

# HYPERCALCIFIED EXTANT AND FOSSIL CHAETETID-TYPE AND POST-DEVONIAN STROMATOPOROID-TYPE DEMOSPONGIAE: SYSTEMATIC DESCRIPTIONS

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## Class DEMOSPONGIAE Sollas, 1885

[Demospongiae SOLLAS, 1885, p. 395] [=Demospongia DE LAUBENFELS, 1955, p. 36]

Porifera with siliceous spicules and/or a fibrous skeleton, or occasionally without a skeleton. Skeleton composed of spongin fibers alone or together with siliceous spicules. Spicules are either monaxonic (either monactine or diactine) or tetraxonic (tetractine), never triaxonic. The axial filament is embedded in a triangular or hexagonal cavity. Spongin almost always present; forms discrete fibers or binds other skeletal elements. Some groups, however, build complex fiber skeletons without spicular elements, and other minor groups produce a hypercalcified basal skeleton in addition to their other skeletal elements, or develop an aragonitic skeleton without spicules. These variants contribute to a wide range of morphological heterogeneity of the class. Aquiferous systems are usually of leucon type. Both oviparous and viviparous reproductive strategies occur (HOOPER & VAN SOEST, 2002b, p. 15). [The date of SOLLAS's (1885) proposed name was discussed by FINKS and RIGBY (2004a, p. 9). Demospongiae is proposed here as the valid name because there are no rules for changing the desinence of higher order taxa, and, in this case, the original spelling adopted by SOLLAS (1885) has been widely accepted and maintained by zoologists. Acceptance of the subclasses Tetractinomorpha LÉVI, 1953, and Ceractinomorpha

LÉVI, 1953, Demospongiae, has diminished in the contemporary literature, as these groups have been recognized to contain polyphyletic taxa (HOOPER & VAN SOEST, 2002b, p. 16–17). This has been confirmed by a recent analysis of the phylogenetic relationships of the orders of Demospongiae based on 18S and 28S rRNA (BORCHIELLINI & others, 2004); so these subclasses will not be used here.] ?*Silurian, Middle Devonian–Holocene.*

## Order HADROMERIDA Topsent, 1894

[*nom. correct.* DE LAUBENFELS, 1936, p. 139, *pro* suborder Hadromerina TOPSENT, 1928, p. 143, *nom. transl. ex* Hadromerina TOPSENT, 1894, p. 6] [=Clavulina VOSMAER, 1887, p. 328, *partim*; =Astromonaxonellida DENDY, 1905, p. 106]

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Demospongiae with monaxonic megascleres (tylostyles, subtylostyles, oxeas, or derivatives) forming radiate or subradiate skeletal arrangement, sometimes only obvious in peripheral skeleton; ectosomal spicules usually smaller than choanosomal ones, and, where present, they may produce a cortical skeleton; spongin often sparse, producing firm non-elastic consistency; microscleres may include various forms of euasters, spirasters, rhabds, microxeas, and/or raphides in trichodragmata, or absent in many taxa (HOOPER & VAN SOEST, 2002c). [FINKS and RIGBY (2004d, p. 724) give the author and date of this order as TOPSENT, 1898, with the following name history: *nom. correct.* DE LAUBENFELS, 1955, p. 39, *pro*

suborder Hadromerina TOPSENT, 1898, p. 93]. ?*Silurian, Middle Devonian–Holocene.*

**Family ACANTHOCHAETETIDAE**  
Fischer, 1970

[Acanthochaetidae FISCHER, 1970, p. 199] [=Tabulospongiidae MORI, 1976, p. 8]

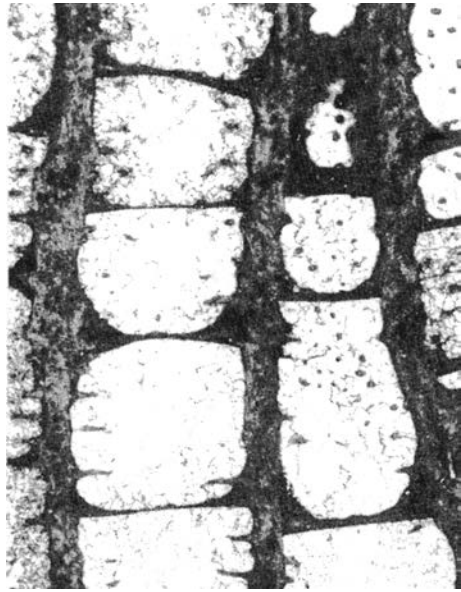
Hypercalcified sponges with a basal calcareous skeleton that is attached to substratum; thin layer of living tissue coating outermost layer of basal skeleton and containing siliceous spiculation of tylostyles as megascleres, and pointing outward; and common, relatively large streptasters. [Based on *Acanthochaetetes wellsi*, the only known living representative of the genus, HARTMAN and GOREAU (1975) and HARTMAN (1982) suggested the sclerosponge family Acanthochaetetidae be classified in a separate order, Tabulospongida. This suggestion is no longer accepted as it overemphasizes the presence of a calcareous skeleton; *Acanthochaetetes* is now assigned to the Hadromerida (RÜTZLER & VACELET, 2002).] *Upper Jurassic–Holocene.*

**Acanthochaetetes** FISCHER, 1970, p. 199 [\**A. seunesi*; OD; holotype, MNHN Institut de Paléontologie, R05599] [=*Acanthochaetetes* IVANOVSKIY, 1973, p. 267, *nom. null.*; =*Tabulospongia* MORI, 1976, p. 2 (type, *T. horiguchii*, OD)]. Domical to columnar basal skeleton of high Mg calcite composed of radially arranged tubules, circular to elliptical in cross section; tubule walls thick, lined with very fine, longitudinally arranged or irregularly clumped spines that are the same microstructurally as walls; tabulae complete, irregularly spaced, horizontal or concave, some with meniscus fillings adjacent to tubule walls; tubules increase by longitudinal fission, less commonly by intertubular budding; microstructure lamellar (irregular *sensu* WENDT, 1979; microlamellar *sensu* CUIF & others, 1979); basal skeleton commonly occurs; spicules are siliceous, whereas basal skeleton is calcitic, composed of iron-rich low Mg calcite (REITNER & ENGESER, 1987, p. 17); tylostyle megascleres from about 200 to 350  $\mu\text{m}$  long; spiraster microscleres approximately 10 to 30  $\mu\text{m}$  in diameter. [The only extant representative is *Acanthochaetetes wellsi* HARTMAN & GOREAU (1975, p. 2–12, fig. 1–9, 11–14, holotype, YPM 9077). Mesozoic material consists of a fragmented but seemingly spheroid skeleton composed of radiating tubes, oval or circular in cross section, ranging from 0.6 mm to 1.2 mm in diameter. Recent material of *A. wellsi*: massive demosponge with calcitic skeleton made up of adjoining vertical

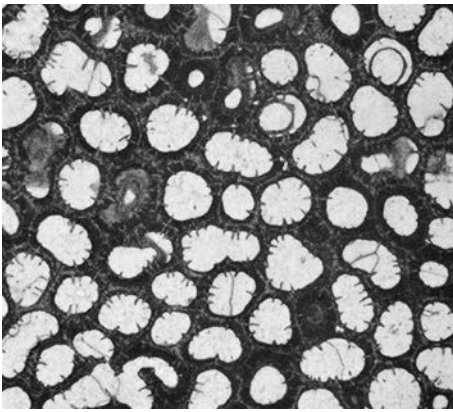
tubes (tubules) with common walls. Basal parts of the tubules partitioned by vertical tabulae. Walls ornamented by spines that are arranged in vertical lines or clumped irregularly. Both walls and spines have a microstructure of stacked lamellae. The surface of the skeleton shows starlike impressions (astrorhizae) from meandering exhalant canals converging upon single oscula. Basal layer with concentric growth lines covering lower surface of sponge. Size ranging from under 1 cm to over 18 cm (diameter of live tissue area). Living tissue (as seen on only extant species, *A. wellsi*) cream colored, coating the calcareous skeleton, in which it is anchored by thin fascicles of collagen fibrils that extend through canaliculi of the skeleton. Choanocyte chambers spherical, 30–35  $\mu\text{m}$  in diameter, choanocytes with periflagellar sleeves. Soft tissue includes masses of pseudogemmules in basal crypts of the tubules, covered by the outermost tabulae that are apparently dormant bodies consisting of clusters of thesocyte-like cells. Intercellular bacteria sparsely distributed in the mesohyl. Neither spongin fibers nor perispicular spongin occur. Siliceous spicules (observed in *A. wellsi*) occur in the living tissue and include erect tylostyles (points toward surface, 286  $\mu\text{m}$  by 3.4  $\mu\text{m}$ , and 7.4  $\mu\text{m}$  head diameter) and spiraster-like and amphister-like microscleres (in three dimensions, being 5  $\mu\text{m}$  by 6 to 20  $\mu\text{m}$  and 28  $\mu\text{m}$ ) localized in a layer in the outer tissue. Microsclere spines are often branched and closely spaced, thus obscuring the axis. Some microscleres can be seen adhering to the calcareous skeleton and may thus become incorporated during fossilization, as described for *A. seunesi* (REITNER & ENGESER, 1983). Growth rate of *A. wellsi* very slow, ranging from 50–450  $\mu\text{m}/\text{yr}$ , according to carbon isotope records (BÖHM & others, 1996; REITNER & GAUTRET, 1996).] *Upper Jurassic–Holocene:* France, Italy, Spain, Greece, *Upper Jurassic–Upper Cretaceous:* France, *Paleocene:* Spain, *Eocene:* western Pacific (New Caledonia, Great Barrier Reef, Okinawa, Guam, Mariana Islands, Philippines, Palau, Japan), *Holocene.*—FIG. 124a–e. \**A. seunesi*; a, high domical to columnar growth form, upper Albian, northern Spain,  $\times 2.75$  (Reitner & Engeser, 1987, p. 14, fig. 2); b, transverse section of tubules in holotype, note spines on tubule walls, Cenomanian, Pyrenees, northern Spain,  $\times 8$  (Fischer, 1970, pl. F,3); c, longitudinal section of tubules, note spines on tubule walls, Cenomanian, Pyrenees, northern Spain,  $\times 7.7$  (Fischer, 1970, pl. F,4); d, detail of longitudinal section of tubules, note spines on tubule walls and meniscus fillings at junction of walls and some tabulae, upper Albian, Cretaceous, d’Alava province, northern Spain,  $\times 68$  (Engeser, Floquet, & Reitner, 1986, pl. 1,6); e, diagrammatic sketch of walls, spines, tabulae, and meniscus fillings associated with some tabulae,  $\times 52.5$  (Fischer, 1970, p. 200, fig. 32).—FIG. 125a–c. \**A. seunesi*; a, SEM photograph of bundles of high-Mg calcite crystals that form the primary central wall structure, upper Albian, northern



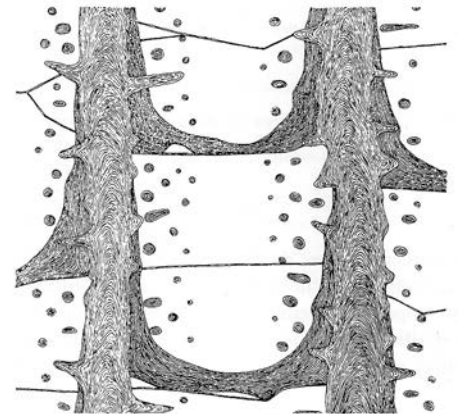
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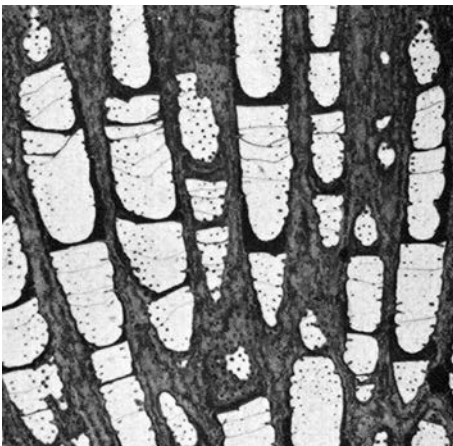
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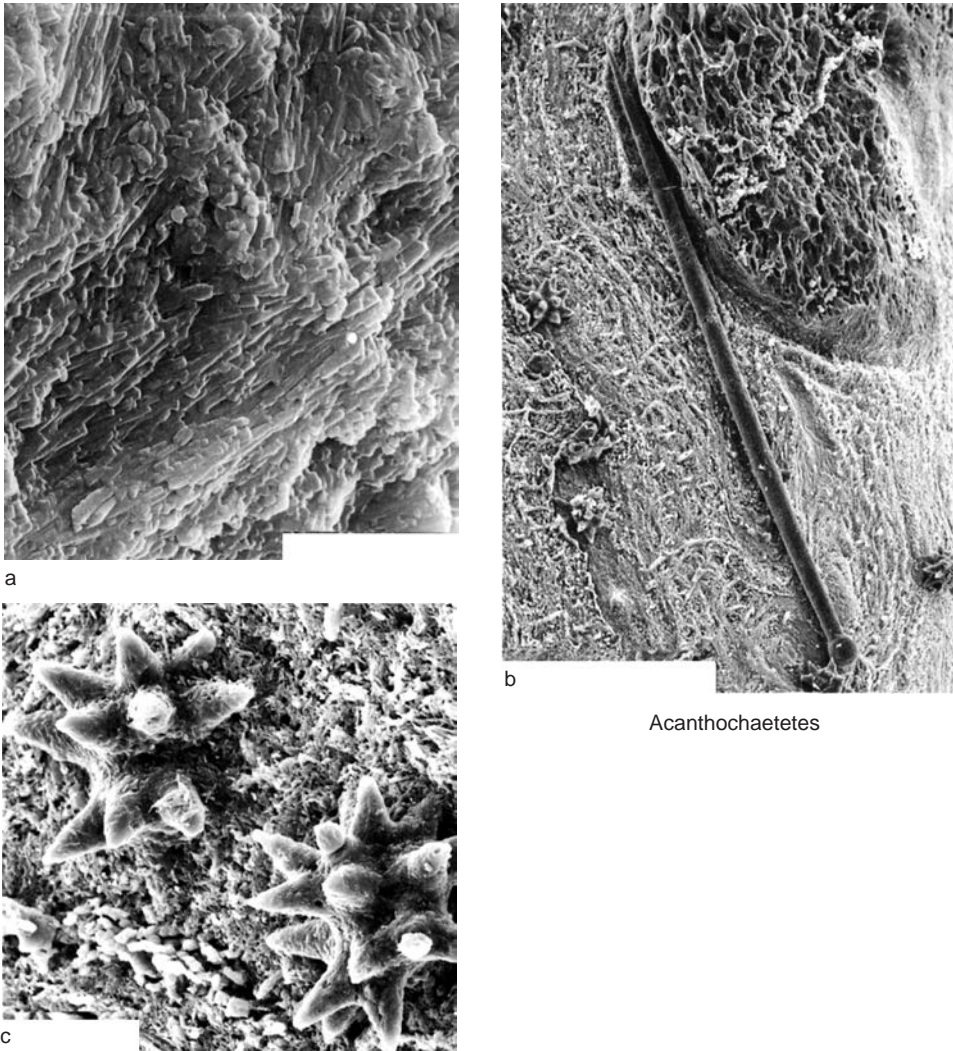


e Acanthochaetetes



c

FIG. 124. Acanthochaetetidae (p. 210–214).



Acanthochaetetes

FIG. 125. Acanthochaetetesidae (p. 210–214).

Spain,  $\times 4750$  (Reitner & Engeser, 1987, p. 14, fig. 4); *b*, SEM photograph of tylostyle megasclere, upper Albian, northern Spain,  $\times 280$  (Reitner & Engeser, 1987, p. 15, fig. 8); *c*, SEM photograph of spiraster microscleres, upper Albian, northern Spain,  $\times 1450$  (Reitner & Engeser, 1987, p. 15, fig. 10).—FIG. 126*a–b*. *A. wellsi* HARTMAN & GOREAU, 1975; *a*, living specimen *in situ* from Touho reef, New Caledonia, 15 m depth,  $\times 0.5$ , and see also Fig. 1.1) (West & others, 2013); *b*, SEM view of surface of a cleaned skeleton, with some spirasters still attached at rim of tubes and a part of skeleton isolated by a basal-layer-like structure, Great Barrier Reef, 15 m,  $\times 38$  (West

& others, 2013); *c*, section through a skeleton, the Philippines, 22 m,  $\times 1.8$  (West & others, 2013); *d*, SEM view of vertical section of skeleton showing surface (top left), tube walls, spines, and horizontal tabulae, the Philippines, 22 m,  $\times 16$  (West & others, 2013); *e*, SEM view of microscleres (spirasters), Great Barrier Reef, 15 m,  $\times 800$  (West & others, 2013); *f*, SEM view of tylostyle, Great Barrier Reef, 15 m,  $\times 500$  (West & others, 2013); *g*, TEM view of a choanocyte, showing a nucleus (*n*), a collar of microvilli (*mv*), a flagellum (*fl*), and a periflagellar sleeve (*ps*),  $\times 7830$  (Boury-Esnault & others, 1990); *h*, TEM view of living tissue (left) and decalcified skeleton (right, *sk*), with spherulose

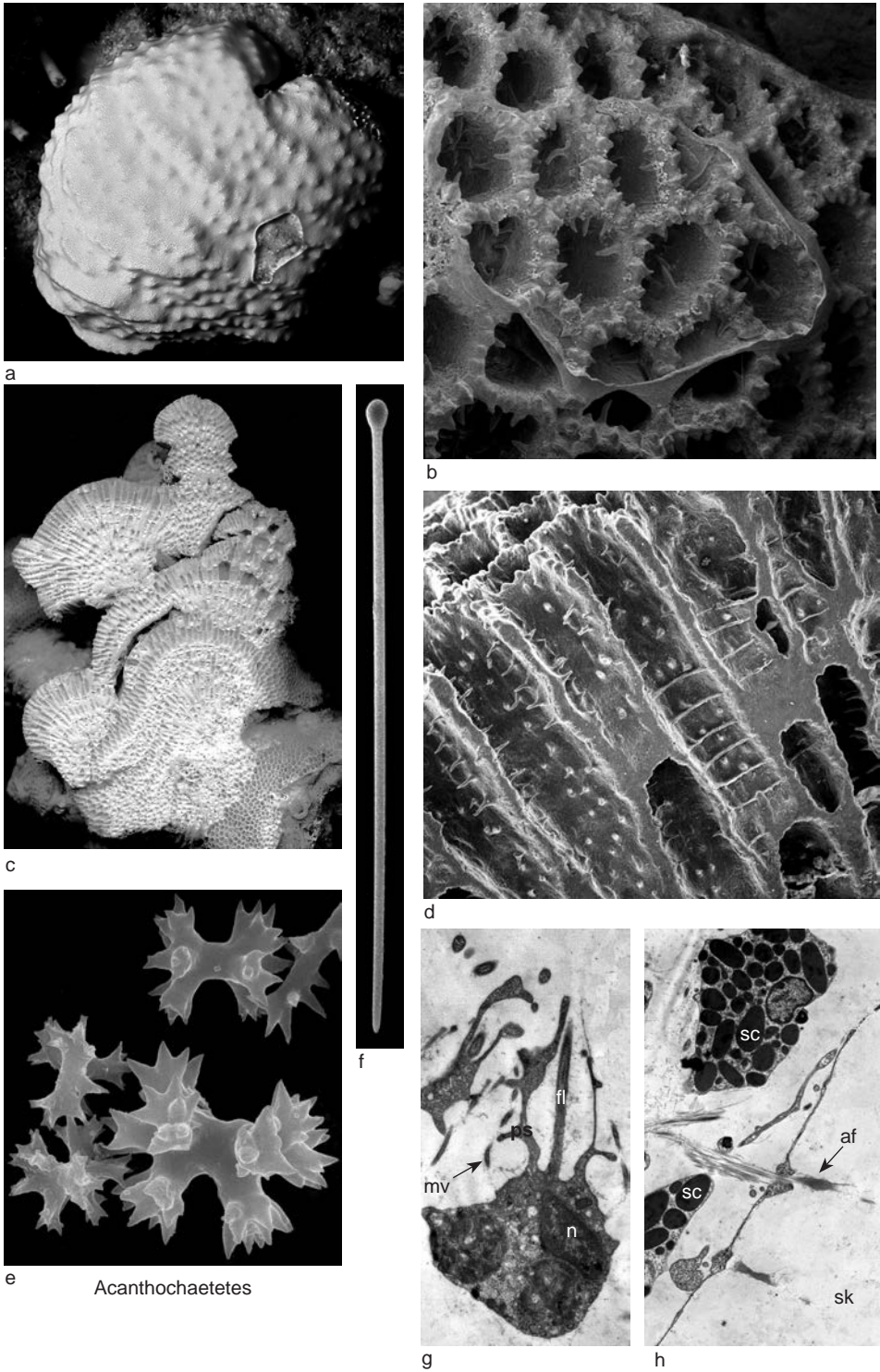


FIG. 126. *Acanthochaetetes* (p. 210–214).

cells (*sc*) and anchoring fascicles of collagen fibrils (*af*),  $\times 5000$  (West & others, 2013; see also *A. wellsii* in Fig. 3.5, Fig. 4.2–4.4).

