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Classification of the Fossil and Living Hypercalcified Chaetetid-Type Porifera (Demospongiae)

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PART E, REVISED, VOLUME 4, CHAPTER 2C: CLASSIFICATION OF THE FOSSIL AND LIVING HYPERCALCIFIED CHAETETID-TYPE PORIFERA (DEMOSPONGIAE)

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The hypercalcified demosponges with a chaetetid calcareous skeleton were originally described as *Chaetetes* by FISCHER VON WALDHEIM, MS in EICHWALD (1829) and subsequently by FISCHER VON WALDHEIM (1830, 1837). SOKOLOV (1955, 1962), who provided a very complete review of the history of the classification of chaetetids, noted that MILNE-EDWARDS and HAIME (1849), placed *Chaetetes* in a separate subfamily, the Chaetetinae, of the Favositidae, a family of the suborder Tabulata Zoantharia. Although it is a minor point, MILNE-EDWARDS and HAIME (1849) did not use Tabulata, but rather *Zoanthaires tabules* as a vernacular name (see HILL, 1981, p. 506). Tabulata, was not introduced as a formal taxonomic entity until MILNE-EDWARDS and HAIME (1850) proposed Zoantharia Tabulata as a suborder.

Subsequently, the subfamily Chaetetinae became the family Chaetetida within the Tabulata (DE FROMENTEL, 1860, 1861). Included within this family were not only chaetetids, but also ". . . tabulates with porous walls, bryozoans, stromatoporoids . . ." and ". . . even some genera of calcareous algae and tetradiids . . ." (SOKOLOV, 1962, p. 259). Thus, *Chaetetes* became a member of the Problematica with suggested representatives allocated to a number of different phyletic homes: sponges, corals, bryozoans, even foraminiferids and algae; depending on the interpretation of its simple skeletal morphology. Referring to chaetetids as well as sphinctozoans, stromatoporoids, and archaeocyaths, WOOD (1990, p. 227) stated the situation well: "The major obstacle to the study of the problematic reef-builders was the absence of conclusive features that could expose a relationship to living forms. The profusion of known representatives of these groups was little help in the solution of the problem. Different workers seized upon different analogies and considered their chosen examples to be crucial, so that these ancient waifs were shunted from one biological group to another." LINDSTRÖM (1873) considered *Chaetetes* a bryozoan, a view strongly supported by PETERHANS (1929) and also indicated by MORET (1966). During the latter part of the 19th century, most investigators considered *Chaetetes* to be a coral, although where within the corals was the subject of some difference of opinion. MILLER (1877) listed them with the Polypi, and in 1889, MILLER placed them within the Coelenterata. DUNCAN (1872) considered *Chaetetes* to be alcyonarian, along with *Monticulipora* and other genera. NEUMAYR (1889) and STRUVE (1898) placed them within the hexacorals. The early 20th century was not much different, in that WEISSERMEL (1927, 1939) created the Chaetokorallen, and OKULITCH (1936b) proposed the order Chaetetina within the schizocorals. LECOMPTE (1939, 1952) noted the difficulties of considering them to be algae and bryozoans, as well as corals, but retained them within the Tabulata. BASSLER (1950) considered them to be tetracorals, and SOKOLOV (1939, 1955, 1962) placed them in the hydrozoans. Within the Hydrozoa, SOKOLOV (1939, 1955, 1962) recognized a discrete group, the Chaetetida, and TESAKOV (1960) and FISCHER (1970) accepted this designation.

Although WOOD (1990, p. 228) indicated that until the late 1960s, most workers considered chaetetids to be hydrozoans, HILL and STUMM (1956) and MÜLLER (1963) retained them in the Tabulata as a separate family. HILL and STUMM (1956, p. 453) suggested that some Mesozoic and Eocene species of chaetetids might be coralline algae. HILL (1981, p. 506) changed the termination of

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

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

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

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

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

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

Besides differences in the morphology of spicules, the mineralogy and microstructure of the tubule walls is different in the extant groups. The original walls are either magnesium calcite or aragonite, and the microstructure may be penicilllate, lamellar,

TABLE 1. Comparison of the microstructures and skeletal mineralogy of extant and fossil hypercalcified demosponges with either a chaetetid or stromatoporoid calcareous skeleton (numerals with lower-case letters and author abbreviations refer to sources provided in the explanation; see below and facing page; new).

