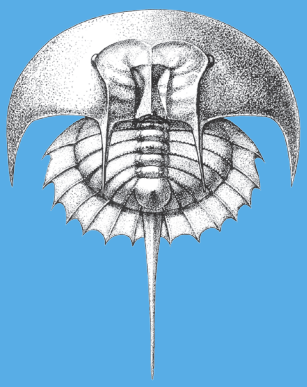

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PART E, REVISED, VOLUME 4, CHAPTER 9F: FUNCTIONAL MORPHOLOGY OF THE PALEOZOIC STROMATOPOROID SKELETON

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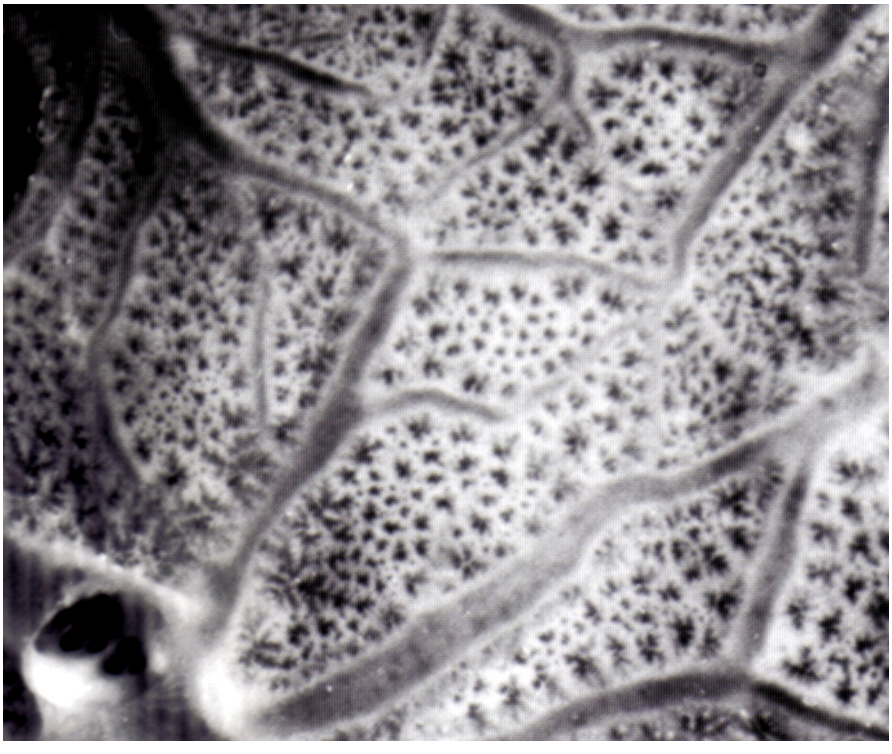
INTRODUCTION

Interpretation of the life processes of long-dead fossil organisms proceeds by comparisons of their morphologic features with engineering models of their possible functions and by comparisons with living organisms of similar form whose functions can be observed directly (Hickman, 1988). For stromatoporoids, both methods are possible, as the laws of fluid mechanics can be applied to their canal systems, and living sponges have some morphologic features of fossil stromatoporoid skeletons.

Until 1970, the Paleozoic stromatoporoids had been considered by most paleontologists to be hydrozoans, but since that time the conviction that they were sponges has grown to a virtual certainty. Evidence for this assignment and evidence against their affinity to other groups, such as the Foraminifera, cyanobacteria, and corals, to which they had been assigned formerly, is presented in the chapter on Morphologic Affinities (*Treatise Online,* Part E, Revised, Volume 4, Chapter 9E). This discussion of their functional morphology is predicated on their placement in the phylum Porifera. Like sponges, the Paleozoic stromatoporoids were sessile, suspension-feeding acoelomate invertebrates that ingested very fine suspended food, such as bacteria, and also probably dissolved organic nutrients. They obtained this food through a water-processing system that included fine, widely distributed pores that pulled sea water into a set of inhalant canals leading to chambers lined with flagellated cells. These flagellated cells and cells in contact with the entering water current trapped a variety of microorganisms and detritus.

"Sponges are little more than highly elaborate manifolds of pipes with lots of small pores and one, or a few, large, commonly apical openings on their surfaces" (Vogel, 1994, p. 38). The laws governing the flow of fluids through these manifolds (and hence the morphology of the organism) are conveniently summarized by Steven Vogel in the book, *Life in Moving Fluids* (2nd ed., 1994). Water is impelled through the tubes by flagellated cells (choanocytes) grouped in minute chambers. The helicoidal beating of the flagella draws water through sievelike villi arranged in a collar at their bases, where food is trapped and ingested. In order to enter the inhalant pores on the outer surface and be available for intracellular digestion in the sponge soft tissue, the nutrient particles can be no more than a few micrometers in diameter and are thought to be largely bacteria. The motion of the flagella also pumps the cleared water out through canals of increasing diameter to external orifices called oscula. The outflow velocity of a single osculum may be as high as 20 cm per second, and, although the contribution of each flagellum is almost infinitely small, the tens of thousands of them that contribute to the water flow allow a sponge to process water equal to its own volume every five seconds (Reiswig, 1974). The most familiar marine sponges are cylindrical or vase shaped, and water enters the outer surface of the vase and exits via an interior cavity (spongocoel) from an osculum at the top. However, the stromatoporoids must have resembled modern encrusting sponges in which openings for inhalant and exhalant water currents share different parts of the same upper surface. Such sponges, and many other features of sponge anatomy, are illustrated by De Vos and others (1991) (Fig. 1,*1*). The relationships between the soft tissue and skeleton of most living sponges is not relevant to the understanding of the function

Stearn, C. W. 2010. Part E, Revised, Volume 4, Chapter 9F: Functional morphology of the Paleozoic stromatoporoid skeleton. Treatise Online 8:1–26, fig. 1–9.



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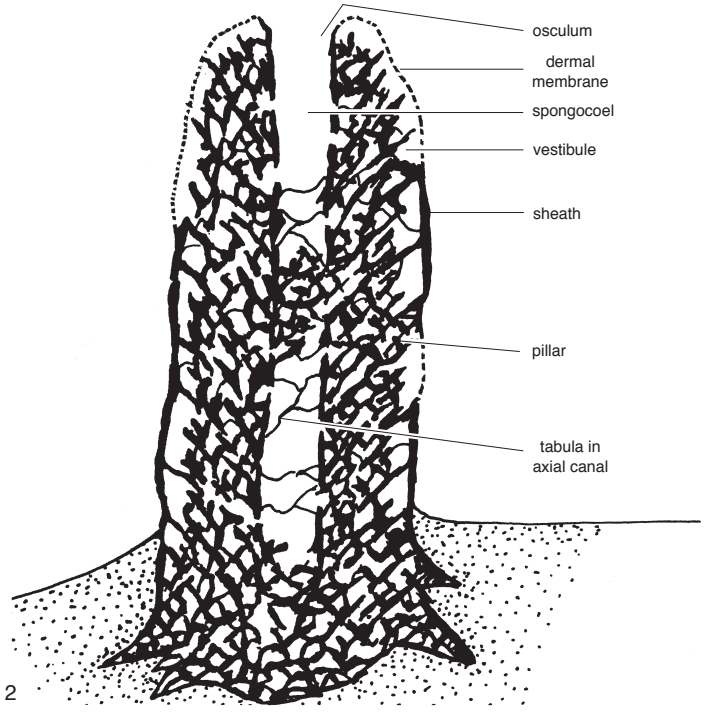

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FIG. 1. *For explanation, see facing page.*

of the skeleton of Paleozoic stromatoporoids, because the great majority of living sponges support their tissues with spicules made of silica, which are bound together by organic compounds subject to decay on death. This structural design is unknown in Paleozoic stromatoporoids. Only the few encrusting sponges of the modern fauna that secreted a basal calcareous skeleton provide a model for these extinct organisms.

The work of Willard HARTMAN and Thomas GOREAU (1970, 1972, 1975) in the late 1960s on the living hypercalcified sponges of Jamaica supplied a specific living model for the extinct Paleozoic stromatoporoids. The skeleton of these sponges is either solid carbonate or the inner cavities, once occupied by soft tissue, are sealed off, abandoned, and fill with sea water as the sponge grows larger. Among the stromatoporoids, only the skeleton of the enigmatic *Lophiostroma* is solid; the rest must have secreted their skeletons, much as hypercalcified sponges such as *Acanthochaetetes* and *Calcifibrospongia* do today. In these genera, soft tissue occupies only the upper interskeletal spaces, and the spaces below this thin living layer contain only water.

COLONIES OR INDIVIDUALS

Lack of evidence for multiple skeletal cavities, tubes, or enclosures suitable to house polyps in the stromatoporoid skeleton has convinced most paleontologists that the group cannot be closely related to clonal cnidarians such as hydrozoans, rugosans, or tabulates. A few paleontologists have modeled the astrorhizae as polyp sites (most recently BOGOYAVLENSKAYA, 1984), but this model does not explain their form, as discussed below (p. 22). The skeletons of several of the living hypercalcified sponges (*Ceratoporella*, *Merlia*, *Acanthochaetetes*) are divided into pseudocalices (small cavities in the upper surface containing units of the filtering system (see Fig. 7, Fig. 8,*1*), but the stromatoporoid skeleton is distinctive in that it must have been essentially continuous across the growing surface.

