TREATISE ON
INVERTEBRATE PALEONTOLOGY

Part E

PORIFERA

Revised
Hypercalcified Porifera
Volume 4

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PART E
PORIFERA
Revised
HYPERCALCIFIED PORIFERA, Volumes 4 and 5

By F. Debrenne, Willard D. Hartman, Stephen Kershaw, P. D. Kruse, Heldur Nestor, J. Keith Rigby Sr., B. Senowbari-Daryan, Colin W. Stearn, Carl W. Stock, Jean Vacelet, Barry D. Webby, Ronald R. West, Philippe Willenz, Rachel A. Wood, and A. Yu. Zhuravlev

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CONTENTS OF VOLUME 4

CONTENTS OF VOLUME 5

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 Paleontological Institute, The University of Kansas, 1475 Jayhawk Blvd., Room 119, Lawrence, Kansas 66045-7594, USA, www.paleo.ku.edu.

PUBLISHED VOLUMES

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Part B. PROTOCTISTA 1 (Charophyta), xvi + 170 p., 79 fig., 9 tables, 2005.

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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.

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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.

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Part H, Revised. BRACHIOPODA, Volume 1 (Introduction), xx + 539 p., 417 fig., 40 tables, 1997.

Part H, Revised. BRACHIOPODA, Volumes 2 and 3 (Linguliformea, Craniiformea, Rhynchonelliformea [part]), xxx + 919 p., 616 fig., 17 tables, 2000.

Part H, Revised. BRACHIOPODA, Volume 4 (Rhynchonelliformea [part]), xxxix + 768 p., 484 fig., 3 tables, 2002.

Part H, Revised. BRACHIOPODA, Volume 5 (Rhynchonelliformea [part]), xlvi + 631 p., 398 fig., 2006.

Part H, Revised. BRACHIOPODA, Volume 6 (Supplement), l + 906 p., 461 fig., 38 tables, CD of compiled references from volumes 1–6, 2007.

Part I. MOLLUSCA 1 (Mollusca General Features, Scaphopoda, Amphineura, Monoplacophora, Gastropoda General Features, Archaeogastropoda, Mainly Paleozoic Caenogastropoda and Opisthobranchia), xxiii + 351 p., 216 fig., 1960.

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 2 (Carboniferous and Permian Ammonoidea), xxix + 258 p., 139 fig., 1 table, 2009.

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; 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.

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Part T. ECHINODERMATA 2 (Crinoidea), Volumes 1–3, xxxviii + 1,027 p., 619 fig., 1978.

Part T, Revised. ECHINODERMATA 2 (Crinoidea), Volume 3. xxix + 261 p., 112 fig., 2011.

Part U. ECHINODERMATA 3 (Asterozoans, Echinozoans), xxx + 695 p., 534 fig., 1966.

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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.

Part W, Revised. MISCELLANEA, Supplement 2 (Conodonta), xxviii + 202 p., frontis., 122 fig., 1981.

THESE VOLUMES

Part E, Revised. PORIFERA, Volumes 4 and 5 (Hypercalcified Porifera). liii + 1223 p., 665 fig., 42 tables, 2015.

VOLUMES IN PREPARATION

Part B. PROTISTA 1 (Chrysomonadida, Coccolithophorida, Diatomacea).

Part F, Revised. CNIDARIA (Scleractinia).

Part G, Revised. BRYOZOA (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 P, Revised. ARTHROPODA 2 (Chelicerata).

Part Q, Revised. ARTHROPODA 3 (Ostracoda).

Part R, Revised. ARTHROPODA 4 (Crustacea Exclusive of Ostracoda).

Part T, Revised. ECHINODERMATA 2 (Crinoidea) (additional volumes).

Part V, Revised. GRAPTOLITHINA.

Part W, Revised. TRACE FOSSILS.

COORDINATING AUTHOR'S PREFACE

Barry D. Webby

Volumes 4 and 5 complete the revision of the *Treatise on Invertebrate Paleontology,* Part E, Porifera. The volumes focus on groups called, collectively, hypercalcified sponges (Termier & Termier, 1973): that is, encompassing all forms that acquired a mainly nonspicular, basal skeleton of calcium carbonate to support and maintain the organism's soft tissues, with it usually mantling above, but occasionally investing part of the associated substrate. The types of hypercalcified skeleton became well adapted, especially in Phanerozoic reef habitats, across a range of distinctly different fossil groups of demosponges and calcareans. The volumes aim: (1) to present comprehensive introductions and systematic descriptions of the main hypercalcified fossil sponge groups—namely, the archaeocyaths, stromatoporoids, and chaetetids; (2) to provide an introduction and systematic descriptions of the comparatively few hypercalcified demosponge and calcarean taxa that are still living; and (3) to add an introduction about the other hypercalcified demosponges and calcareans, represented by the sphinctozoan- and inozoan-type morphologies, to the systematic descriptions of these forms contributed previously in Volume 3 of the *Treatise,* Part E, Porifera, Revised, by Robert M. Finks and J. Keith Rigby (2004d).

Siliceous spicules were secreted by the soft tissue and acted in a variety of support roles in living hypercalcified demosponges. Commonly, they were secondarily accreted to their basal skeletons by calcareous cements. Alternatively, they may have remained as discrete elements in the body of the sponge, or, during the life of the sponge, they may have been initially secreted then reabsorbed in the skeleton, or these siliceous spicules were never secreted. Calcareous spicules, on the other hand, were secreted only in hypercalcified calcareans, with some developing in association with an initial spicular skeleton, or becoming incorporated secondarily in carbonate cementation of the solid basal skeleton. In fossil counterparts, the spicules are seldom recorded in their original state; typically, they show significant levels of diagenetic alteration and are, in consequence, largely preserved as spicule pseudomorphs. Such structures are not uncommon in Mesozoic stromatoporoids (Wood, 1987) and have been identified also in late Paleozoic and Mesozoic chaetetids (Gray, 1980). However, spicule pseudomorphs have not been confirmed positively in the major hypercalcified groups such as archaeocyaths and Paleozoic stromatoporoids.

All the main hypercalcified fossil sponge groups exhibit direct or indirect evidence of aquiferous systems that supported their inferred filter-feeding activities as sponges. These features may comprise: (1) astrorhizal structures as surface impressions in the chaetetids and of surface imprints and internal canals in the stromatoporoids; (2) occurrences of porous outer and inner walls and a central cavity in the archaeocyaths; and (3) astrorhizal structures, pores in outer and inner walls, and a spongocoel (= central cavity) in sphinctozoans and inozoans.

The archaeocyaths, stromatoporoids, and chaetetids are described systematically here, for the first time in a *Treatise* volume, as members of the phylum Porifera. In some contexts, the concept of morphological grade of construction has been applied to these higher-level subdivisions, though independent taxonomic categories up to the level of classes still continue to be maintained for the description of the nonspiculate archaeocyaths and the Paleozoic stromatoporoids. The affinities of these various fossil groups have long been discussed in relation to living sponges and other groups. Kirkpatrick (1908, 1909, 1910a, 1910b, 1910c, 1911, 1912a, 1912b, 1912c, 1912d, 1912e, 1912f) was the first to thoroughly survey the characteristics of a number of living hypercalcified sponges, including the crustlike forms of one species in particular, *Merlia normani* Kirkpatrick, 1908, which he recognized as having siliceous spicules in the living tissue as well as a supplementary calcareous skeleton. In discussion of its possible relationships, he suggested that some Paleozoic fossils, including stromatoporoids, chaetetids, and others, had "essentially the same nature as *Merlia*" (Kirkpatrick, 1912a, p. 502) and that this genus may have been "a solitary survivor" from Paleozoic times. It is unfortunate that his ideas, published in subsequent years, across a broad range of topics on living organisms, fossils, and rocks, became increasingly idiosyncratic and untenable. Nevertheless, he must continue to be credited with recognizing correctly the links between living hypercalcified sponges and the stromatoporoids and chaetetids at a time when these latter groups were consistently treated as hydrozoans.

More than a half century later, Hartman and Goreau (1970, 1972) rediscovered and properly documented many of the living sponges with hypercalcified skeletons in the Caribbean, and, contemporaneously, Vacelet (1964, 1970, 1977a) commenced his remarkable series of discoveries in the Mediterranean and Indo-Pacific, which together allowed poriferan connections to be firmly established for the various fossil groups—such as stromatoporoids and chaetetids, as well the sphinctozoans—that exhibited hypercalcified skeletons.

The Archaeocyatha was treated as a separate phylum between the late 1940s and 1980s, though greater affinities were accorded to the sponges than other groups. However, the rediscoveries of living hypercalcified sponges and the recognition of a chambered, nonspiculate, sphinctozoan called *Vaceletia crypta* (Vacelet, 1977b), which shows close similarities to the architecture and skeletal structure of archaeocyaths, have led to a reappraisal and suggestions that the archaeocyaths are closer taxonomically to phylum Porifera (Debrenne & Vacelet, 1984) than previously thought. More recently, the archaeocyaths were adopted as a separate class of phylum Porifera (see Debrenne, Zhuravlev, & Kruse, 2002, p. 1546).

NOMENCLATURAL CHANGES

Four alternative names—coralline sponges, sclerosponges, pharetronids, and ischyrosponges—have been applied previously to denote broadly equivalent (= synonymous) informal groupings of the presently accepted term hypercalcified sponges (including the hypercalcified demosponges and hypercalcified calcareans, respectively). The coralline sponges were presumably so termed because of their superficial resemblances to coral colonies and occupation as encrustations or other skeletal growths of similar reef-type settings. The term used informally by Hartman (1969, p. 1; Hartman & Goreau, 1970, p. 228) was applied generally to all living sponges with calcified basal skeletons, astrorhizal structures, and spicules, either siliceous or calcareous. The generalized conception of the term has since been broadened to encompass these particular living forms, as well as the array of fossil representatives, particularly of stromatoporoids and chaetetids (see, for example, Wood, 1990b, p. 225–234; Reitner, 1992, p. 1; Wörheide, 1998, p. 1–88; Reitner & others, 2001, p. 219–223, 228, 231–234; Reitner & Wörheide, 2002, p. 58–68).

There is no longer justification for retaining the informal name coralline, especially given that, in terms of taxonomic classification, neither the living forms nor fossil stromatoporoids and chaetetids have diagnostic features in common with representative cnidarian corals and hydrozoans. The only superficial resemblances between hypercalcified sponge groups like stromatoporoids and chaetetids, on the one hand, and tabulate corals, on the other, are, for example, where they develop similar growth habits as a result of sharing similar reef-building habitats. Nevertheless the two groups remain fundamentally different, so the current practice of naming particular types of skeletonized sponge as "coralline" should be discontinued (see WEBBY, 2010, p. 7).

The second name, sclerosponge, is based on class Sclerospongiae HARTMAN & GOREAU (1970, 1972). It was first used in a more restrictive sense to take account of living sponges that exhibited a massive aspicular basal skeleton of calcium carbonate (mainly aragonitic) and siliceous spicules that formed in the thin, overlying, veneerlike layer of living tissue—this latter sometimes becoming entrapped in the calcareous skeletal mass below—and the fossil counterparts, stromatoporoids and chaetetids. HARTMAN and GOREAU (1970, p. 228) proposed this higher taxon mainly to accommodate the remarkable record of living hypercalcified sponge species that they found in the forereef settings of the Caribbean, and their recognition of similarities with astrorhizal-bearing fossil stromatoporoids, as well as some members of the fossil Chaetetidae. Initially, the establishment of the class Sclerospongiae received widespread acceptance, even though HARTMAN and GOREAU (1970, p. 221) acknowledged that "a basal skeletal mass of aragonite [had] arisen independently within several different phylogenetic lines of the Demospongiae," and these same authors (1972, p. 144) admitted that similarities existed between sclerosponges and demosponges, particularly in the organization of their living tissue, cell types, and development (see HARTMAN, 1983, p. 116).

Additionally, Jean VACELET (1964, 1970, 1977a, 1983, 1985), in an important series of hypercalcified sponge discoveries from various parts of the world (in particular the Mediterranean and the Indo-Pacific regions), recognized that modern reef habitats exhibit a wider range of sponge groups than just those represented by a hypercalcified calcareous skeleton and the sclerosponge-type of hypercalcified skeleton with siliceous spicules, this latter regarded as derived from within a number of different orders of the class Demospongiae. Consequently, the higher-level sclerosponge grouping exhibits polyphyletic relationships, and therefore the formal use of the name should be abandoned.

ZITTEL (1878) introduced the third supra-familial group as Pharetrones, a name subsequently amended formally to Pharetronida by DE LAUBENFELS in 1955 (p. 97). VACELET (1991) later recognized such pharetronid-type skeletons as occurring within different subclasses of the Calcarea. They were composed of a massive hypercalcified skeleton—that is, either based on a reinforced spicular skeleton or a nonspicular rigid skeletal mass and usually associated with fused or free calcareous spicules. Consequently within the Calcarea, these pharetronid-type skeletons occur in different calcarean subclasses, and therefore comprise a group, which as a whole must also be interpreted as being polyphyletic in origin (VACELET, 1991, p. 261), and therefore this group name should no longer be used.

The fourth name, ischyrosponges, was based on the supra-familial grouping Ischyrospongiae TERMIER & TERMIER (1973, p. 286) and, as proposed, was likely to have the status of a superclass, given that it was considered to include three classes (Stromatoporoidea, Sclerospongia, and Pharetronidea). However, the name has been little used, even by H. TERMIER and G. TERMIER (1973) to promote this higher-level terminology and clearly proves to represent an even more polyphyletic grouping of forms than the Sclerospongiae, so its use should also be abandoned.

Preference should always be given to describing these forms broadly, and in general terms, as hypercalcified sponges, or, where their more specific relationships are known, as hypercalcified demosponges, hypercalcified calcareans, or heteractinids. The other main subdivision of hypercalcified sponges is based on the important skeletal differences that exist between the main fossil groups. Broadly, these groups comprise the archaeocyathans, chaetetids, stromatoporoids, sphinctozoans, and inozoans, as described herein.

EARLIER *TREATISE* COMPILATIONS

Previously the stromatoporoids and chaetetids were described in *Treatise* volumes as parts of the Coelenterata, and the archaeocyaths were considered to be an independent phylum. The stromatoporoids were regarded initially in the first edition of *Treatise,* Part F, Coelenterata by Marius Lecompte as belonging to class Hydrozoa (LECOMPTE, 1956, p. 107–144), whereas the chaetetids were described as tabulate corals by Dorothy Hill and Erwin Stumm in that same edition of the coelenterate *Treatise* volume (HILL & STUMM, 1956, p. 454–456). Then chaetetids were treated again more comprehensively by Dorothy Hill in Supplement 1 of the *Treatise,* Part F, Coelenterata (HILL, 1981, p. 506–520). The archaeocyaths were twice described as belonging to an independent phylum, first by Vladimir Okulitch, in a part of the first edition of the *Treatise,* Part E (Archaeocyatha and Porifera) (OKULITCH, 1955a, p. 1–20), and second, by Dorothy Hill in the second edition of the *Treatise,* Part E (Archaeocyatha) (HILL, 1972, p. 1–158).

The next revisions of *Treatise,* Part E, Porifera commenced with the publication of Volume 2: Introduction to the Porifera, by Robert M. FINKS, R. E. H. REID, and J. Keith RIGBY (2003), and Volume 3: Porifera (Demospongea, Hexactinellida, Calcarea) by the same authors in 2004. FINKS and RIGBY (2004d, p. 585–764) coauthored a substantial part (about one-third) of Volume 3 that was devoted to the systematic descriptions of the Hypercalcified Sponges, mainly those exhibiting sphinctozoan (= thalamid) and inozoan architectures. Included was a basic outline of the microstructure, morphological features, and the basis for informal subdivision into two groups, the Hypercalcified Demospongea and Hypercalcified Calcarea (FINKS & RIGBY, 2004d, p. 585–594). These groups had been referred to collectively in the past as pharetronids (after order Pharetrones of VON ZITTEL, 1878), with separation into morphological types: the chambered sphinctozoans (alternatively called thalamids, after DE LAUBENFELS, 1955), and the reticular (nonchambered) inozoans (see FINKS, 1983), with both latter names derived from STEINMANN (1882). FINKS and RIGBY (2004d, p. 590) recognized these names based on morphologic types as having some taxonomic value at the family level. However, at higher levels they are not taxonomically useful, as members of both sphinctozoan and inozoan types of constructions occur in both the class Demospongiae and the class Calcarea, and even one demosponge order (Agelasida HARTMAN, 1980b) has representatives of both morphological types, again emphasizing the polyphyly within these forms.

FINKS and RIGBY (2004c, p. 557–583) also included the exclusively Paleozoic (lower Cambrian–Permian) class Heteractinida as an independent, minor, poriferan group. It was also regarded as hypercalcified because, though it has dominantly a spicular skeleton composed of skeletal networks of various calcareous spicule types (mainly octactines, polyactines, or sexiradiates), it also has globular, saucer-shaped, or cylindrical skeletons that commonly become embedded, either partially or more completely, with coatings of cement of nonspicular calcium carbonate. On the other hand, PICKETT (2002, p. 1121) recognized the order Heteractinida as a separate member of the class Calcarea. It represents a group composed of distinctive calcareous octactine to polyactine spicule types and a rigid skeletal framework of nonspicular carbonate.

OUTLINE OF CONTRIBUTIONS TO THIS VOLUME

Much of the stimulus for the present revisions of fossil hypercalcified sponge groups stems from the spectacular rediscoveries from the late 1960s onward of living hypercalcified sponges, first by FINKS and RIGBY (in FINKS, REID, & RIGBY, 2004), and now, herein, in the sections on living hypercalcified

Porifera by Vacelet, Willenz, and Hartman; living and fossil hypercalcified chaetetid-type and post-Devonian stromatoporoid-type Demospongiae by West, Vacelet, Wood, Willenz, and Hartman; and living hypercalcified Calcarea by Vacelet. The so-called living fossils were reported mainly from the dimly lit areas of reefal habitats across a range of settings between sublittoral caves and bathyal cliffs in the tropical to subtropical waters of the Indo-Pacific and Caribbean, and more temperate waters of the Mediterranean and nearby Atlantic (HARTMAN, 1969; HARTMAN & GOREAU, 1970, 1972, 1975; VACELET, 1970, 1977a, 1985; WILLENZ & HARTMAN, 1999).

The rediscoveries of these unique living sponge faunas by Hartman, Vacelet, and others have done much to activate interest among paleontologists, especially those working on the various hypercalcified fossil groups. Consequently, closer linkages have been forged with neontologists, and a number of paleontologists have since applied various functional models based on some of the living hypercalcified forms to morphologically similar fossil taxa. In particular, for a decade or so, Stearn, West, Wood, Debrenne, and Zhuravlev have been attempting to explain aspects of the functional significance, living habits, and microstructures of their fossil taxa (mainly among stromatoporoids, chaetetids, and archaeocyaths), using examples from among the various extant hypercalcified sponge taxons as their models.

Hypercalcified sponges were considered to have acquired a rigid, nonspiculate calcareous basal skeleton in support of their growth within reef habitats by VACELET (1985), WOOD (1987, 1989), and others. They recognized also that the calcareous basal skeleton evolved independently in a number of unrelated sponge lineages through the Phanerozoic, each time developing a similarly convergent form. Furthermore, they regarded the calcareous basal skeleton as representing a morphological grade that appeared and disappeared repeatedly through time, surviving until today in five separate ordinal-level demosponge and three calcarean lines of evolutionary development. These repetitions in the development of a basal skeleton have resulted in many unrelated, relic, living hypercalcified sponge clades and led Vacelet and Wood, in particular, to conclude that the possession of a calcareous basal skeleton had limited phylogenetic significance within the phylum Porifera.

EXTANT AND FOSSIL DEMOSPONGIAE: CHAETETID-TYPE AND POST-DEVONIAN STROMATOPOROID-LIKE TAXA

Volume 4 provides a general introduction with outlines of the respective morphologies, modes of life, ecological significance, geographical distribution, and classification of the living relic sponge faunas, contributed by Vacelet, Willenz, and Hartman. The existing, described living hypercalcified sponge fauna of 19 genera are divided between the 10 genera of class Demospongiae (those belonging to 5 extant orders), and the 9 genera of class Calcarea (that are included in 3 extant orders). This comparatively small number of extant hypercalcified genera represents only about 2.8% of the valid taxa of some 680 living sponge genera known as a result of the recently completed major, collaborative work on global taxonomy (HOOPER, VAN SOEST, & DEBRENNE, 2002); the majority of living sponges lack a mineralized basal skeleton.

Also, in this first part of the present revised Volume 4 are general introductions to the fossil demosponge counterparts of the living taxa, contributed by WEST and WOOD on the chaetetid-type and post-Devonian stromatoporoid-like taxa. In these introductions, they mention the importance of recognizing spicules (or, at least, their pseudomorphs), as had been done earlier by KAŹMIERCZAK (1979), GRAY (1980), and REITNER (1991a) in Carboniferous–Cretaceous chaetetids and by WOOD (1987) for Mesozoic stromatoporoids. Traces of the secondarily entrapped or coated spicules (or spicule pseudomorphs) within their hypercalcified skeletons have been documented by WEST and WOOD, based on their spicules and gross morphology. In addition, they identified in their fossil material evidence of aquiferous systems (for example, presence of astrorhizae on surfaces of chaetetids; see also WEST & CLARK, 1983, fig. 3–4), and other morphological resemblances to extant taxa like *Acanthochaetetes, Merlia,* and *Ceratoporella* that ally these fossil groups to demosponges. Many of these fossil taxa were included previously in cnidarian-based groupings but are now revised and included in higher-level subdivisions of the poriferan class Demospongiae.

The well-illustrated systematic descriptions of extant hypercalcified, and fossil chaetetid- and post-Devonian stromatoporoid-type, demosponge genera are combined for the first time by WEST, VACELET, WOOD, WILLENZ, and HARTMAN in a classification of taxa spread across 8 different orders (2 uncertain) of the class Demospongiae. Included are 48 living and fossil genera (with addition of 5 fossil subgenera). Significantly, the chaetetid-type and stromatoporoid-like genera have separate distributions—that is, as different morphological grades they do not occur together in the same order—which suggests they have some taxonomic significance. On the one hand, chaetetids are distributed across 4 living orders—the Hadromerida, Poecilosclerida, Halichondrida, and possibly Chondrosida, and the stromatoporoid-type genera are presently included in quite different living orders, such as the Agelasida and Haplosclerida.

Another feature of these relationships is seen in the Upper Cretaceous chaetetid demosponge *Stromatoaxinella irregularis,* which WOOD and REITNER (1988) have described as exhibiting tracts of style-like spicule pseudomorphs; they claim the species bears close affinities in its general skeletal organization and microstructure to the middle Mesozoic stromatoporoid-like genus *Dehornella*, on the one hand, and the living genus *Acanthochaetetes* on the other, and that this forms a kind of morphological continuum. However, currently these three genera have been assigned to three different demosponge orders—West and Wood have included *Stromatoaxinella* in order Halichondrida, Wood grouped *Dehornella* in the order Agelasida, and Vacelet, West, and Willenz placed *Acanthochaetetes* in the order Hadromerida—which raises the likelihood that this morphological trend represents one or more convergences owing to their polyphyletic origins.

EXTANT CALCAREA

Descriptions of the extant hypercalcified members of the class Calcarea are also presented by Vacelet in Volume 4. These complement earlier systematic descriptions of the mainly fossil (Mesozoic) hypercalcified genera belonging to the class, which were described by FINKS and RIGBY (2004d, p. 734–762) in Volume 3 of the revised *Treatise*, Part E (Porifera).

LISTS OF POST-DEVONIAN STROMATOPOROID-LIKE TAXA

A large number of nonspicular, post-Devonian, stromatoporoid-like genera, which could not be adequately determined or placed taxonomically in any coherent scheme of classification, were also compiled in an annotated list of 65 genera by Stearn and Stock. Unfortunately, no worker currently specializes in the study of these nonspicular post-Devonian forms. Some of these genera show astrorhizae and are confirmed as sponges, but not all genera exhibit astrorhizae and continue to have problematic relationships. Family affinities, where known, are mentioned, and a list of 15 excluded genera have also been included in Volume 4.

SPHINCTOZOANS, INOZOANS, AND DISJECTOPORIDS

A review of the sphinctozoans and inozoans is presented in the next section by Senowbari-Daryan and Rigby. It complements the systematic descriptions of these hypercalcified demosponge and calcarean groups by FINKS and RIGBY (2004d), incorporated in Volume 3 of the revised *Treatise,* Part E (Porifera). Senowbari-Daryan and Rigby have determined that the sphinctozoans and inozoans are markedly polyphyletic, given that the bulk of the sphinctozoan genera (about 160) occur in 3 demosponge orders: Agelasida (48.5%), Verticillitida (= Vaceletida) (37%), and Hadromerida (11%), and the remainder are calcareans of the order Sphaerocoeliida (3.5%).

In comparison, the inozoan genera (about 100) are represented by the demosponge order Agelasida (70%) and calcarean order Stellispongiida (30%). An additional few sphinctozoan genera are attributed to other poriferan classes, the Hexactinellida, Heteractinida, and the Archaeocyatha (e.g., cosinocyathine archaeocyaths show sphinctozoan-type chambers in early stages of ontogeny [DEBRENNE & WOOD, 1990; SENOWBARI-DARYAN & GARCIA-BELLIDO, 2002a]).

The sphinctozoan morphological grade apparently developed more commonly in sponge lineages than any of the other morphological types of hypercalcified sponges, and, in consequence, was probably the least taxonomically significant morphological type. Other aspects of sphinctozoan and inozoan morphology, their classification, patterns of water circulation, paleoecology, distribution in time and space, and their roles as contributors to reefs are discussed.

The living and fossil (Cretaceous–Tertiary) chambered, nonspiculate, aragonitic hypercalcified sponge *Vaceletia* PICKETT, 1982, is of particular interest as it was originally recognized as an archetypal sphinctozoan, though first allied to calcareans, then to demosponges (VACELET, 1977b, 1979b), and even mentioned as a sole survivor from archaeocyath stock (PICKETT, 1985b). More recently, it has been placed in the demosponge family Verticillitidae STEINMANN, 1882 (see VACELET, 2002b; and FINKS & RIGBY, 2004d). However, by applying molecular-sequencing procedures and other analyses to extant specimens of *Vaceletia,* WORHEIDE (2008) has been able to demonstrate that the taxon is monophyletic and has a precise placement within the extant, nonspiculate, keratose (bath sponge) members of order Dictyoceratida MINCHIN, 1900. The connection is perhaps not surprising, given that modern demosponges can build calcareous and keratose skeletons without spicules (VACELET, 1979b). Nevertheless, the dictyoceratids have only an organic-fiber spongin skeleton, with no trace of an aragonitic skeleton like *Vaceletia.* The fossil taxa that are included in the family Vaceletiidae REITNER & ENGESER, 1985, include only nonspiculate *Vaceletia.* However, within the broader grouping of order Verticillitida TERMIER & TERMIER (in TERMIER, TERMIER, & VACHARD, 1977) (= order Vaceletida of FINKS & RIGBY, 2004d, p. 691), some of these taxa show traces of monaxon spicules—e.g., *Colospongia* LAUBE, 1865, and *Subascosymplegma* DENG, 1981—and these are now excluded from a relationship with *Vaceletia.*

One other problematical group, family Disjectoporidae TORNQUIST, 1901, is described and illustrated by Stearn as comprising 11 Permian–Triassic genera that occur as encrusting forms in reef facies. These taxa have rodlike frameworks and resemble certain living hypercalcified sponges; they are possibly related to inozoan types, but their relationships within the phylum, classified as class and order Uncertain, remains obscure.

GLOSSARY OF TERMS

All authors contributed to the comprehensive glossary of terms. This glossary is applicable to all fossil and extant hypercalcified poriferans described herein (see latter part of Volume 4).

PALEOZOIC STROMATOPOROIDEA AND PULCHRILAMINIDA

The second, major part of this Treatise revision (see first part of Volume 5) is devoted to an introduction to and systematic descriptions of the extinct, Middle Ordovician–Devonian, nonspiculate class Stromatoporoidea *sensu* NICHOLSON & MURIE, 1878, by Stearn, Webby, Nestor, Kershaw, and Stock. The group comprises characteristically large, simple, hypercalcified skeletons of laminar, domical, bulbous, or less commonly, columnar and branching shapes. Internally the skeletal material exhibits repeated growth units, either in networks of pillars and laminae (or cyst plates), or as amalgamated elements; and evidence of aquiferous systems is commonly present. The general morphological forms of the Paleozoic (Mid-Ordovician to Devonian) skeleton may be interpreted to represent a grade of construction that includes a wide range of architectural types: all the known shapes of the Paleozoic skeletons, even columnar and branching growth forms.

Stromatoporoid-grade constructions also developed for a limited time during the early Cambrian in a very small group of porous archaeocyaths (order Kazachstanicyathida KONYUSHKOV, 1967). These constructions also formed during the Jurassic and Cretaceous when another group of spiculate stromatoporoid-grade demosponges appeared (WOOD, 1999, p. 229).

Attempts to establish an ontogenetic succession using the earliest stages of Paleozoic stromatoporoid growth have not been successful. The group is indubitably poriferan, and the nearest living forms are occurrences of hypercalcified demosponges, such as *Ceratoporella, Stromatospongia,* and *Astrosclera* of the family Astroscleriidae (order Agelasida) and *Calcifibrospongia* of the family Calcifibrospongiidae (order Haplosclerida). These extant forms show stellate astrorhizal patterns as surface depressions on upper surfaces where growth has been inhibited beneath exhalant water channel-ways, as originally explained by HARTMAN and GOREAU (1970, p. 224), but it remains very doubtful that these living taxa are directly related to Paleozoic or Mesozoic stromatoporoids. The modern forms are probably merely convergently similar to the ancient forms.

The Paleozoic stromatoporoid taxa have been described and classified using as many consistently preserved morphological characters in their hypercalcified skeletons as possible, though these tend to be limited to a comparatively few internal features and the microstructures. Nevertheless this has provided a workable framework for systematizing the taxa for use in determining such topics as stromatoporoid life history, paleoecology, paleobiogeography, and biostratigraphy.

The origins of the spiculate Mesozoic stromatoporoids remain obscure, but it seems most likely they developed independently of nonspiculate Paleozoic forms, possibly from a demosponge group that was producing siliceous spicules, though they may not have hitherto produced a hypercalcified skeleton.

The Paleozoic class Stromatoporoidea has an essential unity; despite significant imperfections in the stratigraphic record, the group comprises 7 orders and a total of 125 genera that clearly exhibit an early unidirectional evolutionary trend through late Middle to Late Ordovician time, with the group tentatively appearing to be monophyletic. The origins of the earliest order, the Labechiida, remains obscure, though it seems most likely to have evolved from a noncalcified demosponge ancestor during late Mid-Ordovician. Appearances of orders Clathrodictyida and Actinostromida followed, apparently in two separate lines of descent from the Labechiida, during the Late Ordovician. Then derivation of the two other orders occurred: the Stromatoporida from the Clathrodictyida early in the Silurian, and the Syringostromatida from the Actinostromatida in the Silurian (Wenlock). The enigmatic stemlike Amphiporida is another possible offshoot from the Stromatoporida, apparently also early in the Silurian. Representatives of most of these orders, except for the Actinostromatida, then persisted to the major extinction event at the end of Devonian. The Actinostromatida definitely became extinct a little earlier, probably at the end of the Frasnian, and the Syringostromatida only has a doubtful record after the Middle Devonian, and definitely also became extinct by the end of the Devonian.

Webby introduced a new order Pulchrilaminida WEBBY, 2012a, to accommodate the small problematical group (two or three genera) of Early to Mid-Ordovician (Dapingian) reef-building taxa. The group includes forms with large, half-meter diameters; hypercalcified skeletons composed of very thin, sheetlike latilaminae. Tiny (0.5 mm tall) erect, spinose rods, resembling diagenetically replaced (spar-filled) styles protrude above each successive latilamina into overlying thin layers of mud-rock. These structures vaguely resemble the palisade spicules of ectosomal surfaces of some living demosponges (like those in the genus *Suberites* NARDO, 1833, of the hadromerid family Suberitidae SCHMIDT, 1870; see VAN SOEST, 2002a, p. 240–243). The possibly spiculate pulchrilaminids are excluded from the nonspiculate, later Mid-Ordovician to Devonian stromatoporoids, in particular from a close association with the oldest representatives of the class Stromatoporoidea NICHOLSON & MURIE, 1878, namely, members of the order Labechiida KÜHN, 1927.

ARCHAEOCYATHA, RADIOCYATHS, AND CRIBRICYATHS

A comprehensive survey of the class Archaeocyatha BORNEMANN, 1884, is presented in the second part of this *Treatise,* Revised Volume 5, by Debrenne, Zhuravlev, and Kruse. This Early Cambrian group is highly diversified (with 307 genera described); it is nonspiculate and porous, exhibiting a wide variety of skeletal structures, as well as showing differences in the style of its ontogenetic development between the various skeletal groups. The classification is determined using all available data derived from the following three morphological attributes: (1) ontogenetic succession, following heterochronic principles in order to establish the taxonomic hierarchy; (2) functional analysis to allow discrimination between genotypic and phenotypic features; and (3) homologous variability limits that exist between taxa of equivalent levels. The total dataset provides the basis for a complex set of hierarchy-based keys across all levels (orders, suborders, superfamilies, families, and genera) and the recognition of the class Archaeocyatha as a monophyletic taxon (Pierre Kruse, personal communication, April 2008). In terms of hierarchy, the features that appear ontogenetically earlier have the higher taxonomic rank: orders are based on the architecture of the cup, suborders are represented by first-order intervallar structures, superfamilies are recognized from outer wall elements, families are determined using inner wall structures, and genera are based on certain variants of wall and intervallar structures.

The archaeocyaths are recognized as the first group of hypercalcified sponges to display a modular habit, apparently developing this tendency as a part of their colonization of more active reef habitats during the Early Cambrian (WOOD, ZHURAVLEV, & DEBRENNE, 1992). The modular habit arose within the aquiferous system of the sponge organism and was subdivided into multiple functional units. A single functional unit (FRY, 1979) is represented by a number of inhalant openings that lead water to a choanocyte layer and from which exhalant canals direct water away to a single exhalant opening (osculum). In the archaeocyaths, two types of sponges developed, one as a solitary cuplike (unioscular) form and the other exhibiting a modular (multioscular) habit. According to WOOD, ZHURAVLEV, and DEBRENNE (1992), modular is the advanced condition in sponges, whereas the solitary habit is the primitive state. Over 90% of living sponges are modular, whereas archaeocyaths were most commonly represented as a mix of solitary and modular types, with the proportion of modular forms increasing through the Early Cambrian and dominant over solitary types in biohermal settings (WOOD, ZHURAVLEV, & DEBRENNE, 1992).

Archaeocyaths also exhibit a distinctive archaeocyathan grade of construction and are regarded taxonomically as representing an independent class-level taxon (clade) within the phylum Porifera. Currently, they are thought to have closer affinities to the class Demospongiae than to other living classes (DEBRENNE & ZHURAVLEV, 1994). The basic archaeocyathan architecture consists of a conical cup with porous outer and inner walls interconnected with radially arranged vertical plates (septa) and a central cavity; these may be either solitary (dominant) or exhibit a low-integration modular, branching form. A few may develop more complex modular types, such as the catenulate or pseudocerioid forms. Also, within the clade, a number of other distinctive grades of construction have been derived from the basic archaeocyathan morphological type. These comprise thalamid (= sphinctozoan), stromatoporoid, chaetetid, and syringoid architectures that each developed within one specific archaeocyath order or suborder: respectively, the order Capsulocyatha, the order Kazachstanicyathida, the suborder Dictyofavina, and the suborder Syringocnemina. Consequently, these particular grades of construction have real taxonomic significance in identifying the particular higher-level groups within the class Archaeocyatha. Whereas the thalamid architecture of the Capsulocyatha is developed only in solitary forms, the architectures represented in the other three higher-level groups are associated with both solitary and variably integrated modular forms.

Finally, there are two small sections that deal with minor, problematic, Early Cambrian groups: the Radiocyaths and related forms (8 genera), contributed by Kruse, Zhuravlev, and Debrenne; and the Cribricyaths and related forms (16 genera) presented by Zhuravlev and Kruse. Also Debrenne, Zhuravlev, and Kruse provide lists of the Archaeocyatha Nomina Dubia (40 genera); Archaeocyatha and Cribricyatha Nomina Nuda (20 genera); and a list of taxa not Archaeocyatha, Cribricyatha, or Radiocyatha (16 genera).

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In preparing these Revised Volumes 4 and 5 of the *Treatise,* Part E on the Porifera, I have been assisted by a number of specialists, virtually all of them invited in the early years of the project (late 1980s to early 1990s) by the previous *Treatise* Director and Editor, the late Roger L. Kaesler. At the outset, it was our intention only to survey the stromatoporoids, chaetetids, and related living hypercalcified sponge taxa (members of classes Demospongiae and Calcarea with spicules and hypercalcified calcareous basal skeletons), with a team comprising Jean Vacelet and the late Willard Hartman for the living forms, Ron West for the fossil chaetetids, Rachel Wood for the Mesozoic stromatoporoids, and Colin Stearn, Barry Webby, Heldur Nestor, Carl Stock, and Stephen Kershaw for the Paleozoic stromatoporoids. By 1995, however, it was considered desirable to widen the scope of the study to include all the main hypercalcified sponge groups. Consequently, Francoise Debrenne, Pierre Kruse, and Andrey Zhuravlev were added to the team to cover the archaeocyaths (*s.l.*), and Baba Senowbari-Daryan and the late J. Keith Rigby Sr. joined to contribute an introductory section on the sphinctozoan and inozoan architectures of the classes Demospongiae and Calcarea, since the FINKS and RIGBY (2004) of the revised *Treatise*, Part E (Porifera, vol. 3) treated only the systematic descriptions of these groups. Finally, Phillippe Willenz joined as an author early in 2005 to assist in the completion of the section on living hypercalcified sponges with Jean Vacelet and the late Willard Hartman. In my role as Cooordinating Author, I thank them for providing the high-quality, scholarly works that represent arguably the most comprehensive coverage of known ancient and modern hypercalcified sponges ever assembled. I appreciate their maintenance

of patience and faith in the project, their efforts in preparing digitized images of high quality, and perserverance in a long and, at times, thankless task of getting permissions to use copyrighted images. Ron West, Pierre Kruse, and Jean Vacelet, in particular, helped in coordination tasks and review of their sections of the *Treatise* work.

Roger Kaesler, in his role as Editor for more than a decade and a half, remained very supportive and encouraging through all stages of our *Treatise* work, monitoring closely the progress of preparation of our manuscripts and organization of illustrations, until his health began to fail in the latter part of 2005. He always responded in detail to the matters raised by me and other authors and invariably offered helpful advice as to how to solve a particular problem. He took a close personal interest in our work, and shared with us the view, perhaps encouraged by one or two of his departmental colleagues, that carbonate sedimentologists and others studying ancient reefs really needed to have access to such an authoritative, up-to-date *Treatise* volume on the problematical hypercalcified sponge groups. I am grateful to have had the opportunity to work with Roger and much enjoyed the close and cordial relationships we had for so long. Roger L. Kaesler retired in November 2006, and sadly passed away in the following August.

The manuscript and illustrative material was submitted to the *Treatise* office in parts through 2006 and 2007 and has since been processed through the various editorial stages with assistance of the *Treatise* staff. Bruce Lieberman, who acted as Interim Director for a short time in 2006, and then Paul Selden who commenced as new Director and Editor of the *Treatise* in January 2007, have facilitated this process. We are particularly appreciative to them, and to all other members of the Palaeontological Institute staff who have continued to support and help us, especially Jill Hardesty, who as Assistant Editor largely bore most of the responsibility for filing and maintaining our manuscript material after it was submitted. We offer a special thanks to her, for patiently answering our many queries relating to the project during this period through 2007 to 2008—all sorts of editorial matters and information about the work—and she has undertaken a large amount of editorial work in proofing the online chapters of individual sections from May 2009 to mid-2013.

Paul Selden has been largely responsible for an expansion of the Paleontological Institute web site and the development of excellent online facilities that have included the establishment of a new electronic journal called the *Treatise Online.* This latter has permitted us to publish the various sections of our compiled *Treatise* volume—a total of 38 individual chapters that commenced in 2009 and continued through 2010 to early 2013—in advance of this final publication of the consolidated, large volume: the hard copy, blue-covered compendium, which is the *Treatise on Invertebrate Paleontology,* Part E, Revised, Porifera, Volumes 4 and 5, Hypercalcified Porifera. Jill Hardesty, who became the Deputy Director of the Paleontological Institute and Assistant Editor of the *Treatise* near the end of 2009, was the driving force in getting these chapters into publication in the online series, and we thank her most sincerely for that, and all the other *Treatise* staff in Lawrence, Kansas, for their efforts on our behalf. The final bundled version of Hypercalcified Porifera in two *Treatise* volumes was published this year (early in 2015), bringing the long-standing work program of the authors to an end. We are grateful for the continued editorial support of Paul Selden, Jill Hardesty, Elizabeth Brosius, Denise Mayse, and other staff of the Paleontological Institute.

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[1] Willard Hartman, along with Thomas Goreau, confirmed in the early 1970s the presence of relict stocks of living hypercalcified sponges in reef-type habitats of the Caribbean and of the tropical Pacific. Important reinterpretations of problematic fossil groups emerged from these findings.

[2] J. Keith Rigby Sr., was a dedicated, enthusiastic, and highly productive researcher on fossil sponges. Over nearly six decades from the late 1950s, he published more than 140 peer-reviewed papers and monographs on fossil sponges, including descriptions of numerous new fossil assemblages and taxa from many parts of the world and through all periods of the Phanerozoic, from Cambrian to Quaternary. As a Coordinating Author, he completed the compilation of two *Treatise* volumes dealing with fossil sponges, published in 2003 and 2004.

EDITORIAL PREFACE

PAUL A. SELDEN

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, Porifera, Revised, Hypercalcified Porifera, Volumes 4 and 5, continues this trend and has been prepared by a team of specialists, guided by Coordinating Author Barry D. Webby. 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. Among other requirements, the revised *Code* is clear in Chapter 14 that the type genus of family-level taxa must be specified. In this volume we have continued the practice that has characterized most previous volumes of the *Treatise*, namely that the type genus of all family-level taxa is the first listed and diagnosed. 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 family-group. 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, species-group 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 genus-group 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 stemof 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 lower-rank 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 Zoological 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, thoroughly discussed the proposals for regulating suprafamilial nomenclature, as well as many others advocated for inclusion in the new *Code* or recommended for exclusion from it. A decision 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, respectively, are named from the same type genus, since one is not considered to be transferable to the other (*e.g.,* suborder Bellerophontina ULRICH & SCOFIELD, 1897 is not coordinate with superfamily Bellerophontacea 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 family-group level wherever they do not infringe on taxonomic freedom and long-established usage.

4. Authors who accept priority as a determinant in nomenclature of a suprafamilial taxon may change its assigned rank at will, with or without modifying the terminal letters of the name, but such 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 KOBAYASHI, 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 Peck, 1943, p. 465; *emend.,* Peck in Moore & Teichert, 1978, p. 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; =*Lonsdaleia 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 except that diacritical marks have been removed. Where other mandatory changes are required, 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.

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

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. 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 USSR, 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 THESE VOLUMES

Authorship entails both credit and responsibility. As the knowledge of paleontology grows and paleontologists become more specialized, preparation of *Treatise* volumes must necessarily involve larger and larger teams of researchers, each focusing on increasingly narrow aspects of the higher taxon under revision. In these two volumes, we have taken special pains to acknowledge authorship of small subsections. Readers citing the volume are encouraged to pay close attention to the actual authorship of a section or subsection.

Stratigraphic ranges of taxa listed in the systematic descriptions herein 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, Jill Hardesty, and Liz Brosius have faced admirably the formidable task of moving these volumes through the various stages of editing and into production. In this they have been ably assisted by other members of the editorial team, including Denise Mayse, Office

Manager, with her excellent attention to detail while checking the references and various other items, and Mike Cormack with his outstanding computer skills. Brittany Varnado, student assistant, helped with figure preparation and checking and formatting references.

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, Richard A. Robison, and the late Roger L. Kaesler. 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.

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Paul A. Selden
Lawrence, Kansas
December 12, 2014

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 (any provincial terms are presented in brackets in taxonomic descriptions). They are adapted from the International Stratigraphic Chart, compiled by the International Commission on Stratigraphy (ICS; ©2013).

- **Cenozoic Erathem**
  - **Quaternary System**
    - Holocene Series
    - Pleistocene Series
  - **Neogene System**
    - 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 Series
      - Gzhelian Stage
      - Kasimovian Stage
      - Moscovian Stage
      - Bashkirian Stage
    - Mississippian Series
      - Serpukhovian Stage
      - Visean Stage
      - Tournaisian Stage
  - **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
    - Series 3
    - Series 2
    - Terreneuvian Series

REPOSITORIES AND THEIR ABBREVIATIONS

Abbreviations and locations of museums and institutions holding type material, which are used throughout the systematic sections of Volumes 4 and 5, are listed below.

AM, AM.F, AM.FT: Australian Museum (incorporating former Sydney University Palaeontology type collection; see SUP), Sydney, New South Wales, Australia; note that type collections are catalogued using AM.F for specimens and AM.FT for thin sections

AMNH: American Museum of Natural History, New York, USA

BGU: Ministry of Natural Resources and Environmental Protection of Republic of Buryatia (formerly Buryatian Geological Survey), Ulan-Ude, Republic of Buryatia, Russia

BMNH: see NHM

BSP: Bayerische Staatssammlung für Paläontologie und historische Geologie, München, Germany

CE,: Departamento de Paleontología, Universidad Complutense de Madrid, Madrid, Spain

CIGMR: Chengdu Institute of Geology and Mineral Resources, Chengdu, China

CNIGR, TsNIGRm: Central Geological-Exploring Scientific-Research Museum named after F. N. Chernyshev of the All Russian Geological Institute (VSEGEI) of the Ministry of Natural Resources of the Russian Federation, St. Petersburg (formerly Leningrad), Russia; note that TsNIGRm is the newer transliteration

CORD-PZ: Universidad Nacional de Córdoba, Argentina

CSGM, SOAN, TsGM, TsSGM: Central Siberian Geological Museum of the United Institute of Geology, Geophysics, & Mineralogy (OIGGM), Siberian Branch, Russian Academy of Sciences, Akademgorodok, Novosibirsk, Russia; note that there are collections in other centers in Siberia where the SOAN (Siberian Branch of Academy of Sciences) has existed; TsSGM is the newer transliteration

CSGP: Instito Geologico e Minero, Geológicos de Portugal, Lisbon, Portugal

DPI: Geological Museum, Donetsk National Polytechnic University (formerly Donetsk Polytechnic Institute), Donetsk, Ukraine

DVGU: Committee of Natural Resources on the Khabarovsk Region (formerly Far East Territorial Geological Survey, PGO Dal'geologiya) of the Ministry of Natural Resources of the Russian Federation, Khabarovsk, Russia

FMNH: Field Museum of Natural History, Chicago (formerly Walker Museum, University of Chicago), USA

FSL (F.S.L.): Department of Earth Sciences, Faculté des Sciences de Lyon, Université Claude Bernard, Lyon I, Villeurbanne, France

GFCL: Faculté Libre des Sciences de Lille, Université catholique de Lille, France

GML: Geiseltalmuseum Martin Luther, University of Halle, Halle, Germany

GMU: Geological Museum of the State Committee of the Republic of Uzbekistan on Geology and Mineral Resources, Tashkent, Uzbekistan

GNS, IGNS: GNS Science (formerly the Institute of Geological and Nuclear Sciences, and New Zealand Geological Survey, Department of Scientific and Industrial Research), Lower Hutt, New Zealand

GSC: Geological Survey of Canada, Ottawa, Ontario, Canada

GSWA: Geological Survey of Western Australia, Perth, Western Australia, Australia

HBOI: Harbor Branch Oceanographic Institute at Florida Atlantic University, Fort Pierce, Florida, USA

HGT: Tunisian material in H. & G. Termier collection, Muséum National d'Histoire Naturelle, Paris, France; see MNHN

IG: Institute of Geology, Academia Sinica, Beijing, China

IGD: Institute of Geology, Dushanbe, Tadjikistan

IGPS: see TUM

IGNS: see GNS

IGTUT, IGTTU: Institute of Geology, Tallinn University of Technology, Tallinn, Estonia

IPB, PIUB, GPIBo: Institut für Paläontologie, Universität Bonn, Bonn, Germany

IPE: Institut für Paläontologie, Universität Erlangen, Erlangen, Germany; see RA, TTR

IPFUB: Institut für Paläontologie, Freie Universität, Berlin, Germany

IPUM: Instituto di Palaeontologia, Università di Modena, Modena, Italy

IRScNB, RBINSc: Institut Royal Sciences Naturelles Belgique, Brussels (including Lecompte and Willenz collections), Brussels, Belgium

KGU: Siberian Federal University (formerly Krasnoyarsk State University), Krasnoyarsk, Russia

KUMIP: Museum of Invertebrate Paleontology, University of Kansas, Lawrence, Kansas, USA

LGU: St. Petersburg State University, Museum in Faculty of Geology (formerly Leningrad State University), St. Petersburg, Russia

MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA

MIGUP: Museum Instituto di Geologia, Università di Padova, Padova, Italy

MMF: Palaeontological Collection, Geological Survey of New South Wales (formerly Geological & Mining Museum), Londonderry, New South Wales, Australia

MNHB: Museum für Naturkunde der Humboldt-Universität zu Berlin, Geologisch-Paläontologisches Museum, Berlin, Germany

MNHN: Muséum National d'Histoire Naturelle, Paris, France

MUO: Miami University of Ohio, Miami, Ohio, USA

MV: see NMV

NHM: The Natural History Museum, London (formerly BMNH, British Museum, Natural History, London), London, United Kingdom

NIGP, NIGPAS: Nanjing Institute of Geology and Palaeontology, Academia Sinica, Nanjing, China

NMB: Naturhistorisches Museum zu Basel, Basel, Switzerland

NMV, MV: National Museum of Victoria, Melbourne, Victoria, Australia

NYSM: New York State Museum, Albany, USA

PGU: Committee of Natural Resources on the Primor'ye Region (formerly Primor'ye Territorial Geological Survey) of the Ministry of Natural Resources of the Russian Federation, Vladivostok, Russia

PIN: Palaeontological Institute, Russian Academy of Sciences, Moscow, Russia

PIUB: See IPB

PMO: Paleontologisk Museum, University of Oslo, Norway

PU, PUC: Princeton University Collections, Princeton, New Jersey, USA; note that a collection of archaeocyaths donated by the Bedfords were previously housed here, but now have been transferred to the USNM

PUM: Geology, Beijing (formerly Peking) University, Beijing, China

QMF: Queensland Museum, South Brisbane, Queensland, Australia (including the paleontological collections of the University of Queensland, UQF)

RA: Argentine Precordillera type and figured specimens in the Keller & Flügel collection are held in Erlangen; see IPE

RBINSc: see IRScNB

RIGMR: Laboratory of Palaeontology & Stratigraphy of Research Institute of Geology & Mineral Resources, Thanh Xuan, Ha Noi, Vietnam

RM, SCRM (Stearn collection): Redpath Museum, McGill University, Montreal, Canada

ROM: Royal Ontario Museum, Toronto, Ontario, Canada

SAM, SAM.P: South Australian Museum, Adelaide, South Australia, Australia

SAM(C): South African Museum, Cape Town, South Africa

SCRM: See RM

SGPIH: Geological-Paleontological Institute, Universität Hamburg, Hamburg, Germany

SMF, SM: Senckenberg Museum, Frankfurt am Main, Germany

SMNH: Naturhistorisk Riksmuseet, Stockholm, Sweden

SNIIGGiMS: Federal State Bureau "Siberian Scientific Research Institute of Geology, Geophysics & Mineral Resources" of the Russian Federation, Krasnyy Prospect, Novosibirsk, Russia; note that some of these collections have been transferred to CSGM (=TsSGM)

SOAN: Siberian Branch of Academy of Science; note that a number of divisions of this organization have maintained paleontological collections in Krasnoyarsk, Irkutsk, and Ulan-Ude, as well as Novosibirsk, Russia; some of the type material may also have been transferred to the CSGM (=TsSGM)

SUP: Palaeontological collections, University of Sydney, New South Wales, Australia; see AM

SRPMH: Roemer-Pelizaeus Museum, Hildesheim, Germany

SSPHG: Staatliches Sammlung für Paläontologie und Historische Geologie, München, Germany

TPI: Tomsk Polytechnic University, Tomsk, Russia (formerly Tomsk Polytechnic Institute)

TsNIGRA, TsNIGRm, TsNIGRM: see CNIGR

TsSGM: see CSGM

TTR: Turkish type specimens from Tilkideligi Tepe in Cremer collection are held in Erlangen; see IPE

TUM, IGPS: Tohoku University Museum, Sendai, Japan (formerly IGPS, Institute of Geology & Paleontology of Tohoku University)

UAM: University of Alaska Museum, Fairbanks, USA

UCMP: University of California, Museum of Paleontology, Berkeley, California, USA

UG: Universität Graz, Graz, Austria

UGM: Urals Geological Museum of the Urals State Mining University, Ekaterinburg (=Sverdlovsk), Russia

UHR: Hokkaido University, Sapporo, Japan

UM: Paläontologische Sammlung, Geologisch-Paläontologisches Institut, Universität Münster, Münster, Germany

UMMP: Paleontology Museum, University of Michigan, Ann Arbor, Michigan, USA

UQF: University of Queensland, Department of Geology, Brisbane, Queensland, Australia; paleontological collections have now been transferred to the Queensland Museum; see QMF

USNM: National Museum of National History, Smithsonian Institution, Washington, D.C., USA (formerly United States National Museum)

UTGD: University of Tasmania Geology Department, Hobart, Tasmania, Australia

UWA: University of Western Australia, Nedlands, Western Australia, Australia

VNIGRI: All-Union Scientific-Research Geological-Exploring Institute of the Ministry of Natural Resources of the Russian Federation, St Petersburg, Russia

VSEGEI: All-Russian Geological Institute of the Ministry of Natural Resources of the Russian Federation, Sredniy Prospect, St. Petersburg, Russia; note that relevant material has largely been incorporated into museum repositories such as CNIGR (more recently transliterated asTsNIGRm)

VU: Museum of Geology, Victoria University of Wellington, Wellington, New Zealand

XB: Palaeontological Collections of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, Xi'an, Shaanxi Province, China

YaFAN: Museum of Geology of the Institute of Geology of Diamonds and Precious Metals of the Yakutian Scientific Centre of the Siberian Branch of the Russian Academy of Sciences, Yakutsk, Republic of Sakha (Yakutia), Russia

YPM: Yale University, Peabody Museum of Natural History, New Haven, Connecticut, USA; stromatoporoid types of Galloway and St. Jean now housed in the Peabody Museum

ZPAL: Institute of Palaeobiology, Polish Academy of Sciences, Warsaw, Poland

ZSGGU: Closed Company "West Siberian State Geological Trust," PGO Zapsibgeologiya, Novokuznetsk, Kemerova Region, Russia

OUTLINE CLASSIFICATION AND RANGES OF TAXA OF THE HYPERCALCIFIED PORIFERA

BARRY D. WEBBY, Compiler

The outline classification presented below is of fossil and living hypercalcified sponges treated in these volumes. It summaries taxonomic relationships and presents stratigraphic ranges of these supragenic taxa, following best possible correlations. As far as possible, the ranges are are based on the International Stratigraphic Chart, compiled by the International Commission on Stratigraphy (ICS; COHEN & others, 2013).

The presentation is as unified as possible and comprises all the suprageneric divisions treated in these volumes, as well as a number of asterisked family groupings that were listed in the review-style section on chambered sphinctozoan and non-chambered inozoan hypercalcified sponges (see p. 387–395). These latter groups were described previously by FINKS and RIGBY (2004d, p. 585–764) in the *Treatise, Part E, Revised,* Volume 3, and they are shown in this listing as either sphinctozoan skeletal types (denoted by single asterisks) or inozoan types (with double asterisks). Also one family, the Maeandrostiidae, exhibits transitional features between the above-mentioned two skeletal types, and this is shown by a triple asterisk. The fossil orders Stellispongiida and Sphaerocoeliida are included with the Subclass Calcaronea following FINKS and RIGBY (2004d, p. 737–752), rather than in a grouping with subclass Calcinea as preferred by Senowbari-Daryan and Rigby (see p. 387, 391, 392, 394, 395).

In FINKS and RIGBY's (2004d) systematic descriptions on hypercalcified sponges, different morphological types can be distinguished, as follows: (1) inozoan-type morphologies in agelasid demosponges (p. 594–644) as well as in stellispongiid calcareans (p. 738–750); (2) sphinctozoan-type morphologies occurring in a range of agelasid, verticillitid, and hadromerid demosponge orders (p. 646–734) and the sphaerocoeliid calcareans (p. 750–752); and (3) both inozoan- and sphinctozoan-type morphologies developing apparently only in the agelasid demosponge family Maeandrostiidae (p. 644–646).

Largely as a consequence of the strong faunal provincialism, the archaeocyathan representatives have proved difficult to assign within formalized stratigraphic subdivisions of the Cambrian Period. At present only half of the proposed four global Series have been formally named, and five of the ten Stage divisions have not been properly ratified. The undefined subdivisions are presently associated with an interval spanning the "upper-lower" to "lower-middle" parts of the Cambrian, and this includes sequences with the most varied archaeocyathan assemblages. Consequently, Debrenne, Zhuravlev, and Kruse (see p. 909–912) have outlined a biostratigraphic scheme that employs the Siberian archaeocyathan zonal succession in conjunction with the regional stage nomenclature for Siberia. The four Cambrian regional stages are, in ascending order, the Tommotian, Atdabanian, Botomian and Toyonian, and these more or less equate with the largely unnamed "upper-lower" to "lower-middle" Cambrian interval—that is, through the upper part of the Terreneuvian Series (Stage 2 = Tommotian), to the undescribed Series 2, which comprises the Stage 3 (=Atdabanian to early Botomian) and Stage 4 (=late Botomian to Toyonian) interval. The regional units have been further subdivided using the archaeocyathan zonation and identified with four named Tommotian zones (Tom.1–4), four named Atdabanian zones (Atd.1–4), three (only the lowest one named) Botomian zones (Bot.1–3) and three (only the middle zone named) Toyonian, zones (Toy.1–3).

Note also that recent results of rDNA sequencing of the eponymous living genus *Vaceletia* of the family Vaceletiidae by WÖRHEIDE (2008) seems to confirm that this chambered genus is a keratose sponge, and that the group should be transferred to the demosponge Order Dictyoceratida MINCHIN, 1900, from its previous placement within the Order Verticillitida TERMIER & TERMIER in TERMIER, TERMIER, & VACHARD, 1977 (see discussion on p. 273–277).

Phylum Porifera Grant, 1836. *?Cryogenian, Cambrian–Holocene.*
Class Demospongiae Sollas, 1885. *?Silurian, Middle Devonian–Holocene.*
Order Hadromerida Topsent, 1894. *?Silurian, Middle Devonian–Holocene.*
Family Acanthochaetetidae Fischer, 1970. *Upper Jurassic–Holocene.*
Family Suberitidae Schmidt, 1870. *?Silurian, Middle Devonian–Upper Cretaceous (Coniacian).*
Family Spirastrellidae Ridley & Dendy, 1886. *Lower Cretaceous (Albian).*
*Family Celyphiidae de Laubenfels, 1955. *Permian (Guadalupian)–Triassic.*
*Family Ceotinellidae Senowbari-Daryan in Flügel & others, 1978. *Triassic (Ladinian–Carnian).*
*Family Polysiphonidae Girty, 1909. *Permian (Guadalupian)–Triassic.*
Order Chondrosida Boury-Esnault & Lopes, 1985. *Lower Cretaceous (Albian).*
Family Chondrillidae Gray, 1872. *Lower Cretaceous (Albian).*
Order Poecilosclerida Topsent, 1928. *Lower Jurassic–Holocene.*
Family Merliidae Kirkpatrick, 1908. *Lower Jurassic–Holocene.*
Order Halichondrida Gray, 1867. *Triassic–Holocene.*
Family Uncertain. *Upper Triassic–Upper Cretaceous.*
Order Agelasida Hartman, 1980b. *Upper Permian–Holocene.*
Family Astroscleridae Lister, 1900. *Upper Permian–Holocene.*
Family Milleporellidae Yabe & Sugiyama 1935. *Upper Triassic–Eocene.*
Family Actinostromariidae Hudson, 1955c. *Upper Jurassic–Upper Cretaceous.*
Family Actinostromarianinidae Wood, 1987. *Upper Jurassic.*
Family Uncertain. *Triassic (Carnian–Norian)–Jurassic (lower Kimmeridgian).*
*Family Angullongiidae Webby & Rigby, 1985. *Upper Ordovician (Katian).*
*Family Phragmocoeliidae Ott, 1974. *Lower Devonian (Lochkovian)–Triassic (Carnian).*
*Family Intrasporeocoeliidae Fan & Zhang, 1985. *Permian (Guadalupian-Lopingian).*
*Family Cryptocoeliidae Steinmann, 1882. *Silurian (Ludlow)–upper Triassic.*
*Family Palermocoeliidae Senowbari-Daryan, 1990. *upper Triassic.*
*Family Thaumastocoeliidae Ott, 1967. *Upper Ordovician–Triassic (Norian).*
*Family Amphorithalamiidae Senowbari-Daryan & Rigby, 1988. *Permian (Lopingian).*
*Family Polyedridae Termier & Termier in Termier & others, 1977. *Permian (?Arkinskian–Lopingian).*
*Family Aphrosalpingidae Myagkova, 1955. *Upper Ordovician, Silurian (Ludlow) Carboniferous (Pennsylvanian, Permian (Lopingian), Triassic.*
*Family Glomocystospongiidae Rigby, Fan, & Zhang, 1989. *Permian (Lopingian).*
*Family Sebargasiidae de Laubenfels, 1955. *?Ordovician, Carboniferous–Triassic.*
*Family Olangocoeliidae Bechstadt & Brandner, 1970. *middle Triassic.*
*Family Cliefdenellidae Webby, 1969. *Upper Ordovician (Katian).*
*Family Guadalupiidae Girty, 1908. *Carboniferous–Triassic (Norian).*
*Family Tabasiidae Senowbari-Daryan, 2005. *Triassic.*
**Family Catenispongiidae Finks, 1995. *Permian (Artinskian)–Triassic.*
**Family Virgolidae Termier & Termier in Termier & others, 1977. *Permian (Kungurian), Triassic.*
**Family Sphaeropontiidae Rigby & Senowbari-Daryan, 1996. *Permian (Lopingian).*
**Family Exotubispongiidae Rigby & Senowbari-Daryan, 1996. *Permian (Lopingian).*
**Family Sestrostomellidae de Laubenfels, 1955. *Triassic–Lower Cretaceous.*
**Family Pharetrospongiidae de Laubenfels, 1955. *Triassic (Carnian)–Cretaceous.*
**Family Auriculospongiidae Termier & Termier in Termier & others, 1977. *Permian (Asselian, Guadalupian–Lopingian).*
**Family Stellispongiellidae Wu, 1991. *Permian (Guadalupian)–Triassic.*
**Family Preperonidellidae Finks & Rigby, 2004c. *Upper Ordovician–upper Triassic.*
**Family Fissispongiidae Finks & Rigby, 2004c. *Devonian (Eifelian)–Permian (Roadian, or early Guadalupian).*
***Family Maeandrostiidae Finks, 1971. *Carboniferous (middle Pennsylvanian)–Triassic.*
Order Haplosclerida Topsent, 1928. *Upper Carboniferous–Holocene.*
Family Calcifibrospongiidae Hartman, 1979. *Holocene.*
Family Euzkadiellidae Reitner, 1987a. *Lower Cretaceous.*
Family Newellidae Wood, Reitner, & West 1989. *Upper Carboniferous (middle Pennsylvanian).*
Order Dictyoceratida Minchin, 1900. *?Cretaceous, Eocene–Holocene.*
Family Vaceletiidae Reitner & Engeser, 1985. *?Cretaceous, Eocene–Holocene.*
Order Verticillitida Steinmann, 1882. *?lower Cambrian, Cretaceous, ?Cenozoic.*
*Family Solenolmiidae Engeser, 1986. *lower Cambrian–Triassic, ?Jurassic.*
*Family Colospongiidae Senowbari-Daryan, 1990. *lower Cambrian–Triassic.*
*Family Gigantothalamiddae Senowbari-Daryan, 1994. *upper Triassic (Norian).*
*Family Tebagathalamiidae Senowbari-Daryan & Rigby, 1988. *Permian–upper Triassic.*
*Family Annaecoeliidae Senowbari-Daryan, 1978. *upper Triassic.*
*Family Cheilosporitiidae Fischer, 1962. *Triassic (Carnian–Rhaetian).*

*Family Salzburgiidae Senowbari-Daryan & Schafer, 1979. *Permian–Triassic (Rhaetian).*
*Family Cribrothalamiidae Senowbari-Daryan, 1990. *Triassic (Norian–Rhaetian).*
*Family Verticillitidae Steinmann, 1882. *Permian (Guadalupian)–Upper Cretaceous, Paleogene (Eocene).*
Order Uncertain.
Family Burgundiidae Dehorne, 1920. *Upper Jurassic–Lower Cretaceous.*
Family Uncertain. *Upper Triassic, Jurassic, ?Lower Cretaceous, Miocene.*

Class Calcarea Bowerbank, 1864. *?Cambrian, ?Carboniferous ?Permian, ?Jurassic, Cretaceous–Holocene.*
Subclass Calcinea Bidder, 1898. *Holocene.*
Order Murrayonida Vacelet, 1981. *Holocene.*
Family Murrayonidae Dendy & Row, 1913. *Holocene.*
Family Paramurrayonidae Vacelet, 1967a. *Holocene.*
Subclass Calcaronea Bidder, 1898. *?Jurassic, Cretaceous–Holocene.*
Order Lithonida Vacelet, 1981. *?Jurassic, Cretaceous–Holocene.*
Family Minchinellidae Dendy & Row, 1913. *?Jurassic, Cretaceous–Holocene.*
Order Stellispongiida Finks & Rigby, 2004c. *Permian–Holocene.*
**Family Stellispongiidae de Laubenfels, 1955. *Permian–Neogene (Miocene).*
Order Sphaerocoeliida Vacelet, 1979b. *Permian–Cretaceous (Cenomanian).*
*Family Sphaerocoeliidae Steinmann, 1882 *Permian–Cretaceous (Cenomanian).*
Order Baerida Borojevic, Boury-Esnault & Vacelet, 2000. *Pleistocene–Holocene.*
Family Petrobionidae Borojevic, 1979. *Pleistocene–Holocene.*
Family Lepidoleuconidae, Vacelet 1967a. *Holocene.*

Class and Order Uncertain (?Demospongiae or ?Calcarea).
Family Disjectoporidae Tornquist, 1901. *Permian–Triassic.*

Class Heteractinida Hinde, 1887. *lower Cambrian–Permian.*
Order Octactinellida Hinde, 1887. *lower Cambrian–Permian.*
?*Family Nuchidae Pickett, 2002. upper lower–middle Cambrian.

Class Stromatoporoidea Nicholson & Murie, 1878. *Middle Ordovician (Darriwilian)–Lower Carboniferous (Serpukhovian), ?Triassic.*
Order Labechiida Kühn, 1927. *Middle Ordovician (Darriwilian)–Upper Devonian, ?Triassic.*
Family Rosenellidae Yavorsky in Khalfina & Yavorsky, 1973. *Middle Ordovician (Darriwilian)–Upper Devonian.*
Family Labechiidae Nicholson, 1879b. *Middle Ordovician (Darriwilian)–Upper Devonian.*
Family Stromatoceriidae Bogoyavlenskaya, 1969b. *Upper Ordovician (Sandbian–Katian).*
Family Platiferostromatidae Khalfina & Yavorsky, 1973. *Silurian (Llandovery)–Upper Devonian (Famennian).*
Family Stylostromatidae Webby, 1993. *Middle Ordovician (Darrwilian)–Upper Devonian (Famennian).*
Family Aulaceratidae Kühn, 1927. *Middle Ordovician (Darriwilian)–Upper Devonian (Famennian).*
Family Lophiostromatidae Nestor, 1966a. *Middle Ordovician (Darriwilian)–Upper Devonian (Frasnian), ?Triassic.*
Order Clathrodictyida Bogoyavlenskaya, 1969b. *Upper Ordovician (Katian)–Lower Carboniferous (Serpukhovian).*
Family Clathrodictyidae Kühn, 1939a. *Upper Ordovician (Katian)–Lower Carboniferous (Serpukhovian).*
Family Actinodictyidae Khalfina & Yavorsky, 1973. *Upper Ordovician (Katian)–Lower Devonian (Emsian).*
Family Gerronostromatidae Bogoyavlenskaya, 1969b. *Silurian (Llandovery)–Upper Devonian (upper Famennian).*
Family Tienodictyidae Bogoyavlenskaya, 1965c. *Silurian (Llandovery)–Upper Devonian (Frasnian).*
Family Anostylostromatidae Nestor, 2011. Silurian (Ludlow)–Upper Devonian (upper Famennian).
Family Atelodictyidae Khalfina, 1968a. *Lower Devonian–Upper Devonian (upper Famennian).*
Order Actinostromatida Bogoyavlenskaya, 1969b. *Upper Ordovician (Katian)–Upper Devonian (Frasnian).*
Family Actinostromatidae Nicholson, 1886a. *Lower Silurian (Llandovery)–Upper Devonian (Frasnian).*
Family Pseudolabechiidae Bogoyavlenskaya, 1969a. *Lower Silurian (Llandovery)–Upper Silurian (Pridoli).*
Family Plumataliniidae Bogoyavlenskaya, 1969b. *Upper Ordovician (Katian).*
Family Actinostromellidae Nestor, 1966a. *Middle Silurian (Wenlock)–Lower Devonian (Lochkovian).*
Family Densastromatidae Bogoyavlenskaya, 1974. *Lower Silurian (Llandovery)–Lower Devonian (Lochkovian).*
Order Stromatoporellida Stearn, 1980. *Silurian (Pridoli)–Upper Devonian (Famennian).*
Family Stromatoporellidae Lecompte, 1951 in Lecompte, 1951–1952. *Silurian (Wenlock)–Devonian (Frasnian, ?upper Famennian).*
Family Trupetostromatidae Germovsek, 1954. *Silurian (Pridoli)–Upper Devonian (Famennian).*
Family Idiostromatidae Nicholson, 1886a. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian).*
Order Stromatoporida Stearn, 1980. *Silurian (upper Llandovery)–Upper Devonian (Frasnian).*
Family Stromatoporidae, Winchell, 1867. *Silurian (upper Llandovery)–Upper Devonian (Frasnian).*
Family Ferestromatoporidae Khromykh, 1969. *Lower Devonian (?Emsian), Middle-Upper Devonian (Frasnian).*
Family Syringostromellidae Stearn, 1980. *Silurian (upper Llandovery–Upper Devonian (Frasnian).*

- Order Syringostromatida Bogoyavlenskaya, 1969b. *Silurian (Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Famennian).*
  - Family Coenostromatidae Waagen & Wentzel, 1887. Silurian *(Pridoli)–Upper Devonian (Frasnian).*
  - Family Parallelostromatidae Bogoyavlenskaya, 1984. Silurian *(Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Frasnian).*
  - Family Stachyoditidae Khromykh, 1967. *Lower Devonian (?Lochkovian), Middle Devonian (Eifelian)–Upper Devonian (Frasnian, ?Famennian).*
- Order Amphiporida Rukhin, 1938. *?middle Silurian, upper Silurian (Ludlow)–Upper Devonian (Famennian).*
  - Family Amphiporidae Rukhin, 1938. *?middle Silurian, upper Silurian (Ludlow)–Upper Devonian (Famennian).*
- Order and Family Uncertain. *Upper Ordovician (Katian), middle Silurian–Upper Devonian (upper Famennian).*

- Class Uncertain
  - Order Pulchrilaminida Webby, 2012a. *Lower Ordovician (upper Tremadocian)–Middle Ordovician (lower Darriwilian).*
    - Family Pulchrilaminidae Webby, 1993. *Lower Ordovician (upper Tremadocian–Middle Ordovician (lower Darriwilian).*

- Class Archaeocyatha Bornemann, 1884. *Cambrian (Terreneuvian–Furongian).*
  - Order Monocyathida Okulitch, 1935b. *lower Cambrian (Tom.1–Bot.3).*
    - Family Monocyathidae R. Bedford & W. R. Bedford, 1934. *lower Cambrian (Tom.1–Bot.3).*
    - Family Palaeoconulariidae Chudinova 1959. *lower Cambrian (Atd.4–Bot.3).*
    - Family Tumuliolynthidae Rozanov in Rozanov & Missarzhevskiy, 1966. *lower Cambrian (Tom.2–Bot.3).*
    - Family Sajanolynthidae Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1).*
    - Family Globosocyathidae Okuneva, 1969. *lower Cambrian (Atd.2–Bot.1).*
    - Family Favilynthidae Debrenne, 1989. *lower Cambrian (Atd.1–Bot.3).*
  - Order Ajacicyathida R. Bedford & J. Bedford, 1939. *lower Cambrian (Tom.1–Toy.3).*
    - Suborder Dokidocyathina Vologdin, 1957. *lower Cambrian (Tom. 2–Bot.3).*
      - Superfamily Dokidocyathoidea R. Bedford & W. R. Bedford, 1936. *lower Cambrian (Tom.2–Bot.3).*
        - Family Dokidocyathidae R. Bedford & W. R. Bedford, 1936. *lower Cambrian (Tom. 2–Bot.3)*
        - Family Dokidocyathellidae Debrenne, 1964. *lower Cambrian (Atd.2–Bot.1).*
        - Family Cordobicyathidae Perejón, 1975a. *lower Cambrian (Atd.2).*
      - Superfamily Kidrjasocyathoidea Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.2–Bot.1).*
        - Family Kidrjasocyathidae Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.2–Bot.1).*
      - Superfamily Kaltatocyathoidea Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.1–Bot.1).*
        - Family Kaltatocyathidae Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.1–Bot.1).*
      - Superfamily Papillocyathoidea Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.4–Bot.1).*
        - Family Papillocyathidae Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.4–Bot.1).*
      - Superfamily Soanicyathoidea Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.2–Bot.1).*
        - Family Soanicyathidae Rozanov in Zhuraveleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Atd.2–Bot.1).*
        - Family Zhuravlevaecyathidae Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1).*
      - Superfamily Kymbecyathoidea Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.4–Bot.3).*
        - Family Kymbecyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.4–Bot.3).*
    - Suborder Ajacicyathina R. Bedford & J. Bedford, 1939. *lower Cambrian (Tom.1–Toy.3).*
      - Superfamily Bronchocyathoidea R. Bedford & J. Bedford, 1936. *lower Cambrian (Tom.1–Toy.2).*
        - Family Ajacicyathidae R. Bedford & J Bedford, 1939. *lower Cambrian (Tom.1–Toy.2).*
        - Family Densocyathidae Vologdin, 1937b. *lower Cambrian (Atd.1–Bot.3).*
        - Family Bronchocyathidae R. Bedford & J. Bedford, 1936. *lower Cambrian (Atd.1–Bot.3).*
        - Family Ethmocyathidae Debrenne, 1969a. *lower Cambrian (Atd.1–Bot.3).*
        - Family Sajanocyathidae Vologdin, 1956. *lower Cambrian (Atd.1–Toy.2).*
        - Family Bipallicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.2).*
      - Superfamily Pretiosocyathoidea Rozanov, 1969. *lower Cambrian (Atd.1–Bot.2).*
        - Family Robertocyathidae Rozanov, 1969. *lower Cambrian (Atd.2–Bot.1).*
        - Family Pretiosocyathidae Rozanov, 1969. *lower Cambrian (Atd.1–Bot.1).*

Superfamily Erbocyathoidea Vologdin & Zhuravleva in Vologdin, 1956. *lower Cambrian (Atd.1–Toy.3).*

Family Erbocyathidae Vologdin & Zhuravleva in Vologdin, 1956. *lower Cambrian (Atd.1–Tot.3).*

Family Peregrinicyathidae Zhuravleva in Zhuravleva & others, 1967. *lower Cambrian (Bot.1-Bot.2).*

Family Vologdinocyathidae Yaroshevich, 1957. *lower Cambrian (Bot.1–Toy. 2).*

Family Tegerocyathidae Krasnopeeva, 1972. *lower Cambrian (Bot.1–Toy.3).*

Superfamily Tumulocyathoidea Krasnopeeva, 1953. *lower Cambrian (Tom.2–Bot.3).*

Family Tumulocyathidae Krasnopeeva, 1953. *lower Cambrian (Tom.2–Bot.3).*

Family Sanarkocyathidae, Hill, 1972. *lower Cambrian (Atd.3–Bot.1).*

Family Geocyathidae Debrenne, 1964. *lower Cambrian (Atd.1–Bot.1).*

Family Konjuschkovicyathidae Debrenne & Zhuravlev, 2000. *lower Cambrian (Bot.1–Bot.3).*

Superfamily Lenocyathoidea Zhuravleva in Vologdin, 1956. *lower Cambrian (Atd.1–Bot.1).*

Family Torosocyathidae Debrenne, Zhuravlev, & Kruse, 2002. *lower Cambrian (Atd.1–Bot.1).*

Family Japhanicyathidae Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.2–Bot.1).*

Family Lenocyathidae Zhuravleva in Vologdin, 1956. *lower Cambrian (Atd.2–Bot.1).*

Superfamily Annulocyathoidea Krasnopeeva, 1953. *lower Cambrian (Tom.2–Bot.3).*

Family Tumulifungiidae Rozanov in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Tom.2–Bot.3).*

Family Annulocyathidae Krasnopeeva, 1953. *lower Cambrian (Atd.2–Bot.3).*

Family Jakutocarinidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.1–Bot.3).*

Family Gagarinicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.3–Bot.1).*

Superfamily Ethmophylloidea Okulitch, 1937b. *lower Cambrian (Atd.1–Toy.1).*

Family Fallocyathidae Rozanov, 1969. *lower Cambrian (Bot.1–Bot.2).*

Family Gloriosocyathidae Rozanov, 1969. *lower Cambrian (Atd.1–Bot.1).*

Family Kijacyathidae Zhuravleva in Repina & others, 1964. *lower Cambrian (Atd.2–Bot.3).*

Family Carinacyathidae Krasnopeeva, 1953. *lower Cambrian (Atd.1–Bot.3).*

Family Ethmophyllidae Okulitch, 1937b. *lower Cambrian (Atd.4–Toy.1).*

Superfamily Tercyathoidea Vologdin in Simon, 1939. *lower Cambrian (Atd.4–Toy.1).*

Family Piamaecyathellidae Rozanov, 1974. *lower Cambrian (Bot.2).*

Family Botomocyathidae Zhuravleva, 1955b. *lower Cambrian (Atd.4–Bot.3).*

Family Olgaecyathidae Borodina, 1974. *lower Cambrian (Bot.2).*

Family Tercyathidae Vologdin, 1939. *lower Cambrian (Bot.1–Toy.1).*

Superfamily Sigmocyathoidea Krasnopeeva, 1953. *lower Cambrian (Bot.3).*

Family Sigmocyathidae Krasnopeeva, 1953. *lower Cambrian (Bot.3).*

Family Wrighticyathidae Kruse, 1978. *lower Cambrian (Bot.3).*

Suborder Erismacoscinina Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Tom.2–Bot.3).*

Superfamily Salairocyathoidea Zhuravleva in Vologdin, 1956. *lower Cambrian (Tom.2–Bot.3).*

Family Asterocyathidae Vologdin, 1956. *lower Cambrian (Tom.2–Bot.3).*

Family Rudanulidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1–Bot.3).*

Family Salairocyathidae Zhuravleva in Vologdin, 1956. *lower Cambrian (Atd.2–Bot.1).*

Family Crassicoscinidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1988. *lower Cambrian (Atd.4–Bot.1).*

Superfamily Kasyricyathoidea Zhuravleva in Musatov & others, 1961. *lower Cambrian (Atd.1–Bot.3).*

Family Agyrekocyathidae Konyushkov, 1967. *lower Cambrian (Atd.1–Bot.1).*

Family Xestecyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.3).*

Family Kasyricyathidae Zhuravleva in Musatov & others, 1961. *lower Cambrian (Bot.1).*

Family Membranacyathidae Debrenne, Zhuravlev, & Kruse, 2002. *lower Cambrian (Atd.1–Atd.2).*

Superfamily Polycoscinoidea Debrenne, 1964. *lower Cambrian (Atd.3–Bot.3).*

Family Anaptyctocyathidae Debrenne, 1970a. *lower Cambrian (Atd.4–Bot.3).*

Family Polycoscinidae Debrenne, 1964. *lower Cambrian (Atd.3–Bot.3).*

Family Veronicacyathidae Debrenne, Zhuravlev, & Kruse, 2002. *lower Cambrian (Atd.4–Bot.3).*

Family Zonacoscinidae Debrenne, 1971. *lower Cambrian (Bot.1).*

Superfamily Ethmocoscinoidea Zhuravleva, 1957. *lower Cambrian (Atd.2–Bot.3).*

Family Tumulocoscinidae Zhuravleva, 1960b. *lower Cambrian (Atd.2–Bot.1).*

Family Ethmocoscinidae Zhuravleva, 1957. *lower Cambrian (Bot.3).*

Superfamily Coscinoptyctoidea Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.1–Bot.3).*

Family Geyericoscinidae Debrenne & Zhuravlev, 2000. *lower Cambrian (Atd.1–Bot.1).*

Family Coscinoptyctidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.3).*

Family Jebileticoscinidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1).*
Superfamily Sigmocoscinoidea R. Bedford & J. Bedford, 1939. *lower Cambrian (Bot.1–Bot.3).*
Family Sylviacoscinidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1–Bot.3).*
Family Sigmocoscinidae R. Bedford & J. Bedford, 1939. *lower Cambrian (Bot.3).*
Superfamily Porocoscinoidea Debrenne, 1964. *lower Cambrian (Atd.1–Bot.3).*
Family Rozanovicyathidae Korshunov in Zhuravleva, Korshunov, & Rozanov, 1969. *lower Cambrian (Bot.1).*
Family Tatijanaecyathidae Korshunov, 1976. *lower Cambrian (Bot.1).*
Family Porocoscinidae Debrenne, 1964. *lower Cambrian (Atd. 3–Bot.3).*
Superfamily Mootwingeecyathoidea Kruse, 1982. *lower Cambrian (Bot.3).*
Family Mootwingeecyathidae Kruse, 1982. *lower Cambrian (Bot.3).*
Order Putapacyathida Vologdin, 1961. *lower Cambrian (Bot.1–Bot.3).*
Superfamily Alphacyathoidea R. Bedford & J. Bedford, 1939. *lower Cambrian (Bot.1–Bot.3).*
Family Alphacyathidae R. Bedford & J. Bedford, 1939. *lower Cambrian (Bot.1–Bot.3).*
Superfamily Putapacyathoidea R. Bedford & J. Bedford, 1936. *lower Cambrian (Bot.1–Bot.3).*
Family Putapacyathidae R. Bedford & J. Bedford, 1936. *lower Cambrian (Bot.3).*
Superfamily Hupecyathoidea Debrenne, Rozanov, & Zhuravlev, 1990. *lower Cambrian (Atd.4).*
Family Hupecyathidae Debrenne, Rozanov, & Zhuravlev, 1990. *lower Cambrian (Atd.4).*
Superfamily Chabakovicyathoidea Rozanov in Debrenne, Zhuravlev, & Kruse, 2002. *lower Cambrian (Bot.1).*
Family Chabakovicyathidae Rozanov in Debrenne, Zhuravlev, & Kruse, 2002. *lower Cambrian (Bot.1).*
Order Capsulocyathida Zhuravleva in Zhuravleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Tom.1–Bot.3).*
Suborder Capsulocyathina Zhuravleva in Zhuravleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Tom.1–Bot.3).*
Family Cryptoporocyathidae Zhuravleva, 1960b. *lower Cambrian (Tom.1–Bot.3).*
Family Uralocyathellidae Zhuravleva in Zhuravleva, Konyushkov, & Rozanov, 1964. *lower Cambrian (Bot.1).*
Family Tylocyathidae Zhuravlev, 1988. *lower Cambrian (Tom.4–Bot.3).*
Family Fransuasaecyathidae Debrenne, 1964. *lower Cambrian (Atd.1–Bot.1).*
Family Tubericyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1).*
Suborder Coscinocyathina Zhuravleva, 1949. *lower Cambrian (Atd.1–Bot.3).*
Superfamily Coscinocyathoidea Taylor, 1910. *lower Cambrian (Atd.2–Bot.3).*
Family Coscinocyathidae Taylor, 1910. *lower Cambrian (Atd.2–Bot.3).*
Family Mawsonicoscinidae Debrenne & Kruse, 1986. *lower Cambrian (Bot.3).*
Family Coscinocyathellidae Zhuravleva in Vologdin, 1956. *lower Cambrian (Bot.1–Bot.3).*
Superfamily Calyptocoscinoidea Debrenne, 1964. *lower Cambrian (Atd.1–Bot.1).*
Family Calyptocoscinidae Debrenne, 1964. *lower Cambrian (Bot.1).*
Family Tomocyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Atd.1–Atd. 3).*
Superfamily Alataucyathoidea Zhuravleva, 1955b. *lower Cambrian (Atd.1–Atd.2).*
Family Alataucyathidae Zhuravleva, 1955b. *lower Cambrian (Atd.1–Atd.2).*
Superfamily Clathricoscinoidea Rozanov in Repina & others, 1964. *lower Cambrian (Bot.1–Toy.1).*
Family Clathricoscinidae Rozanov in Repina & others, 1964. *lower Cambrian (Bot.1–Toy.1).*
Family Lanicyathidae Debrenne, Rozanov, & Zhuravlev in Debrenne, Zhuravlev, & Rozanov, 1989. *lower Cambrian (Bot.1).*
Order Archaeocyathida Okulitch, 1935b. *lower Cambrian (Tom.1–Toy.3), middle Cambrian, upper Cambrian (Furongian).*
Suborder Loculicyathina Zhuravleva, 1954. *lower Cambrian (Tom.1–Bot.3), upper Cambrian (Furongian).*
Superfamily Loculicyathoidea Zhuravleva, 1954. *lower Cambrian (Tom.1–Bot.3), upper Cambrian (Furongian).*
Family Loculicyathidae Zhuravleva, 1954. *lower Cambrian (Tom.1–Bot.3), upper Cambrian (Furongian).*
Family Eremitacyathidae Debrenne, 1992. *lower Cambrian (Atd.2).*
Superfamily Sakhacyathoidea Debrenne & Zhuravlev, 1990. *lower Cambrian (Tom.2–Atd.2).*
Family Sakhacyathidae Debrenne & Zhuravlev, 1990. *lower Cambrian (Tom. 2–Atd.2).*
Superfamily Chankacyathoidea Yakovlev, 1959. *lower Cambrian (Atd.4–Bot.3).*
Family Chankacyathidae Yakovlev, 1959. *lower Cambrian (Bot.1–Bot.3).*
Family Tchojacyathidae Debrenne & Zhuravlev, 1992b. *lower Cambrian (Atd.4).*
Suborder Anthomorphina Okulitch, 1935b. *lower Cambrian (Bot.1).*
Superfamily Anthomorphoidea Okulitch, 1935b. *lower Cambrian (Bot.1).*
Family Anthomorphidae Okulitch, 1935b. *lower Cambrian (Bot.1).*
Family Shiveligocyathidae Fonin, 1983. *lower Cambrian (Bot.1).*
Suborder Archaeocyathina Okulitch, 1935b. *lower Cambrian (Tom. 2–Toy. 3), middle Cambrian.*
Superfamily Dictyocyathoidea Taylor, 1910. *lower Cambrian (Tom. 2–Toy.1), middle Cambrian.*
Family Dictyocyathidae Taylor, 1910. *lower Cambrian (Tom. 2–Toy.1), middle Cambrian.*
Family Claruscoscinidae Debrenne & Zhuravlev, 1992b. *lower Cambrian (Bot.1–Toy 1).*
Family Pycnoidocoscinidae Debrenne, 1974a. *lower Cambrian (Bot.3).*

Superfamily Archaeocyathoidea Hinde, 1889. *lower Cambrian (Atd.1–Toy. 3).*
Family Archaeopharetridae R. Bedford & W. R. Bedford, 1936. *lower Cambrian (Atd.1–Bot.3).*
Family Archaeocyathidae Hinde, 1889. *lower Cambrian (?Atd.4, Bot.2–Toy. 3).*
Family Archaeosyconidae Zhuravleva, 1954. *lower Cambrian (Bot.1–Bot.3).*
Superfamily Metacyathoidea R. Bedford & W. R. Bedford, 1934. *lower Cambrian (Tom. 2–Bot.3).*
Family Copleicyathidae R. Bedford & J. Bedford, 1937. *lower Cambrian (Tom. 2–Bot.3).*
Family Jugalicyathidae Gravestock, 1984. *lower Cambrian (Atd.4–Bot.2).*
Family Metacyathidae R. Bedford & W. R. Bedford, 1934. *lower Cambrian (Atd.4–Bot.3).*
Superfamily Naimarkcyathoidea Wrona & Zhuravlev, 1996. *lower Cambrian (Bot.3).*
Family Naimarkcyathidae Wrona & Zhuravlev, 1996. *lower Cambrian (Bot.3).*
Superfamily Warriootacyathoidea Debrenne & Zhuravlev, 1992b. *lower Cambrian (Atd. 3–Atd.4).*
Family Warriootacyathidae Debrenne & Zhuravlev, 1992b. *lower Cambrian (Atd.3–Atd.4).*
Superfamily Beltanacyathoidea Debrenne, 1974a. *lower Cambrian (Atd. 3–Bot.3).*
Family Maiandrocyathidae Debrenne, 1974a. *lower Cambrian (Bot.3).*
Family Beltanacyathidae Debrenne, 1974a. *lower Cambrian (Atd. 3–Atd. 4).*
Superfamily Tabellaecyathoidea Fonin, 1963. *lower Cambrian (Bot.2–Bot.3).*
Family Tabellaecyathidae Fonin, 1963. *lower Cambrian (Bot.2-Bot.3).*
Suborder Dictyofavina Debrenne, 1991. *lower Cambrian (Atd.1–Bot.2).*
Superfamily Usloncyathoidea Fonin in Vologdin & Fonin, 1966. *lower Cambrian (Atd.1–Bot.2).*
Family Usloncyathidae Fonin in Vologdin & Fonin, 1966. *lower Cambrian (Atd.1–Bot.2).*
Superfamily Keriocyathoidea Debrenne & Gangloff in Debrenne & Zhuravelev, 1992a. *lower Cambrian (Bot.1–Bot.2).*
Family Keriocyathidae Debrenne & Gangloff in Debrenne & Zhuravelev, 1992a. *lower Cambrian (Bot.1–Bot.2).*
Superfamily Gatagacyathoidea Debrenne & Zhuravlev, 1992a. *lower Cambrian (Bot.2).*
Family Gatagacyathidae Debrenne & Zhuravlev, 1992a. *lower Cambrian (Bot.2).*
Suborder Syringocnemina Okulitch, 1935b. *lower Cambrian (Atd.4–Bot.3).*
Superfamily Auliscocyathoidea Debrenne & Zhuravlev, 1992b. *lower Cambrian (Atd.4–Bot.3).*
Family Auliscocyathidae Debrenne & Zhuravlev, 1992b. *lower Cambrian (Atd.4–Bot.3).*
Superfamily Syringocnemoidea Taylor, 1910. *lower Cambrian (Bot.1-Bot.3).*
Family Tuvacnemidae Debrenne & Zhuravlev 1990. *lower Cambrian (Bot.1–Bot.3).*
Family Syringocnemidae Taylor, 1910. *lower Cambrian (Bot.1–Bot.3).*
Superfamily Kruseicnemoidea Debrenne & Zhuravlev, 1990. *lower Cambrian (Bot.3).*
Family Kruseicnemoidae Debrenne & Zhuravlev, 1990. *lower Cambrian (Bot.3).*
Superfamily Fragilicyathoidea Belyaeva in Belyaeva & others, 1975. *lower Cambrian (Bot.1).*
Family Fragilicyathidae Belyaeva in Belyaeva & others, 1975. *lower Cambrian (Bot.1).*
Order Kazachstanicyathida Konyushkov, 1967. *lower Cambrian (Bot.1–Bot.3).*
Suborder Kazachstanicyathina Konyushkov, 1967. *lower Cambrian (Bot.1–Bot.3).*
Family Korovinellidae Khalfina, 1960a. *lower Cambrian (Bot.1–Bot.3).*
Suborder Altaicyathina Debrenne, 1991. *lower Cambrian (Bot.1–Bot.2).*
Family Altaicyathidae Debrenne & Zhuravlev 1992b. *lower Cambrian (Bot.1- Bot.2)*
Archaeocyatha *Nomina Dubia*
?Class Radiocyatha Debrenne, H. Termier & G. Termier, 1970. *lower Cambrian (Tom. 3–Toy. 2).*
Family Hetairacyathidae R. Bedford & J Bedford, 1937. *lower Cambrian (Tom. 3–Toy. 2).*
Family Uranosphaeridae R. Bedford & J. Bedford, 1936. *lower Cambrian (Bot.1–Bot.3).*
Class Uncertain (probably not allied to Archaeocyatha or Radiocyatha)
Order Acanthinocyathida R. Bedford & W. R. Bedford 1936 *lower Cambrian (Atd.1–Bot.3).*
Family Acanthinocyathidae R. Bedford & W. R. Bedford, 1936. *lower Cambrian (Atd.1–Bot.3).*
Class Cribricyatha Vologdin, 1961 *lower Cambrian (Tom. 2–Bot.3).*
Order Vologdinophyllida Radugin, 1964. *lower Cambrian (Tom.2- Bot.1).*
Superfamily Vologdinophylloidea Radugin, 1964. *lower Cambrian (Tom. 2–Bot.1).*
Family Vologdinophyllidae Ragugin, 1964. *lower Cambrian (Atd.1).*
Family Leibaellidae Jankauskas, 1965. *lower Cambrian (Tom. 2–Bot.1).*
Superfamily Akademiophylloidea Radguin, 1964. *lower Cambrian (Atd.1–Bot.1).*
Family Akademiophyllidae Radugin, 1964. *lower Cambrian (Atd.1–Bot.1).*
Family Striatocyathidae Vologdin & Jankauskas, 1968. *lower Cambrian (Atd.1–Bot.1).*
Order Cribricyathida Vologdin, 1961. *lower Cambrian (Atd.1–Bot.3).*
Superfamily Conoidocyathoidea Vologdin, 1964a. *lower Cambrian (Atd.1–Bot.3).*
Family Concoidocyathidae Vologdin, 1964a. *lower Cambrian (Atd.1–Bot.3).*
Superfamily Pyxidocyathoidea Vologdin, 1964a. *lower Cambrian (Atd.1–Bot.3).*
Family Pyxidocyathidae Vologdin, 1964a. *lower Cambrian (Atd.1–Bot.3).*
Phylum Uncertain (Cribricyath-like Taxa). *lower Cambrian (Atd.1–Bot.3).*
Family Boyarinovicyathidae Zhuravleva in Zhuravleva & others, 1997b. *lower Cambrian (Bot.3).*
Family Uncertain. *lower Cambrian (Atd.1).*

LIVING HYPERCALCIFIED SPONGES

Jean Vacelet, Philippe Willenz, and †Willard D. Hartman

INTRODUCTION

Only a few of the 682 valid sponge genera that comprise the estimated 15,000 species (approximately 7,000 of which are presently described; Hooper & Soest, 2002a) are capable of secreting a rigid calcified skeleton that is generally reinforced with, or complemented by, a spicular skeleton. These sponges have the potential to fossilize, and their fossil counterparts have often been referred to as calcareous sponges by paleontologists. This term is confusing, however, because it is generally used by zoologists to refer only to members of the poriferan class Calcarea. The term hypercalcified sponges is used here for representatives of both the classes Demospongiae and Calcarea, which secrete a complementary calcareous skeleton. These sponges, although few in number in Recent seas, display a high diversity and generally show close affinities to nonhypercalcified sponges, arguing for their classification in various taxa of the classes Demospongiae and Calcarea.

Recent hypercalcified sponges display a certain number of general features that are considered here. Their calcified, coherent skeletons give them the chance of becoming fossilized, and in this respect allow them to develop to closely resemble various ancient reef builders such as the chaetetids, sphinctozoans, inozoans, and stromatoporoids; indeed, they are likely to be survivors of these ancient groups. The study of hypercalcified sponges provides very informative data relevant to fossil groups, which were considered, prior to the 1970s to have rather uncertain affinities. It is important to bear in mind, however, that unlike their fossil relatives, present-day taxa are few in number, with most genera being monotypic and living in cryptic habitats, suggesting that they represent a few survivors of the luxuriant ancient fauna. These few living forms are nevertheless very diverse at the order or class levels and display close affinities with various extant sponge taxa devoid of a hypercalcified skeleton. The large taxonomic diversity of these relict organisms may indicate that occurrences of calcified skeletons developed from many evolutionary lines of descent within the Porifera. The microstructure and composition of the calcified skeletons are also highly diverse—surprisingly more so when compared with present-day calcified cnidarians responsible for reef building—and rather specific in their taxonomic affinities. They live in warm or warm-temperate waters, but unlike their fossil counterparts, are not important reef builders; instead, they live as restricted forms in refuge habitats such as bathyal cliffs and littoral dark caves (Fig. 1–2).

MORPHOLOGICAL TYPES COMPARED WITH FOSSIL ANALOGS

In living hypercalcified sponges, several morphological types or grades of organization are represented, which, in some cases, may correspond to those known as fossils. The diversity is considerably lower in the few survivors than in the ancient fauna, however. Interestingly, the same morphological type may commonly occur in sponges that are clearly differentiated by the spicules, living tissue, and/or microstructure of their calcified skeleton, indicating that the various grades of organization represented in chaetetids, stromatoporoids, inozoans, or sphinctozoans do not correspond to true evolutionary lines.

The chaetetid type corresponds to laminar- or domical-shaped sponges in which the superficial parts of the skeleton

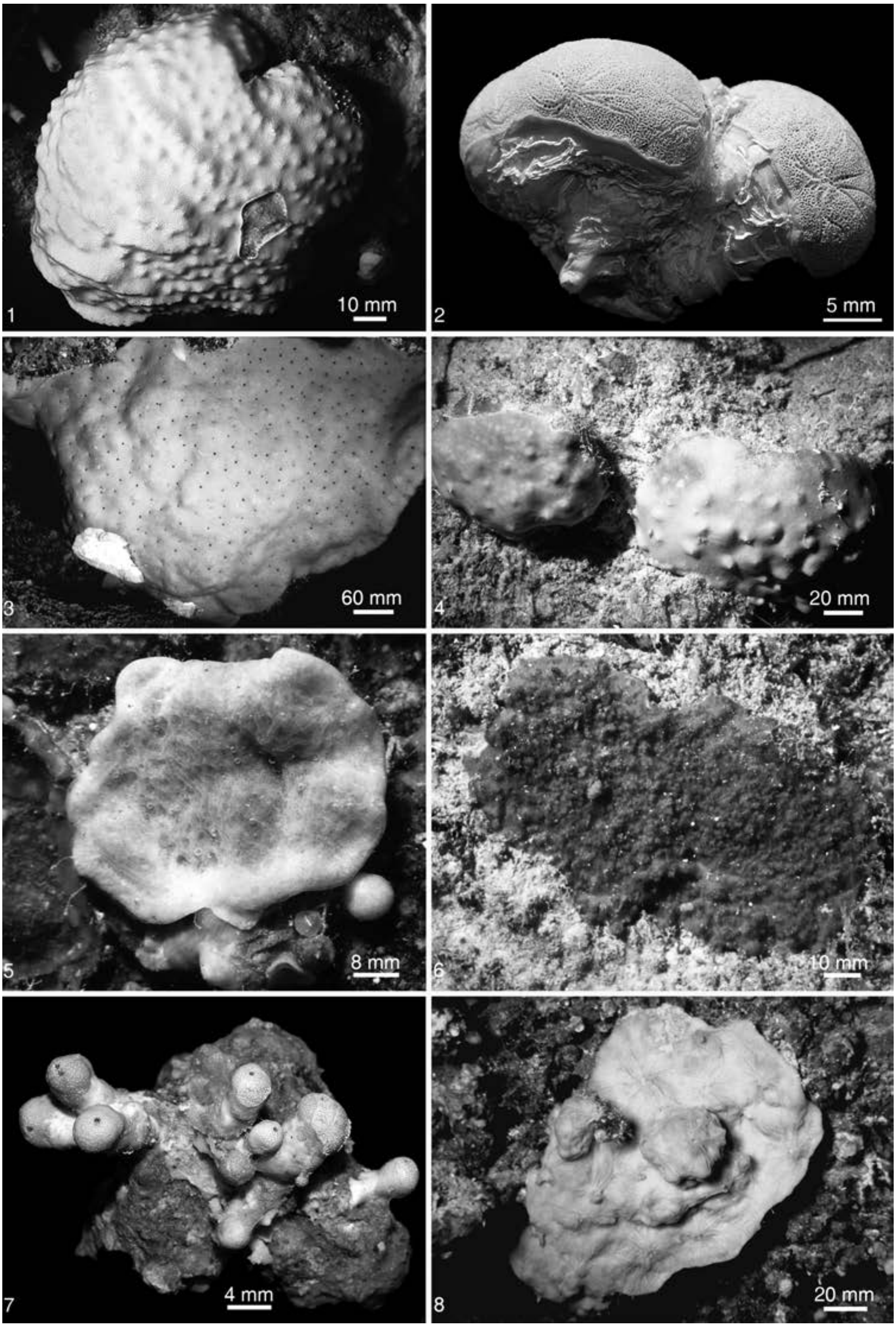

FIG. 1. *(For explanation, see facing page).*

display a honeycomb structure, with more or less hexagonal tubes, somewhat resembling the corallites of scleractinian corals, but smaller. The living tissue occurs as a thin veneer at the surface and within the outer parts of the tubes. The inner parts, often partitioned by horizontal tabulae, may contain reserve cells able to regenerate the sponge (pseudogemmules). The ends of the tubes are infilled by a secondary calcareous deposit, resulting in a very hard skeleton. This type is known in the Ceratoporellidae (without tabulae and pseudogemmules), Merliidae, and Acanthochaetetidae. These three taxa of Demospongiae have no affinities, and their calcareous skeleton, although similarly organized, has a different nature and microstructure. Their structure appears to be similar to that exhibited by some fossil chaetetids, and correlatives seem to be established between Recent and fossil acanthochaetetids (HARTMAN & GOREAU, 1975), and between *Merlia* and the fossil *Blastochaetetes* (GAUTRET, VACELET, & CUIF, 1991). However, the communication canals (or pores) that are present between adjacent tubes in some tabulated fossils of a dubious sponge nature (e.g., in favositids) are not found in living hypercalcified sponges of the chaetetid grade. These canals appear to have no functional significance in a sponge organization. They are more readily explained as a character of cnidarians, providing communication between adjacent polyps.

The stromatoporoid type is strongly reminiscent of the skeleton of some fossil stromatoporoids. It is found in domical to flattened, laminar sponges with a calcified skeleton consisting of a meshwork of tubes, pillars, and laminae. This type is known in *Calcifibrospongia*, with an aragonitic skeleton, which has clear similarities to some Mesozoic stromatoporoids (HARTMAN, 1979), and in *Astrosclera*, where the aragonitic skeleton is spherulitic.

In the sphinctozoid type, the skeleton is external, resulting in a discontinuous growth, with separate chambers linked by a central siphon, as recognized in *Vaceletia*. The skeleton, in aragonite with a microgranular microstructure, has some exact fossil analogs but does not exhibit the full range of morphological structures represented by the diverse record of fossil sphinctozoid sponges. In addition, there are some common points between the morphological organization of *Vaceletia* and that of archaeocyaths. In the latter, the skeleton was likely also to be external, but it had a more elaborate organization, including a double-cup shape and vertically arranged, pseudoseptate partitioning.

The inozoid type is less well defined, occurring in sponges such as *Murrayona*, *Petrobiona*, and some Astroscleridae, where a more or less massive skeleton is enveloped by living tissue.

SKELETON, MICROSTRUCTURE, BIOMINERALIZATION PROCESSES, AND MODES OF PRESERVATION

The living hypercalcified sponges exhibit two types of skeleton: one that is based on a primary spicular skeleton, and the other

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FIG. 1. Hypercalcified demosponges; *1, Acanthochaetetes wellsi* HARTMAN & GOREAU, 1975; living specimen *in situ* from Touho reef, New Caledonia, 15 m (Vacelet, Willenz, & Hartman, 2010); *2, Astrosclera willeyana* LISTER, 1900; dry specimen with astrorhizae, the Philippines, 24 m (Vacelet, Willenz, & Hartman, 2010); *3, Calcifibrospongia actinostromarioides* (HARTMAN, 1979); specimen about 30 × 60 cm *in situ* under an overhang, 30 m, forereef wall, south of Jamaica Bay, southern tip of Acklins Island, Bahamas (Vacelet, Willenz, & Hartman, 2010); *4, Ceratoporella nicholsoni* (HICKSON, 1911); two specimens, *in situ,* 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *5, Goreauiella auriculata* HARTMAN, 1969; *in situ,* 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *6, Hispidopetra miniana* HARTMAN, 1969; *in situ*, 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *7, Vaceletia crypta* (VACELET, 1977b); view from cavities of front coral reef, New Caledonia, 15 m (Vacelet, Willenz, & Hartman, 2010); *8,Willardia caicosensis* (WILLENZ & POMPONI, 1996); holotype, *in situ,* 114 m, northeastern tip of Grand Turk Island prior to collection by Harbor Branch Johnson-Sea Link I submersible (Willenz & Pomponi, 1996). For a color version of this figure, see *Treatise Online,* Number 1 (paleo.ku.edu/treatiseonline).

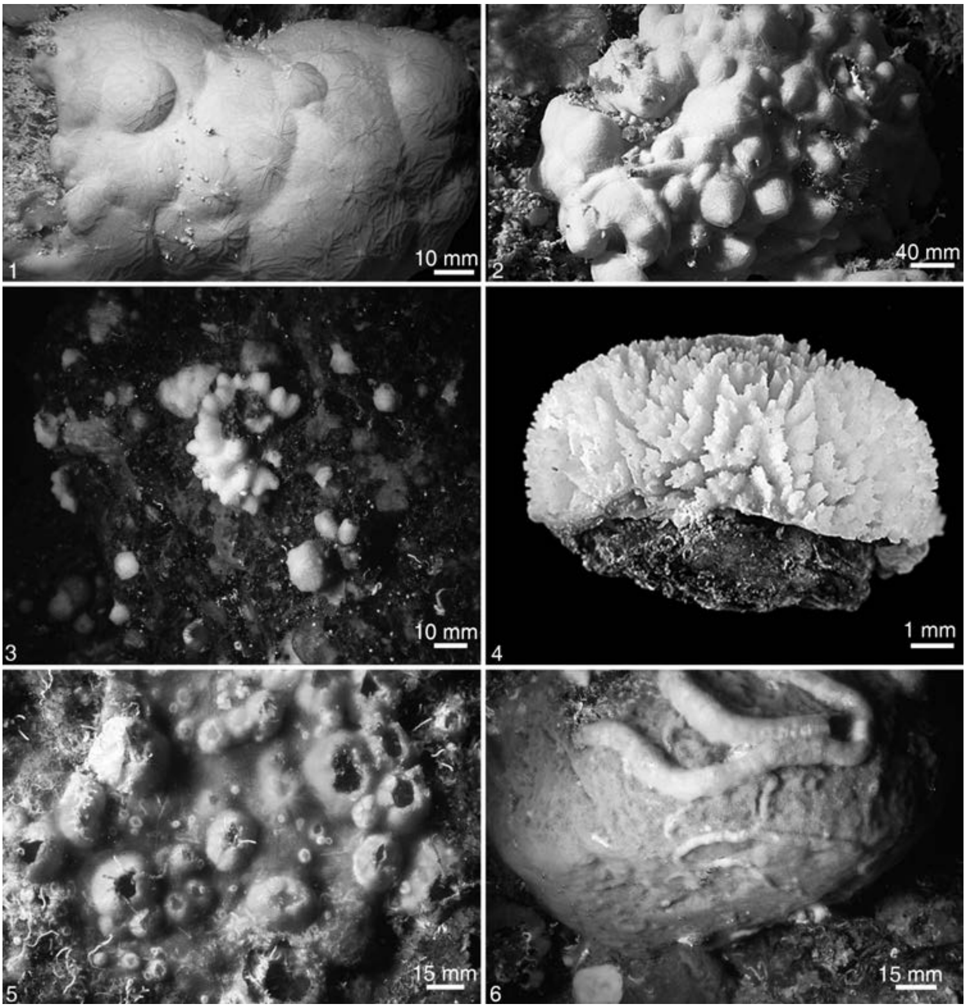

FIG. 2. Hypercalcified demosponges *(Ceratoporella, Stromatospongia, and Merlia)* and a calcarean *(Petrobiona); 1, Ceratoporella nicholsoni* (HICKSON, 1911); *in situ,* 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *2, Stromatospongia norae* HARTMAN, 1969; *in situ,* 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *3, Petrobiona massiliana* VACELET & LÉVI, 1958; *in situ,* 15 m, cave of La Ciotat, northwestern Mediterranean (Vacelet, Willenz, & Hartman, 2010); *4, P. massiliana;* massive skeleton after removal of living tissue (Vacelet, Willenz, & Hartman, 2010); *5, Merlia normani* KIRKPATRICK, 1908; *in situ,* 12 m, cave, Lebanon, Ramkine Island, living tissue covering thin, calcareous skeleton (Vacelet, Willenz, & Hartman, 2010); *6, Merlia deficiens* VACELET, 1980a; *in situ,* 12 m, cave of La Ciotat (northwestern Mediterranean); species is similar to *Merlia normani* but devoid of thin, underlying, calcareous skeleton (Vacelet, Willenz, & Hartman, 2010). For a color version of this figure, see *Treatise Online,* Number 1 (paleo.ku.edu/treatiseonline).

that is not derived from a primary spicular skeleton.

In the first type, found only in the family Minchinellidae of the Calcarea, some of the calcareous spicules are linked together by additional calcareous cement. The cement is made of calcite, as in the spicules, but the microstructure is different. It belongs to the orthogonal type, with crystal fibers in a perpendicular and radial orientation relative to the central axis represented by the spicule. The cement has a variable development, either linking only the basal actines of tetractine spicules, the apical actine of which remains free, or completely surrounding these spicules. In all cases, the living tissue contains free calcareous spicules, generally tangentially arranged in the ectosomal layer and frequently including a special form of triactine: the tuning fork triactine, or diapason. This type of skeleton is thus based on a primary spicule skeleton, which is progressively, and more or less completely, enveloped by calcareous calcitic cement, resulting in a solid skeleton when the cement is well developed. Although chemically very different, these skeletons may morphologically resemble those of some hexactinellid sponges, in which the siliceous spicules are linked and more or less surrounded by a siliceous cement; or like lithistid demosponges, in which the siliceous spicules become zygose through the modified ends of their actines. In representatives of the genus *Plectroninia* (see p. 299), the calcite cement may be poorly developed, with the basal actines of tetractines becoming linked both by a cement and by zygosis of their deformed ends; whereas in *Tulearinia* (see p. 303), a genus of uncertain affinities, the spicules are feebly linked by incomplete zygosis without any cement. The mode of secretion of the calcareous cement has not been investigated and is known only in *Minchinella lamellosa* (see p. 297), where telmatoblasts, columnar cells of the collencyte type, presumed to secrete the cement, have been briefly described (KIRKPATRICK, 1908).

The rigid skeletons obtained by this process form either a basal crust or a reticulate structure, which in the dead parts may be secondarily infiltrated to produce a solid mass. Sponges with this skeleton type may be encrusting, erect lamellar, or more or less massive, and generally small. The diapason, which is found in most of the hypercalcified Calcarea, and which is also known in the fossil representatives, probably has no phylogenetic significance (VACELET, 1991).

The second type, which occurs in a few other members of the class Calcarea—including two genera, *Murrayona* (Fig. 3.1; see p. 294) and *Petrobiona* (see p. 303; see also GILIS & others, 2012), and in all the hypercalcified representatives of the class Demospongiae (10 genera)—forms as a calcareous skeleton that does not derive from a spicular skeleton, although some spicules may be secondarily entrapped. It appears as a primary deposit of calcium carbonate, sometimes secreted on an organic template, but most often secreted by a poorly known process. The calcareous skeleton coexists with a spicule skeleton similar to that found in the nonhypercalcified relatives of these sponges, with the exception of the sphinctozoid *Vaceletia crypta* and some populations of *Astrosclera willeyana*, which are devoid of spicules. In the two genera of Calcarea, the calcareous skeleton is made of calcite. In Demospongiae (Fig. 3.2), it is composed of calcite in two genera (*Acanthochaetetes* and *Merlia*) and of aragonite in eight genera (*Astrosclera, Calcifibrospongia, Ceratoporella, Goreauiella, Hispidopetra, Stromatospongia, Vaceletia,* and *Willardia*). There is no possible confusion with siliceous structures, because a solid, nonspicular siliceous skeleton is unknown in sponges.

The microstructures and the biomineralization processes of the second type of skeleton are highly diverse. All contain a certain amount of organic material. These skeletons are organized in more or less well-defined sclerodermites of the spherulitic, penicillate, or radial flake–spherulitic types. The spherulitic type, with crystal fibers radiating from a central point, is found only in the Recent astrosclerid *Astrosclera willeyana* (see p. 241). In this species, the sclerodermites first appear as intracellular, spheraster-like spherules (Fig. 3.4). When the spherules attain 15–25 µm in diameter, the secreting cells migrate toward the superficial parts of the skeleton, where the spherules are incorporated, and continue their growth asymmetrically (GAUTRET, 1986; CUIF & GAUTRET, 1991; WÖRHEIDE & others, 1997; WÖRHEIDE, 1998). The outline of the intracellular spherule is visible in the central zone of the mature sclerodermites

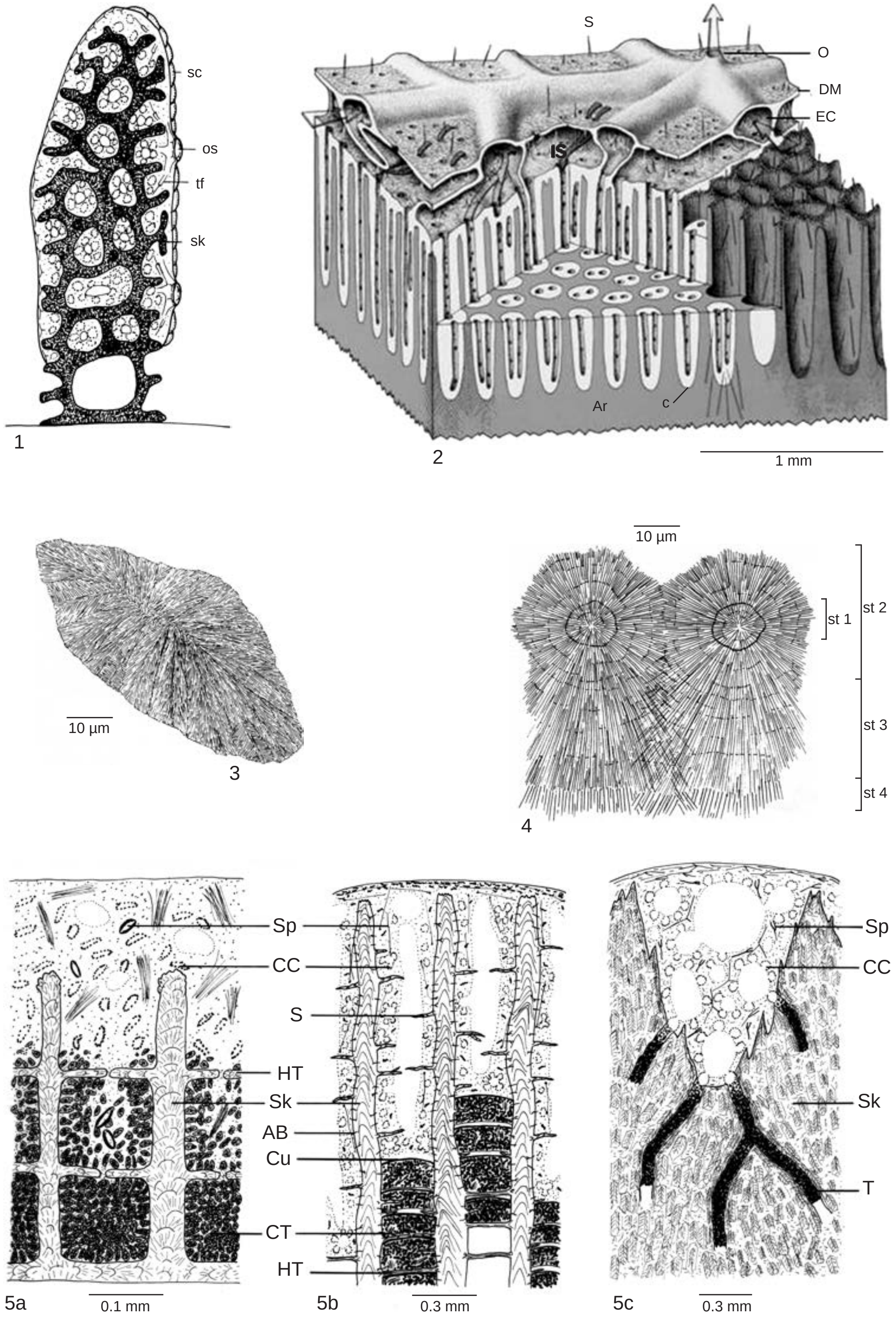

FIG. 3. *(For explanation, see facing page).*

when the skeleton is treated with proteolytic enzymes, and this central zone is more easily dissolved during early diagenesis. The characters of this skeleton, including its mode of synthesis and differential dissolution, are found in diverse Permo-Triassic fossils belonging to various morphological types (Gautret, 1986; Reitner, 1992). Free spheraster-like spherules have been observed in cavities of the skeleton of well-preserved Triassic fossils (Gautret, 1986), indicating a biomineralization process similar to that observed in *Astrosclera*.

Diverse forms of penicillate (also called clinogonal or water jet) microstructure of sclerodermites are observed in other Astroscleridae (*Ceratoporella, Goreauiella, Hispidopetra,* and *Stromatospongia*), in *Merlia,* and in *Murrayona*. Comparable acicular, crystalline, sclerodermite-like patterns are reported in *Calcifibrospongia* (Hartman, 1979) and in *Willardia* (Willenz & Pomponi, 1996). These penicillate sclerodermites are likely secreted by a pinacocyte layer lining the skeleton, which secretes an organic matrix (Willenz & Hartman, 1989; Willenz & Pomponi, 1996) in a biomineralization process certainly different from that of *Astrosclera*, but still poorly known.

Radial flake–spherulitic sclerodermites, in which the crystal fibers are disposed obliquely or perpendicularly to a longitudinal line (Fig. 3.3), are found in *Petrobiona* and have no known fossil counterparts. Two other microstructures are known in which individualized sclerodermites are not distinct. First, a microlamellar microstructure, with crystal fibers aligned in one plane, is found in *Acanthochaetetes*. The skeletal formation takes place within a narrow zone (300–500 nm) between the basopinacoderm and the mature skeleton. The sponge produces threadlike, folded templates (spaghetti fibers of 0.5–2 µm size) that become mineralized (Reitner & Gautret, 1996).

Second, a microgranular, irregular microstructure is found in the sphinctozoan *Vaceletia*. In this species, in which the skeleton is mostly external, growth occurs by the building of successive chambers. The skeleton is secreted on a noncollagenous organic template of the walls of the cupolas and of the pillars, in which are deposited tangled crystal bundles (Vacelet, 1979b; Gautret, 1985; Gautret, Reitner, & Marin, 1996; Reitner & others, 1997). This process may be general in extinct forms with irregular microstructure, including archaeocyaths. In most cases, the basal parts of the skeleton, which is free from living tissue, is infilled by a micritic granular secondary deposit.

The microstructures preserved in living forms are well diversified, but there are others known in fossil representatives that did not survive to the present. For instance, no Recent skeletons are known to be composed of microgranular calcite or spherulitic calcite.

The living sponges with such skeletons belong to diverse morphological types. The massive forms may reach a large size, up to

Fig. 3. Diagrammatic representations of hypercalcified calcareans and demosponges; *1, Murrayona phanolepis* Kirkpatrick, 1910b; diagrammatic section through lamellar specimen, with inhalant face on left and exhalant surface on right; *os,* osculum; *sc,* calcareous scale; *sk,* aspicular calcareous skeleton; *tf,* tuning fork (triactine) (Borojevic, Boury-Esnault, & Vacelet, 1990); *2, Ceratoporella nicholsoni* (Hickson, 1911); diagrammatic three-dimensional representation; *Ar,* aragonite skeleton; *c,* choanosome; *DM,* dermal membrane; *EC,* exhalant canal; *IS,* inhalant space or vestibule; *O,* osculum; *S,* spicule (Willenz & Hartman, 1989; see also Fig. 156*c* and Fig. 355); *3, Petrobiona massiliana* Vacelet & Lévi, 1958; calcitic sclerodermite of radial-flake-spherulitic type (Gautret, 1986); *4, Astrosclera willeyana* Lister, 1900; dissymmetrical spherules of basal zone of skeleton after treatment by a proteolytic enzyme showing initial, intracellular spherule (*st 1*) and successive stages (*st 2–st 4*) of epitaxial growth (Gautret, 1986); *5,* diagrammatic longitudinal section through three living hypercalcified sponges possessing masses of storage cells; *a, Merlia normani* Kirkpatrick, 1908; *b, Acanthochaetetes wellsi* Hartman & Goreau, 1975; *c, Petrobiona massiliana* Vacelet & Lévi, 1958; *AB,* anchoring collagen bundles; *CC,* choanocyte chambers; *CT,* crypt tissue; *Cu,* cuticle; *HT,* horizontal tabulae; *S,* spine; *Sk,* calcareous skeleton; *Sp,* spicules; *T,* trabecular tract (Vacelet, 1990).

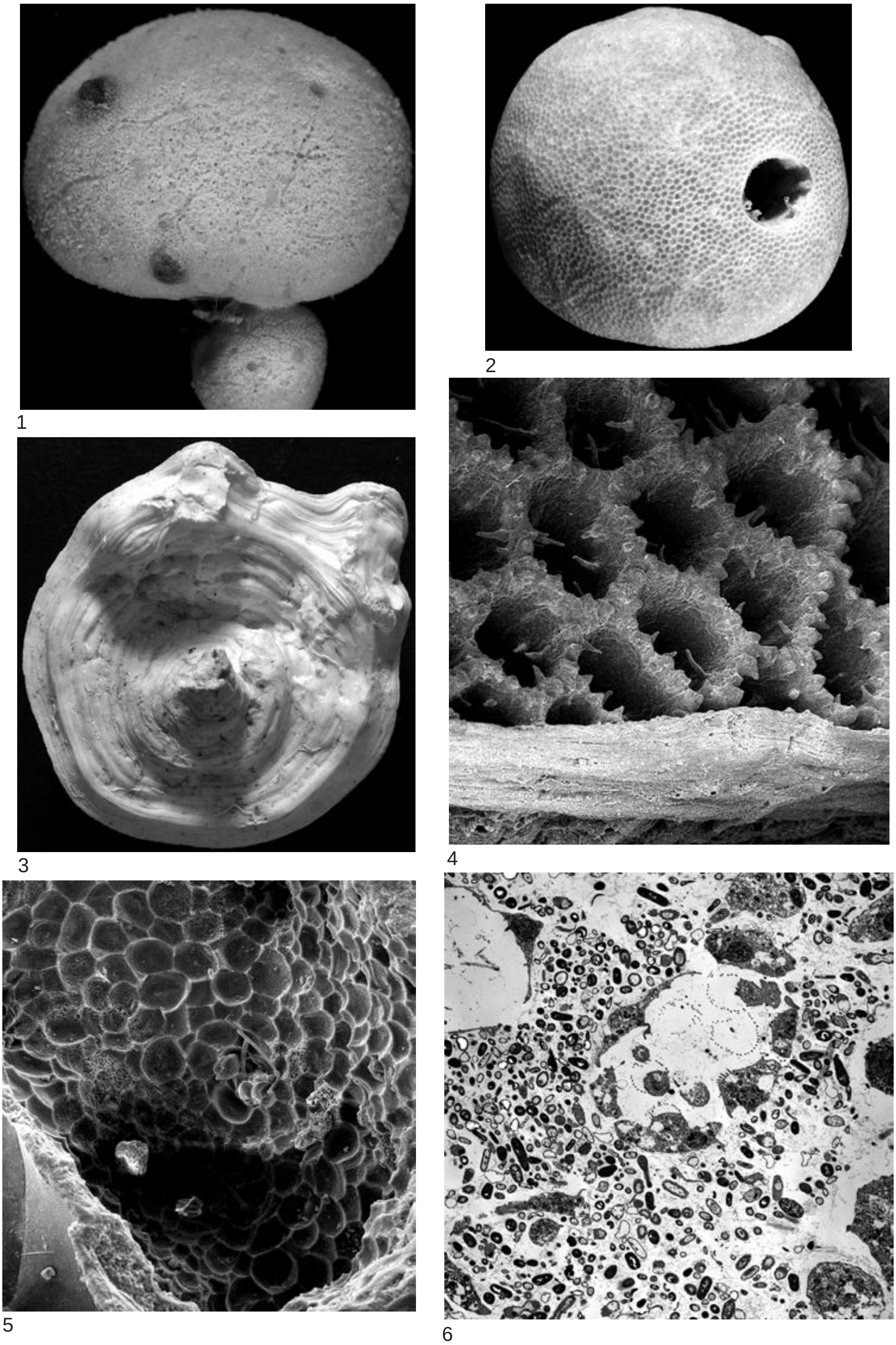

FIG. 4. *(For explanation, see facing page).*

1 m in diameter in some specimens of *Ceratoporella nicholsoni*.

In both types of skeleton, the aquiferous canals generally leave traces on the superficial parts of the skeleton, forming astrorhizae, which often may be marked in the deeper zones of the skeleton (Fig. 4.1–4.2). The basal and lateral surfaces of the dead skeletal mass are covered by an epitheca showing growth lines (Fig. 4.3–4.4), the mode of secretion of which has not been investigated.

MODES OF PRESERVATION

The early diagenesis of the calcareous skeleton has been poorly investigated, although studying the changes in subfossil specimens would be highly instructive. It has been shown that the composition of the organic matrix present in the calcareous skeleton may influence diagenetic processes (Marin & Gautret, 1994). A deposit of micritic aragonite rapidly accumulates in the empty cavities of the basal dead parts of the sponge. Some data are available for the conservation of the spicules included in the calcified skeleton. In *Petrobiona*, the calcitic spicules included in the massive skeleton are well preserved and can be recognized in the earlier growth of the skeleton. In contrast, the siliceous spicules included in the superficial parts of a calcareous skeleton become corroded and totally resorbed from areas of earlier growth in the sponges, with the corresponding cavities being infilled by a variety of calcium carbonate. The spicules that are not included in the solid skeleton or that are feebly attached to the surface of the skeleton (such as the spirasters of *Acanthochaetetes wellsi*) are dispersed at the death of the sponge, and consequently have very few chances to fossilize.

GROWTH RATE, LONGEVITY, AND PROPERTIES OF THE HYPERCALCIFIED SKELETON

The growth rate of sponges with various types of skeleton (discussed above) has been studied in only a few cases. The rate appears remarkably slow as compared to the growth rate of the main reef builders in present-day seas, suggesting that the strategy of reef building by these sponges may have changed significantly through geological time (Willenz & Hartman, 1985, 1999). Growth rate ranges from 180 to 230 µm/yr in *Ceratoporella nicholsoni*, while in *Acanthochaetetes* it has been estimated to reach from only 50 to 100 µm/yr (Reitner & Gautret, 1996). This slow growth rate and the large size of some specimens of *Astrosclera*, *Ceratoporella*, *Acanthochaetetes,* and multi-branched *Vaceletia,* suggest that these sponges may have had a very long life span. The age of specimens of *Ceratoporella nicholsoni* from bathyal environments that are more than 1 m in diameter can be estimated to be more than 1000 yr, and that of decimeter-size specimens of *Acanthochaetetes* from coral reef cavities about 1000 yr as well. In the bathyal zone, the basal part of a 10-cm-thick construction of the branching form of *Vaceletia crypta* was estimated to be 700 yr (Vacelet & others, 1992). Such skeletons have a high potential for providing proxy records of temperature and salinity, extending existing records in the Salinity Maximum Waters of the North Atlantic back to the end of the 19th century

Fig. 4. Epizoans, epitheca, and symbiotic bacteria associated with living hypercalcified sponge taxa. Depth of samples indicated in meters; *1, Astrosclera willeyana* Lister, 1900; astrorhizae and two commensal invertebrates causing bioclaustration inside skeleton, a cirriped (two large black spots) and unidentified cnidarian (small gray spots), Touho, 15 m, New Caledonia, ×2.75 (Vacelet, Willenz, & Hartman, 2010); *2, Acanthochaetetes wellsi* Hartman & Goreau, 1975; astrorhizae and a trace left by unidentified invertebrate, Beautemps-Beaupré, 12 m, New Caledonia, ×2.08 (Vacelet, Willenz, & Hartman, 2010); *3, A. wellsi*; basal part of specimen showing basal peduncle and epitheca, Philippines, 24 m, ×1.8 (Vacelet, Willenz, & Hartman, 2010); *4, A. wellsi;* SEM view of surface and epitheca, Escape Reef, 12 m, Great Barrier Reef, ×40 (Vacelet, Willenz, & Hartman, 2010); *5, Vaceletia crypta* (Vacelet, 1977b); trace of excavating sponge, *Thoosa* sp., in skeleton, New Caledonia, 38 m, ×140 (Vacelet, Willenz, & Hartman, 2010); *6, V. crypta*; TEM view of choanosome, showing choanocyte chambers, archaeocyte cells, and numerous symbiotic bacteria, Kaimon Maru Bank, 245 m, New Caledonia, ×2000 (Vacelet, Willenz, & Hartman, 2010).

(Rosenheim & others, 2004, 2005). Large specimens even reveal the coldest periods of the Little Ice Age at the end of the 17th century (Haase-Schramm & others, 2005). The changes in the anthropogenic lead input to the atmosphere over time have also been detected in the skeleton of *Ceratoporella* (Lazareth & others, 2000). This is essentially related to leaded gasoline consumption after World War II and the following drop in the 1970s, which is linked to a decrease in the use of leaded alkyl additives in gasoline.

The skeleton of *Ceratoporella nicholsoni* is extremely hard, with a compressive strength several times that of cnidarian reef builders and eight times stronger than concrete (Schuhmacher & Plewka, 1981). Although fragmentary and probably not applicable to all living hypercalcified sponges, these results suggest that there may be a tradeoff between mechanical strength and a fast rate of growth (Schuhmacher & Plewka, 1981; Wood, 1990b). Some ancient reef builders had the strategy of slowly building very resistant reefs that were able to withstand hurricanes, whereas modern scleractinian corals build relatively fragile constructions rapidly, and are able to recover comparatively quickly after destructive hurricanes.

MODE OF LIFE

LIVING TISSUE

The living tissue and soft tissue organization are similar to that of the normal Demospongiae and Calcarea. The hypercalcified sponges display the same cell composition and tissue organization as their noncalcified relatives. For instance, *Calcifibrospongia* (family Calcifibrospongiidae), considered to be closely related to members of the family Chalinidae due to the characteristics of their siliceous skeleton, displays the same special hanging type (Langenbruch & Jones, 1990) of choanocyte chambers (Hartman & Willenz, 1990). Four hypercalcified sponges, however, have a special type of living tissue in relation to the presence of a calcareous skeleton. In *Petrobiona*, *Merlia, Acanthochaetetes,* and *Goreauiella*, which are not taxonomically related, reserve cells are packed in cavities at the base of the skeleton (Fig. 3.5; Vacelet, 1990; Willenz & Hartman, 2004). This cellular tissue, pseudogemmulae, is able to regenerate the sponge after death of the superficial tissue and may be responsible for the discontinuous mode of growth, possibly also developing in fossil chaetetids (relatives of *Merlia* and *Acanthochaetetes)*, and perhaps suggesting that pseudogemmulae played an ecological role in periodically harsh environments. In addition, two representatives of Astroscleridae, *Ceratoporella* and *Stromatospongia*, display valvules in their inhalant and exhalant canals, which have not been observed in other sponges (Willenz & Hartman, 1989).

REPRODUCTION

When sexual reproduction has been observed, it proves to occur in a similar way to that of noncalcified relatives. The phenomena is poorly known, however, and some peculiarities need to be reported. Among the Calcarea, the incubated larvae are of the type that are to be expected from their taxonomic affinities, with amphiblastula developing in *Petrobiona* and *Plectroninia*, and blastula produced in *Murrayona* and *Paramurrayona*. A peculiarity, however, is the unusually complex development in *Petrobiona*, in which the fertilization and nutrition of the oocyte, although following the conventional pattern of the Calcaronea, are considerably more elaborate (Gallissian & Vacelet, 1990, 1992). In Demospongiae, the reproductive stages are known in only a few species. *Astrosclera willeyana*, a member of the order Agelasida, incubates parenchymella larvae, whereas the noncalcified Agelasida are oviparous. *Vaceletia crypta*, with affinities to keratose sponges (Wörheide, 2008), is an incubating species with a parenchymella larva, which develops through an unusual coeloblastula stage (Vacelet, 1979a). The fact that sexual reproduction has not been observed in several hypercalcified species that have been frequently studied, such as the other Astroscleridae, *Merlia* spp., and *Acanthochaetetes wellsi,* could suggest they are all oviparous, a condition that is more difficult to diagnose. This would be in agreement with the systematic affinities of Astroscleridae (although there is an exception with the incubating *Astrosclera willeyana*) and Acanthochaetetidae, but not of *Merlia,* which may be expected to be viviparous.

SYMBIOSIS AND COMMENSALISM

Like their noncalcified relatives, the hypercalcified sponges harbor a microflora of symbiotic bacteria. As in nonhypercalcified Demospongiae and Calcarea, there are two main types of associations, one with bacteria relatively few in number and belonging to a single morphotype, and another with a large population of bacteria morphologically and taxonomically highly diverse. This second type occurs in the so-called bacteriosponges. All the representatives of the Calcarea as well as the demosponges *Acanthochaetetes wellsi, Goreauiella auriculata*, and *Merlia* spp., with few bacteria, belong to the first type. In contrast, the sphinctozoan *Vaceletia crypta,* the Astroscleridae *Ceratoporella nicholsoni, Stromatospongia norae*, and *Astrosclera willeyana,* are bacteriosponges (Fig. 4.6). The Astroscleridae have bacteria morphologically similar to those of their close relative *Agelas*, including a special morphotype until now found only in Agelasidae (Vacelet & Donadey, 1977). In *Ceratoporella*, the symbiotic bacteria may represent 20% of the mesohyl volume or 57% of the cellular volume (Willenz & Hartman, 1989; Santavy, Willenz, & Colwell, 1990). Due to their sciaphilic habitat, hypercalcified sponges are never associated with photosynthetic microorganisms such as zooxanthellae or cyanobacteria. However, boring algae of the genus *Ostreobium*, which are able to live in dim light conditions, have been reported in the calcareous skeleton of several species.

Epizoic zoanthids occur occasionally at the surface of *Astrosclera* (Wörheide, 1998) and have been reported in detail in *Calcifibrospongia*, where the colonies cover the entire surface of the sponge with polyps regularly spaced and isolated from the sponge tissues by an armored cyst laid down by the sponge (Willenz & Hartman, 1994). *Astrosclera* and *Acanthochaetetes* could also harbor excavating polychaetes or barnacles that locally inhibit the normal skeletal growth of the host, giving a bioclaustration frequently found in various calcified invertebrates (Fig. 4.1–4.2; Tapanila, 2005). The lower part of the basal skeleton is regularly colonized by sessile organisms, such as thin encrusting sponges, lithistids, Calcarea, bryozoans, Foraminifera, and brachiopods. The basal skeleton can also be heavily invaded by boring sponges of *Aka*, *Cliona, Alectona,* or *Thoosa* (Fig. 4.5).

ECOLOGY AND GEOGRAPHIC DISTRIBUTION

All Recent hypercalcified sponges are sciaphilous, living in very dim light conditions or in total darkness in sublittoral caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundreds of meters for some species (Fig. 5; Vacelet, 1988). Most are found only in tropical or subtropical waters of the Indo-Pacific and West Atlantic zones. There are, however, a few exceptions. Although most of its known representatives are living in the tropical Indo-Pacific, *Plectroninia* (Calcarea) also has deep-sea species with a worldwide distribution, including cold areas, and has been recorded from littoral caves to 1600 m (Vacelet, Boury-Esnault, & Zibrowius, 1989; Könnecker & Freiwald, 2005). The genus *Merlia* (Demospongiae) has representatives with a circumtropical distribution and also occurs in warm temperate seas (Madeira, Mediterranean). *Petrobiona massiliana* (Calcarea) is restricted to sublittoral caves of the warm, temperate Mediterranean.

Under tropical conditions, depth distribution of hypercalcified sponges in the bathyal zone is usually above the thermocline, where

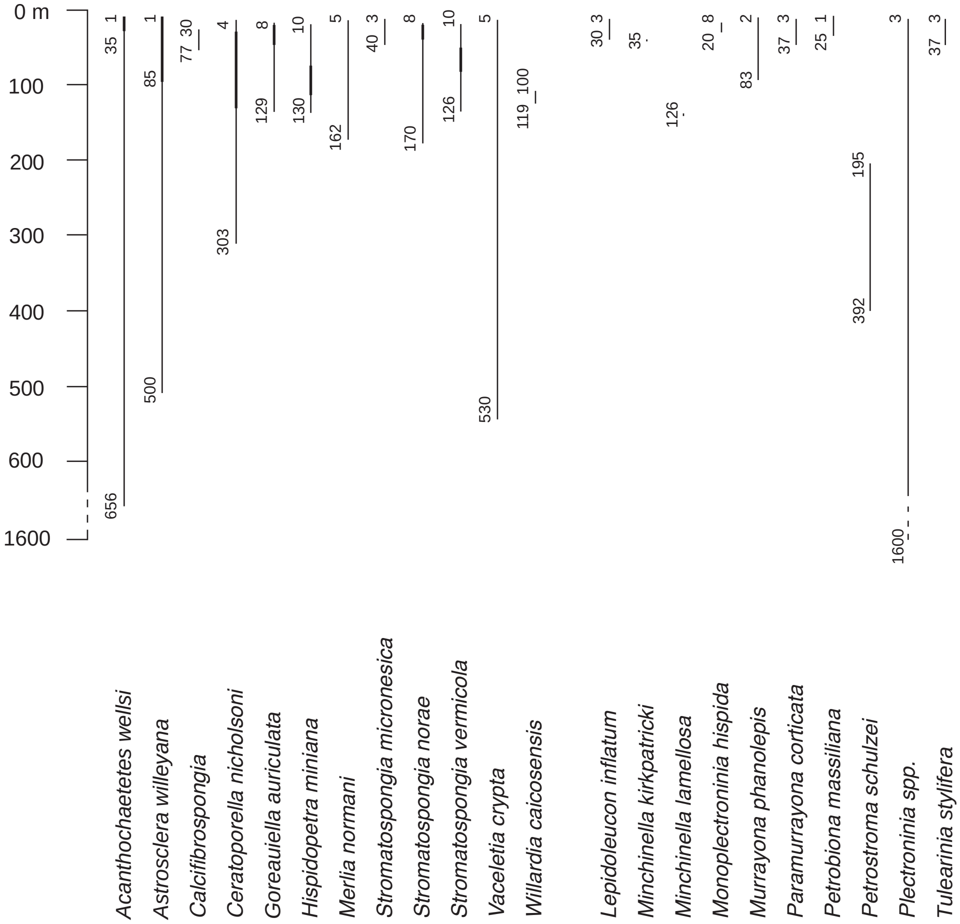

FIG. 5. Depth chart. Vertical distribution of extant hypercalcified taxa of Demospongiae and Calcarea, listed to the left and right sides, respectively. Optimum depth, where known, indicated by thickened bars (adapted from Vacelet, 1988, with addition of some species and unpublished data, Vacelet, 1998).

two species, *Ceratoporella nicholsoni* (LANG, HARTMAN, & LAND, 1975) and *Vaceletia crypta* (VACELET & others, 1992) could replace scleractinian corals as the main reef builders.

This localization in caves and bathyal cliffs, which were difficult to access before SCUBA diving and manned submersibles, may explain why, after the pioneering findings of KIRKPATRICK in the early 20th century, their rediscovery and the renewal of their interpretation are relatively recent. In these environments, most species proved to be, in fact, fairly common. For instance, *Acanthochaetetes wellsi* and *Astrosclera willeyana* appear now to be among the most common species in littoral caves and coral reef tunnels of the Pacific, and thousands of specimens of *Astrosclera*, *Acanthochaetetes*, *Vaceletia*, *Ceratoporella*, and *Petrobiona* have been collected. A few representatives, however, still appear to be quite uncommon or at least restricted to a few localities (representatives of *Calcifibrospongia*, *Willardia*, *Minchinella,* and *Petrostroma*).

Such ecological distribution appears to be different from that of fossil counterparts, which have been important reef builders, most probably in open habitats more or less similar to recent coral reefs. It appears likely that a general shift from open habitats toward cryptic habitats occurred in the survivors of ancient hypercalcified sponges. It has been hypothesized that such a shift occurred under competition with modern reef builders, which have a higher growth rate due to their symbiosis with photosynthetic microorganisms such as zooxanthellae.

The geographic distribution pattern is highly diverse. In the family Astroscleridae, *Astrosclera willeyana* has a large Indo-Pacific distribution, whereas the other genera are mostly distributed in the tropical West Atlantic, with only one Pacific representative. In Acanthochaetetidae, *Acanthochaetetes wellsi* is restricted to the Pacific and *Willardia caicosensis* to the Caribbean. In some widely distributed species, variations occur in different populations, and it is at present difficult to decide whether they represent intraspecific variations or different species. Such uncertainty occurs for *Astrosclera willeyana*, which has an extensive Indo-Pacific distribution from the Red Sea to the Central Pacific and has important spicule variations. Recent studies on rDNA internal transcribed spacer sequences suggest that some populations from the Central Pacific that are devoid of siliceous spicules (VACELET, 1981) may belong to different species (WÖRHEIDE, 1998; WÖRHEIDE & others, 2002). This is not confirmed by mtDNA COI sequences, however, which could be due to a general mtDNA conservation in sponges (WÖRHEIDE, 2006). Similarly, morphological and molecular data both suggest that the sphinctozoan *Vaceletia crypta* actually represents several species (G. WÖRHEIDE & J. VACELET, unpublished results, 2006).

CLASSIFICATION AND EVOLUTION

The living hypercalcified sponges, after having been classified in a high-level taxon, the class Sclerospongiae (HARTMAN & GOREAU, 1970), restricted to those with demosponge affinities, or the class Ischyrospongiae (TERMIER & TERMIER, 1974), including all representatives, are presently classified in various taxa of Demospongiae or Calcarea, according to their living tissue and skeleton characters. Among the Demospongiae, calcified representatives are found in most high-level taxons, the only exceptions being the Astrophorida, Spirophorida (Tetractinellida), and Homoscleromorpha. There is no known calcified Hexactinellida.

This classification appears sound, given the similarities between most of the calcified species and the normal, noncalcified species. A remarkable case is that of the genus *Merlia*, characterized by a highly diagnostic spiculation, including a unique microsclere (clavidisc), in which forms with and without a calcareous skeleton coexist (Fig. 2.5–2.6) (VACELET, 1980a). These forms, according to some authors, are considered as belonging to the same species (SOEST, 1984). *Acanthochaetetes wellsi* has sometimes been classified into the noncalcified genus *Spirastrella*. Most authors, however, consider that the presence of a hypercalcified, calcareous skeleton is a phylogenetically significant character. In a few cases, the affinity between a calcified sponge and its noncalcified relatives has been confirmed by molecular data (CHOMBARD & others, 1997). Only the living sphinctozoan, *Vaceletia crypta*, which has no spicular or fibrous skeleton and a living tissue that does not indicate clear affinities, has been assigned *incertae sedis* within the Demospongiae; but recent results from molecular phylogeny indicate close affinities with the keratose sponge order Dictyoceratida (WÖRHEIDE, 2008). This raises the possibility that some fossil sphinctozoans still included in the order Verticillitida may also have had affinities with keratose sponges.

The living survivors suggest that a more phylogenetic classification, in agreement with the characters of the living tissue, could be considered for the fossil counterparts. It would appear sound to classify together the sponges with a spherulitic skeleton with intracellular secretion of aragonite spherules, known in *Astrosclera* and several Permo-Triassic fossils belonging to various morphological grades (CUIF & GAUTRET, 1991). The microstructure of the calcified skeleton appears to be highly specific, allowing in a few cases to propose a homogeneous classification for the living and the fossil representatives. Fossil examples of the Acanthochaetetidae exhibit affinities with the living Spirastrellidae, and so they may be classified in the order Hadromerida. Fossil chaetetids (see p. 209–292) that have a calcareous skeleton similar in morphology and in microstructure to that of *Merlia*, such as species of *Chaetetes* and *Blastochaetetes* (GAUTRET, VACELET, & CUIF, 1991), may be classified in the Poecilosclerida. Also, there is evidence that stromatoporoids with affinities to *Calcifibrospongia* are members of the order Haplosclerida. However, this classification is difficult to extend to fossil faunas, in which the living tissue and most often the spicules have disappeared, and in which the skeletal microstructure is generally poorly preserved. Furthermore, the fossil forms were certainly more diversified than the few survivors. The few informative cases do not mean that all fossils belonging to the chaetetid and stromatoporoid morphological grades, which were considerably more diversified in the past, actually belong to the taxa defined by the zoologists. In consequence, a classification based mainly on the morphological characters available in fossils has to be maintained, although these morphological grades may not have true taxonomic value.

The number and variety of fossil taxa as compared to the few survivors, which are nevertheless remarkably diversified, suggest that the secretion of a calcified skeleton was more general in the past, especially in periods of high activity in reef construction. The ability to build a calcified skeleton seems to have been lost in most of the Recent sponges, either because of changes in the physicochemical environments or because of competition with more successful reef-builders such as scleractinian corals.

INTRODUCTION TO THE FOSSIL HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

Ronald R. West

In this introduction to chaetetid hypercalcified demosponges, it is pertinent to review briefly the history of relevant extant and fossil species, and key features used to recognize the fossil representatives.

Döderlein (1892, 1897) described *Petrostroma schulzei*, an extant sponge from Japan with a massive calcareous skeleton composed in part of fused spicules. This appears to be the first report of a living sponge with a hypercalcified basal skeleton. Lister (1900) described *Astrosclera willeyana;* then, in 1911, Hickson described *Ceratopora nicholsoni* (now *Ceratoporella nicholsoni*), and Kirkpatrick (1912a) described *Merlia normani*, all three extant taxa with a calcareous skeleton. Kirkpatrick (1912a) noted that *Merlia normani* was of a similar nature to the Paleozoic fossil types, broadly termed *"Monticulipora"* or *"Monticuliporas,"* and he also, importantly, recognized *"Chaetetes"* as being related (Kirkpatrick, 1912c, p. 562).[*] At that time, *Monticulipora* was considered to be a bryozoan by Grabau and Shimer (1909, p. 127) and Zittel (1913, p. 331).

Earlier, Nicholson (1874, p. 500) stated that *Chaetetes* and *Monticulipora* were identical and considered *Monticulipora* to be a tabulate coral (Nicholson, 1879a, p. 201). Still earlier, Duncan (1872) regarded *Chaetetes*, along with *Monticulipora* and other genera, as alcyonarian corals. This is important because (1) the skeleton of *Merlia* is similar to *Chaetetes;* and (2) Nicholson (1879a, p. 201) included *Chaetetes* with *Monticulipora* as tabulate corals. However, Nicholson (1881, p. 79) eventually accepted that, despite the close similarities between the massive types of *Chaetetes* and *Monticulipora,* they were different forms. He did not include *Chaetetes* in his new family, the Monticuliporidae (Nicholson, 1881 p. 90)which was later transferred to the trepostome bryozoans (see Bassler, 1953). Although *Chaetetes* was not included in Grabau and Shimer (1909), it was grouped with tabulate corals by Zittel (1913, p. 117). Though most workers (e.g., Hill, 1981) accepted *Chaetetes* as a tabulate coral, others still considered it to be a bryozoan (e.g., Peterhans, 1929b).

In addition to extant species, fossil species of *Astrosclera* are known from the Triassic, and Reitner (1992), Wörheide (1998), and Reitner and others (2001) considered the calcareous skeleton as being similar to that of fossil stromatoporoids. The calcareous skeleton of both *Merlia* and *Ceratoporella* is similar to that in fossil chaetetids (Hartman & Goreau, 1972; Vacelet, 1990; Reitner, 1992) but the microstructure of these two extant taxa is different (Cuif & Gautret, 1993). However, there is a similarity in the microstructure of *Merlia normani* and the fossils *Chaetetes (Chaetetes) cylindricus* (Fischer von Waldheim, 1837) and *Blastochaetetes bathonicus* (Cuif & Gautret, 1993). The different microstructure in extant *Ceratoporella* and *Astrosclera* is reported in fossil chaetetids from the Permian and Mesozoic (Wendt, 1984; Gautret & Razgallah, 1987; Cuif & Gautret, 1991, 1993).

Although Kirkpatrick (1912a) suggested that chaetetids and other taxa, including stromatoporoids, were siliceous sponges with a supplementary calcareous skeleton, it was not until after Hartman and Goreau (1966, 1970, 1972, 1975, 1976) rediscovered living sponges with a calcareous skeleton in reefal environments

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[*] Quotation marks denote the first reference, in this discussion, of a broader, earlier conception of these generic names.

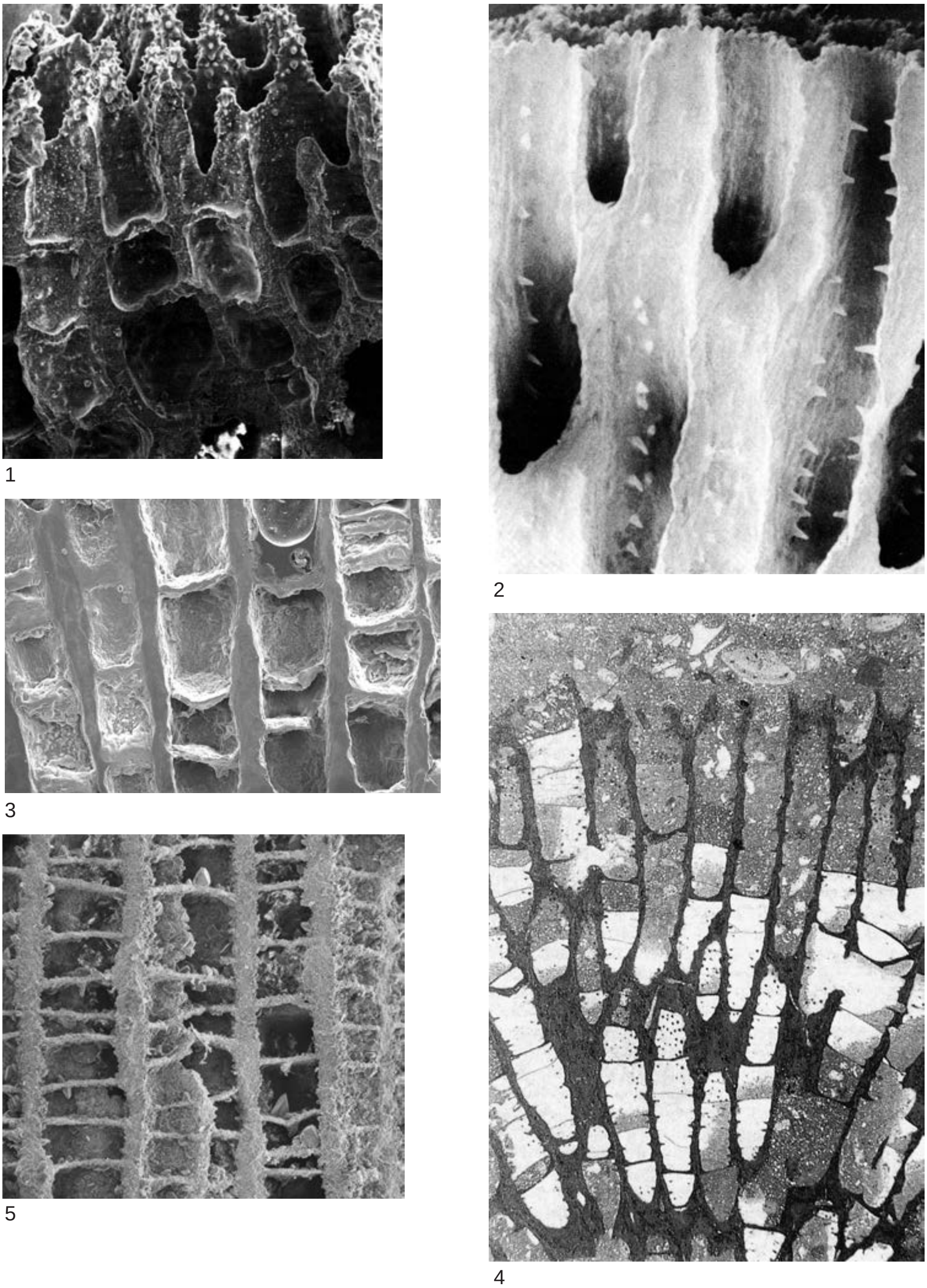
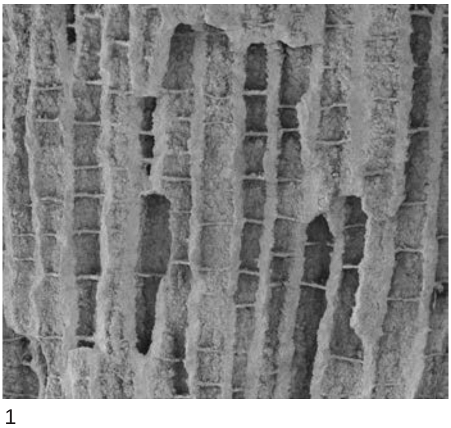


FIG. 6. Rigid aspicular skeletons in chaetetid sponges; *1,* SEM of a longitudinal fracture of *Merlia lipoclavidisca*, an extant form, from La Catedral cave at a water depth of 12 m, Balearic Islands, Mediterranean Sea, ×70 (adapted from Vacelet & Uriz, 1991, p. 172, fig. 2a, with kind permission of Springer Science+Business Media); *2,* SEM of a longitudinal fracture of *Acanthochaetetes wellsi,* an extant form, locality not given, probably a cave at Anae *(Continued on facing page.)*

of the Caribbean and Indo-Pacific regions during the late 1960s and early 1970s that there was some acceptance of this view. Cuif and others (1973) described astrorhizae from Mesozoic (Triassic of Turkey and Cretaceous of Spain) chaetetids. Gray (1980) documented spicule pseudomorphs in Carboniferous chaetetids from the United Kingdom, and West and Clark (1983, 1984) illustrated astrorhizae in Carboniferous (Pennsylvanian) chaetetids from Kansas. Newell (1935) reported the Paleozoic stromatoporoid *Parallelopora* with spicules from the same succession, and Galloway (1957, p. 450) recognized it as a sponge, thus excluding it from this stromatoporoid genus, as did Flügel and Flügel-Kahler (1968, p. 270), who recognized the presence of spicules. A reexamination of Newell's (1935) specimens confirmed their occurrence (Wood, Reitner, & West, 1989).

Other extant sponges with a calcareous skeleton were recognized, and of particular importance was the description of an extant species of the Mesozoic genus of *Acanthochaetetes* as *A. wellsi* by Hartman and Goreau (1975) from cryptic reefal habitats in the Pacific. There are now at least three extant sponge taxa with a calcareous skeleton that resemble the fossil chaetetids. Also, comparing the extant *Ceratoporella nicholsoni* with the calcareous skeleton of fossil chaetetids led Hartman and Goreau (1972) to place the chaetetids in the phylum Porifera and suggested to them that ceratoporellids, with a range back into the Permian, were their descendants. Although a taxonomic home for fossil chaetetids was now better established, there were still problems. Sponges are differentiated taxonomically on the basis of the composition and morphology



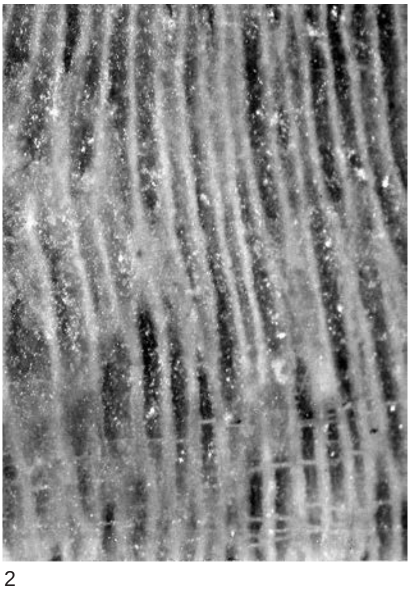


Fig. 7. Rigid aspicular skeletons in chaetetid sponges (continued); *1,* SEM of a longitudinal fracture of *Chaetetes (Chaetetes) radians*, Carboniferous, Pennsylvanian (probably Moscovian), Moscow Basin, Russia, ×15 (West, 2011a); *2,* longitudinal thin section of a chaetetid skeleton, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×14 (West, 2011a).

Fig. 6. *Continued from facing page.*
Island, Guam, ×40 (adapted from Hartman & Goreau, 1975, fig. 6; courtesy of Yale Peabody Museum of Natural History); *3,* longitudinal section (SEM) of *Acanthochaetetes* sp., an extant form, collected live in October 2005 off the Komesu coast, southern Okinawa, at a water depth of 15 m, ×50 (West, 2011a); *4,* longitudinal thin section of *Acanthochaetetes seunesi,* Cretaceous, Cenomanian form, locality not given, probably from the Pyrenees, magnification not given, probably ×10 (adapted from Wood, 1990b, p. 230, fig. 7; for a color version, see *Treatise Online,* Number 20: paleo.ku.edu/treatiseonline); *5,* SEM of a longitudinal fracture of a chaetetid skeleton, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×30 (West, 2011a).

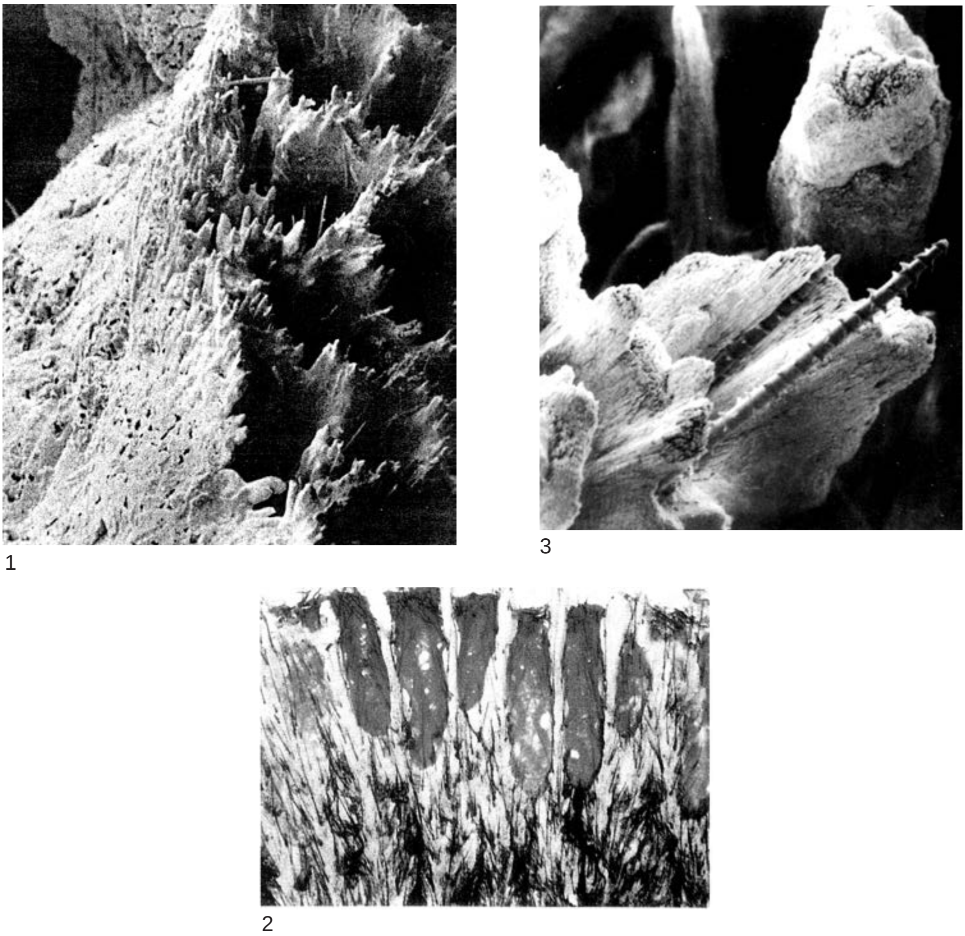


FIG. 8. Rigid spicular skeletons in chaetetid sponges; *1,* SEM of an oblique view of the upper surface of *Ceratoporella nicholsoni,* an extant form, locality not given, probably from the Caribbean, ×70 (adapted from Hartman & Goreau, 1972, fig. 8; courtesy of *Transactions of the Connecticut Academy of Arts and Sciences*); *2,* longitudinal section of *Ceratoporella nicholsoni,* an extant form (note megascleres, dark lines within skeleton), locality not given, probably from the Caribbean, magnification not given, probably ×10 (adapted from Wood, 1990b, p. 228, fig. 5); *3,* SEM of an oblique fracture of *Stromatospongia micronesica*, an extant ceratoporellid sponge, showing siliceous spicules overgrown by the aragonitic skeleton, western Pacific, probably Micronesia, ×370 (adapted from Hartman & Goreau, 1976, p. 347, fig. 14).

of their spicules, and spicules are virtually absent in fossil chaetetids. Additionally, the spicules in the extant genera placed those genera in different poriferan subclasses. WOOD (1990b) summarized the resulting confusion and ultimate solution, namely that the chaetetid skeleton is a grade of organization with no high systematic value, and it belongs in the Tetractinomorpha and Ceractinomorpha, two of the three subclasses of the Demospongiae. Both of these subclasses extend back into the Paleozoic, and, to better understand hypercalcified demosponges with a chaetetid skeleton, it is

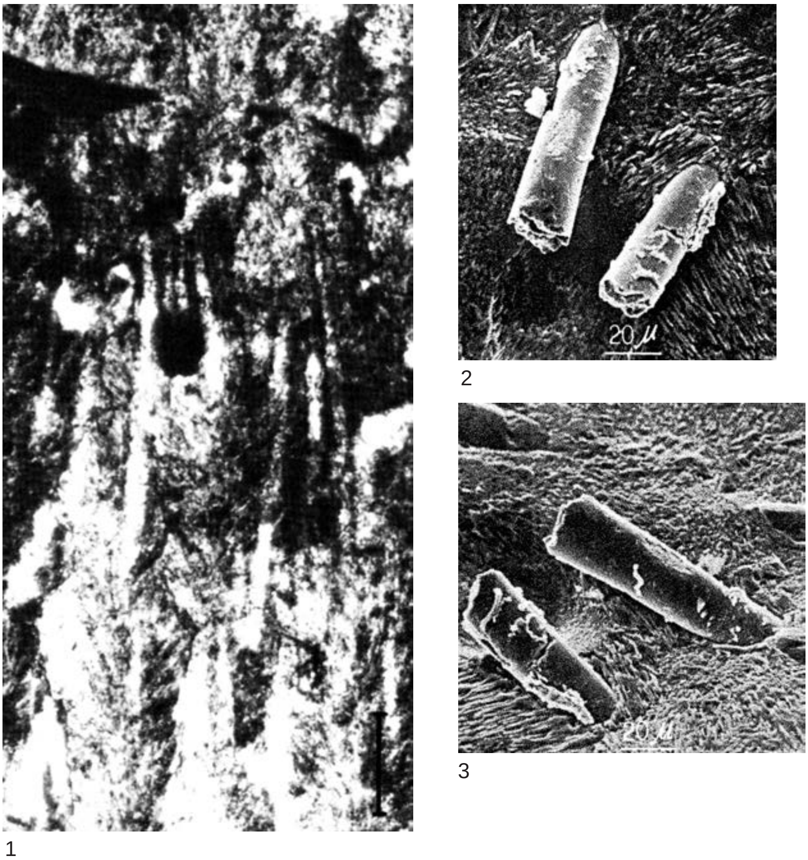


FIG. 9. Rigid spicular skeletons in chaetetid sponges (continued); *1,* longitudinal thin section of *Calcisuberites stromatoporoides,* showing spicules incorporated into high Mg calcite skeleton, Upper Cretaceous (Turonian–Coniacian), near Oberwossen, Bavaria, ×65 (adapted from Reitner, 1992, pl. 23,*3;* courtesy of *Berliner Geowissenschaftliche Abhandlungen,* Free University, Berlin); *2,* SEM of pyritized spicules, pseudomorphs, within basal calcareous skeleton of *Meandripetra zardinii*, Upper Triassic (Carnian), San Cassiano beds near Cortina d'Ampezzo, Italy, ×700 (adapted from Dieci & others, 1977, pl. 2,*3a;* courtesy of *Bollettino della Societa Paleontologica, Italiana*); *3,* same as view *2,* but another area of *Meandripetra zardinii*, ×700 (adapted from Dieci & others, 1977, pl. 2,*3b;* courtesy of *Bollettino della Societa Paleontologica, Italiana*).

necessary to consider, in some detail, their living descendants. However, recent studies (BORCHIELLINI & others, 2004; BOURY-ESNAULT, 2006) have shown that these two subclasses are polyphyletic and their use should be abandoned. Consequently, the fossil genus *Chaetetes* is treated here as a form genus and its constituent subgenera and species also have the status of form taxa.

EXTERNAL MORPHOLOGY

The skeleton of hypercalcified demosponges is a rigid aspicular skeleton (Fig. 6–7), a rigid spicular skeleton (Fig. 8–9),

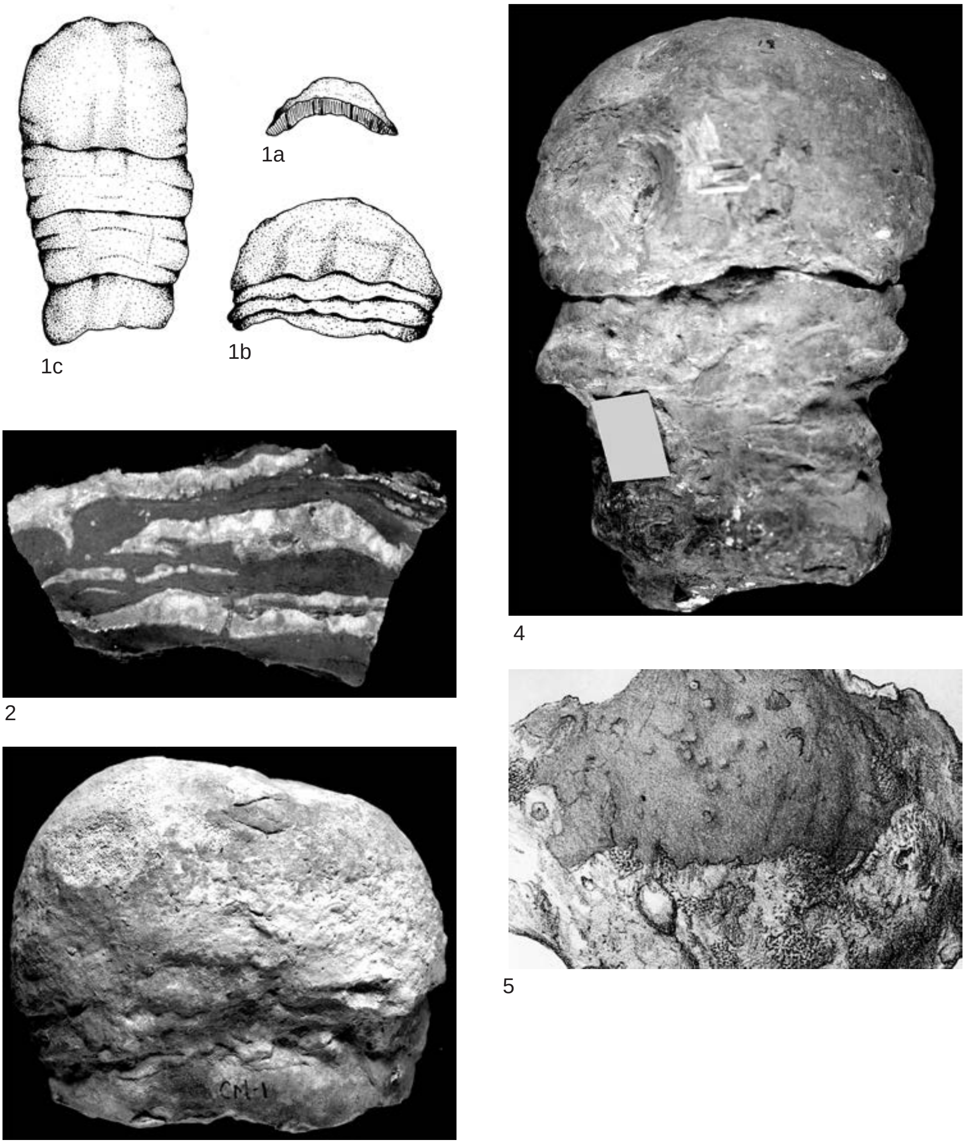


Fig. 10. Basal calcareous skeleton of chaetetid sponges; *1a–c,* basic shapes of chaetetid skeletons; *a,* laminar, *b,* ragged, low domical, *c,* columnar (West & Clark, 1984, p. 339, fig. 3; courtesy of Paleontological Research Institution, Ithaca, New York); *2,* laminar (multiserial, single layer) chaetetids, Carboniferous, Pennsylvanian, southeastern Kansas, ×0.5 (West, 2011a); *3,* domical (multiserial, multilayered) chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.35 (West, 2011a); *4,* columnar (multiserial, multilayered) chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.65 (West, 2011a); *5,* extant *Merlia normani,* a single (multiserial) layer encrusting a volcanic rock, ×0.6 (adapted from Kirkpatrick, 1911, pl. 32,*4;* for a color version, see *Treatise Online,* Number 20: paleo.ku.edu/treatiseonline).

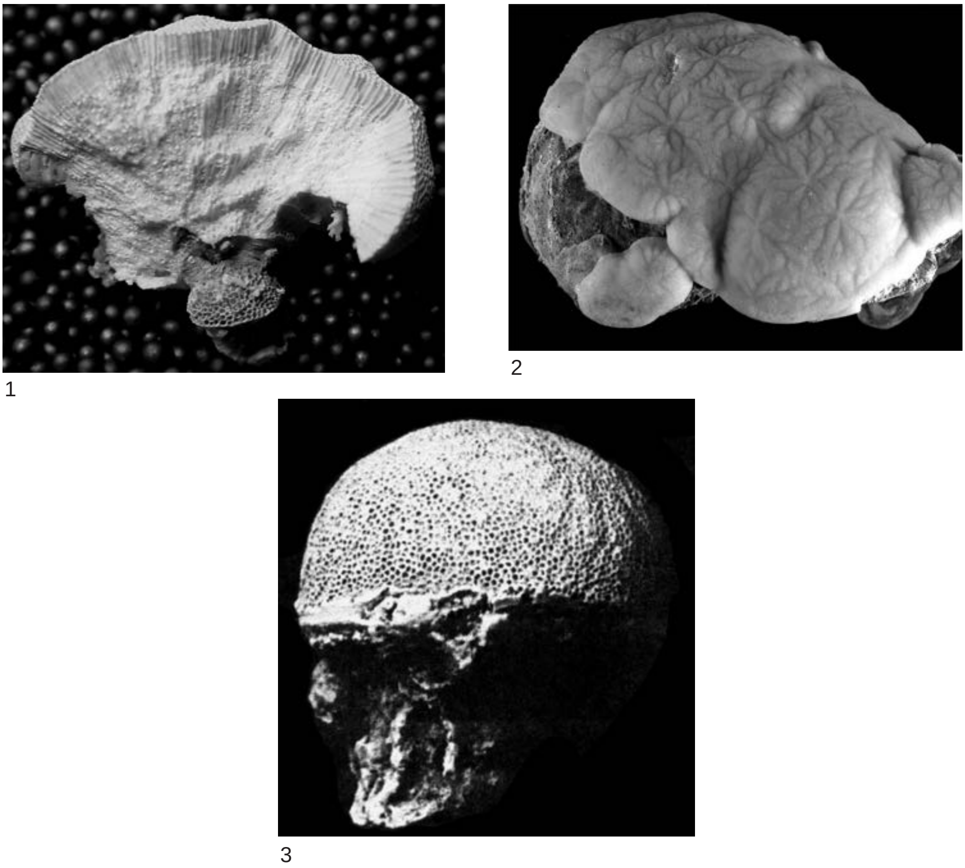
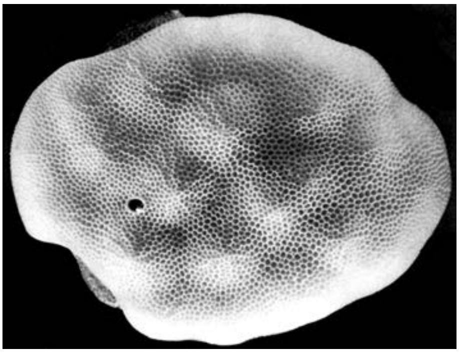


FIG. 11. Basal calcareous skeleton of chaetetid sponges (continued); *1,* extant *Acanthochaetetes* sp., a small domical (multiserial, multilayered) pedunculate specimen, collected live in October 2005 off the Komesu coast, southern Okinawa, at a water depth of 15 m, ×1.7 (West, 2011a); *2,* extant *Ceratoporella nicholsoni*, a small domical (multiserial, multilayered) specimen from Pear Tree Bottom, Runaway Bay, Jamaica, in a tunnel at a depth of 85 feet, ×0.65 (West, 2011a); *3,* a small domical, pedunculate specimen of *Atrochaetetes lagaaiji*, Triassic, Cassian Formation, northern Italy, ×3.3 (adapted from Engeser & Taylor, 1989, p. 51, fig. 8A; courtesy of the Natural History Museum, London).



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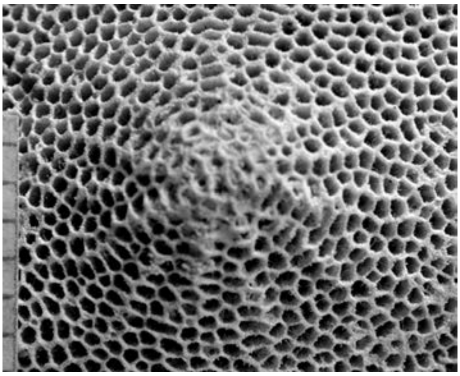

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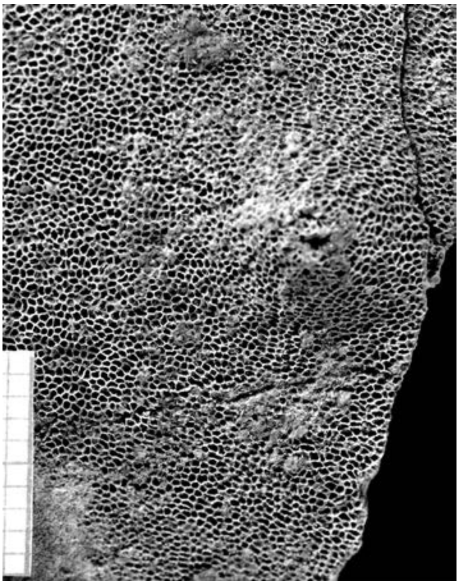

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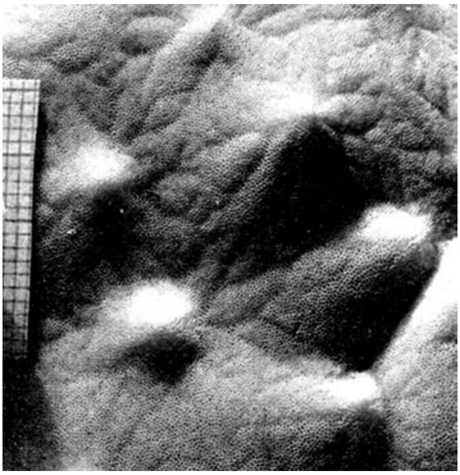

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FIG. 12. External features of chaetetid skeletons: astrorhizae and mamelons; *1, Acanthochaetetes wellsi,* with mamelons and astrorhizae from underwater cave, Anae Island, Guam at 7.5 to 9 m, paratype, YPM No. 9078, ×1.45 (adapted from Hartman & Goreau, 1975, fig. 1; courtesy of Yale Peabody Museum of Natural History); *2, Acanthochaetetes wellsi,* with astrorhizae on mamelon from Augulpelu Reef, Palau Island, southwestern wall of a cave at a depth of 12.2 m, ×4 (West, 2011a); *3,* fossil chaetetid with eroded astrorhizae on mamelon, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×3 (West, 2011a); *4, Ceratoporella nicholsoni,* with mamelons and astrorhizae from subreef tunnel off Runaway Bay, Jamaica, at a depth of 30 m, ×1.5 (adapted from Hartman & Goreau, 1970, p. 211, fig. 6).

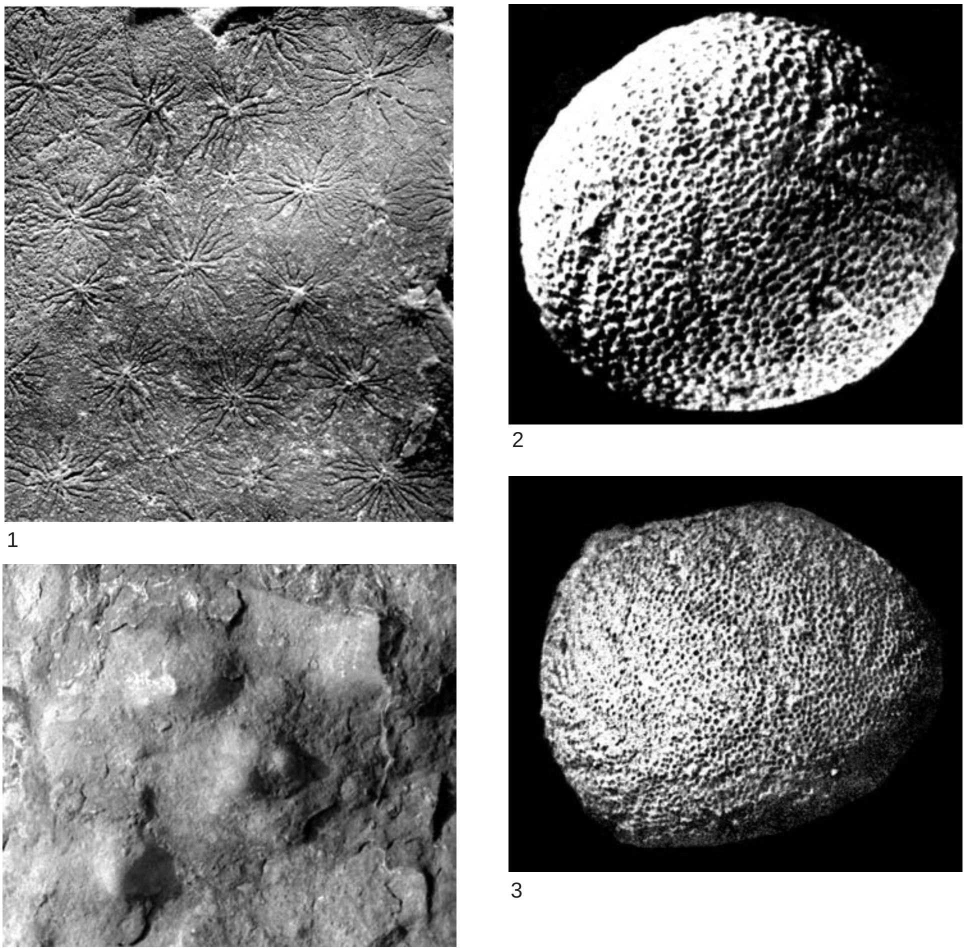


FIG. 13. External features of chaetetid skeletons: astrorhizae and mamelons (continued); *1,* fossil chaetetid with astrorhizae, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×2 (West, 2011a); *2, Cassianochaetetes* sp., with astrorhizae, Triassic, Cassian Formation, northern Italy, ×6.5 (adapted from Engeser & Taylor, 1989, p. 49, fig. 7C; courtesy of the Natural History Museum, London); *3, Atrochaetetes lagaaiji,* with astrorhizae, Triassic, Cassian Formation, northern Italy, ×3.3 (adapted from Engeser & Taylor, 1989, p. 51, fig. 8B; courtesy of the Natural History Museum, London); *4,* upper surface of laminar chaetetid with mamelons, Carboniferous, Pennsylvanian, Laberdie Limestone Member, Pawnee Limestone, Bourbon County, Kansas, ×0.5 (West, 2011a).

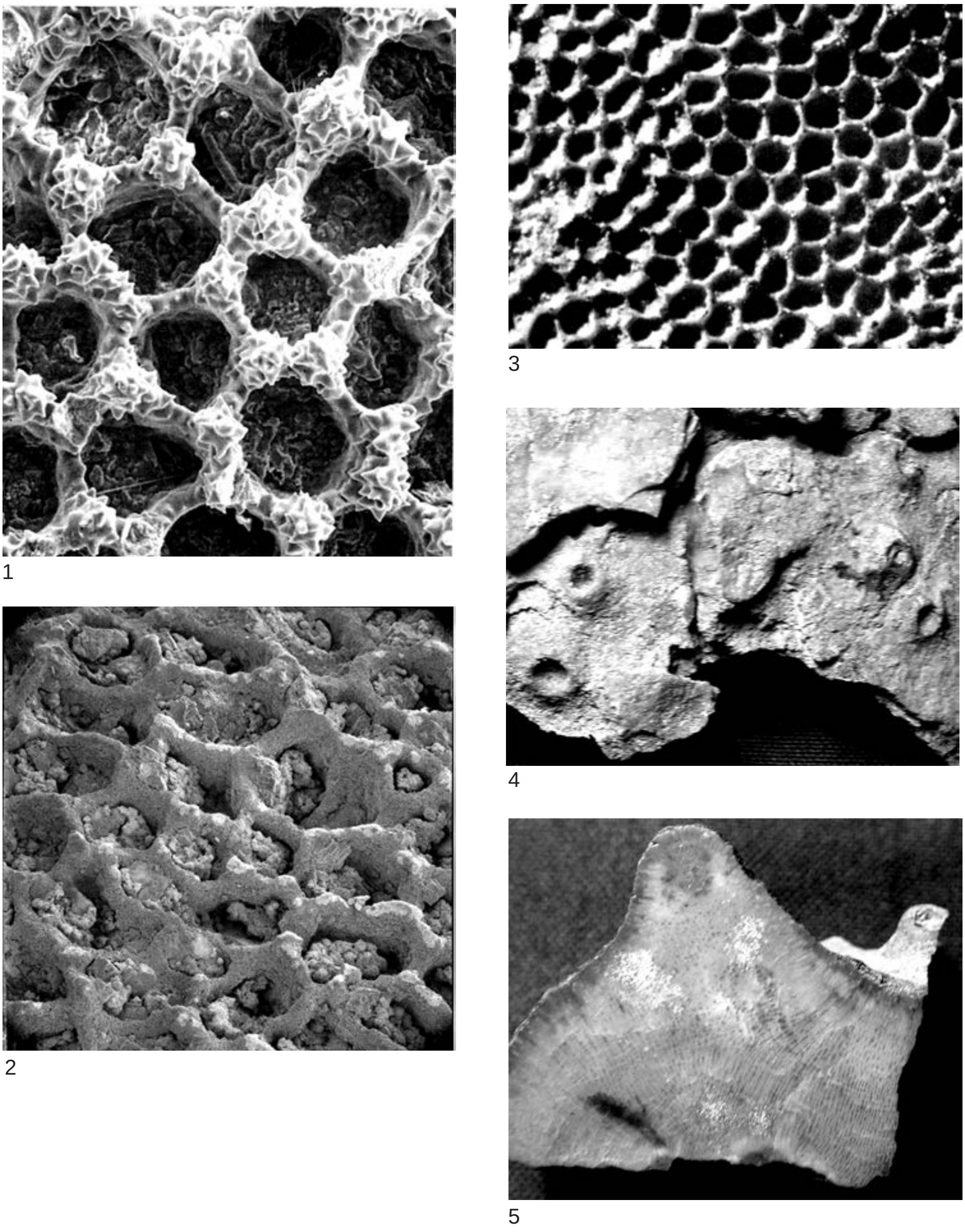


FIG. 14. *(For explanation, see facing page).*

or a combination of both. Morphological features of the exterior of this skeleton are the following: (1) general shape of the calcareous skeleton (Fig. 10–11); (2) surface features such as astrorhizae, mamelons, chimneys, and tubercules (Fig. 12–14); and (3) the numerous, vertically partitioned tubes, or tubules (Fig. 15–16) that compose the calcareous skeleton.

What becomes the rigid calcareous chaetetid skeleton is the result, initially, of sexual reproduction; however, the details of fertilization and larval development in extant taxa are still largely unknown (see p. 10). This sexually produced individual increases asexually (i.e., by cloning; see West & others, 2010) and the resulting clone may become differentiated into functional units, a form of modularity (Wood, Zhuravlev, & Debrenne, 1992). The degree of the structural relationship between the resulting modules may suggest interdependence expressed as low, medium, or high skeletal integration (Wood, Zhuravlev, & Debrenne, 1992, p. 133). Wood, Zhuravlev, and Debrenne (1992, p. 138, fig. 4) illustrated eight different modular-type skeletons recognized in hypercalcified sponges. Chaetetid skeletons are considered to be highly integrated and multiserial, and there are both horizontal and erect multiserial skeletons (Wood, 1999, p. 223, table 6.4). Most chaetetid skeletons are either highly integrated, multiserial, single layered (encrusting), horizontal sheets, or highly integrated, multiserial, multilayered, horizontal (massive) forms (Wood, 1999, p. 223, table 6.4). Wood, Zhuravlev, and Debrenne (1992, p. 135) described some extant hypercalcified sponges ". . . with multiserial massive (e.g., *Ceratoporella*), encrusting (e.g., *Merlia normani*, *Stromatospongia vermicola*) or pedunculate, saucer-shaped morphologies (*Goreauiella auriculata*)." Certainly, the skeleton of *Acanthochaetetes wellsi* should also be considered multiserial and single layered; see External Morphology of the Paleozoic Stromatoporoidea: Shapes and Growth Habits, p. 419–486, for a discussion of an appropriate use of encrust and encrusting. Less common are highly integrated, multiserial, erect chaetetid skeletons (Wood, 1999, p. 223, table 6.4).

Fig. 14. External features of chaetetid skeletons: tubercules and chimneys; *1,* SEM of the surface of *Merlia lipoclavidisca,* an extant form, note tubercules, from La Catedral cave at a water depth of 12 m, Balearic Islands, Mediterranean Sea, ×100 (adapted from Vacelet & Uriz, 1991, p. 172, fig. 2c, with kind permission of Springer Science+Business Media); *2,* SEM of the surface of a fossil chaetetid, note tubercules, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×40 (West, 2011a); *3,* surface of fossil chaetetid with tubercules, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×15 (adapted from West & Clark, 1984, p. 341, pl. 1,*C;* courtesy of Paleontological Research Institution, Ithaca, New York); *4,* surface of fossil chaetetid with chimneys, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma, ×1 (West, 2011a); *5,* longitudinal section of chimney in chaetetid, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma, ×1.3 (West, 2011a).

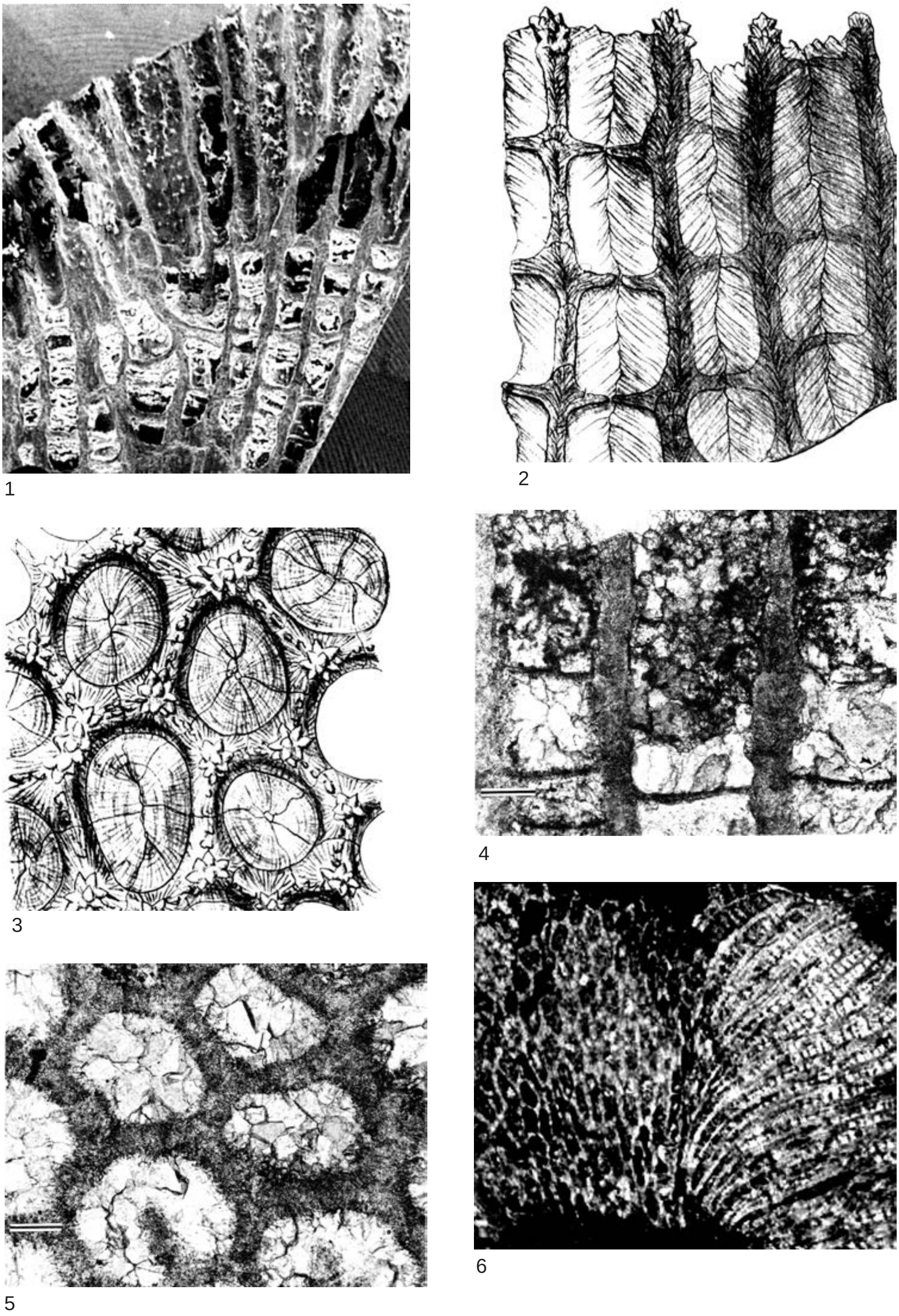


FIG. 15. *(For explanation, see facing page).*

The shape, or gross morphology, of chaetetids is like that of other hypercalcified demosponges, namely: nodular, branching, columnar, laminar, or domical, and may be referred to as the growth form. The relationship between growth morphology and growth form is given in the Glossary (see p. 397–416). As pointed out by WEST and KERSHAW (1991), there are essentially three basic growth forms in chaetetids: laminar, domical, and columnar. These are synonymous, respectively, with what STANTON, CONNOLLY, and LAMBERT (1994) termed tabular, hemispherical, and columnar. In terms of skeletal integration, a multiserial, encrusting growth would produce a laminar form, and the other two growth forms would be the result of a multiserial, massive growth. Domical, multiserial massive skeletons would be roughly equidimensional, and in columnar skeletons, the height would exceed the width. The basic building block of most chaetetids is a thin laminar sheet, and thus one might consider that there is a single growth form: laminar (Fig. 10–11; Fig. 17). As shown in Figure 17, laminar growth can result in domical and columnar masses, as well as in forms with more complex geometries. Such complex geometries are probably the result of environmental perturbations and may be referred to as digitate, branching, anastomosing, or other terms, but essentially they are the result of one or more of the three basic growth forms (Fig. 18–22). Although the calcareous skeleton of chaetetids is composed of tubules, the resulting

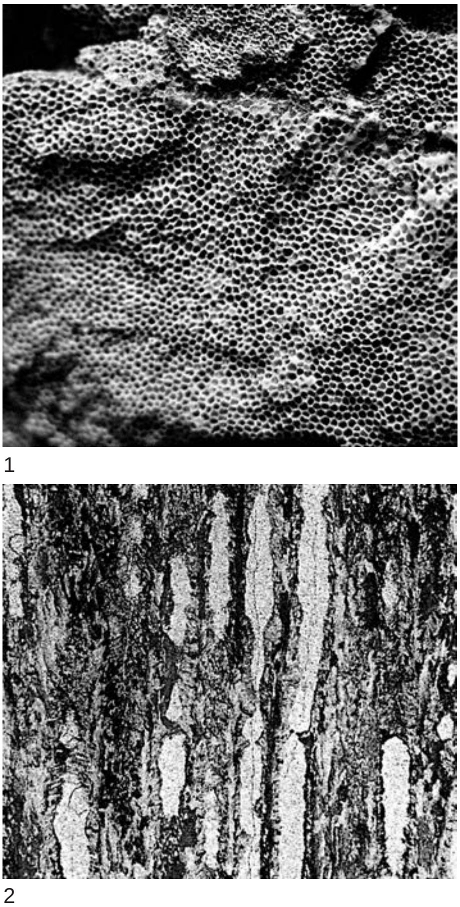


FIG. 16. Internal features of chaetetid skeletons: walls and tubules (continued); *1,* surface expression of tubules in a fossil chaetetid, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Bourbon County, Kansas, ×5 (adapted from Brosius, 2006, p. 42, fig. 58B; courtesy of Kansas Geological Survey, Lawrence); *2,* longitudinal thin section of tubules in *Atrochaetetes alakirensis*, Upper Triassic (Carnian), southwestern Turkey, ×20 (adapted from Cremer, 1995, pl. 25,*2;* courtesy of *Geobios,* Université Lyon).

FIG. 15. Internal features of chaetetid skeletons: walls and tubules; *1,* longitudinal section (SEM) of tubules in *Acanthochaetetes wellsi,* Guam, western Pacific, ×13 (adapted from Reitner, 1991a, p. 196, fig. 11a, with kind permission of Springer Science+Business Media); *2,* longitudinal section of tubules in *Merlia normani,* ×130 (adapted from Kirkpatrick, 1911, pl. 35,*17*); *3,* transverse section of tubules in *Merlia normani,* ×130 (adapted from Kirkpatrick, 1911, pl. 35,*16*); *4,* longitudinal thin section of tubules in a fossil chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×75 (adapted from West & Clark, 1984, p. 341, pl. 1,*B;* courtesy of Paleontological Research Institution, Ithaca, New York); *5,* transverse thin section of tubules in a fossil chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×70 (adapted from West & Clark, 1984, p. 341, pl. 1*A;* courtesy of Paleontological Research Institution, Ithaca, New York); *6,* longitudinal thin section of tubules in a fossil chaetetid, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×12 (West, 2011a).

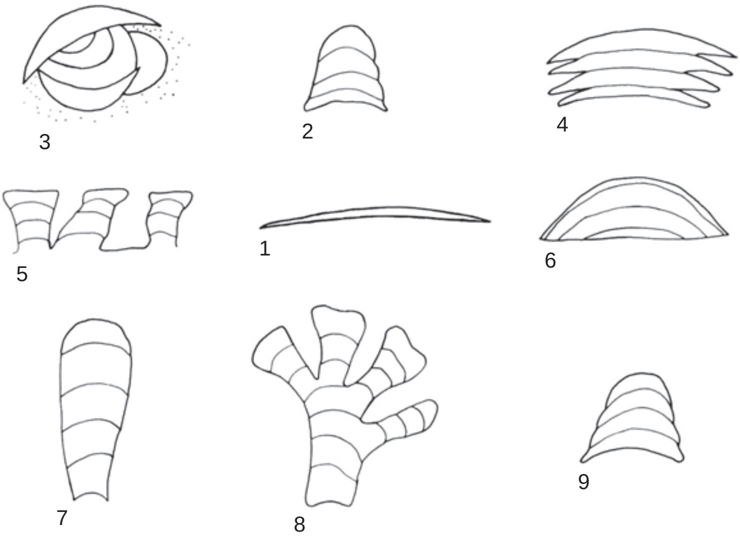
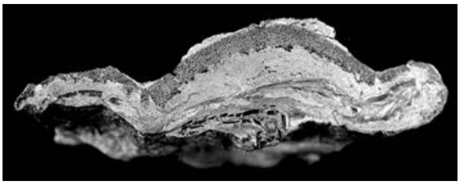


FIG. 17. Possible environmental controls on growth of the chaetetid skeleton, with the basic building block being a laminar accretionary unit; *1,* laminar accretionary unit; *2,* growth on a soft substrate; *3,* turbulence during growth; *4,* periodic sedimentation during growth; *5,* inferred growth to sea level; *6,* no sedimentation during growth; *7–9,* different inferred results of growth in areas of very slow, continuous sedimentation (adapted from Kershaw & West, 1991, p. 342, fig. 7).

shapes and growth habits are similar to that observed in stromatoporoids. WEBBY and KERSHAW (see p. 419–486) discuss in detail the external morphology of Paleozoic stromatoporoids in terms of their shapes and growth habits. In large part, this discussion also applies to chaetetids. STANTON, CONNOLLY, and LAMBERT (1994, fig. 1) illustrated what they considered axial growth and suggested that it might be taxonomically important. Specimens that appear to demonstrate axial growth are often poorly preserved, either partially or completely silicified (STANTON, CONNOLLY, & LAMBERT, 1994), or completely recrystallized. Such diagenetic changes, and others, significantly alter skeletal features. Axial growth in chaetetids may occur, but further study is needed for it to be clearly demonstrated and its possible taxonomic value assessed.

The ancestral part, i.e., initiation, of the calcareous skeleton of extant and fossil chaetetid skeletons is unknown. Thus, it can only be inferred that the entire basal area of any particular chaetetid growth form began at the same time from a thin layer or sheet of soft tissue. Although upward growth of all the tubules from the base appears to be simultaneous, there are differences. Based on studies of thin sections, polished surfaces, and acetate peels, KERSHAW and WEST (1991) reported five different styles of initial growth of the calcareous skeleton in chaetetids. These are shown in Figure 23. Some of these differences appear to be influenced by the substrate (Fig. 23.5; Fig. 24–25), but causes of the other observed differences are currently unknown (Fig. 23.1–23.4). As noted by WEST and KERSHAW (1991,



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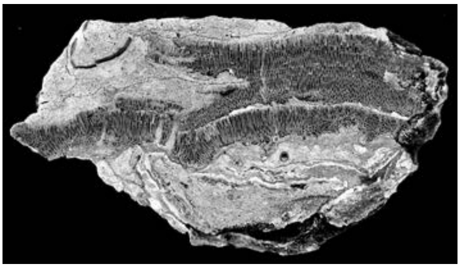

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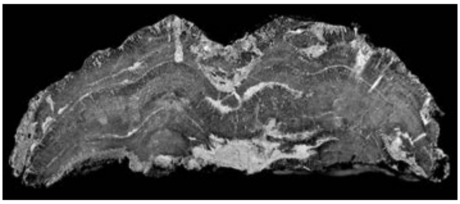

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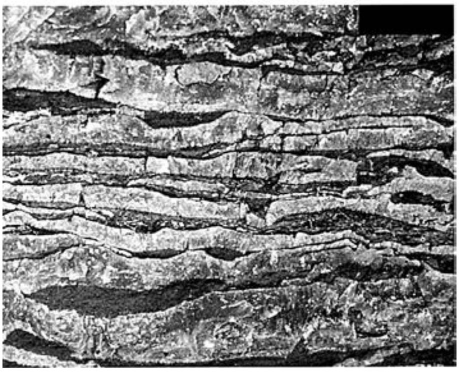

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FIG. 18. Laminar chaetetid growth forms, Carboniferous, Pennsylvanian; *1,* laminar growth of a chaetetid skeleton on an irregular substrate, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.85 (West, 2011a); *2,* laminar growth of a chaetetid skeleton on an oncoid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.85 (West, 2011a); *3,* laminar growth of a chaetetid skeleton on an irregular surface that resulted in a bimodal, low domical form, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.5 (West, 2011a); *4,* laminar to ragged domical chaetetids in a carbonate mudstone, Blackjack Creek Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.1 (West, 2011a); *5,* closely stacked laminar chaetetid skeletons in an argillaceous carbonate mudstone, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas, ×0.45 (adapted from Miller & West, 1997, p. 293, fig. 4A); *6,* bowl-shaped laminar chaetetid skeletons surrounded by argillaceous carbonate mudstone, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas, ×0.35 (adapted from Miller & West, 1997, p. 293, fig. 4B).

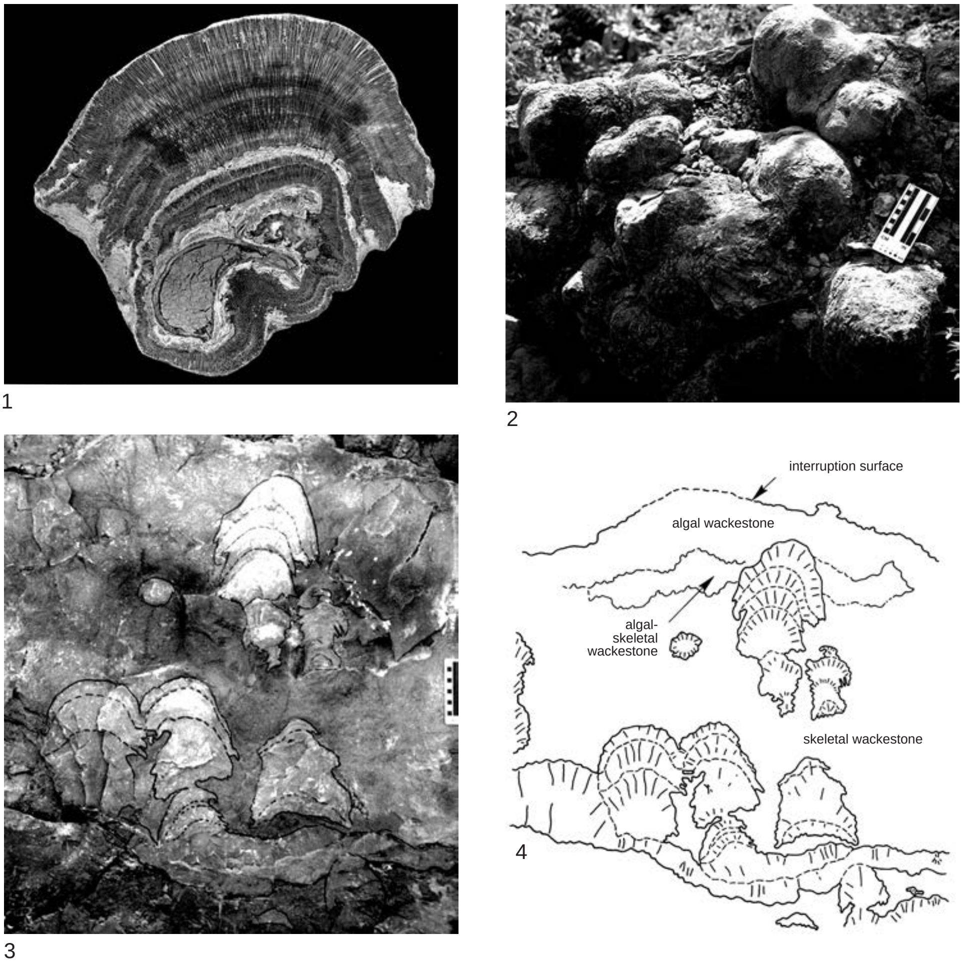


FIG. 19. Domical chaetetid growth forms, Carboniferous, Pennsylvanian; *1,* low domical chaetetid produced by laminar chaetetid encrusting an oncoid that formed around a productid brachiopod valve, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.55 (West, 2011a); *2,* upper surface of domical chaetetids, Higginsville Limestone Member, Fort Scott limestone, Crawford County, Kansas, ×0.075 (West, 2011a); *3,* laminar to ragged, high domical chaetetids, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.075 (West, 2011a); *4,* modified interpretive sketch of area shown in view *3,* ×0.09 (West, 2011a).

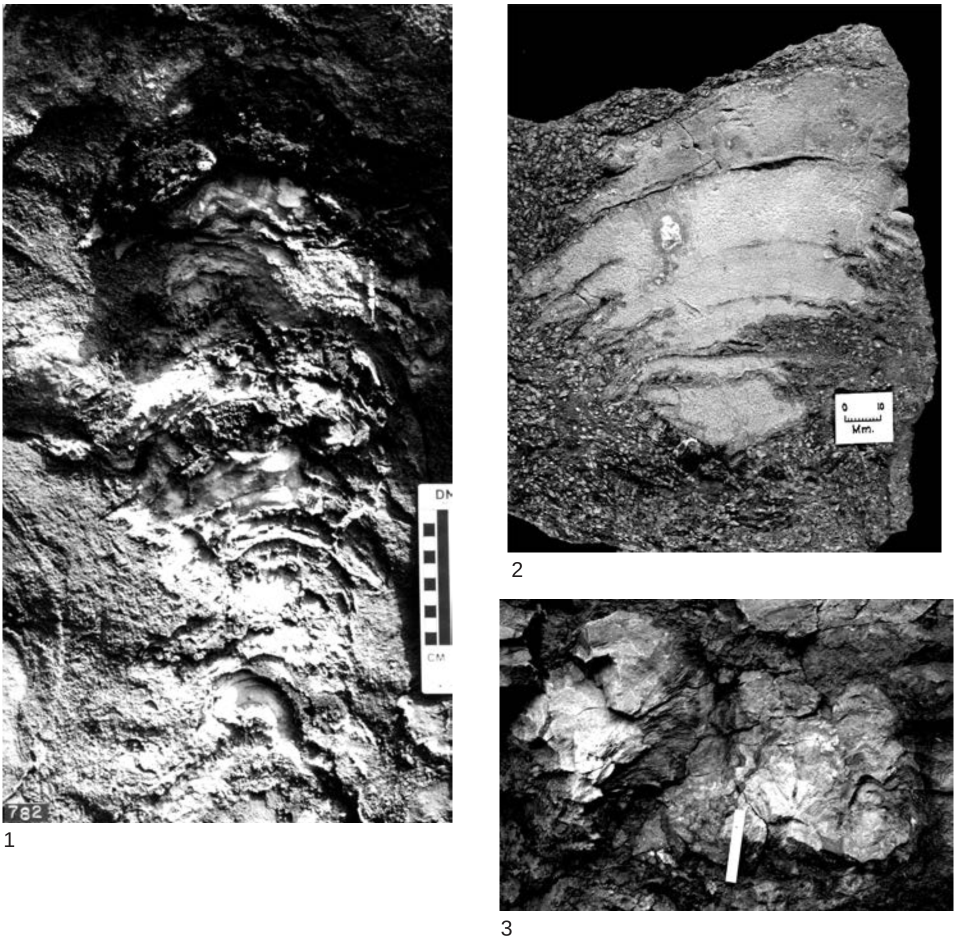


FIG. 20. Domical chaetetid growth forms (continued), Carboniferous, Pennsylvanian; *1,* high domical, ragged chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.2 (West, 2011a); *2,* ragged, domical chaetetid in a fusulinid packstone, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.45 (West, 2011a); *3,* low and high domical chaetetids, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.06 (West, 2011a).

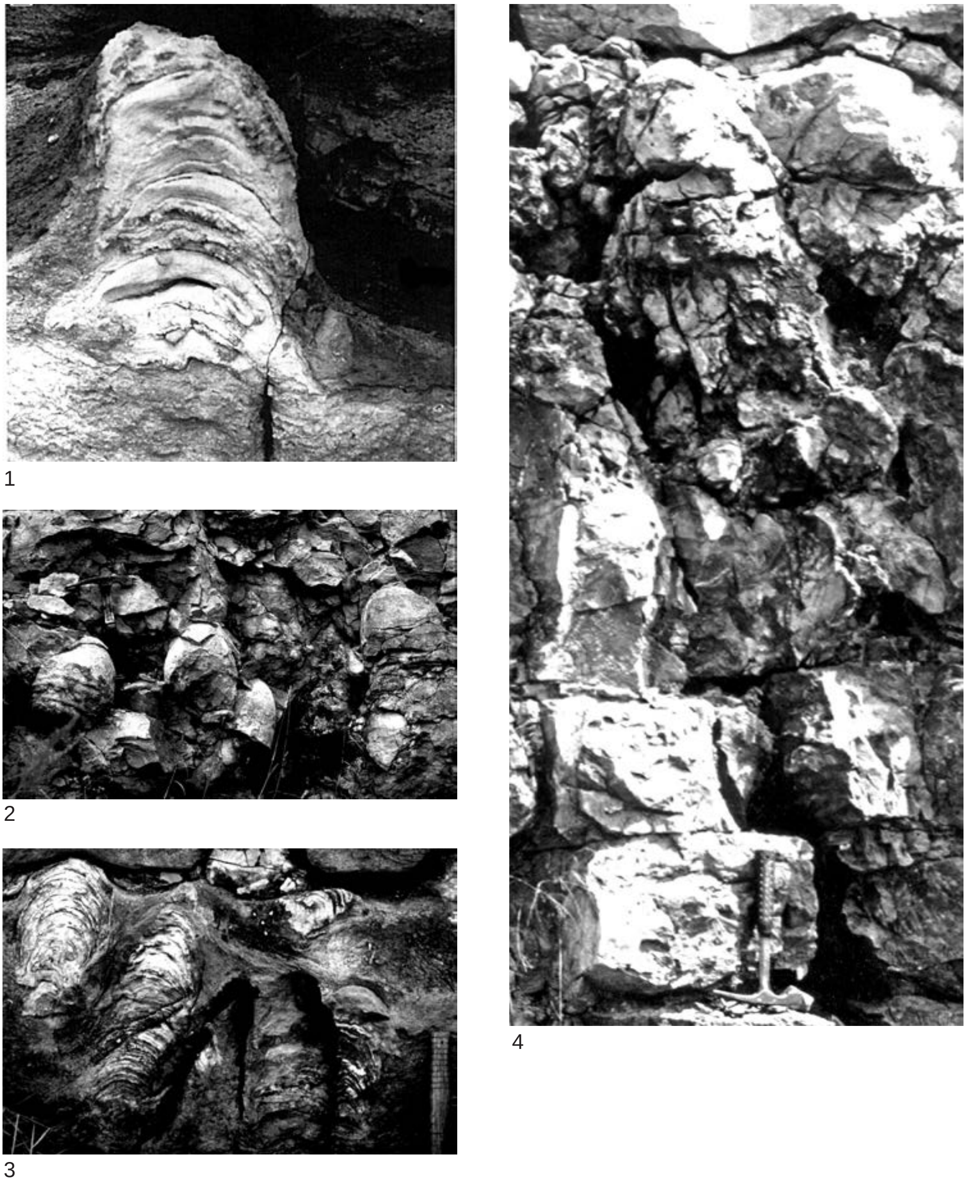


FIG. 21. Columnar chaetetid growth forms, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas; *1,* smooth columnar chaetetid, ×0.25 (adapted from Miller & West, 1997, p. 293, fig. 4E); *2,* mass of columnar chaetetids, ×0.06 (West, 2011a); *3,* smooth to slightly ragged columnar chaetetids, ×0.1 (West, 2011a); *4,* smooth columnar chaetetid, ×0.045 (West, 2011a).

