibers; sometimes canalized by longitudinal canals that run downwardly from positions of covered ostia; loose spicules unknown. Jurassic–Upper Cretaceous.

This family is interpreted more broadly than by SCHRAMMEN (1912) to take in all genera with diplorhytic canalization that is plainly intradictyonal, but the interpretation excludes the Pachyteichismatidae included by ZITTEL (1877b) and DE LAUBENFELS (1955). The skeletal canals do not result from plication of the wall, as claimed by many authors (e.g., ZITTEL, 1877b; SCHRAMMEN, 1912) for some of the genera included (e.g., *Ventriculites* MANTELL, *Rhizopoterion* ZITTEL); in early ontogeny, they arise by progressive differentiation from small, intracortical ostia, identical with those that persist in the adult. Furrowing seen in some genera represents subdermal or subgastral channeling of the dictyonal surface, or sometimes coalescence of series of radial epirhyses.

#### Subfamily VENTRICULITINAE Smith, 1848

[nom. transl. REID, herein, ex Ventriculitidae SMITH, 1848, p. 203]

Typical Ventriculitidae, with epirhyses and aporhyses or their ostia and postica in regular series or not, or with epirhyses or aporhyses more or less replaced by deep, external furrows; superficial structures and basal skeleton formed from anaxial, siliceous outgrowths. *Jurassic–Upper Cretaceous*.

Ventriculites MANTELL, 1822, p. 168 [\*Alcyonium chonoides MANTELL, 1815, p. 402; OD; =Ventriculites radiatus MANTELL, 1822, p. 168, SD POMEL, 1872, p. 89] [=Ocellarioscyphia DE FROMENTEL, 1860a, p. 40 (type, Ventriculites radiatus MANTELL, 1822, p. 168, SD DE LAUBEN-FELS, 1955, p. 106, =Alcyonium chonoides MANTELL, 1815, p. 402); Stelgis POMEL, 1872, p. 149 (type, Ventriculites radiatus MANTELL, 1822, p. 168), which POMEL (1872) changed to Stelgis mantelli for some unknown reason; Cladostelgis POMEL, 1872, p. 150 (type, Verrucospongia damoecornis ROEMER, 1864, p. 45); Pleurostelgis POMEL, 1872, p. 150 (type, Manon miliare REUSS, 1846 in 1845-1846, p. 78)]. Funnel shaped or tonguelike, or with other variants of these shapes; dermal surface variable, typically sculptured to produce alternating tubercles or longitudinal ribs, or combinations of these features: epirhyses open in floors of intervening furrows, in quincunx or not, or more or less obsolete; alternatively surface is sometimes reticulate in aspect, with varying proportions of alternating, simple epirhyses and longitudinal furrows, produced by merger of series of epirhyses; gastral surface with alternating postica of aporhyses, not furrowed; finely porous, dictyonal cortex on dermal side, or both sides; superficial filaments poorly developed or conspicuous on dermal side, where they arch between tubercles or ribs. [Variable (tuberculate, costate, reticulate) development of dermal, skeletal surface is characteristic of the type V. chonoides, of which differently developed individuals have been called V. radiatus MANTELL, V. mammillaris SMITH, and V. decurrens SMITH).] Upper Cretaceous: Europe.-FIG. 347,1a-c. V. striatus SMITH, Germany; a, side view of steeply funnelshaped sponge,  $\times 0.5$ ; *b*, transverse section showing alternating epirhyses and aporhyses; ×1; c, part of skeleton showing lychniscoid structure, ×12 (de Laubenfels, 1955).

- Astropegma POMEL, 1872, p. 84 [\*Ventriculites stellata ROEMER, 1864, p. 18; SD DE LAUBENFELS, 1955, p. 87]. Cup shaped, with thick walls of angular, irregular, lychniscoid mesh; openings grouped into starlike clusters. [Questionably included in the subfamily and family.] Lower Cretaceous: Algeria, Germany.—FIG. 348,3a-b. A. stellata (ROEMER), Peine, Germany; a, thick-walled, cuplike sponge with characteristic starlike, skeletal mesh of outer wall, ×1; b, enlarged section of wall showing finetextured, lychniscoid, skeletal mesh of tracts, approximately ×5 (Roemer, 1840–1841).
- Coscinopora GOLDFUSS, 1826, p. 30 [\*C. infundibuliformis; OD] [=Coscinoscyphia DE FROMENTEL, 1860a, p. 38, obj.; Coccinopora SCHLÜTER, 1870, p. 141, obj.]. Funnel-like or in variants of this shape, with or without stalk; epirhyses and aporhyses radial, separate, closely spaced, arranged alternately in regular, longitudinal series, and in alternate positions in adjacent series; ostia and postica correspondingly quincuncially alternating; ostia round or rhomboidal; postica ovate, elongate longitudinally; finely porous, dictyonal cortex well developed on dermal side, with incorporated dictyonalia lacking distal rays and nodal octahedra; less developed or absent on gastral side where cortical dictyonalia have freely projecting, distal rays that are spines in pinular manner; many lychnisc octahedra solidified in internal meshwork; no superficial meshwork, except where siliceous fibers of basal skeleton coat lower parts. [Difficult to distinguish from some forms of Sporadoscinia POMEL (S. alcyonoides MANTELL) unless skeletal details are preserved. According to SCHRAMMEN (1912, p. 292-293) cortical dictyonalia are sometimes reduced to stauractines.] Upper Cretaceous: Europe.—FIG. 347,4a-b. \*C. infundibuliformis, Quadratenkreide, Cenomanian, Oberg, Germany; a, finely porous, outer, dictyonal cortex seen from inside, with lychniscs and coarser, inhalant ostia; b, upper surface of gastral layer with dictyonalia with projecting, distal, pinular rays, ×45 (Schrammen, 1912).
- Etalloniella OPPLIGER, 1926, p. 35 [\*Étallonia idanensis OPPLIGER, 1915, p. 55; OD]. Cup shaped or broadly obconical to cylindrical with a broad spongocoel, walls thin and lacking differentiated outer layers; dermal surface with numerous small, round to pointed, conical nodes that separate branched furrows, in which occur numerous fine ostia of epirhysal, radial canals that extend straight or slanting to middle of wall and there end blindly, as part of diplorhysal canal system; small postica of aporhysal canals occur scattered in gastral surface; skeleton is regular, fine, lychniscoid meshwork with octahedral lanterns at ray junctions. Jurassic: Europe.—FIG. 347,2a-c. \*E. idanensis (OPPLIGER), Weiss Jura, Upper Jurassic, La Latte near Nantes, France; a, side view of cylindrical fragment with characteristic dermal nodes; b, broad, funnelshaped sponge with stalk and broad, oscular depression, ×1; c, photomicrograph showing lychniscoid skeletal structure, ×50 (Oppliger, 1915).
- Flabellispongia TREST'YAN, 1972, p. 35 [174] [\*F. bicostata; OD]. Leaf-shaped to lamellar or lobate,

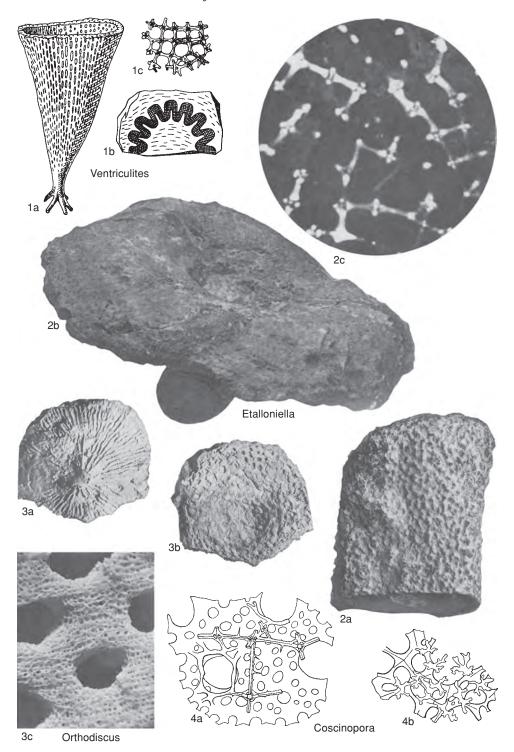


FIG. 347. Ventriculitidae (p. 529-532).

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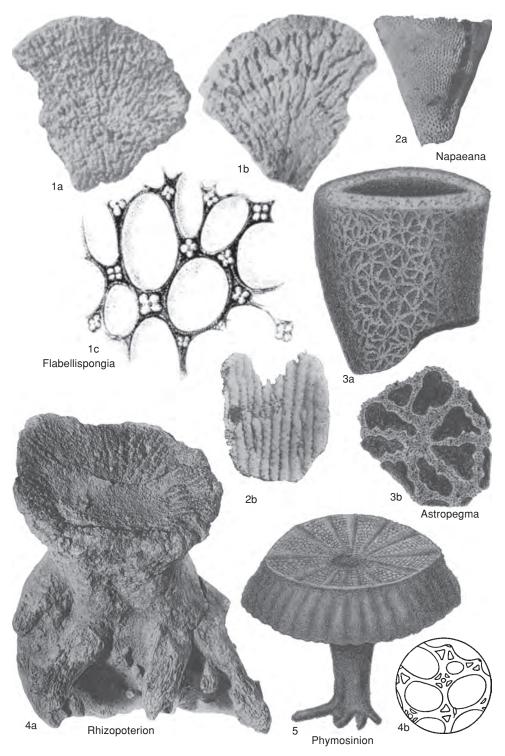


FIG. 348. Ventriculitidae (p. 529-534).

vertically growing, solitary sponges with flat body walls, commonly curved or with flexures and both sides of wall with grooves alternating with ridges; canal system radial with both inhalant and exhalant canals terminating blindly in wall; skeleton lychniscoid with perforated nodes; basal layer with regular structure and both dermal and gastral layers with well-developed cortex of irregular structure. *Cretaceous (Cenomanian):* Russia (middle Dniester region, Moldavia and Ukraine).——FiG. 348,1*a*–*c*. \**F. bicostata*, upper Cenomanian, Naslavcha village, Moldavia; *a*, dermal side of fan-shaped fragment; *b*, gastral side of same, ×1; *c*, photomicrograph showing lychniscoid structure in basal skeleton, ×40 (Trest'yan, 1972).

- ?Leiostracosia SCHRAMMEN, 1902, p. 12 [\*L. punctata; OD] [?=Pachylepisma SCHRAMMEN, 1902, p. 14 (type, P. robusta, M)]. Funnel-like or with variants of this shape, stalked; ostia and epirhyses arranged without order or in longitudinal series between series of aporhyses, sometimes more or less quadratically when in series; aporhyses in regular, longitudinal series, sometimes also grouped quadratically; postica in longitudinal furrows; finely porous, dictyonal cortex on dermal side only; superficial outgrowths short spines on dermal side, denticulate outlines of ostia; forming branching and anastomosing filaments on gastral side. Cretaceous (Barremian-Maastrichtian): France, Barremian-Santonian; Germany, Turonian-Maastrichtian; Europe, Coniacian-Maastrichtian.-FIG. 349, 1a-b. \*L. punctata, Quadratenkreide, Cenomanian, Misburg and Oberg, Germany; a, funnel-like sponge from above with radiating structure where aporhyses are arranged in rows on gastral surface; b, side view of cylindrical stalk with vertical rows of epirhyses, ×0.5 (Schrammen, 1912).-–Fig. 349,1c. L. brandesi SCHRAMMEN, Quadratenkreide, Cenomanian, Oberg, Germany; side view of subcylindrical sponge with irregular, inhalant epirhyses in upper part, but more regular aporhyses on gastral surface of lower spongocoel visible in broken base, ×0.5 (Schrammen, 1912).--Fig. 349,1d. L. robusta SCHRAMMEN, Quadratenkreide, Cenomanian, Misburg, Germany; side view of globular sponge with irregular epirhyses, ×0.5 (Schrammen, 1912).
- Lepidospongia F. A. ROEMER, 1864, p. 9 [\*L. denticulata; OD] [=Plectodermatium SCHRAMMEN, 1902, p. 12 (type, P. fragilis, OD)]. Funnel-like in variants of this shape, or sometimes flabellate; often stalked; strong roots; dermal surface with ostia of epirhyses in longitudinal furrows, between which surface forms regularly bifurcated ribs; aporhyses in longitudinal series, run into ribs of dermal side, not opening in furrows; finely porous, dictyonal cortex on dermal side only or on both sides; superficial filaments of dermal side may arch over furrows; filaments of gastral side form paratangential network, parts of which develop into quadrately arranged, scalelike plates or continuous, transverse bands of finely porous, siliceous material; postica hidden when these structures are fully developed; roots may

be canalized as in *Rhizopoterion* ZITTEL. *Cretaceous* (*Coniacian–Maastrichtian*): Germany, Poland, ?France.——FIG. 349,5*a–b. L. fragilis* (SCHRAM-MEN), Quadratenkreide, Campanian, Misburg, Germany; *a*, dermal surface of funnel-like fragment with radial ribs, ×1; *b*, gastral surface with quadrately arranged plates, ×1 (Schrammen, 1902).

- Licmosinion POMEL, 1872, p. 89 [\*L. cymoria; OD]. Tonguelike, leaflike, or forming convoluted plate; both surfaces with alternating or irregularly distributed apertures of short, radial, skeletal canals that are presumably epirhyses on one side and aporhyses on other; both surfaces with finely porous, dictyonal cortex, with small, intracortical ostia or postica between large apertures. [No known suitable figures.] Lower Cretaceous: Algeria.
- Napaeana DE LAUBENFELS, 1955, p. 87, nom. nov. pro Eudictyon SCHRAMMEN, 1902, p. 15, non MARSHALL, 1875b, nec BISTRAM, 1903, p. 84 [\*Eudictyon striatum SCHRAMMEN, 1902, p. 15; OD] [=Napaea SCHRAMMEN, 1912, p. 273, obj., non ROBINEAU-DESVOIDY, 1830]. Funnel-like, thin walled, stalked; epirhyses and aporhyses regularly alternating in longitudinal series and in adjacent series with ostia and postica quincuncially alternating correspondingly; ostia sometimes in shallow, longitudinal furrows; aporhyses may then also open by small, accessory pores between successive ostia; finely porous, dictyonal cortex on both skeletal surfaces; superficial filaments of gastral side form paratangential network, parts of which develop into scalelike plates or longitudinal bands of finely porous, siliceous material; postica hidden when these structures fully developed. Cretaceous (Coniacian-Maastrichtian): Germany.—FIG. 348,2*a*-*b*. \*N. striata (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg; a, side view of upper, funnel-like part of sponge with regularly spaced ostia; b, gastral surface with longitudinal bands between small postica, ×1 (Schrammen, 1912).
- Orthodiscus SCHRAMMEN, 1924a, p. 25 [\*O. fragilis SCHRAMMEN, 1924a, p. 26; OD]. Discoidal or umbrella-like, stalked, with small, central cavity or not; dermal (=lower) surface with deep, longitudinal furrows between which occur bifurcating ribs; small ostia may be present along floors of these furrows; epirhyses more or less obsolete; gastral (=upper) surface not furrowed; postica large, arranged without order or alternately; aporhyses run into ribs of dermal side; dictyonal cortex on both surfaces; superficial filaments may form network on gastral side. [Possibly only an extreme form of Ventriculites MANTELL.] ?Lower Cretaceous, Upper Cretaceous: Germany, France, Poland.—FIG. 347, 3a-c. \*O. fragilis, Mukronatenkreide, Cenomanian, Misburg, Germany; a, discoidal sponge from below with strong, radial ridges; b, discoidal sponge from above with large postica, ×0.5; c, skeletal net of fragment of upper side, ×4 (Schrammen, 1924a; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Phymosinion POMEL, 1872, p. 89 [\*Coeloptychium muricatum F. A. ROEMER, 1840 in 1840–1841, p. 11; OD]. Bowl shaped or discoidal, with small,

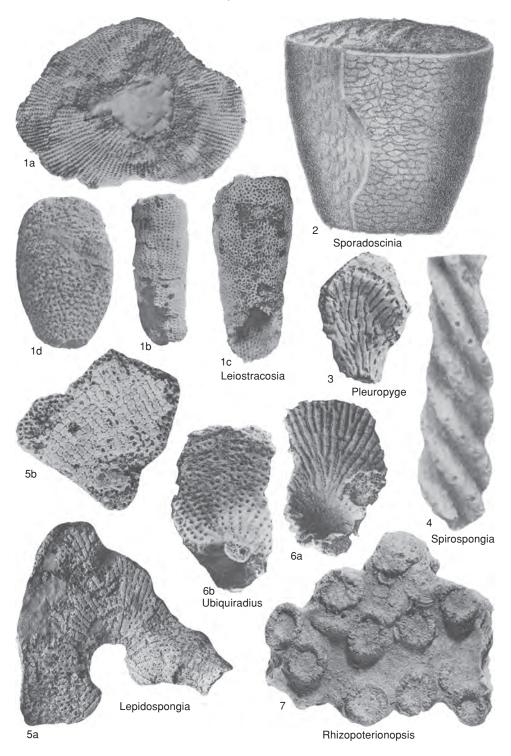


FIG. 349. Ventriculitidae (p. 532-535).

central stalk; dermal surface with ostia of simple epirhyses, arranged alternately or in rough, longitudinal series, and correspondingly arranged, perforated tubercles; gastral side with alternating postica arranged in longitudinal series, along which surface is usually furrowed longitudinally; aporhyses simple, run into tubercles of dermal side, at tops of which they open through small, accessory pores; finely porous, dictyonal cortex on dermal side, less developed or absent on gastral side; no distinct, superficial meshwork. *Upper Cretaceous:* Europe. ——FIG. 348,5. \*P. muricatum (ROEMER), Plänerkalke, Turonian, Alfeld, Germany; gastral surface with tubercles perforated with aporhyses, ×1 (Roemer, 1840–1841).

- Pleuropyge SCHRAMMEN, 1912, p. 274 [\*P. plana; OD]. Bilaterally compressed above a stalk, with parietal oscula or short, open outgrowths along narrow margins; broad sides with irregularly alternating, longitudinal furrows, in floors of which may be ovate or slitlike ostia of short epirhyses; gastral side not furrowed, but with irregularly alternating postica; finely porous cortex on dermal side; incompletely known. [Character of inside from WAGNER (1963, p. 215).] Cretaceous (Turonian-Maastrichian): Germany.——Fig. 349,3. \*P. plana, Quadratenkreide, Cenomanian, Oberg; side view of small, laterally flattened sponge with furrowed, dermal surface and parietal oscula along upper margin, ×1 (Schrammen, 1912).
- Rhizopoterion ZITTEL, 1877b, p. 51 [\*Siphonia cervicornis GOLDFUSS, 1826, p. 18; OD] [=Rhizocheton LACHASSE, 1943, p. 53 (type, Rhizocheton jacobi LACHASSE, 1943, p. 55; OD); ?Retispongia D'ORBIGNY, 1849, p. 547 (type, Scyphia oeynhausii GOLDFUSS, 1831, p. 219; ?Retiscyphia DE FROMENTEL, 1860a, p. 41 (type, Scyphia oeynhausii GOLDFUSS, 1831, p. 219)]. Hollow-cylindrical to funnel-like, or in variants of these shapes, stalked or not, often with massive roots; epirhyses and aporhyses simple, regularly alternating in longitudinal series and in adjacent series, or modified by intercommunication between cavities of same sort and sometimes wholly labyrinthine; ostia alternating in longitudinal series irrespective of internal modifications; sometimes in longitudinal furrows, between which surface forms bifurcate ribs; postica alternating regularly or more or less irregularly; finely porous, dictyonal cortex usually present on both skeletal surfaces; superficial filaments may occur on either side, denticulate outlines of ostia or arch over them, developed similarly on gastral side or form paratangential network above skeletal surface; root often strongly canalized with numerous tubular canals that run downwardly from ostia, which are covered by basal meshwork. [Type species poorly known; probably identical with R. cribrosum (PHILLIPS, 1829 in 1829-1836). Characterization by SCHRAMMEN (1912, p. 271) reflects confusion with Ventriculites MANTELL, due to misidentification of R. cribrosum as V. radiatus MANTELL, as for example by SCRAMMEN (1912, p. 265). Rhizocheton based on a typical Rhizopoterion; proposed because

Rhizopoterion cervicornia (GOLDFUSS) is incompletely known, but not otherwise justified. *Retispongia* exterior as in *Rhizopoterion* species, but inside supposedly without canalar features; this diagnosis based on a figure only; type species identified with *Ventriculites radiatus* MANTELL by GOLDFUSS (1826, p. 16) and others (e.g., SCHRAMMEN, 1912, p. 265) applying that name to *Rhizopoterion cribrosum* (PHILLIPS).] *Cretaceous* (*Albian-Maastrichtian*): Europe.——FIG. 348,4*a-b. R. jacobi* (LACHASSE), upper Campanian, Charentes, France; *a*, side view of funnel-shaped sponge, UPLGS, ×1; *b*, drawing of lychniscoid, skeletal structure, ×100 (Lachasse, 1943; courtesy of Société Géologique de France).

- Rhizopoterionopsis LACHASSE, 1943, p. 51 [\*R. caillauense LACHASSE, 1943, p. 52; OD]. Compound, with multiple funnels arising from a common, branching stock; other characters as in simple forms of Rhizopoterion ZITTEL. Cretaceous (Coniacian–Maastrichtian): France.——FiG. 349,7. \*R. caillauense, upper Campanian, Charentes, France; view from above of branched structure, UPLGS, ×0.50 (Lachasse, 1943; courtesy of Société Géologique de France).
- Spirospongia KRAVTSOV, 1968, p. 124 [401] [\*S. krymica; OD]. Small, solitary sponge with dermal surface marked by three or four, upwardly spiraled, ridgelike folds, the crests of which are perforated by spiral row of large, circular, inhalant ostia to canals that apparently empty into narrow, petalloid, central spongocoel; skeleton lychniscoid in fine lattice, with perforated, nodal expansions. Cretaceous (Maastrichtian): Russia (Crimea).——FIG. 349,4. \*S. krymica, Maastrichtian sandy marl, Bel'bek River; side view of spiraled holotype showing dermal ridges with large, inhalant ostia on their crests, LGI 280/1, ×1 (Kravtsov, 1968).
- Sporadoscinia POMEL, 1872, p. 84 [\*Scyphia retiformis F. A. ROEMER, 1840 in 1840-1841, p. 7; SD RAUFF, 1893, p. 66; =Scyphia decheni GOLDFUSS, 1831, p. 219]. Hollow, cylindrical to funnel-like, or in variants of these shapes; epirhyses and aporhyses radial, separate, or interconnected by tangential passages between cavities of same sort; epirhyses sometimes alternating in series with aporhyses, as in Coscinopora GOLDFUSS, but typically more numerous and arranged without order, in hexagonal groups, in longitudinal series between series of aporhyses, or more or less quadratically; their arrangement sometimes varies through two or more of these conditions; ostia arranged correspondingly, and round, triangular, quadrate, polygonal, irregular, or transversely ovate or slitlike; aporhyses regularly alternating in longitudinal series irrespective of epirhytic variations; postica ovate, elongate longitudinally; finely porous, dictyonal cortex with small, intracortical ostia on both skeletal surfaces; superficial outgrowths absent, inconspicuous, or prominent, sometimes denticulating outlines of ostia or arching over them, or forming paratangential network on gastral side; longitudinal furrowing along series of ostia or postica may occur in oldest

parts, although not typical of genus. *Lower Cretaceous–Upper Cretaceous:* France, Germany, England, Poland; Spain, *Albian.*—FIG. 349,2. \**S. decheni* (GOLDFUSS), Lower Cretaceous, near Peine, Germany; side view of sculptured, cup-shaped sponge with fine, outer pores and elongate pores in gastral surface, ×1 (Roemer, 1841).

Ubiquiradius DE LAUBENFELS, 1955, p. 81 [\*Actinocyclus mirus SCHRAMMEN, 1912, p. 277; OD] [=Actinocyclus SCHRAMMEN, 1912, p. 277 (type, Coeloptychium alternans F. A. ROEMER, 1840 in 1840-1841, p. 10, OD), non EHRENBURG, 1831; Porocyclus Defretin-Lefranc, 1961, p. 69, obj.]. Similar to to Leiostracosia SCHRAMMEN, but with aporhyses more or less replaced by deep, superficial furrows; stalked, widely funnel-like to umbrella shaped with convex, gastral surface; ostia and epirhyses in longitudinal series, sometimes also grouped quadrately; gastral surface deeply furrowed longitudinally, with postica along floors of furrows; epirhyses run into ribs between furrows of gastral side; aporhyses more or less obsolete; finely porous, dictyonal cortex on both skeletal surfaces; superficial outgrowths mainly on dermal side, where filaments may denticulate or arch over ostia. [Named (DE LAUBENFELS, 1955, p. 81) as nom. nov. pro Actinocyclus SCHRAMMEN, 1912, non EHREN-BURG, 1831, but type species of Actinocyclus SCHRAMMEN is Coeloptychium alternans F. A. ROEMER, 1841 in 1840-1841, p. 10 (OD, SCHRAMMEN, 1912, p. 276).] Cretaceous (Coniacian-Maastrichtian): Germany.-FIG 349,6a-b. \*U. mirus (SCHRAMMEN), Quadratenkreide, Cenomanian, Oberg; a, side view of gastral surface with ostia in furrows between ribs; b, dermal surface with rows of inhalant ostia in fine-textured, skeletal structure, ×1 (Schrammen, 1912).

#### Subfamily BOLITESIINAE Schrammen, 1912

[nom. transl. et correct. REID, herein, ex Bolitesidae Schrammen, 1912, p. 197]

Specialized Ventriculitidae with very wide epirhyses and aporhyses, arranged alternately in regular series; epirhyses open through both skeletal surfaces; skeletal meshes filled by networks of anastomosing, siliceous filaments; epirhyses and aporhyses also intercommunicate through small pores in intercanalar partitions. [Made a separate family by SCHRAMMEN (1912, p. 334); but arrangement of canals is of the regular ventriculitid type, as seen for example in Rhizopoterion cribrosum (PHILLIPS), Sporadoscinia alcyonoides (MANTELL); and anastomosing internal filaments correspond with typical, ventriculitid, superficial filaments.] Cretaceous (Coniacian–Maastrichtian).

Bolitesia SCHRAMMEN, 1912, p. 335 [\*B. mirabilis; OD]. Flabellate; base unknown; dermal side with quincuncially alternating ostia of wide epirhyses that run obliquely through wall to gastral side; gastral side with quadrately arranged apertures, which are alternately internal openings of epirhyses and postica of aporhyses that end blindly under dermal surface; dictyonal cortex on both surfaces, not strongly differentiated. *Cretaceous (Coniacian– Maastrichtian):* Germany.—FiG. 350, *Ia–b.* \*B. mirabilis, Quadratenkreide, Cenomanian, Oberg; a, dermal surface of fragment with wide ostia of epirhyses, ×1; b, photomicrograph of skeletal structure of upper surface, ×40 (Schrammen, 1912).

#### Subfamily STAURONEMATINAE Sollas, 1877

[nom. transl. REID, herein, ex Stauronematidae WAGNER, 1963, p. 219, nom. correct. pro Stauronemata SOLLAS, 1877b, p. 23]

Ventriculitidae with tubular, radial epirhyses and aporhyses arranged alternately in longitudinal series and in adjacent series, and with superficial or basal meshwork formed mainly or entirely from dictyonal hexactines. [Interpreted as a small stock diverging from the same source as Ventriculitinae, but distinguished by the spicular character of superficial structures; perhaps most similar to *Coscinopora* GOLDFUSS of Ventriculitinae.] *Lower Cretaceous (Albian)– Upper Cretaceous (Turonian).* 

Stauronema SOLLAS, 1877b, p. 23 [\*S. carteri; OD]. Tongue shaped to triangular and saddle shaped, with small stalk in some individuals, or discoidal following continued growth of broken examples; skeletal framework initially without superficial meshwork, but becoming densely coated on convex (possibly dermal) side by superficial meshwork up to several times thicker; this surface with transverse corrugations or concentric corrugations in discoidal individuals; other primary surface exposed, with regularly alternating, round or ovate apertures of skeletal canals, or concealed by a thin, superficial cover; main superficial mass formed from irregularly oriented, dictyonal hexactines, with or without nodal octahedra, and other beams arising as siliceous outgrowths; this meshwork usually canalized by irregular network of fine, branching and anastomosing canals; surface with cover of fine, branching spinules, and irregular, scattered, small pores through which canal network opens; under this meshwork, or exposed on this side if meshwork absent, round, regularly alternating apertures of radial canals of primary framework; latter mainly regular internally, with nodal octahedra often solidified except in young examples; concave (possibly gastral) dictyonal surface with well-developed, dense cortex; superficial meshwork of this side formed by branched and anastomosed spinules on

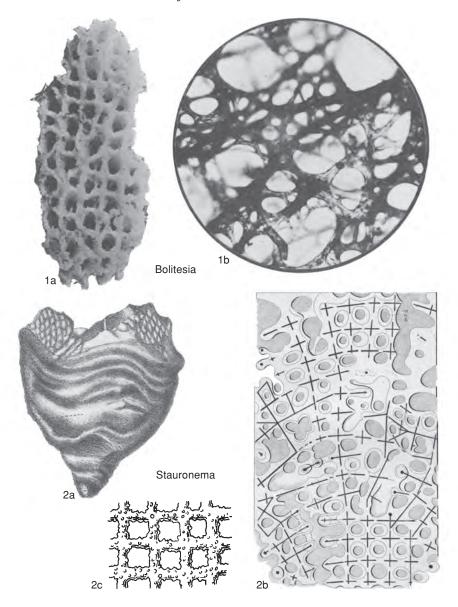


FIG. 350. Ventriculitidae (p. 535-536).

beams at surface, or also containing scattered, paratangential lychniscs. *Lower Cretaceous (Albian)–Upper Cretaceous (Turonian):* Great Britain.——FiG. 350,2*a–c.* \**S. carteri*, Cambridge Upper Greensand, Lower Cretaceous, Folkestone; *a*, side or posterior view of average-sized specimen, with dense mass, below, and oscular plate, above, ×1; *b*, skeletal network of oscular plate with casts of sexiradiate spicules filled with iron pyrite; longitudinal strands vertical and transverse strands more or less horizontal, ×20 (Sollas, 1877b) ; *c*, part of endosomal skeleton with cubical cribwork and thickened rays,  $\times 1$  (de Laubenfels, 1955).

# Subfamily LYCHNISCAULINAE new subfamily

[Lychniscaulinae REID, herein] [type genus, *Lychniscaulus* SCHRAMMEN, 1937, p. 18]

Early Ventriculitidae with epirhyses and aporhyses in alternating, longitudinal series

when in any regular arrangement; without finely porous, cortical coverings or basal or superficial meshwork formed from anaxial, siliceous outgrowths. [Relationship to later forms uncertain, but arrangement of skeletal canals in the type genus *Lychniscaulus* 

SCHRAMMEN is matched in *Leiostracosia* SCHRAMMEN (*Upper Cretaceous*) of Ventriculitinae]. *Upper Jurassic*.

- Lychniscaulus Schrammen, 1937, p. 18 (Schrammen, 1936, p. 180, nom. nud.) [\*L. vannus; OD]. Cylindrical, thick walled, with a deep, narrow, paragastral cavity; dermal side with round ostia of epirhyses, arranged in longitudinal series and more or less quadratically; gastral side with elongate postica arranged similarly; skeletal meshwork regular internally but forming denser and irregular, meshed cortex on dermal side; no superficial structures. Upper Jurassic: Germany.—FIG. 351, 1a-b. \*L. vannus, Weiss Jura, Streitberg; a, side view showing relatively coarse canals regularly arranged in steeply obconical sponge, ×1 (Schrammen, 1936); b, enlargement of outer surface with inhalant ostia in rows through regular, skeletal meshwork, ×5 (Schrammen, 1937).
- Discophyma Oppliger, 1915, p. 43 [\*Stauroderma etalloni Oppliger, 1907, p. 11; SD de Laubenfels, 1955, p. 90] [=Placotelia Oppliger, 1907, p. 13 (type, P. marcoui OPPLIGER, 1907, p. 14, SD REID, herein, ?= Porostoma marginata DE FROMENTEL, 1860a, p. 43, =P. marconi DE LAUBENFELS, 1955, p. 91, nom. null.]. Funnel-like, initially narrow, then widely expanded; upper surface and underside sometimes with concentric corrugations; ostia and postica in rough, longitudinal series, or in concentric rows that may follow corrugations; postica in longitudinal furrows in narrow part or generally; skeletal canals simple, blind, or with fine, lateral branches from simple, main trunks; skeleton more or less irregular, with nodal octahedra absent in parts. [Known only from poorly calcified material. Identity of Placotelia with Discophyma OPPLIGER recognized by OPPLIGER (1926, p. 22), but name Discophyma adopted. Not available under Code Art. 23.2 (ICZN, 1999), as nom. oblit.] Upper Jurassic: Switzerland, France, Poland.—FIG. 351,2a-b. \*D. etalloni (OPPLIGER), Weiss Jura, Andelot, Zürich, Switzerland; a, upper, gastral surface with postica in radial grooves; b, lower or dermal surface with irregularly distributed to obscurely concentric placed inhalant ostia, ×0.25 (Oppliger, 1915).-FIG. 351,2c. D. laciniatum OPPLIGER, Wangenerschichten, Baden, Switzerland; view from above of broad, thin-walled, funnel-shaped sponge with radially ridged, gastral surface perforated by coarse, exhalant ostia, ×0.25 (Oppliger, 1926).—FIG. 351,2d. D. cribratum OPPLIGER, Wangenerschichten, Baden, Switzerland; view into funnelshaped, thin-walled, discoidal sponge with concentric rings of moderately fine, exhalant ostia, ×0.25 (Oppliger, 1926).

#### Family CAMEROSPONGIIDAE Schrammen, 1912

[Camerospongiidae SCHRAMMEN, 1912, p. 312]

Ventriculitid-like Lychniscosa in which marginal surface around terminal osculum is coated by dense, siliceous membrane, and comparable sponges in which blind or open, tubular outgrowths emitted from axial tube or funnel; these types intergrade through sponges with wall externally sculptured as in Ventriculites MANTELL; some depressed or pyriform with marginal membrane then capsulelike; epirhyses and aporhyses simple to labyrinthine where wall is compact; ostia alternating or without order; postica alternating, sometimes in longitudinal series; cavities of tubular outgrowths correspond with aporhyses of other forms; external surface with finely porous, cortical coverings, variably developed, sometimes forming spinelike outgrowths; marginal membrane formed from small, dictyonal hexactines and anastomosing, siliceous filaments, or also incorporating stauractine marginalia; basal skeleton of root processes formed from anastomosing, siliceous fibers. [The intergradation of Camerospongiidae in which tubes are emitted from an axis with others having typical, intradictyonal epirhyses and aporhyses was not known to SCHRAMMEN, who united the former type with cavaediate sponges here referred to the Callicylicinae (Tremabolites ZITTEL) and Coeloptychidae (Cameroptychium LEONHARD). In addition, ZITTEL's (1877b, p. 56-57) characterization of the type Camerospongia D'ORBIGNY was based on Cameroptychium species [C. campanulatum (SMITH), C. schloenbachi (F. A. ROEMER).] The family characterization is emended here accordingly. The group is retained as a separate family because of distinctive specialization but includes forms not distinguishable from Ventriculites MANTELL of the Ventriculitinae except by the marginal membrane (Rhytistamnia POMEL).] Lower Cretaceous (Valanginian)–Upper Cretaceous.

Camerospongia D'ORBIGNY, 1849, p. 548 [\*Scyphia fungiformis GOLDFUSS, 1831, p. 218; OD] [=Cameroscyphia FROMENTEL, 1860a, p. 41, obj.]. Biconical to hemispherical, cushion shaped or

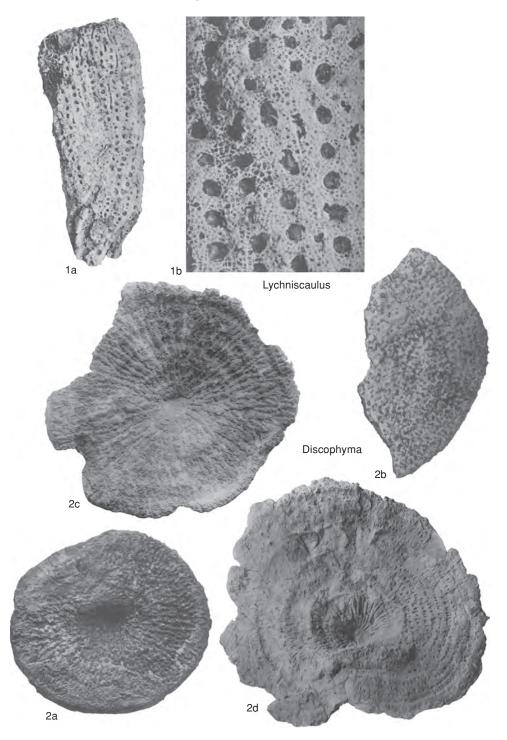


FIG. 351. Ventriculitidae (p. 537).

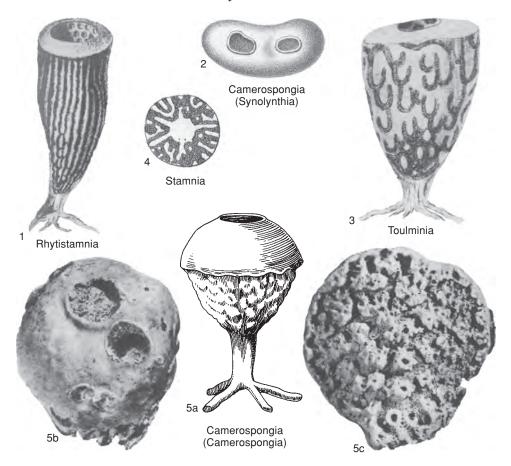


FIG. 352. Camerospongiidae (p. 539-540).

pyriform, with central or marginal root, or forming a colony of marginally attached to completely confluent sponges; upper surface rounded or flattened, formed by siliceous marginal membrane around central osculum with prominent rim, or with more than one osculum in compound examples; underside or lateral surfaces formed by dermal, skeletal surface that may be simply developed with irregularly distributed ostia, or irregularly furrowed to tuberculate with ostia between ribs or tubercles; skeletal canals more or less radial, simple or branched, or continuous labyrinths, also typically wider than intervening skeletal partitions and hence resembling thin-walled tubes; paragastral surface with closely spaced, alternating postica; aporhyses may also open through small, accessory pores on dermal side, sometimes perforate tubercles that become papilliform; dermal surface with finely porous, cortical meshwork that may form spinelike outgrowths, and passes into root structure; gastral side without similar cortex, although accretion of small hexactines may occur. Cretaceous (Valanginian-Maastrichtian): Europe.

- C. (Camerospongia). Solitary, biconical to hemispherical or pyriform, with central or eccentric stalk and roots or sometimes sessile; underside simple reticulate to furrowed or tuberculate, sometimes with prominent, papilliform outgrowths from which solid spines radiate laterally and may unite locally to form bridges. Cretaceous (Valanginian-Maastrichtian): Europe.-FIG. 352,5a. \*C. (C.) fungiformis (GOLDFUSS); side view of complete sponge with basal stalk and rimmed osculum, ×1 (de Laubenfels, 1955). -FIG. 352,5b-c. C. (C.) asymmetrica LAGNEAU-HÉRENGER, Aptian, Can Casanyas Castellet, Catalogne, Spain; b, side view of globular sponge with a cortex and eccentric osculum,  $\times 1$ ; *c*, opposite side showing anastomosing, small tubes, with ostia, that constitute main body of sponge, ×1 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- C. (Synolynthia) POMEL, 1872, p. 76 [\**Choanites subrotundus* MANTELL, 1822, p. 179; OD]. Solitary, hemispherical to cushionlike, with a marginal root or group of roots, or compound,

hemispherical to pyriform with two or more oscula, or forming linear colonies of marginally attached to completely confluent individuals; paragastral cavity or cavities small, pitlike, separate in compound examples; linear colonies formed by budding from side opposite root or roots; dictyonal structure radiating from this margin across body, and continuous through budded individuals. [Essentially intergrading with Camerospongia s.s., but includes compound species and the Cystispongia species of SCHRAMMEN (1912).] Cretaceous (Hauterivian-Maastrichtian): Europe.—FIG. 352,2. C.(S.) reniformis ROEMER, Quadratenkreide, Cenomanian, Ilsenburg, Germany; view from above showing two oscula in cushionlike, small sponge, ×1 (Roemer, 1864).

- Rhytistamnia POMEL, 1872, p. 66 [\* Cephalites longitudinalis SMITH, 1848, p. 281; OD]. Habitus as in Stamnia POMEL, 1872 (p. 66), but dermal surface tuberculate or furrowed longitudinally as in Ventriculites MANTELL of Ventriculitidae; epirhyses simple, with ostia in furrows of dermal side, or more or less obsolete; aporhyses simple, running radially into ribs or tubercles of dermal side; postica alternating; dermal surface with finely porous cortex, with small, intracortical ostia. [Type species not distinguishable from forms of Ventriculites chonoides MANTELL except by marginal membrane.] Cretaceous (Turonian-Maastrichtian): Europe.-FIG. 352, 1. \*R. longitudinalis (SMITH), Chalk, Upper Cretaceous; side view of steeply obconical sponge with furrowed, dermal surface, ×1 (Smith, 1848).
- Stamnia POMEL, 1872, p. 66 [\*Cephalites alternans SMITH, 1848, p. 283; SD DE LAUBENFELS, 1955, p. 107] [=Sestrostamnia POMEL, 1872, p. 66 (type, Cephalites alternans SMITH, 1848, p. 283); ?Tretostamnia POMEL, 1872, p. 70 (type, T. favosa, M); ?Xystrostamnia POMEL, 1872, p. 66 (type, Cephalites paradox SMITH, 1848, p. 283)]. Carrot shaped, with flat, marginal surface, deep, narrow, paragastral cavity, and small stalk and roots; wall compact, with simple, radial or branching, and anastomosing epirhyses and aporhyses; ostia and postica alternating or without order; dermal or both surfaces with finely porous, cortical covering. Cretaceous (Turonian): Europe.-FIG. 352,4. \*S. alternans (SMITH), Chalk, England; transverse section showing broad, central cavity and folded walls, ×1 (Smith, 1847).
- Toulminia ZITTEL, 1877b, p. 56 [\* Cephalites catenifer SMITH, 1848, p. 286; SD DE LAUBENFELS, 1955, p. 90; = Ventriculites benettiae MANTELL, 1822, p. 177, subj.] [=Oncostamnia POMEL, 1872, p. 67, obj.; Phymostamnia POMEL, 1872, p. 67 (type, Cephalites bullatus SMITH, 1848, p. 284, OD); Phalacrus SCHRAMMEN, 1912, p. 321, non PAYKULL, 1800, nom. nov. pro Ornatus DE LAUBENFELS, 1955, p. 90, nom. null.]. Top shaped with compact, outer surface, flat top, and small, basal stalk, or with radiating, tubular outgrowths arising from tubular axis below annular membrane that forms summit; epirhyses typically absent; aporhyses in blind, papil-

liform, or widely open, radial outgrowths, which may be united laterally in groups or connected by secondary bridges at their summits; ends of radial outgrowths round or diamond shaped when closed or papilliform, round or horseshoe shaped to continuously interconnected when freely open; development of these features may vary between different individuals; gastral wall with alternating apertures (postica) that lead into hollow outgrowths; dermal side with or without finely porous, cortical structures, which may form bridges between ends of open outgrowths; gastral meshwork unmodified, or with small hexactines attached to dictyonalia at surface. [Variable development is characteristic of the type species, of which differently developed individuals were types of the nominal species V. benettiae MANTELL, C. catenifer SMITH, C. microta F. A. ROEMER, and C. bullatus SMITH. Type species of Phymostamnia was based on a form of T. benettiae in which tubular outgrowths are terminally diamond shaped with a perforation in the upper angle. This form grades although microta and catenifer forms into typical benettiae, with open tubes continuously connected by secondary bridges.

Ornatus was proposed as a nom. nov. by DE LAUBENFELS (1955, p. 90) for *Phalacrus* SCHRAM-MEN, 1912, p. 321, non PAYKULL, 1800, but the designated type species *P. expectatus* SCHRAMMEN, 1912 was never described by SCHRAMMEN, although three other species were. Sponges are *Toulminia* forms with papilliform or separate open lateral tubes.] *Upper Cretaceous:* Germany.——FIG. 352, 3. \* *T. catenifer* (SMITH), Chalk, Quadratenkreide– Mucronatenkreide; side view of top-shaped sponge with flat top and tubular outgrowth in thick wall, approximately ×1 (Smith, 1848).

#### Family POLYBLASTIDIIDAE Schrammen, 1912

#### [Polyblastidiidae SCHRAMMEN, 1912, p. 194]

Branched-tubular Lychniscosa with threedimensional, skeletal meshwork in which skeletal wall is apparently folded longitudinally; wall with shallow epirhyses but no aporhyses, although gastral side of skeleton deeply furrowed longitudinally; dermal surface of dictyonal framework with shallow, longitudinal furrows, along which are alternating ostia of shallow, pitlike epirhyses, between rounded or slightly tuberculate ribs; gastral side with deep, longitudinal furrows and no aporhyses or postica, although small pores in floors of furrows may perforate ribs of dermal side; some furrows locally intercommunicate through apertures in intervening ridges; dermal side of framework with dictyonal cortex as finely porous, siliceous

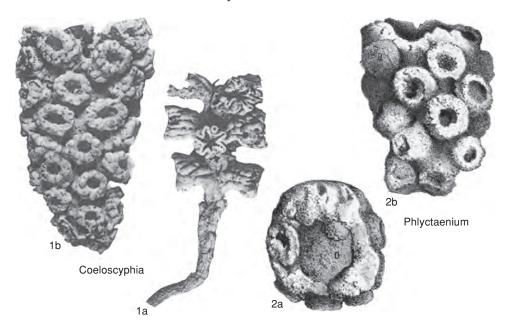


FIG. 353. Polyblastidiidae (p. 541).

membrane; gastral side with no dictyonal cortex, but with anastomosing, superficial filaments that grow out from projecting rays of dictyonalia at surface; basal skeleton formed from siliceous fibers. [Coeloscyphia TATE (=Polyblastidium ZITTEL), was regarded as a ventriculitid by ZITTEL and could be a form in which radial, flagellated chambers or chamber-bearing structures, represented by aporhyses in Ventriculitidae, were replaced by continuous, longitudinal folds of the chamber layer. A similar development occurs in Ubiquiradius DE LAUBENFELS, here placed in the Ventriculitidae because of its apparent relationship to Leiostracosia SCHRAMMEN. The gastral furrows of *Coeloscyphia* were also apparently internal in life, because the superficial filaments grow into and over them.

The nominal genera *Coeloscyphia* TATE and *Polyblastidium* ZITTEL were made types of separate families by DE LAUBENFELS (1855), but their respective type species (*C. sulcata* TATE, *P. luxurians* ZITTEL) are thought here to be based on different specimens of one species, *C. racemosa* (SMITH).] *Upper Jurassic–Cretaceous* (Coniacian).

- Coeloscyphia TATE, 1865, p. 43 [\*C. sulcata; OD; =Brachiolites racemosus SMITH, 1848, p. 364] [=Polyblastidium ZITTEL, 1877b, p. 52 (type, P. luxurians ZITTEL, 1877b, p. 52, OD, =Brachiolites racemosus SMITH, 1848, p. 364]. Axial tube or group of connected tubes, above a stalk with basal roots, emitting radiating, budlike outgrowths with open ends; ends of outgrowths exposing interior structure when incomplete, covered by cortex of dermal side when fully developed. [Polyblastidium ZITTEL, 1877b, is regarded as synonym of Coeloscyphia TATE, 1865, because C. sulcata TATE and P. luxurians ZITTEL are considered identical biologically. Synonymy of P. luxurians and Brachiolites racemosus SMITH, 1848 was recognized by SCHRAMMEN (1912).] Cretaceous (Coniacian-Maastrichtian): Ireland, Germany.-FIG. 353,1ab. \*C. racemosa (SMITH), Quadratenkreide, Cenomanian, Oberg, Germany; a, axial cluster of radiating tubes, above a stalk, where each tube ends in radiating outgrowths; b, obconical cluster of radiating tubes with less distinct, radial structure on their outer ends, ×1 (Schrammen, 1912).
- Phlyctaenium ZITTEL, 1878c, p. 177 [\*Mastospongia cylindrata QUENSTEDT, 1878 in 1877–1878, p. 150; SD DE LAUBENFELS, 1955, p. 89]. Top shaped to cylindrical, outer surface with large nodes, broad osculum, skeleton lychniscoid. Upper Jurassic: Germany.——FIG. 353,2a-b. \*P. cylindratum (QUENSTEDT), Weiss Jura, Kimmeridgian, Friedingen; a, view from above of broad osculum and thick walls; b, view from side of nodose walls, ×1 (Quenstedt, 1877–1878).

#### Family DACTYLOCALYCIDAE Gray, 1867

[Dactylocalycidae GRAY, 1867, p. 505] [=?Lithospongiae DUCHASSAING & MICHELOTTI, 1864, p. 25; Aphrocallistidae SOLLAS, 1877b, p. 23, partim; Macandrospongidae ZITTEL, 1877b, p. 38, partim; Auloplacidae SCHRAMMEN, 1912, p. 227; Euretidae IJIMA, 1927, p. 163, partim]

Lychniscosa with three-dimensional, dictyonal meshwork and single system of intradictyonal skeletal canals as labyrinth of divided and anastomosed, tubular passages that open through both skeletal surfaces, but without connected dermalia or gastralia; cortical meshwork when present formed by modification of outermost primary meshwork, or by secondary accretion of dictyonal hexactines; superficial meshwork and basal skeleton of dictyonal hexactines; lychnisc octahedra may be solidified or largely aborted at surfaces or throughout skeleton; pentactinal dermalia and gastralia and hexaster microscleres in two living genera. [The living type genus Dactylocalyx STUTCH-BURY has usually been placed in the Hexactinosa because of extensive suppression of lychnisc octahedra, which occur only in some specimens of the type species (D.pumiceus STUTCHBURY), and then only in small parts of the skeleton. Analogous suppression of lychnisc octahedra occurs in the fossil Moretiella BREISTROFFER, and in *Caiathiscus* SOLLAS if this is a dactylocalycid. The soft parts of Dactylocalyx are unfortunately not known fully. REISWIG (2002) has discussed the history of interpretation of the family.] Jurassic (Bajocian)-Holocene.

#### Subfamily DACTYLOCALYCINAE Gray, 1867

[nom. transl. REID, herein, ex Dactylocalycidae GRAY, 1867, p. 505]

Sponges of varying habitus, in which skeletal pores are not restricted to special, paragaster-like depressions on either side of wall. Jurassic (Bajocian)–Cretaceous (Maastrictian).

?Calathiscus SOLLAS, 1883, p. 546 [\*C. variolatus; M]. Tubular, straight or horn shaped; skeletal pores without order or locally alternating in vertical rows; skeleton very irregular with many solid nodes and others that have structures that appear to be imperfectly developed octahedra. [Known only from poor, calcified material, not certainly lychniscosan; has been considered ventriculitid (e.g., by HINDE, 1893b, p. 197), but the skeletal canals are labyrinthine, and resemblance to those of *Dactylocalyx* was noted by SOLLAS (1883, p. 546).] *Jurassic (Bajocian):* England.——FIG. 354,2*a*–*b*. \**C. variolatus,* Inferior Oolite, Burton Bradstock; *a*, side view of large, subcylindrical sponge, ×0.5; *b*, drawing of enlarged section of skeletal structure, replaced by calcite, ×50 (Hinde, 1893b).

- Exanthesis REGNARD in MORET, 1926b, p. 231 [\*Plocoscyphia reticulata HINDE, 1884a, p. 135; M] [=Periphora REGNARD, 1926, p. 483 (type, P. robusta, M)]. Body irregularly spreading or columnar, composed of dividing and anastomosing tubes, in columnar forms margins of open, peripheral tubes sometimes growing together locally to make reticulate, peripheral surface; skeletal pores rounded to slitlike or shaped irregularly, similar or differently developed on opposite surfaces, and arranged without order or with rough, longitudinal alignments; skeletal canals sometimes poorly developed; skeletal meshwork more or less regular internally, except when canals are close together, becoming irregular or forming cortex at surfaces; nodal octahedra may be absent in well-developed, cortical meshwork; accretion of dictyonal hexactines may thicken cortical meshwork or build superficial bridges on dermal side. [Exanthesis was described as a new genus by REGNARD (1926, p. 475) in a paper apparently referred to by MORET as "Regnard, in litt."] Cretaceous (Aptian-Maastrichtian): France, England, Spain.
  - E. (Exanthesis). Irregularly spreading to columnar, with peripheral tubes reticulated; skeletal pores round to slitlike or shaped irregularly and similarly or differently developed on opposite surfaces; skeletal canals well developed; distinct, dense, cortical meshwork, thickest on dermal side where accretion of dictyonal hexactines may also be extensive; cortical and superficial dictyonalia without nodal octahedra in most instances. [Periphora REGNARD, 1926 based on an Exanthesis similar to the type E. reticulatus; characters of the latter then not fully known.] Cretaceous (Aptian-Cenomanian): France, England, -FIG. 354,4a-c. \*E. (E.) reticulatus Spain.-(HINDE), Cenomanian; a, side view of irregular sponge of anastomosing tubes, Cape de la Hève, Normandy, France, ×1 (Moret, 1926b; courtesy of Société Géologique de France); b, side view of sponge with apertures of irregular tubes in upper part, Upper Greensand, Eastborne, England,  $\times 0.5$ ; c, fragments of internal skeleton showing so-called lantern development, Upper Greensand, Eastborne, England, ×25 (Hinde, 1884a).
  - E. (Eligma) REGNARD, 1926, p. 484 [\*E. douvillei; M]. Irregularly spreading to roughly columnar, with peripheral tubes mainly separate and often of convoluted shapes; skeletal pores mainly rounded, apart from denticulation by projecting, skeletal rays, and usually similar on both surfaces; skeletal canals well or poorly developed, sometimes more or less limited to enlarged

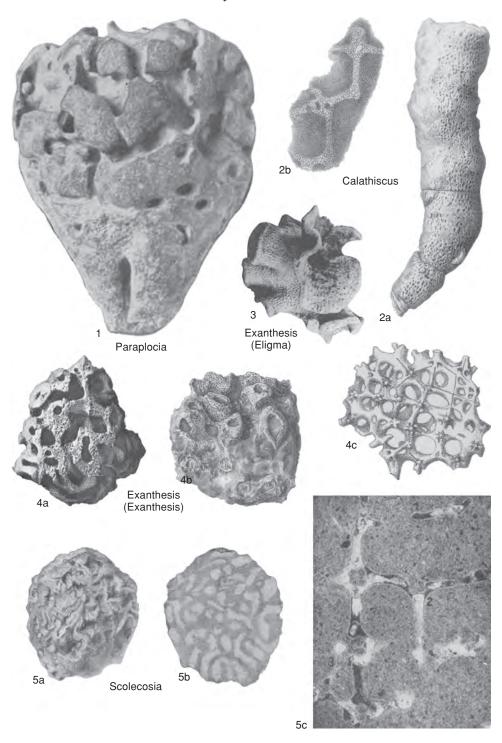


FIG. 354. Dactylocalycidae (p. 542-544).

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skeletal meshes, or only recognizable near surfaces so that no continuous labyrinth is present; meshwork at surfaces not forming definite cortex, although less regular than that of interior, and usually with nodal octahedra. [Type species possibly based on incompletely canalized individuals of *E. (E.) labrosa* (SMITH) because fully canalized examples are otherwise indistinguishable.] *Cretaceous (Albian–Maastrichtian):* France, England.——FIG. 354,3. \*E. (E.) douvillei, chalk of Rouen, Cenomanian, Coulonges-les-Sablons, Orne, France; side view of irregular, small sponge, ×0.66 (Regnard, 1926; courtesy of Société Géologique de France).

- Moretiella BREISTROFFER, 1949, p. 103, nom. nov. pro Moretia Hérenger, 1945, p. 689, non ROBINEAU-DESVOIDY, 1863 [\*Moretia elegans HÉRENGER, 1945, p. 689; OD] [=Neomoretia ZHURAVLEVA in REZVOI, ZHURAVLEVA, & KOLTUN, 1962, p. 46, obj., proposed as a new name for Moretia]. Tubular to funnel-like or flabellate, thick walled; exterior of skeletal framework irregularly sculptured with rounded to slitlike or irregularly shaped, skeletal pores that may have longitudinal alignment; skeletal canals well developed; gastral side smooth but with rounded apertures; skeletal meshwork regular in interior, passing outwardly on both sides into irregular, cortical meshwork that is thick on dermal side; dermal, cortical meshwork loose toward surface, formed partly by accretion of hexactines that also build irregular, superficial bridges across skeletal pores; nodal octahedra absent in cortical meshwork and also more or less extensively in interior. [Placed in a separate family Moretiellidae by HÉRENGER, but skeletal characters similar to those of Exanthesis reticulatus (HINDE).] Cretaceous (Aptian-Cenomanian): Spain.——FIG. 355a-d. \*M. elegans (HÉRENGER), Aptian, Can Casanyas Castellet, Catalogne; a, side view of subcylindrical sponge with elongate, skeletal pores in dermal layer,  $\times 0.5$ ; b, enlargement of part of skeletal net with spines that border some of pores; c, regular, dictyonal, interior, skeletal network interrupted by canals; d, part of gastral surface with dictyonal structure around exhalant ostia partially obscured by a cortex, ×10 (Lagneau-Hérenger, 1962; courtesy of Société Géologique de France).
- Paraplocia POMEL, 1872, p. 104 [\*Spongia labyrinthica MANTELL, 1822, p. 165; OD] [?=Oncotoechus SCHRAMMEN, 1912, p. 308 (type, O. cavernosus SCHRAMMEN, 1912, p. 309, SD DE LAUBENFELS, 1955, p. 91)]. Club shaped, composed of peripherally separate or reticulated, divided and anastomosed tubes, or tubes or solid outgrowths that arise from an axial tube; conditions variable between different individuals; peripheral reticulation of tubes spread variably from lowest parts upwardly; skeletal pores round, arranged without order, or locally opening in sinuous grooves that are imperfectly enclosed canals; skeletal canals well developed; no special cortical meshwork; tubes and cavaedial interspaces of lower parts infilled with secondary, dictyonal meshwork, which is heavily thickened; no

apparent basal attachment. *Cretaceous (Turonian):* Germany.——FIG. 354,1. *P. cavernosa* SCHRAMMEN, Scaphitenplaner, Oppeln; side view of obconical sponge with irregularly anastomosing outgrowths with prominent, small ostia in upper part, ×1 (Schrammen, 1912).

?Scolecosia RAUFF, 1933, p. 54 [\*S. scrobiculata; OD]. Body lenticular, containing labyrinth of vermiform, anastomosed canals that open at surfaces; intervening partitions with simple, regular, skeletal meshwork; further details unknown. [Based on a single, phosphatized pseudomorph.] Cretaceous (Turonian): Germany.—FIG. 354,5a-c. \*S. scrobiculata, Greensand, upper Turonian, Ruhr Valley; a, side view of sponge with labyrinthic canals and skeletal structure,  $\times 1$ ; b, vertical section through sponge showing complex, internal, canal pattern and skeleton,  $\times 1$ ; *c*, thin section showing lychniscoid, skeletal structure partially replaced by phosphorite, ×50 (Rauff, 1933; courtesy of Preussischen Geologischen Landsanstalt, E. Schweizerbart'sche Verlagsbuchhandlung).

#### Subfamily OPHRYSTOMATINAE Schrammen, 1912

[*nom. transl.* REID, 1957b, p. 825, *ex* Ophrystomatidae Schrammen, 1912, p. 197]

Platelike sponges with skeletal canals of one surface restricted to local, paragaster-like depressions that open through a dense, cortical covering, and analogous nodular to hemispherical sponges with a deep, central cavity. [Reduced to subfamily by REID (1957b) on recognition of presence of a dactylocalycid canal system in the first good spicular material; represented in living sponges by the incompletely known "Cystispongia" superstes SCHMIDT (1880).] Cretaceous (Albian–Cenomanian).

Ophrystoma ZITTEL, 1877b, p. 55 [\*Porospongia micrommata F. A. ROEMER, 1864, p. 9; M]. Platelike, sometimes folded irregularly; one surface with alternating or irregularly distributed and rounded to slitlike skeletal pores spaced about their own width apart; other surface imperforate between rounded, paragaster-like pits, with skeletal pores in their walls; surface between these pits formed by dense, irregular meshwork, composed of small, dictyonal hexactines without nodal octahedra; internal meshwork more or less lacunar, forms branched and anastomosed, skeletal trabeculae that are exposed at margins of plate; other skeletal surface with irregular meshwork, not forming a thick cortex; pitted side probably gastral. Cretaceous (Albian-Cenomanian): Germany, England.-FIG. 356,1. \*O. micrommata (ROEMER), Varians-Pläner, Cenomanian, Langelsheim, Germany; plate fragment with irregular rimmed, paragaster-like pits

with spines "*Cystispongia*" superstes SCHMIDT ctyonal, iny canals; *d*, il structure by a cortex, **Ophrystoma** ZITTEL, 1877b, p. 55 [\*

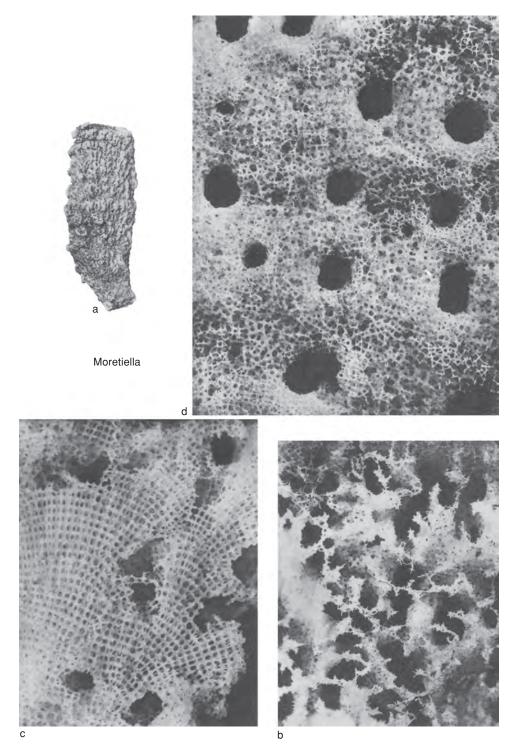


FIG. 355. Dactylocalycidae (p. 544).

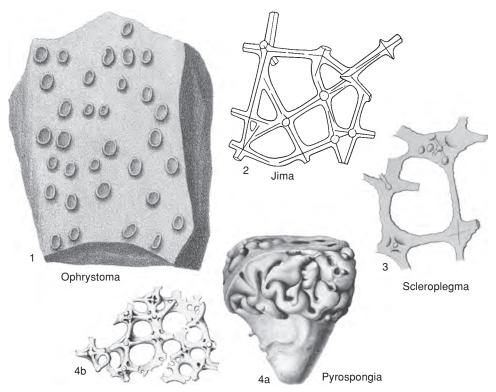


FIG. 356. Dactylocalycidae (p. 544-546).

separated by irregular, dense, skeletal structure, ×1 (Roemer, 1864).

### Subfamily UNCERTAIN

- Jima DE LAUBENFELS, 1955, p. 84, nom. nov. pro Pleurotoma SCHRAMMEN, 1912, p. 257, non EHRENBERG, 1839 [\*Pleurotoma ijimai SCHRAMMEN, 1912, p. 257; M]. Thin-walled, tubular sponges. Upper Cretaceous: Germany.——FIG. 356,2. \*J. ijimai (SCHRAMMEN), Quadratenkreide, Oberg; sample of lychniscoid skeletal structure of thin wall, ×45 (Schrammen, 1912).
- Meandrospongia D'ORBIGNY, 1849, p. 550 [\**M. foliacea;* OD] [=*Maeandrospongia* ROEMER, 1864, p. 52, obj.]. Subcylindrical to steeply obconical meandriform, perhaps branched, thin-walled sponge with many round openings but oscules absent; pores not apparent in original material. [No known suitable figures.] *Cretaceous (Turonian):* Europe.
- Pyrospongia ZAHALKA, 1901, p. 37 [\*P. vrbaei; SD DE LAUBENFELS, 1955, p. 84]. Sponges bulb shaped with thick, high walls of meandering, flexuous, rounded lobes; irregular, radial canals converging to vertical, axial possible spongocoel from small openings on surface; skeleton lychniscoid with promi-

nent lanterns in interior. Upper Cretaceous: Czech Republic, Slovakia.——FiG. 356,4a–b. \*P. urbaei, Couches de Teplice, upper Turonien, Teplice, near Prague; a, side view of bulbous sponge showing structure of walls and canal development,  $\times 0.5$ ; b, skeletal fragment showing lychniscoid structure,  $\times 50$  (Zahálka, 1901).

Scleroplegma SCHMIDT, 1880, p. 56 [\*S. lanterna; SD DE LAUBENFELS, 1955, p. 84]. Cylindrical to kegshaped, thick-walled sponges with a similar-shaped spongocoel; skeleton lychniscoid with round to prismatic mesh spaces and irregular canals. Upper Cretaceous-Holocene: Germany, Atlantic Ocean. ——FIG. 356,3. \*S. lanterna, Holocene, Atlantic Ocean; skeletal fragment showing lychniscoid structure of network, magnification unknown (Schmidt, 1879).

# Family SPORADOPYLIDAE Schrammen, 1937

[Sporadopylidae SCHRAMMEN, 1937, p. 17]

Lychniscosa with three-dimensional, skeletal meshwork and single system of intradictyonal, skeletal canals, in form of quincuncially alternating, radial passages that open through both skeletal surfaces, or of canals of this type that pass into a labyrinth on one side of wall; nodal octahedra well developed or more or less suppressed, sometimes only detectable in small parts of individual sponges. [The family type Sporadopyle ZITTEL and the further included genus Xenoschrammenum DE LAUBENFELS (=Amphiblestrum SCHRAMMEN, 1937, non GRAY, 1848) were stated by SCHRAMMEN (1937, p. 17) to have alternating epirhyses and aporhyses; but the type species S. obliqua (GOLDFUSS) and X. venosum (SCHRAMMEN) have the structure stated here in material identified by SCHRAMMEN.

The radial cavities resemble diarhyses of aphrocallistid Hexactinosa, but their size is more suggestive of chamber-lined canals in some instances.] Upper Jurassic-Cretaceous (Cenomanian).

- Favispongia QUENSTEDT, 1878 in 1877-1878, p. 118 [\*Scyphia obliqua GOLDFUSS, 1826, p. 9; SD SCHRAMMEN, 1937, p. 17] [=Sporadopyle ZITTEL, 1877b, p. 47, obj.]. Tubular to funnel-like, thick walled, usually small; exterior with alternating, round to slitlike, skeletal pores, sometimes also furrowed longitudinally or diagonally; skeletal canals tubular, narrow, pass directly through framework or anastomose on gastral side; internal meshwork regular to more or less irregular, with nodal octahedra well developed; denser, cortical meshwork on dermal side. [Many records refer to Hexactinosa, with which this form has been confused.] Upper Jurassic; ?Lower Cretaceous: Europe .--Fig. 357,1a-b. \*F. obliqua (GOLDFUSS), Weiss Jura, Upper Jurassic, Streitberg, Germany; a, side view showing tubular nature of skeleton and distribution of pores, ×2 (Schrammen, 1937); b, skeletal fragments showing regular network and swollen, nodal octahedra at some junctions, ×20 (Schrammen, 1936).
- Sestrodictyon HINDE, 1884a, p. 101 [\*S. convolutum HINDE, 1884a, p. 102; M]. Irregularly convoluted plates that may pass into funnels by enrollment and union of margins; radial canals freely open on both sides of skeletal framework, or with apertures covered on one side by anastomosing bridges of secondary, dictyonal meshwork that build an irregularly furrowed and perforated secondary surface; those of other side locally in variably developed, longitudinal furrows; this surface also sometimes with small, secondary outgrowths that usually remain separate; lychnisc octahedra rare or absent. *Cretaceous (Albian–Cenomanian):* Switzerland.— FIG. 357,2. \*S. convolutum, Alpine Chalk,

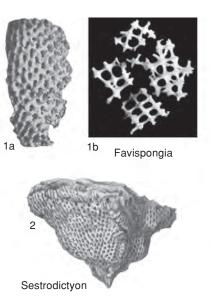


FIG. 357. Sporadopylidae (p. 547).

Appenzell; side view of funnel-like form with coarse openings of radial canals, ×0.5 (Hinde, 1884).

Xenoschrammenum DE LAUBENFELS, 1955, p. 79, nom. nov. pro Amphiblestrum SCHRAMMEN, 1937, p. 57, non GRAY, 1848 [\*Amphiblestrum venosum SCHRAMMEN, 1937, p. 58; OD]. Based on platelike fragments; one side with regularly alternating, ovate apertures, aligned longitudinally, that may become subdivided by secondary partition to form two pores of similar or different sizes; skeletal canals running radially inwardly from this side, through most of framework thickness, then forming a labyrinth that opens through small, rounded pores arranged without order on other side; meshwork fairly regular internally, with dictyonal strands curved strongly to side with pores regularly alternating; lychnisc octahedra only seen locally; irregular meshwork at surfaces. [Funnel-like according to SCHRAMMEN (1937, p. 57), but this habit is not known in the type.] Upper Jurassic, ?Lower Cretaceous: Germany, France, Spain.-FIG. 358a-c. \*X. venosum (SCHRAMMEN), Weiss Jura, Upper Jurassic, Heuchstetten, Germany; a, outer surface of fragment with regular skeleton; b, inner surface of fragment with more irregular skeleton, ×1 (Schrammen, 1937); c, fragment of articulated, skeletal net, ×20 (Schrammen, 1936).—FIG. 358d. X. robustum Lagneau-Hérenger, Hauterivian, Malleval, France; basal part of cylindrical sponge characterized by coarse pores and fibers of skeletal net, ×1 (Lagneau-Hérenger, 1962).-FIG. 358eg. X. fragile LAGNEAU-HÉRENGER, Aptian, Can Casanyas Castellet, Catalogne, Spain; e, broad, plate- to cup-shaped sponge seen from above, ×1; f, enlarged view of gastral surface with dictyonal net between exhalant pores that may be bordered by

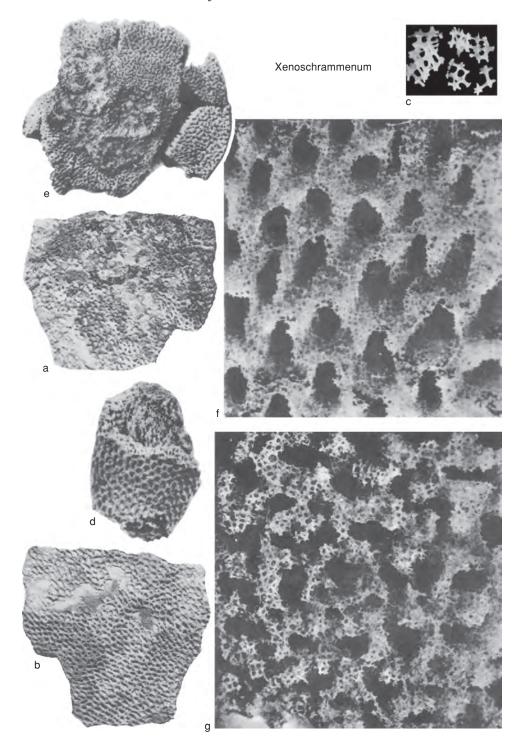


FIG. 358. Sporadopylidae (p. 547-549).

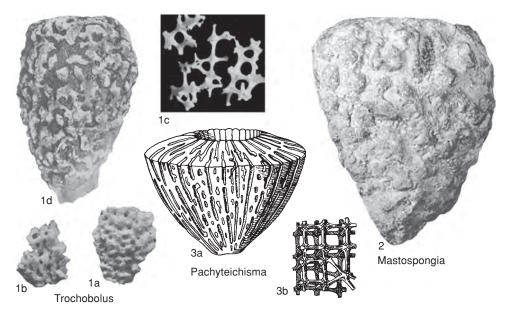


FIG. 359. Pachyteichismatidae (p. 549-550).

spinose ray elements; *g*, enlarged view of dermal surface with coarser, skeletal net that is jagged along pore margins, ×10 (Lagneau-Hérenger, 1962).

### Family PACHYTEICHISMATIDAE Schrammen, 1937

[nom. transl. LAGNEAU-HÉRENGER, 1962, p. 85, ex Pachyteichismatinae Schrammen, 1937, p. 3]

Lychniscosa with three-dimensional, skeletal meshwork; intradictyonal, skeletal canals vary from separate or intercommunicating, longitudinal clefts to continuously labyrinthine passages that open through both skeletal surfaces; external surfaces and walls of canals may show further small, skeletal pores that lead into underlying meshes of skeletal framework; superficial outgrowths and basal skeleton formed from dictyonal hexactines when present. [Skeletal canals of this family were interpreted as cavaedia by SCHRAMMEN (1937, p. 3), who believed them to be formed by radial to labyrinthine convolution of the wall. They interrupt the skeleton in the manner of intradictyonal canals, however, and are broadly comparable with those of Sporadopylidae. The canals are especially large in some species but not larger than intradictyonal schizorhyses of some Tretodictyidae (Hexactinosa).] *Upper Jurassic– Lower Cretaceous.* 

- Pachyteichisma ZITTEL, 1877b, p. 49 [\*P. carteri ZITTEL, 1877b, p. 50; SD DE LAUBENFELS, 1955, p. 87] [=Lancispongia QUENSTEDT, 1877 in 1877-1878, p. 92 (type, L. lopas QUENSTEDT, 1877 in 1877-1878, p. 95, SD REID, herein]. Top shaped with narrow paragaster to funnel-like, thick walled; skeletal canals radial in outer part of wall, become labyrinthine on gastral side; apertures of dermal side in longitudinal series, ovate to cleftlike; between open features may be further blind, radial canals, only open if surface is eroded; apertures of gastral side rounded or shaped irregularly, in longitudinal series or without order, sometimes in longitudinal furrows when arranged serially; skeletal meshwork very regular internally, but forming an irregular trellis work at surfaces; apertures of dermal side sometimes bridged by secondary outgrowths. Upper Jurassic-Lower Cretaceous: Europe; Switzerland, Germany, Kimmeridgian; France, Valanginian-Albian.-FIG. 359, 3a-b. \*P. carteri, Upper Jurassic, Kimmeridgian, Germany; a, side view of thick-walled, top-shaped sponge with alternating epirhyses and aporhyses, ×0.5; b, part of lychniscoid skeleton, ×10 (de Laubenfels, 1955).
- Mastospongia QUENSTEDT, 1877 in 1877–1878, p. 146 [\**M. coniformis* QUENSTEDT, 1877 in 1877–1878, p. 152; SD DE LAUBENFELS, 1955, p. 106]. Top shaped with normal or reduced paragaster, thick walled; skeletal canals as in *Trochobolus* ZITTEL and *Pachyrhachis* SCHRAMMEN, but dermal side has perforated, conical or cylindrical outgrowths. [Comprises a form placed formerly into

Phlyctaenium ZITTEL, but the type of that genus (Mastospongia cylindrata QUENSTEDT, 1877 in 1877–1878, p. 172; SD DE LAUBENFELS, 1955, p. 89) is thought to be a Verrucocoelia (KOLB, 1910 in 1910–1911, p. 203; SCHRAMMEN, 1937, p. 7–8).] Upper Jurassic–Lower Cretaceous: Germany.——FIG. 359,2. \*M. coniformis, Kimmeridgian marls, Upper Jurassic, Bärenthal; side view of top-shaped sponge with low, tubular outgrowths, ZPAL Pf. VIII/218, ×1 (Pisera, 1997; courtesy of Palaeontologica Polonica).

Trochobolus ZITTEL, 1877b, p. 50 [\*T. crassicosta; SD DE LAUBENFELS, 1955, p. 87] [=Pachyrhachis SCHRAMMEN, 1937, p. 5 (type, P. labyrinthica SCHRAMMEN, 1937, p. 7, SD DE LAUBENFELS, 1955, p. 87)]. Cylindrical or top shaped with narrow paragaster, or expanded into funnel or stalked, bowl shapes; skeletal canals labyrinthine; dermal side with apertures arranged alternately, without order, or in reticulating, diagonal or partly longitudinal furrows, between which surface forms ridges or tubercular prominences; apertures of gastral side alternating or without order; skeleton as in Pachyteichisma ZITTEL. [Pachyrhachis used by SCHRAMMEN (1937, p. 5) for thick-walled forms with large, labyrinthine canals, some of which lack superficial furrowing of the dermal side; but furrowing is present in the type designated by DE LAUBENFELS (1955, p. 87); ENGESER and MEHL (1993, p. 190) concluded that Trochobolus may be a younger, subjective synonym of Cyathoplocia POMEL, 1872, because ZITTEL (1877b) placed Scyphia texata GOLDFUSS, 1826, the type species of the latter genus, in Trochobolus.] Upper Jurassic-Lower Cretaceous: Europe; France, Switzerland, Germany, Poland, Spain, Kimmeridgian; France, Albian.—FIG. 359, 1a-c. T. texta SCHRAMMEN, Weiss Jura, Upper Jurassic, Streitberg, Germany; a, side view of small, top-shaped sponge with relatively coarse, irregular inhalant ostia,  $\times 2$ ; b, view of gastral surface of small fragment with irregularly spaced exhalant ostia and texture essentially similar to that of dermal surface,  $\times 2$ ; c, enlarged parts of reticulate, skeletal net, ×20 (Schrammen, 1936). -FIG. 359, 1d. T. labyrinthica SCHRAMMEN, Weiss Jura, Upper Jurassic, Gerstetten, Germany; side view of somewhat coarser species with light matrix filling canals and darker areas with skeletal net preserved, ×0.5 (Schrammen, 1937).

#### Family CYPELLIIDAE Schrammen, 1937

#### [nom. correct. DE LAUBENFELS, 1955, p. 90, pro family Cypelliadae SCHRAMMEN, 1937, p. 10]

Lychniscosa with three-dimensional, dictyonal meshwork, with simple to labyrinthine skeletal canals that open through both surfaces of dictyonal framework; dermal pentactines attached to dermal and marginal surfaces more or less isolated, or numerous and united to form dense, superficial mesh-

work that covers skeletal pores of dictyonal framework; apertures of skeletal canals without order, or in longitudinal or rough, transverse rows on gastral side; dictyonal meshwork mainly irregular, with more or less extensive development of porous, siliceous lamella in some meshes. [The dermalia were called stauractines by SCHRAMMEN (1937, p. 10) but are pentactines in material studied in preparation for this volume. The spicules were previously described as pentactines by ZITTEL (1877b, p. 53) in defining the family type Cypellia POMEL, 1872 (p. 76). Dermal and marginal surfaces are typically continuous so that no distinction can be made between dermalia and marginalia.] Jurassic.

- Cypellia POMEL, 1872, p. 76 [\*Scyphia rugosa GOLDFUSS, 1826, p. 9; OD] [=Phanerochiderma SCHRAMMEN, 1937, p. 11, obj.; Cryptochiderma SCHRAMMEN, 1937, p. 14 (type, Scyphia inberbis QUENSTEDT, 1877 in 1877-1878, p. 125, OD)]. Cylindrical to top shaped with deep, narrow, paragastral cavity, or expanded into funnel or bowl shaped; apertures of skeletal canals arranged without order, or in longitudinal or rough, transverse rows on gastral side; superficial meshwork well developed in fully grown examples; pentactines in single, paratangential layer or numerous and overlapping, united by cementation only, or by branching, siliceous filaments that may thicken into more or less continuous, siliceous lamella in parts. Upper Jurassic: Europe.—FIG. 360, 2a-c. \*C. rugosa (GOLDFUSS), Weiss Jura, Streitberg, Germany; a, nearly complete individual showing growth form of sponge, ×1; b, small individual with superficial meshwork locally lamellar, ×4 (Schrammen, 1937); c, dermalia in reticular net, ×10 (Schrammen, 1936).
- Paracypellia Reid, nom. nov. herein (SCHRAMMEN, 1936, p. 179, nom. nud.; SCHRAMMEN, 1937, p. 13, nom. nud.) [\*Cypellia prolifera ZITTEL, 1878d, p. 61; OD; = Nexispongia libera QUENSTEDT, 1878 in 1877-1878, p. 162, nom. oblit. under Code Art. 23.2 (ICZN, 1999)]. Colonial, with clusters of cylindrical individuals arising from a common base or branching stock; superficial meshwork typically dense, with parts forming more or less continuous, siliceous lamella or scales in which spicules are imbedded; other characters as for Cypellia POMEL, 1872. Upper Jurassic: Germany, Poland .--—Fig. 360, 1a. \*P. prolifera (ZITTEL), Weiss Jura, Streitburg, Germany; spicular structure of outer, superficial scales, ×10 (Schrammen, 1936).-FIG. 360, 1b-c. \*P. prolifera [as Nexispongia libera QUENSTEDT], Weiss Jura, Upper Jurassic, Heuberg, Germany; b, branched colony showing growth form with basal, central stalk, from below; c, branched

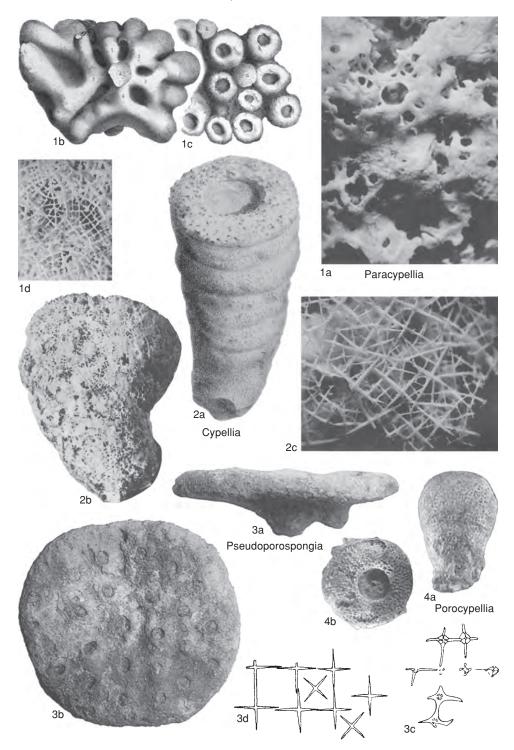
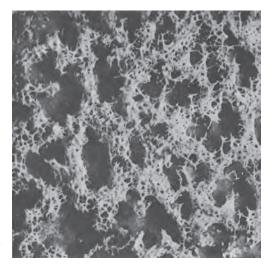


FIG. 360. Cypelliidae (p. 550–552).



Sporadopyge

FIG. 361. Cypelliidae (p. 552).

colony from above, ×0.5 (Quenstedt, 1877– 1878).—FIG. 360, *1d. P. minor* SCHRAMMEN, Weiss Jura, Upper Jurassic, Streitberg, Germany; dermalia, in part over inhalant ostia, ×5 (Schrammen, 1936).

- Porocypellia POMEL, 1872, p. 77 [\*Scyphia pyriformis GOLDFUSS, 1826, p. 10; OD]. Small, hemispherical to club-shaped sponges with single osculum in summit; skeleton lychniscoid with small, octahedral nodes, thickened dermal layer developed; skeleton pierced by numerous, irregularly placed, circular pores. [Included in the family with some question.] Jurassic: Germany.——FIG. 360,4a-b. \*P. pyriformis (GOLDFUSS), Kimmeridgian limestone, Upper Jurassic, Genkingen; a, side view of small, club-shaped sponge with uniform, dermal layer, ZPAL Pf. VIII/ 260, ×2; b, oscular view of same specimen with deep, central spongocoel, ×2 (Pisera, 1997; courtesy of Palaeontologica Polonica).
- Pseudoporospongia Hérenger, 1942, p. 155 [\*P. tarraconensis; OD]. Sponge broadly obconical with flattened, undulating, discoidal upper part, above a distinct stalk; upper surface with ovate oscula 4 to 5 mm in diameter, with slightly elevated rims and separated 1 to 1.5 cm in somewhat irregular, concentric circles around a larger, central opening; principal skeleton lychniscose of small spicules with perforated nodes, dermal layer of reticulated stauractines and other irregularly oriented stauractines. Middle Jurassic (Callovian): Spain (Catalonia).-FIG. 360, 3a-d. \*P. tarraconensis, Terracuques de Llebra Rasquera, northeastern Spain, a, side view of typical specimen showing upper discoidal part and lower stalk, slightly reduced; b, view of upper surface with characteristic ovate oscula arranged in somewhat concentric circles, slightly reduced; c, drawing of lychniscoid

spicular elements of main skeleton, scale unknown; *d*, drawing of dermal net of stauractines, scale unknown (Hérenger, 1942).

Sporadopyge SCHRAMMEN, 1937, p. 16 (SCHRAMMEN, 1936, p. 180, nom. nud.) [\*S. speciosa; M]. Broadly funnel-like to discoidal; exterior with closely spaced, small, skeletal pores, arranged without order; gastral side with larger pores spaced more widely; no continuous superficial meshwork, although dermal pentactines occur fused to surface of skeletal framework. Upper Jurassic: Germany, Poland.——FIG. 361. \*S. speciosa, Weiss Jura, Streitberg, Germany; outer surface of dictyonal skeleton with large, inhalant ostia and small, skeletal pores, ×5 (Schrammen, 1936).

### Family UNCERTAIN

Cavispongia QUENSTEDT, 1877 in 1877-1878, p. 153 [\*Spongites cylindrata QUENSTEDT, 1843, p. 418; SD DE LAUBENFELS, 1955, p. 90]. Massive, large, irregularly obconical sponges without spongocoels but with numerous tightly packed, thin-walled tubes with oscular openings on upper, flat to slightly concave summit; lateral surfaces with irregular outgrowths separated by meandering furrows; skeleton regular with square meshes; may include coarse pentactines as part of dermal skeleton. [Fossils are chiefly casts; included by DE LAUBENFELS (1955) in the Cypellidae, were included in the Neoaulocystidae ZHURAVLEVA, 1962, by PISERA (1997)]. Jurassic: Germany.-FIG. 362, 1a-b. C. cylindrata (QUENSTEDT), Kimmeridgian marls and limestone, Upper Jurassic, Hettingen and Wilmandingen; a, side view of top-shaped sponge with irregular, deep furrows between outgrowths, ZPAL Pf. VIII/73,  $\times$ 1; *b*, summit view with several isolated oscula,

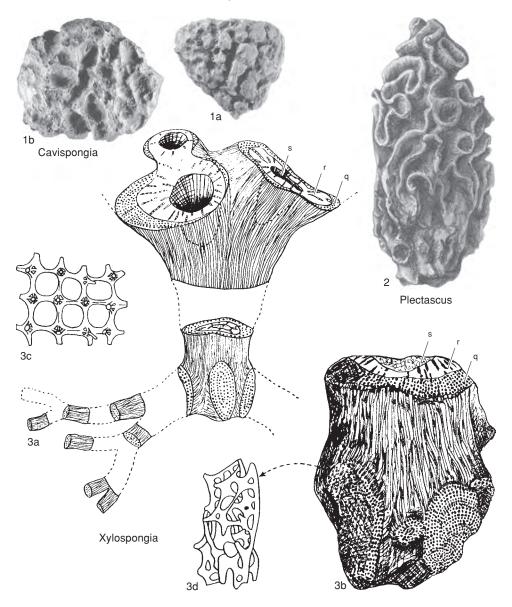


FIG. 362. Uncertain (p. 552-555).

ZPAL Pf. VIII/262, ×1.5 (Pisera, 1997; courtesy of *Palaeontologica Polonica*).

Plectascus SCHRAMMEN, 1912, p. 307 [\*Dendrospongia clathrata F. A. ROEMER, 1864, p. 20; OD] [=Dendrospongia F. A. ROEMER, 1864, p. 20, SD DE LAUBENFELS, 1955, p. 102, nom. oblit.; Code Art. 23.2 (ICZN, 1999)]. Branching and anastomosing tubes; surfaces with quadrately arranged ostia or postica that are in longitudinal furrows on dermal side; further details unknown. [Lychniscosan teste SCHRAMMEN (1912) but resembles some craticulariid Hexactinosa.] Cretaceous (Cenomanian-Turonian): Germany, England.——FIG. 362,2. P. labrosus (SMITH), Upper Greensand, Cenomanian, Folkestone, England; side view of characteristic sponge with folded wall,  $\times 0.5$  (Hinde, 1884a).

Sclerokalia HINDE, 1884a, p. 145 [\*S. cunningtoni; M]. Cup shaped, very thick walled, supposedly unattached; dermal side without canalar features; gastral side with vertical rows of postica of skeletal canals

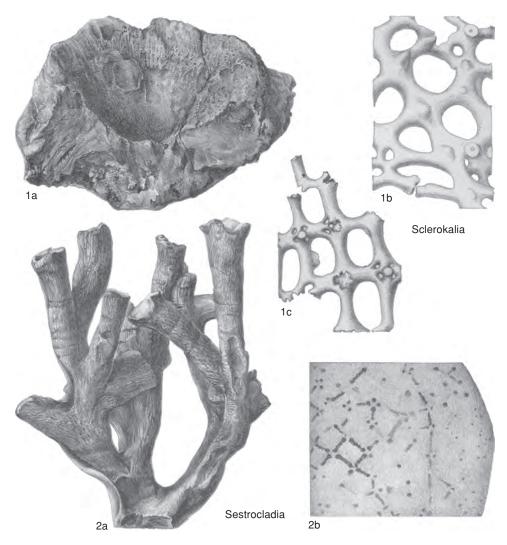


FIG. 363. Uncertain (p. 553-554).

that appear to be shallow; skeletal meshwork regular internally, with nodal octahedra; outer meshwork irregular, without octahedra, and with thick, porous lamella developed at gastral surface. [Based on one imperfect example; possibly a pachyteichismatid with incomplete canalization.] *Cretaceous (Albian):* England.——FIG. 363, 1a-c.~S.*cunningtoni,* Upper Greensand, Warminster, Wiltshire; *a*, side view across broken, thick wall of funnel-shaped sponge with rows of exhalant ostia on gastral surface,  $\times 0.5$ ; *b,* drawing of enlarged, dermal, skeletal net; *c,* drawing of enlarged, spicular mesh immediately interior to dermal layer showing octahedral nodes,  $\times 25$  (Hinde, 1884a). Sestrocladia HINDE, 1884a, p. 117 [\*S. furcatus; M]. Branched, tubular, dermal, skeletal surface with ovate ostia in vague, longitudinal furrows; other details unknown. [Supposedly ventriculitid (HINDE, 1884a, p. 117) or polyblastidiid (DE LAUBENFELS, 1955, p. 89, as coeloscyphiid).] Cretaceous (Cenomanian): England.—FIG. 363,2a-b. \*S. furcatus, Grey Chalk, Dover; a, side view of branched, tubular sponge with dermal ostia in discontinuous, longitudinal furrows, ×0.5; b, drawing of enlarged skeletal structure with octahedral nodes in calcareous replacement, ×25 (Hinde, 1884a).

Xylospongia HERENGER, 1942, p. 176 [\*X. tarraconensis; OD]. Large, steeply obconical sponge with branched, rootlike base, and with upper part where shallow, oscular depressions mark limited branching; upper part of wall layered, with dermal part vertically fibrous and with more or less parallel, longitudinal canals; principal, inner, skeletal layer with regular, lychniscoid structure with perforated nodes and with canals relatively rare and alternating, more or less radial, inhalant and exhalant openings; gastral layer of anastomosing, irregular fibers that are somewhat coarser than dermal layer and with finer, longitudinal canals; rootlike basal parts composed mainly of outer, fibrous layer. Upper Cretaceous (Coniacian-Maastrichtian): Spain.-FIG. 362,3ad. \*X. tarraconensis, Valldarques Lleida, Catalonia, northeastern Spain; a, drawing of reconstruction showing growth form and layered, skeletal structure with outer, longitudinally fibrous part (q), and principal skeleton (r) around shallow, oscular, summit depressions (s), approximately  $\times 0.5$ ; b, fragment showing layered, skeletal structure, with outer, vertically fibrous, dermal layer (q), inner, regular, lychniscoid, skeletal layer (r), and (s) irregular, fibrous, gastral layer, approximately natural size; c, regular, lychniscoid structure of principal, skeletal layer, magnification unknown; d, irregular, skeletal structure of outer, fibrous layer, magnification unknown (Hérenger, 1942).

# Order UNCERTAIN

- Acanothyia POMEL, 1872, p. 68 [\*Camerospongia polydactyla ROEMER, 1864, p. 5; SD DE LAUBENFELS, 1955, p. 94] [=Acanothyra DE LAUBENFELS, 1955, p. 94, nom. null.].Cretaceous (Cenomanian): Germany.
- Antrispongia QUENSTEDT, 1877 in 1877–1878, p. 413
  [\*A. dilabyrinthica; SD DE LAUBENFELS, 1955, p. 94]. The genus might might be included in either the Euretidae or Calypterellidae. Lower Cretaceous: England.
- Baccispongia QUENSTEDT, 1877 in 1877–1878, p. 314 [\*B. baccata; SD DE LAUBENFELS, 1955, p. 94]. Cup shaped, lumpy. Jurassic: Germany.
- Bothroconis KING, 1850, p. 14 [\*B. plana; OD]. Vaselike to flat, creeping sponges with flaring rim; skeletal structure unknown. *Permian:* England.
- Crucispongia QUENSTEDT, 1877 in 1877–1878, p. 164 [\**C. annulata* QUENSTEDT, 1877 in 1877–1878, p. 165; SD DE LAUBENFELS, 1955, p. 94]. Annulate cup. *Jurassic:* Germany.
- Diplopleuriana REID, herein, nom. nov. pro Diplopleura REGNARD, 1926, p. 485, non STIMPSON, 1857 [\*Diplopleura hatoni REGNARD, 1926, p. 485; OD]. Irregular, flattened sponge with short stalk; exterior with numerous irregularly distributed, fine pores; interior surface lacking pores and exhalant canals; skeleton regular lychniscoid. Cretaceous (Cenomanian): France.
- Farreopsis SCHRAMMEN, 1924a, p. 29 [\*F diffusa; OD]. Large, thin-walled sponge of broad, irregularly anastomosing tubes; canal system poorly developed; skeletal structure of fused, cubic meshes; outer, free

radial rays of dermal and gastral hexactines long and conical. *Upper Cretaceous:* Germany.

- Hodsia MOISEEV, 1944, p. 19 (MOISEEV, 1939, p. 816, nom. nud.) [\*H. caucasia; OD]. Cylindrical sponges with narrow, axial spongocoel; thick walls formed of branched, upwardly and outwardly divergent, angular to rounded tracts that roughly parallel coarse canals; these tracts irregularly cross connected with finer tracts and both are interrupted by canals or connecting pores; spicule structure unknown. [The name was proposed by MOISEEV (1939, p. 816) but no description was given until the genus and species were described by MOISEEV in 1944.] Triassic (Norian-Rhaetian): Russia (Caucasus region).-FIG. 364, 1a-b. \*H. caucasia, Norian-Rhaetian sediments, Hosdia Valley; a, transverse section showing thick walls around small, axial spongocoel, with divergent and cross-connecting tracts interrupted by somewhat coarser canals, tracts thickened in dermal and gastral regions, ×4; b, diagonal section showing upwardly divergent and moderately uniform, skeletal structure, ×4 (Moiseev, 1944).
- Lonsda DE LAUBENFELS, 1955, p. 94, nom. nov. pro Conis LONSDALE, 1849, p. 63, non BRANDT, 1835 [\*Conis contortuplicata LONSDALE, 1835, p. 63; OD]. Many-ridged mass. [DE LAUBENFELS, 1955, p. 86, also proposed Lonsda as a new name for Gonis, a misspelling of Conis.] Cretaceous: England.
- ?Pachylepisma SCHRAMMEN, 1902, p. 14 [\*P. robusta; M] [?=Leiostracosia SCHRAMMEN, 1902, p. 12 (type, L. punctata, OD)]. Barrel-shaped to funnel-shaped sponges with broad stem; thick wall around broad spongocoel; exterior marked with numerous irregularly distributed ostia of blind, inhalant canals that alternate in interior with large, exhalant canals; skeleton lychniscoid with common, short spines and exterior with broadened, tangential rays. Upper Cretaceous: Germany.——FIG. 364,2. \*P. robusta, Quadratenkreide, Misburg; side view of holotype showing barrel-shaped form and rough exterior with round, irregularly distributed, exhalant ostia, ×0.5 (Schrammen, 1902).
- Pinnatispongia DONG & KNOLL, 1966, p. 177 [\*P. bengtsoni; OD]. Isolated pentactines with principal, curved ray and four small, propeller-like, lateral rays that diverge nearly normal to central ray at its summit; central ray longer and much thicker and ornamented with three or four rows of nearly parallel barbs that lend featherlike appearance to spicules. *Cambrian (Furongian):* China.—FIG. 364,3. \*P. bengtsoni, Bitiao Formation, middle upper Cambrian, Huayuan, Hunan; side view of type spicule, ×60 (Dong & Knoll, 1996).
- Rugosoderma HOWELL, 1957b, p. 6 [\*R. texasense; OD]. Sponge with numerous thin-walled branches that have small, horizontal, dermal ridges and vertical lines of pits on gastral surface; skeleton reported to be similar to Coeloscyphia, with small knobs at spicule centers. Lower Cretaceous: USA (Texas).—FIG. 364,4. \*R. texasense, Fort Worth

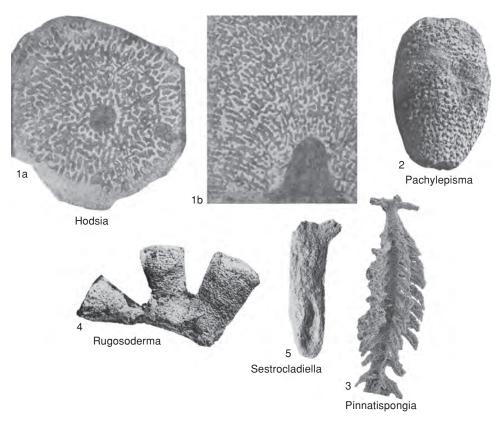


FIG. 364. Uncertain (p. 555-556).

Formation, near Blum, Hill County; side view of holotype showing rough, dermal surface and branching habit, PU 76286, ×1 (Howell, 1957b).
 Sestrocladiella HOWELL, 1957b, p. 5 [\*S. bifurca; OD]. Small, moderately thick-walled sponge as columnar individual that branches in uppermost part; dermal surface indented with irregularly spaced, round pits separated by rounded ridges; pits extending through wall as canals, at least locally; skeleton reported to be similar to that in *Ceoloscyphia*, with small knobs

at spicule centers. *Lower Cretaceous:* USA (Texas). ——FIG. 364,5. \**S. bifurca*, Fort Worth Formation, near Blum, Hill County; side view of holotype showing pitted, dermal surface and small, upper branch of generally columnar form, with diagonal section of broad spongocoel near base, PU 76284, ×1 (Howell, 1957b).

Spongus MANTELL, 1822, p. 164 [\**S. townsendi;* SD DE LAUBENFELS, 1955, p. 94]. Cup shaped. *Cretaceous:* England.

# HETERACTINIDA

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# Class HETERACTINIDA de Laubenfels, 1955

[Heteractinida DE LAUBENFELS, 1955, p. 93]

Sponges in which the spicules, probably originally calcitic, have a hexagonal symmetry, or are derivable therefrom by addition or suppression of rays. *Lower Cambrian– Permian (Cisuralian).* 

## MORPHOLOGY AND PHYLOGENY

The Heteractinida is a minor class of sponges and has only a Paleozoic record. Most characteristic forms have spicules with six rays in one plane, to which are added in later forms a long, proximal ray and sometimes a short distal ray. Such spicules are most commonly and best preserved as calcite, which would seem thus to be their original substance. Their rays are characteristically thick, and suturing between rays and a central disk appears to be absent. Except in Cambrian members and related genera of eiffeliids, the heteractinid sponges have thick body walls consisting of closely packed spicules whose six coplanar rays are subparallel to the outer surface of the sponge. The eiffeliids and several other pre-Carboniferous genera lack skeletal canals as the fossils are now preserved, and their surfaces lack skeletal pores other than interspicular spaces.

Astraeospongium ROEMER, 1852, is the best-known and perhaps most typical member of the class. The mid-Silurian type species, A. meniscus (ROEMER, 1848), has spicules that lack mostly or entirely any proximal and distal rays. Similar concavoconvex, obconical, or discoidal Devonian sponges, also assigned to Astraeospongium, have spicules with a higher proportion of proximal and distal rays.

A globose Silurian species with stronger proximal rays is known, and the Ordovician

genera *Constellatospongia* RIGBY, 1977b, and *Asteriospongia* RIGBY, 1977a, also have spicules with strong, proximal and distal rays. The Silurian *Astraeospongium* may have been ancestral to the Silurian and Devonian *Ensiferites* REIMANN, 1945b, which is also globose to discoidal. *Ensiferites* has spicules in which the proximal ray is very long and stout and the six paratangential rays are relatively short. A consistent feature of these Siluro-Devonian species is the greater stoutness of spicules on upper surfaces compared with those on lower surfaces or in the interior.

VANDERCAMMEN (1950) described a sponge from the Early Carboniferous (Tournaisian) of Belgium that he assigned to Asteractinella HINDE, 1888, a genus originally described by HINDE from isolated, siliceous or silicified spicules from the Visean of Scotland. VANDERCAMMEN's sponge has the form of a thick-walled, plicated obcone, easily derivable from the form of Astraeospongium. Its spicules include some with six paratangential rays and a long proximal ray; others of the same umbrella-like shape with more than six paratangential rays, often with tuberculate distal surfaces; and large, stoutrayed oxyasters, with multiple rays radiating from a common center.