	Merlia	*Acanthochaetetes*	*Astrosclera*	*Ceratoporella*	Chaetetids	Stromatoporoids
Aragonite						
Penicillate				1a (F/R), 4a (C/G)	1a (F/R), 4b*(C/G)	
Spherulitic			1a (F/R), 2a (H/S), 6 (Wt)		1a (F/R), 6 (Wt)	1a (F/R)
Irregular						1a (F/R), 6 (Wt)
Spherulitic compound			5a (Wd)			
Spherulitic elongate				5a (Wd)		
Clinogonal				2a (H/S), 6 (Wt)	6 (Wt)	6 (Wt)
Orthogonal						6 (Wt)
Fibrous centers			7a (Cet)			
Asymmetical				7a (Cet.)		
Mg Calcite						
Penicillate	1b (F/R)				1b (F/R)	
Lamellar		1b (F/R), 2b (H/S), 7b (Cet.)			1b (F/R)	
Water-jet	2b (H/S), 4b (C/G)				4b (C/G)	
Fascicular fibrous	5b (Wd)					
Irregular		5b (Wd), 6 (Wt)			6 (Wt)	
Clinogonal	6 (Wt)				6 (Wt)	6 (Wt)
Spherulitic						6 (Wt)
Orthogonal						6 (Wt)
Trabecular	7b (Cet.)					
Mineralogy not recorded						
Fascicular fibrous	3 (B-E/R)			3 (B-E/R)		
Microlamellar		3 (B-E/R)				
Spherulitic			3 (B-E/R)			

*, some Mesozoic to Recent taxa, but all Paleozoic and some Mesozoic–Recent chaetetids have a water-jet calcite skeleton.

TABLE 1. Explanation.

1. (F/R)

Finks, Robert M., & J. Keith Rigby. 2004. Hypercalcified sponges. *In* R. L. Kaesler, ed., Treatise on Invertebrate Paleontology, Part E, Porifera (Revised), vol. 3. The Geological Society of America, Inc. and The University of Kansas. Boulder, Colorado and Lawrence, Kansas. p. 586–587.

1a. Aragonite

Spherulitic: compound spherulitic, *Astrosclera* and relatives of stromatoporoid morphology, Permo-Triassic genera of inozoans, sphinctozoans, and chaetetids.

Penicillate: clionogonal aragonite, elongate spherulitic, water-jet *Ceratoporella* of chaetetids and inozoans of the Middle Triassic.

Irregular: microgranular aragonite, *Vaceletia* and Triassic sphinctozoans, inozoans, and stromatoporoids.

1b. Mg Calcite

Homogeneous-granular: microgranular Mg calcite, no extant examples, Triassic sphinctozoans and inozoans, best known in *Cassianothalamina* (not included in table).

Lamellar: *Acanthochaetetes,* in Cretaceous to Recent genera with a chaetetid morphology, and the Cretaceous *Calcichondrilla*, an encrusting form with a nonchaetetid morphology.

Penicillate: clinogonal calcite, fascicular fibrous calcite, *Merlia,* and Paleozoic and Mesozoic genera with a chaetetid morphology, such as *Stromatoaxinella*.

(Continued on facing page).

Table 1. Explanation *(continued from facing page)*.

Spherulitic: no extant examples, Cretaceous *Euzkadiella*.
Fibrous: orthogonal Mg calcite, examples in the Calcarea.

2. (H/S)

Hooper, J. N. A., & R. W. M. van Soest, eds. 2002. Systema Porifera, vol. 1. Kluwer Academic/Plenum Publishers. New York, Boston, Dordrecht, London, and Moscow. xlviii + 1101 p.

2a. Aragonite
Spherulitic: *Astrosclera*.
Clinogonal: *Ceratoporella*.

