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Functional Morphology of the Fossil Hypercalcified Chaetetid-Type Porifera (Demospongiae)

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INTRODUCTION

Hypercalcified sponges with a chaetetid skeleton are members of the marine sessile benthos. Extant members occur in areas of very low light or complete darkness in subtidal caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundred meters (Vacelet, 1988) in the Caribbean Sea and Indo-Pacific Ocean. There are three basic components to extant hypercalcified sponges: (1) a thin layer of living tissue, between 1 and 2 mm thick; (2) a rigid basal calcareous skeleton secreted by the living tissue; and (3) siliceous spicules, both megascleres and microscleres, secreted by the living tissue and most often associated with it. Living tissue extends into the calcareous skeleton only a few millimeters. The bulk of the skeleton, unless filled by secondary calcium carbonate, is hollow and during life may have contained seawater. However, if the hollow tubules of the basal calcareous skeleton were filled with seawater, unless protected by a residual organic film, the calcium carbonate of the skeleton would have been adversely affected because of the interaction between calcium carbonate and seawater (Clark, 1976). Spicules may also occur within the skeleton just beneath the layer of living tissue. In some extant taxa, spicules are absent, and in others, there is no calcareous skeleton (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A).

Reasonable inferences about the function of morphological features of fossils requires careful application of the principles of physics to these morphological features and/or knowledge of extant representatives that are morphologically similar and, preferably, taxonomically related. Movement of water to obtain food and expel waste is essential to members of the phylum Porifera, and thus, the physical principles governing the dynamics of fluid flow are useful in understanding this primary function (see also *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F). The extant genera *Acanthochaetetes, Ceratoporella,* and *Merlia* are morphologically similar and, according to some authors (Hartman & Goreau, 1970, 1972; Cuif & Gautret, 1993; Wood, 1990, 1999), taxonomically related to fossil hypercalcified sponges with a chaetetid skeleton.

Skeletal remains of fossil chaetetids consist of two components: pseudomorphs of spicules and a basal calcareous skeleton. Pseudomorphs of both megascleres and microscleres have been recognized. Megascleres are typically simple monaxons, and microscleres are commonly small spherical objects. Any spicules, or pseudomorphs of spicules, present in fossil forms will be contained within the calcareous skeleton. Because the spicules in extant forms are siliceous, the same is assumed for any spicules in fossil forms during life. The calcareous skeleton is composed of vertically arranged contiguous tubes (tubules), and the tubules are most accurately defined as irregular polygons in transverse section. Tabulae, horizontal partitions, commonly occur within the tubules and are readily visible in longitudinal and transverse sections (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 10–11). A foramen (or pore) has been observed near the center of the tabulae in some extant forms, and may be seen in fossil forms (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 29). Features referred to as pseudosepta are visible in tangential sections of some tubules (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 34–35).

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EXTERNAL FEATURES

GROWTH FORM

The chaetetid calcareous skeleton is very simple, both externally and internally. External features include the basal layer, astrorhizae, mamelons, chimneys, and tubercules, though these structures are not always seen. The most obvious aspect of the calcareous skeleton is its general overall shape, which is very similar to that observed in stromatoporoids (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 9B, for a detailed discussion of the shapes and growth habits of Paleozoic stromatoporoids) In chaetetids, there are three basic shapes: laminar, domical, and columnar (West & Kershaw, 1991), which result in a number of variations termed morphotypes by Kershaw and West (1991, fig. 1). These morphotypes can increase in size, or be modified in shape, during life by increasing the number of tubules via longitudinal fission, intertubular increase, peripheral expansion, or the combinations of two or more of these three (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A). Assuming that a laminar accretionary unit (Kershaw & West, 1991, fig. 7) is the basic building block for all of these morphotypes, environmental conditions become the controlling factors. This is not the case in all hypercalcified sponges, namely stromatoporoids. For example, Kershaw (1981) has shown that some stromatoporoid species in the same environment may develop different growth forms. Although future studies might indicate there is a genetic difference between some or all of these different growth forms in fossil chaetetids, our present knowledge suggests that the different growth forms are largely the result of environmental factors.

The basic reason for a calcareous skeleton in chaetetids is no doubt the same as it is for other clonal lower invertebrates that produce similar skeletons, namely other sponges (like stromatoporoids), corals, and bryozoans. All of these groups are suspension feeders, and an elevated feeding surface above the sediment–water interface where the water is less turbid and the water velocity slightly higher is advantageous (Wildish & Kristmanson, 1997). Stearn (2010, *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F) has summarized the possible explanations for a calcareous skeleton in stromatoporoids, and these explanations can, in general, also be applied to chaetetids.

Given the potential importance of turbidity on the growth form of chaetetids, West and Roth (1991) examined the insoluble residues (siliciclastic content) of chaetetid-bearing, and some associated, carbonate rocks. Results of this preliminary study indicated that the siliciclastic content of carbonates containing laminar chaetetids was significantly higher than it was in carbonates containing domical and columnar chaetetids (Tables 1–2). Additionally, West and Roth (1991) compared the siliciclastic content in each of these three different chaetetid carbonates (habitats) to an environment represented by algal carbonates in which chaetetids were absent. There was no significant difference between carbonates containing domical and columnar chaetetids and algal carbonates (Table 2). Based on these results, West and Roth (1991) suggested that laminar chaetetids grew in turbid (dirty) water habitats, and both domical and columnar chaetetids competed with phylloid and other algae in less turbid (cleaner) water environments. Because cleaner water is more favorable for photosynthesizing algae, a low siliciclastic content would be expected. However, the

Table 1. Mean values of percent of silicilastics (insolubles) in chaetetid habitats (different growth forms) and algal environments (carbonates) (new).

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

TABLE 2. Matrix of results of grouped t-tests of mean values of percentages of siliciclastic content (see Table 1); n, number of observations (siliciclastic content); *D,* difference between groups; *ND,* no difference between groups. Differences and no differences are significant at a probability of 0.05 (new).

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

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

GROWTH RATES

Growth rates of 1 mm to 10 mm over several years have been suggested for *Ptychochaetetes*, a Jurassic chaetetid (FABRE & LATHUILIERE, 2007, p. 1539), but these estimates are based on growth rates in corals. Estimates and *in situ* studies of two extant species of hypercalcified sponges with a chaetetid skeleton provide growth rates for these extant forms. The specimens studied were low domical and/or laminar forms, and the results refer to vertical growth and also to lateral expansion of the basal calcareous skeleton in *Ceratoporella nicholsoni. C. nicholsoni* was studied *in situ* by WILLENZ and HARTMAN (1985) in a reef tunnel off the coast of Jamaica for six months (mid-1984 to early 1985) and continued until 1997 (WILLENZ & HARTMAN, 1999). OOMORI and others (1998) estimated the rate of growth in *Acanthochaetetes wellsi* using chemical signatures in growth bands as described by BENAVIDES and DRUFFEL (1986). *In situ* studies of *Acanthochaetetes wellsi* in a dark reef cave in the fringing reef of Lizard Island (Great Barrier Reef) were reported by REITNER and GAUTRET (1996). Based on their study that lasted 320 days, REITNER and GAUTRET (1996) reported an annual growth rate of 0.05–0.1 mm for *A. wellsi.* They further noted (p. 193) that the skeleton formed in a narrow zone between the basopinacoderm and the mature basal skeleton (Fig. 1–2). The rate of growth in *C. nicholsoni* given by DUSTAN and SACCO (1982) and BENAVIDES and DRUFFEL (1986) are relatively the same as those based on the long-term *in situ* study of *C. nicholsoni* in Jamaica that provided an average annual growth rate of 0.21 to 0.23 mm (WILLENZ & HARTMAN, 1999). The basal skeleton of *C. nicholsoni* formed from a layer of basopinacocytes in the mesohyl at the interface between the living tissue and the aragonitic skeleton (WILLENZ & HARTMAN, 1989). Studies of