**Willardia** WILLENZ & POMPONI, 1996, p. 206, fig. 1–22 [\**W. caicosensis* WILLENZ & POMPONI, 1996, p. 208; OD; holotype, RBINSc-POR 49, Brussels; paratypes, NHM 1995.11.3.1, London; HBOI, Harbor Branch; YPM 9360, New Haven]. Plate-like sponge, with calcareous basal skeleton attached to substratum at its center, reaching 4 to 5 mm in thickness. Microstructure of aragonitic skeleton of penicillate spherulitic type. Edges, not attached to substratum, seldom exceeding 2 to 3 mm, usually curled downward, forming an irregular bristled fringe. Individuals reach 15 to 20 cm in width. Surface of living tissue has a velvetlike appearance, due to presence of megasclere brushes protruding through surface of dermal membrane. Living tissue forms a thin veneer of 0.1 to 0.5 mm, filling irregular spaces between erected calcareous processes. Oscules evenly distributed over surface, receiving raised, transparent, anastomosed excurrent canals. Ectosome, mostly hidden under abundant protruding tylostyles, consists of a single layer of flat, superficial exopinacocytes. Choanosome with higher density of choanocyte chambers in central zone. Small eurypylous spherical choanocyte chambers (approximately 17  $\mu\text{m}$  in diameter) with approximately 20 choanocytes per chamber. Choanocytes oblate with an equatorial annular-shaped expansion, a large nucleus, and a long flagellum surrounded at base by a periflagellar sleeve, typical of the order Hadromerida. Central cell, with cytoplasmic processes encircling several flagella. Occurrence of two different types of cells with dense inclusions: spherulous cells densely concentrated beneath exopinacocytes and around aquiferous canals; glyocytes particularly abundant at base of sponge, close to basopinacocytes. Bundles of rough collagen fibrils extending from base of sponge, anchored deep within spaces formed between growing aragonitic crystals, to mesohyl, enveloping base of radiating tylostyles. Neither spongin fibers, nor perispicular spongin occur. Single layer of basopinacocytes lining calcareous skeleton. Intercellular bacteria sparsely distributed in mesohyl. Color yellow to tan orange in life, dark to pale brown in alcohol. Tylostyles, straight or slightly curved, mark oval head, 254–1080  $\mu\text{m}$  by 4.7–15.5  $\mu\text{m}$ . Amphiasters, 15.5–21.7  $\mu\text{m}$  by 10.9–20.2  $\mu\text{m}$ , with short, blunt spines abundant near surface and around canals. *Holocene*: Caribbean (Grand Turk Island, Turks and Caicos Island).—FIG. 127*a–f*. \**W. caicosensis*; *a*, holotype, photographed *in situ* at a depth of 114 m off northeastern tip of Grand Turk Island, prior to collection by Harbor Branch Johnson–Sea Link I submersible, scale bar, 10 cm, and see also Figure 1.8 (Willenz & Pomponi, 1996); *b*, surface of calcareous skeleton after treatment with Perhydrol, showing pillar-shaped processes, scale bar, 1 mm (West & others, 2013); *c*, ground section perpen-

dicular to surface (*s*), with living tissue (*lt*) covering aragonite skeleton (*ar*), light microscopy, scale bar, 100  $\mu\text{m}$  (West & others, 2013); *d*, surface of sponge with radially arranged protruding tylostyles, scale bar, 500  $\mu\text{m}$  (West & others, 2013); *e*, tylostyle protruding from aragonitic skeleton and amphiasters settled on surface during sample preparation, scale bar, 50  $\mu\text{m}$  (Willenz & Pomponi, 1996); *f*, tylostyles and amphiasters (scale bar, 500  $\mu\text{m}$ ), and detail of amphiaster (inset scale bar, 10  $\mu\text{m}$ ) (West & others, 2013).

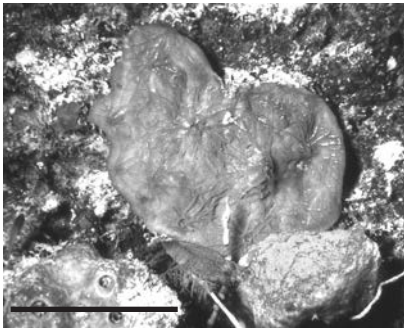
### Family SUBERITIDAE Schmidt, 1870

[*nom. transl. et correct.* VOSMAER, 1887, p. 330, ex Suberitidinae SCHMIDT, 1870, p. 46]

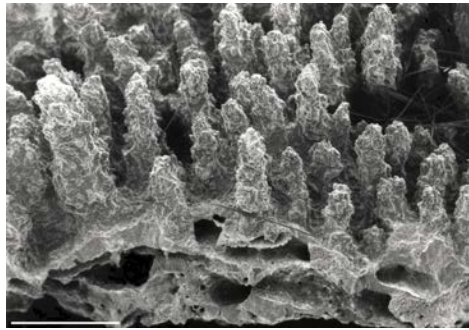
RONALD R. WEST

Globular, ramose, stipitate, massive or encrusting habit. Megascleres usually tylostyles, occasionally styles, strongyloxeas or centotyloxeas; microscleres usually absent, when present confined to microrhabds and trichodragmas. In cross section, megascleres are usually arranged in bouquets at the surface, in massive species becoming progressively confusedly arranged toward the interior, but overall structure may also be strictly radial or showing axial orientation. In one genus, the spicules at the surface are arranged tangentially. There is no recognizable cortex. In thinly encrusting species, spicule orientation is either parallel or perpendicular to the substratum. Modifications of shape and position of the tylostyle heads are common; they can be lobate, pear shaped, drop shaped, or subterminal (description as stated in VAN SOEST, 2002a, p. 227; see also FINKS & RIGBY, 2004a, p. 43, who possibly overlooked SCHMIDT's 1870 citation). ?*Silurian, Middle Devonian–Upper Cretaceous (Coniacian)*.

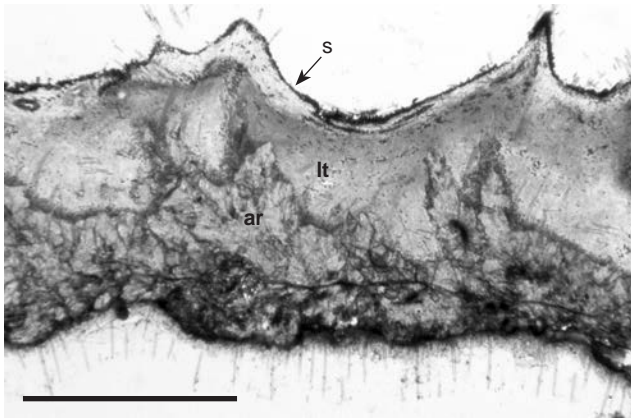
**Calcisuberites** REITNER & SCHLAGINTWEIT, 1990, p. 249 [\**C. stromatoporoides*; OD; holotype no. IPFUB/JR 90]. Hypercalcified demosponge with a high Mg calcite stromatoporoid-grade basal skeleton and a penicillate, water-jet (fascicular fibrous) microstructure; typical hadromerid tylostyle megascleres 700 to 820  $\mu\text{m}$  long and 25 to 30  $\mu\text{m}$  in diameter; plumose, bushlike arrangement of 4 to 5 tylostyles in dermal layer; microscleres unknown. [See also FINKS & RIGBY, 2004a, p. 43.] *Upper Cretaceous (Turonian–Coniacian)*: Germany.—FIG. 128*a–f*. \**C. stromatoporoides*; *a*, growth interruption surface in longitudinal section



a

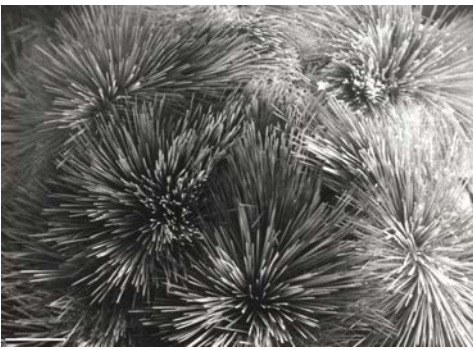


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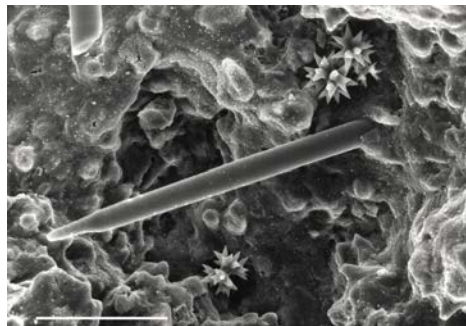


*Willardia*

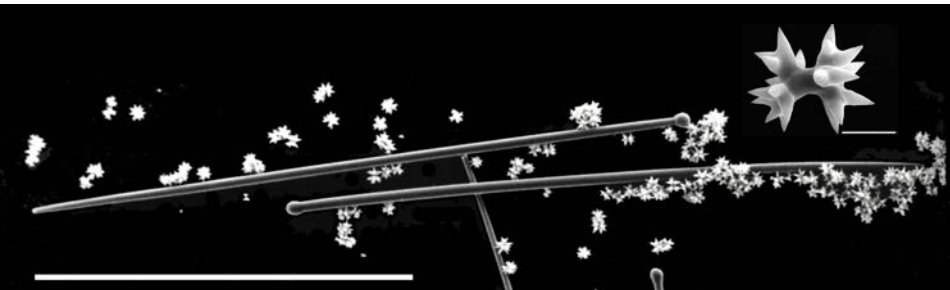
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e



f

FIG. 127. Acanthochaetetidae (p. 214).

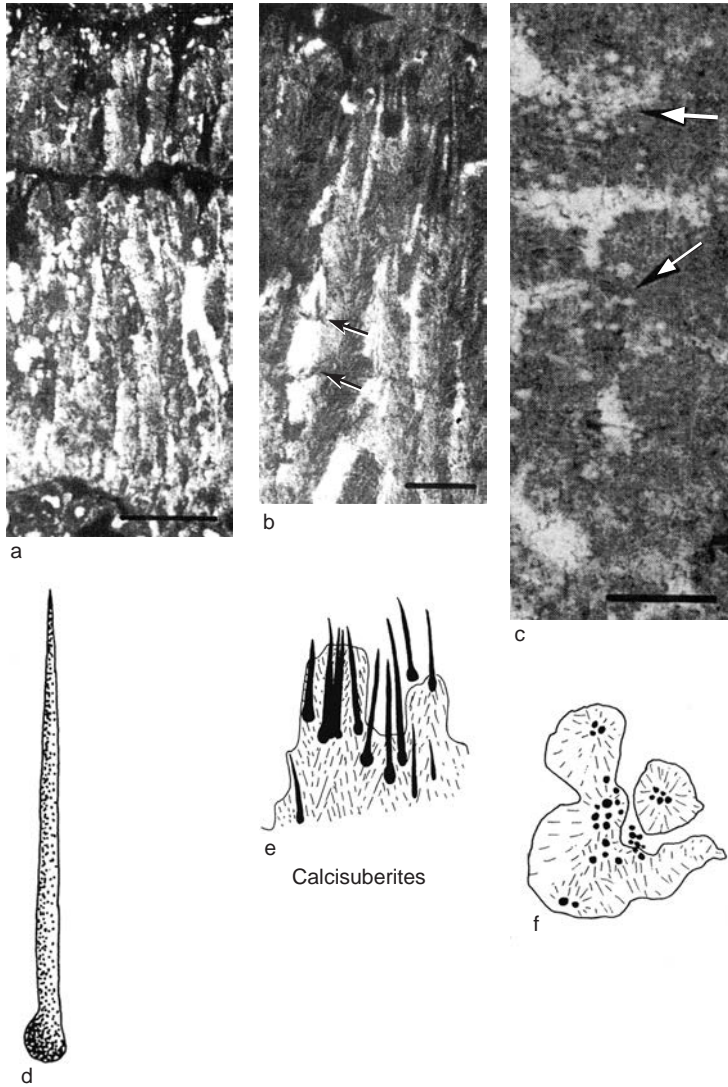


FIG. 128. Suberitidae (p. 214–216).

of basal skeleton,  $\times 8.7$ ; *b*, longitudinal section showing bundles of megascleres in the upper right with *arrows* indicating tabulae in lower left, penicillate, water-jet (fascicular fibrous) microstructure is faintly visible in tubule wall just to right of *arrows*,  $\times 24$ ; *c*, transverse section showing cross sections of bundles of megascleres (small white dots denoted by *arrows*),  $\times 37.5$ ; *d*, diagrammatic sketch of hadromerid tylostyle,  $\times 80$ ; *e*, diagrammatic sketch of megasclere bundles in longitudinal section,  $\times 27.5$ ; *f*, diagrammatic sketch of megasclere bundles in transverse section,  $\times 35$  (Reitner & Schlagintweit, 1990, p. 251, pl. 1).

*Chaetetes* FISCHER VON WALDHEIM MS in EICHWALD, 1829, p. 197 [\**C. cylindricus*; SD OAKLEY, 1936, p. 441; possibly in Eichwald Collection, LGU, Leningrad (but perhaps in Museum of Geological Faculty, St. Petersburg State University)]; LANG, SMITH, and THOMAS (1940, p. 35) considered *C. cylindraceus* congeneric if not conspecific with *C. radians* FISCHER VON WALDHEIM, 1830 and 1837, p. 160, which was erroneously chosen as type species by MILNE-EDWARDS and HAIME (1850–1854, p. lxi), as stated by HILL (1981, p. 508), with spelling of the type species as *cylindraceus*, as does FISCHER (1970) and SOKOLOV (1950)] [= *Chaetites* MICHELIN,



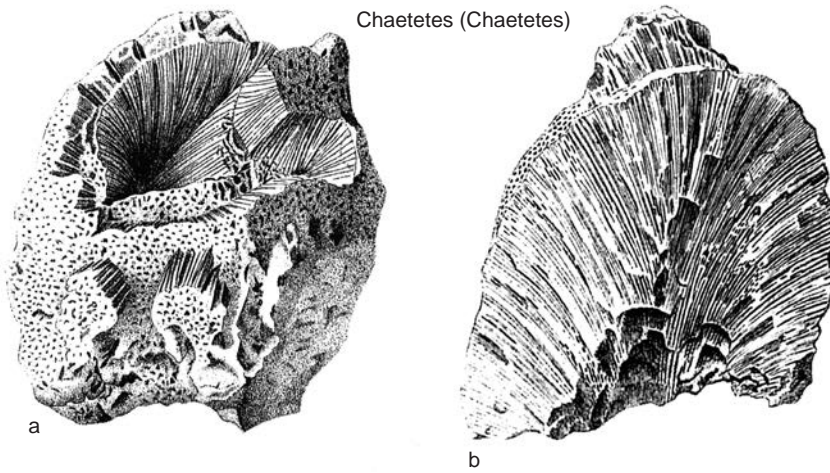


FIG. 129. Suberitidae (p. 216–218).

1844 in 1840–1847, p. 112, *nom null.*; = *Chaetetides* STRAND, 1928b, p. 34, *nom. nov. pro Chaetetes* FISCHER VON WALDHEIM, 1837, p. 159, in case this should prove to be different from *Chaetetes* FISCHER VON WALDHEIM MS in EICHWALD, 1829, p. 197 (LANG, SMITH, & THOMAS, 1940, p. 35, considered *Chaetetides* unnecessary); ?=*Dania* MILNE-EDWARDS & HAIME, 1849, p. 261 (type, *D. huronica*, M; Stokes Collection, possibly MNHN in Paris; Silurian, Drummond Island, Lake Huron, North America), an uncatalogued specimen labeled *D. huronica*, Drummond Island, which may have been used for the schematized figure in MILNE-EDWARDS and HAIME, 1851, pl. 18, 2b, was seen in 1975 by HILL in the Milne-Edwards & Haime Collection of Tabulata, MNHN, Paris (as stated by HILL, 1981, p. 508), but this specimen had a markedly different corallite diameter, = *Danaia* SCUDDER, 1882, p. 101, *nom. null.*]. Growth form columnar, domical, or laminar, may be globular; often with growth interruptions; tubules long, polygonal in transverse section with a common wall; microstructure of walls inferred to be penicillate, water-jet (fascicular fibrous) calcite with aster (possible euaster) microscleres 25 to 35  $\mu\text{m}$  in diameter (REITNER, 1991a, p. 186); tabulae straight or irregular; tubules increase by longitudinal fission, intertubular budding or peripheral expansion. [FISCHER VON WALDHEIM (1837, p. 160) described *Chaetetes cylindricus*, the presumed type species, as having very thin cylindrical tubes. In the same publication, on the same page, he described *C. radians* as being similar to *Calymnopora polymorpha* GOLDFUSS, but the tubes are simple, almost capillary, without diaphragms and at the surface are simple, round, and fine. REITNER (1991a) described a specimen, no. R 27318, labeled "*Chaetetes radians*" in the NHM,

as a new genus and new species, *Chondrochaetetes longitubus*, placing it in the family Chondrosiidae, based on what he considered aster (possible euaster) scleres and because he observed no tylostyles megascleres as seen in *C. mortoni*. The state of preservation (diagenetic alteration, REITNER, 1991a, p. 188) is such that this taxon requires further verification.] ?*Silurian*, Middle Devonian–Upper Jurassic (*Tithonian*): Great Britain, Central Asia, Arctic, China, Japan, Indochina, Middle Devonian–Carboniferous; North America, Middle Devonian–Carboniferous (*Pennsylvanian*); North America, Japan, Mongolia (Karakorum), Permian.

**Chaetetes (Chaetetes)**. Description as for genus. ?*Silurian*, Middle Devonian–Permian: USA (Michigan), ?*Silurian*; Kuznetsk Basin–Kazakhstan, Middle Devonian; Russia ("le calcaire de Moscou"); Great Britain, Central Asia, Arctic, China, Japan, Indochina, Middle Devonian–Carboniferous; North America, Middle Devonian–Carboniferous (*Pennsylvanian*); North America, Japan, Mongolia (Karakorum), Permian.—FIG. 129a. \**C. (C.) cylindricus*, Carboniferous, Russia, St. Petersburg; magnification unknown (Fischer von Waldheim, 1837, pl. 36, 1).—FIG. 129b. *C. (C.) radians* FISCHER VON WALDHEIM, Carboniferous, Russia; this specimen (and the one in Fig. 129a) are presumed to be lost, but might be in the Eichwald collection, St Petersburg; magnification unknown (Fischer von Waldheim, 1837, pl. 36, 3).—FIG. 130a–d. *C. (C.) radians* FISCHER VON WALDHEIM, 1837, Carboniferous, Russia, NHM no. R 27318, labeled as *Chaetetes radians*; a, transverse section showing reduction of tubule size and shape due to diagenetic cement, faint white dots are inferred microscleres,  $\times 26$ ; b, longitudinal section showing

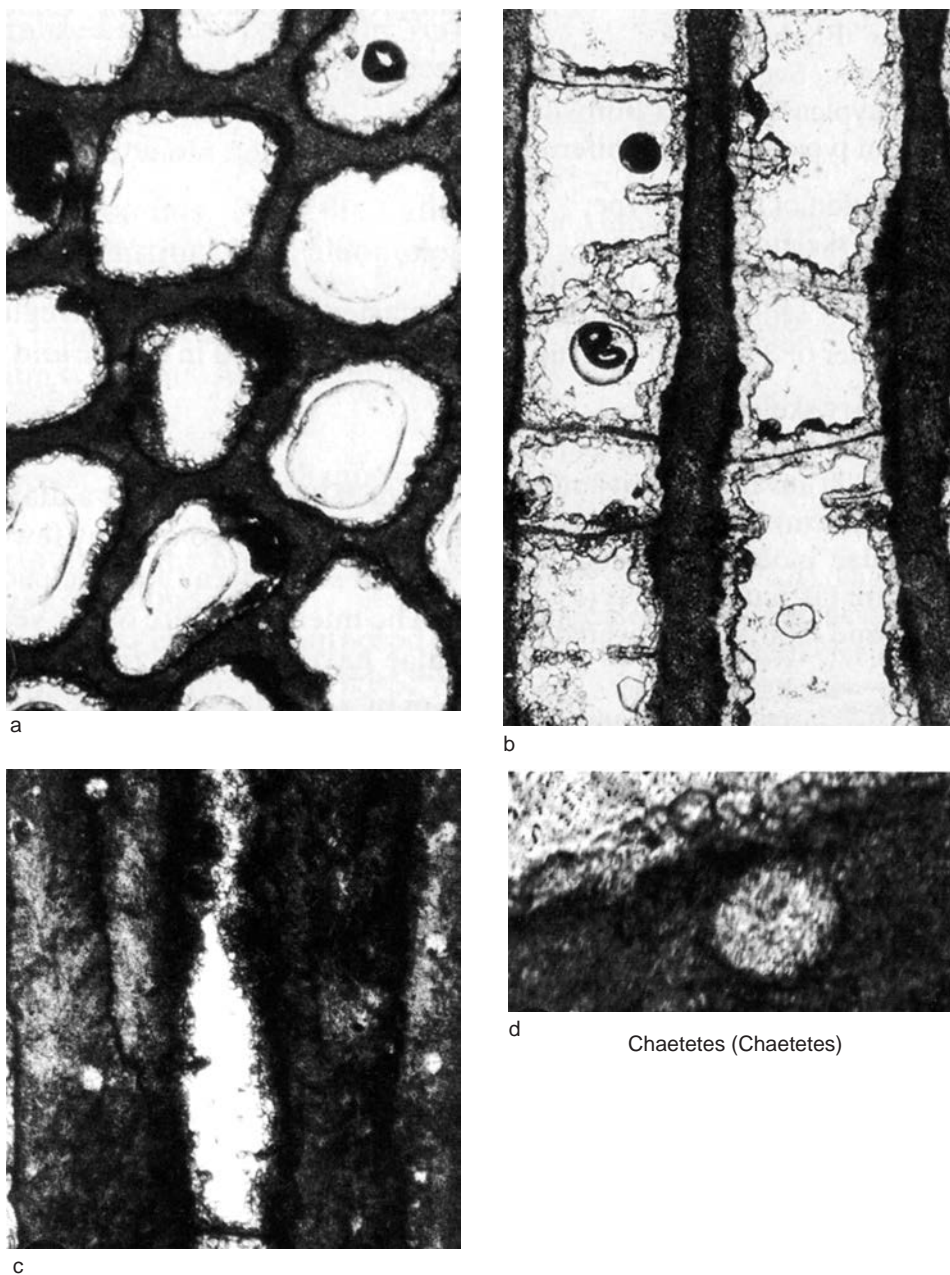


FIG. 130. Suberitidae (p. 216–218).

granular calcite (diagenetic) cement,  $\times 30$ ; *c*, longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure, faint white dots are inferred microscleres,  $\times 45$ ; *d*, detail of inferred microsclere in longitudinal section,  $\times 200$  (Reitner, 1991a, p. 187).

