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Paleogeography and Biostratigraphy of the Hypercalcified Chaetetid-Type Porifera (Demospongiae)

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PART E, REVISED, VOLUME 4, CHAPTER 2F: 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 (Vacelet, Willenz, & Hartman, 2010). 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 lower upper Carboniferous. 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 (Vacelet, Willenz, & Hartman, 2010). The general distribution of the three extant hypercalcified genera with a chaetetid skeleton are as follows: *Merlia*: circumtropical and warm temperate latitudes (Madeira, Mediterranean) (Vacelet, Willenz, & Hartman, 2010); *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.

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 1. 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 2. Hypercalcified demosponges, including chaetetids, are known from five stages in the Carboniferous: Visean, Serpukhovian, Bashkirian, Moscovian, and Kasimovian (Fig. 1–3), but they are most abundant in the Bashkirian and Moscovian. Permian chaetetid reefs are only known from the Guadalupian and Lopingian (Fig. 3–5). Hypercalcified demosponges, including chaetetids, are reported from two Jurassic stages, Oxfordian and Kimmeridgian (Fig. 6). 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. 1–6). 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 2). 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 2).

Although information on the microstructure and spicules, or spicule pseudmorphs, is currently lacking, there are

West, Ronald R. 2012. Part E, Revised, Volume 4, Chapter 2F: Paleogeography and biostratigraphy of the hypercalcified chaetetid-type Porifera (Demospongiae). Treatise Online 37:1–29, 7 fig., 2 tables.

TABLE 1. 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 1 (*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
Upper Carboniferous (Pennsylvanian)	Gzhelian	Hypercalcified demosponges	Tropical	Japan
	Kasimovian–Moscovian–Bashkirian	*Hypercalcified demosponges, with chaetetid reef banks*	Tropical	*western United States, Japan, Kyrgyzstan*
Lower 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 2. Summary of the paleolatitudinal position of reefs that contain, or could contain, chaetetids in the 37 different Phanerozoic stratigraphic intervals listed in Table 1. *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 (new).

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

a number of described taxa that have a chaetetid skeleton and could be hypercalcified 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 West, 2012, table 6). *Chaetetes* (*Boswellia*) and *Pachytheca* are valid chaetetid genera, and occur in the Devonian (West, 2012, table 3). Oliver, Merriam, and Churkin (1975) reported Devonian chaetetids in Alaska and in Devonian reefs from the Cantabrian Mountains in Spain (Méndez-Bedia, Soto, & Fernández-Martinez, 1994; Soto, Méndez-Bedia, & Fernández-Martinez, 1994). 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 lower Carboniferous 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