This is not the place to review the long controversy over whether sponges should be considered individuals or modular organisms. HARTMAN and REISWIG (1973) and FRY (1979) have provided summary discussions. These three, and also FINKS (2003, p. 213), regarded sponges as individuals with unitary control over their aquiferous systems. WOOD, ZHURAVLEV, and DEBRENNE (1992), following others, preferred to characterize most sponges, including stromatoporoids, as modular, and defined the repeated unit as the drainage area of a single osculum (Fig. 2). As applied to stromatoporoids, this would be the tissue and canals draining into a single astrorhizal system. However, the canal systems feeding an osculum may form a continuous, interconnected network over the surface of an encrusting sponge, and the so-called modules, defined on the basis of drainage areas, then have no boundaries in these sponges (Fig. 1,*1*). Also, in living sponges, reorganization of the oscular units of the aquiferous system in dimensions, spacing, and position may take place in a day. Such modules are in no way comparable to the individuals that form the skeletons of clonal animals in the Cnidaria, Bryozoa, or Hemichordata. In a few stromatoporoids, the astrorhizae, immobilized by encasement in the skeleton, maintained their position over long periods, becoming superposed as the skeleton grew; but in most stromatoporoids, the repeated reorganization of the aquiferous system is shown by the scattered distribution of canals observed in longitudinal sections. Evolutionary trends from individuals, through distinct modularity to integration of modules into a whole, have been traced through the Cnidaria (COATES &

FIG. 1. *1,* Surface of the living sponge *Spirastrella* showing network of exhalant canals (De Vos & others, 1991); *2,* reconstruction of digitate stromatoporoid *Amphipora ramosa* (PHILLIPS, 1841) in axial section, showing position of peripheral sheaths and dermal membrane (uncalcified) enclosing vestibules; actual specimens are 3–4 mm in diameter (Stearn, 1997).

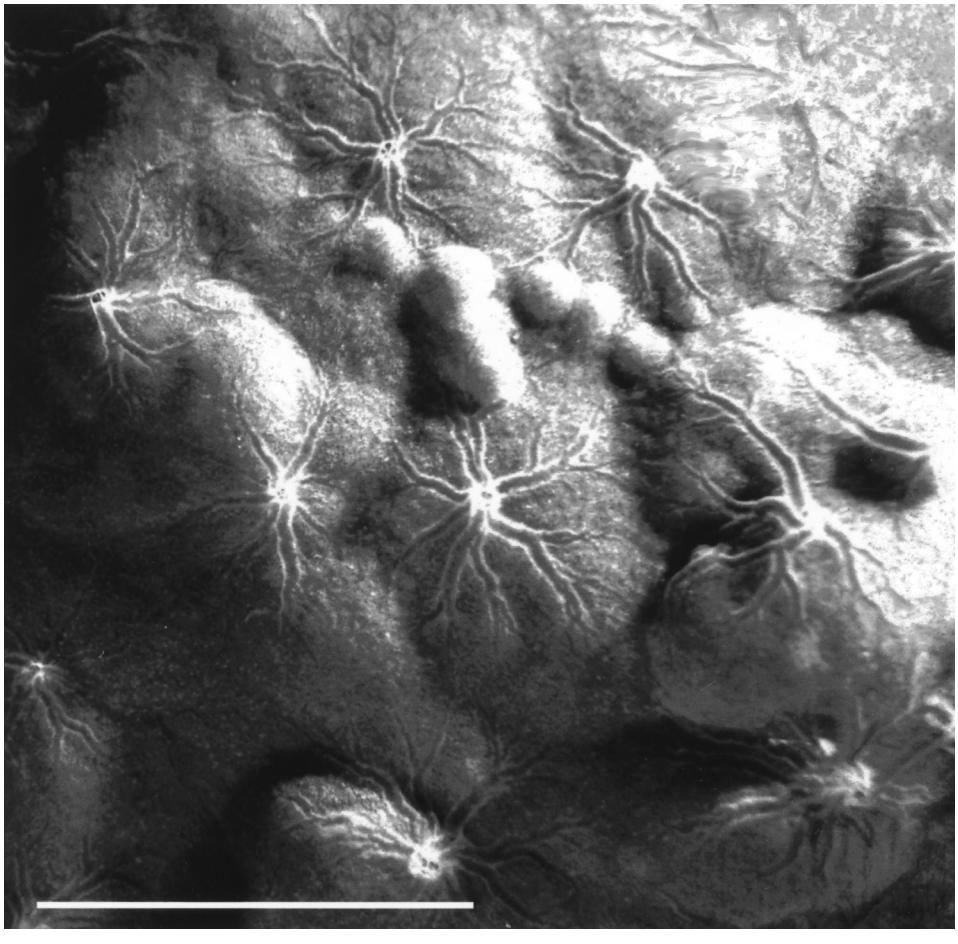


FIG. 2. Exhalant canal system, *Ceratoporella nicholsoni* (HICKSON, 1911), living specimen, Runaway Bay, Jamaica, scale bar, 2 cm (new; courtesy of H. Reiswig).

OLIVER, 1973) and Archaeocyatha (WOOD, ZHURAVLEV, & DEBRENNE, 1992). No such trends are evident in the Paleozoic stromatoporoids. STEARN and PICKETT (1994) have used the term module more appropriately as a skeletal unit added repeatedly during growth (see below).

SPICULES

Paleozoic stromatoporoids differ from most other sponges by their lack of spicules. Although both KIRKPATRICK (1912) and TWITCHELL (1928–1929) reported seeing the remains of spicules in Paleozoic stromatoporoids, their observations have not been confirmed by any later investigations. Although opaline spicules would be unstable in the calcium carbonate environment of the stromatoporoid skeleton, carbonate pseudomorphs might survive, if they were originally present. REITNER and WÖRHEIDE (2002, p. 59, fig. 12) have claimed that a specimen of *"Syringostroma* cf. *borealis* (NICHOLSON, 1875 [sic])," from the Middle Devonian of Spain, is the only Paleozoic stromatoporoid showing spicules, in this case, "aster microscleres." (The taxon referred to here is obscure, as NICHOLSON described only a single species under the name *borealis* in 1891 from the Silurian of Estonia; a species now assigned to

Syringostromella.) The Spanish specimen is here interpreted as showing coarsely cellular microstructure. Spicular pseudomorphs have been reported in late Paleozoic chaetetids and Mesozoic stromatoporoid-like genera (Gray, 1980; Wood & Reitner, 1986) and therefore might be expected to be preserved, at least under some circumstances, if siliceous spicules were secreted by Paleozoic stromatoporoids. As no spicules associated with their basal skeletons have ever been verified, the conclusion that Paleozoic stromatoporoids never did secrete spicules is justified, and deductions about their functional morphology should therefore be based on the assumption that the basal skeleton was their sole supporting structure. The presence of spicules in a late Carboniferous sponge, *Newellia mira* (Newell), as reported by Wood, Reitner, and West (1989), does not modify this statement, as this form (originally described with the stromatoporoid name *Parallelopora mira*) was never accepted by specialists as part of the Paleozoic stromatoporoid group. The relationship of spicules to basal skeletons in living hypercalcified sponges that are used as models for stromatoporoids is further considered under Microstructure (*Treatise Online,* Part E, Revised, Volume 4, Chapter 9D).

FUNCTION OF THE SKELETON AS A WHOLE

Why did stromatoporoids secrete a basal skeleton and why did they grow in forms shared by many clonal lower invertebrates that live in the reef environment? Because such organisms shared encrusting, tabular, domical, columnar, and dendroid shapes, we can conclude that the environmental and genetic controls on their growth were probably similar. The adaptations of these specific growth forms have been discussed by Kershaw (1984, 1998), Kershaw and Brunton (1998), Kano (1990), and several others and are summarized elsewhere (*Treatise Online,* Part E, Revised, Volume 4, Chapter 9B).

The major environmental factor affecting the growth form of stromatoporoids was rate of sedimentation (Kershaw, 1993). It follows that a major function of the skeleton was to raise the sponge above the sediment surface where particles would tend to clog the tiny incurrent pores. A modern sponge's defensive response to sediment is demonstrated when fine sediment is stirred up in storms, and the sponge closes its inhalant porocytes so that the filtration system does not clog (Reiswig, 1971). Because water is clearer higher in the water column, the stromatoporoid sponge gained by growing its top and side feeding surfaces above the turbid bottom waters. In areas of rapid sedimentation, rapid growth of the skeleton was necessary to keep the feeding surfaces from being buried, not just clogged. Why this group of sponges chose to support themselves above the accumulating sediment by means of a basal calcareous skeleton rather than the usual poriferan spicule network is not clear at present. That they did so over a period of 170 million years shows that this was a successful body plan and that the calcareous skeleton is a primitive shared characteristic of this unitary group.

Kazmierczak, Ittekkot, and Degens (1985) postulated that hypercalcified sponges and their ancestors secreted a basal skeleton, because they had to rid themselves of intracellular calcium ions. They believed that cyclic changes in calcium-ion concentrations in the marine environment caused deposition of laminae in stromatoporoids. Reitner and Wörheide (2002, p. 54) have postulated that Ca detoxification was a basic mineralization process in archaeocyaths and sphinctozoans and could be a model for all "irregular, micro-granular basal skeletons of 'stromatoporoid' and 'thalamid' grades of organization."

Schumacher and Plewka (1981) suggested that stromatoporoids built a skeleton of strength and weight to hold them on wave-swept reefs. They implied that the stromatoporoids had a skeleton of solid carbonate like that of the hypercalcified sponge *Ceratoporella*. Only *Lophiostroma*,

a fossil that may not be a stromatoporoid, had such a skeleton. In their porosity and bulk density, stromatoporoids were much like modern reef corals, and their extensive cavities were largely filled with water and minor syntaxial cements in life. However, stromatoporoids, like corals, must have achieved stability in a turbulent environment by means of the rigidity of their skeleton. That they were commonly unable to maintain their position in storms is shown by the ubiquity of broken and displaced specimens.

MISTIAEN (1994) calculated that the average skeletal density of stromatoporoid skeletons increased from about 45% in Ordovician (Caradoc) time to about 75% in early late Devonian (Frasnian) time and then decreased rapidly to the end of the Devonian as labechiids took over. He postulated that, at the close of the Devonian, they lost their skeletons entirely and persisted through the late Paleozoic and earliest Mesozoic as soft-bodied forms, before reappearing as the fossilized stromatoporoid-like forms (see also VACELET, 1985). He related these changes to cycles in chemistry and temperature of sea water as it passed through greenhouse and icehouse phases.