*Regispongia* RIGBY, 1978, has a very similar complement of spicules. It first appeared in the Chesterian (Late Mississippian) and persisted into the lower Permian rocks. It is conicocylindrical with a central cloaca, but large specimens may be externally subplicate, recalling VANDERCAMMEN's sponge in a subdued way. The related *Wewokella* GIRTY, 1912, also possesses tetraradiates, that is, spicules with three coplanar rays and a proximal ray. Such spicules may be regarded as reduced versions of the spicules with six coplanar rays. Other six-rayed spicules have a

rosette of spines at the center of the distal surface, again easy to derive from the Early Carboniferous species. There seems to be little doubt that VANDERCAMMEN's sponge is related to *Wewokella*.

Although these Carboniferous genera differ from Astraeospongium in having multiple spicule rays, the general form of the skeletal net, the stoutness of the spicule rays, and their calcitic composition accords with the earlier genus. These Permo-Carboniferous species possess radial, inhalant and exhalant skeletal canals, although they are not always well developed in many individuals. The Devonian Stellarispongia RIGBY, 1976a, possesses strongly developed skeletal canals within a spicular context like that of Astraeospongium. It is quite possible that Stellarispongia is the connecting link between Astraeospongium and VANDERCAMMEN's Asteractinella. It is already more strongly cup shaped than Astraeospongium but lacks the plicate outline of the Carboniferous form.

Tracing the Astraeospongium lineage back before the Silurian, we find two mid-Ordovician genera, Astraeoconus RIETSCHEL, 1968, and Toquimiella RIGBY, 1967a. Astraeoconus is much thinner walled than Astraeospongium and has a definite cloaca. Its spiculation is entirely of regular sexiradiates with six coplanar rays parallel to the sponge surface, and the body wall is several spicule layers thick. Toquimiella is similar in general form but its sexiradiates are peculiar and also bilaterally symmetrical about a plane parallel to the longitudinal axis of the sponge, a feature that occurs also in some specimens of the Carboniferous Wewokella.

One predicts a Cambrian ancestor of this lineage to have a spiculation of sexiradiates and a very thin walled body. Such skeletons exist in *Jawonya* and *Wagima*, described by KRUSE (1987) from the Middle Cambrian of northern Australia, and in *Eiffelia* WALCOTT, 1920, of the Middle Cambrian Burgess Shale. Neither is a generalized ancestral forms, however, for all three have some advanced structures. *Eiffelia* has a skeleton of regularly oriented and placed, large spicules and similar smaller spicules in a complex skeleton. On the other hand, *Jawonya* and *Wagima* have skeletons of small, irregularly oriented and placed octactines and polyactines, as one would expect in an ancestral form for the *Astraeospongium* lineage, but both Australian Cambrian genera have pronounced, collarlike oscula; and *Wagima* has domed, sievelike screens over the inhalant ostia, as advanced-appearing features.

Two Lower Cambrian genera, Kuraya ROMANENKO, 1968, and Blastasteria DEBRENNE, TERMIER, & TERMIER, 1971, may be early representatives of the lineage. They are characterized by spicules in which the six tangential rays are reflexed at a 45° angle toward the sponge body, a feature that occurs locally also in the late Paleozoic Wewokella, Asteractinella, and Tholiasterella. Otherwise they are globose, thin-walled forms like Eiffelia. The spicules of Blastasteria possess proximal rays, which may be present possibly in Eiffelia but which have not been demonstrated unequivocally. A possible conservative survivor of this early, thin-walled group (RIGBY, 1991a) is the Pennsylvanian Zangerlispongia RIGBY & NITECKI, 1975, with a spiculation of tuberculate sexiradiates.

The peculiar spongelike genus Chancelloria WALCOTT, 1920, occurs with Eiffelia in the Burgess Shale and has a worldwide distribution in rocks of Early and Middle Cambrian age. It and such related forms as Archiasterella Sdzuy, 1969, Allonia Doré & REID, 1965, and Nabaviella MOSTLER & MOSLEH-YAZDI, 1976, and, with some question, Uranosphaera BEDFORD & BEDFORD, 1934, have been considered to be heteractinid sponges by these workers and others (RIGBY & NITECKI, 1975). Chancelloriids were interpreted to be the stem group of all sponges by SDZUY (1969). The chancelloriids are now considered not to be sponges, however, but Coeloscleritophora with an armor of spiny sclerites (BENGTSON, 1990b, p. 45).

An additional group of fossils that have been considered to be possible heteractinid sponges include four genera from the Lower Cambrian of Australia, Siberia, and Morocco. The four genera, associated with archaeocyathids, form a morphological series: Uranosphaera BEDFORD & BEDFORD, 1934, Gonamispongia Korshunov, 1968, Girphanovella ZHURAVLEVA, 1967, and Radiocyathus OKULITCH, 1937. Uranosphaera consists of an external layer of starlike spicules with about twelve reflexed, often branching, tangential rays, that may fuse with those of neighboring spicules. Gonamispongia is very similar, except that all the spicules are fused into a rigid mesh and a proximal ray extends inwardly from the center of each spicule. Girphanovella has an additional inner cloacal lining of similar spicules connected to the outer layer by the proximal rays. Finally, Radiocyathus has both layers coated with a continuous, perforate, calcareous sheet. It is tempting to see in this series the progressive calcification of a system of soft parts (perhaps as much ontogenetic as phylogenetic). Whether these spheroidal to conical objects had the hollow interior filled with a soft thallus, in the manner of the receptaculitids, surrounded by a variably calcified fuzz of branches, or whether they are related to the archaeocyathids, with some kind of pre-metazoan tissue in the intervallum, cannot be settled here. DEBRENNE, TERMIER, and TERMIER (1971) were the first to call attention to the relationship between these four genera and proposed a classification for them, placing them with Kuraya and Blastasteria in the proposed class Radiocvatha. These authors considered the radiocyathids to be more primitive than true sponges, possibly similar to protozoans that may have been ancestral to some metazoans. NITECKI and DEBRENNE (1979) concluded that the radiocyathids may be more closely related to receptaculitids than to archaeocyathids. Inasmuch as they were not included in the 1972 revision of the Archaeocyatha part of Treatise Part E (TEICHERT, 1972) (except Radiocyathus), it seems appropriate to treat them here, although their status as Porifera is doubtful.

Kuraya and Blastasteria, discussed earlier as relatives of Eiffelia, co-occur with the four Lower Cambrian genera of the Uranosphaera-Radiocyathus group. It is not beyond belief that they are all related, as DEBRENNE, TERMIER, and TERMIER (1971) and NITECKI and DEBRENNE (1979) stated. Nevertheless, *Karaya* and *Blastasteria* have symmetrical, unbranched, six-rayed spicules, like those of normal heteractinids, and are therefore treated as such here.

Finally, it should be pointed out that *Leptopoterion* ULRICH, 1889, and *Anomal-oides* ULRICH, 1878, are probably algae related to the receptaculitids (see RAUFF, 1892; RIETSCHEL, 1968a).

As interpreted here, the true heteractinid sponges constitute branched lineages of Eiffelia-Zangerlispongia, and Astraeospongium and its relatives. The Lower Cambrian Kuraya and Blastasteria are the earliest known representatives. Thicknesses of their tangential rays suggests that they may have led directly to Astraeospongium itself, with the slender-rayed Eiffelia as a Cambrian offshoot. We do not know, however, how much iterative evolution has taken place in the heteractinids, and the suggestion is supported chiefly by parsimony. *Eiffelia* may have given rise to the similarly slender-rayed Cambrian Eiffelospongia, Ordovician Toquimiella, and Pennsylvanian Zangerlispongia. In these sublineages there is a common trend from spheroidal to conical shape and the development of a thicker body wall. In Astraeospongium the interior hollow space was eliminated completely. Isolated Ordovician spicules have been assigned to Astraeospongium, but they could well have come from a related genus or genera with a different body form.

*Ensiferites* evolved as early as in the Silurian (sometimes misidentified in collections as *Anomaloides*) and diversified with several species in the Devonian (REIMANN, 1945b; RIGBY, 1979). It is distinguished by a spheroidal to discoidal shape and octactine-based spicules with very stout, proximal rays and six finer, tangential rays. It may represent a side branch of the lineage. *Ensiferites* may have additional rays on distal surfaces of the tangential rays or as supernumerary rays from tips of distal rays, which demonstrates that the potentiality for additional rays was already present in the Devonian.

Stellarispongia is a Devonian relative of Astraeospongium (which also persisted into the Devonian) that differs in having skeletal canals and in resembling a thick-walled cup rather than a thick saucer. In shape it is not far from the lowermost Carboniferous Asteractinella of VANDERCAMMEN (1950), which has added radial plications. In spiculation, however, this is the major break in the history of the heteractinids. All the post-Devonian genera have various polyactines along with sexiradiates and umbrella-shaped septiradiates of the earlier forms. It is possible that the fragmental type materials of Tholiasteralla and Asteractinella of HINDE (1887b, 1888) are not heteractinids but rather siliceous sponges (see REID, 1963b; FINKS, 1960).

There is not such doubt about the completely preserved Asteractinella of VANDER-CAMMEN, however. The slightly later appearing Regispongia (late Mississippian to early Permian) and Pennsylvanian Wewokella could be envisaged easily to have evolved from VANDERCAMMEN's sponge. The cup shape becomes a tube; the new polyactines, as well as the older spicule types, are all retained; and a new simplification sets in, in that the tangential rays of many spicules are reduced to three, making them like the tetraradiates of the typical Calcarea. A tendency to fusion of the spicules by secondary calcite becomes more pronounced in the Permian (Cisuralian) Talpaspongia, which if it differs from Wewokella at all, does so in this and in a broader cloaca and somewhat finer spicules. The heteractinids die out with Talpaspongia in the Artinskian (Leonardian). There is a remote possibility that the Devonian Protoleucon BOLKHOVITINOVA, 1923, is related to Wewokella; this is based on its form and references to star-shaped bodies in its description. It would be worth examining the specimens (which we have not seen) with this in mind. The Pennsylvanian Zangerlispongia in its distal tuberculation suggests relationship to Asteractinella or Tholiasterella, but its thin-walled nature and well-organized skeletal net may indicate a descent from the Eifellia-Toquimiella stock.

## CLASSIFICATION

Heteractinida DE LAUBENFELS, 1955, is used here as the name of the class. That name is distinct from Heteractinellidae HINDE, 1887b, both as a name (the stems differ: heteractin- vs. heteractinell-) and as a concept. DE LAUBENFELS (1955, p. 93) ascribed the name Heteractinida to HINDE, apparently in the belief that he was merely changing the ending. Both names are available for the class because the Code (ICZN, 1999) recognizes class and order level as a single group for the purposes of attribution of authorship but does not require priority. (Heteractinellidae was originally proposed as a suborder.) Differences in concepts of the groups are significant, however. The usage here conforms to that of DE LAUBENFELS's in including both the Octactinellidae and Heteractinellidae in the Heteractinida (as was done earlier by REID, 1963b, p. 234; RIGBY, 1983b, p. 73; 1986a, p. 56). The original Heteractinellidae of HINDE as a concept is equivalent to the family Wewokellidae of the present classification, although emended from HINDE's original definition. In addition to the polyactines that HINDE considered diagnostic, octactines and their derivatives are present in all the species preserved as whole individuals; and, indeed, those polyactines are probably octactine derivatives. Thus, the present classification assigns HINDE's original heteractinellid genera, Asteractinella and Tholiasterella, along with Wewokella and Talpaspongia, to HINDE's Octactinellida, which HINDE originally proposed as a separate and equal category. The order Wewokellida CRONEIS & TOOMEY, 1965, is equivalent to HINDE's suborder Heteractinellidae in its concept.

The Octactinellida are here interpreted as all those sponges centering about *Astraeospongium*, characterized by coarse-rayed spicules composed of radially fibrous calcite and derivable from the plan of an octactine. They are essentially the so-called true heteractinids. The other possible order dealt with here, the Hetaircyathida BEDFORD & BED-FORD, 1937, is not considered to be related to them at all.

The subgroup in which the spicules are primarily radially symmetrical, very coarserayed sexiradiates, or octactines with a long proximal and short, distal ray and in which the body wall consists of solidly and irregularly oriented and packed spicules are placed in the family Astraeospongiidae MILLER, 1889. Kuraya and Blastasteria have relatively thin body walls but are placed here because of the coarseness and irregular orientation of their spicules. Stratigraphic occurrence of these early genera suggests that they may have been ancestral to the thinner-walled eiffeliids, with which they might also be placed on account of their thin wall, and are possibly also ancestral to the later astraeospongiids.

The thin-walled forms with symmetrically arranged, relatively slender-rayed spicules, that either lack proximal and distal rays or have them very weakly developed, are here assigned to the family Eiffeliidae RIGBY, 1986a. They could have resulted from iterative evolution from more typical astraeospongiids, but their concentration in the Cambrian and Ordovician (except for *Zangerlispongia*) suggests they are a natural, early separated group.

The late Paleozoic Wewokellidae KING, 1943, have spicules with more rays (polyactines) and fewer rays (tetraradiates) present alongside the earlier octactine types. They are also characterized by secondary calcareous overgrowth on the spicules and fusion of the skeletons in all but some of the early species. In addition to the octactines, the coarseness of their rays composed of radially fibrous calcite relates them to the typical astraeospongiids. Extra rays in some Ensiferites spicules, as well as skeletal canals in Asteriospongia, Constellatospongia, and Stellarispongia, show that the Ordovician to Devonian astraeospongiids were beginning to approach the morphology of the succeeding wewokellids of the Mississippian.

A dubious order of convenience included here is the group of genera connecting Uranosphaera with Radiocyathus. As discussed above these are probably neither heteractinids nor sponges. Uranosphaera was included by DE LAUBENFELS (1955) in his family Asteractinellidae, equivalent to the Wewokellidae of the present work. Radiocyathus was included by OKULITCH (1955) in the Archaeocyatha but was considered probably not a member by HILL (1972). Nevertheless the two genera are clearly related to one another through Gonamispongia and Girphanovella, and the group must be recognized somehow. DEBRENNE, TERMIER, and TERMIER (1971) proposed a classification of the group, modified only slightly by NITECKI and DEBRENNE (1979), and included within their class Radiocyatha the families Uranosphaeridae, to include the genera Kuraya, Uranosphaera, and Gonamispongia, Girphanovellidae, to include the genera Blastasteria and Girphanovella, and Radiocyathidae, to include Radiocyathus.

A slightly different classification for these problematic fossils is proposed here. The ordinal name Hetairacyathida BEDFORD & BEDFORD, 1937, and the family name Hetairacyathidae BEDFORD & BEDFORD, 1934, are available and valid for this group. (They were based on *Hetairacyathus* BED-FORD & BEDFORD, 1937, a junior synonym of *Radiocyathus*.) It is possible that *Kuraya* and *Blastasteria* belong here also, but a final judgment cannot be made without seeing all the specimens.

A classification of heteractinid sponges published by RIGBY (1976b) differs from that used here by including Eiffelia, Toquimiella, and Zangerlispongia in the Chancelloriidae and by deriving the Wewokellidae from this group, with the Astraeospongiidae, including Astraeoconus, as a side branch. More recent versions (RIGBY, 1986a, 1991a, 1991b) removed Chancelloria from the Heteractinida, erected the family Eiffeliidae for the thin-walled forms, and used the Astraeospongiidae for octactine-based genera and the Wewokellidae for those derived genera with polyactine-based skeletons. ZIEGLER and RIETSCHEL (1970) separated the chancelloriids from the Octactinellida, as here, and included Eiffelia with the octactinellids (as did FINKS, 1967b, 1970 by implication). They considered both groups to be related to the Calcarea and to be separate offshoots of the Dialytina, which they conceived to be the basic calcisponge stock. RIETSCHEL (1968a, p. 16) earlier pointed out that the trigonal symmetry of the octactinellid spicule relates them to the Calcarea and presented much the same distribution of genera as in his later work with ZIEGLER (ZIEGLER & RIETSCHEL, 1970).

# Order OCTACTINELLIDA Hinde, 1887

[*nom. transl.* FINKS & RIGBY, herein, *pro* subclass Octactinellida REID, 1957a, p. 285, *nom. transl. et correct. ex* suborder Octactinellidae HINDE, 1887b, p. 91]

Fundamental spicules with six equally spaced rays either parallel to surface of sponge or irregularly oriented, rays either in one plane or frequently reflexed toward sponge body, and with variably developed proximal and distal rays along an axis at right angles to six; proximal ray usually longer than often suppressed, distal ray, and may be longer than paratangential rays. Earlier forms with only six paratangential rays on most spicules; later forms may suppress alternate three paratangential rays or increase their number; distal ray may be replaced by rays that radiate in all directions of upper hemisphere, and polyasters may be present with rays radiating in all directions of a sphere from common center. Rays usually stoutly and bluntly conical, sometimes bent, may be flattened in paratangential plane, or constricted near crossing, sometimes bearing distal tubercles, may be fused with neighboring rays. These listed features seem to result from deposition of secondary calcite about originally slender, symmetrical ray that lacks possible axial canal; where not recrystallized, both primary and secondary deposits appear to be fibrous calcite, fibers radiating from ray axis. Lower Cambrian–Permian (Cisuralian).

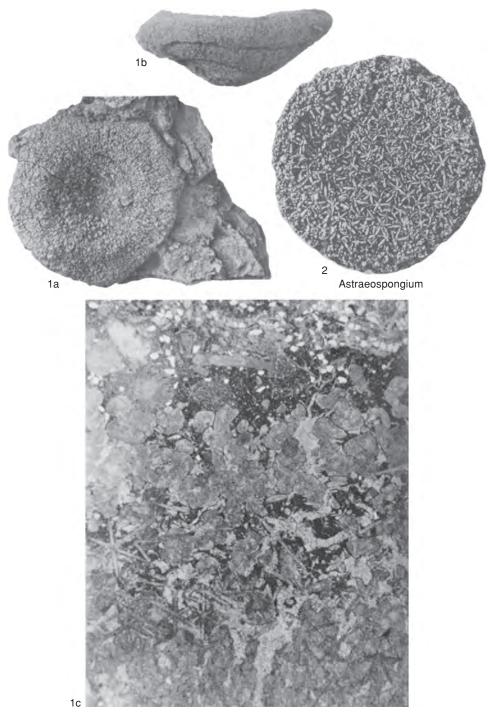
## Family ASTRAEOSPONGIIDAE Miller, 1889

#### [Astraeospongiidae MILLER, 1889, p. 153]

Spicules sexiradiates, septiradiates, or octactines with stout rays; body wall thin in early genera and thick in later ones, composed of several layers of densely packed, irregularly arranged and oriented spicules; body spheroidal, discoid, meniscate, conoidal, or open-cup shaped; osculum and spongocoel developed in early genera (*Kuraya* and *Blastasteria*) but not in later ones. *upper Lower Cambrian–Devonian*.

- Astraeospongium ROEMER, 1852, p. 155 [\*Blumenbachium meniscus ROEMER, 1848, p. 683; OD] [=Octacium SCHLÜTER, 1885, p. 151 (type, O. rhenanum, M); Acanthaspongia M'Coy, 1846, p. 67 (type, A. silurensis, SD DE LAUBENFELS, 1955, p. 78); Acanthospongia ROEMER, 1861, p. 14, obj.]. Sponge discoidal, concavoconvex (concave side up) or squat, inverted cone; no spongocoel preserved, entire sponge filled with closely packed spicules. Spicules sexiradiates, or octactines with short, distal ray and longer, proximal ray; tangential rays may be bent or distorted, and frequently flattened in tangential plane; spicules regularly larger on upper than on lower surface. [Blumenbachium KOENIG, 1820, type species B. globosum KOENIG, 1820, by monotypy, was specifically stated by ROEMER, 1854, not to be a synonym. Even if it were, it would be a nomen oblitum by the Code (ICZN, 1999).] ?Ordovician; Silurian-Devonian: cosmopolitan .-FIG. 365,2. \*A. meniscus (ROEMER), Brownsport Formation, middle Silurian, Perry County, Tennessee, USA; view into shallow, saucer-shaped, gastral area showing several orders of octactine-based spicules, ×1 (Rigby, 1987b).
- Asteriospongia RIGBY, 1977a, p. 123 [\*A. anatrope; OD]. Thick-walled, dome-shaped sponges in which large, nearly vertical, excurrent canals empty onto rounded summit that lacks spongocoel; skeletal net of moderately regularly spaced, but irregularly oriented, small octactines or octactine-based derivatives, such as sexiradiates, in felted mass; outer onefifth of wall dense, produced by calcareous overgrowths on spicules. Middle Ordovician: Canada (District of Franklin, Melville Peninsula, Baffin Island).-FIG. 366, 1a-b. \*A. anatrope, Bad Cache Rapids Limestone, Wildernessian-Barneveldian; a, upper surface of inverted, bowlshaped holotype, with distinctive canals on spongocoel-free, domed surface, GSC 43201, ×1; b, horizontal section with small, octactine spicules, some to right secondarily enlarged, in dense skeleton, perforated by small and large canals, GSC 43202e, ×10 (Rigby, 1977a; courtesy of Minister of Public Works and Government Services Canada, 2000 and the Geological Survey of Canada).
- Blastasteria DEBRENNE, TERMIER, & TERMIER, 1971, p. 442 [\*B. bedfordorum; OD; nom. nov. pro Uranosphaera hexaster BEDFORD & BEDFORD, 1936, p. 10, fig. 39, non BEDFORD & BEDFORD, 1934, p. 7, fig. 36]. Body an invaginated sphere, with broad spongocoel whose lining is continuous with that of exterior over rounded, oscular lip, spicules with six reflexed, tangential rays and longer, proximal ray. [Genus differs from Kuraya in having a spongocoel

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Malluviospongia





FIG. 366. Astraeospongiidae (p. 562).

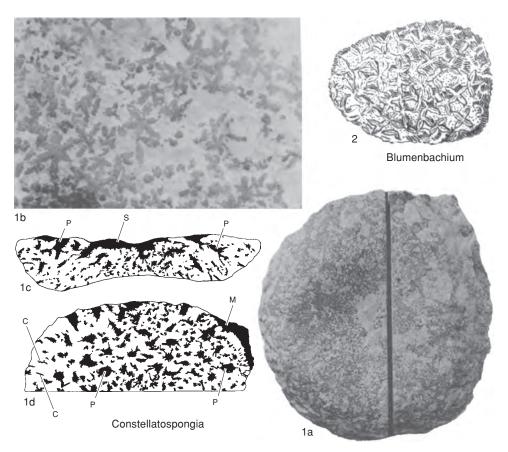


FIG. 367. Astraeospongiidae (p. 562-566).

lining of spicules and in having proximal rays on the spicules.] *Lower Cambrian:* Australia.——FIG. 366,2. \*B. *bedfordorum;* restoration, ×2.4 (Debrenne, Termier, & Termier, 1971; courtesy of Société Géologique de France).

- Blumenbachium KOENIG, 1820, p. 3 [\*B. globosum; M]. Globose to hemispherical sponge with interior filled with irregularly porous material showing obscure concentric and radial structure; arched surface covered with star-shaped, 3- to 5-pointed, spiculelike objects, mostly with four seemingly flattened, tangential rays. [Description based on original illustration.] ?Devonian: Germany.——FIG. 367,2. \*B. globosum; side view of globose holotype with large spicules that dominantly have four tangential rays at sponge surface, scale not given (Koenig, 1820).
- **Constellatospongia** RIGBY, 1977b, p. 131 [\**C. pervia;* OD]. Thick-walled, saucer-shaped sponges, with lateral slopes pierced by large, irregular, parietal gaps that rise approximately normal to outer slopes and empty into broad, shallow spongocoel; intermediate and smaller canals radiate approximately

normal to parietal gaps into dense, spicular, sponge wall; base slightly invaginated, gaps absent; spicules relatively fine octactines with six horizontal rays locally roughly concentric to surface of sponge and marking former positions of exterior sexiradiates or octactines with distal rays aborted; proximal and distal rays essentially same diameter and length as horizontal rays in interior spicules; some exterior spicules with small nodes or irregularities on basic, octactine spicule, probably result of minor secondary calcification. Upper Ordovician: Canada (Manitoba).--FIG. 367,1a-d. \*C. pervia, Churchill River Group, Richmondian, Herriot Creek southwest of Churchill, northern Manitoba; a, uparched base of saucer-shaped holotype, with dimples along lateral slopes at parietal gaps, ×0.5; b, photomicrograph of base exterior with octactine or sexiradiate spicules of two orders of size, some of which have six tangential rays that are knobby with secondary overgrowths, ×5; c, tracing of vertical section through holotype with matrix-filled, parietal gaps (P) and spongocoel (S) shown in black,  $\times 1$ ; d, tracing of horizontal section at approximately

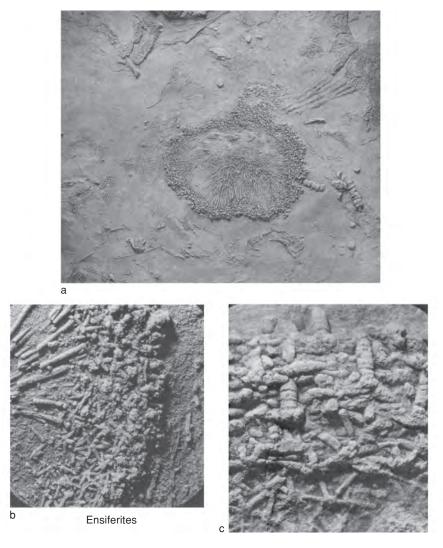
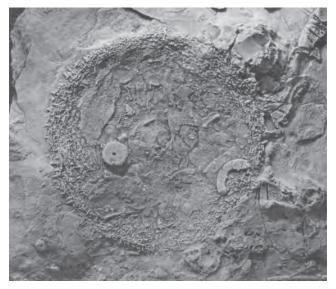


FIG. 368. Astraeospongiidae (p. 566-567).

midheight in holotype showing parietal gaps (P) and smaller canals (C) in interior of sponge, with matrix (M) on margin, GSC 45686, ×1 (Rigby, 1977b; courtesy of Minister of Public Works and Government Services, 2000, and the Geological Survey of Canada).

Ensiferites REIMANN, 1945b, p. 17 [\**E. armatus;* OD]. Sponges irregularly globular, discoidal, or mushroom shaped, possibly hollow; osculum and canal system ill defined or absent; outer spicules consisting of six small and symmetrically disposed, tangential rays, a very much stouter and longer, proximal ray that may be fusiform or abruptly constricted at junction with tangential rays, and a knoblike, distal ray that may have branching; spicules larger on presumed upper surface than on lower one; proximal rays of smaller spicules interspersed among larger ones (on both surfaces) and may be mistaken for monaxons. Interior spicules simple or modified small octactines, irregularly oriented. Comitalialike, fine monaxons also may be present parallel to proximal rays. *Silurian (Wenlock)–Upper Devonian:* USA (New York, Michigan, Tennessee, Arizona). ——FIG. 368*a–c. \*E. armatus,* Onondaga Limestone, Eifelian, Buffalo, New York; *a*, holotype from above with prominent, converging, proximal, spicule rays and dermal layer of matted, tangential rays of octactines, ×1; *b*, photomicrograph of part of skeleton with distinct, tangential rays in dermal layer and long, proximal rays extending into inte-



Ensiferites

FIG. 369. Astraeospongiidae (p. 566-567).

rior of sponge, BMS E16060, ×5; *c*, photomicrograph of outer part of holotype showing short, robust, distal rays and finer, matted, tangential rays, BMS E14876, ×5 (Rigby, Schumacher, & Meader, 1979).—FIG. 369. *E. bennetti* REIMANN, Onondaga Limestone, Eifelian, Buffalo, New York; holotype with central, saucerlike, gastral surface partially obscured by matrix, but with dense, dermal layer well exposed around margin where robust, distal rays project outwardly, ×1 (Rigby, Schumacher, & Meader, 1979).

- Kuraya ROMANENKO, 1968, p. 271 [\*K. sphaerica; OD]. Oblate, spheroidal sponges, thin walled with large osculum; spicules sexiradiates with rays reflexed toward sponge body at 45°. [Genus differs from Eiffelia in reflexion of the paratangential rays and in the irregular arrangement of the spicules.] upper Lower Cambrian: Russia (Siberia), Australia.——FiG. 370, Ia–c. \*K. sphaerica, Lenan, Lower Cambrian limestone, Altay Highlands, Siberia; a, small holotype with spicules having six tangential rays, ZSGU 435/7; b, small paratype with sexiradiate spicules well developed, ZSGU 435/9; c, generalized diagram of sponge body, ×5 (Romanenko, 1968).
- Magenia FINKS, 1995, p. 5 [\**M. david* FINKS, 1995, p. 6; OD]. Sponge oblately globose, possibly hollow, but without osculum; spicules of presumed upper surface with six broad, tangential rays like equilateral triangles, a very short or absent distal ray, and possibly a stout, proximal ray; spicules of presumed lower surface with six slender, tangential rays, a well-developed short to knoblike, distal ray, and a stouter proximal ray about twice length of tangen-

tial rays. *Silurian (Wenlock–Ludlow):* USA (Oklahoma).——FIG. 371*a–c. \*M. david*, Henry house Formation, Pontoon County; *a*, possible upper surface of holotype with broad-rayed octactines; *b*, side and part of basal surface (above) with slender-rayed octactines, ×2; *c*, side of spheroidal holotype showing some spicules with knob as distal ray, USNM 127738, ×10 (Finks, 1995).

Malluviospongia RIGBY & GOODBODY, 1986, p. 345 [\*M. densa RIGBY & GOODBODY, 1986, p. 347; OD]. Saucer- to bowl-shaped or stalked, obconical sponges; thick walls perforated by well-defined, irregularly placed, radial canals that empty into more open canals near spongocoel floor and flank; skeleton of walls zoned with compact, dermal layer of small, lumpy, octactine-based spicules; interior of wall of moderately well organized, clearly defined octactines of several ranks, which grade gastrally into lumpy, coarsely overgrown, grotesque spicules. Lower Devonian-Middle Devonian: Canada (Northwest Territories, Ellesmere Island).-FIG. 365, 1a-c. \*M. densa, Bird Fiord Formation, Eifelian, District of Franklin, southwestern Ellesmere Island; a, vertical view of holotype with simple, open spongocoel and thick walls with grossly lumpy spicules that define radial canals, UA 7535, ×1; b, side view of paratype showing annulate, lower part, UA 7537, ×1; c, photomicrograph of vertical section of paratype showing wellorganized skeleton with ranked octactines in lower, dermal part and lumpy overgrowths on spicules in upper, endosomal and gastral part between dark, matrix-filled canals and beneath quartz-rich fill of spongocoel, UA 7538, ×10 (Rigby & Goodbody,

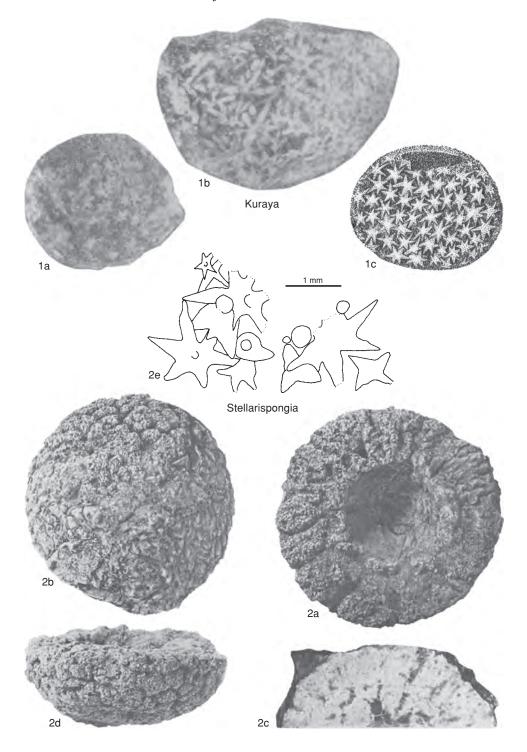


FIG. 370. Astraeospongiidae (p. 567-569).



FIG. 371. Astraeospongiidae (p. 567).

1986; courtesy of *Canadian Journal of Earth Sciences*).

Stellarispongia RIGBY, 1976a, p. 120 [\*S. aspera RIGBY, 1976a, p. 121; OD]. Thick-walled, bowl-shaped sponges with upper surface partly occupied by deep, central, spongocoel depression; strongly developed radial canals may extend from exterior to spongocoel wall, connected laterally by smaller canals parallel to outer surface; canals near surface form deep, radial grooves on upper surface and reticulation on exterior surface; dermal spicules with four to six stout, tangential rays, a knoblike, distal ray (sometimes absent), and probably longer, proximal ray; grotesque, larger spicules produced by overgrowths; smaller, more delicate, interior spicules have six tangential rays consistently developed. Lower Devonian (Emsian): Canada (Ellesmere Island).-FIG. 370,2a-e. \*S. aspera, Blue Fiord Formation, District of Franklin, southwestern Ellesmere Island; *a*, top view of holotype with simple, broad spongocoel and thick walls indented by prominent canals,  $\times 1$ ; *b*, base of holotype with rounded, sculptured exterior,  $\times 1$ ; *c*, side view showing saucerlike shape of sponge, GSC 43208,  $\times 1$ ; *d*, horizontal section through paratype showing coarse, radial canals in thick walls, GSC 43209,  $\times 1$ ; *e*, camera lucida drawings illustrating several ranks of spicules and grotesque larger spicules produced from overgrowths, GSC 43208,  $\times 15$  (Rigby, 1976a; courtesy of *Canadian Journal of Earth Sciences*).

### Family EIFFELIIDAE Rigby, 1986

#### [Eiffeliidae RIGBY, 1986a, p. 56]

Spicules sexiradiates, or septiradiates or octactines with slender rays and very short, proximal and distal rays; spicules of more

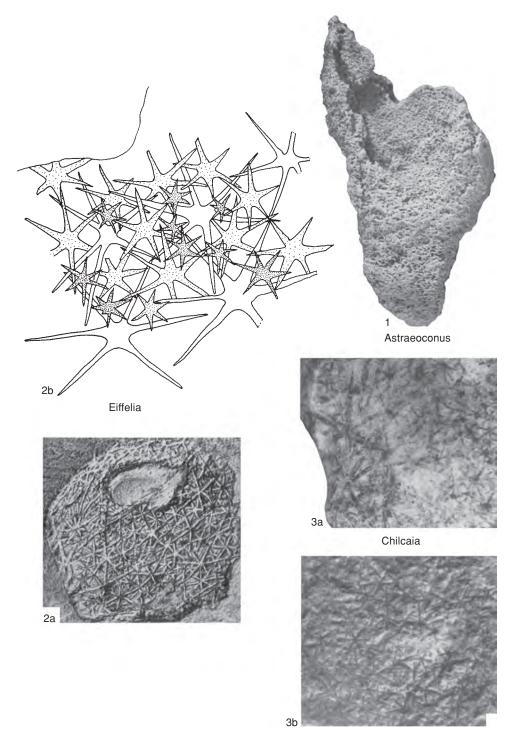


FIG. 372. Eiffeliidae (p. 571-572).

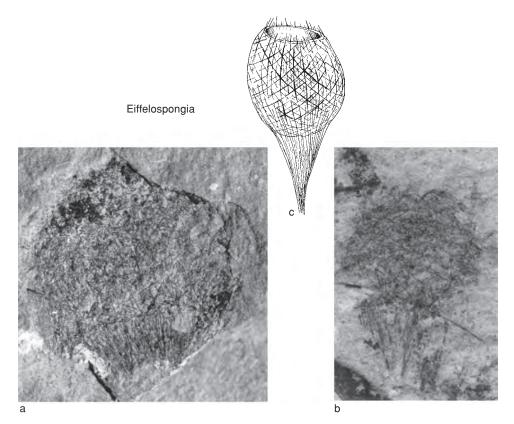


FIG. 373. Eiffeliidae (p. 572).

than one size order arranged more or less quincuncially with relatively uniform orientation; body wall thin; spongocoel and osculum present; sponges globose or obconical. *Lower Cambrian–Carboniferous (Middle Mis*sissippian).

Eiffelia WALCOTT, 1920, p. 323 [\*E. globosa WALCOTT, 1920, p. 324; OD]. Globose, thin-walled sponges with circular osculum; oscular rim enrolled or situated in shallow depression; body wall supported by one or few layers of spicules of at least four size orders, arranged so succeeding orders occur between rays of immediately larger orders, spicules with six long, evenly spaced, thin, tapering rays tangential or reflexed to sponge surface; it is not certain whether seventh, inwardly directed ray was present; spicules regularly and quincuncially arranged and contratangent so that rays outline triangular interspaces. Lower Cambrian-Middle Cambrian: Siberian Platform, Mongolia, China, Europe, Africa, Australia, China, Canada, USA. -FIG. 372,2a-b. \*E. globosa, Stephen Formation, Albertan, Burgess Quarry, Mount Field, British Columbia, Canada; *a*, lectotype showing globose form, open osculum, and thin, skeletal net of ranked, sexiradiate spicules,  $\times 3$  (Walcott, 1920); *b*, camera lucida drawing of part of skeleton showing orientation and positions of ranked sexiradiates in lectotype, USNM 66522,  $\times 3.7$  (Rigby, 1986c).

- Astraeoconus RIETSCHEL, 1968a, p. 17 [\*A. calcarius RIETSCHEL, 1968, p. 18; OD]. Sponge conical, thin walled, with broad, open osculum; spicules regular sexiradiates parallel to sponge surface; interspicular spaces larger on spongocoel surface than on external surface. Lower Ordovician–lower Upper Ordovician: USA (?Colorado), Lower Ordovician; USA (Oklahoma), lower Upper Ordovician.——FIG. 372,1. \*A. calcarius, Bromide Formation, Blackriveran, Criner Hills, Oklahoma; side view of holotype showing obconical form with walls made of regular sexiradiates, SMF 18434, ×4 (Rietschel, 1968a).
- Chilcaia CARRERA, 1994, p. 214 [\*C. bimuralis CARRERA, 1994, p. 215; M]. Discoidal to lamellar sponges with multilayered walls of sexiradiates of at least four ranks, one surface (possibly dermal) of wall with spicules irregularly distributed and grouped by ranks; other side (possibly gastral) with

intermix of spicules of all ranks, but large, first-order sexiradiates rare. *upper Lower Ordovician*: Argentina (San Juan Province).——FIG. 372,3*a–b.* \**C. bimuralis*, San Juan Formation, Llanvirn, Cerro La Chilca, Precordillera; *a*, photomicrograph of part of holotype with sexiradiate spicules of four orders, CEGH-UNC 9335, ×4.5; *b*, regular arrangement of sexiradiate in paratype fragment, CEGH-UNC 6336, ×2.8 (Carrera, 1994; courtesy of *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*).

- Eiffelospongia RIGBY & COLLINS, 2004, p. 88 [\*E. hirsuta; OD]. Small, heteractinid sponges with skeleton of long, thin-rayed sexiradiates in a moderately well organized skeleton, with regularly oriented spicules of at least two ranks; a prominent, basal, goatee-like root tuft is developed; sponges round to oval or keg shaped with deep spongocoel and flat, oscular margin; possible dermal layer principally of irregular monactines. Middle Cambrian: British Columbia, Canada.—FIG. 373a-c. \*E. hirsuta, Trilobite beds, Stephen Shale, Albertan, Mount Stephen; a, diagonally flattened holotype with thin, hexiradiate-based skeleton preserved in upper part and prominent root tuft at base, ROM 43828, ×7; b, paratype with well-preserved, hexiradate spicules in upper globular part of skeleton, above long-rayed oxeas of root tuft, ROM 53543, ×7; c, restoration of species, ×3 (Rigby & Collins, 2004).
- Gondekia RIGBY, 1991b, p. 38 [\*Astraeospongia lancifer REIMAN, 1945a, p. 16; OD]. Thin-walled, saucerto funnel-shaped, eiffeliid sponge with skeleton a felted mass of sexiradiates of at least three ranks with regular spacing and orientation; spicules lacking proximal and distal rays in all ranks; unornamented rays straight and locally flattened and bladelike. Devonian (Givetian): Canada (Ontario), USA (New York).—FIG. 374a-b. \*G. lancifer (REIMAN), Hungry Hollow Formation, Arkona, Ontario, Canada; a, holotype fragment of well-organized sexiradiates in felted skeleton, ×1.4; b, photomicrograph showing three-dimensional relationships of three orders of spicules, BMS 13030, ×7 (Rigby, 1991b).— -FIG. 374c-d. Ludlowville Formation, Givetian, Darian Lakes State Park, western New York; c, small, saucer-shaped sponge from below, with skeleton of felted, small sexiradiates, ×1; d, photomicrograph of closely packed sexiradiates of three ranks, each with six tangential rays in felted skeleton, USNM 463515, ×10 (Rigby, 1994).
- Petaloptyon RAYMOND, 1931, p. 198 [\**P. danei*; OD] [=*Canistrumella* RIGBY, 1986a, p. 58]. Open conical or vasiform to basketlike sponges with alternating, longitudinal panels with and without circular to elliptical, parietal gaps that are circular to polygonal and separated by less than their diameters, occurring in crude, vertical rows; skeleton a felt of spicules principally with five tangential rays although some with four and six also occur, and largely aborted, proximal and distal rays; walls thin; base

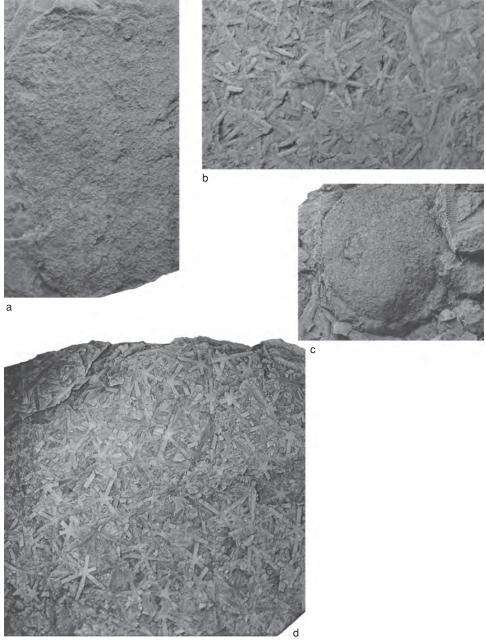
probably stalked. *Middle Cambrian:* Canada (British Columbia).——FIG. 375*a–e.* \**P. danei,* Stephen Formation, *Ogygopsis* shale, Mount Stephen near Field; *a*, figured specimen with alternating panels with and without gaps, ×1; *b*, photomicrograph showing spicules in tracts between gaps and moderately uniformly spaced spicules in panel without gaps, ×5; *c*, photomicrograph of large, five-rayed spicules with centra, ×15; *d*, restoration showing growth form based on fragments and related sponges, approximately natural size; *e*, sketch of spicules showing range of form, most common are five-rayed spicules, ROM 43123, ×25 (Rigby, 1986a).

- Toquimiella RIGBY, 1967a, p. 512 [\*T. curvata; OD]. Sponges low, conical or saucer shaped with flat base; moderately thick walled, presence of spongocoel not established; spicules with six very thin, tangential rays, round node representing distal ray, and possible but not demonstrated proximal ray; two of tangential rays oriented parallel to longitudinal axis of sponge, two lateral rays in upper half of spicule smoothly curve toward top of sponge while lower two lateral rays more abruptly curve toward bottom, with geniculation at midlength; spicules at least three orders of size, with smaller size external to larger; within each size rank spicules are in longitudinal rows overlapping basally, but different ranks arranged quincuncially with respect to one another. Middle Ordovician: USA (Nevada) .-FIG. 376a-b. \*T. curvata, Antelope Valley Formation, Toquima Range; a, photomicrograph of low, obconical holotype with typical spicules on upper right of specimen, MCZ 9391, ×10; b, generalized drawings of ranked spicules characteristic of genus, approximately ×75 (Rigby, 1967a).
- Zangerlispongia RIGBY & NITECKI, 1975, p. 330 [\*Z. richardsoni RIGBY & NITECKI, 1975, p. 331; OD]. Sponge small, obconical, thin-walled cup; at least three ranks of spicules with six tangential rays, no proximal or distal rays, and with tubercles on outer surface of spicule near centrum; spicule ranks arranged quincuncially with overlapping, slightly reflexed rays. Carboniferous (Middle Pennsylvanian): USA (Illinois). FIG. 377a-b. \*Z. richardsoni, Carbondale Formation, Farmington; a, flattened holotype showing steeply obconical form of sponge and its well-preserved, sexiradiate skeleton, ×5; b, photomicrograph of latex mold of holotype showing four ranks of spicules and sculpture of central disc of coarser spicules, FMNH 24821, ×9 (Rigby & Nitecki, 1975).

### Family WEWOKELLIDAE King, 1943

[Wewokellidae R. H. KING, 1943, p. 26] [=suborder Heteractinellidae HINDE, 1887b, p. 92, *emend.*; order Wewokellida CRONEIS & TOOMEY, 1965, p. 12; *emend.*, FINKS & RIGBY, herein]

Spicule rays very stout; spicules including regular septiradiates, often with reflexed rays, septiradiate derivatives with a variable



Gondekia

FIG. 374. Eiffeliidae (p. 572).

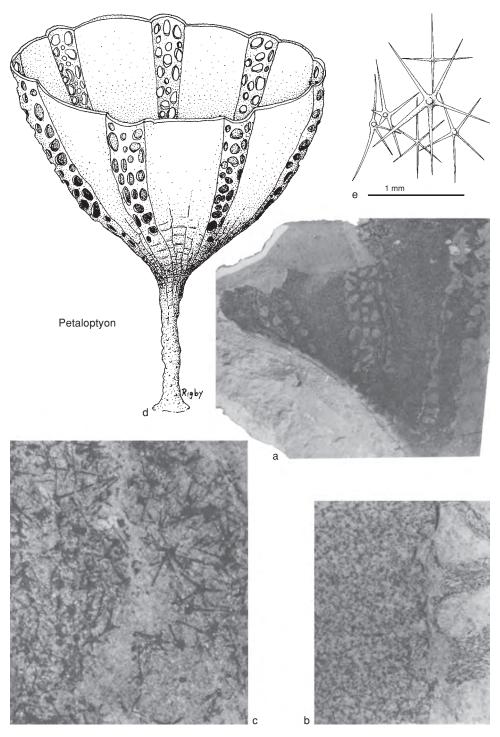


FIG. 375. Eiffeliidae (p. 572).

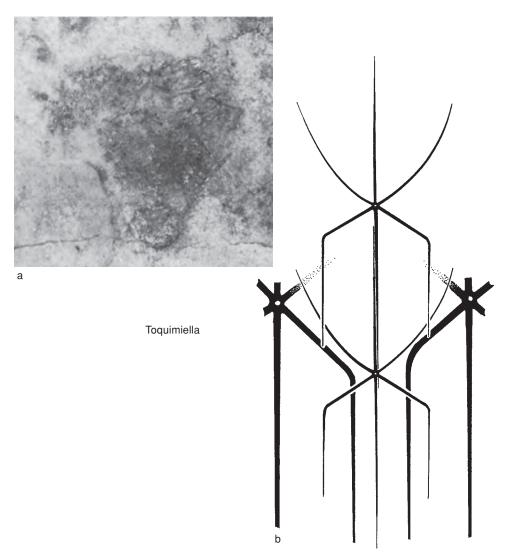
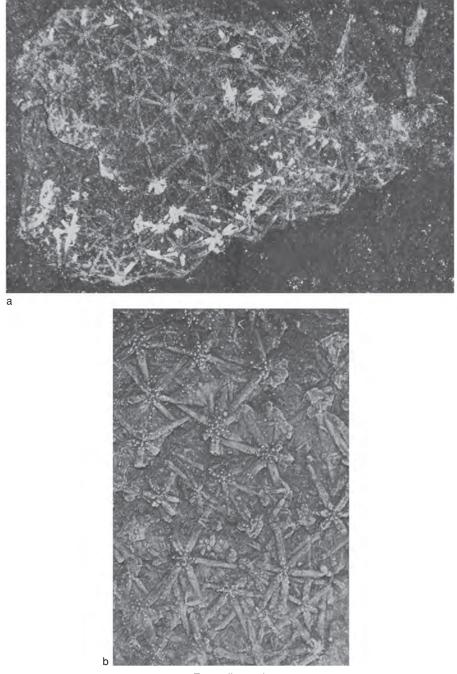


FIG. 376. Eiffeliidae (p. 572).

number of extra tangential and distal rays, tetraradiates with three tangential and one proximal rays, and polyasters with subequal rays radiating in all directions from common center; tangential rays sometimes distally tuberculate; body wall very thick with spicules arranged irregularly and densely packed; inhalant and exhalant canals variably developed; sponge body, where known, cup shaped, obconical, or tubular with more or less well developed spongocoel and osculum. Carboniferous (Mississippian)–Permian (Cisuralian).

Wewokella GIRTY, 1912, p. 121 [\* W. solida; OD]. Sponge body obconical, pyriform, claviform, or conicocylindrical, often irregular and geniculate; large specimens may be longitudinally fluted in upper, widest part; cloaca relatively narrow and body wall thick; cloaca may be only terminal or replaced in lower part by subparallel, longitudinal, exhalant canals; radial, exhalant canals enter cloaca



Zangerlispongia



and radial, inhalant canals lead in from outer surface; principal spicules tetraradiates with three rays parallel to outer surface and 120° from each other (one ray points to base of sponge) and a proximal ray at 90°; less common septiradiates with six tangential rays, two of which are often parallel to longitudinal axis of sponge and longer than others, or else six of equal length and may be reflexed toward proximal ray; on some septiradiates, at outer surface distal ray may be represented by knob or rosette of small rays directed outwardly in all directions; dermal layer of such smaller spicules, together with minute sphaeractines or polyactines that have radiate subequal rays, may occur in patches on surface, especially at points of attachment to shells or crinoid stems; similar polyactines scattered among larger spicules of interior; spicules commonly fused together by secondary calcite deposits; both primary spicule rays and secondary material consist of fibrous calcite with fibers perpendicular to spicule surfaces. Carboniferous (Mississippian-Pennsylvanian): USA (Alabama), Mississippian; USA (Oklahoma, Colorado), Pennsylvanian.-FIG. 378,1ab. \*W. solida, Wewoka Formation, Desmoinesian, Colgate quadrangle, Oklahoma; a, side view of steeply obconical holotype with main body spicules obscured by secondary overgrowth, ×1; b, photomicrograph of central part of holotype with small, triactine spicules among coarser, secondarily enlarged, main body spicules with triactine bases, USNM 12058, ×4 (Rigby, 1978).

- Asteractinella HINDE, 1888, p. 172 [\**A. expansa* HINDE, 1888, p. 173; SD VANDERCAMMEN, 1950, p. 7]. Founded on isolated spicules and fragments of coherent mesh; spicule types including polyactines with one long, proximal ray and six to fourteen rays divergent at various angles, polyactines with dozen or so equal rays radiating in all directions, and polyactines with similar number of tangential rays in one plane, coalescent into broad, central disk beneath which three to four proximal rays diverge; rays conical and blunt. *Carboniferous (Visean):* Scotland.——FIG. 379,2*a*-*c.* \**T. expansa*, Lower Limestone series, Law quarry, Dalry, Ayrshire; assorted typical spicules, ×10 (Hinde, 1887a).
- Regispongia RIGBY, 1978, p. 706 [\* Wewokella contorta KING, 1943, p. 27; OD]. Cylindrical to obconical sponges with shallow to deep spongocoel and thick wall of profusely rayed polyactines and outer, relatively thin, dermal layer of similar, although distinctly smaller, polyactines, minor triactines and octactines also may be present; other spicules may occur as accessory types because of great variation in numbers of rays within polyactines; entire skeletal net weakly to strongly fused by additional calcification; canals irregularly radial and small, because of great irregularity of spicule placement and orientation and because of additional calcification. Carboniferous (Pennsylvanian)– Permian (Cisuralian): North and South America,

Europe, China (Yunnan).——FIG. 378,2*a*–*c*. \**R. contorta* (KING), Graham Formation, Missourian, Jacksboro, Texas, USA; *a*, side view of holotype, subcylindrical sponge with deep spongocoel, UK 58690, ×1; *b*, photomicrograph of dermal part of skeleton of holotype with large, dermal, octactine-based skeleton in center surrounded by other overgrown, polyactine spicules, UK 58690, ×4; *c*, photomicrograph of skeleton of reference specimen where spicules have been grossly calcified and polyactine-based net obscured, USNM 240691, ×4 (Rigby, 1978).

- Talpaspongia KING, 1943, p. 28 [\*T. clavata KING, 1943, p. 29; OD]. Differs from Wewokella in having a broader spongocoel, a thinner body wall, and somewhat finer spicules that are more consistently fused together by secondary deposits. Permian (Aselian–Sakmarian): USA (Texas, New Mexico), China (Guangxi).—FIG. 379, 1a–b. \*T. clavata, Talpa Formation, Runnels County, Texas; a, transverse section of holotype showing large spongocoel and dense skeleton of wall, ×4; b, photomicrograph of transverse section showing swollen spicule rays as light gray circles and rods and canals as darker gray, circular, matrix fillings, Utbeg 8740, ×8 (King, 1943).
- Tholiasterella HINDE, 1887b, p. 76 [\*T. gracilis HINDE, 1887b, pl. 7, 1a-1g; SD DE LAUBENFELS, 1955, p. 93]. Known only from isolated spicules that have six to nine blunt, conical, distally tuberculate, tangential rays radiating from central disk, to which is attached a long proximal ray; spicules with six rays have hexagonal symmetry. [Figure and explanations were published by HINDE in 1887b, and the full description by HINDE in 1888 (p. 168).] Carboniferous (Visean, ?Pennsylvanian): Scotland, Visean; USA (Indiana), ?Pennsylvanian.-FIG. 379, 3a-b. \*T. gracilis, Lower Limestone, Law Quarry, Dalry, Ayrshire, Scotland; a, interior of lectotype fragment of dermal layer with several size ranks of commonly octactine spicules; b, isolated spicule showing sculpture of central disc of polyactine spicule and smaller, attached spicule, ×10 (Hinde, 1887b).

#### Family NUCHIDAE Pickett, 2002

#### [Nuchidae PICKETT, 2002b, p. 1,134]

Small, globular to obconical heteractinids with a coarsely perforate, largely aspiculate wall, and distal oscule with raised, imperforate rim. *Lower Cambrian–Middle Cambrian.* 

Nucha PICKETT & JELL, 1983, p. 90 [\*N. naucum; OD]. Hollow, subspherical chambers with prominent rimmed oscula at both upper and lower poles, wall perforated by closely spaced pores of various sizes; distinct, isolated-appearing chambers

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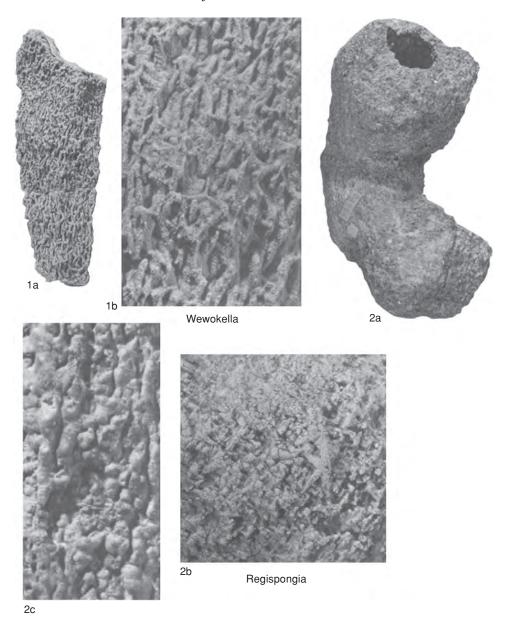


FIG. 378. Wewokellidae (p. 575-577).

probably joined into linear series at poles. *Middle Cambrian:* Australia (New South Wales), Canada.——FiG. 380,*3a–b.* \**N. naucum*, Coonigan Formation, Mootwingee, New South Wales; *a*, oblique view of holotype showing rimmed osculum and porous exowalls; *b*, view from above of globular holotype, NMV P75209, ×4 (Pickett & Jell, 1983).

Jawonya KRUSE, 1987, p. 543 [\**J. gurumal;* OD]. Sponges moderately thin walled, of subspherical to

rounded, obconical chambers with closely spaced exopores that may have radial partitions that project inwardly from pore margins in large specimens. Proximal oscule simple, unelaborated, but distal one with imperforate, asiphonate rim. Octactine and octactine-based, polyactine spicules small and adherent to or embedded in sclerosome, commonly irregularly oriented with reference to sponge axis. *Lower Cambrian-lower Middle Cambrian*: Australia (Northern Territory, South Australia).——FIG.

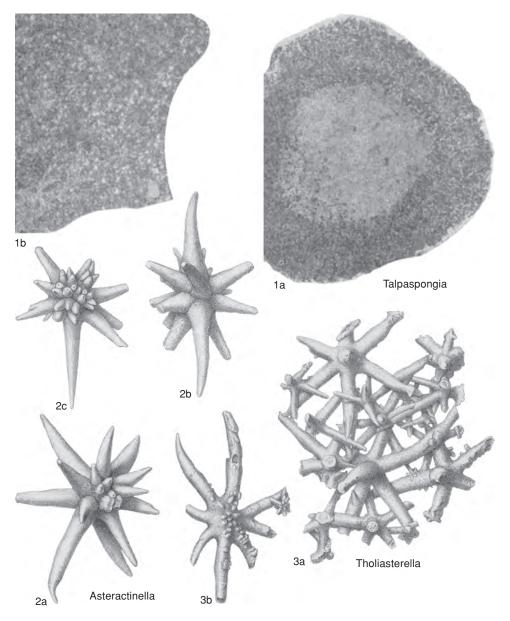


FIG. 379. Wewokellidae (p. 577).

380,2*a*-*c*. \**J. gurumal*, Tindall Limestone, Ordian, Katherine, Northern Territory; *a*, side view of holotype with porous, lower part and upper, collarlike, oscular region, NTGS P8553, ×1; *b*, octactines in paratype; *c*, octactines and polyactines in chamber wall of paratype, NTGS P8575, ×80 (Kruse, 1990).

Wagima KRUSE, 1987, p. 545 [\* W. galbanyin; OD]. Skeleton of thin-walled, subspherical chambers with closely spaced ostia screened externally by domed, multiperforate sieves. Proximal oscule unknown; distal one with imperforate, ambisiphonate rim. Octactine and octactine-based, polyactine spicules small and irregularly oriented and adherent or imbedded in sclerosome. *lower Middle Cambrian:* Australia (Northern Territory).——FIG. 380, *1. \*W. galbanyin*, Tindall Limestone, Ordian, Fenton Airfield; side view of holotype showing subspherical chamber with domed, multiperforate sieves around wall, NTGS P8598, ×1 (Kruse, 1990).

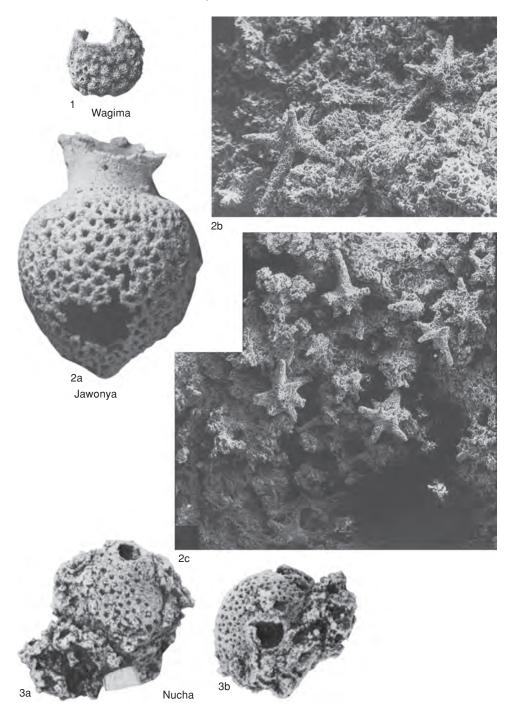


FIG. 380. Nuchidae (p. 577-579).

# Order HETAIRACYATHIDA Bedford & Bedford, 1937

[nom. correct. OKULITCH, 1955, p. 18, pro Hetairacyathina BEDFORD & BEDFORD, 1937, p. 27, nom. nov. pro Heterocyathina OKULITCH, 1935, p. 90, based on invalid generic name]

Double walls thin and sheathlike, strengthened by radiating rods or spicule-like structures. [Considered as possible aberrant archaeocyathans by OKULITCH (1955, p. 18) and HILL (1972, p. 141). Their inclusion here as possible poriferans is questioned.] *Lower Cambrian*.

### Family HETAIRACYATHIDAE Bedford & Bedford, 1937

[Hetairacyathidae BEDFORD & BEDFORD, 1937, p. 27, nom. nov. pro Heterocyathidae BEDFORD & BEDFORD, 1934, p. 6, based on invalid junior homonym, see *Radiocyathus* below]

Organisms spheroidal, conical or tubular with single or double wall enclosing central cavity that may open to exterior by osculumlike opening; each wall composed of starlike objects with eight to twelve rays, radiating from common center and sometimes branching; rays of adjacent stars fusing when in contact; if wall is double, rods connect the two, each rod running from center of a star; interspaces between rays in each wall may be calcified by continuous, perforated sheet, making two porous walls. [These organisms may be variably calcified algae, or archaeocyathids.] *Lower Cambrian.* 

- Girphanovella ZHURAVLEVA, 1967, p. 107 [\*G. girphanovae ZHURAVLEVA, 1967, p. 108; OD]. Spheroidal or tubular with broad cloaca with spicular lining; osculum not known but presumed narrow; spicules with eight to twelve branching, reflexed, tangential rays that fuse with those of neighboring spicules; exterior dermal layer with spicules of two sizes, larger with proximal ray that extends to cloacal lining; spicules of cloacal lining like smaller, dermal ones. [Genus differs from Gonamispongia chiefly having a cloacal lining.] upper Lower Cambrian: Russia (Siberia).-FIG. 381,4a-c. \*G. girphanovae, Lenan; a, weathered surface of spheroidal type specimen showing coarse spicules of dermal layer, ×1; b, transverse section showing doublewalled appearance, ×2; c, spicules of outer layer showing fine and coarse skeletal elements, ×10 (Zhuravleva, 1967).
- Gonamispongia KORSHUNOV, 1968, p. 127 [\*G. ignorabilis KORSHUNOV, 1968, p. 129; OD]. Broadly conical, thin walled (less than 1 mm thick); spicules

with eight to ten tangential rays (less than 1 mm long) radiating from central disk, sometimes bifurcating at ends that fuse to neighboring spicules to form rigid mesh that curls inwardly at oscular rim; much longer, proximal ray (2 mm) extending inwardly from centrum of each spicule. *Lower Cambrian*: Russia (Siberia).——FIG. 381, *la-c.* \* *G. ignorabilis*, Aldanian, Kenyada beds, Gonam River Basin; *a*, vertical section of conical holotype with thin walls and broad spongocoel, ×1; *b*, longitudinal section of sponge showing spicules with several tangential rays that connect to rays of adjacent spicules, ×2; *c*, vertical section showing dense, outer, skeletal layers and spicule with proximal ray, YaFAN, 84,3, ×10 (Korshunov, 1968).

- Radiocyathus OKULITCH, 1937 (April), p. 252, nom. nov. pro Heterocyathus BEDFORD & BEDFORD, 1934, p. 6, non MILNE-EDWARDS & HAIME, 1848 [\*Heterocyathus minor BEDFORD & BEDFORD, 1934, p. 7; OD] [=Hetairacyathus BEDFORD & BEDFORD, 1937 (Sept.), p. 27, nom. nov. pro Heterocyathus BEDFORD & BEDFORD, 1934, p. 6, non MILNE-EDWARDS & HAIME, 1848]. Conical or tubular with solid, but perforated, double wall; on intervallum side of each wall are rodlike, spicule rays in plane of wall, radiating from centers a few millimeters apart; their exterior surfaces tuberculate; proximal ray extending from each center of radiation in outer wall to inner wall. [This genus resembles a Girphanovella in which the space between the spicule rays in the plane of the wall are continuously calcified.] Lower Cambrian: Australia. FIG. 381, 2a-c. \*R. minor (BEDFORD & BEDFORD), Lower Cambrian limestone, Ajax Mine, Beltana, South Australia; a, double walls of obconical or cylindrical holotype that are connected across intervallum by rods or spicules, lower one is outer wall,  $\times 4$ ; b, side view of outer wall with characteristic ridges or lines of tubercles radiating out from separated centers, ×4; c, surface of inner wall with radiating ridges or lines of tubercles, BMNH, ×3 (Bedford & Bedford, 1936).
- Uranosphaera BEDFORD & BEDFORD, 1934, p. 7 [\*U. polyaster; OD]. Spheroidal; round osculum with thickened lip; spicules with about twelve tangential rays, reflexed toward sponge interior and often bifurcated or trifurcated; apparently no proximal or distal rays. Lower Cambrian: South Australia.—
  FIG. 381,3a-b. \*U. polyaster, Lower Cambrian limestone, Ajax Mine, Beltana; a, dermal surface of fragment of hollow, spherical holotype with rimmed, possible oscular opening surrounded by wall composed of polyactinal spicules that have reflexed, interdigitating rays; b, side view of fragment showing strongly reflexed, spicule rays, BMNH, ×4 (Bedford & Bedford, 1936).

# Order and Family UNCERTAIN

Archicladium QIAN & XIAO, 1984, p. 71 [85] [\*A. tridactyles; OD]. Spicules small with several equally spaced, side-by-side rays and central axis pointing

581

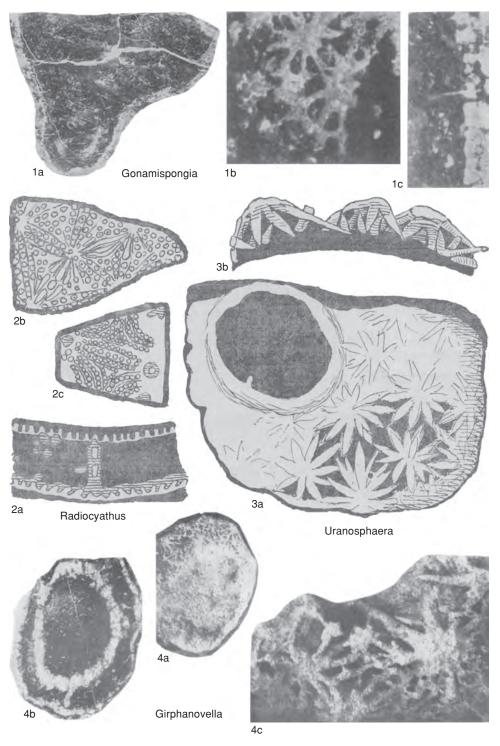


FIG. 381. Hetairacyathidae (p. 581).

in opposite direction; rays long with circular cross section and tapering slightly toward tip; central axis short with rounded end; both rays and axis smooth, without preserved openings. *lower Lower Cambrian*: China (Xinjiang).——FIG. 382,2*a–b.* \**A. tridactyles*, Meishucuan, Yurtus Formation; isolated spicules with short, knoblike axis and opposed parallel rays, *a*, ×50; *b*, ×40 (Qian & Xiao, 1984).

Polycladium QIAN & XIAO, 1984, p. 71 [86] [\*P. yurtusensis; OD]. Small spicules with radial symmetry consisting of central axis, round central disc, and five to seven radiating rays; central axis joining central disc in center; rays abut central disc on upper side; outer surface smooth. [Genus is based on isolated spicules that may belong to chancelloriids and thus are probably not sponges.] lower Lower Cambrian: China (Xinjiang).—FIG. 382,1. \*P. yurtusensis, Meishucuan, Yurtus Formation; isolated spicule with seven reflexed rays and central axis showing through in poorly preserved, central region, ×100 (Qian & Xiao, 1984).

## Class, Order, and Family UNCERTAIN

- Heterostella FEDOROV, 1987, p. 133 [\*H. eleganta FEDOROV, 1987, pl. 35,8–15; OD]. Isolated, starlike, polyactine spicules with distal ray commonly reduced or shorter than proximal ray, or rarely both proximal and distal rays are reduced; four to nine dermal rays straight to slightly curved, of variable lengths, and perpendicular to distal and proximal rays; a slightly convex disc occurring at ray junction; larger spicules with narrow, cylindrical canal. [Possible axial canals in rays of some of the large spicules suggest spicules were originally siliceous; therefore the genus may not be a heteractinid but a hexactinellid. For this reason it is placed in uncertain taxonomic position here.] Lower Cambrian: Russia (Yakutia-Sakha Republic).
- Nabaviella Mostler & Mosleh-Yazdi, 1976, p. 24 [\*N. elegans Mostler & Mosleh-Yazdi, 1976, p. 25; OD]. Siliceous spicules having one central ray that on one end has 3 to 11 recurved, lateral rays and other end may have expanded knob or disc. Eoarchean-Lower Ordovician, ?Middle Ordovician: Iran, Kashmir, Australia, Eoarchean-Upper Cambrian; Kazakhstan, Lower Ordovician, ?Middle Ordovician.-FIG. 383,1a. N. sp., Ajax Limestone, Lower Cambrian, Mt. Scott Range, South Australia; isolated spicule with characteristic, recurved rays, SAMP30222, ×50 (Bengtson, 1990a).-FIG. 383,1b. N. acanthomorpha TIWARI, Precambrian-Cambrian boundary sequence, Pohru Valley, Kashmir; side view of isolated spicule with swollen, acanthose, proximal part and reflexed, upper, lateral rays, WIF, ×10 (Tiwari, 1997).
- Taraxaculum BENGTSON, 1990a, p. 33 [\* T. volans BENGTSON, 1990a, p. 34; OD]. Siliceous spicules with central shaft and four to seven irregularly radiating, lateral rays at one end and opposite end

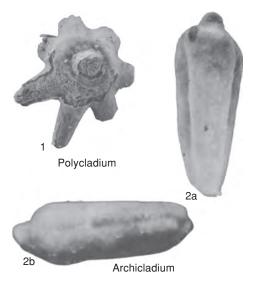


FIG. 382. Uncertain (p. 581-583).

of central shaft pointed or split into two short processes. No axial canal or filament known. *Lower Cambrian:* Australia (South Australia).——FIG. 383,2. \*T. volans, Ajax Limestone, Mt. Scott Range; side view of holotype, isolated spicule with upper, radiating, lateral rays and split, basal part of central shaft, SAMP 30228, ×30 (Bengtson, 1990a).

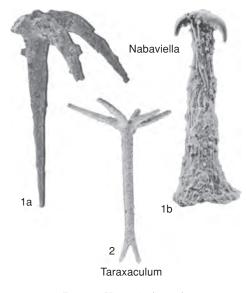


FIG. 383. Uncertain (p. 583).

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# HYPERCALCIFIED SPONGES

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# INTRODUCTION

Many sponges belonging to the subphylum Gelatinosa (i.e., the classes Demospongea and Calcarea) secrete a massive skeleton of calcium carbonate in addition to any spicules, siliceous or calcareous, that they may produce (see summaries by VACELET, 1991; Wood, 1990; Reitner, 1991; Senowbari-Daryan, 1991; Mastandrea & Russo, 1995). Most of these have been assigned to special groups based on the gross morphology of this nonspicular skeleton, such as the Sphinctozoa, Archaeocyatha, Inozoa, Stromatoporoidea, Chaetetida, and possibly Favositida (=Thallocorallia). The calcium carbonate may be either aragonite or calcite, of various microstructures, and secreted either intracellularly or extracellularly. (Intracellular secretion, corresponding to their mode of siliceous spicule production, may be a synapomorphy of the class Demospongea, although extracellular production by various methods almost always accompanies it.) The term basal skeleton (HARTMAN & GOREAU, 1975, p. 3) has been applied generally to this nonspicular calcium carbonate framework, although the earlier term sclerosome (RAUFF, 1913) is available for the material itself, and in some instances (e.g., Sphinctozoa, and probably Archaeocyatha) the skeleton is not confined to the base of the living tissue. The term hypercalcified (TERMIER & TERMIER, 1977a, 1977b) is convenient to use for all sponges that secrete nonspicular calcium carbonate and can include forms that cement spicules together with a calcium-carbonate coating without producing a separate basal skeleton, as in most Heteractinida as well as in many Inozoa of the class Calcarea. It has been suggested (CUIF & GAUTRET, 1991; WOOD, 1990) that ocean chemistry drives the production and mineralogy of the nonspicular carbonate and that symbiotic cyanobacteria may induce or support its precipitation (VACELET, 1983). Nevertheless, the rigid skeleton is adaptive to high wave-energy environments, and the hypercalcified sponges have been significant members of reef communities throughout Phanerozoic time. They have been major reef builders when not outcompeted by other sessile benthos with massive skeletons (WOOD, 1991).

# SECRETION, MINERALOGY, AND MICROSTRUCTURE

The massive calcium carbonate is secreted by several processes, which often characterize particular taxonomic groups. Some groups use more than one process. The mineralogy may also characterize groups, some secreting aragonite, others calcite with variable amounts of magnesium substituting for calcium. It was formerly thought that aragonite and calcite were secreted alternatively or together in the same species or even in the same individual, but recent studies indicate that this is not so (MASTANDREA & RUSSO, 1995). The microstructure of the secreted material also seems to be characteristic of particular groups, inasmuch as it results from the process of secretion. The secretory process is often related to the mode of secretion of the spicular skeleton. For example, demosponge spicules are secreted uniformly intracellularly, and this is also the initial locus of secretion of one type of hypercalcified skeleton, namely that of spherulitic aragonite, although the spherules, following their extrusion from the parent cell, may be enlarged by extracellular secretion. In the Calcarea, on the other hand, both spicules and the hypercalcified skeleton are secreted extracellularly by multiple cells, and both are made of magnesian calcite.

The principal microstructures and mineralogies recognized (see especially

WOOD, 1990; CUIF & GAUTRET, 1991; MASTANDREA & RUSSO, 1995) are as follows.

#### Spherulitic Aragonite

Also called compound spherulitic, this is characteristic of the living demosponge Astrosclera and its relatives, which have stromatoporoid morphology, as well as of a large number of Permo-Triassic genera of inozoan, sphinctozoan, and chaetetid morphology. The spherulites are first produced intracellularly then transported to their skeletal location and simultaneously enlarged by extracellular secretion. Most of the living astrosclerids have acanthostyle spicules, which might place them with the ceractinomorph order Poecilosclerida (SOEST, 1991) except that the spines are verticillate as in the living Agelas, with which VACELET (1983, 1985) and WOOD (1990) placed them, as the order Agelasida, which is presumably also ceractinomorph, although WIEDENMAYER (1994) suggested a tetractinomorph affinity.

### Penicillate Aragonite

Also called clinogonal aragonite, elongate spherulitic, or water-jet structure, this is characteristic of the living demosponge *Ceratoporella*, of chaetetid morphology, which is assigned to the order Agelasida for the same reasons as *Astrosclera*. The aragonite is secreted extracellularly by pinacoderm cells. This morphologic type intergrades with the spherulitic type, inasmuch as spherulites are often extended asymmetrically by extracellular secretion so as to become penicillate. Many Triassic genera of chaetetid as well as inozoan morphology have this structure.

#### Irregular Aragonite

Also called microgranular aragonite, this is found in the living sphinctozoan demosponge *Vaceletia*, a ceractinomorph that cannot be assigned to any order owing to its absence of spicules, as well as a number of Triassic genera of sphinctozoan, inozoan, and stromatoporoid morphologies. The irregularly arranged aragonite needles are secreted over a collagen fiber framework and may be grouped in membrane-bounded, mineralization units with a center of organic matter (GAUTRET, 1985; MASTANDREA & RUSSO, 1995).

#### Homogeneous-Granular Mg Calcite

Also called microgranular Mg calcite, this is not known in any living species but is found in a number of Triassic genera of sphinctozoan and inozoan morphology, the best known of which is *Cassianothalamia*, assigned by REITNER (1987a, 1991) to the tetractinomorph demosponge order Hadromerida on the basis of the presence of tylostyles, spirasters, and euasters. The Cambrian Archaeocyatha also have this microstructure (KRUSE & DEBRENNE, 1989). Whether this indicates a relationship of the Archaeocyatha to the Tetractinomorpha and Hadromerida must, for the present, remain an open question.

#### Lamellar Mg Calcite

Characteristic of the living *Acanthochaetetes*, also assigned to the order Hadromerida on the basis of the presence of tylostyles and spirasters, this microstructure is formed of microcrystals of magnesian calcite aligned in one plane, secreted extracellularly over a matrix of collagen fibers. It is found in a number of euaster-bearing Cretaceous to recent genera of chaetetid morphology as well as a Cretaceous genus *Calcichondrilla* REITNER, 1991, of encrusting, nonchaetetid morphology.

### Penicillate Mg Calcite

Also called clinogonal calcite or fascicular fibrous calcite, this structure is found in the Mississippian and later genus *Chaetetes*, as well as in other Paleozoic and Mesozoic genera of chaetetid morphology, such as *Stromatoaxinella* WOOD & REITNER, 1988. It also includes the living chaetetid genus *Merlia*. The presence of subtylostyles in most of these genera supports an assignment to the ceractinomorph demosponge order Poecilosclerida (SOEST, 1991), also favored by the resemblance of *Merlia* clavidiscs to the diancistras of some poecilosclerids. VACELET and URIZ (1991), however, favored an assignment of *Merlia* to the tylostyle-bearing tetractinomorph order Hadromerida on histologic grounds, questioning the relation of clavidiscs to diancistras.

### Spherulitic Mg Calcite

The only demosponge that clearly has this microstructure is the Cretaceous genus Euzkadiella REITNER, 1987c, of stromatoporoid or quasi-inozoan morphology. It possesses subtylostyles in plumose arrangement, rather similar to many of the chaetetid types with penicillate calcite discussed above. The spicules relate Euzkadiella to the Poecilosclerida (SOEST, 1991), but REITNER (1987c) assigned it to the related order Haplosclerida on the basis of spicule arrangement. The Pennsylvanian stromatoporoid Newellia, which likewise has plumose bundles of subtylostyles, was considered to be related to Euzkadiella by WOOD, REITNER, and WEST (1989). The microstructure of Newellia, however, is microgranular calcite (WOOD, REITNER, & WEST, 1989), at least as preserved. If spherulitic calcite is as related to penicillate calcite as the corresponding aragonitic microstructures are, Euzkadiella and perhaps Newellia may be related to Chaetetes. Petrobiona VACELET & LEVI, 1958, a lithonid calcaronean genus of the class Calcarea, also has a penicillate to spherulitic calcite basal skeleton but is associated with typical calcarean spicules. Murrayona KIRKPATRICK, 1910a, a murrayonid calcinean genus of Calcarea, also has calcite spherulites associated with calcarean spicules.

### Fibrous Mg Calcite

Also called orthogonal Mg calcite, this is characterized by fibers of calcite perpendicular to the surface of the skeletal elements. It is found in several groups of the subclass Calcaronea of the class Calcarea, largely as interspicular cement: in the minchinellids, in the typically inozoan Mesozoic stellispongiids, in the sphaerocoeliid sphinctozoan *Barroisia* (but not in *Tremacystia*, which is granular [REID, 1968d], perhaps diagenetically), and probably in the class Heteractinida.

There may be a large-scale taxonomic significance to basal skeleton mineralogy that is somewhat obscured by current taxonomic disagreements. Aragonite is associated with ceractinomorph demosponges (Types 1–3), assuming the Agelasida to be ceractinomorph, as VACELET (1983, 1985) and WOOD (1990) maintain. Magnesian calcite, on the other hand, is associated with a tetractinomorph demosponge group in two (Types 4 and 5) and possibly three (Type 6) instances, as well as with the class Calcarea (Types 7 and 8). This suggests that Merlia (Type 6) is in fact a tetractinomorph as VACELET and URIZ (1991) maintained and that Euzkadiella (Type 7) is also a tetractinomorph. It may not be without significance that cladistic analysis (in which basal skeleton mineralogy is not one of the characters) shows the Tetractinomorpha to be a sister-group of the Calcarea or Homosclerophora (SOEST, 1991). This line of reasoning supports the assignment of the Agelasida to the Ceractinomorpha.

## MORPHOLOGIC TYPES

As seen from the foregoing discussion, the gross morphology of the basal skeleton is not correlated closely with the microstructure. The microstructure appears to have some taxonomic value at the class and order levels. That is, it is often correlated with spicule form and cytologic or embryologic characters that have been used to establish some of the commonly accepted class-order taxa. The gross morphology, however, may have some significance at the family level. It seems reasonable that major patterns of growth should be genetically controlled and indicate common ancestry. The major morphologic types of hypercalcified sponges are as follows.

#### Sphinctozoan

The basal skeleton (in this instance not really basal) forms a perforated cortex around the soft tissue. The soft tissue grows to a characteristic size and shape and then secretes a calcareous envelope about itself, forming a so-called chamber. After several further chambers are formed in successive bouts of growth, the soft tissue gradually withdraws from the earlier chambers, often forming vesicles to seal off the abandoned spaces. These vesicles, together with pillars, fibers (trabeculae), and tubes that seem to have been formed within the living soft tissue, are referred to collectively as filling tissue. At least some of the tubes and intertrabecular spaces appear to have surrounded major canals in the soft parts. The filling tissue is often indistinguishable from inozoan structure or from the pillars of stromatoporoid structure.

#### Inozoan

This morphologic type is characterized by a basal skeleton of fibrous (trabecular) or anastomosing, tubular form. In many instances the fibers (trabeculae) appear to have been bundles of spicules cemented together and coated by the calcium carbonate. In instances where there are no spicules or only a few scattered, often partly protruding ones, it is likely that the basal skeleton invested spongin fibers previously laid down. The trabeculae usually have a characteristic pattern, often radiating upwardly and outwardly with cross connections between them, as do the spongin fibers and spicule bundles of many nonhypercalcified sponges. They also may anastomose irregularly. A perforated cortex is developed often, and major canal systems may interrupt the trabecular net. The soft tissue of the sponge appears to have occupied the intertrabecular spaces to a significant depth below the upper surface, and the presence of epizoans and inhalant pores well down on the sides of the sponge imply that some of them stood well above the sea floor.

#### Stromatoporoid

This morphology consists of narrow, closely spaced pillars perpendicular to the upper surface of the sponge, with irregular cross connections. Regular enlargements of the cross connections at more or less the

same level occur at closely spaced intervals parallel to the upper surface (latilaminae). Major canal systems, usually exhalant systems about an oscule (astrorhizae), may interrupt the pillars and latilaminae. An imperforate epitheca bearing concentric growth lines may coat the under surface of the entire skeleton. The living tissue of the sponge occupied probably primarily the spaces between the pillars above the last-formed latilamina. The pillars may contain bundles of spicules as in inozoan types, and indeed the only difference between inozoans and stromatoporoids is the larger size and wider spacing of the trabeculae or pillars in inozoans, their less perpendicular relation to the outer surface, and the absence of latilaminae. Inozoan trabeculae outline usually more elaborate and deeper canal systems, implying a greater depth of living tissue within the skeleton as well as a possible absence of periodic growth. Combinations of the stromatoporoid and sphinctozoan type of skeleton are known: the family Guadalupiidae is characterized by a layer of sphinctozoan morphology (the thalamidarium) coated on the exhalant side by a layer of stromatoporoid morphology complete with astrorhizae (the trabecularium). It is possible that the supposed instance of a sphinctozoan coated by a chaetetid (Fistulispongina TERMIER & TERMIER, 1977a) is in fact a single organism as originally proposed.

#### Chaetetid

This morphology consists of spaces of meandriform to polygonal cross section (calicles) outlined by relatively thin walls of calcium carbonate perpendicular to the outer surface of the sponge that may incorporate spicules. Grooves corresponding to exhalant systems about an oscule (astrorhizae) may indent the outer edges of the calicle walls. The walls may be perforated by pores (mural pores) or bear spines projecting into the lumen of the calicle. In most genera horizontal cross partitions (tabulae) occur at intervals in the calicles. (In the ceratoporellids the calicles may also be filled in below with solid skeletal material.) A thin, imperforate epitheca bearing concentric growth lines may coat the entire under surface of the sponge skeleton, being added to at the point where the base meets the upper layer of living tissue. It is apparent that this morphology corresponds not only to that of Chaetete, which has been accepted as a sponge because of the presence of astrorhizae and incorporated spicules (D. I. GRAY, 1980), but also to that of the favositids, which have so far yielded neither astrorhizae nor undisputed spicules, but which may also be sponges (KIRKPATRICK, 1912; HARTMAN & GOREAU, 1975; KAZMIERCZAK, 1984, 1991). Living genera of chaetetid morphology include Merlia KIRKPATRICK, 1908; Ceratoporella HICKSON, 1911; and Acanthochaetetes FISCHER, 1970. In the living forms the soft tissue extends across the entire upper surface above the basal skeleton and fills also each calicle down to the uppermost tabula (or to the solid backfill in some ceratoporellids). In addition, each tabula may have a central pore (in Merlia) or be initially incomplete (in Acanthochaetetes), and the spaces beneath the upper few tabulae may be filled with storage cells that can regenerate the sponge if the surface tissue is destroyed (VACELET, 1991).

### Other Morphologies

The class Calcarea includes several additional morphologic types confined to one or a few genera each that differ to varying degrees from the foregoing. The living *Petrobiona* VACELET & LEVI, 1958, has a massive basal skeleton with a deeply and irregularly pitted surface. The pits are analogous to the calicles of the chaetetid morphology, and the sponge tissue occupies the pits as well as forming a coating over the entire upper surface. Thin, branching canals, ending blindly, extend into the basal skeleton from the lower part of each pit. They contain storage cells and are analogous to the subtabular spaces of chaetetids (VACELET, 1991).

Several genera have a cortex of overlapping scales or flakes derived from the enlargement of triradiates. Except for the osculum and a limited area of inhalant pores, the cortex is imperforate as in many *Sphinctozoa*. In the living calcinean Murrayona KIRK-PATRICK, 1910a such a cortex is underlain by an inozoan trabecular skeleton built of spherulitic to penicillate calcite. Between the principal trabecular basal skeleton and the cortex are unfused spicules of several calcarean types including bundles of tuning fork spicules. In the related Paramurrayona VACELET, 1967a, the inozoan skeleton is completely absent, but the cortical skeleton has an additional layer of irregular, imbricated flakes beneath the outer layer of scales. Loose, calcarean spicules are also present. In the living calcaronean Lepidoleucon VACELET, 1967a the cortex of scales is the only rigid skeleton, the flesh beneath containing only loose spicules of calcarean types. Each of these genera resembles a single chamber of a sphinctozoan, the first having inozoan filling tissue.

In the Jurassic to Holocene calcaronean family Minchinellidae the basal skeleton consists of layers of tetraradiates with the distal ray uniformly directed upwardly, the three proximal rays curving downwardly with clasping terminations, and the whole cemented together with fibrous calcite. Loose calcarean spicules of several types occur in the flesh above the basal skeleton. Except for the regularly layered arrangement and the absence of smaller, coating spicules, this type of basal skeleton is not too different from that of the Jurassic and Cretaceous inozoa with calcarean spicules here assigned to the family Stellispongiidae. It is even closer geometrically to the siliceous, lithistid, dicranoclone skeleton of the Paleozoic demosponge family Hindiidae, presumably a homeomorph inasmuch as (apart from the mineralogic difference of the skeletal material) the megarhizoclones found in some genera (e.g., Scheiella FINKS, 1971b) are not known in any Calcarea.

In the *Heteractinida*, the principal skeleton of octactines (to which are added triactines, tetractines, and polyactines in the Wewokellidae) is almost always fused together by calcite cement. It is not certain whether this is original or diagenetic. Two Cambrian genera, however, *Jawonya* KRUSE, 1987, and *Wagima* KRUSE, 1987, have a cortical, partly imperforate, sphinctozoan type of calcareous basal skeleton that incorporates silicified (or possibly siliceous) octactine or polyactine spicules (or possibly hexactines with extra rays) in what resembles a single sphinctozoan chamber that is certainly original and not diagenetic (KRUSE, 1990).

The archaeocyathan type of skeleton, which will not be discussed further herein, resembles the sphinctozoan type (with some differences in filling tissue) but lacks the repeated units of growth.

### TAXONOMY

Living species of hypercalcified sponges have demonstrated that similar morphologies of the basal skeleton may occur in different classes and orders (WOOD, 1991). The same may be said of mineralogy and microstructure, although these have somewhat greater fidelity to taxa established originally by other means. Cladistic analysis has confirmed that the presence of specific spicule types provides useful synapomorphies for demosponge classification at the ordinal level (SOEST, 1991) and subordinal level (HAJDU, SOEST, & HOOPER, 1994), and it is fortunate that spicules are occasionally preserved in the fossils. A consensus is gradually emerging based on a combination of these characteristics together with data on living forms (VACELET, 1985, 1991; WOOD & REITNER, 1988; BOROJEVIC, BOURY-ESNAULT, & VACELET, 1990; DEBRENNE & WOOD, 1990; WOOD, 1990, 1991; CUIF & GAUTRET, 1991; GAUTRET, VACELET, & CUIF, 1991; Reitner, 1991; Senowbari-Daryan, 1991; Soest, 1991; Debrenne & ZHURAVLEVA, 1994; HAJDU, SOEST, & HOOPER, 1994; STEARN & PICKETT, 1994; WIEDENMAYER, 1994; MASTANDREA & RUSSO, 1995). The classification adopted here is an outgrowth of this consensus.

Because the morphological types called stromatoporoid, chaetetid, and archaeocyathid will be treated in separate volumes of the *Treatise*, those hypercalcified sponges dealt with here are confined to the morphologic types called inozoan and sphinctozoan. The entire class Heteractinida might be regarded as hypercalcified, inasmuch as primary cementation of spicules to one another by calcium carbonate occurs in most genera, but those sponges are treated in a separate section in this volume.

Those assigned to the class Demospongea include the orders Agelasida (both inozoan and sphinctozoan types), Vaceletida (sphinctozoan and inozoan types), Hadromerida (inozoan and sphinctozoan types), and an inozoan group (family Pharetrospongiidae) of uncertain ordinal position. The Agelasida also include genera of chaetetid (e.g., Ceratoporella HICKSON, 1911) and stromatoporoid (e.g., Astrosclera LISTER, 1900) morphologies not dealt with in this volume. Likewise, the Vaceletida include stromatoporoid types (e.g., Burgundia), and the Hadromerida include chaetetid types (e.g., Acanthochaetetes HARTMAN & GOREAU, 1975), also dealt with elsewhere.

Those assigned to the class Calcarea include the orders Murrayonida (inozoan type with quasisphinctozoan elements), Stellispongiida (inozoan type), Sphaerocoeliida (sphinctozoan type), and Lithonida (inozoan type).

# HYPERCALCIFIED DEMOSPONGEA

#### **ORDER AGELASIDA VERRILL, 1907**

Assignment to this group is based on verticillate acanthostyle spicules when present and a basal skeleton of spherulitic or penicillate (clinogonal) aragonite. Among living species verticillate acanthostyles are associated with both spherulitic microstructure (e.g., Astrosclera), which is initially produced intracellularly but enlarged extracellularly, and penicillate microstructure (e.g., Ceratoporella), which is produced extracellularly. Spherulitic skeletons may include laterformed penicillate parts. Although most of the fossil species lack the spicules and are assigned on the basis of skeletal mineralogy and microstructure only, their generally consistent association when both are present supports the assignment (WOOD, 1990;

MASTANDREA & RUSSO, 1995). Some fossil species contain smooth monaxons that are calcite pseudomorphs (presumably) after the original silica (e.g., Thaumastocoelia cassiana STEINMANN, 1882, see MASTANDREA & Russo, 1995, fig. 4.6; and Sestrostomella robusta ZITTEL, 1878b, see WENDT, 1974, fig. 6), and the loss of spines may be diagenetic. On the other hand, the living Hispidopetra HARTMAN, 1969, has only smooth styles associated with a spherulitic aragonite basal skeleton of inozoan type (HARTMAN, 1969). The living Calcifibrospongia HARTMAN, 1979, of stromatoporoid morphology, has smooth strongyles, associated with a spherulitic, aragonite, basal skeleton. It is possible, therefore, that not all hypercalcified sponges with a spherulitic, aragonite, basal skeleton are agelasiids. There is no other basis for assigning the fossils to a different order, however. WIEDENMAYER (1994, p. 66) considered the styles of *Hispidopetra* to have lost their spines and assumed a relationship to the astrosclerid or ceratoporellid group. Indeed, although smooth, they do have the same long, slender form of typical agelasid acanthostyles; so do the strongyles of Calcifibrospongia. The vertical trabeculae of Hispidopetra, bristling with plumosely arranged, smooth styles, are almost identical in diameter and spacing to those of the Permian inozoan Catenispongia FINKS, 1995, which likewise has spherulitic microstructure and may have echinating or plumose, smooth monaxons; the vertical trabeculae of Hispidopetra, although long (7 mm) for a living hypercalcified sponge, are considerably shorter than those of Catenispongia, and the encrusting habit of *Hispidopetra* is quite different from the large, fungiform, osculebearing Catenispongia. Nevertheless, the similarities make a relationship plausible. The Catenispongiidae, as well as other families with smooth monaxons embedded in a spherulitic, basal skeleton, may belong to another order than the Agelasida. One possibility, the Poecilosclerida, is characterized by subtylostyles (SOEST, 1991), but the styles of *Hispidopetra* are not even slightly tylote. The monaxons, perhaps styles, of Thau*mastocoelia, Sestrostomella*, and *Catenispongia* (if this last genus has true spicules) are less slender and more stubby than either the styles of *Hispidopetra* or the acanthostyles of typical agelasids.

Apart from the sclerosponge genera included in the Astroscleridae and Ceratoporellidae, the living species of the Agelasida are confined to the single genus Agelas, which is difficult to place among the demosponges (SOEST, 1991). Its only spicules are the slender, verticillate acanthostyles echinating the spongin fibers, whose presence in Astrosclera, Ceratoporella, Goreauiella, and Stromatospongia, in a similar position relative to the calcareous skeletal elements, are the principal basis for associating them with Agelas, the similar Hispidopetra being also included despite the smoothness of its styles. VACELET (1985, p. 8) was apparently the first to assign them definitely to the family Agelasiidae (with a query in VACELET, 1983) on the basis of spicule and soft tissue affinities. HARTMAN and GOREAU (1970, p. 220), on the other hand, pointed out that the spines are recurved toward the head of the style in the sclerosponges and are not so in Agelas.

Nonverticillate acanthostyles are a relatively neat synapomorphy for the order Poecilosclerida, in particular for the suborders Myxillina and Microcionina (HAJDU, Soest, & Hooper, 1994). Wiedenmayer (1994, p. 66), on the other hand, has stressed the resemblance of the verticillate styles of the sclerosponges to the discasters of Latrunculia and the verticillate sanidasters of Sceptrintus, which two genera he would place in the family Latrunculiidae, near the families Agelasidae and Astroscleridae (=Ceratoporellidae), in the order Hadromerida (WIEDENMAYER, 1994, p. 64, 69, 70, 119). Because of the large number of fossil hypercalcified sponges that have basal skeletons of originally intracellularly produced spherulites of aragonite, similar to those of the Astroscleridae, as well as the uncertainties of the placement of Agelas, it seems appropriate to keep them all in a separate order Agelasida as has been done by VACELET,

WOOD, REITNER, and other investigators. The Agelasida are assigned here to the subclass Ceractinomorpha following the opinions of VACELET (1985) and SOEST (1991).

The evidence for intracellular production of the spherulites is the presence of a core to each spherulite that is delimited by a physical break and that may be mineralogically different from the outer layers of the spherulite, often replaced by iron oxide or sulfide, giving it a dark-colored appearance (CUIF & GAUTRET, 1991). The later extracellularly added layers of aragonite may render the spherulite asymmetrical, or the skeleton may be exclusively produced extracellularly as in some or all living Ceratoporellidae. The asymmetrical spherulites (flaky spherulites of FINKS, 1983a, 1990) are more strongly developed in the secondary filling of original, tissue-filled spaces, and seem characteristic of particular families. Other families (e.g., Ceratoporellidae, Pharetrospongiidae) are characterized by largely, or wholly, penicillate microstructure. In general, however, the families are also defined by common features of gross morphology.

## ORDER VACELETIDA FINKS & RIGBY, HEREIN

This group is defined by the characteristic microstructure of the basal skeleton, namely, irregular-aragonitic (microgranular aragonitic). It is secreted extracellularly over a collagen matrix (VACELET, 1979; WOOD, 1990). The living *Vaceletia* PICKETT, 1982, of sphinctozoan morphology, lacks spicules, as do the fossil genera that have the same microstructure. Its histology and embryology place it in the subclass Ceractinomorpha (VACELET, 1983, 1985) to which the order Vaceletida is here assigned. The families recognized here are defined by gross morphology.

### ORDER HADROMERIDA TOPSENT, 1898

The hadromerids belong to the subclass Tetractinomorpha and are characterized by the presence of tylostyles but no tetraxons and usually some form of astrose microsclere (SOEST, 1991). The hypercalcified species have a basal skeleton of calcite; in those of chaetetid morphology, such as the recent *Acanthochaetetes* HARTMAN & GOREAU, 1975, it is of lamellar microstructure (WOOD, 1990) or alternatively of penicillate microstructure if *Chaetetes* FISCHER DE WALDHEIM, 1829, and its relatives, or *Merlia* KIRK-PATRICK, 1908, are hadromerids; in those of sphinctozoan and inozoan morphology it is of homogeneous-granular, magnesian-calcite microstructure (MASTANDREA & RUSSO, 1995). The families recognized here are defined by gross morphology.

# HYPERCALCIFIED CALCAREA

## ORDER MURRAYONIDA VACELET, 1981

This is the only certain order of hypercalcified sponges in the subclass Calcinea (BOROJEVIC, BOURY-ESNAULT, & VACELET, 1990). As in all members of the class Calcarea, the mineralogy of all skeletal elements is calcite. In the family Murrayonidae there is an inozoan-like, trabecular, aspicular, basal skeleton, plus a cortical skeleton of overlapping scales derived developmentally from triradiate spicules. Isolated spicules of particular form also occur around the osculum, on the inhalant surface, and beneath the cortex. In the family Paramurrayonidae there is a similar cortex of scales, interior bundles of tuning-fork spicules but no aspicular basal skeleton. In the family Lelapiellidae there is a cortex of enlarged, anapodal triradiates (tripods), plus internal bundles of straight biradiates, plus a basal layer of curved biradiates.

## ORDER STELLISPONGIIDA FINKS & RIGBY, HEREIN

This Mesozoic group includes the typical inozoa with spicules characteristic of the class Calcarea. There is considerable doubt concerning their assignment to one or the other of the two well-established subclasses of the Calcarea (Calcinea and Calcaronea), which are based on characters unobservable in fossils, namely, the position of the choanocyte nucleus and the type of larva. The presence of regular triactines (i.e., with rays of equal length and angle) is almost distinctive of the subclass Calcinea (VACELET, 1991, p. 255), but the same author (VACELET, 1991, p. 253) allowed some nonsagittal (i.e., regular) triradiates into the subclass Calcaronea. The Stellispongiida frequently have both types of spicule in the same species. They have a principal skeleton composed of fibers built around one or more triradiates or tetraradiates (including tuningfork spicules) cemented side by side with calcite that at least in some instances has a radial structure (CUIF & others, 1979) and may be coated by a layer of filiform spicules (HINDE, 1893b). Because the living Calcaronea belonging to the order Lithonida often have spicules cemented together with calcite, the Stellispongiida are here placed tentatively in the subclass Calcaronea. The two Mesozoic families (Stellispongiidae and Endostomatidae) are separated according to whether the spicule bundles consist of a larger spicule or spicules coated by smaller ones (Stellispongiidae) or of several subequal spicules (Endostomatidae). The recent family Lelapiidae is also included because it too has spicule bundles (including tuning-fork spicules), although they are not cemented; this last family is clearly calcaronean. The presence of spicule bundles and the tuningfork spicules commonly found within them is not confined to the Calcaronea. They are also present in the living order Murrayonida, which is clearly calcinean (VACELET, 1983, 1985).

## ORDER SPHAEROCOELIIDA VACELET, 1979

These sponges, so far known only as fossils, are characterized by a sphinctozoan morphology. The spicules (variably tetraradiates, triradiates, and derived forms, sagittal where clearly visible) are embedded in a variable amount of fibrous or granular calcite (most thoroughly described by REID, 1968d). The predominance of sagittal spicules in at least two genera (Tremacystia HINDE, 1884a, and Sphaerocoelia STEIN-MANN, 1882) favors but does not require an assignment to the Calcaronea. The triradiates of Barroisia MUNIER-CHALMAS, 1882, on the other hand, "appear to be simply equiradiate where their character can be recognized" (REID, 1968d, p. 7), as in typical Calcinea. The presence in this last genus of tylostyles similar to those of the demosponge order Hadromerida (or Poecilosclerida if they are considered to be subtylostyles), together with the fibrous (rather than granular as in Tremacystia) microstructure of the aspicular calcite, might suggest an assignment elsewhere; but if true triradiates are present, an assignment to the Calcarea and not Demospongea seems to be required. It is worth noting, however, that almost all hypercalcified sponges referred to either Hadromerida the or the Poecilosclerida on the basis of spicules have a calcitic basal skeleton: penicillate in the chaetetids (Hadromerida); lamellar in the acanthochaetetids (Hadromerida); and microgranular in Cassianothalamia and its relatives (Hadromerida), as well as in the stromatoporoid Newellia (Poecilosclerida on the basis of its subtylostyles) (see WOOD, REITNER, & WEST, 1989; CUIF & GAUTRET, 1991; MASTANDREA & RUSSO, 1995). Barroisia is herein retained provisionally in the Sphaerocoeliidae in the absence of more definitive evidence for its relationships.

### ORDER LITHONIDA DOEDERLEIN, 1892

This Jurassic to recent group is clearly assignable to the Calcaronea on the basis of the choanocyte cytology and the larval morphology of the living species. Originally coterminous with the family Minchinellidae, in which the principal skeleton consists of tetraradiates fused together with fibrous calcite, it was expanded by VACELET (1981) to include two other recent, hypercalcified, calcaronean families: the Petrobionidae, in which the principal skeleton is an aspicular mass of spherulitic and penicillate calcite, and the Lepidoleuconidae, in which there is an external armor of overlapping scales derived from the enlargement of equiangular triradiates as in the calcinean order Murrayonida. One might argue that each should be in its own order, but for convenience they are retained here in the order Lithonida.