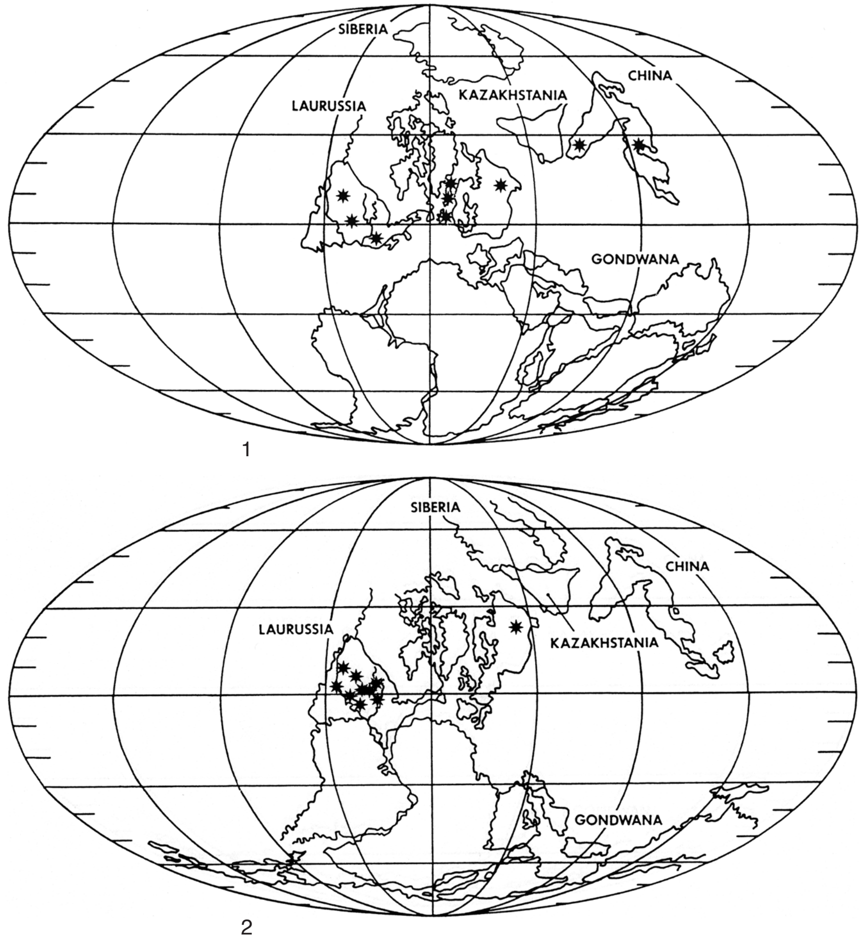

FIG. 1. Distribution of Carboniferous chaetetids; *1,* general distribution of chaetetids during the middle Early Carboniferous (approximately 320–340 Ma; new); *2,* general distribution of chaetetids during the middle Late Carboniferous (approximately 305–320 Ma; new).

also been reported from: Peru (BASSLER, 1950); Akiyoshi-dai, Japan (OTA, 1977, 1968); Taurides, southern Turkey (DENAYER, 2010); Donets Basin, Ukraine (OGAR, 2011); 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 1 and summarized in Table 2, chaetetids also occur in upper Carboniferous reefs of Holm Land, northeastern Greenland

