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 Introduction to the Fossil Hypercalcified Chaetetid-Type Porifera, p. 15–19).

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

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

EXTERNAL FEATURES

GROWTH FORM

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

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

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

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

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

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

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

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

GROWTH RATES

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

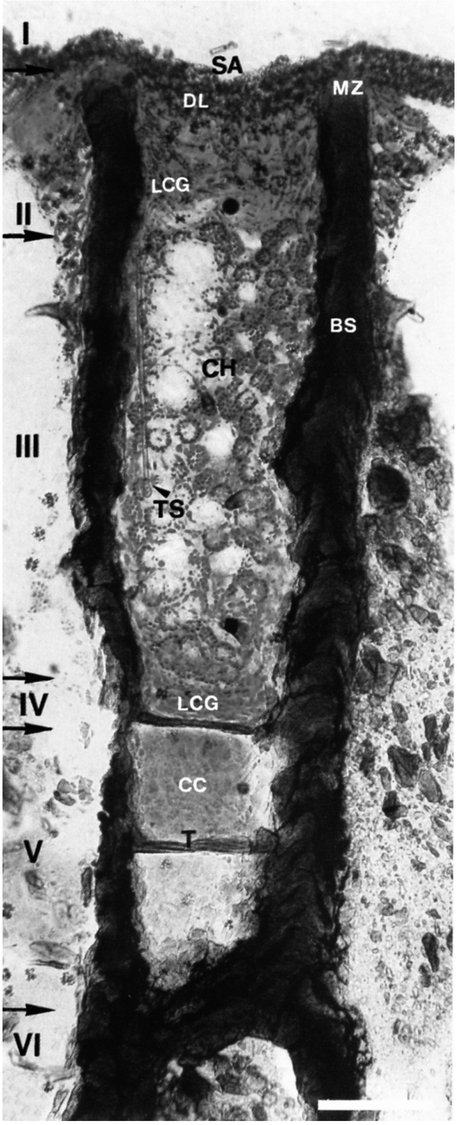

FIG. 58. Growth in *Acanthochaetetes wellsi;* vertical section of a tubule with living tissue. Tubule is divided into six sections: *I,* spiraster microsclere (*SA*) crust; *II,* lower dermal layer (*DL*) with large cells with granules (*LCG*) and skeletal growth fronts (*MZ*); *III,* choanosome (*CH*)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

using $\delta^{13}C$ 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 5–7. Table 5 provides the taxa, age, habitat, growth rate in mm/yr, reference, and pertinent remarks for hypercalcified and nonhypercalcified extant sponges, hermatypic and ahermatypic extant corals, and extant bryozoans. For some sponges and bryozoans, the data are reported as areas, i.e., mm^2/yr. Similar data for Ordovician, Silurian, and Devonian corals are given in Table 6. The same information is given in Table 7 for specimens of extant hermatypic corals from different water depths from the Caribbean and Indo-Pacific. There are data for *Montastrea annularis, Montastrea cavernosa, Porites asteroides*, and *Siderastrea siderea* from the Caribbean, and for *Astreopora myriophthalma, Porites lobata, Goniastrea retiformis, Favia speciosa, Porites lutea,* and *Favia pallida* from the Indo-Pacific. Two aspects of the data in Tables 5 and 7 are particularly obvious and important: (1) the growth rate of all the other clonal invertebrates listed is an order of magnitude greater than the growth rate for either of the two hypercalcified sponges (Table 5); and (2) the growth rate of extant hermatypic corals varies with water depth; often, though not always, the growth is slowest in deeper water (Table 7). In *Oculina varicosa* (Table 5), the ahermatypic form of this species grows faster in deep, cold water than the hermatypic form does in shallow, warmer water.

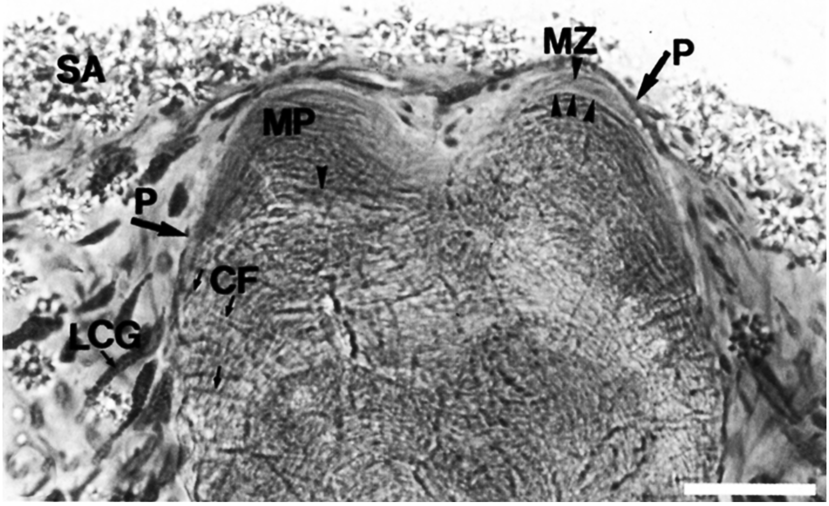

FIG. 59. Growth in *Acanthochaetetes wellsi* (continued); uppermost growing zone of tubule wall, enlargement of upper part of section II in Figure 58. *MP,* mucus-rich parts of basal skeleton within active mineralizing front (*MZ*) beneath basal pinacoderm (*P*), *SA,* spiraster microsclere crust, collagenous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

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

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

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

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

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

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

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

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

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

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

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

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

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

with other encrusting sessile benthos for space on the seafloor.

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

BASAL LAYER

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

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

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

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

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

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

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

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

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

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

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

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

Lophelia pertsua:*Ceratoporella nicholsoni* = 10 mm/yr:X
$7.5:0.175 = 10:X$
$7.5X = 0.175 \times 10$
$X = 0.2$ mm/yr

Lophelia pertsua:*Acanthochaetetes wellsi* =10 mm/yr:X
$7.5:0.075 = 10:X$
$7.5X = 0.075 \times 10$
$X = 0.1$ mm/yr

Oculina varicosa:*Ceratoporella nicholsoni* = 10 mm/yr:X
$16.1:0.175 = 10:X$
$16.1X = 0.175 \times 10$
$X = 0.1$ mm/yr

Oculina varicosa:*Acanthochaetetes wellsi* = 10 mm/yr:X
$16.1:0.075 = 10:X$
$16.1X = 0.075 \times 10$
$X = 0.05$ mm/yr

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

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

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

ASTRORHIZAE

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

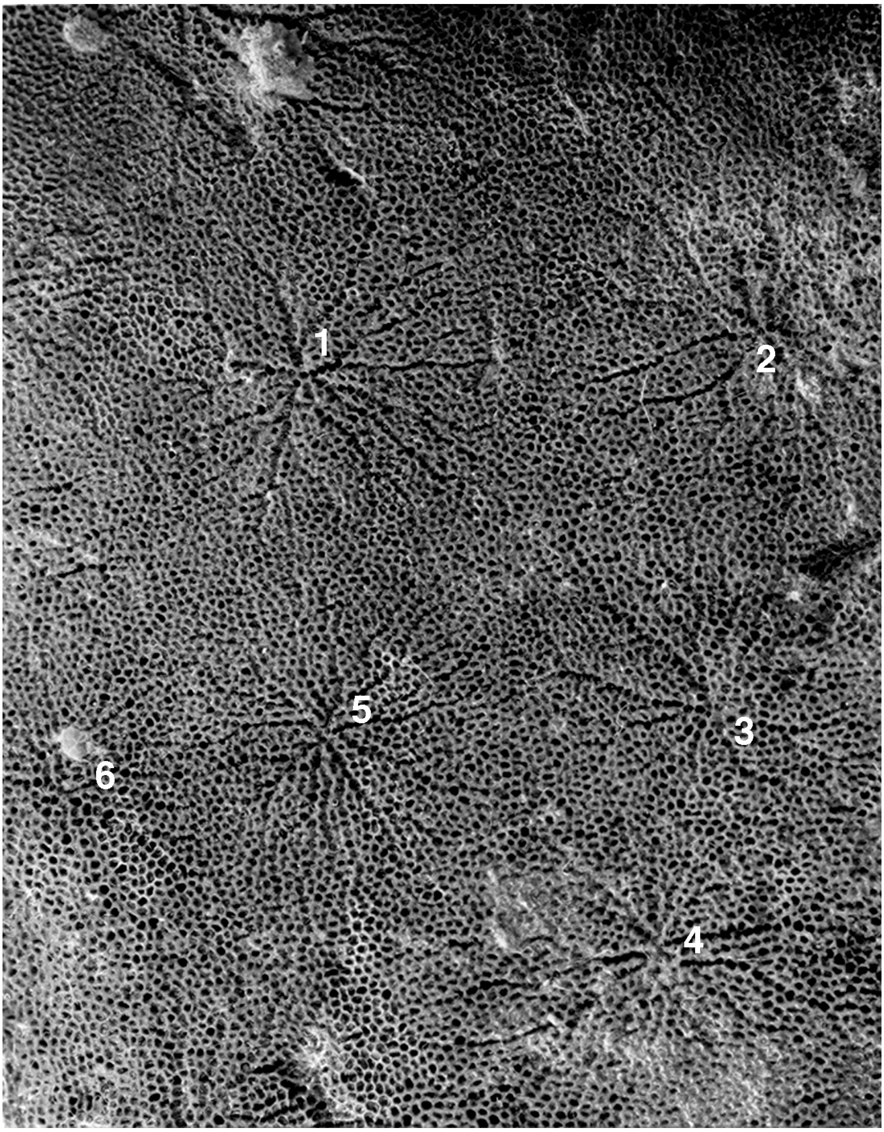

FIG. 60. Six astrorhizae in 10.4 cm^2 area on the surface of a chaetetid, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; see Table 11 for distances between astrorhizae, ×4.1 (West, 2011b).

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

MAMELONS

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

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

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

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

CHIMNEYS

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

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

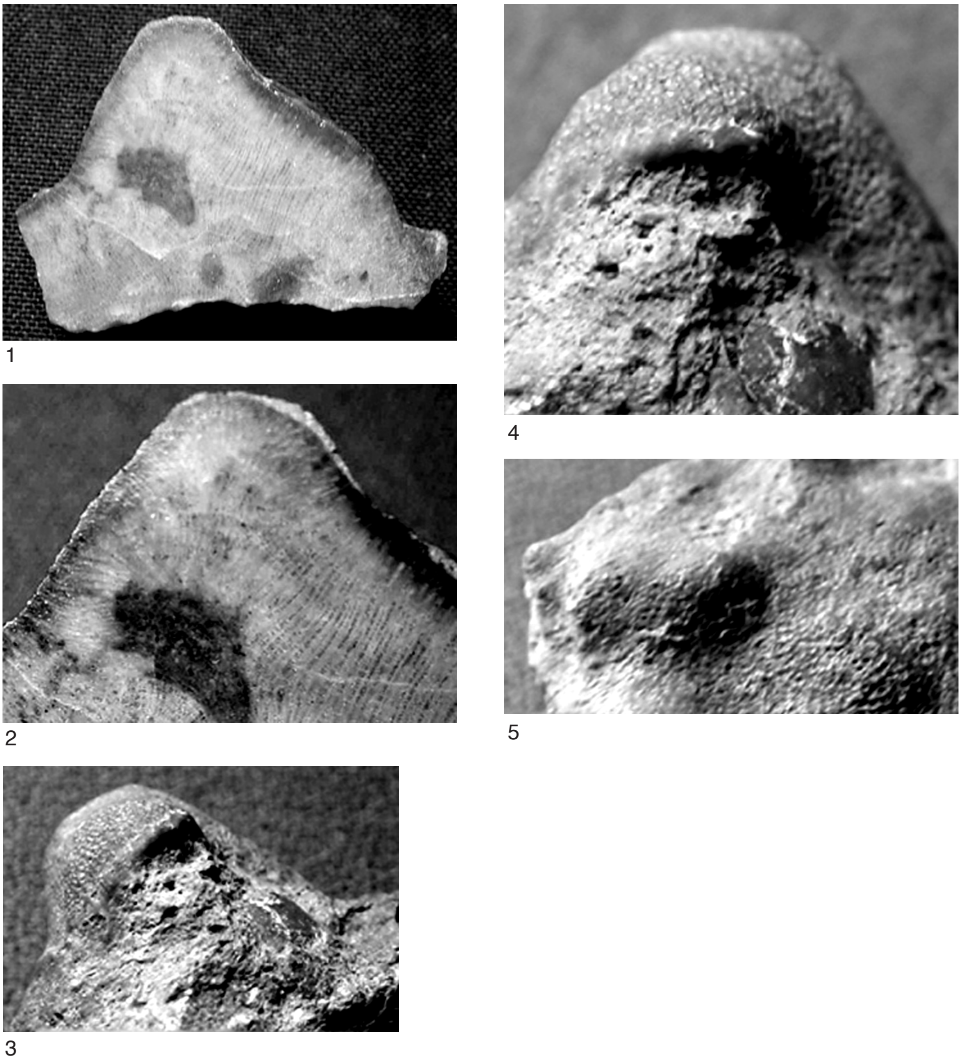

Fig. 61. Tubules in vertically developed mamelons in topotype specimens of *C. (Chaetetes) schucherti* Morgan, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of a vertically developed mamelon, note tubule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

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

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

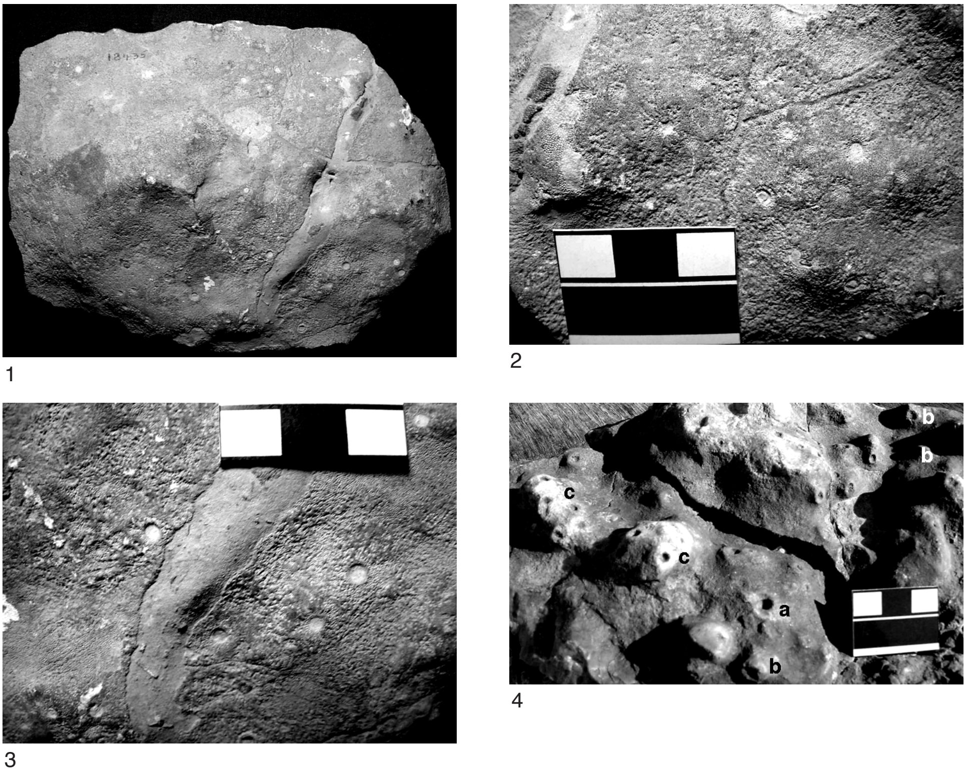

FIG. 62. Circular openings in upper exterior surface of *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of upper exterior surface of holotype; light colored circles are 3 mm holes noted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

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

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

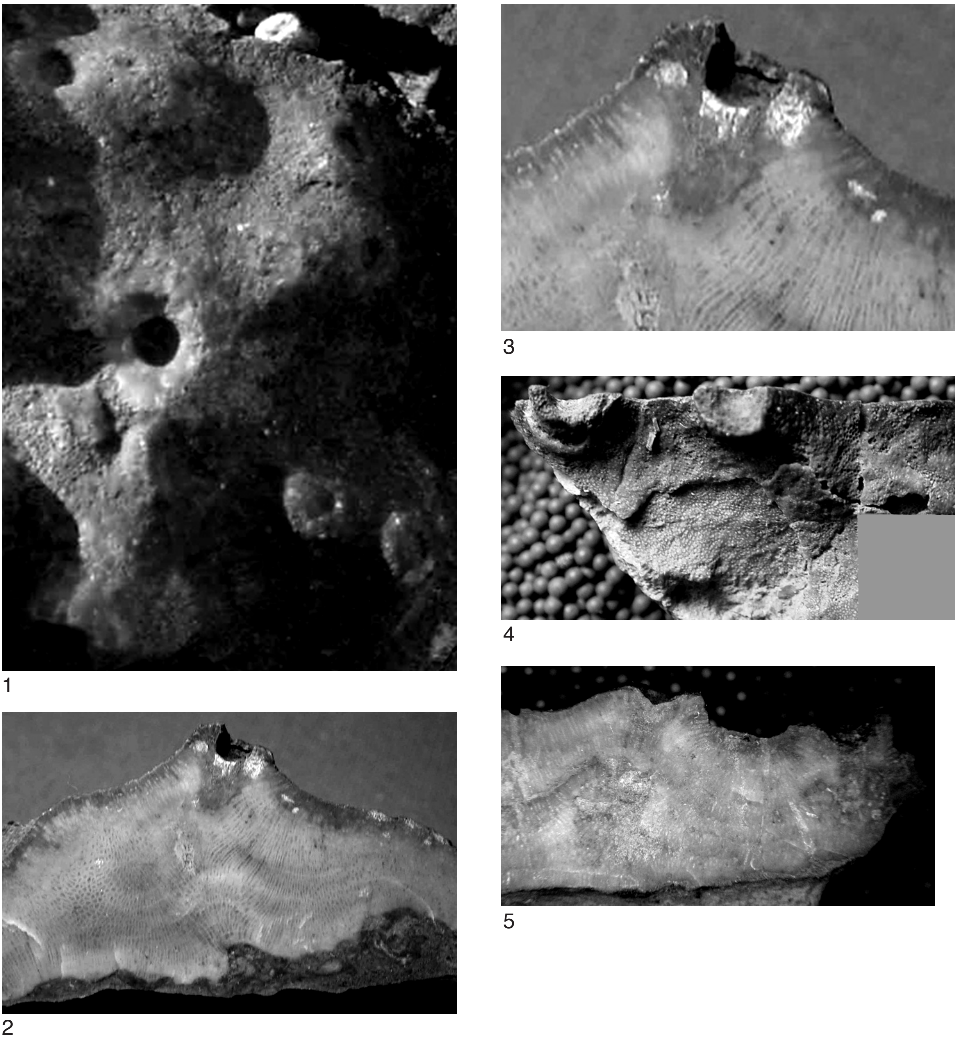

FIG. 63. Chimneys in topotype specimens of *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* plan view of chimneys, the one in left center is slightly abraded, ×1.85; *2,* longitudinal section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