The competitive advantages of many of the clonal organisms that shared growth patterns and environments with stromatoporoids have been considered by COATES and JACKSON (1985), but the applicability of their conclusions, based on corals and bryozoans, to stromatoporoid sponges is in doubt (STEARN, 1982). These organisms are or were typically shallow water, sessile benthos living in reef and level-bottom environments. Such organisms today compete for space (settlement and growth sites), light, and food in hard substrate environments of considerable turbulence.

SKELETAL FRAGMENTS AND PROPAGATION

The highly branched forms and rapid growth rates of many modern scleractinians allow them to overgrow and shade their competitors and to propagate new colonies by fragmentation during tropical storms. Rapidly growing, broken branches soon establish new growth if carried to suitable environments. The fragmentation of stromatoporoids has been considered by KERSHAW and BRUNTON (1998), but there have been no suggestions that this is an adaptation for propagation, and only for dendroid forms, like *Amphipora*, would such breakage have a potential for dispersal.

Several writers have suggested that dendroid branches of such genera as *Amphipora* and *Stachyodes* were high, cylindrical mamelons broken off from tabular or domical bases (BOGOYAVLENSKAYA, 1985; WEBBY, 1993; KERSHAW & BRUNTON, 1998). Rare specimens of *Stachyodes* have been found with a laminar base and fingerlike mamelons (e.g., *S. fasciculata* HEINRICH [STEARN, 1966, p. 118]), but for *Amphipora*, despite the many millions of stems that throng Devonian limestones, no putative bases with broken off mamelons have been demonstrated. The only conclusion is that *Amphipora* stems grew upright (Fig. 1,*2*) with some means of holding themselves vertical in the sediment and that dispersal and propagation by breakage from a tabular or domical base was highly unlikely (STEARN, 1997).

LIGHT DEPENDENCE IN STROMATOPOROIDS

The scleractinians have had great success in modern reefs, becoming the dominant metazoans due to their ability to calcify rapidly with the aid of symbiotic dinoflagellates (identified largely as *Symbiodinium microadriaticum*). Organisms that live by such symbiosis are referred to as mixotrophs, because their metabolic needs are satisfied partly by the ingestion of food and partly by photosynthesis. Mixotrophs are particularly adapted to living in environments of low nutrient supply and productivity, and proof that the stromatoporoids belonged to this group would have important implications for mid-Paleozoic paleoceanography. The

mechanism by which photosynthetic symbionts aid the calcification of reef corals is not completely understood, and the symbionts are not closely associated with the tissues that most actively secrete the skeleton (Constantz, 1986; Cohen & McConnaughey, 2003; Weiner & Dove, 2003). However, this symbiosis allows their skeletons to extend at rates of a few millimeters per year. In contrast, the modern sponges used as models for the Paleozoic stromatoporoids, the hypercalcified sponges, do not have symbionts capable of aiding calcification, grow skeletons much more slowly, and have been relegated to dark, cryptic habitats in the competition for space on modern reefs. On what basis did the stromatoporoids compete with clonal rugosans, tabulates, and trepostome bryozoans with whom they grew on early Paleozoic reefs?

Kershaw (1998) reviewed some of the published data on phototrophism in stromatoporoids. Cowen (1983, 1988), Vacelet (1984), Coates and Jackson (1987), Young and Scrutton (1991), and Wood (1993) speculated on the possibility that the reef-forming trio of the mid-Paleozoic rugosans, tabulates, and stromatoporoids had symbiotic algae that enhanced calcification and growth rate. The rate of calcification evident in the formation of vast Devonian reef tracts has been claimed to be evidence that rapid growth of these organisms was aided by symbiosis. As discussed below, we have no sure measure of the growth rate of any of these organisms, but because they lived in competition for living space over an interval of about 170 million years, their rates were probably roughly comparable, otherwise one would have excluded the others from a rapidly growing reef surface. However, unaided by intracellular symbionts, they all could have grown slowly relative to modern corals. The average rate of upward growth of Devonian reef tracts (that is, the thickness divided by the interval of accumulation) is of the order of a few millimeters per century, which could hardly be considered evidence for rapid growth of the reef builders. Coates and Jackson (1987) did not consider stromatoporoids in their study but concluded that morphological criteria suggest that Siluro-Devonian tabulates contained photosynthetic symbionts. Cowen (1988) used extensive surface area, thinness of living tissue, fast growth, and shallowness of habitat to conclude that stromatoporoids were photosynthetic, but none of these criteria is robust.

Living sponges have many unicellular symbionts, so many (up to 50% of the tissue) that some may be referred to as bacteriosponges (Reiswig, 1981), but they are not the type that aid calcification (Fig. 3). The only sponges harboring dinoflagellate symbionts like the corals are the clionids that bore into the hard tissue of modern corals, and their function in these sponges is problematic (Vacelet, 1984). Most sponge symbionts are cyanobacteria that require light to grow and multiply. Wilkinson (1987) concluded that the photosynthesis of cyanobacteria within sponge tissue makes significant contributions to the energy requirements of sponges on a reef flat on the Great Barrier Reef. Willenz and Hartman (1989) reported that the soft tissue of *Ceratoporella* included nearly 20% bacteria. The lophocytes (collagen-secreting cells) ingest these bacteria for food, but other relationships between the bacteria and the sponge are in doubt. They may aid the sponges in using the dissolved organic matter in sea water (Vacelet, 1984). We cannot know whether stromatoporoids shared the propensity of modern sponges to harbor symbionts, but there is no direct evidence that they did so.

In some specimens of stromatoporoids, Kazmierczak (1976, 1980) has illustrated granular fabrics that he interpreted as fossilized coccoid cyanobacteria. These were not interpreted as symbionts, but, on the basis of these specimens, he has attributed the whole class to the Cyanobacteria, a viewpoint that is rejected here (as discussed in the chapter on Morphologic Affinities, *Treatise Online,* Part E, Revised, Volume 4, Chapter 9E).

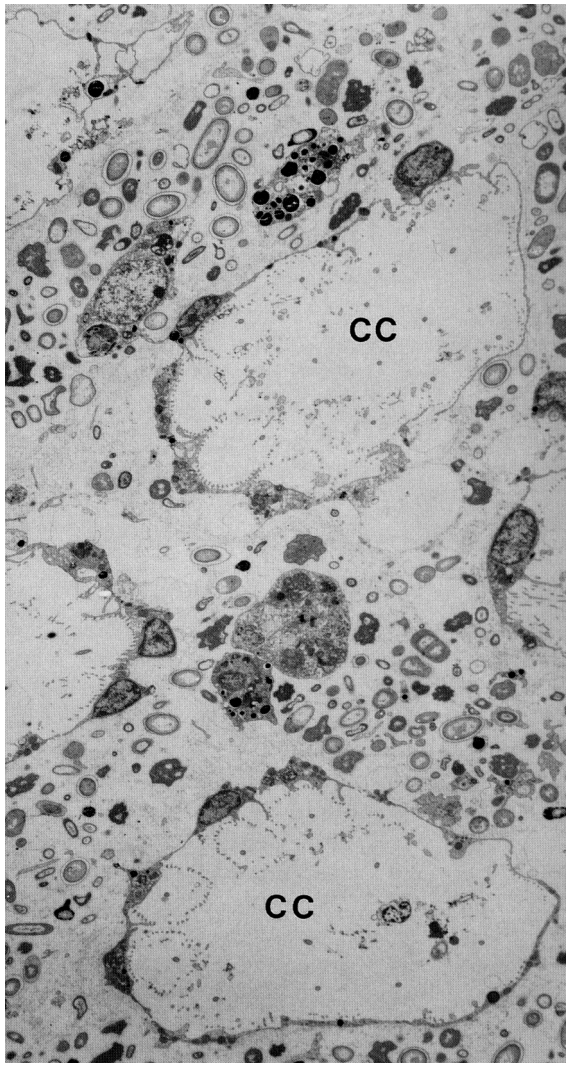


Fig. 3. Symbiotic cyanobacteria, *Ceratoporella nicholsoni* (HICKSON, 1911); Pear Tree Bottom, Jamaica; choanocyte chambers (*cc*), ×2400 (new; courtesy of Ph. Willenz).

ISOTOPE FRACTIONATION

Modern mixotrophic corals secrete a carbonate skeleton that has a distinctive signature of carbon and oxygen isotopes, owing to fractionation of algal photosynthesis.

SWART (1983) summarized the differences between the isotopic ratios in the skeletons of mixotrophic and nonmixotrophic corals. In mixotrophs, he found no correlation between the oxygen and carbon isotopes but a narrow range of values. MALLAMO (1995) has attempted to identify this signature in stromatoporoid skeletal material. Samples of the skeleton were extracted from Devonian and Silurian stromatoporoids using a microdrill to avoid contamination by the gallery fillings. MALLAMO (1995) found $\delta^{13}C$ (PDB) values in the 1.26 to 3.48 range and $\delta^{18}O$ (PDB) in the –9.10 to –4.22 range. Photosynthesis preferentially fixes and

removes ^{12}C, increasing the $^{13}C/^{12}C$ ratio in the skeleton (Norris, 1998). These values showed an enrichment in the ^{13}C isotope and no correlation between the oxygen and carbon isotopes; both results suggest, but are far from proving, that these stromatoporoids could have been mixotrophs. Suggestive also was the correspondence in isotopic signatures between a specimen of *Stromatopora* from Wenlock, England, and that of Triassic corals that Swart and Stanley (1989) suggested were mixotrophs.