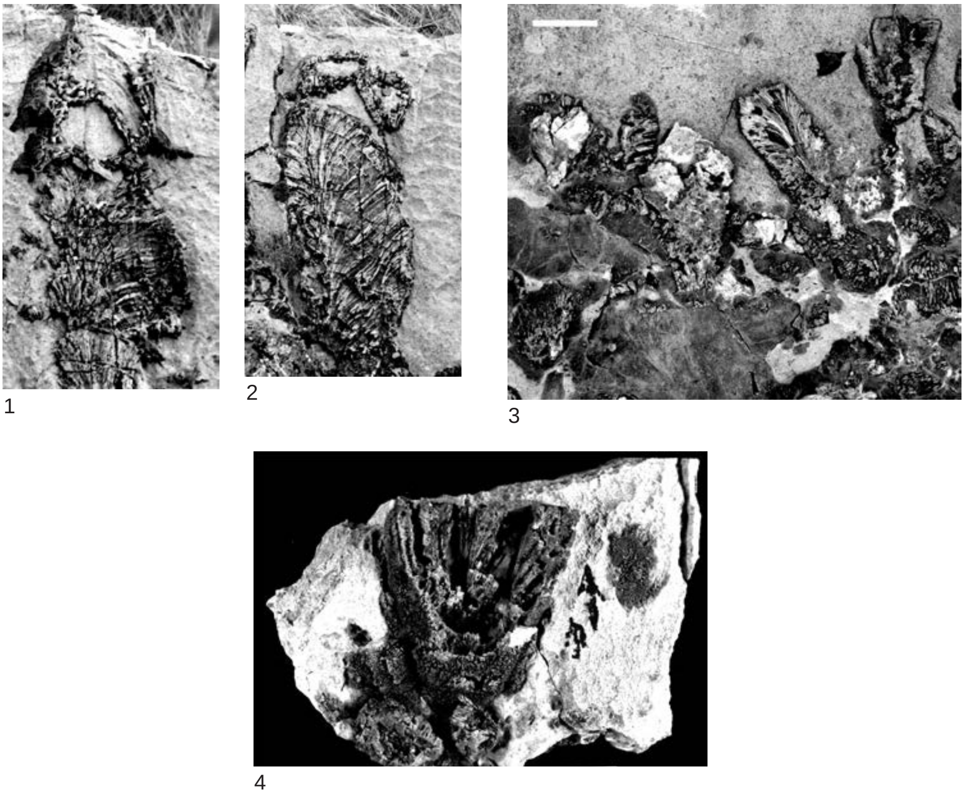


FIG. 22. Columnar chaetetid growth forms (continued), Carboniferous, Pennsylvanian; *1,* largely silicified ragged columnar chaetetid, Horquilla Limestone, Whetstone Mountains, Arizona, ×0.1 (West, 2011a); *2,* largely silicified smooth columnar chaetetid, Horquilla Limestone, Whetstone Mountains, Arizona, ×0.05 (West, 2011a); *3,* largely silicified high domical to columnar chaetetids in an inferred so-called biostrome, Middle Magdalena Group, Hueco Mountains, Texas, ×0.16 (West, 2011a); *4,* largely silicified vase-shaped chaetetid associated with an inferred biostrome, Middle Magdalena Group, Hueco Mountains, Texas, ×0.3 (West, 2011a).

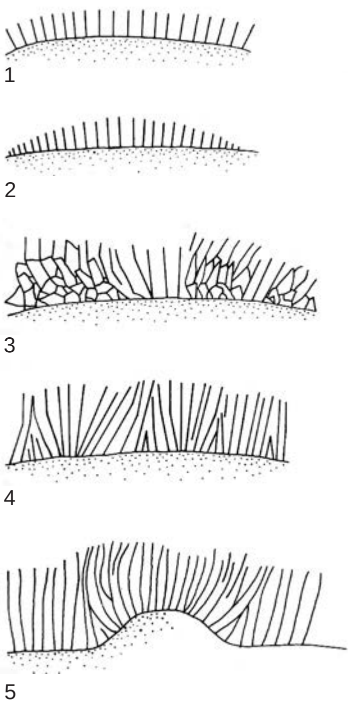


Fig. 23. Styles of initial growth in chaetetids; *1,* uniform tubule growth more or less normal to substrate; an uncommon style, ×3.25; *2,* greater tubule growth in the center; a common style and one that often is the template for continued growth, ×1.2; *3,* upward tubule growth is normal to oblique relative to the substrate, eventually all tubules grow, more or less, normal to the substrate; a common style, ×3; *4,* tubules spread upward and laterally from more than one center of growth, eventually compromised growth occurs at the margins of the different centers of growth; a common style, ×3; *5,* tubule growth associated with positive topographic features, tubules fan out from the positive area; a common style, ×3 (adapted from Kershaw & West, 1991, p. 336, fig. 2A).

p. 446), vertical, uniform growth would produce a laminar form (Fig. 23.1), and vertical, non-uniform growth would produce a domical or columnar form (Fig. 23.2). Growth of some of the initial tubules may be oblique to the substrate and returns to a more vertical position as growth continues (Fig. 23.3). Tubule growth may also proceed from what appears to be two or more growth centers, producing an arrangement of tubules that is complex (Fig. 23.4; Fig. 26).

The amount and rate of sedimentation also plays a role in the gross morphology of chaetetids. Lack of, or very slow, continuous sedimentation results in domical or columnar growth forms with a smooth outer surface (Fig. 17). Episodic sedimentation, which is often recorded as interruptions in the growth of tubules, produces chaetetids with ragged margins, as seen in Figures 27–28. These are not the only two factors that influence the growth form of chaetetids, but these are particularly important. For a fuller discussion of growth forms and habitats, see Kershaw and West (1991), West and Kershaw (1991), and Paleoecology of the Hypercalcified Chaetetid-Type Porifera (p. 127–178) and External Morphology of Paleozoic Stromatoporoids (p. 419–486).

Surface features on chaetetids, such as astrorhizae, chimneys, mamelons, basal layer (basal layer is favored over epitheca, theca, or peritheca to avoid confusion with corals and bryozoans), and tubercules are seldom observed, probably, in part, because of postmortem abrasion, dissolution, or both. All of these, except the basal layer, occur on the upper exterior surface of chaetetids, and even when they are preserved in fossil specimens, they are often broken or muted. Unlike some fossil stromatoporoids and some extant hypercalcified sponges in which astrorhizae can be traced downward into the calcareous skeleton, astrorhizae in chaetetids are confined to the exterior surface (Fig. 18). Serial sectioning of a chaetetid specimen with surface astrorhizae revealed no evidence of these features within the calcareous skeleton. However, CUIF and others (1973, pl. 1,*2*) illustrated a longitudinal section of astrorhizae in *Blastoporella*, but this genus is not currently considered valid because neither spicules nor spicule pseudomorphs have been found.

Although present, the basal layer is rarely seen in fossil forms, but it does occur (Fig. 29) in some very small specimens and on the undersides of laminar forms that have been colonized to some extent by epibionts. Preservation of this feature occurs in specimens collected from mudrocks and has not been observed in any specimens collected from carbonates. The basal layer in fossil chaetetids appears similar to that described from extant forms, with fine concentric growth lines on both (Fig. 29.1–29.4). The basal layer in a section through a specimen of *Acanthochaetetes wellsi* is easily recognized in SEM images, because the microstructure is different from that of the rigid calcareous skeleton (Fig. 29.6). However, the basal layer is not everywhere present in extant forms, no doubt the result of abrasion, dissolution, and/or bioerosion during life. In a fossil specimen, where it could be observed in cross section, it is a very thin (about 0.1 mm or less in thickness), single layer of dark calcite, and the SEM images reveal that it is slightly different from the calcareous skeleton (Fig. 29.5). Although the difference between the basal layer and calcareous skeleton is not as clear in the fossil because of diagenesis, it can be recognized (Fig. 29.7). It is important to note that in both extant and fossil specimens, the outer layer of the skeleton, i.e., the basal layer, is rich in organics. In that a basal layer, like the periostracum in bivalves and brachiopods, functioned, in part at least, as a protection of the more calcareous skeleton (CLARK, 1976), an organic-rich, outer layer is not surprising.

INTERNAL MORPHOLOGY

Irrespective of the growth form, the calcareous skeletons are composed internally of numerous thin-walled tubes that are polygonal (regular to irregular) to meandroid (Fig. 30–31) in transverse or tangential section. These tubes are referred to as tubules, and their walls are tightly joined or shared in common. Pores connecting tubules, referred to as mural

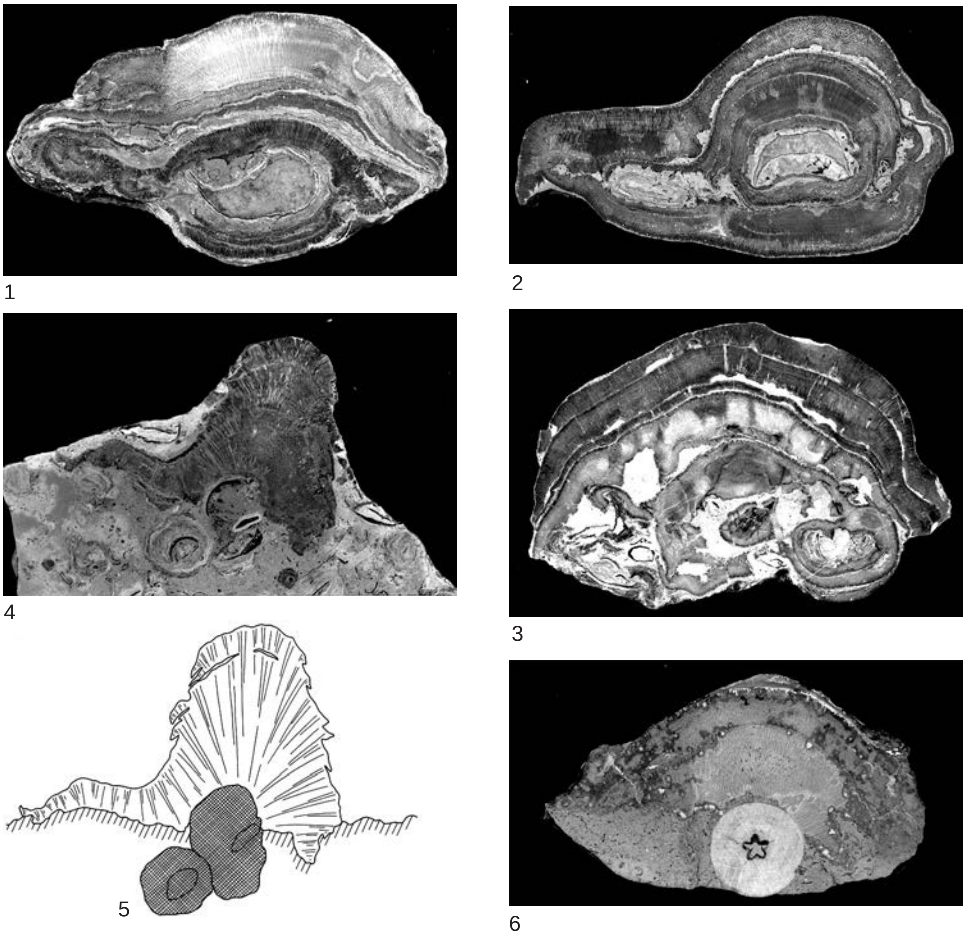


FIG. 24. Influence of substrate irregularities on chaetetid growth, Carboniferous, Pennsylvanian; *1,* oncoid with a productoid brachiopod nucleus, colonized by a laminar chaetetid, followed by a microbial mat; because of this substrate irregularity, a low domical chaetetid skeleton was produced, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.5 (West, 2011a); *2,* chaetetid colonization of two oncoids, producing a complex laminar to smooth, low domical skeleton, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.35 (see West & Kershaw, 1991, p. 449, fig. 2E for interpretive sketch, with kind permission of Springer Science+Business Media); *3,* smooth to slightly ragged, low, domical chaetetid as a result of a substrate irregularity produced by oncoids, skeletal debris, and matrix (carbonate mudstone), Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.3 (West, 2011a); *4,* high domical chaetetid with ragged margins that colonized and grew on an oncoid, substrate is inclined about 30° in a clockwise direction, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.45 (West, 2011a); *5,* interpretive sketch of specimen in view *4,* with the substrate oriented horizontally, depicted by a row of slash marks on either side of large rounded oncoids displayed with a dark stippling, ×0.45 (see also West & Kershaw, 1991, p. 452, fig. 4E, with kind permission of Springer Science+Business Media); *6,* low domical chaetetid that began by colonizing a large crinoid columnal, southeastern Kansas, ×0.6 (West & Kershaw, 1991, p. 449, fig. 2D, with kind permission of Springer Science+Business Media).

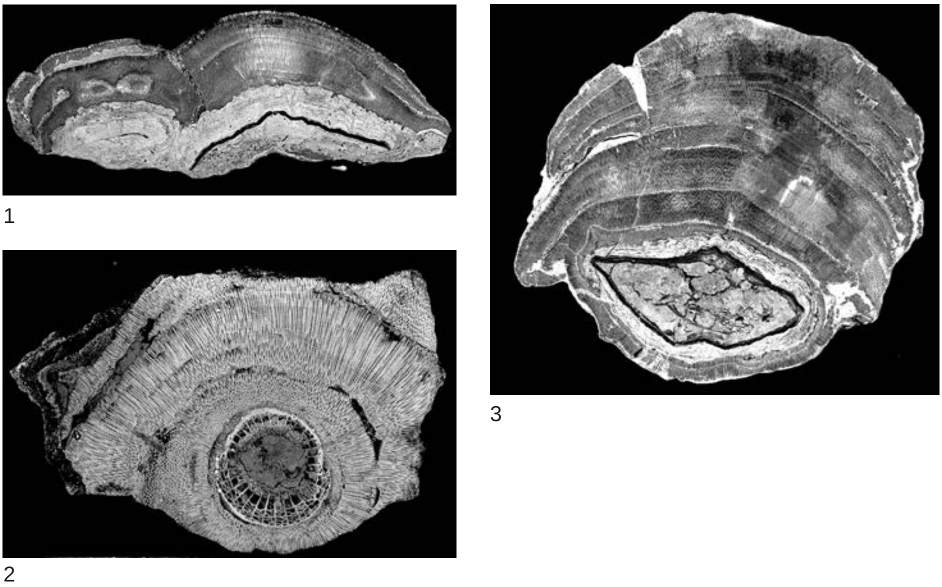


FIG. 25. Influence of substrate irregularities on chaetetid growth, Carboniferous, Pennsylvanian (continued); *1,* laminar to slightly domical chaetetid produced by growth over two oncoids, one of which has a valve of the brachiopod *Neospirifera* as the nucleus, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.5 (West, 2011a); *2,* laminar to slightly domical chaetetid produced by growth over a solitary rugose coral, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×1.9 (West, 2011a; see West & Kershaw, 1991, p. 449, fig. 2A, for interpretive sketch); *3,* domical chaetetid produced by growth over an oncoid with an articulated *Neospirifera* nucleus, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.5 (West, 2011a).

pores in tabulate corals, have been documented in one possible chaetetid genus, *Blastoporella* (Cuif & Ezzoubair, 1991). Longitudinal sections of the calcareous skeleton reveal that the most conspicuous internal morphological features are the tabulae (Fig. 32–33). These are random, irregularly spaced, subhorizontal partitions within tubules that may or may not be aligned between adjacent tubules and are easily observed in polished and thin sections and acetate peels. Generally, the tabulae are thinner than the walls of the tubules, but taphonomic processes can produce thickening or thinning of both (see Fig. 54.2). Because of these taphonomic processes, all measurements, especially those used for taxonomic differentiation, i.e., tubule size, wall thickness, and spacing of tabulae, are of little value (West, 1994). A foramen (Fig. 34) may be present as a circular opening in the tabulae, allowing interconnection between tubular spaces immediately above and below the tabulae. In fossil taxa, the foramen is rarely observed, either because it has been sealed off during later growth or subsequently infilled by taphonomic processes. Spines that have been recognized in such extant forms as *Acanthochaetetes,* if present in fossil taxa, are usually indistinguishable from incomplete tabulae or pseudosepta.

Laminae do not appear to be related to the occurrence of tabulae, but may be associated with closely spaced tabulae. The term as used in chaetetids does not refer to the same features as laminae in stromatoporoids; rather, it is more like what are referred to as latilaminae in stromatoporoids (see Glossary, p. 397–416). Laminae (Fig. 35) in chaetetids are bounded, above and below, by interruptions in the growth of the calcareous skeleton as a result of some disturbance. Thus, the thickness of the lamina will vary depending on the frequency of interruptions, and may thin and thicken laterally. MILLER and WEST (1996) recognized five different types of growth interruption surfaces in chaetetids, all of which may define laminae in the calcareous skeleton (Fig. 36). Tubules may be continuous or discontinuous across some interruptions from one lamina to the next (Fig. 36.1–36.2). Sedimentation, biological encrustation, and/or erosion may also separate laminae (Fig. 36.3–36.6). Erosion process may be biological, physical, chemical, or a combination of all three. Several types of interruption surfaces may occur in a single skeleton, and the type of interruption surface may change across the skeleton (Fig. 36.1–36.2).

Growth of tubules upward and addition of tubules by longitudinal fission, intertubular increase, peripheral expansion, or combinations of all three increase the size of the calcareous skeleton (Fig. 37–38). Lateral growth of the calcareous skeleton occurs when new tubules are formed on the adjacent basal layer or inorganic substrate and are connected to existing tubules, i.e., peripheral expansion (Fig. 37.2). Longitudinal fission and intertubular increase occur within the existing calcareous skeleton. In the former, one pseudoseptum or more (pseudosepta) join to form a new tubule (Fig. 38.2). In intertubular growth, the latter tubule walls separate, and rapid upward growth produces a full-sized tubule (Fig. 37.3; Fig. 38.1).

Particularly conspicuous in transverse and tangential sections is the pseudoseptum (Fig. 39–40). Pseudosepta project into individual tubules from the tubule walls and begin as tiny pustules that might be interpreted as incipient spines. However, serial sections reveal that these pustules expand upward, bladelike, into the tubule as upward growth continues, producing a pseudoseptum and ultimately a new tubule, as noted above. This process of division is called longitudinal fission and, in longitudinal section, might be confused with intertubular increase (see Fig. 37.3). Pseudosepta are most reliably identified from surfaces perpendicular to the long dimension of the tubules, i.e., transverse sections of the calcareous skeleton.

Spicules, siliceous megascleres, and microscleres, are known from extant and fossil forms. However, not all extant or fossil sponges have spicules; VACELET and URIZ (1991, p. 176) stated: "Interestingly, siliceous spicules are somewhat inconstant features in existing calcified demosponges." Most megascleres in chaetetids are tylostyles (Fig. 41–42) with or without spines, and the microscleres are some type of euaster (Fig. 43). Only megascleres are known in *Astrosclera willeyana;* they vary in abundance from high to low, and their morphology varies across different geographic regions (WÖRHEIDE, REITNER, & GAUTRET, 1997; WÖRHEIDE, 1998). Spicules are absent in Central Pacific populations of *Astrosclera willeyana* (VACELET & URIZ, 1991, p. 176). Megascleres in extant forms range in length from 47 µm in some specimens of *Astrosclera* (acanthostyles; Fig. 44) to nearly 600 µm in *Willardia* (tylostyles). Microscleres in extant forms range from 5 µm in *Acanthochaetetes* (amphiasters, diplasters, and spirasters; Fig. 45.1–45.5) to 45 µm in *Merlia* (clavidiscs; Fig. 45.6).

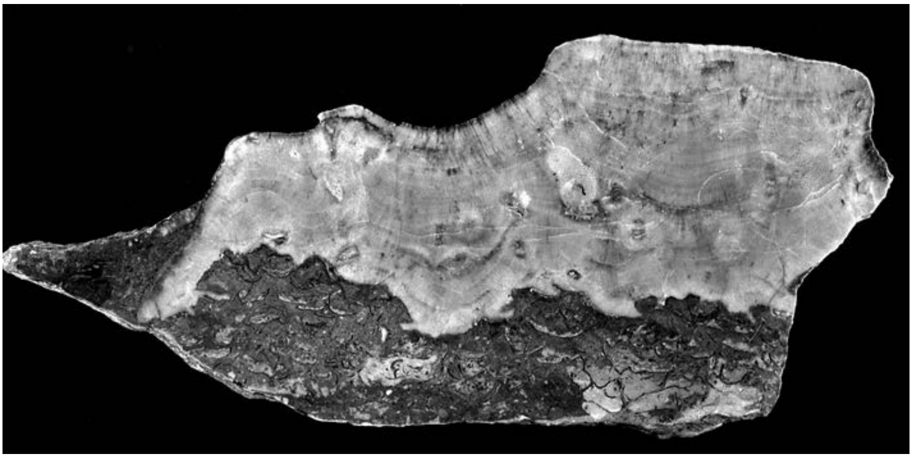


FIG. 26. Tubule complexity in chaetetids; *1,* polished longitudinal section, showing the complexity of tubule interaction in a laminar chaetetid, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma, ×0.6 (West, 2011a); *2,* interpretive sketch of view *1,* ×0.94 (Kershaw & West, 1991, p. 336, fig. 2B).

Environmental factors can have a significant effect on spicule formation in some extant demosponges. URIZ and others (2003, p. 288), referring to the formation of siliceous spicules in sponges, stated that, "Si uptake in sponges has been measured in laboratory experiments (FROHLICH & BARTHEL, 1997; REINCKE & BARTHEL, 1997; MALDONADO, & others, 1999) and may vary according to Si concentration in the water, temperature, and other environmental factors that affect sponge physiology and

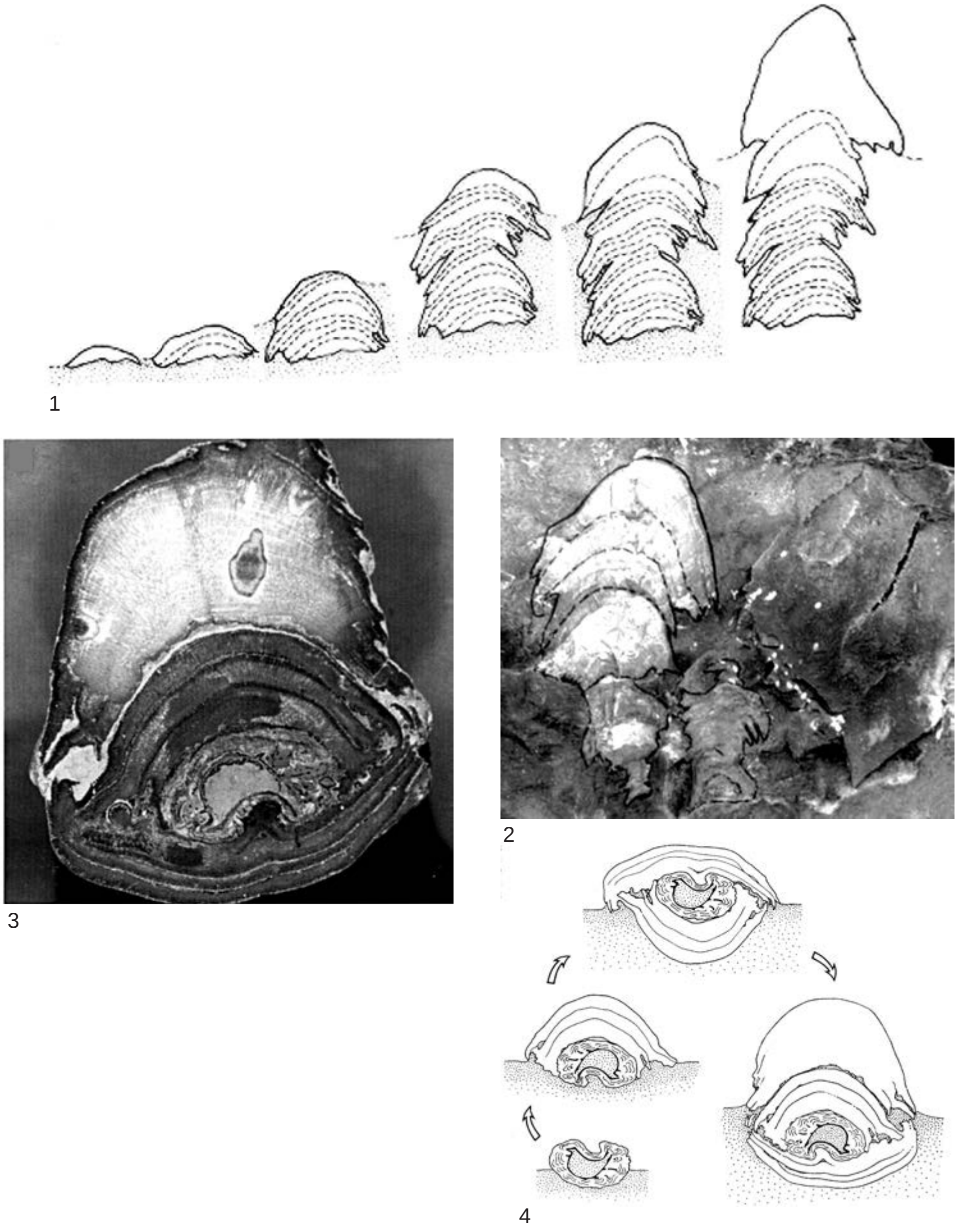


FIG. 27. Inferred development of laminar, domical, and columnar chaetetid skeletons with a ragged margin, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas; *1,* inferred growth sequence of a ragged columnar chaetetid, based on specimens, ×0.09 (Kershaw & West, 1991, p. 338, fig. 3B); *2,* example of a ragged columnar chaetetid for comparison to view *1,* ×0.1 (West, 2011a); *3,* ragged domical chaetetid illustrating multiple disturbances after initiation on an oncoid, ×0.45 (Miller & West, 1997, p. 293, fig. 4F); *4,* inferred sequence of growth events leading to the domical chaetetid shown in view *3,* ×0.19 (Miller & West, 1997, p. 297, fig. 9).

metabolism." Experimental studies have shown that spicules are lacking in sponges grown in water low in silicic acid (Yourassowsky & Rasmont, 1983). Additionally, some extant sponges that lack one or more spicule types in one area but have a full complement of spicules in other areas, is the result, in part, of the silicon concentration in the seawater (Uriz, Turon, & Becerro, 2003, p. 187). Thus, spicule types, absent in natural populations living in waters with a low concentration of silicon, can be produced by artificially increasing the silicic acid concentration (Maldonado & others, 1999). Maldonado and others (1999) suggested that reef-building sponges during the Mesozoic were limited by the availability of silicon. In addition to silicon, experimental studies suggest that iron is necessary for the polymerization of silica to form spicules in demosponges (Müller & others, 2003; Uriz, Turon, & Becerro, 2003). Although megascleres and microscleres are expected in extant forms, environmental factors may preclude their presence. Variation in the spicules of the hypercalcified demosponge *Astrosclera willeyana,* as noted above, may be due to such environmental factors.

Spicules, both megascleres and microscleres, are much less common in fossil hypercalcified demosponges than in extant forms. In addition to the environmental factors noted above, there may be several other explanations; two have been suggested. Most spicules are contained in the soft tissue of extant taxa and are not always incorporated into the calcareous skeleton (Kirkpatrick, 1911; Hartman

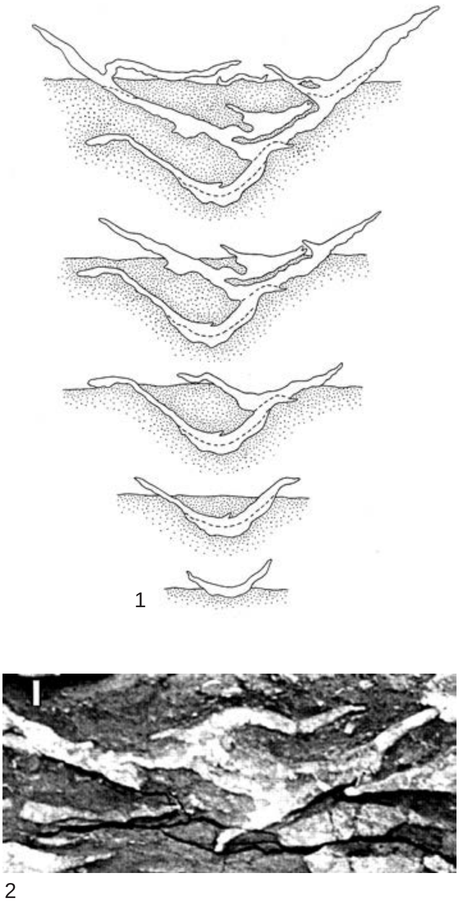


Fig. 28. Inferred development of laminar, domical, and columnar chaetetid skeletons with a ragged margin (continued); *1,* inferred sequence of growth events of some cup-shaped laminar chaetetids, based on specimens, Carboniferous, Pennsylvanian, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas (Miller & West, 1996, p. 295, fig. 6); *2,* example of cup-shaped laminar chaetetids for comparison to view *1,* ×0.3 (adapted from Miller & West, 1997, p. 293, fig. 4B).

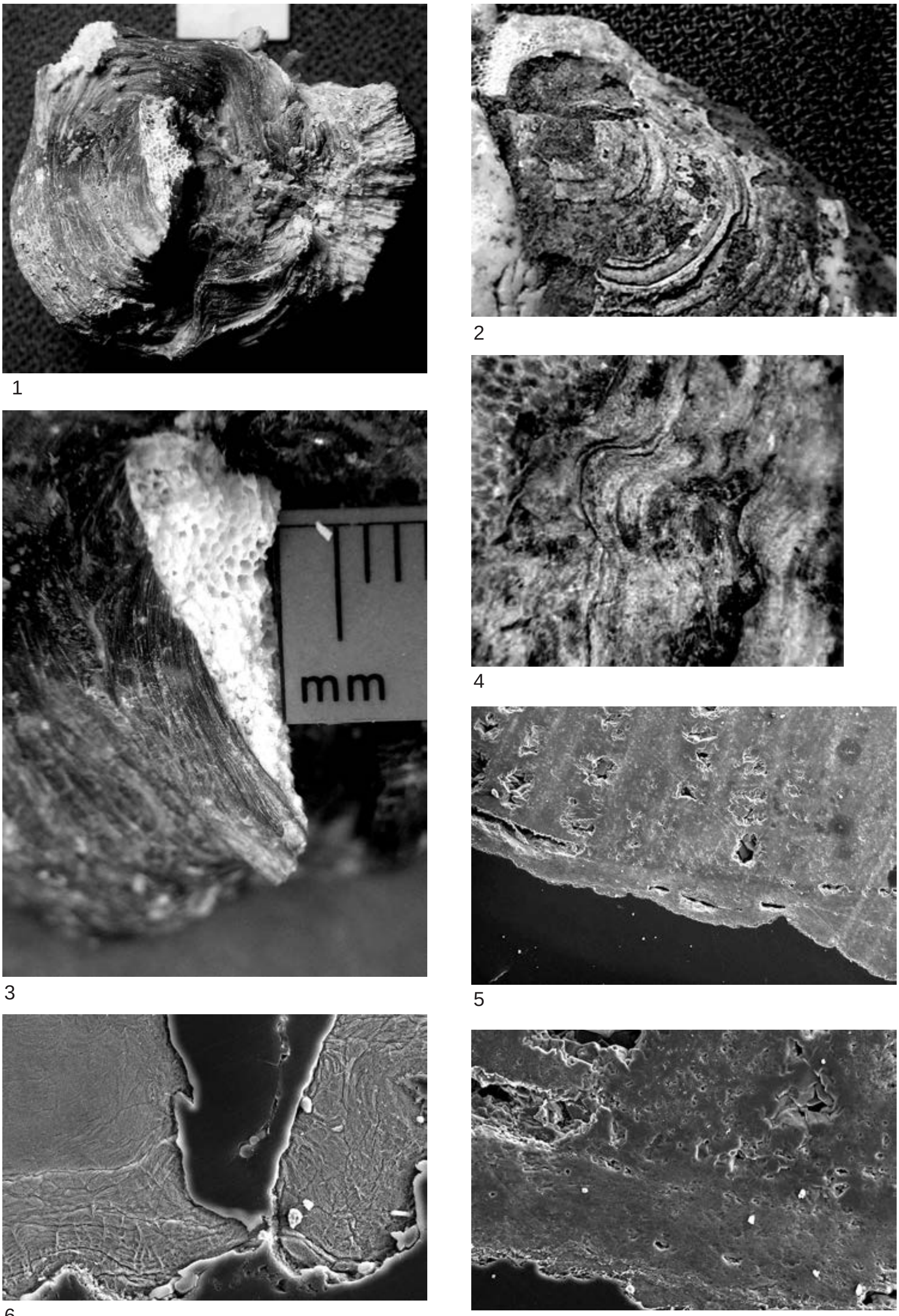


FIG. 29. *(For explanation, see facing page).*

& Goreau, 1975). Silica is unstable in the presence of calcium carbonate, and siliceous spicules are commonly corroded away in older parts of the calcareous skeleton of still-living taxa (Hartman & Goreau, 1970, 1972). Thus, it should not be surprising that spicules are rarely seen in fossil forms.

Given the ease with which silica spicules are corroded from the older parts of the skeleton, any evidence of spicules in fossil forms might be expected to be as pseudomorphs. Spicule pseudomorphs of calcite, pyrite, and iron oxide are known from Mesozoic chaetetids (see Gray, 1980, for summary). The first clear evidence of the poriferan affinities of Paleozoic chaetetids were the spicule pseudomorphs of calcite, pyrite, and silica described by Gray (1980) in chaetetids from the Carboniferous (Mississippian) of England (Fig. 41.6–41.9). Subsequently, Reitner (1991a) documented spicule pseudomorphs, mostly calcite, in both Mesozoic and Paleozoic chaetetids (Fig. 42.1–42.3). Based on what he interpreted as pyrite pseudomorphs of spicules, Kaźmierczak (1984, 1989) suggested a poriferan affinity for some tabulate corals, but Oekentorp (1985) thought that these were the result of boring organisms. These features are similar to what Twitchell (1929) considered spicules in *Stromatopora,* but which Finks (1986) interpreted as pyrite-filled endolithic borings. Wood, Copper, and Reitner (1990) and Copper and Plusquellec (1993) reached similar conclusions for these features described by Kaźmierczak in tabulate corals. Kaźmierczak (1991) presented three cases of what appear to be spicule pseudomorphs in three different favositid tabulate genera. In 1994, Kaźmierczak illustrated well-ordered vertical and subhorizontal tracts of what he interpreted as calcite pseudomorphs of monaxonic sclerites in a Silurian favositid tabulate from Gotland. However, Scrutton (1997, p. 189) regarded these structures as diagenetically altered cores of the trabeculae of the corallite walls. What have been interpreted as calcite spicules have been described from Silurian tabulate corals (Chatterton & others, 2008) but support an affinity with the Octocorallia. Although the morphology of these spicules is not typical of sponges, the growth form and the external and internal morphological features of some tabulates, such as favositids, are similar to chaetetids, and perhaps there is some connection between them as suggested by the pores in the tubule walls of *Blastoporella,* a possible chaetetid genus.

Fig. 29. Basal layer in extant and fossil chaetetids; *1,* underside of extant *Acanthochaetetes wellsi,* showing concentric lines of the basal layer, Chandelier cave near Malakal, Palau, West Carolina Islands, ×1.5 (West, 2011a); *2,* concentric bands of the basal layer on the underside of a fossil chaetetid, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×2 (West, 2011a); *3,* closer view of part of the basal layer of extant *Acanthochaetetes wellsi* shown in view *1,* ×4 (West, 2011a); *4,* closer view of part of the basal layer of the fossil chaetetid shown in view *2,* ×8 (West, 2011a); *5,* SEM of the basal layer of the fossil chaetetid shown in view *2,* the thin area along the base of the tubules in the lower part of the image is the inferred basal layer, ×70 (West, 2011a); *6,* SEM of the basal layer in extant *Acanthochaetetes wellsi* shown in view *1,* basal layer is the area on the left side of the image and the area below the faint light line on the right of the image, ×500 (West, 2011a); *7,* SEM of part of the image shown in view *5,* the inferred basal layer is the lower layer that extends from the middle left of the image to the lower part of the right side of the image, ×300 (West, 2011a).

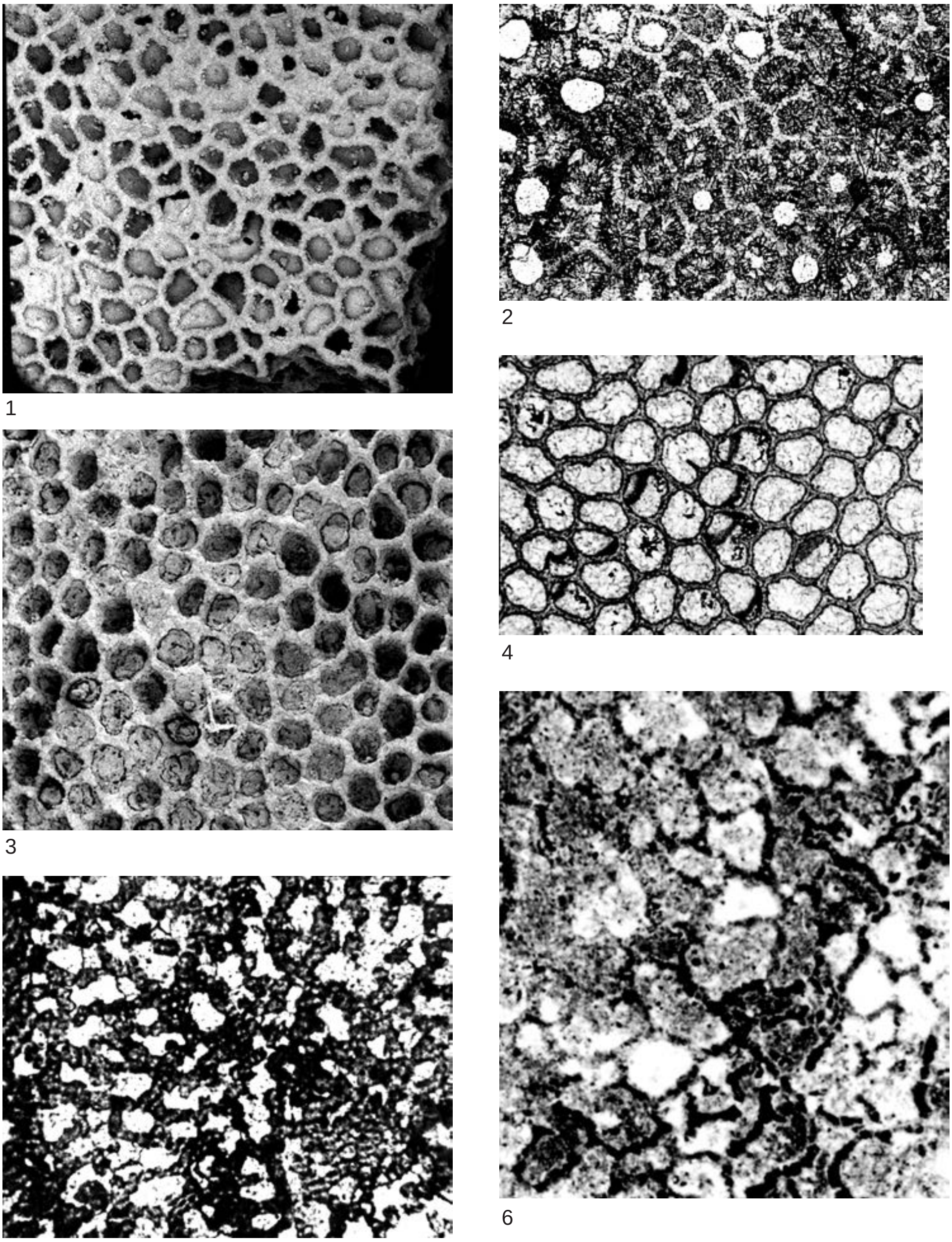


FIG. 30. *(For explanation, see facing page).*

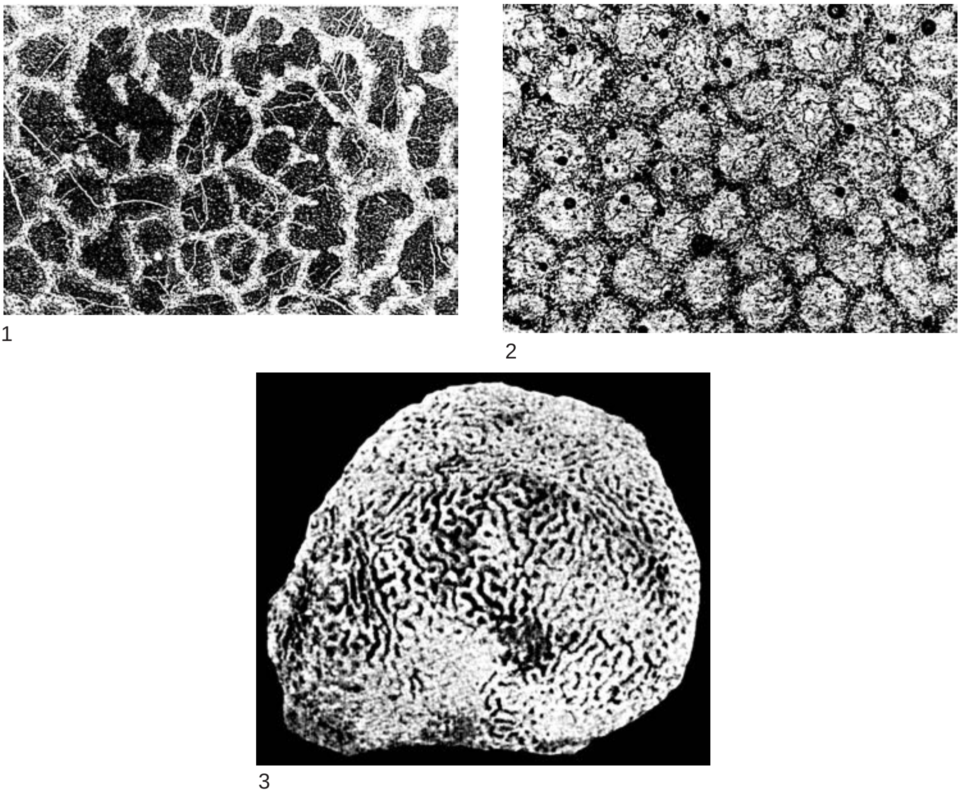


FIG. 31. Shape variation in chaetetid tubules (continued); *1,* transverse thin section of tubules in *Blastochaetetes dolomiticus*, Upper Triassic (Norian), southwestern Turkey, ×17 (adapted from Cremer, 1995, pl. 26,*3*; courtesy of *Geobios,* Université Lyon); *2,* transverse thin section of tubules in ?*Bauneia* sp., Upper Triassic (Norian), southwestern Turkey, ×26 (adapted from Cremer, 1995, pl. 27,*5*; courtesy of *Geobios,* Université Lyon); *3,* view of the surface, showing meandroid shape of tubules in *Meandrioptera zardinii*, Upper Triassic (Carnian), Cassiano beds near Cortina d'Ampezo, Italy, ×2.4 (adapted from Dieci & others, 1977, pl. 1,*2a;* courtesy of *Bollettino della Societa Paleontologica, Italiana*).

FIG. 30. Shape variation in chaetetid tubules; *1,* SEM of transverse view of tubules in *Chaetetes (Chaetetes) radians,* Carboniferous limestone, Miatschkovo, near Moscow, Russia, ×15 (West, 2011a); *2,* transverse thin section of tubules in *Atrochaetetes alakirensis*, Upper Triassic (Norian), southwestern Turkey, ×21 (adapted from Cremer, 1995, pl. 25,*1*); *3,* SEM of transverse view of tubules in a ceratoporillid chaetetid, Permian, Tunisia, ×30 (West, 2011a); *4,* transverse thin section of tubules in *Chaetetopsis favrei*, Lower Cretaceous (Barremian), Crimea, ×11.5 (adapted from Kaźmierczak, 1979, p. 103, fig. 2B; courtesy of E. Schweizerbartsche Verlags, Naegele U Obermiller Science Publishers, Stuttgart, Germany); *5,* transverse thin section of tubules in *Leiospongia polymorpha,* Upper Triassic, Cassian Formation, northern Italy, ×21 (adapted from Engeser & Taylor, 1989, p. 43, fig. 2B; courtesy of the Natural History Museum, London); *6,* transverse thin section of *Chaetetes (Boswellia) mortoni,* Carboniferous, Mississipian (lower Asbian), northern Wales, ×14 (adapted from Gray, 1980, pl. 102,*3*).

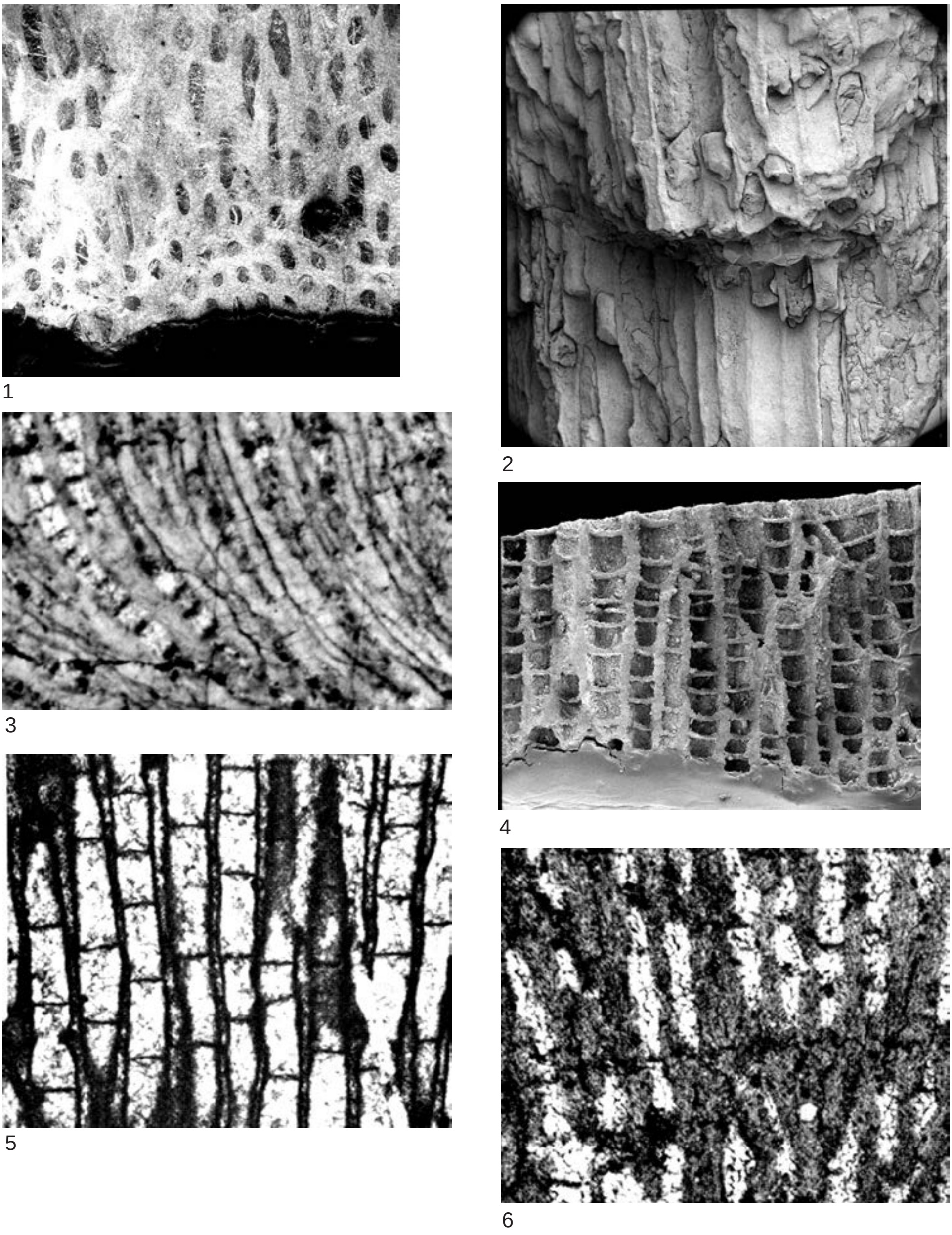


FIG. 32. Walls and tabulae in fossil chaetetids; *1,* SEM of transverse to oblique fracture of a chaetetid, Permian, Tunisia, showing tubule walls and tabulae, ×20 (West, 2011a); *2,* SEM of longitudinal fracture of chaetetid, Carboniferous, Pennsylvanian, Buckhorn Asphalt, Murray County, Oklahoma, ×15 (West, 2011a); *3,* longitudinal thin section of chaetetid, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×36 (West, 2011a); *4,* SEM of longitudinal fracture of a chaetetid, Carboniferous, Pennsylvanian (Moscovian), near Podolsk, Russia, ×15 (West, 2011a); *5,* longitudinal thin section of *Chaetetopsis crinata*, Upper Jurassic (Tithonian, "Portland beds"), Japan, ×15 (adapted from Fischer, 1970, pl. E,*8;* courtesy of *Annales de Paléontologie (Invertébrés),* Elsevier Masson SAS); *6,* longitudinal thin section of *Blastochaetetes capilliformis,* Upper Jurassic (Oxfordian), France, ×15 (adapted from Fischer, 1970, pl. A, fig. 8; courtesy of *Annales de Paléontologie (Invertébrés),* Elsevier Masson SAS).

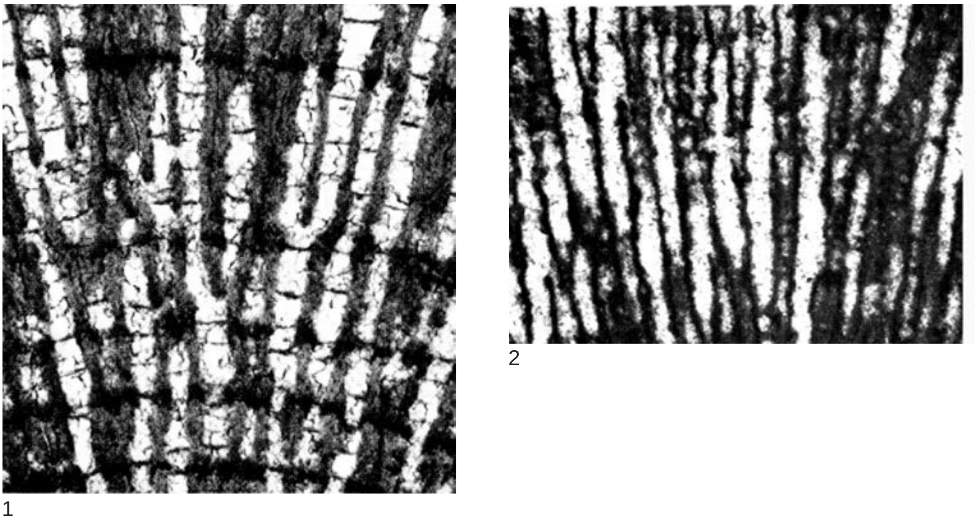


FIG. 33. Walls and tabulae in fossil chaetetids (continued); *1,* longitudinal thin section of *Blastochaetetes bathonicus,* Middle Jurassic (Bathonian), France, ×15 (adapted from Fischer, 1970, pl. B,*4*); *2,* longitudinal thin section of *Ptychochaetetes globosus,* Upper Jurassic (Oxfordian), France, ×15 (adapted from Fischer, 1970, pl. D,*6;* both views courtesy of *Annales de Paléontologie (Invertébrés),* Elsevier Masson SAS).

BIOMINERALIZATION AND MICROSTRUCTURE

Skeletal components of hypercalcified sponges comprise the spicules and the calcareous skeleton. Spicules composed of silica may or may not occur, and even if they are present in extant forms, they are, as noted above, commonly lacking because of taphonomic processes. The calcareous skeleton in extant forms is composed of aragonite or high magnesium calcite (REITNER & WÖRHEIDE, 2002). Calcareous chaetetid skeletons composed of aragonite have been reported from the Mesozoic (CUIF, 1974; DIECI, RUSSO, & RUSSO, 1974a; WENDT, 1974, 1984). SQUIRES (1973) reported at least 5 mol% magnesium carbonate in the walls of chaetetids preserved in the Buckhorn Asphalt, a Carboniferous, Pennsylvanian unit in Oklahoma. The magnesium carbonate of extant chaetetid sponges is between 14 and 20 mol% (WENDT, 1984, p. 327). SQUIRES (1973, p. 98) suggested that the value he obtained could have been higher, in that a thin layer of dolomite rims the walls of the tubules (see his pl. 15, p. 97). Thus, some of the magnesium from the chaetetid skeleton could have been incorporated into the dolomite during diagenesis. Dolomite rims also occur in some of the Carboniferous, Pennsylvanian chaetetids from Kansas (Fig. 46). In most fossil forms, these unstable mineral phases, aragonite and high magnesium calcite, have converted to low magnesium calcite. Because of this recrystallization, the original microstructure of the calcareous skeleton in fossil forms is muted or completely destroyed.

Biomineralization of the spicules and the calcareous skeleton in some extant forms has been well documented (KIRKPATRICK, 1911; VACELET & GARRONE, 1985; WILLENZ & HARTMAN, 1989, 1999; CUIF &

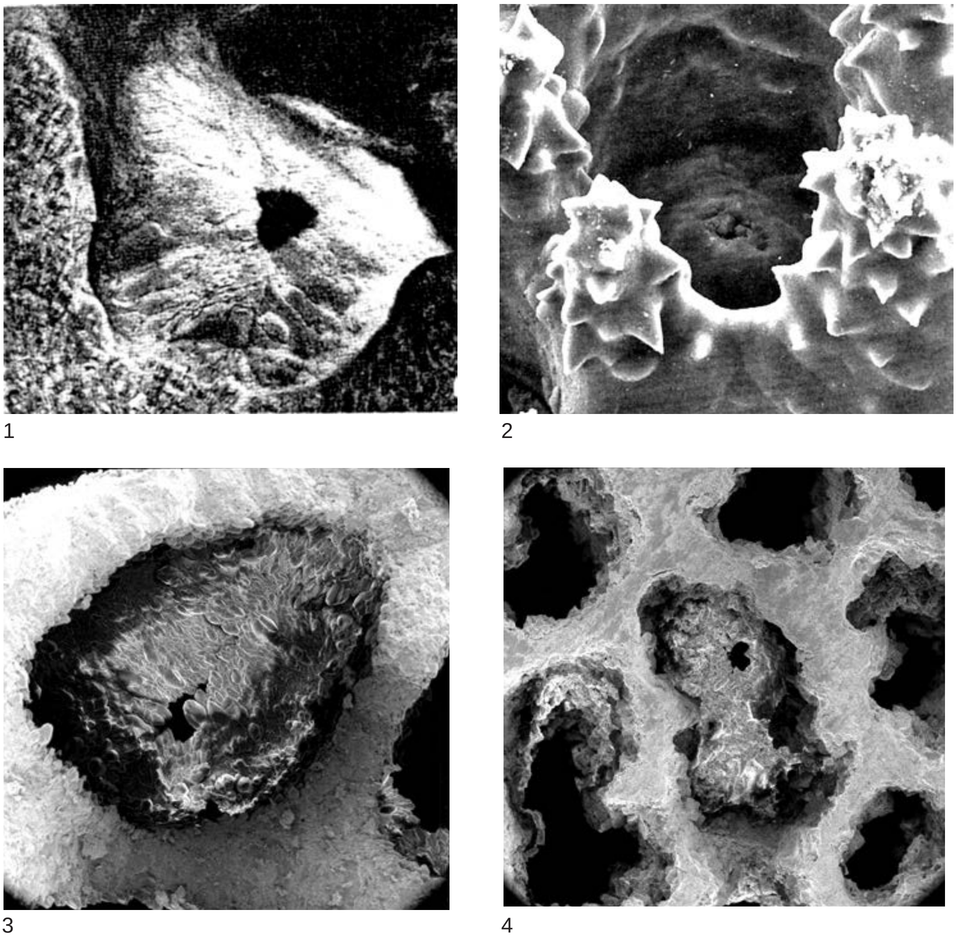


Fig. 34. Foramen in tabulae in extant and fossil chaetetids; *1,* SEM of a possible foramen in a tabula of an extant specimen of *Merlia normani*, Mediterranean Sea, ×350 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. II,*1;* courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, Paris*); *2,* SEM of a possible foramen in a tabula of an extant specimen of *Merlia lipoclavidisca* Vacelet & Uriz, 1991, La Catedral cave, at a water depth of 12 m, Balearic Islands, Mediterranean Sea, ×300 (adapted from Vacelet & Uriz, 1991, p. 172, fig. 2b, with kind permission of Springer Science+Business Media); 3, SEM of a possible foramen in a tabula of *Chaetetes (Chaetetes) radians*, Carboniferous, Pennsylvanian (Moscovian), Moscow Basin, Russia, ×103 (West, 2011a); *4,* SEM of a possible foramen in a tabula of *C. (Chaetetes) radians*, Carboniferous, Pennsylvanian (Moscovian), near Podolsk, south of Moscow, Russia, ×60 (West, 2011a).

Fig. 35. Laminae in fossil chaetetids, Carboniferous, Pennsylvanian; *1,* interlayered chaetetid laminae with algal-microbal mats, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.3 (West, 2011a); *2,* polished longitudinal section of a ragged columnar chaetetid, showing laminae, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.65 (West, 2011a); *3,* differentially weathered longitudinal (vertical) surface of a ragged, high domical chaetetid, showing laminae, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.4 (West, 2011a); *4,* laminae of laminar chaetetids accentuated by weathering, Myrick Station Limestone West, 2011a, Pawnee Limestone, Bourbon County, Kansas, ×0.25 (West, 2011a); *5,* laminar to low domical chaetetids, showing individual laminae in a fusulinid grainstone, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.16 (West, 2011a).

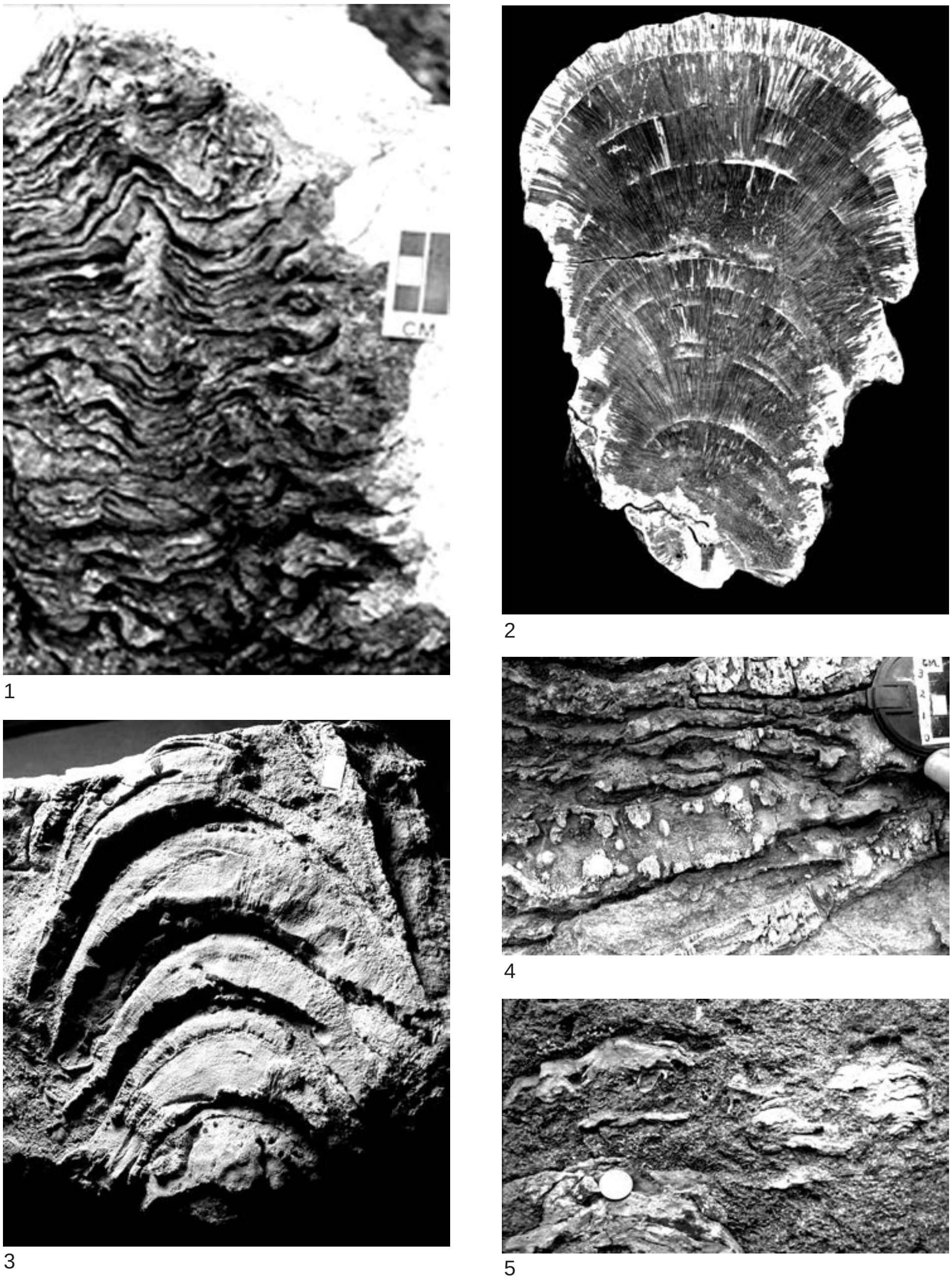


FIG. 35. *(For explanation, see facing page).*

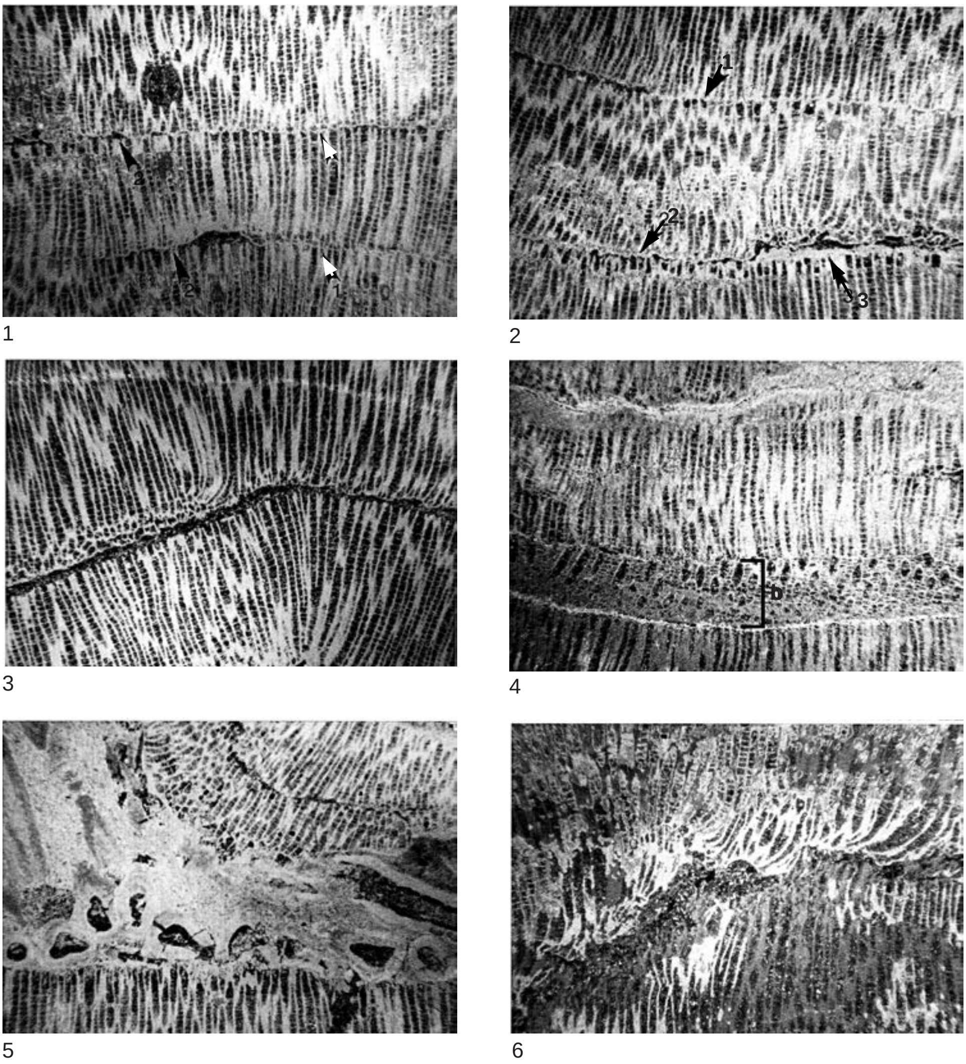


FIG. 36. Five types of growth interruptions observed in chaetetid skeletons, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; all figures are ×6, acetate peel prints; *1,* continuity of tubules across the interruption, type 1 (*arrows*) grades laterally into discontinuity of tubules across the interruption, type 2 (*arrows*); *2,* discontinuity of tubules across the interruption, type 2 (*arrow*), that grades laterally into a thin layer of matrix or matrix filled tubules, type 3 (*arrow*); note that a type 1 interruption (*upper arrow*) occurred after subsequent growth; *3,* thin layer of matrix separating chaetetid laminae, with some tubules below filled with matrix; *4,* chaetetid surface overgrown by fistuliporoid bryozoan (*b*) either coincident with or subsequent to renewed chaetetid growth (type 4 interruption); *5,* chaetetid surface covered by matrix and encrusted by the tabulate coral *Multithecopora* either coincident with or subsequent to renewed chaetetid growth (type 4 interruption); *6,* chaetetid surface locally corroded with evidence of skeletal destruction prior to renewed chaetetid growth (type 5) (adapted from Miller & West, 1997, p. 292, fig. 3A–F).

Gautret, 1991; Reitner, 1992; Gautret, Reitner, & Marin, 1996; Reitner & Gautret, 1996; Wörheide, Reitner, & Gautret, 1996, 1997; Reitner & others, 1997; Wörheide & others, 1997; Wörheide, 1998). However, because of taphonomic processes, little is known of the biomineralization of fossil forms, although it is assumed to be similar, if not identical, to that in extant taxa. Both *Merlia normani* and *Acanthochaetetes wellsi* have a calcareous skeleton similar to that seen in some fossil chaetetids. Kirkpatrick (1911) produced a very careful and detailed study of *Merlia normani*. Using modern techniques, Vacelet (1980a); Gautret, Vacelet, and Cuif (1991); and Cuif and Gautret (1993) described the spicules of *Merlia normani* and compared the microstructure of its calcareous skeleton with that of fossil chaetetids. Because it bears on the occurrence of spicules, it is important to note the differences between the species of *Merlia* (Table 1). Currently four species of *Merlia* are recognized: *normani, lipoclavidisca, deficiens*, and *tenuis* (Vacelet & Uriz, 1991). *M. normani* and *M. lipoclavidisca* have a calcareous skeleton and contain spicules; *M. deficiens* and *M. tenuis* lack a calcareous skeleton but have spicules that place them within the family Merliidae. The megascleres of all four are small tylostyles. The microscleres in *M. normani*, *M. deficiens*, and *M. tenuis* are the very distinctive clavidiscs, but there are no microscleres in *M. lipoclavidisca*. Thus, all extant forms of *Merlia* have tylostyles, but may or may not have a calcareous skeleton and microscleres. Uriz and others (2003, p. 290) suggested that the absence of clavidiscs in *M. lipoclavidisca* is because of the silica-poor water where they live, and that they are present in *M. normani* because it inhabits silica-rich waters. Here again we have evidence relative to the occurrence of spicules in hypercalcified demosponges that is important to the studies of fossils with a chaetetid skeleton.

Table 1. Comparison of the skeletal components of the four species of *Merlia*.

Taxon	Megascleres	Microscleres	Calcareous skeleton
M. normani	tylostyles	clavidiscs	present
M. lipoclavidisca	tylostyles	none	present
M. deficiens	tylostyles	clavidiscs	absent
M. tenuis	tylostyles	clavidiscs	absent

Studies by Hartman and Goreau (1975); Reitner and Engeser (1987); Cuif and Gautret (1991); Reitner (1991a, 1992); Wood (1991b); Gautret, Reitner, and Marin (1996); Reitner and Gautret (1996); Wörheide, Reitner, and Gautret (1996, 1997); Reitner and others (1997); Lange and others (2001); and Reitner and others (2001) using more sophisticated techniques, have examined in some detail the microstructure of *Acanthochaetetes wellsi*. To provide some insight into the possible biomineralization in fossil chaetetids, a brief summary of biomineralization in *A. wellsi* and other hypercalcified demosponges follows (see Living Hypercalcified Sponges, p. 1–14).

Spicules are formed by sclerocyte cells contained within the soft tissue (mesohyl) of the sponge. Studies of *Acanthochaetetes wellsi* show that this soft tissue is only 0.5 to 1 mm thick and contains siliceous tylostyle megascleres, amphiaster-like, and spiraster-like microscleres; some of the microscleres appear to become incorporated into the calcareous skeleton (Rützler & Vacelet, 2002, p. 277). Reitner and others (2001) divided the soft tissue and calcareous skeleton of

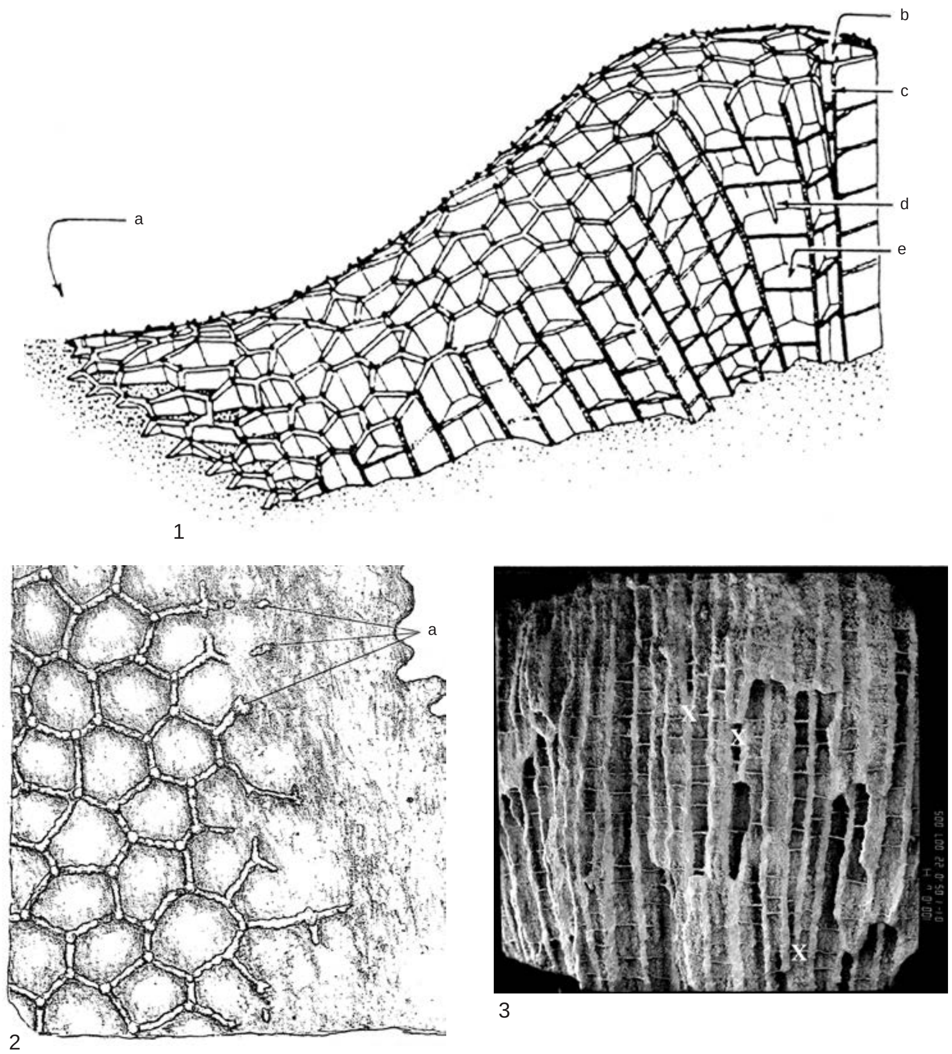


FIG. 37. Skeletal increase in chaetetids; *1,* schematic diagram of chaetetid on a stippled substrate illustrating the methods of skeletal increase and associated morphological features: *a* = area of peripheral expansion; *b* = tubule; *c* = tubule increase by intertubule budding; *d* = pseudosepta and tubule increase by longitudinal fission; *e* = tabulae (adapted from West & Clark, 1983, p. 131, fig. 1; courtesy of Paleontological Research Institution, Ithaca, New York); *2,* peripheral expansion of the skeleton in an extant specimen of *Merlia normani, a* = area of peripheral expansion, ×75 (adapted from Kirkpatrick, 1911, pl. 38,*5*); *3,* SEM of longitudinal fracture of *Chaetetes (Chaetetes) radians,* showing intertubular budding (*white X*), Carboniferous, Moscovian, near Podolsk, Russia, ×5 (West, 2011a).

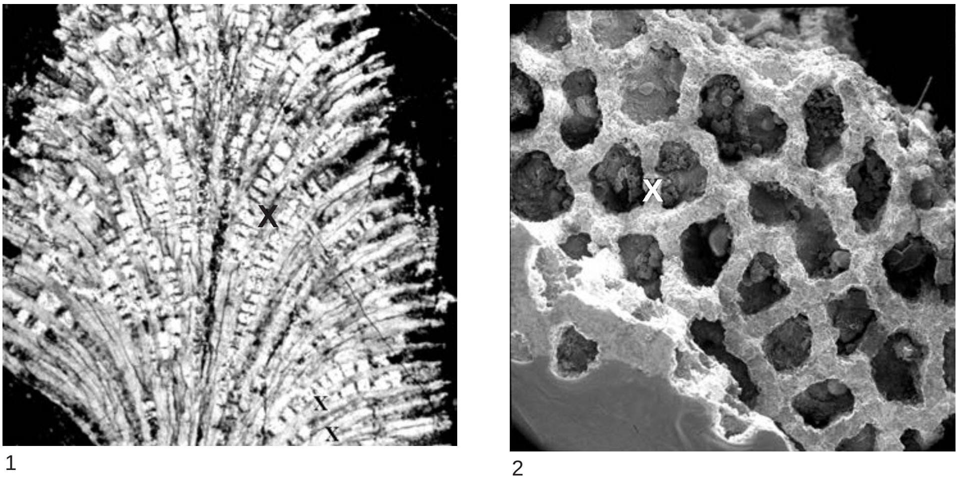


FIG. 38. Skeletal increase in chaetetids (continued); *1,* longitudinal thin section, showing skeleton increase by intertubular budding (*black X*), Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×10 (West, 2011a); *2,* SEM of transverse fracture of *Chaetetes (Chaetetes) radians*, Carboniferous, Pennsylvanian (Moscovian), near Podolsk, Russia, note the joined pseudosepta just above the *white X,* ×30 (West, 2011a).

Acanthochaetetes wellsi into six major zones. These are, from the exterior inward: (1) the dermal area; (2) the internal dermal area; (3) the central part of tubules; (4) the tabulae within the tubules; (5) the space(s) between tabulae; and (6) the nonliving calcareous skeleton. REITNER and others (2001, p. 230), in referring to zone 1, reported that, "the uppermost portion is formed by a thick crust of spiraster microscleres (dermal area, zone 1) and tylostyle megascleres arranged in clearly plumose bundles. . . ."

Some spicules may be entrapped in the calcareous skeleton, resulting in what would be termed a rigid aspicular skeleton (Fig. 6–7). If the spaces within a framework produced by fused or linked spicules are filled by aspicular cement, the skeleton would be referred to as a rigid spicular skeleton (Fig. 8–9). Such a distinction is rarely possible in fossil forms because of taphonomic processes.

WENDT (1984) recognized three different microstructures in the calcareous skeletons of chaetetids: irregular, spherulitic, and clinogonal. Present usage recognizes three basic types of microstructure in the calcareous skeleton of chaetetids: microlamellar, fascicular fibrous, and spherulitic. Three different fascicular fibrous types are recognized: water-jet, penicillate, and trabecular (CUIF & GAUTRET, 1993), but only the former two are found in chaetetids. What WENDT (1984) referred to as irregular is the same as microlamellar, and his clinogonal is the same as fascicular fibrous. WENDT considered water-jet, penicillate, and trabecular as synonyms of clinogonal, and BOURY-ESNAULT and RÜTZLER (1997)

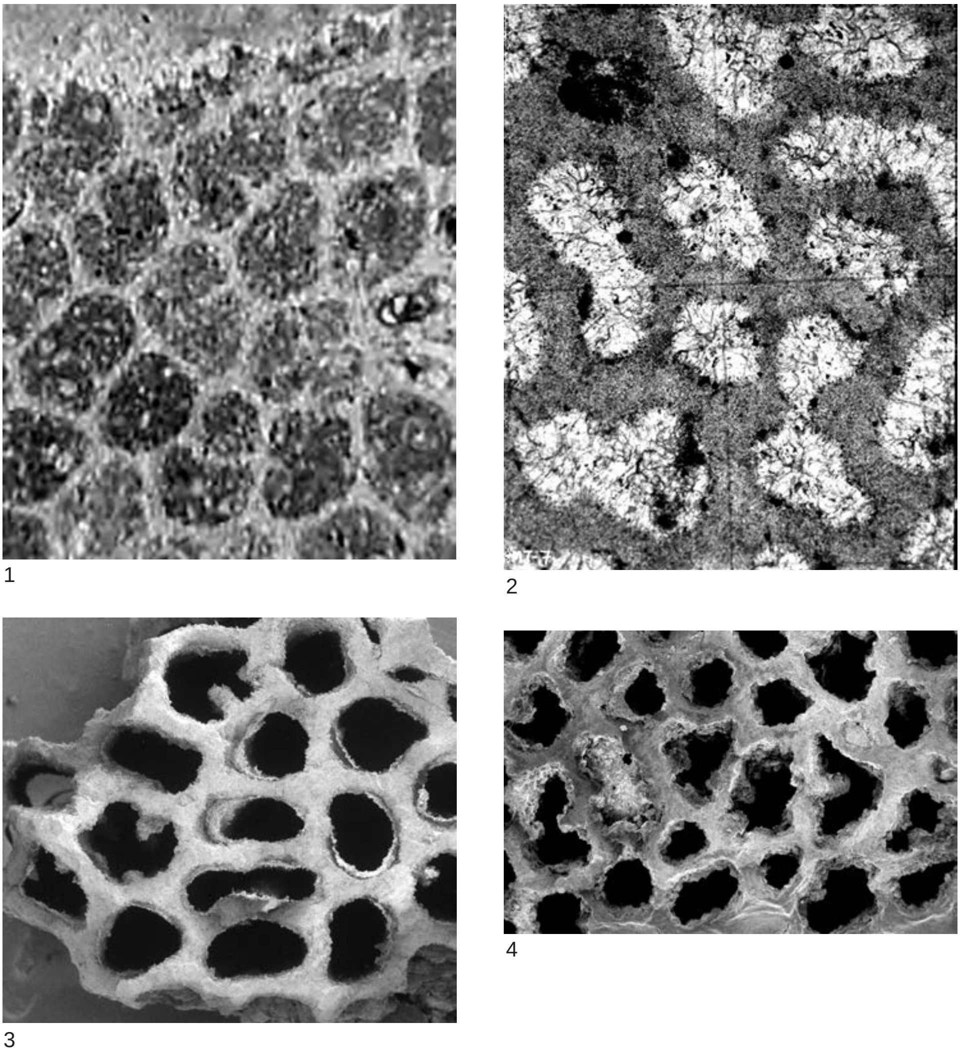


FIG. 39. Pseudosepta in fossil chaetetids; *1,* transverse thin section of chaetetid skeleton, showing tubules with conspicuous pseudosepta, Carboniferous, Pennsylvanian, Bird Springs Formation, near Mountain Springs, Nevada, ×100 (West, 2011a); *2,* transverse thin section of chaetetid skeleton, showing tubules and pseudosepta, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×40 (West, 2011a); *3,* SEM of transverse view of chaetetid skeleton, showing tubules and pseudosepta, Carboniferous, Pennsylvanian (Moscovian), Moscow Basin, Russia, note prominent pseudoseptum in the tubule in the upper center and the two pseudosepta approaching each other in the tubule in the left center, ×25 (West, 2011a); *4,* SEM of transverse view of *Chaetetes (Chaetetes) radians,* showing tubules with pseudosepta, Carboniferous, Pennsylvanian (Moscovian), near Moscow, Russia; note the prominent pseudoseptum in the triangular tubule in the right center and the tubule in the left center with two pseudosepta approaching each other, ×30 (West, 2011a).

considered them to be synonyms of fasciculate fibrous. Thus, the microstructure of the calcareous skeleton of chaetetids may be: microlamellar, spherulitic, water-jet, or penicillate; the last two being two of the three subdivisions of clinogonal and fasciculate fibrous. Cuif and Gautret (1991) pointed out the potential taxonomic value of the microstructure of the calcareous skeleton of fossil and recent sponges, in both Calcispongiae and Demospongiae.

Mineralization of the calcareous skeleton in *Acanthochaetetes wellsi* occurs in three different areas: (1) associated with the thin cover of Mg-rich calcite on collagenous fibers at the top of the walls of the tubules; (2) where the tabulae are being formed; and (3) within older parts of the calcareous skeleton between tabulae where decaying soft sponge tissue produces ammonia (Reitner & Gautret, 1996). Details of the biomineralization in these three areas was described by Reitner and Gautret (1996) and summarized in Reitner and others (2001, p. 230–232). A microlamellar microstructure (Cuif & others, 1979; Wendt, 1979; Reitner & Engeser, 1987) composed of an irregular arrangement of loosely packed crystals, generally with a random orientation, but sometimes arranged such that a lamellar structure is indicated (Wendt, 1984, p. 328), is produced by these processes in *Acanthochaetetes* (Fig. 47). Wendt (1984) referred to this microstructure as irregular.

The calcareous skeleton of the extant genus *Astrosclera*, and some fossil chaetetids from the Permian of Tunisia and the Triassic of Turkey, have a spherulitic microstructure (Wörheide, 1998; Fig. 48). Wörheide (1998) detailed the biocalcification process that produces the calcareous skeleton of *Astrosclera willeyana*, and this process is summarized in Reitner and others (2001).

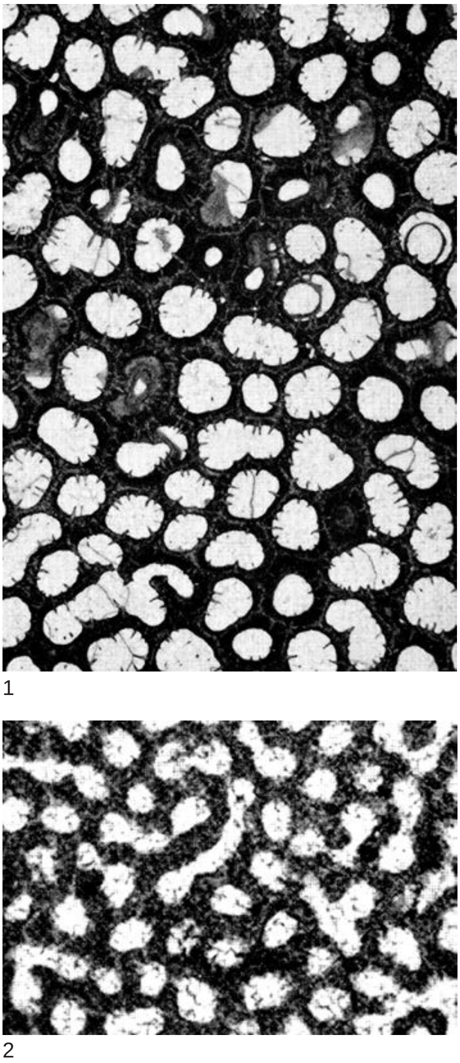


Fig. 40. Pseudosepta in fossil chaetetids (continued); *1,* transverse thin section of *Acanthochaetetes seunesi,* showing tubules and pseudosepta, Upper Cretaceous (Cenomanian), Pyrennees, ×7.5 (adapted from Fischer, 1970, pl. F,*3*); *2,* transverse thin section of *Blastochaetetes capilliformis,* showing tubules and pseudosepta, Upper Jurassic (Oxfordian), France, ×18.7 (adapted from Fischer, 1970, pl. A,*7;* both views courtesy of *Annales de Paléontologie [Invertébrés],* Elsevier Masson SAS).

TABLE 2. Comparison of the microstructures and skeletal mineralogy of extant and fossil hypercalcified demosponges with either a chaetetid or stromatoporoid calcareous skeleton; numerals with lower-case letters and author abbreviations refer to sources provided in the explanation; see below and facing page (West, 2011a).

	Merlia	*Acanthochaetetes*	*Astrosclera*	*Ceratoporella*	Chaetetids	Stromatoporoids
Aragonite						
Penicillate				1a (F/R), 4a (C/G)	1a (F/R), 4b*(C/G)	
Spherulitic			1a (F/R), 2a (H/S), 6 (Wt)		1a (F/R), 6 (Wt)	1a (F/R)
Irregular						1a (F/R), 6 (Wt)
Spherulitic compound			5a (Wd)			
Spherulitic elongate				5a (Wd)		
Clinogonal				2a (H/S), 6 (Wt)	6 (Wt)	6 (Wt)
Orthogonal						6 (Wt)
Fibrous centers			7a (Cet)			
Asymmetical				7a (Cet.)		
Mg Calcite						
Penicillate	1b (F/R)				1b (F/R)	
Lamellar		1b (F/R), 2b (H/S), 7b (Cet.)			1b (F/R)	
Water-jet	2b (H/S), 4b (C/G)				4b (C/G)	
Fascicular fibrous	5b (Wd)					
Irregular		5b (Wd), 6 (Wt)			6 (Wt)	
Clinogonal	6 (Wt)				6 (Wt)	6 (Wt)
Spherulitic						6 (Wt)
Orthogonal						6 (Wt)
Trabecular	7b (Cet.)					
Mineralogy not recorded						
Fascicular fibrous	3 (B-E/R)			3 (B-E/R)		
Microlamellar		3 (B-E/R)				
Spherulitic			3 (B-E/R)			

*, some Mesozoic to Recent taxa, but all Paleozoic and some Mesozoic–Recent chaetetids have a water-jet calcite skeleton.

TABLE 2. Explanation.

1. (F/R)

Finks, Robert M., & J. Keith Rigby Sr. 2004d. Hypercalcified sponges. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part E, Porifera (Revised), vol. 3. The Geological Society of America, Inc. & The University of Kansas. Boulder, Colorado & Lawrence, Kansas. p. 586–587.

1a. Aragonite

Spherulitic: compound spherulitic, *Astrosclera* and relatives of stromatoporoid morphology, Permo-Triassic genera of inozoans, sphinctozoans, and chaetetids.

Penicillate: clionogonal aragonite, elongate spherulitic, water-jet *Ceratoporella* of chaetetids and inozoans of the Middle Triassic.

Irregular: microgranular aragonite, *Vaceletia* and Triassic sphinctozoans, inozoans, and stromatoporoids.

1b. Mg Calcite

Homogeneous-granular: microgranular Mg calcite, no extant examples, Triassic sphinctozoans and inozoans, best known in *Cassianothalamina* (not included in table).

Lamellar: *Acanthochaetetes,* in Cretaceous to Recent genera with a chaetetid morphology, and the Cretaceous *Calcichondrilla*, an encrusting form with a nonchaetetid morphology.

Penicillate: clinogonal calcite, fascicular fibrous calcite, *Merlia,* and Paleozoic and Mesozoic genera with a chaetetid morphology, such as *Stromatoaxinella.*

(Continued on facing page.)

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

Spherulitic: no extant examples, Cretaceous *Euzkadiella*.
Fibrous: orthogonal Mg calcite, examples in the Calcarea.

2. (H/S)

Hooper, J. N. A., & R. W. M. van Soest, eds. 2002a. Systema Porifera, 2 vol. Kluwer Academic/Plenum Publishers. New York, Boston, Dordrecht, London, & Moscow. xlviii + 1708 p.

2a. Aragonite
Spherulitic: *Astrosclera*.
Clinogonal: *Ceratoporella*.
2b. Mg Calcite
Water-jet: *Merlia,* probably the same as penicillate calcite of 1.
Lamellar: *Acanthochaetetes.*

3. (B-E/R)

Boury-Esnault, Nicole, & Klaus Rützler. 1997. Thesaurus of Sponge Morphology. Smithsonian Contributions to Zoology, Number 596:55 p. [Mineralogy not recorded; also here the authors did not recognize separate aragonite and Mg calcite fields].

Fasciculate fibrous: water-jet, penicillate, and trabecular *Merlia;* water-jet, mineralogy not reported; *Ceratoporella,* penicillate.
Microlamellar: *Acanthochaetetes*.
Spherulitic: *Astrosclera*.

4. (C/G)

Cuif, Jean-Pierre, & Pascale Gautret. 1993. Microstructural features of fibrous tissue in the skeletons of some chaetetid sponges. *In* P. Oekentorp-Küster, ed., Proceedings of the VI International Symposium on Fossil Cnidaria and Porifera, Munster Cnidarian Symposium, vol. 1. Courier Forschungsinstitut Senckenberg 164:309–315.

4a. Aragonite
Penicillate: *Ceratoporella*.
4b. Mg Calcite
Water-jet: *Merlia*.
Trabecular: scleractinian corals (not included in table)

5. (Wd)

Wood, Rachel A. 1991b. Non-spicular biomineralization in calcified demosponges. *In* J. Reitner & H. Keupp, eds., Fossil and Recent Sponges. Springer-Verlag. Berlin & Heidelberg. p. 322–340.

5a. Aragonite
Compound spherulitic: *Astrosclera,* probably the same as spherulitic aragonite of 1.
Elongate spherulitic: *Ceratoporella,* probably the same as penicillate aragonite of 1.
5b. Mg Calcite
Fascicular fibrous: *Merlia*, probably penicillate calcite of 1.
Irregular: *Acanthochaetetes,* crystals aligned in one plane, probably lamellar calcite of 1.

6. (Wt)

Wendt, Jobst. 1979. Development of skeletal formation, microstructure, and mineralogy of rigid calcareous sponges from the Late Palaeozoic to Recent. *In* C. Levi & N. Boury-Esnault, eds., Biologie des Spongiaires. Colloques Internationaux du Centre National de la Recherche Scientifique 291:449–457.

Wendt, Jobst. 1984. Skeletal and spicular mineralogy, microstructure and diagenesis of coralline calcareous sponges. Palaeontographica Americana 54:326–336. [Note: the latter reference is an update of the former.]

Mg Calcite or Aragonite
Irregular: aragonite in stromatoporoids and Mg calcite in Cretaceous and Recent "sclerosponges," *Acanthochaetetes*.
Spherulitic: probably aragonite in Carboniferous sclerosponges and in the extant genus *Astrosclera*; probably calcite in a Cretaceous stromatoporoid.
Clinogonal (synonyms = water-jet, trabecular, penicillate): aragonite or calcite in Mesozoic and possibly Paleozoic chaetetids and stromatoporoids; calcitic in *Merlia* and aragonite in *Ceratoporella* and stromatoporoids.
Orthogonal (synonym, fibro-normal): aragonite and calcite in stromatoporoids.

7. (Cet.)

Cuif, Jean-Pierre, Françoise Debrenne, J. G. Lafuste, & Jean Vacelet. 1979. Comparaison de la microstructure du squelette carbonate nonspiculaire d'éponges actuelles et fossiles. *In* C. Levi & N. Boury-Esnault, eds., Biologie des Spongiaires. Colloques Internationaux du Centre National de la Recherche Scientifique 291:459–465.

7a. Aragonite
Spherolites fibreux centres [fibrous spherulitic centers]: *Astrosclera*.
Spherolites asymetriques [asymmetrical spherulites]: *Ceratoporella*.
7b. Mg Calcite
Lamelles presque plates [nearly flat lamellae]: *Acanthochaetetes.*
Trabecules verticals [vertical trabeculae]: *Merlia.*

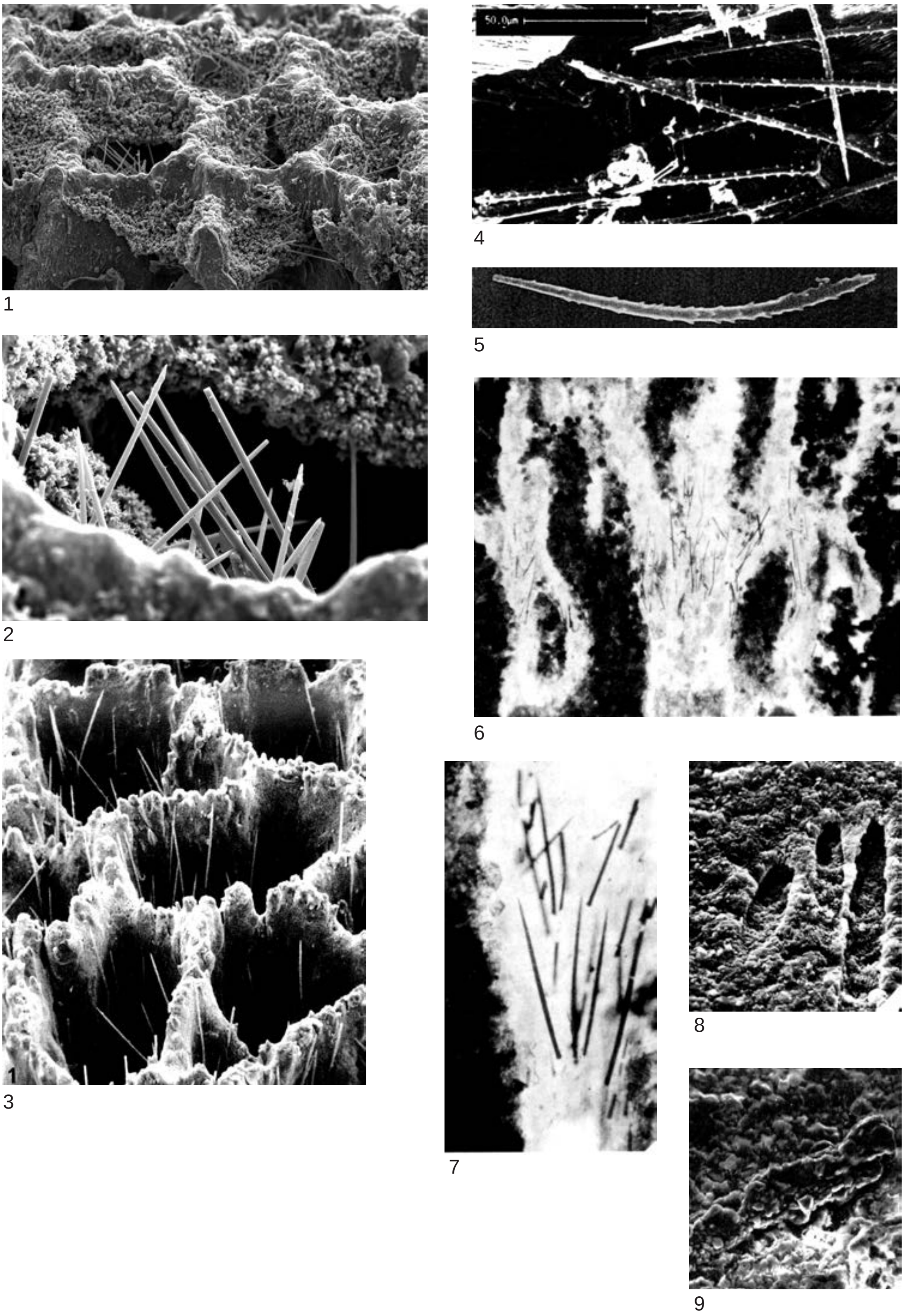


FIG. 41. *(For explanation, see facing page).*

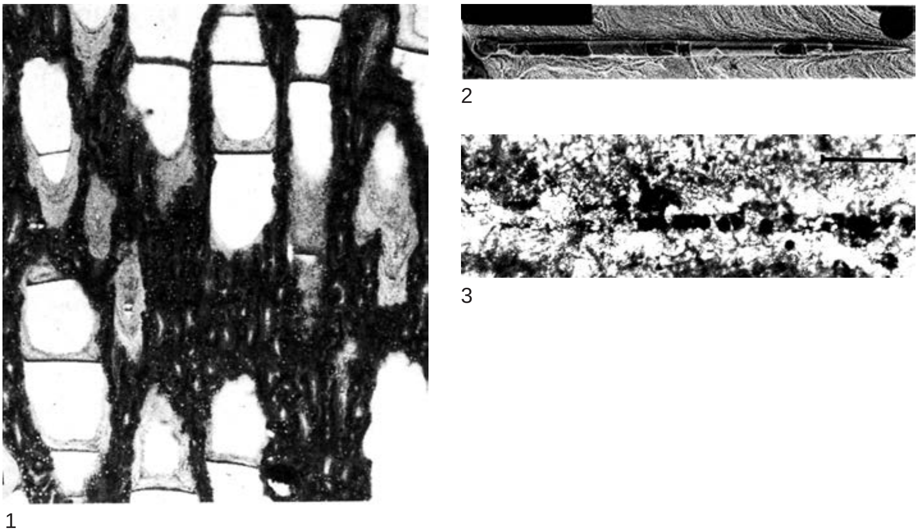


FIG. 42. Pseudomorphs of megasclere tylostyles in fossil chaetetids; *1,* tangential thin section of *Calcistella tabulata,* showing spicule pseudomorphs within tubule walls (white dots within dark areas) from a Cretaceous (possibly Aptian) boulder in an Eocene conglomerate in Greece, ×9 (adapted from Reitner, 1991a, p. 190, fig. 7a); *2,* SEM of a tylostyle from *Acanthochaetetes dendroformis,* Cretaceous, northern Spain, ×145 (adapted from Reitner, 1991a, p. 200, fig. 13c); *3,* longitudinal thin section of a pyritized tylostyle, *Chaetetopsis favrei*, Cretaceous (possibly Aptian) boulder in an Eocene conglomerate, Greece, ×210 (acetate peel print adapted from Reitner, 1991a, p. 185, fig. 5c, all views with kind permission of Springer Science+Business Media).

FIG. 41. Megascleres in chaetetids: tylostyles in extant forms, pseudomorphs in fossil forms; *1,* SEM of surface of *Acanthochaetetes* sp., showing spicules (tylostyles and spirasters) associated with the growing surface; from an extant specimen collected live in October 2005 off the Komesu coast, southern Okinawa, at a water depth of 15 m, ×100 (West, 2011a); *2,* SEM of the tubule on the left side of view *1,* showing the tylostyles, ×500 (West, 2011a); *3,* SEM of the surface of *Ceratoporella nicholsoni,* showing tylostyles of an extant specimen, Jamaica, ×100 (adapted from Hartman & Goreau, 1972, fig. 1; courtesy of *Transactions of the Connecticut Academy of Arts and Sciences*); *4,* SEM of tylostyles of *Ceratoporella nicholsoni,* an extant species, probably Caribbean, ×230 (adapted from Reitner, 1992, pl. 36,*3;* courtesy of *Berliner Geowissenschaftliche Abhandlungen,* Free University, Berlin); *5,* SEM of a tylostyle from *Merlia deficiens,* an extant species, Mediterranean, ×4500 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. 1,*2;* courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, Paris*); *6,* longitudinal thin section of *Chaetetes (Boswellia) mortoni,* showing spicule pseudomorphs (thin dark lines within tubule walls), Carboniferous, Mississipian (lower Asbian), northern Wales, ×30 (adapted from Gray, 1980, pl. 103,*1*); *7,* enlargement of part of view *6,* showing pyritic spicule pseudomorphs, ×87 (adapted from Gray, 1980, pl. 103,*2*); *8,* SEM of longitudinal section of *Chaetetes (Boswellia) mortoni,* showing preferential etching of siliceous spicule pseudomorphs, ×821 (adapted from Gray, 1980, p. 814, fig. 4a); *9,* SEM of longitudinal section of *Chaetetes (Boswellia) mortoni,* showing pyritized spicule pseudomorph, ×667 (adapted from Gray, 1980, p. 814, fig. 4c).

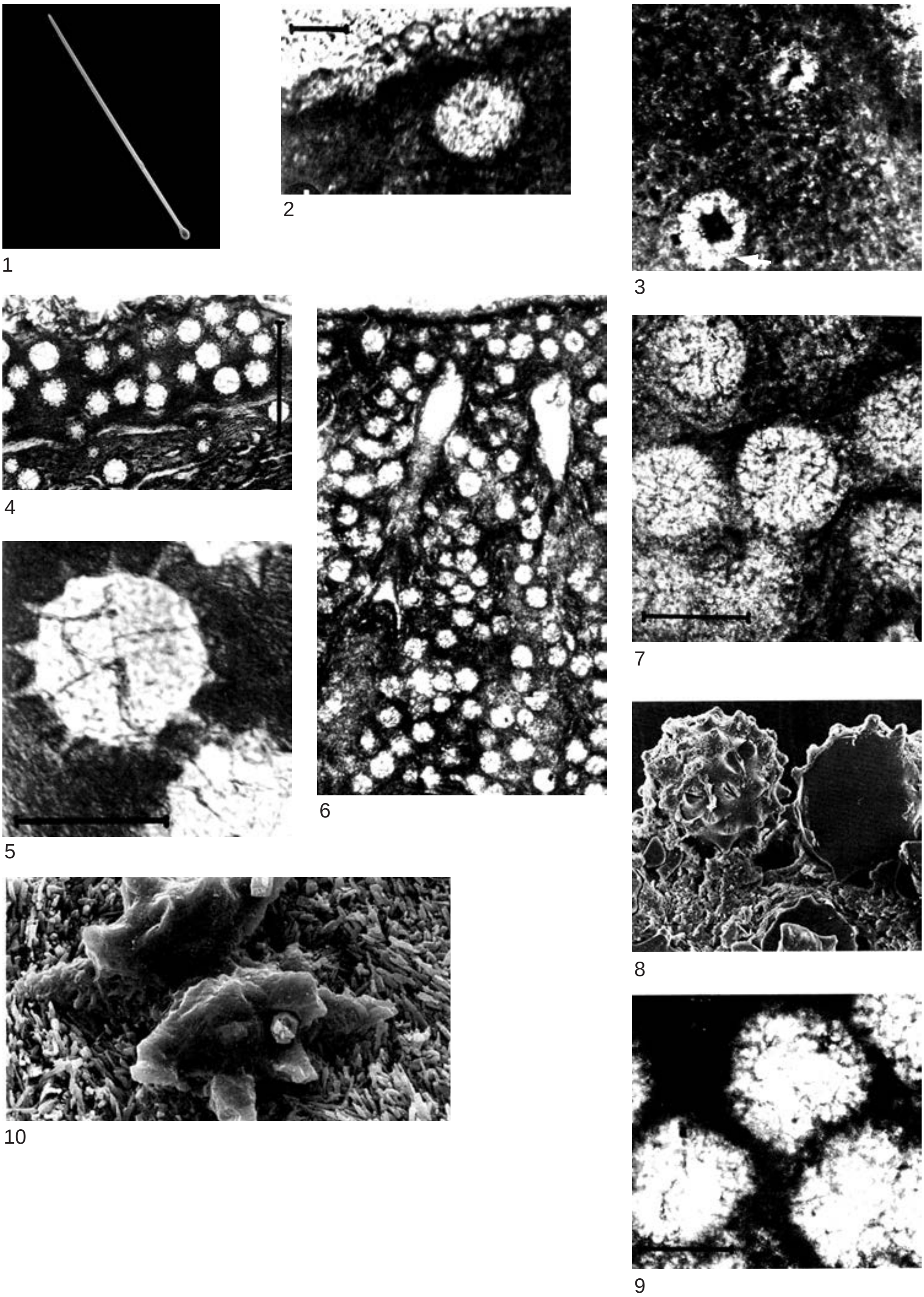


FIG. 43. *(For explanation, see facing page).*

Spherulites are produced within the soft tissue of the sponge. When they are about 15 microns in size, they are transported to the growing tips of the walls and fused together by epitaxial growth, and in some cases, spicules are incorporated, producing a rigid spicular skeleton.

Cuif and others (1979) referred to the microstructure of *Merlia normani* as trabecular and Wendt (1979, 1984) as clinogonal. Boury-Esnault and Rützler (1997) used the term fascicular fibrous, rather than clinogonal, and considered water-jet, trabecular, and penicillate as synonyms of fascicular fibrous. However, Cuif and Gautret (1993) clearly differentiated between the different types of fascicular fibrous microstructures, namely trabecular, penicillate, and water-jet. In taxa with a trabecular microstructure, the orientation of the crystal fibers in the axial part of the trabecula is strongly oblique to the growth direction of the trabecula and does not occur in sponges (Cuif & Gautret, 1993, p. 312). The main difference between the water-jet and penicillate microstructure is in the degree of divergence in the crystal fibers upward in the direction of

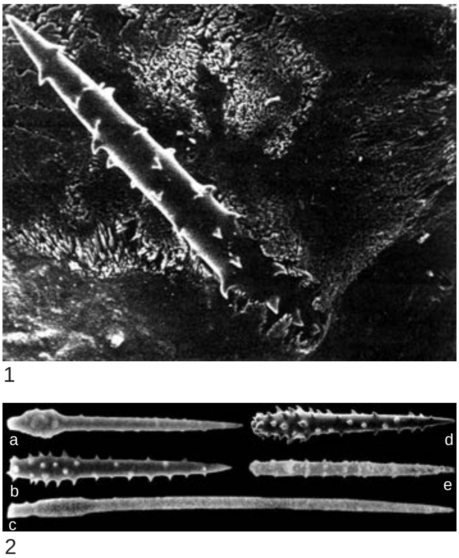


Fig. 44. Variation in acanthostyles in *Astrosclera willeyana; 1,* SEM of an astrosclerid acanthostyle spicule in an extant specimen, Marigondon Cave, Philippines, ×1100 (adapted from Wörheide & others, 1997, pl. III,*2;* courtesy of Real Sociedad Española de Historia Natural, Seccion Geologica, Madrid, Spain); *2,* SEM photos of verticillately spined styles: *a–b,* Indonesia (×400); *c,* Palau (×482); *d,* Philippines (×364); and *e,* Glorieuses Islands (×615) (adapted from Wörheide, 1998, p. 49, pl. 20, with kind permission of Springer Science+Business Media).

Fig. 43. Microscleres in chaetetids: euasters in extant forms; pseudomorphs in fossil forms; *1,* SEM of a siliceous spicule, tylostyle from an extant specimen of *Acanthochaetetes wellsi,* Great Barrier Reef, ×650 (new; courtesy of Jean Vacelet); *2,* thin section of an asterose microsclere pseudomorph in the tubule wall of *Chaetetes (Chaetetes) radians,* Carboniferous, Pennsylvanian, Russia; Reitner (1991a) referred to this specimen as *C. (Chaetetes) radians* and renamed it *Chondrochaetetes longitubus,* ×150 (adapted from Reitner, 1991a, p. 187, fig. 6d); *3,* thin section of asterose microsclere pseudomorphs with pyrite centers (dark areas within lighter circular spicules) in the tubule wall (*white arrow* in lower left points to inferred relict star rays of the microsclere) of *C. (Chaetetes) radians,* Carboniferous, Pennsylvanian, Russia; Reitner (1991a) referred to this specimen as *C. (Chaetetes) radians* and renamed it *Chondrochaetetes longitubus,* ×147 (adapted from Reitner, 1991a, p. 187, fig. 6d); *4,* longitudinal thin section, showing clusters of euasters in the tubule wall of the extant species *Chondrilla grandistellata*, geographic locality not provided, ×29 (adapted from Reitner, 1991a, p. 195, fig. 10a); *5,* enlarged view of the euasters in view *4,* ×200 (adapted from Reitner, 1991a, p. 195, fig. 10b); *6,* longitudinal thin section, showing inferred euaster pseudomorphs in the tubule wall of *Calcichondrilla crustans,* Lower Cretaceous (Albian), northern Spain, ×36.2 (adapted from Reitner, 1991a, p. 192, fig. 8b); *7,* enlarged view of polycrystalline calcite pseudomorphs of inferred euasters in view *6,* ×135 (adapted from Reitner, 1991a, p. 192, fig. 8c); *8,* SEM of euasters in tubule wall of the extant species *Chondrilla grandistellata,* geographic locality not provided, diameter of euasters approximately ×200 (adapted from Reitner, 1991a, p. 190, fig. 7e); *9,* thin section of calcite-filled microscleres, pseudomorphs of inferred euasters, in *Calcistella tabulata* from a Lower Cretaceous (Aptian) boulder in an Eocene conglomerate in Greece, ×220 (adapted from Reitner, 1991a, p. 190, fig. 7d); *10,* SEM of an etched euaster microsclere from the tubule wall of *Acanthochaetetes dendroformis,* Cretaceous, northern Spain, ×2000 (adapted from Reitner, 1991a, p. 200, fig. 13d; views *2–10* with kind permission of Springer Science+Business Media).

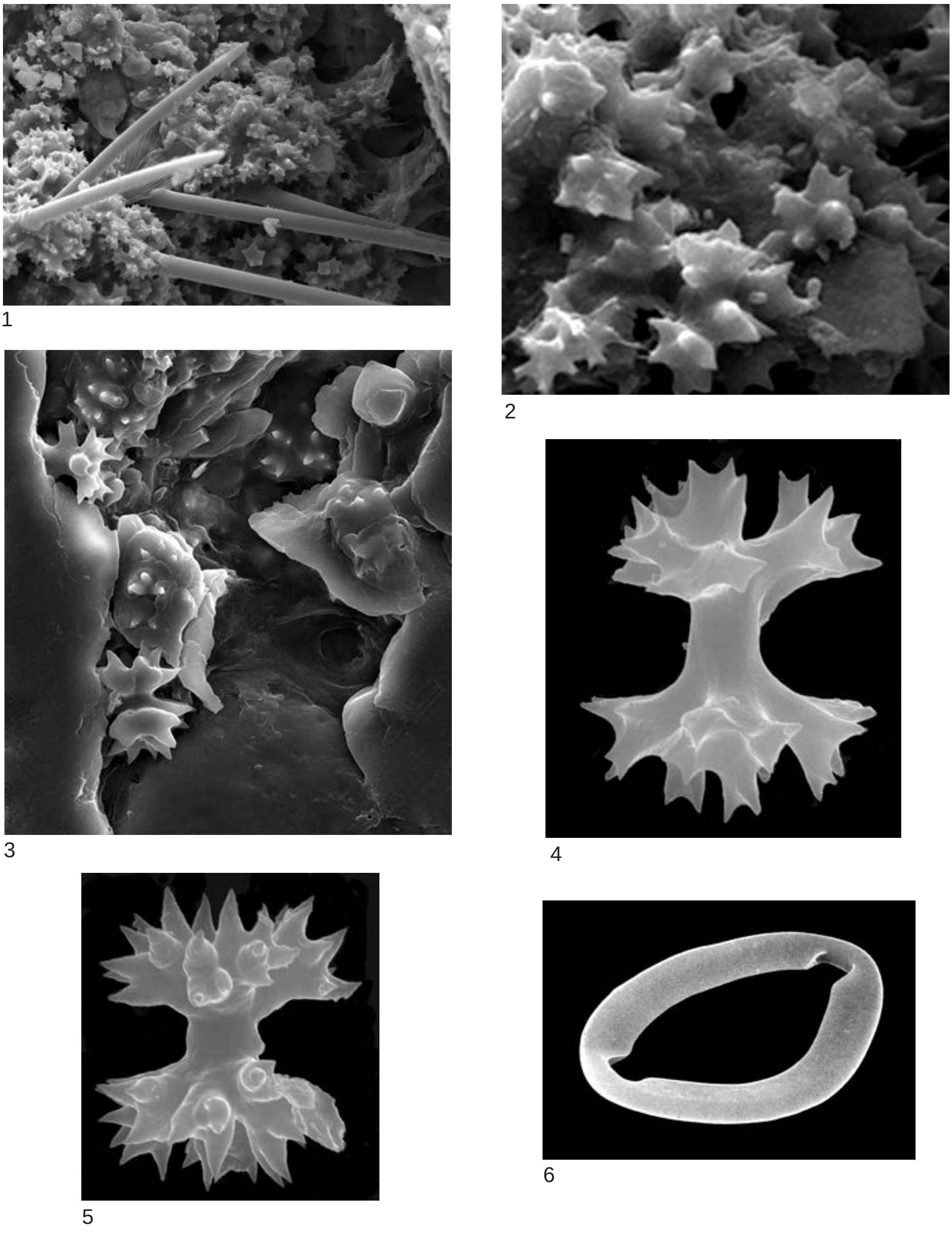


FIG. 45. Microscleres from *Acanthochaetetes* and *Merlia; 1,* SEM of masses of microscleres and a few megascleres (tylostyles) from the growing surface of *Acanthochaetetes* sp., an extant specimen collected live in October 2005 off the Komesu coast, southern Okinawa at a water depth of 15 m, ×1000 (West, 2011a); *2,* enlargement of part of view *1,* showing details of the spirasters, ×4500 (West, 2011a); *3,* SEM of spiraster microscleres from the growing surface of *Acanthochaetetes* sp., an extant specimen collected live in October 2005 off the Komesu coast, southern Okinawa, at a water depth of 15 m, ×1000 (West, 2011a); *4,* SEM of diplaster from an extant specimen of *Acanthochaetetes wellsi,* Great Barrier Reef, ×1320 (West, 2011a); *5,* SEM of several siliceous microscleres from an extant specimen of *Acanthochaetetes wellsi,* Great Barrier Reef, ×1200 (West, 2011a); *6,* SEM of a clavidisc, a meniscoid microsclere from an extant specimen of *Merlia normani,* Great Barrier Reef, ×1760 (West, 2011a).

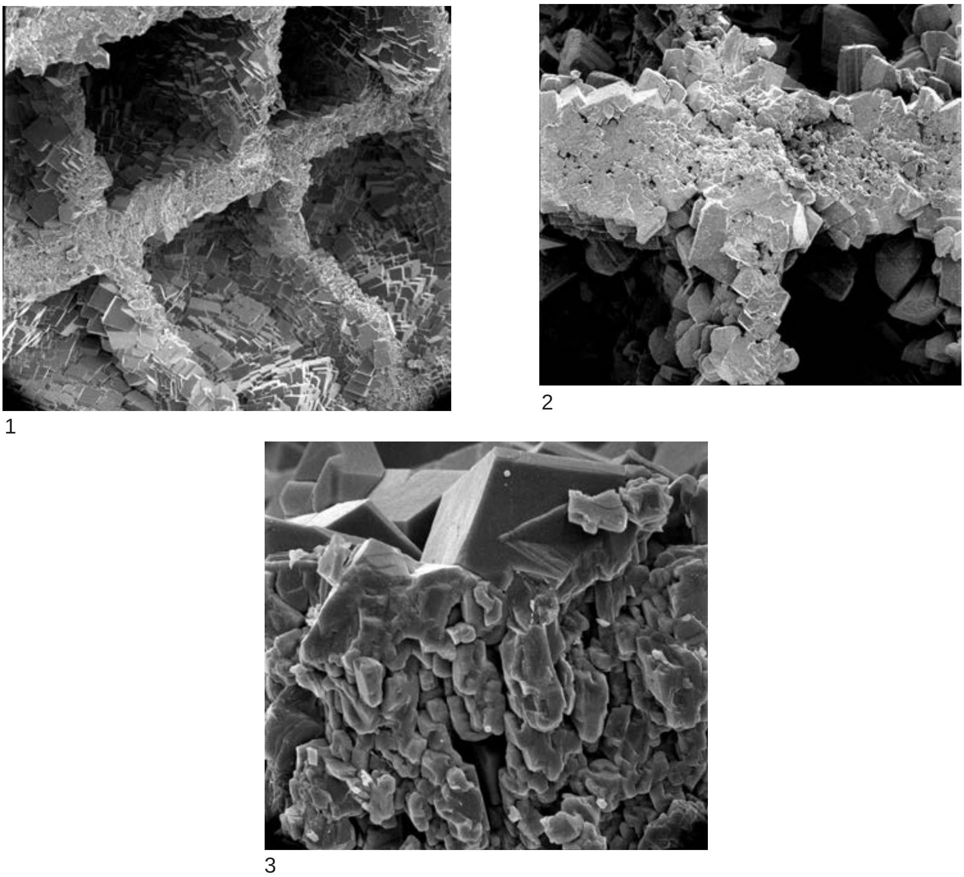
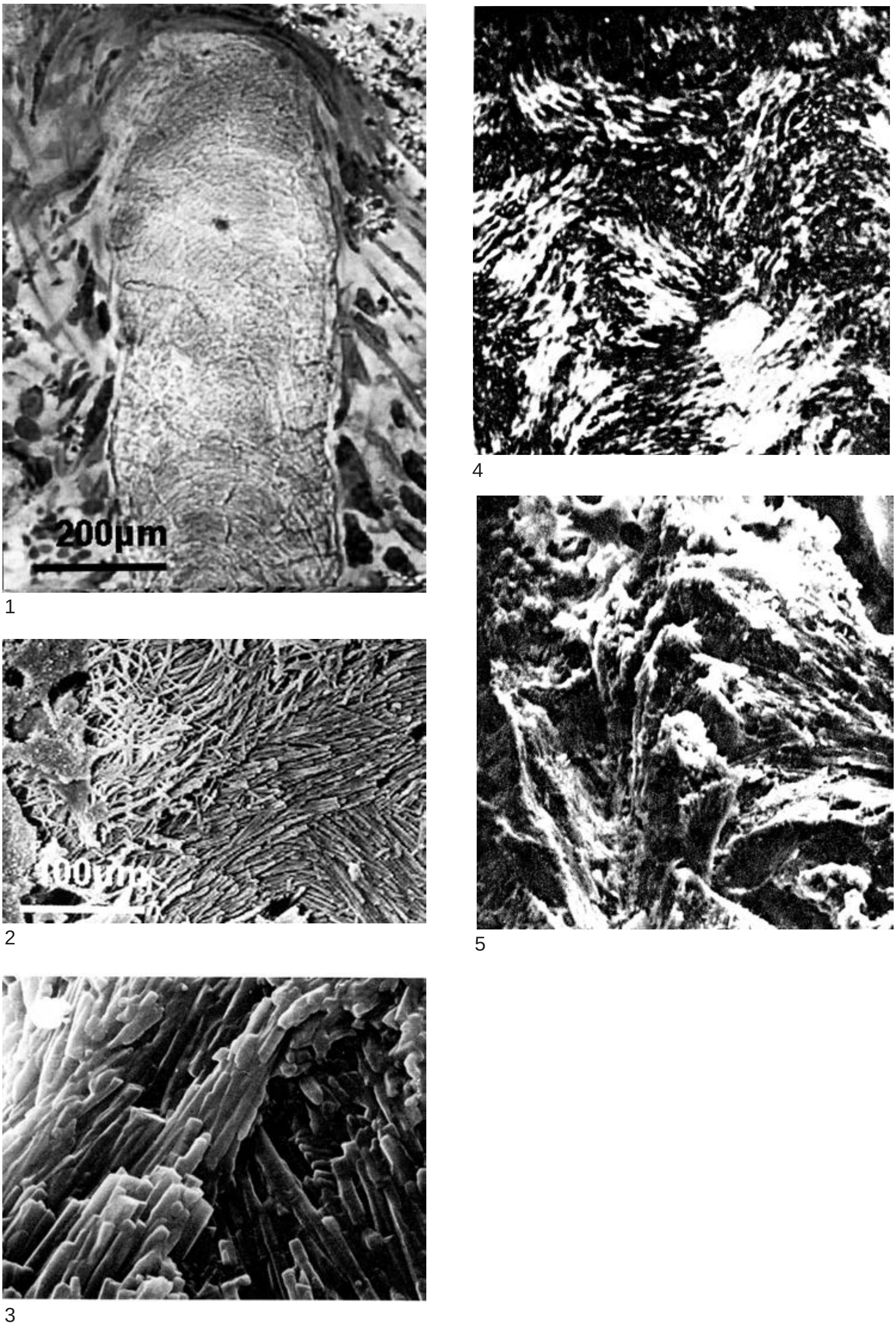


FIG. 46. Dolomite crystals associated with tubule walls and tabulae in a chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone; *1,* SEM of tubule walls and tabulae replaced in part by dolomite, Labette County, Kansas, ×120 (West, 2011a); *2,* enlarged SEM view of tubule wall (horizontal) and tabulae (vertical) replaced in part by dolomite, Labette County, Kansas, ×250 (West, 2011a); *3,* SEM of dolomite rhombs replacing tubule wall, Montgomery County, Kansas, ×1800 (West, 2011a).

growth (CUIF & GAUTRET, 1993). In longitudinal sections, the fibers in a water-jet microstructure fan out upward, and in a penicillate microstructure, the fibers diverge at a very low angle and may appear almost parallel in some views.

Referring to the microstructure of *Merlia normani*, CUIF and GAUTRET (1993, p. 311) stated, "In longitudinal sections, the fibers are vertical in the axial part of the unit..." and bend progressively toward the external part. They comment that this is a typical water-jet (Fig. 49) disposition and noted a similar microstructure in some Carboniferous and Mesozoic (Jurassic and Cretaceous) chaetetids. As noted above, taphonomic processes often obliterate or mute the microstructure in fossil chaetetids, but in some specimens, there is evidence of the original microstructure, and it is fascicular fibrous, water-jet (Fig. 50–51).

The calcareous skeleton of other chaetetids is penicillate, also a type of fascicular fibrous microstructure. The penicillate



1
2
3
4
5

FIG. 47. *(For explanation, see facing page).*

microstructure is easily seen in the extant genus *Ceratoporella* and is also known from fossil chaetetids from the Permian, Triassic, Jurassic, and Cretaceous (Fig. 52; Wendt, 1984; Cuif & Gautret, 1993). Although the term penicillate is used in the *Thesaurus of Sponge Morphology* (Boury-Esnault & Rützler, 1997), Reitner and others (2001) and Vacelet (2002a) referred to the microstructure in *Ceratoporella* as clinogonal. Hartman and Goreau (1970, 1972), Willenz and Hartman (1989), and Reitner and others (2001) described biomineralization in *Ceratoporella*. The calcareous skeleton of *Ceratoporella* is a rigid spicular skeleton in which the crystalline units diverge at a very low angle (Hartman & Goreau, 1970, fig. 17; Wendt, 1984, fig. 1, pl. 2; Wood, 1991b, fig. 5). In spite of taphonomic processes, this microstructure is well preserved in some chaetetids with an original aragonitic skeleton, but less so in those with a calcitic skeleton (Wendt, 1984).

The most recent information on the microstructure and mineralogy of the calcareous skeleton of hypercalcified demosponges is given in Finks and Rigby (2004d). They based their eight different categories on the studies of Wood (1990b), Cuif and Gautret (1991), and Mastandrea and Russo (1995): spherulitic aragonite, penicillate aragonite, irregular aragonite, homogeneous-granular Mg calcite, lamellar Mg calcite, penicillate Mg calcite, spherulitic Mg calcite, and fibrous Mg calcite. How their categories compare with those recognized by others is shown in Table 2, to aid in better understanding and comparing the literature on the different microstructures and skeletal mineralogies of extant and fossil hypercalcified demosponges with either a chaetetid or stromatoporoid calcareous skeleton.

TAPHONOMY (BIOSTRATINOMY AND DIAGENESIS)

Biostratinomic processes (changes between death and final burial) and diagenetic processes (changes after burial) are important in modifying the spicules and the calcareous skeleton of chaetetids. Taphonomic processes identified by Rodriguez (2004) in corals are also important in chaetetids. The 12 taphonomic processes he identified (p. 151), with some modifications and additions, are listed below.

1. Colonization and encrustation by cyanobacteria, algae, bryozoans, foraminifera, corals, sponges, worms, and arthropods, i.e., borings by acrothoracian barnacles (see Fig. 106.3; West & Clark, 1984).

Fig. 47. Microlamellar microstructure in *Acanthochaetetes; 1,* section showing high Mg calcite microstructure and growing tip of a tubule wall, where the mineralization occurs in an extant specimen of *Acanthochaetetes wellsi*, Lizard Island Bonnie Bay reef cave, Great Barrier Reef, Australia, ×95 (adapted from Reitner & others, 1997, pl. *3,2;* courtesy of E. Schweizerbart Science Publishers; for a color version, see *Treatise Online,* Number 20: paleo.ku.edu/treatiseonline); *2,* SEM of part of the zone of initial mineralization that produces the microlamellar microstructure in *Acanthochaetetes wellsi*, an extant species collected from the Lizard Island Bonnie Bay reef cave, Great Barrier Reef, Australia, ×165 (adapted from Reitner & others, 1997, pl. *3,3;* courtesy of E. Schweizerbart Science Publishers); *3,* SEM of calcite microstructure in *Acanthochaetetes seunesi,* Lower Cretaceous (Albian), northern Spain, ×8000 (adapted from Wendt, 1984, p. 331, pl. *1,4;* courtesy of Paleontological Research Institution, Ithaca, New York); *4,* ultrapolished thin section of an extant specimen of *Acanthochaetetes* sp., showing microlamellar microstructure of tubule walls, geographic locality not listed, ×650 (adapted from Cuif & others, 1979, pl. II,*9;* courtesy of CNRS, Paris); *5,* SEM of an extant specimen of *Acanthochaetetes* sp., showing microlamellar microstructure of tubule walls, geographic locality not listed, ×1250 (adapted from Cuif & others, 1979, pl. II,*10;* courtesy of CNRS, Paris).

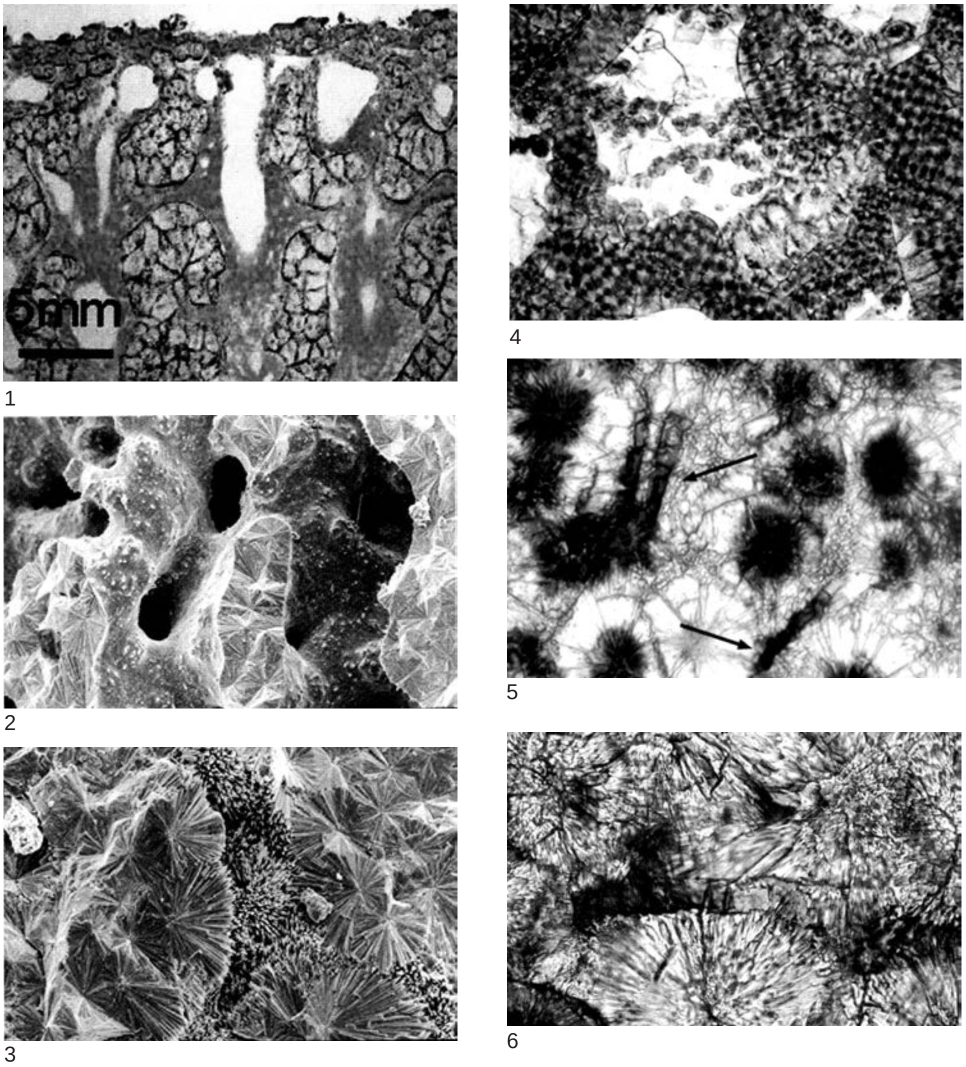


Fig. 48. Spherulitic microstructure in extant and fossil astrosclerid chaetetids; *1,* aragonite spherulites (lighter gray irregular areas that appear brecciated) in a longitudinal section through the living part of an extant specimen of *Astrosclera willeyana,* collected at a depth of 25 m, Ribbon Reef No. 10, Lizard Island, Great Barrier Reef, Australia, ×2.4 (adapted from Reitner & others, 1997, pl. *2,2;* courtesy of E. Schweizerbart Science Publishers); *2,* SEM of smooth walls composed of aragonite spherulites in the skeleton of a Recent specimen of *Astrosclera willeyana,* collected from a reef crest cave of Osprey Reef, Great Barrier Reef, Australia, ×175 (adapted from Wörheide, 1998, pl. 28,*3*); *3,* SEM of aragonite fibers composing the skeleton of a Recent specimen of *Astrosclera willeyana,* collected at a depth of 270 m from the forereef slope of Osprey Reef, Great Barrier Reef, Australia, ×130 (adapted from Wörheide, 1998, pl. 28,*4*); *4,* thin section of spherulitic skeleton (darker areas) of *Astrosclera cuifi,* Upper Triassic (Norian), Turkey, ×50 (adapted from Wörheide, 1998, pl. 30,*1*); *5,* thin section of sub-acanthostyles (*arrows*) in the skeleton of *Astrosclera cuifi*, Upper Triassic (Norian), Turkey, ×220 (adapted from Wörheide, 1998, pl. 30,*6*); *6,* thin section of the spherulitic skeleton with a single sub-acanthostyle between several spherulites in *Astrosclera cuifi,* Upper Triassic (Norian), Turkey, ×467 (adapted from Wörheide, 1998, pl. 30,*8;* views *2–6* with kind permission of Springer Science+Business Media).

2. Bioerosion represented by micro-, meso-, and macroborings, including borings by acrothoracian barnacles (see Fig. 106.3; West & Clark, 1984).

3. Transportation as indicated by abraded surfaces and fragmentation.

4. Infilling of skeletal cavities by sediment and/or cement.

5. Recrystallization (coalescence, euhedralization, micritization).

6. Compression, which produces diagenetic fragmentation.

7. Cementation (micro-dogtooth spar and mosaic calcite).

8. Stylolitization.

9. Silicification.

10. Cleavage.

11. Dissolution.

12. Ferruginization, e.g., pyritization.

Rodriguez (2004, p. 151) pointed out that some of these processes began even before the death of the coral polyps. The same is also true for extant chaetetids in that alteration of the skeleton begins before the death of the organism, as noted by Reitner and Gautret (1996); and it is safe to assume that the same was true for fossil chaetetids.

As noted previously, not all extant hypercalcified demosponges contain spicules during life. Silica-poor water and other environmental factors may preclude the formation of spicules in some extant taxa. When spicules are present, most of them are contained in the soft tissue of extant taxa and are not always incorporated into the calcareous skeleton (Kirkpatrick, 1911; Hartman & Goreau, 1975). Additionally, silica is unstable in the presence of calcium carbonate and siliceous spicules are commonly corroded away in older parts of the calcareous skeleton of still-living taxa (Hartman & Goreau, 1970, 1972). Perhaps, as growth continues, it is more economical to recycle the silica in old spicules than extract it from seawater, given that the silica content in the world ocean may have been low. Ocean water today is undersaturated in silica (Broecker, 1974, p. 33) and averages 2 ppm (Armstrong, 1965, cited in Kennish, 1989, p. 60). Broecker (1974, p. 33) further indicated that hydrous silica dioxide, opal, would readily dissolve in seawater unless protected by some insoluble substance, such as an organic covering. Given the environmental factors that affect spicule formation in living taxa, and taphonomic processes that remove any that do occur, it is not surprising that spicules are relatively rare in fossil forms, and that when they are present, they occur as pseudomorphs (Fig. 41–43). This is unfortunate because spicule composition and morphology are the primary skeletal features upon which sponge systematics is based (Fig. 53.1). Thus, in most fossil specimens of hypercalcified demosponges with a chaetetid skeleton, only the calcareous skeleton is left, and the features it exhibits are less useful for systematic studies. These less useful features are, in order of importance: (1) original mineralogy and microstructure of the calcareous skeleton; and (2) skeletal features such as (a) the size, shape, and arrangement of tubules in transverse section; (b) thickness of walls and tabulae; and (c) spacing of tabulae (Fig. 53.1). Taphonomic processes that alter these features can have a significant negative impact on systematic studies.

Hypercalcified demosponges with a chaetetid skeleton are composed of aragonite or Mg calcite with different microstructures (Table 2) and are thus highly susceptible to diagenetic processes such as recrystallization and replacement (Fig. 46; and see Fig. 54). These diagenetic processes can alter the original mineralogy and microstructure of the skeleton, thus reducing, or eliminating, their systematic usefulness. Although the basic microstructure may remain unchanged in Mesozoic and some upper Paleozoic forms

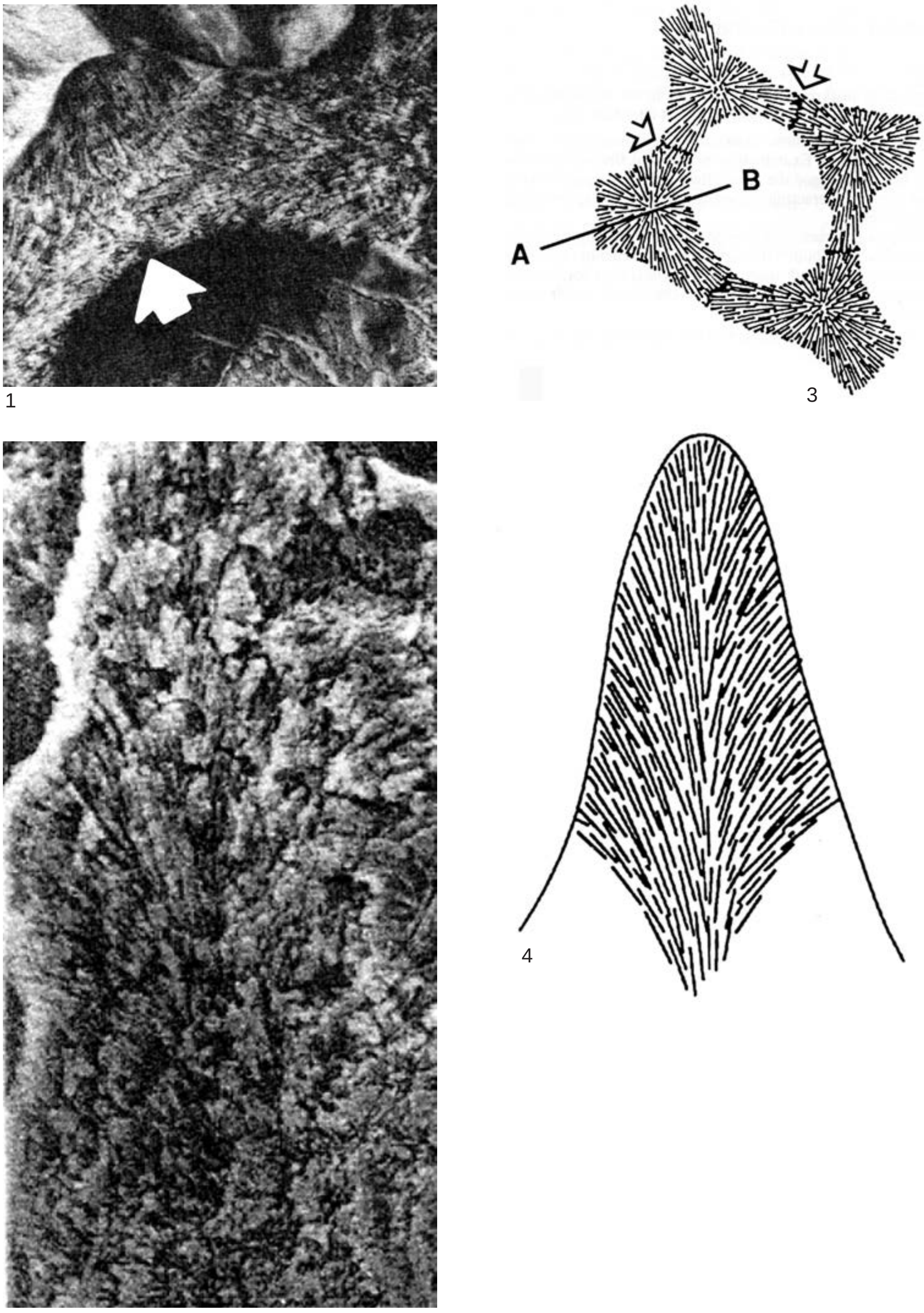


FIG. 49. *(For explanation, see facing page).*

(Fig. 48–52), the size and chemical composition of the crystals forming that structure may change (Cuif & Gautret, 1987; Gautret & Razgallah, 1987; Gautret, Vacelet, & Cuif, 1991; Mastandrea & Russo, 1995; Dauphin, Gautret, & Cuif, 1996). However, even the microstructure of these more recent (Mesozoic) forms can be muted or destroyed (Veizer & Wendt, 1976). Additionally, a diagenetically altered microstructure may mimic the original microstructure in other taxa. For example, micritization can produce a granular microstructure in some taxa, when it was not the original microstructure of the skeleton. Thus, it becomes difficult to separate such diagenetically produced skeletons with a granular microstructure from those in which the original microstructure was/is granular. Gautret (1987) addressed this issue in some extant and Triassic hypercalcified demosponges, and she differentiated between diagenetically produced and original granular microstructural skeletons, using the chemical composition of the skeletons. Along with studies of the major-element composition of chaetetid skeletons (Gautret, 1987), more recent studies have focused on the minor-element and amino acid content of these skeletons (Gautret & Marin, 1993; Marin & Gautret, 1994) as a way of evaluating the effects of diagenesis.

Diagenesis has almost completely destroyed the original microstructure of lower and middle Paleozoic hypercalcified demosponges with a chaetetid skeleton. When careful and detailed studies of the microstructure of chaetetid skeletons is accomplished, the results will probably be much like those reported by Stearn (1966) and Riding (1974a) for stromatoporoids. Only future studies will determine how useful elemental and amino acid compositions of the calcareous skeletons of Paleozoic hypercalcified demosponges will be in learning more about their original composition and microstructure.

With spicules absent or rarely preserved as pseudomorphs, and lacking information on the original composition and microstructure of the calcareous skeleton, the taphonomic impact on the readily visible skeletal features such as tubules,

Fig. 49. Fascicular fibrous water-jet microstructure in *Merlia normani*; *1,* microstructure and junction between walls (*white arrow*) in a polished and etched transverse surface of the extant species *M. normani,* Madeira, ×350 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. II,*4;* courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, Paris*); *2,* water-jet microstructure in a polished and etched longitudinal surface of the extant species *M. normani,* Madeira, ×1167 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. I,*4;* courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, Paris*); *3,* interpretive sketch of a transverse section across a tubule of *M. normani; arrows* indicate junction between walls (possibly junction of pseudosepta), compare with *white arrow* in view *1; line A–B* is the plane of the microstructural unit shown in view *4* (adapted from Cuif & Gautret, 1993, p. 310, fig. 1.1; courtesy of E. Schweizerbartsche Verlags, Naegele U Obermiller Science Publishers); *4,* interpretive sketch of the typical water-jet microstructure in a longitudinal section (*A–B* in view *3*) through a structural unit of *M. normani* (adapted from Cuif & Gautret, 1993, p. 310, fig. 1.2; courtesy of E. Schweizerbart Science Publishers).

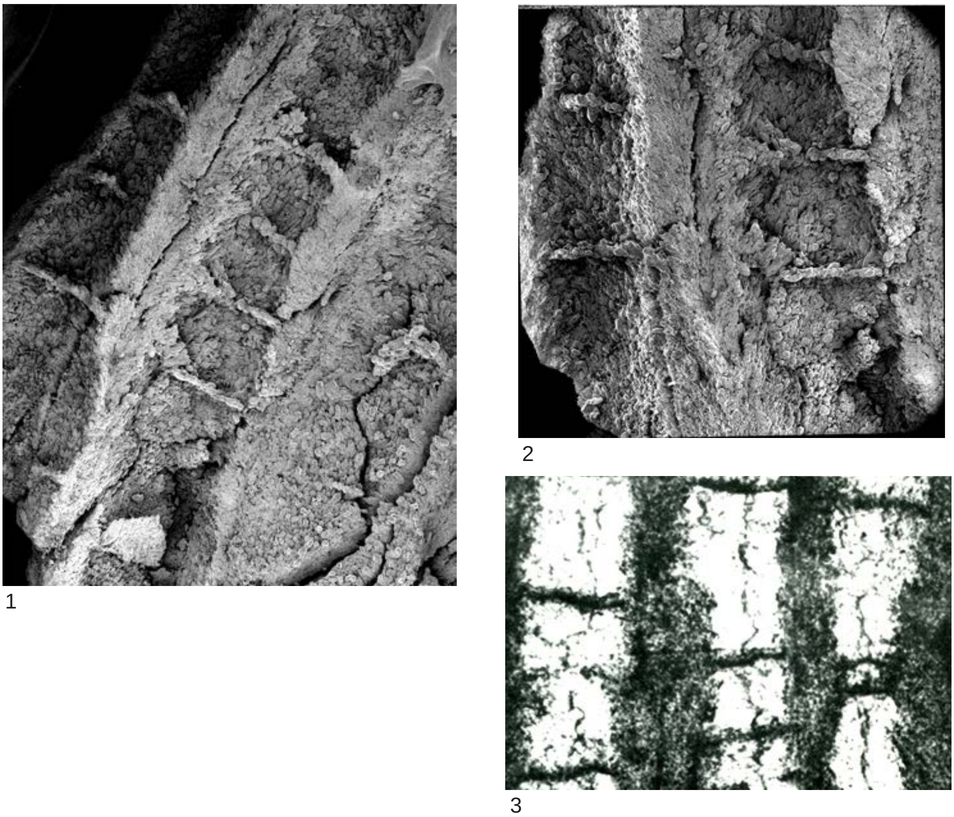


Fig. 50. Fascicular fibrous water-jet microstructure, Carboniferous, Pennsylvanian; *1,* SEM of a tangentially fractured chaetetid skeleton, Moscovian, Moscow Basin, Russia, ×50 (West, 2011a); *2,* enlarged view as seen in an SEM of a longitudinally fractured chaetetid skeleton, Moscovian, Moscow Basin, Russia, ×60 (West, 2011a); *3,* longitudinal thin section of a chaetetid skeleton, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×65 (adapted from Mathewson, 1977, pl. *7,1;* courtesy of Kansas State University).

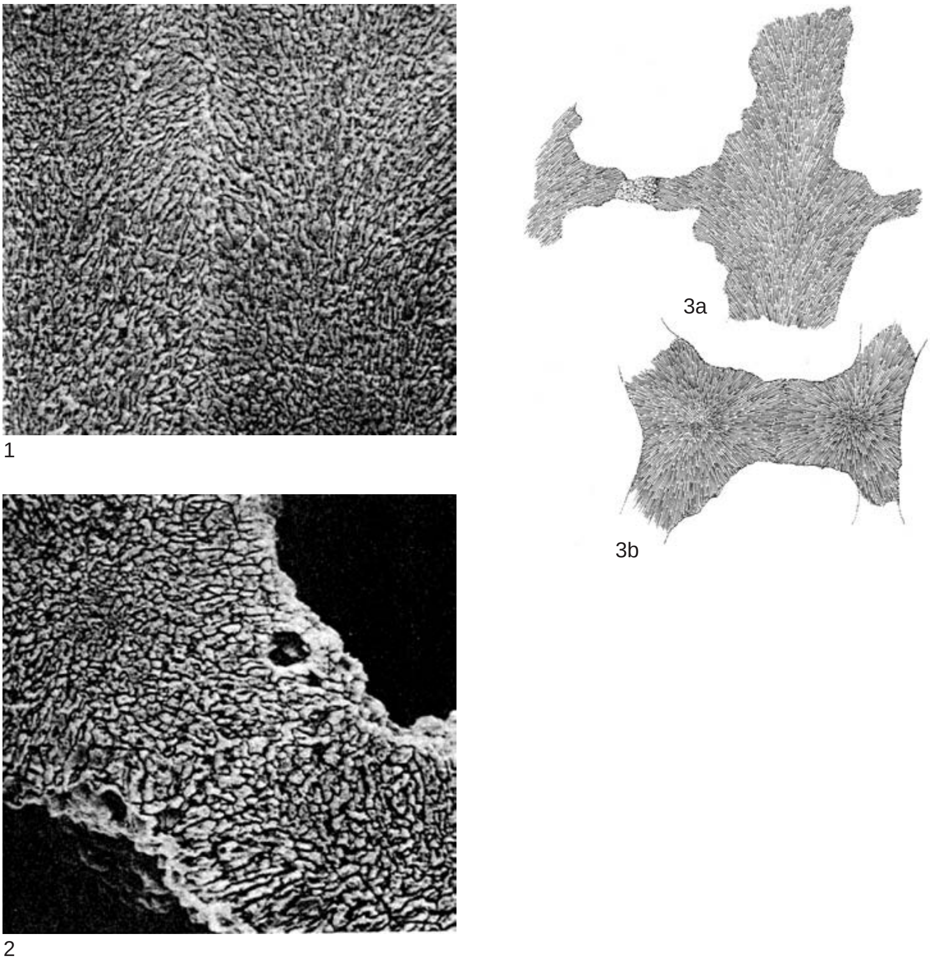
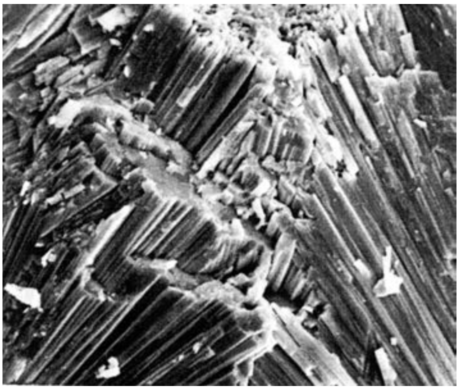


FIG. 51. Fascicular fibrous water-jet microstructure, Carboniferous, Pennsylvanian (continued); *1,* polished and etched longitudinal section of *Chaetetes (Chaetetes) cylindricus,* near Moscow, Russia, ×200 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. III,*1*); *2,* polished and etched transverse section of *C. (Chaetetes) cylindricus*, near Moscow, Russia; note the junction of two microstructural units along a diagonal from the upper right to the lower left, ×200 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. III,*2*); *3,* interpretive sketch of the microstructure of *C. (Chaetetes) cylindricus,* near Moscow, Russia; *a,* longitudinal section, *b,* transverse section; compare *a* to views *1* and *2,* ×80 (adapted from Gautret, Vacelet, & Cuif, 1991, p. 297, fig. 1; all views courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, Paris*).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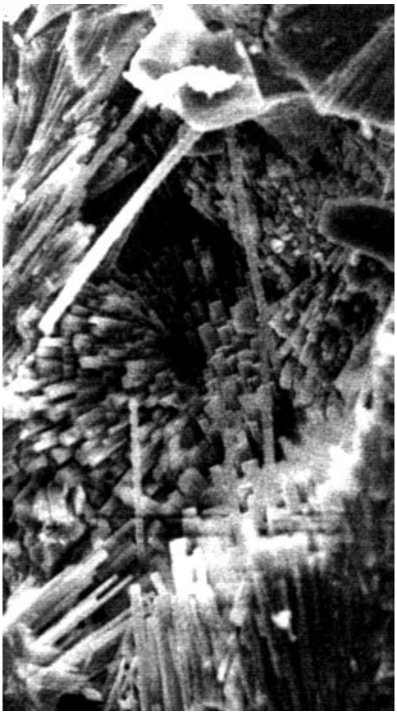
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FIG. 52. Fascicular fibrous penicillate microstructure (clinogonal) in extant and fossil ceratoporellid chaetetids; *1,* SEM of the fascicular fibrous penicillate microstructure (clinogonal) in a fractured surface near the growing tip of a tubule in an extant specimen of *Ceratoporella nicholsoni,* West Indian Caribbean, ×300 (adapted from Hartman & Goreau, 1972, fig. 4; courtesy of *Transactions of the Connecticut Academy of Arts and Sciences*); *2,* SEM of the aragonitic epitaxial backfill that results in the fascicular fibrous penicillate microstructure in a fractured surface of an extant specimen of *Ceratoporella nicholsoni,* Jamaica, ×135 (adapted from Wood, 1991b, p. 329, fig. 5a, with kind permission of Springer Science+Business Media); *3,* SEM of the aragonitic fascicular fibrous penicillate microstructure (clinogonal) in a fractured surface of *Atrochaetetes medius,* Upper Triassic, Italy, ×375 (adapted from Wendt, 1984, p. 331, pl. *1,6;* courtesy of Paleontological Research Institution, Ithaca, New York).

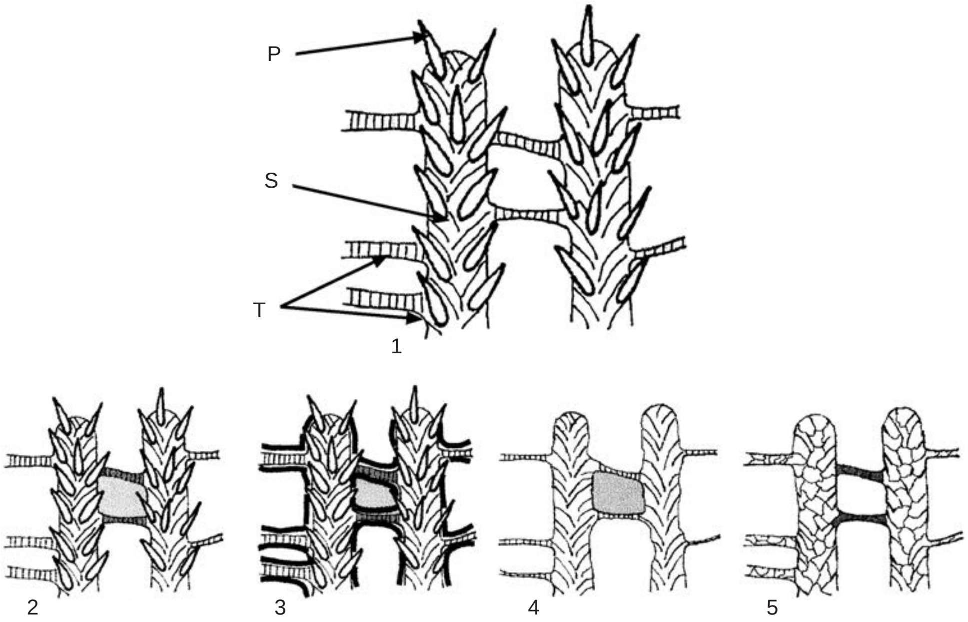

Fig. 53. Categories of skeletal features and potential results of diagenetic processes; *1,* three categories of skeletal features used in systematic studies of chaetetid sponges: *P,* primary, the composition and morphology of mega- and microscleres; *S,* secondary and includes the original mineralogy and microstructure; and *T,* tertiary and includes size, shape and arrangement of tubules in transverse section, thickness of walls and tabulae, and spacing of tabulae (adapted from Wood, 1987, p. 52, fig. 21); *2–5,* diagrams illustrating the potential diagenetic affects on the skeletons of chaetetid sponges; *2,* the original, as depicted, may be affected by the addition and/or subtraction of minerals via interstitial fluids associated with recrystallization, replacement or both (West, 2011a); *3,* results to the original if the walls and tabulae are thickened and intertubular space reduced by deposition of additional inorganic minerals from interstitial fluids (West, 2011a); *4,* results to the original if the spicules are dissolved, the walls and tabulae reduced in thickness, and the intertubular space increased through dissolution via interstitial fluids (West, 2011a); *5,* results if the spicules are dissolved, and the original mineralogy and microstructure is muted or destroyed by recrystallization and/or replacement (West, 2011a).

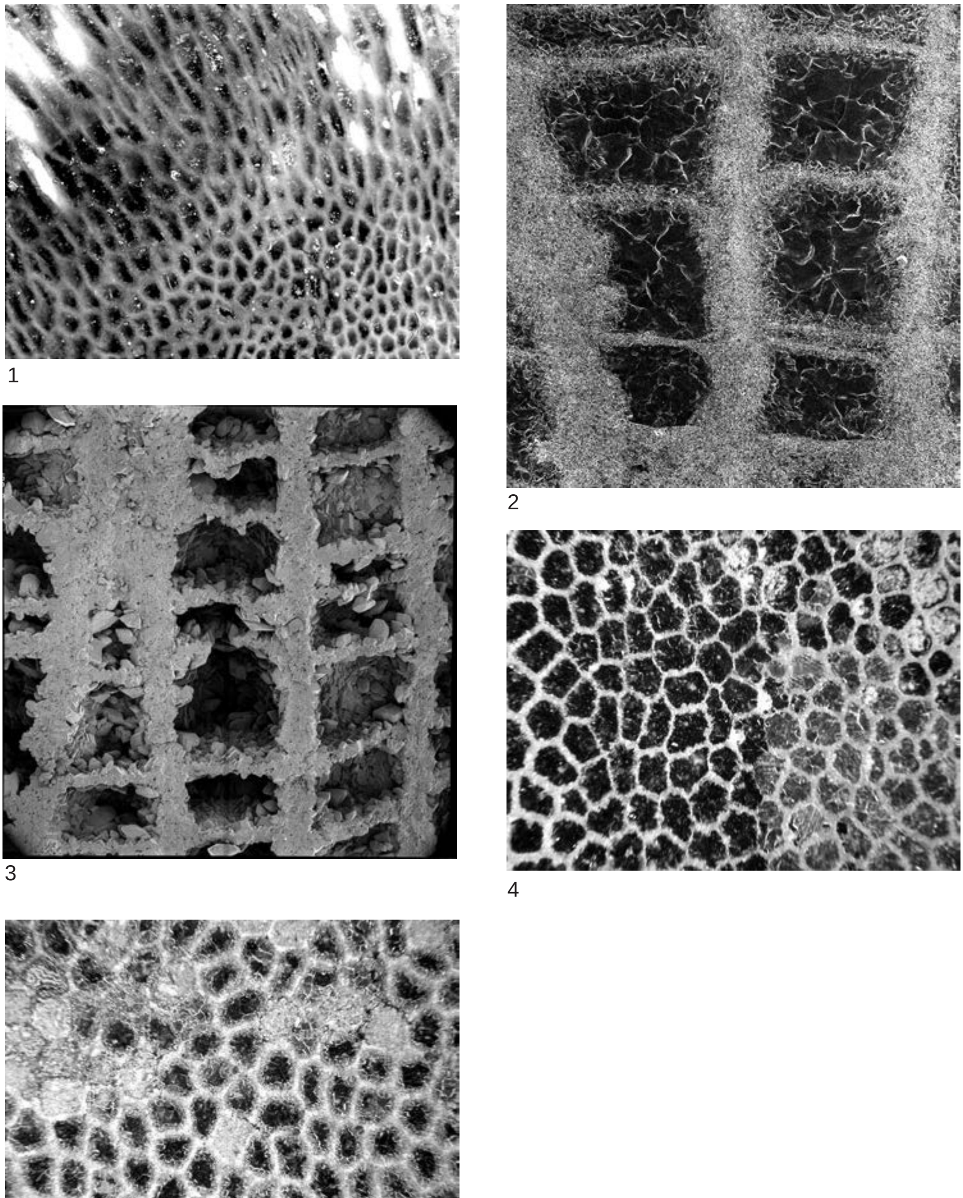

FIG. 54. *(For explanation, see facing page).*

walls, and tabulae must now be examined. Although taphonomic processes rarely modify these features of the calcareous skeleton beyond recognition, they can make it difficult, if not impossible, to separate the mineral component of the original skeleton from that produced taphonomically. There are three areas of mineralization in the calcareous skeleton of *Acanthochaetetes wellsi* (see Reitner & others, 2001), a species that is a reasonable analogue for chaetetid skeletons. One of these, the older parts of the calcareous skeleton between tabulae, is especially important relative to skeletal features. Necrotic (before death) change occurs within this area, because decaying soft sponge tissue produces ammonia (Reitner & Gautret, 1996), creating an environment for the precipitation of calcium carbonate. Such mineralization can increase skeletal features such as wall and tabulae thicknesses, alter the cross-sectional shape of the tubules, and ultimately fill the space completely with precipitated calcium carbonate. Furthermore, it is reasonable to suggest that other processes might produce an acidic environment that could lead to the dissolution of tubule walls and tabulae. Such dissolution would decrease the thickness of the walls and tabulae, and it could even remove tabulae, consequently affecting the distance between tabulae, as well as altering the cross-sectional shape of the tubules. Thus, the size, shape, and arrangement of the tubules and the thicknesses of the walls and tabulae can be altered during life. After death, and during and after final burial, diagenetic processes (physical, chemical, and biological) continue to modify and/or destroy chaetetid skeletons through dissolution and/or chemical precipitation (Fig. 53.2–53.4; West, 1994, p. 401). For example, partial or complete recrystallization and/or silicification of chaetetid skeletons is commonly observed in some Carboniferous specimens (Fig. 54–55).

As noted above, systematic studies require primary features (spicules, which are commonly absent) and secondary

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Fig. 54. Examples of diagenetically altered chaetetid skeletons, Carboniferous, Pennsylvanian; *1,* tangential to transverse thin section, showing chert replacing tubule walls and filling the tubules (white areas in upper right and left corners of image) in a chaetetid skeleton, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×20 (West, 2011a); *2,* longitudinal thin section, showing calcite spar coating tubule walls and tabulae in a chaetetid skeleton, Amoret Limestone Member, Altamont Limestone, Mongomery County, Kansas; note the difference in the thickness of, and space between, tabulae because of the differential coating of tabulae, ×100 (West, 2011a); *3,* SEM of a longitudinal fracture surface, showing the extensive coating, replacement, and filling of the pore spaces in a chaetetid skeleton, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×60 (West, 2011a); *4,* transverse thin section, showing the differences in the wall thicknesses of tubules in a chaetetid skeleton, Bird Springs Formation, Kyle Canyon near Grapevine Spring, Nevada, note that tubule walls in the center are conspicuously thinner than those on either side, ×30 (West, 2011a); *5,* transverse thin section, showing calcite spar coating tubule walls and filling some tubules and obscuring the walls in a chaetetid skeleton, Bird Springs Formation, near Mountain Springs, Nevada, ×30 (West, 2011a).

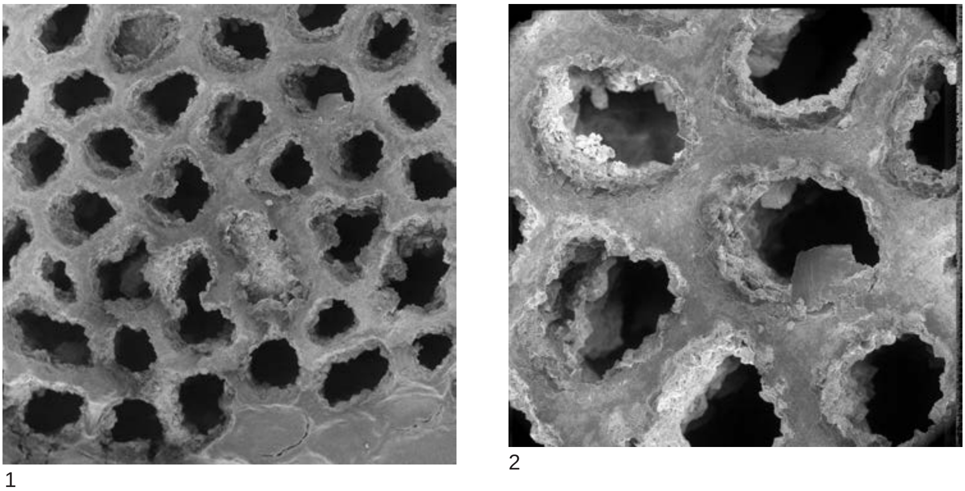
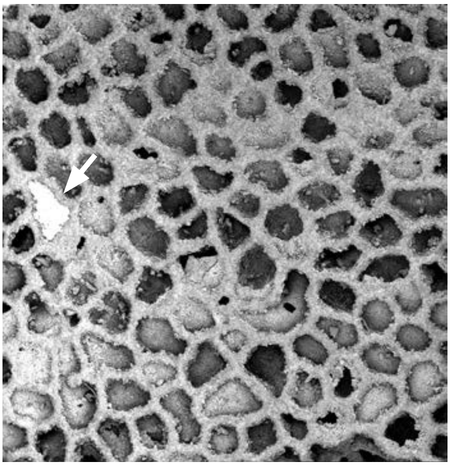


FIG. 55. Examples of diagenetically altered chaetetid skeletons (continued); *1,* SEM of a transverse surface, showing the increase in tubule wall thickness by the addition of mineral deposits in *Chaetetes (Chaetetes) radians,* Carboniferous, Pennsylvanian (Moscovian), near Moscow, Russia, ×30 (West, 2011a); *2,* SEM of the upper right corner of view *1* (note how this diagenetic process affects the cross-section shape of the tubules), ×60 (West, 2011a).

FIG. 56. Similarities and differences between the cross-sectional areas of the tubules from some Carboniferous species of chaetetids; *1,* SEM of transverse surface, showing cross-sectional area (cross-sectional area of a single tubule is illustrated by the white area near center of the left margin, *white arrow*) of tubules in *Chaetetes (Chaetetes) radians* FISCHER VON WALDHEIM, 1830, Pennsylvanian (Moscovian), near Podolsk, south of Moscow, Russia, ×20 (West, 2011a); *2,* matrix showing the results of grouped T-tests of the cross-sectional areas of the tubules in eight different Carboniferous species (designated by *): (a) groups 8 and 9 are from two different thin sections from the same stratigraphic and geographic locality of *Chaetetes (Chaetetes) milleporaceous** MILNE-EDWARDS & HAIME, 1851; (b) groups 21 and 22 are two different areas from the same thin section of the holotype of *Chaetetes (Chaetetes) schucherti** MORGAN, 1924; (c) group 28 is from a thin section of the holotype of *Chaetetes (Chaetetes) eximius** MOORE & JEFFORDS, 1945; (d) group 40 is from a thin section of a paratype of *Chaetetes (Chaetetes) subtilis** MOORE & JEFFORDS, 1945; (e) group 41 is from a thin section of the holotype of *Chaetetes (Chaetetes) favosus** MOORE & JEFFORDS, 1945; (f) group 14 is from a thin section of a chaetetid, Mississippian (upper Visean–Serpukhovian), Kentucky; (g) groups 16 and 20 are of two different thin sections of *C. (Chaetetes) radians* FISCHER VON WALDHEIM, 1830, presumably from the same stratigraphic and geographic locality; and (h) groups 17 and 18 are two different areas on the same thin section of *Chaetetes (Chaetetes) depressus** (Fleming, 1828b); *D,* the groups are different; *ND,* there is no difference between the groups; *D^1,* the same species are different from themselves, although the expected results are that there would be no difference. Significant results are that there are: (1) no differences between: (a) *C. (Chaetetes) milleporaceous** (group 9) and *C. (Chaetetes) schucherti** (group 21); (b) *C. (Chaetetes) eximius** (group 28) and *C. (Chaetetes) schucherti** (group 22); (c) *C. (Chaetetes) favosus** (group 41) and *C. (Chaetetes) schucherti** (group 22); (d) *C. (Chaetetes) milleporaceous** (group 8) and the lower Carboniferous chaetetid (group 14); (e) *C. (Chaetetes) milleporaceous** (group 9) and *C. (Chaetetes) radians* (group 16); (f) *C. (Chaetetes) radians* (group 20) and *C. (Chaetetes) schucherti** (group 22), *C. (Chaetetes) eximius** (group 28) and *C. (Chaetetes) favosus** (group 41); (g) *C. (Chaetetes) depressus** (group 17) and the lower Carboniferous chaetetid (group 14); and (h) *C. (Chaetetes) depressus** (group 18) and *C. schucherti** (group 22), *C. (Chaetetes) eximius** (group 28), and *C. (Chaetetes) radians* (group 20); and (2) that there are differences (D^1) between groups 8 and 9, both *C. (Chaetetes) milleporaceous**; groups 21 and 22, both *C. (Chaetetes) chucherti**; and groups 17 and 18, both *C. (Chaetetes) depressus** (adapted from West, 1994, p. 405, fig. 4; courtesy of E. Schweizerbart Science Publishers).



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Groups													
8													
9	D^1	*C. (C.) milleporaceous*											
21	D	ND											
22	D	D	D^1	*C. (C.) schucherti* holotype									
28	D	D	D	ND	*C. (C.) eximius* holotype								
40	D	D	D	D	D	*C. (C.) subtilis* paratype							
41	D	D	D	ND	D	D	*C. (C.) favosus* holotype						
14	ND	D	D	D	D	D	D	*C. (C.)* sp. Chesterian					
16	D	ND	D	D	D	D	D	D					
20	D	D	D	ND	ND	D	ND	D	D^1	*C. (C.) radians*			
17	D	D	D	D	D	D	D	ND	D	D			
18	D	D	D	ND	ND	D	D	D	D	ND	D^1	*C. (C.) depressus*	
	8	9	21	22	28	40	41	14	16	20	17	18	Groups

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FIG. 56. *(For explanation, see facing page).*

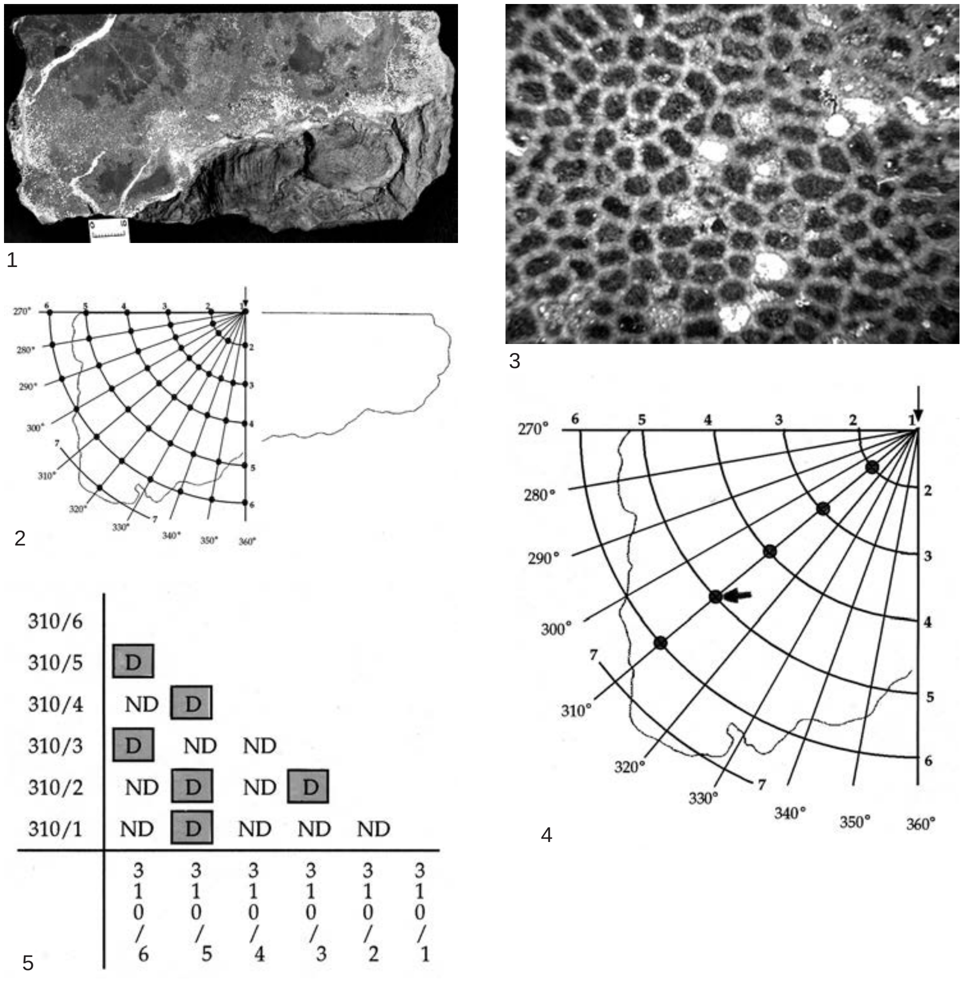

FIG. 57. Similarities and differences between the cross-sectional areas of the tubules from a single laminar chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; *1,* upper surface (transverse section) of polished and etched surface of laminar chaetetid, ×0.4; *2,* outline of polished and etched surface of specimen in view *1,* with superimposed polar coordinates from 270° to 360° (10 rays 10° apart) and 6 arcs, each 13 mm apart; *3,* transverse acetate peel of the area at point 310-5, an example of the 100 tubules for which the cross-sectional area was obtained at each ray-arc intersection, ×30; *4,* sample sites along ray 310 with the one at arc 5 indicated by a *black arrow; 5,* matrix of T-tests comparing the 6 sample sites along ray 310, *ND,* no difference between sites; *D,* there is a difference between sites; expected results are that there would be no differences between any of the sites (West, 2011a).

features (the mineralogical composition and microstructure of the calcareous skeleton). These secondary features are, in numerous cases, extensively modified and, along with absent spicules, are of little value systematically. Therefore, an examination of the skeletal features of chaetetid skeletons alone is unreliable given that such skeletons are polyphyletic (West, 1994). For example, hypercalcified sponges with a chaetetid skeleton occur in at least three orders of the Demospongiae (Hadromerida, Poecilosclerida, and Agelasida) and possibly more. Additionally, taphonomic processes further complicate systematic studies, because they modify such skeletal features as the cross-sectional area of tubules, to the extent that they have little significance (West, 1994, 1995; Fig. 55–56).

FUNCTIONAL MORPHOLOGY OF THE FOSSIL HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

RONALD R. WEST

INTRODUCTION

Hypercalcified sponges with a chaetetid skeleton are members of the marine sessile benthos. Extant members occur in areas of very low light or complete darkness in subtidal caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundred meters (VACELET, 1988) in the Caribbean Sea and Indo-Pacific Ocean. There are three basic components to extant hypercalcified sponges: (1) a thin layer of living tissue, between 1 and 2 mm thick; (2) a rigid basal calcareous skeleton secreted by the living tissue; and (3) siliceous spicules, both megascleres and microscleres, secreted by the living tissue and most often associated with it. Living tissue extends into the calcareous skeleton only a few millimeters. The bulk of the skeleton, unless filled by secondary calcium carbonate, is hollow and during life may have contained seawater. However, if the hollow tubules of the basal calcareous skeleton were filled with seawater, unless protected by a residual organic film, the calcium carbonate of the skeleton would have been adversely affected because of the interaction between calcium carbonate and seawater (CLARK, 1976). Spicules may also occur within the skeleton just beneath the layer of living tissue. In some extant taxa, spicules are absent, and in others, there is no calcareous skeleton (see Introduction to the Fossil Hypercalcified Chaetetid-Type Porifera, p. 15–19).

Reasonable inferences about the function of morphological features of fossils requires careful application of the principles of physics to these morphological features and/or knowledge of extant representatives that are morphologically similar and, preferably, taxonomically related. Movement of water to obtain food and expel waste is essential to members of the phylum Porifera, and thus, the physical principles governing the dynamics of fluid flow are useful in understanding this primary function (see also Functional Morphology of the Paleozoic Stromatoporoid Skeleton, p. 551–574). The extant genera *Acanthochaetetes, Ceratoporella,* and *Merlia* are morphologically similar and, according to some authors (HARTMAN & GOREAU, 1970, 1972; CUIF & GAUTRET, 1993; WOOD, 1990b, 1999), taxonomically related to fossil hypercalcified sponges with a chaetetid skeleton.

Skeletal remains of fossil chaetetids consist of two components: pseudomorphs of spicules and a basal calcareous skeleton. Pseudomorphs of both megascleres and microscleres have been recognized. Megascleres are typically simple monaxons, and microscleres are commonly small spherical objects. Any spicules, or pseudomorphs of spicules, present in fossil forms will be contained within the calcareous skeleton. Because the spicules in extant forms are siliceous, the same is assumed for any spicules in fossil forms during life. The calcareous skeleton is composed of vertically arranged contiguous tubes (tubules), and the tubules are most accurately defined as irregular polygons in transverse section. Tabulae, horizontal partitions, commonly occur within the tubules and are readily visible in longitudinal and transverse sections (see Fig. 15–16). A foramen (or pore) has been observed near the center of the tabulae in some extant forms, and may be seen in fossil forms (see Fig. 34). Features referred to as pseudosepta are visible in tangential sections of some tubules (see Fig. 39–40).

EXTERNAL FEATURES

GROWTH FORM

The chaetetid calcareous skeleton is very simple, both externally and internally. External features include the basal layer, astrorhizae, mamelons, chimneys, and tubercules, though these structures are not always seen. The most obvious aspect of the calcareous skeleton is its general overall shape, which is very similar to that observed in stromatoporoids (see External Morphology of Paleozoic Stromatoporoids, p. 419–486, for a detailed discussion of the shapes and growth habits of Paleozoic stromatoporoids). In chaetetids, there are three basic shapes: laminar, domical, and columnar (West & Kershaw, 1991), which result in a number of variations termed morphotypes by Kershaw and West (1991, fig. 1). These morphotypes can increase in size, or be modified in shape, during life by increasing the number of tubules via longitudinal fission, intertubular increase, peripheral expansion, or the combinations of two or more of these three (see Introduction, p. 15–80). Assuming that a laminar accretionary unit (Kershaw & West, 1991, fig. 7) is the basic building block for all of these morphotypes, environmental conditions become the controlling factors. This is not the case in all hypercalcified sponges, namely stromatoporoids. For example, Kershaw (1981) has shown that some stromatoporoid species in the same environment may develop different growth forms. Although future studies might indicate there is a genetic difference between some or all of these different growth forms in fossil chaetetids, our present knowledge suggests that the different growth forms are largely the result of environmental factors.

The basic reason for a calcareous skeleton in chaetetids is no doubt the same as it is for other clonal lower invertebrates that produce similar skeletons, namely other sponges (like stromatoporoids), corals, and bryozoans. All of these groups are suspension feeders, and an elevated feeding surface above the sediment–water interface where the water is less turbid and the water velocity slightly higher is advantageous (Wildish & Kristmanson, 1997). Stearn, in a later section on the functional morphology of the Paleozoic Stromatoporoid Skeleton (p. 551–574, summarizes the possible explanations for a calcareous skeleton in stromatoporoids, and these explanations can, in general, also be applied to chaetetids.

Given the potential importance of turbidity on the growth form of chaetetids, West and Roth (1991) examined the insoluble residues (siliciclastic content) of chaetetid-bearing, and some associated, carbonate rocks. Results of this preliminary study indicated that the siliciclastic content of carbonates containing laminar chaetetids was significantly higher than it was in carbonates containing domical and columnar chaetetids (Tables 3–4). Additionally, West and Roth (1991) compared the siliciclastic content in each of these three different chaetetid carbonates (habitats) to an environment represented by algal carbonates in which chaetetids were absent. There was no significant difference between carbonates containing domical and columnar chaetetids and algal carbonates (Table 4). Based on these results, West and Roth (1991) suggested that laminar chaetetids grew in turbid (dirty) water habitats, and both domical and columnar chaetetids competed with phylloid and other algae in less turbid (cleaner) water environments. Because cleaner water is more favorable for photosynthesizing algae, a low siliciclastic content would be expected. However, the

Table 3. Mean values of percent of silicilastics (insolubles) in chaetetid habitats (different growth forms) and algal environments (carbonates) (West, 2011b).

	Mean % insolubles	No. of samples
Laminar	25.1	20
Low domical	6.8	8
High domical to columnar	6.0	14
Algal carbonate	4.3	44

Table 4. Matrix of results of grouped t-tests of mean values of percentages of siliciclastic content (see Table 3); n, number of observations (siliciclastic content); *D,* difference between groups; *ND,* no difference between groups. Differences and no differences are significant at a probability of 0.05 (West, 2011b).

Groups	Laminar (n = 20)	Laminar to low domical (n = 8)	Domical to columnar (n = 14)	Algal carbonate (n = 44)	
1					Laminar
2	D				Laminar to low domical
3	D	ND			Domical to columnar
4	D	ND	ND		Algal carbonates
	1	2	3	4	Groups

fact that carbonates containing domical and columnar chaetetids are also low in siliciclastics led West and Roth (1991) to suggest that these chaetetids might have contained some photosynthesizing symbionts like zooxanthellae and competed with the algae for space. Supporting this suggestion is the reported association between autotrophs and bacteria within marine sponges (Wulff, 2006). Erwin and Thacker (2006) reported photosymbionts in reef sponges, and Hill, Lopez, and Harriott (2006) reported sponge-specific cyanobacterial and other bacterial symbionts in Caribbean sponges. Such an association could also explain, to some extent, the tendency for chaetetids in such an environment to develop greater vertical than lateral components of growth. West (1994) suggested that such symbionts might also be responsible for variations observed in the tubule geometry of chaetetids. Even in cleaner water environments, the water at the sediment–water interface would be more turbid, and this could explain why the initial growth of domical and columnar chaetetids was commonly an accretionary laminar unit (Kershaw & West, 1991).

GROWTH RATES

Growth rates of 1 mm to 10 mm over several years have been suggested for *Ptychochaetetes (Ptychochaetetes)*, a Jurassic chaetetid (Fabre & Lathuiliere, 2007, p. 1539), but these estimates are based on growth rates in corals. Estimates and *in situ* studies of two extant species of hypercalcified sponges with a chaetetid skeleton provide growth rates for these extant forms. The specimens studied were low domical and/or laminar forms, and the results refer to vertical growth and also to lateral expansion of the basal calcareous skeleton in *Ceratoporella nicholsoni*. *C. nicholsoni* was studied *in situ* by Willenz and Hartman (1985) in a reef tunnel off the coast of Jamaica for six months (mid-1984 to early 1985) and continued until 1997 (Willenz & Hartman, 1999). Oomori and others (1998) estimated the rate of growth in *Acanthochaetetes wellsi* using chemical signatures in growth bands as described by Benavides and Druffel (1986). *In situ* studies of *Acanthochaetetes wellsi* in a dark reef cave in the fringing reef of Lizard Island (Great Barrier Reef) were reported by Reitner and Gautret (1996). Based on their study that lasted 320 days, Reitner and Gautret (1996) reported an annual growth rate of 0.05–0.1 mm for *A. wellsi.* They further noted (p. 193) that the skeleton formed in a narrow zone between the basopinacoderm and the mature basal skeleton (Fig. 58–59). The rate of growth in *C. nicholsoni* given by Dustan and Sacco (1982) and Benavides and Druffel (1986) are relatively the same as those based on the long-term *in situ* study of *C. nicholsoni* in Jamaica that provided an average annual growth rate of 0.21 to 0.23 mm (Willenz & Hartman, 1999). The basal skeleton of *C. nicholsoni* formed from a layer of basopinacocytes in the mesohyl at the interface between the living tissue and the aragonitic skeleton (Willenz & Hartman, 1989). Studies of *C. nicholsoni* by Lazareth and others (2000)

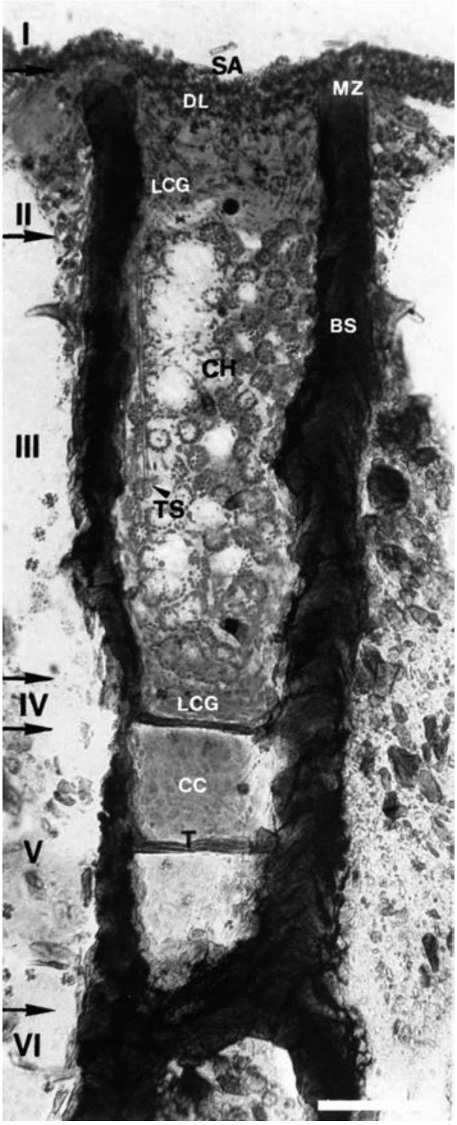

Fig. 58. Growth in *Acanthochaetetes wellsi;* vertical section of a tubule with living tissue. Tubule is divided into six sections: *I,* spiraster microsclere (*SA*) crust; *II,* lower dermal layer (*DL*) with large cells with granules (*LCG*) and skeletal growth fronts (*MZ*); *III,* choanosome (*CH*) and tylostyle megascleres (*TS*); *IV,* basal part with tabula (*T*) formation; *V,* crypt cells (*CC*) [thesocytes, resting-surviving cells]; and *VI,* nonliving basal skeleton (*BS*), ×22.4 (adapted from Reitner & Gautret, 1996, pl. 49,*1;* with kind permission of Springer Science+Business Media; for a color version, see *Treatise Online,* Number 21: paleo.ku.edu/treatiseonline).

using δ^{13}C revealed similar growth rates, and Rosenheim and others (2004) using calcein stain reported an average growth rate of 0.18 mm/yr. However, growth rates vary significantly from one individual to another and within a given individual through time; Willenz and Hartman (1999) reported a growth rate of 0.12 mm/yr for small specimens of *C. nicholsoni.* This is close to the 0.1 mm/yr rate reported for *A. wellsi* (Reitner & Gautret, 1996).

These growth rates of hypercalcified demosponges with a chaetetid skeleton are compared to growth rates reported for other clonal invertebrates in Tables 5–7. Table 5 provides the taxa, age, habitat, growth rate in mm/yr, reference, and pertinent remarks for hypercalcified and nonhypercalcified extant sponges, hermatypic and ahermatypic extant corals, and extant bryozoans. For some sponges and bryozoans, the data are reported as areas, i.e., mm^2/yr. Similar data for Ordovician, Silurian, and Devonian corals are given in Table 6. The same information is given in Table 7 for specimens of extant hermatypic corals from different water depths from the Caribbean and Indo-Pacific. There are data for *Montastrea annularis, Montastrea cavernosa, Porites asteroides*, and *Siderastrea siderea* from the Caribbean, and for *Astreopora myriophthalma, Porites lobata, Goniastrea retiformis*, *Favia speciosa, Porites lutea,* and *Favia pallida* from the Indo-Pacific. Two aspects of the data in Tables 5 and 7 are particularly obvious and important: (1) the growth rate of all the other clonal invertebrates listed is an order of magnitude greater than the growth rate for either of the two hypercalcified sponges (Table 5); and (2) the growth rate of extant hermatypic corals varies with water depth; often, though not always, the growth is slowest in deeper water (Table 7). In *Oculina varicosa* (Table 5), the ahermatypic form of this species grows faster in deep, cold water than the hermatypic form does in shallow, warmer water.

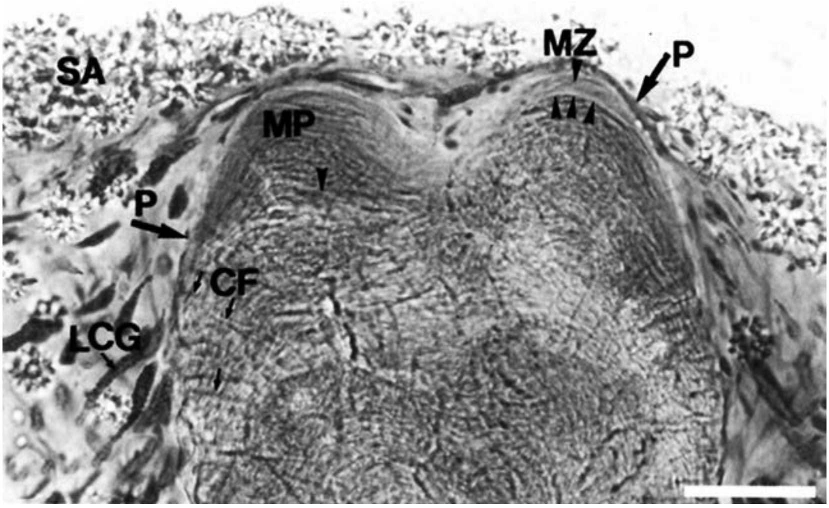

FIG. 59. Growth in *Acanthochaetetes wellsi* (continued); uppermost growing zone of tubule wall, enlargement of upper part of section II in Figure 58. *MP,* mucus-rich parts of basal skeleton within active mineralizing front (*MZ*) beneath basal pinacoderm (*P*), *SA,* spiraster microsclere crust, collagenous fibers (*CF*) within basal skeleton (*arrows*), large cells with granules (*LCG*), ×640 (adapted from Reitner & Gautret, 1996, pl. 49,*2;* with kind permission of Springer Science+Business Media; for a color version, see *Treatise Online,* Number 21: paleo.ku.edu/treatiseonline).

Few data are available on the growth rates of fossil clonal invertebrates. DULLO (2005) provided some data for Pleistocene coral specimens, and MA (1933, 1937a, 1943a, 1943b, 1943c) and FAUL (1943) provided data on Ordovician, Silurian, and Devonian rugose and tabulate corals. But, there are no data on the growth rates of fossil bryozoans or hypercalcified, or other fossil, sponges. MA (1934, 1937b) also documented the growth rate of numerous extant coral taxa from the South Pacific and areas around the Japanese islands. To determine the reliability of the growth rates reported for these fossil corals by MA (1943a, 1943b, 1943c) and FAUL (1943), a comparison was made between growth rates of some extant coral species reported by MA (1937b) with those reported by DULLO (2005) for the same extant species in the same general areas. This comparison (Table 8) shows that the growth rates reported by MA (1937b) are very close to those reported by DULLO (2005) for the same species from the same general area; the difference is less than a millimeter. MA (1943a, 1943b, 1943c) and FAUL (1943) used the same technique in determining the growth rates of fossil corals as MA (1937b) used to determine the growth rates of extant corals. Thus, given the results in Table 8, and the fact that the technique for determining the growth rates of both extant and fossil corals is the same, the growth rate data for fossil corals reported by MA (1943a, 1943b, 1943c) and FAUL (1943) are reasonable growth rate estimates.

Using the growth rates of fossil corals from MA (1943a, 1943b, 1943c) and FAUL (1943) and those of some extant corals and hypercalcified demosponges, it is possible to obtain a rough estimate of the growth rate of some fossil hypercalcified sponges, i.e., those with a chaetetid skeleton. The proportional relationship between the growth rate of an extant coral and the growth rate of an extant hypercalcified demosponge can be used to estimate the growth rate of fossil hypercalcified demosponges, if the growth rate of

TABLE 5. Measured growth rates in mm/yr of extant clonal invertebrates: sponges, corals, and bryozoans; for some sponges and bryozoans, data on growth rate was only available in mm^2/year, as noted on p. 84 (West, 2011b).

Taxa	Habitat	Measured growth rates	Reference	Remarks
Sponges				
Raspailia inaequalis	shallow marine	1–10 mm/yr mean = 5 mm/yr	Kaandorp & Kubler, 2001	
Haliclona oculata	shallow marine	52–78 mm/yr; mean = 65 mm/yr	Kaandorp & Kubler, 2001	tolerates low salinity and silt
Tedania anhelans	shallow marine	160–312 mm^2/yr; mean = 236 mm^2/yr	Knott & others, 2006	littoral to 100 m
Acanthochaetetes wellsi	cryptic marine	0.05–0.1 mm/yr; mean = 0.075 mm/yr	Reitner & Gautret, 1996	water depth = 6–15 m
Ceratoporella nicholsoni	cryptic marine	0.12–0.23 mm/yr; mean = 0.175 mm/yr	Willenz & Hartman, 1999	water depth = 25–29 m
Corals				
Hermatypic	marine	20–80 mm/yr; mean = 50 mm/yr	Wells, 1957	
Hermatypic	marine	9 mm/yr	Krempf, 1934	
Hermatypic	marine reef	6–25 mm/yr; mean = 15.5 mm/yr	Vaughn, 1915	Florida corals
Hermatypic	marine reef	1.1–180 mm/yr; mean = 25.0 mm/yr	Dullo, 2005, table 2	Caribbean Province
Hermatypic	marine reef	3–165 mm/yr; mean = 25.7 mm/yr	Dullo, 2005, table 2	Indo-Pacific Province
Oculina varicosa hermatypic	6 m reef	11.3 mm/yr	Reed, 1981	coastal Florida temp. = 24.6° C
Oculina varicosa ahermatypic	80 m bank	16.1 mm/yr	Reed, 1981	coastal Florida temp. = 16.2° C
Lophelia pertsua ahermatypic	deep-water marine	5–10 mm/yr; mean = 7.5 mm/yr	Fosså, Mortensen, & Furevik, 2002; Mortensen & Rapp, 1998	water depth = 39 to 3000 m; temp. = 6–8° C
Bryozoa				
Membranipora membrancea	marine	720 mm/yr lateral	McKinney & Jackson, 1989	encrusting kelp 0.8–1.2 mm/4–6 hr
Bugula neritina	marine	7300 mm/yr vertical and lateral	McKinney & Jackson, 1989	fouling organism 20 mm/day
Steginoporella sp.	marine	110 mm/yr lateral	McKinney & Jackson, 1989	
Reptadeonella costulata	marine	30–40 mm/yr; lateral mean = 35 mm/yr	McKinney & Jackson, 1989	
Drepanophora tuberculatum	marine	39.6–60 mm^2/yr; mean = 49.8 mm^2/yr	McKinney & Jackson, 1989	2–3 cm^2 (max. size) in 6 months or less
Disporella fimbriata	marine	20.4–39.6 mm^2/yr; mean = 30 mm^2/yr	McKinney & Jackson, 1989	1 cm^2 (max. size) in 3–6 months

fossil corals is known. Extant hypercalcified demosponges for which there are data on growth rates are *Ceratoporella nicholsoni* and *Acanthochaetetes wellsi*, both of which commonly occur in deeper water, cryptic habitats (Table 5). Extant corals from a similar habitat, from which there are growth rate data, are the ahermatypic corals *Oculina varicosa* and *Lophelia pertsua* (Table 5). As noted in the footnote in Table 6, well over 50% of the fossil corals measured by MA (1943a, 1943b, 1943c) had a growth rate of less than 10 mm/yr, and such a growth rate seems appropriate for the calculation of an estimate of the growth rate of fossil hypercalcified demosponges. Results of these calculations are given in Table 9, and the estimated growth rate of fossil hypercalcified

TABLE 6. Estimated growth rates in mm/yr of Paleozoic corals (Ordovician, Silurian, and Devonian) (West, 2011b).

Taxa	Age	Habitat	Estimated growth rates	Reference	Remarks
Heliolites parvistella	Ordovician[1]	marine	1.2 mm/yr	Ma, 1943a, vol. 1	slowest growth of 122 specimens of 46 species of 14 genera
Columnaria alveolata	Ordovician[1]	marine	20.0 mm/yr	Ma, 1943a, vol. 1	fastest growth of 122 specimens of 46 species of 14 genera
Heliolites parvistella	Silurian[2]	marine	1.2 mm/yr	Ma, 1943b, vol. 2	slowest growth of 545 specimens of 145 species of 43 genera
Phaulactis angusta	Silurian[2]	marine	35.0 mm/yr	Ma, 1943b, vol. 2	fastest growth of 545 specimens of 145 species of 43 genera
Keriophyllum proliferum	Devonian[3]	marine	2.0 mm/yr	Ma, 1943c, vol. 3	slowest growth of 494 specimens of 176 species of 32 genera
Tabulophyllum ellipticum	Devonian[3]	marine	30.0 mm/yr	Ma, 1943c, vol. 3	fastest growth of 494 specimens of 176 species of 32 genera
Prismatophyllum sp.[4]	Devonian	marine reef	1.75 mm/yr	Faul, 1943	slowest growth of 33 specimens of 4 species in 1 genus
Prismatophyllum sp.[4]	Devonian	marine reef	6.2 mm/yr	Faul, 1943	fastest growth of 33 specimens of 4 species in 1 genus

[1] 87 of the 122 Ordovician specimens (71%) grew less than 10 mm/yr; [2] 475 of the 545 Silurian specimens (87%) grew less than 10 mm/yr; [3] 318 of the 494 Devonian specimens (64%) grew less than 10 mm/yr; [4] *Prismatophyllum* is now *Hexagonaria.*

demosponges ranges from 0.02 to 0.2 mm/yr. The range of measured growth rates for extant hypercalcified sponges is 0.05 to 0.23 mm/yr (Table 5). Therefore, growth rates are similar in fossil and extant hypercalcified sponges.

Using the estimated minimum and maximum growth rates of fossil hypercalcified demosponges (0.02 mm/yr and 0.2 mm/yr, respectively), the inferred age of a chaetetid mass 2.3 m thick in the Carboniferous of southeastern Kansas (Suchy & West, 2001) is between 11,500 and 115,000 years old. Using the average growth rate, 0.05 mm/yr, of Carboniferous reefs (Table 10), this chaetetid mass would be 46,000 years old, about halfway between the ages based on the estimated annual growth rate of fossil hypercalcified demosponges. Because there are a number of growth interruptions in these Carboniferous chaetetids, these inferred ages are probably minimal.

Regeneration of skeletons of injured specimens was initially slower in *Ceratoporella nicholsoni*, but increased to a normal rate after a year and then increased slightly (Willenz & Hartman, 1999, p. 675). Lehnert and Reitner (1997) reported that lateral regeneration of injured areas of *C. nicholsoni* grew 102 to 154 times faster than vertical growth. Assuming a growth rate of 0.23 mm/yr for vertical growth, Suchy and West (2001, p. 441) calculated that lateral growth would then proceed at the rate of 23 to 35 mm/yr. This rate of lateral expansion of the skeleton may be excessive in that, as Willenz and Hartman (1999, p. 683) noted, Lehnert and Reitner (1997) reported the lateral expansion of the soft tissue, not the skeleton. Although the lateral expansion of the skeleton might have been slower, any increase in the lateral growth rate over the vertical growth rate would be advantageous as these chaetetid sponges competed

TABLE 7. Measured growth rates in mm/yr for specimens of extant hermatypic corals from different water depths from the Caribbean and Indo-Pacific (data from Dullo, 2005, table 1).

Taxa	Habitat	Measured growth rates	Location
Caribbean			
Montastrea annularis	depth < 6 m	8.2 mm/yr	inshore Florida
M. annularis	depth > 6 m	6.3 mm/yr	offshore Florida
M. annularis	depth = 5 m	7.4 mm/yr	Jamaica
M. annularis	depth = 45 m	1.6 mm/yr	Jamaica
Montastrea cavernosa	depth = 10 m	3.6 mm/yr	Jamaica
M. cavernosa	depth =20 m	6.8 mm/yr	Jamaica
M. cavernosa	depth =30 m	4.1 mm/yr	Jamaica
Porites asteroides	depth = 0–1 m	5.0 mm/yr	Jamaica
P. asteroides	depth = 5 m	5.0 mm/yr	Jamaica
P. asteroides	depth = 10 m	3.3 mm/yr	Jamaica
P. asteroides	depth = 30 m	2.3 mm/yr	Jamaica
Siderastrea siderea	depth = 10 m	7.1 mm/yr	Jamaica
S. siderea	depth = 20 m	3.0 mm/yr	Jamaica
S. siderea	depth = 30 m	3.1 mm/yr	Jamaica
Average		**4.8 mm/yr**	
Indo-Pacific			
Astreopora myriophthalma	depth = 6–15 m	13.0 mm/yr	Enewetak
A. myriophthalma	depth = 16–25 m	5.5 mm/yr	Enewetak
Porites lobata	depth = 6–15 m	11.5 mm/yr	Enewetak
P. lobata	depth = 16–25 m	6.0 mm/yr	Enewetak
Porites lutea	depth = 0–5 m	13.5 mm/yr	Enewetak
P. lutea	depth = 6–15 m	11.0 mm/yr	Enewetak
P. lutea	depth = 16–25 m	9.5 mm/yr	Enewetak
P. lutea	depth = >25 m	6.0 mm/yr	Enewetak
Favia pallida	depth = 0–5 m	7.5 mm/yr	Enewetak
F. pallida	depth = 6–15 m	7.0 mm/yr	Enewetak
F. pallida	depth = 16–25 m	7.0 mm/yr	Enewetak
F. pallida	depth = 26–30 m	6.5 mm/yr	Enewetak
Favia speciosa	depth = 0–5 m	4.6 mm/yr	Enewetak
F. speciosa	depth = 6–15m	8.5 mm/yr	Enewetak
F. speciosa	depth = 16–25 m	7.0 mm/yr	Enewetak
Goniastrea retiformis	depth = 0–5 m	10.0 mm/yr	Enewetak
G. retiformis	depth = 6–15 m	9.5 mm/yr	Enewetak
G. retiformis	depth = 16–25 m	6.0 mm/yr	Enewetak
Average		**8.3 mm/yr**	

with other encrusting sessile benthos for space on the seafloor.

Estimates of the growth rates of fossil chaetetids and the ages of chaetetid masses, as outlined above, is, of course, equivocal and may not be realistic. It should be remembered that extant hypercalcified demosponges, those used in this comparison, live in areas of very low light or complete darkness in subtidal caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundred meters (VACELET, 1988). Because of their minor role in post-Paleozoic reefs, this is probably also true for the chaetetid taxa during this time interval. During the Carboniferous (Pennsylvanian), however, they were a major constructor of shallow, subtidal reef mounds in open marine settings (WEST, 1988; SUCHY & WEST, 2001), and thus their annual growth rate may have been much greater. The growth rates presented here are simply to provide some possible indications of longevity and rates of lateral expansion based on those rates in extant taxa.

BASAL LAYER

A very thin feature with concentric growth lines has been observed covering the lower surface in some extant and fossil

TABLE 8. Comparison of measured growth rates in mm/yr of some extant coral taxa from DULLO (2005) and MA (1937b); *μ,* average value (mean) of the number of measurements; *n,* number of measurements (adapted fromWest, 2011b).

Taxa	Region	Measured growth rates	Reference
Atlantic			
Montastera annularis	Florida and Bahamas	μ = 5.8 mm/yr (n = 7)	Ma, 1937b, table 1
M. annularis	Florida and Jamaica	μ = 5.9 mm/yr (n = 4, see Table 6)	Dullo, 2005
Siderastrea siderea	Florida and Bahamas	μ = 3.5 mm/yr (n = 6)	Ma, 1937b, table 1
S. siderea	Jamaica	μ = 4.4 mm/yr (n = 3, see Table 6)	Dullo, 2005
Indo-Pacific			
Favia pallida	Japan and South Pacific	Mean values for different regions range from 2.9-8.3 mm/yr	Ma, 1937b, p. 187
F. pallida	Enewetak	μ = 7.0 mm/yr (n = 4, see Table 6)	Dullo, 2005
Favia speciosa	Japan and South Pacific	Mean values for different regions range from 3.2–9.2 mm/yr	Ma, 1937b, p. 187
F. speciosa	Enewetak	μ = 6.7 mm/yr (n = 3, see Table 6)	Dullo, 2005
Goniastrea retiformis	Japan and South Pacific	Mean values for different regions range from 2.5–7.7 mm/yr	Ma, 1937b, p. 190
G. retiformis	Enewetak	μ = 8.5 mm/yr (n = 3, see Table 6)	Dullo, 2005

forms with a chaetetid skeleton and has also been reported in fossil stromatoporoids (STEARN, 1983b). *Ceratoporella nicholsoni* has a "basal and lateral surface of the skeletal mass covered by an epitheca showing growth lines" (VACELET, 2002a, p. 827). HARTMAN and GOREAU (1972, p. 135) stated that in young specimens of *C. nicholsoni,* the basal layer (their epitheca) is cup shaped, and in larger specimens, it is restricted to the lower surface of the skeleton, commonly obscured where the animal is attached to the substrate. Whether a basal layer, or something similar, is deposited by the sponge upon settlement is unknown, but it does occur on the exposed edges of the basal calcareous skeleton in some chaetetid specimens.

Invertebrates attach to hard substrates in a number of ways, and some demosponges are inferred to use collagenous glue (BROMLEY & HEINBERG, 2006, p. 438). Other sessile clonal invertebrates, such as bryozoans, use an acid mucopolysaccharide secretion (BROMLEY & HEINBERG, 2006, p. 437). In extant hypercalcified demosponges, the basal layer is mostly composed of organic fibers (see Fig. 29), and it is reasonable to suggest that it functioned much like the periostracum in mollusks and other invertebrates with an exoskeleton of calcium carbonate; namely it protected the skeleton from the adverse effects of seawater (CLARK, 1976). STEARN (1983b, p. 145) has suggested that in stromatoporoids, it functioned to inhibit boring organisms from attacking the underside of the skeleton. Although it is rarely visible macroscopically in fossil chaetetids, it has been observed in some specimens and can be differentiated from the basal calcareous skeleton in SEM images of such specimens (see Fig. 29). Because it is thin, appears to be mostly organic in composition, and is exposed to seawater, it is often absent because of physical, chemical, and biological processes during life and after death. Careful study of the contact between the basal calcareous skeleton and the substrate, of both extant and fossil forms, is necessary to determine whether a basal layer, or something similar, is deposited initially when the sponge colonizes the substrate and becomes part of the sessile benthos.

TABLE 9. Estimated growth rates of fossil hypercalcified sponges using the growth rates of appropriate extant corals, hypercalcified sponges, and fossil corals. This table presents the method used here for estimating growth rates for Paleozoic chaetetids. In part A, the ratio between the growth rates of two extant corals, *Lophelia pertsua* and *Oculina varicosa*, from a habitat comparable to that of two extant hypercalcified sponges, *Ceratoporella nicholsoni* and *Acanthochaetetes wellsi,* were set equivalent to the growth rate of a Devonian rugose coral with an analogous compound growth form, *Prismophyllum* (now *Hexagonaria*), relative to an unknown, value herein referred to as *X.* By performing the calculations indicated, the results provide an estimate of the growth rate of a Paleozoic chaetetid. The same method was used to determine the results in part B, using the approximate growth rate determined for Paleozoic corals from the Ordovician, Silurian, and Devonian, based on the data provided in Table 6, instead of that for *Prismophyllum*, and a second estimate of the growth rate of Paleozoic chaetetids was obtained; *μ,* average value (mean) of the number of measurements; *n,* number of measurements (see discussion on p. 86; West, 2011b).

A. Results using data for *Prismophyllum* sp. (now *Hexagonaria*) = 2–6 mm/yr; μ = 4 mm/yr, n = 2 (Faul, 1943).

Lophelia pertsua:*Ceratoporella nicholsoni* = *Prismophyllum*:X
7.5:0.175 = 4:X
7.5X = 0.175 × 4
X = 0.09 mm/yr

Lophelia pertsua:*Acanthochaetetes wellsi* =*Prismophyllum*:X
7.5:0.075 = 4:X
7.5X = 0.075 × 4
X = 0.04 mm/yr

Oculina varicosa:*Ceratoporella nicholsoni* = *Prismophyllum*:X
16.1:0.175 = 4:X
16.1X = 0.175 × 4
X = 0.04 mm/yr

Oculina varicosa:*Acanthochaetetes wellsi* = *Prismophyllum*:X
16.1:0.075 = 4:X
16.1X = 0.075 × 4
X = 0.02 mm/yr

B. Results using a growth rate of 10 mm/yr based on the data contained in Ma (1943a, 1943b, 1943c) for Paleozoic corals from the Ordovician, Silurian, and Devonian (see Table 6).

Lophelia pertsua:*Ceratoporella nicholsoni* = 10 mm/yr:X
7.5:0.175 = 10:X
7.5X = 0.175 × 10
X = 0.2 mm/yr

Lophelia pertsua:*Acanthochaetetes wellsi* =10 mm/yr:X
7.5:0.075 = 10:X
7.5X = 0.075 × 10
X = 0.1 mm/yr

Oculina varicosa:*Ceratoporella nicholsoni* = 10 mm/yr:X
16.1:0.175 = 10:X
16.1X = 0.175 × 10
X = 0.1 mm/yr

Oculina varicosa:*Acanthochaetetes wellsi* = 10 mm/yr:X
16.1:0.075 = 10:X
16.1X = 0.075 × 10
X = 0.05 mm/yr

TABLE 10. Estimated growth rates of Phanerozoic reefs in mm/yr from DULLO (2005, tables 3–4); data converted to mm/yr and averaged for each geological period/system (West, 2011b).

Age	Estimated growth rate	Number of reefs	Dullo table 4 data: reef growth	Dullo table 4 data: framebuilder growth	Dullo table 4: number of reefs
Cenozoic	0.07 mm/yr	8			
Cretaceous	0.07 mm/yr	8			
Jurassic	0.07 mm/yr	9	2.3 mm/yr; range: 1.5-4.3 mm/yr	6 mm/yr; range: 1–11 mm/yr	7
Triassic	0.17 mm/yr	6			
Permian	0.09 mm/yr	6	0.3 mm/yr	4 mm/yr	1
Carboniferous*	0.05 mm/yr	6			
Devonian	0.11 mm/yr	7			
Silurian	0.07 mm/yr	4			
Ordovician	0.03 mm/yr	4			
Cambrian	0.08 mm/yr	4			

*One of these Carboniferous reefs that contains chaetetids is the Horseshoe Atoll Reef Complex in the subsurface of Texas, growth of which is estimated at 34.6 m/myr or 0.0346 mm/yr (Dullo, 2005, p. 42, table 3). See also Stafford (1959) and Toomey and Winland (1973).

ASTRORHIZAE

These stellate patterns of grooves, called astrorhizal canals, are associated with the excurrent canal system and are not commonly observed on fossil chaetetids. When present, they are very shallow grooves that are best seen in light with a low angle of incidence (see Fig. 12–13). Individual astrorhizal canals may be unbranched or show primary and occasionally secondary branches. HARTMAN (1984, p. 306) stated that in the extant form *Acanthochaetetes wellsi,* ". . . astrorhizae are shallow, difficult to see and not infrequently completely absent." Thus they are rarely present on fossil chaetetids. Astrorhizae may occur on one or two or none of the fossil chaetetids that are numerous in any given stratigraphic interval. That is to say, astrorhizae only occur rarely, even when fossil chaetetids are very abundant and make up the entire rock layer. Unlike the astrorhizae in some fossil (stromatoporoids) and some extant hypercalcified sponges, the astrorhizae in chaetetids are confined to the exterior surface of the basal calcareous skeleton; they have not been observed to extend into the interior of this basal skeleton of any of the valid chaetetid genera. CUIF and others (1973, pl. 1,*2*) illustrated a longitudinal section of astrorhizae in *Blastoporella*, but neither spicules nor spicule pseudomorphs have been found in this genus. In general appearance, the astrorhizae in fossil chaetetids are most like those described for *A. wellsi* (HARTMAN & GOREAU, 1975; HARTMAN, 1984). Astrorhizae are absent in *Merlia normani* (HARTMAN & GOREAU, 1975, p. 10), and although they may be absent in *Ceratoporella nicholsoni*, when present, the grooves are deeper, about a millimeter, and cover a larger area (HARTMAN, 1984, p. 306) than in *A. wellsi*. In fossil chaetetids, the astrorhizae cover a circular area of between 10 and 12 mm in diameter (see Fig. 12.3), values within the range covered by astrorhizae in *A. wellsi* (HARTMAN, 1984, p. 306). Within an area of 10.4 cm^2 on the surface of a fossil chaetetid, there are six astrorhizae (Fig. 60), and the distance between the centers of these six range from 8.25 to 27 mm, averaging 16.2 mm (n = 15) (Table 11). In extant forms, astrorhizae are associated with mamelons, but this is not the case in fossil chaetetids. Astrorhizae in fossil chaetetids occur on a relatively smooth to slightly irregular surface, but only rarely do they occur centered on mamelons (see Fig. 12.3). As in extant forms, the function of this stellate pattern of grooves radiating from an osculum are inferred to identify the exhalant canal system in fossil chaetetids. As water is moved through the sponge by the

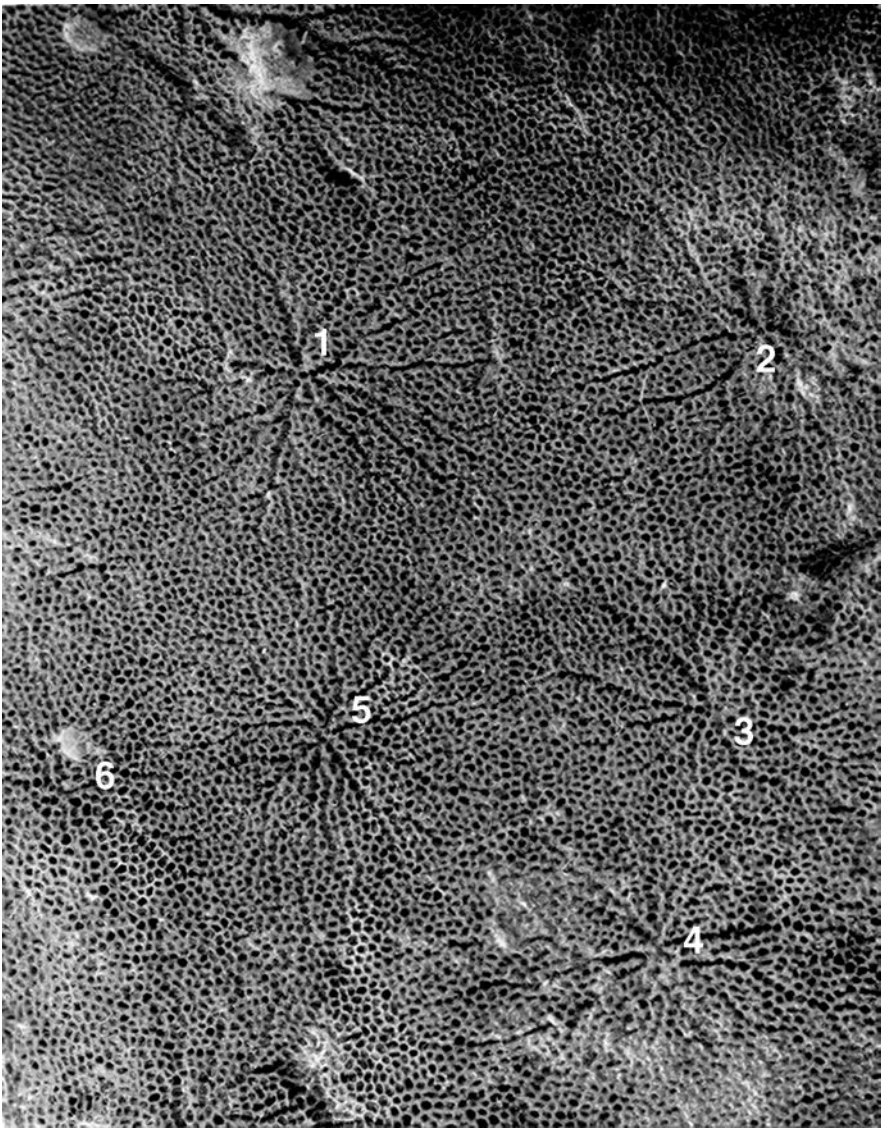

FIG. 60. Six astrorhizae in 10.4 cm^2 area on the surface of a chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; see Table 11 for distances between astrorhizae, ×4.1 (West, 2011b).

flagellated collar cells, it is channeled into the areas of the astrorhizal canals, thence to the osculum (VOGEL, 1994, p. 190–191; 2003, p. 172–173) where it is expelled and carried away by the water currents passing over the surface of the fossil chaetetid, much as occurs in morphologically similar extant forms.

MAMELONS

These features are rounded regular or irregular elevations of the exterior surface of the chaetetid skeleton. They have been observed but are not always present in the extant taxa *Ceratoporella nicholsoni* (HARTMAN & GOREAU, 1970; HARTMAN,

1984) and *Acanthochaetetes wellsi* (Hartman & Goreau, 1975; Hartman, 1984). Although astrorhizae occur on the mamelons of some specimens, they are not present on all mamelons. Astrorhizae are part of the exhalant water circulating systems in these sponges, and some advantage might be realized if the exhalant opening (osculum) is elevated relative to the incurrent openings (ostia) (Hartman, 1984, p. 310). Based on Bernoulli's Principle, water moving over a U-shaped feature is pulled into one opening if the other opening is raised slightly above the surface of the first opening (see Vogel, 1994, p. 72; 2003, p. 149). Experiments by Boyajian and LaBarbera (1987) based on Bernoulli's Principle, suggested that mamelons and associated astrorhizae would be advantageous to taxa living in quiet water. Stearn (see Functional Morphology of the Paleozoic Stromatoporoid Skeleton, p. 551–574) pointed out the reasons why this cannot be applied to all occurrences of forms with astrorhizae associated with mamelons in stromatoporoids. These same reasons are appropriate for fossil chaetetids, as well as for some occurrences of extant hypercalcified demosponges with a chaetetid skeleton. For example, Hartman (1984, p. 310–311), referring to underwater photographs of *in situ* specimens of *C. nicholsoni* stated: "In several photographs a specimen with mamelons occurs directly adjacent to one without mamelons, indicating that an environmental explanation does not apply in these populations." Mamelons are not often observed on fossil chaetetids, and on the rare occurrences when they are present, it is not clear, because of weathering, whether or not they possess astrorhizae (see Fig. 13.4). The tubules composing the mamelons may appear larger than those elsewhere on the upper exterior surface of the basal calcareous skeleton, but this is more apparent than real (Fig. 61).

Table 11. Distance, in mm, between the centers of the six astrorhizae in the 10.4 cm^2 area shown in Figure 60; $n = 15$, $\mu = 16.2$ mm (West, 2011b).

1–2 = 15				
1–3 = 17	2–3 = 12.5			
1–4 = 22	2–4 = 21	3–4 = 8.25		
1–5 = 11.5	2–5 = 19.5	3–5 = 12.25	4–5 = 13	
1–6 = 14.5	2–6 = 27	3–6 = 21	4–6 = 20.5	5–6 = 8.5

CHIMNEYS

Vertically developed mamelons, with an opening (osculum) at or near the apex, that extend well beyond the general growth surface of fossil chaetetids are referred to as chimneys (see Fig. 14.4–14.5). These features have not been recognized in extant hypercalcified demosponges with a chaetetid skeleton. I have only observed chimneys in topotype specimens of a form described by Morgan (1924) as *C. (Chaetetes) schucherti* from Pennsylvanian limestone in Oklahoma (see Fig. 14.4–14.5). Chimneys are not present on the holotype (Fig. 62.1) and are not mentioned in the original description of this species. Morgan (1924, p. 175) noted the presence of ". . . short, round tubes without walls, 3 mm in diameter . . ." (Fig. 62.2) and suggested that these holes ". . . may have been centers of reproduction, goniopores, or they may have been parasitic animals." He noted further that these holes are best seen on weathered surfaces (Fig. 62.3). Similar holes occur on some topotype specimens and they are located: (1) on weathered areas (a in Fig. 62.4); (2) near the top of some cylindrical projections (chimneys) (b in Fig. 62.4); and/or (3) on and around the upper parts of domical to irregularly shaped mamelons (c in Fig. 62.4).

