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Paleoecology of the Hypercalcified  
Chaetetid-Type Porifera (Demospongiae)

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# PART E, REVISED, VOLUME 4, CHAPTER 2E: PALEOECOLOGY OF THE HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

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## INTRODUCTION

The distinction between paleoautoecology (the ecological study of an individual fossil or of small taxonomic groups) and paleo-synecology (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.

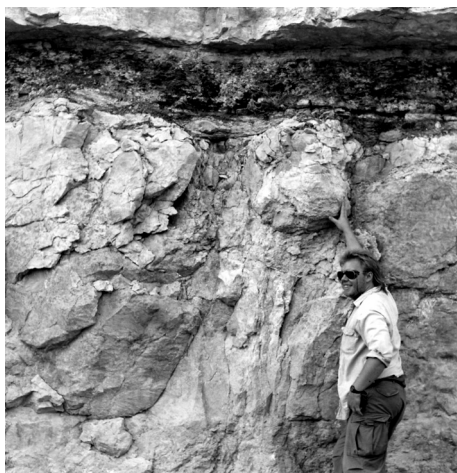
Extant and fossil hypercalcified demosponges with a chaetetid basal calcareous skeleton are exclusively benthic marine invertebrates. Only a few extant hypercalcified demosponges are known, and they occur mostly along bathyal cliffs and in dark littoral caves (VACELET, WILLENZ, & HARTMAN, 2010). KOBLUK 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 WEBBY, 2010: *Treatise Online*, Chapter 8, Glossary, p. 16) 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 upper 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. 1). WEST and CLARK (1983, p. 137) reported upper Carboniferous (Pennsylvanian) columnar chaetetids that were up to 0.8 m in diameter and 1.5 m high (WEST, 2011a, fig. 16.4). WINSTON (1963) documented columnar chaetetids 3 m high in the upper 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 WEST, 2012a, table 4), 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 (late Carboniferous and Permian) and part of the Mesozoic (Middle Triassic into the Cretaceous) but are of lesser importance in reefs during



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FIG. 1. Large chaetetids, Pennsylvanian, upper Carboniferous; 1, rounded upper surfaces of very large high domical to columnar chaetetids projecting above water level, Amoret Limestone Member, Altamont Limestone, Tulsa County, Oklahoma,  $\times 0.02$  (new); 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,  $\times 0.02$  (new); 3, large domical chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 0.02$ ; (adapted from Voegeli, 1992, p. 131, fig. 28; courtesy of the author and Kansas State University).

the Paleogene, Neogene, and Quaternary (HECKEL, 1974; FÜRSICH & WENDT, 1977; FAGERSTROM, 1987; TALENT, 1988; WOOD, 1999; STANLEY, 2001; KIESSLING, FLÜGEL &

GOLONKA, 2002; LEINFELDER & others, 2005; HELM & SCHUELKE, 2006; ALMAZÁN & others, 2007; MINWEGEN, 2007; NAGAI & others, 2007; WEIDLICH, 2007a, 2007b; BLOMEIER,



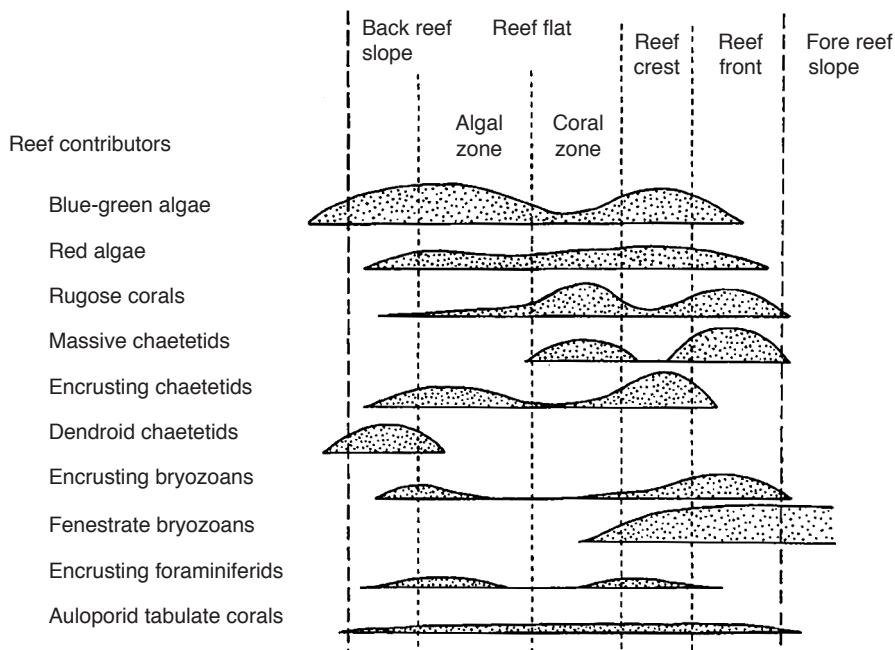


FIG. 2. Distribution of the main reef contributors in the reef facies, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Minami-dai area, Japan (adapted from Sugiyama & Nagai, 1990, p. 11, fig. 2; courtesy of the authors and Akiyoshi-dai Museum of Natural History).

SCHEIBNER, & FORKE, 2009). Where chaetetids are a conspicuous component of reefs, they are commonly part of the constructor guild (WEST, 2011a, fig. 14.2, fig. 16.2), 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. 2–7). In general, it appears that, from the Permian onward, chaetetids functioned in reef building more as binders and less as constructors (Fig. 8).

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; ZAPAIKI & others, 2007; PICKETT, OCH & LEITCH, 2009) and lower Carboniferous (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) in a few places in North America and North Africa (Morocco), but mostly in Europe. A few occurrences have been reported from the Ordovician and Silurian (see WEST, 2011c).

Environmental variables may be grouped into three main categories: physical, chemical, and biological, all of which are inter-related 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

TABLE 1. Some ecological factors important to demosponges; *asterisks*, environmental factors that can be inferred for fossil chaetetids (new).

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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

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demosponges, SARA and VACELET (1973) 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 WEST (2012b).

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 1 are the subdivisions (variables) of topics 2, 4, and 5 as given by SARA and VACELET (1973). An asterisk (in Table 1) 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 occurrence of some

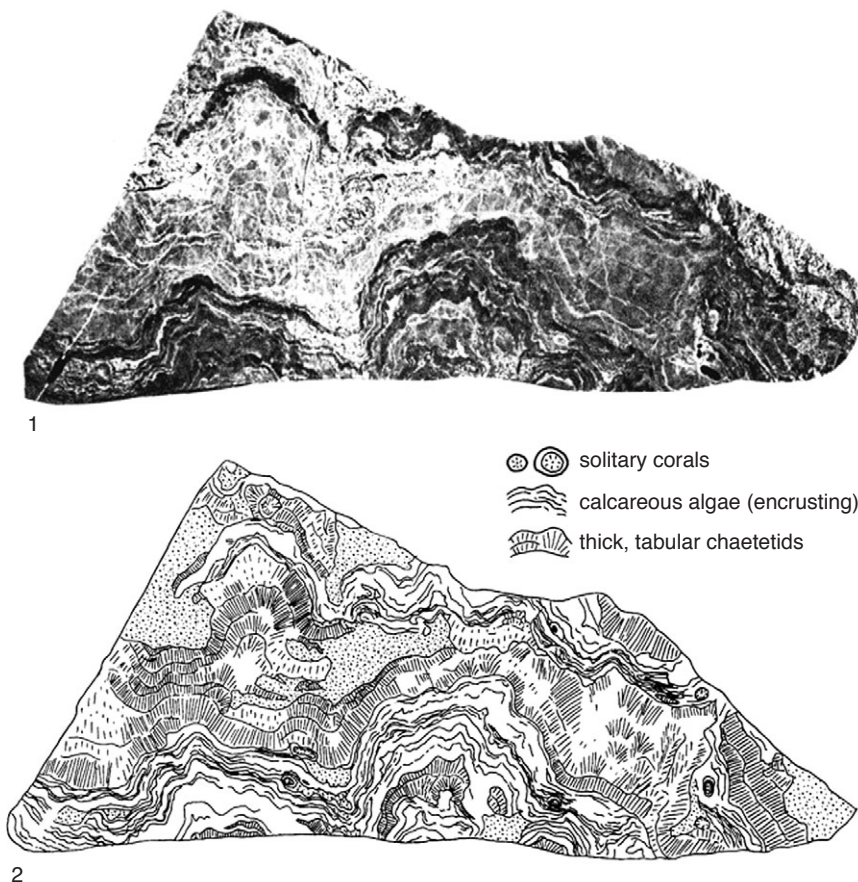


FIG. 3. Reef builders, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan; 1, polished surface of reef boundstone from the reef crest, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan,  $\times 0.29$  (adapted from Nagai, 1992, pl. 24, 1; courtesy of the author and Kyushu University); 2, interpretive sketch of the polished surface in view 1 of the encrusting chaetetid-algal framestone (boundstone),  $\times 0.31$  (adapted from Nagai & others, 1999, p. 37, fig. 22; courtesy of the author and International Symposium on Fossil Cnidaria and Porifera).

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

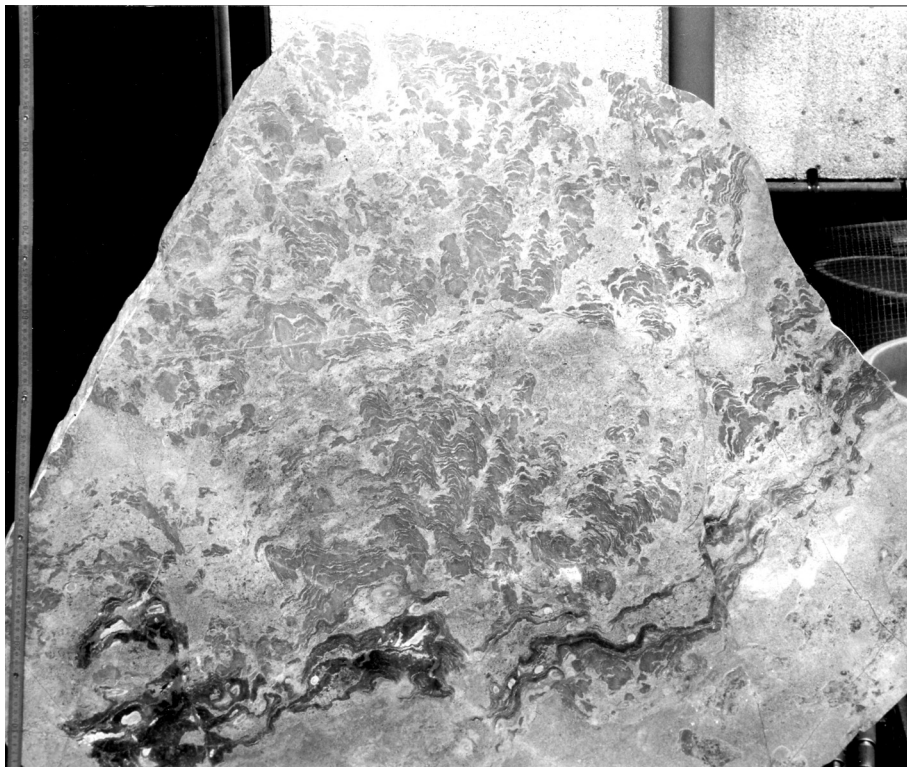


FIG. 4. Polished surface of a large slab from the fore reef facies, Pennsylvanian, upper Carboniferous, Akiyoshi limestone, Akiyoshi-dai, Japan,  $\times 0.11$  (new).

that fossil chaetetids may have contained photosymbionts (CONNOLLY, LAMBERT, & STANTON, 1989; WEST, 1994), 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,



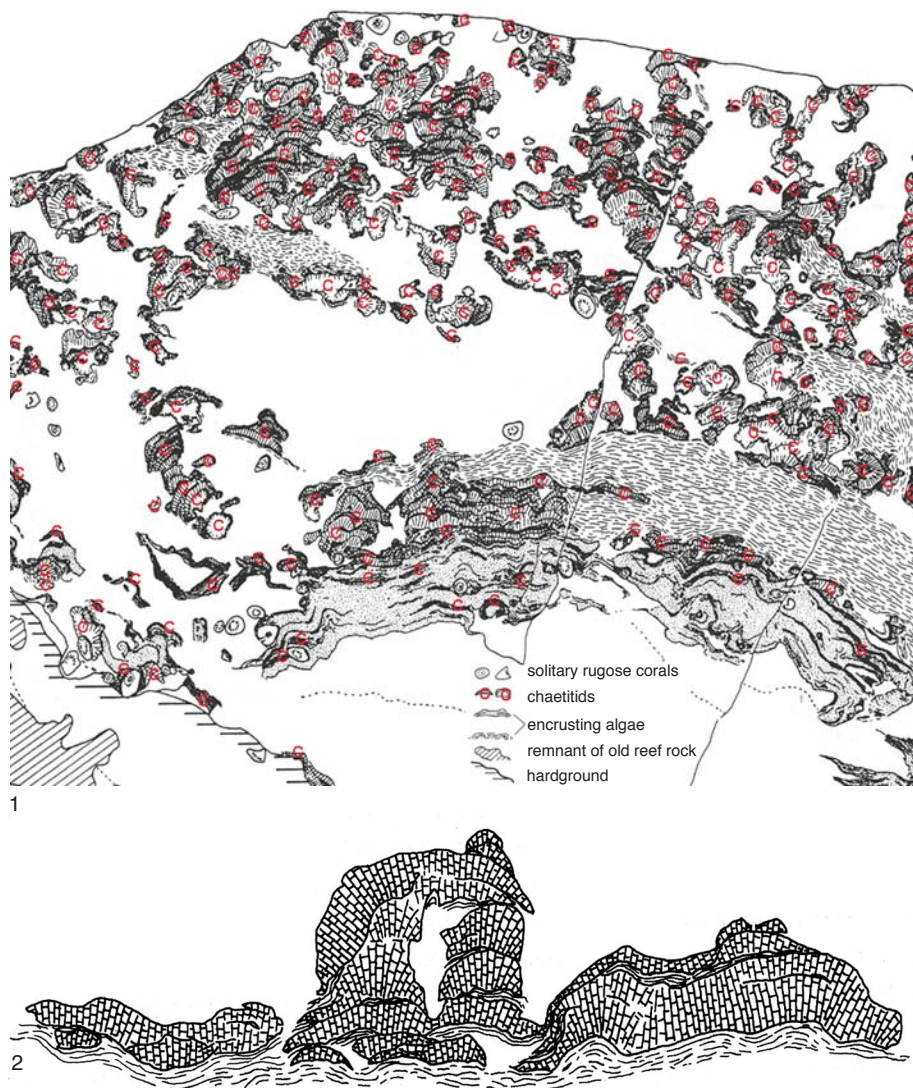


FIG. 5. Polished surfaces of slabs from the reef facies, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan; 1, detailed interpretative sketch of the surface of a large polished slab of chaetetid-algal boundstone,  $\times 0.2$  (adapted from Nagai, 1985, fig. 4); 2, sketch showing the relationship between chaetetids and algal-microbial layers,  $\times 0.67$  (adapted from Nagai, 1985, p. 12, fig. 9b; figures courtesy of the author and Akiyoshi-dai Museum of Natural History).

what is known and understood about the paleoecology 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). See KERSHAW (1998, 2012), DASILVA, KERSHAW, and BOULVAIN (2011a, 2011b), and WEBBY and KERSHAW (2011) for details on these and other aspects of stromatoporoid paleoecology.

As noted in the introductory chapter (WEST, 2011a), the growth form of the

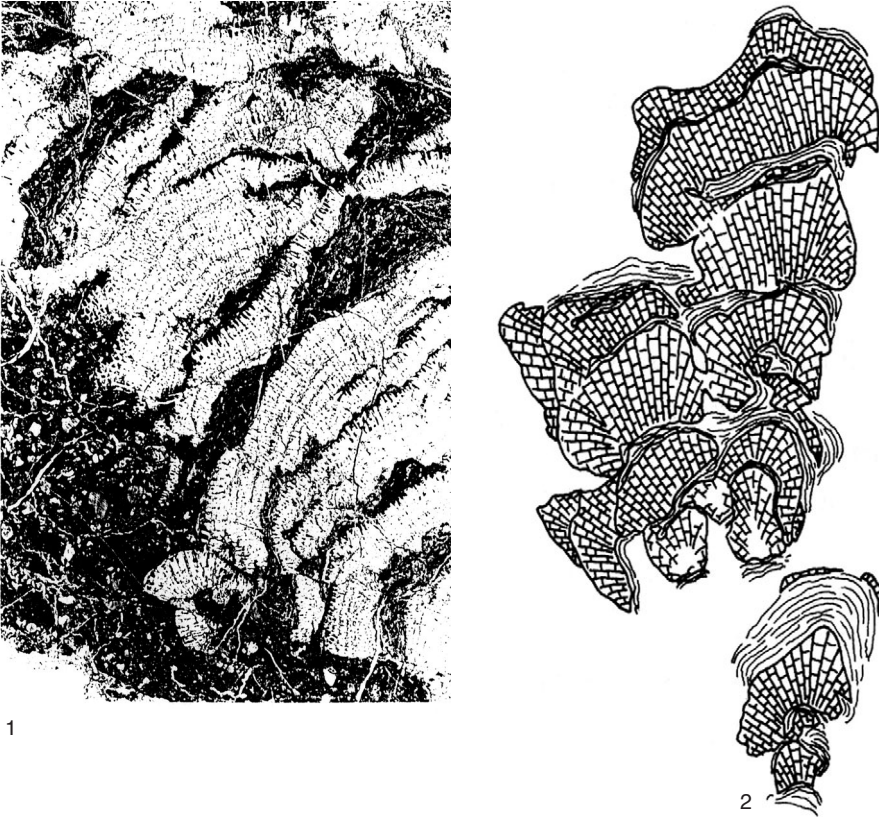


FIG. 6. Details of the relationships between encrusting algae-microbes and chaetetids from the organic reef complex, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan; 1, thin section showing interlayering of thin laminar chaetetids and algal-microbial mats from the organic reef complex,  $\times 1.8$  (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).

basal calcareous skeletons of 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 1 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. 7. Interpretative sketch of the encrusting chaetetid-algal-microbial framestone with attached solitary rugose corals in the reef crest of the organic reef complex, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan,  $\times 0.65$  (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