GROWTH RATES AND GROWTH BANDS

If stromatoporoids were mixotrophs like scleractinians, their rate of calcification was probably rapid. Latilaminar growth (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, p. 25–27), the rhythmic repetition of growth units (latilaminae) commonly separated by growth interruption surfaces, is common in stromatoporoids (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 13,*2,* Fig. 14,*3*). The thickness of these latilaminae is a few millimeters. The repetition of these units suggests that they are annual accretion units, but as yet no proof of their time value has been demonstrated (Young & Kershaw, 2005). On the basis of their observations on nonannual growth banding in domical skeletons of the hypercalcified sponge *Ceratoporella,* Willenz and Hartman (1985) have cautioned that the latilaminae of stromatoporoids should not be assumed to reflect annual cycles.

Meyer (1981) estimated vertical and horizontal growth rates in the Devonian stromatoporoids of Michigan on the basis of the relationships between favositid corals and the stromatoporoids that overgrew them. He assumed that bands defined by the spacing of tabulae in the corals were annual. Using this banding and steplike shape of the coral colony, he determined that the average lateral extension rate of 26 specimens of 3 species of stromatoporoids was between 10 and 23 mm per year. This was sufficient to allow the stromatoporoids to extend laterally over the corals, but their average vertical rate of growth was much lower, between 1.3 and 3 mm per year.

Risk, Pagani, and Elias (1987) described six stromatoporoid thin sections that were repeatedly crossed by bands of microborings that they homologized with those of endolithic algae in modern corals (*Osteobium*). In modern corals, these algae form annual bands immediately below the growing surface. The assumption that the Devonian microborings represent a similar phenomenon yields a growth rate of about 10 mm per year, about the rate of growth of a domical scleractinian such as *Montastrea annularis.* The microborings are not confined to the structural elements of the skeleton but also cross galleries filled with carbonate spar cement. This suggests that they were not formed in the same way as the bands of endolithic algae in modern corals, which are bored soon after the skeleton is secreted and while the interskeletal chambers are empty. How these bands of borings formed is problematic, but they are unlikely to give a reliable growth rate. Similar microborings on the exterior of Ordovician rugose corals have suggested to Elias (1982) that they grew at about 20 mm per year.

Gao and Copper (1997) measured the rates of growth of stromatoporoids from the early Silurian of Manitoulin Island, Canada, using the assumption that the latilaminae are annual additions. They found that the average thickness of the latilaminae in 6 genera ranged from 0.8 to 3.1 mm. They concluded that these results did not clearly indicate whether stromatoporoids were mixotrophic or not.

Young and Kershaw (2005) examined the spacing and nature of the boundaries of latilaminae in stromatoporoids but were unable to conclude whether they were annual or not. Nestor, Copper, and Stock (2010) discussed the seasonal growth bands of stromatoporoids from Anticosti Island and concluded that growth rates of a few millimeters per year were probable.

These rates for stromatoporoids of a few millimeters per year are of the same order of magnitude as those of modern scleractinian corals, but they are much higher than those of living hypercalcified sponges such as *Ceratoporella,* which adds only 0.2 mm per year to its skeleton (Willenz & Hartman, 1985). Since the discovery that hypercalcified sponges secrete a skeleton in isotopic equilibrium with ambient sea water and hence, owing to their slow growth, may preserve a record of ocean chemistry of the last several thousand years, many measurements of their growth rate have been made (Wörheide & others, 1997; Swart & others, 1998; Willenz & Hartman, 1999; Lazareth & others, 2000; Rosenheim & others, 2004). These studies agree that the living hypercalcified sponges grow at rates of less than 1 mm per year and commonly in the 0.2 to 0.3 mm range. The rate for the hypercalcified sponge *Acanthochaetetes* is only 50 µm per year (Reitner & Wörheide, 2002). Whether comparisons of stromatoporoid growth rates to those of their modern analogues has any validity, or relevance to their metabolism, is open to question.

In summary, inadequate evidence suggests that stromatoporoids probably added vertically to their basal skeleton at from 2 mm to 10 mm per year but is equivocal as to their light dependence.

STROMATOPOROID SKELETONS, LIGHT DEPENDENCE, AND REEF STRUCTURE

Light-dependent scleractinians compete for a "place in the sun." For this they grow in upward-spreading forms to overshadow their neighbors. The fragility of such forms in storms is compensated for by their ability to repair rapidly and propagate by fragmentation. The stoutly branching *Acropora palmata* that forms the reef fronts in Caribbean reefs illustrates this reef facies. These enmeshing growth forms are responsible for the cavernous framework structures of modern coral reefs and the ability of such edifices to stand against the attack of storm waves. The common domical and tabular growth forms of the stromatoporoids resemble those of living hypercalcified sponges that are cryptic in habitat and are not adapted to competition with neighbors for light. In mid-Paleozoic stromatoporoid reefs, the framework structure of modern reefs can rarely be demonstrated. Fagerstrom (1987) placed stromatoporoids in his binder guild, but in mid-Paleozoic reefs, the stromatoporoids, where they appear to be in place, grew as isolated organisms, rarely uniting to bind and enclose coarse sediment nor construct a framework. Kershaw (1998) concluded that field studies show that stromatoporoids grew on loose substrates rather than united into frameworks. Inability to form frameworks may account for the low marginal slopes of a few degrees in the profiles of mid-Paleozoic reefs, compared to the almost vertical underwater cliffs that are sustained by modern frame-builders around oceanic islands. These considerations suggest, but certainly do not prove, that the stromatoporoids did not compete with each other, or with other reef builders, for light.

SOFT TISSUE WITHIN THE SKELETON

To what extent was the soft tissue confined to the surface of the skeleton and how much of the skeleton did it penetrate? The living hypercalcified sponges, stromatoporoid analogs, exhibit a range of answers to these questions; in *Ceratoporella,* the soft tissue is entirely superficial; in *Astrosclera,* it fills spaces between skeletal elements deep below the surface. In most post-Ordovician stromatoporoids, the skeletal spaces are filled with calcite spar cement with textures typical of void-filling cements (see Microstructure, *Treatise Online,* Part E, Revised, Volume 4, Chapter 9D). There is no evidence in Paleozoic stromatoporoids that the lower parts of the skeleton were secondarily filled with carbonate by the animal, as in the living sponges *Vaceletia* and *Astrosclera,* in which

living tissue continues to lay down skeletal material well below the surface.

In some specimens of stromatoporoids, the uppermost galleries are distinguished from the spar-filled galleries in the rest of the skeleton by their filling of fine sediment (Fig. 4,*1;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 1,*1*) (STEARN & PICKETT, 1994). These galleries probably contained soft tissue when the organism suddenly died, while the interskeletal spaces below were water filled and sealed off from the soft tissue by tabulae, dissepiments, and laminae. The soft tissue decayed quickly, leaving the path open for sediment to enter before cement filled the empty spaces. Syntaxial cements in water-filled cavities of living corals indicate that abandoned and sealed-off parts of the skeleton may begin to be filled with cement while the coral is still alive at the surface of the skeleton.

At the final growth surfaces of stromatoporoids with laterally persistent laminae (Clathrodictyida, Stromatoporellida), usually only the layer of galleries below the incomplete last lamina has a sedimentary filling, rather than a cement filling. The soft tissue is unlikely to have penetrated deeper into the skeleton, and each completed lamina must have sealed off the interior. In most of the Stromatoporida, sediment surrounds the ends of the pachysteles to a depth of the highest dissepiment in the allotubes. In species with few dissepiments, sediment may penetrate the depth of the last latilamina (Fig. 4,*2*). In these stromatoporoids, the soft tissue presumably occupied the whole last latilamina, as appears to be the case in living *Calcifibrospongia*.

BASAL SKELETON SECRETION IN LIVING HYPERCALCIFIED SPONGES

Living hypercalcified sponges secrete their skeletons in three ways (WOOD, 1991).

1. Basal: through a glucopolysaccharide layer below a basopinacoderm, much like the corals (e.g., *Ceratoporella*).

2. Intracellular: within archaeocytes as spherulites, which are cemented together to form structural elements (e.g., *Astrosclera*).

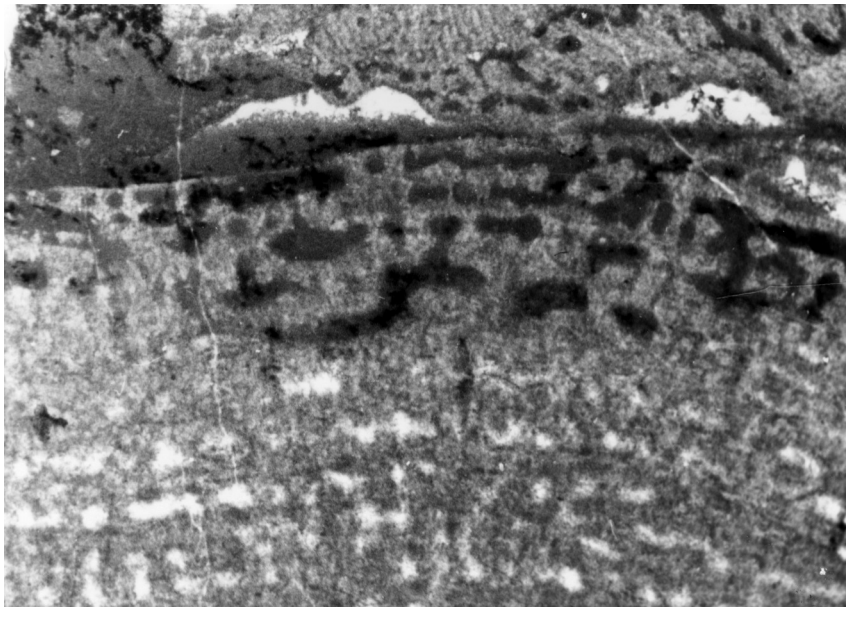
3. Collagenous: inside the soft tissue on an organic matrix (e.g., *Vaceletia*).

The stromatoporoids also appear to have secreted their skeletons using more than one mechanism, certainly methods 1 and 3, and possibly also 2.