# SYSTEMATIC DESCRIPTIONS

# Class DEMOSPONGEA Sollas, 1875

[nom. correct. DE LAUBENFELS, 1955, p. 37, pro Demospongiae SOLLAS, 1875, p. 421]

Spicules of opaline silica are monaxonic or tetraxonic with axial canal of triangular cross section; spongin and mesohyl commonly abundant; architecture of aquiferous system of rhagon type, with small, choanocyte chambers and small choanocytes. *Cryogenian–Holocene.* 

# Subclass CERACTINOMORPHA Lévi, 1953

[*nom. correct.* BERGQUIST, 1967, p. 167, *pro* Céractinomorphes Lévi, 1953, p. 855]

Skeleton generally reticulate and anisotropic; megascleres, when present, monaxonic, never tetraxonic; microscleres, when present, generally sigmas or chelae, never asters; basal skeleton, when present, usually (possibly always) aragonite. *Cambrian– Holocene.* 

# Order AGELASIDA Verrill, 1907

#### [Agelasida VERRILL, 1907, p. 333]

Spicules (if present) long, slender, verticillate acanthostyles (or rarely, smooth styles or strongyles of similar proportions) in plumose or echinating position embedded in spongin fibers or in basal skeleton ; basal skeleton (if present) of spherulitic or penicillate aragonite. [RIGBY & SENOWBARI-DARYAN (1996, p. 26) proposed the new superorder Aspiculata and the new order Inozoida in the class Calcarea to include the following families: Auriculospongiidae TERMIER & TERMIER, 1977; Stellispongiellidae WU, 1991; Peronidellidae WU, 1991; Virgulidae TERMIER & TERMIER, 1977; and the new families Sphaeropontiidae and Exotubispongiidae. They observed (p. 20), however, that their higher classification is an artificial or form classification of these Paleozoic sponges, whose skeletons are made of spherulitic aragonite. Those families are included here in the Agelasida.] *Ordovician–Triassic.* 

## Family CATENISPONGIIDAE Finks, 1995

[Catenispongiidae FINKS, 1995, p. 1]

Aspicular skeleton composed of meandriform, anastomosing trabeculae, outlining anastomosing, tubular spaces of irregular orientation; trabecular microstructure of large (50 to 400  $\mu$ m), isodiametric spherulites of aragonite; larger canals and oscules commonly present; imperforate cortex variably developed; no spicules known with certainty. [This family is separated from the Virgolidae TERMIER & TERMIER, 1977a, on the basis of the irregular rather than radial arrangement of the trabeculae.] *Permian* (*Artinskian*)–*Triassic*.

Catenispongia FINKS, 1995, p. 1 [\*C. agaricus; OD]. Conical-fungiform with strongly convex, upper surface overhanging sides; rugose sides invested with finely porous cortex that bears numerous large, circular pores; interior with meandriform, longitudinal sheets of finely porous trabeculae; sheets outlining longitudinal, laterally anastomosing, canal-like spaces that open on top surface as circular to meandriform, coarse pores; trabecular sheets porous with fine, anastomosing, tubular spaces of circular cross section that open laterally into longitudinal canals as well as on top surface, where they form chains of fine, circular pores between larger, meandriform spaces; large, circular oscules with well-defined margins scattered over top surface, being larger than largest meandriform spaces, and connected to them internally; trabeculae composed of large, isodiametric spherulites; spicules apparently absent but surface of trabeculae showing echinating protrusions, some thin sections showing smooth, strongyle-like, or possibly stylelike (more probably bladed) structures (possibly diagenetic), and large, presumably foreign, monaxon fragments occasionally partly embedded in trabeculae. Permian (Kungurian-Capitanian): USA (Texas) .-FIG. 384,2a-c. \*C. agaricus; a, side view of holotype with lipped ostia in lower, dense, dermal layer and coarse skeleton with larger, exhalant ostia in upper part, Cherry Canyon Formation, Guadalupian, Guadalupe Mountains, ×0.5; b, view from above

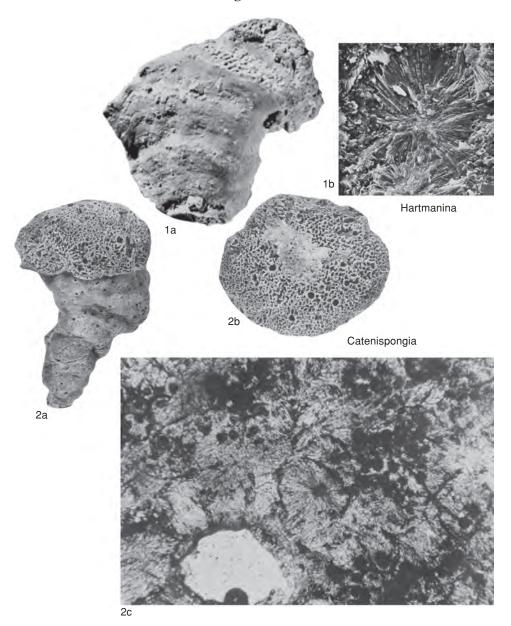


FIG. 384. Catenispongiidae (p. 594-596).

with coarse, exhalant ostia interrupting meandering trabeculae and with fine, intertrabecular spaces, Cherry Canyon Formation, Guadalupian, Guadalupe Mountains, USNM 128060, ×0.5; *c*, photomicrograph showing spherulites in a paratype section, Rhodes Canyon Formation, Leonardian, Glass Mountains, AMNH 44295, ×75 (Finks, 1995).

Hartmanina DIECI, RUSSO, & RUSSO, 1974b, p. 141 [\*Achilleum verrucosum MÜNSTER, 1841, p. 26; OD] [?=Leiospongia D'ORBIGNY, 1849, p. 548, partim, obj.; *Leiofungia* FROMENTEL, 1860a, p. 49, *partim*, obj.]. Conical-fungiform with flat to convex upper surface, overhanging sides; sides covered with rugose, imperforate cortex; top surface bearing circular to meandriform, intertrabecular spaces; no oscules, canals, or pores on sides; trabeculae anastomosing but internal arrangement otherwise unknown; trabeculae composed of medium to large, isodiametric spherulites; spicules absent. [Absence of pores on the sides, as well as absence of pores larger than the

regular, intertrabecular spaces on the top distinguishes this genus from *Catenispongia* FINKS, 1995.] *Triassic:* Europe.——FIG. 384, *Ia–b.* \**H. verrucosum* (MUNSTER), San Cassiano Formation, Carnian, Dolomite Alps, Italy; *a*, side view of holotype with dense, dermal layer and irregular, radial, trabecular spaces on top, ×2; *b*, spherulite of medium dimensions from holotype, SSPHG AS VII 383, ×500 (Dieci, Russo, & Russo, 1974b).

- Ossimimus FINKS, 1995, p. 2 [\*O. robustus; OD]. Large, cylindroid branches bearing scattered, large, circular oscules; surface widely covered with imperforate, dermal layer, the remainder showing small, meandriform, intertrabecular spaces; trabeculae outline uniformly small, anastomosing tubes of circular cross section interpenetrating in every direction but frequently subparallel to outer surface; oscules open into canals of same diameter as oscule and perpendicular to surface, canals penetrate some distance into sponge and communicate with intertrabecular spaces; trabeculae composed of medium-sized, isodiametric spherulites; spicules absent. Permian (Kungurian-Roadian): USA (Texas).-FIG. 385, 2a-b. \*O. robustus, Road Canyon Formation, Leonardian, Glass Mountains; a, subcylindrical, branched, holotype with irregularly distributed oscula over dense, dermal surface, ×0.5; b, photomicrograph of internal, skeletal structure of anastomosing trabeculae, USNM 128066, ×10 (Finks, 1995).
- Stratispongia FINKS, 1995, p. 2 [\*S. cinctuta; OD]. Conical, stipitate, broadly expanding, sometimes branching; concentrically rugose sides semi-corticate, bearing small, meandriform pores and few large, circular ones; top surface bearing small, meandriform, intertrabecular spaces and numerous larger, circular pores; trabeculae solid (but pierced laterally by small, circular pores), meandriform, dominantly vertical and closely spaced; horizontal layers produced by zones of horizontal canals; trabeculae composed of large, isodiametric spherulites; spicules absent. Permian (Artinskian-Capitanian): USA (Texas).-FIG. 385, 1a-b. \*S. cinctuta, Road Canyon Formation, Leonardian, Glass Mountains; a, side view of holotype with smooth, dermal surface and rough top, AMNH 44287, ×1; b, photomicrograph of paratype showing trabeculae outlining anastomosing, tubular spaces, AMNH 44294, ×10 (Finks, 1995).

### Family VIRGOLIDAE Termier & Termier, 1977

[nom. correct. FINKS & RIGBY, herein, pro Virgulidae TERMIER & TERMIER, 1977a, p. 31] [=Tubulispongiidae WU Ya Sheng, 1991, p. 35, partim; Acoelidae WU Ya Sheng, 1991, p. 57, partim; Paracorynellidae WU Ya Sheng, 1991, p. 64]

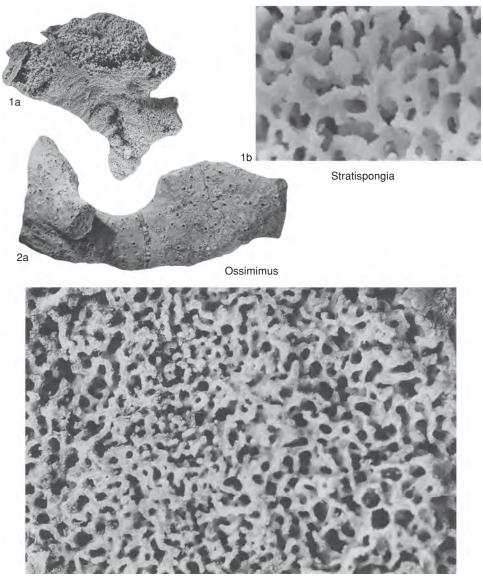
Trabeculae of aspicular skeleton dominantly radial and longitudinal, outlining spaces of subpolygonal to meandriform cross section that may communicate by large, lateral pores; trabecular microstructure of large (50 to 350 μm), isodiametric spherulites, but not demonstrated in type genus; sides covered with imperforate cortex in some genera, including types; calcitic (originally siliceous) monaxons present in some genera but not in type. This family has chaetetid morphology. *Permian–Triassic*.

### Subfamily VIRGOLINAE Termier & Termier, 1977

[nom. transl. et correct. FINKS & RIGBY, herein, ex Virgulidae Termier & Termier, 1977a, p. 31]

Obconical to massive sponges with reticular skeletal net, numerous coarse longitudinal exhalant canals more or less diverge upward into spongocoel, where present; inhalant canals subhorizontal and converge from inhalant pores. *Permian (Kungurian)– Triassic.* 

- Virgola DE LAUBENFELS, 1955, p. 55, nom. nov. pro Virgula GIRTY, 1909, p. 73, non SIMPSON, 1900 [\*Virgula neptunia GIRTY, 1909, p. 74; OD] [=?Pseudovirgula GIRTY, 1909, p. 75, obj.; ?Conosclera WU Ya Sheng, 1991, p. 37 (type, C. vermicula, OD); Ramospongia WU Ya Sheng, 1991, p. 59 (type, R. minor, OD)]. Narrow cylinders branching at acute angles; sides covered with rugose, imperforate cortex; top surface unknown; fine trabeculae outlining narrow, tubular spaces of circular to meandriform cross section that anastomose but are dominantly longitudinal and radial; no larger oscules or canals; trabecular microstructure unknown; spicules unknown. [Genus differs from Ossimimus FINKS, 1995, in the dominantly longitudinal and radial arrangement of the trabeculae; in the absence of larger canals and oscules, in the continuous, imperforate, dermal layer; and in the smaller size of all parts; in addition spherulites are not yet observed. Pseudovirgula GIRTY, 1909, differs in having large pores on the sides at the end of short, tubular projections of the dermal layer leading into short canals of comparable size that interrupt the trabecular mesh; it may also have sphinctozoan-like segmentation; mesh spaces and branch diameter are approximately half that of Virgola.] Permian (Kungurian–Changhsingian): China (Guangxi), Kungurian; USA (Texas), Guadalupian; ?China (Hubei), Tunisia, Changhsingian.——FIG. 386,1a-b. \*V. neptunia (GIRTY), Capitan Formation, Guadalupian, Guadalupe Mountains, Texas; a, transverse section of holotype showing nature of skeleton and lack of spongocoel, USNM 118130, ×4; b, oblique section through branched reference specimen showing coarse, skeletal structure largely uninterrupted by canals or a spongocoel in either branch, USNM 35009, ×4 (Rigby, Senowbari-Daryan, & Liu, 1998).
- Dactylocoelia CUIF, 1979, p. 476 [\*D. cylindrocoelia; OD]. Simple, cylindrical sponges 10 to 12 mm in



2b

FIG. 385. Catenispongiidae (p. 596).

diameter and several centimeters high, with exterior marked only with small, shallow depressions of canal ostia; axial region with moderately open, reticular structure composed of isodiametric, aragonitic spherulites; outer region distinctly more massive, perforated only by horizontal, reticular canals, and composed of aragonite spherulites that are somewhat eccentric in inner part but in outer, massive, distinctive part of skeleton spherulitic fibers oriented toward periphery. *Triassic:* Turkey.——FIG. 386,2*a*–*b.* \**D. cylindrocoelia,* Nappes d'Antalya, Taurus lycien; *a*, longitudinal, fractured sponge,  $\times$ 1; *b*, transverse section across reticulate skeleton of axial region, on left, and through outer wall, on right, showing differences in spherulite structure, approximately  $\times$ 50 (Cuif, 1979).

Intratubospongia RIGBY, FAN, & ZHANG, 1989b, p. 790 [\**I. typica;* OD] [=Dendrosclera WU Ya Sheng, 1991, p. 46 (type, *D. irregularis,* OD); Paracorynella WU Ya Sheng, 1991, p. 64 (type, *P. flexa,* OD); Paristellispongia WU Ya Sheng, 1991, p. 71 (type, *P. parallelica,* OD); Cystospongia WU Ya Sheng, 1991,

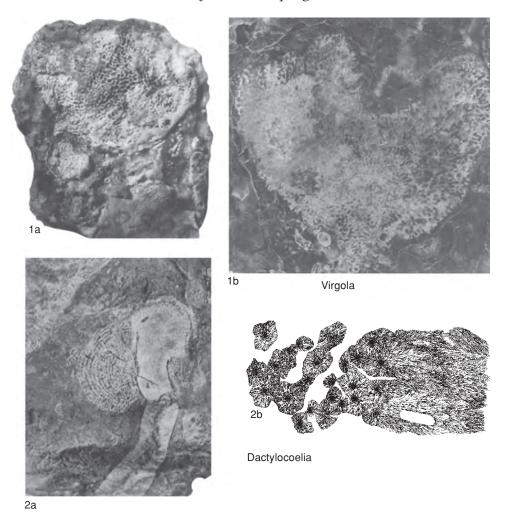


FIG. 386. Virgolidae (p. 596-597).

p. 84 (type, C. guangxiensis, OD)]. Cylindrical to club-shaped sponges that lack a spongocoel but with many large, longitudinal, exhalant canals of various diameters irregularly distributed; inhalant canals essentially horizontal; skeleton of fine fibers; axial cluster of exhalant canals absent. Microstructure and spicules unknown. Permian (Guadalupian-Lopingian): China (Guangxi, Guizhou).-—Fig. 387, 1a-b. \*I. typica, Changxing Formation, Changhsingian, Guangxi; a, longitudinal section of holotype with numerous discontinuous, vertical canals throughout fine, skeletal net, IG 5096, ×2; b, irregular, fibrous, fine-textured skeletal net with dense interruption of skeleton (arrow) in upper part and canals filled with dark matrix below, IGASBA

5247, ×20 (Rigby, Fan, & Zhang, 1989b). Keriocoelia CUIF, 1974, p. 149 [\**K. conica*; OD]. Small, flabellate-conical and stipitate; sides covered with imperforate layer; top surface with circular to submeandriform, intertrabecular spaces or calicles; top edges of trabeculae denticulate; intertrabecular spaces filled in from below by secondary material; trabeculae composed of large, isodiametric spherulites, secondary filling is penicillate in structure; styles present, embedded in spherulitic skeleton. *Triassic:* Europe.—FIG. 388a-c. \*K. conica, San Cassiano Formation, Carnian, Dolomite Alps, Italy; *a*, general morphologic aspect of type specimen,  $\times 3; b$ , photomicrograph of distal surface with alveolar reticulation showing dentate appearance produced by small spherulite,  $\times 20; c$ , spherulites in transverse section,  $\times 30$  (Cuif, 1974; courtesy of *Geobios*).

Reticulocoelia CUIF, 1973, p. 124 [\**R. arborescens;* OD]. Ramose, branches somewhat flattened and lobate; surface bearing only circular to

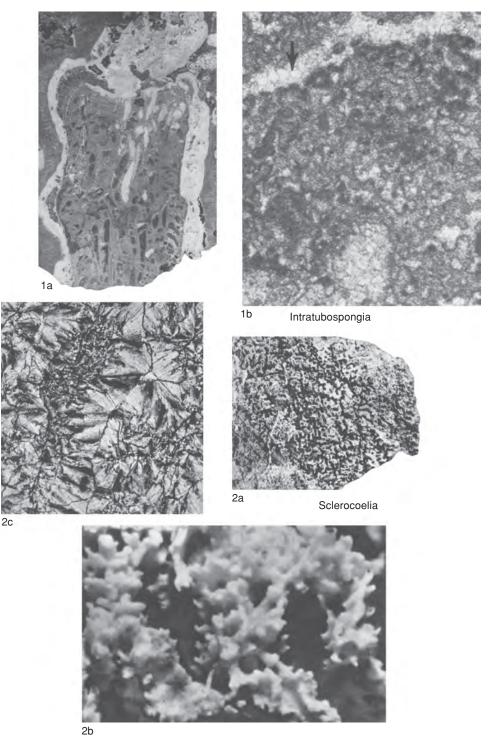


FIG. 387. Virgolidae (p. 597-601).

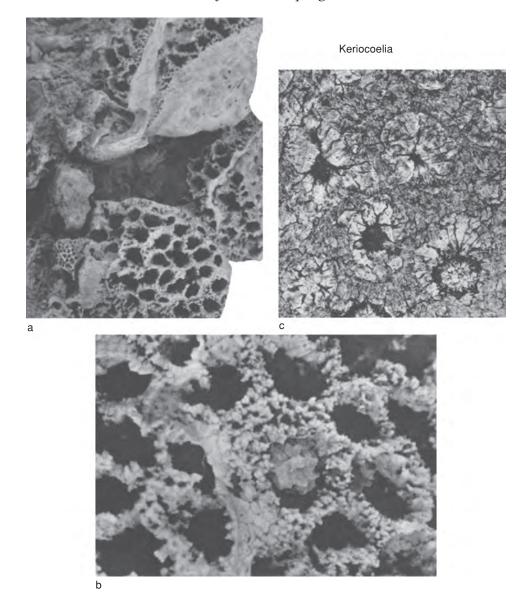


FIG. 388. Virgolidae (p. 598).

meandriform, small, intertrabecular spaces; no larger pores, oscules, or cortex; trabeculae and intertrabecular spaces anastomosing but dominantly longitudinal and distally divergent; trabeculae composed of large, isodiametric spherulites. *Triassic* (*Carnian–Norian*): Turkey.——FIG. 389*a–b.* \*R. *arborescens*, Triassic deposits, Korkuteli; *a*, transverse section of branch of type specimen, ×5; *b*, surface with alveolar development corresponding to homogenous, internal structure, magnification unknown (Cuif, 1973; courtesy of *Geobios*).——FIG. 390a-b. \**R. arborescens*, Triassic deposits, Korkuteli; *a*, spherulite showing irregular orientations in internal, skeletal net, ×100; *b*, drawing of microstructure of skeletal net, with spherulite in interior of trabeculae with layered crust over exterior, scale indicated by bar (Cuif, 1973; courtesy of *Geobios*).

Sclerocoelia CUIF, 1974, p. 147 [\*S. *hispida*; OD]. Thick, encrusting masses whose upper surface bears palmately branched ends of trabeculae that outline meandriform, intertrabecular spaces; intertrabecular spaces below current upper surface completely filled

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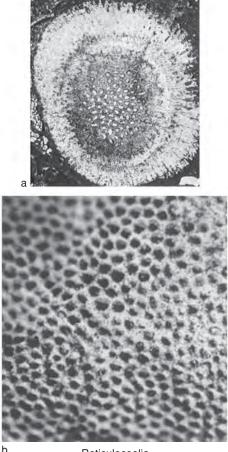
by secondary, trabecular material; primary trabeculae composed of moderately large, isodiametric spherulites that subsequently expand asymmetrically to fill intertrabecular spaces. Calcite (originally silica) acanthostyles embedded in spherulitic skeleton. [This genus differs from others included in this family and was compared by CUIF (1974, p. 149) to the living sclerosponge Goreauiella HART-MAN, 1969, by HARTMAN and GOREAU (1970).] Triassic: Europe.—FIG. 387,2a-c. \*S. hispida, San Cassiano Formation, Dolomite Alps, Italy; a, general morphology of upper surface of type specimen, ×2; b, photomicrograph showing general morphology of outer, vertical processes, ×60; c, photomicrograph under crossed nicols showing large spherulite, ×100 (Cuif, 1974; courtesy of Geobios).

### Subfamily PREEUDINAE Rigby & Senowbari-Daryan, 1996

[Preeudinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 88]

Virgulid sponges lacking large osculum or depression on summit. *Permian (Kungurian– Changhsingian)*.

- Preeudea TERMIER & TERMIER, 1977a, p. 33 [\*P. minima; OD]. Subcylindrical to subspherical, small sponges lacking a spongocoel but with numerous vertical-walled, tubelike, exhalant canals that may be clustered in axial area or distributed throughout sponge; exterior with dense, dermal layer marked by ostia with raised rims; skeleton very fine net of fibers that may be interrupted by obscure, horizontal, inhalant canals; microstructure spherulitic. Permian (Lopingian): Tunisia.—-FIG. 391,1a-d. \*P. minima, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, top of spherical specimen with central bundle of tubular, exhalant canals and dermal surface with rimmed, canal ostia, USNM 463734, ×2; b, side view of conicocylindrical sponge with rimmed, possible inhalant canals, ×2; c, summit of same sponge with cluster of axial canals in shallow, rimmed depression, USNM 463735, ×2; d, restoration showing general canal and skeletal pattern, and tubular or rimmed, inhalant ostia in dermal layer, not to scale (Rigby & Senowbari-Daryan, 1996a).
- Medenina RIGBY & SENOWBARI-DARYAN, 1996a, p. 89 [\*M. laterala; OD]. Single to branched or clubshaped sponges, may be annulate, with numerous longitudinal, exhalant canals clustered side by side in axial area but separation between them increasing toward periphery; horizontal canals developed between exhalant tubes and in outer part of skeleton; walls of both vertical and horizontal canals with numerous small pores; skeletal microstructure spherulitic. Permian (Lopingian): Tunisia.----FIG. 392a-f. \*M. laterala, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, summit view of branched holotype with spongocoels into which empty numerous small, exhalant pores,  $\times$ 1; *b*, side view of holotype, USNM 463728,  $\times$ 1; c, summit view of paratype, half of which shows ostia of numerous longitudinal, exhalant canals,



Reticulocoelia

FIG. 389. Virgolidae (p. 598-600).

USNM 463730,  $\times 2$ ; *d*, side view of weathered paratype with outer, stacked, horizontal canals exposed in upper part,  $\times 2$ ; *e*, micronodose, dense, dermal layer produced by rounded tips of outwardly divergent, skeletal fibers, USNM 463732,  $\times 10$ ; *f*, reconstruction showing relationships of vertical and horizontal canals in interior of obconical sponge, not to scale (Rigby & Senowbari-Daryan, 1996a).

Microsphaerispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 92 [\*M. polyarteria; OD]. Small, spherical sponges with several relatively shallow spongocoels distributed over surface and with low rims; dermal layer perforated by numerous small pores; skeleton of reticulate, relatively coarse fibers; may be attached. Permian (Lopingian): Tunisia.
—FIG. 391,2a-d. \*M. polyarteria, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, paratype with diagnostic sieve plate in exhalant opening, USNM 480227, ×5; b, spherical paratype with rimmed, exhalant openings in

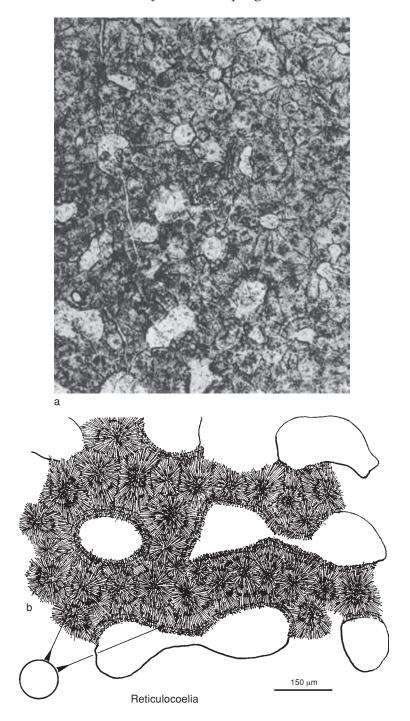


FIG. 390. Virgolidae (p. 598-600).

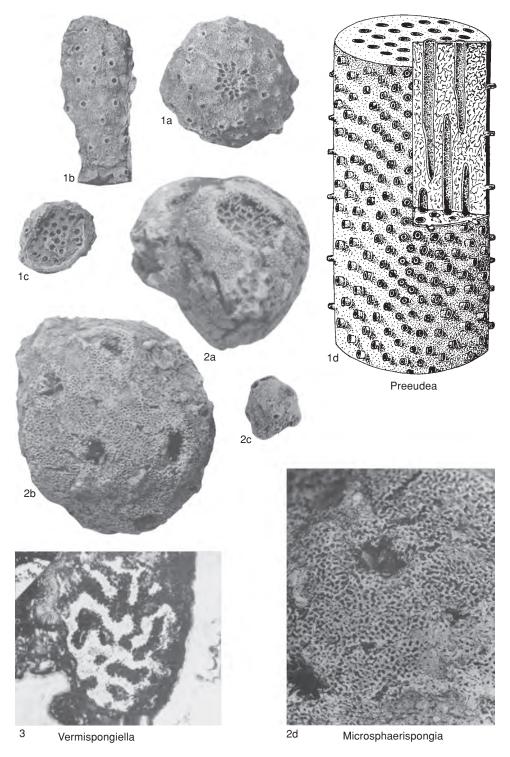


FIG. 391. Virgolidae (p. 601–607).

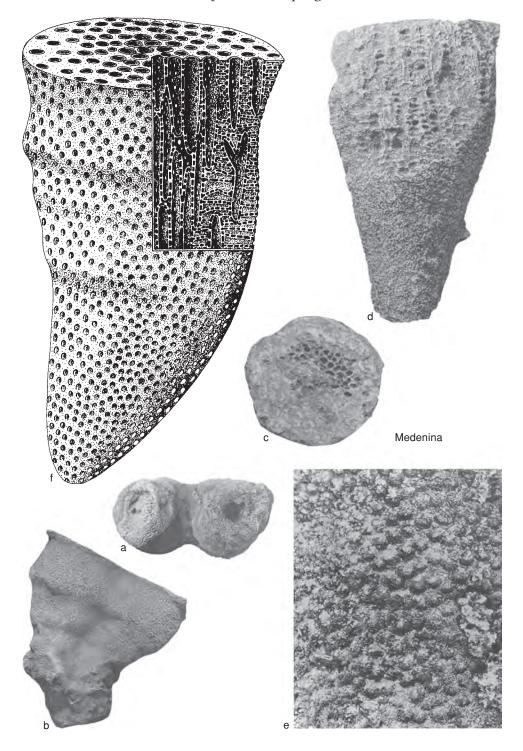


FIG. 392. Virgolidae (p. 601).

Agelasida

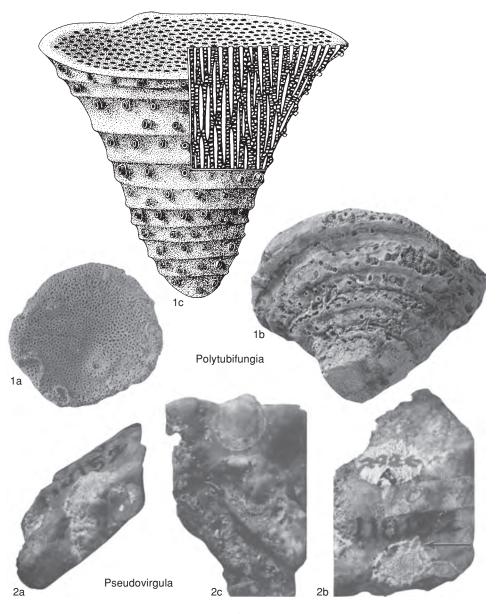


FIG. 393. Virgolidae (p. 605-606).

porous, skeletal net, USNM 480228,  $\times$ 5; *c*, subspherical holotype with rimmed oscula, USNM 480226,  $\times$ 1; *d*, photomicrograph of paratype with scattered, coarse, exhalant ostia and smaller, inhalant ostia and skeletal pores, USNM 480228,  $\times$ 10 (Rigby & Senowbari-Daryan, 1996a).

Polytubifungia RIGBY & SENOWBARI-DARYAN, 1996a, p. 90 [\*P. maxima; OD]. Mushroom-shaped sponges without large, deep spongocoel but with numerous unwalled, coarse, vertical, exhalant canals distributed more or less uniformly throughout entire sponge; fibrous skeleton between canals very fine textured; inhalant canals absent or ill defined in interior but with raised rims on exterior; growth lines clearly developed in dense, dermal layer; microstructure unknown. *Permian (Lopingian):* Tunisia.——FIG. 393,1*a-c.* \**P. maxima,* Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a*, summit of holotype with shallow, broad depression and numerous exhalant ostia, ×1.5; *b*,

605

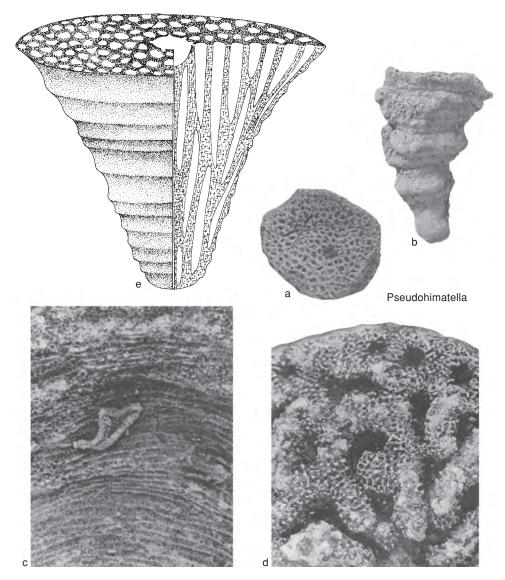


FIG. 394. Virgolidae (p. 608).

oblique side view with numerous inhalant ostia in dense, annulate, dermal layer, USNM 480215, ×2; *c*, reconstruction showing dense, dermal layer with rimmed ostia and skeletal and canal patterns of interior, not to scale (Rigby & Senowbari-Daryan, 1996a).

Pseudovirgula GIRTY, 1909, p. 75 [\**P. tenuis;* OD]. Small, stemlike, cylindrical sponges without a spongocoel but with central region of delicate, reticulate skeleton surrounded by outer, open zone that lacks skeletal net but with irregularly spaced and developed, uparched laminae that subdivide this part of sponge into irregular chambers; open area also with well-developed, coarse, radiating, tubular exaules that extend out from central skeletal region to or beyond the well-defined dermal layer. *Permian (Guadalupian):* USA (Texas).——FIG. 393,2*a*-*c.* \**P. tenuis*, Capitan Limestone, Guadalupe Mountains; *a*, side view of small, cylindrical holotype, ×4; *b*, upper transverse section with prominent exaulos (*arrow*) and dark, unskeletonized layer between light, dermal layer and interior, fibrous skeleton, ×4; *c*, lower surface showing central, fibrous skeleton and outer moat inside well-defined, dermal layer, USNM 118152, ×4 (Rigby, Senowbari-Daryan, & Liu, 1998).

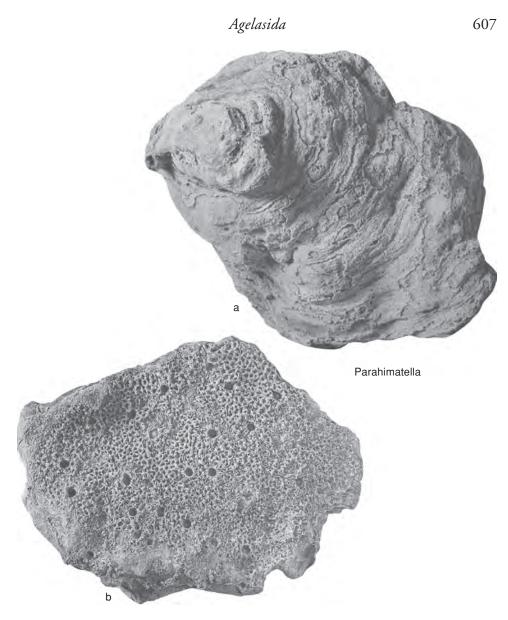


FIG. 395. Virgolidae (p. 608).

Vermispongiella FINKS & RIGBY, herein, nom. nov. pro Vermispongia WU Ya Sheng, 1991, p. 68, non QUENSTEDT, 1878, p. 171, nec WHITFIELD, 1905, p. 298 [\*Vermispongia spiniformis WU Ya Sheng, 1991, p. 68; OD]. Ovate sponges with moderately coarse canals vermiform and interconnected throughout entire sponge; short, excurrent canals not differentiated; skeletal tracts coarse and composed of fibers in irregular structure or in regular lattice; free ends of fibers extending into canals to form spinose-appearing surfaces of skeletal tracts. Permian (Kungurian): China (Guangxi).——FIG. 391,3. \*V. spiniformis (WU), Maokou Formation, Kungurian, Reef of Xiangbo; longitudinal section of holotype, IGASB xb37-2-12, ×2 (Wu Ya Sheng, 1991).

## Subfamily PSEUDOHIMATELLINAE Rigby & Senowbari-Daryan, 1996

[Pseudohimatellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 93]

Virguliid sponges club to mushroom shaped with large osculum in axial part of summit; vertical, exhalant canals not ending in osculum but distributed across summit. *Permian*.



Parahimatella

FIG. 396. Virgolidae (p. 608).

Pseudohimatella RIGBY & SENOWBARI-DARYAN, 1996a, p. 93 [\*Himatella pauciporata PARONA, 1933, p. 37; OD]. Club to mushroom shaped or pearlike without an axial spongocoel but generally one or more large, shallow, osculum-like depressions in axial area of summit; numerous long, coarse, vertical, exhalant canals distributed throughout entire sponge; canals circular to polygonal or irregular in transverse sections; limited horizontal, inhalant canals; rigid skeleton between canals fine, reticulate, fibrous net; dense, dermal layer may have growth lines in lower part; spherulitic microstructure. Permian: Tunisia, Italy (Sicily).---FIG. 394a-e. \*P. pauciporata (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, summit view showing two large, exhalant oscula and numerous coarse, exhalant ostia,  $\times 1$ ; b, side view of annulate, obconical sponge with dense, dermal layer, USNM 480248, ×1; c, photomicrograph of dermal surface with fine microsculpture uninterrupted by canals, USNM 480254, ×10; d, photomicrograph of upper surface with micronodose, broad, skeletal tracts between coarse ostia, USNM 480251, ×10; e, restoration showing canal pattern and dense, dermal layer of obconical sponge, not to scale (Rigby & Senowbari-Daryan, 1996a).

## Subfamily PARAHIMATELLINAE Rigby & Senowbari-Daryan, 1996

[Parahimatellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 94]

Virguliid sponges with fibrous skeleton of coarse spherulites; fibers in vesiculate-

appearing network; numerous deep, widespread spongocoels with oscula on upper surface. *Permian (Lopingian)*.

Parahimatella RIGBY & SENOWBARI-DARYAN, 1996a, p. 94 [\*P. vesiculata; OD]. Broadly obconical or flaring, mushroomlike to annulate, subcylindrical sponges lacking a major axial spongocoel, but with numerous vertical, walled spongocoels with oscula at surface; exhalant canals converging to bases or sides of spongocoels; distinct, small, vertical, inhalant canals extending down from surface into skeleton; skeleton vesiculate of bubblelike chambers arranged in either vertically stacked series or en echelon between canals, each chamber with one or two pores; walls coarsely spherulitic; rodlike elements, possibly foreign, common throughout skeleton. Permian (Lopingian): Tunisia.——FIG. 395a-b. \*P. vesiculata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side and bottom view of sheetlike holotype with dermal surface marked by growth lines, ×1; b, summit view showing numerous irregularly distributed, circular oscula separated by coarse, fibrous skeleton and small, inhalant ostia, USNM 480261, ×1 (Rigby & —Fig. 396. \**P*. Senowbari-Daryan, 1996a).vesiculata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; paratype, SEM photomicrograph of cystlike walls are 50 to 100 µm thick and composed of large spherulites approximately 80 µm in diameter, scale indicated by bar at base, USNM 480261 (Rigby & Senowbari-Daryan, 1996a).

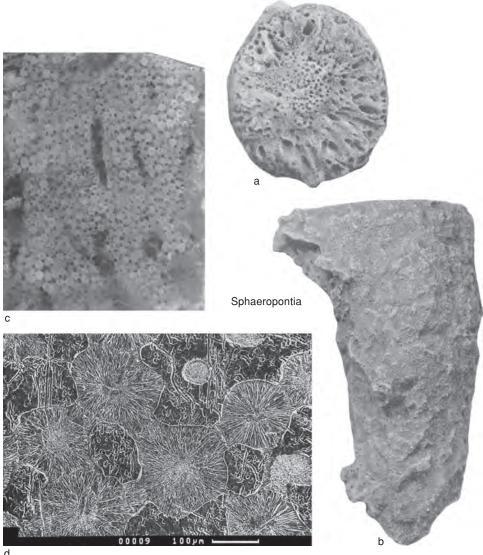


FIG. 397. Sphaeropontiidae (p. 609-610).

## Family SPHAEROPONTIIDAE Rigby & Senowbari-Daryan, 1996

[Sphaeropontiidae RIGBY & SENOWBARI-DARYAN, 1996a, p. 95]

Spherulites separated from one another and connected only by extensions between to form a loosely packed, quasicubic, threedimensional net. [This type of skeleton shows some resemblance to the filling tissue of Intrasporeocoelia FAN & ZHANG, 1985.

The authors of the family (RIGBY & SENOWBARI-DARYAN, 1996a, p. 96) suggest that the sphaeroclone desmas of the lithistid family Astylospongiidae may prove to be spherulites of the type found here, rather than desmas.] Permian (Lopingian).

Sphaeropontia RIGBY & SENOWBARI-DARYAN, 1996a, p. 96 [\*S. regulara; OD]. Conicocylindrical with large, upwardly and outwardly diverging, exhalant canals penetrating spherulitic, skeletal net. Permian

609

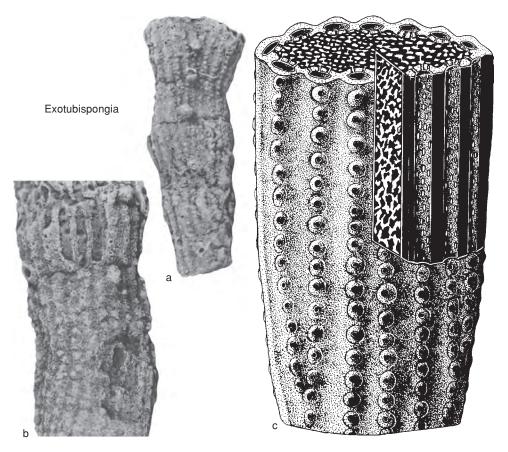


FIG. 398. Exotubispongiidae (p. 610-611).

(Lopingian): Tunisia.——FIG. 397*a–d. \*S. regulara*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a*, summit view of conicocylindrical holotype with numerous radially divergent, exhalant canals and some smaller, nearly vertical, ones in axial area, USNM 480321, ×2; *b*, side view of weathered paratype, USNM 480229, ×2; *c*, polished surface of paratype into nearly transparent calcium carbonate showing spherical spherulites connected by rays in skeletal tracts interrupted by canals, ×10; *d*, SEM photomicrograph of same paratype showing several spherulites and interconnecting, beamlike elements, USNM 480230, scale indicated by bar at base (Rigby & Senowbari-Daryan, 1996a).

## Family EXOTUBISPONGIIDAE Rigby & Senowbari-Daryan, 1996

#### [Exotubispongiidae RIGBY & SENOWBARI-DARYAN, 1996a, p. 97]

Cylindrical to branched, inozoid sponges with several vertical, exhalant, tubelike canals forming part of periphery in dermal part of sponge; inner part with reticular, fibrous skeleton; outer surface with numerous small, pustular pores arranged either in vertical lines along canals or irregularly. *Permian (Lopingian)*.

Exotubispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 97 [\*E. pustulata; OD]. Small, cylindrical or branched sponges with several vertical, tubelike canals in outer ring near periphery; central spongocoel absent; skeleton of upwardly divergent, reticulate fibers; microstructure unknown; vertical canals connect to exterior by numerous small pores that may be pustular and arranged in linear series on ribs along vertical canals or irregularly over dermal surface. Permian (Lopingian): Tunisia.-FIG. 398a-c. \*E. pustulata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side view of incipiently branched holotype with pustular pores in lines, USNM 480231, ×5; b, enlarged side view of paratype with vertically aligned, pustulose pores over vertical canals exposed in upper part, USNM 480235, ×10; c, reconstruction showing exterior and vertical and horizontal sections; coarse, longitudinal canals near periphery have large canals on pustular nodes on surface; inner area with reticular, skeletal fibers, not to scale (Rigby & Senowbari-Daryan, 1996a).

## Family SESTROSTOMELLIDAE de Laubenfels, 1955

[Sestrostomellidae DE LAUBENFELS, 1955, p. 97; emend., FINKS & RIGBY, herein] [=Sestrostomellidae DE LAUBENFELS, 1955, p. 97, parim; Stellispongiidae DE LAUBENFELS, 1955, p. 97, parim; Polysiphonellidae BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 92; Polysiphonellidae WU Ya Sheng, 1991, p. 65]

Sponges of inozoan morphology with vertical canals perpendicular to upper surface and radial canals parallel to it; central cloaca often present; microstructure of spherulitic and clinogonal aragonite with sparse monaxons. *Triassic–Lower Cretaceous*.

- Sestrostomella ZITTEL, 1878b, p. 40 [\*S. robusta; SD DE LAUBENFELS, 1955, p. 97] [=?Palaeoierea LAUBE, 1865, p. 233 (type, Manon? gracilis MÜNSTER, 1841, p. 28, OD); Sestromostella ZITTEL, 1903, p. 62, obj.]. Conical to cylindrical (occasionally with horizontal constrictions) with central cluster of parallel, subequal, exhalant canals that extend deeply into sponge along its axis; canals closely apposed and circular to subpolygonal in cross section; subhorizontal, radial canals empty into them and may be present as radial grooves on convex, top surface; central canals open into shallow, upper depressions. Exterior surface smooth with small, circular to meandriform, inhalant openings between skeletal fibers; imperforate, dermal layer may cover basal part of sponge. Larger, inhalant canals arch inwardly and upwardly parallel to top surface; internal trabeculae forming obscure layers parallel to top surface; intertrabecular spaces circular to meandriform in cross section. Occasional (calcitic, presumably after silica) monaxons may be present among (aragonitic) regular or flaky spherulites composing trabeculae (WENDT, 1974; FINKS, 1983a). Frequently forming bushy colonies of subparallel individuals fused basally and laterally. [Jurassic and Cretaceous homeomorphs with trabeculae composed of a large, central triradiate coated by small, sinuous spicules should not be assigned to this genus; they might be accommodated in Enaulofungia FROMENTEL, 1860a. Palaeoierea LAUBE, 1865, is senior to Sestrostomella if it is indeed a synonym. It is, however, more likely a Thaumastocoelia STEINMANN, 1882 (see p. 664, herein). It can be suppressed under the 50-year rule of the Code (ICZN, 1999).] Triassic-Jurassic: Europe, Iran, Triassic; Canadian Atlantic Shelf, Jurassic.-FIG. 399,1. \*S. robusta, Cassian Formation, Carnian, southern Alps, Italy; a, near longitudinal section of branched, partially recrystallized example showing reticulate structure and axial tubes of spongocoel on left, ×1 (Riedel & Senowbari-Daryan, 1991; courtesy of Springer-Verlag GmbH & Co.).
- Ateloracia POMEL, 1872, p. 228 [\*Cnemidium manon MÜNSTER, 1841, p. 30; SD RAUFF, 1893, p. 71]. Broadly conical, convex, upper surface with central, shallow, cloacal depression, toward which radial, exhalant grooves converge; interior, exhalant canals parallel to upper surface or obliquely convergent on cloaca; inhalant canals perpendicular to upper surface; trabecular mesh fine; sides of sponge invested by dermal layer; trabecular microstructure (WENDT, 1974, p. 503, 507, fig. 1) irregular (aragonitic), partly spherulitic with occasional (calcitic, presumably after silica) monaxons. [Genus differs from Precorynella DIECI, ANTONACCI, & ZARDINI, 1968, in absence of large, radially arranged ostia on the upper surface, in the finer trabecular net, narrower internal canals, and especially the absence of large, axial, vertical, exhalant canals. This name is available for the spherulitic Triassic species usually assigned to Stellispongia D'ORBIGNY, 1849, provided that Cnemidium manon is considered congeneric with the noncloacate, polyosculate species similar to Cnemidium variabile MÜNSTER, 1841. Suitable illustrations for this genus are unavailable.] Triassic: Europe, Timor.
- Brevisiphonella Russo, 1981, p. 5 [\*B. longirima; OD]. Small, compound sponge composed of conicoclavate individuals fused laterally; large, elongate-oval osculum opening into shallow, funnelshaped cloaca at center of each individual, approximately one-third diameter of individual; remainder of surface with fine, meandriform, intertrabecular spaces without dermal layer; skeletal trabeculae outlining anastomosing, tubular spaces; microstructure clinogonal; no spicules known. Triassic (Carnian): Italy.--FIG. 399,4a-e. \*B. longirima, San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; a, side view of holotype; b, diagonal view illustrating several elongate oscula, IPUM 19274; c, side view of branched paratype, IPUM 19275, ×4; d, transverse paratype section showing elliptical spongocoel and lack of defined dermal layer, IPUM 19276, ×8; e, transverse paratype section showing clinogonal microstructure, IPUM 19277, ×200 (Russo, 1981).
- Epitheles FROMENTEL, 1860a, p. 35 [\*Myrmecium hemisphaericum GOLDFUSS, 1826, p. 18; OD] [=Myrmecidium VINASSA DE REGNY, 1901, p. 10, nom. van., nom. nov. pro Myrmecium GOLDFUSS, 1826, p. 18, non LATREILLE, 1825; ?Gymnomyrmecium POMEL, 1872, p. 203 (type, Myrmecium gracile MÜNSTER, 1841, p. 26)]. Typically hemispherical with broadly conical base covered by concentrically wrinkled, dermal layer; narrow, central cloaca opening onto top surface and fed by vertical, central, and upwardly and inwardly curving, lateral, exhalant canals that may crenulate oscular rim; inhalant ostia cover top surface and lead inwardly and downwardly; intertrabecular spaces small and mostly circular in cross section. [Trabecular microstructure of a specimen (AMNH 1281/1) identified by ZITTEL as the type species appears to be small, sinuous bodies, parallel to trabecular surfaces, of the type called by HINDE (1893b, p. 214 et passim.,

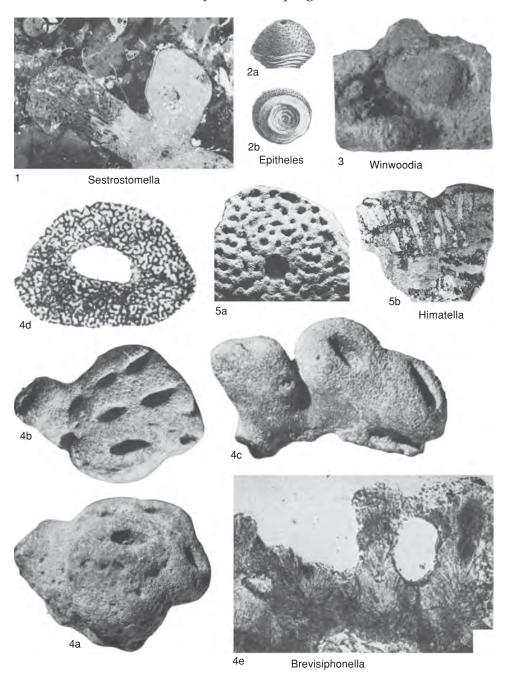


FIG. 399. Sestrostomellidae (p. 611-614).

"filiform sinuous spicules." HURCEWICZ (1975, p. 254, fig. 20 and pl. 30, fig. 1), in a specimen assigned to the same species, identified subequal triactines with subordinate tetractines and diactines, with the basal, dermal layer composed of para-

tangential diactines underlain by a layer of short diactines perpendicular to the surface. The taxonomic position of this genus will have to be determined by a microscopic study of the type specimen. WAGNER (1964, p. 26) placed this genus (as

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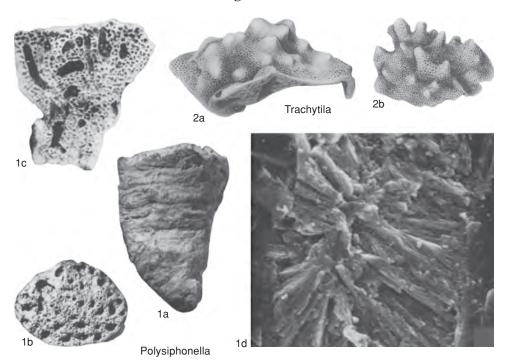


FIG. 400. Sestrostomellidae (p. 613-614).

Myrmecium GOLDFUSS, 1833 and Myrmecidium VINASSA DE REGNY, 1901) in subjective synonymy with *Eusiphonella* ZITTEL, 1878b, but the trabecular microstructure is different.] *Jurassic:* Europe.—. FIG. 399,2*a*-*b*. \**E. hemisphaerica* (GOLDFUSS), ?Corallian Limestone, ?Oxfordian, Upper Jurassic, Thurnau, France; *a*, side view of small, hemispherical sponge with small osculum at summit and irregularly wrinkled, lower, dermal layer, magnification unknown; *b*, view of same sponge from below showing dense, wrinkled, dermal layer, magnification unknown (Fromentel, 1860a).

Himatella ZITTEL, 1878b, p. 29 [\* Tragos milleporatum MÜNSTER, 1841, p. 29; OD]. Broadly conical, flaring upwardly from a narrow base to a width approximately equal to height; top surface gently convex, meeting sides in sharp rim; sides covered with dermal layer, sometimes horizontally rugose; narrow cloaca penetrating most of sponge, opening on center of top surface; top surface showing meandriform, intertrabecular spaces and scattered ostia; some ostia on sides; internal, meandriform, trabecular net often showing periodic thickening parallel to top surface; no interior canals other than intertrabecular spaces. Trabecular microstructure possibly (aragonitic) penicillate or spherulitic with occasional (calcitic, originally siliceous) monaxons (WENDT, 1974, p. 503, 507). Triassic: Europe, Tunisia, Timor.-----FIG. 399,5a-b. H. meandrina TERMIER & TERMIER, Series of Merbah el Oussif,

Changhsingian, Djebel Tebaga, Tunisia; *a*, view from above with central osculum and surrounding skeleton with ostia of vertical canals,  $\times 2$ ; *b*, axial section with prominent, vertical canals in upper part, some of which empty into shallow spongocoel,  $\times 2$  (Termier, Termier, & Vachard, 1977b; courtesy of *Géologie Méditerranéenne*).

- Polysiphonella Russo, 1981, p. 10, non Belyaeva in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93 [\*P. diecii; OD]. Small, conical sponge with flat top covered with ovoid, exhalant openings that communicate with subvertical (possibly anastomosing) canals of interior; intervening skeletal tissue finely trabecular, outlines anastomosing tubular spaces, whose openings are visible on top surface between larger, exhalant pores; sides covered with horizontally rugose epitheca; trabecular microstructure penicillate; no spicules known. Triassic (Carnian): -FIG. 400,1a-d. \*P. diecii, San Cassiano Italy .-Formation, Cortina d'Ampezzo, Dolomite Alps; a, side view of holotype with dense, dermal layer; b, view of holotype summit with numerous, exhalant oscula, IPUM 19285, ×5; c, vertical section of paratype showing several subvertical, exhalant canals in reticulate skeleton, IPUM 19290, ×8; d, paratype, SEM showing irregular, skeletal microstructure, IPUM 19293, ×500 (Russo, 1981).
- Trachytila WELTER, 1911, p. 64 [\**T. tuberosa*; OD]. Sponges with many branches with sharp, wart- or club-shaped expansions that may have oscula at

their ends, intervening dermal area with smaller, probably inhalant, round ostia; basal attachment surface may be irregularly wrinkled or with small, wartlike nodes; vertical canals interrupted by common tabulae; skeletal fibers include poorly preserved, scattered, three-rayed spicules. [Included in the family with some question.] *Lower Cretaceous:* Germany.——FIG. 400,2*a*–*b.* \**T. tuberosa*, Essener Grünsand, Cenomanian, Essen; *a*, side view showing encrusting base and nodular, upper parts of sponge; *b*, view from above of moderately lobate form of genus, ×1 (Welter, 1911).

Winwoodia RICHARDSON & THACKER, 1920, p. 178 [\*W. porula RICHARDSON & THACKER, 1920, p. 179; OD]. Massive sponges, lacking surficial grooves, with or without terminal oscula on summit; numerous inhalant ostia in dermal surface, which lacks a dermal cortex, except possibly present around base. [Included in the family with question.] Middle Jurassic: England.—FIG. 399,3. \*W. porula, upper Inferior Oolite, Gloucestershire; side view of relatively massive, though small, type specimen, ×2 (Richardson & Thacker, 1920).

### Family PHARETROSPONGIIDAE de Laubenfels, 1955

[Pharetrospongiidae DE LAUBENFELS, 1955, p. 98, *partim; emend.*, FINKS & RIGBY, herein]

Basal skeleton of penicillate microstructure of inozoan morphology, consisting of anastomosing trabeculae that outline meandriform, anastomosing, tubular spaces; it is not known if mineralogy is aragonite or calcite; monaxons parallel to length of trabeculae said by earlier authors to be present in type genus and in some others, but they may be referring to penicillate needles. *Permian (Guadalupian)–Cretaceous.* 

## Subfamily PHARETROSPONGIINAE de Laubenfels, 1955

[nom. transl. FINKS & RIGBY, herein, ex Pharetrospongiidae DE LAUBENFELS, 1955, p. 98]

Trabeculae and their interspaces not dominantly vertical and subparallel. *Triassic* (*Carnian*)–*Cretaceous*.

Pharetrospongia SOLLAS, 1877a, p. 249 [\*P. strahani; OD]. Sponge body curving or convoluted plates that may anastomose or form funnel-shaped or subcylindrical bodies; exhalant surface smoother than inhalant, and may have small, circular oscules; otherwise no pores other than intertrabecular spaces, which are circular to meandriform. [Trabeculae of a referred specimen identified by R. E. H. REID and examined by the present author (RMF) has solid, penicillate microstructure with no trace of spicules; supposed parallel monaxons that HINDE (1884a, p. 202) described may have been the penicillate needles.] *Cretaceous:* Europe.—FIG. 401,2a-b. \**P. strahani; a,* side view of cup-shaped specimen with thin walls and reticulate, inner surface, Upper Chalk, Kent, England, ×1; *b,* camera lucida drawing of fibers showing traces of spicules, Upper Greensand, Cambridge, England, ×50 (Hinde, 1884a).

Euepirrhysia Dieci, ANTONACCI, & ZARDINI, 1968, p. 123 [\*E. montanaroae; OD]. Massive (but small) sponge composed of laterally fused, conical individuals; upper surface flat or gently convex, pustulose, with circular, often lipped pore in center of each pustule; much larger, circular oscule in center of each component individual (diameter approximately one-fifth that of individual) surrounded by radiating, dendritic, exhalant canals; upper surface meeting sides in sharp rim or edge; sides covered with horizontally wrinkled epitheca; cylindrical cloaca extending to base of sponge from each oscule; horizontal, exhalant canals enter cloaca from side at regular vertical intervals to produce laminated appearance; closely spaced, vertical canals (possibly inhalant) extend downwardly from each pustule pore on upper surface; remainder of skeleton dense; microstructure unknown; spicules not known. [A second species, E. pusilla (LAUBE, 1865), is represented by solitary, conical individuals; pores of the upper surfaces are largest at the periphery where they form a distinct ring.] Triassic (Carnian-Norian): Italy.—\_FIG. 401, 1a-c. \*E. montanaroae, San Cassiano Formation, Norian, Dolomite Alps; a, view of holotype from above with axial spongocoel in each branch and surface marked by rimmed, possibly inhalant ostia,  $\times 2$ ; b, view from below showing convergent, exhalant canals around three spongocoels, and openings of vertical, possibly inhalant canals, all within dense, dermal layer,  $\times 2$ ; *c*, vertical section with axial spongocoel and walls with regularly spaced levels of exhalant, canal development and vertical canals producing reticulate-appearing skeleton, IPUM 17543, ×2 (Dieci, Antonacci, & Zardini, 1968).

## Subfamily LEIOFUNGIINAE new subfamily

[Leiofungiinae FINKS & RIGBY, herein] [type genus, *Leiofungia* FROMENTEL, 1860a, p. 49]

Conical, imperforate cortex on sides; skeleton dense, with trabeculae subparallel in direction of growth, thin, and outlining narrow, subequal spaces of dominantly meandriform cross section; trabecular microstructure penicillate where known. [The morphology of this subfamily is quasistromatoporoid.] *Permian (Guadalupian)– Cretaceous.* 

Leiofungia FROMENTEL, 1860a, p. 49 [\**Achilleum milleporatum* MUNSTER, 1841, p. 26; OD]. Conicocylindrical with convex, upper surface; sides

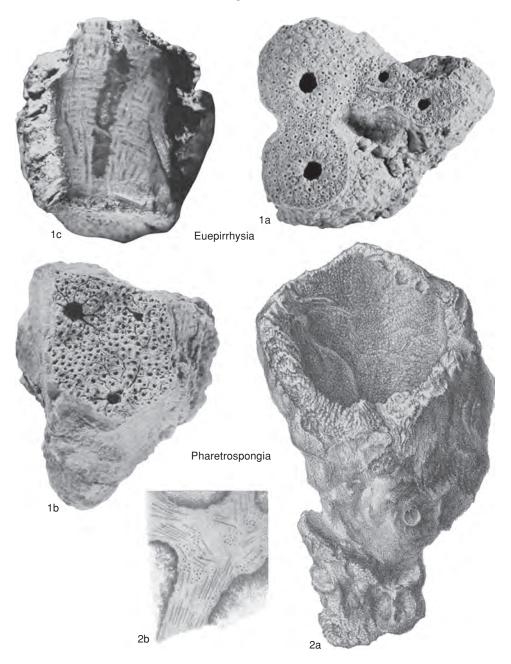


FIG. 401. Pharetrospongiidae (p. 614).

covered with imperforate, dermal layer; pores on upper surface very small, closely spaced, some circular or subpolygonal, but mostly meandriform, as openings of closely spaced, vertical-radial canals separated by thin trabeculae that have penicillate microstructure; it is not known whether type specimens have horizontal cross partitions, as in many sclerosponges; no spicules known. [This genus corresponds to *Leiospongia sensu* DIECI, RUSSO, & RUSSO (1974b, p. 138) *non* D'ORBIGNY (1849, p. 548).] *Triassic:* Europe.——FIG. 402,2*a*-*b*. \**L. milleporata* (MÜNSTER), San Cassiano Formation,

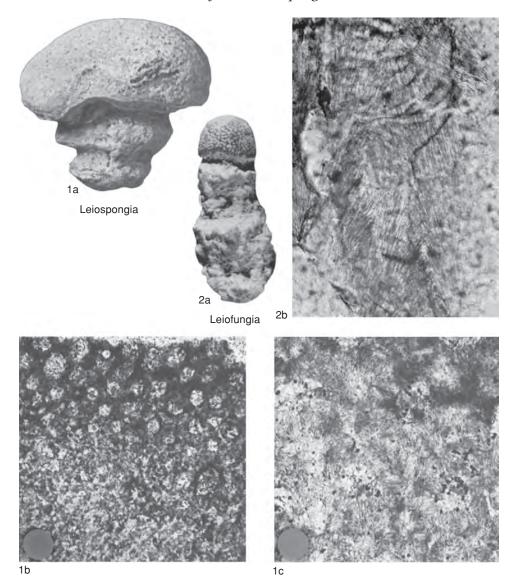


FIG. 402. Pharetrospongiidae (p. 614-618).

Carnian, Dolomite Alps, Italy; *a*, side view of holotype with imperforate, dermal layer and porous, upper surface, ×5; *b*, photomicrograph of longitudinal section with penicillate, crystalline fibers, SSPHG AS VII 445, ×250 (Dieci, Russo, & Russo, 1974b).

- Aulacopagia POMEL, 1872, p. 245 [\*Leiospongia maeandrina D'ORBIGNY, 1850, vol. 1, p. 295; OD]. Resembles Leiofungia FROMENTEL, 1860a, but upper surface bearing meandriform furrows; internal structure unknown and may not be related. [No known suitable figures.] Jurassic: Europe.
- Elasmopagia POMEL, 1872, p. 246 [\**E. anomala*; OD]. Possibly flabellate or vertically laminar sponge with concentrically wrinkled, dermal layer covering sides, porous, skeletal net visible only at top. [Otherwise genus resembles "*Leiospongia* D'ORBIGNY, 1849" (i.e., *Leiofungia* FROMENTEL, 1860a, or *Hartmanina* DIECI, RUSSO, & RUSSO, 1974b) of which it was proposed as a subgenus. It was not illustrated and the internal structure is not known.] *Cretaceous:* France.
- Grossotubenella RIGBY, FAN, & ZHANG, 1989b, p. 794 [\**G. parallela;* OD]. Cylindrical to subcylindrical

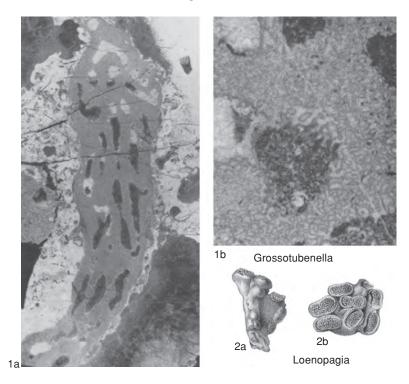


FIG. 403. Pharetrospongiidae (p. 616-618).

sponges without a spongocoel but with a weakly annulate exterior; interior with many coarse, nearly equally spaced, subvertical, subparallel to sinuous, exhalant canals that branch upwardly, infrequently; incurrent canals not evident. Skeleton even textured, composed of fine, vermiform fibers, pierced throughout by small, irregular, skeletal pores; spicules unknown. [Included in the family and subfamily with some question.] Permian (Guadalupian): China (Guangxi).—FIG. 403,1a-b. \*G. parallela, Maokou Formation, Kungurian, Longlin County; a, vertical section of holotype showing cavernous interior with coarse, vertical canals separated by coarse tracts of fine, fibrous skeleton,  $\times 2$ ; *b*, photomicrograph showing fine, fibrous skeleton in tracts between unlined canals, IGASB 5216, ×20 (Rigby, Fan, & Zhang, 1989b).

Leiospongia D'ORBIGNY, 1849, p. 548 [\*Achilleum granulosum MUNSTER, 1841, p. 26; SD FINKS & RIGBY, herein] [=?Hartmanina DIECI, RUSSO, & RUSSO, 1974b, p. 141 (type, Achilleum verrucosum MUNSTER, 1841, p. 25)]. Spheroidal or hemispherical to encrusting sponges with almost straight calicles, divided irregularly by tabulae; walls and tabulae of penicillate, aragonitic structure; distinct dermal layer absent; surface bearing closely spaced, fine, equidimensional pores of subequal size, and edges of intervening trabeculae bearing fine granules; spicules fusiform styles or acanthostyles irregularly present and parallel to growth direction. [Only two species, Achilleum granulosum and A. verrucosum, KLIPSTEIN, 1843 in 1843-1845, were cited (as examples) in connection with Leiospongia when D'ORBIGNY established the genus in November, 1849 (p. 548). Prodrome de Paleontologie, sometimes cited as the first publication of the genus, was published in January, 1850 according to ENGESER and TAYLOR (1989, p. 41-42). According to Article 67.2 of the Code (ICZN, 1999), a nominal species that was not included when a new nominal genus was established cannot be validly designated or indicated as the type species of that genus. Thus the subsequent designation of Achilleum milleporatum MÜNSTER, 1841 as type of Leiospongia D'ORBIGNY, 1849 by DE LAUBENFELS (1955, p. 100) is not valid. Achilleum verrucosum was chosen by DIECI, RUSSO, and Russo (1974b, p. 141) as type of their new genus Hartmanina, which they separated from Leiospongia on the basis of its possession of a spherulitic skeleton rather than a penicillate one, among other features. If one is not to sink Hartmanina into synonymy with Leiospongia, one must choose the remaining species originally included by D'ORBIGNY, namely Achilleum granulosum MÜNSTER, 1841 (the ascription to KLIPSTEIN by D'ORBIGNY is to a subsequent description of MÜNSTER's species) as the type species for Leiospongia. So far as we know, the microstructure of L. granulosum has not been published, nor have we seen the holotype. Hopefully for the retention of Hartmanina, it is not spherulitic, but the finer pores and denser skeleton would justify a separation in any case.] *Triassic*: Europe, Timor.——FIG. 402, *Ia*– c. *L. alpina* (KLIPSTEIN), Cassian Formation, lower Carnian, St. Cassian, Italy; *a*, side view of holotype, BMNH S10462, ×1; *b*, transverse section through calicles, ×35; *c*, spherulitic structure of wall, ×130 (Engeser & Taylor, 1989).

- Loenopagia POMEL, 1872, p. 245 [\* Tragos ramosum KLIPSTEIN, 1843 in 1843-1845, p. 283; OD]. Partly fused, subparallel, conicocylindrical branches, covered laterally by dermal layer; rounded, finely porous upper surface of each branch forming knob on colony surface. [Genus resembles a compound Leiofungia FROMENTEL, 1860a, and could well be that genus, but nothing is known of the internal structure, microstructure, or spicules of Loenopagia.] Triassic: Europe.—FIG. 403,2a-b. \*L. ramosum (KLIPSTEIN), Cassian beds, Tyrol area, Austria; a, side view of branched, small sponge with dense, dermal layer and porous summit,  $\times 1$ ; b, view down onto summit of sponge showing porous, exhalant surfaces of branch tips, ×1 (Klipstein, 1843 in 1843-1845).
- Radicanalospongia RIGBY, FAN, & ZHANG, 1989b, p. 798 [\*R. normala; OD]. Encrusting, commonly forming cylindrical, budding growths with dense, basal layer; pseudocentral, spongocoel-like tube may form where sponges encrusted soft-bodied organisms; many regularly stacked, cylindrical, exhalant canals piercing fibrous skeleton and may assume radial pattern in cylindrical growths; less common and smaller, longitudinal and radial, incurrent canals connecting exhalant canals; skeletal fibers evenly spaced around skeletal canals to produce fine-textured skeleton between coarse canals; spicules and microstructure unknown. Permian (Guadalupian): China (Guangxi).-FIG. 404a-c. \*R. normala, Maokou Formation, Kungurian; a, oblique section of subcylindrical, encrusting holotype with imperforate base over dark, central matrix and stacked, regular series of radial canals, IGASN 5090,  $\times 2$ ; b, encrusting bases of paratype showing radial canals in walls around dark matrix, IGASB 5088,  $\times 2$ ; *c*, photomicrograph of fine, fibrous, skeletal net between uniform, radiating canals in holotype, IGASB 5090, ×10 (Rigby, Fan, & Zhang, 1989b).

### Family AURICULOSPONGIIDAE Termier & Termier, 1977

[Auriculospongiidae TERMIER & TERMIER, 1977a, p. 29] [=Tubulispongiidae WU Ya Sheng, 1991, p. 35]

Sheet- or platelike sponges with one side inhalant and other side exhalant surface, with or without prominent canals; skeleton of fibers parallel to growth direction, with spherulitic microstructure, probably aragonitic. *Permian (Asselian–Changhsingian)*.

### Subfamily AURICULOSPONGIINAE Termier & Termier, 1977

[nom. transl. RIGBY & SENOWBARI-DARYAN, 1996a, p. 26, pro Auriculospongiidae TERMIER & TERMIER, 1977a, p. 29]

Auriculospongiids without inhalant canals but with exhalant canals on one side; interfiber spaces serving as inhalant openings. *Permian (Asselian–Changhsingian)*.

- Auriculospongia TERMIER & TERMIER, 1974, p. 247 [\*Phacellopegma auriculata TERMIER & TERMIER, 1955, p. 625; OD]. Earlike to palmate, bladed sponges with both inhalant and exhalant surfaces marked by tangential, moderately deep furrows that are smaller on inhalant side; skeletal fibers dominantly parallel growth direction and composed of spherulites. Permian (Lopingian): Tunisia.----FIG. 405a-b. \*A. auriculata (TERMIER & TERMIER), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, inhalant side showing irregular, small pores and larger, mounded ostia, ×1; b, diagram of arrangement of skeletal fibers within a club-shaped specimen, not to scale (Rigby & Senowbari-Daryan, 1996a).----FIG. 406a-c. \*A. auriculata (TERMIER & TERMIER), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, exhalant upper surface with a prominent system of divergent furrows in which exhalant ostia are situated, USNM 463571, ×1; b, photomicrograph of upper surface with indented canals separated by irregular nodes of light, skeletal fibers around dark, skeletal pores, USNM 463574, ×10; c, SEM photomicrograph of rigid skeleton composed of spherulites, USNM 463577, scale indicated by bar at base (Rigby & Senowbari-Daryan, 1996a).
- Cavusonella Rigby, Fan, & Zhang, 1989b, p. 796 [\*C. caverna; OD]. Cylindrical, uneven to undulating exteriors; interiors pierced by coarse, irregular openings that may bifurcate upwardly and may make up to one-half sponge volume; prominent, continuous, longitudinal canals and continuous central spongocoel absent; skeleton of irregular fibers in loose, upwardly and outwardly expanding pattern. Permian (Guadalupian-Lopingian): China (Guangxi), Guadalupian; Tunisia, Lopingian.-FIG. 407,1ad. \*C. caverna; a, sublongitudinal section of holotype with irregular, coarse canals in relatively fine, upwardly divergent, fibrous skeleton, Maokou Formation, Kungurian, Guangxi, IGASB 5201, ×2; b, transverse section of paratype with coarse canals in interior, Maokou Formation, Kungurian, Guangxi, IGASB 5195, ×2 (Rigby, Fan, & Zhang, 1989b); c, side view of club-shaped sponge with small, inhalant ostia on ridges between large, exhalant ostia, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia, ×2; d, weathered exterior with uniform, skeletal net in coarse tracts between coarse canals, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia,

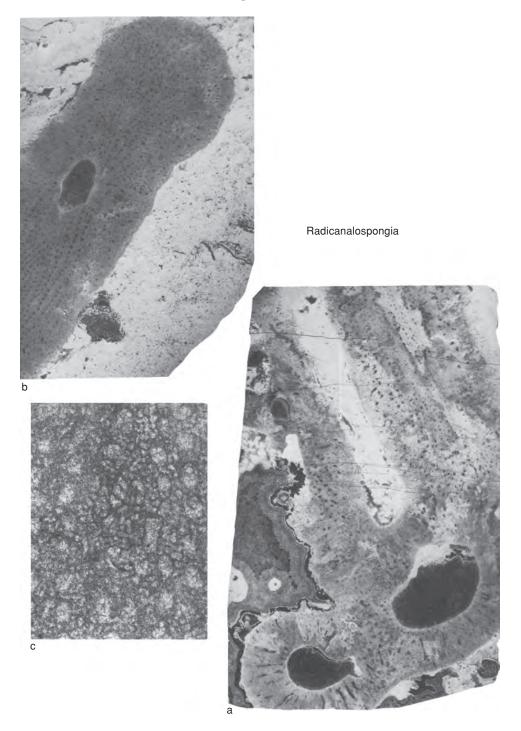


FIG. 404. Pharetrospongiidae (p. 618).

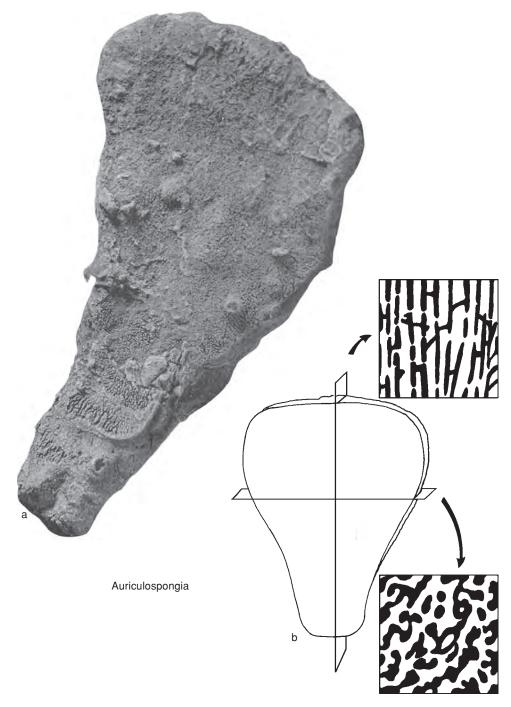
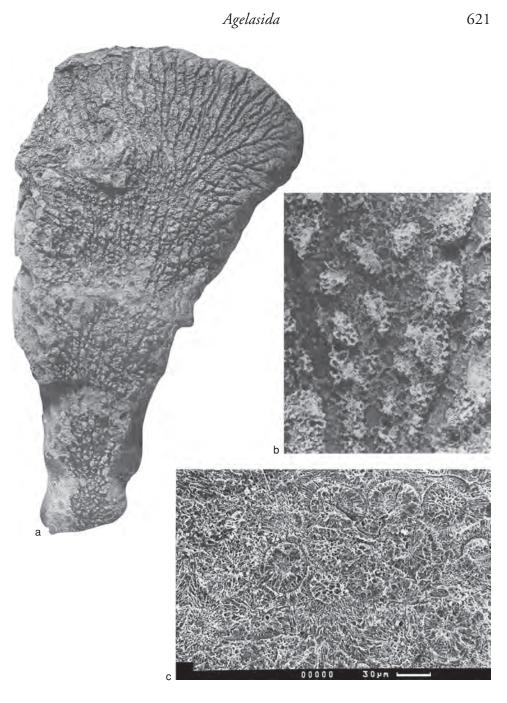
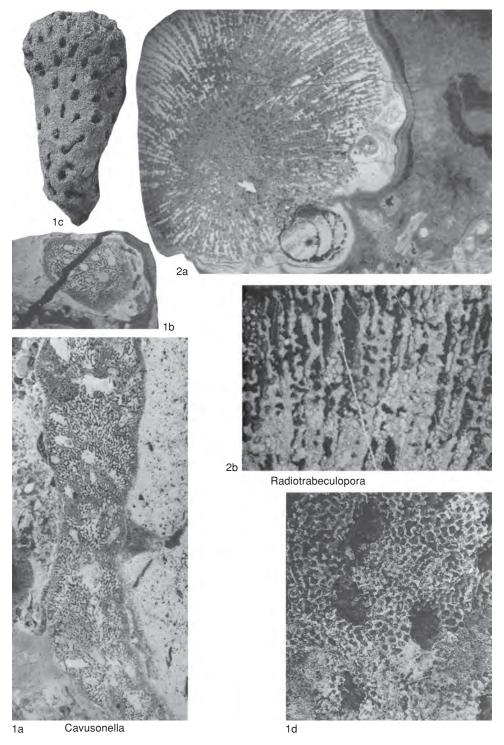


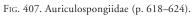
FIG. 405. Auriculospongiidae (p. 618).

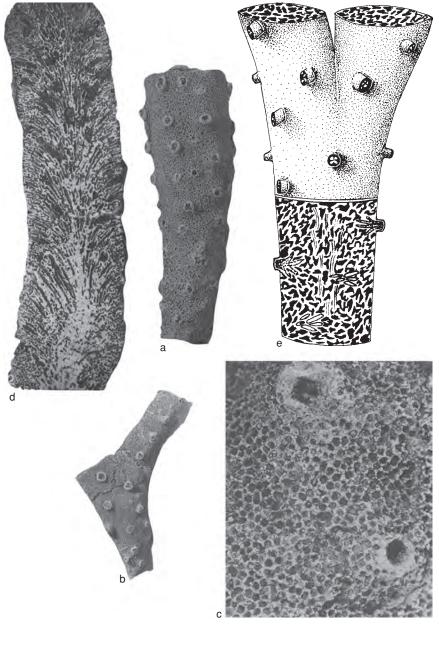


Auriculospongia

FIG. 406. Auriculospongiidae (p. 618).







Daharella

FIG. 408. Auriculospongiidae (p. 624).

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USNM 463589, ×10 (Rigby & Senowbari-Daryan, 1996b).

Radiotrabeculopora FAN, RIGBY, & ZHANG, 1991, p. 56 [\*R. xiangboensis; OD] [=Tubulispongia WU Ya Sheng, 1991, p. 35 (type, T. concentrica, OD); Flabellisclera WU Ya Sheng, 1991, p. 36 (type, F. discreta, OD); Gigantosclera WU Ya Sheng, 1991, p. 38 (type, G. deformis, OD); Gracilitubulus WU Ya Sheng, 1991, p. 39 (type, G. perforatus, OD); Fungispongia WU Ya Sheng, 1991, p. 39 (type, F. circularis WU Ya Sheng, 1991, p. 40, OD)]. Cylindrical to massive, obconical or mushroom- to clubshaped sponges with skeleton of many trabeculae of various diameters that are essentially longitudinal and parallel to each other; trabeculae may merge into single, coarse elements or coarse ones may divide into slender ones; canals between trabeculae diverging upwardly with moderate range of diameters; many smaller pores irregularly interrupting trabeculae; skeletal structure aragonitic with spherulitic microstructure. Permian (Asselian-Changhsingian): USA (California), Asselian-Sakmarian; China (Guangxi, Yunnan), Guadalupian; China (Guangxi, Hubei), Tunisia, Lopingian.—FIG. 407,2a-b. \*R. xiangboensis, Maokou Formation, Kungurian, Xiangbo, Guangxi, China; a, cross section of spheroidal holotype with irregular, radial trabeculae and canals, which has overgrown sphinctozoan sponge at base, projection print of thin section, IGASB 5154, ×2; b, thin section parallel to radial skeleton showing coarse, radial and horizontal trabeculae, coarse pores, and larger canals, IGASB 5154, ×5 (Fan, Rigby, & Zhang, 1991).

### Subfamily DAHARELLINAE Rigby & Senowbari-Daryan, 1996

[Daharellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 34]

Auriculospongiids without exhalant canals, but with distinct, tubelike, inhalant canals; spaces between fibers serving as exhalant openings. *Permian (Changhsingian).* 

Daharella RIGBY & SENOWBARI-DARYAN, 1996a, p. 34 [\*D. ramosa; OD]. Branched to unbranched, cylindrical to palmate sponges that lack a continuous spongocoel or axial bundle of exhalant canals; exterior with numerous circular to starlike, inhalant ostia on tips of tubelike canals; sievelike plate may be developed at base of each ostium, openings may continue into interior as separate, inhalant tubes; skeleton fibrous reticulate. [Daharella lacks an axial spongocoel or common, through-going, longitudinal, exhalant canals. The co-occurring and externally similar-appearing Preeudea has numerous, vertical, exhalant tubes and Djemelia has a well-defined, axial spongocoel.] Permian (Changhsingian): Tunisia. FIG. 408a-e. \*D. ramosa, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side view of branched holotype in which exhalant pores have distinct rims, USNM 463593,  $\times$ 1; *b*, side view of simple paratype with characteristic dermal surface and rimmed ostia, USNM 463952,  $\times$ 2; *c*, photomicrograph of exterior with rimmed, coarse, exhalant ostia in uniform net of fine fibers around skeletal pores, USNM 480411,  $\times$ 10; *d*, longitudinal section showing arrangements of skeletal fibers and canals ending at surface, USNM 463594,  $\times$ 3; *e*, schematic diagram showing skeletal and canal structure of genus, not to scale (Rigby & Senowbari-Daryan, 1996a).

### Subfamily GIGANTOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Gigantospongiinae RIGBY & SENOWBARI-DARYAN, 1996b, p. 351]

Sheetlike to palmate auriculospongiids with both inhalant and exhalant, transverse canals and major, longitudinal, exhalant canals; spongocoels and oscula absent. *Permian* (*Guadalupian*).

Gigantospongia RIGBY & SENOWBARI-DARYAN, 1996b, p. 353 [\*G. discoforma; OD]. Large, discoidal, inozoid sponges with distinct and prominent, divergent to parallel, longitudinal-radial canals, with more irregular, transverse canals generally at right angles or steep angles to dermal-gastral surfaces; limited, astrorhizal development may occur on dermal surface; skeletal tracts subhorizontally and radially divergent, parallel to tubular canals, tracts cross connected by irregular to columnar, vertical, subparallel elements in transverse sections. Skeletal microstructure unknown. Permian (Guadalupian): USA (New Mexico).——FIG. 409*a*-*b*. \**G*. discoforma, Capitan Limestone, Guadalupian, Guadalupe Mountains, New Mexico; a, part of large horizontal holotype, below (left), and reference specimen, above, in field exposure (arrows), scales in inches and centimeters; b, vertical section through holotype showing differentiated, upper and lower layer and canals divergent in direction of growth, scale in centimeters (Rigby & Senowbari-Daryan, 1996b).

### Subfamily SPINOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Spinospongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 37]

Cylindrical to club-shaped auriculospongiids lacking inhalant and exhalant canals; skeleton with prominent, thornlike spines. *Permian (Changhsingian).* 

Spinospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 37 [\*S. radiata; OD]. Cylindrical to club-shaped sponges lacking a central spongocoel or other coarse, exhalant and inhalant canals; exterior marked by tips of spinelike, skeletal elements that

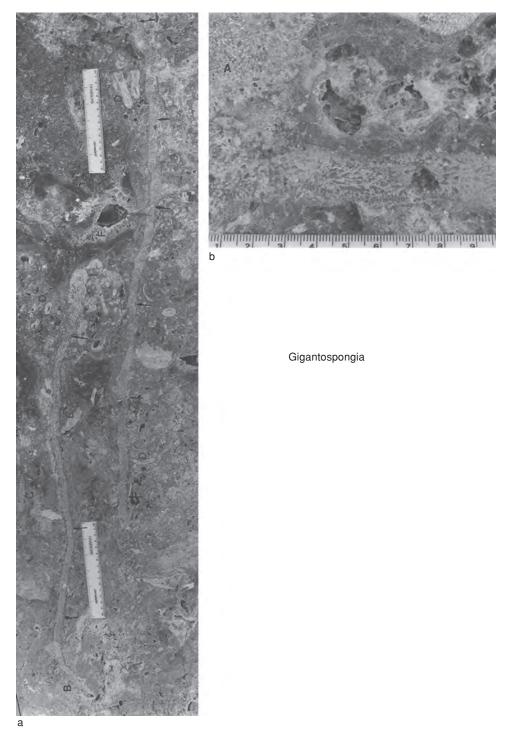


FIG. 409. Auriculospongiidae (p. 624).

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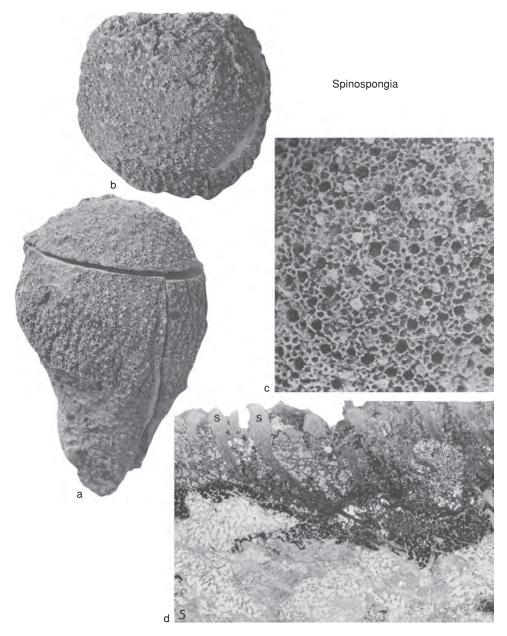


FIG. 410. Auriculospongiidae (p. 624-627).

continue into interior and help form skeleton; coarse, discontinuous openings between spines; interior with reticulate, fibrous skeleton composed of spherulites. *Permian (Changhsingian):* Tunisia.— FIG. 410*a*–*d.* \**S. radiata,* Djebel Tebaga Biohermal Complex, Djebel Tebaga; *a*, side view of rounded, obconical holotype, spherical tips of spinose, skeletal rods show as light dots, small openings between spines do not extend far into interior as canals,  $\times 2$ ; *b*, top view of holotype, spongocoel absent, USNM 464611,  $\times 2$ ; *c*, prominent spines are light, elevated areas in dermal surface of paratype, with skeletal fibers outlining skeletal pores and round, inhalant openings, USNM 463613,  $\times 10$ ; *d*, photomicrograph of section showing spines (*s*) that diverge upwardly and outwardly to dermal surface, internal

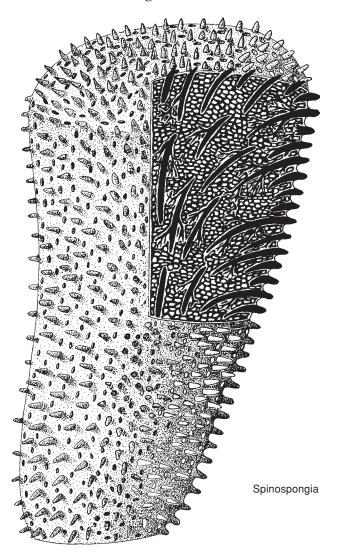


FIG. 411. Auriculospongiidae (p. 624-627).

spaces between spines filled with bubblelike, skeletal tracts, USNM 463615, ×5 (Rigby & Senowbari-Daryan, 1996a).——FiG. 411. \**S. radiata*, Djebel Tebaga Biohermal Complex, Djebel Tebaga; schematic diagram showing outer morphology and structure of skeleton in longitudinal section, not to scale (Rigby & Senowbari-Daryan, 1996a).

### Subfamily ACOELIINAE Wu, 1991

[nom. transl. FINKS & RIGBY, herein, ex Acoeliidae WU Ya Sheng, 1991, p. 57]

Cylindrical to club-shaped or obconical sponges lacking a spongocoel or significant

inhalant and exhalant canals in spherulitic, fibrous, skeletal net. *Permian (Guadalupian–Lopingian)*.

Acoelia WU Ya Sheng, 1991, p. 57 [\*A. ruida; OD]. Sponges moderately large, obconical, curved, with skeleton of thick fibers that are somewhat discontinuous and of moderately uniform diameters; interconnected spaces between fibers circular in longitudinal sections; dermal layer not developed. *Permian (Guadalupian):* China (Guangxi).——FiG. 412,1. \*A. ruida, reef of Xiangbo, Guadalupian; holotype section of irregular, thick fibers lacking coarse canals and dermal layer, xb27-6-2, ×3 (Wu Ya Sheng, 1991).

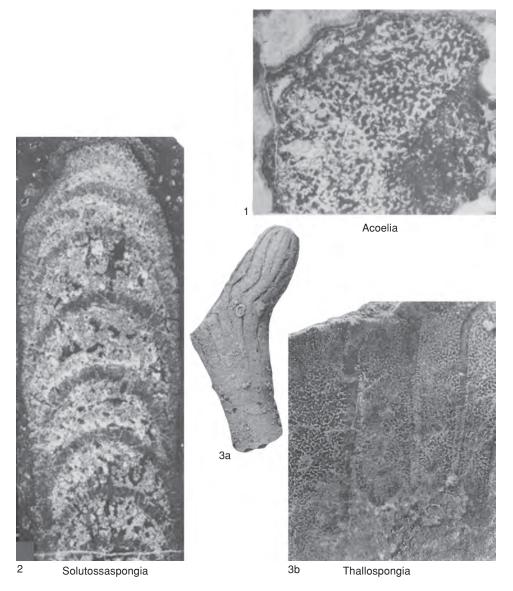


FIG. 412. Auriculospongiidae (p. 627-629).

Solutossaspongia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 25 [\*S. crassimuralis SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 26; OD]. Cylindrical, unbranched sponges with distinct, thick, outer wall; skeleton of interior composed of loose, reticular fibers; spongocoel absent. [SENOWBARI-DARYAN and INGAVAT-HELMCKE (1994) concluded that the family Acoeliidae and the genus Acoelia WU Ya Sheng, 1991, were based on inadequate samples that may have been only tangential sections of other sponges. Solutossaspongia differs from WU's genus in having a thick, outer wall and a loosely packed, fibrous, internal skeleton. They were reluctant to include the genus in the Acoeliidae and instead included it in the inozoa but in family Uncertain.] *Permian (Lopingian):* Thailand.——FiG. 412,2. \*S. crassimuralis, upper Permian limestone, Dorashamian, Phrae; holotype section with thick, outer wall and open, endosomal, reticulate skeleton, BSPGM R15, ×3.5 (Senowbari-Daryan & Ingavat-Helmcke, 1994).

Thallospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 38 [\* T. reticulata; OD]. Branching, solid, small, twiglike sponges lacking spongocoel or major internal, canal system in uniform, upwardly divergent skeleton; upper exterior with impressed, subvertical canals that converge to upper tip. *Permian* (*Lopingian*): Tunisia.——FIG. 412,3*a-b.* \* *T*. *reticulata*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a*, side view of holotype showing branching form, ×2; *b*, photomicrograph of exterior of holotype showing indented, vertical canals in fine, skeletal net, USNM 4480358, ×10 (Rigby & Senowbari-Daryan, 1996a).

### Family STELLISPONGIELLIDAE Wu, 1991

[Stellispongiellidae WU Ya Sheng, 1991, p. 65]

Massive to hemispherical or stemlike to obconical sponges lacking a spongocoel but upper or outer surface including one to several oscula or astrorhizal clusters of exhalant canals; canals of cluster may extend into interior; fibrous skeleton aspiculate, commonly reticulate, with spherulitic microstructure; dense, dermal layer may be present on base. *Permian (Guadalupian)–Triassic (Norian).* 

### Subfamily STELLISPONGIELLINAE Wu, 1991

[*nom. transl.* FINKS & RIGBY, herein, *ex* Stellispongiellidae WU Ya Sheng, 1991, p. 65]

Stellispongiellids in which starlike, oscular clusters of convergent, exhalant canals may be developed on mamelon-like mounds or impressed into generally smooth, upper or outer surface; sponges commonly ramose. *Permian (Guadalupian)–Triassic (Norian).* 

Stellispongiella WU Ya Sheng, 1991, p. 65 [\*Stellispongia bacilla TERMIER & TERMIER, 1955, p. 622; OD] [=Stellispongia TERMIER & TERMIER, 1955, p. 620, obj., non D'ORBIGNY, 1849]. Cylindrical, stemlike to branched or palmate to irregularly encrusting sponges with numerous uniformly distributed oscula to which converge exhalant canals in a stellate pattern; oscula may be on nodes, on smooth exteriors, or impressed into stems; exterior with numerous inhalant pores to short canals that may be lost in skeletal net or may lead to upwardly divergent, axial canals, which connect to radial, exhalant canals and ostia that may occur in tangential, oscular canals or on exterior between oscula; microstructure spherulitic; spongocoel absent. [These Permian sponges were grouped early with similarappearing species in Stellispongia and the Stellispongiidae. Once the spiculate nature of the skeleton of Triassic and probably younger species of Stellispongia became known (REITNER, 1992), however, it was considered important that these aspiculate sponges be separated at generic and family levels.] Permian (Guadalupian-Lopingian): China (Guangxi), Tunisia; Triassic (Norian): -FIG. 413*a*-*d.* \**S. bacilla* (TERMIER & ?Peru.-TERMIER), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view showing coarse, exhalant, astrorhizal canals on nodes with fine skeleton, USNM 480276, ×2; b, branched sponge with astrorhizal canal system on low nodes, USNM 480278, ×1; c, photomicrograph of node with indented, convergent, astrorhizal canals in reticulate, skeletal net, USNM 480412, ×10; d, generalized drawing showing canal patterns in skeleton and general morphology, not to scale (Rigby & Senowbari-Daryan, 1996a).-—Fig. 413e. S. reticulata RIGBY & SENOWBARI-DARYAN, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; side view of holotype with well-preserved, astrorhizal, canal net, USNM 4464648, ×2 (Rigby & Senowbari-Daryan, 1996a).

### Subfamily PRESTELLISPONGIINAE Rigby & Senowbari-Daryan, 1996

[Prestellispongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 49]

Massive to fungiform stellispongiellids with one to several exhalant openings on the summit that extend into interior as clusters of canals; smaller inhalant canals commonly from upper surface and between canals of surficial, starlike, astrorhizal, oscular clusters; skeleton a regular reticulation to one with longitudinally dominant fibers. *Permian (Lopingian).* 

Prestellispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 49 [\*Stellispongia lobata PARONA, 1933, p. 31; OD]. Irregularly obconical to hemispherical or mushroomlike sponges with one to several stellate, oscular clusters of exhalant canals on summit; numerous smaller, vertical or longitudinal inhalant canals in intervening spaces; skeletal structure regular reticulation of small fibers with spherulitic microstructure; spicules absent. Permian (Lopingian): —FIG. 414*a-d.* \**P. lobata* (PARONA), Tunisia.— Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, summit of sponge with several starlike, exhalant, canal clusters and small, inhalant ostia between, USNM 480369; b, side view of irregular, obconical sponge with encrusted, dense, dermal layer; c, summit view of same specimen with exhalant, canal clusters and small, circular, inhalant ostia, USNM 480366, ×1; d, schematic drawing of type (Rigby & Senowbari-Daryan, 1996a).-FIG. 414e. P. permica (PARONA); schematic drawing (Rigby & Senowbari-Daryan, 1996a).——FIG. 414f. P. scapulata RIGBY & SENOWBARI-DARYAN; schematic drawing (Rigby & Senowbari-Daryan, 1996a).

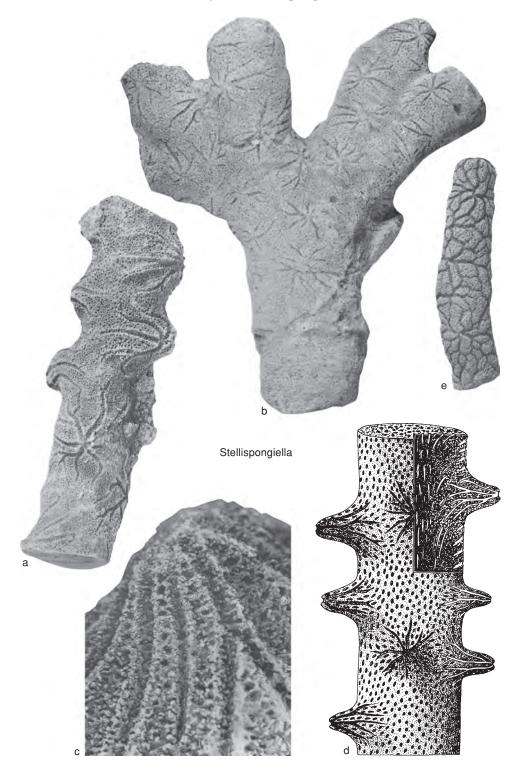


FIG. 413. Stellispongiellidae (p. 629).

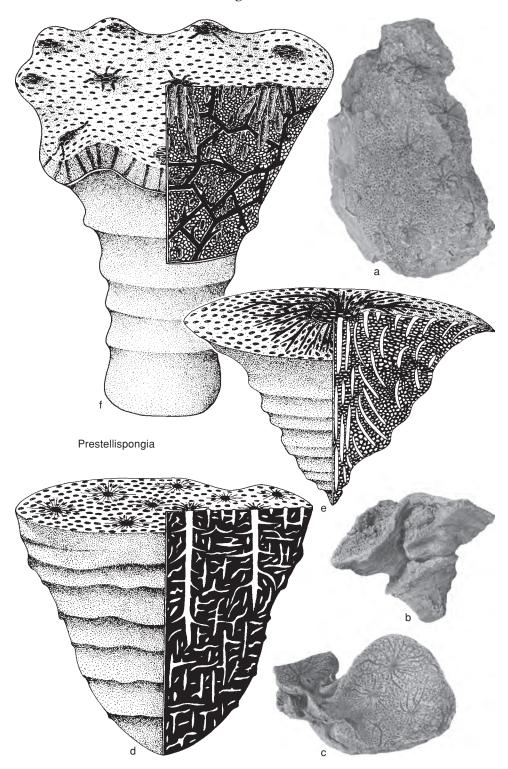
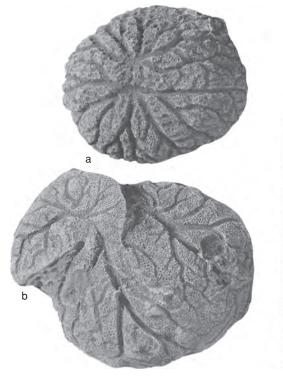


FIG. 414. Stellispongiellidae (p. 629).

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Estrellospongia

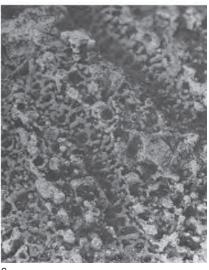


FIG. 415. Stellispongiellidae (p. 632).

### Subfamily ESTRELLOSPONGIINAE Rigby & Senowbari-Daryan, 1996

[Estrellospongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 56]

Massive prestellispongiids that lack oscula and spongocoels but with several astrorhizal clusters of convergent, largely surficial, exhalant canals; coarse openings lacking in fibrous, skeletal net. *Permian (Lopingian)*.

Estrellospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 56 [\*E. grossa; OD]. Irregularly massive, hemispherical to lobate sponges with upper surface marked by one or more astrorhizal systems of coarse, convergent, exhalant canals that are tangential to dermal surface; lacking coarse, vertical, exhalant canals to oscular ostia but with numerous irregularly upward, divergent canals in irregularly but prominently divergent, ladderlike, fibrous skeleton; microstructure spherulitic. Permian (Lopingian): Tunisia.—FIG. 415a-c. \*E. grossa, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel, Tebaga; *a*, holotype summit with multibranched, exhalant canals, USNM 463639, ×1; b, paratype with irregular growth but characteristic canals on summit, USNM 464645, ×1; c, paratype, coarse

fibers exposed in canal grooves of surficial, exhalant canals, with skeletal pores on ridges between, USNM 463644, ×10 (Rigby & Senowbari-Daryan, 1996a).

### Family PREPERONIDELLIDAE new family

[Preperonidellidae FINKS & RIGBY, herein] [=Peronidellidae WU Ya Sheng, 1991, p. 56, partim; Corynellidae WU Ya Sheng, 1991, p. 69] [type genus, Preperonidella FINKS & RIGBY, herein]

Sponges in which exhalant system consists of only spongocoel or cluster of several coarse canals in axial region of sponge; other differentiated canal systems may be absent or well developed; skeletal microstructure spherulitic. Upper Ordovician–Upper Triassic.

# Subfamily PREPERONIDELLINAE new family

[Preperonidellinae FINKS & RIGBY, herein] [type genus, *Preperonidella* FINKS & RIGBY, herein]

Sponges with axial spongocoel but without distinct inhalant and exhalant canals;

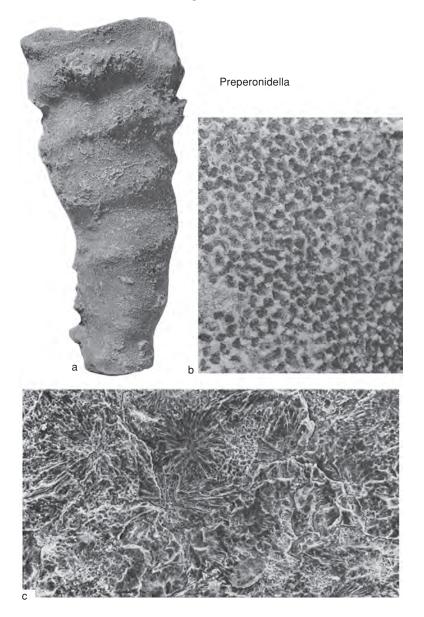


FIG. 416. Preperonidellidae (p. 633-635).