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

TUBERCULES

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

INTERNAL FEATURES

TUBULES

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

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

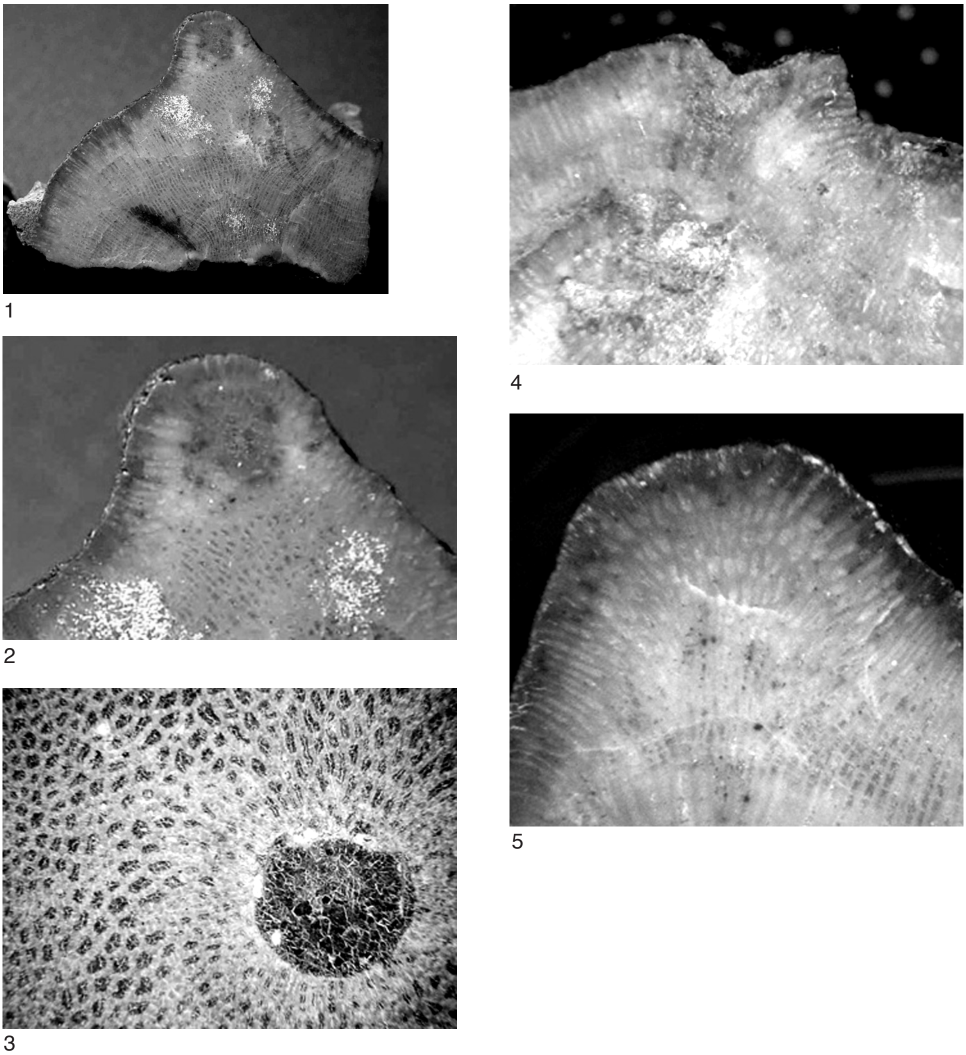

FIG. 64. Arrangement of tubules in vertically developed mamelons with and without circular openings, *C. (Chaetetes) schucherti* MORGAN, 1924, Carboniferous, Pennsylvanian, Homer School Limestone Member, Holdenville Formation, Seminole County, Oklahoma; *1,* longitudinal section of vertically developed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

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

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

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

TABULAE

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

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

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

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

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

PORE (FORAMEN)

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

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

PSEUDOSEPTA

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

SPICULES

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

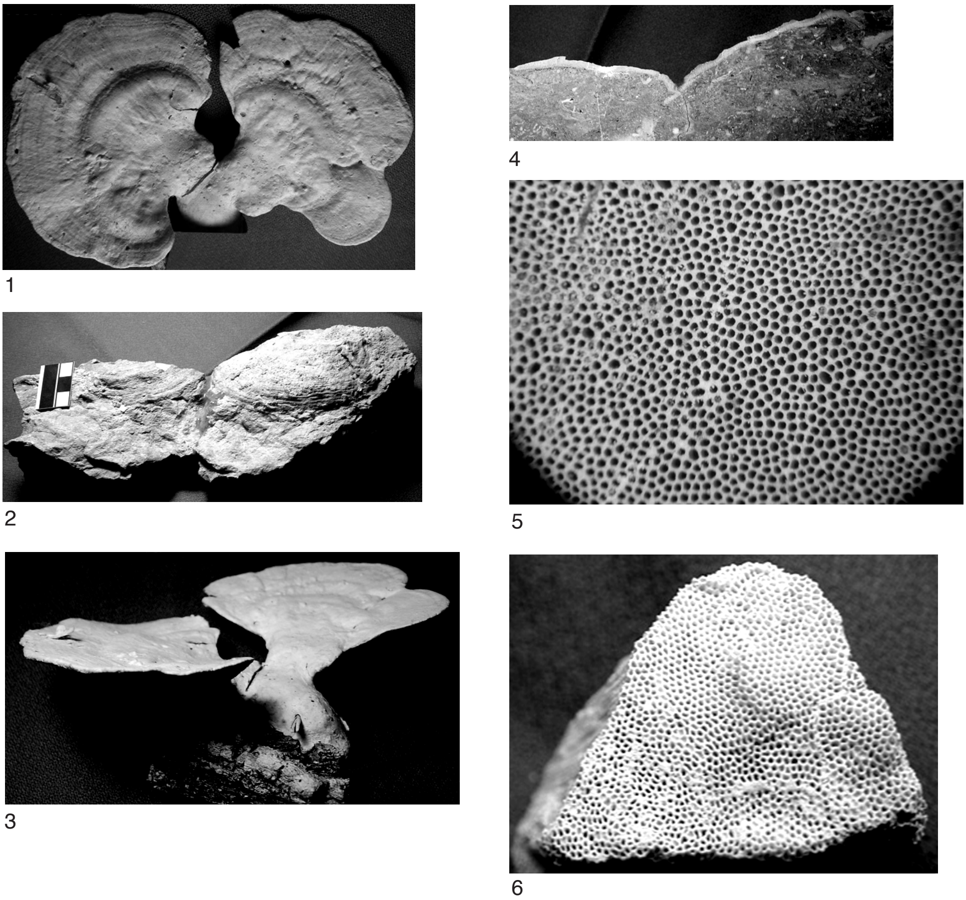

FIG. 65. Comparison of form and structure of laminar chaetetid skeletons with the form and structure of some extant shelf fungus; *1,* upper surface of basic form of an extant shelf fungus, ×0.4; *2,* oblique view of a laminar chaetetid skeleton, Carboniferous, Pennsylvanian, Myrick Station Limestone,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

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

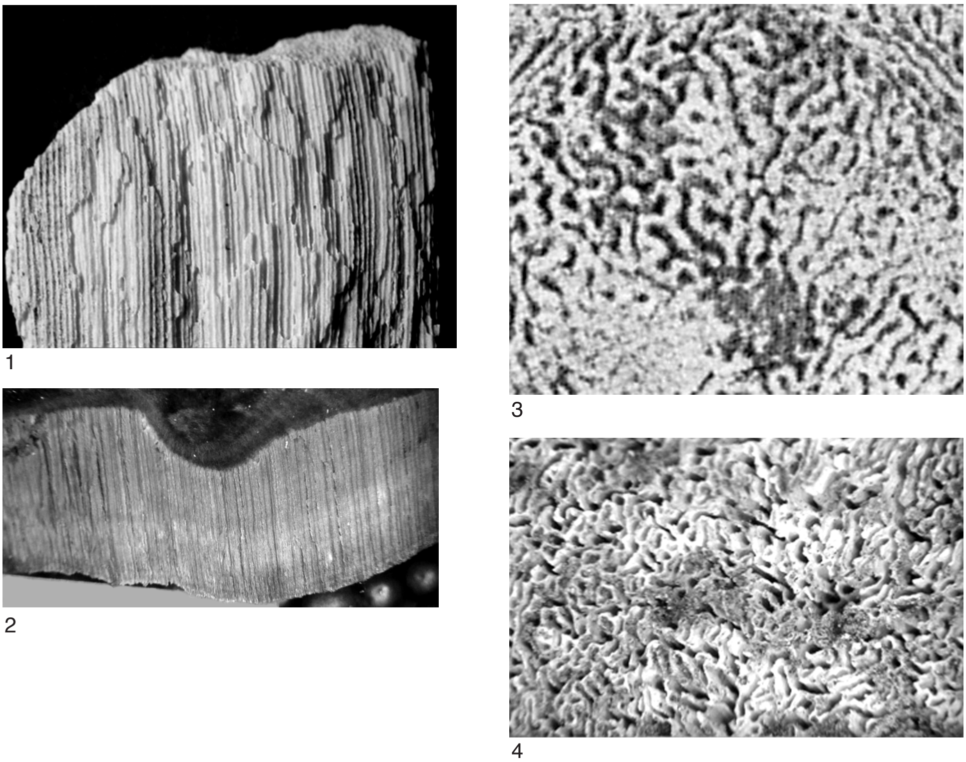

Fig. 66. Comparison of form and structure of laminar chaetetid skeletons with form and structure of some extant shelf fungus (continued); *1,* lateral view of a chaetetid skeleton, Carboniferous, Pennsylvanian (Moscovian), Moscow Basin, Russia, ×1.75 (West, 2011b); *2,* lateral view of mycelium of extant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

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

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

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

Ronald R. West

CLASSIFICATION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

EVOLUTION

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Although chaetetid demosponges are known from the upper Permian (H. TERMIER, G. TERMIER, & VACHARD, 1977; GAUTRET & RAZGALLAH, 1987; FLÜGEL & REINHARDT, 1989), they are absent from the Lower and Middle Triassic. *Atrochaetetes*, *Bauneia*, *Blastochaetetes*, *Blastoporella*, *Cassianochaetetes*, *Ceratoporella*, *Chaetosclera*, *Kemeria*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, and *Sclerocoelia* are known from the lower Upper Triassic (Carnian) of Italy. *Blastoporella*, *Kemeria*, and *Ptychochaetetes (Ptychochaetetes)* are reported from the Upper Triassic of Turkey (see Table 21). The mineralogy and microstructure of the tubule walls are known for all of these genera, and definite spicules (pseudomorphs) are known from *Atrochaetetes*, *Bauneia*, *Blastochaetetes* (CREMER, 1995), *Chaetosclera* (REITNER & ENGESER, 1989a), *Meandripetra* (DIECI & others, 1977), *Ptychochaetetes (Ptychochaetetes)* (CREMER, 1995), and *Scleroscoelia* (DIECI & others, 1977) (Table 20). CUIF (1974) described *Ceratoporella goreaui* from the Saint-Cassian Dolomites (Upper Triassic) of northern Italy, documenting the mineralogy and microstructure, but nothing on the spicules. FÜRSICH and WENDT (1977) reported five undescribed species

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

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

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

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

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

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

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

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

(Continued on facing page).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

PALEOECOLOGY OF THE HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

RONALD R. WEST

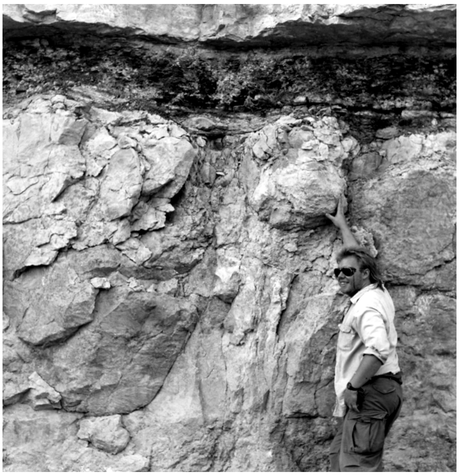
INTRODUCTION

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

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

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

1



3

2

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

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

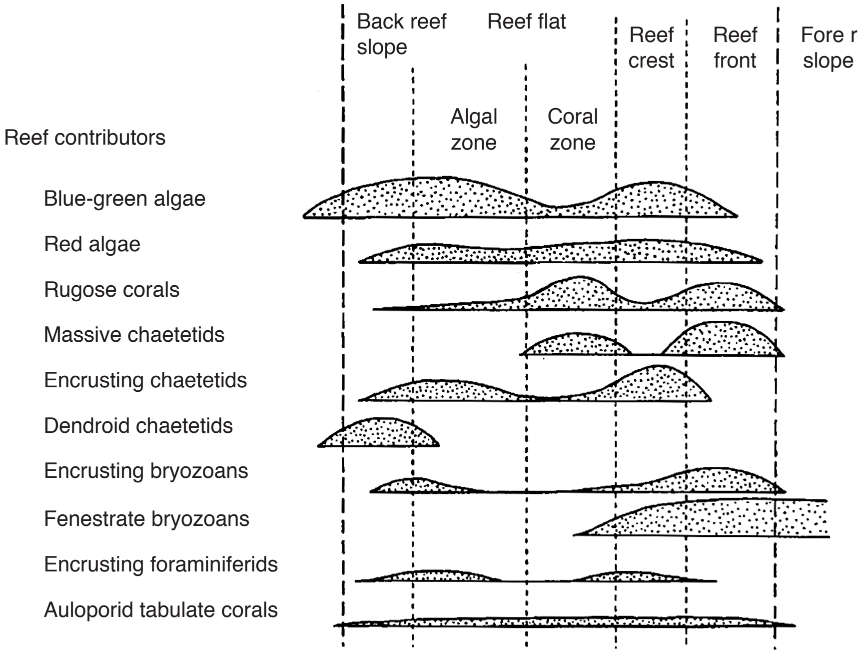


FIG. 68. Distribution of the main reef contributors in the reef facies, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Minami-dai area, Japan (adapted from Sugiyama & Nagai, 1990, p. 11, fig. 2; courtesy of the authors and Akiyoshi-dai Museum of Natural History).

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

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

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

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

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

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

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

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

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

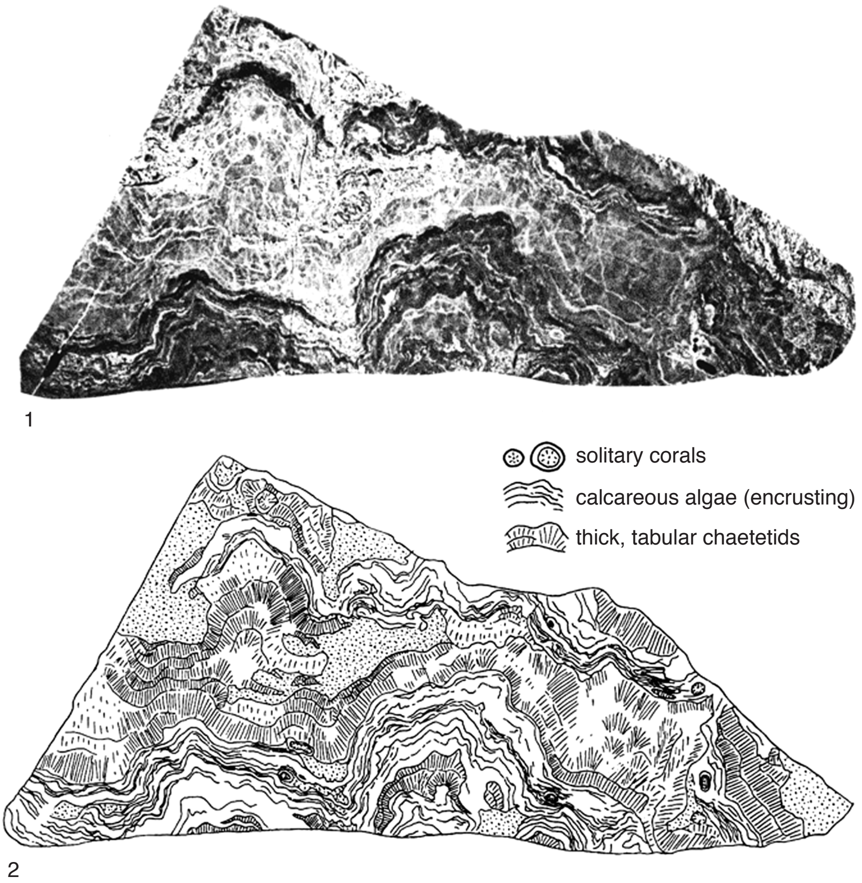


FIG. 69. Reef builders, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* polished surface of reef boundstone from the reef crest, Akiyoshi Limestone, Akiyoshi-dai, Japan, ×0.29 (adapted from Nagai, 1992, pl. 24,*1;* courtesy of the author and Kyushu University); *2,* interpretive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

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

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

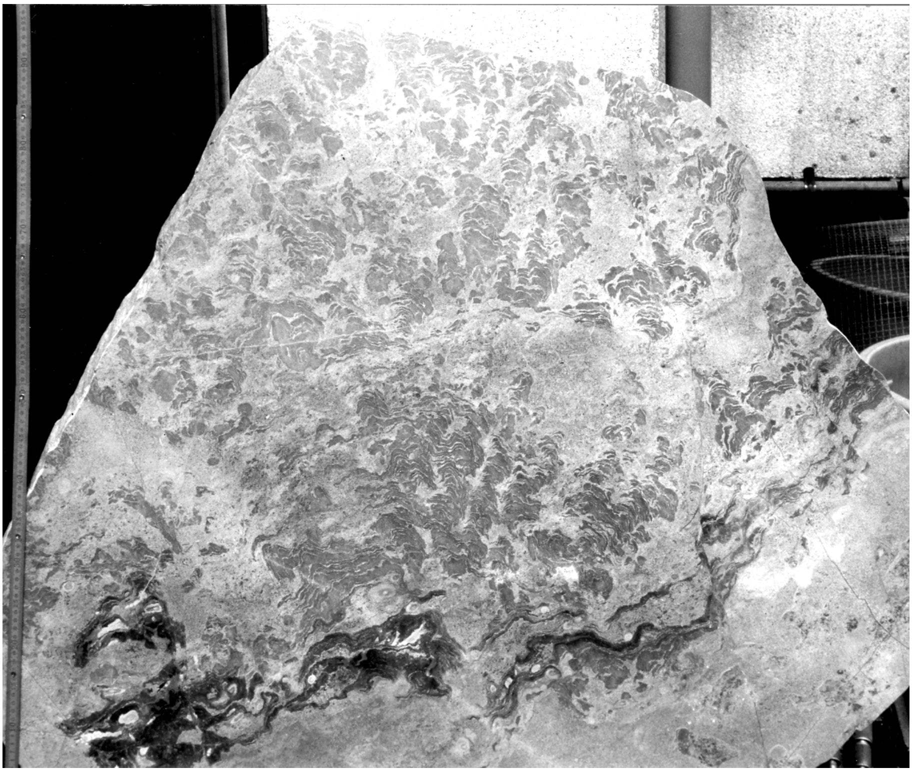


FIG. 70. Polished surface of a large slab from the fore reef facies, Carboniferous, Pennsylvanian, Akiyoshi limestone, Akiyoshi-dai, Japan, ×0.11 (West, 2012b).