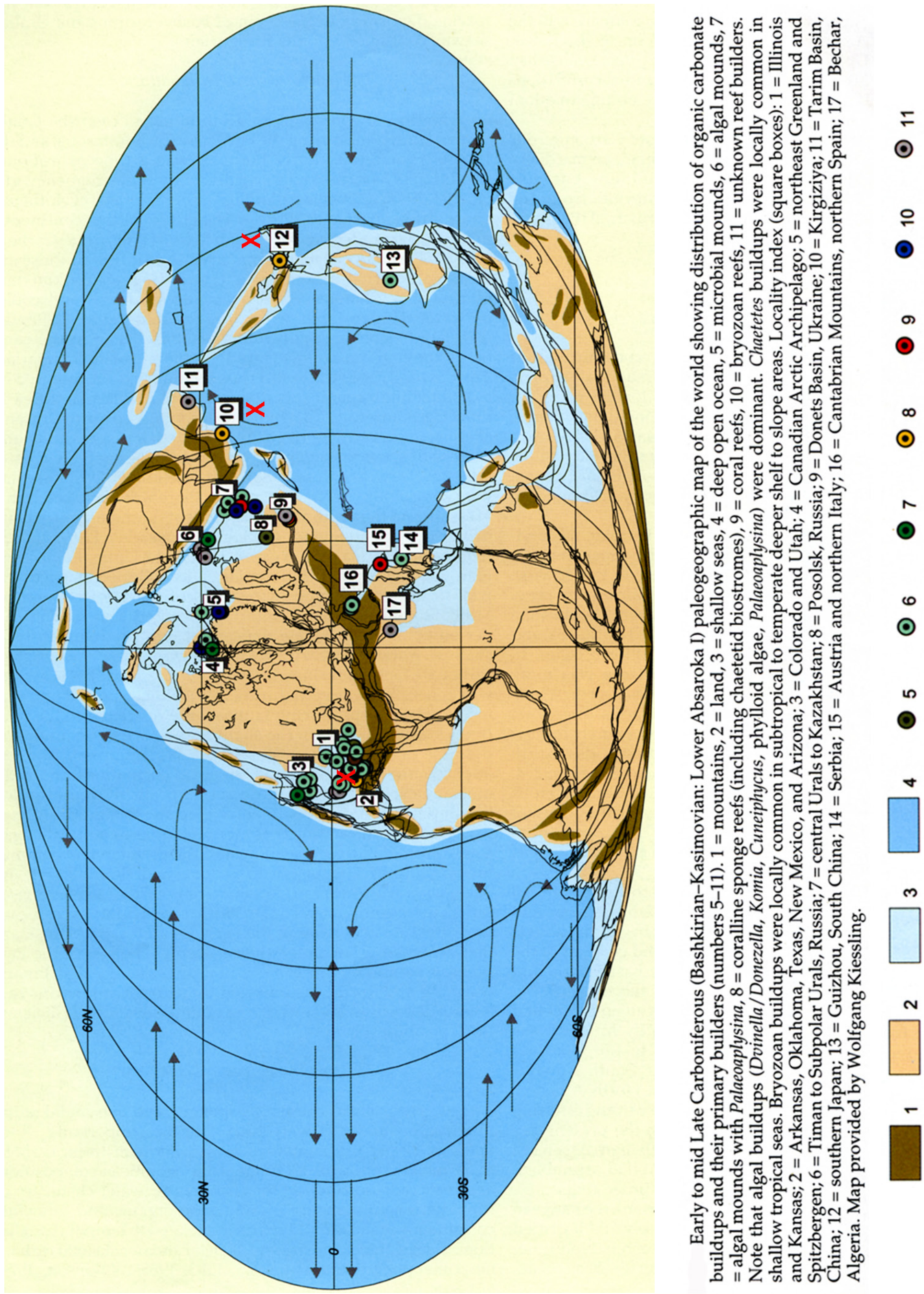

FIG. 2. Carboniferous reefs, those with chaetetids marked with a *red X;* Lower to mid–Upper Carboniferous (Bashkirian–Kasimovian) chaetetid occurrences; red *X* between numbers 1 and 2 and red *X* markings below number 10 and above number 12 are occurrences in the central and western United States, Kyrgyzstan, and Japan respectively (adapted from Wahlman, 2002, p. 274, color fig. 2; courtesy of the author and the Society for Sedimentary Geology).

