PALEOGEOGRAPHY AND BIOSTRATIGRAPHY OF THE HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

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INTRODUCTION

Hypercalcified sponges with a chaetetid skeleton, both fossil and extant, are relatively inconspicuous components of the marine biota. Only a few extant hypercalcified sponges are known, and they occur mostly along bathyal cliffs and in dark littoral caves (see Living Hypercalcified Sponges, p. 1–14). Commonly, the habitats of the extant taxa are associated with reefal environments in tropical or subtropical latitudes in the Indo-Pacific and West Atlantic zones. The general distribution of the three extant hypercalcified genera with a chaetetid skeleton are as follows: *Merlia*, circumtropical and warm temperate latitudes (Madeira, Mediterranean); *Ceratoporella*, tropical latitudes (Caribbean); and *Acanthochaetetes*: tropical latitudes (South Pacific) (Soest & others, 2005). In tropical latitudes, the depth distribution is in the upper bathyal zone (deep forereef), usually above the thermocline, with *Ceratoporella nicholsoni* being the main reef builder between 70 and 105 m depth (Lang, Hartman, & Land, 1975), and then the development of scleractinian coral reefs becomes dominant in the shallower water above. Fossil chaetetids, on the other hand, appear to have thrived in more open marine environments of the shallow continental shelf and were conspicuous reef builders during the Carboniferous.

PALEOBIOGEOGRAPHY

The geographic distribution of fossil chaetetids is not unlike that of extant hypercalcified demosponges with a chaetetid skeleton: it is essentially tropical (Fagerstrom, 1984). Data on the temporal and spatial distribution of reefs during the Phanerozoic in which chaetetids were listed as a reef builders, i.e., chaetetid reefs and hypercalcified demosponges including chaetetids, are shown in Table 26. It also lists data from 37 different stratigraphic intervals (series and stages) that might, on careful study, contain chaetetids, namely hypercalcified demosponges that are unreported or unknown, indeterminate, undifferentiated, and miscellaneous. The latitudinal belt (whether tropical or temperate, and in some cases both) for these series and stages is shown in Table 27. Hypercalcified demosponges, including chaetetids, are known from five stages in the Carboniferous: Visean, Serpukhovian, Bashkirian, Moscovian, and Kasimovian (Fig. 113–115), but they are most abundant in the Bashkirian and Moscovian. Permian chaetetid reefs are only known from the Guadalupian and Lopingian (Fig. 115–117). Hypercalcified demosponges, including chaetetids, are reported from two Jurassic stages, Oxfordian and Kimmeridgian (Fig. 118). All of these occurrences are located in tropical paleolatitudes, except two, which are questionably located in the northern temperate belt (Iran and Japan) during the Jurassic (Oxfordian and Kimmeridgian) (Fig. 113–118). Hypercalcified demosponges that may, on careful study, include chaetetids, are listed as reef builders for six sites, five of which are in tropical paleolatitudes (Table 27). Unreported reef builders, and those listed as unknown, indeterminate, undifferentiated, or miscellaneous at the remaining sites in different stratigraphic intervals could, on careful study, contain chaetetids; most of these are in the tropics (Table 27).

Although information on the microstructure and spicules, or spicule pseudomorphs, is currently lacking, there are a number of described taxa that have a chaetetid skeleton and could be hypercalcified

Table 26. Temporal and spatial distribution of Phanerozoic reefs that contain, or could contain, chaetetids. Hypercalcified demosponges, presumed chaetetids, occur in other stratigraphic intervals as noted in the text; *, only the latitudinal belt (Temperate or Tropical) containing the majority of the occurrences and the general geographic localities of reef builders are indicated, after Kiessling, Flügel, and Golonka (2002), who listed the reef builders as unknown, undifferentiated, miscellaneous, indeterminate, or hypercalcified demosponges (coralline sponges); some were unreported; these five categories are included because chaetetids are, or could have been, involved in the reef building, and as such, suggest intervals and areas for future study; *italics,* stratigraphic intervals and geographic areas where chaetetids have been recognized as important contributors to reef building; #, reef builders are not reported, only whether reefs and reef mounds, mounds biostromes, or unknown buildups occurred (data from Kiessling, Flügel, & Golonka, 2002, and refer only to reefal occurrences).

System	Series and Stage	Reef builder*	Paleolatitude*	Paleogeography*
Neogene	**Pliocene** **Miocene** Tortonian	Unknown	Tropical	southern Spain and southern Italy
	Serravallian–Burdigalian	Unknown	Tropical	Indian Ocean, South Pacific, southeastern Asia, northern Mediterranean coast
Neogene–Paleogene	Aquitanian **Oligocene** Chattian	Unknown	Tropical	South Pacific, New Guinea
Paleogene	Rupelian	Unknown	Tropical	India, southeastern Asia
	Eocene Priabonian	Unknown	Tropical	eastern Africa
	Bartonian–Lutetian	Unknown	S. Temp.	northern Australia
	Bartonian–Lutetian	Unknown	Tropical	India
	Bartonian–Lutetian	Unknown	N. Temp.	Middle East
	Ypresian **Paleocene** Thanetian	Unknown	Tropical	South Africa
Cretaceous	**Upper** Campanian	Unknown	N. Temp.	Greece, Italy
	Lower Aptian–Valanginian	Indeterminate	30° N. Lat.	France, Austria, Germany, northern Italy, Slovenia
	Aptian–Valanginian	Indeterminate	S. Temp.	South Atlantic
	Valanginian	Indeterminate	N. Temp.	Crimea, Ukraine, Turkmenistan
	Valanginian	Indeterminate	Tropical	eastern U.S., Hungary, Spain, France, Italy, Tunisia, Portugal
Jurassic	Tithonian	Indeterminate	Tropical	eastern U.S., Hungary, Spain, France, Italy, Tunisia, Portugal
	Tithonian–Kimmeridgian	Hypercalcified demosponges *Kimmeridgian chaetetids*	Tropical	*Morocco, southern Europe, Saudi Arabia, Iran*
	Oxfordian–Callovian	Hypercalcified demosponges *Oxfordian chaetetids*	Tropical	Egypt, Israel, Lebanon *Mexico, southern Europe, Iran*
	Oxfordian–Callovian	Hypercalcified demosponges	N. Temp.?	Japan

TABLE 26 (*continued from facing page*).

Jurassic	Bathonian–Bajocian	Unknown	Tropical	Georges Bank, Atlantic
	Bathonian–Bajocian	Unknown	S. Temp.	Madagascar
Triassic	Rhaetian–Norian	Hypercalcified demosponges	Tropical	western Tethys, Middle East, southeastern Asia, Japan, western Canada, Alaska (USA)
	Carnian–Ladinian–Anisian	Hypercalcified demosponges	Tropical	essentially Tethyan
Permian	**Lopingian**	*Chaetetid reefs*	Tropical	*Pakistan, southern China*
	Guadalupian	*Chaetetid reefs*	Tropical	?Oman, Pakistan
	Cisuralian Kungurian–Artinskian–Sakmarian	Hypercalcified demosponges	Tropical	western Texas (USA), southern, western China
	Asselian	Hypercalcified demosponges	Tropical	Japan
Carboniferous (Pennsylvanian)	Gzhelian	Hypercalcified demosponges	Tropical	Japan
	Kasimovian–Moscovian–Bashkirian	*Hypercalcified demosponges, with chaetetid reef banks*	Tropical	*western United States, Japan, Kyrgyzstan*
Carboniferous (Mississippian)	Serpukhovian#	Unreported#	Tropical, S. Temp.	United States, Europe, Russia, Iran, China, Afghanistan, Japan
	Visean#	Unreported#	Tropical, S. Temp.	North America, Europe, Russia, Australia, Afghanistan, China, Japan
	Tournaisian#	Unreported#	Tropical, N. and S. Temp.	North America, Europe, Russia, Australia, Afghanistan
Devonian	**Upper** Famennian	Unknown	Tropical, N. and S. Temp.	Australia, Canada, China, Europe, Kazakhstan, Russia
	Frasnian	Unknown	Tropical	northwestern Canada, Russia, Polar Urals, Kazakhstan
	Middle Givetian	Unknown	Tropical	western and northwestern Canada, southern China, Polar Urals
	Lower Emsian–Pragian	Unknown	Tropical	western and northwestern Canada, Polar Urals
	Pragian Lochkovian	Unknown	Tropical	Arctic, northern Urals, Kazakhstan
Silurian	**Pridoli–Ludlow**	Unknown	Tropical	Kazakhstan, Russia
	Ludlow	Unknown	N. Temp.	Kazakhstan, Russia
	Wenlock	Unknown	Tropical	North America, Kazakhstan, Siberia
	Llandovery	Unknown	Tropical	Northwest Territories
Ordovician	**Upper Ordovician** Hirnantian–Katian	Unknown	Tropical	Yakutsk, Russia
	Katian–Sandbian	Miscellaneous	Tropical	northwestern and southeastern Kazakhstan, northwestern Canada
	Middle Ordovician Darriwilian	Undifferentiated	Tropical	North Korea, northern China
	Darriwilian	Undifferentiated	S. Temp.	North Korea, northern China
Ordovician–Cambrian	Tremadocian–Furongian	Unknown	Tropical	North America, Kyrgyzstan, Kazakhstan

Table 27. Summary of the paleolatitudinal position of reefs that contain, or could contain, chaetetids in the 37 different Phanerozoic stratigraphic intervals listed in Table 26. *Note that in some of the 37 stratigraphic intervals containing reefs there is some duplication (even in one interval, tripling) of the number of reefs (West, 2012c).

Reef builder	Number	Tropical	Temperate	30° N. Lat.
Chaetetid reefs	2	2	0	
Hypercalcified demosponges, including chaetetids	3	3	0	
Other hypercalcified demosponges	6	5	1	
*Unknown, indeterminate, undifferentiated, miscellaneous, or unreported reef builders	27	25	12	1

demosponges. To provide a more complete temporal and spatial distribution of chaetetid skeletons, some of these taxa are briefly summarized.

Hypercalcified sponges with a chaetetid skeleton have been reported from Cambrian, Ordovician, Silurian, Devonian, and lower Carboniferous rocks. *Flindersipora bowmani*, an abundant coralomorph in lower Cambrian bioherms in the Flinders Ranges, South Australia, should, according to Sorauf (2000, p. 38) be placed with the chaetetids. However, the numerous, well-developed septa in *Flindersipora bowmani* are a characteristic of tabulate corals and are not currently known in any chaetetid taxa. Interestingly, another characteristic of tabulate corals, namely pores in the walls, has been documented in ?*Blastoporella* (Cuif & Ezzoubair, 1991), a probable chaetetid genus. If septa in chaetetids, as suggested by Sorauf (2000), and pores in tubule walls, as documented in ?*Blastoporella,* are to be considered features of chaetetids, then it is possible that chaetetids and tabulate corals are more closely related than previously thought.

Oakley (1936) described a chaetetid from the Ordovician of the Northwest Territories, Canada, and Norford (1971) described a species of *Chaetetipora* from the Upper Ordovician of Ellesmere Island. Chaetetids were reported from the Upper Ordovician Cincinnati Group by Nicholson (1874) and Mickleborough and Wetherby (1878). Occurrences from the middle Silurian (Clinton) of New York were reported by Nicholson (1874) and Gillette (1947). Some of the taxa (chaetetid species) listed by Mickleborough and Wetherby (1878) are now considered to be bryozoans, and the occurrence of *Chaetetes* (*Chaetetes*) in the Silurian is also queried (see Table 22). *C.* (*Boswellia*) and *Pachytheca* are valid chaetetid genera, and occur in the Devonian (see Table 19). Oliver, Merriam, and Churkin (1975) reported Devonian chaetetids in Alaska, and Méndez-Bedia, Soto, and Fernández-Martinez (1994) and Soto, Méndez-Bedia, and Fernández-Martinez (1994) reported chaetetids in Devonian reefs in the Cantabrian Mountains in Spain. Chaetetids are also found in the subsurface Devonian reefs of Canada (D. L. Kissling, personal communication, 1988). Other Devonian occurrences of chaetetids are in Poland (Nowinski & Sarnecka, 2003), the Ardennes (Belgium, Luxembourg, and France) (Hubert & others, 2007; Zapalski & others, 2007), Germany (May, 1993), Morocco (May, 2008), and Australia (Pickett, Och, & Leitch, 2009).