**Chaetetes (Boswellia)** SOKOLOV, 1939, p. 411 [*\*Chaetetes boswelli* HERITSCH, 1932, p. 221; OD; thin sections, PIOI9, UG, Graz, specimen destroyed *vide* HERITSCH, 1932, p. 221; HILL, 1981, p. 508]. Type species with thick, irregular tubule walls of fascicular fibrous calcite

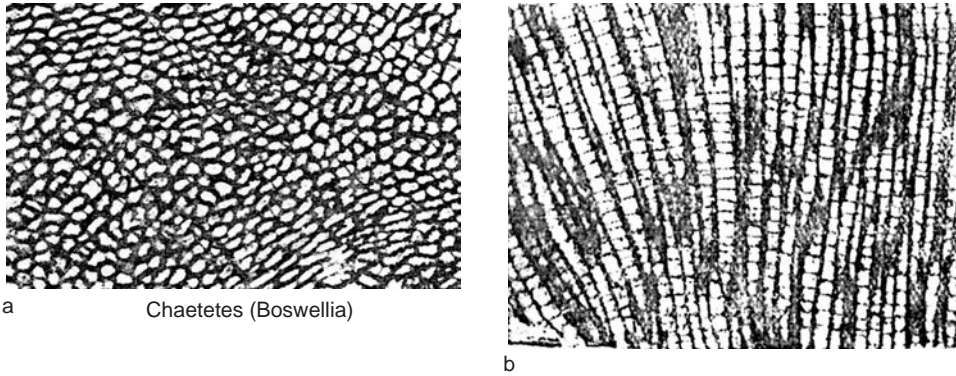


FIG. 131. Suberitidae (p. 216–219).

with megascleres (siliceous) sometimes present; tubules irregular or subpolygonal in transverse section; tubules increase by longitudinal fission that may be incomplete and peripheral expansion (description modified from GRAY, 1980, p. 806). [A modified description from GRAY (1980) and REITNER (1991a), of *Chaetetes (Boswellia) mortoni* GRAY, 1980, is included because details of the primary (spicules) and secondary (mineralogy and microstructure) features are better known for this species than for the type species *C. (B.) boswelli*, as follows: growth form laminar or bulbous; irregular to subpolygonal tubules in transverse section; penicillate, water-jet (fascicular fibrous) tubule walls of inferred Mg calcite; pseudosepta visible in transverse section and as long, irregular ridges in longitudinal section; tabulae well spaced; tubules increase by longitudinal fission and peripheral expansion; monaxon tylostyle megascleres (approximately 7  $\mu\text{m}$  in diameter and 170–275  $\mu\text{m}$  long) as subparallel bundles diverging distally, with their pointed (oxeote) ends directed distally; microscleres unknown. Middle Devonian occurrence is rare.] *Middle Devonian–Carboniferous*: Serbia, Germany, Russia (Moscow and Donets Basins, Urals), Great Britain (Wales), Central Asia.—FIG. 131a–b. \**C. (B.) boswelli* (HERITSCH), D<sub>2</sub>, Carboniferous, northeastern Ukraine, Russia; a, transverse section,  $\times 4$ ; b, longitudinal section,  $\times 4$  (Sokolov, 1950, pl. 8–9).—FIG. 132a–f. *C. (B.) mortoni* GRAY, 1980, lower Carboniferous, northern Wales; a, longitudinal section showing tylostyle megascleres in penicillate, water-jet (fascicular fibrous) tubule wall, paratype NHM no. R4429 (Morton Collection),  $\times 37.5$ ; b, longitudinal section showing arrangement of tylostyle megascleres in tubule walls, paratype NHM no. R4429 (Morton Collection),  $\times 231$  (Gray, 1980, pl. 103); c, diagrammatic sketch of arrangement of tylostyle megascleres in tubule walls,  $\times 100$  (Reitner, 1991a, p. 182); d, single tylostyle megasclere, paratype NHM no.

R4429,  $\times 200$  (Reitner, 1992, pl. 2); e, diagrammatic sketch of tylostyle megasclere,  $\times 400$  (Reitner, 1991a, p. 182); f, three-dimensional reconstruction of basal skeleton,  $\times 11$  (Reitner, 1991a, p. 182).

**Chaetetes (Pseudoseptifer)** FISCHER, 1970, p. 171 [\**Chaetetes beneckeii* HAUG, 1883, p. 174; OD; =*Chaetetes beneckeii* AIRAGHI, 1907, p. 17; =*Chaetetes (Bauneia?) beneckeii* PETERHANS, 1929c, p. 119; =*Chaetetes beneckeii* VIALLI, 1938, p. 65; =*Chaetetes (Pseudoseptifer) beneckeii* FISCHER, 1970, p. 171; although FISCHER (1970) described *Pseudoseptifer* as a subgenus of *Chaetetes*, HILL (1981, p. 519), listed it as a genus; holotype, Upper Jurassic, de Roverè di Velo, Province de Vérone, Italy, original thin sections redescribed by PETERHANS (1929c) in MS]. Growth form domical; tubules irregular polygons, some rounded, in transverse section; tubule walls thick; pseudosepta conspicuous and numerous; tabulae numerous, thin, irregularly spaced; tubules increase by longitudinal fission, rarely intertubular budding and peripheral expansion. [FISCHER (1970, p. 170) described the microstructure as fibrillar; BIZZARINI and BRAGA (1988, p. 145) described it as clinogonal, a synonym of penicillate, water-jet, and fascicular fibrous; aragonite inferred original mineralogy; acanthostyle megascleres documented by BIZZARINI and BRAGA (1988); microscleres unknown.] *Upper Jurassic (Tithonian)*: Italy (Trento–Venetian Prealps).—FIG. 133a–e. \**C. (P.) beneckeii* (HAUG), Saint Anna di Vallarsa, Civic Museum of Rovereto, northern Italy; a–c, upper exterior surface, lower exterior surface, lateral view of basal skeleton,  $\times 0.7$  (adapted from Bizzarini & Braga, 1988, pl. 1,2,3,1); d–e, Malga Fratta, Altopiano dei Setti Comuni, Museum of the Institute of Geology, University of Padova; d, transverse section of basal skeleton, note pseudosepta in lower left,  $\times 3.3$ ; e, enlargement of part of view d showing pseudosepta,  $\times 33$  (adapted from

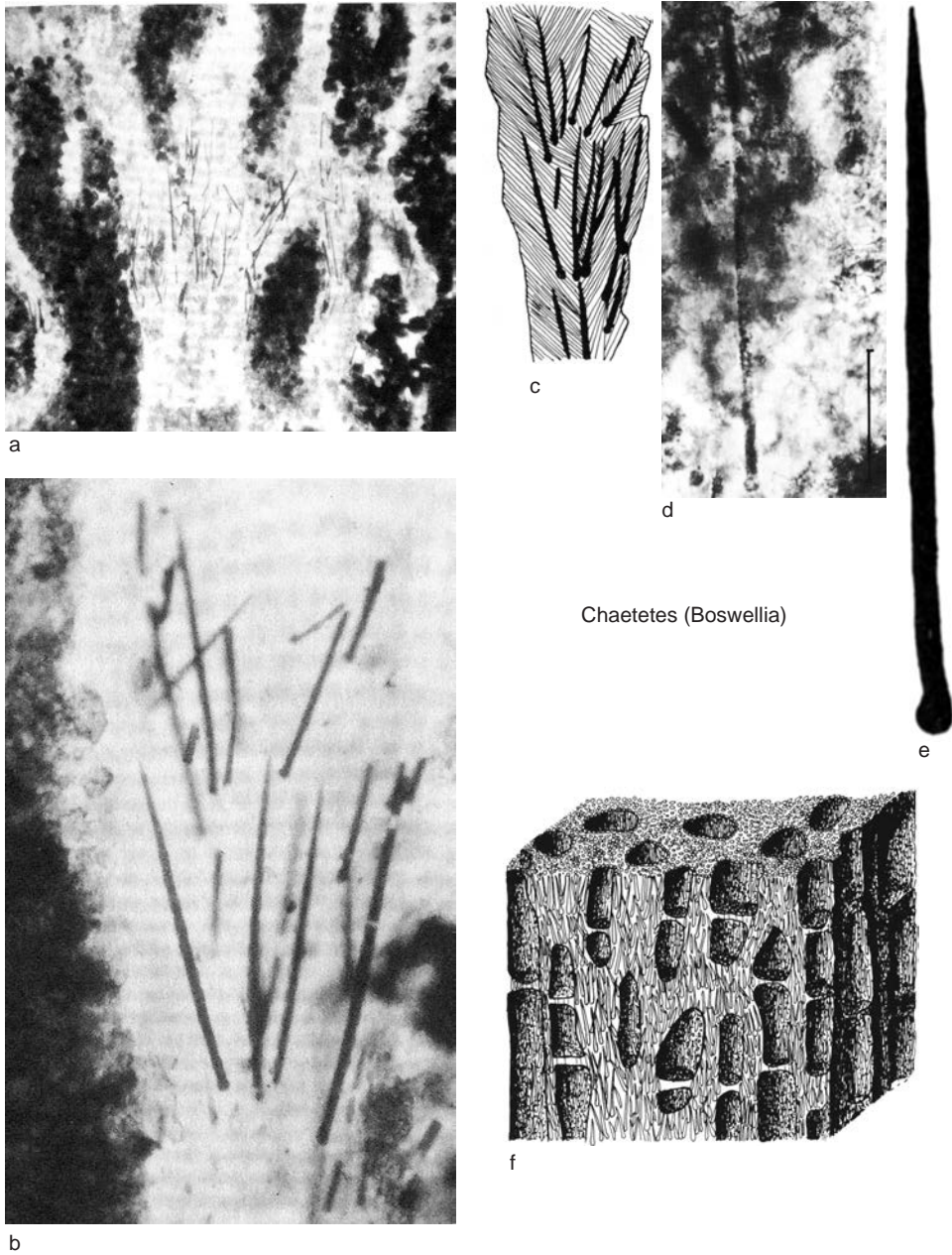
Chaetetes (*Boswellia*)

FIG. 132. Suberitidae (p. 216–219).

Bizzarini & Braga, 1988, pl. 2, 1, 5).—FIG. 134a–b. \**C. (P.) beneckeii* (HAUG), Malga Fratta, Altopiano dei Setti Comuni, Museum of the Institute of Geology, University of Padova; a, longitudinal section of basal skeleton showing pseudosepta (*P*) and tubules increase by longitudinal division,  $\times 15$ ; b, enlargement of part of

view a showing pseudosepta (*P*),  $\times 35$  (adapted from Bizzarini & Braga, 1988, pl. 2, 3–4).—FIG. 134c. *C. (P.) waehneri* HERITSCH, Calcarei Grigi di Noriglio, near Lancia al Col Santo, northern Italy; pseudomorphs of acanthostyle megascleres in penicillate, water-jet (fascicular fibrous, clinogonal) tubule walls (longitudinal

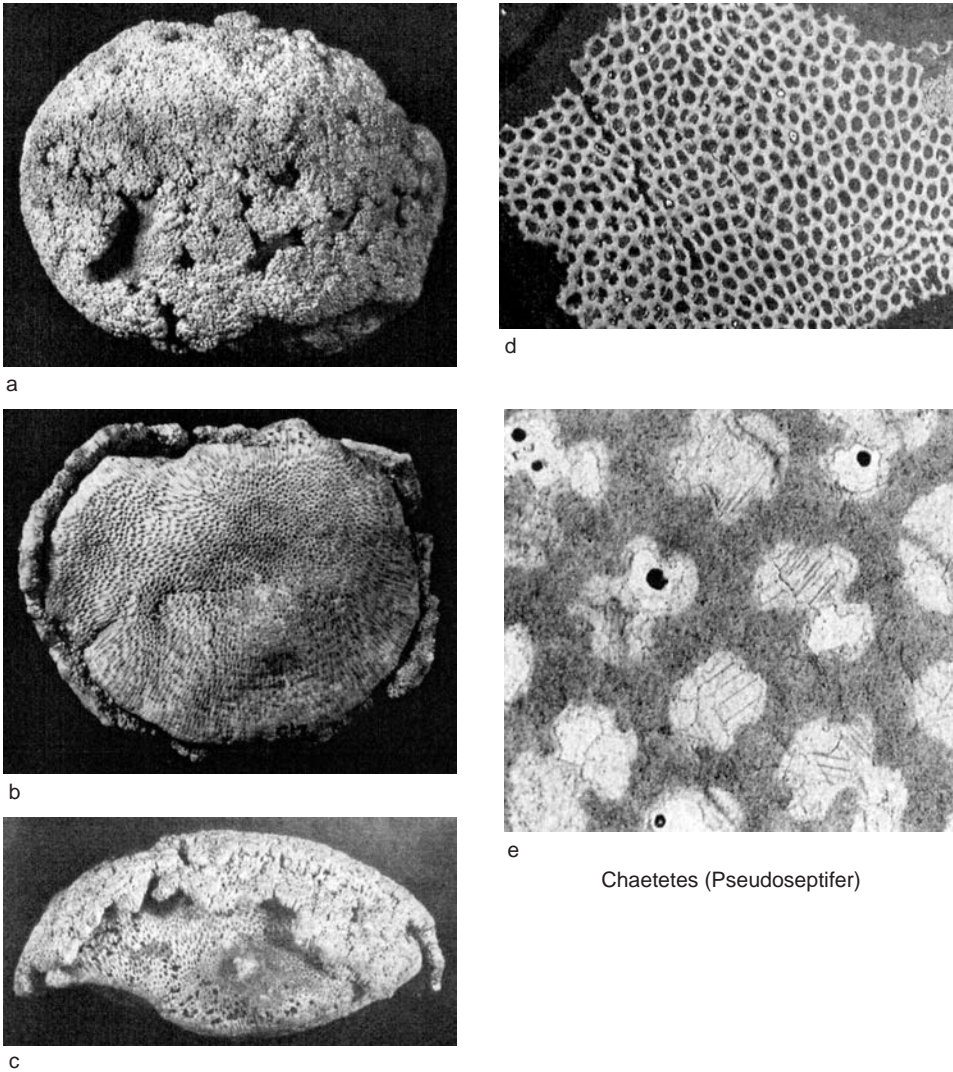
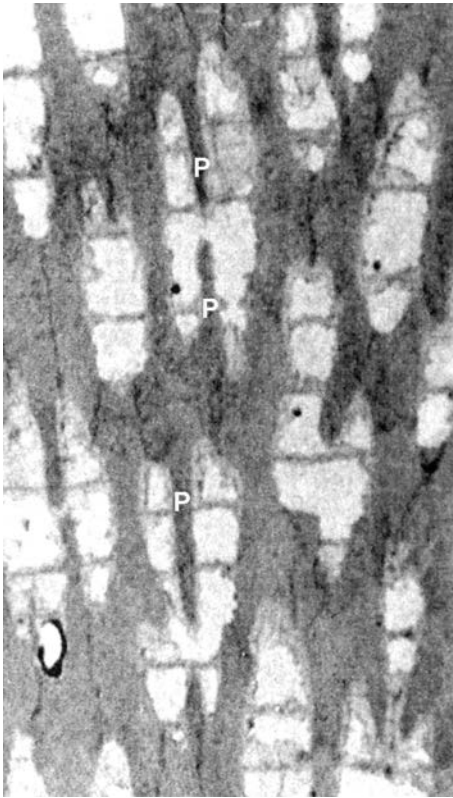


FIG. 133. Suberitidae (p. 216–221).

section), approximately  $\times 218$  (adapted from Bizzarini & Braga, 1988, pl. 5,6).  
**Chaetetopsis** NEUMAYR, 1890, p. 28 [*C. crinata*; OD; no longer in the Neumayr Collection in Vienna, *vide* PETERHANS, 1929c, p. 115; Upper Jurassic (Tithonian), Iwaso Konpira and Torinosuyama, Japan; PETERHANS, 1929c, based his chaetetid interpretation of the genus on the type specimen of *Monotrypa limitata* DENINGER, 1906, p. 64, in the Museum of the University of Freiburg, Upper Jurassic (Tithonian), Capri, Italy. A neotype in MNHM, Paris, named by FISCHER, 1970, p. 197, is unsatisfactory in that it comes from a locality not named by NEUMAYR (Musaki, Japan) and has been greatly

altered by diagenesis (as stated in HILL, 1981, p. 666)]. Growth form domical to globular; tubules in transverse section circular to elliptical, regularly arranged; tubules in longitudinal section long, thin, nearly parallel, with continuous double walls; tabulae thin, abundant, subhorizontal, indistinct, not laterally continuous between tubules; pseudo-septa uncommon; walls defined by a thin marginal edge of granules; remainder of wall irregular crystals similar to tubule fillings; tubules increase by inter-tubular budding, indistinct (description modified from NEUMAYR, 1890; FISCHER, 1970). [Spicules, or spicule pseudomorphs, and the original mineralogy and microstructure are unknown for the type species,



a



c

Chaetetes (Pseudoseptifer)



b

FIG. 134. Suberitidae (p. 216–221).

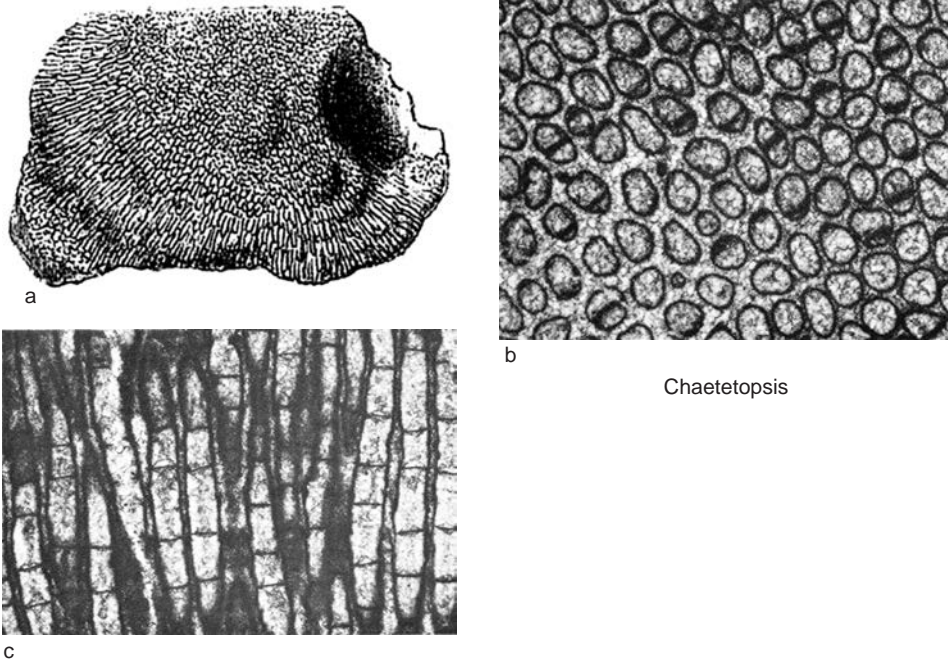


FIG. 135. Suberitidae (p. 221–223).