1. The secretion of the skeletal tissue of some stromatoporoids can be explained as a result of deposition from a basopinacoderm lying at the base of the soft tissue. The soft tissue in this model is entirely separate from, and superficial to, the skeleton. The modern hypercalcified sponge *Ceratoporella* illustrates this pattern. The skeleton of this sponge is secreted at the base of the soft tissue. It forms in an organic matrix beneath a layer of basopinacocytes that appears to control the deposition of the aragonite needles. In addition, monaxon siliceous spicules are formed in the soft tissue by sclerocytes and incorporated in the basal skeleton as it grows upward.

This method of secretion was adduced by STEARN (1975) to explain skeleton formation in all stromatoporoids, but the model has problems with clathrodictyids and stromatoporellids, as explained below. It appears to be a satisfactory explanation for actinostromatids and labechiids, however (Fig. 4,*3*).

2. The open skeletal structure and spherulitic microstructure of the living hypercalcified sponge *Astrosclera* suggested to STEARN (1975) that the skeletons of the Stromatoporida were formed as in this sponge. In *Astrosclera,* the skeleton consists of aragonite spherules a few micrometers in diameter. Each spherule is formed intracellularly in soft tissue and is passed down to the skeletal surface, where it is cemented in place. (Skeleton secretion in *Astrosclera* is described fully by WÖRHEIDE and others [1997]). Proof that skeletons of the order Stromatoporida were ever spherulitic is lacking, and in well-preserved specimens,



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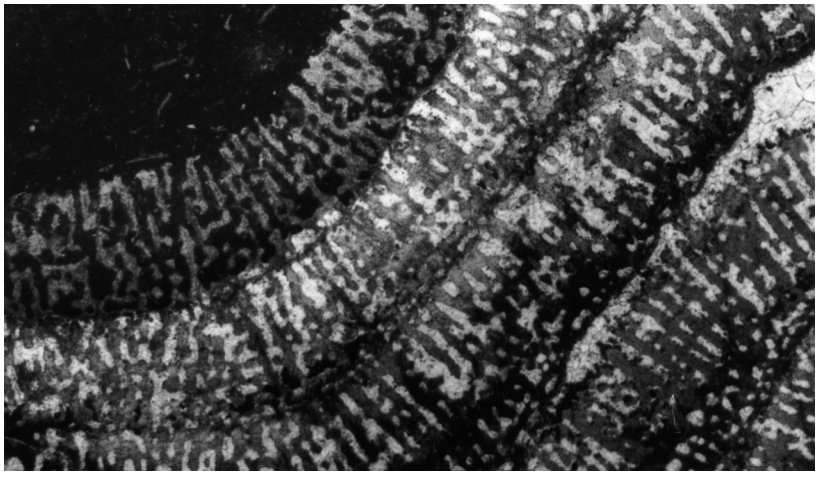

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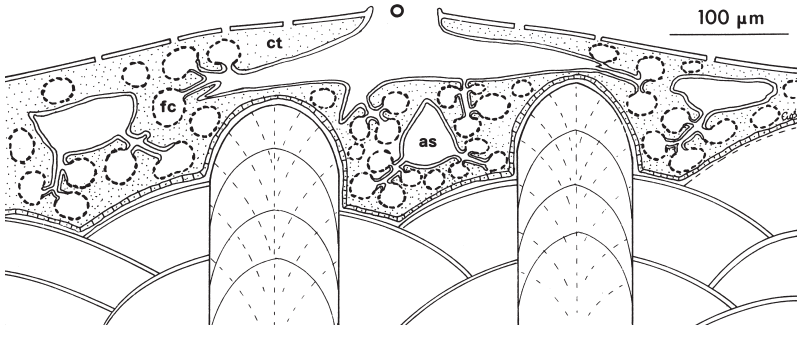

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FIG. 4. *For explanation, see facing page.*

the microstructure appears to have been originally porous (Stearn & Mah, 1987). Reitner and Wörheide (2002) described the various groups of sponges that secrete spherulitic skeletons and conclude that the microstructure has no taxonomic significance. Whether any stromatoporoids skeletons were ever spherulitic or secreted intracellularly remains problematic (see Microstructure, *Treatise Online,* Part E, Revised, Volume 4, Chapter 9D).

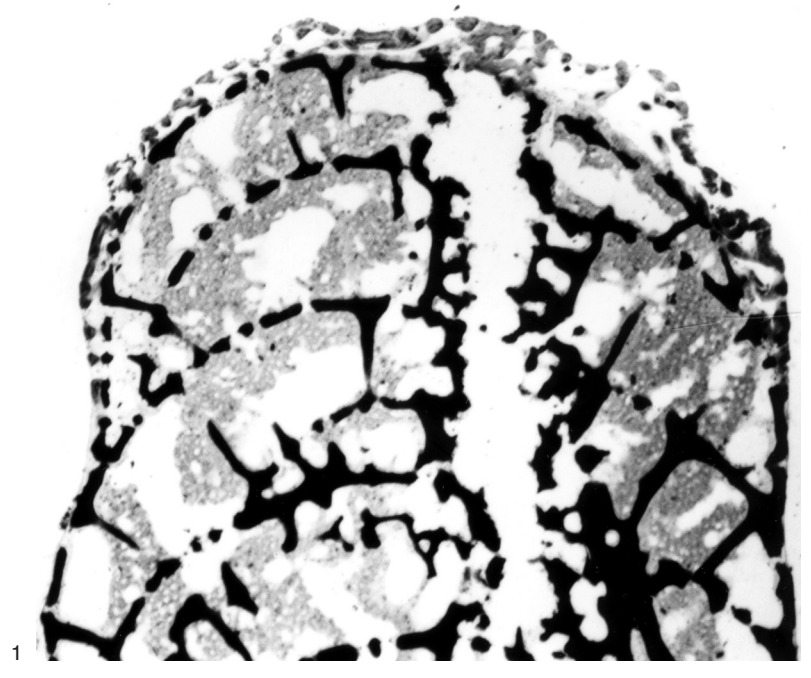
3. In stromatoporoids with skeletons dominated by laminae (the clathrodictyids and stromatoporellids), the laminae and pillars are commonly thinner within the terminal zone, where the galleries are filled with sediment (Fig. 4,*1*). This is the zone that was filled with soft tissue when the animal died. These thinner elements must have been in the process of formation within soft tissue when the animal died. The incomplete structural elements of these groups closely resemble the partially calcified matrix that is an intermediate stage in the secretion of a new chamber in the modern hypercalcified sponge *Vaceletia* and must have been secreted on an organic matrix inside the soft tissue of the surficial layer of the stromatoporoid (Fig. 5,*1*).

The wall of a new chamber in *Vaceletia* is formed just below the thin cell layer (exopinacoderm) that covers the last chamber. A collagenous template or organic matrix forms below this pinacoderm, and within this template, crystals of aragonite appear and grow into a felted layer to form a porous wall (Vacelet, 1979). The pillars within the chambers form by the mineralization of organic strands.

GROWTH MODULES OF LAMINATE STROMATOPOROIDS

The laminae of stromatoporellids are tripartite; that is, they are divided axially by a light layer that may appear continuous or as a line of cellules. Stearn (1975) explained the central light layer as being due to diagenetic leaching of the axis of crystallization of a trabecular aragonite sheet by meteoric waters. Kazmierczak (1971) interpreted it as a growth interruption surface. The nature of this zone is clear in *Simplexodictyon* (Fig. 5,*2;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 4,*2,4*), in which the upper and lower laminar layers part and reunite and may be separated by sediment, epibionts, or calcite cement (Powell, 1991). Each lamina in this genus is composed of two layers locally fused and locally separated. The fundamental unit secreted in successive growth modules within soft tissue consisted of (1) a floor that became the upper layer of an older lamina; (2) a roof that, as the next module was added, became the lower layer of the next tripartite lamina; and (3) the pillars and other structures enclosed between 1 and 2. This growth module is a laterally extensive chamber homologous to the chambers of the sphinctozoans. The modules must have been formed in soft tissue and added to the growing skeleton as units. In genera such as *Stictostroma, Stromatoporella,* and *Trupetostroma,* the axial light zone between the floor and roof of modules is divided into cellules or rounded, discontinuous spaces defining ordinicellular microstructure; that is, the floors and roofs are discontinuously

Fig. 4. *1,* Longtiudinal section, *?Trupetostroma* sp., showing thin, incomplete upper lamina and infiltration of sediment into uppermost galleries that are presumed to have been filled with soft tissue at death, NMV P.141665, Pragian-Emsian Buchan Caves Limestone, eastern Victoria, Australia, ×16 (new); *2,* longitudinal section, *Syringostromella?* cf. *discoidea* (Lonsdale, 1839), SCRM 50-20, Much Wenlock Limestone, Wenlock Edge, Shropshire, England, showing latilamination and sediment penetrating galleries that were presumably filled with soft tissue through whole depth of last latilamina, ×10 (new); *3,* diagrammatic reconstruction of longitudinal section, *Labechia,* showing skeleton of pillars and cyst plates secreted by a basal pinacoderm and soft tissue entirely on surface of skeleton; astrorhizal canals (*as*) lead from choanocyte chambers (*fc*) to an osculum (*o*); water enters choanocyte chambers from fine pores on surface through connective tissue (*ct*) in fine canals not shown on reconstruction; it is not clear whether additional skeleton is formed by formation of cysts within soft tissue and abandonment of sealed-off tissue, or by upward migration of basopinacoderm (Stearn, 1975).