2b. Mg Calcite
Water-jet: *Merlia,* probably the same as penicillate calcite of 1.
Lamellar: *Acanthochaetetes.*

3. (B-E/R)

Boury-Esnault, Nicole, & Klaus Rützler. 1997. Thesaurus of Sponge Morphology. Smithsonian Contributions to Zoology, Number 596:55 p. [Mineralogy not recorded; also here the authors did not recognize separate aragonite and Mg calcite fields].

Fasciculate fibrous: water-jet, penicillate, and trabecular *Merlia;* water-jet, mineralogy not reported; *Ceratoporella,* penicillate.
Microlamellar: *Acanthochaetetes*.
Spherulitic: *Astrosclera*.

4. (C/G)

Cuif, Jean-Pierre, & Pascale Gautret. 1993. Microstructural features of fibrous tissue in the skeletons of some chaetetid sponges. *In* P. Oekentorp-Küster, ed., Proceedings of the VI International Symposium on Fossil Cnidaria and Porifera, Munster Cnidarian Symposium, vol. 1. Courier Forschungsinstitut Senckenberg 164:309–315.

4a. Aragonite
Penicillate: *Ceratoporella*.

4b. Mg Calcite
Water-jet: *Merlia*.
Trabecular: scleractinian corals (not included in table)

5. (Wd)

Wood, Rachel A. 1991. Non-spicular biomineralization in calcified demosponges. *In* J. Reitner & H. Keupp, eds., Fossil and Recent Sponges. Springer-Verlag. Berlin and Heidelberg. p. 322–340.

5a. Aragonite
Compound spherulitic: *Astrosclera,* probably the same as spherulitic aragonite of 1.
Elongate spherulitic: *Ceratoporella,* probably the same as penicillate aragonite of 1.

5b. Mg Calcite
Fascicular fibrous: *Merlia*, probably penicillate calcite of 1.
Irregular: *Acanthochaetetes,* crystals aligned in one plane, probably lamellar calcite of 1.

6. (Wt)

Wendt, Jobst. 1979. Development of skeletal formation, microstructure, and mineralogy of rigid calcareous sponges from the Late Palaeozoic to Recent. *In* C. Levi & N. Boury-Esnault, eds., Biologie des Spongiaires. Colloques Internationaux du Centre National de la Recherche Scientifique 291:449–457.

Wendt, Jobst. 1984. Skeletal and spicular mineralogy, microstructure and diagenesis of coralline calcareous sponges. Palaeontographica Americana 54:326–336. [Note: the latter reference is an update of the former.]

Mg Calcite or Aragonite
Irregular: aragonite in stromatoporoids and Mg calcite in Cretaceous and Recent "sclerosponges," *Acanthochaetetes*.
Spherulitic: probably aragonite in Carboniferous sclerosponges and in the extant genus *Astrosclera*; probably calcite in a Cretaceous stromatoporoid.
Clinogonal (synonyms = water-jet, trabecular, penicillate): aragonite or calcite in Mesozoic and possibly Paleozoic chaetetids and stromatoporoids; calcitic in *Merlia* and aragonite in *Ceratoporella* and stromatoporoids.
Orthogonal (synonym, fibro-normal): aragonite and calcite in stromatoporoids.

7. (Cet.)

Cuif, Jean-Pierre, Françoise Debrenne, J. G. Lafuste, & Jean Vacelet. 1979. Comparaison de la microstructure du squelette carbonate nonspiculaire d'éponges actuelles et fossiles. *In* C. Levi & N. Boury-Esnault, eds., Biologie des Spongiaires. Colloques Internationaux du Centre National de la Recherche Scientifique 291:459–465.

7a. Aragonite
Spherolites fibreux centres [fibrous spherulitic centers]: *Astrosclera*.
Spherolites asymetriques [asymmetrical spherulites]: *Ceratoporella*.

