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Evolution of the Hypercalcified Chaetetid-Type Porifera (Demospongiae)

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

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The chaetetid basal calcareous skeleton, the basis for membership in the order Chaetetida, is polyphyletic (Wood, 1990; and see West, 2011c: *Treatise Online,* Part E, Revised, Volume 4, Chapter 2C, Classification of the fossil and living hypercalcified chaetetid-type Porifera). Genera with a chaetetid skeleton belong to at least three orders of the Demospongiae (the Hadromerida, Poecilosclerida, and Agelasida) and possibly others. The formerly recognized subclasses of the Demospongiae are now abandoned, as suggested by Boury-Esnault (2006), based on the studies of Borchiellini and others (2004). Finks (2003b, p. 265) commented on the possibility of a relationship between demosponges and stromatoporoids, based on Hartman and Goreau (1966). But Finks did not mention the possibility of such a relationship for chaetetids with extant *Ceratoporella,* as noted in other articles by Hartman and Goreau (1972, 1975). Wood and Reitner (1988, p. 213) suggested a morphological continuum between stromatoporoids and chaetetids, noting that, “The distinction previously drawn between ‘stromatoporoids’ and ‘chaetetids’ is artificial.”

As noted in West (2011c), there is some potential overlap between the two subclasses Tetractinomorpha and Ceractinomorpha; see Hooper and van Soest (2002b, p. 16–17) for details. More recently, Borchiellini and others (2004) pointed out that within the clade Demospongiae *sensu stricto,* Tetractinomorpha and Ceractinomorpha are polyphyletic, and for the same reason, Boury-Esnault (2006) has called for the abandonment of these two traditional subclasses. Not only are these subclasses polyphyletic, but some of the families and genera within the classical orders of the Demospongiae are also polyphyletic (Boury-Esnault, 2006).

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

Currently there are 22 taxa (20 genera, 3 subgenera) with a chaetetid basal calcareous skeleton for which reliable information on spicule morphology and tubule wall mineralogy and microstructure is available (Table 1; see also West, 2011c, table 3). Because the spicules of fossil chaetetids are all pseudomorphs, the original mineralogy is unknown but is inferred to have been siliceous, based on knowledge of extant forms such as *Acanthochaetetes wellsi*, *Ceratoporella nicholsoni*, and *Merlia normani*.

There are four taxa (genera) with a chaetetid skeleton for which some meaningful information on the original mineralogy and microstructure of the basal calcareous skeleton is known. However, the presence of pseudomorphs of spicules is unknown or questionable (Table 2; see also West, 2011c, table 4). Therefore, there is some doubt as to the validity of these four genera.

Finally, there are 32 taxa (31 genera, 2 subgenera) for which the original mineralogy and microstructure of the basal calcareous skeleton and pseudomorphs of spicules are either very poorly known or unknown (West, 2011c, table 5). These taxa are based on less reliable skeletal features, as noted above (item 3). Of the 32 taxa in West (2011c, table 5, p. 8), 26 taxa (25 genera and 2 subgenera)

West, Ronald R. 2012. Part E, Revised, Volume 4, Chapter 2D: Evolution of the hypercalcified chaetetid-type Porifera (Demospongiae). Treatise Online 35:1–26, 6 tables.

TABLE 1. Geological range (from the literature) of valid hypercalcified demosponges with a chaetetid skeleton; *, CREMER (1995) documented the microstructure and spicule pseudomorphs in the genus *Bauneia* PETERHANS, 1927, but gave no reasons why he queried the validity of his assignment; **, *Chondrochaetetes* REITNER, 1991, is a junior synonym of *Chaetetes* (new).

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

are considered to be chaetetid form taxa and are best referred to as simply chaetetids or hypercalcified demosponges with a chaetetid skeleton. The remaining 6 taxa (genera), as noted in WEST (2011c, table 5, p. 8), are not considered to be chaetetids and are either worm tubes or corals.

