LIVING HYPERCALCIFIED SPONGES

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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

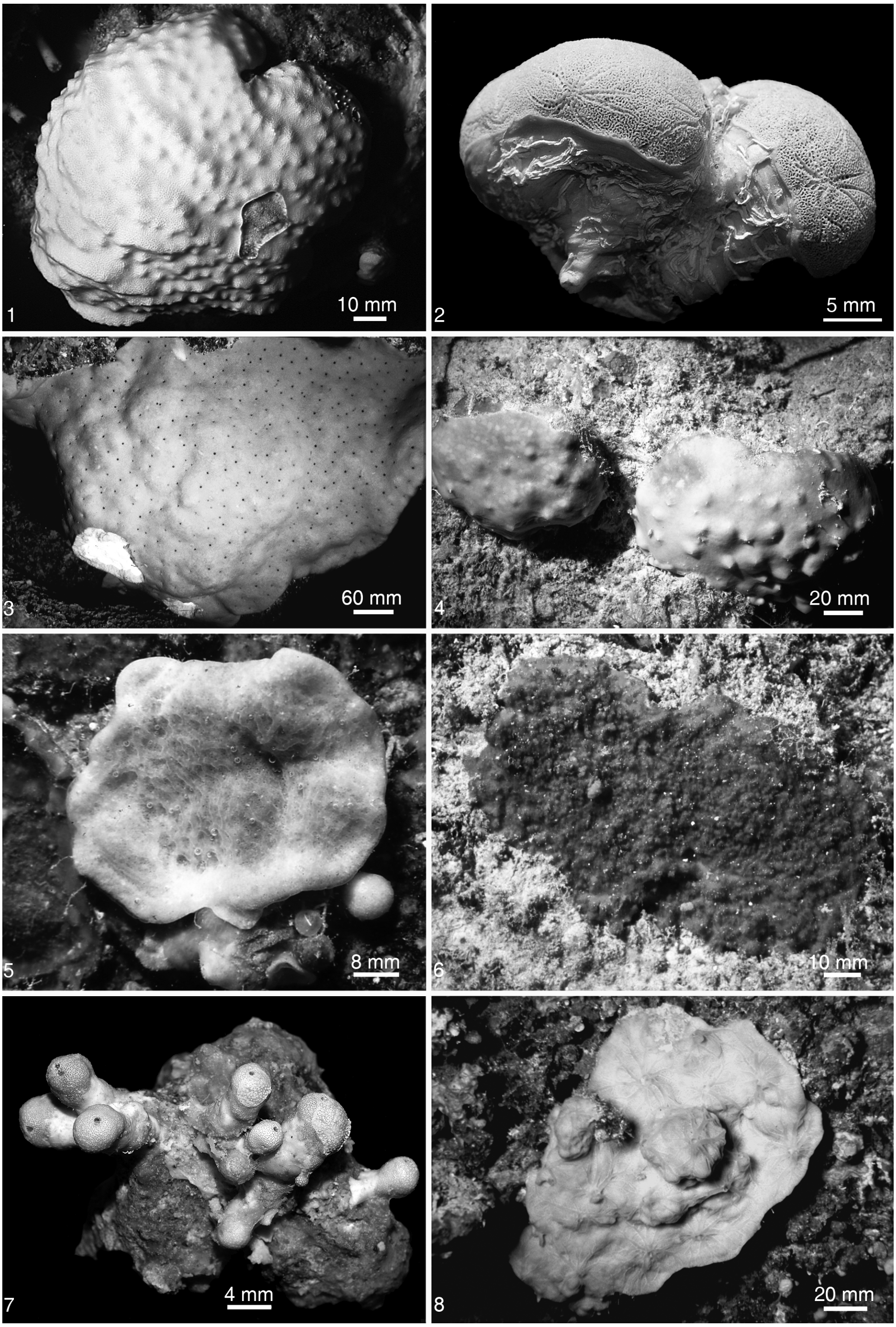

FIG. 1. *(For explanation, see facing page).*

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

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).

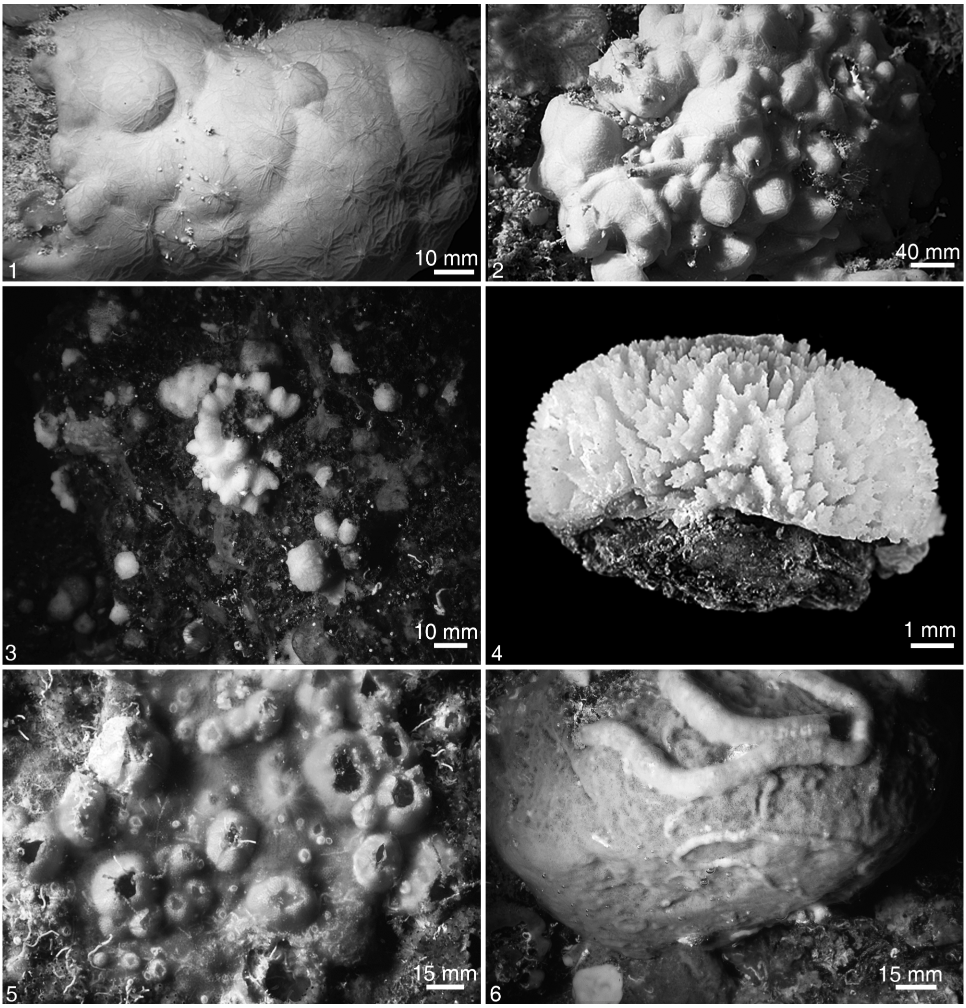

FIG. 2. Hypercalcified demosponges *(Ceratoporella, Stromatospongia, and Merlia)* and a calcarean *(Petrobiona); 1, Ceratoporella nicholsoni* (HICKSON, 1911); *in situ,* 25 m, reef cave, northern coast of Jamaica (Vacelet, Willenz, & Hartman, 2010); *2, Stromatospongia norae* HARTMAN, 1969; *in situ,* 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

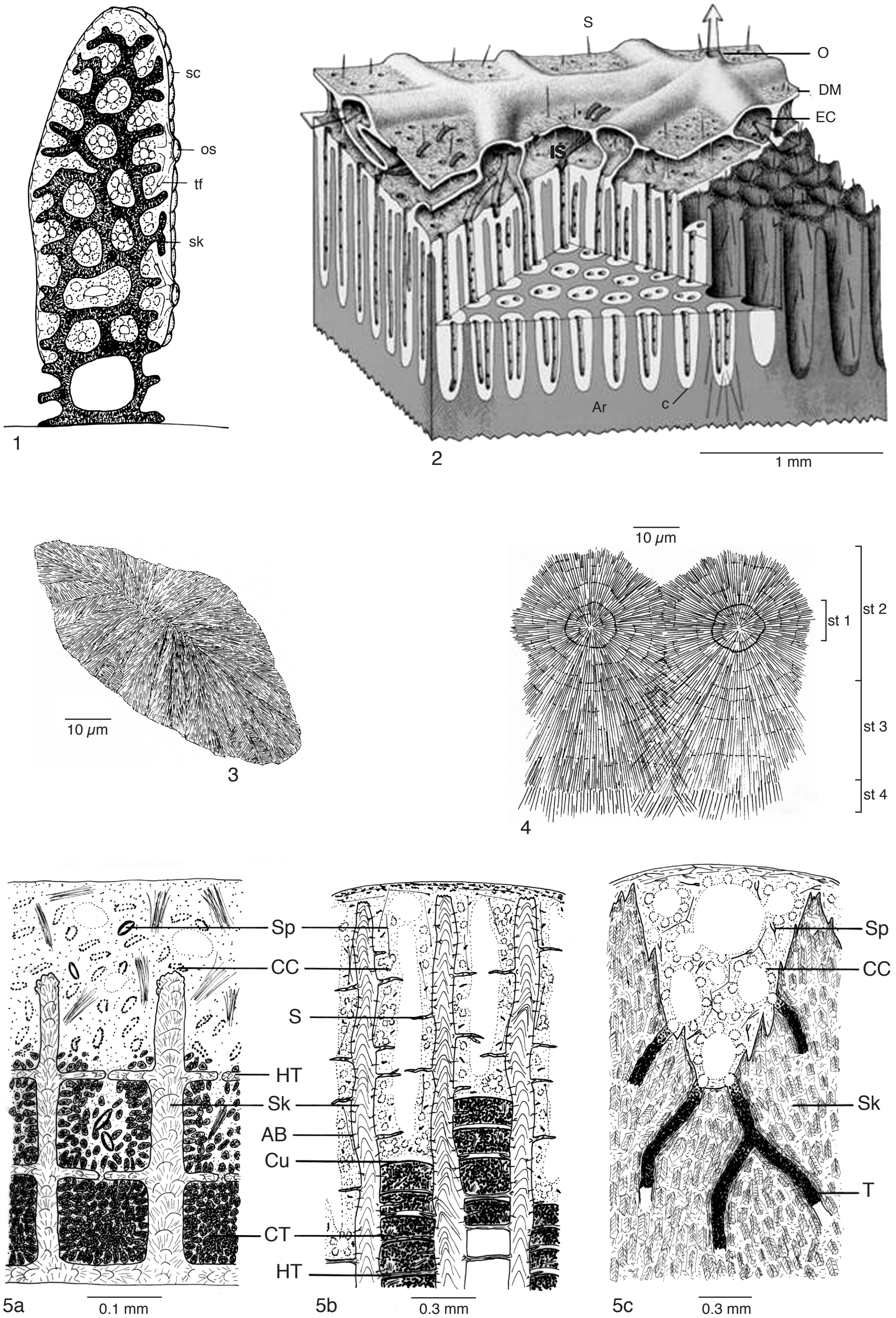

FIG. 3. *(For explanation, see facing page).*

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).

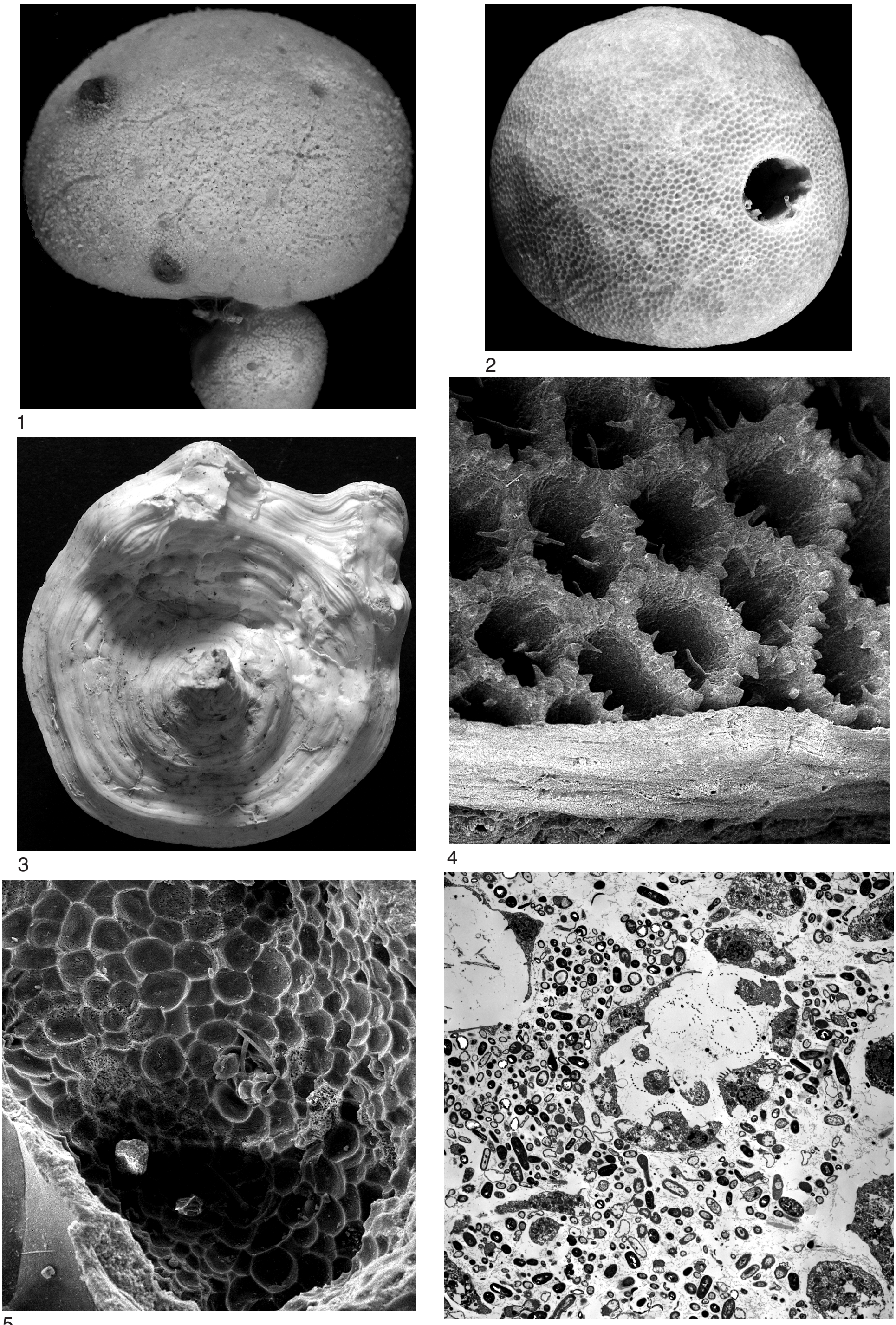

FIG. 4. *(For explanation, see facing page).*

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

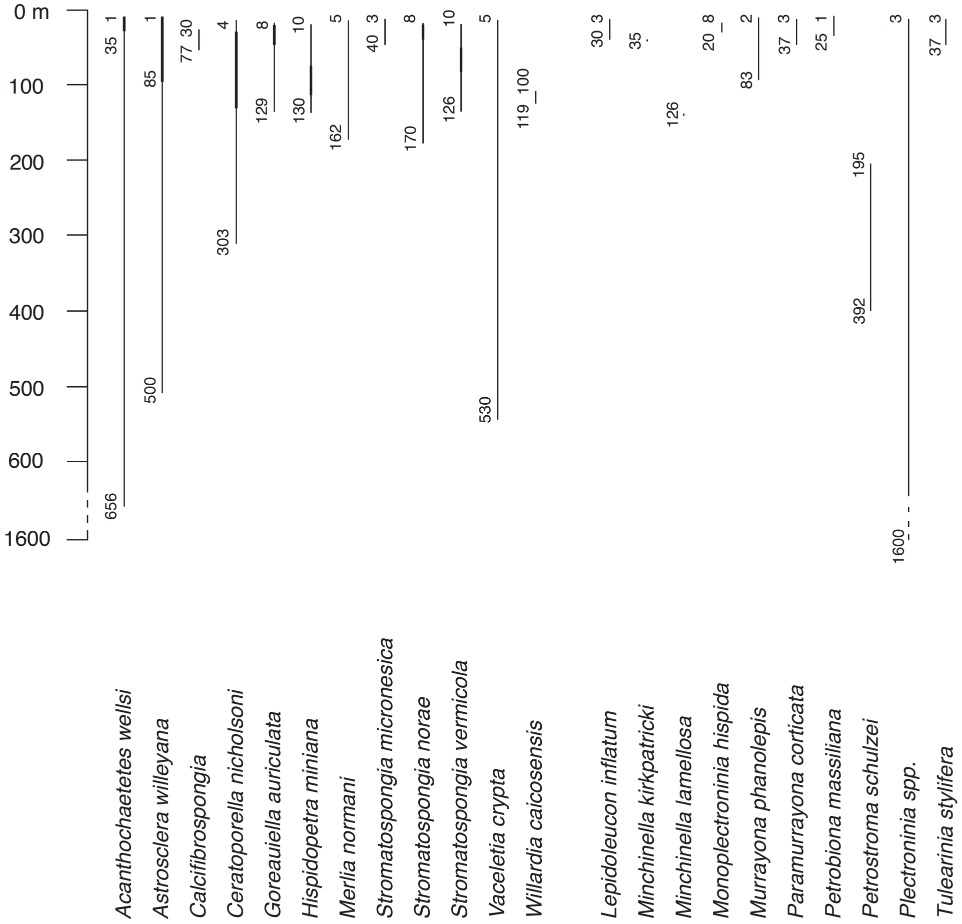

FIG. 5. Depth chart. Vertical distribution of extant hypercalcified taxa of Demospongiae and Calcarea, listed to the left and right sides, respectively. Optimum depth, where known, indicated by thickened bars (adapted from Vacelet, 1988, with addition of some species and unpublished data, Vacelet, 1998).

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.

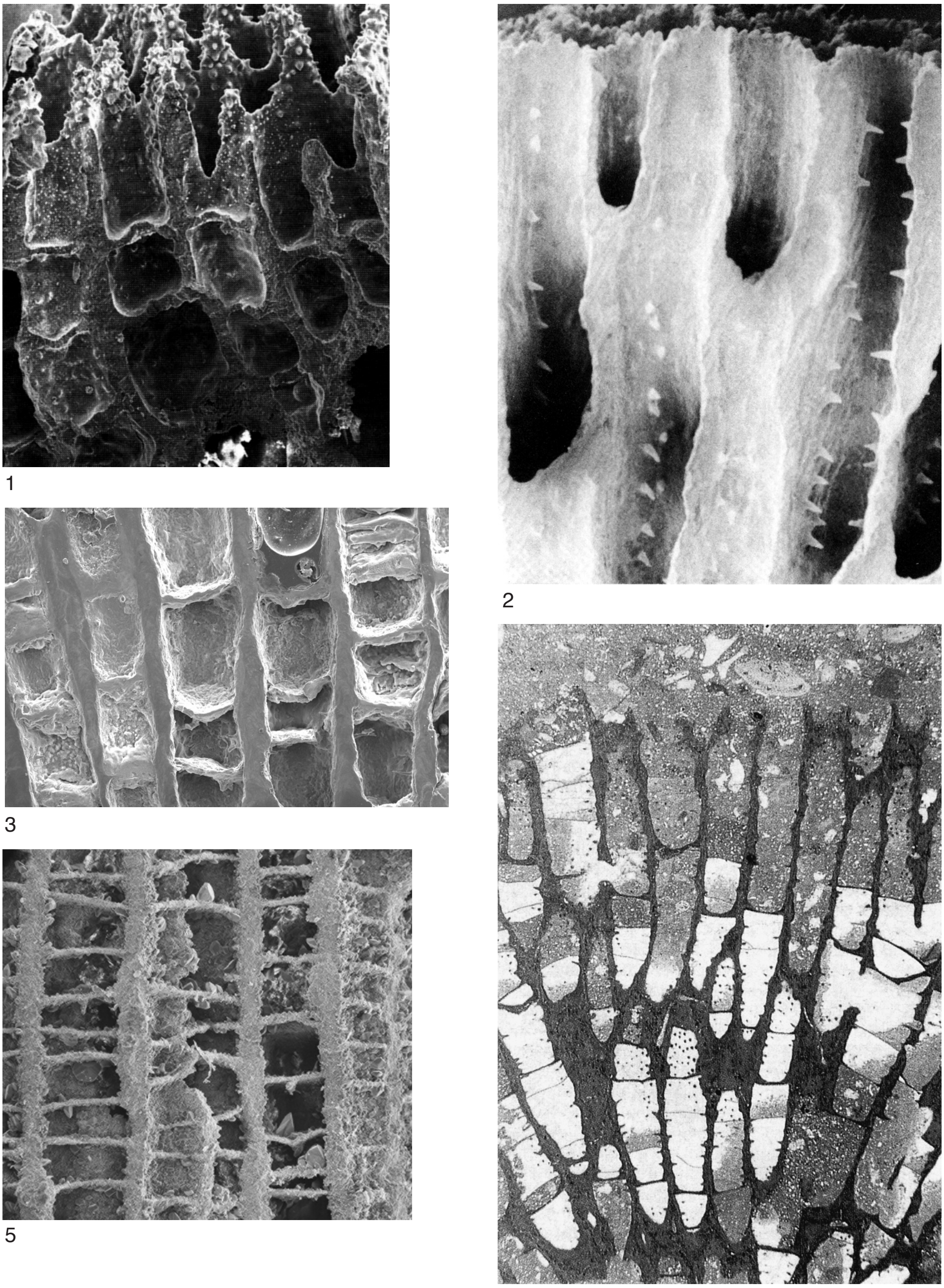
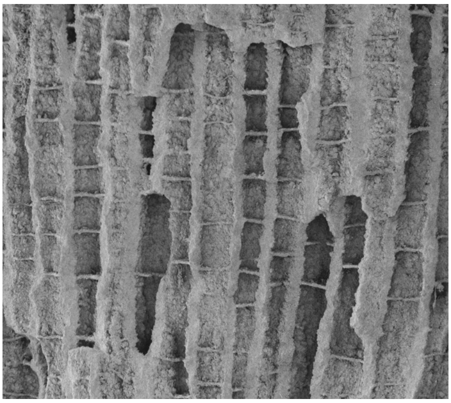


FIG. 6. Rigid aspicular skeletons in chaetetid sponges; *1,* SEM of a longitudinal fracture of *Merlia lipoclavidisca*, an extant form, from La Catedral cave at a water depth of 12 m, Balearic Islands, Mediterranean Sea, ×70 (adapted from Vacelet & Uriz, 1991, p. 172, fig. 2a, with kind permission of 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



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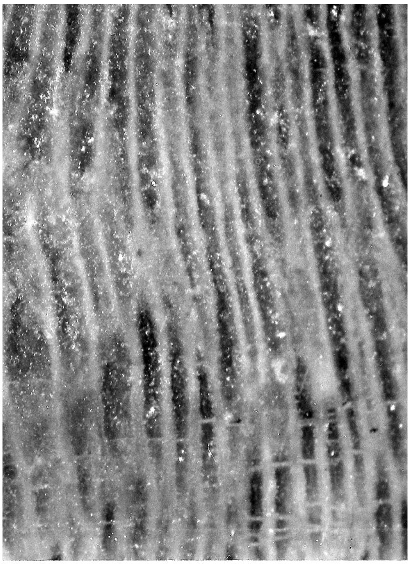

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Fig. 7. Rigid aspicular skeletons in chaetetid sponges (continued); *1,* SEM of a longitudinal fracture of *Chaetetes (Chaetetes) radians*, Carboniferous, Pennsylvanian (probably Moscovian), Moscow Basin, Russia, ×15 (West, 2011a); *2,* longitudinal 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).

