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 eich Wald (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 Favoisitidae, a family of the suborder Tabulata Zoantharia. Although it is a minor point, Milne-Edwards and Haime (1849) did not use Tabulata, but rather Zoaanthaires 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 phylectic 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 different 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 Weissmerl (1927, 1939) created the Chaetokorallen, and Okulitch (1936b) proposed the order Chaetetida 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
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 Thal- lephyta (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 clino- gonal 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), Cuf and others (1973), Cuf 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 Cummings (1912) included the Paleozoic Monticuliporiidae 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 Paleozoic 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 willeymana (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 wellsii* (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 wellsii* 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, Tabulospongia, 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 (CUFF & others, 1973) and Carboniferous chaetetids (WEST & CLARK, 1983, 1984) further strengthen the poriferan affinities of chaetetids. VANE 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 Demospongiae: Tetractinomorpha, Ceractinomorpha, Choristida (for Homoscleromorpha), Clavxinellida, and Lithistida. HOOPER and VAN SOEST (2002a) considered: (1) the lithistids polyphyletic and referred to them as lithistid demosponges (p. 299); and (2) placed Clavxinellida 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 Polecillosclerida, 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 penicillate, 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).

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

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

1. (F/R)

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).
Clinogonal: Acanthochaetetes, in Cretaceous to Recent genera with a chaetetid morphology, and the Cretaceous Calcechondrilla, an encrusting form with a nonchaetetid morphology.
Penicillate: clionogonal 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).

<table>
<thead>
<tr>
<th>Classification Type</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spherulitic: no extant examples, Cretaceous Euzkadiella.</td>
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<tr>
<td>Fibrous: orthogonal Mg calcite, examples in the Calcarea.</td>
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</tr>
<tr>
<td>2a. Penicillate</td>
<td>Ceratoporella.</td>
</tr>
<tr>
<td>2b. Mg Calcite</td>
<td>Water-jet: Merlia, probably the same as penicillate calcite of 1.</td>
</tr>
<tr>
<td>Lamellar: Acanthochaetetes.</td>
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</tr>
<tr>
<td>3. Bourn-Isnault, Nicole, &amp; Klaus Rätzler. 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].</td>
<td></td>
</tr>
<tr>
<td>Fasciculate fibrous: water-jet, penicillate, and trabecular Merlia; water-jet, mineralogy not reported; Ceratoporella, penicillate.</td>
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<tr>
<td>Microlamellar: Acanthochaetetes.</td>
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<tr>
<td>Spherulitic: Astrosclera.</td>
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<tr>
<td>4a. Penicillate</td>
<td>Ceratoporella.</td>
</tr>
<tr>
<td>4b. Mg Calcite</td>
<td>Water-jet: Merlia.</td>
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<tr>
<td>Trabecular: scleractinian corals (not included in table)</td>
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</tr>
<tr>
<td>5a. Aragonite</td>
<td>Compound spherulitic: Astrosclera, probably the same as spherulitic aragonite of 1.</td>
</tr>
<tr>
<td>5b. Mg Calcite</td>
<td>Elongate spherulitic: Ceratoporella, probably the same as penicillate aragonite of 1.</td>
</tr>
<tr>
<td>Mg Calcite or Aragonite</td>
<td>Irregular: aragonite in stromatoporoids and Mg calcite in Cretaceous and Recent &quot;sclerosponges,&quot; Acanthochaetetes.</td>
</tr>
<tr>
<td>Spherulitic: probably aragonite in Carboniferous sponges and in the extant genus Astrosclera; probably calcite in a Cretaceous stromatoporoid.</td>
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</tr>
<tr>
<td>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.</td>
<td></td>
</tr>
<tr>
<td>Orthogonal (synonym, fibro-normal): aragonite and calcite in stromatoporoids.</td>
<td></td>
</tr>
<tr>
<td>7a. Aragonite</td>
<td>Sphérolites fibres centres [fibrous spherulitic centers]: Astrosclera.</td>
</tr>
<tr>
<td>Sphérolites asymétriques [asymmetrical spherulites]: Ceratoporella.</td>
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</tr>
<tr>
<td>7b. Mg Calcite</td>
<td>Lamelles presque plates [nearly flat lamellae]: Acanthochaetetes.</td>
</tr>
<tr>
<td>Trabecules verticales [vertical trabeculae]: Merlia.</td>
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</tbody>
</table>
or spherulitic. As shown in Table 1, the major difference between recent authors is that Hooper and van Soest (2002a) and Cui 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
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: *Parachetaetes*, *Pseudochaetaetes*, *Psychochaetaetes*, *Axiparietes*, *Granatiparietes*, and *Varioparietes*, largely because she felt that the microstructure was the result of diagenetic