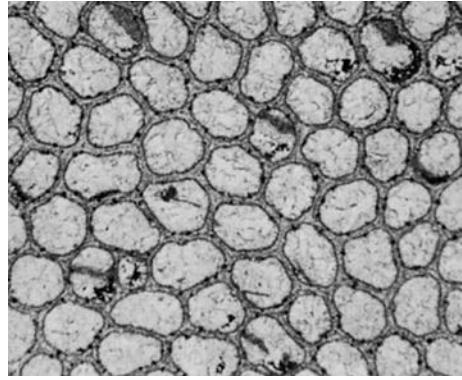
*C. crinata*, but these primary and secondary features have been reported for *C. favrei* (DENINGER, 1906) by KAŻMIERCZAK (1979) and REITNER (1991a) as follows: growth form conical with regular growth ridges on lateral surface; tubules rounded polygonal, subcircular or circular in transverse section, contiguous in longitudinal section; tabulae thin, subhorizontal, and arranged in sets such that a few are aligned between tubules; tubule walls are commonly granular to blocky calcite but inferred to have been fascicular fibrous aragonite; tubules increase by longitudinal fission; monaxon tylostyle pyrite pseudomorph megascleres (120–450  $\mu\text{m}$  long, 5–10  $\mu\text{m}$  in diameter) within tubule walls; microscleres unknown.] *Upper Jurassic (Tithonian)–Lower Cretaceous (Aptian)*: Japan, Italy (Capri), *Tithonian*; Crimea, Greece, *Barremian–Aptian*.—FIG. 135a–c. \**C. crinata*, Portlandian, Jurassic, Japan; a, globular growth form, magnification unknown (Neumayer, 1890, pl. 4); b, transverse section,  $\times 15$ ; c, longitudinal section,  $\times 15$  (Fischer, 1970, pl. E).—FIG. 136a–e. *C. favrei* (DENINGER); a, longitudinal section, Barremian, Crimea,  $\times 27$ ; b, transverse section, Barremian, Crimea,  $\times 25$  (Kaźmierczak, 1979, p. 103–104); c, longitudinal section showing fascicular fibrous microstructure of tubule walls, ?Aptian, Greece,  $\times 347$  (Reitner, 1991a, p. 185); d, longitudinal section showing pyrite pseudomorphs of tylostyle megascleres in tubule walls, Barremian, Crimea,  $\times 150$ ; e, transverse section showing pyrite pseudomorphs of tylostyle mega-

scleres (arrows) in tubule walls, Barremian, Crimea,  $\times 95$  (Kaźmierczak, 1979, p. 103–104).

*Pachythea* SCHLÜTER, 1885, p. 144, non HOOKER, 1861, a plant [\**P. stellimicans*; M; SD BIRENHEIDE, 1985, p. 21, syntypes 138a,b, 204, Schlüter Collection, PIUB; =*Calamopora stromatoporoides* ROEMER, 1880 in 1876–1880, p. 459] [=*Rhaphidopora* NICHOLSON & FOORD, 1886, p. 390 (type, *Calamopora crinalis* SCHLÜTER, 1880, p. 281, OD; syntypes 192, Schlüter Collection (26), PIUB; Middle Devonian, Hillesheim syncline, Eifel, Germany, see SCHLÜTER, 1889, p. 401; =*Pachythea stellimicans* FREARN, 1886, p. 17; =*Pachythea stellimicans* SOKOLOV, 1955, p. 519; =*Pachythea stellimicans* HILL & STUMM, 1956, p. 455; =*Pachythea stellimicans* HILL, 1981, p. 511; =*Pachythea stellimicans* BYRA, 1983, p. 22; =*Pachythea stellimicans* BIRENHEIDE, 1985, p. 21] [=*Rhaphidopora* YABE, 1910, p. 4, *nom. null.*; =*Rhaphidopora* STEARN, 1972, p. 375, *nom. null.* (as stated in HILL, 1981, and BYRA, 1983)]. Growth form laminar; tubules polygonal in transverse section, long and thin longitudinally, most tubules filled with secondary calcite, as in *Ceratoporella*; microstructure penicillate water-jet (fascicular fibrous). [The following was observed in *P. cf. P. stellimicans* of REITNER (1992, p. 152): tabulae microstructure similar to tubule filling; tubule walls inferred to be Mg calcite, tylostyle megasclera (500–800  $\mu\text{m}$  long), arranged in



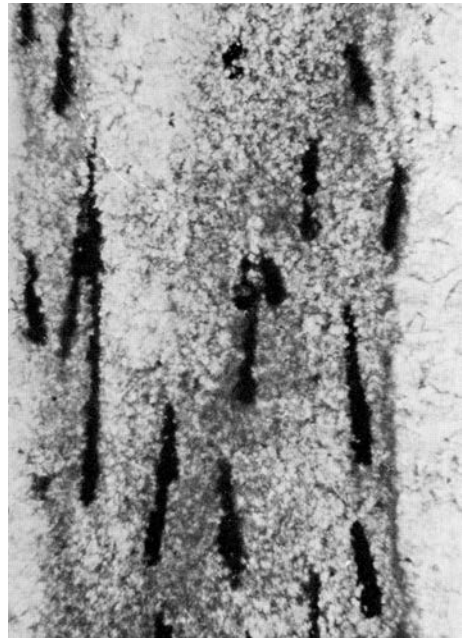
a



b

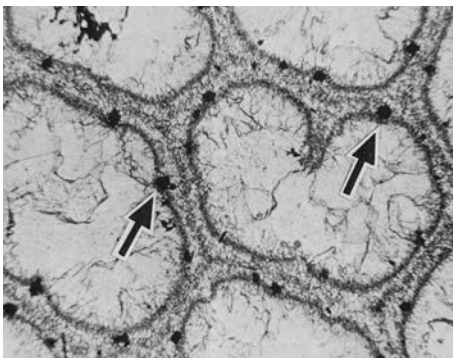


c



d

Chaetetopsis



e

FIG. 136. Suberitidae (p. 221–223).

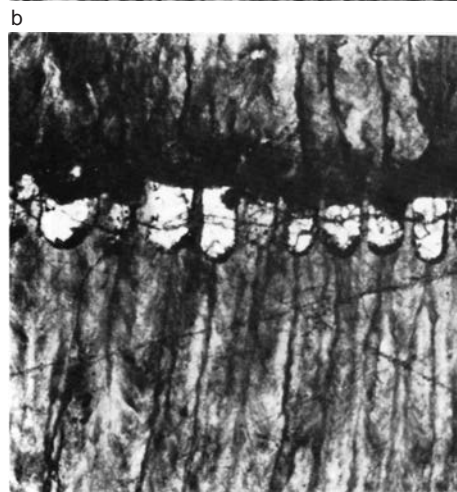
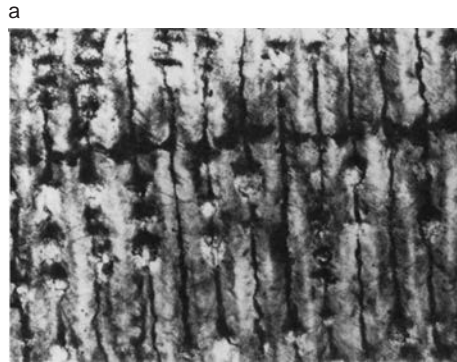
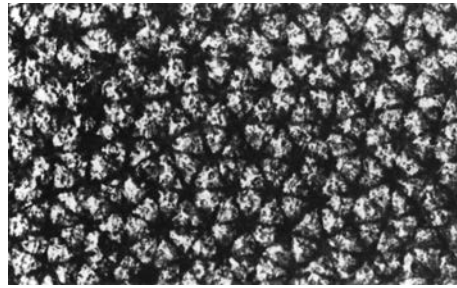


bundles of 5 or 6 in the basal skeleton, reflecting a relict radial structure; microscleres unknown.] *Middle Devonian*: Germany (Eifel), Great Britain, Russia (northern Urals).—FIG. 137*a-c*. \**P. stellimicans*, Eifelian, western Germany; *a*, transverse section of paralectotype,  $\times 20$ ; *b*, longitudinal section of lectotype,  $\times 18.7$ ; *c*, longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure of lectotype,  $\times 21$  (Birenheide, 1985, pl. 1).—FIG. 138*a-c*. *P. cf. P. stellimicans*, Eifelian, northern Spain; *a*, calcite pseudomorph of tylostyle megasclere,  $\times 204$ ; *b*, diagrammatic sketch of tylostyle megasclere,  $\times 270$ ; *c*, diagrammatic reconstruction of basal skeleton,  $\times 52.5$  (Reitner, 1992, p. 153, fig. 30, pl. 22, 6).

**Family SPIRASTRELLIDAE**  
Ridley & Dendy, 1886

[Spirastrellidae RIDLEY & DENDY, 1886, p. 490; *emend.*, RÜTZLER, 2002, p. 220] [=Choanitidae DE LAUBENFELS, 1936, p. 140]

Encrusting demosponges with limestone-excavating capability in early stages but without adult endolithic habit. Exhalant canal system apparent at the surface (particularly obvious in live sponges, when living tissue contracts upon preservation) as meandering, vein-like structures converging on oscula. Skeleton formed by relatively uncommon megascleres in ascending radial tracts and dense layers of microscleres in the ectosomal region and as base layer. Megascleres mainly tylostyles, tracts starting at the sponge base and ending in bouquet-like fashion (spicule points outward) in the ectosomal region or protruding beyond sponge surface; some megascleres oriented at random in choanosome. Microscleres composed of large and stout streptasters (spirasters, diplasters), very common throughout sponge but forming extra-dense cortexlike layers in ectosome and at base (substrate attachment) (diagnosis as quoted in RÜTZLER, 2002, p. 220; see also FINKS & RIGBY, 2004a, p. 43). [RÜTZLER (2002, p. 220) proposed the group as “encrusting sponges with prominent layers of relatively large spirasters, amphistasters or diplasters at the surface and the base or throughout the entire body,” following primarily the conception of the traditional Spirastrellidae



**c** Pachytheca

FIG. 137. Suberitidae (p. 223–225).

of RIDLEY and DENDY (1886, p. 490). Excluded are massive sponges such as *Sphaciospongia* MARSHALL, 1892, and part of the former genus, *Spirastrella sensu lato* with rare and minute spirasters or amphistasters; these latter are now placed in the family Clionidae D'ORBIGNY, 1851

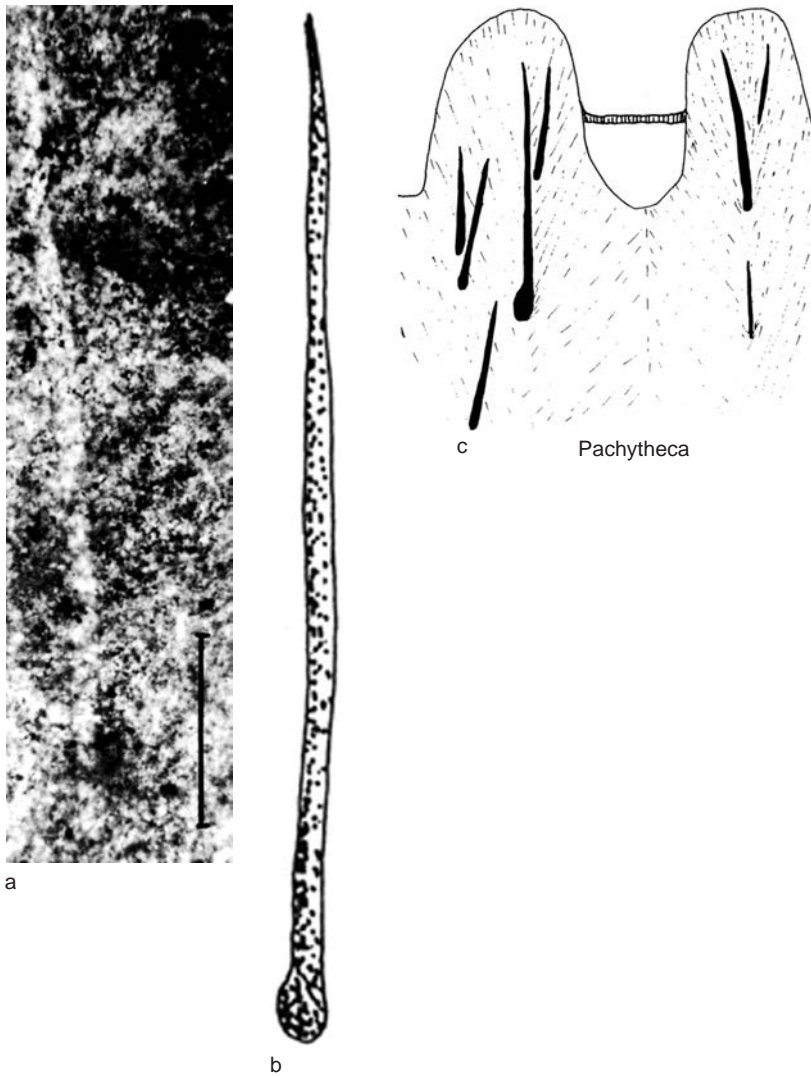


FIG. 138. Suberitidae (p. 223–225).

in 1851–1854; RÜTZLER, 1990; ROSELL & URIZ, 1997.] *Lower Cretaceous (Albian)*.

**Calcispirastrella** REITNER, 1992, p. 149 [*\*C. sphinctozoides*; OD; holotype, IPFUB/JR 1991]. Growth form thalamid-like (egg shaped); multiple pores or ducts in transverse section associated with chambers and/or canal system; large central pores 600–800  $\mu\text{m}$  in diameter with thorny rim; small wall pores approximately 250  $\mu\text{m}$  in diameter associated with smaller pores 100  $\mu\text{m}$  in diameter, inferred as incurrent openings; basal skeleton irregular, granular to prismatic Mg calcite; dermal

layer 80–100  $\mu\text{m}$  thick, with many small (20–25  $\mu\text{m}$ ) spiraster microscleres interspersed with bundles of 6 to 8 tylostyle megascleres (150–200  $\mu\text{m}$  long). *Lower Cretaceous (Albian)*: northern Spain. —FIG. 139a–c. *\*C. sphinctozoides*; a, transverse section showing chambers (arrows), tubes, and canal system,  $\times 6$ ; b, section of dermal layer with crust of small spiraster microscleres and small, plumose arranged, tylostyle megascleres (arrows),  $\times 70$ ; c, longitudinal section of basal skeleton showing microstructure of small, irregular crystals of high Mg calcite (dark areas), light areas are prismatic layers,  $\times 140$  (Reitner, 1992, pl. 24a).

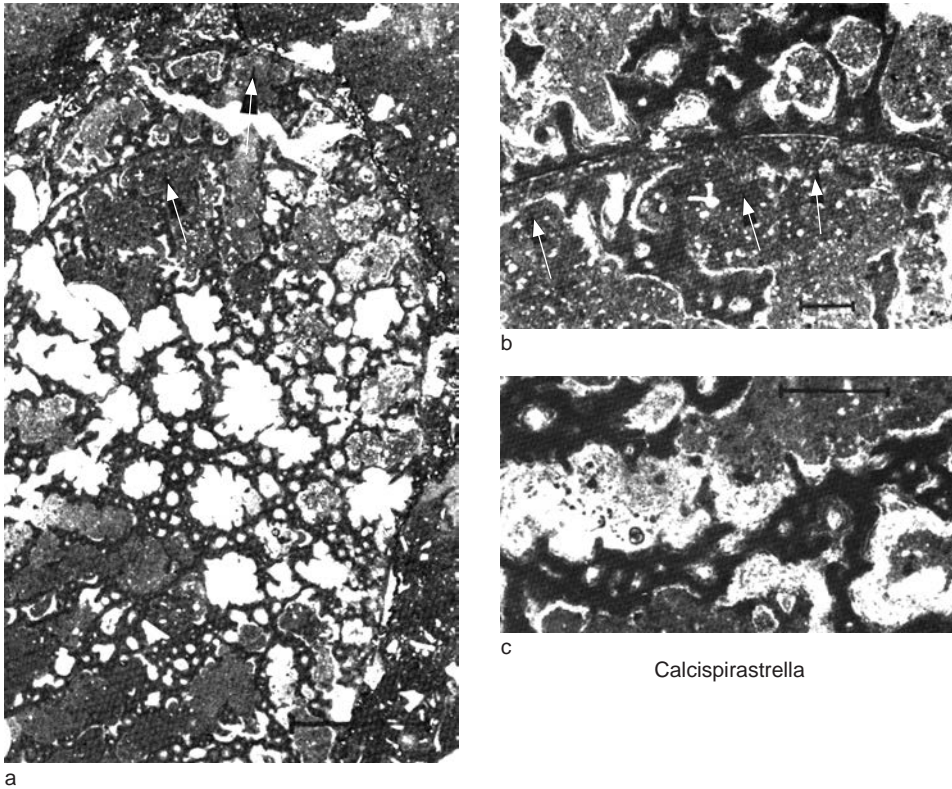


FIG. 139. Spirastrellidae (p. 226).

## Order CHONDROSIDA Boury-Esnault & Lopès, 1985

[Chondrosida BOURY-ESNAULT & LOPÈS, 1985, p. 172]

Encrusting to massive demosponges with a marked cortex enriched with fibrillar collagen, with inhalant apertures localized in pore sieves or cribriporal clones and a skeleton often absent, composed, when present, of nodular spongin fibers or aster microscleres only (never megascleres). Collagen always very abundant. Oviparous. [Diagnosis applies to both order and family; the type genus is *Chondrilla* SCHMIDT, 1862, by original designation; description adapted from BOURY-ESNAULT in HOOPER & VAN SOEST, 2002a, p. 220, p. 291.] *Upper Jurassic–Lower Cretaceous (Albian)*.

## Family CHONDRILLIDAE Gray, 1872

[Chondrillidae GRAY, 1872, p. 461 [=Gummineae SCHMIDT, 1862, p. 37, *nom. oblit.*; =Gumminidae SCHMIDT, 1862, p. 37, *nom. oblit.*; =Chondrosidae SCHULZE, 1877, p. 87; =Chondrissinae LENDENFELD, 1885, p. 14; =Chondrosiidae WIEDENMAYER, 1977, p. 187]

Description as for order. *Upper Jurassic–Lower Cretaceous (Albian)*.

*Calcichondrilla* REITNER, 1991a, p. 191 [*\*C. crustans*; OD; holotype, IPFUB, JR2/89; paratype, IPFUB, JR3/89]. Growth form laminar, crustose; numerous, large euaster (75–100  $\mu\text{m}$  diameter) microscleres (megascleres absent) and inferred excurrent canals in oblique section; irregular lamellar Mg calcite structure of basal skeleton reflects original collagen fibers of an atypical chaetetid (REITNER, 1991a, p. 191). [See also FINKS and RIGBY (2004d, p. 586).] *Lower Cretaceous (Albian)*: northern Spain, United States (Arizona).—FIG. 140a–d. *\*C. crustans*, northern Spain; a, abundant possible euaster microscleres (white spots) in oblique section of holotype,  $\times 14$ ; b, diagrammatic sketch of longitudinal section of calcified collagenous basal skeleton

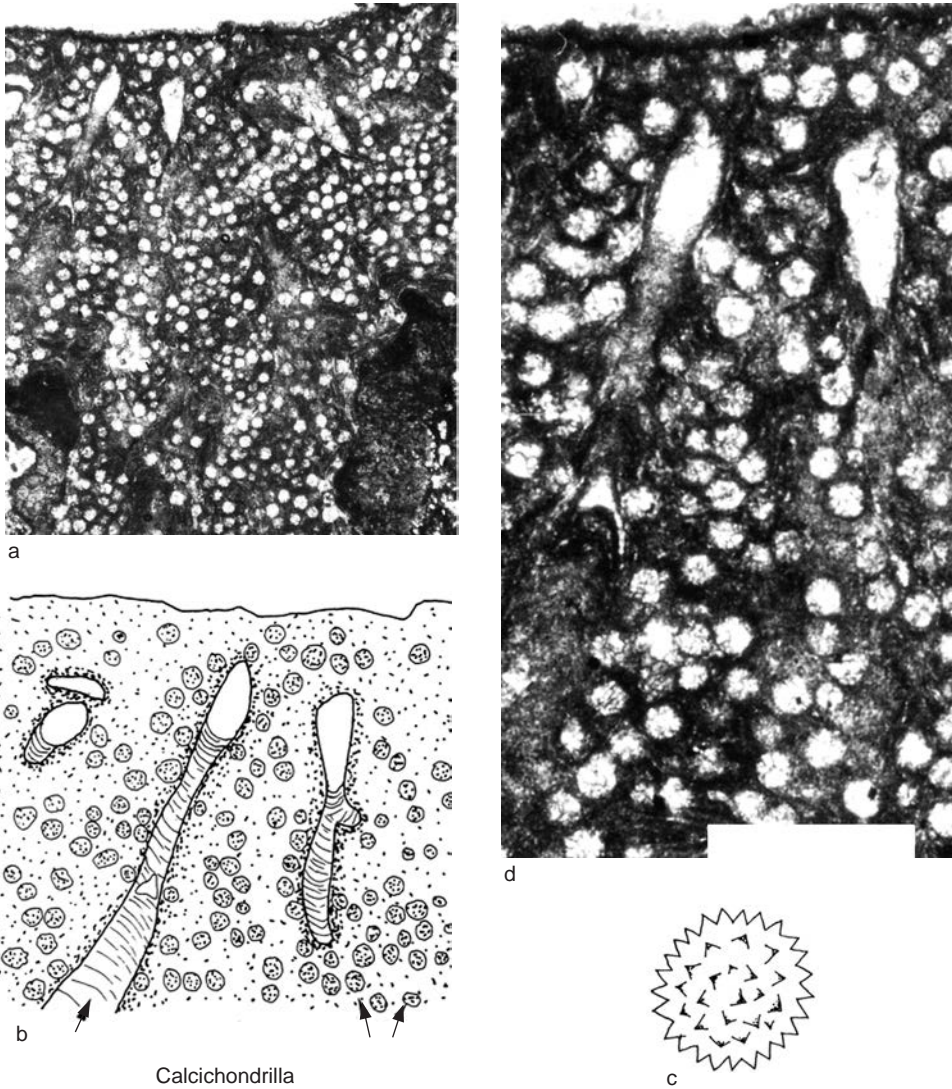


FIG. 140. Chondrillidae (p. 227–228).