7b. Mg Calcite
Lamelles presque plates [nearly flat lamellae]: *Acanthochaetetes.*
Trabecules verticals [vertical trabeculae]: *Merlia.*

or spherulitic. As shown in Table 1, the major difference between recent authors is that Hooper and van Soest (2002a) and Cuif and Gautret (1993) considered the microstructure of *Merlia* to be water-jet, and Finks and Rigby (2004) considered it as penicillate. In terms of more general morphological features, the tubules in some forms, like those in *Ceratoporella*, are filled with calcium carbonate up to the living tissue, and in others, tabulae are present in the tubules. Wood (1990) provided a more complete discussion of the similarities and differences between the different chaetetid skeletons.

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

Although spicules are not always present in extant forms (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, p. 2), they are the primary feature for differentiating poriferan taxa. A meaningful taxonomy is, to some degree, equivocal if spicules are absent, and in chaetetid skeletons spicules, they are commonly absent. There are a number of valid reasons, as noted in Chapter 2A, why spicules are seldom found in fossil chaetetids, and the reader is referred to that chapter. Lacking spicules, namely pseudomorphs of spicules, only secondary skeletal features are left, namely the mineralogy and microstructure of the rigid calcareous skeleton. As noted in Chapter 2A (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, p. 53), the mineralogy and microstructure of the calcareous skeleton can be taxonomically useful. Unfortunately, in most fossil chaetetids, the calcareous skeleton has been taphonomically altered (recrystallized and/or replaced), making it difficult, and commonly impossible, to determine the original mineralogy. By changing the original mineralogy, the original microstructure expressed by that mineralogy is also altered. Thus, in most fossil chaetetids, one is left with the least useful features of the calcareous skeleton upon which to base taxonomic determinations.

Chaetetid skeletons are morphologically very simple (see Wood, 1990, p. 227, on morphological simplicity), with the most commonly preserved features being the size, shape, and arrangement of the tubules, the thicknesses of tubule walls and tabulae, and the spacing between tabulae. Genera and higher taxonomic categories of chaetetids have been based on the general growth form, general shape of the tubules in cross section, thickness of the tubule walls and tabulae, absence of septa and mural pores, and whether new tubules are added by axial, peripheral, or lateral budding. There are very few differences within genera, and between genera and higher taxonomic categories (Hill, 1981). Species of chaetetids have been differentiated primarily on the size of the tubules (commonly the diameter), thickness of the tubule walls, and thickness of the tabulae. To a lesser extent, the spacing between tabulae and the cross-sectional shape of the tubules has been used at the specific level. As shown by West (1994), neither tubule diameter (an inappropriate measure for tubule size, as the tubules are, in cross section, irregular polygons, not circles), tubule wall thickness, nor the cross-sectional area of the tubules (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 51) are valid taxonomic discriminators for Carboniferous species of chaetetids. Comparison of the cross-sectional areas of tubules from different

TABLE 2. HILL's (1981) classification of chaetetid taxa, which she assigned to the coral subclass Tabulata; most of these are now considered to be chaetetid hypercalcified sponge taxa; the taxa above the dashed line are Paleozoic, and those below are post-Paleozoic (new).

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

sites in a single laminar chaetetid from the Carboniferous also reveals the inappropriateness of these features (see *Treatise Online,* Part E, Revised, vol. 4, Chapter 2A, Fig. 52). These weaknesses are inferred to be due, in part, to taphonomic processes (WEST, 1995). The inconsistencies documented in tubule size and wall thickness could also be the result of genetic and/or environmental factors. But whether biological, environmental, or taphonomic, they are not dependable. Consequently, the current state of affairs is that, without spicules and/or the original mineralogy and microstructure of the calcareous skeleton, it is difficult, if not impossible, to systematize hypercalcified demosponges with a chaetetid skeleton.

HILL (1981) listed 8 families within the order Chaetetida, of which 4 were queried, and 29 genera. Thus, not only did HILL doubt the placement and/or validity of the order, she also doubted the validity of most of the families within the order. Seven of the 29 genera are in the 4 queried families (Table 2).

