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Living Hypercalcified Sponges**

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PART E, REVISED, VOLUME 4, CHAPTER 1: 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, 2002) 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 Calcispongiae. The term hypercalcified sponges is used here for representatives of both the classes Demospongiae and Calcispongiae, 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 Calcispongiae.

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
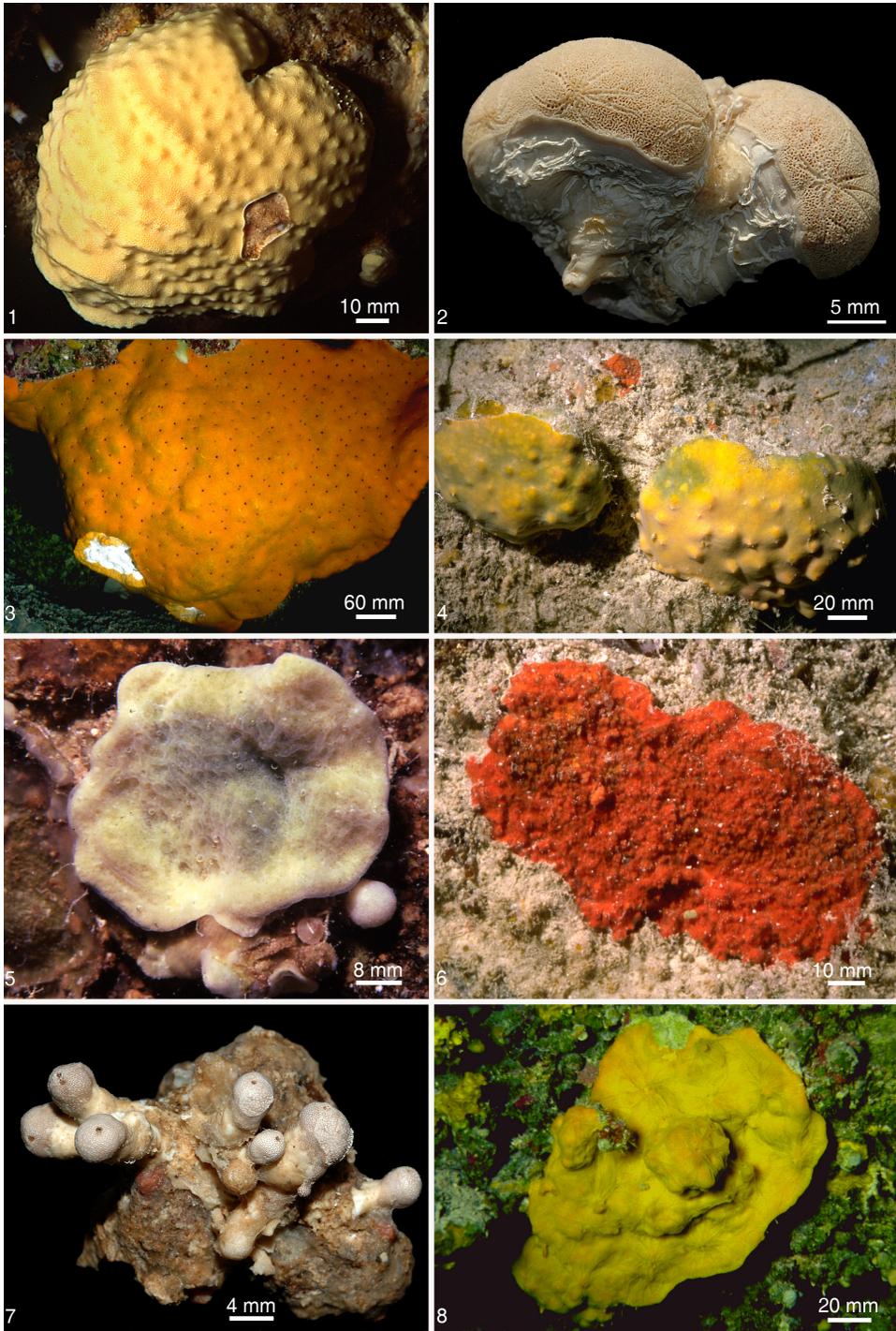
Fig. 1. *For explanation, see facing page.*

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 that is not derived from a primary spicular skeleton.