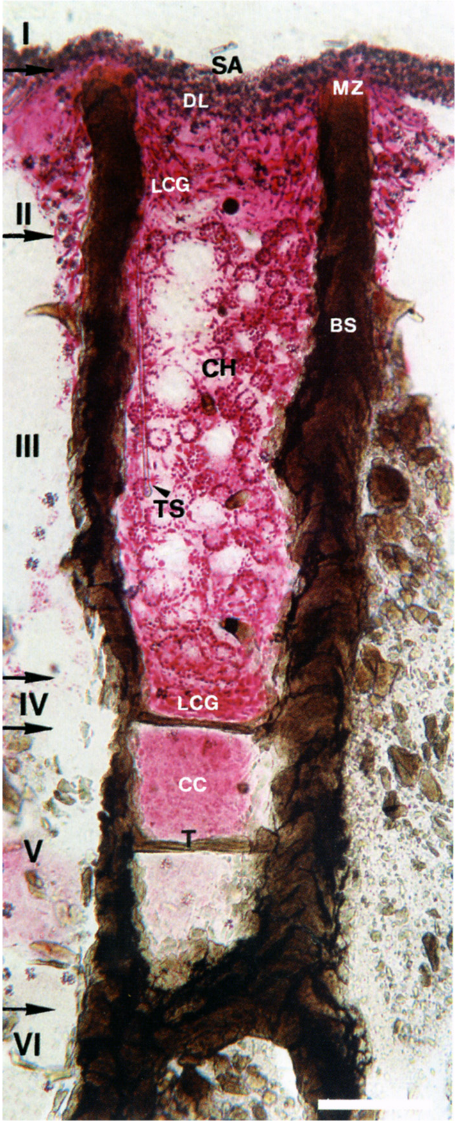

FIG. 1. Growth in *Acanthochaetetes wellsi;* vertical section of a tubule with living tissue. Tubule is divided into six sections: *I,* spiraster microsclere (*SA*) crust; *II,* lower dermal layer (*DL*) with large cells with granules (*LCG*) and skeletal growth fronts (*MZ*); *III,* choanosome (*CH*)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

C. nicholsoni by LAZARETH and others (2000) using $\delta^{13}C$ revealed similar growth rates, and ROSENHEIM and others (2004) using calcein stain reported an average growth rate of 0.18 mm/yr. However, growth rates vary significantly from one individual to another and within a given individual through time; WILLENZ and HARTMAN (1999) reported a growth rate of 0.12 mm/yr for small specimens of *C. nicholsoni.* This is close to the 0.1 mm/yr rate reported for *A. wellsi* (REITNER & GAUTRET, 1996).

These growth rates of hypercalcified demosponges with a chaetetid skeleton are compared to growth rates reported for other clonal invertebrates in Tables 3–5. Table 3 provides the taxa, age, habitat, growth rate in mm/yr, reference, and pertinent remarks for hypercalcified and nonhypercalcified extant sponges, hermatypic and ahermatypic extant corals, and extant bryozoans. For some sponges and bryozoans, the data are reported as areas, i.e., mm^2/yr. Similar data for Ordovician, Silurian, and Devonian corals are given in Table 4. The same information is given in Table 5 for specimens of extant hermatypic corals from different water depths from the Caribbean and Indo-Pacific. There are data for *Montastrea annularis, Montastrea cavernosa, Porites asteroides*, and *Siderastrea siderea* from the Caribbean, and for *Astreopora myriophthalma, Porites lobata, Goniastrea retiformis, Favia speciosa, Porites lutea,* and *Favia pallida* from the Indo-Pacific. Two aspects of the data in Tables 3 and 5 are particularly obvious and important: (1) the growth rate of all the other clonal invertebrates listed is an order of magnitude greater than the growth rate for either of the two hypercalcified sponges (Table 3); and (2) the growth rate of extant hermatypic corals varies with water depth; often, though not always, the growth is slowest in deeper water (Table 5). In *Oculina varicosa* (Table 4), the ahermatypic form of this species grows faster in deep, cold water than the hermatypic form does in shallow, warmer water.

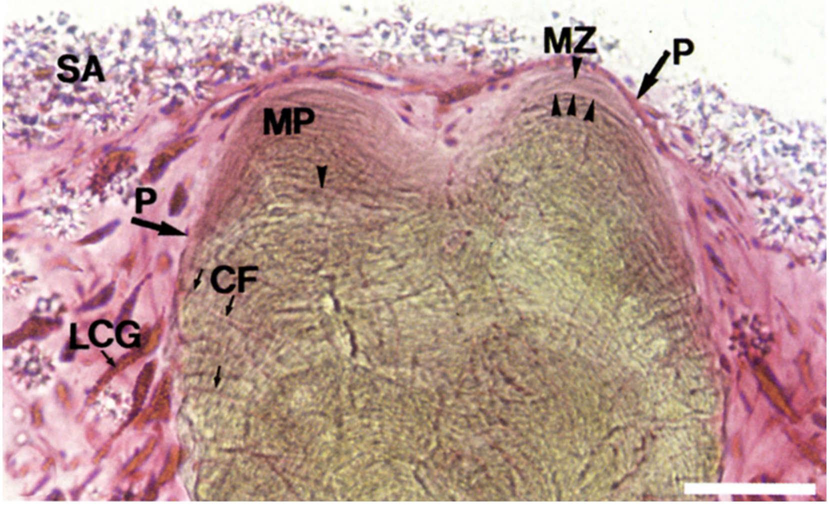

FIG. 2. Growth in *Acanthochaetetes wellsi* (continued); uppermost growing zone of tubule wall, an enlargement of the upper part of section II in Figure 1. *MP,* mucus-rich parts of basal skeleton within the active mineralizing front (*MZ*) beneath the basal pinacoderm (*P*), *SA,* spiraster microsclere crust, collagenous fibers (*CF*) within basal skeleton (*arrows*), large cells with granules (*LCG*), ×640 (adapted from Reitner & Gautret, 1996, pl. 49,*2;* with kind permission of Springer Science+Business Media).

Few data are available on the growth rates of fossil clonal invertebrates. DULLO (2005) provided some data for Pleistocene coral specimens, and MA (1933, 1937a, 1943a, 1943b, 1943c) and FAUL (1943) provided data on Ordovician, Silurian, and Devonian rugose and tabulate corals. But, there are no data on the growth rates of fossil bryozoans or hypercalcified, or other fossil, sponges. MA (1934, 1937b) also documented the growth rate of numerous extant coral taxa from the South Pacific and areas around the Japanese islands. To determine the reliability of the growth rates reported for these fossil corals by MA (1943a, 1943b, 1943c) and FAUL (1943), a comparison was made between growth rates of some extant coral species reported by MA (1937b) with those reported by DULLO (2005) for the same extant species in the same general areas. This comparison (Table 6) shows that the growth rates reported by MA (1937b) are very close to those reported by DULLO (2005) for the same species from the same general area; the difference is less than a millimeter. MA (1943a, 1943b, 1943c) and FAUL (1943) used the same technique in determining the growth rates of fossil corals as MA (1937b) used to determine the growth rates of extant corals. Thus, given the results in Table 6, and the fact that the technique for determining the growth rates of both extant and fossil corals is the same, the growth rate data for fossil corals reported by MA (1943a, 1943b, 1943c) and FAUL (1943) are reasonable growth rate estimates.

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

TABLE 3. Growth rates in mm/yr of extant clonal invertebrates: sponges, corals, and bryozoans; for some sponges and bryozoans, data on growth rate was only available in mm^2/yr , as noted on p. 4 herein (new).

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

fossil corals is known. Extant hypercalcified demosponges for which there are data on growth rates are *Ceratoporella nicholsoni* and *Acanthochaetetes wellsi*, both of which commonly occur in deeper water, cryptic habitats (Table 3). Extant corals from a similar habitat, from which there are growth rate data, are the ahermatypic corals *Oculina varicosa* and *Lophelia pertsua* (Table 3). As noted in the footnote in Table 4, well over 50% of the fossil corals measured by MA (1943a, 1943b, 1943c) had a growth rate of less than 10 mm/yr, and such a growth rate seems appropriate for the calculation of an estimate of the growth rate of fossil hypercalcified demosponges. Results of these calculations are given in Table 7, and the estimated growth rate of fossil hypercalcified

TABLE 4. Growth rates in mm/yr of Paleozoic corals (Ordovician, Silurian, and Devonian) (new).