# skeletal microstructure spherulitic. *Permian* (Guadalupian)–Upper Triassic.

Preperonidella FINKS & RIGBY, nom. nov. herein [\*Peronidella magna RIGBY & SENOWBARI-DARYAN, 1996a, p. 58; OD] [=Peronidella ZITTEL in HINDE, 1893b, p. 213, partim (type, Spongia pistilliformis LAMOUROUX, 1821, p. 88; SD DE LAUBENFELS, 1955, p. 99). Sponges smooth to annulate, columnar to branched, with exhalant canal system only tubular axial spongocoel, although endowall may be pierced by circular endopores in longitudinal rows, dermal layer pierced by small, inhalant ostia; skeletal fibers thin and uniform to variable and thick, and commonly in irregular, reticulate structure; fibers with spherulitic microstructure; dense, dermal layer may be present. [Part of the original *Peronidella* RIGBY & Porifera—Demospongea

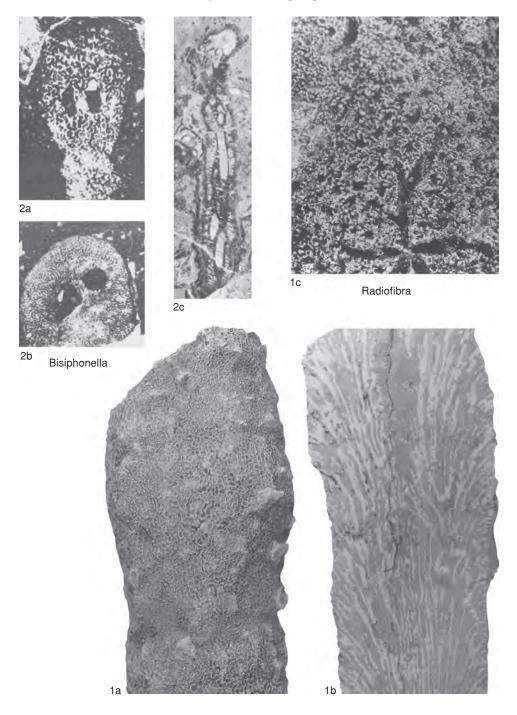


FIG. 417. Preperonidellidae (p. 635).

SENOWBARI-DARYAN, 1996a (see p. 743, herein). Part of Peronidella lacks spicules and is renamed Preperonidella herein, and the family and subfamily names are based on that new name; the original Peronidella and Paronadella are now included in the subfamily Stellispongiinae, p. 739, herein.] Permian (Guadalupian)-Upper Triassic: China (Guangxi, Sichuan), Tunisia, Thailand, USA (Texas, New Mexico), Guadalupian-Lopingian; USA (Oregon), Oman, Peru, Upper Triassic. FIG. 416a-c. \*P. magna (RIGBY & SENOWBARI-DARYAN), Lopingian, Upper Biohermal Complex, Djebel Tebaga, Tunisia; a, side view of annulate, columnar holotype with dermal layer with numerous inhalant pores, USNM 463663, ×1; b, photomicrograph of dermal layer of holotype with numerous skeletal pores defined by relatively robust fibers in almost rectangular, skeletal structure lacking canals, ×10; c, SEM photomicrograph of paratype showing densely packed, large, partially recrystallized spherulites of skeletal fibers, USNM 480422, ×4,500 (Rigby & Senowbari-Daryan, 1996a).

- Bisiphonella WU Ya Sheng, 1991, p. 60 [\*B. cylindrata; OD]. Cylindrical, stemlike sponges with two parallel, axial, walled spongocoels of essentially same size that extend through much of sponge; skeletal fibers in regular to irregular, but relatively uniformly spaced, reticulate net; with or without dermal cortex; short, exaulos-like tubules may extend from spongocoel wall into interior of chambers. Permian (Guadalupian-Lopingian): China (Guangxi), Thai--FIG. 417,2a-c. \*B. cylindrata; a, holotype, land.diagonal section with double, spongocoel tubes in fibrous, reticulate skeleton, Reef of Xiangbo, Guadalupian, Guangxi, IGASB xb27-B-2a, ×2; b, transverse section with two spongocoels in fibrous skeleton, Reef of Xiangbo, Guadalupian, Guangxi, IGASB xb34-2-2, ×2 (Wu Ya Sheng, 1991); c, longitudinal section with two walled, tubular spongocoels cut in lower part, Lopingian, Phrae Province, Thailand, BSPGM R9, ×2 (Senowbari-Daryan & Ingavat-Helmcke, 1994).
- Radiofibra RIGBY & SENOWBARI-DARYAN, 1996a, p. 61 [\*R. lineata; OD]. Cylindrical to subcylindrical sponges that may be branched, all with narrow, deep, axial spongocoel; fibrous skeleton of interior with poorly defined arrangement in transverse sections, but divergent upwardly and outwardly in longitudinal section; spaces between fibers probably canals that diverge upwardly and outwardly toward periphery; short, lateral canals may also occur; microstructure spherulitic. Permian (Lopingian)-Upper Triassic: Tunisia, Lopingian; Iran, Upper Triassic.----FIG. 417, 1a-c. \*R. lineata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view of holotype with coarse, skeletal net,  $\times 2$ ; *b*, polished, longitudinal section with matrix-filled spongocoel and coarse, upwardly divergent fibers,  $\times 2$ ; *c*, photomicrograph of surface showing coarse, skeletal net around

smaller inhalant and larger exhalant openings, USNM 463675, ×10 (Rigby & Senowbari-Daryan, 1996a).

### Subfamily PERMOCORYNELLINAE Rigby & Senowbari-Daryan, 1996

[Permocorynellinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 65]

Sponges in which the axial spongocoel is deep, extending virtually through sponge; inhalant and exhalant canals present as regular or irregular tubes. *Permian (Lopingian)– Upper Triassic.* 

- Permocorynella Rigby & Senowbari-Daryan, 1996a, p. 65 [\*Corynella ovoidalis PARONA, 1933, p. 36; OD]. Spherical, mushroom- or club-shaped sponges with one or two oscula on summit as upper ends of deep spongocoels; radiating and starlike grooves may surround osculum; several vertical, exhalant canals in basal part of sponge empty into base of spongocoel and other higher ones empty into sides of spongocoel, although other upwardly and outwardly divergent, exhalant canals may also occur; horizontal, inhalant canals well defined near periphery of sponge and inhalant pores may be arranged in vertical or horizontal rows; relatively fine, skeletal fibers in regular to reticulate net fill space between canals; skeleton originally primarily aragonite with spherulitic microstructure; lower, dermal surface of mushroom-shaped sponges without pores but with distinct growth lines. Permian (Lopingian)-Upper Triassic: Tunisia, Lopingian; Iran, Upper Triassic.—FIG. 418,2a-d. \*P. ovoidalis (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view with inhalant ostia on ridges between indented, radial, inhalant canals, USNM 463682; b, side view of conicocylindrical form with prominent, inhalant ostia, ×2; c, summit view showing large, central spongocoel and radial canals, with inhalant ostia on ridges between canals, USNM 463685, ×2; d, schematic drawing showing form and canal development, not to scale (Rigby & Senowbari-Daryan, 1996a).
- Djemelia RIGBY & SENOWBARI-DARYAN, 1996a, p. 71 [\*D. amplia; OD]. Single to branched, cylindrical to club-shaped sponges with deep, axial spongocoel; dermal surface with numerous ostia, some of which are on exaules; ostia lead to branched, tubular canals that pass into reticular, fibrous skeleton in interior of wall; spongocoel with distinct wall perforated by well-developed exhalant canals leading into spongocoel. Permian (Lopingian): Tunisia.——FIG. 418, Ia-d. \*D. amplia, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side view of holotype, ×1; b, transverse section showing axial spongocoel and convergent, exhalant canals, USNM 463692, ×2; c, side view of paratype, ×2; d, top view into large, central

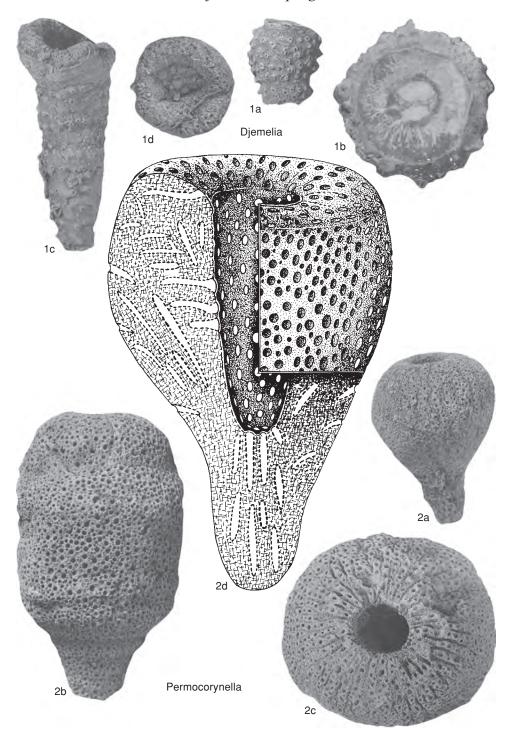


FIG. 418. Preperonidellidae (p. 635-637).

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spongocoel, USNM 463693, ×2 (Rigby & Senowbari-Daryan, 1996a).

Saginospongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 69 [\*S. angusta; OD]. Cylindrical to branched sponges with deep spongocoel in coarse, massive skeleton that appears with radial structure in transverse sections and upwardly divergent in longitudinal sections; internal skeleton of very fine, reticulate or sievelike fibers; microstructure unknown. Permian (Lopingian): Tunisia.—FIG. 419a-c. \*S. angusta, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side view of coarse, textured holotype,  $\times 2$ ; *b*, photomicrograph showing moderately coarse ostia and canals with broad, skeletal tracts with coarse structure, USNM 463677, ×10; c, schematic diagram of skeletal and canal patterns, not to scale (Rigby & Senowbari-Daryan, 1996a).

### Subfamily PRECORYNELLINAE Termier & Termier, 1977

[nom. transl. Finks & Rigby, herein, ex Precorynellidae Termier & Termier, 1977a, p. 45]

Sponges with two or more axial spongocoels or clusters of parallel, coarse, axial, exhalant canals that may be continuations of radial canals; inhalant canals present or absent. Upper Ordovician–Upper Triassic.

Precorynella DIECI, ANTONACCI, & ZARDINI, 1968, p. 126 [\*Cnemidium pyriformis KLIPSTEIN, 1843 in 1843–1845, p. 291; OD] [=?Holosphecion POMEL, 1872, p. 224 (type, H. tuberosum, OD)]. Stipitatespheroidal to obconical or clavate; solitary or laterally fused in small colonies; well-defined, shallow cloaca on top surface surrounded by numerous closely spaced, radial, exhalant grooves that extend well down sides of sponge, alternating with meridional rows of large, inhalant ostia; bottom of cloacal depression covered by radially arranged, closely spaced, large openings of exhalant canals that extend deeply into axial region of sponge; sides of cloaca bearing similar openings of canals that arch upwardly and inwardly parallel to top surface of sponge, being former radial surface grooves. Sponge exterior with small, circular to meandriform, intertrabecular spaces between larger, inhalant ostia, except for imperforate, dermal layer near base; trabeculae of interior layered parallel to top surface with upwardly and outwardly divergent, connecting elements; exhalant canals of interior parallel to arcuate layers except for central, longitudinal group; inhalant canals extending inwardly and downwardy from ostia parallel to connecting elements. Trabecular microstructure of type species spherulitic and penicillate, according to WENDT (1974, p. 503). [Differs from Sestrostomella in presence of cloaca, large canals parallel to top surface, and large ostia on sides.] Permian-Triassic: North America, South America, Europe, Tunisia, Timor.-FIG. 420,2ac. \*P. pyriformis (KLIPSTEIN), San Cassiano Formation, Norian, Dolomite Alps, Italy; *a*, side view of obconical, globose hypotype with dermal surface perforated by numerous inhalant ostia, ×2; *b*, view from above of oscular margin with axial osculum and rows of inhalant ostia, hypotype IPUM 17563, ×2; *c*, longitudinal section showing cluster of vertical, exhalant canal leading to central osculum shallow spongocoel, each canal with an uparched lower part, smaller downwardly arched, inhalant canals showing near dermal layer, IPUM 17565, ×2 (Dieci, Antonacci, & Zardini, 1968).

- Bicoelia RIGBY, SENOWBARI-DARYAN, & LIU, 1998, p. 72 [\*Bisiphonella tubulara Senowbari-Daryan & INGAVAT-HELMCKE, 1994, p. 24; OD]. Cylindrical sponges with two parallel, axial spongocoels, each with separate wall pierced by pores or tubular canals connected to pores in surrounding, reticulate skeleton; distinct, perforated, dermal layer; skeleton between dermal layer and spongocoel walls loose, textured, and partially radially arranged, fibrous network; some horizontal tabulae may occur within spongocoels. Permian (Guadalupian-Lopingian): Thailand, China, USA (New Mexico).-FIG. 420,1a-b. B. guadalupensis RIGBY & SENOWBARI-DARYAN, Capitan Limestone, Capitanian, Guadalupe Mountains, New Mexico; a, holotype (arrow) in a polished section with several other large examples of sponge, all with double spongocoel in axial region, USNM 35175-1, ×2; b, paratype with several transverse sections, each with double spongocoel and coarsely reticulate wall, USNM 35175, ×2 (Rigby, Senowbari-Daryan, & Liu, 1998).
- Imperatoria DE GREGORIO, 1930, p. 39 [\*I. marconii; OD] [?=Bisiphonella WU Ya Sheng, 1991, p. 60 (type, B. cylindrata, OD)]. Sponge with turriculate form, branched to unbranched; each cup- to funnel-shaped, segmentlike element with a horizontal to sloping ramp across its summit and with sharp, outer edge; interior unsegmented, but with upwardly and outwardly directed, moderately coarse, fibrous reticulate skeleton; lacking axial tubes or through-going spongocoel but individual segments may have small oscula above short, coarse, exhalant tubes; upper and lateral, dermal layers smooth and with numerous small pores or with numerous ostia on exaules of outer wall in species questionably included in genus, which also has irregular, horizontal and vertical canals that are largely wanting in other species in genus. Upper Ordovician-Permian: USA (California), Upper Ordovician; Italy (Sicily), Tunisia, ?China, Permian.-FIG. 421,2a. \*I. marconii, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; side view of annulate sponge, USNM 463711, ×1 (Rigby & Senowbari-Daryan, 1996a).——Fig. 421,2b-d. I. voluta RIGBY & SENOWBARI-DARYAN, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; b, side view of holotype showing annulate, turriculate form, ×2; c, view from above with two adjacent, walled oscula in relatively coarse,

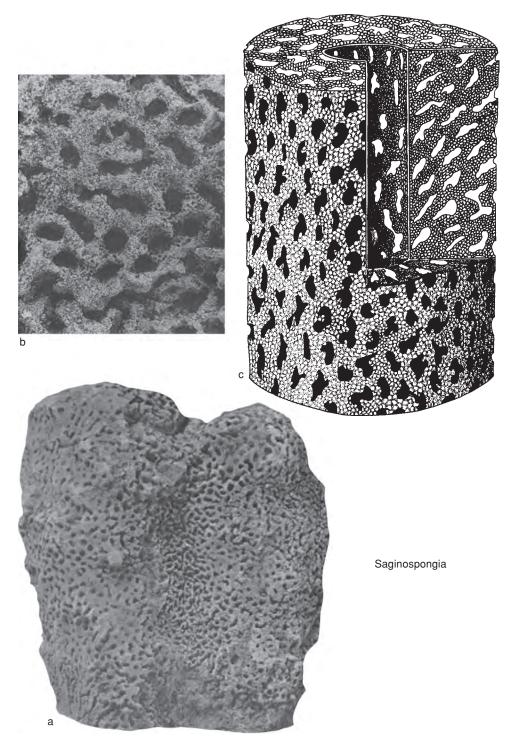
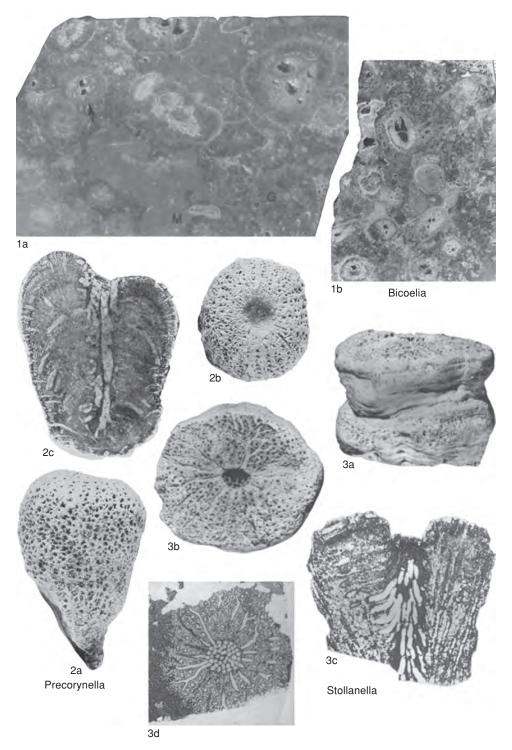


FIG. 419. Preperonidellidae (p. 637).





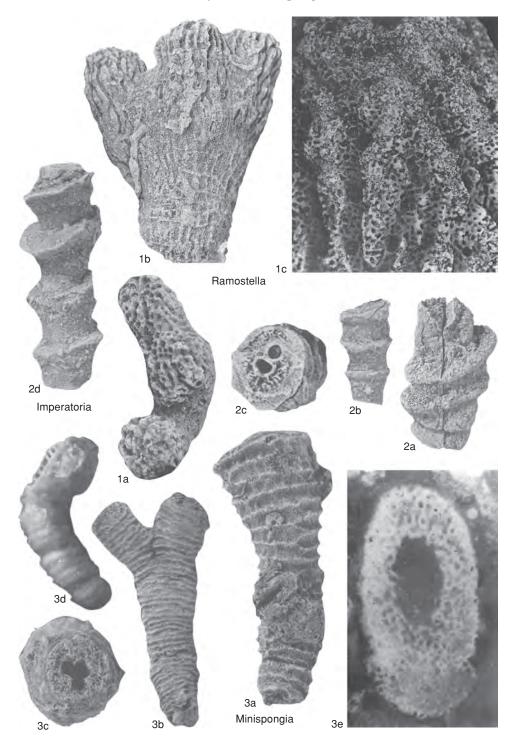


FIG. 421. Preperonidellidae (p. 637-641).

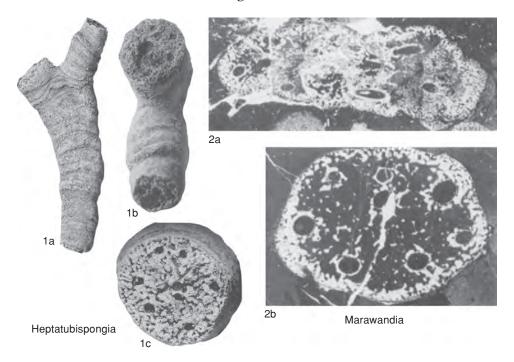


FIG. 422. Preperonidellidae (p. 642).

fibrous skeleton, USNM 463715, ×4; *d*, turriculate paratype, side view, USNM 613712, ×2 (Rigby & Senowbari-Daryan, 1996a).

- Minispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 78 [\*M. carinata; OD]. Tiny, dichotomously branched or cylindrical sponges with one to several united or parallel spongocoels; dermal layer without perforations but with prominent annulations or ridges that may merge laterally in zigzag fashion; skeleton of reticulate fibers. Permian (Guadalupian-Lopingian): Tunisia, USA (New Mexico, Texas). -FIG. 421,*3a–c. \*M. carinata*, Djebel Tebaga Biohermal Complex; Changhsingian, Djebel Tebaga, Tunisia; a, side view of small, annulate to ridged holotype, USNM 463704, ×5; b, side view of branched paratype, USNM 463705, ×5; c, top view showing spongocoel with several parts and surrounding, fibrous wall, USNM 463708, ×5 (Rigby & Senowbari-Daryan, 1996a).-FIG. 421,3d-e. M. constricta (GIRTY), Capitan Limestone, Capitanian, Guadalupe Mountains, Texas; d, side view of small, annulate holotype, USNM 118132, ×2; e, diagonal section through small sponge with relatively coarse, skeletal structure of thin wall, USNM 35175, ×10 (Rigby, Senowbari-Daryan, & Liu, 1998).
- Ramostella RIGBY & SENOWBARI-DARYAN, 1996a, p. 79 [\*R. stipulata; OD]. Cylindrical to branched, small sponges generally with axial cluster of coarse, exhalant canals; lacking transverse, inhalant canals in interior other than moderately coarse, skeletal pores; skeleton upwardly and outwardly expanding

reticulation of fine fibers; upper surface with surficial grooves that converge toward axial, exhalant, canal cluster and that continue longitudinally as undulating and subparallel grooves some distance down in dermal surface of cylindrical flanks; microstructure spherulitic. Permian (Lopingian): Tuni-—FIG. 421, 1a–c. \*R. stipulata, Djebel Tebaga sia.-Biohermal Complex, Changhsingian, Djebel Tebaga; a, top view of holotype showing summits of three short branches,  $\times 2$ ; b, side view showing triangular, palmate form and short branches marked with irregular grooves, but lacking inhalant ostia, USNM 480354, ×2; c, photomicrograph of upper, lateral slope of paratype with subvertical grooves, coarse exhalant ostia, and finer, skeletal pores defined by coarse, skeletal fibers, USNM 480377, ×10 (Rigby & Senowbari-Daryan, 1996a).

Stollanella BIZZARINI & RUSSO, 1986, p. 131 [\*S. diecci; OD]. Sponges simple or branched, steeply obconical with broad base and wrinkled epitheca; axial cluster of subvertical, exhalant canals, as inner, abruptly uparched ends of subhorizontal parts of canals in inner part of wall; oscular surface with shallow spongocoel and several radial furrows; aligned prosopores of subvertical, inhalant canals occurring between furrows; microstructure is micritic. [Aligned, relatively straight, subvertical, inhalant canals penetrate down into the sponge wall from the upper surface in *Stollanella*, in contrast to *Precorynella* where most inhalant canals feed from the lateral, dermal surface. Vertical, inhalant canals are unknown in *Sestrostomella*, and in addition it has a spherulitic microstructure, as does *Precory-nella.*] *Upper Triassic:* Italy.——FIG. 420, 3a-d. \*S. *diecci*, San Cassiano Formation, Carnian, Dolomiti di Braies; *a*, side view of holotype, X2; *b*, view of summit with central spongocoel that has numerous exhalant ostia in gastral wall, X2; *c*, longitudinal section showing large, exhalant canals and smaller, subvertical, inhalant canals, X2; *d*, transverse section with convergent and axial cluster of exhalant canals in holotype, MCSNV 10150, X3 (Bizzarini & Russo, 1986).

### Subfamily HEPTATUBISPONGIINAE Rigby & Senowbari-Daryan, 1996

[Heptatubispongiinae RIGBY & SENOWBARI-DARYAN, 1996a, p. 83]

Sponges in which an axial spongocoel is present with several coarse, longitudinal, exhalant canals regularly spaced in one ringlike layer near periphery. *Permian (Lopingian)–Upper Triassic.* 

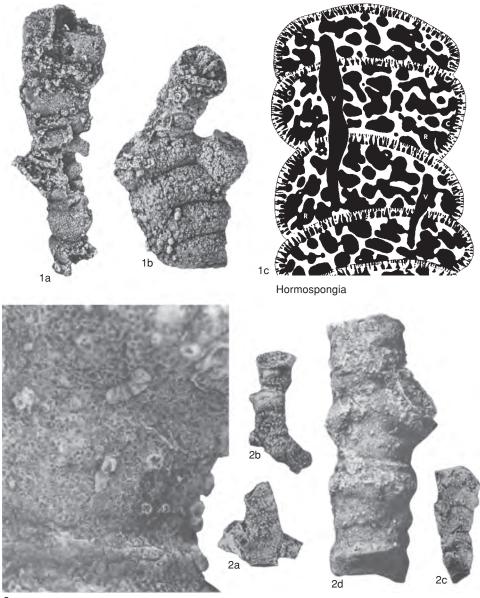
- Heptatubispongia RIGBY & SENOWBARI-DARYAN, 1996a, p. 83 [\*H. symmetrica; OD]. Cylindrical to branched sponges with axial spongocoel or relatively large, axial canal, and usually seven smaller, collateral, vertical canals uniformly spaced in ring near periphery, although numbers of such canals range from six to eight; outer surface with a few ostia; internal skeleton composed of relatively coarse, reticulate fibers; growth lines prominent on exterior. Permian (Lopingian): Tunisia.-FIG. 422, 1a-c. \*H. symmetrica, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, side view of branched holotype,  $\times 2$ ; *b*, summit of left branch, above showing minor, axial, exhalant canals and symmetrically placed, collateral, vertical canals near margin,  $\times 4$ ; *c*, base of holotype with ring of exhalant canals near margin and radial canals around central spongocoel, USNM 463724, ×8 (Rigby & Senowbari-Daryan, 1996a).
- Marawandia Senowbari-Daryan, Seyed-Emami, & AGHANABATI, 1997, p. 312 [\*M. iranica; OD]. Cylindrical, branched sponge with several separated, exhalant tubes, usually of same size and not axially located, that pass through sponge; each tube with distinct wall pierced by openings from sponge interior; outer surface with distinct wall perforated by labyrinthic canal system; loosely packed, skeletal fibers of reticular type fill interior; microstructure and spicular structure not known. Upper Triassic: Iran.—FIG. 422,2a-b. \*M. iranica, reefs within the Nayband Formation, Norian-Rhaetian, Marawand, Iran; a, oblique section of holotype showing several internal, exhalant canals surrounded by skeletal fibers, outer wall with labyrinthic canal system, SPIE M/73, ×5; b, transverse section with eight peripheral, exhalant canals, each with perforated wall, and dense, fibrous, outer wall, SPIE P/324/1, ×10 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997; courtesy of Revista Italiana di Paleontologia e Stratigraphia).

### Family FISSISPONGIIDAE new family

[Fissispongiidae FINKS & RIGBY, herein] [type genus, Fissispongia KING, 1938, p. 499]

Cylindroid; multiple, narrow, central cloacae; trabecular tissue between exowall and endowall outlines anastomosed, tubular spaces that converge inwardly and upwardly to cloacae; interwalls and segmentation variably developed; segments often conical, flaring upwardly; type genus has small ostea and lipped exopores; microstructure of type genus (others not known) very small, isodiametric spherulites (15 to 20 µm). *Devonian (Eifelian)–Permian (Roadian).* 

- Fissispongia KING, 1938, p. 499 [\*F. jacksboroensis; OD] [=?Hormospongia RIGBY & BLODGETT, 1983, p. 773 (type, H. labyrinthica, OD)]. Conicocylindrical, branching, ranging from strongly segmented to unsegmented; segments, when present, strongly conical, expanding upwardly; cloaca narrow, central, and double or very rarely multiple; one cloaca circular in cross section and internally tangent to the second, which wraps around it; endowall of circular cloaca thicker than that of other, which may be locally absent; exowall with very small, closely spaced exopores, together with more widely spaced, larger, circular pores that have strong lips or are at end of spoutlike projections; interwalls absent, even in strongly segmented forms, except for peripheral, incurved part of exowall; interior filled with fine net of trabeculae that outline anastomosed, tubular spaces that tend to be directed inwardly and upwardly, coalescing to enter cloacas through large, circular endopores; endowall between circular cloaca and surrounding one usually imperforate, except where trabecular tube crosses outer cloaca to enter circular one; trabeculae and walls composed of very small, isodiametric spherulites; no spicules. Middle Devonian (?Eifelian), Carboniferous (Middle Pennsylvanian-Roadian): USA (Alaska), ?Eifelian; southcentral and southwestern USA, Middle Pennsylvanian-Upper Pennsylvanian, Asselian–Roadian.——FIG. 423,2a–e. \*F. jacksboroensis, Graham Formation, Virgilian, Jack County, Texas; a-c, three syntypes showing obconical to branching habit and rimmed ostia characteristic of type species, UTBEG K-1467, ×1 (King, 1938); d, side view of annulate, incipiently branched specimen, ×2; e, enlarged part of same sponge showing small, inhalant pores and larger, rimmed pores in dermal layer, OUZC 3013, ×10 (Rigby & Mapes, 2000).
- ?Hormospongia RIGBY & BLODGETT, 1983, p. 775 [\*H. labyrinthica; OD]. Conicocylindrical, branching sponge composed of superposed, conical to discoid segments; one to three narrow, central, vertical cloacae pass through at least several segments; remainder of chamber interior filled with meandri-





Fissispongia

FIG. 423. Fissispongiidae (p. 642-644).

form trabeculae that outline anastomosed, tubular spaces that rise inwardly toward central cloacae; exopores small, circular, and closely spaced on exterior of exowall but merging into wider canals in interior of exowall and communicating with internal, intertrabecular spaces; interwall a continuation of exowall at top of chamber; endowalls incompletely developed; microstructure not known; no spicules known. [This genus is similar to *Fissi-spongia* KING, 1938, but differs in the more variable number of central cloacae, in complexity of canal and pore development, lack of lipped ostia in the dermal layer, and in possibly better developed interwalls.] *Devonian (Eifelian):* USA (Alaska), Australia (New South Wales).——FIG. 423, *Ia-c. \*H. labyrinthica*, Cheeneetnuk Limestone, Eifelian,

Cheeneetnuk River, McGrath Quadrangle, Alaska; *a*, side view of holotype showing uniserial, porous chambers in holotype, UAF 2459, ×2; *b*, branched paratype, UAF 2460, ×2; *c*, generalized vertical section showing vertical (*V*), concentric (*C*), and dominantly radial (*R*) canals within globular chambers and branched pores in walls, approximately ×5 (Rigby & Blodgett, 1983).

### Family MAEANDROSTIIDAE Finks, 1971

#### [Maeandrostiidae FINKS, 1971a, p. 292]

Cylindroidal, cloacate sponges with aspicular skeleton of large, isodiametric spherulites (40 to 140 µm); external cortex with circular, lipped pores, usually large, and, in type genus, meandriform; internal skeleton of meandriform, anastomosing trabeculae outlining radial, upwardly divergent, tubular spaces in Carboniferous and Early Permian species, becoming reduced to radially elongate, vertical pillars between interwalls with radially elongate interpores in some later forms; endowall present; vesicles present in some genera. [This family includes both inozoan-like and sphinctozoanlike forms; the transition between the two types, shown by Early Permian species of Stylopegma KING, 1943, as well as the commonly shared characters of circular, lipped exopores and large, isodiametric spherulites, argues for a phylogenetic unity. The Verticillitidae differ in having a nonspherulitic aspicular skeleton and polygonal exopores in a netlike exowall. Fissispongia KING, 1938, and its relatives differ in having much smaller spherulites and in the multiple, confluent, central cloacae.] Carboniferous (Middle Pennsylvanian)–Triassic.

Maeandrostia GIRTY, 1908, p. 284 [\**M. kansasensis;* OD]. Conicocylindrical to broadly conical, with domical, top surface and central osculum, often branching to form small, flabellate clusters; external cortex may be present locally or widely, pierced by large, circular to meandriform, lipped openings that reveal edges of internal trabeculae, as do areas that are free of cortex; trabeculae outlining anastomosed tubes of circular to meandriform cross section that have prevailingly radial and longitudinal (upwardly diverging) orientation; central cloaca of approximately one-third diameter of sponge lined by cortex or endowall, which truncates intertrabecular spaces and is pierced by pores smaller than these spaces; trabeculae composed of large, isodiametric spherulites; spicules absent. [This genus is a homeomorph of the Mesozoic Eudea LAMOUROUX, 1821, which lacks isodiametric spherulites.] Carboniferous (Middle Pennsylvanian)-Triassic (Anisian): USA (Texas, Oklahoma, Kansas), Italy (Sicily), Yugoslavia (Slovenia), Middle Pennsylvanian-Upper Pennsylvanian, Permian; ?China, Permian; Italy, Anisian.-FIG. 424,2a-c. \*M. kansasensis, Plattsburg Limestone, Desmoinesian-Virgilian, Chanute, Kansas; a, side view of cylindrical syntype,  $\times 1$ ; b, transverse thin section of syntype showing axial spongocoel and vesicular, skeletal material, ×2; c, longitudinal polished section of syntype showing irregularly chambered walls and axial spongocoel, USNM 53468, ×2 (Girty, 1908).

- Adrianella PARONA, 1933, p. 14 [\*A. distefanoi; OD]. Conical; central, possibly cloacal depression on slightly domed, top surface; exterior smooth, pores not preserved; interior composed of meandriform trabeculae that outline anastomosed, tubular canals; trabecular mesh has obscure, concentric layering; trabecular microstructure unknown; spicules unknown. Permian: Sicily.—FIG. 424, 1a-c. \*A. distefanoi, Permian limestone, Palazzo Adriano; a, side view of obconical holotype; b, holotype from above with shallow, axial spongocoel, ×1; c, transverse section showing meandriform trabeculae and small canals that become more common in outer part, all part of syntype suite, ×5 (Parona, 1933).
- Eurysiphonella HAAS, 1909, p. 162 [\*E. steinmanni; OD]. Conicocylindrical; cloaca somewhat more than one-third sponge diameter; chambers high and apparent from segmentation of exterior; exopores, interpores, and endopores small, circular, and closely spaced, endopores a bit larger and interpores a bit smaller than exopores; chambers either completely hollow, contain vesicles, or are filled with irregular, trabecular network; trabecular microstructure unknown; no spicules known. Triassic: Austria.--FIG. 424, 4a-c. \*E. steinmanni, Hallstätter Kalke, Rhaetian, Fischerwiese by Alt-Aussee; a, side view of exterior of type specimen showing segmentation and perforated, chamber walls; b, longitudinal section showing central spongocoel or cloaca with thin walls and hollow, bulbous chambers; c, view from below of broken surface showing central spongocoel and perforate interwall between chambers, ×1 (Haas, 1909).
- Polysiphonaria FINKS, 1997, p. 352 [\*Polysiphonia flabellata FINKS, 1995, p. 4; OD]. Cylindrical branches fused laterally to form flabellate or reticulate shapes; branched at acute angles; no external annulation; closely spaced, moderately large, circular labripores in exowall, with very small exopores between them; multiple, narrow, vertical cloacae with small, vertically elongate endopores; cloacae widely separated and circular in cross section; horizontal interwalls closely spaced with moderately large, closely spaced, radially elongate or

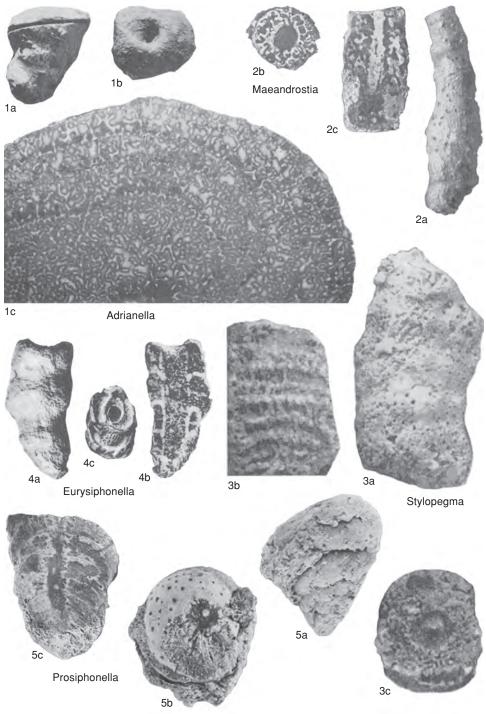


FIG. 424. Maeandrostiidae (p. 644-646).

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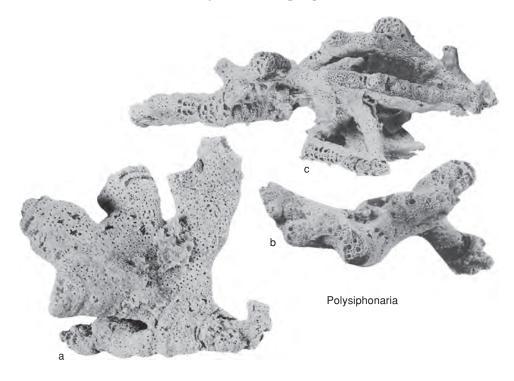


FIG. 425. Maeandrostiidae (p. 644-646).

submeandriform interpores; numerous closely spaced, often coalescent, vertical pillars connect interwalls across low chambers; trabecular microstructure not known; no spicules known. *Permian:* USA (Texas).——FIG. 425*a*–*c.* \**P. flabellata* (FINKS), Road Canyon Formation, Leonardian, Glass Mountains; *a* side view of flabellate, branched holotype; *b*, top view showing multiple branched, tubular spongocoels, AMNH 44309; *c*, paratype with anastomosing branches and parallel, flabellate branches with chambers separated by arched interwalls, AMNH 44316, ×1 (Finks, 1995).

Prosiphonella DIECI, ANTONACCI, & ZARDINI, 1968, p. 138 [\*P. amplectens; OD]. Conical; numerous large, circular exopores, larger exopores lipped; osculum relatively narrow, central; endowall discontinuous because of large endopores; interwall and interpores presumably similar to exowall and exopores; each chamber partially enveloping chamber beneath; chambers low, filled with slender trabeculae forming fine, meandriform mesh in which larger, horizontal canals empty into cloaca; similar large canals perpendicular to exowall extending inwardly and downwardly from large exopores and may branch; trabecular microstructure unknown; no spicules known. Triassic: Europe.-FIG. 424,5a-c. \*P. amplectens, San Cassiano Formation, Norian, Dolomite Alps, Italy; a, side view of holotype with overlapping chambers; b, top of holotype with central spongocoel and rounded summit perforated by coarse, inhalant exopores; *c*, longitudinal section through uparched chambers and prosiphonate spongocoel, IPUM 17596, ×2 (Dieci, Antonacci, & Zardini, 1968).

Stylopegma KING, 1943, p. 18 [\*S. dulce; OD]. Branching cylinders or cones; external segmentation present or absent; prominent, central cloaca (absent in earliest chambers); porous interwalls always present (interpores may be radially elongate); chambers contain vertical, radially elongate, somewhat meandriform and anastomosing trabeculae or vertical, cylindrical pillars (most trabecula-like near interwalls and in earlier species); vesicles may also be present; porous endowall (endopores may be vertically elongate); continuous exowall with circular exopores of one or more sizes, larger usually strongly lipped (labripores); trabeculae, pillars, and walls composed of large, isodiametric spherulites; spicules absent. Permian: USA (Texas).--Fig. 424, 3a-c. \*S. dulce, Leonard Formation, Leonardian, Baylor Mountains; a, side view of holotype exterior with pores in dermal layer, YPM 16594, ×2; b, eroded surface of holotype showing prominent, horizontal, and less regular trabeculae of skeletal net, YPM 16594, approximately ×10; c, transverse section of paratype with prominent, tubular spongocoel and walls with irregular trabeculae, YPM 16597, ×2 (King, 1943).

### Family ANGULLONGIIDAE Webby & Rigby, 1985

[Angullongiidae WEBBY & RIGBY, 1985, p. 211]

Cylindroid with central cloaca; superposed, toroidal chambers containing radial tubes or trabeculae; vesicles may be present; exopores small and numerous; endopores may be locally concentrated; ostia generally present at ends of mamelon-like protrusions; type genus has lamellar secondary lining to wall but microstructure of primary wall not known. [This family bears some resemblance to the Girtyocoeliidae with its ostia and, in some genera, endopores concentrated in a ring, but differs in the presence of numerous exopores and internal, filling tissue in the chambers.] *upper Lower Ordovician–upper Upper Ordovician.* 

- Angullongia WEBBY & RIGBY, 1985, p. 212 [\*A. vesica; OD]. Conicocylindrical, moderately large sponge with superposed, toroidal chambers visible externally; wide, central cloaca approximately one-half sponge diameter; mamelon-like protuberances of exowall may terminate in long ostia; exopores small, circular, widely spaced, lipped; very fine exopores may occur between larger ones; interwall a continuation of exowall, with interpores similar to exopores; endowall (inner spongocoel wall of original authors) continuous with (retrosiphonate) and similar to interwall; dendritic, tubular canals extending inwardly and upwardly from chamber interior to endowall (said to be saclike but peripheral ends may have been intersected obliquely); endowall with fine endopores covering their inner ends; chamber interior lined with thick, secondary, lamellar deposits, through which larger exopores and interpores pass as canals, as is frequently the case with such deposits; remainder of chambers filled with very small vesicles, near walls are subparallel to them; occasional vesicles may occur within cloaca. Middle Ordovician-upper Upper Ordovician: USA (Alaska), Middle Ordovician; New South Wales, upper Upper Ordovician.——FIG. 426,3a-c. \*A. vesica, Angullong Tuff, Ashgill, Cliefden Caves area, New South Wales, Australia; a, longitudinal section of holotype with broad spongocoel and chambers filled with vesiculae, ×2; b, transverse section of holotype where central spongocoel has a distinct endowall and chambers filled with fine vesiculae and saclike sections of tubular canals, SUP51000,  $\times 2$ ; *c*, generalized reconstruction showing form and skeletal structure of sponge, approximately ×2 (Webby & Rigby, 1985).
- Alaskaspongia RIGBY, POTTER, & BLODGETT, 1988, p. 740 [\*A. nana; OD]. Small, conical sponge with superposed, spheroidal to hemispheroidal chambers; narrow, central cloaca one-fifth sponge diameter or less; closely spaced, very small exopores; in-

ner half of interwall formed of trabeculae radiating from endowall and outlining triangular interpores; endopores concentrated in inner part of each chamber; one or more pointed, saclike extensions of chamber drape over exterior of preceding chamber and taper to an exaulos-like tube with terminal opening. upper Lower Ordovician: USA (Alaska). -FIG. 426,2a-b. \*A. nana, unnamed Middle Ordovician sequence, White Mountain area, McGrath Quadrangle; a, side view of holotype showing general obconical form with sagging, adnate chambers increasing upwardly in size, ×2; b, diagonal view into broken chamber showing porous, retrosiphonate, central tube and interwalls, draped exaules showing on lower part of sponge, USNM 417201, ×2 (Rigby, Potter, & Blodgett, 1988).

- Amblysiphonelloides RIGBY & POTTER, 1986, p. 19 [\*A. tubulara; OD]. Conicocylindrical, small, with superposed, discoid chambers; segmentation visible externally; cloaca approximately one-third sponge diameter; exopores small, closely spaced, circular, uniform; exowall continuous with interwall but interpores somewhat smaller than exopores; endopores elongate vertically and same size as interpores; radial tubes, apparently imperforate, lead inwardly from many exopores, occasionally branching inwardly, most end short of endowall but some connect with endopore; microstructure not known; no spicules known. upper Lower Ordovician-upper Upper Ordovician: USA (California).-FIG. 427,2ad. \*A. tubulara, Kangaroo Creek Formation, Llandeilo-Ashgill, Klamath Mountains; a, side view of holotype with low, annular, moniliform chambers, BMNH S10172; b, side view of paratype with porous chamber walls, BMNH S10175, ×2; c, vertical section of silicified sponge showing porous, retrosiphonate, central tube and interwalls, BMNH S10177, ×2; d, diagonal section through paratype showing irregular, tubular, filling structures and porous chamber walls, BMNH S10178, ×10 (Rigby & Potter, 1986).
- Belubulaia WEBBY & RIGBY, 1985, p. 217 [\*B. packhami; OD]. Conicocylindrical, small, occasionally branching sponge with superposed, spheroidal to hemispheroidal segments visible externally; central cloaca one-third to one-fifth sponge diameter; small, circular, closely spaced exopores of varying size; in addition, large ostia are present on ends of mamelon-like protrusions of exowall; interwall continuous with exowall and bearing same pores; endopores somewhat larger than exopores, circular, lipped on chamber side, concentrated in ring at upper end of chamber; occasional vesicles in chambers; microstructure not known; no spicules known. lower Upper Ordovician: Australia (New South Wales).----FIG. 426,1a-c. \*B. packhami, Belubula Limestone, Belubula River; a, side view of holotype with superposed, spheroidal chambers, SUP5105, ×2; b, longitudinally broken paratype showing chambers around central tube with endopores confined to upper parts of chambers, SUP51020,  $\times 5$ ; c, side view of small, paratype

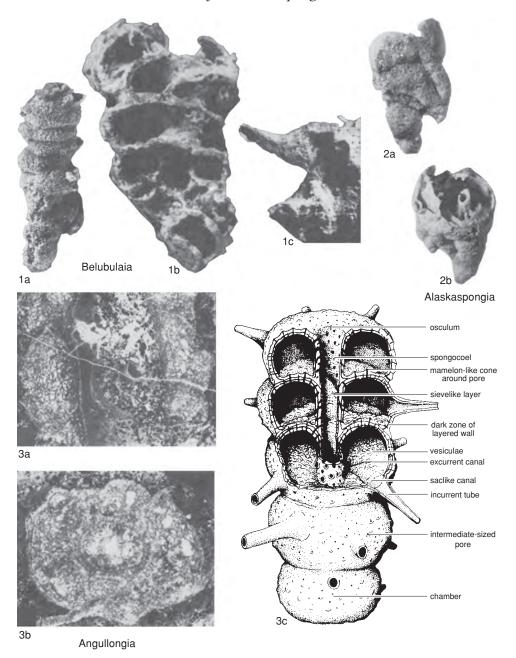


FIG. 426. Angullongiidae (p. 647-650).

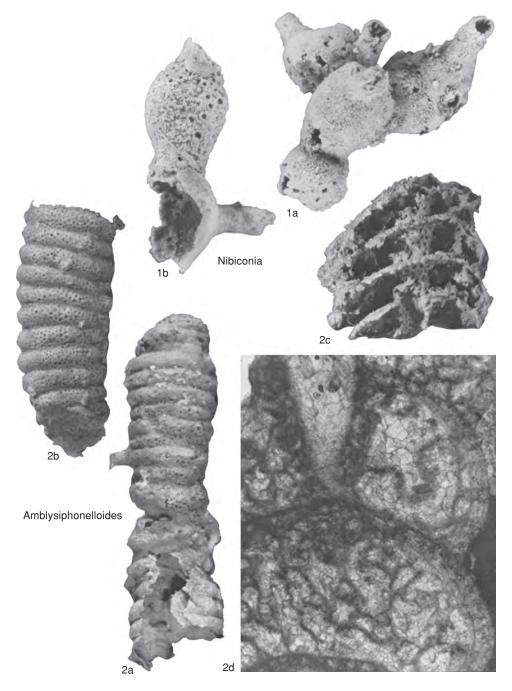
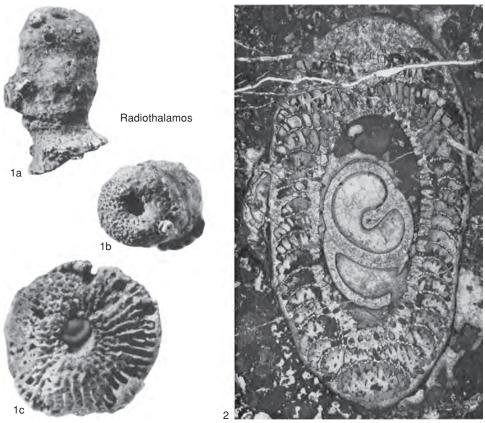


FIG. 427. Angullongiidae (p. 649–650).



Phragmocoelia

FIG. 428. Phragmocoeliidae (p. 650–651).

fragment with tubular ostia on two chamber exowalls, SUP51024, ×4 (Webby & Rigby, 1985). Nibiconia RIGBY & WEBBY, 1988, p. 90 [\**N. adnata;* 

OD]. Irregularly branching sponge of adnate to moderately isolated, swollen chambers with cylindrical Axel, but ill-defined, central spongocoel; chambers lacking vesiculae or other filling structures; chamber walls perforate. *lower Upper Ordovician:* Australia (New South Wales).——FIG. 427, *1a–b.* \**N. adnata*, Sugarloaf Creek breccia of Malongulli Formation, Cliefden Caves area; *a*, holotype of adnate, spindle-shaped chambers with prominent exaules, AMu F66917, X8; *b*, paratype with distinctly porous walls and necked connection between chambers, with tubular exaulos on right, AMu F66919, X8 (Rigby & Webby, 1988).

### Family PHRAGMOCOELIIDAE Ott, 1974

#### [Phragmocoeliidae OTT, 1974, p. 715]

Porate sphinctozoans with septate chamber fillings. *Devonian (Lochkovian)–Triassic (Carnian).* 

Phragmocoelia OTT, 1974, p. 715 [\*P. endersi; OD]. Cylindrical, not externally segmented; cloaca broad with well-developed endowall; endopores circular, closely spaced, and arranged in horizontal rows just above each interwall; additional, smaller endopores irregularly arranged; interpores small, of similar size to smaller endopores except near periphery where they may be same size as exopores; exopores similar in size to larger endopores; chamber height low; chambers containing radial, closely spaced, septalike trabeculae that may break up into radially elongate pillars; trabecular microstructure not known; no spicules observed. Triassic (Carnian): Europe (northern Calcareous Alps).-FIG. 428,2. \*P. endersi, Wettersteinkalk, Autrichian Calcareous Alps, Austria; a, diagonal section of holotype with chambers in single layer around thick-walled, coarsely perforate, axial spongocoel, chambers with septal, filling structures, porous exowall showing near base, BSPGM, ×5 (Ott, 1974; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).

Radiothalamos PICKETT & RIGBY, 1983, p. 738 [\*R. uniramosus; OD]. Conicocylindrical, with super-

posed, low, toroidal chambers visible externally; central cloaca approximately one-fifth to one-sixth sponge diameter; interwall continuous with exowall of preceding chamber; exopores small, circular, closely spaced and of one size, interpores somewhat larger and subangular; endowall incompletely preserved but may be meshlike with large endopores; chambers bearing closely spaced, radial, vertical septa pierced by large, vertically elongate pores; microstructure not known; spicules not known. [Genus somewhat resembles Stylopegma KING, 1943, but the latter has trabeculae that are straight and more regularly radial.] Devonian (Lochkovian-Pragian): Australia (New South Wales) .-----Fig. 428,1a-c. \*R. uniramosus, Garra Formation, Wellington; a, side view of small, silicified holotype with subcylindrical form,  $\times 2$ ; b, view from above showing osculum of central spongocoel and canals of relatively thick walls, MMF 23738, ×2; c, silicified paratype from above showing radial chambers and prospores in thick wall around central spongocoel, MMF 23737, ×2 (Pickett & Rigby, 1983).

### Family INTRASPOREOCOELIIDAE Fan & Zhang, 1985

[Intrasporeocoeliidae FAN & ZHANG, 1985, p. 17] [=Polysiphonellidae BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93, non Polysiphonellidae WU Ya Sheng, 1991, p. 65]

Cylindrical, often branched sponges composed of superposed, overlapping, hemispheroidal chambers with porate walls that apparently lack ostia; central spongocoel absent although chambers may be pierced by longitudinal, open tubes; chamber interiors filled by anastomosing trabeculae that have upward and outward organization; in type genus trabeculae formed of fused spheroidal bodies (possible spherulites). *Permian* (*Guadalupian–Lopingian*).

Intrasporeocoelia FAN & ZHANG, 1985, p. 18 [\*I. hubeiensis; OD]. Cylindrical, branching or spheroidal sponges, composed of superposed, hemispheroidal or meniscoidal, overlapping chambers; exowall-interwall a single unit pierced by closely spaced, small, circular exopores-interpores; outerupper surface microspinose (or microridged, as material is only known from sections); narrow, cloaca-like, vertical tubes, defined by discontinuous endowall, may penetrate a few successive chambers and their interwalls; they are not central and more than one may be present; chambers, especially earlier ones, may be filled by secondary structures analogous to lamellar lining and vesicles of other sphinctozoans, but consisting of spheroidal (or possibly rodlike) bodies fused laterally to form a lining to inner surface of chamber, as well as to form curving, anastomosing trabeculae, with an upward and outward organization, that locally outline circular,

horizontal, canal-like spaces within chambers that are interrupted by larger canals of interwalls; original wall microstructure unknown, but illustrations suggest small, isodiametric spherulites; it is possible that sporelike bodies of filling tissue are abnormally large spherulites; no spicules known. Permian (Guadalupian-Lopingian): China, Tunisia, Italy (Sicily), Greece, Oman, Thailand, Russia.-–Fig. 429, 3a-b. \*I. hubeiensis, Maokou Formation, Guadalupian, Kefeng, Guangxi, China; a, longitudinal section of subcylindrical form with low, arcuate chambers with porous interwalls and sporelike, filling structures that produce stippled-appearing filling on left, IGASB 5099, ×1; b, photomicrograph of sporelike, filling structure in chambers between lighter, porous interwalls, IGASB 5059, ×2 (Rigby, Fan, & Zhang, 1989a).

- Belyaevaspongia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 10 [\*Polysiphonella insolita BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 93; OD] [=Polysiphonella BELYAEVA in BOIKO, Belyaeva, & Zhuravleva, 1991, p. 93, obj., non Russo, 1981; Wu Ya Sheng, 1991, p. 65]. Moniliform imperforate sphinctozoan lacking a spongocoel, but with numerous small tubes that extend through one or two chambers; interiors of chambers hollow or filled with vesiculae. Permian (Lopingian): Thailand, Russia (Primoria, Far East), China.—FIG. 429, 1a-b. \*B. insolita (BELYAEVA), Upper Permian limestone, Dorashamian, Phrae Province, Thailand; a, reference section through chambered sponge with some vesiculae and small tubes that commonly lead to branching points,  $\times 1$ ; b, enlargement of part of same specimen showing perforate, chamber walls and small, perforate tubes (arrows), BSPGM R1, ×2 (Senowbari-Daryan and Ingavat-Helmcke, 1994).
- Rahbahthalamia Weidlich & Senowbari-Daryan, 1996, p. 39 [\*Amblysiphonella? bullifera SENOWBARI-DARYAN & RIGBY, 1988, p. 181; OD]. Single or branched stems of ringlike chambers around axial spongocoel; chambers filled with bubblelike, filling structures; individual bubbles may be interconnected by tubelike or rodlike elements; chamber walls perforated by numerous unbranched pores, which may be oriented obliquely to wall. Permian (Lopingian): Oman, Tunisia, China.-FIG. 430ab. \*R. bullifera (SENOWBARI-DARYAN & RIGBY), Djebel Tebaga reef complex, Changhsingian, Djebel Tebaga, Tunisia; a, holotype section with central, tubular spongocoel with coarser pores than in exowalls and interwalls, chambers with bubblelike, filling structures, USNM 427282, ×3; b, enlarged, single chamber of section from holotype with interconnected, bubblelike, filling structures, USNM 427283, ×1 (Senowbari-Daryan & Rigby, 1988).
- Rhabdactinia YABE & SUGIYAMA, 1934, p. 179 [\*R. columnaria; OD] [=Guangxispongia WU Ya Sheng, 1991, p. 83 (type, G. spinalis, OD)]. Columnar sponges of superimposed, low, concentric chambers; chambers hollow or with scattered, sporelike, filling structures; vertical, exhalant tubes well developed and widely distributed but prominent, central

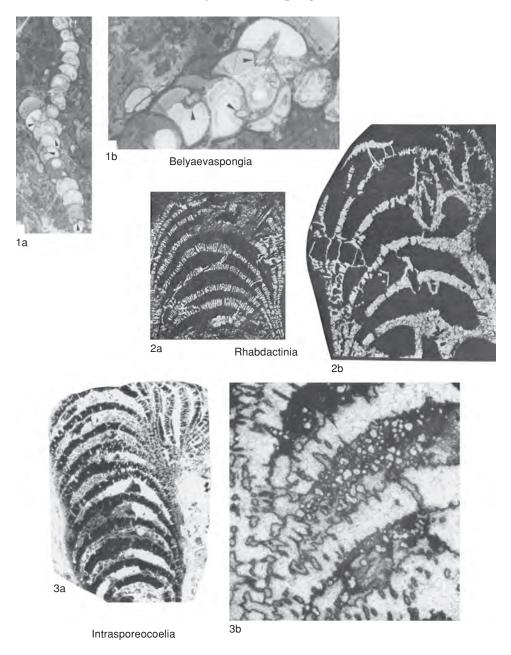


FIG. 429. Intrasporeocoeliidae (p. 651-652).

tube or spongocoel not developed; walls with numerous pores. *Permian (Guadalupian–Lopingian):* Japan, China (Hubei, Guangxi, Zhejiang), Tunisia, Oman, Russia.—FIG. 429,2*a–b.* \**R. columnaria,* Mimikiri Limestone, Tosa Province, Sikoku, Japan; *a*, longitudinal section of type sponge with arcuate chambers and coarsely porous interwall,  $\times 1$ ; *b*, longitudinal section with numerous vertical, exhalant tubes cutting light gray interwalls,  $\times 2$  (Yabe & Sugiyama, 1934).

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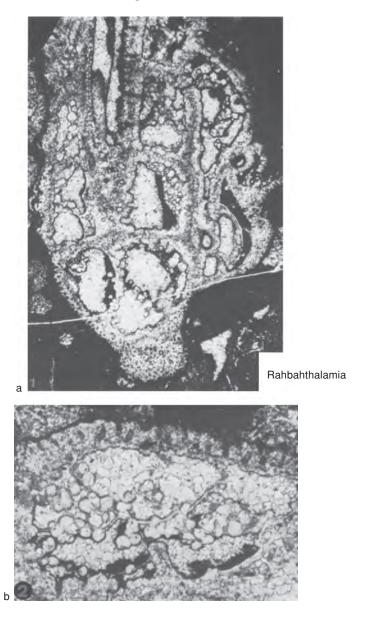


FIG. 430. Intrasporeocoeliidae (p. 651).

# Family CRYPTOCOELIIDAE Steinmann, 1882

[Cryptocoeliidae STEINMANN, 1882, p. 175]

Porate permosphinctans with aragonitic, basal skeleton and trabecular, filling structure; spicular skeleton unknown. *Silurian* (*Ludlow*)–Upper Triassic. Cryptocoelia STEINMANN, 1882, p. 176 [\*C. zitteli; OD]. Cylindrical, composed of overlapped, hemispheroidal or caplike segments, more or less visible on exterior; exowall bearing closely spaced, small, subpolygonal (possibly lobate) exopores, as well as occasional, somewhat larger, lipped, circular exopores; no cloaca or endowall; interwall a continuation of exowall of underlying chamber, doubled by trabecular coating of chamber above; interior of low chambers filled by dominantly vertical, pillarlike trabeculae that show limited, lateral anastomosis and expand laterally at top and bottom of each chamber; they may also outline occasional, large, vertical canals of circular cross section; thin vesicles may occupy spaces between pillars in earlier segments; trabecular microstructure an irregular horizontal lamination, within which STEINMANN (1882) observed irregular, branching bodies of unknown nature. Permian-Upper Triassic: China (Sichuan), Permian; Europe, Iran, Canada (Yukon), Middle Triassic-Upper Triassic; Caucasus region, Russia, Norian; Tajikistan, Carnian-Rhaetian. FIG. 431, 1a-b. \*C. zitteli, Cassian beds, Triassic, Seelande Alps, Austria; a, side view of exterior of holotype made of overlapping, caplike chambers with porous exowalls,  $\times 1$ ; *b*, vertical section of holotype showing chamber structure and vertical, pillarlike trabeculae, ×2 (Steinmann, 1882).

- Anisothalamia SENOWBARI-DARYAN & others, 1993, p. 216 [\*A. minima; OD]. Unbranched to rarely branched stems that lack a spongocoel, with porate interwalls of chambers but aporate exowalls; chambers with some pillar filling structures; skeleton originally aragonite without spicules. [Sections of Anisothalamia may appear similar to tangential sections of Enoplocoelia, but the latter has a spongocoel, which is wanting in Anisothalamia.] Triassic (Anisian): Italy.—\_FIG. 431, 3a-b. \*A. minima, Recoaro to Serla Formation, Olang Dolomite Alps; a, longitudinal section of holotype with thick exowall and arched, perforated interwalls, with pillar structures in chambers (arrows), SPIE 229b,  $\times 20$ ; b, section of reference specimen with partial, secondary calcification of lower walls and perforate interwalls in upper chambers, SPIE R1.5, ×10 (Senowbari-Daryan & others, 1993).
- Antalythalamia SENOWBARI-DARYAN, 1994a, p. 418 [\*A. riedeli; OD]. Moniliform sponges with spherical chambers that lack a spongocoel but have porate walls; large and unbranched pores give sponge exterior a rough, honeycomb-like appearance; filling structure consisting of few but relatively massive columns; numerous vesiculae occur in chamber interiors. [Antalythalamia may appear very similar to Colospongia, but the latter lacks the pillarlike filling structures that are characteristic of the genus and the Cryptocoeliidae. Antalythalamia also appears somewhat similar to the pillar-bearing Amblysiphonella? polyformis SENOWBARI-DARYAN & SCHÄFER, 1986, but the latter has a spongocoel.] Triassic (Norian): Turkey.—FIG. 431,2a-b. \*A. riedeli, Cipit limestone blocks, Taurus Mountains; a, holotype, longitudinal thin section with pillars and vesiculae in seven perforate chambers, SPIE 19 G 11/2, ×10; b, drawing of holotype showing vesiculae and dark pillars in chambers, bar scale 3 mm long (Senowbari-Daryan, 1994a).
- Rigbyspongia DE FREITAS, 1987, p. 840 [\*R. catenulata; OD]. Cateniform, porate, trabeculate sphinctozoan with multisiphonate, axial region; shallow spongocoel into which most equal-sized canals converge and empty; other similar canals exit

through exopores around margin of osculum; numerous vertical pillars are common filling structures in all chambers. [Rigbyspongia was originally included in the family Polysiphoniidae (DE FREITAS, 1987), but that family consists of unsegmented sponges and is not included in the thalamid sponges (SENOWBARI-DARYAN, 1990, p. 104), but in the latter work the genus was included in the Cryptocoeliidae, as it is here.] Silurian (Ludlow): Canada (Cornwallis Island).--FIG. 432,2a-d. \*R. catenulata, Silurian limestone, District of Franklin; a, side view of exterior of holotype, with numerous exopores,  $\times 2$ ; b, longitudinal section with shallow spongocoel in upper part above several vertical, exhalant canals, numerous pillars showing in chambers; c, transverse section showing pillars in outer chambers, GSC 85330, ×2; d, schematic reconstruction showing skeletal and canal patterns with pillars in outer chamber layer, not to scale (De Freitas, 1987; courtesy of Canadian Journal of Earth Sciences).

Sphaerothalamia SENOWBARI-DARYAN, 1994a, p. 420 [\*S. vesiculifera; OD]. Asiphonate, moniliform sponge composed of spherical to hemispherical chambers that increase upwardly in size; chamber walls with dichotomously branching pores; pillarlike elements extending out from chamber interwalls and ectowalls and function as bases for later developing vesiculae, which partially or entirely fill chambers; skeleton possibly aragonitic with irregular microstructure; spicular skeleton composed of monaxons and possible tylostyles, which were incorporated into basal skeleton. [Sphaerothalamia is similar to Antalythalamia but has branching pores in the chamber walls and a spicular skeleton of monaxons.] Triassic (Norian): Turkey .--Fig. 432, 1a-b. \*S. vesiculifera, Cipit limestone blocks, Taurus Mountains; a, holotype, thin section through three chambers with thick, vesicular, filling structures based in part on pillarlike extensions out from walls, bifurcating pores show on exowalls, SPIE 19 G 78/1, ×10; b, drawing of transverse section of paratype showing bifurcating exopores and filling structure pillars in black and vesiculae stippled, SPIE 16 G 49, scale bar, 3 mm (Senowbari-Daryan, 1994a).

## Family PALERMOCOELIIDAE Senowbari-Daryan, 1990

[Palermocoeliidae SENOWBARI-DARYAN, 1990, p. 109]

Porate permosphinctans with radial framework parallel to a well-developed, tubular, canal system in chamber or segment walls. *Upper Triassic.* 

Palermocoelia SENOWBARI-DARYAN, 1990, p. 109 [\**P. tubulifera;* OD]. Permosphinctans with development of a radial, parallel, tubular pore system in chamber walls, which in longitudinal section are composed of trabecular, filling structures simulating that of *Stylothalamia;* skeleton with microgranular

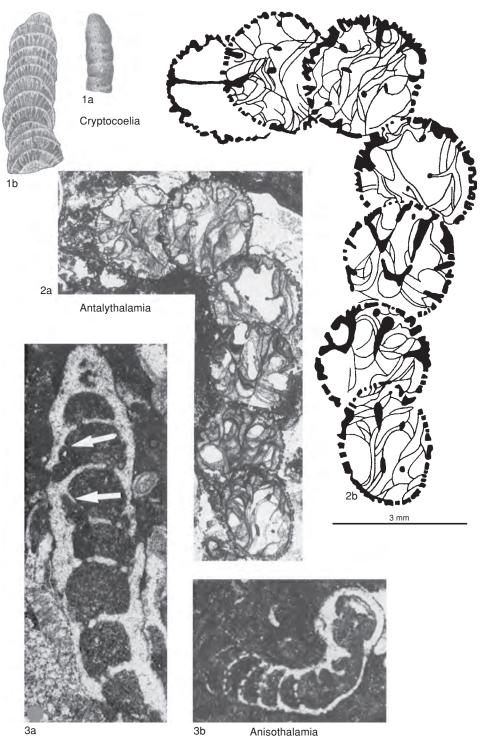


FIG. 431. Cryptocoeliidae (p. 653–654).

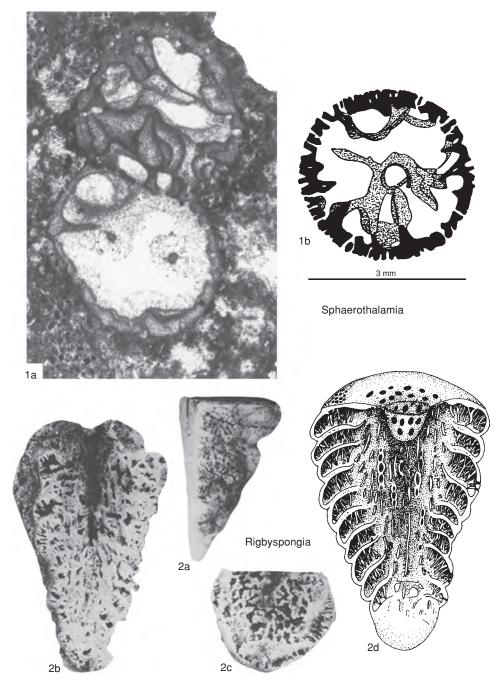


FIG. 432. Cryptocoeliidae (p. 654).

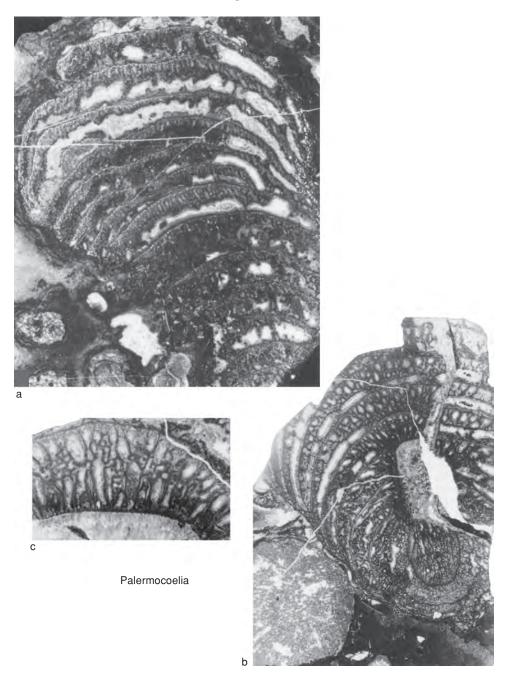


FIG. 433. Palermocoeliidae (p. 654–658).

microstructure, perhaps produced by diagenesis; reticular filling structures developed here and there in older chambers; vesiculae are limited to peripheral parts of older chambers. Upper Triassic: Italy. -FIG. 433a-c. \*P. tubulifera, Triassic reef limestone, Norian-Rhaetian, Palermo, Sicily; a, longitudinal section of holotype with low chambers partially filled with calcite or matrix; tubular pores showing in middle and upper chamber walls, SPIE D/361/2,  $\times$ 4; *b*, transverse section through lower part of holotype with central spongocoel and thick walls with tubular pores, SPIE D/361/3, ×2; c, photomicrograph of spongocoel wall showing tubular structure and intervening filling structure, SPIE D/361/6, ×5 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

### Family GIRTYOCOELIIDAE new family

[Girtyocoeliidae FINKS & RIGBY, herein] [=Amphorithalamiidae SENOWBARI-DARYAN & RIGBY, 1988, p. 201] [type genus, *Girtyocoelia* COSSMANN, 1909, p. 67]

Spheroidal chambers; exowall generally imperforate, with well-developed exauli, that may contain internal cribribulla, in equatorial ring; cloaca present except in juveniles (protocysts), with endopores often concentrated in a ring; filling structures sparse to absent, but vesicles or trabeculae may occur. *Ordovician–Triassic.* 

Girtyocoelia COSSMANN, 1909, p. 67 [\*Heterocoelia beedei GIRTY, 1908, p. 284; OD] [=Heterocoelia GIRTY, 1908, p. 282, obj., non DAHLBOM, 1854; Apocoelia RIGBY, 1984, p. 1,453 (type, A. sphaera RIGBY, 1984, p. 1,456, OD)]. Spherical segments, or spheroidal when in contact, arranged in subparallel, branching, occasionally anastomosing, linear series; segments in each series connected by continuous, narrow, central tube or cloaca that is frequently visible externally between segments and protrudes beyond last segment (prosiphonate); juveniles (protocysts) adnate on shells and other sponges, and initially lack cloaca, although not osculum, and their exauli may be very short or very long; exowall imperforate except for equatorial ring of large, circular exopores at ends of spoutlike exauli or sometimes merely strongly rimmed; at inner end of each exaulos is a hemispherical sieve of smaller, circular pores (cribribulla) that bulges into chamber; inner surface of exowall may have anastomosing network of fibers applied to it, but no fibers are known from lumen of chamber itself; vesicles may be present in lumen; endowall pierced by small to large, circular endopores, often concentrated into two sievelike rings, one near lower and one near upper end of chamber; these rings may bulge into chamber; when successive segments are in contact, interwall double, being two exowalls; cloaca of new branch arising through exowall; exauli of successive segments may occasionally join; long exauli of protocysts may invade other sponges; wall microstructure consists of small (20 to 60 µm), isodiametric spherulites; laminar, secondary layer of clinogonal (penicillate) structure may be present on inside of walls lining chamber; no spicules known. [Early protocysts in which the cloaca has not yet appeared were named Apocoelia by RIGBY (1984, p. 1,453).] Ordovician-Triassic (Carnian): Australia, Ordovician; Austria, upper Bashkirian-Gzhelian; southcentral to southwestern United States, Upper Pennsylvanian, Wordian; Tunisia, Spain, Italy (Sicily), Oman, Venezuela, Thailand, China, Lopingian; Russia, Wordian-Capitanian; Austria, Yugoslavia, Greece, Italy (Sicily), Ladinian-Carnian.--Fig. 434, 1a-e. \*G. beedei (GIRTY), Plattsburg Limestone, Desmoinesian-Virgilian, Chanute, Kansas; a, cluster of several individuals showing growth form,  $\times 1$ ; b, section showing axial spongocoel and globular chambers in branching specimen, ×2; c, section showing chambers separated along axial spongocoel, all part of syntype suite, USNM 53471, ×2 (Girty, 1908); d, silicified specimen with prominent, tubular exaules on each globular chamber, USNM, Glass Mountains, Texas, ×1.5; e, reconstruction showing globular chambers around porous, central tube and with prominent exaules, not to scale (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

Amphorithalamia SENOWBARI-DARYAN & RIGBY, 1988, p. 201 [\*A. cateniformis; OD]. Spheroidal chambers encrusting other surfaces and connected by long, sometimes branching tubes that may be regarded as exauli; one or usually more oval clusters of polygonal pores, surrounded by a low rim, occurring on upper surface of each chamber and may be regarded as cribribulla flush with surface; interior of each chamber filled with fine, meandriform, trabecular net that outlines anastomosing, tubular spaces; exowall aporate; no cloaca; microstructure unknown; no spicules known. [These appear to be protocysts of an unknown adult form (unless paedomorphic); they differ from the protocysts of Girtyocoelia COSSMANN, 1909, in having trabecular, filling tissue and in development of cribribulla-like structures at the surface. They also lack the prominent, central tube distinctive of adult Girtyocoelia. The overall organization, however, is similar to that of Girtyocoelia and they would seem to be related. There are, in fact, traces of trabeculae on the inner surface of the Girtyocoelia exowall. The spelling given here is that used consistently in the original description of the genus and type species. The alternate spelling Amphorothalamia, used in the figure captions, table of contents, and elsewhere in the original publication, is to be regarded as a lapsus calami.] Permian (Lopingian): Tunisia.——FIG. 435,1a-c. \*A. cateniformis, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, attached, flasklike chambers connected by tubes in holotype,  $\times 2$ ; *b*, two chambers of holotype showing distinct ostia, several per chamber, and interior, reticulate, filling structure,  $\times 5$ ; *c*, sketch of holotype,

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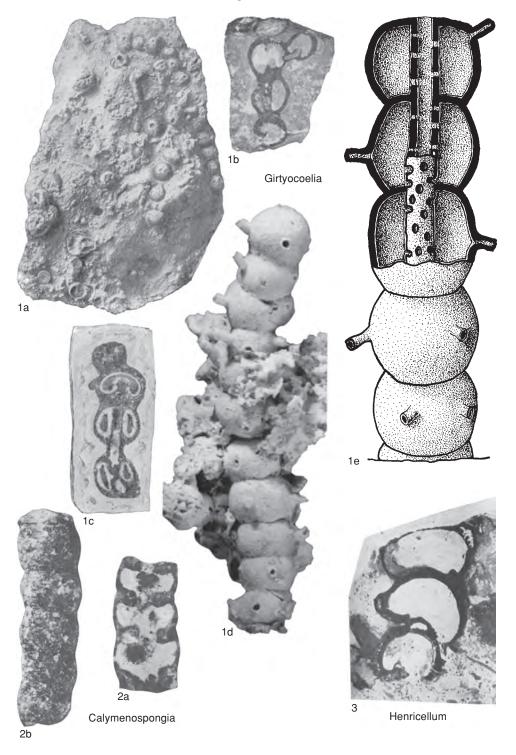


FIG. 434. Girtyocoeliidae (p. 658–660).

either branched stem or two individuals, USNM 427414, approximately ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

- Calymenospongia ELLIOTT, 1963, p. 295 [\*C. kurdistanensis: OD]. Small, uniserial calcisponge, chambers nearly spherical, hollow, fused, double interwalls producing thick layer between chambers; chambers interconnected in interior by single, large osculum through interwalls; exowall with few scattered, relatively coarse, irregularly placed, inhalant ostia. Paleogene (Paleocene): Iraq.—FIG. 434,2ab. \*C. kurdistanensis, Kolosh Formation, Bekhme, Erbil Liwa, northern Iraq; a, holotype showing uniserial growth form, BM S8335; b, vertical section through paratype showing chambers, fused thick interwalls, and thin exowalls, BMS8336, ×25 (Elliott, 1963).
- Enoplocoelia STEINMANN, 1882, p. 166 [\*Scyphia? armata KLIPSTEIN, 1843 in 1843-1845, p. 284; OD]. Cylindrical, not clearly segmented externally; central cloaca about one-fourth sponge diameter; exowall finely porous with circular to vertically elongate, slitlike, meandriform spaces, partly obscured by imperforate cortex, as well as a horizontal row, for each internal segment, of larger, circular exopores with strong lips, or more precisely, a volcano-like protrusion of exowall; chambers low; interwalls sievelike, being pierced by closely spaced, circular interpores of two sizes that are intermediate between sizes of large and small exopores; endopores circular to vertically elongate and size of larger interpores; vertical, trabecular ridges may be attached to chamber side of endowall; chamber lumen free of skeletal structures; walls composed of primary layer of isodiametric spherulites of small to large size; older parts of chambers and cloaca may be largely filled with secondary deposit of clinogonal (penicillate) aragonite; spicules not known. [The specimens of species from the Permian of Sicily are incomplete and questionable.] Permian-Triassic: Tunisia, Italy (?Sicily), Permian; Greece, Italy (Sicily), Austria, Romania, Triassic. -FIG. 435, 3a-b. \*E. armata (KLIPSTEIN), San Cassiano Formation, Carnian-Norian, Dolomite Alps, Italy; a, side view of branched type specimen with lipped exopores,  $\times 2$ ; b, tangential polished section of holotype showing uniformly porous interwalls of low chambers, ×4 (Steinmann, 1882).
- Henricellum WILCKENS, 1937, p. 194 [\*H. insigne; OD]. Spheroidal to hemispheroidal chambers attached in linear series; small, blisterlike chamber attached to outside of each principal chamber and communicates with it by one (or possibly more) small canals through exowall, but there is probably not communication between principal chambers; a few large exopores present on each segment, but wall otherwise imperforate; chamber interior has no skeletal elements; microstructure and spicules not known; outer surface appearing somewhat rough. [Genus is known only from sections and the structure is not well understood. It is conceivable that the blisterlike chambers with their associated canals are exauli with cribribulla, seen in partial view, but

this is conjecture.] Permian (?Wordian-?Capitanian), Triassic: Russia, ?Wordian-?Capitanian; Indonesia, Canada (Yukon), Triassic.—FIG. 434,3. \*H. insigne, Pharetrone Limestone, Upper Triassic, Seran, Moluccas, Indonesia; longitudinal section of holotype with spheroidal chambers lacking filling structures and with rare exopores, S 194, ×2 (Wilckens, 1937; courtesy of Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abt. B).

- Phraethalamia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 21 [\*P. tubulara; OD]. Stemlike, aporate, thalamid sponges with two or more parallel, axial spongocoels that penetrate ringlike, stacked chambers; numerous branched tubes extending from spongocoel wall laterally into hollow chamber interiors, which lack vesiculae and filling structures. [In general size and chamber arrangement, Phraethalamia is similar to Girtyocoelia, but the latter has only a single, axial spongocoel and it lacks the distinctive tubes that extend from the spongocoel wall into the chambers. Such tubes are known in the Permian demosponge Pseudoamblysiphonella SENOWBARI-DARYAN & RIGBY, 1988, and in Barroisia lehmani HILMER & SENOWBARI-DARYAN, 1986, from the Cretaceous of Germany, but both those genera have perforated outer walls.] Permian (Lopingian): Thailand.—FIG. 435,2a-b. \*P. tubulara, upper Permian limestone, Dorashamian, Phrae; a, holotype, longitudinal section through several chambers and two wide, axial canals,  $\times 2$ ; b, drawing of holotype showing spherical, imperforate, chamber walls, double axial canals, and smaller tubes that extend from spongocoel wall into interior of chambers, BSPGM R8, ×1 (Senowbari-Daryan & Ingavat-Helmcke, 1994).
- Polyedra TERMIER & TERMIER, 1955, p. 615 [\*P. tebagaensis; OD]. Cylindrical sponge composed of superposed, spheroidal segments; central cloaca one-third to one-fifth sponge diameter; outer surface of each segment divided into large, polygonal, flat or concave areas, each area bounded by raised rim containing large, circular labripore (or short exaulos) at its center; external surface of sponge, both inside and outside polygonal areas, bearing fine, reticulate sculpture, which is obscurely radial about each labripore; original description states that an internal chamber corresponds to each polygonal area, that these chambers communicate with each other by pores, and that the cloaca is sometimes partitioned longitudinally. [Redescription of topotypes by SENOWBARI-DARYAN and RIGBY (1988, p. 196 ff.; pl. 37,1-8) shows a single chamber for each segment, a cribribulla over the internal end of each exaulos, and small, scattered endopores in the endowall; microstructure not known; no spicules known. As redescribed, this genus differs from Girtyocoelia COSSMANN, 1909, in the polygonal facets and reticulate surface sculpture.] Permian (?Artinskian, Lopingian): Tajikistan, ?Artinskian; Tunisia, Lopingian.—FIG. 436, 1a-d. \*P. tebagaensis, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view of specimen with one rimmed ostium per flattened

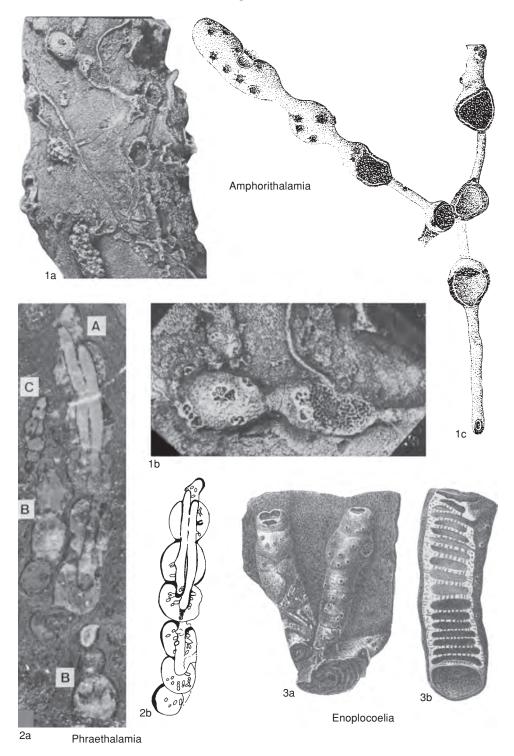


FIG. 435. Girtyocoeliidae (p. 658–660).

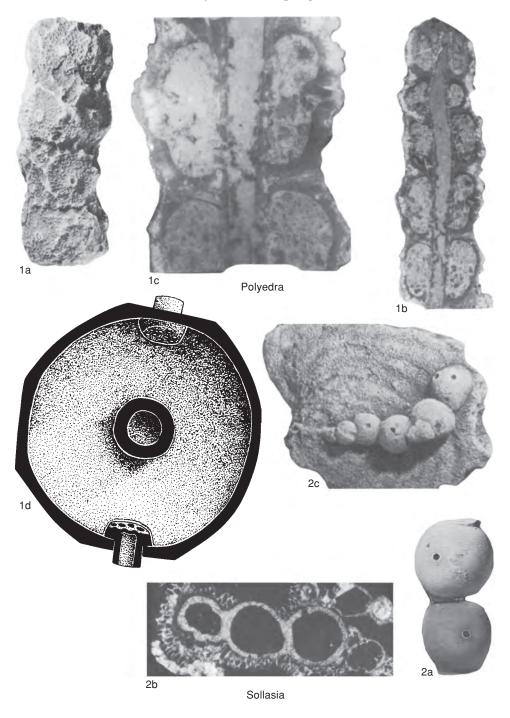


FIG. 436. Girtyocoeliidae (p. 660–664).

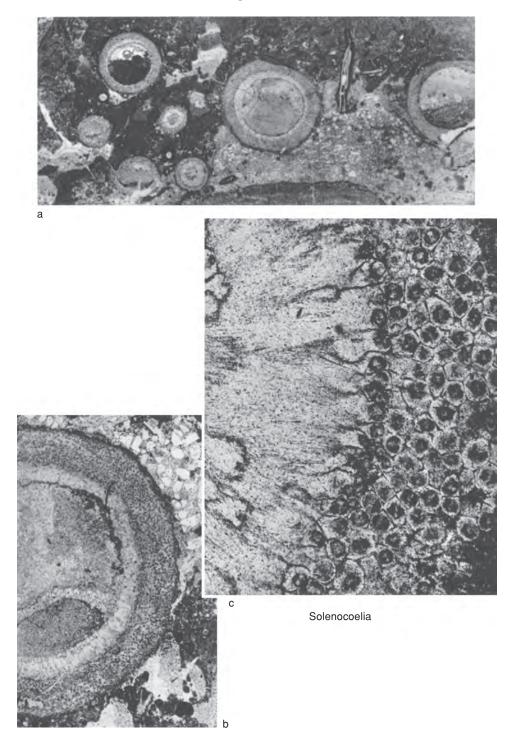


FIG. 437. Girtyocoeliidae (p. 664).

chamber face, which have reticulate, radial sculpture, USNM 427375, ×2; *b*, polished, axial section showing growth form and axial tube, as well as cribribulla on right exowall of second chamber from bottom, ×2; *c*, photomicrograph of lower part of same specimen, with cribribulla at midheight in right exowall of upper chamber, USNM 427377, ×5; *d*, diagram of transverse section showing two ostia with sievelike, cribribulla plates at internal end of short exaules in exowall, and central tube, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

- ?Solenocoelia CUIF, 1973, p. 122 [\*S. cylindracea; OD]. Conical; so-called exowall imperforate; interior without skeletal structures except for occasional thin, curved, tabula-like partition; no pores; primary layer of outer wall and all of tabulae built of small, isodiametric spherulites; outer wall has inner, clinogonal layer; no spicules. [It is doubtful that this is a sponge.] Triassic: Turkey.-FIG. 437 a-c. \*S. cylindracea, Triassic deposits, Carnian-Norian, Korkuteli; a, type, transverse sections of a group of organisms,  $\times 4$ ; b, transverse section with spherulitic structure in both layers of outer wall and in arched plate in interior, ×18; c, photomicrograph showing spherulites in outer wall and strongly asymmetrical ones in interior, ×100 (Cuif, 1973; courtesy of Geobios).
- Sollasia STEINMANN, 1882, p. 151 [\*S. ostiolata; OD]. Spheroidal to barrel-shaped segments in contact in linear series; exowall imperforate except for equatorial ring of large, circular, lipped exopores; no cloaca or endowall, but central osculum at top of each segment; primary layer of exowall of next segment beginning peripherally so that primary interwall is formed by exowall of preceding segment; secondary layer lining lumen of each chamber, coating both sides of interwall; primary layer of exowall or interwall containing fine, anastomosing canals that may be filaments of endolithic fungi or algae; spherulites or spicules not observed. [Permian species in literature poorly known and doubtful.] Carboniferous (Bashkirian)-Triassic (Rhaetian): Spain, Bashkirian; Austria, upper Bashkirian-Gzhelian; Tunisia, Italy (Sicily), Oman, United States (Texas), China and southeastern Asia; Russia, Tajikistan, Guadalupian-Lopingian; ?Hungary, Anisian; Caucasus region, Russia, Carnian-Rhaetian; Italy (Sicily), Norian.-FIG. 436,2a-c. \*S. ostiolata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view of fragment with two chambers, smooth walls, and welldeveloped ostia, USNM 4427384, ×2; b, section through a fragment with three chambers showing double interwalls, lack of filling structures, and granular, spherulitic microstructure in walls that are overgrown with a chaetetid, USNM 427390,  $\times 5$ ; c, specimen illustrating increase in chamber size in early stages of growth, USNM 427394, ×3 (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).

## Family THAUMASTOCOELIIDAE Ott, 1967

[Thaumastocoeliidae Ott, 1967a, p. 15, *partim; emend.*, Finks & Rigby, herein]

Cateniform, without cloaca; cribribullalike pore fields, approximately flush with surface of exowall and surrounded by low rims, occurring equatorially and also forming osculum and interpores. *Middle Ordovician–Triassic.* 

Thaumastocoelia STEINMANN, 1882, p. 153 [\*T. cassiana; OD] [=?Follicatena OTT, 1967a, p. 20 (type, F. cautica OTT, 1967a, p. 22, OD); ?Palaeoierea LAUBE, 1865, p. 233 (type, Manon? gracilis MÜNSTER, 1841, p. 28, OD)]. Cylindrical, segmented; segments spheroidal or barrel shaped; no cloaca; exowall aporate except for a few circular, lipped exopores or circular, sievelike clusters of small, circular exopores (see DIECI & others, 1968, pl. 27,8), clusters depressed below surface and surrounded by external, raised rim (essentially a cribribulla and very short, wide exaulos) [unless the specimen of DIECI and others is a *Follicatena*]; interpores (and terminal oscular field) grouped in large, sievelike cluster bowed down into lower chamber; interior of chambers without skeletal structures; interwall a continuation of exowall of lower chamber covered by secondary layer only of upper chamber; exowall or interwall composed of primary layer of very large, isodiametric spherulites of subpolygonal outline, lined internally by secondary layer of clinogonal (penicillate) structure; supposed, large, calcareous spicules (monaxonic and branching) in secondary layer may be random sections of larger filaments of endolithic fungi or algae, whose finer, irregularly branching filaments have been observed both in secondary layer and also perforating spherulites of primary layer. [Palaeoierea LAUBE, 1865, resembles Thaumastocoelia externally, but its interior structure is unknown; the surface was said to be finely porous, but the large, granular spherulites may have given this impression. It is the senior synonym if truly congeneric. See also Sestromella, p. 611 herein.] Permian (?Cisuralian-?Guadalupian, Lopingian)-Triassic: Oman, China; USA (Texas), ?Permian; Italy, Hungary, Turkey, Tajikistan, Triassic. FIG. 438, 1a-d. \*T. cassiana, San Cassiano Formation, Carnian-Norian, Dolomite Alps, Italy; a, side view with lipped exopores on barrel-shaped chambers of type specimen,  $\times 2$ ; *b*, longitudinal section of type showing porous interwalls and impervious outer walls,  $\times 1$ ; c, view from above of coarsely perforate interwall,  $\times 10$ ; d, section through chamber wall showing large, isodiametric spherulites and supposed spicules that may be penicillate, calcareous elements, ×25 (Steinmann, 1882).

Agelasida

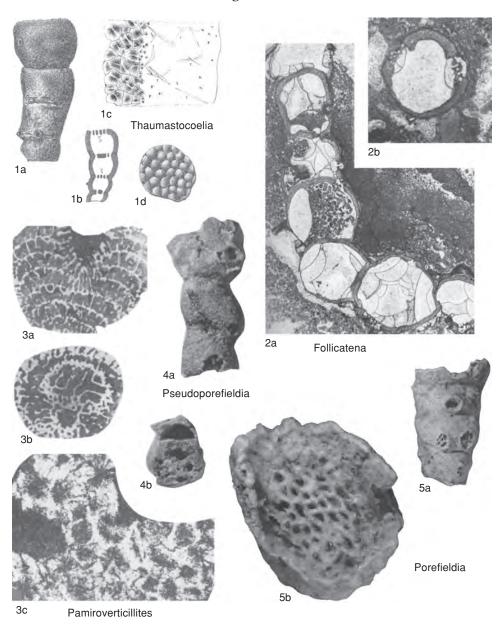


FIG. 438. Thaumastocoeliidae (p. 664-667).

?Follicatena OTT, 1967a, p. 20 [\*F. cautica OTT, 1967a, p. 22; OD]. Spheroidal segments forming chains; cloaca absent; exowall imperforate except for sievelike groups of exopores (cribribullae possibly flush with surface); similar groups of interpores pierce double interwall, pores in wall of lower chamber, with wall of upper chamber absent over entire sievelike group; interior of chambers often filled with numerous vesicles, but no other interior skeletal structures; microstructure unknown; no spicules known. *Permian–Triassic:* Italy (Sicily), Russia Pamir region, Tajikistan, China, *Permian;* Alpine-Mediterranean region, USA (Oregon), Canada (Yukon), *Triassic.*—FIG. 438,2*a–b.* 

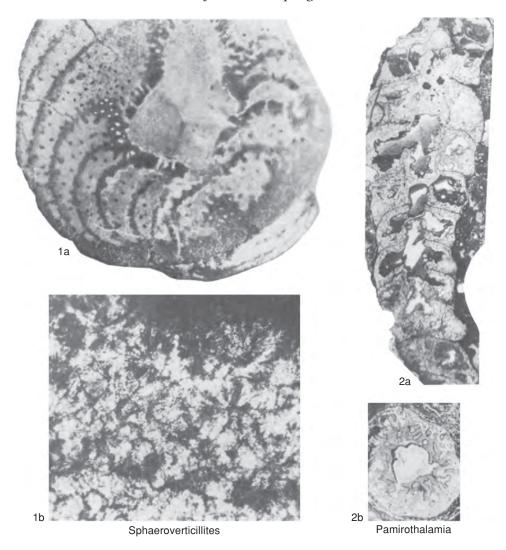


FIG. 439. Thaumastocoeliidae (p. 666-667).

\**E cautica*, Wettersteinkalk, reef facies, Ladinian, Kaisergebirge, Austria; *a*, longitudinal section of holotype with spheroidal chambers and imperforate walls with cribribullae, best seen in upper and lower chambers, BSPGM G 396 a/67, ×2.5; *b*, transverse section of holotype chamber with two distinct cribribulae, BSPGM G 397 a/67, ×5 (Ott, 1967a; courtesy of *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*).

Pamirothalamia BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 135 [\**P. originalis;* OD]. Catenulate sponge with spherical chambers around axial canal that is cryptosiphonate; ostia in distal parts of chambers and on lateral surfaces; chamber walls fragile, in form of possible bars; interwalls double where two chambers juxtaposed and each chamber with complete wall. [Pamirothalamia is similar to Sollasia but has thin, chamber walls and endowall of axial, exhalant structure, somewhat similar to that in Battaglia SENOWBARI-DARYAN & SCHÄFER, 1986.] Triassic: Tajikistan.——FIG. 439,2a-b. \*P. originalis, Triassic limestone, between Aksu River and Dzhilgakochusu River; a, longitudinal section through large sponge with thick exowalls and double interwalls, central, exhalant canal or spongocoel ill defined, MIGT 793-15 116/ 53, ×4; b, transverse section showing complex, inhalant canals in thick walls, MIGT 793-16 116/54, ×4 (Boiko, Belyaeva, & Zhuravleva, 1991).

Pamiroverticillites BOIKO in BOIKO, BELVAEVA, & ZHURAVLEVA, 1991, p. 153 [\*Sphaeroverticillites conicus BOIKO, 1990, p. 123, partim; OD]. Spherical to cup-shaped sponges composed of low, circular chambers that are overlapping, without visible constrictions on dermal surface; dermal surface with equally distributed, round pores; axial spongocoel cylindrical with retrosiphonate chamber walls; chambers with vertical, trabecular filling structures; skeletal structure spherulitic with small spherulites in lower chamber walls, directed downwardly, in possibly parallel rows; spherulites in upper walls large, upwardly directed, and nearly parallel. [Differs from Sphaeroverticillites in growth form and *Preverticillites* in type of filling structures.] Triassic (Norian): Tajikistan. FIG. 438, 3a-c. \*P. conicus (BOIKO), southeastern Pamir; a, vertical section showing low, overlapping chambers with vertical, trabecular filling structures and shallow, axial spongocoel, ×1; b, transverse section with small, axial spongocoel in lower part, and porous chamber walls, ×2; c, photomicrograph of part of wall showing spherulites in wall, MIGT 793-25 116/76, ×50 (Boiko, Belyaeva, & Zhuravleva, 1991).

- Porefieldia RIGBY & POTTER, 1986, p. 37 [\*P. robusta; OD]. Small, conicocylindrical sponges composed of superposed segments, visible on exterior, without cloaca; exowall imperforate but containing two to five, cribribulla-like or craticula-like, elliptical pore fields approximately flush with surface and surrounded by prominent rim; pores subangular and separated by narrow trabeculae; interwalls with interpores of similar shape to craticular (cribribullar) pores, but larger; intervening trabeculae may be crusted on upper surface; thin vesicles may be present in chambers; microstructure not known; no spicules known. [Genus is very similar to Follicatena OTT, 1967a, and Thaumastocoelia STEINMANN, 1882, both from the Triassic.] upper Upper Ordovician: USA (California).-–Fig. 438,5a-b. \*P. robusta, Kangaroo Creek Formation, Ashgill, Klamath Mountains; a, side view of silicified, steeply obconical holotype with prominent pore fields, which may occur several per chamber, as rimmed clusters of ostia,  $\times 2$ ; b, vertical view of broken summit with coarse, sievelike interwalls and moderately thick exowalls, USNM 395885, ×5 (Rigby & Potter, 1986).
- Pseudoporefieldia RIGBY, POTTER, & BLODGETT, 1988, p. 741 [\*P. micella; OD]. Differs from Porefieldia RIGBY & POTTER, 1986, in that the exowall bears small, widely spaced exopores, in addition to pore fields, rather than being imperforate; there is but one lobate pore or pore field per chamber. Middle Ordovician-Upper Ordovician: USA (Alaska).-FIG. 438, 4a-b. \*P. micella, unnamed Middle to Upper Ordovician sequence, White Mountains, McGrath Quadrangle; a, side view of small holotype with irregular growth form and prominent pore fields as inhalant openings, generally one per chamber, ×5; b, view down onto broken upper surface showing large, circular interpores in interwall, USNM 417203, ×5 (Rigby, Potter, & Blodgett, 1988).
- Sphaeroverticillites BOIKO, 1990, p. 122 [\*S. glomeratus BOIKO, 1990, p. 123; OD]. Sponges

large, spherical to cup shaped, with cylindrical, retrosiphonate, axial canal; chambers ringlike, overlapping, without visible constrictions on surface, and with trabecular filling structures; mesostructure spherulitic. *Triassic (Norian):* Tajikistan.——FIG. 439, *1a–b.* \**S. glomeratus*, southwestern Pamir Mountains; *a*, vertical section of holotype showing globose sponge with thick-walled, retrosiphonate, axial canal and porous walls of low, overlapping, chambers that contain vertical, rodlike, trabecular, filling structures, MIGACT 15/I, specimen 173, ×2; *b*, photomicrograph showing spherulitic, skeletal structure in holotype, ×100 (Boiko, Belyaeva, & Zhuravleva, 1991).

## Family APHROSALPINGIDAE Myagkova, 1955

[Aphrosalpingidae МулGKOVA, 1955a, p. 478] [=Spicidae TERMIER & TERMIER, 1977a, p. 41, *partim*; Fistulosponginidae TERMIER & TERMIER, 1977a, p. 38, *partim*; Vesicocaulidae WU Ya Sheng, 1991, p. 91]

Aporate sphinctozoan sponges with deep spongocoel and surrounding chambers either glomerate or catenulate; steeply obconical to subcylindrical with single or branched stems; central tube or spongocoel open or occupied by cluster of axial, exhalant canals; chamber walls may be a single layer or multilayered; exaules, filling structures and intertubes may be present or absent. *upper Upper Ordovician–Triassic.* 

## Subfamily FISTULOSPONGININAE Termier & Termier, 1977

[nom. transl. FINKS & RIGBY, herein, ex Fistulosponginidae TERMIER & TERMIER, 1977a, p. 38] [=Spicidae TERMIER & TERMIER, 1977a, p. 41, partim]

Cylindroid with central cloaca about which a single layer of spheroidal or subpolygonal, single-walled chambers cluster; craticularia at outer end of short exaulos present in each chamber; type genus bearing small exopores as well; endowall has longitudinal canals or ridges. *upper Upper Ordovician–Permian (Lopingian).* 

Fistulosponginina TERMIER & TERMIER, 1977a, p. 38 [\*F. elegans; OD] [=Spica TERMIER & TERMIER, 1977a, p. 41 (type, S. spica, OD), non SWINHOE, 1890, nec SACCO, 1892]. Cylindrical sponge with single layer of spheroidal to subpolygonal chambers surrounding narrow, central cloaca; exowall pierced by cluster of polygonal pores surrounded by low to prominent rim or scattered, large, circular labripores; remainder of exowall minutely porous; interwalls double and penetrated by fine pores as in exowall; endopores larger than fine exopores; endowall said to contain longitudinal canals; no interior structures in chamber except internal lips around large exopores; wall microstructure spherulitic; no spicules known. [Fistulosponginina TERMIER & TERMIER, 1977a, is Spica overgrown by a thin layer of a chaetetid (SENOWBARI-DARYAN & RIGBY, 1988, p. 200), unless this is part of the sponge itself, inasmuch as the agelasid Ceratoporellidae have chaetetid morphology and a spherulitic, aragonite wall structure (WOOD, 1991; MASTANDREA & Russo, 1995) (compare also the stromatoporoidlike trabecularium above the sphinctozoan thalamidarium in the Guadalupiidae).] Permian (Lopingian): Tunisia, Oman.-FIG. 440, 3a-c. \*F. elegans, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view of typical specimen with single, starlike ostia on ends of egglike chambers arranged in vertical rows,  $\times 2$ ; *b*, enlarged side view showing ostia on chamber ends, USNM 427402, ×5; c, polished, vertical section with cross sections of chambers around axial spongocoel, USNM 427405, ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).

- Aphrosalpinx MYAGKOVA, 1955b, p. 639 [\*A. textilis; OD]. Steeply obconical, cylindrical or gobletlike stems, or branched, monoglomerate sponges with generally open, axial spongocoel in middle and upper part, but with axial cluster of small, exhalant tubes in lower part; numerous outer chambers radially arranged, some with prominent, tubular, inhalant exaules in outer wall that may extend inwardly as tubules into chambers; small endopores in inner wall, locally with S-shaped, exhalant canals forming part of reticulate or vermiculate, gastral layer intermediate between cortexlike lining in upper part and axial canal complex in lower part; vesiculae may occur in chambers, particularly in lower part of sponge. Silurian (Ludlow): Russia (northern Urals), USA (Alaska).——FIG. 441, 1a-c. \*A. textilis; a, transverse section showing tubular spongocoel surrounded by radial, cellular layer with prominent, distal exaules, middle Silurian limestone, Ludlovian, McGrath Quadrangle, Alaska, UCG 5592 SD, ×3; b, tangential section through radial chambers showing scalelike sections, with transverse sections of a few exaules showing as small rings in upper left, Heceta Formation, Ludlovian, Tuxekan Island, southeastern Alaska, UCG YP58-3AFL-92, ×4; c, generalized reconstruction showing chamber and exaules development, as well as axial cluster of small, exhalant canals in lower part, not to scale (Rigby & others, 1994; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).
- Cystothalamiella RIGBY & POTTER, 1986, p. 32 [\*C. ducta; OD]. Conicocylindrical sponge composed of spheroidal chambers, polygonal where mutually interfering, clustered about central cloaca that is one-third sponge diameter; exowall imperforate except for short exauli that arise from low mounds and terminate in a craticula; craticular pores subpolygonal; chambers do not communicate with one another, interpores absent; endopores are relatively large, circular to subpolygonal, and closely spaced; endowall bearing irregular, longitudinal ridges on

its inner surface, somewhat similar to rudimentary trabecularium of Cystauletes KING, 1943; vesicles may occur within chambers; microstructure not known; no spicules known. [Genus is similar to the Permian Spica TERMIER & TERMIER, 1977a, except that the latter has sparsely porous exowalls.] upper Upper Ordovician-Silurian (Ludlow): USA (California), upper Upper Ordovician; USA (southeastern Alaska), Ludlow.-FIG. 440,2a-b. \*C. ducta, unnamed limestone, Ashgill, Klamath Mountains, California; a, side view of holotype with circular to polygonal chambers in vertical cluster, each with pronounced exaulos,  $\times 2$ ; b, vertical view showing crescentic chambers around central tube and with short but pronounced exaules, USNM 395880, ×2 (Rigby & Potter, 1986).