Fig. 1. Hypercalcified demosponges; *1, Acanthochaetetes wellsi* Hartman & Goreau, 1975; living specimen *in situ* from Touho reef, New Caledonia, 15 m (Vacelet, new); *2, Astrosclera willeyana* Lister, 1900; dry specimen with astrorhizae, the Philippines, 24 m (Vacelet, new); *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 (Willenz, new); *4, Ceratoporella nicholsoni* (Hickson, 1911); two specimens, *in situ,* 25 m, reef cave, northern coast of Jamaica (Willenz, new); *5, Goreauiella auriculata* Hartman, 1969; *in situ,* 25 m, reef cave, northern coast of Jamaica (Willenz, new); *6, Hispidopetra miniana* Hartman, 1969; *in situ,* 25 m, reef cave, northern coast of Jamaica (Willenz, new); *7, Vaceletia crypta* (Vacelet, 1977); view from cavities of front coral reef, New Caledonia, 15 m (Vacelet, new); *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).
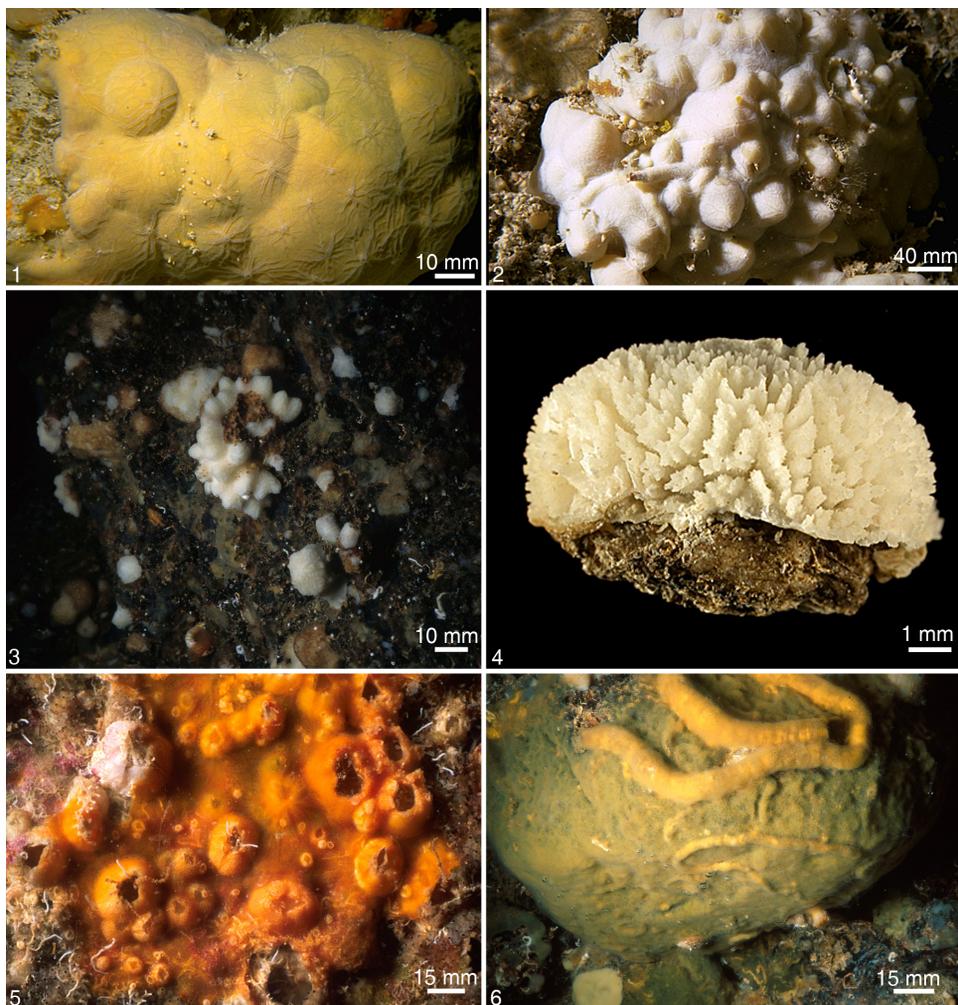
Fig. 2. Hypercalcified demosponges; *1, Ceratoporella nicholsoni* (HICKSON, 1911); *in situ,* 25 m, reef cave, northern coast of Jamaica (Willenz, new); *2, Stromatospongia norae* HARTMAN, 1969; *in situ,* 25 m, reef cave, northern coast of Jamaica (Willenz, new); *3, Petrobiona massiliana* VACELET & LÉVI, 1958; *in situ,* 15 m, cave of La Ciotat, northwestern Mediterranean (Vacelet, new); *4, P. massiliana;* massive skeleton after removal of living tissue (Willenz, new); *5, Merlia normani* KIRKPATRICK, 1908; *in situ,* 12 m, cave, Lebanon, Ramkine island, living tissue covering thin, calcareous skeleton (Vacelet, new); *6, Merlia deficiens* VACELET, 1980; *in situ,* 12 m, cave of La Ciotat (northwestern Mediterranean); species is similar to *Merlia normani* but devoid of thin, underlying, calcareous skeleton (Vacelet, new).