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

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

demosponges ranges from 0.02 to 0.2 mm/yr. The range of measured growth rates for extant hypercalcified sponges is 0.05 to 0.23 mm/yr (Table 3).

Using the estimated minimum and maximum growth rates of fossil hypercalcified demosponges (0.02 mm/yr and 0.2 mm/yr, respectively), the inferred age of a chaetetid mass 2.3 m thick in the Carboniferous of southeastern Kansas (SUCHY & WEST, 2001) is between 11,500 and 115,000 years old. Using the average growth rate, 0.05 mm/yr, of Carboniferous reefs (Table 8), this chaetetid mass would be 46,000 years old, about halfway between the ages based on the estimated annual growth rate of fossil hypercalcified demosponges. Because there are a number of growth interruptions in these Carboniferous chaetetids, these inferred ages are probably minimal.

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

Table 5. Growth rates in mm/yr for specimens of extant hermatypic corals from different water depths from the Caribbean and Indo-Pacific (data from Dullo, 2005, table 1).

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

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

BASAL LAYER

A very thin feature with concentric growth lines has been observed covering the lower surface in some extant and fossil forms with a chaetetid skeleton and has also been reported in fossil stromatoporoids

Table 6. Comparison of growth rates in mm/yr of some extant coral taxa from Dullo (2005) and Ma (1937b); μ, average value (mean) of the number of measurements; n, number of measurements (new).

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

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

Invertebrates attach to hard substrates in a number of ways, and some demosponges are inferred to use collagenous glue (Bromley & Heinberg, 2006, p. 438). Other sessile clonal invertebrates, such as bryozoans, use an acid mucopolysaccharide secretion (Bromley & Heinberg, 2006, p. 437). In extant hypercalcified demosponges, the basal layer is mostly composed of organic fibers (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 24), and it is reasonable to suggest that it functioned much like the periostracum in mollusks and other invertebrates with an exoskeleton of calcium carbonate; namely it protected the skeleton from the adverse effects of seawater (Clark, 1976). Stearn (1983, p. 145) has suggested that in stromatoporoids, it functioned to inhibit boring organisms from attacking the underside of the skeleton. Although it is rarely visible macroscopically in fossil chaetetids, it has been observed in some specimens and can be differentiated from the basal calcareous skeleton in SEM images of such specimens (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 24). Because it is thin, appears to be mostly organic in composition, and is exposed to seawater, it is often absent because of physical, chemical, and biological processes during life and after death. Careful study of the contact between the basal calcareous skeleton and the substrate, of both extant and fossil forms, is necessary to determine whether a basal layer, or something similar, is deposited initially when the sponge colonizes the substrate and becomes part of the sessile benthos.

TABLE 7. Estimates of growth rates of fossil hypercalcified sponges using the growth rates of appropriate extant corals, hypercalcified sponges, and fossil corals. This table presents the method used for estimating growth rates for Paleozoic chaetetids. In part A, the ratio between the growth rates of two extant corals, *Lophelia pertsua* and *Oculina varicosa*, from a habitat comparable to that of two extant hypercalcified sponges, *Ceratoporella nicholsoni* and *Acanthochaetetes wellsi,* were set equivalent to the growth rate of a Devonian rugose coral with an analogous compound growth form, *Prismophyllum* (now *Hexagonaria*), relative to an unknown, X. By performing the calculations indicated, the results provide an estimate of the growth rate of a Paleozoic chaetetid. The same method was used to determine the results in part B, using the average growth rate determined for Paleozoic corals from the Ordovician, Silurian, and Devonian, instead of that for *Prismophyllum*, and a second estimate of the growth rate of Paleozoic chaetetids was obtained; µ, average value (mean) of the number of measurements; n, number of measurements. See text for discussion (p. 6 herein) (new).

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

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

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

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

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

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

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

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

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

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

TABLE 8. Growth rates of Phanerozoic reefs in mm/yr from DULLO (2005, tables 3–4); data converted to mm/yr and averaged for each geological period/system (new).

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

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

ASTRORHIZAE

These stellate patterns of grooves, called astrorhizal canals, are associated with the excurrent canal system and are not commonly observed on fossil chaetetids. When present, they are very shallow grooves that are best seen in light with a low angle of incidence (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 7–8). Individual astrorhizal canals may be unbranched or show primary and occasionally secondary branches. HARTMAN (1984, p. 306) stated that in the extant form *Acanthochaetetes wellsi,* ". . . astrorhizae are shallow, difficult to see and not infrequently completely absent." Thus they are rarely present on fossil chaetetids. Astrorhizae may occur on one or two or none of the fossil chaetetids that are numerous in any given stratigraphic interval. That is to say, astrorhizae only occur rarely, even when fossil chaetetids are very abundant and make up the entire rock layer. Unlike the astrorhizae in some fossil (stromatoporoids) and some extant hypercalcified sponges, the astrorhizae in chaetetids are confined to the exterior surface of the basal calcareous skeleton; they have not been observed to extend into the interior of this basal skeleton of any of the valid chaetetid genera. CUIF and others (1973, pl. 1,*2*) illustrated a longitudinal section of astrorhizae in *Blastoporella*, but neither spicules nor spicule pseudomorphs have been found in this genus. In general appearance, the astrorhizae in fossil chaetetids are most like those described for *A. wellsi* (HARTMAN & GOREAU, 1975; HARTMAN, 1984). Astrorhizae are absent in *Merlia normani* (HARTMAN & GOREAU, 1975, p. 10), and although they may be absent in *Ceratoporella nicholsoni*, when present, the grooves are deeper, about a millimeter, and cover a larger area (HARTMAN, 1984, p. 306) than in *A. wellsi*. In fossil chaetetids, the astrorhizae cover a circular area of between 10 and 12 mm in diameter (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 7.3), values within the range covered by astrorhizae in *A. wellsi* (HARTMAN, 1984, p. 306). Within an area of 10.4 cm^2 on the surface of a fossil chaetetid, there are six astrorhizae (Fig. 3), and the distance between the centers of these six range from 8.25 to 27 mm, averaging 16.2 mm (n = 15) (Table 9). In extant forms, astrorhizae are associated with mamelons, but this is not the case in fossil chaetetids. Astrorhizae in fossil chaetetids occur on a relatively smooth to slightly irregular surface, but they have not been observed centered on mamelons. As in extant forms, the function of this stellate pattern of grooves radiating from an osculum are inferred to identify the