- Nematosalpinx MYAGKOVA, 1995a, p. 478 [\*N. dichotoma MYAGKOVA, 1995a, p. 479; OD]. Small, cylindrical, dichotomously branched, composed of single layer of globular chambers around axial cluster of exhalant canals that extends through sponge; irregularly curved exaules and intertubes may be developed in outer parts of chambers; endopores prominent, moderately coarse openings in endowall opening into exhalant canal cluster. Silurian (Ludlow): Russia (northern Urals), USA (southeastern and southwestern Alaska).-FIG. 441,2a-c. \*N. dichotoma; a, monoglomerate, radial chambers around axial cluster of thick-walled, exhalant canals, Silurian beds, Vishera River, Russia, ×10; b, longitudinal section with well-defined, outer, cellular layer and inner, exhalant, canal cluster, Silurian beds, Vishera River, Russia, FM PE39869, ×10; c, weathered sample with transverse and longitudinal sections through branched specimens, Silurian limestone, Taylor Mountain D-2 Quadrangle, southwestern Alaska, CUG 83RB40, ×2 (Rigby & others, 1994; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).
- Uvacoelia Kügel, 1987, p. 146 [\*U. schellwieni; OD]. Catenulate to glomerate, circular chambers arranged around prosiphonate, central canal or spongocoel; outer, chamber walls not perforated by pores, but each chamber connected to central canal through apopore; growth of new chambers sometimes resulting in lateral displacement of wedges of older chambers. Carboniferous (Pennsylvanian): Aus--FIG. 440, 1a-c. \*U. schellwieni, Auernig tria.beds, Westphalian-Stephanian, Carnic Alps; a, holotype section of spherical chambers with elongate exaules and coarse endopores to central spongocoel, SPIE GP 54, ×5; b, longitudinal section of spherical chambers with elongate exaules, SPIE GP54, ×3; c, generalized restoration, not to scale (Kügel, 1987; courtesy of Facies).

## Subfamily VESICOCAULIINAE Senowbari-Daryan, 1990

[Vesicocauliinae SENOWBARI-DARYAN, 1990, p. 120]

Spiciid sponges with catenulate arrangements of their chambers. *Triassic*.

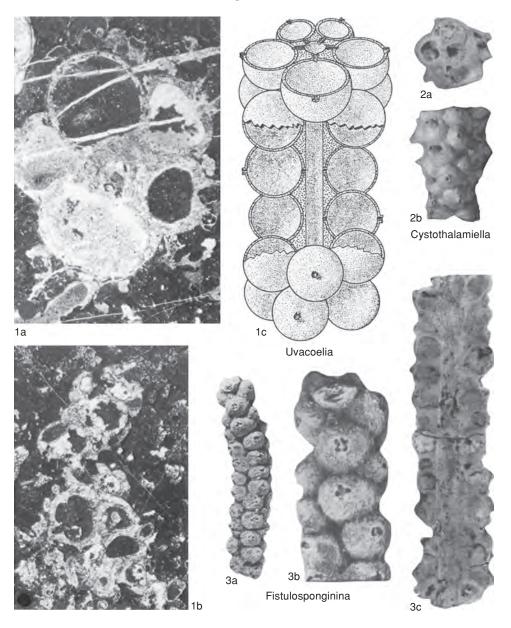


FIG. 440. Aphrosalpingidae (p. 667-668).

Vesicocaulis OTT, 1967a, p. 25 [\*V. alpinus; OD]. Hemispheroidal segments overlapping in chains; exowall imperforate except for sievelike groups of small exopores, each group underlain by a plaque of trabecular tissue (perhaps a cribribulla-like structure); endowall of narrow, central cloaca surrounded by, and continuous with, broad zone of similar trabecular tissue, whose meandriform, anastomosing, small canals tend to run parallel with cloaca, but also opening into it as small, circular endopores, and also communicate with lumen of chamber; remainder of lumen filled with small, thin-walled vesicles that are elongate parallel to exowall; interwall a continuation of exowall of preceding chamber; microstructure unknown; no spicules known. *Triassic:* Austria, Carpathian region, Czech Republic, Slovakia, Italy (Dolomite Alps, Sicily), Greece, Yugoslavia, Hungary.——FiG.

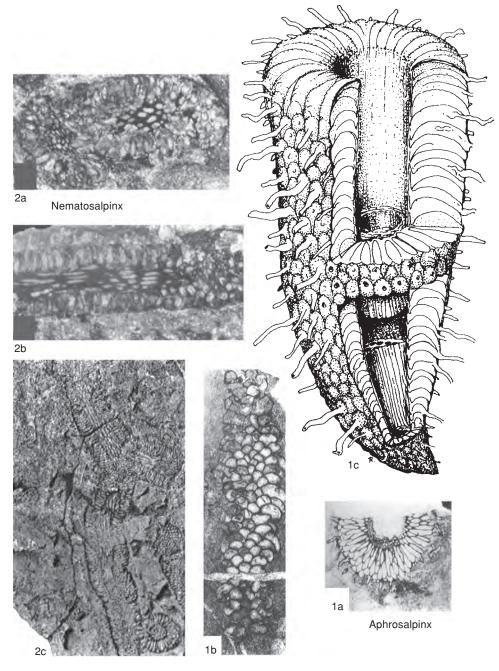


FIG. 441. Aphrosalpingidae (p. 668).

442, *1a–b.* \*V. alpinus, Wettersteinkalk, Ladinian, Karwendel, Austria; *a*, holotype, oblique section through older chambers, filled with vesiculae, and narrow, tubular spongocoel, blanketed with anastomosing, small canals, chamber walls with sievelike

clusters of exopores, A 161 a/67,  $\times$ 5; *b*, transverse section through parts of two chambers filled with vesiculae around narrow, axial spongocoel, and with cribribulla-like pore clusters in upper exowalls, A 161 a/67,  $\times$ 5 (Ott, 1967a; courtesy of *Neues* 

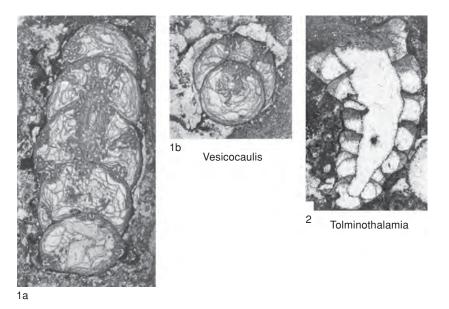


FIG. 442. Aphrosalpingidae (p. 669-671).

Jahrbuch für Geologie und Paläontologie, Monatshefte).

- Russospongia SENOWBARI-DARYAN, 1990, p. 125 [\*Cryptocoelia lupensis SENOWBARI-DARYAN, 1980, p. 182; OD]. Aporate, stemlike sponges with hemispherical chambers in catenulate arrangements; stems with a possible pro- or retrosiphonate spongocoel that extends through entire length of sponge; chambers or segments containing possible septal to trabecular, filling structures; both wall and filling structures have lamellar microstructure; isolated-appearing ostia are common in basal parts of segments; vesiculae also occur; microstructure and spicular skeleton are unknown. [Russospongia differs from Vesicocaulis OTT in having laminate-appearing septal to reticulate, filling structures and from other similar-appearing sponges in having aporate, chamber walls and radially arranged, filling structures.] Triassic (Norian-Rhaetian): Italy (Sicily) .-–Fig. 443,2a-b. \*R. lupensis (SENOWBARI-DARYAN), Triassic reef limestone; a, holotype, longitudinal, cylindrical section of chambers with septal to trabecular, filling structures, Cozzo de Lupo, SPIE P/184, ×2; b, transverse section showing thin, chamber walls and radial, septal, filling structures, Piano di Bataglia, Sicily, SPIE P/438/1, ×2 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).
- Tolminothalamia SENOWBARI-DARYAN, 1990, p. 123 [\*Girtyocoelia carnica SENOWBARI-DARYAN, 1981, p. 109; OD]. Aporate sponges with a retrosiphonate spongocoel with very thin, perforated walls; segment interwalls thicker that outer ectowalls; ostia hardly developed; microstructure of skeleton probably irregular; spicular skeleton not known. Triassic

(Carnian): Italy (Sicily), Yugoslavia (Slovenia). FIG. 442,2. \*T. carnica (SENOWBARI-DARYAN), reef limestone, Huda Juzna, Yugoslavia; longitudinal section with large, thin-walled spongocoel and chambers with somewhat thicker, largely imperforate walls, SPIE thin section 13, ×5 (Senowbari-Daryan, 1990, courtesy Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

Yukonella Senowbari-Daryan & Reid, 1987, p. 900 [\*Y. rigbyi; OD]. Sphinctozoans with catenulate chambers around an ambi- to prosiphonate, central canal consisting of several small canals; some ostia, but not pores, present in outer or ectowall of sponge, but pores are abundant in chamber interwalls; chambers lack filling structures, although a few vesiculae may be present. Triassic (Norian): Canada (Yukon).—FIG. 443,1a-b. \*Y. rigbyi, Lime Peak reef, Lake Laberge area; a, longitudinal section showing porous, chamber interwalls that become imperforate toward exterior, and bundled, exhalant tubes in axial area (top to left), GSC 74608, ×2; b, generalized reconstruction showing dermal surface and skeletal and canal development, not to scale (Senowbari-Daryan & Reid, 1987; courtesy of Canadian Journal of Earth Sciences).

## Subfamily PALAEOSCHADINAE Myagkova, 1955

[*nom. transl.* FINKS & RIGBY, herein, *ex* Palaeoschadidae MYAGKOVA, 1955a, p. 480]

Skeletons with double-layered, thickwalled chambers in which outer layer is

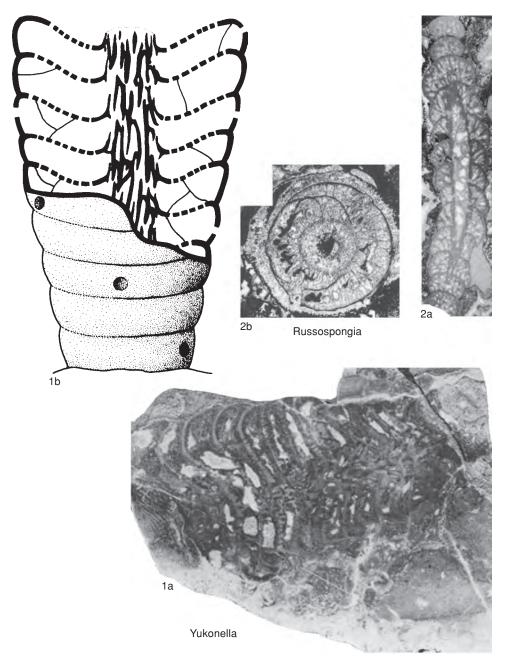


FIG. 443. Aphrosalpingidae (p. 671).

distinctly porous but inner, laminated layer largely lacks pores. *Silurian (Ludlow)*.

Palaeoscheda MYAGKOVA, 1955a, p. 480 [\**P. crassimuralis;* OD]. Irregularly steeply obconical to cylindrical sphinctozoans with one layer of globose,

upwardly arcuate, cystlike chambers around irregular, central tube of several exhalant canals; interwalls and ectowalls double layered with inner, dense layer with only fine, scattered pores, but outer layer with coarse, abundant pores; ectowalls with large, circular ostia from which intertubes extend irregularly

# Agelasida

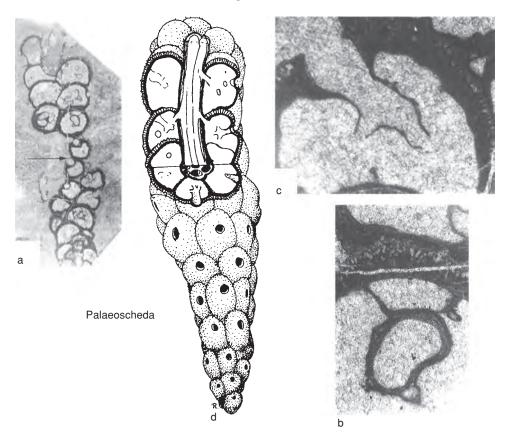


FIG. 444. Aphrosalpingidae (p. 672-673).

into chamber interiors and possibly branch; exaules not developed; endopores obscure to irregular. [The outer layer of chamber walls has coarse pores, but thin sections indicate that these do not penetrate the dense, inner, microcrystalline layer. For this reason the subfamily and genus are tentatively placed here among the aporous sponges but into a distinct subfamily.] Silurian (Ludlow): Russia (northern Urals), USA (southeastern Alaska), Canada (?Northwest Territories).-FIG. 444a-d. \*P. crassimuralis, Heceta Formation, Prince of Wales Island, southeastern Alaska; a, nearly complete, longitudinal section showing globose chambers around spongocoel, in lower part, with intertube connections and ostia (arrow) in chamber walls,  $\times 2$ ; b photomicrograph of coarsely porous interwall, with later added, laminated, upper and lower layers, and vesicula or intertube section below, ×20; c, photomicrograph of intertube interrupting interwall, CUG SB3-7EFL1-90, ×25; d, generalized reconstruction showing relationships of canals to globose chambers, not to scale (Rigby & others, 1994; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).

## Family GLOMOCYSTOSPONGIIDAE Rigby, Fan, & Zhang, 1989

[Glomocystospongiidae RIGBY, FAN, & ZHANG, 1989a, p. 436; *emend.*, FINKS & RIGBY, herein]

Spheroidal to hemispheroidal, aporate chambers arranged in sheets about cavaedial, or perhaps differentiated inhalant and exhalant, spaces with which they communicate by a pore; occasionally, adjacent chambers may communicate by a similar pore, but there are no other pores. [The Triassic *Henricellum* WILCKENS, 1937, was included by the original authors of the family, in addition to the type genus. It, however, does not have the peculiar cavaedial spaces seen in *Glomocystospongia*, and shows more resemblance to the Girtyocoeliidae, with which it is here included (RMF).] *Permian (Lopingian)*.

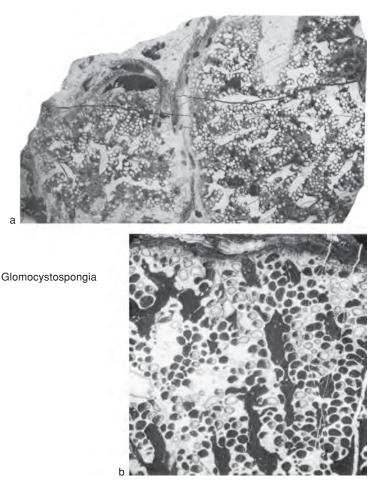


FIG. 445. Glomocystospongiidae (p. 674).

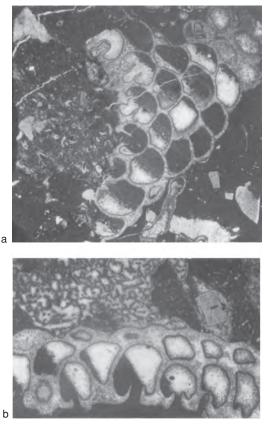
Glomocystospongia RIGBY, FAN, & ZHANG, 1989a, p. 436 [\*G. gracilis; OD]. Sponge massive, explanate or branching-cylindrical, containing subparallel, slitlike, occasionally anastomosing, or dendritic and somewhat radially arranged, possible cavaedial spaces, between which are anastomosing sheets of small, hemispheroidal chambers; convex surfaces of chambers face outwardly and upwardly; each chamber opens by a single, large pore into nearest cavaedial space; very rarely chambers communicate with an adjacent one by a single pore; there are no other pores. [There is a suggestion that spaces may be differentiated into inhalant and exhalant systems, rather than being cavaedia, because some extend radially in from the exterior and end blindly, while other, interior ones are centripetally dendritic, as if exhalant; this is supported by the presence of vesicle-like partitions in some dendritic spaces similar to those that close off disused parts of a cloaca; if so, there must be two openings in each chamber. A referred specimen from Tunisia (SENOWBARI-DARYAN & RIGBY, 1991) contains oxea-like spicules

embedded within the sclerosomal skeleton; they are radial with respect to the sponge, therefore parallel to the surface in the cavaedial walls, but perpendicular and protruding in the chamber walls. The spicules, now calcified or pyritized, are inferred to have been originally siliceous.] Permian (Lopingian): China (Sichuan), Tunisia.-FIG. 445a-b. \*G. gracilis, Changxing Formation, Changhsingian, Sichuan; a, irregular growth form of glomerate chambers around coarse, inhalant-exhalant openings in hemispherical, possibly lobate, branched holotype, ×2; b, photomicrograph showing small, clustered chambers, each with one opening, in single layer around coarse, inhalant-exhalant openings in holotype, IGASB 4021, ×5 (Rigby, Fan, & Zhang, 1989a).

Huayingia RIGBY & others, 1994, p. 98 [\**H. glomerata;* OD]. Nodular, aggregate, foliate to tabular, composed of numerous small, crescentic chambers in vertical section and arched, triangular to spatulate or crescentic in horizontal section; walls imperforate with single large, tubular, retrosiphonate-

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Agelasida



Huayingia

FIG. 446. Glomocystospongiidae (p. 674-675).

appearing ostium per chamber; vesiculae rare within chambers; cribribulla absent. *Permian (Changhsingian):* China (Sichuan, Guizhou).— FIG. 446a-b. \*H. glomerata, Changxing Formation, Changhsingian, Huaying City, Sichuan, China; a, subhorizontal section through holotype plate showing cystose chambers with tubular ostium, in chambers on left, JS0055, ×5; b, vertical section through paratype with arcuate chambers and reflexed, ostial tube in base, JS0056, ×5 (Rigby & others, 1994).

## Family SEBARGASIIDAE de Laubenfels, 1955

[Sebargasiidae DE LAUBENFELS, 1955, p. 101; emend., FINKS & RIGBY, herein] [=Sebargasiidae DE LAUBENFELS, 1955, p. 101, partim; Sphaerosiphonidae STEINMANN, 1882, p. 163, nom. van., partim]

Cylindroid; central cloaca (retrosiphonate); small, circular, closely spaced exopores; wall microstructure spherulitic; no spicules known; vesicles may be present in chambers but not pillars or trabeculae. [Sphaerosiphonidae STEINMANN, 1882, was not based on a nominate genus.] ?Ordovician, Carboniferous-Triassic.

- Sebargasia STEINMANN, 1882, p. 171 [\*S. carbonaria; OD]. Cylindrical, superposed segments visible externally; central cloaca one-third sponge diameter; exopores small, circular, closely spaced; interwall a continuation of exowall of preceding segment with its pores; endowall in continuity with interwall of same segment (retrosiphonate) but with coarse endopores mainly near upper and lower ends of chamber; chambers empty; wall microstructure not known; no spicules known. Carboniferous (Bashkirian): Spain.-FIG. 447,6a-b. \*S. carbonaria, upper Carboniferous limestone, Sebargas, Asturia, northwestern Spain; a, side view of type subcylindrical type specimen, ×1; b, longitudinal section with chambers around tubular spongocoel with moderately coarse endopores, interwalls and exowalls with finer pores,  $\times 2$  (Steinmann, 1882).
- Amblysiphonella Steinmann, 1882, p. 169 [\*A. barroisi Steinmann, 1882, p. 170; OD] [?=Laccosiphonella Aleotti, Dieci, & Russo, 1986, p. 226 (type, Amblysiphonella merlai Parona, 1933, p. 43,

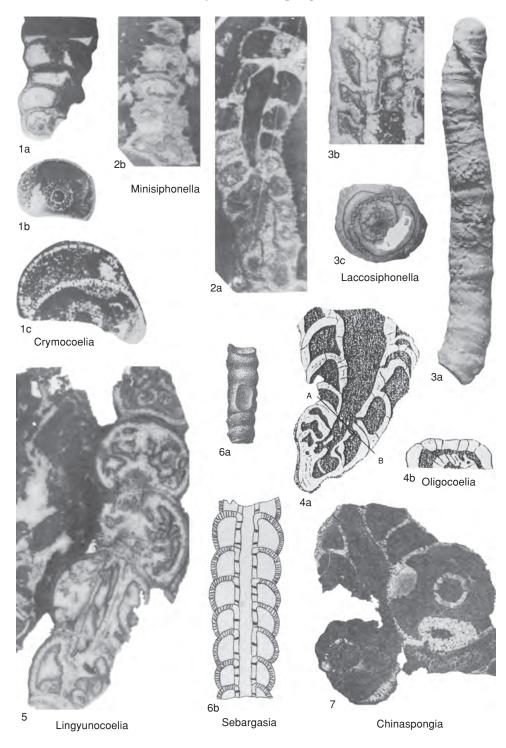


FIG. 447. Sebargasiidae (p. 675–678).

OD); ?=Sebargasia STEINMANN, 1882, p. 171 (type, S. carbonaria; OD); ?=Paramblysiphonella DENG, 1982, p. 254 (type, P. amblysiphonelloides, OD); ?=Lingyunocoelia FAN, WANG, & WU, 2002, p. 339 (type, L. spherica)]. Cylindrical, sometimes subparallel branched segments correspond externally to interior chambers that are in linear series; central cloaca about one-third sponge diameter; exowall with numerous small, circular, closely spaced exopores; interwall a continuation of exowall, below, with similar pores; endowall somewhat thinner and endopores somewhat larger and more widely spaced; interior of chamber and sometimes cloaca may contain imperforate vesicles; wall microstructure small, isodiametric spherulites that may expand asymmetrically into lumens of pore canals and chambers; no spicules known except for a single, possible triradiate (VAN DE GRAAF, 1969, pl. 2,2) that may be foreign. [Because of homeomorphy, the range and distribution are uncertain; the genus should be used only for spherulitic, aspicular forms with only vesicles, and no trabeculae, in the chamber interiors. Sebargasia STEINMANN, 1882, differs chiefly in its fewer, larger endopores, and its smaller exopores; it should probably be considered a junior (page priority) synonym.] ?Cambrian, ?Ordovician, Carboniferous-Triassic: Australia, ?Cambrian; USA (California), ?Ordovician; Kyrgyzstan, Carboniferous; Spain, China, Austria, Bashkirian, Moscovian; USA (Texas), Upper Pennsylvanian; Japan, China, USA (Texas, New Mexico), Tunisia, Italy (?Sicily), Oman, Tajikistan, Armenia, Permian; USA (Oregon), Italy (Sicily), Greece, Iran, Indonesia, China, Peru, Tajikistan, Russia (Caucasus region), Triassic.—FIG. 448,2a-b. \*A. barroisi, Carboniferous limestone, Sebargas, Asturia, northwestern Spain; a, side view of type specimen, ×1; b, longitudinal section showing porous chambers with scattered vesiculae, around perforate tubular spongocoel, exowalls and interwalls are also finely and uniformly perforate, ×2 (Steinmann, 1882).

- Chinaspongia BELYAEVA, 2000, p. 156 [\*C. fani; OD]. Catenulate sponge, porate, forming colonies where adjoining sponges, at a particular phase in development, have common outer walls; in addition to central tubes, lateral ones pass through two or three neighboring chambers; locally these are contiguous with the outer chamber wall. *Permian (Lopingian):* China.——FIG. 447,7. \*C. fani, Maokou Formation, Tonglu, Zhejiang Province; holotype, diagonal section through two subcylindrical branches, each with prominent, central tube and branched, lateral tubes, thin, chamber walls with common, circular, inhalant ostia, FEGI no. 15-MB, thin section 21(1), ×2 (Belyaeva, 2000).
- Crymocoelia BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 118 [\*C. zacharovi; OD]. Uniserial, chambered sponges, subcylindrical lower part and globose upper chambers; retrosiphonate central canal with thin, inner, perforate layer surrounded by outer layer of thin-walled, convergent, exhalant canals to make complex wall; porous

chamber interwalls nearly flat but downflexed near margins where walls overlap; walls porous and relatively thin; early chambers with vesicular filling structures, later ones hollow but uppermost ones with reticular, skeletal material from walls; microstructure with granular, relict texture. Permian (Wordian-Capitanian): Russia (Ukraine).--Fig. 447,1a-c. \* C. zacharovi, Midian, Crimea, River Marta; a, near-vertical section showing uniserial growth form, MFGI 923-5 3a; b, transverse section showing porous exowall of axial spongocoel, MFGI 923-8 4a, ×1; c, oblique section showing porous exowalls and interwalls, with porous, thick endowall of spongocoel in lower center, MFGI 923-5 1, ×2 (Boiko, Belyaeva, & Zhuravleva, 1991).

- ¿Laccosiphonella ALEOTTI, DIECI, & RUSSO, 1986, p. 226 [\*Amblysiphonella merlai PARONA, 1933, p. 43; OD]. Cylindrical; externally segments correspond to low, superposed chambers; cloaca approximately one-third sponge diameter; exopores, interpores, and endopores subequal, small, and closely spaced; endowall thick, in which endopores form short canals that may possibly anastomose; vesicles may be present in chambers; microstructure unknown; no spicules observed. [The only characters that may distinguish this from Amblysiphonella STEINMANN, 1882, assuming the microstructure to be spherulitic aragonite, are the thick endowall and the possibly anastomosing endoporal canals. Anastomosing, poral canals (in all walls), however, are seen in wellpreserved specimens of many sphinctozoan genera, especially if the wall is thick. The thickened endowall is probably not appropriate by itself as a generic distinction.] Permian: Italy (Sicily) .--—Fig. 447, 3a-c. \*L. merlai (PARONA), Permian limestone, Palazzo Adriano, Sosio; a, side view of cylindrical type specimen with weak annulae that correspond to chambers in interior, ×1; b, longitudinal section showing thick, porous endowall of spongocoel and chambers in outer part; c, transverse section showing thin, chamber walls and thick wall of spongocoel, ×2 (Parona, 1933).
- Lingyunocoelia FAN, WANG, & WU, 2002, p. 339 [\*L. spherica; OD]. Moniliform sponge of stacked, spheroidal chambers with an axial spongocoel or cloacal tube; chamber interiors filled with vesiculae or irregular filling material; neither exowalls nor endowalls of central tube have well-defined pores, exowalls also lack tubular exauli. [Lingyunocoelia has the general form of Amblysiphonella or Girtyocoelia with spheroidal chambers and a central, tubular cloaca or spongocoel. Lingyunocoelia is reported to lack pores in both the exowalls and endowalls of the skeleton, but those structures may have been lost because of diagenesis, for faint impressions of pores in both the exowall and endowall are visible in the published figure of the holotype. The holotype appears strikingly similar to Amblysiphonella merla PARONA, 1933.] Permian (Guadalupian): China (Guangxi).-FIG. 447,5. \*L. spherica, Maokou Formation; subvertical section of holotype showing stacked, linear series of spheroidal chambers and axial, central tube, with filling structures in

chambers, faint pores showing in both exowalls and endowalls, particularly in lower chambers, JO651-2, ×2 (Fan, Wang, & Wu, 2002).

- Minisiphonella BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 149 [\*M. cribrata; OD]. Catenulate, chambered colonies in which round to subspherical chambers are very small; axial canal siphonate; outer surface of chambers with distinctive, horizontal ribs. Triassic: Tajikistan.--Fig. 447,2a-b. \*M. cribrata, Triassic limestone, Norian, southeastern Pamir; a, somewhat oblique, longitudinal section of small sponge showing stacked chambers with siphonate, axial spongocoel; coarse, exhalant ostia and finer, more common, inhalant canals in ribbed outer wall, MIGT 191-10 116/50, ×10; b, tangential, vertical section through chamber walls showing ribbed exterior and simple, inhalant ostia throughout walls, MIGT 191-11 116-51, ×10 (Boiko, Belyaeva, & Zhuravleva, 1991).
- Oligocoelia VINASSA DE REGNY, 1901, p. 17 [\*O. zitteli VINASSA DE REGNY, 1901, p. 18; OD]. Conical, curved, not segmented externally; broad, upwardly expanding, central cloaca; some segments possibly incompletely toroidal; exowall bearing small, closely spaced, circular exopores; interwall an upward continuation of exowall, but interpores may be larger and more widely spaced than exopores; endowall a downward continuation of interwall (retrosiphonate) with endopores similar to possible interpores; chamber interior empty; microstructure unknown; spicules not known. Triassic (Carnian): Hungary. FIG. 447, 4a-b. O. zitteli, Veszprém, Jeruzsálemhegy; a, longitudinal section showing form of sponge, its chambers, and central spongocoel, all with thick walls,  $\times 2$ ; b, transverse section showing pores in outer wall and spongocoel wall, along line A-B of view a,  $\times 2$  (Vinassa de Regny, 1901).
- ?Paramblysiphonella DENG, 1982, p. 254 [\*P. amblysiphonelloides; OD]. Straight, cylindrical sponge with more or less annulate exterior produced by subequal chambers, all pierced by central spongocoel; upper wall of each chamber strongly arched upwardly but locally laterally discontinuous in longitudinal sections; wall perforated by numerous small pores, almost circular in cross section; outer walls also pierced by small canals; vesiculae not developed. [Whether this genus is distinct from Amblysiphonella is questionable. A new, detailed description to better document its morphology is necessary (SENOWBARI-DARYAN, 1990, p. 63).] Permian (Cisuralian): Tibet.—FIG. 448,4a-b. \*P. amblysiphonelloides; a, longitudinal section showing broad spongocoel and chambered walls with discontinuous chamber interwalls, NIGPAS 35355; b, transverse section with large spongocoel and some interrupted chamber walls, NIGPAS 35356, ×1 (Deng, 1982).
- Polycystocoelia ZHANG, 1983, p. 11 [\*P. huajiaopingensis; OD] [=Sinocoelia ZHANG & FAN in FAN & ZHANG, 1985, p. 15 (type, S. lepida, OD); Stromatocoelia ZHANG & FAN in FAN & ZHANG, 1985, p. 16 (type, S. asiatica ZHANG & FAN in FAN & ZHANG, 1985, p. 17, OD)]. Cylindrical to cup

shaped to single or branched stems with retrosiphonate, central spongocoel, which may be poorly developed; superposed chambers flattened and caplike, arranged with scalelike appearance; vesiculae and filling structures absent; walls of single layer pierced by numerous interpores and exopores, but coarser ostia not present. Permian (Lopingian)-Triassic (Norian): China (Guangxi), Tunisia, Canada (Yukon), Russia, Lopingian; Tajikistan, -FIG. 449, 1a-b. \*P. huajiaopingensis, Norian.— Changxing Formation, Changhsingian, Lichuan, Hubei, China; a, holotype section with spongocoel in upper part and remainder with coarsely perforate interwalls and exowalls, 0148, ×1.5 (Fan & Zhang, 1985); b, characteristic interwalls pierced by moderately coarse interpores, thin, netlike endowall showing in upper left and exowall on right, IG5070, ×10 (Rigby, Fan, & Zhang, 1989a).

- Pseudoamblysiphonella SENOWBARI-DARYAN & RIGBY, 1988, p. 186 [\*P. polysiphonata; OD]. Conicocylindrical series of superposed, toroidal to fusiform chambers; segmentation visible externally; four to six narrow cloacae clustered in axial region and generally of circular, cross section; exopores small, closely spaced, and circular to submeandriform; exowall curving inwardly at top of chamber to form interwall, which may be partially doubled by succeeding chamber exowall; chambers filled with trabecular tissue that outlines anastomosed tubes that converge dendritically inwardly and upwardly to enter one of axial cloacae; trabeculae appear to be absent from peripheral part of each chamber; microstructure unknown; no spicules known. [This genus differs from Fissispongia KING, 1938, in the larger number of axial cloacae (although rare individuals of Fissispongia have multiple cloacae), in the apparent absence of larger lipped exopores, and in the toroidal form of the chambers.] Permian (Lopingian): Tunisia.-FIG. 448, 3a-c. \*P. polysiphonata, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; a, holotype of ringlike, partially agglomerate chambers, USNM 427307, ×2; b, paratype, transverse section showing branched tubes in interior and perforate exowall, USNM 427309, ×5; c, restoration showing ringlike chambers with branched canals and multiple, exhalant, axial canals, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).
- Pseudoguadalupia TERMIER & TERMIER, 1977a, p. 40 [\*Guadalupia alveolaris PARONA, 1933, p. 49; OD]. Cylindrical sponge composed of superposed, spheroidal chambers; central cloaca approximately onethird sponge diameter; outer surface of exowall bearing closely spaced, circular to polygonal pits with large, circular exopore at bottom of each pit; entire exowall microporous with fine, circular pores; interwall questionably double (i.e., two exowalls in contact); interpores similar to exopores; endopores circular, widely spaced, larger than large exopores; vesicles and small, spherical bodies (as in Intrasporeocoelia FAN & ZHANG, 1985) may be present in chambers; microstructure not known; no spicules known. [Genus is similar to

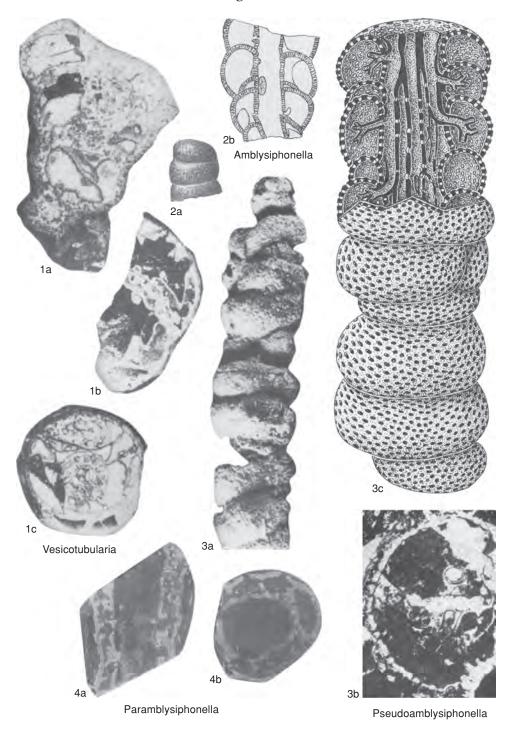


FIG. 448. Sebargasiidae (p. 675–681).

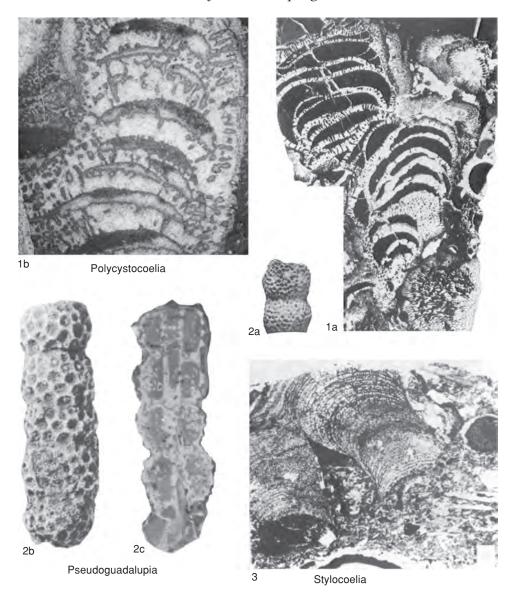


FIG. 449. Sebargasiidae (p. 678-681).

Amblysiphonella STEINMANN, 1882, except for the surface pits.] Permian: Italy (Sicily), Tunisia.— FIG. 449,2a-c. \*P. alveolaria (PARONA); a, side view of small, two-chambered, type fragment with surficial pits and coarse exopores, Permian limestone, Palazzo di Adriano, Sosio, Sicily, ×1 (Parona, 1933); b, side view of characteristic specimen with coarse exopores inside external pits in catenulate, small sponge, Djebel Tebaga reef, Lopingian, Djebel Tebaga, Tunisia, USNM 427381, ×4; c, polished, vertical section showing prominent, central tube and well-defined chambers, Djebel Tebaga reef, Lopingian, Djebel Tebaga, Tunisia, USNM 427383, ×2.5 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Stylocoelia WU Ya Sheng, 1991, p. 86 [\*S. circopora; OD]. Sponges cylindrical, of stacked, low chambers with perforate walls; central spongocoel narrow with perforate walls, chambers with pillar-filling structures that are normal to walls and confined to chambers. Permian (Kungurian): China (Guangxi, Guizhou), Italy (Sicily).—FIG. 449,3. \*S. circopora, Maokou Formation, Reef of Xiangbo, Kungurian, Longlin, Guangxi, China; longitudinal

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section showing low chambers with pillar-filling structures, IGASB xb31-2-1, ×2 (Wu Ya Sheng, 1991).

Vesicotubularia BELYAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 116 [\*V. prima; OD]. Catenulate, chambered sponges with porous walls; chambers initially infilled with vesiculae and later with vesicle-like canals; central spongocoel possibly retrosiphonate and infilled with reticulate tissue; vesiculae participate in construction of chamber walls. [Vesicotubularia is similar to Vesicocaulis OTT, in having all porous walls and vesicle-like canals.] Permian: Russia (Ukraine).—FIG. 448, 1a-c. \*V. prima, Permian limestone, Wordian-Capitanian, Crimea, River Marta; a, vertical section showing growth form and large chambers, MFGI 923-8, 2g,  $\times 2$ ; b, section of exowalls and interwalls showing canals and some vesicular filling structures, MFGI 923-8, 4a, ×5; c, transverse section with vesicular filling structures, MFGI 923-8, 2a, ×5 (Boiko, Belyaeva, & Zhuravleva, 1991).

## Family OLANGOCOELIIDAE Bechstädt & Brandner, 1970

[Olangocoeliidae BECHSTÄDT & BRANDNER, 1970, p. 67]

Spherical aporate chambers, with overlapping to irregularly isolated walls, in series that outline and enclose both spinelike canals or openings. *Middle Triassic*.

Olangocoelia BECHSTÄDT & BRANDNER, 1970, p. 67 [\*O. otti; OD]. Spherical, overlapping, attached to isolated, thin-walled chambers, with sizes measured in millimeters, chambers with isolated pores. [Chambers may also be bound together by stolenlike tubes, according to SENOWBARI-DARYAN (1990, p. 133), who also concluded that the poriferan nature of the fossils is uncertain. Classification with the Foraminifera cannot be ruled out.] Middle Triassic: Italy.——FIG. 450,5a-b. \*O. otti, Olanger Dolomite, upper Anisian, southern Tyrols, Austria; a, holotype, thin section showing sections through thin-walled, irregular chambers filled and surrounded by dark matrix, GII thin section III 17, approximately ×2; b, tangential slice through chambers showing irregular nature of chamber walls, ×20 (Bechstadt & Brandner, 1970; courtesy of Institute für Geologie und Paläontologie, Universitet Innsbruck).

## Family CLIEFDENELLIDAE Webby, 1969

#### [Cliefdenellidae WEBBY, 1969, p. 655]

Sphinctozoans with low, flat to convexupward chambers with imperforate walls; interwalls penetrated by continuous, subvertical, porous, pillarlike tubes; complex, astrorhizae-like, clustered, excurrent, canal system separate from pillarlike, incurrent system and occurring between thin, imperforate interwalls; skeletons of aspicular calcium carbonate (RIGBY & POTTER, 1986, p. 41). *Middle Ordovician–Upper Ordovician*.

- Cliefdenella WEBBY, 1969, p. 655 [\*C. etheridgei; OD]. Sphinctozoan sponges composed of low, platelike, hollow chambers with imperforate interwalls pierced by porous, vertical, pillarlike tubes produced by downward deflection of interwall in retrosiphonate-like, incurrent, canal system; excurrent system or astrorhizal-like canals that converge laterally from chambers and curve vertically into clusters of subvertical, tubelike openings; vertical, incurrent and excurrent tubes not interconnected; vesiculae may occur in early chambers, vertical, porous, incurrent tubes, and in excurrent canals; interwalls may be three layered, with lower and upper, clear layers separated by a medial, dark layer; upper surface commonly denticulate (RIGBY & POT-TER, 1986, p. 41). Middle Ordovician-Upper Ordovician: Australia (New South Wales), USA (Alaska).---FIG. 451a-c. \*C. etheridgei, Cliefden Caves Limestone, Caradoc, Belubula River, New South Wales, Australia; *a*, holotype with prominent, coarse, exhalant, canal clusters through platelike chambers whose interwalls are also pierced by smaller, inhalant canals, SUP 24157, ×4; b, transverse section of part of paratype across exhalant, canal cluster with convergent canals, SUP 24154, ×4; c, transverse section of part of paratype with coarse, exhalant opening and numerous small, inhalant, pillarlike canals through chambers, SUP 24155, ×4 (Webby, 1969).
- Khalfinaea WEBBY & LIN, 1988, p. 152 [\*K. sinensis; OD]. Conicocylindrical or rarely branching, aporate sphinctozoan with low and elongate, gently upwardly arched and stacked chambers, bounded by narrow, ringlike, imperforate exowalls and laminar, uparched interwalls; upper surfaces of interwalls may be denticulate and locally downwardly inflected into regular, nearly vertical, continuous, sometimes porous, incurrent tubes; single, large, central, excurrent tube defined by thickened endowall pierced by small tubes, giving a honeycomb-like appearance; infilled with irregular mesh of primarily randomly oriented, astrorhizal canals of varying sizes, and secondary vesiculae and other thickened (trabecular) tissue, suggesting successive, rather complex, growth interrelationships; vesiculae developed in chambers, incurrent canals and central tubes hollow, rootlike, bracing structures not known. [Khalfinaea is similar to Rigbyetia but has a large, central, excurrent tube with irregular, labyrinthine, astrorhizal canals, vesiculae, or trabecular filling tissue, and is bounded by a well-defined endowall.] Upper Ordovician: China (Xinjiang, Shaanxi), Russia (Altai Sayan).—FIG. 452a-b. \*K. sinensis, Bulongor Formation, Ashgill, Bulongor River, Xinjiang, China; a, longitudinal section showing upwardly arched chambers with honeycomb-like endowall defining a central tube and

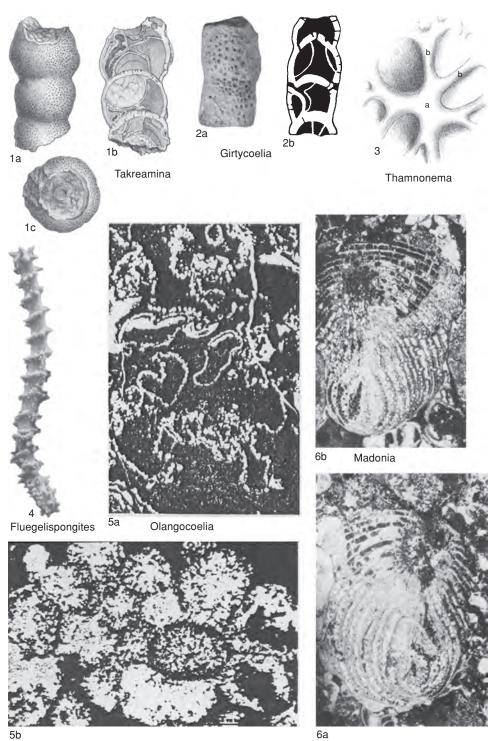


FIG. 450. Olangocoeliidae, Girtycoeliidae, and Uncertain (p. 681–691).

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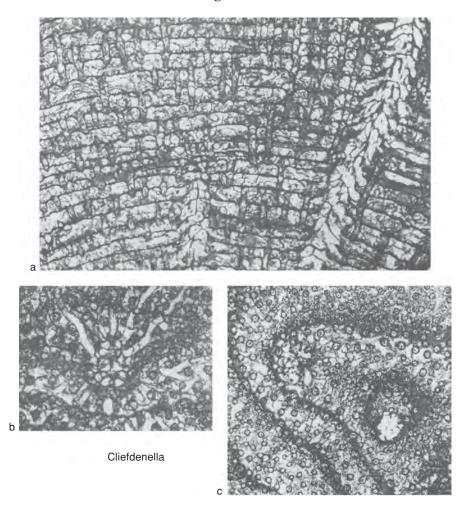


FIG. 451. Cliefdenellidae (p. 681).

with downwardly flexed, inhalant tubes, IGP 18, ×4; *b*, transverse section of paratype with central, exhalant cluster and prominent, central tube surrounded by thick walls of ringlike chambers with vesiculae and other filling structures, with sections of radial, inhalant canals, IGP 21, ×3 (Webby & Lin, 1988).——FIG. 452*c. K. shaanxiensis* WEBBY & LIN, Beiguoshan Formation, Ashgill, Longxian County, Shaanxi, China; longitudinal section of holotype with axial spongocoel surrounded by low chambers with imperforate exowalls, with fine vesiculae and downwardly inclined, inhalant canals, IGP 1, ×4 (Webby & Lin, 1988).

Rigbyetia WEBBY & LIN, 1988, p. 152 [\**Cliefdenella* obconica RIGBY & POTTER, 1986, p. 42; OD]. Obconical to subcylindrical, occasionally branching, aporate sphinctozoan; chambers of low, ringlike, annulated appearance with imperforate exowalls; laminate, gently domed, imperforate interwalls with upper surfaces denticulate and lo-

cally downwardly inflected into vertical to subvertical, porous, incurrent tubes, internally; single, large, central tube of vertically continuous clusters of astrorhizal-like, excurrent canals; this seemingly interconnected with radiating, nearly horizontal, astrorhizal canals of chambers; no clearly defined endowall or endopores developed; vesiculae small and only rare in chambers, not developed elsewhere; hollow, rootlike, bracing structure may be developed. Upper Ordovician: USA (Oregon, California), Australia (New South -FIG. 453a-d. \*R. obconica (RIGBY & Wales).-POTTER), Horseshoe Gulch limestone, Ashgill, Horseshoe Gulch, Klamath Mountains, California; a, side view of exterior of branched holotype with annulate, aporous, dermal layer, ×2; b, other side of holotype with clearly defined, low chambers pierced by tubular, inhalant system where dermal layer has been removed, USNM 395897, ×2; c, view from below of chamber interwall with central cluster of

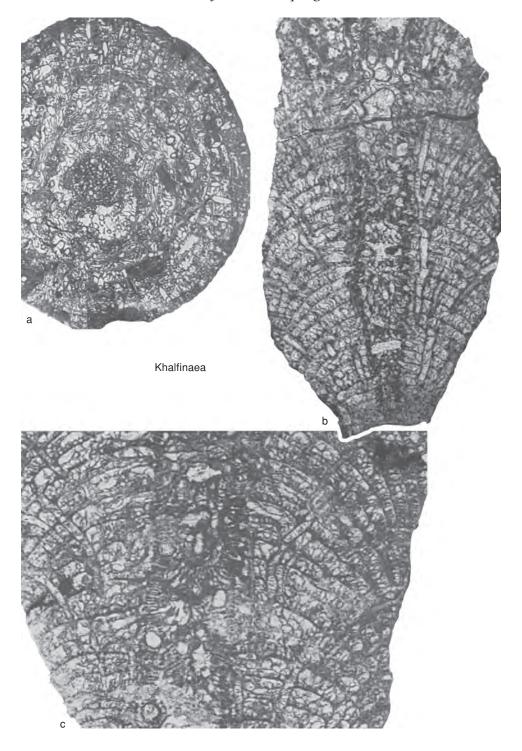


FIG. 452. Cliefdenellidae (p. 681–683).

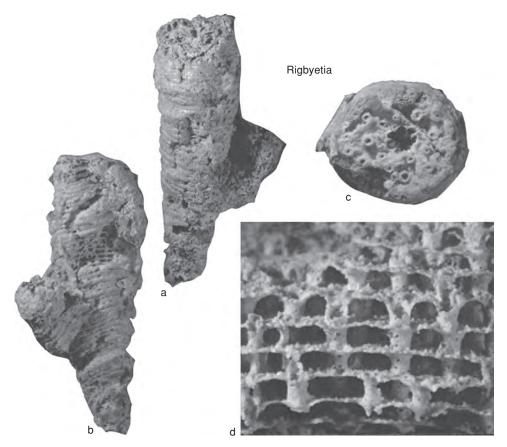


FIG. 453. Cliefdenellidae (p. 683-685).

exhalant canals surrounded by rings of smaller, inhalant canals, USNM 395903, ×5; *d*, enlarged view of paratype showing horizontal interwalls pierced by reflected, inhalant canals, BMNH S10169, ×10 (Rigby & Potter, 1986).

## Family GIRTYCOELIIDAE new family

[Girtycoeliidae FINKS & RIGBY, herein] [type genus, *Girtycoelia* KING, 1933, p. 79]

Cylindroid; cloaca absent; superposed chambers with small, closely spaced, circular exopores; primary walls composed of small (20 to 50  $\mu$ m in *Girtycoelia*) isodiametric spherulites; a secondary lamellar, possibly clinogonal, lining inside of chambers, continuous with vesicles associated with distal withdrawal of sponge tissue from chambers. *Carboniferous (Upper Pennsylvanian)– Triassic.* 

Girtycoelia KING, 1933, p. 79 [\*G. typica; OD]. Spheroidal or hemispheroidal, subequal segments in lin-

ear series that frequently produce subparallel branches that may fuse laterally; no cloaca; exowall with closely spaced, small, subpolygonal to circular exopores of two sizes, as well as occasionally very large, circular ones with raised rims, usually near intersegment suture; imperforate, dermal layer often formed in patches, obliterating small exopores and forming a strong rim about very large ones; imperforate layer may be covered with fine, transverse wrinkles; interwalls continuous with exowall of underlying chamber and interpores same size as small exopores; chamber interiors may contain large vesicles subparallel to exowall and continuous with succession of secondary, imperforate deposits that line chamber interior and mark progressive, distal withdrawal of sponge tissue; walls built of small, isodiametric spherulites, secondary lining lamellar and possibly clinogonal; no spicules known. Carboniferous (Upper Pennsylvanian)-Triassic (Norian): USA (southcentral states), Upper Pennsylvanian; Italy (Sicily), Tajikistan, ?Permian; Russia (Caucasus region), Norian.-FIG. 450,2a-b. \*G. typica, Graford Formation, upper Pennsylvanian, Bridgeport, Wise County, Texas; a, side view of cotype showing porous exowalls of hemispherical chambers

in cylindrical sponge,  $\times 2$ ; *b*, tracing of polished section of cotype showing lack of central, tubular spongocoel in chambers with both exopores and interpores, and scattered vesiculae,  $\times 2$  (King, 1933).

?Takreamina FONTAINE, 1962, p. 205, nom. nov. pro Steinmannia WAAGEN & WENTZEL, 1888, p. 979, non FISCHER, 1886 [\*Steinmannia salinaria ŴAAGEN & WENTZEL, 1888, p. 980; OD] [?=Colospongia LAUBE, 1865, p. 237 (type, Manon dubium MÜNSTER, 1841, p. 28, OD); Waagenium DE LAUBENFELS, 1957, p. 249, nom. nov. pro Waagenella DE LAUBENFELS, 1955, p. 102, obj., non DE KONINCK, 1883, nec YABE & HAYASAKA, 1915]. Spheroidal, subequal segments in linear series, sometimes as subparallel branches that fuse laterally to form flabellate masses; narrow, central, circular osculum in each segment but no endowall (cloaca); exopores small, circular, closely spaced, and of two sizes; interwall a continuation of underlying exowall with its pores and osculum; chambers containing large vesicles but no other skeletal structures; microstructure unknown; no spicules known. [Except for the central osculum and the absence of the large, circular exopores, this genus resembles Girtycoelia KING, 1933. It may also be considered an Amblysiphonella STEINMANN, 1882 that lacks an endowall.] Permian-Triassic: Pakistan, Cambodia, Italy (Sicily), Tunisia, USA (?Texas), China (Guangxi), Permian; Europe, Indonesia (Timor), Triassic.-FIG. 450, 1a-c. \*T. salinaria (WAAGEN & WENTZEL), Productus Limestone, Bilote, Salt Range, India; a, side view of fragmental holotype showing porous exowall of stacked, subspherical chambers,  $\times 1$ ; b, vertical section showing irregularly distributed vesicles of different sizes and central osculum in upper chamber,  $\times 1$ ; c, view from above showing central osculum of upper chamber and porous exowalls, ×1 (Waagen & Wentzel, 1888).

### Family GUADALUPIIDAE Girty, 1909

[Guadalupiidae GIRTY, 1909, p. 79; emend., FINKS & RIGBY, herein]
[=Guadalupiidae GIRTY, 1909, p. 79, partim; Cystothalamiidae GIRTY, 1909, p. 88, partim; Tebagathalamiidae SENOWBARI-DARVAN & RIGBY, 1988, p. 192, partim; Cystauletidae BELVAEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 102, partim; Cystauletidae WU Ya Sheng, 1991, p. 87; Polycystothalamiidae WU Ya Sheng, 1991, p. 92]

Sponges consisting of a sheet (thalamidarium) of similar chambers, whose walls have closely spaced, small, circular pores; on one side of this sheet (exhalant side) is a variably developed layer (trabecularium) of delicate, anastomosing trabeculae, mostly perpendicular to surface, with cross connections, rather similar to those of a stromatoporoid, which may include astrorhizal systems converging on circular, lipped oscules; this double sheet may assume various topological forms, including cylinders, partial cylinders, open cups and palmate branches; chamber interiors hollow except for occasional diaphragms; wall composed of small (20 to 50 µm in *Guadalupia*) isodiametric spherulites. *Carboniferous–Triassic (Norian).* 

- Guadalupia GIRTY, 1909, p. 79 [\*G. zitteliana GIRTY, 1909, p. 80; OD] [=Polyphymaspongia KING, 1943, p. 24 (type, P. explanata KING, 1943, p. 25, OD); Platythalamiella SENOWBARI-DARYAN & RIGBY, 1988, p. 184 (type, P. newelli, OD)]. Auriform, cup shaped, infundibuliform, conicocylindrical, or flat, branching strips (sometimes on different parts of one individual, but also species specific); chambers of thalamidarium quincuncially arranged, elongate between exowall and endowall, cross section cuspate proximally and convex distally (similar to lava pillows), bulging outwardly on exowall (inhalant) side; chambers may be crossed internally by one or more flat, imperforate diaphragms, but otherwise hollow; size and proportions of chambers species specific and constant within individuals; trabecularium on inner or upper side of sponge (exhalant surface), with anastomosing trabeculae dominantly perpendicular to surface, causing it to be hispid; prominent, branching grooves (exhalant or astrorhizal systems) deeply sunk into trabecularium and converging on large, circular oscules with elevated rims, or sometimes on more obscure, central areas; exopores, interpores, and endopores small, circular, and closely spaced, exopores somewhat smaller, and endopores somewhat larger than interpores; interpores may be secondarily closed; microstructure of walls and trabeculae consisting of small, isodiametric spherulites; no spicules observed. [Polyphymaspongia KING, 1943, is a species of Guadalupia with large chambers. Cystothalamia GIRTY, 1909, differs from Guadalupia chiefly in its peculiar growth form; it is here maintained as a separate genus.] Permian (Wordian-Changhsingian): USA (southwestern states), northern Mexico, Italy (Sicily), China, Venezuela, Wordian-Capitanian; Tunisia, China, ?Thailand, Lopingian.-FIG. 454, 1a-c. \*G. zitteliana, Capitan Formation, Guadalupian, Guadalupe Mountains, Texas; a, side view of holotype showing subcylindrical to obconical form, ×1; b, tangential view of section through chambers, ×5; c, section longitudinally through chambers, USNM 118135, ×5 (Girty, 1909).
- ?Cystauletes KING, 1943, p. 31 [\*C. mammilosus; OD]. Long cylinders with multiple branches; broad, central cloaca; chambers quincuncially arranged about cloaca, distally convex and proximally cuspate, forming slight bulges on exterior; no diaphragms observed; exopores, interpores, and endopores small, circular, and closely spaced, approximately equal in size, but endopores more closely spaced than other pores; thin trabecularium lining cloacal surface, consisting of narrow, meandriform ridges separating similar grooves into which endopores open; microstructure small, iso-

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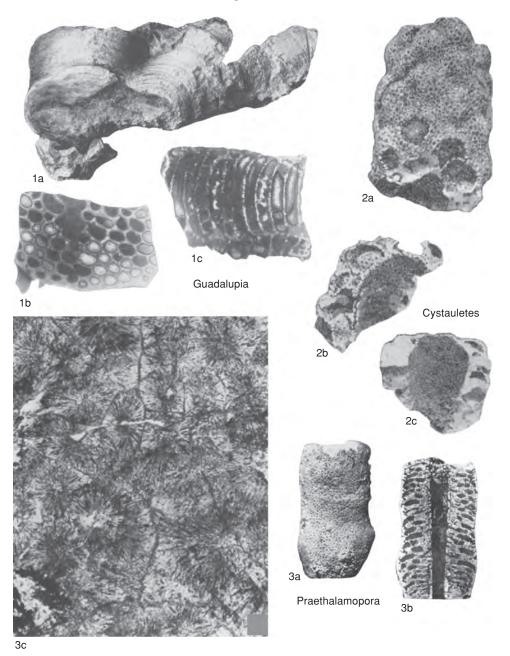


FIG. 454. Guadalupiidae (p. 686-691).

diametric spherulites; no spicules known. [Genus resembles *Discosiphonella*. SENOWBARI-DARYAN (1990, p. 56) has synonymized the two genera but *Discosiphonella* is poorly known and *Cystauletes* should be retained for tubular, branching forms (RMF).] *Carboniferous (Middle Pennsylvanian)–*  Triassic (Norian): USA (Oklahoma), Middle Pennsylvanian; Spain, Moscovian; Italy (Sicily), Japan, Cisuralian; China (Hubei), Russia, Tunisia, Changhsingian; Russia (Northern Caucasus), Norian.—FIG. 454,2a-c. \*C. mammilosus, Pawnee Limestone, Desmoinesian, Nowata, Oklahoma;

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*a*, side view of subcylindrical holotype with mammilose chamber exteriors perforated by common exopores, KU 74131, ×2; *b*, oblique section through part of spongocoel and wall, showing upwardly arcuate interwalls and porous nature of all walls in paratype, KU 74133 ×2; *c*, vertical section through large spongocoel and walls of upwardly arcuate chambers, KU 74132, ×2 (King, 1943).

Cystothalamia GIRTY, 1909, p. 89 [\*C. nodulifera; OD] [=Racemina TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977a, p. 41 (type, R. conica TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977a, p. 42, OD); Polycystothalamia WU Ya Sheng, 1991, p. 92 (type, P. sinuolata, OD)]. Branching, hollow cylinders, with a series of elliptical to slitlike openings from hollow interior along one side of cylinder, that may expand into cuplike, side branches; interior hollow space about half diameter of cylinder and lined by trabecularium; parallel, longitudinal, exhalant grooves and astrorhizal systems occasionally developing on this inner surface, in some instances forming parallel, exhalant tubes that partly or wholly fill portions of inner hollow as in Lemonea SENOWBARI-DARYAN, 1990; chambers of thalamidarium globose, making prominent bulges on exterior; exopores, interpores, and endopores small, circular, and closely spaced, endopores (exhalant) about twice size of exopores (inhalant), and interpores of intermediate size; imperforate diaphragms occasionally present in chambers that are otherwise completely hollow; microstructure spherulitic; no spicules known. [This is essentially a Guadalupia that has been rolled up to form a tube with gaps along one side. The foregoing is based upon the lectotype (USNM 118146, GIRTY, 1909, pl. 31,20; the lateral openings are present on the side not illustrated) plus numerous well-preserved topotypes and near topotypes. The Triassic species in the literature (e.g., OTT, 1967a; DIECI, ANTONACCI, & ZARDINI, 1968) without lateral openings and in which the central hollow is very narrow, possibly without a trabecularium, or in which the hollow is completely filled with a bundle of longitudinal tubes formed from the trabecularium (viz., C. polysiphonata DIECI, ANTONACCI, & ZARDINI, 1968, p. 147) should be referred to other genera. The other fragmentary and poorly preserved cotypes of GIRTY, 1909, are also probably not congeneric with the lectotype.] Carboniferous-Triassic (Ladinian): Kyrgyzstan, Carboniferous; Russia, Permian; USA (Texas), Italy (Sicily), Russia, China (Hubei), Venezuela, ?Cambodia, Guadalupian; China (Hubei, Zhejiang), Tunisia, Changhsingian; Greece, Italy (Sicily), Tajikistan, Carnian-Norian; Germany, Yugoslavia, Ladinian.—FIG. 455, 1a-b. \*C. nodulifera, Delaware Mountain Formation, Guadalupian, Glass Mountains, Texas; a, two silicified specimens showing glomerate chambers with porous walls, ×2; b, polished, longitudinal section through outer wall showing cystose chambers of wall, ×3 (Girty, 1909).-FIG. 455,1c-e. C. guadalupensis (GIRTY), Capitan Formation,

Guadalupian, Guadalupe Mountains, Texas; c, longitudinal, oblique section showing cystose chambers around central spongocoel; d, weakly annulate, cylindrical lectotype with low nodes produced by arcuate, chamber walls; e, lectotype from above showing central spongocoel and chambers of wall, USNM 118150, ×1 (Girty, 1909).

- Diecithalamia SENOWBARI-DARYAN, 1990, p. 58 [\*Cystothalamia polysiphonata DIECI, ANTONACCI, & ZARDINI, 1968, p. 147; OD]. Porate, cylindrical sponge with aragonitic, basal skeleton of irregular microstructure; outer layer of chambers with glomerate arrangement around thick bundle of vertical, axial canals; filling skeleton of reticular type only in area of bundled canals; canal structure prosiphonate; spicular skeleton not known. Triassic (Carnian): Italy, Austria, Italy (Sicily), Greece (Island of Hydra), Yugoslavia.——FIG. 456,1a-b. \*D. polysiphonata (DIECI, ANTONACCI, & ZARDINI), San Cassiano Formation, Carnian, Dolomite Alps, Italy; a, side view of paratype showing glomerate, outer chambers, IPUM 17625, ×2 (Dieci, Antonacci, & Zardini, 1968); b, longitudinal section showing outer, glomerate chambers and inner cluster of vertical, exhalant canals, G/233/1, ×5 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).
- Discosiphonella INAI, 1936, p. 169 [\*D. manchuriensis; OD] [?=Ascosymplegma RAUFF, 1938, p. 195; ?Cystauletes KING, 1943, p. 31 (type, C. mammilosus, OD); ?Lichuanospongia ZHANG, 1983, p. 8 (type, L. typica, OD)]. Sponge as restored resembles a semicircular pocket (or half a pita), long, straight edge open and presumably osculum; sides of pocket are each a thalamidarium of single layer of globose, subpolygonal chambers that bulge externally but are flat on cloacal surface; trabecularium not clearly evident but endowall thicker than exowall; interwalls consistently bulging toward aperture; exopores, interpores, and endopores are subequal and closely spaced; exopores circular but others seen only in section; cloaca traversed by irregular, imperforate partitions, mostly concave toward aperture; chambers may contain imperforate lamellae (diaphragms or possibly vesicles); microstructure unknown; no spicules known. [Genus resembles a compressed, nontubular Cystauletes KING, 1943, in which the aperture is the widest dimension. SENOWBARI-DARYAN (1990, p. 56) has synonymized the two genera but Discosiphonella is poorly known and Cystauletes should be retained for tubular, branching forms (RMF).] Carboniferous (Pennsylvanian)-Triassic (Norian): Manchuria, Pennsylvanian; Thailand, China, Sicily, Lopingian; Peru, Norian. FIG. 455, 2a-c. \*D. manchuriensis, Hsiao-shih Series, Tai-tzu-ho System, Pennsylvanian, Pen-hsihsein, Manchuria; a, side view of weathered exterior of holotype, ×1; b, transverse section near and almost parallel to osculum, ×1; c, diagrammatic restoration showing chambers and osculum at upper margin, ×1 (Inai, 1936; courtesy of Proceedings of the Imperial Academy of Japan).

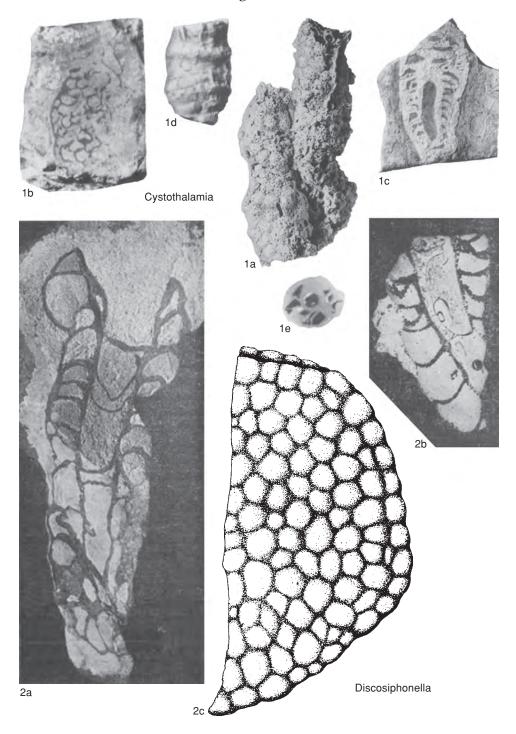


FIG. 455. Guadalupiidae (p. 688).

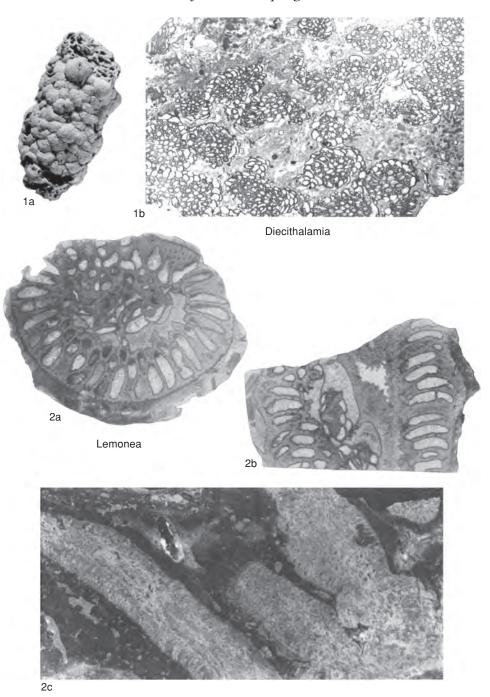


FIG. 456. Guadalupiidae (p. 688–691).

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- Lemonea SENOWBARI-DARYAN, 1990, p. 151 [\*Guadalupia cylindrica GIRTY, 1909, p. 81; OD]. Conical to cylindrical with central cloaca partly or completely filled with parallel, exhalant canals formed from expansion of trabecularium; surrounding thalamidarium as in Guadalupia GIRTY, 1909, with which this intergrades. Cystothalamia GIRTY, 1909, also may have parallel, exhalant canals partly filling cloaca. [Lemonea conica SENOWBARI-DARYAN, 1990, has multiple bundles of parallel, exhalant tubes, each bundle surrounded by a thalamidarium, but the whole forming a single, continuous, conical individual. It probably should be made a separate genus.] Permian (Wordian-Guadalupian): USA (Texas, New Mexico), Tunisia, Italy (Sicily), Yugoslavia, China.-FIG. 456, 2a-c. \*L. cylindrica (GIRTY), Capitan Limestone, Guadalupian, Guadalupe Mountains, Texas; a, transverse section of holotype showing radial chambers around broad spongocoel that contains vesiculae, ×5; b, longitudinal section showing arcuate, radial chambers and vesiculae in spongocoel, ×5 (Girty, 1909); c, polished surface with longitudinal sections of three cylindrical specimens that have characteristic chamber development in their walls and vesiculae of their broad spongocoels, USNM 35019, ×1 (Rigby, Senowbari-Daryan, & Liu, 1998).
- Praethalamopora Russo, 1981, p. 14 [\*P. zardinii; OD]. Cylindrical, chambers not apparent externally; exterior covered with small, closely spaced, circular pores; central cloaca narrow, diameter approximately one-fifth that of sponge; chamber height less than diameter; chambers more or less radially arranged around cloaca and ovoid in section (or alternatively, superposed discoid chambers subdivided by radial partitions); chamber walls perforated by pores; trabecularium not evident; microstructure spherulitic (isodiametric). Triassic (Carnian): Italy.——FIG. 454, 3a-c. \*P. zardinii, San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; a, side view of holotype exterior; b, longitudinal section with a tubular spongocoel and slightly arched chambers on margins, ×2; c, transverse section illustrating spherulitic microstructure, IPUM 19291, ×200 (Russo, 1981).

#### Family UNCERTAIN

- Fluegelispongites MOSTLER, 1994, p. 345 [\*F. trettoensis; OD]. Agelasid sponges characterized by isolated, slender, C- to S-shaped acanthostrongyles that have their spines arranged in spirals. Middle Triassic: Italy.—FIG. 450,4. \*F. trettoensis, Buchensteiner Schichten, Trettoe; isolated holotype, s-shaped acanthostrongyle with spines arranged in spiral, ×300 (Mostler, 1994).
- Madonia SENOWBARI-DARYAN & SCHÄFER, 1986, p. 251 [\**M. conica;* OD]. Porate sphinctozoan with tubular filling structure where tubes are more or less regularly developed; tubes penetrating chamber or

segment roofs and more or less bind segments together; shield-shaped, overlapping chambers arranged around retro- to pseudosiphonate spongocoel; outer segmentation barely visible. [The genus was originally included in the Polytholosidae SEILACHER but the tubes and their orientation in the chamber walls separate the genus from other forms in the family. Segment development and their structure are similar to the cliefdenellids of the Ordovician, but those forms do not have porous walls as in Madonia. For the present Madonia is considered to be of uncertain family relationship.] Triassic (Norian): Italy (Sicily).—FIG. 450,6a-b. \*M. conica, Reef limestone, Norian, Madonie Mountains, Sicily; a, transverse section of holotype showing low, shield-shaped chambers with tubular connections and central canal cut marginally in upper right, SPIE P/244/2, ×2; b, parallel, transverse section showing tubular structures well in lower part and their connections between chamber walls in upper part, SPIE P/244/1, ×2 (Senowbari-Daryan & Schäfer, 1986).

Thamnonema SOLLAS, 1883, p. 549 [\*T. pisiforme; OD]. Small, globular sponge without central cavity; skeleton a network of fibers radiating and branched upwardly from base where three equally spaced, basic fibers originate; summit with larger meshes that appear as small oscules; sides ridged meridionally. *Middle Jurasic:* England.—FIG. 450,3. \*T. pisiforme, Great Oolite, Hampton Down; arrangement of fibers of base; a, primary and, b, secondary fibers radiating from base, c, ×15 (Sollas, 1883).

# Order VACELETIDA new order

#### [Vaceletida FINKS & RIGBY, herein]

Basal skeleton of microgranular aragonite organized in small, irregular units bounded by organic membrane and with organic center, the whole forming a cortex of sphinctozoan morphology, secreted at intervals over newly formed unit of soft tissue; no spicules present in living *Vaceletia* PICKETT, 1982, but some fossils contain imbedded monaxons, as well as dubious spicules of more elaborate form; exopores usually lobate or polygonal in outline. *Lower Cambrian–Holocene.* 

# Family SOLENOLMIIDAE Engeser, 1986

[Solenolmiidae Engeser, 1986, p. 589] [=Deningeriidae Boiko, Belyaeva, & Zhuravleva, 1991, p. 156]

Superposed spheroidal segments; chambers in type genus filled with trabeculae that outline anastomosing tubes that have a dominantly upward and outward orientation (perpendicular to exowall interwall); vesicles present; microstructure microgranular aragonite as in *Vaceletia* PICKETT, 1982. *Lower Cambrian–Triassic, ?Jurassic.* 

# Subfamily SOLENOLMIINAE Senowbari-Daryan, 1990

[Solenolmiinae SENOWBARI-DARYAN, 1990, p. 89]

Solenolmid sponges with catenulate arrangements of chambers. *Lower Cambrian– Triassic, ?Jurassic.* 

- Solenolmia POMEL, 1872, p. 115 [\*Scyphia? manon MÜNSTER, 1841, p. 29; OD] [=Dictyocoelia OTT, 1967b, p. 55, obj.; Solenopsechia POMEL, 1872, p. 155, obj., nom. van.]. Cylindrical, segmented segments spheroidal to barrel shaped; central cloaca about one-third sponge diameter; exopores small, uniform, circular, closely spaced; according to POMEL (1872, p. 115) they open on projections or tubercles arranged in longitudinal rows; interpores same as exopores; endopores somewhat larger and more widely spaced; endowall thicker than exowall and interwalls; chambers filled with trabeculae that outline anastomosing tubes that have a dominantly upward and outward orientation; tubes relatively broad and subpolygonal in cross section; filled with thin vesicles whose plates completely cross tube; trabecular microstructure microgranular aragonite of vaceletid type (WENDT, 1979, p. 454; MASTANDREA & RUSSO, 1995, p. 418); no spicules known. Permian (Lopingian)-Triassic: Tunisia, Sicily, Lopingian; Europe, Oman, Canada (Yukon), Triassic; Tajikistan, Austria, Carnian-Rhaetian.-FIG. 457, 1a-b. \*S. manon (MUNSTER), Wettersteinkalk, Ladinian, Karwendel, Austria; a, weathered, longitudinal section showing tubular spongocoel and reticular filling structure in chambers of wall, BSPGM 1967 II 6, ×1; b, longitudinal section showing nature of chamber walls, porous endowall around spongocoel, and extensive, reticular filling structures, BSPGM thin section G 412 a/67, ×2.5 (Ott, 1967a; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- Ambithalamia SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994, p. 17 [\*A. permica; OD]. Cylindrical, rarely branched sponges without a spongocoel; exterior and interior segmentation poorly developed; possible chamber interwalls or possible growth lines marked by very thin, interrupted (perforated) lines; chamber interiors or internal skeleton of sponge composed of relatively regular fibers of reticular type. Permian (Lopingian): Thailand.— FIG. 457,3a-b. \*A. permica, upper Permian limestone, Dorashamian, Phrae; a, oblique section through holotype (H) and associated sponges of species showing poor segmentation and open, reticulate skeleton, ×4; b, elongate section (B) showing

typical dermal layer and reticulate, endosomal skeleton without a spongocoel, with associated *Bisiphonella* (*A*) and *Solutossaspongia* (*C*), BSPGM R6, ×4 (Senowbari-Daryan & Ingavat-Helmcke, 1994).

- Cryptocoeliopsis WILCKENS, 1937, p. 197 [\*C. gracilis; OD]. Hemispheroidal, overlapping segments; no cloaca; thin exowall or interwall pierced by pores of variable size and irregular distribution; interior of chambers filled with anastomosing trabeculae that have a dominantly upward and outward arrangement; trabeculae outline anastomosing, tubular spaces, some of which are larger than others; microstructure unknown; no spicules known. [May be a synonym of Deningeria WILCKENS, 1937.] Triassic, ?Jurassic: Indonesia, Triassic; Poland, ?Jurassic.-FIG. 458, 1. \*C. gracilis, Pharetrone limestone, Upper Triassic, Seran, Moluccas, Indonesia; longitudinal holotype with spheroidal chambers filled with anastomosing, trabecular filling structures, S 197, ×2 (Wilckens, 1937; courtesy of Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B).
- ?Deningeria WILCKENS, 1937, p. 200 [\*D. camerata; OD] [=?Seranella WILCKENS, 1937, p. 198 (type, S. tenuissima, OD); =? Cryptocoeliopsis WILCKENS, 1937, p. 197 (type, C. gracilis, OD)]. Cylindrical with spheroidal segments; narrow, central cloaca; endowall thin but well developed; interwalls obscure or absent; exowall a thickening of trabecular net; all pores appear to be intertrabecular spaces; interior filled with fine, trabecular net that outlines anastomosing, meandriform, tubular spaces with tendency to upward and outward orientation; microstructure not known; no spicules known. Triassic, ?Jurassic: Indonesia, Italy, Tajikistan, Triassic; Poland, ?Jurassic. FIG. 457, 2. \*D. camerata, Pharetrone limestone, Upper Triassic, Moluccas, Indonesia; longitudinal section of holotype with spheroidal chambers and fine, trabecular filling structure, S 200, ×2 (Wilckens, 1937; courtesy of Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B).
- Panormida SENOWBARI-DARYAN, 1980, p. 186 [\*P. priscae; OD]. Moniliform to dichotomously branched sponges of stacked, strongly conical to dish-shaped chambers; spongocoel pseudosiphonate; coarse, reticulate filling structure. Triassic (Norian-Rhaetian): Italy (Sicily).---FIG. 458,2ab. \*P. priscae, Triassic reef limestone, Norian, Madonia Mountains; a, longitudinal section showing distinctive growth form, with narrow spongocoel in upper part and coarse filling structures in chambers, SPIE P/418, ×1; b, reconstruction showing form of genus and a longitudinal section of upper part of one branch showing perforate spongocoel and outer walls, with coarse, reticulate chamber filling, not to scale (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).
- Paradeningeria SENOWBARI-DARYAN & SCHÄFER, 1979, p. 22 [\*P. alpina; OD]. Porate sponges with prosiphonate, central spongocoel; reticular filling structure in inner parts of chambers is coarse and

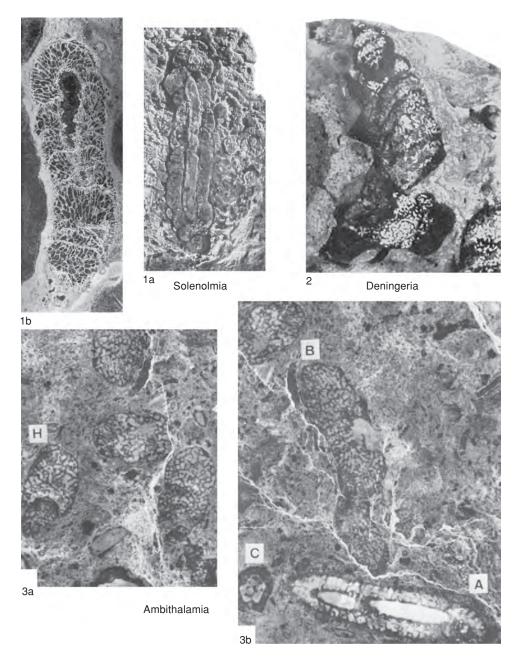


FIG. 457. Solenolmiidae (p. 692).

porous but in outer parts is finer and more compact. *Permian (Guadalupian)–Triassic (Rhaetian):* Ukraine, *Wordian–Guadalupian;* Italy (Sicily), Austria, Yugoslavia, Russia, Iran, USA (Oregon), Canada (Yukon), Tajikistan, *Norian–Rhaetian.*— FIG. 458,*3a–c. \*P. alpina,* Rhaetian reef limestone, Rhaetian, Salzburg, Austria; *a*, holotype, longitudinal section (1) with filling structure in outer parts of chambers, SPIE G/8,  $\times$ 4; *b*, transverse sections showing filling structures inside perforate exowalls, paratype, SPIE SZ/b,  $\times$ 5; *c*, paratype, transverse section with coarse filling structures in interior,

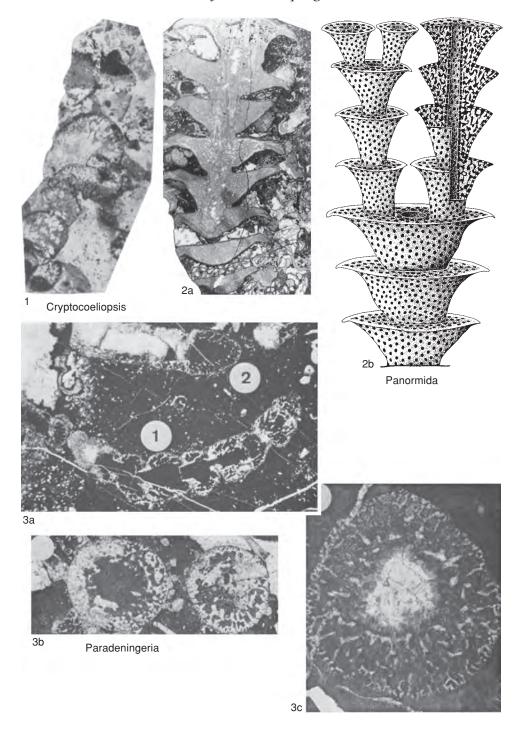


FIG. 458. Solenolmiidae (p. 692–695).

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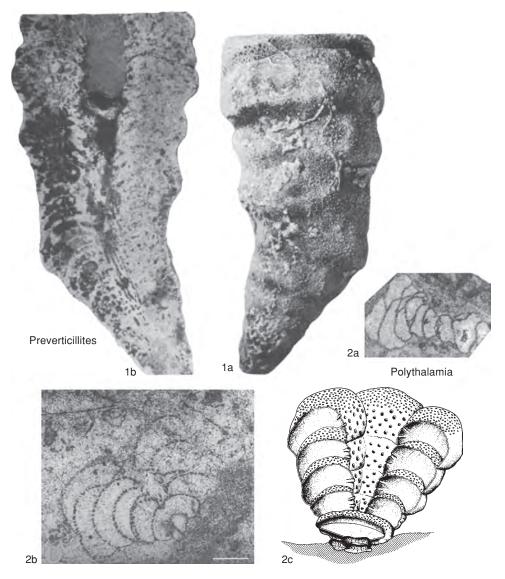


FIG. 459. Solenolmiidae (p. 695-696).

which become finer in outer part of chamber, SPIE G/153/q/2, ×3.9 (Senowbari-Daryan & Schäfer, 1979).

Polythalamia DEBRENNE & WOOD, 1990, p. 436 [\*P. americana; OD]. Globular or irregularly proliferating, chambered sphinctozoan, with thin walls that have numerous regularly arranged exopores and a retrosiphonate, perforate, central spongocoel; without primary filling structures although secondary vesiculae may be present; apparently without spicules, microstructure irregular. [As DEBRENNE & WOOD (1990) pointed out, classification of sphinctozoan sponges is difficult because of the probable polyphyletic origins of the skeletal grade. Placement in the family here, thus, is tentative.] *Lower Cambrian:* USA (Nevada, Alaska).——FIG. 459,2*a*-*c.* \**P. americana*, clasts in Ordovician Valmy Formation, Antler Peak quadrangle, Nevada; *a*, longitudinal section of holotype showing glomerate arrangement and development of axial spongocoel, USNM 434924, ×20; *b*, longitudinal section of chambered paratype with porous walls, USNM 434922, ×10; *c*, generalized reconstruction, approximately ×15 (Debrenne & Wood, 1990).

Preverticillites PARONA, 1933, p. 46 [\**P. columnella;* OD]. Cylindrical; exterior horizontally rugose,

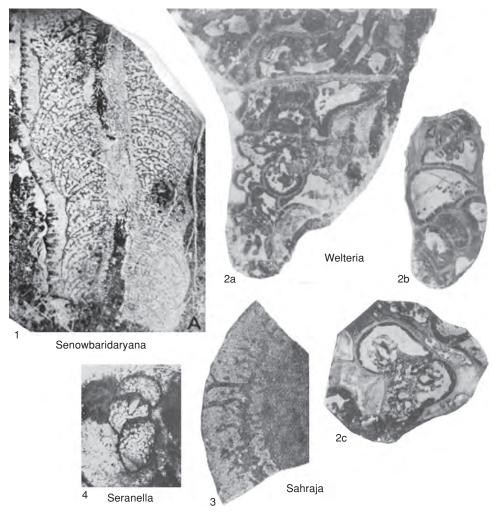


FIG. 460. Solenolmiidae (p. 696-697).

more or less related to interior chambers; exowall possibly minutely porous; narrow, central cloaca about one-fifth sponge diameter; endowall well defined, endopores apparently small; low chambers filled with dominantly radial and vertical, but meandriform and anastomosed, trabeculae that outline tubular spaces; trabecular microstructure not known; no spicules observed. [This genus bears considerable resemblance to early forms of Stylopegma KING, 1943, as well as to Phragmocoelia OTT, 1974. This genus includes the species Verticillites rectangilaris BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 154 and Verticillites convexus BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 174.] Permian-Triassic: Italy (Sicily), Tunisia, Oman, China (Hubei), Russia, Permian; Hungary, Greece, Ladinian-Carnian; Italy (Sicily), Tajikistan, Norian; Tajikistan, Triassic.---FIG.

459,1*a–b.* \**P. columnella*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a*, exterior of annulate, steeply obconical sponge with porous exowall, ×2; *b*, polished, longitudinal section showing prominent, central spongocoel and arcuate chambers with pillar filling structures, USNM 427368, ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Sahraja MOISEEV, 1944, p. 19 (MOISEEV, 1939, p. 816, nom. nud.) [\*S. triassica; OD]. Segmented sponges with broad, central canal; proportionally thick, outer wall and thinner, inner wall separated by a more or less continuous cavity; wall perforated with many branched, radial canals and pores; spicules unknown. [Name proposed by MOISEEV (1939, p. 816) but no description given.] Triassic (Norian-Rhaetian): Russia (Caucacus), Tajikistan (Pamir region), Iran, Turkey.—FIG. 460,3. \*S. triassica,

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Norian–Rhaetian sediments, Valley Sahraja, Caucasus; transverse section showing thicker, outer wall perforated by convergent, inhalant, radial canals that terminate in a cavity that separates thinner, inner and thicker, outer walls,  $\times 3$  (Moiseev, 1944).

- Senowbaridaryana ENGESER & NEUMANN, 1986, p. 153 [\*Verticillites triassicus KOVACS, 1978, p. 690; OD]. Sphinctozoan with chambered structure and reticular, internal structure; isolated chambers comparatively flat; spongocoel pseudosiphonate; microstructure unknown. Middle Triassic-Upper Triassic: Italy, Austria, Hungary, Greece, Russia.—FIG. 460,1.\*S. triassicus (KOVACS), Wetterstein reef limestone, Ladinian-Norian, Tornanádaska, northern Hungary; longitudinal section of holotype with reticular filling structure in uparched, low chambers with very porous walls around tubular spongocoel, MAGI T-0421/A, ×3 (Kovács, 1978; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- ?Seranella WILCKENS, 1937, p. 198 [\*S. tenuissima; OD] [=?Deningeria WILCKENS, 1937, p. 200 (type, D. camerata, OD)]. Cylindrical with spheroidal to hemispheroidal segments; slender, central cloaca; exopores, interpores, and endopores numerous, small, but of more than one size, form unknown; chamber interior filled with fine, trabecular net that outlines anastomosing tubes that connect with pores; microstructure unknown; no spicules known. Triassic: Indonesia.—FIG. 460,4. \*S. tenuissima, Pharetrone limestone, Upper Triassic, Moluccas; longitudinal section of holotype with spheroidal chambers with narrow spongocoel and porous walls, chambers with fine, trabecular filling structure, S 198, ×2 (Wilckens, 1937; courtesy of Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, Abteilung B).
- Welteria VINASSA DE REGNY, 1915, p. 84 [\* W. repleta; OD]. Cylindrical with spheroidal segments externally visible; central cloaca present; few large exopores in each segment, exowall otherwise imperforate; numerous circular interpores in interwall; endowall developed only in vicinity of interwalls (ambisiphonate) where pierced by few large, circular interpores; chamber lumen filled with vesicles; microstructure unknown; no spicules known. Permian-Triassic: ?Oman, Permian; Indonesia (Timor), Triassic; Austria, Italy, Oman, Upper Trias--FIG. 460, 2a-c. \*W. repleta, Triassic, Lelosic. gama, Timor; a, longitudinal section of type with spheroidal segments; b, longitudinal section with tubular spongocoel cut in lower part; c, diagonal section with chambers filled with vesiculae,  $\times 2$ (Vinassa de Regny, 1915).

# Subfamily BATTAGLIINAE Senowbari-Daryan, 1990

[Battagliinae SENOWBARI-DARYAN, 1990, p. 99]

Solenolmid sponges with glomerate arrangement of chambers. *Triassic (Norian– Rhaetian).*  Battaglia SENOWBARI-DARVAN & SCHÄFER, 1986, p. 244 [\*B. major; OD]. Glomerate stems with a pseudosiphonate to retrosiphonate, central canal; central opening filled with bubblelike fabric, but not vesiculae; chamber openings partially filled with reticular filling structure. Triassic (Norian-Rhaetian): Italy (Sicily), Slovenia.——FIG. 461a-b. \*B. major, Reef limestone, Norian, Madonie Mountains, Sicily; a, holotype, longitudinal section with branched canals that lead to central, exhalant canal and reticular filling of glomerate chambers, ×1.5; b, drawing of holotype showing its chambers and canal patterns, SPIE P/424/1, ×1 (Senowbari-Daryan & Schäfer, 1986).

# Family COLOSPONGIIDAE Senowbari-Daryan, 1990

[Colospongiidae SENOWBARI-DARYAN, 1990, p. 63] [=Colospongiidae BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 143; Parauvanellidae WU Ya Sheng, 1991, p. 81; Imbricatocoeliidae WU Ya Sheng, 1991, p. 88]

Porate, thalamid sponges without a central canal or spongocoel and without filling structures; pores of segments unbranched or with only dichotomous branches; basal skeleton primarily aragonitic. *Lower Cambrian– Triassic.* 

## Subfamily COLOSPONGIINAE Senowbari-Daryan, 1990

[Colospongiinae SENOWBARI-DARYAN, 1990, p. 63]

Chambers or segments in linear, moniliform arrangements. *Lower Cambrian– Triassic.* 

Colospongia LAUBE, 1865, p. 237 [\*Manon dubium MÜNSTER, 1841, p. 28; OD] [?=Takreamina FONTAINE, 1962, p. 205, nom. nov. pro Steinmannia WAAGEN & WENTZEL, 1888, p. 979, non FISCHER, 1886 (type, Steinmannia salinaria WAAGEN & WENTZEL, 1888, p. 980, OD), = Waagenium DE LAUBENFELS, 1957, p. 249, nom. nov. pro Waagenella DE LAUBENFELS, 1955, p. 102, obj., non DE KONINCK, 1883, nec YABE & HAYASAKA, 1915]. Spheroidal segments in linear series, successively increasing in size; no cloaca or central osculum; exopores small, subequal, circular, separated by more than their diameter and confined to upper two-thirds or so of each chamber, lower part of exowall secondarily imperforate, except for occasional, large, circular, lipped exopores, which may occur anywhere; interwall and interpores merely top of preceding chamber with its exopores; interior of chamber may contain large vesicles, continuous with secondary linings of chamber wall, convex inwardly and upwardly but no other skeletal tissue; wall microstructure microgranular aragonite as in living Vaceletia PICKETT (MASTANDREA & RUSSO, 1995, p. 418); monaxon spicules imbedded in wall (SENOWBARI-DARYAN, 1989, p. 475). [Descriptions

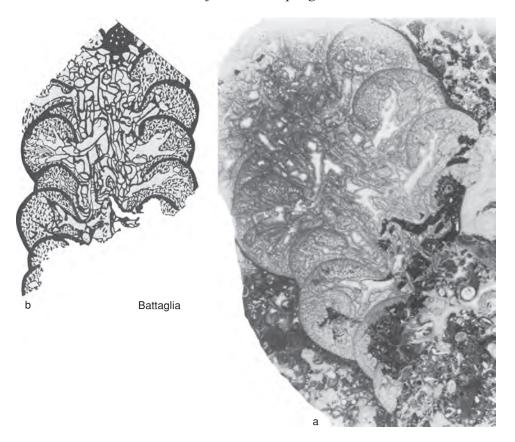


FIG. 461. Solenolmiidae (p. 697).

in the literature (e.g., ZITTEL, 1878b, p. 27; STEINMANN, 1882, p. 172; HERAK, 1943, p. 129; SEILACHER, 1962, p. 738) were of specimens not congeneric with the holotype, which was redescribed by OTT (1967a, p. 50), who considered it congeneric with Girtycoelia KING, 1933. Because the latter genus has spherulitic, aragonite microstructure, the not very exact resemblance in gross morphology must be considered homeomorphic. The species described by SENOWBARI-DARYAN and STANLEY (1988, p. 420), with cribribullae and subpolygonal exopores, is so different from the type species that it should probably be assigned to a new genus.] Carboniferous-Triassic: Europe, USA (Oregon), Canada (Yukon), Peru, Tunisia, Oman, China, India, Timor, Thailand, Russia, Armenia, Tajikistan, Kyrgyzstan.—FIG. 462,2a. \*C. dubia (MÜNSTER), St. Cassian beds, Middle Triassic, St. Cassian, Sud Tyrol, Austria; side view of typical sponge, ×2 (Laube, 1865).—FIG. 462,2b. C. cortexifera SENOWBARI-DARYAN & RIGBY, Biohermal complex, Lopingian, Djebel Tebaga, Tunisia; side view showing outer segmentation and coarse pores in chamber walls, ×2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

- Blastulospongia PICKETT & JELL, 1983, p. 87 [\*B. monothalamos; OD]. Asiphonate, single-chambered, porate sphinctozoans without internal filling structures. [The simple structure and small dimensions of these fossils raise questions about their sponge nature and whether they might be perhaps foraminifera or radiolaria (PICKETT & JELL, 1983; BENGTSON, 1986; MORRIS & MENGE, 1990).] Lower Cambrian-Upper Cambrian: China (Hubei), Lower Cambrian; Australia (New South Wales), Middle Cambrian; Australia (Queensland), Upper Cam--FIG. 462,4a-b. \*B. monothalamos, brian.— Coonigan Formation, Middle Cambrian, Broken Hill quadrangle, New South Wales; a, holotype, spherical chamber with porous exowall,  $\times 20$ ; b, photomicrograph of part of exowall with details of pores, NMV P75150, ×95 (Pickett & Jell, 1983).
- Pseudoimperatoria SENOWBARI-DARYAN & RIGBY, 1988, p. 195 [\*Imperatoria mega RIGBY & POTTER, 1986, p. 23; OD]. Cylindroidal, branching sponge, occasionally anastomosing, composed of

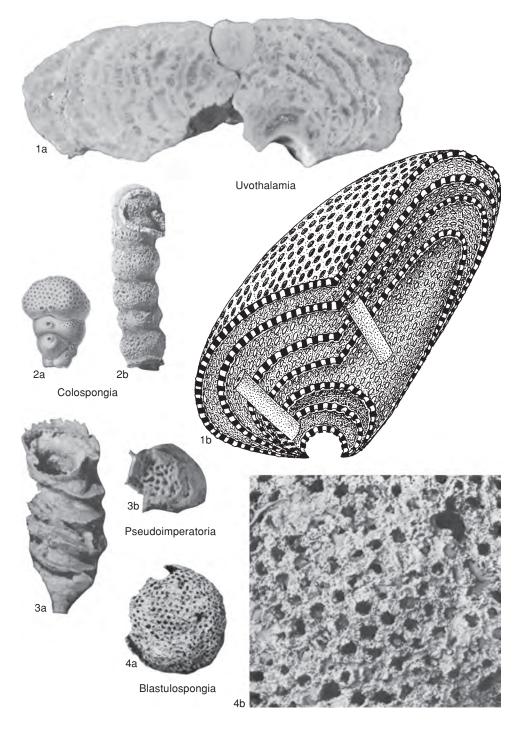


FIG. 462. Colospongiidae (p. 697–701).

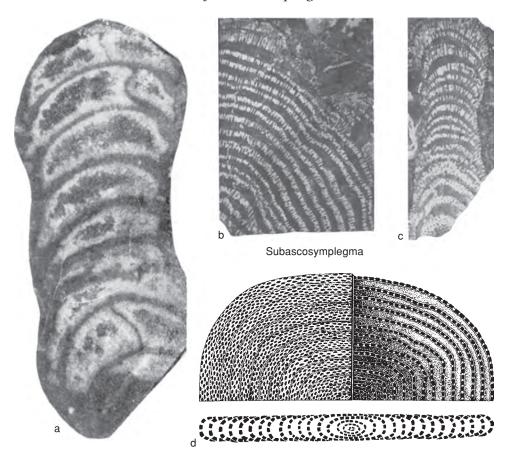


FIG. 463. Colospongiidae (p. 700).

superposed, conical chambers, each flaring to a sharp, upper edge with flat, upper surface; no cloaca; exopores small, widely spaced, of two sizes; interwall sievelike with large, subangular to submeandriform interpores separated by narrow trabeculae; no internal structures in chambers; microstructure not known; no spicules known. upper Lower Ordovician-Permian (Lopingian): USA (California), upper Lower Ordovician-upper Upper Ordovician; Tunisia, Lopingian. Fig. 462, 3a-b. \*P. mega (RIGBY & POTTER), Kangaroo Creek Formation, Ashgill, Klamath Mountains, California; a, side view of holotype showing pronounced, turriculate form, USNM 395862, ×2; b, view from above of porous interwall of paratype with coarse and irregular interpores, USNM 395863, ×2 (Rigby & Potter, 1986).

Subascosymplegma DENG, 1981, p. 425 [\*S. guangxiensis; OD]. Platelike, tabular to flabellate sponges composed of several concentric, annular-appearing to crescentic, cylindrical chambers; walls perforated by numerous small pores; vesiculae may be present or absent within chambers. *Permian (Guadalupian*- Lopingian): China (Hubei, Guangxi), Tunisia.-FIG. 463a. \*S. guangxiensis, Heshan Formation, Changhsingian, Guangxi, China; vertical section of tabular sponge showing superposed chambers with arched, perforated walls, NIGPAS 59977, ×4 (Deng, 1981).—FIG. 463b-d. S. oussifensis TERMIER & TERMIER, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; b, thin section cut parallel to axis of saucerlike surface, with long, low chambers and thick, perforated walls, USNM 427315, ×2; c, thin section normal to sponge surface showing crescentic cross sections of chambers and porous walls, USNM 427316, ×2, d, reconstruction showing arcuate chambers of tabular sponge in horizontal section, above, and vertical section, below, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).

Tristratocoelia SENOWBARI-DARYAN & RIGBY, 1988, p. 188 [\*T. rhythmica; OD]. Superposed, barrelshaped chambers with exowalls pierced by fine, closely spaced exopores, plus occasional lipped, larger exopores; these chambers separated by expanded, dense, thick-walled, ringlike elements that

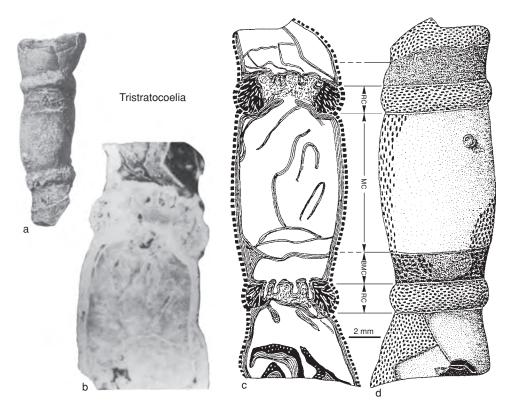


FIG. 464. Colospongiidae (p. 700-701).

form toroidal rolls in exterior and appear as porous, thick interwalls with large interpores in vertical sections; chamber interiors with secondary lamellar lining and vesicles, but no other structure. [This differs from Girtycoelia KING, 1933, in the thickened interwall-exowall complex with its large interpores and external roll. The thick interwalls were originally interpreted as thick-walled, special chambers (so-called ring chambers), but subsequent investigation with additional material (RIGBY, SENOWBARI-DARYAN, & LIU, 1998) indicate that it is not a chamber but a porous interwall. Direction of growth of the sponges is suggested by the upwardly arcuate vesicles in the chamber interiors.] Permian (Lopingian): Tunisia, USA (New Mexico), China, Thailand.—FIG. 464a-d. \*T. rhythmica, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, holotype exterior with two ring chambers and one complete and two fragments of intervening main chambers, ×2; b, polished, axial section showing complex structure of ring chambers and barrel-like main chamber, USNM 427325, ×5; c-d, drawings of vertical, axial section (a), and exterior (b) of holotype; BMC, bottom of main chamber; MC, main chamber; RC, ring chamber, scale indicated by bar (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).

Uvothalamia SENOWBARI-DARYAN, 1990, p. 67 [\*U. planiinvoluta; OD]. Porate sponge composed of low, oval chambers that overlap on sides and top of sponge so segmentation not readily apparent except in sections; chambers without filling structures and vesiculae. Permian (Guadalupian): Italy (Sicily).
 ——FIG. 462,1a-b. \*U. planiinvoluta, Sosio beds; a, cross section of holotype showing low chambers and ovoid growth, SPIE S/15/1, ×2; b, reconstruction showing ovoid growth form with low chambers with perforate walls growing around other organisms, not to scale (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

# Subfamily CORYMBOSPONGIINAE Senowbari-Daryan, 1990

[Corymbospongiinae SENOWBARI-DARYAN, 1990, p. 64]

Glomerate to stratiform arrangement of chambers. Ordovician–Triassic (Rhaetian).

**Corymbospongia** RIGBY & POTTER, 1986, p. 28 [\**C. adnata;* OD]. Clusters of spheroidal to ellipsoidal chambers, possibly encrusting; each chamber bearing long exaulos often arising from a mamelon-like protuberance; exauli of cluster tend to face same

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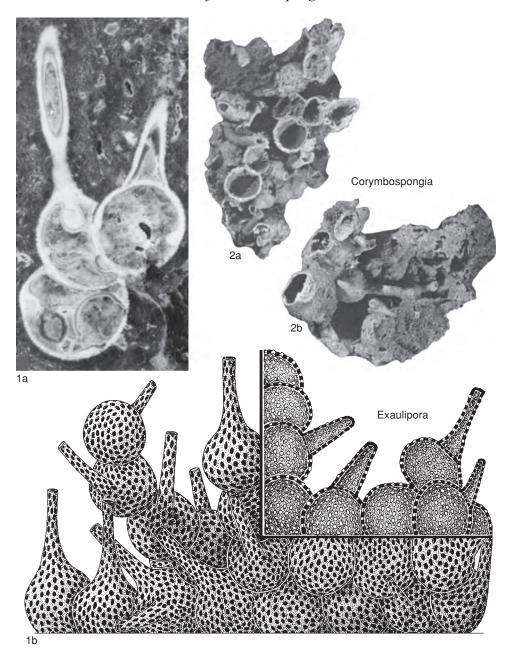


FIG. 465. Colospongiidae (p. 701-703).

direction (possibly upward); chamber walls perforated by small, circular pores that bear lips on inner wall of chamber; adjacent chambers may communicate by these pores but not by exauli; no internal structures except possibly vesicles; microstructure not known; no spicules known. [Genus resembles the protocysts of *Girtyocoelia* COSSMANN, 1909, except for the presence of pores in the walls.] upper Upper Ordovician, ?Permian: USA (California, Alaska), upper Upper Ordovician; USA (Texas), ?Permian.—\_\_\_\_FIG. 465,2a-b. \*C. adnata, Horseshoe Gulch limestone unit, Ashgill, Klamath Mountains, California; a, silicified holotype consisting of adnate to separated, globular chambers with prominent

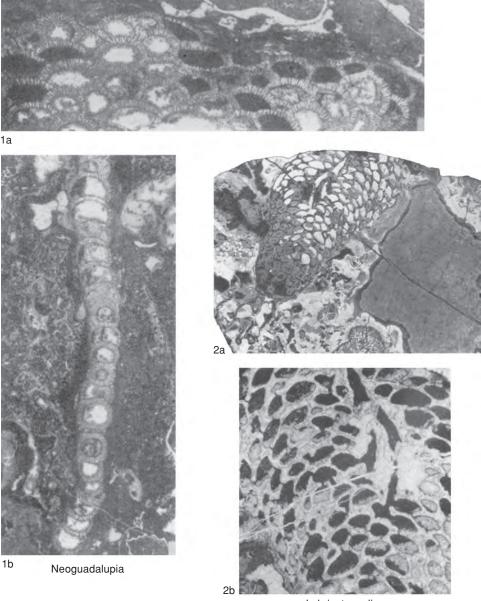
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exaules, BMNH S10163,  $\times$ 2; *b*, silicified paratype with moderately large chambers with porous walls and prominent, tubular exaules, USNM 395904,  $\times$ 2 (Rigby & Potter, 1986).