From an evolutionary standpoint, there are 22 (20 genera and 3 subgenera), or perhaps 26 (22, including the 3 subgenera, with the addition of 4 genera of an unknown spicule morphology), to be placed in a phylogenetic framework. The geologic ranges of the valid taxa (22, including the 3 subgenera) are given in Table 1; and those of the additional 4 inadequately described taxa are included in Table 2. This same information is represented for all 26 taxa in Table 3. Tables 4 and 5 list the basic characteristics of the 22 valid taxa (Table 4), along with the stratigraphic position and the geographic locality of their first and last known occurrences (Table 5). Also included in Tables 4 and 5 are the 4 taxa for which definitive information on the spicules is currently unknown.

TABLE 2. Geological ranges (from the literature) of inadequately known hypercalcified demosponges with a chaetetid skeleton (new).

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

Of the 22 valid taxa, only *Ceratoporella, Chaetetes* (*Chaetetes*), *Chaetetes* (*Boswellia*), *Pachytheca,* and *Spherolichaetetes* are known from the Paleozoic, and of these, only the last 4 are restricted to the Paleozoic (middle Silurian to Permian) (Table 5). Spicules (pseudomorphs) have not been reported from any Silurian chaetetids, and the original mineralogy and microstructure of the tubule walls have been obscured either by recrystallization, silicification, or dolomitization. Thus, the Silurian occurrences are

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

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

questionable. Spicules (tylostyle pseudomorphs) and penicillate calcareous tubule walls have been documented for *Pachytheca* (Reitner, 1992), a genus only known from the Middle Devonian (Eifelian) of northern Spain. Gray (1980) reported spicules (pseudomorphs) in *Chaetetes* (*Boswellia*) from the lower Carboniferous of Wales, and Reitner (1991, p. 181) interpreted the tubule walls to be fascicular fibrous (water-jet) calcite (probably Mg-calcite). Megascleres are unknown from *Chaetetes* (*Chaetetes*), however, probable euasters are present in the fascicular fibrous tubule walls of a specimen from the Carboniferous of Russia (Reitner, 1991, p. 187, fig. 6).

These are the only reported occurrences of spicules in Paleozoic specimens with a chaetetid basal calcareous skeleton (Gray, 1980; Reitner, 1991, 1992). Although the mineralogy and microstructure of the upper Permian genus, *Spherolichaetetes,* is known (Gautret & Razgallah, 1987), spicules are not, thus there is some doubt about its taxonomic affinity (Reitner, 1992). As shown in Table 5, the Permian occurrence of *Ceratoporella* is also questionable. The mineralogy and microstructure of the upper Permian specimens assigned to *Ceratoporella* are known (Termier, Termier, & Vachard, 1977), but spicules are not. This Permian occurrence of *Ceratoporella* is further complicated by the fact that Termier, Termier, and Vachard (1977, p. 27) described *Preceratoporella tunisiana* as a new genus and species in their text, but in explanations of their plates on p. 106, referred to it as *Ceratoporella*? *tunisiana.* The query indicates that assignment of the species to this genus is questionable. The Paleobiology Database (2006) for the Permian *Ceratoporella* shows it as ?*Ceratoporella* sp., and the query

TABLE 4. Basic characteristics of valid taxa from Table 1 and inadequately known taxa from Table 2 (*asterisks*); +, data from CREMER (1995); ++, data from BIZZARINI and BRAGA (1988) (new).

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

here indicates that the entire assignment is doubtful. Obviously, additional study is required.

Definitive data on the spicules (pseudomorphs) and/or tubule wall mineralogy and microstructure for the other Paleozoic taxa with a chaetetid basal calcareous skeleton listed by HILL (1981, table 3, p. 497) are lacking and thus are excluded from the discussion herein (WEST, 2011c, table 5). This excludes the two Upper Ordovician genera, *Chaetetella* and *Chaetetipora* (HILL, 1981, table 3, p. 497), and the range of the order Chaetetida is middle Silurian to Recent. The other Paleozoic chaetetid taxa shown in table 3 of HILL (1981) are now considered to be tabulate corals (WEST, 2011c, table 6).