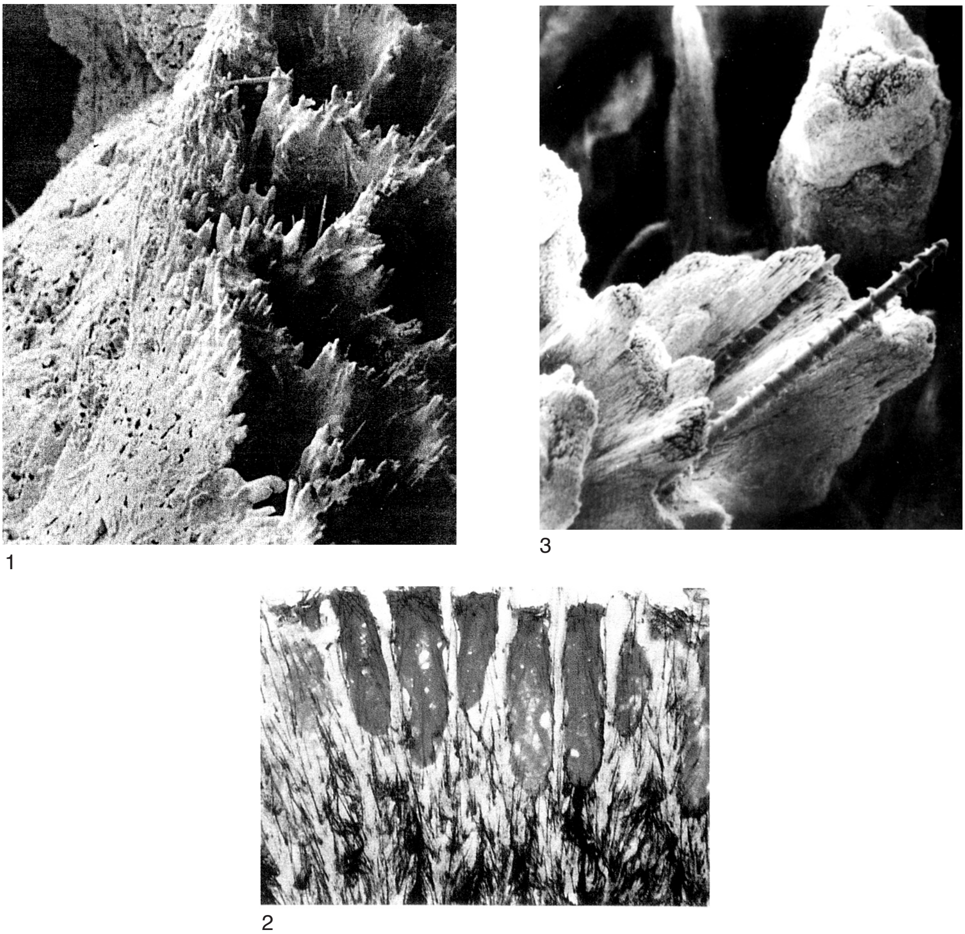

FIG. 8. Rigid spicular skeletons in chaetetid sponges; *1,* SEM of an oblique view of the upper surface of *Ceratoporella nicholsoni,* an extant form, locality not given, probably from the Caribbean, ×70 (adapted from Hartman & Goreau, 1972, fig. 8; courtesy of *Transactions of the Connecticut Academy 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

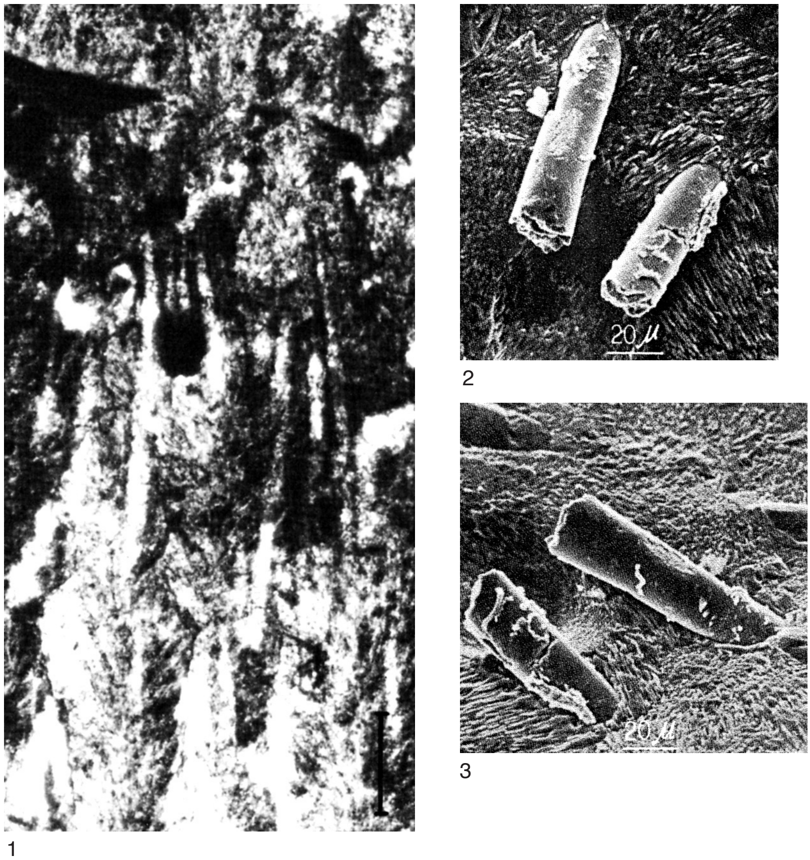

FIG. 9. Rigid spicular skeletons in chaetetid sponges (continued); *1,* longitudinal thin section of *Calcisuberites stromatoporoides,* showing spicules incorporated into high Mg calcite skeleton, Upper Cretaceous (Turonian–Coniacian), near Oberwossen, Bavaria, ×65 (adapted from Reitner, 1992, pl. 23,*3;* 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),

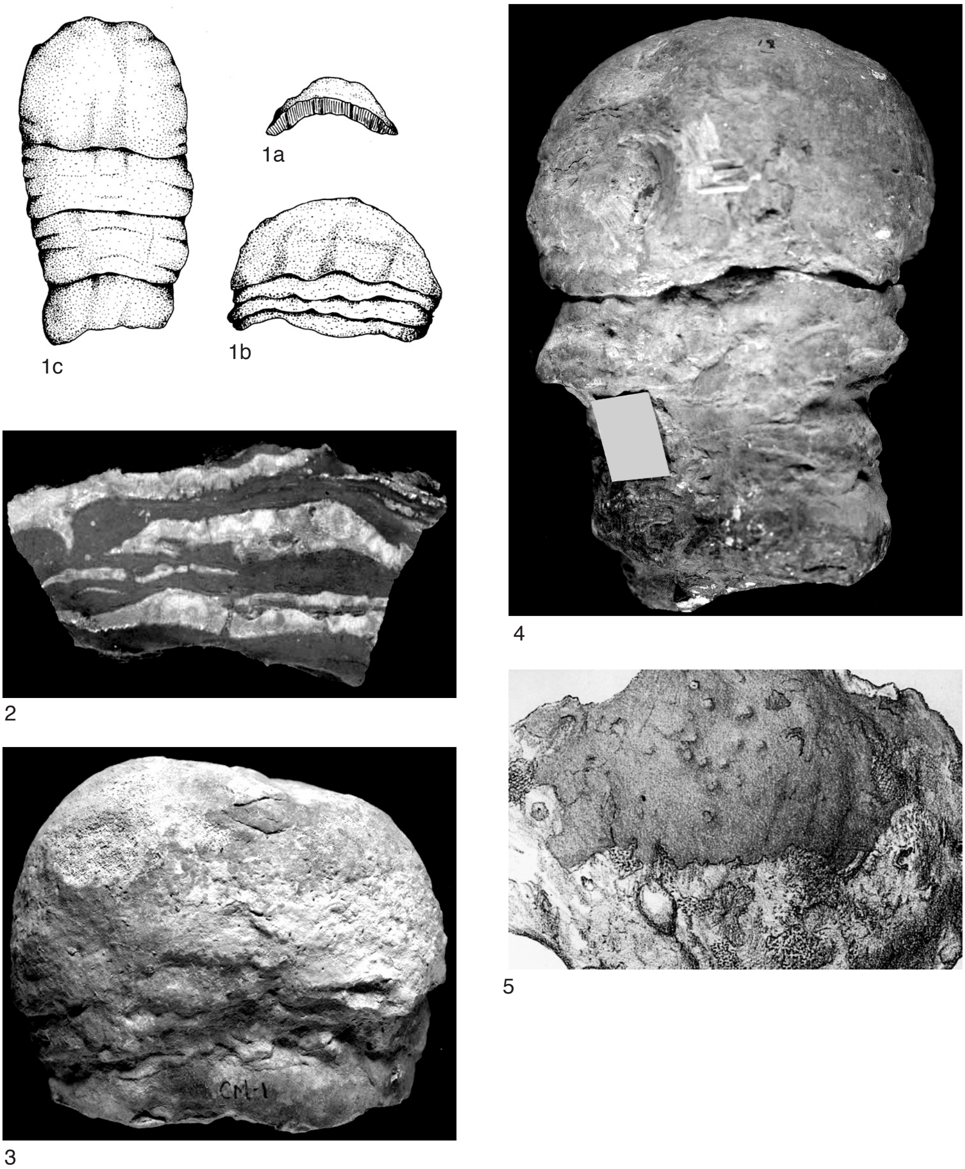

Fig. 10. Basal calcareous skeleton of chaetetid sponges; *1a–c,* basic shapes of chaetetid skeletons; *a,* laminar, *b,* ragged, low domical, *c,* columnar (West & Clark, 1984, p. 339, fig. 3; courtesy of Paleontological Research Institution, Ithaca, New York); *2,* laminar (multiserial, single layer) 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).

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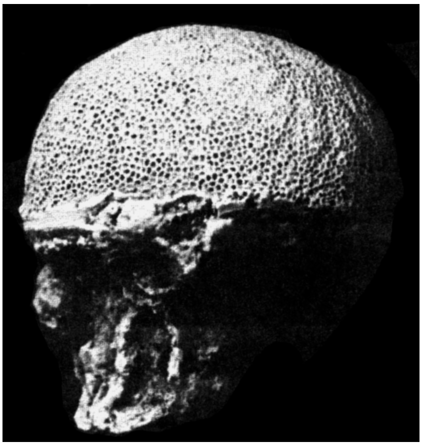

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FIG. 11. Basal calcareous skeleton of chaetetid sponges (continued); *1,* extant *Acanthochaetetes* sp., a small domical (multiserial, multilayered) pedunculate specimen, collected live in October 2005 off the Komesu coast, southern Okinawa, at a water 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).

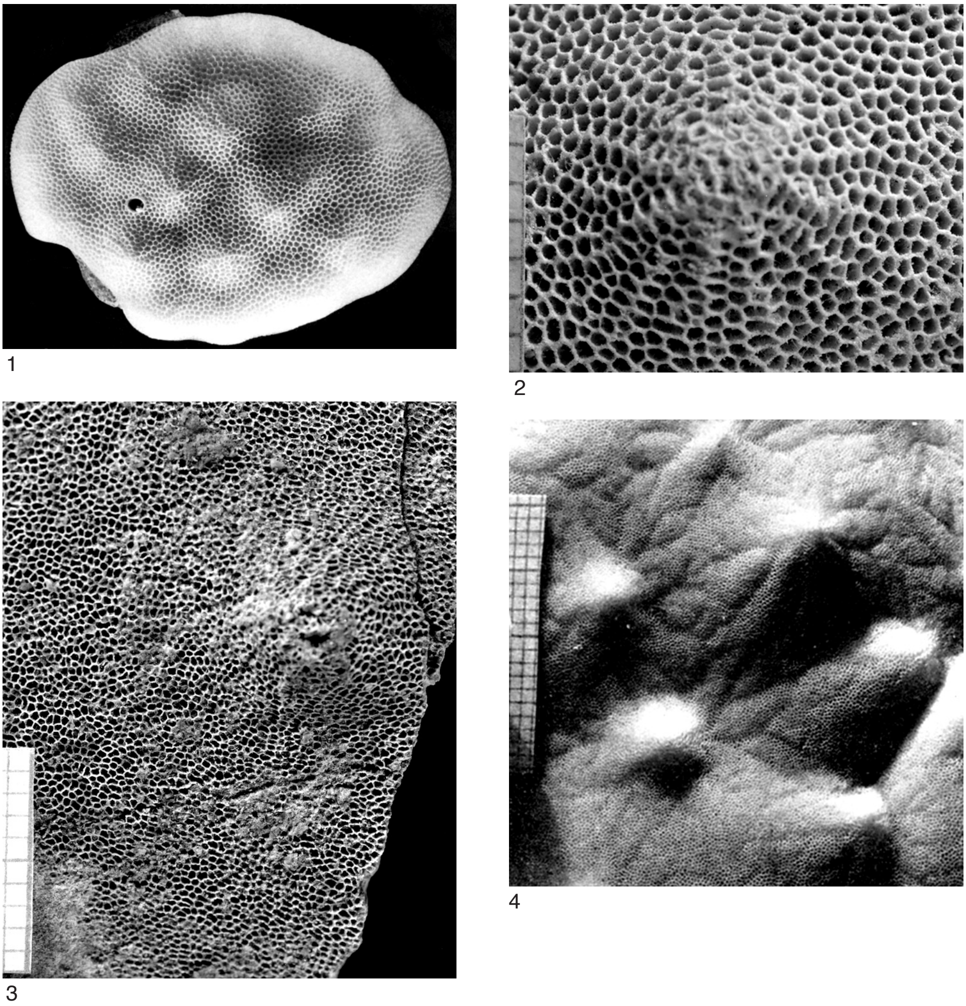


FIG. 12. External features of chaetetid skeletons: astrorhizae and mamelons; *1, Acanthochaetetes wellsi,* with mamelons and astrorhizae from underwater cave, Anae Island, Guam at 7.5 to 9 m, paratype, YPM No. 9078, ×1.45 (adapted from Hartman & Goreau, 1975, fig. 1; courtesy of Yale Peabody Museum of 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).

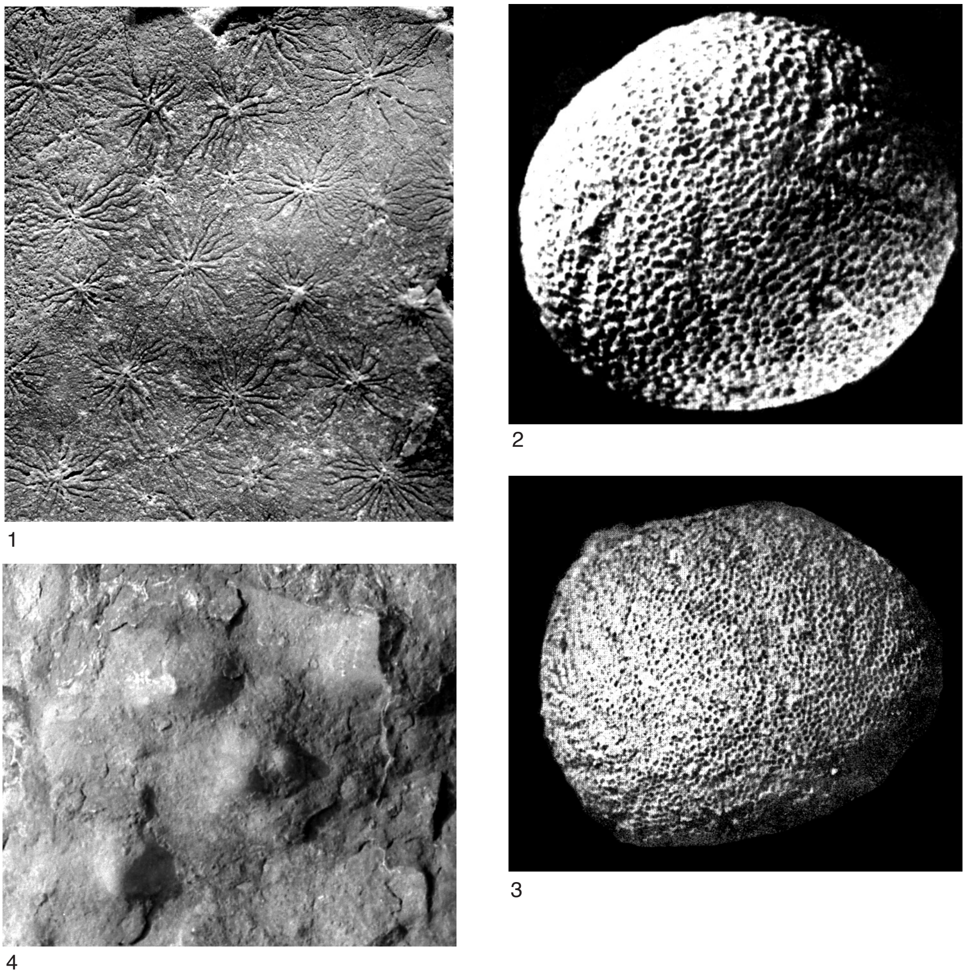


Fig. 13. External features of chaetetid skeletons: astrorhizae and mamelons (continued); *1,* fossil chaetetid with astrorhizae, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×2 (West, 2011a); *2, Cassianochaetetes* sp., with astrorhizae, Triassic, 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).