In the first type, found only in the family Minchinellidae of the Calcispongiae, 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 hexactinellids, 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*, 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*, 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*, 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 Calcispongiae, 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 Calcispongiae (two genera, *Murrayona* [Fig. 3,*1*] and *Petrobiona*), 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 Calcispongiae, 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*. 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 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
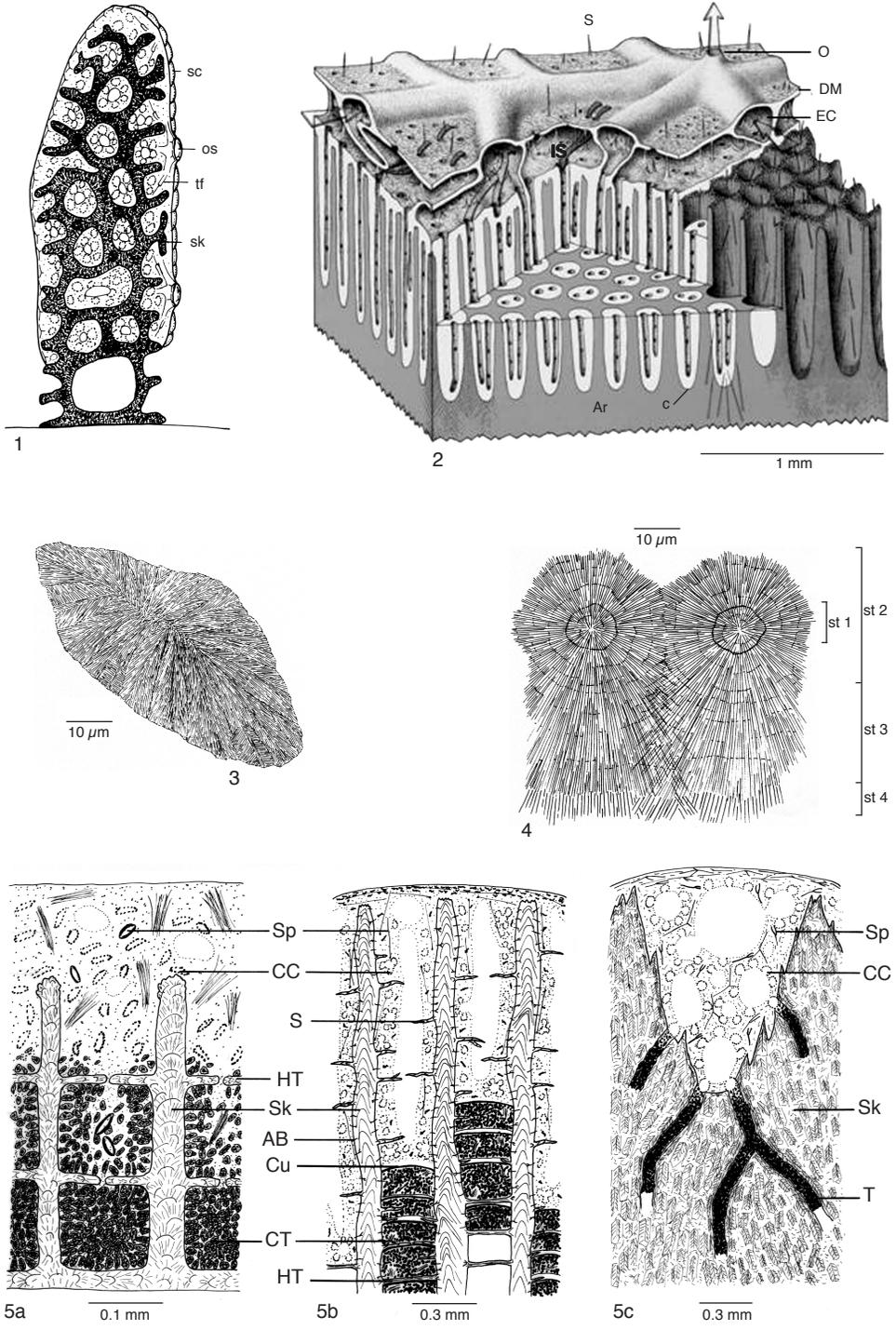
Fig. 3. *For explanation, see facing page.*