More widely distributed are hypercalcified demosponges with a chaetetid skeleton in the Carboniferous, Missisippisan of the United States, as follows: Georgia (Broadhead, 1975; Lord & Walker, 2009; Lord, Walker, & Aretz, 2011); Illinois and Kentucky (Stouder, 1938; Duncan, 1965, 1966; Gutschick, 1965; Trace & McGrain, 1985); western Wyoming (Sando, 1975); Nevada (Arrow Canyon and Goodsprings); and Wellsville Mountains, Utah (West, 1992). Lower Carboniferous chaetetids have also been reported from: Peru (Bassler, 1950); Akiyoshi-dai, Japan (Ota,

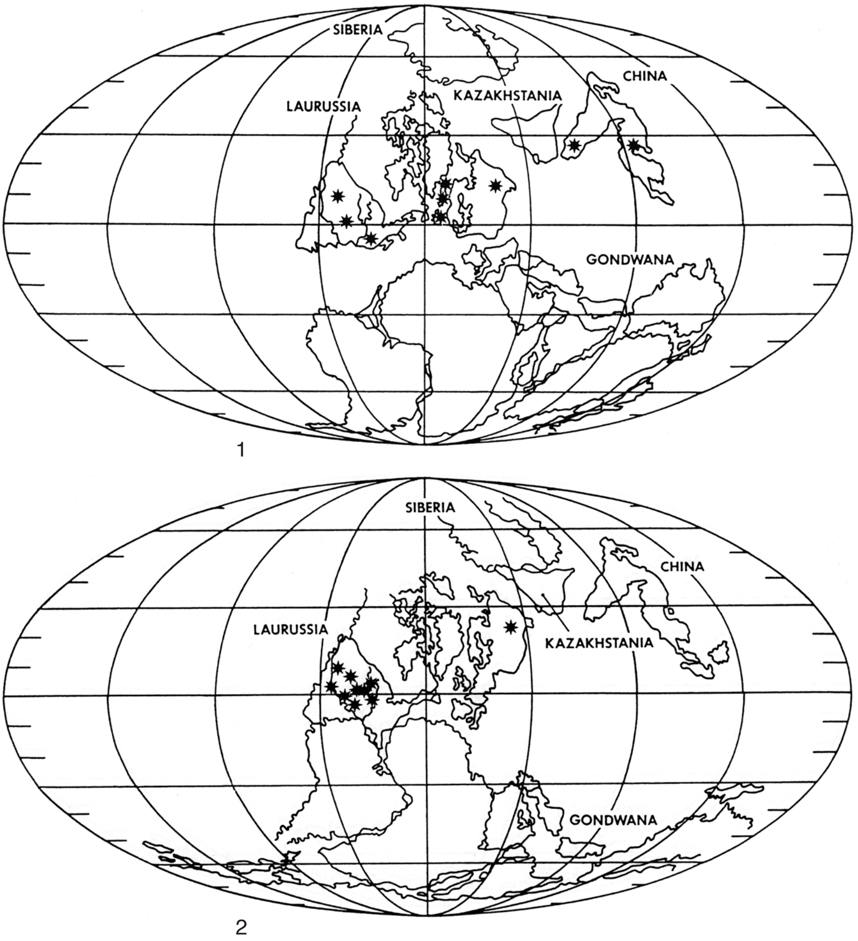
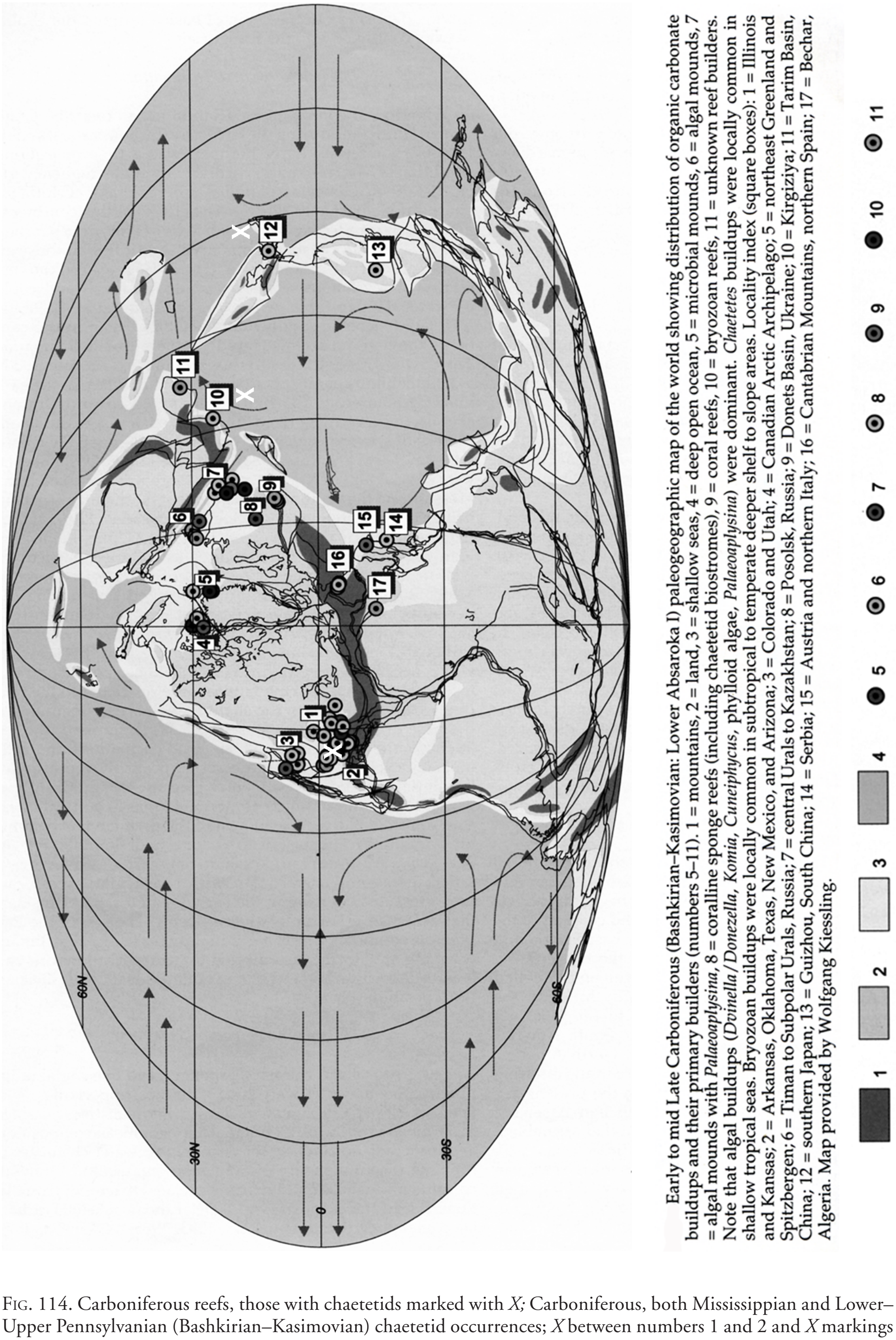


Fig. 113. Distribution of Carboniferous chaetetids; *1,* general distribution of chaetetids during the middle Early Carboniferous, approximately 320–340 Ma (West, 2012c); *2,* general distribution of chaetetids during the middle Late Carboniferous, approximately 305–320 Ma (West, 2012c).

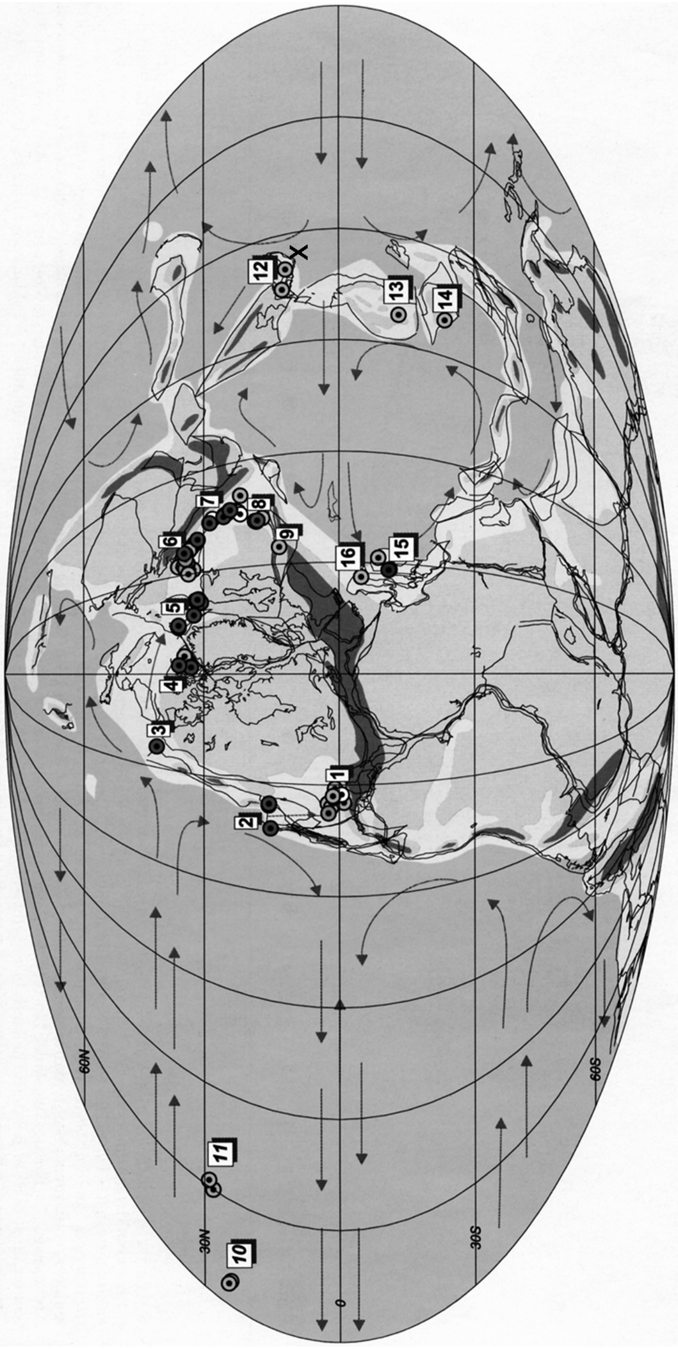
1977, 1968); Taurides, southern Turkey (Denayer, 2010); Donets Basin, Ukraine (Ogar, 2011, 2012); Tiouinine, Morocco (Rodríguez & others, 2011); Derbyshire, England (Wolfenden, 1958); the Great Limestone, Yorkshire, England (Dean, Owen, & Dooris, 2008); Wales (Aretz & Herbig, 2003a); Little Asby Scar, Cumbria, England (Aretz & Nudds, 2007); the Midland Valley, Scotland (Jameson, 1980, 1987); the Anhee Formation of Royseux, Belgium (Aretz, 2001); the Montagne Noire, France (Aretz & Herbig, 2003b); southwestern Spain (Gómez-Herquedas & Rodríguez, 2009); and Cannindah limestone, Queensland, Australia (Shen & Webb, 2008).

Additionally, I have examined numerous specimens of lower Carboniferous chaetetids in museum collections of England, Scotland, Wales, and continental Europe, where they occur more commonly than in the upper Carboniferous rocks of those areas. In addition to the upper Carboniferous sites listed in Table 26 and summarized in Table 27, chaetetids also occur in upper Carboniferous reefs of Holm Land, northeastern Greenland (Stemmerik, 1989), and others are included



Early to mid Late Carboniferous (Bashkirian–Kasimovian: Lower Absaroka I) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–11). 1 = mountains, 2 = land, 3 = shallow seas, 4 = deep open ocean, 5 = microbial mounds, 6 = algal mounds, 7 = algal mounds with *Palaeoaplysina*, 8 = coralline sponge reefs (including chaetetid biostromes), 9 = coral reefs, 10 = bryozoan reefs, 11 = unknown reef builders. Note that algal buildups (*Dvinella/Donezella, Komia, Cuneiphycus,* phylloid algae, *Palaeoaplysina*) were dominant. *Chaetetes* buildups were locally common in shallow tropical seas. Bryozoan buildups were locally common in subtropical to temperate deeper shelf to slope areas. Locality index (square boxes): 1 = Illinois and Kansas; 2 = Arkansas, Oklahoma, Texas, New Mexico, and Arizona; 3 = Colorado and Utah; 4 = Canadian Arctic Archipelago; 5 = northeast Greenland and Spitzbergen; 6 = Timan to Subpolar Urals, Russia; 7 = central Urals to Kazakhstan; 8 = Posolsk, Russia; 9 = Donets Basin, Ukraine; 10 = Kirgiziya; 11 = Tarim Basin, China; 12 = southern Japan; 13 = Guizhou, South China; 14 = Serbia; 15 = Austria and northern Italy; 16 = Cantabrian Mountains, northern Spain; 17 = Bechar, Algeria. Map provided by Wolfgang Kiessling.