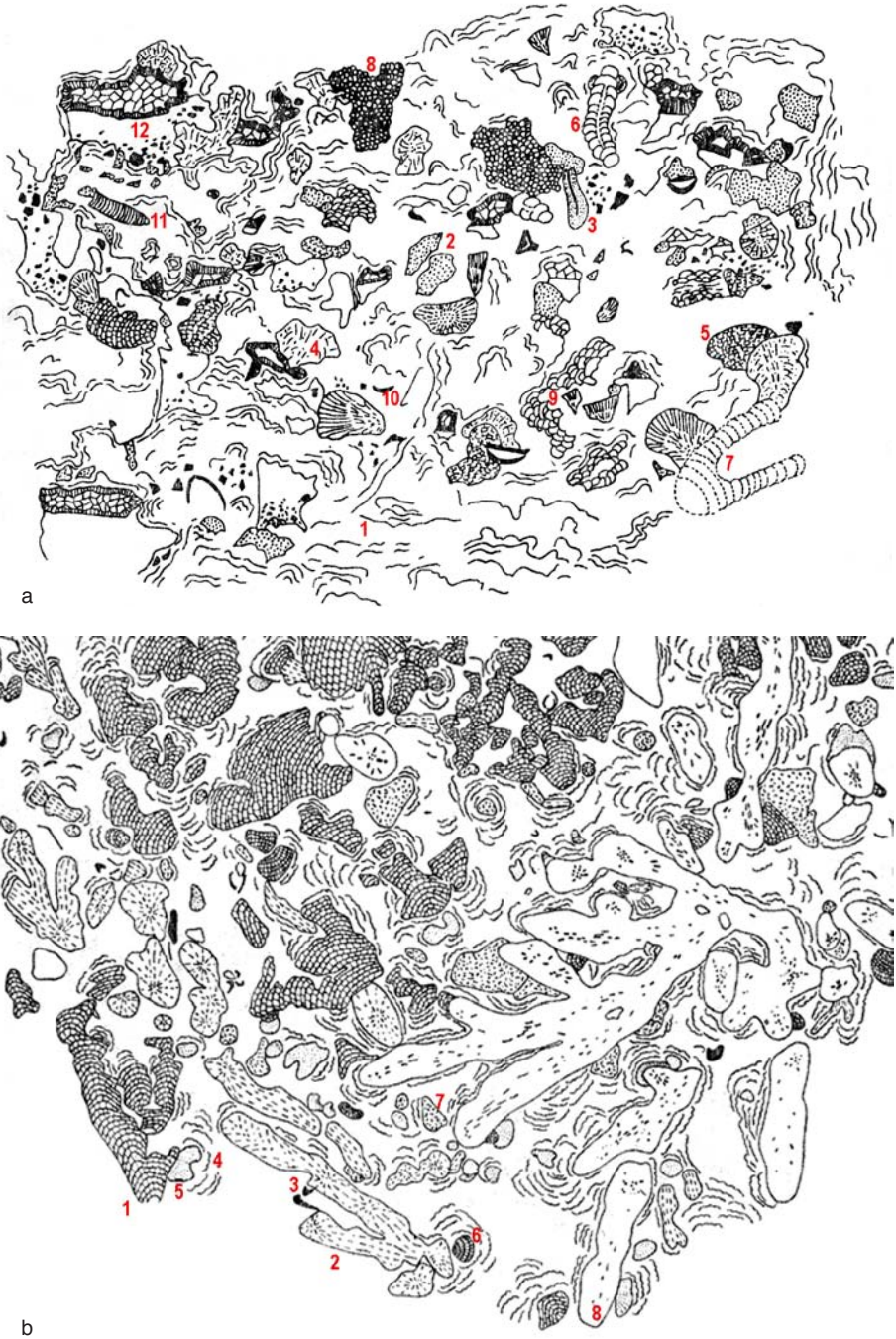


FIG. 8. (For explanation, see facing page).

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 lower Carboniferous (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 upper Carboniferous (Pennsylvanian) (Fig. 9–12; 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 *Acanthochaetes* 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 WEST (2011b). WAHLMAN (2002, p. 290) stated that upper Carboniferous (Pennsylvanian) chaetetid mounds and banks appear to have formed buttresses around the seaward margins of algal mounds (Fig. 13). 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;

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FIG. 8. 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 Rimbiano (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,  $\times 0.43$  (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,  $\times 0.3$  (adapted from Fursich & Wendt, 1977, p. 268, fig. 5; figures courtesy of the authors).

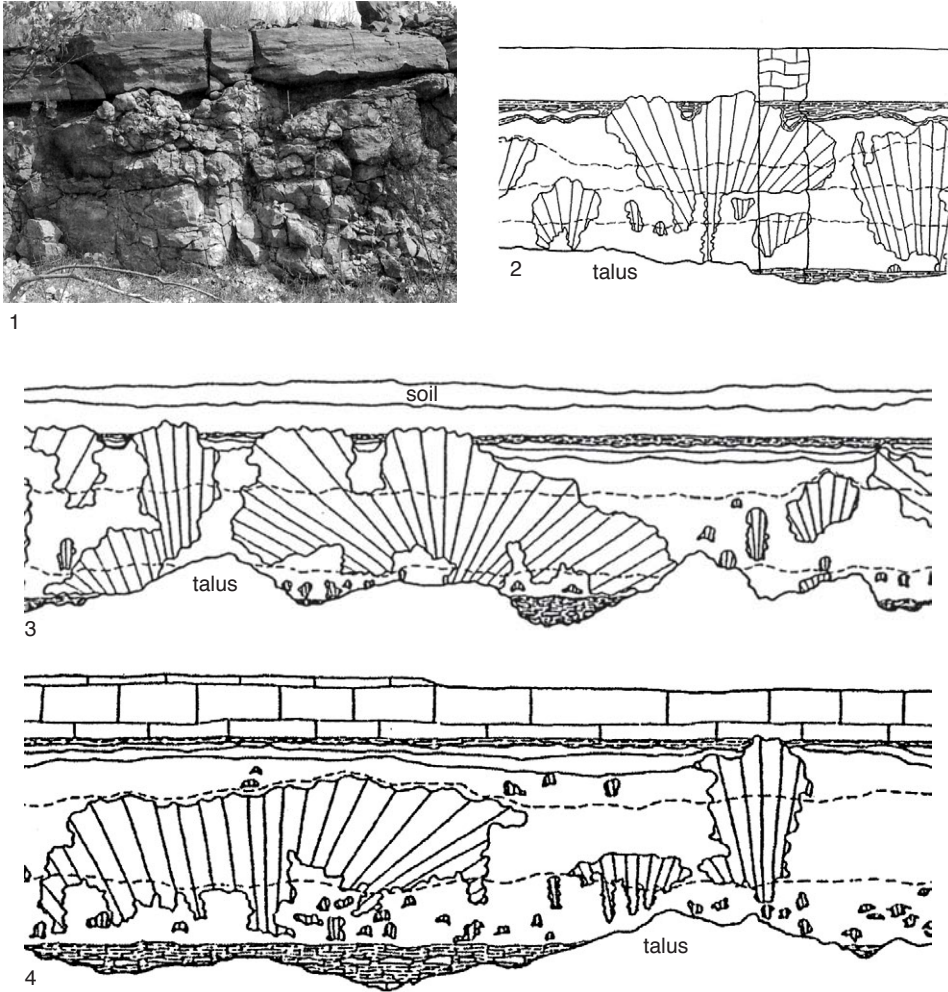


FIG. 9. Chaetetid reef mounds, Pennsylvanian, upper Carboniferous; 1, photograph of an exposure of a chaetetid reef mound in a south-facing wall in the southern part of a quarry, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,  $\times 0.01$  (adapted from Suchy & West, 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 calcilitite with some chert nodules, and white areas above talus line are limestone; 2, photograph in view 1,  $\times 0.01$  (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,  $\times 0.01$  (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,  $\times 0.01$  (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.



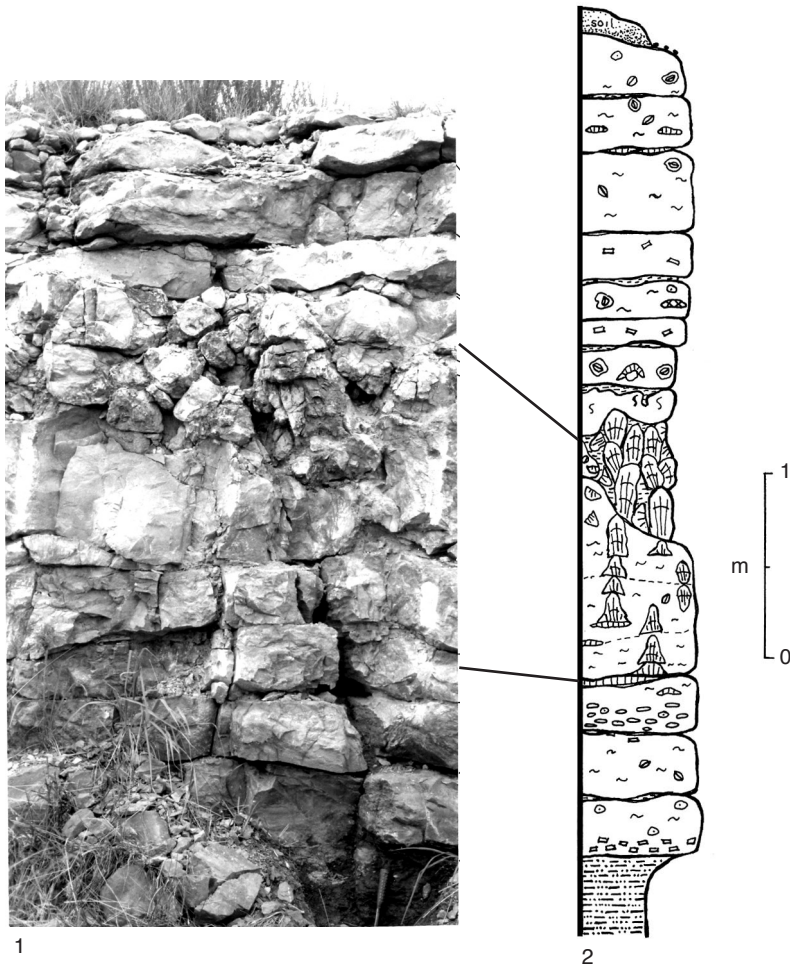


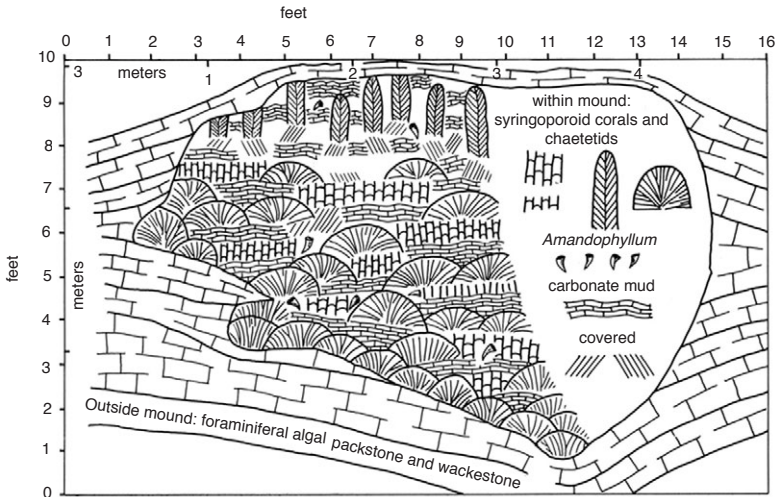
FIG. 10. Further examples of chaetetid reef mounds, Pennsylvanian, upper Carboniferous; 1, photograph of an exposure of part of a chaetetid reef mound in a road cut exposure, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.03$  (adapted from Voegeli, 1992, p. 65, fig. 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).

Association with algal 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, breathing, and excretion 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



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FIG. 11. Chaetetid reef, Pennsylvanian, upper Carboniferous, Texas; 1, photograph of an exposure of a chaetetid reef, Marble Falls Limestone, Mason County, Texas,  $\times 0.01$  (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),  $\times 0.02$  (adapted from Sutherland, 1984, p. 544, fig. 1; figures courtesy of the Paleontological Research Institution, Ithaca, New York).

been postulated for chaetetids (CONNOLLY & STANTON, 1983, 1986; SUTHERLAND, 1984; CONNOLLY, LAMBERT, & STANTON, 1989; VOEGELI, 1992; LEINFELDER & others, 2005). Table 2 lists the criteria that support a shallow water occurrence for middle 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 micro-atolls (Fig. 14–15).

The hydrodynamics of open ocean habitats is a function of current and wave

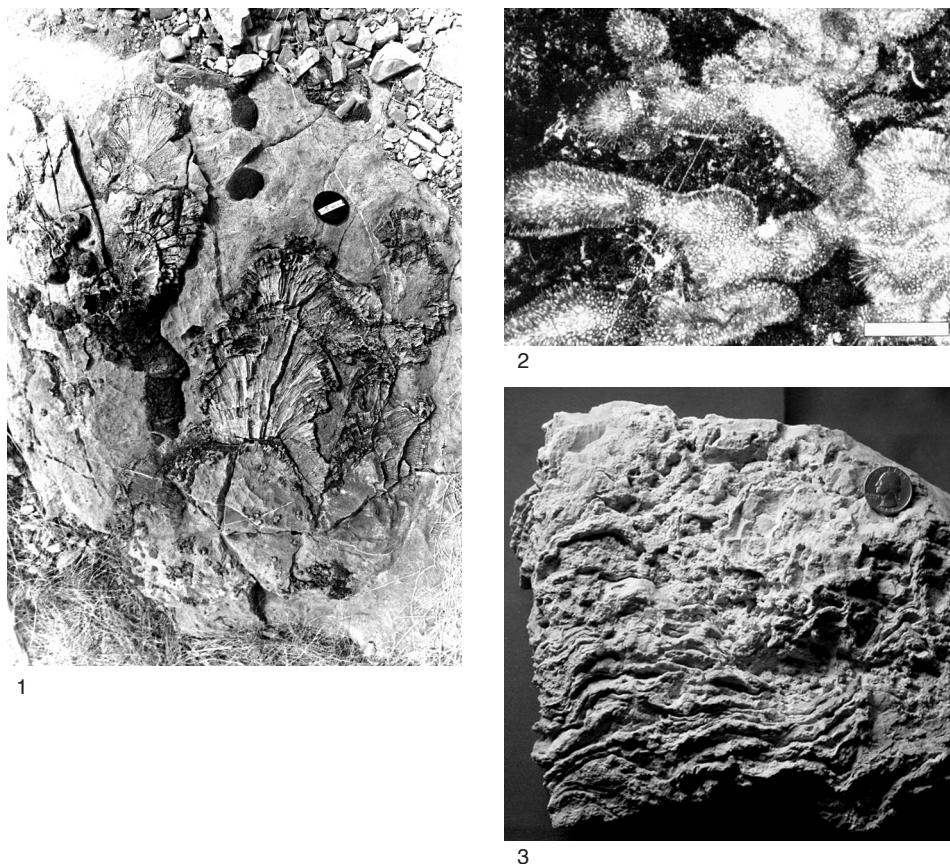


FIG. 12. Chaetetid reefal limestones, Pennsylvanian, upper Carboniferous; 1, photograph of an exposure of columnar chaetetids in a reef bank, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona,  $\times 0.07$  (new); 2, polished surface of a chaetetid boundstone, Cuera Limestone, Playa de La Huelga, Cantabrian Mountains, Spain,  $\times 0.3$  (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,  $\times 0.5$  (new).

energy; in shallow water coastal areas, tidal surges, storm waves, fair weather waves, and currents are 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, breathing, and excretion. 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



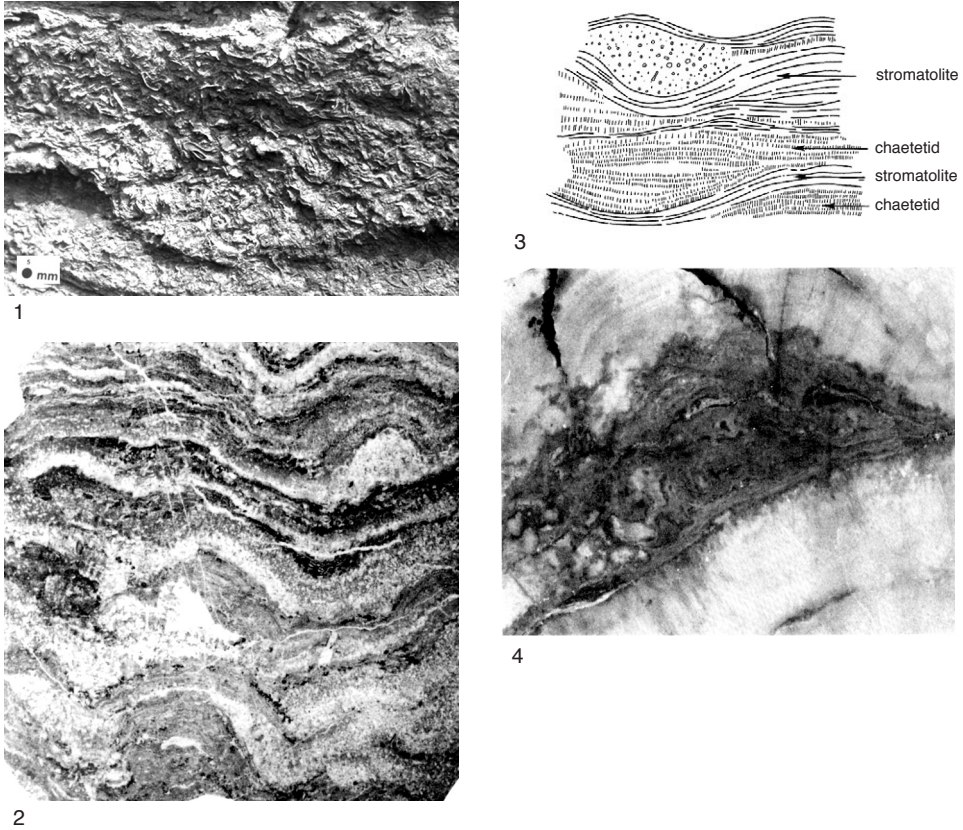


FIG. 13. Details of chaetetids and algal associations, Pennsylvanian, upper Carboniferous; 1, outcrop photograph of the weathered surface of a phylloid algae packstone associated with chaetetids in a reef mound, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.2$  (adapted 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,  $\times 1.7$  (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,  $\times 0.7$  (adapted from Ota, Sugimura, & Ota, 1969, p. 8, fig. 5; courtesy of the authors and Paleontological 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,  $\times 0.8$  (adapted from Sutherland, 1984, p. 547, pl. 1,6; courtesy of the Paleontological Research Institution, Ithaca, New York).

coral colonies were turned over, exposing the sponges. When turbulence, turbidity, and/or 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. 16; 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. 17–20). Some lithologic units containing toppled chaetetids are overlain by lithologies with features suggestive of subaerial exposure (Fig. 17–18). But, there are also examples where, after being disoriented, growth continued such that the initially colonized object (substrate) reveals more than one disturbance (Fig. 20.3–20.4, Fig. 21). Larger and/or denser objects require more hydrodynamic energy to move or topple them. Thus, the size of the chaetetid mass that has

TABLE 2. 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 <i>in situ</i> 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
Syn depositional relief
Disturbed chaetetids, toppled, inverted

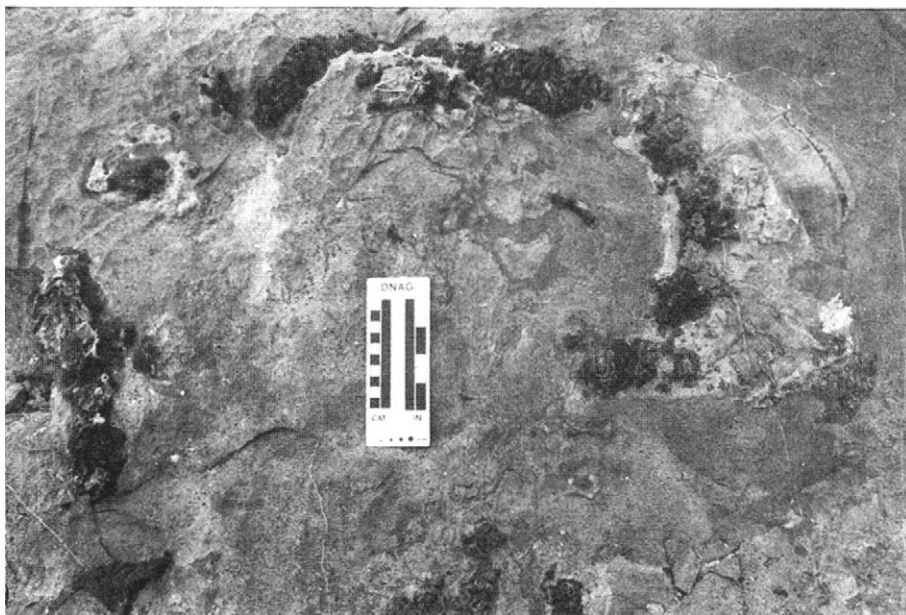


FIG. 14. Upper surface of a chaetetid micro-atoll (scale is in the inferred lagoon, the longest black bar to the left is 10 cm long), Pennsylvanian, upper Carboniferous, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona; dark areas are the tops of chaetetids,  $\times 0.14$  (adapted from Connolly, Lambert, & Stanton, 1989, p. 167, pl. 55.3; courtesy of the authors and Springer-Verlag GmbH & Co.).