- Exaulipora RIGBY, SENOWBARI-DARYAN, & LIU, 1998, p. 48 [\*Corymbospongia(?) permica Senowbari-DARYAN, 1990, p. 69; OD]. Thalamid sponges composed of glomerate clusters of spherical to subspherical, occasionally egg-shaped chambers, that may appear partly moniliform; one or two long, coarse, tubular exaules occurring per chamber; exaules and chamber walls both porous; porous, sievelike plates developed at inner base of exaules; chamber interiors with vesiculae. ?Ordovician, Permian (Guadalupian): USA (?Oregon), ?Ordovician; USA (Texas, New Mexico), China, Guadalupian. FIG. 465, 1a-b. \*E. permica (SENOWBARI-DARYAN), Capitan Limestone, Guadalupian, Guadalupe Mountains, New Mexico; a, holotype, section of three chambers with vesiculae and two with extended exauli, both exowalls and exauli porous, WC/41 SPIE, ×2; b, reconstruction showing growth form and porous walls of chambers and exauli, which are separated from chambers by porous sieve plates, not to scale (Senowbari-Daryan, 1990).
- Imbricatocoelia RIGBY, FAN, & ZHANG, 1989a, p. 419 [\*I. paucipora; OD] [=Squamella BELYAEVA in BELYAEVA & ZHURAVLEVA in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 106 (type, S. lichatchevi, OD)]. Cylindrical to club shaped or spheroidal, with narrow, canal-like, central cloaca in type species, which may be locally multiple and discontinuous in another species or completely absent in a third; chambers small, hemispherical, or bun shaped, arranged in typical guadalupiid fashion, alternating quincuncially and molded to underlying chambers, in multiple ranks around central axis, but not strongly elongate either radially or concentrically; interpores, exopores, and endopores few in number; chambers visible on exterior as nodelike bulges. [The genus is placed with some question in the family.] Permian (Guadalupian-Lopingian): China (Hubei, Guangxi), Oman, Guadalupian-Lopingian; Russia, Wordian-Capitanian.-—Fig. 466,2a-b. \*I. paucipora, Maokou Formation, Kungurian, Guangxi, China; a, holotype, oblique section showing prominent, central tube and crescentic chambers with few coarse interpores,  $\times 1$ ; b, part of holotype showing smooth interwalls pierced by a few interpores and coarse exopores into exhalant canals, IGASB 5046, ×2 (Rigby, Fan, & Zhang, 1989a).
- Lichuanospongia ZHANG, 1983, p. 8 [\*L. typica; OD] [?=Discosiphonella INAI, 1936, p. 169 (type, D. manchuriensis, OD)]. Cylindrical or subcylindrical to obconical sponges composed of low, radially and vertically overlapping, crescentic chambers in scalelike patterns; central tube retrosiphonate with porous, gastral layer; chamber walls double layered with inner one thicker and perforated by coarse pores, but outer one a thin, porous micromesh; vesiculae rare within chambers. [May be a synonym of

Discosiphonella INAI, 1936, p. 169.] Permian (Wordian–Changhsingian): China (Hubei. Guangxi), Lopingian; Russia, Wordian-Capitanian.--FIG. 467a-d. \*L. typica, Wujiaping-Changxing Formation, Lopingian, Xiangbo, Guangxi; a, longitudinal section showing arcuate, overlapping chambers in thin walls around broad, central tube, IGASB 5011, ×1; b, transverse section showing overlapping chambers, IGASB 5006, ×2; c, photomicrograph of tangential section of endowall to central tube, with netlike appearance, IGASB 5003, ×5; d, vertical, tangential section through wall showing overlapping, crescentic chambers with porous interwalls, IGASB 5002, ×5 (Rigby, Fan, & Zhang, 1989a).

- Neoguadalupia ZHANG, 1987, p. 237 [\*N. elegana; OD]. Flat to tabular bodies with subspherical to spherical chambers that are generally superimposed one above other; walls of chambers perforated by numerous small pores; filling structures absent; central cavity or spongocoel absent. Permian (Cisuralian, ?Lopingian), Triassic (?upper Carnian, Norian): China (Guangxi, Yunnan), Cisuralian, ?Lopingian; USA (Oregon), Iran, Russia (Caucasus region), ?upper Carnian, Norian.-FIG. 466,1a-b. \*N. elegana, Maokou Formation, Kungurian, Guangnan County, Yunnan, China; a, horizontal section through broad, platelike holotype with chambers connected by coarse interpores, ×4; b, vertical section through plate showing crescentic chambers added laterally, IGASB 3011, ×2 (Zhang, 1987).
- Parauvanella SENOWBARI-DARYAN & DI STEFANO, 1988, p. 18 [\*P. paronai; OD]. Encrusting masses of superposed, spheroidal to hemispheroidal chambers communicating by closely spaced, circular pores; no internal structures in chambers. [Differs from Uvanella OTT, 1967a, in absence of vesicles and more regular, spheroidal form of chambers.] Permian-Triassic: Italy (Sicily), Tunisia, Oman, USA (Texas), China, Permian; Austria, Iran, Russian Far East, Triassic.-FIG. 468,2. \*P. paronai, Lercara Formation, Cisuralian, Lercara, Sicily; holotype, longitudinal section of superposed, hemispherical chambers, with sponge overgrowing an inozoan, MGUP S/5/207, ×3 (Senowbari-Daryan & Di Stefano, 1988; courtesy of Revista Italiana di Paleontologia e Stratigrafia).
- Platythalamiella SENOWBARI-DARYAN & RIGBY, 1988, p. 184 [\*P. newelli; OD]. [The incompletely preserved specimens on which this genus was based agree almost entirely with the type species of *Guadalupia* GIRTY, 1909 (G. zitteliana GIRTY), except for the absence of a trabecularium, and of diaphragms within the chambers. It is possible that a trabecularium was present but not preserved or recognized. A possible diaphragm is visible in the illustration of the paratype (SENOWBARI-DARYAN & RIGBY, 1988, pl. 29,8, near upper left) and these latter structures are often rare or absent in *Guadalupia* specimens.] Permian (Lopingian)–Upper Triassic (Rhaetian): Tunisia, Timor, Italy, Moluccas, Lopingian; ?Sicily, Norian–Rhaetian.— FIG.



Imbricatocoelia

FIG. 466. Colospongiidae (p. 703).

468, *Ia–b.* \**P. newelli*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a*, holotype, polished horizontal section showing chamber form, thick, perforate walls, and stacking, USNM 427300, ×2; *b*, vertical section through blade of paratype with irregularly overlapping, crescentic, chamber walls, USNM 427301, ×1 (Senowbari-Daryan & Rigby, 1988).

# Family GIGANTOTHALAMIIDAE Senowbari-Daryan, 1994

[Gigantothalamiidae SENOWBARI-DARYAN, 1994a, p. 417]

Sponges with low, crescentic and horizontally extensive chambers with a more or less massive and rounded to irregular, massive

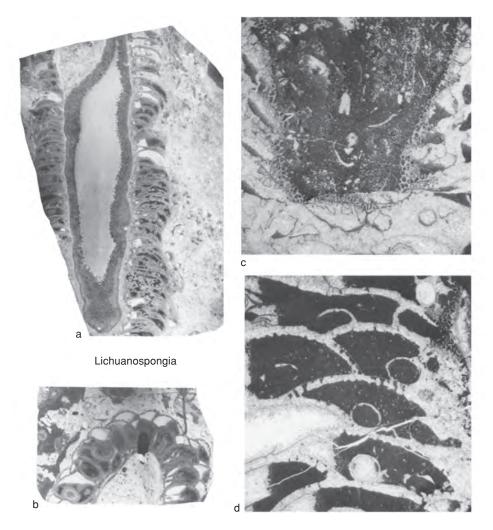


FIG. 467. Colospongiidae (p. 703).

appearance; horizontal growth may exceed vertical growth; segments either hollow or filled with vesiculae; aragonitic, basal skeleton has microspherulitic microstructure; spicular skeleton is not known. *Upper Triassic.* 

Gigantothalamia SENOWBARI-DARYAN, 1994a, p. 417 [\*G. ovoidalis SENOWBARI-DARYAN, 1994a, p. 418; OD]. Spherical to oval or irregularly massive sponges composed of numerous very low, crescentic and horizontally extensive, stacked segments or chambers; segment walls perforated with large, but irregularly placed pores; several single, isolated canals serve as spongocoels for water egress; segments or chambers without filling skeletons and without vesiculae; aragonitic, basal skeleton with spherulitic microstructure; spicules unknown. [Gigantothalamia is similar to Zanklithalamia in growth form, but has single, isolated canals as excurrent features rather than bundles of canals, as in Zanklithalamia.] Triassic (Norian): Turkey.——FIG. 469*a–b.\*G. ovoidalis,* Cipit limestone blocks, lower Norian, Taurus Mountains; *a*, weathered exterior of holotype with short exaules around large pores in center, ×0.8; *b*, longitudinal section showing low chambers with porous walls cut by a few large, exhalant canals, SPIE 19 G 105/1 and 105/2, ×0.8 (Senowbari-Daryan, 1994b).

Zanklithalamia SENOWBARI-DARYAN, 1990, p. 105 [\*Z. multisiphonata; OD]. Gigantic sponges composed of flat, broad chambers pierced by several canal bundles of prosiphonate type that penetrate through skeleton and are vertical or oblique to outer surface; segment or chamber interiors hollow

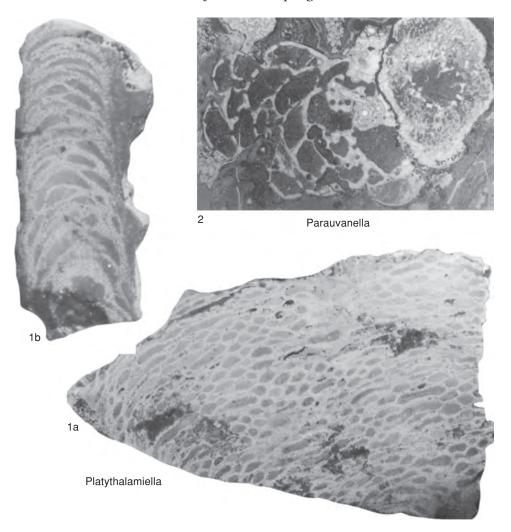


FIG. 468. Colospongiidae (p. 703-704).

or with vertical elements that may be similar to columnar filling structures; vesiculae are rare; primary skeletal mineralogy was probably aragonite; microstructure unknown but probably spherulitic. Upper Triassic: Austria.-FIG. 470a-c. \*Z. multisiphonata, Dachstein reefs, Norian, Berchtesgadener Alps; a, weathered section of holotype with elongate chambers interrupted by faint bundles of vertical, exhalant canals, as in right center, SPIML, Zankl collection, ×0.7; b, section showing elongate chambers cut by faint bundles of exhalant canals in center and upper right center, ×0.7; c, reconstruction showing low chambers with chamber walls, moderately rare pillars, and walls of canals in black, not to scale (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

# Family TEBAGATHALAMIIDAE Senowbari-Daryan & Rigby, 1988

[Tebagathalamiidae SENOWBARI-DARYAN & RIGBY, 1988, p. 192]

Porate sphinctozoans without recognizable outer segmentation in which small spherical to tubular chambers are arranged in one peripheral layer around a very thickwalled spongocoel; each chamber is connected with central tube by only one large, exhalant canal that passes through endowall; few ostia may be present in exowall, in addition to exopores; neither filling tissue nor vesiculae present. *Permian–Upper Triassic.* 

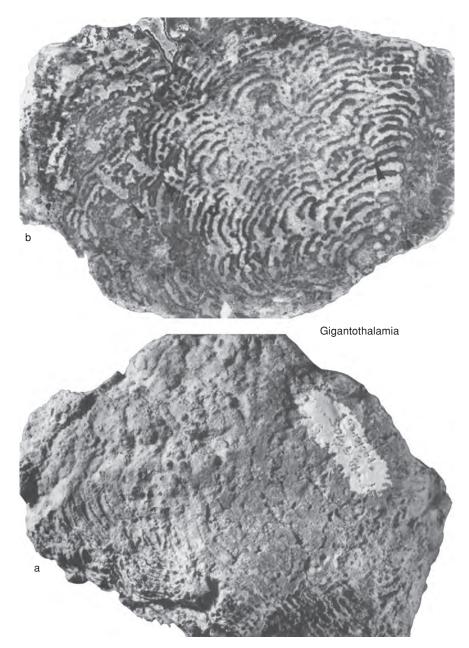


FIG. 469. Gigantothalamiidae (p. 705).

Tebagathalamia SENOWBARI-DARYAN & RIGBY, 1988, p. 192 [\* T. cylindrica; OD] [=Guadalupia DENG, 1982, p. 250 (type, G. sp., OD), non GIRTY, 1909]. Porate cylindrical stems in which radially tubelike chambers have polygonal to subhexagonal cross sections and are arranged in one glomerate layer around thick-walled spongocoel or central tube; segmentation ill defined to unrecognizable in continuous exowall; exowall pierced by fine, closely spaced exopores; interpores slightly larger and more widely spaced; each chamber connected to exhalant, central tube by large, tubular to branched exopore, although such openings from adjacent chambers may unite to form common tubes that empty into spongocoel; microstructure not known; spicules unknown. [The sponges included by DENG in

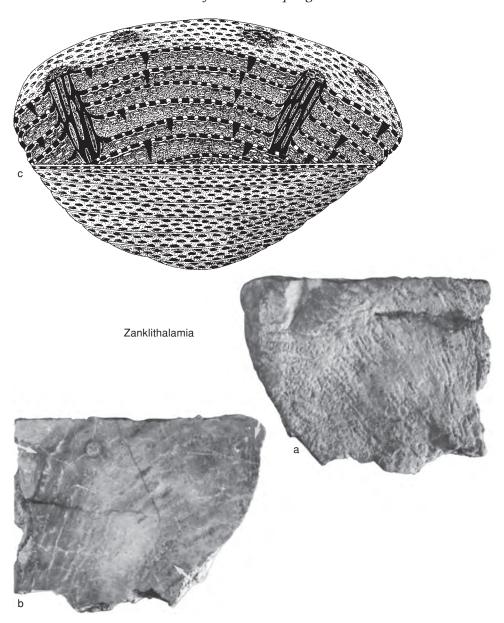


FIG. 470. Gigantothalamiidae (p. 705-706).

Guadalupia sp. are included by SENOWBARI-DARYAN and RIGBY in *Tebagathalamia.*] middle Permianupper Permian: Tunisia, Italy (Sicily), China (Guangxi).—FIG. 471, *Ia-c.* \**T. cylindrica*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; *a*, holotype, oblique section showing polygonal, outer chambers on periphery, with porous walls, and each chamber connected to axial spongocoel by narrow, exhalant canal, USNM 427351, ×4; *b*, small paratype showing polygonal chambers around spongocoel in upper part where exowall has been removed, and small pores where exowall is intact, USNM 427353,  $\times$ 2; *c*, side view of paratype with regular rows of chambers exposed because dermal layer has been removed, USNM 4427355,  $\times$ 2 (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

Annaecoelia SENOWBARI-DARYAN, 1978, p. 207 [\*A. maxima; OD]. Encrusting sponge built of irregularly superposed (glomerate), hemispheroidal chambers; exowall microporous (and pore canals may branch) and continuous about each chamber

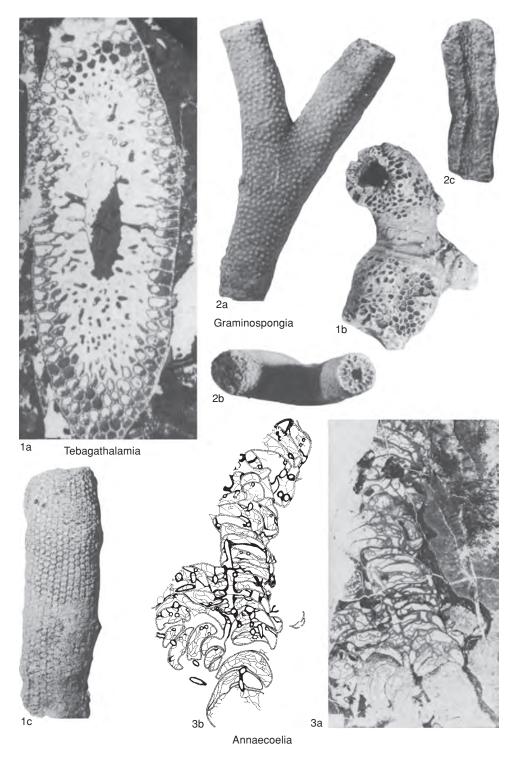


FIG. 471. Tebagathalamiidae (p. 707–710).

(i.e., double where chambers are in contact); exaulos-like tubes arising from some chambers and terminating externally after passing through one or more later chambers that surround and incorporate tubes; tube walls lamellar and imperforate, except for occasional large openings into chambers; vesicles numerous in chambers and in many tubes. Upper Triassic: Austria, Italy (Sicily), Yugoslavia, Oman. -FIG. 471, 3a-b. \*A. maxima, Gruber-Riff limestone, upper Rhaetian, Salzburg, Austria; a, longitudinal thin section of holotype with glomerate, irregular chambers, some of which interconnected by exaulos-like tubes,  $\times 1$ ; *b*, drawing of holotype section showing exaulos-like tubes with thick walls interconnecting irregular chambers with porous interwalls and exowalls and some with vesiculae, SMF 30799c, ×1 (Senowbari-Daryan, 1978; courtesy of Senckenberg Naturforschende Gesellschaft).

Graminospongia TERMIER & TERMIER, 1977a, p. 36 [\*Guadalupia girtyi PARONA, 1933, p. 48; OD] [=Solidothalamia WU Ya Sheng, 1991, p. 91 (type, S. lambdiformis, OD)]. Very thin, branching cylinders; central tube (spongocoel or cloaca) one-tenth to one-fifth branch diameter; exowall with quincuncially arranged, lipped exopores (pustules), each corresponding to an internal, radial chamber; interpores numerous and microscopic; endopores slightly larger than exopores and probably one per chamber; possible rudimentary trabecularium lines cloaca. [An illustration by SENOWBARI-DARYAN and RIGBY (1988, pl. 35,4) showing sublongitudinal, meandriform ridges and canals on the cloacal surface, and these may represent the longitudinal canals reported by the authors of the genus and by ALEOTTI, DIECI, and RUSSO (1986, pl. 3,4). The interpores originally described appear to be oblique cross sections of the chambers. The small size and peculiar exopores of this genus suggest affinities with the dasycladacean algae, but the possible trabecularium strengthens a poriferan assignment.] middle Permian-upper Permian: Italy (Sicily), Tunisia, China.——FIG. 471,2a–c. \*G. girtyi (PARONA), Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga, Tunisia; a, side view of branched specimen with pustulose pores in dermal layer, USNM 427360; b, top of same specimen showing central spongocoel and chambers in wall; c, weathered vertical section showing chambered walls and axial spongocoel, 427362, ×3 (Senowbari-Daryan & Rigby, 1988; courtesy of Facies).

# Family CHEILOSPORITIIDAE Fischer, 1962

#### [Cheilosporitiidae FISCHER, 1962, p. 123]

Porate sphinctozoans with ontogenetic differentiation where asiphonate in initial stages but with a retrosiphonate, central tube in later stages; without filling structures or vesiculae. *Triassic (Carnian–Rhaetian)*.

Cheilosporites WÄHNER, 1903, p. 98 [\*C. tirolensis; OD]. Sphinctozoan sponges in which spongocoel asiphonate in early stages and retrosiphonate in later stages of growth; stems without filling structures and vesiculae. Triassic (Carnian–Rhaetian): Italy (Sicily), Austria, Greece, Jugoslavia, Hungary, Turkey, Norian–Rhaetian; Tajikistan, Carnian– Rhaetian.—FIG. 472,1. \*C. tirolensis, Steinplatten Reef, Rhaetian, northern Calcareous Alps, Italy; thin section including several examples of chambered species cut in various directions and coated by crusts of dark, possible algae, ×3 (Fischer, 1962).

## Family SALZBURGIIDAE Senowbari-Daryan & Schäfer, 1979

[Salzburgiidae SENOWBARI-DARYAN & SCHÄFER, 1979, p. 19]

Porate sphinctozoans with differentiated wall structure; chamber walls double layered; chambers without filling structures. *Permian*—*Triassic (Rhaetian)*.

Salzburgia Senowbari-Daryan & Schäfer, 1979, p. 19 [\*S. variabilis; OD]. Porate sponges with glomerate chamber arrangement, asiphonate but occasionally with retrosiphonate, central canal; chambers with double-layered walls and without filling structures; ostia irregularly distributed. Permian-Triassic (Rhaetian): Italy (Sicily), Oman, China (Guangxi), Permian; Austria, Oman, USA (Oregon), Canada (Yukon), Norian-Rhaetian.—FIG. 472,2a-b. \*S. variabilis, Gruber-Riff, Rhaetian, Salzburg, Austria; a, holotype, thin section with glomerate chambers without filling structures and with central canal, chambers with geopetal structures, ×2; b, photomicrograph showing double-layered walls in two chambers, with older chamber on right and each with thicker, external layer, SPIE A/16/1, ×10 (Senowbari-Daryan & Schäfer, 1979).

# Family CRIBROTHALAMIIDAE Senowbari-Daryan, 1990

[Cribrothalamiidae SENOWBARI-DARYAN, 1990, p. 76]

Simple or branched stems with retrosiphonate spongocoel and glomerate arrangement of chambers; labyrinthic, branched pores in chamber walls; without filling structures but with vesiculae; cribribulla occurring in a well-defined, dermal layer; endowall of spongocoel also has similar appearing layer; inner layers of wall of cribribulla and spongocoel have broad, short canals that appear circular in longitudinal sections and may appear falsely as tubular or spherical filling structures. *Triassic (Norian– Rhaetian)*.

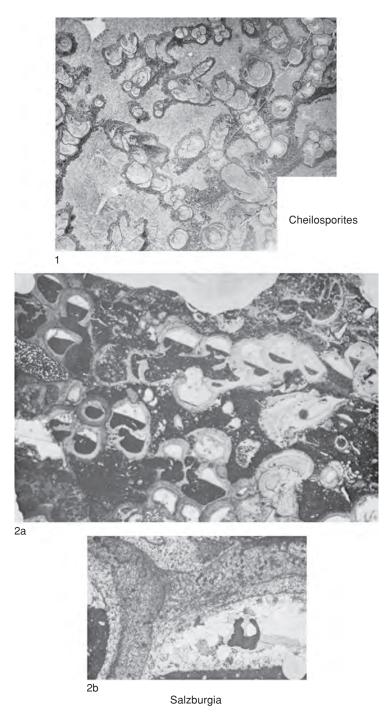


FIG. 472. Cheilosporitiidae and Salzburgiidae (p. 710).

Cribrothalamia SENOWBARI-DARYAN, 1990, p. 76 [\*C. gulloae; OD]. Stems composed of glomerate chambers arranged around retrosiphonate spongocoel; segment walls with labyrinthic, branched pores and additional porous plates as cribribulla in cortex of dermal layer; wall of spongocoel also having development of cribribulla; little filling structure but with vesiculae in interiors of chambers. Triassic (Norian-Rhaetian): Italy (Sicily).-FIG. 473a-c. \*C. gulloae, Triassic reef limestone, Norian, Madonie Mountains; a, holotype of glomerate chambers with coarse pores, spongocoel wall showing in lower part, SGIP MA/10, ×1; b, section through glomerate to irregular chambers, three of which each have cribribulla (arrows), SGMP MG/ 3/2,  $\times 2$ ; c, reconstruction showing glomerate chambers, some with a sievelike cribribulla, around a tubular spongocoel with cribribulla-like endopores, not to scale (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

# Family VERTICILLITIDAE Steinmann, 1882

[Verticillitidae STEINMANN, 1882, p. 172; emend., FINKS & RIGBY, herein] [=Verticillitidae STEINMANN, 1882, p. 172, partim; Polytholosiidae SEILACHER, 1962, p. 785, partim; Stylothalamiidae REITNER & ENGESER, 1985, p. 163, partim; Murguiathalamidae REITNER & ENGESER, 1985, p. 168, partim; Boikothalamiidae REITNER & ENGESER, 1985, p. 169, partim; Ascosymplegmatidae BOIKO, BELTAEVA, & ZHURAVLEVA, 1991, p. 168]

Chambered end cylindroidal with central cloaca (except in *Ascosymplegma* SEILACHER, 1962); exowall netlike with polygonal or lobate exopores closely spaced; where known, microstructure of aspicular skeleton is microgranular aragonite. *Permian* (*Guadalupian*)–Holocene.

# Subfamily VERTICILLITINAE Steinmann, 1882

[nom. transl. FINKS & RIGBY, herein, ex Verticillitidae STEINMANN, 1882, p. 172; emend., FINKS & RIGBY, herein]

Chambers low, containing numerous vertical pillars that frequently branch upwardly below interwall. *Permian (Guadalupian)– Holocene.* 

Verticillites DE FRANCE, 1829, p. 5 [\*V. cretaceus; OD] [=Verticillipora DE BLAINVILLE, 1830, p. 400, obj., nom. van.; Verticillocoelia FROMENTEL, 1860a, p. 30, obj., nom. van.; ?Cystopora POMEL, 1872, p. 229 (type, Verticillites truncatus D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 96, SD DE LAUBENFELS, 1955, p. 105); ?Wienbergia CLAUSEN, 1982, p. 111 (type, Barroisia faxensis RAVN, 1899, p. 24, OD)]. Conicocylindrical, branching; central cloaca about onefifth sponge diameter; smaller, auxiliary cloacas occasionally present; exowall netlike with closely spaced, subpolygonal, sometimes elongate, exopores; interwalls and endowalls the same; endowall with internal, anastomosing, microcanal system (REITNER & ENGESER, 1985); chambers low, upwardly arched, connected by vertical pillars; trabecular microstructure unknown; spicules not known. [In its netlike exowall and vertical pillars, this genus resembles the living and Eocene Vaceletia PICKETT, 1982, as well as the Triassic Stylothalamia OTT, 1967a. Cystopora POMEL, 1872 (p. 229) was stated to differ only in the absence of pillars. Permian and Triassic species appear to belong to Preverticillites PARONA, 1933, which differs from Verticillites in having meandriform trabeculae (walls of possible anastomosing tubes) in chambers rather than pillars.] Cretaceous: Europe.—FIG. 474, 1a-b. \*V. cretaceus, Upper Cretaceous, Maastrichtian, Néhou, Normandie, France; a, side view of holotype showing porous walls of branched sponge, ×1; b, vertical section showing central cloaca and porous interwalls of chambers, ×2 (Reitner & Engeser, 1985).

- Boikothalamia REITNER & ENGESER, 1985, p. 169 [\*Verticillites convexa BOIKO, 1979, p. 79; OD]. Cylindrical; cloaca one-third to one-fifth sponge diameter; chambers low and overlapped by succeeding ones; exowall-interwall netlike with subpolygonal pores; chambers filled with vertical pillars that may branch upwardly; endowall relatively thick with inwardly and upwardly directed canals; possible dichotriaenes imbedded in walls and pillars (cladomes directed upwardly in pillars) are better explained as pseudospicules (see SENOWBARI-DARYAN, 1989). [Except for its supposed spicules, this genus cannot be distinguished from Verticillites DE FRANCE, 1829, although data are not available on microstructure or mineralogy.] Jurassic (Callovian-Kimmeridgian): Siberia, Tajikistan, Greece.—FIG. 474, 3a-b. \*B. convexa (BOIKO), Callovian, Tajikistan; a, longitudinal section of type specimen with narrow spongocoel and uparched chambers with pillar filling structures connected to porous interwalls and exowall, top to left,  $\times 5$ ; b photomicrograph of supposed dichotriaene spicules in calcareous, skeletal element, scale bar, 125 µm (Reitner & Engeser, 1985).
- Marinduqueia YABE & SUGIYAMA, 1939, p. 68 [\*M. mirabilis; OD]. Cylindroid sponges without spines; spongocoel about one-third sponge diameter; chambers very low with numerous pillars that may be arranged in rows and produce a netlike appearance in vertical sections; closely spaced, subpolygonal to polygonal exopores; vesicles occasionally present. [Genus is similar to Vaceletia PICKETT, 1982, but without the lobate or spinose pores.] Paleogene (Eocene): Philippines. FIG. 475, 1a-e. \*M. mirabilis, Island of Marinduque; a, longitudinal section showing spongocoel in upper part and low chambers with pillar filling structures connecting porous interwalls; b, longitudinal section through low chambers with distinctively regular pillars, ×4; c, transverse section through porous interwall and with regular pillars in chambers, ×5; d-e, drawings of type specimens showing chamber

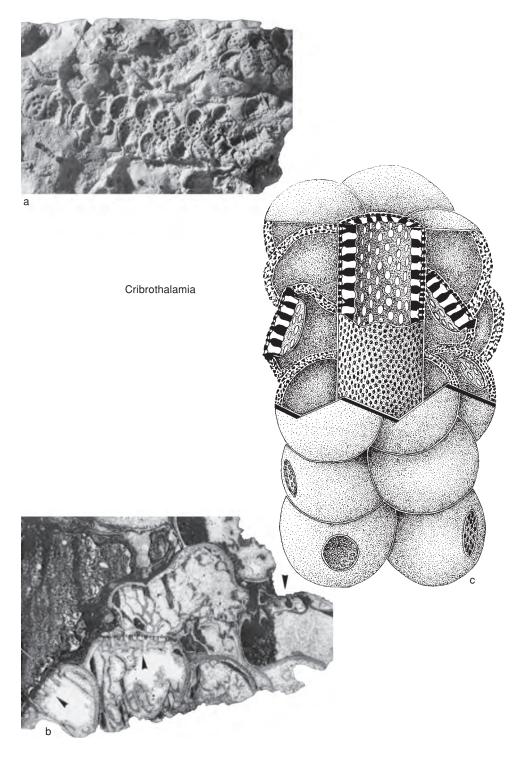


FIG. 473. Cribrothalamiidae (p. 712).

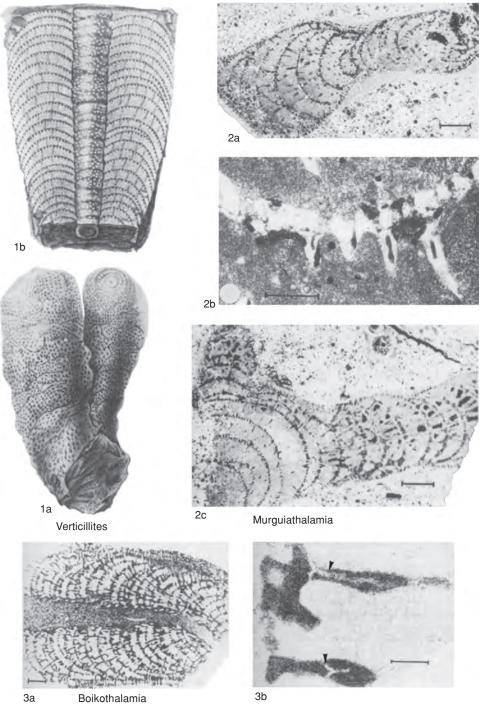


FIG. 474. Verticillitidae (p. 712–717).

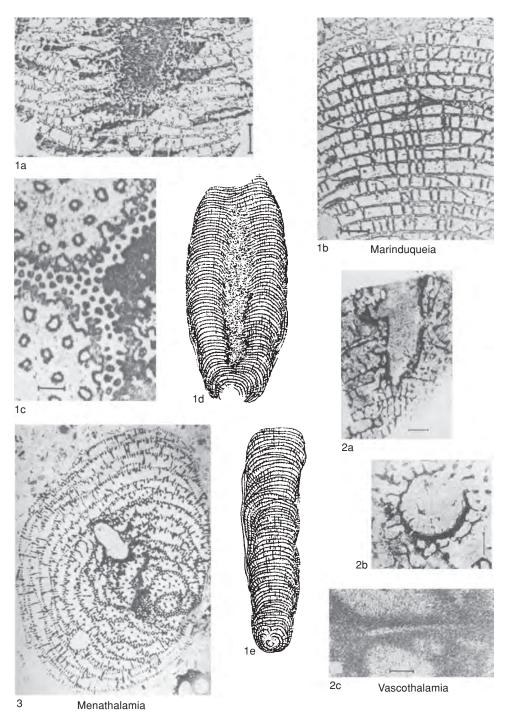


FIG. 475. Verticillitidae (p. 712–717).

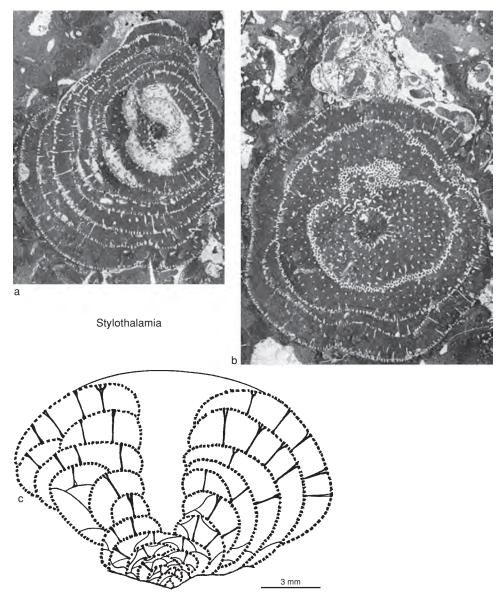


FIG. 476. Verticillitidae (p. 717).

and pillar development and spongocoel, ×1 (Reitner & Engeser, 1985).

?Menathalamia REITNER & ENGESER, 1985, p. 166 [\*M. caniegoensis; OD] [=?Stylothalamia OTT, 1967a, p. 44 (type, S. dehmi, OD)]. Stylothalamid sponges with a deep spongocoel in upper parts, which lack differentiated gastral layer; pores are comparatively small, of variable diameter and round; early skeletal stages without a spongocoel and prosopores may cluster to form astrorhiza-like, exhalant systems; apopores on retrosiphonate, spongocoel wall are of substantial size and irregular form. [Differs from *Stylothalamia* OTT, 1967a, in having more circular and widely spaced pores that may become confluent in early, noncloacate chambers, to form astrorhiza-like or meandriform openings. Genus may be considered a synonym of *Stylothalamia* OTT, 1967a, if the microstructure and mineralogy prove to be the same.] *Cretaceous (Cenomanian):* Spain.—FIG. 475,3. \*M. caniegoensis, Vracon, ?Lower Cenomanian, Caniego, Burgos, northern Spain; transverse section of holotype, negative print, with spongocoel in left center and radiating pillars in low chambers with coarsely porous interwalls, PIFUB 85/4, ×5 (Reitner & Engeser, 1985).

- Murguiathalamia Reitner & Engeser, 1985, p. 168 [\*M. jugoensis; OD]. Broadly conical with broad, open cloaca whose wall merely overlapping interwalls-exowalls of chambers [an alternative interpretation of illustrated sections is a noncloacate sponge with branches]. Chambers relatively high and hemispheroidal (or hemitoroidal) with few pillars; pores circular; pyritic bodies resembling prodichotriaenes embedded in calcareous skeleton (those in pillars have upwardly directed cladome at pillar-interwall junction) are probably pseudospicules (see SENOWBARI-DARYAN, 1989). Cretaceous (upper Albian): Spain.—FIG. 474,2a-c. \*M. jugoensis, sideritic limestone, near Murguía, northern Spain; a, holotype section with moderately high chambers with pillars, ×4; b, photomicrograph of pyrite pseudomorphs of possible megascleres within wall structures, PIFUB 85/5, bar scale, 0.1 mm; c, negative print of tangential section through broad, obconical paratype with retrosiphonate spongocoel and pillars in arcuate chambers, PIFUB 85/6, ×4 (Reitner & Engeser, 1985).
- Stylothalamia OTT, 1967a, p. 44 [\*S. dehmi; OD] [?=Menathalamia REITNER & ENGESER, 1985, p. 166 (type, M. caniegoensis, OD)]. Broadly conical with narrow, central cloaca or without cloaca; chambers low; widely spaced, vertical pillars may branch upwardly, of circular cross section, sometimes hollow, their lumen connecting with that of overlying chamber; imperforate vesicles may be present in earlier chambers; endopores, interpores, and exopores essentially the same, mostly small, closely spaced, and ranging from circular to elongate to subpolygonal or lobate; a few larger, circular pores may be present; trabecular microstructure a feltwork of aragonite needles of vaceletid type (CUIF & others, 1979, p. 460); no spicules known. [Genus is similar to Vaceletia PICKETT, 1982.] Permian (Guadalupian)-Upper Cretaceous: China (Hubei), Guadalupian; Europe, Turkey, Iran, Tajikistan, Triassic; Peru, Morocco, Iran, Lower Jurassic; USA (Texas), Upper Cretaceous.——FIG. 476a-c. \*S. dehmi, Raibler beds, Carnian, Karwendel, Austria; a, transverse section of lower part of holotype with porous walls of circular chambers around narrow spongocoel, and with widely spaced, radial pillars in chambers, 4 mm above base of sponge, BSPGM G 416 a/67, ×4; b, transverse section of holotype above that of view a, with chamber wall cut tangentially near center where pores are well shown, and sections of pillars relatively uniformly distributed in inner two chambers, around spongocoel, 6 mm above base of sponge, BSPGM G 418 a/67, ×4; c, schematic, longitudinal section showing position of transverse sections, view a at level 2 and view b at level 4 (Ott, 1967a; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- Vaceletia Pickett, 1982, p. 241, nom. nov. pro Neocoelia Vacelet, 1977b, p. 509, non McKellar,

1966 [\*Neocoelia crypta VACELET, 1977b, p. 509; OD]. Cylindrical, externally segmented, upper surface domical, sometimes branching; cloaca narrow, about one-eighth sponge diameter; exowall netlike, with subpolygonal or lobate exopores; outer surface of exowall granular and microspinose, microspines alternate with micropores of same diameter; upper surface of interwalls and inner surface of endowall (lining cloaca) same as outer surface of exowall, with interpores and endopores same size and shape as exopores; lower surface of interwall, chamber size of endowall, and surface of pillars, smooth; earlier chambers filled in by secreted sclerosome in layers concave distally; patches of smooth, calcareous deposit partly or wholly cover abandoned, basal part of skeleton exterior, ultimately closing over exopores; trabecular microstructure irregular feltwork of aragonite needles; spicules absent. [Genus is similar to Stylothalamia OTT, 1967a.] Cretaceous (Campanian)-Holocene: Spain, Campanian; Australia, Indo-West Pacific, Eocene-Holocene.-FIG. 477, 1a-c. V. progenitor PICKETT, Pallinup Siltstone, upper Eocene, north of Walpole, Western Australia; a, side view of holotype showing cylindrical branches and minor annulations associated with incremental growth, WAM81.2729, ×1; b, diagonal surface across walls into spongocoel with apopores in gastral layer and irregular, fibrous skeleton, ×10; c, reverse side of fragment with chamberlike increments with pillars and connecting bars, and dermal layer with numerous uniform prosopores, WAM 81.2734, ×10 (Pickett, 1982).

- Vascothalamia REITNER & ENGESER, 1985, p. 162 [\*V. arayaensis; OD]. Steeply obconical to subcylindrical sponges with spongocoel of nearly constant diameter throughout, except in juvenile part of skeleton, and wall with irregular canal system except in juvenile part where not developed; thickened structure of gastral layer producing small apopores; megascleres in basal skeleton monaxons (possible oxeas). Cretaceous (upper Albian): northern Ŝpain. --Fig. 475,2a-c. \*V. arayaensis, limestone reef rubble, lower upper Albian, Ort Araya; a, longitudinal section with thickened, gastral layer to spongocoel and irregular, fibrous skeleton, ×5; b, transverse section through gastral layer around spongocoel and parts of surrounding chamber, ×10; c, oxea megasclere in transverse element of wall, PIFUB 85/3, ×100 (Reitner & Engeser, 1985).
- ?Wienbergia CLAUSEN, 1982, p. 111 [\*Barroisia faxensis RAVN, 1899, p. 24; OD]. Cylindrical with central cloaca approximately one-fifth sponge diameter; chambers moderately high; exopores subpolygonal. [Apart from somewhat higher chambers and absence of branching, genus does not differ from Verticillites DE FRANCE, 1829.] Paleogene (Danian): Denmark.—FIG. 477,2a-c. \*W. faxensis (RAVN), coral limestone, middle Danian, Fakse Sjaelland; a, polished, vertical section (inverted) of lectotype showing central spongocoel and arcuate, sediment-filled chambers with pillars, MMH 15345, ×1; b, side view of exterior of paralectotype showing ornamentation on outer

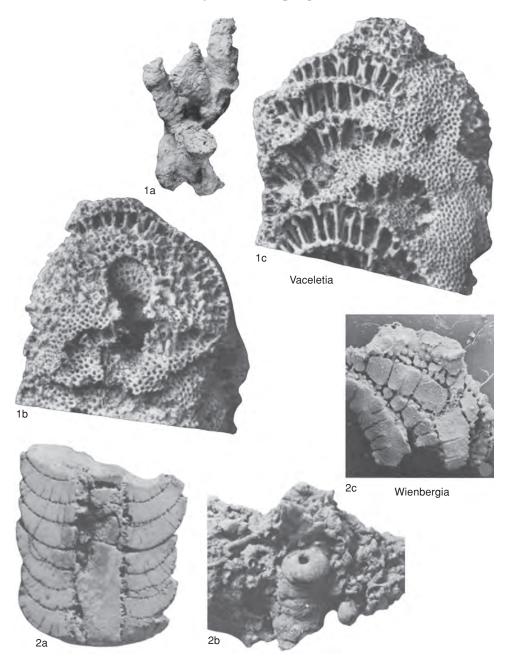


FIG. 477. Verticillitidae (p. 717–719).

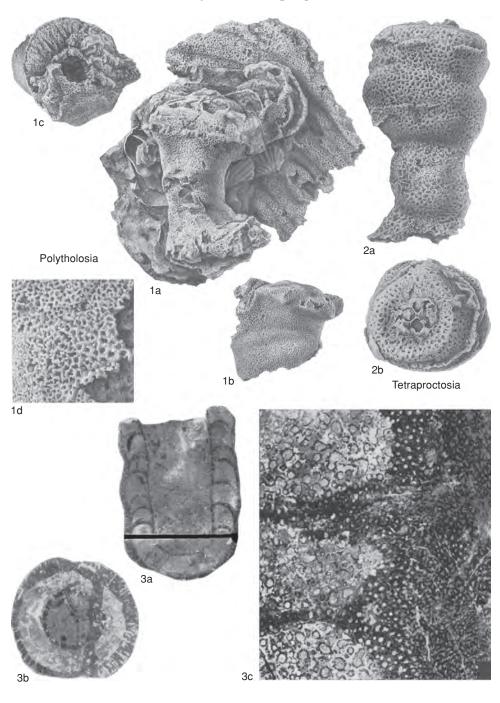
walls, J. P. J. Ravn collection,  $\times 1.5$ ; *c*, details of reference specimen showing chamber interwalls and vertical pillars between them,  $\times 10$  (Clausen, 1982).

# Subfamily POLYTHOLOSIINAE Seilacher, 1962

[*nom. transl.* FINKS & RIGBY, herein, *ex* Polytholosiidae SEILACHER, 1962, p. 785] [=Ascosymplegmatidae BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 168]

Chambers relatively high; no vertical pillars; trabeculae within chambers may outline branching and anastomosing, radial tubes; microstructure not known, but assigned to Verticillitidae on basis of lobate exopores. *Permian (?Lopingian), Triassic.* 

- ?Polytholosia RAUFF, 1938, p. 186 [\*P. complicata; OD] [=?Tetraproctosia RAUFF, 1938, p. 180 (type, T. peruana, OD)]. Cylindrical; exowall netlike with closely spaced, subpolygonal, lobate, or confluent exopores; cloaca one-third to one-fourth sponge diameter; interwall similar to exowall but pores slightly larger; endopores much larger than exopores and interpores; chambers moderately high and partly filled by trabeculae that outline anastomosing, radial tubes leading to endopores; trabeculae chiefly developed on surfaces of interwalls. Trabecular microstructure unknown; no spicules known. [SEILACHER (1962, p. 764-767) described a species from Nevada in which tubes converge inwardly from exopores to form large, radial canals that connect by small canals with parallel, large, radial canals that branch toward endopores, often via a longitudinal canal running along chamber side of endowall; bundle of vertical tubes may substitute for cloaca in early chambers, and diaphragm-like, horizontal, imperforate partitions may occur in lower part of cloaca proper.] Permian (?Lopingian), Triassic: Tunisia, China (Guizhou), ?Lopingian; Peru, USA (Nevada), Triassic; Italy (Sicily), Canada (Yukon), Pamir region, Tajikistan, Norian--FIG. 478, 1a-d. \*P. complicata, Triassic Rhaetian. chert, Ladinian, Nevada Acrotambo near Huacrachuco, Peru; a, side view of subcylindrical type specimen, in lower center and upper right center, intergrown and capped with sheets of Ascosymplegma, upper part and right; b, side view of second type specimen with chambers and porous exowall; c, view from above of same specimen with central spongocoel and radial canals on upper, chamber wall,  $\times 1$ ; *d*, enlarged view of exowall with angular pores that range somewhat in diameter,  $\times 3$ (Rauff, 1938).
- Ascosymplegma RAUFF, 1938, p. 195 [\*A. torosum; OD]. Flat, curving, or undulose sheets whose complete shape is unknown; one species (not type) has fingerlike protrusions; chambers of type species resemble laterally elongate Guadalupia chambers, that is, elongate parallel to growing edge of sponge, pinching out laterally in usual quincuncial arrangement; in other species, however, and in parts of type species, chambers so elongate that they do not terminate laterally within fragmentary specimens; in longitudinal section interwalls meet one surface tangentially and other almost perpendicularly-by analogy with Guadalupia tangent surface is exowall (inhalant) side and perpendicular surface is endowall-trabecularium (exhalant) side [sides of sponge referred to by SEILACHER (1962, pl. 8) and by DIECI & others (1968, pl. 31) as lower and upper, respectively]; no trabecularium apparent; exopores and interpores smaller than endopores; interpores may be secondarily closed and interwalls thickened; walls netlike and pores subpolygonal, especially visible on endowall, with its larger pores, where endopores may be stellate from incipient growth of fibers across them. [The walls and pores are reminiscent of those of Vaceletia PICKETT, 1982; there is a suggestion of trabecular infilling of chambers in some specimens; microstructure is unknown; no spicules are known. May be a synonym of Discosiphonella INAI, 1936.] Triassic: Peru, USA (Nevada), Canada (Yukon), Italy, Russia (Caucasus region).-FIG. 479a-c. \*A. torosum, Triassic chert, ?Ladinian, Acrotambo near Huacrachuco, Peru; a, side view of type showing growth form of chamberlike sheets, overgrowing type of Polytholosia, behind; b, convex, arched growth of chambered-appearing, lower part of type specimen, ×1; c, enlarged view of chamber exowalls with numer-
- ous exopores, ×2 (Rauff, 1938). Nevadathalamia SENOWBARI-DARYAN, 1990, p. 81 [\*Polytholosia cylindrica SEILACHER, 1962, p. 764; OD]. Chambers catenulate in single or branching stems with a retrosiphonate spongocoel and tubular filling structure; pores simple or multiple branched; vesiculae missing or only rarely present. Triassic (Norian-Rhaetian): USA (Nevada), Mexico (Sonora), Canada (Yukon), Austria, Iran.-—Fig. 478, 3a-c. \*N. cylindrica (SEILACHER), Luning Formation, Norian, Pilot Mountains, Nevada; a, longitudinal section of reference specimen showing porous chambers, some with isolated vesiculae, around large spongocoel, ×1; b, transverse section showing endowall around spongocoel thinner than exowall, but both porous,  $\times 1$ ; *c*, outer surface of holotype showing outer sculpture on right, with arcuate, porous, chamber walls in center and tubular filling



Nevadathalamia

FIG. 478. Verticillitidae (p. 719–721).

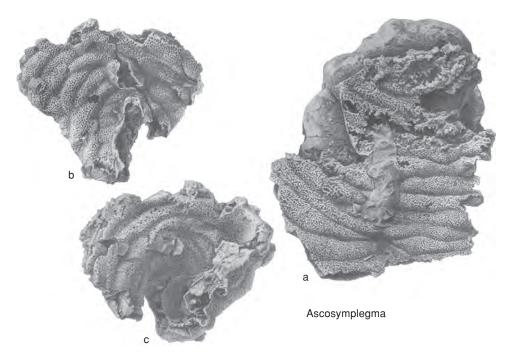


FIG. 479. Verticillitidae (p. 719).

structures in chambers on left, ×2 (Seilacher, 1962).

?Tetraproctosia RAUFF, 1938, p. 180 [\* T. peruana; OD] [=?Polytholosia RAUFF, 1938, p. 186 (type, P. complicata, OD)]. Conicocylindrical but basally expanded for attachment; exowall netlike with closely spaced, subpolygonal, lobate or confluent exopores; cloaca one-third sponge diameter, but subdivided into four subpolygonal, subequal openings at oscular end of sole specimen; interior structures unknown. [This may be an individual variant of Polytholosia RAUFF, 1938, with which it occurs; the exowall is the same.] Triassic: Peru, Pamir region, Tajikistan.-FIG. 478,2a-b. \*T. peruana, Ladinian beds, Middle Triassic, near Huacrachuco, Nevada de Acrotambo, Cordillera blanca, Peru; a, side view, chambered sponge with flared foot, and projecting nodes of tetraproct opening on upper, oscular end, ×2; b, view of tetraproct opening in oscular area, ×2 (Rauff, 1938).

# Subfamily FANTHALAMIINAE Senowbari-Daryan & Engeser, 1996

[Fanthalamiinae SENOWBARI-DARYAN & ENGESER, 1996, p. 269, nom. nov. pro Faniinae SENOWBARI-DARYAN, 1990, p. 83, based on invalid junior homonym]

Polytholosiids with moniliform to uviform arrangement of chambers; without spongocoel. *Triassic (Carnian–Norian,* ?*Rhaetian*).

- Fanthalamia SENOWBARI-DARYAN & ENGESER, 1996, p. 269, nom. nov. pro Fania SENOWBARI-DARYAN, 1990, p. 83, non BARNES & MCDUNNOUGH, 1911 [\*Polytholosia astoma SEILACHER, 1962, p. 760; OD]. Moniliform to irregular stems without spongocoel; exhalant openings or oscula may be developed with various spacing; filling structure is of tubular type and rudimentary to absent; pores are multiple branched; vesiculae have not been observed. Triassic (?Carnian, Norian): Turkey, Russia, ?Carnian; USA (Nevada), Mexico (Sonora), Canada (British Columbia), Norian.-FIG. 480, 1a-c. \*F. astoma (SEILACHER), Luning Formation, Norian, Cedar Mountains, Nevada; a, branched holotype, ×2; b, section of holotype with skeletal pores and ostia between branches of holotype,  $\times 5$ ; *c*, longitudinal section of three stems with chambers of one on left with tubular filling structures, ×1 (Seilacher, 1962).
- Cinnabaria SENOWBARI-DARYAN, 1990, p. 85 [\*Ascosymplegma expansum SEILACHER, 1962, p. 768; OD]. Dish- or saucer-shaped sponges composed of numerous overlapping, tubular chambers arranged in radially concentric or moniliform, stacked series; chamber or segment walls with branching pores; filling structure rudimentary and of granular type through which thick tubes may develop; without spongocoel and vesiculae. *Triassic (Carnian–Norian,* ?Rhaetian): Turkey (Taurus Mountains), *Carnian;* USA (Nevada), Canada (Yukon, British Columbia), India (Himalayan Mountains), Mexico, Norian; Austria, ?Rhaetian.——FIG. 480,2a-b. \*C. expansum (SELACHER), Luning Formation, Norian,

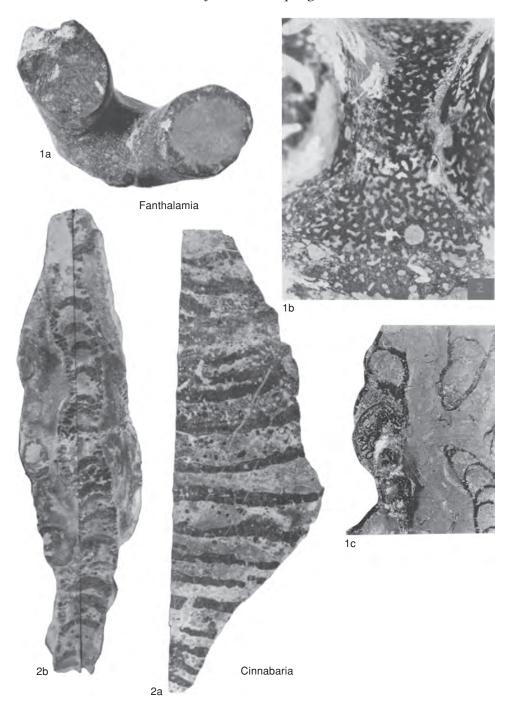


FIG. 480. Verticillitidae (p. 721–723).





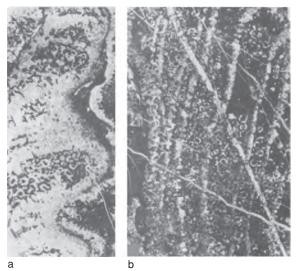
FIG. 481. Verticillitidae (p. 724).

Mina, Mineral County, Nevada; *a*, section normal to plate showing cross sections of stacked, arcuate chambers with porous walls,  $\times 1$ ; *b*, section cut parallel to plate showing long, tubular chambers, SPIT, collections of A. Seilacher,  $\times 1$  (Senowbari-Daryan, 1990; courtesy of *Münchner Geowissenschaftliche Abhandlungen*, Verlag Dr. Friedrich Feil).

# Subfamily POLYSIPHOSPONGIINAE Senowbari-Daryan, 1990

[Polysiphospongiinae SENOWBARI-DARYAN, 1990, p. 88]

Polytholosiids with glomerate arrangement of chambers or segments and with



Platysphaerocoelia

FIG. 482. Uncertain (p. 724).

# through-going spongocoel. *Triassic (Norian–Rhaetian)*.

Polysiphospongia SENOWBARI-DARYAN & SCHÄFER, 1986, p. 249 [\*P. fluegeli; OD]. Sphinctozoans with glomerate arrangement of chambers and tubular filling structure; central canal bundle consisting of multiple, separate canals; canal structure pro- to retrosiphonate. Triassic (Norian-Rhaetian): Italy (Sicily).——FIG. 481*a*-b. \*P. fluegeli, Reef limestone, Norian, Palermo; *a*, longitudinal section of holotype showing prominent, glomerate chambers along margin and irregularly canaled interior lateral to axial cluster of exhalant canals, SPIE P/126/1, ×1.5; *b*, parallel section of holotype that intersects axial cluster of exhalant canals in upper part, and low chambers in lower part, SPIE P/126/2, ×1.5 (Senowbari-Daryan & Schäfer, 1986).

## Family UNCERTAIN

Platysphaerocoelia BOIKO in BOIKO, BELYAEVA, & ZHURAVLEVA, 1991, p. 158 [\**P. aksuensis*; OD]. Massive colonies composed of flat and wide chambers; chamber interiors containing empty, spherical, skeletal elements of various sizes; chamber exowalls thicker than interwalls and with numerous uniform pores. [Genus somewhat similar to *Intrasporocoelia* and *Rhabdactinia* but with massive growth form and in having spherical, skeletal elements forming walls and as filling structures.] *Triassic (Norian–Rhaetian):* Russia (Tajikistan and Pamir regions). ——FIG. 482a-b. \**P. aksuensis,* Triassic limestone, Tajikistan; *a*, tangential section showing chamber cal filling structures; *b*, subvertical section showing

broad chambers with numerous hollow filling structures, ×2 (Boiko, Belyaeva, & Zhuravleva, 1991).

# Subclass TETRACTINOMORPHA Lévi, 1953

[nom. correct. BERGQUIST, 1967, p. 166, pro subclass Tétractinomorphes LEVI, 1953, p. 855]

Generally radiate architecture with ectosomal crust of microscleres; triaenes present in some but not all groups; microscleres asters or sigmaspires; basal skeleton, when present, almost always calcite. Ordovician–Holocene.

# Order HADROMERIDA Topsent, 1898

[nom. correct. DE LAUBENFELS, 1955, p. 39, pro suborder Hadromerina TOPSENT, 1898, p. 93]

Megascleres exclusively tylostyles and other stylote spicules; microscleres (when present) various forms of euasters, spirasters, and microrhabds; architecture radiate with ectosomal crust of microscleres when present; basal skeleton, when present, magnesian calcite, of either lamellar, homogeneous-granular, or penicillate microstructures. [The living *Merlia* KIRKPATRICK, 1908, has been placed in a separate but related order Merliida by VACELET (1979) although others (e.g. HARTMAN & GOREAU, 1970) have placed it in the order Poecilosclerida. The Carboniferous and later *Chaetetes* FISCHER DE WALDHEIM, 1830 in 1830–1837, with its relatives, also may either belong here or with the Poecilosclerida. Both groups have basal skeletons of penicillate calcite unlike other hypercalcified hadromerids.] *Permian– Triassic.* 

#### Family CELYPHIIDAE de Laubenfels, 1955

[Celyphiidae DE LAUBENFELS, 1955, p. 102; emend., FINKS & RIGBY, herein] [=Celyphiidae DE LAUBENFELS, 1955, p. 102, partim; Annaecoeliidae SENOWBARI-DARYAN, 1978, p. 206, partim; Pisothalamiidae SENOWBARI-DARYAN & RIGBY, 1988, p. 203; Alpinothalamiidae SENOWBARI-DARYAN, 1990, p. 137]

Sphinctozoan morphology with hemispheroidal or spheroidal chambers, either glomerate-encrusting or cateniform; filling tissue often of branching tubes; wall structure lamellar; microstructure of microgranular magnesian calcite in those genera that have been investigated; spicules found in some genera include euaster and spiraster microscleres and various monaxon megascleres but not styles. Assignment to order based on mineralogy, microstructure, and microscleres. *Permian (Guadalupian)– Triassic.* 

Celyphia POMEL, 1872, p. 229 [\*Manon submarginatum MÜNSTER, 1841, p. 27; OD]. Earlier chambers smaller than later ones; spheroidal to hemispheroidal chambers encrusting shells or one another to form irregular clusters; exowall imperforate except for large, circular exopores (or oscules) with strong lips or short exauli; interior of chamber containing branched tubules that diverge interiorly from each exopore and open into chamber lumen; still finer trabecular tissue and vesicles have been mentioned and illustrated by various authors, but unclear whether latter specimens are conspecific (or congeneric) with type; exowall structure reported as laminar. [This genus bears some resemblance to protocysts of the agelasid Girtyocoelia COSSMAN, 1909, which are similarly adnate and without the cloaca of the adults. Celyphia, however, is not spherulitic, and has the wall structure of other members of this family, which are more clearly hadromerids. It is possible Celyphia is a juvenile stage of some other genus or else a paedomorphic adult. Branching tubules under each exopore could be analogues of the cribribullae of Girtyocoelia, or they could be exhalant systems as in Pisothalamia (or some one and some the other).] Permian (Wordian)-Cretaceous (Cenomanian): Russia, China, Wordian-Capitanian; Italy, Austria, Hungary, Tajikistan (Pamir region), Turkey, Yugoslavia, Lower Triassic-Upper Triassic; ?Germany, Cenomanian.

- Alpinothalamia SENOWBARI-DARYAN, 1990, p. 137 [\*Cystothalamia bavarica OTT, 1967a, p. 36; OD]. Gross porate to aporate stems composed of glomerate chambers that are in two or more layered positions (polyglomerate), with one or more axially located canal clusters that have a retrosiphonate structure; filling structures absent, but with vesiculae; skeleton of high magnesium calcite with a homogenous, granular microstructure. Middle Triassic-Upper Triassic: Italy, Austria, Yugoslavia, Hungary, Greece, Turkey, Oman, Russia.----FIG. 483,1a-b. \*A. bavarica (OTT), Wettersteinkalk, Middle Triassic, Karwendel-Gebirges, Austria; a, holotype with coarsely porous, axial spongocoel and polyglomerate chambers, BSPGM 1967 II 9, ×2; b, section of counterpart of holotype with multiple, largely imperforate chambers around axial spongocoel and common vesiculae, BSPGM 1331 a/67, ×3.5 (Ott, 1967a; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- Cassianothalamia REITNER, 1987a, p. 573 [\*C. zardinii; OD]. Conical, occasionally branching, with hemispherical, upper surface; narrow, central cloaca appearing in later ontogenetic stages; chambers low, formed by overlapping, hemispherical interwalls connected by numerous vertical pillars that are cylindrical to submeandroid in cross section; neither endowall nor exowall well defined; interpores small, circular, and closely spaced; thin, vertical vesicles connecting pillars occur in earlier, abandoned parts of skeleton; rare spicules found imbedded in skeleton, namely, spiraster and sterraster microscleres and monaxon megascleres; skeleton itself of homogeneous-granular magnesian calcite, found also in Jablonskya, Uvanella, and Zardinia (MASTANDREA & RUSSO, 1995, p. 423). Triassic (Carnian): Austria, Italy, Turkey.--Fig. 484, 3a-d. \*C. zardinii, Cassian Formation, Seeland-Alpe, Dolomite Alps, Italy; a, side view of holotype showing globular form and common, inhalant ostia, ×2; b, view from above showing osculum of shallow spongocoel and uniform, inhalant ostia, MCCA, ×2; c, longitudinal section of paratype showing spongocoel cavity and skeletal structure, PIFUB 87/2, ×4; d, transverse section of paratype showing concentric interwalls and radiating pillars around small spongocoel, PIFUB 87/1, ×1 (Reitner, 1987a; courtesy of Geobios).
- Jablonskyia SENOWBARI-DARYAN, 1990, p. 140 [\*Colospongia andrusovi JABLONSKY, 1975, p. 267; OD]. Catenulate sponge built of hemispheroidal to barrel-shaped chambers without cloaca or endowall; numerous exopores or interpores; chamber interior filled with vesicles in earlier chambers; wall microstructure microgranular magnesian calcite; spicules originally described considered to be pseudospicules by SENOWBARI-DARYAN (1990, p. 140). Triassic (Carnian–Norian): Austria, Italy, Yugoslavia, Romania, Greece, Turkey.—FIG. 485,2a–b.

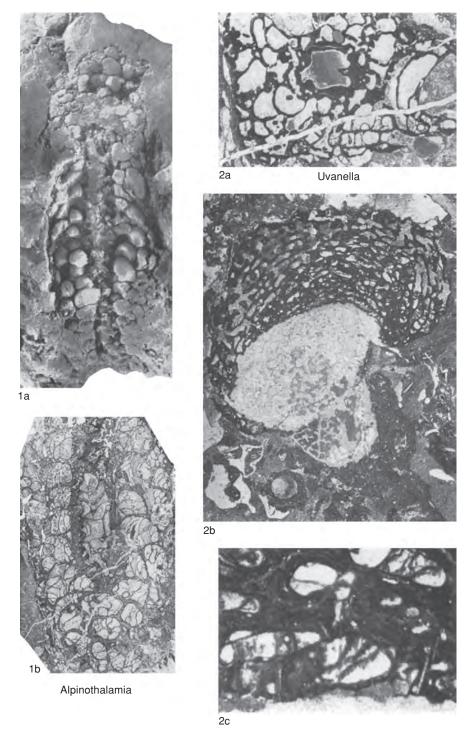
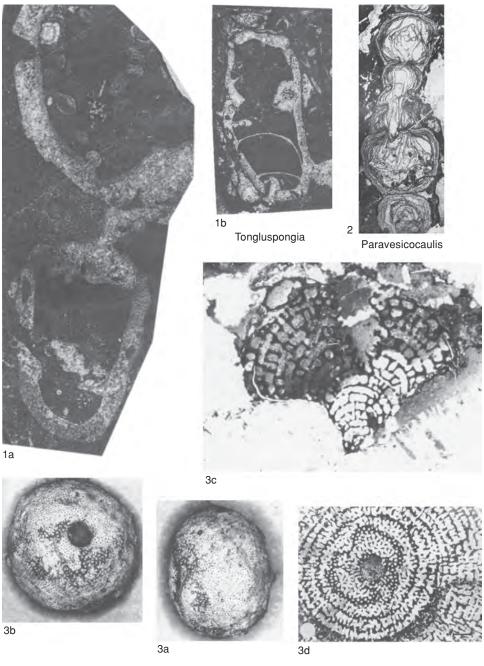


FIG. 483. Celyphiidae (p. 725–732).



Cassianothalamia

FIG. 484. Celyphiidae (p. 725–732).

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\*J. andrusovi (JABLONSKY), San Cassiano Formation, Carnian, Norian, Dolomite Alps, Austria; *a*, longitudinal section with porous walls to hemispheroidal chambers and with vesiculae in early chambers, but absent in later ones, SPIE D/69/9/4, ×4; *b*, transverse sections of two specimens showing light, pore fillings in dark, chamber walls, with vesiculae in chamber interiors, SPIE H/52, ×4 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

- Leinia SENOWBARI-DARYAN, 1990, p. 144 [\*L. schneeburgensis; OD]. Porate, cylindrical sponge made of very low and shield-shaped chambers or segments; spongocoel retrosiphonate, extending through sponge; chambers hollow, without vesiculae; basal skeleton composed of high magnesium calcite with granular microstructure; spicules unknown. Triassic (Carnian): Austria, Greece (Hydra).-FIG. 486,1a-b. \*L. schneeburgensis, Upper Triassic limestone, Carnian, Hochschwab, Austria; a, longitudinal thin section, holotype, with low, shield-shaped chambers and retrosiphonate spongocoel, chambers walls porous, SPIE 29E26/2, ×1.5; b, oblique section of reference specimen with broad spongocoel and with porous chamber walls, SPIE E23/1, ×1.5 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).
- Loczia VINASSA DE REGNY, 1901, p. 16 [\*L. cryptocoelioides; OD]. Conicocylindrical; coated with dermal layer bearing widely and irregularly spaced, small pores; no osculum on rounded, upper surface, which also bears dermal layer; interior with closely spaced, horizontal, skeletal elements connected by less continuous, vertical ones, suggesting latilaminae and pillars of a stromatoporoid, with central area in which vertical elements are more continuous; trabecular microstructure showing curvilinear elements parallel to course of skeletal elements, here interpreted as a laminar wall structure. Triassic: Hungary, Austria. FIG. 487, 2a-b. \*L. cryptocoelioides, Upper Triassic, Veszprém, Jeruzsálemhegy, Bakony, Austria, a, side view of typical specimen showing general growth form,  $\times 1$ ; b, enlarged vertical section of interior showing horizontal fibers and less continuous, vertical, pillarlike fibers, approximately ×3 (Vinassa de Regny, 1901).
- Montanaroa Russo, 1981, p. 12 [\*M. dolomitica; OD]. Spheroidal, cateniform, summit opening a circular, cribrate plate surrounded by low rim; same structure serving as interpores between chambers; remainder of exowall imperforate except for rare, lipped ostia; no internal structures except for occasional, thin vesicles lining inner surface of exowall; exowall layered with irregular microstructure. [The layered wall and summit cribrate plate as in Pisothalamia are the principal reasons for placing this genus in the family.] Triassic (Carnian): Italy. -FIG. 487, 3a-d. \*M. dolomitica, San Cassiano Formation, Cortina d'Ampezzo, Dolomite Alps; a, side view of chambered holotype,  $\times 9$ ; b, view of summit of holotype with cribrate osculum, IPUM 19295, ×9; c, longitudinal section showing cham-

bered growth and cribrate oscula, ×8; *d*, microstructure of irregular type in layered wall, IPUM 19298, ×150 (Russo, 1981).

- Pamirocoelia BOIKO in BOIKO, BELYAEVA, & ZHURAV-LEVA, 1991, p. 133 [\*P. sphaerica; OD]. Chambers spherical to conical and forming glomerate colonies without central spongocoel or axial canal; distal part of chambers with up to four ostia covered with very thin, perforate membrane; chamber walls solid and imperforate.[Differs from related sponges in having the distinct, fine, porous membrane over the distal ostia in the imperforate wall and in absence of an axial exhalant structure.] Triassic (Norian-Rhaetian): Tajikistan.-FIG. 487,1a-c. \*P. sphaerica, Triassic limestone, southeastern Pamir, River Karauldandaly; a, cluster of spheroidal chambers with coarse, inhalant ostia in thick walls, MIGT 191-x-1,116/4, ×3; b, transverse section with distinctive inhalant canals in pore fields and possible small, central, exhalant canal in center, MIGT 191-x-1, 116/4, ×10; c, photomicrograph of section through pore field in lower left of b, with screen over ostia shown only as aligned, dotlike sections of elements, MIGT 191-x-1, 116/4, ×25 (Boiko, Belyaeva, & Zhuravleva, 1991).
- Paravesicocaulis Kovács, 1978, p. 689 [\*P. concentricus; OD]. Spheroidal segments forming chain; exowall pierced by very small, closely spaced exopores (150 to 200 µm); endowall apparently absent, but vesicles subparallel with exowall filling chambers and outlining discontinuous, central, tubular space corresponding to cloaca; more widely spaced vesicles, some horizontal, may occur in this space; interwall merely two exowalls in contact, pierced by central opening width of cloaca, which corresponds to terminal osculum; wall said to be nonspherulitic and composed of several layers; no spicules known. Triassic (Ladinian-Rhaetian): Austria, Hungary, Yugoslavia, Ladinian-Carnian; Italy (Sicily), Greece, Iran, Tajikistan, Norian-Rhaetian.—FIG. 484,2. \*P. concentricus, Wetterstein reef limestone, Ladinian-middle Carnian, Tornanádaska, northern Hungary; longitudinal section of holotype of spheroidal chambers with vesicles that outline central, tubular space equivalent to spongocoel in some, and with interwalls as double exowalls, MHGI T-430/A, ×5 (Kovács, 1978; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- **Pisothalamia** SENOWBARI-DARYAN & RIGBY, 1988, p. 206 [\**P. spiculata;* OD]. Spheroidal segments; central, circular oscule one-fifth sponge diameter or less, in a depression of exowall that bulges downwardly to form spheroidal, cribribulla-like structure bearing small, closely spaced interpores; exowall bearing numerous, scattered, large, circular exopores, each of which bears internal cribribulla; very small exopores between them connect with branching tubes within exowall; chambers lined with lamellar, secondary tissue that also invests partly fused, oolith-like bodies that fill lower parts of chamber; comparable lamellar tissue fills oscular cribribulla, lamellae run upwardly and inwardly to

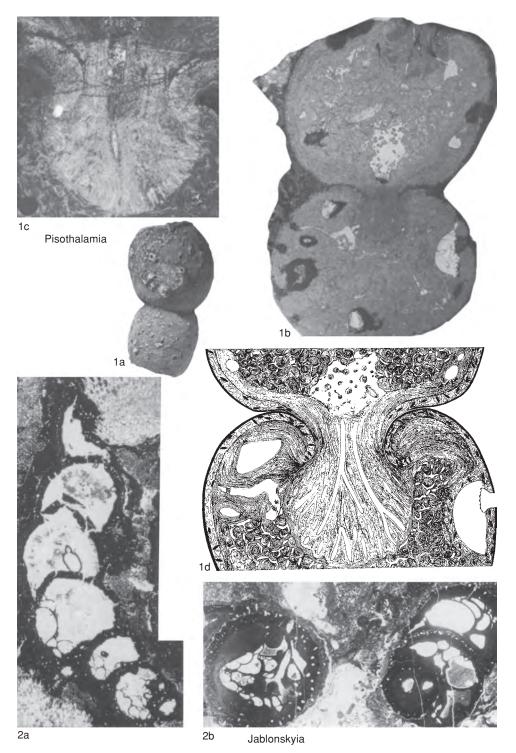


FIG. 485. Celyphiidae (p. 725–732).

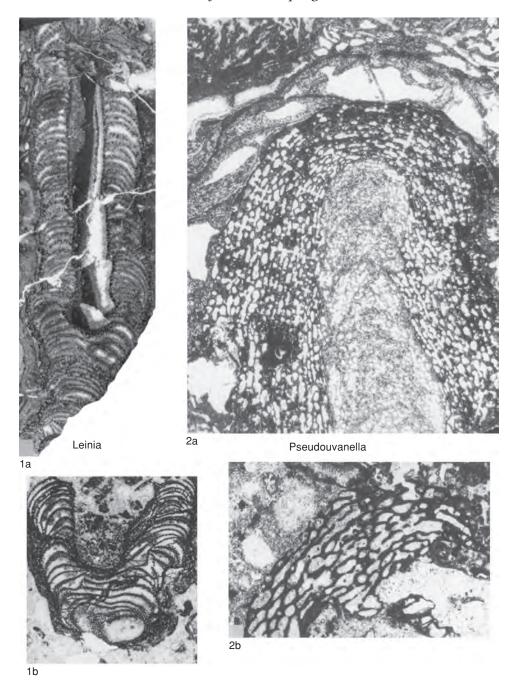


FIG. 486. Celyphiidae (p. 728-732).

outline subparallel, dendritic canals that arise at interpores and converge upwardly; imbedded in exowall are thin, curved, oxea or strongyle-like bodies (presumably limonite after pyritized opal) that are irregularly arranged, but more concentrated near oscule, and occasionally occur in lamellar tissue, especially near cribribullae. [Apart from the spicules and the ooids, the latter of which also occur in the agelasid *Intrasporeocoelia* FAN & ZHANG, 1985, the structure of this sponge resembles the

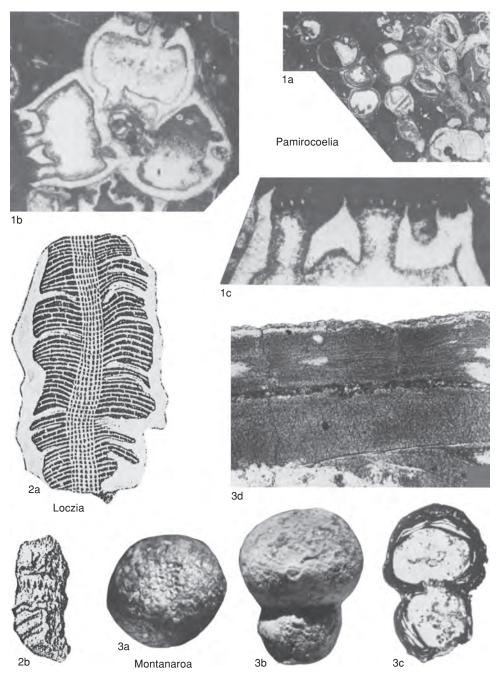


FIG. 487. Celyphiidae (p. 728).

thaumastocoeliids, but even more *Montanaroa* RUSSO, 1981, which has an oscular cribribulla. The lamellar tissue and ooids may be secondary deposits formed as the sponge tissue withdrew from the chamber, and correspond to vesicles of other sphinctozoans, but are here interpreted as homologues of the branching tubes present in *Celyphia* and other members of the family.] *Permian (Lopingian):* Tunisia.—FIG. 485,1*a*-*d.* \**P. spiculata*, Djebel Tebaga Biohermal Complex, Changhsingian, Djebel Tebaga; *a*, small paratype with several rimmed ostia in each chamber, USNM 427421,  $\times 2$ ; *b*, longitudinal section of holotype with saclike structures in oscular areas in each of two chambers,  $\times 2$ ; *c*, peel of structure between chambers showing canal details and laminate structure,  $\times 5$ ; *d*, drawing of oscular system between chambers showing complex canal pattern and laminate structure, as well as dark, rodlike spicules in exowalls and interwalls and pisoid filling structures within chambers, not to scale (Senowbari-Daryan & Rigby, 1988; courtesy of *Facies*).

- Pseudouvanella SENOWBARI-DARYAN, 1994a, p. 422 [\*P. parallela; OD]. Aporate and incrusting sponges composed of numerous oblong segments, whose long axis developed perpendicular to growth direction; segment walls not straight but bent undulatory or wavy; in various places upper or younger wall of chamber bends backwardly or downwardly to form column with broad base; locally merger of chamber walls produces walls double thickness of regular segment walls; pillars similar to those of stromatoporoids or stylothalamiids, very numerous; vesiculae may be developed locally in some chambers; spicules unknown. [Placement in the family is uncertain, but the genus appears similar to Uvanella and it is tentatively included here.] Triassic (Norian): Turkey.—FIG. 486,2a-b. \*P. parallela, Cipit limestone, lower Norian, Taurus Mountains, southern Turkey; a, holotype with relatively thick walls of oblong segments, encrusting inozoan sponge and, in turn, encrusted by sponge with lenticular structure, SPIE "Trias Türkei" 19 F29/2, ×4; b, section of irregular, older, interconnected segments of reference specimen, SPIE "Trias Türkei" 19 G102/4, ×10 (Senowbari-Daryan, 1994b).
- Tongluspongia BELYAEVA, 2000, p. 42 [156] [\* T. yangae; OD]. Sponge with large, irregularly shaped, noncatenulate chambers that are irregularly joined with or without tubes; chamber walls with outer, granoblastic layer and inner, faintly recrystallized layer with spherulitic relicts; walls massive, imperforate but pierced by large, isolated, solitary ostia that may have rims or extend short distances above walls; walls may contain a few monaxial spicules; vesiculae or outgrowths of skeletal material from walls may occur in chamber interiors. upper Permian (Wuchiapingian): China (Zhejiang Prov--FIG. 484, 1a-b. \*T. yangae, Maokou Forince).mation, Maokouan, Tonglu; a, holotype, diagonal, longitudinal section of large, irregular, thick-walled chambers, with coarse, thick, outer layer and thinner, finer textured, inner layer, both pierced by coarse ostia, FEGI no. 165-MB, no. 14(2), ×5; b, longitudinal section with arched vesiculae in lower part of chamber, and coarse-textured, thick chamber walls, FEGI no. 14(4),  $\times 2$  (Belyaeva, 2000).
- Uvanella OTT, 1967a, p. 38 [\*U. irregularis; OD]. Hemispheroidal, encrusting masses of more or less concentrically layered, blisterlike chambers or irregular, interconnecting spaces between latilaminalike and pillarlike structures reminiscent of stromatoporoids; chambers intercommunicate

through small, irregular pores in their walls; chambers of earlier, abandoned parts of skeleton filled with thin-walled vesicles crossing narrow, vertical dimension of chamber; wall microstructure irregularly laminar of homogeneous-granular magnesian calcite (MASTANDREA & RUSSO, 1995, p. 423); one specimen contains vertically oriented oxeas in its basal part, the spicules crossing chamber lumens and walls alike. [It is possible that these spicules belong to the underlying inozoan sponge on which the Uvanella is growing.] middle Permian-Triassic (Rhaetian): China (Guangxi), middle Permian-upper Permian; Europe, Alpine-Mediterranean area, Ladinian-Carnian; Italy (Sicily), Greece, Iran, Oman, Tajikistan, ?Canada (Yukon), Norian-Rhaetian.—FIG. 483,2a-c. \*U. irregularis, Wettersteinkalk, Norian, Jovenspitze, Austria; a, holotype, tangential section showing irregular chambers and distinct pores in walls, BSPGM 1340 a/67, ×5; b, longitudinal section of reference specimen encrusting an inozoan, showing layered, blisterlike chambers and vesiculae in early chambers, BSPGM G 411 a/67, ×5; c, photomicrograph of walls of basal chambers with monaxon spicules, which may be from encrusted sponge below, BSPGM 1340 a/67, ×40 (Ott, 1967a; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).

## Family CEOTINELLIDAE Senowbari-Daryan, 1978

[Ceotinellidae Senowbari-Daryan in Flugel, Lein, & Senowbari-Daryan, 1978, p. 165]

Aporate sponges with a reticular-tubular filling structure (in *Ceotinella* tubes developed exclusively in periphery); other segmentation hardly recognizable; basal skeleton composed of high magnesium calcite with granular and homogenous microstructure; spicular skeleton not known. *Triassic* (*Ladinian–Carnian*).

Ceotinella PANTIC, 1975, p. 154 [\*C. mirunae; OD]. Aporate, cylindrical to conicocylindrical sponges without, or with barely recognizable, outer segmentation, but interior segmented; segments separated in peripheral part of skeleton by radial, septal elements of erect, tubular-formed sections; reticular filling structures developed near spongocoel; through-going spongocoel ambisiphonate; skeletal microstructure granular. Triassic (Ladinian-Carnian): Yugoslavia, Ladinian; Austria, Yugoslavia, Greece (Hydra), Italy (Sicily), Turkey, Oman, Carnian.-FIG. 488,4. \*C. mirunae, Kleine Reef, Ladinian, Huda Juzna, Yugoslavia; transverse section with thick exowall and axial spongocoel, peripheral tubular-formed sections, and inner, reticulate filling structures, SPIE H/36/2, ×10 (Senowbari-Daryan, 1990; courtesy of Münchner Geowissenschaftliche Abhandlungen, Verlag Dr. Friedrich Feil).

Hadromerida

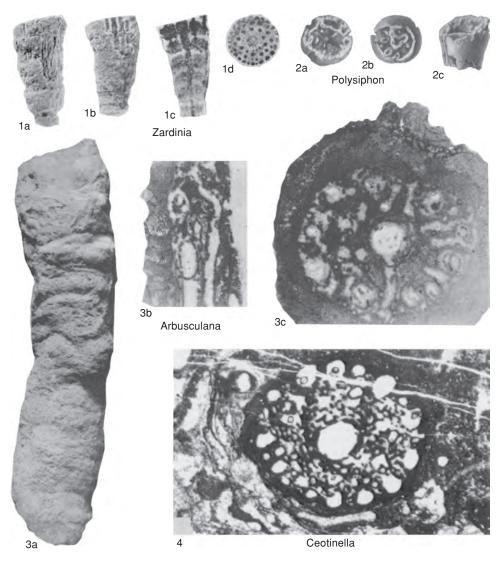


FIG. 488. Ceotinellidae and Polysiphonidae (p. 732-734).

#### Family POLYSIPHONIDAE Girty, 1909

#### [Polysiphonidae GIRTY, 1909, p. 86]

Cylindroid; narrow, central cloaca surrounded by ring of longitudinal canals, connected to cloaca by horizontal, radial canals; interwalls may be absent and external segmentation variably developed; fine, trabecular net may fill rest of chamber, but not in poorly preserved type genus; microstructure homogeneous-granular magnesian calcite in Zardinia but not known in other genera, which are assigned here on basis of resem-

## blance to Zardinia in gross morphology. Permian-Triassic.

Polysiphon GIRTY, 1909, p. 87 [\*P. mirabile; OD]. Conical fragments; imperforate exowall; discontinuous, narrow, central cloaca defined by imperforate endowall from which imperforate tubes branch upwardly and outwardly to end tangent to inner side of exowall, forming peripheral ring of tubes; intervening interior space empty as preserved. [Type material too fragmentary to characterize but resembles Arbuscula PARONA, 1933, and Zardinia DIECI, ANTONACCI, & ZARDINI, 1968.] Permian (Guadalupian): USA (Texas).——FIG. 488,2a-c. \*P. mirabile, Bell Canyon Formation, Guadalupe

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Mountains; *a*, silicified holotype from above; *b*, holotype from below; *c*, side view of holotype,  $\times 3$  (Girty, 1909).

- ?Arbusculana FINKS & RIGBY, herein, nom. nov. pro Arbuscula PARONA, 1933, p. 22, non BOLIVAR, 1855 [\*Arbuscula contortiplicata PARONA, 1933, p. 22; OD]. Cylindrical, with horizontal folds and grooves on surface; narrow, central cloaca; external pores fine, intertrabecular spaces; interior with fine, trabecular net that forms anastomosing tubules; halfway between outer surface and cloacal surface is a ring of large, longitudinal tubes of circular cross section, about half diameter of cloaca; large, radial canals enter cloaca through large pores and also communicate with longitudinal tubes through short branches; no interwalls; exowall and endowall not clearly differentiated from trabecular net; trabecular microstructure unknown; no spicules known. Permian: Italy (Sicily), USA (?Texas).-FIG. 488, 3a-c. \*A. contortiplicata (PARONA), Permian limestone, Palazzo di Adriano, Sosio, Sicily; a, side view of annulate, cylindrical sponge, ×1; b, longitudinal section with narrow spongocoel and somewhat smaller, subparallel, vertical canal, both as interruptions in trabecular, skeletal net,  $\times 2$ ; c, transverse section with axial spongocoel and ring of smaller, vertical tubes in outer part of sponge, in trabecular skeletal net, all part of syntype suite, ×2 (Parona, 1933).
- Zardinia Dieci, Antonacci, & Zardini, 1968, p. 139 [\*Z. perisulcata; OD] [=?Arbusculana FINKS & RIGBY, herein, p. 734, nom. nov. pro Arbuscula PARONA, 1933, p. 22 (type, A. contortiplicata, OD), non BOLIVAR, 1855]. Conical, externally segmented; narrow, central cloaca surrounded by ring of smaller, longitudinal canals near periphery of sponge and sometimes an additional ring or rings nearer cloaca; exowall present, exopores possibly absent; endowall with large, circular endopores; endowall thicker immediately above and below interwalls (ambisiphonate); interwalls with large, circular interpores corresponding to longitudinal canals, latter otherwise unbounded other than by trabecular ends; remaining interior of chambers filled with fine, trabecular net that defines anastomosing tubules of circular cross section; trabecular microstructure of homogeneous-granular magnesian calcite (MASTANDREA & RUSSO, 1995, p. 423); no spicules known. [Genus differs from Arbusculana FINKS & RIGBY (herein, p. 734, nom. nov. pro Arbuscula PARONA, 1933), in the presence of exowall, endowall, and interwalls, together with the resulting segmentation. Inasmuch as the same range of structure is shown within Fissispongia KING, 1938, Zardinia could be considered a junior subjective synonym of Arbusculana.] Triassic: Italy, Austria, Hungary, Yugoslavia, Greece, Turkey, Oman.—FIG. 488,1*a-d. \*Z. perisulcata*, San Cassiano Formation, Norian, Dolomite Alps, Italy; a, side view of weakly annulate holotype with some vertical, exhalant canals visible in upper part where dermal layer has been eroded away, IPUM 17597,  $\times 2.5$ ; b, side view of paratype with dense, dermal layer, below, and parts of vertical, exhalant canals,

above, IPUM 17598,  $\times 2.5$ ; *c*, longitudinal section of paratype showing chamber interwalls perforated by axial spongocoel and vertical, exhalant canals, IPUM 17599,  $\times 2.5$ ; *d*, transverse section at level of interwall with sections of central spongocoel and several vertical canals, IPUM 17600,  $\times 2.5$  (Dieci, Antonacci, & Zardini, 1968).

# Class CALCAREA Bowerbank, 1864

[Calcarea BOWERBANK, 1864, p. 160] [=class Calcispongea DE BLAINVILLE, 1834, p. 494, nom. transl. et correct. DE LAUBENFELS, 1955, p. 95, ex order Calcispongiae DE BLAINVILLE, 1834, p. 494; Calcarosa HAECKEL, 1872b; Megamastictora SolLus, 1887, p. 421]

Spicules and aspicular basal skeleton, if present, of magnesian calcite secreted extracellularly. Spicules include triradiates (three rays in one plane) and derived forms. *Lower Cambrian–Holocene*.

#### Subclass CALCINEA Bidder, 1898

#### [Calcinea BIDDER, 1898, p. 73]

Choanocyte nucleus basal; larva a parenchymella (coeloblastula); spicules normally include equiangular and equiradiate triradiates. *Holocene*.

# Order CLATHRINIDA Hartman, 1958

[Clathrinida HARTMAN, 1958a, p. 108]

Skeleton composed exclusively of separate spicules. This order includes families Clathrinidae MINCHIN, 1900, p. 110 (type genus, Clathrina GRAY, 1867, p. 557); Soleneiscidae BOROJEVIC & others, 2002, p. 1,144 (type genus, Soleneiscus BOROJEVIC & others, 2002, p. 1,144); Levinellidae BOROJEVIC & BOURY-ESNAULT, 1986, p. 444 (type genus, Levinella BOROJEVIC & BOURY-ESNAULT, 1986, p. 444); Leucaltidae DENDY & Row, 1913, p. 736 (type genus, Leucaltis HAECKEL, 1872b, p. 142); Leucascidae DENDY, 1893, p. 71 (type genus, Leucascus DENDY, 1893, p. 72); Leucettidae BOROJEVIC, 1968, p. 207 (type genus, Leucetta HAECKEL, 1872b, p. 118). Holocene.

# Order MURRAYONIDA Vacelet, 1981

[Murrayonida VACELET, 1981, p. 315]

Skeleton of overlapping calcite scales forming cortex, or trabecular, basal skeleton

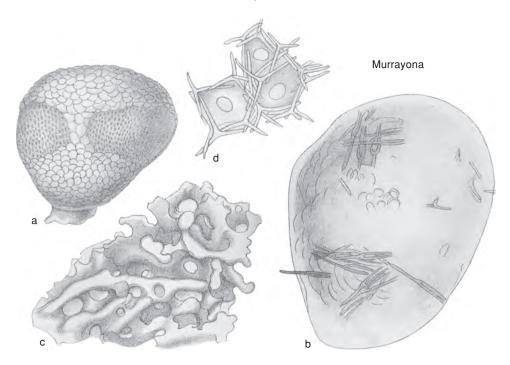


FIG. 489. Murrayonidae (p. 735).

of spherulitic to penicillate calcite, or bundles of spicules; tuning fork spicules usually present. *Holocene*.

## Family MURRAYONIDAE Kirkpatrick, 1910

[nom. transl. DENDY & ROW, 1913, p. 741, ex Murrayoninae Kirkpatrick, 1910a, p. 132]

Basal skeleton rigid, aspicular network of calcite; cortex mainly overlapping calcareous plates in oscular region and of small triactines in lower walls; choanosome includes free, diapason triactines. *Holocene*.

Murrayona KIRKPATRICK, 1910a, p. 127 [\*M. phanolepis; OD]. Spheroidal, stipitate; single, circular oscule at summit; remainder of surface covered by imperforate layer of overlapping but unfused, subcircular, planoconvex scales, except for equatorial groove bearing closely spaced, small, inhalant pores outlined by bundled triradiates; laminar forms also occur, with one side bearing scales and multiple oscules, other side similar to an equatorial groove; between scales and principal skeleton is thin layer of unfused triradiates, both equiangular and sagittal, as well as bundles of tuning-fork spicules; principal skeleton built of flattened, curved, anastomosing trabeculae outlining anastomosing, tubular spaces, which contain central canal lined by choanocyte chambers; scales of calcite and developed from triradiates with flattened, laterally expanded rays; trabeculae of principal skeleton calcitic and built solely of flaky spherulites, whose radiating fibrillae give trabecular surface a microhispid character; choanocyte nuclei basal, larva a blastule. [An endolithic alga (Osterobium queketti BORNET & FLAHAUT, fide VACELET, 1977a, p. 349) commonly penetrates both scales and trabeculae.] Holocene: Indo-Pacific .----- FIG. 489a-d. \*M. phanolepis, Indian Ocean, Christmas Island; a, side view of small type specimen showing inner, fibrous, calcareous skeleton and outer layer of imbricate scales, ×5; b, inner surface of one scale with loosely adhering, tuning-fork spicules, ×100; c, broken surface of inner part of skeleton showing curving trabeculae, ×20; d, part of pore area with three pores and surrounding, triradiate spicules, ×125 (Kirkpatrick, 1910a; courtesy of the Royal Society, London).

## Family PARAMURRAYONIDAE Vacelet, 1967

#### [Paramurrayonidae VACELET, 1967a, p. 49]

Choanosomal skeleton of bundles of diapason triactines without rigid structure; cortex with outer layer of aspicular, overlapping, calcareous plates and inner layer of free plates. *Holocene*.

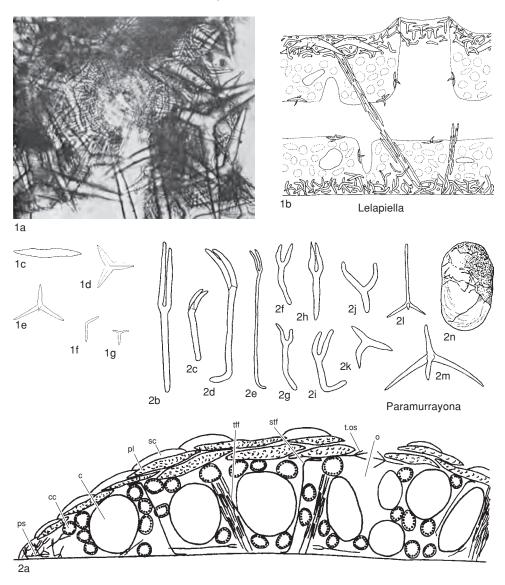


FIG. 490. Paramurrayonidae (p. 736-737).

Paramurrayona VACELET, 1967a, p. 49 [\*P. corticata; OD]. Encrusting, very small; surface covered with overlapping, oval scales, beneath which is denser layer of imbricated, irregular, rectangular flakes, apparently derived from scales; both types of body composed of radially fibrous calcite and surfaces mammellonated; no intermediates between flakes or scales and spicules; interior of sponge containing vertical bundles of tuning-fork spicules; central oscule penetrating layers of flakes and scales and surrounded by ring of quadriradiates with paired rays tangent to oscule and fourth ray pointing obliquely upward to oscular center; peripheral areas of sponge with free sagittal and equiangular quadriradiates and triradiates; choanocyte nuclei basal; larva possibly a parenchymella; scales and flakes penetrated by an endolithic fungus. *Holocene:* Madagascar, Malagasy.——FIG. 490,2*a*-*n*. \**P*. *corticata*, Grand Récif de Tuléar, Madagascar; *a*, schematic drawing through encrusting sponge showing canals, *c*; choanocyte chambers, *cc*; supporting tuning-fork spicules, *stf*; surface scales, *sc*; fibers of tuning-fork spicules, *tff*; oscula, *o*; calcareous plates, *pl*; peripheral spicules, *ps*; tetractines of oscula, *t.os; b–i*, spicules including tuning fork spicules of several types, ×200 (*b–d*, *f–i*), ×100 (*d–e*); *j–k*, triactines, ×200; *l–n*, tetractine, perioscular tetractine, scale, ×100 (Vacelet, 1967a).

Lelapiella VACELET, 1977a, p. 358 [\*L. incrustans; OD]. Encrusting, very small; one, rarely two, oscules with rim; inhalant pores scattered over surface; cortical layer of large, anapodal, equiangular triradiates with papillose, upper surface, together with smaller diactines bent at 120°; latter also forming dense, basal layer; two layers connected by oblique bundles of straight, parallel diactines; oscule surrounded by paired rays of sagittal triradiates and internal canals by equiangular quadriradiates whose fourth ray is directed toward lumen; choanocyte nucleus questionably basal; larva not known. Holocene: Indo-Pacific.—FIG. 490,1a-g. \*L. incrustans, Grand Reef of Tuléar, and in Mozambique Channel, Indian Ocean; a, photomicrograph of oscula and surrounding spicules seen from above, MNHN J.V.-76-2, ×70; b, diagram of general structural and spicule organization, ×50; cg, characteristic spicules including c, diactine of fibers  $\times 100$ ; d, triactine of outer skeleton,  $\times 50$ ; e, tetractine of canal, ×100; *f*, curved diactine, ×50; g, perioscular triactine, ×50 (Vacelet, 1977a; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

# Subclass CALCARONEA Bidder, 1898

[Calcaronea BIDDER, 1898, p. 73]

Choanocyte nucleus apical; larva an amphiblastula; triradiates predominantly sagittal except in Lapidoleuconidae. *Lower Cambrian–Holocene*.

## Order LEUCOSOLENIDA Hartman, 1958

[Leucosoleniida HARTMAN, 1958a, p. 108]

Asconoid. [Family included is Leucosoleniidae MINCHIN, 1900, p. 110 (type genus, *Leucosolenia* BOWERBANK, 1862, p. 1,094).] *Holocene*.

## Order SYCETTIDA Bidder, 1898

#### [Sycettida BIDDER, 1898, p. 73]

Syconoid or leuconoid. Families included are Sycettidae DENDY, 1893, p. 72 (type genus, *Sycetta* HAECKEL, 1872b, p. 235); Grantiidae DENDY, 1893, p. 72 (type genus, *Grantia* FLEMING, 1828, p. 524); Leuconiidae VOSMAER, 1887, p. 373 (type genus, *Leuconia* GRANT, 1833, p. 199); Heteropiidae DENDY, 1893, p. 75 (type genus, *Heteropia* CARTER, 1886, p. 47); Amphoriscidae DENDY, 1893, p. 76 (type genus, *Amphoriscus* HAECKEL, 1870, p. 238); plus the families treated below. *Carboniferous– Holocene*.

#### Family GRANTIIDAE Dendy, 1893

[Grantiidae DENDY, 1893, p. 72]

Sycon architecture persistent within an enclosing dermis or cortex, inhalant and exhalant systems consistently developed. *Carboniferous–Holocene*.

- Grantia FLEMING, 1828, p. 524 [\*Spongia compressa FABRICIUS, 1780, p. 448; OD]. Syconoid sponges with cortex of tangential triactines or tetractines and smaller, perpendicular diactines; choanosome spicules may include larger triactines and diactines, which may protrude on dermal surface. *Holocene:* cosmopolitan.——FIG. 491,*3. G. socialis* BORO-JEVIC, New Caledonia; diagram of transverse section showing spicule composition of cortex above and principal skeleton below; *a*, atrium, *ar*, articulate choanosomal skeleton, *as*, atrial skeleton composed of tangential triactines and tetractines, *cx*, cortex, *ss*, subatrial spicules, thickness 700 µm (Borojevic, 1967).
- Protoleucon BOLKHOVITINOVA, 1923, p. 67 [\*P. pavlovi; OD]. Cylindrical sponges with deep spongocoel; skeleton of vermiform looping fibers forming either irregular swellings or hollow, irregularly curved tubes; large canals extending in from dermal surface to interior of sponge; smaller canals also present. Carboniferous: Russia.——FiG. 491,1a-c. \*P. pavlovi, Krasnaya Pakhra, Moscow region; a,view from above showing relatively thin walls around matrix-filled spongocoel, ×2; b, view of gastral surface with irregular ostia, ×2; c, skeletal fibers in tangential section, ×10 (Rezvoi, Zhuravleva, & Koltun, 1962).
- Protosycon ZITTEL, 1878b, p. 48 [\*Scyphia punctata GOLDFUSS, 1826, p. 10; OD]. Resembles Grantia. Upper Jurassic: Germany.—FIG. 491,4a-d. \*P. punctatum (GOLDFUSS); a, side view of small sponge, ×1; b-d, diact, triacts, and tetract spicules, ×150 (de Laubenfels, 1955).

#### Family LEUCONIIDAE Vosmaer, 1887

[nom. correct. DE LAUBENFELS, 1955, p. 96, pro Leuconidae VOSMAER, 1887, p. 373]

Initially similar to Grantiidae but developing simple, rhagon architecture, generally with single spongocoel of simple type. *Lower Jurassic, Holocene.* 

Leuconia Grant, 1833, p. 199 [\*Spongia nivea Grant, 1826, p. 339; SD Bowerbank, 1862, p. 1,094] [see 738

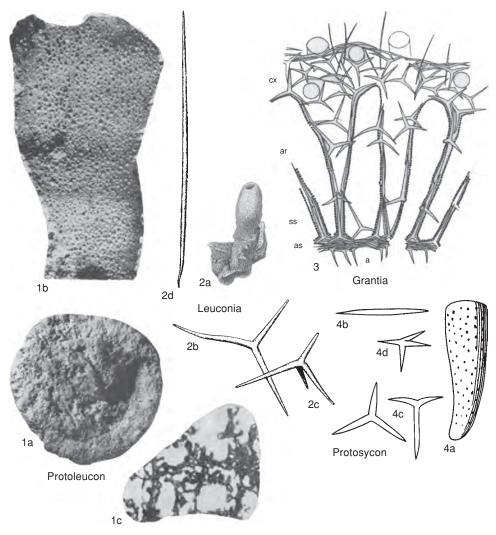


FIG. 491. Grantiidae and Leuconiidae (p. 737–738).

BURTON, 1963, p. 232 for extensive synonymy of *Leuconia*]. Simple, rhagon sponges with dermal triacts over endosomal diactines, triactines, and tetractines. *Lower Jurassic–Holocene:* England, *Lower Jurassic;* cosmopolitan, *Holocene.*—FIG. 491,2*a–d. L. walfordi* (HINDE), middle Lias, Northhampton, England; *a*, side view of small sponge, ×10; *b–d*, spicules from species, ×100 (Hinde, 1893b).