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

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

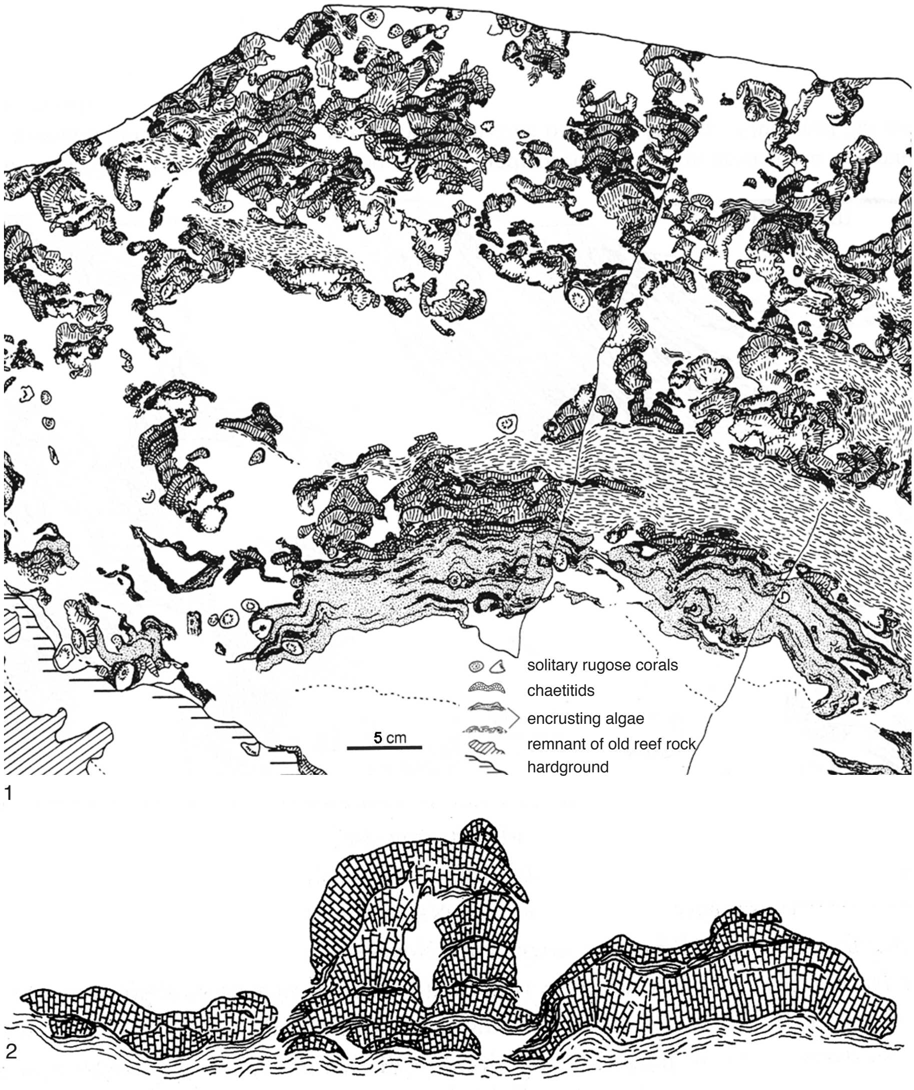


FIG. 71. Polished surfaces of slabs from the reef facies, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* detailed interpretative sketch of the surface of a large polished slab of chaetetid-algal boundstone, ×0.2 (adapted from Nagai, 1985, fig. 4; for a color version, see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

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

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

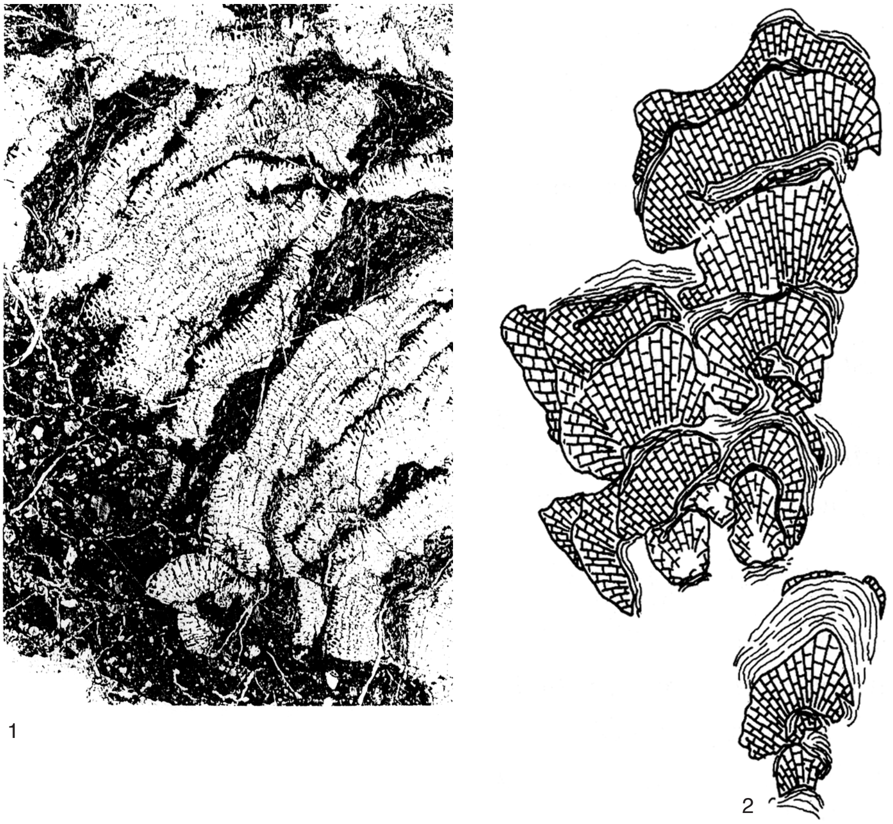


FIG. 72. Details of the relationships between encrusting algae–microbes and chaetetids from the organic reef complex, Carboniferous, Pennsylvanian, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* thin section showing interlayering of thin laminar chaetetids and algal–microbial mats from the organic reef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

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

PHYSICAL AND CHEMICAL FACTORS

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

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

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

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

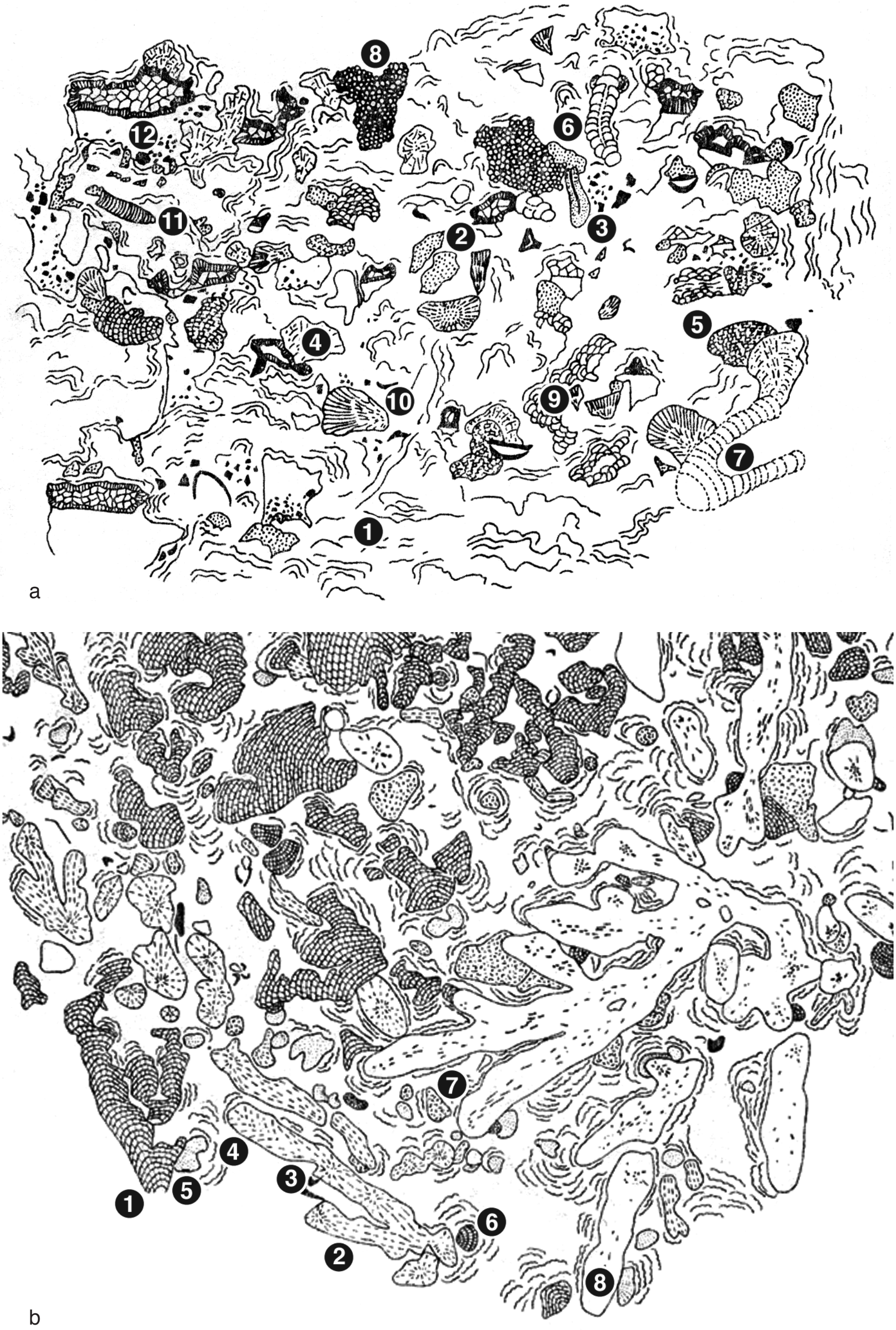


FIG. 74. *(For explanation, see facing page).*

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

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

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

HIGH DOMICAL AND COLUMNAR FORMS

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

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

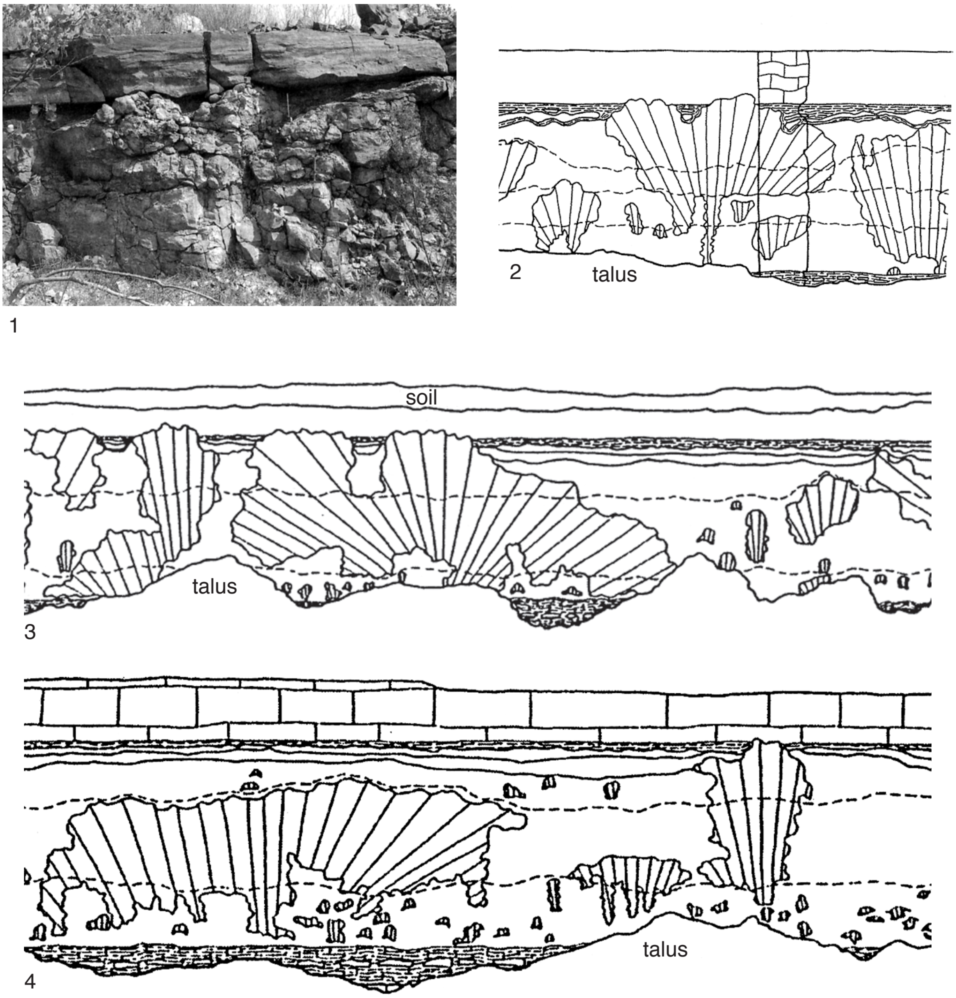


FIG. 75. Chaetetid reef mounds, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of a chaetetid reef mound in a south-facing wall in the southern part of a quarry, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×0.01 (adapted from Suchy & West, 2001, p. 429,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

SUCHY & WEST, 2001; WEST, NAGAI, & SUGIYAMA, 2001; SANO, FUJII, & MATSUURA, 2004; SANO, 2006). Such occurrences might indicate that, rather than competitors, chaetetids and algae were mutually tolerant in these environments. Or, perhaps, as illustrated by PRECIADO and MALDONADO (2005, p. 149), for some extant situations, the presence of the algae created a favorable habitat for the sponge, in this case the chaetetid. Association with algal

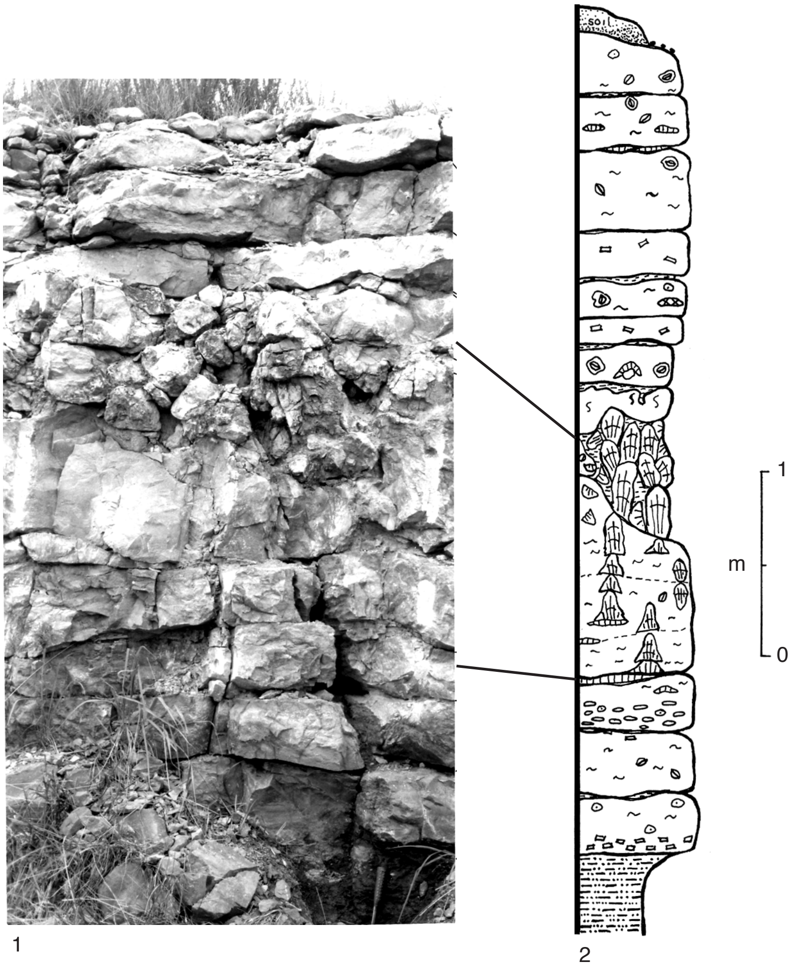


FIG. 76. Further examples of chaetetid reef mounds, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of part of a chaetetid reef mound in a road cut exposure, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.03 (adapted from Voegeli, 1992, p. 65, fig. 19); *2,* graphic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

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

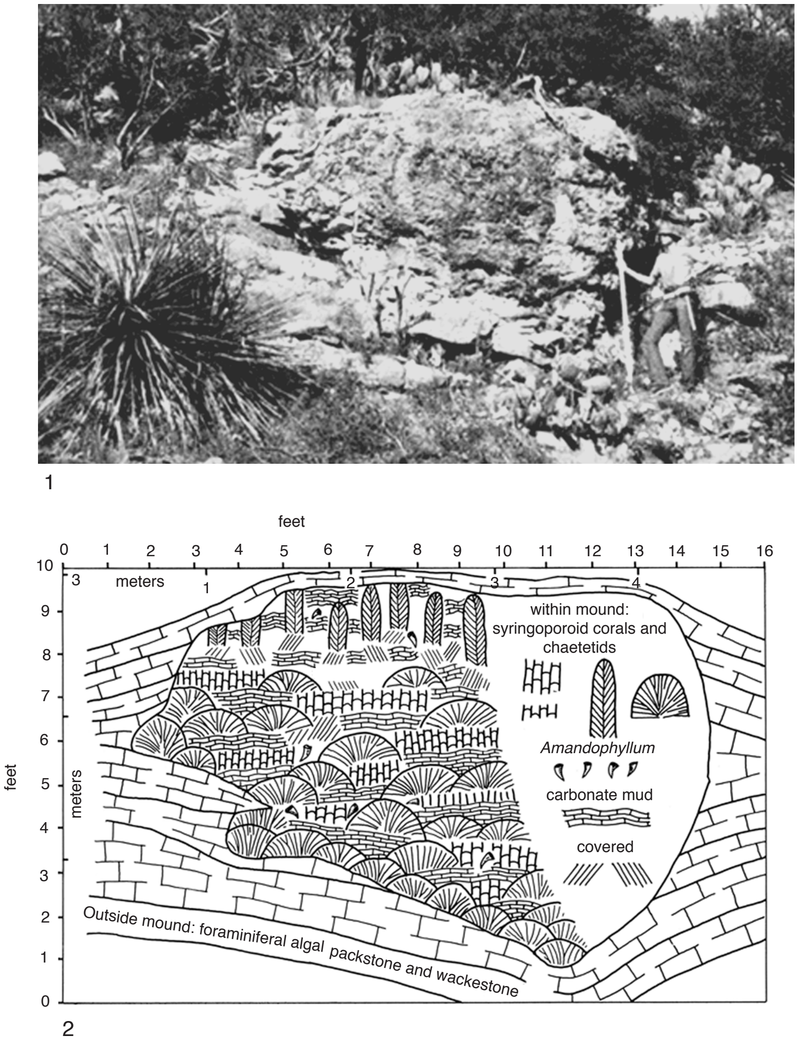


FIG. 77. Chaetetid reef, Carboniferous, Pennsylvanian, Texas; *1,* photograph of an exposure of a chaetetid reef, Marble Falls Limestone, Mason County, Texas, ×0.01 (adapted from Sutherland, 1984, p. 547, pl. 1,*1*); *2,* interpretative sketch of view *1,* showing domical and columnar chaetetids with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

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

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

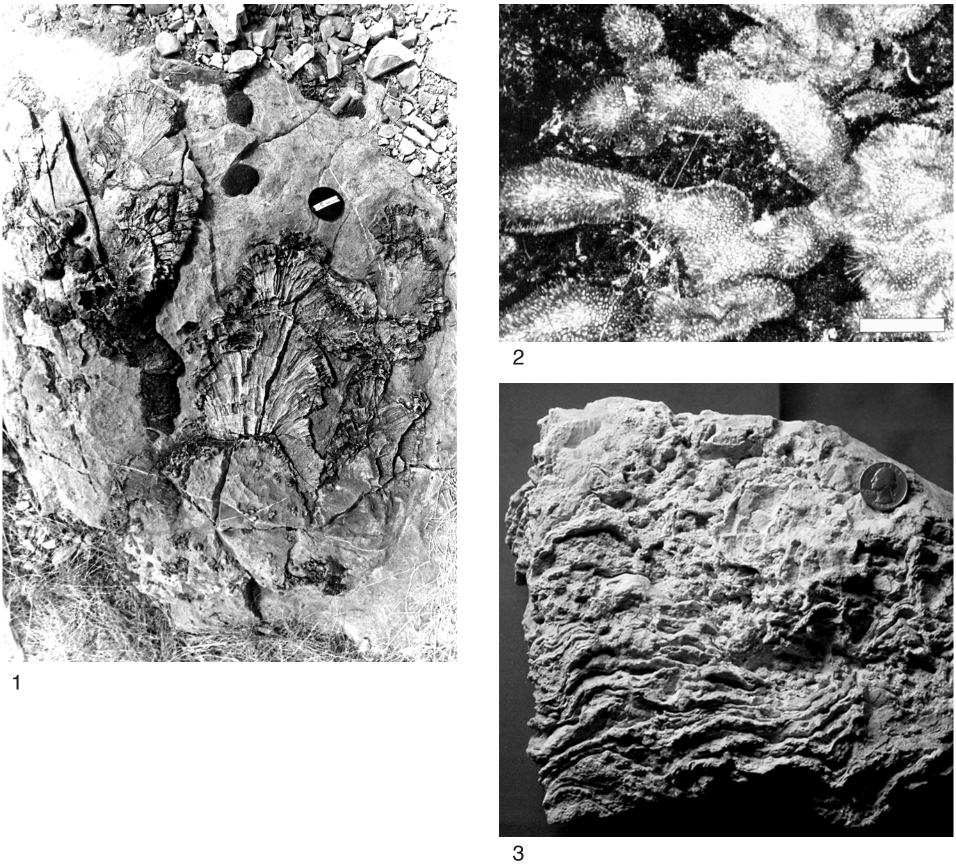


Fig. 78. Chaetetid reefal limestones, Carboniferous, Pennsylvanian; *1,* photograph of an exposure of columnar chaetetids in a reef bank, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona, ×0.07 (West, 2012b); *2,* polished surface of a chaetetid boundstone, Cuera Limestone, Playa de La Huelga,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