At, or near, the top of these chimneys is a 3 mm diameter opening (Fig. 63.1, Fig. 63.4) which, based on vertical sections, extends downward 6 to 8 mm to near the base of the chimney (Fig. 63.2–63.3, Fig. 63.5). These tubes are now filled with an argillaceous carbonate matrix or sparry calcite. The distance between these 3 mm diameter openings ranges from 9 to 20

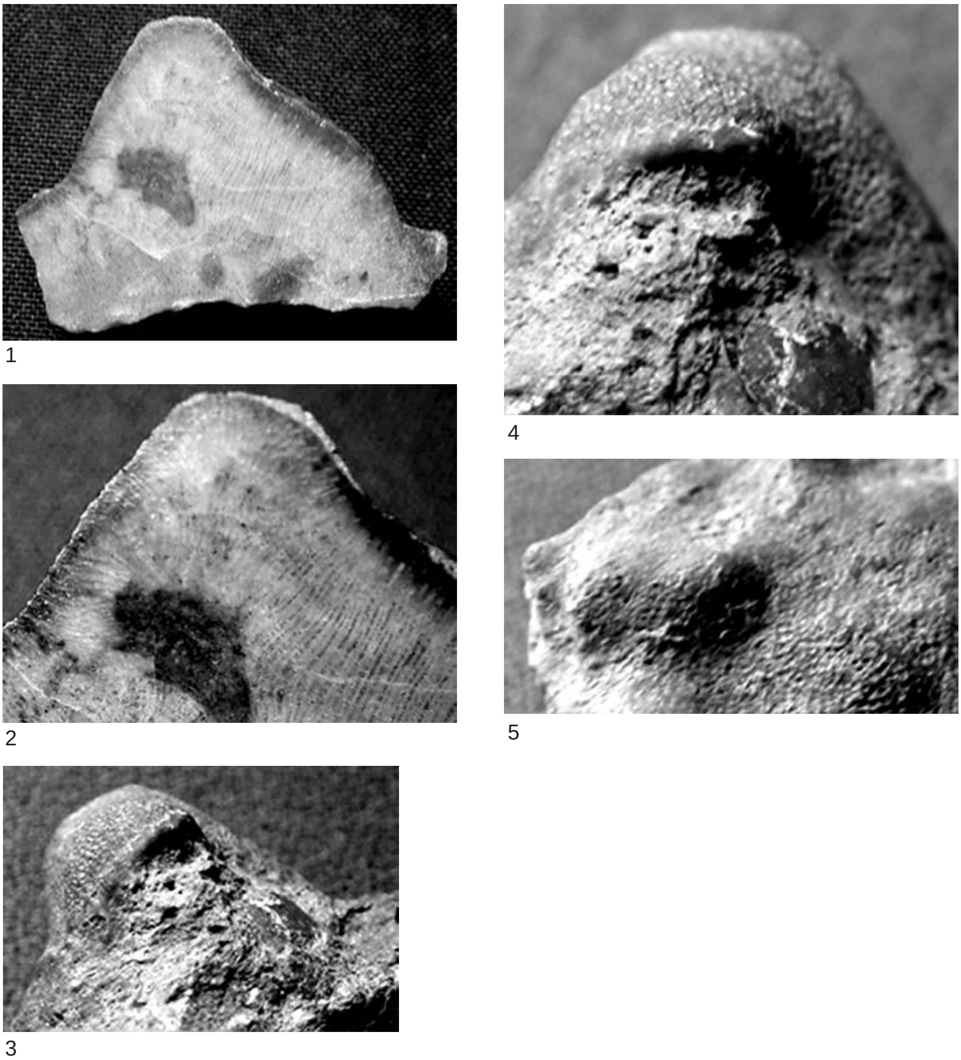

FIG. 61. Tubules in vertically developed mamelons in topotype specimens of *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of a vertically developed mamelon, note tubule size, ×1; *2,* enlarged view of vertically developed mamelon in view *1,* ×2; *3,* oblique view of vertically developed mamelon in view *1,* ×2.9; *4,* enlarged view of *3,* ×4.6; *5,* plan view of exterior of vertically developed mamelons, ×3.8 (West, 2011b).

mm and averages 12.5 mm (n = 12). This is about the same as the average distance, 16.2 mm, between the centers of astrorhizae in fossil chaetetids (Table 10). Given the similarity in spacing, and the fact that astrorhizae are considered the area of the exhalant water system, it may be suggested that the openings at the top of vertically developed mamelons, i.e., chimneys, functioned as oscula. Openings associated with exhalant fluid flow and referred to as chimneys occur in the bryozoan *Membranipora membranacea* (DASSOW, 2006).

Although it may be that some vertically developed mamelons were associated with the exhalant movement of water, such

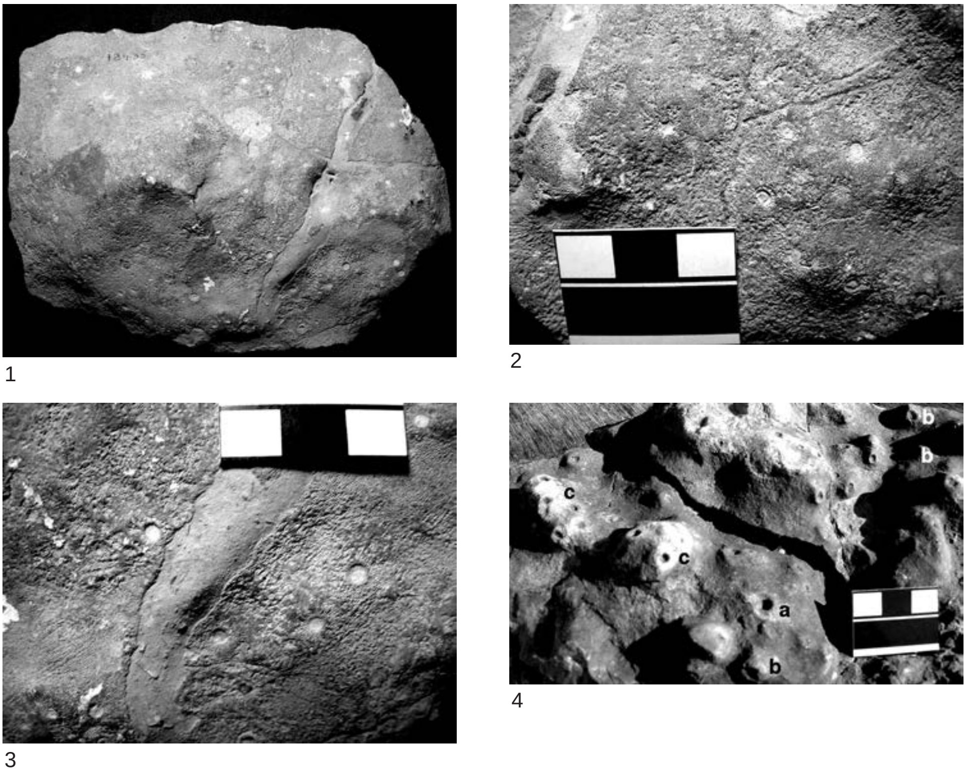

FIG. 62. Circular openings in upper exterior surface of *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of upper exterior surface of holotype; light colored circles are 3 mm holes noted by MORGAN, 1924, ×0.25; *2,* part of upper exterior surface of holotype showing 3 mm diameter holes; note that some, but not all, of these holes are associated with mamelons, ×0.8; *3,* same as view *2,* but slightly enlarged and of a different area; holes in this view are not associated with obvious mamelons, ×0.85; *4,* upper exterior surface of a topotype specimen showing location of 3 mm diameter holes: *a,* on a weathered area, *b,* near top of vertically developed mamelons, i.e., chimneys, and *c,* on and around upper areas of domical to irregularly shaped mamelons, ×0.4 (West, 2011b).

circular openings are not restricted to the top of vertically extended mamelons and occur elsewhere on the calcareous skeleton (Fig. 63.4). It is possible that all, or some, of these circular openings are the result of an associated symbiotic soft-bodied invertebrate, i.e., sponge, coral, or worm. Holes of the same diameter as these, 3 mm, but much shallower, only 1 mm, have been observed in extant specimens of *Ceratoporella nicholsoni* and are the sites of commensal zoanthideans (soft corals) that grew on the surface of the sponge (HARTMAN & GOREAU, 1970, p. 209). Smaller holes, 1.5 to 2.5 mm in diameter, also occur in extant specimens of *C. nicholsoni* (HARTMAN, 1984, p. 311) and are attributed to *Siphonodictyon,* an excavating member of the boring clionid sponges (HARTMAN, 1984, p. 311). RÜTZLER (1971, p. 1) noted that he had frequently observed the deep-yellow sponge chimneys of *Siphonodictyon* protruding from living coral heads. Hydroids are also known to be symbiotic on, or inside of, sponges (PUCE & others, 2005).

Tubules that surround the circular tubes in *C. (Chaetetes) schucherti* radiate out from the tubes a distance of from 5 to 10 mm and then turn upward (MORGAN, 1924, p. 175). This

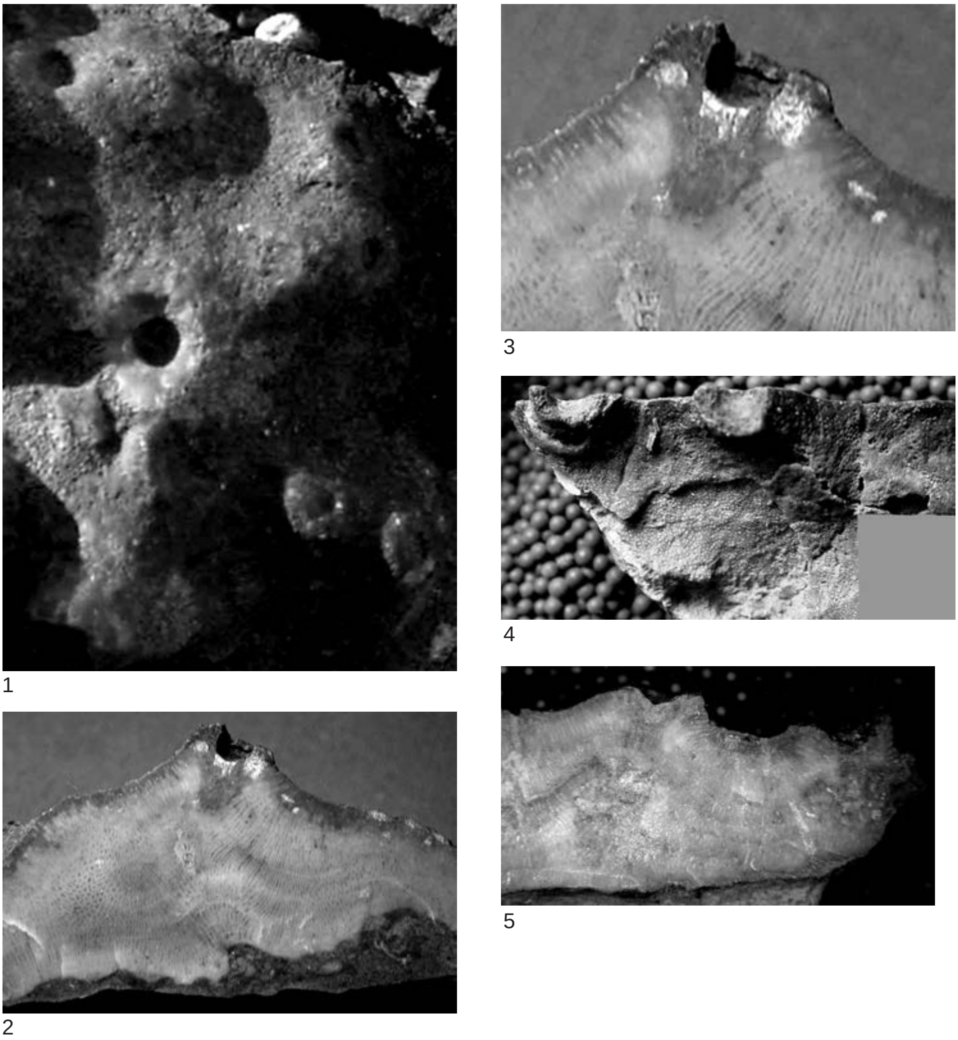

FIG. 63. Chimneys in topotype specimens of *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of chimneys, the one in left center is slightly abraded, ×1.85; *2,* longitudinal section of chimney showing depth of a partially filled hole at top of vertically developed mamelon with a chimney, ×1.25; *3,* enlarged view of upper part of chimney with partially filled hole in view *2,* ×2; *4,* plan view of two adjacent chimneys, ×1.9; *5,* longitudinal section of two adjacent chimneys seen in plan view in view *4,* ×2.15 (West, 2011b).

same arrangement occurs in topotype specimens with mamelons, including those with a circular opening at the top, i.e., chimneys (Fig. 64). The vertically extended mamelons were constructed by tubules that fanned out as they grew upward, and the circular openings associated with some mamelons appear to have been excavated later. Tubules associated with these circular openings do not appear to be distorted; there is nothing that resembles the abnormal growth around the suggested vermiform symbiotics illustrated by WEST and CLARK (1984, pl. 2,*F*). Although some of these circular openings could have been oscula, others were excavated after skeletal growth, but before death; they could also be postmortem features.

TUBERCULES

These structures that resemble tiny spines are small, slightly raised, calcareous projections. They occur at the junction between two or more tubules at the top of the basal calcareous skeleton, where the thin soft tissue is presumed to have been in contact with the skeleton. These have been observed in *Merlia normani* (Hajdu & van Soest, 2002) and in some well-preserved fossil chaetetid skeletons (see Fig. 14.2–14.3). Perhaps they have had some value in helping anchor the thin layer of soft tissue to the basal calcareous skeleton. However, it is more likely that they are simply the result of the arrangement of the calcite crystals from which the basal skeleton is/was constructed. The microstructure and mineralogy of *Merlia* and fossil chaetetids is considered to be penicillate Mg calcite (Finks & Rigby, 2004c; see Table 2). Water-jet Mg calcite has also been used to describe the microstructure and mineralogy (Cuif & Gautret, 1993; Hooper & van Soest, 2002a; and see Table 2). In either case, the calcite crystals that compose the walls of the tubules fan outward at a relatively high angle (see Cuif & Gautret, 1993). As the walls of two or more tubules come into contact and join, the merging of bundles of crystals in each could result in a projection above the adjacent walls of the tubules producing tubercules. For example, the upper edges of the tubules in *Acanthochaetetes wellsi* are crenulated, and each crenulation corresponds to upwardly directed undulations of the lamellar crystalline units of calcite that make up the walls of the tubules (Hartman & Goreau, 1975, p. 3).

INTERNAL FEATURES

TUBULES

The chaetetid skeleton is dominantly composed of tubules. In longitudinal section, they are more or less straight, but in transverse section, they exhibit meandroid- to irregularly polygonal–shaped outlines (see Fig. 15–16, Fig. 30–31). Co-joining of walls with adjacent tubules results in a honeycomb-like construction, although the tubules have a much more irregular profile in transverse section. To attempt to understand the role of the tubules in chaetetid skeletons of hypercalcified demosponges, it is useful to examine the relationship between the tubules that compose the basal calcareous skeleton and the soft, living tissue in extant taxa.

Initiation of a calcareous skeleton in chaetetids would have provided a stable, rigid platform for the efficient functioning of the aquiferous system, an advantage in some environments. However, if the environment provided such substrates, as is common in environments with firm to hard surfaces, i.e., reefs, a rigid platform may have been readily available in the form of dead or diseased surfaces of other clonal organisms, such as corals and bryozoans. In environments with soft, loose substrates, similar colonization sites would have been provided by the shells of other invertebrates, such as mollusks and brachiopods. Glaessner (1962) suggested that initially a skeleton could have been the means by which organisms disposed of metabolic waste products; in the case of most invertebrate skeletons, one such waste product is calcium. Similarly, Simkiss (1977) noted the harmfulness of excessive levels of Ca in cells and suggested that the excretion of such excessive Ca led to biocalcification as the cells detoxified. More recently, Reitner and Gautret (1996, p. 193), referring to *Acanthochaetetes wellsi,* stated that the "... main controlling factor of calcification is the deposition of a physiological surplus of Ca^{2+}, a toxic metabolic waste product." This could result in an initial basal calcareous skeleton in chaetetids, because, based on studies of extant forms such as *Ceratoporella*, *Acanthochaetetes*, and *Merlia*, the only part of the calcareous skeleton that contains living tissue is the uppermost millimeter or two. The bulk of domical, columnar, and some

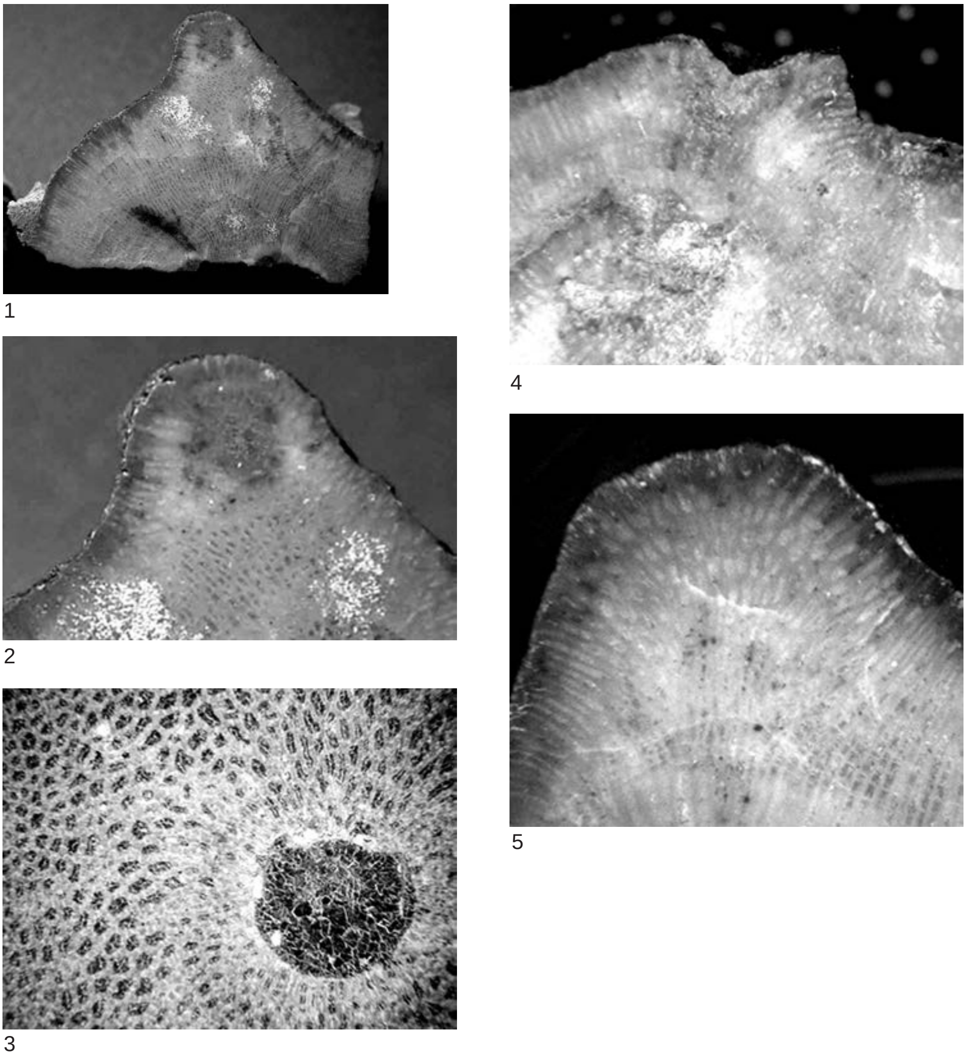

FIG. 64. Arrangement of tubules in vertically developed mamelons with and without circular openings, *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of vertically developed mamelon with a tube (chimney) in a topotype specimen, ×0.9; *2,* enlargement of upper part of chimney figured in view *1,* ×3; *3,* transverse thin section of tube in vertically developed mamelon (chimney) in the holotype, tube filled with sparry calcite, ×6.7; *4,* longitudinal section of vertically developed mamelons with shallow tube (chimney) in a topotype specimen, ×5; *5,* longitudinal section in a vertically developed mamelon in a topotype specimen, ×5 (West, 2011b).

laminar chaetetid skeletons in extant taxa (and inferred in fossil forms) appear to have little, if anything, to do with the living tissue. Over time, there may have been some genetic component that favored the development of a basal calcareous skeleton (see KIRKPATRICK, 1911, p. 690–691). For example, lateral expansion of such a skeleton would permit the sponge to dominate more of the substrate and provide a larger base for upward (vertical) growth yet still remain a fairly stable structure. Lateral expansion and upward growth from a smaller base occurs in fossil chaetetids (see Fig. 19.3–19.4, Fig. 20.2). Something similar has been documented in *Ceratoporella nicholsoni*, an extant taxon, where the young forms are cone shaped or pedunculate, and the mature forms are massive and mound shaped (VACELET, 2002a, p. 827). HARTMAN and GOREAU (1975, p. 3) also reported a stalked condition in some specimens of *A. wellsi*, supporting a tendency, in some cases, for upward growth. An example of an extant pedunculate specimen of *Acanthochaetetes* sp. can be seen in Figure 11.1. With vertical growth of the skeleton, the thin layer of living tissue would be positioned higher in the water column. Such a position would be advantageous for an organism that depends on dissolved and suspended matter in the water it pumps through its pores.

The tubule walls of *Acanthochaetetes wellsi, Ceratoporella nicholsoni,* and *Merlia normani*, all extant taxa, are either aragonite or Mg calcite. Arrangement of the crystals of these minerals produces either a penicillate (water-jet) or lamellar microstructure (see Table 2) in these taxa. In most fossil chaetetids, the original mineralogy has, as a result of taphonomic processes (recrystallization), changed to low Mg calcite. But the original mineralogy is inferred to have been Mg calcite, and the microstructure is penicillate, as in the extant genus *Merlia*. The basal calcareous skeleton of Pennsylvanian chaetetids preserved in asphalt in Oklahoma was reported by SQUIRES (1973; and see Introduction, p. 15–80) to contain 5 mol% Mg calcite, but unfortunately he did not document the microstructure of the tubule walls in these specimens.

REITNER and GAUTRET (1996, pl. 49,*1*) illustrated the relationship between the thin layer of living tissue and the tubules of the basal calcareous skeleton in *Acanthochaetetes wellsi*. The living tissue is confined to the space above the outermost horizontal partition (tabulae) in the tubule and is 1.2 to 2.0 mm thick (HARTMAN & GOREAU, 1975, p. 3). In *Merlia normani*, the relationship between the soft tissue and the basal calcareous skeleton is similar, with a thin layer of living tissue that contains the choanosomal tissue and spicules (HAJDU & VAN SOEST, 2002, p. 691–692). The living tissue in *Ceratoporella nicholsoni* is 1.5 mm thick and extends into tubules that lack horizontal partitions (tabulae) (VACELET, 2002a, p. 827). The innermost parts of the tubules in this species are filled with aragonite, and the soft tissue in the outermost part of "each (tubule) [calicular unit of VACELET] corresponds to a single inhalant and exhalant canal" (VACELET, 2002a, p. 827). Essentially, the basal calcareous skeleton is a pitted platform composed of tubules (pits) with a horizontal partition upon which the thin layer of living tissue rests and is somewhat protected. KIRKPATRICK (1911, p. 690) suggested support and shelter for the function of this pitted outer surface in *Merlia normani*. Given the similarity of the basal calcareous skeletons in fossil chaetetids to those in extant taxa, one can safely assume a similar function for the skeleton of the fossils.

TABULAE

The tabulae are horizontal partitions that subdivide the tubules in some fossil and extant chaetetid skeletons and are commonly thinner than the tubule walls (see Fig. 32–33). If present, these discrete calcareous plates are generally flat or slightly curved and parallel to the growth surface in both fossil and extant specimens. The outermost tabula, in extant forms, forms a floor for the overlying thin layer of living tissue (see REITNER & GAUTRET, 1996, pl. 49,*1*). Thus the tabula functions as the base upon which the soft tissue rests, and they may or may not be perforated by a foramen that may or may not be subsequently infilled with calcite. The space containing the soft living tissue and the spaces between successive tabulae below the living tissue in extant specimens are referred to as crypts. Tabulae in *Acanthochaetetes wellsi* are irregularly spaced, may be slightly convex, horizontal, or slightly concave, and do not necessarily occur at the same level in adjacent tubules; however, they may be at the same level in a few tubules in a limited area (Hartman & Goreau, 1975, p. 3). This also applies to fossil chaetetids (West & Clark, 1984), and in some fossil specimens, the tabulae are incomplete. Such incompleteness of tabulae could be due to an opening where perforated by a foramen or produced by dissolution.

The space beneath the tabulae upon which the living tissues is supported and the next lower tabulae often contain crypt cells, also known as archaeocytes, thesocytes, gemmules, resting, or surviving cells. All of these terms refer to a resistant asexual reproductive body (see Boury-Esnault & Rützler, 1997, p. 10–18). Thus, they are similar to resting spores that some fungi and plants produce during adverse times, and they are capable of generating a fully functioning organism under favorable conditions. These crypt cells may occur in one or more of the intertabular spaces (crypts) below the outermost tabulae that support the currently live tissue. In *Merlia normani,* there may be as many as five of these intertabular storage spaces filled with crypt cells in any given tubule (Kirkpatrick, 1911, pl. 32,*9–10*). Archaeocytes in *M. normani* are well illustrated by Reitner (1992, p. 239, fig. 66e). It is unlikely that crypt cells will be preserved in fossil chaetetids, and they have not been reported in fossil specimens. However, it is possible that if a living chaetetid were smothered by a sudden influx of sediment and the thin layer of living tissue were preserved, crypt cells could be preserved.

It is suggested that tabulae were generated during stressful times when the sponge produced and sealed off gemmules to protect them until more favorable conditions returned. Hartman and Goreau (1975, p. 3) noted that it is characteristic of *Acanthochaetetes wellsi* to die back for unknown intervals of time, perhaps erratically, and for new groups of tubules (calicles of Hartman & Goreau, 1975) to appear at a level above the previous living surface with three or more generations of dead, flattened masses of skeleton overlying one another. This same behavior can be inferred through studies of the different growth forms and occurrences of fossil chaetetids. Because tabulae do not necessarily occur at the same level in adjacent tubules, each tubule, or in some cases, small groups of tubules, are responding to unfavorable conditions by producing tabulae at different times and places across the living surface. Likewise, the irregularity in spacing between tabulae in adjacent tubules suggests a response by individual tubules to environmental conditions that results in the production of tabulae.

Based on current understanding, it appears that the primary function of tabulae represented a platform to support the layer of living tissue and a secondary function of older tabulae is/was to protect the asexual reproductive bodies during unfavorable environmental episodes. Tubules might have also provide some strength and stability to the skeleton, but with each tubule sharing one or more of its walls with adjacent tubules, there seems to have been little need for additional reinforcement.

As noted above, the basal calcareous skeleton of some chaetetid skeletons looks very much like the honeycombs constructed by bees. There is also a striking resemblance between these sponge skeletons and the structure of mycelium, the typical vegetative structure of some fungi, and, to some extent, in the sheetlike growth form of some tree fungi (Fig. 65–66). Fungi and sponges with a chaetetid skeleton are fairly simple organisms, and perhaps it is not surprising that both generate somewhat similar structures to house and protect asexual reproductive bodies.

PORE (FORAMEN)

A more or less circular opening near the center of individual tabulae in hypercalcified demosponges with a chaetetid skeleton is referred to as a pore, or foramen. KIRKPATRICK (1911) called such an opening a foramen, and that term is defined by BOURY-ESNAULT and RÜTZLER (1997, p. 39, fig. 208) as a "circular pore in laminae connecting adjoining interlamellar spaces." By laminae, they appear to mean tabulae, because they identify the foramen as being in a tabula in BOURY-ESNAULT and RÜTZLER (1997, p. 39, fig. 208). Tabulae in *Acanthochaetetes wellsi* are continuous and lack a foramen (HARTMAN & GOREAU, 1975), but a foramen is present in the tabulae of *Merlia normani* (KIRKPATRICK, 1911; REITNER, 1992, p. 239, fig. 66e). The occurrence of incomplete tabulae in fossil chaetetids might suggest the occurrence of foramina, but there are other explanations for incomplete tabulae in fossil chaetetids, as noted above. What has been identified as a foramen in a fossil chaetetid is illustrated in Figure 34. Tubular spaces between tabulae contain gemmules in some extant forms; the same may be reasonably inferred for fossil chaetetids. A foramen would permit the movement and/or exchange of cellular matter and also for egress of the asexual reproductive bodies to the surface of the basal calcareous skeleton with the return of favorable environmental conditions. There seems to be no other reasonable explanation for its existence, and the fact that such an opening has not been documented in *A. wellsi* indicates that it may not have been essential for regenerative growth.

Before we are able to more fully understand fossil chaetetids, the reproductive biology and larval history of the extant hypercalcified demosponges with chaetetid skeletons needs to be better known. As REITNER (1991a, p. 208) stated relative to sponges with a basal calcareous skeleton ". . . we must know more about the ontogeny of young sponges after settlement of the larva."

PSEUDOSEPTA

Features that are apparently known only from fossils with a chaetetid skeleton are pseudosepta (see WEST & CLARK, 1984). These calcareous structures are associated with longitudinal fission, one of the three ways the number of tubules in the basal calcareous skeleton may be increased. Pseudosepta first appear as small, slightly raised areas (nodes) on the interior wall of the tubule (see Fig. 39–40). One or more nodes may occur in any given tubule, which divides it into equal or unequal parts. With upward growth, the nodes expand outward and upward, parallel to the direction of the growth axis, resulting in septa-like features. As two pseudosepta within a tubule approach each other, the parent tubule increases in size. Eventually, the pseudosepta may extend across the tubule, or merge with others, subdividing the original tubule into two or more new tubules. Generally, the division of the parent tubule is along its shortest horizontal dimension. Therefore, pseudosepta are associated with the growth and expansion of the basal calcareous skeleton.

SPICULES

These features, a component of the soft tissue and the mineral skeleton, are typically composed of silica in extant forms, but when observed in fossil forms, they are pseudomorphs of calcite, pyrite, or iron oxide (see Fig. 41–43). In extant forms, and some fossil chaetetids, there are both megascleres and microscleres. In the extant taxa, *Acanthochaetetes wellsi*, *Ceratoporella nicholsoni*, and *Merlia normani*, spicules are largely confined to the thin layer of soft tissue. HARTMAN and GOREAU (1975, p. 4) stated that siliceous spicules are not incorporated into the basal calcareous skeleton of *A. wellsi,* but RÜTZLER and VACELET (2002, p. 277) indicated that some microscleres that adhere to the tubule

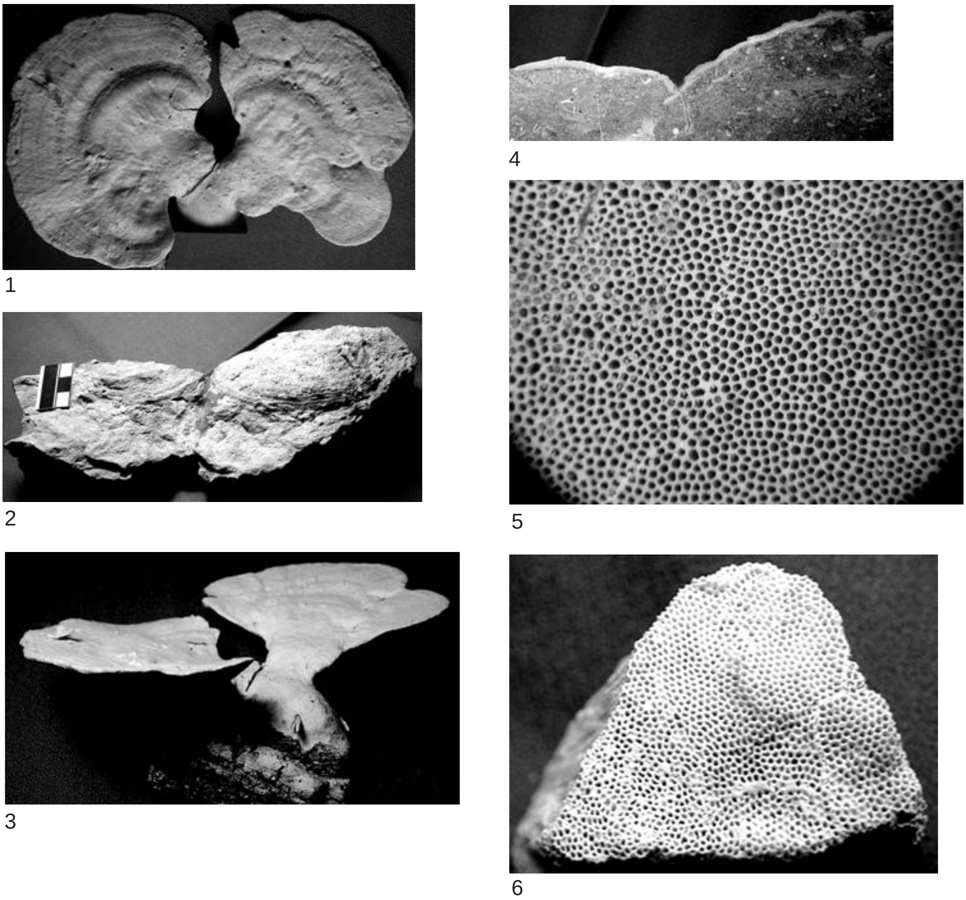

FIG. 65. Comparison of form and structure of laminar chaetetid skeletons with the form and structure of some extant shelf fungus; *1,* upper surface of basic form of an extant shelf fungus, ×0.4; *2,* oblique view of a laminar chaetetid skeleton, Carboniferous, Pennsylvanian, Myrick Station Limestone, Pawnee Limestone, Bourbon County, Kansas, compare with view *1,* ×0.2; *3,* lateral view of extant shelf fungus figured in view *1,* ×0.5; *4,* longitudinal section of chaetetid skeleton figured in view *2,* thin, arcuate white lines are laminar chaetetid skeleton with darker matrix below, compare with view *3,* ×0.3; *5,* lower surface of an extant shelf fungus showing irregular polygons that compose mycelium, ×7; *6,* upper surface of a chaetetid skeleton, Carboniferous, Pennsylvanian (Moscovian), Moscow Basin, Russia, compare with view *5,* ×2 (West, 2011b).

walls may be incorporated into the skeleton during fossilization. Although some spicules are trapped in the tubule walls of *C. nicholsoni*, they are progressively dissolved in the basal calcareous skeleton (VACELET, 2002a, p. 827). In *M. normani*, the megascleres occur as bundles along the sides and bottom of the open crypts, but rarely in the lower crypts (KIRKPATRICK, 1911, p. 670, fig. 2, pl. 33,*3*). Microscleres in this species are contained along the surface of the soft living tissue (KIRKPATRICK, 1911, p. 670, pl. 33,*3*). Because siliceous spicules are rarely incorporated into the basal calcareous skeleton of extant forms, they are commonly absent in fossil chaetetids. When they do occur in fossils, they are pseudomorphs, because of the ease with which siliceous spicules are

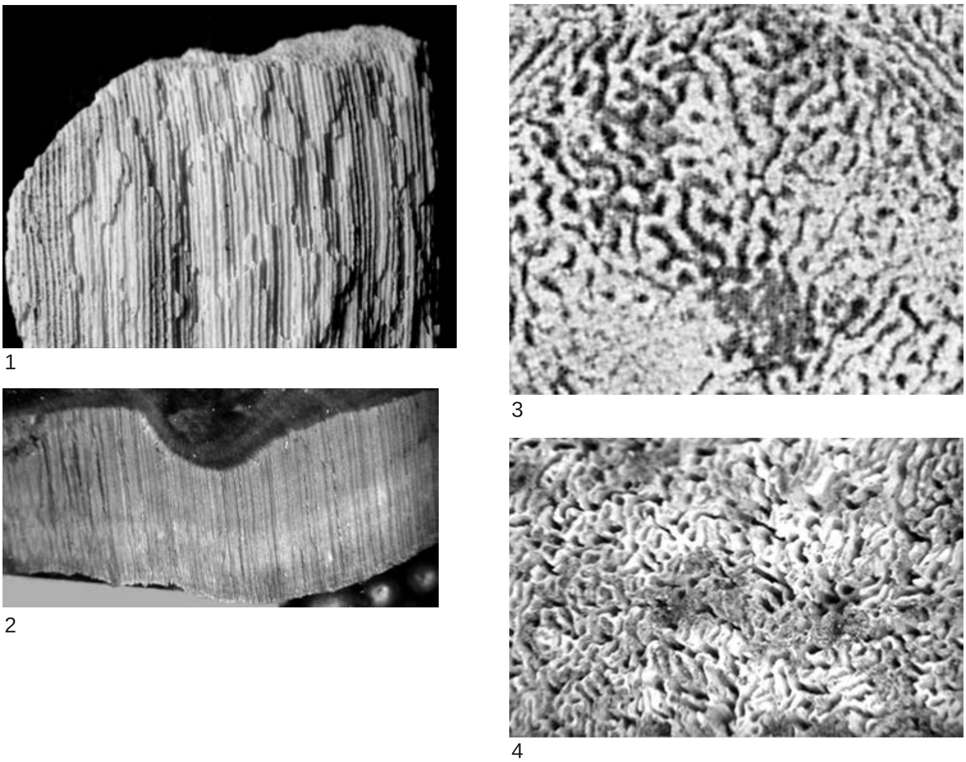

Fig. 66. Comparison of form and structure of laminar chaetetid skeletons with form and structure of some extant shelf fungus (continued); *1,* lateral view of a chaetetid skeleton, Carboniferous, Pennsylvanian (Moscovian), Moscow Basin, Russia, ×1.75 (West, 2011b); *2,* lateral view of mycelium of extant shelf fungus in Figure 65.5, compare with view *1,* ×4 (West, 2011b); *3,* upper surface of *Meandriptera zardinii*, Upper Triassic (Carnian), St. Cassiano beds near Cortina d'Ampezo, Italy, showing the meandroid shape of the tubules, ×4 (adapted from Dieci & others, 1977, pl. 1,*2a;* courtesy of *Bollettino della Società Paleontologica, Italiana*); *4,* lower surface of an extant shelf fungus showing the meandroid structure of the mycelium, compare with view *3,* ×5 (West, 2011b).

dissolved, as noted in extant taxa. Megascleres in fossil chaetetids are thin tylostyle-like features (see Fig. 41–42), and microscleres are more or less dark spheres, commonly seen as circles in sectioned specimens (see Fig. 43).

The main purpose of megascleres is the maintenance of rigidity in the sponge soft tissue (Bergquist, 1978; Koehl, 1982). Although it might seem that soft sponge tissue containing siliceous spicules would be a deterrent to a number of sponge predators, this is not necessarily the case. Bergquist (1978, p. 94) noted that grazing of sponges by opistobranchs, echinoderms, fish, and turtles is common, and that any defense against predation is biochemical. Peters and others (2006) concluded chemical defense explained the unpalatability of the sponges they studied. Finks (2003a, p. 214–216) suggested that spicules provided protection and a structural advantage. Finks suggested they were protected against predation, but also discouraged the settlement of larvae of sessile organisms. Jones, Blum, and Pawlik (2005) have studied the relationship between chemical and physical defenses against consumers of some marine sponges and concluded that in some cases, the spicules are a deterrent to predation. How much of the above is applicable to extant hypercalcified demosponges with a chaetetid skeleton, and thus potentially to fossil chaetetids, is presently unknown.

CLASSIFICATION AND EVOLUTION OF THE FOSSIL AND LIVING HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

Ronald R. West

CLASSIFICATION

The hypercalcified demosponges with a chaetetid calcareous skeleton were originally described as *Chaetetes* by Fischer von Waldheim, MS in Eichwald (1829) and subsequently by Fischer von Waldheim (1830, 1837). Sokolov (1955, 1962), who provided a very complete review of the history of the classification of chaetetids, noted that Milne-Edwards and Haime (1849), placed *Chaetetes* in a separate subfamily, the Chaetetinae, of the Favositidae, a family of the suborder Tabulata Zoantharia. Although it is a minor point, Milne-Edwards and Haime (1849) did not use Tabulata, but rather *Zoanthaires tabules* as a vernacular name (see Hill, 1981, p. 506). Tabulata, was not introduced as a formal taxonomic entity until Milne-Edwards and Haime (1850–1854) proposed Zoantharia Tabulata as a suborder.

Subsequently, the subfamily Chaetetinae became the family Chaetetida within the Tabulata (de Fromentel, 1860b, 1861). Included within this family were not only chaetetids, but also "…tabulates with porous walls, bryozoans, stromatoporoids…" and "…even some genera of calcareous algae and tetradiids…" (Sokolov, 1962, p. 259). Thus, *"Chaetetes"* became a member of the Problematica with suggested representatives allocated to a number of different phyletic homes: sponges, corals, bryozoans, even foraminiferids and algae, depending on the interpretation of its simple skeletal morphology.[*] Referring to chaetetids as well as sphinctozoans, stromatoporoids, and archaeocyaths, Wood (1990b, p. 227) stated the situation well: "The major obstacle to the study of the problematic reef-builders was the absence of conclusive features that could expose a relationship to living forms. The profusion of known representatives of these groups was little help in the solution of the problem. Different workers seized upon different analogies and considered their chosen examples to be crucial, so that these ancient waifs were shunted from one biological group to another." Lindström (1873) considered *Chaetetes* a bryozoan, a view strongly supported by Peterhans (1929b) and also indicated by Moret (1966). During the latter part of the 19th century, most investigators considered *Chaetetes* to be a coral, although where within the corals was the subject of some difference of opinion. Miller (1877) listed them with the Polypi, and in 1889, Miller placed them within the Coelenterata. Duncan (1872) considered *Chaetetes* to be alcyonarian, along with *"Monticulipora"* and other genera. Neumayr (1889) and Struve (1898) placed them within the hexacorals. The early 20th century was not much different, in that Weissermel (1927, 1939) created the Chaetokorallen,

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[*] Quotation marks around generic names denote the first reference, in this section, to a broader, earlier conception of a generic name.

and Okulitch (1936b) proposed the order Chaetetina within the schizocorals. Lecompte (1939, 1952b) noted the difficulties of considering them to be algae and bryozoans, as well as corals, but retained them within the Tabulata. Bassler (1950) considered them to be tetracorals, and Sokolov (1939, 1955, 1962) placed them in the hydrozoans. Within the Hydrozoa, Sokolov (1939, 1955, 1962) recognized a discrete group, the Chaetetida, and Tesakov (1960) and Fischer (1970) accepted this designation.

Although Wood (1990b, p. 228) indicated that until the late 1960s, most workers considered chaetetids to be hydrozoans, Hill and Stumm (1956) and Müller (1963) retained them in the Tabulata as a separate family. Hill and Stumm (1956, p. 453) suggested that some Mesozoic and Eocene species of chaetetids might be coralline algae. Hill (1981, p. 506) changed the termination of the name for the order designed by Okulitch (1936b) from Chaetetina to the Chaetetida but queried its placement within the subclass Tabulata. Hill (1981, p. 506) noted that ". . . in thin section chaetetids were homomorphic with members of other categories within the Coelenterata, but also with members of the Bryozoa, Porifera (sclerosponges), and Thallophyta (solenoporids)." Hill stated (1981, p. 506), "I am regarding them as Anthozoa Tabulata for lack of a better choice." By taking this decision, the geologic range of the Tabulata was extended into the Mesozoic and Cenozoic. Although clearly defined septa and pores connecting adjacent tubules were lacking, other features seemed to support the inclusion of chaetetids within the Tabulata. These other features were (1) the presence of tabulae, then considered to be an exclusively coelenterate feature; (2) the microstructure of the tubule walls, then described as clinogonal tufts in single ranks of longitudinal monacanths; and (3) the method of tubule increase (Hill, 1981, p. 506–507). In the section on post-Paleozoic Chaetetida, Hill (1981) discussed the studies by Hartman and Goreau (1970, 1972) on extant sponges and by Fischer (1970), Cuif and others (1973), Cuif and Fischer (1974), and by others on Mesozoic chaetetids. In these discussions, Hill suggested indirectly that some or all of the post-Paleozoic genera that she considered to be valid might be sponges. However, she did not include them in the stratigraphic distribution chart for the Tabulata, retaining only taxa that were exclusively Paleozoic.

Studies during the late 19th and early to middle 20th centuries are particularly significant relative to understanding the phyletic position of *Chaetetes*. Recall that in 1872, Duncan considered *Chaetetes*, along with *Monticulipora,* as alcyonarian corals. The close relationship between *Chaetetes* and *Monticulipora* at that time is illustrated by the fact that James (1881) considered the former to be a subgenus of the latter. However, as noted by Sokolov (1955, p. 106), Bassler (1906) and Cumings (1912) included the Paleozoic Monticuliporidae within the phylum Bryozoa (order Trepostomata). Consequently, the bryozoan genera were excluded from the Chaetetidae (Sokolov, 1955, p. 106), leaving them in the phylum Coelenterata. Kirkpatrick (1912a, p. 502) stated, ". . . that numerous Palaeozoic fossils coming under the old-fashioned term '*Monticulipora*' are of essentially the same nature as *Merlia*. . . ." Thus, irrespective of their phyletic membership, whether tabulate coral or bryozoan, the morphological similarity between *Merlia normani,* an extant sponge with siliceous spicules and a calcareous skeleton, and the fossil *Chaetetes,* was recognized by way of *Monticulipora*.

Other extant sponges with a calcareous skeleton were also known at that time: viz., *Petrostroma schulzei* (DÖDERLEIN, 1892, 1897); *Astrosclera willeyana* (LISTER, 1900); and *Ceratoporella nicholsoni* (HICKSON, 1911). But, it was *Merlia normani*, now recognized as a hypercalcified demosponge, that was suggested by KIRKPATRICK (1912a) to be the living descendant of some Paleozoic chaetetid fossils.

During the late 1960s and early 1970s, HARTMAN and GOREAU (1966, 1970, 1972, 1975, 1976) rediscovered living sponges with calcareous skeletons from the cryptic reef environments of the Caribbean and Indo-Pacific. The impact of their studies is well summarized by WOOD (1990b), with the basic aspects relative to chaetetids noted below. HARTMAN and GOREAU (1970) proposed a new class, the Sclerospongiae of the phylum Porifera, for extant forms with a calcareous skeleton. Comparison between external and internal features of extant sclerosponges and fossil chaetetids led HARTMAN and GOREAU (1972) to recognize the Chaetetida as an order within the class Sclerospongiae, along with the order Ceratoporellida. In placing chaetetids in the Sclerospongiae, HARTMAN and GOREAU (1972, p. 146–147) noted the following resemblances to *Ceratoporella:* ". . . a similar arrangement and size range of contiguous tubes that divide by longitudinal fission, shared common walls between adjacent tubes, have a trabecular microstructure, and trend toward meandroid configuration in some instances." In *Ceratoporella nicholsoni*, the calcareous tubes (tubules) ". . . are filled in solidly beneath the living tissue" (HARTMAN & GOREAU, 1972, p. 146). The finding of tabulae in the tubules of the extant sclerosponge *Acanthochaetetes wellsi* (HARTMAN & GOREAU, 1975) strengthened the poriferan affinity of fossil chaetetids. The presence of tabulae had previously been restricted to the Cnidaria (WOOD, 1990b, p. 228). Tabulae in *Acanthochaetetes wellsi* and the absence of spicules in the calcareous skeleton in this extant form are two features common to most fossil chaetetids. In the systematics of the Porifera, HARTMAN (1980, p. 25) listed four orders with extant members in the Sclerospongiae: Stromatoporoida, Ceratoporellida, Tabulospongida, and Merliida. The Chaetetida was not included as an order by HARTMAN (1980), even though it was given as an order by HARTMAN and GOREAU (1972), as noted above. Given the features of the calcareous skeleton, fossil chaetetids might be placed in any one of the latter three of the four orders listed by HARTMAN (1980).

Documentation of spicule pseudomorphs in Carboniferous chaetetids (GRAY, 1980) and astrorhizae in Mesozoic (CUIF & others, 1973) and Carboniferous chaetetids (WEST & CLARK, 1983, 1984) further strengthen the poriferan affinities of chaetetids. VAN SOEST (1984) and VACELET (1985) showed that variations in the spicules and other soft-tissue features in extant members of the Sclerospongiae could easily be accommodated within the Demospongiae and that the class Sclerospongiae was polyphyletic. Studies by REITNER (1987a, 1987b, 1987c) and WOOD (1987) supported this interpretation, and the class Sclerospongiae has now been abandoned. "Chaetetids were proposed to be an assortment of demosponges" (Wood, 1990b, p. 229), and the former systematic group Chaetetida based on the calcareous skeleton was redefined as a morphological grade with no high systematic value. Molecular data (Chombard & others, 1997) also demonstrated the polyphyly of the Sclerospongiae. The calcareous skeleton of those taxa within the questionable order Chaetetida (Hill, 1981) is therefore more properly referred to as a chaetetid skeleton. Hypercalcified demosponge is currently the favored general category for all demosponges with a calcareous skeleton, including chaetetids.

Hooper and van Soest (2002b) recognized three subclasses in the Demospongiae: Tetractinomorpha, Ceractinomorpha, and Homoscleromorpha. Hooper and van Soest (2002b, p. 16–17) pointed out some potential overlap in an important phylogenetic character between the suborders Tetractinomorpha and Ceractinomorpha. Finks and Rigby (2004d) recognized five subclasses within the Demospongiae: Tetractinomorpha, Ceractinomorpha, Choristida (for Homoscleromorpha), Clavaxinellida, and Lithistida. Hooper and van Soest (2002a) considered: (1) the lithistids polyphyletic and referred to them as lithistid demosponges (p. 299); and (2) placed Clavaxinellida in synonymy with the order Halichondrida, a ceractinomorph demosponge (p. 721). Boury-Esnault (2006, p. 205) stated: "The two traditional subclasses Tetractinomorpha and Ceractinomorpha are polyphyletic and it is proposed that they be abandoned." This polyphyletic situation is not new, because Hartman and Goreau in 1972 stated (p. 144), "A chaetetiform skeleton has developed independently several times during the course of evolution." Currently, chaetetid skeletons occur in at least three demosponge orders: the Hadromerida, the Poecilosclerida, the Agelasida, and possibly in others. The morphology of the spicules is the primary criteria for differentiating sponges, and in hypercalcified demosponges the mineralogy and microstructure is also important.

Besides differences in the morphology of spicules, the mineralogy and microstructure of the tubule walls is different in the extant groups. The original walls are either magnesium calcite or aragonite, and the microstructure may be penicilllate, lamellar, or spherulitic. As shown in Table 2 (see p. 56–57), the major difference between recent authors is that Hooper and van Soest (2002a) and Cuif and Gautret (1993) considered the microstructure of *Merlia* to be water-jet, and Finks and Rigby (2004d) considered it as penicillate. In terms of more general morphological features, the tubules in some forms, like those in *Ceratoporella*, are filled with calcium carbonate up to the living tissue, and in others, tabulae are present in the tubules. Wood (1990b) provided a more complete discussion of the similarities and differences between the different chaetetid skeletons.

Features used to taxonomically differentiate hypercalcified demosponges fall into three categories. In order of decreasing usefulness, these are: (1) spicule composition and morphology; (2) the original mineralogy and microstructure of the calcareous skeleton; and (3) skeletal features such as size, shape, and arrangement of tubules. These are what Reitner (1991a) referred to as primary skeleton (spicules morphology) and secondary skeleton (mineralogy and microstructure of the tubule walls). Although the third set of features are those most often available in fossil chaetetids, their taxonomic value is suspect because of biological factors, i.e., genetics, environmental conditions during growth, and/or taphonomic processes (see below).

Although spicules are not always present in extant forms (see p. 17, 47–65), they are the primary feature for differentiating poriferan taxa. A meaningful taxonomy is, to some degree, equivocal if spicules are absent, and in chaetetid skeletons spicules, they are commonly absent. There are a number of valid reasons why spicules are seldom found in fossil chaetetids (see p. 38–43). Lacking spicules, namely pseudomorphs of spicules, only secondary skeletal features are left, namely the mineralogy and microstructure of the rigid calcareous skeleton. The mineralogy and microstructure of the calcareous skeleton can be taxonomically useful. Unfortunately, in most fossil chaetetids, the calcareous skeleton has been taphonomically altered (recrystallized and/or replaced), making it difficult, and commonly impossible, to determine the original mineralogy. By changing the original mineralogy, the original microstructure expressed by that mineralogy is also altered. Thus, in most fossil chaetetids, one is left with the least useful features of the calcareous skeleton upon which to base taxonomic determinations.

Chaetetid skeletons are morphologically very simple (see WOOD, 1990b, p. 227, on morphological simplicity), with the most commonly preserved features being the size, shape, and arrangement of the tubules, the thicknesses of tubule walls and tabulae, and the spacing between tabulae. Genera and higher taxonomic categories of chaetetids have been based on the general growth form, general shape of the tubules in cross section, thickness of the tubule walls and tabulae, absence of septa and mural pores, and whether new tubules are added by axial, peripheral, or lateral budding. There are very few differences within genera, and between genera and higher taxonomic categories (HILL, 1981). Species of chaetetids have been differentiated primarily on the size of the tubules (commonly the diameter), thickness of the tubule walls, and thickness of the tabulae. To a lesser extent, the spacing between tabulae and the cross-sectional shape of the tubules has been used at the specific level. As shown by WEST (1994), neither tubule diameter (an inappropriate measure for tubule size, as the tubules are, in cross section, irregular polygons, not circles), tubule wall thickness, nor the cross-sectional area of the tubules (see Fig. 56) are valid taxonomic discriminators for Carboniferous species of chaetetids. Comparison of the cross-sectional areas of tubules from different sites in a single laminar chaetetid from the Carboniferous also reveals the inappropriateness of these features (see Fig. 57). These weaknesses are inferred to be due, in part, to taphonomic processes (WEST, 1995). The inconsistencies documented in tubule size and wall thickness could also be the result of genetic and/or environmental factors. But whether biological, environmental, or taphonomic, they are not dependable. Consequently, the current state of affairs is that, without spicules and/or the original mineralogy and microstructure of the calcareous skeleton, it is difficult, if not impossible, to systematize hypercalcified demosponges with a chaetetid skeleton.

HILL (1981) listed 8 families within the order Chaetetida, of which 4 were queried, and 29 genera. Thus, not only did HILL doubt the placement and/or validity of the order, she also doubted the validity of most of the families

TABLE 12. HILL's (1981) classification of chaetetid taxa, which she assigned to the coral subclass Tabulata; most of these are now considered to be chaetetid hypercalcified sponge taxa; the taxa above the dashed line are Paleozoic, and those below are post-Paleozoic (West, 2011c).

Order	Family	Subfamily	Genus	Subgenus
?Chaetetida	Chaetetidae	Chaetetinae	*Chaetetes*	*Chaetetes*
				Boswellia
			?*Carnegiae*	
			Chaetetella	*Chaetetella*
				Chaetetiporella
			Litophyllum	
			Pachytheca	
			?*Spongiothecopora*	
			?*Staphylopora*	
		Chaetetiporinae	*Chaetetipora*	
			Fistulimurina	
		Moskoviinae	*Moskovia*	
	Cryptolichenariidae		*Cryptolichenaria*	
			Amsassia	
			Porkunites	
	?Desmidoporidae		*Desmidopora*	
			Nodulipora	
			Schizolites	
	?Tiverinidae		*Tiverina*	
			Barrandeolites	
	?Lamottiidae		*Lamottia*	
	?Lichenariidae		*Lichenaria*	
	Favosichaetetidae		*Favosichaetetes*	
			Guizhouchaetetes	
— —	— —	— —	— —	— —
	Chaetetidae		*Atrochaetetes*	
			Bauneia	
			?*Blastochaetetes*	
			Pseudoseptifer	
	Acanthochaetetidae		*Acanthochaetetes*	
			Diplochaetetes	
			Septochaetetes	

within the order. Seven of the 29 genera are in the 4 queried families (Table 12).

As noted above, HILL (1981) separated the Paleozoic chaetetids (the first 26 taxa [22 genera and 4 subgenera] in Table 12) from the post-Paleozoic chaetetids (the last 7 taxa in Table 12). Genera that HILL (1981, p. 520) removed from the Chaetetida were: *Parachaetetes, Pseudochaetetes, Ptychochaetetes, Axiparietes, Granatiparietes*, and *Varioparietes,* largely because she felt that the microstructure was the result of diagenetic alteration of solenoporacean walls. *Axiparietes* and *Varioparietes* were described as genera by SCHNORF-STEINER (1963), but FISCHER (1970) considered them to be subgenera of *Ptychochaetetes*. Documentation by CREMER (1995) of the microstructure and spicule pseudomorphs in Upper Triassic specimens of *Ptychochaetetes* from southwestern Turkey clearly establishes it as a valid chaetetid

TABLE 13. Currently valid fossil chaetetid taxa based on pseudomorphs of spicules and the original mineralogy and microstructure of calcareous skeleton. Unless these features are identifiable, the use of these taxa is inappropriate and should be avoided (West, 2011c).

Acanthochaetetes Fischer, 1970
Atrochaetetes Cuif & Fischer, 1974
Bauneia Peterhans, 1927
  [Cremer (1995) documented the microstructure and spicule pseudomorphs in this genus and queried it but did not provide reasons]
Blastochaetetes Dietrich, 1919
Calcichondrilla Reitner, 1991a
Calcispirastrella Reitner, 1992
Calcistella Reitner, 1991a
Calcsuberites Reitner & Schlagintweit, 1990
Ceratoporella Hickson, 1911
Chaetetes (Chaetetes) Fischer von Waldheim in Eichwald, 1829
  [*Chondrochaetetes* Reitner, 1991a, is a junior synonym]
Chaetetes (Boswellia) Sokolov ,1939
Chaetetes (*Pseudoseptifer)* Fischer, 1970
Chaetetopsis Neumayr, 1890
Chaetosclera Reitner & Engeser, 1989a
Keriocoelia Cuif, 1974
Leiospongia d'Orbigny, 1849b
Meandripetra Dieci & others, 1977
Merlia Kirkpatrick, 1908
Neuropora (Lamouroux), 1821
Pachytheca Schlüter, 1885
Ptychochaetetes (Ptychochaetetes) Koechlin, 1947
Ptychochaetetes (Varioparietetes) Bodergat, 1975
Sclerocoelia Cuif, 1974

TABLE 14. Fossil chaetetid taxa for which some meaningful information on the original mineralogy and microstructure of the calcareous skeleton is known, but the presence of pseudomorphs of spicules is unknown or questionable. Until more reliable data are available, these taxa are queried (West, 2011c).

Blastoporella Cuif & Ezzoubair, 1991
Cassianochaetetes Engeser & Taylor, 1989
Kermeria Cuif & Ezzoubair, 1991
Sphaerolichaetetes Gautret & Razgallach, 1987

TABLE 15. Fossil taxa for which the original mineralogy and microstructure of the basal calcareous skeleton and pseudomorphs of spicules are either very poorly known or unknown. These taxa are based on unreliable gross morphological features. They are therefore considered to be chaetetid form taxa and are best referred to as doubtful chaetetids or hypercalcified demosponges, possibly with a chaetetid skeleton. Taxa below the dashed line are not currently considered to be chaetetids (West, 2011c).

?*Carnegiea* Girty, 1913
Cassianopora Bizzarini & Braga, 1978
Chaetetella (Chaetetella) Sokolov, 1962
Chaetetella (Chaetetiporella) Sokolov, 1950
Chaetetipora Struve, 1898
Conosclera Wu, 1991
Fistulimurina Sokolov, 1947
Flabellisclera Wu, 1991
Fungispongia Wu, 1991
Gigantosclera Wu, 1991
Gracilitubulus Wu, 1991
Leiochaetetes Andri & Rossi, 1980
Litophyllum Etheridge, 1899
Mirispongia Wu, 1991
Moskovia Sokolov, 1950
Pamirochaetetes Boĭko, 1979
Parabauneia Wu, 1991
Planochaetetes Solovjeva, 1980
Preceratoporella Termier, H., G. Termier, & D. Vachard, 1977 (note that Reinhardt [1988] called this genus *Praeceratoporella,* which is a misspelling)
Septochaetetes Rios & Almela, 1944
Siphostroma Steiner, 1932
Solenopora Dybowski, 1877, by Riding, 2004
Spinochaetetes C. T. Kim in Yang, Kim, & Chow, 1978
?*Spongiothecopora* Sokolov, 1955
Tubulispongia Wu, 1991
Zlambachella Flügel, 1961a

— — — — — — — —

Diplochaetetes Weissermel, 1913 (suggested to be worm tubes by Fischer, Galli Oliver, & Reitner, 1989)
Favosichaetetes Yang, 1978 (has mural pores—probably a tabulate)
Guizhouchaetetes Yang, 1978 (has mural pores—probably a tabulate)
Lovcenipora Giattini, 1902 (considered to be a tabulate coral by Giattini [1902] and Vinassa de Regny [1915]; considered to be a chaetetid by Senowbari-Daryan and Maurer [2008]; has mural pores—probably a tabulate)
Pachythecopora Deng, 1982d (has mural pores—probably a tabulate)
Pseudomillestroma Deng, 1982d (probably a milleporoid coral)

genus. HILL (1981, p. 666) also considered *Chaetetopsis* as an unrecognizable genus, because it was ". . . greatly altered by diagenesis." However, KAŹMIERCZAK (1979) illustrated monaxon spicule pseudomorphs in a specimen of *Chaetetopsis favrei* from the Lower Cretaceous of the Crimea. Based on the internal micromorphology (preservation precluded recognition of spicules or spicule pseudomorphs and the mineralogy and microstructure of the skeleton) of *Solenopora spongioides*, the type species, RIDING (2004) considered it to have a chaetetid skeleton. This returns *Solenopora spongioides* to the chaetetids, as originally assigned by DYBOWSKI in 1877, and raises questions about other supposed solenoporaceans, such as the 6 genera noted above by HILL (1981). As pointed out previously, taphonomic processes can be of considerable importance to studies of the systematics of chaetetids as well as to other fossils with a similar skeleton.

Currently, there are 23 chaetetid taxa (20 genera 5 subgenera) from which pseudomorphs of spicules have been identified, and for which the original mineralogy and microstructure of the calcareous skeleton is known (Table 13).

Because of the lack of pseudomorphs of spicules, and until more reliable data are available on the original mineralogy and microstructure of the calcareous skeleton, another four taxa are regarded as having a less certain status (Table 14).

Spicules, or spicule pseudomorphs, original mineralogy, and microstructure of the basal skeleton are either inadequately known, or unknown from 26 of the 32 taxa listed in Table 15, and these are considered to be chaetetid form taxa. The other 6 taxa in Table 15, those below the dashed line, are currently considered to be either worm tubes or corals, as noted. HILL (1981) considered 10 of the 32 taxa in Table 15 to be chaetetids (compare Tables 12 and 15). The remaining 22 taxa in Table 15 were either unknown to HILL or were described, redescribed, or considered to be chaetetids since HILL's 1981 work.

An additional 11 taxa, listed by HILL (1981) as chaetetids, are rejected from the group; they are more likely to be tabulate corals (Table 16).

In conclusion, the classification of chaetetids has had a long and varied history and with the recent assignment of the type species of the solenoporacean algae to the chaetetids (RIDING, 2004), there remains more work to be done. Given the difficulties generated by taphonomic processes and the simple morphology of the calcareous skeleton, further careful studies are needed. With the rediscovery of extant forms in the 1960s and 1970s following the pioneering efforts of KIRKPATRICK in the early 1900s, it is now apparent that chaetetid skeletons have evolved (or developed) more than once, in more than one clade, of the hypercalcified demosponges.

EVOLUTION

The chaetetid basal calcareous skeleton, the basis for membership in the order Chaetetida, is polyphyletic (WOOD, 1990b; and see p. 107–114). Genera with a chaetetid skeleton belong to at least three orders of the Demospongiae (the Hadromerida, Poecilosclerida, and Agelasida) and possibly others. The formerly recognized subclasses of the Demospongiae are now abandoned, as suggested by BOURY-ESNAULT (2006), based on the studies of BORCHIELLINI and others (2004). FINKS (2003b, p. 265) commented on the possibility of a relationship between demosponges and stromatoporoids, based on Hartman and Goreau (1966). But Finks did not mention the possibility of such a relationship for chaetetids with extant *Ceratoporella,* as noted in other articles by Hartman and Goreau (1972, 1975). Wood and Reitner (1988, p. 213) suggested a morphological continuum between stromatoporoids and chaetetids, noting that, "The distinction previously drawn between 'stromatoporoids' and 'chaetetids' is artificial."

As noted previously (p. 107–110), there is some potential overlap between the two subclasses Tetractinomorpha and Ceractinomorpha; see Hooper and van Soest (2002b, p. 16–17) for details. More recently, Borchiellini and others (2004) pointed out that within the clade Demospongiae *sensu stricto,* Tetractinomorpha and Ceractinomorpha are polyphyletic, and for the same reason, Boury-Esnault (2006) has called for the abandonment of these two traditional subclasses. Not only are these subclasses polyphyletic, but some of the families and genera within the classical orders of the Demospongiae are also polyphyletic (Boury-Esnault, 2006).

Features necessary for a meaningful taxonomic classification of chaetetid calcareous skeletons are, in order of importance: (1) spicule composition and morphology, both megascleres and microscleres; (2) the original mineralogy and microstructure of the calcareous skeleton; and (3) skeletal features, such as size, shape, and arrangement of tubules. As noted elsewhere, the first two are the most important features, but commonly they are absent, leaving only the third upon which to base a taxonomy. Unfortunately, these features of the tubules are not reliable (West, 1994).

Currently there are 23 taxa (20 genera, 5 subgenera) with a chaetetid basal calcareous skeleton for which reliable information on spicule morphology and tubule wall mineralogy and microstructure is available (Table 13; Table 17). Because the spicules of fossil chaetetids are all pseudomorphs, the original mineralogy is unknown but is inferred to have been siliceous, based on knowledge of extant forms such as *Acanthochaetetes wellsi*, *Ceratoporella nicholsoni*, and *Merlia normani.*

Table 16. Taxa not considered to be chaetetids; they are most likely tabulate corals (West, 2011c).

?*Staphylopora* Le Maitre, 1956
Cryptolichenaria Sokolov, 1955
Amsassia Sokolov & Mironova, 1959
Porkunites Klaamann, 1966
Desmidopora Nicholson, 1886d
Nodulipora Lindström, 1873
Schizolites Preobrazhenskiy, 1968
Tiverina Sokolov & Tesakov, 1968
"Barrandeolites" Sokolov & Prantl in Sokolov, 1965
Lamottia Raymond, 1924
Lichenaria Winchell & Schuchert, 1895

There are four taxa (genera) with a chaetetid skeleton for which some meaningful information on the original mineralogy and microstructure of the basal calcareous skeleton is known. However, the presence of pseudomorphs of spicules is unknown or questionable (Table 14; Table 18). Therefore, there is some doubt as to the validity of these four genera.

Finally, there are 32 taxa (31 genera, 2 subgenera) for which the original mineralogy and microstructure of the basal calcareous skeleton and pseudomorphs of spicules are either very poorly known or unknown (Table 15). These taxa are based on less reliable skeletal features, as noted above (item 3). Of the 32 taxa in Table 15, 26 taxa (25 genera and 2 subgenera) are considered to be chaetetid form taxa and are best referred to as simply chaetetids or hypercalcified demosponges with a chaetetid skeleton. The remaining 6 taxa (genera), as noted in Table

15, are not considered to be chaetetids and are either worm tubes or corals.

From an evolutionary standpoint, there are 23 (20 genera and 5 subgenera), or perhaps 27 (23, including the 3 subgenera, with the addition of 4 genera of an unknown spicule morphology), to be placed in a phylogenetic framework. The geologic ranges of the valid taxa (23, including the 5 subgenera) are given in Table 17; and those of the additional 4 inadequately described taxa are included in Table 18. This same information is represented for all 27 taxa in Table 19. Table 20 and Table 21 list the basic characteristics of the 23 valid taxa (Table 20), along with the stratigraphic position and the geographic locality of their first and last known occurrences (Table 21). Also included in Table 20 and Table 21 are the 4 taxa for which definitive information on the spicules is currently unknown.

Of the 23 valid taxa, only *Ceratoporella, Chaetetes* (*Chaetetes*), *Chaetetes* (*Boswellia*), *Pachytheca,* and *Spherolichaetetes* are known from the Paleozoic, and of these, only the last 4 are restricted to the Paleozoic (middle Silurian to Permian) (Table 21). Spicules (pseudomorphs) have not been reported from any Silurian chaetetids, and the original mineralogy and microstructure of the tubule walls have been obscured either by recrystallization, silicification, or dolomitization. Thus, the Silurian occurrences are questionable. Spicules (tylostyle pseudomorphs) and penicillate calcareous tubule walls have been documented for *Pachytheca* (Reitner, 1992), a genus only known from the Middle Devonian (Eifelian) of northern Spain. Gray (1980) reported spicules (pseudomorphs) in *Chaetetes* (*Boswellia*) from the Carboniferous (Mississippian) of Wales, and Reitner (1991a, p. 181) interpreted the tubule walls to be fascicular fibrous (water-jet) calcite (probably Mg-calcite). Megascleres are unknown from *Chaetetes* (*Chaetetes*), however, probable euasters are present in the fascicular fibrous tubule walls of a specimen from the Carboniferous of Russia (Reitner, 1991a, p. 187, fig. 6).

These are the only reported occurrences of spicules in Paleozoic specimens with a chaetetid basal calcareous skeleton (Gray, 1980; Reitner, 1991a, 1992). Although the mineralogy and microstructure of the upper Permian genus, *Spherolichaetetes,* is known (Gautret & Razgallah, 1987), spicules are not, thus there is some doubt about its taxonomic affinity (Reitner, 1992). As shown in Table 21, the Permian occurrence of *Ceratoporella* is also questionable. The mineralogy and microstructure of the upper Permian specimens assigned to *Ceratoporella* are known (H. Termier, G. Termier, & Vachard, 1977), but spicules are not. This Permian occurrence of *Ceratoporella* is further complicated by the fact that H. Termier, G. Termier, and Vachard (1977, p. 27) described *Preceratoporella tunisiana* as a new genus and species in their text, but in explanations of their plates on p. 106, referred to it as *Ceratoporella*? *tunisiana.* The query indicates that assignment of the species to this genus is questionable. The Paleobiology Database (2006) for the Permian *Ceratoporella* shows it as ?*Ceratoporella* sp., and the query here indicates that the entire assignment is doubtful. Obviously, additional study is required.

Definitive data on the spicules (pseudomorphs) and/or tubule wall mineralogy and microstructure for the other Paleozoic taxa with a chaetetid basal calcareous skeleton listed by Hill (1981, table 3, p. 497) are lacking and, thus, are excluded from

Table 17. Geological ranges (from the literature) of valid hypercalcified demosponges with a chaetetid skeleton; *, Cremer (1995) documented the microstructure and spicule pseudomorphs in the genus *Bauneia* Peterhans, 1927, but gave no reasons why he queried the validity of his assignment; **, *Chondrochaetetes* Reitner, 1991a, is a junior synonym of *Chaetetes* (West, 2012a).

Genus	Geologic range
Acanthochaetetes Fischer, 1970	Upper Jurassic, Upper Cretaceous–Holocene
Atrochaetetes Cuif & Fischer, 1974	Upper Triassic–Upper Jurassic or Lower Cretaceous
Bauneia Peterhans, 1927*	Upper Triassic–Upper Jurassic
Blastochaetetes Dietrich, 1919	Upper Triassic–Upper Cretaceous
Calcichondrilla Reitner, 1991a	Lower Cretaceous
Calcispirastrella Reitner, 1992	Lower Cretaceous
Calcistella Reitner, 1991a	Upper Jurassic–Lower Cretaceous
Calcisuberites Reitner & Schlagintweit, 1990	Cretaceous (Turonian–Coniacian)
Ceratoporella Hickson, 1911	?Permian, Triassic–Holocene
Chaetetes (*Chaetetes*) Fischer von Waldheim in Eichwald, 1829**	?Silurian, Triassic–Permian
Chaetetes (*Boswellia*) Sokolov, 1939	Middle Devonian–Carboniferous
Chaetetes (*Pseudoseptifer*) Fischer, 1970	Upper Jurassic
Chaetetopsis Neumayr, 1890	Upper Jurassic–Lower Cretaceous
Chaetosclera Reitner & Engeser, 1989a	Upper Triassic
Keriocoelia Cuif, 1974	Upper Triassic
Leiospongia d'Orbigny, 1849b	Upper Triassic
Meandripetra Dieci & others, 1977	Upper Triassic
Merlia Kirkpatrick, 1908	Lower Jurassic–Holocene
Neuropora Bronn, 1825	Middle Jurassic–Lower Cretaceous
Pachytheca Schlüter, 1885	Middle Devonian
Ptychochaetetes (Ptychochaetetes) Koechlin, 1947	Upper Triassic–Upper Jurassic
Ptychochaetetes (Varioparietetes) Bodergat, 1975	Miocene
Sclerocoelia Cuif, 1974	Upper Triassic

this discussion (Table 15). This excludes the two Upper Ordovician genera, *Chaetetella* and *Chaetetipora* (Hill, 1981, table 3, p. 497), and the range of the order Chaetetida is middle Silurian to Recent. The other Paleozoic chaetetid taxa shown in table 3 of Hill (1981) are now considered to be tabulate corals (Table 16).

Although chaetetid demosponges are known from the upper Permian (H. Termier, G. Termier, & Vachard, 1977; Gautret & Razgallah, 1987; Flügel & Reinhardt, 1989), they are absent from the Lower and Middle Triassic. *Atrochaetetes*, *Bauneia*, *Blastochaetetes*, *Blastoporella*, *Cassianochaetetes*, *Ceratoporella*, *Chaetosclera*, *Kemeria*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, and *Sclerocoelia* are known from the lower Upper Triassic (Carnian) of Italy. *Blastoporella*, *Kemeria*, and *Ptychochaetetes (Ptychochaetetes)* are reported from the Upper Triassic of Turkey (see Table 21). The mineralogy and microstructure of the tubule walls are known for all of these genera, and definite spicules (pseudomorphs) are known from *Atrochaetetes*, *Bauneia*, *Blastochaetetes* (Cremer, 1995), *Chaetosclera* (Reitner & Engeser, 1989a), *Meandripetra* (Dieci & others, 1977), *Ptychochaetetes (Ptychochaetetes)* (Cremer, 1995), and *Scleroscoelia* (Dieci & others, 1977) (Table 20). Cuif (1974) described *Ceratoporella goreaui* from the Saint-Cassian Dolomites (Upper Triassic) of northern Italy, documenting the mineralogy and microstructure, but nothing on the spicules. Fürsich and Wendt (1977) reported five undescribed species

TABLE 18. Geological ranges (from the literature) of inadequately known hypercalcified demosponges with a chaetetid skeleton (West, 2012a).

Genus	Geologic range
Blastoporella Cuif & Ezzoubair, 1991	Upper Triassic
Cassianochaetetes Engeser & Taylor, 1989	Upper Triassic
Kemeria Cuif & Ezzoubair, 1991	Upper Triassic
Spherolichaetetes Gautret & Razgallah, 1987	Upper Permian

TABLE 19. Chart of the generalized first (X), last (†), only (Ø), and extant (Δ) occurrences (stratigraphically) of valid taxa from Table 17 and inadequately known taxa from Table 18 (numbers underlined). Questionable occurrences are queried (?). The 23 valid taxa include *Chaetetes* (*Chaetetes*) and 2 other subgenera for *Chaetetes: C.* (*Boswellia*) and *C.* (*Pseudoseptifer*). Range abbreviations are as follows: *Q-H,* Holocene; *Q-Pl,* Pleistocene; *N,* Neogene; *Pa,* Paleogene; *K,* Cretaceous; *J,* Jurassic; *Tr,* Triassic; *P,* Permian; *C-P,* Carboniferous, Pennsylvanian; *C-M,* Carboniferous, Mississippian; *D,* Devonian; *S,* Silurian; *O,* Ordovician; *Cm,* Cambrian. Numbers correspond to genera as follows: *1, Acanthochaetetes; 2, Atrochaetetes; 3, Bauneia; 4, Blastochaetetes; 5, Blastoporella; 6, Calcichondrilla; 7, Calcispirastrella; 8, Calcistella; 9, Calcisuberites; 10, Cassianochaetetes; 11, Ceratoporella; 12, Chaetetes (Chaetetes)*; *13, Chaetetes* (*Boswellia*); *14, Chaetetes* (*Pseudoseptifer*); *15, Chaetetopsis; 16, Chaetosclera; 17, Kemeria; 18, Keriocoelia; 19, Leiospongia; 20, Meandripetra; 21, Merlia; 22, Neuropora; 23, Pachytheca; 24, Ptychochaetetes (Ptychochaetetes); 25, Ptychochaetetes (Varioparietes); 26, Spherolichaetetes; 27, Sclerocoelia* (adapted from West, 2012a).

Range	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Q-H	Δ										Δ										Δ						
Q-Pl																											
N																									Ø		
Pa																											
K		†		†		Ø	Ø	†	Ø						†							†					
J	X		†					X						Ø	X						X	X		†			
Tr		X	X	X	Ø					Ø	X					Ø	Ø	Ø	Ø	Ø				X		Ø	
P											?	†													Ø		
C-P																											
C-M													†														
D													X										X				
S												?															
O																											
Cm																											

TABLE 20. Basic characteristics of valid taxa from Table 17 and inadequately known taxa from Table 18 (*asterisks*); +, data from CREMER (1995); ++, data from BIZZARINI and BRAGA (1988) (West, 2012a).

Genus	Megascleres	Microscleres	Mineralogy	Microstructure
Acanthochaetetes Fischer, 1970	tylostyles	euasters, pirasters, amphiasters	Mg calcite	lamellar
Atrochaetetes Cuif & Fischer, 1974	tylostyles+	unknown	aragonite	fascicular fibrous penicillate, water-jet
Bauneia Peterhans, 1927	tylostyles+	unknown	aragonite	penicillate, water-jet
Blastochaetetes Dietrich, 1919	tylostyles+	unknown	aragonite, Mg calcite	penicillate, water-jet
*Blastoporella** Cuif & Ezzoubair, 1991	unknown	unknown	?aragonite	penicillate, water-jet
Calcichondrilla Reitner, 1991a	unknown	large euasters	Mg calcite	irregular to lamellar
Calcispirastrella Reitner, 1992	tylostyles	spirasters	Mg calcite	irregular to granular to prismatic
Calcistella Reitner, 1991a	unknown	asters (?euasters)	Mg calcite	micritic
Calcisuberites Reitner & Schlagintweit, 1990	tylostyles	unknown	?Mg calcite	penicillate, water-jet
*Cassianochaetetes** Engeser & Taylor, 1989	unknown	unknown	aragonite	spherulitic
Ceratoporella Hickson, 1911	tylostyles	unknown	aragonite	penicillate
Chaetetes (Chaetetes) Fischer von Waldheim in Eichwald, 1829	unknown	asters (?euasters)	unknown, but calcite inferred	fascicular fibrous, penicillate, water-jet
Chaetetes (Boswellia) Sokolov, 1939	tylostyles	unknown	?Mg calcite	penicillate, water-jet
Chaetetes (Pseudoseptifer) Fischer, 1970	acanthostyles++	unknown	?aragonite	clinogonal, penicillate
Chaetetopsis Neumayr, 1890	tylostyles	unknown	?aragonite	?fascicular fibrous
Chaetosclera Reitner & Engeser, 1989a	tylostyles	unknown	aragonite	spherulitic
*Kemeria** Cuif & Ezzoubair, 1991	unknown	unknown	?aragonite	penicillate, water-jet
Keriocoelia Cuif, 1974	styliform	unknown	aragonite	spherulitic
*Leiospongia** d'Orbigny, 1849b	acanthostyles or fusiform	unknown	aragonite	spherulitic
Meandripetra Dieci & others, 1977	acanthostyles: straight to curved	unknown	aragonite	penicillate, water-jet
Merlia Kirkpatrick, 1908	tylostyles	clavidiscs, raphides, spiny monoactines	Mg calcite	penicillate, water-jet
Neuropora Bronn, 1825	tylostyles	unknown	?Mg calcite	penicillate, water-jet
Pachytheca Schlüter, 1885	tylostyles	unknown	?Mg calcite	penicillate, water-jet
Ptychochaetetes (Ptychochaetetes) Koechlin, 1947	tylostyles+	unknown	?aragonite	penicillate, water-jet
Ptychochaetetes (Varioparietes) Bodergat, 1975	tylostyles+	unknown	?aragonite	penicillate, water-jet
Sclerocoelia Cuif, 1974	acanthostyles	unknown	aragonite	penicillate, water-jet
*Spherolichaetetes** Gautret & Razgallah, 1987	unknown	unknown	aragonite	spherulitic

TABLE 21. Stratigraphic and geographic occurrences of valid taxa from Table 17 and inadequately known taxa from Table 18 (*asterisks*).

Genus	First occurrence	Location	Last occurrence	Location	Source
Acanthochaetetes	Upper Jurassic	Italy, France, Greece, Spain	Holocene	western Pacific	Fischer, 1970; Hartman & Goreau, 1975
Atrochaetetes	Triassic (lower Carnian)	Italy, St. Cassian, southwestern Turkey	Jurassic–Cretaceous	northwestern Turkey	Cuif & Fischer, 1974; Engeser & Taylor, 1989; Cuffey, Basile, & Lisenbee, 1979
Bauneia	Triassic (Carnian)	Oman, Turkey, Tajikistan	Jurassic (Tithonian)	Portugal, Czech Republic, Italy	Cremer, 1995; Paleobiology Database, 2006
Blastochaetetes	Triassic (Norian and Carnian)	Asia Minor (Turkey)	Cretaceous (Maastrichtian)	Italy, Spain, France	Hill, 1981; Paleobiology Database, 2006
_Blastoporella_*	Triassic (Carnian)	northern Italy	Triassic (Norian)	Turkey	Cuif & Ezzoubair, 1991
Calcichondrilla	Cretaceous (middle Albian)	northern Spain, Arizona	Cretaceous (middle Albian)	northern Spain, Arizona	Reitner, 1991a
Calcispirastrella	Cretaceous (middle Albian)	northern Spain	Cretaceous (middle Albian)	northern Spain	Reitner, 1992
Calcistella	Jurassic (lower Tithonian)	Germany (Bavaria)	Cretaceous (Albian)	Greece	Reitner, 1991a, 1992
Calcisuberites	Cretaceous (Turonian–Coniacian)	Germany (Bavaria)	Cretaceous (Turonian –Coniacian)	Germany (Bavaria)	Reitner & Schlagintweit, 1990; Reitner, 1992
_Cassianochaetetes_*	Triassic (lower Carnian)	Italy, St. Cassian	Triassic (lower Carnian)	Italy, St. Cassian	Engeser & Taylor, 1989
Ceratoporella	?Permian, Triassic	Tunisia, Italy	Holocene	Caribbean	Reitner, 1992; H. Termier, G. Termier, & Vachard, 1977; Vacelet, 2002a
Chaetetes (*Chaetetes*)	?Silurian	North America	Permian	North America, Asia	Hill, 1981
Chaetetes (*Boswellia*)	Middle Devonian (rare)	Europe, central Asia	Carboniferous Mississippian	Europe (western Serbia)	Hill, 1981
Chaetetes (*Pseudoseptifer*)	Upper Jurassic	northern Italy	Upper Jurassic	northern Italy	Bizzarini & Braga, 1988
Chaetetopsis	Jurassic (Tithonian and Kimmeridgian)	Italy (Capri), Japan	Cretaceous (Aptian–Albian)	Greece, Crimea	Kaźmierczak, 1979; Hill, 1981; Reitner, 1991a
Chaetosclera	Triassic (upper Carnian)	Italy	Triassic (upper Carnian)	Italy	Reitner & Engeser, 1989a
_Kemeria_*	Triassic (Carnian)	northern Italy	Triassic (Norian)	Turkey	Cuif & Ezzoubair, 1991
Keriocoelia	Triassic (Carnian)	northern Italy	Triassic (Carnian)	northern Italy	Cuif, 1974; Dieci & others, 1977
Leiospongia	Triassic (lower Carnian)	Italy, St. Cassian	Triassic (Lower Carnian)	Italy, St. Cassian	Engeser & Taylor, 1989
Meandripetra	Triassic (Carnian)	Italy, St. Cassian	Triassic (Carnian)	Italy, St. Cassian	Dieci & others, 1977
Merlia	Lower Jurassic	Austria	Holocene	Caribbean, eastern Atlantic, Mediterranean, Indo-Pacific	Mostler, 1990; Vacelet & Uriz, 1991
Neuropora	Middle Jurassic	Germany	Lower Cretaceous	Germany	Kaźmierczak & Hillmer, 1974
Pachytheca	Devonian (Eifelian)	northern Spain	Devonian (Eifelian)	northern Spain	Hill, 1981; Reitner, 1992

(Continued on facing page).

TABLE 21. *(Continued from facing page).*

Ptychochaetetes (Ptychochaetetes)	Triassic (Norian)	Turkey, Tajikistan	Jurassic (Kimmeridgian)	Spain, Jabaloyes	Cremer, 1995; Termier & Termier, 1976
Ptychochaetetes (Varioparietes)	Neogene (Miocene)	France	Neogene (Miocene)	France	Bodergat, 1975
*Spherolichaetetes**	lower upper Permian	southern Tunisia	upper upper Permian	Greece, China	Flügel & Reinhardt, 1989
Sclerocoelia	Triassic (Carnian)	northern Italy	Triassic (Carnian)	northern Italy	Cuif, 1974

of *Ceratoporella* in the patch reefs of the Cassian Formation (Upper Triassic) of the southern Alps. ENGESER and TAYLOR (1989) stated that it is possible that there are monaxon spicules in *Leiospongia*, but no spicule pseudomorphs are recorded from *Cassianochaetetes*. Thus, of the 13 Triassic genera, only 10 are valid: *Atrochaetetes, Bauneia*, *Blastochaetetes*, *Ceratoporella*, *Chaetosclera*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, *Ptychochaetetes (Ptychochaetetes)*, and *Sclerocoelia* (Table 20). Additionally, *Atrochaetetes, Bauneia, Blastochaetetes,* and *Ptychochaetetes (Ptychochaetetes)* occur in the Jurassic, along with *Chaetetes* (*Pseudoseptifer*) (Table 21). Also, *Atrochaetetes* and *Blastochaetetes* extend into the Cretaceous. Furthermore, *Ptychochaetetes (Varioparietes)* occurs in the Miocene of France (BODERGAT, 1975; TERMIER & TERMIER, 1976), and *Ceratoporella* is a well-known, extant genus. The other five valid genera, *Chaetosclera*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, and *Sclerocoelia* are restricted to the Carnian of Italy (see Table 21).

The mineralogy and microstructure of the tubule walls, as well as spicules and/or pseudomorphs of spicules, are known from the remaining nine genera, namely: *Acanthochaetetes*, *Calcichondrilla, Calcispirastrella*, *Calcistella*, *Calcisuberites*, *Chaetetes* (*Pseudoseptifer*), *Chaetetopsis*, *Merlia*, and *Neuropora* (Table 20). The first occurrence of *Acanthochaetetes*, *Calcistella*, *Chaetetes* (*Pseudoseptifer*), and *Chaetetopsis* is in the Jurassic. *Chaetetes* (*Pseudoseptifer*) is known only from the Lower Jurassic of northern Italy, but *Calcistella* and *Chaetetopsis* extend into the Cretaceous (Albian), and *Acanthochaetetes* extends into the Holocene. *Calcichondrilla*, *Calcispirastrella*, *Calcisuberites*, and *Neuropora* are only known from the Cretaceous (see Table 21). The characteristic clavidisc microscleres of *Merlia* occur in the Lower Jurassic of Austria (MOSTLER, 1990), and the basal skeleton has been reported from the Eocene of Spain (BARRIER & others, 1991). *Merlia* is widely distributed in the world's oceans today (see VACELET & URIZ, 1991). *Acanthochaetetes* and *Merlia* are the only two extant genera in this group of nine genera.

No exhaustive attempt has been made to fill completely the gaps between these first and last occurrences for the 26 taxa (both valid and inadequately known) recorded in Table 19. Certainly, hypercalcified demosponges with a chaetetid basal calcareous skeleton occur in some of the intervening intervals. For example, chaetetids are well known from the Carboniferous (Mississippian) of England and the Carboniferous (Pennsylvanian) of North America and Russia, as well as from numerous Mesozoic reefal settings. In spite of this, there are still some large stratigraphic gaps, such as absences of any reported or confirmed Neogene occurrences of *Acanthochaetetes*. *Tabulospongia* described by MORI (1976, 1977), now *Acanthochaetetes* (REITNER & ENGESER, 1983), was reported by NAKAMORI (1986) from Pleistocene reef limestones from Miyako-jima, Ryukyu Islands, and I have collected *Acanthochaetetes* in reef limestones of the Minatogawa Formation (upper Pleistocene) exposed on the southern coast of Okinawa. More recently, MILLET and KIESSLING (2009) reported *Acanthochaetetes* from Pleistocene coral reef terraces on the island of Efate in the Vanuatu Archipelago. This genus is also reported from the Cretaceous of Spain (REITNER, 1991a; WILMSEN, 1996), and Bulgaria (TCHECHMEDJIEVA, 1986); the Upper Jurassic of Portugal (G. TERMIER, H. TERMIER, & RAMALHO, 1985); the Paleocene of France (PACAUD, MERLE, & MEYER, 2000; MONTENAT, BARRIER, & OTT D'ESTEVOU, 2002); and the Eocene of Spain (RIOS & ALMELA, 1944). Some possible reasons for such stratigraphic gaps are: (1) failure to recognize chaetetids; (2) misidentification once recognized; and/or (3) skeletal mineralogy and subsequent taphonomic alteration of it. Recognition of chaetetids as hypercalcified demosponges has not yet been fully recognized; some carbonate geologists (SCHOLLE & ULMER-SCHOLLE, 2002) still list them as tabulate corals.

Although chaetetids are obvious members of some Paleozoic reefs, particularly during the Carboniferous, they are not conspicuous members of post-Paleozoic reefs. The extant taxa, i.e., *Acanthochaetetes*, *Ceratoporella*, and *Merlia,* live under conditions of very low light or in complete darkness in subtidal caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundred meters (VACELET, 1988; see also Living Hypercalcified Sponges, p. 11–13). It appears, based on their minor role in post-Paleozoic reefs, that they may have also been restricted to such habitats during the Mesozoic and Cenozoic. Thus, they could be easily overlooked, and taphonomic processes would make their recognition even more difficult.

Whether chaetetid basal calcareous skeletons are calcite or aragonite may well be a function of seawater chemistry. STANLEY (2006) has pointed out that the skeletons of simple biologic organisms, such as sponges, corals, and bryozoans, can be expected to reflect the chemistry of ambient seawater, particularly in terms of the Mg/Ca ratio. If the molar ratio of Mg to Ca is below 1.0, low-Mg calcite is produced; if that ratio is above 1.0, the result is high-Mg calcite; and when that ratio is above 2.0, both high-Mg calcite and aragonite will be produced (STANLEY, 2006, p. 215). Current knowledge indicates that the basal calcareous skeletons of chaetetids were either aragonite or high-Mg calcite, both of which are unstable and are easily affected by taphonomic processes. Recrystallization and/or replacement, both diagenetic processes, result in the destruction of features critical to accurate identification, namely: spicules, original mineralogy of both spicules and the basal skeleton, and the microstructure of the basal skeleton.

Hooper and van Soest (2002b) in *Systema Porifera* placed *Acanthochaetetes* in the order Hadromerida, class Demospongiae, and *Merlia* in the order Poecilosclerida, class Demospongiae. Reitner (1991a) summarized the current phylogenetic theories, both monophyletic and polyphyletic, relative to those genera with a basal calcareous skeleton. Using 17 features, Reitner (1991a) constructed 2 cladograms, 1 monophyletic and 1 polyphyletic, for the relationship between the genera of the order Hadromerida with a basal calcareous skeleton. Reitner concluded that a polyphyletic origin for the basal calcareous skeleton is the most probable (1991a, p. 208), although he also indicated that a monophyletic origin cannot be ruled out if young adult sponges of these genera do not contain a basal calcareous skeleton. Thus, further study, particularly of the ontogeny of demosponges such as *Acanthochaetetes*, is required. Reitner (1992), in his monograph on hypercalcified demosponges (his so-called coralline sponges), presented cladograms for all of the taxa of this group, including the order Poecilosclerida with further comments on the order Hadromerida.

In that spicules are commonly absent in fossil chaetetids, Cuif and Gautret (1991, 1993) suggested that a careful study of the mineralogy and microstructure of the basal calcareous skeleton might be useful phylogenetically. As noted in the Introduction (p. 47–65) in a study of the microstructure of the chaetetids, Cuif and Gautret (1993) have shown that, though commonly considered synonyms, there is a recognizable difference between penicillate, trabecular, and water-jet microstructures. Their results indicated that the simple trabecular microstructure does not occur in hypercalcified demosponges with a chaetetid skeleton. They concluded that there are two basic microstructures, one of calcite and one of aragonite, observed in chaetetid skeletons from the Carboniferous to the Holocene. It was suggested that these features could be used as the basis for two separate clades: a penicillate aragonite clade and a water-jet calcite clade.

Based on the observations by Lafuste and Fischer (1971), Cuif and Gautret (1993) noted the similarity of the tubule wall microstructure between *Merlia normani*, *Chaetetes (Chaetetes) cylindraceus,* and some specimens of *Blastochaetetes* from the Jurassic; these are members of the water-jet calcite clade. Members of the penicillate aragonite clade are, from oldest to youngest: ceratoporellids from the Permian and Triassic, and the extant genus *Ceratoporella*. The Triassic ceratoporellid had been considered to be *Blastochaetetes*, but Cuif and Ezzoubair (1991) proposed separating them from *Blastochaetetes s.s.* Specimens of *Blastochaetetes s.s.* with a water-jet calcite microstructure occur in the Jurassic. Cuif and Gautret (1993, p. 314, fig. 5) noted the relationship between the stratigraphic occurrence of these two clades and the changes in seawater chemistry proposed by Sandberg (1983).

It has been possible, using geochemical data, to infer the basic seawater chemistry of the Phanerozoic ocean and divide the Phanerozoic based on the dominant carbonate minerals, i.e., calcite versus aragonite seas (Sandberg, 1983, 1984, 1985; Fuchtbauer & Hardie, 1976, 1980; Hardie, 1996; Stanley & Hardie, 1998, 1999; Montanez, 2002; Stanley, Reis, & Hardie, 2002). Stanley (2006) discussed the influence of seawater chemistry on biomineralization and predicted the skeletal mineralogy of the dominant reef

Table 22. Grouping of valid taxa from Table 17 and inadequately known taxa from Table 18 (*asterisks*) based on known or inferred mineralogy including the known or inferred microstructure of each. Note: Based on the studies by Cuif and Ezzoubair (1991), *Blastochaetetes* is separated into a calcite (*s.s.*) form and an aragonite (*s.l.*) form, as noted in the text; *Q-H,* Quaternary–Holocene; *Q-Pl,* Quaternary–Pleistocene; *N,* Neogene; *Pa,* Paleogene; *K,* Cretaceous; *J,* Jurassic; *Tr,* Triassic; *P,* Permian; *C,* Carboniferous; *D,* Devonian; *S,* Silurian (West, 2012a).

	Q-H	Q-Pl	N	Pa	K	J	Tr	P	C	D	S	Microstructure
Mg Calcite												
Acanthochaetetes	X	X		X	X	X						lamellar
Blastochaetetes s.s.						X						penicillate, water-jet
Calcichondrilla					X							irregular lamellar
Calcispirastrella					X							irregular, granular, prismatic
Calcistella					X	X						micritic
Calcisuberites					X							penicillate, water-jet
Chaetetes (*Chaetetes*)								X			?	fascicular fibrous, penicillate, water-jet
Chaetetes (*Boswellia*)									X	X		penicillate, water-jet
Merlia	X	X	X	X	X	X						penicillate, water-jet
Neuropora					X							penicillate, water-jet
Pachytheca										X		penicillate, water-jet
Aragonite												
Atrochaetetes					X	X	X					fascicular fibrous, penicillate, water-jet
Bauneia						X	X					penicillate, water-jet
Blastochaetetes s.l.					X		X					penicillate, water-jet
*Blastoporella**							X					penicillate, water-jet
*Cassianochaetetes**							X					spherulitic
Ceratoporella	X				X		X	?				penicillate
Chaetetes (*Pseudoseptifer*)						X						clinogonal, penicillate
Chaetetopsis					X	X						?fascicular fibrous
Chaetosclera							X					spherulitic
*Kemeria**							X					penicillate, water-jet
Keriocoelia							X					spherulitic
Leiospongia							X					spherulitic
Meandripetra							X					penicillate, water-jet
Ptychochaetetes (Ptychochaetetes)						X						penicillate, water-jet
Ptychochaetetes (Varioparietes)			X									penicillate, water-jet
Sclerocoelia							X					penicillate, water-jet
*Spherolichaetetes**								X				spherulitic

builders during the Phanerozoic. Based on data from Stanley (2006), the original mineralogy of the basal calcareous skeletons of chaetetids may be predicted. Chaetetids that may occur in the Cambrian to the mid-early Carboniferous interval (which is seemingly equivalent to the Sepukhovian-Bashkirian boundary event at the end of the Mississippian) should be low-Mg calcite (Calcite I interval of Stanley, 2006, p. 218). Those from the mid-early Carboniferous to mid-Jurassic interval should be aragonite or high-Mg calcite in composition (Aragonite II interval of Stanley, 2006, p. 218–219). Chaetetid skeletons from the mid-Jurassic to the Eocene should be low-Mg calcite (Calcite II of Stanley, 2006, p. 219–220), and skeletons of extant chaetetids and those occurring back to the Oligocene should be aragonite or high-Mg calcite (Aragonite III interval of Stanley, 2006, p. 220).

The original mineralogy of the basal calcareous skeleton of 17 of the taxa listed in Table 20 is known; mineralogy of another taxon, *Chaetetes* (*Chaetetes*), is unknown but inferred to be calcite, and there is some question as to the original skeletal mineralogy of the remaining eight: *Bauneia, Chaetetes* (*Boswellia*), *Chaetetes* (*Pseudoseptifer*), *Chaetetopsis, Kemeria, Neuropora, Pachytheca,* and *Ptychochaetetes* (see Table 20). Based on the work of Stanley (2006), noted above, the original mineralogy of *Chaetetes* (*Boswellia*), *Chaetetopsis, Neuropora, Pachytheca,* and *Ptychochaetetes* should be low-Mg calcite, and *Bauneia* and *Chaetetes* (*Pseudoseptifer*) should be aragonite. However, Jurassic specimens of *Bauneia, Chaetetes* (*Pseudoseptifer*), *Chaetetopsis,* and *Ptychochaetetes* could be low-Mg calcite or aragonite, because the contact between the Aragonite II and Calcite II intervals is about Mid-Jurassic. *Kemeria,* as well as Triassic specimens of *Blastochaetetes* (Table 22), are in the Aragonite II interval, as given by Stanley (2006). However, the skeletal mineralogy of *Blastochaetetes,* from the Upper Jurassic and Cretaceous, should be low-Mg calcite, not aragonite (Table 22), to conform to the intervals of Stanley (2006).

The reported original skeletal mineralogy of the Permian, Triassic, and Lower Jurassic taxa (Table 20 and Table 22) are compatible with the Aragonite II interval of Stanley (2006) and would suggest an ambient seawater chemistry with an Mg/Ca ratio greater than 2.0. The occurrence of *Atrochaetetes* with an aragonite skeleton in the Upper Jurassic and Cretaceous part of the Calcite II interval is anomalous, although its first occurrence is in the Aragonite II interval (Triassic). The situation is similar for the three extant taxa. *Acanthochaetetes* is first known in the Upper Jurassic (Table 21), the Calcite II interval, and as an extant form in the Aragonite III interval. *Ceratoporella* is first known from the Permian and *Merlia* from the Lower Jurassic (Table 21), both in the Aragonite II interval, and both range across Calcite II into the present, Aragonite III interval.

The situation relative to the original microstructure is even more complicated than that of the original skeletal mineralogy (see Table 20). Penicillate and water-jet have been used interchangeably; and other microstructures, such as lamellar, irregular, and spherulitic, are also recognized. Thus, a penicillate aragonite and a water-jet calcite clade are not mutually exclusive, and taxa with neither a penicillate nor a water-jet microstructure are excluded.

Irrespective of the questionable original skeletal mineralogy of some taxa and the differences relative to the study of STANLEY (2006), there may be two clades, as seen in Table 22: a Phanerozoic calcite clade and a largely post-Paleozoic aragonite clade. These clades do not correlate with the seawater chemistry curves first proposed by SANDBERG (1983) and subsequently modified by SANDBERG (1983, 1984, 1985), STANLEY and HARDIE (1999), MONTANEZ (2002), and STANLEY (2006). Interestingly, some of the taxa that are reported as aragonite occur first in the Triassic, the Aragonite II interval of STANLEY (2006), but also occur in the Upper Jurassic and Cretaceous, his Calcite II interval (Table 22). In addition to clarifying the microstructure of chaetetid basal skeletons, the mineralogy of these skeletons also needs to be more closely examined. WEBB, WÖRHEIDE, and NOTHDURFT (2003) pointed out the potential usefulness of rare-earth element analyses of the skeletal components of extant and fossil sponges, including chaetetids and stromatoporoids, relative to seawater chemistry and biomineralization.

The classification, and thus the phylogeny, of sponges is based on certain aspects of their soft part anatomy and the mineralogy and morphology of their spicules. In addition, the mineralogy and microstructure of the tubule walls of hypercalcified demosponges with a chaetetid basal calcareous skeleton are also important.

Evolutionary aspects of hypercalcified demosponges may be found in the calcareous skeletons as suggested by WOOD and REITNER (1988). They redescribed the upper Cretaceous *Blastochaetetes irregularis* (MICHELIN) as *Stromatoaxinella irregularis* based on preserved spicule pseudomorphs and their arrangement. Referring to the calcareous skeleton of *Stromatoaxinella irregularis,* WOOD and REITNER (1988, p. 221) noted that the spiculation reflected an arrangement found in Recent chaetetid demosponges, but that the calcareous skeleton is more labyrinthine, a presumed stromatoporoid characteristic. The microstructure of *S. irregularis* is identical to that in *Dehornella*, a Mesozoic stromatoporoid (WOOD & REITNER, 1988, p. 221). This led WOOD and REITNER (1988, p. 222, fig. 9) to suggest a morphological continuum between the calcareous skeletons of *Dehornella*, a Mesozoic stromatoporoid, and extant chaetetids such as *Acanthochaetetes*. The calcareous skeleton of *Stromatoaxinella irregularis*, formerly *Blastochaetetes irregularis,* occupies an intermediate position in this morphological continuum. Results of my examination of specimens of *Stromatoaxinella irregularis* from the Spanish Santonian (Cretaceous), collected, identified, and provided by Alex Nogués in Barcelona, are consistent with those presented by WOOD and REITNER (1988). Such studies are important and necessary, and the ability to isolate and compare molecular data from sponges is increasing and will aid in testing this, and other, hypotheses.

Molecular data has shown that the class Sclerospongiae (HARTMAN & GOREAU, 1970) is polyphyletic (CHOMBARD & others, 1997). More recently, molecular data indicates that the two subclasses of the Demospongiae are polyphyletic (BORCHIELLINI & others, 2004), and therefore their use as subclass subdivisions should be discontinued. In addition, molecular studies are shedding new light on the variation within the phylum Porifera (WÖRHEIDE, SOLÉ-CAVA, & FROMONT, 2004), on their origins and links within metazoans (LARROUX & others, 2006), and their phylogeography (WÖRHEIDE, SOLÉ-CAVA, & FROMONT, 2004; WÖRHEIDE, 2006; WÖRHEIDE, SOLÉ-CAVA, & HOOPER, 2005), leading to greater understanding of processes controlling the geographic distributions of their lineages by constructing genealogies of populations and genes. Such studies will, along with more complete information on the morphology of spicules and the mineralogy and microstructure of chaetetid basal calcareous skeletons, permit a better understanding and explanation of the phylogeny of hypercalcified demosponges.

PALEOECOLOGY OF THE HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

RONALD R. WEST

INTRODUCTION

The distinction between paleoautoecology (the ecological study of an individual fossil or of small taxonomic groups) and paleosynecology (the whole fossil assemblage), is not sharp, but it is convenient (AGER, 1963, p. 31). However, such a distinction in fossil chaetetids is not particularly useful, because sponges are clonal organisms. Each tubule within the chaetetid (sponge) clone functions more or less independently of adjacent tubules. Individuals are not recognized within the clone that makes up the calcareous skeleton. Areas of tubules associated with astrorhizae are sometimes referred to as modules, but these are not individuals in a biological sense. Additionally, the chaetetid skeleton is polyphyletic and the current taxonomy of these forms is in a state of flux. The following addresses the physical, chemical, and biological factors that are paleoecologically important to an understanding of fossil chaetetids, especially in the context of the ecology of extant demosponges, both hypercalcified and others.

Extant and fossil hypercalcified demosponges with a chaetetid basal calcareous skeleton are exclusively benthic marine invertebrates. Only a few extant hypercalcified demosponges are known, and they occur mostly along bathyal cliffs and in dark littoral caves (see p. 1–14). KOBLUK and VAN SOEST (1989) reported *Merlia normani* at depths of 18 to 30 m in the cavities of coral reefs at Bonaire. *Merlia normani* also occurs in semi-submerged caves in the Mediterranean (CORRIERO & others, 2000). Although they did not specify the taxa, RASMUSSEN and BRETT (1985) reported that hypercalcified sponges (they used the term sclerosponges, which is a term now considered to be obsolete; see Glossary, p. 412) were the most abundant, comprising over 10% of the preservable skeletonized taxa in cavities at 105 and 125 m at St. Croix. In these cryptic refugia, most genera are small, but massive specimens of *Ceratoporella nicholsoni*, up to a meter in diameter, have been reported (HARTMAN & GOREAU, 1970, p. 232). Some shallow-water Carboniferous (Pennsylvanian) chaetetids rival the above-reported extant forms in size, with fossil domical and columnar forms reaching a diameter of 0.75 m (Fig. 67). WEST and CLARK (1983, p. 137) reported Carboniferous (Pennsylvanian) columnar chaetetids that were up to 0.8 m in diameter and 1.5 m high (see Fig. 21.4). WINSTON (1963) documented columnar chaetetids 3 m high in the Carboniferous (Pennsylvanian) of central Texas, and SUTHERLAND (1984) described chaetetid reefs that were 3.3 m high and 4.6 m in diameter, in the same area. LANG, HARTMAN, and LAND (1975) reported that *Ceratoporella nicholsoni* is the primary frame builder at depths between 70 and 105 m at Discovery Bay on the northern coast of Jamaica. Although the range of *Ceratoporella* probably extends back to the Permian (see Table 21), it has not been reported as a primary frame builder in any of these older reefs.

Extant genera that are germane to a discussion of fossil hypercalcified demosponges with a chaetetid skeleton are *Acanthochaetetes*, *Ceratoporella*, and *Merlia*. Unlike most of these extant taxa, fossil chaetetids were a conspicuous component of reefal and associated environments during the late Paleozoic—Carboniferous (Pennsylvanian) and Permian—and part of the Mesozoic (Middle Triassic into the Cretaceous) but are of lesser importance in reefs during the Paleogene, Neogene, and Quaternary (HECKEL, 1974; FÜRSICH & WENDT, 1977; FAGERSTROM, 1987; TALENT, 1988; WOOD, 1999; STANLEY, 2001b;

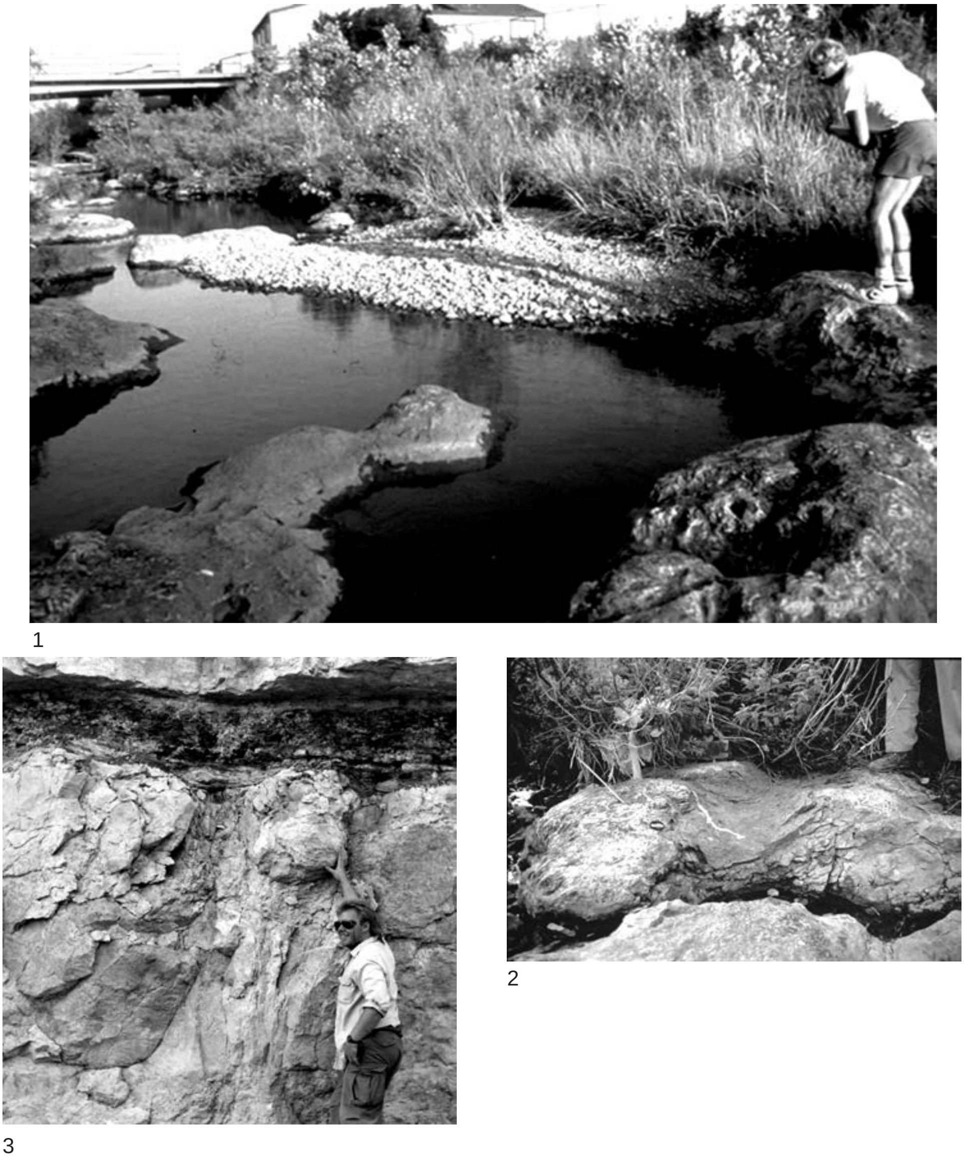

FIG. 67. Large chaetetids, Carboniferous, Pennsylvanian; *1,* rounded upper surfaces of very large high domical to columnar chaetetids projecting above water level, Amoret Limestone Member, Altamont Limestone, Tulsa County, Oklahoma, ×0.02 (West, 2012b); *2,* closer view of the upper surfaces of three large high domical to columnar chaetetids, Amoret Limestone Member, Altamont Limestone, Tulsa County, Oklahoma; note the draping mudrock between the two chaetetids in the center of the photograph, ×0.02 (West, 2012b); *3,* large domical chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.02; (adapted from Voegeli, 1992, p. 131, fig. 28; courtesy of the author and Kansas State University).

KIESSLING, FLÜGEL & GOLONKA, 2002; LEINFELDER & others, 2005; HELM & SCHUELKE, 2006; ALMAZÁN & others, 2007; MINWEGEN, 2007; NAGAI & others, 2007; WEIDLICH, 2007a, 2007b; BLOMEIER, SCHEIBNER, & FORKE, 2009). Where chaetetids are a conspicuous component of reefs, they are commonly part of the constructor guild (see Fig. 19.2,

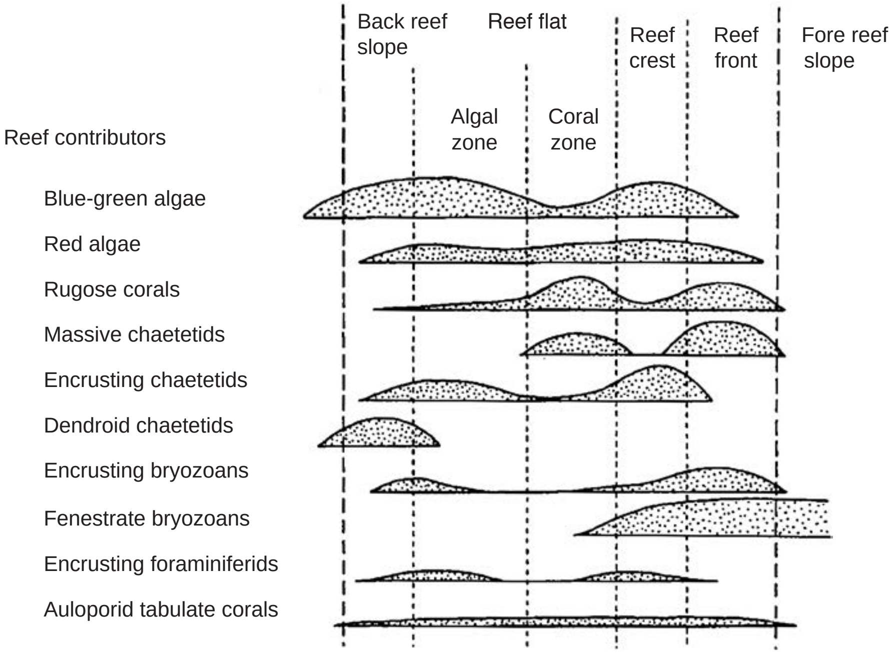

FIG. 68. Distribution of the main reef contributors in the reef facies, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Minami-dai area, Japan (adapted from Sugiyama & Nagai, 1990, p. 11, fig. 2; courtesy of the authors and Akiyoshi-dai Museum of Natural History).

Fig. 21.2), but they may also serve as binders (FÜRSICH & WENDT, 1977; FAGERSTROM, 1984, 1987; BERNECKER & WEIDLICH, 1994; LEINFELDER & others, 2005; WEIDLICH, 2007a, 2007b). In addition to constructors (NAGAI, 1985; NAGAI & others, 2007), in the Akiyoshi Organic Reef Complex, SUGIYAMA and NAGAI (1994) and NAGAI and others (2007) also reported them as sediment bafflers and binders in this complex (Fig. 68–73). A similar situation is reported by NAKAZAWA (2001) in the Omi Lindstone of central Japan. In general, it appears that, from the middle Permian (NAKAZAWA, UENO, & FUJIKAWA, 2012) onward, chaetetids functioned in reef building more as binders and less as constructors (Fig. 74).

Although most conspicuous in the upper Paleozoic and part of the Mesozoic, chaetetids also occur in carbonate facies of Devonian rocks (OLIVER & others, 1975; D. L. KISSLING, personal communication, 1988; MAY, 1993, 2008; MÉNDEZ-BEDIA, SOTO, & FERNÁNDEZ-MARTINEZ, 1994; SOTO, MÉNDEZ-BEDIA, & FERNÁNDEZ-MARTINEZ, 1994; NOWINSKI & SARNECKA, 2003; HUBERT & others, 2007; ZAPAISKI & others, 2007; PICKETT, OCH & LEITCH, 2009) and Carboniferous (Mississippian) rocks in a few places in North America and North Africa (Morocco), but mostly in Europe (GUTSCHICK, 1965; ARETZ & HERBIG, 2003a, 2003b; ARETZ & NUDDS, 2007; SHEN & WEBB, 2008; DEAN, OWEN, & DOORIS, 2008; GÓMEZ-HERGUEDAS & RODRÍGUEZ, 2009; LORD & WALKER, 2009; LORD, WALKER, & ARETZ, 2011). A few occurrences have been reported from the Ordovician and Silurian (see discussion of classification and evolution, p. 105–114).

Environmental variables may be grouped into three main categories: physical, chemical, and biological, all of which are interrelated and interdependent; a change in one may affect one or several variables in one or more of the three. Thus, it is difficult to ascribe a specific effect to a specific variable. In considering the ecology of the Demospongiae, including hypercalcified demosponges, SARA and VACELET (1973)

TABLE 23. Some ecological factors important to demosponges; *asterisks*, environmental factors that can be inferred for fossil chaetetids (West, 2012b).

- Physicochemical variables (topic 2)
  - *Temperature
  - *Light
  - *Hydrodynamics
  - *Sedimentation
  - *Substrate
  - *Water depth
  - *Desiccation or exposure
  - *Salinity
  - Dissolved gases
  - Suspended matter
    - Inorganic: minerals
    - Organic: nutrients
  - Pollution
- Synecology (topic 4)
  - *Epibioses
    - Sponges as epibionts
    - Epibionts on sponges
    - Stratification and evolution of demosponge growth: competition and cooperation relative to substrate
  - *Relations between demosponges and between demosponges and other sessile organisms
  - Predation
  - *Endobionts: commensal and parasitic
  - *Association with algae and bacteria endobionts
    - Association with bacteria
    - Association with cyanophytes
    - Association with unicellular algal eukaryotes
    - Association with multicellular algae
  - Conclusions
- Spatial distribution (topic 5)
  - *Quantitative distribution
  - Distribution in the Mediterranean
    - Middle and infralittoral
    - Circalittoral
    - Bathyal
  - Distribution in northeastern Atlantic
  - Distribution in the middle tropics
  - Distribution in Polar seas
  - Distribution in the deep benthos
  - Distribution in fresh water
  - Distribution in brackish water
  - Distribution in polluted water

discussed six major topics: (1) larval ecology; (2) physicochemical factors; (3) life cycle; (4) synecology; (5) spatial distribution; and (6) geographic distribution, variability, and speciation. Of these six, some aspects of topics 2, 4, and to some extent 5, can be addressed relative to fossil chaetetids. Information on topics 1 and 3 are not available for fossil chaetetids, and topic 6 for fossil forms is considered in the discussion of paleobiogeography and biostratigraphy below (see p. 179–192).

Direct observation and measurement, both natural and experimental, of ecologically important variables relative to extant taxa are important and useful in understanding the paleoecology of fossil forms. However, such direct data cannot be obtained for fossils. Thus, our paleoecological knowledge of fossil chaetetids must rely heavily on inferences based on a careful study of the lithologic context of *in situ* chaetetid occurrences and their associated organisms.

Listed in Table 23 are the subdivisions (variables) of topics 2, 4, and 5 as given by Sara and Vacelet (1973). An asterisk (in Table 23) indicates a variable for which some information can be reasonably inferred from the lithologic context of the fossils.

Although all physical and chemical factors are controlled to some extent by geographical factors, information relative to the hydrodynamics (turbulence), sedimentation (turbidity), substrate, water depth, salinity, and desiccation can be inferred from the lithology within which fossil chaetetids are preserved and the fossil organisms with which they are associated. Obviously, information on dissolved gases and suspended matter and the effects of pollution is unavailable, but the fact that chaetetid sponges occur and are preserved in the rock record indicates that oxygen and suspended matter necessary for survival (nutrition and skeletal formation) were available during the life span recorded by the basal calcareous skeleton of these sponges. Wood (1995) considered Carboniferous chaetetids as occurring in nutrient-limited environments, and Kötter and Pernthaler (2002) studying *in situ* feeding in cavity-dwelling sponges classed the extant form, *Merlia normani,* as a facultative coelobite (generally cavity dwellers, coelobites, that occur within crevices in reefs but also may occur on the outer surface of the reefs) with a higher filtration rate than obligate coelobite (cavity dwellers, coelobites that occur exclusively within crevices) sponges. The

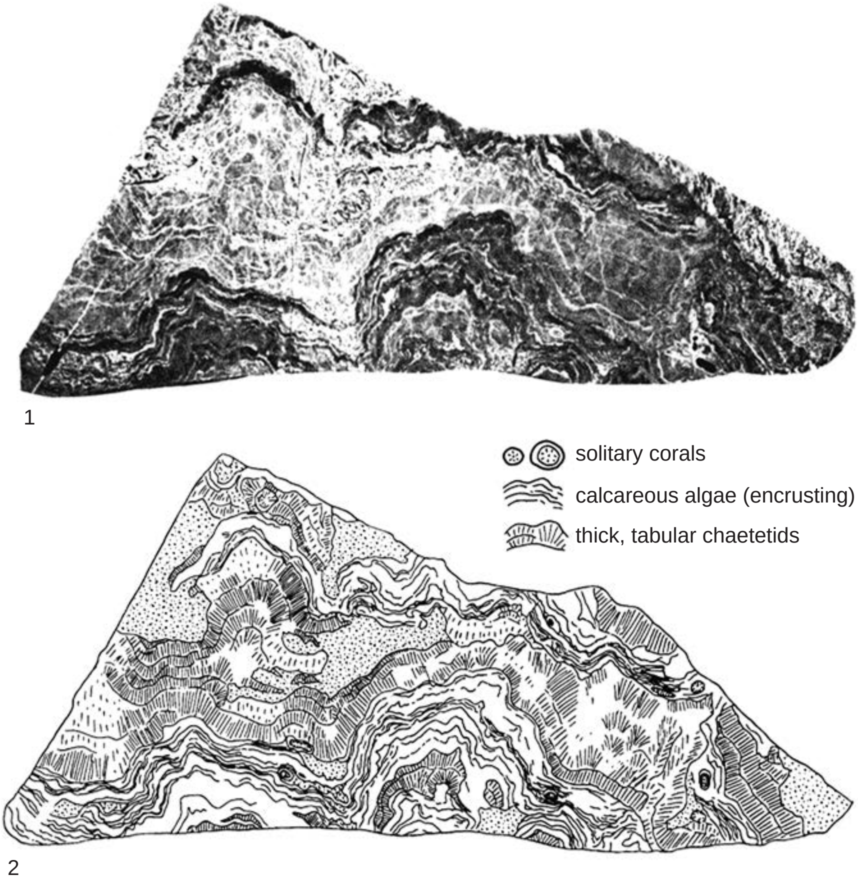

FIG. 69. Reef builders, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* polished surface of reef boundstone from the reef crest, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.29 (adapted from Nagai, 1992, pl. 24,*1;* courtesy of the author and Kyushu University); *2,* interpretive sketch of the polished surface in view *1* of the encrusting chaetetid-algal framestone (boundstone), ×0.31 (adapted from Nagai & others, 1999, p. 37, fig. 22; courtesy of the author and International Symposium on Fossil Cnidaria and Porifera).

occurrence of some sponges, including *Merlia normani*, in coral reef cavities is dependent on the availability of dissolved and particulate carbon sources in the ambient water (DE GOEIJ & others, 2008, p. 139).

With the exception of predation and endobionts, the fossil record provides some useful information on the community ecology of chaetetids, namely epibionts and the relationship between chaetetids and associated fossilized sessile and vagrant benthos. Both invertebrates and vertebrates prey on extant marine sponges (SARA & VACELET, 1973; WULFF, 2006), and grazing traces or other evidence of organically induced injury might, if preserved in fossils, indicate predation. As yet, no such evidence has been reported for fossil chaetetids. Sponges host a variety of uni- and multicellular symbionts, some of which are photosymbionts (SARA & VACELET, 1973; RÜTZLER, 1990). Endosymbionts, including endolithic blue-green algae (Cyanobacteria), have been reported from the skeletons of some extant hypercalcified demosponges but not the soft tissue (HARTMAN, 1984). It has been suggested that fossil chaetetids may

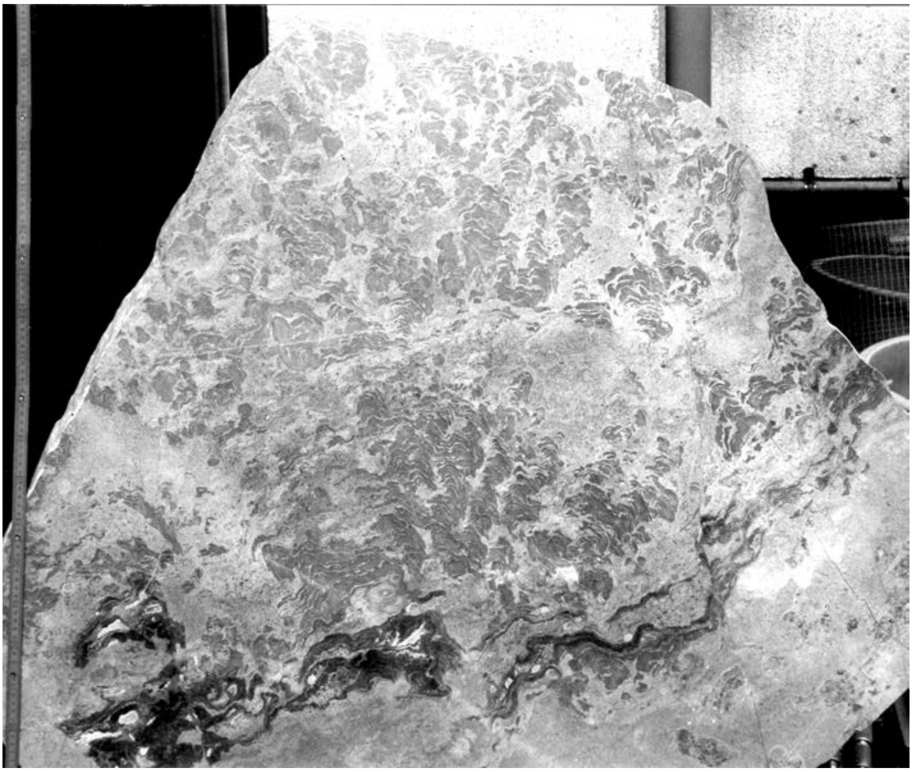

FIG. 70. Polished surface of a large slab from the fore reef facies, Carboniferous, Pennsylvanian, Akiyoshi limestone, Akiyoshi-dai, Japan, ×0.11 (West, 2012b).

have contained photosymbionts (CONNOLLY, LAMBERT, & STANTON, 1989; WEST, 1994; FINKS, 2010a), but the evidence is equivocal, as it is for Paleozoic corals (WOOD, 1999). However, COPPER (2002, p. 221) gave four good reasons why Paleozoic reef builders had photosymbionts, namely: (1) Paleozoic reefs developed on large, tropical, shallow water platforms well within the photic zone; (2) Paleozoic reef builders, including stromatoporoids, had a growth rate, size, and modularity similar to extant reef builders; (3) given the Neoproterozoic ancestry of dinoflagellates, and their presence as primary photosymbionts today, it seems reasonable that such a symbiotic relationship would have developed in Paleozoic reef builders; and (4) the skeletal complexity of Paleozoic corals approaches that exhibited by extant hermatypic corals. Obviously, more study is needed, particularly on extant hypercalcified demosponges, as indicated by HARTMAN (1984).

CONNOLLY, LAMBERT, and STANTON (1989) have summarized the paleoecology of some middle Carboniferous (Lower and Middle Pennsylvanian) chaetetids. WEST and KERSHAW (1991) reviewed chaetetid habitats, and KERSHAW and WEST (1991) related chaetetid growth to environmental factors. FÜRSICH and WENDT (1977) documented the occurrence of chaetetids in Cassian (Triassic) patch reefs, and LEINFELDER and others (2005) discussed the paleoecology of chaetetids and other reef builders in some Jurassic reefs. Basically, the paleoecology of fossil chaetetid sponges is similar to that of stromatoporoids. Both are hypercalcified sponges, and both skeletal types filled similar roles in the environment. Thus, what is known and understood about the paleo-

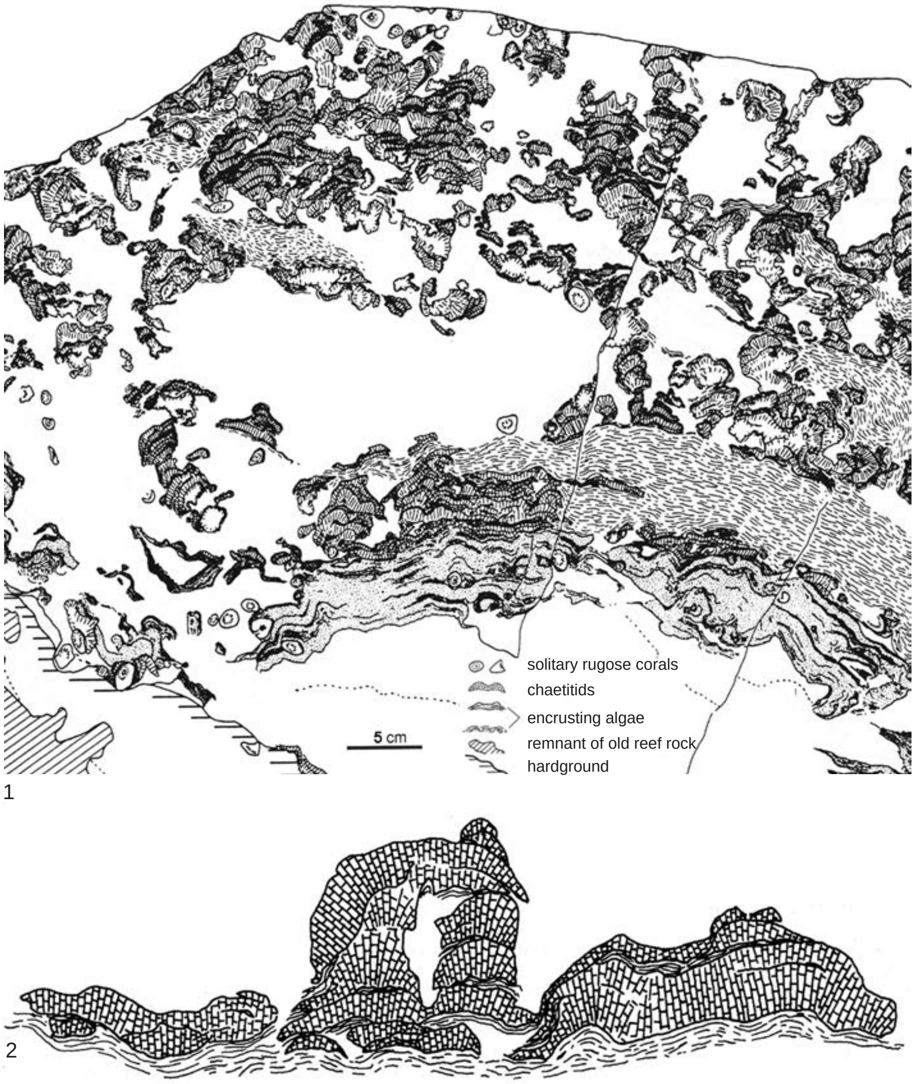

FIG. 71. Polished surfaces of slabs from the reef facies, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* detailed interpretative sketch of the surface of a large polished slab of chaetetid-algal boundstone, ×0.2 (adapted from Nagai, 1985, fig. 4; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline); *2,* sketch showing the relationship between chaetetids and algal-microbial layers, ×0.67 (adapted from Nagai, 1985, p. 12, fig. 9b; figures courtesy of the author and Akiyoshi-dai Museum of Natural History).

ecology of stromatoporoids can be applied, more or less, equally to chaetetids. Optimum environments for stromatoporoids are marine waters above 20 m in depth, with open circulation, in tropical (less than 30°) paleolatitudes (SCRUTTON, 1998, p. 39, fig. 30C). For details on these and other aspects of stromatoporoid paleoecology, see KERSHAW (1998) and DA SILVA, KERSHAW, and BOULVAIN (2011a, 2011b), and see the External Morphology and Paleoecology sections of Paleozoic stromatoporoids, below (p. 419–486; p. 631–651).

As noted previously (see p. 7), the growth form of the basal calcareous skeletons of

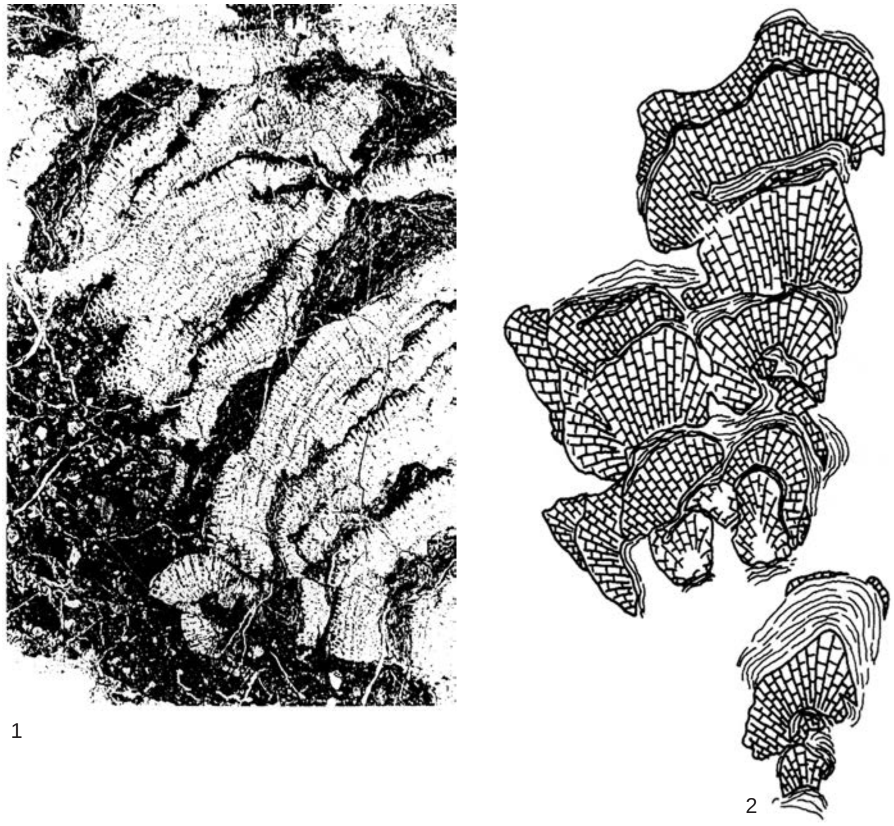

FIG. 72. Details of the relationships between encrusting algae–microbes and chaetetids from the organic reef complex, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* thin section showing interlayering of thin laminar chaetetids and algal–microbial mats from the organic reef complex, ×1.8 (adapted from Nagai, 1992, pl. 38,*2;* courtesy of the author and Kyushu University); *2,* interpretative sketch showing the production of columnar masses by the successive overgrowths of chaetetids and algal-microbial mats from the organic reef (adapted from Nagai, 1985, p. 12, fig. 9a; courtesy of the author and Akiyoshi-dai Museum of Natural History).

fossil chaetetids may be laminar, domical, or columnar, and they appear to be controlled, in part, by environmental factors. Those environmental factors indicated by an asterisk in Table 23 are addressed, and because they are interrelated and interdependent, it is most convenient to consider them together (e.g., temperature, water depth, light, hydrodynamics, sedimentation, desiccation, salinity, and substrate).

PHYSICAL AND CHEMICAL FACTORS

Temperature, light (depth), and turbulence are important factors in the geographic and bathymetric distribution of demosponges. Generally, subtidal (littoral) demosponges (*sensu lato*) are sciaphilous (shade-loving), but some prefer areas of strong illumination (SARA & VACELET, 1973). MEROZ-FINE, SHEFER, and ILAN (2005) addressed the interdependence of depth, light, and turbulence on the morphology and physiology of an extant demosponge species in four different environments. Two environments were in relatively calm water (a shallow cave and deep water) and two in more turbulent high-energy habitats (a shallow exposed site and a tidal pool). Sponge clones from exposed environments

FIG. 73. Interpretative sketch of the encrusting chaetetid-algal–microbial framestone with attached solitary rugose corals in the reef crest of the organic reef complex, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.65 (adapted from West, Nagai, & Sugiyama, 2001, p. 138, fig. 5; courtesy of the authors and Tohoku University Museum).

were larger than those from deeper water, and those from tide pools and exposed environments contained more structural silica than those from calmer water. The oxea spicules of sponge clones from calmer environments were significantly shorter than those in clones from more exposed environments. When clones from calm habitats were transplanted into more exposed habitats, the percentage of spicules to dry weight of those clones increased significantly. The effect of these physical and chemical factors may, in part, explain some of the differences in the growth form and size, as well as the rarity of spicules, in fossil chaetetids.

Examination of the available data on the distribution of Phanerozoic reefs (KIESSLING, FLÜGEL, & GOLONKA, 2002) indicates that

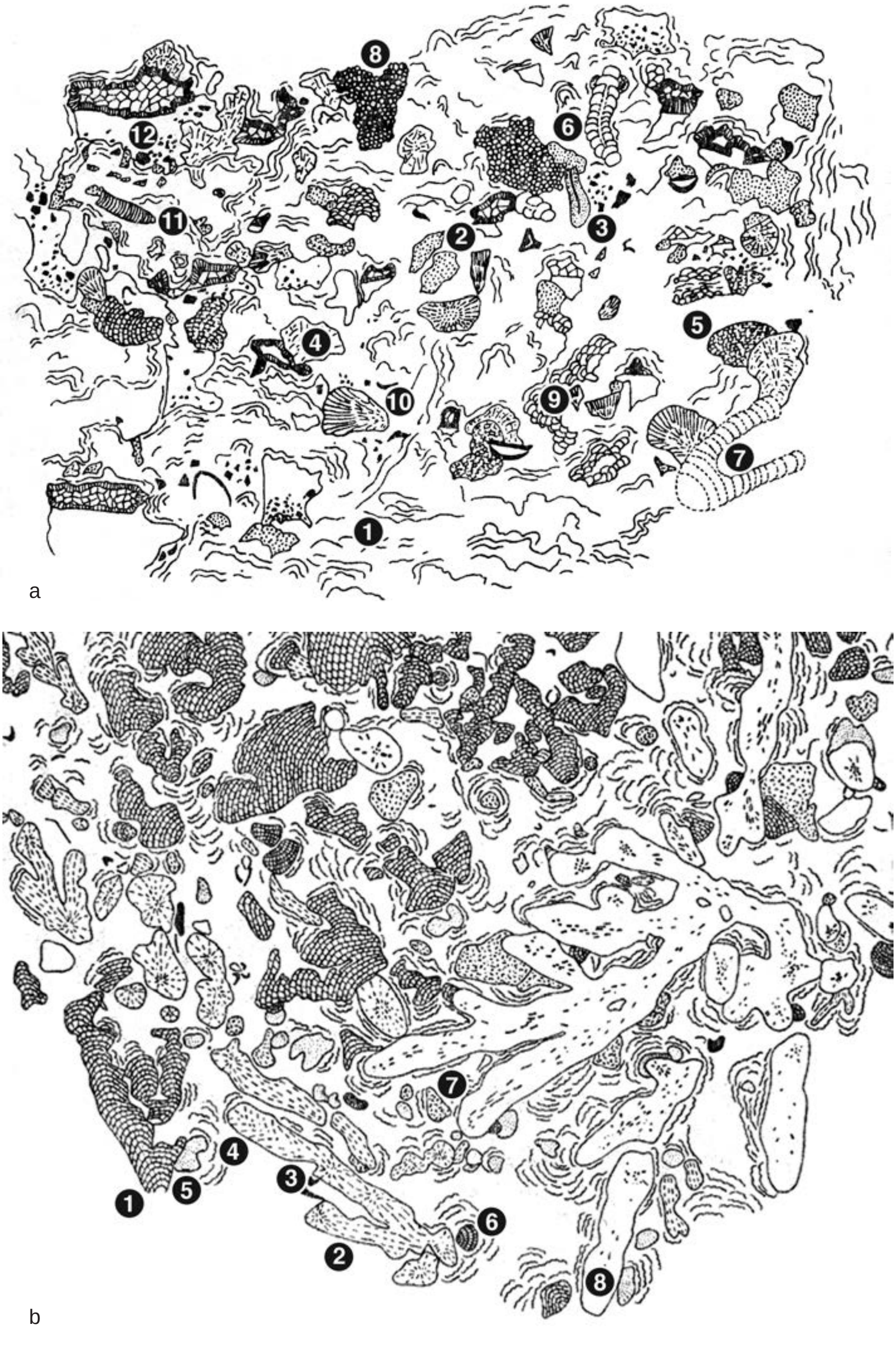

FIG. 74. *(For explanation, see facing page).*

the vast majority of them occur in what were tropical latitudes in marine waters of the shallow shelf. Hypercalcified demosponges with a chaetetid skeleton are components of some of these reefs. ARETZ and NUDDS (2007, p. 377) reported chaetetids as contributors to Carboniferous, Mississippian (upper Visean) reefal carbonates that developed in shallow, well-agitated shoal environments, and LORD and WALKER (2009) and LORD, WALKER, and ARETZ (2011) reported them as the first succession stage in a Mississippian (Serpukhovian, Bangor Limestone) reef in Georgia. Chaetetids are particularly conspicuous as constructors of reef mounds and banks in the Carboniferous (Pennsylvanian) (Fig. 75–78; WEST, 1988; WOOD, 2001; WAHLMAN, 2002, p. 290). The paleolatitudinal position of these chaetetid-bearing reefal limestones, and their inferred shallow water setting, suggest that fossil chaetetids preferred warm marine waters, unlike their extant descendants that occur in deeper, and thus cooler, water habitats. However, there are cryptic intertidal occurrences reported in Palau (SAUNDERS & THAYER, 1987). Living specimens of *Acanthochaetetes* sp. off the Komesu coast in Okinawa occur in caves and overhanging spurs above fair weather wave base from water depths of 4 to 26 m (NAGAI & others, 2007). On an overcast day, the illumination at these sites was between 1 and 14 lux (1 lux = 1 lumen per square meter). Thus, even though some extant forms inhabit the photic zone, the available light in these environments is very low.

However, it is not uncommon to find fossil chaetetids in limestones with phylloid and other algae, as noted in the previous discussion of their functional morphology (see p. 81–104). WAHLMAN (2002, p. 290) stated that Carboniferous (Pennsylvanian) chaetetid mounds and banks appear to have formed buttresses around the seaward margins of algal mounds (Fig. 79). These might be considered analogous to the algal ridges that buttress the seaward margins of present-day coral reefs.

HARTMAN and GOREAU (1970, p. 232) commented on the high bulk density of *Ceratoporella nicholsoni,* and studies of the mechanical resistance of extant reef builders indicates that for *C. nicholsoni:* (1) the compressive strength of the skeleton is eight times stronger than concrete; (2) the stress-strain ratio is considerably greater than it is for the skeletons of extant reef-building corals; and (3) the resistance to abrasion is approximately twice that of marble (SCHUHMACHER & PLEWKA, 1981, p. 280). This skeletal strength is attributed to the more massive, less porous skeleton of *Ceratoporella nicholsoni*. Although diagenetically unaltered skeletons of fossil chaetetids are more porous than the skeleton of *C. nicholsoni,* they were massive and less fragile, and more like the extant hypercalcified demosponge than modern reef building corals.

HIGH DOMICAL AND COLUMNAR FORMS

High domical and columnar fossil chaetetids often occur with algal limestones (WEST & CLARK, 1983, 1984; NAGAI, 1985; CONNOLLY, LAMBERT, & STANTON, 1989; WEST & KERSHAW, 1991; WU, 1991; SUGIYAMA & NAGAI, 1994; MINWEGEN, 2001;

FIG. 74. Chaetetids as minor components, binders rather than constructors, in patch reefs, Cassian Formation, Triassic; what have been referred to as indeterminate "sclerosponges" and "sclerosponges" but are most likely chaetetids, as indicated. *a,* Interpretative sketch of a polished slab from an algal-foraminiferid patch reef, Cassian Formation, Triassic, Valle di Rimbianeo (Misutina), Italy; *1,* algal crusts; *2,* sessile foraminiferids; *3, Peronidella* sp., an inozoan sponge; *4,* indeterminate Inozoa; *5,* indeterminate stromatoporoids; *6, Dictyocoelia manon* (MÜNSTER), a sphinctozoan sponge; *7, Amblysiphonella* sp., a sphinctozoan sponge; *8, Uvanella* sp. A; *9, Uvanella* sp. B. (*Uvanella* is a hadromerid sponge); *10,* indeterminate "sclerosponge" (chaetetid); *11,* serpulid tubes; *12,* geopetal cavities, ×0.43 (adapted from Fursich & Wendt, 1977, p. 280, fig. 9); *b,* interpretative sketch of a cross section through a calcareous sponge-coral patch reef, Cassian Formation, Triassic, Seelandalpe, north of Schluderbach, Italy; *1,* stromatoporoids; *2,* scleractinian corals; *3,* brachiopod and mollusk shells; *4,* encrusting algae; *5,* "sclerosponges" (chaetetids); *6, Circopora* sp., a sphinctozoan sponge; *7,* Inozoa; *8, Sestrostomella robusta*, an agelasid sponge, ×0.3 (adapted from Fursich & Wendt, 1977, p. 268, fig. 5; figures courtesy of the authors; for color versions, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline).

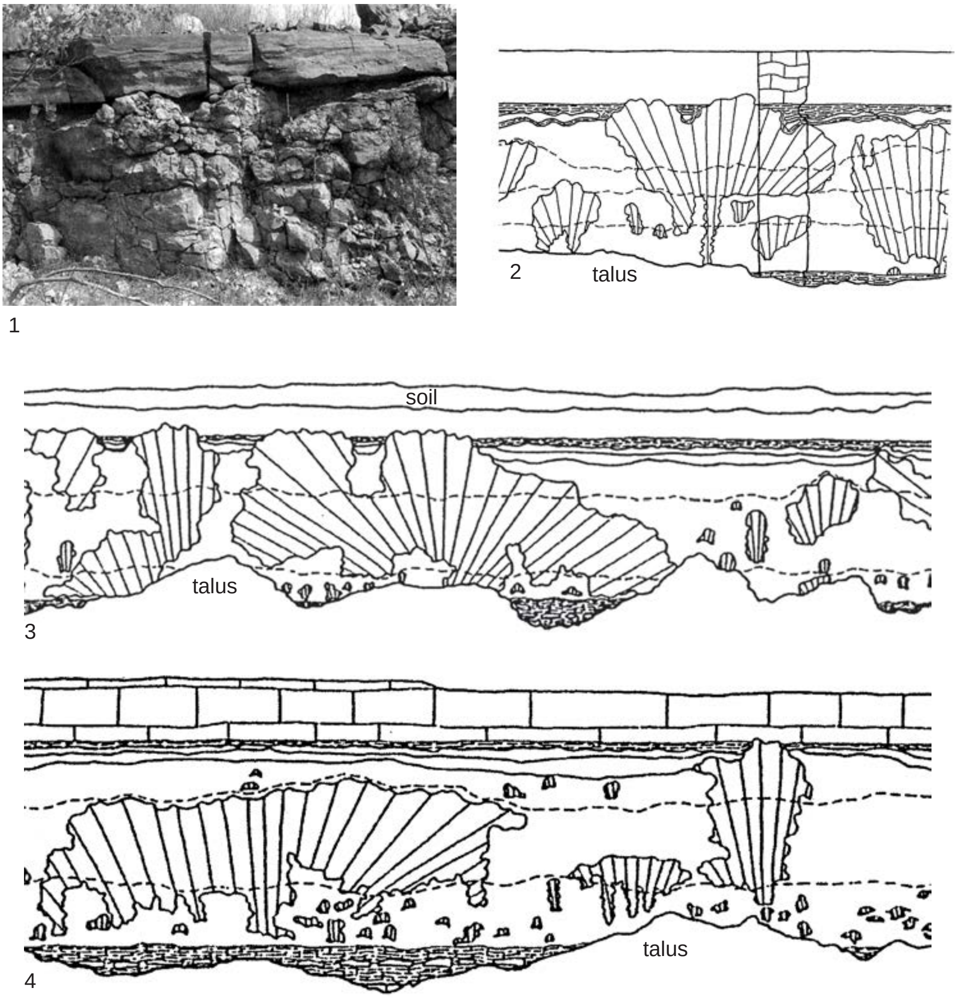

FIG. 75. Chaetetid reef mounds, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of a chaetetid reef mound in a south-facing wall in the southern part of a quarry, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.01 (adapted from Suchy & West, 2001, p. 429, fig. 5); *2–4,* interpretive sketches; thin dashed lines at top of figures denote a thin mudrock layer, thicker dark areas above the talus is an algal calcilutite with some chert nodules, and white areas above talus line are limestone; *2,* photograph in view *1,* ×0.01 (adapted from Suchy & West, 2001, p. 429, fig. 5); *3,* chaetetid reef mound in the west-facing wall in the northern part of a quarry, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.01 (adapted from Suchy & West, 2001, p. 435, fig. 9A); *4,* chaetetid reef mound in the south-facing wall in the northern part of a quarry, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.01 (adapted from Suchy & West, 2001, p. 436, fig. 10B; figures courtesy of the authors and the Society for Sedimentary Geology).

Suchy & West, 2001; West, Nagai, & Sugiyama, 2001; Sano, Fujii, & Matsuura, 2004; Sano, 2006). Such occurrences might indicate that, rather than competitors, chaetetids and algae were mutually tolerant in these environments. Or, perhaps, as illustrated by Preciado and Maldonado (2005, p. 149), for some extant situations, the presence of the algae created a favorable habitat for the sponge, in this case the chaetetid. Association with algal

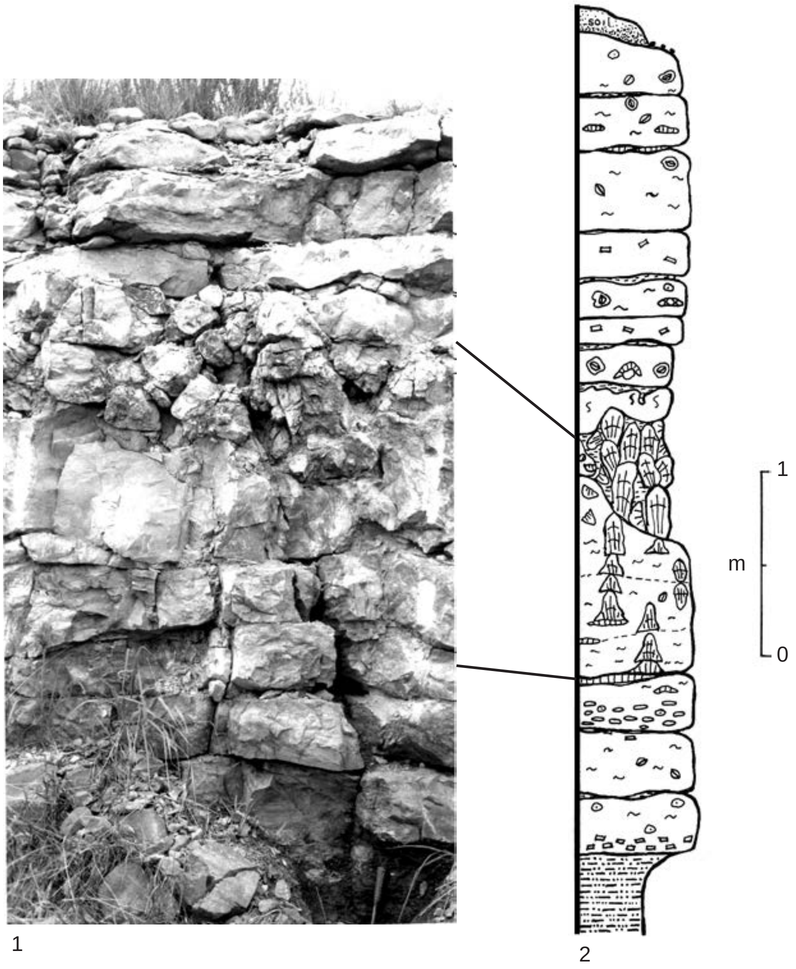

FIG. 76. Further examples of chaetetid reef mounds, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of part of a chaetetid reef mound in a road cut exposure, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.03 (adapted from Voegeli, 1992, p. 65, fig. 19); *2,* graphic section of photograph in view *1,* showing the position of abundant large domical to columnar chaetetids, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas (adapted from Voegeli, 1992, p. 65, fig. 19; figures courtesy of the author and Kansas State University).

limestones indicates that fossil chaetetids were successful in the photic zone, and as buttresses, they were tolerant of high-energy conditions. Water turbulence is known to be important to extant demosponges (*sensu lato*); if turbulence is too high, the settlement of larvae is inhibited and adults are damaged, if too low, the feeding, respiring, and excreting are affected (SARA & VACELET, 1973). LAUBENFELS (1950) reported as optimal, a current of 3 km/hr for extant taxa, with higher or lower values being more limiting. In areas of excess turbulence, demosponges (*sensu lato*) that normally inhabit more open water are found in cracks and cavities of rocks (SARA & VACELET, 1973). Although extant hypercalcified demosponges are commonly found in such sheltered shallow water habitats, their fossil ancestors flourished in more open, turbulent environments. Deep to very shallow subtidal environments have been postulated for chaetetids (CONNOLLY & STANTON,

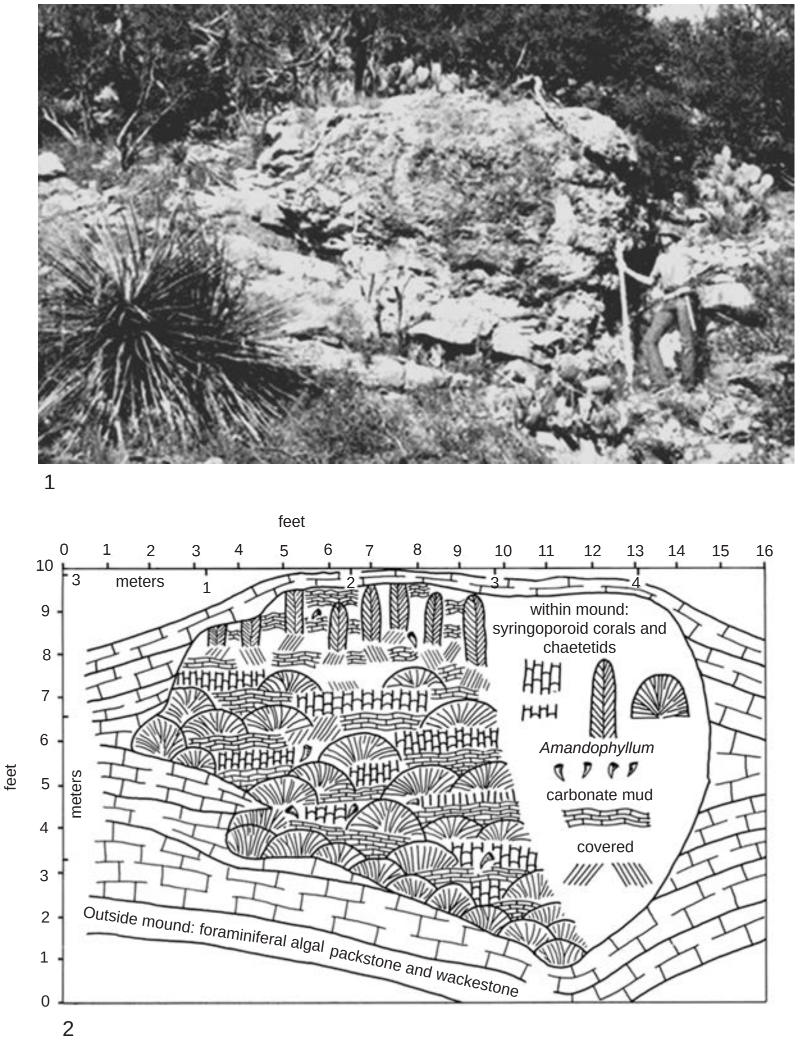

FIG. 77. Chaetetid reef, Carboniferous, Pennsylvanian, Texas; *1,* photograph of an exposure of a chaetetid reef, Marble Falls Limestone, Mason County, Texas, ×0.01 (adapted from Sutherland, 1984, p. 547, pl. 1,*1*); *2,* interpretative sketch of view *1,* showing domical and columnar chaetetids with associated corals and micrite (carbonate mud), ×0.02 (adapted from Sutherland, 1984, p. 544, fig. 1; figures courtesy of the Paleontological Research Institution, Ithaca, New York).

1983, 1986; SUTHERLAND, 1984; CONNOLLY, LAMBERT, & STANTON, 1989; VOEGELI, 1992; LEINFELDER & others, 2005). Table 24 lists the criteria that support a shallow water occurrence for Carboniferous (Lower and Middle Pennsylvanian) chaetetids. Based on the flat tops of individual vase-like growth forms of chaetetids in a Carboniferous (Pennsylvanian) chaetetid reef bank, CONNOLLY, LAMBERT, and STANTON (1989) suggested that the chaetetids grew up to sea level in a low energy environment, which resulted in this unusual growth form that, in plan view, resembles microatolls (Fig. 80–81).

The hydrodynamics of open ocean habitats is a function of current and wave energy; in shallow water coastal areas, tidal surges, storm waves, fair weather waves, and currents are

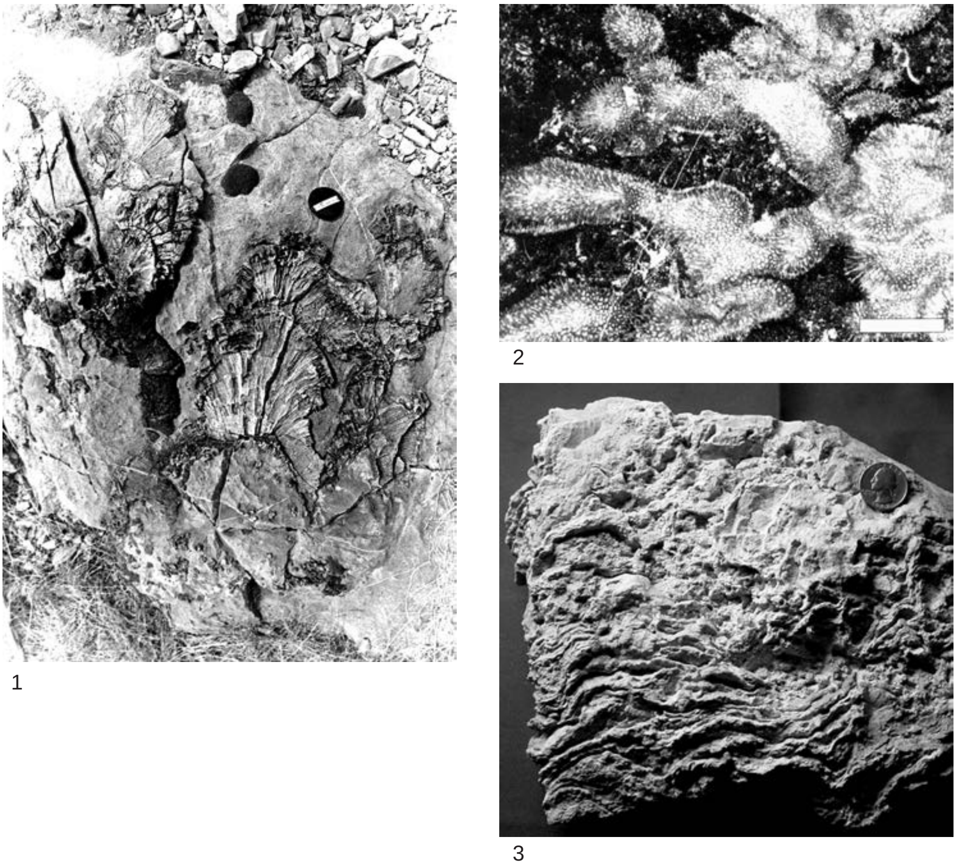

FIG. 78. Chaetetid reefal limestones, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of columnar chaetetids in a reef bank, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona, ×0.07 (West, 2012b); *2,* polished surface of a chaetetid boundstone, Cuera Limestone, Playa de La Huelga, Cantabrian Mountains, Spain, ×0.3 (adapted from Minwegen, 2001, p. 110, pl. 4,*2;* courtesy of the author and Kölner Forum für Geologie und Paläontologie); *3,* weathered surface of laminar chaetetids and algal-microbial mats from the reef core, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.5 (West, 2012b).

all important. Turbulence has a direct effect on the particle size and amount of sediment suspended in the water. If the seabed is composed of loose, coarse sediment grains and the turbulence is high, then the amount of sediment suspended in the water may be high, i.e., high turbidity. On the other hand, if the available sediment grains are small, then high turbulence may remove them from the area. High turbidity, whether the result of coarse suspended sediment and high energy, or fine suspended sediment and low energy, can be detrimental to attached benthic organisms, such as sponges, that feed by filtering the water. Sponges inhabiting unprotected areas will be abraded if the suspended sediment is coarse grained and the energy (turbulence) is high. If the suspended particles are fine grained and energy relatively low or zero, the inhalant pores of the sponge may become clogged by deposited sediment, which impairs feeding, respiring, and excreting. BAKUS (1968, p. 45) noted that deposition of small- and medium-sized silt grains was detrimental, either by burial, or clogging, of the canals and chambers of sponges that inhabited the undersides of coral colonies, given the evidence when coral colonies were turned over, exposing the sponges. When turbulence, turbidity, and/or

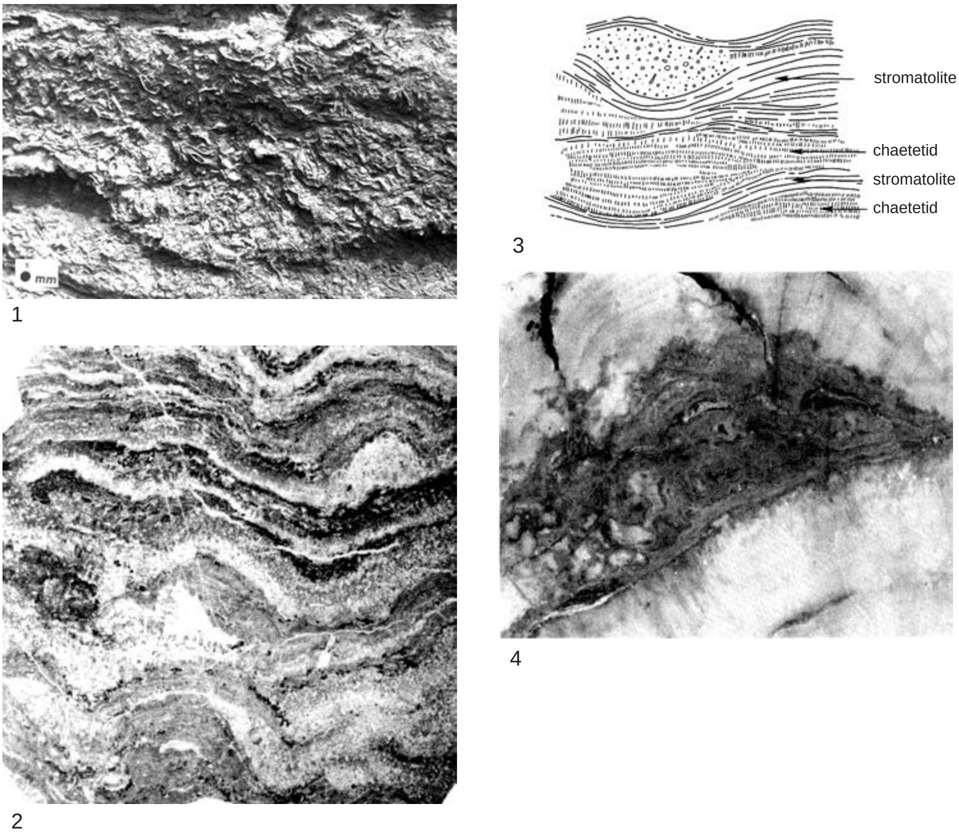

FIG. 79. Details of chaetetids and algal associations, Carboniferous, Pennsylvanian; *1,* outcrop photograph of the weathered surface of a phylloid algae packstone associated with chaetetids in a reef mound, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.2 (adapted from Voegeli, 1992, p. 75, fig. 22; courtesy of the author and Kansas State University); *2,* vertical thin section of laminar chaetetids and stromatolitic (algal-microbial) layers, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×1.7 (adapted from Ota, 1968, pl.4,*2;* courtesy of the author and Akiyoshi-dai Museum of Natural History); *3,* interpretative sketch of chaetetid and stromatolite (algal-microbial) layers in the reef limestone, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.7 (adapted from Ota, Sugimura, & Ota, 1969, p. 8, fig. 5; courtesy of the authors and Palaeontological Society of Japan); *4,* laminar chaetetid below, overlain by an algal-foraminiferal-microbial layer that is in turn overlain by a low domical chaetetid, Marble Falls Limestone, Mason County, Texas, ×0.8 (adapted from Sutherland, 1984, p. 547, pl. 1,*6;* courtesy of the Paleontological Research Institution, Ithaca, New York).

sedimentation are detrimental, demosponges (*sensu lato*) survive on vertical surfaces or on the undersides of overhanging surfaces (SARA & VACELET, 1973). Whether this has played a role in the cryptic habitats of extant hypercalcified demosponges is unclear, though *Merlia normani* is considered to be a facultative coelobite (cavity dweller) (KÖTTER & PERNTHALER, 2002).

As constructors in shallow shelf environments, fossil chaetetids existed in environments from high to very low energy. Extant encrusting and/or massive sponges on subtidal hard surfaces, including cobbles, in areas of high current velocity, are oriented parallel to the current direction (GINN, LOGAN, & THOMAS, 2000). Paleocurrent data from a Carboniferous (Pennsylvanian) limestone suggests the orientation of domical to columnar chaetetids associated with this limestone (Fig. 82; SUCHY & WEST, 2001, p. 433) is compatible with the observations of these extant sponges. High domical and columnar chaetetids that were narrow at the base and wider near the top and not supported by surrounding sediment were susceptible to being toppled by high-energy events. Although there is evidence that high domical and columnar growth forms were toppled, probably by storms, there are similar sized and larger chaetetids that appear to have been undisturbed by such events (Fig. 83–86). Some lithologic units containing toppled chaetetids are overlain by lithologies with features suggestive of subaerial exposure (Fig. 83–84). But, there are also examples where, after being disoriented, growth continued such that the initially colonized object (substrate) reveals more than one disturbance (Fig. 86.3–86.4, Fig. 87). Larger and/or denser objects require more hydrodynamic energy to move or topple them. Thus, the size of the chaetetid mass that has been toppled and/or moved around provides some indication of the relative hydrodynamic energy in that environment. As growth continued, the chaetetid

TABLE 24. Criteria suggesting or implying a shallow-water occurrence for chaetetids. These criteria are based on direct observation, close stratigraphic association, or implied by the comments of one or more of 30 authors (see Connolly, Lambert, & Stanton, 1989, for references) (adapted from Connolly, Lambert, & Stanton, 1989, table 3).

Bioherms, banks, mounds
Chaetetid breccia and/or fragments
Chaetetid micro-atolls
Coarse bioclastics on the lee side of *in situ* chaetetids
Fenestra
Grainstones
Intraclasts
Flattened upper surfaces of chaetetid skeletons
Mudcracks, shrinkage cracks, sun cracks
Oncolites
Oolites
Penecontemporaneous dolomite
Peritidal indicators
Phylloid algal mounds
Proximity to strandline
Stromatolites
Subaerial exposure—paleosols
Syndepositional relief
Disturbed chaetetids, toppled, inverted

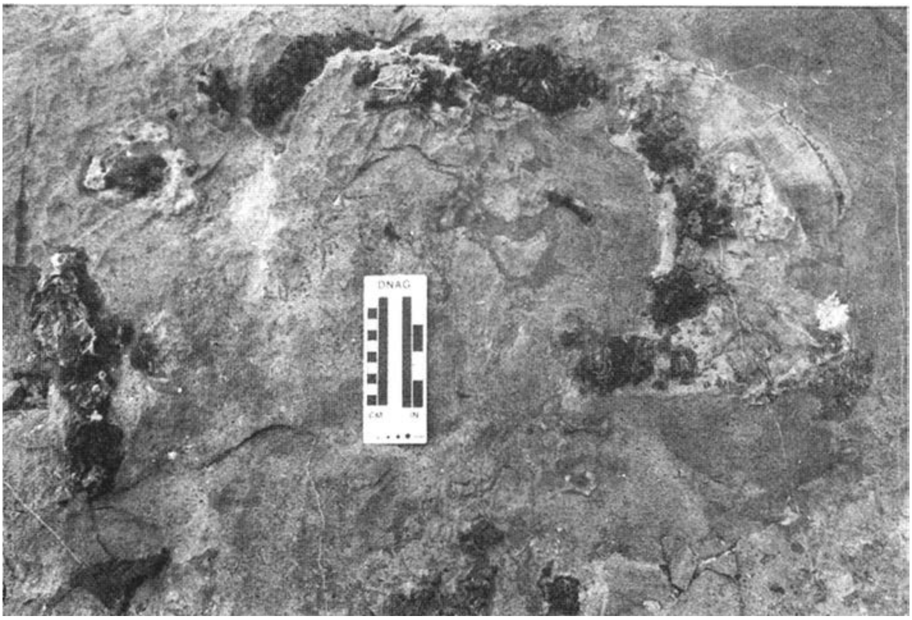

FIG. 80. Upper surface of a chaetetid micro-atoll (scale is in the inferred lagoon, the longest black bar to the left is 10 cm long), Carboniferous, Pennsylvanian, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona; dark areas are the tops of chaetetids, ×0.14 (adapted from Connolly, Lambert, & Stanton, 1989, p. 167, pl. 55,*3;* courtesy of the authors and Springer-Verlag GmbH & Co.).

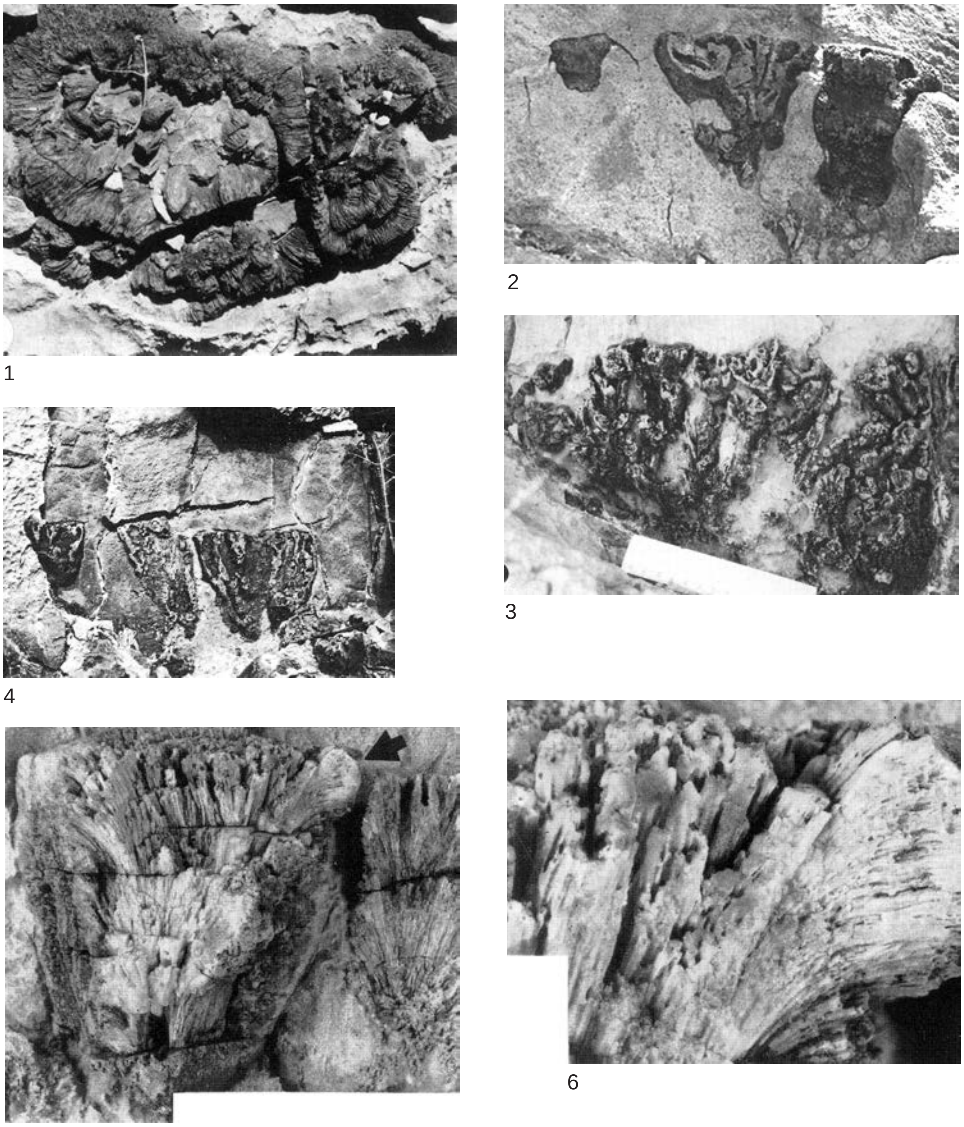

FIG. 81. Flared chaetetids and micro-atolls, Carboniferous, Pennsylvanian; *1,* upper surface of a small chaetetid micro-atoll, limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×0.3 (adapted from Stanton, Connolly, & Lambert, 1994, p. 367, fig. 2.6; courtesy of the authors and Springer-Verlag GmbH & Co.); *2,* lateral view of silicified chaetetids with lateral flaring at a common horizon, limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×0.35 (West, 2012b); *3,* lateral view of fused silicified chaetetids with lateral flaring at a common horizon in an inferred biostrome, limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×0.2 (adapted from Connolly, Lambert, & Stanton, 1989, p. 167, pl. 55,*1;* courtesy of the authors and Springer-Verlag GmbH & Co.); *4,* lateral view of silicified chaetetids with lateral flaring at a common horizon from another part of the inferred biostrome figured in view *3,* limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×0.1 (adapted from Connolly, Lambert, & Stanton, 1989, p. 165, pl. 54,*5;* courtesy of the authors and Springer-Verlag GmbH & Co.); *5,* close-up of the lateral flaring chaetetid showing tubules, limestone of the Middle

(Continued on facing page.)

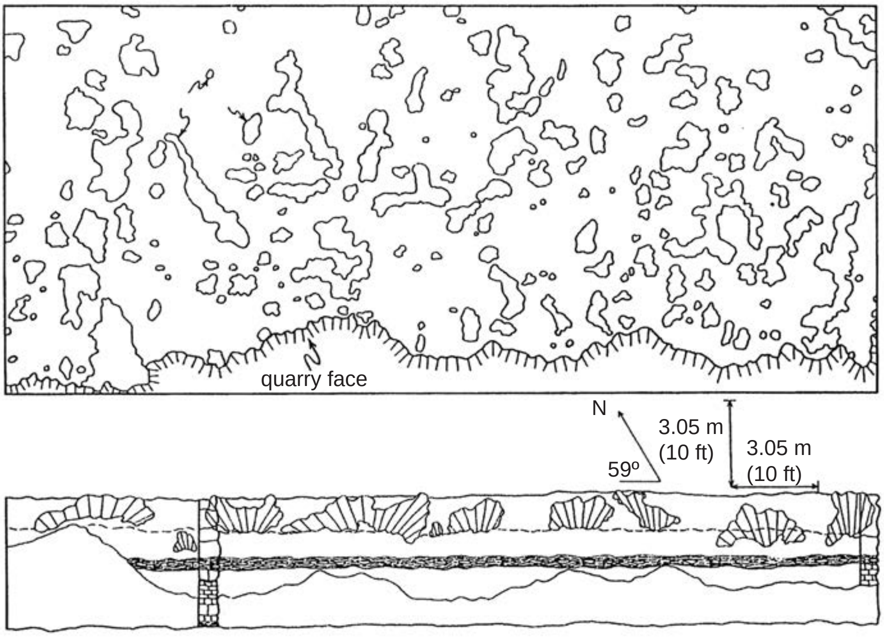

FIG. 82. Inferred current direction from the southwest (lower left), based on the shape and orientation of chaetetids and associated cross-laminated calcarenites. Upper diagram is a map of an exposed bedding plane surface in a quarry, and the lower diagram is the vertical face associated with that quarry map, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, 59° west of north refers to the orientation of the quarry face in both views (planar and vertical), as do the vertical and horizontal scale bars, ×0.004 (adapted from Suchy & West, 2001, p. 434, fig. 8; courtesy of the authors and the Society for Sedimentary Geology).

mass reached a size that was not easily moved, though upward growth continued (Fig. 86.3–86.4). Some high domical to columnar forms extended several centimeters above the seabed (Fig. 86.1). In some cases, the margins of such masses are ragged (Fig. 86.2), presumably due to sediment influx, but they managed to cope with the influx and survive (Fig. 88.3–88.4). There are also occurrences where sediment was piled up along the margins of domical chaetetids, suggesting that growth was only slightly faster than the rate of sedimentation (Fig. 86.1, Fig. 89.1–89.2). Partial or complete burial of the living surfaces of some chaetetids by sediment is indicated by tubules now filled with micrite (Fig. 89.3, Fig. 90.1–90.2; see also Fig. 36.1), but rejuvenation may follow such disruptive events (Fig. 88.3–88.4). Sponges possess high regenerative capacities. They may undergo tissue regression during adverse environmental conditions and then generate a functional morphology when favorable conditions recur (FELL, 1993, p. 1–2). The reef-building constructors were mainly domical to columnar shapes that, though not the most common chaetetid growth forms, occupied the most active environments.

LAMINAR AND LOW DOMICAL FORMS

The most common role of fossil chaetetids in reef building was as binders that inhabited

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FIG. 81. *(Continued from facing page).*
Magdalena Group, Hueco Mountains, Texas, ×0.7 (adapted from Stanton, Connolly, & Lambert, 1994, p. 368, fig. 3.7; courtesy of the authors and E. Schweizerbartsche Verlags, Naegele u. Obermiller Science Publishers); *6,* close-up of the area in the upper right center of view *5,* showing the outward bent, flared tubules, limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×3 (adapted from Stanton, Connolly, & Lambert, 1994, p. 368, fig. 3.6; courtesy of the authors and E. Schweizerbartsche Verlags, Naegele u. Obermiller Science Publishers).

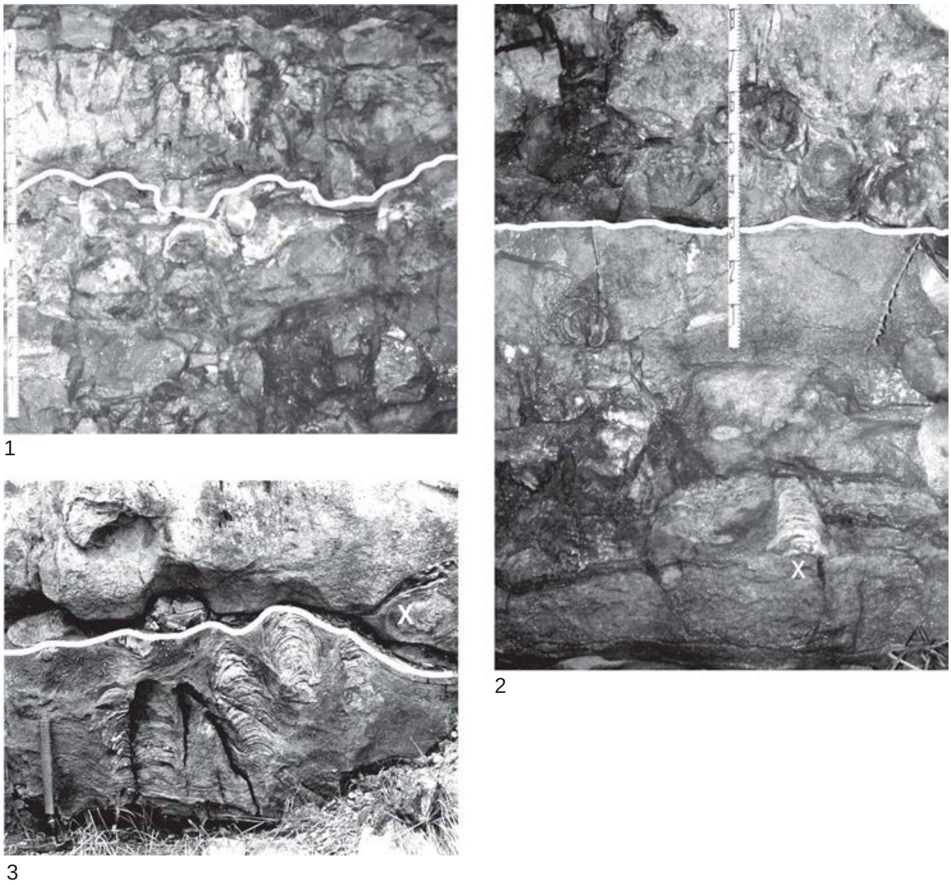

FIG. 83. Chaetetids and associated erosion, Carboniferous, Pennsylvanian; *1,* toppled chaetetids and an erosion surface at the white line, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.05 (West, 2012b); *2,* close view of toppled chaetetid interval above the white line in Amoret Limestone Member, Altamont Limestone, Labette County, Kansas; lateral equivalent at the same locality as shown in view *1;* note the high domical chaetetid with ragged margins above *white X,* ×0.06 (West, 2012b); *3,* columnar chaetetids with smooth to ragged margins in the interval below the disturbed interval, white line, seen in view *2;* note the base, in the overlying disturbed interval, of a toppled large domical or columnar chaetetid, *white X* near the right margin of the photo, ×0.06 (West, 2012b).

more sheltered environments. A laminar to low domical growth form characterizes these binders (Fig. 90.3). The percentage of siliciclastics (insolubles) is higher in lithologies containing laminar growth forms (Fig. 90.4) than it is in lithologies containing domical and columnar forms (the main constructors of reef mounds) (WEST & ROTH, 1991; see Tables 3–4), but ragged laminar and low domical to compound domical forms also occur in higher energy environments where packstones and grainstones were deposited (Fig. 89.4; and see Fig. 35.5).

Demosponges (*sensu lato*), with few exceptions, are limited to waters of normal marine salinity (SARA & VACELET, 1973), but many extant taxa can survive some exposure if they are located in low intertidal environments on the undersides of ledges or stones (BURTON, 1949). In some extant species, periods of emergence may actually be favorable (LAUBENFELS, 1947). Fossil chaetetids may have tolerated some subaerial exposure and desiccation, but they also were disoriented (toppled) in shallow water environments and truncated by exposure (Fig. 83.1, Fig. 91).

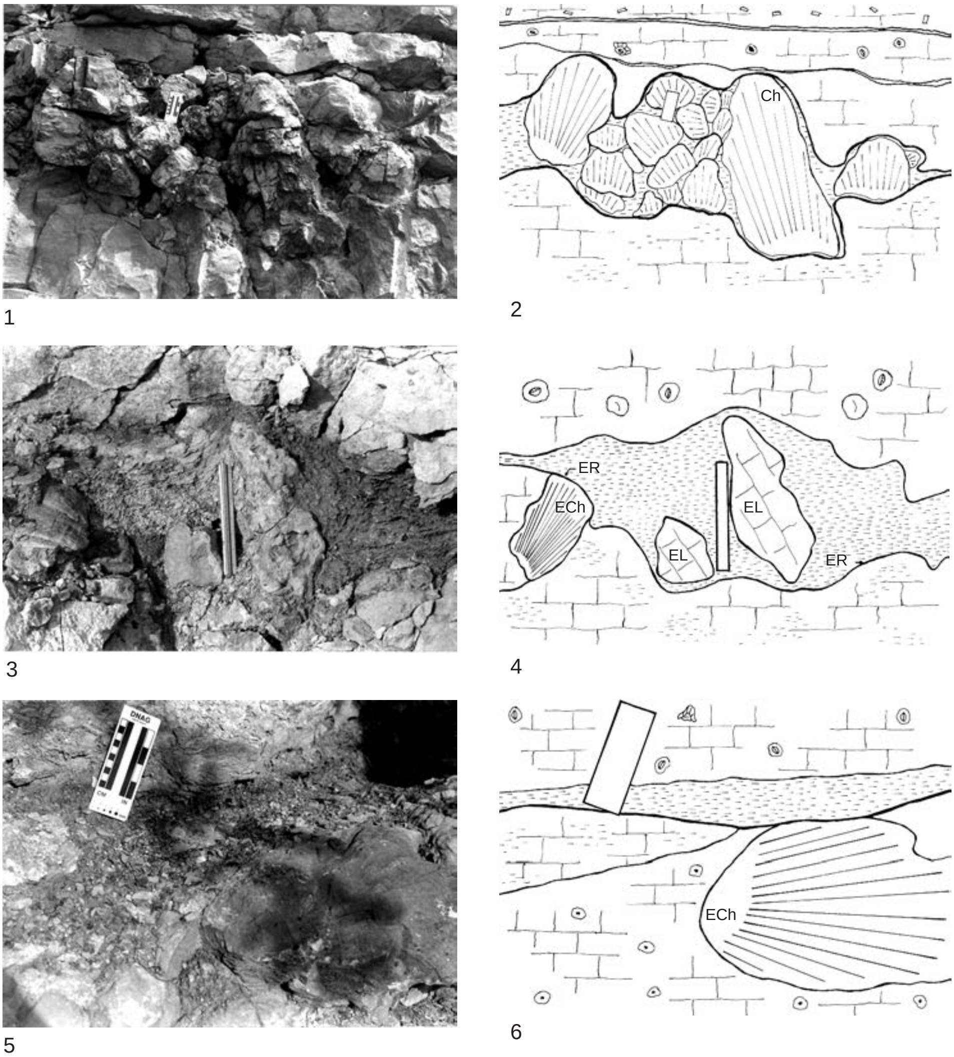

FIG. 84. Further examples of chaetetids and associated erosion, Carboniferous, Pennsylvanian; *1,* disturbed and toppled domical and columnar chaetetids, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.25 (adapted from Voegeli, 1992, p. 139, fig. 31); *2,* interpretative sketch of view *1, Ch,* chaetetid, ×0.25 (adapted from Voegeli, 1992, p. 139, fig. 31); *3,* eroded chaetetids associated with erosion surface and eroded limestone blocks encased in a mudrock matrix, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.1 (adapted from Voegeli, 1992, p. 25, fig. 8); *4,* interpretative sketch of view *3,* erosion surface (*ER*) and eroded limestone blocks (*EL*), eroded chaetetid (*ECh*), ×0.1 (adapted from Voegeli, 1992, p. 25, fig. 8); *5,* detail of eroded chaetetid in the disturbed interval and associated oncolitic limestones and mudrocks, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.1 (adapted from Voegeli, 1992, p. 55, fig. 17); *6,* interpretative sketch of view *5,* eroded chaetetid (*ECh*), ×0.1 (adapted from Voegeli, 1992, p. 55, fig. 17; figures courtesy of the author and Kansas State University).

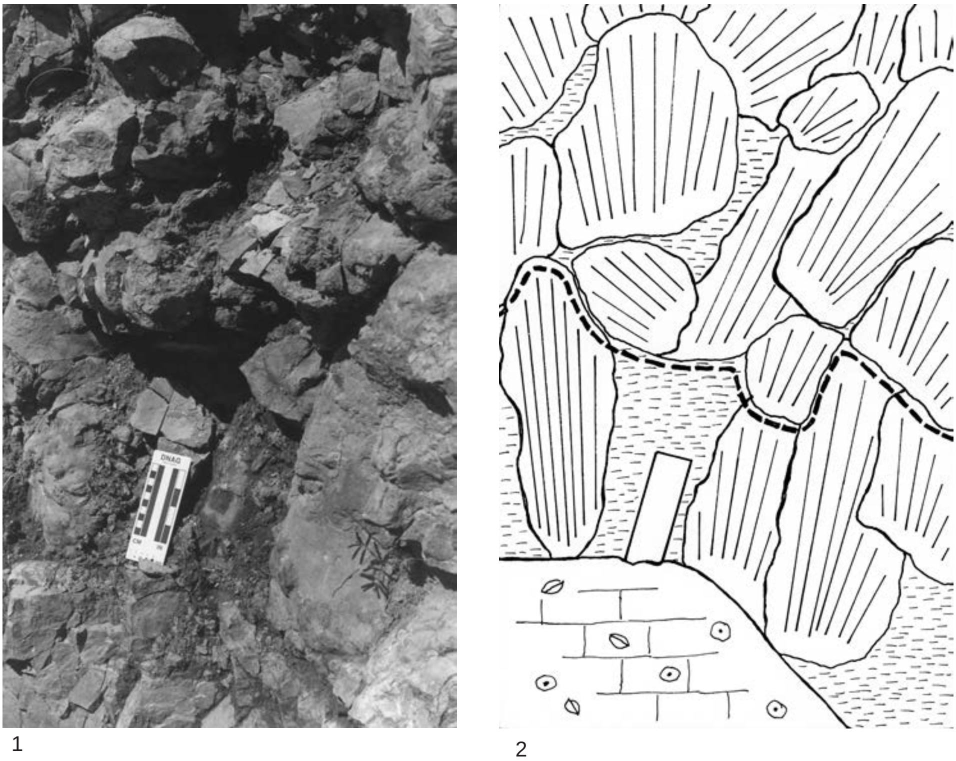

FIG. 85. Erosion, sediment draping, and rejuvenation; *1,* evidence of two episodes of erosion in the disturbed chaetetid interval, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.1 (adapted from Voegeli, 1992, p. 134, fig. 29); *2,* interpretative sketch of view *1,* scale is positioned on the first erosion surface (*solid line*), *dashed line* indicates the position of a second erosion surface; columnar chaetetids grew on the lower surface and were less disturbed than those above the upper erosion surface, ×0.1 (adapted from Voegeli, 1992, p. 134, fig. 29; figures courtesy of the author and Kansas State University).

FIG. 86. Further examples of erosion, sediment draping, and rejuvenation; *1,* sediment, now a grainstone to wackestone, draped on, and over, a high domical chaetetid with smooth margins, based on the draped sediment; the top of the chaetetid is inferred to have been several centimeters above the sea floor during life, ×0.2 (adapted from Voegeli, 1992, p. 162, fig. 39; courtesy of the author and Kansas State University); *2,* tall columnar chaetetids with smooth to ragged margins, suggesting episodic sedimentation and a current direction from right to left, Carboniferous, Pennsylvanian, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona, ×0.05 (see also Connolly, Lambert, & Stanton, 1989, p. 167, pl. 55,*5;* courtesy of the authors and Springer-Verlag GmbH & Co.); *3,* interpretative sketch from the polished surface of a high domical chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, showing three episodes (generations) of growth caused by overturning. Initial growth was on the algal-micobial encrustation, an oncolite, followed by overturning, more growth, more algal-microbial encrustation, and final growth, ×0.45 (adapted from Voegeli, 1992, p. 152, fig. 37; courtesy of the author and Kansas State University); *4,* interpretative sketch from the polished surface of a high domical chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas showing three episodes (generations) of growth caused by overturning. Initial growth was on an algal-microbial coated lithoclast, ×0.3 (adapted from Voegeli, 1992, p. 142, fig. 33; courtesy of the author and Kansas State University).

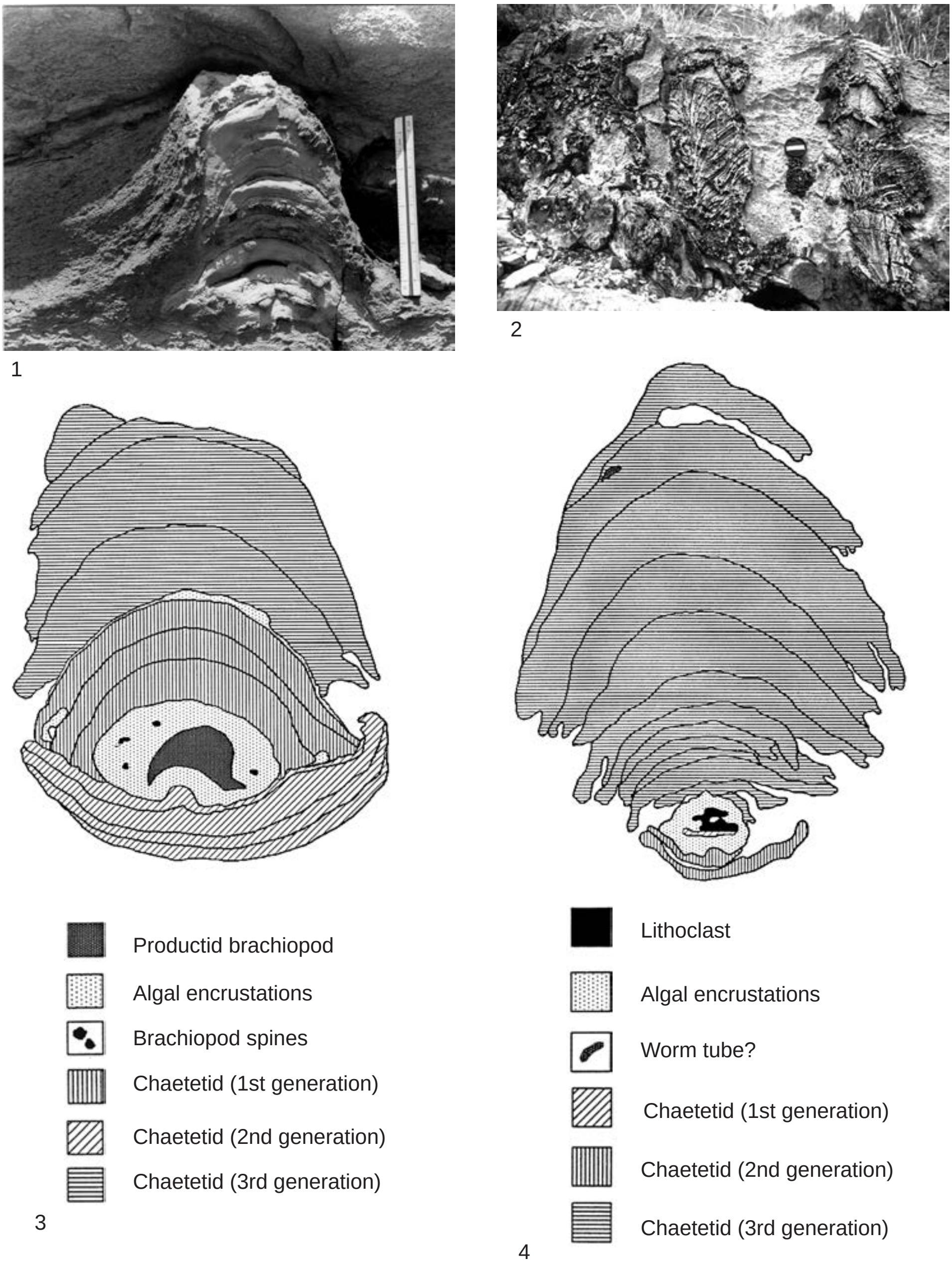

FIG. 86. *(For explanation, see facing page).*

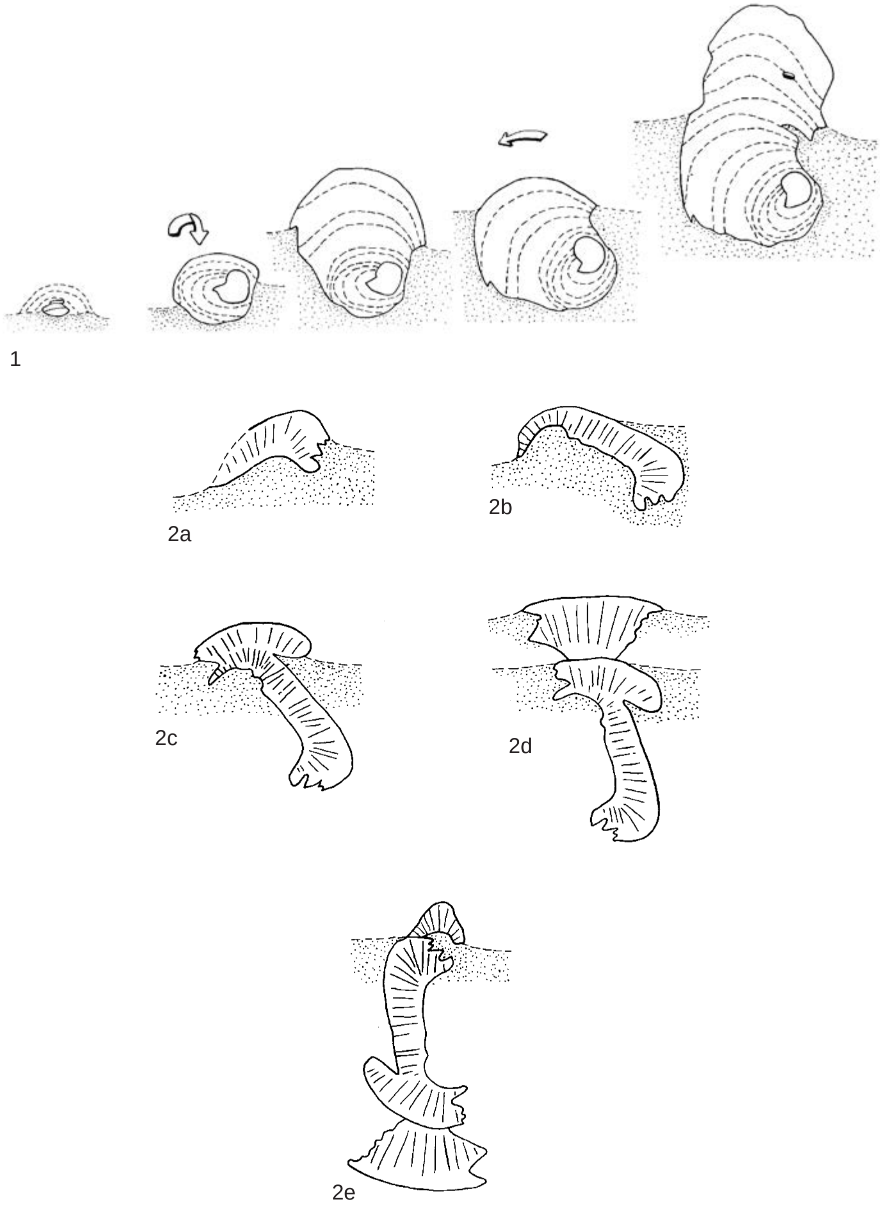

Fig. 87. Inferred growth stages of chaetetids based on interruption partings, Carboniferous, Pennsylvanian; *1,* interpretative sketches based on a vertical section of a high domical chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas showing changes in shape as a result of periodic disturbance and movement during life, *arrow* to left indicates that mass has been turned over 360° prior to the increase in size shown in third image, and *arrow* just right of center indicates that mass has been rotated about 90° to the left prior to the increase in size, as shown in the fifth image, ×0.1 (adapted from Kershaw & West, 1991, p. 338, fig. 3.A); *2a–e,* interpretative sketches of a complex chaetetid in a coarse bioclastic limestone, Blackjack Creek Limestone Member, Fort Scott Limestone, Crawford County, Kansas showing the affects of periodic disturbance and sedimentation, ×0.2 (adapted from Kershaw & West, 1991, p. 340, fig. 5; figures courtesy of the authors and *Lethaia*).

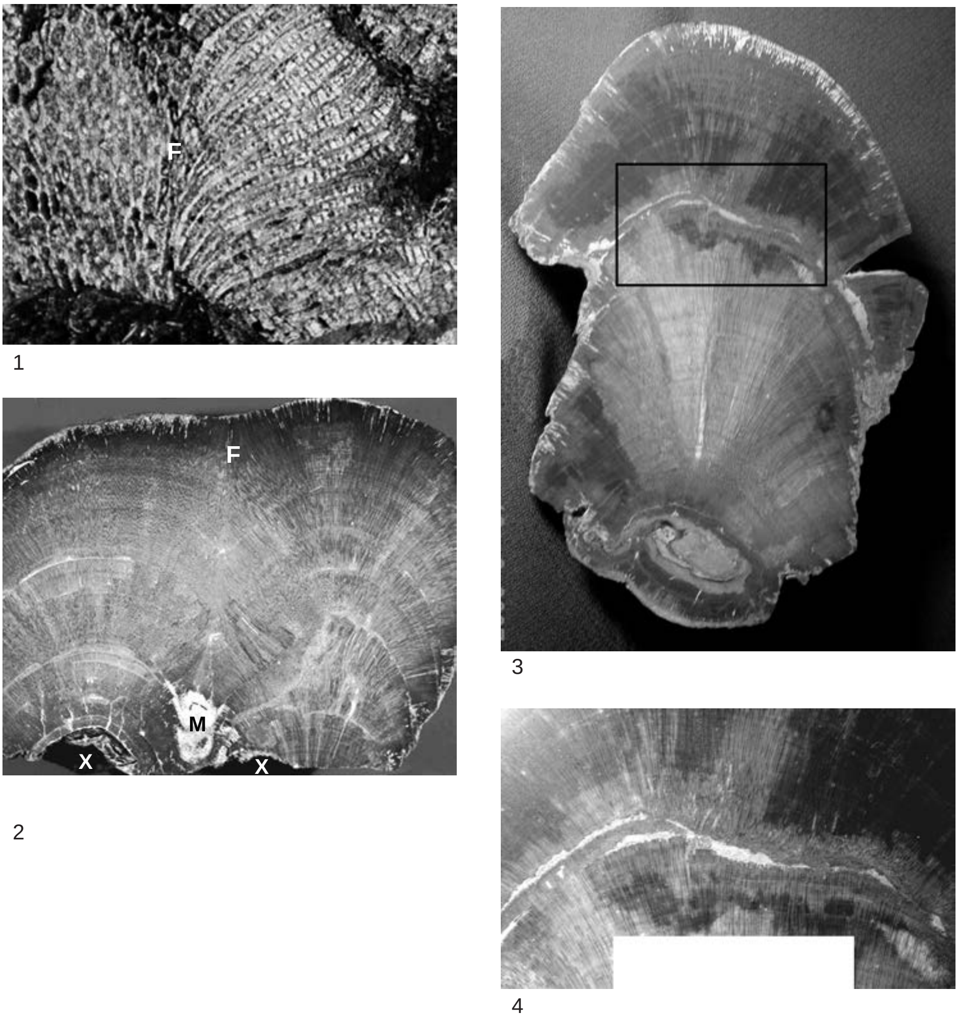

FIG. 88. Fusion and rejuvenation in chaetetids, Carboniferous, Pennsylvanian; *1,* fusion in domical chaetetids, Akiyoshi Limestone, Akiyoshi-dai, Japan; *F,* plane of fusion (just above and left of center), ×14.5 (West, 2012b); *2,* fusion of two high domical chaetetids each began on an algal-microbially encrusted brachiopod valve, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; *M,* matrix; *F,* plane of fusion, *X,* algal-microbial encrusted brachiopod shells, ×0.37 (West, 2012b); *3,* rejuvenation in a columnar chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, after an event that nearly smothered the living surface, ×0.5 (adapted from West & Clark, 1984, p. 343, pl. 2,*C;* courtesy of the authors and the Paleontological Research Institution, Ithaca, New York); *4,* detail of interruption surface, as outlined in view *3,* ×0.12 (West, 2012b).

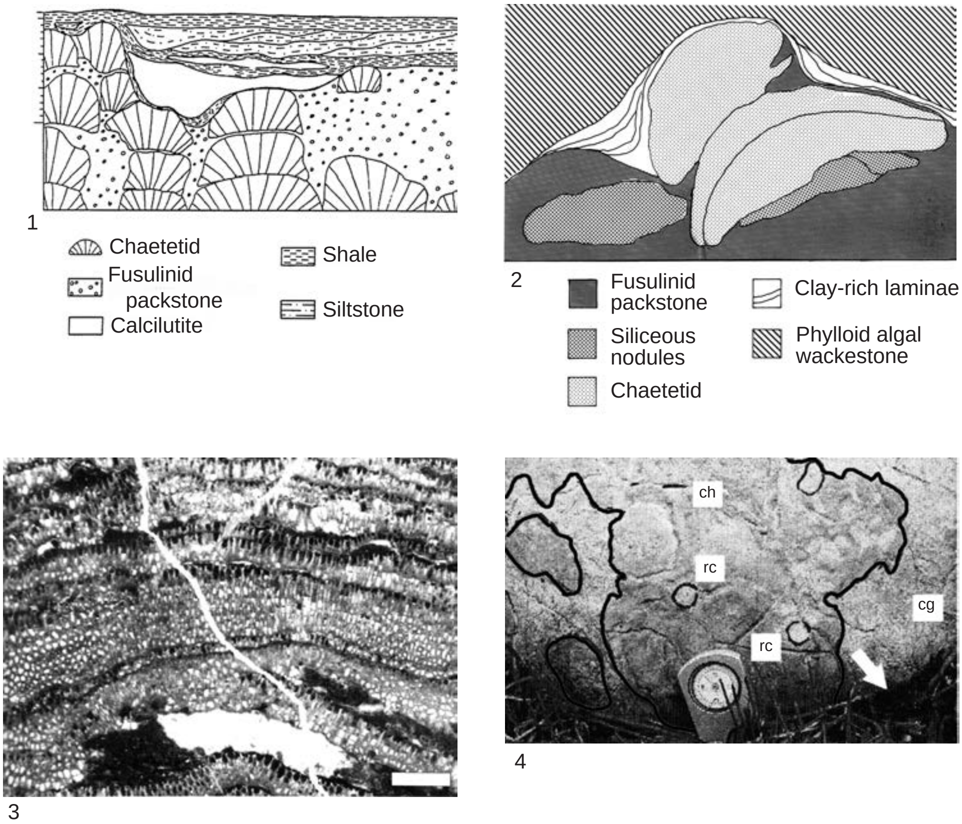

FIG. 89. Chaetetid substrates and associated lithologies, Carboniferous, Pennsylvanian; *1,* interpretative sketch of an exposure of columnar chaetetids in a fusulinid packstone, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas smothered by calcilutite (carbonate mudstone), shale (mudrock), and siltstone; note the draping mudrock on the middle chaetetid, ×0.03 (adapted from Suchy & West, 2001, p. 432, fig. 7; courtesy of the authors and the Society for Sedimentary Geology); *2,* interpretative sketch of an exposure of a slightly disturbed domical chaetetid on a siliceous nodule (nodule is probably a diagenetic feature) in a fusulinid packstone smothered by clay that is overlain by phylloid algal wackestone, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; note the draped clay-rich laminae, ×0.3 (adapted from Voegeli, 1992, p. 128, fig. 27; courtesy of the author and Kansas State University); *3,* matrix-filled chaetetid tubules (3 to 4 mm below top of photo), Cuera limestone, Hontoria, Cantabrian Mountains, Spain, ×0.3 (adapted from Minwegen, 2001, p. 113, pl. 5,*1;* courtesy of the author and Kölner Forum für Geologie und Paläontologie); *4,* irregular chaetetids (*ch*) are outlined in black and incorporated solitary rugose corals (*rc*), in small black circles in a coarse-grained crinoidal grainstone (*cg*), Akiyoshi Llimestone, Akiyoshi-dai, Japan, *white arrow* indicates stratigraphic up direction, ×0.2 (adapted from Sano, 2006, p. 174, fig. 5C; courtesy of the author; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline).

Generally, demosponges (*sensu lato*) prefer an irregular, firm to hard substrate, but some live on mobile substrates if they are attached to a solid object (SARA & VACELET, 1973). Extant specimens of *Acanthochaetetes* sp. colonize small mounds of coralline algae on a rippled, sandy slope in water 80 to 100 m deep off the Komesu coast in Okinawa (NAGAI & others, 2007) (Fig. 92). As a conspicuous part of the sessile benthos, the composition and texture of the substrate were important to chaetetids. As noted by KERSHAW and WEST (1991), three aspects of the substrate appear to have been important to chaetetids: composition, consistency, and profile. In terms of consistency and composition, JAMESON (1980, p. 130–136)

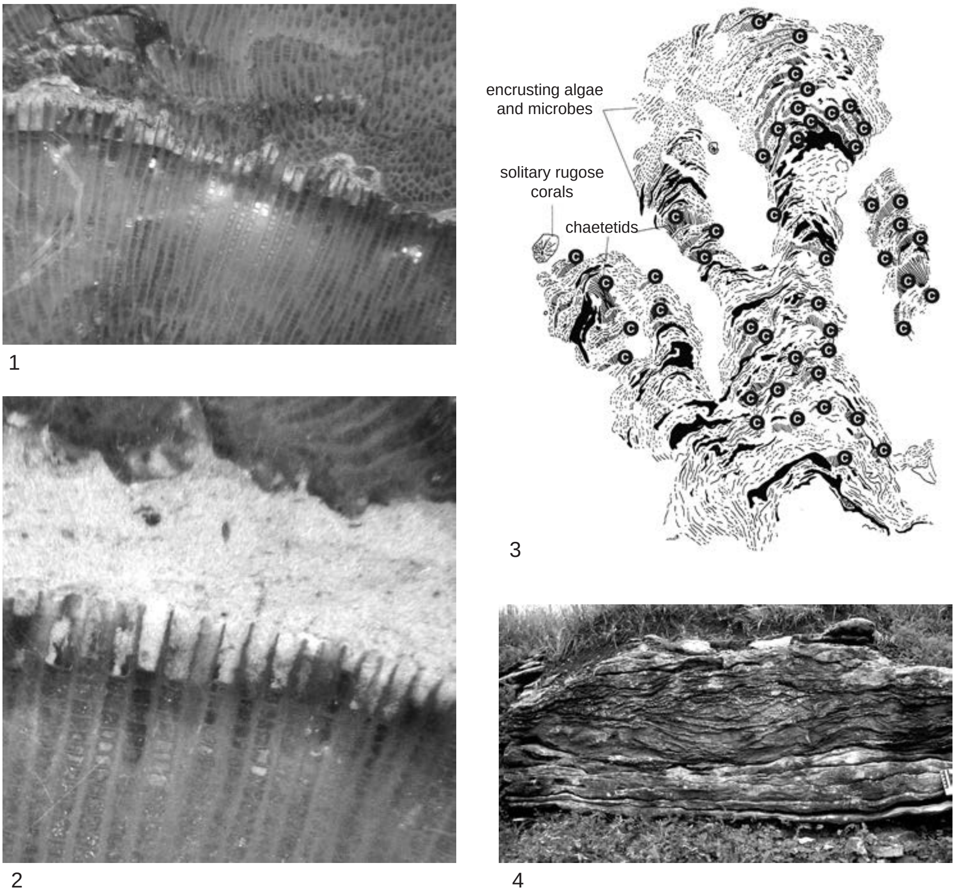

FIG. 90. Further examples of chaetetid substrates and associated lithologies, Carboniferous, Pennsylvanian; *1,* micrite-filled chaetetid tubules, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×10 (West, 2012b); *2,* detail view of part of the area in view *1,* of the micrite-filled tubules in the chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×20 (West, 2012b); *3,* interpretative sketch of a polished slab of the reef flat, Akiyoshi Limestone, Akiyoshi-dai, Japan of associated algal-microbial layers and laminar chaetetid (*C*), ×0.4 (adapted from Nagai, 1979, p. 665, fig. 7; courtesy of the author; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline); *4,* outcrop of laminar chaetetids in an insoluble, mud-rich matrix, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas, ×0.3 (West, 2012b).

recognized four general types of substrates: gels, plastic, firm, and granular. Gels are argillaceous with a thixotropic (becoming fluid when shaken) surface and remain as a gel until buried. Plastic substrates are slightly firmer than gels and are often argillaceous biomicrosparites. Fine-grained biomicrosparites with very little clay (<5%) that are slightly lithified are classed as firm. A gradual change from gel to plastic to firm is not uncommon. Granular substrates have a supporting framework of coarse skeletal debris, and depending on the hydrodynamic energy of the environment, provide suitable surfaces for colonization by sessile benthos. Broken fragments of *Siphonodendron* provided hard surfaces for chaetetid colonization in a Carboniferous (Mississippian, Visean) reef bank in Great Britain (ARETZ & NUDDS, 2007). Chaetetids are common in Serpukhovian echinoderm grainstone-packstones and calcareous sand

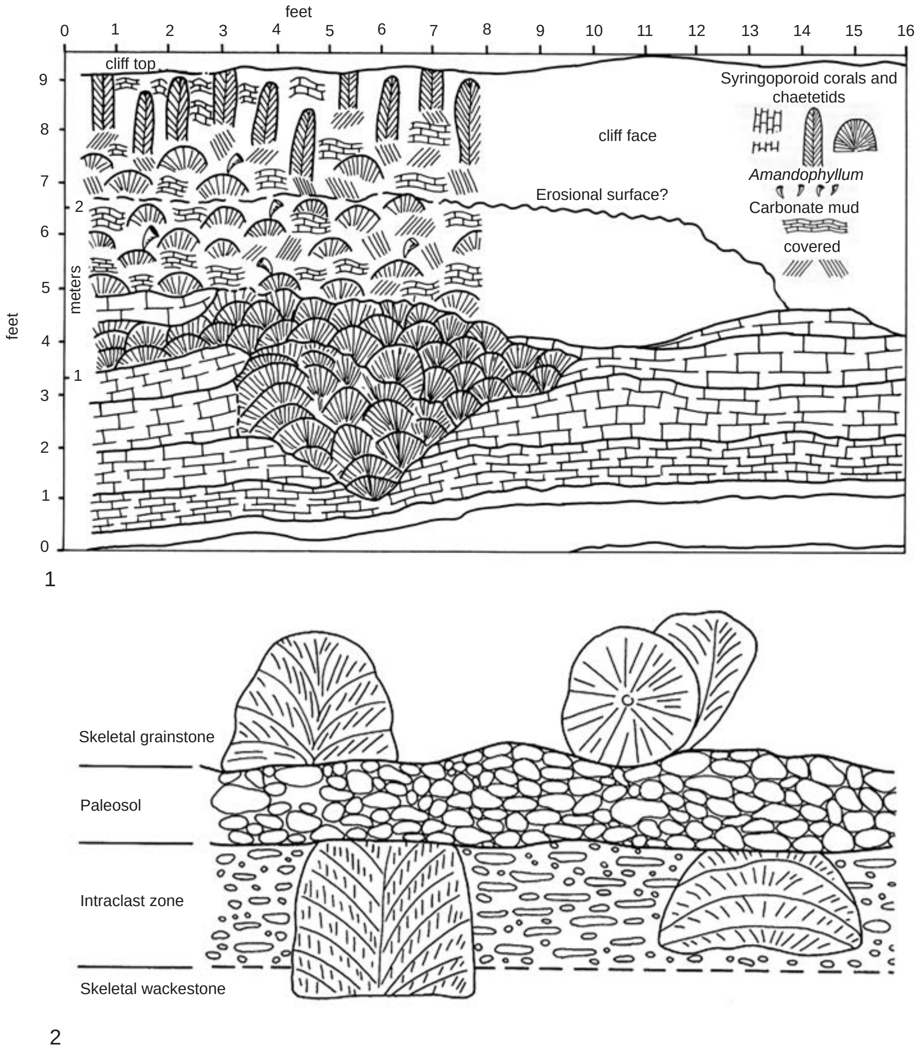

FIG. 91. Erosional surfaces and mobile sediment as chaetetid substrates; *1,* interpretative sketch of the vertical exposure of a chaetetid bank, where chaetetids colonized an inferred erosional surface, Carboniferous, Pennsylvanian, Marble Falls Limestone, Mason County, Texas, ×0.02 (adapted from Sutherland, 1984, p. 545, fig. 3, courtesy of the Paleontological Research Institution, Ithaca, New York); *2,* interpretative sketch of truncated domical chaetetids at the top of an intraclast interval followed by paleosol development; subsequent colonization of the paleosol by domical chaetetids in a skeletal grainstone environment, some of which were toppled with renewed upward growth (upper right), ×0.25 (adapted from Connolly, Lambert, & Stanton, 1989, p. 154, fig. 6; courtesy of the authors and Springer-Verlag GmbH & Co.).

shoals (Gómez-Herguedas & Rodríguez, 2009). The relationships between these substrates and other factors, namely, growth form or habit, size, distribution, and lithofacies, for chaetetids is shown in Figure 93. Fistuliporid bryozoans inhabit similar environments and are potential competitors; they are included in Figure 93 for comparison.