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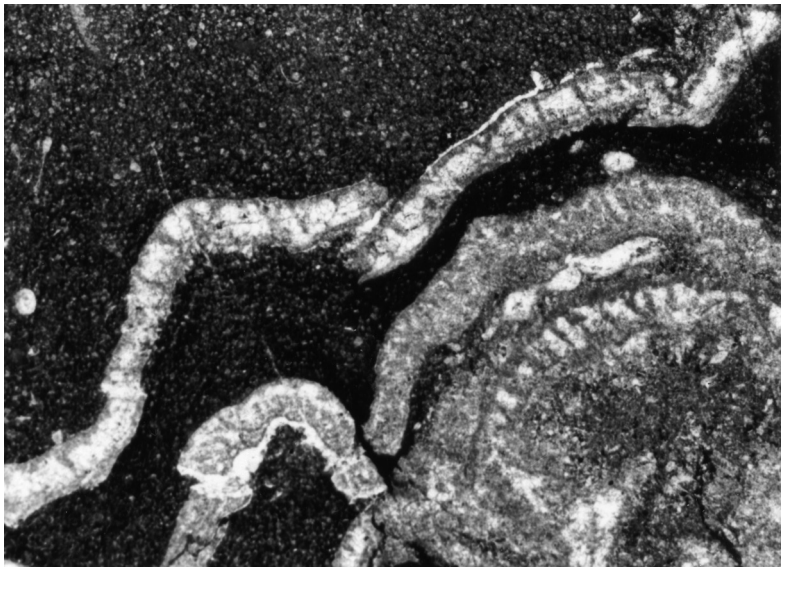

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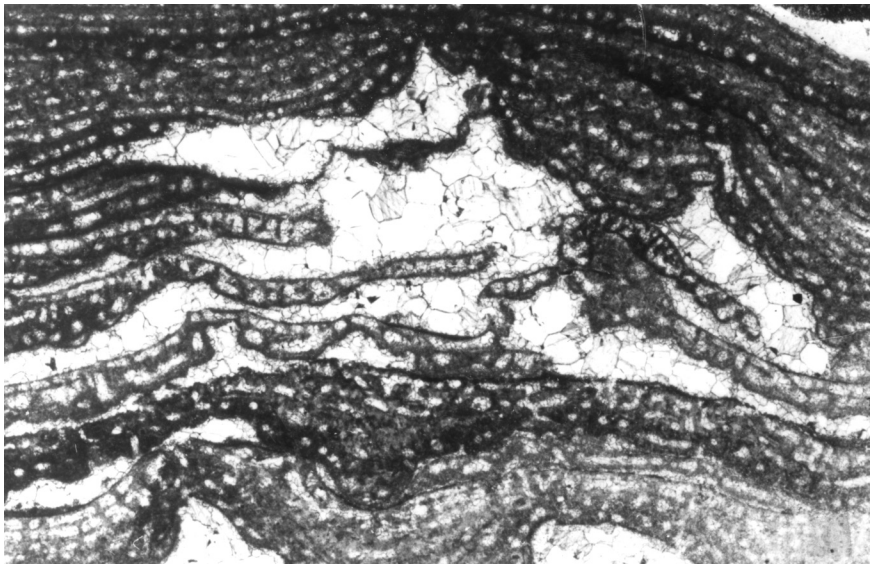
FIG. 5. *1,* Cross section of soft tissue and skeleton of living sphinctozoan sponge *Vaceletia* in process of secreting a new chamber in organic matrix of soft tissue; soft tissue does not completely fill chambers; empty spaces are canals; new, incompletely mineralized chamber appears irregular, probably as a result of some deformation during preparation, ×35 (Vacelet, 1979; photo courtesy of J. Vacelet); *2,* growth modules of upper and lower laminae and enclosed pillars separated from main skeleton and surrounded by sediment; *Simplexodictyon* sp., AM.FT 15018, upper Silurian, Narragal Limestone, New South Wales, Australia, ×10 (new, courtesy of B. Webby).



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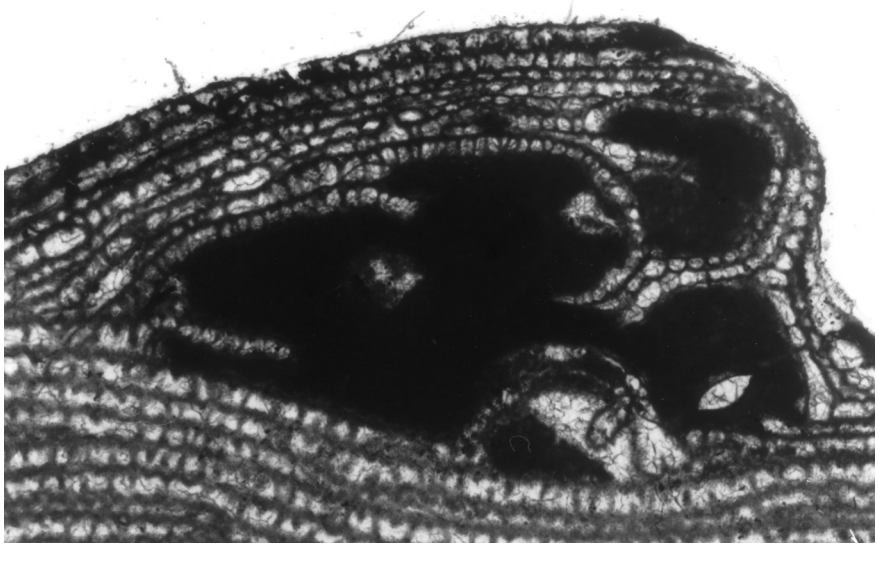

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FIG. 6. *1,* Growth modules consisting of upper and lower laminae and enclosed pillars projecting into a spar-filled cavity, presumably once filled with sediment; *Stictostroma maclareni* STEARN, 1966, SCRM 80-88, Frasnian, Kakisa Formation, Great Slave Lake area, Northwest Territories, Canada, ×4.25 (Stearn & Pickett, 1994); *2,* laminae of a clathrodictyid, *Petridiostroma incrustatum* NESTOR, COPPER, & STOCK, 2010, separated from main skeleton and supported by sediment in a cavity; SCRM 133-1, Llandovery, Jupiter Formation, Anticosti Island (specimen collected by P. Copper), ×10 (new).

fused, leaving cellules between them (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 4,*1*). Many species otherwise typical of the skeletal structure of *Stromatoporella* show only scattered areas of ordinicellular laminae or none at all. The irregularity of development of this ordinicellular microstructure has been attributed to preservational factors but may be caused by original lateral variation in the way in which the modules were fused into the skeleton.

Modules consisting of the upper and lower layers of two successive tripartite laminae and the intervening pillars may project laterally into spar-filled areas that were originally cavities (Fig. 6,*1*) in stromatoporellids, such as *Stictostroma* and *Stromatoporella.* The occurrence of these projections in genera of the Clathrodictyida, such as *Atelodictyon, Petridiostroma,* and *Hammatostroma,* indicates that this group also secreted skeletons in modules. The differences in appearance of laminae between the Stromatoporellida (1) and Clathrodictyida (2) may be due to the way in which the modules were added to the skeleton. In the Clathrodictyida (Fig. 6,*2*), which have single-layered laminae, the floors of the modules are the upper surfaces of the module below and no special floor is secreted. The stromatoporellid (1) and clathrodictyid (2) patterns of module secretion may be homologous to sphinctozoan chambers formed when (1) the primary wall forms a floor as well as a roof (e.g., the sphinctozoan, *Celyphia*); and (2) when it forms only a roof, as in most sphinctozoans. The formation of some growth modules that project into the surrounding sediment in some laminate stromatoporoids may be difficult to reconstruct (Fig. 5,*2,* Fig. 6,*2*), but sediment must have accumulated between intervals of module construction in these specimens.

As noted above, most laminate stromatoporoids have smooth upper surfaces formed by the last lamina, and no sediment penetrates the last galleries that are sealed by this last lamina. In these specimens, modules in the process of calcification within soft tissue and insufficiently fused to the old skeleton have been disrupted and swept away when the soft tissue decayed. Only in exceptional circumstances, when the module was incomplete but sufficiently formed to be fused to the skeleton, was it left behind when the soft tissue decayed and was preserved by the infiltration of sediment into the incompletely sealed galleries.

A thin, calcareous sheath that envelops certain genera is a puzzling skeletal feature through which water must flow in freely. It is most conspicuous in *Amphipora* (Stearn, 1997) (Fig. 1,*2;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 16E, Fig. 42) but was noted by Nicholson (1886, p. 59–60) on several domical and encrusting stromatoporoids and by Nicholson (1886), Zukalova (1971), and Cockbain (1984) on *Stachyodes.* In order for water to enter the interior of the fossil sponge, either this sheath must have been perforated by minute pores or it covered only parts of the animal that were nonfunctional. Stearn (1997) has suggested that this sheath is similar to the dermal membrane that overlies the open space called the vestibule above the skeletal material in the hypercalcified sponges *Ceratoporella* and *Stromatospongia* (Fig. 7). The dermal membrane is minutely porous and allows water into the vestibule, where it is drawn into the choanocyte chambers. Stellate water canals within the vestibule isolate exhalant water from inhalant water and direct it to oscula that penetrate the dermal membrane. The calcification of the membrane as the inhalant surface becomes nonfunctional in older, damaged, or buried parts of the skeleton would produce a skeletal structure similar to the peripheral membranes in *Amphipora* and other genera.