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

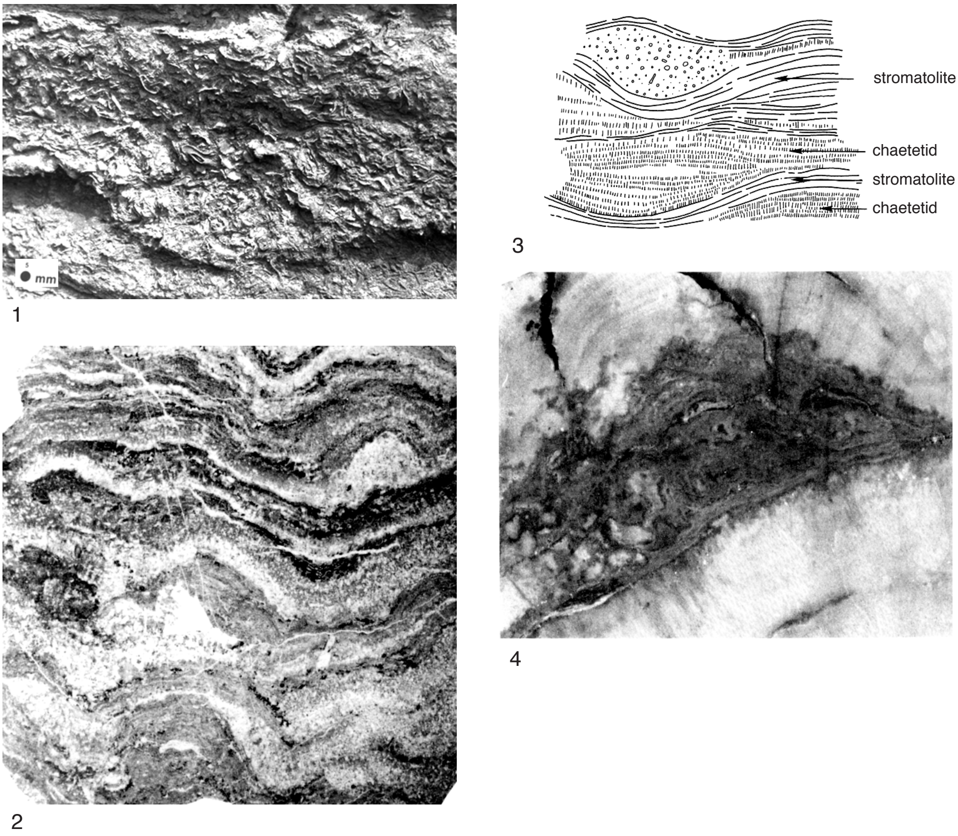


FIG. 79. Details of chaetetids and algal associations, Carboniferous, Pennsylvanian; *1,* outcrop photograph of the weathered surface of a phylloid algae packstone associated with chaetetids in a reef mound, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.2 (adapted from Voegeli,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

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

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

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

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

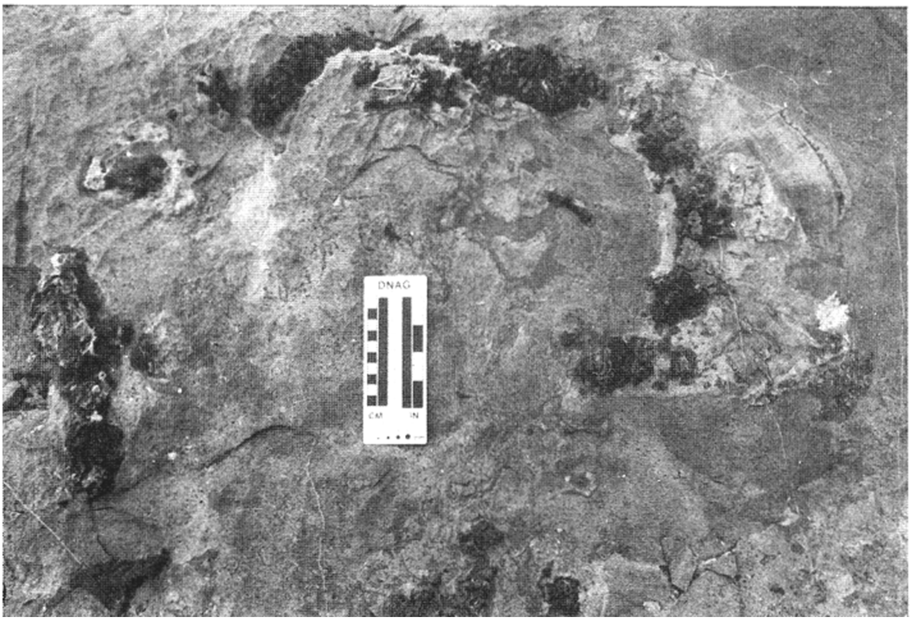


FIG. 80. Upper surface of a chaetetid micro-atoll (scale is in the inferred lagoon, the longest black bar to the left is 10 cm long), Carboniferous, Pennsylvanian, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona; dark areas are the tops of chaetetids, ×0.14 (adapted from Connolly, Lambert,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

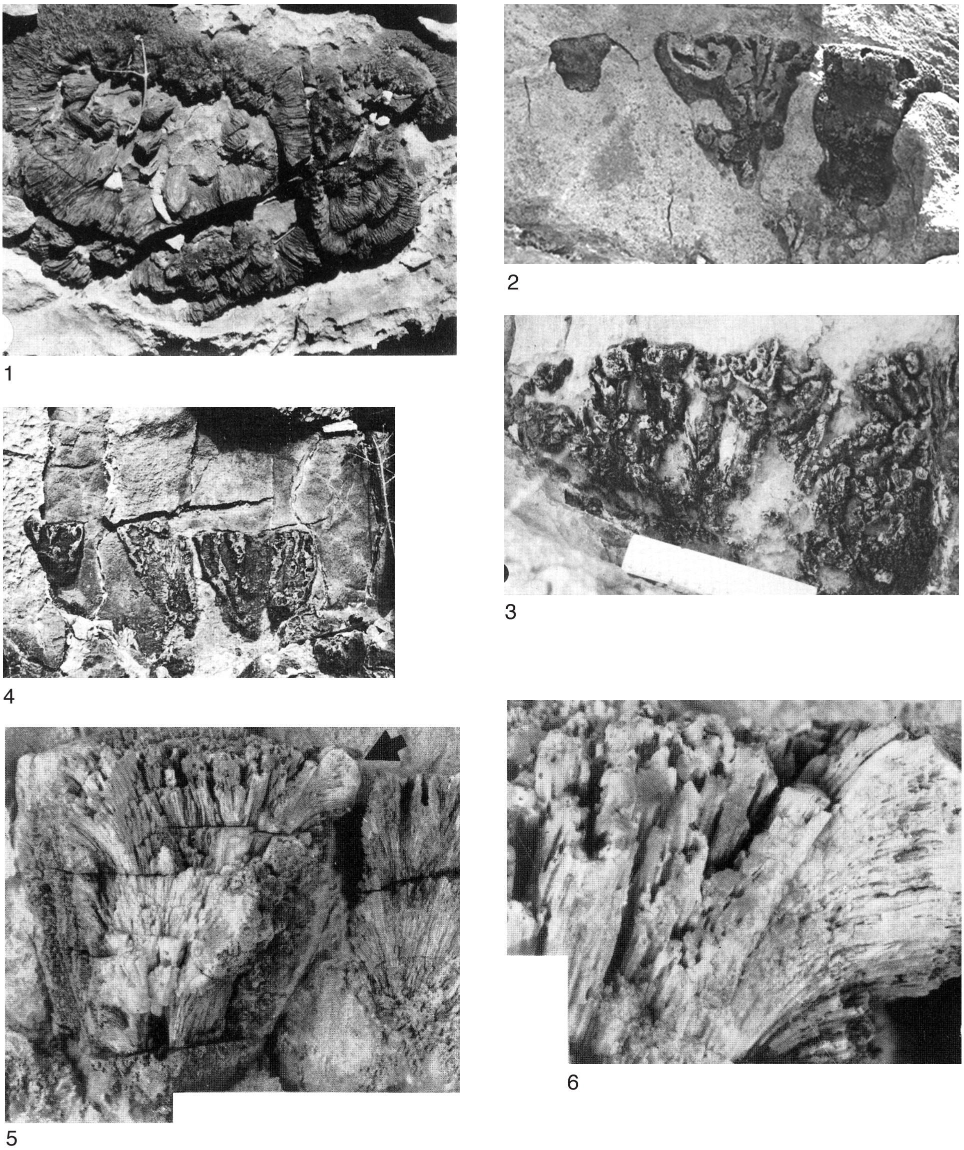


FIG. 81. Flared chaetetids and micro-atolls, Carboniferous, Pennsylvanian; *1,* upper surface of a small chaetetid micro-atoll, limestone of the Middle Magdalena Group, Hueco Mountains, Texas, ×0.3 (adapted from Stanton, Connolly, & Lambert, 1994, p. 367, fig. 2.6; courtesy of the authors and Springer-Verlag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

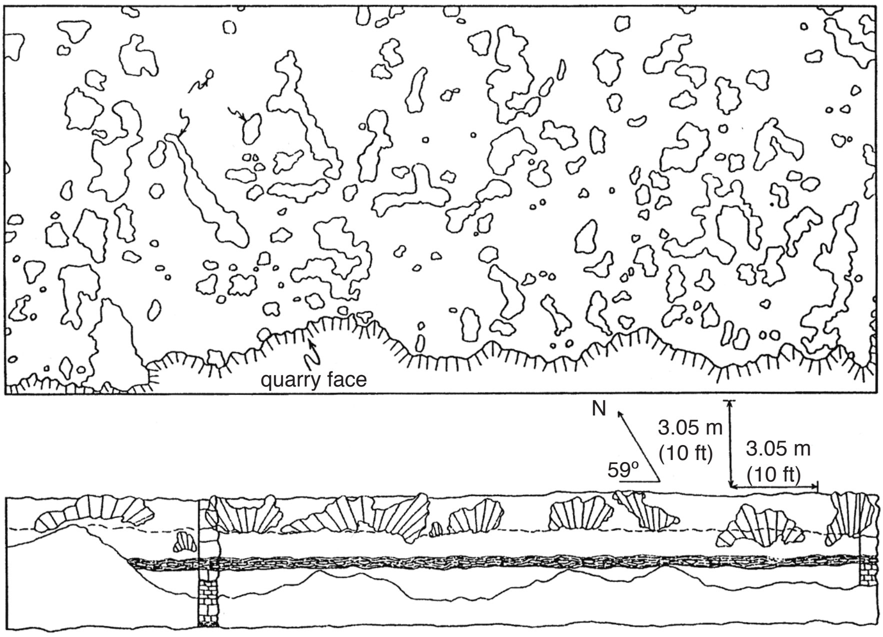


FIG. 82. Inferred current direction from the southwest (lower left), based on the shape and orientation of chaetetids and associated cross-laminated calcarenites. Upper diagram is a map of an exposed bedding plane surface in a quarry, and the lower diagram is the vertical face associated with that quarry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

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

LAMINAR AND LOW DOMICAL FORMS

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

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

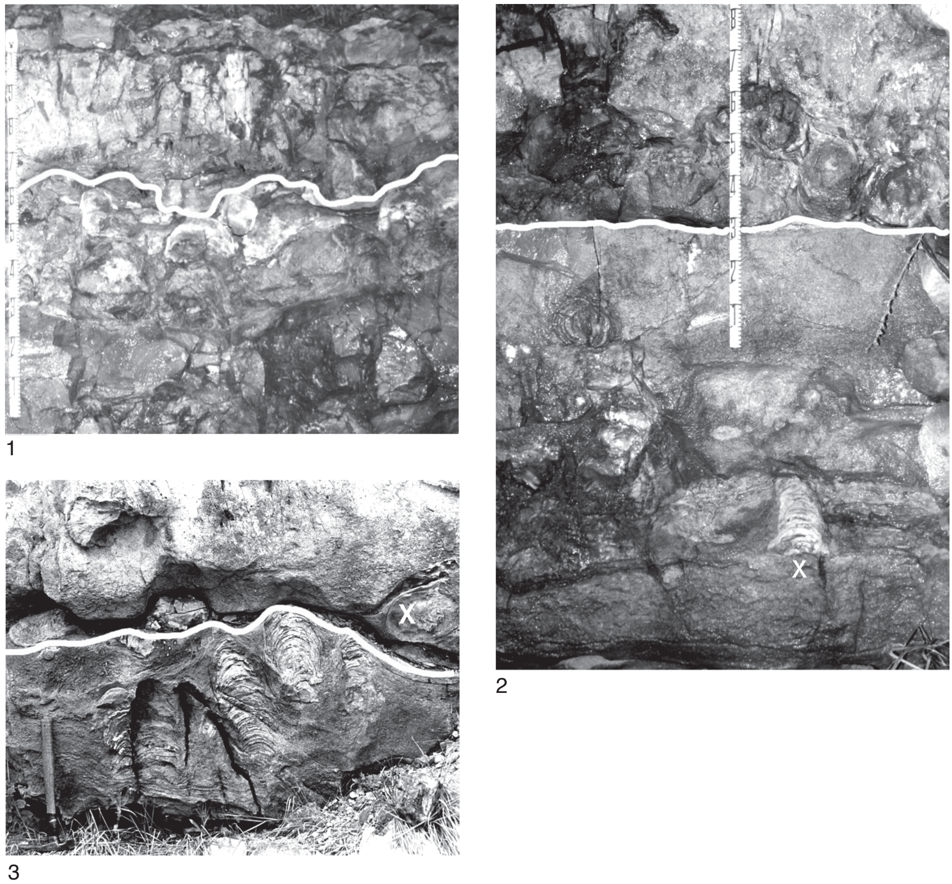

Fig. 83. Chaetetids and associated erosion, Carboniferous, Pennsylvanian; *1,* toppled chaetetids and an erosion surface at the white line, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.05 (West, 2012b); *2,* close view of toppled chaetetid interval above the white line in Amoret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

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

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

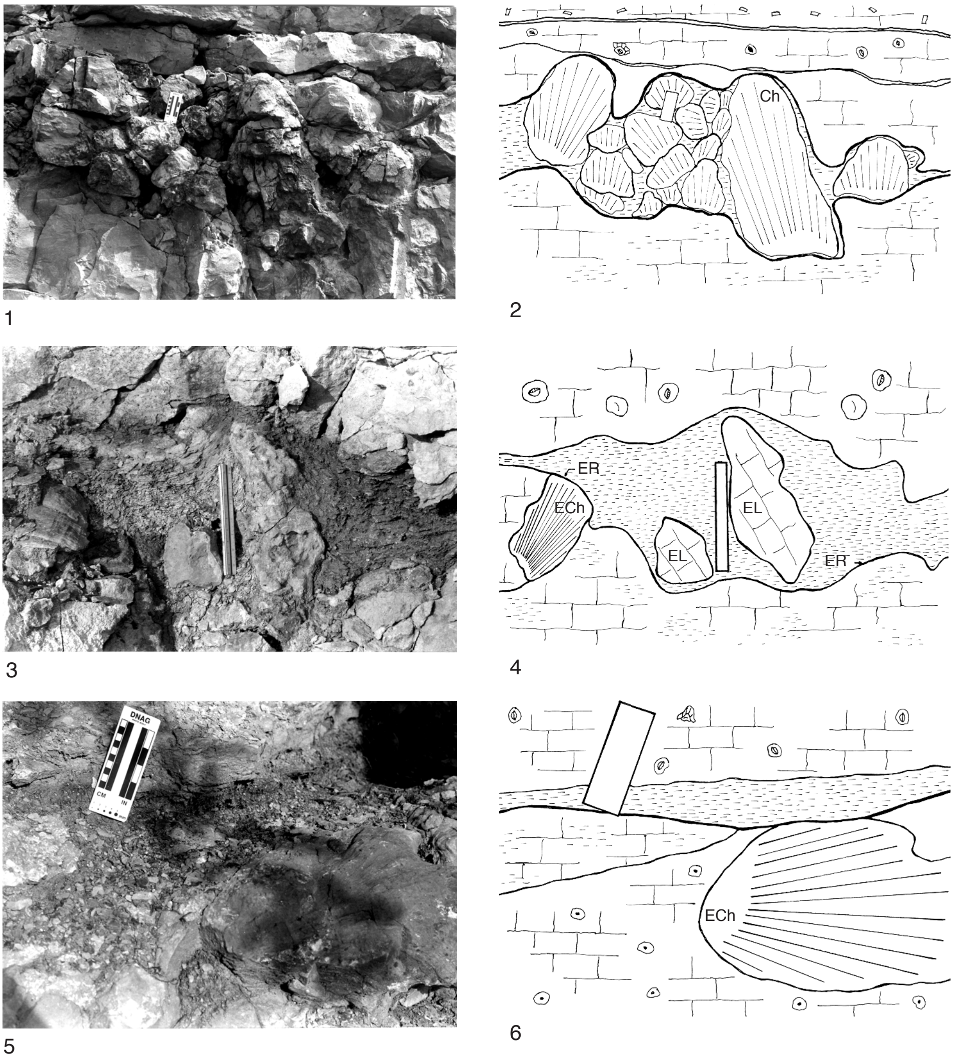

FIG. 84. Further examples of chaetetids and associated erosion, Carboniferous, Pennsylvanian; *1,* disturbed and toppled domical and columnar chaetetids, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.25 (adapted from Voegeli, 1992, p. 139, fig. 31); *2,* interpretative sketch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

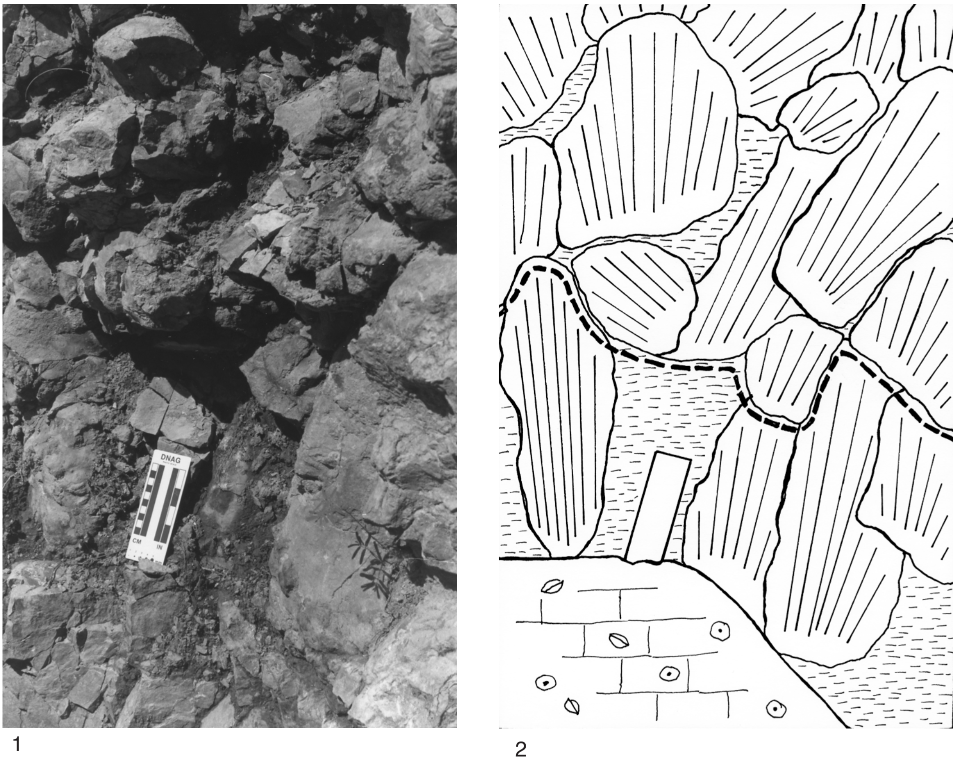

Fig. 85. Erosion, sediment draping, and rejuvenation; *1,* evidence of two episodes of erosion in the disturbed chaetetid interval, Carboniferous, Pennsylvanian, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, ×0.1 (adapted from Voegeli, 1992, p. 134, fig. 29); *2,* interpretative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