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**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).**

<table>
<thead>
<tr>
<th>Order</th>
<th>Family</th>
<th>Subfamily</th>
<th>Genus</th>
<th>Subgenus</th>
</tr>
</thead>
<tbody>
<tr>
<td>?Chaetetida</td>
<td>Chaetetidae</td>
<td>Chaetetinae</td>
<td>Chaetetes</td>
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<td></td>
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<td>Chaetetes</td>
<td><em>Boswellia</em></td>
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<td>?Carnegieia</td>
<td>Chaetetella</td>
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<td>Chaetetella</td>
<td>Chaetetiporella</td>
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<td>Litophyllum</td>
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<td>Pachyphora</td>
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<td>?Spongiosthecopora</td>
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<td>?Sphychipora</td>
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<tr>
<td>Chaetetiporinae</td>
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<td>Chaetetipora</td>
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<td></td>
<td>Moskoviinae</td>
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<td>Fistulimurina</td>
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<td></td>
<td>Cryptolichenariidae</td>
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<td>Cryptolichenaria</td>
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<td></td>
<td>Amsasia</td>
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<td>Porkunites</td>
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<td></td>
<td>?Desmidoporida</td>
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<td>Desmidopora</td>
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<td>Nodulipora</td>
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<td>Schizolites</td>
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<td>?Tiverinida</td>
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<td>Tiverina</td>
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<td>Barrandeolites</td>
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<tr>
<td>?Lamottida</td>
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<td>Lamottia</td>
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<tr>
<td>?Lichenariida</td>
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<td>Lichenaria</td>
<td></td>
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<tr>
<td>Favosichaetetidae</td>
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<td></td>
<td>Favosiachaetaetes</td>
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<td>Guizhouchaetetes</td>
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<td></td>
<td>Chaetetidae</td>
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<td>Atrochaetetes</td>
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<td></td>
<td>Baunica</td>
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<td></td>
<td>?Blastochaetetes</td>
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<td></td>
<td>Pseudopectifer</td>
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<td></td>
<td>Acanthochaetaetes</td>
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<td></td>
<td>Diplochaetetes</td>
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<td></td>
<td>Septochaetetes</td>
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<td></td>
<td>Acanthochaetetidae</td>
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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).

<table>
<thead>
<tr>
<th>Taxa</th>
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<tbody>
<tr>
<td>Acanthochaetetes Fischer, 1970</td>
</tr>
<tr>
<td>Astrochaetetes Cuif &amp; Fischer, 1974</td>
</tr>
<tr>
<td>Baumea Peterhans, 1927</td>
</tr>
<tr>
<td>[Cremer (1995) documented the microstructure and spicule pseudomorphs in this genus and queried it but did not provide reasons]</td>
</tr>
<tr>
<td>Blastochaetetes Dietrich, 1919</td>
</tr>
<tr>
<td>Calcichondrilla Reitner, 1991</td>
</tr>
<tr>
<td>Calcispirastrella Reitner, 1992</td>
</tr>
<tr>
<td>Calciestella Reitner, 1991</td>
</tr>
<tr>
<td>Calcisuberites Reitner &amp; Schlagintweit, 1990</td>
</tr>
<tr>
<td>Ceratoporella Hickson, 1911</td>
</tr>
<tr>
<td>Chaetetes (Chaetetes) Fischer von Waldheim in Eichwald, 1829</td>
</tr>
<tr>
<td>[Chondrochaetetes Reitner, 1991, is a junior synonym]</td>
</tr>
<tr>
<td>Chaetetes (Bauwelia) Sokolov, 1939</td>
</tr>
<tr>
<td>Chaetetes (Pseudoseptifer) Fischer, 1970</td>
</tr>
<tr>
<td>Chaetotopias Neumayr, 1890</td>
</tr>
<tr>
<td>Chaetosclera Reitner &amp; Engeser, 1989</td>
</tr>
<tr>
<td>Keriocellia Cuif, 1974</td>
</tr>
<tr>
<td>Leiospongia Orbigny, 1849</td>
</tr>
<tr>
<td>Meandripetra Dieci &amp; others, 1977</td>
</tr>
<tr>
<td>Merlia Kirkpatrick, 1908</td>
</tr>
<tr>
<td>Neuropora (Lamouroux), 1821</td>
</tr>
<tr>
<td>Ptychitheca Schuter, 1885</td>
</tr>
<tr>
<td>Ptychochaetetes Koechlin, 1947</td>
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<tr>
<td>Sclerocellia Cuif, 1974</td>
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</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>Taxa</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blastoporella Cuif &amp; Ezouzoubair, 1991</td>
</tr>
<tr>
<td>Cassianochaetetes Engeser &amp; Taylor, 1989</td>
</tr>
<tr>
<td>Kermeria Cuif &amp; Ezouzoubair, 1991</td>
</tr>
<tr>
<td>Sphaerolichaeetes Gautret &amp; Razgallach, 1987</td>
</tr>
</tbody>
</table>