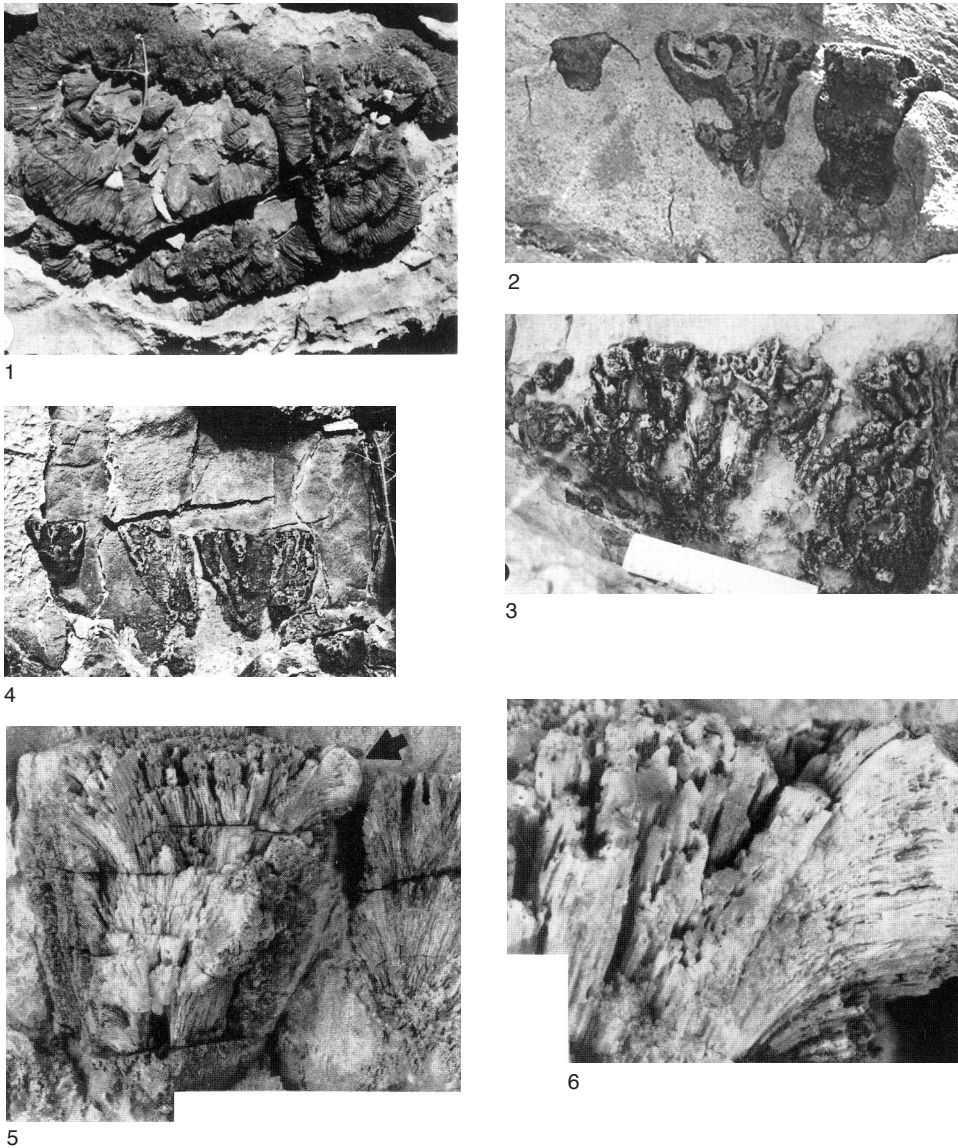


FIG. 15. Flared chaetetids and micro-atolls, Pennsylvanian, upper Carboniferous; 1, upper surface of a small chaetetid micro-atoll, limestone of the Middle Magdalena Group, Hueco Mountains, Texas,  $\times 0.3$  (adapted from Stanton, Connolly, & Lambert, 1994, p. 367, fig. 2.6; courtesy of the authors 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,  $\times 0.35$  (new); 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,  $\times 0.2$  (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,  $\times 0.1$  (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).

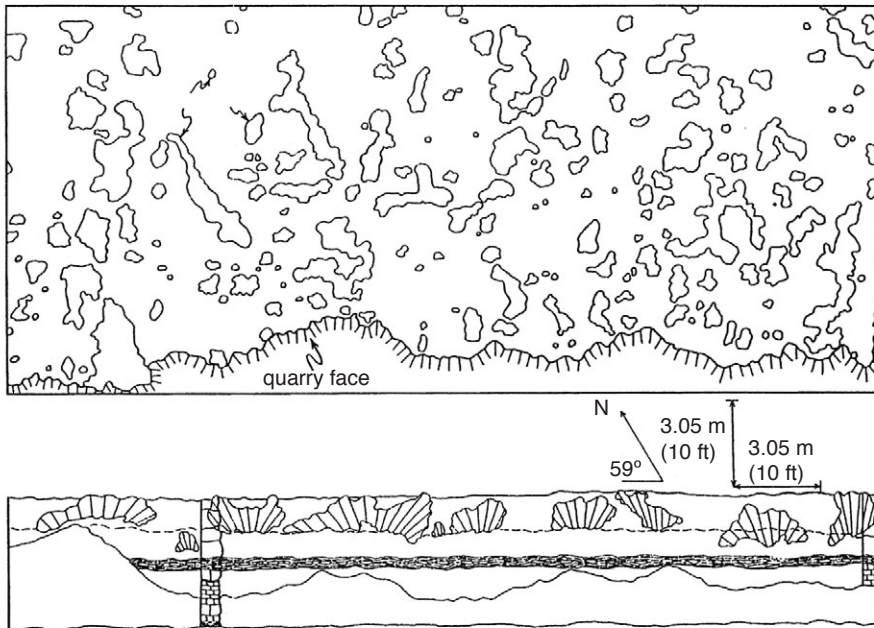


FIG. 16. Inferred current direction from the southwest (lower left), based on the shape and orientation of chaetetids and associated cross-laminated calcarenites. Upper diagram is a map of an exposed bedding plane surface in a quarry, and the lower diagram is the vertical face associated with that quarry map, Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,  $59^\circ$  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,  $\times 0.004$  (adapted from Suchy & West, 2001, p. 434, fig. 8; courtesy of the authors and the Society for Sedimentary Geology).

been toppled and/or moved around provides some indication of the relative hydrodynamic energy in that environment. As growth continued, the chaetetid mass reached a size that was not easily moved, though upward growth continued (Fig. 20.3–20.4). Some high domical to columnar forms extended several centimeters above the seabed (Fig. 20.1). In some cases, the margins of such masses are ragged (Fig. 20.2), presumably due to sediment influx, but they managed to cope with the influx and survive (Fig. 22.3–22.4). 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 sedimenta-

tion (Fig. 20.1, Fig. 23.1–23.2). Partial or complete burial of the living surfaces of some chaetetids by sediment is indicated by tubules now filled with micrite (Fig. 23.3, Fig. 24.1–24.2; see also WEST, 2011a, fig. 31.1), but rejuvenation may follow such disruptive events (Fig. 22.3–22.4). 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

Fig. 15. (Continued from facing page).

Magdalena Group, Hueco Mountains, Texas,  $\times 0.7$  (adapted from Stanton, Connolly, & Lambert, 1994, p. 368, fig. 3.7; courtesy of the authors and E. Schweizerbartsche Verlags, Naegle 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,  $\times 3$  (adapted from Stanton, Connolly, & Lambert, 1994, p. 368, fig. 3.6; courtesy of the authors and E. Schweizerbartsche Verlags, Naegle u. Obermiller Science Publishers).



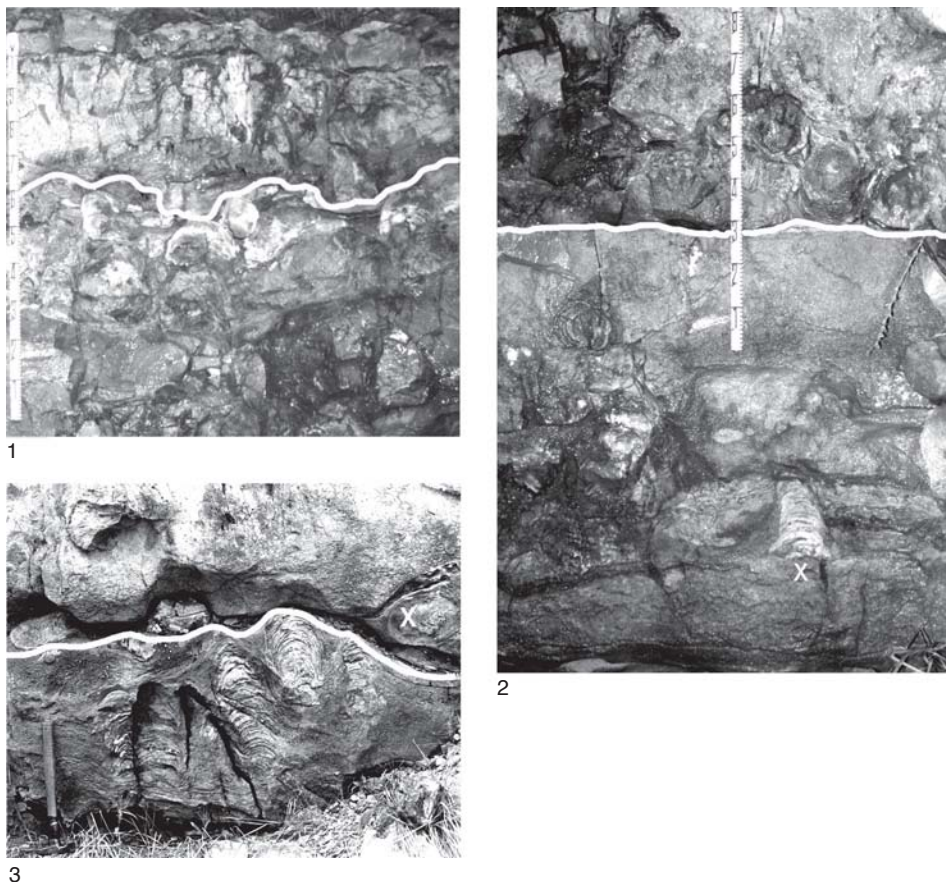


FIG. 17. Chaetetids and associated erosion, Pennsylvanian, upper Carboniferous; 1, toppled chaetetids and an erosion surface at the white line, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.05$  (new); 2, close view of toppled chaetetid interval above the white line 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*,  $\times 0.06$  (new); 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,  $\times 0.06$  (new).

inhabited more sheltered environments. A laminar to low domical growth form characterizes these binders (Fig. 24.3). The percentage of siliciclastics (insolubles) is higher in lithologies containing laminar growth forms (Fig. 24.4) than it is in lithologies containing domical and columnar forms (the main constructors of reef mounds) (WEST & ROTH, 1991; and see WEST, 2011b, tables 1–2), but ragged laminar and low domical to compound domical forms also occur in higher energy environments where packstones and grain-

stones were deposited (Fig. 23.4; see also WEST, 2011a, fig. 30.5).

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

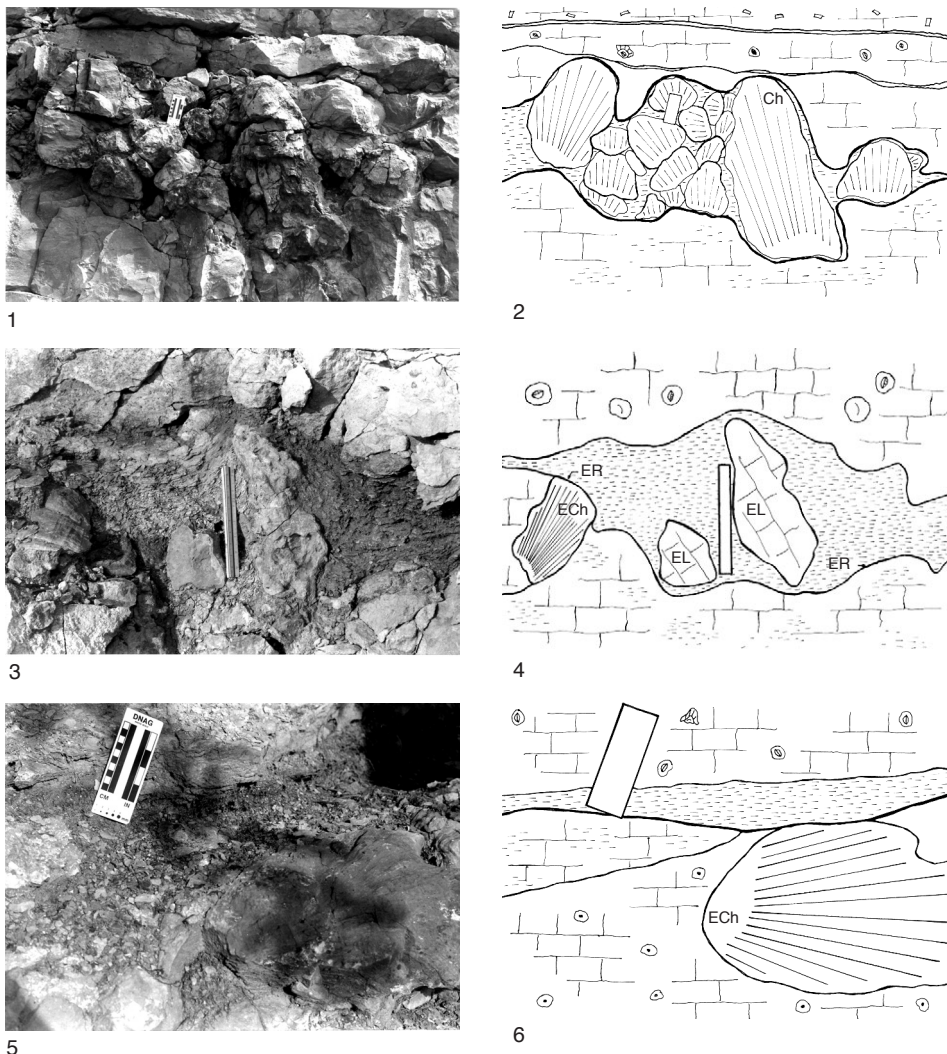


FIG. 18. Further examples of chaetetids and associated erosion, Pennsylvanian, upper Carboniferous; 1, disturbed and toppled domical and columnar chaetetids, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.25$  (adapted from Voegeli, 1992, p. 139, fig. 31); 2, interpretative sketch of view 1, *Ch*, chaetetid,  $\times 0.25$  (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,  $\times 0.1$  (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*),  $\times 0.1$  (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,  $\times 0.1$  (adapted from Voegeli, 1992, p. 55, fig. 17); 6, interpretative sketch of view 5, eroded chaetetid (*ECh*),  $\times 0.1$  (adapted from Voegeli, 1992, p. 55, fig. 17; figures courtesy of the author and Kansas State University).