Chaetetids are most commonly found in carbonate rocks, such as argillaceous limestones, micrites (carbonate mudstones), wackestones, packstones, and grainstones. Such substrates may be loose or partially

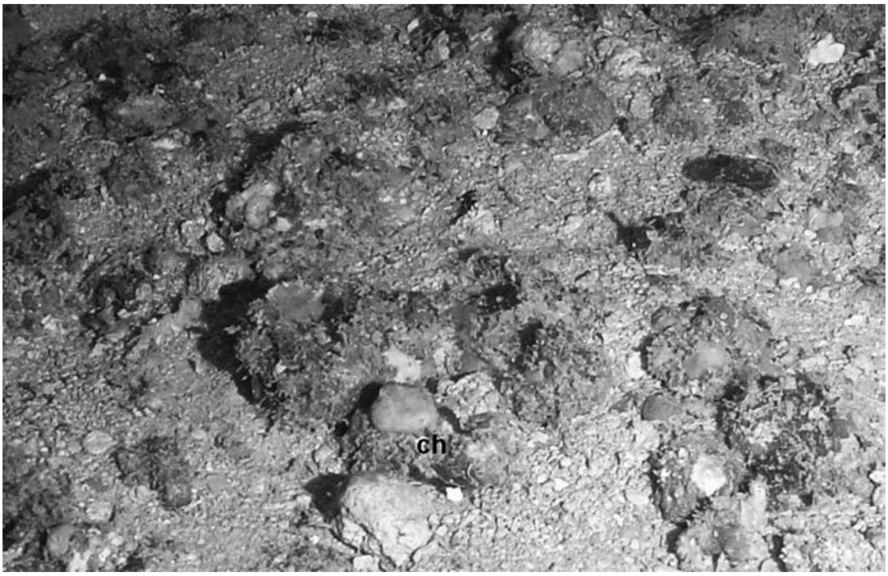

FIG. 92. Extant specimen of *Acanthochaetetes* sp. attached to a small mound of coralline algae (*ch* in lower left center of photo) at a depth of 85 m off the Komesu coast, southern Okinawa, ×0.4 (adapted from Nagai & others, 2007, fig. 4f; courtesy of the authors and the editor of the Abstracts volume of the Xth International Symposium on Fossil Cnidaria and Porifera, A, P. Karpinsky Russian Geological Research Institute; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline).

to completely lithified. As loose grains, there could be some degree of mobility, depending on the hydrodynamics at any given time. Results of such mobile substrates are illustrated by changes in the growth direction (Fig. 87.2). However, chaetetids, like stromatoporoids, also existed on muddy substrates and within siliciclastic sequences (Fig. 90.4, Fig. 91.2; see also Fig. 18.6). WALKER (1972, fig. 24, 27) described chaetetid bioherms and biostromes on a shale substrate overlain by algal mounds in a coarse, well-sorted sandstone, as well as in an arkosic conglomerate (Fig. 94.1–94.3). KERSHAW, WOOD, and GUO (2006) described three different relationships between Silurian stromatoporoids and muddy substrates. These were: (1) growth on a soft substrate; (2) encrusting a hard substrate; and (3) formation of cavities. The first two are commonly associated with stromatoporoids that have a smooth basal surface and the latter has a corrugated basal surface. Direct colonization on fine-grained sediments usually occurred when the sediment covered large skeletal grains, such as brachiopod shells, and provided a topographic high for attachment. Such direct colonization of muddy substrates has not been observed in chaetetids, but it cannot be ruled out. The basal surfaces of chaetetids, when available, are commonly irregular and often exhibit concentric ridges and bands, perhaps corrugations. Cavities created by corrugations as described by KERSHAW, WOOD, and GUO (2006) may also occur in chaetetids because of the irregularity of their basal surface.

All three chaetetid growth forms (laminar, domical, columnar) may grow over loose, soft substrates, but some hard or firm irregularity seems to be necessary for initial colonization (Fig. 94.4; see also KERSHAW & WEST, 1991; WEST & KERSHAW, 1991; see Fig. 24–25). In some cases, as growth continued, other firm to hard objects were incorporated into the growing skeleton (Fig. 94.5; see also Fig. 24.3). Hydrodynamics, tides, waves, or currents may have removed some of this loose sediment and created ephemeral cryptic habitats for encrusters on the undersides of

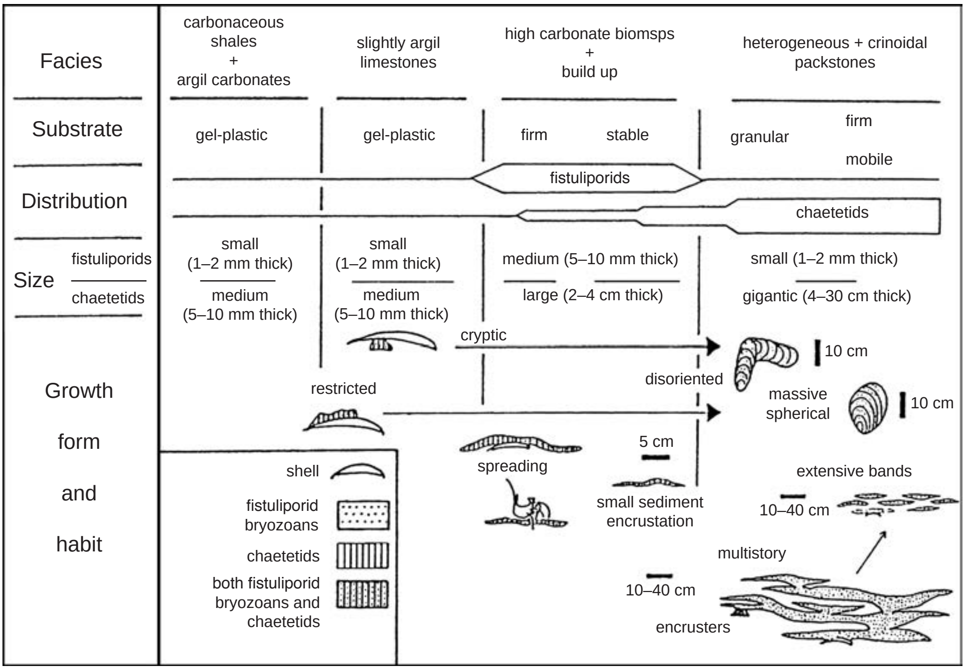

FIG. 93. Relationships between four types of substrates (gel, plastic, firm, and granular) and growth form or habit, size, distribution, and lithofacies, for chaetetids and fistuliporid bryozoans; note that both bryozoans and chaetetids occur as spreading forms in plastic to firm substrates, where competition could occur. As defined by JAMESON (1980, p. 125), a gel refers to thixotropic behavior, that is to liquefy under stress (shock) but returns to its original state after the stress is removed; plastic ideally refers to uniform deformation under stress with the resulting shape retained after the stress is removed; *argil,* argillaceous; *biomsps,* biomicrosparites (adapted from Jameson, 1980, p. 377, fig. 14.9; courtesy of University of Edinburgh).

the chaetetids (Fig. 95–96; JAMESON, 1980; SUCHY & WEST, 1988). The paleoecology of such marine hard substrate associations has been reviewed by TAYLOR and WILSON (2003).

Protecting the calcareous skeleton from the toxicity of seawater (CLARK, 1976) and possibly deterring encrusting epibiota is a thin organic layer, the basal layer (or epitheca) in extant hypercalcified demosponges (HARTMAN & GOREAU, 1972). What appears to be a similar feature occurs on the basal surfaces of some fossil chaetetids (see Fig. 29). This organic basal layer is, in some members of the Demospongiae, inferred to be a collagenous glue (BROMLEY & HEINBERG, 2006). Because this basal layer is thin and only secreted along the growing margin of the base of the calcareous skeleton, it is easily removed and/or modified by physical, chemical, and/or biological activity. One such modification can be by associated invertebrates that attach to any exposed areas of the basal layer. Such cryptic niches may be ephemeral because of the ease with which they can become filled by available sediment.

BIOLOGICAL FACTORS

Finding a place to attach in habitats where physical and chemical conditions are favorable is the first of many biological interactions involving chaetetids. Competition for a place on the seabed, where space is commonly limited, can result in competitive interactions. Available substrate is commonly very limited and competition for it intense. In the photic zone, perhaps the most likely spatial competitor of fossil chaetetids were algae. CANDELAS and CANDELAS (1963) and

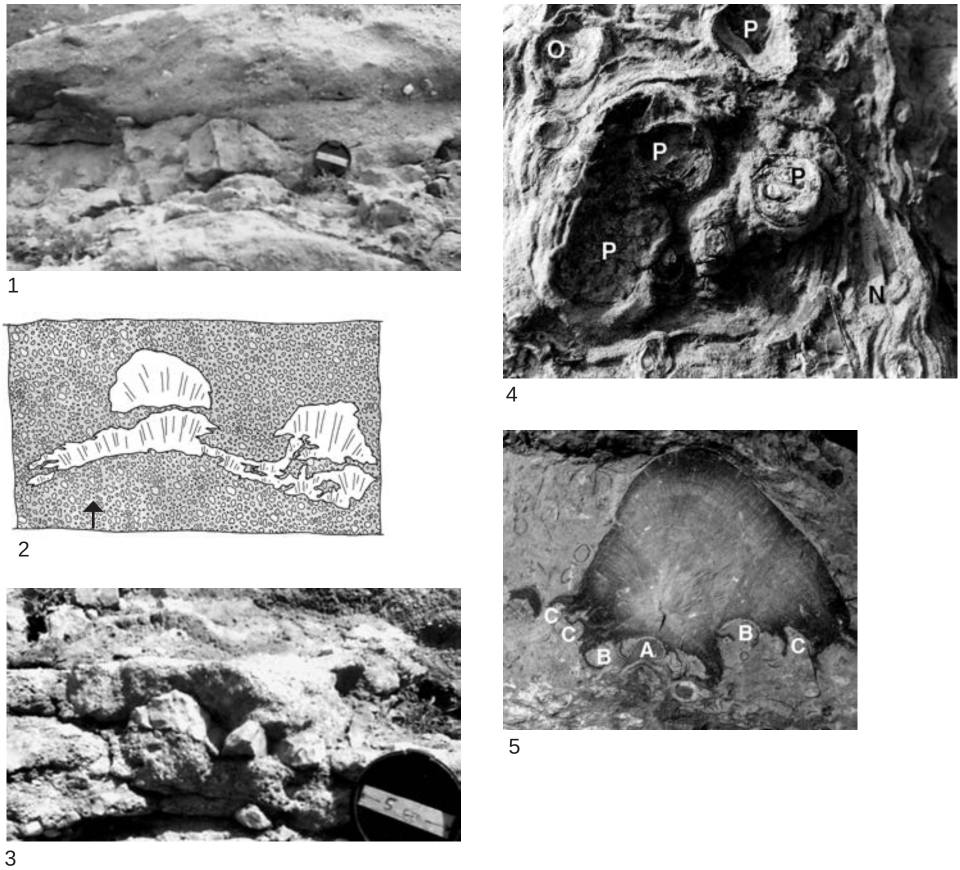

FIG. 94. Substrates and relationships, Carboniferous, Pennsylvanian; *1,* laminar to low domical chaetetids on an arkose substrate, Resolution Member, Minturn Formation, Resolution Mountain near Camp Hale, Eagle County, Colorado, ×0.09 (West, 2012b); *2,* interpretative sketch of view *1;* note the separation (fission) into two low domical chaetetids, *arrow,* stratigraphic up direction, ×0.09 (West, 2012b); *3,* closer view of low domical and laminar chaetetids on an arkose substrate, Resolution Member, Minturn Formation, Resolution Mountain, Camp Hale, Eagle County, Colorado, ×0.14 (West, 2012b); *4,* base of large domical chaetetids, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, showing initiation of chaetetid growth on brachiopod shells (*P,* productids, *N, Neospirifera*) and oncoids (*O*) that later merged (fused) and spread outward over a loose grained substrate, forming a large domical chaetetid, ×0.3 (West, 2012b); *5,* polished vertical section of a domical chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, that began on a productid brachiopod valve (*A*) and then grew outward and upward, incorporating other brachiopod valves and oncoids (*B*), creating overhangs or cavities (*C*) on a substrate of loose sediment, ×0.16 (adapted from Voegeli, 1992, p. 141, fig. 32; courtesy of the author and Kansas State University).

RÜTZLER (1965) have suggested spatial competition between algae and some extant demosponges (*sensu lato*). However, PRECIADO and MALDONADO (2005), who examined spatial competition between sponges and macroalgae in a rocky subtidal environment, concluded that environmental factors, other than the presence of algae, determined the location for sponges in that environment. The holdfasts of some algae provided a suitable substrate for some sponges (PRECIADO & MALDONADO, 2005, p. 149).

The association of fossil chaetetids with phylloid and other algae indicates that spatial competition between them may have existed in some environments in the past. A favorable environment may also lead to

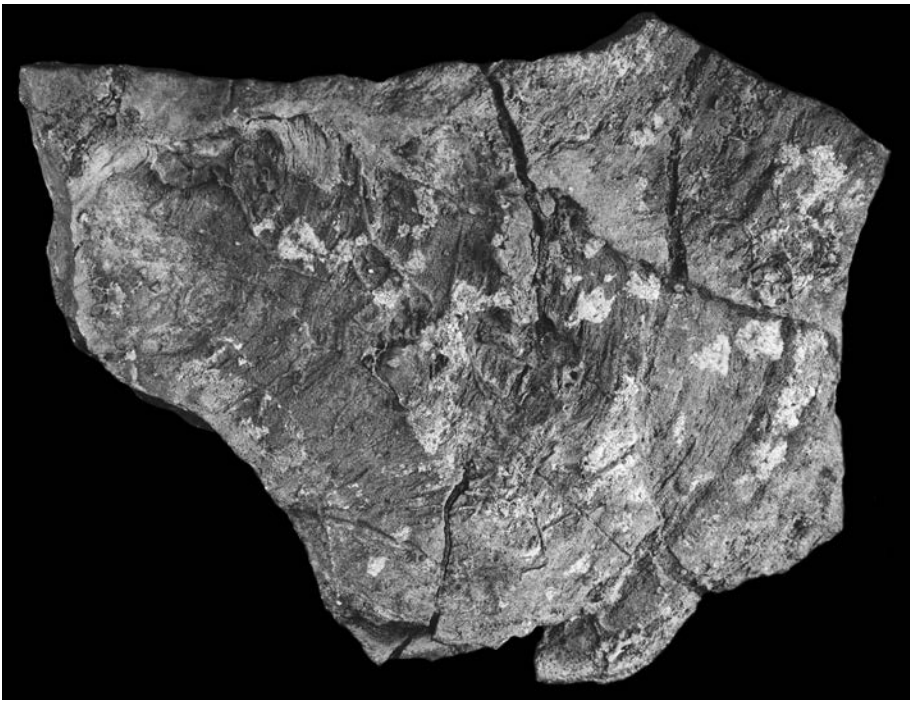

FIG. 95. Cryptic biota on part of the lower surface, the underside, of a laminar chaetetid, Carboniferous, Pennsylvanian, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, ×0.7 (adapted from Suchy & West, 1988, p. 407, fig.2A; courtesy of the authors and the Society for Sedimentary Geology).

spatial competition with other, nonphotosynthesizing, sessile benthos: sponges, corals, bryozoans, cementing brachiopods and bivalves, as well as tube-building worms, such as the serpulids. These encrusting forms may themselves become substrates for chaetetids and representatives of other groups producing a vertical succession of encrusters.

FAGERSTROM and others (2000) recognized four types of live-live interactions: (1) direct aggressive (encrusting overgrowth); (2) indirect-passive (depriving others of resources, such as sunlight by growing above them); (3) stand-offs (avoidance by minimizing contact); and (4) overwhelming (one volumetrically or numerically overwhelms the other). It is difficult, commonly impossible, to differentiate live-live interactions from live-dead interactions in the fossil record. However, careful comparison with the results of known interactions in extant taxa of the same phylogenetic group can be useful in inferring potential live-live interactions in their fossil ancestors (FAGERSTROM & others, 2000; WEST & others, 2011). Distortion of the margins of the skeleton, and/or internal skeletal features may indicate live-live interactions. Thin, lenticular skeletal margins and associated skeletal distortion suggest live-live competition (Fig. 97–100). When skeletal distortion is lacking, the association may be that of a live chaetetid growing on and/or over a dead skeleton; however a live-live relationship cannot be ruled out (Fig. 99.2; see also HARTMAN, 1984, fig. 12). What have been interpreted as live-live stand-offs, presumably because of genetic differences, also occur in fossil chaetetids (Fig. 100; FAGERSTROM & others, 2000).

Other types of live-live interactions between clonal marine invertebrates are fission and fusion. WEST and others (2010) and FAGERSTROM and WEST (2011) recognized three types of fusion in clonal

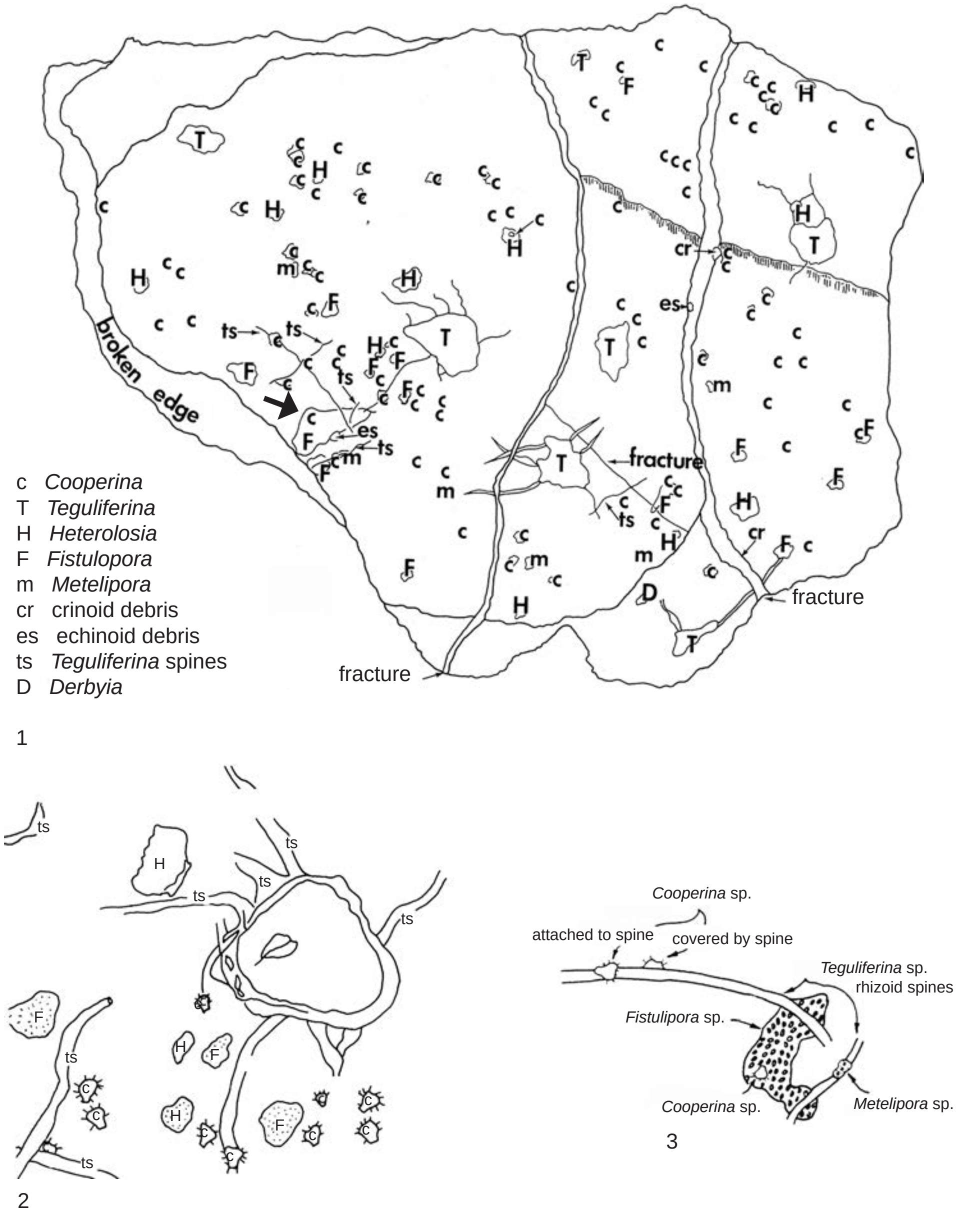

FIG. 96. Laminar chaetetid and cryptic biota; *1,* map of Figure 95 showing the location and identity of the cryptic biota. Because of their small size, the location of worm tubes, *Spirorbis,* and foraminiferid *Tetrataxis* are omitted, ×0.8 (adapted from Suchy & West, 1988, p. 407, fig. 2B; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline); *2,* detail map of the area around the large brachiopod *Teguliferina* (*T*) specimen, just left of center in view *1,* letter designation for taxa are the same as in view *1,* ×1.85 (West, 2012b); *3,* generalized sketch of the area designated by the *arrow* on left of view *1,* indicating the positions of the encrusters to each other (adapted from Suchy & West, 1988, p. 407, fig. 3; figures courtesy of the authors and the Society for Sedimentary Geology).

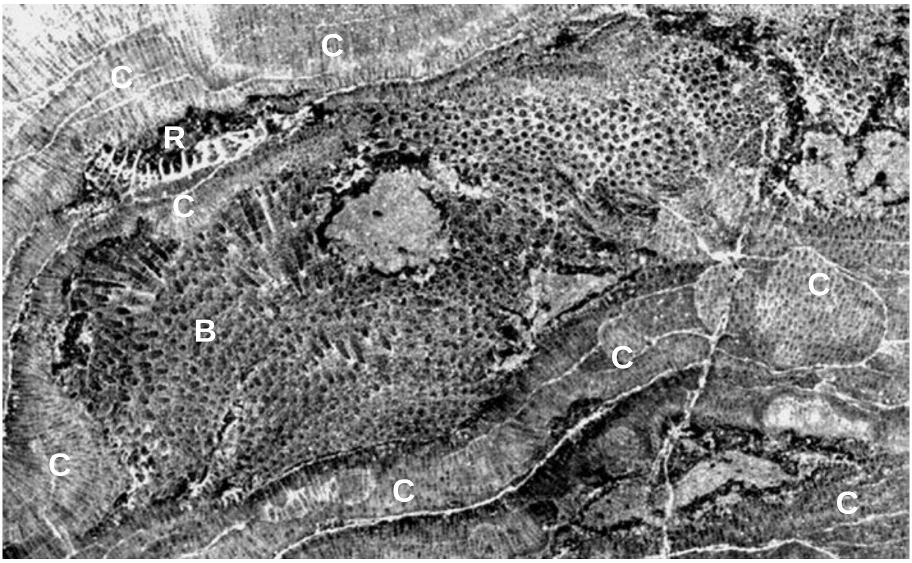

FIG. 97. Inferred live-live spatial competition between chaetetids (*C*), fistuliporid bryozoans (*B*), and a solitary rugose coral (*R*), Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×3 (West, 2012b).

invertebrates. These are: (1) interclone fusion of two or more clones, each grown from its own larva; (2) intraclone fusion among parts of the same clone, having its origin from one larva (including recovery from partial degradation, self-overgrowth, and branch fusion); and (3) quasifusion between a live clone margin, bud, or polyp, and a dead portion (margin, stem, corallite) of the same, or a different clone. Both fission and fusion have been recognized in fossil chaetetids (Fig. 101). Another example of fission is shown in Figure 94.1–94.2. Intra-clonal fusion in fossil chaetetids is more easily recognized (Fig. 88.1, Fig. 101). Recognition of inter-clonal fusion is often more difficult, if not impossible, because it requires the identification of the points of origin of the two clones (Fig. 88.2).

Once established on the substrate, a rapid rate of expansion, i.e., rapid growth rate, is a significant advantage. The growth rates of extant hypercalcified demosponges is slow (see Functional Morphology section, p. 85–89), and, given that it was likely to be similar in fossil chaetetids, it was not much of an advantage. It is currently unknown whether extant hypercalcified demosponges and/or their fossil ancestors were equipped with allelochemicals and/or secondary metabolites that inhibited, or arrested, the growth of spatial competitors. Allelochemical deterrence is a mechanism documented for some sponges (JACKSON & BUSS, 1975; PAUL, 1992). Given the slow rate of expansion of hypercalcified demosponges, chemical deterrents would have been advantageous.

Although a succession of encrusting organisms (Fig. 102–104) may represent live-live interactions, they could also represent live-dead interactions. Death of part, or all, of a given encruster may provide a suitable substrate for the next one. *Girvanella,* a cyanobacterium, was the main colonizer in some Serpuhkovian mounds but alternated with chaetetids. The chaetetids also encrusted corals, providing a surface for subsequent attachment of corals (GÓMEZ-HERGUEDAS & RODRÍGUEZ, 2009).

A successful competitor may overwhelm an encruster (Fig. 99.2) or the encruster may die as a result of disease, predation, smothering (burial by sediment), and/or exposure (erosion). Evidence of the cause(s) of death in

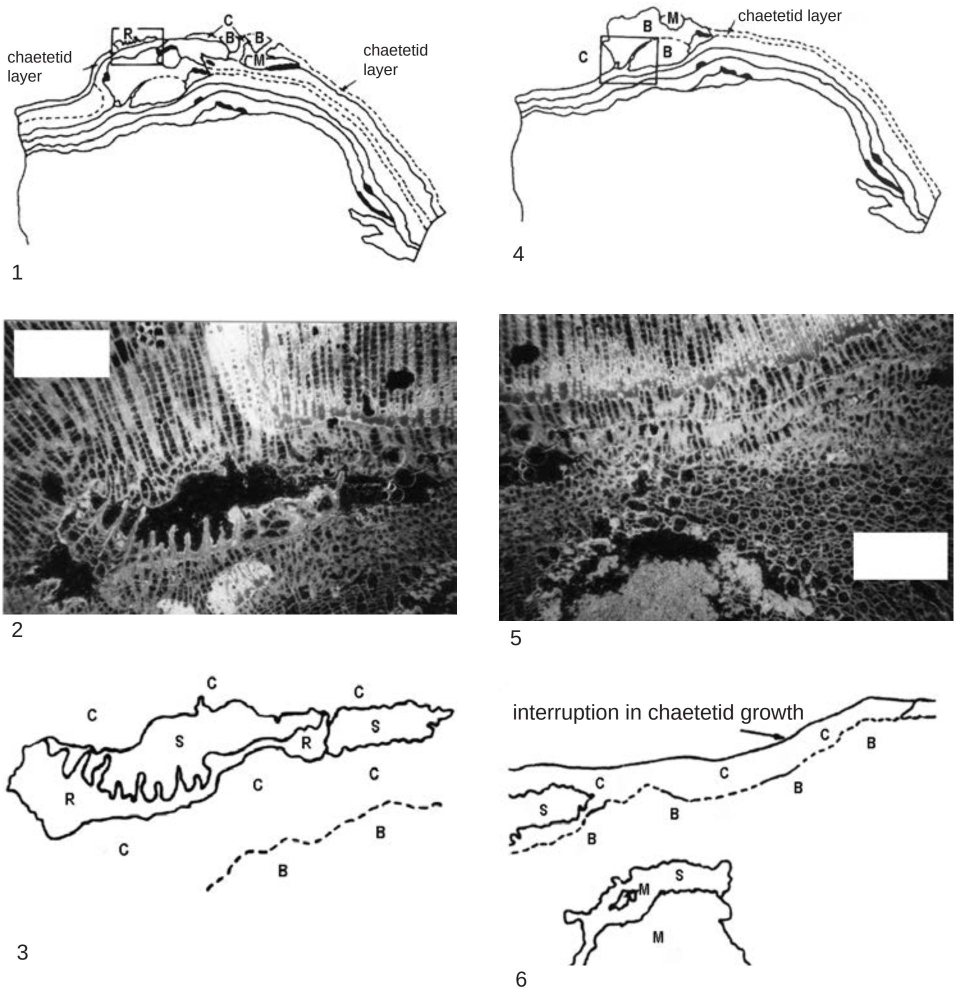

FIG. 98. Chaetetids and inferred live-live spatial competition, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; *1,* interpretative sketch of the upper part of the area in Figure 97 (*R* denotes the position of solitary rugose coral) showing the interaction between the chaetetid and the coral and the chaetetid (*C*) and the fistuliporid bryozoan (*B*); *M,* matrix×0.55 (modified from Fagerstrom & others, 2000, p. 13, fig. 2 stage V); *2,* acetate peel print of rectangular area shown in view *1;* note distortion of chaetetid tubules just below the coral and the interface between the chaetetid and fistuliporid bryozoan, ×5.25 (adapted from Fagerstrom & others, 2000, p. 9, pl. 3,*7a*); *3,* interpretative sketch of interactions in view *2,* between chaetetids (*C*), a fistuliporid bryozoan (*B*), and a solitary rugose coral (*R*); *S,* calcite spar; both the chaetetid tubules and bryozoan zooecia are distorted at the interface between them; compare with view *2* (adapted from Fagerstrom & others, 2000, p. 9, pl. 3,*7b*); *4,* interpretative sketch of area just below and slightly right of that shown in view *1,* with several layers of chaetetid and associated features removed (the two closely spaced dashed parallel lines in view *1* and view *4* denote the same areas); *C,* chaetetid; *B,* fistuliporid bryozoan; *M,* matrix, ×0.55 (adapted from Fagerstrom & others, 2000, p. 13, fig. 2, stage III); *5,* acetate peel print of rectangular area shown in view *4,* chaetetid tubules and zooecia of the fistuliporid bryozoan are distorted along the interface between them, ×5.25 (adapted from Fagerstrom & others, 2000, p. 9, pl. 3,*3a*); *6,* interpretative sketch of interactions in view *5, C,* chaetetid; *B,* fistuliporid bryozoan; *S,* calcite spar; *M,* matrix; both the chaetetid tubules and bryozoan zooecia are distorted along the interface between them; compare with view *5* (adapted from Fagerstrom & others, 2000, p. 9, pl. 3,*3b;* figures courtesy of the authors and Springer-Verlag GmbH & Co.).

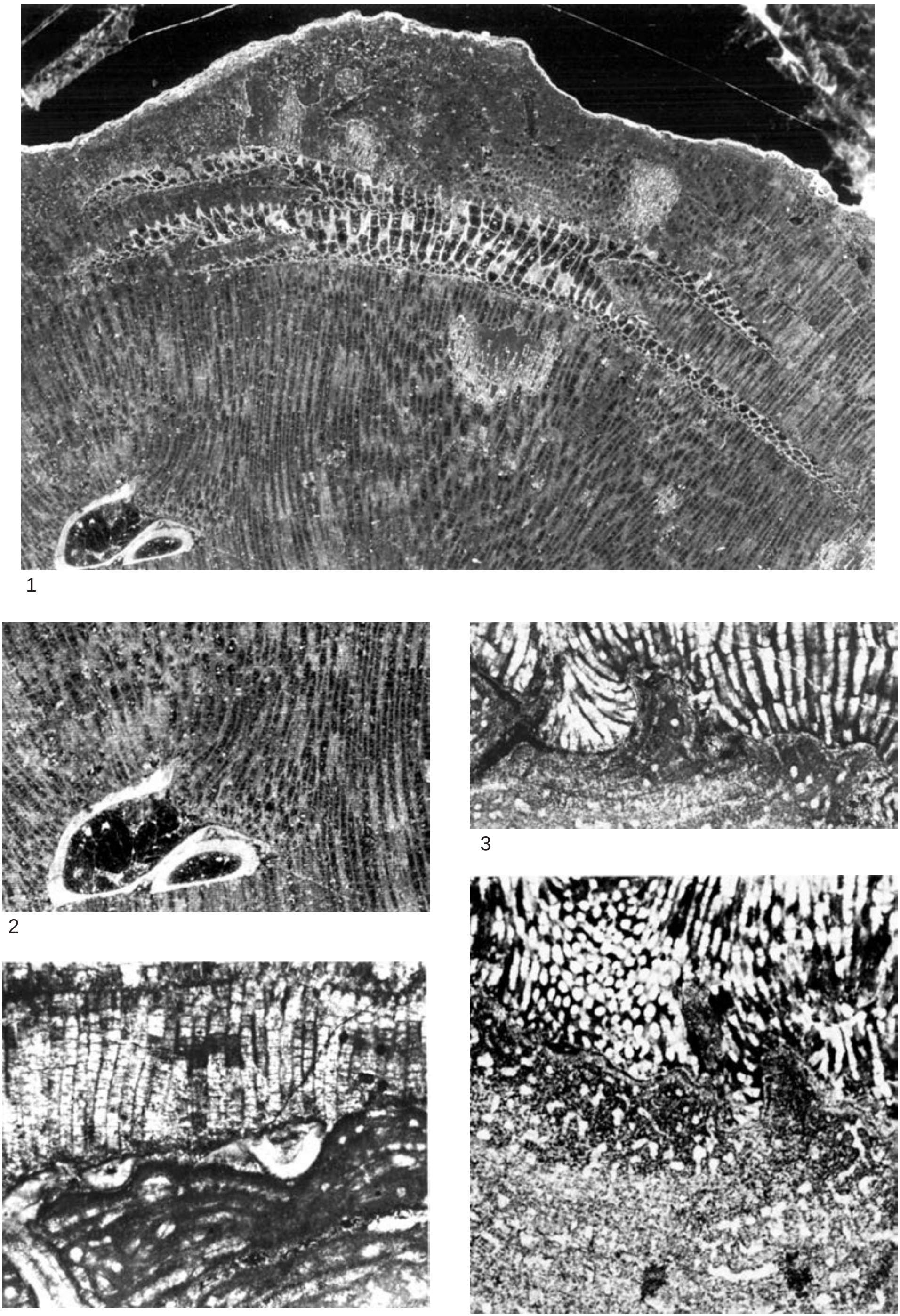

FIG. 99. *(For explanation, see facing page).*

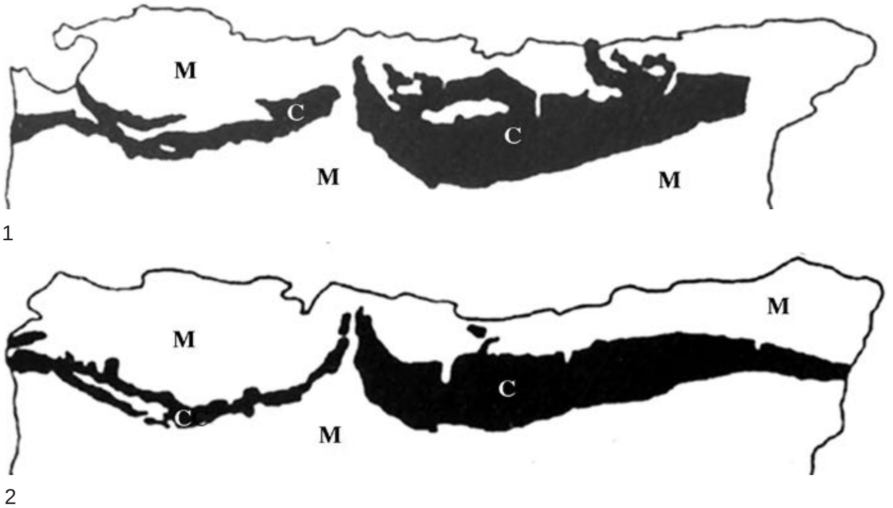

Fig. 100. Inferred live-live stand-off interaction between chaetetids; *1,* stand-off interaction between chaetetid clones (*C,* black areas), Carboniferous, Pennsylvanian, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas; *M,* matrix, ×0.5 (adapted from Fagerstrom & others, 2000, p. 12, fig. 1.D, slab 2, surface b); *2,* opposite side of stand-off interaction between chaetetid clones (*C,* black areas) in view *1,* Carboniferous, Pennsylvanian, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas; *M,* matrix (slab 2 is 2.5 cm thick), ×0.5 (adapted from Fagerstrom & others, 2000, p. 12, fig. 1.D, slab 2, surface c; figures courtesy of the authors and Springer-Verlag GmbH & Co.).

chaetetids is commonly equivocal and subject to inferences based on preserved features of the skeletal margins and internal skeletons. Interruption partings in fossil chaetetids are common and often provide some indication of death in some specimens (see Fig. 36).

The reaction of extant demosponges (*sensu lato*) to epibionts on the living surface is varied, and may: (1) be repulsive to all epibionts, or (2) allow only specific taxa as epibionts. Besides these two categories, there are species in some groups that are almost completely covered by algae, bryozoans, and/or other sponges (Topsent, 1928; Rützler, 1970). This latter condition is due to the presence of a well-developed spicular layer

Fig. 99. Inferred live-live spatial interactions between chaetetids and other encrusting benthos; *1,* negative print of a polished vertical section showing inferred live-live interaction between a chaetetid and the bryozoan *Tabulopora*?, based on the mutual distortion of skeletons, Carboniferous, Mississippian, upper Visean, Brigantian, A. Orionastraea Band, Bradwell Dale, Derbyshire, United Kingdom, ×3.6 (adapted from Fagerstrom & others, 2000, pl. 4,*1;* courtesy of the authors and Springer-Verlag GmbH & Co.); *2,* negative print of an enlarged view of area in the lower left corner of view *1,* inferred as chaetetid overwhelming the spirorbid tube, ×9 (modified from Fagerstrom & others, 2000, p. 9, pl. 3,*8;* courtesy of the authors and Springer-Verlag GmbH & Co.); *3,* inferred live-live interaction based on the skeletal distortion at the interface between a chaetetid and the stromatoporoid *Salairella,* Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia, with the chaetetid progressively overwhelming the stromatoporoid, ×8 (adapted from Zhen & West, 1997, p. 275, fig. 3.E; courtesy of the authors and *Alcheringa*); *4,* distorted final growth surface of the stromatoporoid *Salairella* in an inferred live-live interaction with the overlying chaetetid, Middle Devonian, Givetian, Burdekin Formation, northern Queensland, Australia, ×10 (adapted from Zhen & West, 1997, p. 275, fig. 3.D; courtesy of the authors and *Alcheringa*); *5,* basal layer of a chaetetid encrusting tabulate corals that had encrusted the stromatoporoid, a possible live-live interaction between the three taxa, Middle Devonian, Givetian, Burdelin Formation, Regan's Quarry, Reid Gap, northern Queensland, Australia, ×8 (adapted from Zhen & West, 1997, p. 276, fig. 4.A; courtesy of the authors and *Alcheringa*).

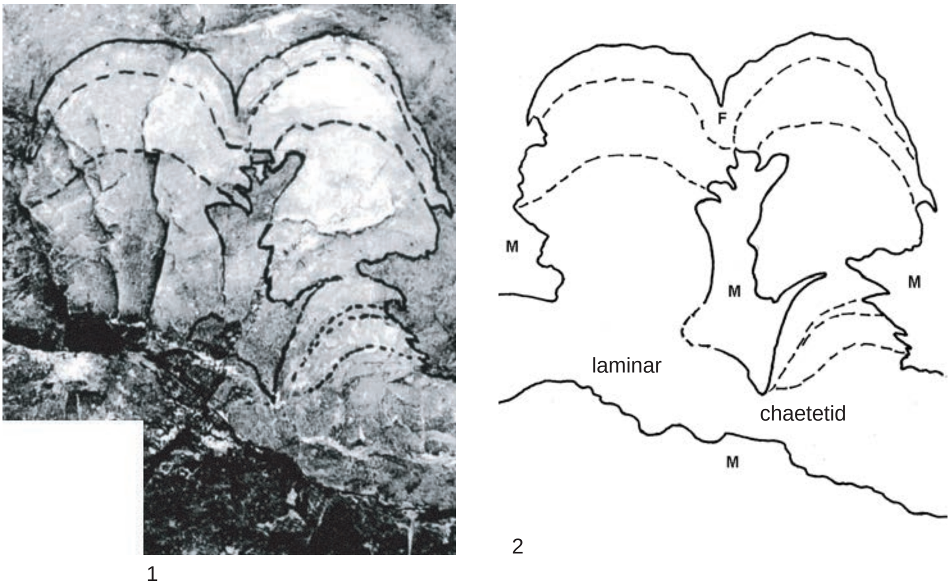

FIG. 101. Fusion and rejuvenation in chaetetids; *1,* fission and fusion in a chaetetid that began as a laminar form, followed by fission and growth into two columnar chaetetids with ragged margins (*dashed lines* are interruption partings) that fused, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.15 (West, 2012b); *2,* interpretive sketch of view *1; M,* matrix; *F,* plane of fusion, ×0.15 (West, 2012b).

that covers all but specialized inhalant areas and serves as an available substrate; such camouflage may provide some degree of protection (SARA & VACELET, 1973).

Serpulid polychaetes, zoanthideans (soft corals), scleractinian corals, clinoid and other sponges, barnacles, brachiopods, and gastropods are considered to be animal symbionts and are associated with the extant hypercalcified demosponges *Ceratoporella nicholsoni* and *Astrosclera willeyana* (HARTMAN, 1984; see also the previous discussion of chimneys, p. 93–96). Such associations occur during the life of the hypercalcified demosponges (HARTMAN, 1984, fig. 12–18), but may also occur after death of part, or all, of the living surface of the sponge. Because extant hypercalcified demosponges die back locally and then overgrow the same area later, they provide unique opportunities for other encrusting organisms (HARTMAN, 1984, p. 312). Very small holes (0.5 to 1.0 mm in diameter) in live *Acanthochaetetes* sp. collected from the shallow waters off the Komesu coast in Okinawa may be the

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FIG. 102. Associated encrusters and successive overgrowths, Carboniferous, Pennsylvanian; *1,* interpretative sketch of the polished surface of a slab, Akiyoshi Limestone, Akiyoshi-dai, Japan, showing associated encrusters and successive overgrowths, ×0.35 (adapted from Sugiyama & Nagai, 1990, p. 20, fig. 7; courtesy of the authors and Akiyoshi-dai Museum of Natural History; for a color version, see *Treatise Online,* Number 36: paleo.ku.edu/treatiseonline); *2,* vertical section of a laminar to low domical chaetetid that was overgrown by *Multithecopora*, a tabulate coral, that subsequently was overgrown by a laminar chaetetid, followed by successive layers of skeletal mud (matrix) and laminar chaetetids, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.3 (West, 2012b); *3,* weathered vertical section of a laminar chaetetid overgrown by a dome-shaped mass of *Multithecopora*, a tabulate coral, that was subsequently overgrown by a low domical chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; *Ch,* chaetetid; *Co,* tabulate coral, ×0.14 (West, 2012b); *4,* transverse thin section of a solitary rugose coral encrusted initially by a thin algal-microbial mat that was subsequently completely encrusted by a chaetetid, Blackjack Creek Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×1.7 (West, 2012b).

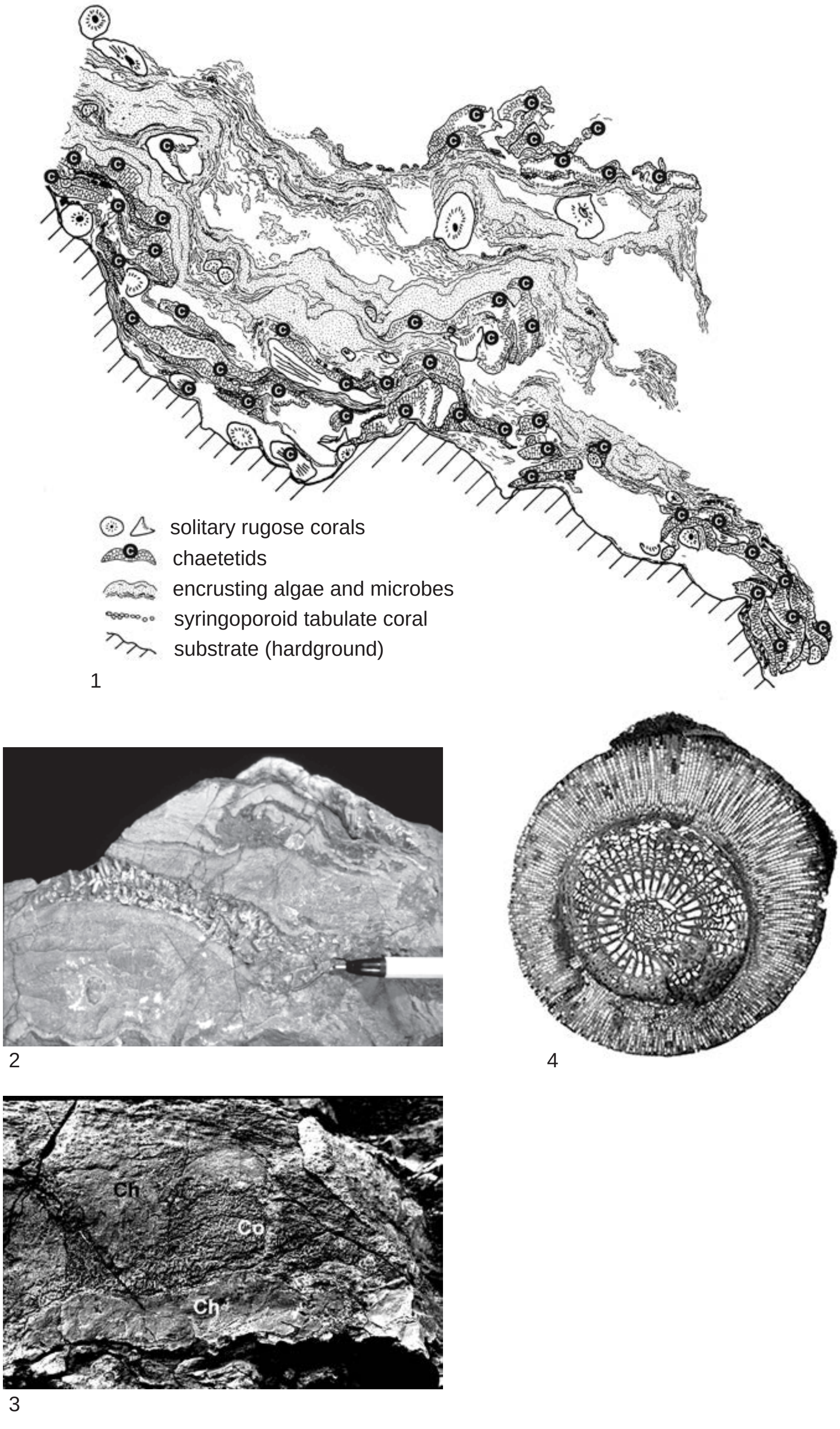


FIG. 102. *(For explanation, see facing page).*

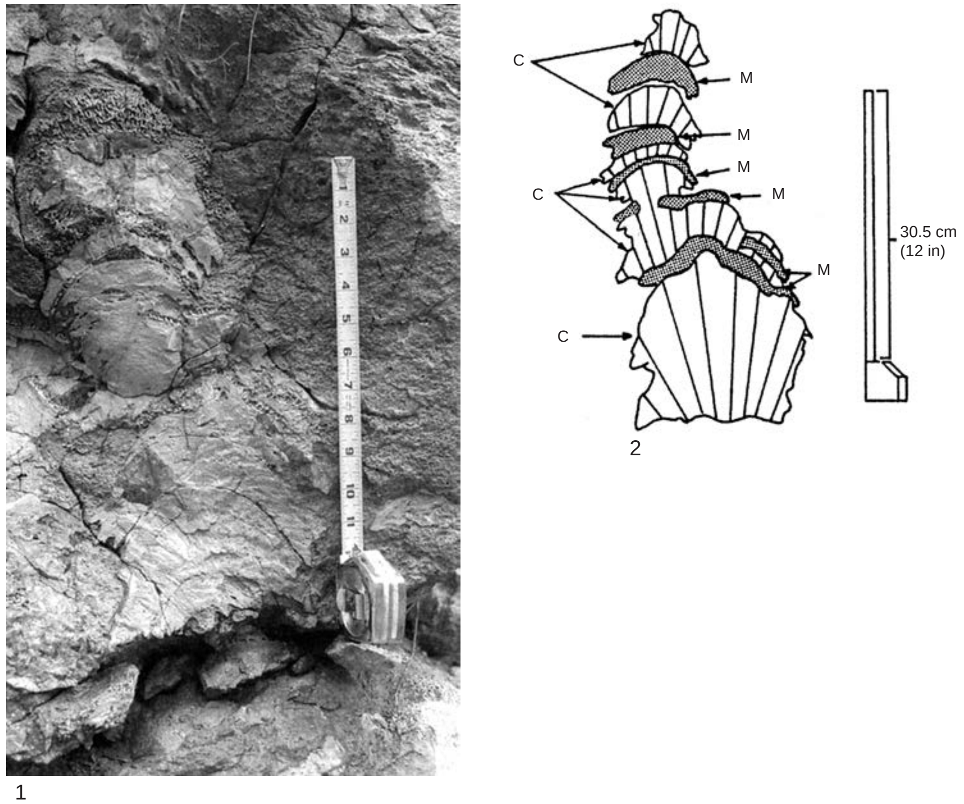


FIG. 103. Further examples of associated encrusters and successive overgrowths; *1,* weathered vertical surface of a succession of chaetetid and *Multithecopora* overgrowths in a fusulinid packstone, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.17; *2,* interpretative sketch of view *1, C,* chaetetid, *M, Multithecopora,* ×0.12 (adapted from Suchy & West, 2001, p. 438, fig. 11C; courtesy of the authors and the Society for Sedimentary Geology).

FIG. 104. Successive events preserved in a low domical chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; *1,* complex history of a low domical chaetetid revealed by a series of laminar chaetetids interrupted by sediment influx and other encrusters (algal-microbial mats) and boring organisms, ×0.6 (adapted from Mathewson, 1977, p. 142 pl. 5,*1;* courtesy of the author and Kansas State University); *2,* enlarged view of the incorporated oncoid in the lower left of view *1;* note that the oncoid has been rotated 180° relative to its orientation in view *1*; initially a brachiopod valve was encrusted by an algal-microbial mat that was subsequently bored and then encrusted by a laminar chaetetid, ×1.4; *3,* enlarged view of the upper left quarter of view *2,* showing the sequence as reported for view *2,* bored algal-microbial encrustation on the brachiopod valve followed by a laminar chaetetid, a thin layer of micrite (sediment on the right) and then another laminar chaetetid, ×2.6; *4,* enlarged view of the upper right quarter of view *2,* showing the borings in the algal-microbal encrustation on the brachiopod valve, ×3 (West, 2012b).

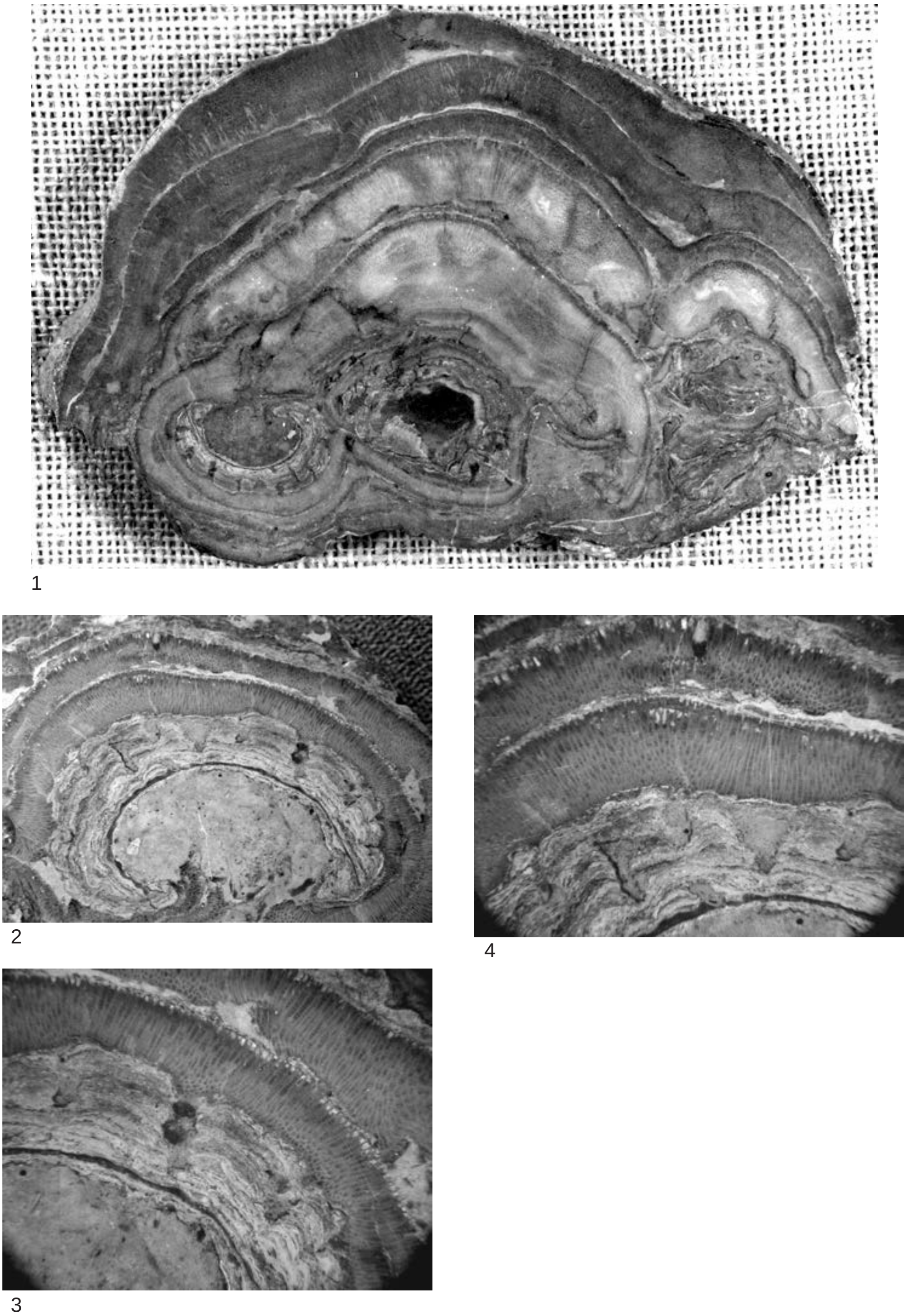


FIG. 104. *(For explanation, see facing page).*

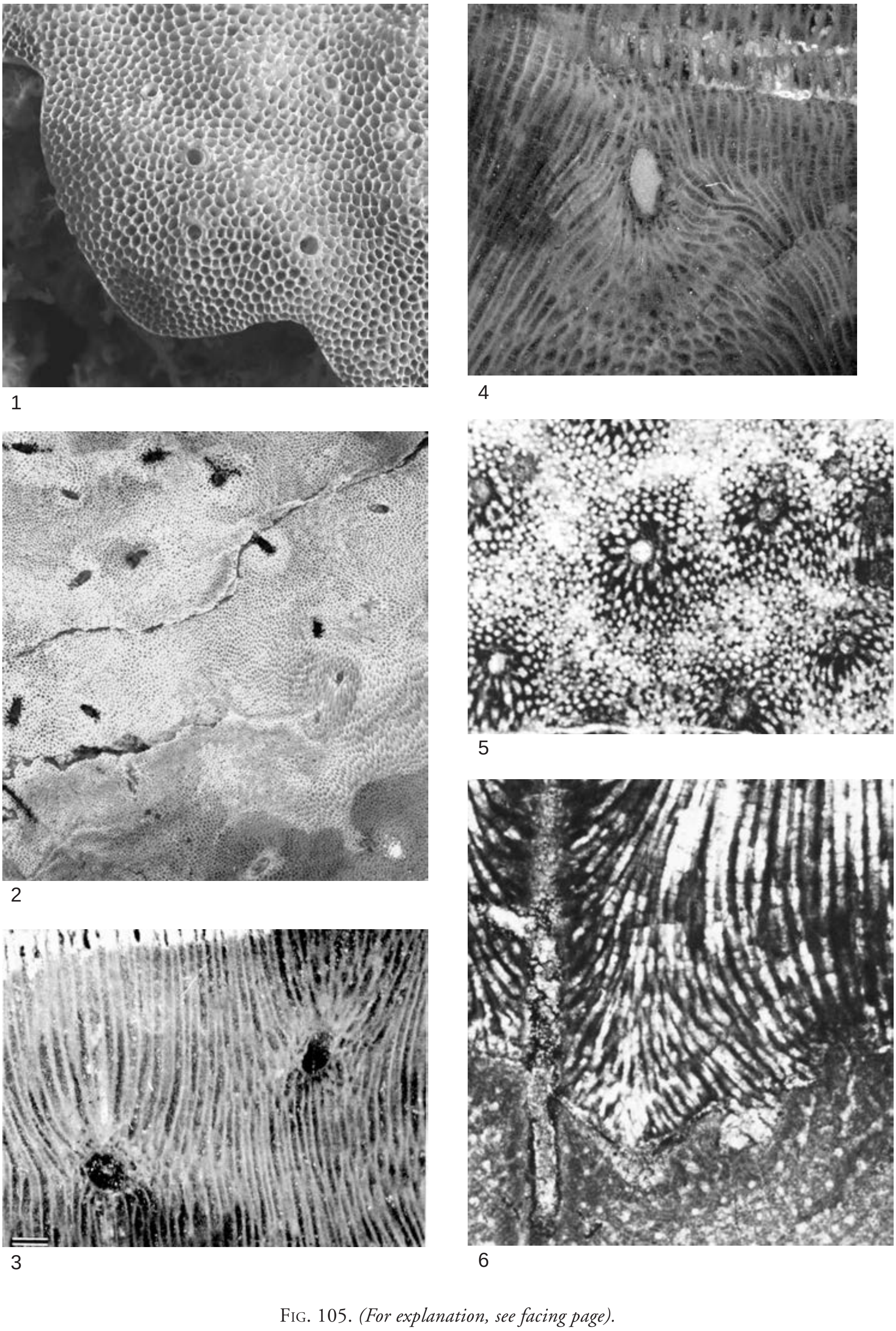


FIG. 105. *(For explanation, see facing page).*

result of polychaete worms, zoanthideans (soft corals), or clinoid (excavating) sponges (Fig. 105.1). It is difficult to determine in fossil chaetetids whether any epibionts occupied the skeleton during life or invaded it after death. However, distortion of the tubules, rather than truncated tubules, suggests that some live-live disturbance was responsible for the distortion of the tubules. Distortion of tubules in a Carboniferous chaetetid has been attributed to an association with a so-called parasitic organism described as *Streptindytes chaetetiae* (OKULITCH, 1936a). BERTRAND and others (1993) described sinuous openings in the calcareous skeleton of a Devonian chaetetid as *Trypanopora* and *Torquaysalpinx*. All three of these genera were attributed to the activity of worms. Based on the distortion of tubules associated with holes in some chaetetid specimens, as illustrated by OKULITCH (1936a), WEST and CLARK (1983), and ZHEN and WEST (1997), it is suggested that worms also invaded some Devonian and Carboniferous (Pennsylvanian) chaetetids (Fig. 105.2–105.6). Similar tubelike features have been reported in tabulate corals and are considered to be evidence of parasitism rather than commensalism (ZAPALSKI, 2007).

Unlike specimens with distorted tubules, there are openings in the calcareous skeleton of chaetetids that, based on their shape in plan view, and/or the orientation of the truncation of their tubules, suggest the activity of boring organisms (Fig. 106.1–106.3). These features have been referred to as *Trypanites* (DEVRIES, 1955; MATHEWSON, 1977). DEVRIES (1955) illustrated other features that WEST and CLARK (1983, 1984) suggested might be *Caulostrepsis*, and others as either *Rogerella* or *Zapfella*. *Trypanites* and *Caulostrepsis* (Fig. 106.2) are inferred to be worm borings: a polychaete and *Polypora*-type worm, respectively; *Rogerella* and *Zapfella* are the borings of acrothoracican barnacles (Fig. 106.3; WEST & CLARK, 1984). Acrothoracican borings have also been recognized in ?*Coelocladiella*, a fossil demosponge (GUNDRUM, 1979). Shapes similar to inferred acrothoracican barnacle borings also occur in living specimens of *Acanthochaetetes* sp. (Fig. 106.4). Openings in some living specimens of *Acanthochaetetes* sp. clearly truncate the tubules, indicating invasion of a boring organism during the life of the chaetetid (Fig. 106.5–106.6).

Compared with other reefs, both fossil and Holocene, the diversity of chaetetid reef mounds is low; however, other sessile and free living suspension-feeders, as well as vagrant deposit feeders, and nektic invertebrates occur with them (Table 25). Data in this table represents a detailed study of one limestone member at four different geographic localities. Obviously, only recognized, preserved taxa are included, and thus, it is biased, but it is a reasonable estimate of the diversity and relative density of invertebrates associated with this Carboniferous (Pennsylvanian) chaetetid reef mound. Based on the data in Table 25 (foraminiferids are omitted from

FIG. 105. Inferred worm tubes in chaetetid skeletons; *1,* upper surface of an extant specimen of *Acanthochaetetes* sp., showing small openings that could have been produced by polychaetes, zoanthideans, and/or clinoid sponges; collected live off the Komesu coast, southern Okinawa, Japan at a water depth of 16 m, ×3 (West, 2012b); *2,* inferred worm tubes and/or possible borings in the upper surface of a chaetetid skeleton, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×7.5 (West, 2012b); *3,* polished vertical section of inferred worm tubes in a chaetetid skeleton, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; note distortion of tubules adjacent to the spar-filled holes, ×5 (adapted from West & Clark, 1984, p. 343, pl. 2,*F;* courtesy of the authors and the Paleontological Research Institution, Ithaca, New York); *4,* polished oblique section of an inferred worm tube in a chaetetid skeleton, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; note the distorted tubules adjacent to the micrite-filled hole, ×5.3 (West, 2012b); *5,* transverse thin section of inferred worm tubes in a chaetetid skeleton, Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia; note the distortion of tubules adjacent to the spar-filled holes, ×7.5 (adapted from Zhen & West, 1997, p. 276, fig. 4C; courtesy of the authors and *Alcheringa*); *6,* longitudinal thin section of an inferred worm tube that extends from the skeleton of the stromatoporoid *Salairella* into the skeleton of the chaetetid, Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia; note distortion of both skeletons, ×10 (adapted from Zhen & West, 1997, p. 275, fig. 3C; courtesy of the authors and *Alcheringa*).

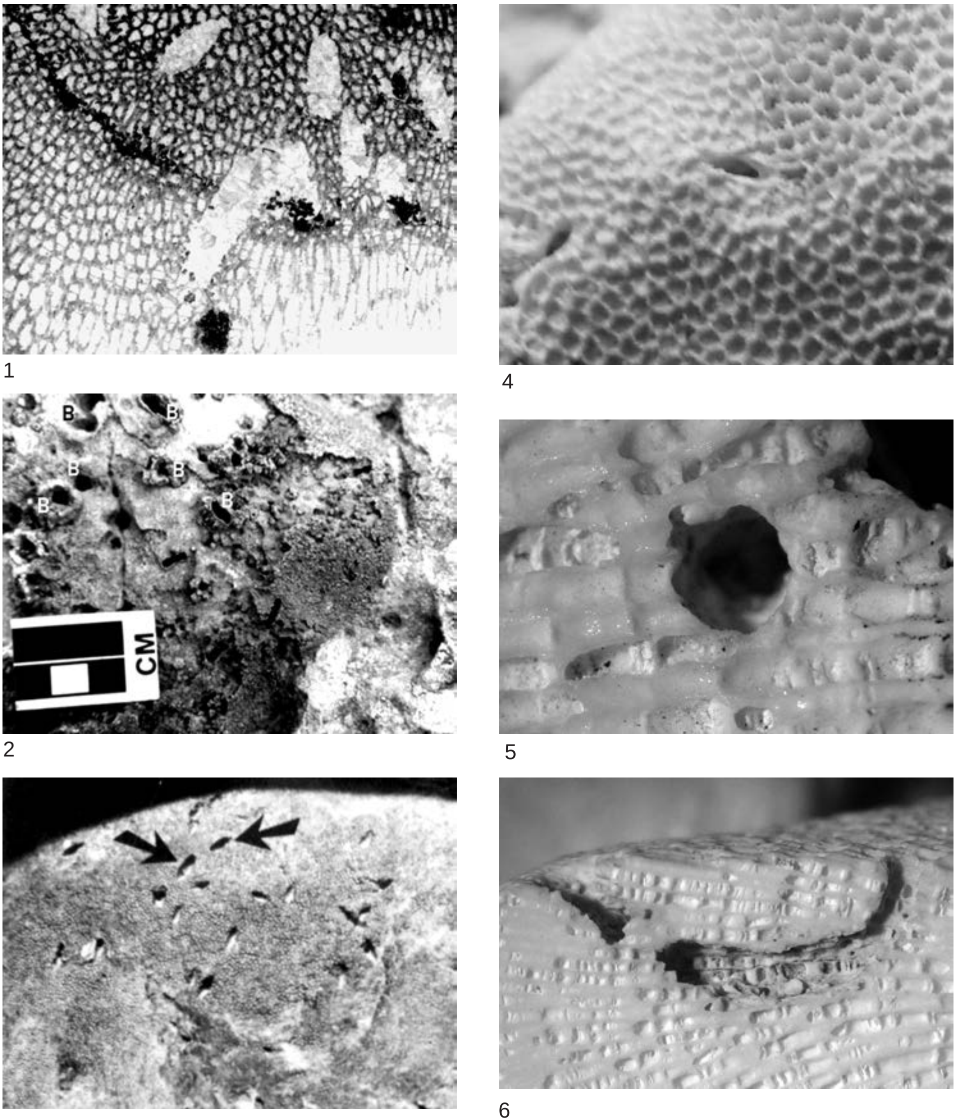


Fig. 106. Inferred borings in chaetetid skeletons; *1,* Transverse to oblique thin section of chaetetid from the Carboniferous, Pennsylvanian, Piedraslungas Limestone, Piedraslungas, Cantabrian Mountains, Spain; note the lack of tubule distortion adjacent to the spar-filled holes, ×6 (adapted from Minwegen, 2001, p. 137, pl. 17,*2;* courtesy of the author and Kölner Forum für Geologie und Paläontologie); *2,* weathered and partially silicified upper surface of a domical chaetetid with holes, designated with five *white* and one *black B*, similar to those described as *Trypanites* and *Caulostrepsis*, Carboniferous, Pennsylvanian, Blackjack Creek Limestone Member, Fort Scott Limestone, Crawford County, Kansas, scale in cm and inches (West, 2012b); *3,* upper surface of a domical chaetetid with teardrop-shaped holes (*black arrows*) interpreted as acrothoracican barnacle borings (*Rogerella* or *Zapfella*), Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×1.5 (adapted from Mathewson, 1977, p. 148, pl. 8,*1;* courtesy of the author and Kansas State University); *4,* upper surface of an extant specimen of *Acanthochaetetes* sp. with tear-drop openings suggestive of borings; collected live off the Komesu coast, southern Okinawa, Japan, at a water depth of 15 m, ×7 (West, 2012b); *5,* upper surface of an extant specimen of *Acanthochaetetes* sp. with a round opening suggestive of a boring; collected from off the Komesu coast, southern Okinawa; note that there is no distortion of the tubules, ×17 (West, 2012b); *6,* longitudinal section through an inferred boring in an extant specimen of *Acanthochaetetes* sp. from off the Komesu coast, southern Okinawa; note that there is no distortion of the tubules, ×3.7 (West, 2012b).

TABLE 25. Invertebrates associated with chaetetid reef mounds. The first letter in hyphenated entries refers to whether it is epifanual (*E*) or infaunal (*I*), the second letter indicates whether it is attached (*A*), free-living (*F*), vagrant (*V*), or nektic (*N*), and the third letter indicates whether it was a suspension (*S*) feeder, deposit (*D*) feeder, or carnivore (*C*); *slashes* indicate that the entity had two or three mode of mobility and/or feeding; question marks indicate that the feeding type is questionable (adapted from Voegeli, 1992, table 1, p. 153).

Organisms	Inferred ecological niche	Conspicuous	Present
Phylloid Algae	P	X	
Algal-microbial mats	P	X	
Foraminiferids			
Fusulinids	E-F-D?	X	
Tetrataxis	E-A-S?		X
Globovalvulina	E-F-D?		X
Endothyra	E-F-D?		X
Sponges			
Girtyocoelia	E-A-S		X
Corals			
Lophophylidium	E-A-S		X
Multithecopora	E-A-S		X
Bryozoans	E-A-S		X
Brachiopods			
Composita	E-A-S	X	
Crurithyris	E-A-S		X
Hustedia	E-A-S		X
Lingula	I-A-S		X
Mesolobus	E-F-S		X
Neochonetes	E-F-S		X
Neospirifera	E-F-S		X
Productids	E-A/F-S	X	
Mollusks			
Bivalves			
Aviculopecten	E-F-S		X
Edmondia	E-F-S		X
Gastropods			
Bellerophontids	E-V-D		X
Low-spired	E-V-D/C		X
High-spired	E-V-D/C		X
Omphaiotrocus	E-V-D		X
Straparollus	E-V-D		X
Cephalopods	E-N-C		X
Worm tubes	I-A-S		X
Arthropods			
Ostracodes	E/I-V/N-D/C	X	
Trilobites	E-V-D/C		X
Barnacle borings	I-A-S	X	
Echinoderms			
Crinoids	E-A-S	X	X
Echinoids	E-V-D/C		

the following percentage calculations because their ecological niche is queried), 23 of 26 taxa (88%) are epifaunal, 17 of 26 (65%) are attached or free living, and 17 of 26 (65%) are suspension feeders.

The association with such a high percentage of other suspension feeding invertebrates may be related, in part, to the availability and usefulness of available organic matter and nutrients in the environment. Some extant demosponges (*sensu lato*) use the very fine fraction of available organics that is poorly used by other filter (suspension) feeders (SARA & VACELET,

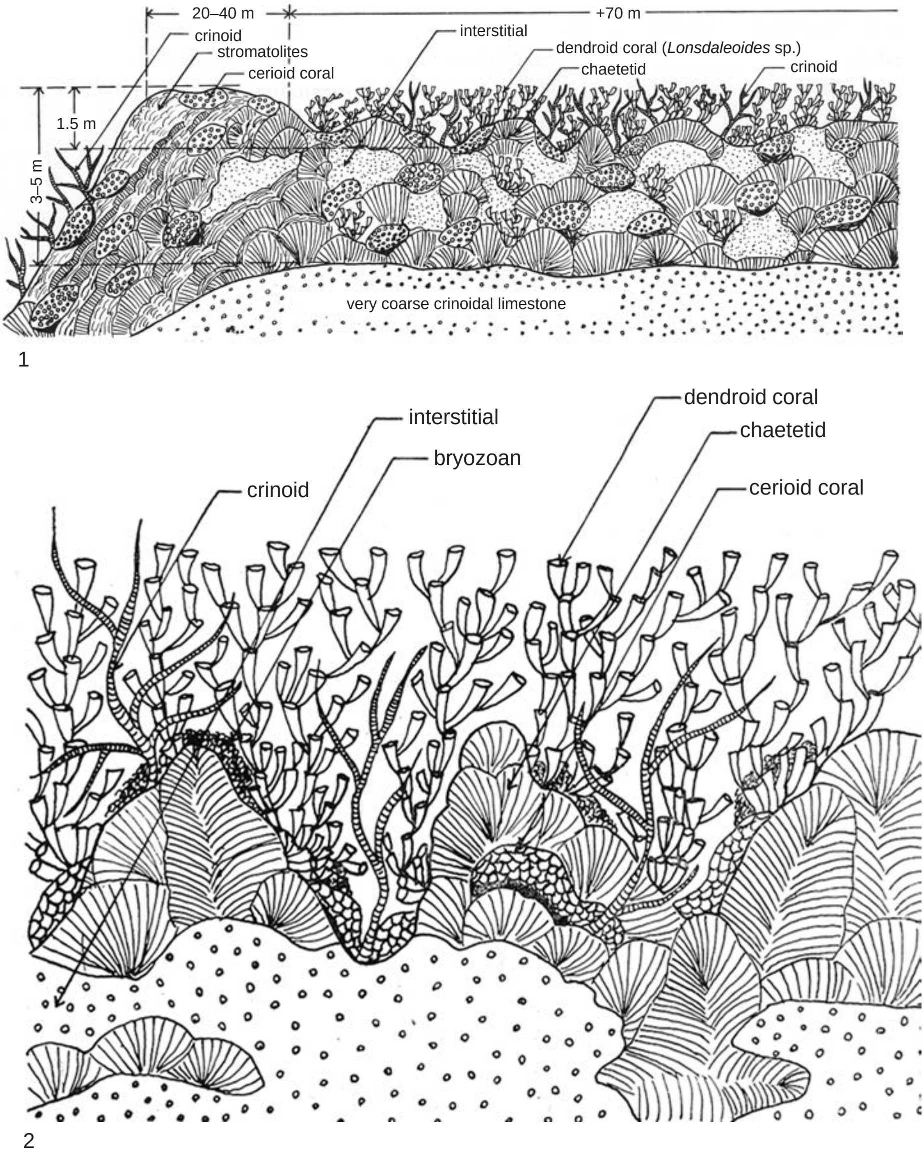


FIG. 107. Schematic diagrams of the reef mound at the Sumitomo quarry, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* relationship between chaetetids, associated sessile suspension feeders, and interstitial sediment on a very coarse clastic crinoidal substrate, ×0.005 (adapted from Ota, 1968, p. 31, fig. 12); *2,* detailed schematic diagram of part of view *1* (adapted from Ota, 1968, p. 31, fig. 13, in part; figures courtesy of the author and Akiyoshi-dai Museum of Natural History).

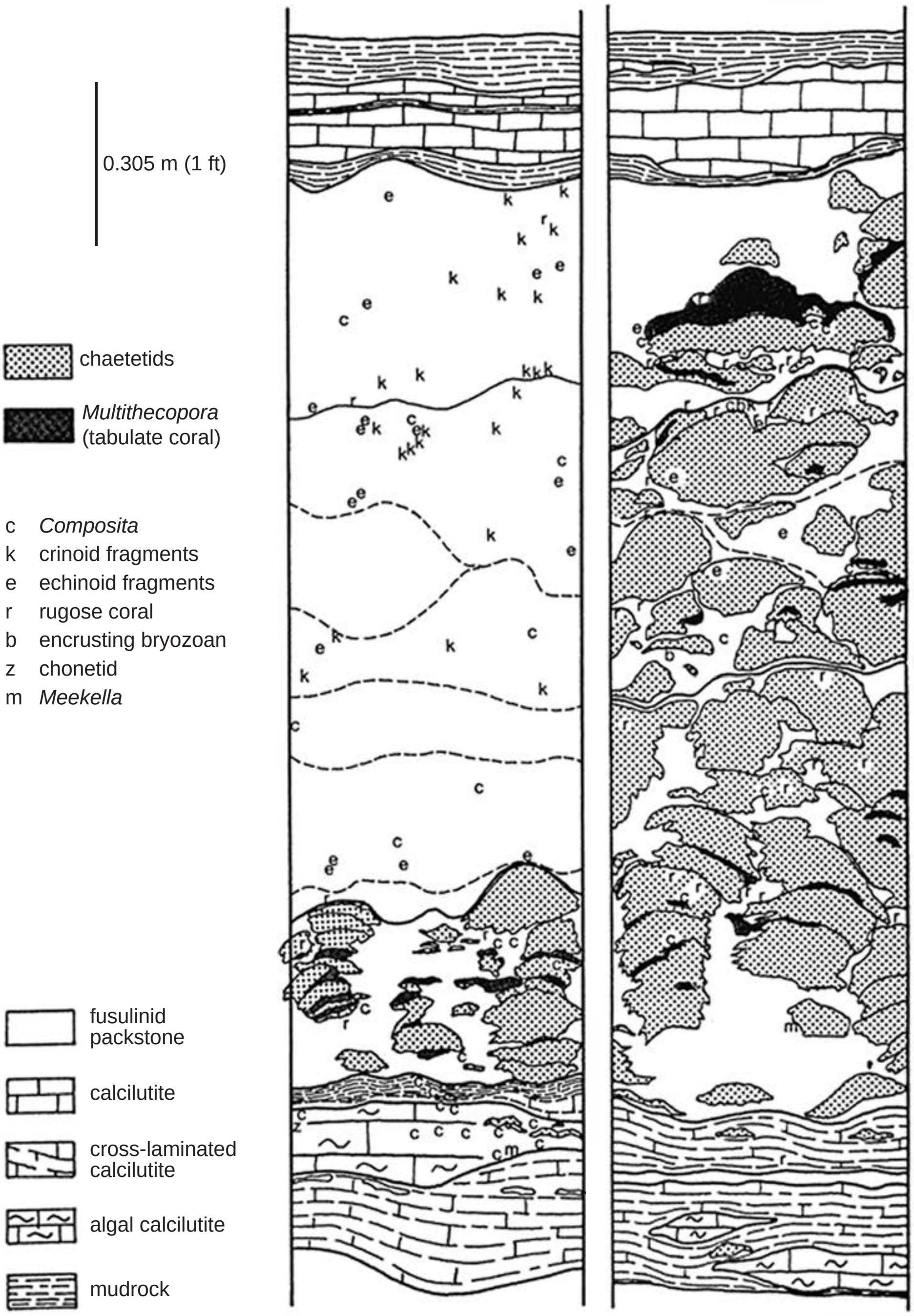


FIG. 108. Interpretative diagram of chaetetids, associated organisms, and lithologies at two different vertical sequences in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas (adapted from Suchy & West, 2001, p. 440, fig. 12; courtesy of the authors and the Society for Sedimentary Geology).

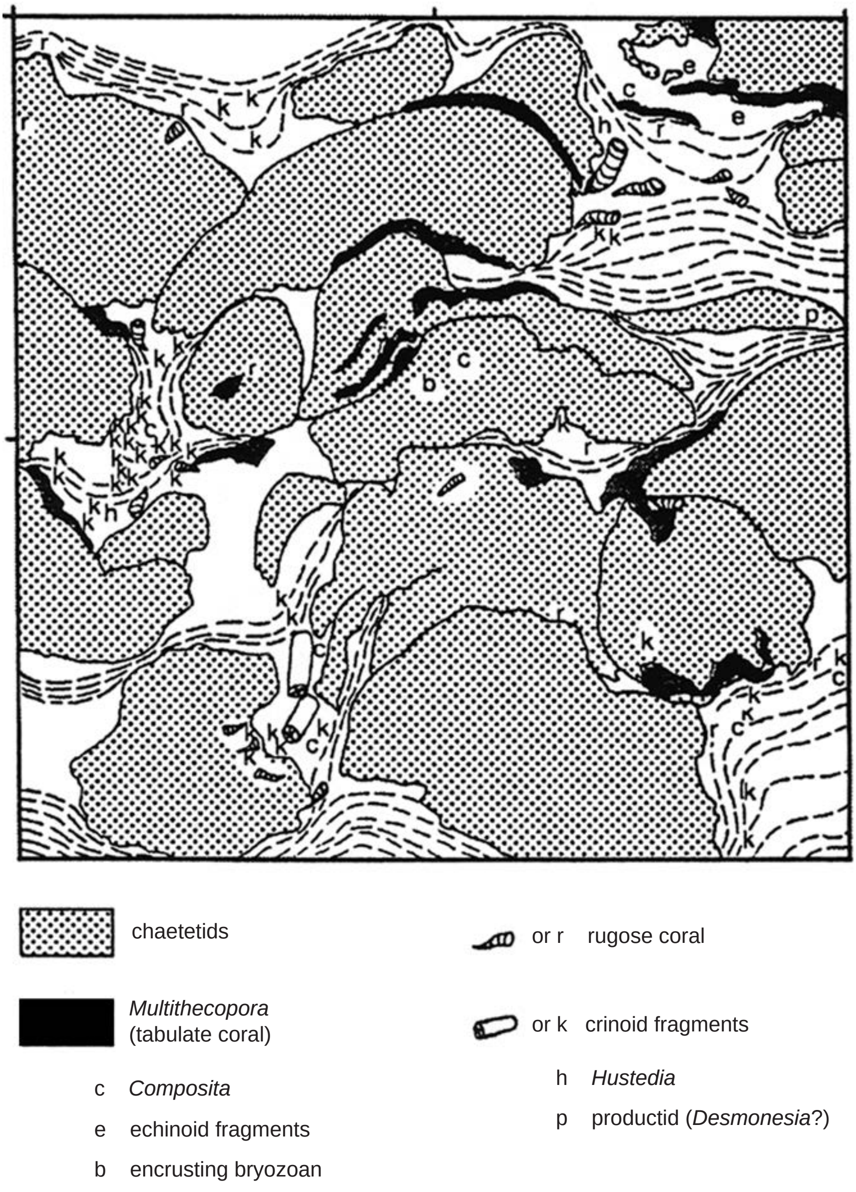


FIG. 109. Distribution of organisms in a 0.6 m^2 (2 $foot^2$) area on a vertical surface in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; transportation of the crinoid and echinoid fragments is apparent, and other taxa are in inferred life position; matrix is a cross-laminated fusulinid wackestone, and the laminations are accurately drawn, ×0.18 (adapted from Suchy & West, 2001, p. 441, fig. 13; courtesy of the authors and the Society for Sedimentary Geology).

1973, p. 494). If this is true for hypercalcified demosponges, then there is less competition for the food they require and adequate food for the other filter (suspension) feeders. Schematics (Fig. 107) illustrate the occurrence of some of these suspension-feeders in a Carboniferous (Pennsylvanian) chaetetid reef. The tabulate coral, *Multithecopora*, encrusting bryozoans, most solitary rugose corals, and some articulate brachio-

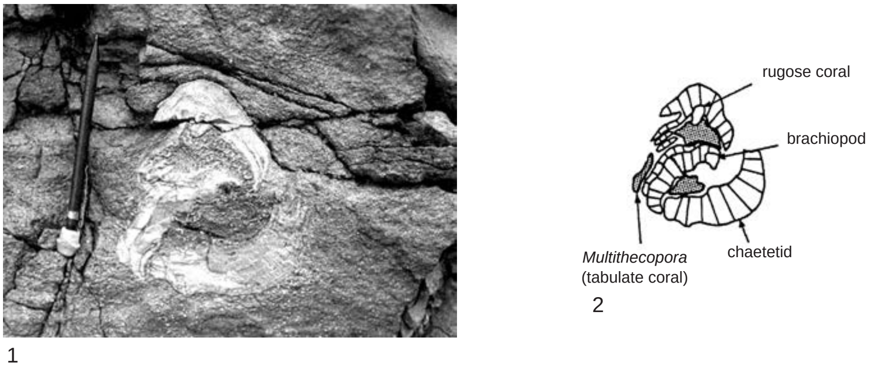


Fig. 110. Details of the relationships between chaetetids, associated organisms, and lithologies in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; *1,* relationship between three episodes of chaetetid growth and associated corals and a brachiopod on a weathered vertical surface, matrix is a fusulinid wackestone, ×0.2 (adapted from Suchy & West, 2001, p. 438, fig. 11B, in part); *2,* interpretative sketch of view *1,* ×0.1 (adapted from Suchy & West, 2001, p. 438, fig. 11B, in part; figures courtesy of the authors and the Society for Sedimentary Geology).

pods are in life position (Fig. 108–110). Corals, both rugosans and tabulates, especially syringoporoids like *Multithecopora*, are commonly associated with Paleozoic chaetetids, particularly during the middle Carboniferous (Lower and Middle Pennsylvanian) when chaetetids were most abundant. *Multithecopora* may provide the initial substrate for chaetetids (Fig. 108); most often growing on upper surfaces, or the upper surfaces of the ragged margins of domical to columnar chaetetids. Successive overgrowths of *Multithecopora* and chaetetids can produce domical (Fig. 110.1–110.2) and/or columnar structures (Fig. 103). Commonly, *Multithecopora* encrustations are thin (Fig. 102.2, Fig. 111.1–111.2), but they also form domical structures (Fig. 102.3).

Although colonial rugose corals occur with chaetetids (Sutherland, 1984), solitary rugose corals are more often encountered. They might have attached to the edges and/or upper surfaces (Fig. 77, Fig. 91.1, Fig. 109) or might have served as substrates for chaetetids and be completely covered by the sponge skeleton (Fig. 89.4, Fig. 102.4). Jameson (1980, p. 358) reported solitary rugose corals attached to chaetetids from the Petershill Formation Carboniferous (Mississippian) of Scotland. Some solitary rugose corals attached to the sheltered undersides of laminar chaetetids and grew around the edges and upward (Fig. 111.3–111.4).

Corals commonly occur on the upper surfaces of chaetetids, but other associated invertebrates are most often encountered on the sheltered undersides of the basal layer of chaetetids. Certain spine-bearing brachiopods (*Cooperina*, *Teguliferina*, and *Heterolosia*) appeared to favor these cryptic areas (Fig. 95–96, Fig. 111.5–111.7). From the Carboniferous (Middle Pennsylvanian) in Nevada, Perez-Huerta (2003) suggested a similar occurrence of the brachiopod *Heteralosia* (*sic*) *slocomi* as encrusting what he referred to as a chaetetid-like tabulate coral, probably a chaetetid sponge. Aulostegid brachiopods, along with spirorbid worm tubes, are attached to the undersides of laminar chaetetids in the Petershill Formation Carboniferous (Mississippian) of Scotland (Jameson, 1980, fig. 14-3a). Although they have not been observed, these genera also probably occur under the overhanging, ragged margins of domical and columnar chaetetids, like the small brachiopod *Thecidellina* that is attached to the undersides of some extant hypercalcified demosponges (Jackson,

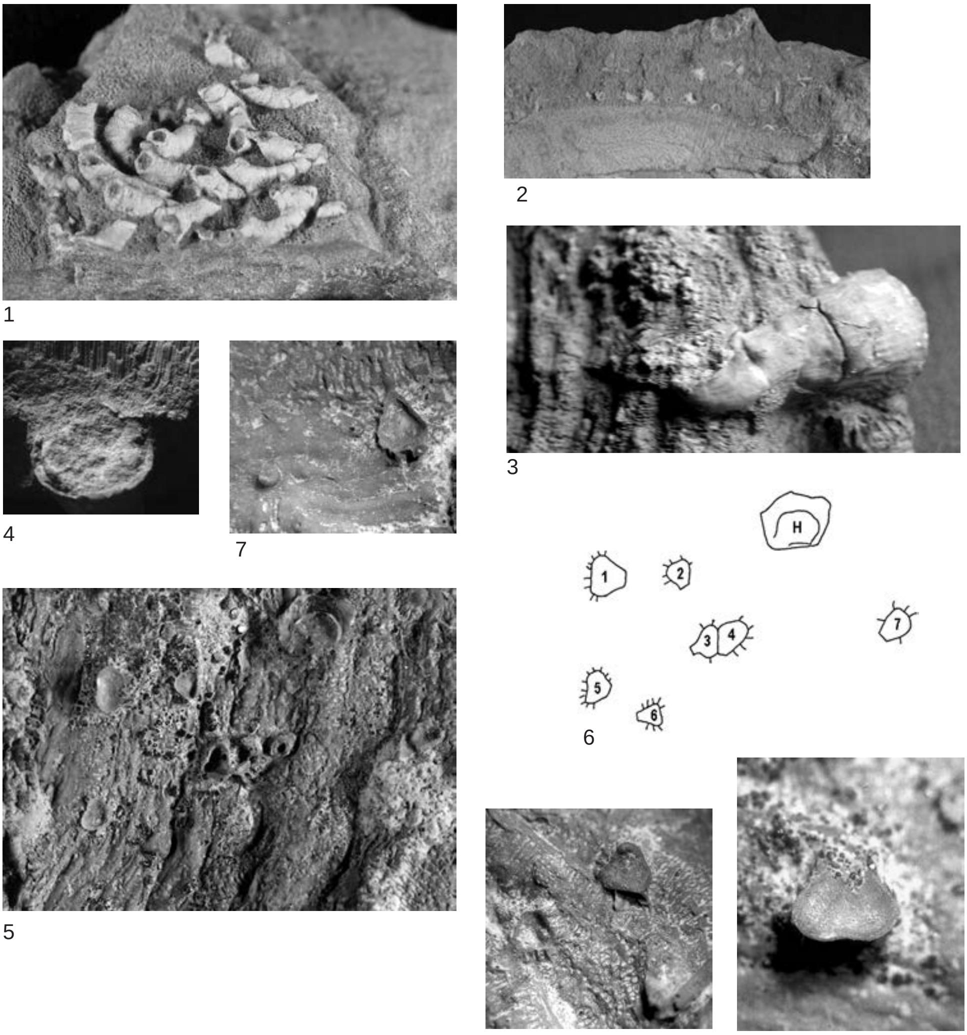


FIG. 111. Details of some specific invertebrate fossils associated with chaetetids, Carboniferous, Pennsylvanian; *1,* upper surface of the tabulate coral *Multithecopora* sp. attached to the upper surface of a chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×2 (adapted from West & Clark, 1984, p. 343, pl. 2,*D;* courtesy of the authors and the Paleontological Research Institution, Ithaca, New York); *2,* vertical view of *Multithecopora* sp. attached to the upper surface of a laminar chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.85 (West, 2012b); *3,* solitary rugose coral attached to the outer edge of the underside of a laminar chaetetid that has grown around the edge, suggesting a positive phototrophic reaction, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, ×1.7 (West, 2012b); *4,* a lateral view looking into the calyx of the solitary rugose coral in view *3,* ×1.25 (West, 2012b); *5,* brachiopods, *Cooperina* sp. and *Heterolosia* sp., attached to the lower surface of a laminar chaetetid, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, ×2.7 (West, 2012b); *6,* interpretative sketch of view *5,* showing the spatial distribution of *Heterolosia* sp. (*H*) and seven numbered specimens of *Cooperina* sp., ×2.4 (West, 2012b); *7,* pedicle valve of *Cooperina* sp. (upper right) and spirorbid worm tube (lower left) attached to the underside of a laminar chaetetid, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, ×7 (West, 2012b); *8,* spines cementing two specimens of *Cooperina* sp. to the underside of a laminar chaetetid, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa; specimen in the left center is a pedicle valve, the one in the upper center is articulated, ×7 (West, 2012b); *9,* articulated specimen of *Cooperina* sp. attached to the underside of a laminar chaetetid, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, with ventral margin tilted away from attachment surface, ×10 (West, 2012b).

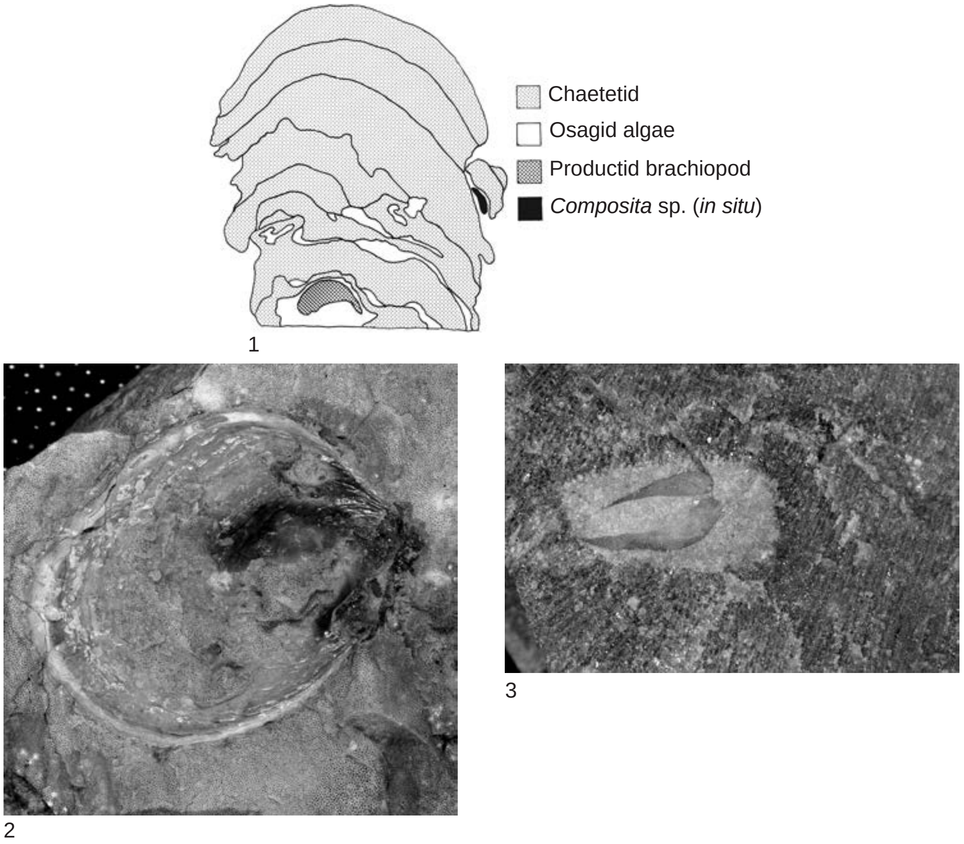


Fig. 112. Details of some further specific invertebrate fossils associated with chaetetids from the Carboniferous, Pennsylvanian; *1,* high domical chaetetid with ragged margins, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; initial laminar chaetetid encrusted an algal-microbially (osagid) encrusted hydrodynamically unstable productid valve; note the *in situ Composita* sp. beneath a now-broken overhanging laminae, ×0.3 (adapted from Voegeli, 1992, p. 159, fig. 38; courtesy of the author and Kansas State University); *2,* lower valve of what is interpreted as *Pseudomonotis*, an oyster-like bivalve, attached (cemented) to the upper surface of a domical chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×1.15 (West, 2012b); *3,* butterflied, smooth-valved bivalve, probably *Edmondia*, in a matrix-filled cavity within a domical chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×1.9 (West, 2012b).

Goreau, & Hartman, 1971; Saunders & Thayer, 1987). Brachiopods associated with the ragged margins of chaetetids and interstitial spaces in chaetetid reef mounds are pedunculate (*Composita* and *Hustedia*), cemented (*Meekella*), and presumed free-living chonetids (Fig. 108–110, Fig. 112.1). The attachment of terebratuliform brachiopods *Composita* and *Dielasma* to Carboniferous (Mississippian) chaetetids has also been documented (Jameson, 1980, p. 355).

Encrusting bryozoans *Fistulipora* and *Metelipora* occur in these cryptic niches (Fig. 95–96) and occasionally on the upper surfaces of chaetetids. Fistuliporid bryozoans are commonly attached to both the upper and lower surfaces of some Carboniferous (Mississippian) chaetetids (Jameson, 1980, p. 353). Some *Fistulipora* and *Tabulopora*(?) are reported as being chaetetid competitors (Fig. 97–98, Fig. 99.1; Fagerstrom & others, 2000). Figure 93 illustrates some of the environmental factors that are inferred to be involved in this competition. Chaetetids are not the only demosponges encrusted by bryozoans. GUNDRUM (1979) reported membraniporiform bryozoans attached to ?*Coelocladiella*.

Bivalves inferred to having been attached and/or nestling also occur with chaetetids. An imprint, interpreted as the lower valve of *Pseudomonotis*, an oyster-like bivalve, was attached to the upper surface of a domical Carboniferous (Pennsylvanian) chaetetid (Fig. 112.2). Also in a domical chaetetid are the smooth, butterflied valves of a small bivalve, probably *Edmondia*, that appears to have been nestled in a small flask-shape cavity and is now surrounded by micrite (Fig. 112.3).

Most of the preserved invertebrates associated with chaetetid reef mounds are suspension feeders, but vagrant deposit feeders are also present (8 of 26 taxa, or 31%; Table 25). Invertebrates in this niche group are less often preserved, because most are mollusks and their skeletons are more easily altered or destroyed by taphonomic processes. Members of the chaetetid reef mounds with articulated skeletons (trilobites, crinoids, and echinoids) most often occur as disarticulated fragments. Sometimes a number of disarticulated parts occur in close association with each other, suggesting *in situ* disarticulation. One such example of an echinoid is illustrated by SUCHY and WEST (2001, fig. 11E).

In large part, this chapter has focused on factors that occur during the life of chaetetids, and a number of these factors result in injury and/or death of these hypercalcified sponges. However, as noted above, some of these factors continue and/or are initiated after the death of the chaetetid. These postmortem processes fall within the realm of taphonomy, and are, as noted by PERRY and HEPBURN (2008), especially important when attempting to unravel and understand potential ecological relationships in reefs, a common chaetetid habitat.

PALEOGEOGRAPHY AND BIOSTRATIGRAPHY OF THE HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

RONALD R. WEST

INTRODUCTION

Hypercalcified sponges with a chaetetid skeleton, both fossil and extant, are relatively inconspicuous components of the marine biota. Only a few extant hypercalcified sponges are known, and they occur mostly along bathyal cliffs and in dark littoral caves (see Living Hypercalcified Sponges, p. 1–14). Commonly, the habitats of the extant taxa are associated with reefal environments in tropical or subtropical latitudes in the Indo-Pacific and West Atlantic zones. The general distribution of the three extant hypercalcified genera with a chaetetid skeleton are as follows: *Merlia*, circumtropical and warm temperate latitudes (Madeira, Mediterranean); *Ceratoporella*, tropical latitudes (Caribbean); and *Acanthochaetetes*: tropical latitudes (South Pacific) (SOEST & others, 2005). In tropical latitudes, the depth distribution is in the upper bathyal zone (deep forereef), usually above the thermocline, with *Ceratoporella nicholsoni* being the main reef builder between 70 and 105 m depth (LANG, HARTMAN, & LAND, 1975), and then the development of scleractinian coral reefs becomes dominant in the shallower water above. Fossil chaetetids, on the other hand, appear to have thrived in more open marine environments of the shallow continental shelf and were conspicuous reef builders during the Carboniferous.

PALEOBIOGEOGRAPHY

The geographic distribution of fossil chaetetids is not unlike that of extant hypercalcified demosponges with a chaetetid skeleton: it is essentially tropical (FAGERSTROM, 1984). Data on the temporal and spatial distribution of reefs during the Phanerozoic in which chaetetids were listed as a reef builders, i.e., chaetetid reefs and hypercalcified demosponges including chaetetids, are shown in Table 26. It also lists data from 37 different stratigraphic intervals (series and stages) that might, on careful study, contain chaetetids, namely hypercalcified demosponges that are unreported or unknown, indeterminate, undifferentiated, and miscellaneous. The latitudinal belt (whether tropical or temperate, and in some cases both) for these series and stages is shown in Table 27. Hypercalcified demosponges, including chaetetids, are known from five stages in the Carboniferous: Visean, Serpukhovian, Bashkirian, Moscovian, and Kasimovian (Fig. 113–115), but they are most abundant in the Bashkirian and Moscovian. Permian chaetetid reefs are only known from the Guadalupian and Lopingian (Fig. 115–117). Hypercalcified demosponges, including chaetetids, are reported from two Jurassic stages, Oxfordian and Kimmeridgian (Fig. 118). All of these occurrences are located in tropical paleolatitudes, except two, which are questionably located in the northern temperate belt (Iran and Japan) during the Jurassic (Oxfordian and Kimmeridgian) (Fig. 113–118). Hypercalcified demosponges that may, on careful study, include chaetetids, are listed as reef builders for six sites, five of which are in tropical paleolatitudes (Table 27). Unreported reef builders, and those listed as unknown, indeterminate, undifferentiated, or miscellaneous at the remaining sites in different stratigraphic intervals could, on careful study, contain chaetetids; most of these are in the tropics (Table 27).

Although information on the microstructure and spicules, or spicule pseudomorphs, is currently lacking, there are a number of described taxa that have a chaetetid skeleton and could be hypercalcified

Table 26. Temporal and spatial distribution of Phanerozoic reefs that contain, or could contain, chaetetids. Hypercalcified demosponges, presumed chaetetids, occur in other stratigraphic intervals as noted in the text; *, only the latitudinal belt (Temperate or Tropical) containing the majority of the occurrences and the general geographic localities of reef builders are indicated, after Kiessling, Flügel, and Golonka (2002), who listed the reef builders as unknown, undifferentiated, miscellaneous, indeterminate, or hypercalcified demosponges (coralline sponges); some were unreported; these five categories are included because chaetetids are, or could have been, involved in the reef building, and as such, suggest intervals and areas for future study; *italics,* stratigraphic intervals and geographic areas where chaetetids have been recognized as important contributors to reef building; #, reef builders are not reported, only whether reefs and reef mounds, mounds biostromes, or unknown buildups occurred (data from Kiessling, Flügel, & Golonka, 2002, and refer only to reefal occurrences).

System	**Series and Stage**	**Reef builder***	**Paleolatitude***	**Paleogeography***
Neogene	**Pliocene** **Miocene** Tortonian	Unknown	Tropical	southern Spain and southern Italy
	Serravallian–Burdigalian	Unknown	Tropical	Indian Ocean, South Pacific, southeastern Asia, northern Mediterranean coast
Neogene–Paleogene	Aquitanian **Oligocene** Chattian	Unknown	Tropical	South Pacific, New Guinea
Paleogene	Rupelian	Unknown	Tropical	India, southeastern Asia
	Eocene Priabonian	Unknown	Tropical	eastern Africa
	Bartonian–Lutetian	Unknown	S. Temp.	northern Australia
	Bartonian–Lutetian	Unknown	Tropical	India
	Bartonian–Lutetian	Unknown	N. Temp.	Middle East
	Ypresian **Paleocene** Thanetian	Unknown	Tropical	South Africa
Cretaceous	**Upper** Campanian	Unknown	N. Temp.	Greece, Italy
	Lower Aptian–Valanginian	Indeterminate	30° N. Lat.	France, Austria, Germany, northern Italy, Slovenia
	Aptian–Valanginian	Indeterminate	S. Temp.	South Atlantic
	Valanginian	Indeterminate	N. Temp.	Crimea, Ukraine, Turkmenistan
	Valanginian	Indeterminate	Tropical	eastern U.S., Hungary, Spain, France, Italy, Tunisia, Portugal
Jurassic	Tithonian	Indeterminate	Tropical	eastern U.S., Hungary, Spain, France, Italy, Tunisia, Portugal
	Tithonian–Kimmeridgian	Hypercalcified demosponges *Kimmeridgian chaetetids*	Tropical	*Morocco, southern Europe, Saudi Arabia, Iran*
	Oxfordian–Callovian	Hypercalcified demosponges *Oxfordian chaetetids*	Tropical	Egypt, Israel, Lebanon *Mexico, southern Europe, Iran*
	Oxfordian–Callovian	Hypercalcified demosponges	N. Temp.?	Japan

TABLE 26 (*continued from facing page*).

Jurassic	Bathonian–Bajocian	Unknown	Tropical	Georges Bank, Atlantic
	Bathonian–Bajocian	Unknown	S. Temp.	Madagascar
Triassic	Rhaetian–Norian	Hypercalcified demosponges	Tropical	western Tethys, Middle East, southeastern Asia, Japan, western Canada, Alaska (USA)
	Carnian–Ladinian–Anisian	Hypercalcified demosponges	Tropical	essentially Tethyan
Permian	**Lopingian**	*Chaetetid reefs*	Tropical	*Pakistan, southern China*
	Guadalupian	*Chaetetid reefs*	Tropical	?Oman, Pakistan
	Cisuralian Kungurian–Artinskian–Sakmarian	Hypercalcified demosponges	Tropical	western Texas (USA), southern, western China
	Asselian	Hypercalcified demosponges	Tropical	Japan
Carboniferous (Pennsylvanian)	Gzhelian	Hypercalcified demosponges	Tropical	Japan
	Kasimovian–Moscovian–Bashkirian	*Hypercalcified demosponges, with chaetetid reef banks*	Tropical	*western United States, Japan, Kyrgyzstan*
Carboniferous (Mississippian)	Serpukhovian#	Unreported#	Tropical, S. Temp.	United States, Europe, Russia, Iran, China, Afghanistan, Japan
	Visean#	Unreported#	Tropical, S. Temp.	North America, Europe, Russia, Australia, Afghanistan, China, Japan
	Tournaisian#	Unreported#	Tropical, N. and S. Temp.	North America, Europe, Russia, Australia, Afghanistan
Devonian	**Upper** Famennian	Unknown	Tropical, N. and S. Temp.	Australia, Canada, China, Europe, Kazakhstan, Russia
	Frasnian	Unknown	Tropical	northwestern Canada, Russia, Polar Urals, Kazakhstan
	Middle Givetian	Unknown	Tropical	western and northwestern Canada, southern China, Polar Urals
	Lower Emsian–Pragian	Unknown	Tropical	western and northwestern Canada, Polar Urals
	Pragian Lochkovian	Unknown	Tropical	Arctic, northern Urals, Kazakhstan
Silurian	**Pridoli–Ludlow**	Unknown	Tropical	Kazakhstan, Russia
	Ludlow	Unknown	N. Temp.	Kazakhstan, Russia
	Wenlock	Unknown	Tropical	North America, Kazakhstan, Siberia
	Llandovery	Unknown	Tropical	Northwest Territories
Ordovician	**Upper Ordovician** Hirnantian–Katian	Unknown	Tropical	Yakutsk, Russia
	Katian–Sandbian	Miscellaneous	Tropical	northwestern and southeastern Kazakhstan, northwestern Canada
	Middle Ordovician Darriwilian	Undifferentiated	Tropical	North Korea, northern China
	Darriwilian	Undifferentiated	S. Temp.	North Korea, northern China
Ordovician–Cambrian	Tremadocian–Furongian	Unknown	Tropical	North America, Kyrgyzstan, Kazakhstan

TABLE 27. Summary of the paleolatitudinal position of reefs that contain, or could contain, chaetetids in the 37 different Phanerozoic stratigraphic intervals listed in Table 26. *Note that in some of the 37 stratigraphic intervals containing reefs there is some duplication (even in one interval, tripling) of the number of reefs (West, 2012c).

Reef builder	Number	Tropical	Temperate	30° N. Lat.
Chaetetid reefs	2	2	0	
Hypercalcified demosponges, including chaetetids	3	3	0	
Other hypercalcified demosponges	6	5	1	
*Unknown, indeterminate, undifferentiated, miscellaneous, or unreported reef builders	27	25	12	1

demosponges. To provide a more complete temporal and spatial distribution of chaetetid skeletons, some of these taxa are briefly summarized.

Hypercalcified sponges with a chaetetid skeleton have been reported from Cambrian, Ordovician, Silurian, Devonian, and lower Carboniferous rocks. *Flindersipora bowmani*, an abundant coralomorph in lower Cambrian bioherms in the Flinders Ranges, South Australia, should, according to SORAUF (2000, p. 38) be placed with the chaetetids. However, the numerous, well-developed septa in *Flindersipora bowmani* are a characteristic of tabulate corals and are not currently known in any chaetetid taxa. Interestingly, another characteristic of tabulate corals, namely pores in the walls, has been documented in ?*Blastoporella* (CUIF & EZZOUBAIR, 1991), a probable chaetetid genus. If septa in chaetetids, as suggested by SORAUF (2000), and pores in tubule walls, as documented in ?*Blastoporella,* are to be considered features of chaetetids, then it is possible that chaetetids and tabulate corals are more closely related than previously thought.

OAKLEY (1936) described a chaetetid from the Ordovician of the Northwest Territories, Canada, and NORFORD (1971) described a species of *Chaetetipora* from the Upper Ordovician of Ellesmere Island. Chaetetids were reported from the Upper Ordovician Cincinnati Group by NICHOLSON (1874) and MICKLEBOROUGH and WETHERBY (1878). Occurrences from the middle Silurian (Clinton) of New York were reported by NICHOLSON (1874) and GILLETTE (1947). Some of the taxa (chaetetid species) listed by MICKLEBOROUGH and WETHERBY (1878) are now considered to be bryozoans, and the occurrence of *Chaetetes* (*Chaetetes*) in the Silurian is also queried (see Table 22). *C.* (*Boswellia*) and *Pachytheca* are valid chaetetid genera, and occur in the Devonian (see Table 19). OLIVER, MERRIAM, and CHURKIN (1975) reported Devonian chaetetids in Alaska, and MÉNDEZ-BEDIA, SOTO, and FERNÁNDEZ-MARTINEZ (1994) and SOTO, MÉNDEZ-BEDIA, and FERNÁNDEZ-MARTINEZ (1994) reported chaetetids in Devonian reefs in the Cantabrian Mountains in Spain. Chaetetids are also found in the subsurface Devonian reefs of Canada (D. L. Kissling, personal communication, 1988). Other Devonian occurrences of chaetetids are in Poland (NOWINSKI & SARNECKA, 2003), the Ardennes (Belgium, Luxembourg, and France) (HUBERT & others, 2007; ZAPALSKI & others, 2007), Germany (MAY, 1993), Morocco (MAY, 2008), and Australia (PICKETT, OCH, & LEITCH, 2009).

More widely distributed are hypercalcified demosponges with a chaetetid skeleton in the Carboniferous, Missisippisan of the United States, as follows: Georgia (BROADHEAD, 1975; LORD & WALKER, 2009; LORD, WALKER, & ARETZ, 2011); Illinois and Kentucky (STOUDER, 1938; DUNCAN, 1965, 1966; GUTSCHICK, 1965; TRACE & MCGRAIN, 1985); western Wyoming (SANDO, 1975); Nevada (Arrow Canyon and Goodsprings); and Wellsville Mountains, Utah (WEST, 1992). Lower Carboniferous chaetetids have also been reported from: Peru (BASSLER, 1950); Akiyoshi-dai, Japan (OTA,

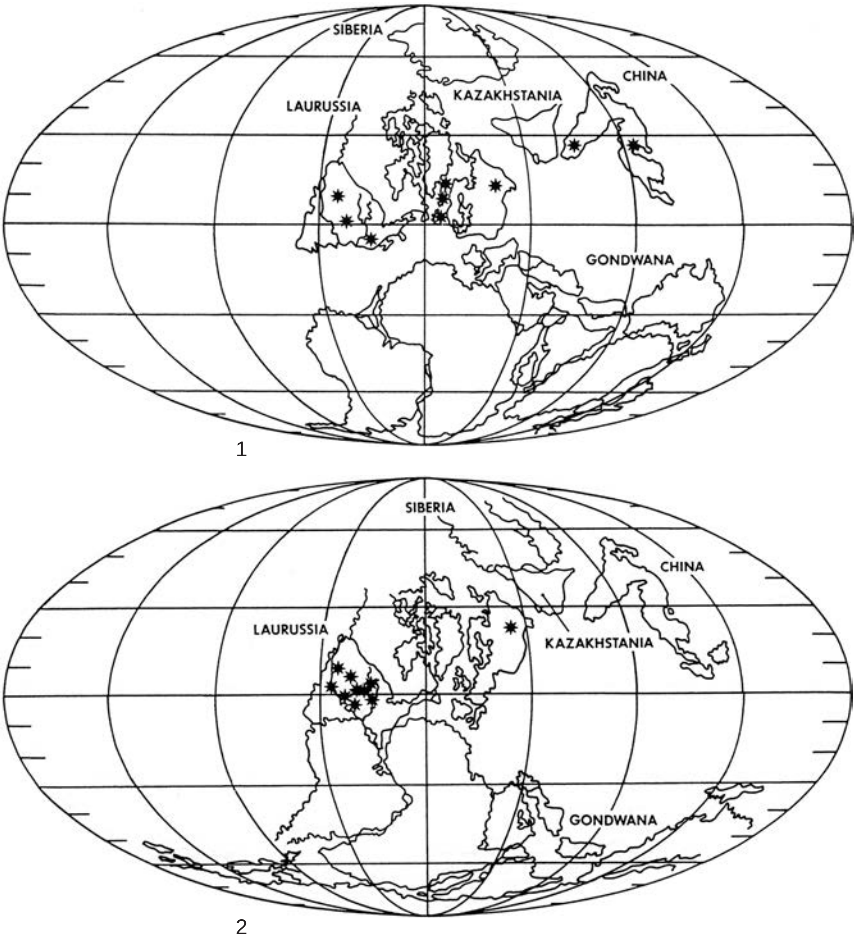
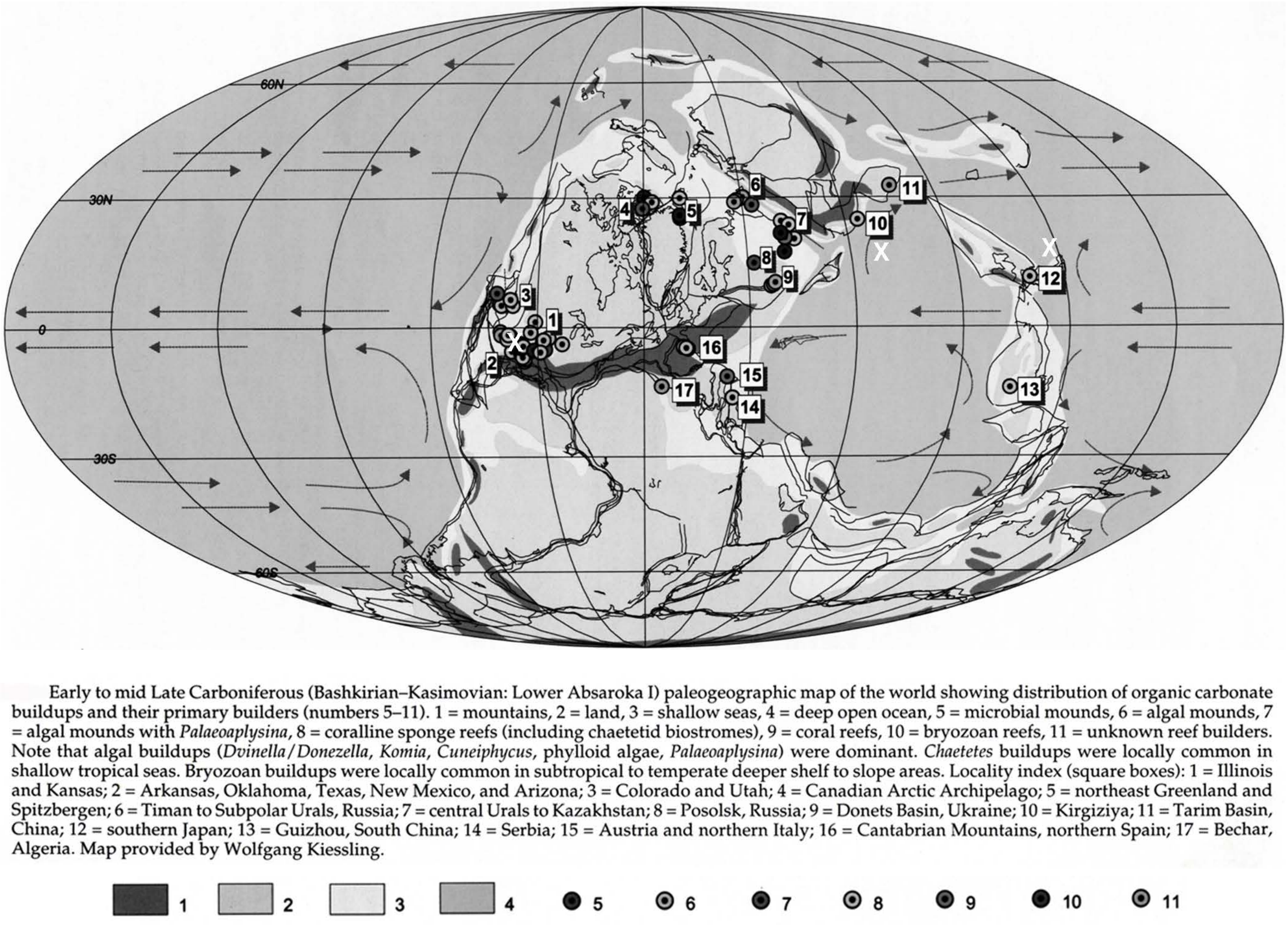


FIG. 113. Distribution of Carboniferous chaetetids; *1,* general distribution of chaetetids during the middle Early Carboniferous, approximately 320–340 Ma (West, 2012c); *2,* general distribution of chaetetids during the middle Late Carboniferous, approximately 305–320 Ma (West, 2012c).

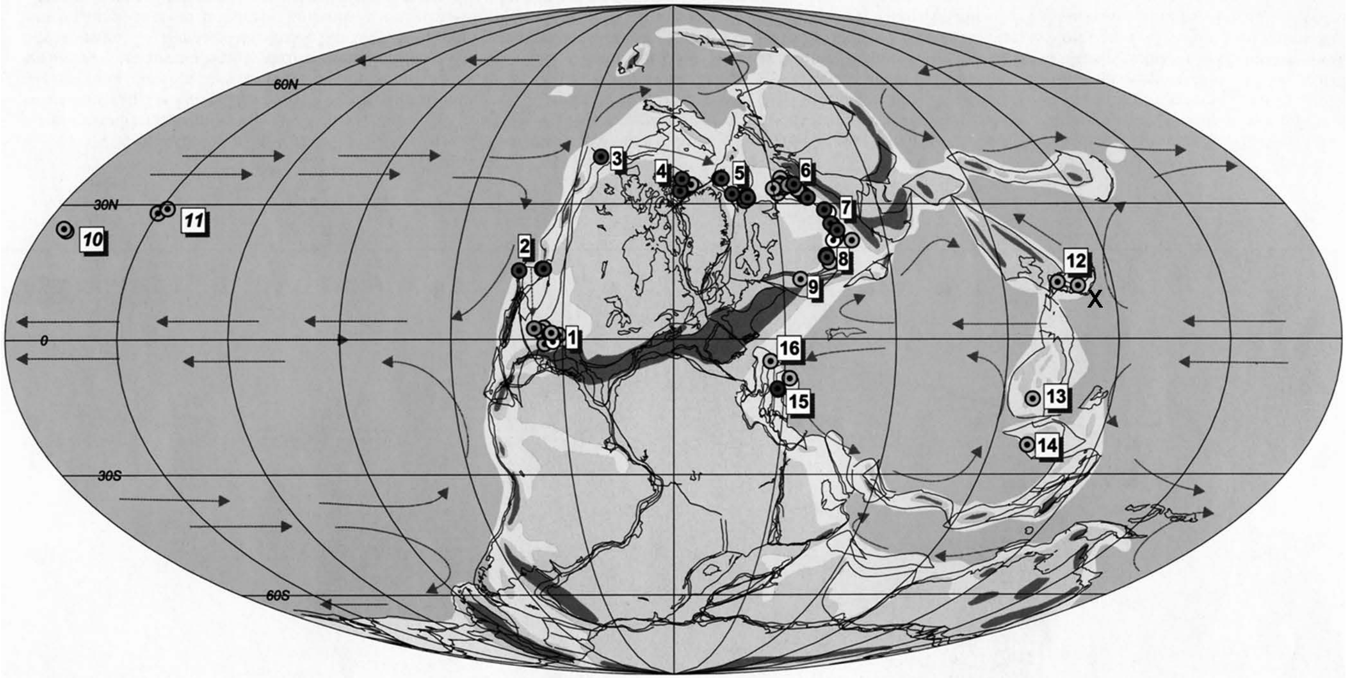
1977, 1968); Taurides, southern Turkey (DENAYER, 2010); Donets Basin, Ukraine (OGAR, 2011, 2012); Tiouinine, Morocco (RODRÍGUEZ & others, 2011); Derbyshire, England (WOLFENDEN, 1958); the Great Limestone, Yorkshire, England (DEAN, OWEN, & DOORIS, 2008); Wales (ARETZ & HERBIG, 2003a); Little Asby Scar, Cumbria, England (ARETZ & NUDDS, 2007); the Midland Valley, Scotland (JAMESON, 1980, 1987); the Anhee Formation of Royseux, Belgium (ARETZ, 2001); the Montagne Noire, France (ARETZ & HERBIG, 2003b); southwestern Spain (GÓMEZ-HERQUEDAS & RODRÍGUEZ, 2009); and Cannindah limestone, Queensland, Australia (SHEN & WEBB, 2008).

Additionally, I have examined numerous specimens of lower Carboniferous chaetetids in museum collections of England, Scotland, Wales, and continental Europe, where they occur more commonly than in the upper Carboniferous rocks of those areas. In addition to the upper Carboniferous sites listed in Table 26 and summarized in Table 27, chaetetids also occur in upper Carboniferous reefs of Holm Land, northeastern Greenland (STEMMERIK, 1989), and others are included



Early to mid Late Carboniferous (Bashkirian–Kasimovian: Lower Absaroka I) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–11). 1 = mountains, 2 = land, 3 = shallow seas, 4 = deep open ocean, 5 = microbial mounds, 6 = algal mounds, 7 = algal mounds with *Palaeoaplysina*, 8 = coralline sponge reefs (including chaetetid biostromes), 9 = coral reefs, 10 = bryozoan reefs, 11 = unknown reef builders. Note that algal buildups (*Dvinella/Donezella, Komia, Cuneiphycus*, phylloid algae, *Palaeoaplysina*) were dominant. *Chaetetes* buildups were locally common in shallow tropical seas. Bryozoan buildups were locally common in subtropical to temperate deeper shelf to slope areas. Locality index (square boxes): 1 = Illinois and Kansas; 2 = Arkansas, Oklahoma, Texas, New Mexico, and Arizona; 3 = Colorado and Utah; 4 = Canadian Arctic Archipelago; 5 = northeast Greenland and Spitzbergen; 6 = Timan to Subpolar Urals, Russia; 7 = central Urals to Kazakhstan; 8 = Posolsk, Russia; 9 = Donets Basin, Ukraine; 10 = Kirgiziya; 11 = Tarim Basin, China; 12 = southern Japan; 13 = Guizhou, South China; 14 = Serbia; 15 = Austria and northern Italy; 16 = Cantabrian Mountains, northern Spain; 17 = Bechar, Algeria. Map provided by Wolfgang Kiessling.

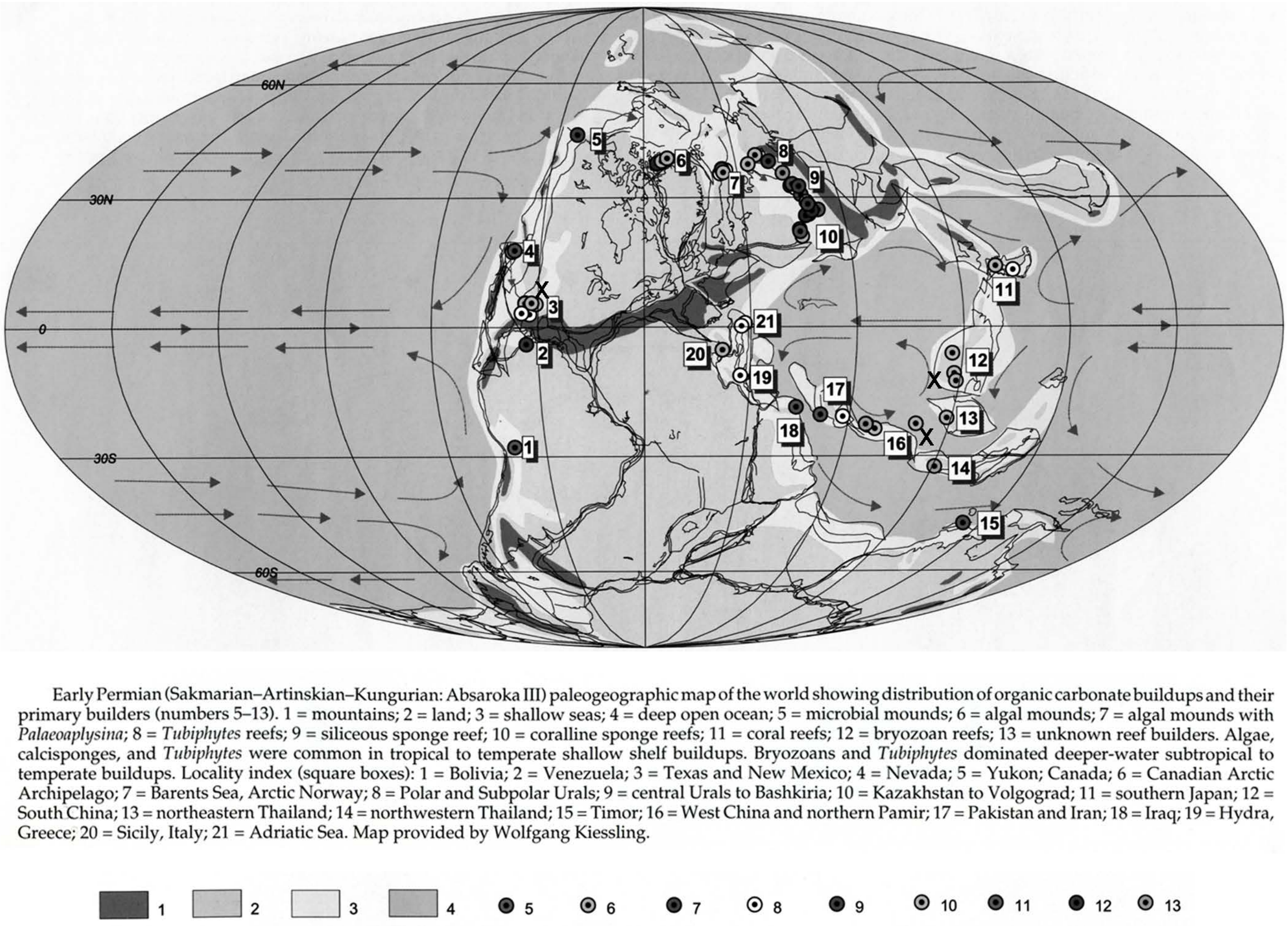
FIG. 114. Carboniferous reefs, those with chaetetids marked with *X;* Carboniferous, both Mississippian and Lower–Upper Pennsylvanian (Bashkirian–Kasimovian) chaetetid occurrences; *X* between numbers 1 and 2 and *X* markings below number 10 and above number 12 are occurrences in the central and western United States, Kyrgyzstan, and Japan respectively (adapted from Wahlman, 2002, p. 274, color fig. 2; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Latest Carboniferous and earliest Permian (Gzhelian–Asselian: Absaroka II) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–11). 1 = mountains; 2 = land; 3 = shallow seas; 4 = deep open ocean; 5 = microbial mounds; 6 = algal mounds; 7 = algal mounds with *Palaeoaplysina*; 8 = *Tubiphytes* reefs; 9 = coralline sponge reefs; 10 = bryozoan reefs; 11 = unknown reef builders. Phylloid algal buildups dominated shallow-water tropical seas, and in the Asselian, calcisponges became more common. In subtropical to temperate seas, *Palaeoaplysina* (with varying amounts of intermixed phylloid algae) dominated buildups in shallow water, and *Tubiphytes* and bryozoans dominated in deeper shelf to slope buildups. Locality index (square boxes): 1. = Texas and New Mexico; 2 = Idaho and California; 3 = Yukon, Canada; 4 = Canadian Arctic Archipelago and North West Territories; 5 = Barents Sea and Spitzbergen; 6 = Subpolar Urals and Timan–Pechora Basin, Russia; 7 = central Urals to Bashkiria, Russia; 8 = Pricaspian Basin, Kazakhstan to Volgograd, Russia; 9 = Donets Basin, Ukraine; 10 = Sikhote–Alin, Russia (paleoposition hypothetical); 11 = Koryak, Russia (paleoposition hypothetical); 12 = Japan; 13 = Guizhou, South China; 14 = Loei, Thailand; 15 = Serbia and Hungary; 16 = Austria. Map provided by Wolfgang Kiessling.

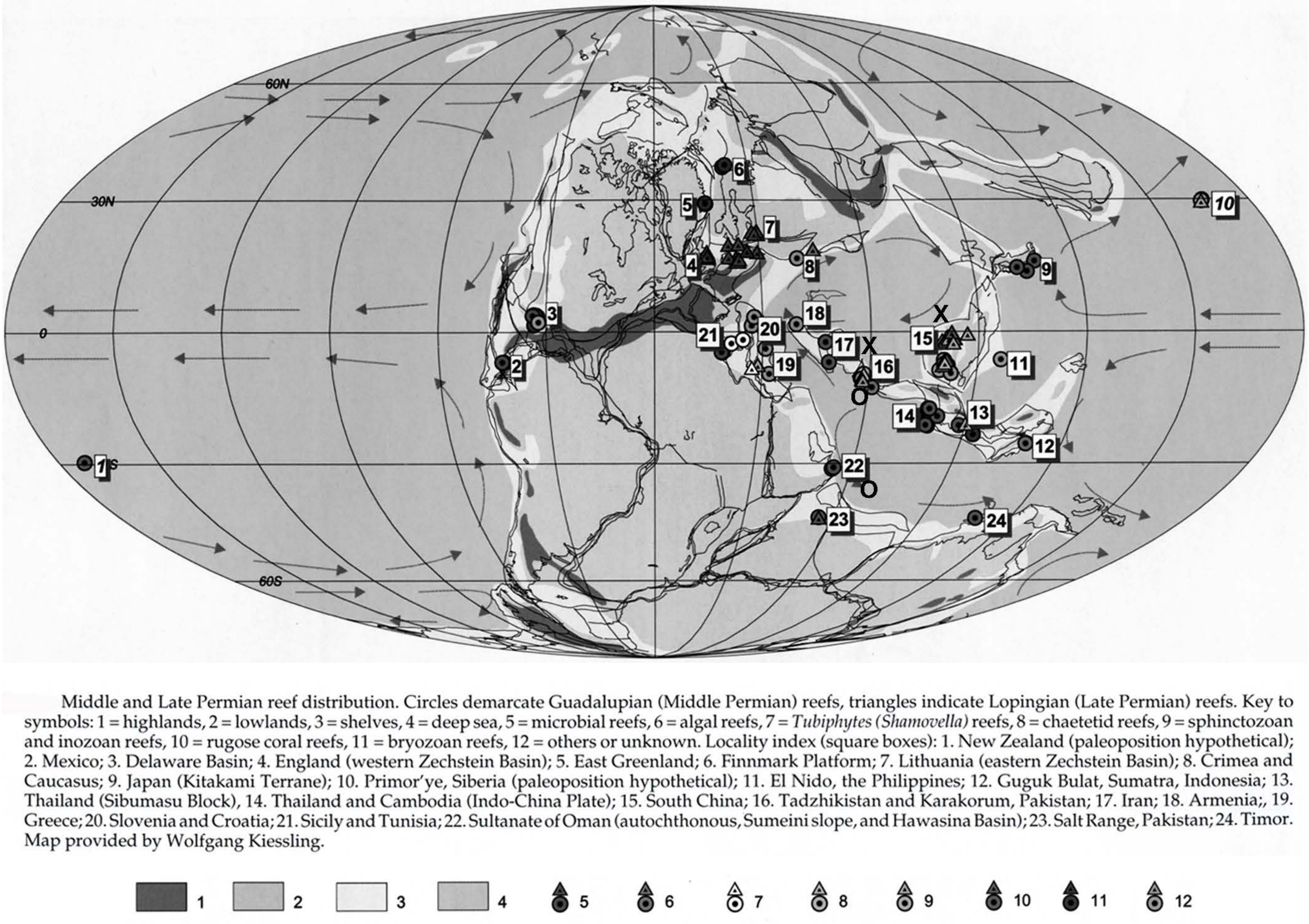
■ 1 ▨ 2 ☐ 3 ▨ 4 ● 5 ◉ 6 ● 7 ⊙ 8 ◉ 9 ● 10 ◉ 11

FIG. 115. Carboniferous and lower Permian reefs, those with hypercalcified demosponges marked with *X;* Carboniferous, Upper Pennsylvanian (Gzhelian) to lowermost Permian, Lower Cisuralian (Asselian) hypercalcified demosponge locality; *X* below and slightly right of number 12 is the Japanese (Akiyoshi) site (adapted from Wahlman, 2002, p. 275, color fig. 3; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Early Permian (Sakmarian–Artinskian–Kungurian: Absaroka III) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–13). 1 = mountains; 2 = land; 3 = shallow seas; 4 = deep open ocean; 5 = microbial mounds; 6 = algal mounds; 7 = algal mounds with *Palaeoaplysina;* 8 = *Tubiphytes* reefs; 9 = siliceous sponge reef; 10 = coralline sponge reefs; 11 = coral reefs; 12 = bryozoan reefs; 13 = unknown reef builders. Algae, calcisponges, and *Tubiphytes* were common in tropical to temperate shallow shelf buildups. Bryozoans and *Tubiphytes* dominated deeper-water subtropical to temperate buildups. Locality index (square boxes): 1 = Bolivia; 2 = Venezuela; 3 = Texas and New Mexico; 4 = Nevada; 5 = Yukon; Canada; 6 = Canadian Arctic Archipelago; 7 = Barents Sea, Arctic Norway; 8 = Polar and Subpolar Urals; 9 = central Urals to Bashkiria; 10 = Kazakhstan to Volgograd; 11 = southern Japan; 12 = South China; 13 = northeastern Thailand; 14 = northwestern Thailand; 15 = Timor; 16 = West China and northern Pamir; 17 = Pakistan and Iran; 18 = Iraq; 19 = Hydra, Greece; 20 = Sicily, Italy; 21 = Adriatic Sea. Map provided by Wolfgang Kiessling.

FIG. 116. Lower Permian reefs, those with hypercalcified demosponges marked with *X;* lower Permian (Sakmarian, Artinskian, and Kungurian) **hypercalcified demosponge localities;** *X* markings above and to left of number 3, between numbers 13 and 16, and to lower left of number 12 refer to western Texas, southern and western China, respectively (adapted from Wahlman, 2002, p. 276, fig. 4; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Middle and Late Permian reef distribution. Circles demarcate Guadalupian (Middle Permian) reefs, triangles indicate Lopingian (Late Permian) reefs. Key to symbols: 1 = highlands, 2 = lowlands, 3 = shelves, 4 = deep sea, 5 = microbial reefs, 6 = algal reefs, 7 = *Tubiphytes (Shamovella)* reefs, 8 = chaetetid reefs, 9 = sphinctozoan and inozoan reefs, 10 = rugose coral reefs, 11 = bryozoan reefs, 12 = others or unknown. Locality index (square boxes): 1. New Zealand (paleoposition hypothetical); 2. Mexico; 3. Delaware Basin; 4. England (western Zechstein Basin); 5. East Greenland; 6. Finnmark Platform; 7. Lithuania (eastern Zechstein Basin); 8. Crimea and Caucasus; 9. Japan (Kitakami Terrane); 10. Primor'ye, Siberia (paleoposition hypothetical); 11. El Nido, the Philippines; 12. Guguk Bulat, Sumatra, Indonesia; 13. Thailand (Sibumasu Block), 14. Thailand and Cambodia (Indo-China Plate); 15. South China; 16. Tadzhikistan and Karakorum, Pakistan; 17. Iran; 18. Armenia;, 19. Greece; 20. Slovenia and Croatia; 21. Sicily and Tunisia; 22. Sultanate of Oman (autochthonous, Sumeini slope, and Hawasina Basin); 23. Salt Range, Pakistan; 24. Timor. Map provided by Wolfgang Kiessling.

FIG. 117. Permian reefs, those with chaetetids marked with *X* or *O;* Permian (Guadalupian and Lopingian) chaetetid occurrences; *O* markings just below number 22 and to the lower left of number 16 are Guadalupian occurrences in Oman and Pakistan, respectively; *X* markings between numbers 16 and 17 and above number 15 (Lopingian) are occurrences in Pakistan and southern China, respectively (adapted from Weidlich, 2002, p. 352, fig. 8; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).

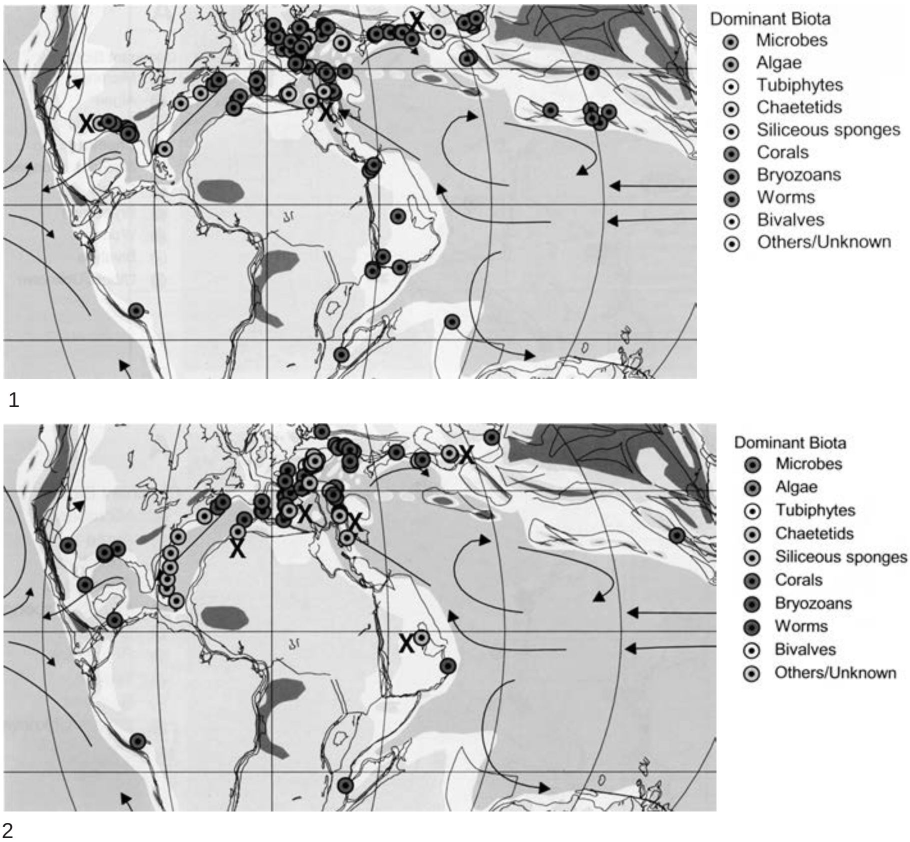


FIG. 118. Jurassic reefs, those with chaetetids marked with *X; 1,* Upper Jurassic (Oxfordian) chaetetid occurrences; *X* markings are localities in Mexico, southern Europe, and Iran (adapted from Leinfelder & others, 2002, p. 481, color fig. 5A; courtesy of the author and the Society for Sedimentary Geology); *2,* Upper Jurassic (Kimmeridgian) chaetetid occurrences; *X* markings are localities in Morocco, southern Europe, Iran, and Saudi Arabia (adapted from Leinfelder & others, 2002, p. 482, color fig. 6A; courtesy of the author and the Society for Sedimentary Geology; for color versions, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).

in the collections of the Canadian Geological Survey from Ellesmere Island (Canadian Arctic).

Post-Paleozoic chaetetids are represented in fossil sponge communities of Lower and middle Cretaceous rocks in Arizona and northern Spain (REITNER, 1989). Chaetetids also occur in Paleogene and Neogene rocks, as shown in Table 26, and in Pleistocene reef limestones of Okinawa (MORI, 1976; 1977; NAKAMORI, 1986) and the Vanuatu Archipelago (MILLET & KIESSLING, 2009). Living specimens occur in the fringing coral reefs of Okinawa (NAGAI & others, 2007).

Some of the occurrences noted in the preceding paragraphs are in series and stages that are listed as unreported in Table 26, such as the lower Cambrian, lower Carboniferous, and part of the Lower Cretaceous. However, all of the sites mentioned above are situated on currently available paleogeographic maps, in positions either in the tropics or in warm temperate settings. Thus, the paleogeographic distribution of fossil chaetetids is the same as for their extant descendants in tropical to warm temperate zones. Although chaetetids were never really conspicuous and never formed large reefs, they did, during the late Paleozoic, produce significant reef mounds and banks in shallow water, open marine environments (West, 1988; Wahlman, 2002). Prior to the upper Paleozoic, they appear to have had a smaller and less significant role in Paleozoic reef communities. It is important to note that the skeletal morphology of chaetetids is similar to that of a number of Paleozoic tabulate corals, as well as some bryozoan colonies. Because workers in the Paleozoic commonly relate forms they collect in the field to tabulate corals rather than chaetetids, more careful study of tabulate corals, such as lichenarids and chaetetids is needed (see also discussion on p. 6).

Extant, and most post-Paleozoic chaetetids, are also small and relatively inconspicuous in the relatively more diverse reef communities of the Mesozoic, occurring in cryptic and/or deeper bathyal environments. As small occupants of such environments, they are easily overlooked, which may be part of the reason why they have rarely been reported.

BIOSTRATIGRAPHY

Hypercalcified demosponges with a chaetetid skeleton occur in four orders of the Demospongiae: Hadromerida, Chondrosida, Poecilosclerida, Agelasida, and possibly also the Halichondrida (*Chaetosclera* and *Neuropora*). In addition, there are five genera, *Atrochaetetes, Bauneia, Blastochaetetes, Meandripetra, Ptychochaetetes (Ptychochaetetes),* and *P. (Varioparietes)* for which the order and family are uncertain. The order Hadromerida contains the following taxa: *Acanthochaetetes, Calcisuberites, Chaetetes* (*Chaetetes*), *C.* (*Boswellia*), *C.* (*Pseudoseptifer*), *Chaetetopsis, Pachytheca,* and *Calcispirastrella*. *Ceratoporella*, *Blastoporella*, *Kemeria*, *Keriocoelia*, *Leiospongia*, and *Sclerocoelia* are in the order Agelasida; the placement of *Cassianochaetetes* and *Spherolichaetetes* in this order is questionable. Currently, the only genus in the order Poecilosclerida is *Merlia*. The oldest and longest ranging valid chaetetid taxa extend from the ?Silurian to the Recent (see Table 19, Table 22). There are more valid chaetetid genera in the Mesozoic than in the Paleozoic, with the greatest number (ten), in the Triassic. Of these ten, five genera (*Atrochaetetes, Bauneia, Blastochaetetes, Ceratoporella*, and *Ptychochaetetes*) extend beyond the Triassic (see Table 19, Table 22). There are also three other chaetetid genera in the Triassic that are inadequately known, because spicules, or spicule pseudomorphs, have not yet been recognized (see Table 19, Table 22). Of the three extant genera, *Acanthochaetetes, Ceratoporella,* and *Merlia,* only the last is known from the Paleogene (Eocene and Oligocene) and Neogene (Miocene).

It is interesting that there are so many valid chaetetid genera (ten) in the Triassic and so few in the Paleozoic (three). Although a number of tabulate and rugose corals survived the extinctions at the end of the Ordovician and the end of the Devonian, none survived the extinction at the end of the Paleozoic (Permian) (Sepkoski, 2002). Heterocorals appeared first in the Upper Devonian (Famennian) and continued into the Carboniferous, but they are unknown from the Permian (Sepkoski, 2002, p. 61). The class Stromatoporoidea (Stearn & others, 1999, p. 11; and see Paleozoic Stromatoporoidea, p. 707) is only reported from the Paleozoic, where they were important reef builders during the Late Ordovician, Silurian, and Devonian, and none is confirmed to have survived beyond the Devonian. Habitats occupied by these corals and stromatoporoids would have been available to other organisms that survived the extinctions at the end of the Devonian and the end of the Permian. A tentative occurrence of *Ceratoporella,* an extant chaetetid genus, is reported from the Permian (H. Termier, G. Termier, & Vachard, 1977), so perhaps chaetetids occupied these available niches during the Triassic but were eventually replaced by scleractinian corals and Mesozoic stromatoporoids. At the same time, the preservation potential of any fossil is decreased the longer it is subjected to natural processes, namely

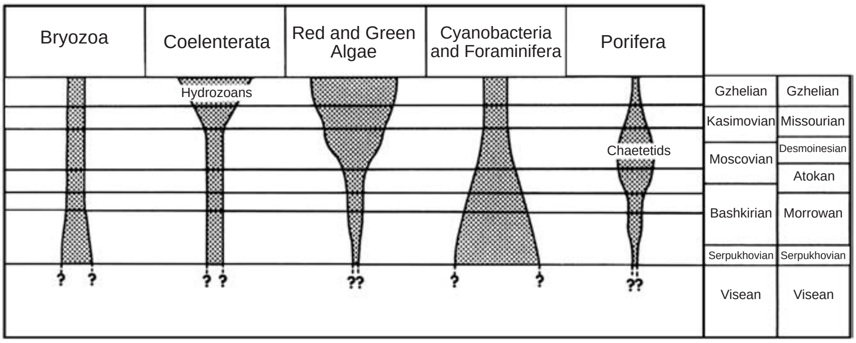


Fig. 119. Relative abundance (skeletal biovolume) in relation to the major groups of reef builders, upper Carboniferous reef mounds; time scale on the far right is the regional scale for North America, and the other one is the International time scale (adapted from West, 1988, p. 157, fig. 1; courtesy of the author and the Society for Sedimentary Geology).

diagenetic processes, and thus the older and less well-preserved Paleozoic forms may not have been recognized and/or were confused with tabulate corals, as noted on the previous page.

The currently known first and last occurrences of the 22 valid genera of hypercalcified demosponges with a chaetetid skeleton are listed in Table 19, along with the 4 genera for which definitive information on spicules or spicule pseudomorphs is lacking. Of these 22 valid genera, 19 are known only from the Mesozoic, 3 valid genera are exclusively Paleozoic, the living *Ceratoporella* has questionably been reported from the Permian, and the oldest occurrence of *Merlia* is in the Jurassic. Although the generic diversity is greatest in the Mesozoic, conspicuous reef building chaetetids were most abundant during the upper Carboniferous (Wood, 1990b). Because of their small size and minor roles in the generally more diverse Mesozoic reef communities, chaetetids are often unrecognized.

The five time slices in which chaetetids were abundant enough to be important in the construction of reefs are upper Carboniferous (Bashkirian–Kasimovian), Permian (Guadalupian and Lopingian), and Jurassic (Oxfordian and Kimmeridgian) (Table 26). Although they are specifically listed as reef builders during these five intervals, they are most conspicuous during the upper Carboniferous (Bashkirian, Moscovian, and Kasimovian). The reason(s) for their abundance during this time interval is not clear, but it could be related to the fact that the diversity of the reef mounds was low during this period of time. With less competition, chaetetid skeletons may have grown larger, forming more conspicuous reefal structures.

Two aspects of this concentration in the upper Carboniferous (Bashkirian–Kasimovian) deserve comment. First, chaetetids, based on field collecting and examination in some museum collections, appear to be more widespread and conspicuous in the lower Carboniferous (Mississippian) of most of Europe (Spain is an exception) than in the United States (Fig. 113.1–113.2). Kiessling, Flügel, and Golonka (2002, p. 708) noted that the status of the mid-Carboniferous event between the Serpukhovian and Bashkirian, as a major global extinction event, was ambiguous; however, their data indicated a first-order reef crisis. The upper Carboniferous (Pennsylvanian) in Europe is more siliciclastic, as it is also in the eastern United States. Consequently, in all of these regions, it appears that the environments available during the upper Carboniferous were rather unsuitable for chaetetids. However, that does not explain the rarity of chaetetids in the largely carbonate sequence of most of the lower Carboniferous (Mississippian) in the central and western United States. It also does not explain the similarity between the poriferan and coral assemblages of Spain and the North American midcontinent during the upper Carboniferous, especially during the Moscovian (García-Bellido & Rodríguez, 2005). If, as documented by García-Bellido and Rodríguez (2005), there was a marine connection between the Paleotethys Sea and the Panthalassan Ocean during the Moscovian, then it seems reasonable to infer that such a connection existed earlier, i.e., during the lower Carboniferous through into the Bashkirian (lower upper Carboniferous).

The second aspect is the rather sudden, almost complete, disappearance of chaetetids from the upper Carboniferous (Kasimovian–Gzhelian) through the Permian. There are a few reported occurrences of chaetetids in the Kasimovian (most of the Missourian) of the United States, but currently there are no known Gzhelian (Virgilian) (West, 1992) or lower Permian (Asselian) occurrences in the United States. Wahlman (2002) recorded upper Carboniferous (Gzehlian) and lower Permian (Asselian) hypercalcified demosponges from Japan (Fig. 115; Table 26) and from the lower Permian (Sakmarian, Artinskian, and Kungurian) of western Texas and southern and western China (Fig. 116; Table 26). Chaetetid reefs occur in the upper Permian (Guadalupian and Lopingian) of Oman, Pakistan, and southern China (Fig. 117; Table 26; Weidlich, 2002, 2007a, 2007b; Weidlich & Bernecker, 2003). Phylloid algae (Fig. 119) were the dominant reef builders during the Late Carboniferous and earliest Permian, not only in the western and central United States but also in southern Europe and southern China (Wahlman, 2002, p. 322). Calcareous algae, especially rhodophytes and chlorophytes, were abundant and diverse (Wray, 1968, 1970, 1977) and apparently more successful than chaetetids in the open marine shallow waters of the continental shelf and epicontinental seas. However, chaetetids survived in the more turbid, less illuminated, and, as suggested by Wood (1995, fig. 5), nutrient-limiting waters of these environments. Perhaps this was the beginning of their retreat into the deeper water and/or cryptic habitats they inhabit today.

The biostratigraphy of hypercalcified demosponges with a chaetetid skeleton is affected by: (1) the skeletal architecture–organizational grade, which is polyphyletic; (2) the sporadic occurrence of valid chaetetid genera (see Table 19); and (3) the taphonomic processes that often altered and/or destroyed the original skeletal microstructure and spicules, making generic and specific identification difficult, if not impossible. As noted above, Cambrian and Ordovician chaetetid-like forms have been reported, but the oldest currently valid chaetetid taxon is the questionable occurrence of *Chaetetes* (*Chaetetes*) in the Silurian. Valid chaetetid genera and subgenera extend to the Recent and are most abundant during the Bashkirian and Moscovian, an interval that, based on current knowledge, is the acme zone of chaetetid sponges (Fig. 119).

A number of stratigraphic gaps exist between the currently known first and last appearances of the valid chaetetid genera (see Table 19), as well as many blanks and unknowns in the temporal and spatial distribution of chaetetids (Table 26). More thorough globally oriented investigations of chaetetid sponges are required to achieve the fullest possible understanding of the paleobiogeography and biostratigraphic development of this group.

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INTRODUCTION TO POST-DEVONIAN HYPERCALCIFIED SPONGES (STROMATOPOROID TYPE)

RACHEL WOOD

EXTERNAL MORPHOLOGY

GROSS MORPHOLOGY

As with most epibenthic invertebrates, calcified sponges display a wide range of gross morphologies and sizes, which may be more an expression of environmental controls than phylogeny. Modular organisms (those that show a repetition of functional units or individuals) have particularly flexible morphologies, which appear to be designed for life under varied rates of sedimentation, hydrodynamic energies, and substrate types. Some species have fixed morphologies and sizes, others show variation according to setting, and yet others show evidence that individuals can adapt to changing energy and sediment regimes, as shown by changing growth styles over the individual's lifetime.

Mesozoic stromatoporoids tend generally to be smaller than Paleozoic representatives, but they fall into the same three main groups of branching, laminar, and massive morphologies. The full range of gross morphologies they exhibit is listed in Table 28, together with their growth form, and an interpretation of the environments in which such forms most commonly grew (compiled from KISSLING & LINEBACK, 1967; KERSHAW, 1998). Growth form denotes the organization of functional units and follows the scheme outlined by COATES and JACKSON (1985). Laminar forms are subdivided into those that formed a permanent attachment to a hard substrate (encrusting) and those that grew upon soft sediment (recumbent). Detailed descriptions of the gross morphologies and growth forms are given in the Glossary (p. 397–415).

SURFACE FEATURES

Most Mesozoic stromatoporoids show open, porous surfaces, where the skeletal elements form a network. Other surface features fall into two categories: first are those structures related to the immediate hydrodynamic conditions under which an individual grew. These are oscular chimneys, mamelons, and subsidiary branches. Oscular chimneys are tubelike elongations bearing exhalant, oscular pores; mamelons are rounded, moundlike elevations that often bear astrorhizae or oscular pores. Subsidiary branches represent further skeletal development from either of these structures. All these structures enabled the sponge to increase the diameter of supply and thus avoid recycling of exhalant water (FRY, 1979). The presence or absence of such structures cannot always, however, be attributed to large-scale environmental causes. For example, adjacent individuals of the living chaetetid, *Ceratoporella,* show varied mamelon development. Reconstruction of hydrodynamic regimes should therefore only be considered when the range of surface features of an assemblage is available.

The second category of surface features reflects the organization and position of the aquiferous filtration system in relationship to the areas of skeletogenesis. The skeleton of a sponge serves to support the aquiferous system and will reflect the position of this when the soft tissues have gone. Most Mesozoic stromatoporoids possess complex traces of the intricate canal systems within their skeletons, often as ramifying unwalled spaces within the skeleton, which open out into astrorhizae on the upper surfaces. As the individual grows, successive layers are superimposed.

TABLE 28. Gross morphology and growth form of Mesozoic stromatoporoids, together with inferred environments in which each form most commonly occurred (Wood, 2011).

Gross morphology	Growth form	Inferred hydrodynamic regime	Inferred sedimentation rate
branching-delicate	pseudocolonial (uniserial)	low energy	high
branching-delicate	pseudocolonial (uniserial)	moderate energy	moderate
branching	multiserial erect	low-moderate energy	moderate
laminar-recumbent	multiserial	variable energy	low
laminar-encrusting	multiserial	high energy	low
massive: hemispherical, nodular	multiserial encrusting	moderate-high energy	low
massive: columnar, conical	multiserial encrusting	low-moderate energy	high

The form of the aquiferous system is largely dictated by the relative thickness of soft tissue and can thus be an important clue in soft-tissue reconstructions. For example, astrorhizae, the unwalled traces of the stellate, branching, exhalant canal system, are expressed in the fossilizable skeleton only when the soft tissue is sufficiently thin for the exhalant canals to be directly adjacent to the areas of calcification—i.e., the aquiferous system is essentially surficial. In contrast, oscular pores will be present within the skeleton only if the soft tissue is thick and the aquiferous system is penetrative and enclosed within the upper portions of the calcareous skeleton. Here, the exhalant canal traces are expressed as ramifying canals within the skeleton and not as superficial astrorhizal furrows. Ostia do not normally have any skeletal expression, although the tubules in chaetetids may correspond to the placing of one or more ostia, as noted in the living chaetetid *Ceratoporella.*

As in Paleozoic representatives, many Mesozoic stromatoporoids show a concentric layered appearance on the undersurface of hand specimens or when viewed in longitudinal thin section. These layers are periodic skeletal growth increments known as latilaminae. They are formed by alternating changes in the thickness or spacing of skeletal elements, or by a periodicity in the arrangement of the secondary skeleton. They may also be produced by preservational differences in the skeletal elements, perhaps due to varying amounts of organic material, leading to differing diagenetic susceptibility. Latilamination appears to be a reflection of different rates or types of skeletal growth and may indicate some cyclicity, possibly seasonal, of the environment in which stromatoporoids grew.

INTERNAL MORPHOLOGY

CONSTRUCTION OF THE SKELETON

The skeletal construction of many living calcified sponges consists of four successive growth stages: (1) organic skeleton; (2) spicular framework; (3) primary calcareous skeleton; (4) secondary calcareous skeleton (filling tissue). Some or all of these growth stages are inferred to have been present in Mesozoic stromatoporoids and are illustrated schematically in Figure 120.

1. Fine collagen fibers, known as spongin, occur in many sponges and in all demosponges. Spongin fibers are a few millimeters in diameter and are formed by numerous collagenous fibers 10 µm or less in diameter. Spongin is secreted by spongeocytes and is found in varying quantities in different groups.

2. Siliceous and calcareous spicules are known from Mesozoic stromatoporoids, placing their possessors in the classes Demospongiae and Calcarea, respectively. Spicules are secreted by sclerocytes. In demosponges, an axial filament appears within the sclerocyte, which serves as the template for silicification. Collenocyte cells are probably active in moving spicules to their final positions, at which point basal exopinacocytes engulf the spicules and cover them with a layer of spongin.

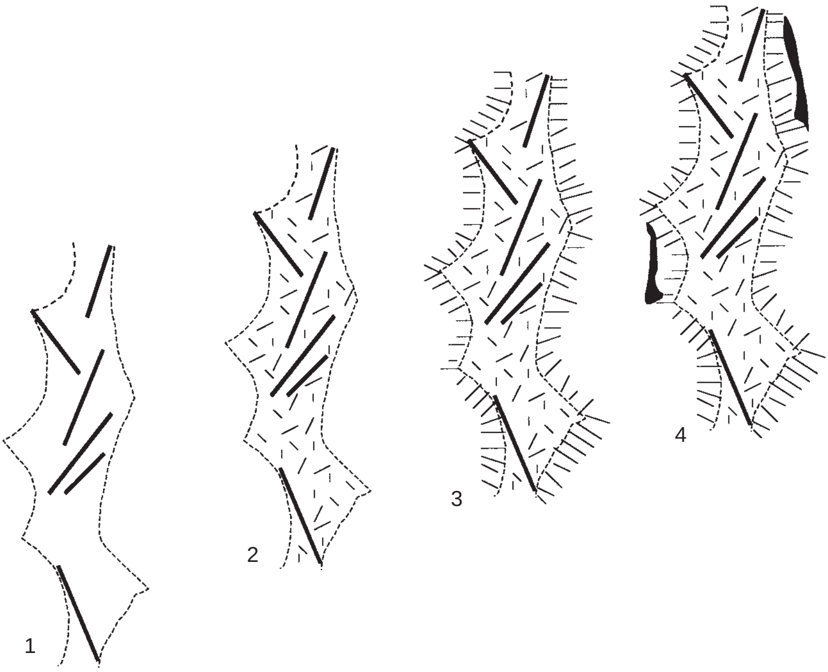


FIG. 120. Schematic illustration of the four successive skeletal growth stages inferred to have been present in Mesozoic stromatoporoids; *1,* primary spicule framework, probably bound with an organic matrix *(dotted lines);* 2, primary calcareous skeleton of irregular microstructure, forming meniscus-like around projecting spicules; 3,secondary calcareous skeleton forming orthogonal fibrous rim; 4, filling tissue of irregular tabulae (shown in black) (adapted from Wood, 1987).

Spicules are thus trapped and interconnected within the skeleton of spongin, from which the spicules echinate (protrude upward and outward from the fibers). As more spicules are moved into place and join the skeletal network, all parts of the spicule-spongin complex become covered with a similar layer of exopinacocytes. The skeleton of siliceous spicules and spongin fibers provides support for the soft parts of the sponge; in demosponge cultures raised in a silica-free medium, the aquiferous system fails. Spicules are highly variable in morphology and organization, and they often show considerable variety within different histological parts of an individual. Spicule tracts (bunches of spicules) may show an axial condensation from which they diverge in a plumose (as in Milleporellidae) or a plumulo-reticulate arrangement (as in Actinostromarianinidae), which radiate to the surface of the sponge.

3. The form of the primary calcareous skeleton is often determined by the position of the organic skeleton and may also be influenced by the positioning of the spicular skeleton.

The resultant primary calcareous skeletal elements fall into two categories: radial and concentric elements (Fig. 121). Radial elements may be pillars (of limited length) or columns (more continuous). Concentric elements are known as pillar-lamellae (short, discontinuous elements contiguous with pillars or columns) or laminae (independently secreted, continuous elements). Laminae are often punctured by pores, which are interpreted as oscular openings, as found in *Burgundia* (see Fig. 185*a–f*). Astrorhizae are often limited to interlaminar areas where laminae are present, although there may be some connection between successive generations. In some forms, the radial skeletal elements initiate from an axial

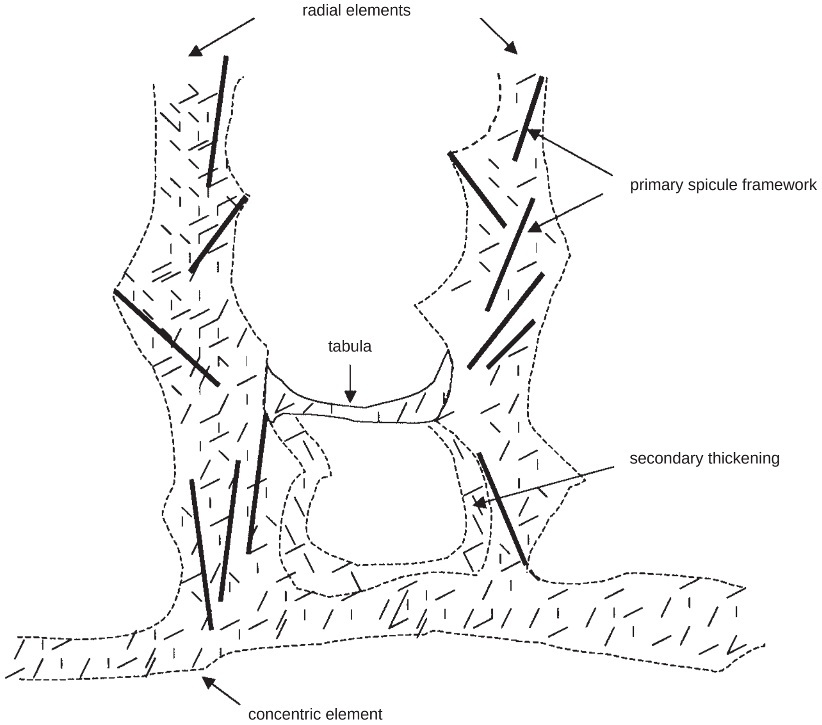


FIG. 121. Nomenclature of the skeletal elements in Mesozoic stromatoporoids (adapted from Wood, 1987).

condensed area (e.g., *Actinostromarianina,* Fig. 170,*3a–b*).

Sometimes the skeleton of Mesozoic stromatoporoids forms a reticulum where no distinction between radial and concentric elements can be made. This is often the case in the undifferentiated juvenile skeletal tissue at the base of stromatoporoid skeletons.

4. Only the peripheral areas of most calcified sponge skeletons are open, water-supplied frameworks covered by or filled with living soft tissue. Abandoned, older parts of the skeleton no longer occupied by living tissue are sectioned off or secondarily infilled by skeletal structures, which also provide a support platform for the soft tissue. A variety of secondarily precipitated structures (tabulae, secondary thickening, and backfill) constructed of various microstructures are common in Mesozoic stromatoporoids (Fig. 121). Tabulae are platelike, straight or curved elements that span between radial elements, parallel to the growth surface of the individual or across exhalant canal traces and oscular tubes. They may be precipitated at irregular intervals (independently) during the lifetime of the sponges or aligned as periodical growth increments. Tabulae often show a greater degree of alignment in forms with inferred thin veneers of tissue. They may be thin and of irregular microstructure or relatively thick, fibrous structures. Some Recent calcified chaetetid sponges possess tabulae (*Merlia* spp., *Acanthochaetetes* spp., and *Ceratoporella* sp.), but most other forms, especially *Ceratoporella*-like forms, form a backfill of solid skeleton, which may completely occlude the primary pore spaces that formerly housed the living tissue. The backfilling tissue forms syntaxially upon the primary skeleton, and, generally, the two components cannot be easily distinguished. Sometimes the development of backfill is limited to a secondary thickening of the

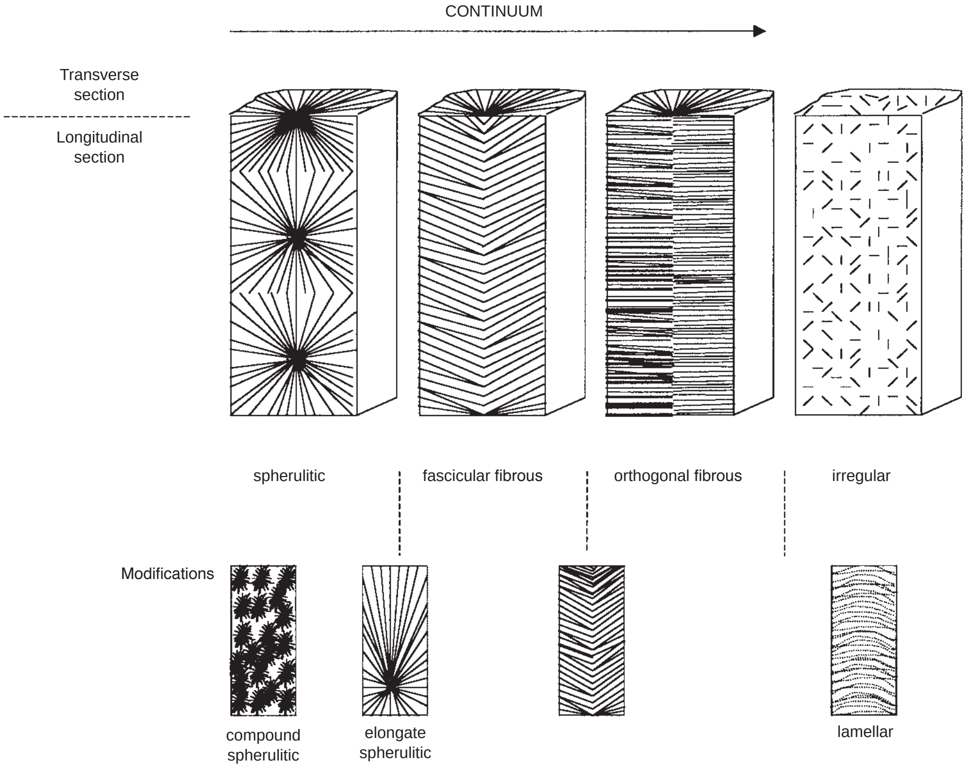


FIG. 122. Four main microstructural types of calcareous skeleton found in Mesozoic stromatoporoids, illustrated schematically as they appear in sections through a radial element. Modifications of these types are shown below the illustrations of the main types (adapted from Wood, 1987).

skeleton, especially the radial elements. It is not clear whether this overgrowth of crystals in optical continuity is an organic or inorganic process. Often, secondary backfill can initiate from a tabula, as found in *Ceratoporella.* Here, the distinction between types of filling tissue can be an arbitrary one. In other cases, such as the Cretaceous–Recent chaetetid *Acanthochaetetes,* tabulae may form contiguously with the primary skeleton, making a distinction between primary and secondary skeleton also problematic.

The following relationships have been determined between these three skeletal products in calcified sponges.

1. The calcified skeleton is precipitated directly within an aspiculate spongin framework or matrix, e.g., *Vaceletia* (Recent sphinctozoan) and possibly *Burgundia* (Mesozoic stromatoporoid).

2. Spicules are present, but only incorporated into the skeleton by chance, e.g., *Acanthochaetetes* (Recent chaetetid) and *Blastochaetetes irregularis* WOOD & REITNER, 1988 (Mesozoic chaetetid).

3. The calcified skeleton is precipitated around a primary spicule framework or lattice, e.g., *Petrobiona* (Recent calcarean) and *Actinostromaria* sp. (Mesozoic stromatoporoid).

4. The acicular crystals of the calcified skeleton initiate from the spicule bases within tracts, e.g., *Calcifibrospongia* (Recent stromatoporoid) and *Dehornella* (Mesozoic stromatoporoid).

5. The calcified skeleton is precipitated within a spongin matrix, which drapes,

meniscus-like, around a spicule framework, e.g., *Actinostromarianina lecompti* (Mesozoic stromatoporoid).

In addition to latilaminae, growth interruption surfaces may also be detected within longitudinal sections. These represent periods of considerable soft-tissue loss, due to sediment incursions or scour events, and may be followed by encrustation of the resulting free skeletal surface. The stromatoporoid soft tissue may subsequently regrow over some or all of the area, and skeletal growth will recommence. The undersurfaces, or within the skeleton, may also show epithecae. These are solid, platelike deposits of secondary tissue, which are often continuous across growth surfaces. When such structures appear within the skeleton, they are interpreted as having been precipitated in response to adverse environmental conditions.

MODES OF PROLIFERATION

Branches in Mesozoic stromatoporoids often arise from a basal nodule by either a dichotomy (longitudinal fission) or budding, which initiates from the axial part of the skeleton. Mode of branching affects the resultant branching form. Individuals may show a fasciculate arrangement of the branches.

BIOMINERALIZATION AND MICROSTRUCTURE

Sponges not only produce a diverse variety of microstructural fabrics (Fig. 122), but also form them via several biomineralization mechanisms. These mechanisms can be classed within genetic subdivisions, which are described below. This has the advantage of separating microstructures that have previously been classified together under the same descriptive heading, but which clearly have different modes of genesis (Wood, 1991b). Table 29 summarizes information concerning the supposed nonspicular biomineralization mechanisms found in Recent calcified demosponges, their products, and systematic distribution.

All biomineralization mechanisms employed by calcified sponges appear to precipitate crystals from beneath an organic layer that, to varying extents, acts as a template. The distribution of nucleation sites, presumably determined by organic tissue organization, also appears to be an important factor in determining the resultant microstructural type. In most cases, with the exception of irregular microstructures, the crystals are precipitated with their c-axes oriented perpendicular to the pinacoderm. When all three skeletal elements are present, the sequence of precipitation is always the same: (1) spicule formation, transportation, and orientation; (2) spongin-collagen fibers to bind the spicules in place; (3) calcareous skeleton precipitation.

The terms biologically induced, organic matrix-mediated (Lowenstam, 1981), and biologically controlled (Mann, 1983) have been established for describing the varying degrees of control of the organic component. Calcified demosponges appear to show representatives from all these types.

MINERALIZATION OF A COLLAGENOUS MATRIX

In this mode, the calcareous skeleton is wholly defined by the extent of a preformed collagenous framework of spongin that becomes calcified. This would seem to indicate an organic matrix-mediated mechanism, in which the cell manipulates an organic framework upon which regulated mineralization occurs (Lowenstam, 1981). Spicules may or may not play a role, but, where present, they appear to act as a framework around which the organic matrix is precipitated, and in the case of fibrous microstructures, they act as nucleation sites for the acicular crystal growth. Two living sponges calcify via calcification of an organic matrix, but they are systematically unrelated and produce totally different microstructures.

Vaceletia, a Recent aspiculate dictyoceratid (formerly verticillitid) sphinctozoan, produces a skeleton composed of a feltwork of aragonitic microfibrils known as microgranular

TABLE 29. Summary table of biomineralization mechanisms found in Recent calcified demosponges and calcareans, their products, and their systematic distribution (adapted from Wood, 2011).

Systematics	Genus	Biomineralization mechanism	Microstructure and mineralogy
Class Demospongiae			
Order Agelasida			
Family Astroscleridae	*Astrosclera*	intracellular	spherulitic aragonite
	Ceratoporella	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
	Stromatospongia	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
Order Haplosclerida			
Family Calcifibrospongiidae	*Calcifibrospongia*	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
Order Hadromerida			
Family Acanthochaetetidae	*Willardia*	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
	Acanthochaetetes	secretory pinacoderm	microlamellar calcite
Order Poecilosclerida			
Family Merliidae	*Merlia*	secretory pinacoderm	pencillate (fascicular fibrous) calcite
Order Dictyoceratida (formerly Verticillitida)			
Family Vaceletiidae	*Vaceletia*	noncollagenous organic template	microgranular irregular aragonite
Class Calcarea			
Order Lithonida			
Family Minchinellidae	*Plectroninia, Minchinella*	secretion by telmatoblasts	orthogonal calcite
Order Murrayonida			
Family Murrayonidae	*Murrayona*	secretory pinacoderm	pencillate (fascicular fibrous) calcite
Order Baeriida			
Family Petrobionidae	*Petrobiona*	secretory pinacoderm	radial flake (fascicular fibrous) calcite

irregular microstructure. New chambers are added periodically, and they initiate by the formation of a collagenous template below the upper pinacoderm layer. Mineralization first occurs within isolated spherical regions, extending along the length of the new chamber wall (GAUTRET, 1985). Crystals first form bundles of disoriented acicular rods (compact in the terminology of GAUTRET, 1985), which later become more granular (composite in the terminology of GAUTRET, 1985) during a further phase of precipitation. In some parts of the skeleton, the bundles may show a preferred orientation parallel to the collagenous fibers between which they grow. The pillars that support the hemispherical chambers form during the first mineralization phase by mineralization of organic strands. Older, abandoned chambers become filled with layered lenses of irregular microstructures, and although it is not clear whether these are the result of inorganic or organic mineralization, their form does suggest an organic origin.

Nonspicular fossil sphinctozoans, which bear an irregular calcareous skeleton, are inferred, by suggested affinity to *Vaceletia,* to have possessed a similar mode of biomineralization. In addition, spiculate stromatoporoids, e.g., *Newellia mira* (Carboniferous haplosclerid), and the calcitic species *Actinostromarianina lecompti* (Jurassic agelasid), bear irregular calcareous skeletons that appear to drape around a primary spicular skeleton, also implying direct mineralization of a collagenous template (Wood, 1987; Wood, Reitner, & West, 1989).

Calcifibrospongia (Recent haplosclerid stromatoporoid) also biomineralizes by calcification of an organic matrix. Here, the calcareous skeleton precipitates around a lattice of siliceous strongyles that are bound within spongin fibers. The calcareous skeleton forms elongate sclerodermites 60–110 µm long. Hartman (1979) suggested that the centers of calcification may form simultaneously within a particular length of fiber, where the acicular aragonite crystals grow out in all directions from each center until they reach the boundary of the organic fiber, or are stopped by the crystals of a neighboring sclerodermite. Spicules frequently appear to serve as the nuclei for the sclerodermites. *Calcifibrospongia* can show deposits of epithecal material varying from 40–250 µm thick, representing planes of the successive dieback and regrowth of the skeleton, but no other filling tissue or secondary skeleton is present.

Euzkadiella (Cretaceous haplosclerid stromatoporoid) possesses a microstructure similar to *Calcifibrospongia,* and although this form was originally calcitic rather than aragonitic, it has been inferred to have formed by the same process (Reitner, 1987a).

SECRETORY PINACODERM

Here, calcified sponges produce a calcareous skeleton by precipitation through a secretory pinacoderm via a thin mucous- or fluid-filled (possible polysaccharide) layer, resembling the process found in calcareous algae. This would indicate a biologically controlled mechanism of precipitation, in which the cell appears to act as a causative agent and in some way controls the precipitation of minerals (Mann, 1983). The muco-polysaccharide layer might provide a migration path and medium for joining Ca^{2+} and CO_{32-} ions, as known in scleractinian corals. This layer may also serve, to a lesser extent, as a template controlling the configuration of crystals. Several forms are at present collected under this subheading, until more details allow us to refine the scheme.

The calcareous skeletons of *Ceratoporella* (agelasid chaetetids) and *Acanthochaetetes* (hadromerid chaetetids) are thought to be produced by this mechanism. In *Ceratoporella,* the calcareous skeleton is formed of acicular or fibrous crystals arranged in a modified spherulitic form known as penicillate. Hartman and Goreau (1975) observed this skeleton to form around clots of organic matrix (possibly spongin) surrounding the heads of some spicules. Thus, to some extent, the positioning of the calcareous skeleton appears to be determined by the placing of the spicule and spongin frameworks. In the acanthochaetetids, the high-Mg calcite skeleton has an irregular microstructure of crystals (1–8 µm long) oriented in one plane only, giving the appearance of a microlamellar microstructure in longitudinal section. Instead of the abandoned parts of the skeleton being filled with a secondary epitaxial backfill, the portions below the living tissue are sectioned off by a series of tabulae or horizontal partitions. Growth of the tubule walls is incremental and layered, and the spines and tabulae grow in an integrated way as outgrowths form the calicle walls. However, secondarily precipitated tabulae are also known. The microscleres form a dense layer at the surface of the living tissue, while the tylostyles are aligned parallel to the tubule walls. In living forms, the spicules are not incorporated into the calcareous skeleton, but in fossil representatives they are, although by chance (Reitner

& ENGESER, 1983). The megascleres tend to occur parallel to the tubule walls, and the microscleres within the tabulae, perhaps indicating the formation of the latter near the living tissue surface. Nanometer-sized organic fibers act as the matrix for calcification, and the tubule wall centers are richest in organic material. Collagenous strands extend into the calcareous skeleton, which seem to act as anchorage points for the soft tissue, as noted in some scleractinian corals. The exhalant canals sometimes leave impressions on the skeletal surface as in *Ceratoporella.* Both *Ceratoporella* and *Acanthochaetetes* have considerable fossil records, extending to the upper Permian and Upper Cretaceous, respectively.

Many Mesozoic stromatoporoids, such as the Milleporellidae, are inferred to have formed their calcareous skeletons by this method (WOOD, 1987). These forms produce fascicular fibrous skeletons, similar to those of *Ceratoporella.*

PASSIVE SECRETORY PINACODERM (CEMENT)

Orthogonal microstructure is common in many fossil calcified sponges, including fossil demosponges. They are also found in some living calcarean sponges (e.g., *Minchinella*). This simple microstructural type could be explained by the cement-like precipitation of acicular crystals with their c-axis parallel to a secretory membrane. They would, as such, constitute a biologically induced precipitation mechanism, in which the cell appears to act as a causative agent in the precipitation of minerals, but where the cell has little control (LOWENSTAM, 1981). The Upper Jurassic agelasid stromatoporoid *Actinostromaria* forms a primary calcareous orthogonal skeleton upon a spicule lattice. *Actinostromarianina lecompti* shows a primary irregular calcareous skeleton and a secondary orthogonal fibrous one, which has a banded distribution, forming latilaminae throughout the growth of the individual (see Fig. 170,*3a–b*). This would seem to point to the mediation of some periodic environmental effect, such as warmer temperatures, causing an intermittent biologically induced precipitation.

INTRACELLULAR ORIGIN

Astrosclera (a Recent agelasid stromatoporoid) is the only known calcified sponge whose calcareous skeleton has an intracellular origin. The basal calcareous skeleton of *Astrosclera* consists of a fine reticulum of aragonite with no differentiation into pillars and laminae. Calcareous spherules are formed intracellularly by amoebocytes as small nuclei (15 µm) near the surface of the sponge and then transported to a position where they grow larger by epitaxial growth and add to the general calcareous skeletal network to produce a compound spherulitic microstructure. The spherules are known to possess an organic calcification center of approximately 7 mm in diameter, and they show several organic rich layers, one of which corresponds to the attachment of the spherules to the skeletal wall, where it is emplaced by a covering organic envelope. The living tissue penetrates the mesh of the skeleton to a depth of approximately 10 mm, and a secondary deposit of acicular calcite crystals partially fills the abandoned inner skeletal reticulum. In the Indian Ocean, *Astrosclera* secretes siliceous acanthostyles, but Pacific populations largely lack them; although, when present, the spicules are incorporated into the calcareous skeleton. There appears to be no discernible direct relationship between the spicules and the positioning of the calcareous skeleton; they are incorporated by chance. Below the pinacoderm are large exhalant canals, 60–80 µm in diameter, that branch downward and outward into the skeletal tissue to form astrorhizal-like structures. No tabulae are known, but secondary epitaxial backfill occurs as penicillate tufts in the abandoned parts of the skeleton.

A wide variety of fossil calcified demosponges are known that show this aragonitic spherulitic microstructural type, especially

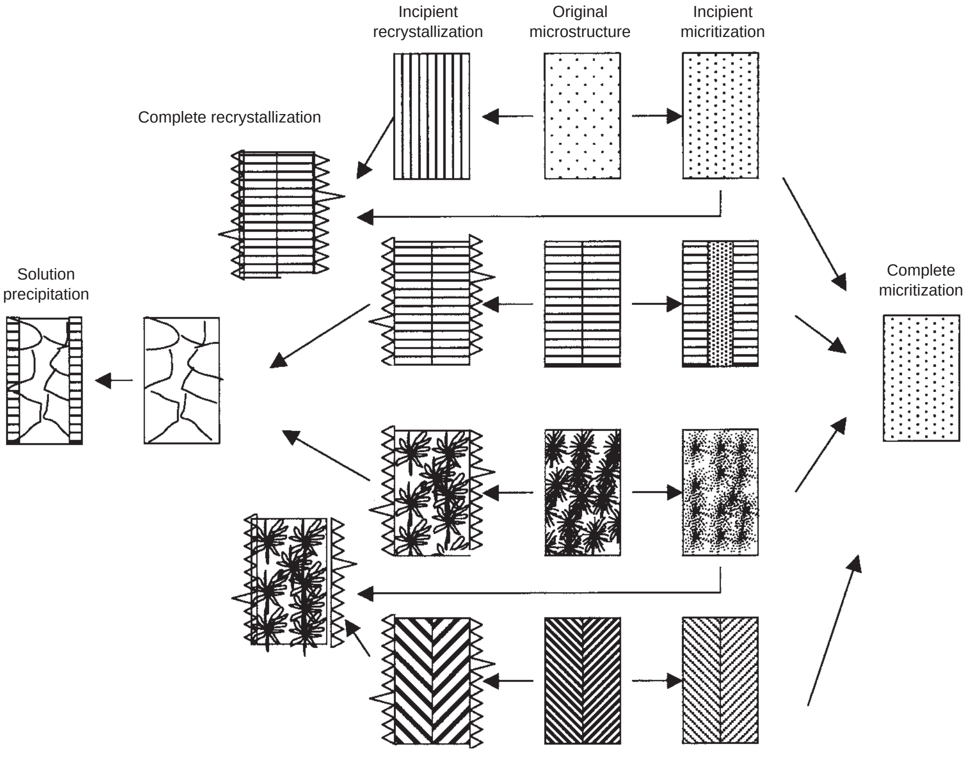


FIG. 123. Suggested diagenetic trends found in the calcareous skeletons of fossil calcified sponges; see Fig. 122 for additional microstructure symbols (adapted from Wendt, 1984; Wood, 1987).

from the Upper Triassic of Italy and Turkey. *Astrosclera* is considered to have an Upper Triassic age (see Hypercalcified Extant and Fossil Chaetetid-Type and Post-Devonian Stromatoporoid-Type Demospongiae: Systematic Descriptions, p. 209–292). However, although the biomineralization mechanism was probably the same, taxonomic affinity cannot be assumed until we have spicule confirmation.

MINERALOGY

Living calcified sponges may be aragonitic (e.g., *Ceratoporella*) or high-Mg calcite (e.g., *Acanthochaetetes* and *Merlia*). Although our sample size is small, mineralogical type has some stability within families, but not at higher taxonomic levels. Mineralogical composition therefore appears to be of low phylogenetic significance and to have arisen independently within different families.

Due to the fine microstructural preservation of many Mesozoic stromatoporoids, their original mineralogy is inferred to have been low-Mg calcite (WOOD, 1987). However, forms with original aragonite preservation are known from several Carboniferous (Pennsylvanian), middle to upper Permian, and Upper Triassic localities.

It is clear that the mineralogy of calcified sponges has varied throughout the Phanerozoic. Although our knowledge is patchy, especially from the Tertiary, aragonitic forms are only known from the Carboniferous (Pennsylvanian) to Upper Triassic, and Recent (WOOD, 1987; STANLEY & HARDIE, 1998). These periods correspond to the aragonite facilitating phases of SANDBERG (1983) and suggest that mineralogy of sponge calcareous skeletons may be under such environmental rather than taxonomic controls. Taxa with different mineralogies coexisted, such as the chaetetid genera *Acanthochaetetes* (high-Mg calcite) and *Ceratoporella* (aragonite) and milleporellid stromatoporoids (possibly low-Mg calcite), during the Upper Jurassic to Upper Cretaceous. Perhaps the calcareous skeletons in these groups arose during their appropriate facilitating phases (Wood, 1987). We require a greater diagenetic understanding, valid phylogenetic allocations, and far more material if we are to fully assess the significance and controls of mineralogical composition in calcified sponges.

DIAGENESIS

DIAGENESIS OF THE CALCAREOUS SKELETON

Diagenetic alteration is significant in stromatoporoids, as it may enhance, modify, or destroy primary skeletal characteristics.

Wendt (1984) and Wood (1987) have described diagenetic trends in Mesozoic stromatoporoids in which they distinguished three independent processes: alteration of mineralogy, alteration of microstructure, and the formation of diagenetic pseudostructures. Stromatoporoids are also subject to the range of diagenetic replacements found in other calcareous fossils, such as chertification.

ALTERATION OF MINERALOGY

Although there are several locations within upper Paleozoic and Mesozoic strata that yield forms with original aragonite preservation, most fossil sponge material, including most Mesozoic stromatoporoids, is now low-Mg calcite. Low-Mg calcite is the most stable mineralogy under normal diagenetic conditions, and originally low-Mg forms tend to retain their original mineralogy and possess well-preserved microstructures. Originally high-Mg calcite always reverts to low-Mg calcite, sometimes with loss of microstructural detail, as known from fossil acanthochaetetids, but aragonitic forms tend to be wholly recrystallized with no or few traces of primary microstructure.

ALTERATION OF MICROSTRUCTURE

Wendt (1984) described microstructural alteration from aragonitic Permian and Triassic material in terms of micritization, cementation, and recrystallization (transformation). Figure 123 shows suggested diagenetic trends found in the calcareous skeletons of fossil calcified sponges (adapted from Wendt, 1984, and Wood, 1987). Completely micritized, recrystallized structures and solution precipitation may be derived from any of the four original microstructures (see Fig. 122).

Micritization

Micritization is attributed to the decomposition of organic matrices with biominerals. The final result is the complete breakdown of the original crystal arrangement and the formation of irregularily organized granular crystals between 1 and 8 µm in length.

Micritization appears preferentially to attack areas in the microstructure most accessible to percolated fluids or where organic matter was concentrated. In orthogonal microstructure, micritization starts from the central axis of calcification and may increase in width, to eventually totally obscure the original fibers. The centers and edges of spherules are the most susceptible areas in spherulitic microstructures. Fascicular fibrous microstructure appears to be least susceptible to micritization.

Cementation

Modern calcified demosponges show the rapid precipitation of micritic aragonite within the empty cavities formed in abandoned basal parts of the skeleton.

Two phases of cementation are often found within the skeletons of Mesozoic stromatoporoids. (1) Early rim cements, precipitated epitaxially to the microstructural fibers of the skeletal elements. Syntaxial crystal growth may also occur in forms with fibrous microstructures, leading to thickening of the skeletal elements. Aragonitic calcareous sponges often show acicular aragonite crystals growing isopachously from the skeletal elements, including the tabulae. (2) Later drusy or equant cements within the interskeletal pore space. The preservation of spicules within the interskeletal spaces, or projecting into the interskeletal spaces, indicates that this cementation can occur before the diagenetic breakdown of the spicules. Since Recent calcified sponge spicules are known to dissolve during the lifetime of individuals (Hartman & Goreau, 1970), this cementation must be a very early diagenetic event.

Recrystallization

In Mesozoic stromatoporoids, recrystallization leads to a general increase in crystal size. During early recrystallization, the individual crystals in the three fibrous microstructures will maintain their acicular nature, but continued recrystallization will cause the growth of more equidimensional crystals. Previously micritized specimens can be recrystallized to form coarse mosaics with residual micritized areas.

DIAGENETIC PSEUDOSTRUCTURES

Pseudolamellar structure and scalenohedral pseudostructure have been noted in Mesozoic stromatoporoids (Wendt, 1984; Wood, 1987). Under SEM, pseudolamellar structure consists of interlocked, curved, bladed crystals, 5–10 µm thick and a few mm long. Wendt suggested that microlamellar structure is probably derived from a calcitic irregular microstructure showing some parallel orientation. Scalenohedra appear as saw-toothed formations or indentations projecting toward the center of the skeletal elements. A similar structure has been characterized by Bathurst (1975) as being a recrystallization fabric.

DIAGENESIS OF SPICULES

Spicules have been found in several Mesozoic stromatoporoid genera from many localities with differing diagenetic histories. They may be originally siliceous (demosponges) or calcareous (calcareans) and are often incorporated into the calcareous skeleton. In Recent calcified demosponges, spicules consist of hydrated amorphous silica (Hartman & Goreau, 1970; Jones, 1979). Recent calcareans have single crystal high-Mg calcite spicules. Minor amounts of SO_4^{2-}, Sr^{2+}, and Na^+ have also been found in calcitic spicules (Jones, 1979). Use of standard carbonate stains greatly enhances the visibility of fossil spicules. It is still unclear whether the absence of microscleres is due to nonsecretion or to their increased susceptibility to diagenetic loss.

Spicule diagenesis begins during the lifetime of Recent calcified demosponges. The processes are not fully known but have been partially described by Hartman and Goreau (1970) and Hartman (1979).

Due to the thermodynamic instability of inphase silica and calcite, silica spicules begin to corrode at high pH. Pitting of the spicule surface and corrosion of the acanthostyle spines and of the projecting tips have been noted in Recent and fossil forms (Gray, 1980; Hartman, 1980a). This corrosion of spicules during the lifetime of a sponge starts in the older parts of the specimen. Hartman and Goreau (1970) noted that spicule dissolution sometimes starts from the axial filament; in other cases, the head of the spicule is most susceptible. Eventually, spicule cavities or molds are left. The subsequent diagenetic history of the spicules appears to be detemined by the role they played in relation to the calcareous skeleton.

Originally Siliceous Spicules

Early diagenetic processes have nearly always replaced the amorphous silica of demosponge spicules by a secondary polycrystalline mosaic of $CaCO_3$, SiO_2, or FeS_2, or a single crystal pseudomorph of SiO_2.

Early Diagenesis

During life, spicules may be wholly free or incorporated partially or fully into the primary or secondary calcareous skeleton. In forms that produce a secondary backfill, the spicule molds may become filled with a syntaxial growth of calcite crystals, making it impossible to determine the original placing and presence of the spicules.

Later Diagenesis

If not totally obliterated by epitaxial skeletal growth, the mold may be subsequently filled with other minerals.

Calcite Pseudomorphs

Calcite pseudomorphs may be mono- or polycrystalline. Where calcite pseudomorphs are found, the microstructure of the calcareous skeleton is always well preserved. Pseudomorph boundaries are only apparent when they are covered with a thin micrite envelope or when they are of different calcite mineralogy from the calcareous skeleton as shown by staining. Otherwise, the pseudomorphs appear as spicule ghosts as in *Parastromatopora japonica,* described by Hartman and Goreau (1970, fig. 16). Here, the spicules are recognized by their crystallographic difference from the fibers of the calcareous skeleton microstructure. The calcite pseudomorphs tend to be found in the core areas of the specimens, which have been partially protected from later leaching of corrosive pore waters.

In forms where the originally siliceous spicules formed a primary skeletal framework, the calcite pseudomorphs are rarely found projecting into the interskeletal spaces. Most frequently, they terminate abruptly due to corrosion of the projecting tips. In *Blastochaetetes irregularis* Wood & Reitner, 1988, where calcareous pseudomorphs are preserved within the tubules, the areas of spicule contact with the calcareous skeleton are more poorly preserved than in areas where spicules are encased by spar within the pore space. The skeletal calcite appears to have a corrosive effect upon the spicules.

Calcite pseudomorphs are also susceptible to micritization. All stages, from well-preserved pseudomorphs with a thin micritized coating, through badly micritized, but discernible spicules forming diffuse elongate and circular lighter areas, to a totally micritized central zone within the calcareous skeletal elements are noted.

Pyrite Pseudomorphs

Pyrite pseudomorphs appear as agglomerates or as chains of pyrite crystals (see *Actinostromarianina lecompti,* Fig. 170,*3b*). They are often shorter than calcite pseudomorphs, but both pseudomorph types are frequently found together in the same specimen (Wood & Reitner, 1986) indicating that pyritization has occurred either after partial dissolution of the silicious spicule or as replacement of the calcite pseudomorph. Examples have been found in which threads of pyrite are seen forming within calcite pseudomorphs. Pyritization appears to nucleate upon the organic axial filament, probably due to bacterial activity, and this may occur at a very early stage of diagenesis.

Pyrite pseudomorphs are often found in large numbers near the outer edges of specimens (see Wood & Reitner, 1986, pl. 35,*3*), and pseudomorphs can remain after total obliteration of the calcareous skeleton by subsequent silicification.

Siliceous Spicule Pseudomorphs

Siliceous spicule pseudomorphs are occasionally found in Mesozoic stromatoporoids. They are found in chertified areas of specimens, often where the calcified skeleton has been totally obliterated and can be exceptionally well preserved.

The typical corrosion and pitting features noted by Hartman and Goreau (1970) in Recent calcified demosponge spicules are seen on these pseudomorphs. Axial canals are preserved, but no acanthostyle spines are noted. Considering their excellent preservation, it is therefore unlikely that they were originally acanthostyles.

Siliceous spicule pseudomorphs sometimes appear dark brown and microgranular. The axial canals are not visible, and the brownish granular appearance and high relief of some pseudomorphs suggest that the original spicule mineralogy has been altered. Gray (1980) noted that the occurrence of this microgranular silica within spicule pseudomorphs and not within the chalcedonic silica walls, as well as the retention of delicate spicule corrosion features, are good evidence of an original mineralogy of opal A in fossil calcified demosponges, as in their extant relatives.

PRESENT CLASSIFICATION

The following lines of evidence suggest that the formation of a basal calcareous skeleton in sponges is a simple process and that sponges can calcify with relative ease.

1. Calcareous skeletons have a wide systematic distribution within the Porifera. Calcified demosponges are known from the orders Haplosclerida, Agelasida, Hadromerida, and Poecilosclerida. Calcified calcareans are known from both the Calcinea and the Calcaronea.

2. Different microstructures and seemingly different biomineralization mechanisms are present within closely related forms. For example, both *Astrosclera* and *Ceratoporella* are haplosclerids, but one produces a spherulitic microstructure with an intracellular origin and the other an elongate spherulitic one via a secretory pinacoderm. In addition, members of the same clade appear to have independently produced different calcareous mineralogies and microstructures at different times (e.g., *Newellia mira* and *Euzkadiella erenoensis*) (Wood, Reitner, & West, 1989).

3. The closest relatives of Recent calcified forms are noncalcified (e.g., *Spirastrella* to *Acanthochaetetes,* and *Agelas* to *Astrosclera* and *Ceratoporella*).

4. Some species appear to have a facultative ability to calcify. There are four species of the genus *Merlia,* but only two produce a calcareous skeleton.

5. The crystals precipitated by sponges do not have a unique crystal habit, trace element, or isotopic composition, which points to a minimal intervention of biological processes. The $\delta^{18}O$ signature of calcified demosponges all fall within the field of normal seawater, indicating that little vital fractionation occurs (e.g., Rosenheim & others, 2004).

6. The favored polymorph of calcified demosponge calcareous skeletons follows the oscillating trend first proposed by Sandberg (1983) and Stanley and Hardie (1998).

It is clear that the mere possession of a calcareous skeleton has little higher taxonomic significance. In addition, the calcareous skeleton is convergent in many characteristics.

Gross Morphology

Although the gross morphology of Mesozoic stromatoporoids is often subject to environmental control, there does appear to be stability within some species. However, gross morphology can be used only as a subsidiary generic or specific feature, and then only with caution.

Surface Features

Stromatoporoid surface features are an expression of the relative thickness of soft tissue, the aquiferous system required to drain it, and the position of this system relative to the areas of skeletogenesis. These features may not always be consistent within a species and hence can only be used as subsidiary species characteristics.

Spicular Skeleton

In Mesozoic stromatoporoids, spicule type and arrangement are the best taxonomic criteria available, and the only criteria of use in high-level systematic allocation. They offer the only indication of taxonomic affinity within the Porifera. However, it is highly likely in the evolution of demosponges that the basic monaxon megasclere spicule has evolved several times. For this reason, much stress has been laid upon the use of microscleres for demosponge systematics. Unfortunately, the majority of known Mesozoic stromatoporoid spicules are monaxon megascleres and few microscleres have been found.

The following relationships have been determined between the primary spicule framework and the secondary calcified skeleton.

1. A calcified skeleton without spicular skeleton (e.g., *Vaceletia, Burgundia*).

2. Spicules present, but placing is independent of calcified skeleton: i.e., spicules are incorporated into the skeleton by chance (e.g., *Blastochaetetes irregularis* WOOD & REITNER, 1988*, Ceratoporella*).

3. The calcified skeleton is precipitated around a primary spicule framework or lattice:

3a. The crystals of the calcareous skeleton initiate from spicule bases: e.g., *Dehornella.*

3b. The calcified skeleton is precipitated around a spicule framework: e.g., *Actinostromarianina lecompti* and *Actinostromaria* sp.

The way in which forms construct their skeletons is taken to be of family level and lower taxonomic significance when combined with spicule data.

Microstructure

Microstructure seems to be the result of the form of organic template and the biomineralization mechanism or mechanisms employed by the sponge. Microstructure of the calcareous skeleton may be a highly specific characteristic that allows placement of aspiculate fossil forms within particular orders. Some combinations of microstructure and mineralogy, however, are known only in the fossil record, and data about the systematic distribution of biomineralization mechanisms in sponges is insufficient to assess the relative status of differing microstructures. It would seem probable that biologically controlled precipitations (e.g., intracellular spherulites) would have greater higher systematic use than biologically induced ones (e.g., orthogonal cement).

Internal Organization of the Calcareous Skeleton

REISWIG (1975) stated in his study of the aquiferous systems of three living marine demosponges that the aquiferous systems of two unrelated species, *Halichondria panicea* (order Halichondrida) and *Haliclona permollis* (order Haplosclerida) were so similar that it was impossible to make species determinations of desilicified sections on the basis of canal organization alone. This suggests that the construction and organization of the aquiferous system can only be used as a very low-level taxonomic criterion.

The internal organization of the sponge calcareous skeleton can be taken to be a direct reflection of soft-tissue and aquiferous system organization and will be of low systematic significance. In general, forms that have a thin veneer of tissue and, therefore, show traces of the exhalant canal system as astrorhizal grooves or ridges in the surface of the calcareous skeleton produce a compact skeletal network with little or no internal traces of the aquiferous system. In contrast, forms that have a greater thickness of living tissue have penetrating aquiferous systems, thus producing an open calcareous skeleton.

Some skeletal features have been found to be extremely variable: e.g., presence or absence of laminae. These can also no longer be used as significant taxonomic features.

Mineralogy

Mineralogy appears to be of low phylogenetic significance, having arisen independently within several living calcified demosponge families. It is proposed that this feature not be used beyond the family level. The Porifera, both living and fossil, remains one of the most difficult groups to systematize and hence construct reliable phylogenies. Although cladistic analyses have been attempted for Recent poriferans, these have as yet proved most inconclusive, due to the lack of understanding of the various character states. With no soft tissue and uncommon spicule preservation and the dominance of skeletal features that are of no higher taxonomic importance, this situation is compounded for fossil forms. The possibility of much further insight remains bleak.

The following classification outline is adopted in this *Treatise* for Mesozoic and

Cenozoic stromatoporoids. The placing of families in the Porifera has been determined by their spiculation; those families with no spiculate representatives remain as *incertae sedis* within the Porifera. The phylum allocation of some families remains uncertain.

Class DEMOSPONGIAE Sollas, 1885
  Order HADROMERIDA Topsent, 1894
    Family ACANTHOCHAETETIDAE Fischer, 1970
    Family SUBERITIDAE Schmidt, 1870
    Family SPIRASTRELLIDAE Ridley & Dendy, 1886
  Order CHONDROSIDA Boury-Esnault & Lopès, 1985
    Family CHONDRILLIDAE Gray, 1872
  Order POECILOSCLERIDA Topsent, 1928
    Family MERLIIDAE Kirkpatrick, 1908
  Order HALICHONDRIDA Gray, 1867
    Family UNCERTAIN
  Order AGELASIDA Hartman, 1980b
    Family ASTROSCLERIDAE Lister, 1900
  Family MILLEPORELLIDAE Yabe & Sugiyama, 1935
    Family ACTINOSTROMARIIDAE Hudson, 1955c
    Family ACTINOSTROMARIANINIDAE Wood, 1987
    Family UNCERTAIN
  Order HAPLOSCLERIDA Topsent, 1928
    Family CALCIFIBROSPONGIIDAE Hartman, 1979
    Family EUZKADIELLIDAE Reitner, 1987a
    Family NEWELLIDAE Wood, Reitner, & West, 1989
  Order DICTYOCERATIDA Minchin, 1900
    Family VACELETIIDAE Reitner & Engeser, 1985
  Order UNCERTAIN
Class CALCAREA Bowerbank, 1864
    Family BURGUNDIIDAE Dehorne, 1920
    Family UNCERTAIN
  Subclass CALCINEA Bidder, 1898
  Order MURRAYONIDA Vacelet, 1981
    Family MURRAYONIDAE Dendy & Row, 1913
    Family PARAMURRAYONIDAE Vacelet, 1967a
  Subclass CALCARONEA Bidder, 1898
  Order LITHONIDA Vacelet, 1981
    Family MINCHINELLIDAE Dendy & Row, 1913
  Order BAERIIDA Borojevic, Boury-Esnault, & Vacelet, 2000
    Family PETROBIONIDAE Borojevic, 1979
    Family LEPIDOLEUCONIDAE Vacelet, 1967a

HYPERCALCIFIED EXTANT AND FOSSIL CHAETETID-TYPE AND POST-DEVONIAN STROMATOPOROID-TYPE DEMOSPONGIAE: SYSTEMATIC DESCRIPTIONS

Ronald R. West, Jean Vacelet, Rachel A. Wood, Philippe Willenz, and †Willard D. Hartman

Class DEMOSPONGIAE Sollas, 1885

[Demospongiae Sollas, 1885, p. 395] [=Demospongea de Laubenfels, 1955, p. 36]

Porifera with siliceous spicules and/or a fibrous skeleton, or occasionally without a skeleton. Skeleton composed of spongin fibers alone or together with siliceous spicules. Spicules are either monaxonic (either monactine or diactine) or tetraxonic (tetractine), never triaxonic. The axial filament is embedded in a triangular or hexagonal cavity. Spongin almost always present; forms discrete fibers or binds other skeletal elements. Some groups, however, build complex fiber skeletons without spicular elements, and other minor groups produce a hypercalcified basal skeleton in addition to their other skeletal elements, or develop an aragonitic skeleton without spicules. These variants contribute to a wide range of morphological heterogeneity of the class. Aquiferous systems are usually of leucon type. Both oviparous and viviparous reproductive strategies occur (Hooper & van Soest, 2002b, p. 15). [The date of Sollas's (1885) proposed name was discussed by Finks and Rigby (2004a, p. 9). Demospongiae is proposed here as the valid name because there are no rules for changing the desinence of higher order taxa, and, in this case, the original spelling adopted by Sollas (1885) has been widely accepted and maintained by zoologists. Acceptance of the subclasses Tetractinomorpha Lévi, 1953, and Ceractinomorpha Lévi, 1953, Demospongiae, has diminished in the contemporary literature, as these groups have been recognized to contain polyphyletic taxa (Hooper & van Soest, 2002b, p. 16–17). This has been confirmed by a recent analysis of the phylogenetic relationships of the orders of Demospongiae based on 18S and 28S rRNA (Borchiellini & others, 2004); so these subclasses will not be used here.] *?Silurian, Middle Devonian–Holocene.*

Order HADROMERIDA Topsent, 1894

[*nom. correct.* de Laubenfels, 1936, p. 139, *pro* suborder Hadromerina Topsent, 1928, p. 143, *nom. transl. ex* Hadromerina Topsent, 1894, p. 6] [=Clavulina Vosmaer, 1887, p. 328, *partim*; =Astromonaxonellida Dendy, 1905, p. 106]

Jean Vacelet, Ronald R. West, and Philippe Willenz

Demospongiae with monaxonic megascleres (tylostyles, subtylostyles, oxeas, or derivatives) forming radiate or subradiate skeletal arrangement, sometimes only obvious in peripheral skeleton; ectosomal spicules usually smaller than choanosomal ones, and, where present, they may produce a cortical skeleton; spongin often sparse, producing firm non-elastic consistency; microscleres may include various forms of euasters, spirasters, rhabds, microxeas, and/or raphides in trichodragmata, or absent in many taxa (Hooper & van Soest, 2002c). [Finks and Rigby (2004d, p. 724) give the author and date of this order as Topsent, 1898, with the following name history: *nom. correct.* de Laubenfels, 1955, p. 39, *pro* suborder Hadromerina Topsent, 1898, p. 93]. *?Silurian, Middle Devonian–Holocene.*

Family ACANTHOCHAETETIDAE Fischer, 1970

[Acanthochaetetidae Fischer, 1970, p. 199] [=Tabulospongiidae Mori, 1976, p. 8]

Hypercalcified sponges with a basal calcareous skeleton that is attached to substratum; thin layer of living tissue coating outermost layer of basal skeleton and containing siliceous spiculation of tylostyles as megascleres, and pointing outward; and common, relatively large streptasters. [Based on *Acanthochaetetes wellsi*, the only known living representative of the genus, Hartman and Goreau (1975) and Hartman (1982) suggested the sclerosponge family Acanthochaetetidae be classified in a separate order, Tabulospongida. This suggestion is no longer accepted as it overemphasizes the presence of a calcareous skeleton; *Acanthochaetetes* is now assigned to the Hadromerida (Rützler & Vacelet, 2002).] *Upper Jurassic–Holocene.*

Acanthochaetetes Fischer, 1970, p. 199 [**A. seunesi*; OD; holotype, MNHN Institut de Paléontologie, R05599] [=*Acantochaetetes* Ivanovskiy, 1973, p. 267, *nom. null.;* =*Tabulospongia* Mori, 1976, p. 2 (type, *T. horiguchii*, OD)]. Domical to columnar basal skeleton of high Mg calcite composed of radially arranged tubules, circular to elliptical in cross section; tubule walls thick, lined with very fine, longitudinally arranged or irregularly clumped spines that are the same microstructurally as walls; tabulae complete, irregularly spaced, horizontal or concave, some with meniscus fillings adjacent to tubule walls; tubules increase by longitudinal fission, less commonly by intertubular budding; microstructure lamellar (irregular *sensu* Wendt, 1979; microlamellar *sensu* Cuif & others, 1979); basal skeleton commonly occurs; spicules are siliceous, whereas basal skeleton is calcitic, composed of iron-rich low Mg calcite (Reitner & Engeser, 1987, p. 17); tylostyle megascleres from about 200 to 350 µm long; spiraster microscleres approximately 10 to 30 µm in diameter. [The only extant representative is *Acanthochaetetes wellsi* Hartman & Goreau (1975, p. 2–12, fig. 1–9, 11–14, holotype, YPM 9077). Mesozoic material consists of a fragmented but seemingly spheroid skeleton composed of radiating tubes, oval or circular in cross section, ranging from 0.6 mm to 1.2 mm in diameter. Recent material of *A. wellsi:* massive demosponge with calcitic skeleton made up of adjoining vertical tubes (tubules) with common walls. Basal parts of the tubules partitioned by vertical tabulae. Walls ornamented by spines that are arranged in vertical lines or clumped irregularly. Both walls and spines have a microstructure of stacked lamellae. The surface of the skeleton shows starlike impressions (astrorhizae) from meandering exhalant canals converging upon single oscula. Basal layer with concentric growth lines covering lower surface of sponge. Size ranging from under 1 cm to over 18 cm (diameter of live tissue area). Living tissue (as seen on only extant species, *A. wellsi*) cream colored, coating the calcareous skeleton, in which it is anchored by thin fascicles of collagen fibrils that extend through canaliculi of the skeleton. Choanocyte chambers spherical, 30–35 µm in diameter, choanocytes with periflagellar sleeves. Soft tissue includes masses of pseudogemmules in basal crypts of the tubules, covered by the outermost tabulae that are apparently dormant bodies consisting of clusters of thesocyte-like cells. Intercellular bacteria sparsely distributed in the mesohyl. Neither spongin fibers nor perispicular spongin occur. Siliceous spicules (observed in *A. wellsi*) occur in the living tissue and include erect tylostyles (points toward surface, 286 µm by 3.4 µm, and 7.4 µm head diameter) and spiraster-like and amphiaster-like microscleres (in three dimensions, being 5 µm by 6 to 20 µm and 28 µm) localized in a layer in the outer tissue. Microsclere spines are often branched and closely spaced, thus obscuring the axis. Some microscleres can be seen adhering to the calcareous skeleton and may thus become incorporated during fossilization, as described for *A. seunesi* (Reitner & Engeser, 1983). Growth rate of *A. wellsi* very slow, ranging from 50–450 µm/yr, according to carbon isotope records (Böhm & others, 1996; Reitner & Gautret, 1996).] *Upper Jurassic–Holocene*: France, Italy, Spain, Greece, *Upper Jurassic–Upper Cretaceous*; France, *Paleocene*; Spain, *Eocene*; western Pacific (New Caledonia, Great Barrier Reef, Okinawa, Guam, Mariana Islands, Philippines, Palau, Japan), *Holocene.*——Fig. 124*a–e.* **A. seunesi; a,* high domical to columnar growth form, upper Albian, northern Spain, ×2.75 (Reitner & Engeser, 1987, p. 14, fig. 2); *b,* transverse section of tubules in holotype, note spines on tubule walls, Cenomanian, Pyrenees, northern Spain, ×8 (Fischer, 1970, pl. F,*3*); *c,* longitudinal section of tubules, note spines on tubule walls, Cenomanian, Pyrenees, northern Spain, ×7.7 (Fischer, 1970, pl. F,*4*); *d,* detail of longitudinal section of tubules, note spines on tubule walls and meniscus fillings at junction of walls and some tabulae, upper Albian, Cretaceous, d'Alava province, northern Spain, ×68 (Engeser, Floquet, & Reitner, 1986, pl. 1,*6*); *e,* diagrammatic sketch of walls, spines, tabulae, and meniscus fillings associated with some tabulae, ×52.5 (Fischer, 1970, p. 200, fig. 32).——Fig. 125*a–c.* **A. seunesi; a,* SEM photograph of bundles of high-Mg calcite crystals that form the primary central wall structure, upper Albian, northern

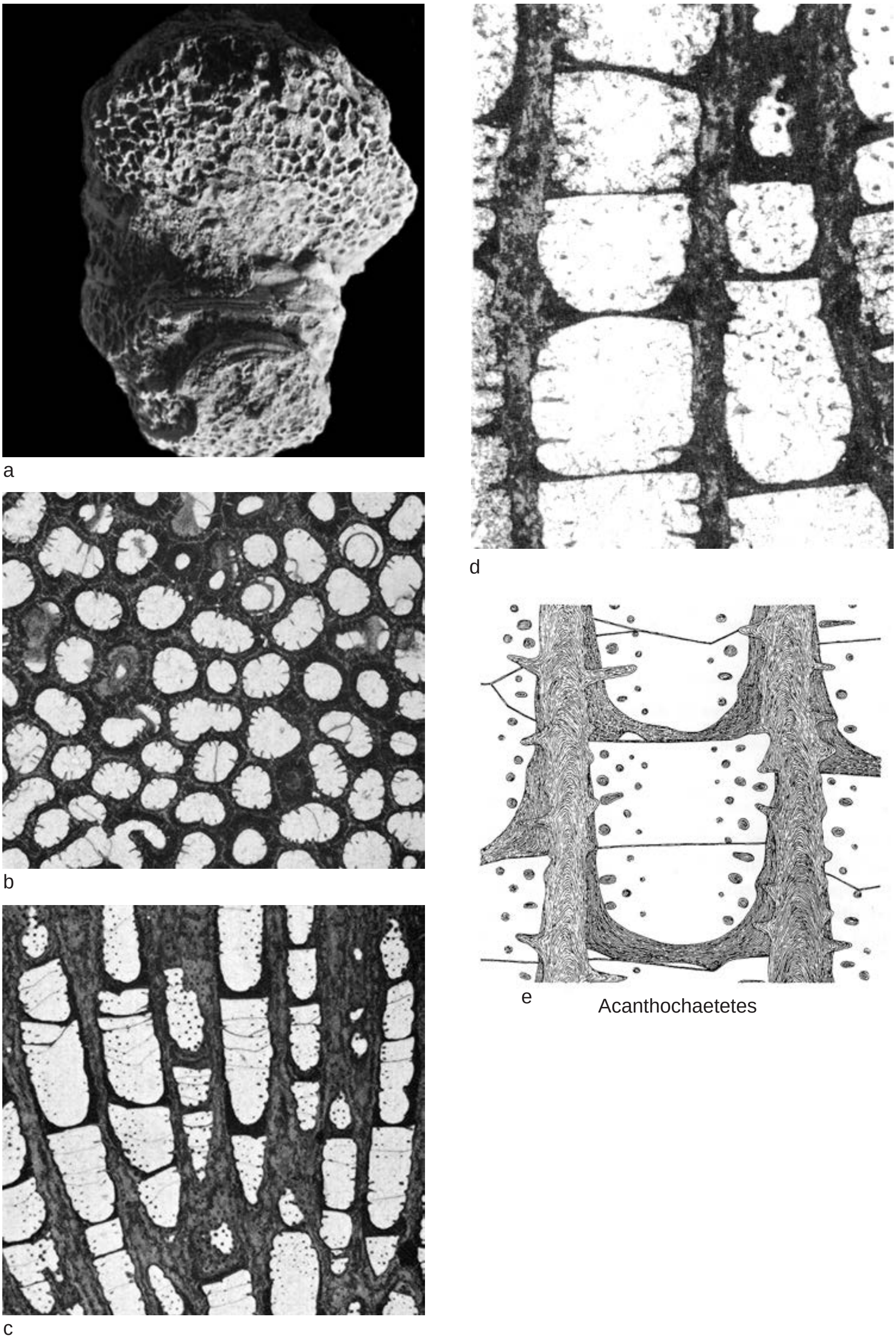


Fig. 124. Acanthochaetetidae (p. 210–214).