The taxonomic and phylogenetic significance of the calcareous skeleton of hypercalcified sponges has been considered insignificant by some sponge workers who rely entirely on the arrangement and form of spicules as guides to systematic relationships (e.g., Vacelet, 1985; Wood, 1990; Reitner

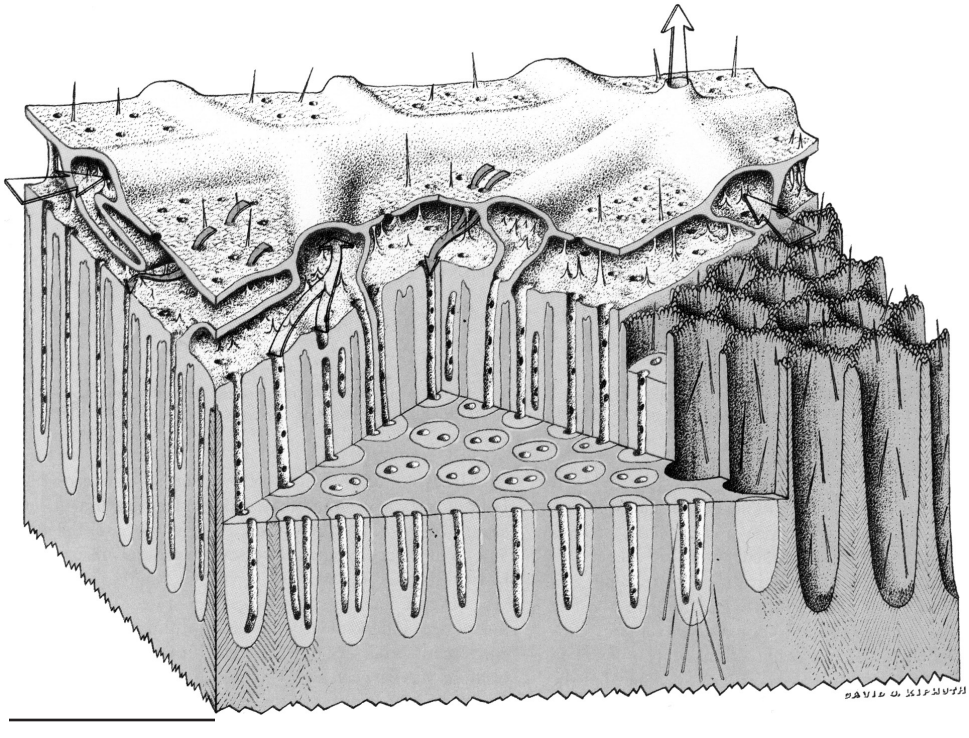

FIG. 7. Diagrammatic reconstruction of relationship between soft tissue and skeleton of *Ceratoporella nichsolsoni* (HICKSON, 1911) showing flow of water into ostia, through vestibule, into choanocyte chambers and out via astrorhizal canals to osculum; scale bar, 1 mm (Willenz & Hartman, 1989).

& WÖRHEIDE, 2002). They pointed out that the calcareous skeleton is secreted by various mechanisms (see above), in various mineralogies, and by genera belonging to various orders of sponges (Haplosclerida, Axinellida, Hadromerida, Choristida, Vaceletida, Keratosa, and Poecilosclerida) (WOOD, 1989) that are defined on the basis of their spicules and soft tissue organization. The basal skeleton therefore must be easy to secrete without much investment of biological energy; that is, it is facultative and therefore of little systematic value (WOOD, 1989). That the basal skeletons of demosponges, such as *Ceratoporella,* have an isotopic signature ($\delta^{18}O$) that is close to that of ambient sea water, is taken as further proof of its facultative nature (see above). The conclusion that the hypercalcified skeleton of these sponges is not only useless in establishing relationships, but may be misleading, is disturbing to paleontologists who have no choice but to base classification and phylogeny on these skeletal fossils. However, until some new key to unlocking the phylogeny of the Paleozoic stromatoporoids is found, paleontologists can proceed only as if features of the basal skeleton have systematic value.

FUNCTIONS OF SPECIFIC STRUCTURAL ELEMENTS

Specific functions and adaptations cannot be ascribed to the skeletal architecture of stromatoporoids. Until more information is available about restriction of species to facies indicative of specific ancient environments, such speculation is idle. These sponges must have adapted various combinations of pillars, laminae, and dissepiments, involving structural elements to lift their feeding

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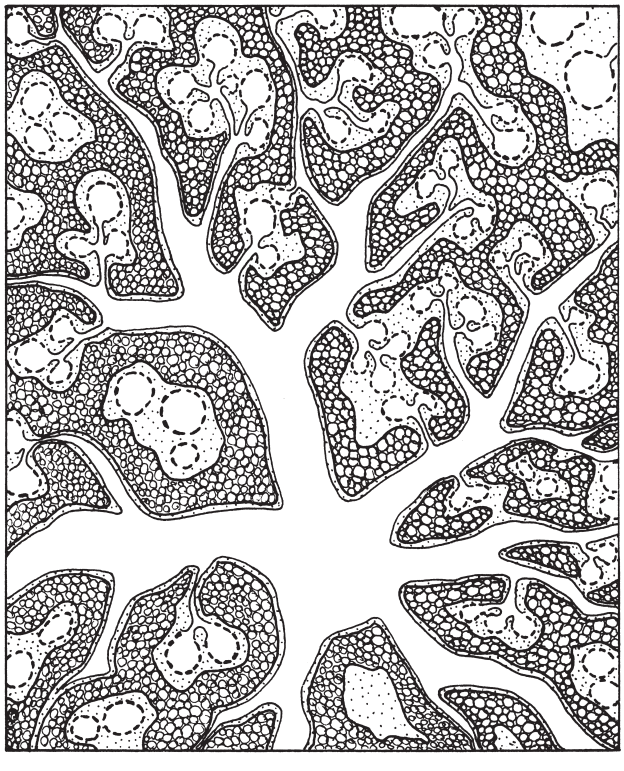

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FIG. 8. *1,* Surface of skeleton of *Ceratoporella nicholsoni* (HICKSON, 1911) showing astrorhizal grooves branching and leading to mamelons on surface, SCRM 99-2, Runaway Bay, Jamaica, ×3 (Stearn, 1972); *2,* reconstruction of tangential section of astrorhizal system in a stromatoporoid, order Stromatoporida; branching canals connect to subspherical choanocyte chambers in gallery space; skeletal material is reconstructed as cellular; largest canals about 0.1 mm across (Stearn, 1975).

surfaces from the substrate. Presumably, the structural elements were selected to optimize support, extension of the intake surface, passage of canals, isolation of inhalant from exhalant water, rigidity, energy cost, rate of growth, and resistance to parasites and predators. The specific advantages of such specialized structural elements as, for example, ring pillars in *Stromatoporella*, to survival of the species is presently unknown. Horizontal elements, such as dissepiments, laminae, and astrorhizal tabulae, were apparently secreted to seal off the unused part of the skeleton from the living tissue. Because the stromatoporoid sponge must have been physiologically incapable of lifting itself in its skeleton in growing, as cnidaria polyps do, the abandoned soft tissues must have been sealed off and left to decay (as illustrated by the living hypercalcified sponge *Vaceletia;* Vacelet & others, 1992).

Although the surfaces of modern sponges are attacked by organisms whose relatives would have been contemporaries of the stromatoporoids, no evidence of such predation has been described from these fossils and, if present, would be difficult to distinguish from mechanical damage.

The adaptive significance of only the astrorhizae, mamelons, and growth form have been investigated; the interpretation of growth form is discussed in another chapter (*Treatise Online,* Part E, Revised, Volume 4, Chapter 9B).

MAMELONS

Many growth surfaces have these regularly spaced, radially symmetrical mounds with a few millimeters of relief. In typical skeletons, they are the sites of oscular openings of astrorhizae (Fig. 8,*1;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 10,*1,3*).

The function of mamelons is related to the need to separate the incoming from outgoing water streams to increase the efficiency of feeding. Water processed to remove microorganisms, nutrients, and oxygen exhaled from oscula should not be sucked back into inhalant pores (ostia) on the surrounding surface. Fry (1979) has summarized Bidder's Diameter of Supply concept to the spacing of oscula on the surface of encrusting sponges. The jet from an osculum should be able to diffuse water already cleaned away from the inhalant pores, and the sponge's anatomy and physiology is adapted to maximize this mechanism. Raising oscula on mamelons above the inhalant surface of an encrusting sponge is one strategy to achieve this, and in some living sponges, it results in the oscula being raised on high chimneys.

Boyajian and LaBarbera (1987) investigated the effect of the flow of ambient sea water over mamelons on which astrorhizae were centered to explain the function and form of the mamelons on the growth surface. The stromatoporoid surface was simulated by a model and the astrorhizae by radial grooves on its flanks. When water in a flume was passed over the model, the difference in velocity of the current near the base of the model mamelon (slowed by friction with the substrate) and that at the top caused a pressure differential defined by Bernoulli's Law, which pulled water marked by a dye stream up the astrorhizal grooves to the mamelon summit. Boyajian and LaBarbera (1987) suggested that the experiment showed that the flow of water across mamelons would have helped the stromatoporoid in circulating water through the astrorhizal canals. As Vogel (1994) explained, although this principle can be applied to the circulation of fluids in burrows of marine worms and gophers, its application to stromatoporoids is not as evident as the experiment suggests, for the following reasons.

1. Astrorhizae are not grooves open at their lower ends in the sides of mamelons as modeled, but enclosed tubes embedded in the skeleton. Although tubes were tried in the experiment, no results are reported.

2. Many stromatoporoids have astrorhizae without mamelons or between mamelons, i.e., the association of mamelons and

astrorhizae is not as universal as implied in the experiment.

3. Boyajian and LaBarbera (1987) suggested that mamelated surfaces should characterize stromatoporoids that lived in environments of low current velocities, where their circulatory system would need to be supplemented by the pressure differential, and pointed out that the mamelate hypercalcified sponge *Ceratoporella* lives in caves and at depth in Jamaican waters where currents are light. They suggested that ancient current conditions might be determined from mamelon and astrorhizal form. However, the reverse of this argument might be used; that is, in order for the mechanism proposed to be an effective aid to the circulation of sponges, a constant current must cross the surface, and the stronger the better. The occurrence of mamelons on *Ceratoporella* could be taken to indicate that no relationship exists between currents and mamelons.

4. The flagella of sponges living in calm water seem quite capable of maintaining circulation in astrorhizae without the aid of this mechanism.

5. No relationship between the form or presence of astrorhizae or mamelons and the current regime of the environment of living or fossils sponges has been demonstrated.