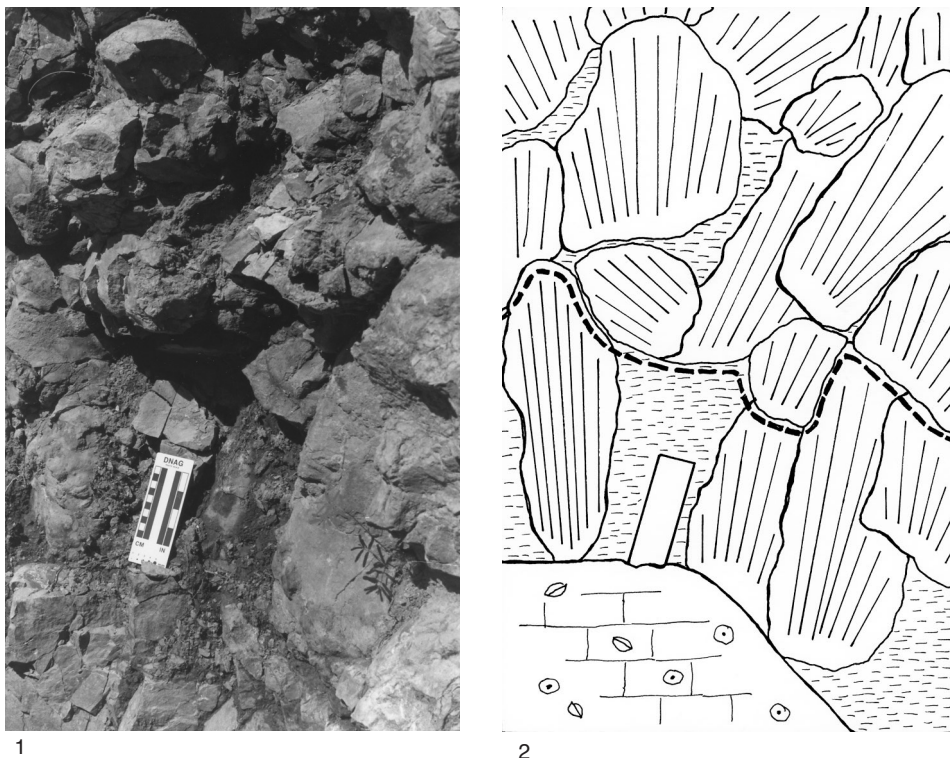
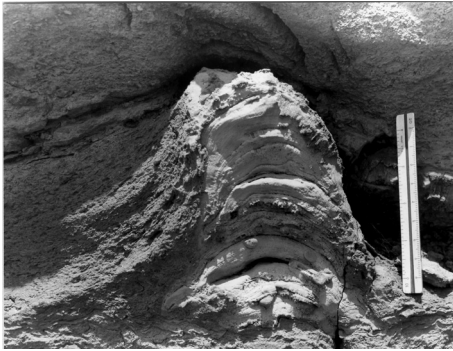


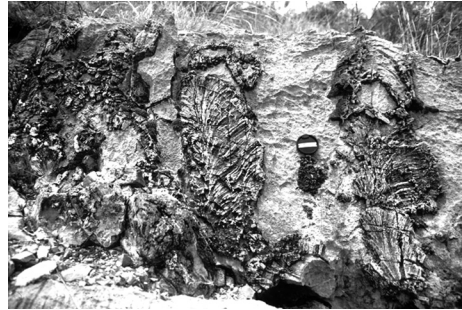
FIG. 19. Erosion, sediment draping, and rejuvenation; 1, evidence of two episodes of erosion in the disturbed chaetetid interval, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.1$  (adapted from Voegeli, 1992, p. 134, fig. 29); 2, interpretative 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,  $\times 0.1$  (adapted from Voegeli, 1992, p. 134, fig. 29; figures courtesy of the author and Kansas State University).

FIG. 20. 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,  $\times 0.2$  (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, Pennsylvanian, upper Carboniferous, Horquilla Limestone, Dry Canyon, Whetstone Mountains, Arizona,  $\times 0.05$  (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, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas, showing three episodes (generations) of growth caused by overturning. Initial growth was on the algal-microbial encrustation, an oncolite, followed by overturning, more growth, more algal-microbial encrustation, and final growth,  $\times 0.45$  (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, Pennsylvanian, upper Carboniferous, 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,  $\times 0.3$  (adapted from Voegeli, 1992, p. 142, fig. 33; courtesy of the author and Kansas State University).

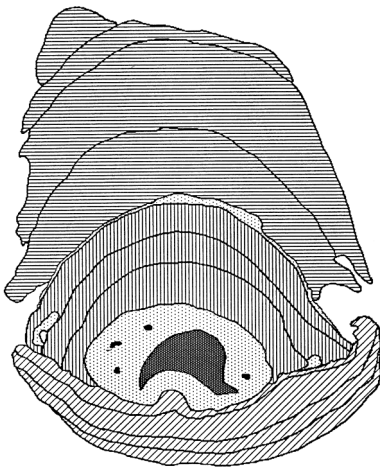










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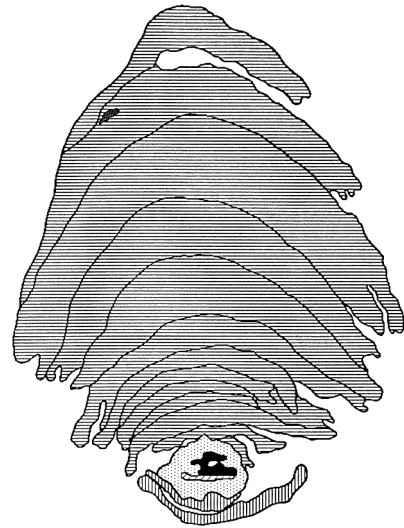








2



-  Productid brachiopod
-  Algal encrustations
-  Brachiopod spines
-  Chaetetid (1st generation)
-  Chaetetid (2nd generation)
-  Chaetetid (3rd generation)

3



-  Lithoclast
-  Algal encrustations
-  Worm tube?
-  Chaetetid (1st generation)
-  Chaetetid (2nd generation)
-  Chaetetid (3rd generation)

4

FIG. 20. (For explanation, see facing page).



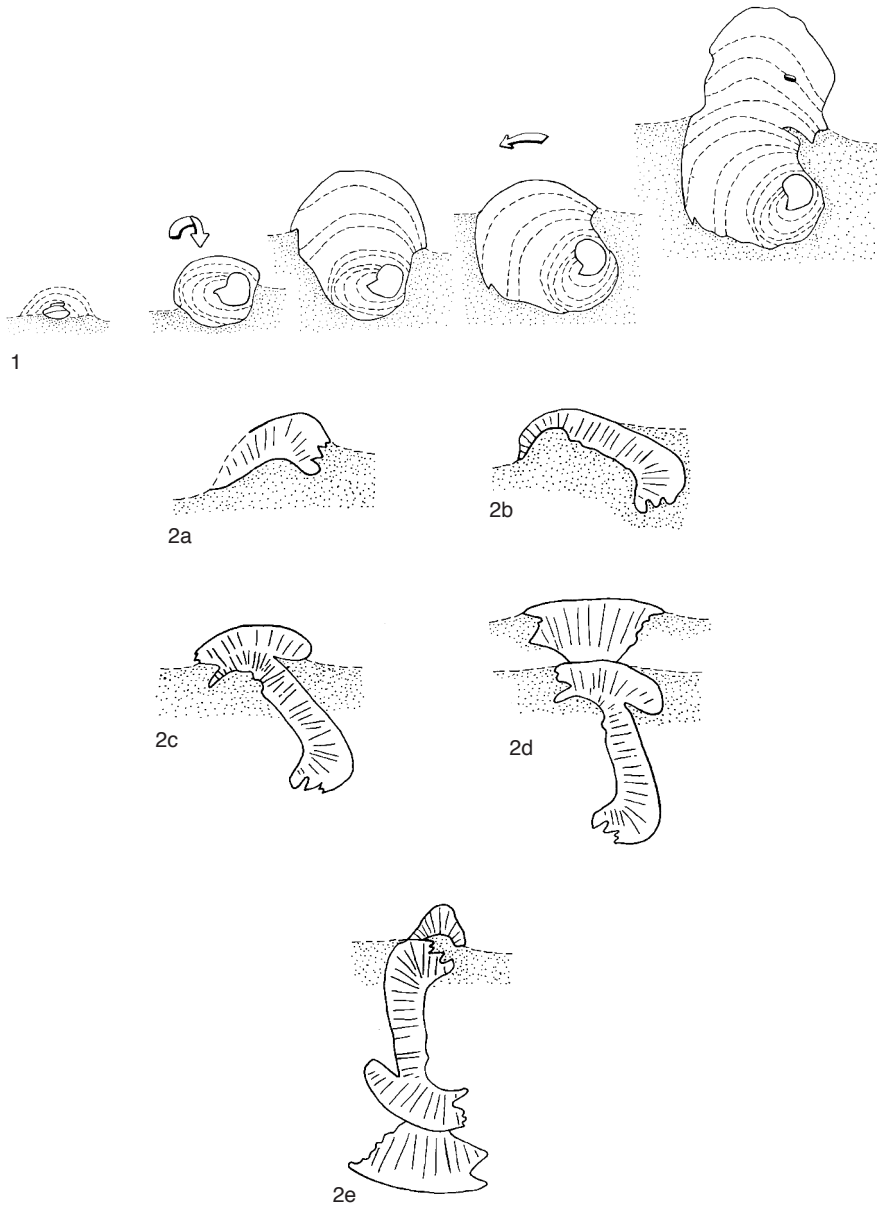


FIG. 21. Inferred growth stages of chaetetids based on interruption partings, Pennsylvanian, upper Carboniferous; 1, interpretative sketches based on a vertical section of a high domical chaetetid, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas showing changes in shape as a result 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,  $\times 0.1$  (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,  $\times 0.2$  (adapted from Kershaw & West, 1991, p. 340, fig. 5; figures courtesy of the authors and *Lethaia*).

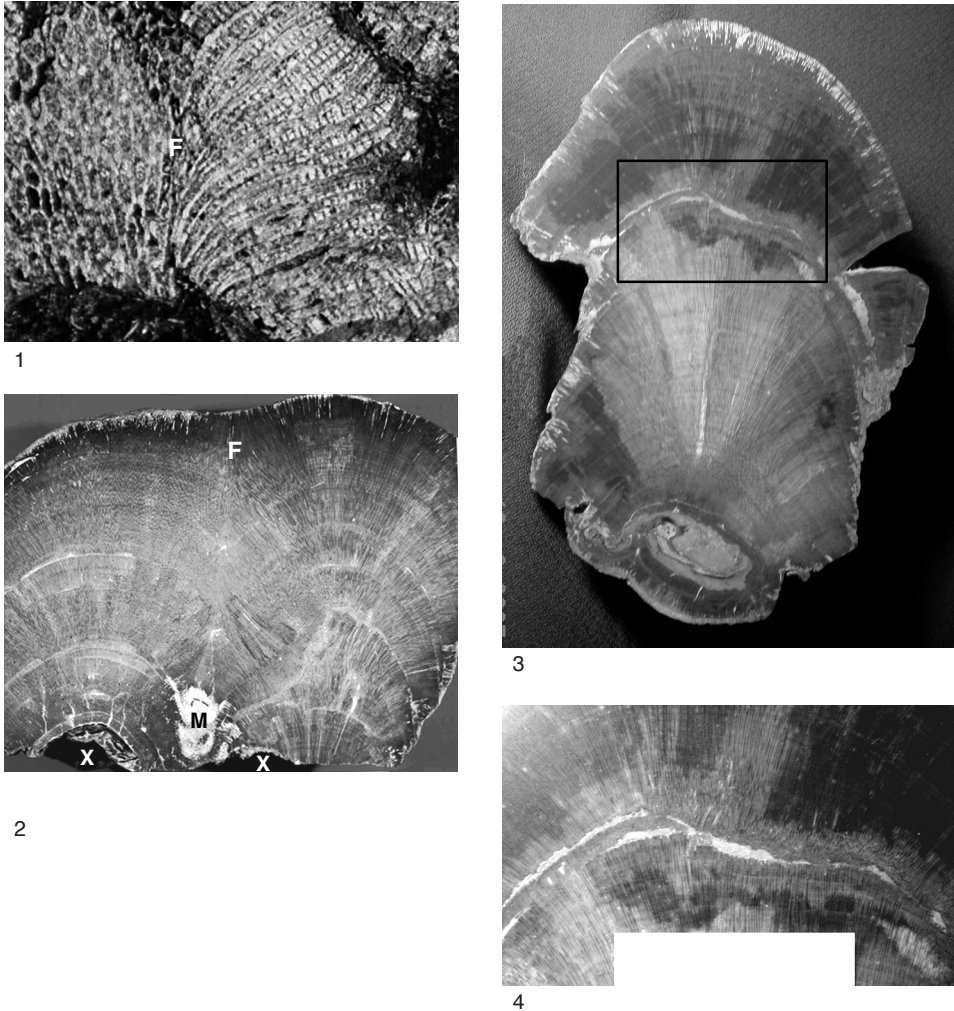


FIG. 22. Fusion and rejuvenation in chaetetids; 1, fusion in domical chaetetids, Pennsylvanian, upper Carboniferous, Akiyoshi Limestone, Akiyoshi-dai, Japan; *F*, plane of fusion (just above and left of center),  $\times 14.5$  (new); 2, fusion of two high domical chaetetids each began on an algal-microbially encrusted brachiopod valve, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; *M*, matrix; *F*, plane of fusion, *X*, algal-microbial encrusted brachiopod shells,  $\times 0.37$  (new); 3, rejuvenation in a columnar chaetetid, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas, after an event that nearly smothered the living surface,  $\times 0.5$  (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,  $\times 0.12$  (new).

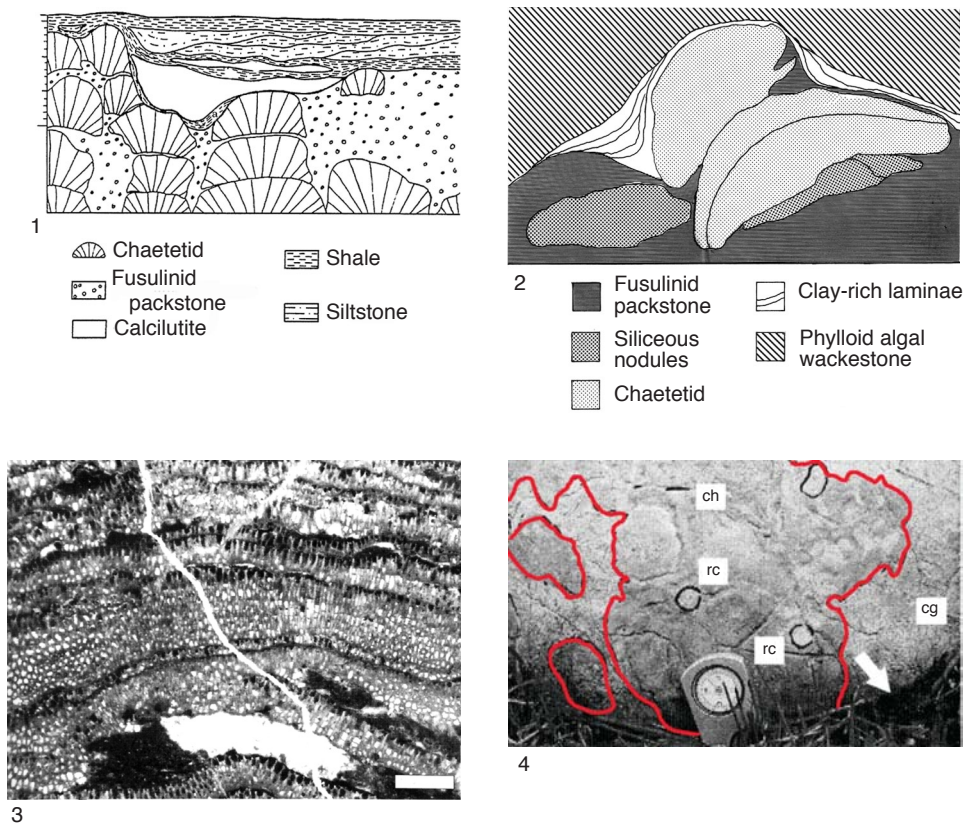


FIG. 23. Chaetetid substrates and associated lithologies, Pennsylvanian, upper Carboniferous; 1, interpretative sketch of an exposure of columnar chaetetids in a fusulinid packstone, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas smothered by calcilitite (carbonate mudstone), shale (mudrock), and siltstone; note the draping mudrock on the middle chaetetid,  $\times 0.03$  (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,  $\times 0.3$  (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,  $\times 0.3$  (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 red and incorporated solitary rugose corals (*rc*), in small black circles in a coarse-grained crinoidal grainstone (*cg*), Akiyoshi Limestone, Akiyoshi-dai, Japan, *white arrow* indicates stratigraphic up direction,  $\times 0.2$  (adapted from Sano, 2006, p. 174, fig. 5C; courtesy of the author).

(toppled) in shallow water environments and truncated by exposure (Fig. 17.1, Fig. 25).

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. 26). 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

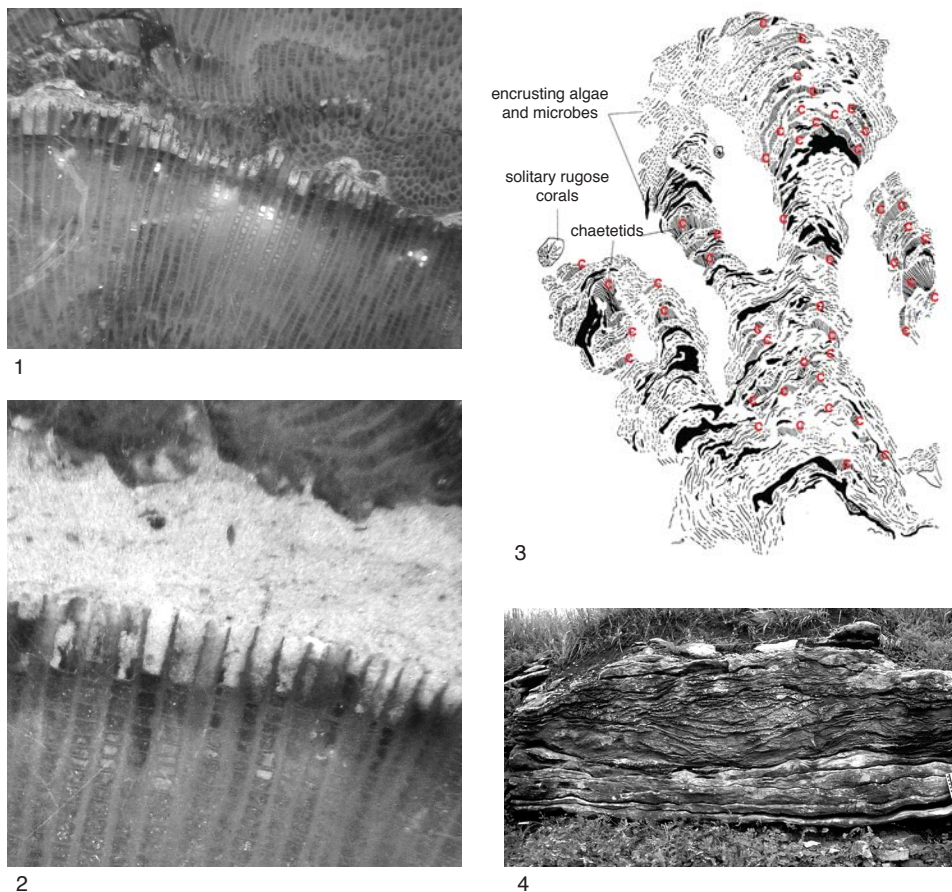
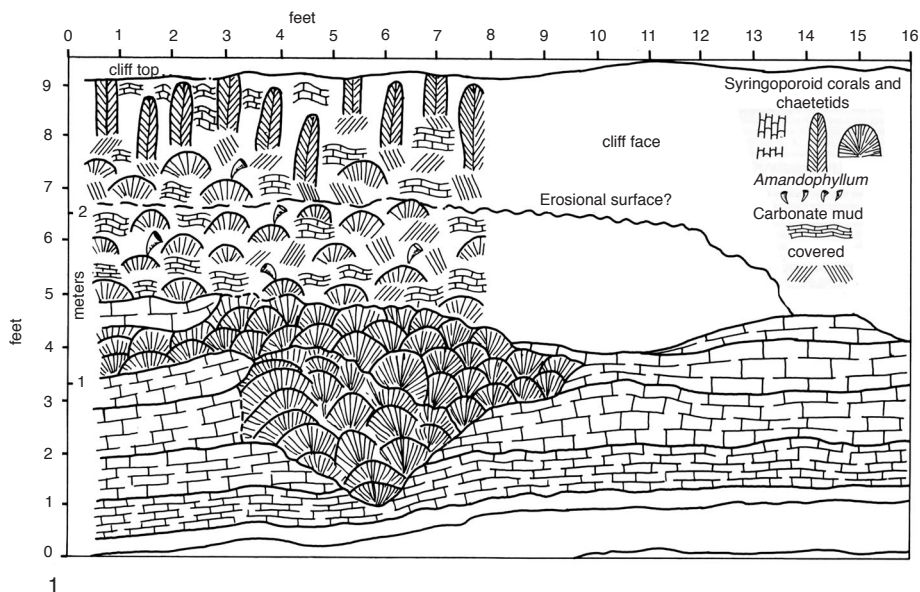


FIG. 24. Further examples of chaetetid substrates and associated lithologies, Pennsylvanian, upper Carboniferous; 1, micrite-filled chaetetid tubules, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 10$  (new); 2, detail view of part of the area in view 1, of the micrite-filled tubules in the chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 20$  (new); 3, interpretative sketch of a polished slab of the reef flat, Akiyoshi Limestone, Akiyoshi-dai, Japan of associated algal-microbial layers and laminar chaetetid (red C),  $\times 0.4$  (adapted from Nagai, 1979, p. 665, fig. 7; courtesy of the author); 4, outcrop of laminar chaetetids in an insoluble, mud-rich matrix, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas,  $\times 0.3$  (new).