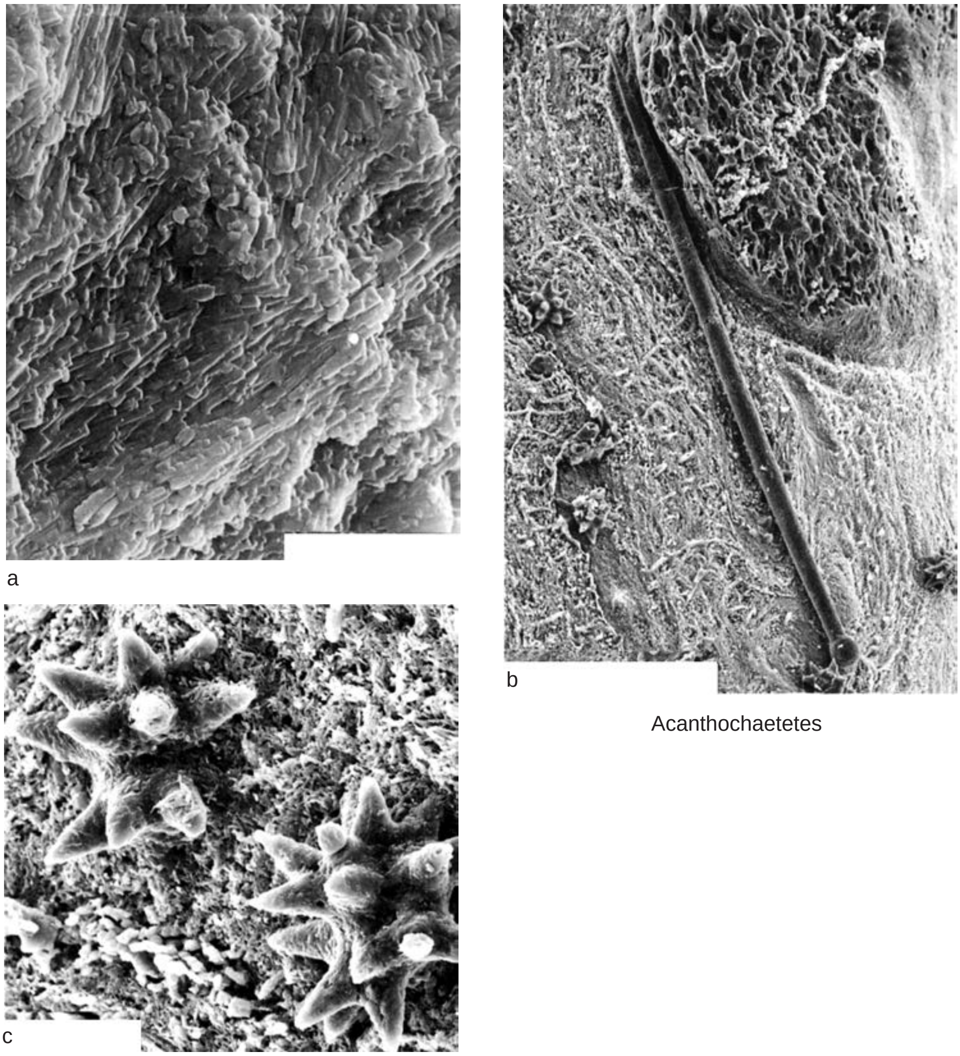


FIG. 125. Acanthochaetetidae (p. 210–214).

Spain, ×4750 (Reitner & Engeser, 1987, p. 14, fig. 4); *b,* SEM photograph of tylostyle megasclere, upper Albian, northern Spain, ×280 (Reitner & Engeser, 1987, p. 15, fig. 8); *c,* SEM photograph of spiraster microscleres, upper Albian, northern Spain, ×1450 (Reitner & Engeser, 1987, p. 15, fig. 10).——FIG. 126*a–h. A. wellsi* HARTMAN & GOREAU, 1975; *a,* living specimen *in situ* from Touho reef, New Caledonia, 15 m depth, ×0.5, and see also Fig. 1.1) (West & others, 2013); *b,* SEM view of surface of a cleaned skeleton, with some spirasters still attached at rim of tubes and a part of skeleton isolated by a basal-layer–like structure, Great Barrier Reef, 15 m, ×38 (West & others, 2013); *c,* section through a skeleton, the Philippines, 22 m, ×1.8 (West & others, 2013); *d,* SEM view of vertical section of skeleton showing surface (top left), tube walls, spines, and horizontal tabulae, the Philippines, 22 m, ×16 (West & others, 2013); *e,* SEM view of microscleres (spirasters), Great Barrier Reef, 15 m, ×800 (West & others, 2013); *f,* SEM view of tylostyle, Great Barrier Reef, 15 m, ×500 (West & others, 2013); *g,* TEM view of a choanocyte, showing a nucleus (*n*), a collar of microvilli (*mv*), a flagellum (*fl*), and a periflagellar sleeve (*ps*), ×7830 (Boury-Esnault & others, 1990); *h,* TEM view of living tissue (left) and decalcified skeleton (right, *sk*), with spherulous

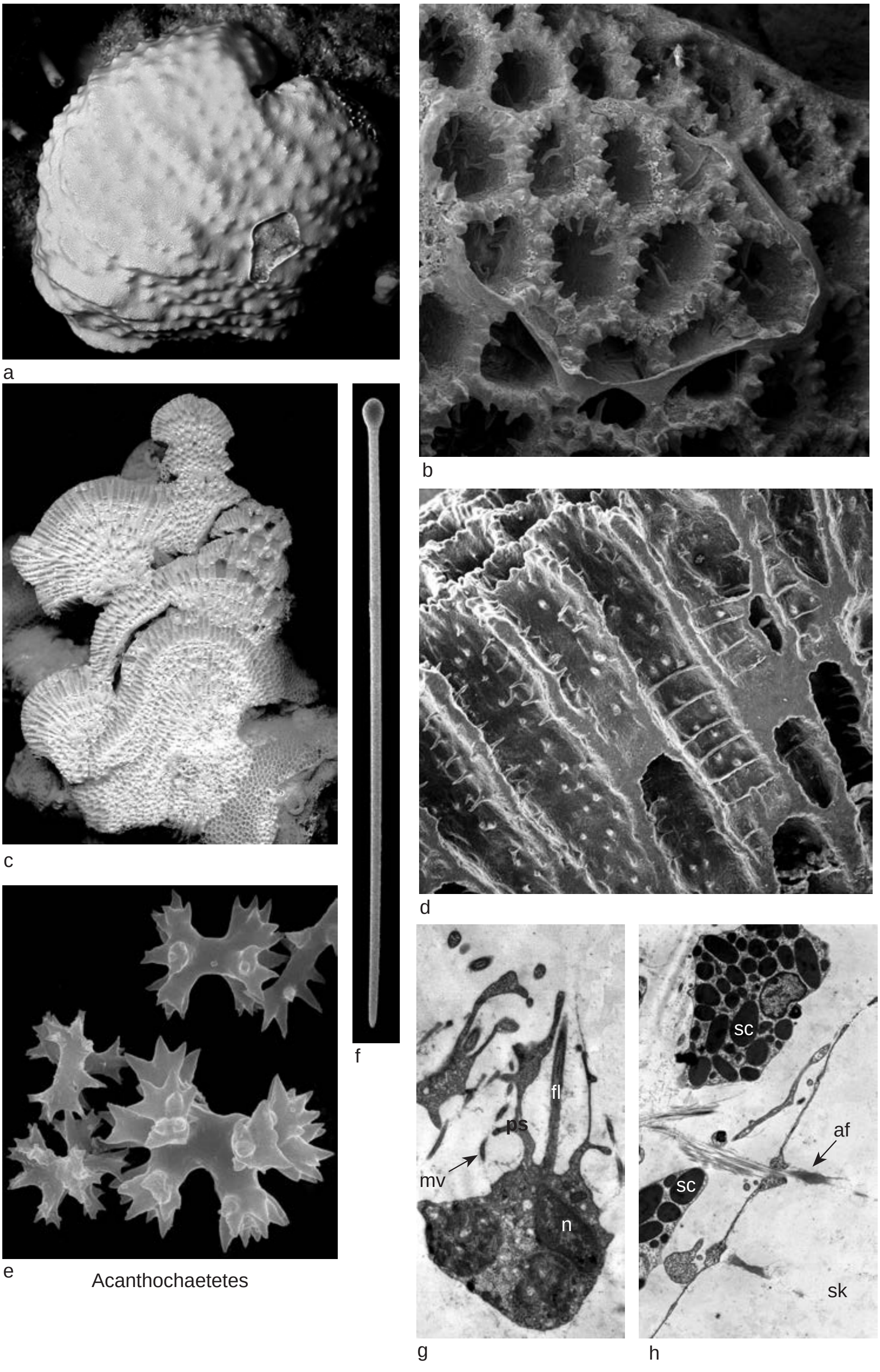


FIG. 126. Acanthochaetetidae (p. 210–214).

cells (*sc*) and anchoring fascicles of collagen fibrils (*af*), ×5000 (West & others, 2013; see also *A. wellsi* in Fig. 3.5, Fig. 4.2–4.4).

Willardia WILLENZ & POMPONI, 1996, p. 206, fig. 1–22 [**W. caicosensis* WILLENZ & POMPONI, 1996, p. 208; OD; holotype, RBINSc-POR 49, Brussels; paratypes, NHM 1995.11.3.1, London; HBOI, Harbor Branch; YPM 9360, New Haven]. Plate-like sponge, with calcareous basal skeleton attached to substratum at its center, reaching 4 to 5 mm in thickness. Microstructure of aragonitic skeleton of penicillate spherulitic type. Edges, not attached to substratum, seldom exceeding 2 to 3 mm, usually curled downward, forming an irregular bristled fringe. Individuals reach 15 to 20 cm in width. Surface of living tissue has a velvetlike appearance, due to presence of megasclere brushes protruding through surface of dermal membrane. Living tissue forms a thin veneer of 0.1 to 0.5 mm, filling irregular spaces between erected calcareous processes. Oscules evenly distributed over surface, receiving raised, transparent, anastomosed excurrent canals. Ectosome, mostly hidden under abundant protruding tylostyles, consists of a single layer of flat, superficial exopinacocytes. Choanosome with higher density of choanocyte chambers in central zone. Small eurypylous spherical choanocyte chambers (approximately 17 µm in diameter) with approximately 20 choanocytes per chamber. Choanocytes oblate with an equatorial annular-shaped expansion, a large nucleus, and a long flagellum surrounded at base by a periflagellar sleeve, typical of the order Hadromerida. Central cell, with cytoplasmic processes encircling several flagella. Occurrence of two different types of cells with dense inclusions: spherulous cells densely concentrated beneath exopinacocytes and around aquiferous canals; glycocytes particularly abundant at base of sponge, close to basopinacocytes. Bundles of rough collagen fibrils extending from base of sponge, anchored deep within spaces formed between growing aragonitic crystals, to mesohyl, enveloping base of radiating tylostyles. Neither spongin fibers, nor perispicular spongin occur. Single layer of basopinacocytes lining calcareous skeleton. Intercellular bacteria sparsely distributed in mesohyl. Color yellow to tan orange in life, dark to pale brown in alcohol. Tylostyles, straight or slightly curved, mark oval head, 254–1080 µm by 4.7–15.5 µm. Amphiasters, 15.5–21.7 µm by 10.9–20.2 µm, with short, blunt spines abundant near surface and around canals. *Holocene*: Caribbean (Grand Turk Island, Turks and Caicos Island).——FIG. 127*a–f*. **W. caicosensis*; *a,* holotype, photographed *in situ* at a depth of 114 m off northeastern tip of Grand Turk Island, prior to collection by Harbor Branch Johnson–Sea Link I submersible, scale bar, 10 cm, and see also Figure 1.8 (Willenz & Pomponi, 1996); *b,* surface of calcareous skeleton after treatment with Perhydrol, showing pillar-shaped processes, scale bar, 1 mm (West & others, 2013); *c,* ground section perpendicular to surface (*s*), with living tissue (*lt*) covering aragonite skeleton (*ar*), light microscopy, scale bar, 100 µm (West & others, 2013); *d,* surface of sponge with radially arranged protruding tylostyles, scale bar, 500 µm (West & others, 2013); *e,* tylostyle protruding from aragonitic skeleton and amphiasters settled on surface during sample preparation, scale bar, 50 µm (Willenz & Pomponi, 1996); *f,* tylostyles and amphiasters (scale bar, 500 µm), and detail of amphiaster (inset scale bar, 10 µm) (West & others, 2013).

Family SUBERITIDAE Schmidt, 1870

[*nom. transl. et correct.* VOSMAER, 1887, p. 330, *ex* Suberitidinae SCHMIDT, 1870, p. 46]

RONALD R. WEST

Globular, ramose, stipitate, massive or encrusting habit. Megascleres usually tylostyles, occasionally styles, strongyloxeas or centotylote oxeas; microscleres usually absent, when present confined to microrhabds and trichodragmas. In cross section, megascleres are usually arranged in bouquets at the surface, in massive species becoming progressively confusedly arranged toward the interior, but overall structure may also be strictly radial or showing axial orientation. In one genus, the spicules at the surface are arranged tangentially. There is no recognizable cortex. In thinly encrusting species, spicule orientation is either parallel or perpendicular to the substratum. Modifications of shape and position of the tylostyle heads are common; they can be lobate, pear shaped, drop shaped, or subterminal (description as stated in VAN SOEST, 2002a, p. 227; see also FINKS & RIGBY, 2004a, p. 43, who possibly overlooked SCHMIDT's 1870 citation). *?Silurian, Middle Devonian–Upper Cretaceous (Coniacian).*

Calcisuberites REITNER & SCHLAGINTWEIT, 1990, p. 249 [**C. stromatoporoides;* OD; holotype no. IPFUB/JR 90]. Hypercalcified demosponge with a high Mg calcite stromatoporoid-grade basal skeleton and a penicillate, water-jet (fascicular fibrous) microstructure; typical hadromerid tylostyle megascleres 700 to 820 µm long and 25 to 30 µm in diameter; plumose, bushlike arrangement of 4 to 5 tylostyles in dermal layer; microscleres unknown. [See also FINKS & RIGBY, 2004a, p. 43.] *Upper Cretaceous (Turonian–Coniacian):* Germany.——FIG. 128*a–f*. **C. stromatoporoides; a,* growth interruption surface in longitudinal section

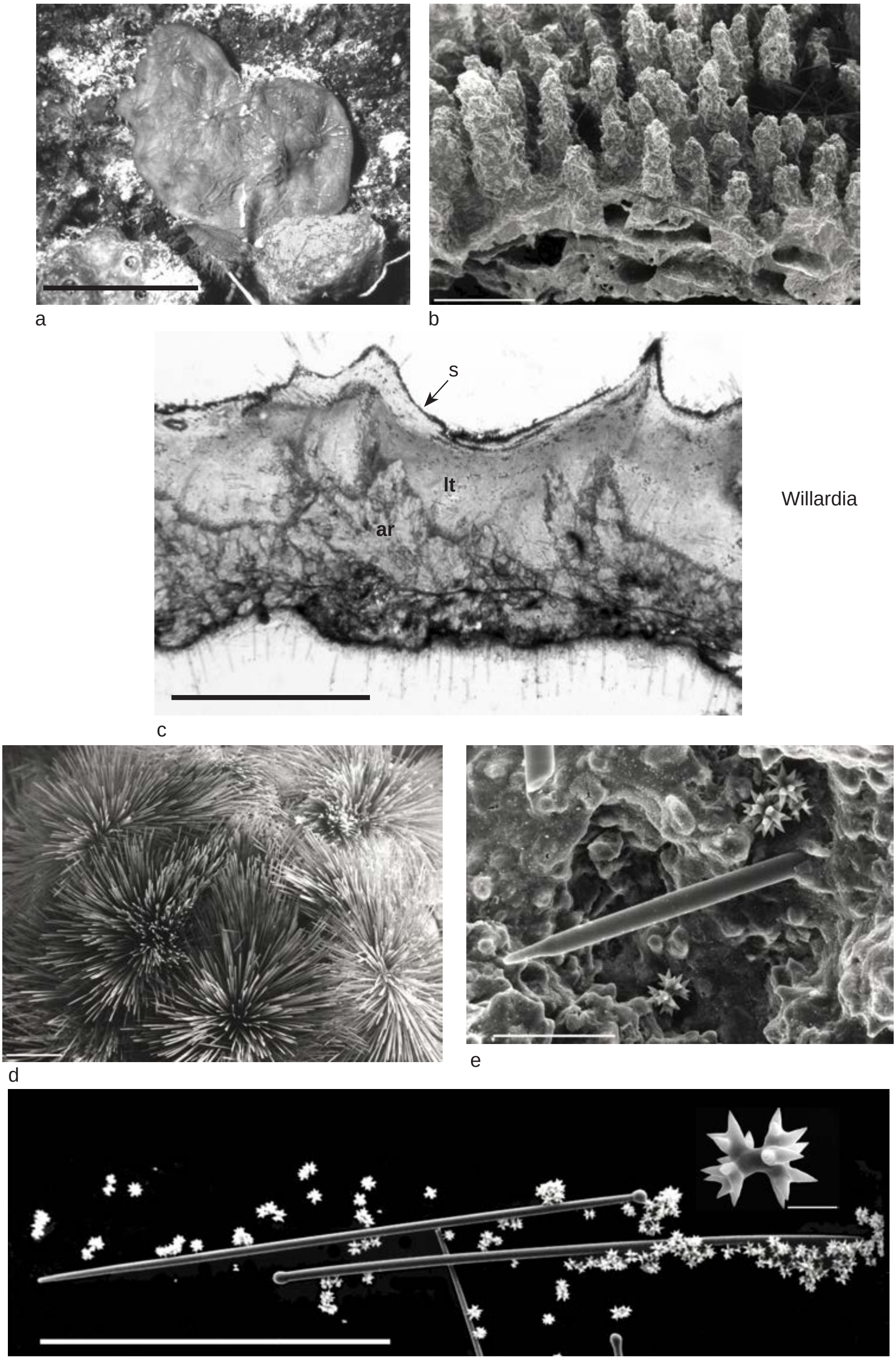


FIG. 127. Acanthochaetetidae (p. 214).

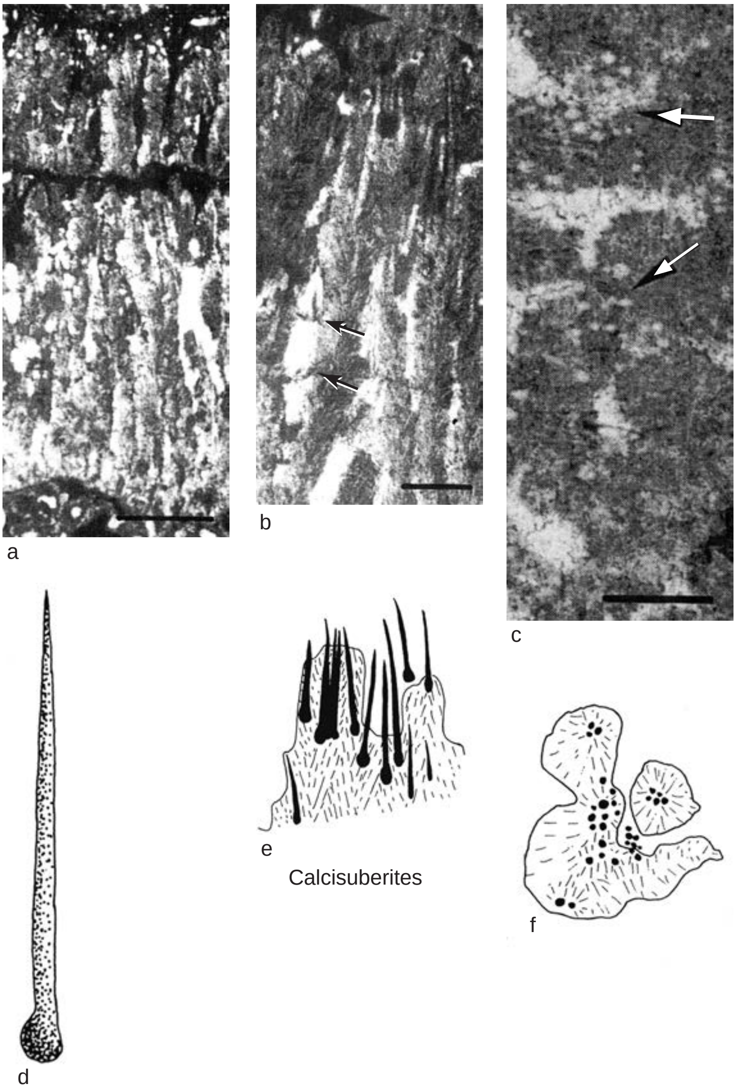


FIG. 128. Suberitidae (p. 214–216).

of basal skeleton, ×8.7; *b,* longitudinal section showing bundles of megascleres in the upper right with *arrows* indicating tabulae in lower left, penicillate, water-jet (fascicular fibrous) microstructure is faintly visible in tubule wall just to right of *arrows,* ×24; *c,* transverse section showing cross sections of bundles of megascleres (small white dots denoted by *arrows*), ×37.5; *d,* diagrammatic sketch of hadromerid tylostyle, ×80; *e,* diagrammatic sketch of megasclere bundles in longitudinal section, ×27.5; *f,* diagrammatic sketch of megasclere bundles in transverse section, ×35 (Reitner & Schlagintweit, 1990, p. 251, pl. 1).

Chaetetes FISCHER VON WALDHEIM MS in EICHWALD, 1829, p. 197 [**C. cylindricus*; SD OAKLEY, 1936, p. 441; possibly in Eichwald Collection, LGU, Leningrad (but perhaps in Museum of Geological Faculty, St. Petersburg State University); LANG, SMITH, and THOMAS (1940, p. 35) considered *C. cylindraceus* congeneric if not conspecific with *C. radians* FISCHER VON WALDHEIM, 1830 and 1837, p. 160, which was erroneously chosen as type species by MILNE-EDWARDS and HAIME (1850–1854, p. lxi), as stated by HILL (1981, p. 508), with spelling of the type species as *cylindraceus*, as does FISCHER (1970) and SOKOLOV (1950)] [=*Chaetites* MICHELIN,

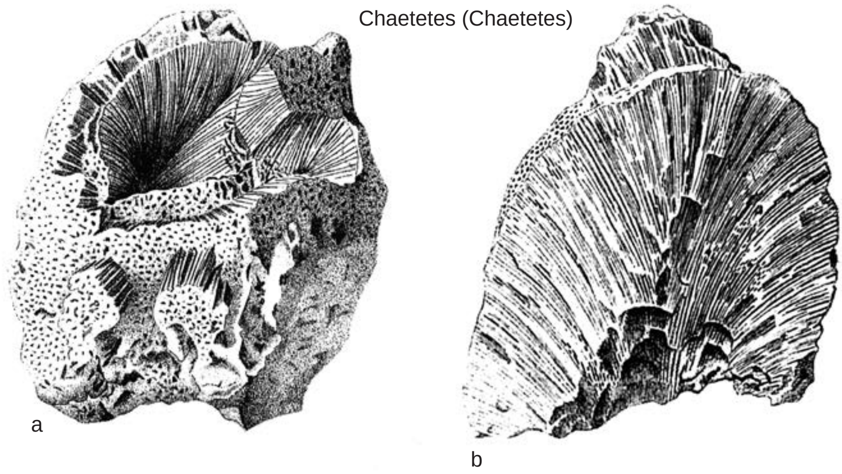
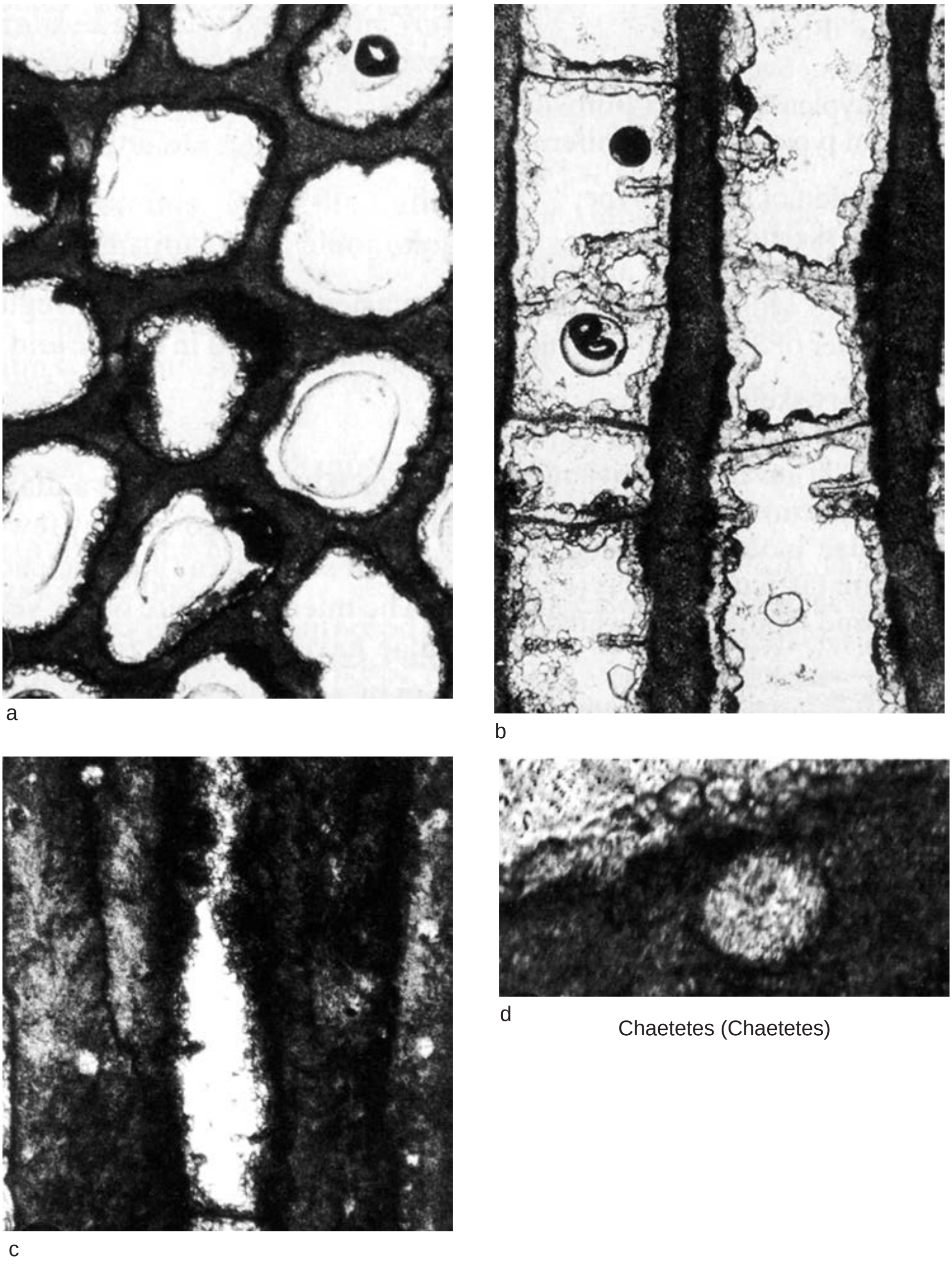


Fig. 129. Suberitidae (p. 216–218).

1844 in 1840–1847, p. 112, *nom null.; =Chaetetides* Strand, 1928b, p. 34, *nom. nov. pro Chaetetes* Fischer von Waldheim, 1837, p. 159, in case this should prove to be different from *Chaetetes* Fischer von Waldhelm MS in Eichwald, 1829, p. 197 (Lang, Smith, & Thomas, 1940, p. 35, considered *Chaetetides* unnecessary); ?=*Dania* Milne-Edwards & Haime, 1849, p. 261 (type, *D. huronica*, M; Stokes Collection, possibly MNHN in Paris; Silurian, Drummond Island, Lake Huron, North America), an uncatalogued specimen labeled *D. huronica*, Drummond Island, which may have been used for the schematized figure in Milne-Edwards and Haime, 1851, pl. 18,*2b,* was seen in 1975 by Hill in the Milne-Edwards & Haime Collection of Tabulata, MNHN, Paris (as stated by Hill, 1981, p. 508), but this specimen had a markedly different corallite diameter, =*Danaia* Scudder, 1882, p. 101, *nom. null.*]. Growth form columnar, domical, or laminar, may be globular; often with growth interruptions; tubules long, polygonal in transverse section with a common wall; microstructure of walls inferred to be penicillate, water-jet (fascicular fibrous) calcite with aster (possible euaster) microscleres 25 to 35 µm in diameter (Reitner, 1991a, p. 186); tabulae straight or irregular; tubules increase by longitudinal fission, intertubular budding or peripheral expansion. [Fischer von Waldheim (1837, p. 160) described *Chaetetes cylindricus*, the presumed type species, as having very thin cylindrical tubes. In the same publication, on the same page, he described *C. radians* as being similar to *Calmnopora polymorpha* Goldfuss, but the tubes are simple, almost capillary, without diaphragms and at the surface are simple, round, and fine. Reitner (1991a) described a specimen, no. R 27318, labeled "*Chaetetes radians*" in the NHM, as a new genus and new species, *Chondrochaetetes longitubus,* placing it in the family Chondrosiidae, based on what he considered aster (possible euaster) scleres and because he observed no tylostyles megascleres as seen in *C. mortoni*. The state of preservation (diagenetic alteration, Reitner, 1991a, p. 188) is such that this taxon requires further verification.] *?Silurian, Middle Devonian–Upper Jurassic (Tithonian):* Great Britain, Central Asia, Arctic, China, Japan, Indochina, *Middle Devonian–Carboniferous*; North America, *Middle Devonian–Carboniferous (Pennsylvanian)*; North America, Japan, Mongolia (Karakorum), *Permian.*

Chaetetes (Chaetetes). Description as for genus. *?Silurian, Middle Devonian–Permian:* USA (Michigan), *?Silurian*; Kuznetsk Basin–Kazakhstan, *Middle Devonian*; Russia ("le calcaire de Moscou"); Great Britain, Central Asia, Arctic, China, Japan, Indochina, *Middle Devonian–Carboniferous*; North America, *Middle Devonian–Carboniferous (Pennsylvanian)*; North America, Japan, Mongolia (Karakorum), *Permian.*——Fig. 129*a.* **C. (C.) cylindricus*; Carboniferous, Russia, St. Petersburg; magnification unknown (Fischer von Waldheim, 1837, pl. 36,*1*).——Fig. 129*b. C. (C.) radians* Fischer von Waldheim, Carboniferous, Russia; this specimen (and the one in Fig. 129a are presumed to be lost, but might be in the Eichwald collection, St Petersburg); magnification unknown (Fischer von Waldheim, 1837, pl. 36,*3*).——Fig. 130*a–d. C. (C.) radians* Fischer von Waldheim, 1837, Carboniferous, Russia, NHM no. R 27318, labeled as *Chaetetes radians*; *a,* transverse section showing reduction of tubule size and shape due to diagenetic cement, faint white dots are inferred microscleres, ×26; *b,* longitudinal section showing



Chaetetes (Chaetetes)

FIG. 130. Suberitidae (p. 216–218).

granular calcite (diagenetic) cement, ×30; *c,* longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure, faint white dots are inferred microscleres, ×45; *d,* detail of inferred microsclere in longitudinal section, ×200 (Reitner, 1991a, p. 187).

Chaetetes (Boswellia) Sokolov, 1939, p. 411 [**Chaetetes boswelli* Heritsch, 1932, p. 221; OD; thin sections, PIOI9, UG, Graz, specimen destroyed *fide* Heritsch, 1932, p. 221; Hill, 1981, p. 508]. Type species with thick, irregular tubule walls of fascicular fibrous calcite

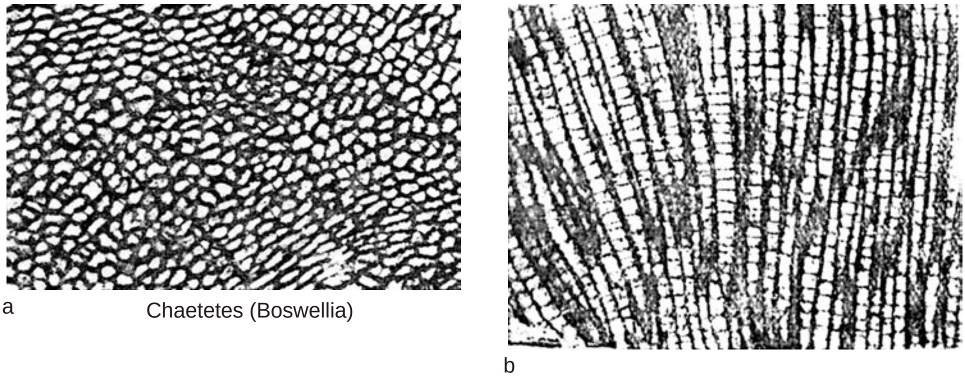


FIG. 131. Suberitidae (p. 216–219).

with megascleres (siliceous) sometimes present; tubules irregular or subpolygonal in transverse section; tubules increase by longitudinal fission that may be incomplete and peripheral expansion (description modified from Gray, 1980, p. 806). [A modified description from Gray (1980) and Reitner (1991a), of *Chaetetes (Boswellia) mortoni* Gray, 1980, is included because details of the primary (spicules) and secondary (mineralogy and microstructure) features are better known for this species than for the type species *C. (B.) boswelli,* as follows: growth form laminar or bulbous; irregular to subpolygonal tubules in transverse section; penicillate, water-jet (fascicular fibrous) tubule walls of inferred Mg calcite; pseudosepta visible in transverse section and as long, irregular ridges in longitudinal section; tabulae well spaced; tubules increase by longitudinal fission and peripheral expansion; monaxon tylostyle megascleres (approximately 7 µm in diameter and 170–275 µm long) as subparallel bundles diverging distally, with their pointed (oxeote) ends directed distally; microscleres unknown. Middle Devonian occurrence is rare.] *Middle Devonian–Carboniferous*: Serbia, Germany, Russia (Moscow and Donets Basins, Urals), Great Britain (Wales), Central Asia.——FIG. 131*a–b*. **C. (B.) boswelli* (Heritsch), D$_2$, Carboniferous, northeastern Ukraine, Russia; *a,* transverse section, ×4; *b,* longitudinal section, ×4 (Sokolov, 1950, pl. 8–9).——FIG. 132*a–f. C. (B.) mortoni* Gray, 1980, lower Carboniferous, northern Wales; *a,* longitudinal section showing tylostyle megascleres in penicillate, water-jet (fascicular fibrous) tubule wall, paratype NHM no. R4429 (Morton Collection), ×37.5; *b,* longitudinal section showing arrangement of tylostyle megascleres in tubule walls, paratype NHM no. R4429 (Morton Collection), ×231 (Gray, 1980, pl. 103); *c,* diagrammatic sketch of arrangement of tylostyle megascleres in tubule walls, ×100 (Reitner, 1991a, p. 182); *d,* single tylostyle megasclere, paratype NHM no. R4429, ×200 (Reitner, 1992, pl. 2); *e,* diagrammatic sketch of tylostyle megasclere, ×400 (Reitner, 1991a, p. 182); *f,* three-dimensional reconstruction of basal skeleton, ×11 (Reitner, 1991a, p. 182).

Chaetetes (Pseudoseptifer) Fischer, 1970, p. 171 [**Chaetetes beneckei* Haug, 1883, p. 174; OD; =*Chaetetes beneckei* Airaghi, 1907, p. 17; =*Chaetetes (Bauneia?) beneckei* Peterhans, 1929c, p. 119; =*Chaetetes beneckei* Vialli, 1938, p. 65; =*Chaetetes (Pseudoseptifer) beneckei* Fischer, 1970, p. 171; although Fischer (1970) described *Pseudoseptifer* as a subgenus of *Chaetetes*, Hill (1981, p. 519), listed it as a genus; holotype, Upper Jurassic, de Roverè di Velo, Province de Vérone, Italy, original thin sections redescribed by Peterhans (1929c) in MS]. Growth form domical; tubules irregular polygons, some rounded, in transverse section; tubule walls thick; pseudosepta conspicuous and numerous; tabulae numerous, thin, irregularly spaced; tubules increase by longitudinal fission, rarely intertubular budding and peripheral expansion. [Fischer (1970, p. 170) described the microstructure as fibroradial; Bizzarini and Braga (1988, p. 145) described it as clinogonal, a synonym of penicillate, water-jet, and fascicular fibrous; aragonite inferred original mineralogy; acanthostyle megascleres documented by Bizzarini and Braga (1988); microscleres unknown.] *Upper Jurassic (Tithonian):* Italy (Trento–Venetian Prealps).——FIG. 133*a–e*. **C. (P.) beneckei* (Haug), Saint Anna di Vallarsa, Civic Museum of Rovereto, northern Italy; *a–c,* upper exterior surface, lower exterior surface, lateral view of basal skeleton, ×0.7 (adapted from Bizzarini & Braga, 1988, pl. 1,*2,3,1*); *d–e,* Malga Fratta, Altopiano dei Setti Communi, Museum of the Institute of Geology, University of Padova; *d,* transverse section of basal skeleton, note pseudosepta in lower left, ×3.3; *e,* enlargement of part of view *d* showing pseudosepta, ×33 (adapted from

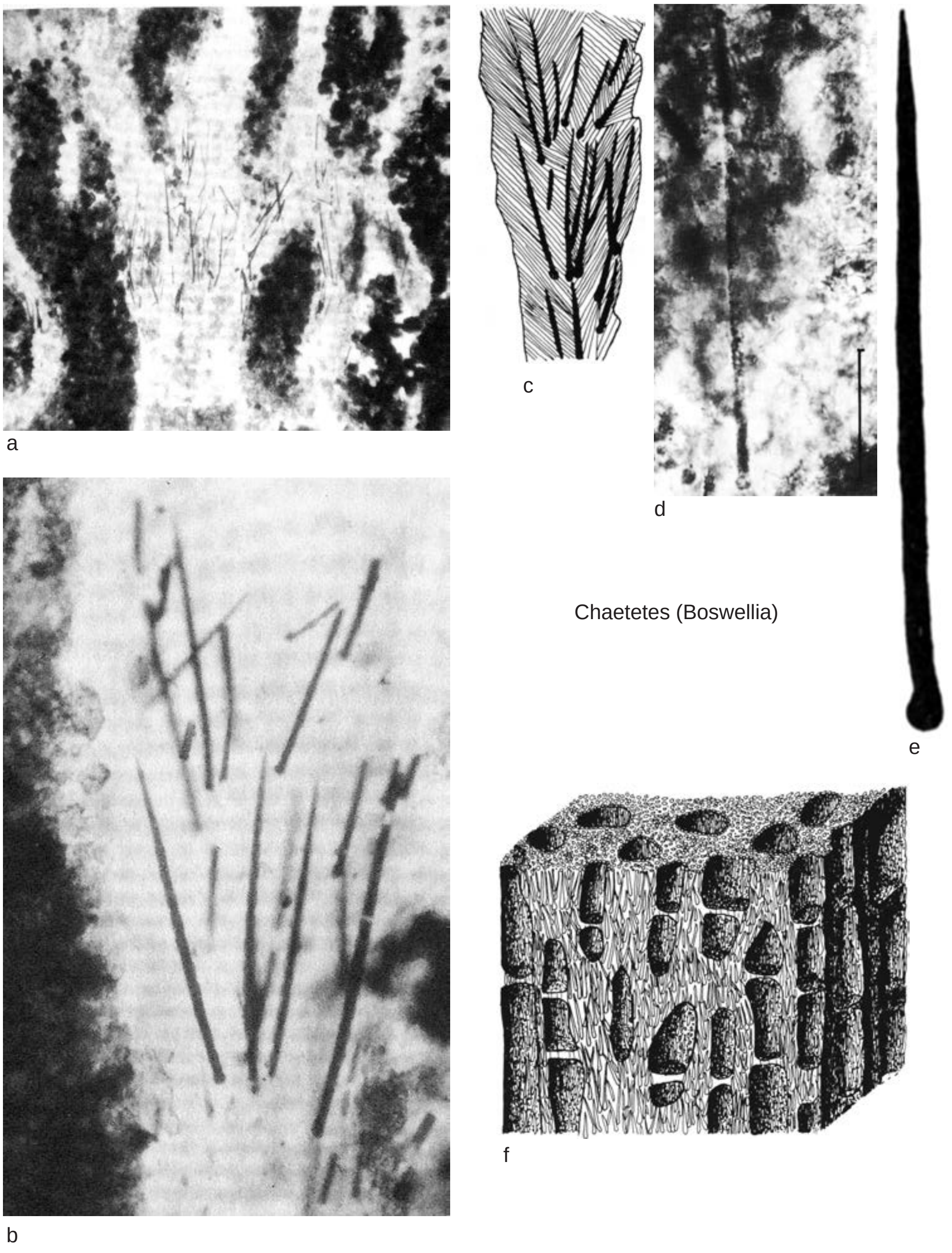


FIG. 132. Suberitidae (p. 216–219).

Bizzarini & Braga, 1988, pl. 2,*1,5*).——FIG. 134*a–b*. **C. (P.) beneckei* (HAUG), Malga Fratta, Altopiano dei Setti Communi, Museum of the Institute of Geology, University of Padova; *a,* longitudinal section of basal skeleton showing pseudosepta (*P*) and tubules increase by longitudinal division, ×15; *b,* enlargement of part of view *a* showing pseudosepta (*P*), ×35 (adapted from Bizzarini & Braga, 1988, pl. 2,*3–4*).——FIG. 134*c*. *C. (P.) waehneri* HERITSCH, Calcari Grigi di Noriglio, near Lancia al Col Santo, northern Italy; pseudomorphs of acanthostyle megascleres in penicillate, water-jet (fascicular fibrous, clinogonal) tubule walls (longitudinal

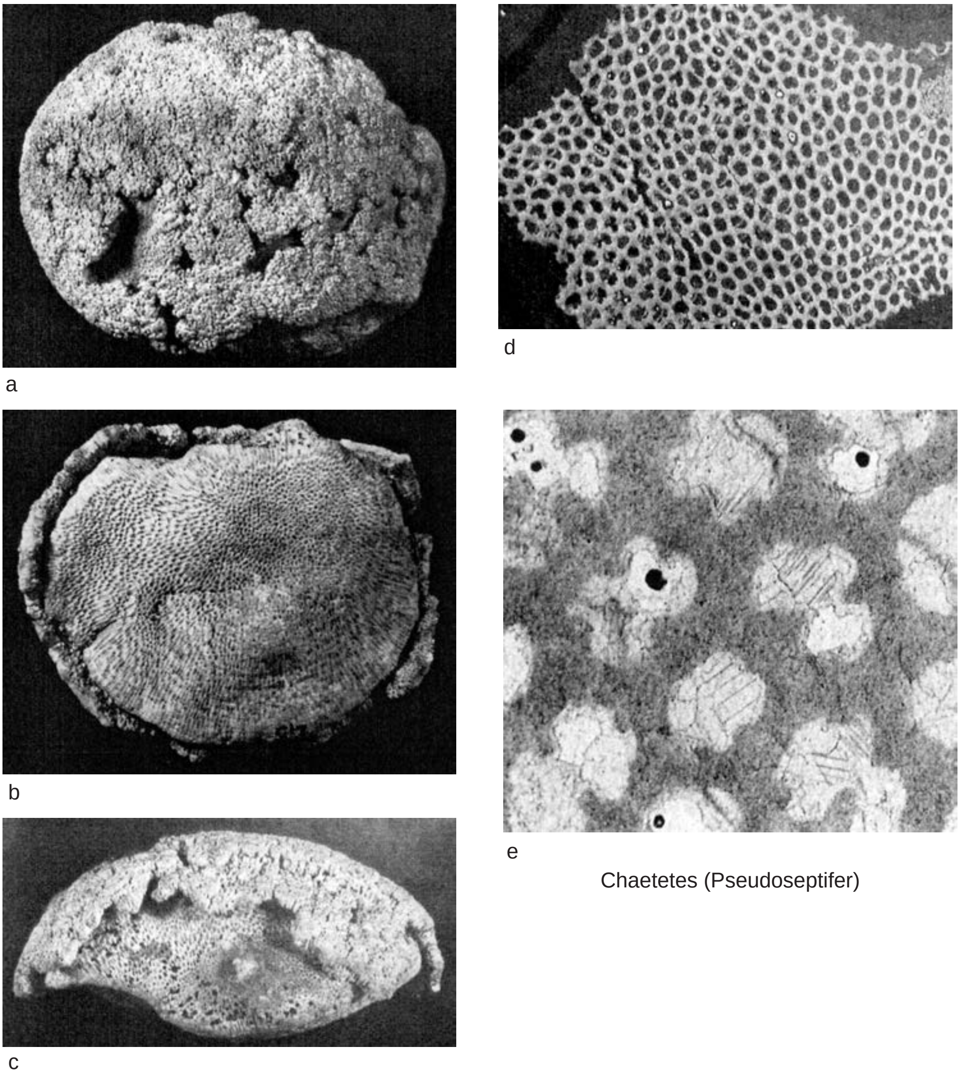
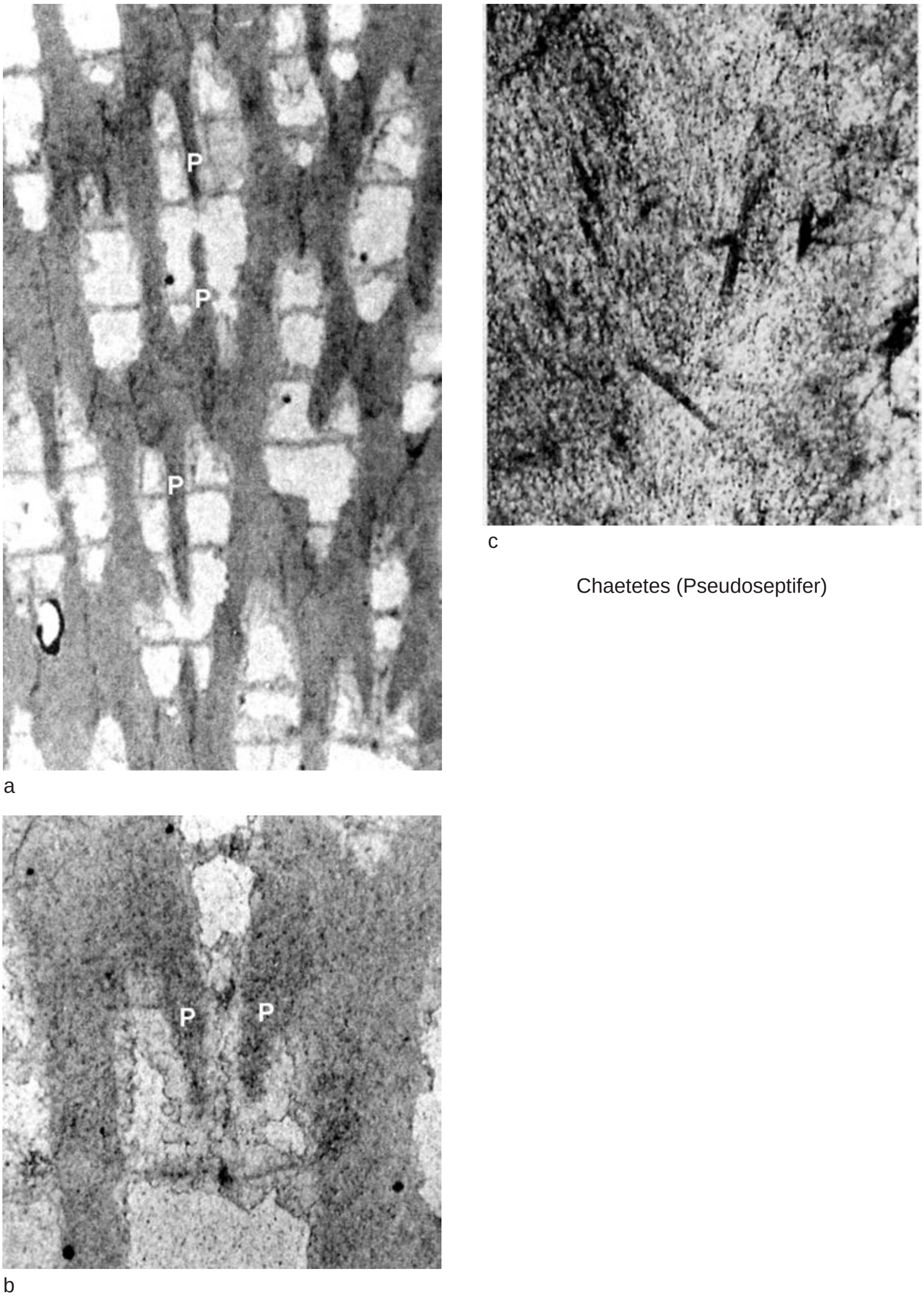


FIG. 133. Suberitidae (p. 216–221).

section), approximately ×218 (adapted from Bizzarini & Braga, 1988, pl. 5,*6*).

Chaetetopsis NEUMAYR, 1890, p. 28 [**C. crinata*; OD; no longer in the Neumayr Collection in Vienna, *fide* PETERHANS, 1929c, p. 115; Upper Jurassic (Tithonian), Iwaso Konpira and Torinosuyama, Japan; PETERHANS, 1929c, based his chaetetid interpretation of the genus on the type specimen of *Monotrypa limitata* DENINGER, 1906, p. 64, in the Museum of the University of Freiburg, Upper Jurassic (Tithonian), Capri, Italy. A neotype in MNHM, Paris, named by FISCHER, 1970, p. 197, is unsatisfactory in that it comes from a locality not named by NEUMAYR (Musaki, Japan) and has been greatly altered by diagenesis (as stated in HILL, 1981, p. 666)]. Growth form domical to globular; tubules in transverse section circular to elliptical, regularly arranged; tubules in longitudinal section long, thin, nearly parallel, with continuous double walls; tabulae thin, abundant, subhorizontal, indistinct, not laterally continuous between tubules; pseudosepta uncommon; walls defined by a thin marginal edge of granules; remainder of wall irregular crystals similar to tubule fillings; tubules increase by intertubular budding, indistinct (description modified from NEUMAYR, 1890; FISCHER, 1970). [Spicules, or spicule pseudomorphs, and the original mineralogy and microstructure are unknown for the type species,



Chaetetes (Pseudoseptifer)

FIG. 134. Suberitidae (p. 216–221).

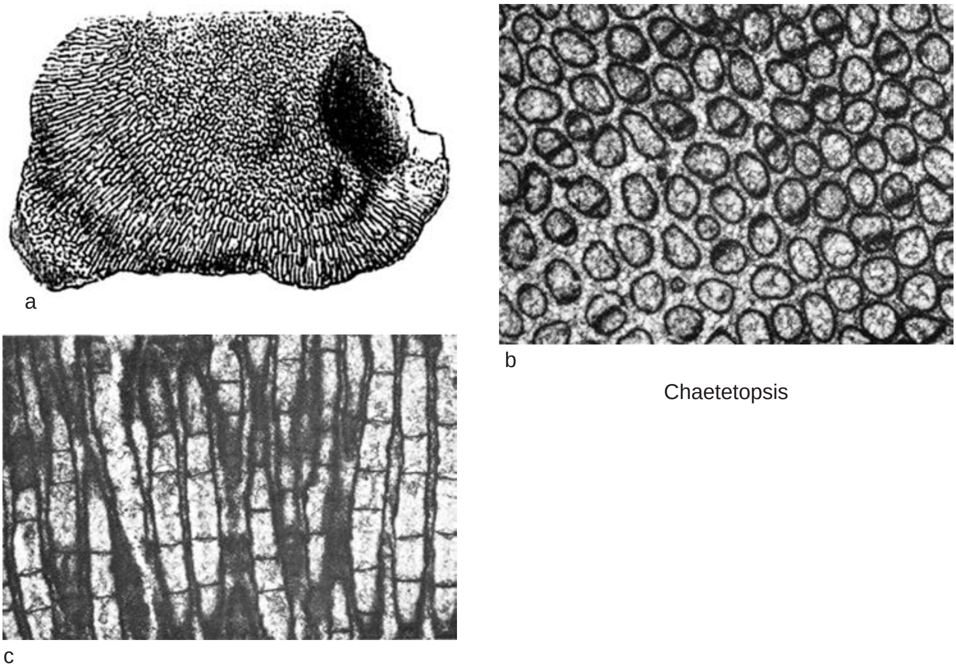


Fig. 135. Suberitidae (p. 221–223).

C. crinata, but these primary and secondary features have been reported for *C. favrei* (Deninger, 1906) by Kaźmierczak (1979) and Reitner (1991a) as follows: growth form conical with regular growth ridges on lateral surface; tubules rounded polygonal, subcircular or circular in transverse section, contiguous in longitudinal section; tabulae thin, subhorizontal, and arranged in sets such that a few are aligned between tubules; tubule walls are commonly granular to blocky calcite but inferred to have been fascicular fibrous aragonite; tubules increase by longitudinal fission; monaxon tylostyle pyrite pseudomorph megascleres (120–450 µm long, 5–10 µm in diameter) within tubule walls; microscleres unknown.] *Upper Jurassic (Tithonian)–Lower Cretaceous (Aptian):* Japan, Italy (Capri), *Tithonian;* Crimea, Greece, *Barremian–Aptian.*——Fig. 135*a–c.* **C. crinata*, Portlandian, Jurassic, Japan; *a,* globular growth form, magnification unknown (Neumayer, 1890, pl. 4); *b,* transverse section, ×15; *c,* longitudinal section, ×15 (Fischer, 1970, pl. E).——Fig. 136*a–e. C. favrei* (Deninger); *a,* longitudinal section, Barremian, Crimea, ×27; *b,* transverse section, Barremian, Crimea, ×25 (Kaźmierczak, 1979, p. 103–104); *c,* longitudinal section showing fascicular fibrous microstructure of tubule walls, ?Aptian, Greece, ×347 (Reitner, 1991a, p. 185); *d,* longitudinal section showing pyrite pseudomorphs of tylostyle megascleres in tubule walls, Barremian, Crimea, ×150; *e,* transverse section showing pyrite pseudomorphs of tylostyle megascleres (*arrows*) in tubule walls, Barremian, Crimea, ×95 (Kaźmierczak, 1979, p. 103–104).

Pachytheca Schlüter, 1885, p. 144, *non* Hooker, 1861, a plant [**P. stellimicans*; M; SD Birenheide, 1985, p. 21, syntypes 138a,b, 204, Schlüter Collection, PIUB; =*Calamopora stromatoporoides* Roemer, 1880 in 1876–1880, p. 459] [?=*Rhaphidopora* Nicholson & Foord, 1886, p. 390 (type, *Calamopora crinalis* Schlüter, 1880, p. 281, OD; syntypes 192, Schlüter Collection (26), PIUB; Middle Devonian, Hillesheim syncline, Eifel, Germany, see Schlüter, 1889, p. 401; =*Pachytheca stellimicans* Frech, 1886, p. 17; =*Pachytheca stellimicans* Spriestersbach, 1942, p. 126; =*Pachytheca stellimicans* Sokolov, 1955, p. 519; =*Pachytheca stellimicans* Hill & Stumm, 1956, p. 455; =*Pachytheca stellimicans* Hill, 1981, p. 511; =*Pachytheca stellimicans* Byra, 1983, p. 22; =*Pachytheca stellimicans* Birenheide, 1985, p. 21] [=*Raphidiopora* Yabe, 1910, p. 4, *nom. null.;* =*Rhaphidiopora* Stearn, 1972, p. 375, *nom. null.* (as stated in Hill, 1981, and Byra, 1983)]. Growth form laminar; tubules polygonal in transverse section, long and thin longitudinally, most tubules filled with secondary calcite, as in *Ceratoporella*; microstructure penicillate water-jet (fascicular fibrous). [The following was observed in *P.* cf. *P. stellimicans* of Reitner (1992, p. 152): tabulae microstructure similar to tubule filling; tubule walls inferred to be Mg calcite, tylostyle megasclera (500–800 µm long), arranged in

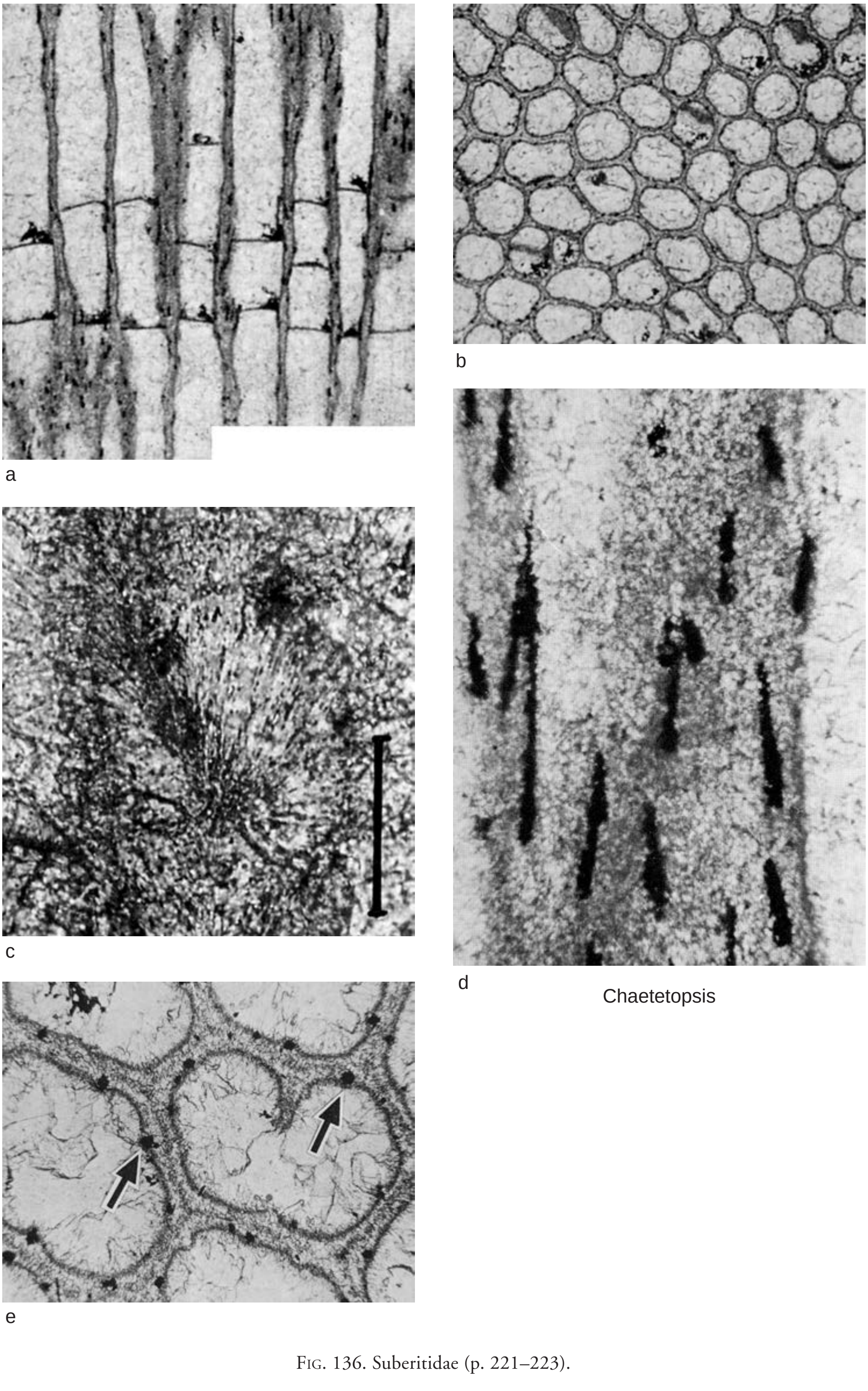


FIG. 136. Suberitidae (p. 221–223).

bundles of 5 or 6 in the basal skeleton, reflecting a relict radial structure; microscleres unknown.] *Middle Devonian*: Germany (Eifel), Great Britain, Russia (northern Urals).——FIG. 137*a–c*. **P. stellimicans,* Eifelian, western Germany; *a,* transverse section of paralectotype, ×20; *b,* longitudinal section of lectotype, ×18.7; *c,* longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure of lectotype, ×21 (Birenheide, 1985, pl. 1).——FIG. 138*a–c*. *P.* cf. *P. stellimicans*, Eifelian, northern Spain; *a,* calcite pseudomorph of tylostyle megasclere, ×204; *b,* diagrammatic sketch of tylostyle megasclere, ×270; *c,* diagrammatic reconstruction of basal skeleton, ×52.5 (Reitner, 1992, p. 153, fig. 30, pl. 22, *6*).

Family SPIRASTRELLIDAE
Ridley & Dendy, 1886

[Spirastrellidae RIDLEY & DENDY, 1886, p. 490; *emend.,* RÜTZLER, 2002, p. 220] [=Choanitidae DE LAUBENFELS, 1936, p. 140]

Encrusting demosponges with limestone-excavating capability in early stages but without adult endolithic habit. Exhalant canal system apparent at the surface (particularly obvious in live sponges, when living tissue contracts upon preservation) as meandering, vein-like structures converging on oscula. Skeleton formed by relatively uncommon megascleres in ascending radial tracts and dense layers of microscleres in the ectosomal region and as base layer. Megascleres mainly tylostyles, tracts starting at the sponge base and ending in bouquet-like fashion (spicule points outward) in the ectosomal region or protruding beyond sponge surface; some megascleres oriented at random in choanosome. Microscleres composed of large and stout streptasters (spirasters, diplasters), very common throughout sponge but forming extra-dense cortexlike layers in ectosome and at base (substrate attachment) (diagnosis as quoted in RÜTZLER, 2002, p. 220; see also FINKS & RIGBY, 2004a, p. 43). [RÜTZLER (2002, p. 220) proposed the group as "encrusting sponges with prominent layers of relatively large spirasters, amphiasters or diplasters at the surface and the base or throughout the entire body," following primarily the conception of the traditional Spirastrellidae of RIDLEY and DENDY (1886, p. 490). Excluded are massive sponges such as *Spheciospongia* MARSHALL, 1892, and part of the former genus, *Spirastrella sensu lato* with rare and minute spirasters or amphiasters; these latter are now placed in the family Clionaidae D'ORBIGNY, 1851

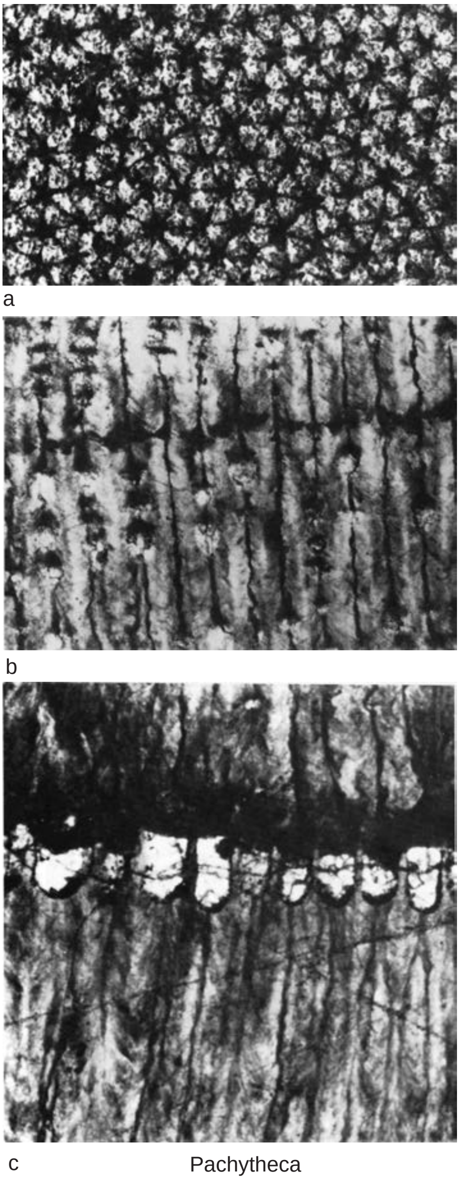


FIG. 137. Suberitidae (p. 223–225).

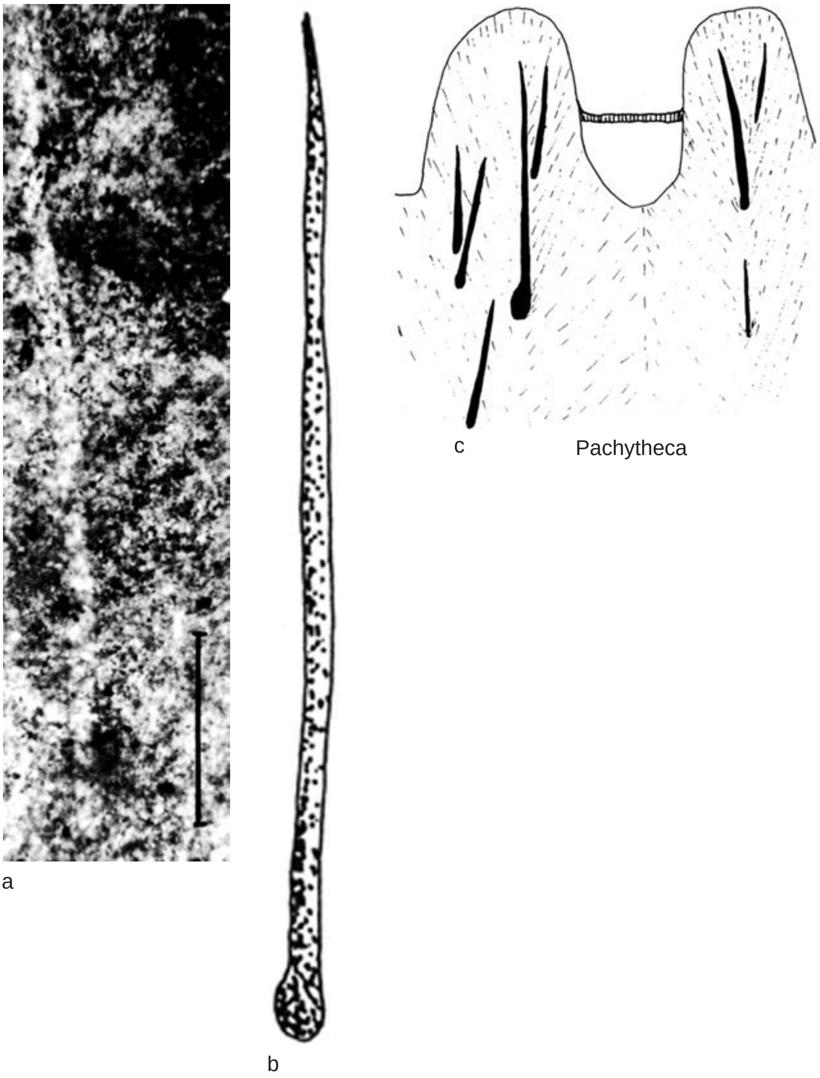


FIG. 138. Suberitidae (p. 223–225).

in 1851–1854; RÜTZLER, 1990; ROSELL & URIZ, 1997.] _Lower Cretaceous (Albian)._

Calcispirastrella REITNER, 1992, p. 149 [*_C. sphinctozoides_; OD; holotype, IPFUB/JR 1991]. Growth form thalamid-like (egg shaped); multiple pores or ducts in transverse section associated with chambers and/or canal system; large central pores 600–800 µm in diameter with thorny rim; small wall pores approximately 250 µm in diameter associated with smaller pores 100 µm in diameter, inferred as incurrent openings; basal skeleton irregular, granular to prismatic Mg calcite; dermal layer 80–100 µm thick, with many small (20–25 µm) spiraster microscleres interspersed with bundles of 6 to 8 tylostyle megascleres (150–200 µm long). _Lower Cretaceous (Albian):_ northern Spain.——FIG. 139_a–c_. *_C. sphinctozoides_; _a,_ transverse section showing chambers (_arrows_), tubes, and canal system, ×6; _b,_ section of dermal layer with crust of small spiraster microscleres and small, plumose arranged, tylostyle megascleres (_arrows_), ×70; _c,_ longitudinal section of basal skeleton showing microstructure of small, irregular crystals of high Mg calcite (dark areas), light areas are prismatic layers, ×140 (Reitner, 1992, pl. 24a).

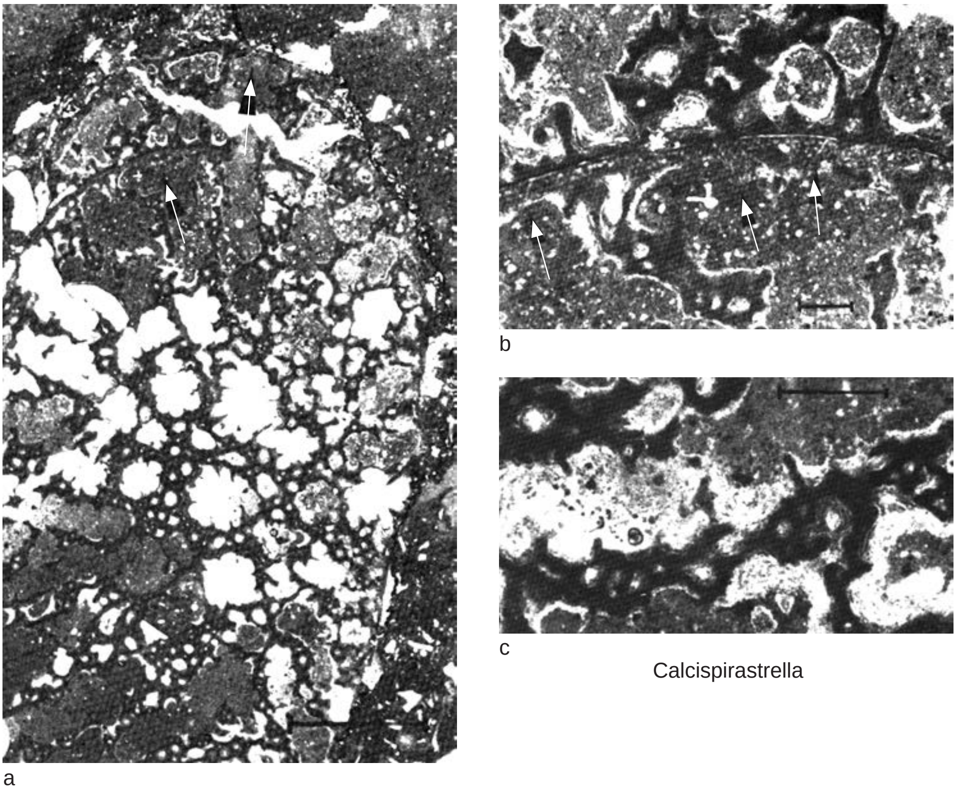


FIG. 139. Spirastrellidae (p. 226).

Order CHONDROSIDA Boury-Esnault & Lopès, 1985

[Chondrosida Boury-Esnault & Lopès, 1985, p. 172]

Encrusting to massive demosponges with a marked cortex enriched with fibrillar collagen, with inhalant apertures localized in pore sieves or cribriporal clones and a skeleton often absent, composed, when present, of nodular spongin fibers or aster microscleres only (never megascleres). Collagen always very abundant. Oviparous. [Diagnosis applies to both order and family; the type genus is *Chondrilla* Schmidt, 1862, by original designation; description adapted from Boury-Esnault in Hooper & van Soest, 2002a, p. 220, p. 291.] *Upper Jurassic–Lower Cretaceous (Albian).*

Family CHONDRILLIDAE Gray, 1872

[Chondrillidae Gray, 1872, p. 461 [=Gummineae Schmidt, 1862, p. 37, *nom. oblit.;* =Gumminidae Schmidt, 1862, p. 37, *nom. oblit.*; =Chondrosidae Schulze, 1877, p. 87; =Chondrissinae Lendenfeld, 1885, p. 14; =Chondrosiidae Wiedenmayer, 1977, p. 187]

Description as for order. *Upper Jurassic–Lower Cretaceous (Albian).*

Calcichondrilla Reitner, 1991a, p. 191 [**C. crustans;* OD; holotype, IPFUB, JR2/89; paratype, IPFUB, JR3/89]. Growth form laminar, crustose; numerous, large euaster (75–100 µm diameter) microscleres (megascleres absent) and inferred excurrent canals in oblique section; irregular lamellar Mg calcite structure of basal skeleton reflects original collagen fibers of an atypical chaetetid (Reitner, 1991a, p. 191). [See also Finks and Rigby (2004d, p. 586).] *Lower Cretaceous (Albian):* northern Spain, United States (Arizona).——FIG. 140*a–d.* **C. crustans,* northern Spain; *a,* abundant possible euaster microscleres (white spots) in oblique section of holotype, ×14; *b,* diagrammatic sketch of longitudinal section of calcified collagenous basal skeleton

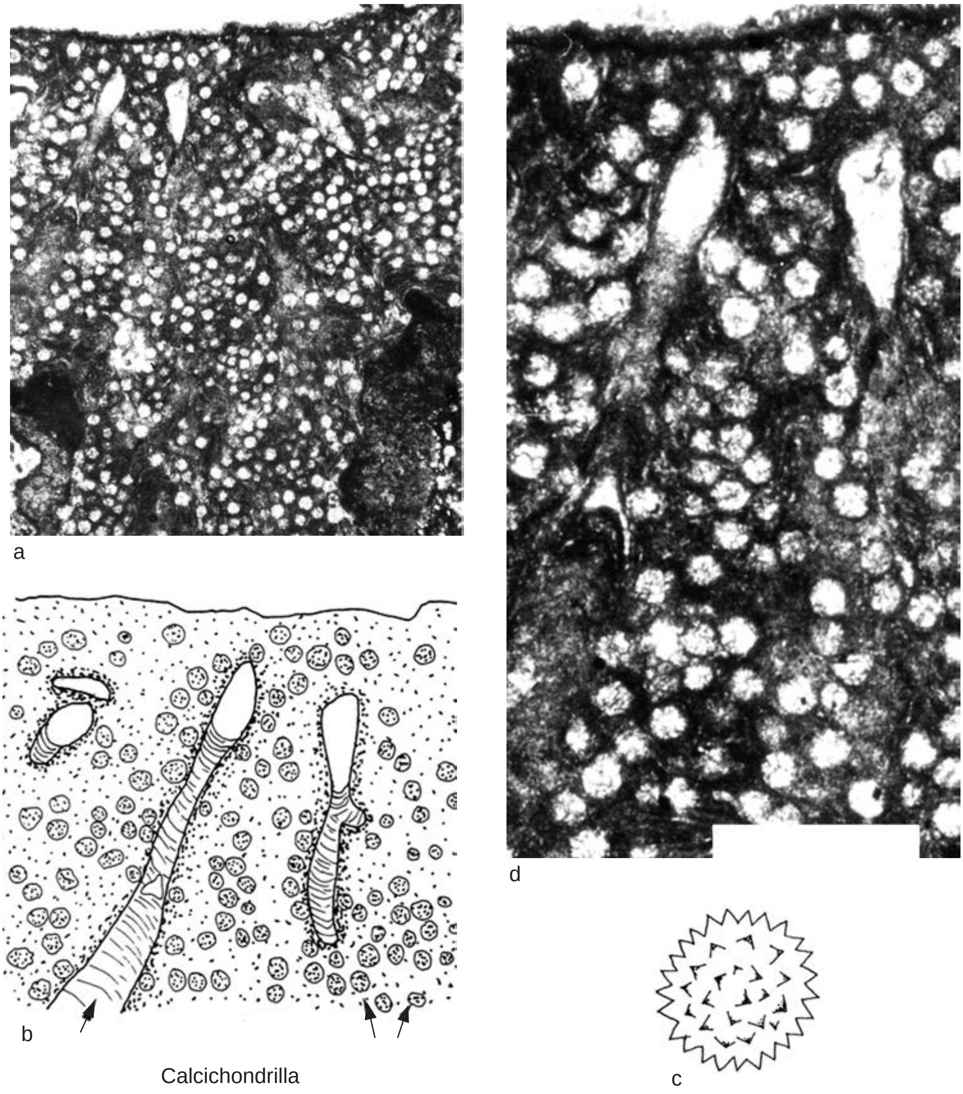


FIG. 140. Chondrillidae (p. 227–228).

(stippled area), tubes of canal system (*arrow* in lower left), and possible eusater microscleres (*arrows* in lower right), ×32.5 (Reitner, 1991a, p. 192); *c,* sketch of inferred morphology of a euaster microsclere, ×220 (Reitner, 1992, p. 159); *d,* enlargement of upper left area of view *a* showing tubes of canal system and abundant microscleres, ×61.2 (Reitner, 1991a, p. 192).——FIG. 141. **C. crustans,* lamellar microstructure of calcified collagenous basal skeleton of holotype in oblique section, ×125 (Reitner, 1991a, p. 192).

Calcistella REITNER, 1991a, p. 188 [**C. tabulata* REITNER, 1991a, p. 189; OD; holotype, IPFUB, JR I /89)]. Growth form domical with large tubules; tubule walls thick with numerous sparite-filled pores and canals of inferred excurrent system; tabulae thin, subhorizontal to slightly arched, micritic calcite, as are the tubule walls; micritic Mg calcite basal skeleton with large (50–65 µm diameter) possible euaster microscleres with relict spines (megascleres unknown); original atypical chaetetid skeleton inferred to be collagen fibers (Reitner, 1991a, p. 189). *Upper Jurassic (Tithonian), Lower Cretaceous (?Aptian, Albian):* Germany (Bavaria), *Tithonian;* Greece (Arachova), *?Aptian, Albian.*——Fig. 142*a–c*. **C. tabulata*, ?Aptian, Albian, Greece; *a,* thick tubule walls with canal system of basal skeleton in oblique section, ×11; *b,* longitudinal section of tubule walls and tabulae, gray lamellar areas are granular calcite inferred to have been associated with upward growth of soft tissue, ×18; *c,* enlargement of part of view *a* showing microscleres (white dots) and internal canals (gray areas), ×25 (Reitner, 1991a, p. 190).——Fig. 143*a–c*. **C. tabulata*, ?Aptian, Albian, Greece; *a,* calcite-filled molds of possible euaster microscleres, ×380 (Reitner, 1991a, p. 190); *b,* sketch of inferred possible euaster microsclere, ×400; *c,* diagrammatic sketch of longitudinal section of calcified collagenous basal skeleton (*arrow* in upper right, stippled area), tubes of canal system (*arrow* in lower center), and possible euaster microscleres (*arrows* in upper section), ×10 (Reitner, 1992, p. 157).

Order POECILOSCLERIDA Topsent, 1928

Jean Vacelet and Ronald R. West

[*nom. correct.* de Laubenfels, 1955, p. 21, 38, *pro* Poecilosclerina Topsent, 1928, p. 41, 43] [=Poeciloscleridae Topsent, 1894, p. 10]

Demospongiae with skeleton composed of discrete siliceous spicules; main skeleton composed of megascleres (monactinal, diactinal, or both) and spongin; fibers in various stages of development; both fiber and mineral skeletons always show regional differentiation of megascleres into distinct ectosomal and choanosomal components; microscleres include meniscoid forms, such as chelae (unique to the order), sigmas and sigmancistra derivatives, and other diverse forms such as toxas, raphides, microxeas, and discate microrhabds; order is predominantly viviparous with incompletely ciliated parenchymella larvae; one oviparous family (Raspailiidae), and another suspected oviparous family (Rhabderemiidae), is also included (diagnosis as stated by Hooper & van Soest, 2002d, p. 403; see also Finks & Rigby, 2004a, p. 49). *Lower Jurassic–Holocene.*

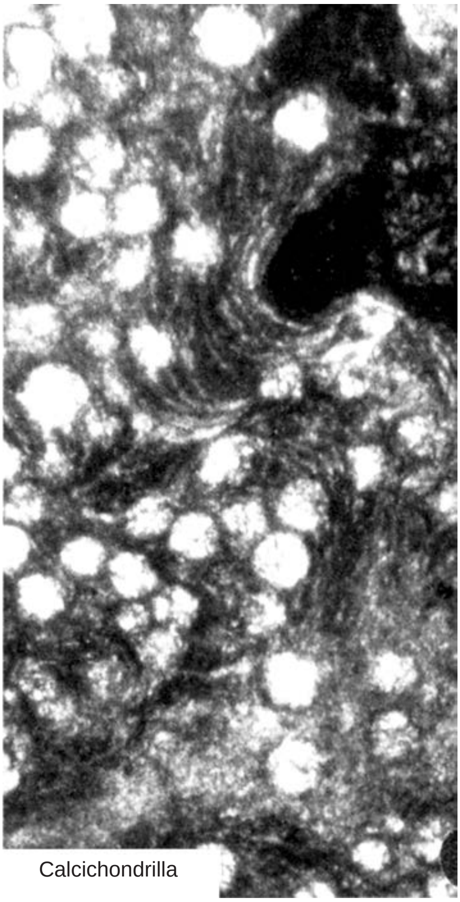


Fig. 141. Chondrillidae (p. 227–228).

Family MERLIIDAE Kirkpatrick, 1908

[Merliidae Kirkpatrick, 1908, p. 510]

Thin crusts consisting of a chaetetid-like calcareous basal skeleton (i.e., formed of a layered system of calcareous chambers), the outer layer of which is filled with sponge tissue and siliceous spicules. Basal skeleton made up of high magnesium calcite with a water-jet type microstructure. Spiculation consists of thin tylostyles arranged in wispy plumose bundles, unique keyhole-type microscleres called clavidiscs, rugose raphides, and small commata-like spicules appearing monactinal. Calcareous skeleton or clavidiscs may be absent (description modified from Hajdu & van Soest, 2002). [The monogeneric

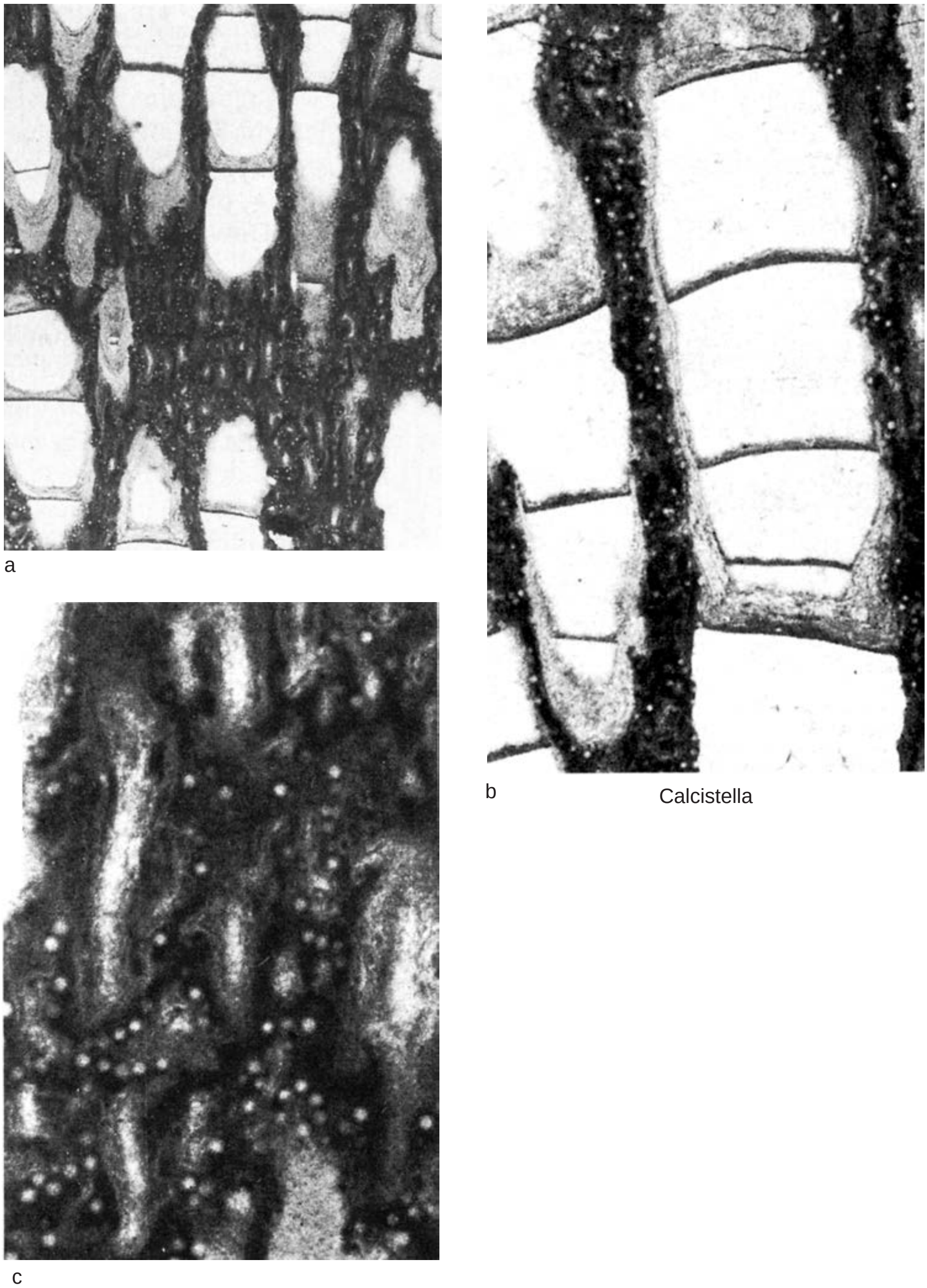


FIG. 142. Chondrillidae (p. 228–229).

family Merliidae is presently classified in the order Poecilosclerida (class Demospongiae), owing to its spicule characters and especially given the resemblance between the clavidiscs and the diancistras of Hamacanthidae GRAY, 1872 (HAJDU, 2002, p. 665). However, this relationship needs to be confirmed by molecular systematics. The microstructure and arrangement of the calcareous skeleton both suggest close affinities between Merliidae and Paleozoic and Jurassic chaetetids (GAUTRET, VACELET, & CUIF, 1991).] *Lower Jurassic–Holocene.*

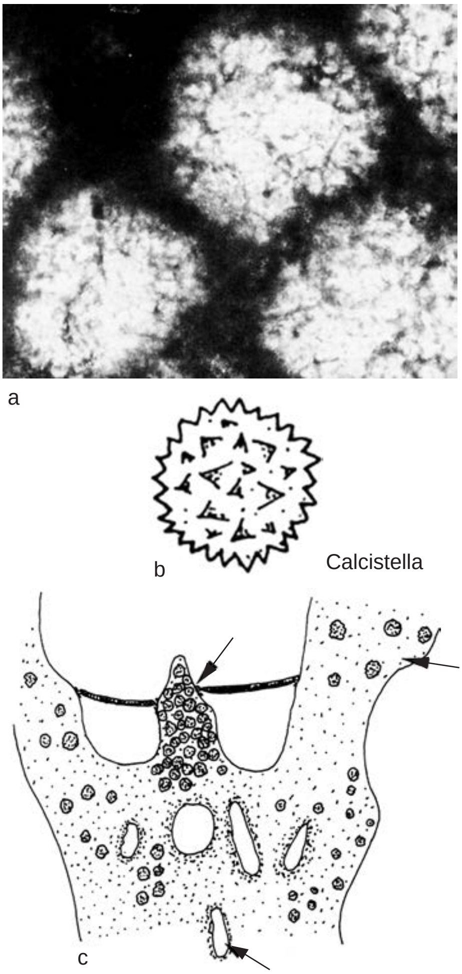


FIG. 143. Chondrillidae (p. 228–229).

Merlia KIRKPATRICK, 1908, p. 510 [**M. normani;* OD; KIRKPATRICK, 1908, p. 510, holotype NHM 1911.4.7.10] [=*Noronha* KIRKPATRICK, 1909, p. 47 (type, *N. scalariformis*, OD)]. Thin, crustlike, calcareous basal skeleton present or absent; where present, composed of vertically arranged tubes partitioned by tabulae to form layered series of chambers; those of outer layer filled with choanosomal tissue and spicules, while those beneath occupied by undifferentiated cell masses (crypt tissue). Spicules include thin tylostyles, clavidiscs, raphides and commata, though clavidiscs not always present. Microstructure of water-jet type. Type species is encrusting, 1–1.5 mm thick, subcircular to irregular crusts, which may cover surfaces larger than 100 cm^2. Living tissue somewhat transparent, with a superficial system of small canals converging toward poorly visible oscules, covering a calcareous basal skeleton. Surface smooth, microscopically slightly hispid, finely granular when dry. Color yellow-orange to red in life, clearer in preservative. Living tissue including a thin dermal membrane, a choanosome partly contained in the tubes of the calcareous skeleton, and accumulations of reserve cells in the basal crypts of the skeleton (pseudogemmulae). Choanosome has ascending bundles of tylostyles, slightly diverging at surface. Choanocyte chambers spherical, approximately 25 µm in diameter, pseudogemmulae appearing as moniliform cylinders after decalcification, made of large cells similar to gemmular archaeocytes, 15–20 µm in diameter and filled in with reserve inclusions, and, additionally, collagen fibrils of the mesohyl often forming dense fascicles and belonging to the smooth type. Calcareous basal skeleton made of a system of regularly honeycombed tubes 120–150 µm in diameter, with walls 40–60 µm thick and a pillar with tuberculate elevations at each angle. Siliceous spicules not entrapped in the calcareous skeleton. Calcareous skeleton made of high magnesium calcite, with a clinogonal (or water-jet, fasciculate) microstructure. Microstructural elements arranged vertically in axis of center of pillars, fanning out laterally along an increasing angle to build walls and tabulae. Spicules comprise slender tylostyles, straight with a poorly marked oval head, 120–160 by 0.7–2 µm, clavidiscs that are more abundant near surface, varying from ring shaped, 40–50 by 30 µm and 3 µm thick, to 62 by 38 µm, with a well-developed margin and two key-hole notches, as well as rugose raphides in trichodragmata, 40–90 µm, and commata 15 µm. Clavidiscs and commata are sometimes absent (KIRKPATRICK, 1911; HAJDU & VAN SOEST, 2002). Other Recent species comprise: *M. lipoclavidisca* VACELET & URIZ, 1991, which lacks clavidiscs, possibly because it occupied a silicon-poor environment (based on specimens from Lebanon; unpublished data [J. VACELET, July 2003]; therefore it probably is a synonym of *M. normani*); *M. deficiens* VACELET, 1980b, has a wide circumtropical distribution like *M. normani* but also extends to Pacific localities; and *M. tenuis* HOSHINO, 1990, occurs in Japan. Both the latter lack a basal skeleton, so they do not share all the same derived generic characters (synapomorphies) as the type species. Recent material shows that

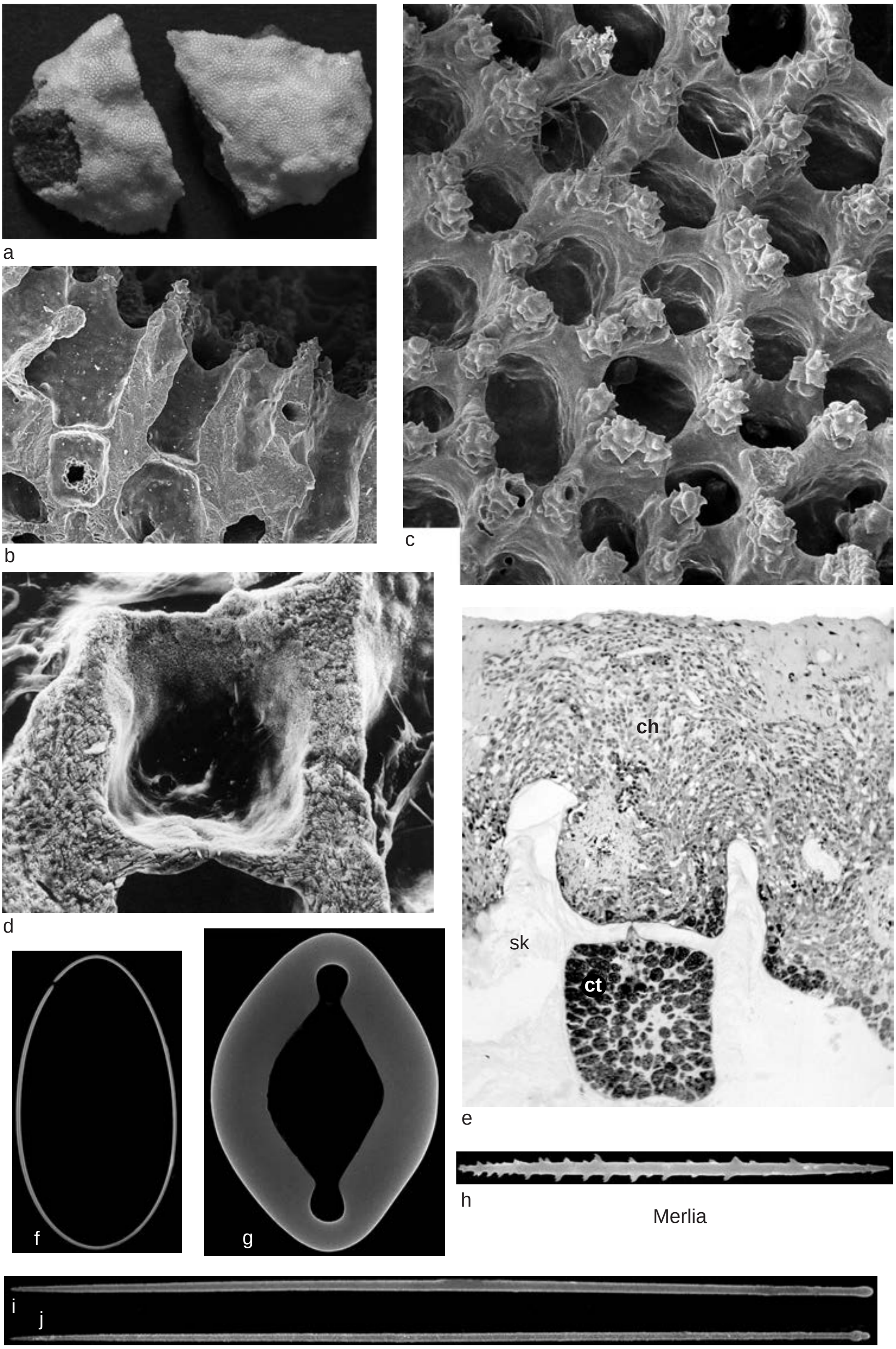


FIG. 144. Merliidae (p. 231–234).

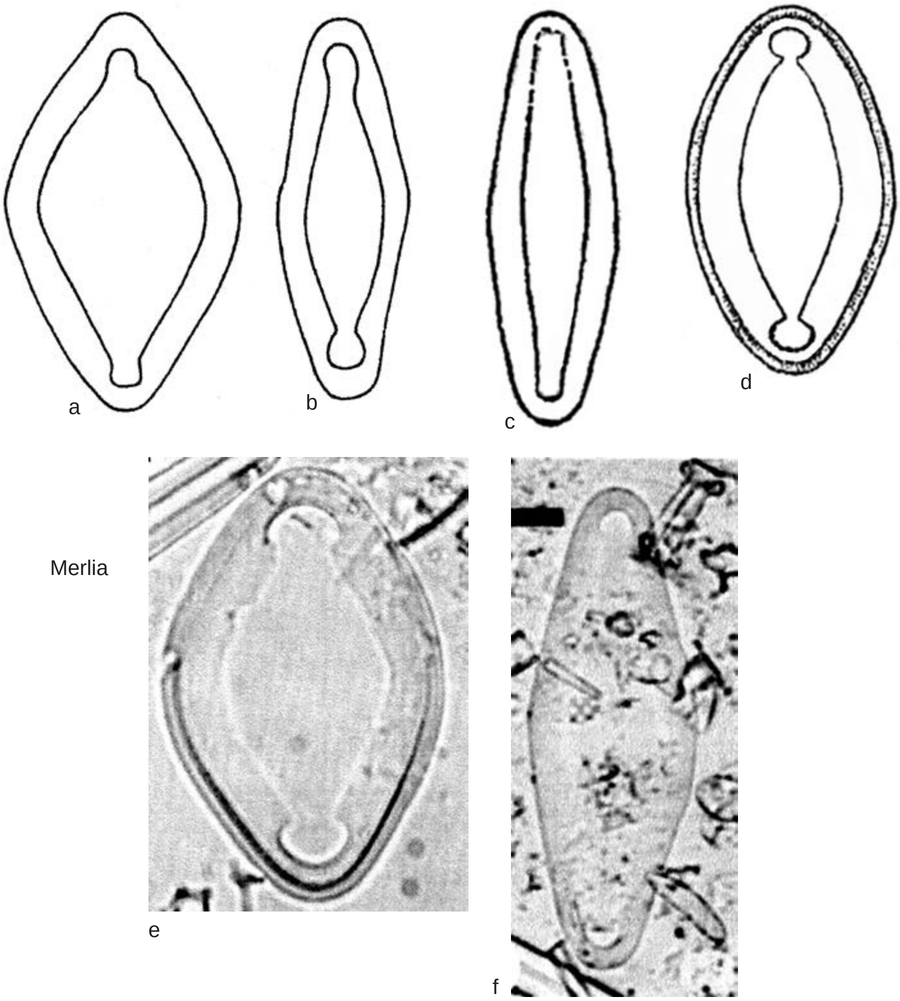


FIG. 145. Merliidae (p. 231–234).

in superficial analysis, the calcified *Merlia* are very frequently confused with bryozoans, suggesting that fossil specimens are more numerous than recorded. The absence of observation of reproduction stages suggests that these sponges are oviparous. Merliid sponges commonly lived in semidark caves, 5–15 m depth, in cryptic habitats of coral reefs, and on deeper rocky substrata down to 165 m; always in dim light conditions and warm temperate to circumtropical tropical waters. [The fossil record includes calcareous skeletons resembling *M. normani* from the Miocene of Spain (BARRIER & others, 1991), and distinctive and diagnostic spicules (clavidiscs) have been recorded from the following localities: Lower Jurassic of Austria (MOSTLER, 1990); Upper Cretaceous of northern Germany (WIEDENMAYER, 1994, p. 68, fig. 24.3 after SCHRAMMEN, 1924, pl. 4,*14;* termed psellium); Oligocene of New Zealand (*M. morlandi* HINDE & HOLMES, 1892); and Eocene and Miocene from Deep Sea Drilling Program (DSDP) cores in the western Central Atlantic (BUKRY, 1978). Spicule occurrences at these localities are not associated with reefs, suggesting the species lacked a calcareous skeleton, as in *M. deficiens* and *M. tenuis* (WIEDENMAYER, 1994).] *Lower Jurassic–Holocene:* Austria, *Lower Jurassic*; northern Germany, *Upper Cretaceous;* New Zealand, *Oligocene*; western Central Atlantic (clavidiscs only), *Eocene–Miocene;* Spain (skeletons of type species), *Miocene;* Madeira, Mediterranean, Caribbean, Red Sea and Indian Ocean and subfossil (ca. 1.5 k.y.) cave in Crete (type species), *Holocene.*——FIG. 144*a–j.* **M. normani; a,* dry specimen, Banc Ampère, western Atlantic, 56–75 m, ×2.6 (West & others, 2013); *b,* SEM

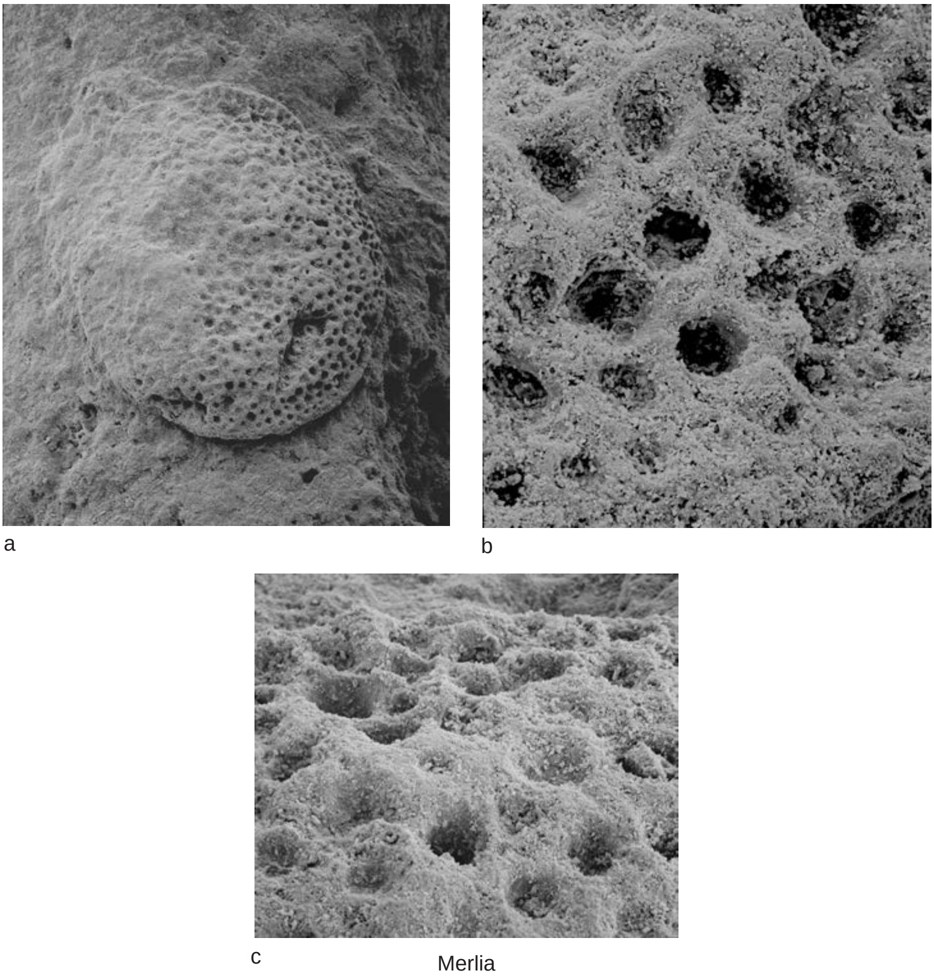
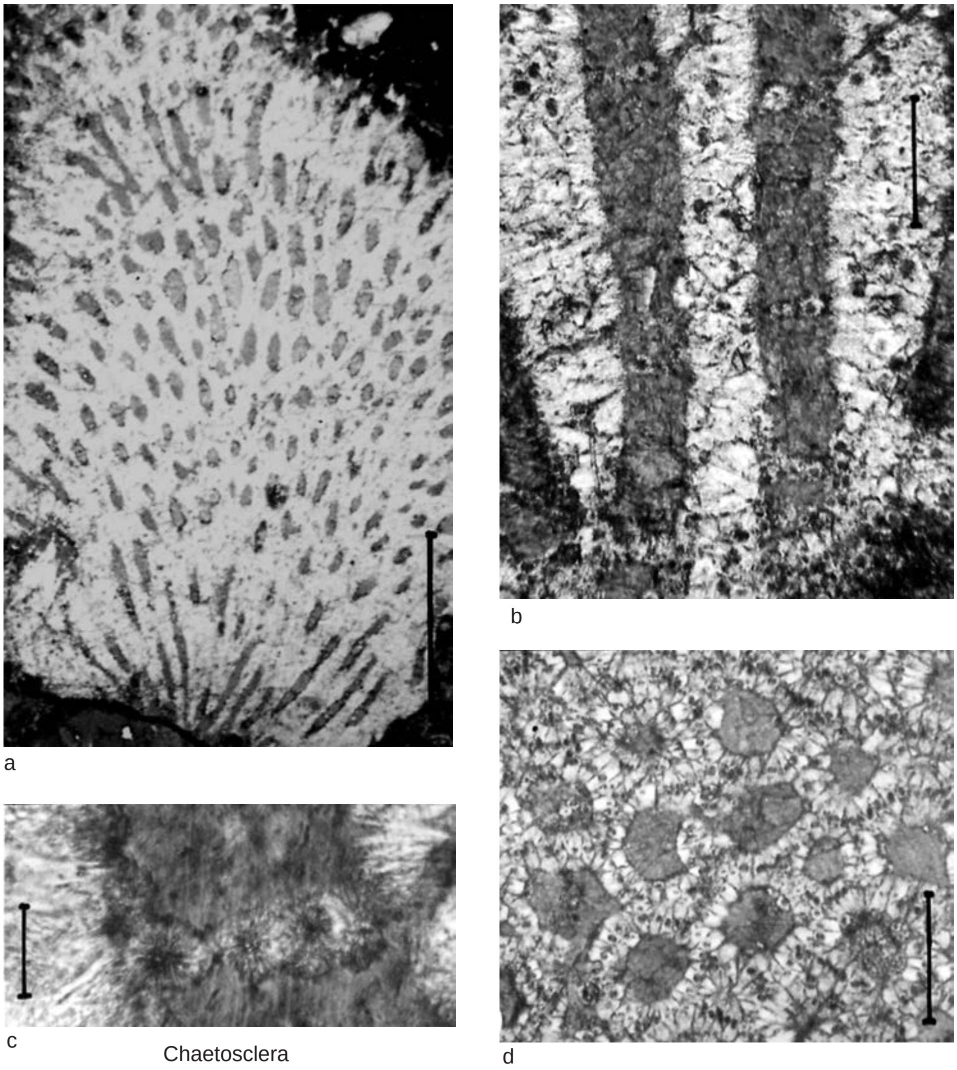


FIG. 146. Merliidae (p. 231–234).

view of a vertical section of skeleton illustrating tubes and tabulae that form a roof over basal crypts, Banc Ampère, western Atlantic, 80 m, ×560 (West & others, 2013); *c,* SEM view of surface of skeleton, Banc Ampère, western Atlantic, 80 m, ×90 (West & others, 2013); *d,* SEM view of vertical section of skeleton, after mild treatment with dilute formic acid, showing microstructure of tube walls and horizontal tabulae, ×250 (Gautret, Vacelet, & Cuif, 1991); *e,* section through a decalcified specimen showing living tissue (*ch,* choanosome; *ct,* crypt tissue or pseudogemmula) and traces of organic material in decalcified skeleton (*sk*), ×180 (Vacelet, 1990); *f–j,* SEM views of spicules, Porto Santo, 110 m depth, specimen housed in NHM; *f,* immature stage of clavidisc, ×670; *g,* clavidisc, ×1500; *h,* rugose raphide, ×1400; *i–j,* tylostyles, ×800 (West & others, 2013).——FIG. 145*a–f. Merlia* sp.; *a–b,* clavidisc, lower Jurassic, northern Calcareous Alps, northern Italy, magnification unknown (Mostler, 1990, pl. 17); *c,* clavidisc, upper Cretaceous, northern Germany, ×253 (Wiedenmayer, 1994, p. 68, adapted from Schrammen, 1924, pl. 4); *d,* clavidisc, Oamaru Diatomite, Eocene–Oligocene, New Zealand, ×373 (Hinde & Holmes, 1892, pl. 9); *e,* clavidisc, Middle Eocene, DSDP Core 391A, Blake Nose, western Central Atlantic, ×460 (Bukry, 1978, pl. 14); *f,* clavidisc, lower Miocene, Deep Sea Drilling Project Core 390A, Blake–Bahamas Basin, western Central Atlantic, ×800 (Bukry, 1978, pl. 14).——FIG. 146*a–c. Merlia* sp., Miocene, Spain; *a,* SEM photograph of upper surface of basal skeleton, ×25; *b,* SEM oblique photograph of upper surface of basal skeleton, ×200; *c,* SEM photograph of enlargement of part of upper surface in view *a,* ×220 (West & others, 2013).



Chaetosclera

FIG. 147. Uncertain (p. 236).

Order HALICHONDRIDA Gray, 1867

RONALD R. WEST and RACHEL A. WOOD

[*nom. correct.* VAN SOEST & HOOPER, 2002a, p. 721, *pro* Halichondriida WIEDENMAYER, 1977, p. 148, *nom. correct. pro* Halichondrides LÉVI, 1953, p. 853, *nom. correct. pro* Halichondrina VOSMAER, 1887, p. 335, *nom. correct. pro* Halichondriadae GRAY, 1867, p. 518] [=Axinellides LÉVI, 1953, p. 853; =Clavaxinellides LÉVI, 1956, p. 167, *partim*; =Clavaxinellida LÉVI, 1957, p. 181, *partim*; =Axinellida LÉVI, 1957, p. 181, *partim;* =Claraxinellida LÉVI, 1957, p. 183, *lapsus calami*]

Demospongiae with styles, oxeas, strongyles, or intermediate spicules, of widely diverging sizes, and not functionally localized; skeleton plumoreticulate, dendritic, or confused; microsleres, if present, microxeas and/or trichodragmas (diagnosis and name history as stated in VAN SOEST & HOOPER, 2002a, p. 721). See also FINKS and RIGBY (2004a, p. 46). If the three genera in the following family Uncertain belong to this order, then the stratigraphic range of the order should be *Triassic–Holocene*.

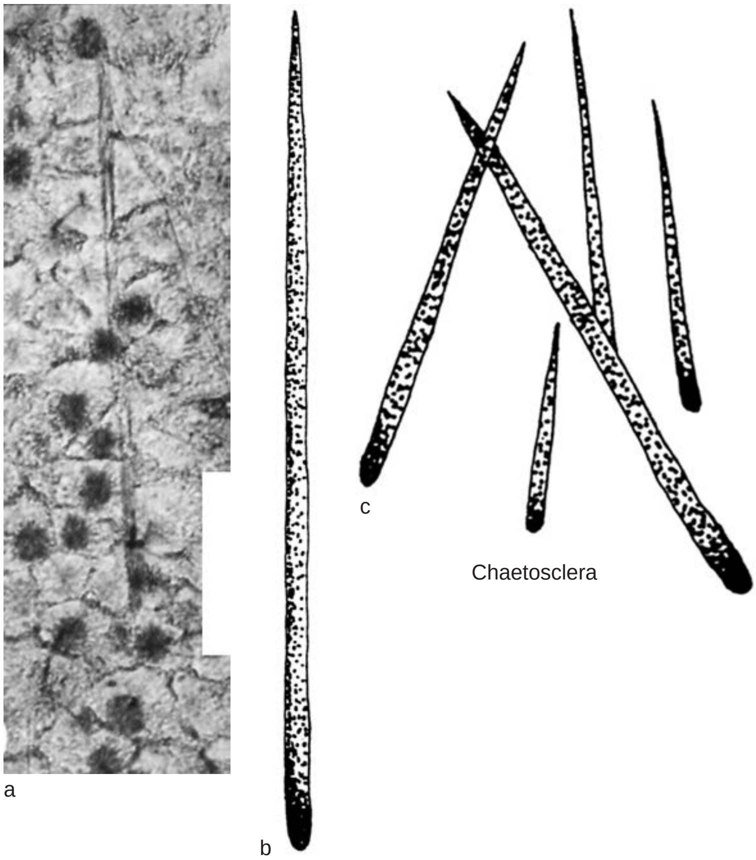


FIG. 148. Uncertain (p. 236).

Family UNCERTAIN

Chaetosclera Reitner & Engeser, 1989a, p. 160 [**C. klipsteini*; OD; holotype, IPFUB, JR 89/12; paratype, NHM, D54224]. Growth form domical to pyriform, small; tubules polygonal in transverse section, long, with tabulae; tubule walls and tabulae composed of spherulitic aragonite; originally opal tylostyle megascleres (175–300 µm long, 2–4 µm in diameter) preserved as Fe calcite pseudomorphs, arranged in bundles of 3 to 4, pointing outward in tubule walls, some along internal side of tubules; microscleres unknown. *Upper Triassic (Carnian)*: northern Italy (Dolomite Alps).——FIG. 147*a–d*. **C. klipsteini*; *a,* tangential section of basal skeleton of holotype, IPFUB JR 89/12, ×4.8; *b,* longitudinal section of holotype, IPFUB JR89/12, showing tubule walls (light vertical areas) and poorly preserved tabulae (light horizontal areas near base of figure), ×170; *c,* detail of tabulae showing spherulitic microstructure in holotype, IPFUB JR 89/12, ×600; *d,* transverse section of paratype showing spherulitic microstructure of tubule walls (light areas with diagenetically altered dark centers), ×170 (Reitner & Engeser, 1989a, pl. 1).——FIG. 148*a–c*. **C. klipsteini*; *a,* spherulitic tubule wall of holotype, and some spherules appear to extend into a tylostyle megasclere, suggesting that they are secondary structures, IPFUB JR 89/12, ×392 (Reitner & Engeser, 1989a, pl. 1); *b,* sketch of tylostyle megasclere, ×433; *c,* sketch of cluster of tylostyle megascleres, ×360 (Reitner, 1992, p. 199).

Neuropora Bronn, 1825, p. 43 [**Chrysaora spinosa* Lamouroux, 1821, p. 83; OD; =*Neuropora spinosa* Lamouroux in Bronn, 1825, p. 43; =*Chrysaora spinosa* Lamouroux in Michelin, 1846 in 1840–1847, p. 237; =*Acanthopora lamourouxi* Haime, 1854, p. 216; =*Neuropora spinosa* Haime, 1854, p. 214; =*Neuropora spinosa* Lamouroux in Bassler, 1953, p. 68; =*Neuropora spinosa* Walter, 1969, p. 44]. Growth form laminar to columnar (branching), often with

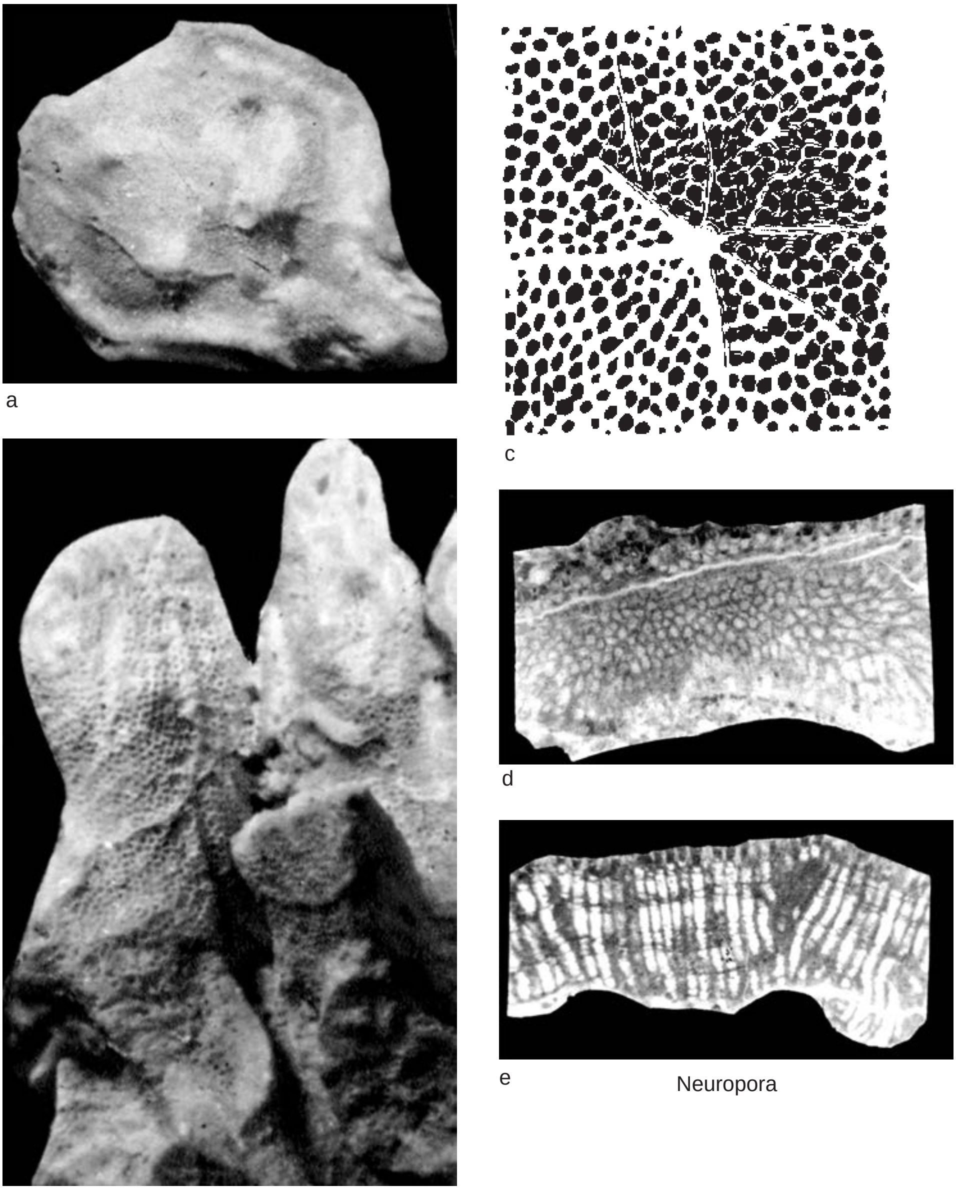


FIG. 149. Uncertain (p. 236–238).

surface mamelons, astrorhizae, and small buds; tubules irregular polygons in transverse section; in longitudinal section, tubules long, narrow, diverging from a point and becoming parallel in upper part of basal skeleton; may be filled with epitaxial cement and resemble *Ceratoporella*. [The mineralogy, microstructure, and spicules and/or spicule pseudomorphs are unknown from the neotype, *N. spinosa*, but these features and the original mineralogy are inferred from studies of *N. pustulosa* (ROEMER, 1839); tubule walls Mg calcite (inferred) penicillate, water-jet (fascicular fibrous) microstructure; microstructure of tabulae semispherulitic to clinogonal; tylostyle megascleres 100–200 µm long and 5–7 µm in diameter, in bundles of 3 to 4, with distal ends

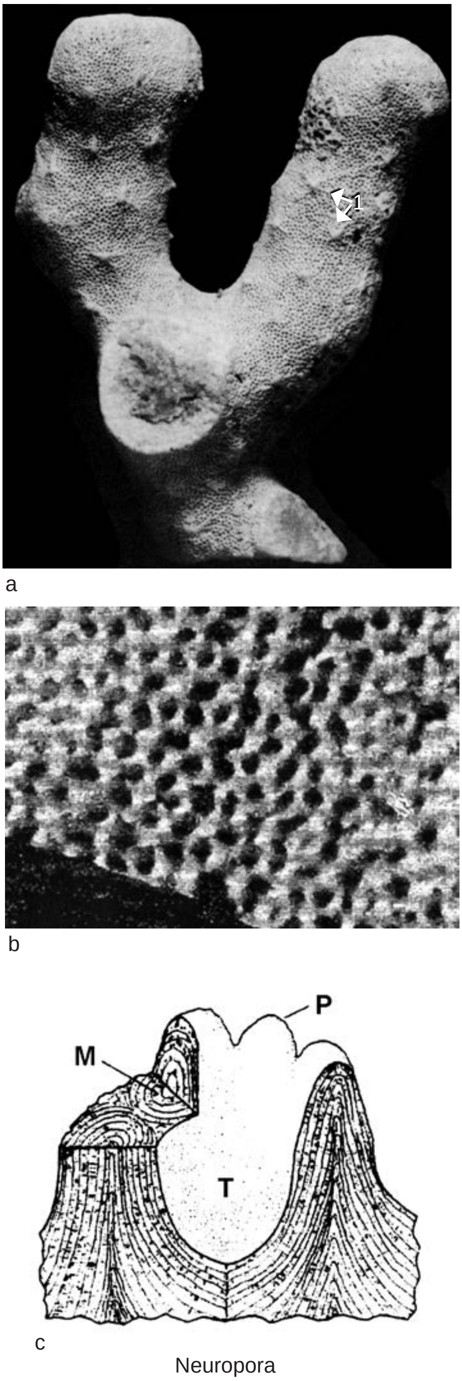


Fig. 150. Uncertain (p. 236–238).

pointing toward sponge surface, some attached proximally to tubule walls and projecting into tubules; microscleres unknown (description modified from Walter, 1969 (specimens are in the collections of the Department of Earth Sciences, Faculté des Sciences de Lyon [F.S.L.]); Kaźmierczak & Hillmer, 1974 (specimens are in the collections of the Geological-Palaeontological Institute of the University of Hamburg [SGPIH] and the Roemer-Pelizaeus Museum, Hildesheim [SRPMH]); Reitner, 1992.] *Middle Jurassic (Bathonian)–Lower Cretaceous (Hauterivian)*: France, *Bathonian*; Germany, *Hauterivian*.——Fig. 149*a–e*. **N. spinosa* (Lamouroux); *a,* exterior surface of basal skeleton of neotype, no. 490 F.S.L., upper Bathonian, Langrune-sur-Mer, Calvados, France, ×4.7; *b,* exterior of branching columnar basal skeleton, no. 28 972 F.S.L., upper Bathonian, Blainville, Calvados, France, ×7.5 (Walter, 1969, pl. 18–19); *c,* surface feature (possible astrorhiza), Bathonian, France, ×18 (Bassler, 1953, p. 67); *d,* transverse to tangential section of basal skeleton, no. 38 094 F.S.L., upper Bathonian, Blainville, Calvados, France, ×9.9; *e,* longitudinal section of basal skeleton, no. 38 174 F.S.L., upper Bathonian, Ranville, Calvados, France, ×10 (Walter, 1969, pl. 18–19).——Fig. 150*a–c*. *N. pustulosa* (Roemer, 1839), Hauterivian, northwestern Germany; *a,* fused columnar branching basal skeleton, note stellate pattern (*1* and *arrows*), ×2.3 (Reitner, 1992, pl. 34); *b,* surface view of tubules, SGPIH 1726, Achim, ×35; *c,* diagrammatic sketch of tubule surface; *T,* tubule; *P,* pustules; *M,* mamelon-like columns with inferred microstructure, ×500 (Kaźmierczak & Hillmer, 1974, p. 447, pl. II).——Fig. 151*a–d*. *N. pustulosa* (Roemer, 1839), Hauterivian, northwestern Germany; *a,* calcite pseudomorph of tylostyle megasclere, ×590; *b–c,* diagrammatic sketch of tylostyle megascleres, ×450; *d,* pseudomorphs of two tylostyle megascleres, ×360 (Reitner, 1992, p. 206, pl. 34).

Stromatoaxinella Wood & Reitner, 1988, p. 215 [**Chaetetes irregularis* Michelin, 1847 in 1840–1847, p. 306; M; holotype, NHM no. 5481]. Calcareous skeleton with tracts of long, thin, loosely plumose styles preserved mainly in secondary filling tissue within tubules; only rarely incorporated into outer parts of tubule walls; walls formed by fusion of adjacent columns, primary fascicular fibrous microstructure. *Upper Cretaceous (Santonian)*: France, Spain.——Fig. 152*a–b*. **S. irregularis* (Michelin), light photomicrograph, NHM no. 5481, Collades de Bastus, Spain; *a,* longitudinal thin section, ×20; *b,* longitudinal thin section, ×100 (Wood & Reitner, 1988, p. 216).——Fig. 153. **S. irregularis* (Michelin), light photomicrograph, NHM no. 5481, Collades de Bastus, Spain; foramina and aligned tabulae in longitudinal-oblique thin section, ×50 (Wood & Reitner, 1988, p. 216).

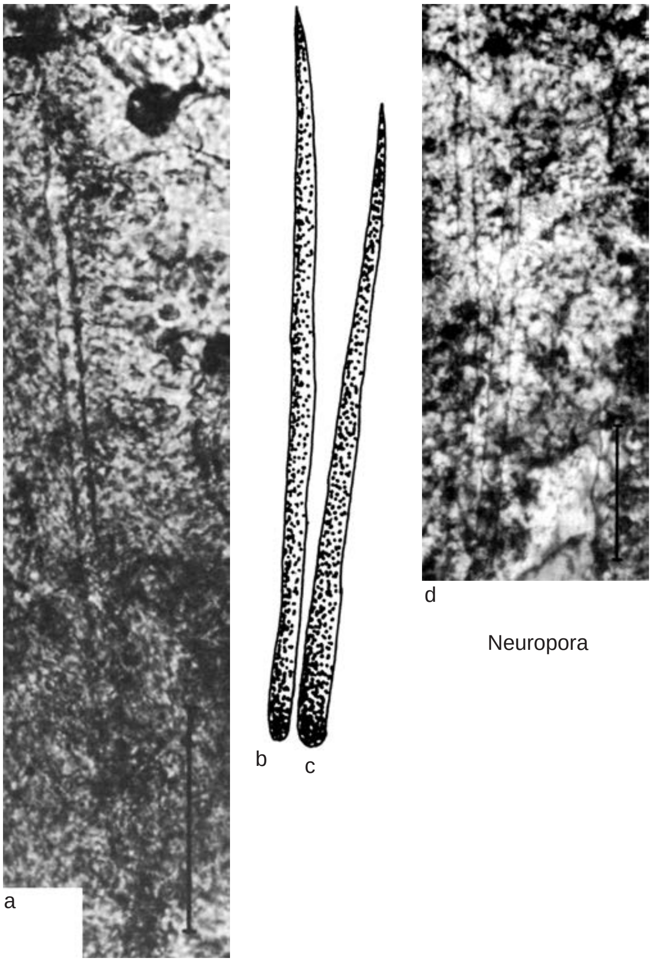


FIG. 151. Uncertain (p. 236–238).

Order AGELASIDA Hartman, 1980

JEAN VACELET, PHILIPPE WILLENZ, RONALD R. WEST, AND †WILLARD D. HARTMAN

[Agelasida HARTMAN, 1980b, p. 29]

Demospongiae with verticillately spined monactine megascleres, coring or echinating a system of anastomosing spongin fibers, or echinating the limestone walls of a basal skeleton in which they are progressively entrapped; if present, basal skeleton of spherulitic or penicillate aragonite. [FINKS and RIGBY (2004d, p. 594) proposed VERRILL (1907, p. 333) as author of the order, whereas HOOPER and VAN SOEST (2002a, p. 819) retained HARTMAN (1980b) as the author, based on the same type genus. VERRILL (1907) proposed only the family name Agelasidae, whereas the order Agelasida was formally proposed independently by HARTMAN (1980b). A former editor of the *Treatise* (see KAESLER in FINKS, REID, & RIGBY, 2004, p. xix), following the *Code*

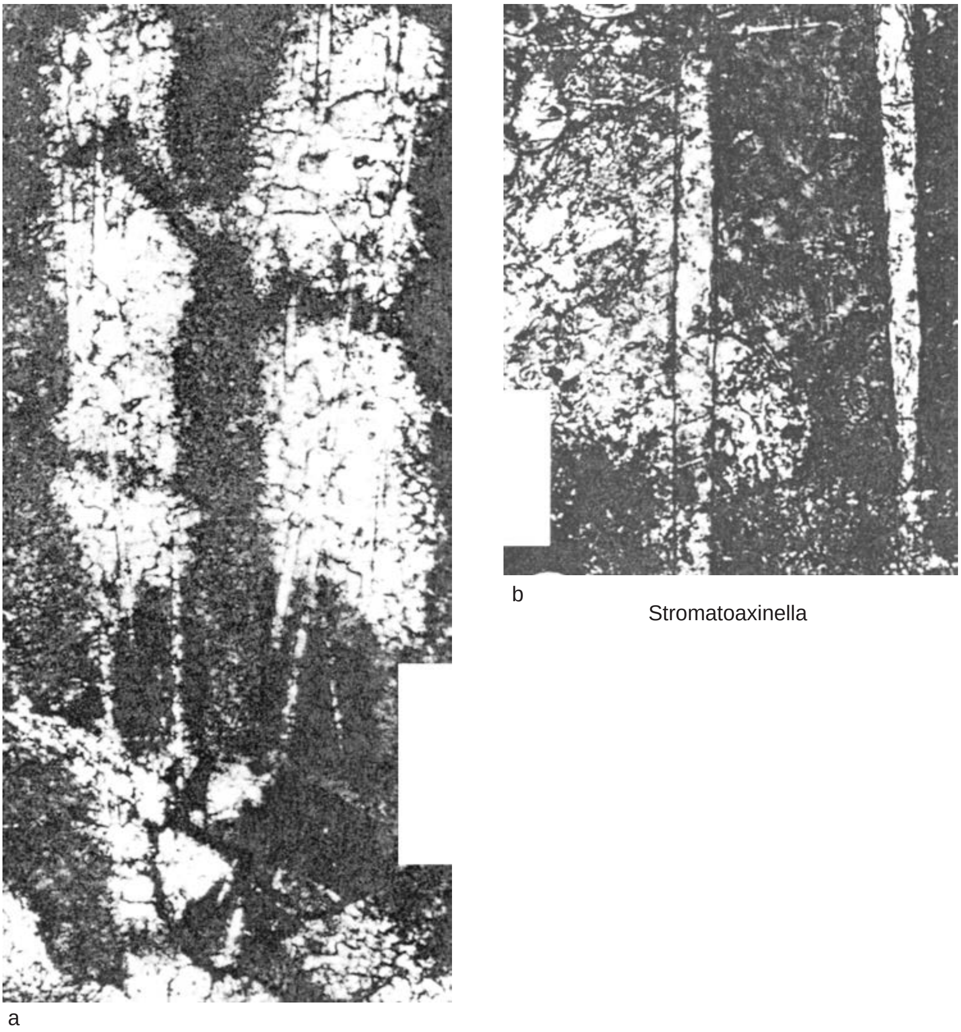


FIG. 152. Uncertain (p. 238).

of Zoological Nomenclature (ICZN, 1999), has drawn a classificatory and nomenclatorial distinction between suprafamilial and family group taxa; consequently, the family name Agelasidae VERRILL, 1907, is not considered to be transferable to a suprafamilial taxon while retaining the same author. Order Agelasida HARTMAN, 1980, is therefore the preferred usage. FINKS and RIGBY (2004d) include in this order several families of Paleozoic sponges of uncertain affinities whose skeleton is made of spherulitic aragonite.] *upper Permian–Holocene.*

Family ASTROSCLERIDAE Lister, 1900

[Astroscleridae LISTER, 1900, p. 479] [=Ceratoporellidae HARTMAN & GOREAU, 1972, p. 136]

Agelasida with verticillately spined styles, occasionally smooth styles, and a basal calcareous skeleton made of spherulitic or clinogonal sclerodermites in aragonite (VACELET, 2002a). [Monophyly of the family presently is not well established for the Recent representatives; *Astrosclera* with spherulitic microstructure and with incubated parenchymella larvae, other genera with penicillate microstructure and unknown reproduction, suggesting a possible future splitting into two families: Astroscleridae Lister, 1900, and Ceratoporellidae Hartman & Goreau, 1972. Two genera are placed questionably in this family: *Cassianochaetetes* and *Spherolichaetetes*; for discussion, see those genus entries.] *upper Permian–Holocene.*

Astrosclera Lister, 1900, p. 459 [**A. willeyana;* OD; holotype NHM 1990.1019.1]. Massive growth form. Meandroid or reticulate calcareous skeleton in aragonite, composed of spherulitic sclerodermites of intracellular origin and further epitaxial growth. Living tissue inside irregular lacunae of superficial calcareous skeleton. Superficial canals etching an astrorhizal system on surface of calcareous skeleton. Siliceous styles of variable shape, often echinating in the calcareous skeleton, sometimes absent (diagnosis as stated by Vacelet, 2002a, p. 825). Type species massive, globular, bulbous, cushion shaped, or cylindrical. Young specimens encrusting, growing upward into a cylindrical structure, with a dead stalk and a living head progressively becoming rounded and larger than the stalk (bulbous shape). In largest specimens, shape subspherical with a stalk hidden by head margins growing down toward substratum. Growth rings visible, but without any trace of regeneration or budding. Bathyal specimens mostly cylindrical. Size usually 0.5–2.5 cm, up to 25 cm in diameter. Texture stony. Color orange. Surface smooth, irregularly mammillate in some large specimens. Oscules small, 2–5/cm^2, in the center of an astrorhizal system etched into skeleton. Living tissue located at surface and inside irregularly reticulated lacunae of superficial (1–8 mm thick) calcareous skeleton. No special ectosomal differentiation. Choanocyte chambers small, approximately 15 µm in diameter. Exhalant canals bearing a valvule near the aphodus. Tissue containing a high density of morphologically diverse intercellular bacteria. No well-defined spherulous cells. Basal calcareous skeleton in aragonite, alveolar in surface and with an organization more or less similar to that of fossil stromatoporoids, solid in the backfilled central parts. Tabulae absent. Basal parts externally covered by a basal layer. Sometimes associated with zoanthids, which are included in basal skeleton. Microstructure spherulitic, built up of sclerodermites 10–60 µm in diameter, with crystal fibers, 1–3 µm in diameter, arranged in a radiate structure. Sclerodermites intracellularly secreted as granules that pass through spheraster-like stage and are incorporated into superficial parts of solid skeleton when their size is 20–25 µm (Lister, 1900; Gautret, 1986; Wörheide & others, 1997). Siliceous acanthostyles dispersed in the living tissue. In some specimens, acanthostyles entrapped by their bases within the calcareous skeleton, obliquely echinating the basal skeleton. Acanthostyles usually with a swelling in basal third, but highly variable in shape, size, and abundance, according to geographic distribution. In Indian Ocean, acanthostyles 42–87 µm by 2.5–11 µm, with verticillated spines generally well developed; spines absent in the Red Sea. In West Pacific, acanthostyles 47–164 µm by 1.7–10.5 µm, sometimes vestigial or absent, with an irregular spination. Siliceous spicules absent

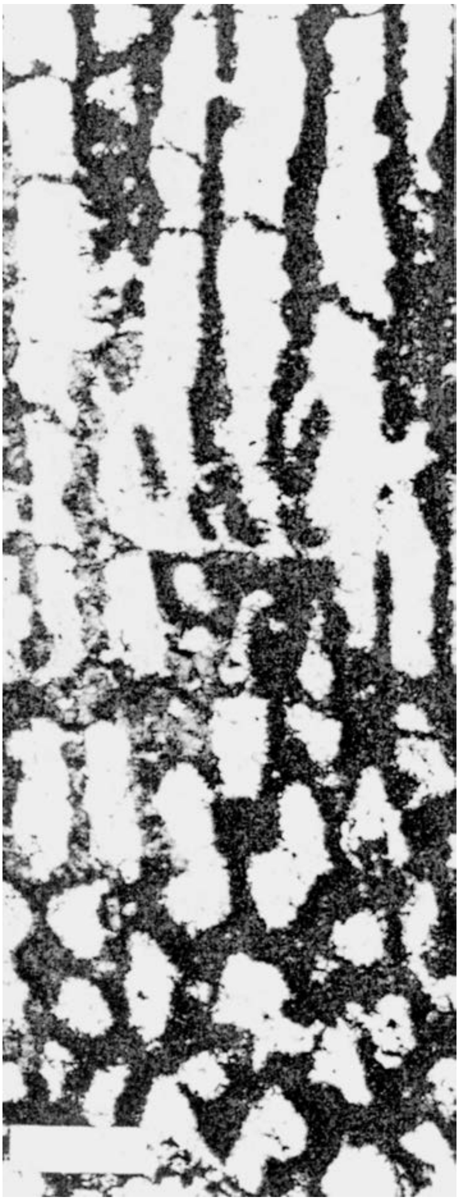

Stromatoaxinella

Fig. 153. Uncertain (p. 238).

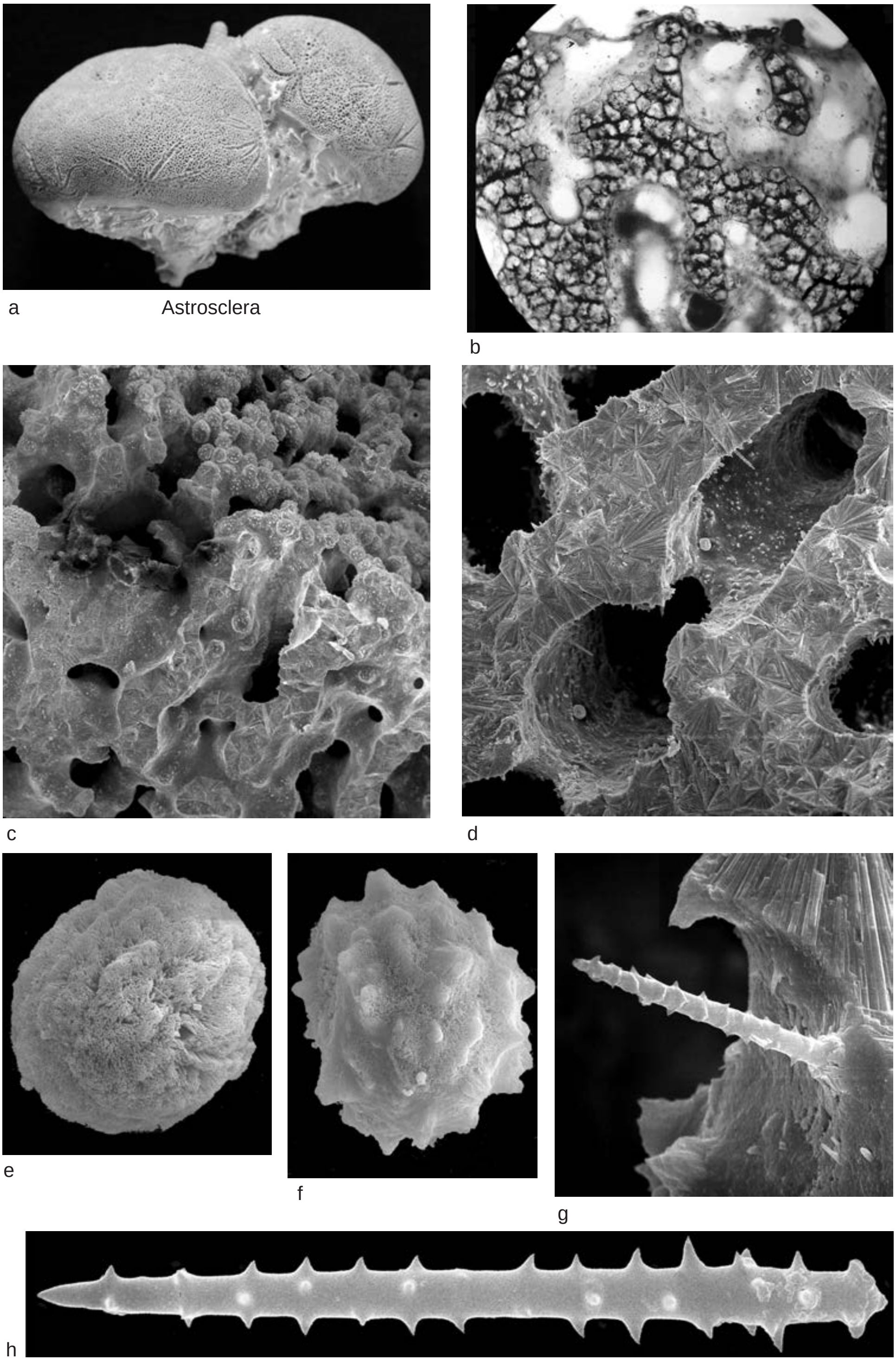


FIG. 154. Astroscleridae (p. 241–243).

in Central Pacific. Reproduction viviparous, by incubated parenchymella. Growth rate of the skeleton approximately 0.2 mm/yr (Wörheide, 1998). Common on undersurfaces of coral rubble, reef cavities, caves, deep cliffs, 1–185 m depth. (modified from Vacelet, 2002a, p. 827). Other Recent species: a single species has been formerly described. However, recent results using molecular data suggest the presence of several distinct species (Wörheide, personal communication, 2005). Fossil records: *Astrosclera cuifi* Wörheide, 1998, described as a Triassic representative from Turkey (Wörheide, 1998), with spherulitic basal skeleton and acanthostyles. Other fossils from upper Permian and Upper Triassic, with spherulitic microstructure but without spicules and showing various grades of skeletal construction, are more uncertain relatives. A similar mode of skeletal secretion has been demonstrated in some of these fossils (Gautret, 1986). [No fossil record of the genus exists between the Triassic and the Recent, so the genus is regarded as a Lazarus-taxon (Wörheide, 1998; Reitner & Wörheide, 2002, p. 64).] *Upper Triassic–Holocene*: Turkey, *Upper Triassic;* Red Sea, Madagascar, Seychelles, Comoro Islands, Christmas Island, Mascarene islands, Philippines, Indonesia, Great Barrier Reef, New Caledonia, Guam, Enewetak, French Polynesia, Japan, *Holocene.*——Fig. 154*a–h.* **A. willeyana*; *a*, dry specimen with astrorhizae, Philippines, water depth 24 m, MNHN DJV152, ×1.7 (West & others, 2013; see also Fig. 1.2); *b*, section through skeleton and living tissue with free spherules near surface (top) and two oocytes in choanosome, MNHN DJV152, ×43 (West & others, 2013); *c,* SEM view of surface (top right) and a fracture through skeleton with protruding spicules, Mayotte Island, water depth 25 m, ×43 (West & others, 2013); *d,* SEM view of fracture through skeleton, without siliceous spicule, Marquesas Islands, 90–130 m depth, ×120 (West & others, 2013); *e–f,* SEM views of free stages of growth of skeletal spheroliths, Marquesas Islands, 90–130 m, ×1100 (West & others, 2013); *g,* SEM view of spicule protruding from skeleton, Mayotte Island, 25 m depth, ×1300 (West & others, 2013); *h,* SEM view of acanthostyle spicule, Mayotte Island, 25 m depth, ×2100 (West & others, 2013).

?Cassianochaetetes Engeser & Taylor, 1989, p. 43 [**Catenipora orbignyanus* Klipstein, 1845 in 1843–1845, p. 288; OD; holotype, NHM S10465 (specimen and 2 thin sections); as the only recognizable syntype, this is designated as the holotype] [=*Leiofungia* de Fromentel, 1860b, p. 49 (type, *Achilleum milleporatum* Münster, 1841, p. 26, OD); =*Leiospongia* de Laubenfels, 1955, p. 100 (type, *Achilleum milleporatum* Münster, 1841, p. 26, OD de Laubenfels, 1955, p. 26)]. Growth form small, fungiform with convex upper surface; basal layer well developed with growth lines; tubules irregular polygons in transverse view; tubules long, slightly curved; tabulae, if present, with flat upper surface and tufted lower surface or as tubule narrowing or irregular tubule occlusions; tubule walls elongate aragonite spherules (recrystallized); megascleres and microscleres unknown (description modified from Engeser & Taylor, 1989, p. 43–46). [For more on the taxonomic history of this genus and assigned species, see Engeser and Taylor (1989, p. 43–49). This genus is placed questionably in the family Astroscleridae because, although it has the typical spherulitic microstructure, spicules are unknown and the skeletal construction appears to be somewhat different.] *Upper Triassic (Carnian):* Italy.——Fig. 155*a–e.* **C. orbignyanus* (Klipstein), holotype, Cassian Formation, northern Italy; *a,* specimen magnification unknown (Klipstein, 1845 in 1843–1845, pl. 19,*20a*); *b,* lateral view showing mushroom shape and basal layer, ×4.7; *c,* upper surface showing shape of tubules, ×4.4; *d,* longitudinal section showing radiating tubules, ×5.2; *e,* enlarged view of longitudinal section showing recrystallized tubule walls, ×17.5 (Engeser & Taylor, 1989, p. 45).

Ceratoporella Hickson, 1912, p. 351, *nom. nov. pro Ceratopora* Hickson, 1911, p. 200, *non* Grabau, 1899, p. 414, coelenterate [**Ceratopora nicholsoni* Hickson, 1911, p. 200; OD]. Massive growth form, mound shaped when mature, with regularly spaced mamelons; young individuals cone shaped or pedunculate. Color orange in life. Mound-shaped specimens up to 100 cm in diameter and 50 cm in thickness on deep fore reef, extraordinarily tough and heavy. Basal and lateral surfaces of the skeletal mass covered by a basal layer showing growth lines. Superficial parts of basal calcareous skeleton marked by closely spaced tubules, 0.2–0.5 mm across and 1–1.2 mm deep, irregularly polygonal, ranging from 150 µm to 300–400 µm in diameter. Lumen of tubules filled in with aragonite in inner part of basal skeleton. Basal skeleton made of sclerodermites with a clinogonal microstructure, consisting of closely packed crystalline units that diverge at a low angle. Siliceous spicules are styles, 206–298 µm by 3.1–4 µm, bearing regular whorls of spines, free in living tissue or obliquely entrapped in tubule wall and their bases surrounded by collagen microfibrils. Entrapped siliceous spicules progressively dissolved within basal calcareous skeleton. Living tissue forming a thin veneer at surface of calcareous skeleton and extending downward into each tubule; total thickness of living tissue 1.5 mm. Each tubulae unit corresponds to a single inhalant and exhalant canal. Canals bearing special valvules. Choanocyte chambers small, 20.7 µm in mean diameter. Exhalant collecting system leaving stellate depressions (astrorhizae) on surface of skeleton. Intercellular symbiotic bacteria abundant and highly diverse in shape. Growth rate of skeleton in Jamaican caves varying from 0.21–0.23 mm/yr measured experimentally *in situ* (Willenz & Hartman, 1999), up to 0.23–0.43 mm/yr based on U-Th age measurements (Haase-Schramm & others, 2003) or 0.20–0.60 mm/yr based on calculation from Sr/Ca data (Haase-Schramm & others, 2005). Depth range: 8–184 m. [Regular tubulae structure of the skeleton is reminiscent of the

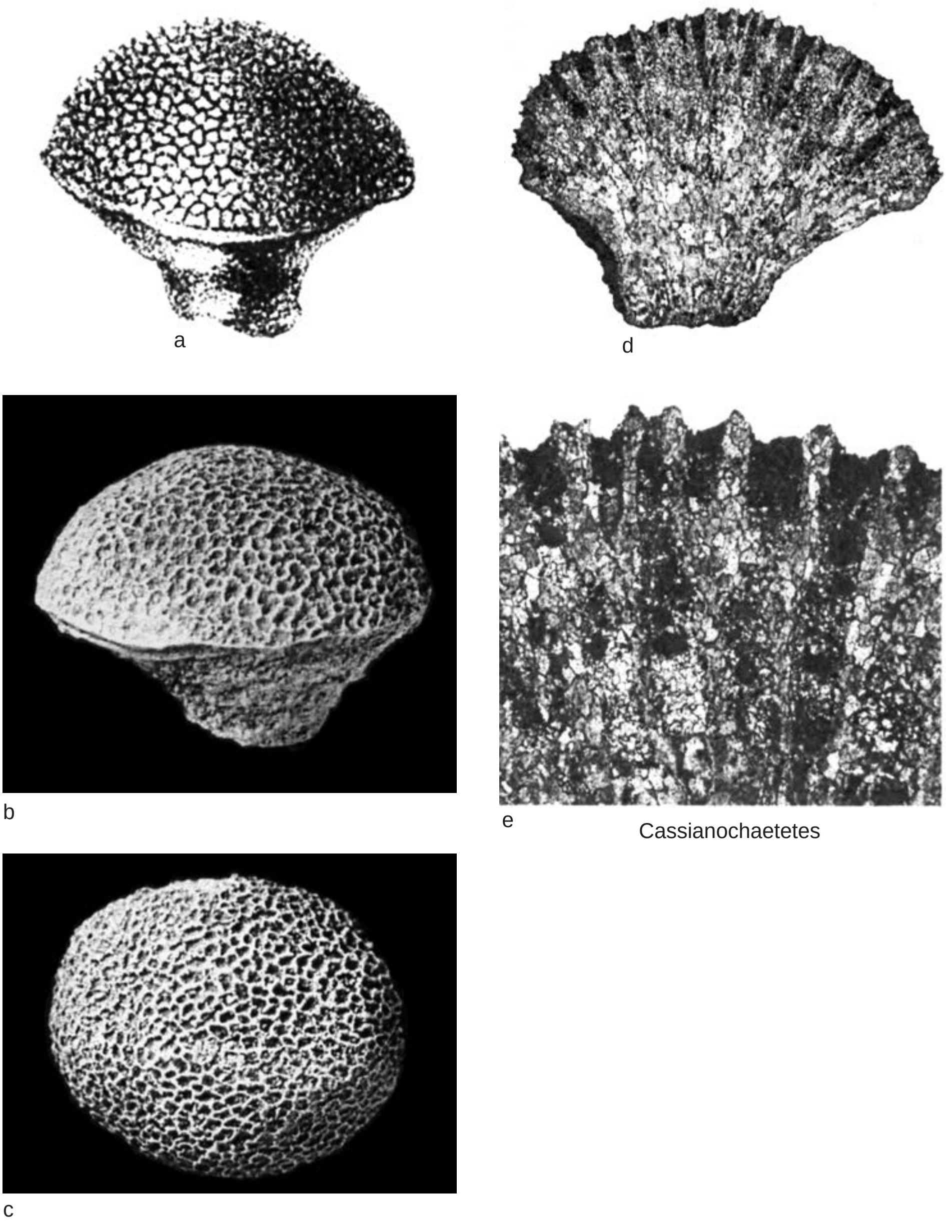


FIG. 155. Astroscleridae (p. 243).

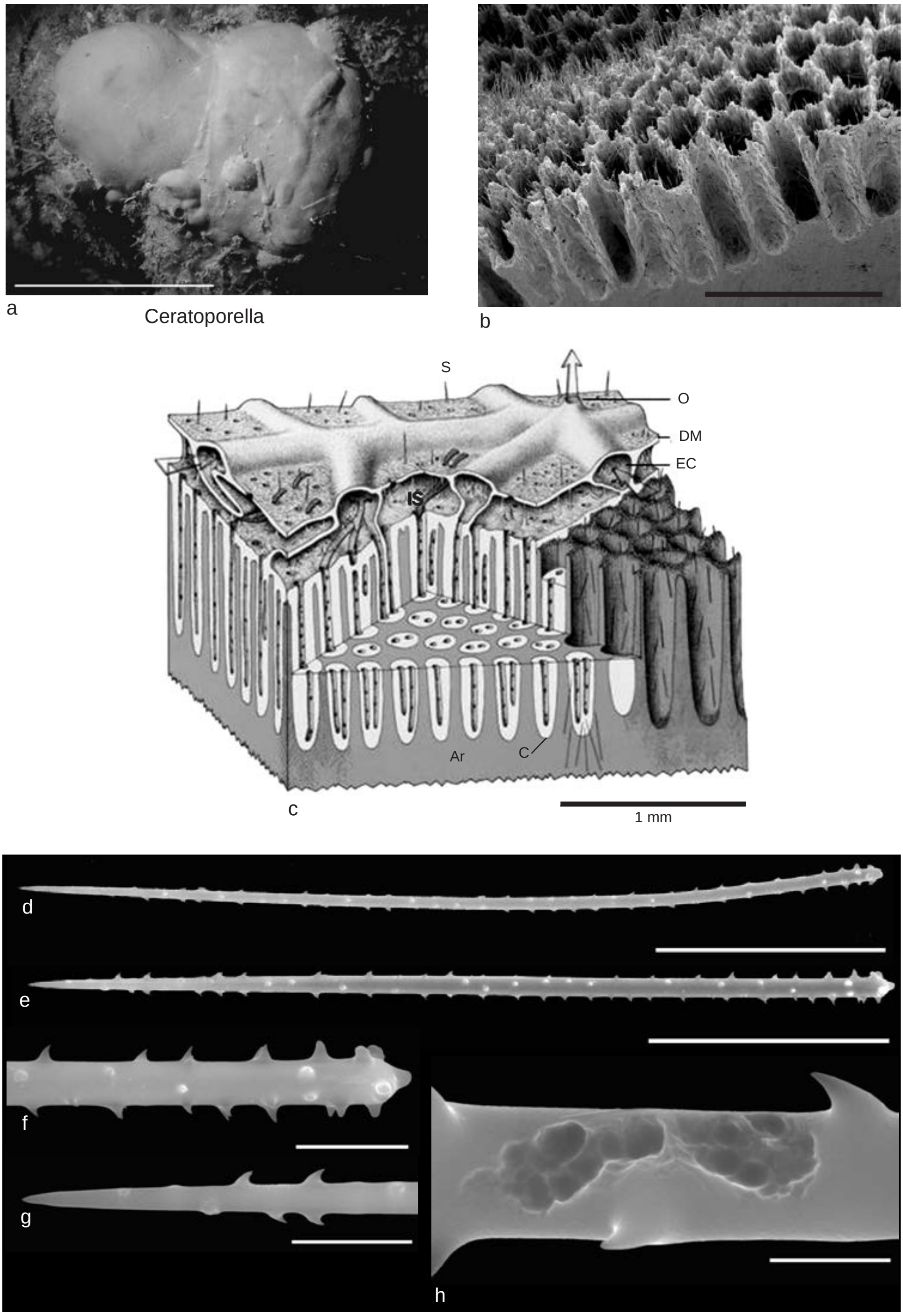


FIG. 156. Astroscleridae (p. 243–246).

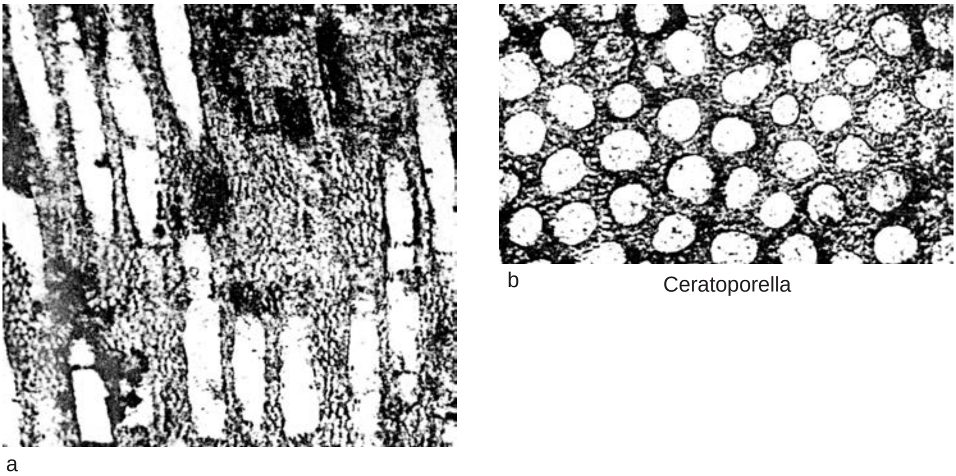


FIG. 157. Astroscleridae (p. 243–246).

calcified demosponges *Merlia* KIRKPATRICK, 1908, family Merliidae, and *Acanthochaetetes* FISCHER, 1970, family Spirastrellidae. The genus, however, is easily distinguished from these by the microstructure and composition of the skeleton and by the spicule complement (VACELET, 2002a). Fossil forms of this genus have been reported from Tunisia, as ?*Ceratoporella* sp., by H. TERMIER, G. TERMIER, and VACHARD (1977), and REITNER (1992) has described *Ceratoporella breviacanthostyla* from Italy.] *?upper Permian, Triassic (Carnian)–Holocene*: Tunisia, *?upper Permian*; northern Italy, *Carnian*; Bahamas, Belize, Cuba, Jamaica, *Holocene*.——FIG. 156*a–h*. **C. nicholsoni* (HICKSON), RBINSc-POR.095; *a,* underwater photograph of specimen with diameter about 12 cm, at depth of 25 m in reef cave on northern coast of Jamaica (not collected; see also Fig. 2.1), scale bar, 10 cm; *b,* surface of calcareous skeleton showing tubules with protruding siliceous spicules, scale bar, 1 mm; *c,* three-dimensional representation; *Ar,* aragonite skeleton; *C,* choanosome; *DM,* dermal membrane; *EC,* exhalant canal; *IS,* inhalant space or vestibule; *O,* osculum; *S,* spicule (Willenz & Hartman, 1989; see also Fig. 3.2 and Fig. 355); *d–e,* spined styles, scale bars, 50 µm; *f–g,* details of extremities of spicules, scale bars, 10 µm; *h,* detail of eroded spicule, scale bar, 2 µm (West & others, 2013).——FIG. 157*a–b*. ?*C*. sp., ?upper Permian, Tunisia; *a,* holotype, longitudinal section, No. HGT.T81, in the collection of H. & G. Termier (Paris), ×17.5; *b,* transverse section, ×17.5 (H. Termier, G. Termier, & Vachard, 1977, pl. 6).——FIG. 158*a–f*. *C. breviacanthostyla* REITNER, 1992, Carnian, northern Italy; *a,* longitudinal section of holotype, IPFUB/JR 1989, ×6.2; *b,* fractured vertical section of paratype showing microstructure (*1*) and open tubule (*2*); *open arrow* indicates sponge surface, IPFUB/JR 1989, ×100; *c,* enlargement of part of view *a* showing short iron calcite pseudomorphs of acanthostyles (*1,* area of *black arrows*); *open arrow* indicates direction to sponge surface, ×32.5; *d,* agelasid acanthostyle, ×750; *e–f,* sketches of two agelasid acanthostyles, ×550 (Reitner, 1992, p. 220, pl. 37).

Goreauiella HARTMAN, 1969, p. 16 [**G. auriculata* HARTMAN, 1969, p. 17; OD; holotype YPM no. 6858]. Auriculate or saucerlike form, with edges upturned or curled downward, attached by a broad peduncle. Color light yellow in life. Size up to 16 cm in diameter and 3 mm in thickness. Basal skeleton thin, made up of aragonitic sclerodermites, with numerous arborescent, spinose processes, 0.5–1.1 mm in height, and multibranching patterns of higher processes draining to edge of skeleton. Microstructure consisting of sclerodermites with crystals radiating in all directions from centers of calcification (clinogonal type with divergent irregular linear elements). Siliceous spicules are strongyles bearing whorls of spines, 35–124 µm by 1.3–1.9 µm (mean 60–68 µm by 2.3–2.7 µm), becoming embedded in basal skeleton first by one end provided with rounded knobs. Living tissue forming a thin veneer, filling space between superficial processes of basal skeleton. Oscules 300 µm in diameter, opening out along edge of sponge. Eurypylous choanocyte chambers 18–20 µm in diameter. Intercellular symbiotic bacteria scarce. Occasionally associated with zoanthids that induce formation of processes in calcareous skeleton. In specimens from Jamaica, masses of storage cells packed with various inclusions and resembling gemmular thesocytes occur at base of living tissue, between processes of aragonite skeleton. Alternatively, spermatic cysts containing primary spermatocytes can occur in same region of mesohyl. Depth range: 8–70 m in caves and deep fore reef. *Holocene:* Bahamas, Belize, Jamaica.——FIG. 159*a–i*. **G. auriculata,* RBINSc-POR.097; *a,* seen *in situ* at depth of 25 m in reef cave on northern coast of Jamaica, scale bar, 1 cm (see also

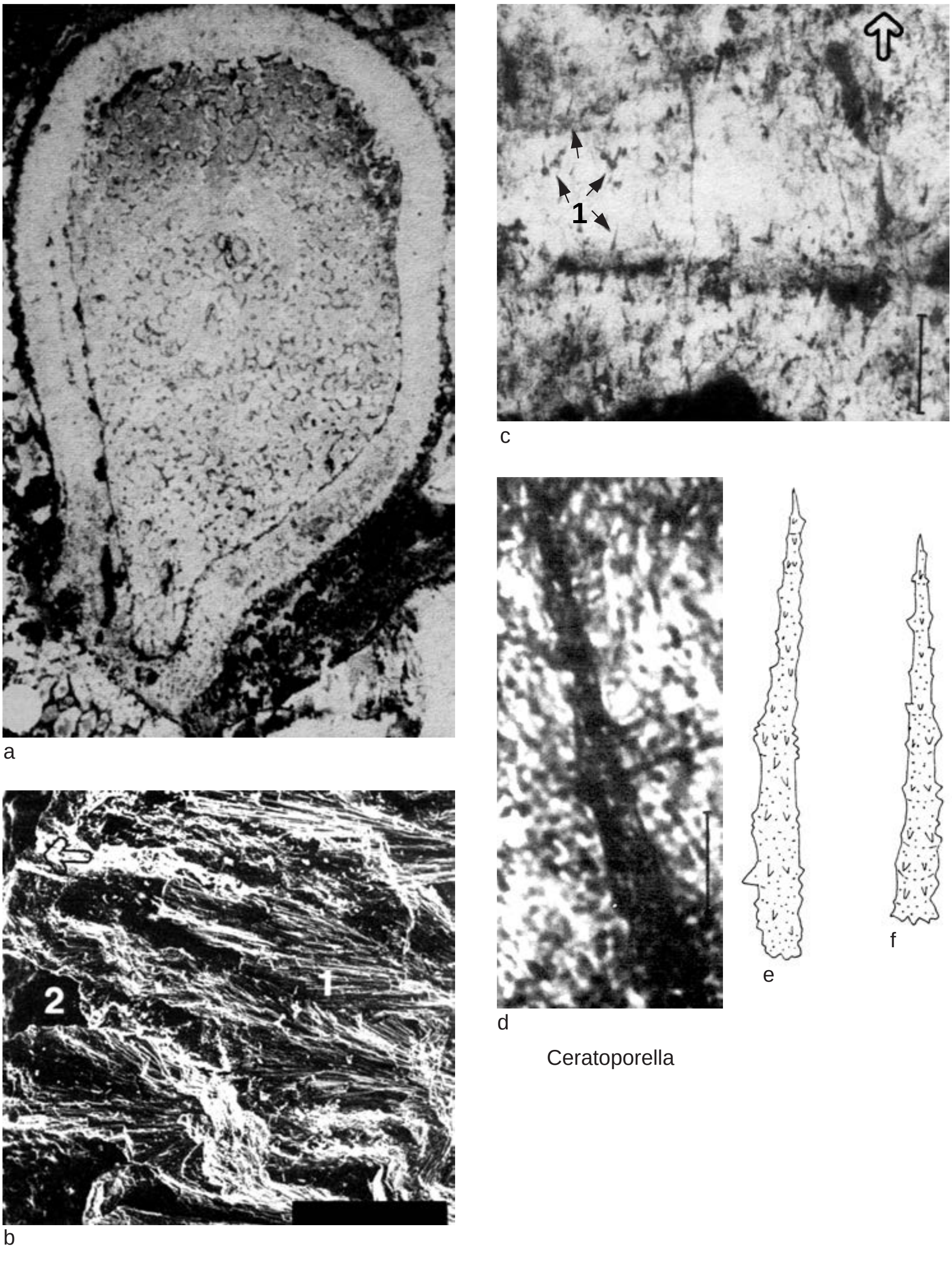


FIG. 158. Astroscleridae (p. 243–246).

Fig. 1.5); *b,* ground section perpendicular to sponge surface, through aragonite skeleton and living tissue (*ar,* aragonitic skeleton; *c,* choanosome; *dm,* dermal membrane; *s,* spicules), scale, 100 µm; *c,* SEM view of skeleton with arborescent processes, scale bar, 1 mm; *d,* SEM view of arborescent aragonitic processes with protruding spicules (*s*), scale bar, 100 µm; *e–i,* strongyles of three different shapes (*e–g,* scale bar, 20 µm), and details of partially dissolved siliceous spicules (*h–i,* scale bars, 5 µm, 2 µm), as seen within basal calcareous skeleton (West & others, 2013).

Hispidopetra HARTMAN, 1969, p. 12 [**H. miniana;* OD; holotype YPM no. 6853]. Encrusting to

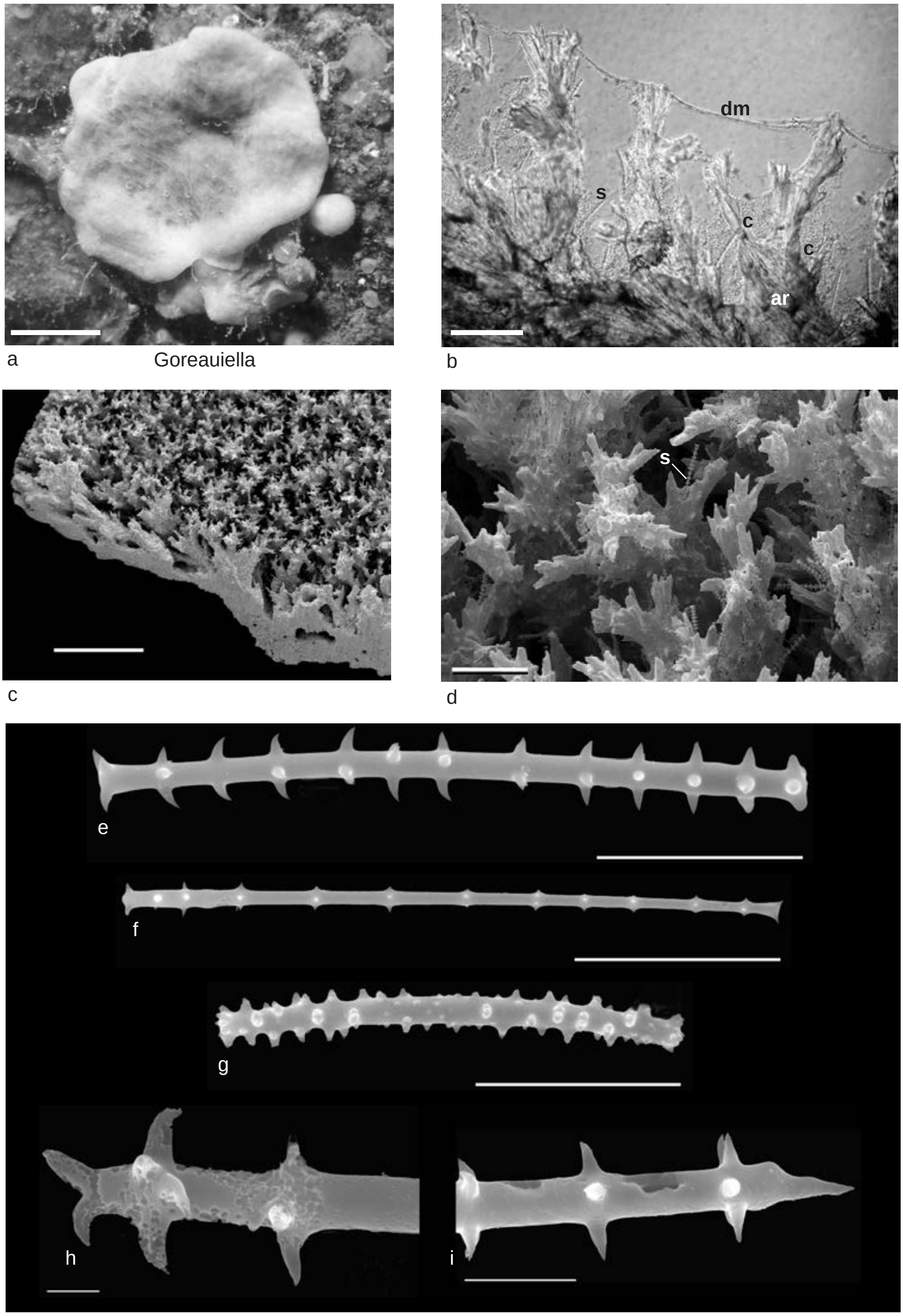


FIG. 159. Astroscleridae (p. 246–247).

massive Astroscleridae with smooth styles and basal skeleton bearing long superficial processes. Type species encrusting to dome shaped or massive. Basal skeleton made up of aragonitic sclerodermites, devoid of astrorhizae, with surface covered with superficial, arborescent, spinose processes up to 7 mm high. Microstructure consisting of sclerodermites with crystals radiating in all directions from centers of calcification (clinogonal type with divergent, irregular, linear elements). Color carmine to vermilion in life. Size reaching 15 cm in diameter and 3 cm in height. Spicules smooth, slightly curved styles, varying greatly in length, range of means 269–301 µm by 5.4–7.4 µm, with an overall range 125–818 µm by 1.3–10.4 µm, partially (by the head) or totally entrapped in basal skeleton. Some spicules show evidence of erosion after entrapment in aragonite. Eurypylous choanocyte chambers, 6–18 µm in diameter. Frequently overgrown by serpulid worms. Depth range: 10–95 m in caves and deep fore reef. [Reitner (1992) reported a fossil species, *H. triassica.*] *Upper Triassic–Holocene:* Italy, *Upper Triassic*; Bahamas, Belize, Jamaica, *Holocene*.——Fig. 160*a–l*. **H. miniana*, RBINSc-POR.098; *a,* seen *in situ* at depth of 25 m in reef cave on northern coast of Jamaica, scale bar, 2 cm (see also Fig. 1.6); *b,* surface of calcareous skeleton showing arborescent knoblike processes, scale, 2 mm; *c,* detail of arborescent process with aragonite crystals projected in all directions and protruding siliceous stylote spicules, scale bar, 200 µm; *d,* detail of siliceous spicule sticking out of aragonite skeleton, scale bar, 50 µm; *e–l,* curved styles (*e–i,* scale bar, 100 µm), varying greatly in length; detail of tips of styles with typically irregular shape (*j–k;* scale bar, 5 µm); and detail of an eroded spicule (*l*) as found entrapped in aragonite, scale bar, 5 µm (West & others, 2013).——Fig. 161*a–e*. *H. triassica* Reitner, 1992, holotype, Carnian, Dolomites, northern Italy; *a,* basal skeleton nearly completely filled by synepitaxial cement, younger part showing partially open tubules (*1*), IPFUB/JR 1989, ×6.5; *b,* long monaxon tylostyles in basal skeleton, ×80; *c,* bundles of monocrystalline ferroan calcite spicule pseudomorphs, IPFUB/JR 1989, ×177; *d,* tangential section of slightly curved ferroan calcite spicule pseudomorph, IPFUB/JR 1989, ×142; *e,* monaxon tylostyle, ×217 (Reitner, 1992, pl. 31–32).

?Spherolichaetetes Gautret & Razgallah, 1987, p. 67 [**S. spheroides;* OD; holotype CP196U3-23, paratype CP196U3-25, repository of both types unknown]. Growth form laminar to low domical; tubules irregular polygons in transverse section; in longitudinal section, tubules long, continuous, with tabulae; increase by intertubular budding or longitudinal fission; tubule walls aragonite spherules; megascleres and microscleres unknown. [This genus is placed questionably in the family Astroscleridae because, although it has typical spherulitic microstructure, spicules are unknown, and the skeletal construction appears to be somewhat different.] *upper Permian (lower part)–upper Permian (upper part):* Tunisia (Jebel Tébaga), *upper Permian (lower part)*; China, Greece, *upper Permian (upper part).*——Fig. 162*a–c*. **S. spheroides*, Tunisia; *a,* external morphology of basal skeleton of paratype, CP196U3-25, ×1.9; *b,* internal morphology of basal skeleton of specimen in view *a*, ×1.9; *c,* enlarged view of exterior of specimen in view *a* showing new tubule (*white X*) produced by intertubular budding, ×102 (Gautret & Razgallah, 1987, pl. 1, 4).——Fig. 163*a–c*. **S. spheroides*, Tunisia; *a,* internal morphology of basal skeleton of holotype, CP196U3-23, showing continuous tubule walls and tabulae, ×1.3; *b,* spherulitic microstructure, symmetrical spherulite at end of tubule wall, ×800; *c,* asymmetrical spherulite near basal part of tubule, ×800 (Gautret & Razgallah, 1987, pl. 1, 4).

Stromatospongia Hartman, 1969, p. 2 [**S. vermicola* Hartman, 1969, p. 3; OD; holotype YPM no. 6376]. Encrusting to massive Astroscleridae with verticillately spined styles, and basal skeleton associated with calcareous tubes of serpulid worms. Type species encrusting to massive, with an aragonitic basal skeleton always growing in association with tangled masses of serpulid worms. Surface of basal skeleton ornamented with processes 0.8 to 2 mm high. Living tissue forming a thin veneer in spaces between processes of basal skeleton. Color apricot to light salmon pink in life. Size up to 40 cm in diameter and 10 cm in height. Basal skeleton superficially marked by numerous upright, multibranched processes, 1.5–2 mm high, with the living tissue extending down into irregular spaces left between processes. Sclerodermites with aragonite crystals radiating in all directions from centers of calcification usually located around spicule heads (clinogonal type with water-jet elements). Siliceous verticillately spined styles (acanthostyles), 75–519 µm by 3.3–13 µm, with a mean of 165–187 µm by 6.2–8 µm, with whorls of spines on shaft, more or less completely overgrown by aragonite. Eurypylous choanocyte chambers, 16–20 µm in diameter. Association with serpulids appears obligatory. Depth range: 10–95 m under overhangs of deep fore reefs. Other Recent species include *S. norae* Hartman, 1969, and *S. micronesica* Hartman & Goreau, 1976. *S. norae* occurs in the Caribbean, with or without association with serpulids. Basal mass of aragonite only reaches 4 cm in height. Surface processes of calcareous skeleton are lamellate in form, shorter and more closely spaced than in *S. vermicola*. Acanthostyles are similar in shape to those of *S. vermicola* but longer and thinner, 75–519 µm by 2.7–9.1 µm, with mean values of 195–215 µm by 5.5–6.1 µm. Spicules embedded in aragonite as the calcareous skeleton grows upward, and some of them become partially eroded. Color varies from cream to ecru beige.

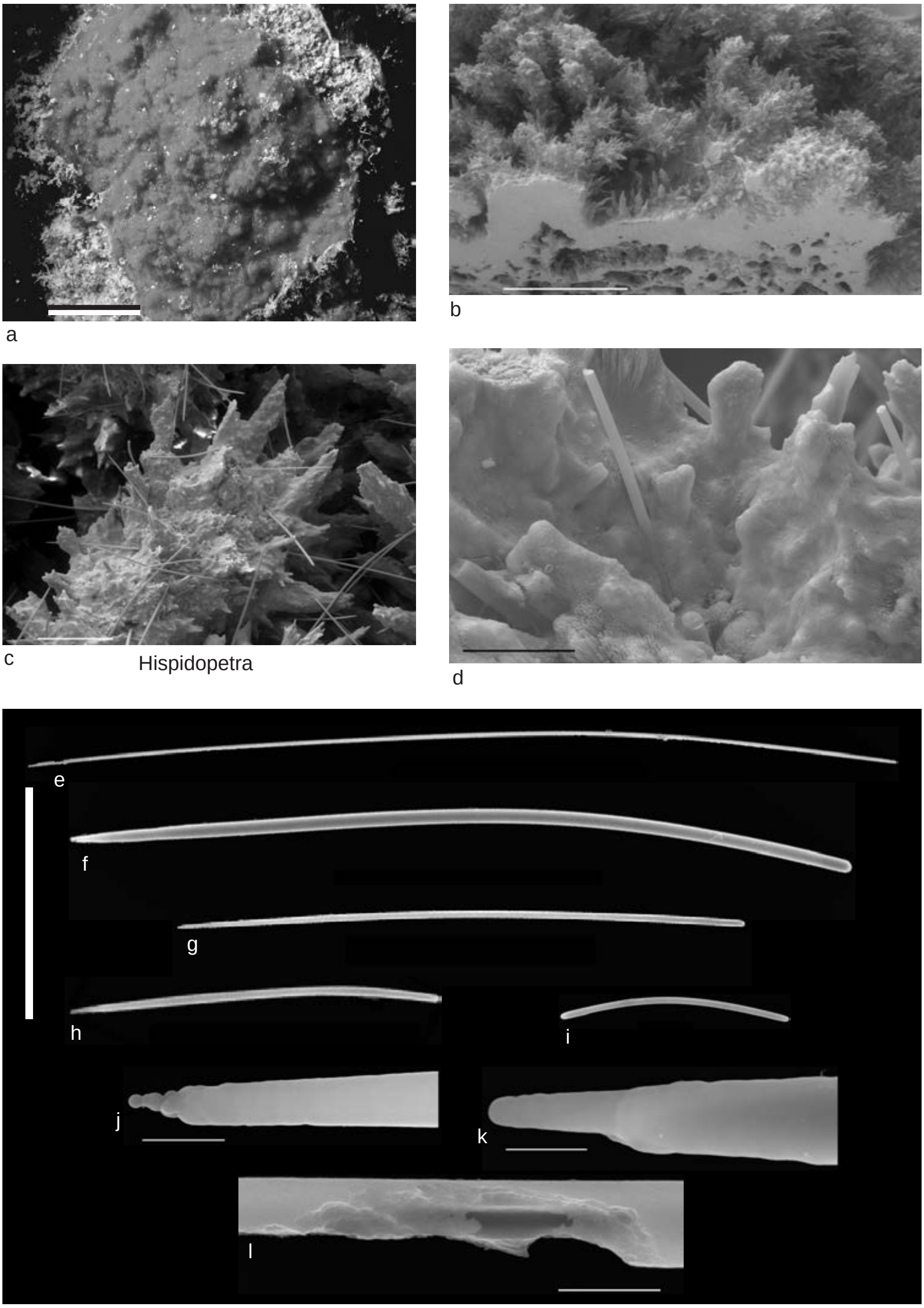


FIG. 160. Astroscleridae (p. 247–249).

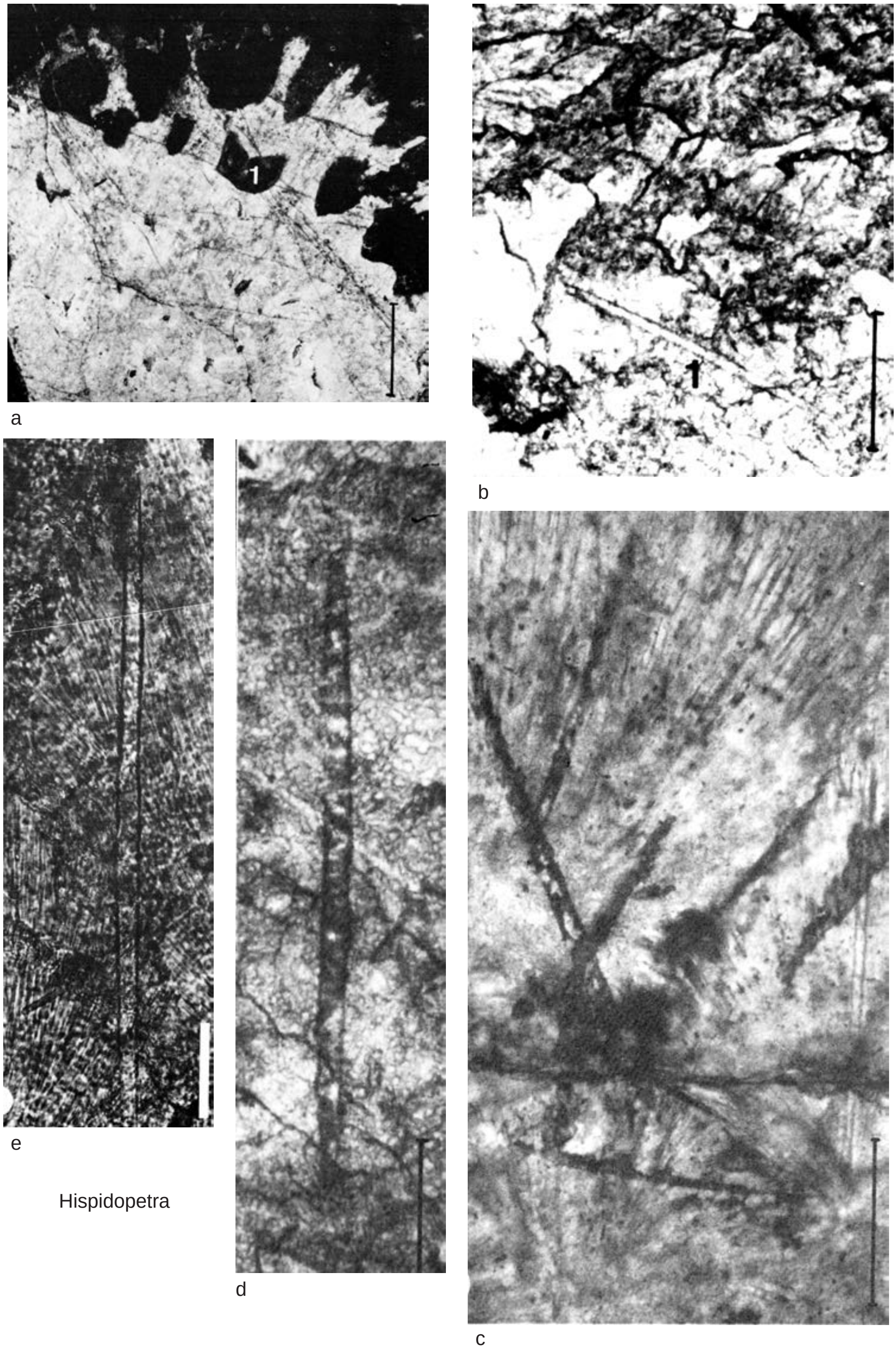


FIG. 161. Astroscleridae (p. 247–249).

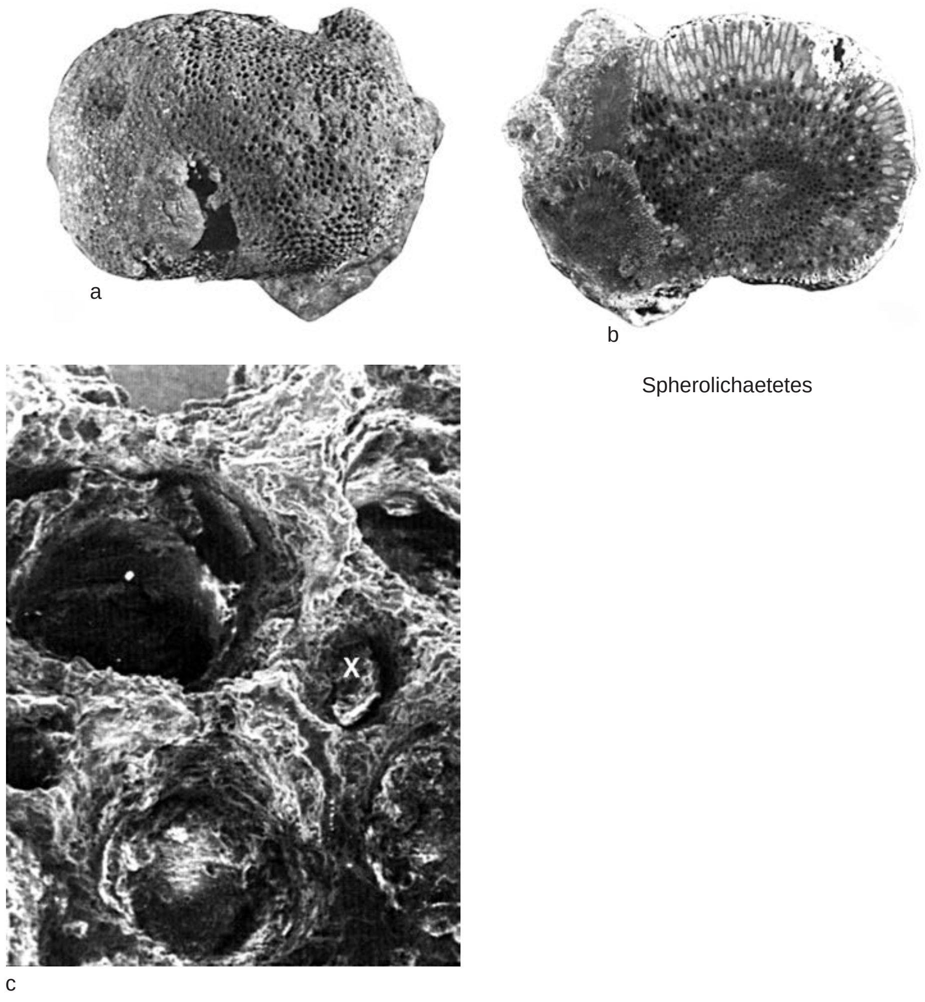


FIG. 162. Astroscleridae (p. 249).

Intercellular symbiotic bacteria abundant and highly diverse in shape; *S. micronesica* HARTMAN & GOREAU, 1976, occurs in the Pacific with a more variable form of surface processes of aragonite skeleton and smaller acanthostyles. Color varies from cream through yellowish cream to yellow-tan to ochre. [The genus is possibly synonymous with *Ceratoporella* (HARTMAN & GOREAU, 1972; WILLENZ & HARTMAN, 1989). Its superficial skeleton, however, is devoid of the regular tubules highly characteristic of *Ceratoporella.* Illustrations of the type species are poor, and S. *norae* better illustrates the characters of the genus.] *Holocene*: Bahamas, Jamaica, Pacific Ocean.——FIG. 164*a–j*. *S. norae,* RBINSc-POR.096; *a,* seen *in situ*, at a depth of 25 m in a reef cave on northern coast of Jamaica, scale bar, 2 cm (see also Fig. 2.2); *b,* SEM view of skeleton with surface processes, scale bar, 1 mm (West & others, 2013); *c,* three-dimensional representation of living tissue and aragonite skeleton; *Ar,* aragonite skeleton; *C,* choanosome; *DM,* dermal membrane; *EC,* exhalant canal; *IS,* inhalant space or vestibule; *O,* osculum; *S,* spicule (Willenz & Hartman, 1989); *d–j,* acanthostyles of three different shapes (*d–f,* scale bar, 50 µm); details of extremities of spicules (*g–h,* scale bars, 10 µm), eroded spicule with detail (*i–j,* scale bars, 20 µm, 5 µm respectively (West & others, 2013).

Family MILLEPORELLIDAE Yabe & Sugiyama, 1935

Rachel A. Wood

[Milleporellidae Yabe & Sugiyama, 1935, p. 152, 158] [=Millestrominidae Gregory, 1898, p. 339; =Milleporididae Yabe & Sugiyama, 1935, p. 158; =Milleporelloidae Alloiteau, 1952, p. 392; =Millestromidae Hudson, 1953, p. 885; =Parastromatoporidae Hudson, 1959, p. 312]

Calcified agelasids with spicule framework of club-shaped styles in a plumose arrangement in vertical elements only. Microscleres absent. Primary calcareous skeleton dominated by radial elements of orthogonal or fascicular fibrous microstructure initiated at bases of spicules. Massive encrusting or dendroid gross morphology. Secondary calcareous skeleton, where present, growing epitaxially on primary. Traces of aquiferous system as astrorhizae and/or oscula. [The name family Millestrominidae Gregory, 1898, never won general acceptance by later workers; indeed it has been largely ignored and probably should remain so, in accordance with Article 40.2, ICZN (1999, p. 46). The later-introduced family group name Milleporellidae Yabe & Sugiyama, 1935, has, on the other hand, been adopted by most later workers either in the original, more restricted, or in a broader conception, of the family. Wood (1987 p. 50) recommended this latter approach, merging members of both of Yabe and Sugiyama's (1935) families, the Milleporellidae and Milleporididae. These were formerly distinguished (see Hudson, 1959) on differences in arrangements between their aquiferous systems, but Wood (1987, p. 50) considered these differences to have no significance at the taxonomic level. Consequently, given the exclusion of Gregory's (1898) family name for the reasons stated above, Wood (1987) concluded that the name Milleporellidae should take priority as the senior family group name; Lecompte, 1952a, p. 25; Lecompte, 1956, p. 138; Galloway, 1957, p. 457. The inclusion of family Parastromatoporidae Hudson, 1959, was proposed by Wood (1987) due to finding of identical club-shaped styles in a plumose arrangement, and on the basis that astrosystems alone were insufficient diagnostic characteristics.] *Upper Triassic–Eocene.*

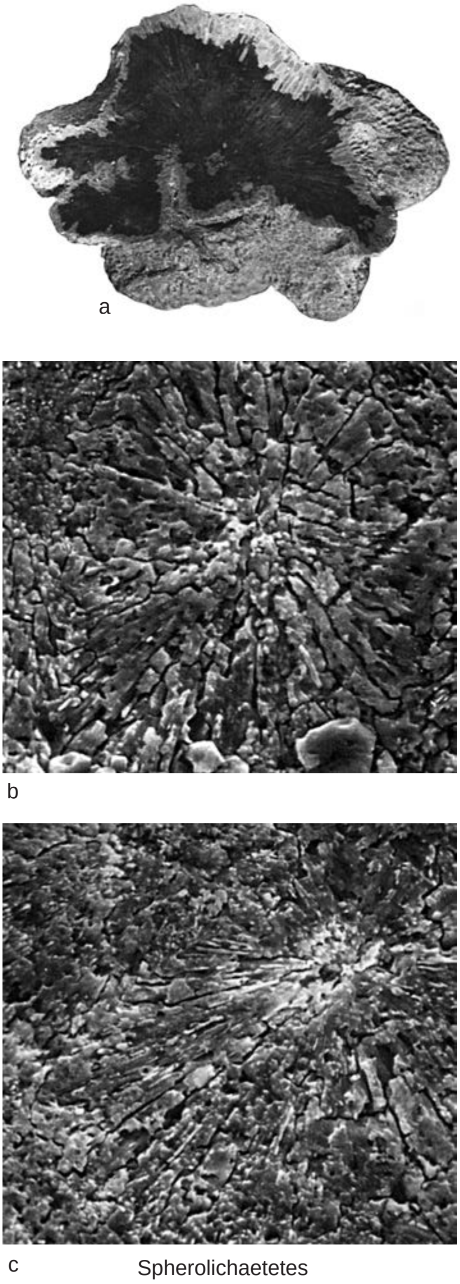


Fig. 163. Astroscleridae (p. 249).

?Milleporella Deninger, 1906, p. 67 [**M. sardoa*; OD; =*M. ichnusae* Deninger, 1906, p. 62] [=*Istriactis*

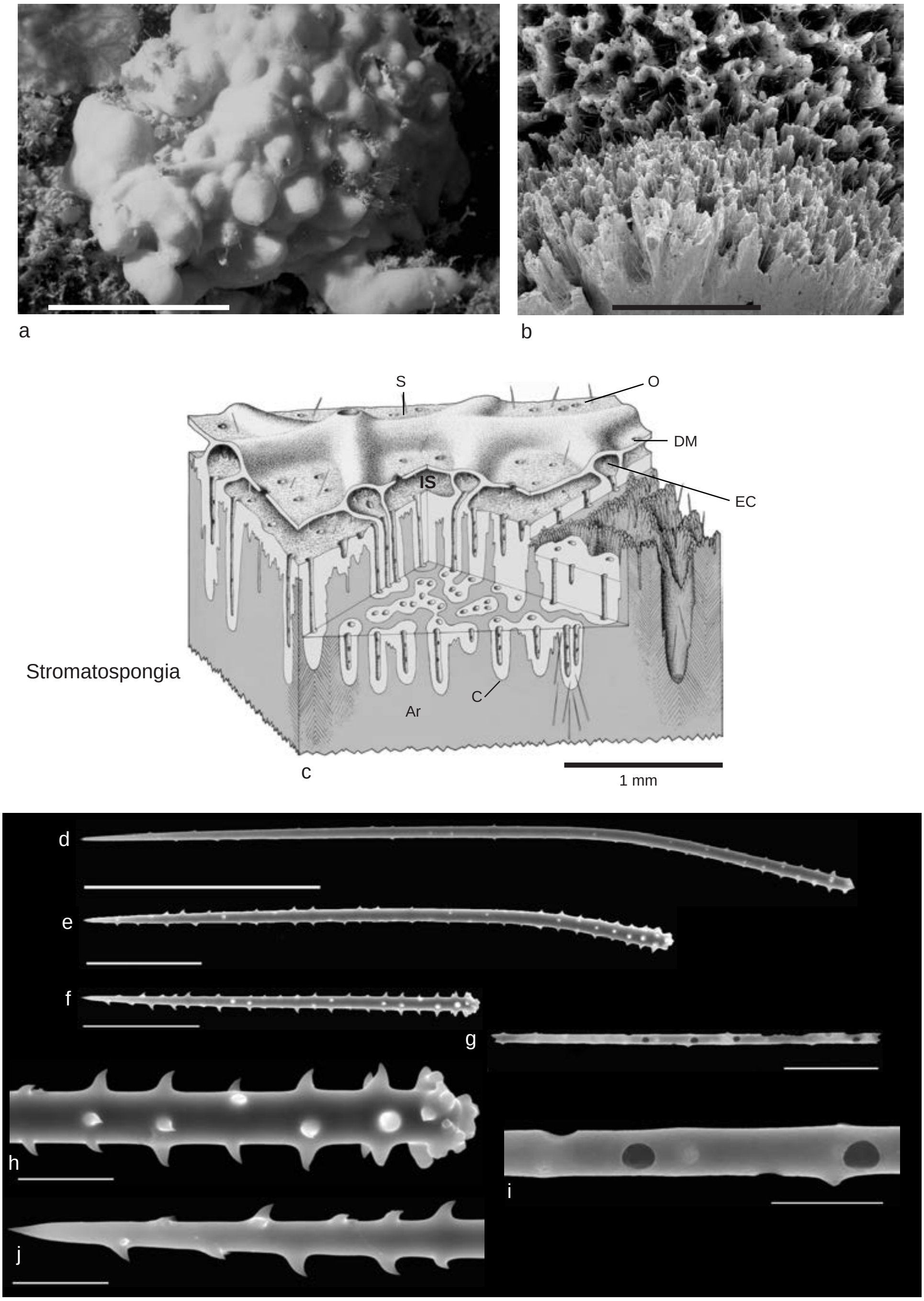


FIG. 164. Astroscleridae (p. 249–252).

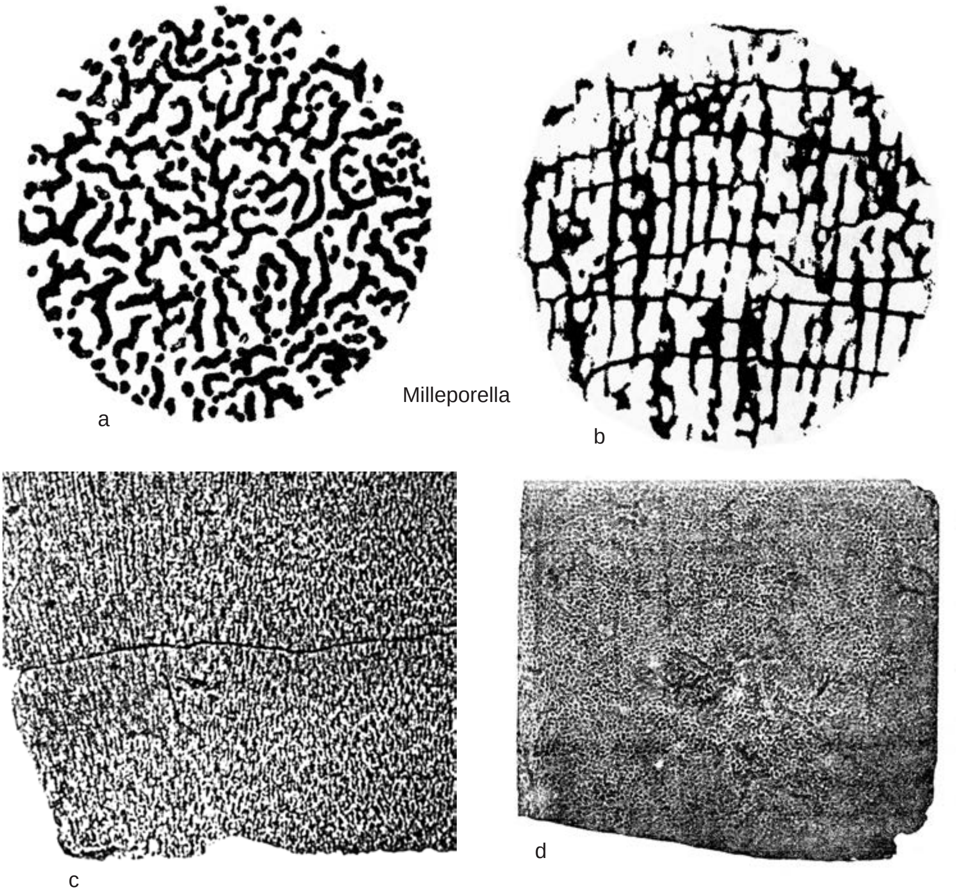


FIG. 165. Milleporellidae (p. 253–255).

Munier-Chalmas, MS in coll. of Dehorne, 1920, p. 99, *nom. nud.* (type, *M. adriatica* Dehorne, 1920, p. 99, OD; =*Milleporella marticensis* Dehorne, 1920, p. 100)]. No spicules noted to date. Presumed calcified agelasids with primary calcareous skeleton dominated by radial elements of fascicular fibrous microstructure. Massive encrusting or dendroid gross morphology. Secondary calcareous skeleton growing epitaxially on primary. Traces of aquiferous system as astrorhizae and/or oscula. [Deninger (1906) described *Milleporella* and *M. sardoa* as a new genus and new species, but only illustrated *M. ichnusae* n. g. n. sp. Likewise, Dehorne (1920) did not illustrate *Istriactis sardoa* but illustrated *I. marticensis*. It is therefore assumed that *M. sardoa* is an invalid name and is replaced herein by *Milleporella ichnusae. M. ichnusae* Deninger, 1906, and *M. marticensis* Dehorne, 1920, are illustrated herein; type specimens thought to be lost. The genus name is listed as questionable because so far no spicules have been found.] *Jurassic–Eocene*: Europe.——Fig. 165*a–b*. **M. ichnusae*, Upper Cretaceous, Sardinia; *a*, transverse section; *b*, longitudinal section, magnifications unknown, specimens thought to be lost (Deninger, 1906, pl. VII,*8a–b*).——Fig. 165*c–d. M. marticensis* Dehorne, 1920, upper Cretaceous, Hippurites beds of Martigues, Bouches-du-Rhône, France; *c*, transverse section, ×3; *d*, tangential section of same specimen as view *c,* showing stellar channels, similar to astrorhizae, ×2.7 (Dehorne, 1920, pl. XVI,*1–2*).

Dehornella Lecompte, 1952a, p. 16 [**Stromatoporella hydractinoides* Dehorne, 1920, p. 77; OD; holotype, Geological Laboratory, Sorbonne, pl. 6,*2,* and thin sections a–c] [=*Astroporina* Hudson, 1960, p. 196 (type, *A. stellifera* Hudson, 1960, p. 197, OD, holotype, NHM, pl. 27,*1–2*)]. Densely packed, plumose arrangement of club-shaped style spicules 110–135 µm long, 13.5–17 µm wide; continuous

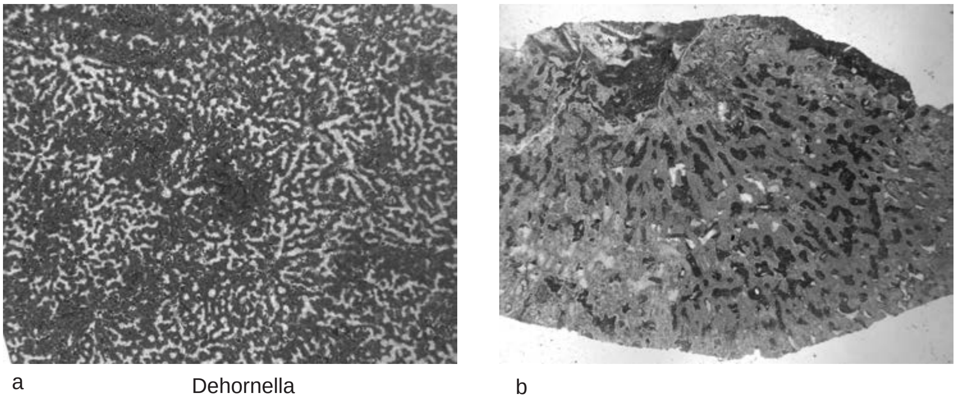


FIG. 166. Milleporellidae (p. 255–256).

fascicular fibrous vertical elements 100–300 µm wide; subordinate pillar-lamellae; often with marked astrorhizae, latilaminae, and tabulae; type material has been lost. Two other included species: *D. harrarensis* (WELLS, 1943, p. 50) exhibits an open reticulum, vertical elements generally 250–300 µm wide, few tabulae, and styles that do not project, Oxfordian, Kurtcha, Harrar Province, Ethiopia, with wider distribution in upper Oxfordian–lower Aptian, Austria, France, Israel, Sinai, Ethiopia, Oman); *D. crustans* (HUDSON, 1960, p. 191), exhibits densely packed plumose styles that project, and vertical elements with anastomizing columns, abundant astrorhizae, and aligned tabulae; lower Kimmeridgian, Makhtesh Hagadol, Israel, with wider distribution in Kimmeridgian, Israel, Dakkar, Somalia. *Upper Jurassic–Lower Cretaceous:* Portugal, Austria, France, Israel, Sinai, Lebanon, Egypt, Ethiopia, Somalia, Oman.——FIG. 166*a–b. D. harrarensis* (WELLS), light photomicrographs, lower Kimmeridgian, Wadi Bik, Ruus al Jebel, Oman; *a,* transverse section, NHM no. 4844c, ×4 (West & others, 2013); *b,* longitudinal section, NHM no. 4868a, ×6 (West & others, 2013).——FIG. 167,*1a–c. D. crustans* HUDSON, light photomicrographs, NHM no. 5170c, lower Kimmeridgian, Makhtesh Hagadol, Israel; *a,* longitudinal section, ×4 (West & others, 2013); *b,* longitudinal section, ×20 (West & others, 2013); *c,* longitudinal section of plumose spicule tract, ×100 (West & others, 2013).

Murania KAŹMIERCZAK, 1974, p. 341 [**M. lafeldi*; OD; holotype, ZPAL.Pf.1/1a–b]. Sheetlike, massive, or fasciculate calcareous skeleton of vertically arranged prismatic columns (pillars) that encase densely packed plumose arrays of club-shaped styles. [One other species, *M. reitneri*, is known from the Kimmeridgian, Austria, and the holotype is illustrated herein; *M. reitneri* only differs from the type species in one respect: having more slender columns, up to 0.32 mm diameter (mean of 0.32 mm), as compared with columns of the type species, which are up to 0.5 mm in diameter (mean of 0.3 mm).] *Upper Triassic–Lower Cretaceous*: Austria, *Kimmeridgian;* Italy, *Upper Triassic;* Slovakia, Germany, Spain, Gulf of Mexico, *Lower Cretaceous*.——FIG. 167,*2a. *M. lafeldi*, Z.Pal.Pf.I/1b, transverse section, ×40 (courtesy of Kaźmierczak, 1974).——FIG. 167,*2b–c. M. reitneri* SCHLAGINTWEIT, light photomicrographs, holotype BSP 2003 X-5, Bayerische Staatssamlung für Paläontologie und historische Geologie, Munich, Kimmeridgian, Krahstein, Austria; *b,* transverse section, ×8; *c,* transverse section, ×35 (West & others, 2013).

Parastromatopora YABE & SUGIYAMA, 1935, p. 183 [**Stromatopora japonica* YABE, 1903, p. 2; OD; holotype, University of Hokkaidu, UHR 00445] [=*Epistromatopora* YABE & SUGIYAMA, 1935, p. 183, obj.]. Milleporellidae with short styles 60 µm in length, 18 µm wide, with fascicular fibrous continuous columns, pillar-lamellae absent or subordinate, and numerous aligned tabulae. One other species, *P. libani* HUDSON, 1954c, p. 659, has columns forming tubules; no pillar-lamellae; canals converge toward central osculum and occurs in the upper Oxfordian–lower Kimmeridgian, Lebanon, Israel, and Yemen. [Type is not illustrated as spicules are not well preserved.] *Upper Jurassic (upper Oxfordian–lower Kimmeridgian):* Japan, Lebanon, Israel, Yemen.——FIG. 168,*1a–b. P. libani* HUDSON, light photomicrographs, NHM no. 4789, lower Kimmeridgian, Toumatt, Lebanon, Israel; *a,* transverse section, ×8; *b,* transverse section, ×8 (West & others, 2013).

Promillepora DEHORNE, 1920, p. 97 [**P. pervinquieri;* M; =*Stromatopora douvillei* DEHORNE, 1920, p. 20, lectotype by LECOMPTE, 1952a, p. 23] [=*Amorphospongia* D'ORBIGNY, 1847, p. 178, *nom. nud.*]. Milleporellidae with short styles, maximum length 50 µm, 12 µm width in a loose plumose arrangement; fascicular fibrous microstructure; abundant, radially extensive tabulate oscula with no astrorhizae. [*Stromatopora douvillei* DEHORNE,

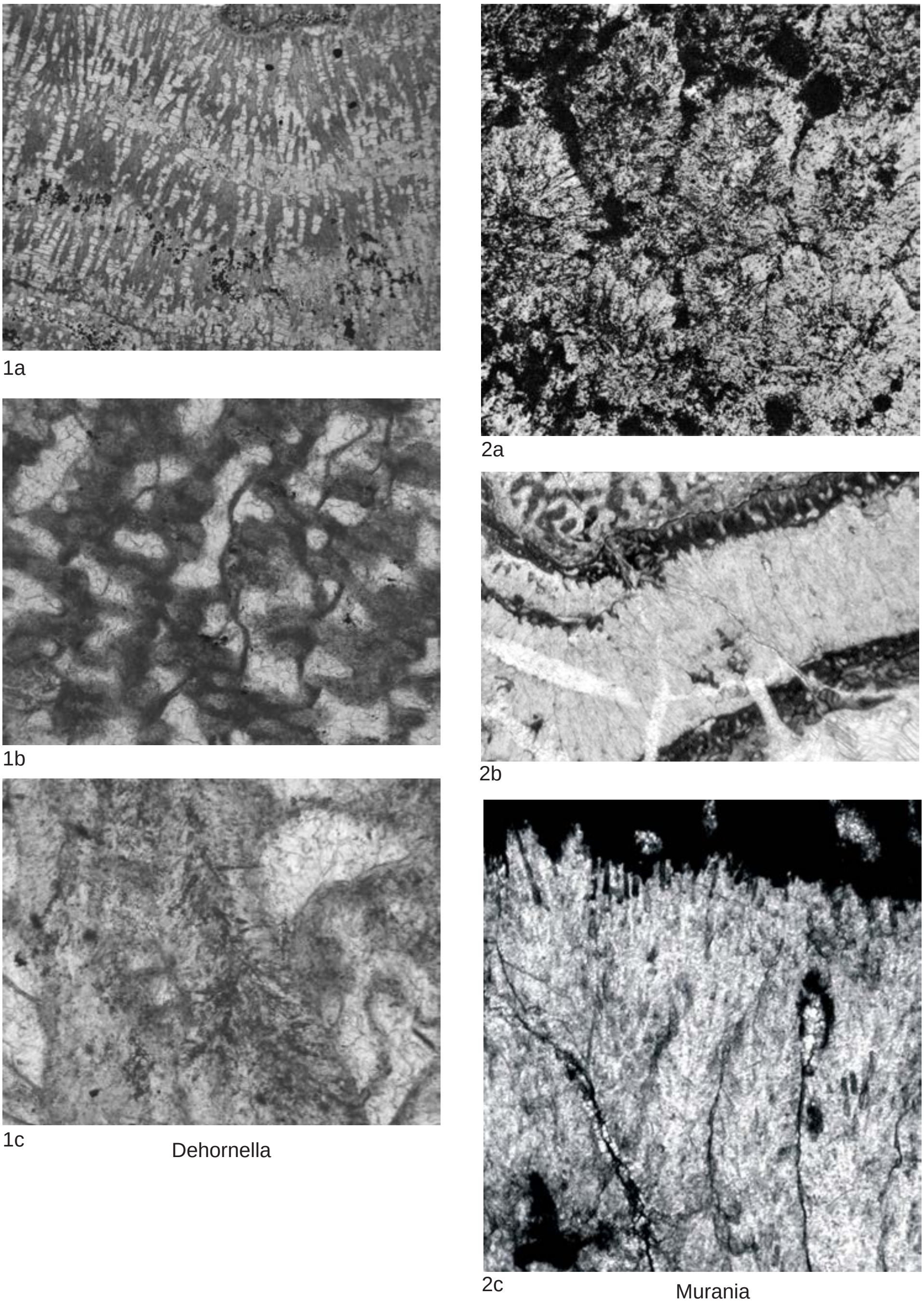
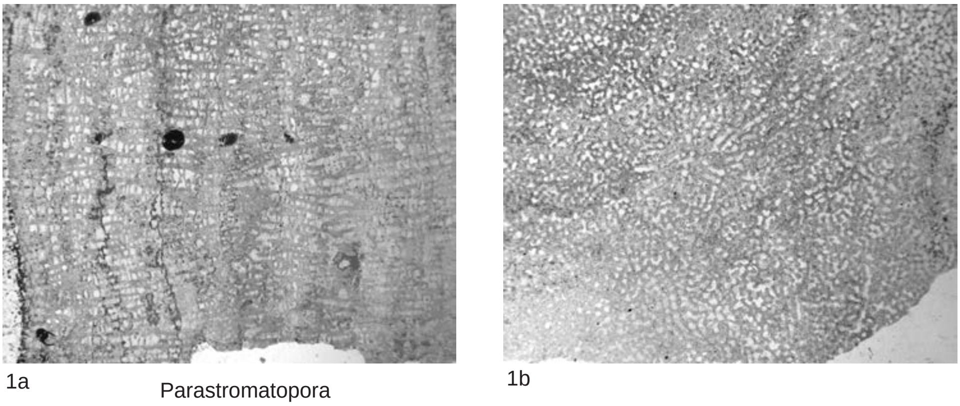
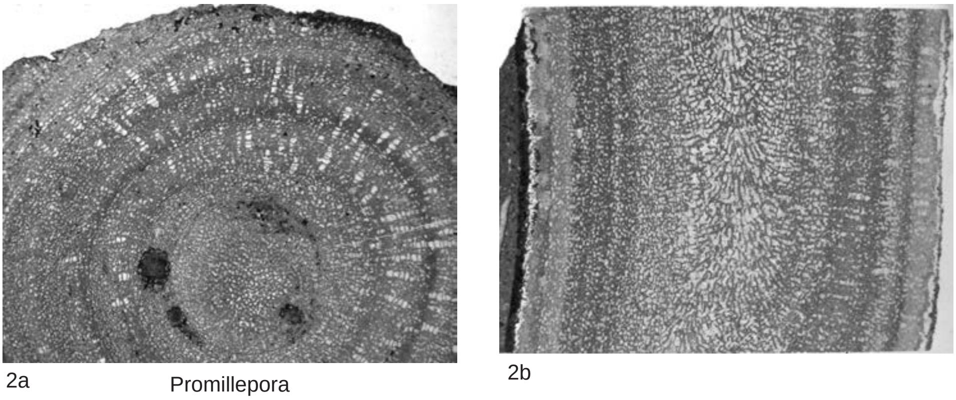


FIG. 167. Milleporellidae (p. 255–256).



Parastromatopora



Promillepora

Fig. 168. Milleporellidae (p. 256–258).

1920, p. 20, has a common straight tabulate oscula, 140–300 µm in diameter.] *Upper Jurassic (upper Oxfordian–lower Kimmeridgian)*: Israel, Tunisia.——Fig. 168,*2a–b.* **P. pervinquieri,* light photomicrograph, lower Kimmeridgian, Makhtesh Hagadol, Israel; *a,* transverse section, NHM no. 4898A, ×7; *b,* transverse section, NHM no. 4901a, ×7 (West & others, 2013).

Shuqraia Hudson, 1954a, p. 218 [**Milleporidium zuffardi* Wells, 1943, p. 51; OD; holotype AMNH 252900–259001]. Styles maximum of 80 µm long, 7 µm wide; regular columns forming tubules; orthogonal to fascicular fibrous skeleton. Type species with fibrous tabulae upon primary skeleton and loosely packed plumose styles; its distribution occurs in Israel, Ethiopia, Somalia, and Yemen; *S. hudsoni* (Wood, 1987, p. 60–62) is another species with commonly stacked astrorhizae, with distribution restricted to Yemen. *Upper Jurassic (upper Oxfordian–lower Kimmeridgian):* Yemen, Israel, Ethiopia, Somalia, Yemen, ?Japan.——Fig. 169,*1a–b.* **S. zuffardi* (Wells), light photomicrograph, lower Kimmeridgian, Shuqra, southern Yemen; *a,* longitudinal section, NHM no. 4485B, ×6; *b,* transverse section, NHM no. 4505, ×15 (West & others, 2013).——Fig. 169,*1c–d. S. hudsoni* (Wood), light photomicrograph, upper Oxfordian, Alam Abayadh, northern Yemen; *c,* tangential section, NHM no. 4570A, ×7; *d,* transverse section, NHM no. 4639a, ×8 (West & others, 2013).