Where mamelons and astrorhizae are associated in stromatoporoids, the association is more likely to be controlled by the need to separate incoming from outgoing water under still conditions than by an adaptation to take advantage of pressure differences caused by currents. Where the surface is swept by currents, the problem of recycling of water is much less.

ASTRORHIZAE

For more than 150 years, the canal systems that shaped the astrorhizae have been considered the key to understanding the systematic position of the stromatoporoids (Fig. 8,*2;* and see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 10–13). The features of the astrorhizae that require explanation by a model of their functions are the following.

1. Most canals are not bounded by discrete walls but are represented by clear spaces (astrorhizal paths) through the skeletal elements communicating in three dimensions with the galleries. Some canals are bordered by a wall pierced with pores.

2. On growth surfaces, the traces of astrorhizal canals may be grooves or ridges.

3. The canals decrease in diameter regularly away from the centers of the astrorhizae. At the centers they are bent upward to join single, or multiple, ascending canals.

4. Most canals decrease in diameter distally until they cannot be distinguished from the galleries. Rarely the distal tips of the canals of adjacent astrorhizae join to form a network.

5. Astrorhizae may be superposed, forming columns, or they may be scattered in the skeleton.

6. Not all species or genera show them.

7. The canals may be crossed by simple tabulae.

8. Astrorhizae tend to be uniform in size, form, and spacing throughout the skeleton of a species; that is, they are distinctive of particular species.

Early in the history of the study of stromatoporoids, paleontologists (Nicholson & Murie, 1878; Solomko, 1885) recognized the similarity of the astrorhizae to the exhalant, water-gathering systems of sponges. Carter (1877) reasoned that the canals were homologous to the hydrorhizal system of the hydrozoan *Hydractinia*. This system links the zooids of the hydroid and allows them to exchange nutrients by diffusion. His views convinced Nicholson (1886) to abandon his former position that stromatoporoids were sponges and to ascribe them to the Hydrozoa. Nicholson's influence was so great that, although a few continued to affirm the sponge model (Kirkpatrick, 1912; Heinrich, 1914; Twitchell, 1928–1929), the hydrorhizal model of the astrorhizae became orthodoxy for the next

85 years (e.g., Kühn, 1927; Lecompte, 1951, 1956; Galloway, 1957; Flügel & Flügel-Kahler, 1968; Bogoyavlenskaya, 1984). Reasons for rejecting the hypothesis that astrorhizae are homologous to hydrozoan hydrorhizae have been reviewed by Stearn (1972). Hydrorhizal tubes should be of constant diameter along their length, always join into a continuous network, and conform at their branching points with the laws of fluid diffusion (LaBarbera & Boyajian, 1991). The astrorhizae fulfill none of these requirements.

Jordan (1969), Kazmierczak (1969), and Nguyen Hung (2001) have postulated that the astrorhizae are foreign organisms that have invaded the stromatoporoid skeleton. The integration of the canals into the skeleton and their uniformity within species makes this hypothesis unlikely. As explained in the Internal Morphology chapter (*Treatise Online,* Part E, Revised, Volume 4, Chapter 9C), some radially branching tubes of astrorhizae formed within Devonian stromatoporoids do appear to be traces of a parasitic organism. They are characterized by: (1) greater diameters than normal astrorhizal canals (which may also be present in the same skeleton; Kazmierczak, 1969); (2) distinct walls; (3) abundant, closely spaced, curved dissepiments, rather than widely spaced tabulae (see *Treatise Online,* Part E, Revised, Volume 4, Chapter 9C, Fig. 16,*1*). The affinity of the organism forming these walled tubes is unknown. Kazmierczak (1976) later changed his interpretation of astrorhizae to accord with his hypothesis that stromatoporoids belonged in the Cyanophyta. He proposed that the astrorhizae represent ". . . *in situ* developed new coccoid colonies . . . ." (p. 51) and that modern counterparts can be found in the radially filamentous juvenile stages of colonial coccoid cyanophytes. The viewpoint that stromatoporoids were cyanophytes was effectively rebutted by Riding and Kershaw (1977) and LaBarbera and Boyajian (1991).

Since the work on hypercalcified sponges of Hartman and Goreau (1970), who revived and documented Kirkpatrick's (1912) suggestion that astrorhizae proved the poriferan nature of stromatoporoids, most paleontologists have been convinced that these canal systems are homologous to the exhalant systems of encrusting sponges. If the astrorhizae carried the exhalant water from the stromatoporoid sponge, then their design should be optimized for this use by natural selection. The optimum design of such a system in organisms was defined as Murray's Law, or $Q = kd^3$, where Q is the flow through a vessel and d is its radius (Vogel, 1994). Murray's Law describes a bulk-flow transport system that minimizes the metabolic costs of moving fluid through the system and the metabolic costs of maintaining the system (Ziegler, 1995). Where a canal (such as an astrorhizal canal) branches into two or more tributaries, the relationship between their radii, $d_{n,}$ is indicated as:

$$d_0^3 = d_1^3 + d_2^3 + \ldots d_n^3$$

That is, the sum of the cubes of the radii of the tributaries equals the cube of the radius of the vessel they join. Measurements by Ziegler (1995) show that the canal systems of two marine sponges are compatible with Murray's Law and that it can be used to assess the sponge affinity of enigmatic fossils.

LaBarbera and Boyajian (1991) considered three hypotheses to explain the function of astrorhizae: (1) the canals represent the traces of symbiotic organisms; (2) they represent diffusion canals; or (3) they carried a bulk flow of water to serve trophic-respiratory functions. Each of these hypotheses can be accepted or rejected on the basis of the anatomy of the branching points in the tributary system of the astrorhizae. If the canals are diffusion channels, such as postulated by those who favor a hydrozoan affinity, then the sum of the squares of the diameters of the daughter canals below a branch point should equal the square of the diameter of the canal into which they lead. If the bulk flow system was constructed so that both the resistance to flow and some cost associated with the volume of the system

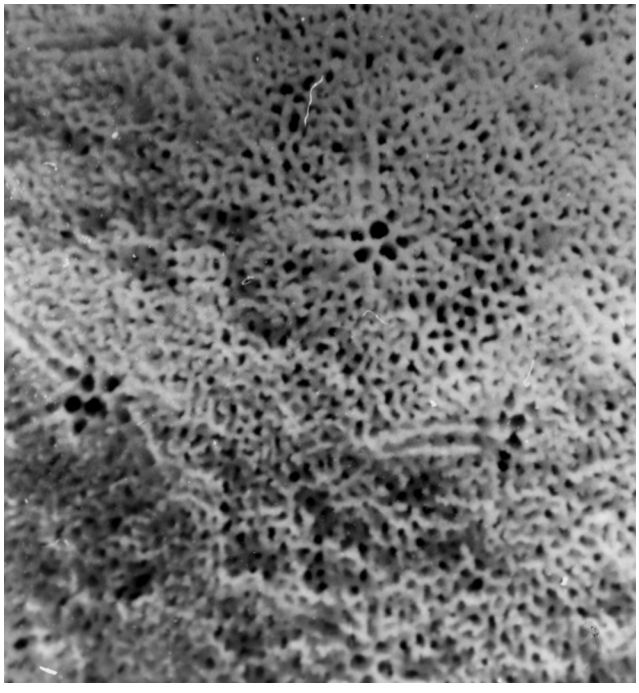

FIG. 9. Surface of skeleton, *Astrosclera willeyana* LISTER, 1900, showing astrorhizal canals on surface and penetrating into skeleton, SCRM 99-3, Guam, Anae Island, ×10 (new).

were minimized, then the sum of the cubes of the diameters of the daughters should equal the cube of the diameter of the canal to which they lead. By measuring the branching points in several specimens from the Devonian of Michigan, LABARBERA and BOYAJIAN (1991) showed that the diameters of the canals corresponded well with Murray's Law and did not support the other hypotheses. They concluded that their study showed the astrorhizae were likely to be the exhalant canals of sponges.

The living hypercalcified sponges provide models for the astrorhizal systems of stromatoporoids (Fig. 7, Fig. 8,*2*). In *Ceratoporella,* the soft tissue forms a thin (1.5 mm) layer on the surface of a domical solid skeleton of aragonite (Fig. 7, Fig. 8,*1*). WILLENZ and HARTMAN (1989) have described how water traverses the upper soft tissue surface through porocytes, with openings only a few micrometers across. The incoming water enters a vestibule cavity beneath the surface and passes by canals, into the choanocyte chambers located in regularly spaced depressions in the skeletal surface. Water cleaned of nutrients is impelled from the choanocyte chambers and gathered into tubes of steadily increasing diameter, joining others as tributaries that lead through the vestibules onto the surface to central oscula (Fig. 8,*1*). The astrorhizal canals leave vague depressions on the skeletal surface, because secretion of the skeleton is inhibited beneath them (Fig. 7). No trace of these surficial astrorhizal canals is preserved in the skeleton as it is secreted. In *Goreauiella,* the canal system is similar but leaves ridges instead of depressions in the basal skeleton. In *Merlia,* the exhalant canals are entirely superficial and leave no trace on the skeleton. In *Astrosclera,* the skeleton has many internal cavities filled with soft tissue, and the astrorhizal canals reach downward into the cavities and are outlined by skeletal

tissue (Fig. 9). In *Vaceletia,* the living tissue filled with canals of various sizes occupies several of the younger chambers (Fig. 5,*I*).

The preservation of open astrorhizal canals in the skeletons of many stromatoporoids indicates that they must have been functional in the soft tissue that occupied the upper layers of the skeleton, otherwise they would not have been accommodated by skeletal modifications. These open canals would have been points of entry to abandoned parts of the skeleton for destructive organisms, unless sealed off as the sponge grew upward. To seal them, the sponge appears to have calcified the valvules, layers of tissue that extend across the canals in living hypercalcified sponges to regulate water flow, forming astrorhizal tabulae. The level at which permanent astrorhizal tabulae were introduced in these canals may serve as an indicator of the depth of penetration of soft tissue in the skeleton.

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