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

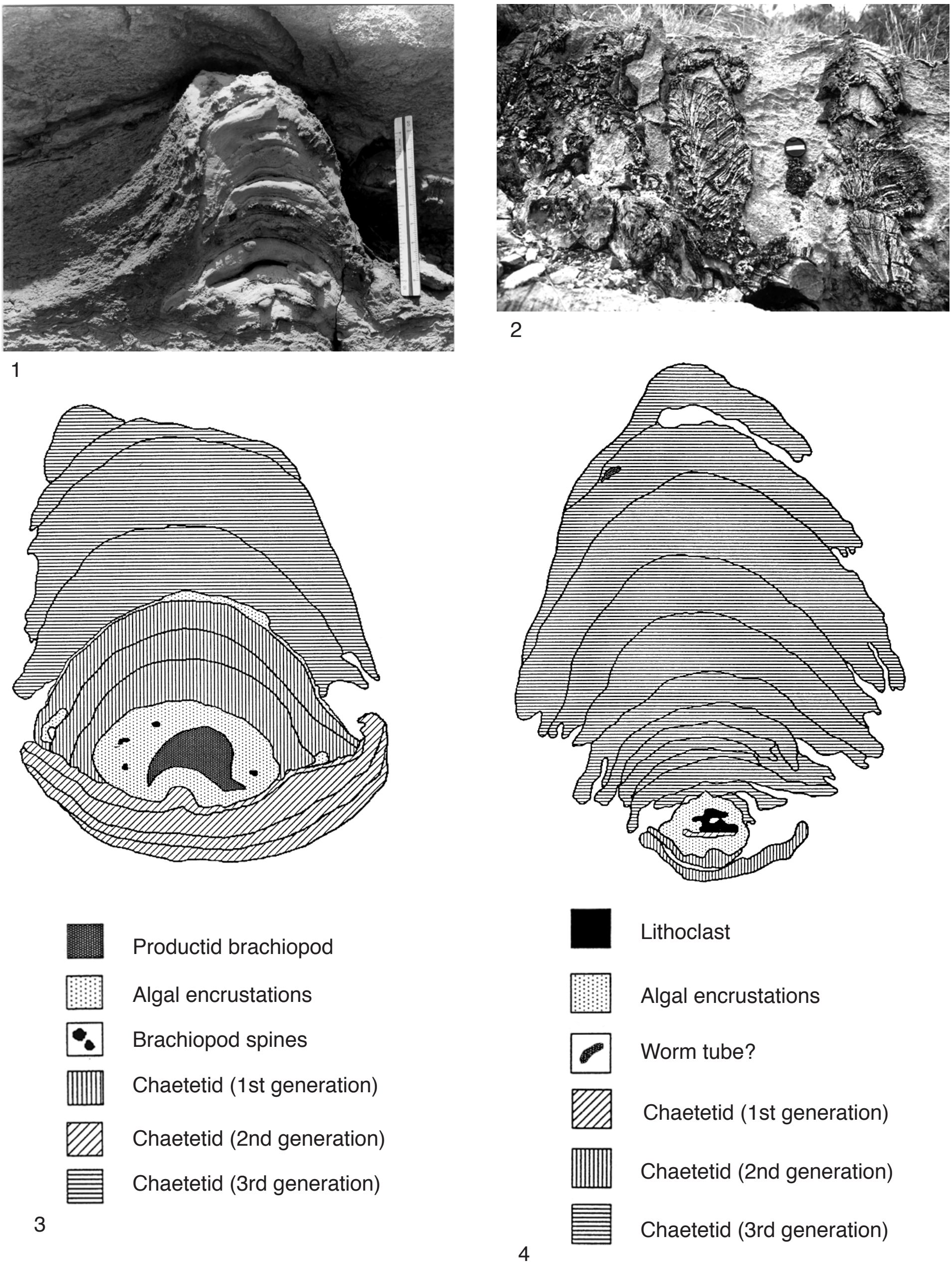

FIG. 86. *(For explanation, see facing page).*

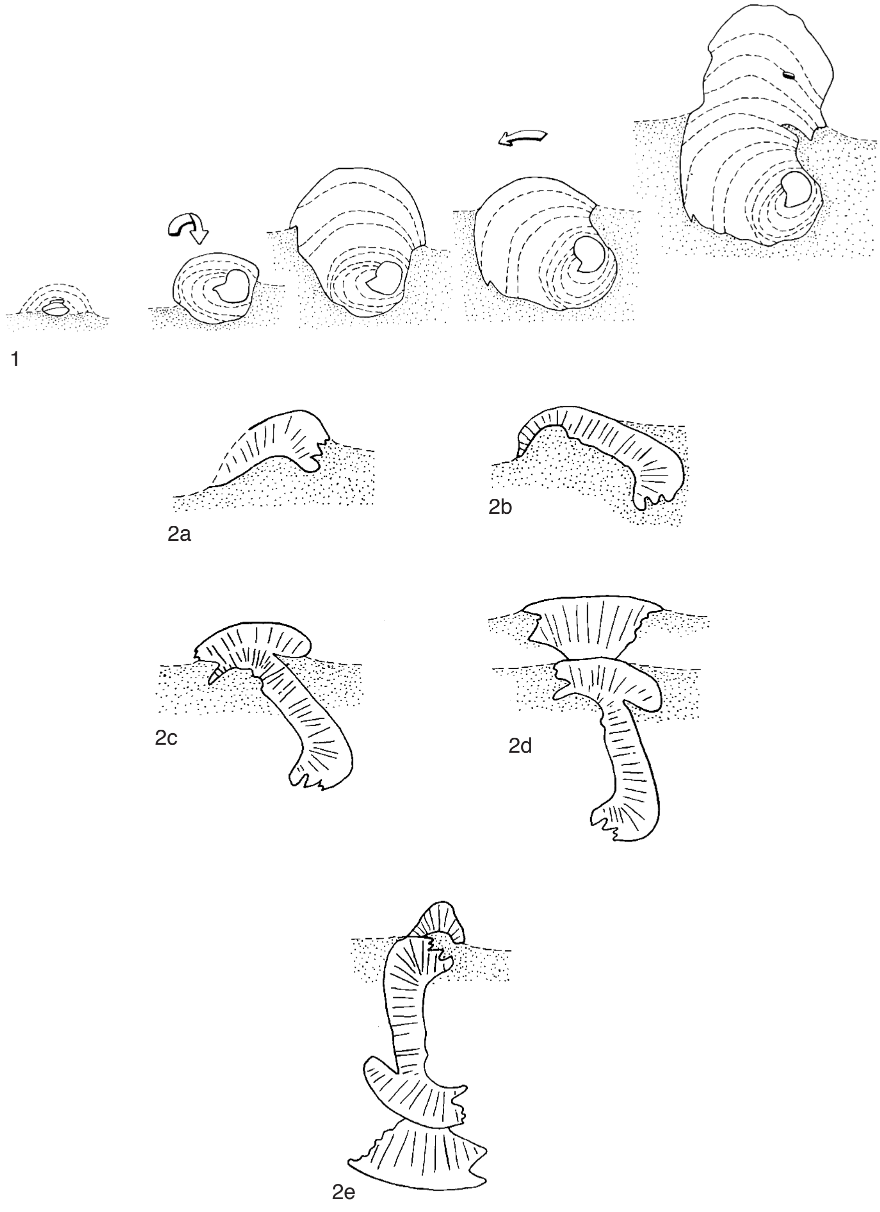

FIG. 87. Inferred growth stages of chaetetids based on interruption partings, Carboniferous, Pennsylvanian; *1,* interpretative sketches based on a vertical section of a high domical chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas showing changes in shape as a result of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

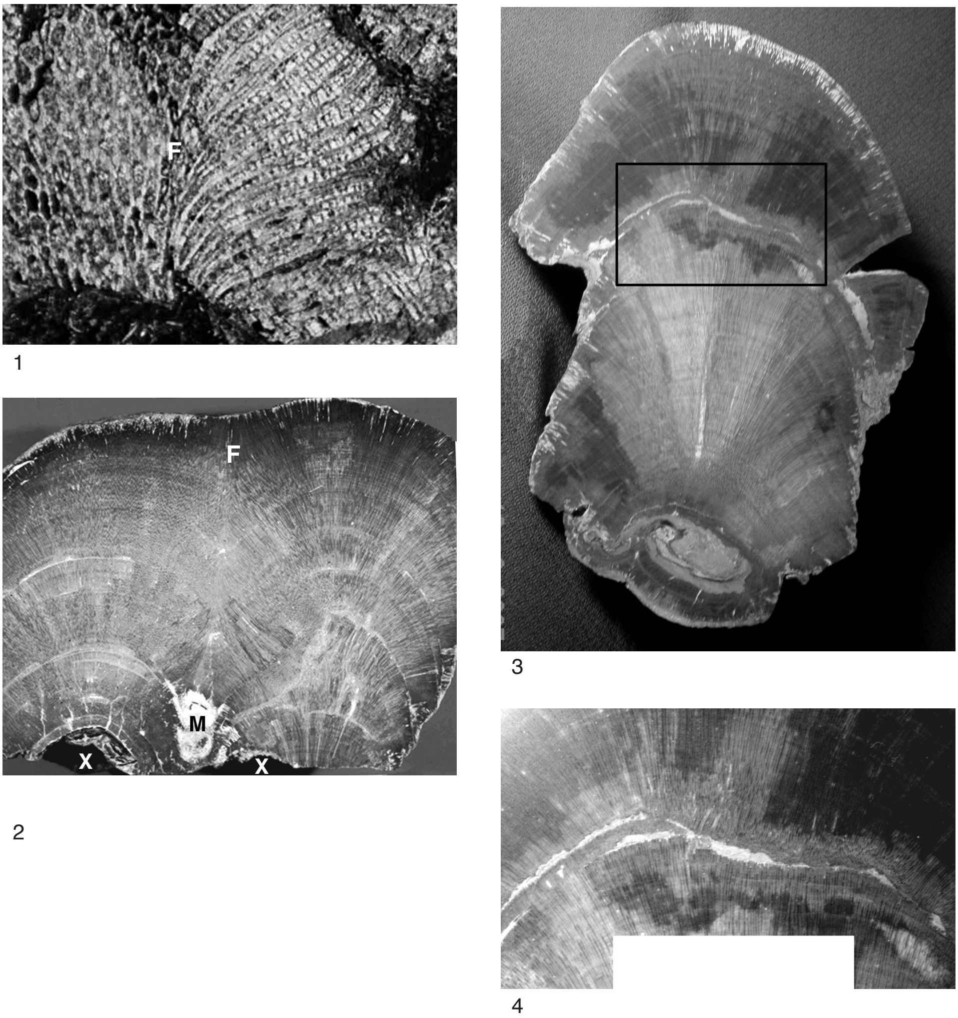

FIG. 88. Fusion and rejuvenation in chaetetids, Carboniferous, Pennsylvanian; *1,* fusion in domical chaetetids, Akiyoshi Limestone, Akiyoshi-dai, Japan; *F,* plane of fusion (just above and left of center), ×14.5 (West, 2012b); *2,* fusion of two high domical chaetetids each began on an algal-microbially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

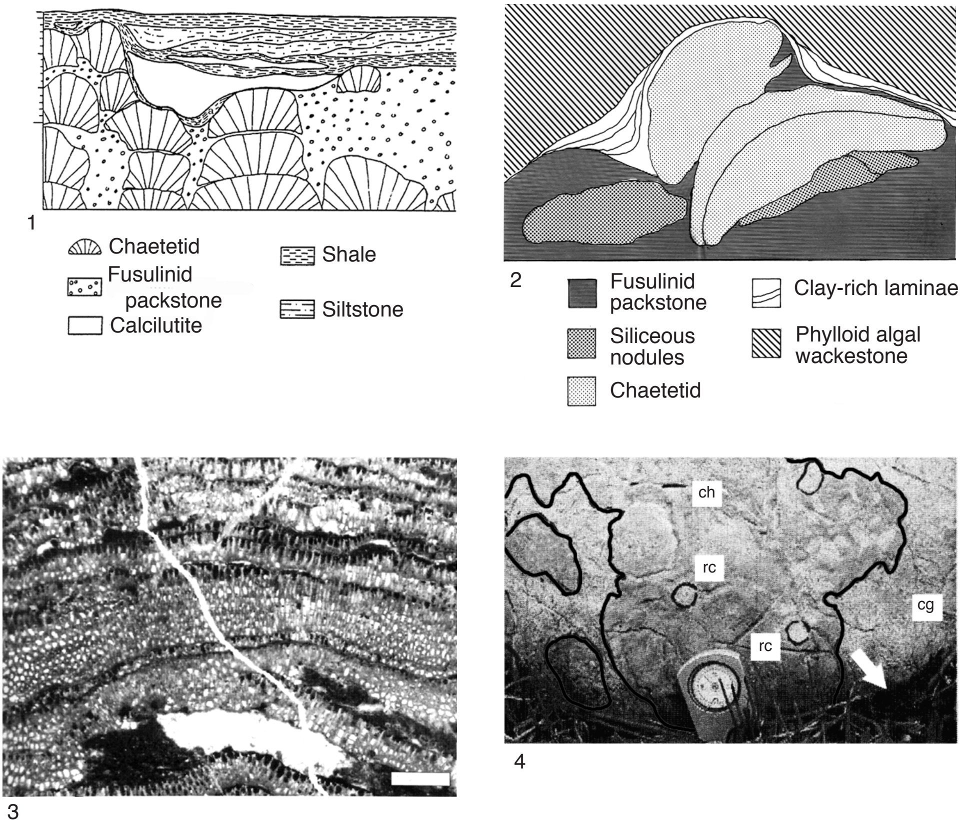

FIG. 89. Chaetetid substrates and associated lithologies, Carboniferous, Pennsylvanian; *1,* interpretative sketch of an exposure of columnar chaetetids in a fusulinid packstone, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas smothered by calcilutite (carbonate mudstone),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

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

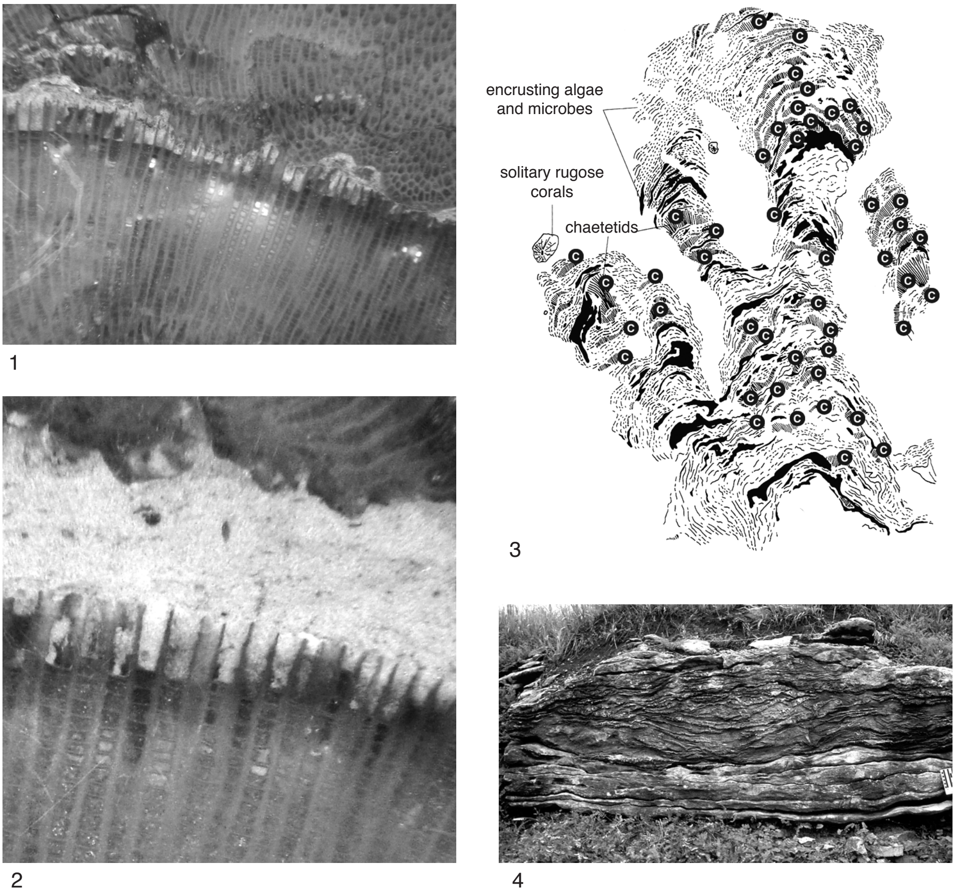

FIG. 90. Further examples of chaetetid substrates and associated lithologies, Carboniferous, Pennsylvanian; *1,* micrite-filled chaetetid tubules, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, ×10 (West, 2012b); *2,* detail view of part of the area in view *1,* of the micrite-filled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

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

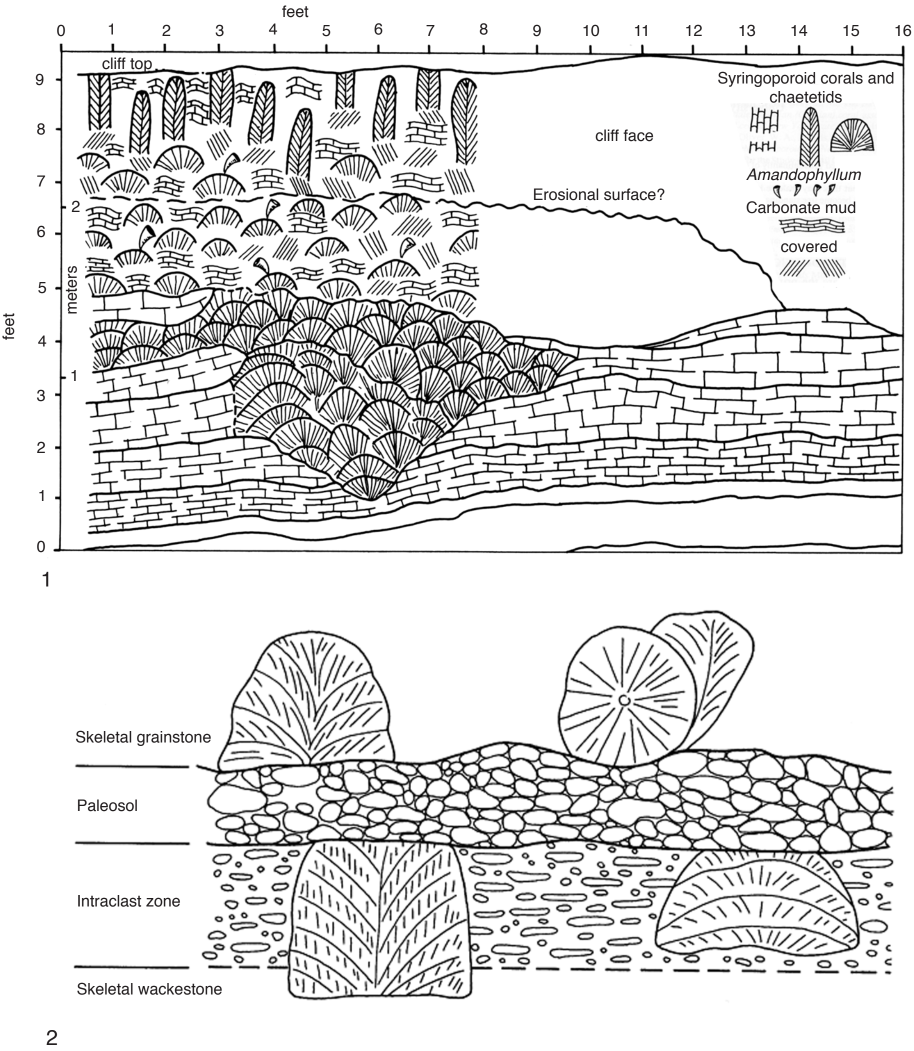

FIG. 91. Erosional surfaces and mobile sediment as chaetetid substrates; *1,* interpretative sketch of the vertical exposure of a chaetetid bank, where chaetetids colonized an inferred erosional surface, Carboniferous, Pennsylvanian, Marble Falls Limestone, Mason County, Texas, ×0.02 (adapted from Sutherland,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

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

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

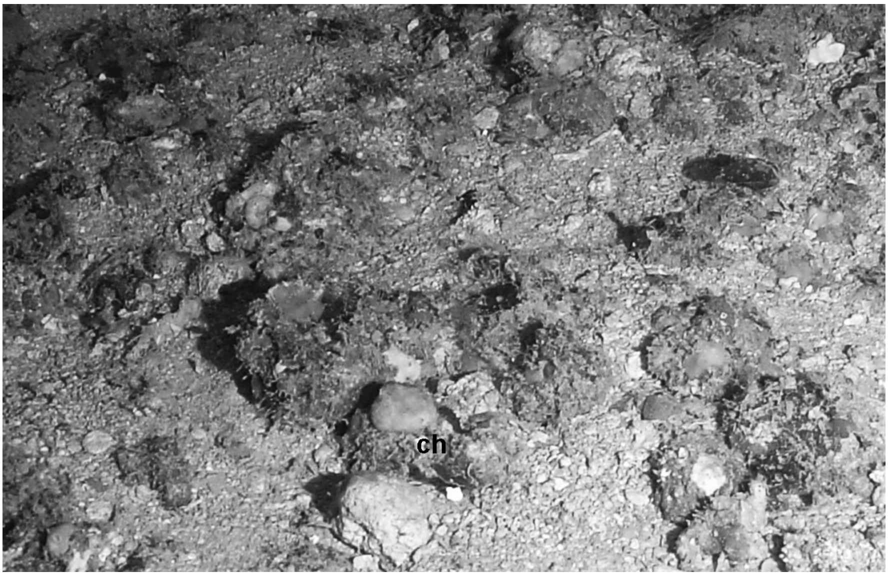

FIG. 92. Extant specimen of *Acanthochaetetes* sp. attached to a small mound of coralline algae (*ch* in lower left center of photo) at a depth of 85 m off the Komesu coast, southern Okinawa, ×0.4 (adapted from Nagai & others, 2007, fig. 4f; courtesy of the authors and the editor of the Abstracts volume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

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

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

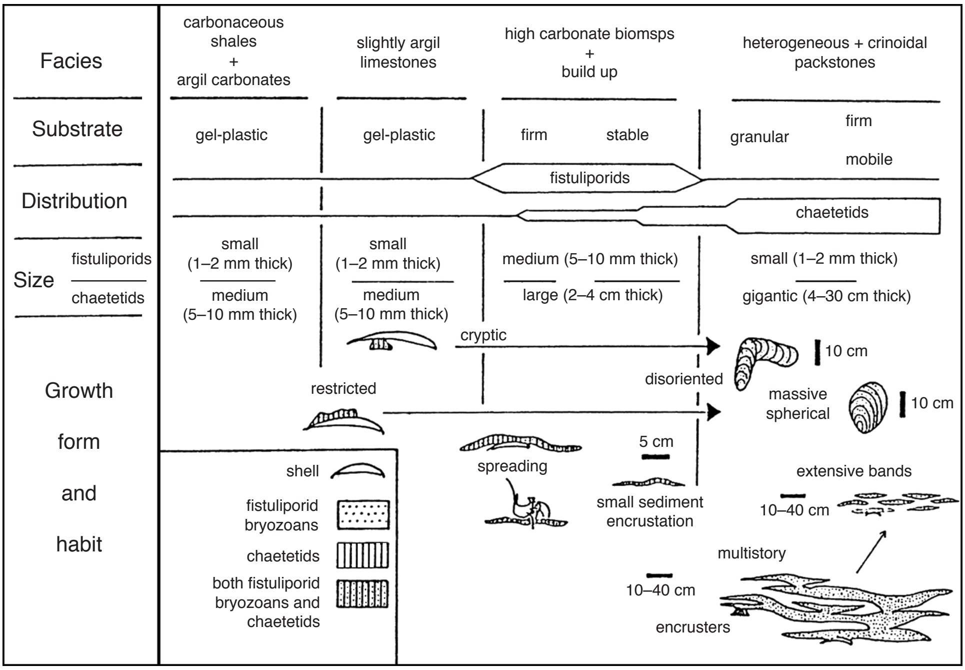

Fig. 93. Relationships between four types of substrates (gel, plastic, firm, and granular) and growth form or habit, size, distribution, and lithofacies, for chaetetids and fistuliporid bryozoans; note that both bryozoans and chaetetids occur as spreading forms in plastic to firm substrates, where competition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

the chaetetids (Fig. 95–96; Jameson, 1980; Suchy & West, 1988). The paleoecology of such marine hard substrate associations has been reviewed by Taylor and Wilson (2003).