Steinerina Hudson, 1956b, p. 518, *nom. nov. pro Steineria* Hudson, 1956a, p. 722, *non* Micoletzky, 1922, p. 119, nematode [**Stromatopora romanica* Dehorne, 1918, p. 221; OD; holotype, Geological Laboratory Sorbonne Specimen 27, Hudson, 1956] [=*Romanactis* Munier-Chalmas, *nom. nud.,* MS in coll. of Dehorne, 1920, p. 88]. Milleporellidae with short pillars of fascicular fibrous microstructure up to 300 µm in length; abundant tabular astrorhizal canals up to 560 µm in diameter; secondary epitaxial skeleton and common aligned tabulae. [One other species, *S. somaliensis* (=*Milleporidium somaliense* Zuffardi-Comerci, 1931, p. 70), has an open reticulum with pillars up to 230 µm in diameter and occurs in the upper Oxfordian–lower Kimmeridgian of Israel, Oman, and Somalia. Illustrations

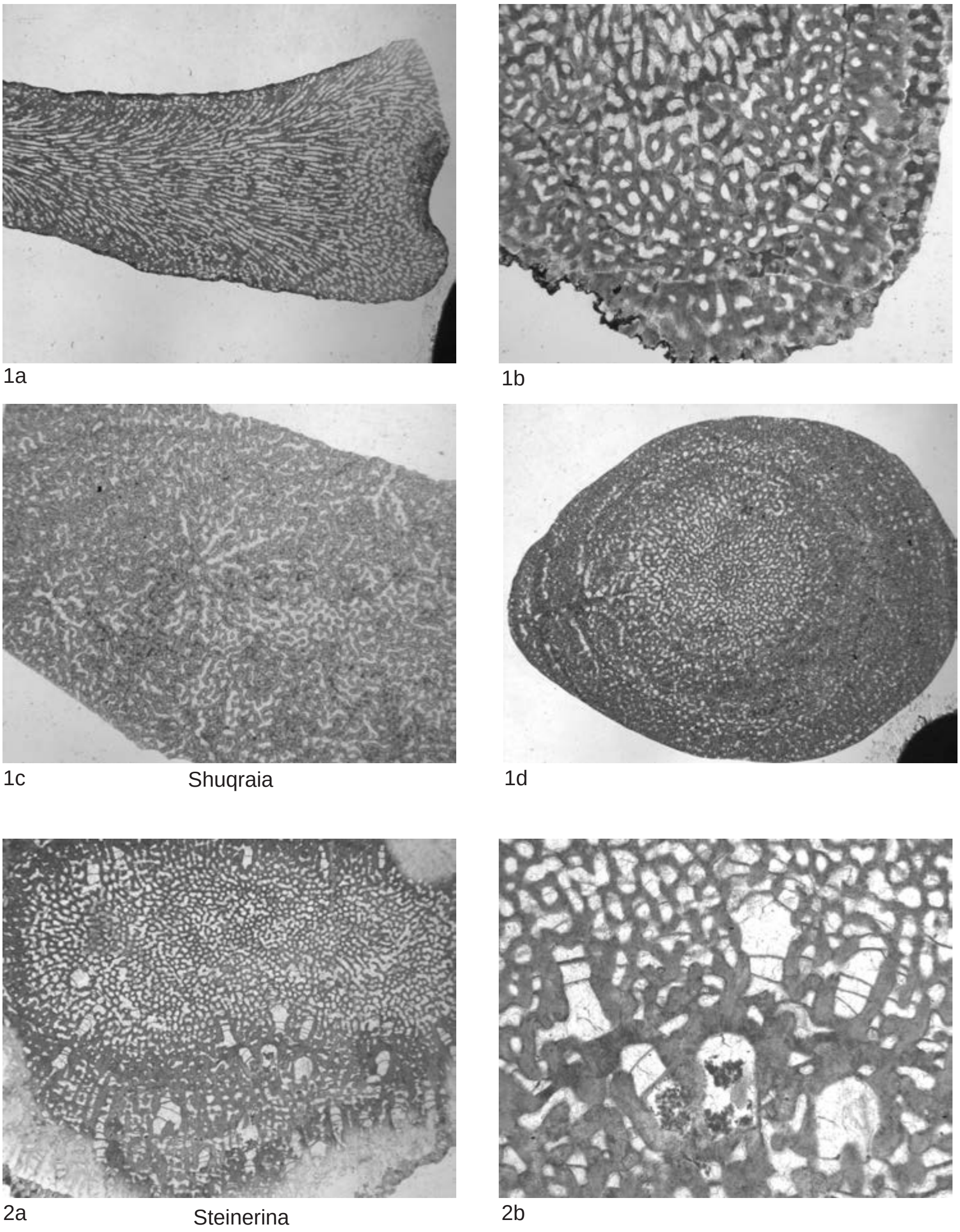


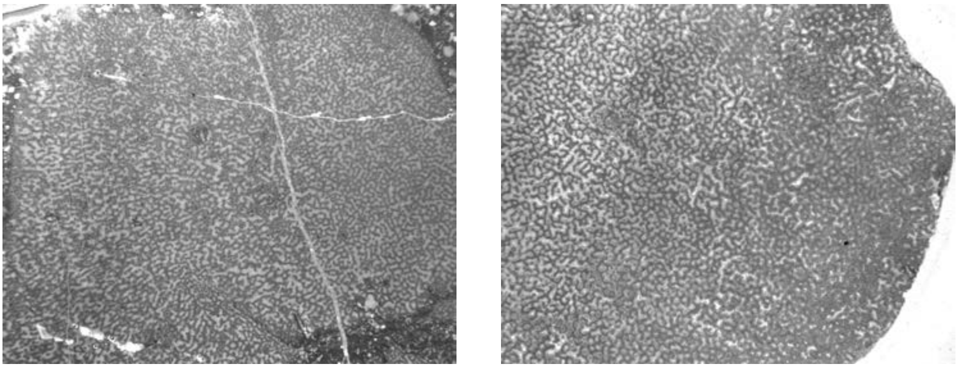
Fig. 169. Milleporellidae (p. 258–259).

of the type species are unavailable as the type material has been lost.] *Upper Jurassic (upper Oxfordian–lower Kimmeridgian):* Romania, Israel, Oman, Somalia.——Fig. 169,*2a–b. S. somaliensis* (Zuffardi-Comerci, 1931), light photomicrograph, NHM no. 4973B, Wadi Bekr, Haushi, Oman; *a,* transverse section, ×7; *b,* transverse section, ×35 (West & others, 2013).

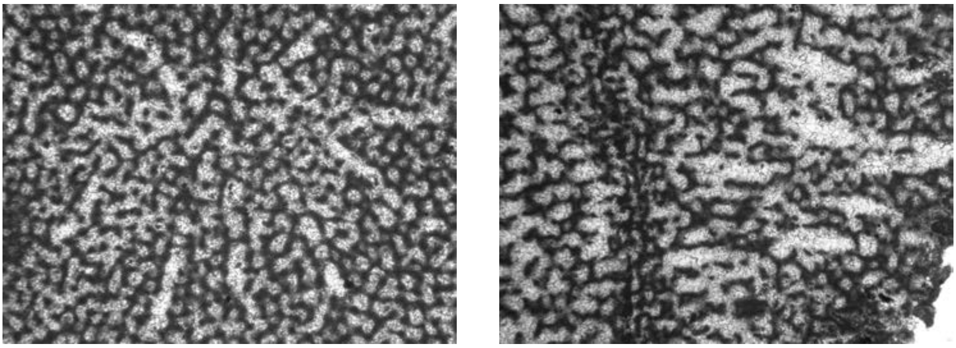
Family ACTINOSTROMARIIDAE Hudson, 1955

[Actinostromariidae Hudson, 1955c, p. 238] [=Stromatorhizidae Hudson, 1957, p. 5]

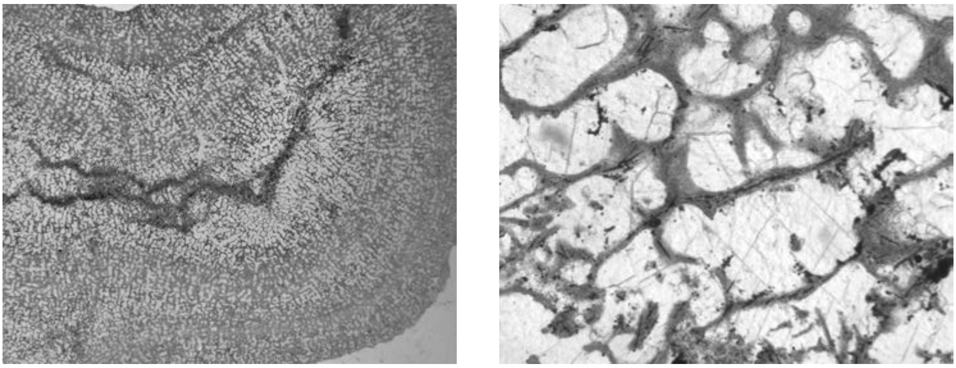
Calcareous skeleton with an open reticulate arrangement of pillars and pillar-lamellae



Actinostromaria



Actostroma



Actinostromarianina

FIG. 170. Actinostromariidae and Actinostromarianinidae (p. 260–261).

composed of a spicule framework of styles and possible triaxines, and an enclosing fibrous orthogonal microstructure; possible triaxines placed at pillar-lamellae junctions (description adapted from WOOD, 1987, p. 70). *Upper Jurassic–Upper Cretaceous.*

Actinostromaria MUNIER-CHALMAS in TORNQUIST, 1901, p. 1116 (HAUG, 1909, pl. 97, no text, *nom. nud.*) [**A. stellata* DEHORNE, 1915, p. 733; SD DEHORNE, 1915, p. 733; according to DEHORNE (1915, p. 733), MUNIER-CHALMAS neither described nor illustrated *A. stellata,* and thus a holotype was not originally designated, and now type material has been lost]. Open reticulate arrangement of pillars and pillar-lamellae with fibrous orthogonal microstructure with a spicule framework of styles and possible triaxines. *Upper Jurassic–Upper Cretaceous*: France, Slovakia, Japan.——Fig. 170,*1a–b. A.* sp., light photomicrograph, upper Oxfordian, Trnovski Gost, Slovenia; *a,* longitudinal section, NHM no. H 5491, ×8; *b,* transverse section, NHM no. H 5492, ×8 (West & others, 2013).

Actostroma Hudson, 1958, p. 91 [**A. damesini* Hudson, 1958, p. 92; OD; holotype, NHM 4890; =*Actostroma nasri* Hudson, 1958, p. 95; =*Actostroma kuhni* Hudson, 1958, p. 96]. Primary calcareous skeleton encloses spicule framework of intramural styles and possible triaxines; skeletal elements orthogonal to fascicular fibrous. Abundant astrorhizal canals and oscula, sometimes tabulate styles and possible triaxines; skeletal elements dominantly pillars and pillar-lamellae, forming partially open to closed tubule-like mesh; tabulae only seen in astrorhizal canals; latilaminae and mamelons commonly present; nodular, encrusting, or dendroid external morphology. *Upper Jurassic (lower Kimmeridgian)*: Israel, ?China.——Fig. 170,*2a–b.* **A. damesini*, light photomicrograph, Israel; *a,* transverse section, NHM no. 4891a, ×15; *b,* longitudinal section, NHM no. 4892a, ×15 (West & others, 2013).

Family ACTINOSTROMARIANINIDAE Wood, 1987

[Actinostromarianinidae Wood, 1987, p. 74]

Calcareous skeleton with long thin styles or tylostyles in a radial arrangement and an irregular or orthogonal fibrous microstructure. *Upper Jurassic (upper Oxfordian–upper Kimmeridgian).*

Actinostromarianina Lecompte, 1952a, p. 9 [**Stromatopora milleporoides var. romanica* Dehorne, 1920, p. 87; OD; there is no indication of a designated holotype in Dehorne (1920, p. 86–88); apparently the type material is lost]. Thin styles or tylostyles (180 µm length by 8 µm width) arranged in loose, radial manner, with densely packed central axis; primary calcareous skeleton of irregular or fascicular fibrous microstructure; secondary calcareous skeleton may or may not be present; granular, aligned tabulae; nodular or dendroid morphology; astrorhizae weakly developed or indistinguishable. *A. lecompti* Hudson, 1955c, p. 230 (Milan, 1969, p. 179) has a secondary calcareous skeleton in form of orthogonal rim, sometimes forming latilaminae. Primary calcareous skeleton of irregular microstructure. Another species, *A. praesalevensis* (Zuffardi-Comerci, 1931, p. 49) (Yabe & Sugiyama, 1935; Hudson, 1955c, p. 230) has a nodular morphology and primary calcareous skeleton of fascicular fibrous microstructure forming pillars 70–250 µm and pillar-lamellae (50–70 µm diameter). Aligned tabulae between 15–30 µm thick. No discernible astrorhizal systems in form of orthogonal rim, sometimes forming latilaminae. *Upper Jurassic (upper Oxfordian–upper Kimmeridgian):* France, Romania, Ethiopia, Yemen, Iraq.——Fig. 170,*3a–b. A. lecompti* Hudson, light photomicrograph, NHM no. 4608a, upper Kimmeridgian, Alam Abayadh, northern Yemen; *a,* transverse section, ×5; *b,* transverse section, ×30 (West & others, 2013).

Family UNCERTAIN

Ronald R. West and Rachel A. Wood

Blastoporella Cuif & Ezzoubair, 1991, p. 264 [**Blastochaetetes karachensis* Cuif & Fischer, 1974, p. 11; OD; *Blastoporella karachensis* Cuif & Fischer, 1974, p. 11–12 is designated as the "standard species" (currently in J.-P. Cuif collections of the Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris; it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN) for *Blastoporella,* in Cuif and Ezzoubair, 1991, p. 264, but neither a holotype nor paratypes were designated. The earlier (original) description of *Blastochaetetes karachensis* (Cuif & Fischer, 1974, p. 11–12, pl. III,*2–3*), however, did refer to these unnumbered images as the holotype, and illustrated (pl. III, *4–5*) two other unnumbered specimens as well (see Fig. 172*c*)]. Growth form domical, fungiform to conical with astrorhizae; tubules irregularly shaped (alveolar) in transverse section with connecting pores; irregular tubule shape due to connecting pores clearly visible in longitudinal section; tubules increase by longitudinal fission, rarely by intertubular budding; penicillate, water-jet (fascicular fibrous) aragonitic microstructure; megacleres and microscleres unknown (description modified from Cuif & Fischer, 1974; Cuif & Ezzoubair, 1991). *Triassic (Carnian–Norian):* northern Italy (Dolomites), *Carnian;* Turkey (Alakir Çay), *Norian.*——Fig. 171*a–d.* **B. karachensis* (Cuif & Fischer), Carnian, Triassic, northern Italy; *a,* topotype, upper exterior surface of fungiform basal skeleton with astrorhizae, ×1.5; *b,* topotype, longitudinal section of astrorhizae, ×10; *c,* topotype, transverse section of astrorhizae, ×14 (Cuif & others, 1973, pl. 1); *d,* holotype, transverse section showing connections (pores) between tubules, ×17 (Cuif & Fischer, 1974, pl. III,*5*).——Fig. 172*a–e.* **B. karachensis* (Cuif & Fischer), Carnian, Triassic, northern Italy; *a,* topotype, transverse section of tubules showing connection (pore) between two tubules (*black X*) in lower left, ×28 (Cuif & Ezzoubair, 1991, pl. 2); *b,* holotype, longitudinal section showing connections between tubules, ×15 (Cuif & Fischer, 1974, pl. III,*3*); *c,* longitudinal section of another specimen showing connections between tubules, ×22.5 (Cuif & Fischer, 1974, pl. III,*5*); *d,* topotype, longitudinal section of tubules showing connection (pore) between tubules (*white X*), ×52; *e,* topotype,

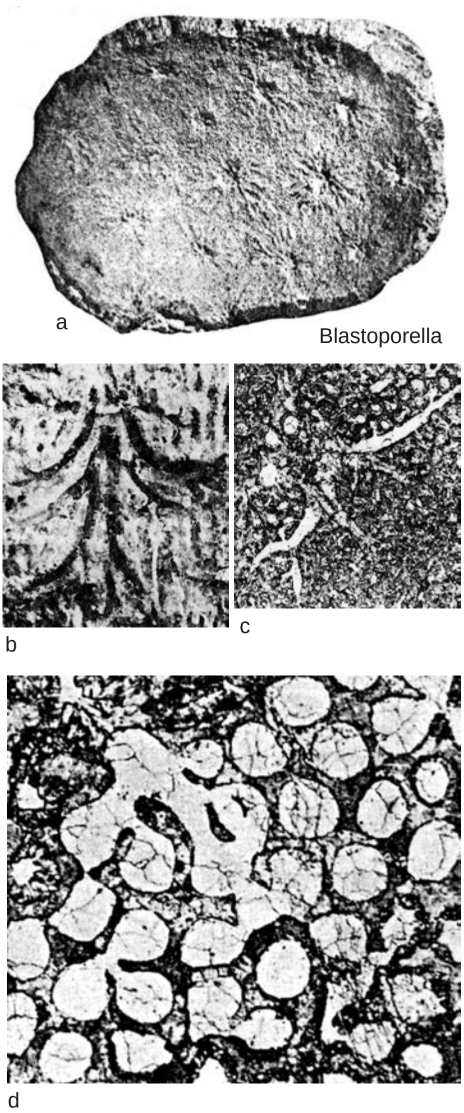


FIG. 171. Uncertain (p. 261–262).

tangential section showing penicillate, water-jet (fascicular fibrous) microstructure of tubule walls, ×400 (Cuif & Ezzoubair, 1991, pl. 2).

Kemeria Cuif & Ezzoubair, 1991, p. 264 [**K. pachytheca*; OD; unnumbered holotype, from near Kemer village; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN)]. Growth form, irregular, nodular, composed of jointed tubules; tubule walls alveolar, characterized by superimposed layers of bundles of penicillate fibers in transverse and longitudinal section, some with small pores; penicillate, water-jet (fascicular fibrous possible aragonite) microstructure; some tubules filled by secondary fascicular crystals; megascleres and microscleres unknown (description based on Cuif & Ezzoubair, 1991). [It is uncertain whether all the views are from parts of the holotype, or some include parts of other type specimens, or represent different, undesignated specimens.] *Triassic (Carnian–Norian):* northern Italy (Dolomite Alps), *Carnian;* Turkey (Alakir Çay), *Norian.*——Fig. 173*a–b.* **K. pachytheca*; *a,* transverse section of tubules with walls composed of numerous penicillate units, each unit going to extinction in transmitted polarized light, ×12.5; *b,* enlargement of part of view *a* showing details of penicillate microstructure of tubule walls, ×100 (Cuif & Ezzoubair, 1991, pl. 2).——Fig. 174*a–d.* **K. pachytheca*; *a,* SEM of penicillate water-jet (fascicular fibrous) microstructure of tubule walls, ×93; *b,* enlargement of view *a* of penicillate water-jet (fascicular fibrous) microstructure of tubule walls, ×217; *c,* slightly oblique longitudinal section showing an opening (pore, *white X*) between two tubules, note penicillate microstructure, ×26; *d,* secondary fascicular crystals filling tubules, inferred to be continuous, ×156 (Cuif & Ezzoubair, 1991, pl. 2).

Keriocoelia Cuif, 1974, p. 149 [**K. conica;* OD; Cuif (1974) did not designate a holotype nor paratypes; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN). Dieci and others (1977) studied 12 topotype specimens (including IPUM 19091, 19092, 19093) and 9 unnumbered specimens, all of which are in the Zardini Collections, IPUM]. Growth form low domical, fungiform with well-developed basal layer; tubules irregular polygons in plan view increasing distally by addition of small spherulites that produce a notched appearance; compact mass produced by secondary penicillate filling of tubules; tubule walls spherulitic aragonite; styliform megascleres and microscleres unknown (Dieci & others, 1977). [See also *Keriocoelia* in Finks & Rigby (2004d, p. 598).] *Triassic (Carnian):* Italy.——Fig. 175*a–f.* **K. conica,* Cassian Formation, northern Italy; *a,* lateral view of basal skeleton of topotype, IPUM 19091, note fungiform growth form and basal layer, ×3.6; *b,* upper surface of basal skeleton of topotype, IPUM 19091, ×3.9 (Dieci & others, 1977, pl. 1); *c,* irregular upper (distal) surface of tubules due to continuous addition of small spherules, ×13.6; *d,* transverse section showing spherulitic microstructure of tubule walls and partial to complete filling of tubules with penicillate aragonite, ×30; *e,* detailed drawing

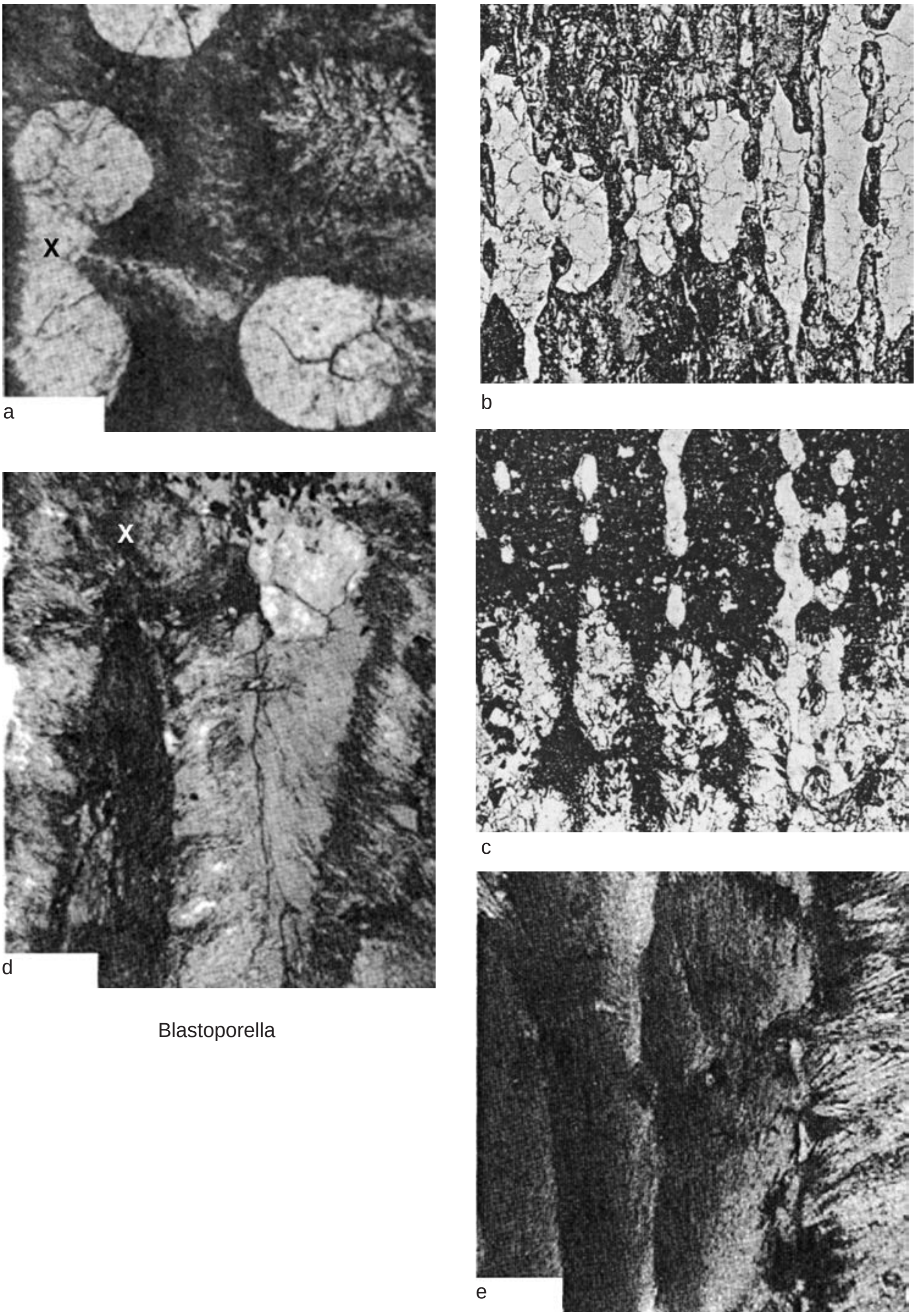
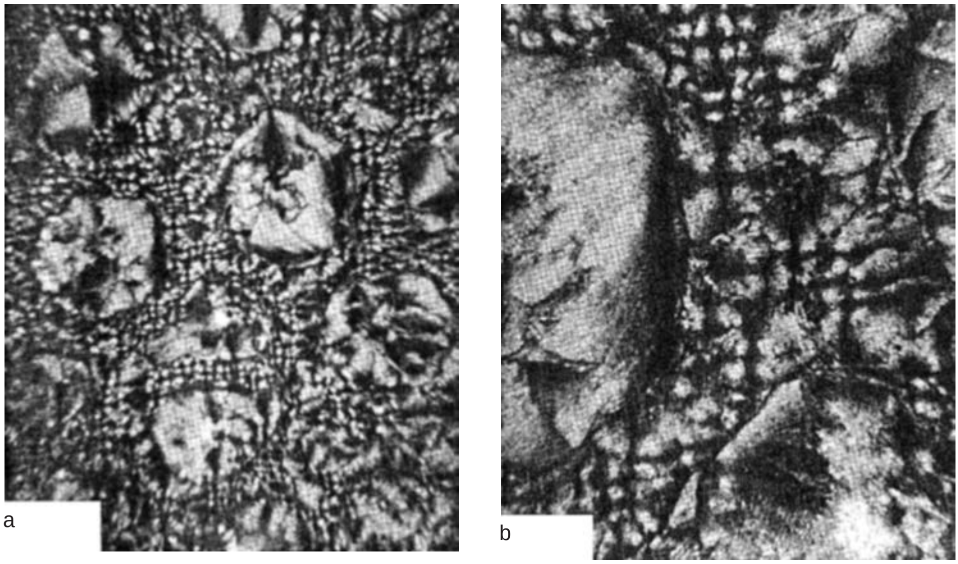


FIG. 172. Uncertain (p. 261–262).



Kemeria

FIG. 173. Uncertain (p. 262).

of transverse section, tubule walls composed of perfectly centered spherules; subsequently, tubules filled with fascicular rods of aragonite, ×85 (Cuif, 1974, p. 150, pl. 31); *f,* thin section, topotype, IPUM 19093, showing stylifom megascleres, ×700 (Dieci & others, 1977, pl. 3).

Leiospongia D'ORBIGNY, 1849b, p. 548 [**Achilleum verrucosum* MÜNSTER, 1841, p. 26; SD ENGESER & TAYLOR, 1989, p. 40] [=*Leiofungia* de FROMENTEL, 1860b, p. 49, obj.; =*Hartmanina* DIECI, RUSSO, & RUSSO, 1974b, p. 141, obj.]. Growth form domical to small columnar, some fungiform; basal layer well developed with growth ridges; tubules polygon in plan view with irregularly spaced tabulae; tubules increase by longitudinal fission or intertubular budding; walls and tabulae composed of spherulitic aragonite. [Spicules and/or spicule pseudomorphs are unknown from the type species, *L. verrucosum,* but acanthostyle or fusiform megascleres are known, arranged parallel to growth direction in *Leiospongia* sp.; microscleres unknown (ENGESER & TAYLOR, 1989, fig. 3F; DIECI, RUSSO, & RUSSO, 1974b); see also *Hartmanina* FINKS & RIGBY, 2004d, p. 595. For more on the taxonomic history of this genus and assigned species, see ENGESER and TAYLOR (1989, p. 40–43) and DIECI, RUSSO, and RUSSO (1974b).] *Triassic (Carnian):* northern Italy.——FIG. 176*a–b.* **L. verrucosum* (MÜNSTER), lectotype, AS VII 383 in collections at SSPHG, Cassian Formation; *a,* lateral view of basal skeleton of lectotype, ×2; *b,* spherulitic microstructure of basal skeleton, ×950 (Dieci, Russo, & Russo, 1974b, pl. 51–52).——FIG. 176*c–d. L. alpina* (KLIPSTEIN, 1845 in 1843–1845), holotype, S10462, NHM, Cassian Formation; *c,* lateral view, ×4.4; *d,* basal view showing basal layer, ×4.4 (Engeser & Taylor, 1989, p. 41).——FIG. 177*a–c. L.* sp., figured as *Calamopora (?) gnemidium* by KLIPSTEIN (1845 in 1843–1845, pl. 19,*15b*), S10464 NHM, Cassian Formation; *a,* lateral view of specimen, ×4.9; *b,* SEM photograph of upper surface showing tubule shapes, ×38; *c,* tylostyle megasclere in tubule wall, ×475 (Engeser & Taylor, 1989, p. 44).

Sclerocoelia CUIF, 1974, p. 147 [**S. hispida;* OD; CUIF (1974) did not designate a holotype, nor paratypes; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN). DIECI and others (1977) studied one topotype specimen in the Zardini Collections, IPUM no. 19097]. Growth form laminar, compact, thick; delicate, arborescent

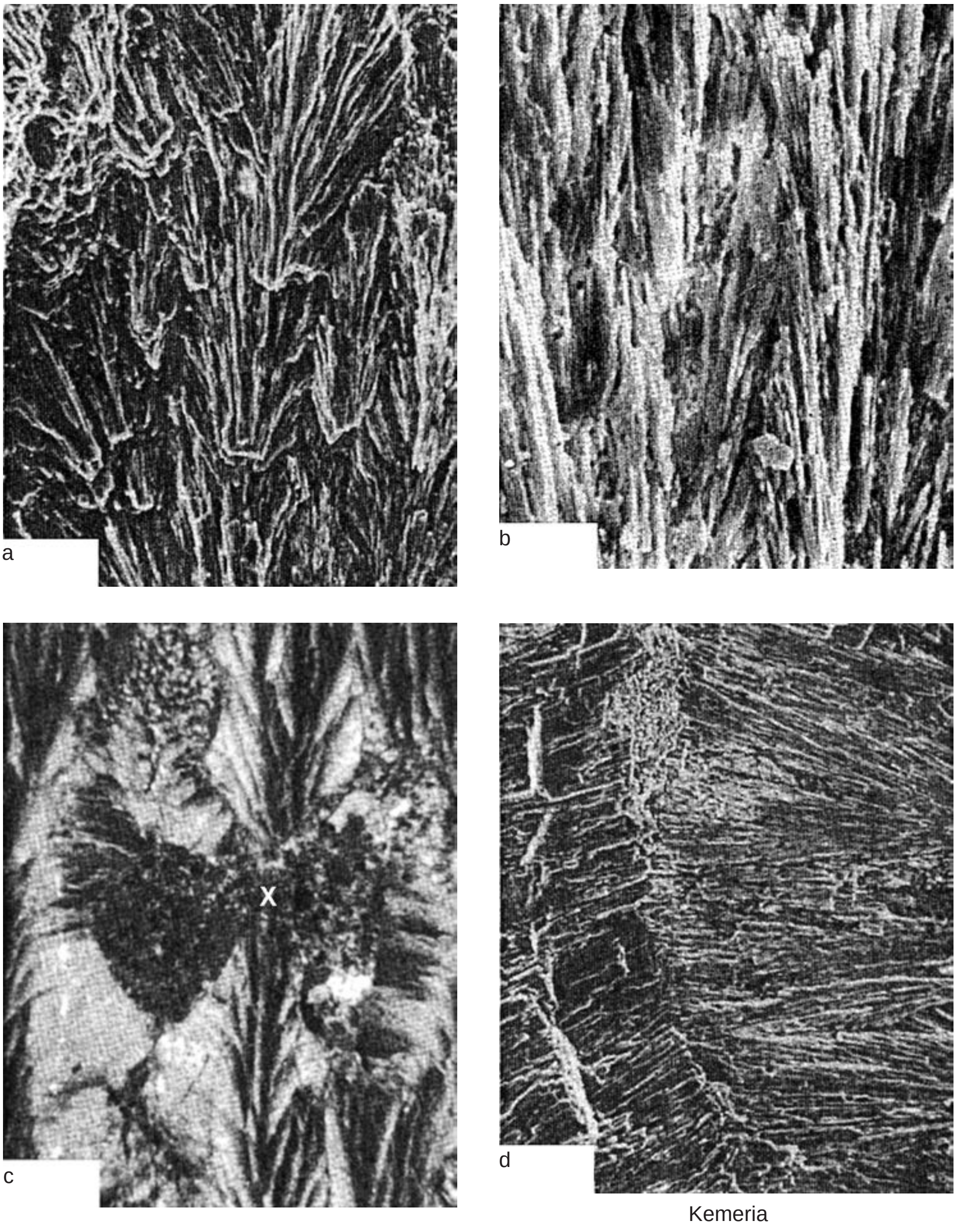


FIG. 174. Uncertain (p. 262).

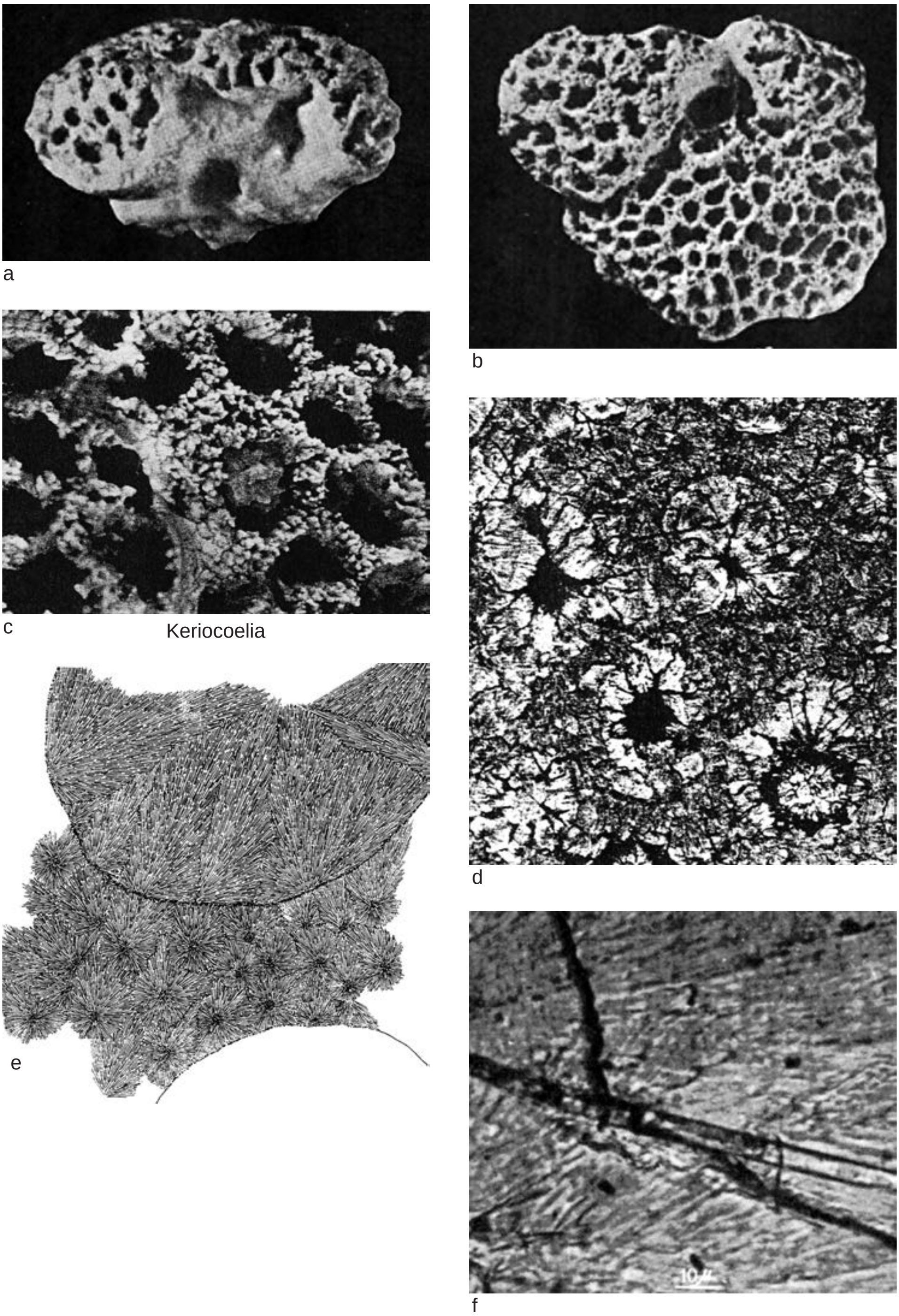


FIG. 175. Uncertain (p. 262–264).

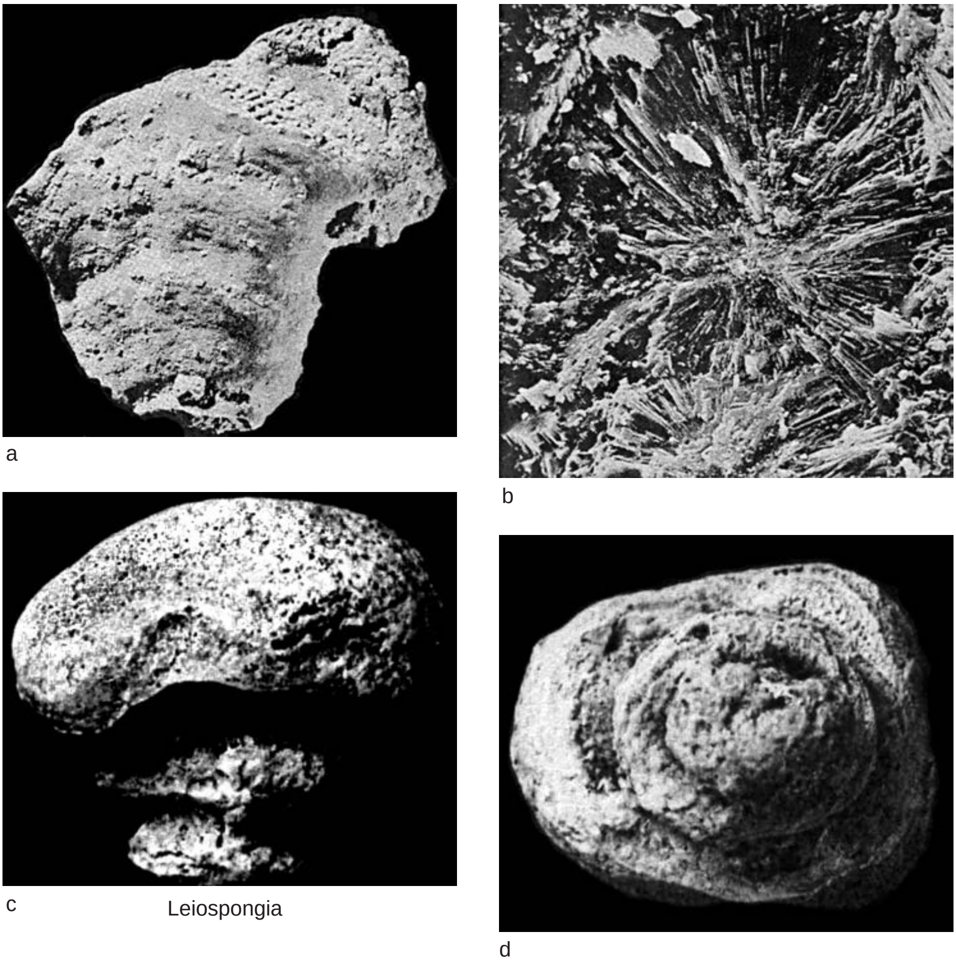


FIG. 176. Uncertain (p. 262–264).

calcareous processes on growing surface resulting in felted appearance; aragonitic penicillate, water-jet (fascicular fibrous) secondary microstructure filling tubules is continuous with primary aragonitic spherulitic microstructure of tubule walls; acanthostyle megascleres 45 to 77 µm long, numerous; microscleres unknown (description modified from CUIF, 1974; DIECI & others, 1977; see also FINKS & RIGBY, 2004d, p. 600–601). *Triassic (Carnian):* Italy.——FIG. 178*a–d*. **S. hispida*, Cassian Formation, northern Italy; *a,* morphology of upper surface, ×3; *b,* detail of upper surface of vertical (tubule) walls, ×44; *c,* penicillate, water-jet (fascicular fibrous) secondary microstructure of topotype IPUM 19097, ×450 (Dieci & others, 1977, pl. 2); *d,* transverse section in transmitted polarized light of primary spherulitic microstructure that forms tubule walls, ×115 (Cuif, 1974, p. 148, pl. 30).——FIG. 179*a–d*. **S. hispida*, Cassian Formation, northern Italy; *a,* detailed drawing of transverse section of spherules that form vertical processes (possible tubule walls), compare with view *d,* ×60 (Cuif, 1974, p. 148, fig. 4); *b,* pseudomorph acanthostyle megasclere in topotype IPUM 19097, oriented diagonally relative to crystalline fibers of basal skeleton, ×2000; *c,* pseudomorph acanthostyle megasclere in topotype, IPUM 19097, embedded in crystalline fibers of basal skeleton, ×2000 (Dieci & others, 1977, pl. 2,*1b,1a*); *d,* mold of part of an acanthostyle megasclere (fragment of spicule is visible

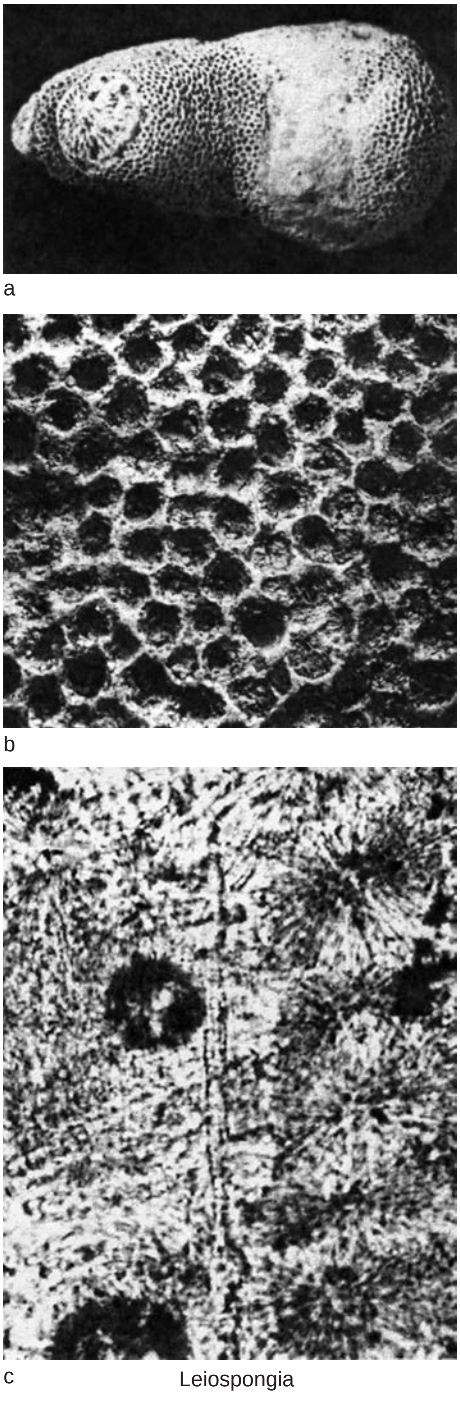


FIG. 177. Uncertain (p. 264).

on left side of illustration) in topotype IPUM 19097, ×2000 (adapted from Dieci & others, 1977, pl. 2,*1c*).

Sobralispongia SCHMID & WERNER, 2005, p. 655 [**S. densespiculata;* OD; holotype CSGP 4217]. Encrusting calcified agelasid with spicule framework of club-shaped styles and subtylostyles with plumose arrangement in vertical elements only; asterlike microscleres; primary calcareous skeleton dominated by radial elements of orthogonal or fascicular fibrous or irregular microstructure; meandroid surface features. *Upper Jurassic (lower Kimmeridgian):* Portugal.——FIG. 180*a–c*. **S. densespiculata*, Sobral del Monte Agraco; *a,* longitudinal section, CSGP 4217, ×6; *b,* oblique section, light photomicrograph, holotype CSGP 4217, ×9; *c,* longitudinal section, light photomicrograph, specimen BSP 2003 IV 4d, ×26 (Schmid & Werner, 2005).

Order HAPLOSCLERIDA Topsent, 1928

[*nom. correct.* DE LAUBENFELS, 1955, p. 37, *pro* Haplosclerina TOPSENT, 1928, p. 66] [=Nepheliospongida BERGQUIST, 1980, p. 4]

JEAN VACELET, PHILIPPE WILLENZ,
and †WILLARD D. HARTMAN

Demospongiae in which the main skeleton is partially or entirely composed of isodictyal, anisotropic, or isotropic, occasionally alveolate reticulation of spongin fibers and/or spicules, with uni- to multispicular tracts of diactinal spicules forming triangular, rectangular, or polygonal meshes. Megascleres are exclusively oxeote or strongylote, bonded together with collagenous spongin or closed within spongin fibers; microscleres, if present, may include sigmas and/or smooth toxas (both frequently centrangulate), microxeas or microstrongyles, and in one group amphidiscs (VAN SOEST & HOOPER, 2002b, p. 831); FINKS and RIGBY (2004a, p. 53) attributed the order Haplosclerida to TOPSENT, 1898, as follows: "*nom. correct.* DE LAUBENFELS, 1955, p. 37, *pro* Haplosclerina TOPSENT, 1898, p. 93;" however, Haplosclerina is not mentioned on p. 93 of TOPSENT, 1898; FINKS and RIGBY (2004a) also followed DE LAUBENFELS (1955, p. 37). *Carboniferous (Pennsylvanian)–Holocene.*

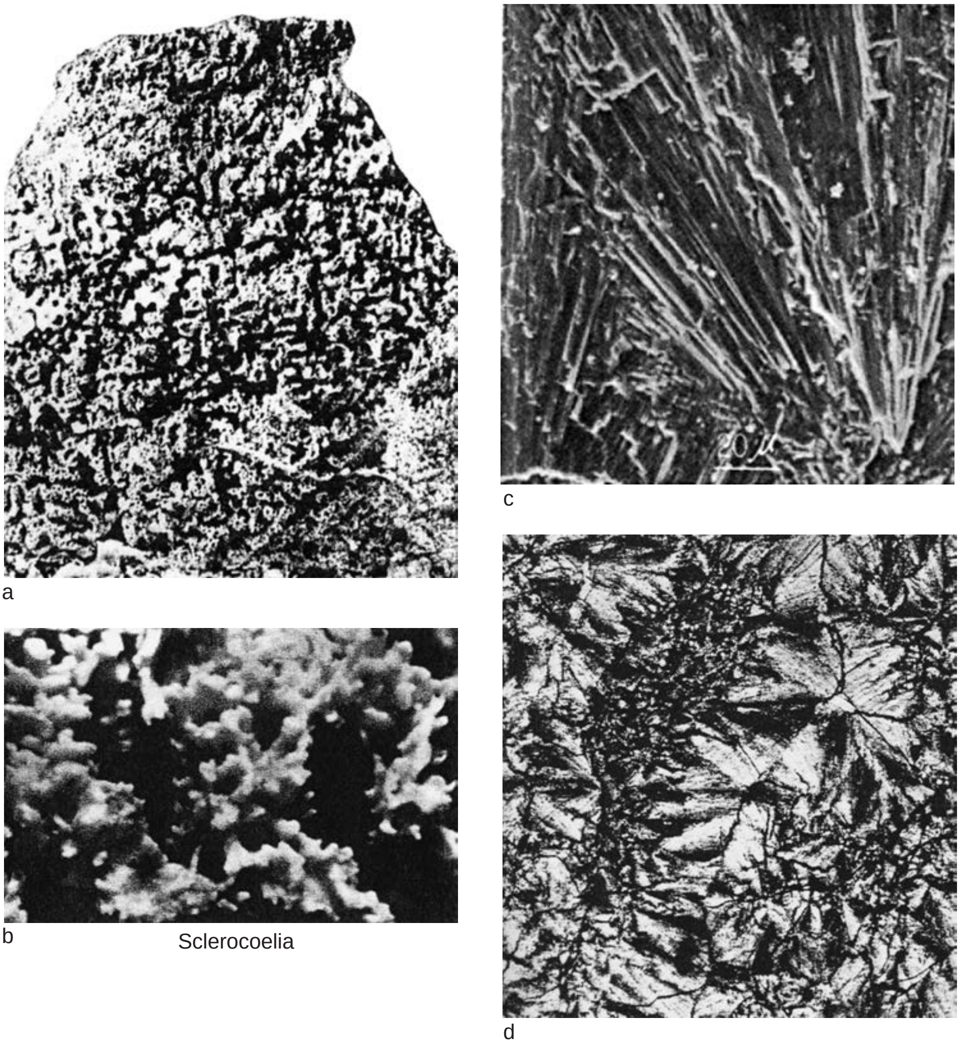


FIG. 178. Uncertain (p. 264–268).

Family CALCIFIBROSPONGIIDAE Hartman, 1979

[Calcifibrospongiidae HARTMAN, 1979, p. 473]

Semiglobular or flattened aragonitic masses covered by a thin veneer of organic tissue. Surface with evenly scattered, depressed oscules. Siliceous skeleton composed of a reticulation of thin strongyles. No ectosomal specialization. Aragonitic basal skeleton consists of a meshwork of tubes, pillars, and lamellae that intergrade peripherally with spicular skeleton. Canal system penetrates aragonitic meshwork to a varying degree, depending on episodes of growth (VAN SOEST, 2002b, p. 918). *Holocene.*

Calcifibrospongia HARTMAN, 1979, p. 468 [**C. actinostromarioides;* M; holotype YPM no. 9114]. Description as for family. Type species mushroom

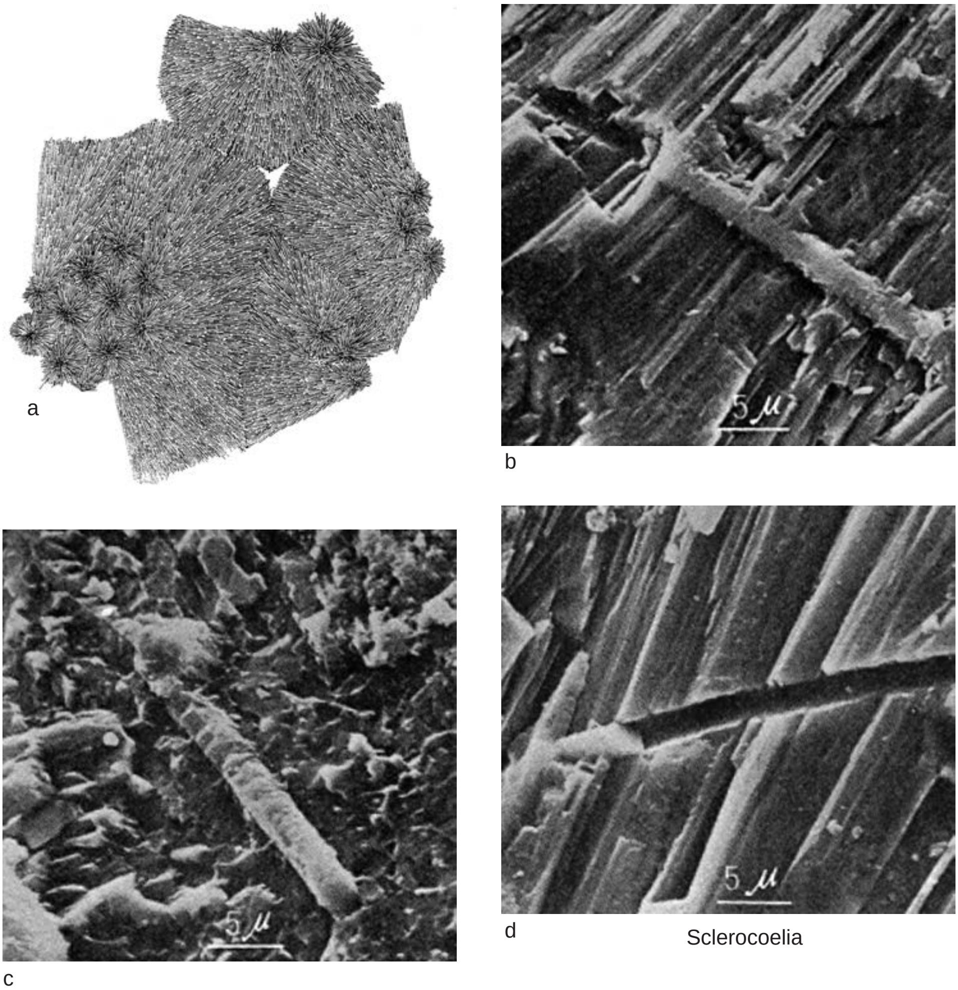


FIG. 179. Uncertain (p. 264–268).

shaped (smaller specimens), dome shaped to flattened with a broad base of attachment. Size up to 30 cm by 30 cm by 10 cm. Surface smooth when alive, provided with many evenly distributed, rounded, slightly depressed oscules, with a faint trace of astrorhizae. Color brownish tan or tannish orange alive. Soft parts—apart from the pinacoderm—entirely incorporated in basal calcareous skeleton. Calcareous skeleton is laid down within the organic fibers that surround the tracts of siliceous spicules. Microstructure of aragonite is organized as acicular crystalline units with spherulitic or sclerodermite-like patterns. The inhalant canals lead into system of cavities of calcareous skeleton, and likewise exhalant canals run through calcareous mass over a considerable distance to end in vestibules immediately underneath pinacoderm. Ectosomal region is supported for a small distance by free siliceous spicules arranged in a uni- or paucispicular isodictyal reticulation. In subectosomal region, spicule tracts, which are aligned in collagenous matrix, become focal points for calcification, and further down into sponge, spicules become entirely enclosed in calcium carbonate. Siliceous skeletal meshes and calcareous cavities match closely in size, smaller meshes varying from 55–175 µm in diameter, many larger ones represented by various canals and tubes. Choanocyte chambers, about 20 µm in diameter, and mesohyl tissues are found to a variable depth within calcareous basal mass and are rich in symbiotic prokaryotes. In larger specimens, a layer of 1.5–3 cm thick is alive, underneath which there are dead layers of similar thickness marking intervals of death and regeneration. Spicules are thin, gently curved strongyles, 130–210 µm by 3–6 µm. Both ends often produce numerous concentric additions. Epizoic zoanthids grow on surface of some specimens, with polyps regularly spaced and isolated from sponge within an armored cyst laid down by sponge and reinforced with strongyles. Occurs in shaded, deep reef habitats (HARTMAN, 1979; WILLENZ & HARTMAN, 1994; VAN SOEST, 2002b). *Holocene*: Carribean (Bahamas).——FIG. 181*a–i*. **C. actinostromarioides*, RBINSc-POR.061; *a,* underwater photograph of specimen about 30 cm by 60 cm, under an overhang at depth of 30 m on forereef wall south of Jamaica Bay, southern tip of Acklins Island, Bahamas, scale, 15 cm (see also Fig. 1.3); *b,* part of calcareous skeleton with large exhalant canal in center, and smaller exhalant canals entering main one laterally, scale bar, 2 mm; *c,* enlargement of surface of skeleton, with small round holes that are inhalant canals, scale, 500 µm; *d,* detail of aragonitic skeleton with protruding siliceous spicules, scale, 100 µm; *e,* pattern of siliceous spicules in exopinacoderm, scale, 200 µm; *f–i,* siliceous spicules with thin, slightly curved strongyle (*f,* scale, 50 µm); ends of strongyles with numerous concentric additions (*g–h,* scale, 5 µm); *i,* eroded strongyle as found enclosed in calcareous skeleton, showing a general surface pitting, scale, 2 µm (West & others, 2013).

Family EUZKADIELLIDAE Reitner, 1987

[Euzkadiellidae REITNER, 1987a, p. 204]

RACHEL A. WOOD and RONALD WEST

Calcified hapolosclerids with a reticulate spicular skeleton and a spherulitic calcareous skeleton. *Lower Cretaceous.*

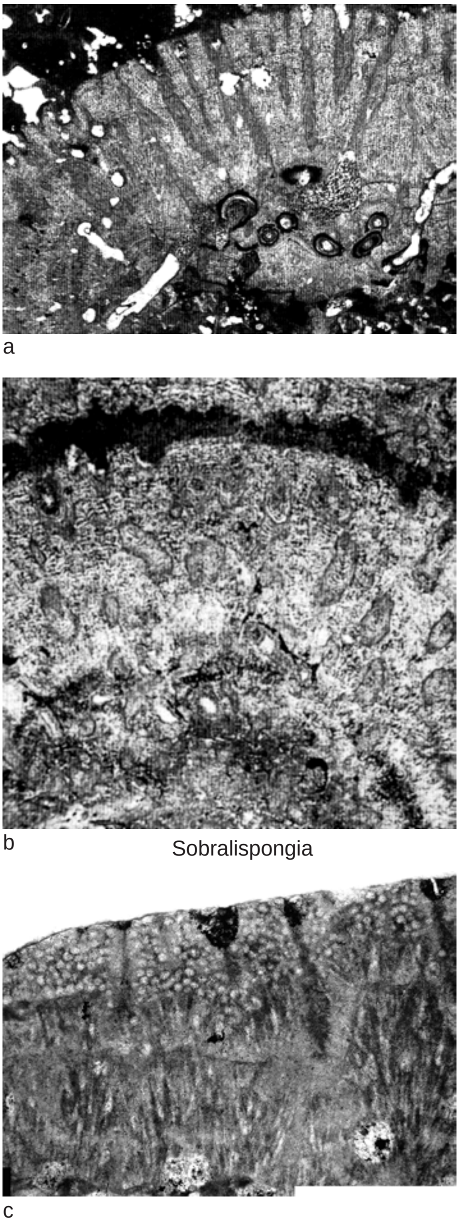


FIG. 180. Uncertain (p. 268).

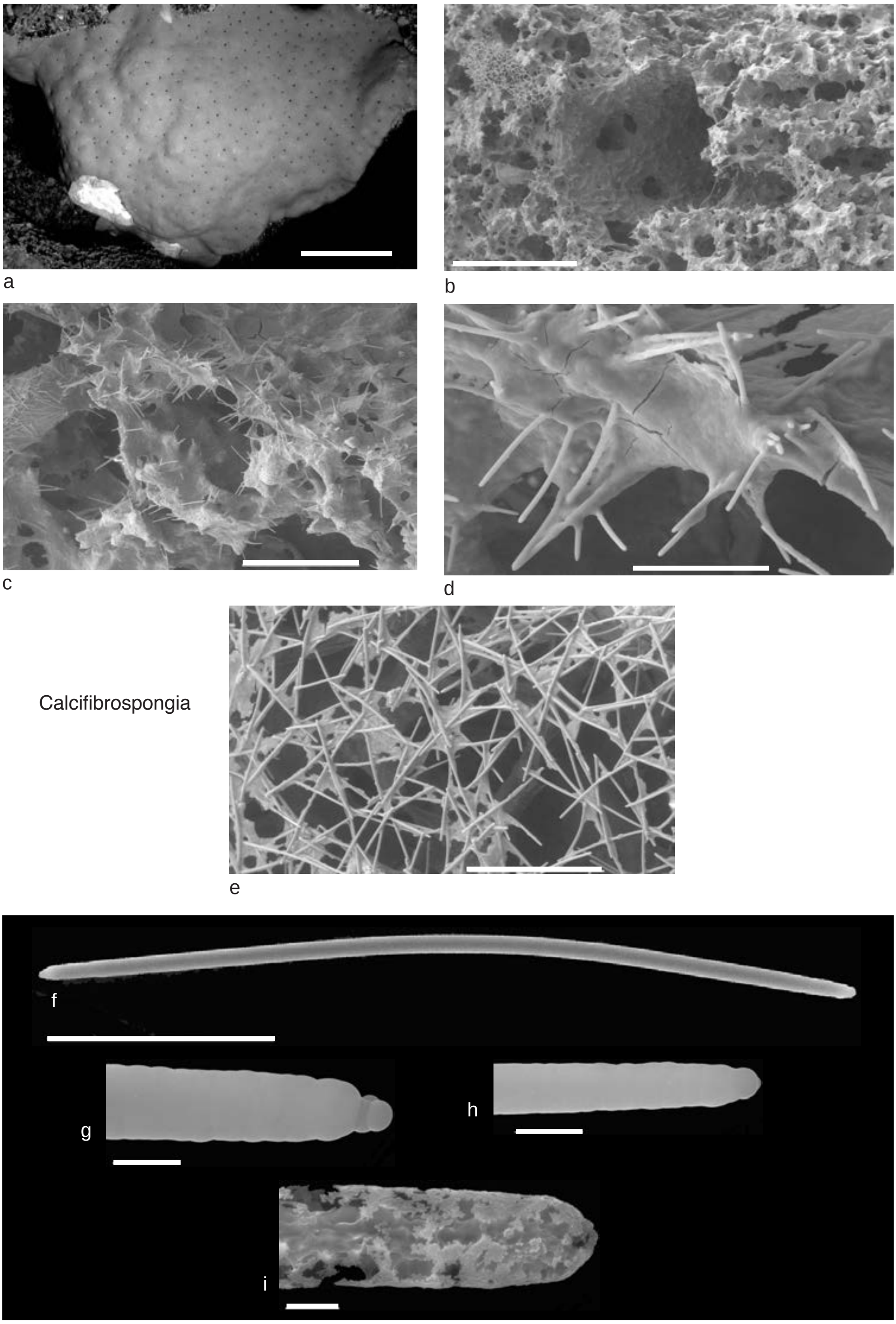


FIG. 181. Calcifibrospongiidae (p. 269–271).

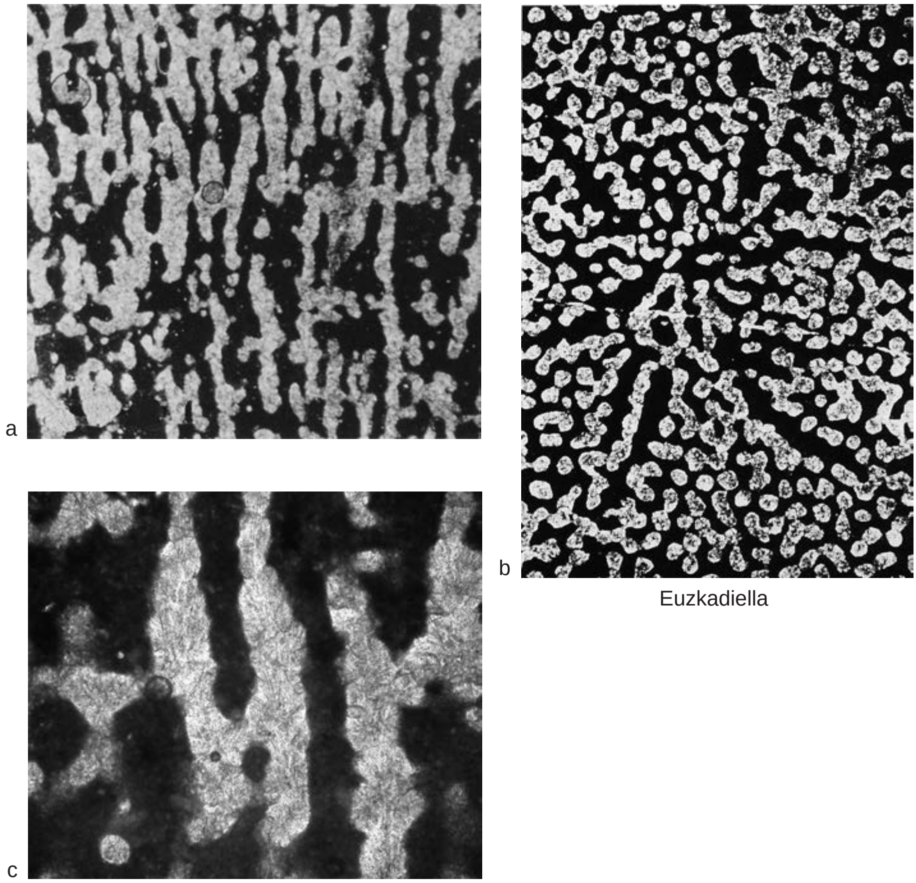


FIG. 182. Euzkadiellidae (p. 273).

Euzkadiella REITNER, 1987a, p. 204 [**E. erenoensis;* OD; holotype NHM H 5478a]. Plumose skeleton of large subtylostyles and oxes, as well as transversely arranged smaller strongyle spicules that form a reticulate pattern and astrorhizae; spherulitic calcareous skeleton. *Lower Cretaceous*: Spain.——FIG. 182*a–c.* **E. erenoensis*, light photomicrograph, NHM H 5478a, Ereño, Guipuzco Province; *a,* longitudinal section, ×4 (Reitner, 1987a, p. 207, fig. 3c); *b,* longitudinal section, ×25 (West & others, 2013); *c,* transverse section, ×3 (Reitner, 1987a, p. 207, fig. 3c).

Family NEWELLIDAE Wood, Reitner, & West, 1989

[Newellidae WOOD, REITNER, & WEST, 1989, p. 86]

Calcified hapolosclerids with a regular isodactyl arrangement of megasleres, with a secondary aragonitic skeleton. *Carboniferous (Middle Pennsylvanian).*

Spongonewellia ÖZDIKMEN, 2009, p. 212, *nom. nov. pro Newellia* WOOD, REITNER, & WEST, 1989, p. 86, *non* ANDRÉ, 1962, arachnid [**Parallelopora mira* NEWELL, 1935, p. 341; OD; holotype, University of Kansas, KUMIP 58231]. Radial plumose styles, subtylostyles, and strongyles and transverse strongyles forming lateral connections. *Carboniferous (Middle Pennsylvanian):* USA (Kansas).——FIG. 183*a–c.* **S. mira* (NEWELL), longitudinal section, KUMIP 58231, Anderson County; *a,* light photomicrograph, ×10; *b,* SEM, ×186; *c,* SEM, ×500 (Wood, Reitner, & West, 1989, p. 88–89).

Order DICTYOCERATIDA Minchin, 1900

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

JEAN VACELET

Demospongiae that have a spongin fiber skeleton constructed in an anastomosing

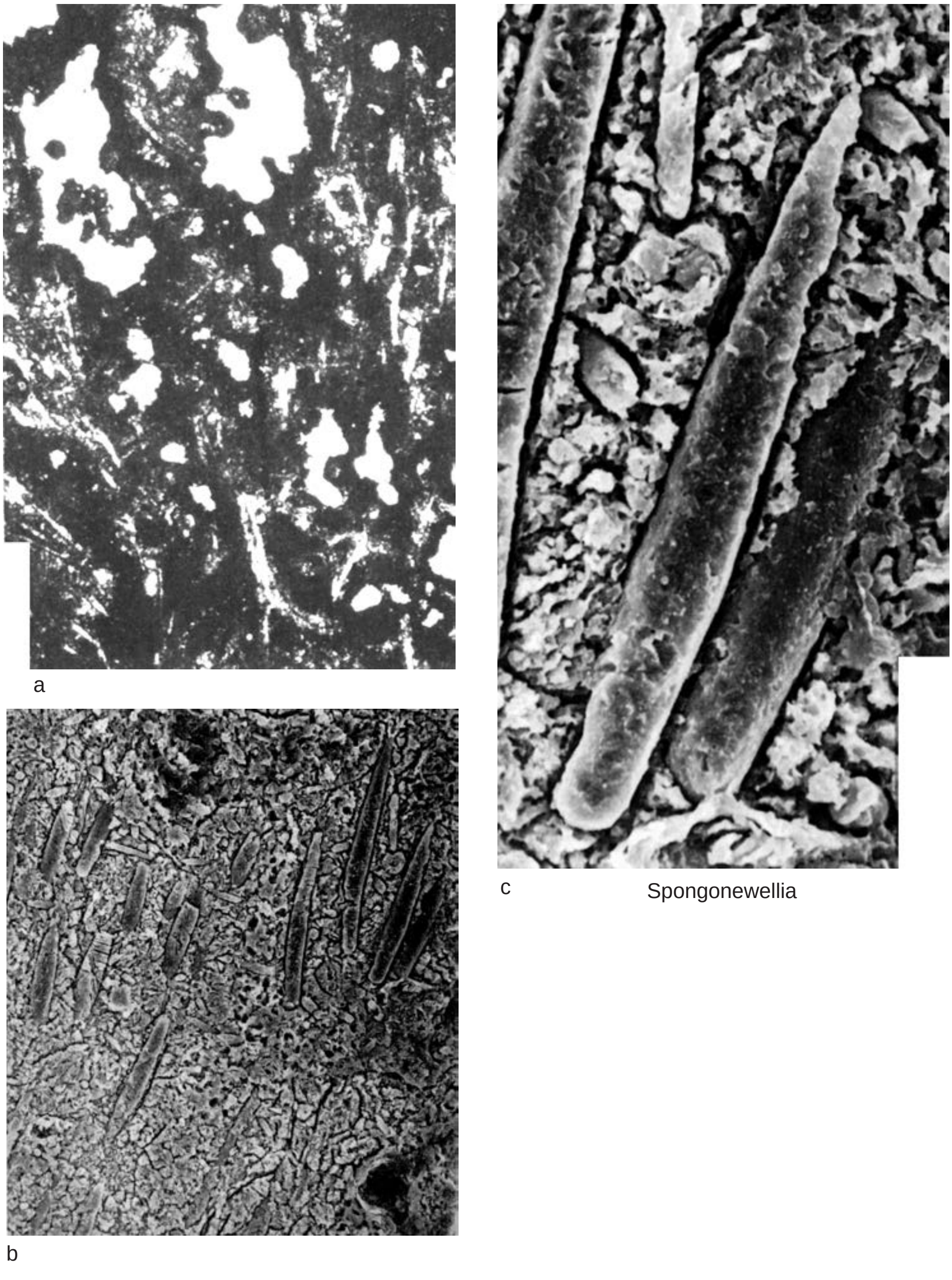


FIG. 183. Newellidae (p. 273).

plan. Choanocyte chambers are either diplodal or eurypylous. Larvae are incubated parenchymellae with a posterior ring or cap of long cilia. Also, chambered hypercalcified sponges (so-called Sphinctozoa) of the siphonate type that are devoid of fiber and spicule skeleton, with aragonitic, porate external wall, may occur within the order. [Four families of the Dictyoceratida exhibit nonmineralized, nonspicular, horny (that is, keratose) members, including the well-known bath sponges (adapted from COOK &

Bergquist, 2002, p. 1021), with only one of these families (the family Dysideidae Gray, 1867) being represented as having a fossil record: three of its listed genera range from the Jurassic to Holocene (see Finks & Rigby, 2004a, p. 44). Previously this order was defined as lacking a mineralized or spicule skeleton. However, the additional family added here, Vaceletiidae Reitner & Engeser (1985, p. 163), is comprised of chambered hypercalcified sponges of siphonate type, having an aragonitic, porate external wall and lacking a fiber or spiculate skeleton. This family is referred to on the basis of the analyses of rDNA sequences, proving that its eponymous, monophyletic genus *Vaceletia* is a keratose demosponge (Wörheide, 2008, p. 433).] *?Cretaceous, Eocene–Holocene.*

Family VACELETIIDAE
Reitner & Engeser, 1985

[Vaceletiidae Reitner & Engeser, 1985, p. 163]

Chambered Dictyoceratida with a calcified skeleton of the sphinctozoan siphonate type, with atrium of almost constant diameter and a special atrium wall. No secondary canal system in atrium wall. Spicule and fiber skeleton totally lacking. Chambers low, containing numerous vertical pillars. Exopores simple. Exowall, interwall, and endowall with the same pattern of perforation (description adapted from Reitner & Engeser, 1985, and amended to accommodate this family as a keratose sponge; see Wörheide, 2008). *?Cretaceous, Eocene–Holocene.*

Family Vaceletiidae was first recognized, based both in living and fossil forms as type genus *Vaceletia* Pickett, 1982, and fossil (Eocene) genus, *Marinduqueia* Yabe & Sugiyama, 1939, in the original conception of Reitner and Engeser (1985, p. 163), as a member of the order Verticillitida Termier & Termier in H. Termier, G. Termier, & Vachard, 1977 (only included in part in the family Verticillitidae Steinmann, 1882). However, other authors have treated the family Vaceletiidae as a junior synonym of family Verticillitidae Steinmann, 1882, within the order Verticillitida Termier & Termier in H. Termier, G. Termier, & Vachard, 1977 (see Senowbari-Daryan, 1990, p. 48; and Senowbari-Daryan & García-Bellido, 2002a, p. 1521), and subfamily Verticillitinae Steinmann, 1882, of family Verticillitidae (see Finks & Rigby, 2004d, p. 712, and Senowbari-Daryan & Rigby, 2011, p. 70). Nine genera have been maintained in the subfamily, including the type genus *Verticillites* Defrance, 1829, the living and fossil *Vaceletia*, and fossil *Marinduqueia* (see Finks & Rigby, 2004d, p. 712, and Senowbari-Daryan & Rigby, 2011, p. 70).

It should be noted that both orders Verticillitida Termier & Termier in H. Termier, G. Termier, & Vachard, 1977 (see Senowbari-Daryan & García-Bellido, 2002a, p. 1521, table 1) and Vaceletida Rigby, 2004a (p. 4), 2004c (p. 691) that include family Verticillitidae Steinmann, 1882, were validly constituted, though their overall family compositions are rather different. The order Vaceletida Finks & Rigby, 2004d, was given a broader conception, incorporating many more families and exhibiting more widely ranging stratigraphic records (e.g., Cambrian and Permian). The relationships of a number of these families, especially those containing Cambrian taxa, need to be further assessed. The order Verticillitida, with its narrower scope, should retain priority of usage.

The status of Vaceletiidae (following Reitner & Engeser, 1985, p. 163) remains uncertain: whether it should be reinstated as an independent family and be transferred only with type genus *Vaceletia* and possibly *Marinduqueia* to the order Dictyoceratida; or whether the morphologically closely related genera (*Vaceletia* plus eight fossil genera) belonging to the subfamily Verticillitinae should all be transferred to the Dictyoceratida (see compilation of Finks & Rigby, 2004d, p. 712–719, and list in Senowbari-Daryan & Rigby, 2011, p. 70). Possibly future comparative work on the fossil taxa may help resolve the taxonomic relationships, for example, by intensive studies of the microstructures within their skeletons. However, for the present, it seems best to transfer only the type genus *Vaceletia* (and possibly *Marinduqueia*) of the family Vaceletiidae to the order Dictyoceratida, and leave all the other genera still considered to be fossil sphinctozoans as verticillitinid and verticillitid members of the order Verticillitida Termier & Termier in H. Termier, G. Termier, & Vachard, 1977, as followed by Finks and Rigby (2004d) and Senowbari-Daryan and Rigby (2011).

Vaceletia Pickett, 1982, p. 241, *nom. nov. pro Neocoelia* Vacelet, 1977b, p. 509, *non* McKellar, 1966 [**Neocoelia crypta* Vacelet, 1977b, p. 509; OD; holotype, MNHN DJV39]. Cylindrical, solitary or irregularly branching, with chambered skeleton of siphonate type composed of an irregular arrangement of aragonite crystals. Spicules and spongin fibers absent. Inhalant openings in outer wall of porate type, with simple exopores provided with spines extending toward center of aperture. Exowall, interwall, and endowall with same pattern of perforation. Exhalant canal siphonate, sometimes with longitudinal dividing wall. Regular, pillar-like filling structures in chambers. Earlier chambers filled in by calcareous deposit, which also partly or wholly covers surface of basal part of skeleton. [The type species is cylindrical, with irregular swellings and constrictions marking successive chambers, solitary or irregularly branching. Living part 5–9 mm high and 3 mm in diameter. Dead bases of the same diameter, with a variable development, often covered by a thin epitheca and filled in with a secondary deposit. Color of living tissue grey in life, and in alcohol, skeleton white. Skeleton of living part made of series of thin-walled, crescent-shaped chambers, 0.6 mm high near center, traversed by cylindrical central canal (siphon or atrium), 0.7–0.9 mm in diameter, with proper wall. Dome-shaped walls of chamber supported by regular pillars, 40–50 µm in diameter, perpendicular to wall and regularly spaced. Walls from chamber and atrium all 50 µm thick, bearing apertures regularly arranged, 100 µm in diameter, with variable number of short radial spines. Spicules and spongin fibers absent, both in skeleton and in living tissue. Living tissue located inside chambers, except thin pinacoderm lying on surface of outer wall and bearing ostia. Osculum apical, 0.5–0.8 mm in diameter. Ostia 25–50 µm in diameter, unique in center of each aperture of outer chamber wall. Choanocyte chambers aphodal, 40–45 µm in diameter, with short aphodus. Tissue containing a high density of morphologically diverse intercellular bacteria. Microstructure of skeleton microgranular, consisting of a feltwork of aragonite crystals organized into nodules with noncalcified center (Gautret, 1985). Skeleton secreted as an organic template that is subsequently mineralized (Vacelet, 1979b; Reitner & Wörheide, 2002). Reproduction viviparous, by incubated parenchymella. Large distribution throughout Indo-West Pacific area, in semi-closed cavities of coral reef-front caves and bathyal environments, 10–530 m depth. Only a single Recent species, the type *V. crypta,* has been described. However, in bathyal environments and in some reef caves, this sponge may have a branching, colonial mode of growth, enabling it to build large aggregates up to 30 cm in diameter and probably more (Vacelet & others, 1992; Wörheide & Reitner, 1996), thus retaining the building capabilities of its fossil counterparts. The skeleton is more heavily calcified, with thicker pillars and chamber walls, with a longitudinal wall dividing the central canal. These variations, as well as others presently undescribed, may either be specific, meaning that there are several species of living sphinctozoans, or may indicate a large morphological plasticity, which could have implications for interpretation of fossil species. The fossil record includes two species, *V. progenitor* Pickett, 1982, and *V. faxensis* (Ravn, 1899), respectively, from the Eocene of Australia and Denmark (Clausen, 1982; Pickett, 1982), and a doubtful species from the Campanian of Spain (Reitner, 1992). In the absence of spicules and a fibrous skeleton, the affinities of *Vaceletia* in terms of other extant orders of Demospongiae remain uncertain. However, recent results of molecular taxonomy indicate an affinity with keratose sponges of the order Dictyoceratida (Lavrov, Wang, & Kelly, 2008; Wörheide, 2008), while some spiculate fossil representatives of order Verticillitida suggest an uncertain affinity with Haplosclerida (Reitner & Wörheide, 2002). The genus *Vaceletia* is here classified in family Vaceletiidae, as suggested by Wörheide (2008). The family is here classified in Dictyoceratida, with a tentative redefinition of the order. At this time it cannot be determined whether other fossil members of the former Verticillitida are possibly comparable to keratose sponges or distinct from this group.] *?Cretaceous, Eocene–Holocene:* Spain, *?Cretaceous;* Western Australia, *Eocene;* tropical Indo-West Pacific, *Holocene.*——Fig. 184*a–f.* **V. crypta* (Vacelet); *a,* view of specimens from cavities of front coral reef, New Caledonia, 15 m water depth, ×1.6 (West & others, 2013); *b*, fragment of an aggregate built by colonial, bathyal form, Norfolk Ridge, 250 m, ×0.6 (West & others, 2013); *c,* SEM view of vertical section of skeleton, with dead bases bored by a *Thoosa* sp., New Caledonia, 25 m, ×12.5 (West & others, 2013); *d,* SEM view of surface of skeleton, partially covered by epitheca, Norfolk Ridge, 250 m, ×127 (West & others, 2013); *e*, section through skeleton and living tissue, Great Barrier Reef, 10 m, ×80 (West & others, 2013); *f,* section through skeleton and living tissue of growing specimen, showing skeleton, with template of new chamber (top) and living tissue, ×60 (Vacelet, 1979b).

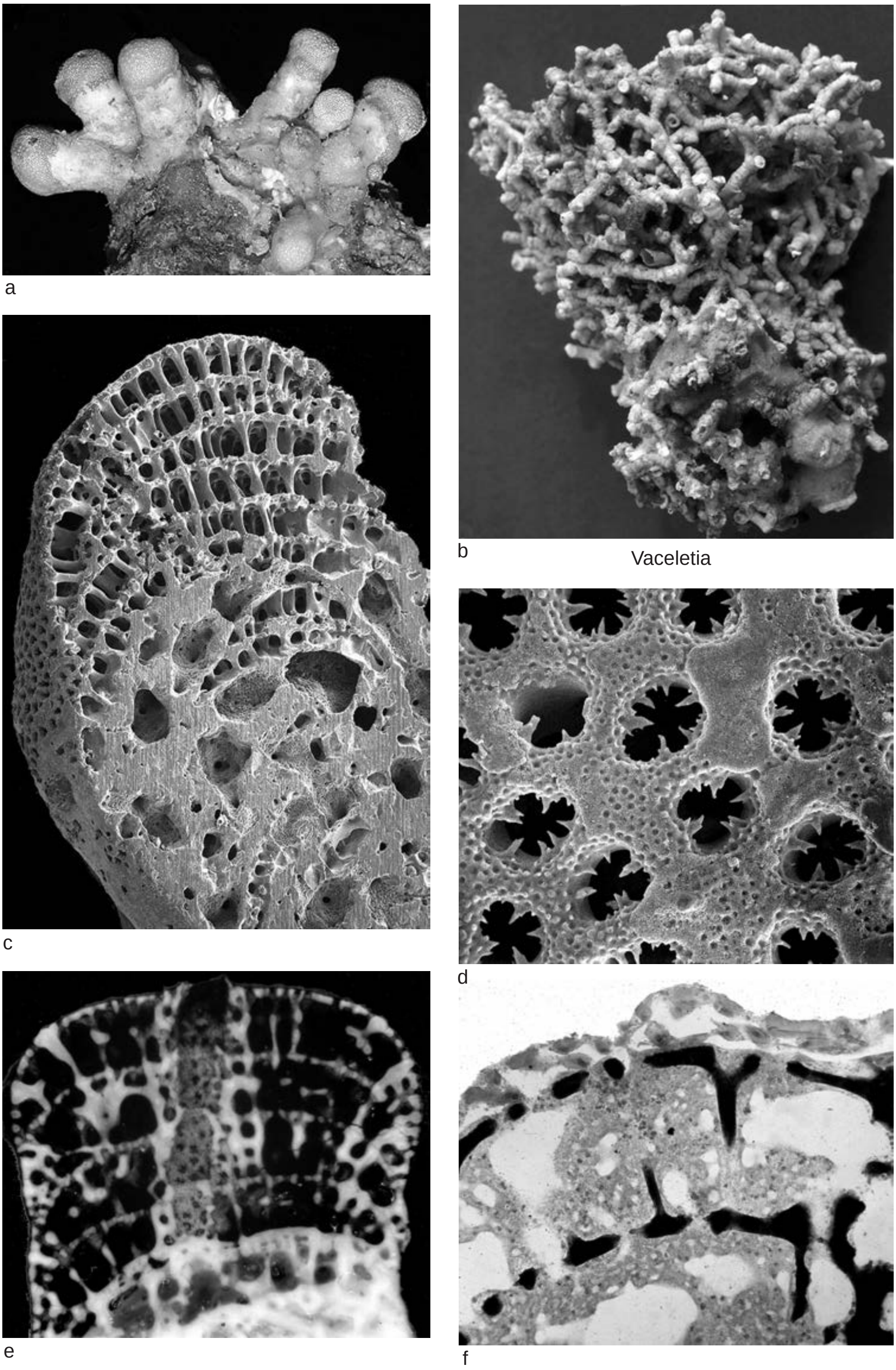
Order UNCERTAIN

Family BURGUNDIIDAE Dehorne, 1920

Rachel A. Wood

[*nom. correct.* Hudson, 1954b, p. 48, *pro* Burgundides Dehorne, 1920, p. 69]

Possible aspiculate calcified demosponges with a fibrous microstructure and concentric



Vaceletia

FIG. 184. Vaceletiidae (p. 276).

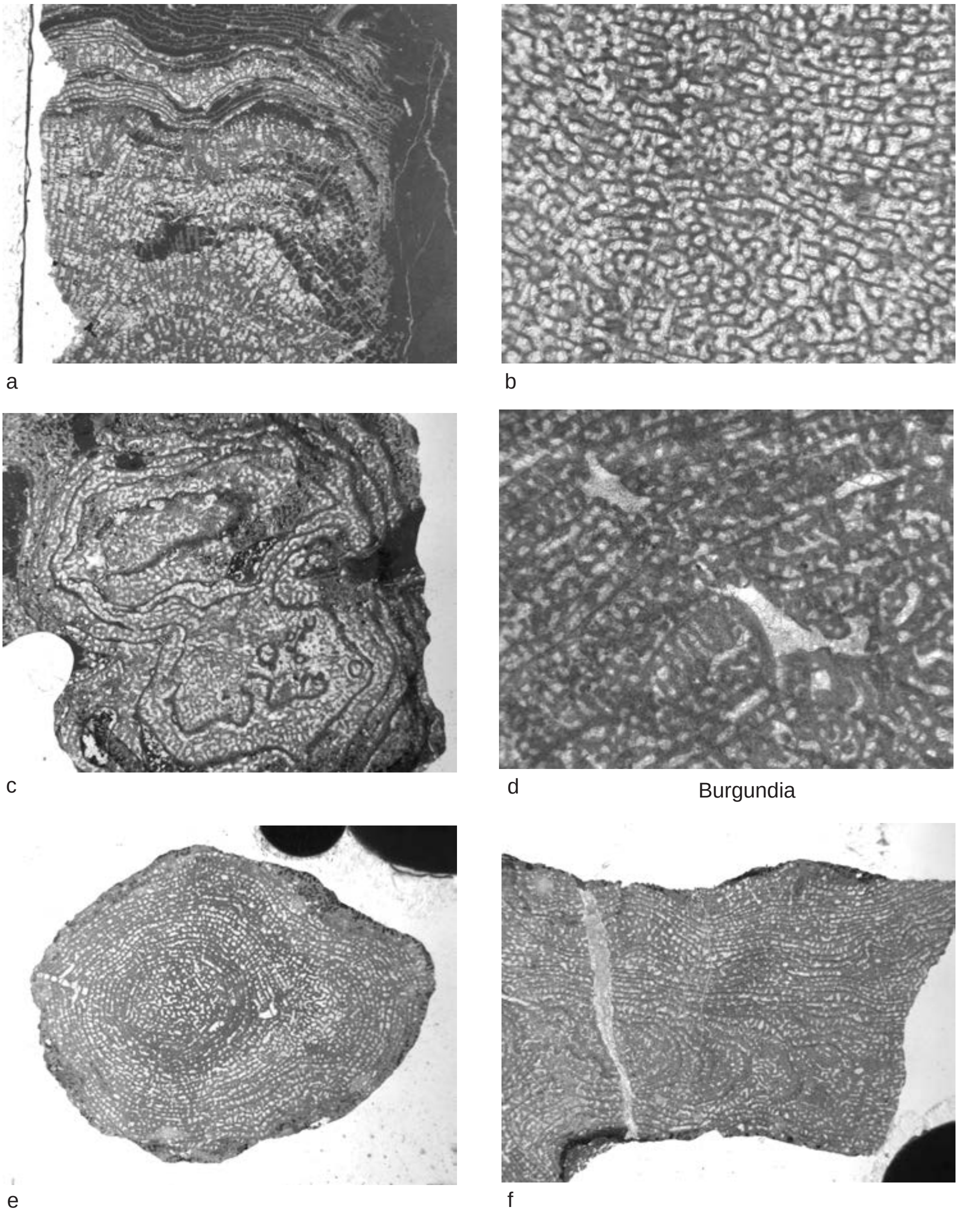


FIG. 185. Burgundiidae (p. 278–281).

perforated laminae. Aquiferous system may or may not bear tabulate oscula and astrorhizae. *Upper Jurassic–Lower Cretaceous.*

Burgundia DEHORNE, 1916, p. 430 [**B. trinorchii* DEHORNE, 1916, p. 431; OD; holotype, Geological Laboratory Sorbonne, fig. 1, collection of Munier-Chalmas; =*Circoporella semiclathrata* HAYASAKA, 1917, p. 58; =*Plassenia alpine* YABE & SUGIYAMA, 1931a, p. 113; =*Burgundia semiclathrata* HAYASAKA, 1917, p. 56; STEINER, 1932, p. 184; =*Burgundia* cf. *semiclathrata* HAYASAKA, 1917, p. 56; KELLAWAY & SMITH, 1938, pl. 21,*5;* =*Circoporella semiclathrata* HAYASAKA, 1917, p. 56; YABE & SUGIYAMA, 1941a, p. 39; =*Burgundia barremensis* YAVORSKY, 1957, p. 27; ?=*Burgundia alpina* YABE & SUGIYAMA, 1931a, p. 113; FENNINGER & HOTZL, 1965, p. 39] [?=*Stromatoporidium* VINASSA DE REGNY, 1915,

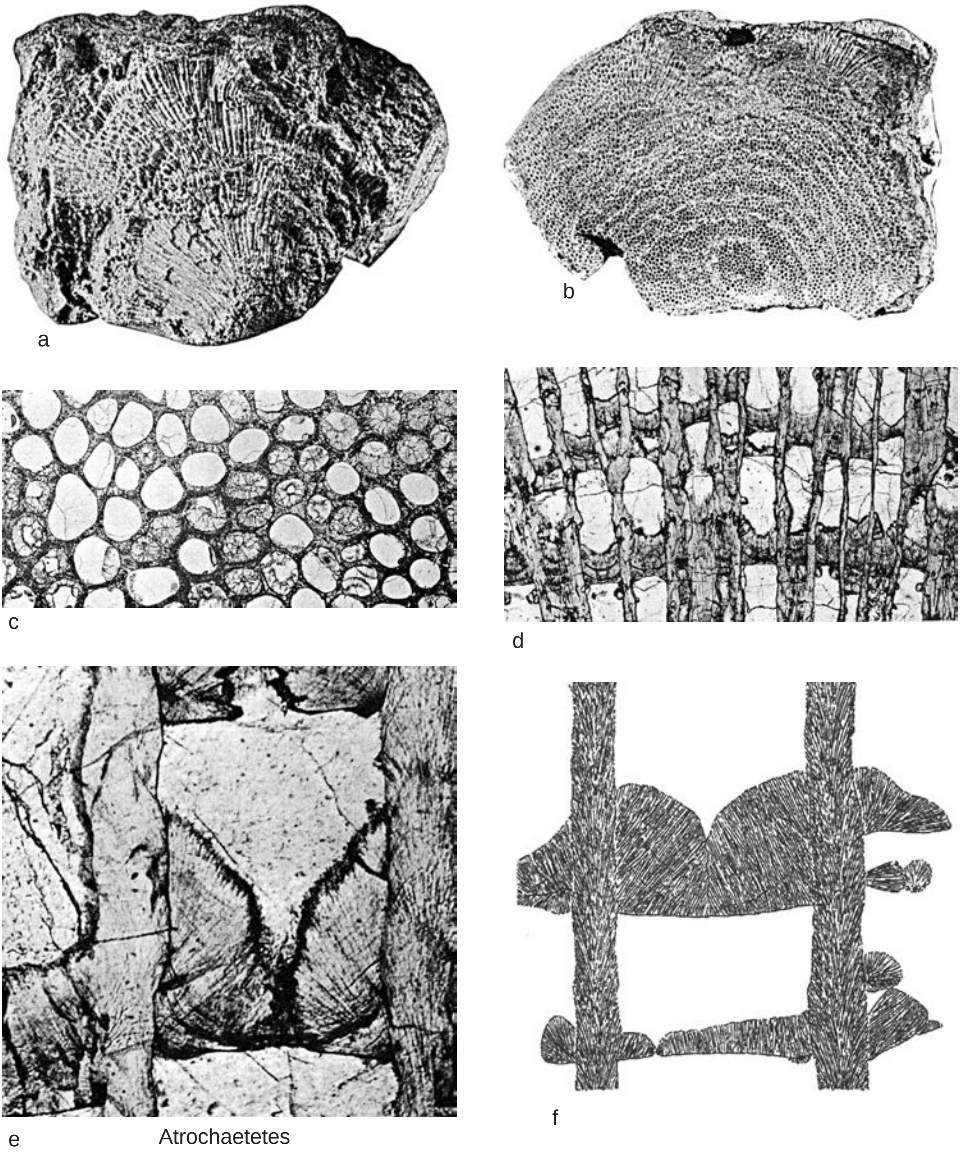


FIG. 186. Uncertain (p. 281–283).

p. 108 (type, *S. globosum*, OD); =*Circoporella* HAYASAKA, 1917, p. 57 (type, *C. semiclatharata,* OD); =*Plassenia* YABE & SUGIYAMA, 1931a, p. 113 (type, *P. alpina,* OD); =*Bekhmeia* HUDSON, 1954b, p. 48 (type, *B. wetzeli* HUDSON, 1954b, p. 49, OD)]. Burgundiid with ability to produce tabulae. Microstructure ranging from orthogonal to fascicular fibrous. Massive, nodular or dendroid gross morphology. Aquiferous units may possess tabulate oscula and/or astrorhizae (see WOOD, 1987). Type species is massive or nodular with vertical elements of 40–70 µm diameter; holotype from Portlandian, Upper Jurassic, Saone et Loire, Vers, France; type species distributed through upper Oxfordian–Hauterivian, France, Spain, Russia, and Japan. Another species, *B. ramosa* PFENDER, 1937, p. 133, has a coarse reticulum or normally short-branched vertical elements (pillars) of 50–90 µm diameter but no axial reticulum; synonyms are as follows: =*Burgundia ramosa* PFENDER, 1937,

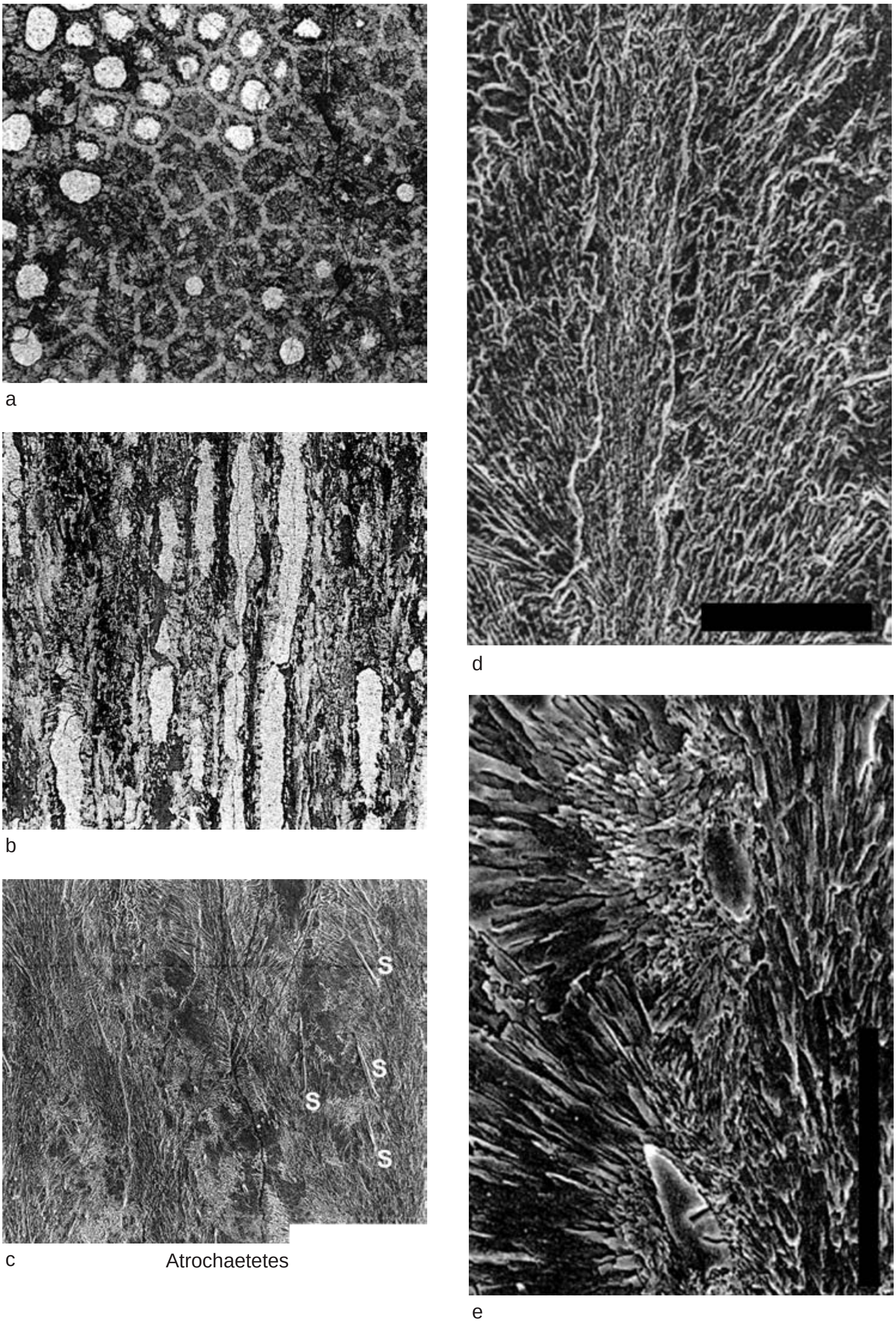


FIG. 187. Uncertain (p. 281–283).

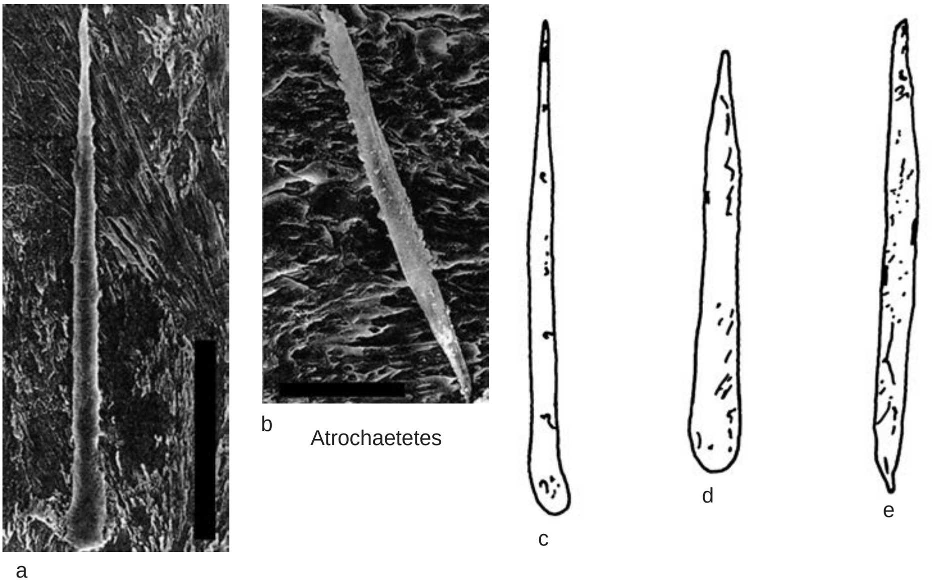


Fig. 188. Uncertain (p. 281–283).

p. 133; =*Burgundia campanae* Pfender, 1937, p. 135; =*Burgundia steinerae* Hudson, 1955c, p. 228; Fenninger, Flügel, & Hötzl, 1963, p. 235; =*Burgundia steinerae* Hudson, 1955c, p. 228; Fenninger & Hötzl, 1965, p. 40; =*Burgundia mammelonata* Fenninger & Hötzl, 1965, p. 40; =*Burgundia semiclathrata* (Hayasaka, 1917, p. 57); Turnšek & Masse, 1973, p. 237; =*Burgundia massiliensis* Turnšek & Masse, 1973, p. 237; =*Burgundia steinerae* Hudson, 1955c, p. 228; Dong & Wang, 1983, p. 417; this species extends from upper Oxfordian–Hauterivian, France, Spain, Syria, Iraq, and China. A third species, *B. wetzeli* (Hudson, 1954b, p. 49), is a nodular or dendroid *Burgundia* with an axial nonlaminate reticulum formed of tubules, and an outer laminate reticulum with simple unbranched pillars limited to one interlaminar space; and stacked astrorhizal systems with tabulate oscula; synonyms are as follows: =*Bekmeia wetzeli* Hudson, 1954b, p. 49; =*Burgundia wetzeli* Hudson, 1954b, p. 48; =*Burgundia wetzeli* Turnšek & Masse, 1973, p. 223; it occurs in the Hauterivian, France, Spain, and Iraq. *Upper Jurassic–Lower Cretaceous*: France, Spain, Syria, Iraq, Yemen, China, Russia, Japan.——Fig. 185*a–b*. **B. trinorchii*, light photomicrograph, Portlandian, Villereouse, France; *a,* longitudinal section, NHM no. 4044, ×15; *b,* transverse section, NHM no. 3594, ×20 (West & others, 2013).——Fig. 185*c–d. B. ramosa* Pfender, light photomicrograph, upper Oxfordian, Wadi Leeben, Sharwain Range, Qishn, Yemen; *c,* transverse section, NHM no. H 4615 a, ×15; *d,* upper Hauterivian, Cretaceous, La Mounine, Marseille, France; longitudinal section, NHM no. H 5486, ×30 (West & others, 2013).——Fig. 185*e–f. B. wetzeli* (Hudson), light photomicrograph, Hauterivian, Bekhme Gorge, Iraq; *e,* transverse section, NHM no. 4428 b, part of holotype, ×3; *f,* longitudinal section, NHM no. 4431, ×3 (West & others, 2013).

Family UNCERTAIN

Ronald R. West

Atrochaetetes Cuif & Fischer, 1974, p. 7 [**A. tamnifer* Cuif & Fischer, 1974, p. 8, fig. 2; pl. I,*1;* pl. II,*1–3;* pl. IV,*4–5*; OD; specimen is illustrated as holotype (unnumbered), and although not specified, it is assumed that specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN)]. Growth form domical to conical; tubules irregular polygons in transverse section; tubules continuous, subparallel in longitudinal section; tabulae subhorizontal, commonly thickened by fan-shaped deposit extending into tubules at junction of tabulae and tubule walls; penicillate aragonitic microstructure; tubules

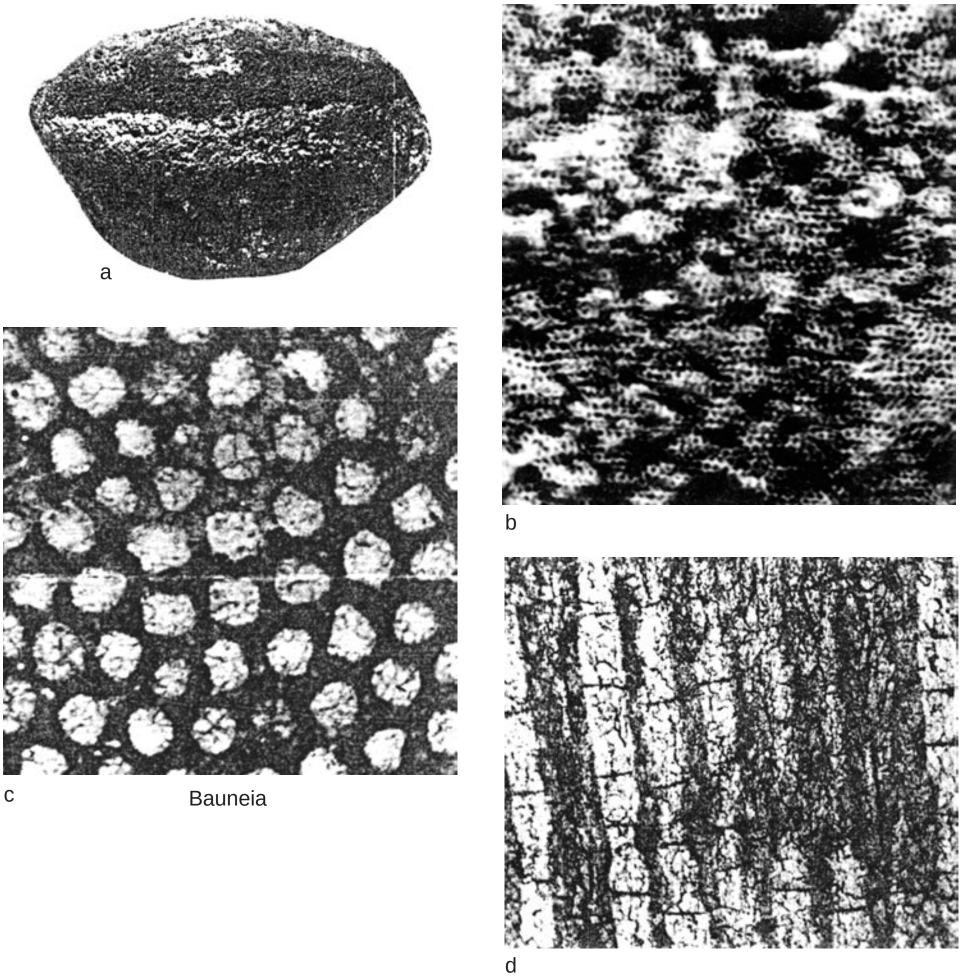


FIG. 189. Uncertain (p. 283–284).

increase commonly by intertubular budding, rarely longitudinal fission. Spicules and/or spicule pseudomorphs unknown from type species, but spicule pseudomorphs and additional information on the microstructure from three specimens of *A. alakirensis* CUIF & FISCHER (1974, p. 9–10) from the same stratigraphic and geographic locality as *A. tamnifer* are reported by CREMER (1995). *A. alakirensis*: growth form domical to conical with distinct growth bands associated with quasi-tabulae where tufts of crystal fibers (secondary wall) merge; true tabulae unknown; tubules polygonal to circular in transverse section of variable size; tubules long, subparallel in longitudinal section; aragonite inferred original mineralogy; primary tubule wall microstructure penicillate, water-jet (fascicular fibrous); secondary wall tufts of crystal fibers attached to primary tubule walls; tubules increase by intertubular budding and longitudinal fission; calcite monaxon tylostyle megasclere pseudomorphs in secondary wall, some attached to primary tubule wall, extending (pointed ends) into tubules; three types of monaxon tylostyle megascleres (2.4–15 µm wide and 53–292 µm long): short, thick (53–97 µm long), long, slender (110–292 µm), and rare oxes (58–80 µm long); microscleres unknown (CREMER, 1995, p. 166–170). *Upper Triassic (Carnian)–Upper Jurassic, ?Lower Cretaceous:* Turkey (Anatalya Region), *Carnian–Norian;* northwestern Turkey, *Upper Jurassic, ?Lower Cretaceous.*——FIG. 186*a–f.* **A. tamnifer*, Carnian, Triassic, Turkey, all images are from unnumbered holotype in the J. P. Cuif collection; *a,* lateral view of basal skeleton, ×0.8; *b,* polished surface of basal skeleton, ×0.85; *c,* transverse section, ×9; *d,* longitudinal section, ×7.5; *e,* longitudinal section showing microstructure and fan-shaped deposits at junction of tabulae and tubule walls, ×52; *f,* detailed drawing of microstructure of tubule walls and fibroradial deposits associated with some tabulae, compare with view *e,* ×55 (Cuif & Fischer, 1974, pl. I, fig. 1–2, *d,e;* pl. II, fig. 1, *c;* pl. IV, fig. 4–5, *a,b;*).——Fig. 187*a–e. A. alakirensis* Cuif & Fischer, Carnian–Norian, Anatalya Region, Turkey, Paleontological Institute, University of Erlangen–Nurnberg (IPE); *a,* transverse section of generally polygonal tubules, secondary walls (darker color) increase thickness of tubule walls, specimen 19F40, ×21; *b,* primary (light colored) and secondary (darker colored) tubule walls in longitudinal section, specimen 19F40, ×17.6; *c,* longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure and megascleres in secondary walls (*white S*), specimen 19F40, ×80; *d,* longitudinal section of primary (center) and secondary (both sides) tubule walls, specimen 19F40, ×317; *e,* longitudinal section of calcification centers of two areas in secondary tubule wall (tufts of crystal fibers), specimen 19F43, ×800 (Cremer, 1995, p. 168, pl. 25).——Fig. 188*a–e. A. alakirensis* Cuif & Fischer, Carnian–Norian, Anatalya Region, Turkey, Paleontological Institute, University of Erlangen–Nurnberg (IPE); *a,* typical tylostyle megasclere with knoblike rounded end, specimen 19F40, ×567; *b,* less common are oxea megasclere, pointed at both ends, specimen 19F43, ×900; *c–e,* diagrammatic sketches of three types of megascleres observed in this species, *c,* ×500, *d,* ×750, *e,* ×1000 (Cremer, 1995, p. 168, pl. 25).

Bauneia Peterhans, 1927, p. 389 [**Monotrypa multitabulata* Deninger, 1906, p. 63; M; Deninger Collection, University of Freiburg, Germany; =*Chaetetes capri* Angelis d'Ossat, 1905, p. 12, *fide* Fischer, 1970, p. 176, Royal Geological Museums (Rome or Naples)] [?=*Pseudomonotrypa* Reshetkin, 1926, p. 7, for two or more species from the Crimean Jurassic; see also Yavorsky, 1947, p. 22; Fischer (1970, p. 174) stated that no type species had been chosen, *fide* Hill, 1981, p. 519]. Growth form globular, nodular; tubules on upper surface felted, irregular polygons in transverse section; tubules long, subparallel in longitudinal section, divided by thin, irregularly spaced, subhorizontal tabulae; tubules increase by intertubular budding and longitudinal fission; penicillate, water-jet (fascicular fibrous) microstructure. [Spicules and/or spicule pseudomorphs are unknown in the type species, but Cremer (1995, p. 172–173) provided the following information on the spicules and the inferred aragonitic microstructure of a single specimen identified as ?*Bauneia* sp.: tubules subpolygonal to elliptical in transverse section; tubules increase by intertubular budding; microstructure of primary and secondary tubule walls penicillate, water-jet (fascicular fibrous) with secondary wall commonly filling tubules; calcite monaxon tylostyle megasclere pseudomorphs (82–140 µm long, 7–11 µm wide) without preferred arrangement in primary and secondary wall, most attached

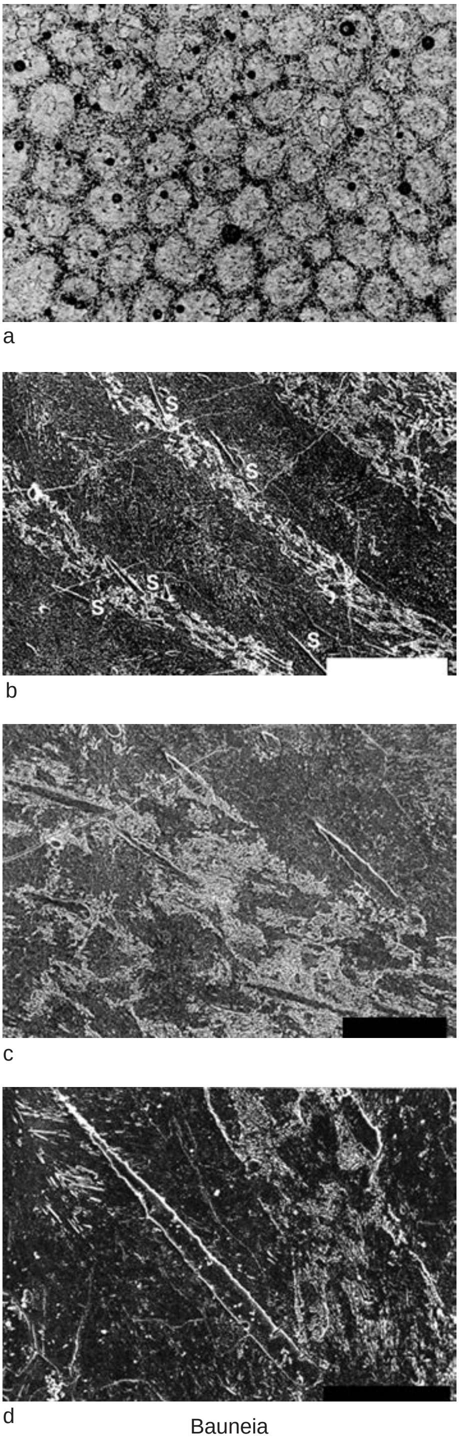


Fig. 190. Uncertain (p. 283–284).

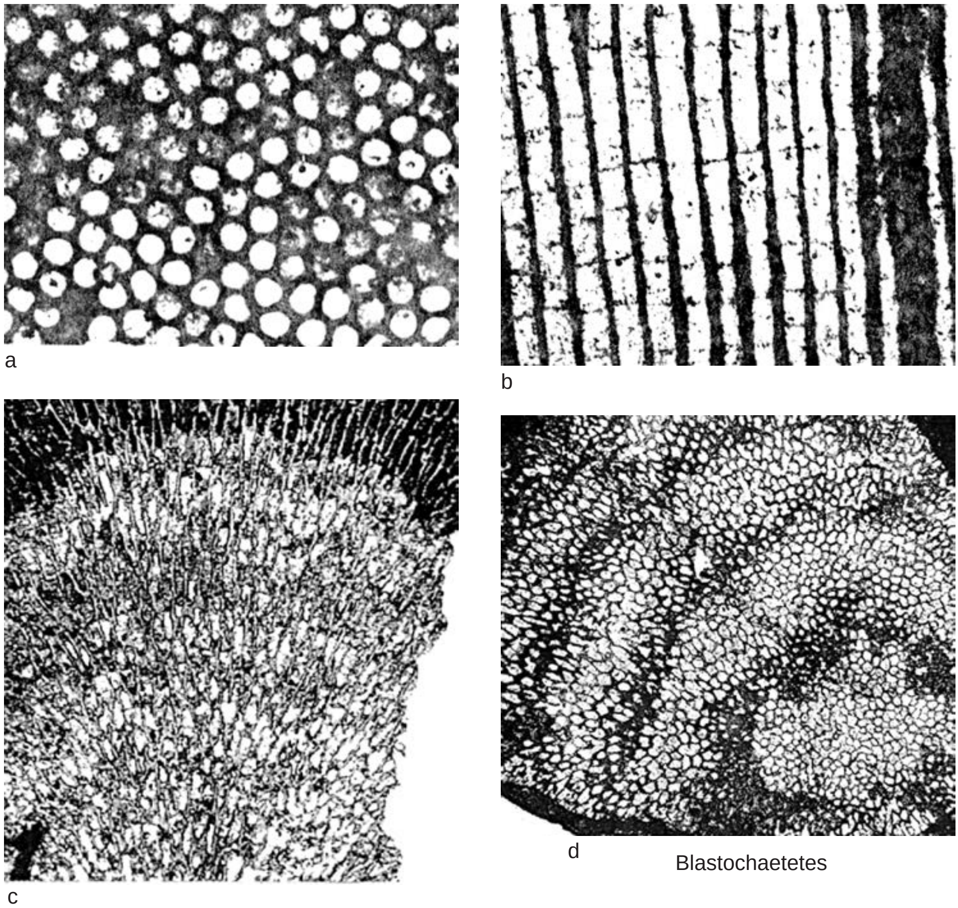


Fig. 191. Uncertain (p. 284–287).

via rounded end to, or in, primary wall; microscleres unknown.] *Triassic (Norian)–Upper Jurassic (Tithonian)*: Turkey (Anatolya), Oman, Tajikistan, *Norian*; Italy, Portugal, Czech Republic, *Oxfordian, Tithonian*.——Fig. 189*a–d*. **B. multitabulata* (Deninger), Tithonian, Italy; *a,* lateral view of basal skeleton, ×0.8; *b,* detail of external surface, ×4; *c,* transverse section, ×29; *d,* longitudinal section, ×25 (Peterhans, 1927, pl. X–XI).——Fig. 190*a–d*. ?*B.* sp. Norian, Turkey, Deninger Collection, University of Freiburg, Germany and the Royal Geological Museums (Rome or Naples); *a,* transverse section showing subpolygonal to elliptical tubules, 19E9/2c, ×19.5; *b,* longitudinal section showing spicular basal skeleton (*white S,* spicules), 19E9/2c, ×70; *c,* enlargement of part of view *b* showing tylostyle megascleres attached in primary wall (mottled area) of tubules, ×167; *d,* tylostyle megasclere in secondary wall of tubule with rounded end in primary wall of tubule, 19E9/2c, ×300 (Cremer, 1995, pl. 27).

Blastochaetetes Dietrich, 1919, p. 210 [**Chaetetes capilliformis* Michelin, 1844 in 1840–1847, p. 112; OD]. Growth form domical to columnar

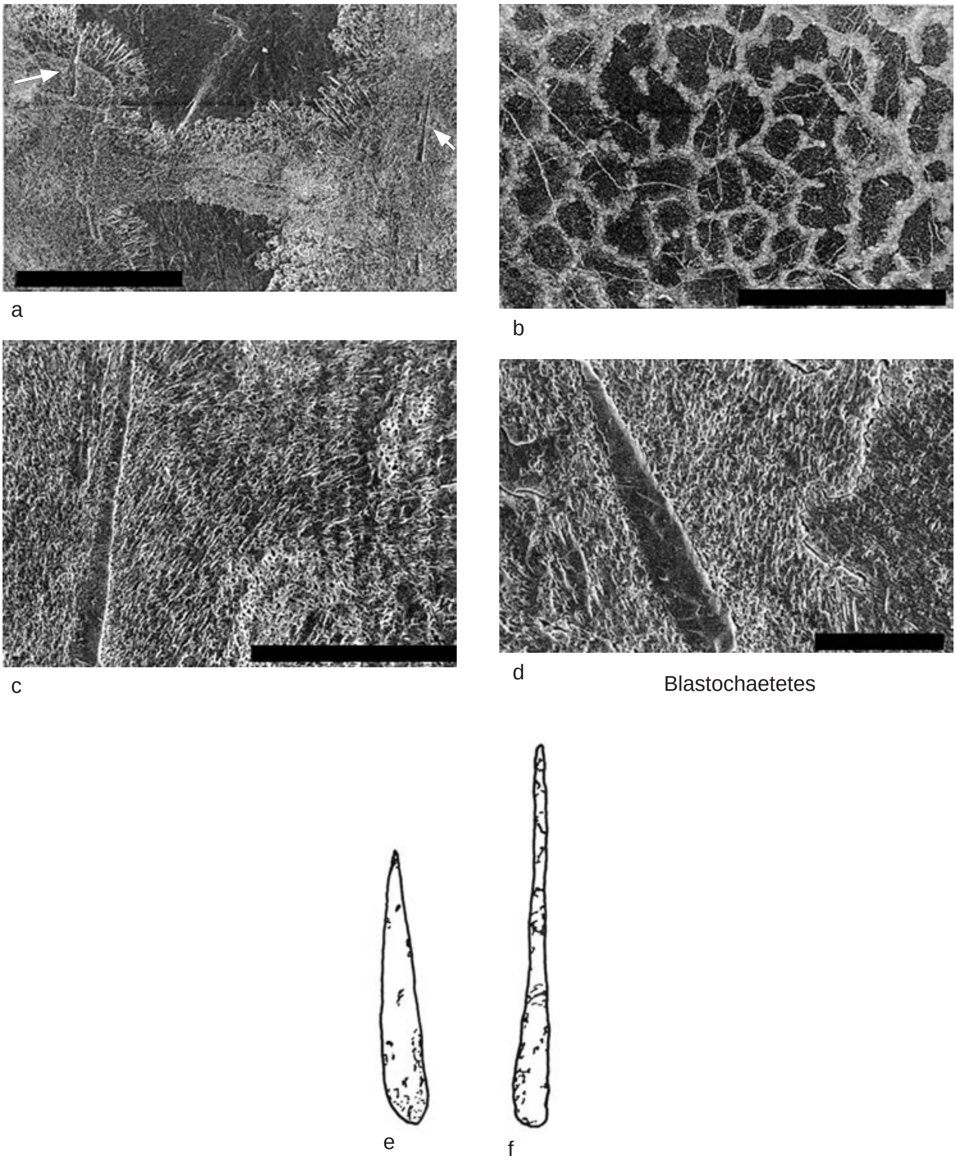


FIG. 192. Uncertain (p. 284–287).

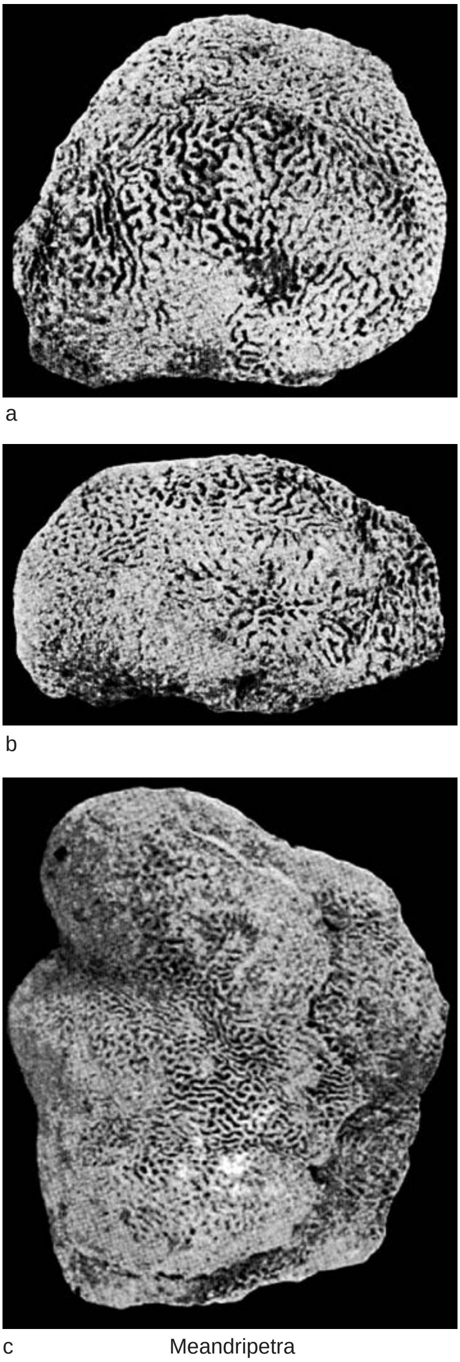


FIG. 193. Uncertain (p. 287–289).

(possible branching); tubules polygonal in transverse section, filled with drusy calcite; pseudosepta present; tubules long, diameter varies, imperforate; tabulae thin, horizontal or slightly tilted, irregularly placed; tubules increase by intertubular budding, rarely by longitudinal fission; aragonite or Mg calcite inferred original mineralogy. [Dietrich (1919) based his genus on specimens from the Oxfordian of Chatel-Censoir, Yonne, France, that he referred to Michelin's species; Dietrich's types were interpreted by Fischer (1970) as a new species of *Bauneia*, and if Dietrich's description of his specimens is taken as his designation of them as types, then *Blastochaetetes* would become a senior synonym of *Bauneia* Peterhans, 1927. However, Fischer recognized *Chaetetes capilliformis* Michelin, 1844 in 1840–1847, p. 112 (in Michelin Collection of the NMNH, Paris, Oxfordian, Jurassic, Saint Mihiel, Meuse, France) as the type specimen; *fide* Hill, 1981, p. 519. Whereas neither microstructure and spicules nor spicule pseudomorphs have been recognized in the type species, another species exhibits some of these details. Bizzarini and Braga (1978, p. 44–46) first described *Blastochaetetes dolomiticus* from the Carnian Dolomite Alps of Italy (holotype MIGUP no. 26064; paratypes MIGUP nos. 28=6065-66), and Cremer (1995, p. 170–172) provided a more complete diagnosis and description of *B. dolomiticus*, based on specimens from the Norian of Turkey, in the Cremer collection in the Paleontological Institute, University of Erlangen-Nurnberg, IPE): growth form domical to conical, growth bands distinct; in transverse section, tubules irregular polygons, vary in size and shape with pseudsepta; tubule walls with knoblike thickenings in longitudinal section; tabulae frequent, plain to concave, often with thickened margins, irregularly spaced; tubules increase by intertubular budding and longitudinal fission; primary wall layer penicillate, water-jet (fascicular fibrous) microstructure; secondary wall layer thin, epitaxial fibrous calcite; calcite pseudomorph tylostyle megascleres (49–109 µm long) long, slender, and short, club shaped in both primary and secondary wall layers, lacking preferred orientation; microscleres unknown (description adapted from Cremer, 1995, p. 170–172).] *Triassic (Carnian)–Upper Cretaceous:* Italy, Turkey, *Carnian–Norian*; France, Italy, Spain, *Jurassic (Tithonian)–Upper Cretaceous.*——FIG. 191*a–b.* **B. capilliformis* (Michelin), Tithonian, France, unnumbered specimens; *a,* transverse section of basal skeleton, ×20; *b,* longitudinal section of basal skeleton, ×20 (Peterhans, 1929b, pl. VI).——FIG. 191*c–d. B. dolomiticus* Bizzarini & Braga, Norian, Tilkideligi Tepe and B., Alankoyu, Turkey; *c,* longitudinal section of basal skeleton, specimen TTR/1a, ×3.8; *d,* transverse section of basal skeleton, specimen TTM12, ×2.6 (Cremer,

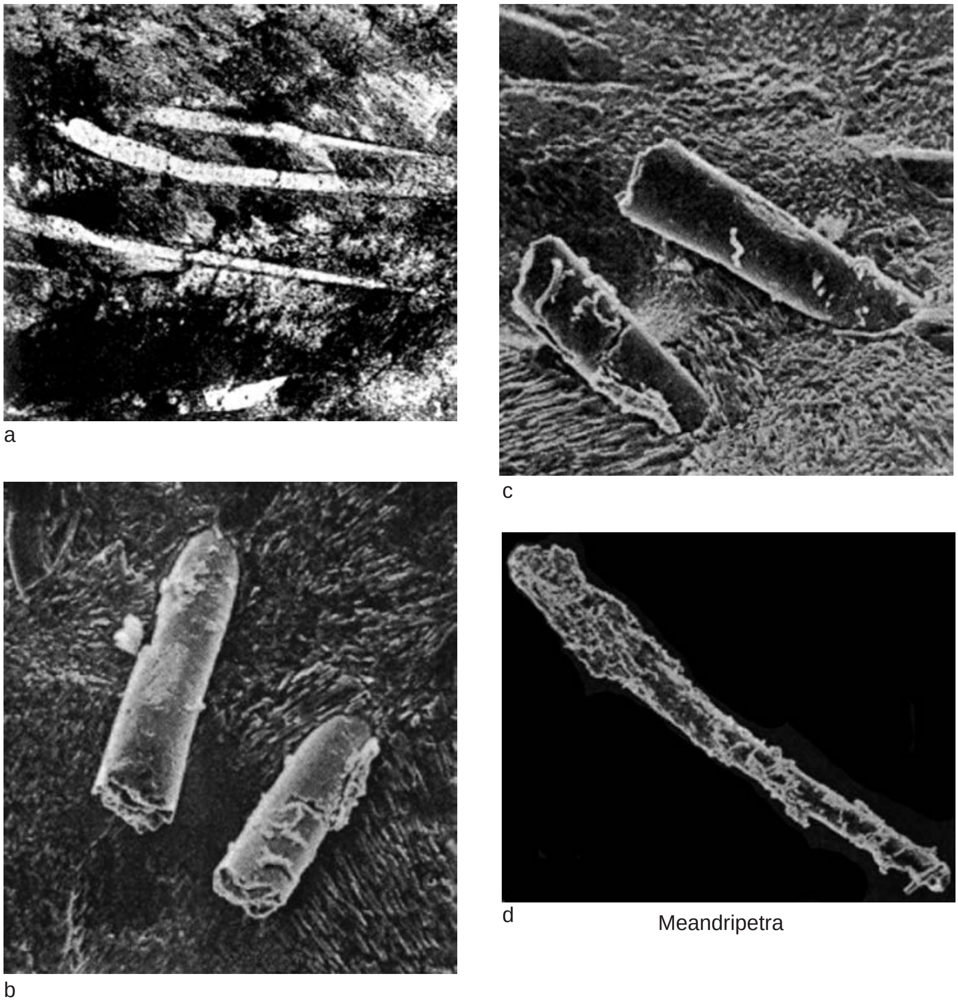


FIG. 194. Uncertain (p. 287–289).

1995, p. 170, pl. 26).——FIG. 192*a–f. B. dolomiticus* BIZZARINI & BRAGA, Norian, Tilkideligi Tepe and B., Alankoyu, Turkey; *a,* tabula between tubule walls, *white arrows* indicate tylostyle megascleres embedded in primary wall of specimen TTR/1a, ×130; *b,* irregular tubule shape and pseudosepta in transverse section of specimen TTH12, ×16.5; *c,* penicillate, water-jet (fascicular fibrous) microstructure of primary tubule walls, with embedded slender, tylostyle megasclere, ×400; *d,* unnumbered specimen with short clublike tylostyle megasclere, ×900; *e–f,* diagrammatic sketches of tylostyle megascleres from an unnumbered specimen, ×750, ×675 (Cremer, 1995, p. 170, pl. 26).

Meandripetra DIECI & others, 1977, p. 232 [**M. zardinii*; OD; holotype 19094, paratype 19095; Zardini Collection, IPUM]. Growth domical to fungiform; tubules meandroid on upper surface; short, lamellate distal processes; in longitudinal section, tubules filled with secondary calcite deposits, except distal 2–3 mm; tubules increase by longitudinal fission; aragonitic penicillate, water-jet (fascicular fibrous) microstructure; straight to slightly curved tylostyle megascleres occur as pseudomorphs, some of pyrite, and molds; microscleres unknown. *Triassic (Carnian):* Italy.——FIG. 193*a–c.* **M. zardinii*, Cassian Formation, Alpe di Specie, near Cortina d'Ampezzo, northern

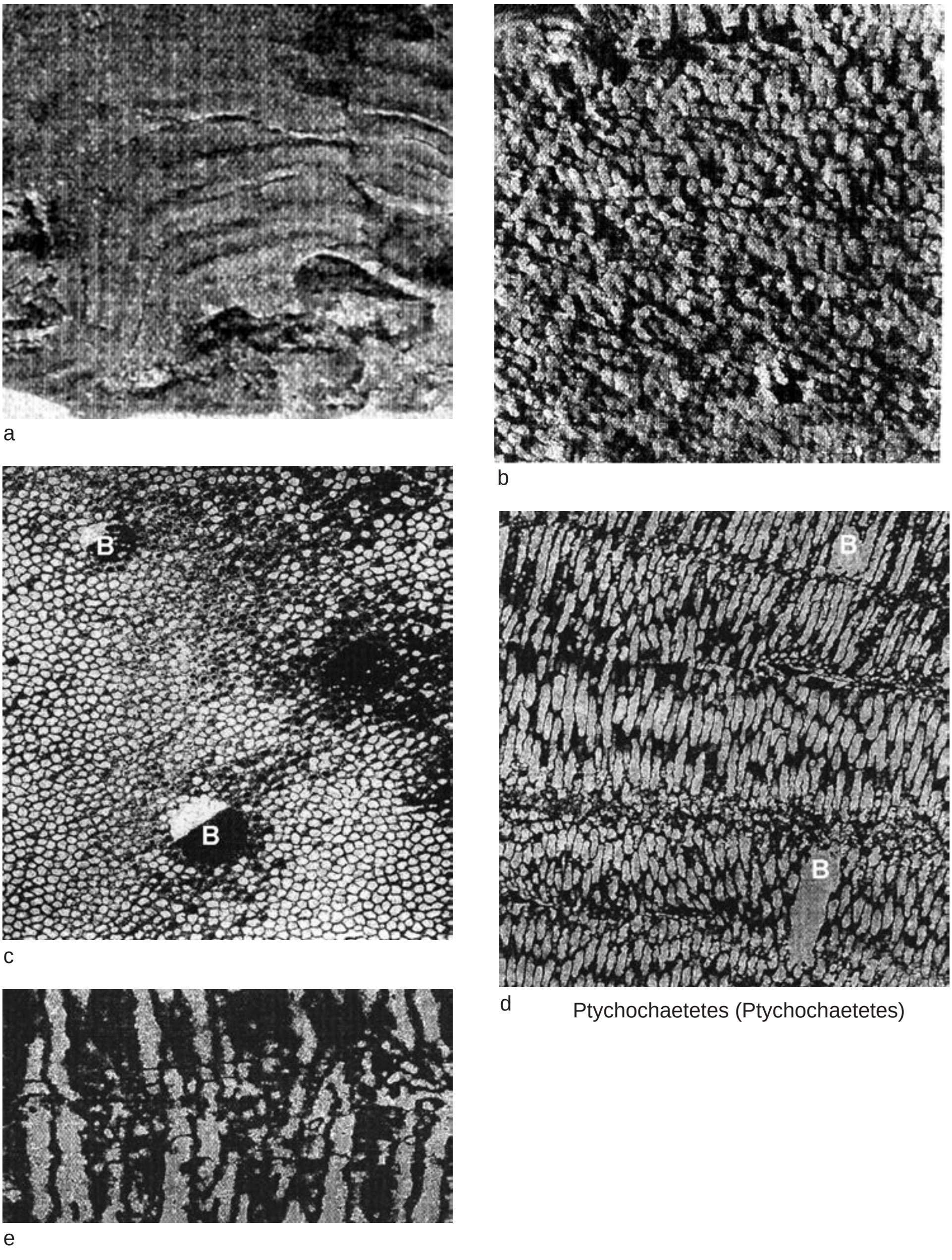


FIG. 195. Uncertain (p. 289–291).

Italy; *a,* holotype, upper surface of basal skeleton, IPUM 19094, ×2.5; *b,* holotype, lateral view of basal skeleton, IPUM 19094, ×2.5; *c,* paratype, upper surface of basal skeleton, IPUM 19095, ×1.9 (Dieci & others, 1977, pl. 1–3).——FIG. 194*a–d.* **M. zardinii*, Cassian Formation, Alpe di Specie, near Cortina d'Ampezzo, northern Italy; *a,* paratype, straight to slightly curved tylostyle megascleres in thin section, IPUM 19095, ×110; *b,* paratype, pyritic pseudomorphs of tylostyle megascleres in penicillate, water-jet (fascicular fibrous) microstructure of tubule walls, IPUM 19095, ×500; *c,* paratype, pyritic pseudomorphs of tylostyle megascleres in tubule walls, IPUM 19095, ×500; *d,* paratype, isolated pyritized pseudomorph of slightly curved, encrusted tylostyle megasclere, IPUM 19095, ×170 (Dieci & others, 1977, pl. 1–3).

Ptychochaetetes KOECHLIN, 1947, p. 4 [**P. ramosus* KOECHLIN, 1947, p. 4–6, pl. 1,*1–2,* pl. 2,*1–4;* OD]. Growth form laminar to low domical with distinct interruption partings; tubules of compacted granular calcite; tubules rounded polygons in transverse section with large openings, inferred borings, partially filled with calcite; pseudosepta present; tubules elongate, slightly curved in longitudinal section; tabulae thin, more or less at same level in adjacent tubules; tubule walls with and without pores, composed of radial fibers; tubules increase by longitudinal fission and intertubular budding. [Spicules and/or spicule pseudomorphs are not known from the type species, *P. ramosus*, but TERMIER and TERMIER (1976) documented pyrite pseudomorphs of monaxon tylostyle megascleres, the primary and secondary tubule walls, and the thin tabulae in a Kimmeridgian specimen of *Ptychochaetetes* sp. from Spain. CREMER (1995) also documented the microstructure and calcite pseudomorphs of tylostyle monaxon megascleres in a Triassic specimen of *Ptychochaetetes* sp. from Turkey: long, slender to club-shaped tylostyles (77–192 µm long, 7–11 µm wide) usually in secondary wall, but may be in, or attached to, the primary wall; microscleres unknown; and microstructure of both walls penicillate, water-jet (fascicular fibrous), inferred to be aragonite; quasi-tabulae formed by thickened secondary walls at level of tabulae. *Triassic (Norian)–Miocene (Burdigalian):* Turkey (Tilkideligi Tepe), Tajikistan, *Norian*; Austria, Portugal, Switzerland, Spain, *Jurassic (Kimmeridgian);* France (l'Ain), *Miocene (Burdigalian).*

Ptychochaetetes (Ptychochaetetes). Description as for genus. *Triassic (Norian)–Jurassic (Kimmeridgian):* Turkey (Tilkideligi Tepe), Tajikistan, *Norian*; Austria, Portugal, Switzerland, Spain, *Kimmeridgian.*——FIG. 195*a–e.* **P. (P.) ramosus*, type specimens in Naturhistorisches Museum, Basel, Kimmeridgian, Switzerland; *a,* holotype, general laminar growth form, NMB A 390, ×1.5 (note: vertical lines are not part of the specimen); *b,* holotype, corroded granular calcite tubules on upper surface, NMB A 390, ×7.3; *c,* tangential section, nearly transverse,

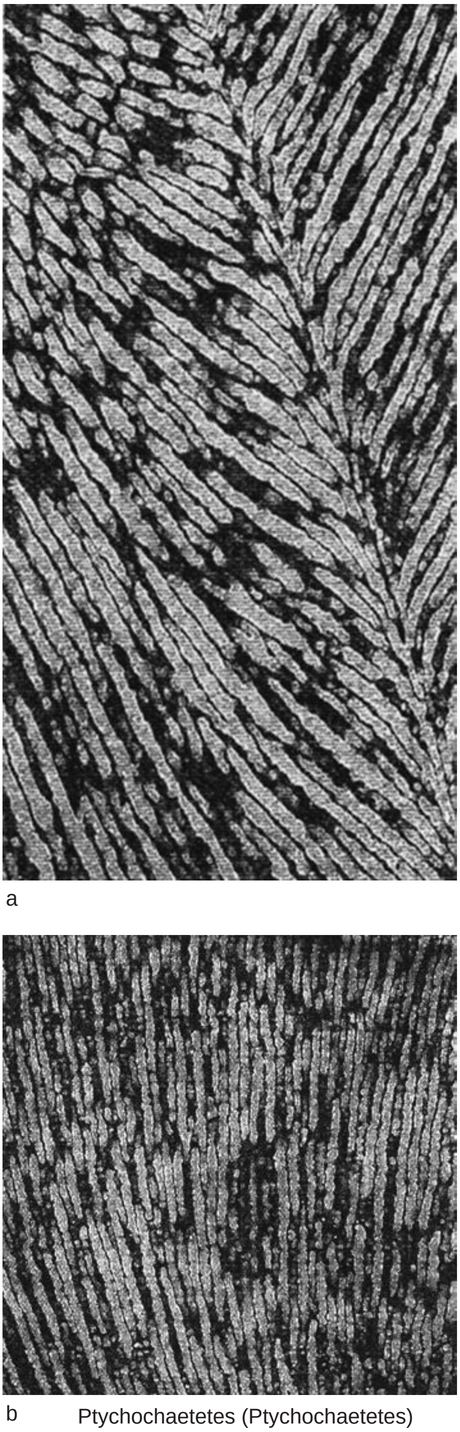
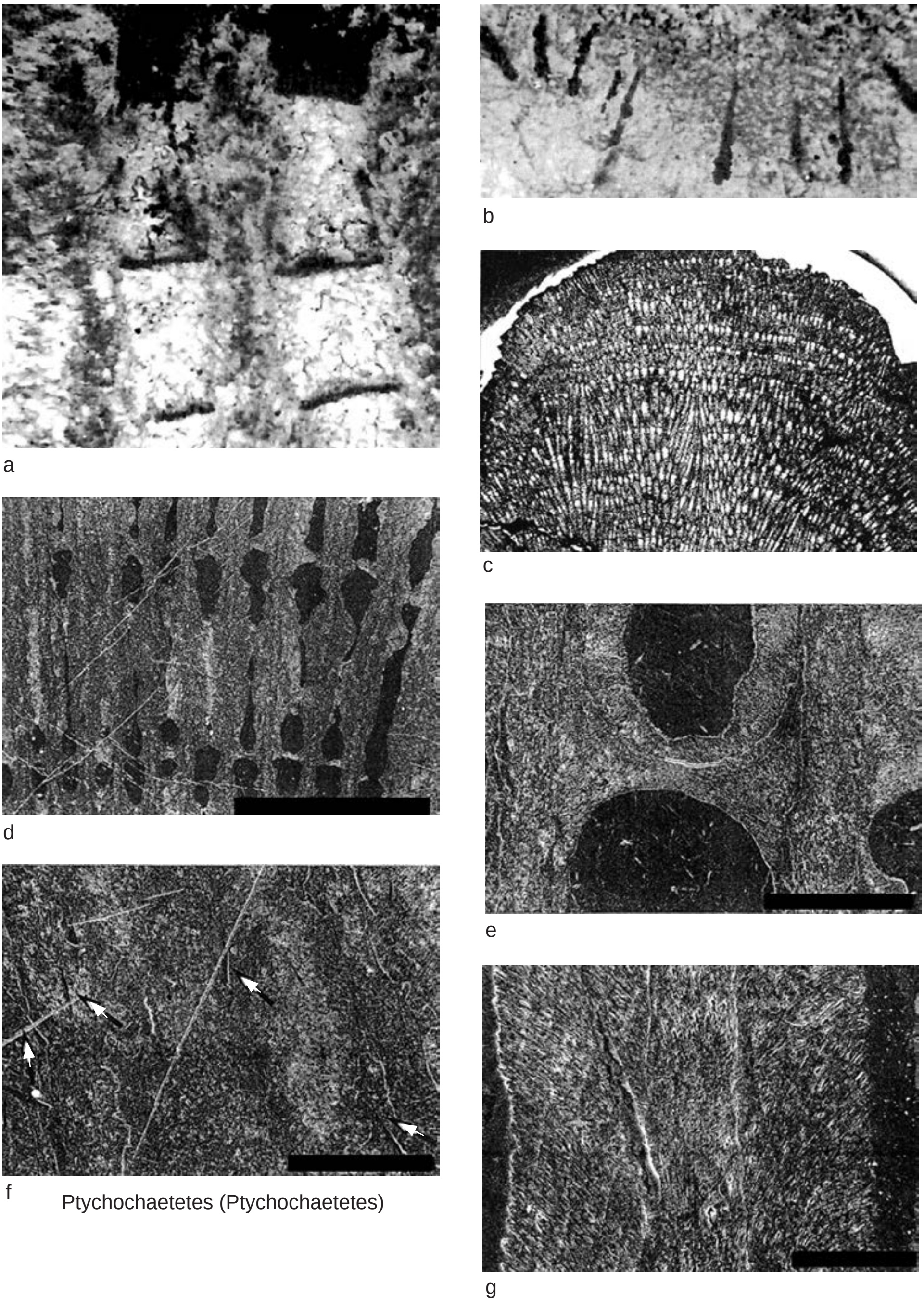


FIG. 196. Uncertain (p. 289–291).



Ptychochaetetes (Ptychochaetetes)

FIG. 197. Uncertain (p. 289–291).

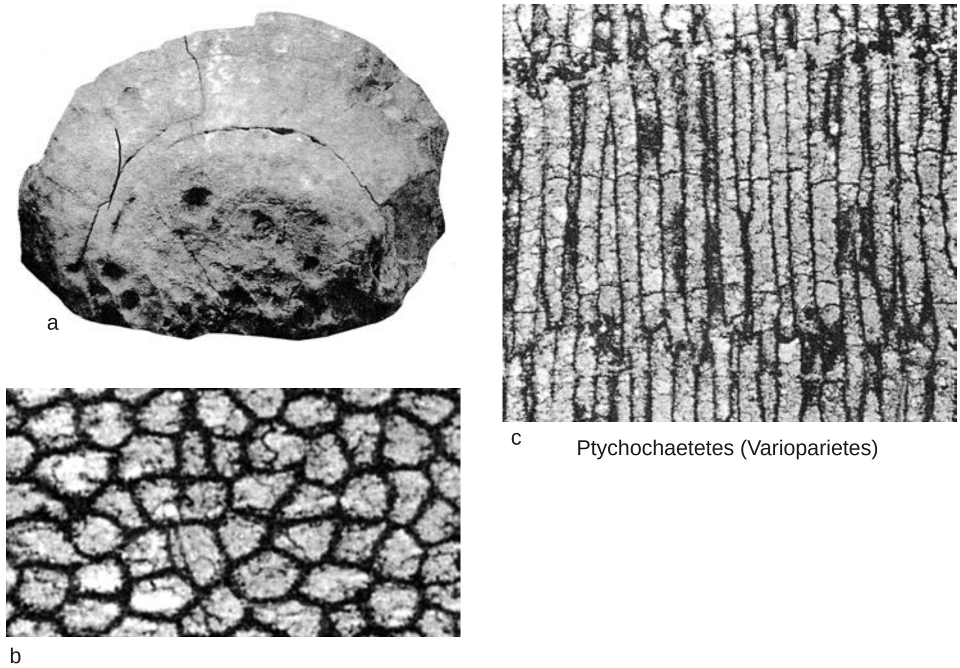


Fig. 198. Uncertain (p. 289–291).

showing cross sectional shape of tubules; note large holes partially filled (geopetal) with calcite (*white B*), possibly borings, ×7.5; *d,* second nondesignated type specimen (invalidly named a type species) in a slightly oblique section shows tubules and what appear to be growth interruptions and possible borings (*white B*), ×6.4; *e,* enlargement of longitudinal section of another type specimen (invalidly named as type species) showing irregularities in tubules at apparent growth interruptions, ×42 (Koechlin, 1947, pl. 1–2).——Fig. 196*a–b.* **P. (P.) ramosus*, other type specimens in Naturhistorisches Museum, Basel, Kimmeridgian, Switzerland; *a,* longitudinal section showing apparent branching of tubules as result of oblique contact during growth, ×7.5; *b,* longitudinal section of elongate, curved tubules, ×7.9 (Koechlin, 1947, pl. 1–2).——Fig. 197*a–b. P. (P.)* sp. Termier & Termier, Kimmeridgian, Jabaloyes, Spain; *a,* enlargement of specimen in longitudinal section, ×79; *b,* iron oxide pseudomorphs of monaxon tylostyle megascleres near upper surface of another specimen, ×179 (Termier & Termier, 1976, pl. 1).——Fig. 197*c–g. P. (P.)* sp. Cremer, Norian, Tilkideligi Tepe, Turkey; *c,* longitudinal section of domical form, TTR20 specimen in Cremer collection in Erlangen, Germany (IPE), ×1.9; *d,* longitudinal section of tubules with tabulae at same level in adjacent tubules, TTR20, ×16; *e,* longitudinal section of primary tubule walls and secondary basal skeleton, TTR20, ×120; *f,* tylostyle megascleres (*white arrows*) embedded in both primary tubule walls and secondary basal skeleton, TTR20, ×105; *g,* tylostyle megasclere attached to penicillate, water-jet (fascicular fibrous, clinogonal) primary wall of tubule; note the microstructure of primary wall and secondary basal skeleton are the same, TTR20, ×300 (Cremer, 1995, pl. 26–27).

Ptychochaetetes (Varioparietes) Bodergat, 1975, p. 293 [**P. (V.) resurgens;* OD; Department of Earth Sciences, Claude-Bernard University, Lyon, France, collection no. 5 090 26 192 02]. Growth form domical; tubules in transverse section irregular polygons with pseudosepta; tubules long, subparallel with thin tabule at more or less the same level in adjacent tubules. *Miocene (Burdigalian):* France (l'Ain).——Fig. 198*a–c.* **P. (V.) resurgens*; *a,* lower surface of basal skeleton, holotype, no. FSL 171 000, ×0.4; *b–c,* paratype, no. FSL 171 007; *b,* transverse section, ×67; *c,* longitudinal section, ×30 (Bodergat, 1975, pl. 27–28).

ACKNOWLEDGMENTS

Ronald R. West

Over the years, numerous individuals from many parts of the world have contributed to my efforts to learn more about

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HYPERCALCIFIED EXTANT CALCAREA: SYSTEMATIC DESCRIPTIONS

Jean Vacelet

Class CALCAREA Bowerbank, 1864

[Calcarea Bowerbank, 1864, p. 160] [=Calcispongia de Blainville, 1830, p. 494]

Marine Porifera exhibiting mineral skeleton composed entirely of calcium carbonate. Skeleton represented by free diactine, triactine, tetractine spicules, that may be combined with a solid basal calcitic skeleton or basal spicules, either cemented together or completely embedded in an enveloping calcareous cement. Aquiferous system may be asconoid, syconoid, sylleibid, or leuconoid. Members of the Calcarea are viviparous, and their larvae are blastulae (diagnosis modified from Manuel & others, 2002, p. 1103). [The calcitic sponges exhibit monocrystalline calcareous spicules and have been grouped previously in either the Calcarea or the Calcispongia. The Calcispongia was a name proposed by de Blainville (1830) for a genus, and then other early workers (e.g., Johnston, 1842; Haeckel, 1872) adopted it for wider use in recognizing the entire higher level subdivision of the group. Much later, Manuel and others (2002, p. 1103), in their major *Systema Porifera* project overview of this higher level subdivision employing Calcispongia and Calcarea, recognized that, through the 20th century, the preferred usage of these two names was the Calcarea. Also, some doubt existed about the validity of the taxonomic name Calcispongia, and that it should continue to be used as a class-level taxon, given that de Blainville (1830) and other 19th century workers had recognized the original genus as a synonym of *Grantia* Fleming, 1828a. Nevertheless, Manuel and others (2003, p. 311), and Manuel (2006, p. 226) have recently proposed a two-fold subdivision of the two group names: that Calcispongia be retained as the crown-based clade name, and Calcarea be employed for the stem-based clade. Manuel's (2006, p. 226) suggestions are to reserve the name Calcispongia for the crown group, including the living calcareous sponge representatives and probably most, if not all, of their extinct relatives, and to employ the Calcarea for members of the stem group, which comprises not only all the representatives of the Calcispongia but also the exclusively Paleozoic Heteractinida Hinde, 1887 (Cambrian–Permian). These proposals have not yet been considered for general approval of sponge workers and to be ratified or formally abandoned. In the meantime, all calcareous sponges are described herein as being exclusively calcareans; they comprise a confirmed Mesozoic to Recent record, plus a doubtful earlier (Carboniferous–Permian) record, based on a few scattered, poorly documented occurrences (see Finks & Rigby, 2004d), and the possibly early Cambrian genus *Gravestockia* Reitner, 1992, which should be included in the class, because it has a "rigid skeleton of tetractine desmas" (Finks & Rigby, 2004d, p. 758). Class Calcarea is subdivided into two subclasses, Calcinea and Calcaronea, based on several independent characters. This subdivision has been recently confirmed by molecular characters (Voigt, Wülfing, & Wörheide, 2012).] *?Cambrian, ?Carboniferous, ?Permian, ?Jurassic, Cretaceous–Holocene.*

Subclass CALCINEA Bidder, 1898

[Calcinea Bidder, 1898, p. 73]

Calcarea with a regular (equiangular and equiradiate) or exceptionally parasagittal or sagittal triactines and/or a basal system of tetractines. In addition to the free spicules, there may be a nonspicular basal calcareous skeleton. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinucleate with spherical nuclei. Basal body of flagellum is not adjacent to nucleus. Calcinea incubate coeloblastula larvae (MANUEL & others, 2002, p. 1109). *Holocene*.

Order MURRAYONIDA Vacelet, 1981

[Murrayonida VACELET, 1981, p. 314]

Calcinea with reinforced skeleton consisting of a rigid network of calcite, of calcareous plates, or of spicule tracts generally composed of diapason triactines. Canal system leuconoid (VACELET & others, 2002a, p. 1153). [The order is comprised of three monotypic families, one of which, Lelapiellidae BOROJEVIC, BOURY-ESNAULT, & VACELET (1990), is not hypercalcified. There is no fossil record for this order.] *Holocene*.

Family MURRAYONIDAE Dendy & Row, 1913

[Murrayonidae DENDY & ROW, 1913, p. 741]

Murrayonida in which the basal skeleton is composed of a rigid, calcareous, aspicular network. Cortex composed chiefly of overlapping calcareous scales in oscular zone, and of small triactines in pore zone. Choanosomal skeleton including free diapason triactines (VACELET & others, 2002a, p. 1153). *Holocene*.

Murrayona KIRKPATRICK, 1910b, p. 127 [**M. phanolepis;* M; holotype, NHM 1937.8.6.1]. Diagnosis as for family. Type species is globular, pyriform, or lamellate. Consistency hard, stony. Color white. Lamellate specimens with a distinct inhalant and exhalant surface, globular ones with special, generally equatorial, inhalant areas. Cortical skeleton of inhalant areas made up of a tangential reticulation of triactines. Exhalant surfaces covered by scales originating from equiangular triactines. Diapason triactines isolated under the scales, not building tracts. Osculum surrounded by circlet of special triactines with long lateral actines. Basal skeleton reticulate, with meandroid structure, made up of fused, irregularly shaped, calcitic sclerodermites with vague clinogonal microstructure, generally without entrapped spicules. Aquiferous system leuconoid with basinucleated choanocytes. Embryo of blastula type (VACELET & others, 2002a). A single species, recorded from underwater caves and deep fore reef of Eastern Indian Ocean (Christmas Island) and Western and Central Pacific, 2–83 m depth. Meandroid structure of basal skeleton resembles stromatoporoid organization. Skeleton may be able to fossilize, but no fossil representative has yet been recognized (REITNER, 1992). *Holocene*: Eastern Indian Ocean, Western and Central Pacific.——FIG. 199*a–f*. **M. phanolepis,* Moorea, Central Pacific; *a*, view of specimen with living tissue (Vacelet, 1977a); *b*, SEM view of fracture of skeleton of another specimen near surface (top); *c*, SEM view of surface of skeleton on exhalant face, with trace of an osculum and a trapped superficial scale; *d*, SEM view of surface of skeleton on inhalant face; *e*, SEM view of microstructure on a fracture; *f*, calcareous scale (Vacelet, 2012); see also Fig. 3,*1*, herein, with diagrammatic section through a lamellar specimen of *M. phanolepis*, with inhalant face on left and inhalant one on right (Borojevic, Boury-Esnault, & Vacelet, 1990).

Family PARAMURRAYONIDAE Vacelet, 1967

[Paramurrayonidae VACELET, 1967a, p. 49]

Murrayonida with choanosomal skeleton made up of fascicles of diapason triactines without any rigid structure. Cortical skeleton composed chiefly of superficial layer of overlapping calcareous scales and internal layer of free calcareous plates. [Paramurrayonidae differs from Murrayonidae mainly by the absence of a rigid aspicular skeleton, which is replaced by a cortical layer of calcareous plates. Such a cortical skeleton is slightly reminiscent of the external skeleton found in fossil and Recent sphinctozoans. However, the plates are not fused but simply loosely joined by organic material, forming a nonfossilizable skeleton, and the body is not segmented (VACELET & others, 2002a, p. 1154).] *Holocene*.

Paramurrayona VACELET, 1967a, p. 49 [**P. corticata;* M; holotype, MNHN C1968-153]. Diagnosis as for family. Type species encrusting, roughly circular, 2–5 mm in diameter, 0.5 mm thick. Color brown, with a glistening, smooth surface. Surface covered with a layer of overlapping oval scales, 150–400 µm in maximum diameter, deriving from triactines. Underlying layer of

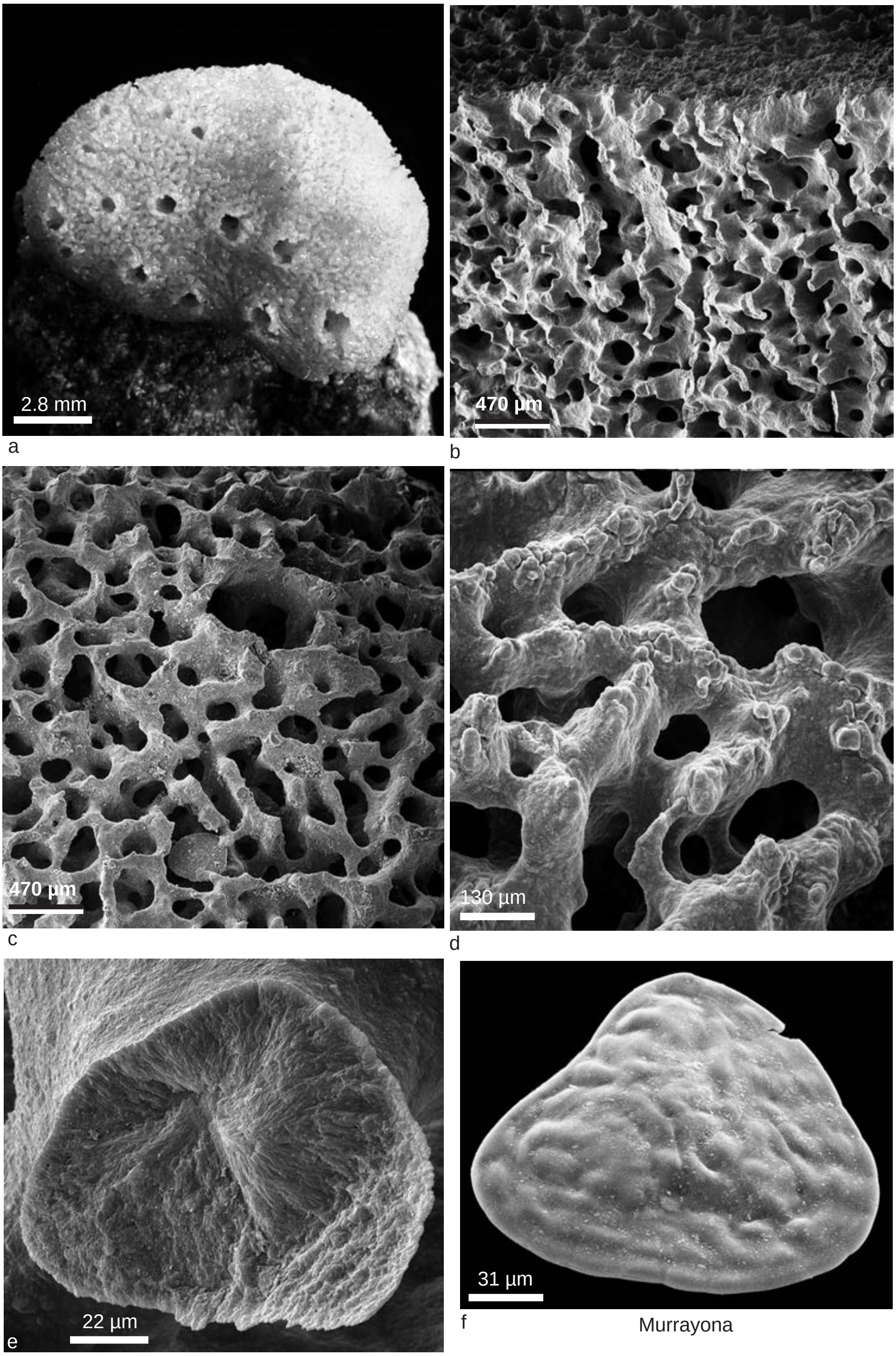

FIG. 199. Murrayonidae (p. 294).

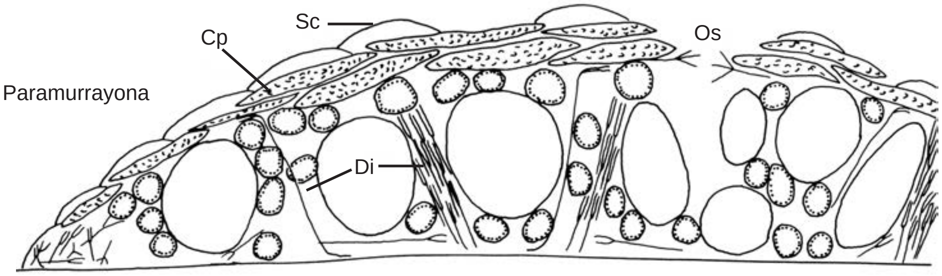

FIG. 200. Paramurrayonidae (p. 294–296).

calcitic plates, mostly rectangular, up to 1 mm in length and 50–100 µm thick. Choanosomal skeleton composed exclusively of diapason triactines, generally disposed in fascicles. Osculum 250 µm in diameter, approximately central in a zone devoid of scales and plates, surrounded by a circlet of special tetractines. Inhalant areas presumably located at periphery of sponge, where a few triactines, diapasons, and tetractines are localized. Aquiferous system leuconoid with basinucleated choanocytes. Embryo of blastula type. A single species, recorded from underwater caves and microcavities of coral reefs in Indian Ocean (Madagascar), Pacific Ocean (New Caledonia) and Caribbean (Jamaica) (VACELET & others, 2002a). *Holocene:* Indian Ocean, Western Pacific, and Caribbean.——FIG. 200. **P. corticata,* diagrammatic section; *Di,* diapason triactines, single or in tracts; *Cp,* calcareous plates; *Os,* osculum; *Sc,* calcareous scales (Vacelet, 1967a).

Subclass CALCARONEA
Bidder, 1898

[Calcaronea BIDDER, 1898, p. 73]

Calcarea with diactines and/or sagittal triactines and tetractines, rarely also with regular spicules. In addition to free spicules, there may be a rigid basal skeleton, nonspicular or spicular (with spicules cemented together or completely embedded in an enveloping calcareous cement). In ontogeny, first spicules to be produced are diactines in settled larva. Choanocytes are apinucleate, and basal system of flagellum is adjacent to apical region of nucleus. Calcaronea incubate amphiblastula larvae (description modified from MANUEL & others, 2002, p. 1109). *?Jurassic, Cretaceous–Holocene.*

Order LITHONIDA
Vacelet, 1981

[Lithonida VACELET, 1981, p. 315] [=*Stereina* DE LAUBENFELS, 1955, p. 99, *partim*]

Calcaronea with reinforced skeleton consisting of linked or cemented basal actines or tetractines. Diapason spicules generally present. Canal system leuconoid (description modified from VACELET & others, 2002b). [VACELET (1981, p. 315) proposed the order Lithonida to include the calcaronean families Petrobionidae and Lepidoleuconidae, based on the subfamily Lithoninae DÖDERLEIN, 1898. However, the Lepidoleuconidae was transferred to Baerida by BOROJEVIC, BOURY-ESNAULT, and VACELET (2000), and the Petrobionidae subsequently transferred also to the Baerida (MANUEL & others, 2003) and herein.] *?Jurassic, Cretaceous–Holocene.*

Family MINCHINELLIDAE
Dendy & Row, 1913

[Minchinellidae DENDY & ROW, 1913, p. 739] [=Porosphaeridae DE LAUBENFELS, 1955, p. 99, *partim*; =Bactronellidae DE LAUBENFELS, 1955, p. 100, *partim*]

Basal skeleton consisting of a network of tetractines cemented or linked together by their basal actines, which are linked by zygosis of irregularly curved or expanded ends. Linkage either a complex zygosis, often reinforced by a calcareous cement of variable development that can completely embed whole network, or a simple entanglement. Microstructure of cement of orthogonal type. Superficial skeleton made of free spicules, mostly tangentially disposed in dermal membrane, generally including diapasons.

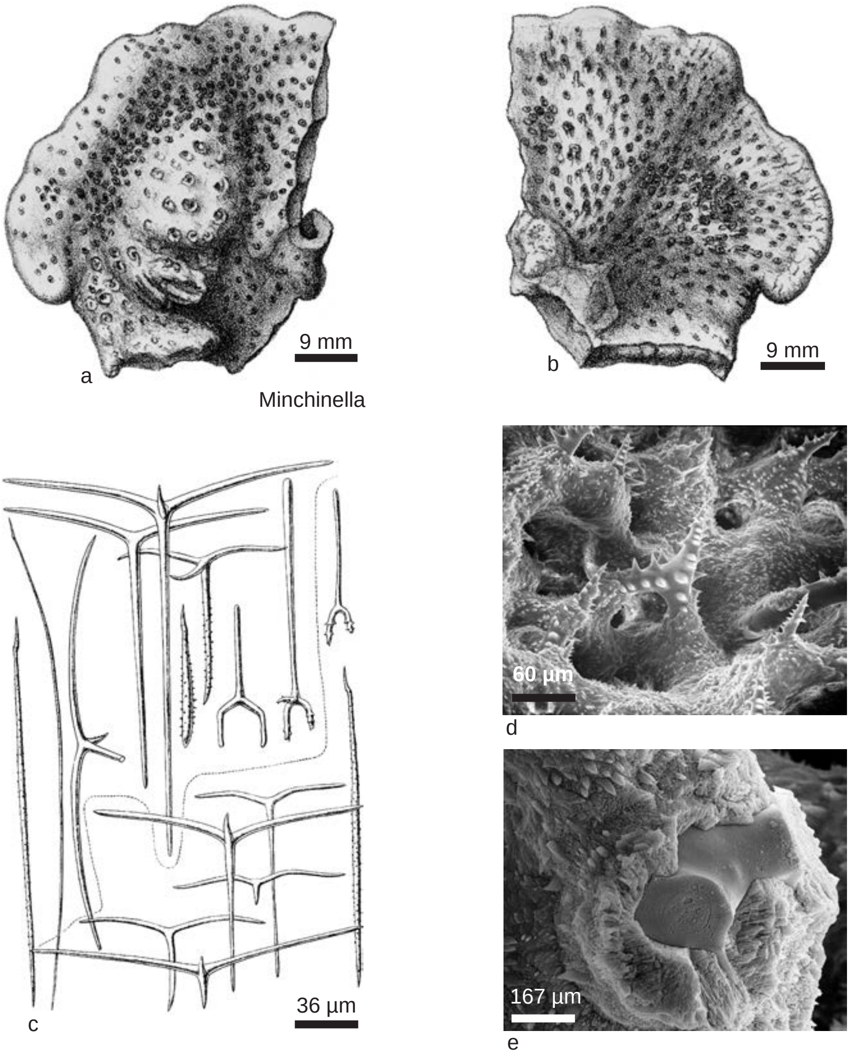

FIG. 201. Minchinellidae (p. 297–298).

[The family includes five Recent genera, one of which (*Tulearinia*), is poorly calcified and of uncertain affinity, and six fossil genera that range from Jurassic–Paleogene in age (*Porosphaera* STEINMANN, 1878; *Bactronella* HINDE, 1884; *Porosphaerella* WELTER, 1911; *Sagittularia* WELTER, 1911; *Retispinopora* BRYDONE, 1912; *Muellerithalamia* REITNER, 1987c). The diagnosis of the fossil and Recent genera are in need of revision, based on a careful reexamination of the type material. A *Treatise* coverage of systematic descriptions of the fossil genera is presented elsewhere (see FINKS & RIGBY, 2004d, p. 754–756).] *?Jurassic, Cretaceous–Holocene.*

Minchinella KIRKPATRICK, 1908, p. 504 [**M. lamellosa;* OD; holotype, NHM 1900.10.22.1A]. Minchinellidae in which main skeleton consists of one category of tetractines linked together into rigid network by their basal actines and subsequently embedded in enveloping cement. Cortical skeleton composed of free spicules, diactines, triactines, diapasons, and tetractines. Type species erect lamellar, with narrow base of attachment, 6.4 mm wide, 5.1 mm high, and 6.5 mm thick (holotype). Paratype smaller and ear shaped. Consistency hard, rigid. Poral face with pore chimneys, up to 3 mm in height and 1 mm in diameter, ending in drumlike membrane. Oscular face with cylindrical chimneys, 2 mm high, with a contracted end. Color in alcohol buff to brown, white at the rim. Choanocyte chambers 32.5 µm in diameter, with choanocytes showing hourglass modification due to poor preservation. Skeleton of both surfaces composed of an ectosomal layer of spinose diactines. Skeleton of poral and oscular chimneys composed of outer coat of spinose diactines, with axis vertical or oblique to long axis of tube, several layers of triactines and tetractines with apical ray projecting into lumen of tube, and fringe of bristlelike diactines round poral orifice. At base of chimneys, triactines and tetractines with spinose rays become partially cemented together. Main skeleton a firm reticulation with ovoid or rectangular meshes, 140–190 µm in total diameter, made of solid strands composed of spinose tetractines, with actines more or less completely embedded in calcitic cement of fibrillar, orthogonal microstructure. Apical ray is last to be embedded and, when free, pointing toward lumen. Diactines of several types, generally spinose, thicker on oscular face, 87–234 by 3.8–7.5 µm. Sagittal triactines generally smooth, unpaired actine 104–156 by 5–9.5 µm, paired actines 49–87 µm. Diapason triactines not aligned in tracts, with smooth shaft, 133 µm long and prongs smooth or spinose, 25 µm long. Tetractines similar to triactines, with apical actine 17 µm long. Cemented tetractines in a single size, with conical spines. Pacific Ocean (Vanuatu), 128 m depth. [A second species, *M. kirkpatricki* Vacelet, 1981, from New Caledonia, differs mostly by nonlamellar shape and absence of aquiferous chimneys.] *Holocene*: southwestern Pacific Ocean.——Fig. 201*a–e*. **M. lamellosa,* Api, New Hebrides, holotype; *a*, oscular surface; *b*, poral surface; *c*, spicules of poral and oscular surfaces (Kirkpatrick, 1908); *d*, SEM view of basal skeleton of partially embedded tetractines; *e*, SEM view of fracture in basal skeleton, showing a tetractine and cement (Vacelet, 1991).

Monoplectroninia Pouliquen & Vacelet, 1970, p. 439 [**M. hispida*; M; holotype, NHM 1970.4.24.1]. Minchinellidae in which main skeleton is composed of a basal layer made of one category of small tetractines linked together by their basal actines, while their apical actine remains free and points outward. Cortical skeleton made of free spicules, diactines, triactines, diapasons, and tetractines (Vacelet & others, 2002b, p. 1187). Monotypic genus differs from Recent representatives of *Plectroninia* in having basal skeleton devoid of large tetractines. Type species, small encrusting, 1.0–1.1 mm in diameter, 0.5 mm thick, white, with hispid surface. Cortical layer with layer of tangential smooth triactines and oblique spinose diactines. Osculum in cortical layer surrounded by circlet of tangential tetractines with spinose apical actine pointing toward lumen and smooth basal actines. Smooth diapasons dispersed in basal skeleton, not aligned in tracts. Main skeleton basal, made of a few layers of small spinose tetractines linked by basal actines, with apical actine remaining free and pointing outward. Choanocyte chambers irregularly tubular. Mediterranean (Marseille), dark submarine caves, 8–20 m depth (Vacelet & others, 2002b). *Holocene*: Mediterranean.——Fig. 202*a–d*. **M. hispida*, Cape Morgiou cave, Marseille, 15 m depth; *a*, SEM view of basal skeleton of fused tetractines; *b*, SEM view of basal skeleton with fused tetractines and a diapason (Vacelet, 2012); *c,* spicules: *Ca,* ectosomal triactines; *Cb,* periosculartetractines; *Cc,* perioscular diactines; *Cd,* ectosomal diactines; *Ce,* diapason triactines; *Cf,* fused tetractines of basal skeleton; *d*, ectosome, with ectosomal spicules and tetractines forming a circlet around osculum, and a fragment of basal skeleton (Pouliquen & Vacelet, 1970).

Petrostroma Döderlein, 1892, p. 145 [**P. schulzei;* M; holotype, NHM 99.7.14.1] [not *Petrostroma* Stearn, 1991, p. 617, stromatoporoid; *Petridiostroma* Stearn, 1992, p. 531, *nom. nov. pro Petrostroma* Stearn, 1991]. Minchinellidae with large tetractines fused by their basal actines, forming radial lines that are linked by smaller tetractines, also fused by their basal actines. Cortical skeleton composed of free spicules, triactines, diapason, and tetractines. Type species a massive base from which arises several short, cylindrical branches, dichotomously divided at their ends, of stony consistency. Color whitish to yellowish. Cortical skeleton made of free triactines and tetractines and of bundles of diapasons. Main skeleton of inner part a firm reticulation of ascending and diverging strands made of fused tetractines, which are linked by secondary strands of smaller tetractines fused by their basal actines. Tetractines of main skeleton bearing some conical spines, with apical actines remaining most often free. Free spicules smooth tetractines and triactines in several layers (with a few spinose tetractines), with rays 100 µm by 400 µm × 10 µm; diapasons aligned in tracts, 25–50 µm in diameter (Vacelet & others, 2002b, p. 1188). [The Recent representative has not been found again since its original description (Döderlein, 1892, 1898). Contrary to *Minchinella*, the tetractines linked by their basal actines are not subsequently embedded in a secondary cement. The mode of junction of the tetractines is rather similar to that in *Plectroninia* and *Monoplectroninia*. *Petrostroma* may represent a growth form of sponges similar to Recent representatives of *Plectroninia*, which are thinly encrusting and thus do not develop such a complex system of ascending and radiating lines; in which case, the two genera could be synonyms. This question is pending examination of new material and a revision of the fossil genera of Jurassic–Miocene age being allocated to the family Minchinellidae (Vacelet & others, 2002b).] *Cretaceous–Holocene:* France (Haute-Savoie), *Cretaceous*; Japan (Sagami Bay, 195–392 m depth), *Holocene.*——Fig. 203*a–e*. **P.*

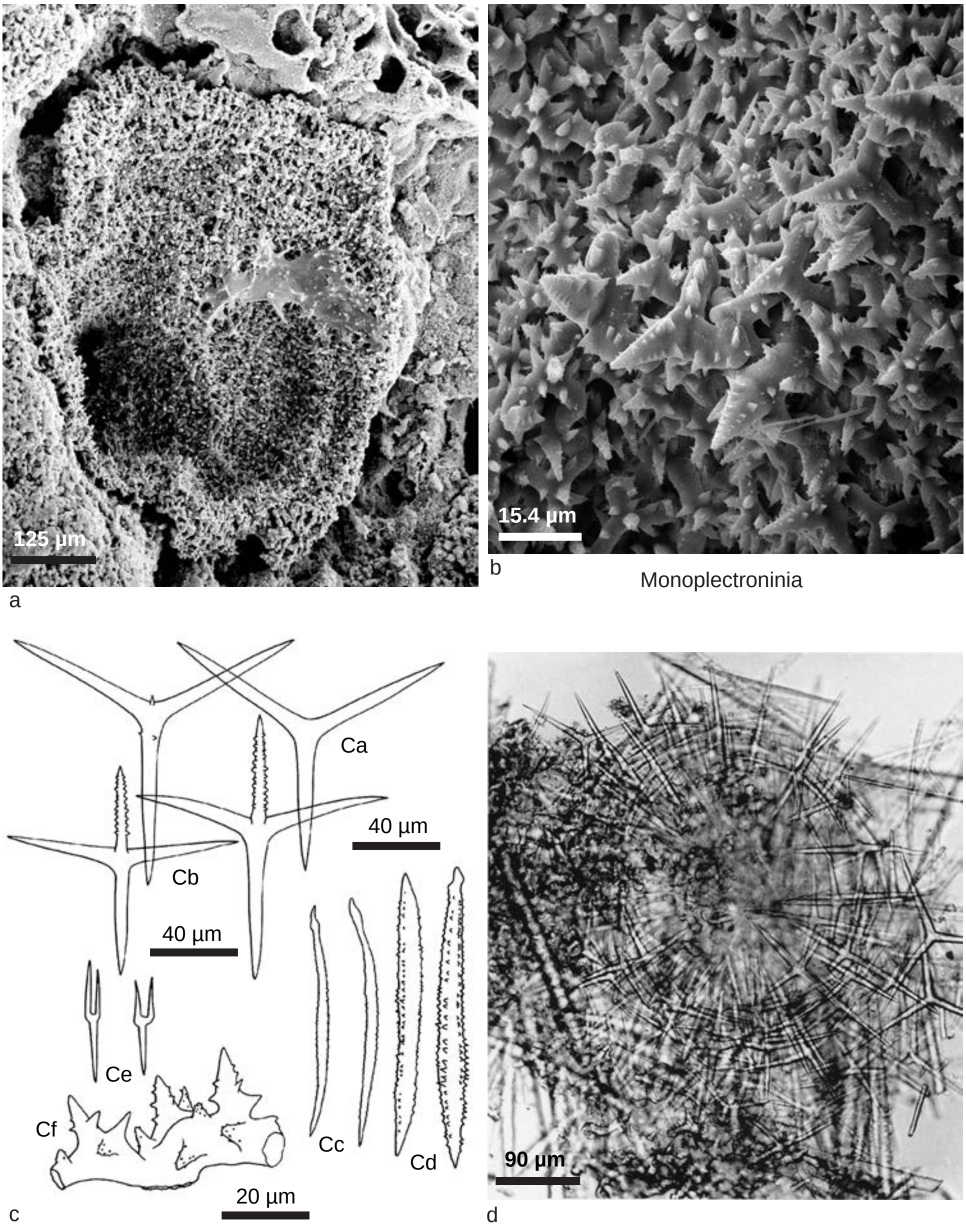

FIG. 202. Minchinellidae (p. 298).

schulzei, *a,* general view; *b,* ectosomal layer with ostia, triactines, and tetractines, and bundles of diapason; *c*, section through outer part of basal skeleton, with primary radial strands and secondary strands; *d,* small and large fused tetractines of basal skeleton; *e,* diapason triactine (Döderlein, 1898).

Plectroninia HINDE, 1900, p. 51 [**P. halli;* OD; holotype, NMV P14357]. Minchinellidae with basal skeleton made up of two types of fused tetractines, a layer composed of large tetractines and a layer of small tetractines. Tetractines fused by basal actines, with apical actine remaining free and pointing outward. Basal actines attached by simple zygosis in small tetractines, zygosis reinforced by cement layer in large tetractines. Cortical skeleton of free spicules tangentially arranged (VACELET & others, 2002b,

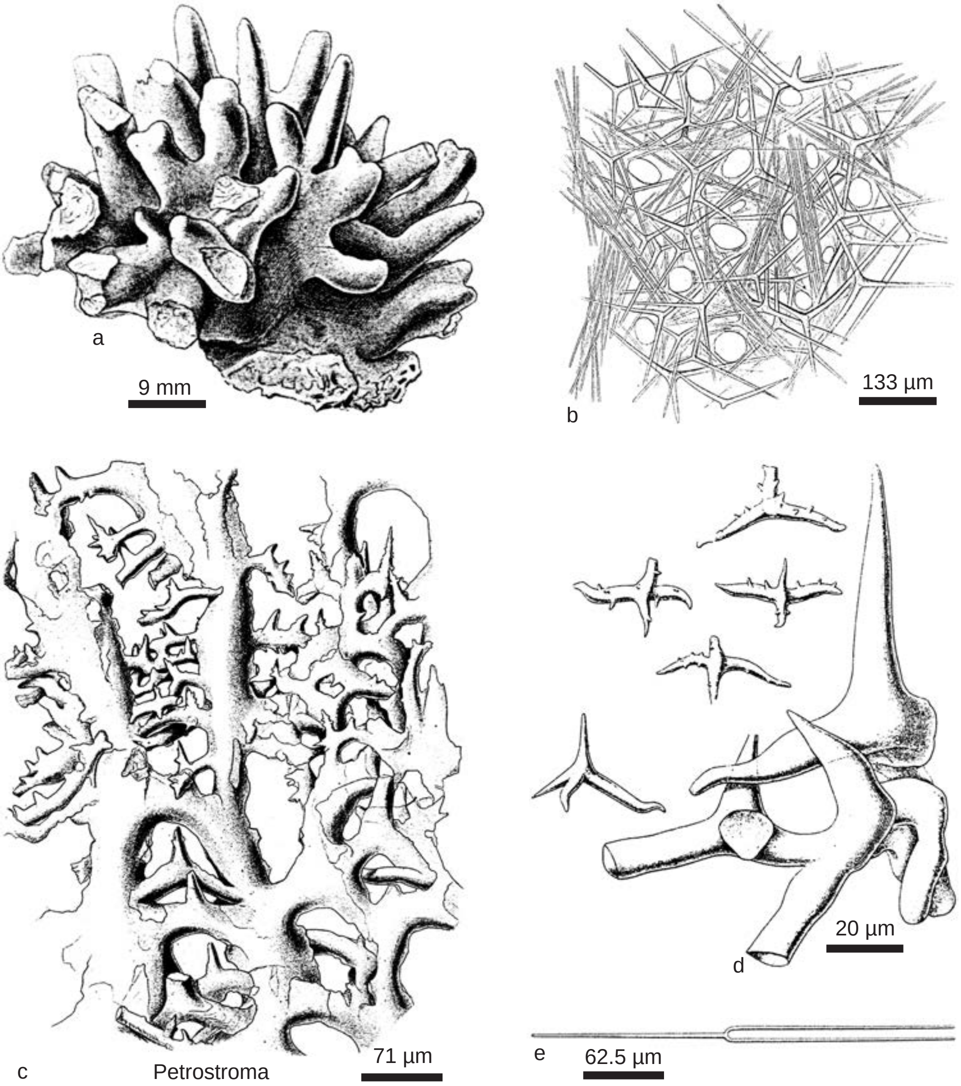

FIG. 203. Minchinellidae (p. 298–299).

p. 1188). Type species turbinate in shape, 16 mm high by 18 mm in greatest width. Sides covered by spicular dermal layer, partly preserved, interior skeleton firm, stony. Surface skeleton composed of free spicules tangentially disposed, with superficial layer of diactines, up to 610 µm by 10 µm, lying in parallel, overlying a layer made of diactines, triactines, and tetractines, including rare diapasons. Basal skeleton a multilayered reticulation made up of spinose tetractines, with basal actines unequal and irregularly curved, linked by expanded ends to basal actines of adjoining spicules, and with apical actine remaining free and pointed toward surface of sponge. Tetractines simply attached by expanded ends to basal actines of adjoining tetractines in outer layers, the apposition being reinforced by thin calcitic cement in inner layers, where tetractines have different size. Traces of canals radiating from summit of sponge present, 200–500 µm in diameter (VACELET & others, 2002b). [Type species is from the lower part of the middle Miocene in the Fyansford Formation, north of Geelong, Victoria, Australia (PICKETT, 1983); and another undescribed fossil species is from the upper Miocene of southeastern Spain (BARRIER & others, 1991). There are 13 Recent species, with a highly diverse dermal

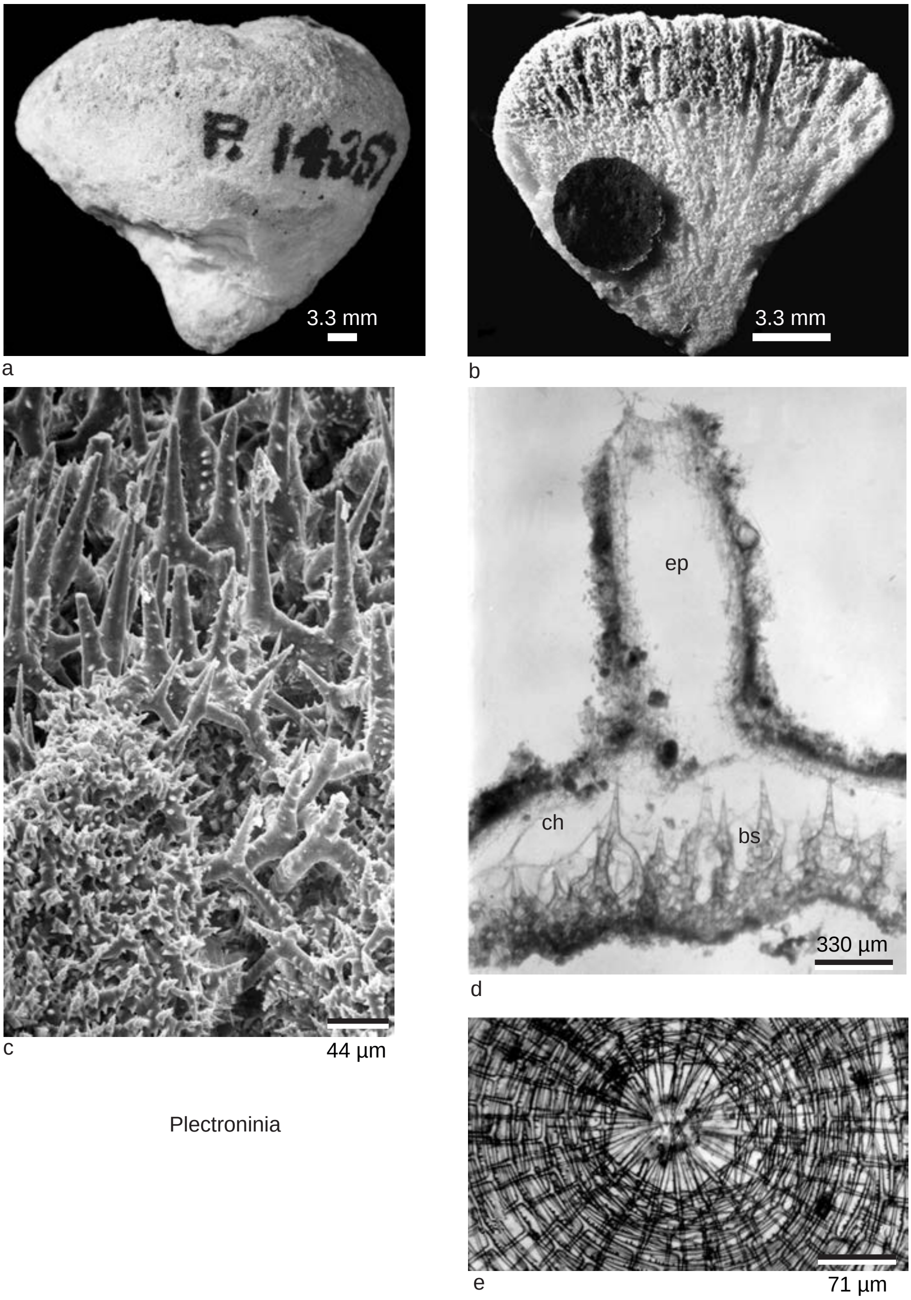

FIG. 204. Minchinellidae (p. 299–303).

skeleton of tangential spicules, in shallow water caves of the Indo-Pacific and Mediterranean, and in the bathyal zone, up to 1600 m depth with a large distribution. Recent species display an encrusting shape, and their allocation to the same genus as the fossil *Plectroninia halli* is not certain. In both Recent and fossil taxa, the basal skeleton of fused tetractines is composed of two different layers of fused tetractines, but contrary to the fossil species, in which the layer of small tetractines is superficial,

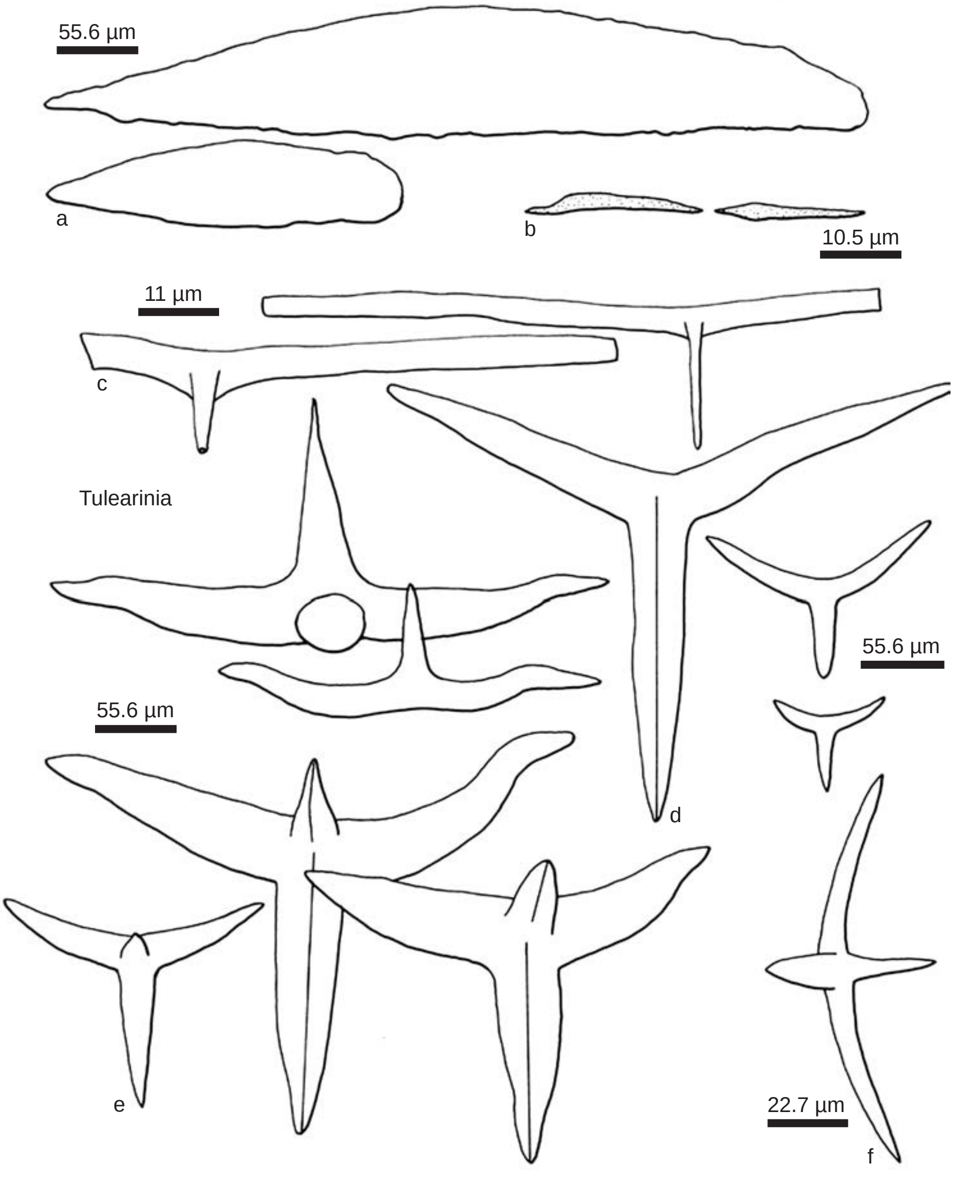

FIG. 205. Minchinellidae (p. 303).

this layer in Recent species is basal with regard to the layer of large tetractines. These Recent taxa could be classified alternatively in the genus *Bactronella* (Jurassic), as suggested by FINKS, HOLLOCHER, and THIES (2011). Another approach could be to describe them as comprising a new genus, but the introduction is dependent on a revision of the fossil genera in the Minchinellidae (VACELET & others, 2002b).] *?Jurassic, Cretaceous–Holocene:* Germany, USA (North Carolina), *Cretaceous*; Australia (Victoria), Spain, *Miocene;* Indopacific, Mediterranean, bathyal ocean, *Holocene*.——FIG. 204*a–b*. **P. halli;* general view of holotype (Pickett, 1983, p. 106).——FIG. 204*c*. *P. neocaledoniense* VACELET, SEM view of basal skeleton made up of small and large fused tetractines, 25 m depth, New Caledonia (Vacelet & others, 2002b).——FIG. 204*d*. *P. hindei* KIRKPATRICK, section through Mediterranean specimen, Marseille, 5 m depth; *ep,* exhalant papillae; *ch,* choanosome; *bs,* basal skeleton (Pouliquen & Vacelet, 1970).——Fig. 204*e*. *P. vasseuri* Vacelet, cortical skeleton of tangential triactines and osculum with a circlet of tetractines, Tuléar, Madagascar, 6 m depth (Vacelet, 1967b).

Tulearinia Vacelet, 1977a, p. 354 [**T. stylifera*; M; holotype, MNHN J.V.-76-1]. Minchinellidae in which basal skeleton consists of tetractines with basal actines interwoven but not cemented, and with underlying layers of triactines linked in same way (Vacelet & others, 2002b, p. 1190). Type species small, encrusting, 3 mm in maximum diameter, 0.7–0.8 mm thick. Color white, surface hispid, with osculum 0.4 mm in diameter, lined by thin triactines and a few tetractines. Surface skeleton composed of an outer layer of thick tangential or oblique diactines, and a layer of tangential triactines, overlying choanosome zone. Choanocyte chambers 55–75 µm in diameter, surrounded by microdiactines; canals lined by special tetractines, choanocytes apinucleate. Under choanosome, basal skeleton made of several layers of tetractines interwoven by basal actines, with apical actine pointing toward surface, and basal layer of interwoven triactines. Indian Ocean (Madagascar, La Réunion), New Caledonia, in submarine caves of the front reef, 3–37 m depth (Vacelet & others, 2002b). [This genus is monotypic and assigned with some reservation to the family Minchinellidae. Diapasons are absent; the basal skeleton is not solidly linked, and the spicules are only slightly entangled together through their crooked ends, without the true zygosis that characterizes Minchinellidae. This mode of union may be seen either as a transitional stage to the minchinellid structure or as a convergent mode of skeletal reinforcement in the high energy habitat of the tunnels of front reefs. The affinity of the genus thus remains rather uncertain.] *Holocene*: Indian Ocean and southwestern Pacific.——Fig. 205*a–f*. **T. stylifera*, spicules of holotype; *a*, diactines from outer layer; *b*, microdiactines; *c*, perioscular triactines; *d*, triactines; *e*, tetractines from basal network; *f*, tetractine from canals (Vacelet, 1977a).

Order BAERIDA Borojevic, Boury-Esnault, & Vacelet, 2000

[Baerida Borojevic, Boury-Esnault, & Vacelet, 2000, p. 249]

Leuconoid Calcaronea with skeleton either composed exclusively of microdiactines, or in which microdiactines constitute exclusively or predominantly a specific sector of skeleton, such as choanoskeleton or atrial skeleton. Large or giant spicules are frequently present in cortical skeleton, from which they may partially or fully invade choanoderm. In sponges with reinforced cortex, inhalant pores may be restricted to sievelike ostia-bearing region. Dagger-shaped, small tetractines (pugioles) are frequently sole skeleton of exhalant aquiferous system. An aspicular calcareous skeleton may be present (diagnosis modified from Borojevic & others, 2002). [The order contains four families, two of which, Baeriidae and Trichogypsidae, are not hypercalcified, and are not treated here.] *Pleistocene–Holocene*.

Family PETROBIONIDAE Borojevic, 1979

[Petrobionidae Borojevic, 1979, p. 529]

Baerida of thickly encrusting or subspherical growth form. Basal skeleton composed of a solid mass of calcite consisting of elongated sclerodermites that form a series of crests between which lies living tissue, with survival structures made of reserve cells filling small canaliculi of the skeleton. Aquiferous system leuconoid. Free spicules triactines, tuning-fork triactines (diapasons), pugiole tetractines, and microdiactines. Spicules randomly trapped within the massive skeleton do not dissolve (description modified from Vacelet & others, 2002b, p. 1191). [The monogeneric family Petrobionidae was classified in the order Lithonida in *Systema Porifera* (Vacelet & others, 2002b). A recent reevaluation of morphological and molecular characters suggests a classification in the order Baerida (Manuel & others, 2003). No counterpart of the skeleton microstructure older than 30,000 years is known in the fossil record.] *Pleistocene–Holocene.*

Petrobiona Vacelet & Lévi, 1958, p. 318 [**P. massiliana;* M; holotype, MNHN C. 1968.814]. Diagnosis as for family. Type species massive, subspherical or multilobate with a dead stalk in calm environments, encrusting in high energy environments. Maximum size of living head 1.0–1.2 cm in diameter, with stalk 2 cm long, up to 6 cm in diameter when encrusting. Texture stony. Color pure white. Surface smooth. Oscules apical in subspherical or multilobate specimens, 0.6–0.8 mm in diameter. Living tissue located at surface and between crests of basal skeleton, with choanosome 600 µm thick, anchored in basal skeleton by tracts of reserve cells filling canaliculi 50–90 µm in diameter. Aquiferous system leuconoid, choanocyte chambers 50–80 µm in diameter. Spicules: sagittal triactines (actines

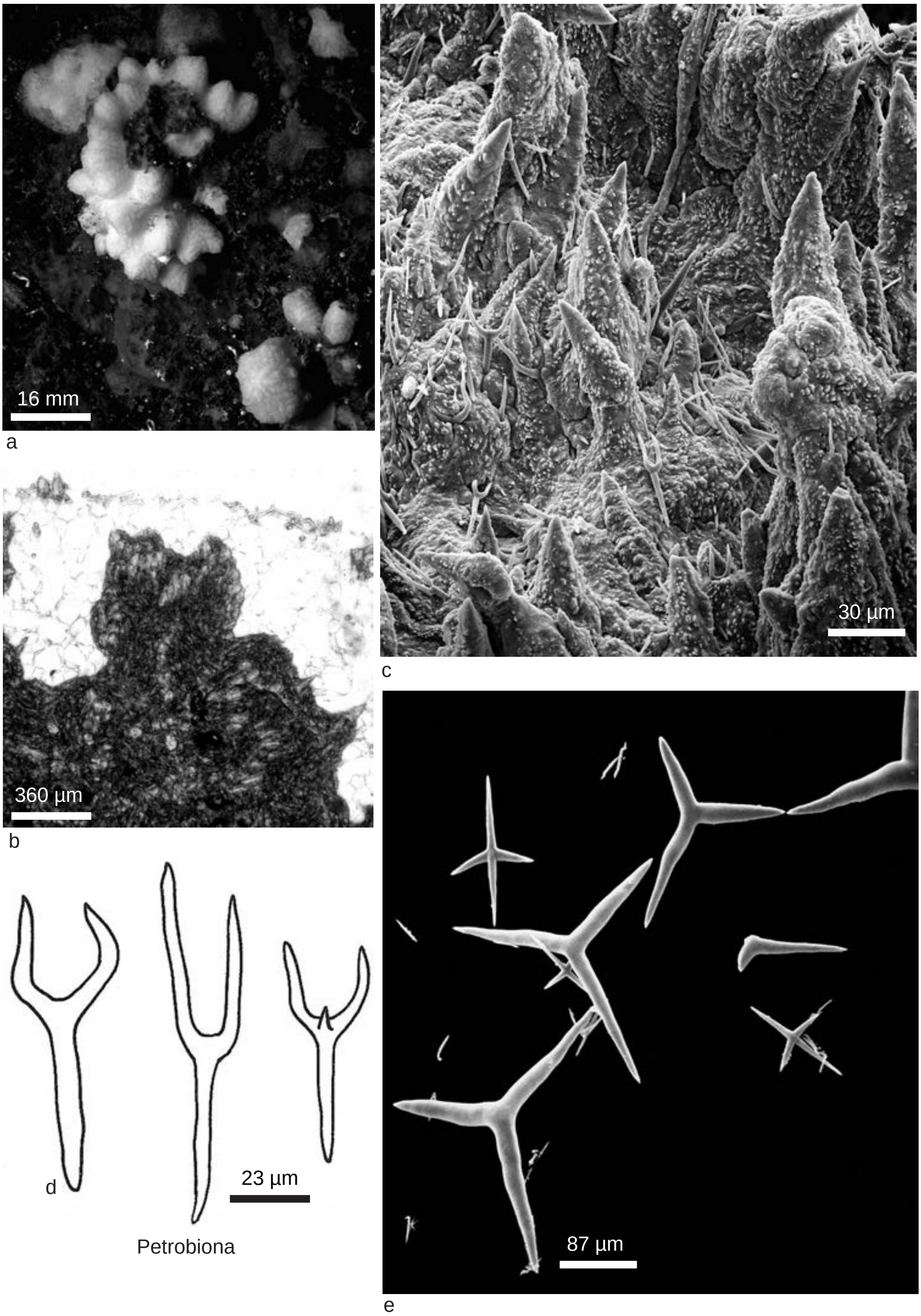

FIG. 206. Petrobionidae (p. 303–305).

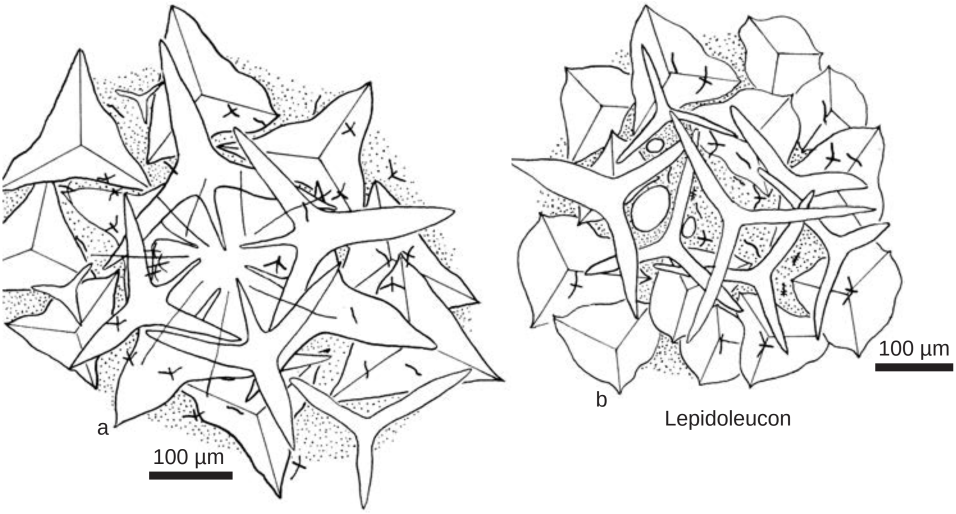

FIG. 207. Lepidoleuconidae (p. 305–306).

25–200 µm by 6–40 µm), tuning-fork (diapason) triactines (basal actine 30–70 µm by 5–8.5 µm; lateral actines 20–50 µm by 4–7 µm), pugiole tetractines in two categories (lateral actines 40–130 µm by 22–28 µm and 16–40 µm by 5.5–8.5 µm, axial actines 8–100 µm by 10–28 µm and 30–70 µm by 5.5–8.5 µm), rugose microdiactines 30–60 µm by 2–3 µm. Basal calcareous skeleton in calcite, solid, with crests and depressions on surface, built up of elongate, irregular sclerodermites, with radial orientation of crystals from longitudinal axis, 80–150 µm in maximum size. Some spicules entrapped in basal skeleton, randomly arranged and showing no sign of dissolution. Reproduction by amphiblastula larva, with unusually complex nourishment process of oocyte and embryo. A single species in Mediterranean: eastern basin (Adriatic, Ionian Sea, Crete, Malta, Tunisia), western part of the western basin (not recorded west of the Rhone delta and Algeria). Common near entrance of dark caves, more rarely on undersurface of stones, 0.5–25 m depth. Fossil skeletons recorded from a cave on Crete that emerged 1500 years ago (VACELET, 1980b) and from Pleistocene cliffs of southern Italy dating back 30,000 years (VACELET, 1991). *Pleistocene–Holocene*: Mediterranean caves.——FIG. 206*a–e*. **P. massiliana*; *a,* several specimens *in situ* in Marseille cave, 10 m (Vacelet, 2012); *b*, section through apical zone, showing massive skeleton, choanocyte chambers, and surface spicules (Vacelet, 2012); *c*, SEM view of skeleton surface with tuning-fork spicules partially entrapped (Vacelet, 1991); *d*, tuning-fork triactines (Vacelet, 1964); *e*, calcareous spicules, triactines, pugioles, and microdiactines (Vacelet, 2012). See also Fig. 3,*5c,* herein, calcitic sclerodermite of the so-called flake-spherulitic or fibro-radial type in *Petrobiona massiliana* (GAUTRET, 1986); and diagrammatic vertical section through three living hypercalcified sponges possessing masses of storage cells in Fig. 3,*5a–c,* herein).

Family LEPIDOLEUCONIDAE Vacelet, 1967

[Lepidoleuconidae VACELET, 1967a, p. 54]

Baerida with leuconoid organization and irregular outer layer of scales derived from triactines. Choanoskeleton exclusively composed of scattered microdiactines. Ostia localized in a special area where triactines are not transformed into scales. Osculum with a circlet of modified tetractines. [The calcareous superficial scales derived from triactines are reminiscent of the scales of Murrayonidae and Paramurrayonidae in subclass Calcinea. The organization of the skeleton, however, is similar to that of other Baerida.] *Holocene.*

Lepidoleucon VACELET, 1967a, p. 54 [**L. inflatum;* M; holotype, MNHN C1968-149]. Diagnosis as for family. Type species tiny, hemispherical, 0.4–1 mm in diameter, covered by several superficial layers of triangular or rounded scales, 160 µm in maximum diameter, deriving from triactines. Osculum single, central, with a circlet made by inflated lateral actines of special tetractines, whose apical actine is directed toward center of aperture. Ostia localized in lateral area, devoid of scales and bearing large triactines. Color yellowish or brownish. Choanoskeleton exclusively composed of microdiactines. Aquiferous system leuconoid, with apinucleated choanocytes. Amphiblastula larvae (BOROJEVIC & others, 2002, p. 1199). *Holocene*: Indian Ocean (Madagascar), Western and Central Pacific (New Caledonia, Tuamotu Islands), in underwater caves and tunnels of the fore-reef zone, 3–30 m depth.——FIG. 207*a–b*. **L. inflatum; a*, surface view of osculum, with tetractines, triactines, scales, microdiactines, and microtetractines; *b*, surface view of inhalant area, with triactines, scales, microdiactines, and microtetractines (Vacelet, 1967a).

A LIST OF UPPER PALEOZOIC–MESOZOIC STROMATOPOROID-LIKE GENERA; AND EXCLUDED TAXA

Colin W. Stearn and Carl W. Stock

For over a century, certain upper Paleozoic to Mesozoic fossils of marine sessile benthic organisms with calcareous skeletons, many containing astrorhizae, were included with the Ordovician–Devonian Stromatoporoidea, and many of these were included in the same families as the earlier Paleozoic genera (e.g., Kühn, 1939b; Lecompte, 1956). The biological affinities of many of these upper Paleozoic and Mesozoic genera are still in doubt. Like the Stromatoporoidea, they have been assigned to a variety of invertebrate groups such as the hydrozoans, sponges, bryozoans, and foraminiferans. The hydrozoan affinity was strongly supported (e.g., Lecompte, 1956) by the similarities of some Jurassic–Cretaceous forms to Recent Hydrozoa (see Morphologic Affinities of the Paleozoic Stromatoporoidea to Other Fossil and Recent Groups, p. 543–549). Only relatively recently have some genera among the Mesozoic forms been found to contain spicules or spicule pseudomorphs (e.g., G. Termier, H. Termier, & Ramalho, 1985; H. Termier, G. Termier, & Ramalho, 1985; Wood, 1987) that demonstrate a relationship with the demosponges. Some of the nonspicular forms contain astrorhizae, diagnostic of the Porifera, that confirm they are sponges, but not all genera contain astrorhizae.

In the 19th century, before thin sections became a standard method of research, many genera of calcareous crusts were established with inadequate diagnoses and illustrations. Some of these have been determined to be inorganic tufas, stromatolites formed by cyanobacteria, poorly preserved corals and sponges, or calcareous algae. Most are impossible to identify consistently, cannot be traced through type specimens, and have been noted in the literature only in the original description. Kühn (1939b, p. 60–62) gave an extensive list of these useless genera, which is not repeated here. A few of the genera that have received some comment in the literature are listed below; for others, the reader is referred to Kühn's (1939b) list and Finks and Rigby (2004d).

Upper Paleozoic–Mesozoic stromatoporoid-like fossils are more difficult to study than their Ordovician–Devonian analogs. This difference is due to the limited number of paleontologists studying the late Paleozoic–Mesozoic forms. As Stock (2001) noted, for the period 1926–2000, there were 734 publications on Ordovician–Devonian stromatoporoids, but only 230 on Carboniferous–Cretaceous forms. Whereas 6 paleontologists (R. G. S. Hudson; A. Schnorf-Steiner; G. Termier; H. Termier; D. Turnšek; R. Wood) produced more than 10 publications on Jurassic–Cretaceous stromatoporoid-like taxa from 1926 to 2000, 14 paleontologists did the same for the Ordovician–Devonian stromatoporoids (O. V. Bogoyavlenskaya; D.-Y. Dong; E. Flügel; S. Kershaw; V. G. Khromykh; A. I. Lessovaya; B. Mistiaen; H. Nestor; V. N. Riabinin; J. St. Jean; C. W. Stearn; C. W. Stock; B. D. Webby; V. I. Yavorsky). A large number of publications are representative of a major research commitment by the author to a particular taxon. Clearly, this relatively large number of specialists, in many cases interacting with each other on a regular basis, led to a more coherent understanding of the earlier stromatoporoids than was possible for later stromatoporoid-like forms.

The above-noted uncertainties with regard to the taxonomic position of many of the upper Paleozoic–Mesozoic, nonspicular, stromatoporoid-like taxa, the lack of a coherent, consistent classification system for this taxon, and the additional lack of anyone currently specializing in the study of the nonspicular stromatoporoid-like forms has discouraged the authors from presenting here a systematic paleontology of the group. In this alphabetical list of stromatoporoid-like genera, the geologic systems from which type species were collected are indicated. Excluded taxa (either not stromatoporoid-like poriferans or not Porifera) are listed on p. 310.

Actinostromina Germovšek, 1954, p. 351 [**A. oppidana*; OD]. *Upper Jurassic:* Slovenia.

Adriatella Milan, 1969, p. 180 [**A. poljaki* Milan, 1969, p. 181; OD]. *Upper Jurassic.*

Aksaeporella Boĭko, 1979, p. 57 [**A. arta* Boĭko, 1979, p. 58; OD]. [Boĭko (1979) placed this genus in the stromatoporoids, but it also resembles chaetetids and hydrozoans.] *Upper Triassic*: Tadjikistan (Pamirs).

Aphralysia Garwood, 1914, p. 268 [**A. carbonaria* Garwood, 1914, p. 269; OD]. [Several authors (e.g., Pia, 1937) have considered the genus to be a stromatoporoid, but Galloway (1957) returned it to the algae.] *Carboniferous (Missippian):* England (Westmoreland).

Astrostylopsis Germovšek, 1954, p. 361 [**A. slovenica*; OD] [=*Trupetostromaria* Germovšek, 1954, p. 365 (type, *T. circoporea,* OD)]. *Upper Jurassic:* Slovenia.

Atelostroma Dong & Wang, 1983, p. 417 [**A. jurassicum* Dong & Wang, 1983, p. 418; OD]. *Upper Jurassic:* China (Xizang).

Axiotubullina Dong & Wang, 1983, p. 419 [**A. columna;* OD]. *Upper Jurassic:* China (Xizang).

Baastadiostroma Brood, 1972, p. 404 [**B. typicum*; OD]. *Upper Cretaceous:* Sweden.

Burgundostromaria Turnšek, 1970, p. 199 [**B. zlatibornensis* Turnšek, 1970, p. 200; OD]. *Upper Cretaceous:* Serbia.

Cassianostroma Flügel, 1960, p. 51 [**C. kupperi* Flügel, 1960, p. 51–52; OD]. *Triassic:* Italy.

Ceraostroma Kühn, 1926, p. 413 [**C. steinmanni*; OD]. *Jurassic:* Austria.

Circopora Waagen & Wentzel, 1887, p. 957 [**C. foveolata* Waagen & Wentzel, 1887, p. 958–960; OD]. *Permian, ?Triassic:* Pakistan, Austria, Russia, Indonesia.

Coenostella Turnšek, 1966, p. 355 [**C. thomasi* Turnšek, 1966, p. 356; OD]. *Upper Jurassic:* Slovenia.

Convexistroma Boĭko, 1984b, p. 62 [**C. irregularis;* OD]. *Lower Jurassic:* Tadjikistan (Pamirs).

Crimestroma Yavorsky, 1947, p. 16 [**C. borissiaki;* OD]. *Upper Jurassic:* Ukraine (Crimea).

Cylicopsis Le Maître, 1935, p. 43 [**Stromatomorpha (Cylicopsis) atlantis* Le Maître, 1935, p. 43; OD]. *Lower Jurassic:* Morocco.

Dehornaeporella Termier in G. Termier, H. Termier, & Ramalho, 1985, p. 204 [**Stromatopora choffati* Dehorne, 1917a, p. 118; OD]. [G. Termier, H. Termier, & Ramalho (1985) noted the presence of monaxon spicules (styles) in the type species.] *Upper Jurassic:* Egypt (Sinai), Israel, Oman, Portugal, Slovenia.

Dongqiastroma Dong & Wang, 1983, p. 415 [**D. lamellatum;* OD]. *Upper Jurassic:* China (Xizang).

Dongqiastromaria Dong & Wang, 1983, p. 417 [**D. grossa;* OD]. *Upper Jurassic:* China (Xizang).

Desmopora Yavorsky, 1947, p. 17 [**D. listrigonorum;* OD]. *Upper Jurassic:* Ukraine (Crimea).

Disparistromaria Schnorf, 1960b, p. 439 [**D. tenuissima* Schnorf, 1960b, p. 440; OD]. *Cretaceous:* Switzerland.

Ellipsactinia Steinmann, 1878, p. 116 [**E. ellipsoidea* Steinmann, 1878, p. 117; OD]. *Upper Jurassic*: Austria.

Emscheria Schnorf-Steiner, 1958, p. 461 [**E. netherensis* Schnorf-Steiner, 1958, p. 462; OD]. *Upper Cretaceous:* France.

Gurumdistroma Boĭko, 1984b, p. 65 [**G. astrorhizoides;* OD]. *Lower Jurassic:* Tadjikistan (Pamirs).

Hudsonella Turnšek, 1966, p. 361 [**H. otlicensis* Turnšek, 1966, p. 362; OD]. *Upper Jurassic:* Slovenia.

Incrustospongia Molineux, 1994, p. 980 [**I. meandrica* Molineux, 1994, p. 980–981; OD]. [Finks & Rigby (2004c) placed this laminated encrusting form in Demospongiae, order and family Uncertain.] *Carboniferous (Pennsylvanian):* USA (Texas).

Jillua Krumbeck, 1913, p. 134 [**J. tubifera;* OD]. [Comments in Flügel & Sy (1959); see also Yabe & Sugiyama (1935) and Kühn (1939b), who based the genus on surface features only.] *Upper Triassic:* Indonesia.

Komia Korde, 1951, p. 181 [**K. abundans;* OD] [=*Ungdarella* Maslov, 1956, p. 73 (type, *U. americana;* OD), *non* Korde, 1951, *non* Toomey & Johnson, 1968, p. 577]. [Although originally described as an alga and confirmed as such by Stock & others (1992), Wilson, Waines, & Coogan (1963) placed these fossils in the Stromatoporoidea.] *Carboniferous (Pennsylvanian):* Japan, Russia (Urals), USA (southwestern states).

Lamellata Flügel & Sy, 1959, p. 60 [**L. wahneri* Flügel & Sy, 1959, p. 61; OD]. [The genus was compared with *Ellipsactinia, Nigriporella,* and *Sphaeractinia* by Flügel & Sy (1959). Konishi (1959) wrote that the genus is a synonym of *Tubiphytes* Maslov.] *Upper Triassic:* Austria, Greece (Corfu).

Lithopora Tornquist, 1900, p. 128 [**L. koeneni;* OD]. *Triassic:* Italy.

Milleporidium Steinmann, 1903, p. 2 [**H. remesi;* OD]. *Upper Jurassic:* Austria.

Millestroma Gregory, 1898, p. 340 [**M. nicholsoni* Gregory, 1898, p. 341; OD]. [The genus is composed of bundles of fine tubes that suggest affinity to the bryozoans (Dehorne, 1920); however, Gregory (1898) placed it in the hydrozoans.] *Upper Cretaceous:* Egypt.

Myrioporina Kühn, 1939b, p. 34 [**Myriopora verbeeki* Volz, 1904, p. 187; OD]. [Hudson (1956a) considered that *Myriopora* of Reuss (1846) was a *lapsus calami* for *Myriapora* de Blainville (1830) and that *Myriopora* Volz, 1904, was a homonym of *Myriopora* Reuss and *Myriapora* de Blainville and hence was not available, and to resolve the nomenclatural problem, he recognized Kühn's genus *Myrioporina* as valid to replace the names that de Blainville, Reuss, and Volz had used for this taxon.] *Jurassic:* Indonesia (Sumatra).