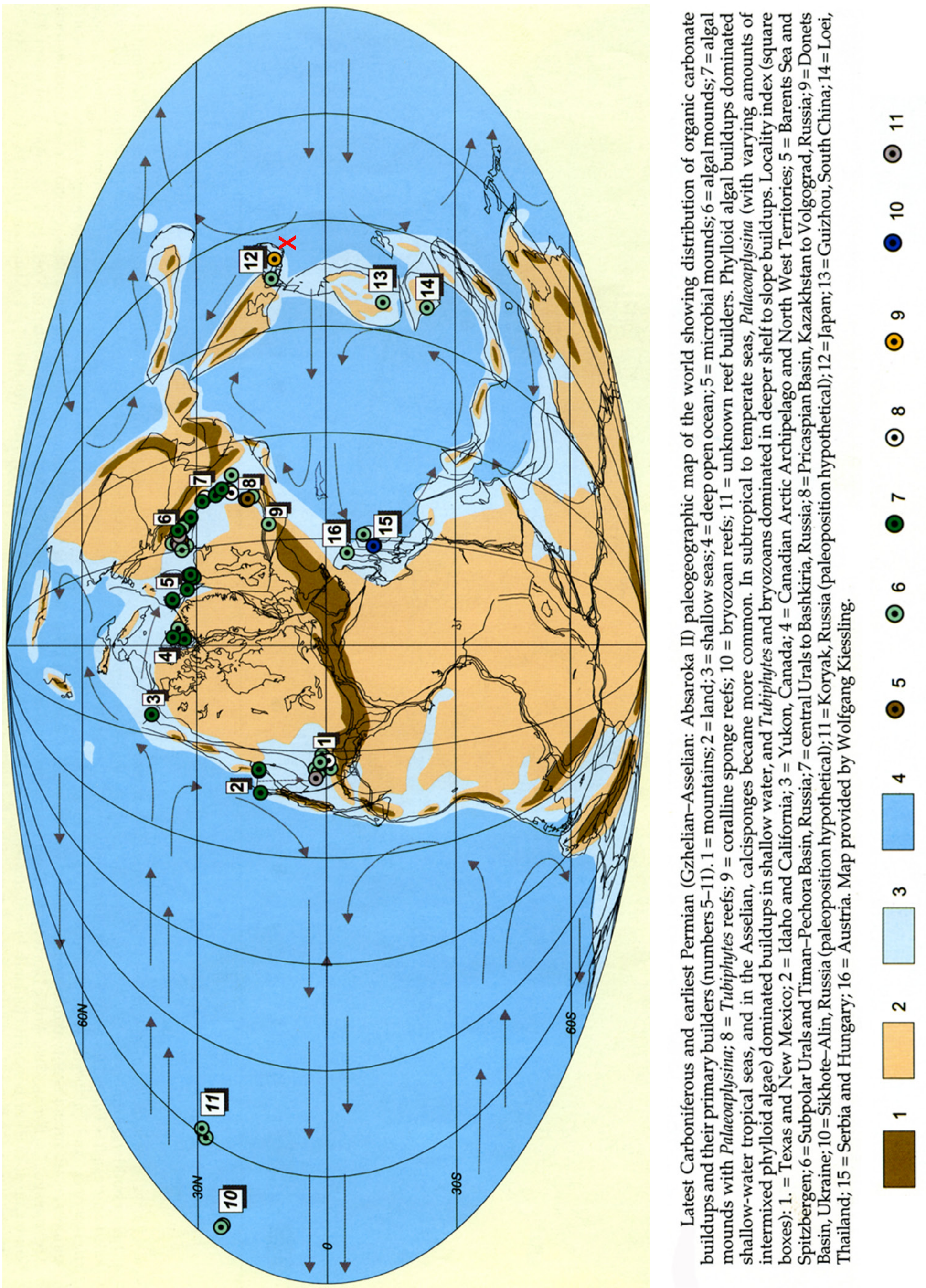

FIG. 3. Upper Carboniferous and lower Permian reefs, those with hypercalcified demosponges marked with a *red X;* uppermost Carboniferous (Gzhelian) and lowest (Asselian) Permian hypercalcified demosponge localities; *X* below and slightly right of number 12 is the Japanese (Akiyoshi) site (adapted from Wahlman, 2002, p. 275, color fig. 3; courtesy of the author and the Society for Sedimentary Geology).