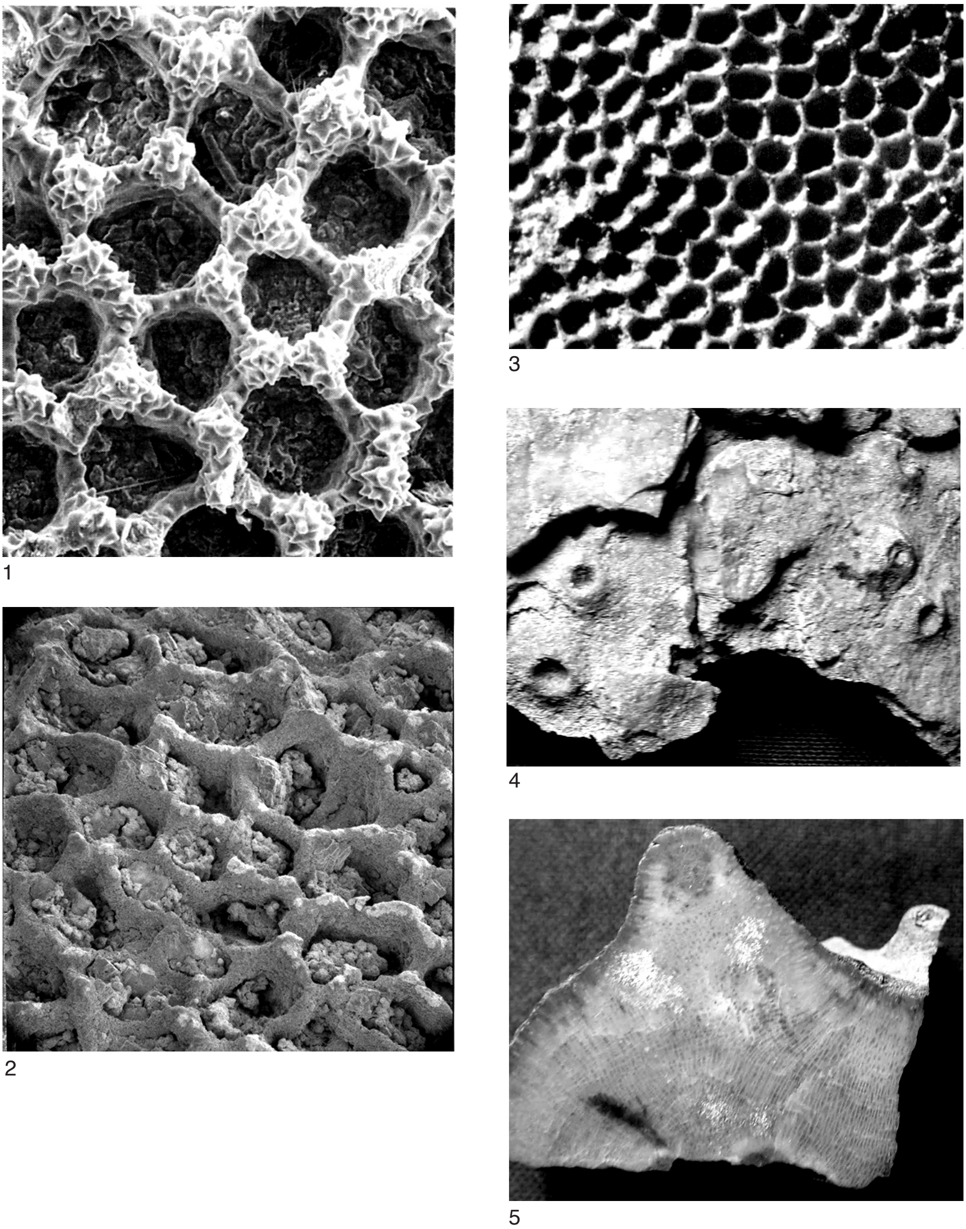


FIG. 14. *(For explanation, see facing page).*

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).

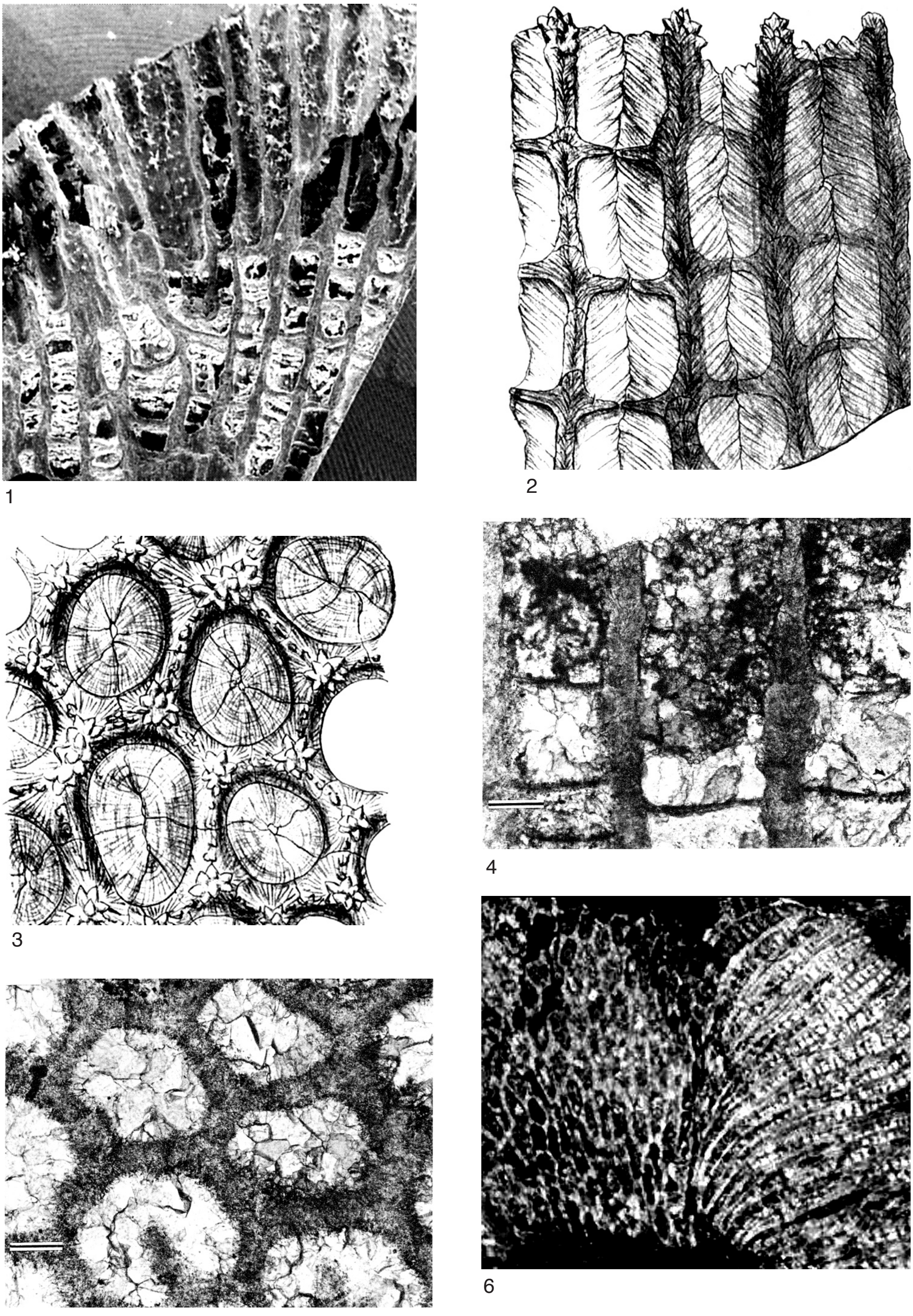


FIG. 15. *(For explanation, see facing page).*

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

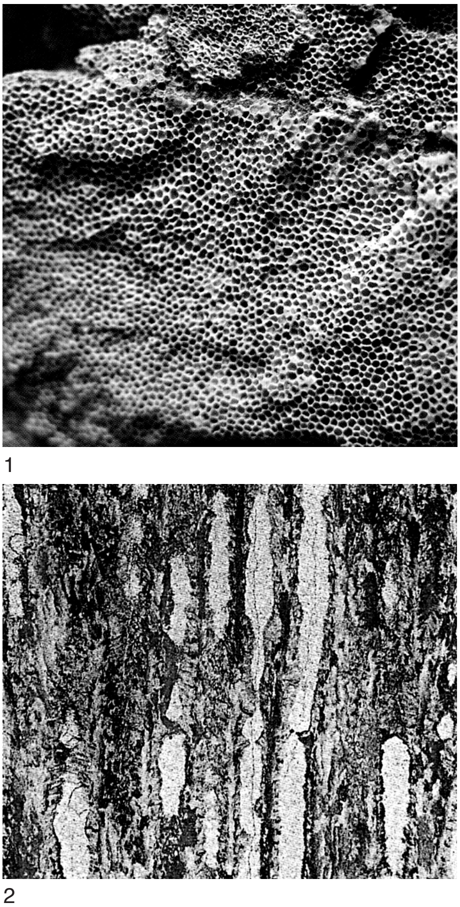


Fig. 16. Internal features of chaetetid skeletons: walls and tubules (continued); *1,* surface expression of tubules in a fossil chaetetid, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Bourbon County, Kansas, ×5 (adapted from Brosius, 2006, p. 42, fig. 58B; courtesy 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).

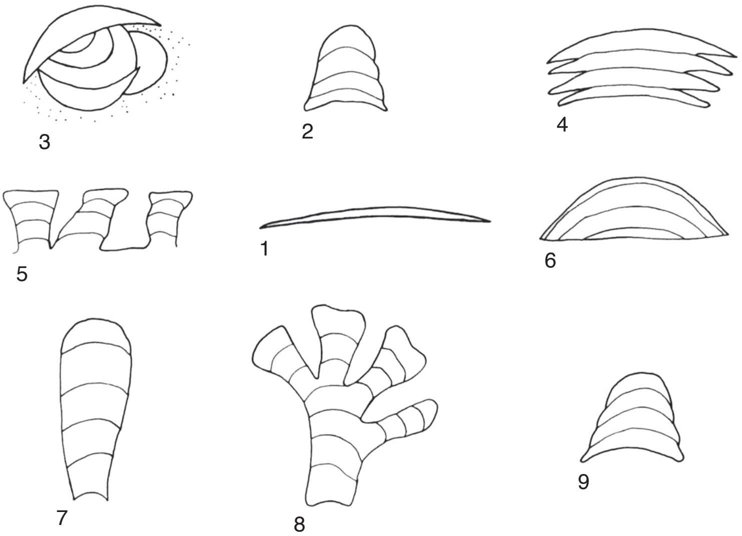


FIG. 17. Possible environmental controls on growth of the chaetetid skeleton, with the basic building block being a laminar accretionary unit; *1,* laminar accretionary unit; *2,* growth on a soft substrate; *3,* turbulence during growth; *4,* periodic sedimentation during growth; *5,* inferred growth 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,

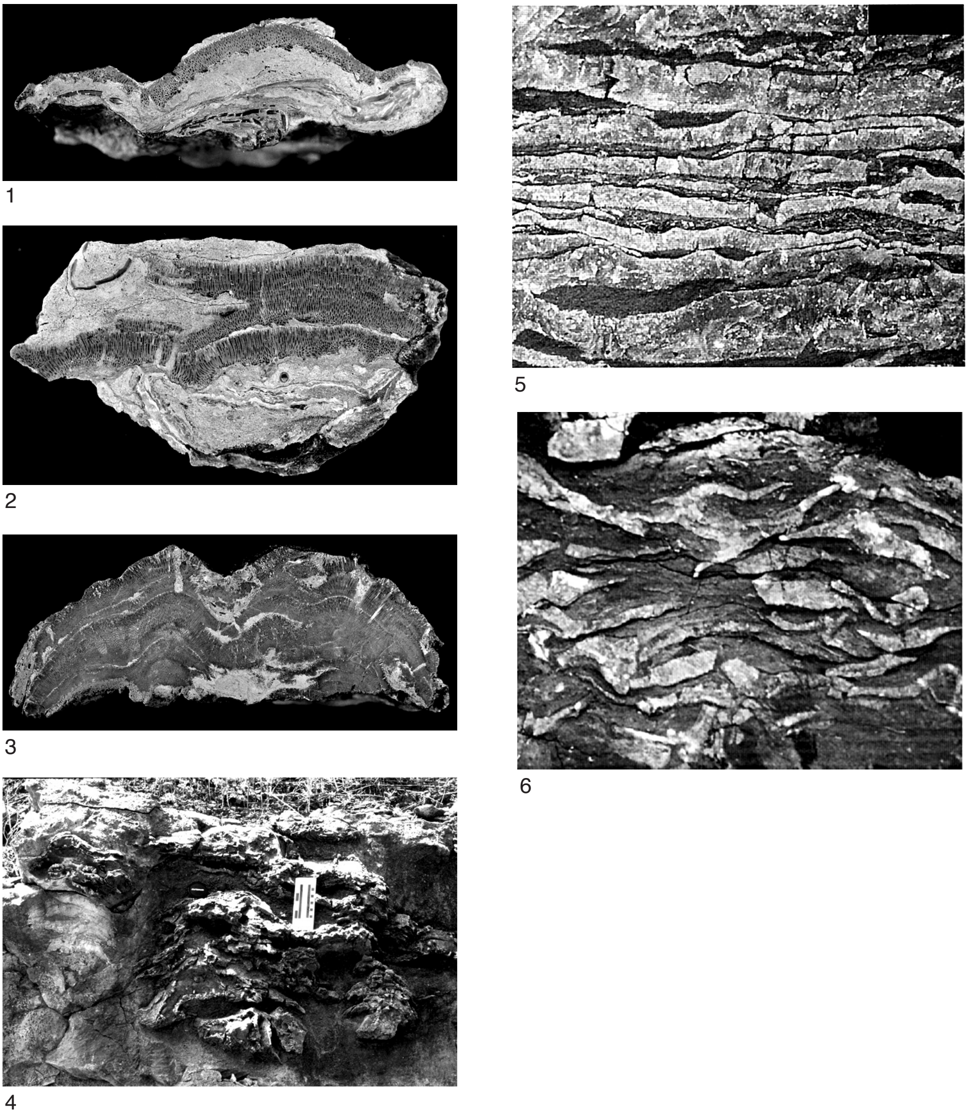


FIG. 18. Laminar chaetetid growth forms, Carboniferous, Pennsylvanian; *1,* laminar growth of a chaetetid skeleton on an irregular substrate, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.85 (West, 2011a); *2,* laminar growth of a chaetetid skeleton on an oncoid, Amoret Limestone 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).

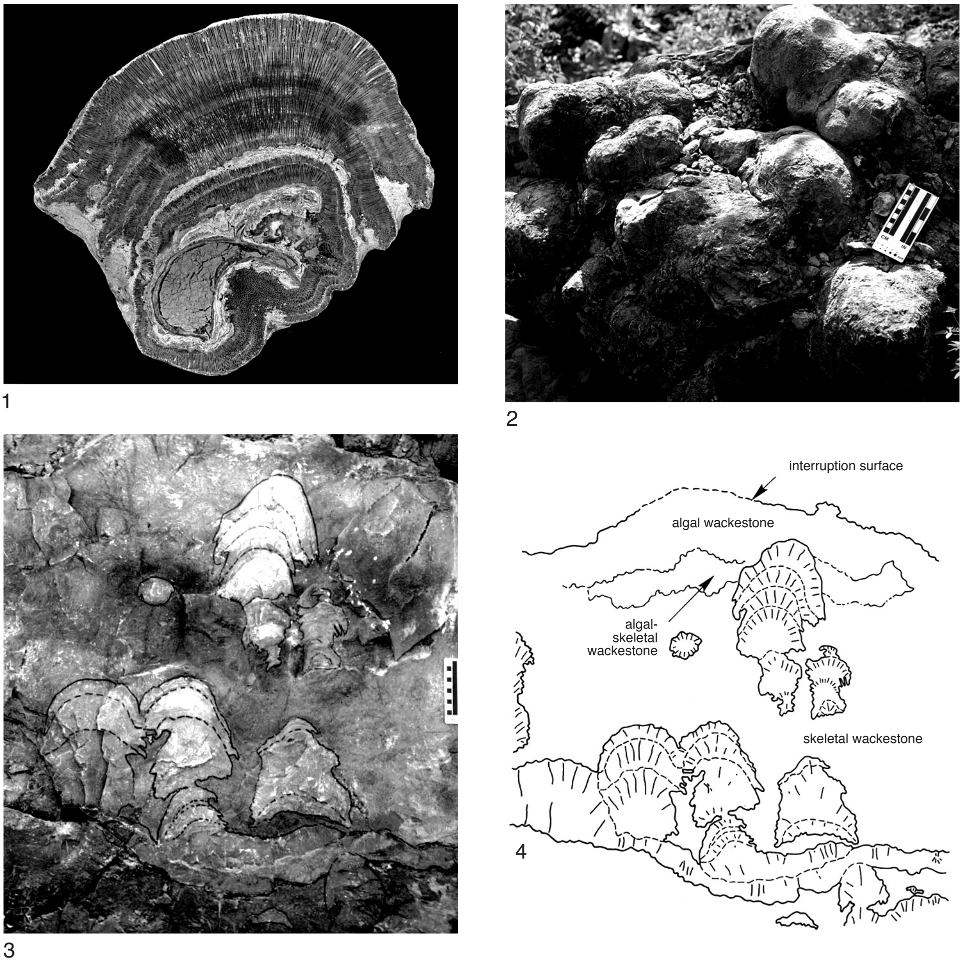


FIG. 19. Domical chaetetid growth forms, Carboniferous, Pennsylvanian; *1,* low domical chaetetid produced by laminar chaetetid encrusting an oncoid that formed around a productid brachiopod valve, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×0.55 (West, 2011a); *2,* upper 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).

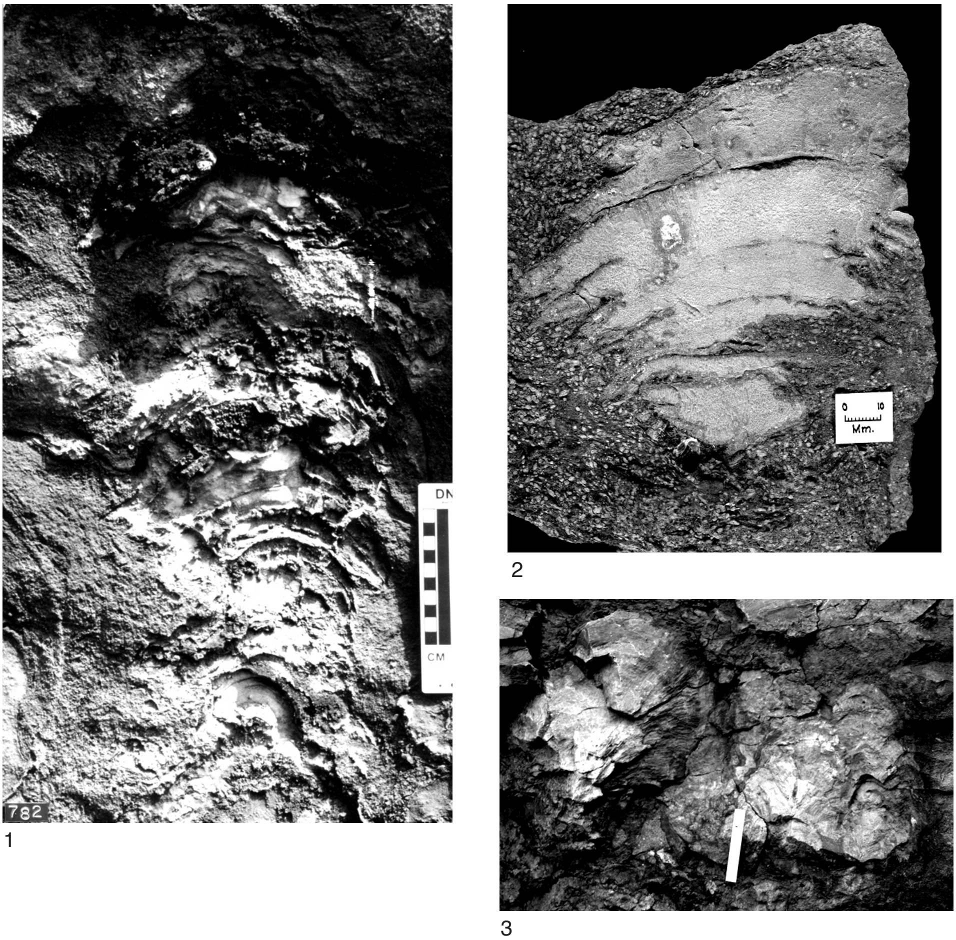


FIG. 20. Domical chaetetid growth forms (continued), Carboniferous, Pennsylvanian; *1,* high domical, ragged chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.2 (West, 2011a); *2,* ragged, domical chaetetid in a fusulinid packstone, Higginsville Limestone Member, Fort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

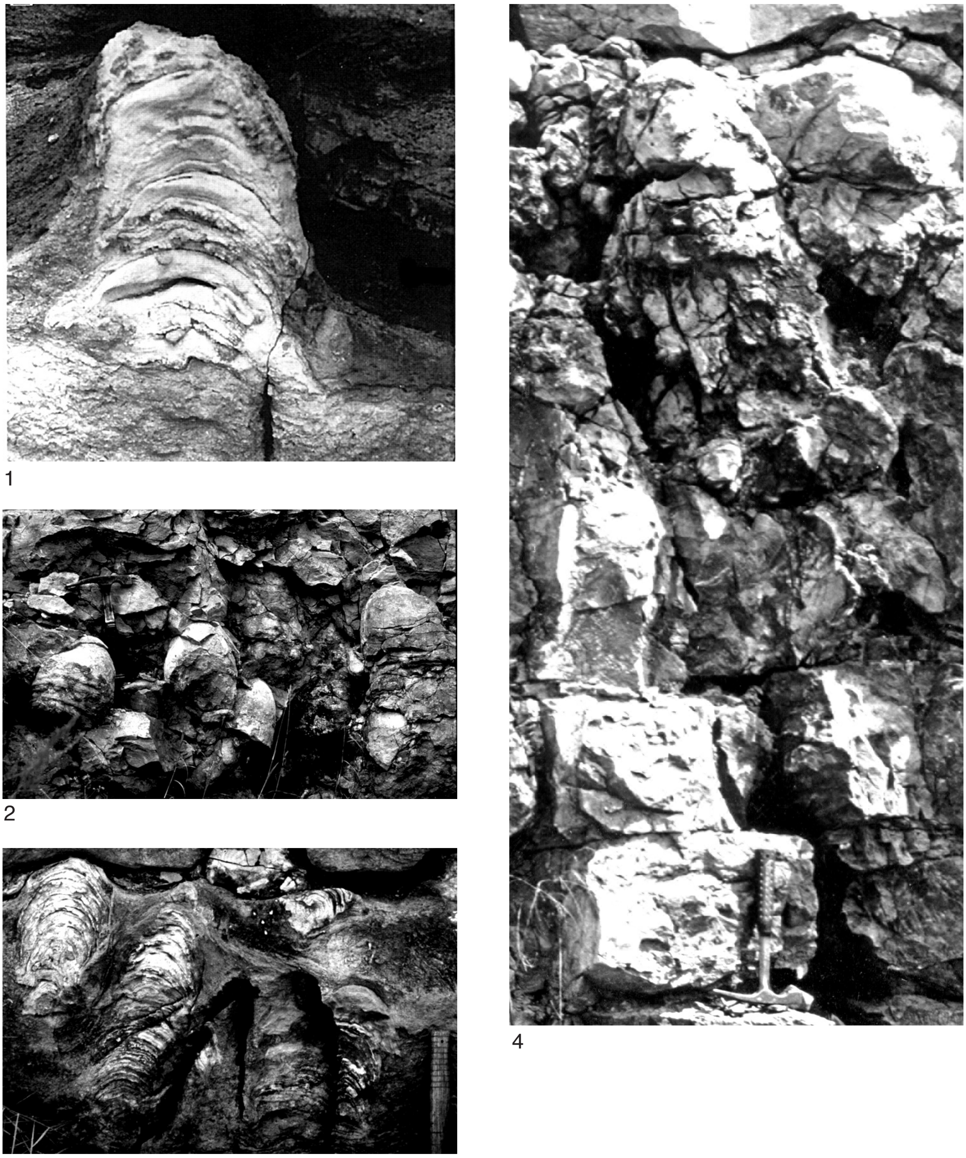


FIG. 21. Columnar chaetetid growth forms, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas; *1,* smooth columnar chaetetid, ×0.25 (adapted from Miller & West, 1997, p. 293, fig. 4E); *2,* mass of columnar chaetetids, ×0.06 (West, 2011a); *3,* smooth to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