Palaeoaplysina Krotow, 1888, p. 549 [**P. laminaeformis*; OD; neotype P209-3 (Tchuvaschov, 1973)] [=*Mezenia* Stuckenberg, 1895, p. 130 (type, *M. rozeni*, OD); Flügel, 1961b; =*Uralotimania* Riabinin, 1915, p. 23 (type, *U. reticulata,* OD)]. [This is a common reef-forming fossil organism of the lower Permian and Carboniferous rocks of western and arctic North America and Russia. It has a unique cellular microstructure and a complex system of internal canals parallel to the base in the lower part, bending upward to the upper surface. The genus has generally been assigned to either the hydrozoans or sponges and suggestions that it is an alga are rejected by recent researchers. Recent papers on this common fossil include: Davies (1971); Davies & Nassichuk (1973, 1986); Watkins & Wilson (1989).] *Carboniferous (Pennsylvanian)–lower Permian:* Canada (arctic islands, Yukon), Russia (Urals, Russian platform), USA (California, Idaho).

Palaeomillepora Gabilly & Lafuste, 1957, p. 355 [**P. liasica;* OD]. *Lower Jurassic:* France.

Paradehornella Boĭko, 1989, p. 56 [**P. astriferum;* OD]. *Middle Jurassic*: Tadjikistan (Pamirs).

Paramilleporella Fenninger in Fenninger & Hötzl, 1965, p. 20 [**P. gracilis;* OD]. *Upper Jurassic:* Austria.

Paratubuliella Dong & Wang, 1983, p. 423 [**P. pertabulata;* OD]. *Upper Jurassic:* China (Xizang).

Parksia Lecompte, 1952a, p. 24 [**Stromatopora douvillei* Dehorne, 1918, p. 220; OD]. *Upper Jurassic:* Tunisia.

Paronaria Termier & Termier, 1984, p. 236 [**Parkeria provali* Parona in Parona, Crema, & Prever, 1909, p. 161; OD]. *Cretaceous:* Italy.

Periomipora H.Termier, G. Termier, & Ramalho, 1985, p. 980 [**P. elegantissima;* OD]. [H. Termier, G. Termier, & Ramalho (1985) noted the presence of monaxon spicules in the type species.] *Upper Jurassic:* Portugal.

Reticullina Turnšek, 1966, p. 364 [**R. rectiangularis* Turnšek, 1966, p. 365; OD]. *Upper Jurassic:* Slovenia.

Rhizoporidium Parona in Parona, Crema, & Prever, 1909, p. 158 [**R. irregulare;* OD]. *Cretaceous:* Italy.

Sarawakia Hashimoto, 1973, p. 210 [**S. ellipsactinoides* Hashimoto, 1973, p. 211; OD]. *Upper Jurassic:* Malaysia (Sarawak).

Saresiastroma Boĭko, 1989, p. 57 [**S. conceptum* Boĭko, 1989, p. 58; OD]. *Middle Jurassic:* Tadjikistan (Pamirs).

Sarmentofascis G. Termier, H. Termier, & Vachard, 1977, p. 146 [**Cladocoropsis cretacica* Turnšek, 1968, p. 357; OD]. *Lower Cretaceous:* Montenegro.

Scaniostroma Brood, 1972, p. 396 [**S. gracilis*; OD]. Resembles the spongiomorphs (see discussion of this group, p. 311). *Upper Cretaceous:* Sweden.

Sedekiastroma Boĭko, 1984b, p. 60 [**S. liassica* Boĭko, 1984b, p. 61; OD]. *Lower Jurassic:* Tadjikistan (Pamirs).

Shamovella Rauser-Chernousova, 1950, p. 17 [**S. obscura* Maslov, 1956, p. 82; SD Riding, 1993; see discussions regarding the validity of *Shamovella* versus *Tubiphytes:* Riding & Guo (1992); Riding (1993); Riding & Barkham (1999)] [=*Tubiphytes* Maslov, 1956, p. 82 (type, *T. obscurus*; OD); =*Nigriporella* Rigby, 1958, p. 584 (type, *N. magna*, OD, lost); Permian, Texas, USA]. [Riding & Guo (1992) discussed the possible affinity of this widespread fossil as a cyanobacterium, hydrozoan, rhodophyte, poriferan, or foraminiferan and concluded that it is most likely a sponge.] *Carboniferous–Cretaceous (mainly Permian).*

Siphostroma Steiner, 1932, p. 79 [**S. arzieri* Steiner, 1932, p. 99; OD]. [Discussed by Yabe & Sugiyama (1935), Kühn (1939b), and Lecompte (1952a).] *Cretaceous:* Switzerland.

Sphaeractinia Steinmann, 1878, p. 115 [**S. diceratina;* OD]. *Upper Jurassic:* Austria.

Sporadoporidium Germovšek, 1954, p. 370 [**S. rakoveci;* OD]. *Upper Jurassic:* Slovenia.

Steinerella Lecompte, 1952a, p. 26 [**Stromatopora mecosola* Steiner, 1932, p. 103; OD]. *Lower Cretaceous:* Switzerland.

Stromatoporellata Bakalow, 1910, p. 5 [**S. mammillaris;* OD]. [Described on the basis of surface characteristics only. Holotype not available (see Flügel & Sy, 1959).] *Upper Triassic:* Bulgaria.

Stromatoporellina Kühn, 1927, p. 550 [**Stromatoporella haugi* Dehorne, 1917b, p. 70; OD] [=*Astrorhizopora* Schnorf-Steiner, 1958, p. 454 (type, *Stromatoporella haugi* Dehorne, 1917b, p. 70, OD)]. *Upper Cretaceous:* France.

Stromatoporina Kühn, 1927, p. 550 [**Stromatopora tornquisti* Deninger, 1906, p. 66; OD]. *Triassic:* Italy (Sardinia).

Stromatorhiza Bakalow, 1906, p. 13 [**Thamnaraea*? *granulosa* Koby, 1888, p. unknown; OD]. [Hudson (1955a) gave the most complete discussion and suggested synonymy with *Cylicopsis* Le Maitre, *Astrostylopsis* Germovšek, and *Trupetostromaria* Germovšek.] *Jurassic:* Switzerland.

Stromatostroma Bakalow, 1910, p. 4 [**S. triassicum*; OD]. *Triassic:* Bulgaria.

Tauripora Yavorsky, 1947, p. 16 [**T. astroites* Yavorsky, 1947, p. 16–17; OD]. *Permian*: Crimea.

Tosastroma Yabe & Sugiyama, 1935, p. 158 [**T. tokunagai* Yabe & Sugiyama, 1935, p. 185; OD]. *Upper Jurassic:* Japan.

Tubuliella Turnšek, 1966, p. 357 [**T. fluegeli;* OD]. *Upper Jurassic:* Slovenia.

Tubulopareites Schnorf, 1960a, p. 430 [**T. constans* Schnorf, 1960a, p. 432; OD]. *Upper Cretaceous:* France.

Xizangstromatopora Dong, 1981, p. 118 [**X. densata* Dong, 1981, p. 119; OD]. *Upper Jurassic:* China (Xizang).

Yezoactinia Hashimoto, 1960, p. 95 [**Y. shotombestuensis* Hashimoto, 1960, p. 96; OD]. *Upper Jurassic:* Japan.

EXCLUDED TAXA

Aprutinopora Parona in Parona, Crema, & Prever, 1909, p. 150 [**A. osimoi* Parona in Parona, Crema, & Prever, 1909, p. 151; OD]. [Questionably a bryozoan (Kühn, 1939b).] *Cretaceous:* Italy.

Cerkesia Moiseev, 1944, p. 24 [**C. robinsoni* Moiseev, 1944, p. 25; OD] [=*Cercessia* Flügel, 1961b, p. 74, *lapsus calami*]. [Moiseev (1944) suggested relationships with the actinostromatids, siphonostromids, and burgundiids, but his illustrations suggest this may be a bryozoan. Used by only Moiseev.] *Upper Triassic:* Georgia and Russia (Caucasus).

Cycloporidium Parona in Parona, Crema, & Prever, 1909, p. 157 [**C. tuberiforme;* OD]. ["Description and illustration very unclear" (Kühn, 1939b, p. 58).] *Cretaceous*: Italy.

Elephantaria Oppenheim, 1930, p. 1 [**E. lindstroemi* Oppenheim, 1930, p. 2; OD]. [Possibly a scleractinian coral.] *Cretaceous:* Austria.

Lichuanopora Fan, Rigby, & Zhang, 1991, p. 66 [**L. bancaoensis;* OD]. [Skeleton consists of open, longitudinal tubes with walls penetrated by pores. Possibly a hydrozoan.] *upper Permian:* China (Hubei).

Likinia Ivanova & Ilkhovsky in Ilkhovsky, 1973, p. 11 [**L. nikitini;* OD]. [May be a hydrozoan.] *Carboniferous:* Russia (Oka River).

Lophiostroma Nicholson, 1891a, p. 160 [**Labechia? schmidtii* Nicholson, 1886a, p. 16; OD]. [Sugiyama (1939) used this lower Paleozoic genus for calcareous crusts, identifying them as belonging to the genus *Lophiostroma.* Also, Mori (1980, p. 238–239) recorded *Lophiostroma ozawai* Yabe & Sugiyama, 1931a, as a brachiopod shell. A brief discussion of the need to exclude these "calcareous crusts" from a relationship with the type species of *Lophiostroma (?Labechia) schmidtii* (Nicholson, 1891a), is also included in the systematic descriptions of the Labechiida, p. 749.] *Carboniferous–Permian*: Japan.

Megastroma Montanaro-Gallitelli, 1954, p. 79 [**M. lecomptei;* OD]. [Flügel & Flügel-Kahler (1968) suggested this may be an inorganic structure.] *Permian:* Italy (Sicily).

Neostroma Tornquist, 1901, p. 1117 [**N. sumatraense;* OD]. [Flügel (1961b) synonymized this genus with the scleractinian coral *Actinacis* d'Orbigny.] *Cretaceous:* Indonesia (Sumatra).

Parkeria Carpenter in Carpenter & Brady, 1870, p. 724 [**P. sphaerica* Carter, 1877, p. 61; OD] [=*Millarella* Carter, 1888, p. 178 (type, *M. cantabrigiensis*, OD)]. [A hydrozoan cnidarian (Termier & Termier, 1984).] *Cretaceous:* England, India.

Porosphaera Steinmann, 1878, p. 120 [**Millepora globularis* Phillips, 1829, p. 155; OD]. [In Calcarea (Finks & Rigby, 2004d, p. 756).] *Upper Cretaceous:* Czech Republic, England, France, Germany.

Rhizostromella Parona in Parona, Crema, & Prever, 1909, p. 160 [**R. apenndina;* OD]. ["Description and illustration worthless" (Kühn, 1939b, p. 62).] *Cretaceous:* Italy.

Sphaerostromella Yabe & Sugiyama, 1931a, p. 123 [**S. shikokuensis;* OD]. [The skeleton is spherical with zooids like a bryozoan. It has been considered to be a bryozoan (Kühn, 1939b), hydrozoan (Flügel, 1961b), or not a stromatoporoid (Flügel & Flügel-Kahler, 1968).] *Carboniferous:* Japan.

Stromactinia Vinassa de Regny, 1911, p. 19 [**S. triassica* Vinassa de Regny, 1911, p. 20; OD]. [Steiner (1932) related this genus to *Ellipsactinia.* Flügel (1961b, p. 71) placed it in the alga *Sphaerocodium.*] *Upper Triassic:* Hungary (Lake Balaton).

Stromaporidium Vinassa de Regny, 1915, p. 108 [**S. globosum;* OD]. [The genus has been placed in the Hydrozoa (Vinassa de Regny, 1915), algae (Parona, 1928; Sugiyama, 1939), or *incerta sedis* (Flügel & Sy, 1959).] *Upper Triassic:* Indonesia.

Thalaminia Steinmann, 1878, p. 112 [**Ceriopora crispa* Goldfuss, 1826, p. 38; OD]. [According to Flügel (1961b, p. 71), this is a nonstromatoporoid sponge, but Finks, Reid, and Rigby (2004) did not include it with the Porifera.] *Upper Jurassic–Lower Cretaceous:* France.

SYSTEMATIC DECRIPTIONS OF THE CLASS AND ORDER UNCERTAIN: FAMILY DISJECTOPORIDAE

COLIN W. STEARN

The reef facies of the Permian and Late Triassic in the Tethyan faunal realm contains encrusting and domical carbonate fossils of organisms composed of rods that form a framework. These fossils are now composed of calcite but may originally have been aragonite, as many show recrystallization microfabrics. Their systematic position has been controversial, and they have commonly been placed in the Hydrozoa (KÜHN, 1939b; LECOMPTE, 1956; FLÜGEL & SY, 1959) and also referred to as late Paleozoic stromatoporoids. Like the stromatoporoids, their framework skeleton is commonly traversed by tabulated longitudinal and tangential canals or tubes. These have suggested an affinity to the Cnidaria and particularly to the Hydrozoa, but similar tubes are found in several groups of hypercalcified sponges. Now that the Paleozoic stromatoporoids are recognized as having structures closely resembling living hypercalcified sponges, the disjectoporids are here tentatively placed in the Porifera, but their affinity with the major groups of this phylum is obscured by their total lack of preserved spicules.

The spongiomorphs, Middle Triassic to Upper Cretaceous carbonate fossils, are composed of a framework of largely longitudinal rods that resembles that of the disjectoporids. They have been linked to the disjectoporids and also considered to have been hydrozoans (e.g., FLÜGEL & SY, 1959). However, recent work by GAUTRET and associates (GAUTRET, EZZOUBAIR, & CUIF, 1992; GAUTRET, DAUPHIN, & CUIF, 1994) has shown that the spongiomorphs are cnidarians related to the scleractinian superfamily Poriticae GRAY, 1842. They are therefore not considered further in this volume devoted to the hypercalcified sponges.

Class and Order UNCERTAIN (?DEMOSPONGIAE or ?CALCAREA)

Family DISJECTOPORIDAE Tornquist, 1901

[Disjectoporidae TORNQUIST, 1901, p. 1121; LECOMPTE, 1956, p. 138; KÜHN, 1939b, p. 48; FLÜGEL & SY, 1959, p. 14] [=Coenostromidae WAAGEN & WENTZEL, 1887, p. 925, *partim*; =Coenostromatidae WENTZEL, 1889, p. 18; *non* Coenostromatidae WAAGEN & WENTZEL; STEARN & others, 1999]

Laminar, incrusting, and irregular carbonate skeletons composed of a three-dimensional meshwork of longitudinal and tangential rods (trabeculae), thickened and fused where they intersect, enclosing rounded interspaces, forming an irregular grid in longitudinal sections. Skeletal framework traversed by long, tabulated tubes (canals) and irregular, poorly defined, tangential canal systems. *Permian–Triassic.*

Disjectopora WAAGEN & WENTZEL, 1887, p. 947 [**D. milleporaeformis* WAAGEN & WENTZEL, 1887, p. 948; OD]. Laminar, encrusting to domical skeleton composed of longitudinal (or radial) and tangential (or concentric) rods, intersecting and thickening at subspherical nodes to form irregular, three-dimensional grid. Interspace voids rounded, subspherical, irregularly superposed, aligned tangentially in longitudinal section, giving skeleton concentric banding. Tangential rods may appear to unite into tangential sheets, or laminae, perforated by rounded pores approximately the diameter of nodes where rods thicken at intersections. Vaguely defined, locally tabulated, longitudinal, cylindrical voids approximately twice the diameter of interspaces widely scattered in skeleton. In tangential section, rods cut as circles between

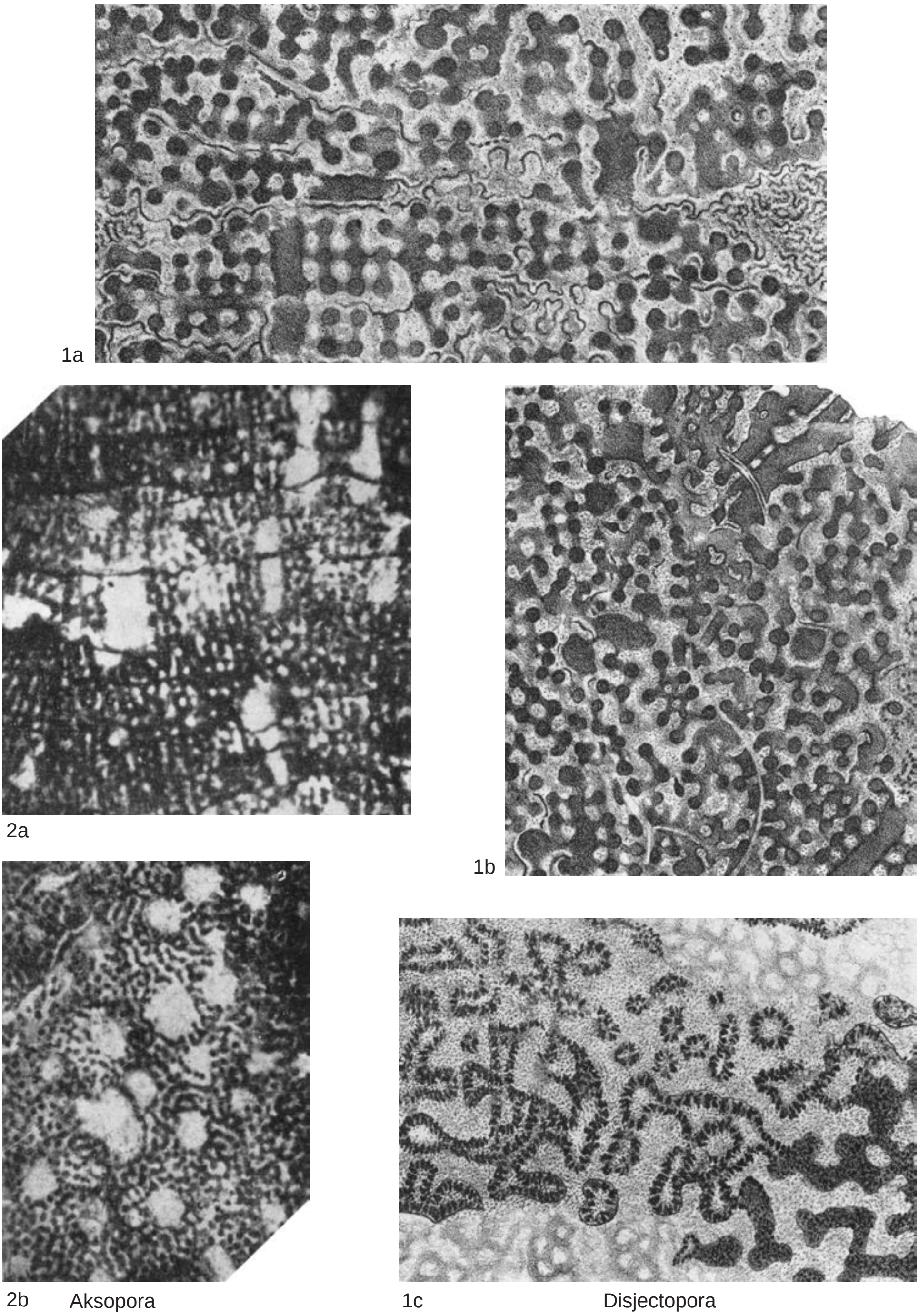

FIG. 208. Disjectoporidae (p. 311–313).

nets of tangential rods and joined into irregular masses perforated by round pores where section cuts nets. Poorly defined, tangential canal systems may be evident. *upper Permian–Upper Triassic, ?Upper Jurassic:* Pakistan, South China, Japan, Italy, Indonesia, ?Canada (eastern continental shelf).——Fig. 208,*1a–c*. **D. milleporaeformis*, Salt Range, Pakistan; *a,* longitudinal section, ×50; *b,* tangential section, ×50; *c,* part of longitudinal section (*a*) in altered state, ×100 (Waagen & Wentzel, 1887).

Aksopora Boĭko, 1970b, p. 50 [497] [**A. tenuitrabeculata*; OD] [=*Aksupora* Boĭko, 1979, p. 55 (type, *A. tenuitrabeculata* Boĭko, 1979, p. 56, *lapsus calami*)]. Skeleton domical, composed of longitudinal rods, regularly joined by tangential rods to form porous, tangential laminae that produce latilamination. Network of rods traversed by long, wide, tabulated, longitudinal canals without walls, passing through several latilaminae. In tangential section, rods joined into network with round interspaces. Astrorhizae inconspicuous. Similar to *Pamiropora* but with longer longitudinal canals. *Upper Triassic:* Pamir Mountains, Tadjikistan.——Fig. 208,*2a–b*. **A. tenuitrabeculata,* holotype, IGD1492, Norian–Rhaetian; *a,* longitudinal section through axis of skeleton showing longitudinal canal system, ×6; *b,* tangential section, ×6 (Boĭko, 1970b).

Arduorhiza Wentzel, 1889, p. 1–24 [**Carterina pyramidata* Waagen & Wentzel, 1887, p. 945–947; OD] [=*Carterina* Waagen & Wentzel, 1887, p. 944, obj., *non* Brady, 1884, a foraminiferan; =*Carta* Stechow, 1921, p. 253, obj; =*Carterinula* Strand, 1928a, p. ?1–8 (see Lecompte, 1956, p. 138; Stock & others, 1992, p. 10; no type species designated, according to Stock & others, 1992)]. Skeleton conical with apex down, formed of highly irregular meshwork of rods without prominent or extensive longitudinal or tangential elements, enclosing subspherical interspaces, traversed by wide, prominent, longitudinal canals without walls, and similar tangential, serpentine, and radial canals prominent in tangential section. Tabulae rare. Type shows some canals divided radially by thin, so-called pseudosepta with swollen tips; canals may be an overgrown, parasitic, or commensural organism (Fig. 209*c*). *upper Permian:* Pakistan (Salt Range), Slovenia.——Fig. 209*a–c*. **A. pyramidata*, Salt Range; *a,* tangential section showing canal systems and subspherical interspaces (matrix is dark), ×50; *b,* longitudinal section (matrix is dark), ×50; *c,* fractured surface showing minute canals with so-called pseudosepta (matrix is white), ×30 (Waagen & Wentzel, 1887).

Balatonia Vinassa de Regny, 1908, p. 13–14 [**B. koechi* Vinassa de Regny, 1908, p. 14–17; OD). Domical to upwardly expanding carbonate skeletons, a few centimeters across, with interior zones of open, irregular structure and peripheral zones dominated by closely set, longitudinal rods. In interior zone, rods, about 50 micrometers wide, irregular in cross section, join to form open network with vermiform interspaces generally radiating outward from axial growth center. In peripheral zones, rods, mostly longitudinal, anastomosing, joined at intervals by swelling that may be aligned locally tangentially but not sufficiently to produce concentric laminae or marked latilamination. In tangential section of peripheral zones, rods of irregular cross section enclose vermiform and labyrinthine interspaces. Large (up to 0.2 mm diameter), round, longitudinal, sparsely tabulated canals present in the peripheral zones of some specimens or species. *?middle Permian, Upper Triassic:* ?South China, Austria, Hungary.——Fig. 210,*1a–c*. **B. koechi*, Lake Balaton, Hungary; *a,* longitudinal section of peripheral zone, ×5; *b,* tangential section of interior zone, ×5; *c,* longitudinal section, ×7 (Vinassa de Regny, 1911).

Cancellistroma Wu, 1991, p. 98 [**C. ramosa*; OD] [=*Concentristroma* Wu, 1991, p. 99 (type, *C. eucalla*, OD); =*Tubulistroma* Wu, 1991, p. 100 (type, *T. irregularis*, OD); =*Fungistroma* Wu, 1991, p. 101 (type, *F. daemonia*, OD)]. Skeleton ramose, highly irregular or encrusting, composed of longitudinal and tangential rods, swollen at their intersections, forming a grid in which one or the other is more prominent. Skeleton traversed by longitudinal tubes or canals wider than interspaces between rods, in some species of several different sizes. Tangential canal systems present in some species. *middle Permian:* China (Guangxi).——Fig. 211,*1*. **C. ramosa*, holotype, longitudinal section, No. XB36-4-5, Maoku Formation, Xiangbo, ×2 (Wu, 1991).

Irregulatopora Waagen & Wentzel, 1887, p. 951 [**I. undulata* Waagen & Wentzel, 1887, p. 952; OD]. Laminar to encrusting skeleton of highly irregular longitudinal and tangential rods, thickened to nodes at their intersections, enclosing rounded voids in both longitudinal and vertical sections, forming an irregular meshwork penetrated by longitudinal and tangential canals. Longitudinal canals short, without walls, subcircular in cross section, with widely scattered tabulae. Tangential canals irregular, short, vermiform openings in meshwork, without evident pattern. Similar to *Disjectopora* but more irregular. *upper Permian, ?Upper Triassic:* Pakistan, ?Indonesia.——Fig. 211,*2a–b*. **I. undulata*, Salt Range, Pakistan; *a,* tangential section, ×5; *b,* longitudinal section, dark areas are interspaces or canals, ×38 (Waagen & Wentzel, 1887).

Pamiropora Boĭko, 1970b, p. 49 [492] [**P. concentrica*; OD]. Skeleton domical, irregular to columnar, composed of distinct axial and peripheral zones. In axial zone, rods merge into continuous network to enclose longitudinal cylindrical canals. In peripheral zone, rods (about 50 micrometers across) largely separate but joined at intervals to form dense laminae. Tabulated, longitudinal canals (about 0.3 mm in diameter) common in

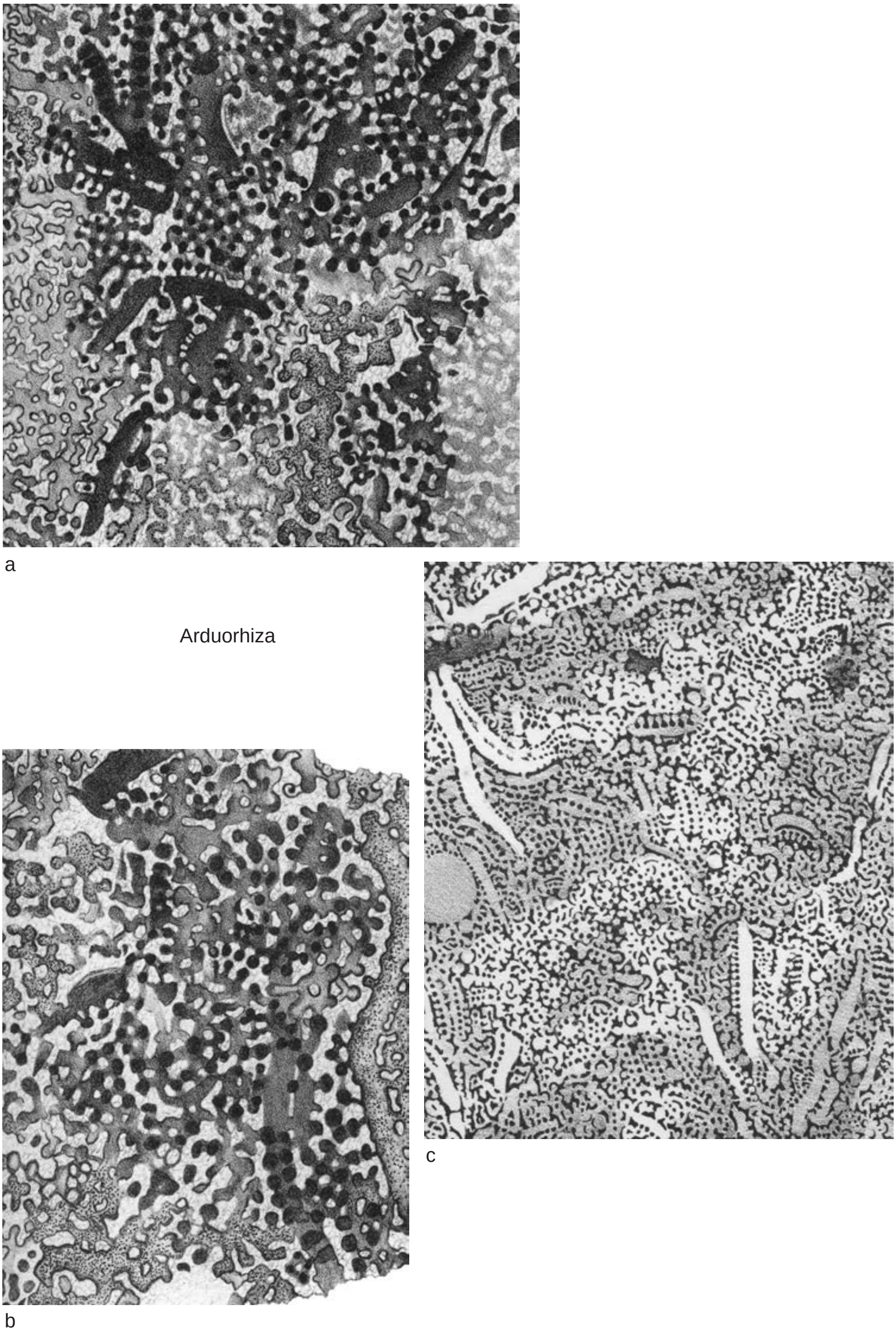

FIG. 209. Disjectoporidae (p. 313).

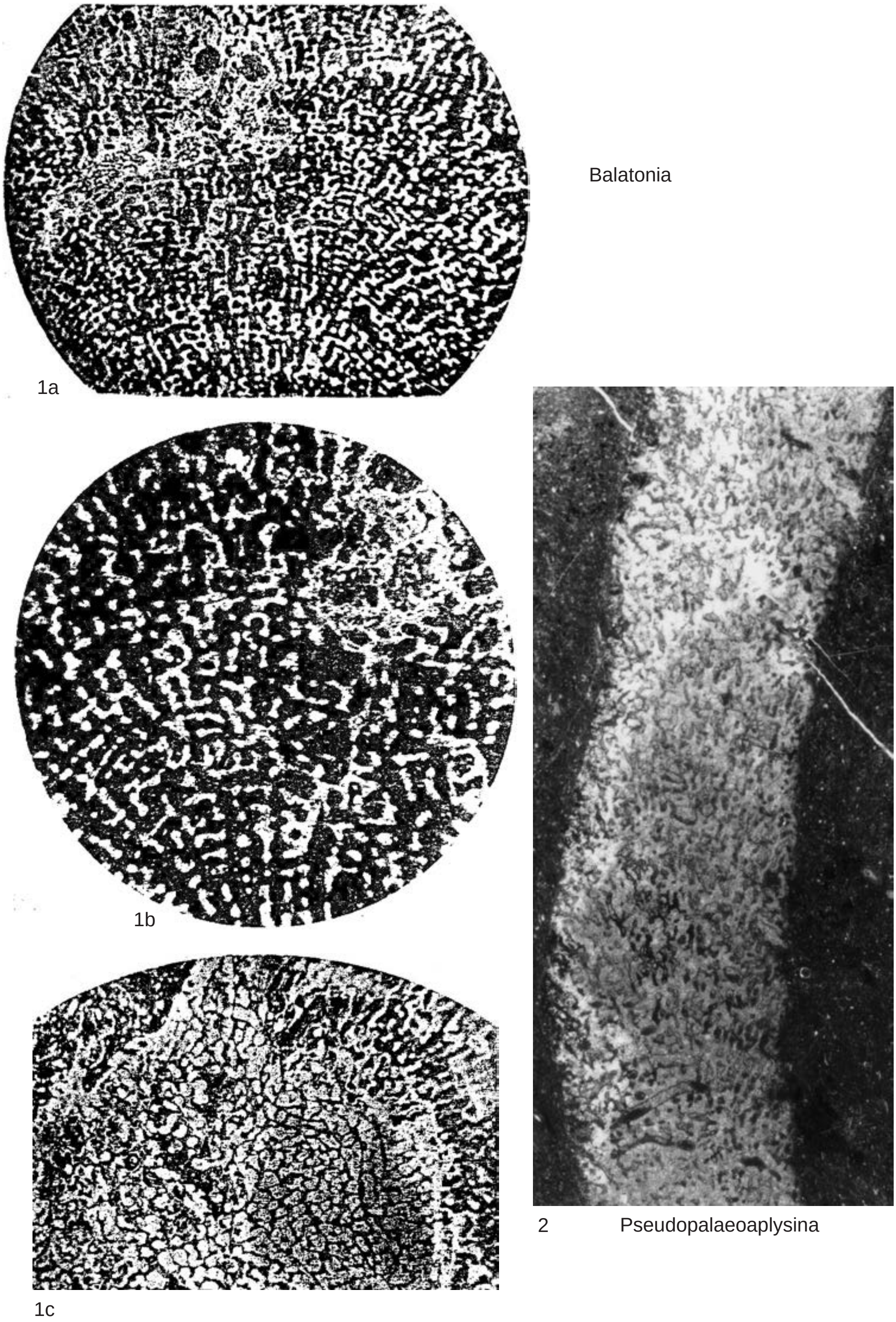

FIG. 210. Disjectoporidae (p. 313–319).

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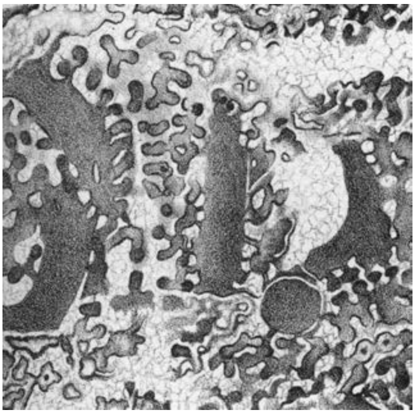
Cancellistroma



2a Irregulatopora

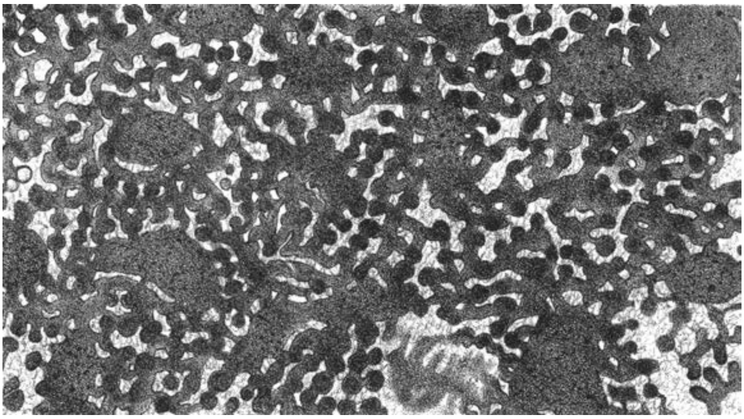


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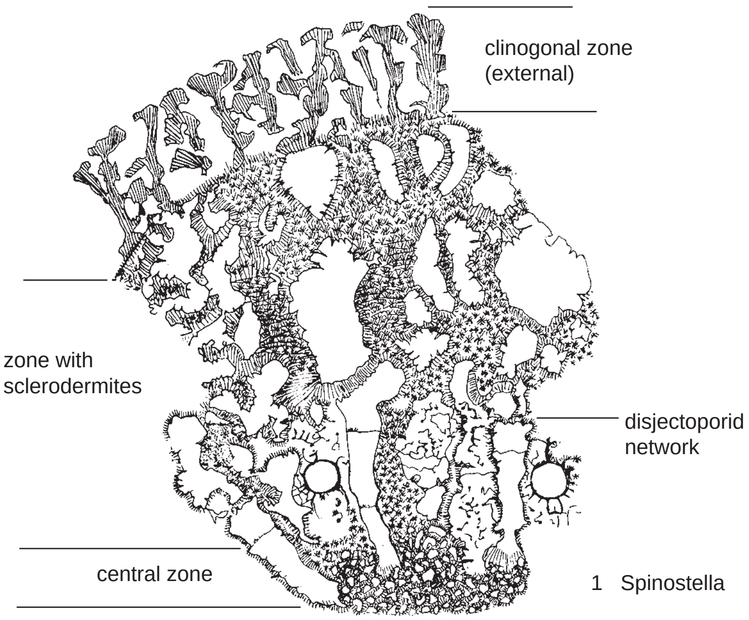
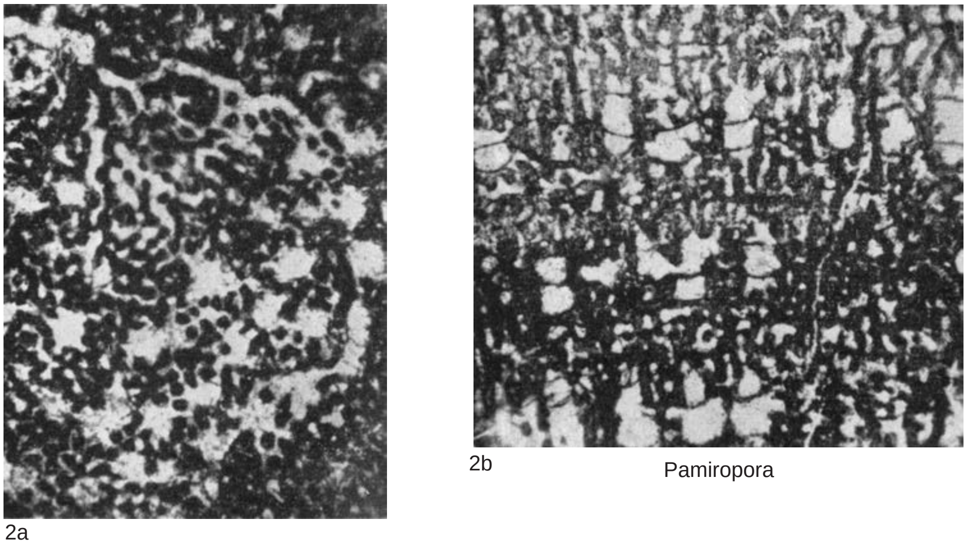
FIG. 211. Disjectoporidae (p. 313).



1 Spinostella



Pamiropora

FIG. 212. Disjectoporidae (p. 313–320).

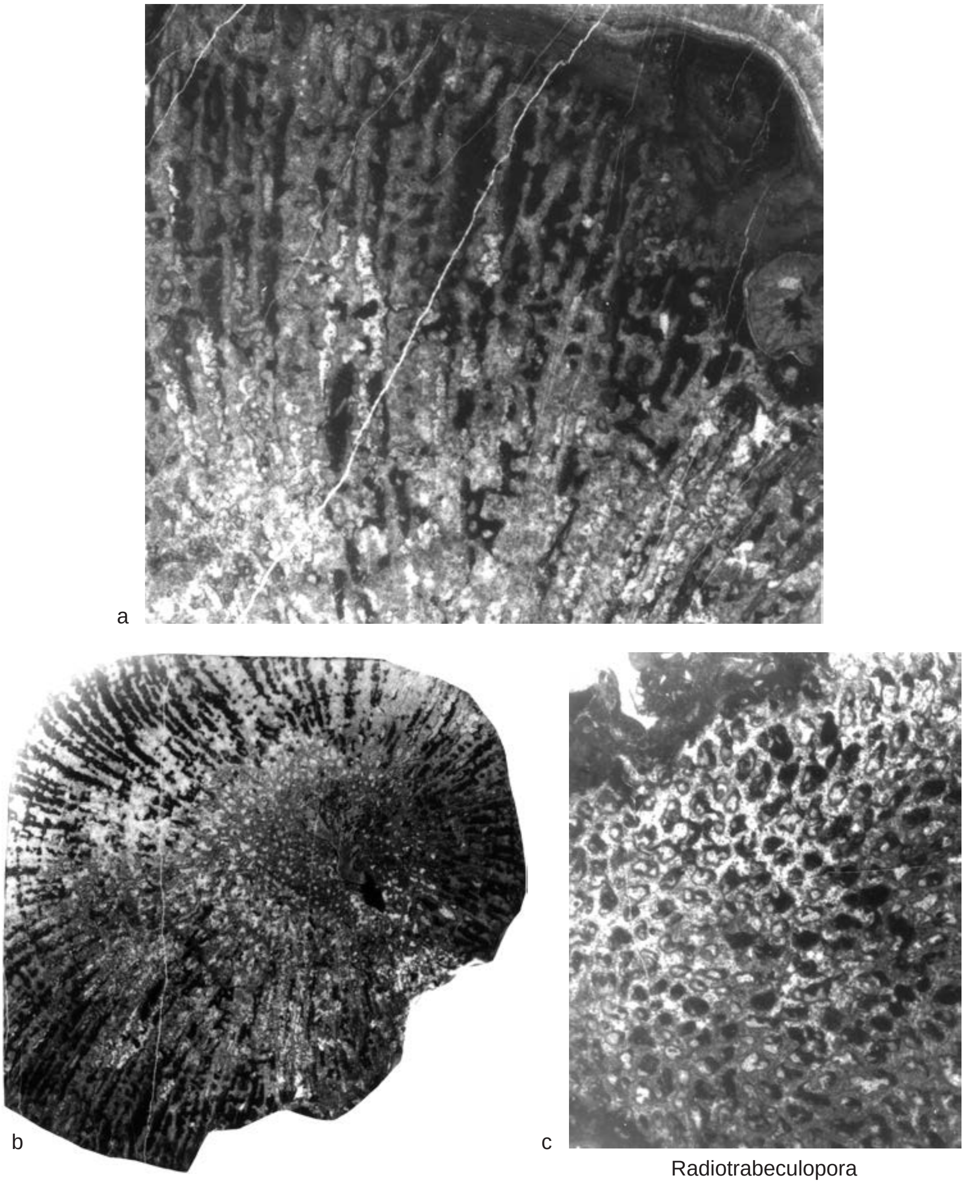


FIG. 213. Disjectoporidae (p. 319–320).

peripheral zone, in concentric zones separated by zones without canals, resulting in prominent latilamination. In tangential section, smaller canals in form of astrorhizae common. *Upper Triassic:* Tadjikistan (Pamir Mountains).——FIG. 212,*2a–b*. **P. concentrica; a*, longitudinal section, peripheral zone, ×16; *b,* tangential section showing astrorhiza and cut rods, IGD 1500, Norian–Rhaetian, southeastern Pamirs, ×16 (Boǐko, 1970b).

Pseudopalaeoaplysina FAN, RIGBY, & ZHANG, 1991, p. 66 [**P. sinensis;* OD]. Skeleton thin plate (about 0.5 mm), apparently attached at one edge, with smooth lateral sides, composed of rods fanning outward and upward from axial plane. Rods dividing outward, discontinuous in longitudinal section, circular in cross section, or more commonly united irregularly laterally to enclose longitudinal interspaces of circular, labyrinthine, and serpentine cross sections.

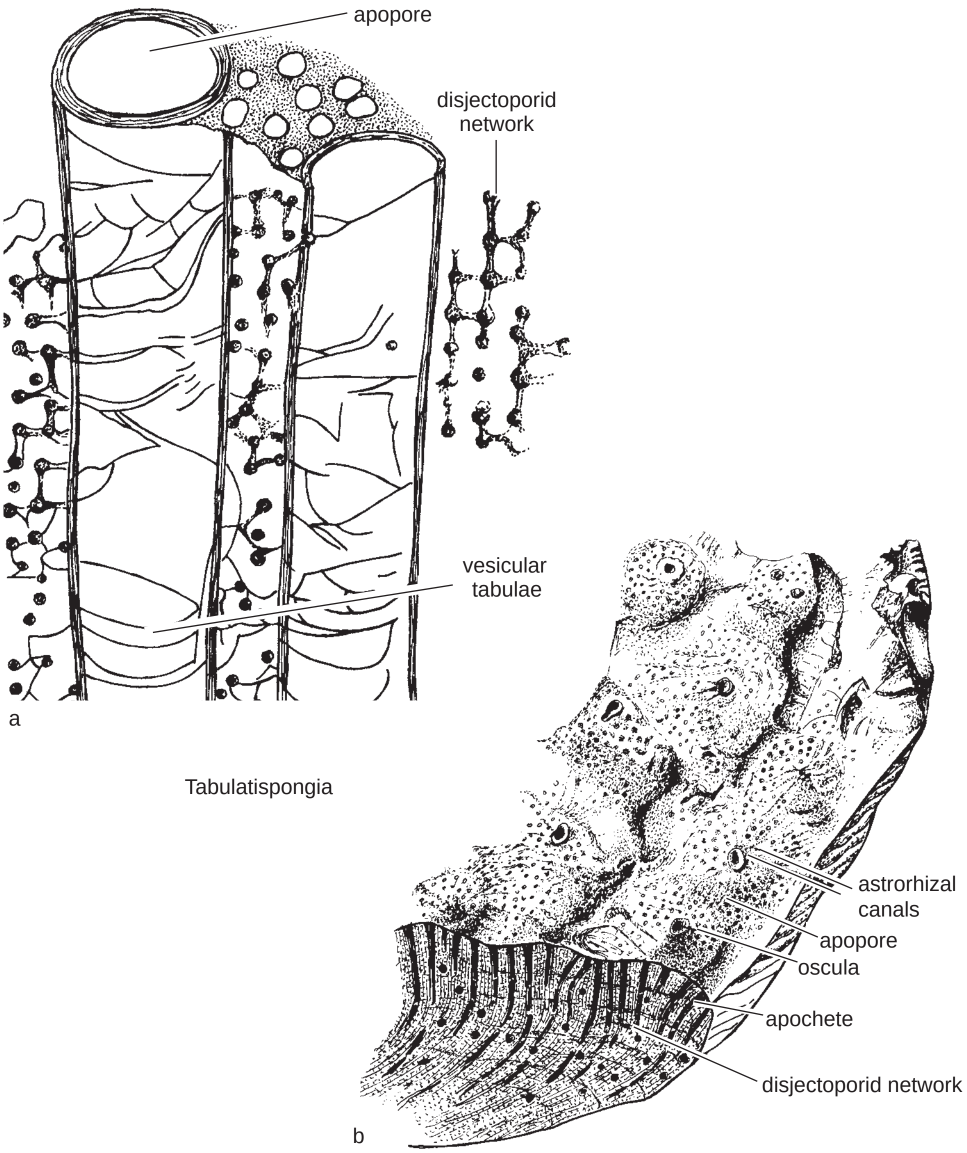


FIG. 214. Disjectoporidae (p. 320).

Interspaces, where circular in section, may resemble longitudinal canals but not crossed by dissepiments or tabulae and completely infiltrated by sedimentary matrix. Tangential structures inconspicuous. *middle Permian:* China (Guangxi).——FIG. 210,*2*. **P. sinensis*, holotype, IG0094, Maoku Formation, Xiangbo, longitudinal section, ×2 (Stearn, 2010a).

Radiotrabeculopora FAN, RIGBY, & ZHANG, 1991, p. 56 [**R. xiangboensis;* OD] [=*Tubulispongia* WU, 1991, p. 35 (type, *T. concentrica,* OD); =*Flabellisclera* WU, 1991, p. 36 (type, *F. discreta,* OD); =*Gigantosclera* WU, 1991, p. 38 (type, *G. deformis*, OD); =*Gracilitubulus* WU, 1991, p. 39 (type, *G. perforatus*, OD); =*Fungispongia* WU, 1991, p. 39 (type, *F. circularis*, OD) (see FINKS & RIGBY, 2004d, p. 624)]. Skeleton irregular, encrusting to columnar, composed of central and peripheral zones. Peripheral zones composed of longitudinal rods, merging and dividing but generally parallel, interrupted by numerous small pores, united by short bridges (nodelike swellings) that are not aligned to form persistent tangential structures, in type species breaking up into nodes (i.e., beaded). Interspaces longitudinally elongated, approximately width of rods (about 0.5 mm). In axial zones, rods merge to enclose subcylindrical interspaces, producing a continuous network structure traversed by astrorhizal canals in some species. *lower Permian–upper Permian:* USA (California), South China (Guangxi, Yunnan), Tunisia.——FIG. 213*a–c*. **R. xiangboensis*, Maoku Formation, Xiangbo, China; *a,* holotype, longitudinal section in peripheral zone showing rods joined by short bridges, IG 5154, ×5; *b,* section of whole holotype showing peripheral and axial zones, IG 5154, ×2; *c,* tangential section of axial zone, paratype, IG 5155, ×4 (Stearn, 2010a).

Spinostella TERMIER & TERMIER, 1980, p. 4 [**S. praecursor;* OD; no number or repository given]. Skeleton cylindrical; composed of three zones: an axial zone of chaetetid-like, honeycomb structure; an intermediate zone of irregular, spherulitic, structural elements traversed by wide, open canals lined with small spines, and rarer tabulated canals; an outer zone of irregular but dominantly radial structural elements of fasciculate microstructure, and a surface showing canals of astrorhizal form. [This is not a typical disjectoporid and does not have the framework of rods of this group; however, it was placed by TERMIER & TERMIER (1980) in the family Disjectoporidae. The holotype, as they noted, shows many features of the Ceratoporellidae.] *upper Permian:* Tunisia (Djebel Tebaga).——FIG. 212,*1*. **S. praecursor*, drawn from holotype; section of segment of cylindrical skeleton from axial to peripheral zones, ×57.5 (Termier & Termier, 1980).

Tabulatispongia TERMIER & TERMIER, 1977a, p. 30 [**T. stromatoporoides;* OD]. Skeleton tabular, encrusting, composed or an open, rectilinear, three-dimensional grid of finely fibrous, longitudinal and tangential rods that expand into nodes where they fuse. Longitudinal canals with distinct walls and irregular, numerous tabulae, traverse skeleton, leading to pores on surface at crests of mamelons and centers of tangential astrorhizal canal systems. *upper Permian:* Tunisia (Djebel Tebaga).——FIG. 214*a–b*. **T. stromatoporoides*, ?drawn from holotype; *a,* longitudinal section, diagrammatic, approximately ×25; *b,* longitudinal section and surface diagram, approximately ×1 (Termier & Termier, 1977b).

SPHINCTOZOAN AND INOZOAN HYPERCALCIFIED SPONGES: AN OVERVIEW

B. SENOWBARI-DARYAN and †J. KEITH RIGBY SR.

INTRODUCTION

Many sponges that secrete a rigid skeleton composed of calcium carbonate, which may be aragonite or calcite (high- or low-Mg calcite), are included in the hypercalcified sponges in TERMIER and TERMIER (1973, 1977). Additionally, different types of spicular skeletons of calcite or siliceous mineralogy may be embedded within the rigid skeletons. Sponges with chambered construction are included in the group, termed Sphinctozoa, and those nonchambered representatives are included in the group termed Inozoa. These two groups were united in classic works in the Pharetronida (a division now regarded as obsolete; see Glossary, p. 410). Because of the polyphyletic nature of both of these groups, these terms cannot be used as systematic categories for classification of these sponges. The terms Sphinctozoa and Inozoa are used here for morphologically chambered or nonchambered sponges, respectively, without taking their systematic position into consideration.

The chambered Sphinctozoa and nonchambered Inozoa have been previously assigned to the Calcarea but are now largely included in the Demospongiae. They represent polyphyletic hypercalcified sponge groups and range stratigraphically from the Cambrian to the Recent. Their external and internal morphology, occurrence of spicules, mineralogy and microstructure of their rigid skeletons, their roles as reef builders, their stratigraphic record and geographic distribution, patterns of evolution and extinction, and a short review of the classification are discussed. A list of known sphinctozoan and inozoan genera, with their stratigraphic occurrences, are also presented here (p. 387–395).

Hypercalcified sponges, including sphinctozoans, inozoans, stromatoporoids, archaeocyaths, and chaetetids are important groups of carbonate-producing invertebrates occurring in Phanerozoic reef ecosystems and in shallow-water biotopes. Archaeocyaths in the Cambrian, stromatoporoids in the Ordovician to Devonian, and inozoans, sphinctozoans, and chaetetids in the late Paleozoic and Mesozoic, particularly in the Permian and Triassic, are the main inhabitants of shallow-water biotopes and reef-building organisms.

The evolution of inozoan and sphinctozoan hypercalcified sponges was influenced by two significant events, one at the end of the Paleozoic era and the other at the end of the Triassic period, and by several other relatively minor extinction events. More than 90% of sponge genera became extinct during both of those major events, and no described Permian sponge species have been recognized in pioneer Middle Triassic reefs. However, several morphologically identical or similar genera, the so-called Lazarus taxa (JABLONSKI, 1986), reappear in the Upper Triassic (Norian) record. The event at the end of the Triassic was also dramatic for both the inozoans and sphinctozoans, for almost all documented sponge taxa in those groups became extinct. Only one genus of sphinctozoan, *Stylothalamia,* survived the Triassic-Jurassic boundary event. Again, morphologically identical or similar sphinctozoan and inozoan taxa reappear in the Upper Jurassic record.

HISTORY

Because most Recent sponges bear skeletal components composed of spongin or spicules, fossil sponges with a rigid skeleton but without spicules (due to their initial lack or to loss related to recrystallization) have been assigned to different groups of organisms. For example, the stromatoporoids have been assigned to hydrozoans. Some have been classified as a separate phylum (phylum Archaeocyatha) or to other fossil groups, like the Chaetetida. All of these groups are now included in the Porifera (HOOPER, VAN SOEST, & DEBRENNE, 2002; Stromatoporoidea: STEARN, 1972, 1975a, 2010b; VACELET, 1985; WOOD, 1987, 1990a; STEARN & PICKETT, 1994; STEARN & others, 1999; COOK, 2002; Archaeocyatha: HARTMAN & GOREAU, 1970, 1975; GRAY, 1980; DEBRENNE & VACELET, 1984; RIGBY & others, 1993; DEBRENNE & ZHURAVLEV, 1994; DEBRENNE, ZHURAVLEV, & KRUSE, 2002; Chaetetida: REITNER & WÖRHEIDE, 2002; and see Classification and Evolution of the Fossil and Living Hypercalcified Chaetetid-Type Taxa, p. 105–114).

The so-called Pharetronida [including the chambered Sphinctozoa STEINMANN (1882) or Thalamida DE LAUBENFELS (1955), and nonchambered Inozoa STEINMANN (1882), sponges with a rigid calcareous skeleton] were generally attributed to the Calcarea in the past. No special attention was paid to their spicular skeletons, which may have been embedded within the calcareous rigid skeleton in some representatives of both groups. Detailed investigations during the last half-century, especially those investigations including scanning electron microscopy, have shown that both the sphinctozoan and inozoan groups are polyphyletic in origin. Both appeared for the first time in the Cambrian and occur in the geologic record up to the Recent. Because of their significantly different morphologies, the Sphinctozoa and Inozoa are treated separately on the following pages.

SPHINCTOZOANS

Chambered skeletal construction, with or without spicular skeletons, and with different skeletal mineralogy (aragonitic and calcitic) and microstructure, has developed independently several times in different sponge groups during the geologic past. For example, archaeocyathan chambered sponges are known from the Cambrian and later (e.g., *Archaeosycon, Cerbicanicyathus:* DEBRENNE, ZHURAVLEV, & ROZANOV, 1989; DEBRENNE & WOOD, 1990; DEBRENNE, 1992; ZHURAVLEV, 1989). Other examples include the Silurian agelasid demosponges *Nematosalpinx* and *Aphrosalpinx* (MYAGKOVA, 1955a, 1955b; RIGBY, NITECKI, & others, 1994; FINKS & RIGBY, 2004d), the Cambrian heteractinid chambered sponges *Nucha, Wagima,* and *Jawonya* (PICKETT & JELL, 1983; KRUSE, 1987; PICKETT, 2002), the Jurassic–Cretaceous calcarean chambered sponges *Barroisia* MUNIER-CHALMAS in STEINMANN, 1882, and *Muellerithalamia* REITNER, 1987c, among others, along with the hexactinellid chambered sponges (*Casearia* QUENSTEDT, 1858, *Dracolychnos* WU & XIAO, 1989; RIGBY, WU, & FAN, 1998, Triassic–Jurassic), and demosponge chambered sponges (e.g., *Celyphia* POMEL, 1872; *Radiocella* SENOWBARI-DARYAN & WURM, 1994). These may be the majority of late Paleozoic and Mesozoic chambered sponges. Because of the lack of rigid calcareous skeletons, representatives of chambered hexactinellids and lithistid demosponges (*Radiocella*) are not treated in this section, though chambered archaeocyaths are discussed below (see systematic descriptions of the Archaeocyatha, p. 1025–1035).

EXTERNAL MORPHOLOGY

We include in the term external morphology all features of sphinctozoan sponges that are visible and recognizable from the skeletal exterior. External features of sphinctozoan sponges include: (1) outer segmentation; (2) sponge shape; (3) chamber shape; (4) arrangement of the chambers; (5) inhalant canals or ostia in exowalls and their patterns; and (6) exhalant canals or oscula. The major morphological elements of sphinctozoan sponge skeletons are shown in Figure 215.

Outer Segmentation

Chambered organization is the most important characteristic feature of sphinctozoan sponges, separating them from other hyper-

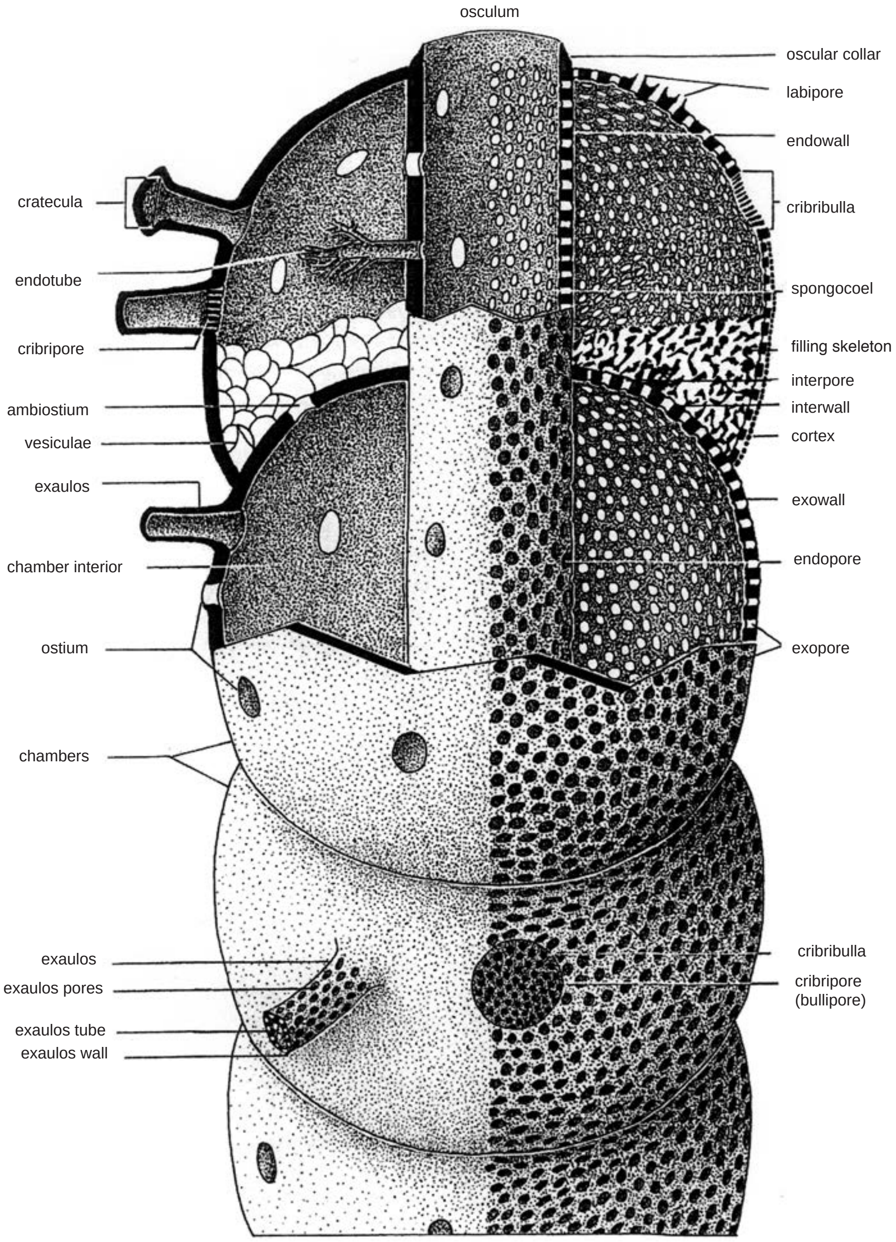


FIG. 215. Major morphological skeletal elements of sphinctozoan sponges. On the right, main characteristic features of the porate forms, and on the left, aporate forms. Of the filling skeleton structures, only the reticular type, on the right, and the vesicular type, on the left, are shown in the interior of the last chamber. Skeletal elements like those in the aporate sponges may also occur in porate representatives (adapted from Senowbari-Daryan, 1990).

calcified sponge groups. Outer segmentation corresponds generally to internal segmentation. However, due to overlap of earlier chambers by younger, later chambers in some representatives, especially those taxa with crescentlike chambers (e.g., the Triassic genus *Senowbaridaryana,* Fig. 216–217, or *Zardinia,* Fig. 218), outer segmentation may be totally

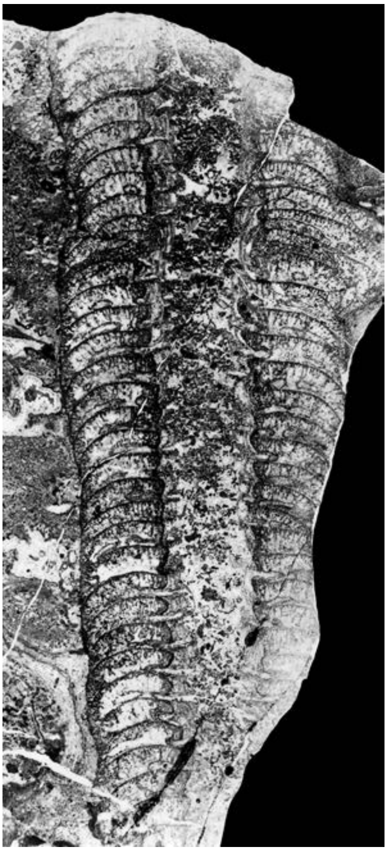


FIG. 216. *Senowbaridaryana hydriotica* SENOWBARI-DARYAN, 1990. Outer segmentation of this porate and siphonate sphinctozoan is totally lacking, but the chambered construction can be seen after cutting the specimen in longitudinal section. Crescentlike chambers contain reticular filling skeleton; Carnian, Triassic, Hydra, Greece, ×1.7 (Senowbari-Daryan & Schäfer, 1983).

lacking or hard to recognize. The chambered sphinctozoan construction of such sponges is recognizable only after cutting into their skeletons in longitudinal sections. Transverse sections of such sponges appear as several concentric circular walls arranged one inside the other. Outer annulation of skeletons, which generally reflects growth stages, does not consistently indicate internal segmentation.

Single-chambered sphinctozoans are very rare, but have been reported from the Cambrian of Australia (*Nucha* PICKETT & JELL, 1983; *Blastulospongia* PICKETT & JELL, 1983; *Jawonya* KRUSE, 1983; *Wagima* KRUSE, 1987; and later only from the Upper Triassic of Vancouver Island, Canada, as the species *Nucha*? *vancouverensis* STANLEY, 1998).

Sponge Shape

Those multichambered sphinctozoan sponges with a constant chamber diameter are usually cylindrical in shape (Fig. 219.3–219.7). Club-shaped skeletons occur in some taxa (e.g., the Permian species *Lemonea conica* SENOWBARI-DARYAN, 1990, or *Senowbaridaryana conica,* Fig. 217, Fig. 220), where the sponge or chamber diameters increase during sponge growth. Representatives of sheetlike or flattened forms also occur with hemispherical chambers arranged in one layer (e.g., the Permian genus *Neoguadalupia* ZHANG, 1987) or two layers (e.g., *Platythalmiella* SENOWBARI-DARYAN & RIGBY, 1988), or occur with tubelike chambers (e.g., the Permian genus *Subascosymplegma* DENG, 1981) (Fig. 219.10, Fig. 221). Aggregate forms composed of clusters of chambers (e.g., Permian *Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1998; see Fig. 219.8, Fig. 222), or irregularly shaped sphinctozoans (e.g., *?Polysiphonaria* FINKS, 1997) occur also in Permian and Triassic deposits. Sphinctozoans are usually single, unbranched stems. Dichotomously branched taxa (e.g., *Nevadathalamia ramosa* SENOWBARI-DARYAN & REID, 1987) or rejuvenated skeletons are rare (e.g., *Panormida priscae* SENOWBARI-DARYAN, 1980b; Fig. 223). Marginal displacements of chamber walls have been observed, for example, in the Triassic species *Vesicocaulis reticuliformis* JABLONSKY, 1972 (SENOWBARI-DARYAN, 1990).

Shape of Chambers

Spherical to hemispherical chambers are the most common shapes in sphinctozoan sponges, as, for example, in some species of *Colospongia* or *Sollasia* (Fig. 224–225). Other chambers may be barrel shaped, as in some species of *Amblysiphonella,* or crescentlike, as in *Cryptocoelia* (Fig. 226) or *Zardinia* (Fig. 218). Chambers that are flattened rectangular (*Enoplocoelia, Tolminothalamia*),

FIG. 217. *Senowbaridaryana conica* (SENOWBARI-DARYAN & SCHÄFER, 1986). Marginal axial section through the conical sponge. Diameters of crescentlike chambers increase rapidly during growth of the sponge. The chamber interiors contain small tubes that are more or less parallel to the axis of the sponge; Norian, Triassic, Sicily, ×3 (Senowbari-Daryan & Schäfer, 1986).

funnel shaped (*Panormida,* Fig. 223) or tubelike (*Cinnabaria* or *Subascosymplegma,* Fig. 221) occur also in other chambered sponges.

Arrangement of Chambers

The arrangement of chambers in multibranched sphinctozoans may be moniliform. In asiphonate species, hemispherical to subspherical chambers are arranged one above the other, as, for example, in the porate genus *Colospongia* (Fig. 224) or the aporate genus *Sollasia* (Fig. 225). Chamber arrangement may be catenulate, where ringlike chambers are stacked one above the other in siphonate species, as in the porate genera *Amblysiphonella* (Fig. 227) and *Polytholosia* or in the aporate genus *Girtyocoelia* (Fig. 228). Occurrences of several egg-shaped or cystlike chambers, arranged in one or more glomerate layers (like kernels of an ear of corn) around a spongocoel, are known from chambered sponges with either aragonitic or Mg-calcitic skeletons (Fig. 219.5–219.6, Fig. 220, Fig. 229–230). A glomerate arrangement of the chambers was developed very early in calcitic chambered sponges, in the Cambrian chambered archaeocyath genus *Polythalamia* DEBRENNE & WOOD (1990; see also FINKS & RIGBY, 2004d, p. 695, fig. 459,*2a–c;* and see also Fig. 82.3) and as well in the Silurian genera *Palaeoscheda* MYAGKOVA (1955a) and *Aphrosalpinx* MYAGKOVA (1955b; see RIGBY, NITECKI, & others, 1994). Arrangement of cystlike chambers in one or more layers around the spongocoel occurs also in Carboniferous

FIG. 218. *Zardinia cylindrica* SENOWBARI-DARYAN & SCHÄFER, 1983. Longitudinal section of sponge, with Mg-calcite mineralogy, exhibiting a retrosiphonate type of spongocoel and crescentlike chambers; because of overlap of older chambers by younger ones, the exowalls are thicker than interwalls and endowalls; *Z. cylindrica*, like other species of the genus, is characterized by tubular canals that diverge upward and outward through internal filling skeleton and chamber walls, to open in exterior of sponge; Carnian, Triassic, Hydra, Greece, ×3 (Senowbari-Daryan & Schäfer, 1983).

and Permian taxa and again, once more, in Norian forms. For example, the Carboniferous and Permian genus *Discosiphonella* INAI, 1936, is characterized by one layer of cystlike chambers around the spongocoel, and the contemporaneous *Cystothalamia* GIRTY (1908a) or *Diecithalamia* SENOWBARI-DARYAN (1990; Fig. 229) by more layers of chambers around the spongocoel (GARICÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004). *Discosiphonella,* as an example of a so-called Lazarus fauna (JABLONSKI, 1986), is not known from the Lower and Middle Triassic but appears again in the Norian Upper Triassic (SENOWBARI-DARYAN & LINK, 1998). The Ladinian–Carnian, Mg-calcitic sphinctozoan genus *Alpinothalamia* SENOWBARI-DARYAN, 1990 (Fig. 230) is also characterized by chambers that are arranged in more than one layer around the spongocoel. Glomerate arrangement of the cystlike chambers around the spongocoel occurs also in the Jurassic calcarean genus *Thalamopora* (ROEMER, 1840).

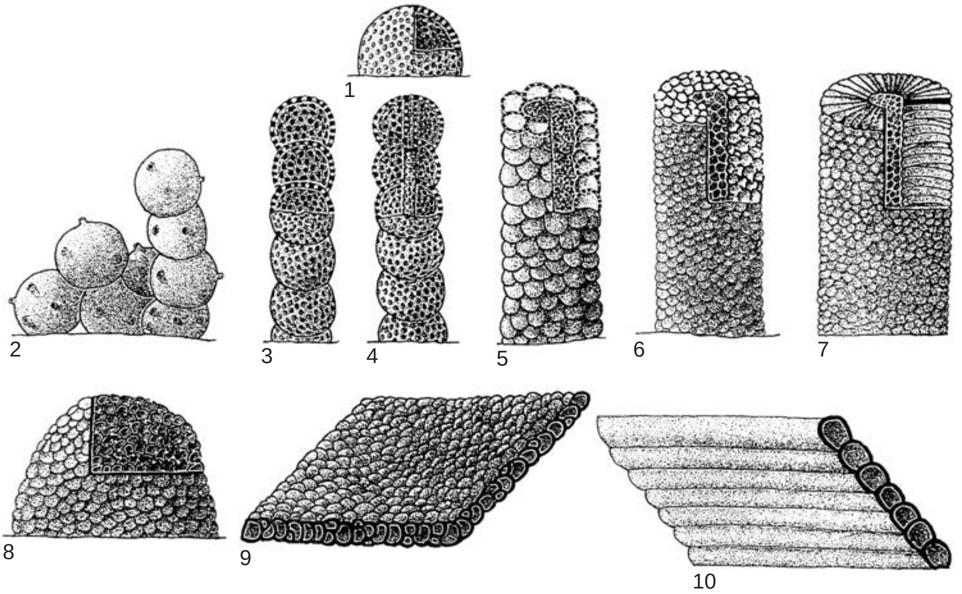


FIG. 219. Main growth shapes of sphinctozoan sponges. *1,* Single chambered (e.g., the heteractind genus *Blastulospongia* PICKETT & JELL); *2,* moniliform (e.g., *Celyphia* POMEL); *3,* moniliform (e.g., *Colospongia* LAUBE); *4,* catenulate (e.g., *Amblysiphonella* STEINMANN); *5,* monoglomerate (e.g., *Discosiphonella* INAI); *6,* polyglomerate (e.g., *Cystothalamia* GIRTY); *7,* stratiform (e.g., *Lemonea* SENOWBARI-DARYAN); *8,* uviform (e.g., *Uvanella* OTT); *9,* platyform, stratiform (e.g., *Neoguadalupia* ZHANG); and *10,* platyform, tubular (e.g., *Subascosymplegma* DENG) (adapted from Senowbari-Daryan, 1990).

Inhalant Canals or Ostia in Exowalls and Their Patterns

Two kinds of inhalant canal systems are recognized in sphinctozoan sponges, based on their sizes and their distribution patterns in the exowall. These systems were termed porate and aporate by SEILACHER (1962). The porate type is characterized by small openings, termed pores (or exopores), that are usually less than 1 mm in diameter and are evenly distributed in the external wall. The numbers of such pores may reach 100 or more in a single chamber. These pores may have circular or oval cross sections. In some genera, such as in the Triassic genus *Nevadathalamia* or the Recent *Vaceletia,* spinelike elements may extend into the interior of the pores. Most pores, however, are simple, though dichotomously branched, multibranched, and labyrinthic-branched pore systems occur in some genera (Fig. 231).

The Permian species *Follicatena permica* SENOWBARI-DARYAN, 1990 (Fig. 232), which has a chamber construction like that of *Colospongia,* has chamber walls with screenlike cribribulla, each with numerous small openings termed cribripores (bullipores). Pores combined with ostia, sometimes termed ostial pores (as in the Upper Triassic species *Colospongia dubia* LAUBE, see SENOWBARI-DARYAN, 1990, pl. 40,*8–9;* FINKS & RIGBY, 2004d, fig. 462,*2a*), or pores combined with cribribulla with cribripores (as in the Upper Triassic species *Colospongia wahleni* SENOWBARI-DARYAN & STANLEY, 1988), are known from exceptional examples.

Aporate sphinctozoans are characterized by chamber walls with large openings, termed ostia, which are usually larger than 1 mm in diameter, and usually fewer than 10 ostia occur per chamber. The ostia may be depressed or have elevated rims, or even have rims that are extended, tubelike, as, for example, in *Girtyocoelia* (Fig. 228). The

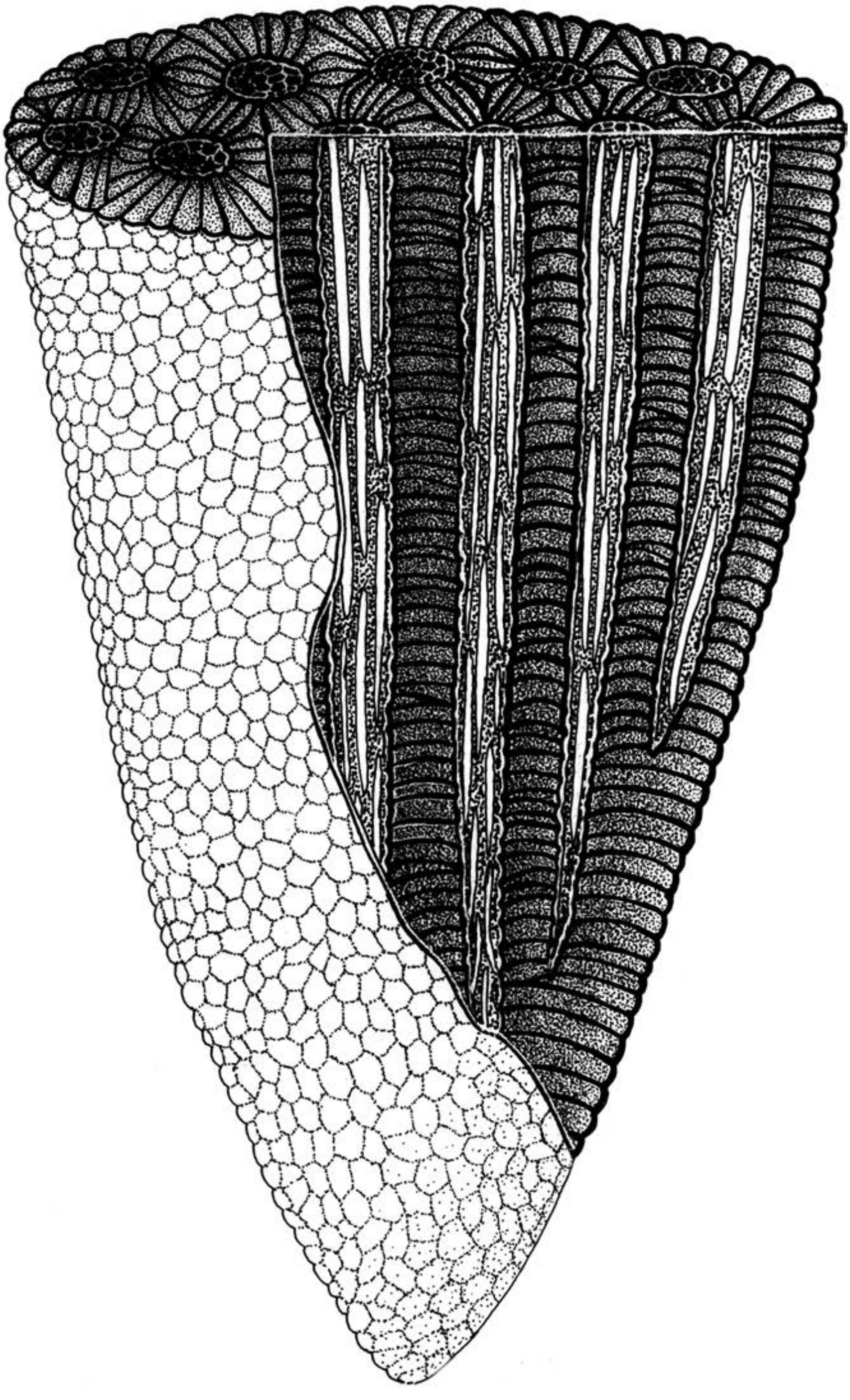


FIG. 220. Reconstruction of *Lemonea conica* SENOWBARI-DARYAN showing the conical shape of the sponge, bundles of spongocoels, and the stratiform chambers arranged radially around the spongocoels; chamber walls are perforated, but the pores are not shown; schematic, not to scale (Senowbari-Daryan, 1990).

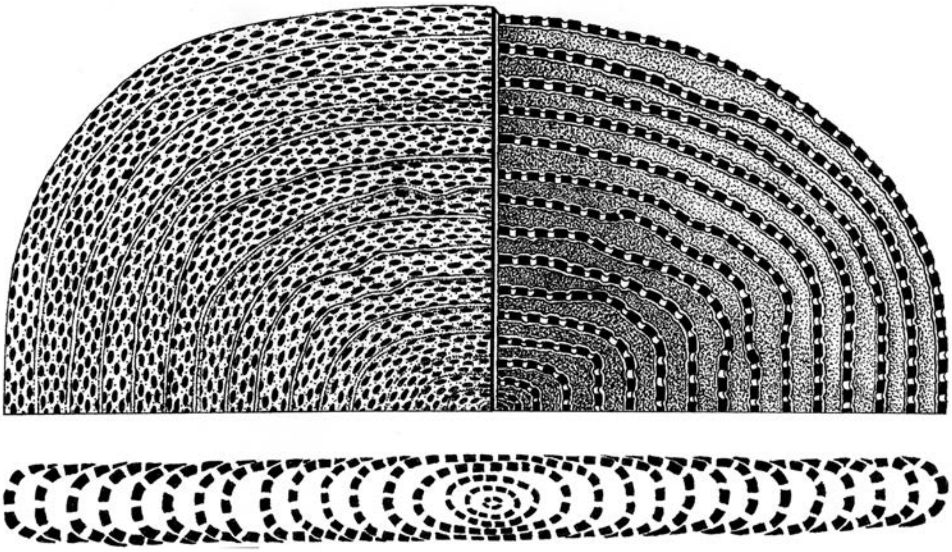


FIG. 221. Reconstruction of *Subascosymplegma oussifensis* (TERMIER & TERMIER, 1977b). The sheetlike or hemispherical sponge is composed of arcuate, tubelike chambers, and the younger chambers overlap preceding chambers; upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Senowbari-Daryan & Rigby, 1988).

latter openings are called exaules (sing., exaulos). The exaulos tube may be perforated with exaulos pores, as, for example, in the Permian genus *Exaulipora* RIGBY, SENOWBARI-DARYAN, & LIU, 1988 (Fig. 222), or it may be aporate, as in *Girtyocoelia* (Fig. 228). The inner end of some exaules in aporate forms may have screenlike cribribulla, like those in some of the porate sphinctozoans, such as in *Exaulipora* (Fig. 222).

Exhalant Canals or Oscula

The tops of some siphonate sphinctozoan sponges, like *Amblysiphonella,* may have a single large opening, an osculum, or several openings, or oscula, grouped as canal bundles and commonly located axially. Such axial canal bundles may occupy more than 70% of the whole sponge diameter, as, for example, in the Triassic species *Diecithalamia polysiphonata* DIECI, ANTONACCI, & ZARDINI, 1968 (Fig. 229). Where a retrosiphonate axial tube or spongocoel is formed by downward extension of upper chamber walls (Fig. 233), the diameter of the osculum commonly appears larger than the diameter of the spongocoel. In most other types of constructions (Fig. 233), the diameter of the osculum corresponds to the diameter of the spongocoel.

The spongocoel wall (endowall) may have pores or openings of the same size as those in the exowalls or interwalls, but they also may be different (Fig. 227–228). Several individual spongocoels may be present in large, laterally extended sphinctozoan sponges, as in the Triassic species *Cryptocoelia lata* SENOWBARI-DARYAN & SCHÄFER, 1983 (Fig. 234), or separate spongocoel bundles may be developed, as in the Permian species *Lemonea conica* SENOWBARI-DARYAN, 1990 (Fig. 220). In the Triassic *Zanklithalamia multisiphonata* SENOWBARI-DARYAN, 1990, such bundles may pass through the whole sponge body.

Starlike exhalant canal openings, an astrorhizal system, may be developed in a variety of stromatoporoid and inozoan sponges, and have been observed in a few genera of sphinctozoan sponges. In the Ordovician genus *Cliefdenella* WEBBY, 1969, or in the Triassic genus *Tabasia* SENOWBARI-DARYAN, 2005a, exhalant canals end in a starlike astrorhizal system (see WEBBY, 1969, 1979a,

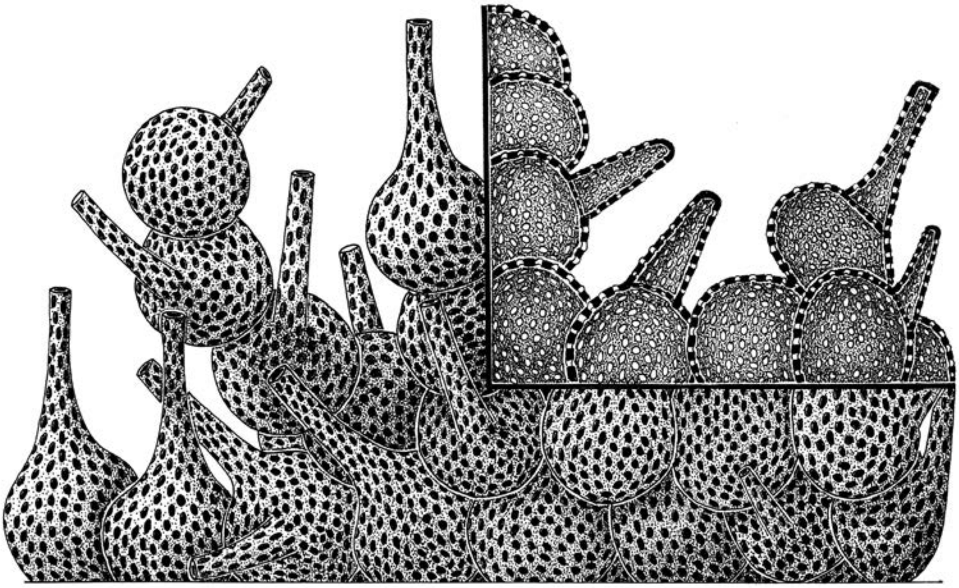


FIG. 222. Reconstruction of *Exaulipora permica* (SENOWBARI-DARYAN), Permian, Guadalupe Mountains, Texas and New Mexico, United States, showing perforated exaulos walls and the cribribulla with cribripores at the base of the exaules; vesiculae occur within the interior of the segment, but they are not shown (Senowbari-Daryan, 1990).

1986; STOCK, 1981; WEBBY & LIN, 1988). In the Permian sheetlike or funnel-shaped species *Guadalupia explanata* (KING, 1943), one side of the sheets commonly has several astrorhizal canals that served as exhalant canals (Fig. 235).

INTERNAL MORPHOLOGY

Internal morphologic elements are characteristic features that can be observed after cutting the skeleton. These features include the internal segmentation and chamber shape, internal walls (interwalls and endowalls) and their characteristics, such as whether they are double or single layered, their thickness, and patterns of perforation. Also included are spongocoels and their formation type, and the types of filling skeletons within chamber interiors.

Internal Segmentation

The internal segmentation, a most important feature of sphinctozoan sponges, usually corresponds to outer segmentation. However, a few taxa, especially those with crescentlike chamber shapes (Fig. 216, Fig. 218), have distinct internal segmentation (see also *Cassianothalamia* REITNER, 1987b; *Uvothalamia* SENOWBARI-DARYAN, 1990), but their outer segmentation is poorly developed, or even totally lacking.

Interwalls, the walls between chambers, may have the same thickness as exowalls of the same chambers, but they also may be different. Perforation patterns of interwalls usually correspond to those of the exowalls, but they also may be different in some taxa, as in some species of *Amblysiphonella* or in *Girtyocoelia* (Fig. 227–228).

Internal Canal System

There are three types of exhalant canal systems in sphinctozoan sponges. These were called the *Colospongia*-type, *Sphaerocoelia*-type, and *Amblysiphonella*-type by SENOWBARI-DARYAN (1990) (Fig. 236). The *Colospongia*-type (Fig. 224, Fig. 236.3) system is without a separate siphon or spongocoel and was called asiphonate by SEILACHER (1962). It is assumed

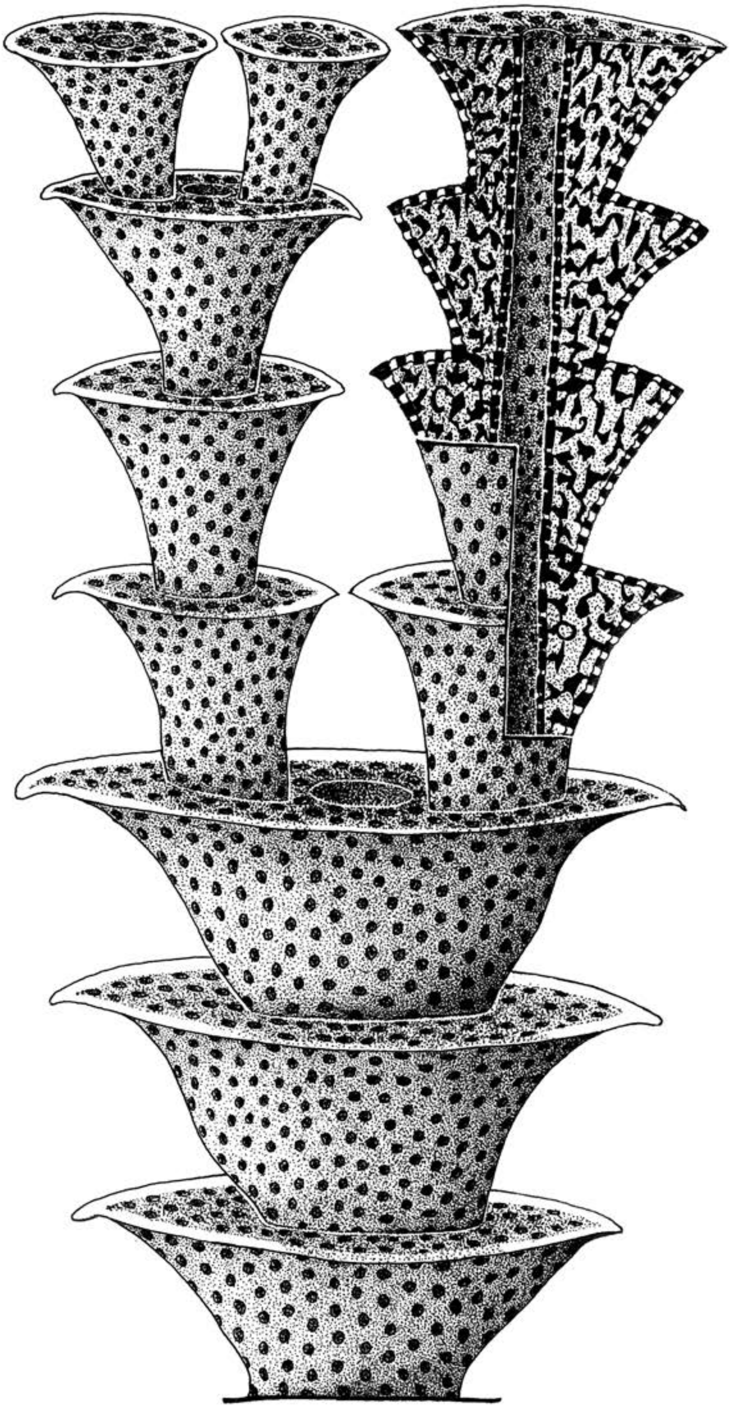


FIG. 223. Reconstruction of *Panormida priscae* SENOWBARI-DARYAN. The porate and siphonate sponge is characterized by funnel-shaped chambers and rejuvenescence; chamber interiors are filled with reticular filling structure; Norian, Triassic, Sicily; schematic, not to scale (Senowbari-Daryan, 1990).

FIG. 224. *Colospongia catenulata* OTT, 1967. Longitudinal section through five spherical-hemispherical chambers arranged in a moniliform series, one above another; chamber walls are pierced by uniform, equal-sized, and evenly distributed pores; chamber interiors contain some vesiculae; Ladinian–Carnian, Triassic, Wetterstein Limestone, Austria, ×5 (Senowbari-Daryan & Rigby, 2011).

that pores in the exowalls (exopores) served as the inhalant canal system, and that pores at the top of chambers (interpores) served as exhalant openings. In the *Sphaerocoelia*-type, each chamber top is pierced by a single large pore or osculum that served as the exhalant opening (Fig. 225, Fig. 236.2). This system was called cryptosiphonate by SEILACHER (1962). The siphonate *Amblysiphonella*-type (Fig. 227, Fig. 236.1) system is characterized by development of a true spongocoel, separated from the chamber by its own wall (endowall). The exhalant system types of SEILACHER (1962), thus, are largely characterized by the type of spongocoel formation. In retrosiphonate sponges, the chamber roofs are curved downward, growing until they merge with roofs of preceding chambers, as, for example, in *Amblysiphonella* (Fig. 233.4). In ambisiphonate sponges, chamber roofs grew upward and arched horizontally toward the osculum. That system is recognizable by a large pore in the middle of the endowall, as, for example, in *Barroisia* (Fig. 233.5). Prosiphonate sponges are characterized by upward growth of chamber roofs, as, for example, in *Girtyocoelia* (Fig. 233.6). It should be mentioned that recognition of the spongocoel type is not always easy, sometimes it is virtually impossible.

Thicknesses and perforation patterns of the spongocoel wall (endowall) may be the same as, or different from, those of the interwalls or exowalls (Fig. 227–228).

In some taxa, as in the Triassic species *Zardinia cylindrica* SENOWBARI-DARYAN, 1990, for example, numerous additional inhalant canals converge inward through the internal filling structure and chamber walls from the outside of the sponge, and coarser exhalant canals open into the spongocoel through the inner part of the wall (Fig. 218). Some of the inhalant canals have small convergent branches near the dermal surface.

Filling Skeleton

Chamber interiors of some sphinctozoan sponges lack any internal structures, but many others have skeletal elements within chambers formed while the chambers were functional parts of the biologic activity of the sponges. These special kinds of skeletal elements are called filling skeletons or filling structures. Six types of filling skeletons have been recognized in chambered sphinctozoan sponges, including: reticular, trabecular, tubular, septate, sporelike, and pisolitic skeletons (Fig. 237). A combination of two filling skeletons (septate + reticular) is an exceptional case and has been reported only in the Triassic genus *Ceotinella* PANTIC, 1975 (Fig. 237). Vesiculae may occur with (*Cryptocoelia)* or without (*Colospongia, Sollasia*) other internal structures within the same sponge (SENOWBARI-DARYAN, 1990). Vesiculae are not considered here to be elements of a filling skeleton, because they sealed off older chambers or parts of chambers and pores that were no longer occupied or used

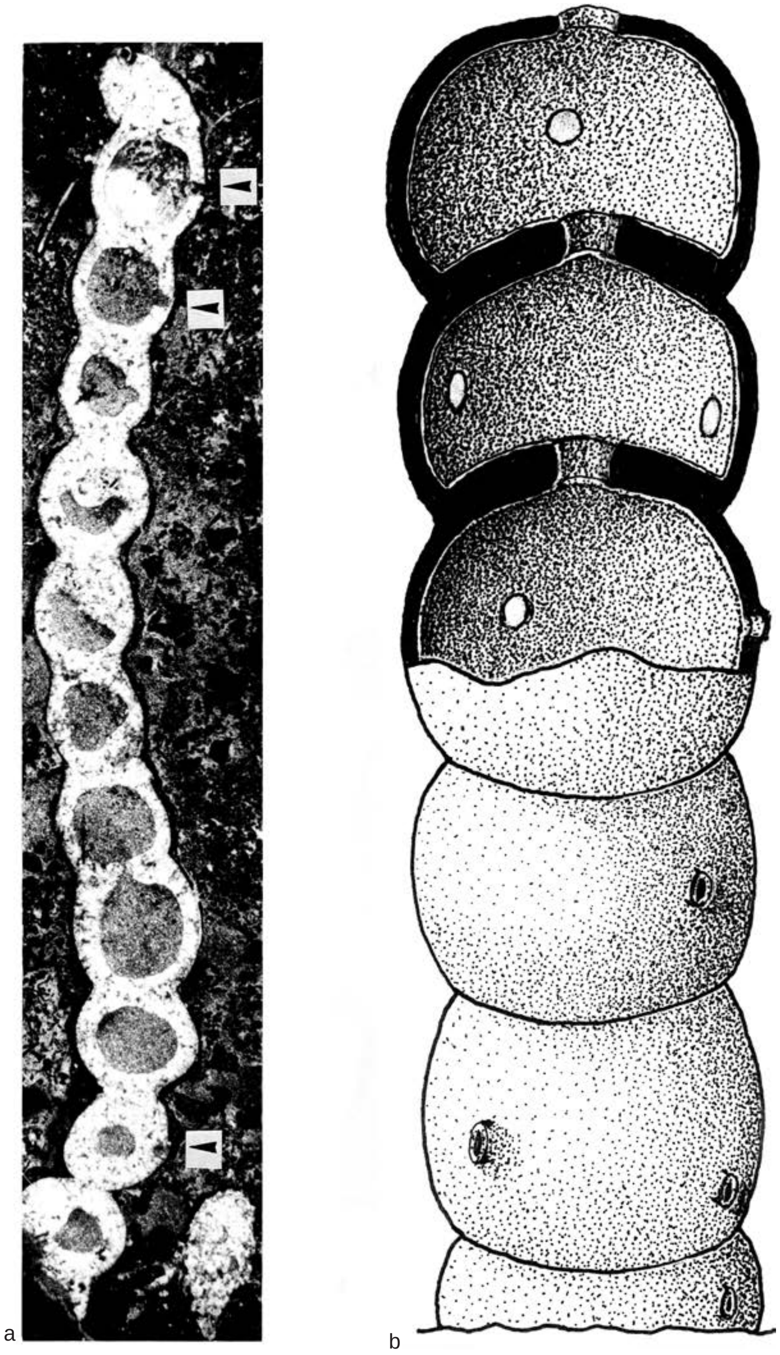


FIG. 225. *Sollasia ostiolata* STEINMANN, 1882, an abundant and cosmopolitan sphinctozoan sponge in Carboniferous and Permian deposits; *a,* longitudinal section cuts through numerous moniliform cryptosiphonate chambers with thick, aporate chamber walls; *arrows* indicate large openings (ostia) in few chambers cut by the section; lower Permian, Sosio valley, Sicily, ×4.6 (adapted from Senowbari-Daryan & Di Stefano, 1988a); *b,* reconstruction showing large opening in the roofs of the chambers and weakly rimmed ostia in the exowalls (adapted from Senowbari-Daryan, 1990).

FIG. 226. *Cryptocoelia zitteli* STEINMANN, 1882, an abundant sponge within the Ladinian–Carnian reefs in the western Tethys. Longitudinal section through the sponge shows numerous crescentlike chambers in a moniliform arrangement; spongocoel is cut in upper part of the sponge; chamber interiors are filled with trabecular (pillarlike) filling skeleton showing distinct lamination (see Fig. 234); Carnian, Triassic, Slovenia, ×3.3 (Senowbari-Daryan, 1981).

by the sponge. Vesiculae, their secretion processes in several stages, and the sealing of pores by vesiculae are shown in Figure 238, in the Triassic genus *Jablonskyia* SENOWBARI-DARYAN, 1990.

A filling skeleton has not been reported from Cambrian sphinctozoans. Cambrian segmented sponges with different filling skeletons, described in the literature as archaeocyaths, are not considered in this section. Most Ordovician representatives of sphinctozoans also lack a filling skeleton. The oldest type of internal filling skeleton seems to be the tubular type, where tubes extend into the chamber interiors from exopores of the exowall in the Ordovician species *Amblysiphonelloides tubulara* RIGBY & POTTER, 1986, from the Klamath Mountains, northern California. Similar tubes may also occur in *Girtyocoelia canna,* described by the same authors from the same locality. The large, coarse, pillar-like vertical tubes in *Cliefdenella* WEBBY, 1969, extend through several flattened low chambers and with the small vertical tubes that pierce only a few layers serving as exhalant tubes. They provide good examples of fine and coarse exhalant structures in the basic water vascular system and are not classified as filling structures. They are totally different from the tubular elements that are more or less horizontal, running perpendicular to the sponge axis in *Amblysiphonelloides* RIGBY & POTTER, 1986 (see WEBBY, 1969; WEBBY & MORRIS, 1976; RIGBY & POTTER, 1986). Later tubular filling skeleton elements occur in several genera, in the Permian genus *Pseudoamblysiphonella* SENOWBARI-DARYAN & RIGBY, 1988, and in the Triassic genus *Polytholosia* RAUFF, 1938. Tubular filling skeletons are not known from Jurassic and younger sphinctozoans.

Trabecular (pillar-like) filling skeletons (Fig. 237, Fig. 239) appear first in the Silurian genus *Rigbyspongia* DE FREITAS, 1987, from Cornwallis Island, Canadian Arctic. This type of filling skeleton is common in Permian to Triassic sphinctozoans, as well as in Cretaceous–Paleogene/Neogene representatives, and in the modern *Vaceletia crypta* (VACELET, 1977b; PICKETT, 1982).

Reticular filling skeletons (Fig. 237, Fig. 240) seem to have developed originally in the Ordovician species *Amblysiphonella reticulata* RIGBY & POTTER (1986), but are well known in the Middle Devonian genus *Hormospongia*, described by RIGBY and BLODGETT (1983) from central Alaska. This type of filling skeleton is common in Permian and Triassic representatives, but in the post-Triassic record it is known only

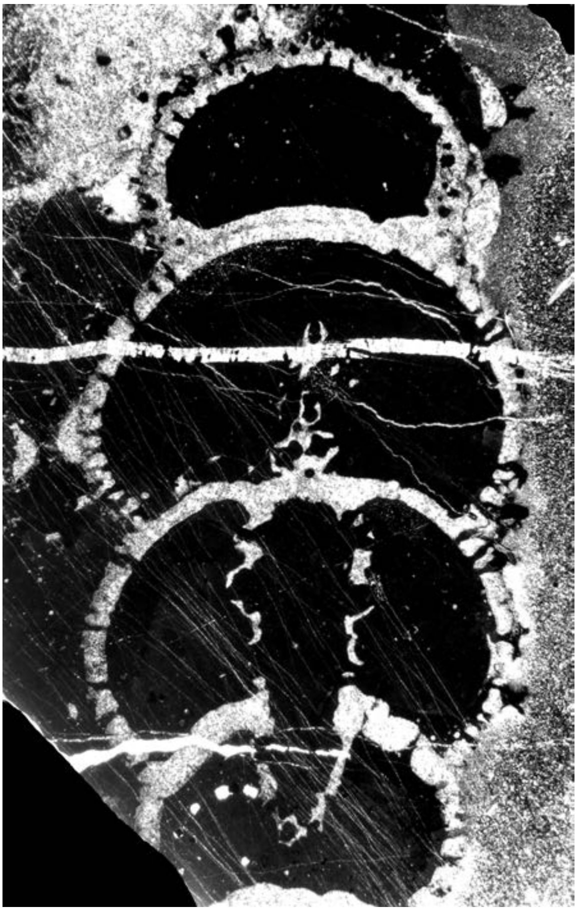


Fig. 227. *Amblysiphonella* sp. Marginal axial section exhibiting hemispherical chambers with perforated exowalls; interwalls are aporate and double layered; endowall is thinner than the exo- and interwalls and is pierced by large and unevenly distributed openings; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×4 (Senowbari-Daryan & Rigby, 2011).

from the Jurassic calcarean genus *Muellerithalamia* Reitner, 1987b.

Sporelike filling skeletons (Fig. 237) are not common and, until now, have been described only from Permian examples, such as *Intrasporeocoelia* (Fan & Zhang, 1985; Rigby, Fan, & Zhang, 1988), and from the Triassic genus *Delijania* Senowbari-Daryan, 2005a.

A pisolitic-like filling skeleton (Fig. 237) is only known from the genus *Pisothalamia,* described from the upper Permian of southern Tunisia by Senowbari-Daryan and Rigby (1988).

Septate-type filling skeletons (Fig. 237) occur in the Devonian genus *Radiothalamos* Pickett & Rigby, 1983, and in the Triassic genus *Phragmocoelia* Ott, 1974.

Two kinds of filling skeleton do not normally occur within the same sponge. The Triassic genus *Ceotinella* Pantic (1975), however, is exceptional, for in that genus peripheral septate and axially reticular filling skeletons (Fig. 237) occur in the same sponge chambers.

It should be mentioned that internal filling skeletons are more common in porate than in aporate representatives of sphinctozoans.

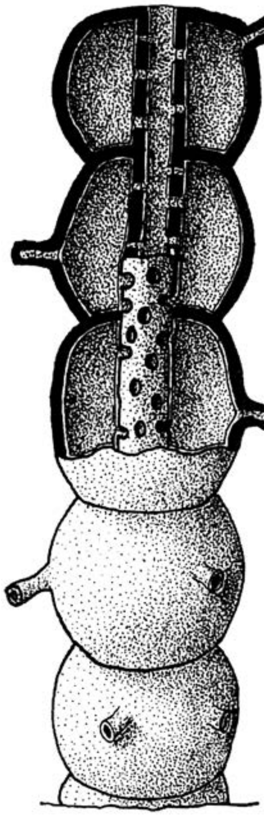


FIG. 228. Reconstruction of *Girtyocoelia beedei* (GIRTY, 1908b) showing unevenly perforated endowall of the spongocoel, and aporate exowalls with sporadic ostia with tubular exaulos; similar to *Sollasia, Girtyocoelia* is also an abundant and cosmopolitan sponge in Carboniferous and Permian deposits; schematic, not to scale (adapted from Senowbari-Daryan, 1990).

This is probably related to the lesser skeletal resistance of the porate construction, caused by perforation of the chamber walls. It was probably a benefit for these sponges to stabilize their skeletons by secreting the internal filling structure.

Spicules

The only living sponge with sphinctozoan construction, *Vaceletia* (VACELET, 1977b), does not have a spicular skeleton. Fossil sphinctozoan sponges commonly lack spicules, possibly because they were not preserved, or they were initially rare.

There are no reports of occurrences of spicules in sphinctozoan archaeocyaths. However, REITNER (1991b, 1992) reported spicules in close proximity to the nonchambered coscinocyathid and other archaeocyaths in lower Cambrian reefs of South Australia, suggesting the spicules were either entrapped during secondary skeletal-forming processes of the archaeocyaths, or secreted from within their primary skeletons. DEBRENNE and ZHURAVLEV (1992b), however, considered it more likely that the spicules, like certain trilobite fragments, were entirely incorporated in archaeocyathan secondary skeletons from debris that lay close by on the sea floor. Indeed, none had a primary skeletal origin, as confirmed by DEBRENNE, ZHURAVLEV, and KRUSE's more general statement that "no undoubted spicules have been recorded from the primary skeleton of archaeocyaths" (see p. 885). Polyactines have been reported in the single-chambered Cambrian sphinctozoan heteractinid sponge *Jawonia* (KRUSE, 1987; DEBRENNE & WOOD, 1990; REITNER, 1992; PICKETT, 2002). Sphinctozoan hexactinellid sponges have chambered skeletons composed of hexactine spicules arranged in a latticelike structure, as shown in an Upper Triassic Iranian species of *Casearia* (Fig. 241). Sphinctozoan construction with both spicular and rigid skeletons is not known in the hexactinellids. Lithistid demosponges with skeletons composed of tetractine spicules arranged in a latticelike structure, without a rigid skeleton, are known only in the Upper Triassic genus *Radiocella* (SENOWBARI-DARYAN & WÜRM, 1994) from the Alps.

In so-called classic sphinctozoan sponges, *sensu* STEINMANN (1882), spicules have been reported from only a few upper Paleozoic and Triassic representatives. Monaxon siliceous spicules, replaced by calcite, pyrite, or other minerals, were reported from some Permian forms, including *Pisothalamia spiculata* SENOWBARI-DARYAN & RIGBY, 1988, and *Subascosymplegma oussifensis* (TERMIER & TERMIER, 1977b), and from some Triassic genera with aragonitic skeletal microstructure, such as in *Colospongia* LAUBE, 1865, *Celyphia* POMEL, 1872, *Thaumastocoelia* STEINMANN, 1882, or with Mg-calcitic skeletal mineralogy, as in *Cassianothalamia* REITNER, 1987b (SENOWBARI-DARYAN, 1989, 1990, 1991; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a; SENOWBARI-DARYAN & RIGBY, 1988; REITNER, 1987c, 1990, 1992). The spicular skeletons of all these taxa are composed of monactine macroscleres (Fig. 242). Possible microscleres are known only from the Carnian species *Cassianothalamia zardinii* REITNER, 1987b, which has a Mg-calcitic rigid skeleton (REITNER, 1987c, 1990). However, ENGESER and APPOLD (1988) did not find microscleres in *Cassianothalamia.* The identification of some cavities within the pillar-filling structures as spicules in some Mesozoic sphinctozoan sponges (*Murguiathalamia* REITNER & ENGESER, 1985, or *Vascothalamia* REITNER & ENGESER, 1985) by REITNER and ENGESER (1985) and REITNER (1990, 1992) seems to be a misinterpretation, as discussed in detail by SENOWBARI-DARYAN (1990, p. 23). Calcitic triactine spicules have been found in several Jurassic and Cretaceous genera: in *Barroisia* MUNIER-CHALMAS, 1882 (QUENSTEDT 1858; SEILACHER, 1962; SENOWBARI-DARYAN & ABATE, 1996; SENOWBARI-DARYAN & GARCIA-BELLIDO, 2002a); *Sphaerocoelia* STEINMANN, 1882; and *Muellerithalamia* REITNER, 1987c (REID, 1967, 1968; DEBRENNE & LAFUSTE, 1972; SENOWBARI-DARYAN, 1989, 1990; REITNER, 1990, 1992). The different basic spicules present in skeletons of hypercalcified sphinctozoan sponges indicate the polyphyletic nature of this group.

Mineralogy and Microstructure of the Rigid Skeleton

Because of strong recrystallization, the original mineralogy of the rigid skeleton of early Paleozoic sphinctozoans is not known (RIGBY & POTTER, 1986). However, the granular microstructure of those Silurian chambered sponges, described as archaeocyaths by previous authors and redescribed by RIGBY, NITECKI, and others (1994) as sphinctozoans, strongly suggests an original skeletal mineralogy of high-Mg calcite. The similarities of mineralogy and microstructure of sphinctozoan sponges and archaeocyaths were discussed by KRUSE and DEBRENNE (1989) and ZHURAVLEV (1989). The skeletal mineralogy of representatives of these sponges is not discussed in detail in this section.

FIG. 229. *Diecithalamia polysiphonata* (DIECI, ANTONACCI, & ZARDINI, 1968). The longitudinal section exhibits cystlike chambers arranged in two or more layers (polyglomerate) around an axial spongocoel that is composed of several individual tubes; Carnian, Triassic, Hydra, Greece, ×3 (Senowbari-Daryan & Rigby, 2011).

The primary skeletal mineralogy (now aragonite or neomorphic calcite) of the majority of upper Paleozoic and Mesozoic sphinctozoans was aragonite, like in the Recent *Vaceletia* (VEIZER & WENDT, 1976; WENDT, 1977, 1978, 1979, 1984, 1990; GAUTRET, 1985; SENOWBARI-DARYAN, 1990). Sphinctozoans with Mg-calcitic mineralogy (up to 11 Mol% $MgCO_3$; RUSSO & others, 1991) appeared in the Middle Triassic (Anisian), became abundant in the Ladinian and Carnian (*Alpinothalamia* SENOWBARI-DARYAN, 1990;

FIG. 230. *Alpinothalamia bavarica* (OTT, 1967), a porate-aporate sponge, with Mg-calcite skeletal mineralogy, composed of numerous cystlike chambers arranged in two or more layers around an axial spongocoel that has a thick endowall; Carnian, Triassic, Sicily, ×1.5 (Senowbari-Daryan & Abate, 1986).

Cassianothalamia REITNER, 1987b; *Stylothalamia* OTT, 1967), and became extinct at the end of the Triassic. However, the only documented sphinctozoan sponge that survived beyond the Triassic–Jurassic boundary, *Stylothalamia columnaris* (LE MAITRE, 1935), is known from several localities (see SENOWBARI-DARYAN & HAMEDANI, 1999). The high-Mg calcite of its skeleton is not proven, and the skeletal preservation suggests that the primary skeletal mineralogy of this sponge seems to have been aragonite. Both aragonitic and high-Mg-calcitic mineralogy of the rigid skeleton also occurs in Jurassic–Cretaceous sphinctozoan sponges, some of which were described as hydrozoans (e.g., *Actinostromaria* CHALMAS in DEHORNE, 1920; this genus is now considered to be an agelasid demosponge of stromatoporoid type; see the introduction to post-Devonian hypercalcified demosponges, p. 201 and 206).

The processes of biomineralization in hypercalcified sponges in general were discussed by SIMKISS (1986), and STEARN and PICKETT (1994), and of sphinctozoans and inozoans in particular, by GAUTRET (1985), GAUTRET and CUIF (1989), CUIF and GAUTRET (1991), WENDT (1979, 1990), FINKS (1990), and REITNER and others (1997). Figure 243 shows these processes of calcification in the Triassic genus *Jablonskyia* SENOWBARI-DARYAN, 1990; for a detailed description see SENOWBARI-DARYAN (1997).

The six principal types of microstructures known in sphinctozoan sponges include (Fig. 244): (1) spherulitic, (2) irregular, (3) orthogonal, (4) clinogonal, (5) lamellar, and (6) microgranular (DEBRENNE & LAFUSTE, 1972; CUIF, 1973, 1974, 1979; CUIF & others, 1979; CUIF & others, 1990; SENOWBARI-DARYAN, 1990, 1991; SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a; WENDT, 1979, 1984, 1990).

The earliest known microstructure of sphinctozoan sponges seems to be of lamellar type, reported from the Ordovician genus *Angullongia* by WEBBY and RIGBY (1985) and RIGBY and POTTER (1986). WENDT (1984), in contrast to JONES (1979), concluded that lamellar microstructure was caused by a diagenetic process and was not developed as a primary structure in the sponges. However, the excellent aragonitic preservation of the rigid skeleton of *Celyphia submarginata* MÜNSTER, 1841 (Fig. 242), from the Cassian Formation (Dolomite, Italy), suggests that the lamellar microstructure in this sponge is primary (SENOWBARI-DARYAN, 1990, 1991; REITNER, 1992). Lamellar microstructure is also known from the other Triassic genus *Montanaroa* RUSSO (1981).

The spherulite type of microstructure in sphinctozoans is known from several

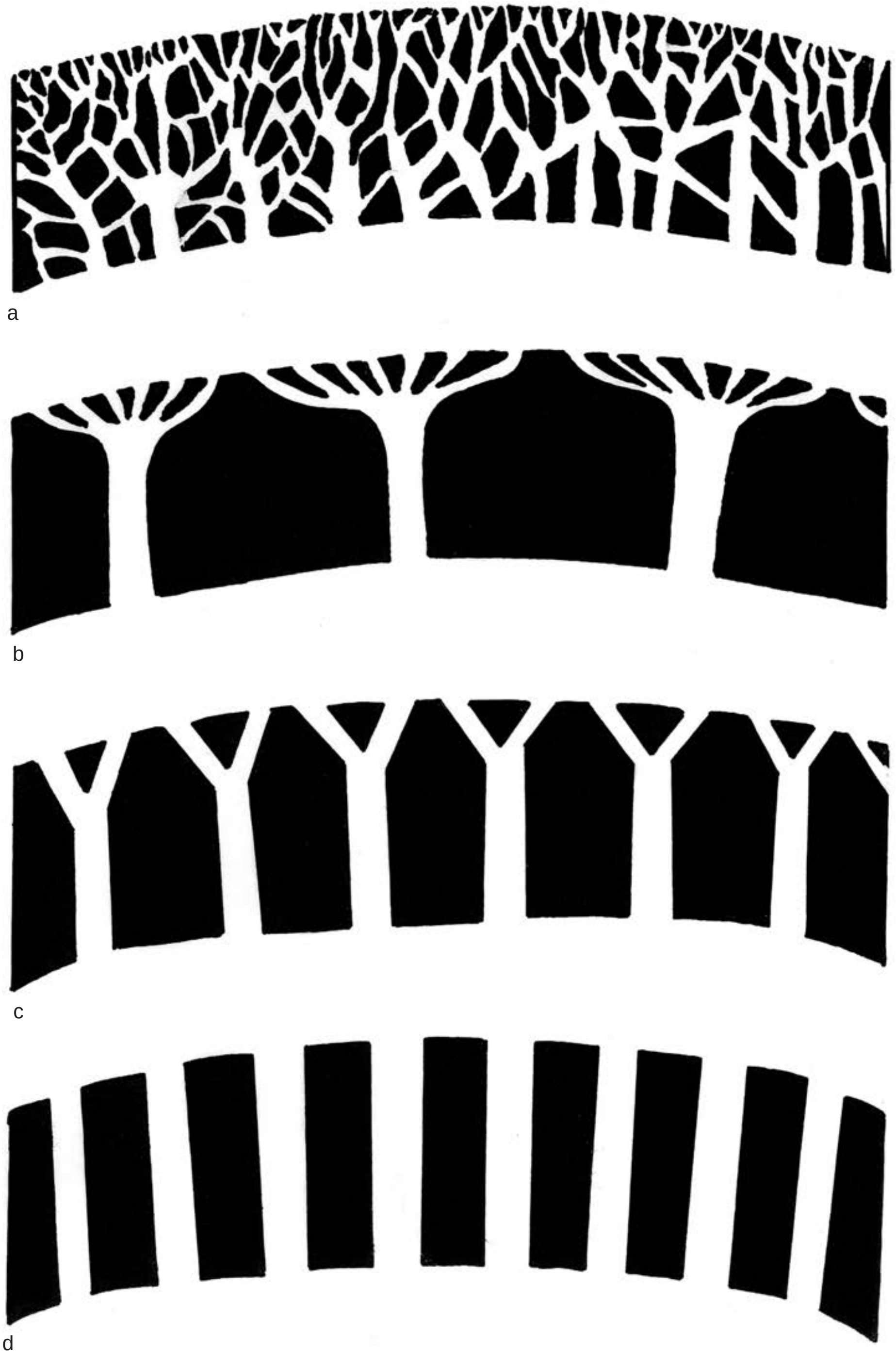


FIG. 231. Perforation pattern in porate sphinctozoans; *a,* labyrinthic branched pores, *b,* multibranched pores, *c,* dichotomously branched pores, and *d,* single pores; schematic, not to scale (Senowbari-Daryan, 1990).

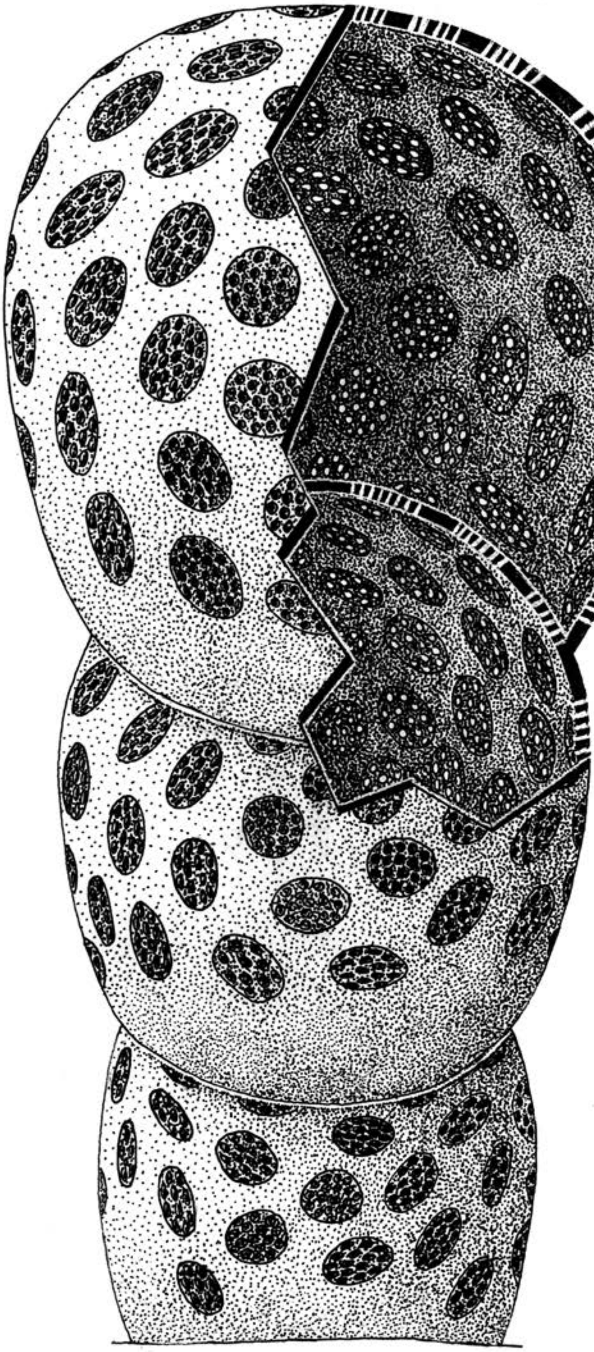
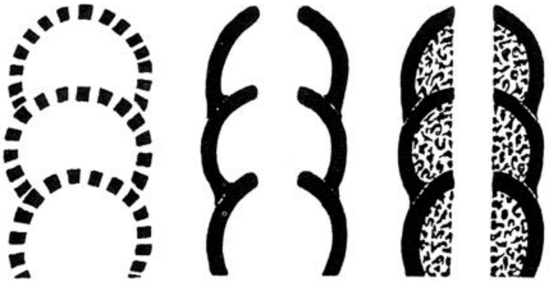
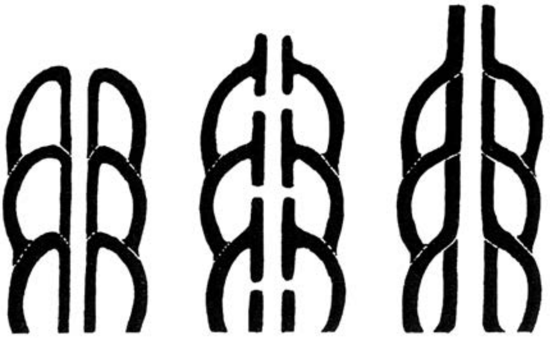


FIG. 232. Reconstruction of *Follicatena permica* SENOWBARI-DARYAN, 1990. The exowall and interwalls of this moniliform and *Colospongia*-like sponge contains numerous openings in the chamber walls of cribribulla with cribripores; cribribulla are not developed near bases of the chambers; species is known from the Permian of Sicily; schematic, not to scale (Senowbari-Daryan, 1990).



1 asiphonate 2 cryptosiphonate 3 pseudoosiphonate



4 retrosiphonate 5 ambisiphonate 6 prosiphonate

FIG. 233. Theoretical consideration of SEILACHER (1962) for the formation of canals in sphinctozoan sponges. *1,* Asiphonate, *Colospongia*; *2,* cryptosiphonate, *Sollasia; 3,* pseudosiphonate, *Senowbaridaryana*; *4,* retrosiphonate, *Amblysiphonella; 5,* ambisiphonate, *Barroisia*; and *6,* prosiphonate, *Girtyocoelia*. The recognition of retrosiphonate, ambisiphonate, and prosiphonate types is not always easy (adapted from Seilacher, 1962).

Carboniferous and Permian genera, such as *Sollasia* and *Girtyocoelia*. Spherulitic microstructure is the most common type in upper Paleozoic and Triassic sphinctozoans with an aragonitic skeletal mineralogy (GAUTRET, 1985; WENDT, 1990; MASTANDREA & RUSSO, 1995). These spherulites are of different sizes in various taxa.

Granular microstructure (irregular micritic, MÜLLER-WILLE & REITNER, 1993) is typical of sphinctozoan sponges with high-Mg-calcite mineralogy, such as the Triassic genera *Cassianothalamia* REITNER, 1987b, *Uvanella* OTT, 1967, or *Alpinothalamia* SENOWBARI-DARYAN, 1990. Granular microstructure is also developed in some Jurassic and Cretaceous chambered sponges, such as in *Boikothalamia convexa* (BOĬKO, 1981), and other sponges described as hydrozoans in the literature (the Upper Jurassic genus *Actinostromaria* CHALMAS in DEHORNE, 1920), although this genus is now regarded as an agelasid demosponge of stromatoporoid type (see p. 201, 206).

The aragonitic rigid skeleton of modern *Vaceletia* is composed of irregularly arranged needles of aragonite (GAUTRET, 1985; WENDT, 1990; CUIF & GAUTRET, 1991; WOOD, 1991b; MASTANDREA & RUSSO, 1995). Irregular microstructure is known also from some fossil representatives with aragonitic skeletal mineralogy, such as the Triassic genera *Colospongia* LAUBE, 1865, or *Solenolmia* POMEL, 1872.

Clinogonal microstructure has been reported from the secondary (internal) layer of the skeletal wall in the Triassic species *Thaumastocoelia cassiana* STEINMANN, 1882 (see FINKS & RIGBY, 2004d, p. 664).

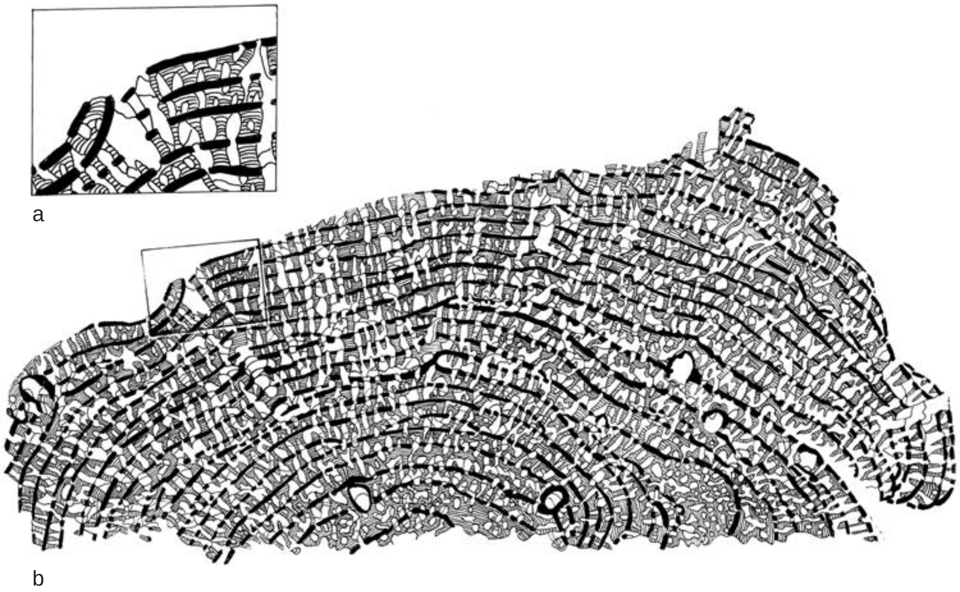


FIG. 234. *Cryptocoelia lata* SENOWBARI-DARYAN & SCHÄFER, 1983. Drawing of a longitudinal thin section exhibiting laterally extended chambers, numerous upward and outward radiating exhalant canals, and the lamellar structured trabecular (pillarlike) filling skeleton within the chamber interiors, as in *Cryptocoelia zitteli* STEINMANN, 1882; Carnian, Triassic, Hydra, Greece; *a,* ×6, *b,* ×3 (Senowbari-Daryan & Schäfer, 1983).

PALEOBIOLOGY, PATTERNS OF WATER CIRCULATION, AND PALEOECOLOGY

In the living chambered sponge *Vaceletia,* only the last added, or youngest, chambers are occupied with living soft body (VACELET, 1979b). This is also true in some other hypercalcified sponges, such as *Ceratoporella* HICKSON, 1911, in which only about 1 mm is occupied by the soft body (HARTMAN & GOREAU, 1966, 1970), or in *Astrosclera willeyana* LISTER, 1900, in which only about 1 cm of the youngest part of the skeleton is occupied by the soft body (WÖRHEIDE & others, 1997). This suggests that in fossil chambered sponges, the living sponge body, perhaps, was also limited to the last chambers. This assumption is supported by observations of some internal skeletal structures. For example, vesiculae are interpreted as a type of secondary skeletal element that may occur more abundantly within older chambers. They may partially or entirely, internally, seal off the inhalant pores of the exowalls (Fig. 238). In addition, other kinds of internal skeletal structures, which are interpreted as support organs of the skeleton, are commonly observed within the older chambers. The rigid exoskeleton (chamber walls) was probably covered by a thin organic membrane, like in modern *Vaceletia*.

As discussed above in the section on Internal Canal System (p. 330), there were principally three types of exhalant canal systems in sphinctozoan sponges (Fig. 236). These were termed *Colospongia*-type, *Sphaerocoelia*-type, and *Amblysiphonella*-type by SENOWBARI-DARYAN (1990). The *Colospongia*-type, called asiphonate by SEILACHER (1962), is without a separate spongocoel. Thus, it is assumed that the lateral pores of the exowalls served as inhalant canals. Water entered via these inhalant canals and then circulated through the small choanocyte chambers, located within the chamber interiors, and then exited through the interpores that served as exhalant canals. The large openings in chamber interwalls in the *Sphaerocoelia*-type

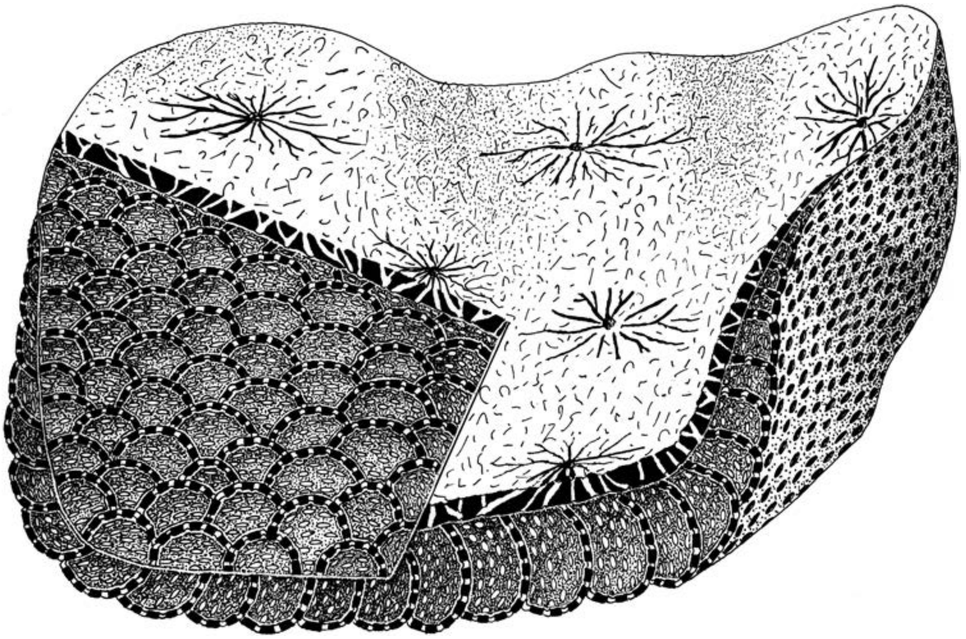


FIG. 235. Reconstruction of *Guadalupia explanata* (KING, 1943) is characterized by numerous hemispherical chambers arranged beside and above one another. Exowalls on the lower outside are perforated (inhalant pores), and the opposite upper surface bears several astrorhizal canal systems that served as exhalant canals. The sponge is abundant in Permian reefs, Guadalupe Mountains, Texas and New Mexico, United States; schematic, not to scale (Senowbari-Daryan, 1990).

system likely served as exhalant canals. A spongocoel was most probably developed, which extended as a tubular large opening through the whole sponge and was bounded by soft tissue within the chamber interiors. The *Amblysiphonella*-type system had an axial canal (or a bundle of axial canals). Water passed through exopores into the chamber interiors, and after circulation in choanocyte chambers, exited through the axial canals and osculum. Similar occupation of the main chambers by smaller choanocyte chambers and the passage of water through the skeleton in some chambered archaeocyaths were reconstructed by ZHURAVLEV (1989).

According to KRUSE (1987), Cambrian sphinctozoans did not live in reef environments. Ordovician to Carboniferous hypercalcified sphinctozoans are commonly found in what were shelf sediments. Sedimentological and paleontological data indicate that during the latest lower Permian to the middle Permian, sphinctozoans changed their biotope. Middle and upper Permian and Triassic sphinctozoans inhabited shallow-water environments, mainly reef or reefal biotopes. Cretaceous sphinctozoans are also found in deposits of similar environments (REITNER & ENGESER, 1985). Sedimentological and paleontological data indicate that sphinctozoans lived mostly in low-energy environments, below wave base, in the photic zone, usually at depths of 15–50 m (SENOWBARI-DARYAN & RIGBY, 1988; SENOWBARI-DARYAN, 1991). According to FAGERSTROM (1984), the different shapes and growth types of Permian sphinctozoans suggest they functioned in three different ways in the reef communities: as bafflers and sediment traps, as frame builders, and as sediment binders.

The modern sphinctozoan sponge *Vaceletia* lives in cryptic habitats on outer slopes of coral reefs in the Indo-Pacific region

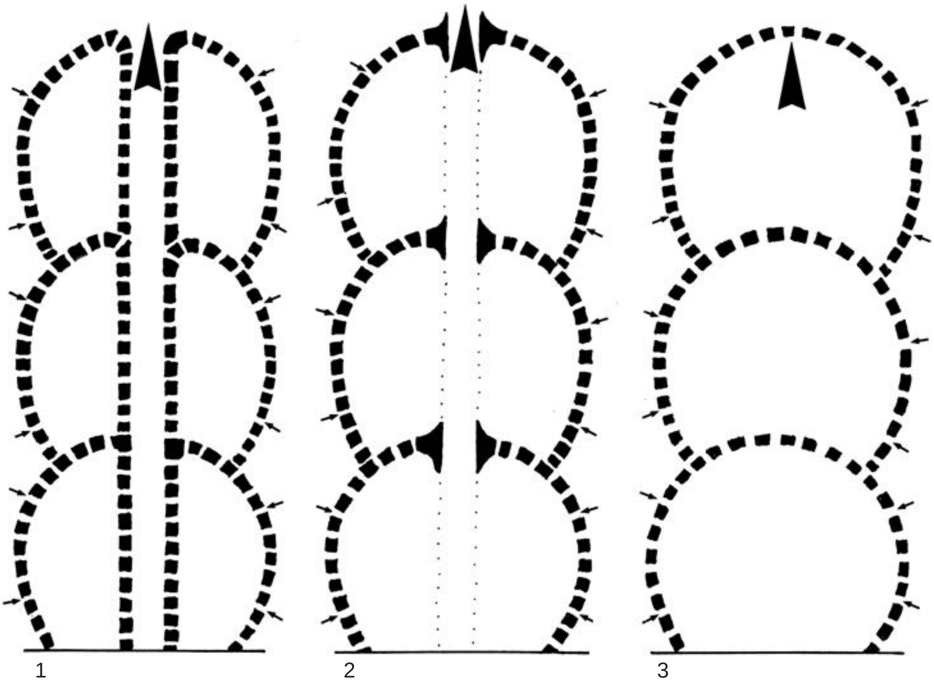


FIG. 236. Three principal types of water circulation in sphinctozoan sponges. *1, Amblysiphonella*-type, *2, Sphaerocoelia*-type, and *3, Colospongia*-type; *small arrows* indicate direction of inhalant water motion; *large arrows* indicate direction of exhalant water currents (Senowbari-Daryan, 1990).

at depths of 15–38 m (VACELET, 1979b; BASILE, CUFFEY, & KONICH, 1984). However, the majority of Permian and Triassic sphinctozoan sponges were upright, growing organisms attached to hard substrates on the sea bottom. The observation and interpretation of WOOD, DICKSON, and KIRKLAND-GEORGE (1994, 1996) that most sphinctozoans of the Permian Capitan reef were cryptobionts inhabiting cavities made by other organisms were not confirmed by other workers (RIGBY, SENOWBARI-DARYAN, & LIU, 1998; FAGERSTROM & WEIDLICH, 1999a; NEWELL, 2001; NOÉ, 2003).

REVIEW OF CLASSIFICATION

STEINMANN (1882) was the first author to classify chambered sponges. He placed them in four families, based on the combination of the presence or absence of a spongocoel and the type of filling skeleton within the chamber interiors. GIRTY (1908a) added two additional families to STEINMANN's (1882) families. DE LAUBENFELS (1955) was the next author to add two more families to the sphinctozoan sponges. Based on the external pattern of perforation (porate or aporate), SEILACHER (1962) created two superfamilies (Porata and Aporata) and assigned all known families to these superfamilies. Later, SEILACHER's superfamilies were raised to suborder ranks by PICKETT and RIGBY (1983). The SEILACHER (1962) classification was also modified by OTT (1967). Based on the presence of or lack of a spicular skeleton, and its chemical composition (siliceous or carbonate) and on the mineralogical composition of the rigid skeleton (aragonite or Mg calcite), SENOWBARI-DARYAN (1990) classified the chambered sponges into six orders (compare RIGBY & others, 1993).

1. Sphaerocoeliida WENDT, 1979. Calcareous spicular skeleton, calcitic rigid skeleton primary aragonite? Calcarea?; Jurassic.

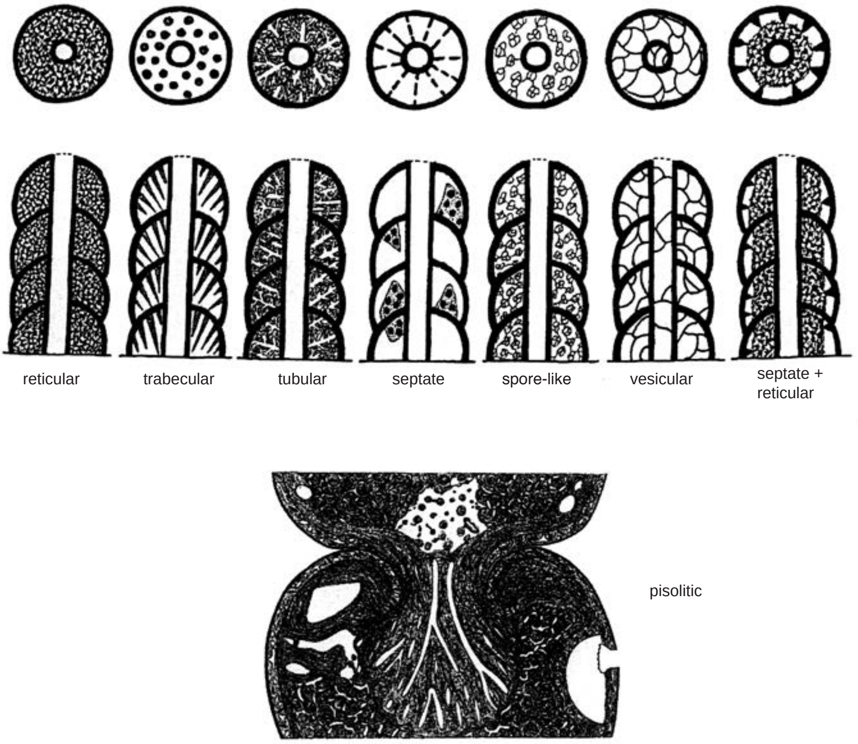


FIG. 237. Appearance of different types of filling skeleton known in the sphinctozoans, as seen in longitudinal and transverse sections. Vesiculae may occur separately or in combination with other types of filling skeleton (adapted from Senowbari-Daryan, 1990).

2. Verticillitida TERMIER & TERMIER (in H. TERMIER, G. TERMIER, & VACHARD, 1977). With or without primary siliceous spicules, rigid skeleton composed of aragonite. Demospongiae; Triassic–Recent.

3. Permosphincta TERMIER & TERMIER, 1974. Aragonitic rigid skeleton lacking spicules. Demospongiae? Calcarea?; Cambrian–Cretaceous.

4. Pisothalamida SENOWBARI-DARYAN & RIGBY, 1988. Siliceous spicular skeleton composed of primary monaxons, with an aragonitic rigid skeleton and pisolitic internal filling structure. Demospongiae; Permian.

5. Hadromerida (*partim*), according to REITNER (1987c). Probably monactine megascleres and sphaeraster microscleres. Demospongiae, Triassic (the only genus of this taxon—*Cassianothalamia*—was assigned to the new family Cassianothalamiidae by REITNER (1987b), order Hadromerida. MÜLLER-WILLE and REITNER (1993) moved the genus *Cassianothalamia* to the family Geoiidae within the order Astrophorida.

6. Guadalupiida TERMIER & TERMIER (in H. TERMIER, G. TERMIER, & VACHARD, 1977). Without spicules, calcitic rigid skeleton (according to FINKS, 1983, rigid skeleton is primary aragonite). Demospongiae; Permian.

Finally, chambered sponges without a spicular skeleton but with rigid skeletons composed of high-Mg-calcite mineralogy were united in the order Uncertain by SENOWBARI-DARYAN (1990). These fossils range in age from Middle to Upper Triassic.

WU (1991, 1995) classified the sphinctozoan sponges into five suborders, based on differences in their exhalant canal systems: Asiphonata (without a spongocoel); Siphonata (with an axial canal or an axial canal bundle); Vasculata (with a central conduit

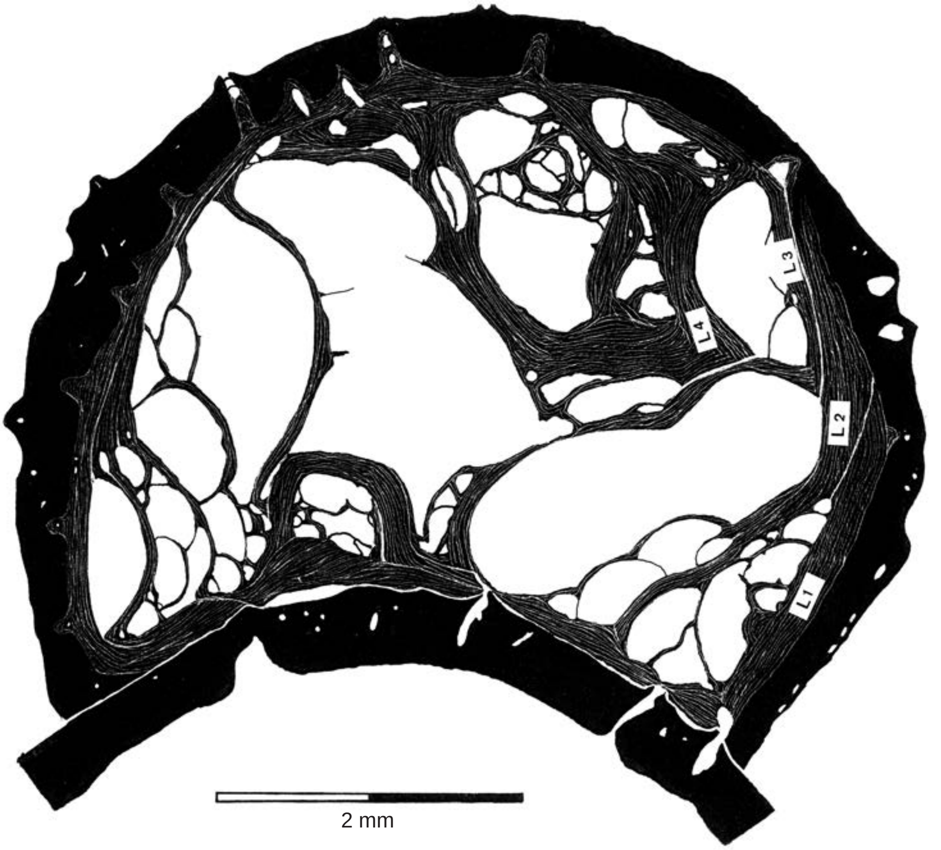


FIG. 238. A chamber of *Jablonskyia andrusovi* (JABLONSKY) showing vesiculae secreted in at least four stages (*L1–L4*). The exopores are sealed off by different stages of vesiculae (Senowbari-Daryan, 1990).

or central conduit bundle); Polysiphonata (having more than one exhalant tube or vertical tube bundle scattered in the whole sponge); and Polyvasculata (having more than one vertical conduit or vertical conduit bundle scattered in the whole sponge). Numerous old and new families established by WU (1991) were assigned by him to these suborders.

Because of their polyphyletic nature, the chambered sponges were assigned to different sponge classes, including Heteractinida, Demospongiae, Calcarea, Hexactinellida, and Archaeocyatha, Hexactinellida, and Archaeocyatha by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002a). Most sphinctozoans are classified into different orders within the demosponges. In addition, a separately listed bibliography of fossil sphinctozoans was provided by SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002b).

FINKS and RIGBY (2004d) followed the frame of the classification of SENOWBARI-DARYAN and GARCÍA-BELLIDO (2002a), with some revision and modification. They assigned most hypercalcified chambered sponges to the class Demospongea (=Demospongiae), subclass Ceractinomorpha, orders Agelasida and Vaceletida; and subclass Tetractinomorpha, order Hadromerida.

In summary, because of the polyphyletic nature of chambered sponges, their preservation problems, and because of gaps in their occurrences and documented evolution during Earth history, the systematic

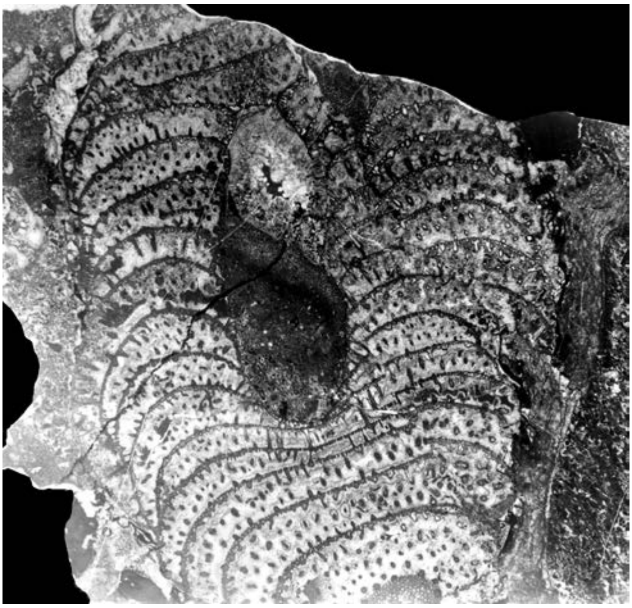


FIG. 239. *Stylothalamia hydriotica* SENOWBARI-DARYAN, 1990. This retrosiphonate sponge exhibits the trabecular (pillarlike) filling skeleton within the chamber interiors; pillars appear as points when cut transversely; Carnian, Triassic, Hydra, Greece, ×2.2 (Senowbari-Daryan, 1990).

classification of this group of sponges is still unsatisfactory. There is limited agreement about the importance of different features of hypercalcified sphinctozoan sponges among different workers, thus leading to different classifications. Also, there is not an exact boundary between the sphinctozoans and sponges with other similar fossils, described as stromatoporoids, hydrozoans, or archaeocyaths. There are numerous Cambrian genera, described as archaeocyaths, that have internal and external constructions like those of upper Paleozoic or Mesozoic representatives. Also, the mineralogy and microstructure of the rigid skeletons of some of them are apparently the same. For example, the lower Cambrian chambered *Gerbicanicyathus* BELYAEVA (see DEBRENNE, ZHURAVLEV, & KRUSE, 2002, fig. 52/G, I) and *Clathricoscinus popovi* VLASOV, 1961, described as archaeocyaths, have the same construction and the same perforation of chamber walls as that in the Paleozoic and Triassic *Amblysiphonella* (see ZHURAVLEV, 1989). Their difference from *Amblysiphonella* is in skeletal mineralogy. However, an *Amblysiphonella*- or *Gerbicanicyathus*-type sponge with the same skeletal mineralogy (high-Mg calcite) is also known as *Leinia* SENOWBARI-DARYAN (1990) from Upper Triassic (Carnian) deposits. Also, the internal filling structures (especially of trabecular type) in several Cambrian archaeocyaths and Mesozoic sphinctozoans are identical. For example, the Cambrian species *Nochoroicyathus mirabilis* ZHURAVLEVA and the Jurassic species *Boikothalamia convexa* (=*Verticillites convexus* BOĬKO, 1981) can hardly be differentiated (compare ZHURAVLEVA & MYAGKOVA, 1987, pl. 1,*1;* BOĬKO in ZHURAVLEVA & MYAGKOVA, 1981, pl. 40,*2;* BOĬKO in BOĬKO, BELYAEVA, & ZHURAVLEVA, 1991, pl. 64,*3b*). Numerous other analogous examples could be added to this list. The phylogeny of archaeocyaths was discussed by ZIEGLER and RIETSCHEL (1970) and ROWLAND (2001), and the possible connection of chambered archaeocyaths and sphinctozoan sponges has been previously discussed by ZHURAVLEVA (1970) and DEBRENNE and VACELET (1984).

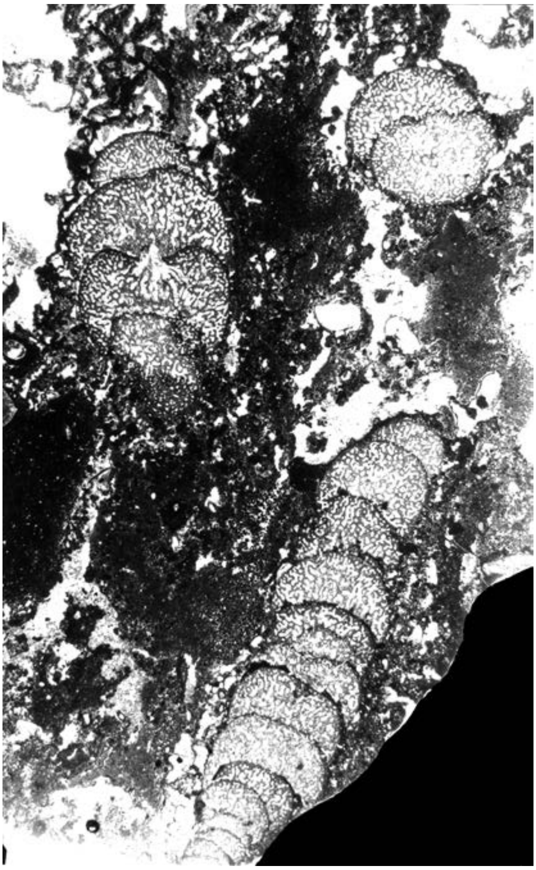


FIG. 240. *Solenolmia manon* (MÜNSTER, 1841). Longitudinal and oblique sections exhibiting reticular filling skeleton in chamber interiors; axial canal is cut in one specimen, on the left; Ladinian–Carnian, Triassic, Dolomites, Italy, ×2.5 (Senowbari-Daryan & Rigby, 2011).

PATTERNS OF EVOLUTION AND EXTINCTION

During the last few decades, numerous papers have been published about mass extinction or bio-events during Phanerozoic time. Numerous papers have treated the different groups of marine and nonmarine organisms. However, no extinction data about the sponges in general, nor about the sphinctozoan sponges in particular, are available in either RAUP and SEPKOSKI (1982, 1984) or SEPKOSKI (1986, 1990), nor in publications of other workers treating extinctions at the Permo–Triassic boundary or the Triassic–Jurassic boundary (Permo–Triassic: RAUP & BOYAJIAN, 1988; ERWIN, BOWRING, & YUGAN, 2002; Triassic–Jurassic: BENTON, 1986, 1988, 1991; HALLAM, 1990, 1996, 2002; HALLAM & GOODFELLOW, 1990; HALLAM & WIGNALL, 1997), although the chambered sponges were the main reef builders in late Paleozoic and in Triassic time. Some general observations about the evolution, extinction, and diversification of sphinctozoan sponges in Phanerozoic time are presented below.

To date, about 160 genera of various types of hypercalcified, chambered sponges have been described. Chambered archaeocyaths and hexactinellids are excluded here. For details see the summary, below, of classification and stratigraphic occurrences (p. 386–395) and SENOWBARI-DARYAN & GARCÍA-BELLIDO (2002a).

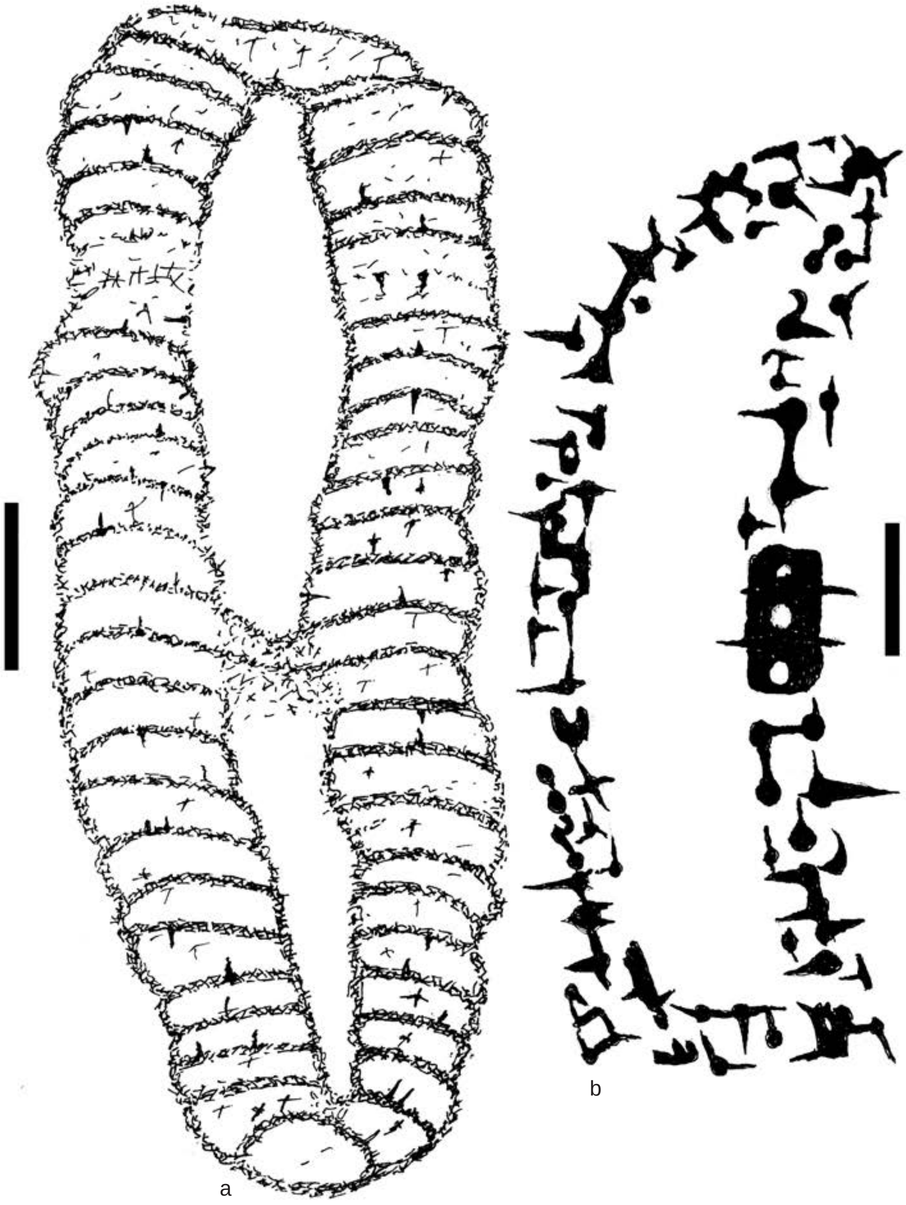


FIG. 241. Lattice skeleton of chambered hexactinellid sponge *Casearia* sp., upper Norian, Triassic, Nayband Formation, Iran. *a,* Longitudinal section showing lattice arrangement of hexactine spicules forming chamber walls, scale bar, 1 cm; *b,* magnification of one chamber showing arrangement of individual hexactines within the chamber and spongocoel walls, scale bar, 1 mm (Senowbari-Daryan & Rigby, 2011).

Cambrian

Six genera have been reported from the Cambrian (Fig. 245). Five of them are limited to the Cambrian, and only the genus *Amblysiphonella* continued into the Ordovician. Fifty percent of Cambrian genera (three genera: *Jawonia, Nucha,* and *Wagima*; see PICKETT, 2002) belong to the heteractinid sponges.

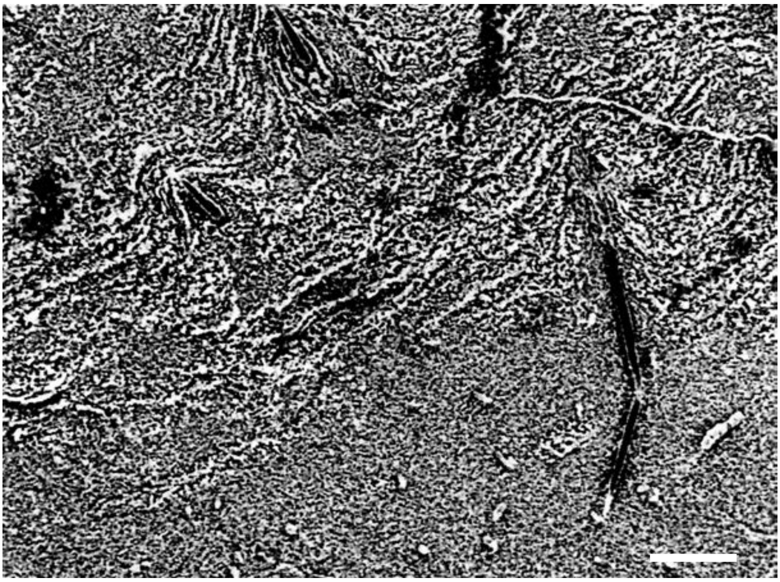


FIG. 242. Monaxon spicules imbedded in the chamber wall of the Triassic species *Celyphia submarginata* (MÜNSTER, 1841). Spicules are located in the center of wavy lamellar microstructure; Carnian, Triassic, Cassian Formation, Dolomites, Italy, scale bar, 30 µm (Senowbari-Daryan, 1990).

Ordovician

Fifteen genera have been reported from the Ordovician, and 14 of them are new in the Ordovician. Only the genus *Amblysiphonella* survived from the Cambrian assemblage. The Ordovician marked the first radiation of sphinctozoan sponges. However, of these 15 Ordovician genera, only the genus *Cystothalamiella* survived the Ordovician–Silurian boundary event, which also affected many other benthic organisms (see BRENCHLEY, 1989). *Amblysiphonella* has been reported from the Cambrian and Ordovician and also occurs in the Carboniferous, Permian, and Triassic, but it has not been reported from the Silurian or Devonian. *Amblysiphonella* could be another genus that survived the Ordovician–Silurian event but still has not been reported from the Silurian. *Pseudoimperatoria* is another genus reported from the Ordovician and Permian but not from the Silurian–Carboniferous. The possible extinction of 14 genera produced a generic extinction rate of 93%. Ordovician sponge diversification was summarized, in general, by CARRERA and RIGBY (2004).

Silurian

Five genera of sphinctozoans are known from the Silurian (Fig. 245), and four of them are new. Only *Cystothalamiella* survived from the Ordovician.

Devonian

Only two hypercalcified sphinctozoan sponges, *Hormospongia* and *Radiothalamos,* are known from the Devonian. Both of them are new in the Devonian, and they are limited to this period.

Carboniferous

The Carboniferous (Fig. 245) marked the second diversification period of hypercalcified sphinctozoan sponges. Eight genera, with numerous species, are known from deposits at many different localities of this period. Six of these eight genera first appear in the Carboniferous. Only *Amblysiphonella* ranges

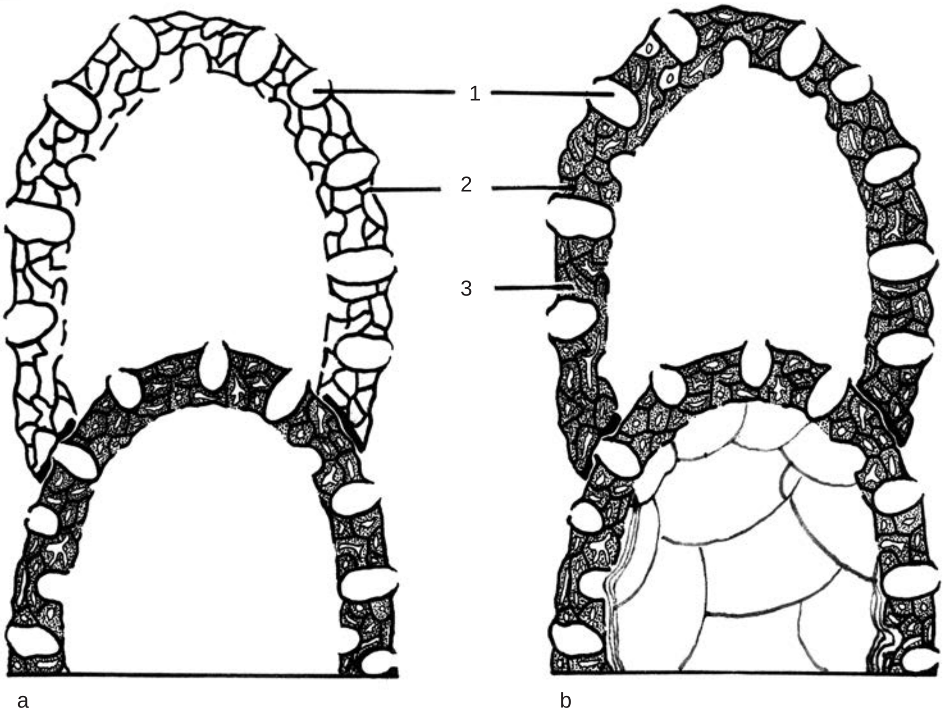


FIG. 243. Biomineralization process of the chamber walls in *Jablonskyia adrusovi* (JABLONSKY). The initial calcification started the thin labyrinthic lines within the wall (*a*) and proceeded from these lines into the interspaces (*b*); rodlike or labyrinthic systems of spaces remained free from calcification and may be changed with spicules. *1,* exopores, *2,* lines of initial calcification of the first mineralization stage, and *3,* full calcification of the spaces between lines of initial calcification; schematic, not to scale (Senowbari-Daryan, 1997).

up from the Cambrian and *Girtyocoelia* has been reported also from the Ordovician.

Permian

The Permian is the third and most significant diversification period of hypercalcified sphinctozoan sponges in Paleozoic time. At least 60 genera are known; of these 52 appear in the Permian as new. Six genera range up from the Carboniferous and 2 genera range up from the Ordovician.

The Permian–Triassic boundary event was the second and most significant extinction event for hypercalcified sphinctozoan sponges at the end of Paleozoic time. Of the known 60 genera in the Permian, 38 genera became extinct and only 22 genera survived the Permian–Triassic boundary event, for an extinction rate of approximately 63% at the genus level. However, it should be noted that no Permian species have been reported from deposits of the Lower Triassic and Anisian time (SENOWBARI-DARYAN & others, 1993).

Triassic

The Triassic was the fourth diversification period for chambered sponges. About 83 genera, with more than 200 species, have been described from the Triassic. The diversification of the hypercalcified sphinctozoans with rigid aragonitic skeletons increased rapidly in the Triassic. Chambered sponges with high-Mg-calcite mineralogy appeared in the Anisian, and the number of these taxa also increased during Ladinian and Carnian time. Sphinctozoan hexactinellids with

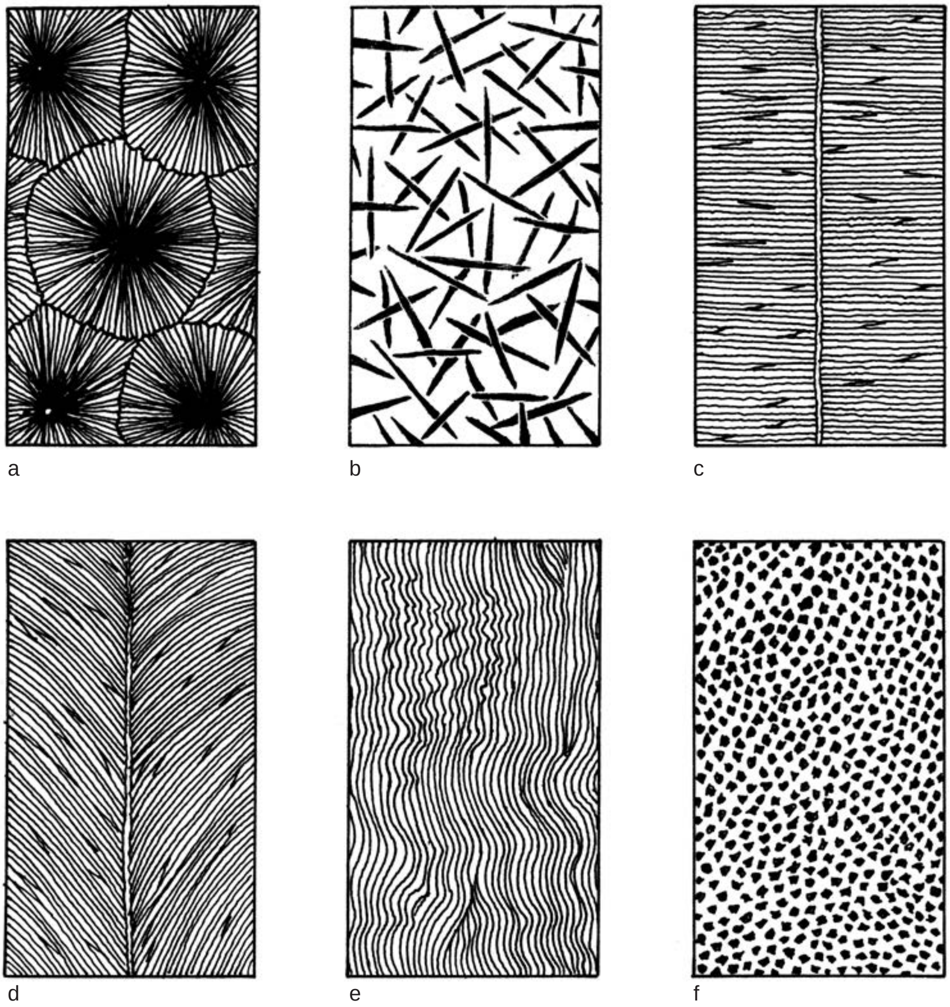


FIG. 244. Different microstructures known in sphinctozoan sponges. *a,* Spherulitic, *b,* irregular, *c,* orthogonal, *d,* clinogonal, *e,* lamellar, and *f,* microgranular; note that spherulitic, clinogonal, and granular types of microstructure also apply to certain inozoans (see p. 362–366); schematic, not to scale (Senowbari-Daryan, 1990).

hexactine spicular skeletons appeared for the first time in the Carnian. Only one genus of chambered lithistid demosponge is known from the Norian, and it was reported from Gosaukamm, Austria (SENOWBARI-DARYAN & WÜRM, 1994).

Of the 83 hypercalcified sphinctozoan genera known from the Triassic, 61 genera are new and 22 genera survived from the Paleozoic. However, there is a major break in the record, for no sphinctozoan sponges have been reported from the Lower Triassic (Scythian), and no Paleozoic chambered species have been found in Anisian reefs (SENOWBARI-DARYAN & others, 1993).

The number of sphinctozoan taxa greatly increased during the Middle and Upper Triassic (Carnian). In addition to aragonitic sphinctozoans, a large number of sphinctozoans with high-Mg-calcite mineralogy appeared. At the Carnian–Norian boundary, or in the lower Norian, some 12–17 million years before the end of the Triassic (STANLEY, 2001a), another extinction event changed the radiation of sphinctozoan sponges considerably. Almost all representatives with high-Mg-calcite mineralogy became extinct; those with aragonitic skeletons were less affected by this extinction. According to FLÜGEL and SENOWBARI-DARYAN (2001), about 50% of sphinctozoan sponges, at the generic level, disappeared during upper Carnian–lower Norian time. However, few of the so-called conservative taxa, such as *Colospongia* and *Amblysiphonella,* survived this extinction event. The Norian diversification produced many new taxa with both simple and complex constructions. The number of taxa seems to have decreased during the uppermost Triassic, which ended with a significant extinction event at the Triassic–Jurassic boundary.

Comparing Triassic sphinctozoan assemblages with those of the Permian, the Ladinian and Carnian sponge faunas exhibit few similarities to those of the upper Paleozoic sphinctozoans. On the other hand, the similarity of Permian and Norian–Rhaetian assemblages is much greater. For example, the genera *Discosiphonella*, *Polycystocoelia,* and *Platythalamiella* are known from Permian and Norian–Rhaetian deposits, but not from Lower and Middle Triassic and Carnian occurrences. Most of the conservative Carboniferous–Permian genera, like *Discosiphonella, Sollasia, Colospongia,* and *Amblysiphonella,* survived, but only a few of the so-called progressive genera survived beyond the Permian–Triassic extinction event. Similar Norian reappearances of taxa from other phyla that seemed to have disappeared at the end of the Paleozoic have been reported by other authors: for example, the Paleozoic strophomenid brachiopod *Gosaukammerella* (SENOWBARI-DARYAN & FLÜGEL, 1996) and phylloid algae (R. P. REID, 1986).

The Triassic–Jurassic event terminated the major evolutionary burst of Triassic sphinctozoan sponges. Of the 83 known Triassic genera, 82 genera became extinct at the Carnian–Norian, or at the end-Norian extinction event, which is a generic extinction rate of about 98%. Only the genus *Stylothalamia* survived beyond the Triassic–Jurassic boundary. *Stylothalamia columnaris* LE MAITRE, 1935, is the only sphinctozoan species known from the Lower Jurassic (Liassic) at several localities in the world (South America: HILDEBRANDT, 1971, 1981; SENOWBARI-DARYAN & STANLEY, 1994; North Africa: SCHROEDER, 1984; Europe: BECCARELLI BAUCK, 1986; see SENOWBARI-DARYAN & HAMEDANI, 1999).

Jurassic

As noted above, only one species of sphinctozoan sponge, *S. columnaris,* is known from the Lower Jurassic. Both the hypercalcified sphinctozoans with various filling structures (e.g., *Boikothalamia*), and the hexactinellid representative, e.g., *Casearia,* appear again in the Middle and Upper Jurassic. Calcarean sphinctozoans, including *Barroisia, Thalamopora, Sphaerocoelia,* and *Muellerithalamia,* also appear in the Upper Jurassic. Only four genera of hypercalcified chambered sponges are known from the Upper Jurassic. Some of these genera continued into the Cretaceous.

Cretaceous

To date, only ten Cretaceous hypercalcified sphinctozoans are known from several combined localities, especially from Europe (REITNER & ENGESER, 1985, 1989b; ENGESER & NEUMANN, 1986; HILLMER & SENOWBARI-DARYAN, 1986). Apparently, only two genera survived the Cretaceous–Tertiary boundary, which is an extinction rate of 90%.

Paleogene–Neogene

Only two or three Paleogene–Neogene sphinctozoan sponge genera are known. *Vaceletia* (PICKETT, 1982) is the only living sphinctozoan sponge. For more information see SENOWBARI-DARYAN, 1990; SENOWBARI-DARYAN and GARCÍA-BELLIDO, 2002a.

Holocene

Only one genus of chambered sponge, *Vaceletia*, has been reported as occurring in the Holocene.

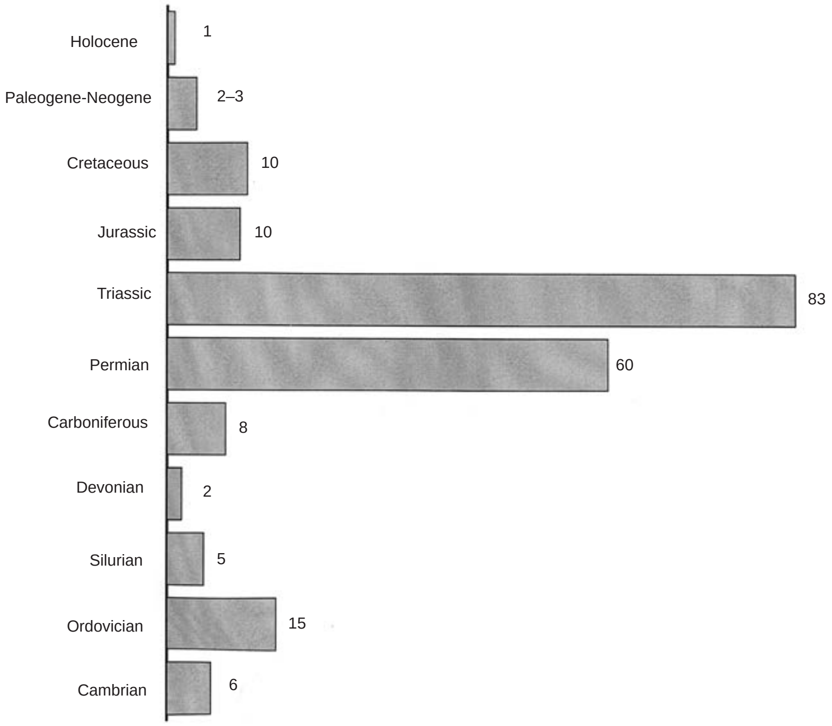


FIG. 245. Number of hypercalcified sphinctozoan genera per geologic period through the Phanerozoic (chambered hexactinellid genera are not considered in this diagram; Senowbari-Daryan & Rigby, 2011).

Figure 245 shows the number of sphinctozoan sponge genera occurring per period through Earth history.

INOZOANS

Like sphinctozoan sponges, the inozoans (Inozoa STEINMANN, 1882) are polyphyletic. Although some Triassic taxa, such as *Sestrostomella* (see REITNER, 1992) and Jurassic inozoan sponges like *Peronidella* HINDE, 1893, secreted spicular skeletons, almost all Triassic and Permian representatives of the group lack a spicular skeleton. For that reason, RIGBY and SENOWBARI-DARYAN (1996a) suggested separation of inozoan sponges without spicular skeletons into the Inozoida, and those with a spicular skeleton into the Inozoa. Without taking spicular skeletons differences into consideration, the morphologic features of both groups are discussed here.

EXTERNAL MORPHOLOGY

Sponge Shape

Shapes of inozoan sponges are usually cylindrical, like *Peronidella* HINDE, 1893, for example, or *Stollanella* BIZZARINI & RUSSO, 1986; but club- or mushroom-shaped taxa, as, for example, *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a, or sheetlike taxa, such as *Auriculospongia* TERMIER & TERMIER, 1974, or irregularly massive to hemispherical taxa, such as *Estrellospongia* RIGBY & SENOWBARI-DARYAN, 1996a, are also known. Figure 246 shows the principal general shapes of inozoans.

Both single and multibranched growth types also occur, such as the Upper Triassic multibranched species *Peronidella iranica* SENOWBARI-DARYAN, 2003 (Fig. 247). Inozoan sponges are commonly less than

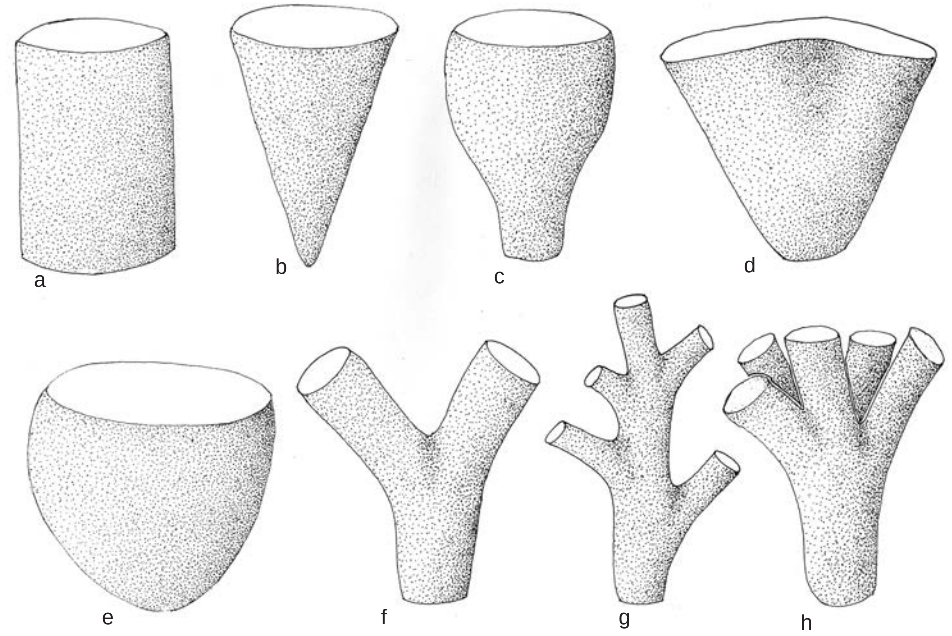


FIG. 246. General shapes of skeletons of inozoan sponges. *a,* cylindrical, *b,* arcuate conical, *c,* conical to club shaped, *d,* tabular, *e,* hemispherical, *f,* single dichotomously branched, *g–h,* dichotomously multibranched; schematic, not to scale (Senowbari-Daryan & Rigby, 2011).

10 cm in diameter, although large species, up to 2.5 m diameter, like the platelike Permian *Gigantospongia discoforma* RIGBY & SENOWBARI-DARYAN, 1996b, are exceptional. Annulated, screwlike, or externally segmented forms also occur, as, for example, the Permian genera *Imperatoria* DE GREGORIO, 1930, and *Minispongia* RIGBY & SENOWBARI-DARYAN, 1996a. Outer dermal surfaces of inozoans may be smooth or characterized by having distinct growth lines. The major skeletal elements of inozoans are shown in Figure 248.

External Inhalant Canals

Outer surfaces of inozoans may totally lack perforations, but the majority of these sponges are perforated by numerous small pores, or by less abundant large openings, termed ostia (Fig. 249–250). Sponges with a distinct cortex or dermal layer commonly have pores or ostia, but in representatives without a dermal layer, communication from the outside to the sponge interior is accomplished through spaces between skeletal fibers, as, for example, in *Peronidella* HINDE, 1893. Pores or ostia may have circular or oval cross sections. Ostia are usually separated, single, circular openings, as in the Permian genus *Djemelia* RIGBY & SENOWBARI-DARYAN, 1996a, but starlike ostia or two or more combined ostia that may be united into groups, also occur, as, for example, in some species of the genus *Daharella* RIGBY & SENOWBARI-DARYAN, 1996a. Both ostia types may be rimmed or have tubelike projections, termed exaules. Exaules of inozoans are usually less than 1 mm long, and exaules, like those observed in some sphinctozoan representatives, such as in *Girtyocoelia* COSSMAN, 1909 (Fig. 228), have not been reported in inozoans. The two types of openings (pores and ostia) of inhalant canals usually do not occur together in the same sponge.

In sheetlike representatives of inozoan sponges, the opposite surfaces may have similar porosity, or be different. For example, in the

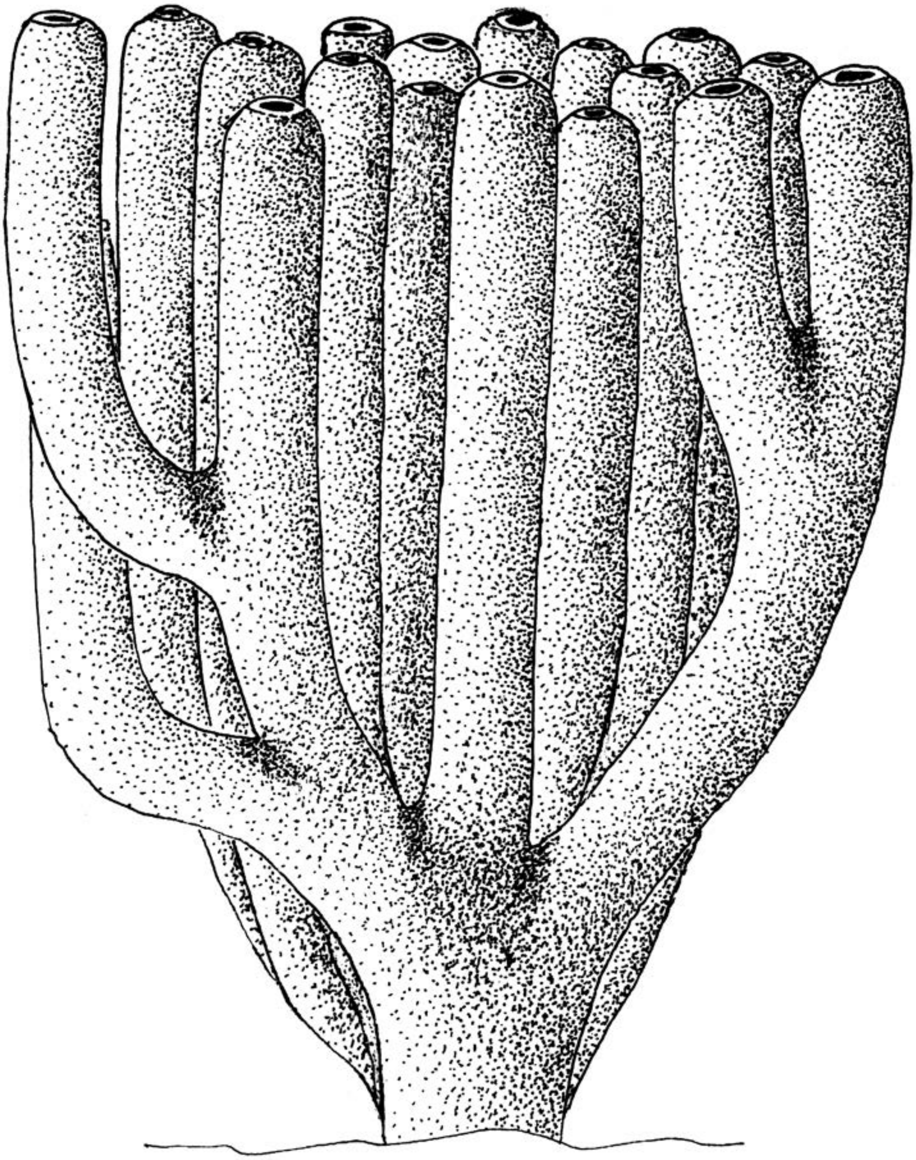


FIG. 247. Reconstruction of multibranched inozoan sponge *Peronidella iranica* SENOWBARI-DARYAN, 2003; Norian–Rhaetian, Triassic, reefs within Nayband Formation, Iran (Senowbari-Daryan, 2003).

Permian genus *Auriculospongia* TERMIER & TERMIER, 1974 (see Fig. 259.1), or in the Triassic genus *Aliabadia* SENOWBARI-DARYAN (2005a), the opposite sides are totally different.

External Exhalant Canals

As mentioned above, some inozoan sponges lack an axial spongocoel, especially those with sheetlike construction, but representatives of cylindrical- or club-shaped taxa may also be without distinct exhalant canals, as, for example, the Permian genus *Daharella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 249) or the Triassic genus *Molengraaffia* VINASSA DE REGNY, 1915.

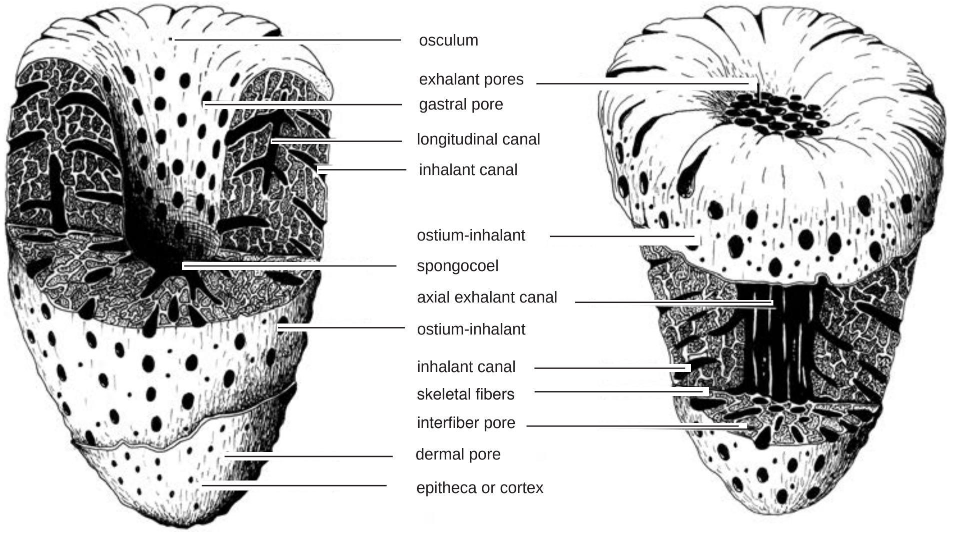


FIG. 248. Major skeletal elements of inozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

Some inozoans are characterized by only one osculum (e.g., *Peronidella* HINDE, 1893), and others by several oscula (e.g., *Sestrostomella* ZITTEL, 1878; Fig. 251), which are visible as one or several openings at the top of the sponge (Fig. 251; see also DIECI, ANTONACCI, & ZARDINI, 1968, pl. 25–26). In representatives with a single spongocoel, that spongocoel may be circular, oval, or starlike in cross section. Oscula of spongocoels may be located in depressions or on elevations. Upper surfaces of some inozoans may have numerous oscula across the top of the sponge (e.g., the Permian genera *Polytubispongia* RIGBY & SENOWBARI-DARYAN, 1996a [Fig. 250], or *Medenina* RIGBY & SENOWBARI-DARYAN, 1996a). These and other types of oscula extend as spongocoels into the sponge interior.

Starlike arrangements of exhalant canals in an astrorhizal system are developed in a variety of genera in inozoan sponges. For example, tops of the Permian sponge *Prestellispongia lobata* (PARONA, 1933), which has a conical shape, are occupied by one or more astrorhizal systems (see DIECI, ANTONACCI, & ZARDINI, 1968; RIGBY & SENOWBARI-DARYAN, 1996a). Several astrorhizal systems cover the outer surface of the cylindrical and massive genus *Stellispongiella* WU (see TERMIER & TERMIER, 1955; RIGBY & SENOWBARI-DARYAN, 1996a). The astrorhizal systems may be located on elevations (mamelons) (Fig. 252, Fig. 259.4) or not.

INTERNAL MORPHOLOGY

Spongocoels

Some inozoans possess only one axial spongocoel (e.g., *Peronidella* HINDE, 1893) (Fig. 259.2), and others have several axial spongocoels (e.g., *Sestrostomella* ZITTEL, 1878 [Fig. 251], or *Stollanella* BIZZARINI & RUSSO, 1986 [Fig. 253]). These spongocoels may pass vertically or longitudinally through the whole sponge from near the base up to the summit (e.g., *Sestrostomella*), or it may be limited to only the upper part of the sponge (e.g., the Permian genus *Pseudohimatella* RIGBY & SENOWBARI-DARYAN, 1996a). The spongocoel may have its own skeletal wall (Fig. 254), or it may be surrounded by the fibrous skeleton of the entire sponge wall, without a distinct separate inner layer (Fig. 255). Several sponges possess numerous vertical spongocoels that are distributed through the whole sponge (see Fig. 259.3) (e.g., the Permian genera *Preeudea* TERMIER & TERMIER, 1977a, or *Polytubifungia* RIGBY & SENOWBARI-DARYAN, 1996a; Fig.

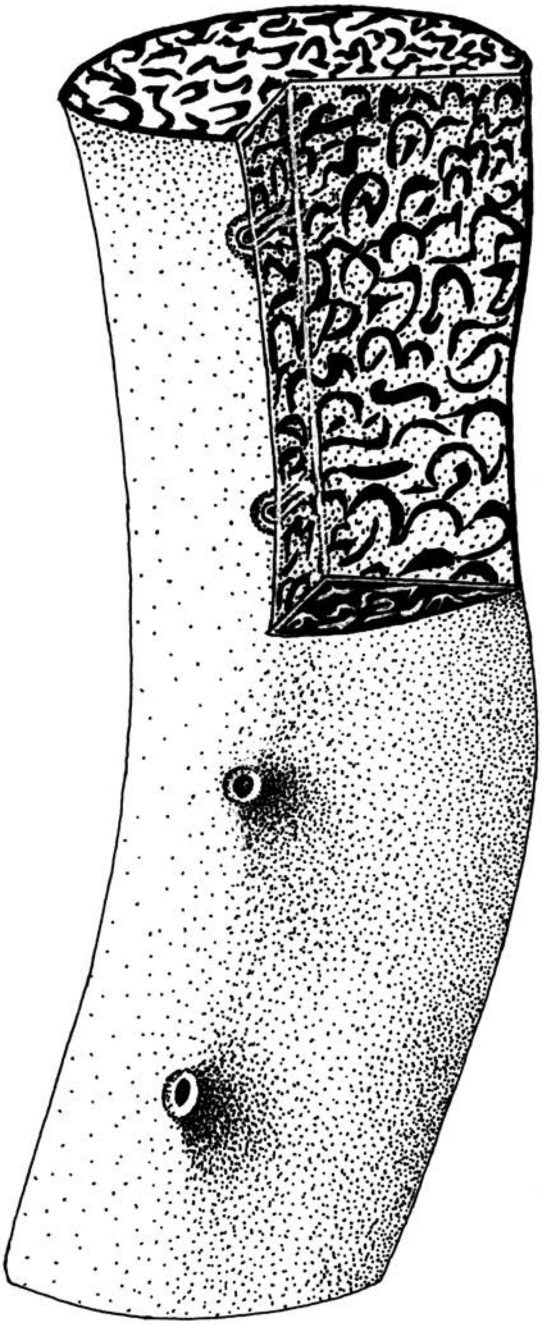


FIG. 249. Reconstruction of asiphonate inozoan sponge *Daharella micella* RIGBY & SENOWBARI-DARYAN, 1996a. Water passed through rimmed ostia and out through interfiber spaces; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

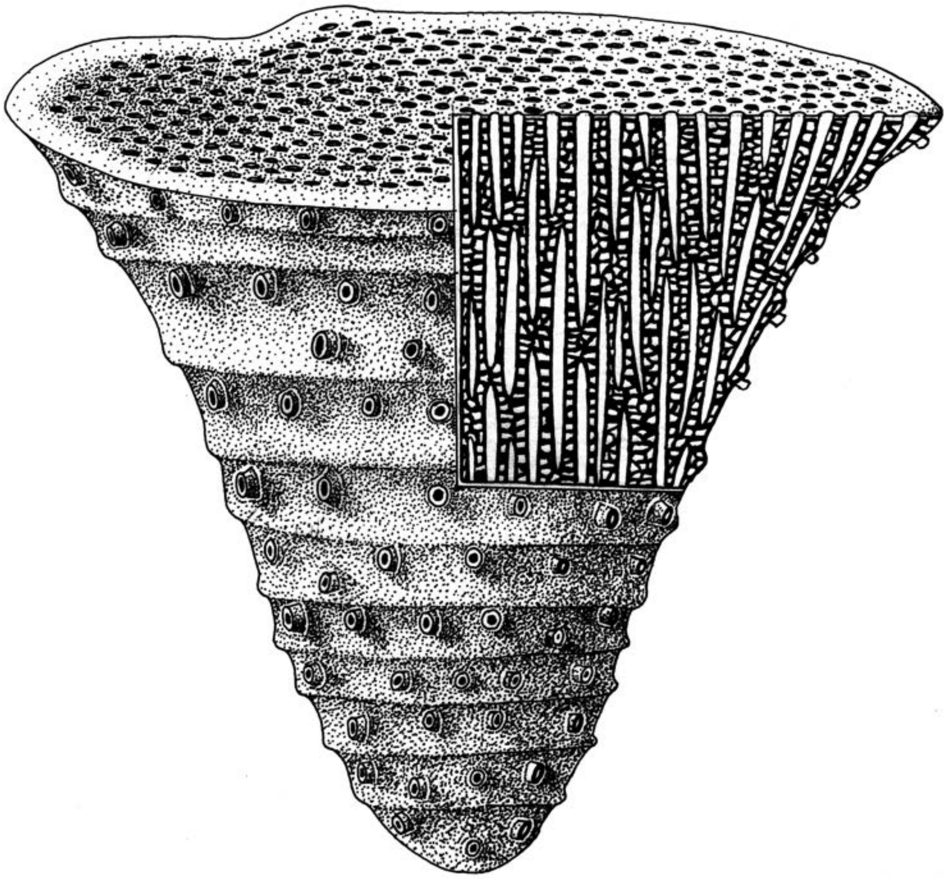


FIG. 250. Reconstruction of *Polytubispongia maxima* RIGBY & SENOWBARI-DARYAN, 1996a; externally annulate conical sponge bearing numerous rimmed ostia on the dermal surface that serve as inhalant canals; exhalant canals are numerous, more or less parallel tubes that are distributed through whole sponge; sponge is known from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

250). The Permian genus *Pseudohimatella* RIGBY & SENOWBARI-DARYAN, 1996a, is characterized by a shallow axial spongocoel and numerous additional small spongocoels that pass vertically through the whole sponge. The Triassic genus *Marawandia* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, possesses several spongocoels that are usually located near the periphery of the sponge (Fig. 254). In the Permian genus *Exotubispongia* RIGBY & SENOWBARI-DARYAN, 1996a, the interior of the sponge is filled with a reticular fibrous skeleton, but the more outer part of the sponge is marked by numerous vertical canals (Fig. 256).

Internal Inhalant and Exhalant Canals

Outer ostia continue as tubes into the relatively thick sponge wall in some inozoans, as, for example, in the Permian genus *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 255, Fig. 257), or in the Jurassic genus *Endostoma* ROEMER, 1864 (=*Corynella* ZITTEL, 1878). These tubes may be called inhalant tubes or canals (Fig. 255). Spongocoels of these sponges may have a distinct, separate wall that is pierced by openings called gastral pores. Gastral pores may continue into the sponge wall as radial tubes, which are termed exhalant tubes, or canals. Inhalant

FIG. 251. *Sestrostomella robusta* ZITTEL; oblique sections; sponge is characterized by a bundle of axial tubes that may range up to 20 individual tubes. Additional small tubes are also present, and they diverge upward and outward to dermal surface of sponge; concentric lines in sponge wall reflect growth lines; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×2.5 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

and exhalant tubes are usually not connected directly with each other. These tubes may have a pierced wall or may be surrounded by the fibrous skeleton of the sponge wall. Inhalant and exhalant canals are usually oriented horizontally, but they are also commonly longitudinal and parallel to the axial spongocoel (Fig. 255). In some genera, the exhalant canals may converge upward and open into the spongocoel, as in *Sestrostomella* ZITTEL, 1878 (Fig. 251), or they may be outwardly divergent within the sponge wall and open at the sponge surface, as in *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 255, Fig. 257), or in *Stollanella* BIZZARINI & RUSSO, 1986 (Fig. 235).

Astrorhizal systems, common in stromatoporoids and Recent hypercalcified sponges such as *Ceratoporella,* occur in a variety of inozoan sponges. For example, the Permian–Triassic genus *Stellispongiella* WU, 1991, is a massive, rodlike sponge that is characterized by astrorhizal exhalant canals, which in some specimens are located within mamelon-like elevations (Fig. 252). Also, summits of some other genera, such as the Permian–Triassic genus *Prestellispongia* RIGBY & SENOWBARI-DARYAN, 1996a, and the Triassic genus *Stellispongia* D'ORBIGNY (see DIECI, ANTONACCI, & ZARDINI, 1968), have several astrorhizal exhalant canal systems.

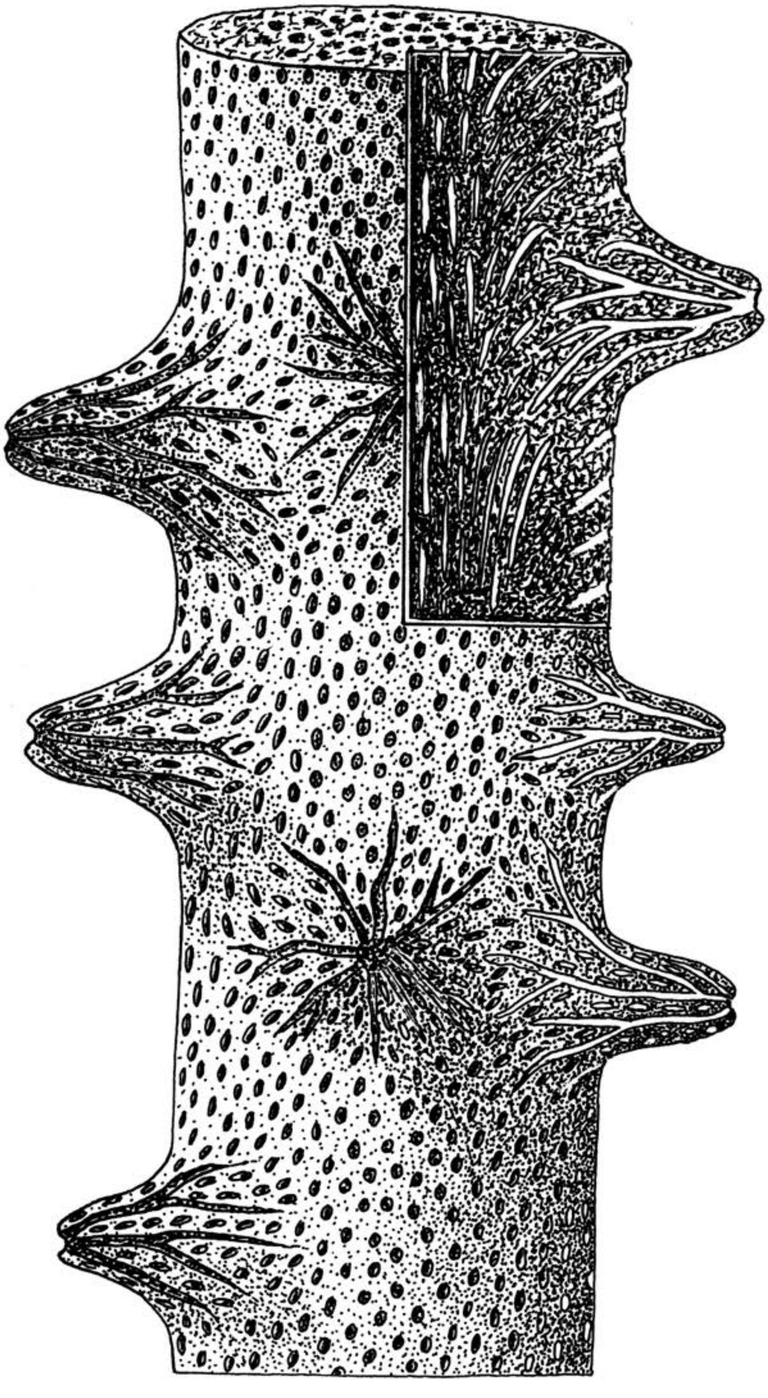


FIG. 252. Reconstruction of *Stellispongiella bacilla* (TERMIER & TERMIER, 1977b), a cylindrical inozoan sponge from upper Permian, Djebel Tebaga, Tunisia; astrorhizal systems served as exhalant canals and are located on sharp moundlike elevations; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

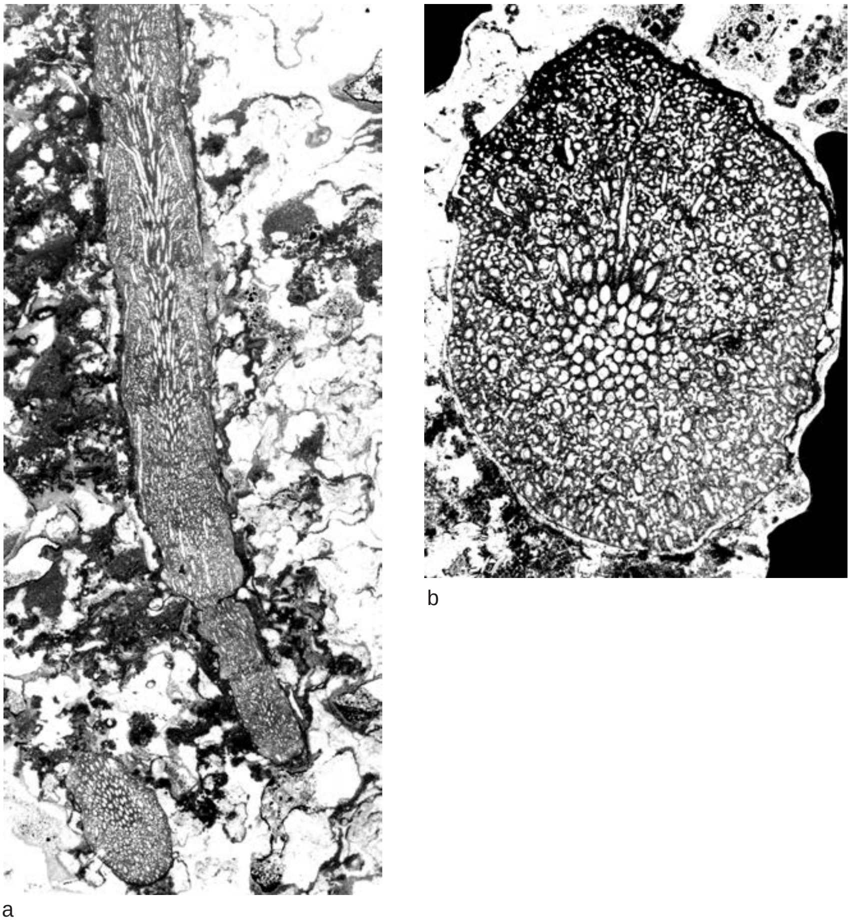


FIG. 253. *Stollanella diecii* BIZZARINI & RUSSO, 1986. *a,* Longitudinal, ×1.5, and *b,* transverse, ×5, sections of cylindrical inozoan sponge. It has Mg-calcite skeletal mineralogy and is characterized by an axial canal bundle composed of up to approximately 50 individual tubes; additional smaller tubes around axial bundle diverge upward and outward toward dermal surface of sponge; Ladinian–Carnian, Triassic, Dolomites, Italy (Senowbari-Daryan & Rigby, 2011).

Structure of Rigid Skeleton

Walls of the majority of inozoan sponges are composed of reticulate skeletal fibers. Thicknesses and orientations of such skeletal fibers may vary across different parts of the same sponge skeleton. Fibers in *Auriculospongia* TERMIER & TERMIER, 1974, are linearly arranged parallel to the growth direction and may be associated with some transverse fibers, but they appear unoriented in sections perpendicular to the growth direction (see RIGBY & SENOWBARI-DARYAN, 1996a, fig. 12). In the Triassic genera *Molengraaffia* VINASSA DE REGNY, 1915, and *Anguispongia* SENOWBARI-DARYAN, 2005b, orientations of fibers are totally different in sections cut parallel or perpendicular to the growth direction (see SENOWBARI-DARYAN, 2005b). Walls around axial spongocoels in some Triassic sponges are composed only of tubes that diverge upward and outward. These tubes are interconnected with other tubes by numerous intertubular pores.

Spicules

Investigations of well-preserved Permian inozoan sponges from Djebel Tebaga, Tunisia

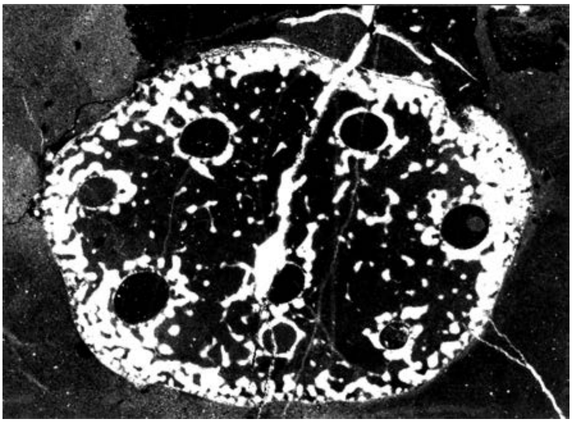


FIG. 254. *Marawandia iranica* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997. Cylindrical inozoan sponge, seen here in transverse section, has several (6–8) usually peripherally located spongocoel tubes with more or less distinct exowalls pierced by labyrinthic branched pores; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×12 (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997).

by scanning electron microscopy by WENDT (1977, 1978, 1979, 1984) and RIGBY and SENOWBARI-DARYAN (1996a) show that these sponges lack calcareous or siliceous spicular skeletons. Detailed discussion of whether the spicules were originally lacking, or were lost secondarily during diagenesis, was given by RIGBY and SENOWBARI-DARYAN (1996a).

In contrast to the Permian inozoans, spicules have been found in some Triassic and Jurassic inozoan sponges. For example, spicules occur in the Triassic genera *Sestrostomella* ZITTEL, 1878, and *Stellispongia* D'ORBIGNY, 1849b, and in the Jurassic genus *Peronidella* ZITTEL in HINDE, 1893 (see REITNER, 1992).

Mineralogy and Microstructure of the Rigid Skeleton

Modifications of calcite, aragonite, and Mg calcite are known from fossil inozoan representatives. Because of replacement of aragonite by calcite, primary skeletal mineralogy is not known for lower Paleozoic (Cambrian–Carboniferous) inozoans. However, traces of spherulitic microstructure, like those in Paleozoic stromatoporoids that point to an original primary aragonite composition (STEARN, 1972), are also preserved in some Carboniferous inozoans, suggesting a primary aragonitic mineralogy of these taxa (WENDT, 1984). Certain aragonitic skeletal mineralogy was reported from upper Permian inozoans of Djebel Tebaga, Tunisia (WENDT, 1977, 1979; RIGBY & SENOWBARI-DARYAN, 1996a). The majority of inozoan sponges from other Permian localities of the world are recrystallized. As a result, the primary skeletal mineralogy of sponges from these localities is not known.

Aragonite skeletal mineralogy is known also from numerous Triassic taxa, such as *Eudea polymorpha* (KLIPSTEIN), *Leiospongia involuta* (KLIPSTEIN), and *Peronidella lorenzi* ZITTEL, or *Sestrostomella robusta* ZITTEL (DIECI, RUSSO, & RUSSO 1974a; WENDT, 1974, 1975, 1979, 1990; MÜLLER-WILLE & REITNER, 1993; MASTANDREA & RUSSO, 1995).

Mg-calcitic mineralogy is very rare in Triassic inozoans but does seem to be present. For example, it is present in *Stollanella* BIZZARINI & RUSSO, 1986, which, according to the authors, has a micritic, irregular, or homogenous skeletal texture, as described in examples from the Carnian Cassian Formation (Dolomites, northern Italy). It is also present in some as yet undescribed Norian–Rhaetian species from southern Turkey.

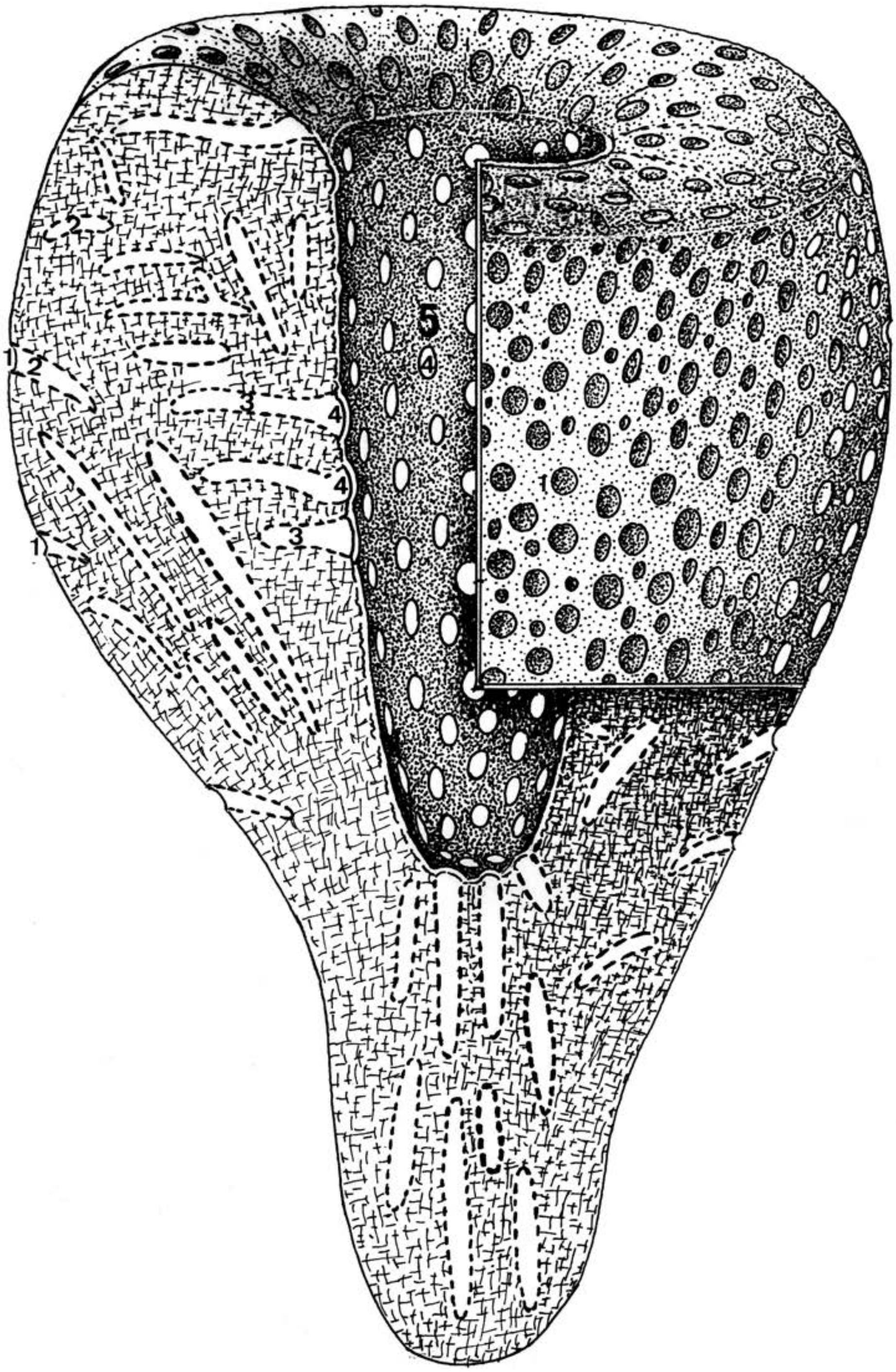


FIG. 255. Reconstruction of *Permocorynella* RIGBY & SENOWBARI-DARYAN, 1996a, showing *1,* exopores or ostial pores, *2,* inhalant canals, *3,* exhalant canals, *4,* endopores, and *5,* deep spongocoel. Spaces between the inhalant and exhalant canals are filled with reticular fiber skeleton; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

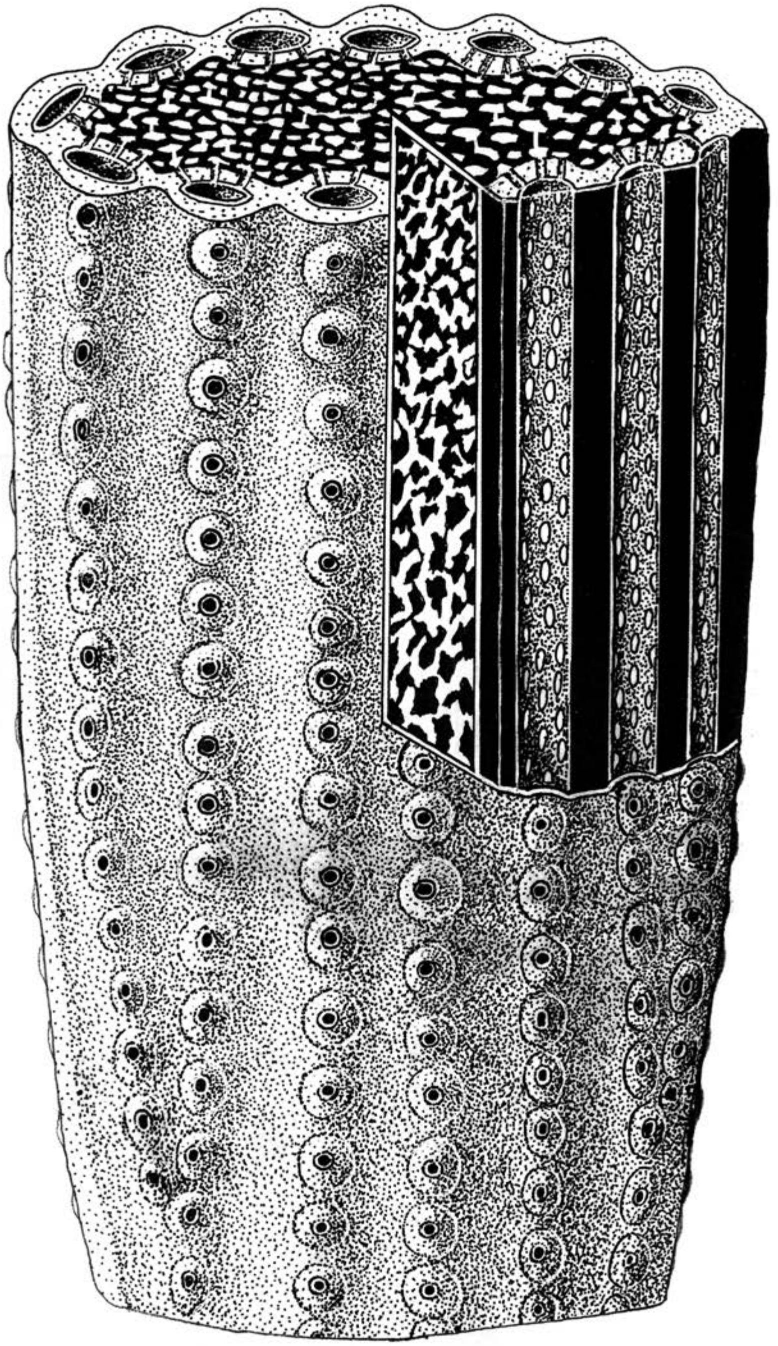


FIG. 256. Reconstruction of *Exotubispongia pustulata* RIGBY & SENOWBARI-DARYAN, 1996a; sponge has numerous vertical peripheral tubes that are connected by pores to spaces in the internal reticular skeleton and to the dermal surface through numerous ostia located on pustulelike elevations. The sponge is known, to date, only from upper Permian, Djebel Tebaga, Tunisia; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

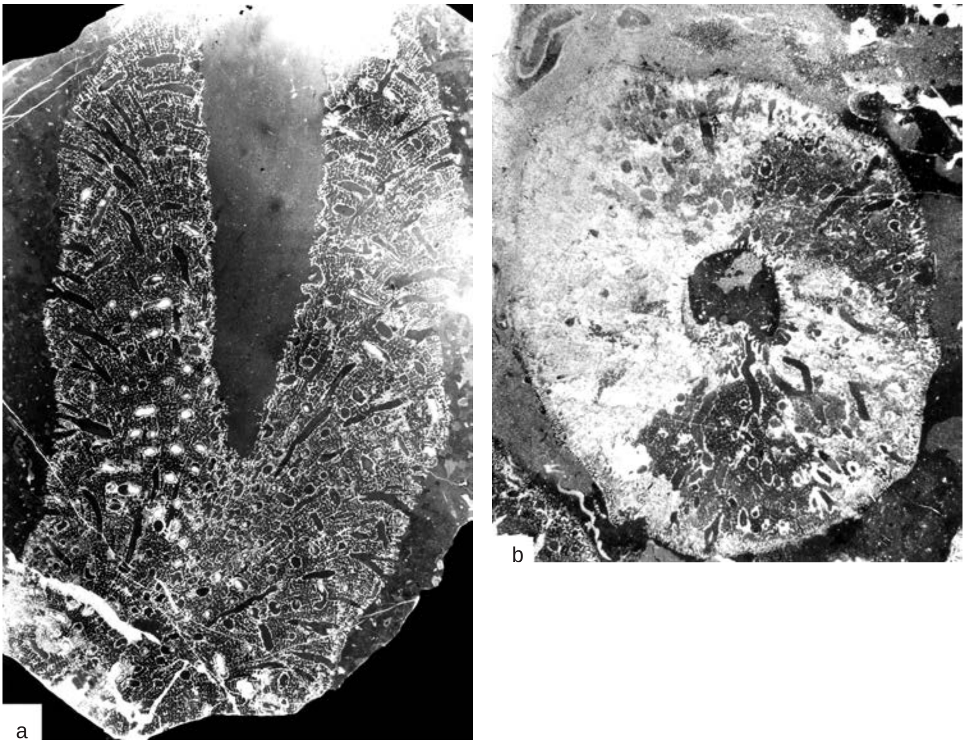


FIG. 257. *Permocorynella maxima* SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997, as seen in *a,* longitudinal and *b,* transverse sections. Sponge is characterized by an axial spongocoel and numerous additional branched tubes that diverge upward and outward to become perpendicular to dermal surface of sponge; Norian–Rhaetian, Triassic, Nayband Formation, Iran, ×2 (Senowbari-Daryan & Rigby, 2011).

WENDT (1979, 1984, 1990) concluded that principally five types of microstructure occur within the inozoan sponges. He listed them as: (1) granular; (2) irregular; (3) spherulitic; (4) clinogonal; and (5) orthogonal. More than one microstructure type may occur in primary and secondary skeletons within the same sponge skeleton.

A granular microstructure (Fig. 244) was observed, for example, in the Permian–Triassic genus *Himatella* ZITTEL, 1878 (WENDT, 1979), and an irregular microstructure is known from the Triassic genus *Eudea* (WENDT, 1979, 1990; MASTANDREA & RUSSO, 1995).

Spherulitic microstructure (Fig. 244), the most common microstructure in inozoan sponges, is known from the majority of Permian and Triassic genera. It has been recognized, e.g., in Permian *Sphaeropontia* RIGBY & SENOWBARI-DARYAN, 1996a (Fig. 258), and in the Triassic genera *Sestrostomella* ZITTEL, 1878 (DIECI, ANTONACCI, & ZARDINI, 1968; WENDT, 1979; MASTANDREA & RUSSO, 1995), or *Peronidella* (DIECI, ANTONACCI, & ZARDINI, 1968; MÜLLER-WILLE & REITNER, 1993). A list of Permian inozoan sponges with spherulitic microstructure from Djebel Tebaga, Tunisia was given by RIGBY and SENOWBARI-DARYAN (1996a), with sizes of spherulites in those sponges ranging from 30–100 µm.