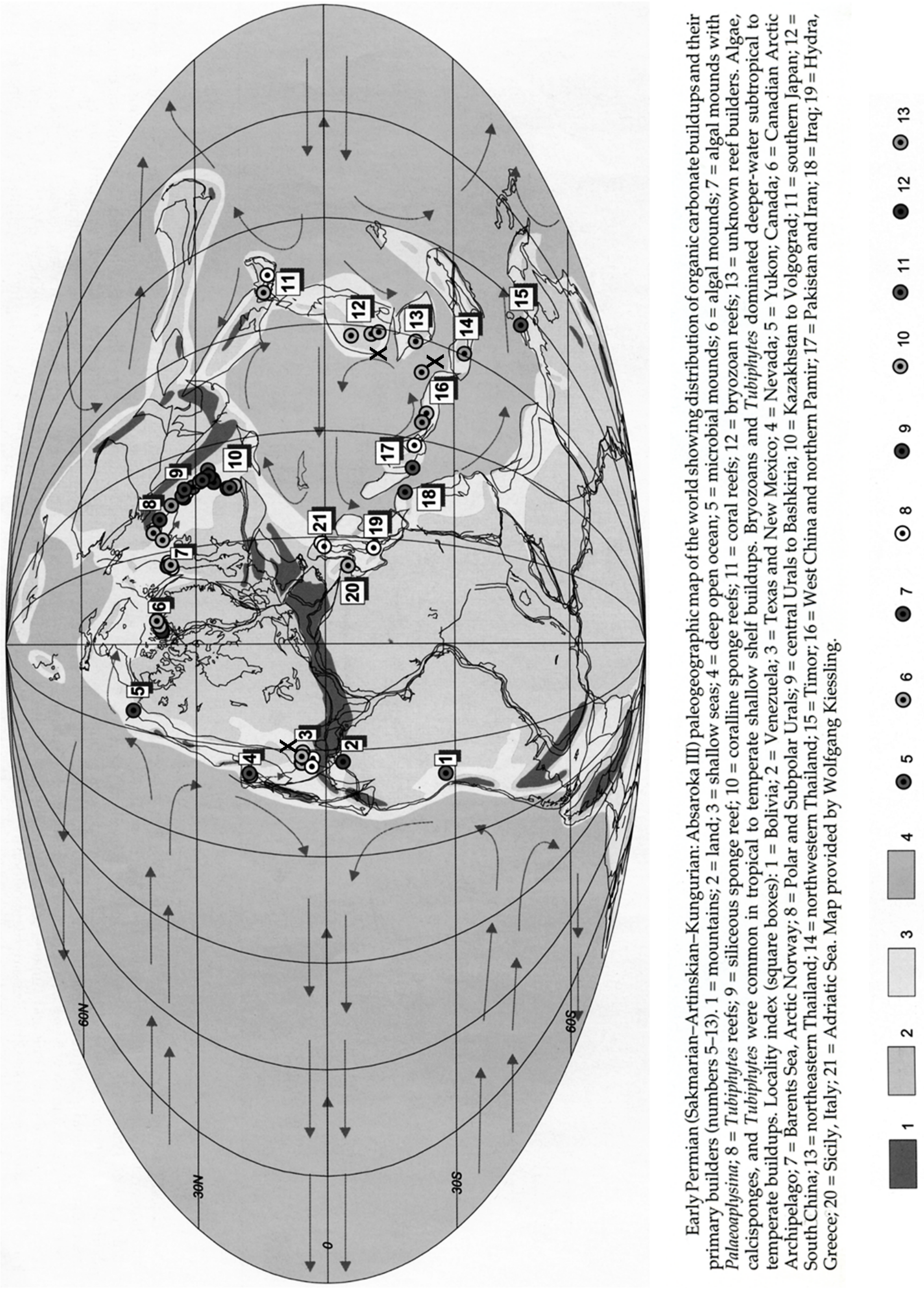
FIG. 114. Carboniferous reefs, those with chaetetids marked with *X;* Carboniferous, both Mississippian and Lower–Upper Pennsylvanian (Bashkirian–Kasimovian) chaetetid occurrences; *X* between numbers 1 and 2 and *X* markings below number 10 and above number 12 are occurrences in the central and western United States, Kyrgyzstan, and Japan respectively (adapted from Wahlman, 2002, p. 274, color fig. 2; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Latest Carboniferous and earliest Permian (Gzhelian–Asselian: Absaroka II) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–11). 1 = mountains; 2 = land; 3 = shallow seas; 4 = deep open ocean; 5 = microbial mounds; 6 = algal mounds; 7 = algal mounds with *Palaeoaplysina;* 8 = *Tubiphytes* reefs; 9 = coralline sponge reefs; 10 = bryozoan reefs; 11 = unknown reef builders. Phylloid algal buildups dominated shallow-water tropical seas, and in the Asselian, calcisponges became more common. In subtropical to temperate seas, *Palaeoaplysina* (with varying amounts of intermixed phylloid algae) dominated buildups in shallow water, and *Tubiphytes* and bryozoans dominated in deeper shelf to slope buildups. Locality index (square boxes): 1. = Texas and New Mexico; 2 = Idaho and California; 3 = Yukon, Canada; 4 = Canadian Arctic Archipelago and North West Territories; 5 = Barents Sea and Spitzbergen; 6 = Subpolar Urals and Timan–Pechora Basin, Russia; 7 = central Urals to Bashkiria, Russia; 8 = Pricaspian Basin, Kazakhstan to Volgograd, Russia; 9 = Donets Basin, Ukraine; 10 = Sikhote-Alin, Russia (paleoposition hypothetical); 11 = Koryak, Russia (paleoposition hypothetical); 12 = Japan; 13 = Guizhou, South China; 14 = Loei, Thailand; 15 = Serbia and Hungary; 16 = Austria. Map provided by Wolfgang Kiessling.

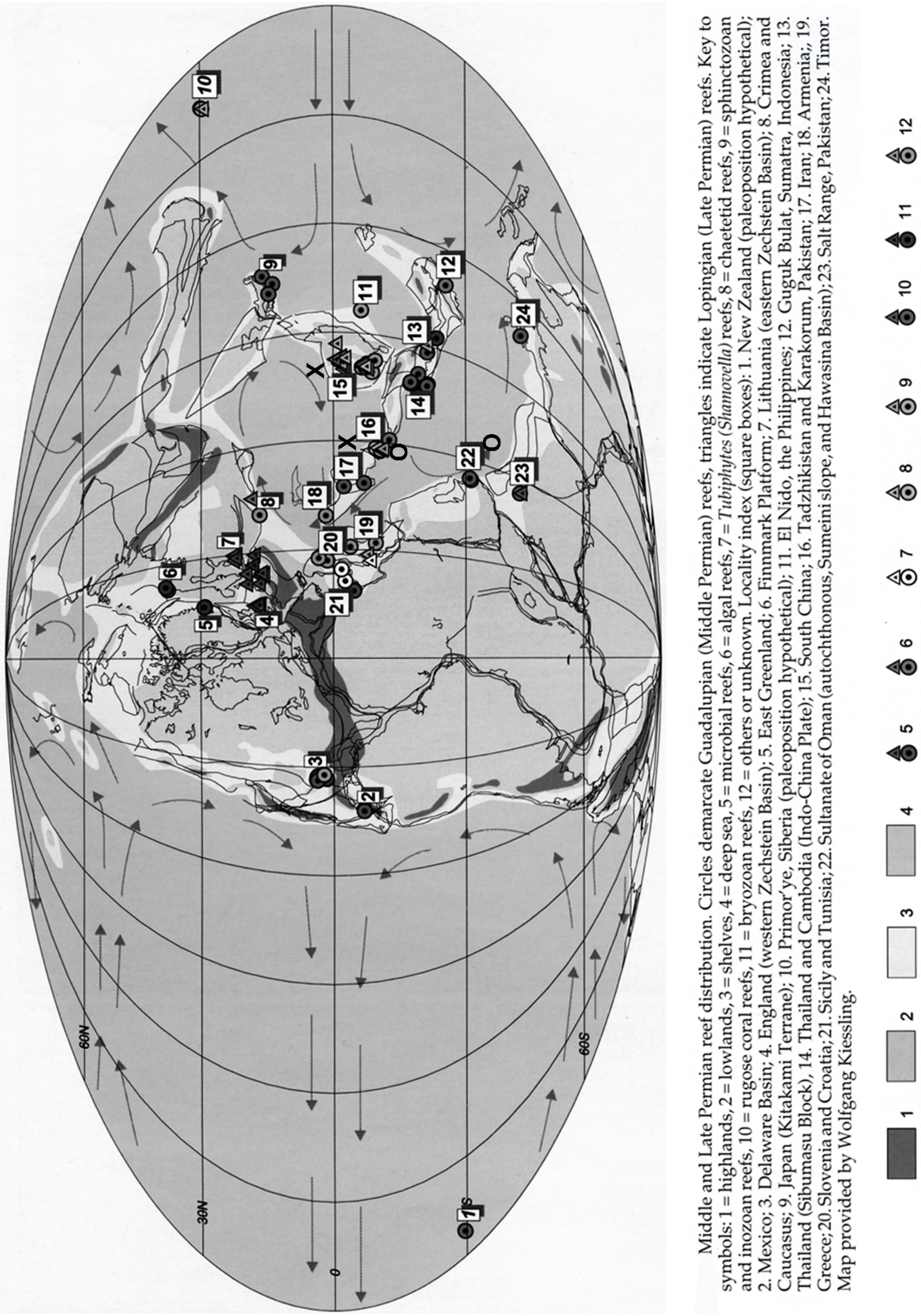
▨ 1 ▨ 2 ☐ 3 ▨ 4 ● 5 ◉ 6 ● 7 ◉ 8 ◉ 9 ● 10 ◉ 11

Fig. 115. Carboniferous and lower Permian reefs, those with hypercalcified demosponges marked with *X;* Carboniferous, Upper Pennsylvanian (Gzhelian) to lowermost Permian, Lower Cisuralian (Asselian) hypercalcified demosponge locality; *X* below and slightly right of number 12 is the Japanese (Akiyoshi) site (adapted from Wahlman, 2002, p. 275, color fig. 3; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Early Permian (Sakmarian–Artinskian–Kungurian: Absaroka III) paleogeographic map of the world showing distribution of organic carbonate buildups and their primary builders (numbers 5–13). 1 = mountains; 2 = land; 3 = shallow seas; 4 = deep open ocean; 5 = microbial mounds; 6 = algal mounds; 7 = algal mounds with *Palaeoaplysina;* 8 = *Tubiphytes* reefs; 9 = siliceous sponge reef; 10 = coralline sponge reefs; 11 = coral reefs; 12 = bryozoan reefs; 13 = unknown reef builders. Algae, calcisponges, and *Tubiphytes* were common in tropical to temperate shallow shelf buildups. Bryozoans and *Tubiphytes* dominated deeper-water subtropical to temperate buildups. Locality index (square boxes): 1 = Bolivia; 2 = Venezuela; 3 = Texas and New Mexico; 4 = Nevada; 5 = Yukon; Canada; 6 = Canadian Arctic Archipelago; 7 = Barents Sea, Arctic Norway; 8 = Polar and Subpolar Urals; 9 = central Urals to Bashkiria; 10 = Kazakhstan to Volgograd; 11 = southern Japan; 12 = South China; 13 = northeastern Thailand; 14 = northwestern Thailand; 15 = Timor; 16 = West China and northern Pamir; 17 = Pakistan and Iran; 18 = Iraq; 19 = Hydra, Greece; 20 = Sicily, Italy; 21 = Adriatic Sea. Map provided by Wolfgang Kiessling.

FIG. 116. Lower Permian reefs, those with hypercalcified demosponges marked with *X;* lower Permian (Sakmarian, Artinskian, and Kungurian) **hypercalcified demosponge localities;** *X* markings above and to left of number 3, between numbers 13 and 16, and to lower left of number 12 refer to western Texas, southern and western China, respectively (adapted from Wahlman, 2002, p. 276, fig. 4; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).



Middle and Late Permian reef distribution. Circles demarcate Guadalupian (Middle Permian) reefs, triangles indicate Lopingian (Late Permian) reefs. Key to symbols: 1 = highlands, 2 = lowlands, 3 = shelves, 4 = deep sea, 5 = microbial reefs, 6 = algal reefs, 7 = *Tubiphytes* (*Shamovella*) reefs, 8 = chaetetid reefs, 9 = sphinctozoan and inozoan reefs, 10 = rugose coral reefs, 11 = bryozoan reefs, 12 = others or unknown. Locality index (square boxes): 1. New Zealand (paleoposition hypothetical); 2. Mexico; 3. Delaware Basin; 4. England (western Zechstein Basin); 5. East Greenland; 6. Finnmark Platform; 7. Lithuania (eastern Zechstein Basin); 8. Crimea and Caucasus; 9. Japan (Kitakami Terrane); 10. Primor'ye, Siberia (paleoposition hypothetical); 11. El Nido, the Philippines; 12. Guguk Bulat, Sumatra, Indonesia; 13. Thailand (Sibumasu Block), 14. Thailand and Cambodia (Indo-China Plate); 15. South China; 16. Tadzhikistan and Karakorum, Pakistan; 17. Iran; 18. Armenia;, 19. Greece; 20. Slovenia and Croatia; 21. Sicily and Tunisia; 22. Sultanate of Oman (autochthonous, Sumeini slope, and Hawasina Basin); 23. Salt Range, Pakistan; 24. Timor. Map provided by Wolfgang Kiessling.

FIG. 117. Permian reefs, those with chaetetids marked with *X* or *O;* Permian (Guadalupian and Lopingian) chaetetid occurrences; *O* markings just below number 22 and to the lower left of number 16 are Guadalupian occurrences in Oman and Pakistan, respectively; *X* markings between numbers 16 and 17 and above number 15 (Lopingian) are occurrences in Pakistan and southern China, respectively (adapted from Weidlich, 2002, p. 352, fig. 8; courtesy of the author and the Society for Sedimentary Geology; for a color version, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).