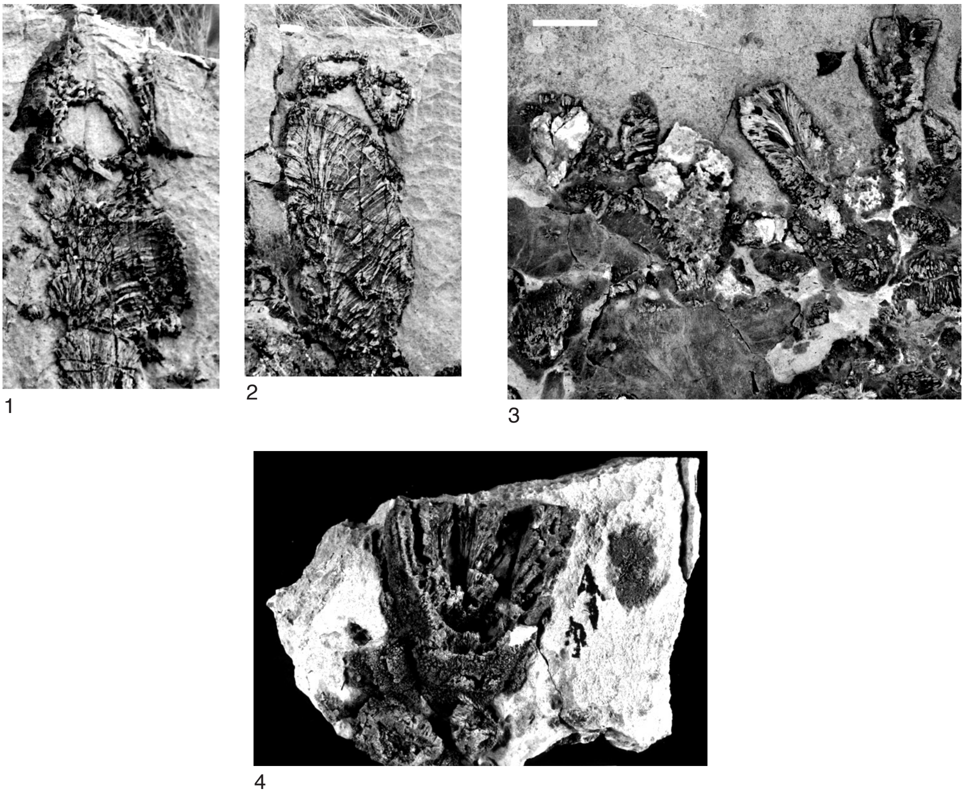


FIG. 22. Columnar chaetetid growth forms (continued), Carboniferous, Pennsylvanian; *1,* largely silicified ragged columnar chaetetid, Horquilla Limestone, Whetstone Mountains, Arizona, ×0.1 (West, 2011a); *2,* largely silicified smooth columnar chaetetid, Horquilla Limestone, Whetstone Mountains, Arizona, ×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).

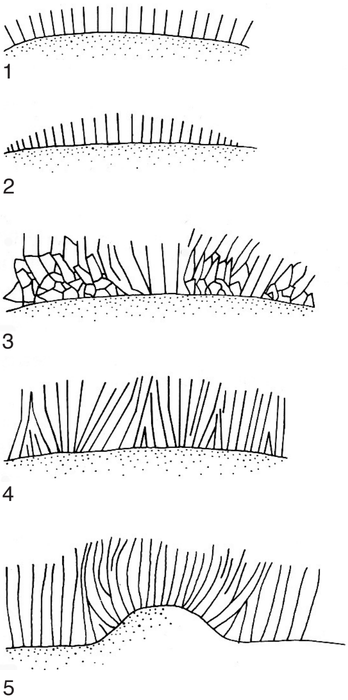


FIG. 23. Styles of initial growth in chaetetids; *1,* uniform tubule growth more or less normal to substrate; an uncommon style, ×3.25; *2,* greater tubule growth in the center; a common style and one that often is the template for continued growth, ×1.2; *3,* upward tubule growth is normal to oblique 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

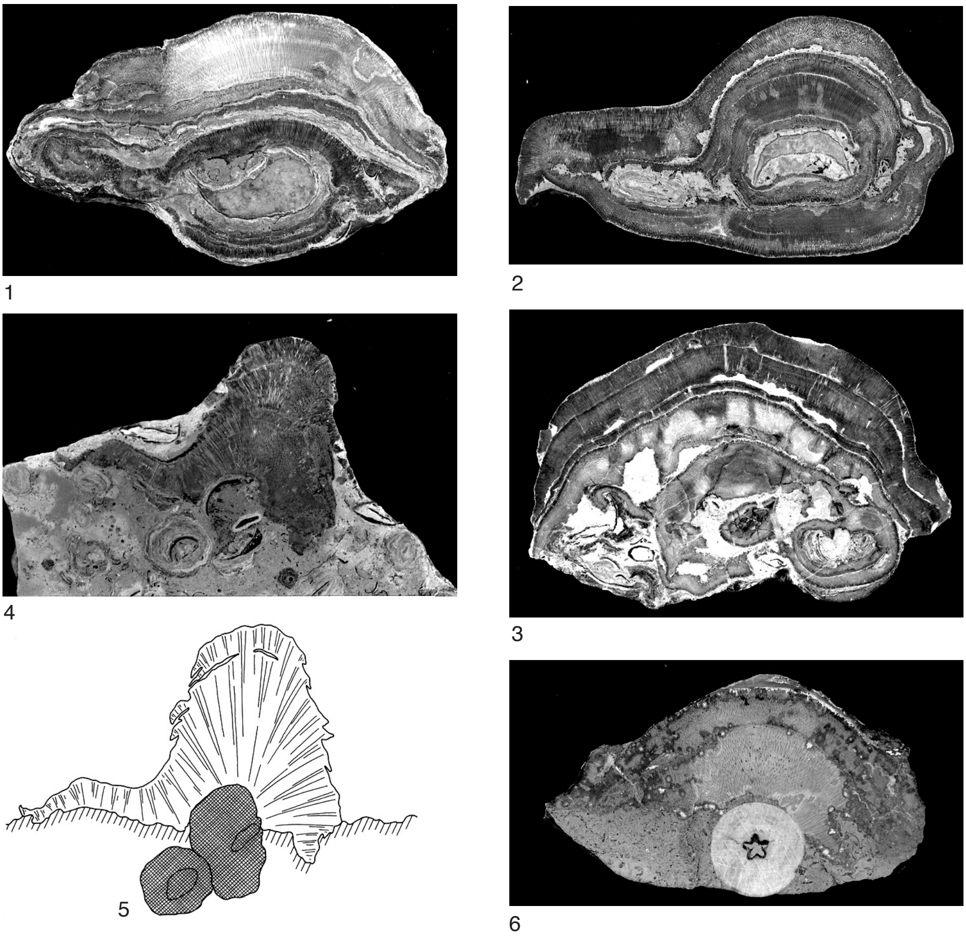


FIG. 24. Influence of substrate irregularities on chaetetid growth, Carboniferous, Pennsylvanian; *1,* oncoid with a productoid brachiopod nucleus, colonized by a laminar chaetetid, followed by a microbial mat; because of this substrate irregularity, a low domical chaetetid skeleton was produced, Amoret 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).

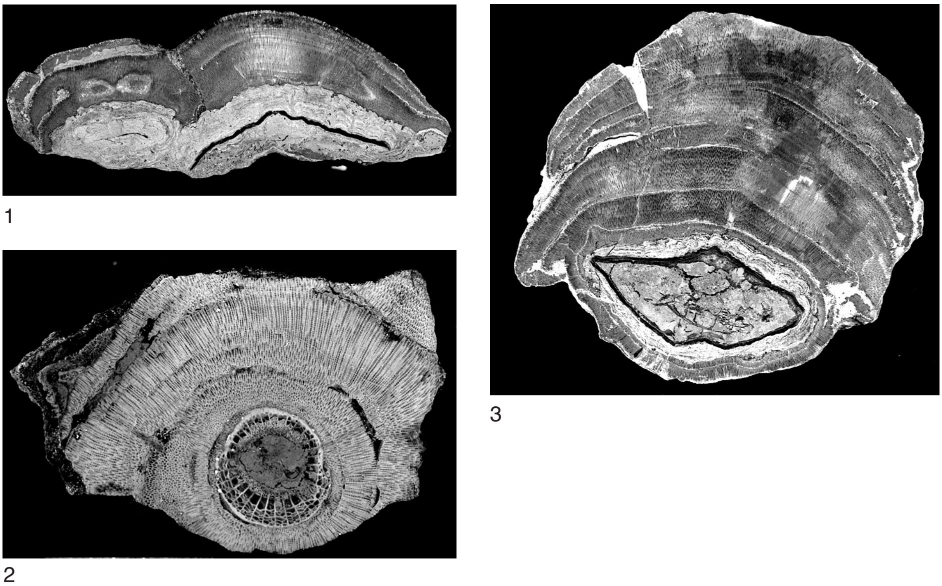


FIG. 25. Influence of substrate irregularities on chaetetid growth, Carboniferous, Pennsylvanian (continued); *1,* laminar to slightly domical chaetetid produced by growth over two oncoids, one of which has a valve of the brachiopod *Neospirifera* as the nucleus, Amoret Limestone Member, Altamont Limestone, 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).

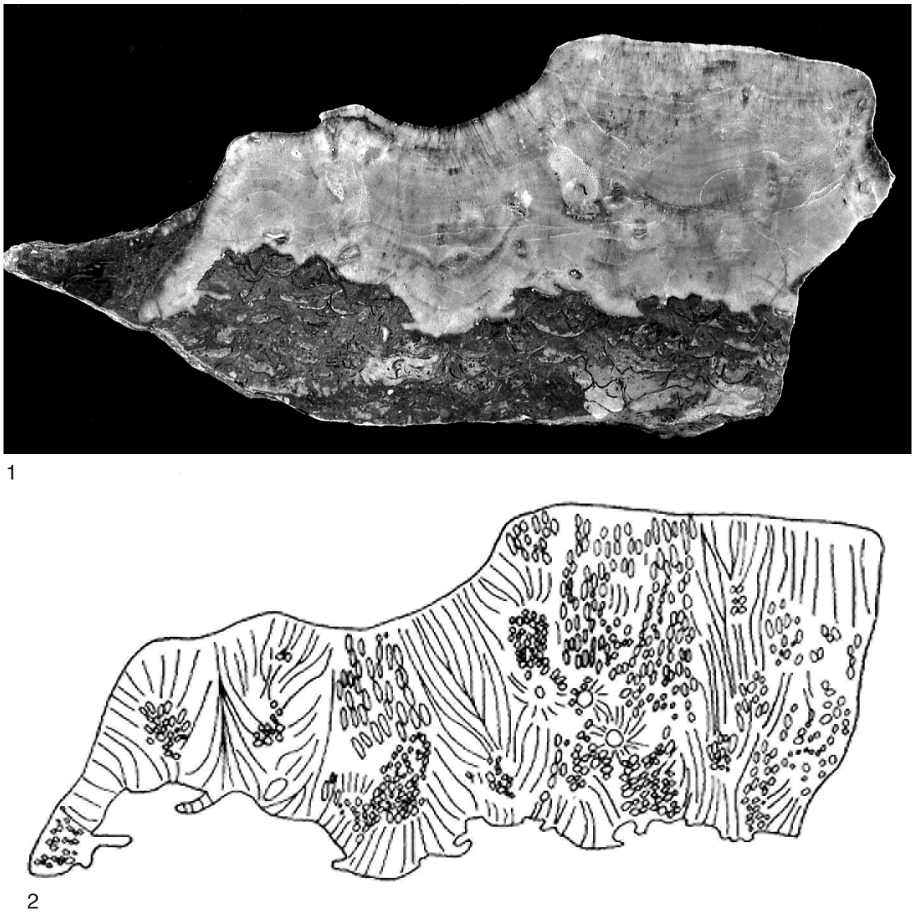


FIG. 26. Tubule complexity in chaetetids; *1,* polished longitudinal section, showing the complexity of tubule interaction in a laminar chaetetid, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma, ×0.6 (West, 2011a); *2,* interpretive sketch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

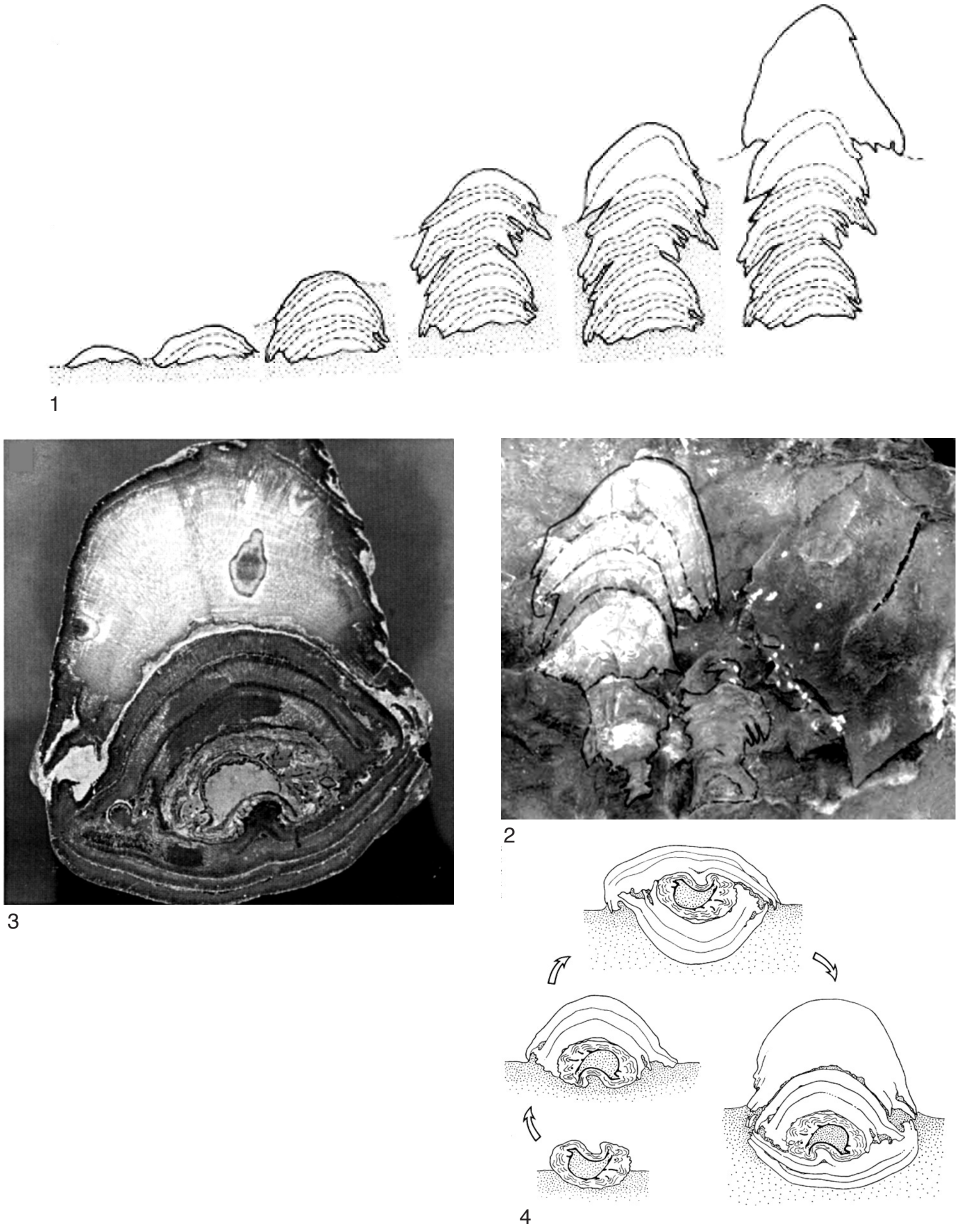


FIG. 27. Inferred development of laminar, domical, and columnar chaetetid skeletons with a ragged margin, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas; *1,* inferred growth sequence of a ragged columnar chaetetid, based on specimens, ×0.09 (Kershaw & 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

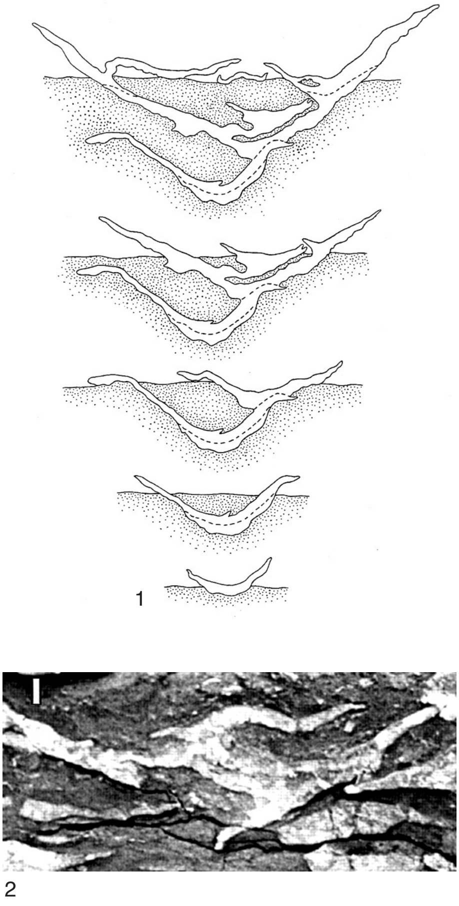
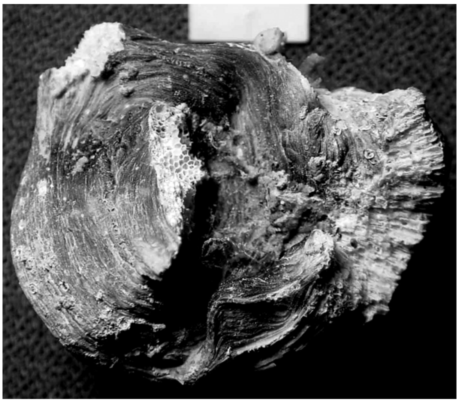


Fig. 28. Inferred development of laminar, domical, and columnar chaetetid skeletons with a ragged margin (continued); *1,* inferred sequence of growth events of some cup-shaped laminar chaetetids, based on specimens, Carboniferous, Pennsylvanian, Myrick Station Limestone Member, Pawnee Limestone, Bourbon 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).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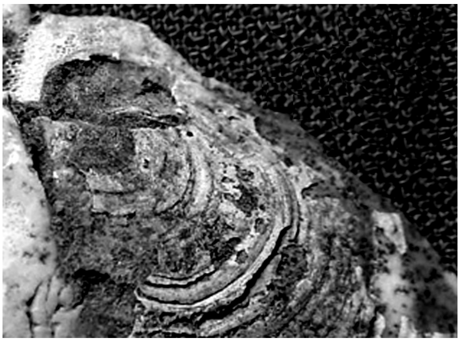
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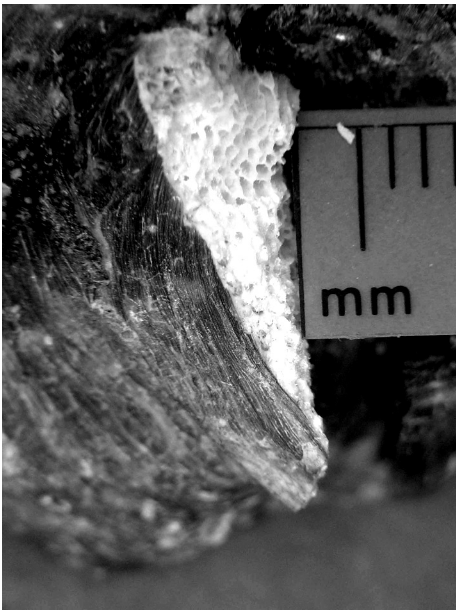

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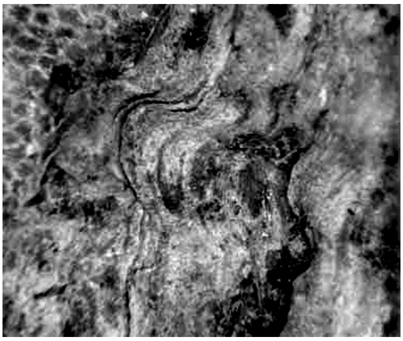
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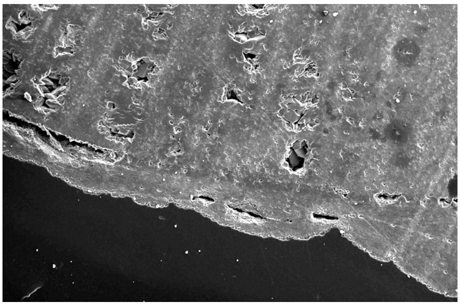
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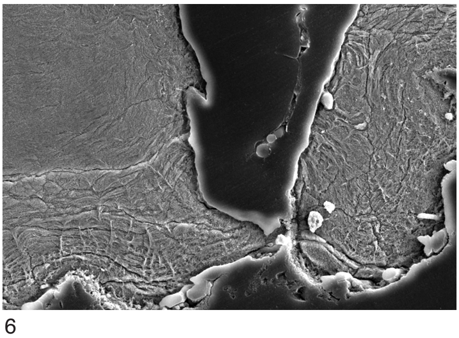
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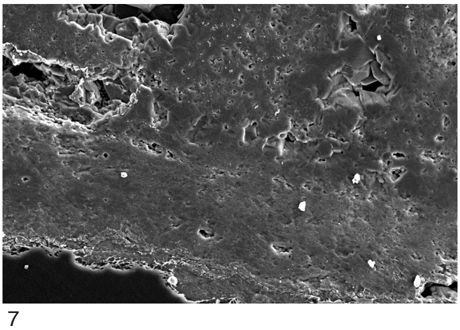
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FIG. 29. *(For explanation, see facing page).*

& 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).