Although chaetetid demosponges are known from the upper Permian (TERMIER, TERMIER, & VACHARD, 1977; GAUTRET & RAZGALLAH, 1987; FLUGEL & REINHARDT,

TABLE 5. Stratigraphic and geographic occurrences of valid taxa from Table 1 and inadequately known taxa from Table 2 (*asterisks*).

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

1989), they are absent from the Lower and Middle Triassic. *Atrochaetetes*, *Bauneia*, *Blastochaetetes*, *Blastoporella*, *Cassianochaetetes*, *Ceratoporella*, *Chaetosclera*, *Kemeria*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, and *Sclerocoelia* are known from the lower Upper Triassic (Carnian) of Italy. *Blastoporella*, *Kemeria*, and *Ptychochaetetes* are reported from the Upper Triassic of Turkey (see Table 5). The mineralogy and microstructure of the tubule walls are known for all of these genera, and definite spicules (pseudomorphs) are known from *Atrochaetetes*, *Bauneia*, *Blastochaetetes* (CREMER, 1995), *Chaetosclera* (REITNER & ENGESER, 1989), *Meandripetra* (DIECI & others, 1977), *Ptychochaetetes* (CREMER, 1995), and *Scleroscoelia* (DIECI & others, 1977) (Table 4). CUIF (1974) described *Ceratoporella goreaui* from the Saint-Cassian Dolomites (Upper Triassic) of northern Italy, documenting the mineralogy and microstructure, but nothing on the spicules. FÜRSICH and WENDT (1977) reported five undescribed species of *Ceratoporella* in the patch reefs of the Cassian Formation (Upper Triassic) of the southern Alps. ENGESER and TAYLOR (1989) stated that it is possible that there are monaxon spicules in *Leiospongia*, but no spicule pseudomorphs are recorded from *Cassianochaetetes*. Thus, of the 13 Triassic genera, only 10 are valid: *Atrochaetetes, Bauneia*, *Blastochaetetes*, *Ceratoporella*, *Chaetosclera*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, *Ptychochaetetes*, and *Sclerocoelia* (Table 4). Additionally, *Atrochaetetes, Bauneia, Blastochaetetes,* and *Ptychochaetetes* occur in the Jurassic, along with *Chaetetes* (*Pseudoseptifer*) (Table 5). Also, *Atrochaetetes* and *Blastochaetetes* extend into the Cretaceous. Furthermore, *Ptychochaetetes* occurs in the Miocene of France (BODERGAT, 1975; TERMIER & TERMIER, 1976), and *Ceratoporella* is a well-known, extant genus. The other five valid genera, *Chaetosclera*, *Keriocoelia*, *Leiospongia*, *Meandripetra*, and *Sclerocoelia* are restricted to the Carnian of Italy (see Table 5).

The mineralogy and microstructure of the tubule walls, as well as spicules and/or pseudomorphs of spicules, are known from the remaining nine genera, namely: *Acanthochaetetes*, *Calcichondrilla, Calcispirastrella*, *Calcistella*, *Calcisuberites*, *Chaetetes* (*Pseudoseptifer*), *Chaetetopsis*, *Merlia*, and *Neuropora* (Table 4). The first occurrence of *Acanthochaetetes*, *Calcistella*, *Chaetetes* (*Pseudoseptifer*), and *Chaetetopsis* is in the Jurassic. *Chaetetes* (*Pseudoseptifer*) is known only from the Lower Jurassic of northern Italy, but *Calcistella* and *Chaetetopsis* extend into the Cretaceous (Albian), and *Acanthochaetetes* extends into the Holocene. *Calcichondrilla*, *Calcispirastrella*, *Calcisuberites*, and *Neuropora* are only known from the Cretaceous (see Table 5). The characteristic clavidisc microscleres of *Merlia* occur in the Lower Jurassic of Austria (MOSTLER, 1990), and the basal skeleton has been reported from the Eocene of Spain (BARRIER & others, 1991). *Merlia* is widely distributed in the world's oceans today (see VACELET & URIZ, 1991). *Acanthochaetetes* and *Merlia* are the only two extant genera in this group of nine genera.