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

BIOLOGICAL FACTORS

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

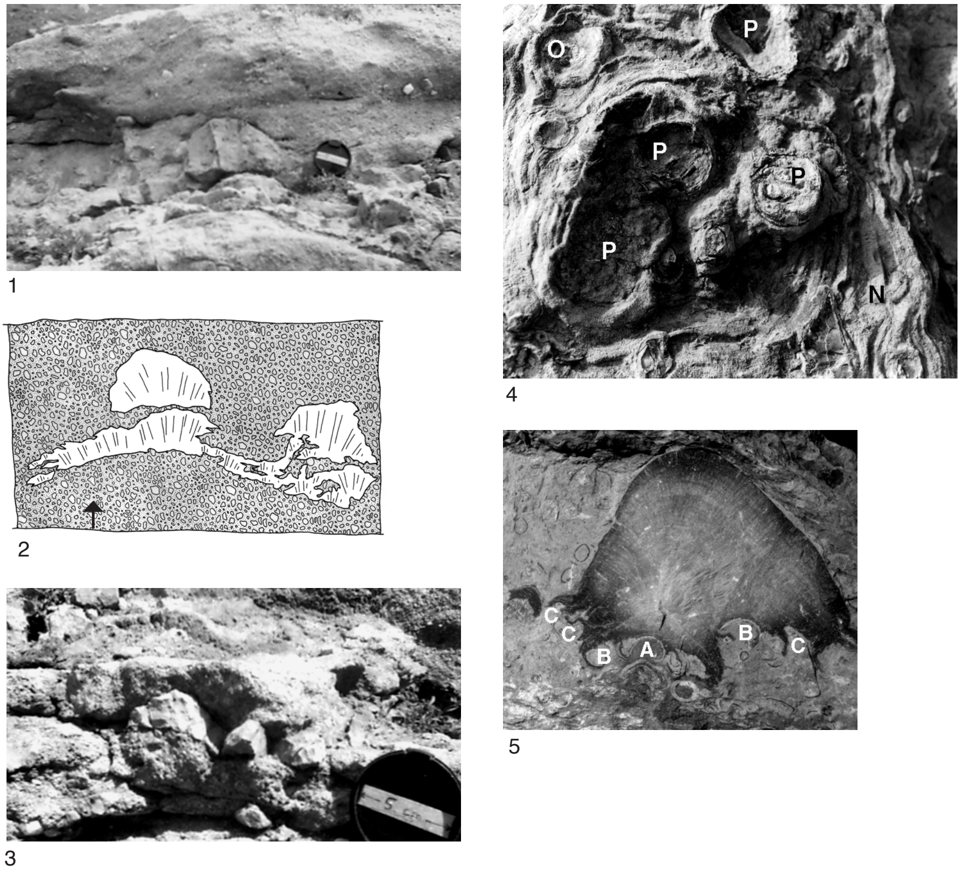

Fig. 94. Substrates and relationships, Carboniferous, Pennsylvanian; *1,* laminar to low domical chaetetids on an arkose substrate, Resolution Member, Minturn Formation, Resolution Mountain near Camp Hale, Eagle County, Colorado, ×0.09 (West, 2012b); *2,* interpretative sketch of view *1;* note the separation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

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

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

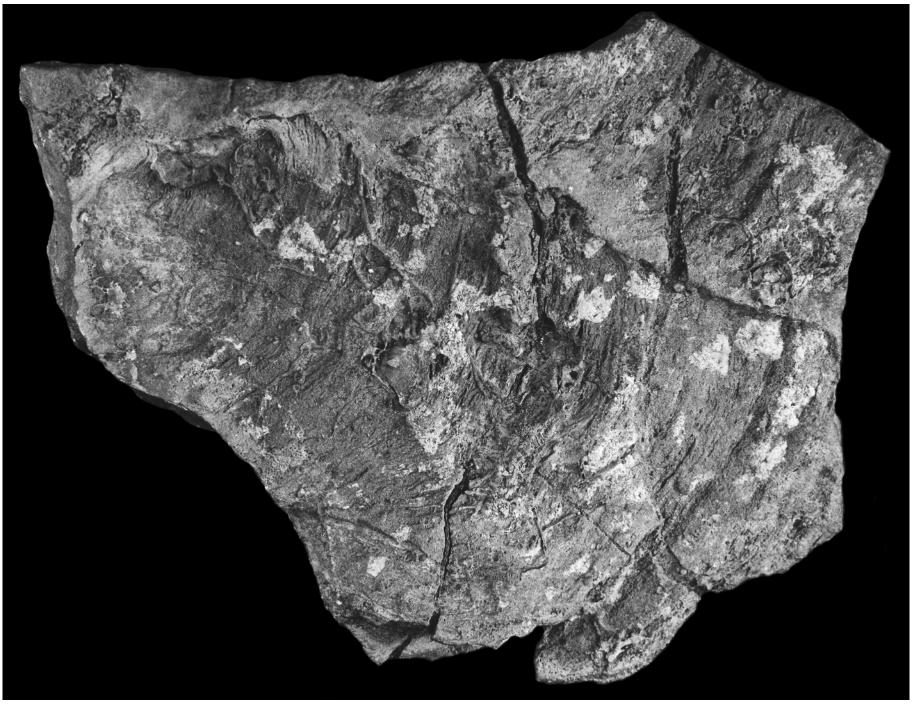

FIG. 95. Cryptic biota on part of the lower surface, the underside, of a laminar chaetetid, Carboniferous, Pennsylvanian, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa, ×0.7 (adapted from Suchy & West, 1988, p. 407, fig.2A; courtesy of the authors and the Society for Sedimentary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

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

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

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

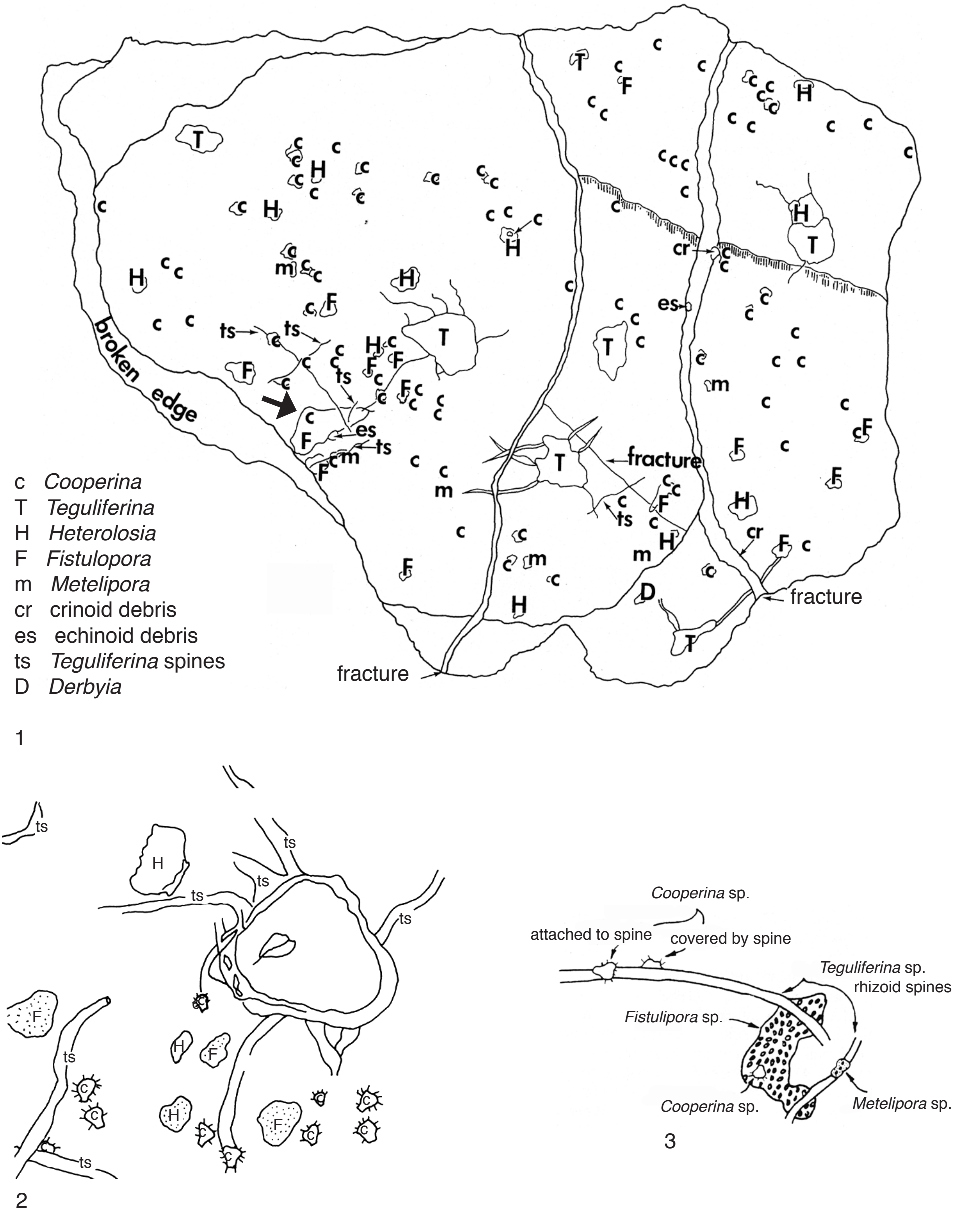

FIG. 96. Laminar chaetetid and cryptic biota; *1,* map of Figure 95 showing the location and identity of the cryptic biota. Because of their small size, the location of worm tubes, *Spirorbis,* and foraminiferid *Tetrataxis* are omitted, ×0.8 (adapted from Suchy & West, 1988, p. 407, fig. 2B; for a color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

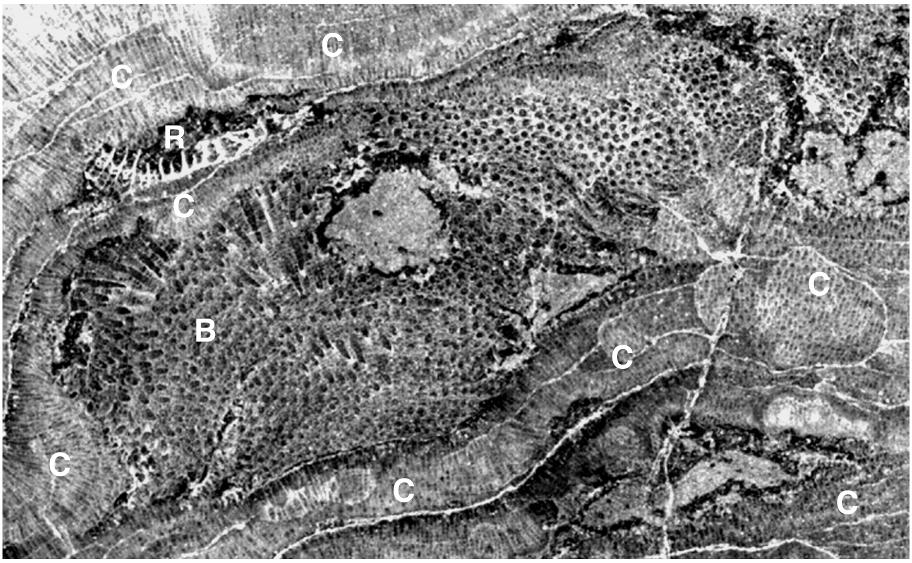

FIG. 97. Inferred live-live spatial competition between chaetetids (*C*), fistuliporid bryozoans (*B*), and a solitary rugose coral (*R*), Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×3 (West, 2012b).

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

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

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

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

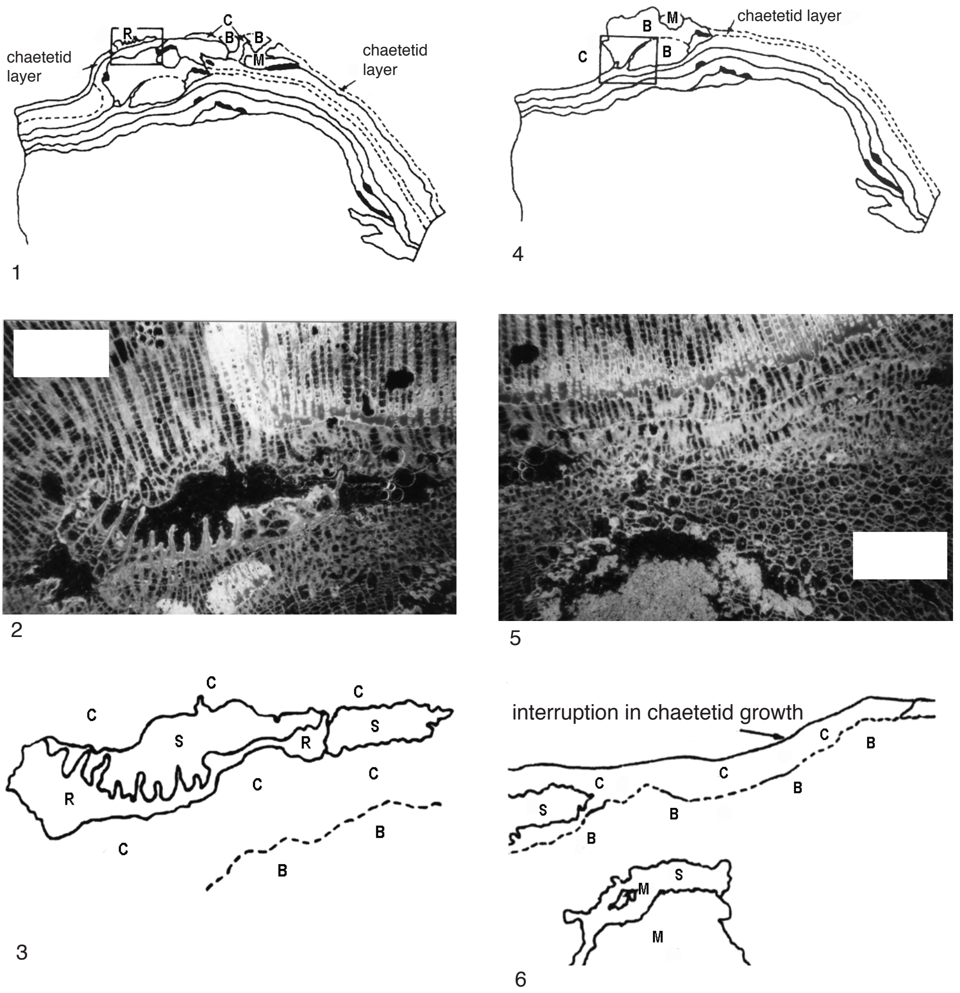

FIG. 98. Chaetetids and inferred live-live spatial competition, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; *1,* interpretative sketch of the upper part of the area in Figure 97 (*R* denotes the position of solitary rugose coral) showing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

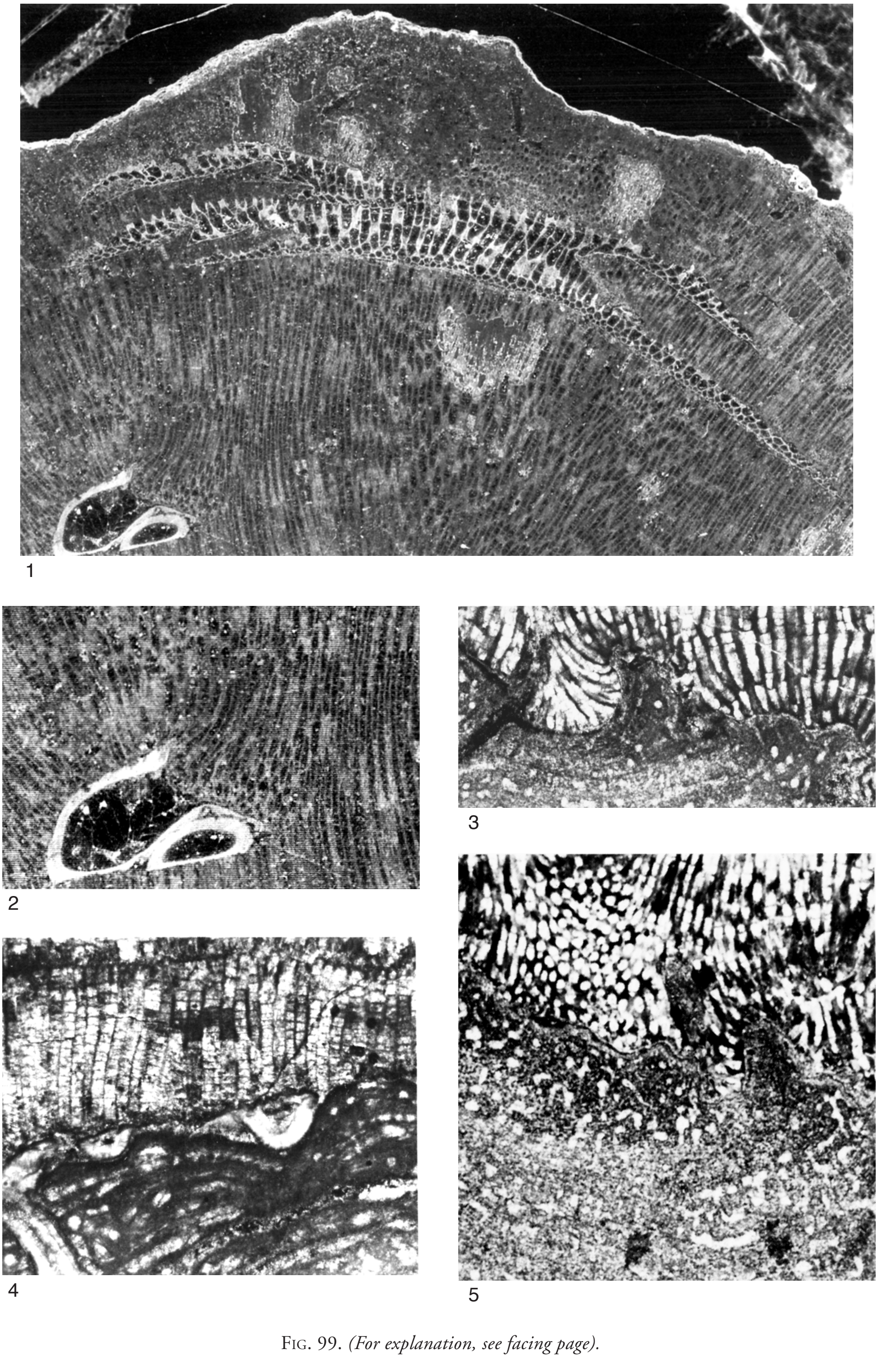

FIG. 99. *(For explanation, see facing page).*

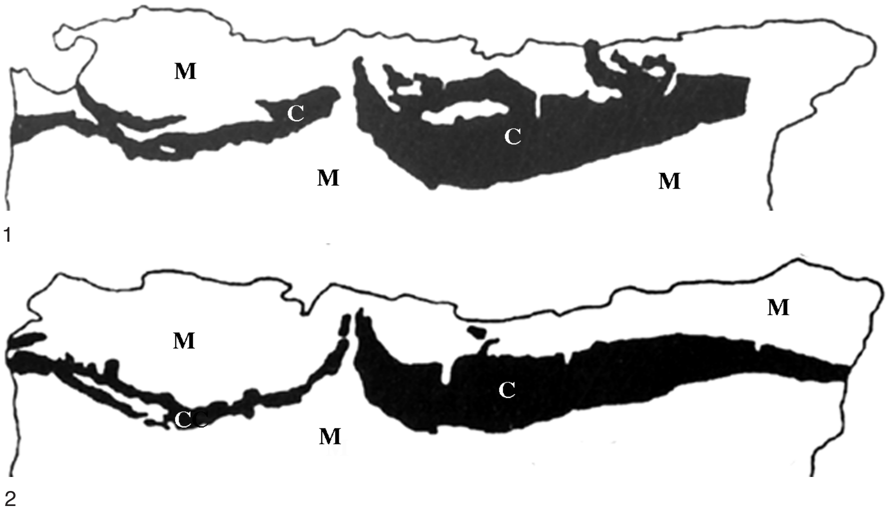

Fig. 100. Inferred live-live stand-off interaction between chaetetids; *1,* stand-off interaction between chaetetid clones (*C,* black areas), Carboniferous, Pennsylvanian, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas; *M,* matrix, ×0.5 (adapted from Fagerstrom & others,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