(stippled area), tubes of canal system (*arrow* in lower left), and possible eusater microscleres (*arrows* in lower right),  $\times 32.5$  (Reitner, 1991a, p. 192); *c*, sketch of inferred morphology of a euaster microsclere,  $\times 220$  (Reitner, 1992, p. 159); *d*, enlargement of upper left area of view *a* showing tubes of canal system and abundant microscleres,  $\times 61.2$  (Reitner, 1991a, p. 192).—FIG. 141. \**C. crustans*, lamellar microstructure of calcified collagenous

basal skeleton of holotype in oblique section,  $\times 125$  (Reitner, 1991a, p. 192).  
**Calcastella** REITNER, 1991a, p. 188 [*\*C. tabulata* REITNER, 1991a, p. 189; OD; holotype, IPFUB, JR I /89)]. Growth form domical with large tubules; tubule walls thick with numerous sparite-filled pores and canals of inferred excurrent system; tabulae thin, subhorizontal to slightly arched, micritic calcite, as are the tubule

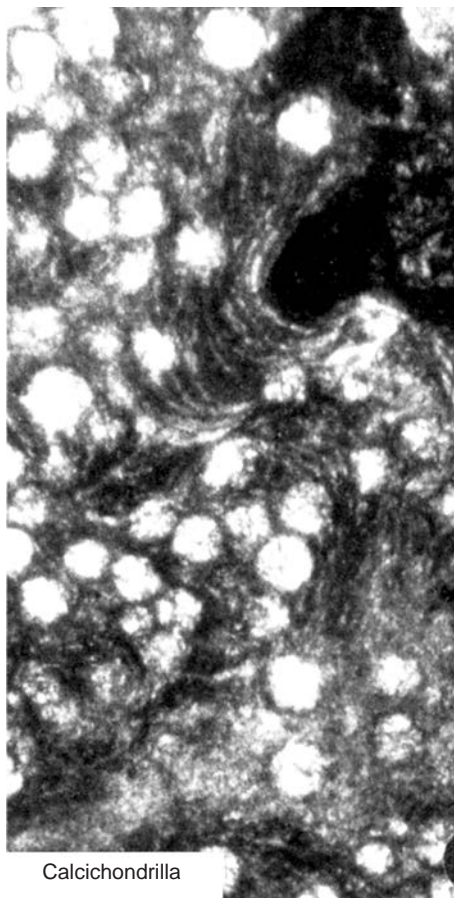
walls; micritic Mg calcite basal skeleton with large (50–65  $\mu\text{m}$  diameter) possible euaster microscleres with relict spines (megascleres unknown); original atypical chaetetid skeleton inferred to be collagen fibers (REITNER, 1991a, p. 189). *Upper Jurassic (Tithonian), Lower Cretaceous (?Aptian, Albian):* Germany (Bavaria), *Tithonian*; Greece (Arachova), *?Aptian, Albian*.—FIG. 142a–c. \**C. tabulata*, *?Aptian, Albian, Greece*; a, thick tubule walls with canal system of basal skeleton in oblique section,  $\times 11$ ; b, longitudinal section of tubule walls and tabulae, gray lamellar areas are granular calcite inferred to have been associated with upward growth of soft tissue,  $\times 18$ ; c, enlargement of part of view a showing microscleres (white dots) and internal canals (gray areas),  $\times 25$  (Reitner, 1991a, p. 190).—FIG. 143a–c. \**C. tabulata*, *?Aptian, Albian, Greece*; a, calcite-filled molds of possible euaster microscleres,  $\times 380$  (Reitner, 1991a, p. 190); b, sketch of inferred possible euaster microsclere,  $\times 400$ ; c, diagrammatic sketch of longitudinal section of calcified collagenous basal skeleton (arrow in upper right, stippled area), tubes of canal system (arrow in lower center), and possible euaster microscleres (arrows in upper section),  $\times 10$  (Reitner, 1992, p. 157).

## Order POECILOSCLERIDA Topsent, 1928

JEAN VACELET and RONALD R. WEST

[*nom. correct.* DE LAUBENFELS, 1955, p. 21, 38, *pro* Poecilosclerina TOPSENT, 1928, p. 41, 43] [=Poeciloscleridae TOPSENT, 1894, p. 10]

Demospongiae with skeleton composed of discrete siliceous spicules; main skeleton composed of megascleres (monactinal, diactinal, or both) and spongin; fibers in various stages of development; both fiber and mineral skeletons always show regional differentiation of megascleres into distinct ectosomal and choanosomal components; microscleres include meniscoid forms, such as chelae (unique to the order), sigmas and sigmancistra derivatives, and other diverse forms such as toxas, raphides, microxeas, and discate microrhabds; order is predominantly viviparous with incompletely ciliated parenchymella larvae; one oviparous family (Raspailiidae), and another suspected oviparous family (Rhabderemiidae), is also included (diagnosis as stated by HOOPER & VAN SOEST, 2002d, p. 403; see also FINKS & RIGBY, 2004a, p. 49). *Lower Jurassic–Holocene*.



Calcichondrilla

FIG. 141. Chondrillidae (p. 227–228).

## Family MERLIIDAE Kirkpatrick, 1908

[Merliidae KIRKPATRICK, 1908, p. 510]

Thin crusts consisting of a chaetetid-like calcareous basal skeleton (i.e., formed of a layered system of calcareous chambers), the outer layer of which is filled with sponge tissue and siliceous spicules. Basal skeleton made up of high magnesium calcite with a water-jet type microstructure. Spiculation consists of thin tylostyles arranged in wispy plumose bundles, unique keyhole-type microscleres called clavidiscs, rugose raphides, and small commata-like spicules appearing monactinal. Calcareous skeleton or clavidiscs may be absent (description modified from HAJDU & VAN SOEST, 2002). [The monogeneric



a



b

Calcistella



c

FIG. 142. Chondrillidae (p. 228–229).

family Merliidae is presently classified in the order Poecilosclerida (class Demospongiae), owing to its spicule characters and especially given the resemblance between the clavidiscs and the diancistras of Hamacanthidae GRAY, 1872 (HAJDU, 2002, p. 665). However, this relationship needs to be confirmed by molecular systematics. The microstructure and arrangement of the calcareous skeleton both suggest close affinities between Merliidae and Paleozoic and Jurassic chaetetids (GAUTRET, VACELET, & CUIF, 1991).] *Lower Jurassic–Holocene.*

**Merlia** KIRKPATRICK, 1908, p. 510 [\**M. normani*; OD; KIRKPATRICK, 1908, p. 510, holotype NHM 1911.4.7.10] [= *Noronha* KIRKPATRICK, 1909, p. 47 (type, *N. scalariformis*, OD)]. Thin, crustlike, calcareous basal skeleton present or absent; where present, composed of vertically arranged tubes partitioned by tabulae to form layered series of chambers; those of outer layer filled with choanosomal tissue and spicules, while those beneath occupied by undifferentiated cell masses (crypt tissue). Spicules include thin tylostyles, clavidiscs, raphides and commata, though clavidiscs not always present. Microstructure of water-jet type. Type species is encrusting, 1–1.5 mm thick, subcircular to irregular crusts, which may cover surfaces larger than 100 cm<sup>2</sup>. Living tissue somewhat transparent, with a superficial system of small canals converging toward poorly visible oscules, covering a calcareous basal skeleton. Surface smooth, microscopically slightly hispid, finely granular when dry. Color yellow-orange to red in life, clearer in preservative. Living tissue including a thin dermal membrane, a choanosome partly contained in the tubes of the calcareous skeleton, and accumulations of reserve cells in the basal crypts of the skeleton (pseudogemmulae). Choanosome has ascending bundles of tylostyles, slightly diverging at surface. Choanocyte chambers spherical, approximately 25 µm in diameter, pseudogemmulae appearing as moniliform cylinders after decalcification, made of large cells similar to gemmular archaeocytes, 15–20 µm in diameter and filled in with reserve inclusions, and, additionally, collagen fibrils of the mesohyl often forming dense fascicles and belonging to the smooth type. Calcareous basal skeleton made of a system of regularly honeycombed tubes 120–150 µm in diameter, with walls 40–60 µm thick and a pillar with tuberculate elevations at each angle. Siliceous spicules not entrapped in the calcareous skeleton. Calcareous skeleton made of high magnesium calcite, with a clinogonal (or water-jet, fasciculate) microstructure. Microstructural elements arranged vertically in axis of center of pillars, fanning out laterally along an increasing angle to build walls and tabulae. Spicules comprise slender tylostyles, straight with a poorly marked oval head, 120–160 by 0.7–2 µm, clavidiscs

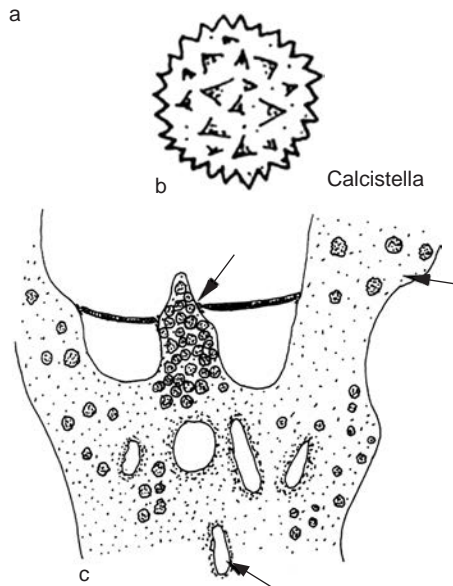
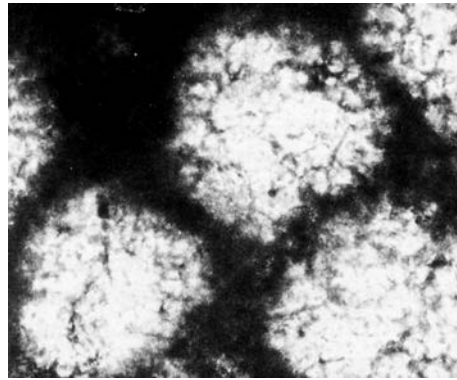


FIG. 143. Chondrillidae (p. 228–229).

that are more abundant near surface, varying from ring shaped, 40–50 by 30 µm and 3 µm thick, to 62 by 38 µm, with a well-developed margin and two key-hole notches, as well as rugose raphides in trichodragmata, 40–90 µm, and commata 15 µm. Clavidiscs and commata are sometimes absent (KIRKPATRICK, 1911; HAJDU & VAN SOEST, 2002). Other Recent species comprise: *M. lipoclavidisca* VACELET & URIZ, 1991, which lacks clavidiscs, possibly because it occupied a silicon-poor environment (based on specimens from Lebanon; unpublished data [J. VACELET, July 2003]; therefore it probably is a synonym of *M. normani*); *M. deficiens* VACELET, 1980b, has a wide circumtropical distribution like *M. normani* but also extends to Pacific localities; and *M. tenuis* HOSHINO, 1990, occurs in Japan. Both the latter lack a basal skeleton, so they do not share all the same derived generic characters (synapomorphies) as the type species. Recent material shows that

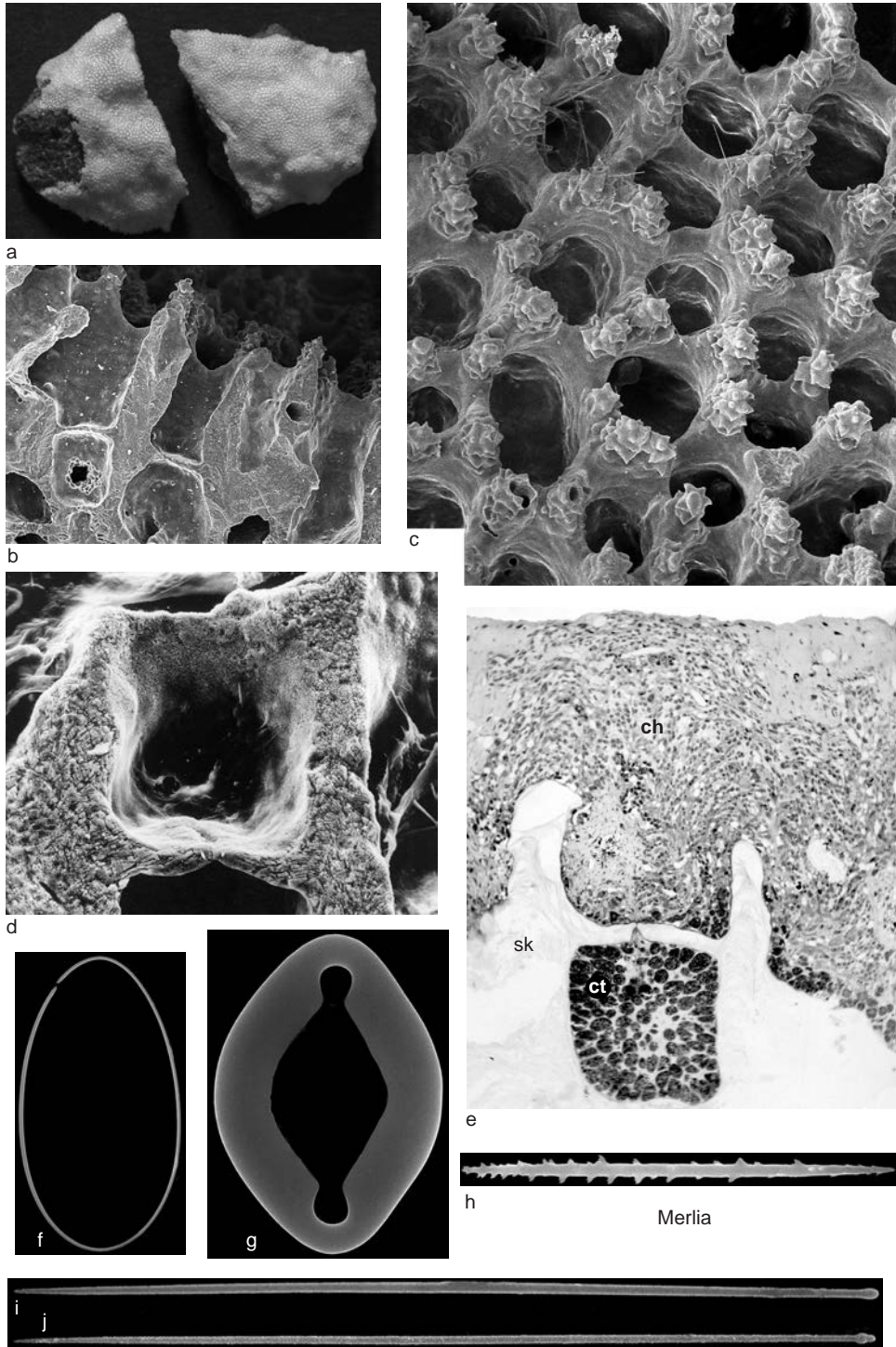


FIG. 144. Merliidae (p. 231–234).



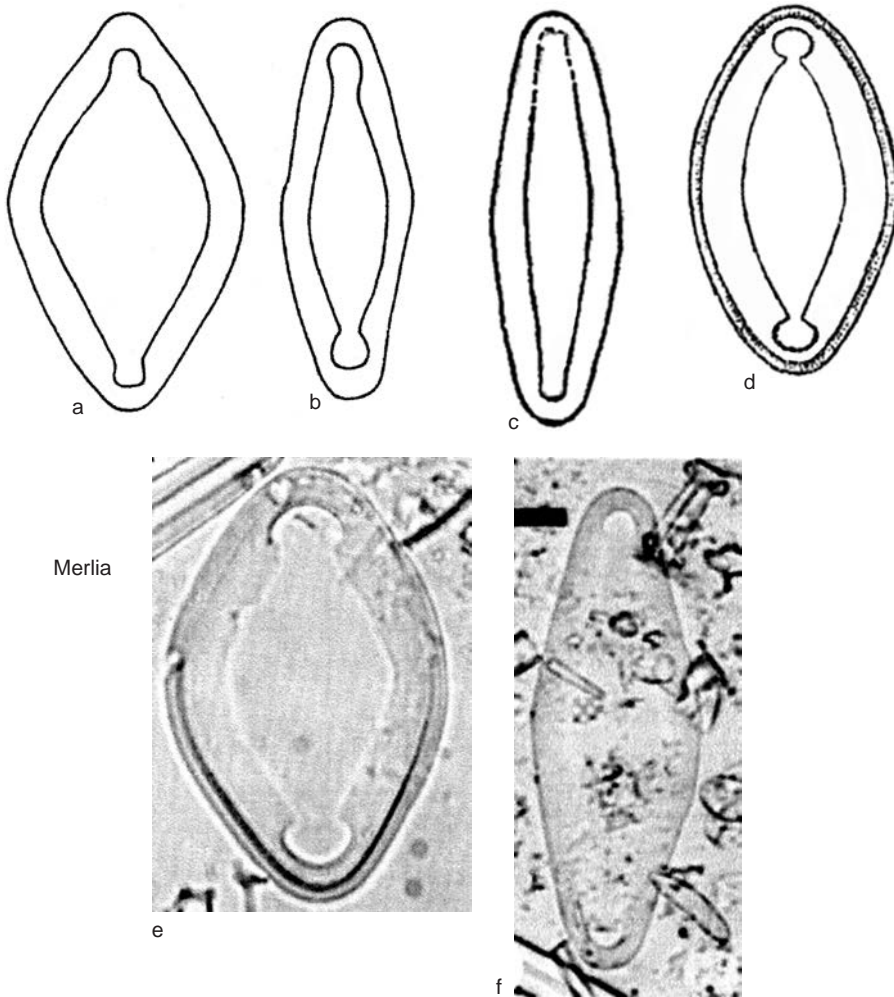


FIG. 145. Merliidae (p. 231–234).

in superficial analysis, the calcified *Merlia* are very frequently confused with bryozoans, suggesting that fossil specimens are more numerous than recorded. The absence of observation of reproduction stages suggests that these sponges are oviparous. Merliid sponges commonly lived in semidark caves, 5–15 m depth, in cryptic habitats of coral reefs, and on deeper rocky substrata down to 165 m; always in dim light conditions and warm temperate to circum-tropical tropical waters. [The fossil record includes calcareous skeletons resembling *M. normani* from the Miocene of Spain (BARRIER & others, 1991), and distinctive and diagnostic spicules (clavids) have been recorded from the following localities: Lower Jurassic of Austria (MOSTLER, 1990); Upper Cretaceous of northern Germany (WIEDENMAYER, 1994,

termed psellium); Oligocene of New Zealand (*M. morlandi* HINDE & HOLMES, 1892); and Eocene and Miocene from Deep Sea Drilling Program (DSDP) cores in the western Central Atlantic (BUKRY, 1978). Spicule occurrences at these localities are not associated with reefs, suggesting the species lacked a calcareous skeleton, as in *M. deficiens* and *M. tenuis* (WIEDENMAYER, 1994).] Lower Jurassic–Holocene: Austria, Lower Jurassic; northern Germany, Upper Cretaceous; New Zealand, Oligocene; western Central Atlantic (clavids only), Eocene–Miocene; Spain (skeletons of type species), Miocene; Madeira, Mediterranean, Caribbean, Red Sea and Indian Ocean and subfossil (ca. 1.5 k.y.) cave in Crete (type species), Holocene.—FIG. 144a–j. \**M. normani*; a, dry specimen, Banc Ampère, western Atlantic, 56–75 m,  $\times 2.6$  (West & others, 2013); b, SEM

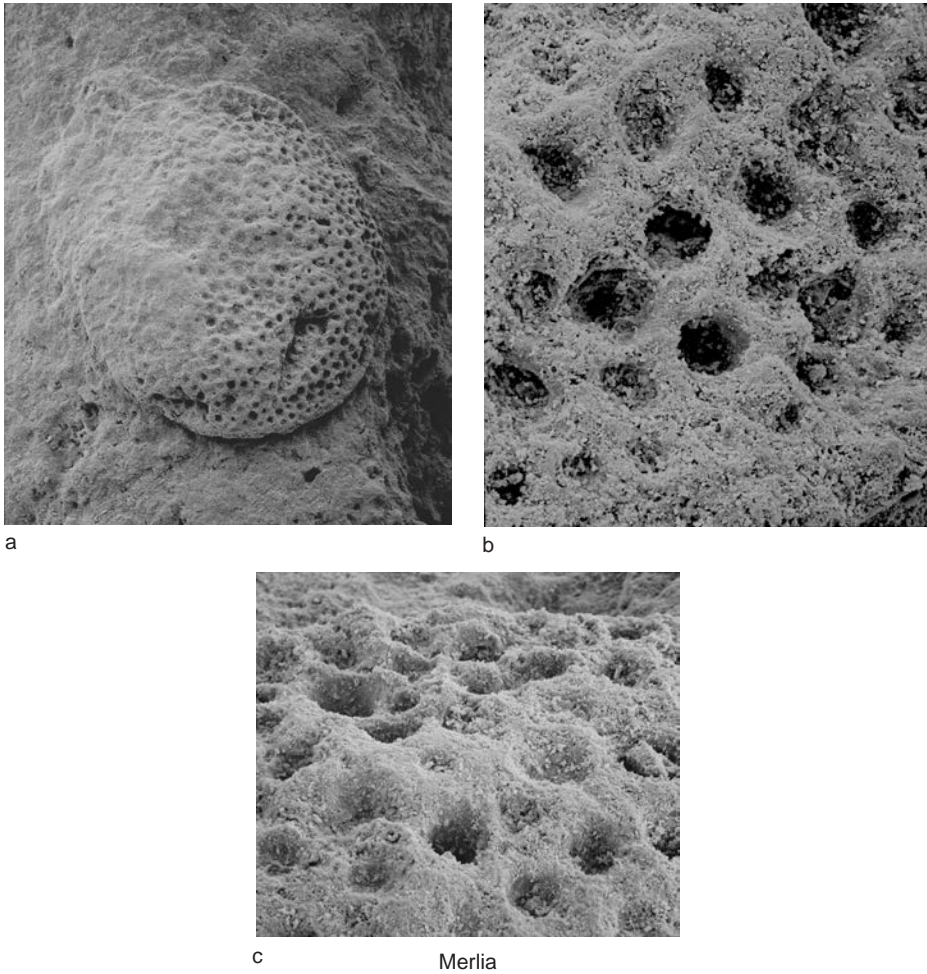


FIG. 146. Merliidae (p. 231–234).