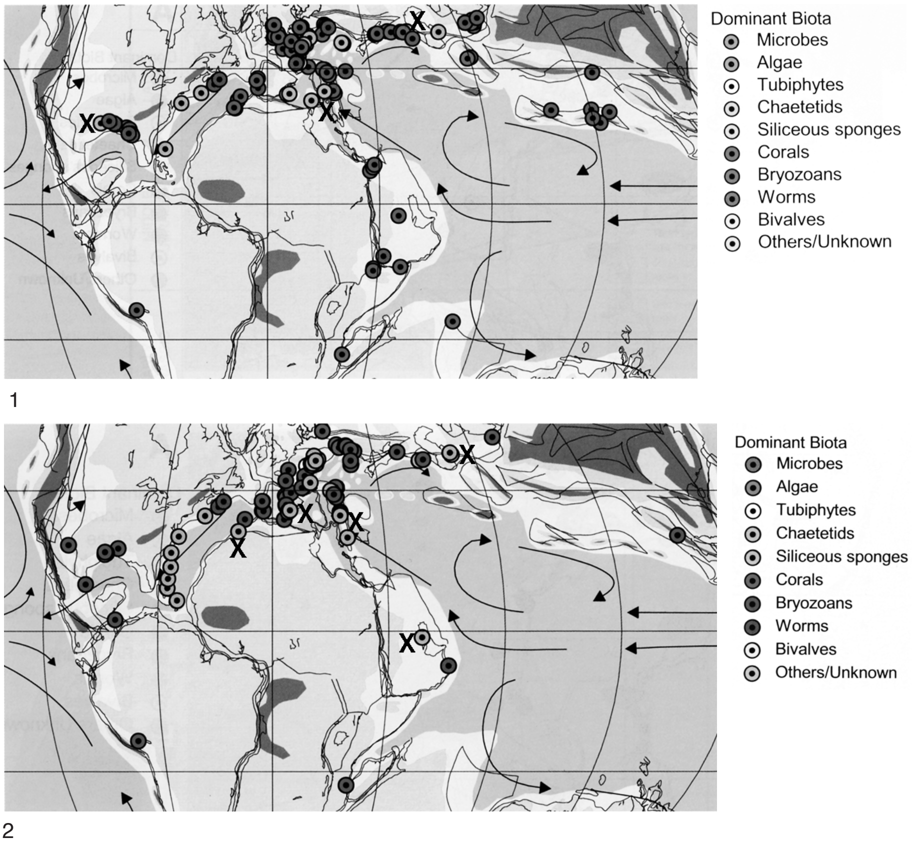


FIG. 118. Jurassic reefs, those with chaetetids marked with *X; 1,* Upper Jurassic (Oxfordian) chaetetid occurrences; *X* markings are localities in Mexico, southern Europe, and Iran (adapted from Leinfelder & others, 2002, p. 481, color fig. 5A; courtesy of the author and the Society for Sedimentary Geology); *2,* Upper Jurassic (Kimmeridgian) chaetetid occurrences; *X* markings are localities in Morocco, southern Europe, Iran, and Saudi Arabia (adapted from Leinfelder & others, 2002, p. 482, color fig. 6A; courtesy of the author and the Society for Sedimentary Geology; for color versions, see *Treatise Online,* Number 37: paleo.ku.edu/treatiseonline).

in the collections of the Canadian Geological Survey from Ellesmere Island (Canadian Arctic).

Post-Paleozoic chaetetids are represented in fossil sponge communities of Lower and middle Cretaceous rocks in Arizona and northern Spain (REITNER, 1989). Chaetetids also occur in Paleogene and Neogene rocks, as shown in Table 26, and in Pleistocene reef limestones of Okinawa (MORI, 1976; 1977; NAKAMORI, 1986) and the Vanuatu Archipelago (MILLET & KIESSLING, 2009). Living specimens occur in the fringing coral reefs of Okinawa (NAGAI & others, 2007).

Some of the occurrences noted in the preceding paragraphs are in series and stages that are listed as unreported in Table 26, such as the lower Cambrian, lower Carboniferous, and part of the Lower Cretaceous. However, all of the sites mentioned above are situated on currently available paleogeographic maps, in positions either in the tropics or in warm temperate settings. Thus, the paleogeographic distribution of fossil chaetetids is the same as for their extant descendants in tropical to warm temperate zones. Although chaetetids were never really conspicuous and never formed large reefs, they did, during the late Paleozoic, produce significant reef mounds and banks in shallow water, open marine environments (West, 1988; Wahlman, 2002). Prior to the upper Paleozoic, they appear to have had a smaller and less significant role in Paleozoic reef communities. It is important to note that the skeletal morphology of chaetetids is similar to that of a number of Paleozoic tabulate corals, as well as some bryozoan colonies. Because workers in the Paleozoic commonly relate forms they collect in the field to tabulate corals rather than chaetetids, more careful study of tabulate corals, such as lichenarids and chaetetids is needed (see also discussion on p. 6).

Extant, and most post-Paleozoic chaetetids, are also small and relatively inconspicuous in the relatively more diverse reef communities of the Mesozoic, occurring in cryptic and/or deeper bathyal environments. As small occupants of such environments, they are easily overlooked, which may be part of the reason why they have rarely been reported.

BIOSTRATIGRAPHY

Hypercalcified demosponges with a chaetetid skeleton occur in four orders of the Demospongiae: Hadromerida, Chondrosida, Poecilosclerida, Agelasida, and possibly also the Halichondrida (*Chaetosclera* and *Neuropora*). In addition, there are five genera, *Atrochaetetes, Bauneia, Blastochaetetes, Meandripetra, Ptychochaetetes (Ptychochaetetes),* and *P. (Varioparietes)* for which the order and family are uncertain. The order Hadromerida contains the following taxa: *Acanthochaetetes, Calcisuberites, Chaetetes* (*Chaetetes*), *C.* (*Boswellia*), *C.* (*Pseudoseptifer*), *Chaetetopsis, Pachytheca,* and *Calcispirastrella*. *Ceratoporella*, *Blastoporella*, *Kemeria*, *Keriocoelia*, *Leiospongia*, and *Sclerocoelia* are in the order Agelasida; the placement of *Cassianochaetetes* and *Spherolichaetetes* in this order is questionable. Currently, the only genus in the order Poecilosclerida is *Merlia*. The oldest and longest ranging valid chaetetid taxa extend from the ?Silurian to the Recent (see Table 19, Table 22). There are more valid chaetetid genera in the Mesozoic than in the Paleozoic, with the greatest number (ten), in the Triassic. Of these ten, five genera (*Atrochaetetes, Bauneia, Blastochaetetes, Ceratoporella*, and *Ptychochaetetes*) extend beyond the Triassic (see Table 19, Table 22). There are also three other chaetetid genera in the Triassic that are inadequately known, because spicules, or spicule pseudomorphs, have not yet been recognized (see Table 19, Table 22). Of the three extant genera, *Acanthochaetetes, Ceratoporella,* and *Merlia,* only the last is known from the Paleogene (Eocene and Oligocene) and Neogene (Miocene).

It is interesting that there are so many valid chaetetid genera (ten) in the Triassic and so few in the Paleozoic (three). Although a number of tabulate and rugose corals survived the extinctions at the end of the Ordovician and the end of the Devonian, none survived the extinction at the end of the Paleozoic (Permian) (Sepkoski, 2002). Heterocorals appeared first in the Upper Devonian (Famennian) and continued into the Carboniferous, but they are unknown from the Permian (Sepkoski, 2002, p. 61). The class Stromatoporoidea (Stearn & others, 1999, p. 11; and see Paleozoic Stromatoporoidea, p. 707) is only reported from the Paleozoic, where they were important reef builders during the Late Ordovician, Silurian, and Devonian, and none is confirmed to have survived beyond the Devonian. Habitats occupied by these corals and stromatoporoids would have been available to other organisms that survived the extinctions at the end of the Devonian and the end of the Permian. A tentative occurrence of *Ceratoporella,* an extant chaetetid genus, is reported from the Permian (H. Termier, G. Termier, & Vachard, 1977), so perhaps chaetetids occupied these available niches during the Triassic but were eventually replaced by scleractinian corals and Mesozoic stromatoporoids. At the same time, the preservation potential of any fossil is decreased the longer it is subjected to natural processes, namely

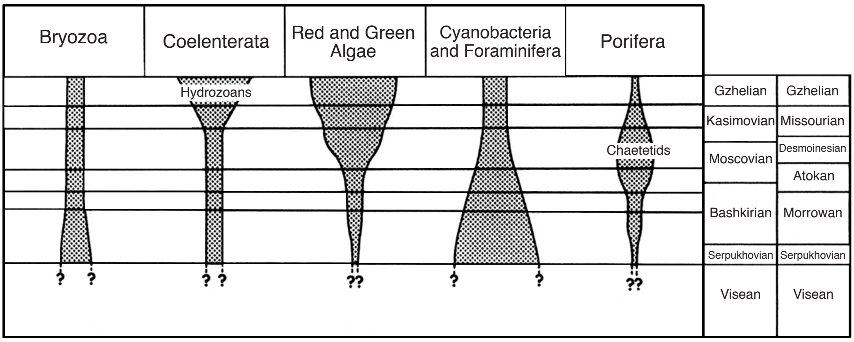


FIG. 119. Relative abundance (skeletal biovolume) in relation to the major groups of reef builders, upper Carboniferous reef mounds; time scale on the far right is the regional scale for North America, and the other one is the International time scale (adapted from West, 1988, p. 157, fig. 1; courtesy of the author and the Society for Sedimentary Geology).

diagenetic processes, and thus the older and less well-preserved Paleozoic forms may not have been recognized and/or were confused with tabulate corals, as noted on the previous page.

The currently known first and last occurrences of the 22 valid genera of hypercalcified demosponges with a chaetetid skeleton are listed in Table 19, along with the 4 genera for which definitive information on spicules or spicule pseudomorphs is lacking. Of these 22 valid genera, 19 are known only from the Mesozoic, 3 valid genera are exclusively Paleozoic, the living *Ceratoporella* has questionably been reported from the Permian, and the oldest occurrence of *Merlia* is in the Jurassic. Although the generic diversity is greatest in the Mesozoic, conspicuous reef building chaetetids were most abundant during the upper Carboniferous (WOOD, 1990b). Because of their small size and minor roles in the generally more diverse Mesozoic reef communities, chaetetids are often unrecognized.

The five time slices in which chaetetids were abundant enough to be important in the construction of reefs are upper Carboniferous (Bashkirian–Kasimovian), Permian (Guadalupian and Lopingian), and Jurassic (Oxfordian and Kimmeridgian) (Table 26). Although they are specifically listed as reef builders during these five intervals, they are most conspicuous during the upper Carboniferous (Bashkirian, Moscovian, and Kasimovian). The reason(s) for their abundance during this time interval is not clear, but it could be related to the fact that the diversity of the reef mounds was low during this period of time. With less competition, chaetetid skeletons may have grown larger, forming more conspicuous reefal structures.

Two aspects of this concentration in the upper Carboniferous (Bashkirian–Kasimovian) deserve comment. First, chaetetids, based on field collecting and examination in some museum collections, appear to be more widespread and conspicuous in the lower Carboniferous (Mississippian) of most of Europe (Spain is an exception) than in the United States (Fig. 113.1–113.2). KIESSLING, FLÜGEL, and GOLONKA (2002, p. 708) noted that the status of the mid-Carboniferous event between the Serpukhovian and Bashkirian, as a major global extinction event, was ambiguous; however, their data indicated a first-order reef crisis. The upper Carboniferous (Pennsylvanian) in Europe is more siliciclastic, as it is also in the eastern United States. Consequently, in all of these regions, it appears that the environments available during the upper Carboniferous were rather unsuitable for chaetetids. However, that does not explain the rarity of chaetetids in the largely carbonate sequence of most of the lower Carboniferous (Mississippian) in the central and western United States. It also does not explain the similarity between the poriferan and coral assemblages of Spain and the North American midcontinent during the upper Carboniferous, especially during the Moscovian (García-Bellido & Rodríguez, 2005). If, as documented by García-Bellido and Rodríguez (2005), there was a marine connection between the Paleotethys Sea and the Panthalassan Ocean during the Moscovian, then it seems reasonable to infer that such a connection existed earlier, i.e., during the lower Carboniferous through into the Bashkirian (lower upper Carboniferous).

The second aspect is the rather sudden, almost complete, disappearance of chaetetids from the upper Carboniferous (Kasimovian–Gzhelian) through the Permian. There are a few reported occurrences of chaetetids in the Kasimovian (most of the Missourian) of the United States, but currently there are no known Gzhelian (Virgilian) (West, 1992) or lower Permian (Asselian) occurrences in the United States. Wahlman (2002) recorded upper Carboniferous (Gzehlian) and lower Permian (Asselian) hypercalcified demosponges from Japan (Fig. 115; Table 26) and from the lower Permian (Sakmarian, Artinskian, and Kungurian) of western Texas and southern and western China (Fig. 116; Table 26). Chaetetid reefs occur in the upper Permian (Guadalupian and Lopingian) of Oman, Pakistan, and southern China (Fig. 117; Table 26; Weidlich, 2002, 2007a, 2007b; Weidlich & Bernecker, 2003). Phylloid algae (Fig. 119) were the dominant reef builders during the Late Carboniferous and earliest Permian, not only in the western and central United States but also in southern Europe and southern China (Wahlman, 2002, p. 322). Calcareous algae, especially rhodophytes and chlorophytes, were abundant and diverse (Wray, 1968, 1970, 1977) and apparently more successful than chaetetids in the open marine shallow waters of the continental shelf and epicontinental seas. However, chaetetids survived in the more turbid, less illuminated, and, as suggested by Wood (1995, fig. 5), nutrient-limiting waters of these environments. Perhaps this was the beginning of their retreat into the deeper water and/or cryptic habitats they inhabit today.