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

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

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

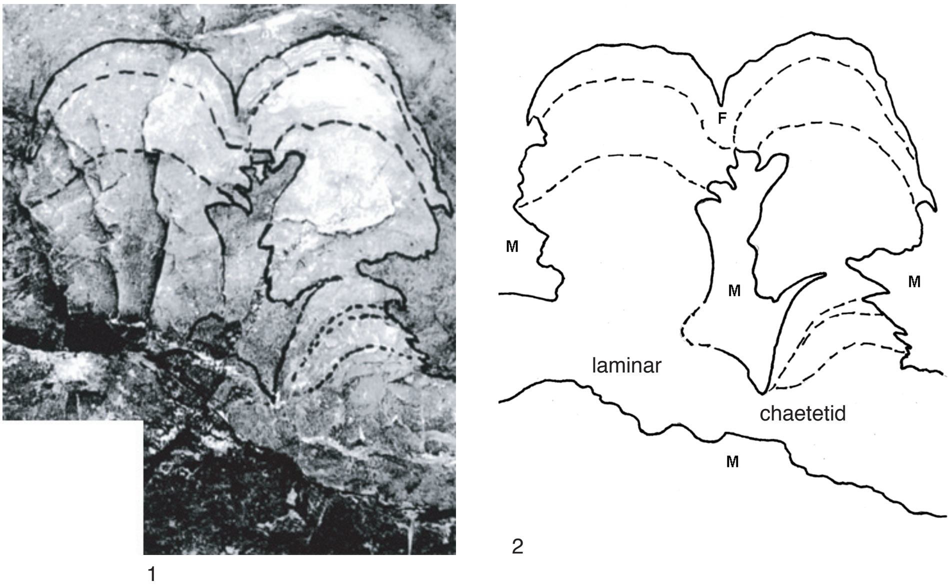

FIG. 101. Fusion and rejuvenation in chaetetids; *1,* fission and fusion in a chaetetid that began as a laminar form, followed by fission and growth into two columnar chaetetids with ragged margins (*dashed lines* are interruption partings) that fused, Carboniferous, Pennsylvanian, Amoret Limestone Member,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

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

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

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

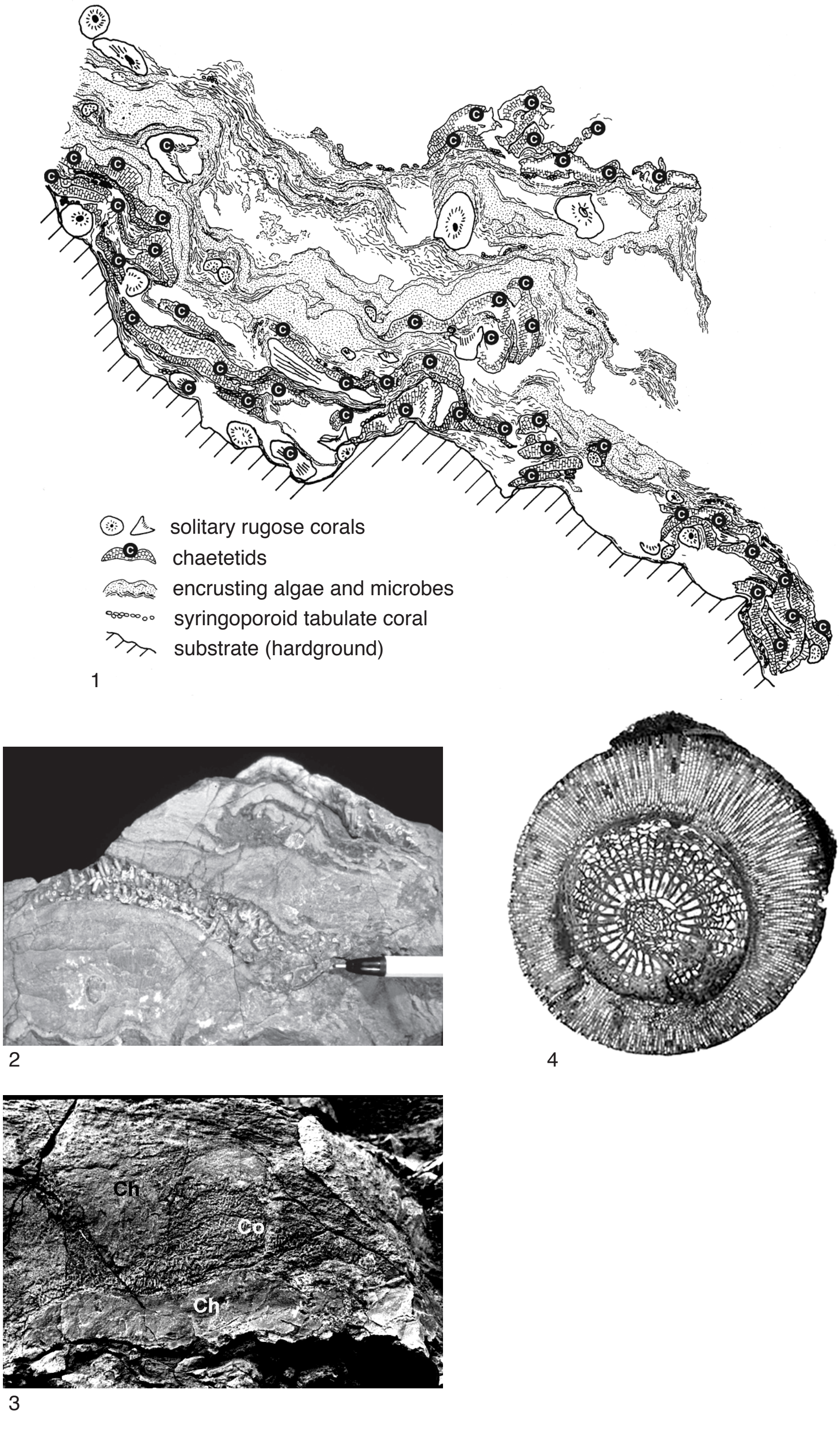

FIG. 102. *(For explanation, see facing page).*

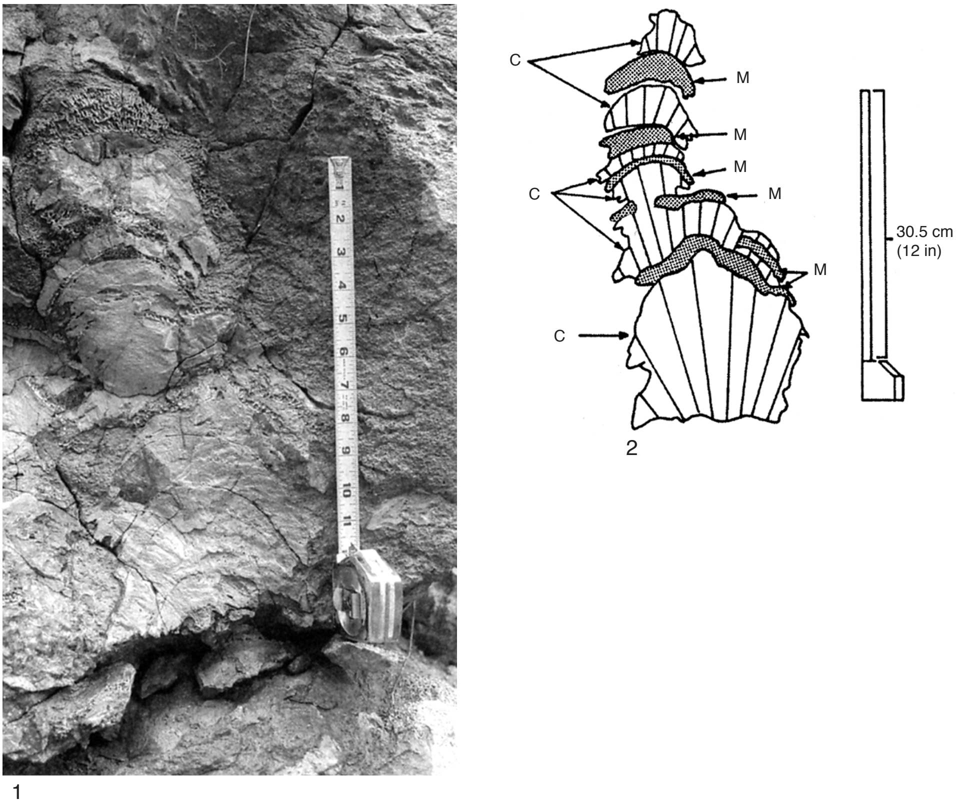

FIG. 103. Further examples of associated encrusters and successive overgrowths; *1,* weathered vertical surface of a succession of chaetetid and *Multithecopora* overgrowths in a fusulinid packstone, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,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

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

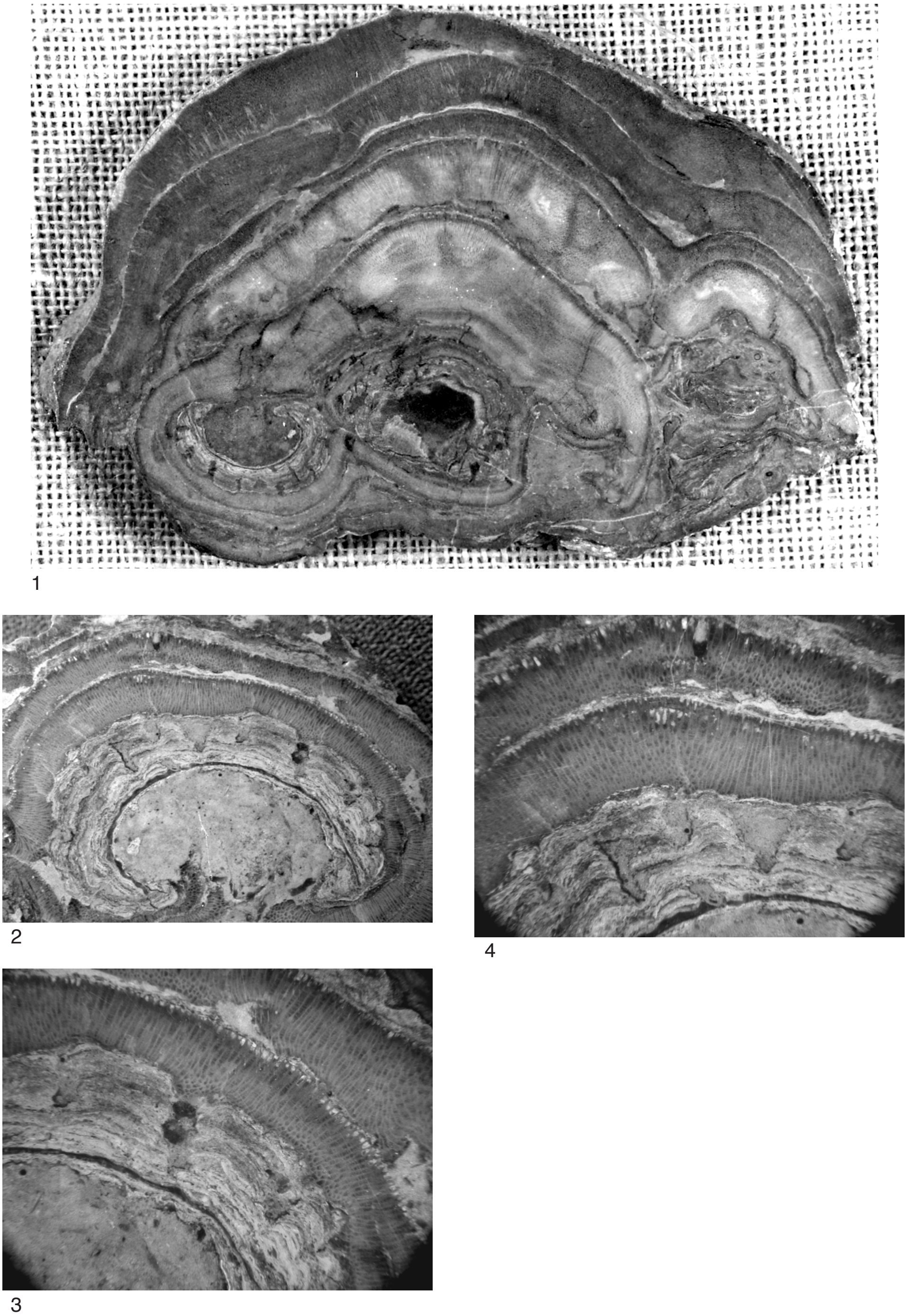

FIG. 104. *(For explanation, see facing page).*

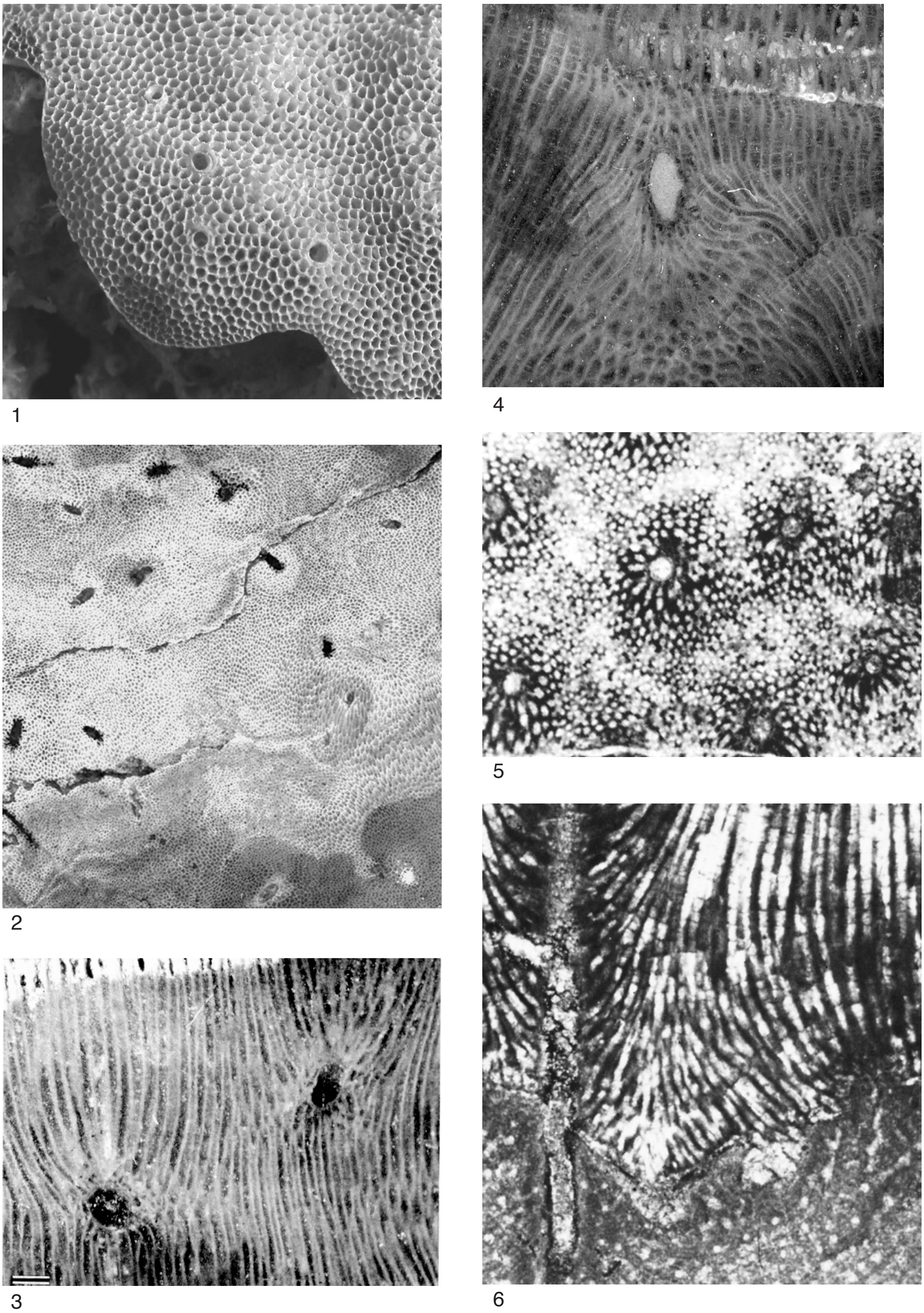

Fig. 105. *(For explanation, see facing page).*

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

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

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

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

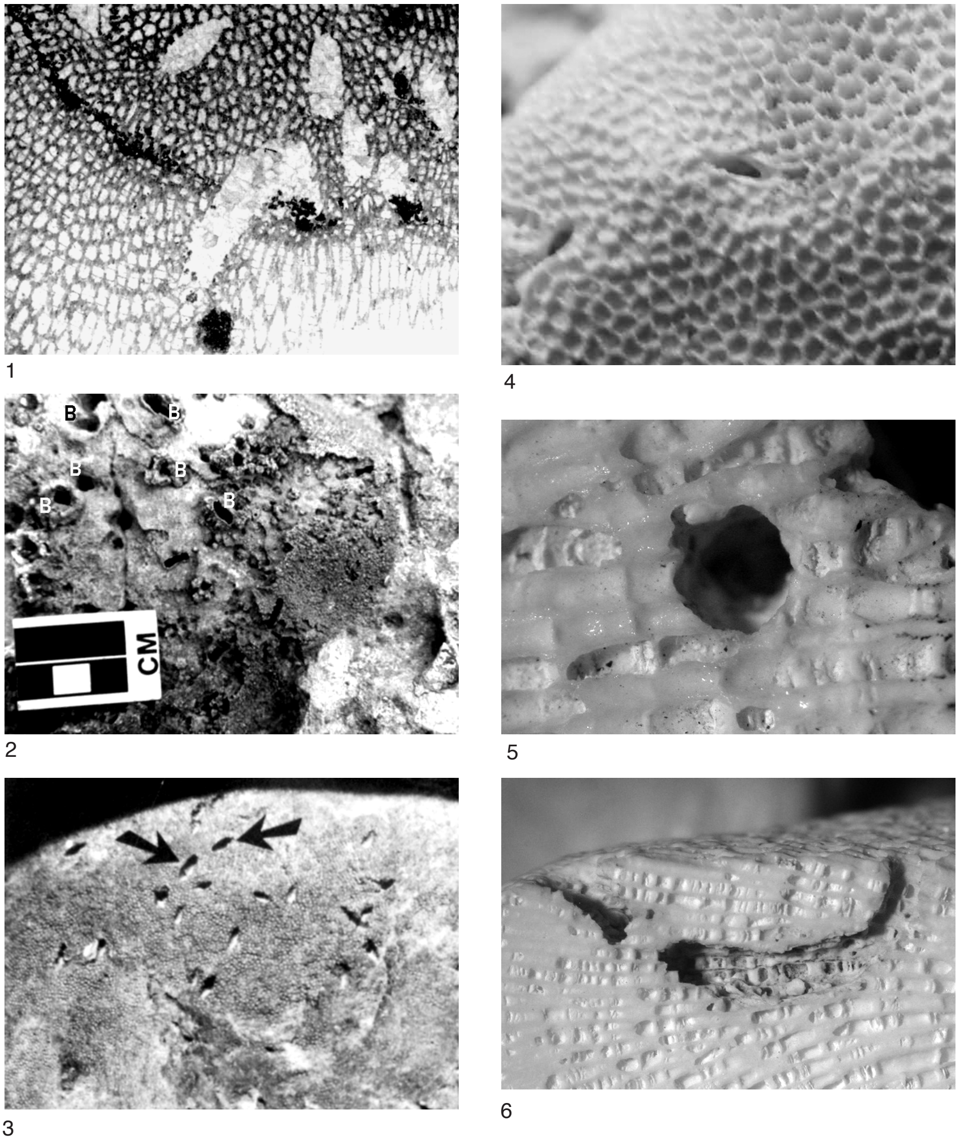

FIG. 106. Inferred borings in chaetetid skeletons; *1,* Transverse to oblique thin section of chaetetid from the Carboniferous, Pennsylvanian, Piedraslungas Limestone, Piedraslungas, Cantabrian Mountains, Spain; note the lack of tubule distortion adjacent to the spar-filled holes, ×6 (adapted from Minwegen,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