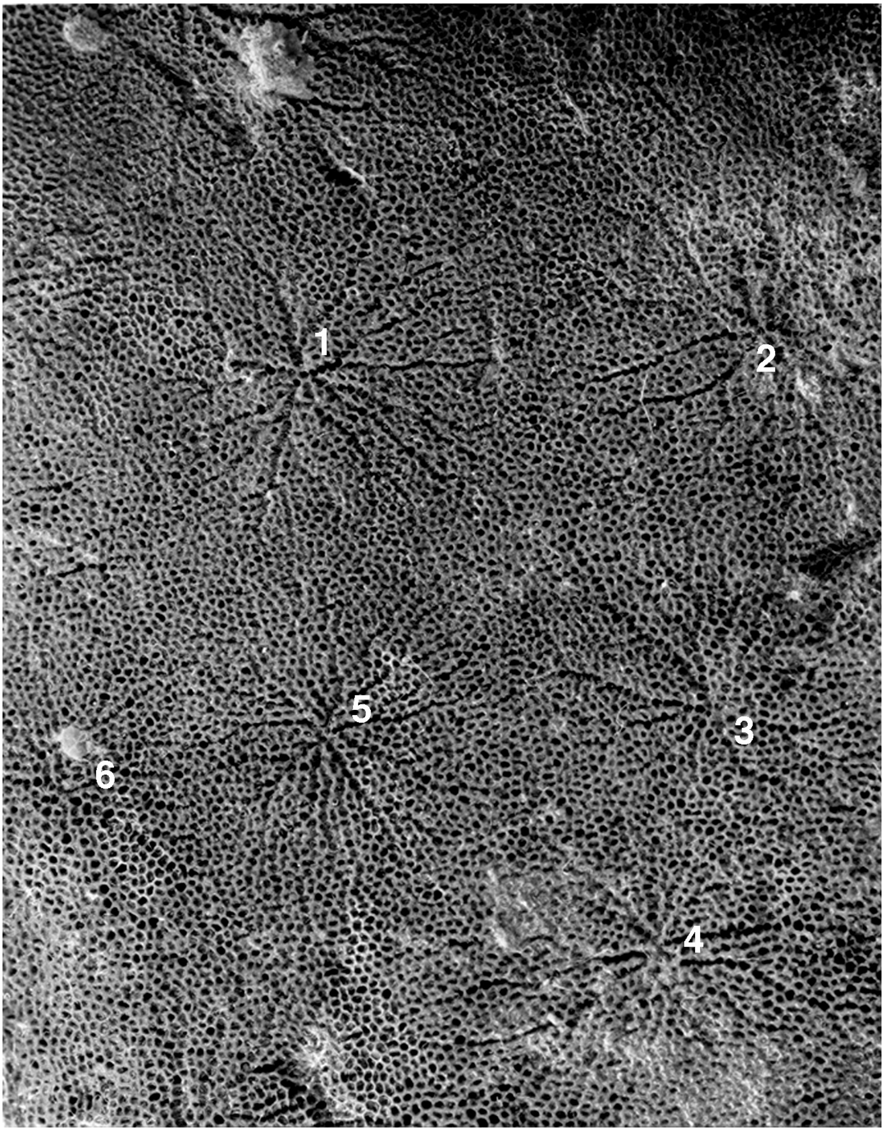

FIG. 3. Six astrorhizae in 10.4 cm^2 area on the surface of a chaetetid, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; see Table 9 for distances between astrorhizae, ×4.1 (new).

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

MAMELONS

These features are rounded regular or irregular elevations of the exterior surface of the chaetetid skeleton. They have been observed but are not always present in the extant taxa *Ceratoporella nicholsoni* (Hartman & Goreau, 1970; Hartman, 1984) and *Acanthochaetetes wellsi* (Hartman & Goreau, 1975; Hartman, 1984). Although astrorhizae occur on the mamelons of some specimens, they are not present on all mamelons. Astrorhizae are part of the exhalant water circulating systems in these sponges, and some advantage might be realized if the exhalant opening (osculum) is elevated relative to the incurrent openings (ostia) (Hartman, 1984, p. 310). Based on Bernoulli's Principle, water moving over a U-shaped feature is pulled into one opening if the other opening is raised slightly above the surface of the first opening (see Vogel, 1994, p. 72; 2003, p. 149). Experiments by Boyajian and LaBarbera (1987) based on Bernoulli's Principle, suggested that mamelons and associated astrorhizae would be advantageous to taxa living in quiet water. Stearn (2010, *Treatise Online,* Part E, Revised, vol. 4, Chapter 9F) has pointed out the reasons why this cannot be applied to all occurrences of forms with astrorhizae associated with mamelons in stromatoporoids. These same reasons are appropriate for fossil chaetetids, as well as for some occurrences of extant hypercalcified demosponges with a chaetetid skeleton. For example, Hartman (1984, p. 310–311), referring to underwater photographs of *in situ* specimens of *C. nicholsoni* stated: "In several photographs a specimen with mamelons occurs directly adjacent to one without mamelons, indicating that an environmental explanation does not apply in these populations." Mamelons are not often observed on fossil chaetetids, and on the rare occurrences when they are present, it is not clear, because of weathering, whether or not they possess astrorhizae (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 8.4). The tubules composing the mamelons may appear larger than those elsewhere on the upper exterior surface of the basal calcareous skeleton, but this is more apparent than real (Fig. 4).

Table 9. Distance, in mm, between the centers of the six astrorhizae in the 10.4 cm^2 area shown in Figure 3; n = 15, μ = 16.2 mm (new).

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

CHIMNEYS

Vertically developed mamelons, with an opening (osculum) at or near the apex, that extend well beyond the general growth surface of fossil chaetetids are referred to as chimneys (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 9.4–9.5). These features have not been recognized in extant hypercalcified demosponges with a chaetetid skeleton. I have only observed chimneys in topotype specimens of a form described by Morgan (1924) as *Chaetetes schucherti* from upper Carboniferous limestone in Oklahoma (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 9.4–9.5). Chimneys are not present on the holotype (Fig. 5.1) and are not mentioned in the original description of this species. Morgan (1924, p. 175) noted the presence of ". . . short, round tubes without walls, 3 mm in diameter . . ." (Fig. 5.2) and suggested that these holes ". . . may have been centers of reproduction, goniopores, or they may have been parasitic animals." He noted further that these holes are best seen on weathered surfaces (Fig. 5.3). Similar holes occur on some topotype specimens and they are located: (1) on weathered areas (a in Fig. 5.4); (2) near the top of some cylindrical projections (chimneys) (b in Fig. 5.4); and/or (3) on and around the upper parts of domical to irregularly shaped mamelons (c in Fig. 5.4).

At, or near, the top of these chimneys is a 3 mm diameter opening (Fig. 6.1, Fig. 6.4) which, based on vertical sections, extends downward 6 to 8 mm to near the base of the chimney (Fig. 6.2–6.3, Fig. 6.5). These tubes are now filled with an argillaceous

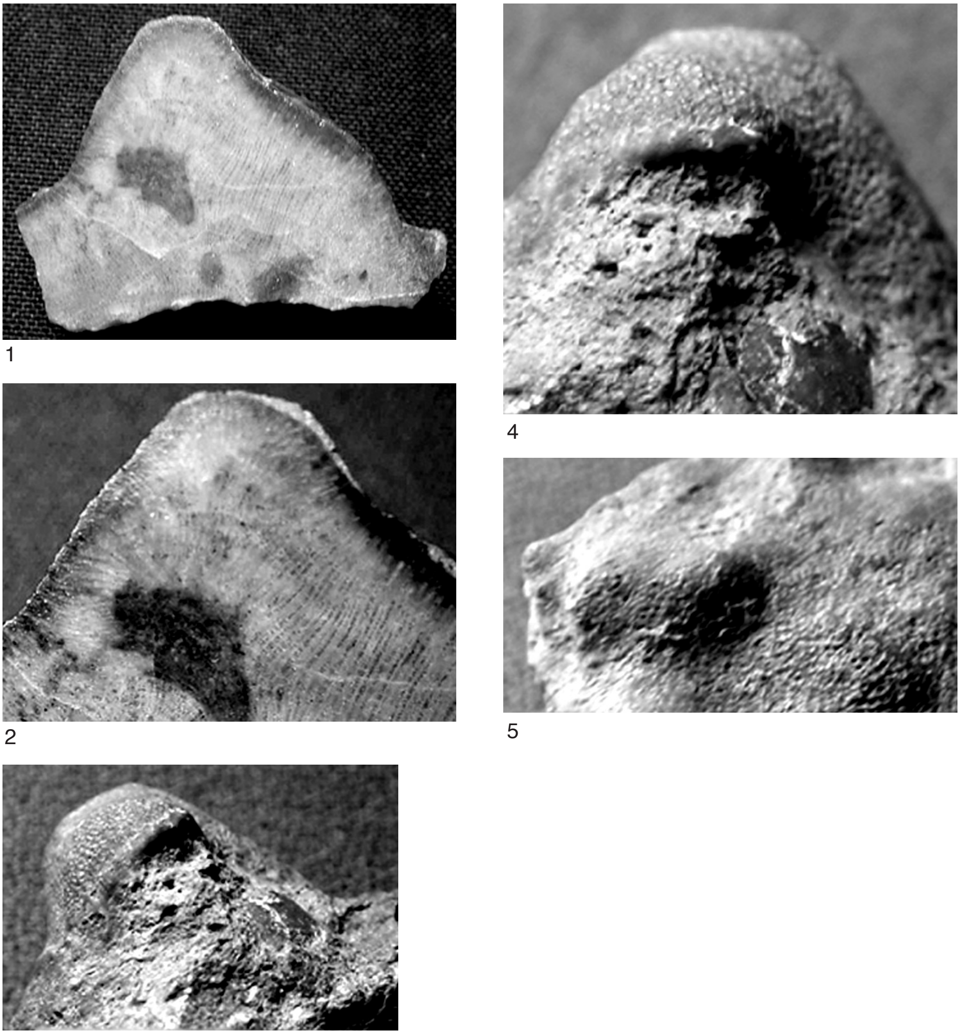

FIG. 4. Tubules in vertically developed mamelons in topotype specimens of *Chaetetes schucherti* MORGAN, 1924, Pennsylvanian, upper Carboniferous, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of a vertically developed mamelon, note tubule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