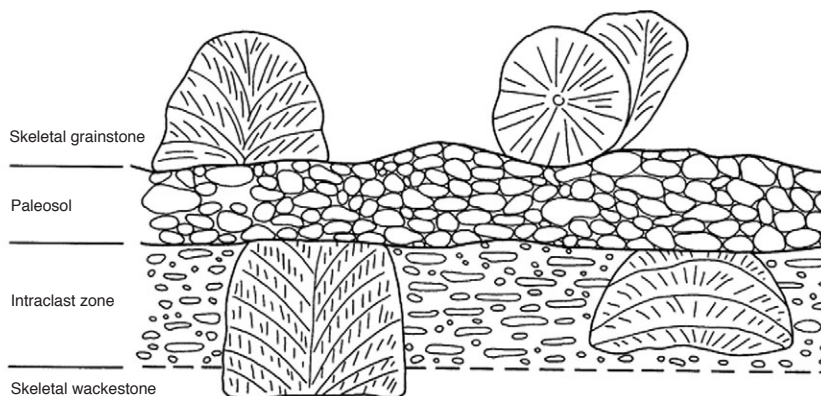
composition, JAMESON (1980, p. 130–136) recognized four general types of substrates: gels, plastic, firm, and granular. Gels are argillaceous with a thixotropic (becoming fluid when shaken) surface and remain as a gel until buried. Plastic substrates are slightly firmer than gels and are often argillaceous biomicroparites. Fine-grained biomicroparites 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 lower Carboniferous (Visean) reef bank in Great Britain (ARETZ & NUDDS, 2007). Chaetetids are common in Serpukhovian echinoderm grainstone-packstones and





1



2

FIG. 25. 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, Pennsylvanian, upper Carboniferous, Marble Falls Limestone, Mason County, Texas,  $\times 0.02$  (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 topped with renewed upward growth (upper right),  $\times 0.25$  (adapted from Connolly, Lambert, & Stanton, 1989, p. 154, fig. 6; courtesy of the authors and Springer-Verlag GmbH & Co.).

calcareous sand 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 27. Fistuliporid bryozoans inhabit similar environments and are potential

competitors; they are included in Figure 27 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. 26. 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,  $\times 0.4$  (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).

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. 21.2). However, chaetetids, like stromatoporoids, also existed on muddy substrates and within siliciclastic sequences (Fig. 24.4, Fig. 25.2; see also WEST, 2011a, fig. 13.6). 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. 28.1–28.3). 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. 28.4; see also KERSHAW & WEST, 1991; WEST & KERSHAW, 1991; WEST, 2011a, fig. 19–20). In some cases, as growth continued, other firm to hard objects were incorporated into the growing skeleton (Fig. 28.5; see also WEST, 2011a, fig. 19.3). Hydrodynamics, tides, waves, or currents may have removed some of this loose sediment and created ephemeral cryptic habitats for encrusters on the undersides of the chaetetids (Fig. 29–30; JAMESON, 1980; SUCHY

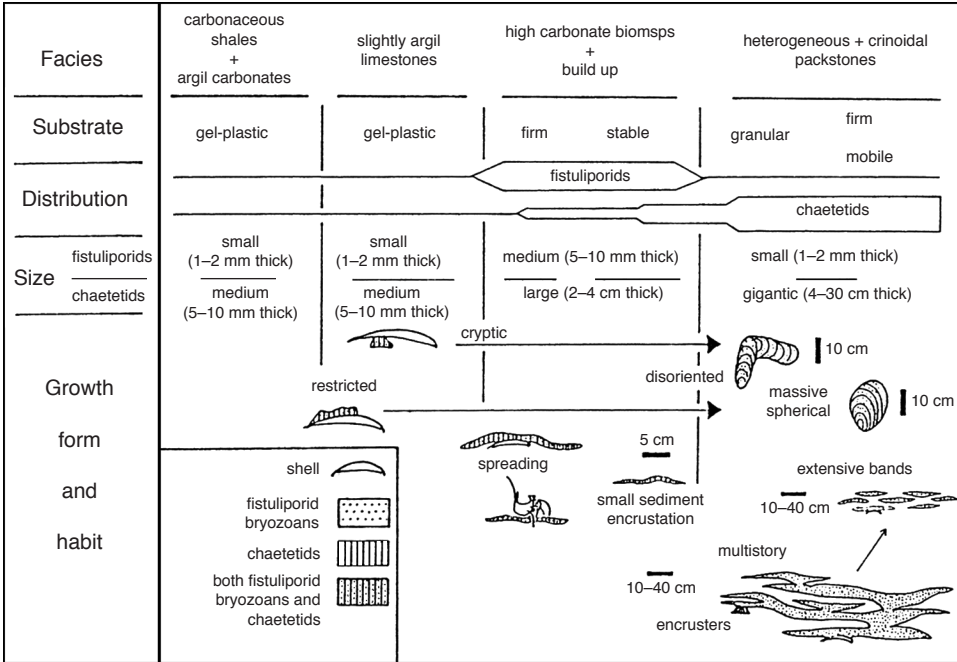


FIG. 27. Relationships between four types of substrates (gel, plastic, firm, and granular) and growth form or habit, size, distribution, and lithofacies, for chaetetids and fistuliporid bryozoans; note that both bryozoans and chaetetids occur as spreading forms in plastic to firm substrates, where competition 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).

& 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 (WEST, 2011a, fig. 24). 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 RÜTZLER (1965) have suggested spatial competition between algae and some



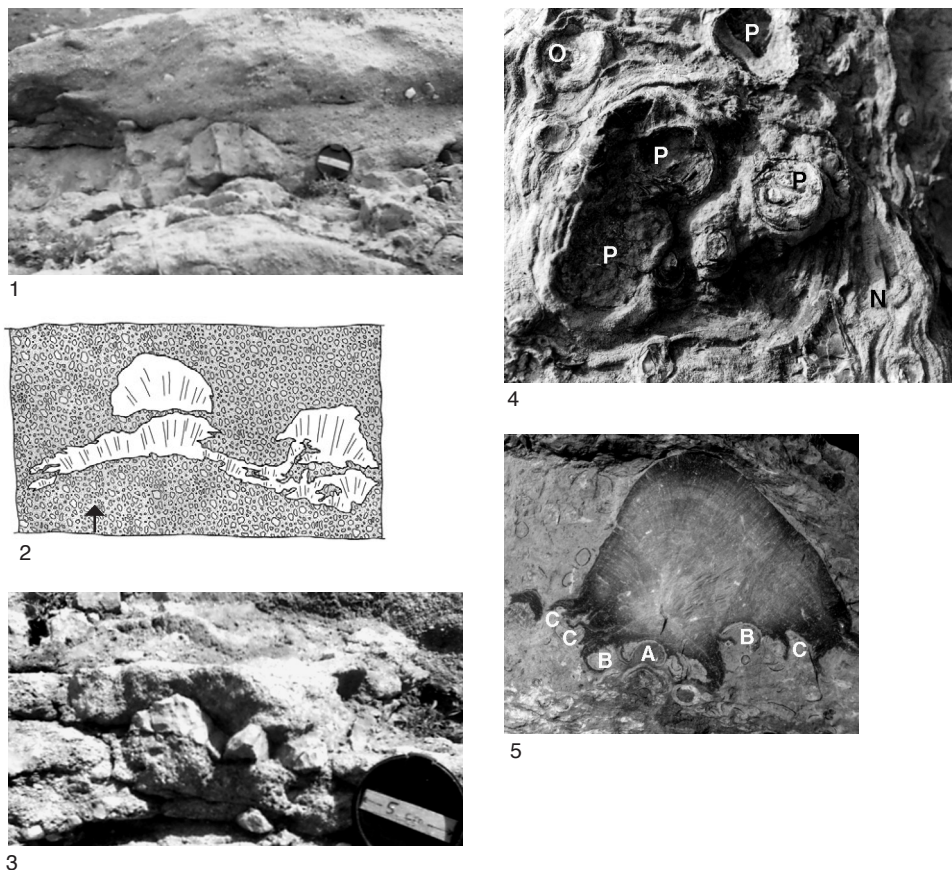


FIG. 28. Substrates and relationships, Pennsylvanian, upper Carboniferous; 1, laminar to low domical chaetetids on an arkose substrate, Resolution Member, Minturn Formation, Resolution Mountain near Camp Hale, Eagle County, Colorado,  $\times 0.09$  (new); 2, interpretative sketch of view 1; note the separation (fission) into two low domical chaetetids, *arrow*, stratigraphic up direction,  $\times 0.09$  (new); 3, closer view of low domical and laminar chaetetids on an arkose substrate, Resolution Member, Minturn Formation, Resolution Mountain, Camp Hale, Eagle County, Colorado,  $\times 0.14$  (new); 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,  $\times 0.3$  (new); 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,  $\times 0.16$  (adapted from Voegeli, 1992, p. 141, fig. 32; courtesy of the author and Kansas State University).

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 spatial competition with other, nonphotosynthesizing, sessile benthos: sponges,

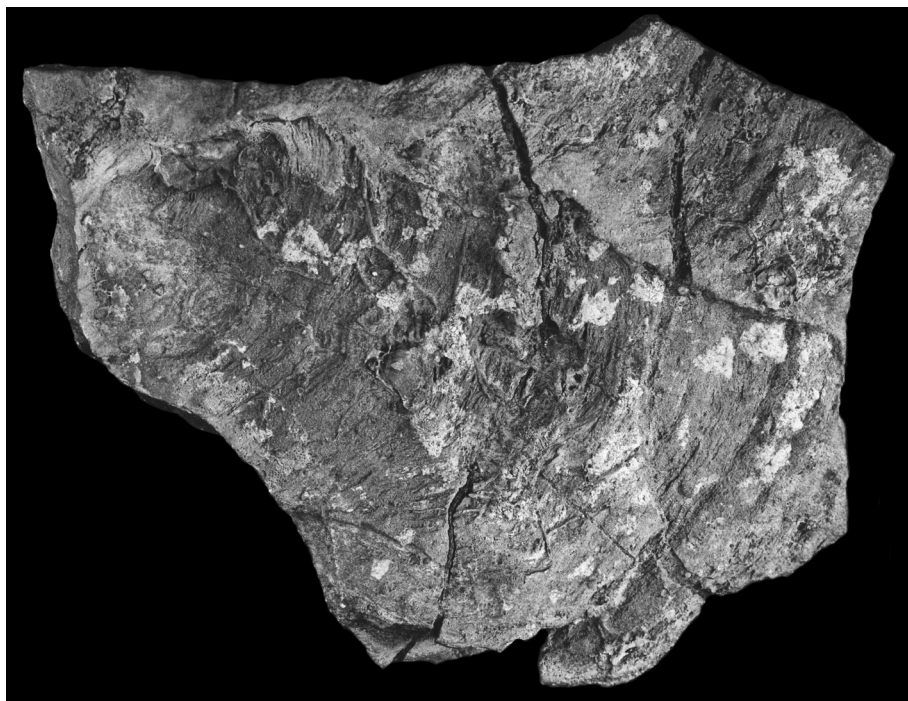


FIG. 29. Cryptic biota on part of the lower surface, the underside, of a laminar chaetetid, Pennsylvanian, upper Carboniferous, Coal City Limestone Member, Pawnee Limestone, Appanoose County, Iowa,  $\times 0.7$  (adapted from Suchy & West, 1988, p. 407, fig.2A; courtesy of the authors and the Society for Sedimentary Geology).

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. 31–34). 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. 33.2; 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. 34; FAGERSTROM & others, 2000).

Other types of live-live interactions between clonal marine invertebrates are fission and fusion. WEST and others (2011) and FAGERSTROM and WEST (2011) recognized three types of fusion in clonal invertebrates. These are: (1) interclone fusion of two or more clones, each grown from its own

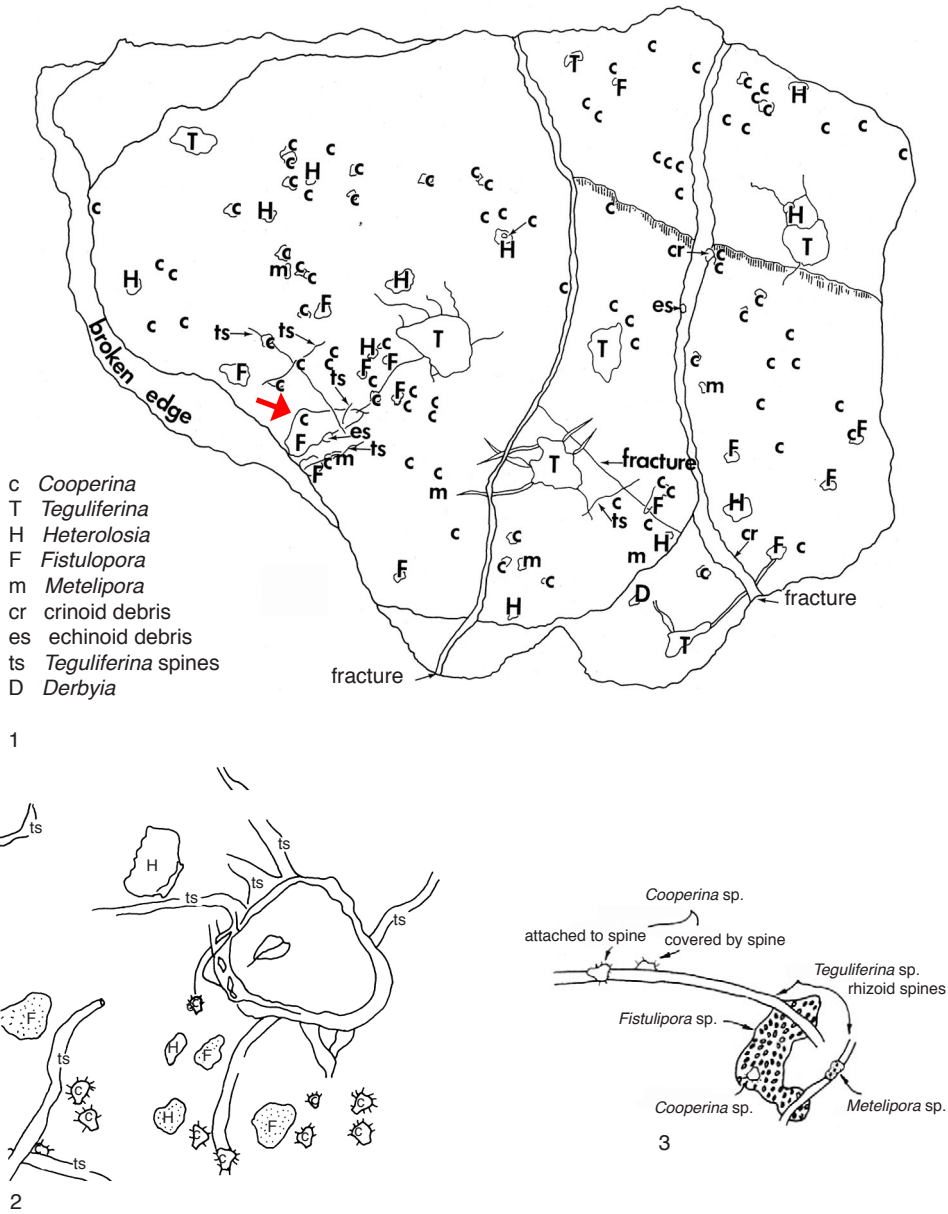


FIG. 30. Lamellar chaetetid and cryptic biota; 1, map of Figure 29 showing the location and identity of the cryptic biota. Because of their small size, the location of worm tubes, *Spirorbis*, and foraminiferid *Tetrataxis* are omitted,  $\times 0.8$  (adapted from Suchy & West, 1988, p. 407, fig. 2B); 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,  $\times 1.85$  (new); 3, generalized sketch of the area designated by the red 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).