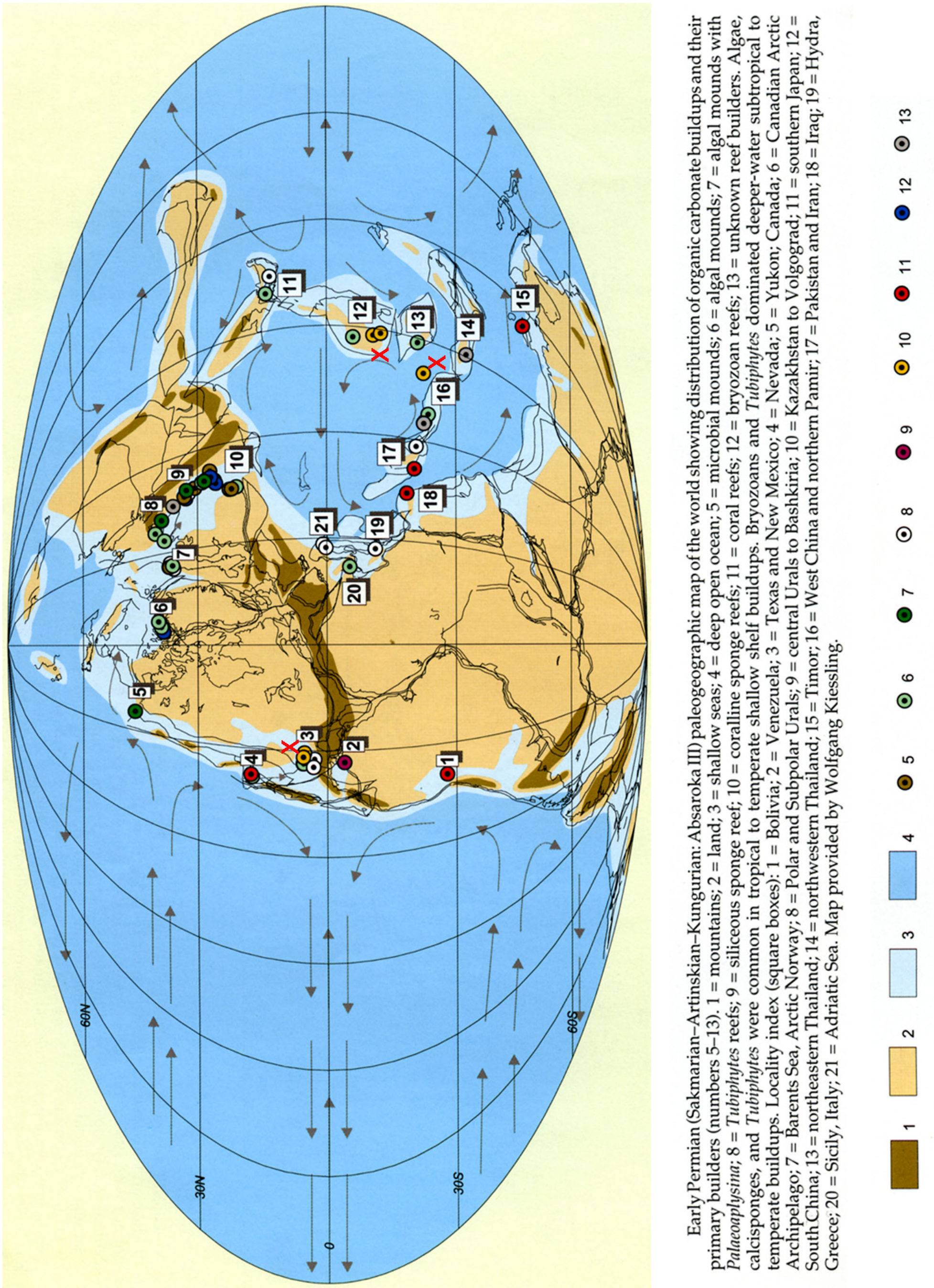

FIG. 4. Lower Permian reefs, those with hypercalcified demosponges marked with a *red X;* lower Permian (Sakmarian, Artinskian, and Kungurian) hypercalcified demosponge localities; *X* markings above and to left of number 3, between numbers 13 and 16, and to lower left of number 12 refer to western Texas, southern and western China, respectively (adapted from Wahlman, 2002, p. 276, fig. 4; courtesy of the author and the Society for Sedimentary Geology).