carbonate matrix or sparry calcite. The distance between these 3 mm diameter openings ranges from 9 to 20 mm and averages 12.5 mm (n = 12). This is about the same as the average distance, 16.2 mm, between the centers of astrorhizae in fossil chaetetids (Table 8). Given the similarity in spacing, and the fact that astrorhizae are considered the area of the exhalant water system, it may be suggested that the openings at the top of vertically developed mamelons, i.e., chimneys, functioned as oscula. Openings associated with exhalant fluid flow and referred to as chimneys occur in the bryozoan *Membranipora membranacea* (DASSOW, 2006).

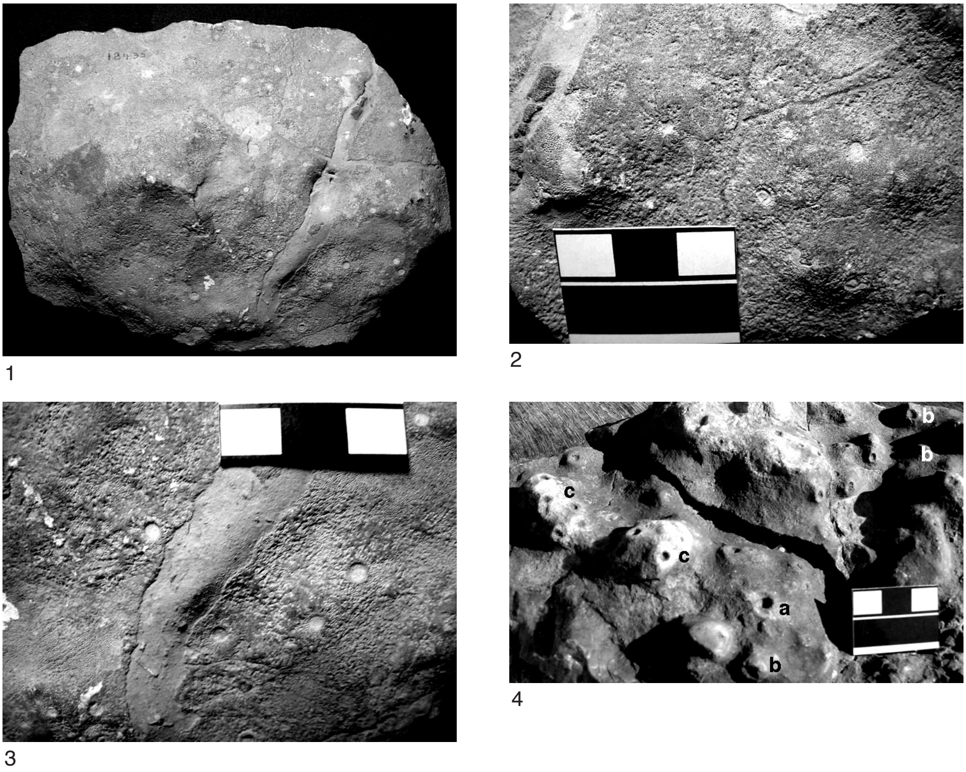

FIG. 5. Circular openings in the upper exterior surface of *Chaetetes schucherti* MORGAN, 1924, Pennsylvanian, upper Carboniferous, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of upper exterior surface of the holotype; light colored circles are the 3 mm holes noted by MORGAN, 1924, ×0.25; *2,* part of the upper exterior surface of the holotype showing 3 mm diameter holes; note that some, but not all, of these holes are associated with mamelons, ×0.8; *3,* same as view *2,* but slightly enlarged and of a different area; holes in this view are not associated with obvious mamelons, ×0.85; *4,* upper exterior surface of a topotype specimen showing the location of the 3 mm diameter holes: *a,* on a weathered area, *b,* near the top of vertically developed mamelons, i.e. chimneys, and *c,* on and around the upper areas of domical to irregularly shaped mamelons, ×0.4 (new).

Although it may be that some vertically developed mamelons were associated with the exhalant movement of water, such circular openings are not restricted to the top of vertically extended mamelons and occur elsewhere on the calcareous skeleton (Fig. 6.4). It is possible that all, or some, of these circular openings are the result of an associated symbiotic soft-bodied invertebrate, i.e., sponge, coral, or worm. Holes of the same diameter as these, 3 mm, but much shallower, only 1 mm, have been observed in extant specimens of *Ceratoporella nicholsoni* and are the sites of commensal zoanthideans (soft corals) that grew on the surface of the sponge (HARTMAN & GOREAU, 1970, p. 209). Smaller holes, 1.5 to 2.5 mm in diameter, also occur in extant specimens of *C. nicholsoni* (HARTMAN, 1984, p. 311) and are attributed to *Siphonodictyon,* an excavating member of the boring clionid sponges (HARTMAN, 1984, p. 311). RÜTZLER (1971, p. 1) noted that he had frequently observed the deep-yellow sponge chimneys of *Siphonodictyon* protruding from living coral heads. Hydroids are also known to be symbiotic on, or inside of, sponges (PUCE & others, 2005).