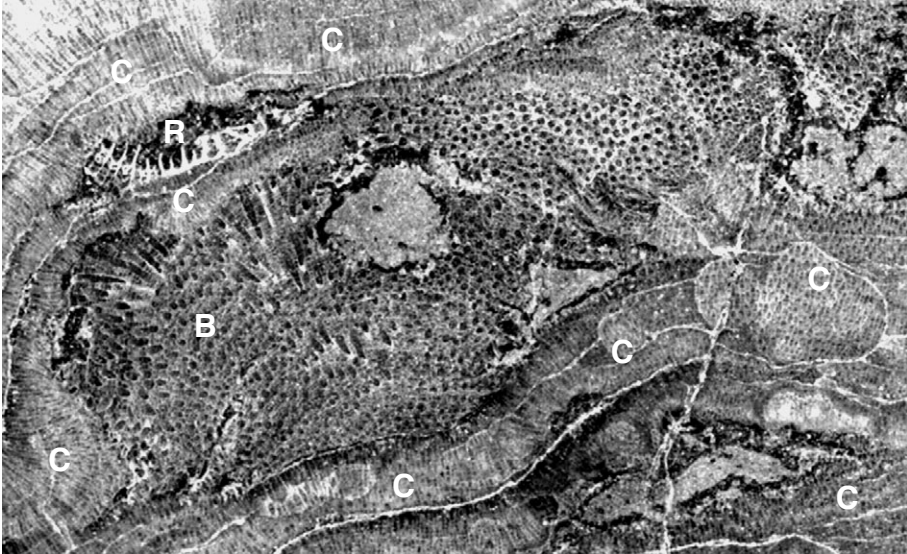


FIG. 31. Inferred live-live spatial competition between chaetetids (C), fistuliporid bryozoans (B), and a solitary rugose coral (R), Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,  $\times 3$  (new).

larva; (2) intracclone 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, or corallite) of the same, or a different clone. Both fission and fusion have been recognized in fossil chaetetids (Fig. 35). Another example of fission is shown in Figure 28.1–28.2. Intra-clonal fusion in fossil chaetetids is more easily recognized (Fig. 22.1, Fig. 35). Recognition of interclonal fusion is often more difficult, if not impossible, because it requires the identification of the points of origin of the two clones (Fig. 22.2).

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 discussion of growth rates in WEST, 2011b), 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. 36–38) 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. 33.2) or the encruster may die as a result of disease, predation, smothering (burial by sediment), and/or exposure (erosion). Evidence of the cause(s)

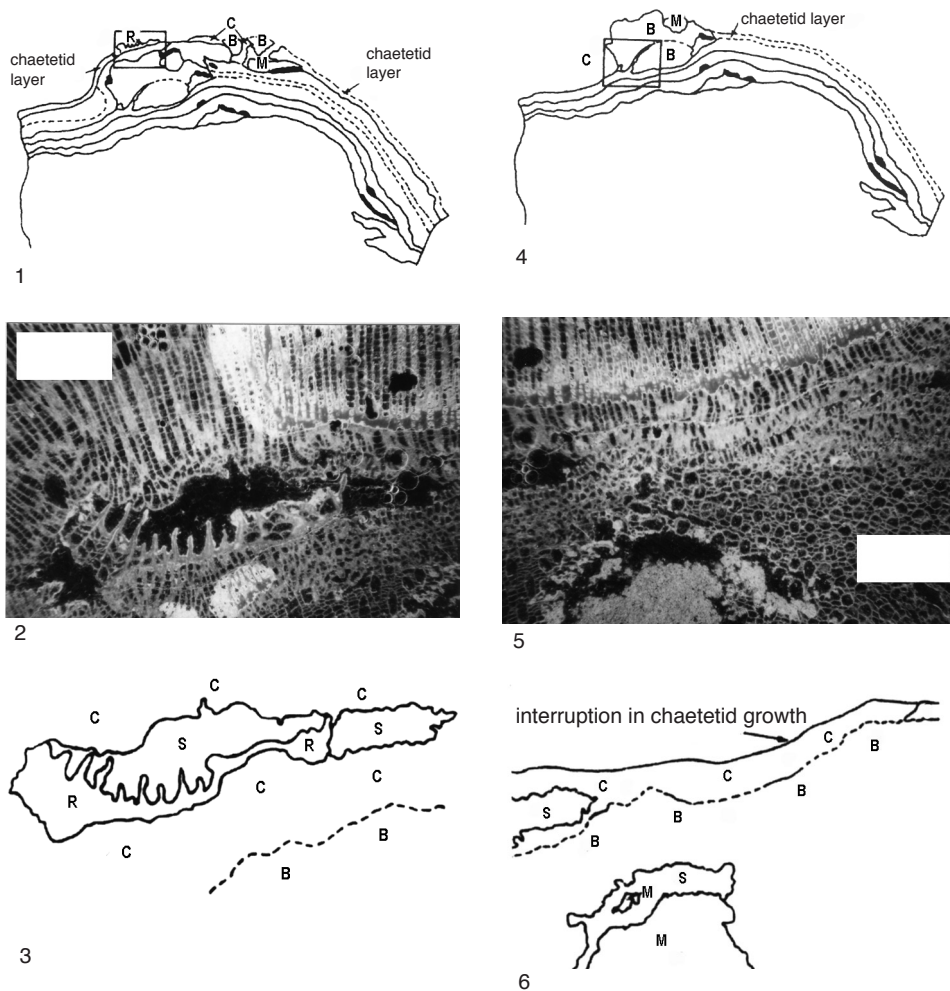
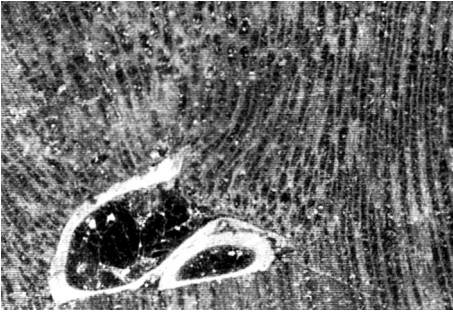


FIG. 32. Chaetetids and inferred live-live spatial competition, Pennsylvanian, upper Carboniferous, Higginville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; 1, interpretative sketch of the upper part of the area in Figure 31 (*R* denotes the position of solitary rugose coral) showing the interaction between the chaetetid and the coral and the chaetetid (*C*) and the fistuliporid bryozoan (*B*); *M*, matrix,  $\times 0.55$  (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,  $\times 5.25$  (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,  $\times 0.55$  (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,  $\times 5.25$  (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.).

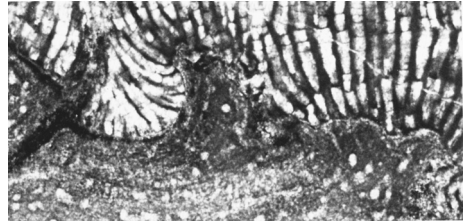




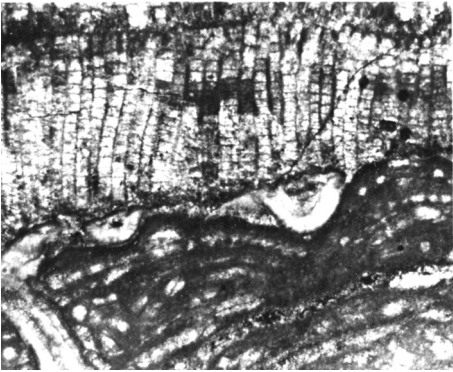
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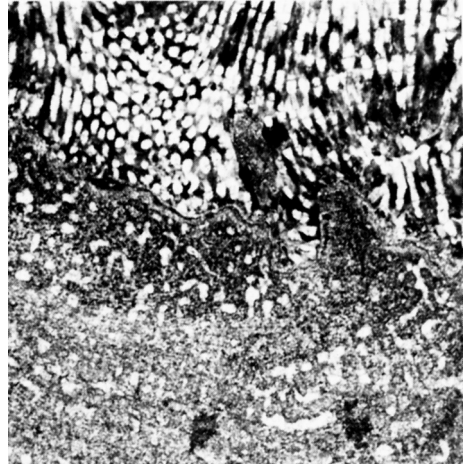
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FIG. 33. (For explanation, see facing page).



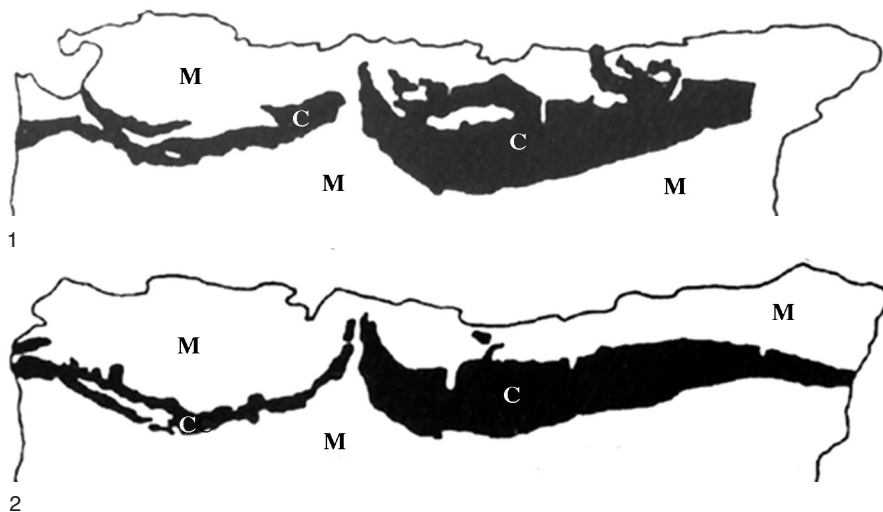


FIG. 34. Inferred live-live stand-off interaction between chaetetids; 1, stand-off interaction between chaetetid clones (C, black areas), Pennsylvanian, upper Carboniferous, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas; M, matrix,  $\times 0.5$  (adapted from Fagerstrom & 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, Pennsylvanian, upper Carboniferous, Myrick Station Limestone Member, Pawnee Limestone, Bourbon County, Kansas; M, matrix (slab 2 is 2.5 cm thick),  $\times 0.5$  (adapted from Fagerstrom & others, 2000, p. 12, fig. 1.D, slab 2, surface c; figures courtesy of the authors and Springer-Verlag GmbH & Co.).

of death in 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 WEST, 2011a, fig. 31).

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/

FIG. 33. 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, Brigantian, upper Viséan, lower Carboniferous, A. Orionastraea Band, Bradwell Dale, Derbyshire, United Kingdom,  $\times 3.6$  (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,  $\times 9$  (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 *Salairrella*, Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia, with the chaetetid progressively overwhelming the stromatoporoid,  $\times 8$  (adapted from Zhen & West, 1997, p. 275, fig. 3.E; courtesy of the authors and *Alcheringa*); 4, distorted final growth surface of the stromatoporoid *Salairrella* in an inferred live-live interaction with the overlying chaetetid, Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia,  $\times 10$  (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, Givetian, Middle Devonian, Burdekin Formation, Regan's Quarry, Reid Gap, northern Queensland, Australia,  $\times 8$  (adapted from Zhen & West, 1997, p. 276, fig. 4.A; courtesy of the authors and *Alcheringa*).

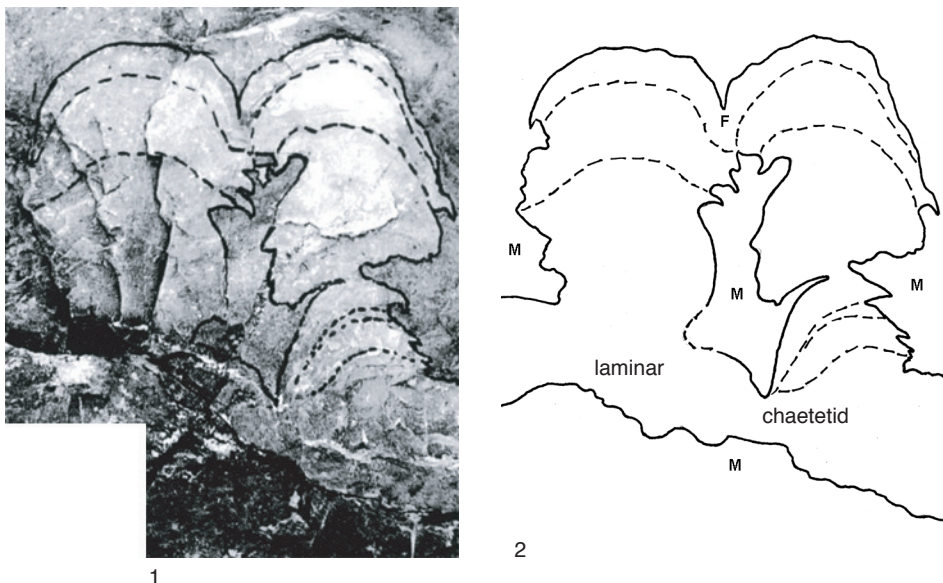


FIG. 35. Fusion and rejuvenation in chaetetids; 1, fission and fusion in a chaetetid that began as a laminar form, followed by fission and growth into two columnar chaetetids with ragged margins (*dashed lines* are interruption partings) that fused, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Labette County, Kansas,  $\times 0.15$  (new); 2, interpretive sketch of view 1; *M*, matrix; *F*, plane of fusion,  $\times 0.15$  (new).

or other sponges (TOPSENT, 1928; RÜTZLER, 1970). This latter condition is due to the presence of a well-developed spicular layer 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 discussion of chimneys in WEST, 2011b). 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

FIG. 36. Associated encrusters and successive overgrowths, Pennsylvanian, upper Carboniferous; 1, interpretive sketch of the polished surface of a slab, Akiyoshi Limestone, Akiyoshi-dai, Japan, showing associated encrusters and successive overgrowths,  $\times 0.35$  (adapted from Sugiyama & Nagai, 1990, p. 20, fig. 7; courtesy of the authors and Akiyoshi-dai Museum of Natural History); 2, vertical section of a laminar to low domical chaetetid that was overgrown by *Multiithecopora*, 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,  $\times 0.3$  (new); 3, weathered vertical section of a laminar chaetetid overgrown by a dome-shaped mass of *Multiithecopora*, 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,  $\times 0.14$  (new); 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,  $\times 1.7$  (new).

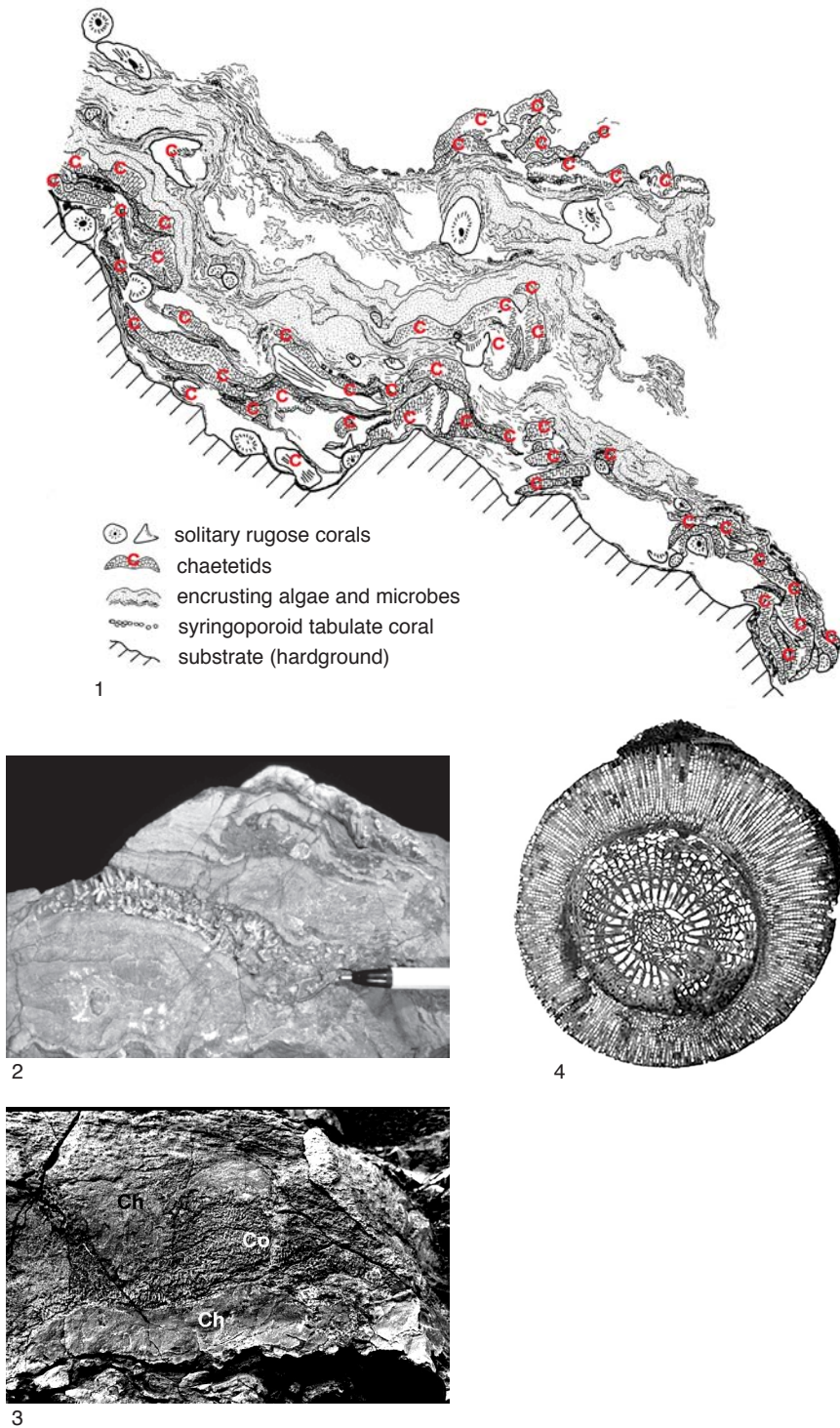


FIG. 36. (For explanation, see facing page).