## Order STELLISPONGIIDA new order

[Stellispongiida FINKS & RIGBY, herein]

Calcaronea with an inozoan basal skeleton. *Permian–Holocene*.

## Family STELLISPONGIIDAE de Laubenfels, 1955

[Stellispongiidae DE LAUBENFELS, 1955, p. 97; emend., FINKS & RIGBY, herein] [=Stellispongiidae DE LAUBENFELS, 1955, p. 97, partim; Elasmostomatidae DE LAUBENFELS, 1955, p. 98, partim; Discococliidae DE LAUBENFELS, 1955, p. 99, partim; Elasmococliidae DE LAUBENFELS, 1955, p. 99, partim]

Trabeculae of central spicule or spicules coated by smaller spicules. [The majority of Jurassic genera have a single central spicule while the majority of Cretaceous genera have multiple central spicules.] *Permian– Neogene (Miocene).* 

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#### Subfamily STELLISPONGIINAE de Laubenfels, 1955

[nom. transl. FINKS & RIGBY, herein, ex Stellispongiidae DE LAUBENFELS, 1955, p. 97; emend., FINKS & RIGBY, herein]

## Multiple central spicules in trabeculae. Permian–Paleogene (Eocene).

Stellispongia D'ORBIGNY, 1849, p. 549 [\* Tragos stellatum GOLDFUSS, 1826, p. 14; OD] [=Operytis POMEL, 1872, p. 229, obj.; ?Trachysphecion POMEL, 1872, p. 223 (type, Spongia stellata LAMOUROUX, 1821, p. 89; SD RAUFF, 1893, p. 71); ?Diasterofungia DE FROMENTEL, 1861, p. 358 (type, D. insignis, OD)]. Bun-shaped or tuberoid, with flattened base covered by concentrically wrinkled, dermal layer; upper surface bearing mamelons, each with astrorhiza-like, exhalant, groove system without central osculum or pore cluster; entire upper surface covered with small, circular, intertrabecular pores, some clearly larger than others. [Trabecular microstructure of the type species, which is Cretaceous (Cenomanian), was described by DUNIKOWSKI (1883, p. 318, pl. 4,5) as having triradiates in the middle of trabecular and sagittal tetraradiates on outside with unpaired rays projecting into lumen of intertrabecular space, such as typical of oscular assemblies of living, nonpharetronid Calcarea. Triassic specimens belonging to Cnemidium variabile MÜNSTER, 1841 (which has been considered incorrectly the type species by many authors) have penicillate (aragonitic) to irregular, partly spherulitic microstructure (WENDT, 1974, p. 503-507; 1979, p. 454) or spherulitic microstructure (FINKS, 1983a, p. 64, 69; but this is perhaps Stellispongia subsphaerica DIECI, ANTONACCI, & ZARDINI, 1968), or sinuous bodies (possibly flaky, asymmetric spherulites) (STEINMANN, 1882, p. 180, pl. 9,2; RAUFF, 1938, p. 197 ff., pl. 21,30.2). WENDT (1974, p. 507) cited occasional monaxons for the Triassic Stellispongia manon (MÜNSTER) but no triradiates. The Triassic sponges with spherulitic or penicillate, aragonitic basal skeletons should not be assigned to Stellispongia. They are agelasid demosponges. Ateloracia POMEL, 1872 (p. 228), (q.v.) with type Cnemidium manon MÜNSTER, 1841, is available. HINDE (1893b, p. 226) established Holcospongia for Jurassic and Cretaceous species assigned to Stellispongia because he considered (incorrectly) the Triassic Cnemidium variabile MUNSTER to be the type (this is the source of the SD cited by DE LAUBENFELS, 1955, p. 97). It is questionable, however, whether HINDE's Jurassic species of Holcospongia (among which is the type) are congeneric with the Cretaceous type of Stellispongia. Nonspiculate, Paleozoic sponges originally included in Stellispongia (TERMIER & TERMIER, 1955, 1973, 1977a) have been placed in Stellispongiella WU Ya Sheng (1991) by RIGBY and SENOWBARI-DARYAN (1996a), in the family Stellispongiellidae WU Ya Sheng, 1991. That classification is followed here.] ?Jurassic, Cretaceous: Europe.—FIG. 492,4. \*S.

stellata (GOLDFUSS), Upper Cretaceous, Cenomanian, Essen, Germany; camera lucida drawing of spicules around canal, with coarser triradiates near opening and smaller ones associated with monaxons farther away, ×50 (Dunikowski, 1883).

- Amorphofungia FROMENTEL, 1860a, p. 50 [\*Achilleum tuberosum GOLDFUSS, 1829, p. 93; OD]. Tuberous and lobate; closely spaced, small, subcircular, and subequal pores represent openings of more or less radial and anastomosing, intertrabecular spaces; microstructure and spicules not known. Jurassic: Germany.—FIG. 492, 1. \*A. tuberosa (GOLDFUSS), upper beds of Jurassic limestone, Hattheim; fragment showing lobate, tuberose form with small, inhalant ostia to irregularly convergent, trabecular spaces, shown in broken surfaces, ×1 (Goldfuss, 1833).
- Amorphospongia D'ORBIGNY, 1849, p. 550, non FROMENTEL, 1860a [\*Achilleum truncatum GOLDFUSS, 1829, p. 93; SD FINKS & RIGBY, herein]. Cylindrical, branching; surface bearing circular to submeandriform pores of subequal size, and coated in patches with dermal layer; pores separated by thin trabeculae and presumably represent openings of internal, intertrabecular spaces; microstructure and spicules unknown. [GOLDFUSS (1829, p. 93) said that the skeletal net has great similarity to that of the type specimen of Pachytilodia ZITTEL, 1878b. The other species originally included by D'ORBIGNY (1849, p. 550), Achilleum chirotonum GOLDFUSS (1826, p. 2), appears to be a hexactinellid. DE LAUBENFELS'S (1955, p. 104) designation of Achilleum tuberosum GOLDFUSS, 1829, as the type is invalid; this species was not originally included by D'ORBIGNY (1849, p. 550) when he established the genus. That species is the valid type of FROMENTEL, 1860a.] Jurassic: Germany.
- Blastinoidea RICHARDSON & THACKER, 1920, p. 182 [\*B. frithica; OD]. Minute, spherical to subspherical sponges similar to *Stellispongia*, but surface smooth and without furrows; no osculum visible and dermal cortex not developed. *Middle Jurassic:* England.——FIG. 493,7. \*B. frithica, middle Inferior Oolite, Gloucestershire; side view of subspherical type specimen, ×2 (Richardson & Thacker, 1920).
- **Conocoelia** ZITTEL, 1878b, p. 34 [\**Siphonocoelia* crassa FROMENTEL, 1861, p. 360; SD DE LAUBEN-FELS, 1955, p. 99]. Broadly conical with flattish top; solitary or with budded individuals springing from top edge; central, deep cloaca narrow and funnel shaped; outer surface porous but with horizontal constrictions; no internal canals except intertrabecular spaces; meandriform, trabecular mesh showing horizontal layering; trabecular microstructure large, central, tri- or tetraradiates coated by smaller, sinuous spicules (HINDE, 1884a, p. 177–178). Lower Cretaceous: Europe.
- Diaplectia HINDE, 1884a, p. 193 [\*D. auricula; SD DE LAUBENFELS, 1955, p. 98] [=?Trachyphlyctia POMEL, 1872, p. 237 (type, Spongia helvelloides

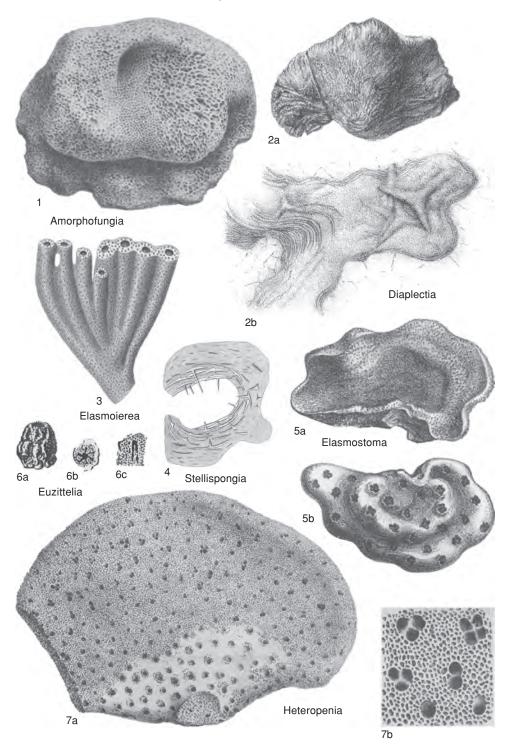


FIG. 492. Stellispongiidae (p. 739-741).

LAMOUROUX, 1821, p. 87)]. Ear, fan, or cup shaped, stipitate; trabeculae dominantly subparallel and vertical; no pores other than intertrabecular spaces; no dermal layer; trabecular microstructure consisting of large, central, tri- and tetraradiates coated by small, sinuous spicules, small pitchfork spicules reported. *Jurassic:* Europe.——FIG. 492,2*a*-*b.* \**D. auricula*, Inferior Oolite, Middle Jurassic, Cheltenham, England; *a*, ear-shaped type specimen viewed from below, ×1; *b*, camera lucida drawing of interior fiber showing large, three- and four-rayed spicules with minute, sinuous spicules bordering fiber, ×75 (Hinde, 1884a).

- Elasmoierea FROMENTEL, 1860a, p. 34 [\**E. sequana;* OD] [=*Elasmocoelia* ROEMER, 1864, p. 31, obj., *nom. van.*]. Erect, plicate, sometimes branching laminae with many vertical, exhalant canals (or narrow cloacae) opening in single row (occasionally several abreast) on upper edge; sides of lamina may bulge around each cloaca; sides of lamina covered with small, closely spaced pores; trabecular microstructure of *E. faringdonesis* (MANTELL), according to HINDE (1884a, p. 177), consists of tri- and tetraradiates with some "slender filiform spicules." *Lower Cretaceous:* Europe.——FIG. 492,3. \**E. sequana*, Hils, near Berklingen, northern Germany; side view of branched sponge with aligned oscula on upper edge, ×1 (Roemer, 1864).
- ?Elasmostoma FROMENTEL, 1860a, p. 42 [\*E. frondescens FROMENTEL, 1860a, p. 43; OD] [=?Heteropenia POMEL, 1872, p. 153 (type, Manon peziza GOLDFUSS, 1826, p. 3, SD DE LAUBENFELS, 1955, p. 105)]. Ear or bracket shaped, with attachment near middle of straight side; concentrically rugose parallel to semicircular growing edge; one surface (possibly exhalant) covered with dermal layer pierced by irregularly circular, large pores (possible oscules); this surface is convex in type species, therefore questionably exhalant; other (possibly inhalant) surface covered by small, irregular, intertrabecular spaces. [HINDE (1884a, p. 193) described the trabecular microstructure of Tragos acutimargo ROEMER, 1839 (which he, as well as ZITTEL, 1878b, p. 44, considered a senior subjective synonym of the type species) as large, central, tri- and tetraradiates coated by smaller, sinuous spicules. The concave face bears the dermal layer and oscules in T. acutimargo, according to POMEL (1872, p. 151-152). This genus is externally similar to some species of Raphidonema HINDE, 1884a, but differs in the presence of large, central spicules in the center of the trabeculae.] Jurassic (Oxfordian)-Paleogene (Eocene): Poland, Germany, Oxfordian; Europe, Cretaceous; Mexico, Eocene. FIG. 492,5a-b. \*E. frondescens, Neocomian, Lower Cretaceous, St. Dizier, Germany, a, dermal surface of irregular, small sponge with small, inhalant ostia, ×1; b, gastral view of same sponge with several relatively large, exhalant oscula, ×1 (Fromentel, 1860a).
- Euzittelia ZEISE, 1897, p. 329 [\**E. magnifica;* OD]. Sponges bud to rounded club shaped, with upper

surface marked by elongate furrows that have networks of horizontal elements; sponges characterized by well-developed spongocoel or paragaster, which extends full length of sponge, and well-developed aporhysal or exhalant canal system; radial, aporhysal canals penetrate approximately halfway through sponge wall and terminate distally with irregular, blunt ends; inhalant canal system has not been recognized; skeletal fibers range 0.1 to 0.3 mm thick, but individual spicules have not been recognized. Jurassic-Cretaceous: Europe .--Fig. 492,6a-c. \*E. magnifica, Stramberger Schichten, Germany; a, side view of small, furrowed sponge, Palaeontologisches Museum München, ×1; b, horizontal section showing axial spongocoel and radial, exhalant canals,  $\times 1$ ; *c*, vertical section with tubular, axial spongocoel and cellular-appearing skeleton, ×1 (Zeise, 1897).

- ?Heteropenia POMEL, 1872, p. 153 [\*Manon peziza GOLDFUSS, 1826, p. 3; SD DE LAUBENFELS, 1955, p. 105] [=Catagma SOLLAS, 1878, p. 354, SD DE LAUBENFELS, 1955, p. 105, obj.; ?Elasmostoma FROMENTEL, 1860a, p. 42-43 (type, E. frondescens DE FROMENTEL, 1860a, p. 43, OD)]. Cup shaped with short stalk or foot; basal part may be covered with dermal layer; concave (possibly exhalant) surface bearing fine, closely spaced, round pores; convex (possibly inhalant) surface bearing meandriform, intertrabecular spaces and small, round pores arranged more or less quincuncially; latter lead into canals that rise obliquely to, but not through, concave surface. [This description is based on POMEL's description (1872, p. 153) but agrees roughly with the figure of Manon peziza of GOLDFUSS (1833, pl. 5,1) which POMEL cited, although less so with GOLDFUSS's other figures of that species. They seemingly all share the unusual feature of larger pores on the convex, outer surface, a feature shared also with the type species of Elasmostoma FROMENTEL, 1860a. POMEL stated (1872, p. 153) that the type, Heteropenia peziza POMEL, 1872, resembled Manon peziza sufficiently to be considered identical, but clearly implied that the type specimen was not one of GOLDFUSS's original lot. DE LAUBENFELS (1955, p. 105) unambiguously designated Manon peziza GOLDFUSS as the type.] Cretaceous (Cenomanian): Europe.-FIG. 492, 7a-b. \*H. peziza (GOLDFUSS), St. Petersburg and Essen, Ruhr region, Germany; a, view of upper surface with coarse, exhalant pores, ×1; b, enlarged part of upper, gastral surface showing variation in exhalant openings, approximately ×4 (Goldfuss, 1833).
- Pachymura WELTER, 1911, p. 58 [\*P. goldfussi; OD]. Cup to goblet-shaped sponge with markedly elongate funnels of gastric cavity; canal system not defined, skeletal fibers coarse with irregular orientation, and composed of parallel, possibly threerayed spicules. Lower Cretaceous: Germany.— FIG. 493,2. \*P. goldfussi, Essener Grünsand, Cenomanian, Tourtia of Essen; side view of irregular, funnel-shaped sponge with porous walls, ×1 (Welter, 1911).

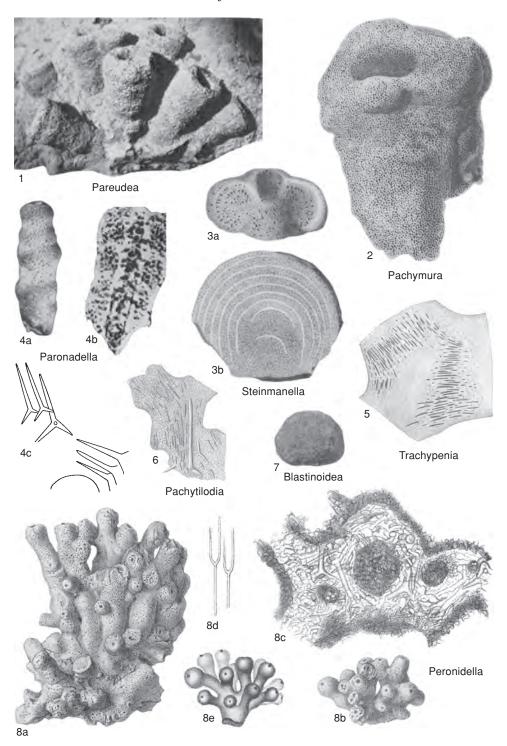


FIG. 493. Stellispongiidae (p. 739-745).

- Pachytilodia ZITTEL, 1878b, p. 46 [\*Scyphia infundibuliformis GOLDFUSS, 1826, p. 12; OD]. Very large, goblet or cup shaped with short stalk; smaller, younger individuals pear shaped with shallow depression on top; no pores other than coarse, irregular, intertrabecular spaces; trabecular microstructure, according to DUNIKOWSKI (1883, p. 322), consisting of monaxons parallel to length of fibers and very large triradiates. Cretaceous: Europe.—FIG. 493,6. \*P. infundibuliformis (GOLD-FUSS), Upper Cretaceous, Cenomanian, Essen, Germany; camera lucida drawing of parallel monaxons, ×50 (Dunikowski, 1883).
- Pareudea ÉTALLON, 1859b, p. 542 [\*Scyphia bronnii GOLDFUSS, 1829, p. 91; SD DE LAUBENFELS, 1955, p. 106] [=*Eusiphonella* ZITTEL, 1878b, p. 34, obj.] Tubular, cylindrical to conical, solitary or branching; central cloaca one-third total diameter; osculum may have stellate outline from short, radial slits; meandriform trabeculae thickened at surface to outline larger and smaller, circular pores; imperforate dermal layer may be present near base. [HINDE (1893b, p. 219) added further diagnostic features of horizontal, exhalant canals that enter the cloaca in vertical rows of elongate pores, producing the oscular slits, and whose presence distinguishes the genus from Peronidella ZITTEL in HINDE, 1893b. HINDE (loc. cit.) illustrated the trabecular microstructure of Eusiphonella prolifera HINDE, 1893b, as multiple, central, large triradiates coated by a few filiform or sinuous spicules; this would distinguish it somewhat from the more numerous central spicules of Peronidella. HINDE (1884a, p. 178) also noted triradiates in the dermal layer of the type species. It should be noted that GOLDFUSS's (1829, p. 91, pl. 33,9) original description and illustration of the type species is indistinguishable in gross form from Peronidella and does not have radial slits. WAGNER (1964, p. 27 and pl. 5, 1a-c) chose as lectotype a branching group of somewhat conical individuals and emphasized the presence of the short, longitudinal, radial slits in the cloacal wall (HINDE's rows of elongate pores) as a diagnostic character. WAGNER placed Epitheles FROMENTEL, 1860a (as Myrmecium GOLDFUSS, 1826 and Myrmecidium VINASSA DE REGNY, 1901) in subjective synonymy, but their trabecular microstructure is different, as is also their spheroidal form. HINDE, 1893b, p. 219, designated Scyphia bronnii MÜNSTER in GOLDFUSS, 1829, as type of Eusiphonella ZITTEL, 1878b; the same species was the first cited and described by ÉTALLON (1859b, p. 542) under his new genus Pareudea, and was designated as type of that earlier genus by DE LAUBENFELS (1955, p. 106).] Upper Triassic-Upper Jurassic: Peru, Upper Triassic; Peru, Lower Jurassic; England, Poland, France, Germany, Oxfordian; Czech Republic, Slovakia, Tithonian; Italy, Upper Jurassic. FIG. 493,1. \*P. bronnii (GOLDFUSS), Weissjura Zeta, Upper Jurassic, Nattheim, southern Germany; lectotype, branched cluster with exhalant ostia in rows in spongocoels, BSPGM AS VII 254, ×1.5 (Wagner, 1964).
- Paronadella Rigby & Senowbari-Daryan, 1996a, p. 61 [\*Peronidella proramosa HURCEWICZ, 1975, p. 272; OD]. Sponge single or branched, cylindrical with deep spongocoel that extends nearly through entire sponge; inhalant and exhalant canals or pores absent, with interconnected fiber spaces within wall; spicular skeleton composed of di-, tri-, or tetraclones not united with calcareous cement. [This may be a Paleozoic representative of Triassic and younger peronidellids with spicules.] Permian-Jurassic (Oxfordian): Italy (Sicily), Permian; Poland, Oxfordian. FIG. 493, 4a-c. \*P. proramosa (HURCEWICZ), Jurassic limestone, upper Oxfordian, Wydrznów, Polish Jura Chain, Poland; a, holotype, side view, UL Sp. VII/131, ×2; b, longitudinal section with cylindrical spongocoel and reticulate, almost chambered-appearing skeleton, UL Sp. VII/ 142,  $\times$ 5; c, sketch of sagittal tetractines from UL Sp. VII/26, ×85 (Hurcewicz, 1975; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).
- Peronidella ZITTEL in HINDE, 1893b, p. 213, partim [\*Spongia pistilliformis LAMOUROUX, 1821, p. 88; SD DE LAUBENFELS, 1955, p. 99] [=Siphonocoelia FROMENTEL, 1860a, p. 31 (type, Scyphia elegens GOLDFUSS, 1826, p. 6, OD); Discoelia FROMENTEL, 1861, p. 357 [360] (type, Scyphia cymosa MICHELIN, 1847 in 1840-1847, p. 249, SD RAUFF, 1893), =Discocoelia DE LAUBENFELS, 1955, p. 99, obj., lapsus calami, nom. nov. pro Polycoelia FROMENTEL, 1860a, p. 32, non KING, 1849; Coeloscyphia TATE, 1865, p. 43 (type, C. sulcata, SD DE LAUBENFELS, 1955, p. 87), nom. van. pro Polycoelia FROMENTEL, 1860a, p. 32; Dendrocoelia LAUBE, 1865, p. 233 (type, D. dichotoma, SD FINKS & RIGBY, herein), nom. van. pro Polycoelia FROMENTEL, 1860a, p. 32; Pliocoelia POMEL, 1872, p. 242, jr. obj. syn. of Discoelia FROMENTEL, 1861, p. 357 [360]; Loenocoelia POMEL, 1872, p. 243 (type, L. ramosa, OD); ?Coeloconia POMEL, 1872, p. 248 (type, Scyphia cylindrica GOLDFUSS, 1826, p. 5, partim); ?Dyoconia POMEL, 1872, p. 248 (type, Scyphia cylindrica GOLDFUSS, 1826, p. 5, partim); ?Vermispongiae QUENSTEDT, 1877 in 1877-1878, p. 171, obj., =Dermispongia ZITTEL, 1878b, p. 30, lapsus calami; ?Radicispongia QUENSTEDT, 1877 in 1877-1878, p. 179 (type, Spongites radiciformis GOLDFUSS, 1826, p. 10); Peronella ZITTEL, 1878b, p. 30, obj., non GRAY, 1855, nec MOERCH, 1863]. Branching cylinders arising from common base and partly fused laterally; may also be solitary; top of cylinder rounded with central osculum; deep, central cloaca; surface pores only regular, intertrabecular spaces; imperforate, dermal layer present on basal part of each branch; trabecular microstructure of Jurassic type species according to HINDE (1893b, p. 214) consists of triradiates, and possibly tetraradiates, including tuning-fork spicules, very closely intermingled; fibers sometimes coated by thin layer of filiform, sinuous spicules that may also line cloaca. [HURCEWICZ (1975, p. 268) described nontopotype material referred to the type species and stated that tetraradiates predominate in the fibers

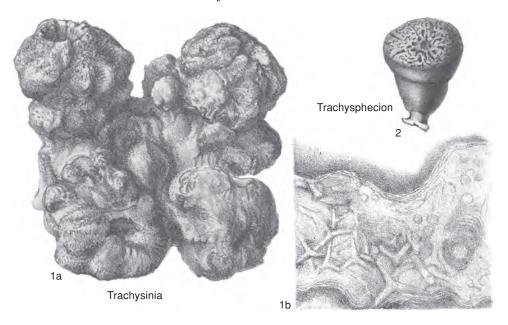


FIG. 494. Stellispongiidae (p. 745).

and that the dermal layer consists of densely spaced, sagittal triradiates with their apical rays set obliquely outward. WENDT (1974, p. 503) characterized the microstructure of some Triassic species referred to Peronidella as composed of irregularly arranged needles of aragonite without spicules (i.e., they would be vacelitid demosponges) and DIECI, RUSSO, and RUSSO (1974a) described other Triassic specimens as spherulitic (i.e., they would be agelasid demosponges). The nonspicular, pre-Jurassic species should not be referred to Peronidella. They are demosponges. Jurassic and Cretaceous species whose microstructure has been published appear to conform to that of the type species. Several of the genera cited in the synonymy with a query are senior to Peronidella. The oldest of these is Siphonocoelia FROMENTEL, 1860a (type, Scyphia elegans GOLDFUSS, 1826). Their microstructure is not known.] Jurassic-Cretaceous, Holocene: Europe, Canadian Atlantic Shelf, Mediterranean Sea. FIG. 493,8a-e. \*P. pistilliformis (LAMOUROUX); a, branched cluster showing mode of growth and size of branches, Great Oolite, Upper Jurassic, Bath, United Kingdom, ×1; b, smaller cluster with smaller branches to show range of form in type species, Great Oolite, Upper Jurassic, Bath, United Kingdom, ×1; c, camera lucida drawing of part of sponge showing spicule structure of fibers, Great Oolite, Upper Jurassic, Bath, United Kingdom, ×60; d, drawing of tuning fork spicules from same section, Great Oolite, Upper Jurassic, Bath, United Kingdom, ×200 (Hinde, 1893b); e, side view of small type cluster showing form of branches, Holocene, Mediterranean Sea, near Caen, France, ×1 (Lamouroux, 1822).

- Steinmanella WELTER, 1911, p. 66 [\*S. latidorsata WELTER, 1911, p. 67; SD DE LAUBENFELS, 1955, p. 98]. More or less sheetlike sponges with fibrous, skeletal structure somewhat similar to Elasmostoma or Sestrostomella; general structure of more or less parallel layers; coarse canal system absent but short, twisted fibers on under surface around larger and smaller pores. [Included in the family with some question.] Upper Cretaceous: Germany.——FIG. 493,3a-b. \*S. latidorsata, Essen Grünsand, Cenomanian, Essen; a, upper or gastral surface with shallow depression and moderately coarse, exhalant ostia, ×1; b, surface of leaflike sponge with parallel, ridgelike beams showing expansion of skeleton, ×2 (Welter, 1911).
- Trachypenia POMEL, 1872, p. 152 [\*Manon stellatum GOLDFUSS, 1826, p. 3; SD FINKS & RIGBY, herein]. Auriform, infundibuliform, or frondose, thin sheets; possible exhalant surface covered with meandriform, intertrabecular spaces that converge upon small, circular, evenly spaced pores to form fine-grained pattern of stellate domains; opposite (possibly inhalant) surface covered with more or less circular, intertrabecular spaces that tend to form zones of larger and smaller pores parallel to growing edge of sponge zones corresponding to obscure growth rugae; no dermal layer; internal, intertrabecular spaces meandriform; no larger canals; trabecular microstructure consisting of larger, central spicule or spicules (tri- or possibly tetraradiates) surrounded by small, sinuous monaxons parallel to trabecular surface. [HINDE (1884a, p.

200) referred this species to his genus Raphidonema and reported the microstructure as of small, sinuous triradiates. DUNIKOWSKI (1883, p. 320), added monaxons as well, recognized sagittal triradiates, and illustrated (pl. 2 (38),2) larger, central spicules. The very characteristic stellate pattern of trabeculae and absence of a dermal layer separate this genus from *Elasmostoma* FROMENTEL, 1860a. The same characters, as well as spicular differences, separate it from the type of Raphidonema HINDE, 1884a.] Cretaceous: Europe.—FIG. 493,5. \*T. stellata (GOLDFUSS), Upper Cretaceous, Cenomanian, Essen, Germany; camera lucida drawing showing large, triradiate spicules surrounded by smaller monaxons, ×50 (Dunikowski, 1883).

- Trachysinia HINDE, 1884a, p. 189 [\**T. aspera*; SD DE LAUBENFELS 1955, p. 97]. Tubular with shallow to deep, central cloaca; exterior knobby; generally bushy colonies with several individuals fused basally; radial, exhalant canals may enter cloaca but interior with few canals except coarse, intertrabecular spaces; trabecular microstructure consisting of multiple, central, tri- and tetraradiates coated by smaller, sinuous spicules (HINDE, 1884a, p. 189). *Jurassic:* Europe.—FIG. 494, *Ia-b.* \**T. aspera*, Couche a polypiers, Middle Jurassic, Caen, France; *a*, type specimen from above with knobby exterior, ×1; *b*, camera lucida drawing showing three- and four-rayed spicules within a fiber, ×72 (Hinde, 1884a).
- ?Trachysphecion POMEL, 1872, p. 223 [\*Spongia stellata LAMOUROUX, 1821, p. 89; SD RAUFF, 1893, p. 71]. Conical, irregular; slightly convex, upper surface bearing one or more oscules, with coarsely stellate outline produced by radial canals or pores surrounding them. [HINDE (1884a, p. 186) stated that the trabecular microstructure consists of central, irregular triradiates or tetraradiates coated by small, sinuous spicules. Genus may be synonymous with Stellispongia D'ORBIGNY, 1849 (q. v.).] Jurassic, Holocene: Europe.—FIG. 494,2. \*T. stellata (LAMOUROUX), Holocene, Mediterranean Sea near Caen, France; side view of small, obconical form with stellate-appearing osculum on rounded summit, ×1 (Lamouroux, 1822).

## Subfamily HOLCOSPONGIINAE new subfamily

[Holcospongiinae FINKS & RIGBY, herein] [type genus, Holcospongia HINDE, 1893b, p. 225]

## Single, central spicule in trabeculae. *Per*mian–Neogene (Miocene).

Holcospongia HINDE, 1893b, p. 225 [\*Spongia floriceps PHILLIPS, 1829 in 1829–1836, p. 126; SD HURCEWICZ, 1975, p. 259]. Digitiform individuals or branches united by common base; longitudinal grooves running down sides of each branch, radiating from summit; osculum or cloaca limited or absent; internal canals, other than intertrabecular spaces, not well developed; dermal layer covers base of sponge; trabeculae contain central, tri- or tetraradiate coated by several layers of "filiform spicules" or "sinuous spicules" (HINDE, 1893b, p. 225, 227), parallel to trabecular surface. [Foregoing based on type species; other species include solitary, ovoid individuals with same characters, as well as specimens in which triradiates occur imbedded in the dermal layer; species with summit, exhalant, pore clusters or oscular depressions may or may not belong here. HINDE did not designate a type, and we have found no earlier designation of a type than this one, which is, in fact, the first of HINDE's described species.] Middle Jurassic-Upper Jurassic: Europe, ?Peru. FIG. 495, 6a-b. \*H. floriceps (PHILLIPS), Lower Coral Rag, Upper Jurassic, Hackness, Yorkshire, United Kingdom; a, side view of small type specimen with small oscula and surrounding radial canals, York Museum, ×1; b, drawing of spicular structure of fibers from type specimen, ×60 (Hinde, 1893b).

- ?Actinospongia D'ORBIGNY, 1849, p. 548 [\*A. ornata; OD] [=Actinofungia FROMENTEL, 1860a, p. 49, nom. van.]. Appears somewhat similar to Leiospongia, but with very convex, upper part without an oscule and with dermal surface with irregular, radiating structure. Jurassic (Bathonian): Europe.
- Astrospongia ÉTALLON, 1859a, p. 151 [\*Achilleum costatum GOLDFUSS, 1829, p. 94; OD] [=Blastinia ZITTEL, 1878b, p. 42, obj.; ?Actinospongia D'ORBIGNY, 1849, p. 548 (type, A. ornata, OD); ?Actinofungia FROMENTEL, 1860a, p. 49, nom. van. pro Actinospongia D'ORBIGNY, 1849, p. 548; ?Praeoculospongia GERASSIMOV, 1960 (type, P. epiconcha, OD)]. Hemispherical with broadly conical base covered with concentrically wrinkled, dermal layer; upper portion corrugated by prominent, meridional ridges that radiate from summit and alternate with corresponding sulci, both widening downwardly. No pores (nor canals probably) except circular to meandriform, intertrabecular spaces. Trabeculae consist of triradiates according to HINDE (1893b, p. 246), but in a specimen identified by ZITTEL as being of the type species, smaller "filiform spicules" coat a central spicule, as in Holcospongia. [ÉTALLON (1859b, p. 151) clearly designated Achilleum costatum GOLDFUSS, 1829 as type. The citation of Astrospongia subcostata ÉTALLON, 1859b, as type by DE LAUBENFELS (1955, p. 104) is incorrect (RMF).] Jurassic: Europe.-FIG. 495, 3. \*A. costata (GOLDFUSS), Jurakalkes, Streitberg, Germany; side view of globose sponge with wrinkled, lower, dermal layer and radially ridged, upper part, ×3 (Goldfuss, 1833).
- Enaulofungia FROMENTEL, 1860a, p. 48 [\*E. corallina; OD] [=?Holcospongia HINDE, 1893b, p. 225 (type, H. floriceps HINDE, 1893b, p. 226, SD FINKS & RIGBY, herein); Desmospongia ÉTALLON, 1863, p. 422 (type, Spongia semicinctus QUENSTEDT, 1877 in 1877–1878, p. 219, =Enaulofungia pedunculata MÜLLER, 1984, p. 32)]. Spheroidal, sometimes stipitate; shallow, oscular depression at summit, containing exhalant, pore cluster toward which radial, bifurcating, exhalant grooves converge from

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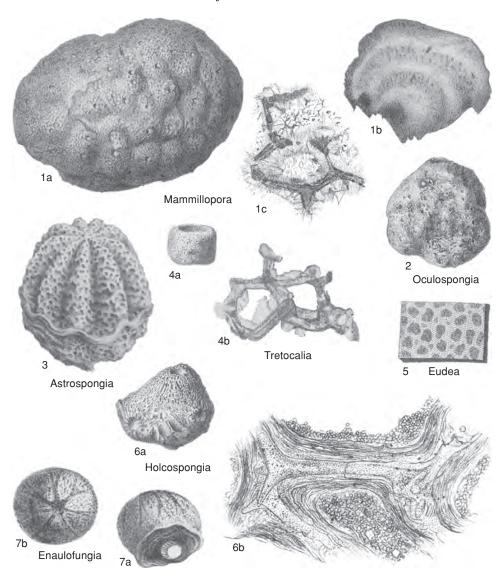


FIG. 495. Stellispongiidae (p. 745-748).

sides of sponge. Trabecular microstructure of topotypes unknown, but HINDE (1884a, p. 186) referred British specimens to the type species, which have a central, tri- or tetraradiate coated by sinuous filiform spicules. [This genus differs from typical *Holcospongia* HINDE, 1893b, in the presence of the summit depression with pore cluster and in being solitary. HINDE (1893b, p. 226) considered this genus (as *Enaulospongia, lapsus calami*) to be a synonym of *Holcospongia*, which would sink the latter into synonymy.] ?*Triassic, Jurassic*, ?*Cretaceous*: Iran, ?*Triassic*; Europe, *Jurassic*, ?*Creta*- *ceous.*—FIG. 495,7*a–b.* \**E. corallina*, Oxfordian, Jurassic, Champlitte, France, *a*, diagonal view from below of spheroidal sponge with short stalk and exhalant grooves extending upwardly from near flared base, ×0.5; *b*, view from above with exhalant cluster on summit with convergent exhalant grooves, ×0.5 (Fromentel, 1860a).

Eudea LAMOUROUX, 1821, p. 46 [\**E. clavata*; OD] [=*Epeudea* FROMENTEL, 1860a, p. 27–28 (type, *Eudea cribraria* MICHELIN, 1847 in 1840–1847, p. 251); *Orispongia* QUENSTEDT, 1877 in 1877– 1878, p. 195 (type, *O. globata*, OD); *?Conispongia*  ÉTALLON, 1859a, p. 150 (type, C. thurmani, SD RAUFF, 1893, p. 72 ); ?Elasmeudea POMEL, 1872, p. 234 (type, E. cribaria MICHELIN, 1847 in 1840-1847, pl. 48,8c,d); ?Stegeudea FROMENTEL, 1864, p. 26, nom. null. (misspelled Stegendea, a typographical error)]. Club shaped, occasionally branched; deep, central cloaca with terminal osculum; sides of sponge and walls of cloaca largely covered with dermal layer bearing characteristic large, lipped, irregular openings through which trabecular interspaces are visible; uncovered top of sponge showing intertrabecular spaces directly; trabecular microstructure of Jurassic species bundles of parallel diactines, with subordinate, regular triradiates and tetraradiates, with some diactines bent like paired rays of tuning-fork spicule (KRAUTTER, 1994); HINDE (1893b) described a central spicule (possible triradiate) coated by diactines; Triassic species have felted, aragonite needles in layers parallel to trabecular surfaces, as in Vaceletia, and no spicules (DIECI, RUSSO, & Russo, 1974a, p. 101; Mastandrea & Russo, 1995, p. 418). [Inasmuch as the type species is Jurassic, the Triassic species require a new generic name; they are demosponges belonging to the order Vaceletida. The Pennsylvanian Maeandrostia GIRTY, 1908, is a homeomorph with spherulitic microstructure. It is an agelasid demosponge and is not related to the Triassic so-called eudeas with vaceletid microstructure, nor to Eudea itself. Epeudea FROMENTEL, 1860a, and Elasmeudea POMEL, 1872, have as types different topotype specimens of the same Jurassic species (Eudea cribraria MICHELIN, 1847 in 1840-1847) except for one specimen in common (MICHELIN, 1847 in 1840-1847, pl. 58,8c). ZITTEL (1878b, p. 26) synonymized this species with the type species of Eudea (E. clavata LAMOUROUX, 1821); both are from the same locality and formation. The large, lipped openings in the dermal layer, which expose the internal trabeculae, give this possible form genus its characteristic appearance. They are present on the small, attached specimens of the type species of Conispongia ÉTALLON, 1859a, which may be a juvenile Eudea (RMF).] Triassic, Jurassic, Holocene: Europe, Iran.-FIG. 495,5. \*E. clavata, Holocene, Mediterranean Sea, near Caen, France; side view of branched sponge with coarser, inhalant openings in lower part than around rounded, upper part and osculum, ×1 (Lamouroux, 1822).

Mammillopora BRONN, 1825, p. 15 [\*Lymnorea mamillosa (sic) LAMOUROUX, 1821, p. 77; OD]
[=Lymnorea LAMOUROUX, 1821, p. 77, obj., non PERON & LESUEUR, 1810; Limnorea GOLDFUSS, 1826, p. 14, obj., nom. van. pro Lymnorea LAMOUROUX, 1821, p. 77; Lymnoreotheles FROMENTEL, 1860a, p. 34, obj., nom. van. pro Lymnorea LAMOUROUX, 1821, p. 77; Inobolia HINDE, 1884a, p. 184 (type, I. inclusa HINDE, 1884a, p. 185, M); ?Placorea POMEL, 1872, p. 225, obj.; ?Gymnorea POMEL, 1872, p. 225 (type, Polycoelia gemmans FROMENTEL, 1860a, pl. 4,4, SD RAUFF, 1893, p. 71); ?Dichorea POMEL, 1872, p.

225 (type, Lymnorea michelini D'ORBIGNY, 1850 in 1850-1852, vol. 1, p. 325, OD); Lymnorella HINDE, 1893b, p. 234, obj., nom. van. pro Lymnorea LAMOUROUX, 1821, p. 77; ?Orecyta DE LAUBENFELS, 1955, p. 49 (type, Limnorea nobilis ROEMER, 1864, p. 37, OD), nom. nov. pro Cytorea POMEL, 1872, p. 225, non LAPORTE, 1849]. Hemispherical to flabellate with conical base covered by concentrically wrinkled, imperforate layer (i.e., laterally fused, cylindrical branches within a common envelope); upper surface composed of subequal, knoblike protuberances, each bearing a central osculum that may merge with radial, slitlike, exhalant canals to form a stellate outline; rest of upper surface covered with pores that open into intertrabecular spaces; according to HINDE (1884a, p. 161, 184; 1893b, p. 234 ff.) trabeculae composed of central triradiate or tetraradiate, surrounded by fibrous calcite that may have traces of filiform spicules. [HINDE (1893b, p. 236) reported tuning-fork spicules (sagittal triradiates with parallel, paired rays) from the fibers, as well as (in topotype material) dermal triradiates (HINDE, 1884a, p. 184 and pl. 35,1a). HINDE (1893b, p. 235) synonymized Inobolia HINDE, 1884a with Mammillopora (as Lymnorella) citing as the only significant difference the absence or rarity of oscules and exhalant canals. If filiform spicules truly coat the fibers, Mammillopora is very similar to the Cretaceous Stellispongia D'ORBIGNY, 1849 (q.v.) but differs in having a single, central spicule. HURCEWICZ (1975, p. 276) described a similar spicular structure to that described by HINDE, but in a different species, which need not be congeneric with the type. HINDE (1884a, p. 160-161) considered Mammillopora (as Lymnorea) as the typical example of a trabecular structure consisting of a single spicule coated by minimal, structureless calcite. However, HINDE later (1893b, p. 235) cited the occasional presence of filiform spicules in this outer layer. This would render his Lymnorea type of fiber distinct only in degree from his Sestrostomella type (as found in post-Triassic Sestrostomella) with a large, central spicule surrounded by filiform spicules. Although BRONN (1825, p. 15) did not cite any species when he established Mammillopora, he clearly intended it as a replacement name for the homonymous Lymnorea LAMOUROUX, 1821, p. 77.] Jurassic, ?Cretaceous, Holocene: Europe, Iran.-FIG. 495, 1a-c. \*M. mamillosa (LAMOUROUX), Inferior Oolite, Middle Jurassic, Cheltenham, England; a, large specimen with nodular surface and numerous ostia,  $\times 1$ ; b, vertical section with alternating, concentric growth and development of exhalant canals, ×1; c, drawing of part of section showing axial spicules and surrounding, largely recrystallized parts of skeletal fibers, which in other specimens are composed of filiform spicules, ×60 (Hinde, 1893b).

Oculospongia FROMENTEL, 1860a, p. 37 [\*O. neocomiensia; OD] [=Homalorea POMEL, 1872, p. 225 (type, Tremospongia dilatata ROEMER, 1864, p. 40, OD); Sphecidion POMEL, 1872, p. 223 (type, Manon tubuliferum GOLDFUSS, 1826, p. 2, OD); ?Stenocoelia FROMENTEL, 1861, p. 357 (type, S. ferryi, OD); ?Crispispongia QUENSTEDT, 1877 in 1877-1878, p. 197 (type, C. expansa, SD DE LAUBENFELS, 1955, p. 100)]. Sponge massive, encrusting, rounded to conical with broad, convex top; few small, circular oscules, sometimes lipped, scattered singly over top surface; remaining surface of top and sides covered with coarse pores representing intertrabecular spaces; such pores may be vertically elongate on sides; horizontal layers of denser skeleton or horizontal constrictions imply periodic growth; obscure grooves may be present on upper surface; small patches of imperforate, dermal layer may be present; trabeculae, which are sheetlike and curve about tubular interspaces, are minutely spinose. [According to HURCEWICZ (1975, p. 245 and pl. 34,4) trabeculae (of a referred Jurassic species not the type) are built of subparallel, smooth and spinose triactines, both regular and sagittal, and the dermal layer is built of two layers of regular triactines with those in the outer layer being smaller and set obliquely to produce a spinose surface. HINDE (1884a, p. 192; 1893b, p. 240), however, described two Jurassic species (the type is Cretaceous) as having a central spicule coated by "sinuous filiform spicules." GREGORIO (1930, p. 47) proposed Virmula as a subgenus of Oculospongia, to include the new species Oculospongia (Virmula) notans, but Virmula was treated as a separate genus by DE LAUBENFELS (1955, p. 99), without explanation. This sponge should probably be treated as a subgenus, as was done by GREGORIO.] Permian, ?Triassic, Jurassic, Cretaceous: Sicily, Permian; Europe, ?Triassic, Jurassic, Cretaceous.—FIG. 495,2. O. dilatate (ROEMER), Lower Greensand, Cretaceous, Farringdon, Berkshire, England; upper surface of characteristic sponge, ×1 (Hinde, 1884a).

- Tremospongia D'ORBIGNY, 1849, p. 548 [\*Lymnorea sphaerica MICHELIN, 1846 in 1840-1847, p. 216; OD] [=Orosphecion POMEL, 1872, p. 222 (type, Manon pulvinarium GOLDFUSS, 1826, p. 2, OD); Aplosphecion POMEL, 1872, p. 222 (type, A. radiciformis, OD); Synopella ZITTEL, 1878b, p. 42, obj.]. Spheroidal with conical base covered by concentrically wrinkled, imperforate, dermal layer; surface of spheroidal part bearing numerous small clusters of exhalant openings; remainder of upper surface reveals trabeculae and intertrabecular spaces; trabecular microstructure unknown. [External form suggests relationship to Mammillopora BRONN, 1825. Aplosphecion POMEL, 1872, has only a single exhalant, pore cluster but resembles otherwise the others.] Cretaceous (Turonian): Europe.
- Tretocalia HINDE, 1900, p. 62 [\*T. pezica; OD]. Small, simple, cup-shaped to cylindrical sponges with flat base and funnel- to cup-shaped spongocoel; dermal and gastral surfaces with numerous small, round ostia and minute, irregular interspaces; wall moderately thick and pierced by exhalant canals that parallel dermal surface and

expressed on dermal surface as vertical furrows; skeleton a continuous, anastomosing, regular mesh of small fibers cored by ill-defined spicules, either singly or side by side; gastral wall differentiated and basal and lower, dermal layer locally preserved. [Tentatively included in the family. The Eocene age given by HINDE (1900) is in error (PICKETT, 1983, p. 107).] *Neogene (Miocene):* Australia.——FIG. 495, *4a–b.* \* *T. pezica,* Sherwood Marl, Flinders, Victoria; *a*, side view of small, cupshaped sponge, X1; *b*, transverse section with spicule-cored, skeletal fibers, ×60 (Hinde, 1900).

## Family ENDOSTOMATIDAE new family

[Endostomatidae FINKS & RIGBY, herein] [type genus, *Endostoma* ROEMER, 1864, p. 39]

Trabeculae of several subequal spicules cemented together. ?Lower Triassic-?Midde Triassic, Upper Triassic (Norian)-Paleogene (Eocene).

Endostoma ROEMER, 1864, p. 39 [\*Scyphia foraminosa GOLDFUSS, 1829, p. 86; SD DE LAUBENFELS, 1955, p. 97] [=Tubulospongia COURTILLER, 1861, p. 135 (type, T. insignis, SD DE LAUBENFELS, 1955, p. 108); ?Polyendostoma ROEMER, 1864, p. 39 (type, P. sociale, SD DE LAUBENFELS, 1955, p. 100); ?Astrolmia POMEL, 1872, p. 115 (type, Cnemidium astrophorum GOLDFUSS, 1829, p. 97; OD); ?Syncalpia POMEL, 1872, p. 116 (type, Cnemidium astrophorum GOLDFUSS, 1829, p. 97, SD RAUFF, 1893, p. 68); ?Holosphecion POMEL, 1872, p. 224 (type, H. tuberosum, OD); Corynella ZITTEL, 1878b, p. 35, obj.]. Conicocylindrical, usually simple but sometimes several basally conjoined, characterized by deep, central cloaca; principal, exhalant canals enter cloaca subhorizontally, and on top surface occur as radial grooves converging on osculum; other canals essentially intertrabecular spaces; patches of imperforate dermal layer may cover lower parts of sponge. According to HINDE (1884a, p. 160) fibers are bundles of subparallel, extremely slender triradiates, and paratangential dermal triand tetraradiates may be present locally. [Observations by FINKS appear to confirm HINDE's interpretation of the fibers. DUNIKOWSKI (1883, p. 316) noted a predominance of irregular triradiates. HURCEWICZ (1975, pl. 29,2) illustrated paratangential, knobby triradiates on the surface of the dermal layer of a Jurassic species, whose trabeculae have the structure described by HINDE. Absence of longitudinal slits in the cloacal wall and absence of large central spicules in trabeculae separate this from Eusiphonella ZITTEL, 1878b. The type species is Cretaceous; Permo-Triassic species with spherulitic microstructure once assigned here were separated off as Precorynella DIECI, ANTONACCI, & ZARDINI, 1968. They are agelasid demosponges. DE LAUBENFELS's (1955, p. 97) selection of Scyphia foraminosa GOLDFUSS, 1829, as type makes this ge-

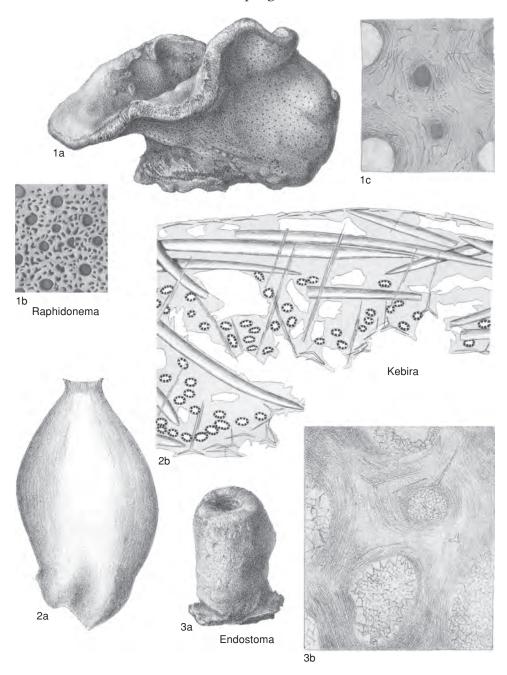


FIG. 496. Endostomatidae and Lelapiidae (p. 748-750).

nus an objective senior synonym of the betterknown *Corynella* ZITTEL, 1878b, for which the same species was selected by HINDE, 1884a, p. 179.] *Triassic (Norian)–Cretaceous:* Europe, *?Triassic, Jurassic–Cretaceous;* Iran, *Norian–Rhaetian.*——FIG. 496, 3a-b. \**E. foraminosa* (GOLDFUSS), Lower Greensand, Cretaceous, Farringdon, England; *a*, side view of small, subcylindrical sponge with prominent osculum and spongocoel, ×1; *b*, camera lucida drawing of skeletal relationships showing filiform, three-rayed spicules making up skeletal fibers, ×72 (Hinde, 1884a).

Raphidonema HINDE, 1884a, p. 197 [\*R. contortum; SD DE LAUBENFELS, 1955, p. 99]. Cup shaped, with irregular and wavy outline and relatively thin walls; wall composed of anastomosing, tubular spaces of narrow bore, separated by skeletal trabeculae; larger, straighter tubes more or less perpendicular to inner (exhalant) surface of cup (presumably containing exhalant canals) are spaced quincuncially, penetrating most of wall and opening as pores of same diameter on inner surface (near top of sponge they run obliquely upward); intervening intertrabecular spaces (tubes) open as small, circular pores on both outer and inner surfaces, through a thickened surface layer of skeleton; lower part of inner surface may be so thickened as to obliterate these small pores; fibers (trabeculae) composed of numerous sinuous, laminar or threadlike bodies subparallel to fiber surface, which were interpreted by HINDE (1884a, p. 197 ff.) as triactines with one reduced ray. Cretaceous-Paleogene (Eocene): Europe, Cretaceous; India, Eocene. FIG. 496, 1a-c. \*R. contortum, Lower Greensand, Farringdon, Berkshire, England; a, side view of specimen with convolute walls with small, inhalant ostia, ×1; b, enlargement of dermal surface with circular, inhalant ostia and intervening skeletal net, ×5; c, camera lucida drawing of part of interior skeleton with thin, threadlike bodies that HINDE (1884a) interpreted as triradiate spicules in fibers, ×50 (Hinde, 1884a).

## Family LELAPIIDAE Dendy & Row, 1913

[Lelapiidae DENDY & ROW, 1913, p. 784]

Spicules organized in tracts. Holocene.

- Lelapia GRAY, 1867, p. 557 [\*L. australis; OD] [=Paralelapia HOZAWA, 1923, p. 185 (type, Lelapia nipponica Hara, 1894, p. 369, OD); ?Kebira Row, 1909, p. 210 (type, K. uteoides, OD)]. Sponge cylindrical or club shaped with central cloaca and terminal oscule; inhalant pores scattered over surface; dermal layer of sagittal triradiates and microxeas; interior with crisscrossing bundles of tuning-fork spicules, their paired rays usually facing gastrally, as well as separate, irregularly arranged, very large oxeas; gastral layer of sagittal triradiates, and rare sagittal quadriradiates (with short fourth ray facing cloaca); oscule surrounded by vertical palisade of oxeas; choanocyte nuclei apical; larva not known. [Paralelapia HOZAWA, 1923 differs only in the subdermal location of the large oxeas and in the radial arrangement of the tuning-fork bundles, which start from the unpaired rays of gastral triradiates, a condition also seen in the type species.] Holocene: Indo-Pacific.
- ?Kebira Row, 1909, p. 210 [\*K. uteoides; OD]. Ovoid with central cloaca and terminal osculum; dermal layer of small, sagittal triradiates underlain by very

large oxeas oriented longitudinally; gastral layer of small, equiangular and sagittal triradiates; in choanosome between these two layers are radial bundles of sagittal triradiates whose paired rays, uniformly directed gastrally, are vestigial bumps; choanocyte nuclear position and larva not known. [The chief distinction between this genus and Lelapia GRAY, 1867, lies in the vestigial, paired rays of the tuning-fork spicules, for contrary to Row's opinion (1909, p. 210) it seems possible for vestigial rays to curve sufficiently to form tuning forks with continued growth, and the bundled spicules need not be regarded as a fundamentally different kind of spicule in this genus.] Holocene: Red Sea. FIG. 496, 2a-b. \*K. uteoides, Tela Tela Kebira, Red Sea, Sudan; a, side view of flaskshaped sponge, ×6; b, longitudinal section through sponge showing distribution of large oxeas and smaller, triradiate spicules, ×40 (Row, 1909).

# Order SPHAEROCOELIIDA Vacelet, 1979

[Sphaerocoeliida Vacelet, 1979, p. 492] [=suborder Sphinctozoa Steinmann, 1882, p. 149, *partim*; order Thalamida de Laubenfels, 1955, p. 100, *partim*]

Cortex of calcite with embedded, calcite spicules; no trabeculae; body organized in chains of modular segments. *Permian– Cretaceous (Cenomanian).* 

#### Family SPHAEROCOELIIDAE Steinmann, 1882

[Sphaerocoeliidae Steinmann, 1882, p. 150; emend., Finks & Rigby, herein] [=Sphaerocoeliidae Steinmann, 1882, p. 150, partim; Barroisiidae de Laubenfels, 1955, p. 101, partim]

Cylindroid, composed of superposed chambers without internal structures; central osculum in each chamber, endowall present only in *Barroisia* MUNIER-CHALMAS, 1882; exopores subpolygonal (circular in *Tremacystia* HINDE, 1884a); calcareous, sagittal triradiates embedded in calcite wall; in addition, tetraradiates present except in *Barroisia*, monaxons except in *Tremacystia*. *Permian–Cretaceous (Cenomanian)*.

Sphaerocoelia STEINMANN, 1882, p. 162 [\**Thala-mopora michelini* SIMONOWITSCH, 1871, p. 31; OD]. Spheroidal to hemispheroidal segments clearly marked externally, increasing in size noticeably in a curved or bent, linear series; large, central osculum at top of each chamber but no endowall; closely spaced, circular or subpolygonal exopores; interwall with its pores a continuation of exowall of preceding chamber. [HINDE (1884a, p. 173) reported interwall is double; STEINMANN (1882, p. 162) said

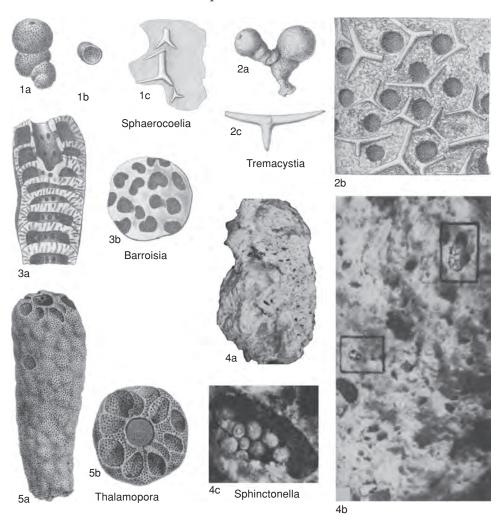


FIG. 497. Sphaerocoeliidae (p. 750-752).

wall built of small, curved monaxons closely packed, but DUNIKOWSKI (1883, p. 317) reported also triradiates (sagittal in his illustration) and a few tetraradiates from topotypes assigned to the same species. In view of homeomorphy of similar Cretaceous forms, and uncertainty as to spicule complement of the type, reported distribution outside the type locality and stratigraphic age (or even within it) must remain doubtful.] Permian-Cretaceous (Cenomanian): Tunisia, Permian; Germany (Essen), France, Czech Republic, Slovakia, Jurassic-Cretaceous (Cenomanian).—FIG. 497, 1a-c. \*S. michelini (SIMONOWITSCH), Cenomanian beds, Essen area, Germany; a, side view of small type with spheroidal, porous chambers,  $\times 2$ ; *b*, view from above showing central osculum and surrounding, coarse pores, ×10 (Steinmann, 1882); c, camera

lucida drawing showing triradiate spicules in a fragment, ×50 (Dunikowski, 1883).

Barroisia MUNIER-CHALMAS, 1882, p. 425 [\*Tubipora anastomosans MANTELL, 1838, p. 636; OD]. Conicocylindrical branching tubes without external segmentation; central cloaca about one-third sponge diameter; exowall netlike with subpolygonal, substellate exopores; interwalls gently arched distally, chambers low, interpores polygonal; endowall continuous, with horizontal whorl of large, circular endopores in each chamber; exowall consisting of inner layer of felted triradiates parallel to wall and outer layer of penicillately arranged tylostyles, tylote ends outwardly, both embedded in finely fibrous groundmass (REID, 1968d, p. 3). [MUNIER-CHALMAS's publication is dated June 5, 1882. STEINMANN, 1882, p. 163, ascribed the genus to MUNIER-CHALMAS but noted it as a manuscript name. Inasmuch as STEINMANN's publication bears only the date 1882 (published as the second of two Bande for the Jahrgang 1882), and Article 21 of the Code (ICZN, 1999) states that in the absence of evidence for a day or month of publication, the date of publication is to be taken as the last day of the year, it would be consistent both with the Code and with STEINMANN's intentions to ascribe the genus solely to MUNIER-CHALMAS (RMF).] Cretaceous (Aptian-Albian, Cenomanian): Czech Republic, Slovakia, England, France, Germany, Greece, Spain, Romania.——FIG. 497, 3a-b. \*B. anastomosans (MANTELL), Aptian, Blangy, northern France; a, longitudinal section showing tubular spongocoel with coarse endopores, and porous interwalls and exowalls,  $\times 3$ ; b, transverse section of exowall with irregular, inhalant ostia, ×10 (Steinmann, 1882).

- Sphinctonella HURCEWICZ, 1975, p. 280 [\*S. trestiani; OD]. Massive, sometimes encrusting; composed of blisterlike chambers of irregularly ovate cross section, numerous small chambers interspersed between fewer larger ones; chamber walls microvesicular; small pores in chamber walls communicating with these vesicular spaces, while larger pores communicating between chambers [it is unclear whether some of these vesicular spaces and chambers might not be tubular and anastomosing]; chamber lumens generally empty but some contain obscure, spheroidal bodies or tubular structures; walls said to contain "traces of small, densely spaced numerous monactines and some triactines" (HURCEWICZ, 1975, p. 281). [The genus was placed with some question into the family Cryptocoeliidae by SENOWBARI-DARYAN (1990) because of the uncertain character of the tubular filling structure but is included here in the Sphaerocoeliidae because of the reported spicules.] Jurassic (Oxfordian): Poland.—FIG. 497,4a-c. \*S. trestiani, Jurassic beds, Kujawy; a, holotype, broken surface, with chambers of various sizes, ×1; b, enlarged surface of holotype with chambers indicated, ×8; c, enlarged chamber with filling structures, UL Sp VII/2, ×10 (Hurcewicz, 1975; courtesy of Acta Palaeontographica Polonica, Polska Akademia Nauk).
- Thalamopora ROEMER, 1840 in 1840–1841, p. 21 [\*Thalamopora (Ceriopora) cribrosa GOLDFUSS, 1826, p. 32; OD]. Conicocylindrical, small, occasionally branching; central cloaca one-fourth or more of sponge diameter; surrounded by thalamidarium of globose chambers; exopores and interpores subequal, circular, small, numerous, and closely spaced; single larger endopore communicating with cloaca from inner, narrow end of each chamber; no trabecularium. [DUNIKOWSKI (1883, p. 323) stated that he has observed triradiates in the wall, and STEINMANN (1882, p. 168) stated that sections of spicules similar to those of *Barroisia* MUNIER-CHALMAS, 1882, are vis-

ible locally in cut sections on a few specimens. Genus resembles *Cystauletes* KING, 1943, perhaps homeomorphically.] *Cretaceous (Cenomanian):* Germany.——FIG. 497,5a-b. \**T. cribrosa* (GOLDFUSS), Mergelgrande, near Essen, Ruhr region; *a*, side view of typical sponge showing subcylindrical, chambered form with central spongocoel, ×2; *b*, view from above showing central, tubular spongocoel and surrounding, radially arranged chambers, ×3 (Goldfuss, 1833).

Tremacystia HINDE, 1884a, p. 171 [\* Verticillites dorbignyi HINDE, 1882, p. 192; SD DE LAUBENFELS, 1955, p. 101]. Spheroidal, overlapping segments in short, upwardly expanding, branching series, last chamber being noticeably larger and more globose; small, circular, central osculum at top of each chamber, but endowall absent; exopores small, circular, separated slightly more than their diameter; interwall an extension of underlying exowall with its pores; one specimen of type series has imperforate, endowall-like, central tube in terminal chamber, which is of similar structure to a vesicle in preceding chamber; walls composed of small, very thin (filiform), sagittal triradiates with nearly orthogonal, paired rays curved about pores, generally reduced third ray directed away from them (or else completely missing); outside these smaller spicules are larger, sagittal triradiates and tetraradiates, with paired rays often subhorizontal, unpaired ray directed downwardly, and fourth ray, when present, directed inwardly; spicules uncemented or partly to completely embedded in granular calcite, which may be diagenetic; small, sagittal triradiates found on surfaces of imperforate tube and vesicle, their paired rays horizontal and unpaired ray directed downwardly, being much more reduced on inner side of tube (REID, 1969a, p. 2-3). Cretaceous (Albian-Cenomanian): England, France.—FIG. 497,2a-c. \*T. dorbignyi (HINDE), Upper Greensand, Wiltshire, England; a, side view of branching, figured specimen with globose chambers, ×1; b, part of outer wall with circular, inhalant ostia and large, tetraradiate spicules of dermal layer,  $\times 30$ ; c, detached tetraradiate spicules from dermal layer, ×50 (Hinde, 1884a).

# Order LITHONIDA Doederlein, 1892

[Lithonida DOEDERLEIN, 1892, p. 143] [=Lithonia VACELET, 1981, p. 325; emend., VACELET, 1981, p. 325; Stereina de LAUBENFELS, 1955, p. 99, partim]

Hypercalcified Calcaronea. Jurassic-Holocene.

## Family LEPIDOLEUCONIIDAE Vacelet, 1967

[Lepidoleuconiidae VACELET, 1967a, p. 54]

External armor of scales derived from triradiates; choanosomal skeleton of scat-

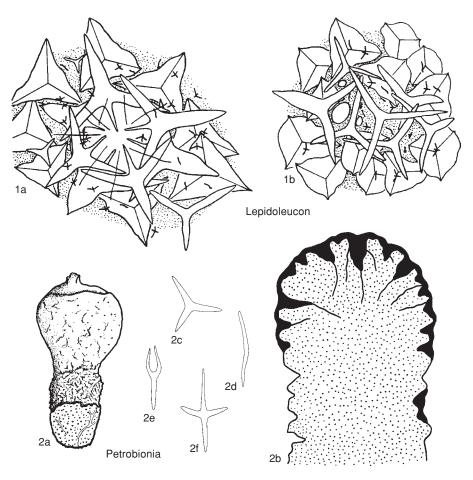


FIG. 498. Lepidoleuconiidae and Petrobionidae (p. 753-758).

# tered microdiactines; oscular area with modified tetractines. *Holocene*.

Lepidoleucon VACELET, 1967a, p. 54 [\*L. inflatum; OD]. Domical, encrusting, very small; central, circular osculum and lateral, oval, inhalant area form only openings in armor of triangular to circular, overlapping scales derived from enlargement of equiangular triradiates; inhalant area supported by nonenlarged, equiangular triradiates; osculum surrounded by partially enlarged, equiangular tetraradiates whose short, fourth ray (in the same plane) is directed toward oscular center, as are smaller monaxons radially arranged; sponge interior containing only microbiradiates and microtetraradiates with spinose microbiradiates in inhalant area; choanocyte nucleus apical, and larva an amphiblastula. Holocene: Indo-Pacific. FIG. 498, 1a-b. \*L. inflatum, reefs at Tulear and Songeritelo, Madagascar; a, drawing of spicule arrangement around osculum, includes microdiactine and tetractines as well as larger triactines and tetractines, some of which are enlarged into triactine-based scales,  $\times 100$ ; *b*, drawing of spicule arrangement around inhalant zone with same types of spicules,  $\times 100$  (Vacelet, 1967a).

## Family MINCHINELLIDAE Dendy & Row, 1913

[Minchinellidae DENDY & ROW, 1913, p. 739] [=Minchinellidae DENDY & ROW, 1913, p. 739, partim; Porosphaeridae DE LAUBENFELS, 1955, p. 99, partim; Bactronellidae DE LAUBENFELS, 1955, p. 100, partim]

Principal skeleton composed of layers of tetraradiates with three curving, downwardly directed rays and one straight, upwardly directed ray, spicules cemented together with fibrous calcite. Additional spicules, including tuning forks, loose in flesh. [The order Lithonida DOEDERLEIN, 1892, as originally defined (group Lithones) is coterminous with the family Minchinellidae. VACELET (1981, p. 315) expanded the definition to include the other calcaronean families with a massive skeleton, namely the Petrobionidae and the Lepidoleuconidae.] *Jurassic–Holocene*.

- Minchinella KIRKPATRICK, 1908, p. 504 [\*M. lamellosa; OD]. Flabellate or ear-shaped sponge with one flat side inhalant and other exhalant; inhalant and exhalant chimneys of soft parts represented in rigid skeleton by raised, circular rims occurring in radial rows on inhalant surface, more scattered and larger on exhalant one; principal skeleton formed of spinose tetraradiates with one straight, distal ray and three arcuate, proximal rays, cemented together by coating of radially fibrous calcite (clino- to orthogonal, WENDT, 1979, p. 454) with a finely papillose surface; loose spicules of soft parts including surface layer of spinose monaxons, chimneys also surrounded by apparatus of sagittal triradiates with unpaired ray parallel to axis of chimney, pointing downwardly, and paired rays nearly at right angles to it, along with similar quadriradiates, their fourth ray pointing toward chimney axis; unpaired ray is generally longer than paired rays in both spicule types but may be shorter in some spicules; tuningfork spicules also present in basal parts of chimneys; leuconoid sponge hermaphroditic and incubating a parenchymella larva; nucleus of choanocytes is apical. Holocene: Indo-Pacific. FIG. 499, 1a-e. \*M. lamellosa, Api, New Hebrides; a, dermal surface of holotype; b, gastral surface of holotype,  $\times 1$ ; c, quadriradiate, long, gastral ray and nearly equal basal rays; d, tuning fork spicule; e, monaxon from surface of oscular chimney, ×200 (Kirkpatrick, 1908; courtesy of Taylor & Francis, Annals and Magazine of Natural History).
- Bactronella HINDE, 1884a, p. 205 [\*B. pusillum; OD]. Sponge club shaped, branching, discoid, or encrusting; principal skeleton formed of spinose quadriradiates with very long, distal ray and three shorter, arcuate, proximal rays with terminal, clasping expansions, spicules arranged so that distal rays line up to form more or less continuous, radial rods and proximal rays outlining radial canals; smaller triradiates with orthogonal, proximal rays may connect larger spicules laterally; net fused together by microhispid smaller spicules; dermal layer covering much of outer surface, spicules of which could not be observed in type species but which in referred species consisting of tangent monaxons and sagittal triradiates; basal layer consisting of uncemented quadriradiates, similar to those of principal skeleton, together with smooth triradiates and quadriradiates. [The basal layer was described by HINDE (1900, p. 59 ff.) from the type species and the associated Bactronella parrula HINDE from Victoria, Australia. VACELET (1967a, p. 49) suggested that several Holocene species that

he described as *Plectroninia* might be better referred to *Bactronella*.] *Jurassic–Neogene (Miocene), ?Holocene:* Germany, *Jurassic;* France, *Cretaceous;* USA (North Carolina), *Eocene;* Australia (Victoria), *Miocene;* Madagascar, Mozambique, *?Holocene.*—FIG. 499,*3a–c. \*B. pusillum,* Upper Jurassic, probably from Thurnau, Bavaria, Germany; *a*, side view of small type specimen, ×2; *b*, part of transverse section showing canals in outer part and general appearance of central part, ×20; *c*, part of three-rayed spicule showing spinous character of rays, ×200 (Hinde, 1884a).

- Muellerithalamia REITNER, 1987b, p. 95 [\* Verticillites extensus LANG, 1985, p. 5; OD]. Minchinellid sponge with calcitic, basal skeleton that may be chambered but without regular, thalamid structure; cylindrical spongocoel may be present; microstructure orthogonal to hemispherical; internal structure irregular (reticulate) to trabecular; prosopores and apopores developed; rigid spicules present within trabecular structures of basal skeleton; spicules are modified monactines, triaenes, and calthrops. Upper Jurassic: southern Germany. FIG. 500, 1a-c. \*M. extensus (LANG), Frankenalb; a, longitudinal section showing irregular, chambered structure and axial spongocoel,  $\times 2$ ; *b*, part of outer wall of *a*, with small, inhalant prosopores but larger apopores (arrows), ×4; c, drawing of part of basal skeleton with spicules, ×10 (Reitner, 1987b).
- Petrostroma DOEDERLEIN, 1892, p. 145 [\*P. schulzei; OD]. Branching twigs arising from encrusting, basal, laminar expansion; principal skeleton composed of quadriradiates cemented together in continuous net with upwardly and outwardly radiating elements (fused distal rays of possible quadriradiates) connected laterally by thinner elements, and showing denser growth laminations parallel to branch tip; principal quadriradiates generally smooth and oriented with three arched, proximal rays facing inwardly and straight, pointed distal ray faced outwardly; more irregular and spinose, smaller quadriradiates fill in mesh spaces near surface; dermal layer of loose spicules including smooth, sagittal triradiates and tetraradiates plus crisscrossing bundles of parallel, tuning-fork spicules. [No known suitable figures.] Cretaceous-Paleogene (Eocene): Germany, France, Cretaceous; Japan, Eocene.
- Plectroninia HINDE, 1900, p. 51 [\**P. halli;* OD]. Sponge fig shaped, cake shaped, or crustlike; sides covered with dermal layer, large, exhalant canals perpendicular to upper surface with equivalent grooves on side of upper margin; principal skeleton formed of spinose quadriradiates with long, pointed, distal ray and three shorter, curved, proximal rays with terminal expansions, organized roughly into layers with distal rays outwardly and proximal rays fixed to underlying spicules by terminal expansions and by investing calcite cement with microhispid surface; orientation is not uniform and concentric and radial, organization is not evident; dermal layer of uncemented spicules

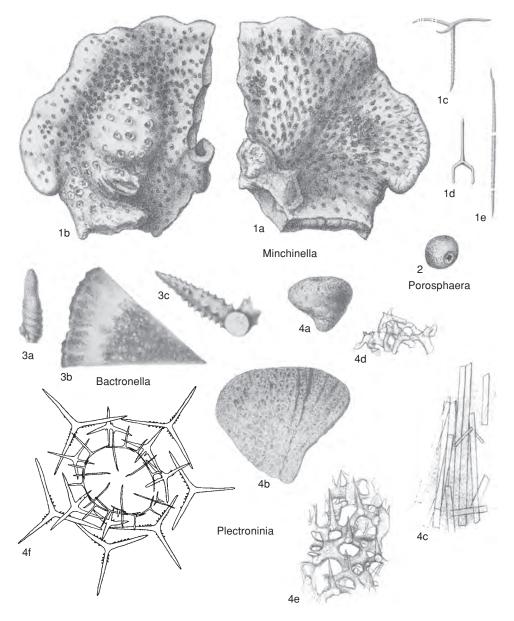


FIG. 499. Minchinellidae (p. 754-756).

consisting of outer thatch of smooth monaxons oriented vertically (perpendicular to top growing edge) under which is layer of irregularly oriented, small monaxons, smooth triradiates, and tetraradiates (both symmetrical and sagittal), tuningfork spicules, and small, loose spicules similar to those of principal net; basal layer consisting of spicules as in principal net but small and uncemented; periodic intercalations of basal layer, sometimes accompanied by dermal-type spicules, may occur within principal skeleton, parallel to upper surface of sponge, and presumably indicate periodic interruptions (possibly seasonal) in growth; choanoctye chambers in upper layer of principal skeleton, storage cells (thesocytes) may be present in basal layer (VACELET, 1967b, p. 124). *Cretaceous–Holocene:* Europe, *Cretaceous;* USA (North Carolina), *Eocene;* Australia (Victoria), *Miocene;* Indo-Pacific, Mediterranean, *Holocene.* ——FIG. 499,4*a*–*e.* \**P. halli,* Miocene, Fyansford Formation, Moorabool River, Victoria, Australia; *a*, side view of holotype, ×1; *b*, vertical section showing canal development, ×2; *c*, fragment of dermal layer with long, lance-shaped to styliform monaxial spicules, ×100; *d*, fragment of basal layer, ×100; *e*, vertical section of skeletal mesh showing radial arrangement of apical rays and manner of junction of other rays, ×50 (Hinde, 1900).—FIG. 499,4*f. P. pulchella* VACELET, Holocene, reef at Tulear, Madagascar; drawing of spicule arrangement around oscule with representative spicules, ×100 (Vacelet, 1967a).

- Porosphaera STEINMANN, 1878, p. 120 [\*Millepora globularis PHILLIPS, 1829 in 1829-1836, p. 186; OD]. Spheroidal to hemispheroidal, latter forms with concentrically wrinkled, concave base, and varying from oblate to prolate; spheroidal forms may have meridional, exhalant grooves, sometimes branched, converging on one end, which may be produced into mamelon; spheroidal forms may be penetrated wholly or partly by central tube that appears to be mold of attachment to seaweed stem or similar object; patches of a dermal layer may occur on outer surface, in addition to concentrically wrinkled, basal layer of hemispheroidal form; narrow, subequal, closely spaced, radial canals radiate from center of sponge or from center of flat base when present, and open as circular pores at surface; principal skeleton consisting of quadriradiates with long, pointed, sometimes laterally spined, distal ray and three short, bowed, proximal rays with terminal, clasping expansions, ensemble of such spicules fused into continuous net by coating of cement; basal, dermal layer of small monaxons parallel to edge of sponge, outside of which is thatch of similar spicules arranged radially; upper, dermal layer composed of tangential, small, smooth triradiates, quadriradiates, and monaxons, not otherwise oriented, except that local, concentric arrangements of monaxons external to rest appear to have surrounded a pore. Cretaceous: Europe, USA.-FIG. 499,2. \*P. globularis (PHILLIPS), Chalk, Upper Cretaceous, Yorkshire, United Kingdom; small, globular sponge, YM, ×1 (Phillips, 1836 in 1829-1836).
- Porosphaerella WELTER, 1911, p. 16 [\*P. subglobosa WELTER, 1911, p. 23; OD]. Club shaped, sometimes clustered or branched, sometimes encrusting; base always concave with concentrically wrinkled, dermal layer; longitudinal sections having longitudinal, subparallel, wide, skeletal fibers that presumably represent fused, superposed, distal rays of quadriradiates, connected by thin, horizontal elements, widely spaced but at same level across sponge, and possibly representing smaller quadriradiates with orthogonal, proximal rays, or else repeated basal layers with monaxons; no spicules observed in concentrically wrinkled, dermal layer at base of sponge, but possible cross sections of such spicules were seen in horizontal elements of sponge interior. [Externally, this genus resembles some specimens of Porosphaera described

by HINDE (1904, pl. 1,27–28), as well as *Bactronella* HINDE, 1884a.] *Cretaceous:* Germany, France.——FIG. 500,4*a*–*b.* \**P. subglobosa*, Essener Grünsand, Cenomanian, Essen, Germany; *a*, view from above of encrusting, globular to nodose form,  $\times 1$ ; *b*, part of dermal skeleton showing coarse, skeletal fibers connected by thin, weblike elements, spinose rays may have arisen from coarse, fiber junctions,  $\times 29$  (Welter, 1911).

- Retispinopora BRYDONE, 1912, p. 112 [\*R. arbusculum; SD DE LAUBENFELS, 1955, p. 107]. Very small, conoidal or stalagmite-like sponges with concave, sometimes expanded base that may bear few concentric wrinkles; surface pores formed by interspicular spaces of principal skeleton, which is built of anapodal triradiates similar to those of Porosphaera STEINMANN, 1878. [Except for their very small size, these sponges resemble Porosphaera with which they may occur; it is possible that they are merely juveniles of that genus.] Cretaceous-Paleogene (Danian): England, Cretaceous; Denmark, Danian.-FIG. 500,2. \*R. arbusculum, Chalk of Hants, Upper Cretaceous, Cosham, England; side view of small, porous, conoidal sponge, ×12 (Brydone, 1912).
- Sagittularia WELTER, 1911, p. 33 [\*S. adfixa WELTER, 1911, p. 34; OD]. Hemispheroidal or encrusting; concave base covered with concentrically wrinkled, dermal layer; principal skeleton built of superposed layers of large, anapodal quadriradiates with long, spinose, distal ray and short, proximal rays fused by cement into continuous, horizontal layers; between these larger spicules are smaller quadriradiates cemented into fine meshwork; spicules of basal dermal layer not ascertainable. Cretaceous: Germany, France.—FIG. 500, 3a-b. \*S. adfixa, Essener Grünsand, Cenomanian, Essen, Germany; a, side view of globose, typical specimen, ×1; b, enlarged section of skeleton showing coarse rhabdome with axial canal and interconnecting, fine meshwork, ×29 (Welter, 1911).
- Tulearinia VACELET, 1977a, p. 354 [\*T. stylifera; OD]. Encrusting, very small; circular oscule; coarse, styliform monaxons in surface layer, both tangential and protruding, together with large, sagittal triradiates interlaced to form cortex; sponge interior with microdiactines; basal layer of large, sagittal quadriradiates with fourth ray directed upwardly and remaining, somewhat irregular rays interlaced and underlain by layer of smaller, sagittal triradiates; oscule enclosed by paired rays of thin triradiates, and of tetraradiates whose fourth ray is directed toward oscular center; choanocyte nucleus apical. Holocene: Indian Ocean.-FIG. 500,5a-e. \*T. stylifera, off Island of Réunion; a, photomicrograph of section perpendicular to surface of oscular opening margined by triradiate spicules, MNHN J.V.-76-1, ×65; b-e, characteristic spicules including surficial diactines, tetractines of basal network, perioscular triactines, perioscular tetractines, ×50 (Vacelet, 1977a; courtesy of Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

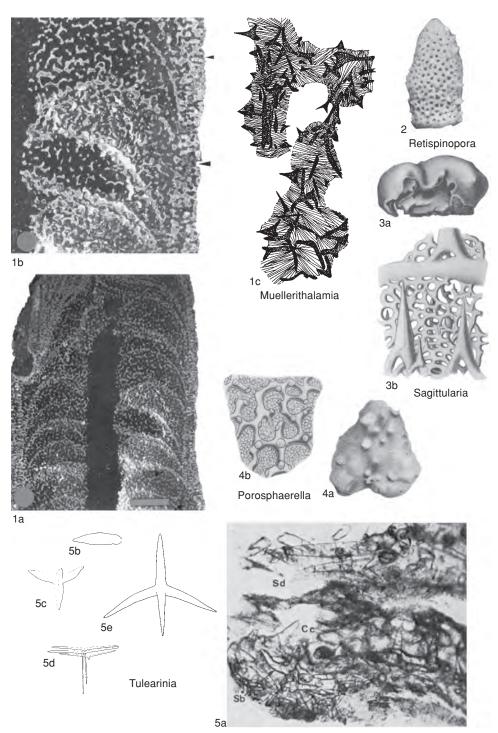


FIG. 500. Minchinellidae (p. 754–756).

#### Family PETROBIONIDAE Borojevic, 1979

[Petrobionidae BOROJEVIC, 1979, p. 529]

Massive skeleton of spherulitic and penicillate calcite with irregular pits containing flesh of sponge; loose, calcareous spicules also present. *Holocene*.

Petrobionia VACELET & LÉVI, 1958, p. 318 [\*P. massiliana; OD]. Globular, cylindrical, or club shaped; principal skeleton a nearly solid mass of irregular magnesian calcite spherulites and areas of penicillate structure; upper surface deeply and irregularly pitted, in which spaces living tissues are lodged, with extensions into branching tunnels that penetrate more deeply into massive skeleton; spicules of flesh including sagittal quadriradiates and triradiates whose paired rays surround oscules, paired rays of quadriradiates being nearly orthogonal, tuning-fork spicules, and microdiactines; choanocyte nucleus apical and larva amphiblastula. Holocene: Mediterranean.-FIG. 498,2a-f. \*P. massiliana, Gulf of Marseille; a, drawing of side view showing growth form,  $\times 1$ ; b, schematic, longitudinal section showing living tissue in black over massive, internal structure,  $\times 2$ ; *c*-*f*, spicules of sponge, ×100 (Vacelet & Lévi, 1958).

# Order and Family UNCERTAIN

Gravestockia REITNER, 1992, p. 99 [\*G. pharetroniensis; OD]. Small, upright sponges that possess a rigid skeleton of tetractine desmas, with uncemented, monaxial spicules and regular triaenes in dermal skeleton; tetractines with branched ray tips comparable to zygomes in demosponges; each spicule a single crystal of calcite. [Taxonomic position of the sponge is uncertain, but REITNER (1992, p. 100) concluded that it is not a heteractinid form. PICKETT (2002a, p. 1,119) suggested that the genus is similar to modern, lithonine, calcareous sponges, and hence the genus is tentatively included here.] Lower Cambrian: South Australia. FIG. 501a-c. \*G. pharetroniensis, Flinders Range, Atdabanian; a, holotype section of sponge that grew on an archaeocyathan, IPFUB/JR 1992/1, ×10; b, section of choanosomal skeleton composed principally of calcareous, desmalike spicules, scale bar, 100 µm; c, enlarged section of free dermal triaene, REM back scatter image, scale bar, 100 µm (Reitner, 1992).

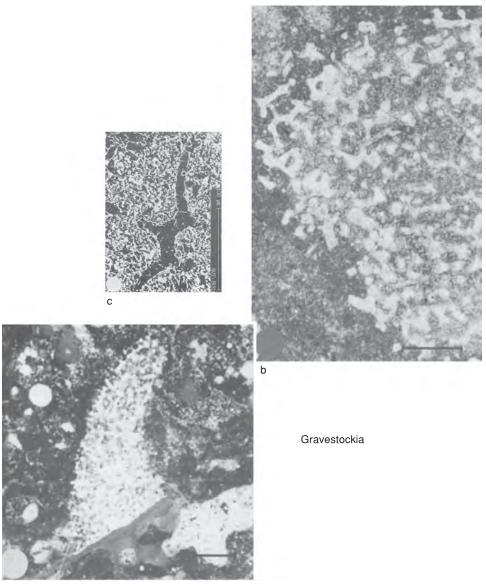
# Class and Order UNCERTAIN Family POLYACTINELLIDAE Mostler, 1985

#### [Polyactinellidae MOSTLER, 1985, p. 14]

Sponges whose forms are unknown, but which are characterized by distinctive, calcareous spicules with three-rayed, basic structure but which may have 3, 5, 6, 9, or 12 additional rays developed. *Lower Cambrian–Permian*.

- Polyactinella MOSTLER, 1985, p. 15 [\*P. furcata; OD] [?=Dodecaactinella REIF, 1968, p. 741 (type, D. oncera, OD)]. Spicules with six rays that diverge from a central point, three of which are short and three of which are longer and bifurcate distally into two rays, to produce a nine-rayed spicule. Lower Cambrian-Middle Cambrian: Sardinia.——FIG. 502,1. \*P. furcata, archaeocyathid limestone of Matoppa Member, Lower Cambrian, Iglesiente, southwestern Sardinia; type spicule with three short rays and three longer primary rays that bifurcate, ×100 (Mostler, 1985; courtesy of Naturwissenschaftlich-Medizinischer Verein in Innsbruck).
- Bengtsonella MOSTLER, 1996b, p. 228 [\*B. australiensis; OD]. Sponges characterized by threerayed spicules whose distal ray tips are trifurcate and whose proximal ray segments are very short; medial ray of trifurcate tip short and two diverging long and curved. Lower Cambrian: South Australia.——FIG. 502,4. \*B. australiensis, Ajar Limestone, Mt. Scott Range; holotype spicule showing distinctive ray development, ×200 (Mostler, 1996b).
- ?Dodecaactinella REIF, 1968, p. 741 [\*D. oncera; OD] [?=Polyactinella MOSTLER, 1985, p. 15 (type, P. furcata, OD)]. Spicules with six initial rays that diverge from a central point, three shorter and three longer, trifurcating distally to produce spicules with 12 rays. [BENGTSON (1990a) placed Polyactinella and Sardospongia into synonymy with Dodecaactinella. MEHL and LEHNERT (1997) later concluded that there are no transition forms between Dodecaactinella and Sardospongia and that those genera should be kept separate. They also concluded that there are transition forms between Dodecaactinella and Polyactinella and that those genera should be combined.] Lower Cambrian-Upper Ordovician: Sardinia, Siberia, Argentina, Australia.-FIG. 502,2a-b. \*D. oncera, Borkholmer beds, Upper Ordovician, Borkholm, Estonia; holotype spicules, SPIT Po 1352/24, ×40 (Reif, 1968; courtesy of Neues Jahrbuch für Geologie und Paläontologie, Monatshefte).
- Dvorcia NEKVASILOVA & STEMPROKOVA, 1960, p. 403 [\*D. mira; OD]. Sponges characterized by synphobetractine spicules whose two lower rays are fused at their tips; lower rays may be much shorter than upper rays. Lower Ordovician-Permian: Czech Republic, Slovakia, Sweden.— FIG. 502,5a-b. \*D. mira, Lower Devonian, Bohemia; isolated spicules showing variation in growth form, ×75 (Mostler, 1996b).
- Kucerella MOSTLER, 1996b, p. 233 [\*K. prokopensis; OD]. Sponges characterized by synphobetractines whose lower rays are greatly swollen and partially fused. Lower Devonian (Pragian): Czech Republic, Slovakia.——FIG. 502,3. \*K. prokopensis; isolated

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а

FIG. 501. Uncertain (p. 758).

spicule showing characteristic swollen, lower rays, ×200 (Mostler, 1996b).

Phobetractinia REIF, 1968, p. 739 [\*P. polymorpha; OD]. Triradiate spicules with angles between rays 120 degrees; one main ray unpaired but other two dichotomously branched, with rays that may be parallel as in phobetractines or may converge as in synphobetractine spicules. Lower Cambrian-Carboniferous (Mississippian), Permian: Sweden, Estonia, Argentina, Sicily.—FIG. 502,7a-c. \*P. polymorpha, limestone; a, phobetractine with three lower rays, Lower Cambrian, western Sardinia, ×100; b, synphobetractine with converging lower rays, Ordovician, Sweden, ×100; c, drawing of phobetractine spicule with named rays, not to scale (Mostler, 1985; courtesy of Naturwissenschaftlich-Medizinischer Verein in Insbruck).

Praephobetractinia KOZUR, 1991, p. 589 [\*P. eocambrica; OD]. Isolated spicules, primarily three-rayed, with rays separated at 120 degrees; 760

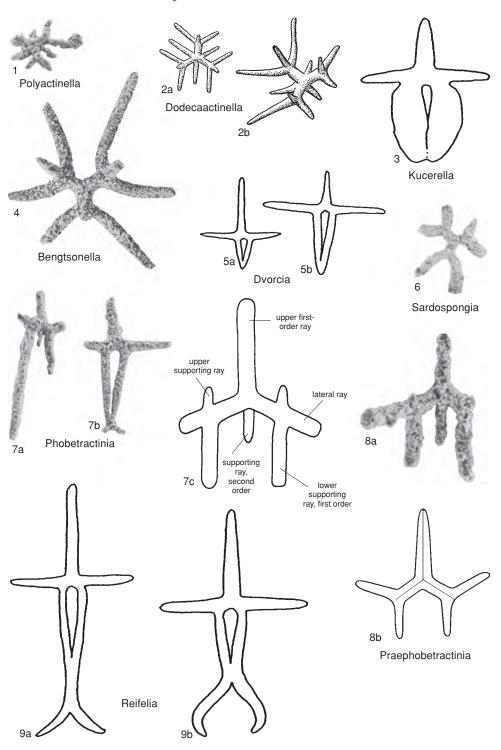


FIG. 502. Polyactinellidae (p. 758-762).

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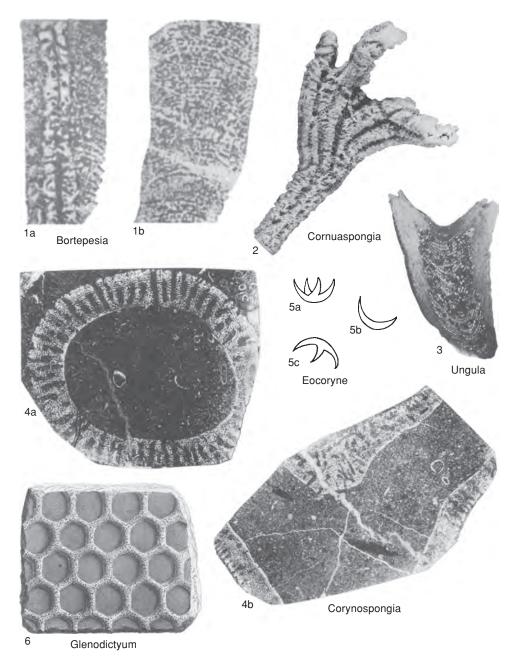


FIG. 503. Uncertain (p. 762-764).

upper ray long and unbranched, but two lower rays each with two secondary rays at 120 percent from main ray and with one of those being parallel, long, upper ray. *Lower Cambrian–Middle Or dovician:* Sardinia.—FIG. 502,8*a–b.* \**P. eocambrica,* Lower Cambrian archaeocyathid bioherm, Iglesiente, southwestern Sardinia; *a*, holotype, triradiate spicule with lower branched rays and upper, unbranched main ray, GII, unnumbered, ×200 (Mostler, 1985); b, drawing of idealized complete spicule, not to scale (Kozur, 1991; courtesy of *Naturwissenschaftlich-Medizinischer Verein in Innsbruck*).

Reifelia MOSTLER, 1996b, p. 232 [\**R. diffissa*; OD]. Sponges characterized by synphobetractine spicules whose two lower, curved rays are fused at some distance from their origins, but whose ray tips diverge distally. *lower Silurian–Carboniferous* (Mississippian): Austria (Karnian Alps), *lower Silurian*; Czech Republic, Slovakia, *Pragian*; Ireland, Afghanistan, Mississippian.—FIG. 502,9a-b. \*R. diffisa; drawings of restored spicules showing general form of distinctive, lower, partially fused rays, approximately ×100 (Mostler, 1996b).

Sardospongia MOSTLER, 1985, p. 16 [\*S. triradiata; OD]. Triradiate spicules with 120 degrees between the dichotomously or trichotomously branching rays; no accessory, central rays present. Lower Cambrian–Middle Cambrian, ?Middle Ordovician: Sardinia, Argentina, Australia.——FIG. 502,6. \*S. triradiata, concretionary limestone, Middle Cambrian, Iglesiente, southwest Sardinia; type, triradiate spicule with branched rays, ×100 (Mostler, 1985; courtesy of Naturwissenschaftlich-Medizinischer Verein in Innsbruck).

## Class and Order UNCERTAIN

- Alasonia SIRKOVA, 1938a, p. 16 [\*A. remesi; OD]. Jurassic: Czech Republic, Slovakia.
- Aphlebospongia SIRKOVA, 1938a, p. 13 [\*A. remesi; OD]. Jurassic: Czech Republic, Slovakia.
- Astrofungia GREGORIO, 1883, p. 121 [\*A. cidariformis; SD DE LAUBENFELS, 1955, p. 100]. ?Cretaceous: Italy.
- Atikokania WALCOTT, 1912, p. 17 [\*A. lawsoni; OD]. Cylindrical to elongate conical with cloaca-like, central cavity surrounded by radiating and concentric, skeletal strands. [Treated as a trace fossil by HÄNTZSCHEL (1975, p. 171).] *Eoarchean– Neoproterozoic:* Canada.
- Bortepesia BOIKO, 1984, p. 35 [\*B. cylindrica; OD]. Cylindrical to branched, colonial sponges with relatively narrow but deep spongocoels or broad, exhalant canals; dermal layer thin, rough, porous; interior skeleton with moderately regularly spaced, upwardly arcuate, transverse or horizontal fibers, more or less connected by irregular, vertical fibers; microstructure bundled and spherulitic. Upper Triassic: Tadjhikistan (Pamir).-FIG. 503, 1a-b. \*B. cylindrica, Norian, southeastern Pamir; a, vertical, axial section of holotype with parallel, thickwalled, exhalant canals or spongocoels, surrounded by porous, chambered, outer part of endosome,  $\times 2$ ; b, tangential vertical section through outer endosome of holotype showing upwardly arcuate, transverse fibers of chambers with porous walls, specimen oop No. II/II, ×2 (Boiko, 1984)
- Coniatopenia POMEL, 1872, p. 152 [\**Elasmostoma peziza* ROEMER, 1864, p. 46; OD]. *Cretaceous:* Germany.
- **Cornuaspongia** SENOWBARI-DARYAN, 1994b, p. 66 [\**C. longidepressa*; OD]. Multi-branched, handlike to antlerlike sponge without spongocoel; each branch with one or more grooves running through or across branch with large openings in grooves; branches with oval cross sections; spicule structure unknown. *Upper Triassic-Jurassic*: Peru.——FIG.

503,2. \*C. longidepressa, Pucará Group, Chaquipuquio; side view of holotype showing growth form and longitudinal grooves, ×1 (Senowbari-Daryan, 1994b).

- Corynospongia DENG, 1990, p. 317 [319] [\*C. tubuliforma DENG, 1990, p. 318; OD]. Tubular, branching sponge with prominent spongocoel with a moderately distinct, dense, gastral layer and rows of coarse, horizontal, radial canals that are cross connected by finer canals; spicule structure unknown. Permian (Cisuralian): China (Sichuan). FIG. 503,4a-b. \*C. tubuliforma, Maokou Formation, Kungurian, Xingwen County, southern Sichuan; a, transverse section of one branch showing large, central spongocoel and thick walls with horizontal rows of prominent, large, radial canals that extend through wall and are cross connected by many fine canals, holotype, ×1.5; b, longitudinal section of parts of two branches, each with broad spongocoel and walls pierced by coarse, radial canals, holotype, ×1 (Deng, 1990).
- Cotyliscus R. H. KING, 1943, p. 34 [\**C. ewersi;* OD]. Cuplike sponges with canals penetrating walls. *Carboniferous (Mississippian):* Texas.
- Diestosphecion POMEL, 1872, p. 223 [\* Tremospongia grandis ROEMER, 1864, p. 40; OD]. Cretaceous: Germany.
- Diplostomella REID, herein, nom. nov. pro Diplostoma FROMENTEL, 1860a, p. 42, non RAFINESQUE, 1817, nec COBBOLD, 1861, nec EBENSBERGER, 1962 [\*Diplostoma neocomiensis FROMENTEL, 1860a, p. 42; OD]. Sponge porous platelike, riddled with small ostia on both sides. Lower Cretaceous: France.
- Dyocopanon POMEL, 1872, p. 226 [\*Scyphia monilifera ROEMER, 1864, p. 37]. Cretaceous: Germany.
- Eflugelia VACHARD in MASSE & VACHARD, 1979, p. 34 [\*Cuneiphycus johnsoni FLÜGEL, 1966, p. 34, non MAMET & ROUX, 1977]. Attached, regularly laminate of weakly undulating meshwork; small branches; general form conical, sometimes biconical; walls hyaline to granular. Carboniferous (Pennsylvanian)-Permian (Lopingian): Africa, Europe, Asia.
- Eocoryne MATTHEW, 1886, p. 30 [\**E. geminum;* OD]. Relatively large, peculiarly shaped spicules 1.5 to 2.0 mm long. *Middle Cambrian:* Canada.——FIG. 503,*5a–c.* \**E. geminum;* isolated spicules, approximately ×10 (de Laubenfels, 1955).
- Glenodictyum VON DER MARCK, 1876, p. 68 [\*G. hexagonum; OD]. Skeleton with conspicuous, hexagonal network in which mesh spaces are 12 to 15 mm across and intervening skeletal elements are up to 5 mm wide. Cretaceous: Germany.——Fic. 503,6. \*G. hexagonum; fragment of skeleton with hexagonal structure, ×0.5 (Von der Marck, 1876).
- Holocoelia STEINMANN, 1913, p. 86 [\**H. toulai*; SD DE LAUBENFELS, 1955, p. 102]. *Cretaceous:* Germany (Baden).
- Lamellispongia BOIKO, 1984, p. 31 [\*L. gelevus; OD]. Platelike or bladelike, weakly flexed sponges without major, axial, or vertical canals, but with small,

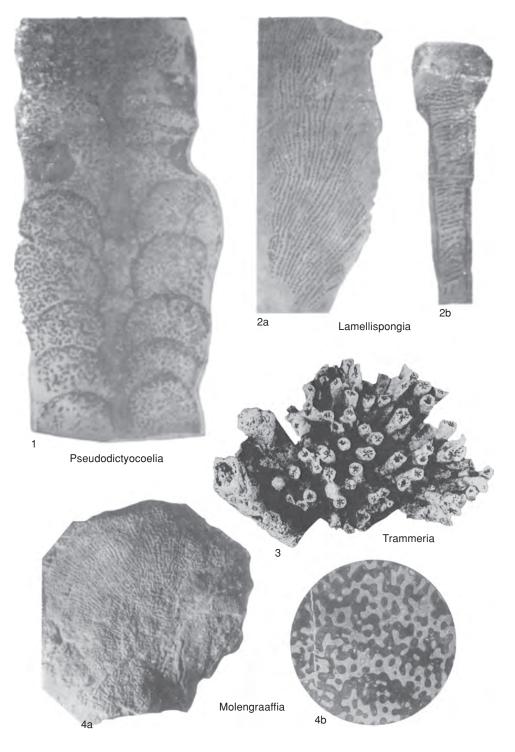


FIG. 504. Uncertain (p. 762-764).

horizontal canals that pierce plate; skeleton with upwardly divergent, major fibers cross connected with finer fibers; skeleton of spherulites 0.05 to 0.07 mm in diameter. *Upper Triassic:* Tadjhikistan (Pamir).——FIG. 504,2*a*–*b.* \**L. gelevus*, uppermost Norian, southeastern Pamir; *a*, dermal surface of thin, bladelike holotype with upwardly and outwardly divergent, ladderlike, skeletal tracts, ×2; *b*, vertical, longitudinal section of holotype with horizontal, skeletal tracts and transverse canals, specimen oop No. 5/II, ×10 (Boiko, 1984).

- Megalelasma Počta, 1903a, p. 9 [\**M. dispansum;* OD]. Inverted, cone-shaped sponge with thin walls; skeletal structure poorly preserved. *Upper Cretaceous (Cenomanian):* Czech Republic, Slovakia.
- Misraea MAITHY & BABU, 1987, p. 224 [\**M. vindhyanensis;* OD]. *Paleoproterozoic– Neoproterozoic:* India.
- Molengraaffia VINASSA DE REGNY, 1915, p. 80 [\*M. regularis; OD] [=Molengraafia DE LAUBENFELS, 1955, p. 100, nom. null.]. Skeleton of moderately coarse fibers, 0.2 mm in diameter, spaced 0.5 mm apart in regular, reticulate structure; interconnected canals round, diameter of 0.5 mm, and with skeletal fibers converge to, and surround, a moderately large, central area; spicule structure unknown. Triassic: East Indies.—FIG. 504,4a-b.
   \*M. regularis, Fatu Kaoniki, Timor; a, side view of sponge showing upwardly divergent canal and skeletal structure, ×1; b, cross section showing round canals and interconnected, skeletal fibers, ×5 (Vinassa de Regny, 1915).
- Oligoplagia HERAK, 1944, p. 130 [\**O. carnica;* OD]. [Distinguished from related genera by having horizontal walls or tabulae in ovate cylindrical stems, with common, open (but barely visible in the walls), eye-shaped pores.] *Triassic:* Austria.
- Plectinia Počta, 1903b, p. 122 [\*P. minuta; SD DE LAUBENFELS, 1955, p. 100]. Cretaceous: Czech Republic, Slovakia.
- Polycnemiseudea FROMENTEL, 1860a, p. 29 [\*Cnemidium gregarium D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 285; OD]. Upper Cretaceous: France.
- Pseudodictyocoelia BOIKO, 1984, p. 32 [\*P. elongata; OD.] Cylindrical, chambered sponge with deep,

axial spongocoel; chamber walls distinctly porous, thicker, and more compact than moderately uniformly spaced, branched and interwoven, fibrous, chamber-filling structures; entire skeleton composed of spherulites 0.02 to 0.04 mm in diameter. *Upper Triassic:* Tadjhikistan (Pamir).——FIG. 504,1. \*P. elongata, uppermost Norian, base of Aktash Mountains, southeastern Pamir; vertical, axial section of holotype showing upwardly arcuate, porous chambers, filled with endosomal, skeletal mesh, surrounding axial spongocoel, specimen oop No. 8/II, ×2 (Boiko, 1984).