The biostratigraphy of hypercalcified demosponges with a chaetetid skeleton is affected by: (1) the skeletal architecture–organizational grade, which is polyphyletic; (2) the sporadic occurrence of valid chaetetid genera (see Table 19); and (3) the taphonomic processes that often altered and/or destroyed the original skeletal microstructure and spicules, making generic and specific identification difficult, if not impossible. As noted above, Cambrian and Ordovician chaetetid-like forms have been reported, but the oldest currently valid chaetetid taxon is the questionable occurrence of *Chaetetes* (*Chaetetes*) in the Silurian. Valid chaetetid genera and subgenera extend to the Recent and are most abundant during the Bashkirian and Moscovian, an interval that, based on current knowledge, is the acme zone of chaetetid sponges (Fig. 119).

A number of stratigraphic gaps exist between the currently known first and last appearances of the valid chaetetid genera (see Table 19), as well as many blanks and unknowns in the temporal and spatial distribution of chaetetids (Table 26). More thorough globally oriented investigations of chaetetid sponges are required to achieve the fullest possible understanding of the paleobiogeography and biostratigraphic development of this group.

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INTRODUCTION TO POST-DEVONIAN HYPERCALCIFIED SPONGES (STROMATOPOROID TYPE)

RACHEL WOOD

EXTERNAL MORPHOLOGY

GROSS MORPHOLOGY

As with most epibenthic invertebrates, calcified sponges display a wide range of gross morphologies and sizes, which may be more an expression of environmental controls than phylogeny. Modular organisms (those that show a repetition of functional units or individuals) have particularly flexible morphologies, which appear to be designed for life under varied rates of sedimentation, hydrodynamic energies, and substrate types. Some species have fixed morphologies and sizes, others show variation according to setting, and yet others show evidence that individuals can adapt to changing energy and sediment regimes, as shown by changing growth styles over the individual's lifetime.

Mesozoic stromatoporoids tend generally to be smaller than Paleozoic representatives, but they fall into the same three main groups of branching, laminar, and massive morphologies. The full range of gross morphologies they exhibit is listed in Table 28, together with their growth form, and an interpretation of the environments in which such forms most commonly grew (compiled from KISSLING & LINEBACK, 1967; KERSHAW, 1998). Growth form denotes the organization of functional units and follows the scheme outlined by COATES and JACKSON (1985). Laminar forms are subdivided into those that formed a permanent attachment to a hard substrate (encrusting) and those that grew upon soft sediment (recumbent). Detailed descriptions of the gross morphologies and growth forms are given in the Glossary (p. 397–415).

SURFACE FEATURES

Most Mesozoic stromatoporoids show open, porous surfaces, where the skeletal elements form a network. Other surface features fall into two categories: first are those structures related to the immediate hydrodynamic conditions under which an individual grew. These are oscular chimneys, mamelons, and subsidiary branches. Oscular chimneys are tubelike elongations bearing exhalant, oscular pores; mamelons are rounded, moundlike elevations that often bear astrorhizae or oscular pores. Subsidiary branches represent further skeletal development from either of these structures. All these structures enabled the sponge to increase the diameter of supply and thus avoid recycling of exhalant water (FRY, 1979). The presence or absence of such structures cannot always, however, be attributed to large-scale environmental causes. For example, adjacent individuals of the living chaetetid, *Ceratoporella,* show varied mamelon development. Reconstruction of hydrodynamic regimes should therefore only be considered when the range of surface features of an assemblage is available.

The second category of surface features reflects the organization and position of the aquiferous filtration system in relationship to the areas of skeletogenesis. The skeleton of a sponge serves to support the aquiferous system and will reflect the position of this when the soft tissues have gone. Most Mesozoic stromatoporoids possess complex traces of the intricate canal systems within their skeletons, often as ramifying unwalled spaces within the skeleton, which open out into astrorhizae on the upper surfaces. As the individual grows, successive layers are superimposed.

Table 28. Gross morphology and growth form of Mesozoic stromatoporoids, together with inferred environments in which each form most commonly occurred (Wood, 2011).

Gross morphology	Growth form	Inferred hydrodynamic regime	Inferred sedimentation rate
branching-delicate	pseudocolonial (uniserial)	low energy	high
branching-delicate	pseudocolonial (uniserial)	moderate energy	moderate
branching	multiserial erect	low-moderate energy	moderate
laminar-recumbent	multiserial	variable energy	low
laminar-encrusting	multiserial	high energy	low
massive: hemispherical, nodular	multiserial encrusting	moderate-high energy	low
massive: columnar, conical	multiserial encrusting	low-moderate energy	high

The form of the aquiferous system is largely dictated by the relative thickness of soft tissue and can thus be an important clue in soft-tissue reconstructions. For example, astrorhizae, the unwalled traces of the stellate, branching, exhalant canal system, are expressed in the fossilizable skeleton only when the soft tissue is sufficiently thin for the exhalant canals to be directly adjacent to the areas of calcification—i.e., the aquiferous system is essentially surficial. In contrast, oscular pores will be present within the skeleton only if the soft tissue is thick and the aquiferous system is penetrative and enclosed within the upper portions of the calcareous skeleton. Here, the exhalant canal traces are expressed as ramifying canals within the skeleton and not as superficial astrorhizal furrows. Ostia do not normally have any skeletal expression, although the tubules in chaetetids may correspond to the placing of one or more ostia, as noted in the living chaetetid *Ceratoporella.*

As in Paleozoic representatives, many Mesozoic stromatoporoids show a concentric layered appearance on the undersurface of hand specimens or when viewed in longitudinal thin section. These layers are periodic skeletal growth increments known as latilaminae. They are formed by alternating changes in the thickness or spacing of skeletal elements, or by a periodicity in the arrangement of the secondary skeleton. They may also be produced by preservational differences in the skeletal elements, perhaps due to varying amounts of organic material, leading to differing diagenetic susceptibility. Latilamination appears to be a reflection of different rates or types of skeletal growth and may indicate some cyclicity, possibly seasonal, of the environment in which stromatoporoids grew.

INTERNAL MORPHOLOGY

CONSTRUCTION OF THE SKELETON

The skeletal construction of many living calcified sponges consists of four successive growth stages: (1) organic skeleton; (2) spicular framework; (3) primary calcareous skeleton; (4) secondary calcareous skeleton (filling tissue). Some or all of these growth stages are inferred to have been present in Mesozoic stromatoporoids and are illustrated schematically in Figure 120.

1. Fine collagen fibers, known as spongin, occur in many sponges and in all demosponges. Spongin fibers are a few millimeters in diameter and are formed by numerous collagenous fibers 10 µm or less in diameter. Spongin is secreted by spongeocytes and is found in varying quantities in different groups.

2. Siliceous and calcareous spicules are known from Mesozoic stromatoporoids, placing their possessors in the classes Demospongiae and Calcarea, respectively. Spicules are secreted by sclerocytes. In demosponges, an axial filament appears within the sclerocyte, which serves as the template for silicification. Collenocyte cells are probably active in moving spicules to their final positions, at which point basal exopinacocytes engulf the spicules and cover them with a layer of spongin.

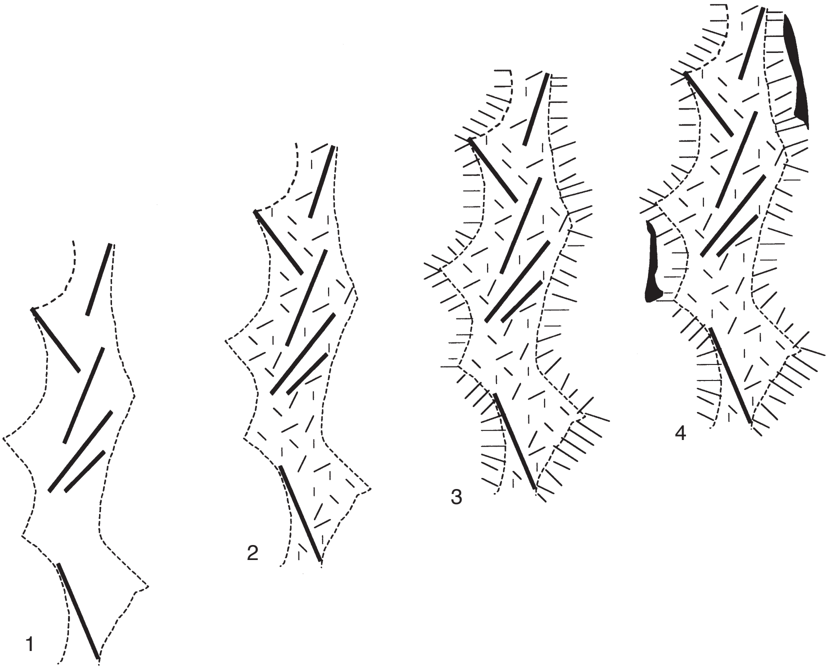

FIG. 120. Schematic illustration of the four successive skeletal growth stages inferred to have been present in Mesozoic stromatoporoids; *1,* primary spicule framework, probably bound with an organic matrix *(dotted lines);* 2, primary calcareous skeleton of irregular microstructure, forming meniscus-like around projecting spicules; 3,secondary calcareous skeleton forming orthogonal fibrous rim; 4, filling tissue of irregular tabulae (shown in black) (adapted from Wood, 1987).

Spicules are thus trapped and interconnected within the skeleton of spongin, from which the spicules echinate (protrude upward and outward from the fibers). As more spicules are moved into place and join the skeletal network, all parts of the spicule-spongin complex become covered with a similar layer of exopinacocytes. The skeleton of siliceous spicules and spongin fibers provides support for the soft parts of the sponge; in demosponge cultures raised in a silica-free medium, the aquiferous system fails. Spicules are highly variable in morphology and organization, and they often show considerable variety within different histological parts of an individual. Spicule tracts (bunches of spicules) may show an axial condensation from which they diverge in a plumose (as in Milleporellidae) or a plumulo-reticulate arrangement (as in Actinostromarianinidae), which radiate to the surface of the sponge.

3. The form of the primary calcareous skeleton is often determined by the position of the organic skeleton and may also be influenced by the positioning of the spicular skeleton.

The resultant primary calcareous skeletal elements fall into two categories: radial and concentric elements (Fig. 121). Radial elements may be pillars (of limited length) or columns (more continuous). Concentric elements are known as pillar-lamellae (short, discontinuous elements contiguous with pillars or columns) or laminae (independently secreted, continuous elements). Laminae are often punctured by pores, which are interpreted as oscular openings, as found in *Burgundia* (see Fig. 185*a–f*). Astrorhizae are often limited to interlaminar areas where laminae are present, although there may be some connection between successive generations. In some forms, the radial skeletal elements initiate from an axial

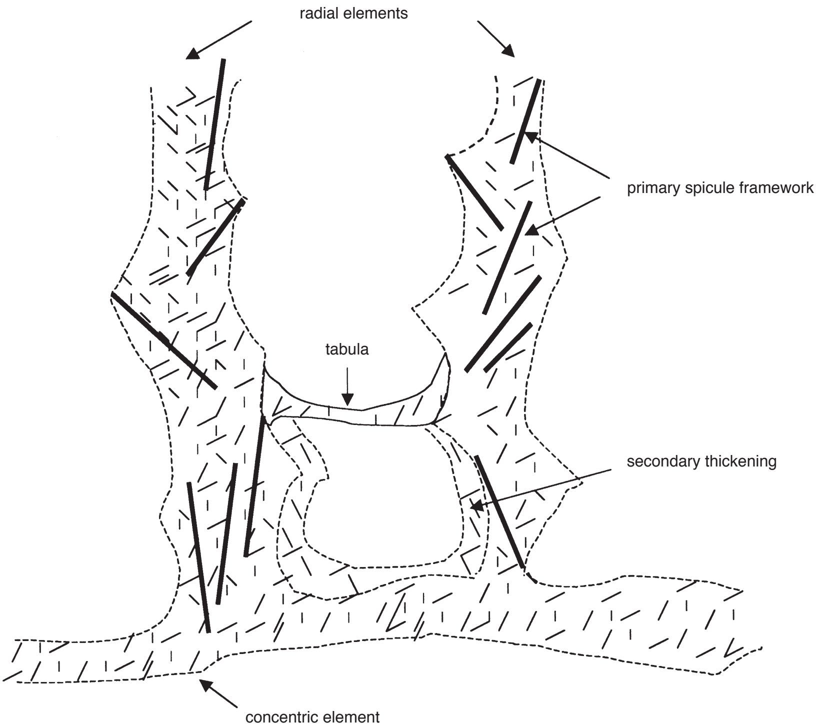

FIG. 121. Nomenclature of the skeletal elements in Mesozoic stromatoporoids (adapted from Wood, 1987).

condensed area (e.g., *Actinostromarianina,* Fig. 170,*3a–b*).

Sometimes the skeleton of Mesozoic stromatoporoids forms a reticulum where no distinction between radial and concentric elements can be made. This is often the case in the undifferentiated juvenile skeletal tissue at the base of stromatoporoid skeletons.