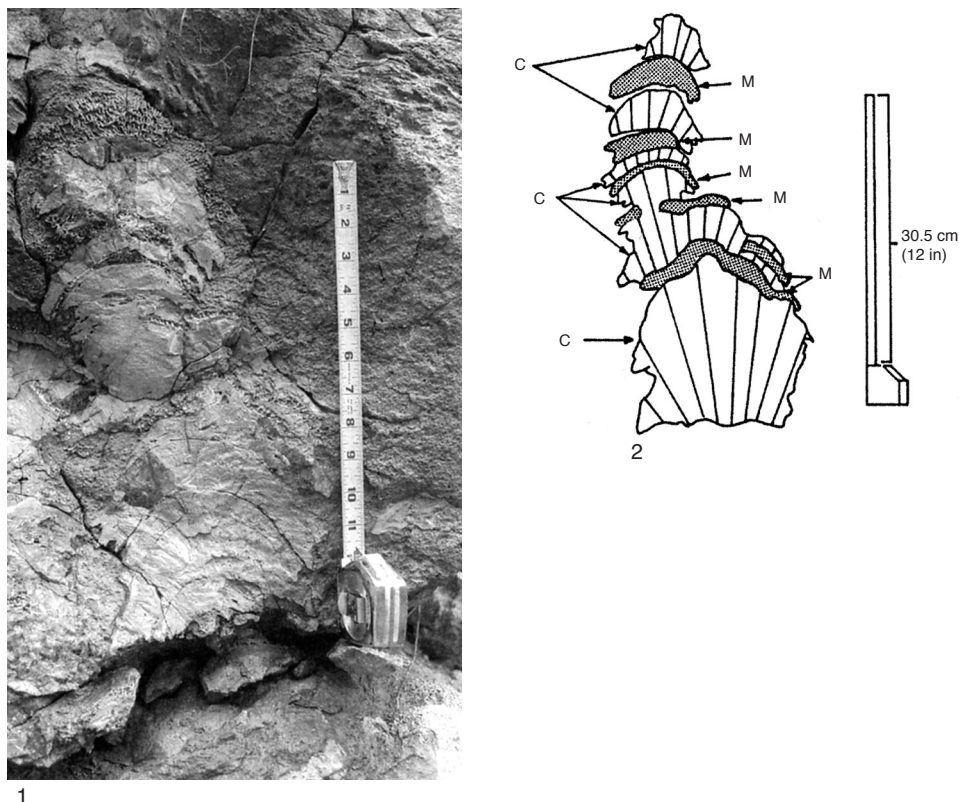
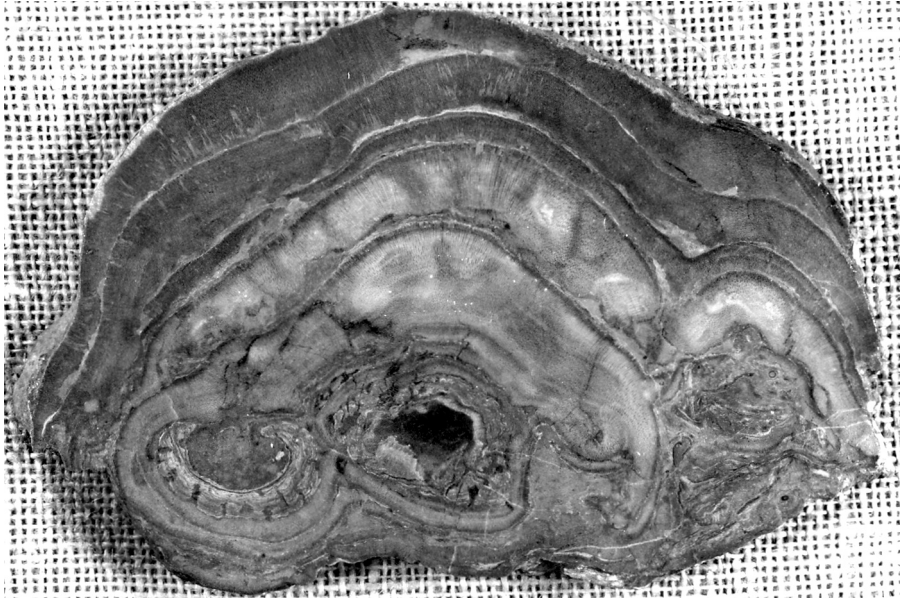


FIG. 37. Further examples of associated encrusters and successive overgrowths; 1, weathered vertical surface of a succession of chaetetid and *Multiithecopora* overgrowths in a fusulinid packstone, Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,  $\times 0.17$ ; 2, interpretative sketch of view 1, C, chaetetid, M, *Multiithecopora*,  $\times 0.12$  (adapted from Suchy & West, 2001, p. 438, fig. 11C; courtesy of the authors and the Society for Sedimentary Geology).

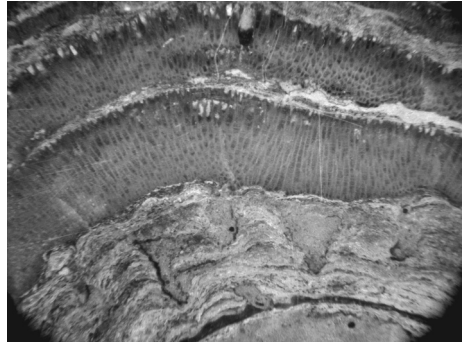
FIG. 38. Successive events preserved in a low domical chaetetid, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; 1, complex history of a low domical chaetetid revealed by a series of laminar chaetetids interrupted by sediment influx and other encrusters (algal-microbial mats) and boring organisms,  $\times 0.6$  (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  $180^\circ$  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,  $\times 1.4$ ; 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,  $\times 2.6$ ; 4, enlarged view of the upper right quarter of view 2, showing the borings in the algal-microbial encrustation on the brachiopod valve,  $\times 3$  (new).



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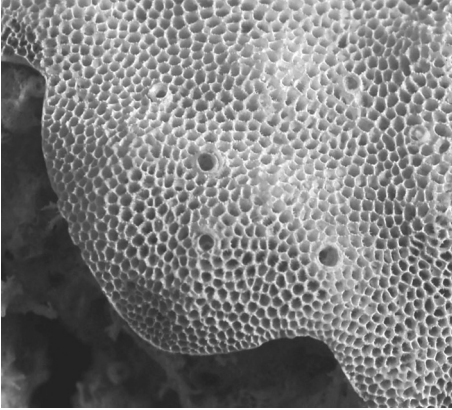
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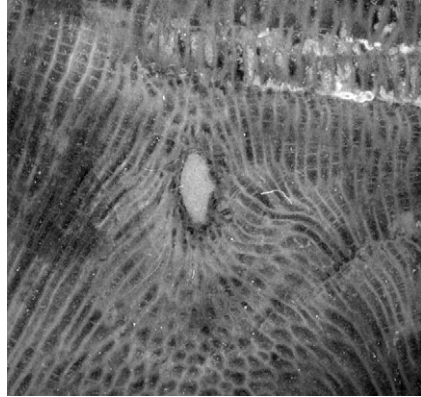
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FIG. 38. (For explanation, see facing page).

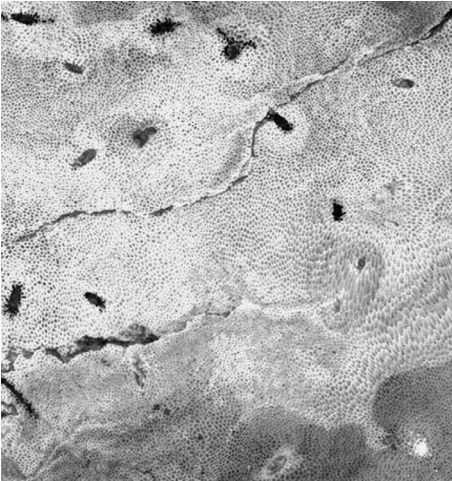




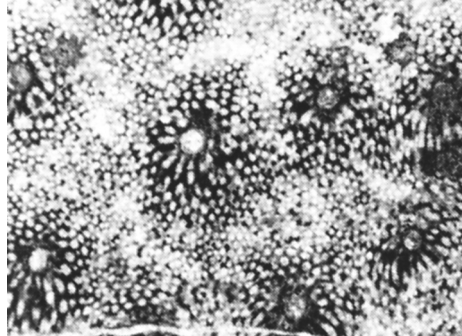
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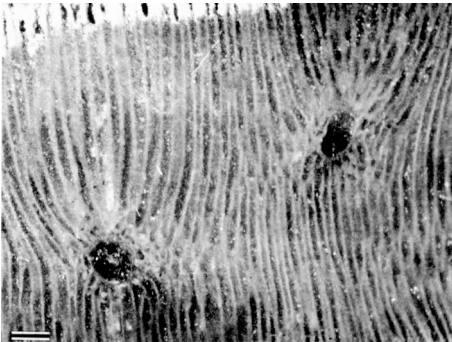
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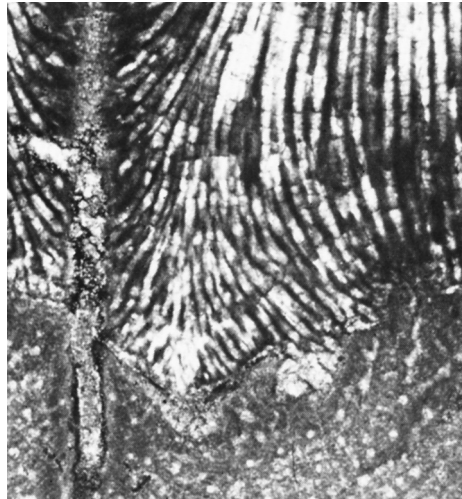
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FIG. 39. (For explanation, see facing page).



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 result of polychaete worms, zoanthideans (soft corals), or clinoid (excavating) sponges (Fig. 39.1). 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. 39.2–39.6). 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 nature of the truncation of their tubules, suggest the activity of boring organisms (Fig. 40.1–40.3). 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. 40.2) are inferred to be worm borings: a polychaete and *Polypora*-type worm, respectively; *Rogerella* and *Zapfella* are the borings of acrothoracican barnacles (Fig. 40.3; WEST & CLARK, 1984). Acrothoracican borings have also been recognized in ?*Coelocladia*, a fossil demosponge (GUNDRUM, 1979). Shapes similar to inferred acrothoracican barnacle borings also occur in living specimens of *Acanthochaetetes* sp. (Fig. 40.4). 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. 40.5–40.6).

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 nektonic invertebrates occur with them (Table 3). 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,

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FIG. 39. 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,  $\times 3$  (new); 2, inferred worm tubes and/or possible borings in the upper surface of a chaetetid skeleton, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 7.5$  (new); 3, polished vertical section of inferred worm tubes in a chaetetid skeleton, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; note distortion of tubules adjacent to the spar-filled holes,  $\times 5$  (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, Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; note the distorted tubules adjacent to the micrite-filled hole,  $\times 5.3$  (new); 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,  $\times 7.5$  (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 *Salairrella* into the skeleton of the chaetetid, Givetian, Middle Devonian, Burdekin Formation, northern Queensland, Australia; note distortion of both skeletons,  $\times 10$  (adapted from Zhen & West, 1997, p. 275, fig. 3C; courtesy of the authors and *Alcheringa*).

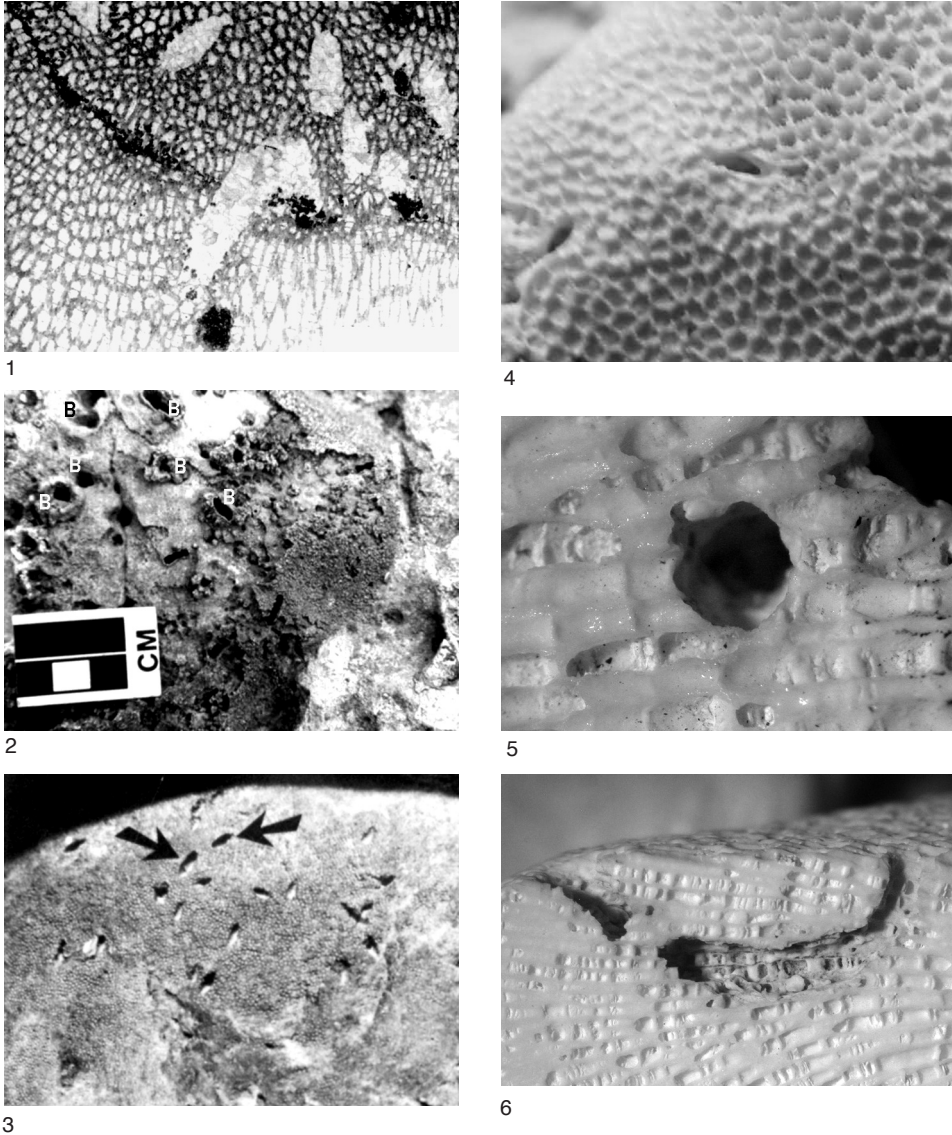


FIG. 40. Inferred borings in chaetetid skeletons; 1, Transverse to oblique thin section of chaetetid from the Pennsylvanian, upper Carboniferous, Piedraslungas Limestone, Piedraslungas, Cantabrian Mountains, Spain; note the lack of tubule distortion adjacent to the spar-filled holes,  $\times 6$  (adapted 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 B* and one *black B*, similar to those described as *Trypanites* and *Caulostrepsis*, Pennsylvanian, upper Carboniferous, Blackjack Creek Limestone Member, Fort Scott Limestone, Crawford County, Kansas, scale in cm and inches (new); 3, upper surface of a domical chaetetid with teardrop-shaped holes (*black arrows*) interpreted as acrothoracican barnacle borings (*Rogerella* or *Zapfella*), Pennsylvanian, upper Carboniferous, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 1.5$  (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,  $\times 7$  (new); 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,  $\times 17$  (new); 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,  $\times 3.7$  (new).

TABLE 3. Invertebrates associated with chaetetid reef mounds. the first letter in hyphenated entries refers to whether it is epifaunal (*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).

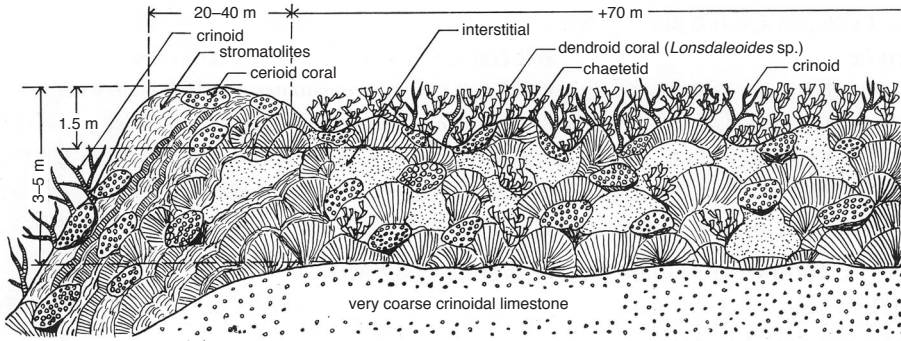
Organisms	Inferred ecological niche	Conspicuous	Present
Phylloid Algae	P	X	
Algal-microbial mats	P	X	
Foraminiferids			
Fusulinids	E-F-D?	X	
<i>Tetrataxis</i>	E-A-S?		X
<i>Globovalvulina</i>	E-F-D?		X
<i>Endothyra</i>	E-F-D?		X
Sponges			
<i>Girtyocoelia</i>	E-A-S		X
Corals			
<i>Lophophylidium</i>	E-A-S		X
<i>Multithecopora</i>	E-A-S		X
Bryozoans	E-A-S		X
Brachiopods			
<i>Composita</i>	E-A-S	X	
<i>Crurithyris</i>	E-A-S		X
<i>Hustedia</i>	E-A-S		X
<i>Lingula</i>	I-A-S		X
<i>Mesolobus</i>	E-F-S		X
<i>Neochonetes</i>	E-F-S		X
<i>Neospirifera</i>	E-F-S		X
Productids	E-A/F-S	X	
Mollusks			
Bivalves			
<i>Aviculopecten</i>	E-F-S		X
<i>Edmondia</i>	E-F-S		X
Gastropods			
<i>Bellerophontids</i>	E-V-D		X
Low-spired	E-V-D/C		X
High-spired	E-V-D/C		X
<i>Omphaiotrocus</i>	E-V-D		X
<i>Sstraparollus</i>	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		

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 3 (foraminiferids are omitted from the following percentage calculations because their ecological niche is queried), 23 of 26 taxa (88%) are epifaunal,

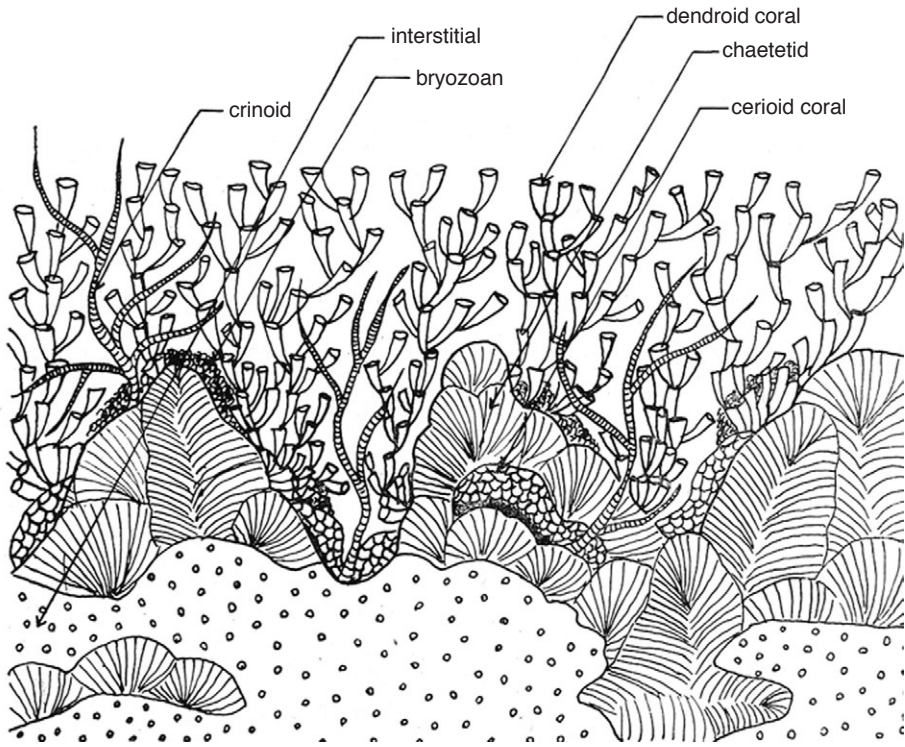
17 of 26 (65%) are attached or free living, and 17 of 26 (65%) are suspension feeders.

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





1



2

FIG. 41. 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,  $\times 0.005$  (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).