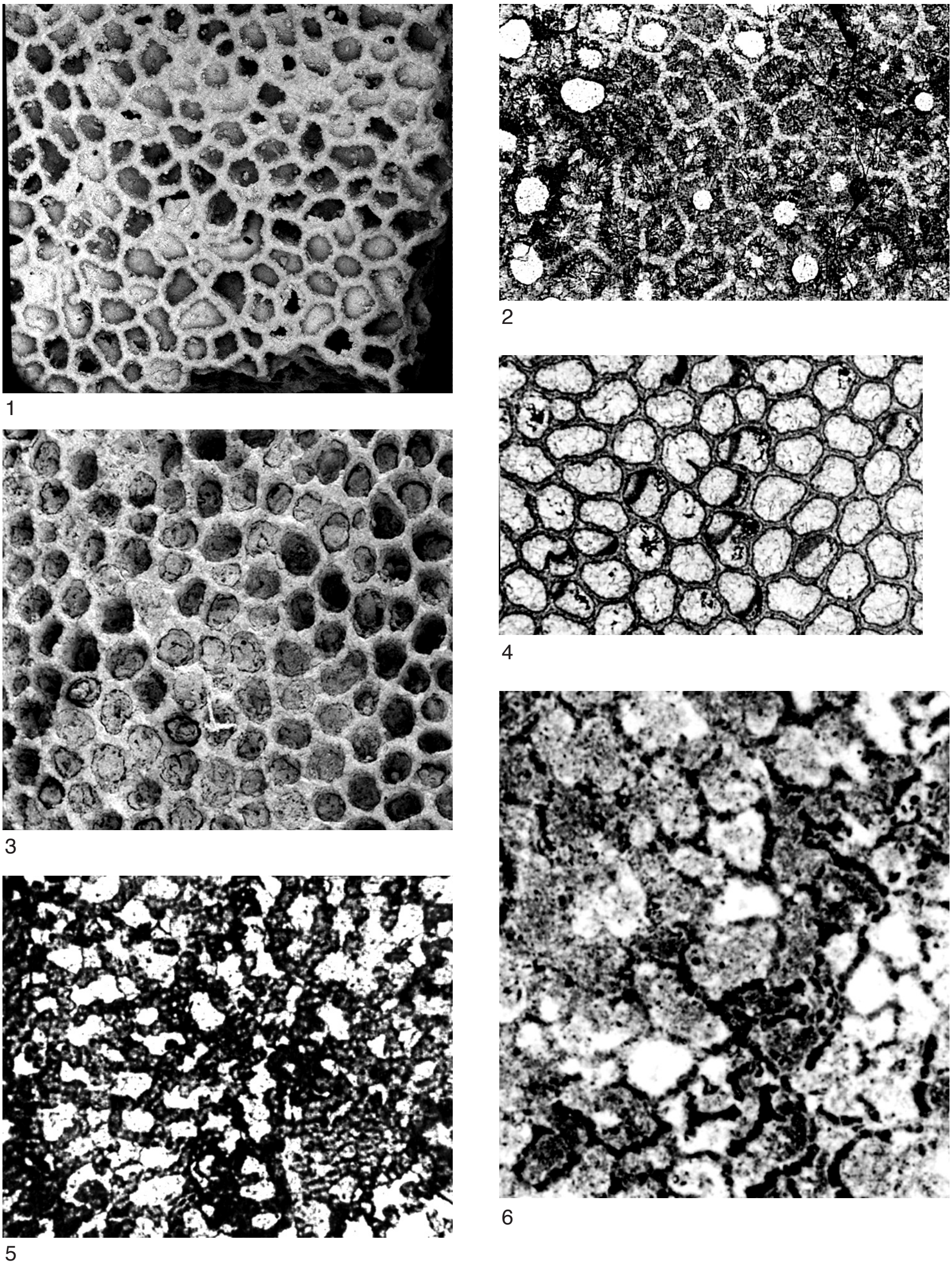


FIG. 30. *(For explanation, see facing page).*

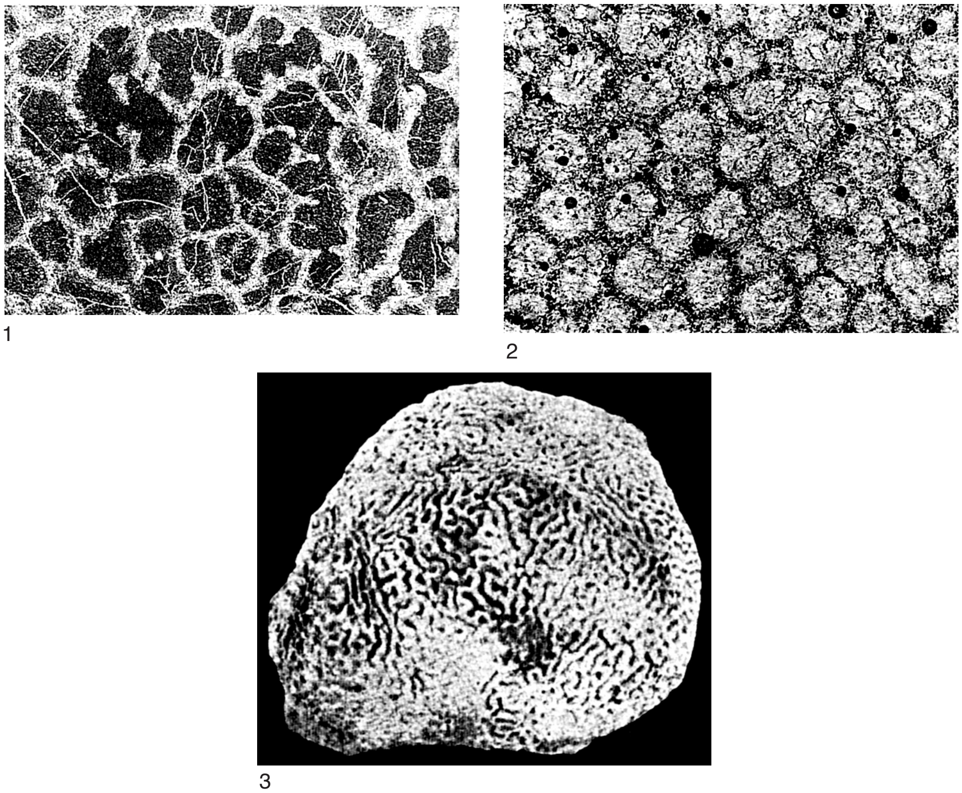


FIG. 31. Shape variation in chaetetid tubules (continued); *1,* transverse thin section of tubules in *Blastochaetetes dolomiticus*, Upper Triassic (Norian), southwestern Turkey, ×17 (adapted from Cremer, 1995, pl. 26,*3*; courtesy of *Geobios,* Université Lyon); *2,* transverse thin section of tubules 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*).

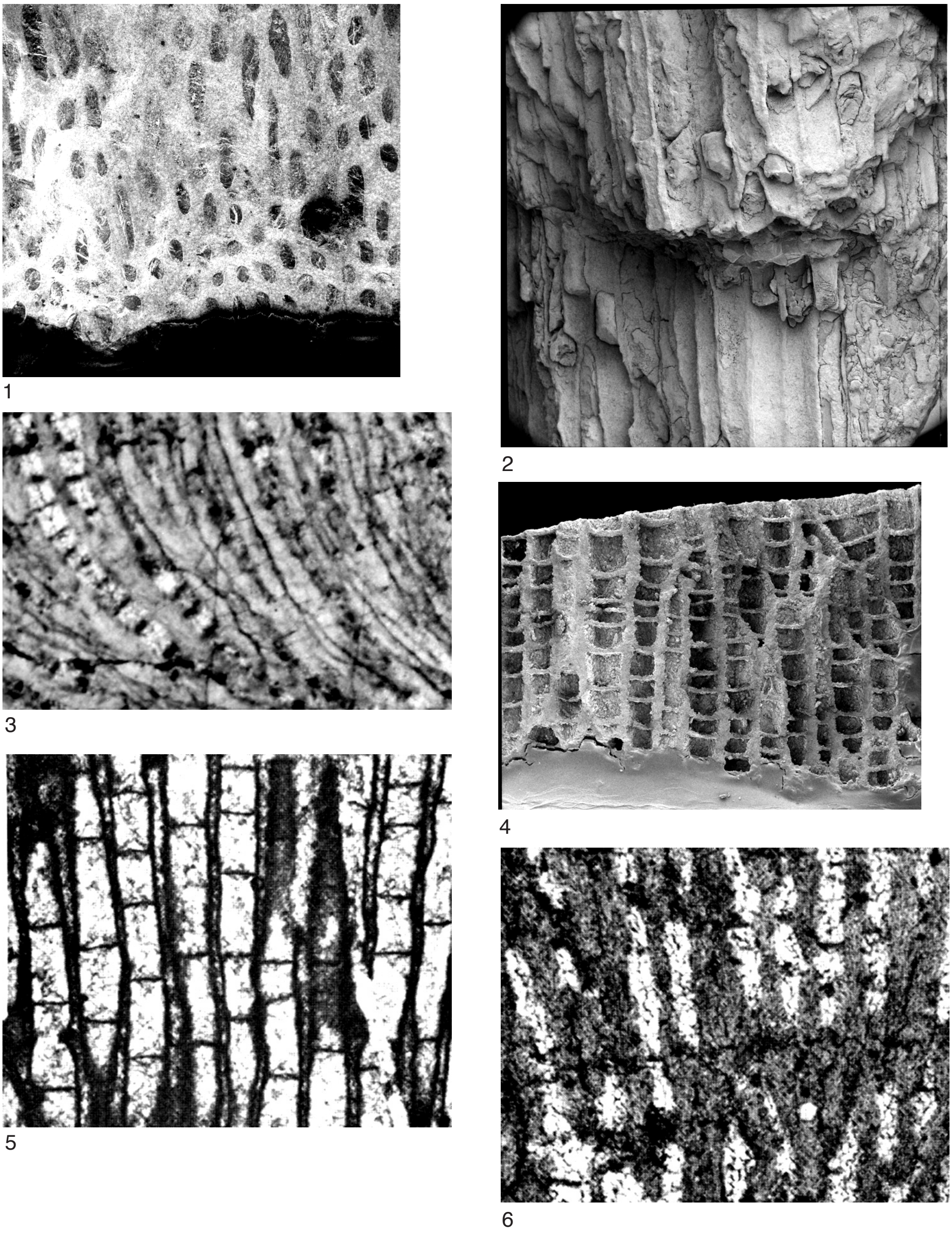


FIG. 32. Walls and tabulae in fossil chaetetids; *1,* SEM of transverse to oblique fracture of a chaetetid, Permian, Tunisia, showing tubule walls and tabulae, ×20 (West, 2011a); *2,* SEM of longitudinal fracture of chaetetid, Carboniferous, Pennsylvanian, Buckhorn Asphalt, Murray County, Oklahoma, ×15 (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).

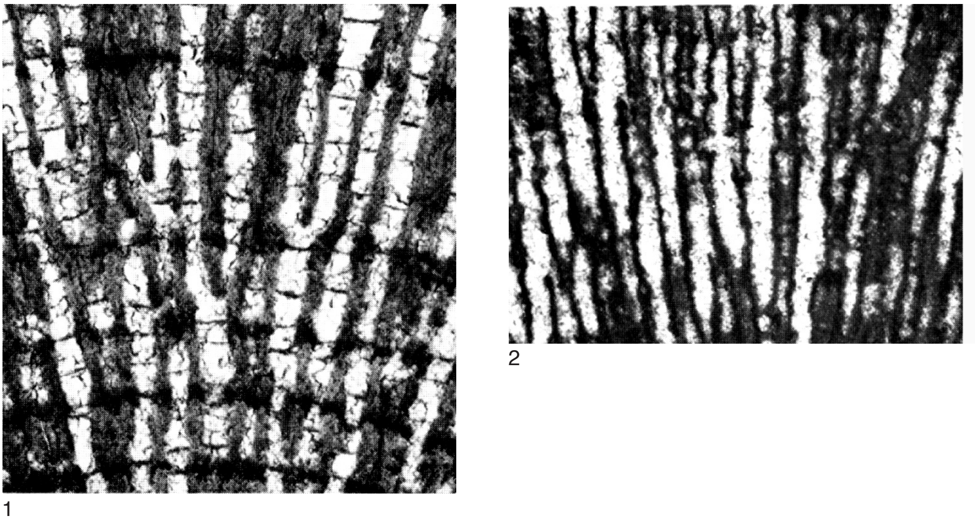


FIG. 33. Walls and tabulae in fossil chaetetids (continued); *1,* longitudinal thin section of *Blastochaetetes bathonicus,* Middle Jurassic (Bathonian), France, ×15 (adapted from Fischer, 1970, pl. B,*4*); *2,* longitudinal thin section of *Ptychochaetetes globosus,* Upper Jurassic (Oxfordian), France, ×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 &

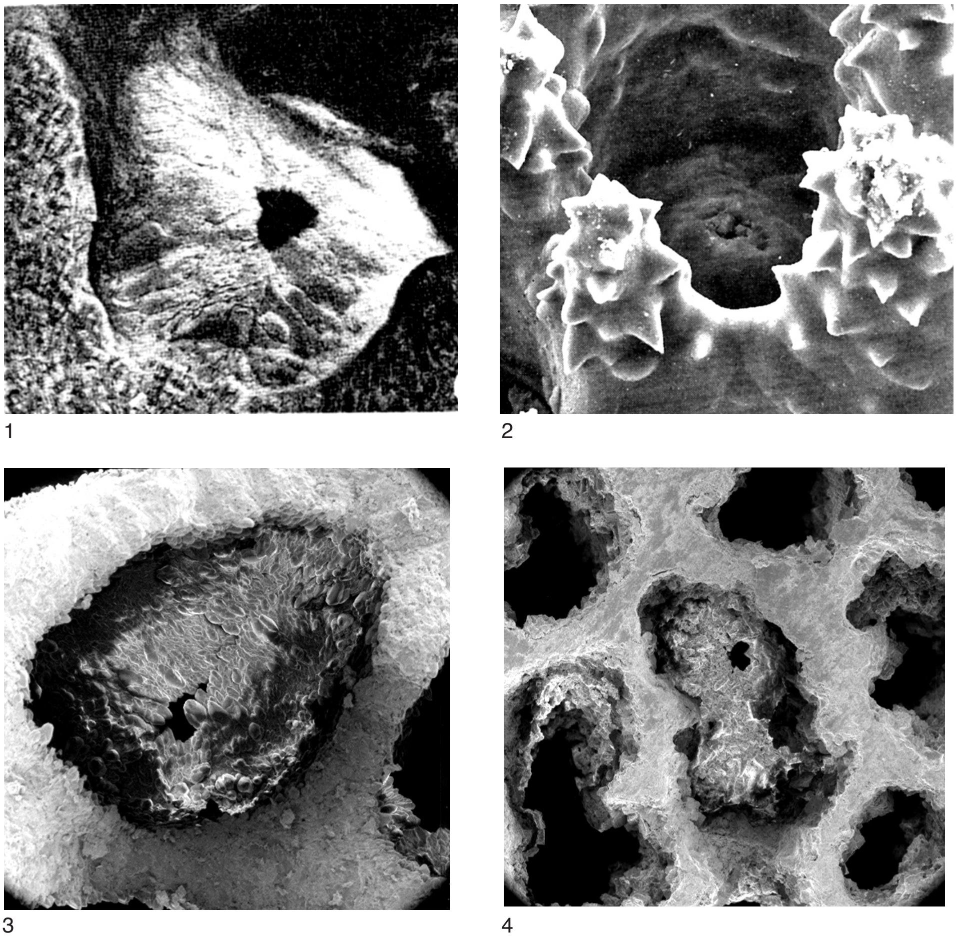


Fig. 34. Foramen in tabulae in extant and fossil chaetetids; *1,* SEM of a possible foramen in a tabula of an extant specimen of *Merlia normani*, Mediterranean Sea, ×350 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. II,*1;* courtesy of *Publications Scientifiques du Muséum national d'Histoire naturelle, 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).