- Rauffia ZEISE, 1897, p. 326 [\*R. clavata; OD]. Lower Triassic–Upper Cretaceous: Europe.
- Scribroporella Spriesterbach, 1935, p. 477 [\*S. socialis; OD]. Middle Devonian: Germany.
- Strambergia ZEISE, 1897, p. 330 [Strambergia sp.; OD]. Lower Triassic–Upper Cretaceous: Europe.
- Trammeria SENOWBARI-DARYAN, 1994b, p. 65 [\*T. dendroida; OD]. Multibranched, coral-like sponge, spongocoel with starlike cross section passing through entire branches and producing radially arranged, skeletal sections; numerous exhalant canals with oval pores in vertical rows ending in spongocoel; spicule structure unknown. Triassic-Jurassic: Peru.—FIG. 504,3. \*T. dendroida, Upper Triassic, Pucará Group, Shalipayco; holotype from above showing bushy form and sections of branches with starlike spongocoels, ×1 (Senowbari-Daryan, 1994b).
- Ungula TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977a, p. 85 [\*U. kaisini; OD]. Steeply obconical to dentiform, with outer, relatively dense crust of fibrous, lamellar structure around inner layered, more porous, vesicular, central part where layers rise upwardly in obconical fashion toward margin and merge with or terminate against outer crust. No distinct canals; possible concave operculum with same microstructure as outer crust. [Poriferan nature of the specimen is questionable.] Permian (Lopingian): Tunisia.-FIG. 503,3. \*U. kaisini, Djebel Tebaga; longitudinal section of holotype showing finely fibrous, lamellate, thick, outer wall and thin, capping, possible operculum, and layered, more coarsely vesicular, interior structure, collection H. & G. Termier, ×5 (Termier & Termier, 1977a).

# UNRECOGNIZABLE SUPPOSED SPONGES

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Many supposed sponge genera described in the early development of paleontology were inadequately documented because methods of ascertaining skeletal details and microstructure of sponge fossils were not available. If original type material were to be reexamined using modern techniques, perhaps some of them might prove to be recognizable, as has been the case with a few forms listed as unrecognizable in the 1955 sponge volume of the *Treatise*.

As noted by DE LAUBENFELS (1955), unfortunately many fossils, particularly sponges, have been so altered during preservation that their microstructure and other critical details of their skeletons are not preserved. This makes definition and classification difficult, in spite of all efforts to understand them. Consequently, in the following compilation, names are listed alphabetically because too little information is available to place them in a meaningful classification.

- Achilleum OKEN, 1815, p. 81 [\**A. manus;* SD DE LAUBENFELS, 1955, p. 104]. *Cretaceous–Holocene:* Europe.
- Adelphocoelia Étallon, 1859a, p. 136 [\**Scyphia propinqua* GOLDFUSS, 1829, p. 89; OD]. *Jurassic:* Europe.
- Alcyoniolithes BLUMENBACH, 1815, p. 24 [\*A. stadensis; OD] [=Alcyonolithes DE LAUBENFELS, 1955, p. 104, nom. null.]. Age and locality uncertain.
- Amorphocoelia Étallon, 1859a, p. 136 [\*A. incrustans; OD]. Jurassic: Europe.
- Angidia POMEL, 1872, p. 122 [\**A. cribrosa;* SD DE LAUBENFELS, 1955, p. 104]. *Paleogene–Neogene:* Algeria.
- Aplorytis POMEL, 1872, p. 229 [\*Lymnorea bajocensis D'ORBIGNY, 1850 in 1850–1852, p. 294; OD; as cited by POMEL, but not listed in genus by D'ORBIGNY; but D'ORBIGNY, 1850 in 1850–1852, vol. 1, p. 294 cites as *Cnemidium bajocense* D'ORBIGNY, 1847]. Conical with imperforate, dermal layer covering all but broad, convex, upper surface; radial, exhalant grooves converging on center of summit; exhalant pores open only into these grooves; internal structures and fiber microstructure unknown. [No known suitable figures.] *Jurassic:* Europe.

- Araeoplocia POMEL, 1872, p. 104 [\*Achilleum morchella GOLDFUSS, 1826, p. 2; SD RIGBY, herein]. [The subsequent designation of Meandrospongia annulata ROEMER, 1864, p. 53, as the type species of the genus by DE LAUBENFELS (1955, p. 104) is invalid because the species was not mentioned by POMEL (1872).] Devonian.
- Arthrocypellia POMEL, 1872, p. 77 [\*Scyphia articulata GOLDFUSS, 1826, p. 9; OD]. Devonian.
- Asteriscosella CHRIST, 1925, p. 1 [\*A. nassovica; OD]. Devonian: Germany.
- Asteropagia POMEL, 1872, p. 245 [\*Asterospongia globosa ROEMER, 1864, p. 50; SD de LAUBENFELS, 1955, p. 104]. Cretaceous: Europe.
- Astrolmia POMEL, 1872, p. 115 [\*Cnemidium astrophorum GOLDFUSS, 1829, p. 97; OD]. Cretaceous: Europe.
- Atelosphecion POMEL, 1872, p. 224 [\*A. commutatum; OD]. Paleogene–Neogene: Algeria.
- Badinskia POMEL, 1872, p. 84 [\*B. lobata; OD]. Paleogene-Neogene: Algeria.
- Batalleria Hérenger, 1946b, p. 46 [\*B. cylindrata Hérenger, 1946b, p. 47; OD]. Cretaceous: Spain.
- Batospongia ULRICH in MILLER, 1889, p. 154 [\*B. spicata ULRICH in MILLER, 1889, p. 155; OD]. Sponge possibly globose, no cloaca; radialreticulate, somewhat meandriform spiculofibers; fiber an open, porous, uncored mesh of monaxons (probably oxeas) tangent to surface of fiber, echinated by numerous smooth monaxons (possible oxeas) at approximately 90° to fiber; smaller desmoids of uncertain form may also be present as a coating on fiber but poor preservation makes this uncertain. [This genus does not clearly belong to the dystactospongiids but is difficult to place elsewhere unless with the haplistiids. Probable dystactospongiid (unrecognizable).] Carboniferous (Pennsylvanian): USA (Illinois).-FIG. 505, 1a-c. \*B. spicata, Lower Coal Measures, Pennsylvanian, Seville; *a*, lower side of holotype from which dermal layer has been removed, ×1; b, cluster of silicified spicules; c, inner side of basal dermal layer, ISM, ×18 (Ulrich & Everett, 1890).
- Bembixastrum SCHRAMMEN, 1924b, p. 129 [\*\*B. granulosum MÜNSTER in GOLDFUSS sp.;" OD]. Identity of only cited species uncertain and no diagnosis given; type species may be *Cnemidium* granulosum MÜNSTER in GOLDFUSS, 1829, p. 97, regarded by ZITTEL (1878a, p. 110) as a synonym of *Cnemidiastrum stellatum* (GOLDFUSS). Age and locality uncertain, but probably *Jurassic*: Germany (Streitberg).
- Bicupula COURTILLER, 1861, pl. 35 [\**B. gratiosa*; SD DE LAUBENFELS, 1955, p. 104]. *Upper Cretaceous:* France.
- Biopalla WALLACE, 1878, p. 369 [\*B. keokuki; OD]. Carboniferous: Iowa.

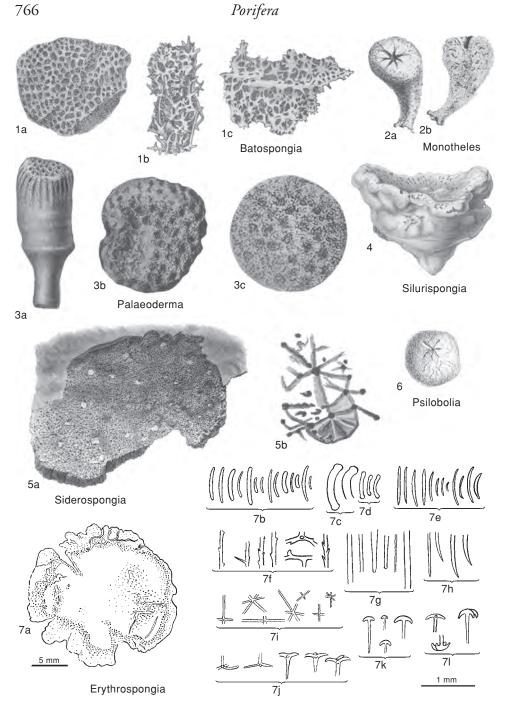


FIG. 505. Uncertain (p. 765-771).

- Bonneyia SOLLAS, 1873, p. 79 [\**B. bacilliformis;* SD RIGBY, herein]. *Lower Cretaceous:* Europe.
- Bothriopeltia POMEL, 1872, p. 81 [\**Cribrospongia* baugieri D'ORBIGNY, 1850 in 1850–1852, vol. 1, p. 388; SD RAUFF, 1893, p. 66]. *Cretaceous:* Europe.
- Bottonaecyathus RODIONOVA, 1967, p. 87 [\*B. astraeformis; OD]. Solitary, rarely colonial; steeply obconical to cylindrical forms with distinct, central spongocoel; prominent, subhorizontal radial exhalant canals unevenly distributed and locally may extend through thick walls from small, dermal pores or inhalant ostia to larger, gastral exhalant ostia. Skeleton of radial rows of longitudinal and transverse rods, united tangentially. [Genus was included by HILL (1972, p. 107) in the Archaeocyatha, but it may be a spiculate sponge.] Lower Cambrian: Russia (Altay-Sayan), Morocco.—FIG. 506a-b. \*B. astraeformis, Sanashtikgol'skiy horizon, Altay-Sayan region; a, diagrammatic transverse section showing coarse exhalant canals and central spongocoel surrounded by thick walls; b, diagram showing radial canals in both longitudinal and transverse sections of cylindrical fossil, ×2 (Hill, 1972).
- Broseocnemis POMEL, 1872, p. 81 [\*B. asperata; OD]. Jurassic: Algeria.
- Bursispongia QUENSTEDT, 1878 in 1877–1878, p. 506 [\**B. bursata;* OD]. *Jurassic:* Germany.
- Calpia POMEL, 1872, p. 116 [\*Cribrospongia cariosa ROEMER, 1864, p. 13; OD]. Devonian.
- Calymmospongia Štrand, 1928, p. 33 [\**Cystispongia subglobosa* ROEMER, 1864, p. 8; SD RAUFF, 1893, p. 65] [=*Calymma* POMEL, 1872, p. 73, obj., *non* HUEBNER, 1823]. *Cretaceous:* Europe.
- **Camerocoelia** ÉTALLON, 1859a, p. 134. Type species, age, and locality uncertain.
- Catalopia POMEL, 1872, p. 205 [\**C. gemmans;* OD]. *Cretaceous:* Algeria.
- Cephalocoelia ÉTALLON, 1859a, p. 136 [\**C. gresslyi;* OD]. *Jurassic:* Germany.
- Ceriopeltia POMEL, 1872, p. 81 [no species] [=*Ceriopelta* DE LAUBENFELS, 1955, p. 104, *nom. null.*]. Age and locality uncertain.
- Chenendroscyphia FROMENTEL, 1860a, p. 40 [\**Chenendopora marginata* MICHELIN, 1847 in 1840–1847, p. 129; OD]. Age and locality uncertain.
- Chitoracia POMEL, 1872, p. 227 [\**C. roemeri* POMEL, 1872, p. 227; SD RAUFF, 1893, p. 71]. *Devonian*.
- Cladocalpia POMEL, 1872, p. 117 [\* Tubulospongia dendroides COURTILLER, 1861, pl. 33,3; SD DE LAUBENFELS, 1955, p. 104]. Upper Cretaceous: Europe.
- Cladocinclis POMEL, 1872, p. 110 [\*Amorphospongia dumosa D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 188; OD]. Cretaceous: Europe.
- Cladopagia POMEL, 1872, p. 246 [no species]. Age and locality uncertain.
- Cladosmila POMEL, 1872, p. 240 [\*?*Anthophyllum proliferum* GOLDFUSS, 1826, p. 46; OD]. Age and locality uncertain.

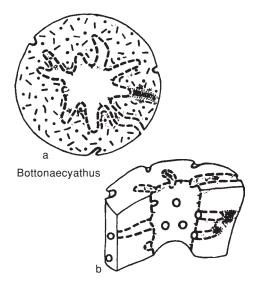


FIG. 506. Uncertain (p. 767).

- Clionothes LEES & THOMAS, 1919, p. 605 [\*C. lizardensis; OD]. Carboniferous (Mississippian): USA (Iowa).
- Cnemicoelia ÉTALLON, 1859a, p. 145. Type species, age, and locality uncertain.
- Cnemidium GOLDFUSS, 1826, p. 14 [\*C. lamellosum; SD MILLER, 1889, p. 157]. Upper Cretaceous: Europe.
- Cnemipsechia POMEL, 1872, p. 155 [\*C. fungiaeformis; OD]. Paleogene-Neogene: Algeria.
- Cnemiracia POMEL, 1872, p. 227 [\*Stellispongia aperta; SD DE LAUBENFELS, 1955, p. 104]. Cretaceous: Europe.
- Coelosphaeridium C. F. ROEMER, 1885, p. 57 [\*C. cyclocrinophilum; OD]. Age and locality uncertain.
- Coelosmila POMEL, 1872, p. 239 [\* Ceriopora favosa GOLDFUSS, 1826, p. 38; SD DE LAUBENFELS, 1955, p. 104]. Cretaceous: Europe.
- Collojerea POMEL, 1872, p. 176 [\*Siphonia ramosa MICHELIN, 1847 in 1840–1847, p. 141; OD]. Devonian.
- Colpoplocia POMEL, 1872, p. 104 [\**Plocoscyphia michelini* D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 188; SD RAUFF, 1893, p. 67]. *Upper Jurassic:* Europe.
- Confervites BRONGNIART, 1828, p. 35 [\**C. fasciculata;* SD de LAUBENFELS, 1955, p. 104]. *Jurassic:* Europe.
- Corthya POMEL, 1872, p. 109 [no species]. Age and locality uncertain.
- Cribrocoelia Étallon, 1859a, p. 134 [\**C. striata;* SD DE LAUBENFELS, 1955, p. 104]. *Jurassic:* Europe.
- Cribroscyphia FROMENTEL, 1860a, p. 38 [\*Scyphia polyommata GOLDFUSS, 1826, p. 8; OD]. Upper Jurassic: Europe.

- Criccospongia MOSTLER, 1986, p. 348 [no type species]. Upper Triassic: Austria, Italy.
- Cupulospongia D'ORBIGNY, 1849, p. 550 [\*Scyphia porosa ROEMER, 1840 in 1840–1841, p. 7; SD RIGBY herein] [=Cupulochonia FROMENTEL, 1860a, p. 44, obj.] [Subsequent designation of Tragos patella GOLDFUSS, 1833, as the type species by DE LAUBENFELS (1955, p. 104) is invalid because that species was earlier listed (DE LAUBENFELS, 1955, p. 48) as the subsequently designated type species for Hyalotragos ZITTEL, 1878a.] Upper Jurassic: France.
- Cyathoplocia POMEL, 1872, p. 103 [\*Scyphia texata GOLDFUSS, 1826, p. 7; OD]. Age and locality uncertain.
- Cyclospongia MILLER, 1892, p. 615 [\*C. discus; OD]. Devonian: USA (Indiana).
- Cylindrospongia F. A. ROEMER, 1864, p. 21 [\*C. *abreviata*; SD DE LAUBENFELS, 1955, p. 104]. Cretaceous: Europe.
- Cyronella BEEDE, 1899, p. 129. Type species, age, and locality uncertain.
- Cystoloena POMEL, 1872, p. 76 [\* Cystispongia undulata ROEMER, 1864, p. 8; SD RAUFF, 1893, p. 65]. Cretaceous: Europe.
- Cystopora POMEL, 1872, p. 229 [\*Verticillites truncatus D'Orbigny, 1850 in 1850–1852, vol. 2, p. 96; SD DE LAUBENFELS, 1955, p. 105]. Cretaceous: Europe.
- Dendrospongia F. A. ROEMER, 1864, p. 20 [\*D. clathrata; SD DE LAUBENFELS, 1955, p. 105]. Cretaceous: Europe.
- Dercites CARTER, 1871, p. 130 [\**D. haldonensis*; OD] [=*Dercitites* SOLLAS, 1880c, p. 587, *nom. null.*]. *Lower Cretaceous:* Europe.
- Desmospongia Étallon, 1863, p. 422 [\*Spongia semicinctus QUENSTEDT, 1878 in 1877–1878, p. 215; OD]. Jurassic: Europe.
- Dichoplectella MATTHEW, 1891, p. 149 [\*D. *irregularis*; OD]. *Cambrian:* Canada (Acadia).
- Dichorea POMEL, 1872, p. 225 [\*Lymnorea michelini D'ORBIGNY, 1850 in 1850–1852, vol. 1, p. 325; OD]. Upper Jurassic: Europe.
- Dictyocladia POMEL, 1872, p. 86 [\*D. ramosa; OD]. Upper Jurassic: Europe.
- Dictyosmila POMEL, 1872, p. 240 [\*D. reteporiformis; OD]. Cretaceous: Europe.
- Didesmospongia ÉTALLON, 1864, p. 422 [no species]. *Jurassic:* Europe.
- Diseudea FROMENTEL, 1860a, p. 28 [\**Siphonia lagenaria* MICHELIN, 1847 in 1840–1847, p. 250; OD] [=*Copanon* POMEL, 1872, p. 226, obj.]. *Middle Jurassic:* Europe.
- Distheles FROMENTEL, 1860a, p. 36 [\*D. depressa; OD]. Jurassic: Europe.
- Dolispongia QUENSTEDT, 1877 in 1877–1878, p. 297 [\**Scyphia maeandrina* GOLDFUSS, 1829, p. 88; SD DE LAUBENFELS, 1955, p. 105]. *Jurassic:* Germany.
- Donatispongia MALFATTI, 1901, p. 299 [\*D. patellaris; OD]. Paleogene–Neogene: Europe.
- Dulmius GREGORIO, 1930, p. 48 [\*D. innovatus; OD]. Permian: Sicily.
- Elasmeudea POMEL, 1872, p. 234 [\**Eudea cribraria* MICHELIN, 1847 in 1840–1847, p. 251; SD RAUFF, 1893, p. 72]. *Cretaceous:* Europe.

- Eligmaella RIGBY, herein, nom. nov. pro Eligma REGNARD, 1926, p. 484, non HUBNER, 1819 [\*Eligma douvilli REGNARD, 1926, p. 484; OD]. Cretaceous: France.
- Emplociata RIGBY, herein, nom. nov. pro Emplocia POMEL, 1872, p. 103, non HERRICH-SCHAEFFER, 1856 [\*Brachiolites foliaceus T. SMITH, 1848, p. 364; OD]. Cretaceous: Europe.
- Enteropycnus DE LAUBENFELS, 1955, p. 105, nom. nov. pro Pychnogaster SCHRAMMEN, 1924a, p. 30, non GRAELL, 1851 [\*Pycnogaster texturatus SCHRAMMEN, 1924a, p. 30; OD]. Cretaceous: Germany.
- Erythrospongia HUDSON, 1929, p. 185 [\*E. lithodes; OD]. Cylindrical to irregularly bulbous; possibly with central cloaca and osculum; large, parallel, possible rhabdodiactines paratangential to outer surface; cortex or body wall containing small, curved, possible rhabdodiactines, most strongylelike, some oxeote, together with hexactines, pentactines, clemes, and fragments with dianchorate and quadrianchorate terminations; presumed microscleres are spinose microhexactines and micropentactines, as well as seeming hexasters that range from simply branched microhexactines to polyactinal, euaster-like forms. [These could be burrows lined with assorted, foreign spicules.] Carboniferous (Visean): England.-FIG. 505,7a-l. \*E. lithodes, Yoredale Series, northwestern Yorkshire; a, drawing of section through sponge nodule,  $\times 2$ ; bl, isolated macroscleres from nodule by etching in weak acid: b, monaxons, c-d, tylotes; e, oxeas; f, broken spinose spicules; g-h, curved spicule fragments; *i*, hexactines; *j-l*, pentactine-based spicules, ×15 (Hudson, 1929).
- Eucoscinia POMEL, 1872, p. 83 [\**Scyphia cancellata* GOLDFUSS, 1829, p. 89; SD de LAUBENFELS, 1955, p. 105]. *Cretaceous:* Europe.
- Evinospongia Stoppani, 1860, p. 90 [\**E. cerea;* SD de LAUBENFELS, 1955, p. 105]. *Triassic:* Italy.
- Exosinion POMEL, 1872, p. 91 [\*Ventriculites gracilis ROEMER, 1864, p. 20; OD]. Cretaceous: Europe.
- Favospongia HINDE, 1888, p. 179 [\*F. ruthveni; OD]. upper Silurian: Europe.
- Floriania RIGBY, herein, nom. nov. pro Floria GREGORIO, 1930, p. 47, non LOEW, 1879 [\*Floria permiana GREGORIO, 1930, p. 48; OD]. Permian: Sicily.
- Forospongia D'ORBIGNY, 1849, p. 549 [\* Tragos acetabulum GOLDFUSS, 1826, p. 13; OD]. Jurassic: Europe.
- Fungispongia RINGUEBERG, 1884, p. 147 [\*F. irregularis; OD]. Silurian: USA.
- Gemmellarella PARONA, 1933, p. 21 [\*G. permica; OD]. Permian: Europe.
- Goniocoelia Étallon, 1859a, p. 136. Type species, age, and locality uncertain.
- Goniospongia D'ORBIGNY, 1849, p. 548 [\*G. schlotheimii; OD] [=Gonioscyphia FROMENTEL, 1860a, p. 40, obj.]. Upper Jurassic: France.
- Graptospongia RUEDEMANN, 1934, p. 68 [\**G. pusilla;* OD]. *Ordovician:* USA (New York).
- Gymnomyrmecium POMEL, 1872, p. 203 [\**Myrmecium gracile* MÜNSTER, 1841, p. 26; OD]. Club shaped, without dermal layer; shallow, cloacal

depression at top. [Differs from *Epitheles* FRO-MENTEL, 1860a, in absence of dermal layer and shallower cloaca. A topotype identified by ZITTEL has sinuous spicules of the same size as those of *Epitheles*, but the trabecular mesh is much finer, and lacks the large internal canals; no known suitable figures.] *Triassic:* Europe.

- Gymnorea POMEL, 1872, p. 225 [\**Polycoelia gemmans* FROMENTEL, 1860a, pl. 4,4; SD RAUFF, 1893, p. 71]. *Cretaceous:* Europe.
- Hallisida POMEL, 1872, p. 230 [\*Hallirhoa lycoperdites LAMOUROUX, 1821, p. 72; OD]. Cretaceous: Europe.
- Hemicoetis POMEL, 1872, p. 102 [\*Scyphia tenuis ROEMER, 1840 in 1840–1841, p. 9; OD]. Devonian.
- Hemipenia POMEL, 1872, p. 153 [\*Oculispongia polymorpha ROEMER, 1864, p. 48; SD DE LAUBENFELS, 1955, p. 105]. Devonian.
- Hemispongia D'ORBIGNY, 1849, p. 549 [\**H. rouyana;* OD]. *Cretaceous:* Europe.
- Herpophlyctia POMEL, 1872, p. 237 [\*H. subregularis; OD]. Paleogene-Neogene: Algeria.
- Herpothis POMEL, 1872, p. 247 [\*H. saheliensis; OD]. Paleogene–Neogene: Algeria.
- Heterosmila POMEL, 1872, p. 239 [\*H. diastoporiformis; OD]. Paleogene–Neogene: Algeria.
- Holcosinion POMEL, 1872, p. 90 [\*Ocellaria laticostata ROEMER, 1864, p. 17; SD DE LAUBENFELS, 1955, p. 105]. Devonian.
- Holoracia POMEL, 1872, p. 227 [\*Cnemidium turbinatum MÜNSTER, 1841, p. 30; SD RAUFF, 1893, p. 71]. Cretaceous: Europe.
- Holosphecion POMEL, 1872, p. 224 [\*H. tuberosum; OD]. Stipitate-spheroidal with variably developed, dermal layer; shallow, summit depression containing cluster of exhalant openings from which radiate rows of smaller, exhalant openings. Internal characters not known. External features somewhat similar to *Precorynella* and *Monotheles*, so far as POMEL's description permits comparison. [POMEL assigned the Triassic type of *Precorynella* to this genus as a second species; no known suitable figures.] ?Triassic, ?Jurassic (fide RAUFF, 1893, p. 71): Europe; ?Paleogene-?Neogene: Algeria.
- Homalorea POMEL, 1872, p. 225 [\* Tremospongia dilatata ROEMER, 1864, p. 40; OD]. Devonian.
- Homolpia POMEL, 1872, p. 105 [\*Spongus townsendi MANTELL, 1822, p. 164; OD]. Devonian.
- Homoptychium POMEL, 1872, p. 69 [\*Coeloptychium deciminum ROEMER, 1864, p. 3; OD]. Cretaceous: Europe.
- Hylospongia SOLLAS, 1873, p. 79 [\**H. patera;* SD RIGBY, herein]. *Lower Cretaceous:* Europe.
- Hystrispongia ULRICH in MILLER, 1889, p. 160 [=Hystriospongia ULRICH, 1890b, p. 245, nom. null.]. Carboniferous: USA.
- Isophyllum DE LAUBENFELS, 1955, p. 105, nom. nov. pro Coelophyllum SCHRAMMEN, 1924a, p. 150, non SCUDDER, 1875 [\*Coelophyllummarginatum SCHRAM-MEN, 1924a, p. 150; OD]. Cretaceous: Germany.
- Kazakovicyathus KONYUSHKOV, 1972, p. 130 [\*K. sajanicus; OD]. Lower Cambrian: Russia.
- Labyrintholites SINTZOVA, 1879, p. 17 [\*L. varians; SD DE LAUBENFELS, 1955, p. 106]. Cretaceous: Russia.

- Leptomitosia Вонм, 1927, p. 189 [\*L. dubia; OD]. *Cretaceous:* Europe.
- Lithosiella RIGBY, herein, non. nov. pro Lithosia POMEL, 1872, p. 252, non FABRICIUS, 1789 [\*Turonia radiata COURTILLER, 1861, pl. 40,9–10; OD]. [See also DE LAUBENFELS, 1955, p. 106.] Cretaceous: Europe.
- Lithospongites CARTER, 1873, p. 439 [\*L. kittoni CARTER; SD DE LAUBENFELS, 1955, p. 106]. Carboniferous: Europe.
- Loboptychium SCHRAMMEN, 1924a, p. 27 [\*L. concavum; SD de LAUBENFELS, 1955, p. 106]. Devonian.
- Lodanella KAYSER, 1885, p. 207 [\*L. mira; OD]. Lower Cretaceous: Europe.
- Loenocoelia POMEL, 1872, p. 243 [\*L. ramosa; SD RAUFF, 1893, p. 72]. Cretaceous: Algeria.
- Madrespongia QUENSTEDT, 1877 in 1877–1878, p. 212 [\**M. trichotomoides*; SD DE LAUBENFELS, 1955, p. 106]. *Upper Jurassic:* Germany.
- Maeandroptychium SINTZOVA, 1879, p. 5 [\*M. polymorfum SINTZOVA, 1879, p. 10; SD DE LAUBENFELS, 1955, p. 106]. Cretaceous: Russia.
- Manon Oken, 1815, p. 76 [\**Spongia dichotoma* LINNE, 1767, p. 1296; SD de LAUBENFELS, 1955, p. 106]. *Cretaceous, Holocene:* Europe.
- Mantellia PARKINSON, 1822, p. 53 [no species]. Cretaceous: United Kingdom.
- Mastoscinia POMEL, 1872, p. 106 [\**Scyphia verrucosa* GOLDFUSS, 1826, p. 7; SD DE LAUBENFELS, 1955, p. 106]. *Cretaceous:* Europe.
- Megaspongia QUENSTEDT, 1877 in 1877–1878, p. 45 [\**M. tessellata* QUENSTEDT, 1877 in 1877–1878, p. 48; SD DE LAUBENFELS, 1955, p. 106]. *Jurassic:* Europe.
- Megastroma DAWSON, 1883, p. 12 [\**M. laminosum;* OD]. *Carboniferous (Mississippian):* Canada (Brookfield, Nova Scotia).
- Miassocyathus FOMIN, 1963, p. 17 [\**M. lobanovae*; OD]. *Middle Devonian:* Russia (eastern Ural Mountains).
- Monamona DE LAUBENFELS, 1955, p. 106, nom. nov. pro Mona SMITH, 1911, p. 149, non HULST, 1888 [\*Mona monensis SMITH, 1911, p. 149; OD]. Carboniferous: Isle of Man.
- Monilites Carter, 1871, p. 132 [\**M. haldonensis;* SD DE LAUBENFELS, 1955, p. 106]. *Devonian.*
- Monotheles FROMENTEL, 1860a, p. 35 [\*M. neocomiensis; OD] [=Distheles FROMENTEL, 1860a, pl. 2,7 (type, D. depressa, OD); Cnemicopanon POMEL, 1872, p. 227, nom. van., obj.]. Globular-stipitate or pyriform with deep, exhalant grooves often radiating from central, summit osculum; very shallow cloaca; no dermal layer. Trabecular microstructure unknown, and genus may not be related to Epiheles. [Distheles differs from Monotheles only in being colonial rather than solitary; no known figures of type species.] Lower Cretaceous: Europe.-FIG. 505,2a-b. M. stellata FROMENTEL, Neocomian, Germany; a, side view of obconical sponge, exhalant grooves around osculum,  $\times 1$ ; b, vertical section through same specimen with shallow spongocoel and canal structure, ×1 (Fromentel, 1860a).

- Nanodiscites SOLLAS, 1880d, p. 387 [\**N. parvus;* OD]. *Cretaceous:* Europe.
- Nelumbosium Gregorio, 1930, p. 69 [\*N. primum; OD]. Permian: Sicily.
- Nexispongia QUENSTEDT, 1877 in 1877–1878, p. 162 [\**N. libera;* OD]. *Jurassic:* Germany.
- Nudispongia QUENSTEDT, 1877 in 1877–1878, p. 220 [\**N. cribrata* QUENSTEDT, 1877 in 1877–1878, p. 219; SD de LAUBENFELS, 1955, p. 106]. *Jurassic:* Germany.
- Occultus KRASNOPEEVA in REZVOI, ZHURAVLEVA, & KOLTUN, 1962, p. 58 [\*Archaeospongia radiata KRASNOPEEVA, 1937; OD]. ?Precambrian-Lower Cambrian: Russia.
- Ocellarioscyphia FROMENTEL, 1860a, p. 40 [\*Ventriculites radiatus MANTELL, 1822, p. 168; SD DE LAUBENFELS, 1955, p. 106]. Cretaceous: England.
- Oegophymia POMEL, 1872, p. 141. Type species, age, and locality uncertain.
- Olynthia POMEL, 1872, p. 76 [\*Manon marginatum MÜNSTER, 1841, p. 27; SD RAUFF, 1893, p. 65]. *Cretaceous:* Europe.
- Operytis POMEL, 1872, p. 229 [\*Tragos stellatum GOLDFUSS, 1826, p. 14; OD] [=Actinopagia POMEL, 1872, p. 245 (type, Actinospongia stellata ROEMER, 1864, p. 48, OD)]. Cretaceous: Europe.
- Orispongia QUENSTEDT, 1877 in 1877–1878, p. 192 [\*Spongites perforatus QUENSTEDT, 1877 in 1877– 1878, p. 100; SD DE LAUBENFELS, 1955, p. 106]. Jurassic: Germany.
- Pachaena SOLLAS, 1880d, p. 392 [\*P. hindi; OD]. Cretaceous: Europe.
- Pachastrellites SOLLAS, 1880d, p. 390 [\*P. fusifer; OD]. *Cretaceous:* Europe.
- Pachycinclis POMEL, 1872, p. 110 [\*Amorphospongia carantonensis D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 188; OD]. Cretaceous: Europe.
- Pachypegma SCHRAMMEN, 1924a, p. 31 [\*P. macrostoma; OD]. Cretaceous: Europe.
- Pachytoechia POMEL, 1872, p. 230 [\*Cnemidium parva ÉTALLON, 1859b, p. 544; OD]. [=Pachytoecia ZITTEL, 1878b, p. 35, nom. null.]. Cretaceous: Europe.
- Palaeoderma GERTH, 1927, p. 116 [\*P. tubulosa; OD]. Cylindroidal and stipitate with gently concave, upper surface; stalk and lower part of main body covered with imperforate, dermal layer; upper surface covered with large, exhalant pores that open from vertical canals that run through body of sponge; outermost such canals form vertical grooves on sides of upper part; dendroclone rows perpendicular to upper surface. Permian (Lopingian): Timor. FIG. 505, 3a-c. \*P. tubulosa, upper Permian limestone, Besleo; a, side view of holotype with lower stalk and numerous ostia of vertical, exhalant canals on upper surface,  $\times 1$ ; *b*, summit of holotype with ostia of exhalant canals,  $\times 2$ ; c, transverse section through upper part showing sections of vertical canals uniformly distributed in dense skeleton, ×3 (Gerth, 1929; courtesy of E. Schweizerbart'sche Verlagsbuchhandlung).
- Palaeoieriea LAUBE, 1865, p. 233 [\*Manon? gracilis MUNSTER, 1841, p. 28; OD]. Age and locality uncertain.

- Paracinclis POMEL, 1872, p. 110 [\*Amorphospongia digitata D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 188; OD]. Cretaceous: Europe.
- Paraglossotubenella ZHANG & ZHANG, 1990, p. 430 [ \*P. magma; OD]. No description nor type locality given. Permian: China.
- Paramelonella HOWELL, 1956, p. 30 [\*P. etheridegi; OD]. [Worm burrow trace fossil (see PICKETT, 1983, p. 110).] Permian (Artinskian): Western Australia.
- Paramorphospongia HOWELL, 1956, p. 34 [\*P. globosa; OD]. Small, encrusted pebble of sandstone (PICKETT, 1983, p. 111). *Permian (Artinskian):* Western Australia.
- Paramoudra BUCKLAND, 1817, p. 413 [no species]. Upper Cretaceous: Ireland.
- Parenia Počta, 1885, p. 19 [\*P. oculata; OD]. Cretaceous: Bohemia.
- Peregrinellus RIGBY, herein, nom. nov. pro Peregrinus KRASNOPEEVA, 1940, p. 32, non KIRKALDY, 1904 [\*Pachytheca conica KRASNOPEEVA, 1934; OD]. Precambrian: Kuznetsk Ala Tau, Russia.
- Periphora REGNARD, 1926, p. 483 [\*P. robusta; OD]. *Cretaceous:* Europe.
- Perispongia D'ORBIGNY, 1849, p. 548 [\*P. reflexa; OD]. Jurassic (Oxfordian): France.
- Phragmoscinia POMEL, 1872, p. 83 [\*Scyphia decorata GOLDFUSS, 1829, p. 90; OD]. Cretaceous: Europe.
- Phymatocoelia POMEL, 1872, p. 242 [\*Scyphia uvaeformis GIEBEL, 1850, p. 57; OD]. [The type species was listed by GIEBEL (1852, p. 181) as being from the Kreidegebirge.] Devonian: France.
- Phymatolpia POMEL, 1872, p. 105 [\*Brachiolites tuberosus SMITH, 1848, p. 354; OD]. Cretaceous: Europe.
- Phymocoetis POMEL, 1872, p. 102 [\*Ocellaria interrupta ROEMER, 1864, p. 17; OD]. Devonian.
- Pilosphecion POMEL, 1872, p. 223 [\* Tragos acutemarginatum KLIPSTEIN, 1843 in 1843–1845, p. 282; SD RAUFF, 1893, p. 71]. Cretaceous: Europe.
- Placorea POMEL, 1872, p. 225 [\**Limnorea mammillaris* ROEMER, 1864, p. 37; OD]. *Cretaceous:* Europe.
- Planispongia QUENSTEDT, 1877 in 1877–1878, p. 317 [\**P. auriformis* QUENSTEDT, 1877 in 1877–1878, p. 318, SD DE LAUBENFELS, 1955, p. 107]. *Jurassic:* Europe.
- Plectodocis POMEL, 1872, p. 103 [\*Brachiolites fenestratus SMITH, 1848, p. 367; OD]. Cretaceous: Europe.
- Plesiocnemis POMEL, 1872, p. 80 [\**P. siphonioides;* SD RAUFF, 1893, p. 66]. *Upper Jurassic:* Algeria.
- Plethocoetis POMEL, 1872, p. 101 [\*Laocoetis irregularis; SD DE LAUBENFELS, 1955, p. 107]. Paleogene-Neogene: Algeria.
- Plococoelia Étallon, 1863, p. 427 [\**P. obscura;* OD]. *Jurassic:* France.
- Polycantha SOLLAS, 1873, p. 79 [\*P. etheridgii; OD]. Lower Cretaceous: Europe.
- Polyozia POMEL, 1872, p. 91 [\*P. ropalina; OD]. Paleogene-Neogene: Algeria.
- Polyproctus SCHRAMMEN, 1924a, p. 151 [\**P. tuberosus;* SD de LAUBENFELS, 1955, p. 107]. *Cretaceous:* Europe.

- Polyscyphia SINTZOVA, 1879, p. 19 [\*P. pseudocoeloptychium SINTZOVA, 1879, p. 20; OD]. Cretaceous: Russia.
- Porosmila FROMENTEL, 1860a, p. 46 [\**P. martini;* OD]. *Lower Jurassic:* Europe.
- Protocoelia WU Ya Sheng, 1991, p. 67 [\*P. vermiformis; OD]. Permian (Cisuralian): China.
- Pseudosiphonia Courtiller, 1861, pl. 28,1–2 [\*P. tuberculata; OD]. Cretaceous: Europe.
- Psilobolia POMEL, 1872, p. 230 [\*P. metaeformis; OD]. Globular, small, with central group of postica and short, radiating furrows at summit; short aporhyses radiating downwardly and outwardly from postica, with central one largest; no cortex; other skeletal characters unknown. [Position uncertain; but compared with Astrobolia by ZITTEL, 1878b, p. 116.] Neogene (Miocene): Algeria.—FIG. 505,6. \*P. metaeformis, Djebel Djambeida; view from above of globular sponge with central postica and radial furrows, ×1 (Pomel, 1872).
- Pterosmila POMEL, 1872, p. 240 [\**Ceriopora alata* GOLDFUSS, 1826, p. 38; SD DE LAUBENFELS, 1955, p. 107]. *Cretaceous:* Europe.
- Pulvillus Carter, 1878, p. 137 [\**P. thomsoni;* SD DE LAUBENFELS, 1955, p. 107]. *Carboniferous:* Scotland, United Kingdom.
- Puppispongia GREGORIO, 1930, p. 70 [\**P. prostrema;* OD]. *Permian:* Sicily.
- Quenstedtella DE LAUBENFELS, 1955, p. 107, nom. nov. pro Vermispongia WHITFIELD, 1905, p. 298, non QUENSTEDT, 1878 in 1877–1878 [\*Vermispongia hamiltonensis WHITFIELD, 1905, p. 298; OD]. Cretaceous: USA (Indiana).
- Radicispongia QUENSTEDT, 1877 in 1877–1878, p. 179 [\**R. radiciformis;* OD]. *Jurassic:* Europe.
- Rauffella ULRICH, 1889, p. 235 [\**R. filosa* ULRICH, 1889, p. 237; SD MILLER, 1889, p. 163]. Ordovician: USA.
- **Reteporites** WALCH, 1776?, *non* LAMOUROUX, 1821, p. 50]. Type species, age, and locality uncertain.
- Retia SOLLAS, 1873, p. 79 [\**R. simplex;* SD RIGBY, herein]. *Lower Cretaceous:* Europe.
- Rhabdaria BILLINGS, 1865, p. 357 [\**R. fragilis;* SD MILLER, 1889, p. 164]. *Cambrian–Ordovician:* USA.
- Rhabdocoetis POMEL, 1872, p. 102 [\*Ocellaria cancellata ROEMER, 1864, p. 17; OD]. Cretaceous: Germany.
- Rhipidotaxis OPPLIGER, 1921a, p. 205 [No species designated]. Funnel-shaped sponge with rhizoclone spicules. *Jurassic:* Switzerland.
- Rhiposinion POMEL, 1872, p. 91 [\* Ventriculites decurrens SMITH, 1848, p. 215; OD]. Cretaceous: Europe.
- Rhizogonima POMEL, 1872, p. 159 [\*Rhizospongia digitata COURTILLER, 1861, p. 120; OD]. Cretaceous: Europe.
- Rhytidolpia POMEL, 1872, p. 105 [\* Ventriculites striatus SMITH, 1848, p. 212; OD]. Cretaceous: Europe.
- Rhyzospongia D'ORBIGNY, 1849, p. 548 [\*Polypotecia pictonica MICHELIN, 1847 in 1840–1847, p. 147; OD] [=Rhysospongia D'ORBIGNY, 1850 in 1850– 1852, p. 286, obj., non CHARLESWORTH, 1848;

Risospongia FROMENTEL, 1860a, p. 39, obj.; Rizoscyphia FROMENTEL, 1860a, p. 39, obj.]. Upper Cretaceous: France.

- Satratus DE LAUBENFELS, 1955, p. 107 [\*Strephochetus brainerdi SEELEY, 1902, p. 156; OD] [=Strephorhetus VOSMAER, 1887, p. 402, obj.]. [SEELEY (1902, p. 157) proposed the species Strephochetus atratus (S. atratus) and apparently, through some confusion, the new genus Satratus was listed by DE LAUBENFELS (1955, p. 107), but that genus was not proposed by SEELEY.] Middle Ordovician: USA (Vermont).
- Sciadosinion POMEL, 1872, p. 91 [\*Coeloptychium plicatellum ROEMER, 1840 in 1840–1841, p. 11; OD]. Cretaceous: Europe.
- Scyphia OKEN, 1815, p. 77 [\*Spongia scyphiformis ESPER, 1794, p. 277; SD DE LAUBENFELS, 1936, p. 26]. Hollow, obconical sponges. Over 200 poorly described, fossil species from many systems have been assigned incorrectly to this genus, merely because they were hollow, obconical forms, although in other respects they are very diverse. [No certain fossils of the genus are known.] *Holocene*.
- Scythia D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 284. Type species, age, and locality uncertain. [The genus was listed by DE LAUBENFELS (1955, p. 107) but a search of publications of D'ORBIGNY failed to turn up the term, and it is considered a misprint of *Scyphia*.]
- Sestrimia POMEL, 1872, p. 71 [\*Manon impressum GOLDFUSS, 1829, p. 95; OD]. Cretaceous: Europe.
- Shuqraiopsis JANSA, TERMIER, & TERMIER, 1983, p. 202 [\*S. abenakiensis; OD]. Only sections known, and these include vertically curved, reticulate networks that are interrupted by numerous pores or canals; fused network includes so-called pillars that have circular sections and suggest fusion of desmas; skeletal elements are reported to appear similar to recrystallized lithistid structures. [Identification of spicule type is uncertain, and position in the Astylospongiidae, as was suggested by the authors, is unlikely.] Jurassic: Canadian Atlantic Shelf.
- Siderospongia TRAUTSCHOLD, 1870, p. 233 [\*S. sirensis; OD]. Broadly saucer shaped with numerous oscules on concave surface; both external form and internal, spicular arrangement similar to that of Anthaspidella; poorly known. Carboniferous (Mississippian): Russia (Moscow basin).——FIG. 505,5ab. \*S. sirenis, Kaluga; a, concave, upper surface of type specimen showing skeletal net interrupted by open oscules, ×0.5; b, circular dots of cross sections of trabs connected by long axis of dendroclones, ×4 (Trautschold, 1870).
- Silurispongia MARTIN-WISMAR, 1878b, p. 65 [\*S. conus; OD]. Conical with gently concave, upper surface that bears pores arranged in radial rows converging on center; spicules unknown. [Poorly known, but may be a senior synonym of *Trochospongia* and *Zittelella.*] *?Silurian:* Germany (glacial drift).——FIG. 505,4. \*S. conus, glacial erratic, Lochemerberg; side view of obconical sponge with broad spongocoel marked by radial rows of exhalant ostia, dermal layer dense, ×0.5 (Martin-Wismar, 1878b).

- Solenothyia POMEL, 1872, p. 68 [\**Camerospongia* schlönbachii ROEMER, 1864, p. 5; OD]. *Cretaceous:* Europe.
- Sparsispongia D'ORBIGNY, 1849, p. 549 [\* Tragos rugosum GOLDFUSS, 1829, p. 96; SD RIGBY, herein]. [ENGESER and MEHL (1993, p. 188) observed that designation by DE LAUBENFELS (1955, p. 107) of S. polymorpha GOLDFUSS (1831, p. 215), as the type species of Sparsispongia is not valid because that species was not mentioned by D'ORBIGNY (1849), and that the type species must be selected from Tragos rugosum GOLDFUSS, 1826, or Manon pulvinarium GOLDFUSS, 1826. The latter species was selected as the type species of Orosphecion by POMEL, 1872.] Jurassic: Europe.
- Sphecidion POMEL, 1872, p. 223 [\**Manon tubuliferum* GOLDFUSS, 1826, p. 2; OD]. *Cretaceous:* Europe.
- Spheciopsis POMEL, 1872, p. 224 [\*Achilleum poraceum KLIPSTEIN, 1843 in 1843–1845, p. 281; OD]. Cretaceous: Europe.
- Sphenodictya HERZER, 1901, p. 30 [\*S. cornigera; SD DE LAUBENFELS, 1955, p. 107]. Carboniferous (Pennsylvanian): USA (Marietta, Ohio).
- Sphenopoterium MEEK & WORTHEN, 1860, p. 447 [\*S. compressum MEEK & WORTHEN, 1860, p. 448; SD DE LAUBENFELS, 1955, p. 107]. Carboniferous: USA.
- Spongarium MURCHISON, 1839, p. 696 [\*S. edwardsii; OD] [=Spongiarum BRÖNN, 1848, p. 1192, obj.]. Silurian: Europe.
- Spongillopsis GEINITZ, 1864, p. 517 [\*S. dyadica; SD DE LAUBENFELS, 1955, p. 107]. Permian: Europe.
- Spongoconia POMEL, 1872, p. 249 [\*S. angulosa; SD DE LAUBENFELS, 1955, p. 107]. Paleogene–Neogene: Algeria.
- Spongopagia POMEL, 1872, p. 246 [\*Spongia informis MICHELIN, 1847 in 1840–1847, p. 217; OD]. Cretaceous: Europe.
- Spongospira StOEHR, 1880, p. 120 [\**S. florealis;* OD]. Age and locality uncertain.
- Sporocalpia POMEL, 1872, p. 117 [\*Plocoscyphia morchella POMEL, 1872, p. 117; SD de LAUBENFELS, 1955, p. 107]. Cretaceous: Europe.
- Sporosinion POMEL, 1872, p. 90 [\* Ventriculites impressus SMITH, 1848, p. 205; SD RAUFF, 1893, p. 66]. Cretaceous: Europe.
- Spumispongia QUENSTEDT, 1877 in 1877–1878, p. 402 [\*S. punctata QUENSTEDT, 1877 in 1877–1878, p. 401; SD DE LAUBENFELS, 1955, p. 107]. Jurassic: Europe.
- Stamnocnemis POMEL, 1872, p. 80 [\*Cnemidium rouyana D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 96; OD]. Cretaceous: Europe.
- Stegendea FROMENTEL, 1875, p. 168 [=Stegeudea FROMENTEL, 1864, p. 26, nom. null.]. Triassic-Cretaceous: Europe.

- Stenocoelia FROMENTEL, 1861, p. 357 [\*S. ferryi; OD]. Conical, sometimes stipitate, upper surface with scattered oscules. Trabecular microstructure not known. [The limited information concerning this genus suggests it is similar to Oculospongia FROMENTEL, 1860a, or perhaps Mammillopora BRONN, 1825. FROMENTEL (1861, p. 357) compared it to Discoelia FROMENTEL, 1861, which appears to be a synonym of Peronidella ZITTEL in HINDE, 1893b.] Cretaceous (Berriasian-Hauterivian): France.
- Streblia POMEL, 1872, p. 207 [\*S. tuberiformis; SD DE LAUBENFELS, 1955, p. 107]. Paleogene-Neogene: Algeria.
- Strephochetus SEELEY, 1885, p. 357 [\*S. ocellatus; SD MILLER, 1889, p. 165] [=Strephorhetus VOSMAER, 1887, p. 402, nom. null.]. Middle Ordovician: USA (Vermont).
- Striataspongia HOWELL, 1957a, p. 1 [\**S. cylindrica;* OD]. *Upper Devonian:* Western Australia.
- Stromatopagia POMEL, 1872, p. 245 [\*?Sparsispongia radiosa D'ORBIGNY, 1850 in 1850–1852, vol. 1, p. 109]. Cretaceous: Europe.
- Sulcispongia QUENSTEDT, 1877 in 1877–1878, p. 81
   [\*S. incisa QUENSTEDT, 1877 in 1877–1878, p. 82;
   SD DE LAUBENFELS, 1955, p. 108]. Jurassic: Germany.
- Syncalpia POMEL, 1872, p. 116 [\*Cnemidium astrophorum GOLDFUSS, 1829, p. 97; SD RAUFF, 1893, p. 68]. Cretaceous: Europe.
- Taothis POMEL, 1872, p. 246 [\*Polytrema pavonia D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 278; OD]. Triassic-Cretaceous: Europe.
- Taseoconia POMEL, 1872, p. 249 [\*T. obovata; OD]. Paleogene-Neogene: Algeria.
- Testaspongia QUENSTEDT, 1878 in 1877–1878, p. 539 [\**T. craniolaris* QUENSTEDT, 1878 in 1877–1878, p. 540; SD de LAUBENFELS, 1955, p. 108]. *Triassic– Cretaceous:* Europe.
- Tethylites SOLLAS, 1880d, p. 390 [\*T. cretaceus; OD]. Cretaceous: Europe.
- Tetrasmila FROMENTEL, 1860a, p. 46 [\**T. corallina;* OD]. *Upper Jurassic:* Europe.
- Textispongia QUENSTEDT, 1877 in 1877–1878, p. 60 [\**T. coarctata;* SD DE LAUBENFELS, 1955, p. 94]. *Jurassic:* Germany.
- Thalamospongia D'ORBIGNY, 1850 in 1850–1852, vol. 2, p. 96 [\* *T. cottaldina;* OD] [= *Thalamosmila* FROMENTEL, 1860a, p. 45, obj.]. *Triassic–Cretaceous:* Europe.
- Thecospongia ÉTALLON, 1859b, p. 551 [\* *T. gresslyi;* OD]. *Jurassic:* France.
- Tholothis POMEL, 1872, p. 246 [\*Polytrema urceolata (LAMOUROUX, 1839, pl. 1,11); SD RIGBY, herein]. *Triassic–Cretaceous:* Europe. [POMEL (1872) listed the species *Polytrema convexa* and *P. urceolata*

(LAMOUROUX), as cited by D'ORBIGNY, as members of the genus, but, of the two, only the latter was named in the study by D'ORBIGNY (1850 in 1850– 1852, vol. 2, p. 279). Hence, *P. urceolata* should be considered as the type species, and not the former, as proposed by DE LAUBENFELS (1955, p. 108).]

- Thrachythyia POMEL, 1872, p. 68 [\**Cephalites capitata* SMITH, 1848, p. 288; OD]. *Cretaceous:* Europe.
- Thyronia POMEL, 1872, p. 67 [\*Cephalites seriatoporus ROEMER, 1864, p. 7; OD]. Triassic-Cretaceous: Europe.
- Thyia POMEL, 1872, p. 68, nom. nud. [Thyia is a large general line with no species, but it includes the genus Thrachythyia.] Cretaceous: Europe.
- Toriscodermia WISNIOWSKI, 1889a, p. 674 [No species]. Loose spicules. *Jurassic:* Europe.
- Trachysinion POMEL, 1872, p. 90 [\* Ventriculites tuberculosum ROEMER, 1864, p. 19; SD DE LAUBENFELS, 1955, p. 108]. Cretaceous: Germany.
- Tretolmia POMEL, 1872, p. 115 [\*Scyphia psilopora GOLDFUSS, 1826, p. 9; OD]. Cretaceous: Europe.
- Tretolopia POMEL, 1872, p. 204 [\*T. sparsa; SD DE LAUBENFELS, 1955, p. 108]. ?Paleogene-?Neogene: ?Algeria.
- Trinacrianella RIGBY, herein, nom. nov. pro Trinacriella PARONA, 1933, p. 32, non DEL-GUERCIO, 1913 [\*Trinacriella retusa PARONA, 1933, p. 33; OD]. Permian: Italy.
- Trioxites RAFINESQUE-SCHMALTZ, 1839, p. 380 [\**Achilleum dubium* GOLDFUSS, 1826, p. 9; OD]. Age and locality uncertain.
- Triphyllactis SOLLAS, 1880d, p. 390 [\**T. elegans;* OD]. Age and locality uncertain.
- Triposphaerilla WISNIOWSKI, 1889b, p. 235 [\**T. poctae;* OD]. *Jurassic:* Europe.
- Ttachycnemis POMEL, 1872, p. 79 [\* T. rugosa; OD] [=Trachycnemis RAUFF, 1893, p. 66, nom. null.]. Cretaceous: Europe.
- Tubispongia QUENSTEDT, 1877 in 1877–1878, p. 190 [\**T. caecau* QUENSTEDT, 1877 in 1877–1878, p. 191; SD DE LAUBENFELS, 1955, p. 108]. *Jurassic:* Germany.
- Tubulospongia COURTILLER, 1861, pl. 31,1 [\* T. insignis; SD de LAUBENFELS, 1955, p. 108]. Cretaceous: France.
- Vermispongia QUENSTEDT, 1877 in 1877–1878, p. 171, non WU Ya Sheng, 1991, p. 68 [\*V. wittlingensis QUENSTEDT, 1877 in 1877–1878, p. 230; OD]. Triassic–Cretaceous: Germany.
- Vomacispongites DE LAUBENFELS, 1955, p. 108, nom. nov. pro Spongites SCHLOTHEIM, 1820, p. 369, non OKEN, 1814 [\*Spongites pertusus SCHLOTHEIM, 1820, p. 371; OD]. Cretaceous: Europe.

## GENERA INCORRECTLY ASSIGNED TO PORIFERA BUT BELONGING TO OTHER TAXA

Acanthochonia HINDE, 1884 (receptaculitid).

Alcyonium LINNÉ, 1758 (ascidian).

- Alveolites LAMOUROUX, 1801 (coelenterate).
- Anomaloides ULRICH, 1878 (receptaculitid).
- Anthelia Lamouroux, 1816 (coelenterate).
- Anthophyllum Schweigger, 1820 (coelenterate).
- Bebryce PHILLIPI, 1842 (coelenterate).
- Calceolispongia Etheridge, 1915 (crinoid). Camarocladia Miller, 1889 [\**C. dichotoma;* OD].
- Cambrian-Ordovician. (trace fossil).
- Cellepora GMELIN, 1789 (bryozoan).
- Cerionites MEEK & WORTHEN, 1868 (receptaculitid)
- Ceriopora GOLDFUSS, 1833 (bryozoan).
- Choanites MANTELL, 1822 (ascidian).
- Cyclocrinites EICHWALD, 1842 (receptaculitid).
- Cylindrites GOEPPERT, 1842 (alga).
- Dictyocrinus HALL, 1859, (receptaculitid)
- Eschara LAMOUROUX, 1801 (bryozoan).
- Fibularia LAMOUROUX, 1816 (echinoderm).
- Fungites MARTINI, 1762 (coelenterate).
- Heliolites DANA, 1846 (coelenterate).
- Hydnopora PHILLLIPI, 1836 (bryozoan).
- Ichnospongia RIGBY, 1980 (trace fossil, burrow)
- Ischadites MURCHISON, 1839 (receptaculitid)
- Isis LINNÉ, 1758 (coelenterate).
- Kaiyangites QIAN & YIN, 1984 (possible conodont or uncertain taxonomy)
- Lepidolites ULRICH, 1889 (receptaculitid).
- Lichenopora DE FRANCE, 1823 (coelenterate).
- Millepora LINNÉ, 1758 (coelenterate).
- Nidulites SALTER, 1851 (receptaculitid)
- Palaeacis MEEK & WORTHEN, 1860 (coelenterate).
- Palaeospongia D'ORBIGNY, 1849 (receptaculitid, =Ischadites)
- Pasceolus BILLINGS, 1857 (receptaculitid)
- Polypatina ARENDT, 1956 (coelenterate, =Palaeacis)
- Receptaculites DE BLAINVILLE, 1830 (receptaculitid)
- Retopora LAMOUROUX, 1801 (bryozoan).
- Somphospongia BEEDE, 1899, p. 128 [\*S. multiformis; OD]. Carboniferous: USA (Coal Measures, Kansas), (alga).
- Sphaerospongia PENGELLY, 1861 (receptaculitid).
- Theonoa LAMOUROUX, 1821 (bryozoan).
- Vintonia NITECKI & RIGBY, 1965, p. 1,374 [\*V. doris; OD]. Carboniferous (Mississippian): USA (Fayetteville Shale, Arkansas), (plant, seedfern).

### RANGES OF TAXA

The stratigraphic distribution of the Porifera recognized in this volume is shown graphically in the range chart (Table 1).

Because of the very long stratigraphic ranges of many higher taxa of Porifera, ranges in the chart are rather broad in order to ensure that all periods are included. For more detailed stratigraphic information, refer to the systematic section of the volume.

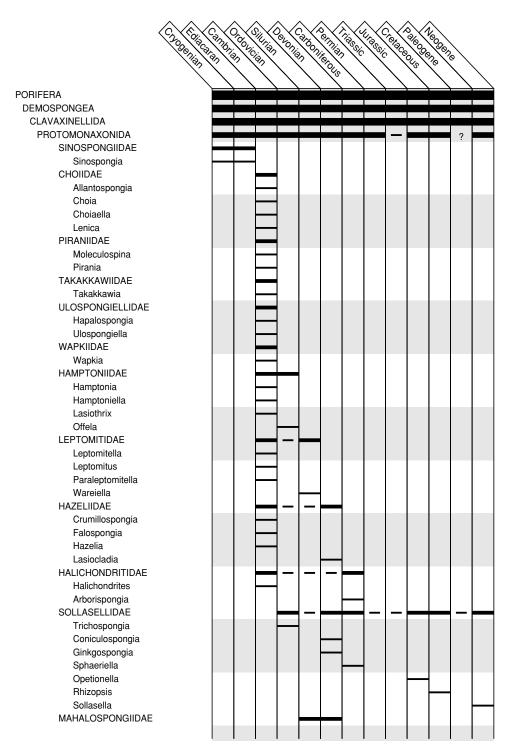
The following chart was compiled using software developed for the Paleontological

Institute by Kenneth C. Hood and David W. Foster.

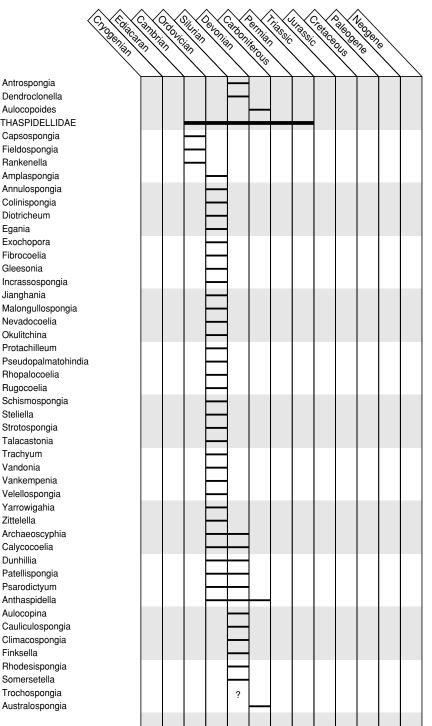
It must be emphasized that the order of taxa in this chart is governed entirely by their stratigraphic range and, within that, by alphabetical order and differs in some cases from the taxonomic order in the systematic part of the volume. No taxonomic conclusions should be drawn from the position of taxa in this chart.

[	
Explanation of Table	1
PHYLUM	
CLASS	
SUBCLASS	
ORDER	
SUBORDER	
SUPERFAMILY	
FAMILY	
SUBFAMILY	
Genus	
Subgenus	
Occurrence questionable	????
Occurrence inferred	

TABLE 1. Stratigraphic Distribution of the Porifera.



(Cz.	Kaje Canton Seenjan and the	Ordouroa	Devo han on	Catoonije	triasse tous	JUI ASSIC	A A REOUS	Neogene ene	
Mahalospongia HELIOSPONGIIDAE Coelocladia Coelocladiella Heliospongia Neoheliospongia Spitsbergenia TETHYIDAE Tethya									?
CLAVULINA CLIONAIDAE Clionolithes						-			
Runia Palaeosabella Entobia Clionoides Filuroda				? ?	_		+		+
Cliona Alectona Thoosa ADOCIIDAE				-					
Aka SUBERITIDAE Calcisuberites Rhopaloconus									?
Suberites SPIRASTRELLIDAE Ditriaenella Spirastrella									?
CERACTINOMORPHA LITHISTIDA ORCHOCLADINA STREPTOSOLENIDAE									
Gallatinospongia ?Orlinocyathus Wilbernicyathus Allosaccus			_						
Aulocopella Edriospongia Eospongia Hesperocoelia			=						
Hudsonospongia Lissocoelia ?Ozarkocoelia Streptosolen									
Verpaspongia Aulocopium Perissocoelia									



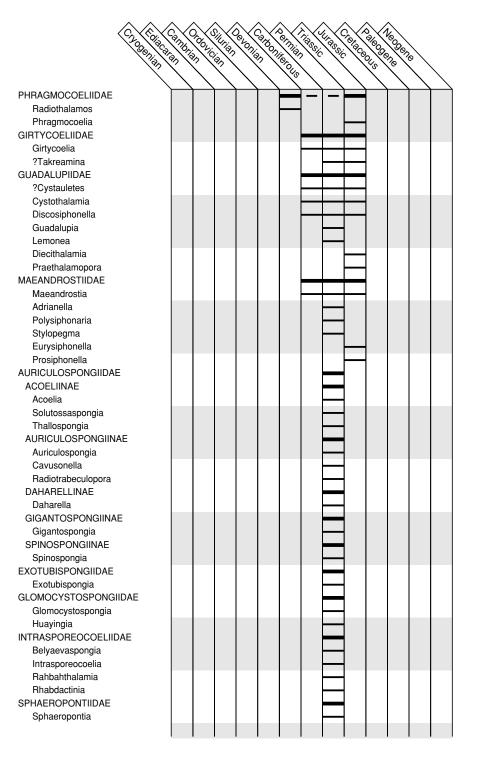
ANTHASPIDELLIDAE Capsospongia Fieldospongia Rankenella Amplaspongia Annulospongia Colinispongia Diotricheum Egania Exochopora Fibrocoelia Gleesonia Incrassospongia Jianghania Malongullospongia Nevadocoelia Okulitchina Protachilleum Rhopalocoelia Rugocoelia Schismospongia Steliella Strotospongia Talacastonia Trachyum Vandonia Vankempenia Velellospongia Yarrowigahia Zittelella Archaeoscyphia Calycocoelia Dunhillia Patellispongia Psarodictyum Anthaspidella Aulocopina Cauliculospongia Climacospongia Finksella Rhodesispongia Somersetella Trochospongia

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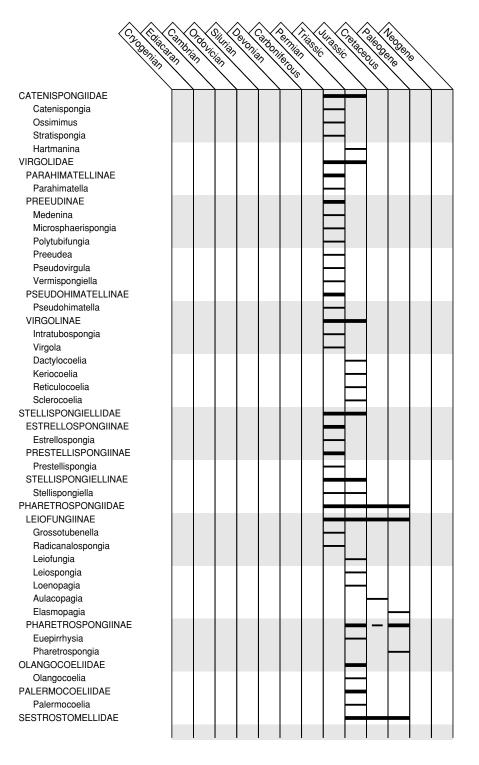
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Brianispongia Canningella Cockbainia Fistulosospongia Isispongia Playfordiella Syringelasma Jereina Virgaspongia Phacellopegma Aulacospongia Incrustospongiella Mastophyma Multistella Palaeojerea Palaeophyma Pseudomultistella Pycnospongia Timidella Tschernyschevostuckenbergia Virgaspongiella ASTYLOSPONGIIDAE Astylostroma Caliculospongia Camellaspongia Phialaspongia Astylospongia Carpospongia Caryospongia Caryospongia Caryospongia Astylospongial Caryoconus Palaeomanon Astyloscyphia Astylotuba Attungaia Devonoscyphia												
Garraspongia Globispongia Jazwicella Malinowskiella Inglispongia Ellesmerespongia Raanespongia CHIASTOCLONELLIDAE Syltispongia Chiastoclonella Allassospongia					?							
Rutkowskiella				F								

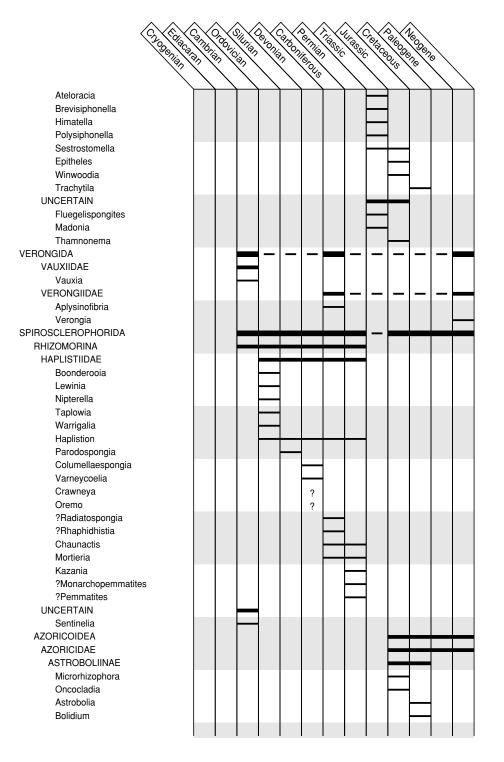
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Defordia													
Insulipora													
Pseudovirgulopsis													
ANTHRACOSYCONIDAE													
Devonospongia							_						
Anthracosycon													
Collatipora													
Dactylites											_		
?Laubenfelsia													
AGELASIDA			?										
SEBARGASIIDAE			? ?	?		_							
Amblysiphonella			' ?	' ?	_	_							
Sebargasia			·	L ,									
Chinaspongia													
Crymocoelia													
?Laccosiphonella													
?Lingyunocoelia													
?Paramblysiphonella													
Pseudoamblysiphonella							-						
Pseudoguadalupia								_					
Stylocoelia							-						
Vesicotubularia													
Polycystocoelia													
Minisiphonella								-					
Oligocoelia								-	_				
ANGULLONGIIDAE													
Alaskaspongia													
Amblysiphonelloides													
Angullongia													
Belubulaia													
Nibiconia		_							_				
CLIEFDENELLIDAE													
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Rigbyetia THAUMASTOCOELIIDAE													
Porefieldia					_	_	_						
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?Follicatena													
Thaumastocoelia													
Pamirothalamia													
Pamiroverticillites								-					
Sphaeroverticillites													
APHROSALPINGIDAE						—			_				
FISTULOSPONGININAE						—							
Cystothalamiella													
Aphrosalpinx													

Crocenary Constant	Carnorie An	Proovician	Devon	Carponing Aponing	arnian stringer	July sic	Crete Sic	R 3/600	Weogene	,	
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Uvacoelia											
Fistulosponginina											
PALAEOSCHADINAE											
Palaeoscheda											
VESICOCAULIINAE											
Russospongia											
Tolminothalamia								_			
Vesicocaulis								_			
Yukonella								_			
PREPERONIDELLIDAE											
PRECORYNELLINAE								_			
Imperatoria						_	_				
Bicoelia						_	_				
Minispongia						_	_				
Ramostella						-					
Precorynella						_		-			
Stollanella							_	-			
HEPTATUBISPONGIINAE						-					
Heptatubispongia						-					
Marawandia								-			
PERMOCORYNELLINAE											
Djemelia						_					
Saginospongia					_	_		_		_	
PREPERONIDELLINAE											
Bisiphonella Preperonidella											
Radiofibra											
GIRTYOCOELIIDAE									_		
Girtyocoelia											
Sollasia											
Amphorithalamia						_					
Phraethalamia											
Polyedra											
Enoplocoelia						_		_			
Henricellum							?	-			
?Solenocoelia							_	-			
Calymenospongia											
CRYPTOCOELIIDAE					-		_				
Rigbyspongia											
Cryptocoelia						-					
Anisothalamia											
Antalythalamia											
Sphaerothalamia								-			
FISSISPONGIIDAE											
?Hormospongia											
Fissispongia					?						
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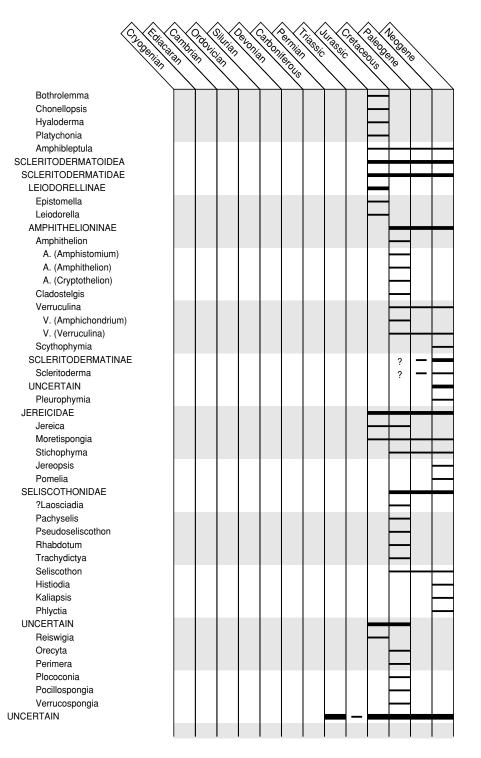
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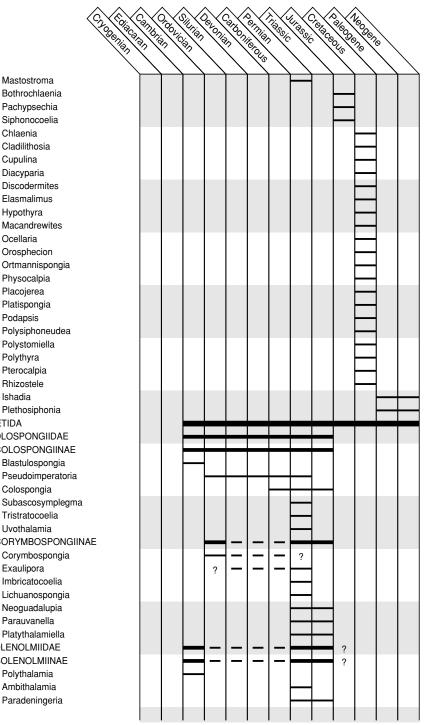




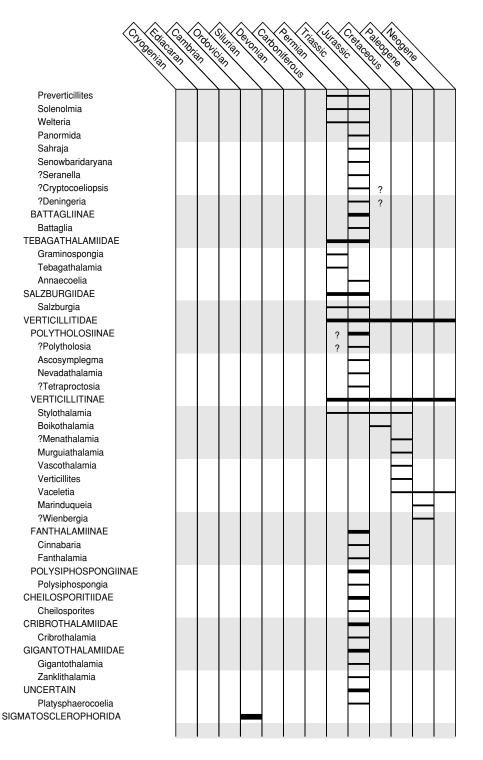
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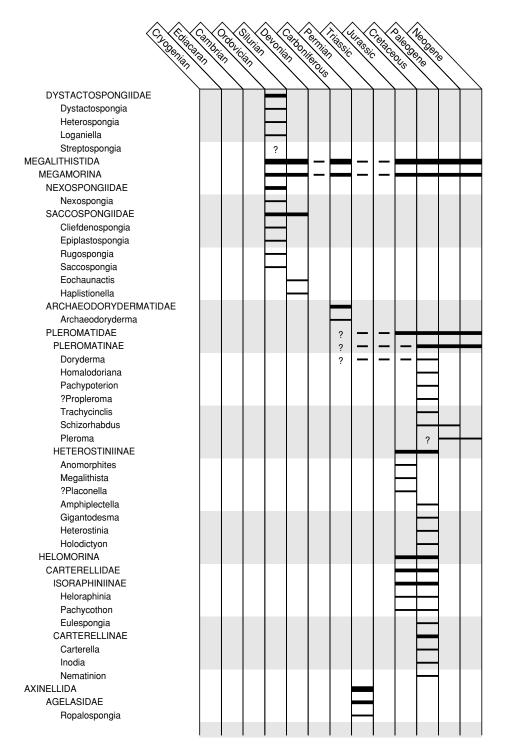
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AULOSOMINAE										-			
?Polyrhizophora									ŀ				
Yrrhiza									-				
Aulosoma													
Coelosphaeroma													
Oncodona													
Stachyspongia				_									
CYTORACIINAE											-	_	
Cnemispongia									Ē				
Cytoracia									Ē				?
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LEIOCHONIINAE													
Leiochonia													
Pseudocytoracea Soutolio													
Scytalia SIPHONIDIINAE										- E			
Pachysalax													
AZORICINAE													
Coscinostoma													
Plinthodermatium											_		
Chonella													_
Pliobolia										_  -			
Azorica											?	_	
Cnemaulax												_	_
?Plioboliopsis												_	
CNEMIDIASTRIDAE										_	_	_	_
Cnemopeltia									ŀ	_			
C. (Cnemopeltia)									-	_			
C. (Tremastrum)									ŀ	_			
Corallidium									ŀ	_			
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PLATYCHONIODEA													_
ARETOTRAGOSIDAE													
Aretotragos													
DISCOSTROMATIDAE													
DISCOSTROMATINAE													
Discostroma													
Hyalospongia Hyalotragos													
Proseliscothon													
PYRGOCHONIINAE													
?Patanophyma													
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P. (Actinostrombus)									ļ				
P. (Pyrgochonia)									ļ				
PLATYCHONIIDAE													

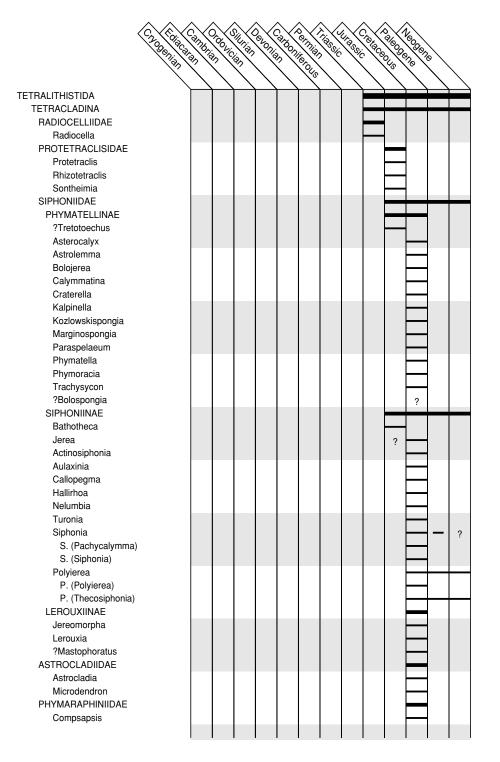




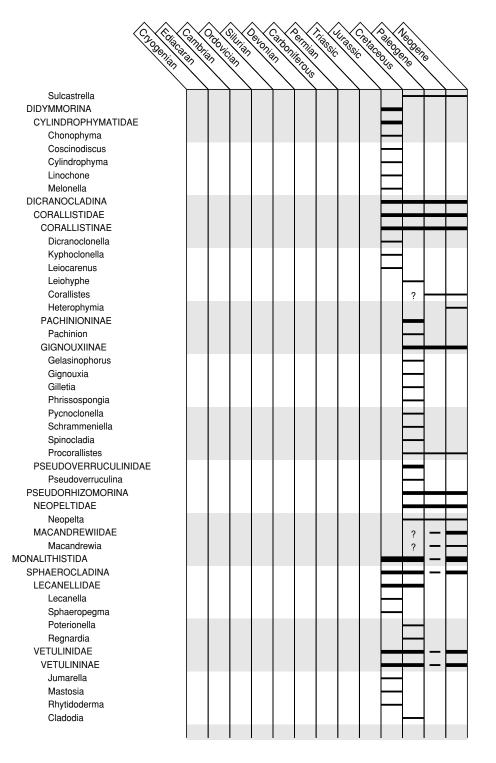
Pachypsechia Siphonocoelia Chlaenia Cladilithosia Cupulina Diacyparia Discodermites Elasmalimus Hypothyra Macandrewites Ocellaria Orosphecion Ortmannispongia Physocalpia Placojerea Platispongia Podapsis Polysiphoneudea Polystomiella Polythyra Pterocalpia Rhizostele Ishadia Plethosiphonia VACELETIDA COLOSPONGIIDAE COLOSPONGIINAE Blastulospongia Pseudoimperatoria Colospongia Subascosymplegma Tristratocoelia Uvothalamia CORYMBOSPONGIINAE Corymbospongia Exaulipora Imbricatocoelia Lichuanospongia Neoguadalupia Parauvanella Platythalamiella SOLENOLMIIDAE SOLENOLMIINAE Polythalamia Ambithalamia Paradeningeria

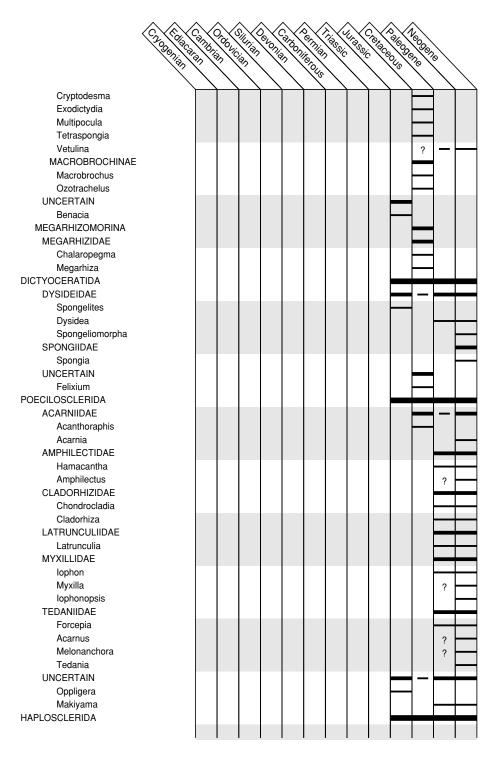


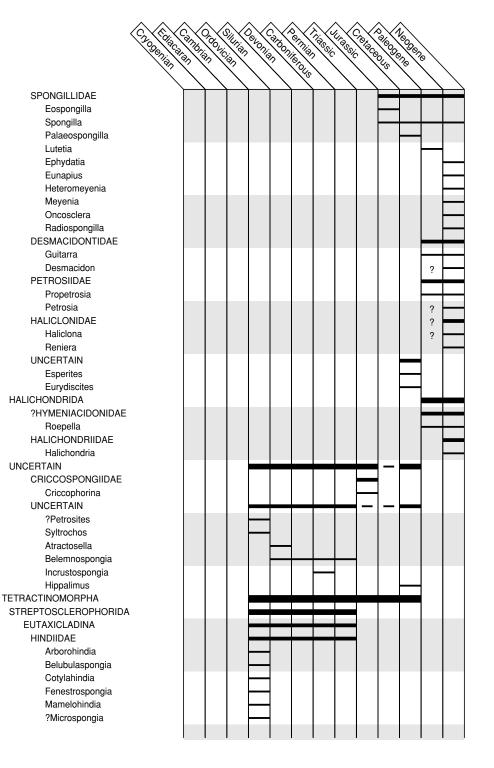




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Cycloclema											
Lopadophorus Pholidocladia											
P. (Pholidocladia)											
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Phymaraphinia											
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Prokaliapsis											
P. (Prokaliapsis)										_	
PLINTHOSELLIDAE											
Ingentilotus											
Plinthosella											
Pycnodesma										_	
CHENENDOPORIDAE										?	
Chenendopora											
?Dimorphina										_	
Microcladina										- 1	
?Tragalimus										?	
THEONELLIDAE											_
PHYMAPLECTIINAE											
Phymaplectia										?	
Thamnospongia											
THEONELLINAE										?	
Colossolacis		_					_	_			_
Leiophyllum											
?Placoscytus											
Rhoptrum Stellettites											
Racodiscula										, _	
Discodermia											
Theonella										· · ·	
ACROCHORDONIINAE										:	
Acrochordonia											
Eustrobilus											
Pseudojerea										_	
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Pachycorynea											
Rhopalospongia											
Verrucodesma											
Zitteleus UNCERTAIN											
Vermiculissimum											
vormounsantum											

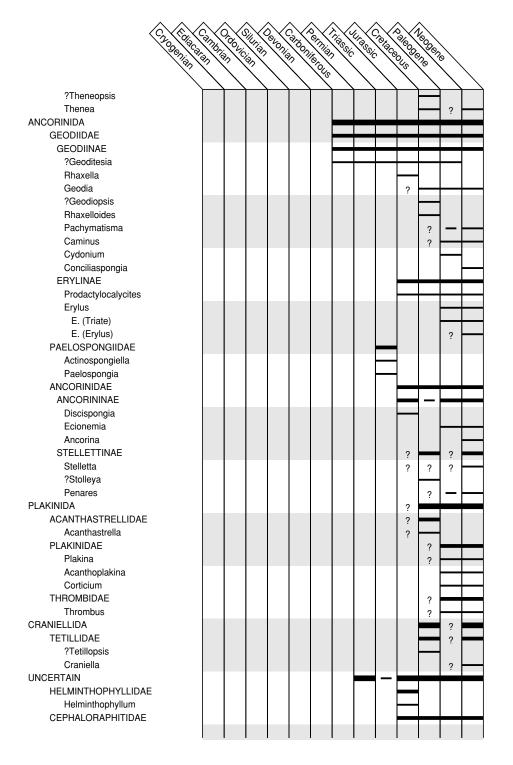


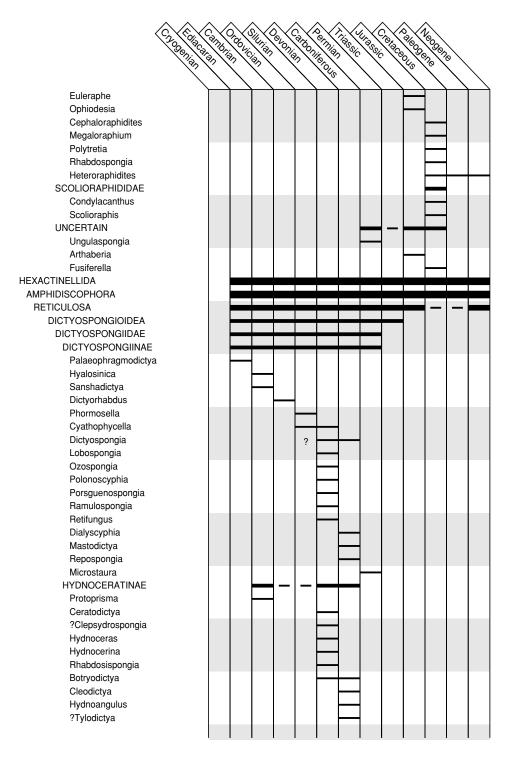




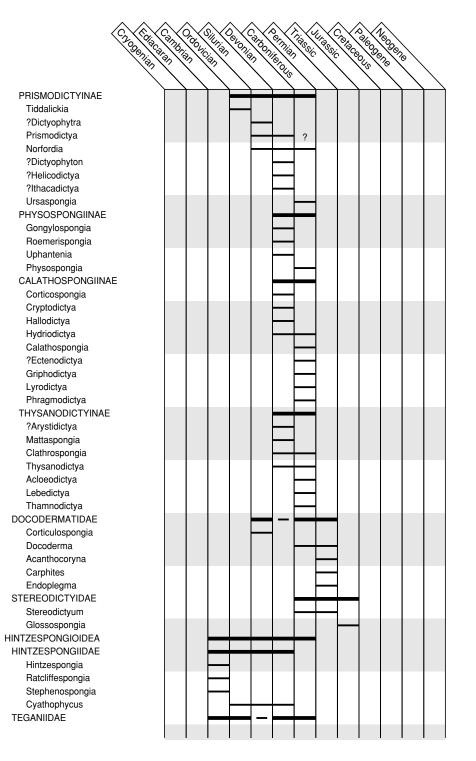
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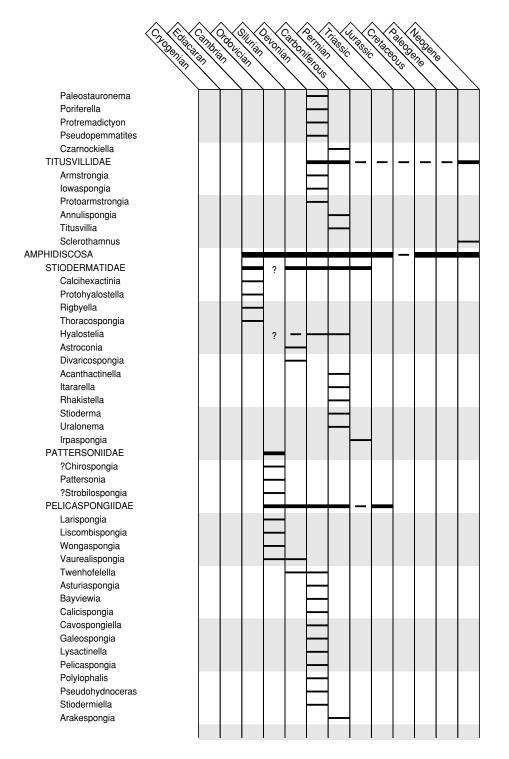
Cho		1008 FTR
Palmatohindia		
Hindia		
Sphaerolites		
Sadleria		
Scheielloides		
Scheiia		
Scheiella		
HADROMERIDA		
POLYSIPHONIDAE		
?Arbusculana		
Polysiphon		
Zardinia		
CELYPHIIDAE		
Pisothalamia		
Tongluspongia		
Uvanella		
Celyphia		
Alpinothalamia		
Cassianothalamia		
Jablonskyia		
Leinia		
Loczia		
Montanaroa		
Pamirocoelia		
Paravesicocaulis		
Pseudouvanella		
CEOTINELLIDAE		
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CHORISTIDA		
PACHASTRELLIDA		
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Pachastrella	? <b>— —</b> ? 2 <b>— —</b> 2	? ?
Nethea		?
CALTHROPELLINAE		?
Calthropella		?
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Helobrachium		
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COSTAMORPHIIDAE		
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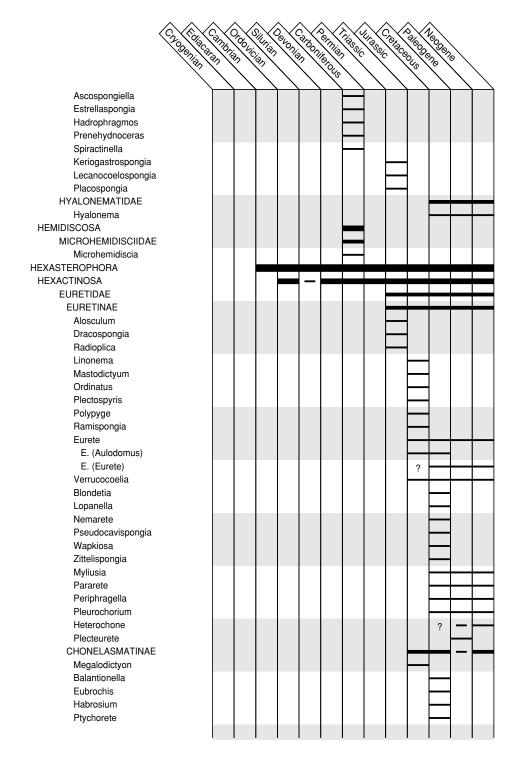


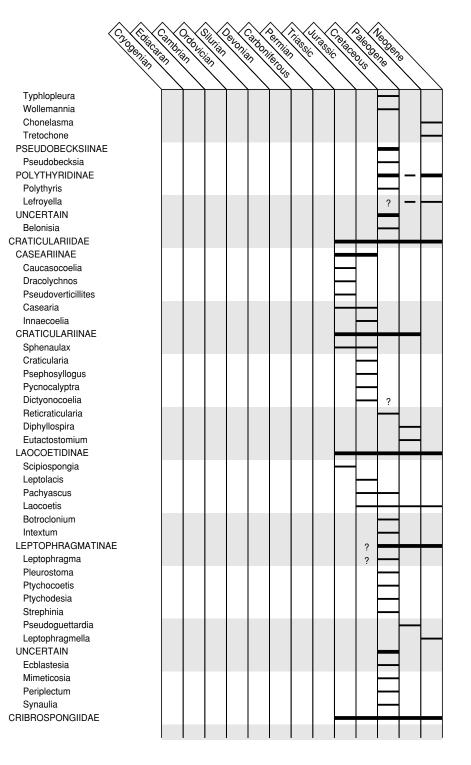


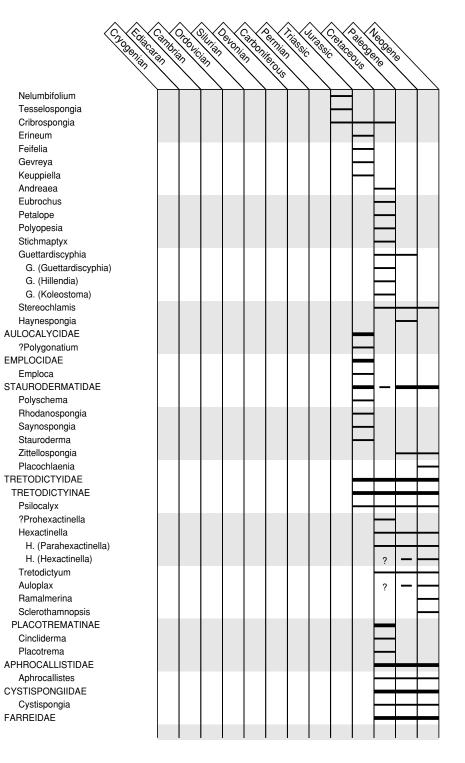
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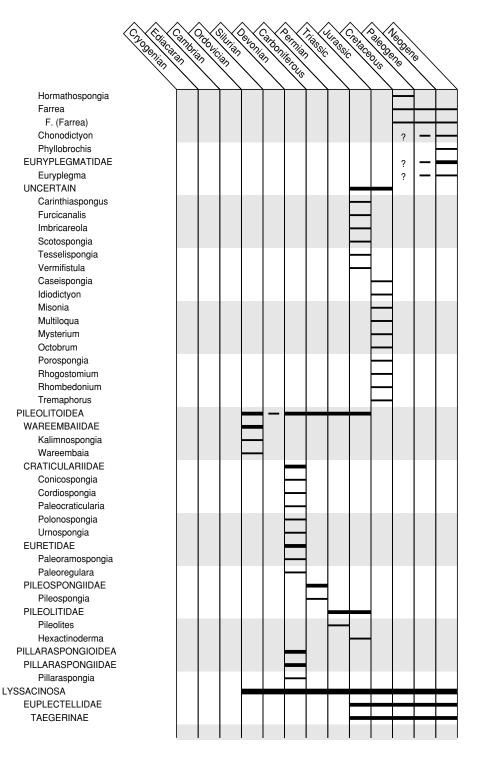


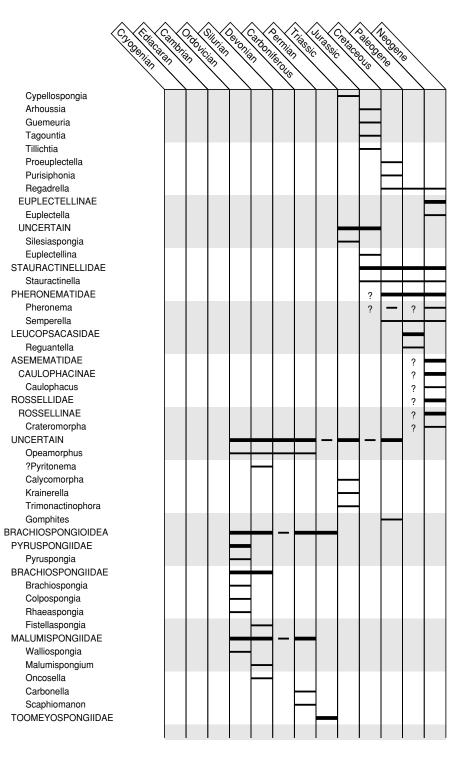


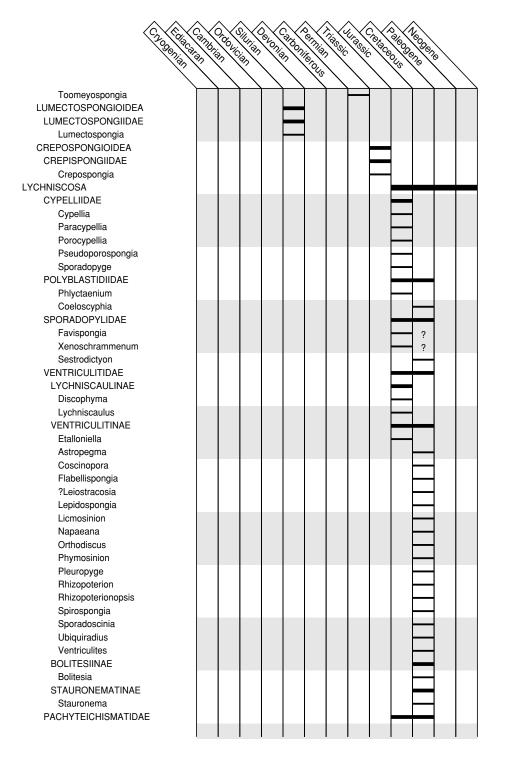




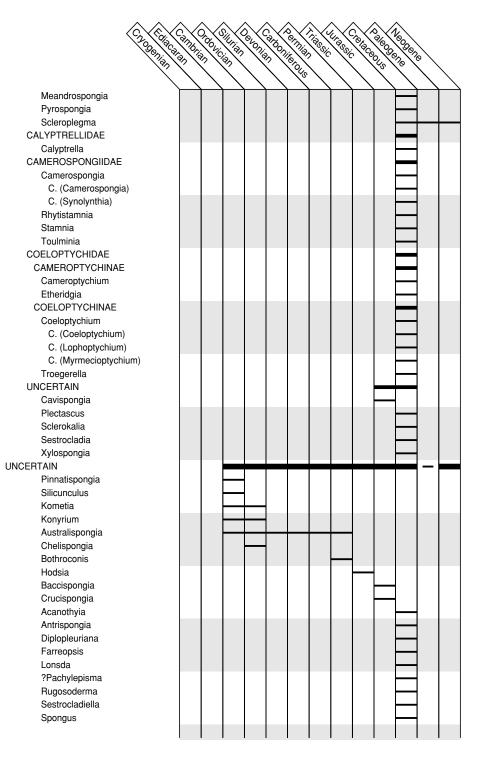


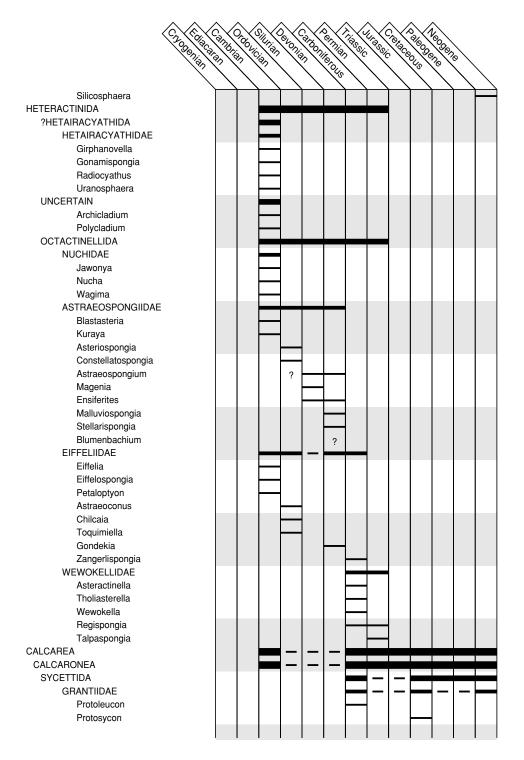




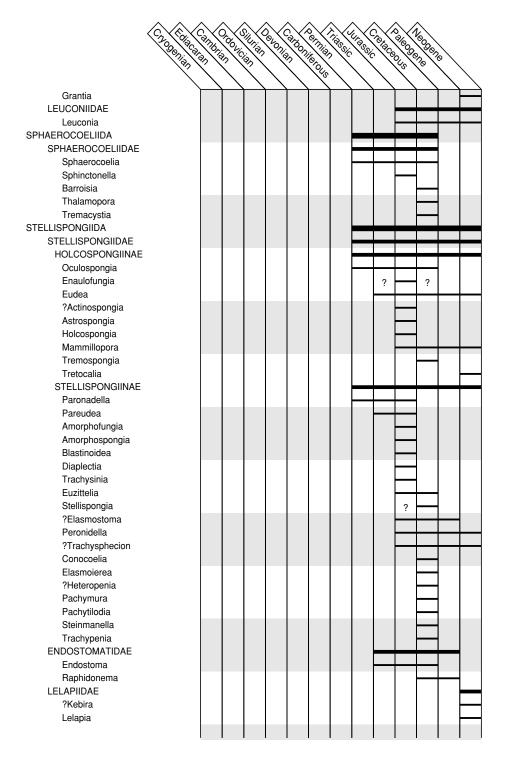


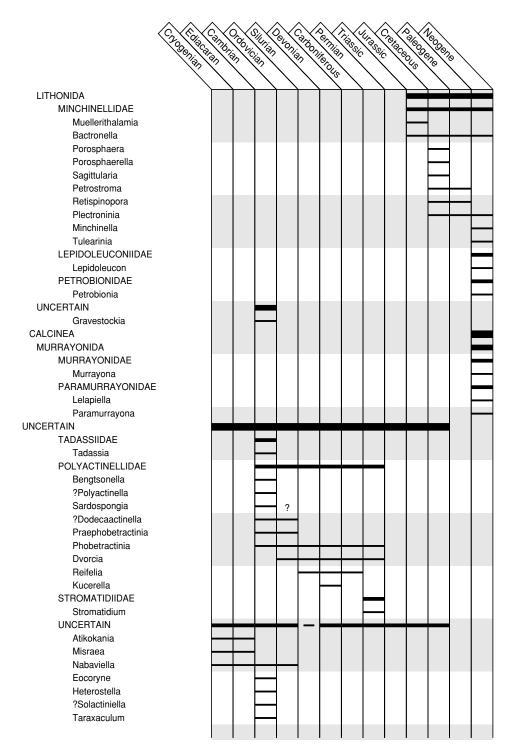
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Mastospongia Pachyteichisma Trochobolus CALLODICTYONIDAE CALLODICTYONINAE Coscinaulus							
Desmoderma Beaussetia Callodictyonella Cinclidella Diplodictyon Pleurope							
Porochonia Regnardielasma CALLICYLICINAE Ceriodictyon Brachiolites							
Centrosia Cephalites Tremabolites Callicylix C. (Cyclostigma)							
C. (Callicylix) MICROBLASTIDINAE Microblastidium Spirolophia BECKSINAE Becksia							
Discoptycha Oncolpia O. (Oncolpia) O. (Polyptycha) Plocoscyphia Sarophora							
Manzonispongia DACTYLOCALYCIDAE DACTYLOCALYCINAE ?Calathiscus Exanthesis	E						
E. (Eligma) E. (Exanthesis) Moretiella Paraplocia ?Scolecosia OPHRYSTOMATINAE							
Ophrystoma UNCERTAIN Jima							

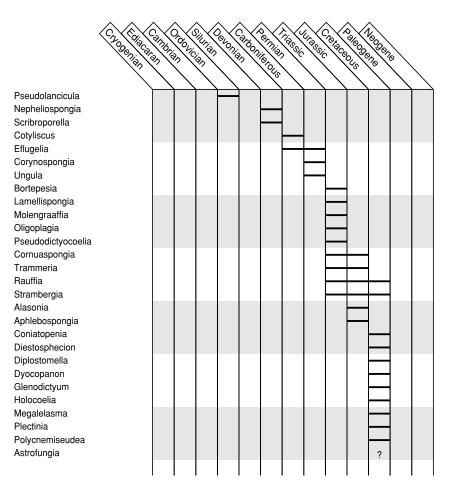




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