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).

<table>
<thead>
<tr>
<th>Taxa</th>
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<tbody>
<tr>
<td>?Carnegiea Girty, 1913</td>
</tr>
<tr>
<td>Cassianopora Bezzarin &amp; Braga, 1978</td>
</tr>
<tr>
<td>Chaetetella (Chaetetella) Sokolov, 1962</td>
</tr>
<tr>
<td>Chaetetella (Chaetetiporella) Sokolov, 1950</td>
</tr>
<tr>
<td>Chaetetipora Struve, 1898</td>
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<tr>
<td>Conoiclastina Wu, 1991</td>
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<tr>
<td>Fisulimurina Sokolov, 1947</td>
</tr>
<tr>
<td>Flabelliscierna Wu, 1991</td>
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<tr>
<td>Fungiporina Wu, 1991</td>
</tr>
<tr>
<td>Fungiosclera Wu, 1991</td>
</tr>
<tr>
<td>Graciliubulus Wu, 1991</td>
</tr>
<tr>
<td>Leiochaetetes Andri &amp; Russo, 1980</td>
</tr>
<tr>
<td>Lithophyllum Etheridge, 1899</td>
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<tr>
<td>Mirisiporina Wu, 1991</td>
</tr>
<tr>
<td>Moskvitam Sokolov, 1950</td>
</tr>
<tr>
<td>Panmnrchaetetes Bokko, 1979</td>
</tr>
<tr>
<td>Parabaumea Wu, 1991</td>
</tr>
<tr>
<td>Planochaetetes Solovjeva, 1980</td>
</tr>
<tr>
<td>Preceratoporella Termier, H., G. Termier, &amp; D. Vachard, 1977 (note that Reinhardt (1988) called this genus Preceratoporella, which is a misspelling)</td>
</tr>
<tr>
<td>Septochaetetes Rios &amp; Almela, 1944</td>
</tr>
<tr>
<td>Siphosetaria Steiner, 1932</td>
</tr>
<tr>
<td>Solenopora Dybowski, 1877, by Riding, 2004</td>
</tr>
<tr>
<td>?Spongiothecopora Sokolov, 1955</td>
</tr>
<tr>
<td>Tubulispornia Wu, 1991</td>
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<tr>
<td>Zambachella Flogel, 1961</td>
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<tr>
<th>Taxa</th>
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<tbody>
<tr>
<td>Diplochaetetes Weissermel, 1913 (suggested to be worm tubes by Fischer, Galli Oliver, &amp; Reitner, 1989)</td>
</tr>
<tr>
<td>Fuoschitaeetes Yang, 1978 (has mural pores—probably a tabulate)</td>
</tr>
<tr>
<td>Guizouchaetetes Yang, 1978 (has mural pores—probably a tabulate)</td>
</tr>
<tr>
<td>Lovenipora 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)</td>
</tr>
<tr>
<td>Pachybaeopora Deng, 1982 (has mural pores—probably a tabulate)</td>
</tr>
<tr>
<td>Pseudomillestroma Deng, 1982 (probably a milleporoid coral)</td>
</tr>
</tbody>
</table>
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, *Kazmierczak* (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 *Dybowsky* 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).

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.

**ACKNOWLEDGMENTS**

Over the years, numerous individuals from many parts of the world have contributed to my efforts to learn more about chaetetid sponges, and I sincerely thank all of them. I am particularly
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