4. Only the peripheral areas of most calcified sponge skeletons are open, water-supplied frameworks covered by or filled with living soft tissue. Abandoned, older parts of the skeleton no longer occupied by living tissue are sectioned off or secondarily infilled by skeletal structures, which also provide a support platform for the soft tissue. A variety of secondarily precipitated structures (tabulae, secondary thickening, and backfill) constructed of various microstructures are common in Mesozoic stromatoporoids (Fig. 121). Tabulae are platelike, straight or curved elements that span between radial elements, parallel to the growth surface of the individual or across exhalant canal traces and oscular tubes. They may be precipitated at irregular intervals (independently) during the lifetime of the sponges or aligned as periodical growth increments. Tabulae often show a greater degree of alignment in forms with inferred thin veneers of tissue. They may be thin and of irregular microstructure or relatively thick, fibrous structures. Some Recent calcified chaetetid sponges possess tabulae (*Merlia* spp., *Acanthochaetetes* spp., and *Ceratoporella* sp.), but most other forms, especially *Ceratoporella*-like forms, form a backfill of solid skeleton, which may completely occlude the primary pore spaces that formerly housed the living tissue. The backfilling tissue forms syntaxially upon the primary skeleton, and, generally, the two components cannot be easily distinguished. Sometimes the development of backfill is limited to a secondary thickening of the

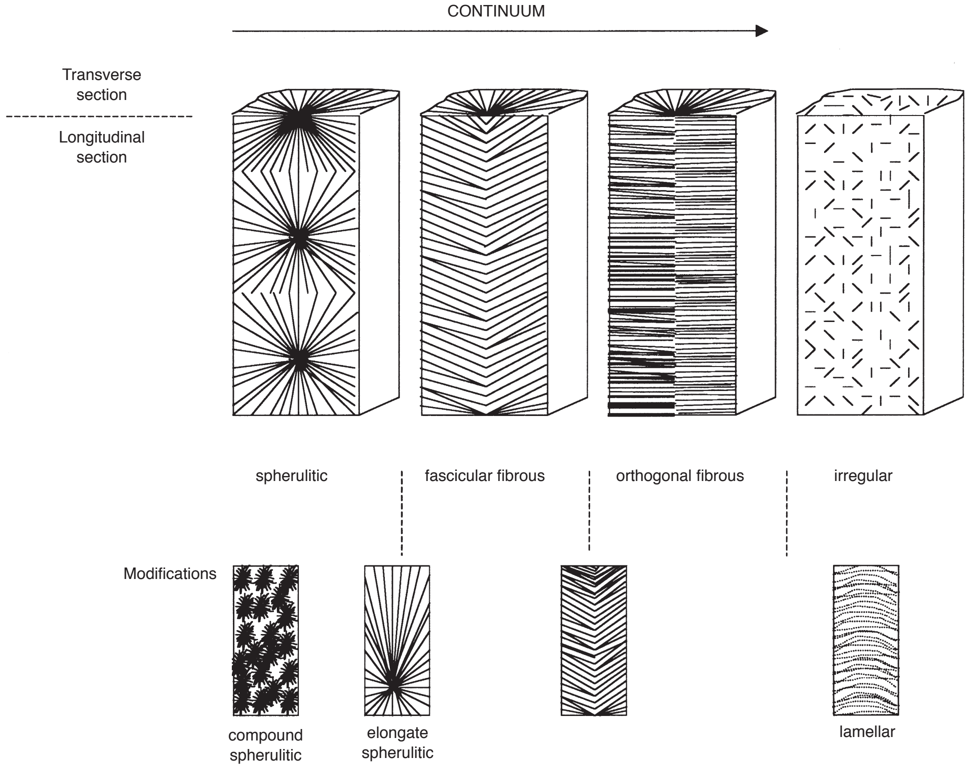

FIG. 122. Four main microstructural types of calcareous skeleton found in Mesozoic stromatoporoids, illustrated schematically as they appear in sections through a radial element. Modifications of these types are shown below the illustrations of the main types (adapted from Wood, 1987).

skeleton, especially the radial elements. It is not clear whether this overgrowth of crystals in optical continuity is an organic or inorganic process. Often, secondary backfill can initiate from a tabula, as found in *Ceratoporella.* Here, the distinction between types of filling tissue can be an arbitrary one. In other cases, such as the Cretaceous–Recent chaetetid *Acanthochaetetes,* tabulae may form contiguously with the primary skeleton, making a distinction between primary and secondary skeleton also problematic.

The following relationships have been determined between these three skeletal products in calcified sponges.

1. The calcified skeleton is precipitated directly within an aspiculate spongin framework or matrix, e.g., *Vaceletia* (Recent sphinctozoan) and possibly *Burgundia* (Mesozoic stromatoporoid).

2. Spicules are present, but only incorporated into the skeleton by chance, e.g., *Acanthochaetetes* (Recent chaetetid) and *Blastochaetetes irregularis* WOOD & REITNER, 1988 (Mesozoic chaetetid).

3. The calcified skeleton is precipitated around a primary spicule framework or lattice, e.g., *Petrobiona* (Recent calcarean) and *Actinostromaria* sp. (Mesozoic stromatoporoid).

4. The acicular crystals of the calcified skeleton initiate from the spicule bases within tracts, e.g., *Calcifibrospongia* (Recent stromatoporoid) and *Dehornella* (Mesozoic stromatoporoid).

5. The calcified skeleton is precipitated within a spongin matrix, which drapes,

meniscus-like, around a spicule framework, e.g., *Actinostromarianina lecompti* (Mesozoic stromatoporoid).

In addition to latilaminae, growth interruption surfaces may also be detected within longitudinal sections. These represent periods of considerable soft-tissue loss, due to sediment incursions or scour events, and may be followed by encrustation of the resulting free skeletal surface. The stromatoporoid soft tissue may subsequently regrow over some or all of the area, and skeletal growth will recommence. The undersurfaces, or within the skeleton, may also show epithecae. These are solid, platelike deposits of secondary tissue, which are often continuous across growth surfaces. When such structures appear within the skeleton, they are interpreted as having been precipitated in response to adverse environmental conditions.

MODES OF PROLIFERATION

Branches in Mesozoic stromatoporoids often arise from a basal nodule by either a dichotomy (longitudinal fission) or budding, which initiates from the axial part of the skeleton. Mode of branching affects the resultant branching form. Individuals may show a fasciculate arrangement of the branches.

BIOMINERALIZATION AND MICROSTRUCTURE

Sponges not only produce a diverse variety of microstructural fabrics (Fig. 122), but also form them via several biomineralization mechanisms. These mechanisms can be classed within genetic subdivisions, which are described below. This has the advantage of separating microstructures that have previously been classified together under the same descriptive heading, but which clearly have different modes of genesis (Wood, 1991b). Table 29 summarizes information concerning the supposed nonspicular biomineralization mechanisms found in Recent calcified demosponges, their products, and systematic distribution.

All biomineralization mechanisms employed by calcified sponges appear to precipitate crystals from beneath an organic layer that, to varying extents, acts as a template. The distribution of nucleation sites, presumably determined by organic tissue organization, also appears to be an important factor in determining the resultant microstructural type. In most cases, with the exception of irregular microstructures, the crystals are precipitated with their c-axes oriented perpendicular to the pinacoderm. When all three skeletal elements are present, the sequence of precipitation is always the same: (1) spicule formation, transportation, and orientation; (2) spongin-collagen fibers to bind the spicules in place; (3) calcareous skeleton precipitation.

The terms biologically induced, organic matrix-mediated (Lowenstam, 1981), and biologically controlled (Mann, 1983) have been established for describing the varying degrees of control of the organic component. Calcified demosponges appear to show representatives from all these types.

MINERALIZATION OF A COLLAGENOUS MATRIX

In this mode, the calcareous skeleton is wholly defined by the extent of a preformed collagenous framework of spongin that becomes calcified. This would seem to indicate an organic matrix-mediated mechanism, in which the cell manipulates an organic framework upon which regulated mineralization occurs (Lowenstam, 1981). Spicules may or may not play a role, but, where present, they appear to act as a framework around which the organic matrix is precipitated, and in the case of fibrous microstructures, they act as nucleation sites for the acicular crystal growth. Two living sponges calcify via calcification of an organic matrix, but they are systematically unrelated and produce totally different microstructures.

Vaceletia, a Recent aspiculate dictyoceratid (formerly verticillitid) sphinctozoan, produces a skeleton composed of a feltwork of aragonitic microfibrils known as microgranular

TABLE 29. Summary table of biomineralization mechanisms found in Recent calcified demosponges and calcareans, their products, and their systematic distribution (adapted from Wood, 2011).

Systematics	Genus	Biomineralization mechanism	Microstructure and mineralogy
Class Demospongiae			
Order Agelasida			
Family Astroscleridae	*Astrosclera*	intracellular	spherulitic aragonite
	Ceratoporella	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
	Stromatospongia	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
Order Haplosclerida			
Family Calcifibrospongiidae	*Calcifibrospongia*	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
Order Hadromerida			
Family Acanthochaetetidae	*Willardia*	secretory pinacoderm	pencillate (fascicular fibrous) aragonite
	Acanthochaetetes	secretory pinacoderm	microlamellar calcite
Order Poecilosclerida			
Family Merliidae	*Merlia*	secretory pinacoderm	pencillate (fascicular fibrous) calcite
Order Dictyoceratida (formerly Verticillitida)			
Family Vaceletiidae	*Vaceletia*	noncollagenous organic template	microgranular irregular aragonite
Class Calcarea			
Order Lithonida			
Family Minchinellidae	*Plectroninia, Minchinella*	secretion by telmatoblasts	orthogonal calcite
Order Murrayonida			
Family Murrayonidae	*Murrayona*	secretory pinacoderm	pencillate (fascicular fibrous) calcite
Order Baeriida			
Family Petrobionidae	*Petrobiona*	secretory pinacoderm	radial flake (fascicular fibrous) calcite

irregular microstructure. New chambers are added periodically, and they initiate by the formation of a collagenous template below the upper pinacoderm layer. Mineralization first occurs within isolated spherical regions, extending along the length of the new chamber wall (Gautret, 1985). Crystals first form bundles of disoriented acicular rods (compact in the terminology of Gautret, 1985), which later become more granular (composite in the terminology of Gautret, 1985) during a further phase of precipitation. In some parts of the skeleton, the bundles may show a preferred orientation parallel to the collagenous fibers between which they grow. The pillars that support the hemispherical chambers form during the first mineralization phase by mineralization of organic strands. Older, abandoned chambers become filled with layered lenses of irregular microstructures, and although it is not clear whether these are the result of inorganic or organic mineralization, their form does suggest an organic origin.

Nonspicular fossil sphinctozoans, which bear an irregular calcareous skeleton, are inferred, by suggested affinity to *Vaceletia,* to have possessed a similar mode of biomineralization. In addition, spiculate stromatoporoids, e.g., *Newellia mira* (Carboniferous haplosclerid), and the calcitic species *Actinostromarianina lecompti* (Jurassic agelasid), bear irregular calcareous skeletons that appear to drape around a primary spicular skeleton, also implying direct mineralization of a collagenous template (Wood, 1987; Wood, Reitner, & West, 1989).

Calcifibrospongia (Recent haplosclerid stromatoporoid) also biomineralizes by calcification of an organic matrix. Here, the calcareous skeleton precipitates around a lattice of siliceous strongyles that are bound within spongin fibers. The calcareous skeleton forms elongate sclerodermites 60–110 µm long. Hartman (1979) suggested that the centers of calcification may form simultaneously within a particular length of fiber, where the acicular aragonite crystals grow out in all directions from each center until they reach the boundary of the organic fiber, or are stopped by the crystals of a neighboring sclerodermite. Spicules frequently appear to serve as the nuclei for the sclerodermites. *Calcifibrospongia* can show deposits of epithecal material varying from 40–250 µm thick, representing planes of the successive dieback and regrowth of the skeleton, but no other filling tissue or secondary skeleton is present.

Euzkadiella (Cretaceous haplosclerid stromatoporoid) possesses a microstructure similar to *Calcifibrospongia,* and although this form was originally calcitic rather than aragonitic, it has been inferred to have formed by the same process (Reitner, 1987a).

SECRETORY PINACODERM

Here, calcified sponges produce a calcareous skeleton by precipitation through a secretory pinacoderm via a thin mucous- or fluid-filled (possible polysaccharide) layer, resembling the process found in calcareous algae. This would indicate a biologically controlled mechanism of precipitation, in which the cell appears to act as a causative agent and in some way controls the precipitation of minerals (Mann, 1983). The muco-polysaccharide layer might provide a migration path and medium for joining Ca^{2+} and CO_{32-} ions, as known in scleractinian corals. This layer may also serve, to a lesser extent, as a template controlling the configuration of crystals. Several forms are at present collected under this subheading, until more details allow us to refine the scheme.