view of a vertical section of skeleton illustrating tubes and tabulae that form a roof over basal crypts, Banc Ampère, western Atlantic, 80 m,  $\times 560$  (West & others, 2013); *c*, SEM view of surface of skeleton, Banc Ampère, western Atlantic, 80 m,  $\times 90$  (West & others, 2013); *d*, SEM view of vertical section of skeleton, after mild treatment with dilute formic acid, showing microstructure of tube walls and horizontal tabulae,  $\times 250$  (Gautret, Vacelet, & Cuif, 1991); *e*, section through a decalcified specimen showing living tissue (*cb*, choanosome; *ct*, crypt tissue or pseudogemmula) and traces of organic material in decalcified skeleton (*sk*),  $\times 180$  (Vacelet, 1990); *f–j*, SEM views of spicules, Porto Santo, 110 m depth, specimen housed in NHM; *f*, immature stage of clavidisc,  $\times 670$ ; *g*, clavidisc,  $\times 1500$ ; *h*, rugose raphide,  $\times 1400$ ; *i–j*, tylostyles,  $\times 800$  (West & others, 2013).—FIG. 145*a–f*. *Merlia*

sp.; *a–b*, clavidisc, lower Jurassic, northern Calcareous Alps, northern Italy, magnification unknown (Mostler, 1990, pl. 17); *c*, clavidisc, upper Cretaceous, northern Germany,  $\times 253$  (Wiedenmayer, 1994, p. 68, adapted from Schrammen, 1924, pl. 4); *d*, clavidisc, Oamaru Diatomite, Eocene–Oligocene, New Zealand,  $\times 373$  (Hinde & Holmes, 1892, pl. 9); *e*, clavidisc, Middle Eocene, DSDP Core 391A, Blake Nose, western Central Atlantic,  $\times 460$  (Bukry, 1978, pl. 14); *f*, clavidisc, lower Miocene, Deep Sea Drilling Project Core 390A, Blake–Bahamas Basin, western Central Atlantic,  $\times 800$  (Bukry, 1978, pl. 14).—FIG. 146*a–c*. *Merlia* sp., Miocene, Spain; *a*, SEM photograph of upper surface of basal skeleton,  $\times 25$ ; *b*, SEM oblique photograph of upper surface of basal skeleton,  $\times 200$ ; *c*, SEM photograph of enlargement of part of upper surface in view *a*,  $\times 220$  (West & others, 2013).

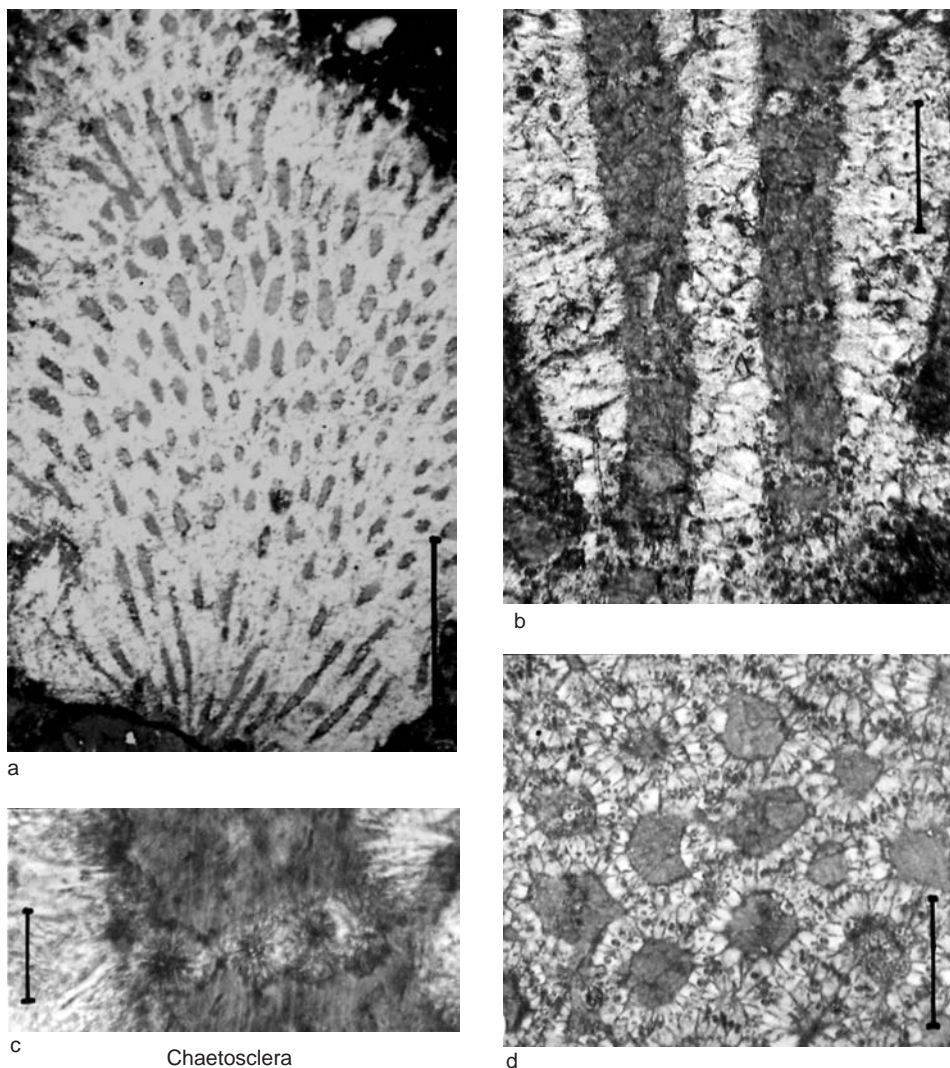


FIG. 147. Uncertain (p. 236).

## Order HALICHONDRIDA Gray, 1867

RONALD R. WEST and RACHEL A. WOOD

[*nom. correct.* VAN SOEST & HOOPER, 2002a, p. 721, *pro* Halichondriida WIEDENMAYER, 1977, p. 148, *nom. correct. pro* Halichondrides LEVI, 1953, p. 853, *nom. correct. pro* Halichondrina VOSMAER, 1887, p. 335, *nom. correct. pro* Halichondriadae GRAY, 1867, p. 518] [=Axinellides LEVI, 1953, p. 853; =Clavaxinellides LEVI, 1956, p. 167, *partim*; =Clavaxinellida LEVI, 1957, p. 181, *partim*; =Axinellida LEVI, 1957, p. 181, *partim*; =Claraxinellida LEVI, 1957, p. 183, *lapsus calami*]

Demospongiae with styles, oxeas, strongyles, or intermediate spicules, of

widely diverging sizes, and not functionally localized; skeleton plumoreticulate, dendritic, or confused; microscleres, if present, microxeas and/or trichodragmas (diagnosis and name history as stated in VAN SOEST & HOOPER, 2002a, p. 721). See also FINKS and RIGBY (2004a, p. 46). If the three genera in the following family Uncertain belong to this order, then the stratigraphic range of the order should be *Triassic–Holocene*.

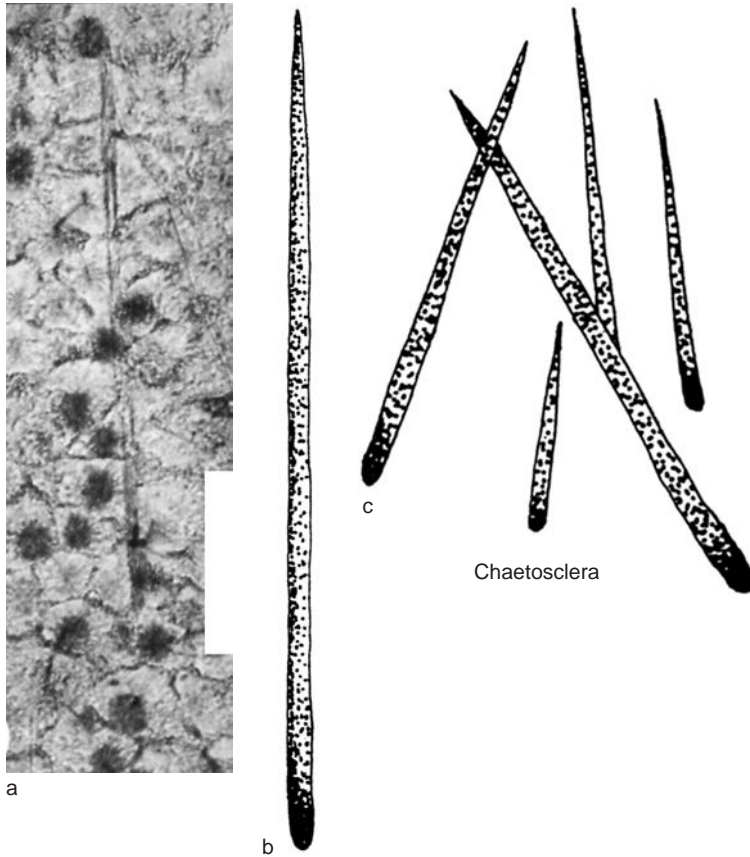


FIG. 148. Uncertain (p. 236).

### Family UNCERTAIN

**Chaetosclera** REITNER & ENGESER, 1989a, p. 160 [*\*C. klipsteini*; OD; holotype, IPFUB, JR 89/12; paratype, NHM, D54224]. Growth form domical to pyriform, small; tubules polygonal in transverse section, long, with tabulae; tubule walls and tabulae composed of spherulitic aragonite; originally opal tylostyle megascleres (175–300  $\mu\text{m}$  long, 2–4  $\mu\text{m}$  in diameter) preserved as Fe calcite pseudomorphs, arranged in bundles of 3 to 4, pointing outward in tubule walls, some along internal side of tubules; microscleres unknown. *Upper Triassic (Carnian)*: northern Italy (Dolomite Alps).—FIG. 147a–d. *\*C. klipsteini*; a, tangential section of basal skeleton of holotype, IPFUB JR 89/12,  $\times 4.8$ ; b, longitudinal section of holotype, IPFUB JR 89/12, showing tubule walls (light vertical areas) and poorly preserved tabulae (light horizontal areas near base of figure),  $\times 170$ ; c, detail of tabulae showing spherulitic microstructure in holotype, IPFUB

JR 89/12,  $\times 600$ ; d, transverse section of paratype showing spherulitic microstructure of tubule walls (light areas with diagenetically altered dark centers),  $\times 170$  (Reitner & Engeser, 1989a, pl. 1).—FIG. 148a–c. *\*C. klipsteini*; a, spherulitic tubule wall of holotype, and some spherules appear to extend into a tylostyle megasclere, suggesting that they are secondary structures, IPFUB JR 89/12,  $\times 392$  (Reitner & Engeser, 1989a, pl. 1); b, sketch of tylostyle megasclere,  $\times 433$ ; c, sketch of cluster of tylostyle megascleres,  $\times 360$  (Reitner, 1992, p. 199).

**Neuropora** BRONN, 1825, p. 43 [*\*Chrysaora spinosa* LAMOUROUX, 1821, p. 83; OD; =*Neuropora spinosa* LAMOUROUX in BRONN, 1825, p. 43; =*Chrysaora spinosa* LAMOUROUX in MICHELIN, 1846 in 1840–1847, p. 237; =*Acanthopora lamourouxi* HAIME, 1854, p. 216; =*Neuropora spinosa* HAIME, 1854, p. 214; =*Neuropora spinosa* LAMOUROUX in BASSLER, 1953, p. 68; =*Neuropora spinosa* WALTER, 1969, p. 44]. Growth form laminar to columnar (branching), often with

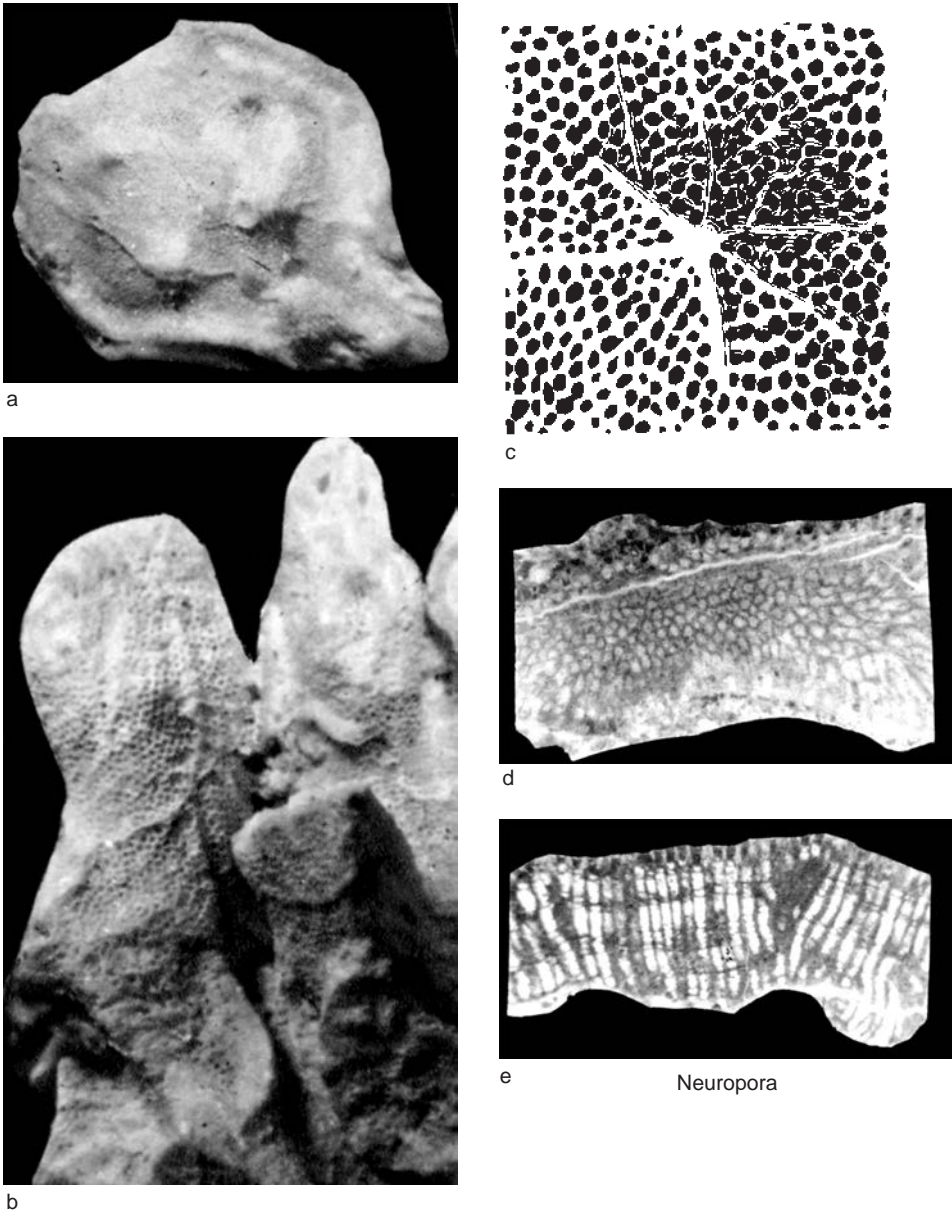


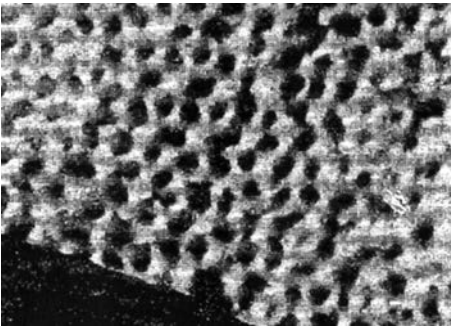
FIG. 149. Uncertain (p. 236–238).

surface mamelons, astrorhizae, and small buds; tubules irregular polygons in transverse section; in longitudinal section, tubules long, narrow, diverging from a point and becoming parallel in upper part of basal skeleton; may be filled with epitaxial cement and resemble *Ceratoporella*. [The mineralogy, microstructure, and spicules and/or spicule pseudomorphs are unknown from the

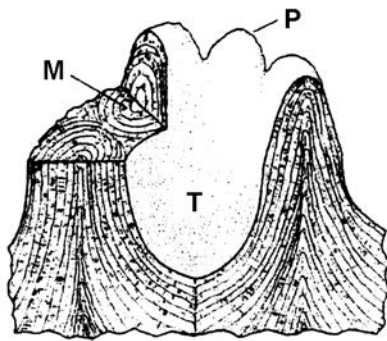
neotype, *N. spinosa*, but these features and the original mineralogy are inferred from studies of *N. pustulosa* (ROEMER, 1839); tubule walls Mg calcite (inferred) penicillate, water-jet (fascicular fibrous) microstructure; microstructure of tabulae semispherulitic to clinogonal; tylostyle megascleres 100–200  $\mu\text{m}$  long and 5–7  $\mu\text{m}$  in diameter, in bundles of 3 to 4, with distal ends



a



b



c

Neuropora

FIG. 150. Uncertain (p. 236–238).

pointing toward sponge surface, some attached proximally to tubule walls and projecting into tubules; microscleres unknown (description modified from WALTER, 1969 (specimens are in the collections of the Department of Earth Sciences, Faculté des Sciences de Lyon [F.S.L.]); KAZMIERCZAK & HILLMER, 1974 (specimens are in the collections of the Geological-Palaeontological Institute of the University of Hamburg [SGPIH] and the Roemer-Pelizaeus Museum, Hildesheim [SRPMH]); REITNER, 1992.) *Middle Jurassic (Bathonian)–Lower Cretaceous (Hauterivian)*: France, Bathonian; Germany, Hauterivian.—

FIG. 149a–e. \**N. spinosa* (LAMOUROUX); a, exterior surface of basal skeleton of neotype, no. 490 F.S.L., upper Bathonian, Langrune-sur-Mer, Calvados, France,  $\times 4.7$ ; b, exterior of branching columnar basal skeleton, no. 28 972 F.S.L., upper Bathonian, Blainville, Calvados, France,  $\times 7.5$  (Walter, 1969, pl. 18–19); c, surface feature (possible astrorhiza), Bathonian, France,  $\times 18$  (Bassler, 1953, p. 67); d, transverse to tangential section of basal skeleton, no. 38 094 F.S.L., upper Bathonian, Blainville, Calvados, France,  $\times 9.9$ ; e, longitudinal section of basal skeleton, no. 38 174 F.S.L., upper Bathonian, Ranville, Calvados, France,  $\times 10$  (Walter, 1969, pl. 18–19).—FIG. 150a–c. *N. pustulosa* (ROEMER, 1839), Hauterivian, northwestern Germany; a, fused columnar branching basal skeleton, note stellate pattern (*I* and arrows),  $\times 2.3$  (Reitner, 1992, pl. 34); b, surface view of tubules, SGPIH 1726, Achim,  $\times 35$ ; c, diagrammatic sketch of tubule surface; *T*, tubule; *P*, pustules; *M*, mamelon-like columns with inferred microstructure,  $\times 500$  (Kazmierczak & Hillmer, 1974, p. 447, pl. II).—FIG. 151a–d. *N. pustulosa* (ROEMER, 1839), Hauterivian, northwestern Germany; a, calcite pseudomorph of tylostyle megasclere,  $\times 590$ ; b–c, diagrammatic sketch of tylostyle megascleres,  $\times 450$ ; d, pseudomorphs of two tylostyle megascleres,  $\times 360$  (Reitner, 1992, p. 206, pl. 34).

*Stromatoaxinella* WOOD & REITNER, 1988, p. 215 [*Chaetetes irregularis* MICHELIN, 1847 in 1840–1847, p. 306; *M*; holotype, NHM no. 5481]. Calcareous skeleton with tracts of long, thin, loosely plumose styles preserved mainly in secondary filling tissue within tubules; only rarely incorporated into outer parts of tubule walls; walls formed by fusion of adjacent columns, primary fascicular fibrous microstructure. *Upper Cretaceous (Santonian)*: France, Spain.—FIG. 152a–b. \**S. irregularis* (MICHELIN), light photomicrograph, NHM no. 5481, Collades de Bastus, Spain; a, longitudinal thin section,  $\times 20$ ; b, longitudinal thin section,  $\times 100$  (Wood & Reitner, 1988, p. 216).—FIG. 153. \**S. irregularis* (MICHELIN), light photomicrograph, NHM no. 5481, Collades de Bastus, Spain; foramina and aligned tabulae in longitudinal-oblique thin section,  $\times 50$  (Wood & Reitner, 1988, p. 216).