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

Although chaetetids are obvious members of some Paleozoic reefs, particularly during the Carboniferous, they are not conspicuous members of post-Paleozoic reefs. The extant taxa, i.e., *Acanthochaetetes*, *Ceratoporella*, and *Merlia,* live under conditions of very low light or in complete darkness in subtidal caves, crevices, and tunnels of coral reefs, or on cliffs in the upper bathyal zone down to a few hundred meters (Vacelet, 1988; see also Vacelet, Willenz, & Hartman, 2010). It appears, based on their minor role in post-Paleozoic reefs, that they may have also been restricted to such habitats during the Mesozoic and Cenozoic. Thus, they could be easily overlooked, and taphonomic processes would make their recognition even more difficult.

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

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

In that spicules are commonly absent in fossil chaetetids, Cuif and Gautret (1991, 1993) suggested that a careful study of the mineralogy and microstructure of the basal calcareous skeleton might be useful phylogenetically. As noted by West (2011a) in a study of the microstructure of the chaetetids, Cuif and Gautret (1993) have shown that, though commonly considered synonyms, there is a recognizable difference between penicillate, trabecular, and water-jet microstructures. Their results indicated that the simple trabecular microstructure does not occur in hypercalcified demosponges with a chaetetid skeleton. They concluded that there are two basic microstructures, one of calcite and one of aragonite, observed in chaetetid skeletons from the Carboniferous to the Holocene. It was suggested that these features could be used as the basis for two separate clades: a penicillate aragonite clade and a water-jet calcite clade.

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

It has been possible, using geochemical data, to infer the basic seawater chemistry of the Phanerozoic ocean and divide the Phanerozoic based on the dominant carbonate minerals, i.e., calcite versus aragonite seas (Sandberg, 1983, 1984, 1985; Fuchtbauer & Hardie, 1976, 1980; Hardie, 1996; Stanley & Hardie, 1998, 1999; Montanez, 2002; Stanley, Reis, & Hardie, 2002). Stanley (2006) discussed the influence of seawater chemistry on biomineralization and predicted the skeletal mineralogy of the dominant reef builders during the Phanerozoic. Based on data from Stanley (2006), the original mineralogy of the basal calcareous skeletons of chaetetids may be predicted. Chaetetids that may occur in the Cambrian to the mid-early Carbonifeous interval should be low-Mg calcite (Calcite I interval of Stanley, 2006, p. 218), and those from the mid-Early Carboniferous to Mid-Jurassic interval should be aragonite or high-Mg calcite in composition (Aragonite II interval of Stanley, 2006, p. 218–219). Chaetetid skeletons from the Mid-Jurassic to the Eocene should be low-Mg calcite (Calcite II of Stanley, 2006, p. 219–220), and skeletons of extant chaetetids and those occurring back to the Oligocene should be aragonite or high-Mg calcite (Aragonite III interval of Stanley, 2006, p. 220).