The calcareous skeletons of *Ceratoporella* (agelasid chaetetids) and *Acanthochaetetes* (hadromerid chaetetids) are thought to be produced by this mechanism. In *Ceratoporella,* the calcareous skeleton is formed of acicular or fibrous crystals arranged in a modified spherulitic form known as penicillate. Hartman and Goreau (1975) observed this skeleton to form around clots of organic matrix (possibly spongin) surrounding the heads of some spicules. Thus, to some extent, the positioning of the calcareous skeleton appears to be determined by the placing of the spicule and spongin frameworks. In the acanthochaetetids, the high-Mg calcite skeleton has an irregular microstructure of crystals (1–8 µm long) oriented in one plane only, giving the appearance of a microlamellar microstructure in longitudinal section. Instead of the abandoned parts of the skeleton being filled with a secondary epitaxial backfill, the portions below the living tissue are sectioned off by a series of tabulae or horizontal partitions. Growth of the tubule walls is incremental and layered, and the spines and tabulae grow in an integrated way as outgrowths form the calicle walls. However, secondarily precipitated tabulae are also known. The microscleres form a dense layer at the surface of the living tissue, while the tylostyles are aligned parallel to the tubule walls. In living forms, the spicules are not incorporated into the calcareous skeleton, but in fossil representatives they are, although by chance (Reitner

& ENGESER, 1983). The megascleres tend to occur parallel to the tubule walls, and the microscleres within the tabulae, perhaps indicating the formation of the latter near the living tissue surface. Nanometer-sized organic fibers act as the matrix for calcification, and the tubule wall centers are richest in organic material. Collagenous strands extend into the calcareous skeleton, which seem to act as anchorage points for the soft tissue, as noted in some scleractinian corals. The exhalant canals sometimes leave impressions on the skeletal surface as in *Ceratoporella.* Both *Ceratoporella* and *Acanthochaetetes* have considerable fossil records, extending to the upper Permian and Upper Cretaceous, respectively.

Many Mesozoic stromatoporoids, such as the Milleporellidae, are inferred to have formed their calcareous skeletons by this method (WOOD, 1987). These forms produce fascicular fibrous skeletons, similar to those of *Ceratoporella.*

PASSIVE SECRETORY PINACODERM (CEMENT)

Orthogonal microstructure is common in many fossil calcified sponges, including fossil demosponges. They are also found in some living calcarean sponges (e.g., *Minchinella*). This simple microstructural type could be explained by the cement-like precipitation of acicular crystals with their c-axis parallel to a secretory membrane. They would, as such, constitute a biologically induced precipitation mechanism, in which the cell appears to act as a causative agent in the precipitation of minerals, but where the cell has little control (LOWENSTAM, 1981). The Upper Jurassic agelasid stromatoporoid *Actinostromaria* forms a primary calcareous orthogonal skeleton upon a spicule lattice. *Actinostromarianina lecompti* shows a primary irregular calcareous skeleton and a secondary orthogonal fibrous one, which has a banded distribution, forming latilaminae throughout the growth of the individual (see Fig. 170,*3a–b*). This would seem to point to the mediation of some periodic environmental effect, such as warmer temperatures, causing an intermittent biologically induced precipitation.

INTRACELLULAR ORIGIN

Astrosclera (a Recent agelasid stromatoporoid) is the only known calcified sponge whose calcareous skeleton has an intracellular origin. The basal calcareous skeleton of *Astrosclera* consists of a fine reticulum of aragonite with no differentiation into pillars and laminae. Calcareous spherules are formed intracellularly by amoebocytes as small nuclei (15 µm) near the surface of the sponge and then transported to a position where they grow larger by epitaxial growth and add to the general calcareous skeletal network to produce a compound spherulitic microstructure. The spherules are known to possess an organic calcification center of approximately 7 mm in diameter, and they show several organic rich layers, one of which corresponds to the attachment of the spherules to the skeletal wall, where it is emplaced by a covering organic envelope. The living tissue penetrates the mesh of the skeleton to a depth of approximately 10 mm, and a secondary deposit of acicular calcite crystals partially fills the abandoned inner skeletal reticulum. In the Indian Ocean, *Astrosclera* secretes siliceous acanthostyles, but Pacific populations largely lack them; although, when present, the spicules are incorporated into the calcareous skeleton. There appears to be no discernible direct relationship between the spicules and the positioning of the calcareous skeleton; they are incorporated by chance. Below the pinacoderm are large exhalant canals, 60–80 µm in diameter, that branch downward and outward into the skeletal tissue to form astrorhizal-like structures. No tabulae are known, but secondary epitaxial backfill occurs as penicillate tufts in the abandoned parts of the skeleton.

A wide variety of fossil calcified demosponges are known that show this aragonitic spherulitic microstructural type, especially

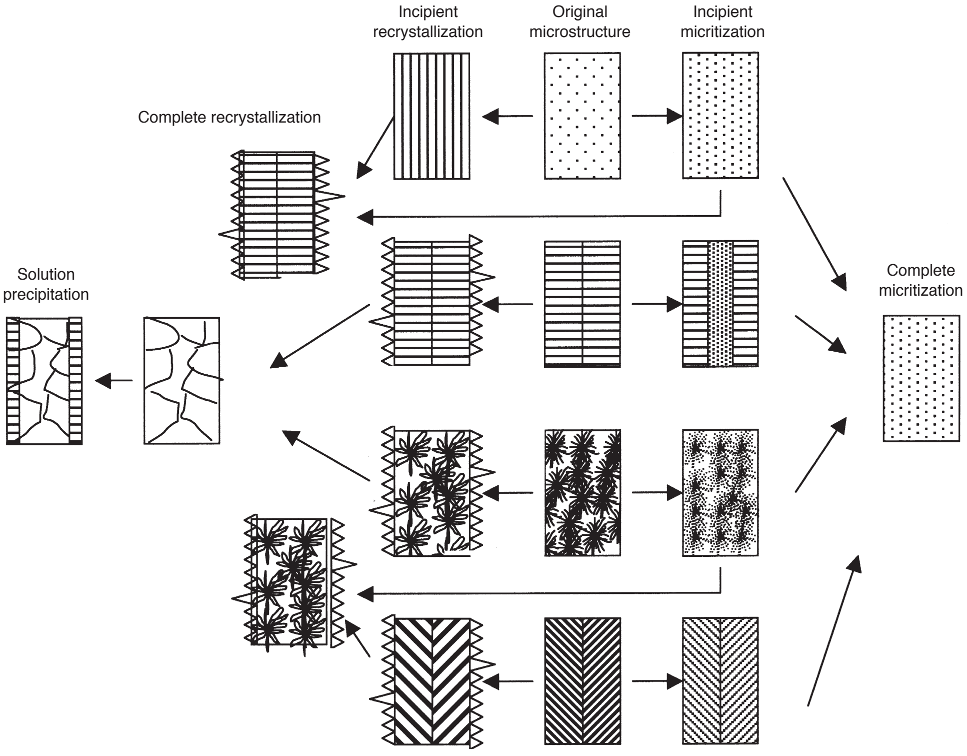

FIG. 123. Suggested diagenetic trends found in the calcareous skeletons of fossil calcified sponges; see Fig. 122 for additional microstructure symbols (adapted from Wendt, 1984; Wood, 1987).

from the Upper Triassic of Italy and Turkey. *Astrosclera* is considered to have an Upper Triassic age (see Hypercalcified Extant and Fossil Chaetetid-Type and Post-Devonian Stromatoporoid-Type Demospongiae: Systematic Descriptions, p. 209–292). However, although the biomineralization mechanism was probably the same, taxonomic affinity cannot be assumed until we have spicule confirmation.

MINERALOGY

Living calcified sponges may be aragonitic (e.g., *Ceratoporella*) or high-Mg calcite (e.g., *Acanthochaetetes* and *Merlia*). Although our sample size is small, mineralogical type has some stability within families, but not at higher taxonomic levels. Mineralogical composition therefore appears to be of low phylogenetic significance and to have arisen independently within different families.

Due to the fine microstructural preservation of many Mesozoic stromatoporoids, their original mineralogy is inferred to have been low-Mg calcite (WOOD, 1987). However, forms with original aragonite preservation are known from several Carboniferous (Pennsylvanian), middle to upper Permian, and Upper Triassic localities.

It is clear that the mineralogy of calcified sponges has varied throughout the Phanerozoic. Although our knowledge is patchy, especially from the Tertiary, aragonitic forms are only known from the Carboniferous (Pennsylvanian) to Upper Triassic, and Recent (WOOD, 1987; STANLEY & HARDIE, 1998). These periods correspond to the aragonite facilitating phases of SANDBERG (1983) and suggest that mineralogy of sponge calcareous skeletons may be under such environmental rather than taxonomic controls. Taxa with different mineralogies coexisted, such as the chaetetid genera *Acanthochaetetes* (high-Mg calcite) and *Ceratoporella* (aragonite) and milleporellid stromatoporoids (possibly low-Mg calcite), during the Upper Jurassic to Upper Cretaceous. Perhaps the calcareous skeletons in these groups arose during their appropriate facilitating phases (Wood, 1987). We require a greater diagenetic understanding, valid phylogenetic allocations, and far more material if we are to fully assess the significance and controls of mineralogical composition in calcified sponges.

DIAGENESIS

DIAGENESIS OF THE CALCAREOUS SKELETON

Diagenetic alteration is significant in stromatoporoids, as it may enhance, modify, or destroy primary skeletal characteristics.

Wendt (1984) and Wood (1987) have described diagenetic trends in Mesozoic stromatoporoids in which they distinguished three independent processes: alteration of mineralogy, alteration of microstructure, and the formation of diagenetic pseudostructures. Stromatoporoids are also subject to the range of diagenetic replacements found in other calcareous fossils, such as chertification.

ALTERATION OF MINERALOGY

Although there are several locations within upper Paleozoic and Mesozoic strata that yield forms with original aragonite preservation, most fossil sponge material, including most Mesozoic stromatoporoids, is now low-Mg calcite. Low-Mg calcite is the most stable mineralogy under normal diagenetic conditions, and originally low-Mg forms tend to retain their original mineralogy and possess well-preserved microstructures. Originally high-Mg calcite always reverts to low-Mg calcite, sometimes with loss of microstructural detail, as known from fossil acanthochaetetids, but aragonitic forms tend to be wholly recrystallized with no or few traces of primary microstructure.

ALTERATION OF MICROSTRUCTURE

Wendt (1984) described microstructural alteration from aragonitic Permian and Triassic material in terms of micritization, cementation, and recrystallization (transformation). Figure 123 shows suggested diagenetic trends found in the calcareous skeletons of fossil calcified sponges (adapted from Wendt, 1984, and Wood, 1987). Completely micritized, recrystallized structures and solution precipitation may be derived from any of the four original microstructures (see Fig. 122).

Micritization

Micritization is attributed to the decomposition of organic matrices with biominerals. The final result is the complete breakdown of the original crystal arrangement and the formation of irregularily organized granular crystals between 1 and 8 µm in length.

Micritization appears preferentially to attack areas in the microstructure most accessible to percolated fluids or where organic matter was concentrated. In orthogonal microstructure, micritization starts from the central axis of calcification and may increase in width, to eventually totally obscure the original fibers. The centers and edges of spherules are the most susceptible areas in spherulitic microstructures. Fascicular fibrous microstructure appears to be least susceptible to micritization.

Cementation

Modern calcified demosponges show the rapid precipitation of micritic aragonite within the empty cavities formed in abandoned basal parts of the skeleton.

Two phases of cementation are often found within the skeletons of Mesozoic stromatoporoids. (1) Early rim cements, precipitated epitaxially to the microstructural fibers of the skeletal elements. Syntaxial crystal growth may also occur in forms with fibrous microstructures, leading to thickening of the skeletal elements. Aragonitic calcareous sponges often show acicular aragonite crystals growing isopachously from the skeletal elements, including the tabulae. (2) Later drusy or equant cements within the interskeletal pore space. The preservation of spicules within the interskeletal spaces, or projecting into the interskeletal spaces, indicates that this cementation can occur before the diagenetic breakdown of the spicules. Since Recent calcified sponge spicules are known to dissolve during the lifetime of individuals (Hartman & Goreau, 1970), this cementation must be a very early diagenetic event.

Recrystallization

In Mesozoic stromatoporoids, recrystallization leads to a general increase in crystal size. During early recrystallization, the individual crystals in the three fibrous microstructures will maintain their acicular nature, but continued recrystallization will cause the growth of more equidimensional crystals. Previously micritized specimens can be recrystallized to form coarse mosaics with residual micritized areas.

DIAGENETIC PSEUDOSTRUCTURES

Pseudolamellar structure and scalenohedral pseudostructure have been noted in Mesozoic stromatoporoids (Wendt, 1984; Wood, 1987). Under SEM, pseudolamellar structure consists of interlocked, curved, bladed crystals, 5–10 µm thick and a few mm long. Wendt suggested that microlamellar structure is probably derived from a calcitic irregular microstructure showing some parallel orientation. Scalenohedra appear as saw-toothed formations or indentations projecting toward the center of the skeletal elements. A similar structure has been characterized by Bathurst (1975) as being a recrystallization fabric.

DIAGENESIS OF SPICULES

Spicules have been found in several Mesozoic stromatoporoid genera from many localities with differing diagenetic histories. They may be originally siliceous (demosponges) or calcareous (calcareans) and are often incorporated into the calcareous skeleton. In Recent calcified demosponges, spicules consist of hydrated amorphous silica (Hartman & Goreau, 1970; Jones, 1979). Recent calcareans have single crystal high-Mg calcite spicules. Minor amounts of SO_4^{2-}, Sr^{2+}, and Na^+ have also been found in calcitic spicules (Jones, 1979). Use of standard carbonate stains greatly enhances the visibility of fossil spicules. It is still unclear whether the absence of microscleres is due to nonsecretion or to their increased susceptibility to diagenetic loss.