Tubules that surround the circular tubes in *Chaetetes schucherti* radiate out

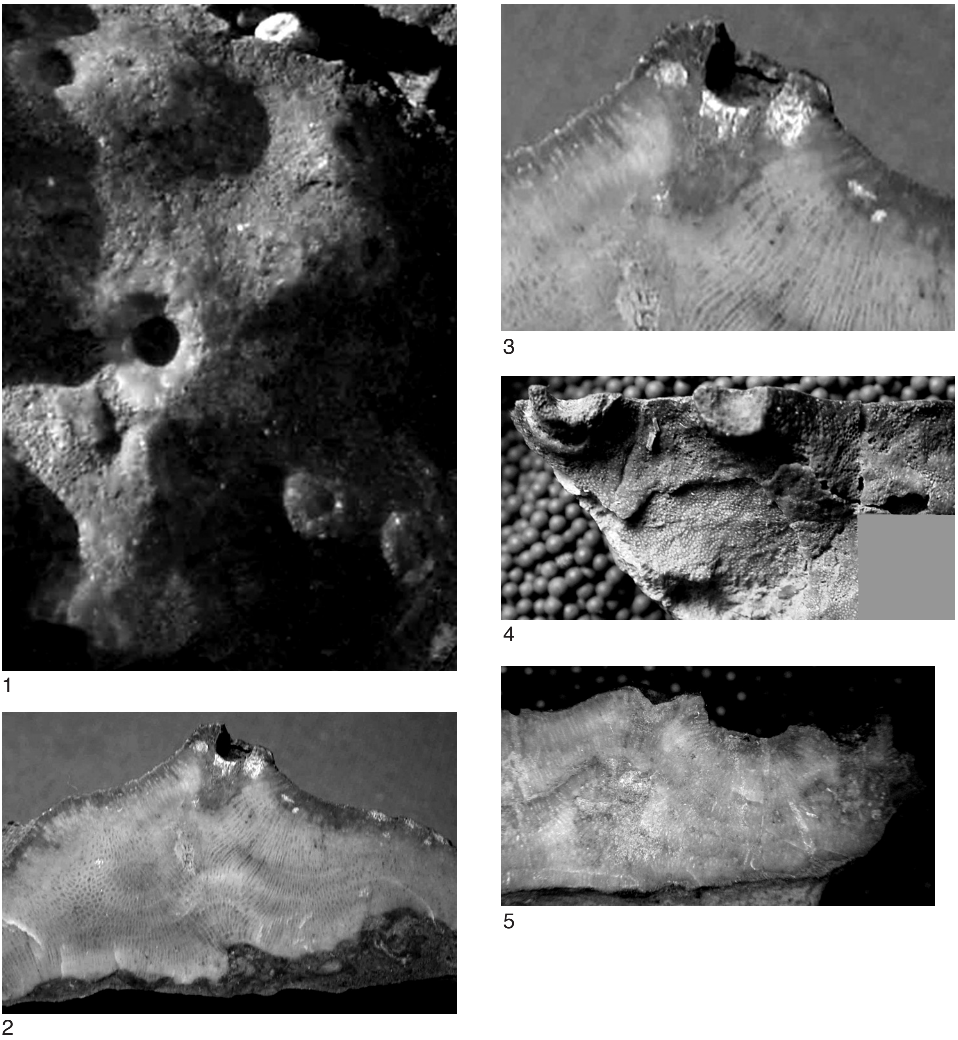

FIG. 6. Chimneys in topotype specimens of *Chaetetes schucherti* MORGAN, 1924, Pennsylvanian, upper Carboniferous, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of chimneys, the one in the left center is slightly abraded, ×1.85; *2,* longitudinal section of chimney showing the depth of a partially filled hole at the top of the vertically developed mamelon with a chimney, ×1.25; *3,* enlarged view of the upper part of the chimney with the partially filled hole in view *2,* ×2; *4,* plan view of two adjacent chimneys, ×1.9; *5,* longitudinal section of the two adjacent chimneys seen in plan view in view *4,* ×2.15 (new).

from the tubes a distance of from 5 to 10 mm and then turn upward (MORGAN, 1924, p. 175). This same arrangement occurs in topotype specimens with mamelons, including those with a circular opening at the top, i.e., chimneys (Fig. 7). The vertically extended mamelons were constructed by tubules that fanned out as they grew upward, and the circular openings associated with some mamelons appear to have been excavated later. Tubules associated with these circular openings do not appear to be distorted; there is nothing that resembles the abnormal growth around the suggested vermiform symbiotics illustrated by WEST and CLARK (1984, pl. 2,*F*). Although some of these circular openings could have been oscula, others were excavated after skeletal growth, but before death; they could also be postmortem features.

TUBERCULES

These structures that resemble tiny spines are small, slightly raised, calcareous projections. They occur at the junction between two or more tubules at the top of the basal calcareous skeleton, where the thin soft tissue is presumed to have been in contact with the skeleton. These have been observed in *Merlia normani* (HAJDU & VAN SOEST, 2002) and in some well-preserved fossil chaetetid skeletons (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 9.2–9.3). Perhaps they have had some value in helping anchor the thin layer of soft tissue to the basal calcareous skeleton. However, it is more likely that they are simply the result of the arrangement of the calcite crystals from which the basal skeleton is/was constructed. The microstructure and mineralogy of *Merlia* and fossil chaetetids is considered to be penicillate Mg calcite (FINKS & RIGBY, 2004; see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Table 2). Water-jet Mg calcite has also been used to describe the microstructure and mineralogy (CUIF & GAUTRET, 1993; HOOPER & VAN SOEST, 2002a; and see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Table 2). In either case, the calcite crystals that compose the walls of the tubules fan outward at a relatively high angle (see CUIF & GAUTRET, 1993). As the walls of two or more tubules come into contact and join, the merging of bundles of crystals in each could result in a projection above the adjacent walls of the tubules producing tubercules. For example, the upper edges of the tubules in *Acanthochaetetes wellsi* are crenulated, and each crenulation corresponds to upwardly directed undulations of the lamellar crystalline units of calcite that make up the walls of the tubules (HARTMAN & GOREAU, 1975, p. 3).

INTERNAL FEATURES

TUBULES

The chaetetid skeleton is dominantly composed of tubules. In longitudinal section, they are more or less straight, but in transverse section, they exhibit meandroid- to irregularly polygonal–shaped outlines (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 10–11, Fig. 25–26). Co-joining of walls with adjacent tubules results in a honeycomb-like construction, although the tubules have a much more irregular profile in transverse section. To attempt to understand the role of the tubules in chaetetid skeletons of hypercalcified demosponges, it is useful to examine the relationship between the tubules that compose the basal calcareous skeleton and the soft, living tissue in extant taxa.

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

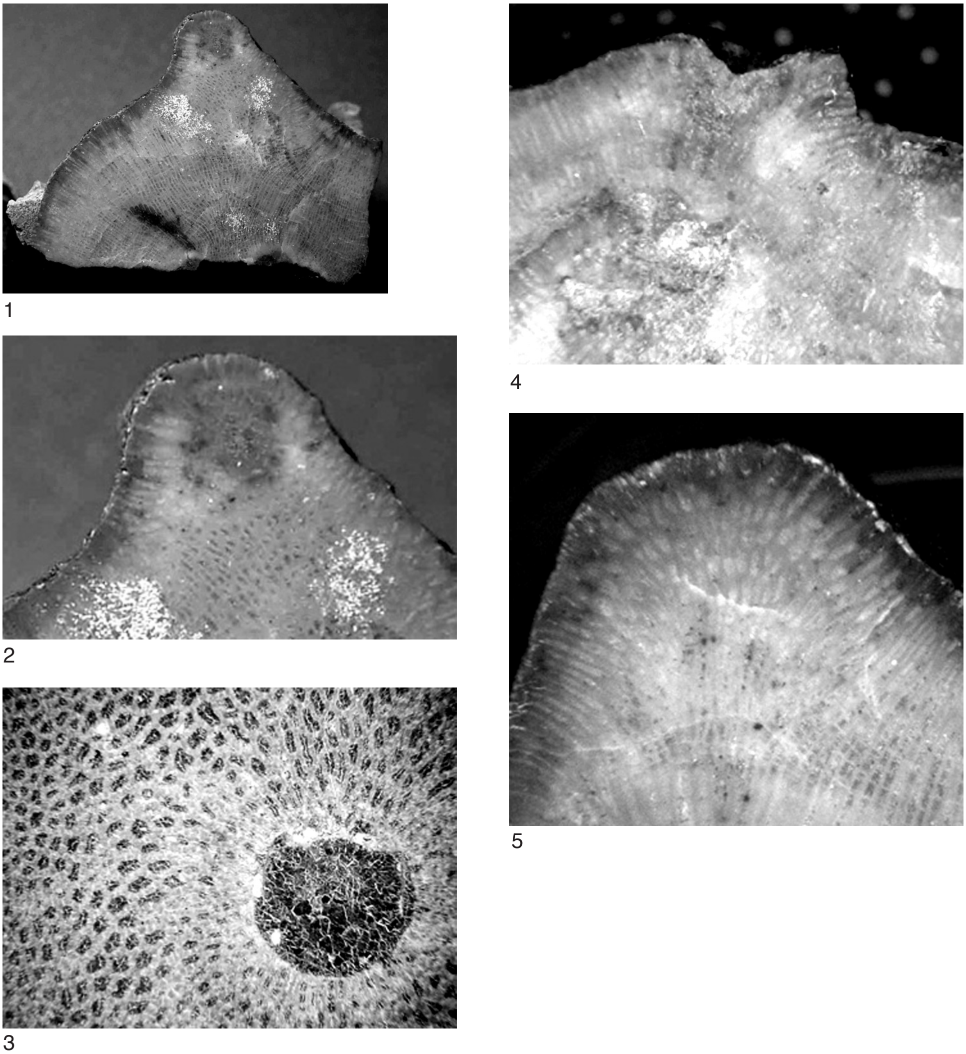

FIG. 7. Arrangement of tubules in vertically developed mamelons with and without circular openings, *Chaetetes schucherti* MORGAN, 1924, Pennsylvanian, upper Carboniferous, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of vertically developed mamelon with a tube (chimney) in a topotype specimen, ×0.9; *2,* enlargement of upper part of chimney figured in view *1,* ×3; *3,* transverse thin section of tube in vertically developed mamelon (chimney) in the holotype, tube filled with sparry calcite, ×6.7; *4,* longitudinal section of vertically developed mamelons with shallow tube (chimney) in a topotype specimen, ×5; *5,* longitudinal section in a vertically developed mamelon in a topotype specimen, ×5 (new).