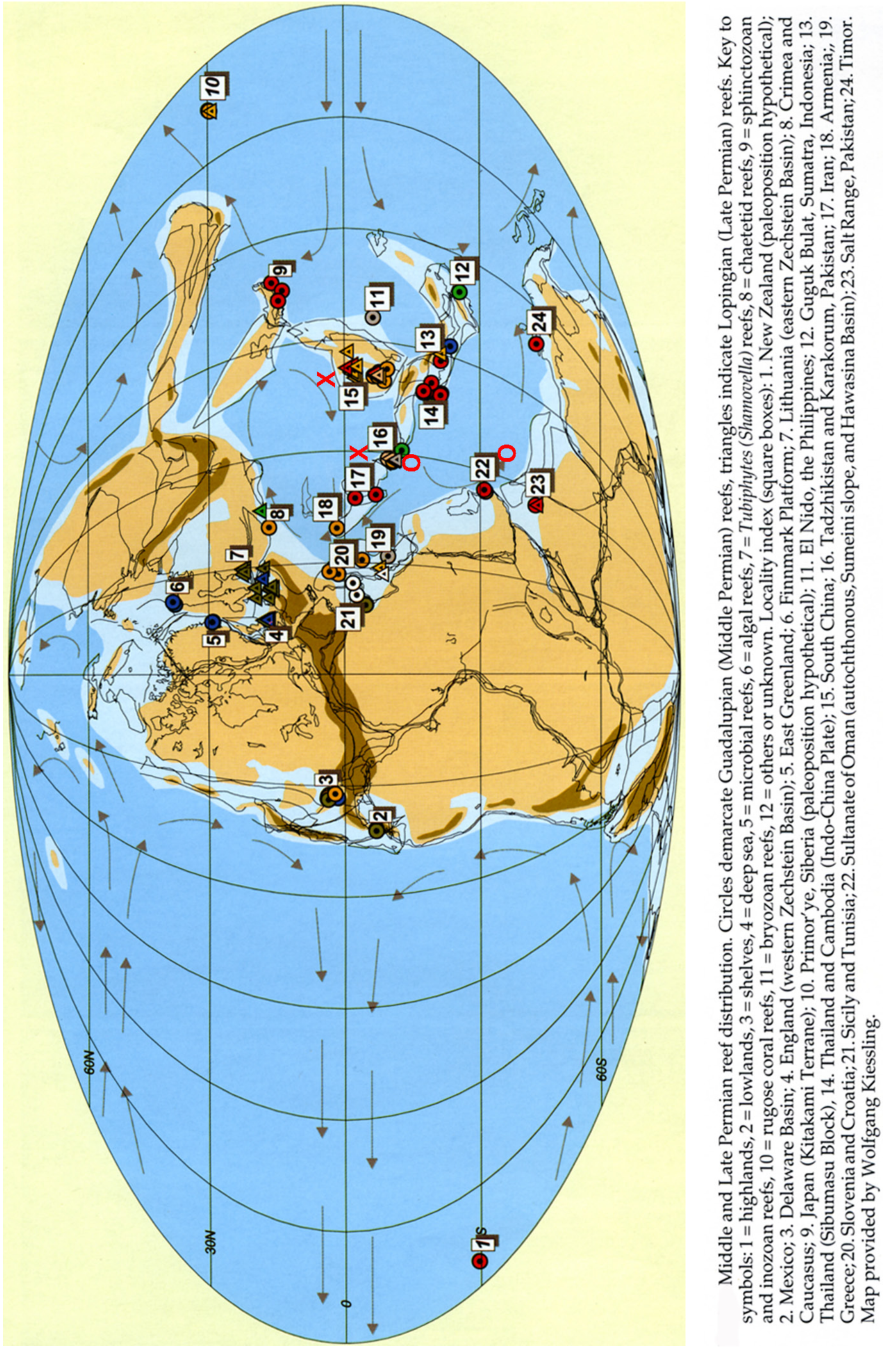

FIG. 5. Permian reefs, those with chaetetids marked with a *red X* or *O;* middle (Guadalupian) and upper (Lopingian) Permian chaetetid occurrences; *O* markings just below number 22 and to the lower left of number 16 are Guadalupian occurrences in Oman and Pakistan, respectively; *X* markings between 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).