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 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,*1–2*). The basal and lateral surfaces of the dead skeletal mass are covered by an epitheca showing growth

FIG. 3. *1, Murrayona phanolepis* KIRKPATRICK, 1910; 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); *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).
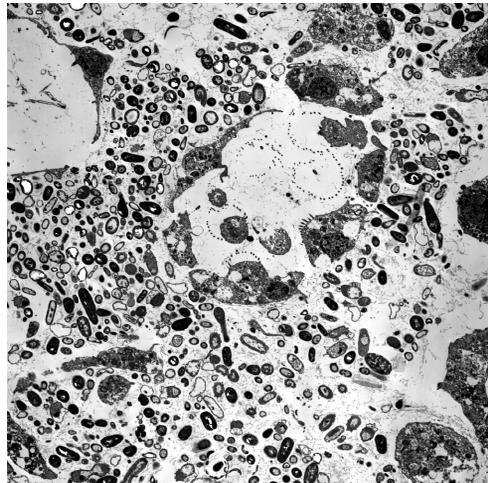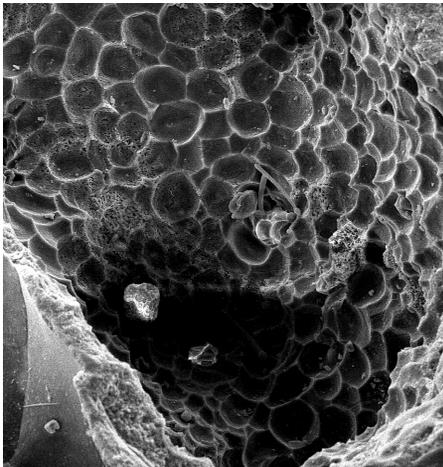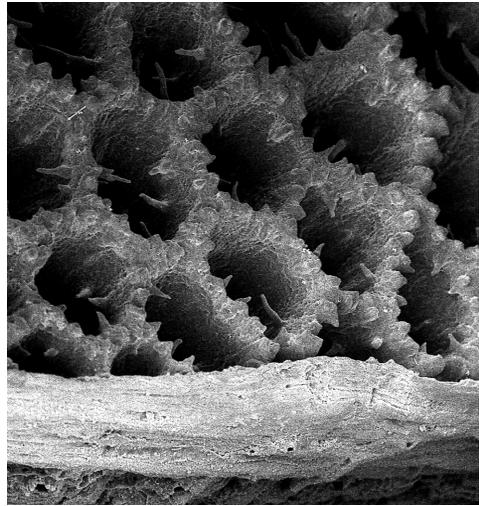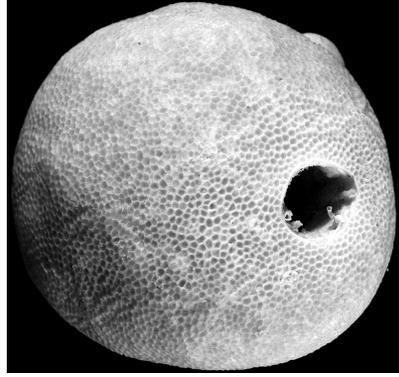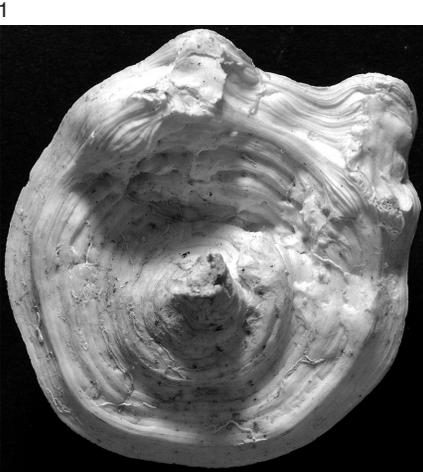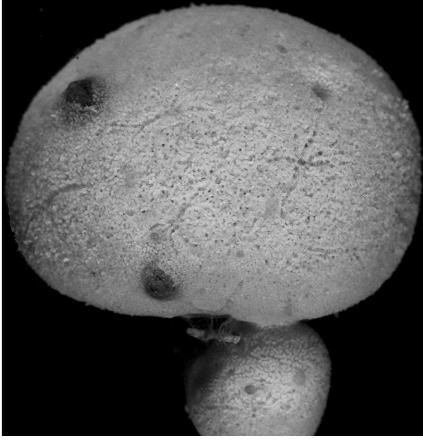
FIG. 4. *For explanation, see facing page.*

lines (Fig. 4,*3–4*), 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 (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).

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, new); *2, Acanthochaetetes wellsi* HARTMAN & GOREAU, 1975; astrorhizae and a trace left by unidentified invertebrate, Beautemps-Beaupré, 12 m, New Caledonia, ×2.08 (Vacelet, new); *3, A. wellsi*; basal part of specimen showing basal peduncle and epitheca, Philippines, 24 m, ×1.8 (Vacelet, new); *4, A. wellsi;* SEM view of surface and epitheca, Escape Reef, 12 m, Great Barrier Reef, ×40 (Vacelet, new); *5, Vaceletia crypta* (VACELET, 1977); trace of excavating sponge, *Thoosa* sp., in skeleton, New Caledonia, 38 m, ×140 (Vacelet, new); *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, new).