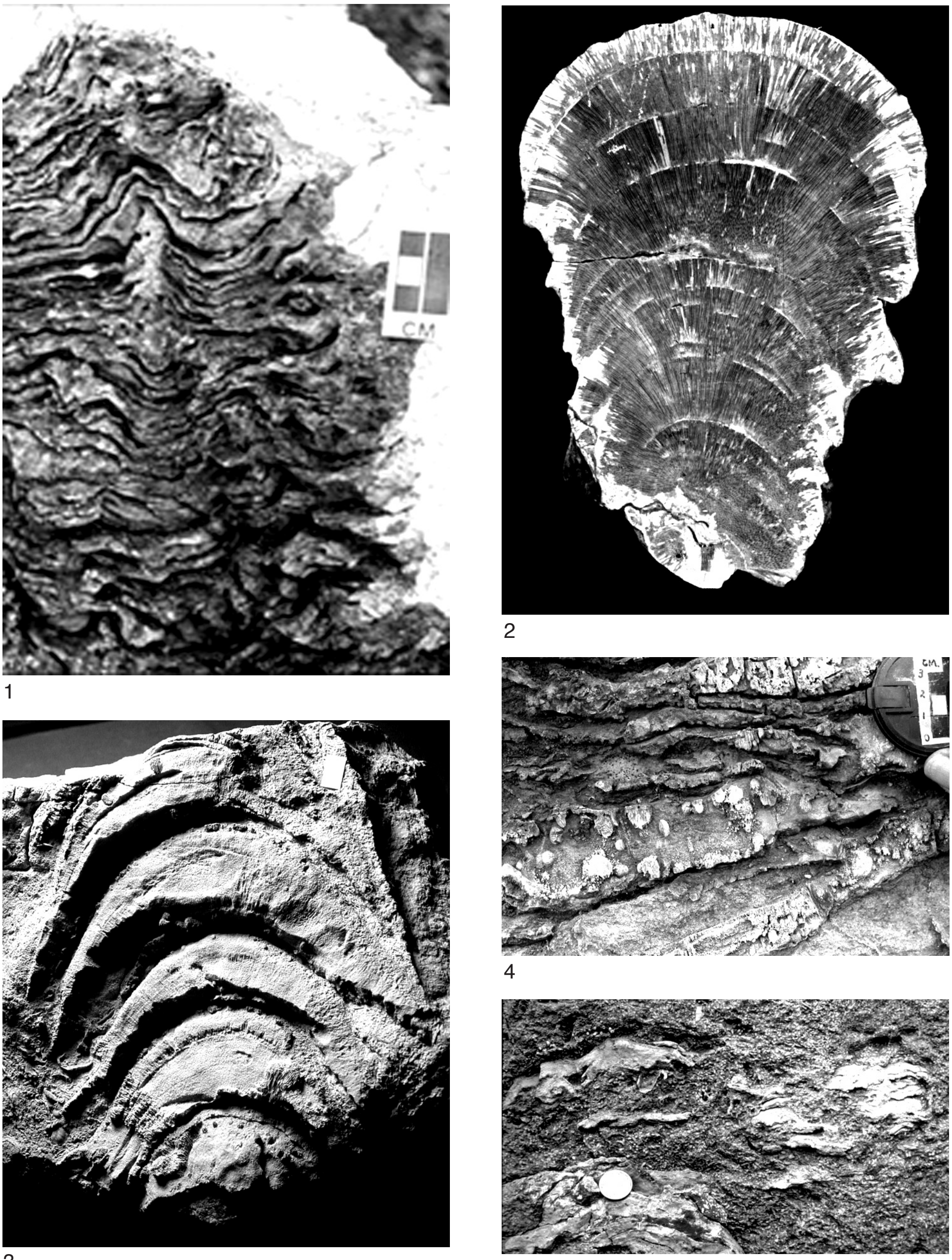


FIG. 35. *(For explanation, see facing page).*

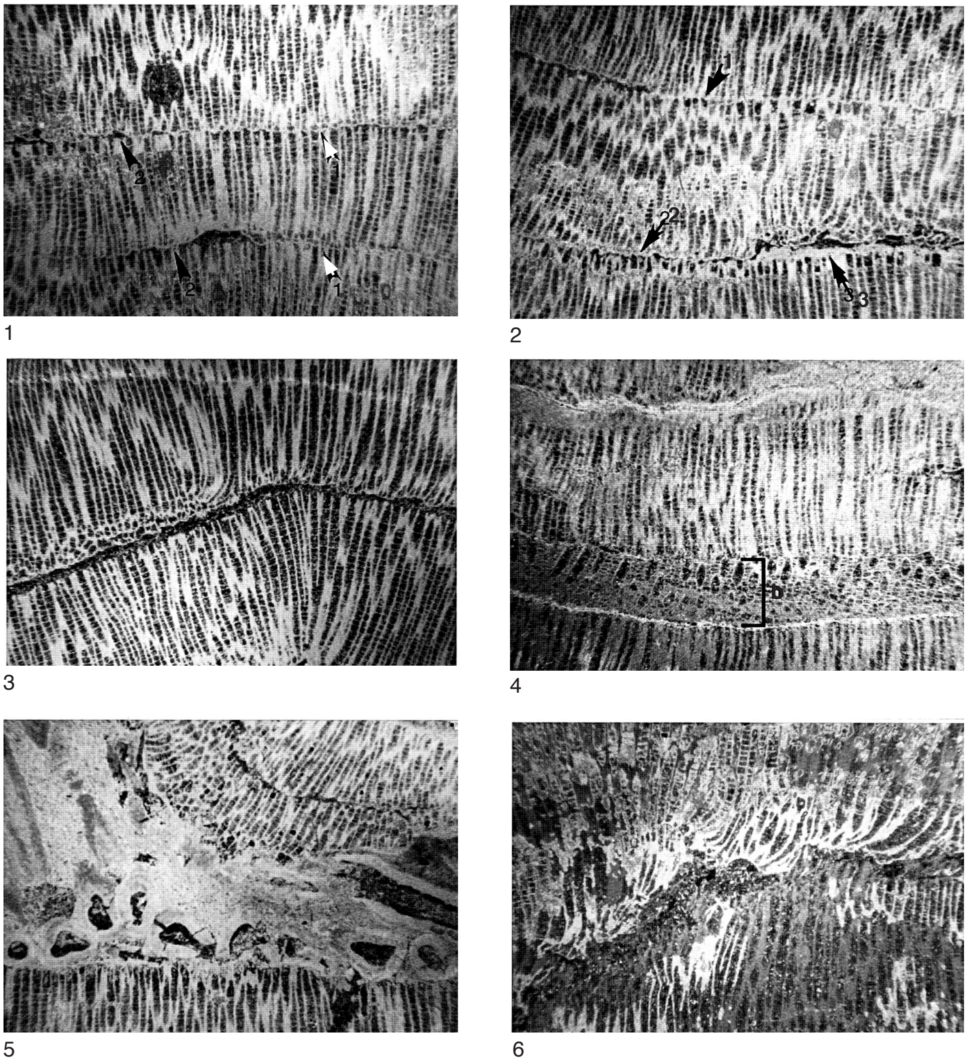


FIG. 36. Five types of growth interruptions observed in chaetetid skeletons, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; all figures are ×6, acetate peel prints; *1,* continuity of tubules across the interruption, type 1 (*arrows*) grades 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

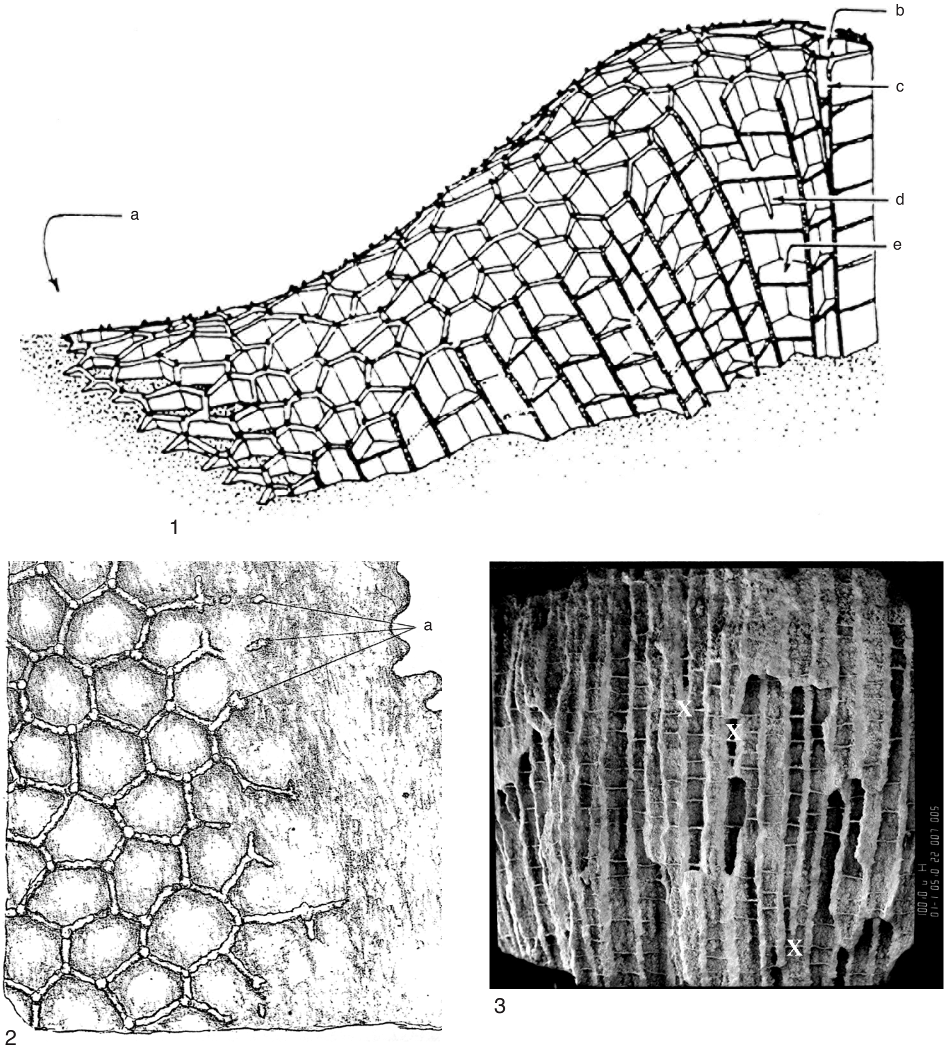


FIG. 37. Skeletal increase in chaetetids; *1,* schematic diagram of chaetetid on a stippled substrate illustrating the methods of skeletal increase and associated morphological features: *a* = area of peripheral expansion; *b* = tubule; *c* = tubule increase by intertubule budding; *d* = pseudosepta 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).

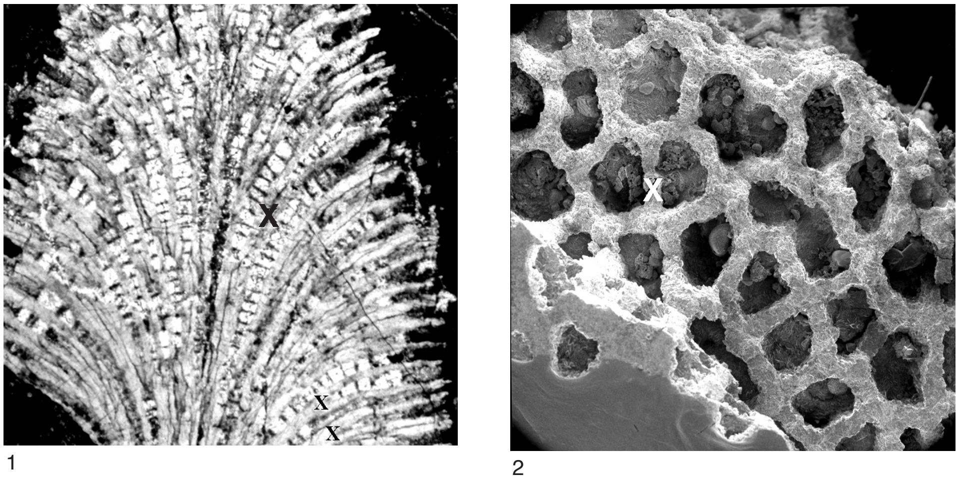


FIG. 38. Skeletal increase in chaetetids (continued); *1,* longitudinal thin section, showing skeleton increase by intertubular budding (*black X*), Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×10 (West, 2011a); *2,* SEM of transverse fracture of *Chaetetes (Chaetetes) radians*, Carboniferous, 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)

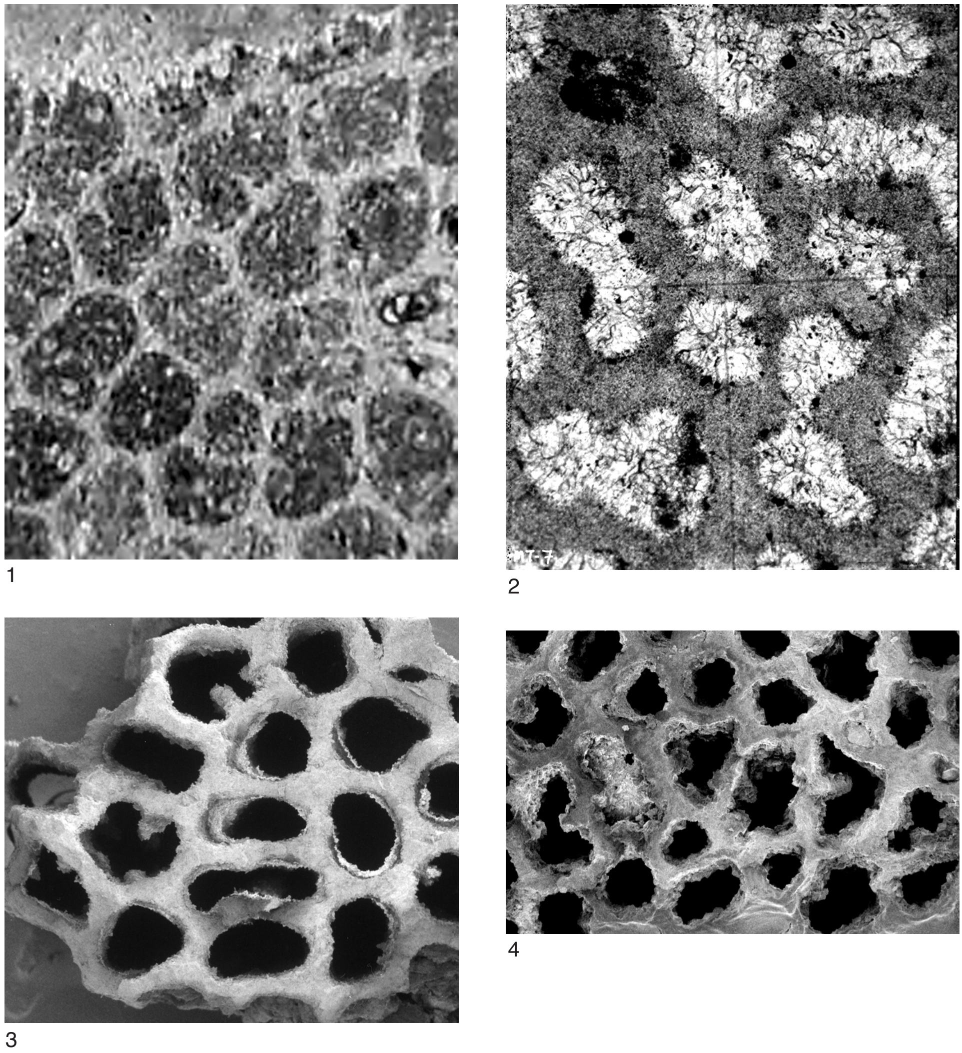


FIG. 39. Pseudosepta in fossil chaetetids; *1,* transverse thin section of chaetetid skeleton, showing tubules with conspicuous pseudosepta, Carboniferous, Pennsylvanian, Bird Springs Formation, near Mountain Springs, Nevada, ×100 (West, 2011a); *2,* transverse thin section of chaetetid skeleton, showing 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).

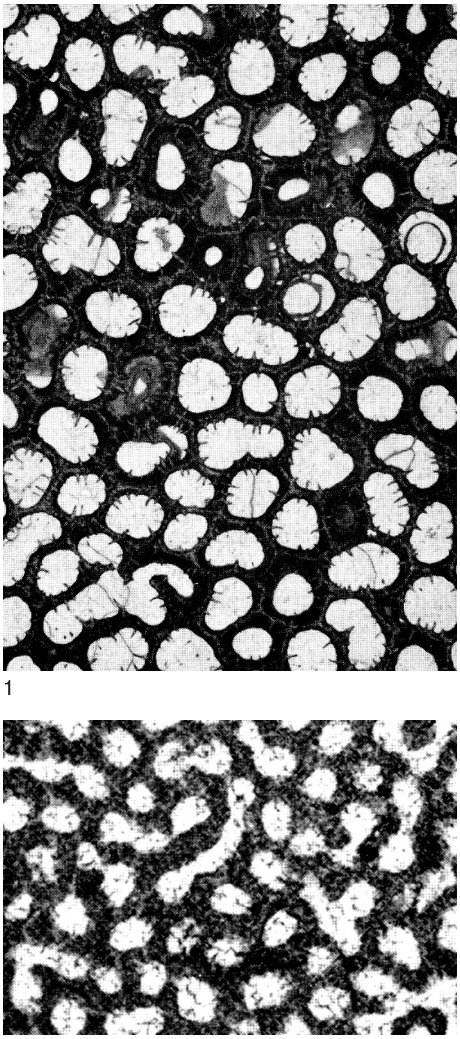


FIG. 40. Pseudosepta in fossil chaetetids (continued); *1,* transverse thin section of *Acanthochaetetes seunesi,* showing tubules and pseudosepta, Upper Cretaceous (Cenomanian), Pyrennees, ×7.5 (adapted from Fischer, 1970, pl. F,*3*); *2,* transverse thin section of *Blastochaetetes capilliformis,* 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.*

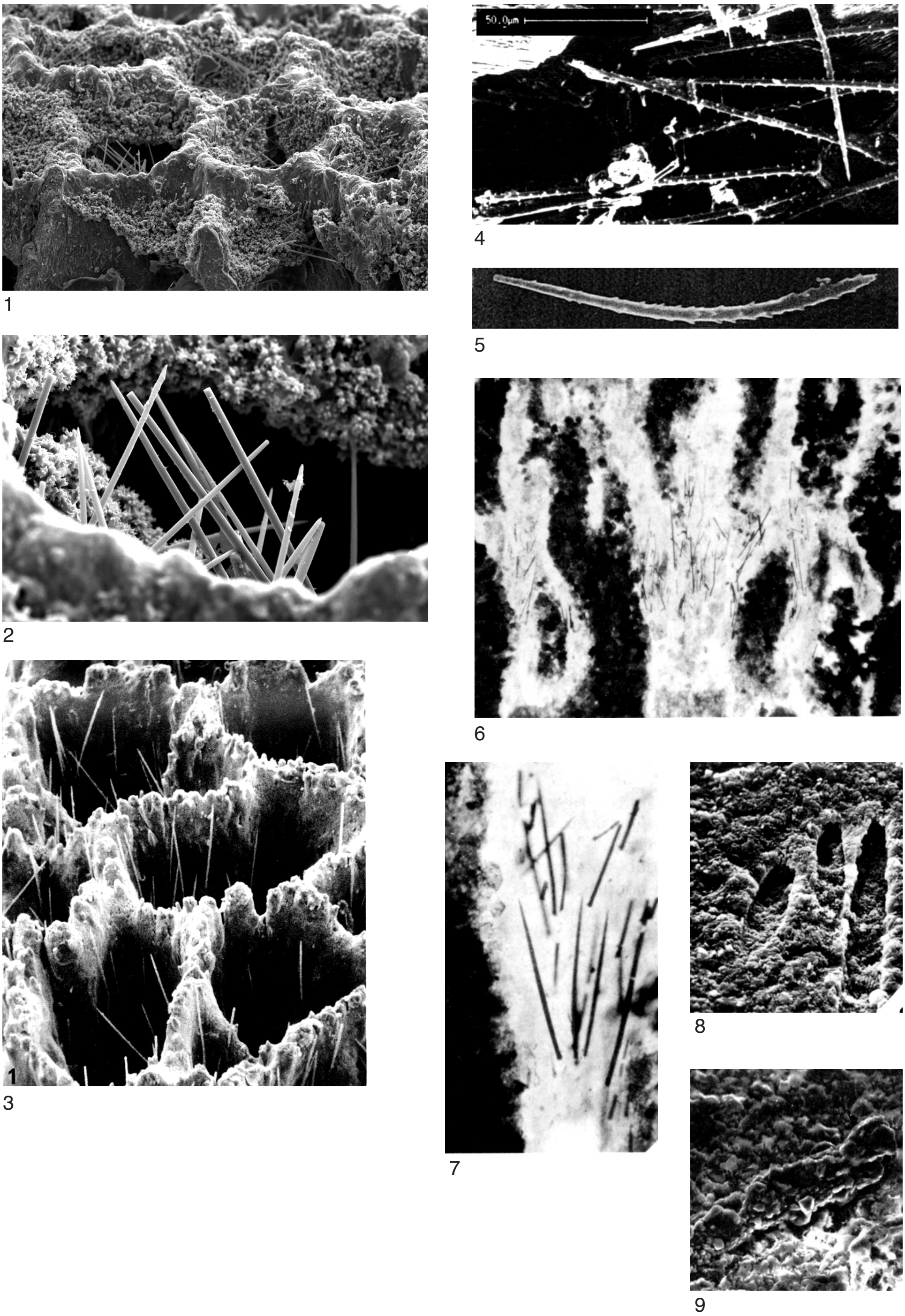


Fig. 41. *(For explanation, see facing page).*

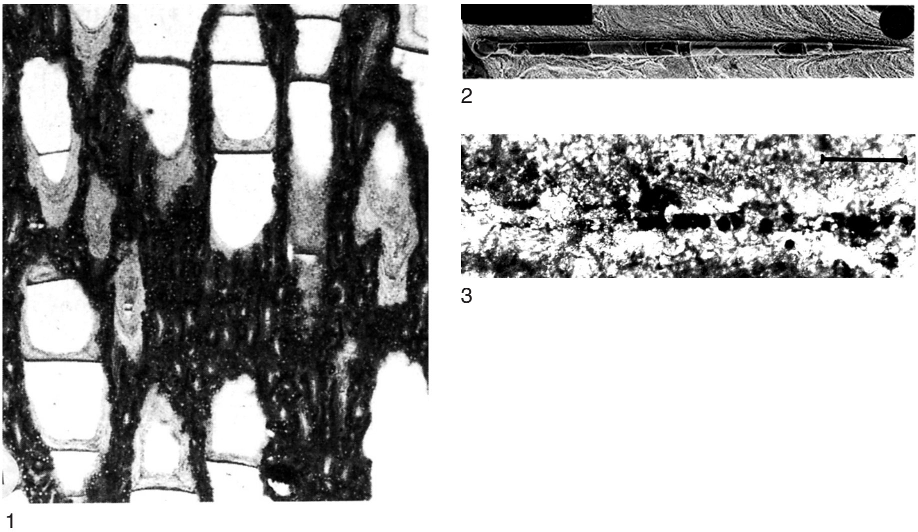


FIG. 42. Pseudomorphs of megasclere tylostyles in fossil chaetetids; *1,* tangential thin section of *Calcistella tabulata,* showing spicule pseudomorphs within tubule walls (white dots within dark areas) from a Cretaceous (possibly Aptian) boulder in an Eocene conglomerate in Greece, ×9 (adapted from 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).