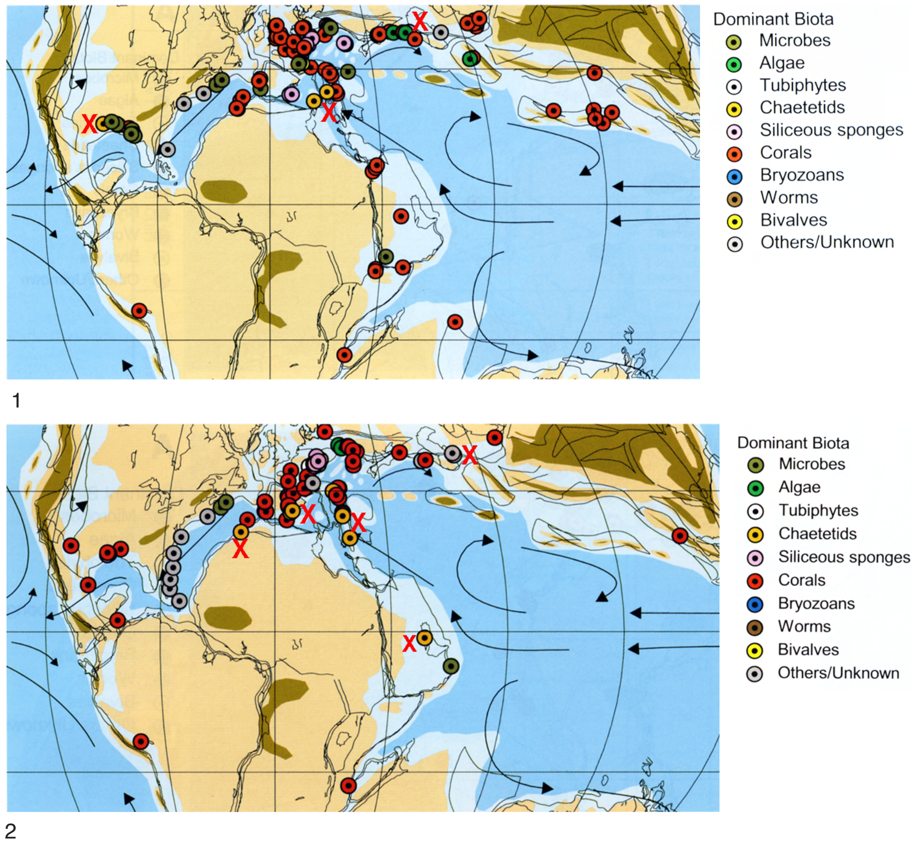

FIG. 6. Jurassic reefs, those with chaetetids marked with a *red X; 1,* Oxfordian chaetetid occurrences; *X* markings are localities in Mexico, southern Europe, and Iran (adapted from Leinfelder & others, 2002, p. 481, color fig. 5A; courtesy of the author and the Society for Sedimentary Geology); *2,* 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).

(STEMMERIK, 1989), and others are included 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, 1987d). Chaetetids also occur in Paleogene and Neogene rocks, as shown in Table 1, 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 1, 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 page 6 herein).

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,* and *Ptychochaetetes,* 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 (West, 2012, tables 3, 6). 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 (West, 2012, tables 3, 6). There are also three other chaetetid genera in the Triassic that are inadequately known, because spicules, or spicule pseudomorphs, have not yet been recognized (West, 2012, tables 3, 6). 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 *Treatise Online,* Part E, Revised vol. 4, Chapter 16A) 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 (Termier, 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 diagenetic processes, and thus the older and less

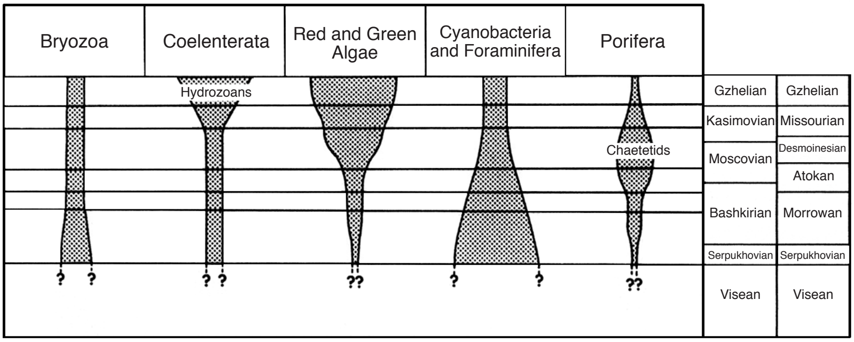

FIG. 7. Relative abundance (skeletal biovolume) in relation to the major groups of reef builders, upper Carboniferous reef mounds; time scale on the far right is the regional scale for North America, and the other one is the International time scale (adapted from West, 1988, p. 157, fig. 1; courtesy of the author and the Society for Sedimentary Geology).

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 WEST (2012, table 3), 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, 1990). 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 1). 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. 1.1–1.2). 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. 3; Table 1) and from the lower Permian (Sakmarian, Artinskian, and Kungurian) of western Texas and southern and western China (Fig. 4; Table 1). Chaetetid reefs occur in the upper Permian (Guadalupian and Lopingian) of Oman, Pakistan, and southern China (Fig. 5; Table 1; Weidlich, 2002, 2007a, 2007b; Weidlich & Bernecker, 2003). Phylloid algae (Fig. 7) 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 (West, 2012, table 3); 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. 7).

A number of stratigraphic gaps exist between the currently known first and last appearances of the valid chaetetid genera (West, 2012, table 3), as well as many blanks and unknowns in the temporal and spatial distribution of chaetetids (Table 1). 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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