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, 1990). 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 Calcispongiae. 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 Calcispongiae, 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 Astro-

scleridae (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 Calcispongiae, 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 Calcispongiae 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,*1–2;* TAPANILA, 2005). The lower part of the basal skeleton is regularly colonized by sessile organisms, such as thin encrusting sponges, lithistids, Calcispongiae, 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* (Calcispongiae) 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* (Calcispongiae) 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 two species, *Ceratoporella nicholsoni* (LANG, HARTMAN, & LAND, 1975) and *Vaceletia crypta* (VACELET & others, 1992) could replace scleractinian corals as the main reef builders.
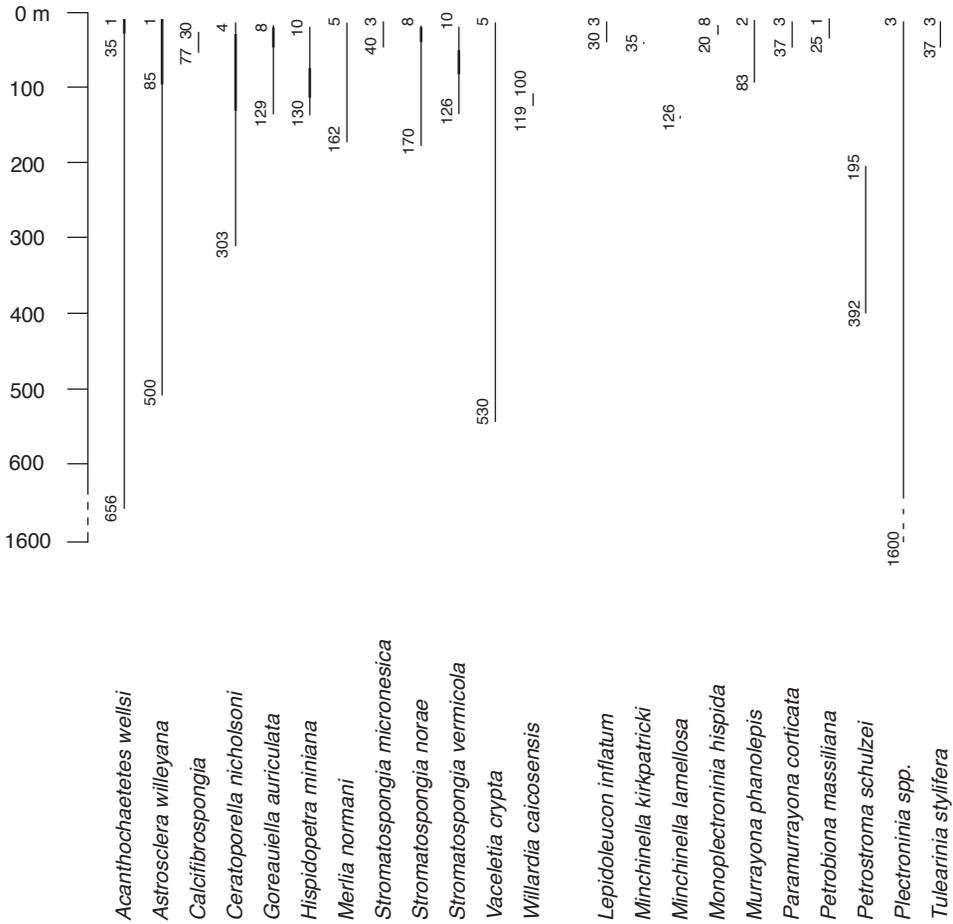
FIG. 5. Depth chart. Vertical distribution of extant hypercalcified Demospongiae and Calcispongiae. Optimum depth, where known, indicated by thickened bars (adapted from Vacelet, 1988, with addition of some species and unpublished data, Vacelet, 1998).

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 Calcispongiae, 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. 2,5–6) (Vacelet, 1980). 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 the living tissue of which does not indicate clear affinities, was *incertae sedis* in the Demospongiae; but recent results from molecular phylogeny indicate close affinities with the keratose sponge order Dictyoceratida (Wörheide, 2008). This suggests that some fossil sphinctozoans of the order Verticillitida also could 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. The fossil Chaetetidae 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.

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