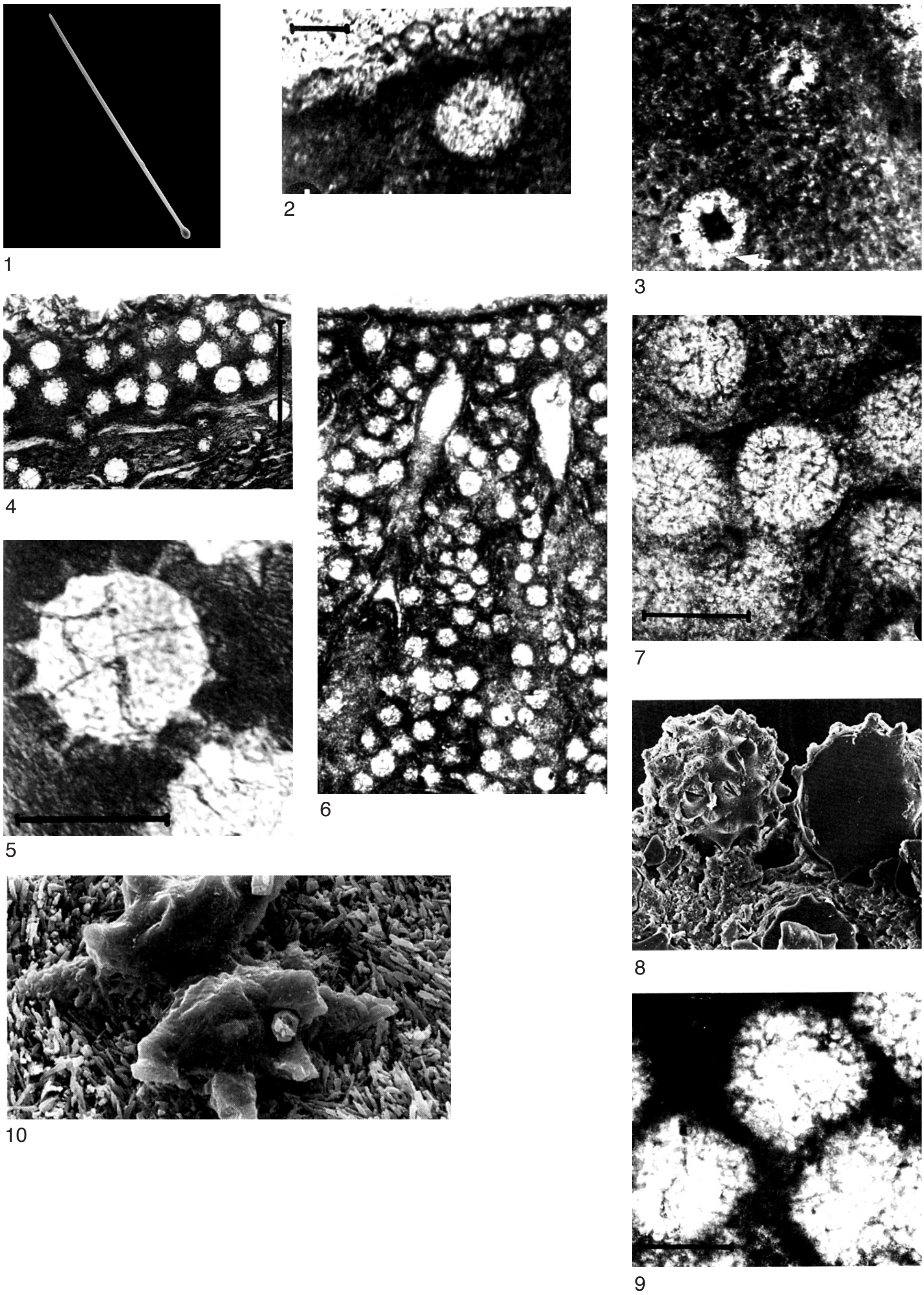


FIG. 43. *(For explanation, see facing page).*

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

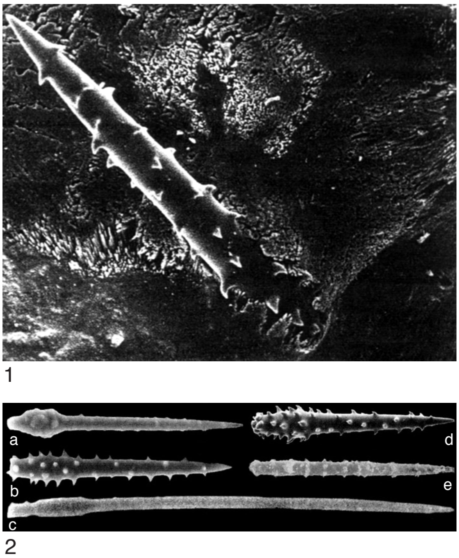


Fig. 44. Variation in acanthostyles in *Astrosclera willeyana; 1,* SEM of an astrosclerid acanthostyle spicule in an extant specimen, Marigondon Cave, Philippines, ×1100 (adapted from Wörheide & others, 1997, pl. III,*2;* courtesy of Real Sociedad Española de Historia Natural, Seccion Geologica, Madrid, 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).

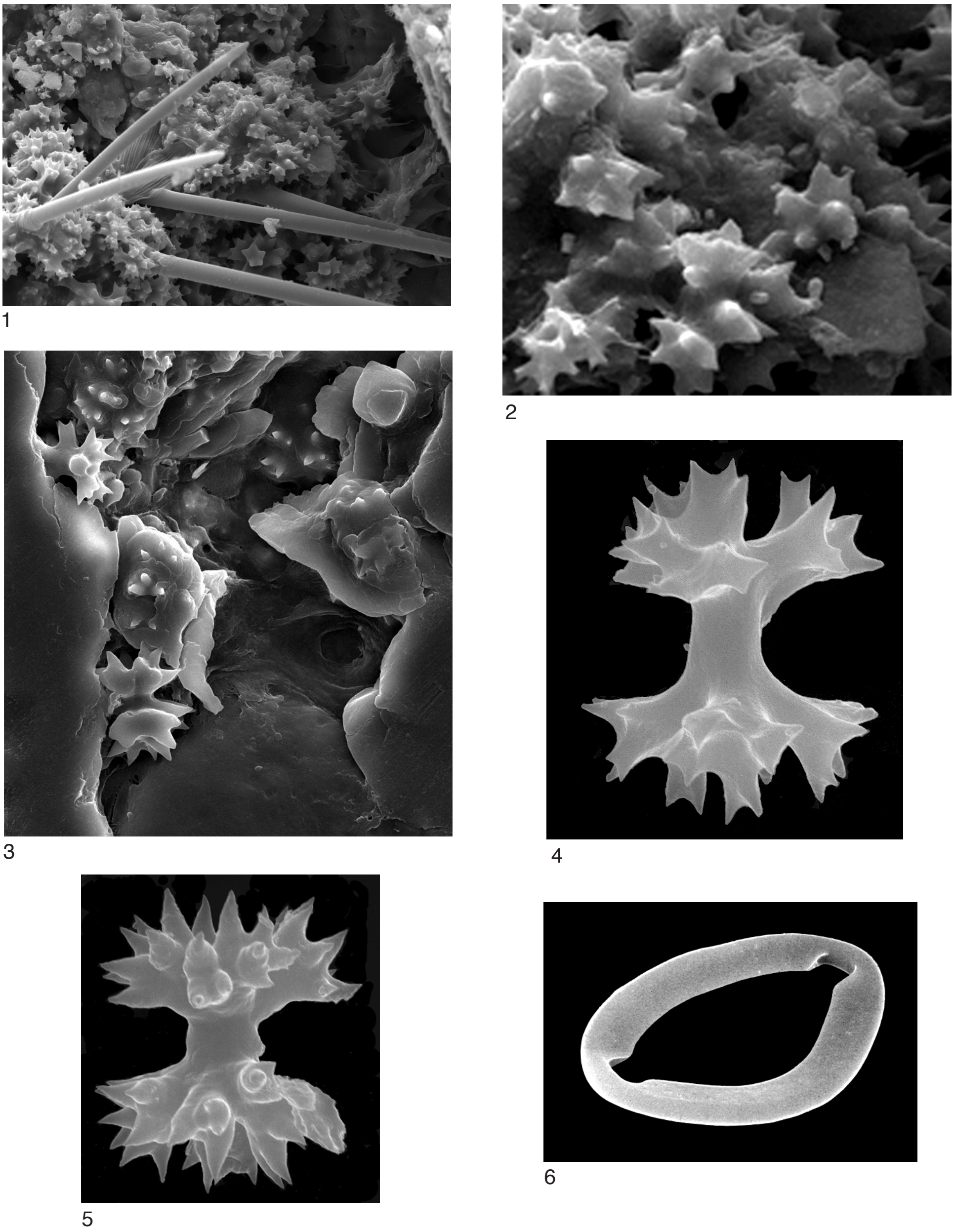


FIG. 45. Microscleres from *Acanthochaetetes* and *Merlia; 1,* SEM of masses of microscleres and a few megascleres (tylostyles) from the growing surface of *Acanthochaetetes* sp., an extant specimen collected live in October 2005 off the Komesu coast, southern Okinawa at a water depth of 15 m, ×1000 (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).

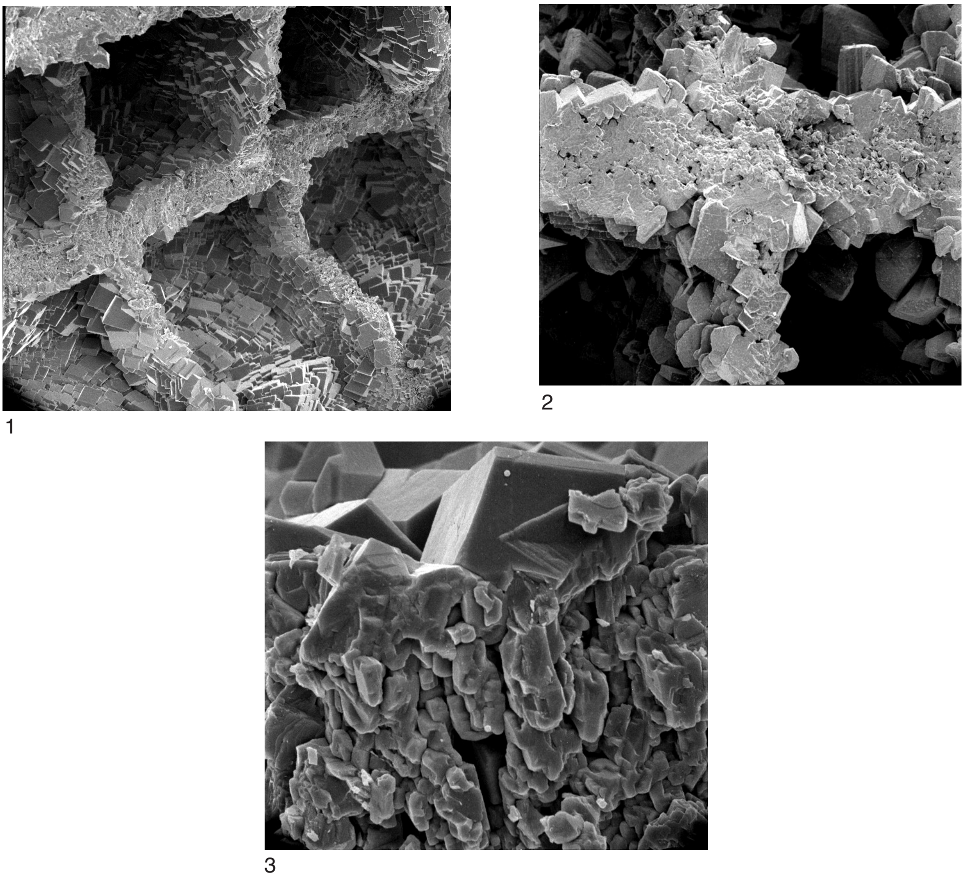


FIG. 46. Dolomite crystals associated with tubule walls and tabulae in a chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone; *1,* SEM of tubule walls and tabulae replaced in part by dolomite, Labette County, Kansas, ×120 (West, 2011a); *2,* enlarged SEM view of tubule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

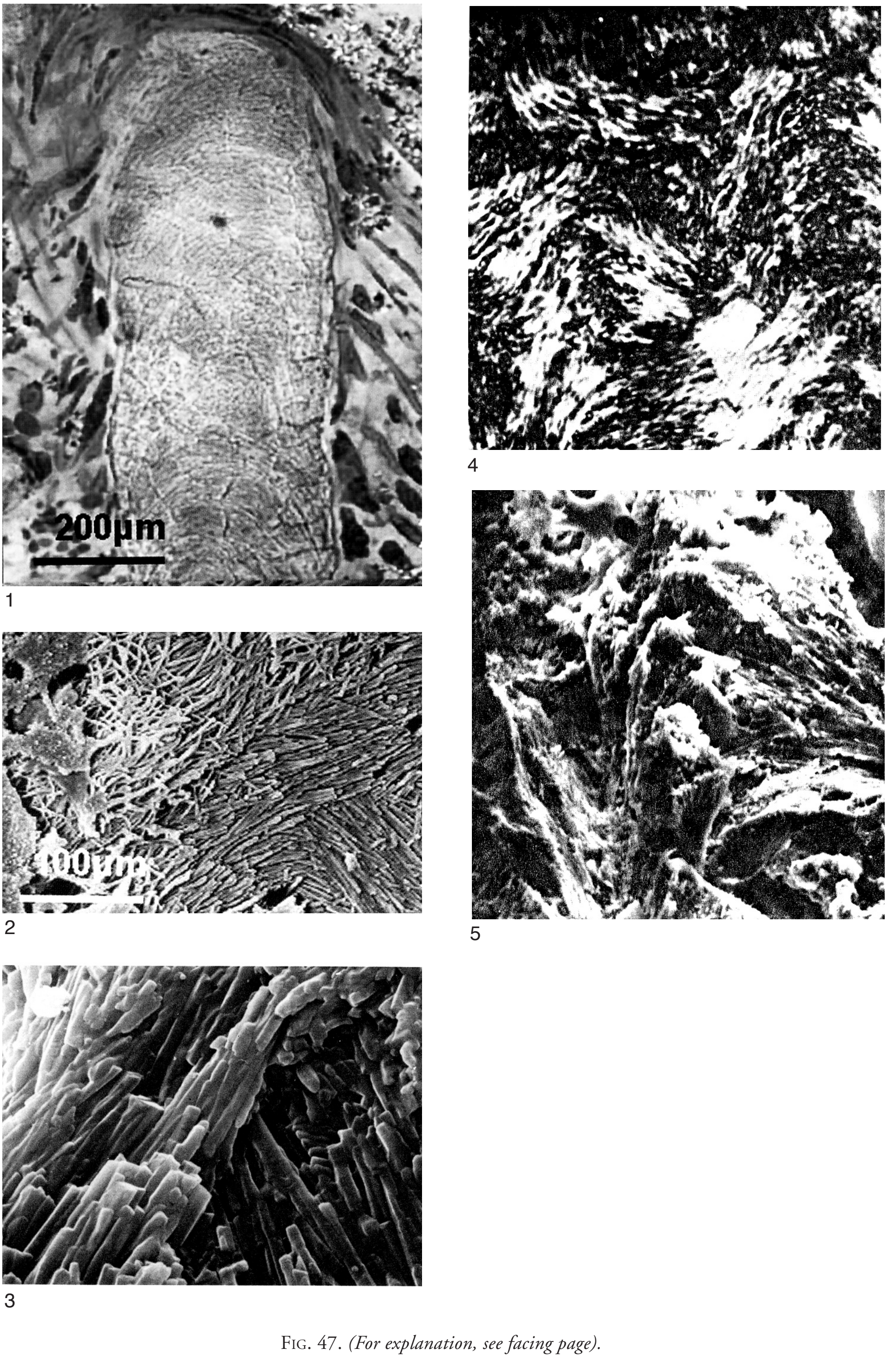


FIG. 47. *(For explanation, see facing page).*

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).

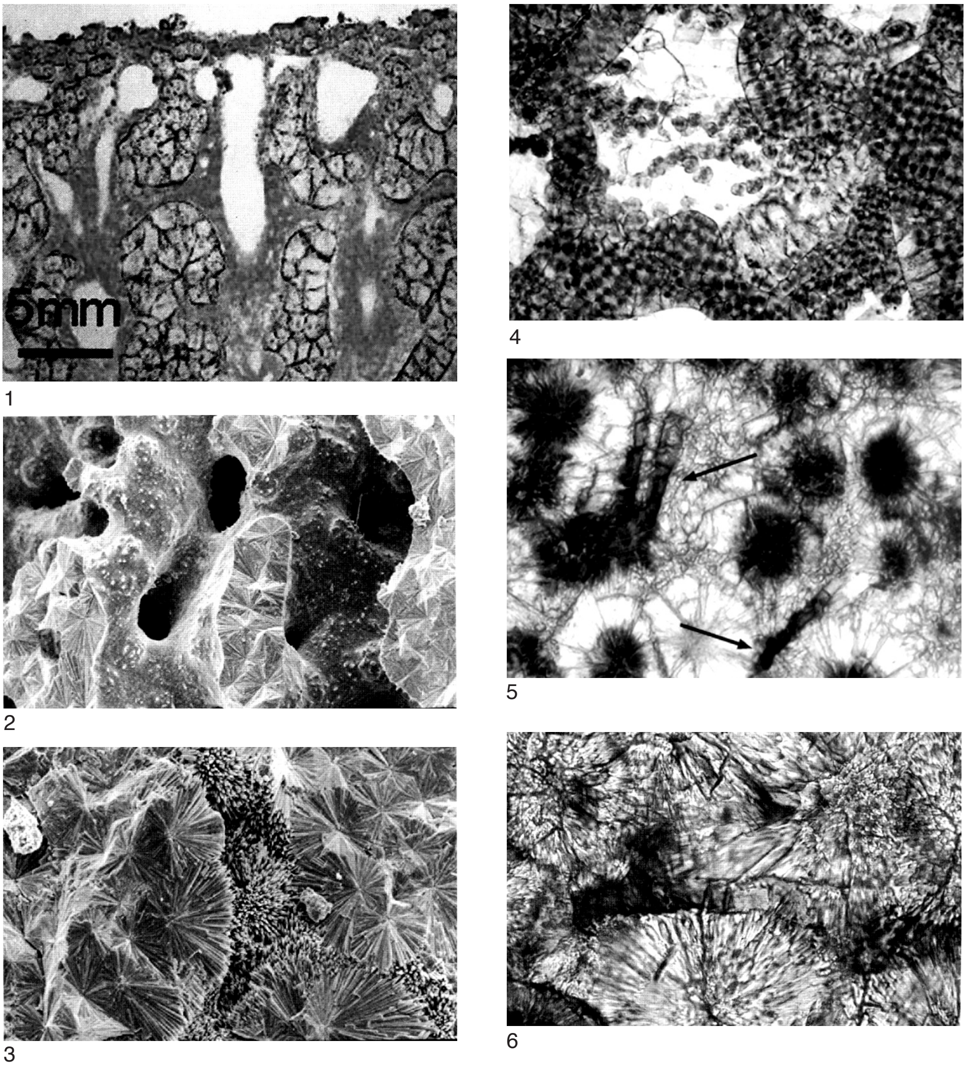


FIG. 48. Spherulitic microstructure in extant and fossil astrosclerid chaetetids; *1,* aragonite spherulites (lighter gray irregular areas that appear brecciated) in a longitudinal section through the living part of an extant specimen of *Astrosclera willeyana,* collected at a depth of 25 m, Ribbon Reef 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

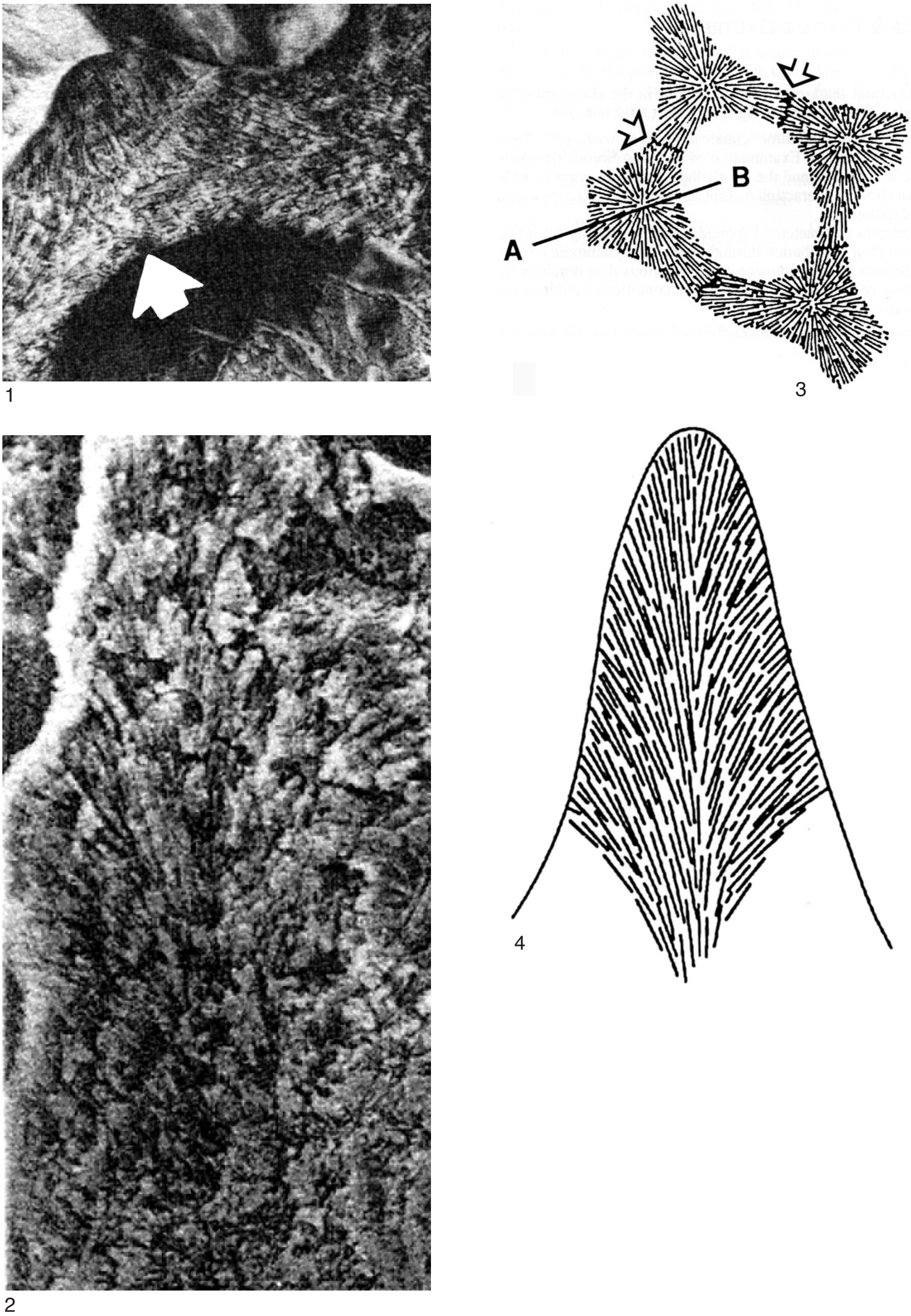


FIG. 49. *(For explanation, see facing page).*

(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).