As noted above, HILL (1981) separated the Paleozoic chaetetids (the first 26 taxa [22 genera and 4 subgenera] in Table 2) from the post-Paleozoic chaetetids (the last 7 taxa in Table 2). Genera that HILL (1981, p. 520) removed from the Chaetetida were: *Parachaetetes, Pseudochaetetes, Ptychochaetetes, Axiparietes, Granatiparietes*, and *Varioparietes,* largely because she felt that the microstructure was the result of diagenetic

TABLE 3. Currently valid fossil chaetetid taxa based on pseudomorphs of spicules and the original mineralogy and microstructure of calcareous skeleton. Unless these features are identifiable, the use of these taxa is inappropriate and should be avoided (new).

Acanthochaetetes FISCHER, 1970
Atrochaetetes CUIF & FISCHER, 1974
Bauneia PETERHANS, 1927
[CREMER (1995) documented the microstructure and spicule pseudomorphs in this genus and queried it but did not provide reasons]
Blastochaetetes DIETRICH, 1919
Calcichondrilla REITNER, 1991
Calcispirastrella REITNER, 1992
Calcistella REITNER, 1991
Calcsuberites REITNER & SCHLAGINTWEIT, 1990
Ceratoporella HICKSON, 1911
Chaetetes (Chaetetes) FISCHER VON WALDHEIM in EICHWALD, 1829
[*Chondrochaetetes* REITNER, 1991, is a junior synonym]
Chaetetes (Boswellia) SOKOLOV ,1939
Chaetetes (*Pseudoseptifer)* FISCHER, 1970
Chaetetopsis NEUMAYR, 1890
Chaetosclera REITNER & ENGESER, 1989
Keriocoelia CUIF, 1974
Leiospongia D'ORBIGNY, 1849
Meandripetra DIECI & others, 1977
Merlia KIRKPATRICK, 1908
Neuropora (LAMOUROUX), 1821
Pachytheca SCHLUTER, 1885
Ptychochaetetes KOECHLIN, 1947
Sclerocoelia CUIF, 1974

TABLE 4. Fossil chaetetid taxa for which some meaningful information on the original mineralogy and microstructure of the calcareous skeleton is known, but the presence of pseudomorphs of spicules is unknown or questionable. Until more reliable data are available, these taxa are queried (new).

Blastoporella CUIF & EZZOUBAIR, 1991
Cassianochaetetes ENGESER & TAYLOR, 1989
Kermeria CUIF & EZZOUBAIR, 1991
Sphaerolichaetetes GAUTRET & RAZGALLACH, 1987

TABLE 5. Fossil taxa for which the original mineralogy and microstructure of the basal calcareous skeleton and pseudomorphs of spicules are either very poorly known or unknown. These taxa are based on unreliable gross morphological features. They are therefore considered to be chaetetid form taxa and are best referred to as doubtful chaetetids or hypercalcified demosponges, possibly with a chaetetid skeleton. Taxa below the dashed line are not currently considered to be chaetetids (new).

?*Carnegiea* GIRTY, 1913
Cassianopora BIZZARINI & BRAGA, 1978
Chaetetella (Chaetetella) SOKOLOV, 1962
Chaetetella (Chaetetiporella) SOKOLOV, 1950
Chaetetipora STRUVE, 1898
Conosclera WU, 1991
Fistulimurina SOKOLOV, 1947
Flabellisclera WU, 1991
Fungispongia WU, 1991
Gigantosclera WU, 1991
Gracilitubulus WU, 1991
Leiochaetetes ANDRI & RUSSO, 1980
Lithophyllum ETHERIDGE, 1899
Mirispongia WU, 1991
Moskovia SOKOLOV, 1950
Pamirochaetetes BOIKO, 1979
Parabauneia WU, 1991
Planochaetetes SOLOVJEVA, 1980
Preceratoporella TERMIER, H., G. TERMIER, & D. VACHARD, 1977 (note that REINHARDT (1988) called this genus *Praeceratoporella,* which is a misspelling
Septochaetetes RIOS & ALMELA, 1944
Siphostroma STEINER, 1932
Solenopora DYBOWSKI, 1877, by RIDING, 2004
Spinochaetetes C. T. KIM in YANG, KIM, & CHOW, 1978
?*Spongiothecopora* SOKOLOV, 1955
Tubulispongia WU, 1991
Zlambachella FLÜGEL, 1961