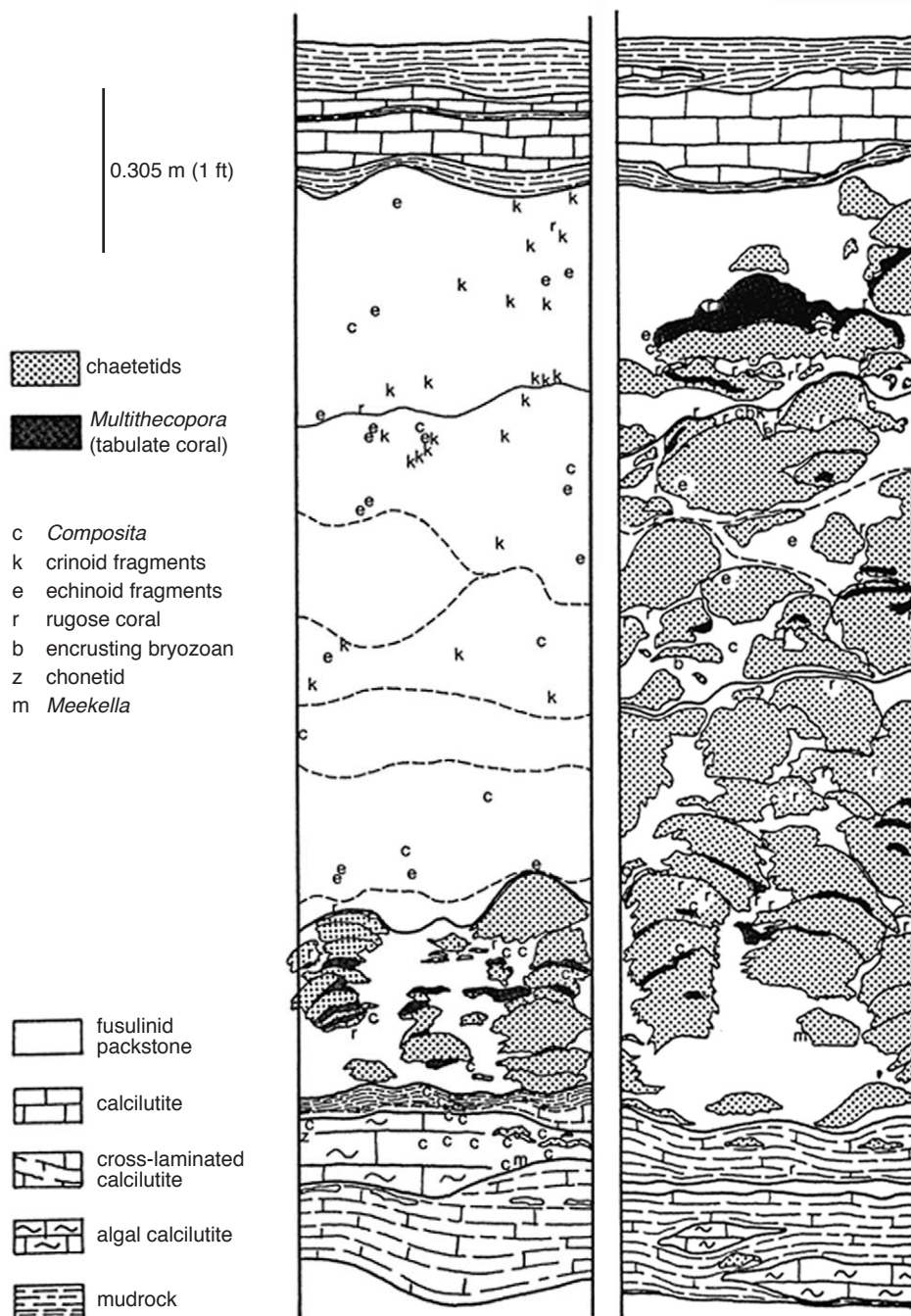


FIG. 42. Interpretative diagram of chaetetids, associated organisms, and lithologies at two different vertical sequences in a chaetetid reef mound exposed in a quarry, Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas (adapted from Suchy & West, 2001, p. 440, fig. 12; courtesy of the authors and the Society for Sedimentary Geology).



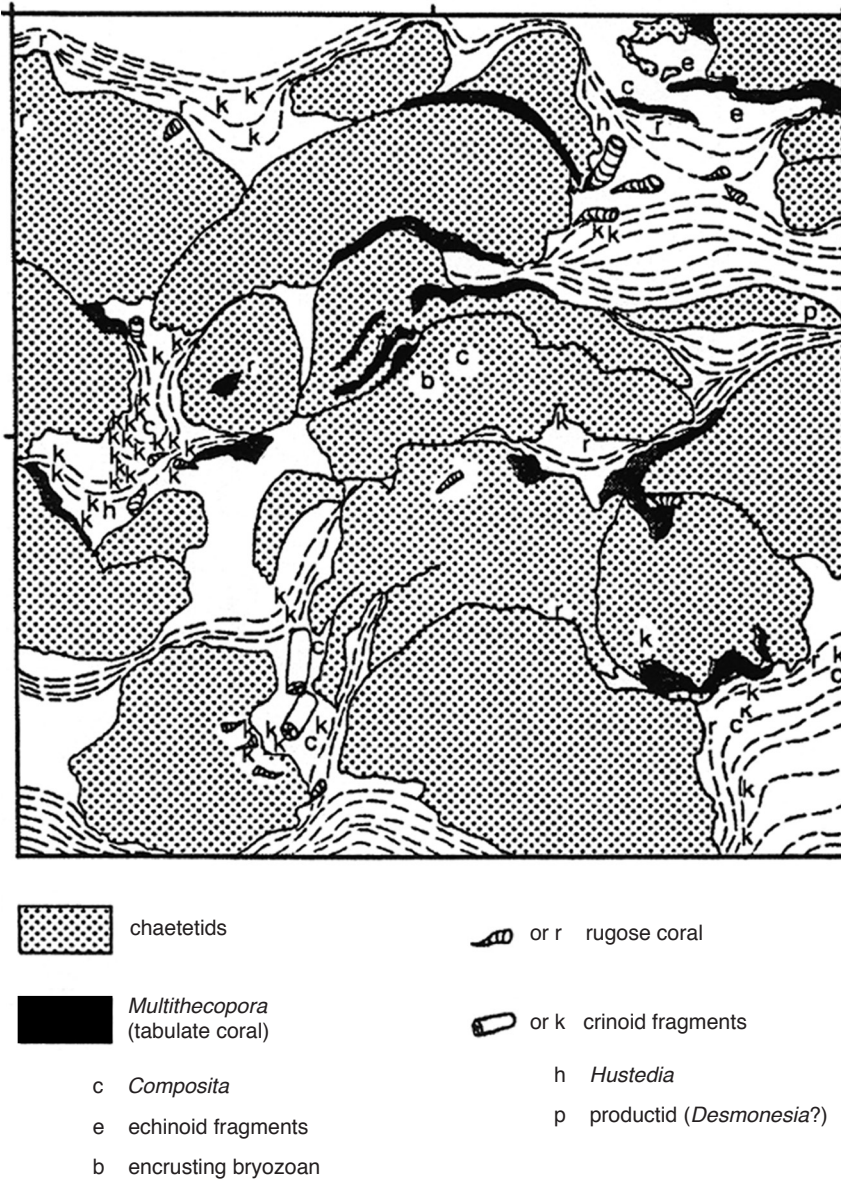


FIG. 43. Distribution of organisms in a 0.6 m<sup>2</sup> (2 foot<sup>2</sup>) area on a vertical surface in a chaetetid reef mound exposed in a quarry, Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; transportation of the crinoid and 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. X0.18 (adapted from Suchy & West, 2001, p. 441, fig. 13; courtesy of the authors and the Society for Sedimentary Geology).

fraction of available organics that is poorly used by other filter (suspension) feeders (SARA & VACELET, 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. 41) illustrate the occurrence of some of these suspension-feeders in a Carboniferous (Pennsylvanian) chaetetid reef. The tabulate coral,



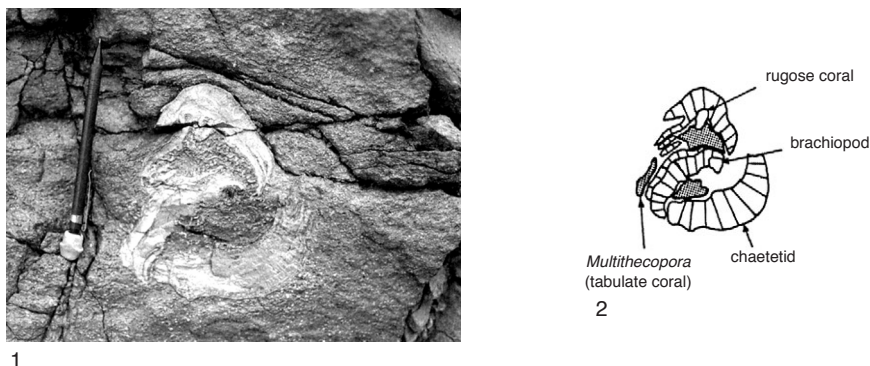


FIG. 44. Details of the relationships between chaetetids, associated organisms, and lithologies in a chaetetid reef mound exposed in a quarry, Pennsylvanian, upper Carboniferous, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas; 1, relationship between three episodes of chaetetid growth and associated corals and a brachiopod on a weathered vertical surface, matrix is a fusulinid wackestone,  $\times 0.2$  (adapted from Suchy & West, 2001, p. 438, fig. 11B, in part); 2, interpretative sketch of view 1,  $\times 0.1$  (adapted from Suchy & West, 2001, p. 438, fig. 11B, in part; figures courtesy of the authors and the Society for Sedimentary Geology).

*Multithecopora*, encrusting bryozoans, most solitary rugose corals, and some articulate brachiopods are in life position (Fig. 42–44). 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. 42); 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. 44.1–44.2) and/or columnar structures (Fig. 37). Commonly, *Multithecopora* encrustations are thin (Fig. 36.2, 45.1–45.2), but they also form domical structures (Fig. 36.3).

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. 11, Fig. 25.1, Fig. 43) or might have served as substrates for chaetetids and be completely covered by the sponge skeleton (Fig. 23.4, Fig. 36.4). JAMESON (1980, p. 358) reported solitary rugose corals attached to chaetetids from

the Petershill Formation (lower Carboniferous) of Scotland. Some solitary rugose corals attached to the sheltered undersides of laminar chaetetids and grew around the edges and upward (Fig 45.3–45.4).

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 *Heteralosia*) appeared to favor these cryptic areas (Fig. 29–30, Fig. 45.5–45.7). From the upper 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 (lower Carboniferous) 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

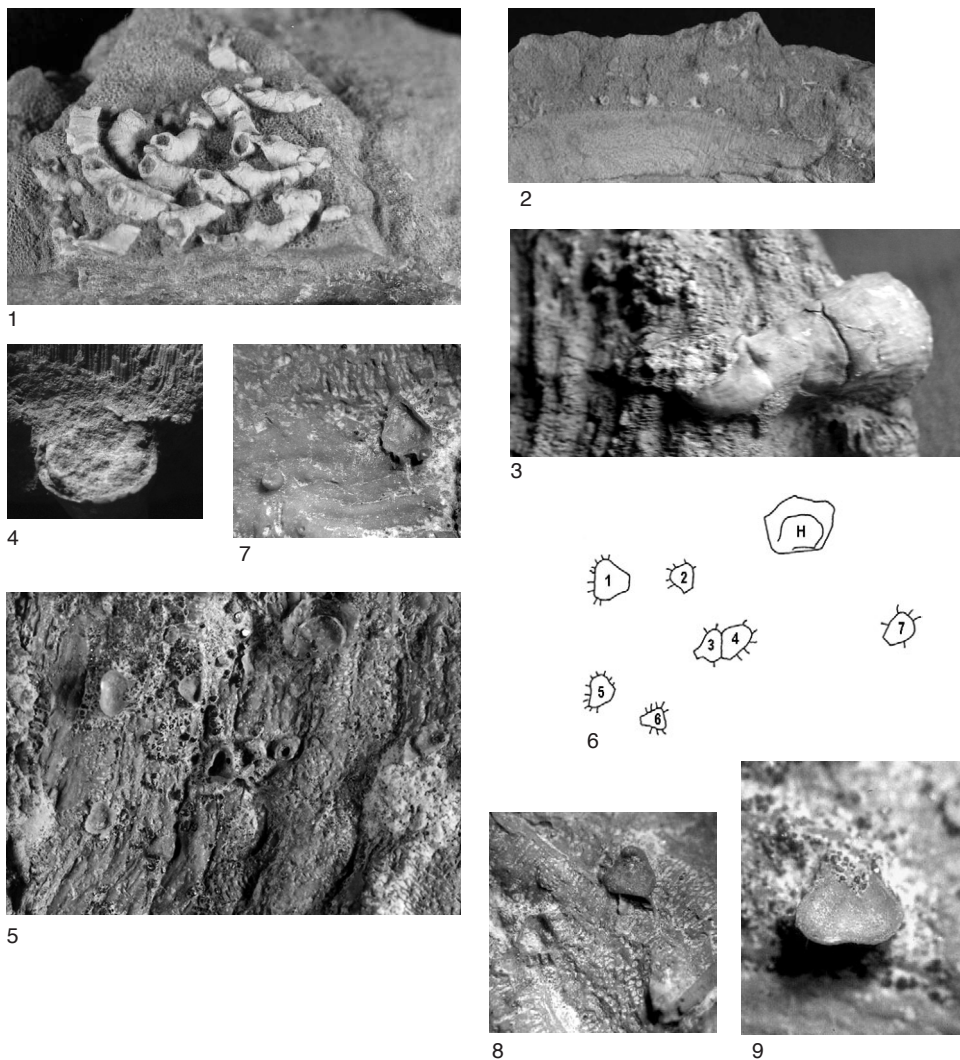


FIG. 45. Details of some specific invertebrate fossils associated with chaetetids, Pennsylvanian, upper Carboniferous; 1, upper surface of the tabulate coral *Multithecopora* sp. attached to the upper surface of a chaetetid, Higginsville Limestone Member, Fort Scott Limestone, Crawford County, Kansas,  $\times 2$  (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,  $\times 0.85$  (new); 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,  $\times 1.7$  (new); 4, a lateral view looking into the calyx of the solitary rugose coral in view 3,  $\times 1.25$  (new); 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,  $\times 2.7$  (new); 6, interpretative sketch of view 5, showing the spatial distribution of *Heterolosia* sp. (H) and seven numbered specimens of *Cooperina* sp.,  $\times 2.4$  (new); 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,  $\times 7$  (new); 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,  $\times 7$  (new); 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,  $\times 10$  (new).

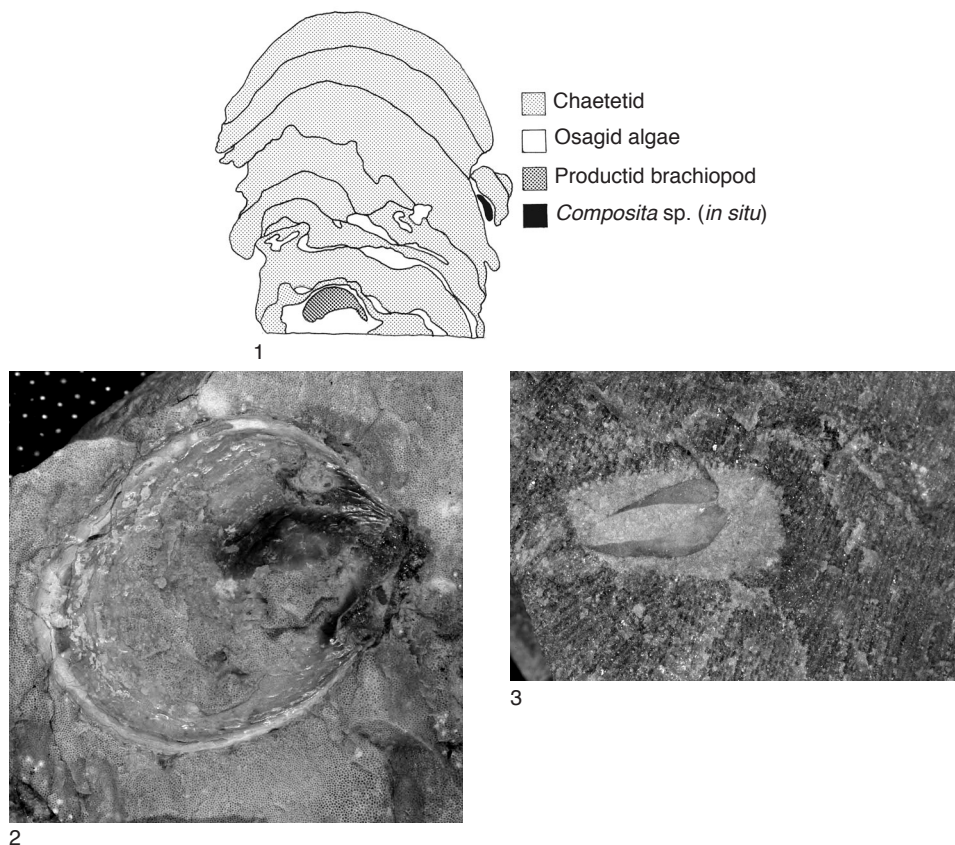


FIG. 46. Details of some further specific invertebrate fossils associated with chaetetids from the Pennsylvanian, upper Carboniferous; 1, high domical chaetetid with ragged margins, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas; initial laminar chaetetid encrusted an algal-microbially (osagid) encrusted hydrodynamically unstable productid valve; note the *in situ* *Composita* sp. beneath a now-broken overhanging laminae,  $\times 0.3$  (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,  $\times 1.15$  (new); 3, butterflyed, smooth-valved bivalve, probably *Edmondia*, in a matrix-filled cavity within a domical chaetetid, Amoret Limestone Member, Altamont Limestone, Montgomery County, Kansas,  $\times 1.9$  (new).

to the undersides of some extant hypercalcified demosponges (JACKSON, 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. 42–44, Fig. 46.1). The attachment of terebratuliform brachiopods *Composita* and *Dielasma* to lower Carbonif-

erous chaetetids has also been documented (JAMESON, 1980, p. 355).

Encrusting bryozoans *Fistulipora* and *Metelipora* occur in these cryptic niches (Fig. 29–30) and occasionally on the upper surfaces of chaetetids. *Fistuliporid* bryozoans are commonly attached to both the upper and lower surfaces of some lower Carboniferous chaetetids (JAMESON, 1980, p. 353). Some *Fistulipora* and *Tabulopora*(?) are reported as being chaetetid competi-



tors (Fig. 31–33.1; FAGERSTROM & others, 2000). Figure 27 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 *Coelocladia*.

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. 46.2). Also in a domical chaetetid are the smooth, butterflyed 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. 46.3).

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 3). 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.

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