could result in a basal calcareous skeleton in chaetetids, at least initially, because, based on studies of extant forms such as *Ceratoporella*, *Acanthochaetetes*, and *Merlia*, the only part of the calcareous skeleton that contains living tissue is the uppermost millimeter or two. The bulk of domical, columnar, and some laminar chaetetid skeletons in extant taxa (and inferred in fossil forms) appear to have little, if anything, to do with the living tissue. Over time, there may have been some genetic component that favored the development of a basal calcareous skeleton (see KIRKPATRICK, 1911, p. 690–691).

For example, lateral expansion of such a skeleton would permit the sponge to dominate more of the substrate and provide a larger base for upward (vertical) growth yet still remain a fairly stable structure. Lateral expansion and upward growth from a smaller base occurs in fossil chaetetids (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 14.3–14.4, Fig. 15.2). Something similar has been documented in *Ceratoporella nicholsoni*, an extant taxon, where the young forms are cone shaped or pedunculate, and the mature forms are massive and mound shaped (Vacelet, 2002, p. 827). Hartman and Goreau (1975, p. 3) also reported a stalked condition in some specimens of *A. wellsi*, supporting a tendency, in some cases, for upward growth. An example of an extant pedunculate specimen of *Acanthochaetetes* sp. can be seen in *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Figure 6.1. With vertical growth of the skeleton, the thin layer of living tissue would be positioned higher in the water column. Such a position would be advantageous for an organism that depends on dissolved and suspended matter in the water it pumps through its pores.

The tubule walls of *Acanthochaetetes wellsi, Ceratoporella nicholsoni,* and *Merlia normani*, all extant taxa, are either aragonite or Mg calcite. Arrangement of the crystals of these minerals produces either a penicillate (water-jet) or lamellar microstructure (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Table 2) in these taxa. In most fossil chaetetids, the original mineralogy has, as a result of taphonomic processes (recrystallization), changed to low Mg calcite. But the original mineralogy is inferred to have been Mg calcite, and the microstructure is penicillate, as in the extant genus *Merlia*. The basal calcareous skeleton of Pennsylvanian chaetetids preserved in asphalt in Oklahoma was reported by Squires (1973; see also *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A) to contain 5 mol% Mg calcite, but unfortunately he did not document the microstructure of the tubule walls in these specimens.

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

TABULAE

The tabulae are horizontal partitions that subdivide the tubules in some fossil and extant chaetetid skeletons and are commonly thinner than the tubule walls (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 27–28). These discrete calcareous plates are generally flat or slightly curved and parallel to the growth surface in both fossil and extant specimens, where they occur. The outermost tabula, in extant forms, forms a floor for the overlying thin layer of living tissue (see Reitner & Gautret, 1996, pl.

49,*1*). Thus the tabula function as the base upon which the soft tissue rests, and they may or may not be perforated by a foramen that may or may not be subsequently infilled with calcite. The space containing the soft living tissue and the spaces between successive tabulae below the living tissue in extant specimens are referred to as crypts. Tabulae in *Acanthochaetetes wellsi* are irregularly spaced, may be slightly convex, horizontal, or slightly concave, and do not necessarily occur at the same level in adjacent tubules; however, they may be at the same level in a few tubules in a limited area (HARTMAN & GOREAU, 1975, p. 3). This also applies to fossil chaetetids (WEST & CLARK, 1984), and in some fossil specimens, the tabulae are incomplete. This incompleteness could be due to an opening where perforated by a foramen or produced by dissolution.

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

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

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

As noted above, the basal calcareous skeleton of some chaetetid skeletons looks very much like the honeycombs constructed by bees. There is also a striking resemblance between these sponge skeletons and the structure of mycelium, the typical vegetative structure of some fungi, and, to some extent, in the sheetlike growth form of some tree fungi (Fig. 8–9). Fungi and sponges with a chaetetid skeleton are fairly simple organisms, and perhaps it is not surprising that both generate somewhat similar structures to house and protect asexual reproductive bodies.

PORE (FORAMEN)

A more or less circular opening near the center of individual tabulae in hypercalcified demosponges with a chaetetid skeleton is referred to as a pore, or foramen. Kirkpatrick (1911) called such an opening a foramen, and that term is defined by Boury-Esnault and Rützler (1997, p. 39, fig. 208) as a "circular pore in laminae connecting adjoining interlamellar spaces." By laminae, they appear to mean tabulae, because they identify the foramen as being in a tabula in Boury-Esnault and Rützler (1997, p. 39, fig. 208). Tabulae in *Acanthochaetetes wellsi* are continuous and lack a foramen (Hartman & Goreau, 1975), but a foramen is present in the tabulae of *Merlia normani* (Kirkpatrick, 1911; Reitner, 1992, p. 239, fig. 66e). The occurrence of incomplete tabulae in fossil chaetetids might suggest the occurrence of foramina, but there are other explanations for incomplete tabulae in fossil chaetetids, as noted above. What has been identified as a foramen in a fossil chaetetid is illustrated in *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Figure 29. Tubular spaces between tabulae contain gemmules in some extant forms; the same may be reasonably inferred for fossil chaetetids. A foramen would permit the movement and/or exchange of cellular matter and also for egress of the asexual reproductive bodies to the surface of the basal calcareous skeleton with the return of favorable environmental conditions. There seems to be no other reasonable explanation for its existence, and the fact that such an opening has not been documented in *A. wellsi* indicates that it may not have been essential for regenerative growth.

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

PSEUDOSEPTA

Features that are apparently known only from fossils with a chaetetid skeleton are pseudosepta (see West & Clark, 1984). These calcareous structures are associated with longitudinal fission, one of the three ways the number of tubules in the basal calcareous skeleton may be increased. Pseudosepta first appear as small, slightly raised areas (nodes) on the interior wall of the tubule (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 34–35). One or more nodes may occur in any given tubule, which divides it into equal or unequal parts. With upward growth, the nodes expand outward and upward, parallel to the direction of the growth axis, resulting in septa-like features. As two pseudosepta within a tubule approach each other, the parent tubule increases in size. Eventually, the pseudosepta may extend across the tubule, or merge with others, subdividing the original tubule into two or more new tubules. Generally, the division of the parent tubule is along its shortest horizontal dimension. Therefore, pseudosepta are associated with the growth and expansion of the basal calcareous skeleton.