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

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

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

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

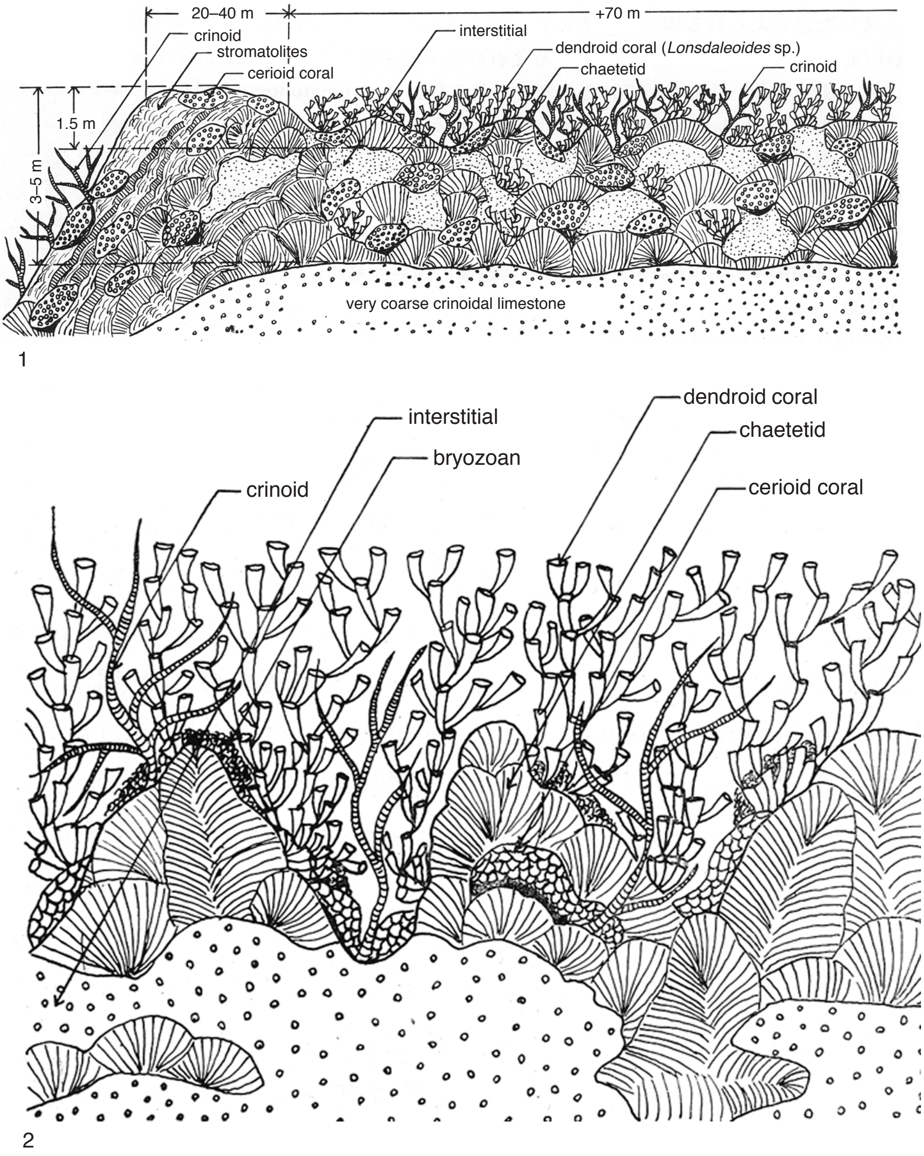

FIG. 107. Schematic diagrams of the reef mound at the Sumitomo quarry, Akiyoshi Limestone, Akiyoshi-dai, Japan; *1,* relationship between chaetetids, associated sessile suspension feeders, and interstitial sediment on a very coarse clastic crinoidal substrate, ×0.005 (adapted from Ota, 1968, p. 31, fig.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

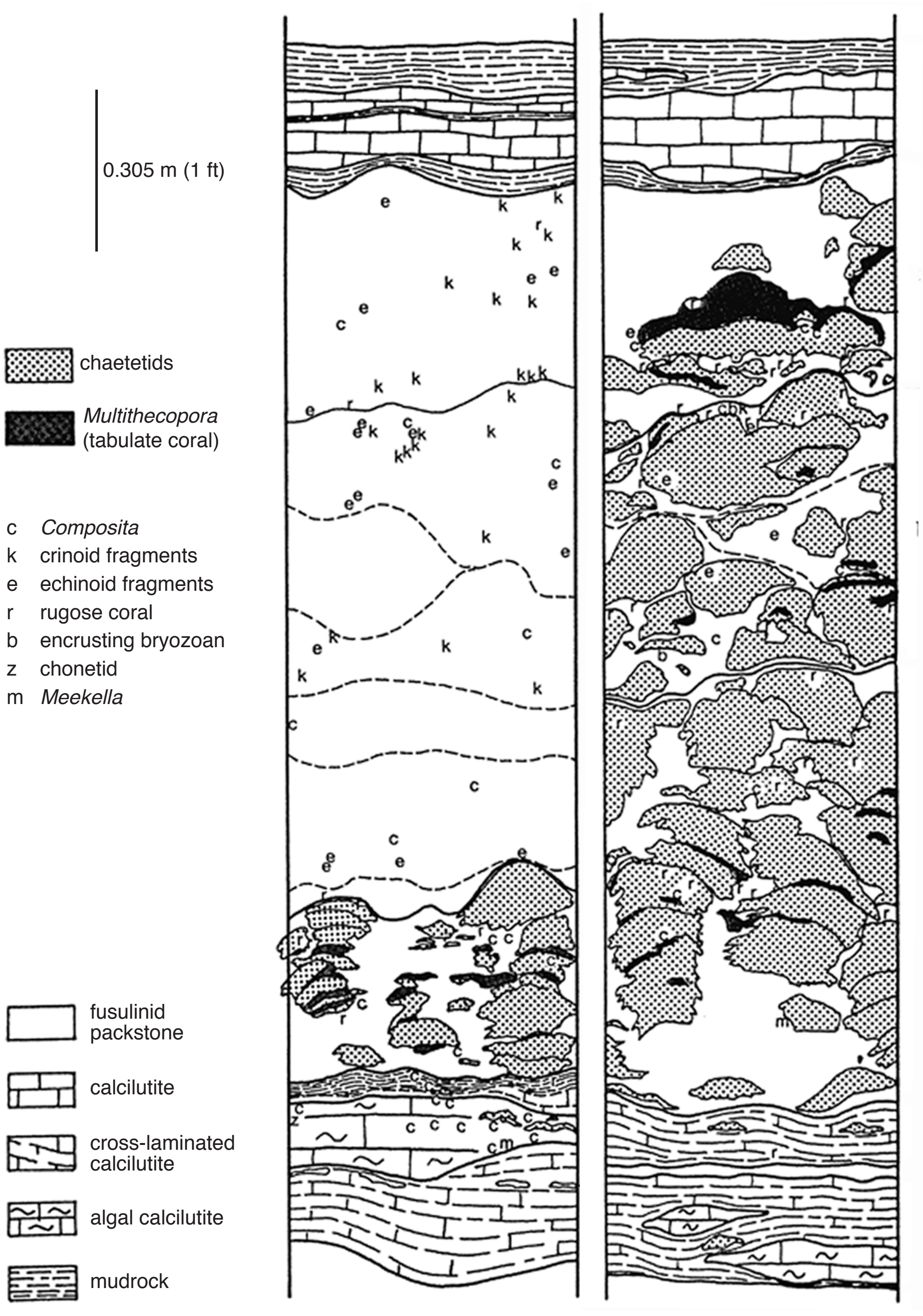

FIG. 108. Interpretative diagram of chaetetids, associated organisms, and lithologies at two different vertical sequences in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas (adapted from Suchy & West,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

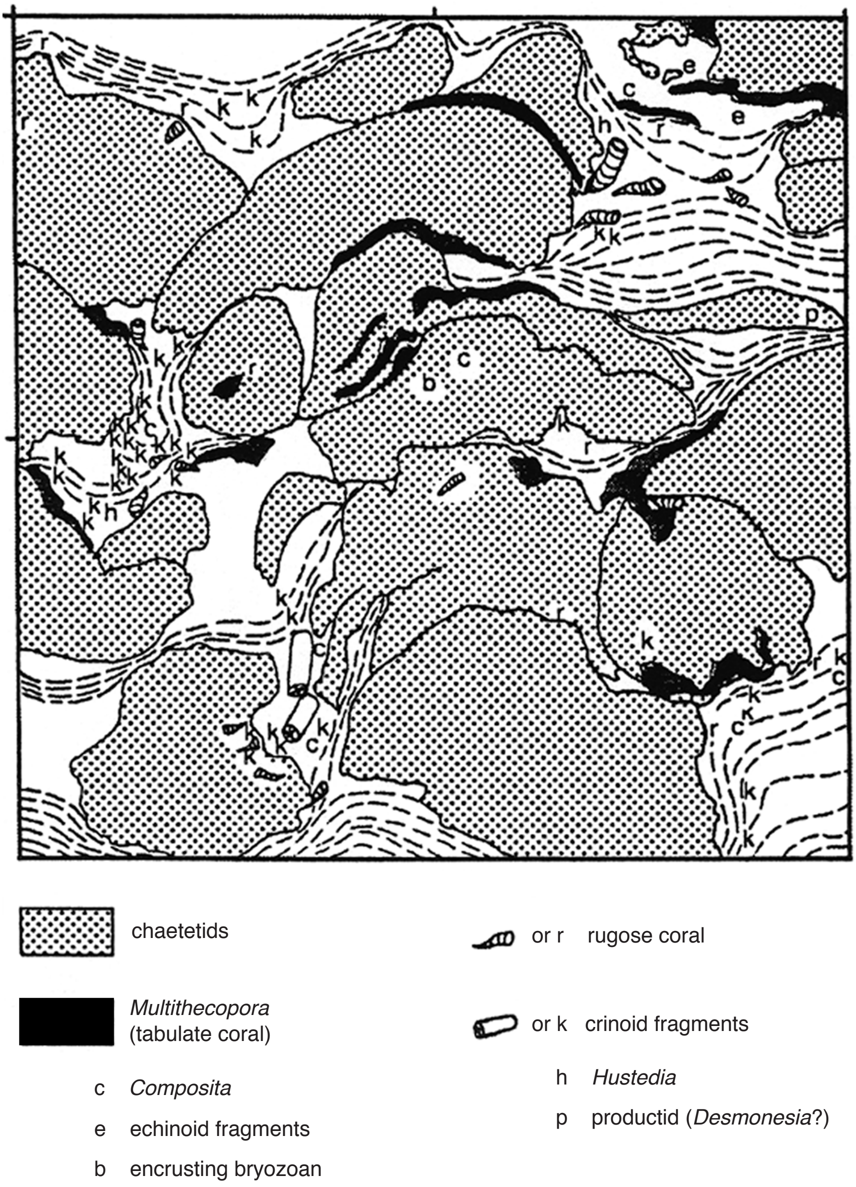

FIG. 109. Distribution of organisms in a 0.6 m^2 (2 foot^2) area on a vertical surface in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; transportation of the crinoid and echinoid fragments is apparent,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

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

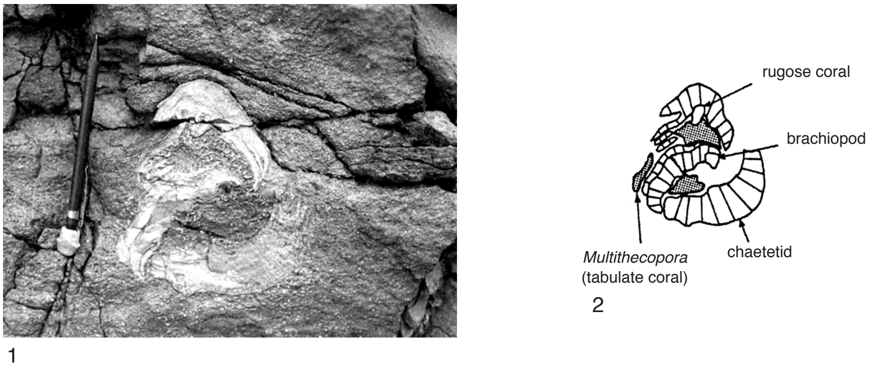

FIG. 110. Details of the relationships between chaetetids, associated organisms, and lithologies in a chaetetid reef mound exposed in a quarry, Carboniferous, Pennsylvanian, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; *1,* relationship between three episodes of chaetetid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

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

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

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

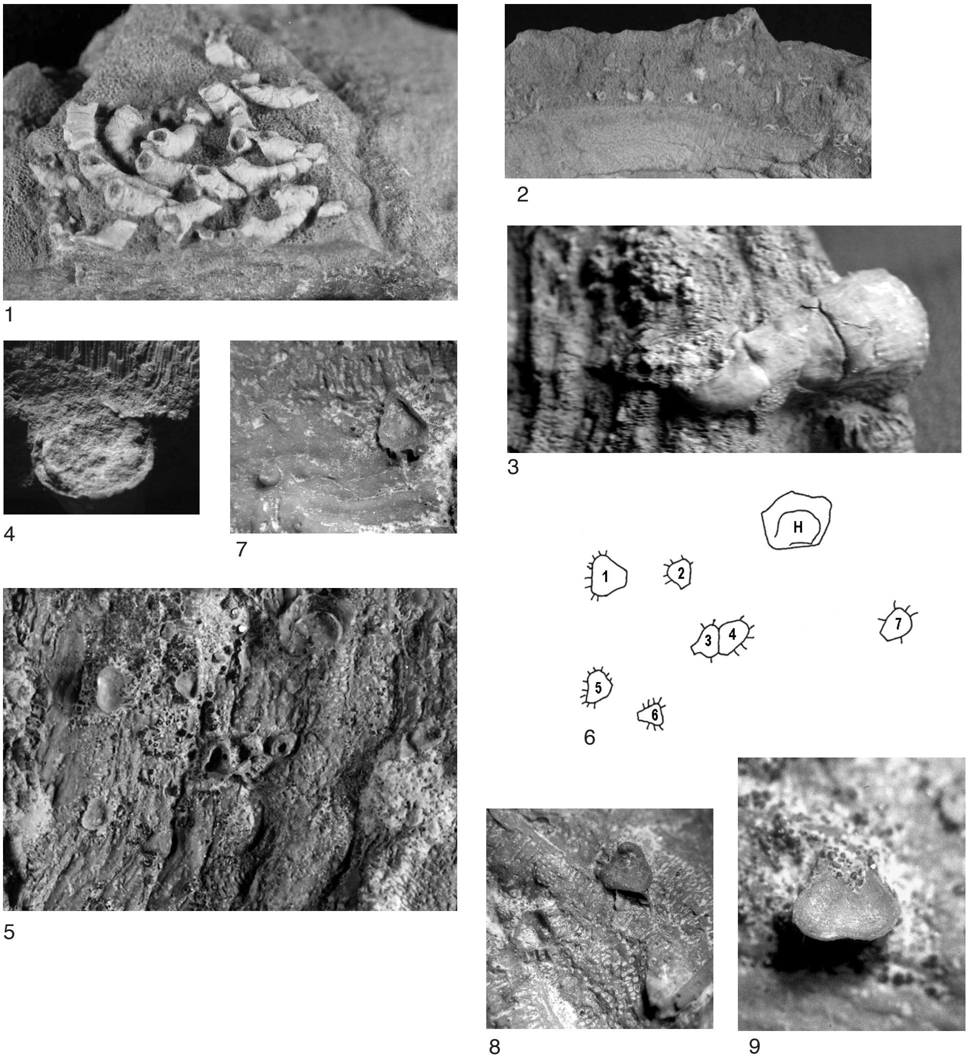

FIG. 111. Details of some specific invertebrate fossils associated with chaetetids, Carboniferous, Pennsylvanian; *1,* upper surface of the tabulate coral *Multithecopora* sp. attached to the upper surface of a chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas, ×2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

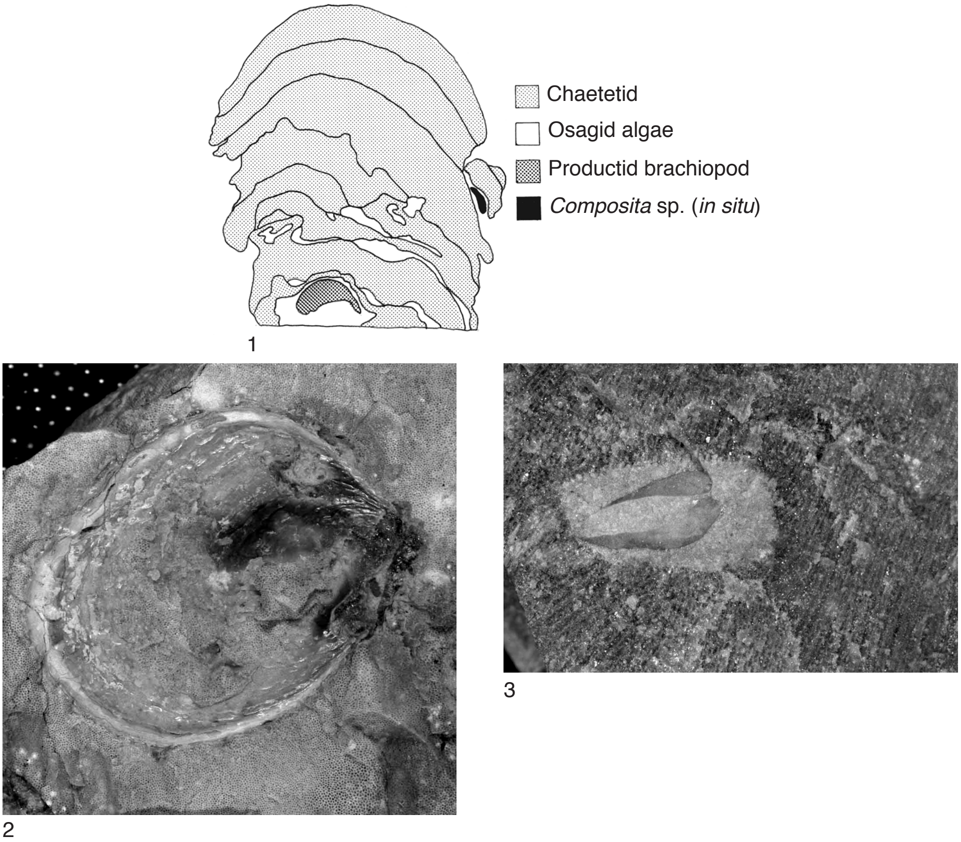

Fig. 112. Details of some further specific invertebrate fossils associated with chaetetids from the Carboniferous, Pennsylvanian; *1,* high domical chaetetid with ragged margins, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; initial laminar chaetetid encrusted an algal-microbially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

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

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

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

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

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