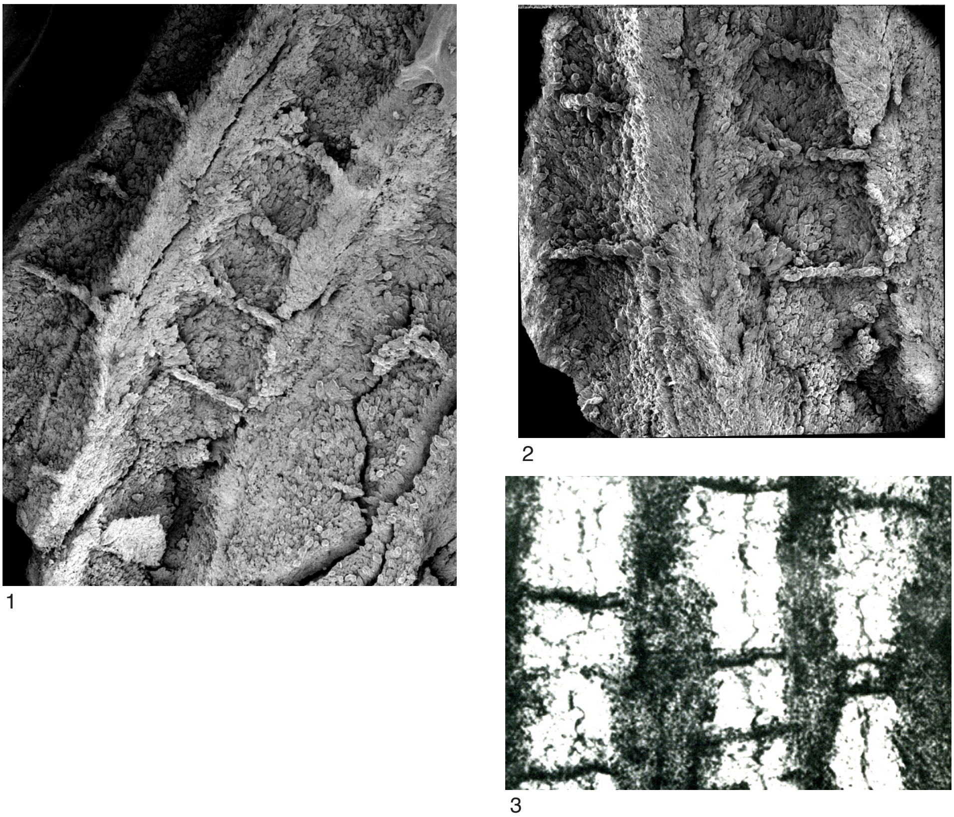


Fig. 50. Fascicular fibrous water-jet microstructure, Carboniferous, Pennsylvanian; *1,* SEM of a tangentially fractured chaetetid skeleton, Moscovian, Moscow Basin, Russia, ×50 (West, 2011a); *2,* enlarged view as seen in an SEM of a longitudinally fractured chaetetid skeleton, Moscovian, Moscow Basin, 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).

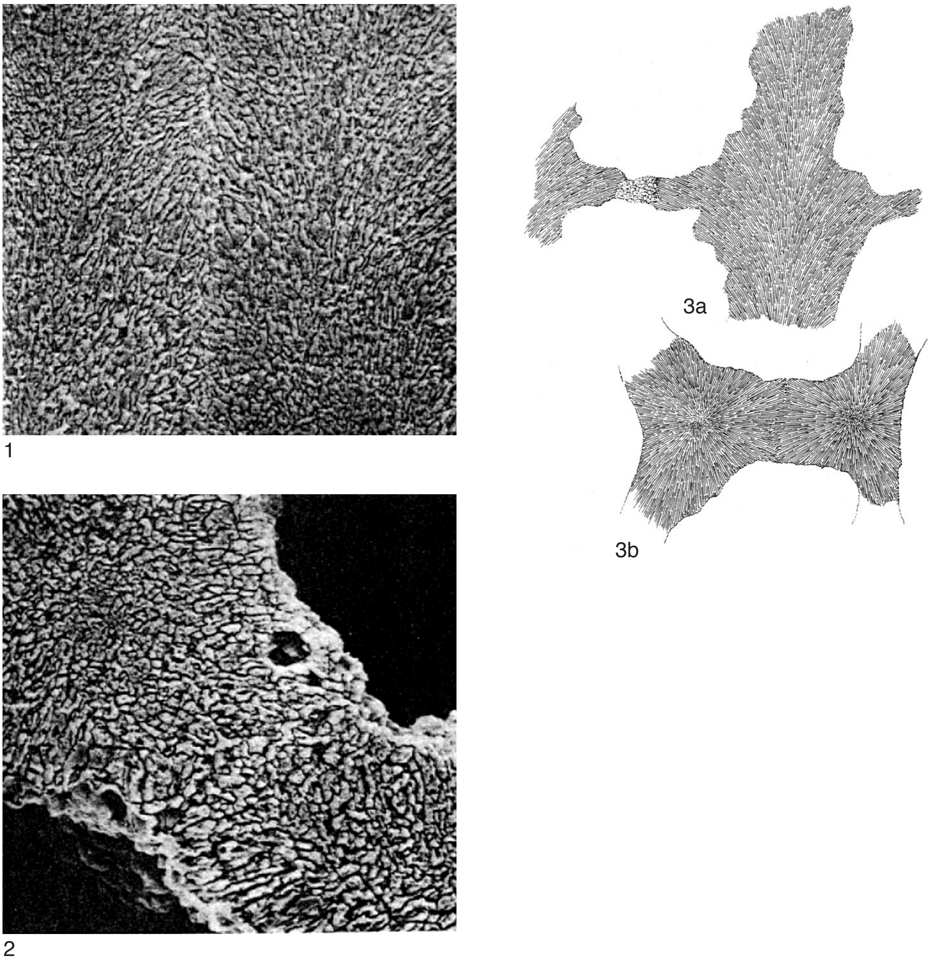


FIG. 51. Fascicular fibrous water-jet microstructure, Carboniferous, Pennsylvanian (continued); *1,* polished and etched longitudinal section of *Chaetetes (Chaetetes) cylindricus,* near Moscow, Russia, ×200 (adapted from Gautret, Vacelet, & Cuif, 1991, pl. III,*1*); *2,* polished and etched transverse 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*).

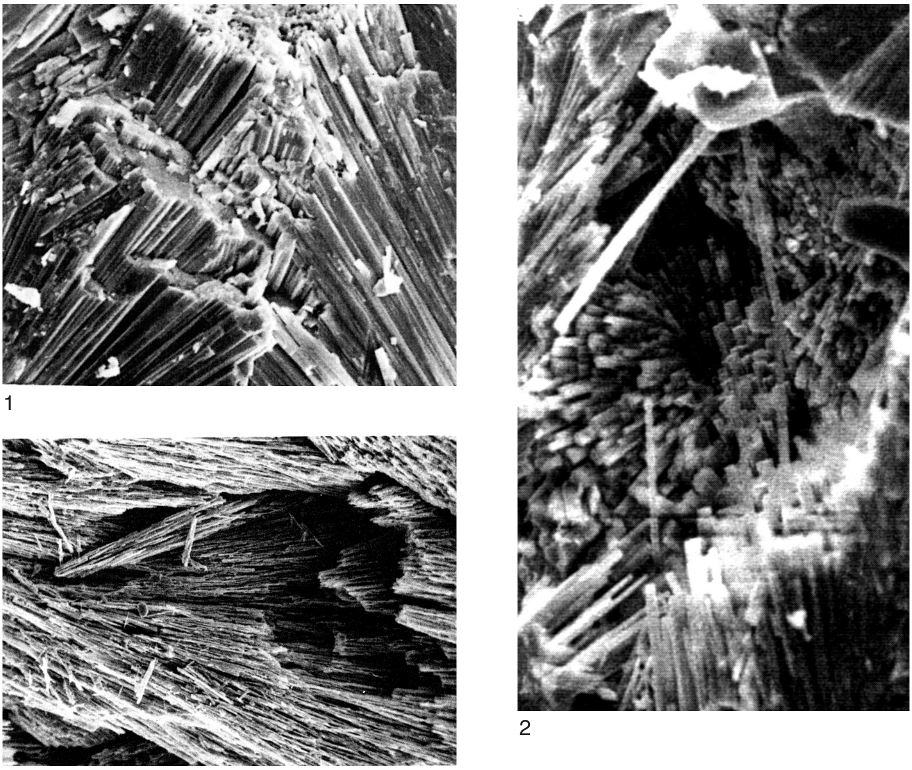


Fig. 52. Fascicular fibrous penicillate microstructure (clinogonal) in extant and fossil ceratoporellid chaetetids; *1,* SEM of the fascicular fibrous penicillate microstructure (clinogonal) in a fractured surface near the growing tip of a tubule in an extant specimen of *Ceratoporella nicholsoni,* West 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).

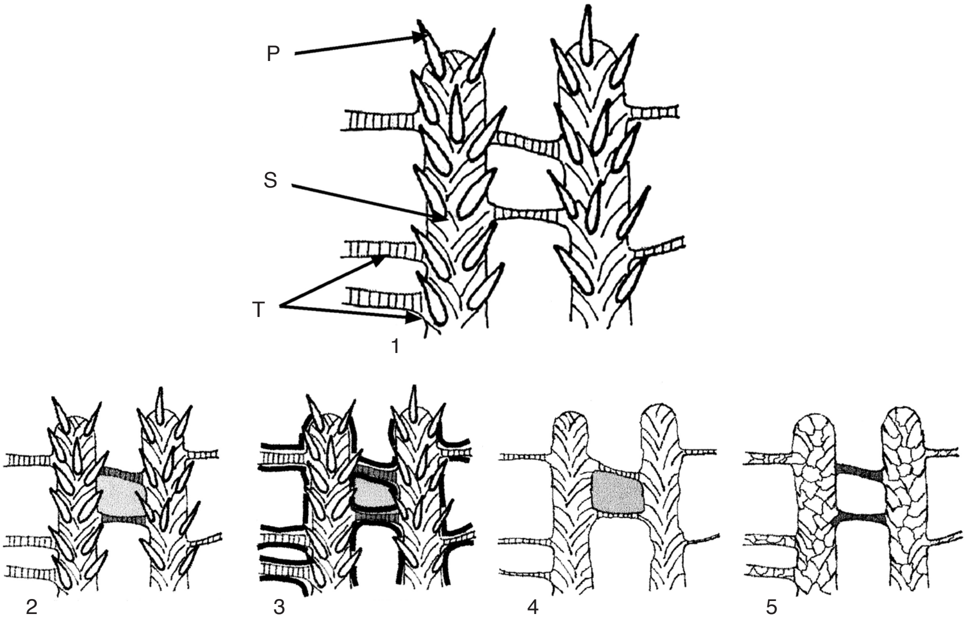


FIG. 53. Categories of skeletal features and potential results of diagenetic processes; *1,* three categories of skeletal features used in systematic studies of chaetetid sponges: *P,* primary, the composition and morphology of mega- and microscleres; *S,* secondary and includes the original mineralogy 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).

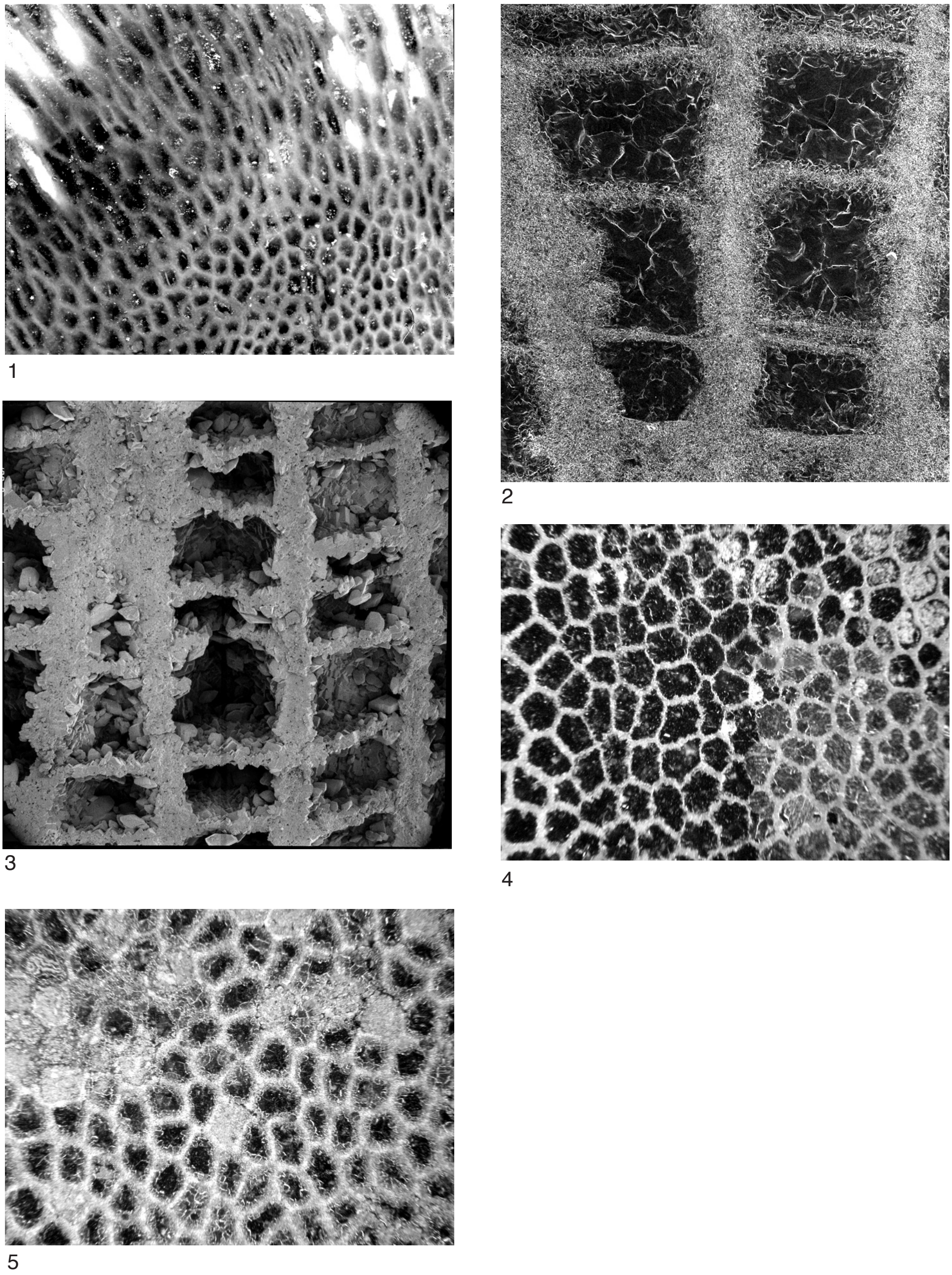


FIG. 54. *(For explanation, see facing page).*

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

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).

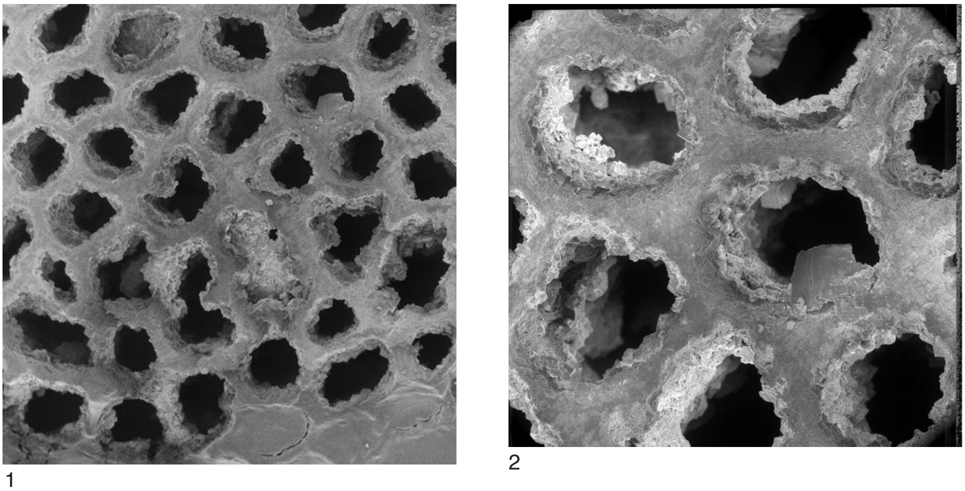
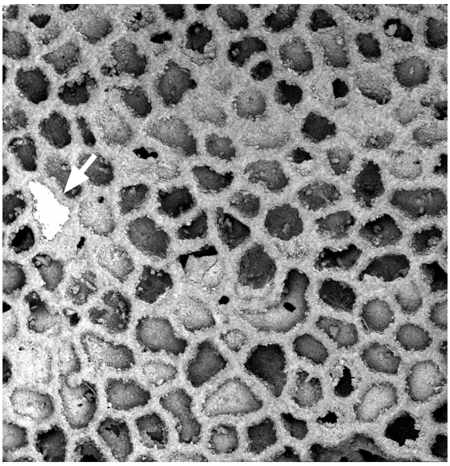


Fig. 55. Examples of diagenetically altered chaetetid skeletons (continued); *1,* SEM of a transverse surface, showing the increase in tubule wall thickness by the addition of mineral deposits in *Chaetetes (Chaetetes) radians,* Carboniferous, Pennsylvanian (Moscovian), near Moscow, Russia, ×30 (West, 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).

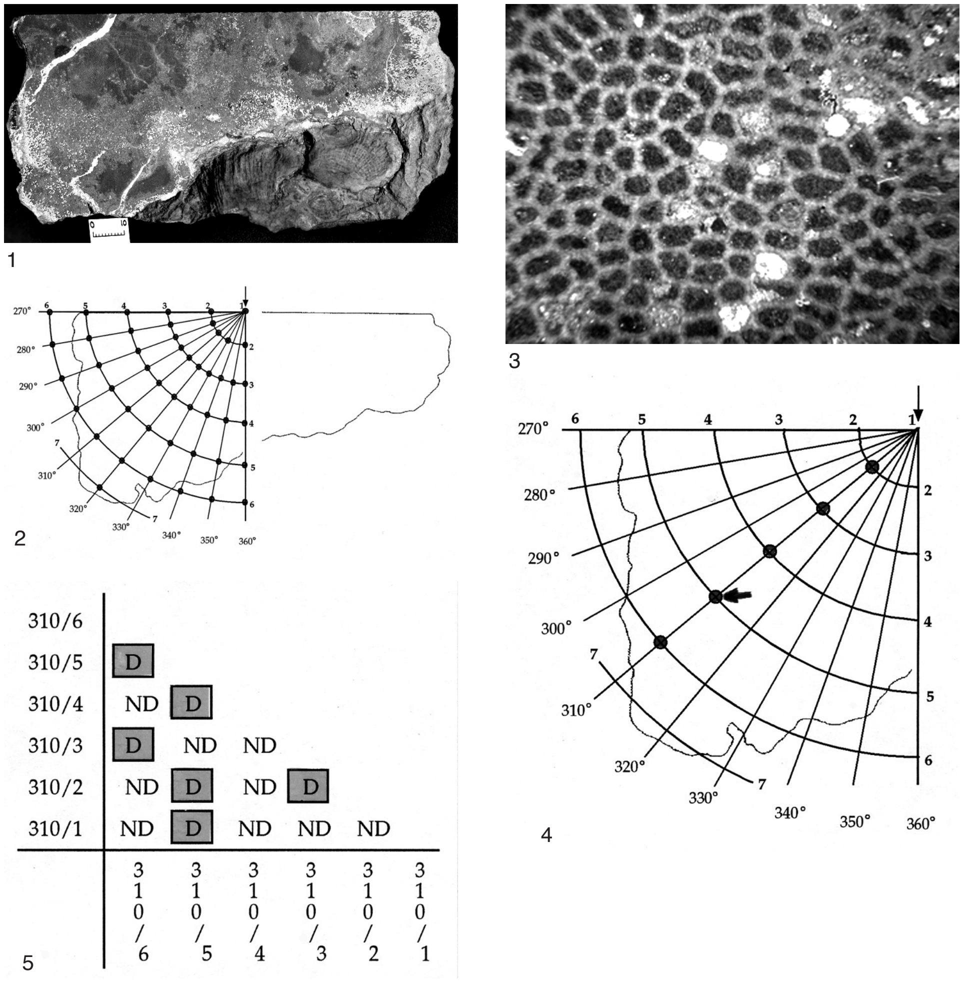


1

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

2

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



	310/6	310/5	310/4	310/3	310/2	310/1
310/6						
310/5	D					
310/4	ND	D				
310/3	D	ND	ND			
310/2	ND	D	ND	D		
310/1	ND	D	ND	ND	ND	

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).