SPICULES

These features are a component of the mineral skeleton, typically composed of silica in extant forms, but when observed in fossil forms, they are pseudomorphs of calcite, pyrite, or iron oxide (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 36–38). In extant forms, and some fossil chaetetids, there are both megascleres and microscleres. In the extant taxa, *Acanthochaetetes wellsi*, *Ceratoporella nicholsoni*, and *Merlia normani*, spicules are largely confined to the thin layer of soft tissue. Hartman and Goreau (1975, p. 4) stated that siliceous spicules are not incorporated into the basal

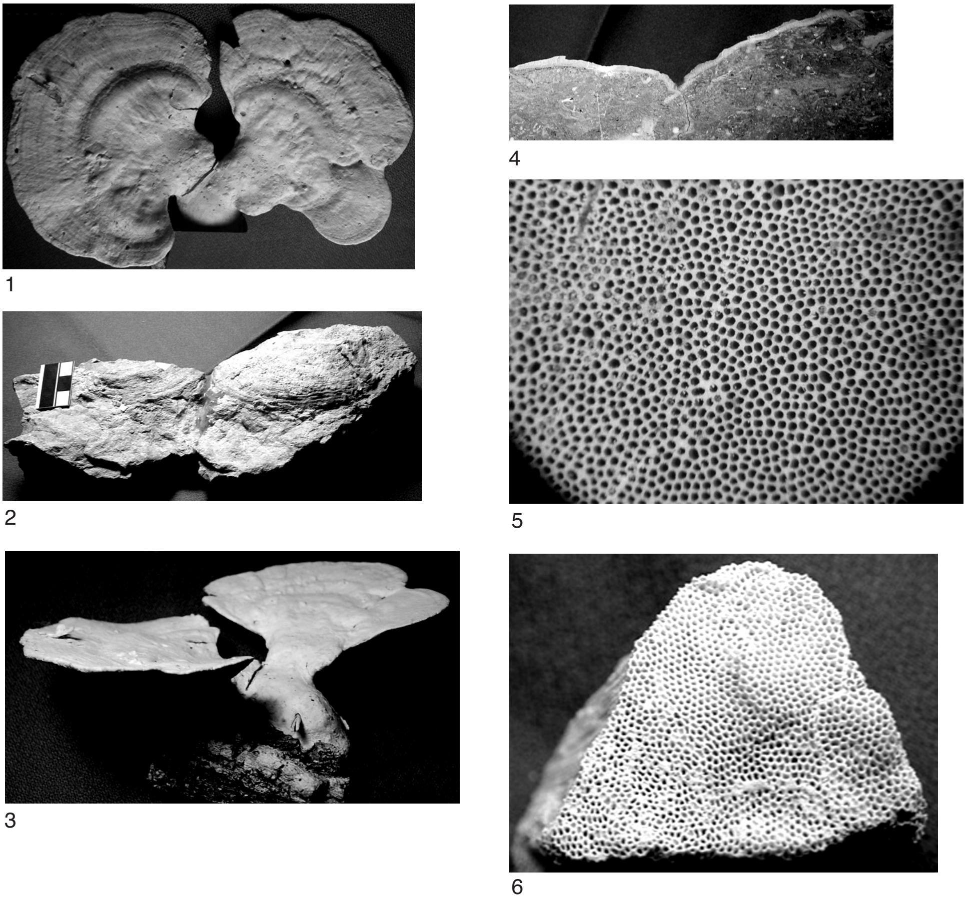

FIG. 8. Comparison of form and structure of laminar chaetetid skeletons with the form and structure of some extant shelf fungi; *1,* upper surface of the basic form of an extant shelf fungi, ×0.4; *2,* oblique view of a laminar chaetetid skeleton, Pennsylvanian, upper Carboniferous, Myrick Station Limestone, Pawnee Limestone, Bourbon County, Kansas, compare with view *1,* ×0.2; *3,* lateral view of extant shelf fungi figured in view *1,* ×0.5; *4,* longitudinal section of chaetetid skeleton figured in view *2,* the thin, arcuate white lines are the laminar chaetetid skeleton with darker matrix below, compare with view *3,* ×0.3; *5,* lower surface of an extant shelf fungi showing the irregular polygons that compose the mycelium, ×7; *6,* upper surface of a chaetetid skeleton, Moscovian, upper Carboniferous, Moscow Basin, Russia, compare with view *5,* ×2 (new).

calcareous skeleton of *A. wellsi,* but RÜTZLER and VACELET (2002, p. 277) indicated that some microscleres that adhere to the tubule walls may be incorporated into the skeleton during fossilization. Although some spicules are trapped in the tubule walls of *C. nicholsoni,* they are progressively dissolved in the basal calcareous skeleton (VACELET, 2002, p. 827). In *M. normani,* the megascleres occur as bundles along the sides and bottom of the open crypts, but rarely in the lower crypts (KIRKPATRICK, 1911, p. 670, fig. 2, pl. 33,*3*). Microscleres in this species are contained along the surface of the soft living tissue (KIRKPATRICK, 1911, p. 670, pl. 33,*3*). Because siliceous spicules are rarely incorporated into the basal calcareous skeleton of extant forms, they are commonly absent in fossil chaetetids. When they do occur in fossils, they are pseudomorphs, because of the ease with which siliceous spicules are dissolved, as noted in extant taxa. Megascleres in fossil chaetetids are thin tylostyle-like features (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A,

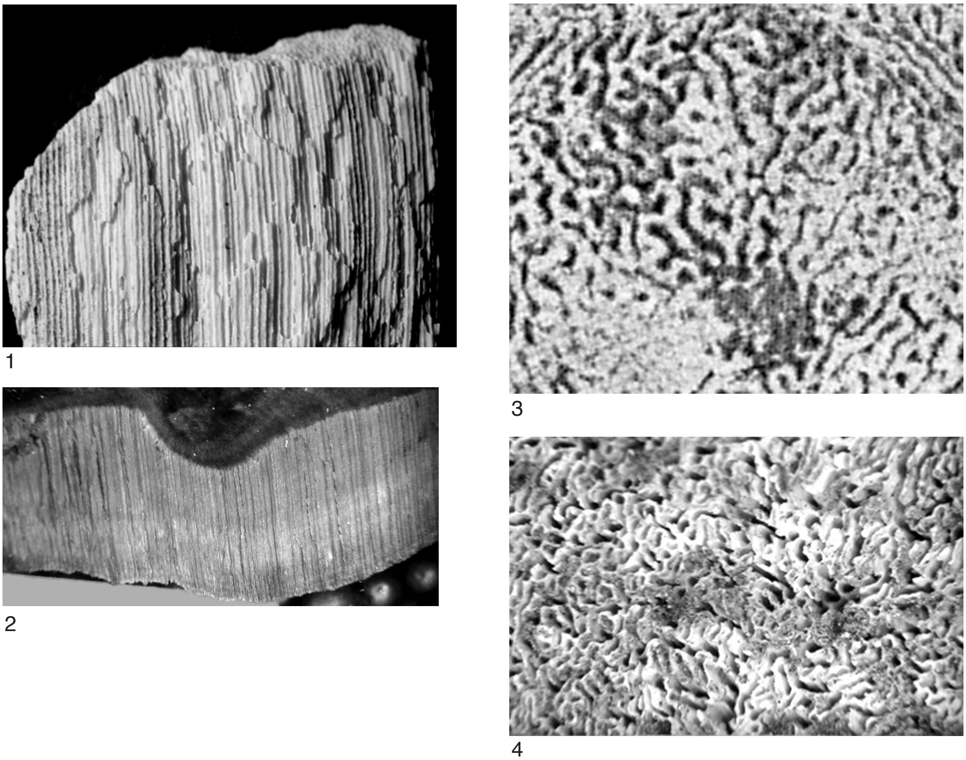

Fig. 9. Comparison of form and structure of laminar chaetetid skeletons with the form and structure of some extant shelf fungi (continued); *1,* lateral view of a chaetetid skeleton, Moscovian, upper Carboniferous, Moscow Basin, Russia, ×1.75 (new); *2,* lateral view of the mycelium of the extant shelf fungi figured in view Fig. 8.5, compare with view *1,* ×4 (new); *3,* upper surface of *Meandriptera zardinii*, Carnian, Upper Triassic, St. Cassiano beds near Cortina d'Ampezo, Italy, showing the meandroid shape of the tubules, ×4 (adapted from Dieci & others, 1977, pl. 1,*2a;* courtesy of *Bollettino della Società Paleontologica, Italiana*); *4,* lower surface of an extant shelf fungi showing the meandroid structure of the mycelium, compare with view *3,* ×5 (new).

Fig. 36–37), and microscleres are more or less dark spheres, commonly seen as circles in sectioned specimens (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 38).

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

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