The original mineralogy of the basal calcareous skeleton of 17 of the taxa listed in Table 4 is known; mineralogy of another taxon, *Chaetetes* (*Chaetetes*), is unknown but inferred to be calcite, and there is some question as to the original skeletal mineralogy of the remaining eight: *Bauneia, Chaetetes* (*Boswellia*), *Chaetetes* (*Pseudoseptifer*), *Chaetetopsis, Kemeria, Neuropora, Pachytheca,* and *Ptychochaetetes* (see Table 4). Based on the work of Stanley (2006), noted above, the original mineralogy of *Chaetetes* (*Boswellia*), *Chaetetopsis, Neuropora, Pachytheca,* and *Ptychochaetetes* should be low-Mg calcite, and *Bauneia* and *Chaetetes* (*Pseudoseptifer*) should be aragonite. However, Jurassic specimens of *Bauneia, Chaetetes* (*Pseudoseptifer*), *Chaetetopsis,* and *Ptychochaetetes* could be low-Mg calcite or aragonite, because the contact between the Aragonite II and Calcite II intervals is about Mid-Jurassic. *Kemeria,* as well as Triassic specimens of *Blastochaetetes* (Table 6), are in the Aragonite II interval, as given by Stanley (2006). However, the skeletal mineralogy of *Blastochaetetes,* from the Upper Jurassic and Cretaceous, should be low-Mg calcite, not aragonite (Table 6), to conform to the intervals of Stanley (2006).

Table 6. Grouping of valid taxa from Table 1 and inadequately known taxa from Table 2 (*asterisks*) based on known or inferred mineralogy including the known or inferred microstructure of each. Note: Based on the studies by Cuif and Ezzoubair (1991), *Blastochaetetes* is separated into a calcite (*s.s.*) form and an aragonite (*s.l.*) form, as noted in the text; *Q-H,* Quaternary–Holocene; *Q-Pl,* Quaternary–Pleistocene; *N,* Neogene; *Pa,* Paleogene; *K,* Cretaceous; *J,* Jurassic; *Tr,* Triassic; *P,* Permian; *C,* Carboniferous; *D,* Devonian; *S,* Silurian (new).

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

The reported original skeletal mineralogy of the Permian, Triassic, and Lower Jurassic taxa (Tables 4 and 6) are compatible with the Aragonite II interval of Stanley (2006) and would suggest an ambient seawater chemistry with an Mg/Ca ratio greater than 2.0. The occurrence of *Atrochaetetes* with an aragonite skeleton in the Upper Jurassic and Cretaceous part of the Calcite II interval is anomalous, although its first occurrence is in the Aragonite II interval (Triassic). The situation is similar for the three extant taxa. *Acanthochaetetes* is first known in the Upper Jurassic (Table 5), the Calcite II interval, and as an extant form in the Aragonite III interval. *Ceratoporella* is first known from the Permian and *Merlia* from the Lower Jurassic (Table 5), both in the Aragonite II interval, and both range across Calcite II into the present, Aragonite III interval.

The situation relative to the original microstructure is even more complicated than that of the original skeletal mineralogy (see Table 4). Penicillate and water-jet have been used interchangeably; and other microstructures, such as lamellar, irregular, and spherulitic, are also recognized. Thus, a penicillate aragonite and a water-jet calcite clade are not mutually exclusive, and taxa with neither a penicillate nor a water-jet microstructure are excluded.

Irrespective of the questionable original skeletal mineralogy of some taxa and the differences relative to the study of STANLEY (2006), there may be two clades, as seen in Table 6: a Phanerozoic calcite clade and a largely post-Paleozoic aragonite clade. These clades do not correlate with the seawater chemistry curves first proposed by SANDBERG (1983) and subsequently modified by SANDBERG (1983, 1984, 1985), STANLEY and HARDIE (1999), MONTANEZ (2002), and STANLEY (2006). Interestingly, some of the taxa that are reported as aragonite occur first in the Triassic, the Aragonite II interval of STANLEY (2006), but also occur in the Upper Jurassic and Cretaceous, his Calcite II interval (Table 6). In addition to clarifying the microstructure of chaetetid basal skeletons, the mineralogy of these skeletons also needs to be more closely examined. WEBB, WÖRHEIDE, and NOTHDURFT (2003) pointed out the potential usefulness of rare-earth element analyses of the skeletal components of extant and fossil sponges, including chaetetids and stromatoporoids, relative to seawater chemistry and biomineralization.

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

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

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

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