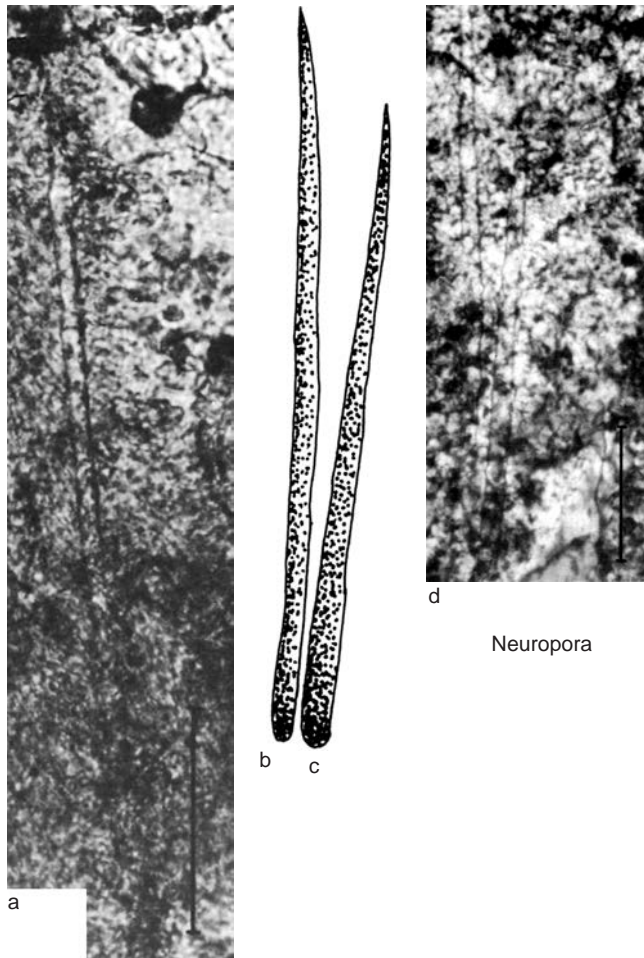


FIG. 151. Uncertain (p. 236–238).

## Order AGELASIDA Hartman, 1980

JEAN VACELET, PHILIPPE WILLENZ, RONALD R. WEST, AND  
†WILLARD D. HARTMAN

[Agelasida HARTMAN, 1980b, p. 29]

Demospongiae with verticillately spined monactine megascleres, coring or echinating a system of anastomosing spongin fibers, or echinating the limestone walls of a basal skeleton in which they are progressively entrapped; if present,

basal skeleton of spherulitic or penicillate aragonite. [FINKS and RIGBY (2004d, p. 594) proposed VERRILL (1907, p. 333) as author of the order, whereas HOOPER and VAN SOEST (2002a, p. 819) retained HARTMAN (1980b) as the author, based on the same type genus. VERRILL (1907) proposed only the family name Agelasidae, whereas the order Agelasida was formally proposed independently by HARTMAN (1980b). A former editor of the *Treatise* (see KAESLER in FINKS, REID, & RIGBY, 2004, p. xix), following the *Code*



FIG. 152. Uncertain (p. 238).

of *Zoological Nomenclature* (ICZN, 1999), has drawn a classificatory and nomenclatorial distinction between suprafamilial and family group taxa; consequently, the family name *Agelasidae* VERRILL, 1907, is not considered to be transferable to a suprafamilial taxon while retaining the same author. Order *Agelasida* HARTMAN, 1980, is therefore the preferred usage. FINKS and RIGBY (2004d) include in this order several families of Paleozoic sponges of uncertain affinities whose skeleton is made of spherulitic aragonite.] *upper Permian–Holocene.*

#### Family ASTROSCLERIDAE Lister, 1900

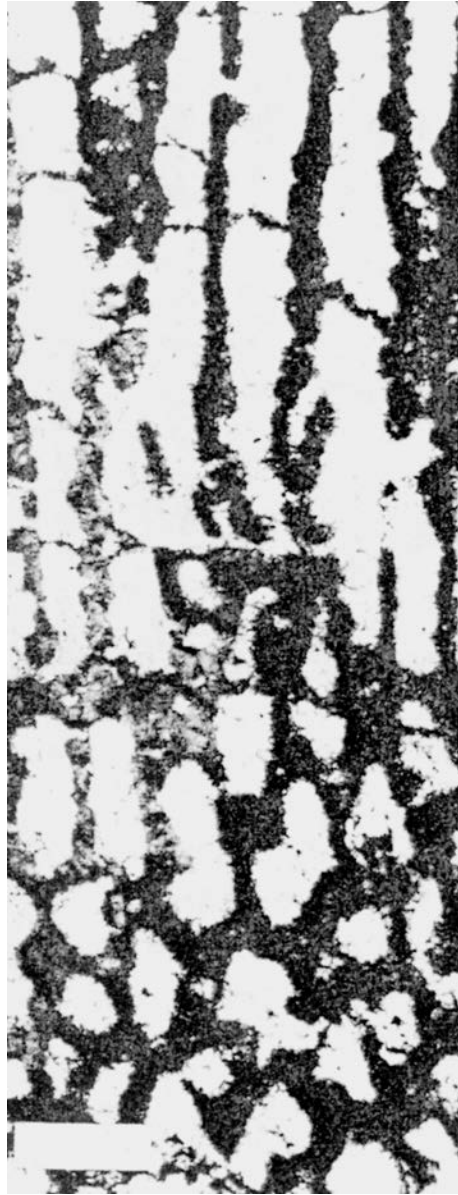
[*Astroscleridae* LISTER, 1900, p. 479] [=*Ceratoporellidae* HARTMAN & GOREAU, 1972, p. 136]

Agelasida with verticillately spined styles, occasionally smooth styles, and a basal calcareous skeleton made of spherulitic or clinogonal sclerodermites in aragonite (VACELET, 2002a). [Monophyly of the family presently is not well established for the Recent representatives; *Astrosclera* with spherulitic microstructure and with incubated parenchymella larvae, other genera with penicillate



microstructure and unknown reproduction, suggesting a possible future splitting into two families: Astroscleridae LISTER, 1900, and Ceratoporellidae HARTMAN & GOREAU, 1972. Two genera are placed questionably in this family: *Cassianochaetetes* and *Spherolichaetetes*; for discussion, see those genus entries.] upper Permian–Holocene.

**Astrosclera** LISTER, 1900, p. 459 [*A. willeyana*; OD; holotype NHM 1990.1019.1]. Massive growth form. Meandroid or reticulate calcareous skeleton in aragonite, composed of spherulitic sclerodermites of intracellular origin and further epitaxial growth. Living tissue inside irregular lacunae of superficial calcareous skeleton. Superficial canals etching an astrorhizal system on surface of calcareous skeleton. Siliceous styles of variable shape, often echinating in the calcareous skeleton, sometimes absent (diagnosis as stated by VACELET, 2002a, p. 825). Type species massive, globular, bulbous, cushion shaped, or cylindrical. Young specimens encrusting, growing upward into a cylindrical structure, with a dead stalk and a living head progressively becoming rounded and larger than the stalk (bulbous shape). In largest specimens, shape subspherical with a stalk hidden by head margins growing down toward substratum. Growth rings visible, but without any trace of regeneration or budding. Bathyal specimens mostly cylindrical. Size usually 0.5–2.5 cm, up to 25 cm in diameter. Texture stony. Color orange. Surface smooth, irregularly mammillate in some large specimens. Oscules small, 2–5/cm<sup>2</sup>, in the center of an astrorhizal system etched into skeleton. Living tissue located at surface and inside irregularly reticulated lacunae of superficial (1–8 mm thick) calcareous skeleton. No special ectosomal differentiation. Choanocyte chambers small, approximately 15 μm in diameter. Exhalant canals bearing a valvule near the aphodus. Tissue containing a high density of morphologically diverse intercellular bacteria. No well-defined spherulous cells. Basal calcareous skeleton in aragonite, alveolar in surface and with an organization more or less similar to that of fossil stromatoporoids, solid in the backfilled central parts. Tabulae absent. Basal parts externally covered by a basal layer. Sometimes associated with zoanths, which are included in basal skeleton. Microstructure spherulitic, built up of sclerodermites 10–60 μm in diameter, with crystal fibers, 1–3 μm in diameter, arranged in a radiate structure. Sclerodermites intracellularly secreted as granules that pass through spheraster-like stage and are incorporated into superficial parts of solid skeleton when their size is 20–25 μm (LISTER, 1900; GAUTRET, 1986; WÖRHEIDE & others, 1997). Siliceous acanthostyles dispersed in the living tissue. In some specimens, acanthostyles entrapped by their bases within the calcareous skeleton, obliquely echinating the basal skeleton. Acanthostyles usually



*Stromatoxinella*

FIG. 153. Uncertain (p. 238).

with a swelling in basal third, but highly variable in shape, size, and abundance, according to geographic distribution. In Indian Ocean, acanthostyles 42–87 μm by 2.5–11 μm, with verticillated spines generally well developed; spines absent in the Red Sea. In West Pacific, acanthostyles 47–164 μm by 1.7–10.5 μm, sometimes vestigial or absent, with an irregular spination. Siliceous spicules absent

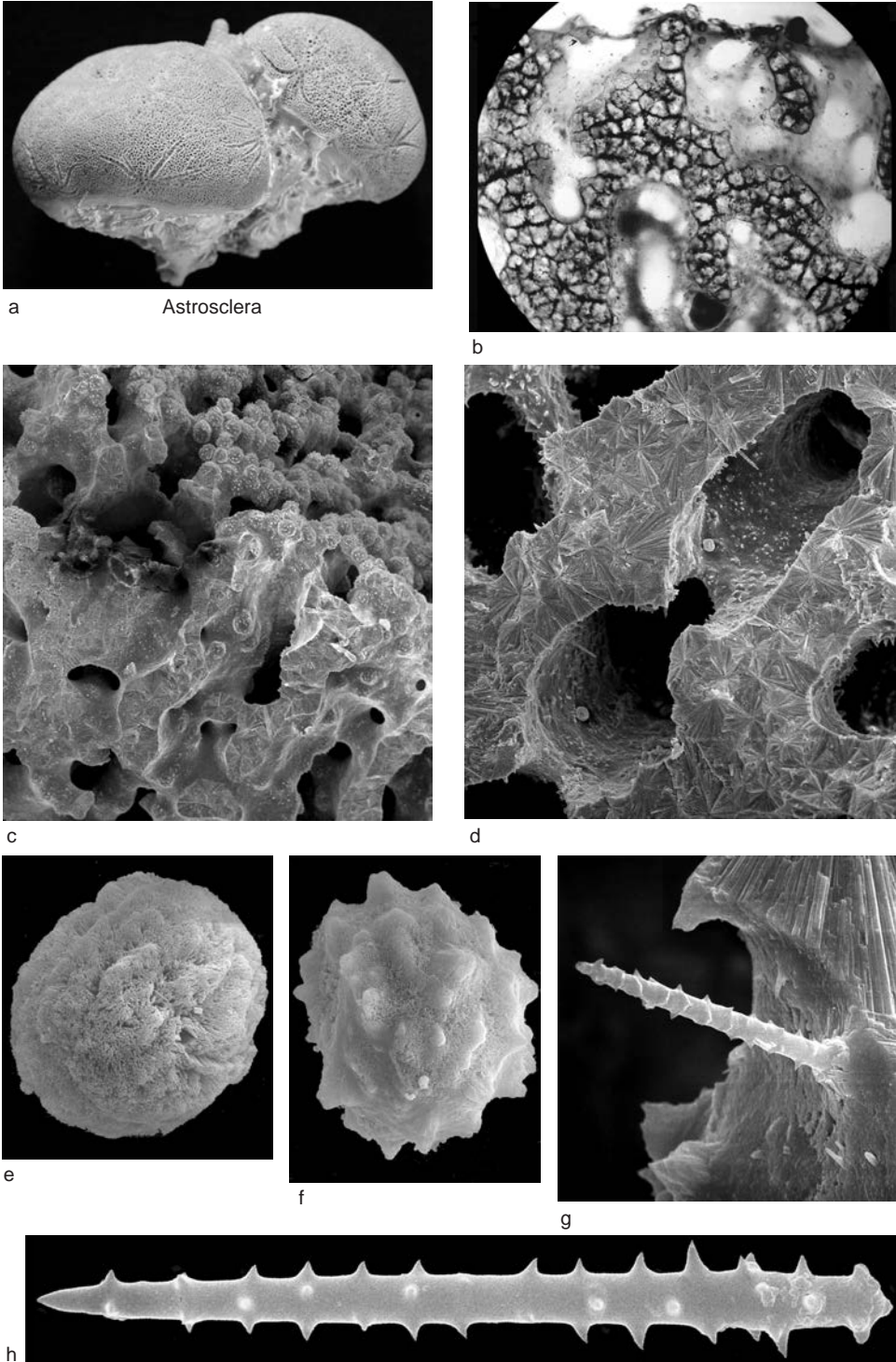


FIG. 154. Astroscleridae (p. 241–243).

in Central Pacific. Reproduction viviparous, by incubated parenchymella. Growth rate of the skeleton approximately 0.2 mm/yr (WÖRHEIDE, 1998). Common on undersurfaces of coral rubble, reef cavities, caves, deep cliffs, 1–185 m depth. (modified from VACELET, 2002a, p. 827). Other Recent species: a single species has been formerly described. However, recent results using molecular data suggest the presence of several distinct species (WÖRHEIDE, personal communication, 2005). Fossil records: *Astrosclera cuiji* WÖRHEIDE, 1998, described as a Triassic representative from Turkey (WÖRHEIDE, 1998), with spherulitic basal skeleton and acanthostyles. Other fossils from upper Permian and Upper Triassic, with spherulitic microstructure but without spicules and showing various grades of skeletal construction, are more uncertain relatives. A similar mode of skeletal secretion has been demonstrated in some of these fossils (GAUTRET, 1986). [No fossil record of the genus exists between the Triassic and the Recent, so the genus is regarded as a Lazarus-taxon (WÖRHEIDE, 1998; REITNER & WÖRHEIDE, 2002, p. 64).] *Upper Triassic–Holocene*: Turkey, *Upper Triassic*; Red Sea, Madagascar, Seychelles, Comoro Islands, Christmas Island, Mascarene islands, Philippines, Indonesia, Great Barrier Reef, New Caledonia, Guam, Enewetak, French Polynesia, Japan, *Holocene*.—FIG. 154a–h. \**A. willeyana*; a, dry specimen with astrorhizae, Philippines, water depth 24 m, MNHN DJV152,  $\times 1.7$  (West & others, 2013; see also Fig. 1.2); b, section through skeleton and living tissue with free spherules near surface (top) and two oocytes in choanosome, MNHN DJV152,  $\times 43$  (West & others, 2013); c, SEM view of surface (top right) and a fracture through skeleton with protruding spicules, Mayotte Island, water depth 25 m,  $\times 43$  (West & others, 2013); d, SEM view of fracture through skeleton, without siliceous spicule, Marquesas Islands, 90–130 m depth,  $\times 120$  (West & others, 2013); e–f, SEM views of free stages of growth of skeletal spherulites, Marquesas Islands, 90–130 m,  $\times 1100$  (West & others, 2013); g, SEM view of spicule protruding from skeleton, Mayotte Island, 25 m depth,  $\times 1300$  (West & others, 2013); h, SEM view of acanthostyle spicule, Mayotte Island, 25 m depth,  $\times 2100$  (West & others, 2013).

?*Cassianochaetetes* ENGESER & TAYLOR, 1989, p. 43 [\**Catenipora orbignyana* KLIPSTEIN, 1845 in 1843–1845, p. 288; OD; holotype, NHM S10465 (specimen and 2 thin sections); as the only recognizable syntype, this is designated as the holotype] [= *Leiofungia* DE FROMENTEL, 1860b, p. 49 (type, *Achilleum milleporatum* MÜNSTER, 1841, p. 26, OD); = *Leiospongia* DE LAUBENFELS, 1955, p. 100 (type, *Achilleum milleporatum* MÜNSTER, 1841, p. 26, OD DE LAUBENFELS, 1955, p. 26)]. Growth form small, fungiform with convex upper surface; basal layer well developed with growth lines; tubules irregular polygons in transverse view; tubules long, slightly curved; tabulae, if present, with flat upper surface and tufted lower surface or as tubule narrowing or irregular tubule occlusions; tubule walls elongate

aragonite spherules (recrystallized); megascleres and microscleres unknown (description modified from ENGESER & TAYLOR, 1989, p. 43–46). [For more on the taxonomic history of this genus and assigned species, see ENGESER and TAYLOR (1989, p. 43–49). This genus is placed questionably in the family Astroscleridae because, although it has the typical spherulitic microstructure, spicules are unknown and the skeletal construction appears to be somewhat different.] *Upper Triassic (Carnian)*: Italy.—FIG. 155a–e. \**C. orbignyana* (KLIPSTEIN), holotype, Cassian Formation, northern Italy; a, specimen magnification unknown (Klipstein, 1845 in 1843–1845, pl. 19, 20a); b, lateral view showing mushroom shape and basal layer,  $\times 4.7$ ; c, upper surface showing shape of tubules,  $\times 4.4$ ; d, longitudinal section showing radiating tubules,  $\times 5.2$ ; e, enlarged view of longitudinal section showing recrystallized tubule walls,  $\times 17.5$  (Engeser & Taylor, 1989, p. 45).

*Ceratoporella* HICKSON, 1912, p. 351, *nom. nov. pro Ceratopora* HICKSON, 1911, p. 200, *non* GRABAU, 1899, p. 414, coelenterate [\**Ceratopora nicholsoni* HICKSON, 1911, p. 200; OD]. Massive growth form, mound shaped when mature, with regularly spaced mamelons; young individuals cone shaped or pedunculate. Color orange in life. Mound-shaped specimens up to 100 cm in diameter and 50 cm in thickness on deep fore reef, extraordinarily tough and heavy. Basal and lateral surfaces of the skeletal mass covered by a basal layer showing growth lines. Superficial parts of basal calcareous skeleton marked by closely spaced tubules, 0.2–0.5 mm across and 1–1.2 mm deep, irregularly polygonal, ranging from 150  $\mu$ m to 300–400  $\mu$ m in diameter. Lumen of tubules filled in with aragonite in inner part of basal skeleton. Basal skeleton made of sclerodermites with a clinogonal microstructure, consisting of closely packed crystalline units that diverge at a low angle. Siliceous spicules are styles, 206–298  $\mu$ m by 3.1–4  $\mu$ m, bearing regular whorls of spines, free in living tissue or obliquely entrapped in tubule wall and their bases surrounded by collagen microfibrils. Entrapped siliceous spicules progressively dissolved within basal calcareous skeleton. Living tissue forming a thin veneer at surface of calcareous skeleton and extending downward into each tubule; total thickness of living tissue 1.5 mm. Each tubulae unit corresponds to a single inhalant and exhalant canal. Canals bearing special valves. Choanocyte chambers small, 20.7  $\mu$ m in mean diameter. Exhalant collecting system leaving stellate depressions (astrorhizae) on surface of skeleton. Intercellular symbiotic bacteria abundant and highly diverse in shape. Growth rate of skeleton in Jamaican caves varying from 0.21–0.23 mm/yr measured experimentally *in situ* (WILLENZ & HARTMAN, 1999), up to 0.23–0.43 mm/yr based on U-Th age measurements (HAASE-SCHRAMM & others, 2003) or 0.20–0.60 mm/yr based on calculation from Sr/Ca data (HAASE-SCHRAMM & others, 2005). Depth range: 8–184 m. [Regular tubulae structure of the skeleton is reminiscent of the

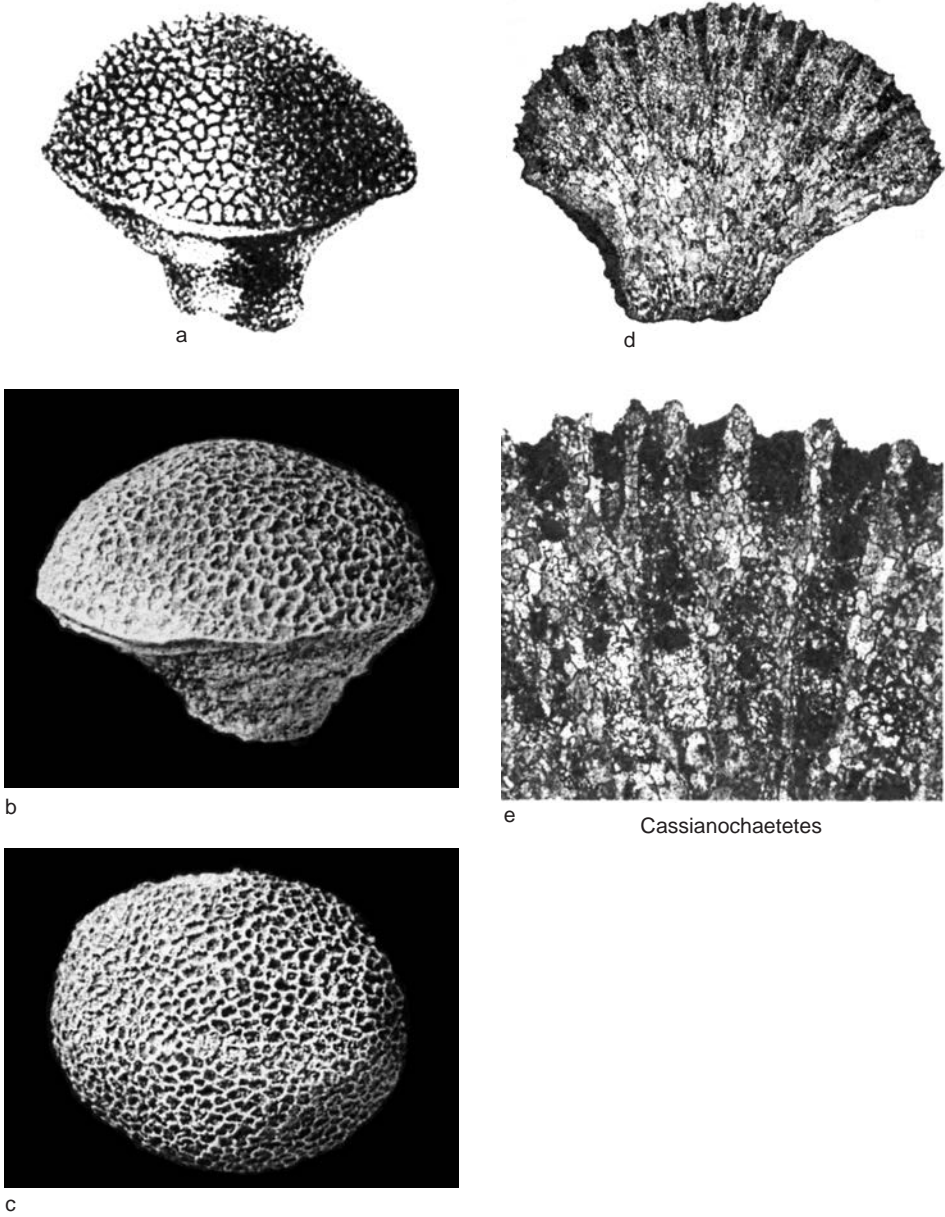


FIG. 155. Astrocleridae (p. 243).