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Diplochaetetes WEISSERMEL, 1913 (suggested to be worm tubes by FISCHER, GALLI OLIVER, & REITNER, 1989)
Favosichaetetes YANG, 1978 (has mural pores—probably a tabulate)
Guizouchaetetes YANG, 1978 (has mural pores—probably a tabulate)
Lovcenipora GIATTINI, 1902 (considered to be a tabulate coral by GIATTINI [1902] and VINASSA DE REGNY [1915]; considered to be a chaetetid by SENOWBARI-DARYAN and MAURER [2008]; has mural pores—probably a tabulate)
Pachythecopora DENG, 1982 (has mural pores—probably a tabulate)
Pseudomillestroma DENG, 1982 (probably a milleporoid coral)

alteration of solenoporacean walls. *Axiparietes* and *Varioparietes* were described as genera by SCHNORF-STEINER (1963), but FISCHER (1970) considered them to be subgenera of *Ptychochaetetes*. Documentation by CREMER (1995) of the microstructure and spicule pseudomorphs in Upper Triassic specimens of *Ptychochaetetes* from southwestern Turkey clearly establishes it as a valid chaetetid genus. HILL (1981, p. 666) also considered *Chaetetopsis* as an unrecognizable genus, because it was "... greatly altered by diagenesis." However, KAŹMIERCZAK (1979) illustrated monaxon spicule pseudomorphs in a specimen of *Chaetetopsis favrei* from the Lower Cretaceous of the Crimea. Based on the internal micromorphology (preservation precluded recognition of spicules or spicule pseudomorphs and the mineralogy and microstructure of the skeleton) of *Solenopora spongioides*, the type species, RIDING (2004) considered it to have a chaetetid skeleton. This returns *Solenopora spongioides* to the chaetetids, as originally assigned by DYBOWSKI in 1877, and raises questions about other supposed solenoporaceans, such as the 6 genera noted above by HILL (1981). As pointed out previously, taphonomic processes can be of considerable importance to studies of the systematics of chaetetids as well as to other fossils with a similar skeleton.

Currently, there are 22 chaetetid genera and subgenera from which pseudomorphs of spicules have been identified, and for which the original mineralogy and microstructure of the calcareous skeleton is known (Table 3).

Because of the lack of pseudomorphs of spicules, and until more reliable data are available on the original mineralogy and microstructure of the calcareous skeleton, another four taxa are regarded as having a less certain status (Table 4).

Spicules, or spicule pseudomorphs, original mineralogy, and microstructure of the basal skeleton are either inadequately known, or unknown from 26 of the 32 taxa listed in Table 5, and these are considered to be chaetetid form taxa. The other 6 taxa in Table 5, those below the dashed line, are currently considered to be either worm tubes or corals, as noted. HILL (1981) considered 10 of the 32 taxa in Table 5 to be chaetetids (compare Tables 2 and 5). The remaining 22 taxa in Table 5 were either unknown to HILL or were described, redescribed, or considered to be chaetetids since HILL's 1981 work.

An additional 11 taxa, listed by HILL (1981) as chaetetids, are rejected from the group; they are more likely to be tabulate corals (Table 6).

TABLE 6. Taxa not considered to be chaetetids; they are most likely tabulate corals (new).

?*Staphylopora* LE MAITRE, 1956
Cryptolichenaria SOKOLOV, 1955
Amsassia SOKOLOV & MIRONOVA, 1959
Porkunites KLAAMANN, 1966
Desmidopora NICHOLSON, 1886
Nodulipora LINDSTRÖM, 1873
Schizolites PREOBRAZHENSKIY, 1968
Tiverina SOKOLOV & TESAKOV, 1968
Barrandeolites SOKOLOV & PRANTL in SOKOLOV, 1965
Lamottia RAYMOND, 1924
Lichenaria WINCHELL & SCHUCHERT, 1895

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

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