Spicule diagenesis begins during the lifetime of Recent calcified demosponges. The processes are not fully known but have been partially described by Hartman and Goreau (1970) and Hartman (1979).

Due to the thermodynamic instability of inphase silica and calcite, silica spicules begin to corrode at high pH. Pitting of the spicule surface and corrosion of the acanthostyle spines and of the projecting tips have been noted in Recent and fossil forms (Gray, 1980; Hartman, 1980a). This corrosion of spicules during the lifetime of a sponge starts in the older parts of the specimen. Hartman and Goreau (1970) noted that spicule dissolution sometimes starts from the axial filament; in other cases, the head of the spicule is most susceptible. Eventually, spicule cavities or molds are left. The subsequent diagenetic history of the spicules appears to be detemined by the role they played in relation to the calcareous skeleton.

Originally Siliceous Spicules

Early diagenetic processes have nearly always replaced the amorphous silica of demosponge spicules by a secondary polycrystalline mosaic of $CaCO_3$, SiO_2, or FeS_2, or a single crystal pseudomorph of SiO_2.

Early Diagenesis

During life, spicules may be wholly free or incorporated partially or fully into the primary or secondary calcareous skeleton. In forms that produce a secondary backfill, the spicule molds may become filled with a syntaxial growth of calcite crystals, making it impossible to determine the original placing and presence of the spicules.

Later Diagenesis

If not totally obliterated by epitaxial skeletal growth, the mold may be subsequently filled with other minerals.

Calcite Pseudomorphs

Calcite pseudomorphs may be mono- or polycrystalline. Where calcite pseudomorphs are found, the microstructure of the calcareous skeleton is always well preserved. Pseudomorph boundaries are only apparent when they are covered with a thin micrite envelope or when they are of different calcite mineralogy from the calcareous skeleton as shown by staining. Otherwise, the pseudomorphs appear as spicule ghosts as in *Parastromatopora japonica,* described by HARTMAN and GOREAU (1970, fig. 16). Here, the spicules are recognized by their crystallographic difference from the fibers of the calcareous skeleton microstructure. The calcite pseudomorphs tend to be found in the core areas of the specimens, which have been partially protected from later leaching of corrosive pore waters.

In forms where the originally siliceous spicules formed a primary skeletal framework, the calcite pseudomorphs are rarely found projecting into the interskeletal spaces. Most frequently, they terminate abruptly due to corrosion of the projecting tips. In *Blastochaetetes irregularis* WOOD & REITNER, 1988, where calcareous pseudomorphs are preserved within the tubules, the areas of spicule contact with the calcareous skeleton are more poorly preserved than in areas where spicules are encased by spar within the pore space. The skeletal calcite appears to have a corrosive effect upon the spicules.

Calcite pseudomorphs are also susceptible to micritization. All stages, from well-preserved pseudomorphs with a thin micritized coating, through badly micritized, but discernible spicules forming diffuse elongate and circular lighter areas, to a totally micritized central zone within the calcareous skeletal elements are noted.

Pyrite Pseudomorphs

Pyrite pseudomorphs appear as agglomerates or as chains of pyrite crystals (see *Actinostromarianina lecompti,* Fig. 170,*3b*). They are often shorter than calcite pseudomorphs, but both pseudomorph types are frequently found together in the same specimen (WOOD & REITNER, 1986) indicating that pyritization has occurred either after partial dissolution of the silicious spicule or as replacement of the calcite pseudomorph. Examples have been found in which threads of pyrite are seen forming within calcite pseudomorphs. Pyritization appears to nucleate upon the organic axial filament, probably due to bacterial activity, and this may occur at a very early stage of diagenesis.

Pyrite pseudomorphs are often found in large numbers near the outer edges of specimens (see WOOD & REITNER, 1986, pl. 35,*3*), and pseudomorphs can remain after total obliteration of the calcareous skeleton by subsequent silicification.

Siliceous Spicule Pseudomorphs

Siliceous spicule pseudomorphs are occasionally found in Mesozoic stromatoporoids. They are found in chertified areas of specimens, often where the calcified skeleton has been totally obliterated and can be exceptionally well preserved.

The typical corrosion and pitting features noted by HARTMAN and GOREAU (1970) in Recent calcified demosponge spicules are seen on these pseudomorphs. Axial canals are preserved, but no acanthostyle spines are noted. Considering their excellent preservation, it is therefore unlikely that they were originally acanthostyles.

Siliceous spicule pseudomorphs sometimes appear dark brown and microgranular. The axial canals are not visible, and the brownish granular appearance and high relief of some pseudomorphs suggest that the original spicule mineralogy has been altered. GRAY (1980) noted that the occurrence of this microgranular silica within spicule pseudomorphs and not within the chalcedonic silica walls, as well as the retention of delicate spicule corrosion features, are good evidence of an original mineralogy of opal A in fossil calcified demosponges, as in their extant relatives.

PRESENT CLASSIFICATION

The following lines of evidence suggest that the formation of a basal calcareous skeleton in sponges is a simple process and that sponges can calcify with relative ease.

1. Calcareous skeletons have a wide systematic distribution within the Porifera. Calcified demosponges are known from the orders Haplosclerida, Agelasida, Hadromerida, and Poecilosclerida. Calcified calcareans are known from both the Calcinea and the Calcaronea.

2. Different microstructures and seemingly different biomineralization mechanisms are present within closely related forms. For example, both *Astrosclera* and *Ceratoporella* are haplosclerids, but one produces a spherulitic microstructure with an intracellular origin and the other an elongate spherulitic one via a secretory pinacoderm. In addition, members of the same clade appear to have independently produced different calcareous mineralogies and microstructures at different times (e.g., *Newellia mira* and *Euzkadiella erenoensis*) (WOOD, REITNER, & WEST, 1989).

3. The closest relatives of Recent calcified forms are noncalcified (e.g., *Spirastrella* to *Acanthochaetetes,* and *Agelas* to *Astrosclera* and *Ceratoporella*).

4. Some species appear to have a facultative ability to calcify. There are four species of the genus *Merlia,* but only two produce a calcareous skeleton.

5. The crystals precipitated by sponges do not have a unique crystal habit, trace element, or isotopic composition, which points to a minimal intervention of biological processes. The $\delta^{18}O$ signature of calcified demosponges all fall within the field of normal seawater, indicating that little vital fractionation occurs (e.g., ROSENHEIM & others, 2004).

6. The favored polymorph of calcified demosponge calcareous skeletons follows the oscillating trend first proposed by SANDBERG (1983) and STANLEY and HARDIE (1998).

It is clear that the mere possession of a calcareous skeleton has little higher taxonomic significance. In addition, the calcareous skeleton is convergent in many characteristics.

Gross Morphology

Although the gross morphology of Mesozoic stromatoporoids is often subject to environmental control, there does appear to be stability within some species. However, gross morphology can be used only as a subsidiary generic or specific feature, and then only with caution.

Surface Features

Stromatoporoid surface features are an expression of the relative thickness of soft tissue, the aquiferous system required to drain it, and the position of this system relative to the areas of skeletogenesis. These features may not always be consistent within a species and hence can only be used as subsidiary species characteristics.

Spicular Skeleton

In Mesozoic stromatoporoids, spicule type and arrangement are the best taxonomic criteria available, and the only criteria of use in high-level systematic allocation. They offer the only indication of taxonomic affinity within the Porifera. However, it is highly likely in the evolution of demosponges that the basic monaxon megasclere spicule has evolved several times. For this reason, much stress has been laid upon the use of microscleres for demosponge systematics. Unfortunately, the majority of known Mesozoic stromatoporoid spicules are monaxon megascleres and few microscleres have been found.

The following relationships have been determined between the primary spicule framework and the secondary calcified skeleton.

1. A calcified skeleton without spicular skeleton (e.g., *Vaceletia, Burgundia*).

2. Spicules present, but placing is independent of calcified skeleton: i.e., spicules are incorporated into the skeleton by chance (e.g., *Blastochaetetes irregularis* WOOD & REITNER, 1988*, Ceratoporella*).

3. The calcified skeleton is precipitated around a primary spicule framework or lattice:

3a. The crystals of the calcareous skeleton initiate from spicule bases: e.g., *Dehornella.*

3b. The calcified skeleton is precipitated around a spicule framework: e.g., *Actinostromarianina lecompti* and *Actinostromaria* sp.

The way in which forms construct their skeletons is taken to be of family level and lower taxonomic significance when combined with spicule data.

Microstructure

Microstructure seems to be the result of the form of organic template and the biomineralization mechanism or mechanisms employed by the sponge. Microstructure of the calcareous skeleton may be a highly specific characteristic that allows placement of aspiculate fossil forms within particular orders. Some combinations of microstructure and mineralogy, however, are known only in the fossil record, and data about the systematic distribution of biomineralization mechanisms in sponges is insufficient to assess the relative status of differing microstructures. It would seem probable that biologically controlled precipitations (e.g., intracellular spherulites) would have greater higher systematic use than biologically induced ones (e.g., orthogonal cement).

Internal Organization of the Calcareous Skeleton

REISWIG (1975) stated in his study of the aquiferous systems of three living marine demosponges that the aquiferous systems of two unrelated species, *Halichondria panicea* (order Halichondrida) and *Haliclona permollis* (order Haplosclerida) were so similar that it was impossible to make species determinations of desilicified sections on the basis of canal organization alone. This suggests that the construction and organization of the aquiferous system can only be used as a very low-level taxonomic criterion.

The internal organization of the sponge calcareous skeleton can be taken to be a direct reflection of soft-tissue and aquiferous system organization and will be of low systematic significance. In general, forms that have a thin veneer of tissue and, therefore, show traces of the exhalant canal system as astrorhizal grooves or ridges in the surface of the calcareous skeleton produce a compact skeletal network with little or no internal traces of the aquiferous system. In contrast, forms that have a greater thickness of living tissue have penetrating aquiferous systems, thus producing an open calcareous skeleton.

Some skeletal features have been found to be extremely variable: e.g., presence or absence of laminae. These can also no longer be used as significant taxonomic features.

Mineralogy

Mineralogy appears to be of low phylogenetic significance, having arisen independently within several living calcified demosponge families. It is proposed that this feature not be used beyond the family level. The Porifera, both living and fossil, remains one of the most difficult groups to systematize and hence construct reliable phylogenies. Although cladistic analyses have been attempted for Recent poriferans, these have as yet proved most inconclusive, due to the lack of understanding of the various character states. With no soft tissue and uncommon spicule preservation and the dominance of skeletal features that are of no higher taxonomic importance, this situation is compounded for fossil forms. The possibility of much further insight remains bleak.

The following classification outline is adopted in this *Treatise* for Mesozoic and

Cenozoic stromatoporoids. The placing of families in the Porifera has been determined by their spiculation; those families with no spiculate representatives remain as *incertae sedis* within the Porifera. The phylum allocation of some families remains uncertain.

- Class DEMOSPONGIAE Sollas, 1885
  - Order HADROMERIDA Topsent, 1894
    - Family ACANTHOCHAETETIDAE Fischer, 1970
    - Family SUBERITIDAE Schmidt, 1870
    - Family SPIRASTRELLIDAE Ridley & Dendy, 1886
  - Order CHONDROSIDA Boury-Esnault & Lopès, 1985
    - Family CHONDRILLIDAE Gray, 1872
  - Order POECILOSCLERIDA Topsent, 1928
    - Family MERLIIDAE Kirkpatrick, 1908
  - Order HALICHONDRIDA Gray, 1867
    - Family UNCERTAIN
  - Order AGELASIDA Hartman, 1980b
    - Family ASTROSCLERIDAE Lister, 1900
  - Family MILLEPORELLIDAE Yabe & Sugiyama, 1935
    - Family ACTINOSTROMARIIDAE Hudson, 1955c
    - Family ACTINOSTROMARIANINIDAE Wood, 1987
    - Family UNCERTAIN
  - Order HAPLOSCLERIDA Topsent, 1928
    - Family CALCIFIBROSPONGIIDAE Hartman, 1979
    - Family EUZKADIELLIDAE Reitner, 1987a
    - Family NEWELLIDAE Wood, Reitner, & West, 1989
  - Order DICTYOCERATIDA Minchin, 1900
    - Family VACELETIIDAE Reitner & Engeser, 1985
  - Order UNCERTAIN
- Class CALCAREA Bowerbank, 1864
    - Family BURGUNDIIDAE Dehorne, 1920
    - Family UNCERTAIN
  - Subclass CALCINEA Bidder, 1898
    - Order MURRAYONIDA Vacelet, 1981
      - Family MURRAYONIDAE Dendy & Row, 1913
      - Family PARAMURRAYONIDAE Vacelet, 1967a
  - Subclass CALCARONEA Bidder, 1898
    - Order LITHONIDA Vacelet, 1981
      - Family MINCHINELLIDAE Dendy & Row, 1913
    - Order BAERIIDA Borojevic, Boury-Esnault, & Vacelet, 2000
      - Family PETROBIONIDAE Borojevic, 1979
      - Family LEPIDOLEUCONIDAE Vacelet, 1967a