Clinogonal microstructure (Fig. 244) occurs in the Triassic species *Stellispongia variabilis* (WENDT, 1979, 1984). According to WENDT (1975, 1979, 1984), the Triassic sponge *Cassianostroma küpperi* FLÜGEL has a clinogonal microstructure. *Cassianostroma* was originally described as a hydrozoan by

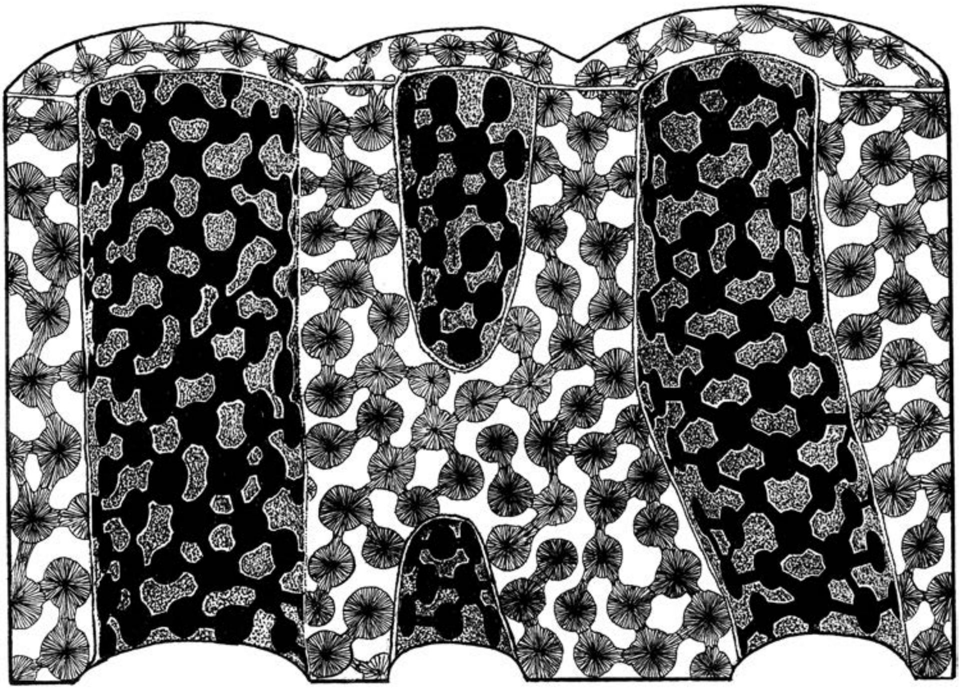


FIG. 258. Spherulitic microstructure of *Sphaeropontia regulara* RIGBY & SENOWBARI-DARYAN, 1996a, upper Permian, Djebel Tebaga, Tunisia. This type of microstructure is most abundant in aragonitic inozoan and sphinctozoan sponges; schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

FLÜGEL (1960), but it also may be considered as an inozoan sponge. However, according to FLÜGEL (1960, p. 55) the "radial-strahligen Bau der 'Radial-Struktur'" should be classified as spherulitic. Similar (or identical) sponges from the same horizon and locality, but with irregular microstructure, were described as *Stromatowendtia* RUSSO, MASTANDREA, & BARACCA, 1994.

The occurrence of an orthogonal type microstructure (Fig. 244) is not proven in Triassic inozoans.

PALEOBIOLOGY, PATTERNS OF WATER CIRCULATION, AND PALEOCOLOGY

Possible water circulation patterns in Permian inozoan sponges of Djebel Tebaga, Tunisia, were discussed by RIGBY and SENOWBARI-DARYAN (1996a). They differentiated four main patterns (Fig. 259).

1. *Auriculospongia*-type: in these sheetlike sponges, water moved essentially horizontally.
2. *Peronidella*-type: cylindrical or club-shaped sponges with inhalant openings on side surfaces, and with one or several spongocoels open at the summit; passage of water was horizontal and then vertical.
3. *Pseudohimatella*-type: cylindrical or club-shaped sponges without differentiated inhalant openings on side surfaces, but at the top of the sponge, and associated there with one or several spongocoels; passage of water was vertically downward, then horizontal, and then vertically upward.
4. *Stellispongiella*-type: sponges where inhalant and exhalant openings are both located on side surfaces; passage of water was horizontal, then vertical, and then horizontal.

Similar water movement patterns also may have been present in Mesozoic inozoan sponges.

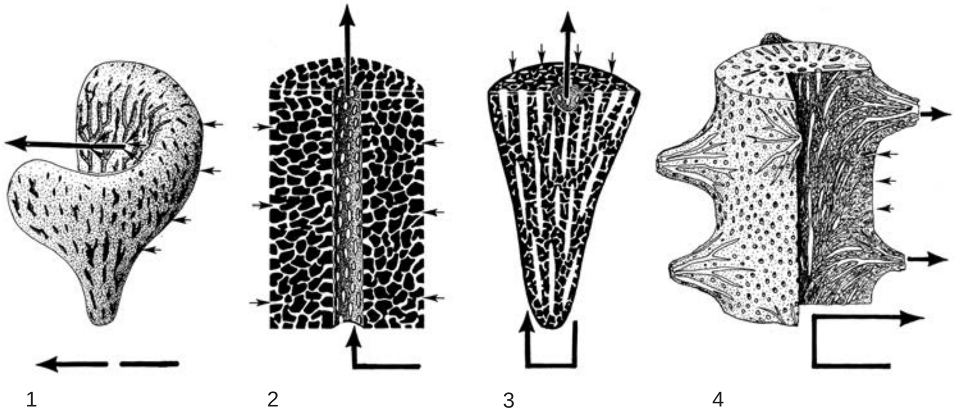


FIG. 259. Pathways of water movement in inozoan sponges. *Small arrows* indicate inhalant current directions; *large arrows* indicate exhalant directions. *1, Auriculospongia*-type (pathway: inhalant = horizontal, exhalant = horizontal); *2, Peronidella*-type (pathway: inhalant = horizontal, exhalant = vertically upward); *3, Pseudohimatella*-type (pathway: inhalant = vertically downward, exhalant = vertically upward); *4, Stellispongiella*-type (pathway: inhalant = horizontal, exhalant = horizontal); schematic, not to scale (Rigby & Senowbari-Daryan, 1996a).

Inozoan sponges, as important late Paleozoic and Triassic reef builders, lived in the same biotopes as the sphinctozoan sponges and likely had functions similar to those of the sphinctozoans, discussed previously (see p. 341–342).

REVIEW OF CLASSIFICATION

A summary of the review of classification of inozoan sponges by earlier authors was given by RIGBY and SENOWBARI-DARYAN (1996a). In the same publication, they subdivided the inozoans of STEINMANN (1882) into two orders: the Inozoa, which includes those with a spicular skeleton; and the Inozoida, which includes those without a spicular skeleton. Sponges from both the Inozoa and the Inozoida were placed in the classes Demospongea (=Demospongiae), and Calcarea by FINKS and RIGBY (2004d). They subdivided the hypercalcified sponges and placed them into the following subclass to ordinal level groupings.

- Class Demospongiae
  - Subclass Ceractinomorpha LÉVI, 1953
    - Order Agelasida VERRILL, 1907
    - Order Vaceletida FINKS & RIGBY, 2004d
  - Subclass Tetractinomorpha LÉVI, 1953
    - Order Hadromerida TOPSENT, 1898
- Class Calcarea
  - Subclass Calcinea BIDDER, 1898
    - Order Clathrinida HARTMAN, 1958
    - Order Murrayonida VACELET, 1981
  - Subclass Calcaronea BIDDER, 1898
    - Order Leucosolenida HARTMAN, 1958
    - Order Sycettida BIDDER, 1898
    - Order Stellispongiida FINKS & RIGBY, 2004d
    - Order Sphaerocoeliida WENDT, 1979
    - Order Lithonida DÖDERLEIN, 1892

PATTERNS OF EVOLUTION AND EXTINCTION

Inozoans, like the sphinctozoans, had pulses of major diversification separated by times of extinction during the late Paleozoic and Mesozoic, and had reduced records, to near total extinction, in the Cenozoic. These records have not been widely published, although the prominence of both of these groups in the Permian and Triassic records is well known. Currently, approximately 100 genera of various hypercalcified inozoan sponges have been described, including forms now placed dominantly in the Demospongiae, but including several Mesozoic and Cenozoic genera placed in the Calcarea as well.

Figure 260 shows the abundance and number of inozoan genera reported to date from each geologic period through the Phanerozoic.

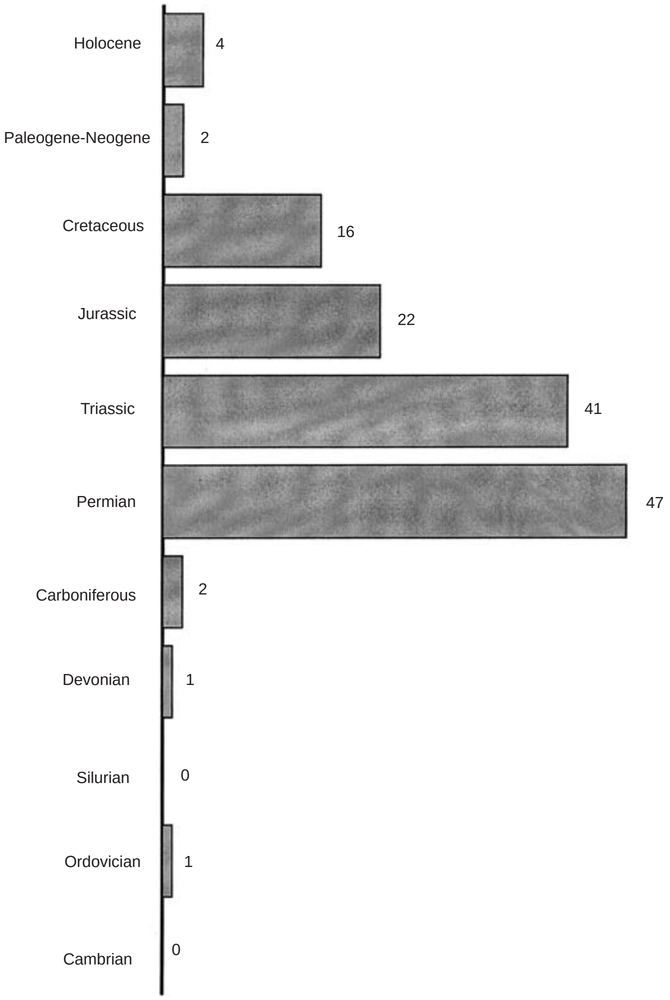


FIG. 260. Number of inozoan genera per geologic period through the Phanerozoic. Genera that have been described as hydrozoans are not considered in the diagram (Senowbari-Daryan & Rigby, 2011).

Cambrian

No inozoan sponges have been described from the Cambrian.

Ordovician

The single genus *Imperatoria,* based on the species *I. mega* has been reported as inozoan by RIGBY and POTTER (1986) from the Upper Ordovician Kangaroo Creek Formation, Klamath Mountains, northern California. This sponge was attributed to the sphinctozoan genus *Pseudoimperatoria* by SENOWBARI-DARYAN and RIGBY (1988).

Silurian

No Silurian inozoan sponges have been documented to date.

Devonian

The genus *Fissispongia* KING, 1938, is the only inozoan sponge currently reported from the Devonian. The genus is a moderately long-ranging form that first appeared in the Middle Devonian (?Eifelian), of Alaska

(RIGBY & BLODGETT, 1983), but which ranges up through the Carboniferous into the lower Permian in the south-central United States.

Carboniferous

Only two genera of inozoan sponges have been reported from the Carboniferous, including *Fissispongia,* cited above, and the somewhat similar long-ranging genus *Maeandrostia* GIRTY, 1908b. These sponges marked the base of major expansions of the inozoans that took place during the Permian, for *Maeandrostia* also ranges from the upper lower Carboniferous, through the Permian, into the lower Middle Triassic.

Permian

The Permian marks the first major pulse of diversification of the hypercalcified sponges with inozoan skeletal structure. Presently, 47 genera of inozoans have been described from the Permian, and 46 of these genera appear in the Permian as new forms. With that taxonomic expansion, the inozoans also became more geographically widespread, as noted in Stratigraphic and Geographic Occurrences (p. 371).

The Permian–Triassic boundary extinction event had a major impact on the inozoan sponges, as it did on the sphinctozoan forms, and fossils of other phyla too. Of the 47 inozoan genera reported from the Permian, only 15 or 16 survived into the Triassic, so that the extinction rate was approximately 70%.

Triassic

Of the 41 inozoan genera known from the Triassic, 25 or 26 genera are new and 15 or 16 genera survived from the Permian. As with the sphinctozoans, there is a major break in the record, for no inozoans are known from the Lower Triassic (Scythian), and only *Maeandrostia* GIRTY, 1908b, see above, has been found in Anisian reefs of northern Italy (SENOWBARI-DARYAN & others, 1993). Inozoan sponge taxa increased greatly in number during the Middle and Upper Triassic, and a second pulse of sponge diversification was produced. As with the inozoans, however, the number of taxa decreased sharply toward the end of the Triassic, and a second major extinction event occurred at the Triassic–Jurassic boundary. Only *Sestrostomella,* and questionably *Stellispongiella,* among the demosponges, and *Stellispongia, Pareudea, Eudea,* and *Oculospongia* among the Calcarea, and *Cornuaspongia* and *?Trammeria* among the class and order Uncertain inozoans, survived into the Jurassic beyond the boundary event. From the Triassic on through the Cenozoic, the Calcarea play an ever increasingly significant role in the evolutionary development of the inozoans.

Jurassic

A third pulse of inozoan diversification resulted in the documented occurrence of 22 new inozoan genera, along with 6 genera that survived beyond the boundary extinction event into the Jurassic, which had an extinction rate of about 73%. This has resulted in a known Jurassic inozoan fauna of 22 genera. Of these, the 5 genera, *Sestrostomella, Epitheles, Winwoodia, Aulocopagia,* and *Stellispongiella* are classed with the Demospongiae, and the remainder are classed with the Calcarea (FINKS & RIGBY, 2004a, 2004d). Except for *Sestrostomella,* which was reported from the Canadian Atlantic Shelf, all other Jurassic inozoan genera have been reported from localities in Europe, around the western end of the Tethyan seaway, an area that continued as a major locus of evolution of these forms.

Cretaceous

A total of 16 to 18 genera of inozoan sponges have been reported, and 2 more are questionably reported from the Cretaceous. Of these, 10 or 12 genera are new forms and 6 are carry-over elements from the Jurassic. Only *Trachytila, Pharetrospongia,* and *Elasmopagia* are demosponge forms, and the remainder of these Cretaceous inozoans are genera of the moderately rapidly evolving family Stellispongiidae, of the Calcarea (Finks & Rigby, 2004a, 2004d). All of these Cretaceous inozoans have been reported from localities in Europe, which, again, was the locus of inozoan evolution for the period.

Paleogene–Neogene

Only two inozoan genera are documented from deposits of these ages. *?Elasmostoma* has been reported from the Eocene of Mexico, and *Tretocalia* from the Miocene of Australia (Finks & Rigby, 2004d, p. 741, 748). The lower and mid-Cenozoic record of inozoans is one of near extinction of sponges with this skeletal structure.

Holocene

Four genera of inozoans have been reported as occurring in the Holocene. These include: *Trachysphecion* Pomel, 1872; *Eudea* Lamouroux, 1821; *Mammillopora* Bronn, 1825, and *Peronidella* Zittel in Hinde, 1893, all from the Mediterranean Sea near France, and all are now included in the Calcarea (Finks & Rigby, 2004d, p. 743–747). These inozoans are living representatives of genera that first appeared in the early Mesozoic.

TEMPORAL AND SPATIAL DISTRIBUTION OF SPHINCTOZOANS AND INOZOANS

STRATIGRAPHIC AND GEOGRAPHIC OCCURRENCES

In general, sphinctozoan and inozoan sponges have a lower and mid-latitude distribution throughout their history and have relatively limited geographic distributions through much of the early Paleozoic. However, they became more widely distributed and considerably more diverse during the Permian and Triassic and became increasingly less diverse and more geographically limited during the later Mesozoic and Cenozoic (Fig. 245, Fig. 261–272).

The heteractinids *Jawonya* and *Wagima,* which occur in the lower and lower middle Cambrian in the Northern Territory (Kruse, 1983, 1990) of Australia, are the oldest forms included by some in the sphinctozoans. Moderate faunules of early sphinctozoans, including *Blastulospongia* and *Amblysiphonella,* and the heteractinid *Nucha,* are also the earliest sphinctozoan forms and have been reported from middle Cambrian rocks of New South Wales (Pickett & Jell, 1983). Other documented Cambrian occurrences are the single-genus records of *Polythalamia* from the lower Cambrian of Alaska and Nevada, in western North America (Debrenne & Wood, 1990), and the upper Cambrian occurrence of *Blastulospongia* from Hubei, China (Conway Morris & Chen, 1990), and from Queensland, Australia (Bengtson, 1986; Fig. 261).

Sponges described as archaeocyaths from the Cambrian could be attributed to the inozoans, but they are not discussed here. The inventory of sphinctozoan and inozoan sponges treated here is based on cited publications and on the works of Finks and Rigby (2004a, 2004b, 2004d).

The oldest nonarchaeocyath sponge, *Imperatoria mega* (Rigby & Potter, 1986), was described as being an inozoan from Ordovician rocks of the eastern Klamath Mountains of northestern California. This sponge was attributed to the sphinctozoan genus *Pseudoimperatoria* by Senowbari-Daryan and Rigby (1988).

Five genera of Ordovician sphinctozoans, *Cliefdenella, Angullongia, Belubulaia, Nibiconia,* and *Rigbyetia* (Fig. 262), have been documented from New South Wales, Australia by Webby (1969), Webby and Rigby (1985), Rigby and Webby (1988), and Webby and Lin (1988). From western North America, nine Ordovician genera have been reported from northern California and Oregon (Rigby & Potter, 1986; Webby & Lin, 1988), including *Amblysiphonella, Amblysiphonelloides, Angullongia, Corymbospongia, Cystothalamiella, Exaulipora, Porefieldia, Pseudoimperatoria,* and *Rigbyetia.*

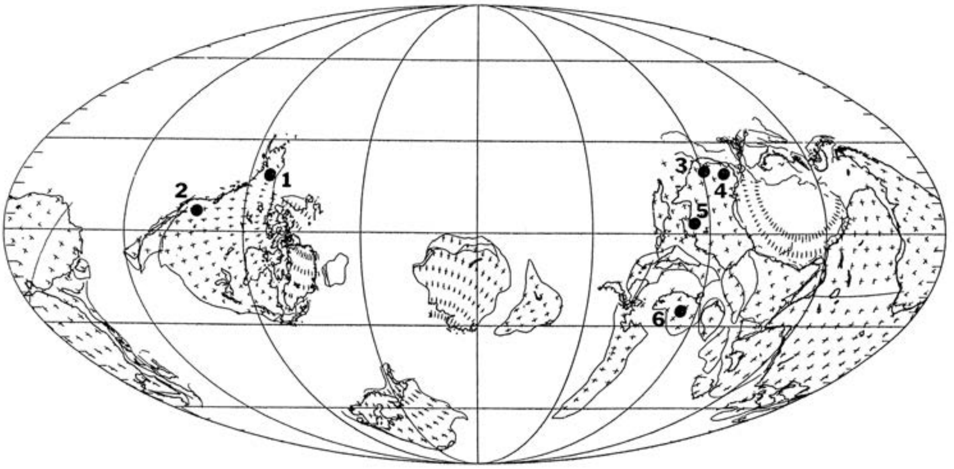


FIG. 261. Paleogeographic distribution of localities from where Cambrian sphinctozoans have been reported: *1,* Tatonduk River, eastern Alaska, United States; *2,* Antler Peak quadrangle, Nevada, United States; *3,* Queensland, Australia; *4,* New South Wales, Australia; *5,* Northern Territory, Australia; *6,* Hubei, China (base map adapted from Scotese & McKerrow, 1990).

Five genera of Ordovician sphinctozoans, including *Alaskaspongia, Angullongia, Cliefdenella, Corymbospongia,* and *Pseudoporefieldia,* have been documented from Alaska and the Yukon Territory (STOCK, 1981; RIGBY, POTTER, & BLODGETT, 1988). These are the most diverse Ordovician sphinctozoan faunules documented to date, and they mark an early period of diversification of sponges with these types of chambered skeletons. *Khalfinaea* WEBBY & LIN, 1988, has been reported from the Shaanxi and Xinjiang provinces of China and the Altai Sayan region of Russia, and it is the only

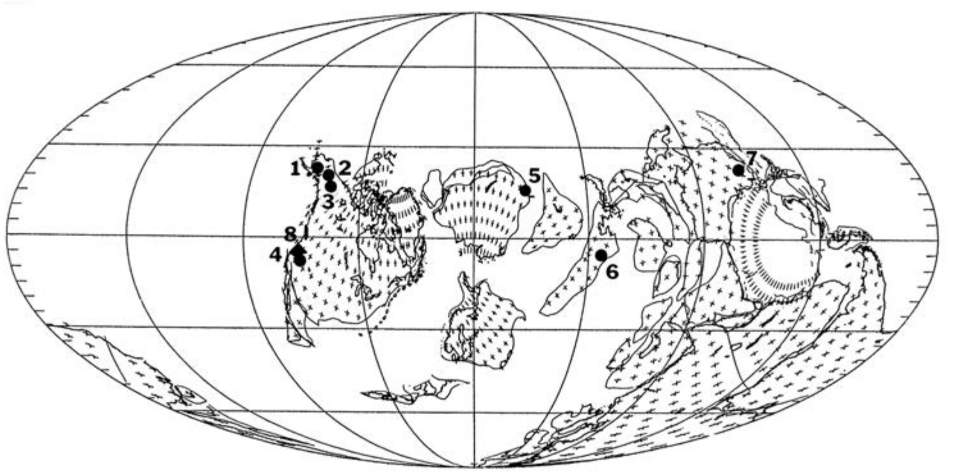


FIG. 262. Paleogeographic distribution of localities from where Ordovician sphinctozoan (*circles*) and inozoan (*triangle*) sponges have been reported. Sphinctozoans occur at localities: *1,* McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; *2,* Livengood quadrangle, east-central Alaska, United States; *3,* Jones Ridge, Yukon Territory, Canada; *4,* Antler Peak quadrangle, Nevada; *5,* Altai Sayan, eastern Kazakhstan, Russia; *6,* Hubei, China; *7,* New South Wales, Australia. Inozoans have been reported from locality *8,* Klamath Mountains, Oregon (base map adapted from Scotese & McKerrow, 1990).

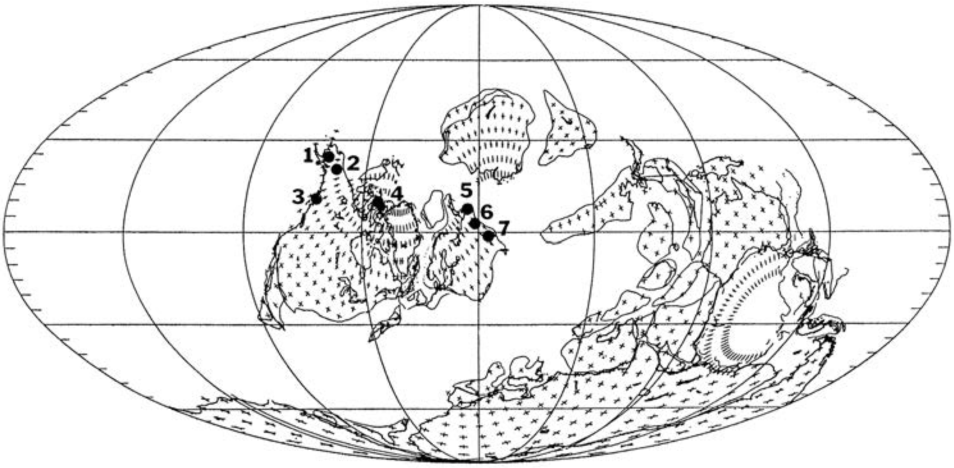


Fig. 263. Paleogeographic distribution of localities from where Silurian sphinctozoan sponges have been reported: *1,* Taylor Mountains D-2 quadrangle, southwestern Alaska, United States; *2,* White Mountain area, McGrath A-4 and A-5 quadrangles, west-central Alaska, United States; *3,* Seaotter Sound area, southeastern Alaska, United States; *4,* Cornwallis Island, District of Franklin, Northwest Territories, Canada; *5,* Pay-Khoy, Cape Belyi Nos, northern Russia; *6,* western slope of Northern Ural Mountains, Russia; *7,* eastern slope of Central Ural Mountains, Russia; no inozoans have been reported from the Silurian (base map adapted from Scotese & McKerrow, 1990).

Ordovician sphinctozoan sponge described from these areas (Fig. 262).

Silurian sphinctozoan sponges have somewhat more limited diversity and geographic occurrences than those of the Ordovician (Fig. 263). Silurian sphinctozoans have been reported from Pay-Khoy, Cape Belyi Nos, and the Northern and Central Ural Mountains of Russia (Myagkova, 1955a, 1955b; Zhuravleva & Myagkova, 1974a, 1974b, 1981, 1987), and from southeastern, south-central, and southwestern Alaska in North America, where *Aphrosalpinx, Nematosalpinx,* and *Palaeoscheda* have been recovered (Rigby,

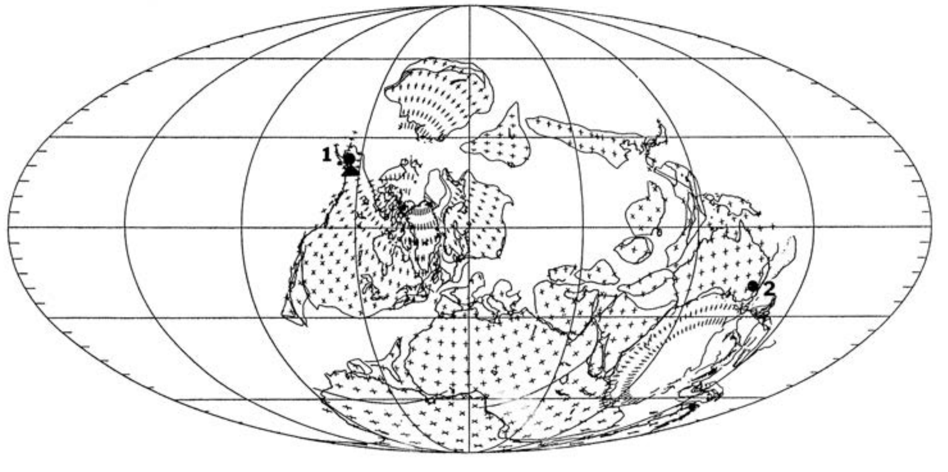


Fig. 264. Paleogeographic distribution of localities from where Devonian sphinctozoan (*circles*) and inozoan (*triangle*) sponges have been reported: *1,* McGrath area, west-central Alaska, United States, where both sphinctozoan and inozoan sponges occur; *2,* New South Wales, Australia (base map adapted from Scotese & McKerrow, 1990).

NITECKI, & others, 1994). The marked similarity of aphrosalpingid sphinctozoan sponges of Alaska and Russia suggests significant paleobiogeographic relationships between the Alexander terrane of southeastern Alaska and the Nixon Fork terrane of west-central Alaska with that of the Ural Mountains, as was earlier suggested by RIGBY, NITECKI, and others (1994). *Aphrosalpinx* MYAGKOVA, 1955b, and *Palaeoscheda* MYAGKOVA, 1955a, are known from the Silurian of both the northern Ural Mountains and southeastern Alaska. *Nematosalpinx* MYAGKOVA, 1955a, is known from both the Ural Mountains and southwestern Alaska. It is associated with *Cystothalamiella* RIGBY & POTTER, 1986, in the latter area.

Rigbyspongia DE FREITAS, 1987, was described from Ludlovian rocks from Cornwallis Island, Arctic Canada. It is the only sphinctozoan reported from that region.

Sphinctozoans were markedly restricted, both geographically and taxonomically, in the Devonian (Fig. 264). *Hormospongia* RIGBY & BLODGETT, 1983, has been reported from the Eifelian of the McGrath area of southwestern Alaska, the type area, and from New South Wales, Australia (PICKETT & POHLER, 1993). *Radiothalamos* PICKETT & RIGBY, 1983, the other known Devonian sphinctozoan, was described from the earlier Lower Devonian of New South Wales. The questionable inozoan, *Fissispongia,* has been reported from the Devonian of Alaska (RIGBY & BLODGETT, 1983). It is the only possible Devonian inozoan known to date, and *Fissispongia* is considered to be a sphinctozoan by some workers.

Carboniferous sphinctozoans are known principally from lands bordering the Tethyan Seaway (Fig. 265), but no major diverse sphinctozoan Carboniferous assemblages have been reported from the region. Three genera, *Amblysiphonella, Colospongia,* and *Sollasia*, have been reported from Austria (LAUBE, 1865; PELZMANN, 1930; LOBITZER, 1975; KÜGEL, 1987), and five genera, *Amblysiphonella, Cystothalamia, Discosiphonella, ?Sebargasia,* and *Sollasia* from Spain (STEINMANN, 1882; GARCÍA-BELLIDO, 2002; GARCÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004). *Sollasia* has recently been reported from the United Kingdom (RIGBY & MUNDY, 2000), and *Amblysiphonella* and *Discosiphonella* from China (INAI, 1936). *Amblysiphonella* and other sponges have also been reported from the upper Carboniferous of Nebraska and Texas (CLARKE, 1897; GIRTY, 1908b, 1915; KING, 1933, 1938, 1943; TOOMEY, 1979), at some distance from the Tethyan region. As in earlier occurrences, these fossil localities were also at tropical to subtropical paleolatitudes.

Carboniferous inozoans are also limited geographically and taxonomically. *Maeandrostia* GIRTY, 1908b, was first described from the Pennsylvanian of Kansas, but it has also been reported from Texas and Oklahoma (Fig. 265), as has the questionable inozoan *Fissispongia* (KING, 1938; RIGBY & MAPES, 2000). *Maeandrostia* has also been reported as occurring in Carboniferous deposits of Sicily and the former Yugoslavia, along the western margin of the Tethyan seaway (FINKS & RIGBY, 2004d, p. 644).

Sphinctozoans are significant faunal elements in Permian assemblages from around the margin of the Tethyan seaway and in isolated lower latitude areas in western North and South America (Fig. 266; RIGBY & SENOWBARI-DARYAN, 1995). Several major assemblages have been described from the Tethyan seaway area, and these occurrences have been documented in FINKS and RIGBY (2004d). For example, 20 genera have been documented from Sicily (PARONA, 1933; SENOWBARI-DARYAN, 1980a, 1990; SENOWBARI-DARYAN & DI STEFANO, 1988a), 27 genera from Tunisia (TERMIER & TERMIER, 1955; H. TERMIER, G. TERMIER, & VACHARD, 1977; SENOWBARI-DARYAN & RIGBY, 1988, 1991) in the western part of the Tethyan seaway margin, and 15 genera from Oman (WEIDLICH & SENOWBARI-DARYAN, 1996), on the southern seaway margin. Sphinctozoans are also significant faunal elements from various localities in China, where 34 genera have been described (HAYASAKA, 1918; DENG, 1982a, 1982b; ZHANG, 1983, 1987; Fan & Zhang, 1985; Reinhardt, 1988; Rigby, Fan, & Zhang, 1988, 1989a; Flügel & Reinhardt, 1989; Rigby, Fan, & others, 1994; Belyaeva, 2000; Fan, Wang, & Wu, 2002).

Sphinctozoan sponges of Russia have been extensively documented in the major work by Boĭko, Belyaeva, and Zhuravleva (1991), where faunas from the different regions were treated in separate chapters in the volume. Permian sponges from Middle Asia (southern Tian-Shan, Karatchatyr Mountains), from North Pamir (Darwaz and Piotr I Mountains), from the Far East (southern Primorsky Krai), from Armenia, and from the Crimea are documented in separate chapters, along with later chapters on Triassic and Jurassic sphinctozoans.

Less diverse sphinctozoan assemblages are known from the Permian of Greece (Guernet & Termier, 1969; Flügel & Reinhardt, 1989), Pakistan (Waagen & Wentzel, 1888), Iran (Senowbari-Daryan & Hamedani, 2002; Senowbari-Daryan, Rashidi, & Hamedani, 2005), India (De Koninck, 1863), Thailand (Senowbari-Daryan & Ingavat-Helmcke, 1994), Indonesia (Wilckens, 1937), Cambodia (Mansuy, 1913, 1914), and Japan (Hayasaka, 1918; Akagi, 1958; Igo, Igo, & Adachi, 1988), as occurrences are traced around the Tethyan seaway margin. In most of these areas, only one or two sphinctozoan genera have been reported, although seven genera have been reported from Thailand and six from Tajikistan in Russia.

In North America, nine sphinctozoans, including *Amblysiphonella, Cystothalamia, Exaulipora, Guadalupia, Lemonea, Parauvanella, ?Polysiphonaria, Preverticillites,* and *Tristratocoelia,* have been reported as being part of the sponge assemblage from the Permian reef complex of the Guadalupe Mountains and related areas in Texas and New Mexico (Girty, 1908a; King, 1943; Senowbari-Daryan, 1990; Finks, 1995, 1997; Rigby, Senowbari-Daryan, & Liu, 1998).

A modest faunule of five sphinctozoan genera has been described from western Venezuela (Rigby, 1984), as the only suite of Permian sphinctozoans documented to date from South America. This assemblage includes *Colospongia, Cystothalamia, Guadalupia,* and *Girtyocoelia*.

The Permian marked a major expansion, both taxonomically and geographically, in the occurrence of inozoan sponges (Fig. 267). Major inozoan assemblages have been collected and described from Permian rocks in Tunisia (Termier & Termier, 1955, 1974; H. Termier, G. Termier, & Vachard, 1977; Rigby & Senowbari-Daryan, 1996a), where approximately 30 genera have been described. Somewhat less extensive inozoan faunas have been described from various localities in eastern and southeastern China (Rigby, Fan, & Zhang, 1989b; Fan, Rigby, & Zhang, 1991; Wu, 1991; Rigby, Fan, & others, 1994), and from the Texas–New Mexico region in the United States (Girty, 1908a; King, 1943; Finks, 1995; Rigby, Senowbari-Daryan, & Liu, 1998), where 12 genera are documented. In a major addition to the Guadalupe Mountain assemblage, Rigby and Bell (2006), described 5 additional genera from Guadalupian Permian rocks of the Guadalupe Mountains.

Less diverse Permian inozoan faunules have been documented from Italy (Sicily), (Parona, 1933; Aleotti, Dieci, & Russo, 1986; Senowbari-Daryan & Di Stefano, 1988a), Thailand (Senowbari-Daryan & Ingavat-Helmcke, 1994), Iran (Senowbari-Daryan, Rashidi, & Hamedani, 2005), around the western end of the Tethyan seaway, where four genera have been documented in each of those localities, and where one genus, *Peronidella,* has been reported from the Permian of Hungary (H. W. Flügel, 1973).

In the western part of North America, a single Permian inozoan genus, *Radiotrabeculopora,* has been reported from east-central California (Rigby, Linder, & Stevens, 2004). This genus has been interpreted as a disjectoporid-type hypercalcified sponge that has possible inozoan relationships (see p. 319).

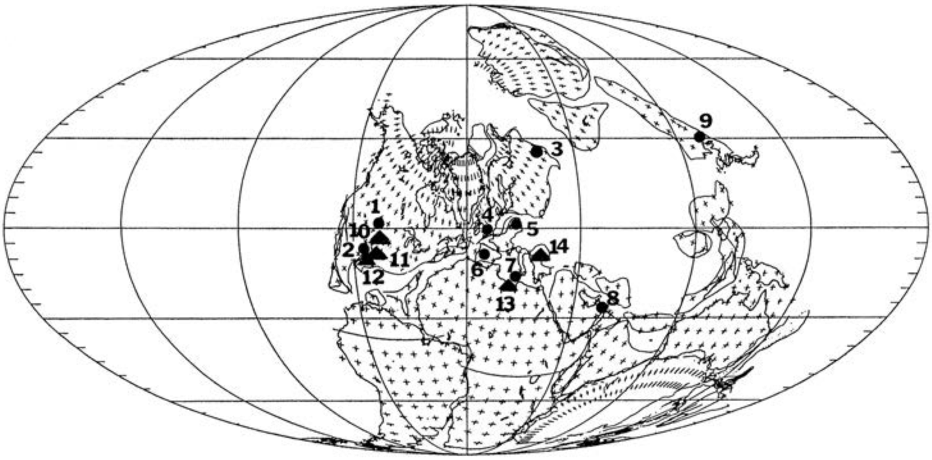


FIG. 265. Paleogeographic distribution of localities from where Carboniferous sphinctozoan (*circles*) and inozoan (*triangles*) sponges have been reported. Sphinctozoan sponges have been reported from localities: *1,* Nebraska, United States; *2,* Texas, United States; *3,* Russia, in general; *4,* Yorkshire, United Kingdom; *5,* Austria; *6,* Spain; *7,* Sicily, Italy; *8,* Oman; *9,* Manchuria, China. Inozoans have been reported from localities: *10,* Kansas, United States; *11,* Oklahoma, United States; *12,* Texas, United States; *13,* Sicily, Italy; *14,* former Yugoslavia (base map adapted from Scotese & McKerrow, 1990).

Triassic sphinctozoans underwent a major taxonomic burst, and they have been reported from a greater number of localities than sphinctozoan faunas from any earlier period of geologic time (Fig. 268). These occurrences are cited in FINKS and RIGBY (2004c). Like Permian faunas, Triassic sphinctozoans have been reported widely from margins of the Tethyan seaway and from the western parts of North and South America. The most diverse

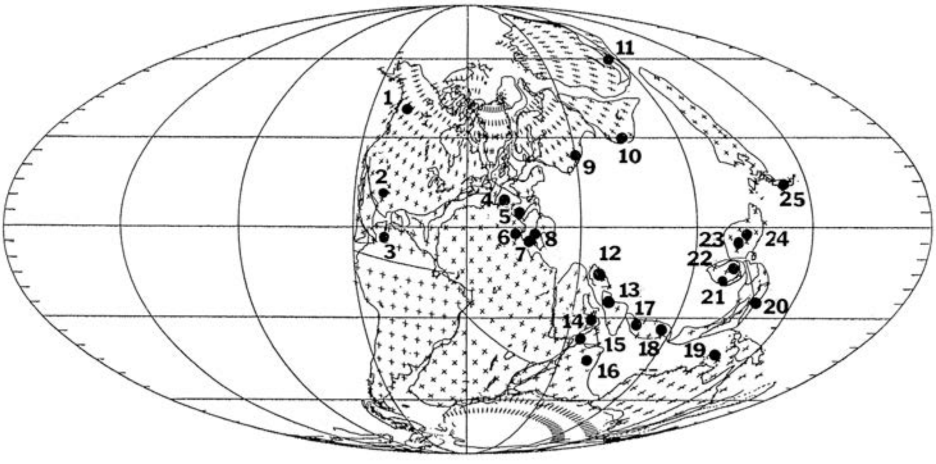


FIG. 266. Paleogeographic distribution of localities from where Permian sphinctozoan sponges have been reported: *1,* British Columbia, Canada; *2,* Guadalupe Mountain region, Texas and New Mexico, United States; *3,* western Venezuela; *4,* Spain; *5,* Sicily; *6,* Tunisia; *7,* Greece; *8,* former Yugoslavia; *9,* Ukraine; *10,* Tajikistan; *11,* Russian Far East; *12,* Turkey; *13,* Iran; *14,* Oman; *15,* Pakistan; *16,* India; *17,* Caucasus, Russia; *18,* Tibet; *19,* Timor; *20,* Indonesia; *21,* Thailand; *22,* Cambodia; *23,* Sichuan-Guizhou, China; *24,* Hubei, China; *25,* Japan (base map from Scotese & McKerrow, 1990).

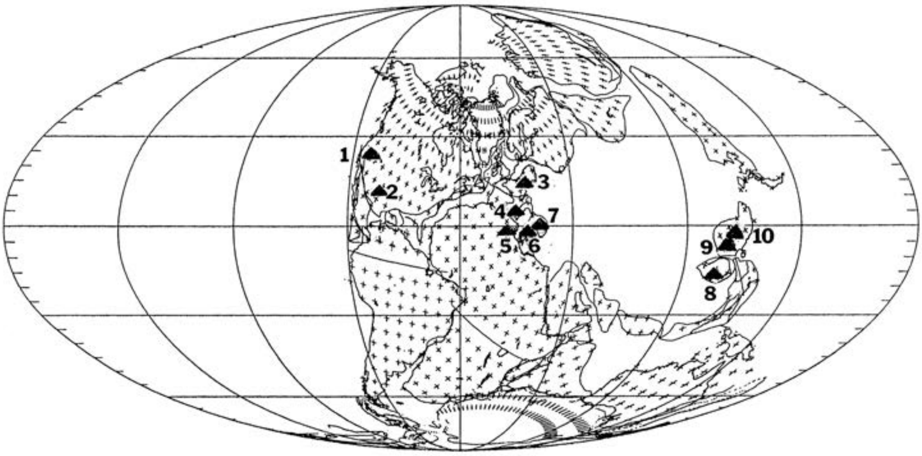


FIG. 267. Paleogeographic distribution of localities from where Permian inozoan sponges have been reported: *1,* east-central California, United States; *2,* Guadalupe Mountain region, Texas and New Mexico, United States; *3,* Europe in general; *4,* Sicily, Italy; *5,* Tunisia; *6,* former Yugoslavia; *7,* Hungary; *8,* Thailand; *9,* Guangxi and Guizhou area, southeastern China; *10,* Hubei area, eastern China (base map adapted from Scotese & McKerrow, 1990).

faunas are those from southeastern European and Middle Eastern countries.

North American assemblages were mainly collected from the western part of the United States, Canada, and Mexico. SENOWBARI-DARYAN and REID (1987) described a moderate assemblage of sphinctozoans from the Stikine terrane, from the southern Yukon, in westernmost Canada. Sphinctozoans there are part of sponge reefs and interreef accumulations, and the occurrence of 14 sphinctozoan genera has been

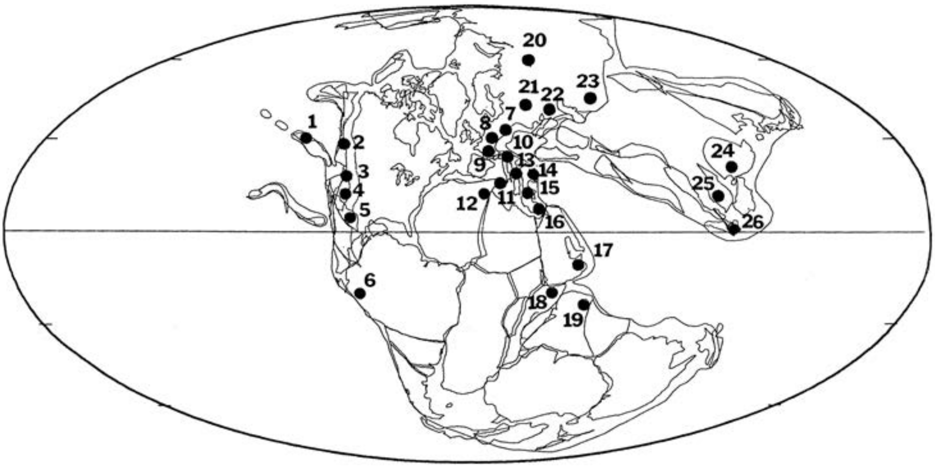


FIG. 268. Paleogeographic distribution of localities from where Triassic sphinctozoan sponges have been reported: *1,* Stikine terrane, southern Yukon Territory, Canada; *2,* Quesnel Range, southern British Columbia, Canada; *3,* Wallowa Mountains, eastern Oregon, United States; *4,* Mineral County, western Nevada, United States; *5,* Sonora, Mexico; *6,* central Peru; *7,* former Czechoslovakia; *8,* Germany; *9,* France; *10,* northern Italy; *11,* Sicily; *12,* Tunisia; *13,* former Yugoslavia; *14,* Hungary; *15,* Greece; *16,* Turkey; *17,* Oman; *18,* Iran; *19,* Himalayan Mountains, northern, India; *20,* Northern Ural Mountains, Russia; *21,* Ukraine; *22,* Caucasus region, Russia; *23,* Tajikistan and Pamir regions; *24,* Sichuan, China; *25,* Thailand; *26,* Timor (base map from Scotese, 2001).

documented from the area. An additional genus, *Fanthalamia,* has been documented from Triassic rocks in the Quesnel Range, in southern British Columbia (Stanley & Senowbari-Daryan, 1999). Farther to the southeast, in eastern Oregon, three sphinctozoan genera, *Polycystocoelia, Neoguadalupia,* and *Nevadathalamia,* have been reported from the Triassic of the Wallowa Mountains by Senowbari-Daryan and Stanley (1988). *Fanthalamia* Senowbari-Daryan & Engeser (1996), and *Cinnabaria* Senowbari-Daryan (1990) occur in Triassic deposits in Nevada and British Columbia. The close tie of these assemblages with Chinese faunas is suggested because some of these genera are characteristic of Tethyan faunas and, as suggested by Senowbari-Daryan and Reid (1987), some of the genera documented in Yukon suites had been previously reported only from Tethyan localities, and others from both American and Tethyan localities. They suggested that such a mixture might reflect the origin of the Stikine terrane as an island in the ancestral Pacific Ocean, between the Tethys region and North America.

The occurrence of *Nevadathalamia* Senowbari-Daryan, 1990, in Nevada, is geographically intermediate between occurrences of that sponge in the Yukon region of Canada, to the north, and from Sonora, Mexico, to the south, where it occurs with *Fanthalamia* and *Cinnabaria,* as reported by Senowbari-Daryan (in Stanley & others, 1994) and Senowbari-Daryan, Stanley, and Gonzalez-Leon (2001).

The only Triassic sphinctozoans thus far reported from South America are from Peru (Rauff, 1938; Senowbari-Daryan, 1994b), where occurrences of *Amblysiphonella, Discosiphonella,* and *Polytholosia* have been documented. Generically diverse major faunas of Triassic sphinctozoans have been reported from southeastern Europe (Fig. 268), with 29 genera of sponges from the Alps (Münster, 1841; Laube, 1865; Pomel, 1872; Steinmann, 1882; Ott, 1967; Dieci, Antonacci, & Zardini, 1968; Senowbari-Daryan, 1978, 1981, 1990; Senowbari-Daryan & Schäfer, 1979; Senowbari-Daryan & Riedel, 1987). From Austria, 27 genera have been reported (Münster, 1841; Steinmann, 1882; Ott, 1967; Dieci, Antonacci, & Zardini, 1968; Ott in Kraus & Ott, 1968; Wolff, 1973; Ott, 1974; Senowbari-Daryan, 1978, 1990; Senowbari-Daryan & Schäfer, 1979; Dullo, 1980; Engeser & Neuman, 1986; Senowbari-Daryan & Riedel, 1987; Senowbari-Daryan & Würm, 1994). From Italy, primarily Sicily, 15 genera have been reported (Senowbari-Daryan, 1980b; Senowbari-Daryan & Abate, 1986; Senowbari-Daryan & Schäfer, 1986; Senowbari-Daryan & Di Stefano, 1988b); and from southern Italy (Calabria) where 6 genera have been described by Senowbari-Daryan and Zamparelli (1999, 2003), and Senowbari-Daryan, Abate, and others (1999). Sphinctozoan sponge faunas from the Carpathians include 17 genera (Münster, 1841; Steinmann, 1882; Vinassa de Regny, 1901, 1908; Scholz, 1972; Mello, 1975; Balogh & Kovacs, 1976; Kovács, 1978a; Senowbari-Daryan, 1978, 1990; Senowbari-Daryan & Riedel, 1987; Riedel & others, 1988; Flügel & others, 1991 in 1991–1992); and those from southern European countries (Greece, Romania, and the former Yugoslavia) include 16 genera (Pantic, 1975; Senowbari-Daryan, 1981, 1982, 1990; Senowbari-Daryan & Schäfer, 1983; Senowbari-Daryan & Riedel, 1987; Riedel & Senowbari-Daryan, 1989).

Diverse sphinctozoan assemblages are known from Turkey, where at least 18 Triassic genera have been documented (Riedel, 1990; Senowbari-Daryan, 1990, 1994a; Senowbari-Daryan & Link, 1998; Senowbari-Daryan, Link, & García-Bellido, 2003), and from Tajikistan, where 22 genera have been cited in Triassic faunas (Boĭko, 1984a, 1990; Boĭko, Belyaeva, & Zhuravleva, 1991). Primary sources for Tajikistan occurrences of most of these genera are not cited, but the genera are listed from Tajikistan in Finks and Rigby (2004d).

Less diverse Triassic sphinctozoan collections have also been documented from various areas in western Russia, including the Caucasus (Moiseev, 1944; Boĭko, 1990; Boĭko, Belyaeva, & Zhuravleva, 1991), where 10 genera have been documented; and from the Pamir region (Boĭko, 1986), where 3 genera are cited. Single Triassic sphinctozoan genera are known from the Northern Urals (Myagkova, 1955a) and from the Ukraine–Crimea region (Boĭko, Belyaeva, & Zhuravleva, 1991). In addition, 11 different genera are listed as occurring in Russia, presumably western Russia, by Finks and Rigby (2004d) (Myagkova, 1955a, 1955b; Senowbari-Daryan, 1990; Boĭko, Belyaeva, & Zhuravleva, 1991).

Less diverse faunules are known from Romania, where 4 Triassic sphinctozoan genera are cited in Finks and Rigby (2004d), including *Amblysiphonella, Enoplocoelia, Solenolmia,* and *Stylothalamia* (Steinmann, 1882; Senowbari-Daryan & Riedel, 1987; Riedel & Senowbari-Daryan, 1988; Senowbari-Daryan, 1990). The 2 genera *Solenolmia* and *Vesicocaulus* have been identified from the Triassic of the former Czechoslovakia (Jablonsky, 1972; Senowbari-Daryan & Riedel, 1987; Senowbari-Daryan, 1990). In the area around the southwestern part of the Tethyan seaway, Triassic sphinctozoans have also been collected from Iran, where the occurrence of 25 genera has been reported (Senowbari-Daryan & Hamedani, 1999; Senowbari-Daryan, 2005a; Finks & Rigby, 2004d). Triassic sphinctozoans reported from Oman include 10 genera (Senowbari-Daryan, 1990; Bernecker, 1996; Senowbari-Daryan, Bernecker, & others, 1999; Finks & Rigby, 2004d). Only the genus *Cinnabaria,* described as *Colospongia catenulata* by Bhargava and Bassi (1985), has been reported from India.

In the southeastern part of the seaway margin, reported occurrences of Triassic sphinctozoans from China include *Dracolychnos* Wu & Xiao, 1989, and *Casearia*; both genera are now included in the Hexactinellida (Reid, 2004, p. 486). These genera and other hexactinellids are not included in this presentation. From the Moluccas (Indonesia), five genera of Triassic sphinctozoans have been described (Wilckens, 1937) and four genera from Timor (Vinassa de Regny, 1915; Senowbari-Daryan, 1990).

Triassic inozoan occurrences are primarily focused around the Tethyan margin (Fig. 269). Large faunules of Triassic inozoans have been reported from Italy, where ten genera have been documented from the Dolomite Alps of northern Italy (Dieci, Antonacci, & Zardini, 1968; Cuif, 1974; Russo, 1981; Bizzarini & Russo, 1986; Engeser & Taylor, 1989; Riedel & Senowbari-Daryan, 1991), and two genera from the Island of Sicily (Senowbari-Daryan & Schäfer, 1986).

Elsewhere in Europe, 2 genera are known from the Triassic of Austria (Klipstein, 1843–1845; Haas, 1909), and 10 from several countries in Europe in general (Finks & Rigby, 2004d). A single Triassic inozoan genus, *Himatella,* has been reported from Tunisia (H. Termier, G. Termier, & Vachard, 1977). Three genera, *Dactylocoelia, Reticulocoelia,* and *Peronidella,* have been documented from the Triassic of Turkey (Cuif, 1973; Riedel, 1990), and at least 12 genera from Iran (Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997; Senowbari-Daryan, 2005b). *Peronidella* is the only inozoan genus reported from Oman (Bernecker, 1996), but 4 inozoan genera have been reported from Timor, including *Ateloracia, Himatella, Leiospongia,* and *Precorynella* (Wilckens, 1937; Finks & Rigby, 2004d). In contrast to the rich sphinctozoan fauna known from the Pamir Mountains and the Caucasus, the inozoan fauna of this region is poorly known. However, Moiseev (1944) reported the occurrence of 2 genera (*Molengraaffia* and *Hodsia*) from Caucasus, and Doronov, Gazdzicki, and Melnikova (1982) reported the occurrence of 3 genera (*Precorynella, Corynella,* and *Molengraaffia*) from the southeastern Pamir Mountains.

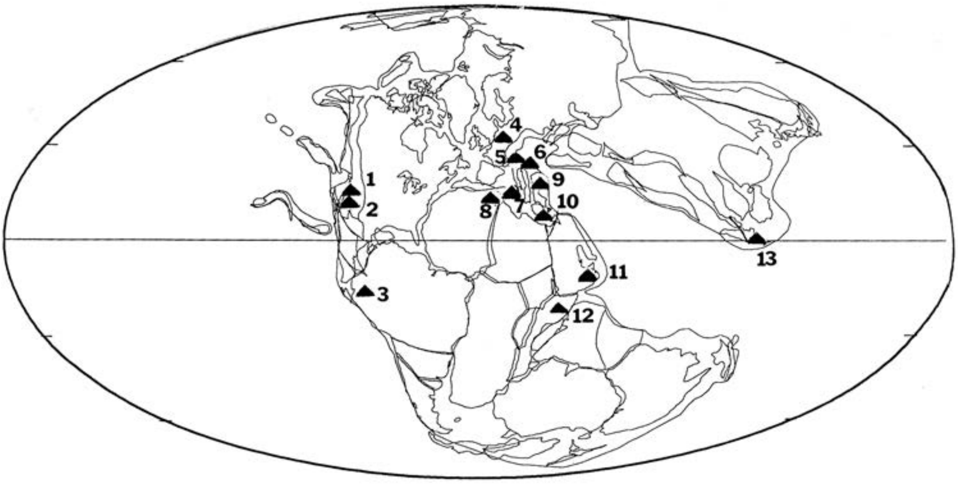


FIG. 269. Paleogeographic distribution of localities from where Triassic inozoan sponges have been reported: *1,* Wallowa Mountains, eastern Oregon, United States; *2,* Mineral County, western Nevada, United States; *3,* Peru; *4,* Europe, in general; *5,* Dolomite Alps, northern Italy; *6,* Austria; *7,* Sicily; *8,* Tunisia; *9,* Hungary; *10,* Turkey; *11,* Oman; *12,* Iran; *13,* Timor (base map adapted from Scotese, 2001).

Preperonidella is the only Triassic inozoan genus reported from Oregon, in the western United States. *Stellispongia* has been described from the Triassic of Peru (RAUFF, 1938), where *Preperonidella,* as *Peronidella,* has also been reported (SENOWBARI-DARYAN, 1994b). *Corynella* and *Eusiphonella* (treated in FINKS & RIGBY, 2004d, p. 743, 748, as junior synonyms of *Endostoma* and *Pareudea,* respectively), as well as questionable *Stellispongiella,* were also listed as inozoan sponges from Peru (SENOWBARI-DARYAN, 1994b, p. 57) and are now considered to belong to the Calcarea, rather than to the Demospongiae like most

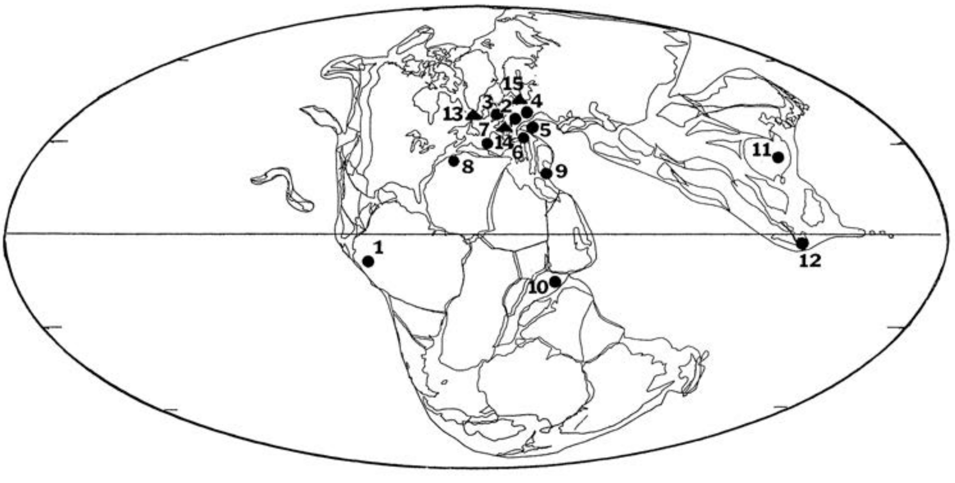


FIG. 270. Paleogeographic distribution of localities from where Jurassic sphinctozoan (*circles*) and inozoan (*triangles*) sponges have been reported. Sphinctozoans occur at localities: *1,* Peru; *2,* England, United Kingdom; *3,* Germany; *4,* Poland; *5,* former Czechoslovakia; *6,* Italy; *7,* Portugal; *8,* Morocco; *9,* Greece; *10,* China; *11,* Moluccas; *12,* Cambodia. Inozoans occur at localities: *13,* eastern Atlantic shelf, Canada; *14,* France; *15,* Germany (base map adapted from Scotese, 2001).

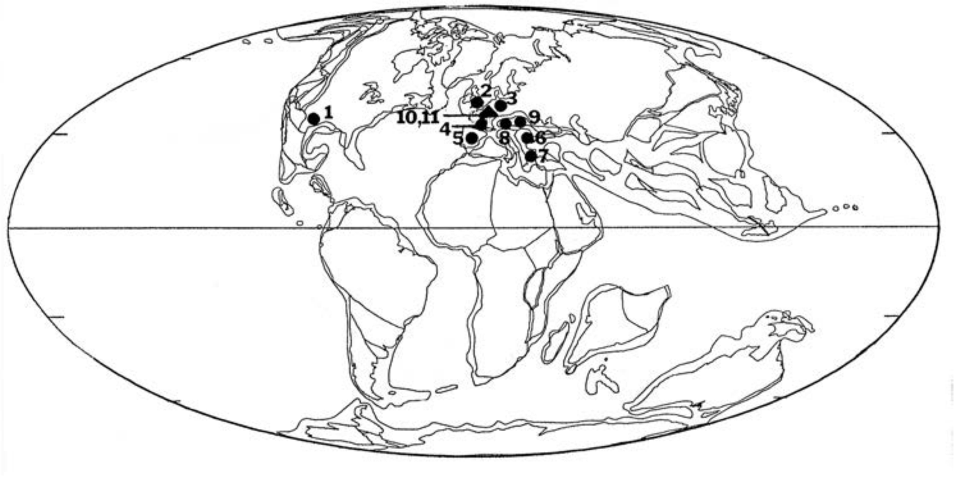


FIG. 271. Paleogeographic distribution of localities from where Cretaceous sphinctozoan (*circles*) and inozoans (*triangles*) sponges have been reported. Sphinctozoans occur at localities: *1,* Texas, United States; *2,* United Kingdom; *3,* Germany; *4,* France; *5,* Spain; *6,* Romania; *7,* Greece; *8,* Switzerland; *9,* Austria. Inozoans occur at localities: *10,* Germany; and *11,* France (base map adapted from Scotese, 2001).

other inozoans. *Cornuaspongia* and *?Trammeria* were also described from the Triassic of Peru by SENOWBARI-DARYAN (1994b). They are also considered as probable inozoans, but their taxonomic positions in class and order are uncertain (FINKS & RIGBY, 2004d, p. 762, 764).

Diversity and geographic spread of sphinctozoan sponges in the Jurassic record is markedly reduced from that of the Triassic, although the major focus of occurrences is still along western margins of the Tethyan seaway (Fig. 270). For example, *?Deningeria* and *Sphinctonella* have been reported from

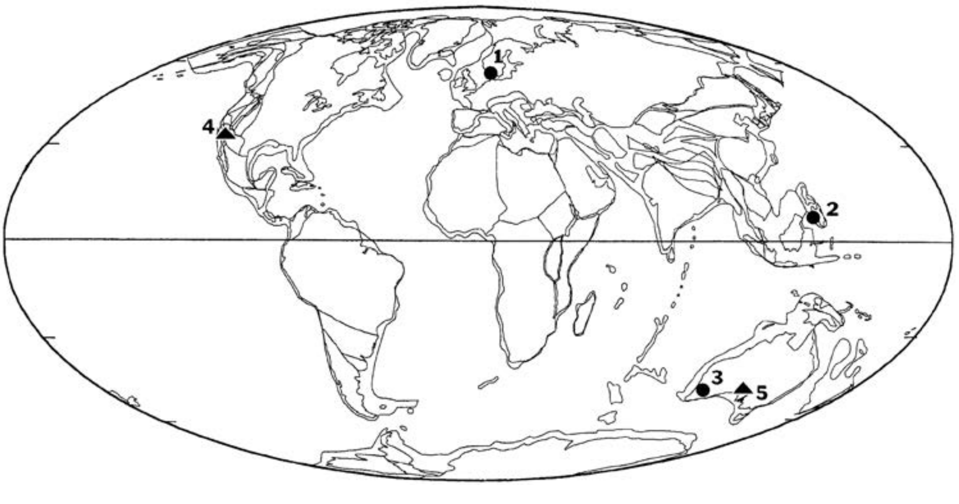


FIG. 272. Paleogeographic distribution of localities from where Paleogene–Neogene sphinctozoan and inozoan sponges have been reported. Sphinctozoan sponges (*circles*) have been reported from: *1,* Denmark (Paleocene); *2,* Marinduque, Philippine Islands, (Eocene); *3,* southwestern Australia (Eocene); and inozoan sponges (*triangles*) have been reported from: *4,* Mexico (Eocene); and *5,* Australia (Miocene) (base map adapted from Scotese, 2001).

Poland (HURCEWICZ, 1975); *Barroisia* and *Muellerithalamia* from Germany (QUENSTEDT, 1858; REITNER, 1987c), the latter two genera included in the Calcarea (FINKS & RIGBY, 2004d). *Barroisia, Sphaerocoelia,* and *Thalamopora* have been reported from the Czech Republic and Slovakia (ZEISE, 1897) and *Thalamopora* from Portugal (G. TERMIER, H. TERMIER, & RAMALHO, 1985). *Barroisia* has also been reported from the United Kingdom (KEEPING, 1883) and from Italy (SENOWBARI-DARYAN & ABATE, 1996), and *Boikothalamia* has been reported from Spain (REITNER & ENGESER, 1985). *Casearia,* a hexactinellid chambered sponge, is not treated in detail here, but it has been reported from along the eastern margin of the Tethyan realm from China (WU & XIAO, 1989; RIGBY, WU, & FAN, 1998), from central Iran, the western Tethys (Germany), and northern Tethys (Pamir Mountains) (MÜLLER, 1974; BOĬKO, 1990; SENOWBARI-DARYAN & HAMEDANI, 1999).

Only a single Lower Jurassic sphinctozoan, *Stylothalamia*, has been reported from the American continents (Fig. 270) and that was from Peru (HILDEBRANDT, 1971; SENOWBARI-DARYAN & STANLEY, 1994). *Stylothalamia* has also been reported from European countries (RADOIČIĆ, 1966; PALLINI & SCHIAVINOTTO, 1981; SCHIAVINOTTO, 1984; BECCARELLI BAUCK, 1986; BROGLIO LORIGA & others, 1991), and from northern Africa (SCHROEDER, 1984). From the Upper Jurassic, the genera *Barroisia, Boikothalamia, Sphaerocoelia, Thalamopora*, and *Verticillites* have been reported from several different European countries by various authors (see SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a). The occurrence of ?*Cryptocoeliopsis* WILCKENS, 1937, or *?Deningeria* WILCKENS, 1937, has been reported from Poland (HURCEWICZ, 1975).

Jurassic inozoans are more diverse than contemporaneous sphinctozoans, but they are still less geographically extensive and less diverse that those of the Triassic (Fig. 270). Several calcareous sponges that are considered as inozoans, including *Endostoma, ?Elasmostoma, Enaulofungia, Pareudea,* and *Eudea,* have been reported from the Jurassic of Germany (WAGNER, 1964; MÜLLER, 1984); from Italy (BIZZARINI, BRAGA, & MASTANDREA, 1987); and from Greece (BONNEAU & TERMIER, 1975). The single genus *Epitheles,* based on species included in *Myrmecium*, has been reported from France, along with the questionable *Aulocopagia* POMEL, 1872. *Winwoodia* (RICHARDSON & THACKER, 1920) has been documented from England. An additional 12 genera of the family Stellispongiidae, within the Calcarea, are included in the list of inozoans appended below, and all are reported as occurring in the Jurassic deposits of Europe. Undescribed inozoan sponges are abundant in Jurassic deposits of the Shotori Mountains in northeastern Iran (SENOWBARI-DARYAN, personal observation). The only reported inozoan from the Jurassic of North America is *Sestrostomella*, from the Canadian Atlantic Shelf (FINKS & RIGBY, 2004d, p. 611). Six genera were reported by RAUFF (1938) and SENOWBARI-DARYAN (1994b) from Peru in South America.

Cretaceous geographic spread of sphinctozoan sponges is even more restricted than that of the Jurassic, but the focus is still in western European countries (Fig. 271). The most diverse faunas have been found in Spain (SCHROEDER & WILLEMS, 1983; SCHROEDER, 1984; REITNER & ENGESER, 1985; REITNER, 1987c), where five genera have been reported, followed by faunules from Germany (STEINMANN, 1882; DUNIKOWSKI, 1883; WELTER, 1911; HILLMER & SENOWBARI-DARYAN, 1986) and France (DELEMATTE, TERMIER, & TERMIER, 1986; TERMIER & TERMIER, 1985a, 1985b), where four genera have been documented from both countries. Single genera have been reported from other European localities, including *Stylothalamia* from Austria (ENGESER & NEUMANN, 1986; SENOWBARI-DARYAN, 1990), *Stylothalamia* from Greece (SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a), and *Barroisia* from Romania, Switzerland (STEINMANN, 1882), and England (HINDE, 1882, 1884; REID, 1968).

Stylothalamia is the only sphinctozoan genus reported from the Cretaceous of North America, where specimens of the genus were recovered from central Texas by Wells (1934).

Cretaceous inozoans are more diverse than contemporaneous sphinctozoans, but they are certainly more geographically limited than in the Jurassic record, for Cretaceous occurrences have been reported principally from European localities (Fig. 271). *Pharetrospongia strahani* Sollas, 1877, for example, was reported from England, as the figured specimen in Finks and Rigby (2004d, p. 614), although the genus is cited there as occurring in Europe, which would suggest a broader distribution. *Elasmopagia* Pomel, 1872, is the only Cretaceous inozoan-type demosponge reported to date from France, and it was not illustrated when proposed. *Trachytila* Welter, 1911, is likewise the only Cretaceous inozoan demosponge reported from Germany.

Sixteen genera that are included in the family Stellispongiidae de Laubenfels, 1955, class Calcarea, by Finks and Rigby (2004d, p. 739–747) are considered to have inozoan skeletal structure (see appended list below, p. 383). Twelve of these genera are documented from Cretaceous deposits of Europe, and two more are reported as questionably present there in the Cretaceous (Lamouroux, 1821; Bronn, 1825; de Fromentel, 1860a; Roemer, 1864; Pomel, 1872; Zittel, 1878; Hinde, 1884, 1893; Zeise, 1897; Welter, 1911; Finks & Rigby, 2004d).

Cenozoic sphinctozoans are certainly geographically and taxonomically limited, for they have been described from only three localities (Fig. 272). Only two genera have been documented from a European country: *Verticillites* and *?Wienbergia* from Denmark (Ravn, 1899; Clausen, 1982). In addition to the European occurrence, only the single genus *Marinduqueia* has been described from the Eocene of the Philippine Islands (Yabe & Sugiyama, 1939), and an Eocene species of the living genus *Vaceletia* has been reported from Western Australia (Pickett, 1982).

Reported Paleogene-Neogene inozoans are limited to the occurrence of ?*Elasmostoma* de Fromentel, 1860a, from the Eocene of Mexico (Finks & Rigby, 2004d, p. 741), and *Tretocalia* Hinde, 1900, from the Miocene of Australia (Pickett, 1983). Four inozoan genera of the class Calcarea, including the stellispongiinids *Trachysphecion* Pomel, 1872, and *Peronidella* Zittel in Hinde, 1893, and the holcospongiinids *Eudea* Lamouroux, 1821, and *Mammillopora* Bronn, 1825, have been reported from the Holocene (Finks & Rigby, 2004d, p. 743–747).

ROLES OF SPHINCTOZOANS AND INOZOANS AS CONTRIBUTORS TO REEFS

Hypercalcified inozoan and sphinctozoan sponges (including archaeocyaths, stromatoporoids, and chaetetids) were the most abundant metazoan contributors to the formation of invertebrate reefs during the Paleozoic and early Mesozoic (Wood, 1990b, 1991b; Kiessling, 2001b). Only the roles of sphinctozoans and inozoans as contributors to reefs and reefal deposits, and their abundance, are treated in the following discussions.

CAMBRIAN–CARBONIFEROUS

In contrast to abundant archaeocyaths in the Cambrian and stromatoporoids in Ordovician to Devonian reefs, inozoan and sphinctozoan sponges were not abundant reef builders during this time interval, but both groups are known from reefs or reefal deposits from some localities (Ordovician: Webby & Rigby, 1985; Rigby & Potter, 1986; Rigby, Potter, & Blodgett, 1988; Rigby & Webby, 1988; Webby & Lin, 1988; Silurian: de Freitas, 1987; Rigby, Nitecki, & others, 1994; Rigby & Chatterton, 1999; Devonian: Rigby & Blodgett, 1983; see also Rigby & Chatterton, 1999).

Contemporary with the chaetetids, inozoan and sphinctozoan sponges became more important contributors among the sponge association in the upper Carboniferous. Individually rich, but with low diversity, sponge faunas have been described from bedded shallow-water carbonates from the Carnic Alps, Austria (PELZMANN, 1930; LOBITZER, 1975; KÜGEL, 1987), from Spain (STEINMANN, 1882; VAN DE GRAAF, 1969; GARCÍA-BELLIDO & RIGBY, 2004; GARCÍA-BELLIDO, SENOWBARI-DARYAN, & RIGBY, 2004); and from Kansas, Texas, and Oklahoma (GIRTY, 1908b; KING, 1933, 1938, 1943; RIGBY & MAPES, 2000) in the United States.

PERMIAN

Sphinctozoan and inozoan sponges are among the most significant contributors in Permian metazoan reefs (KIESSLING, 2001b; WEIDLICH, 2002). Both groups are abundant in lower Permian sponge *Tubiphytes-Archaeolithoporella* reef boulders of Sicily (SENOWBARI-DARYAN & DI STEFANO, 1988a), or in bedded reefal bioconstructions of Iran (SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005).

Inozoan- and sphinctozoan-dominated middle and upper Permian reefs occur worldwide (for a summary, see RIGBY & SENOWBARI-DARYAN, 1995; WEIDLICH, 2002). Both groups have been described from reefs or reefal limestones from several localities in Texas and New Mexico, in the United States (for a summary, see FAGERSTROM & WEIDLICH, 1999a, 1999b; NOÉ, 2003; sponges described by GIRTY, 1908b; FINKS, 1960; RIGBY & SENOWBARI-DARYAN, 1996a, 1996b; RIGBY, SENOWBARI-DARYAN, & LIU, 1998); from Venezuela (RIGBY, 1984); from Sicily (PARONA, 1933; ALEOTTI, DIECI, & RUSSO, 1986; SENOWBARI-DARYAN, 1990; FLÜGEL, DI STEFANO, & SENOWBARI-DARYAN, 1991); from Tunisia (TERMIER & TERMIER, 1974; H. TERMIER, G. TERMIER, & VACHARD, 1977; SENOWBARI-DARYAN & RIGBY, 1988; RIGBY & SENOWBARI-DARYAN, 1996a); from Pakistan (WAAGEN & WENTZEL, 1888); from Japan (HAYASAKA, 1918; AKAGI, 1958; IGO, IGO, & ADACHI, 1988); from China (FAN & ZHANG, 1985; FLÜGEL & REINHARDT, 1989; RIGBY, FAN, & ZHANG, 1989a, 1989b; FAN, RIGBY, & JINGWEN, 1990; FAN, RIGBY, & ZHANG, 1991; WU, 1991; RIGBY, FAN, & others, 1994; RIGBY, FAN, & NAIREN, 1995; BELYAEVA, 2000; FAN, WANG, & WU, 2002); from Oman (WEIDLICH & SENOWBARI-DARYAN, 1996); from Iran (SENOWBARI-DARYAN & HAMEDANI, 2002; RIGBY, SENOWBARI-DARYAN, & HAMEDANI, 2005; SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005); from Caucasia (see BOĬKO, BELYAEVA, & ZHURAVLEVA, 1991); from Thailand (SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994); and from the former Yugoslavia (FLÜGEL, KOCHANSKY-DEVIDE, & RAMOVS, 1984; SREMAC, 2005).

TRIASSIC

Hypercalcified sponges, including the group of spongiomorphid fossils described as hydrozoans by early workers (now considered to be sponges, such as *Spongiomorpha* FRECH, 1890, and *Disjectopora* WAAGEN & WENTZEL, 1888; see also Summary of Classification, p. 386, below), and chaetetids were among the most significant contributors to Middle and Late Triassic reefs (FLÜGEL & SENOWBARI-DARYAN, 2001; FLÜGEL, 2003). FLÜGEL (2003) concluded that hypercalcified sponges made up to 50–75% of the bulk of Late Triassic reefs. Inozoans and sphinctozoans are particularly abundant in Upper Triassic reefs. Of these, the sphinctozoans seem to be more abundant than the inozoans. Sponges with aragonitic and Mg-calcitic mineralogy are both represented. Generic diversity, complexity, and the dimensions of both groups increased from the Anisian to the Carnian and reached its maximum development during the Norian. The diversity of both groups seems to have decreased during the uppermost Norian or Rhaetian stage, and their importance as principal contributors, bafflers, and framebuilders was taken over by scleractinian corals.

Middle Triassic sphinctozoan- and inozoan-dominated reefs or reefal carbonates are known from numerous localities in the western Tethys (Alps: OTT, 1967; DULLO & LEIN, 1980; BRADNER & RESCH, 1981; FOIS & GAETANI, 1981, 1984; HENRICH, 1982; SENOWBARI-DARYAN & others, 1993; RÜFFER & ZAMPARELLI, 1997; EMMERICH & others, 2005; for more information, see FLÜGEL & SENOWBARI-DARYAN, 2001), and from the Apennines (SENOWBARI-DARYAN, ABATE, & others, 1999). Sphinctozoans have been reported from the Middle to Upper Triassic of the western Tethys (from the Alps of Austria: ZANKL, 1969; SENOWBARI-DARYAN, 1978, 1980a, 1990; SENOWBARI-DARYAN & SCHÄFER, 1979; SCHÄFER, 1979; DULLO & LEIN, 1980; for more information, see FLÜGEL, 1981, 2003; FLÜGEL & SENOWBARI-DARYAN, 2001); from northern Italy (MÜNSTER, 1841; DIECI, ANTONACCI, & ZARDINI, 1968; RUSSO, 1981; BIZZARINI & RUSSO, 1986); from southern Italy (MASTANDREA & RETTORI, 1989; SENOWBARI-DARYAN & ZAMPARELLI, 1999, 2003); from the Carpathians (JABLONSKY, 1971, 1972, 1975; BALOGH & KOVÁCS, 1976; KOVÁCS, 1978a, 1978b; FLÜGEL & others, 1992 in 1991–1992); from the former Yugoslavia (SENOWBARI-DARYAN, 1981, 1982; RAMOS & TURNSEK, 1984; TURNSEK, BUSER, & OGORELEC, 1987); and from Greece (SCHÄFER & SENOWBARI-DARYAN, 1982; SENOWBARI-DARYAN, 1982; SENOWBARI-DARYAN & SCHÄFER, 1983; SENOWBARI-DARYAN, MATARANGAS, & VARTIS-MATARANGAS, 1996).

Triassic sphinctozoan- and inozoan-dominated reefs and reefal limestones are also known from the southern Tethys (Sicily: SENOWBARI-DARYAN, 1980b; SENOWBARI-DARYAN, SCHÄFER & ABATE, 1982; SENOWBARI-DARYAN & ABATE, 1986; SENOWBARI-DARYAN & SCHÄFER, 1986; SENOWBARI-DARYAN & DI STEFANO, 1988b; from Turkey: CUIF, 1973; SENOWBARI-DARYAN, 1994a; SENOWBARI-DARYAN & LINK, 1998; SENOWBARI-DARYAN, LINK, & GARCÍA-BELLIDO, 2003, and from Oman: BERNECKER, 1996; SENOWBARI-DARYAN, BERNECKER, & others, 1999). These types of deposits are also known from the northern Tethys (Caucasus: MOISEEV, 1944; BOĬKO, BELYAEVA, & ZHURAVLEVA, 1991), and from the central Tethys (SENOWBARI-DARYAN, 1996, 2005a; SENOWBARI-DARYAN, SEYED-EMAMI, & AGHANABATI, 1997).

Sphinctozoan and inozoan sponges have been described from other Norian–Rhaetian reefs from the western Tethys (VINASSA DE REGNY, 1915; WILCKENS, 1937; RÖHL & others, 1991), and from around the Panthalassian ocean from North America (Nevada: STANLEY, 1979; British Columbia, Canada: STANLEY & SENOWBARI-DARYAN, 1999; Yukon, Canada: SENOWBARI-DARYAN & REID, 1987) and South America (SENOWBARI-DARYAN, 1994b).

Occurrences of approximately 16 sphinctozoan genera in Middle Triassic reefs and 55 genera in Upper Triassic reefs have been recorded. Inozoan sponges of Triassic deposits are not well known. They are represented by approximately 41 genera, but there are many more undescribed taxa.

In Jurassic deposits and reefs, siliceous sponges are more abundant than hypercalcified sponges in general, and especially the sphinctozoan and inozoan sponges. Based on the abundance of reef builders, LEINFELDER (2001) described three types of Jurassic reefs, and discussed them as coral reefs, siliceous sponge reefs, and pure microbiolite reefs. Although some sphinctozoan sponges are known from Upper Jurassic reefs, they do not play an important role in shallow-water environments. Inozoans, excluding those just described as stromatoporoids, are significantly more abundant than sphinctozoans in Jurassic deposits, and especially in Upper Jurassic deposits.

Jurassic sphinctozoans and inozoans are known in reef associations from Italy (SCHIAVINOTTO, 1984; BECARELLI BAUCK, 1986; BIZZARINI, BRAGA, & MASTANDREA, 1987; BROGLIO LORICA & others, 1991), Germany (QUENSTEDT, 1858; ZITTEL, 1879; WAGNER, 1964; LANG, 1985; REITNER, 1987c), Switzerland (OPPLIGER, 1929), France (POMEL, 1872), the former Yugoslavia (RADOIČIĆ, 1966), Greece (BONNEAU & TERMIER, 1975), Morocco (SCHROEDER, 1984), Poland (HURCEWICZ, 1972, 1975), and Peru (HILDEBRANDT, 1971, 1981; SENOWBARI-DARYAN, 1994b).

The abundance of both sphinctozoans and inozoans increased during the Cretaceous.

Several taxa have been described, especially from the Cretaceous of Spain (Schroeder & Willems, 1983; Reitner & Engeser, 1985; Reitner, 1987d), and Germany (Hillmer & Senowbari-Daryan, 1986).

In summary, the hypercalcified sponges (including archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, and inozoans) are the dominant metazoan fossil groups in Cambrian to Permian reefs. Among the invertebrates, sphinctozoan and inozoans were the main reef builders of Permian and Triassic reefs. In the uppermost Triassic (Rhaetian), scleractinian corals became more abundant than the hypercalcified sponge groups. The role of corals as the main reef builders continued to rise until Recent times, with the exception of the Cretaceous, when rudist bivalve reefs developed.

TECHNIQUES FOR STUDY

Sphinctozoans and inozoans are calcareous forms where both external and internal structures are critical for taxonomic evaluation. As a result, these fossils are prepared for examination and description much like bryozoans or stromatoporoids. Thin sections or polished sections of the skeletons provide primary information on those structures. Vertical axial sections that show the internal and dermal elements, coupled with similarly complete transverse sections, are normally important for analysis of elongate forms. Sections at high angles to and parallel to surfaces in platelike forms are also both necessary for adequate documentation of their structure, as in other fossil groups. In some forms, it may be helpful to prepare tangential or oblique sections to show chamber patterns and structures. Sections or polished surfaces should be prepared large enough to show the general structure of the fossil, rather than only a small part.

It is sometimes helpful to etch polished surfaces or sections with very dilute (3–5%) or concentrated (100%) acetic acid. Etched surfaces should be frequently checked during processing, compared to see which preparation is most productive on the particular samples, and that technique then applied for final preparation. Low-relief etched surfaces are necessary for examination of microstructure and spicules by scanning electron microscopy.

Silicified fossils of these groups are normally prepared for study by etching them in dilute hydrochloric or acetic acids. This allows encasing matrix to be removed so that details of the individual skeletons can be examined. Where the skeletons are very delicate, they may be embedded in epoxy, and after cutting the skeletons, they can be examined.

SUMMARY OF CLASSIFICATION AND STRATIGRAPHIC OCCURRENCES

The following is a list of all the currently recognized chambered (Sphinctozoa) and nonchambered (Inozoa) hypercalcified sponge genera and their stratigraphic occurrences.

Most aspects of the systematic classification proposed by Finks and Rigby (2004d, p. 585–764) have continued to be used here, but there are some important changes, as follows.

1. Demospongiae Sollas, 1885, is here maintained as class group name, given its widespread use and general acceptance by zoologists and paleontologists. The ICZN Code (1999) has not stipulated a consistent form of ending for class group names, although one attempt was made in the first *Treatise* Part E volume (Moore, 1955), including the change de Laubenfels (1955) made to poriferan class divisions, viz., "Demospongea, Hyalospongea and Calcispongea."
2. Subclasses Tetractinomorpha and Ceractinomorpha Lévi, 1953, have proven to exhibit polyphyletic relationships, and this has led to suggestions that use of these two traditional subclasses should be abandoned (Boury-Esnault, 2006).
3. Order Vaceletida Finks & Rigby (2004d, p. 691) is broadly constituted to incor-

porate many families and a wide scope of stratigraphic records but does not have priority over order Verticillitida TERMIER & TERMIER, 1977a; note also the recent common usage of this ordinal subdivision by VACELET, 2002b, p. 1097, and SENOWBARI-DARYAN and GARCÍA-BELLIDO, 2002a, p. 1521, is preferred here.

4. Calcispongiae DE BLAINVILLE, 1830, p. 494, and Calcarea BOWERBANK, 1864, p. 160, have been widely used as alternative class-level group names. The original spelling of DE BLAINVILLE (1830) was Calcispongia, but most subsequent authors have preferred to use the class-level name Calcarea for sponges with calcareous spicules (see more detailed discussion on p. 293).
5. In the FINKS and RIGBY (2004d) classification, the two subclasses of the Calcarea are the Calcinea and Calcaronea, with the former including two orders (Murrayonida and Clathrinida), and the latter with five orders (Leucosolenida, Sycettida, Stellispongiida, Sphaeocoeliida, and Lithonida). This contrasts with the new classification presented in this section, which only involves subclass Calcinea, with mainly sphinctozoan types grouped into two orders (Sphaerocoeliida and Lithonida) and inozoan types grouped within one order (Stellospongiida). The subclass Calcaronea is no longer considered to contain sphinctozoan or inozoan sponges.

The list of hexactinellid, lithistid, and heteractinid sphinctozoans are included, as well as the demosponge and calcarean representatives. For references that are not listed in this presentation, see FINKS, REID, and RIGBY (in KAESLER, 2004, p. 812–855). Stratigraphic abbreviations: C, Cambrian; O, Ordovician; S, Silurian; D, Devonian; Ca, Carboniferous; P, Permian; T, Triassic; J, Jurassic; Cr, Cretaceous; Ce, Cenozoic; R, Recent. A question mark before the genus name means either the family affiliation or the validity of the genus is uncertain.

SPHINCTOZOA

- Class Demospongiae SOLLAS, 1885
  - Order Agelasida VERRILL, 1907
    - Family Angullongiidae WEBBY & RIGBY, 1985
      - *Angullongia* WEBBY & RIGBY, 1985 (O)
      - *Alaskaspongia* RIGBY, POTTER, & BLODGETT, 1988 (O)
      - *Amblysiphonelloides* RIGBY & POTTER, 1986 (O)
      - *Belubulaia* WEBBY & RIGBY, 1985 (O)
      - *Nibiconia* RIGBY & WEBBY, 1988 (O)
    - Family Phragmocoeliidae OTT, 1974
      - *Phragmocoelia* OTT, 1974 (T)
      - ?*Baghevangia* SENOWBARI-DARYAN, RASHIDI, & HAMEDANI, 2005 (P)
      - *Radiothalamos* PICKETT & RIGBY, 1983 (D)
    - Family Intrasporeocoeliidae FAN & ZHANG, 1985
      - *Intrasporeocoelia* FAN & ZHANG, 1985 (P)
      - *Belyaevaspongia* SENOWBARI-DARYAN & INGAVAT-HELMCKE, 1994 (P)
      - *Delijania* SENOWBARI-DARYAN, 2005a (T)
      - *Rahbahthalamia* WEIDLICH & SENOWBARI-DARYAN, 1996 (P)
      - *Rhabdactinia* YABE & SUGIYAMA, 1934 (P)
    - Family Cryptocoeliidae STEINMANN, 1882
      - *Cryptocoelia* STEINMANN, 1882 (P–T)
      - *Anisothalamia* SENOWBARI-DARYAN & others, 1993 (T)
      - *Antalythalamia* SENOWBARI-DARYAN, 1994a (T)
      - ?*Calabrispongia* SENOWBARI-DARYAN & ZAMPARELLI, 2003 (T)

Rigbyspongia de Freitas, 1987 (S)
Sphaerothalamia Senowbari-Daryan, 1994a (T)
Family Palermocoeliidae Senowbari-Daryan, 1990
Palermocoelia Senowbari-Daryan, 1990 (T)
Family Thaumastocoeliidae Ott, 1967
Subfamily Thaumastocoeliinae Ott, 1967
Thaumastocoelia Steinmann, 1882 (P–T)
?*Calymenospongia* Elliott, 1963 (Ce)
?*Follicatena* Ott, 1967 (P–T)
Henricellum Wilckens, 1937 (P–T)
Pamirothalamia Boĭko in Boĭko, Belyaeva, & Zhuravleva, 1991 (T)
Pamiroverticillites Boĭko in Boĭko, Belyaeva, & Zhuravleva, 1991 (T)
Porefieldia Rigby & Potter, 1986 (O)
Pseudoporefieldia Rigby, Potter, & Blodgett, 1988 (O)
?*Solenocoelia* Cuif, 1973 (T)
Sollasia Steinmann, 1882 (Ca–T)
Sphaeroverticillites Boĭko, 1990 (T)
Subfamily Enoplocoeliinae Senowbari-Daryan, 1990
Enoplocoelia Steinmann, 1882 (P–T)
Girtyocoelia Cossmann, 1909 (O–T)
Girtyocoeliana Rigby & others, 2005 (O)
Naybandella Senowbari-Daryan, 2005a (T)
Phraethalamia Senowbari-Daryan & Ingavat-Helmcke, 1994 (P)
Family Amphorithalamiidae Senowbari-Daryan & Rigby, 1988
Amphorithalamia Senowbari-Daryan & Rigby, 1988 (P)
Family Polyedridae Termier & Termier, 1977a
Polyedra Termier & Termier, 1977a (P)
Family Aphrosalpingidae Myagkova, 1955b
Subfamily Fistulospongiinae Termier & Termier, 1977a
?*Fistulosponginina* Termier & Termier, 1977a (P)
Aphrosalpinx Myagkova, 1955b (S)
Cystothalamiella Rigby & Potter, 1986 (O–S)
Nematosalpinx Myagkova, 1955a (S)
Uvacoelia Kügel, 1987 (Ca)
Subfamily Vesicocauliinae Senowbari-Daryan, 1990
Vesicocaulis Ott, 1967 (T)
Russospongia Senowbari-Daryan, 1990 (T)
Tolminothalamia Senowbari-Daryan, 1990 (T)
Yukonella Senowbari-Daryan & Reid, 1987 (T)
Subfamily Palaeoschadinae Myagkova, 1955a
Palaeoscheda Myagkova, 1955a (S)
Family Glomocystospongiidae Rigby, Fan, & Zhang, 1989a
Glomocystospongia Rigby, Fan, & Zhang, 1989a (P)
Huayingia Rigby, Fan, & others, 1994 (P)
Family Sebargasiidae de Laubenfels, 1955
?*Sebargasia* Steinmann, 1882 (Ca)
Amblysiphonella Steinmann, 1882 (?C, ?O, Ca–T)
Calabrisiphonella Senowbari-Daryan & Zamparelli, 2003 (T)
Chinaspongia Belyaeva, 2000 (P)

Crymocoelia Belyaeva in Boĭko, Belyaeva, & Zhuravleva, 1991 (P)
?*Laccosiphonella* Aleotti, Dieci, & Russo, 1986 (P)
?*Lingyunocoelia* Fan, Wang, & Wu, 2002 (P)
Minisiphonella Boĭko in Boĭko, Belyaeva, & Zhuravleva, 1991 (T)
?*Oligocoelia* Vinassa de Regny, 1901 (T)
?*Paramblysiphonella* Deng, 1982c (P)
Polycystocoelia Zhang, 1983 (P–T)
Pseudoamblysiphonella Senowbari-Daryan & Rigby, 1988 (P)
Pseudoguadalupia Termier & Termier, 1977a (P)
Stylocoelia Wu, 1991 (P)
Vesicotubularia Belyaeva in Boĭko, Belyaeva, & Zhuravleva, 1991 (P)
Family Olangocoeliidae Bechstädt & Brandner, 1970
Olangocoelia Bechstädt & Brandner, 1970 (T)
Family Cliefdenellidae Webby, 1969
Cliefdenella Webby, 1969 (O)
Khalfinaea Webby & Lin, 1988 (O)
Rigbyetia Webby & Lin, 1988 (O)
Family Guadalupiidae Girty, 1908a
Guadalupia Girty, 1908a (P)
?*Cystauletes* King, 1943 (Ca–T)
Cystothalamia Girty, 1908a (Ca–T)
Diecithalamia Senowbari-Daryan, 1990 (T)
Discosiphonella Inai, 1936 (Ca–T)
Lemonea Senowbari-Daryan, 1990 (P)
Praethalamopora Russo, 1981 (T)
Family Tabasiidae Senowbari-Daryan, 2005a
Tabasia Senowbari-Daryan, 2005a (T)
?*Madonia* Senowbari-Daryan & Schäfer, 1986 (T)
Order Verticillitida Termier & Termier, 1977a
Family Solenolmiidae Engeser, 1986
Subfamily Solenolmiinae Engeser, 1986
Solenolmia Pomel, 1872 (P–T)
?*Adrianella* Parona, 1933 (P)
Ambithalamia Senowbari-Daryan & Ingavat-Helmcke, 1994 (P)
?*Cryptocoeliopsis* Wilckens, 1937 (T, ?J)
?*Deningeria* Wilckens, 1937 (T, ?J)
Hormospongia Rigby & Blodgett, 1983 (D)
Panormida Senowbari-Daryan, 1980b (T)
Paradeningeria Senowbari-Daryan & Schäfer, 1979 (P–T)
?*Polysiphonaria* Finks, 1997 (P)
Polythalamia Debrenne & Wood, 1990 (C); described as a capsulocyathid archaeocyath by Debrenne, Zhuravlev, & Kruse (see p. 918)
Preverticillites Parona, 1933 (P)
Prosiphonella Dieci, Antonacci, & Zardini, 1968 (T)
Sahraja Moiseev, 1944 (T)
Senowbaridaryana Engeser & Neumann, 1986 (T)
?*Seranella* Wilckens, 1937 (T)
Welteria Vinassa de Regny, 1915 (P–T)
Subfamily Battagliinae Senowbari-Daryan, 1990

- *Battaglia* Senowbari-Daryan & Schäfer, 1986 (T)

Family Colospongiidae Senowbari-Daryan, 1990

Subfamily Colospongiinae Senowbari-Daryan, 1990

- *Colospongia* Laube, 1865 (Ca–T)
- *Blastulospongia* Pickett & Jell, 1983 (C)
- *Pseudoimperatoria* Senowbari-Daryan & Rigby, 1988 (O–P)
- *Subascosymplegma* Deng, 1981 (P)
- *Tristratocoelia* Senowbari-Daryan & Rigby, 1988 (P)
- *Uvothalamia* Senowbari-Daryan, 1990 (P)

Subfamily Corymbospongiinae Senowbari-Daryan, 1990

- *Corymbospongia* Rigby & Potter, 1986 (O, ?P)
- *Exaulipora* Rigby, Senowbari-Daryan, & Liu, 1998 (?O, P)
- *Imbricatocoelia* Rigby, Fan, & Zhang, 1989a (P)
- *Lichuanospongia* Zhang, 1983 (P)
- *Neoguadalupia* Zhang, 1987 (P–T)
- *Parauvanella* Senowbari-Daryan & Di Stefano, 1988a (P–T)
- *Platythalamiella* Senowbari-Daryan & Rigby, 1988 (P–T)
- *Shotorispongia* Senowbari-Daryan, Rashidi, & Hamedani, 2006

Subfamily Kashanelliinae Senowbari-Daryan, 2005b

- *Kashanella* Senowbari-Daryan, 2005a (T)

Family Gigantothalamiidae Senowbari-Daryan, 1994a

- *Gigantothalamia* Senowbari-Daryan, 1994a (T)
- *Zanklithalamia* Senowbari-Daryan, 1990 (T)
- *Lucaniaspongia* Senowbari-Daryan, Abate, & others, 1999 (T)

Family Tebagathalamiidae Senowbari-Daryan & Rigby, 1988

- *Tebagathalamia* Senowbari-Daryan & Rigby, 1988 (P)
- *Graminospongia* Termier & Termier, 1977a (P)

Family Annaecoeliidae Senowbari-Daryan, 1978 (T)

- *Annaecoelia* Senowbari-Daryan, 1978 (T)

Family Cheilosporitiidae Fischer, 1962

- *Cheilosporites* Wähner, 1903 (T)

Family Salzburgiidae Senowbari-Daryan & Schäfer, 1979

- *Salzburgia* Senowbari-Daryan & Schäfer, 1979 (P–T)

Family Cribrothalamiidae Senowbari-Daryan, 1990

- *Cribrothalamia* Senowbari-Daryan, 1990 (T)

Family Verticillitidae Steinmann, 1882

Subfamily Verticillitinae Steinmann, 1882

- *Verticillites* Defrance, 1829 (J–Ce)
- *Boikothalamia* Reitner & Engeser, 1985 (J)
- *Marinduqueia* Yabe & Sugiyama, 1939 (Ce); this genus has recently been given an alternative assignment to that presented here and classified within the Order Dictyoceratida, Family Vaceletiidae (see discussion, p. 273–275)
- ?*Menathalamia* Reitner & Engeser, 1985 (Cr)
- *Murguiathalamia* Reitner & Engeser, 1985 (Cr)
- *Stylothalamia* Ott, 1967 (P–Cr)
- *Vaceletia* Pickett, 1982 (Cr–R) this genus has recently been given an alternative assignement to that presented here and classified within the Order Dictyoceratida, Family Vaceletidae (see discussion, p. 273–275).
- *Vascothalamia* Reitner & Engeser, 1985 (Cr)

?*Wienbergia* Clausen, 1982 (Ce)
Subfamily Polytholosiinae Seilacher, 1962
Polytholosia Rauff, 1938 (P–T)
?*Ascosymplegma* Rauff, 1938 (T)
Nevadathalamia Senowbari-Daryan, 1990 (T)
?*Tetraproctosia* Rauff, 1938 (T)
Subfamily Fanthalamiinae Senowbari-Daryan & Engeser, 1996
Fanthalamia Senowbari-Daryan & Engeser, 1996 (T)
Cinnabaria Senowbari-Daryan, 1990 (T)
Iranothalamia Senowbari-Daryan, 2005a (T)
Subfamily Polysiphospongiinae Senowbari-Daryan, 1990
Polysiphospongia Senowbari-Daryan & Schäfer, 1986 (T)
Family Uncertain
Platysphaerocoelia Boĭko in Boĭko, Belyaeva, & Zhuravleva, 1991 (T)
Order Hadromerida Topsent, 1898
Family Celyphiidae de Laubenfels, 1955
Celyphia Pomel, 1872 (P–T, Cr)
Alpinothalamia Senowbari-Daryan, 1990 (T)
Cassianothalamia Reitner, 1987b (T)
Jablonskyia Senowbari-Daryan, 1990 (T)
Leinia Senowbari-Daryan, 1990 (T)
Loczia Vinassa De Regny, 1901 (T)
Montanaroa Russo, 1981 (T)
Pamirocoelia Boĭko in Boĭko, Belyaeva, & Zhuravleva, 1991 (T)
Paravesicocaulis Kovács, 1978a (T)
Pisothalamia Senowbari-Daryan & Rigby, 1988 (P)
Pseudouvanella Senowbari-Daryan, 1994a (T)
Tongluspongia Belyaeva, 2000 (P)
Uvanella Ott, 1967 (P–T)
Family Ceotinellidae Senowbari-Daryan in Flügel, Lein, & Senowbari-Daryan, 1978
Ceotinella Pantic, 1975 (T)
Family Polysiphonidae Girty, 1908a
Polysiphon Girty, 1908a (P)
Arbusculana Finks & Rigby, 2004d (P)
?*Zardinia* Dieci, Antonacci, & Zardini, 1968 (T)
Subclass Lithistida Schmidt, 1870
Order Tetralithistida Lagneau-Hérenger, 1962
Suborder Tetracladina Zittel, 1878
Family Radiocelliidae Senowbari-Daryan & Würm, 1994
Radiocella Senowbari-Daryan & Würm, 1994 (T)
Class Calcarea Bowerbank, 1869
Subclass Calcinea Bidder, 1898
Order Sphaerocoeliida Vacelet, 1979b
Family Sphaerocoeliidae Steinmann, 1882
Sphaerocoelia Steinmann, 1882 (P–Cr)
Barroisia Munier-Chalmas, 1882 (J–Cr)
Sphinctonella Hurcewicz, 1975 (J)
Thalamopora Roemer, 1840 (J–Cr)
Tremacystia Hinde, 1884 (Cr)

Order Lithonida Döderlein, 1892
Family Minchinelliidae Dendy & Row, 1913
Muellerithalamia Reitner, 1987c (J)
Class and Order Uncertain
Pseudodictyocoelia Boĭko, 1984a (T)
Class Hexactinellida Schmidt, 1870
Subclass Hexasterophora Schulze, 1887
Order Hexactinosa Schrammen, 1903
Family Craticulariidae Rauff, 1893
Subfamily Caseariinae Schrammen, 1937
Casearia Quenstedt, 1858 (T–J)
Caucasocoelia Boĭko, 1990 (T)
Dracolychnos Wu & Xiao, 1989 (T)
Innaecoelia Boĭko, 1990 (J)
Pseudoverticillites Boĭko, 1990 (T)
Class Heteractinida de Laubenfels, 1955
Order Octactinellida Hinde, 1887
Family Nuchidae Pickett, 2002
Nucha Pickett & Jell, 1983 (C)
Jawonya Kruse, 1987 (C)
Wagima Kruse, 1987 (C)

INOZOA

The following list contains only the confirmed fossil inozoan sponges. Representatives of modern calcareous algae, including some inozoan taxa described as algae, are not listed here.

Class Demospongiae Sollas, 1885
Order Agelasida Verrill, 1907
Family Catenispongiidae Finks, 1995
Catenispongia Finks, 1995 (P)
Hartmanina Dieci, Russo, & Russo, 1974b (T); described as an obj. syn. of *Leiospongia* d'Orbigny, 1849b, a chaetetid as per Engeser & Taylor, 1989, and classified by West and Wood as an agelasid (see p. 264).
demosponge
Ossiminus Finks, 1995 (P)
Stratispongia Finks, 1995 (P)
Family Virgolidae Termier & Termier in H. Termier, G. Termier, & Vachard, 1977
Subfamily Virgolinae Termier & Termier in H. Termier, G. Termier, & Vachard, 1977
Virgola de Laubenfels, 1955 (P)
Dactylocoelia Cuif, 1979 (T)
Intratubospongia Rigby, Fan, & Zhang, 1989b (P)
Keriocoelia Cuif, 1974 (T); described as a chaetetid as per Dieci & others, 1977, and classified by West and Wood as an agelasid demosponge (see p. 262)
Reticulocoelia Cuif, 1973 (T)
Sclerocoelia Cuif, 1974 (T); described as a chaetetid as per Dieci & others, 1977, and West and Wood classified as an agelasid demosponge (see p. 264)
Subfamily Preeudinae Rigby & Senowbari-Daryan, 1996a
Preeudea Termier & Termier in H. Termier, G. Termier, & Vachard, 1977 (P)
Medenina Rigby & Senowbari-Daryan, 1996a (P)
Microsphaerispongia Rigby & Senowbari-Daryan, 1996a (P)

Polytubifungia Rigby & Senowbari-Daryan, 1996a (P)
Pseudovirgula Girty, 1908a (P)
Vermispongiella Finks & Rigby, 2004c (P)
Subfamily Pseudohimatellinae Rigby & Senowbari-Daryan, 1996a
Pseudohimatella Rigby & Senowbari-Daryan, 1996a (P)
Subfamily Parahimatellinae Rigby & Senowbari-Daryan, 1996a
Parahimatella Rigby & Senowbari-Daryan, 1996a (P)
Family Sphaeropontiidae Rigby & Senowbari-Daryan, 1996a
Sphaeropontia Rigby & Senowbari-Daryan, 1996a (P)
Family Exotubispongiidae Rigby & Senowbari-Daryan, 1996a
Exotubispongia Rigby & Senowbari-Daryan, 1996a (P)
Family Sestrostomellidae de Laubenfels, 1955
Sestrostomella Zittel, 1878 (T–J)
Brevisiphonella Russo, 1981 (T)
Epitheles de Fromentel, 1860a (J)
Himatella Zittel, 1878 (P–T)
Polysiphonella Russo, 1981 (T)
Trachytila Welter, 1911 (Cr)
Winwoodia Richardson & Thacker, 1920 (J)
Family Pharetrospongiidae de Laubenfels, 1955
Subfamily Pharetrospongiinae de Laubenfels, 1955
Pharetrospongia Sollas, 1877 (Cr)
Euepirrhysia Dieci, Antonacci, & Zardini, 1968 (T)
Subfamily Leiofungiinae Finks & Rigby, 2004d
Leiofungia de Fromentel 1860a (T)
Aulacopagia Pomel, 1872 (J)
Elasmopagia Pomel, 1872 (Cr)
Grossotubenella Rigby, Fan, & Zhang, 1989b (P)
Leiospongia d'Orbigny, 1849b (T); described as a chaetetid, as per Engeser & Taylor, 1989, and classified by West and Wood as an agelasid demosponge (see p. 264)
Loenopagia Pomel, 1872 (T)
Radicanalospongia Rigby, Fan, & Zhang, 1989b (P)
Family Auriculospongiidae Termier & Termier, 1977b
Subfamily Auriculospongiinae Rigby & Senowbari-Daryan, 1996a
Auriculospongia Termier & Termier, 1974 (P)
Anguispongia Senowbari-Daryan, 2005b (T)
Cavusonella Rigby, Fan, & Zhang, 1989b (P)
Molengraaffia Vinassa de Regny, 1915 (T)
Radiotrabeculopora Rigby, Fan, & Zhang, 1989b (P); described as belonging to the family Disjectoporidae (order ?Inozoa) by Stearn (see p. 319)
Subfamily Daharelliinae Rigby & Senowbari-Daryan, 1996a
Daharella Rigby & Senowbari-Daryan, 1996a (P)
Aliabadia Senowbari-Daryan, 2005b (T)
Subfamily Gigantospongiinae Rigby & Senowbari-Daryan, 1996a
Gigantospongia Rigby & Senowbari-Daryan, 1996a (P)
Subfamily Spinospongiinae Rigby & Senowbari-Daryan, 1996a
Spinospongia Rigby & Senowbari-Daryan, 1996a (P)
Subfamily Acoeliinae Wu, 1991
?*Acoelia* Wu, 1991 (=*Molengraaffia* Vinassa de Regny, 1915) (P)

          - *Solutossaspongia* Senowbari-Daryan & Ingavat-Helmcke, 1994 (P)
      - Family Stellispongiellidae Wu, 1991
        - Subfamily Stellispongiellinae Wu, 1991
          - *Stellispongiella* Wu, 1991 (P–T)
          - *Lutia* Senowbari-Daryan, 2005a (T)
        - Subfamily Prestellispongiinae Rigby & Senowbari-Daryan, 1996a
          - *Prestellispongia* Rigby & Senowbari-Daryan, 1996a (P)
        - Subfamily Estrellospongiinae Rigby & Senowbari-Daryan, 1996a
          - *Estrellospongia* Rigby & Senowbari-Daryan, 1996a (P)
      - Family Preperonidellidae Finks & Rigby, 2004d
        - Subfamily Preperonidellinae Finks & Rigby, 2004d
          - *Preperonidella* Finks & Rigby, 2004d (P–T)
          - *Bisiphonella* Wu, 1991 (P)
          - *Radiofibra* Rigby & Senowbari-Daryan, 1996a (P–T)
        - Subfamily Permocorynellinae Rigby & Senowbari-Daryan, 1996a
          - *Permocorynella* Rigby & Senowbari-Daryan, 1996a (P–T)
          - *Djemelia* Rigby & Senowbari-Daryan, 1996a (P)
          - *Saginospongia* Rigby & Senowbari-Daryan, 1996a (P)
        - Subfamily Precorynellinae Termier & Termier, 1977b
          - *Precorynella* Dieci, Antonacci, & Zardini, 1968 (P–T)
          - *Bicoelia* Rigby & Senowbari-Daryan, 1996a (P)
          - *Imperatoria* de Gregorio, 1930 (O, P)
          - *Minispongia* Rigby & Senowbari-Daryan, 1996a (P)
          - *Ramostella* Rigby & Senowbari-Daryan, 1996a (P)
          - *Stollanella* Bizzarini & Russo, 1986 (T)
        - Subfamily Heptatubispongiinae Rigby & Senowbari-Daryan, 1996a
          - *Heptatubispongia* Rigby & Senowbari-Daryan, 1996a (P)
          - *Marawandia* Senowbari-Daryan, Seyed-Emami, & Aghanabati, 1997 (T)
      - Family Fissispongiidae Finks & Rigby, 2004d
          - *Fissispongia* King, 1938 (D–Ca)
      - Family Maeandrostiidae Finks, 1971
          - *Maeandrostia* Girty, 1908b (Ca–T)
          - *Stylopegma* King, 1943 (P)
- Class Calcarea Bowerbank, 1869
  - Subclass Calcinea Bidder, 1898
    - Order Stellispongiida Finks & Rigby, 2004d
      - Family Stellispongiidae de Laubenfels, 1955
        - Subfamily Stellispongiinae de Laubenfels, 1955
          - *Stellispongia* d'Orbigny, 1849b (?J, Cr)
          - *Amorphospongia* d'Orbigny, 1849b (J)
          - *Blastinoidea* Richardson & Thacker, 1920 (J)
          - *Conocoelia* Zittel, 1878 (Cr)
          - *Diaplectia* Hinde, 1884 (J)
          - *Elasmoierea* de Fromentel, 1860a (Cr)
          - ?*Elasmostoma* de Fromentel, 1860a (J, Cr–Ce)
          - *Euzittelia* Zeise, 1897 (J–Cr)
          - ?*Heteropenia* Pomel, 1872 (Cr)
          - *Lutia* Senowbari-Daryan, 2005a (T)
          - *Pachymura* Welter, 1911 (Cr)

Pachytilodia Zittel, 1878 (Cr)
Pareudea Étallon, 1859 (T–J)
Paronadella Rigby & Senowbari-Daryan, 1996a (P–J)
Peronidella Zittel in Hinde, 1893 (J–Cr, R)
Steinmanella Welter, 1911 (Cr)
Trachypenia Pomel, 1872 (Cr)
Trachysinia Hinde, 1884 (J)
Trachysphecion Pomel, 1872 (J, R)
Subfamily Holcospongiinae Finks & Rigby, 2004d
Holcospongia Hinde, 1893 (J)
Actinospongia d'Orbigny, 1849b (J)
Astrospongia Étallon, 1859 (J)
Calicia Dullo & Lein, 1980 (T)
Enaulofungia de Fromentel, 1860a (?T, J, ?Cr)
Eudea Lamouroux, 1821 (T–J, R)
Mammillopora Bronn, 1825 (J, ?Cr, R)
Oculospongia de Fromentel, 1860a (P, ?T, J–Cr)
Tremospongia d'Orbigny, 1849b (Cr)
Tretocalia Hinde, 1900 (Ce)
Class and Order Uncertain
Bortepesia Boĭko, 1984a (T)
Cornuaspongia Senowbari-Daryan, 1994b (T–J)
?*Corynospongia* Deng, 1990 (P)
Lamellispongia Boĭko, 1984a (T)
?*Trammeria* Senowbari-Daryan, 1994b (T–J)

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GLOSSARY OF TERMS APPLIED TO THE HYPERCALCIFIED PORIFERA

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This glossary covers all the major groups of hypercalcified sponges, including the fossil representatives of the Archaeocyatha, Stromatoporoidea, Chaetetida, Sphinctozoa, and Inozoa, and as well the living hypercalcified members of the classes Demospongiae and Calcarea. It includes the terms used to describe the wide range of morphological types of nonspiculate basal calcareous skeletons. It also includes relevant spicule terminology for the well-preserved fossil skeletons exhibiting spicule traces and for describing the spicules associated with the living hypercalcified basal skeletons, as well as those loosely aggregated in soft tissues of their upper growing surfaces. The glossary reflects the scope and wide-ranging progress made in research on the various hypercalcified sponge groups over the past 40 years. Many of the terms defined in the glossary are discussed and illustrated in the introductory chapters of this volume.

Parts of this compilation are based significantly on the following works: (1) Boury-Esnault and Rützler's (1997) *Thesaurus on Sponge Morphology* (with its terminology focused on extant forms); (2) parts of Hooper and van Soest's (2002a) *Systema Porifera* that deal with the terminology of fossil Sphinctozoa (contributed by Senowbari-Daryan and Garcia-Bellido) and the Archaeocyatha (with its separate glossary contributed by Debrenne, Zhuravlev, and Kruse); (3) the contribution on Paleozoic stromatoporoids by Stearn and others (1999), also with a separate glossary; and (4) the fossil sponge glossary in the *Treatise on Invertebrate Paleontology,* Part E, Revised, vol. 2, contributed by Reid and Rigby (2003). An etymology of the Greek words used in the formation of sponge terminology, nomenclature, and taxon names by Boury-Esnault and Rützler (1997) and Hooper and van Soest (2002a) is presented in Voultsiadou and Gkelis (2005).

The terms defined here in alphabetical order as being of greater importance in this *Treatise* volume are listed in bold and singular, and the groups of hypercalcified sponges to which they apply are denoted at the end of each entry by abbreviations in bold and square brackets. These latter are identified (special interests of authors are included in parentheses) as follows: **Ar**, archaeocyaths (Debrenne, Zhuravlev, Kruse); **Ch**, chaetetids (West); **Cr**, cribricyaths (Zhuravlev, Kruse); **Di**, disjectoporids (Stearn); **Ex**, extant forms (Vacelet, Willenz); **In**, inozoans (Senowbari-Daryan, Rigby); **Ms**, Mesozoic stromatoporoids (Wood); **Ps**, Paleozoic stromatoporoids (Stearn, Webby, Nestor, Stock, Kershaw); **Pu**, pulchrilaminids (Webby); **Ra**, radiocyaths (Kruse, Zhuravlev, Debrenne); **Sp**, sphinctozoans (Senowbari-Daryan, Rigby). Some nonspiculate stromatoporoid-like forms (Stearn, Stock) from the Mesozoic are also denoted by **Ms**.

Each entry in the alphabetically arranged glossary list includes the specific term, then one or more sentences defining the term, followed by a listing of additional terms that are included for comparative purposes to the defined term. Other terms that are viewed as having lesser importance are also listed as synonyms (syn.); these are mainly regarded as superfluous (or obsolete). A few other terms are entered in the glossary with italics, and contributing authors regard these as obsolete; consequently they are not recommended for continued use by workers on hypercalcified sponges. Two examples are (1)the so-called coralline sponges, a term that is more or less synonymous with hypercalcified sponges but inappropriately named, even allowing for some that show a superficial resemblance to corals; and (2) the Sclerospongiae, an artifical (polyphyletic) grouping of living forms exhibiting demosponge affinities, with solid calcareous skeletons and, as well, fossil stromatoporoids and chaetetids.

The presentation of this consolidated glossary has involved entering terminology across a number of different hypercalcified sponge groups, and this has resulted in some multiple listings with a term having been introduced independently by workers in a number of different groups. Consequently, the definitions vary greatly: in some cases they describe very similar structures, and in other examples the features given a common name represent entirely unrelated structures. For example, whereas the term astrorhiza seems to define homologous structures across a number of different groups, the term tabula appears to represent completely unrelated types of structures across various groups. In preparing this consolidated glossary, we maintain the separated multiple entries for each term using an italicized *or* between each successive entry. The only other alternative was to present separate glossaries for each group, but this seemed a less satisfactory approach, given the longer-term aim to produce an entirely unified nomenclature for the hypercalcified sponges.

Though the archaeocyathan terms used here derive mainly from the summary in DEBRENNE, ZHURAVLEV, and KRUSE (2002), they were originally proposed by a number of workers, most notably DEBRENNE, ROZANOV, and ZHURAVLEV (1990, p. 205); ZHURAVLEV, DEBRENNE, and WOOD (1990); WOOD, ZHURAVLEV, and DEBRENNE (1992); and DEBRENNE and ZHURAVLEV (1992b, p. 34, 58). In addition, some general terms were taken from VLASOV (1962); ROZANOV (1973, p. 62–77); WENDT (1980); WOOD (1987); and MEYEN (1988).

The Paleozoic stromatoporoid terms compiled here have been compiled from the glossary list in STEARN and others (1999, p. 5–10). This was the first attempt since the late 1950s (GALLOWAY, 1957, p. 350–360) to produce a concise, simplified, yet comprehensive list of morphological terms in English. BOGOYAVLENSKAYA (1968, 1984), KHALFINA (1972), and BOL'SHAKOVA (1973) provided other morphological summaries.

A glossary of Mesozoic stromatoporoid terms was compiled by WOOD (1987), and, prior to the summary of morphological terminology in SENOWBARI-DARYAN and GARCIA-BELLIDO (2002a), there was a comprehensive coverage of the morphological terminology of sphinctozoans assembled by SENOWBARI-DARYAN (1990).

A divergence of opinion exists between the usages of the term stromatoporoid among authors of the chapters dealing with Mesozoic taxa. Wood (p. 193–208, 209–292) has treated the term stromatoporoid as representing a grade of organization of the hypercalcified skeleton, and so the term is viewed as having little or no taxonomic significance. The spiculate relationship is considered by Wood to have prime importance in classifying the Mesozoic taxa and in assigning them to the class Demospongiae; or, where spicules are lacking, the taxa are placed in *incertae sedis* of the Porifera. The second opinion stems from the long-standing perception among Paleozoic workers that the term stromatoporoid is taxonomically important: it remains the basis for recognition of the Ordovician–Devonian class Stromatoporoidea as an independent, unified, and exclusively nonspiculate group. Given this background, Stearn and Stock (p. 307–310) regarded the comparatively limited and uncertain record of nonspiculate, upper Paleozoic–Mesozoic forms as being stromatoporoid-like taxa, with uncertain links to early to mid-Paleozoic Stromatoporoidea.

It should be noted that the list of Paleozoic stromatoporoid terms presented in this glossary is additionally classified into those terms that are: (1) related to skeletal form and structure (skeleton = sk); (2) structures parallel to growth surfaces (tangential = ts); (3) structures normal to growth surfaces (longitudinal = ls); (4) related to the aquiferous filtration system (aquiferous = aq); and (5) related to microstructural type (microstructure = mi). One of the supplementary categories in parentheses (above) has been added to each Paleozoic stromatoporoid term listed in the glossary.

It is important also to distinguish growth orientations within laminar, domical, and bulbous stromatoporoid skeletons, as well as to the different orientations of thin sections used to study them. In particular, growth takes place *longitudinally* as the organism extends outwardly through successive growth surfaces, and *tangentially* as it extends laterally, parallel to successive growth surfaces. For studying columnar and dendroid skeletons, three different orientations are used: *longitudinally*, in the direction of the long axis of the column or branch; *transversely*, at right angles to the long axis; and *tangentially*, in the direction of the long axis, but offset to near the outer margin of the column or branch. In the *transverse* cut, structures are parallel to growth toward the periphery of branch, but normal to growth in the axial region.

Thin sections used in studying archaeocyaths and chaetetids are typically cut in two main orientations: *longitudinally* and *transversely* (perpendicular to and parallel to the growth surface, respectively).

Other abbreviations used in the Glossary are listed below.

S2a: *Systema Porifera*, vol. 2, Debrenne, Zhuravlev, and Kruse, 2002, p. 1539–1699, Class Archaeocyatha Bornemann, 1884.

S2b: *Systema Porifera*, vol. 2, Senowbari-Daryan and Garcia-Bellido, 2002a, p. 1511–1533, Fossil sphinctozoan: chambered sponges (polyphyletic).

Th: *Thesaurus on Sponge Morphology* (edited by Boury-Esnault & Rützler, 1997, Smithsonian Contributions to Zoology 596:1–55).

Tr: *Treatise on Invertebrate Paleontology*, Part E, Revised, Volume 2 (Reid & Rigby, 2003), glossary for Porifera, p. 177–190.

References herein are to figures and terms used within these two volumes of the Treatise on Invertebrate Paleontology, Part E, Revised, Volumes 4 and 5. This glossary represents a comprehensive listing of terms used for fossil hypercalcified poriferans. Less complete are the set of terms compiled for extant representatives of the hypercalcified poriferans—a more complete listing of these is contained in Boury-Esnault and Rützler (1997), available online (http://www.sil.si.edu/smithsoniancontributions/zoology/pdf_hi/sctz-0596.pdf).

acanthostyle. Single-axis spicule that bears small spines (or spinules), one blunt end and one pointed end; normally a megasclere (Th, fig. 216; Tr, p. 177) [**Ms, Ch, Ex**].

acosmoreticular (mi). A microreticulate microstructure where the orientation of micropillars and microcolliculi is without order [**Ps**].

allotube (ls). An elongate space within the skeleton aligned normal to the growth surface, meandriform or irregular in tangential section, bounded by amalgamate net of pachysteles and pachystromes, internally divided by dissepiments in orders Stromatoporida and Syringostromatida (Fig. 324.4; Fig. 329.3–329.4 (syn., pseudozooidal tube, coenotube) [**Ps**].

altoid wall. In Kazachstanicyathida, a simple outer wall of lintels linking distal ends of pillars to form a continuous plate pierced by frequent polygonal pores (Fig. 516c) (syn., simple wall of *Altaicyathus*-type; Debrenne & Zhuravlev, 1992b) [**Ar**].

amalgamate structure (sk). Three-dimensional network in which discrete, persistent, tangential structural elements are poorly defined (Fig. 321.5–321.6) [**Ps**].

ambiostium. A large exopore in interwall at the junction of two chambers, that opens into both chambers (S2b, fig. 1) [**Sp, In**].

ambisiphonate. Condition in which a spongocoel or axial tube is formed by growth upward from the chamber floor and downward from the roof. Usually the two parts do not grow completely together, leaving a ring of perforations or exopores (S2b, p. 1515, fig. 10) [**Sp, In**].

ambitopic mode of life. Like a number of other Paleozoic benthic organisms (Jaanusson, 1979a, p. 269), many stromatoporoids were capable of maintaining markedly different types of substrate preferences, first as attached forms during early growth stages, and then switching to live essentially freely on unconsolidated substrates, like level-bottom muddy settings, through their remaining life history [**Ps**].

amphiaster. A microsclere with rays radiating from both ends of a shaft. The rays are shorter than the shaft (Th) [**Ex**].

amphiblastula. Hollow, ovoid larva, with anterior (flagellated) and posterior (nonflagellated) groups of cells, typical of Calcaronea (Th) [**Ex**].

annulation. A ringlike structure marked by either a constriction or expansion in the outer wall of the skeleton [**Sp, In**].

annulus (pl., **annuli**). Ring-shaped (annular) plate separating horizontal files of wall openings (alone or in combination with other wall types); develops on external surface of outer walls or internal (central cavity) surface of inner walls; may be of planar, S-shaped, or V-shaped section (Fig. 501; S2a, p. 1689, fig. 19–21) [**Ar**].

anthoid wall. In Anthomorphina, a simple outer wall comprising transverse lintels linking adjacent pseudosepta to form a single row of slightly subquadrate large pores; additional lintels may delineate additional, discontinuous pore rows (Fig. 516a–516b) (syn., simple wall of *Anthomorpha*-type; Debrenne & Zhuravlev, 1992b) [**Ar**].

apical actine (ray). Fourth actine of a tetractine that is joined to the basal triradiate system (Th) [**Ex**].

apochete. Exhalant canal [**Sp, In**].

apopore. Exhalant pore [**Sp, In**].

apopyle. Opening of a choanocyte chamber into an exhalant canal (Th, p. 8, fig. 37) [**Ex**].

aporate. Without pores [**Sp, In**].

aporose septum. Septal pores absent. See septum (S2a, p. 1692, fig. 39H) [**Ar**].

aquiferous system. Whole water-conducting system of a sponge between the ostia and the osculum, comprising the inhalant system, choanocyte chambers, and exhalant system (Th, p. 8, fig. 37) [**Ms, Ch, Ex**].

aquiferous unit. Portion of the sponge that is a more or less functionally independent water-conducting system, comprising associated ostia, inhalant system, choanocyte chambers, and exhalant system, and has its drainage converging on a single osculum. See functional unit and module, which are treated as equivalents) (S2a, p.1689, fig. 3) [**Ar, Ms, Ch, Ex**].

archaeocyathan architecture. Skeletal structure with radial-longitudinal and/or radial-transverse partitions in intervallum. See architecture (Fig. 491b; S2a, p. 1689, fig. 2A, C) [**Ar**].

architecture. Type of primary skeletal structure. See archaeocyathan architecture, chaetetid architecture, stromatoporoid architecture, thalamid architecture (Fig. 491; S2a, p. 1689, fig. 1); syn., growth pattern [**Ar**].

asiphonate. Without a spongocoel or axial canals (S2b, p. 1519, fig. 10) [**Sp, In**].

asiphonate exhalant system. Condition in sphinctozoan sponges where any form of axial canal is lacking (S2b, p. 1513) [**Sp**].

aster. Any polyactinal (multi-rayed) microsclere in which the processes diverge from a common center or axial shaft (Tr, p. 178; Hooper & Wiedenmayer, 1994, p. 38, fig. 117–131) [**Ms, Ch, Ex**].

astrorhiza (pl., **astrorhizae**) (aq). A set of radiating (stellate) and branching canals, grooves, ridges, and openings of exhalant canal system of primary skeleton, as imprints converging to a single osculum (or closely spaced oscula) on terminal growth surface of skeleton; the structures may be associated with mamelons (Fig. 326.1–326.5; Fig. 327.2–327.4; Fig. 328.1–328.4; S2a, p. 1689, fig. 61F; Th, p. 36, fig. 203, 210; Tr, p. 178); syn., excurrent canal traces, astrosystem, stellate venations [**Ar, Ps, Ms, Ch, Ex, Sp, In**].

astrorhizal canal (aq). Part of a stellate, radiating, and/or branching, exhalant canal system within the skeleton (both longitudinally and tangentially oriented), composed of walled tubes, or where preserved without walls, as astrorhizal paths. In chaetetids, they are confined to the external surface. Canals may be partitioned by tabulae or dissepiments (syn., lateral tube, transverse astrotube, lateral canal) [**Ps, Ms, Ch, Ex**].

astrorhizal path. See astrorhizal canal (Fig. 327.2–327.3) [**Ps**].

astrotube. The terms lateral and axial astrotubes have been applied to distribution of oscula on Mesozoic stromatoporoids (Hudson, 1958); now obsolete [**Ms**].

atrium. An exhalant aquiferous cavity receiving water from one or more exhalant canals or apopyles and conducting it to one or more oscula) (Th, p. 8, fig. 40; Tr, p. 178); syn., spongocoel, preoscular cavity, cloaca [**Ms, Ch, Ex**]; *or* spongocoel (Th, p. 8, fig. 40) [**Sp, In**].

attached microporous sheath. Microporous sheath attached directly to carcass pore lintels; may be continuous (covering entire surface of carcass) or discontinuous (covering each carcass pore separately). See microporous sheath (Fig. 504.2–504.3; S2a, p. 1690, fig. 44D, G) [**Ar**].

autotube (ls). An elongate space between pachysteles with circular to subcircular outline in tangential section [**Ps**].

axial. The central (older) part of a skeletal branch [**Ms, Ch**].

axial canal (aq). Longitudinally oriented median structure of the astrorhizal system in domical, laminar, bulbous, and irregular skeletons that may be analogous to the axial canal in some columnar to dendroid stromatoporoids; may be tabulated (Fig. 329.1; Fig. 349.2; Fig. 476*a*) [**Ps**]; *or* spongocoel [**Sp, In**].

axial tube. Spongocoel, or a combination of discontinuous but aligned tubelike structures in interwalls [**Sp, In**].

backfill. Secondarily secreted calcareous filling material that grows syntaxially over the primary calcareous skeleton. Backfill may partially or fully occlude the primary pore space. See secondary calcareous skeleton [**Ms, Ch**].

baculus (pl., **baculi**). Longitudinal, rodlike element on external surface of outer wall [**Cr**].

bar. Radial-transverse lintel separating pores in a uniporous septum; biconcave in plan and with elongate cross section. See rod, uniporous septum (Fig. 496.3; S2a, p. 1689) [**Ar**].

barrel-shaped chamber shape. Chambers with nearly flat interwalls, but with bulging sides at midheight in subcylindrical structure [**Sp, In**].

basal calcareous skeleton. Hypercalcified sponges composed of either a rigid aspiculate or rigid spiculate skeleton, or a combination of both; the basal skeleton of calcium carbonate is considered by analogy with living hypercalcified sponges to have underlain a mantling layer of living tissue during its upward and outward growth. See rigid aspicular skeleton, rigid spicular skeleton [**Ps, Ms, Ch, Ex**].

basal layer (ts). A thin, dense, initial investment of skeletal material at the base of a stromatoporoid or chaetetid skeleton, with associated basal surface with either smooth or concentrically arranged, wrinkled, fine to coarse striae; basal layer is typically confined to undersides of laminar-domical shaped skeletons but may extend to lateral surfaces of small, cup-shaped skeletons; may be synonymous with epitheca of corals and extant hypercaclcified sponges but is not of secondary origin; the basal layer was produced in an inital stage of the growth process, as part of the basal phase of STEARN (1989a); in chaetetids, the basal layer appears to be organic [**Ps, Ch**].

basal phase (ts). A unit distinguished by structures different from those of the mature skeleton, formed in the initial growth of skeletal material across the surface of the sediment or hard substrate, or resumption of growth at the base of a latilamina (Fig. 329.2; Fig. 330.3) [**Ps**].

basic wall. Wall constructed only of marginal intervallar structures with additional lintels between. See rudimentary wall (Fig. 514c; Fig. 515b; S2a, p. 1689, fig. 60L) [**Ar**].

bisiphonate. Sponges with two spongocoels [**Sp, In**].

bowl-like cup. Widely conical cup. See cup (Fig. 581,*2;* S2a, p. 1690, fig. 69A) [**Ar**].

bract. S-shaped, cupped, or tubular plate incompletely covering a single pore; develops on external surface of outer wall or internal (central cavity) surface of inner wall. See fused bract, scale, pore tube (Fig. 500a–500b; S2a, 1689, fig. 44C) [**Ar**].

branching canal. Canal completely divided at a point along the length into two or more subsidiary canals. See canal (Fig. 503a; S2a, p. 1689, fig. 22J) [**Ar**].

branching gross morphology. Spreading out in branches; syn., dendritic, dendroid, foliose, fasciculate, ramose, digitate, phaceloid [**Ms, Ch, Ex**].

branching modular organization. Type of modular organization generated either by longitudinal subdivision or by external or interseptal budding. See modular organization; syn., dendroid, ramose (Fig. 492; S2a, p. 1691, fig. 60F–G) [**Ar**].

budding. Type of asexual reproduction in which parent cup is distinct from its progeny, though contiguous with them. [This budding terminology does not apply to chaetetids.] See external budding, intercalicular budding, interseptal budding (Fig. 522; S2a, p. 1689, fig. 9) [**Ar**].

bulbous growth morphology. Having the form of bulbous calcareous skeleton [**Ms, Ch, Ex**].

bullipore. Pore of a cribribulla (S2b, fig. 1) [**Sp, In**].

buttress. Complex, aporose structure of secondary skeleton consisting of several lamellar elements and extending from outer surface of primary skeleton to connect it with any firm substrate. See exocyathoid buttress, tersioid buttress (Fig. 552; S2a, p. 1689) [**Ar**].

calcareous skeleton. The calcareous skeletal material of hypercalcified demosponges and calcareans, both aspiculate and spiculate. See basal calcareous skeleton, skeleton; syn., coenosteum [**Ms, Ch, Ex**].

calicle. Longitudinal, tubelike, intervallar structure that can be hexagonal or tetragonal in cross section. See facet (Fig. 510a; S2a, p. 1689, fig. 71A–B) [**Ar**]; *or calicle.* Not recommended as a chaetetid morphological term because of its cnidarian connotations; replaced by tubule (see definition, p. 415) [**Ch**].

calthrop. Equiangular tetraxon with equal rays, so-called from resemblance to the four-pointed weapon known as a calthrop; may be a mega- or microsclere (Th, p. 42, fig. 228) [**Ms, Ch, Ex**].

cambroid wall. In Loculicyathina, a simple outer wall consisting of a continuous plate pierced by simple pores; pores may be rounded, irregularly rounded, or irregularly quadrate (Fig. 515c–515f); syn., simple wall of *Cambrocyathellus*-type; DEBRENNE & ZHURAVLEV, 1992b) [**Ar**].

canal. Wall opening of length greater than diameter. See branching canal, communicating canal, noncommunicating canal, S-shaped canal, subdivided canal, V-shaped canal, spongiose wall [S2a, p. 1689] [**Ar**]; *or* internal passage for water circulation, may be single or dichotomously to multidichotomously branched, or labyrinthic branched. See groovelike canal, fully roofed canal, exopore (S2b, p. 1519, fig. 8) [**Sp, In**].

canal system. Inhalant and exhalant canals for water circulation within the sponge [**Sp, In**].

carcass. Layer of otherwise simple pores and intervening lintels, the latter supporting microporous sheath in walls of microporous sheath type (S2a, p. 1689, fig. 27B) [**Ar**].

cassiculate structure (sk). Formed by oblique skeletal elements joined to enclose diamond-shaped galleries in a network like that of a chainlink fence (Fig. 322.1) [**Ps**].

cateniform. Catenulate or moniliform structure [**Sp, In**].

catenulate. Arrangement of ringlike chambers in moniliform structure around one or more spongocoels (S2b, p. 1515, fig. 4) [**Sp, In**].

catenulate modular organization. Chainlike modular organization consisting of individuals united laterally with one or two others; generated by incomplete longitudinal subdivision. See modular organization (Fig. 495b; S2a, p. 1691, fig. 41K) [**Ar**].

cavaedia (pl.). Large, deep indentations between folds in a plicate dermal surface of a sponge [**Sp, In**].

cellular (mi). Speckled skeletal material filled with closely spaced, irregularly distributed, subspherical, clear areas (cellules) that appear to have been voids in the structural element (Fig. 338.1; Fig. 339.1; Fig. 343.2) [**Ps**].

cellules (mi). See cellular [**Ps**].

cemented (fused) spicule. Interlocked or adjacent spicules firmly linked by calcareous cement; the cement may be restricted to the junction area or may progressively encase the entire spicule (Th, p. 36, fig. 204) [**Ms, Ch, Ex**].

central cavity. Space within two-walled cup, bounded externally by inner wall (S2a, p. 1690) [**Ar**].

chaetetid architecture. Skeletal structure consisting of calicles in archaeocyaths. [Use of the term tubules is preferred in chaetetids.] See architecture (Fig. 491e; S2a, p. 1689, fig. 2D) [**Ar**].

chamber. Space in a thalamid cup bounded by adjacent arched tabulae and their contiguous walls (S2a, p. 1690) [**Ar**]; *or* hollow, superposed, or laterally attached, major structures in sphinctozoan skeleton (S2b, fig. 1) [**Sp**].

chamber shape. Form of hollow major structures of the sponge skeleton. See barrel-shaped chamber shape, crescentic chamber shape, flattened chamber shape, funnel-shaped chamber shape, hemispherical chamber shape, tubular chamber shape, spheroidal chamber shape, rectangular chamber shape [**Sp**].

chamber wall. The skeletal structure that defines an individual chamber and may be subdivided into an exowall, interwall, and endowall [**Sp, In**].

chimney. Vertically developed mamelons bearing oscula, both of which protrude beyond the general growth surface [**Ms, Ch, Ex**]; *or* see exaulos [**Ar, Sp, In**].

clathrate wall. Wall consisting of a carcass of slitlike pores supporting a layer of more closely spaced, longitudinal ribs with or without transverse linking lintels. See pseudoclathrate wall (S2a, p. 1690, fig. 38E, J, 50F, H) [**Ar**].

clavidisc. Specialized microsclere, comprising an ovate disc with an elongate central perforation [**Ms, Ch, Ex**].

clinogonal microstructure. Elongate microstructural elements are divergent from a common axis at angles of less than 45° and may be penicillate, of thin pencil-like elements, or water-jet of divergent, irregular, linear elements or trabecular, of rods of anastomosing filaments, which may form an irregular mesh or web. Penicillate and water-jet are confirmed as basic types of clinogonal microstructure in sponges, but trabecular represents a cnidarian condition (not known in sponges), consequently an obsolete term in relation to sponges. Note also fascicular fibrous microstructure is broadly synonymous with clinogonal microstructure (Wendt, 1984; Boury-Esnault & Rützler, 1997) [**Ch, Sp, In, Ms, Ex**].

clinoreticular (mi). A microreticulate microstructural type where micropillars are inclined upward and outward from subcolumn axes; note that subcolumns in the syringostromatids have been been referred to as pillars [**Ps**].

cloaca. See spongocoel [**Sp, In**].

cloacal. Of the cloaca or spongocoel [**Sp, In**].

coarsely porous porosity. Pore diameter greater than lintel width; pores rounded to polygonal in outline. See porosity (Fig. 494b; Fig. 509a; S2a, p. 1691, fig. 56F) [**Ar**].

coeloblastula (blastula). Hollow larva composed of an envelope of morphologically similar equipotent cells, to which a few, larger, nonflagellated cells may be added at the posterior pole (Th) [**Ex**].

coenostele (ls). Not recommended because of its cnidarian connotations. See pachystele [**Ps**].

coenosteum (sk). See skeleton. The term is not recommended for continued use in describing the solid calcified skeleton of stromatoporoid sponges. [It remains applicable to cnidarians that exhibit a common colonial skeleton, and to Bryozoa with vesicular or solid skeletal material between zooecia.] [**Ps, Ms**].

coenostrome (ts). Not recommended because of its cnidarian connotations. See pachystrome; syn., coenostrom [**Ps**].

coenotube (ls). Not recommended because of its cnidarian connotations. See allotube [**Ps**].

collencyte. Cell with branching pseudopods, involved in the secretion of collagen (Th, p. 12, fig. 49) [**Ex**].

colliculus (pl., **colliculi**) (ts). A rod attached to a pillar that joins other such rods to form a net parallel to the growth surface in the order Actinostromatida; hence the laminae in this group are composed of colliculi (Fig. 321.1–321.2) [**Ps**].

column (ls). Skeletal structure (of macrostructure level) in which the arrangement of skeletal elements differs from that of intercolumn areas. The difference is commonly in the concentration and width of astrorhizae, pillars, or other longitudinal structures. See mamelon column (Fig. 325.5) [**Ps**]; *or* radial structural element of the calcareous skeleton, which appears vertical in longitudinal section. Greater degree of continuity and size than pillars; syn., vertical element, radial pillar, vertical lamella [**Ms**].

columnar gross morphology. Elongate forms with a circular or subcircular cross section; syn., cylindrical [**Ms, Ch, Ex**].

comma (pl., **commas**). A curved microstyle (Th) [**Ex**].

communicating canal. Canal connected to its neighbors either by pores piercing mutual canal walls or by anastomosing. See canal (Fig. 503b; S2a, p. 1689, fig. 25E, 31E–F, 37E–F); syn., perforate canal [**Ar**].

compact (mi). Specks are distributed evenly throughout the skeletal elements so that the elements have no regular internal microstructure [**Ps**].

compensation. Morphogenetic process involving the addition of a microporous sheath-screen or other elements in response to oligomerization (S2a, p. 1690) [**Ar**].

completely porous septum. Septal pores distributed frequently and uniformly over entire septum. See septum (Fig. 496a–496b; S2a, p. 1691, fig. 22H, 24B) [**Ar**].

compound wall. Wall in which component pores or cells bear spinelike elements projecting inward from their lintels; spines may unite across pore orifice to form micropores (complete pore subdivision) or remain incompletely connected (incipient pore subdivision) (Fig. 516d; S2a, p. 1690, fig. 67F, 68F, respectively) [**Ar**].

concentrically porous wall. Wall in which pores are grouped into more or less discrete clusters corresponding to cells bounded by adjacent radial-longitudinal partitions and tangential synapticulae (Fig. 514d; Fig. 516e); syn., centripetal wall of Gravestock, 1984) [**Ar**].

conical cup. Cup in form of inverted cone. See cup (S2a, p. 1690, fig. 13C) [**Ar**].

conical gross morphology. Having the form of an inverted cone [**Ms, Ex**].

contemporary phase (ls). A unit of skeletal growth of characteristic structure that displaces others, tangentially reflecting different structures formed contemporaneously along the growth surface (e.g., areas exhibiting structures unique to those formed by the superposition of mamelons) (Fig. 322.5, Fig. 325.5) [**Ps**].

coralline sponges. So named because of their superficial resemblances to groups of skeletonized, colonial organisms like tabulate corals in the Paleozoic and scleractinian corals in the Mesozoic to Recent; and also because of the many associations where sponges occur in reef-building habitats. Both these connotations are misleading, however: coralline is not a sponge-derived morphological term, and it has no place in the broader taxonomic classification and/or evolutionary development of sponges, either hypercalcified or otherwise. Consequently, the expression coralline, even as part of a general informal usage, should be discontinued. The term *coralline demosponges* is similarly a misnomer [**Ps, Ms, Ch, Sp, In, Ex**].

corallite. Not recommended because the term has cnidarian connotations [**Ms, Ch**].

corolla. Star-shaped, convex-downward, umbrella-like structure projecting from external surface of a cup and consisting of hollow, closed shafts and their connecting membranes; part of primary skeleton (Fig. 493e–493f; S2a, p. 1690, fig. 53J–L) [**Ar**].

cortex (pl., **cortices**). Thin, rindlike external layer of the rigid skeleton, usually with a structure different from that of the interior part of the skeleton (S2b, fig. 1) [**Sp, In**].

cortical. Of the cortex [**Sp, In**].

craticula (pl., **craticulae**). A screenlike element across the outer end of an exaulos (S2b, fig. 1) [**Sp, In**].

craticular pore. An opening or pore in a craticula [**Sp, In**].

crenulate. Wall in which each intersept is individually folded to form smoothly rounded bulge directed away from the intervallum (S2a, p. 1690, fig. 74A–B); syn., turgescent [**Ar**].

crenulation (ls). A small, upward inflection of a cyst plate or lamina (Fig. 387,*2a–b*) [**Ps**].

crescentic chamber shape. Chambers that are C-shaped, or shaped like the moon in its first quarter [**Sp, In**].

cribribulla (pl., **cribribullae**). Blisterlike sieve at the inner end of an exaulos (S2b, fig. 1) [**Sp, In**].

cribripore. Pores in sievelike or screenlike cribribulla (S2b, fig. 1) [**Sp, In**].

cryptosiphonate. Condition in sphinctozoan sponges in which chambers communicate through an aperture or group of apertures through the interwall between chambers (S2b, p. 1513, 1519, fig. 10) [**Sp**].

cryptosiphonate exhalant system. Condition in sphinctozoan sponges where skeletal chambers communicate through an aperture or group of apertures in chamber interwalls, without an axial tube (S2b, p. 1513) [**Sp**].

cup. Calcareous archaeocyathan skeleton. See bowl-like cup, conical cup, cylindrical cup, domal cup, juvenile cup, multichambered cup, platelike cup, sheetlike cup, single-chambered cup (S2a, p. 1690, fig. 1) [**Ar**].

cyathiform. Cup shaped [**Sp, In**].

cylindrical cup. Narrowly conical cup approaching form of cylinder. See cup (Fig. 502c; Fig. 509c; S2a, p. 1690, fig. 12J) [**Ar**].

cyst (ts). The space enclosed by the cyst plate [**Ps**].

cyst plate (ts). An upwardly and outwardly convex (in a few taxa, flat or concave) skeletal plate parallel to the growth surface in the order Labechiida, with most family representatives exhibiting cyst plates of variable sizes and shapes (rarely very large), and in places showing denticles on their tops. Branching to columnar members of family Aulaceratidae exhibit two types of cyst plates—large, stacked to overlapping cyst plates within axial columns; and much smaller, commonly imbricated, structural elements in lateral zones that Copper, Stock, and Jin (2013, p. 671) have now chosen to call "microcyst plates." This unfortunately has wider implications, given the bulk of labechiids exhibit smaller to medium-sized cyst plates and that a stabilized nomenclature for recording all these structures has existed for more than a half century (see Galloway, 1957). (Fig. 318.5; Fig. 391*g;* Fig. 392*e*); syn., microcyst plate [**Ps**].

denticle. Flattened, toothlike projection from free edge of an annulus (Fig. 501.5; S2a, p. 1690, fig. 20A,C) [**Ar**]; *or* short, solid, skeletal rod raised above the surface of cyst plates, and may extend from flanks of some pillars in the order Labechiida (incorporates villi of Galloway, 1957) (Fig. 321.4; Fig. 322.5) [**Ps**].

dermal. Outer surface or part of a sponge [**Sp, In**].

desma. Typically an interlocking megasclere of varied geometry that contributes to the main body of skeleton of lithistid demosponges (Th) [**Ex**].

diapason (tuning-fork spicule). Sagittal triactine with parallel, paired rays (Th) [**Ex**].

diaphragm. Thin, flat, or convex membrane narrowing orifice of a simple pore (Fig. 499.1; S2a, p. 1690, fig. 19C, left) [**Ar**]; *or* more or less rigid plate subdividing chamber interiors [**Sp, In**].

dichotomous exopore. A pore that subdivides once into two branches in the outer part of the wall [S2b, fig. 8] [**Sp, In**].

dictyonal network. Three-dimensional intervallar structure comprising radial and longitudinal lintels of taeniae (in which pores are subtetragonal) linked by tangential synapticulae at each interpore node to form an orthogonal, scaffoldlike network of equidimensional units (Fig. 509b–509c; S2a, p. 1690, fig. 60J, M) [**Ar**].

diplaster. An astrose microsclere in which the rays or spines radiate from two slightly distant points (Th) [**Ex**].

dissepiment (ts). An upwardly convex or inclined plate occupying interlaminar space; the term is also applied to partitions in allotubes, autotubes, and astrorhizal canals; not always easy to distinguish from tabulae in astrorhizal canals and interlaminar spaces; also dissepiments in places partition some peripheral vesicles of the amphiporids (Fig. 319.1; Fig. 319.3; Fig. 325.3) [**Ps**].

domal cup. Cup in form of domelike plate. See cup (S2a, p. 1690, fig. 61A) [**Ar**].

domical growth morphology. Having a calcareous skeleton with a domical growth form [**Ms, Ch, Ex**].

echinating. Megascleres that protrude from the spongin plate, a fiber, or a spicule tract (Th, p. 30, fig. 173) [**Ms, Ch, Ex**].

encrusting growth habit. Forms with a low height-to-width ratio that demonstrably encrust a substrate or another organism; syn., matlike gross morphology [**Ms, Ch, Ex**].

encrusting growth morphology. Exhibiting a matlike skeletal form seen to encrust substrate or other organism [**Ms, Ch, Ex**].

encrusting mode of life. These types of stromatoporoid organisms may be distinguished from their ambitopic counterparts by remaining in occupation of hard substrates throughout most of their life history; they are especially commonly associated with reef habitats [**Ps**].

encrusting modular organization. Modular organization in the form of a multioscular plate whose lower surface is attached to substrate. See modular organization (Fig. 492; S2a, p. 1691, fig. 61A) [**Ar**].

endocameral. Within the chambers of sphinctozoan (or informally termed thalamid) sponges [**Sp**].

endopore. Opening through the wall of a spongocoel or endowall (S2b, fig. 1) [**Sp, In**].

endotube. Tube that pierces the endowall and extends into the chamber interior from the endowall in a sphinctozoan sponge (S2b, fig. 1) [**Sp**].

endowall. The wall between the spongocoel and surrounding chamber (S2b, fig. 1) [**Sp, In**].

entrapped spicules. Calcareous or siliceous spicules that are not part of the primary spicule framework but are enclosed progressively within the calcareous solid skeleton during growth (Th, p. 36, fig. 205) [**Ms, Ch, Ex**].

enveloping skeletal growth (sk). This condition occurs where growth of a succeeding latilamina (or lamina) overlaps the previous latilamina when the living tissue was able to entirely mantle the calcareous skeleton from its top to lower lateral extremities, and to remain free from any contamination from associated sediment [**Ps**].

epitheca (pl., **epithecae**) (ts). Thin, wrinkled, calcareous covering of the basal surface of the skeleton of fossil hypercalcified sponges, probably representing initial growth. Problematic term, given its long-established cnidarian and bryozoan connotations; preferentially replaced by descriptive term basal layer for fossil stromatoporoids and chaetetids, whereas epitheca continues to be used by specialists on extant hypercalcified taxa [**Ps, Ch**]; *or* thin, wrinkled, calcareous basal layer of finer structure than the superjacent, normal skeleton that covers the dead basal part of the rigid calcareous demosponge skeleton, and considered to be of secondary origin (Th, p. 36, fig. 203) [**Ms, Ex**].

euaster. A collective term for astrose microscleres in which the rays radiate from a central point (Th, p. 44, fig. 223, 258, 275, 276, 279, 291) [**Ms, Ch, Ex**].

exaulos (pl., **exaules**). Protruding, spoutlike extension of outer walls. See chimney in *Retilamina* (Debrenne & James, 1981) (Fig. 495.5; S2a, p. 1690, fig. 61A, 75H; S2b, fig. 1) [**Ar, Sp, In**].

excurrent. See exhalant [**Sp, In**].

excurrent canal. See exhalant canal (Th, p. 8, fig. 37) [**Sp, In**].

exhalant. Allowing the outward flow of water (syn., excurrent) [**Sp, In**].

exhalant canal. Canal that forms a part of the exhalant system and is lined by the apopinocoderm; allows discharge of water from the sponge interior; syn., excurrent canal [**Sp, In**].

exhalant canal system. Part of the aquiferous system between the apopyle and oscule (Th, p. 8, fig. 37) [**Ms, Ch, Ex**].

exhalant opening. Opening through which water exits; may be through an exhalant or gastral pore, if larger, or an exopore, if smaller [**Sp, In**].

exhalant system. Arrangement of canals or other openings through which water exits a sponge or a chamber. See asiphonate exhalant system, cryptosiphonate exhalant system, siphonate exhalant system; syn., excurrent canal system) [**Sp, In**].

exocyathoid buttress. Zoned buttress encrusting primary cup, in which each zone consists of concentric plates connected by radial plates. See buttress (Fig. 522a; S2a, p. 1689, fig. 56C, D) [**Ar**].

exopore. Pore that pierces the outer wall of a chamber. Several types of openings are included here, including single, dichotomous, multidichotomous, and labyrinthic exopores (S2b, fig. 1) [**Sp**].

exowall. External wall of a chamber (S2b, fig. 1) [**Sp**].

external budding. Bud on outer wall of parent cup. See budding (Fig. 492; S2a, p. 1689, fig. 60G) [**Ar**].

facet. Any flat face of a calicle or syrinx (Fig. 510a–510d; S2a, p. 1690, fig. 72A–D) [**Ar**].

fascicular fibrous microstructure. General term for microstructure of crystal fibers fanning outward and radiating upward. See clinogonal microstructure (Th, p. 36, fig. 206) [**Ms, Ch, Ex**].

fiber. A column (strand, thread) of spongin forming a reticulate or dendritic skeleton, with or without indigenous spicules or foreign material (Th, p. 30, fig. 160, 170) [**Ms, Ch, Ex**].

fiber skeleton. Aragonitic or calcitic rigid skeleton of inozoans and sphinctozoans [**Sp, In**].

fibrous (mi). Specks and crystal boundaries aligned. In laminae, this alignment is transverse; in pillars, it may curve upward and outward from the axis in a water-jet or feather structure (Fig. 336.1; Fig. 345.1) [**Ps**].

filling material (filling tissue). Secondary calcareous skeleton that partitions or fills abandoned parts of the skeleton (Th, p. 38, fig. 207) [**Ms, Ch, Ex**].

filling structure (or **skeleton**). Elements of the skeleton filling within chambers of sphinctozoan sponges; may be reticulate, trabecular, tubular, radially septate, sporelike, pisolitic, vesicular, or a combination, such as septate-reticulate (S2b, p. 1513, fig. 1, 11) [**Sp**].

finely porous porosity. Pore diameter less than lintel width. See porosity (Fig. 494c; S2a, p. 1691, fig. 62D) [**Ar**].

first-order intervallar structure. Intervallar structure directly connecting both walls. See intervallar structure, pseudoseptum, septum, taenia (S2a, p. 1690) [**Ar**].

flattened chamber shape. Chambers with relatively low heights as compared to their diameters [**Sp**].

foramen (pl., **foramina**). Circular aperture in tabulae of chaetetid skeletons, allowing interconnection between adjoining intertabular spaces (Th, p. 38, see label "fo" shown on fig. 208) [**Ch**]; *or foramen* (ts). See pore [**Ps, Ms**].

fully roofed canal. Canal enclosed within the skeleton [**Sp, In**].

functional unit. The portion of water-conducting system of a sponge draining a single osculum; comprised of ostia, the inhalant system, choanocyte chambers, and exhalant system [**Ms, Ch, Ex**].

fungiform. Shaped like a mushroom [**Sp, In**].

funnel-shaped chamber shape. Chambers that are like an inverted cone, with a hole or small tube at the lower or narrow end [**Sp**].

fused bract. Neighboring bracts of the same horizontal file, incompletely amalgamated to form a single structure covering two or more openings in a wall, rarely forming a complete circle. Fused bracts are planar or S-shaped in longitudinal profile (S2a, p. 1690, fig. 61B–C); syn., pseudoannulus [**Ar**].

gallery (sk). The three-dimensional interlaminar space between adjacent pillars and bounded above and below by laminae or pachystromes; may contain other structural elements (e.g., dissepiments). The term is not usually applied in the Labechiida [**Ps**].

gastral. Inner surface or part of a sponge wall around a spongocoel [**Sp, In**].

globular gross morphology. Exhibiting a globular-shaped calcareous skeleton [**Ms, Ch, Ex**].

glomerate. Arrangement of the chambers like the seeds in an ear of corn or the grapes in a cluster [**Sp, In**].

granular (or **microgranular**) **microstructure**. Composed of irregular grains or granules [**Sp, In**].

groovelike canal. Canal impression in the skeleton as a groove in the dermal layer, marking the position of a canal that was not covered by skeletal material [**Sp, In**].

gross morphology. The overall shape of the calcareous skeleton. Often subject to considerable environmental control. See nodular gross morphology, branching gross morphology, columnar gross morphology, conical gross morphology, encrusting gross morphology, laminar gross morphology, domical gross morphology. It does not include other parts of external morphology, such as surface features (e.g., mamelons, traces of astrorhizae) [**Ms, Ch, Ex**].

growth axis. Represents the direction the skeleton grew in nodular, branching, columnar, conical, and domical forms, perpendicular to the growth surface [**Ms, Ch, Ex**].

growth banding. Banding in skeleton of some hypercalcified sponges reflects variations in growth due to a range of external and possibly internal controls. Three styles of banding are recognized: (1) density banding; (2) growth interruption banding; (3) postmortem banding (YOUNG & KERSHAW, 2005); the first two styles reflect periodic changes in growth (syn., latilaminae), but the third style is produced by secondary processes of diagenesis and compaction [**Ps**].

growth form (sk). Overall shape or morphotype; may be laminar, domical, bulbous, irregular, columnar, dendroid, digitate, or digitolaminar. Laminar, domical, irregular, bulbous, and digitolaminar forms may interfinger (in places giving ragged skeletal outlines) at their outer edges with surrounding sediment, whereas columnar, dendroid, and digitate forms tend to have smooth outer margins. Among Paleozoic stromatoporoids, the domical to laminar shapes are most common (and include the largest), and the other main shapes, arranged in decreasing order of abundance, are: irregular, bulbous (moderately common), columnar, digitate, dendroid to digitolaminar (less common to rare). [**Ps, Ch**].

growth habit. The growth habits reflect different levels of skeletal integration of the modular organization and may be associated with the growth morphologies (given in parentheses) and defined in separate entries. See pseudocolonial growth habit (branching), multiserial erect growth habit (branching), multiserial encrusting-encrusting growth habit (laminar, encrusting), multiserial encrusting-massive growth habit (nodular, conical, hemispherical) [**Ms, Ch, Ex**].

growth module. See module [**Ps**].

growth surface (ts). Any level in the skeleton where addition to the surface is contemporaneous; basal and terminal refer to the first and last surfaces of skeletal growth (Fig. 318.1; Fig. 352.1–352.2) [**Ps**]; *or* any contemporaneous surface on or within the skeleton [**Ms, Ch, Ex**].

hemispherical chamber shape. Chambers with relatively flat bases but spheroidal roofs [**Sp**].

hemispherical gross morphology. Having a flat base and a convex upper surface; syn., massive gross morphology, domical gross morphology [**Ms, Ch, Ex**].

hypercalcified sponges. The original term hypercalcified sponges (Termier & Termier, 1973) is a generalized, informal name to describe sponges that have secreted excessive amounts of solid, nonspiculate, calcium carbonate to their basal skeletons. The name has been used for nearly four decades to recognize a wide variety of fossil sponges—groups that include the archaeocyaths, stromatoporoids, chaetetids, sphinctozoans, and inozoans, as well as a relatively small number of questionably related lines of living Demospongiae and Calcarea; in most cases, the skeletons were confined more or less entirely to the bases of the living tissue, but this was not always so in the sphinctozoans, nor in all probability, in the archaeocyaths. Additionally the term hypercalcified has for convenience been applied to certain spiculate groups, those where the spicules have been cemented together with calcium carbonate coatings without producing a completely fused basal skeleton, as in the class Heteractinida, and in some inozoans (Finks & Rigby, 2004c, p. 585) of the class Calcarea. In the interests of stability in sponge nomenclature, it is important that the informal term **hypercalcified sponges** be maintained exclusively for the combined living and fossil members of both formal classes Demospongiae and Calcarea. To avoid confusion, it must be clearly distinguished from the terms **calcareous sponges** or **calcifying sponges** that are rather informal names, usually reserved by zoologists for use in describing members of the class Calcarea. See *coralline sponges* [**Ar, Ps, Ms, Ch, Sp, In, Ex**].

incurrent. See inhalant [**Sp, In**].

incurrent canal. See inhalant canal [**Sp, In**].

independent microporous sheath. Microporous sheath supported above carcass by short rods arising from carcass pore lintels; this sheath type is invariably continuous. See microporous sheath (Fig. 504a; Fig. 505h–505i; S2a, p. 1690, fig. 27B, 54G, I) [**Ar**].

individual. A single skeleton, composed of one or more functional units, representing one individual. In biological terms, this represents all the cellular components and all the interactions of their components within the pinacocyte envelope [**Ms, Ch, Ex**].

inhalant. Through which water enters [**Sp, In**].

inhalant canal. Any canal forming part of the inhalant system and lined by the prosopinacoderm (Th, p. 8) [**Ms, Ch, Ex**]; *or* any canal for passage of inhalant water leading into sponge interior, which would have initially had a lining of prosopinacoderm [**Sp, In**].

inner cavity. Space within one-walled cup, bounded externally by the wall (S2a, p. 1690) [**Ar**].

inner wall. Inner of two concentric walls in two-walled cups (S2a, p. 1690) [**Ar**].

Inozoa (Steinmann, 1882) or **inozoans**. Nonchambered, usually cylindrical or club-shaped sponges with both rigid and additionally spiculate skeleton (calcareans, demosponges) [**In**].

Inozoida (Rigby & Senowbari-Daryan, 1996a), or **inozoides**. Nonchambered, usually cylindrical or club-shaped sponges with rigid skeletons but without spicules; hence assignments to calcarean or demosponge groups remain uncertain [**In**].

intercalicular budding. Bud inside a single calicle. See budding (Fig. 492; S2a, p. 1689, fig. 62F) [**Ar**].

interlaminar space. Area or space enclosed between two successive laminae [**Ps, Ms**].

internal filling skeleton. See filling structure [**Sp, In**].

interpore. Pore in interwalls between chambers (S2b, fig. 1) [**Sp, In**].

intersept. That part of a wall or intervallum bounded by adjacent radial-longitudinal partitions (septa, taeniae) (S2a, p. 1690) [**Ar**].

interseptal budding. Bud in intervallum. See budding (Fig. 492; S2a, p. 1689, fig. 62F); syn., interparietal [**Ar**].

interseptal plate. Second-order intervallar structure in form of porous plate linking adjacent radial-longitudinal partitions (septa, taeniae) (Fig. 555,*3;* S2a, p. 1690, fig. 29D–E) [**Ar**].

interskeletal space. Referring to the spaces between any skeletal elements. See gallery, chamber, coenospace, coenotube [**Ms, Ex**].

intertabula (pl., **intertabulae**). That part of a wall or intervallum bounded by adjacent tabulae (S2a, p. 1690) [**Ar**].

intertube. Small tube that connects chambers through interwalls [**Sp, In**].

intertubular increase. Budding of the rigid calcareous skeleton involves the separation of tubule walls where they meet at an angle (at each intersection) and gradual expansion to full-sized tubule size with upward growth; syn., intercalicle budding [**Ch**].

intervallar cell. Part of intervallum bounded by adjacent radial-longitudinal partitions and tangential synapticulae (S2a, p. 1690) [**Ar**].

intervallar structure. Any skeletal element in the intervallum. See first-order intervallar structure, second-order intervallar structure (S2a, p. 1690) [**Ar**].

intervallum. Space enclosed between walls of a two-walled cup (S2a, p. 1690) [**Ar**].

interwall. The wall or walls between two adjacent chambers (S2b, fig. 1) [**Sp, In**].

invaginated wall. Inner wall closed at base and contiguous with tabula (S2a, 1690) [**Ar**].

irregular gross morphology. Having an irregularly shaped calcareous skeleton [**Ms, Ch, Ex**].

irregular microstructure. Irregular (felt) microstructure in which tangled linear crystal fibers have no preferred orientation (e.g., *Vaceletia*). Shape and nature of crystal fibers may be diverse or with unaligned and irregularly spaced elements (Th, p. 38, fig. 209); syn., granular, compact, freely micritic [**Ms, Ch, Sp, In, Ex**].

Ischyrospongiae (Termier & Termier, 1973). Introduced originally as a class to accommodate the extant Calcarea and Demospongiae with a solid calcareous skeleton and the fossil stromatoporoids and chaetetids, but the group name was seldom used, as it initially lacked priority over the Sclerospongiae Hartman & Goreau (1970), only remaining applicable to extant calcareans. However, use of the Termiers's name has been discontinued since Vacelet (1985) established the group as polyphyletic; hence the term is obsolete [**Ps, Ms, Ch, Sp, Ex**].

isodiametric. Of equal diameter, as in isodiametric spherulites in some skeletal structures [**Sp, In**].

isodictyal. An isodictyal skeleton exhibits an arrangement of spicules in simple, triangular meshes with single monaxons united tip to tip around each side (Th, p. 32; Tr, p. 183) [**Ms, Ch, Ex**].

juvenile cup. That portion of a cup generated prior to complete development of all mature structures. See cup (Fig. 497a; Fig. 497c; S2a, p. 1690, fig. 62G–H) [**Ar**].

labripore. Exopores surrounded by a distinct external lip or rim [S2b, fig. 1] [**Sp, In**].

labyrinthic exopore. A pore that subdivides several times into a labyrinth or network of interconnected branches in the wall (S2b, fig. 8) [**Sp, In**].

lamella. A term introduced by Lecompte (1956), for lamina, but now obsolete [**Ps**].

lamellar microstructure. Laminate microstructure of thin layers that may be smooth and more or less uniform, to undulating and irregular [**Sp, In**].

lamina (pl., **laminae**) (ts). A tangentially extensive skeletal plate or net parallel to the growth surface; it may be single-layered or tripartite; i.e., with a less opaque central zone, a line of cellules in the central zone (ordinicellular) or an opaque central microlamina, or it may be composed of multiple microlaminae (Fig. 317.2; Fig. 320.1) [**Ps**]; *or* a continuous, concentric, calcareous sheet parallel to the growth surface, and perpendicular to radial skeletal elements, e.g., the long axes of chaetetid tubules. Laminae in chaetetids are bounded above and below by growth interruptions, and in that sense they are more analogous to latilaminae of stromatoporoids than to stromatoporoid laminae; syn., lamella *pars*, coenosteal lamella, thecal lamella [**Ms, Ch**].

laminar gross morphology. Forms with a low height-to-width ratio that are free living, i.e., that do not appear to be attached to a hard substrate; syn., tabular gross morphology [**Ms, Ch, Ex**].

laminar-encrusting gross morphology. Exhibiting overall shape as matlike or tabular growth form that may be free-living or encrusting [**Ms, Ch, Ex**].

latilamina (pl., **latilaminae**). A tangentially continuous set of layers of skeletal material of the calcareous skeleton, visible as periodic growth bands bounded above and below by phase changes or growth interruption surfaces (Fig. 329.2; Fig. 330.3) [**Ps, Ms**].

leuconoid. Aquiferous system in which the choanocytes are restricted to discrete choanocyte chambers, which are dispersed in the mesohyl (Th) [**Ex**].

lintel. Skeletal structure separating and bounding adjacent pores (S2a, p. 1690) [**Ar**].

lipped pore. Labripore [**Sp, In**].

loculus (pl., **loculi**). That part of an intervallum delimited by two adjacent septa-taeniae and two adjacent tabulae (S2a, p. 1690) [**Ar**].

longitudinal fission. Increase in the rigid calcareous skeleton by the development of one or more pseudosepta that subdivide the tubule into equal or unequal parts; commonly the subdivision is across the shortest transverse dimension of the tubule (West & Clark, 1984) [**Ch**].

longitudinal fold. In a two-walled cup, the fold of one wall or mutual folds of both walls to impart a succession of more or less regular transverse annulations of the cup (Fig. 534,*5;* S2a, p. 1690, fig. 16A) [**Ar**].

longitudinal subdivision. Type of asexual reproduction by which the parent cup divides into two or more cups of equal sizes; syn., longitudinal fission (Fig. 492; S2a, p. 1690, fig. 9, 59F, 60F–G) [**Ar**].

louver. Plate incompletely covering two or more adjacent pores or intersepts in the same horizontal file; intermediate between fused bract and annulus (Fig. 500c–500d; Fig. 500f; S2a, p. 1691, fig. 18B) [**Ar**].

macrostructure. Pertains to visible internal skeletal structures in low magnification (up to ×10) using oriented thin sections. See lamina, pillar, cyst plate, dissepiment [**Ps**]; wall, tubule, tabula, lamina, pseudosepta [**Ch**].

mamelon (ts). An updomed area of skeletal material on the terminal growth surface (Fig. 326.1; Fig. 326.3) [**Ps**]; *or* rounded regular or irregular elevation of the skeleton surface; may or may not show correlation with astrorhizae; syn., monticule [**Ms, Ch, Ex**].

mamelon column (ls). A structure composed of upwardly inflected laminae, cyst plates or pachystromes formed by superposition of mamelons (Fig. 325.4–325.5) [**Ps**].

massive. Solid mass (a skeleton of relatively large bulk but not specifically shaped) [**Sp, In**].

massive gross morphology. Characteristically showing a bulky, nondescript type of calcareous skeleton [**Ms, Ch, Ex**].

massive modular organization. Type of modular organization (bulky skeleton) generated by contiguous addition of new aquiferous units. See modular organization (Fig. 492; S2a, p. 1691, fig. 71A, 75A, E) [**Ar**].

meandroid. A flexuous pattern shown by tubules in transverse section as opposed to discrete, regular, or irregular polygons [**Ch**].

megapillar (ls). A rodlike structure of a larger order of magnitude than a pillar. Megapillars can be distinguished in taxa having two sizes of pillars, such as *Bifariostroma*, *Oslodictyon*, *Yabeodictyon*, *Actinodictyon, Belemnostroma* [**Ps**].

megasclere. Major supporting spicule; the larger size group where two distinct size categories exist. Generally with a length greater than 100 µm [**Ms, Ch, Ex**].

melanospheric (mi). Specks are concentrated in closely spaced, irregularly distributed, subspherical opaque areas separated by clear areas (Fig. 338.2–338.3) [**Ps**].

membrane tabula. Second-order intervallar structure developed in same plane in one or several intersepts by fusion of spines. See tabula (Fig. 511; S2a, p. 1692, fig. 10) [**Ar**].

mesohyl. Part of sponge enclosed in pinacoderm and choanoderm (Th, p. 12) [**Ex**].

microcolliculus (pl., **microcolliculi**) (ts). A very fine, tangentially oriented rod that with other such rods forms a network joining micropillars within microreticulate microstructure [**Ps**].

microcyst plate (ts). A term proposed by Copper, Stock, and Jin (2013, p. 671), but its use should be discontinued as it contributes little towards achieving a more simplified and unified nomenclature of cyst plate terminology within the Labechiida. See cyst plate [**Ps**].

microgranular microstructure. Diverse microstructure composed of equant micrite-sized grains or crystals; in some cases, anhedral crystals have randomly oriented c-axes (Fig. 521; Th, p. 8, fig. 211; S2a, p. 1691) [**Ar, Ms, Ch, Ex**].

microlamellar microstructure. Structure in which the crystal fibers are disposed in crisscross layers, mostly parallel to the growing surface of the skeleton (e.g., *Acanthochaetetes)* (Th, p. 41, fig. 212) [**Ch, Ms, Ex**].

microlamina (pl., **microlaminae**) (ts). A thin, compact, laterally persistent plate that may be part of a lamina, or a single element parallel to the growth surface, or may consist of microcolliculi (Fig. 322.3) [**Ps**].

micropillar (ls). A very fine, rodlike, longitudinal structural element within microreticulate microstructures [**Ps**].

microporous sheath. Thin skeletal plate supported by lintels of carcass pores and pierced by micropores of lesser diameter; develops on external surface of outer wall or internal (central cavity side) surface of inner wall. See attached microporous sheath, independent microporous sheath (Fig. 504; S2a, p. 1690); syn., microporous membrane [**Ar**]; *or* an external layer of nesasters in some radiocyath genera; comprises anastomosing rays and tangential linking cross pieces (Fig. 658,*1a*) [**Ra**].

microreticulate (mi). Structural elements composed of micropillars and microcolliculi giving a three-dimensional network of fine posts and beams. See acosmoreticular, clinoreticular, orthoreticular (Fig. 339.3) [**Ps**].

microsclere. Accessory spicule of often ornate shape; the smaller size group where two size categories exist. Spicules generally smaller than 100 µm (Th, p. 44) [**Ms, Ch, Ex**].

microstructure. Crystal arrangement of calcareous skeleton that forms the skeletal elements, as seen under high power using a light microscope and/or an SEM. See irregular microstructure, microgranular microstructure, microlamellar microstructure, penicillate microstructure, clinogonal microstructure, orthogonal microstructure, spherulitic microstructure, trabecular microstructure, water-jet microstructure, fascicular fibrous microstructure, lamellar microstructure (Fig. 521; S2a, p. 1690; S2b, p. 1520, fig. 12); syn., ultrastructure, skeletal material, skeletal tissue [**Ar, Ms, Ch, Sp, In, Ex**]; *or* see compact, fibrous, striated, tubulate, cellular, melanospheric, microreticulate (three types), ordinocellular, vacuolate [**Ps**].

modular organization. Skeleton incorporating two or more aquiferous units united by common intervallar structures. See branching modular organization, catenulate modular organization, encrusting modular organization, massive modular organization, pseudocerioid modular organization (Fig. 492; Fig. 495; S2a, p. 1691, fig. 9) [**Ar**].

module. Functional unit of the poriferan aquiferous filtration system, serving a fixed volume of cells. A sponge module consists of incurrent pores (ostia), a connective canal system of incurrent and excurrent canals, and a common exhalant opening (osculum). In fossil sponges, a module is defined by the extent and influence of each osculum that may be expressed by the catchment area of the astrorhizae. See functional unit, aquiferous unit [**Ar, Ms, Ch, Ex**]; *or* fundamental construction unit of the skeleton of Stromatoporellida and Clathrodictyida consisting of a floor that becomes the upper layer of a tripartite lamina (and is absent in the clathrodictyids), a roof that becomes the lower layers of the succeeding lamina, and the pillars and other structures enclosed between these layers; alternatively termed a growth module. Note that this concept of a sponge module relates to the secretion of successive structural elements (floors and posts) rather than the organization of aquiferous units (Fig. 353.2; Fig. 354.1–354.2) [**Ps**].

monaxon. Linear, nonradiate spicule, or a spicule type not having more than two rays along one axis (Th, p. 44) [**Ms, Ch, Ex**].

moniliform. Linear arrangement of the chambers in asiphonate sphinctozoans (S2b, p. 1512, 1515, fig. 4) [**Sp**].

monoglomerate. Arrangement of several cystlike chambers in a single layer around one or more axial spongocoel(s) (S2b, p. 1512, 1515, fig. 4) [**Sp, In**].

monoplatyform. Chambers forming plates a single chamber layer thick, with chambers laterally adjacent to one another (S2b, p. 1512, 1515, fig. 4) [**Sp, In**].

monticule (ts). A small mamelon in Paleozoic stromatoporoids. See mamelon [**Ps**].

multichambered cup. Cup incorporating two or more chambers. See cup (Fig. 491c; S2a, p. 1690, fig. 2B2, 52G–H) [**Ar**].

multidichotomous exopore. A pore that subdivides once into several branches in the outer part of the wall (S2b, fig. 8) [**Sp, In**].

multiperforate tumulus. Tumulus with several pores, each pore surmounting a small papilla. See tumulus (Fig. 506c–506e; S2a, p. 1692, fig. 31N) [**Ar**].

multiserial encrusting-encrusting growth habit. A form with a low height-to-width ratio, composed of many laterally connected modules. See laminar-encrusting gross morphology [**Ms, Ch, Ex**].

multiserial encrusting-massive growth habit. A form with a high height-to-width ratio that is composed of many modules. The modules are often bound both laterally across the growth surface and along the growth axis of the skeleton, with no skeletal separation between them. Often the skeleton consists of many superposed modules, though only surficial modules will be active. See nodular gross morphology, columnar gross morphology, conical gross morphology, hemispherical gross morphology [**Ms, Ch, Ex**].

multiserial erect growth habit. Where more than one laterally connected functional module is present on each skeletal branch at any one time. See branching gross morphology [**Ms, Ch, Ex**].

nesaster. Primary constituent of inner or outer wall; solid, starlike structure consisting of 6 to 20 coplanar rays radiating from a central boss. In some genera, nesasters additionally bear an external microporous sheath. See microporous sheath (Fig. 658,*1b;* Fig. 659*b;* Fig. 660,*2a–c*); syn., aster, rosette [**Ra**].

netlike porosity. Pore diameter much greater than lintel width; pores polygonal in outline. See porosity (Fig. 499i; S2a, p. 1691, fig. 49D, 62A, C); syn., retiform porosity, reticulate porosity [**Ar**].

nodular gross morphology. Almost spherical, often composed of a number of nodular growths. See globular gross morphology, irregular gross morphology, subspherical gross morphology, bulbous gross morphology, massive gross morphology [**Ms, Ch, Ex**].

noncommunicating canal. Canal lacking connecting pores or any other communication with adjacent canals. See canal (Fig. 502; S2a, p. 1689, fig. 23H); syn., imperforate canal [**Ar**].

non-enveloping skeletal growth (sk). A type of growth condition that occurs where a succeeding latilamina (or lamina) fails to completely overlap the preceeding latilamina, giving a smooth appearance in cases where comparatively rapid upward growth was maintained, or it develops a ragged appearance when sediment spreads across lower parts of lateral margins of the skeleton [**Ps**].

oligomerization. Morphogenetic process involving decrease in number of pores or pore rows per intersept with accompanying increase in size of individual pores (S2a, 1691) [**Ar**].

ontogeny. The development during the course of an individual's life history; has not been recognized in either stromatoporoids or chaetetids; probably the term should be regarded as obsolete in these groups [**Ms, Ch**]. Skeletal ontogeny is recognized in archaeocyaths, however. See skeletal ontogeny [**Ar**].

orbicyathoid. See transverse fold (Fig. 494c; S2a, p. 1691, fig. 16D–E) [**Ar**].

ordinicellular (mi). Axial planes of laminae are marked by a layer of subspherical clear areas (cellules), giving laminae a three-layered, or tripartite, appearance in longitudinal section. Where divisions between these cellules are missing, the semicontinuous, clear middle layer accentuates this tripartite appearance. In some tripartite laminae, the central layer may be more opaque than those above and below (Fig. 320.1; Fig. 434*c*) [**Ps**].

organic skeleton. Spongin or collagenous part of mechanical support found in demosponges [**Ms, Ch, Ex**].

orthogonal microstructure. Microstructure in which the crystal fibers are in perpendicular and radial orientation relative to a central axis (Th, p. 40, fig. 213) [**Ms, Ch, Ex**]; *or* elongate microstructural elements diverging from a common axis at high angles to produce a radial, fibrous microstructure (Th, p. 40, fig. 213) [**Sp, In**].

orthoreticular (mi). Microreticulate microstructure where micropillars are normal to laminae-pachystromes and the microlaminae are parallel to the laminae [**Ps**].

oscule. See osculum [**Sp, In**].

osculum (pl., **oscula**). One (or more) openings through which water discharges from a sponge to the exterior; usually located at top of sponge (Th, p. 8, fig. 8, 38; S2b, fig. 1); syn., lateral astrotube, axial astrotube [**Ar, Ms, Ch, Sp, In, Ex**].

ostial pore. Proposed as new term for small inhalant apertures through external wall of calcarous skeleton [**Sp, In**].

ostium (pl., **ostia**). Any opening in the exopinacoderm through which water enters the living sponge. The term should be reserved for small inhalant apertures through living tissue. For inhalant apertures through calcareous walls of fossil skeletons, for example, the exowall of sphinctozoans, the general term pore remains available, or more specifically, ostial pore may be applied (Th, p. 8, fig. 45) [**Sp, Ex**].

outer wall. Outer of two concentric walls in two-walled cups (S2a, p. 1691) [**Ar**].

pachystele (ls). A wall-like part of the amalgamate net, either meandriform or fused to form a closed, continuous network in tangential section of orders

Stromatoporida and Syringostromatida (Fig. 321.5–321.6); syn., coenostele [**Ps**].

pachystrome (ts). A part of the amalgamate net that parallels the growth surface in the orders Stromatoporida and Syringostromatida (Fig. 321.5–321.6); syn., coenostrome [**Ps**].

palmate. With palms or with handlike structure [**Sp, In**].

papilla (pl., **papillae**) (ls). A raised, rounded extension of a pillar on the terminal growth surface [**Ps**].

paragaster. Spongocoel [**Sp, In**].

paralamina (pl., **paralaminae**) (ts). A planar skeletal plate that traverses single-layered, chevron-shaped laminae of a few genera of the order Clathrodictyida (Nestor, 1966a) [**Ps**].

pectinate tabula. Second-order intervallar structure developed in same plane in all or most intersepts and consisting of bolster(s) and centripetal spines in mutually opposed, comblike arrangement. See tabula (Fig. 534,*4c;* S2a, p. 1692, fig. 15H) [**Ar**].

pellis. Simple, aporose structure of secondary skeleton externally enveloping outer wall (S2a, p. 1691, fig. 59A) [**Ar**].

pelta (pl., **peltae**). In Monocyathida, a transverse, convex or concave primary skeletal structure, the direct extension of the wall, roofing inner cavity, and with central sag bearing an orifice (Fig. 507.1–507.2a–b; S2a, p. 1691, fig. 2G, 12H) [**Ar**].

penicillate microstructure. Crystal fibers fanning outward and radiating upward in a freely divergent manner (e.g., *Ceratoporella*). This microstructure is a subdivision of the broader clinogonal and fascicular fibrous microstructural types. See fascicular fibrous microstructure, clinogonal microstructure (Th, p. 40) [**Ch**].

periloph. Raised rim around an exopore or inhalant pore (formerly ostium); shorter than tubular exaulos. See labripore [**Sp, In**].

peripheral. Outer (younger) part of a skeletal branch [**Ms, Ch**].

peripheral expansion. Increase in the rigid calcareous skeleton by the development from the thin growing edge (soft tissue), of new, full-sized tubules on a preexisting substrate that fuse with preexisting tubules of the skeleton (West & Clark, 1983) [**Ch**].

peripheral membrane. See sheath [**Ps**].

peripheral vacuole. A cellule that occupies a space between a pillar-pachystele, small interconnecting processes, and an adjacent, thin, curved plate resembling a dissepiment (previously termed peripheral membrane and cyst plate) of a few trupetostromatid genera (e.g., *Hermatostroma, Hermatoporella*) (Fig. 323.2; Fig. 324.2) [**Ps**].

peripheral vesicle (ls). Elongated, bubble-like, gallery space forming part of a sporadically developed row along the inner side of the sheath of amphiporid stromatoporoids; in some cases partitioned by dissepiments (Fig. 476*b*) [**Ps**].

peripterate. Ribbonlike element spirally coiled along cup axis to form outer wall (Fig. 665,*2*) [**Cr**].

*Pharetronida (*Zittel, 1878). Former grouping for sphinctozoan and inozoan sponges (polyphyletic) [**Sp, In**].

phase (sk). A part of the skeleton characterized by a change of growth structure either longitudinally (successive) or tangentially (contemporary). Divided into basal phase, contemporary phase, spacing phase, successive phase, and terminal phase (Fig. 329.5; Fig. 330.1) [**Ps**].

pillar (ls). A skeletal rod (rarely a plate); may be long, columnar, continuous through laminae and interlaminar spaces, or may be confined to an interlaminar space, upwardly conical, spool shaped, grading into upwardly or downwardly inflected laminae in Paleozoic stromatoporoids. Pillars of order Labechiida may be circular, irregular, meandriform, or bladed (with or without flanges) in tangential section. A series of short, superposed interlaminar pillars in families Trupetostromatidae and Gerronostromatidae that may be difficult to distinguish from long, continuous pillars unless the traces of laminae cross them. See ring pillar (Fig. 317.3; Fig. 319.5; Fig. 321.2; Fig. 322.2; Fig. 323.3–323.4) [**Ps**]; *or* pillars are relatively short and discontinuous. See column; syn., vertical lamella, radial pillar [**Ms**]; *or* rodlike structure connecting adjacent tabulae and may extend through tabulae (Fig. 656,*1a–b;* Fig. 657; S2a, p. 1691, fig. 2F, 51F, 75G–H) [**Ar**]; *or* rodlike elements extending between interwalls of successive chambers [**Sp**].

pillar-lamellae. Horizontal elements that are part of the primary calcareous skeleton; short, discontinuous, concentric elements, contiguous with pillars or columns; syn., horizontal lamellae, concentric lamellae, lamellae *pars*, transverse lamellae) [**Ms**].

pinacocyte. Cell delimiting the sponge from the external milieu and always in a layer one-cell deep only (Th, p. 14, fig. 49, 51, 59) [**Ex**].

pinacoderm. Surface lined by pinacocytes (Th, p. 14, fig. 49) [**Ex**].

pisolitic filling structure (or **skeleton**). Composed of small, round-to-ellipsoidal calcium carbonate bodies with concentric and radial internal structure [**Sp, In**].

platelike cup. Conical cup in which apical angle of cone approaches 180°. See cup (Fig. 615,*1a–b;* S2a, p. 1690, fig. 58A) [**Ar**].

plate tabula. First-order intervallar structure in form of porous plate. See tabula (Fig. 498; S2a, p. 1692, fig. 40C, 43F) [**Ar**].

plicate wall. Wall in which each intersept is individually folded to form sharp, mid-interseptal longitudinal ridge, directed away from intervallum and separating planar to subplanar lateral flanks (Fig. 493a; S2a, p. 1691, fig. 42A); syn., asteroid, stellate [**Ar**].

plumose. A type of skeletal construction made of primary fibers or spicule tracts from which skeletal elements radiate obliquely (Th, p. 34, fig. 192) [**Ms, Ch, Ex**].

polyactine. A spicule with many growth axes [**Ms, Ch, Ex**].

polyglomerate. Arrangement of chambers around one or more axial spongocoel(s) in two or more layers (S2b, p. 1512, 1515, fig. 4) [**Sp, In**].

polyplatyform. Chambers forming plates composed of two or more flat layers, with chambers laterally adjacent to one another (S2b, p. 1512, 1515, fig. 4) [**Sp, In**].

polysiphonate. Sponges with more than two spongocoels [**Sp, In**].

porate. With pores. Sphinctozoans whose chamber walls (at least the exowall) contain small and equally distributed openings of the same size [**Sp**].

pore. General term for any small opening of a calcareous wall through which water passes. On external walls of hypercalcified sponges, such pores may represent inhalant apertures (the term ostia was previously applied to these structures but should be reserved for inhalant openings through the exopinacoderm of living sponges). See ostial pore [**Sp, In**]; *or* restricted to openings piercing any primary skeletal structure, of diameter greater than thickness of that structure. See slitlike pore, stirrup pore, subdivided pore (S2a, p. 1691) [**Ar**]; *or* an opening of rounded section through a lamina (foramen of GALLOWAY, 1957, is a large pore) [**Ps, Ms**].

pore field. Cluster of pores, particularly if in flat area surrounded by a low rim, in an exowall [**Sp, In**].

pore tube. Structure of elongate, scooplike to tubular shape, completely or almost completely covering a single pore (Fig. 520a–520b; S2a, p. 1691, fig. 64A–D, 70C) [**Ar**]; *or* longitudinally oriented, canal-like tubes that developed by the superposition of pores, which were first pierced by the original cyst plates or laminae. The pore tubes are considered to be primary structures and typically have sparry calcite infills; see labechiid genus *Forolinia* (NESTOR, COPPER & STOCK, 2010, p. 57, pl. 2a–b, 4a–b). However, this same type of structure has been inferred to be a product of selective dissolution of pillarlike elements by diagenetic processes and secondary infilling of the "tube" with sparry calcite, as seems likely in many examples of the labechiid genus *Stromatocerium;* see discussion in the Labechiida (p. 710–711) and illustrations of the so-called "pore tubes" (hollow pillars or wall-less "rods") in KAPP and STEARN (1975, fig. 3) and Webby (1979b, p. 248, fig. 5A–D) [**Ps**].

porosity. Character of pore arrangement in a primary skeletal structure. See coarsely porous porosity, finely porous porosity, netlike porosity, slitlike porosity, septum, pseudoseptum, taenia (S2a, p. 1691) [**Ar**].

primary calcareous skeleton. Initially formed calcareous skeleton and well differentiated from an enveloping secondary calcareous skeleton. [Paleozoic stromatoporoids do not show such a clear-cut differentiation into primary and secondary skeletal growth, and to some extent this applies to chaetetids as well.] (Th, p. 40, fig. 207) [**Ms, Ch, Ex**]; *or* that part of skeleton formed during ontogeny (primary growth of individual) by biologically controlled processes and serving as the locus for principal life functions (Fig. 521a–521c; S2a, p. 1691, fig. 4) [**Ar**].

primary spicule framework. Framework of arranged spicules around which the predominantly primary calcareous skeleton is precipitated (Th, p. 40, fig. 207) [**Ms, Ch, Ex**].

prosiphonate. A type of spongocoel in which individual chamber roofs or interwalls grew upward to form the spongocoel (S2b, p. 1519, fig. 10) [**Sp**].

prosopore. Inhalant pore [**Sp, In**].

prosopyle. Opening of an inhalant canal into a choanocyte chamber (Th, p. 8, see label "pro" in fig. 37) [**Ex**].

pseudocerioid modular organization. Massive type of modular organization consisting of individuals united laterally with two or more other individuals; generated by incomplete longitudinal subdivision. See modular organization (Fig. 495c; Fig. 523c; S2a, p. 1691, fig. 25A) [**Ar**].

pseudoclathrate wall. Wall consisting of a layer of closely spaced, longitudinal ribs and transverse linking lintels supported by short rods above quadrate intervallar cells. See also clathrate wall (Fig. 612,*1b;* S2a, p. 1691, fig. 55D) [**Ar**].

pseudocolonial growth habit. Having only one active functional module present on each skeletal branch. See branching gross morphology [**Ms, Ch, Ex**].

pseudogemmule. Accumulation of gemmular archaeocytes in basal cavities of a solid skeleton or hypercalcified skeleton (Th) [**Ex**].

pseudolamellar microstructure. Diagenetic alteration of the microstructure, producing parallel plates of recrystallized crystals and giving an internally layered appearance in transverse section [**Ms**].

pseudoseptum (pl., **pseudosepta**). Radial-longitudinal first-order intervallar structure formed by irregularly porous, planar-to-subplanar partition, developed during ontogeny from initial taenial structure; may be coarsely porous or finely porous. See porosity (Fig. 494; S2a, p. 1691, fig. 57E, 59G) [**Ar**]; *or* calcareous structure that subdivides (or longitudinally partitions) tubules; pseudosepta are associated with the growth and expansion of the rigid calcareous skeleton. See longitudinal fission [**Ch**].

pseudosiphonate. A type of spongocoel that lacks a true axial tube but with a tubular axial passage that may or may not be outlined by an endocameral structure (S2b, p. 1519, fig. 10) [**Sp, In**].

pseudospicules. Linear, spicule-like elements of spongin or spongin-related materials in living forms, or of secondary mineral fillings of primary or secondary linear openings within skeletal structures in fossil examples [**Sp, In**].

pseudotaenial network. Three-dimensional intervallar structure, comprising taeniae linked by synapticulae at each interpore node (Fig. 509; S2a, p. 1691, fig. 64A–D, 66F–G, 67D–E) [**Ar**].

pseudozooidal tube. A term introduced by GALLOWAY (1957) but because of its hydrozoan and/or bryozoan connotations, it is here replaced by allotube [**Ps**].

pugiole tetractine. Dagger-shaped, cruciform, or harpoonlike tetractine (BOROJEVIC, BOURY-ESNAULT, & VACELET, 2000) [**Ex**].

pustula (pl., **pustulae**). Wall structure covering an individual wall pore, in form of low cone or hemispherical dome pierced by a single central orifice (Fig. 517d; S2a, p. 1691, fig. 59K) [**Ar**].

radial. Elements radiating outward from a central point or area [**Ms, Ch**].

radial canal. Radially directed inhalant or exhalant canal [**Sp, In**].

radiate. Spicule with three or more radiating growth axes, or referring to radiating arrangement of megascleres [**Ms, Ch, Ex**].

radiate skeleton. A type of skeleton in which the structural components diverge from a central region toward the sponge surface (Th, p. 34, fig. 194) [**Ms, Ch, Ex**].

radicatus (pl., **radicati**). Dense lamellar structure of secondary skeleton anchoring the cup to a substrate (ZHURAVLEVA & MYAGKOVA, 1981, fig. 7; S2a, p. 1690, fig. 1); syn., epitheca [**Ar**].

raphide. A very thin, hairlike microsclere, often in bundles called trichodragmas (Th) [**Ex**].

rectangular chamber shape. Chambers that have four sides and are quadrangular [**Sp**].

recurrence. Morphogenetic polymorphic set of features regularly repeating along the same vector in each series of homologous variability (S2a, p. 1691) [**Ar**].

redimiculus (pl., **redimiculi**). Narrow, aporose, radial-longitudinal plate projecting externally or internally from a wall (Fig. 499f–499g; S2a, p. 1691, fig. 51B) [**Ar**].

regular spicule. Triactine or tetractine spicule with basal rays of equal length and with equal angles (120° between them, when projected into a plane perpendicular to the optic axis) (Th) [**Ex**].

reticular. Endocameral structure consisting of an irregularly three-dimensional network of beams of skeleton (S2b, fig. 11) [**Sp, In**].

reticulate filling structure (or **skeleton**). Composed of a three-dimensional network of fibers or other linear elements [**Sp, In**].

reticulate skeleton. General organization of skeleton consists of a three-dimensional network of fibers, tracts, lines, and/or individual spicules (Th, p. 34, fig. 155–158, 163, 175, 176, 180, 195); syn., reticulum [**Ms, Ch, Ex].**

retrosiphonate. A type of spongocoel formed by downward or backward extension of the chamber walls in sphinctozoans (S2b, p. 1519, fig. 10) [**Sp, In**].

rhagon. Earliest functional stage with multiple choanocyte chambers and aquiferous canals, typical for Demospongiae (Th, p. 18, fig. 86) [**Ms, Ch, Ex**].

rib. Narrow longitudinal plate linking annuli to wall (S2a, p. 1691, fig. 19G–H) [**Ar**].

rigid aspicular skeleton. A skeleton that originates from the direct secretion of aspiculate elements made of calcium carbonate; siliceous or calcareous spicules may be secondarily entrapped in the skeleton during the growth process. See basal calcareous skeleton (Th, p. 40, fig. 208) [**Ms, Ch**].

rigid skeleton. Skeleton of hypercalcified sponges that is not flexible; either aspiculate, spiculate, or both, and irrespective of whether it developed initially from a completely fused basal calcarous skeleton or not [**Sp, In**].

rigid spicular skeleton. Skeleton in which the main framework is first made up of fused or linked spicules that may later be invested by an aspiculate cement (Th, p. 40, fig. 204) [**Ms, Ch**].

rim. In two-walled cups, a planar-to-convex primary skeletal structure developed by the direct extension of one wall to unite with the other, creating intervallum roofing (Fig. 507.3–Fig. 507.4; S2a, p. 1691, fig. 26B) [**Ar**].

ring pillar. Short pillar that appears as a hollow cone formed by upward inflection of a lamina (e.g., *Stromatoporella*) [**Ps**].

rod. Radial-transverse lintel separating pores in a uniporous septum; of uniform diameter and circular cross section. See bar, uniporous septum (S2a, p. 1691) [**Ar**]; *or* rodlike skeletal elements for disjectoporids, either longitudinal or tangential, forming the three-dimensional skeletal network (Fig. 208,*1–2*); syn., trabecula, concentrirod, radirod) [**Di**].

rudimentary wall. Wall constructed only of marginal intervallar structures. See basic wall (Fig. 515a; S2a, p. 1691, fig. 71C–D) [**Ar**].

sagittal spicule. Triactine or tetractine with two equal angles (paired angles) and one dissimilar angle (unpaired angle) at the center, when projected into a plane perpendicular to the optic axis (Th) [**Ex**].

scale. Triangular or circular spicule derived from a triactine (Th) [**Ex**]; *or* curved, S-shaped or V-shaped plate spanning and incompletely covering two or more laterally adjacent pores; develops on external surface of outer wall or internal (central cavity) surface of inner wall. See bract, spine **[Ar].**

scalenohedral structure. Diagenetic pseudostructure caused by recrystallization. Forming a sawtooth arrangement of fibers that appear darker in thin section [**Ms, Ch**].

sclere. Spicule [**Sp,In**].

sclerocyte. Cell involved in spicule formation. In demosponges with intracellular secretion, sclerocytes are characterized by numerous mitochondria and the presence of spicule-axial filaments. In calcareans, where secretion is extracellular, sclerocytes have septate junctions between them (Th, p. 14, fig. 49, 69) [**Ex**].

sclerodermite. Aggregate of crystals forming a microstructural unit of the calcareous skeleton (Th, p. 40, fig. 215) [**Ms, Ch, Ex**].

sclerosome. Calcareous cement or nonspiculate calcium carbonate that unites spicules or forms skeletal fibers that then become imbedded (Tr p. 187) [**Sp, In**].

Sclerospongiae (Hartman & Goreau, 1970). This group was introduced as a separate class to include extant Demospongiae with solid calcareous skeletons and fossil counterparts (stromatoporoids, chaetetids, and sphinctozoans), but this combination proved to include polyphyletic relationships (Vacelet, 1985); hence the term is obsolete. No hypercalcified calcareans were associated with this group [**Ps, Ms, Ch, Sp, Ex**].

secondary calcareous skeleton. Skeletal components formed after the deposition of the primary skeleton, enveloping and/or infilling space between the initial elements; not easy to distinguish in chaetetids (Fig. 521.1d; Th, p. 40, fig. 207; S2a, p. 1691, fig. 4) [**Ar, Ms, Ch**].

secondary thickening. A type of secondary calcareous material that precipitates as simple aporose structures in multiple layers of enveloping elements upon the primary skeleton; difficult to differentiate in chaetetids (S2a, p. 1691, fig. 4) [**Ar, Ms, Ch**].

second-order intervallar structure. Intervallar structure developed upon first-order structures. See intervallar structure (S2a, p. 1690) [**Ar**].

segment. Term used by some authors for a chamber of a sphinctozoan [**Sp**].

segmentation. Subdivision of some linear sphinctozoan sponges into chambers, often marked by annulations of outer walls at chamber junctions [**Sp**].

segmented tabula. Plate tabula being a direct extension of outer and/or inner walls. See tabula (Fig. 512; S2a, p. 1692, fig. 66D–E) [**Ar**].

septate filling structure (or **skeleton**). Composed of vertical, bladelike elements that are commonly radially arranged [**Sp, In**].

septate-reticulate filling structure (or **skeleton**). Composed of a combination of two types of filling structures: septate and reticulate. Such combinations of these and other filling structures are rare [**Sp, In**].

septum (pl., **septa**). Radial-longitudinal, first-order intervallar structure in form of planar partition, ontogenetically fully developed (apart from porosity) from its inception. See aporose septum, completely porous septum, sparsely porous septum, uniporous septum (S2a, p. 1692); syn., pariety [**Ar**].

shaft. Radial-transverse element linking one nesaster of outer wall with corresponding nesaster of inner wall; of uniform diameter and circular cross section (Fig. 658,*1a*) [**Ra**].

sheath (ls). Imperforate, calcified, commonly discontinuous, thin outer wall that bounds the stem fragments of the order Amphiporida and the family Stachyoditidae; has contact with and is supported by outer extensions of the skeletal network (pillars with lateral processes, amalgamate, or pachystele-like structural elements) (Fig. 349.2; Fig. 476*a–b*); syn., peripheral membrane [**Ps**].

sheetlike cup. Cup in form of vertical or horizontal plate. See cup (Fig. 615,*1a–b;* S2a, p. 1690) [**Ar**].

sieve plate. Screenlike or perforated plate in an osculum or across a spongocoel below the level of the osculum [**Sp, In**].

simple tumulus. Tumulus with a single, typically downwardly oriented pore. See tumulus (Fig. 506a–506b; S2a, p. 1692, fig. 30L, 47B) [**Ar**].

single-chambered cup. Cup incorporating one chamber only. See cup (Fig. 491d; S2a, p. 1690, fig. 2B1, 52A) [**Ar**].

single exopore. A single, tubular, unbranched opening (S2b, fig. 8) [**Sp, In**].

siphon. Spongocoel [**Sp, In**].

siphonate. Having a distinct spongocoel [**Sp, In**].

siphonate exhalant system. Condition in sphinctozoan sponges where skeletal chambers communicate through an axial tube (S2b, p. 1513) [**Sp, In**].

skeletal ontogeny. Development of the primary skeleton through the lifetime of the organism, from juvenile to adult [**Ar**].

skeletal structure (sk). Frameworks (laminae, pillars, and other elements) of the basal calcareous skeleton dominated by gridlike combinations of structural elements that characterize the main orders of the class Stromatoporoidea: (a) domes (cyst plates) and pillars in order Labechiida; (b) floors (laminae) and pillars in order Clathrodictyida and order Stromatoporellida; (c) beams (colliculi) and pillars in order Actinostromatida; and (d) an amalgamate structure composed of floors (pachystromes) and walls (pachysteles) in orders Stromatoporida and Syringostromida (**Ps**).

skeletal tracts. A column of aligned megascleres (Th, p. 34, fig. 201) [**Ms, Ch**].

skeleton. All hard parts secreted by the living organism in support and protection of itself above the substrate, thus avoiding mantling sediment and/or overgrowth by competitors (Th, p. 34); syn., coenosteum, colony, coenosarcal tissue, coenochyme. Given the connotations these five synonyns have with colonial organisms (in particular cnidarians), their continued use in sponge terminology should not be maintained [**Ps, Ms, Ch, Ex**].

slitlike pore. Pore in form of a transversely oriented slit. See pore (Fig. 498e; Fig. 499j; Fig. 512c; S2a, p. 1691, fig. 21M, 40G, J) [**Ar**].

slitlike porosity. Pores elongate-elliptical in outline. See porosity (Fig. 498e; Fig. 499j; Fig. 512c; S2a, p. 1691, fig. 40J) [**Ar**].

spacing phase (ts). A unit distinguished by changes in the spacing of laminae, cysts, or pachystromes (Fig. 317.4; Fig. 329.5) [**Ps**].

sparsely porous septum. Septal pores distributed frequently and uniformly over part of septum only or irregularly or infrequently distributed. See septum (Fig. 496d–496e; S2a, p. 1692, fig. 21G) [**Ar**].

speck (mi). An equidimensional opaque body in skeletal material of a stromatoporoid a few micrometers across that is the smallest (microgranule size) unit of microstructure seen in the light microscope (Fig. 335.2) [**Ps**].

spheroidal chamber shape. Chambers that are globose or essentially spherical [**Sp**].

spherulite. Skeletal microstructure composed of spherulites that are composed of crystals radiating from a common center (Th, p. 40, fig. 215; S2b, fig. 12) [**Sp, In, Ch**].

spherulitic microstructure. Globular (centric or excentric) arrangement of crystal fibers or skeletal elements radiating from a common center (e.g., *Astrosclera*) (Th, p. 40, fig. 215); syn., spheroidal microstructure [**Ms, Ch, Sp, In, Ex**].

Sphinctozoa (Steinmann, 1882; =Thalamida de Laubenfels, 1955), or **sphinctozoans**. General terms applied to chambered sponges. Because of polyphyletic nature of chambered sponges, the terminology is not taxonomically valid (demosponges, calcareans) [**Sp**].

spicular. Of or pertaining to spicules [**Ms, Ch, Sp, In, Ex**].

spiculate. Consisting of spicules, or spicule-bearing [**Ms, Ch, Sp, In, Ex**].

spiculate skeleton. Framework of arranged spicules [**Ms, Ch, Ex**].

spicule. A discrete, mineralized skeletal element, generally composed of silica or calcium carbonate, and secreted by sclerocytes. Spicules typically formed as more or less elongated rays with pointed, rounded, or more elaborated terminations, arranged along one or more axes (Th, p. 34, fig. 195) [**Ms, Ch, Sp, In, Ex**].

spine. Skeletal structure comprising a narrow, elongate, and typically tapering process projecting freely from any skeletal element; a spine is distinguished from a bract by the relatively small, circular-to-subcircular attachment area and a needlelike-to-thornlike shape (acicular to flattened) of the former. For inner walls, spines are considered as ornamental elements of simple walls; whereas bracts, together with scales, are a family diagnostic character. The distinction is difficult to appreciate, as there are no distinct morphological boundaries in the continuum from spines to cupped bracts (e.g., in the *Anapyctocyathus-Erugatocyathus* group, in which the whole continuum of structures may be seen). See bract, scale (S2a, p. 1692, fig. 67K) [**Ar**].

spinose rod (ls). A slender, upwardly tapering rod, usually with spar-replaced center and resembling a spine (Fig. 487) [**Pu**].

spongin. Skeletal substance in Demospongiae consisting of collagen microfibrils of approximately 10 nm diameter (Th, p. 34, fig. 160, 170, 176, 185, 200) [**Ms, Ch, Ex**].

spongiose wall. Massive inner wall consisting of elaborately waved, communicating canals (Fig. 556,*1a–b;* Fig. 556,*2;* S2a, p. 1692, fig. 39E–F) [**Ar**].

spongocoel. Large central canal or canals for exhalant (or excurrent) water. If only a single spongocoel is present, it is usually axially situated. If more spongocoels are present, they may be grouped in axial bundles or distributed throughout the sponge body [**Sp, In, Ex**].

spongocyte. Cell secreting spongin fibers (Th, p. 14, fig. 49, 71, *spo* = spongin) [**Ex**].

spore-like filling structure or skeleton. Composed of hollow sporelike structures that may be attached to one another or arranged in a network [**Sp, In**].

S-shaped canal. Canal with S-shaped aspect in longitudinal section. See canal (Fig. 502c; S2a, p. 1689, fig. 28K–L, 59L) [**Ar**].

stem (sk). Term applied to fragmentary parts of branches of dendroid-shaped skeletons of the order Amphiporida [**Ps**].

stipule. Leaflike appendage arising from canal-bract junction in a wall with a longitudinal, V-shaped appearance, or subdividing subspherical chambers in outer walls of some Ethmophylloidea (Fig. 503c; S2a, p. 1692, fig. 32F, 34C–F, 36C–E, 49C) [**Ar**].

stirrup pore or canal. Pore or canal located at the junction of a wall and a septum or tabula. Typically, a stirrup pore or canal is accompanied by a semicircular indentation in the septal or tabular margin. See pore, canal (Fig. 496c; S2a, p. 1691, fig. 17A) [**Ar**].

stratiform. Sheetlike growth form consisting of single layer of chambers. Also, arrangement of tubelike chambers around one or more spongocoels (S2b, p. 1512, 1515, fig. 4) [**Sp, In**].

stratocyst (ts). A term introduced by Bogoyavlenskaya (1984, p. 11) for long and low cyst plates resembling microlaminae. Not recommended for continued use, as it duplicates more commonly accepted usages of “long and low cyst plates,” and “long-low cyst plates,” especially in the Labechiida [**Ps**].

streptaster. Aster in which the rays proceed from an axis that is usually spiral (Th) [**Ex**].

striae (pl.). Transverse platelike elements of inner wall (Fig. 664,*2c*) [**Cr**].

striated (mi). Specks concentrated in short, rodlike bodies; a microstructure apparently unique to *Stachyodes* (Fig. 474*d–e*) [**Ps**].

stromatoporoid architecture. Skeletal structure with mattresslike chambers containing pillars, bearing superficial resemblance to some stromatoporoids. See architecture (Fig. 516c; Fig. 656,*1a–b;* Fig. 657; S2a, p. 1689, fig. 2E) [**Ar**].

strongyle. An isodiametric, diactinal megasclere with rounded ends (Th, p. 46, fig. 280) [**Ms, Ch, Ex**].

style. Monaxon spicule with one end pointed, the other (head or base) blunt; normally a megasclere (Th, p. 46, fig. 282) [**Ms, Ch, Ex**].

subcolumn (ls). A structure of subcircular cross section that consists of micropillars and microcolliculi arranged in an acosmoreticular or clinoreticular pattern; in syringostromatids, the term pillar has been used an an alternative [**Ps**].

subdivided canal. Canal bearing processes projecting inward from its wall. See canal (Fig. 517e–517f; S2a, p. 1689, fig. 70A–E) [**Ar**].

subdivided pore. Pore with more or less well-developed subdivision, ranging from radially directed spines to complete microporous sheath. See pore, compound wall (Fig. 516d; Fig. 517a; S2a, p. 1691, fig. 67G–H, 69A) [**Ar**].

subspherical growth morphology. Having a subspherically shaped calcareous skeleton [**Ms, Ch, Ex**].

successive phase (ts). A unit of growth distinguished and bounded by longitudinal changes in structure within the skeleton; the phase may be terminal, basal, or spacing (Fig. 330.1) [**Ps**].

superposed astrorhizae. Successive generations of astrorhizae that have formed along the same radial axis (Fig. 323.4; Fig. 328.2); syn., stacked astrorhizae, astrorhizal cylinders, astrorhizal columns, astrorhizal corridors, astrocolumns [**Ps, Ms**].

synapticula (pl., **synapticulae**). Second-order intervallar structure comprising narrow tangential rod linking adjacent, longitudinally oriented first-order intervallar structures (Fig. 560a; S2a, p. 1692, fig. 32A) [**Ar**].

syrinx (pl., **syringes**). First-order intervallar structure comprising porous radial tube of hexagonal or tetragonal cross section (Fig. 510.2a–d; S2a, p. 1692, fig. 72A–D) [**Ar**].

tabellar wall. Wall consisting of longitudinal ribs linked by flattened transverse lintels (S2a, p. 1692, fig. 70H–I) [**Ar**].

tabula (pl., **tabulae**). Transverse porous partition linking both walls of a two-walled cup. See membrane tabula, pectinate tabula, plate tabula, segmented tabula (Fig. 498; Fig. 511–512; S2a, p. 1692) [**Ar**]; *or* flat to gently curved plates that partition astrorhizal canals (Fig. 325.1; Fig. 329.1) and localized areas of interlaminar space; they commonly develop tangentially and may be difficult to distinguish from dissepiments. Also, irregular, complete to incomplete plates within the axial canal of the order Amphiporida and other dendroid to columnar growth forms (*Stachyodes, Idiostroma*) (Fig. 325.1; Fig. 329.1; Fig. 349.2) [**Ps**]; *or* a discrete calcareous plate, generally flat or slightly curved parallel to the growth surface, which, as a floor, partitions the basal part of the skeletal cavity; this plate may or may not be perforated by a foramen that may or may not be subsequently infilled and is commonly thinner than the tubule walls. These distinctive features, which are present in both Mesozoic stromatoporoids and chaetetids, do not appear to be homologous with tabulae of archaeocyaths or Paleozoic stromatoporoids [**Ms, Ch, Ex**].

tabular. Platelike [**Sp, In**].

tabular wall. Wall that is an outward or inward extension of a tabula or chamber-forming segment (Fig. 498c; S2a, p. 1692, fig. 54C) [**Ar**].

tabulate osculum. Osculum in stromatoporoids that has been repeatedly partitioned by secondarily deposited tabulae; syn., zooidal tube, superposed galleries, zooidal tubule, major autotube [**Ms**].

tabulum. Platelike elements that divide skeletal cavity. Relationship between the term tabulum and the tabulae of other hypercalcified groups remains unknown [**Sp, In**].

taenia (pl., **taeniae**). First-order intervallar structure; nonplanar, often dichotomous, radial-longitudinal partitions in intervallum; may be coarsely or finely porous. See porosity (Fig. 508; S2a, p. 1692) [**Ar**].

terminal phase (ts). Consists of the last units of skeletal growth that preserve a change in structure [**Ps**].

tersioid buttress. Tubular buttress consisting of concentric envelope and infilling platy elements. See buttress (Fig. 522; S2a, p. 1689, fig. 42B) [**Ar**].

tetractine. A spicule with four rays (Th, p. 26, fig. 144) [**Ex**].

Thalamida (DE LAUBENFELS, 1955). Former grouping of sphinctozoans [**Sp**].

thalamid architecture. Skeletal structure with subspherical chambers. See architecture (Fig. 491c; S2a, p. 1689, fig. 2B1–B2) [**Ar**].

thalamidarium. Single layer of chambers in a stratiform or sheetlike sphinctozoan sponge in which chambers are convex toward the growing edge [**Sp**].

toroidal. Growth form having an open or doughnut-shaped coil [**Sp, In**].

trabeculae (pl.). Filling structure composed of regular rodlike or beamlike pillars supporting roof over the bottom of chambers in sphinctozoans; in living hexactinellid sponges, the same term is used for divided and anastomosed, protoplasmic filaments that form a network of water-filled interspaces (S2b, fig. 11) [**Sp, In**].

trabecular filling structure of skeleton. Composed of parallel or slightly diverging, rod- or beamlike elements supporting chamber walls [**Sp, In**].

trabecular microstructure. Where the crystal fibers are symmetrically arranged around the growth axis and axial fibers are absent (a cnidarian condition that is unknown in sponges).

transverse fold. In a two-walled cup, fold of one wall or mutual folds of two walls to impart a succession of more or less regular, longitudinal annulations of cup (Fig. 494c; S2a, p. 1692, fig. 58A); syn., orbicyathoid [**Ar**].

triactine. A spicule with three rays (Th, p. 26, fig. 148, 150–153) [**Ms, Ch, Ex**].

tubercule. Small, slightly raised calcareous projections, like tiny spines, that occur at the junction between two or more tubules at the top of the basal calcareous skeleton, where the thin soft tissue is presumed to have been in contact with the skeleton [**Ch**].

tubiform. Polyplatyform with tubelike chambers, laterally or vertically adjacent, forming platelike structures (S2b, p. 1513) [**Sp, In**].

tubular. Arrangement of skeletal elements with appearance of closely packed tubes [**Ms, Ch**]; *or* endocameral filling structure usually consisting of branched tubes between the openings of exowalls and endowalls (S2b, fig. 11) [**Sp, In**].

tubular chamber shape. Chambers that are linear and pipelike [**Sp**].

tubular filling structure of skeleton. Composed of small, tubelike elements that may be curved, irregularly oriented, and often bifurcated [**Sp, In**].

tubulate (mi). Clear, vermiform areas extending irregularly through the speckled skeletal material; best shown in *Clathrocoilona* (Fig. 337.2) [**Ps**].

tubule. The tubes that constitute the basal calcareous skeleton of chaetetid hypercalcified demosponges; exhibiting meandroid- to irregularly polygonal-shaped outlines in tangential section; syn., calicle, pseudocalyx (pl., pseudocalices) [**Ch**].

tubulus (pl., **tubuli**). Complex structure of secondary skeleton consisting of tubular structure in central cavity (S2a, p. 1692, fig. 66G) [**Ar**].

tumulus (pl., **tumuli**). Outer wall structure in shape of a discrete, hollow subspherical dome covering an individual wall opening. See multiperforate tumulus, simple tumulus (Fig. 506; S2a, p. 1692) [**Ar**].

tylostyle. A style with a tyle (globular swelling) at the base (Th, p. 48, fig. 493) [**Ms, Ch, Ex**].

uniporous septum. Septum with single longitudinal row of pores of diameter subequal to intervallum width; pores separated by bars or rods. See septum, bar, rod (Fig. 496c; S2a, p. 1692, fig. 13B–C) [**Ar**].

unpaired actine. The ray of a triactine or of a triradiate basal system of a tetractine, lying in the plane of bilateral symmetry of sagittal spicules (not the basal ray) (Th) [**Ex**].

uviform. Sponges with chambers clustered to form irregular aggregates (S2b, p. 1512, fig. 4) [**Sp, In**].

vacuolate (mi). Scattered subspherical voids larger than cellules (about 100 µm) within compact laminae and pillars, as in *Trupetostroma* (Fig. 340.3; Fig. 481*a*) [**Ps**].

vermiculate. Irregularly sinuous [**Sp, In**].

verticillately spined style. Acanthostyle with spines arranged in regular rows; the term is used for the spicules of Astroscleridae and Agelasidae (Vacelet, 2002a) [**Ex**].

vesicle. Simple, aporose, bubble-like structure of secondary skeleton (Fig. 521.3; S2a, p. 1692, fig. 4, 59L–M) [**Ar**].

vesicle or **vesicular skeleton**. Filling structure of bubblelike imperforate diaphragms, usually within chambers, but rarely in a spongocoel, or in exhalant and inhalant canals (S2b, fig. 11) [**Sp, In**].

vesicular filling structure (or **skeleton**). Composed of small, blister- or bubblelike elements that are upwardly or laterally convex [**Sp, In**].

villi. An obsolete term used by Galloway (1957) that is incorporated in the definition of denticle [**Ps**].

V-shaped canal. Canal with V-shaped aspect in longitudinal section; may be upright or inverted. See canal (Fig. 502d; S2a, p. 1689, fig. 49C–D); syn., geniculate [**Ar**].

wall. The calcareous element, or elements, that define(s) the basal skeleton of the individual in solitary hypercalcified demosponges, or the constituent modules of modular hypercalcified demosponges. In chaetetids, the microstructure is commonly fascicular, but may be either water jet, penicillate, or spherulitic when unaltered [**Ch**]; *or* see altoid wall, anthoid wall, basic wall, cambroid wall, concentrically porous wall, clathrate wall, compound wall, inner wall, outer wall, plicate wall, pseudoclathrate wall, rudimentary wall, spongiose wall, tabellar wall, tabular wall [**Ar**].

water-jet microstructure. Where crystal fibers progressively fan outward around the growth axis (e.g., *Merlia*). This microstructure is a subdivision of the broader clinogonal and fascicular fibrous microstructural types. See fascicular fibrous microstructure, clinogonal microstructure (Th) [**Ch, Ex**].

zygosis. Mode of junction between siliceous desmas or calcareous tetractines by the interlocking of their terminal or lateral expansions. A secondary cement may be present (Th) [**Ex**].