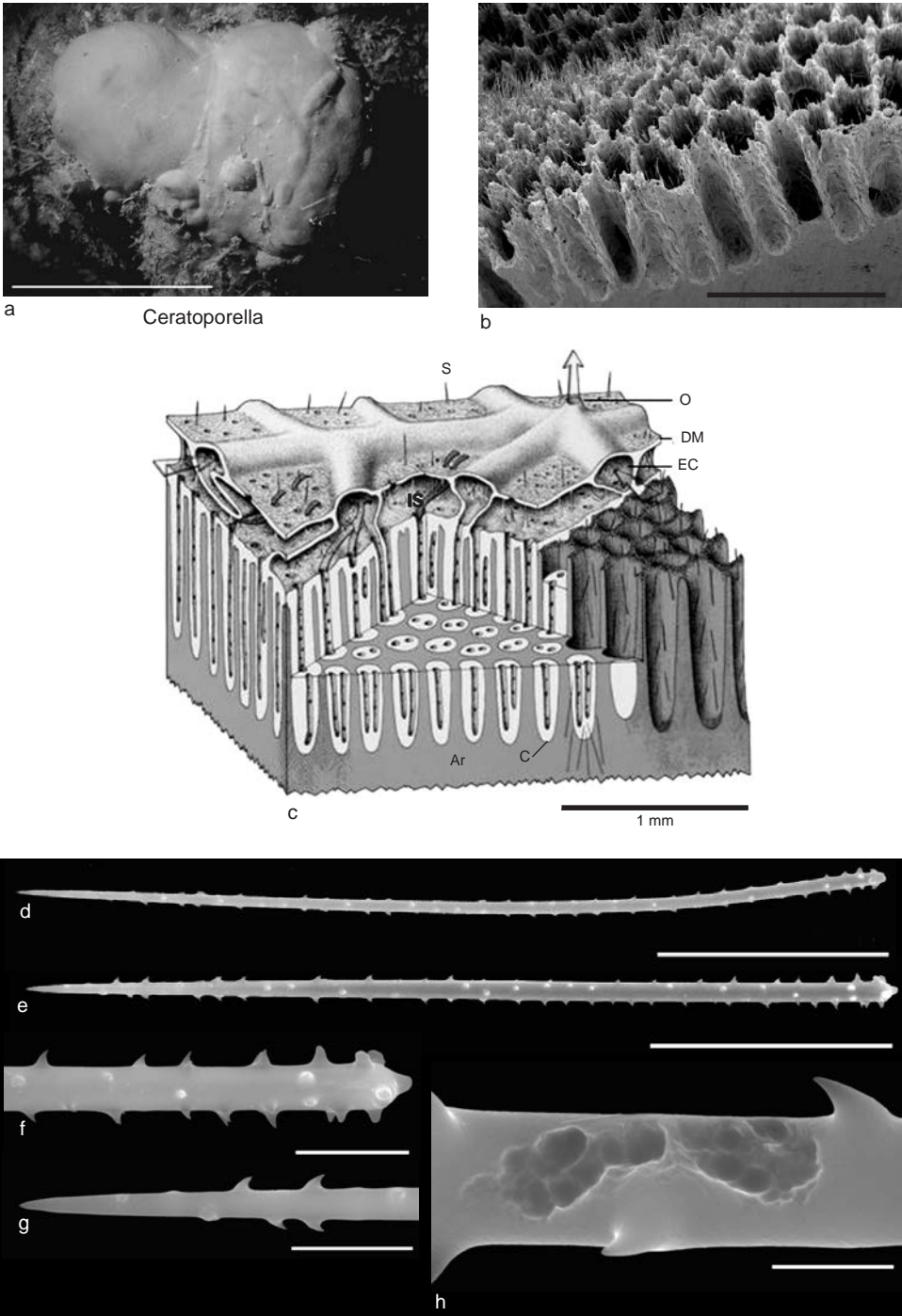


FIG. 156. Astroscleridae (p. 243–246).

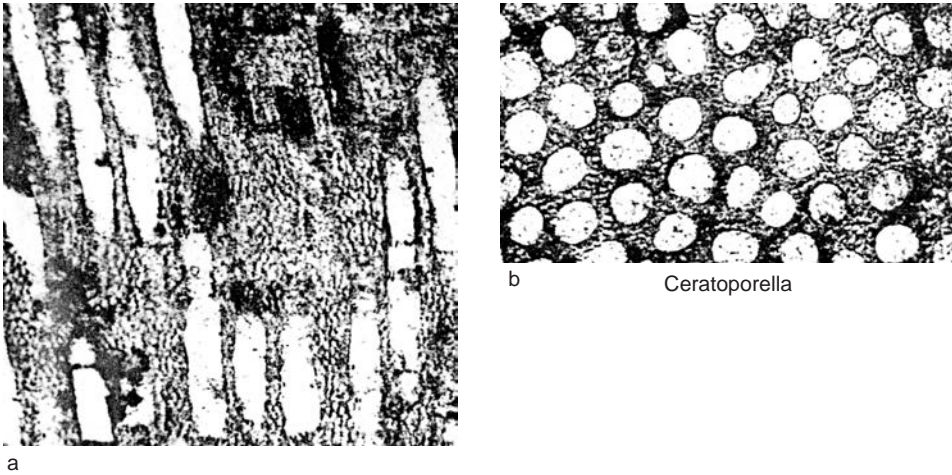


FIG. 157. Astroscleridae (p. 243–246).

calcified demosponges *Merlia* KIRKPATRICK, 1908, family Merliidae, and *Acanthochaetetes* FISCHER, 1970, family Spirastrellidae. The genus, however, is easily distinguished from these by the microstructure and composition of the skeleton and by the spicule complement (VACELET, 2002a). Fossil forms of this genus have been reported from Tunisia, as ?*Ceratoporella* sp., by H. TERMIER, G. TERMIER, and VACHARD (1977), and REITNER (1992) has described *Ceratoporella breviacanthostyla* from Italy.] ?upper Permian, Triassic (Carnian)–Holocene: Tunisia, ?upper Permian; northern Italy, Carnian; Bahamas, Belize, Cuba, Jamaica, Holocene.—FIG. 156a–b. \**C. nicholsoni* (HICKSON), RBINSc-POR.095; *a*, underwater photograph of specimen with diameter about 12 cm, at depth of 25 m in reef cave on northern coast of Jamaica (not collected; see also Fig. 2.1), scale bar, 10 cm; *b*, surface of calcareous skeleton showing tubules with protruding siliceous spicules, scale bar, 1 mm; *c*, three-dimensional representation; *Ar*, aragonite skeleton; *C*, choanosome; *DM*, dermal membrane; *EC*, exhalant canal; *IS*, inhalant space or vestibule; *O*, osculum; *S*, spicule (Willenz & Hartman, 1989; see also Fig. 3.2 and Fig. 355); *d–e*, spined styles, scale bars, 50  $\mu$ m; *f–g*, details of extremities of spicules, scale bars, 10  $\mu$ m; *b*, detail of eroded spicule, scale bar, 2  $\mu$ m (West & others, 2013).—FIG. 157a–b. ?*C. sp.*, ?upper Permian, Tunisia; *a*, holotype, longitudinal section, No. HGT.T81, in the collection of H. & G. Termier (Paris),  $\times 17.5$ ; *b*, transverse section,  $\times 17.5$  (H. Termier, G. Termier, & Vachard, 1977, pl. 6).—FIG. 158a–f. *C. breviacanthostyla* REITNER, 1992, Carnian, northern Italy; *a*, longitudinal section of holotype, IPFUB/JR 1989,  $\times 6.2$ ; *b*, fractured vertical section of paratype showing microstructure (1) and open tubule (2); open arrow indicates sponge surface, IPFUB/JR 1989,  $\times 100$ ; *c*, enlargement of part of view *a* showing short iron calcite pseudomorphs of acanthostyles (1, area of black arrows);

*open arrow* indicates direction to sponge surface,  $\times 32.5$ ; *d*, agelasid acanthostyle,  $\times 750$ ; *e–f*, sketches of two agelasid acanthostyles,  $\times 550$  (Reitner, 1992, p. 220, pl. 37).

*Goreauella* HARTMAN, 1969, p. 16 [\**G. auriculata* HARTMAN, 1969, p. 17; OD; holotype YPM no. 6858]. Auriculate or saucerlike form, with edges upturned or curled downward, attached by a broad peduncle. Color light yellow in life. Size up to 16 cm in diameter and 3 mm in thickness. Basal skeleton thin, made up of aragonitic sclerodermites, with numerous arborescent, spinose processes, 0.5–1.1 mm in height, and multibranching patterns of higher processes draining to edge of skeleton. Microstructure consisting of sclerodermites with crystals radiating in all directions from centers of calcification (clinogonal type with divergent irregular linear elements). Siliceous spicules are strongyles bearing whorls of spines, 35–124  $\mu$ m by 1.3–1.9  $\mu$ m (mean 60–68  $\mu$ m by 2.3–2.7  $\mu$ m), becoming embedded in basal skeleton first by one end provided with rounded knobs. Living tissue forming a thin veneer, filling space between superficial processes of basal skeleton. Oscules 300  $\mu$ m in diameter, opening out along edge of sponge. Eurypylous choanocyte chambers 18–20  $\mu$ m in diameter. Intercellular symbiotic bacteria scarce. Occasionally associated with zoanths that induce formation of processes in calcareous skeleton. In specimens from Jamaica, masses of storage cells packed with various inclusions and resembling gemmular thesocytes occur at base of living tissue, between processes of aragonite skeleton. Alternatively, spermatocysts containing primary spermatocytes can occur in same region of mesohyl. Depth range: 8–70 m in caves and deep fore reef. Holocene: Bahamas, Belize, Jamaica.—FIG. 159a–i. \**G. auriculata*, RBINSc-POR.097; *a*, seen *in situ* at depth of 25 m in reef cave on northern coast of Jamaica, scale bar, 1 cm (see also

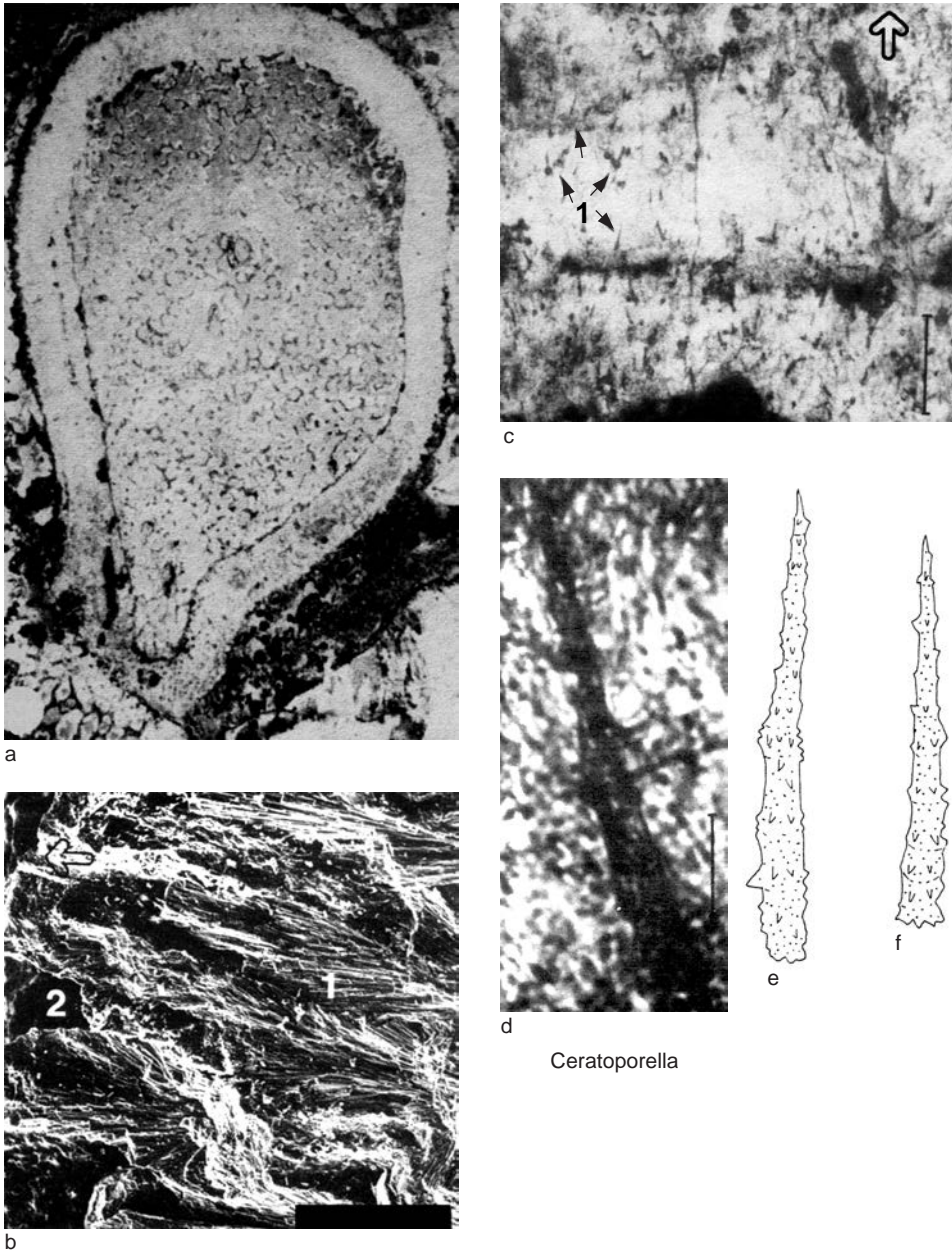


FIG. 158. Astroscleridae (p. 243–246).

Fig. 1.5); *b*, ground section perpendicular to sponge surface, through aragonite skeleton and living tissue (*ar*, aragonitic skeleton; *c*, choanosome; *dm*, dermal membrane; *s*, spicules), scale, 100  $\mu$ m; *c*, SEM view of skeleton with arborescent processes, scale bar, 1 mm; *d*, SEM view of arborescent aragonitic processes with protruding spicules (*s*), scale bar, 100

$\mu$ m; *e–i*, strongyles of three different shapes (*e–g*, scale bar, 20  $\mu$ m), and details of partially dissolved siliceous spicules (*b–i*, scale bars, 5  $\mu$ m, 2  $\mu$ m), as seen within basal calcareous skeleton (West & others, 2013).

*Hispidopetra* HARTMAN, 1969, p. 12 [\**H. miniana*; OD; holotype YPM no. 6853]. Encrusting to

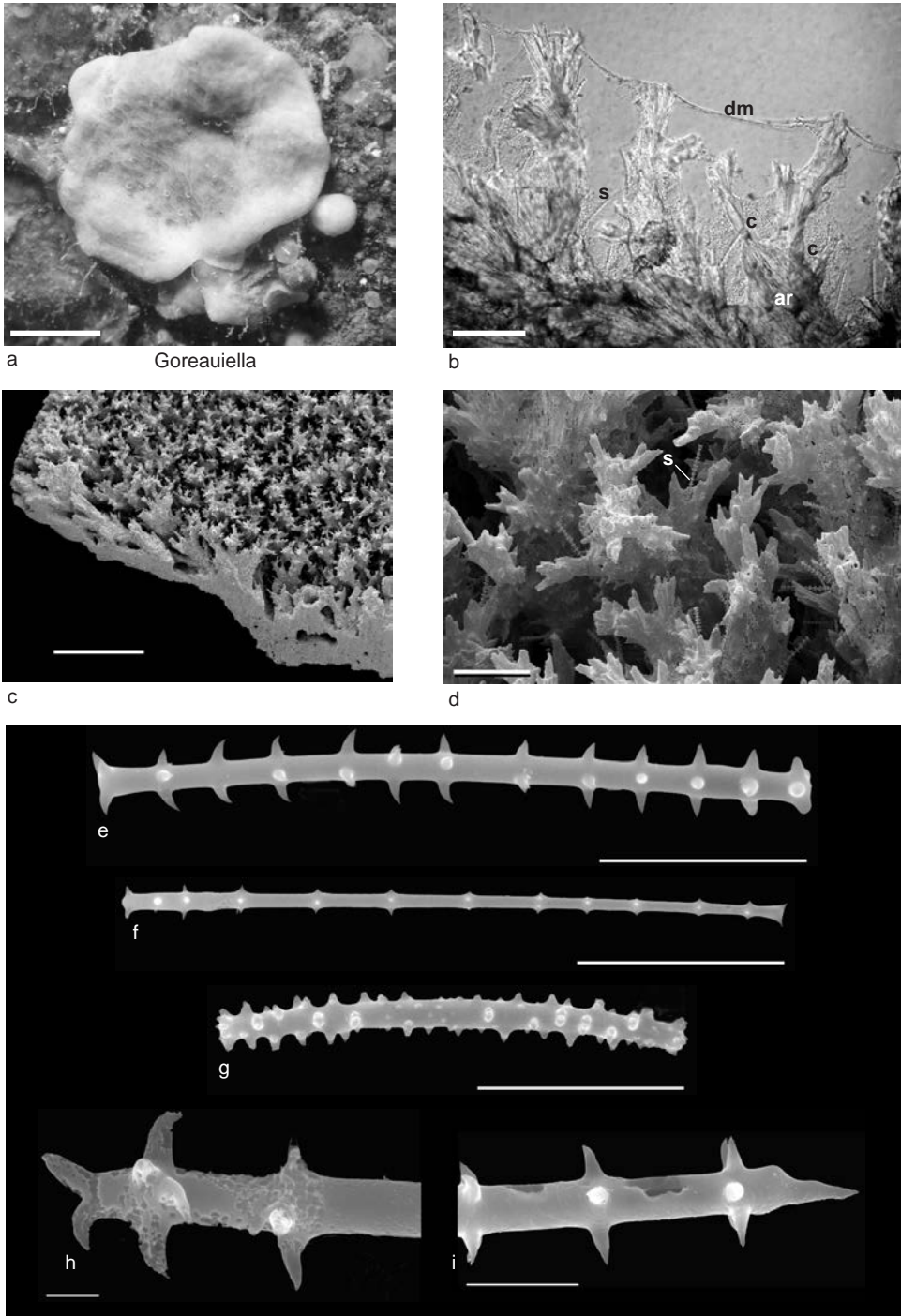


FIG. 159. Astroscleridae (p. 246–247).



massive Astroscleridae with smooth styles and basal skeleton bearing long superficial processes. Type species encrusting to dome shaped or massive. Basal skeleton made up of aragonitic sclerodermites, devoid of astrorrhizae, with surface covered with superficial, arborescent, spinose processes up to 7 mm high. Microstructure consisting of sclerodermites with crystals radiating in all directions from centers of calcification (clinoagonal type with divergent, irregular, linear elements). Color carmine to vermilion in life. Size reaching 15 cm in diameter and 3 cm in height. Spicules smooth, slightly curved styles, varying greatly in length, range of means 269–301  $\mu\text{m}$  by 5.4–7.4  $\mu\text{m}$ , with an overall range 125–818  $\mu\text{m}$  by 1.3–10.4  $\mu\text{m}$ , partially (by the head) or totally entrapped in basal skeleton. Some spicules show evidence of erosion after entrapment in aragonite. Eurypylous choanocyte chambers, 6–18  $\mu\text{m}$  in diameter. Frequently overgrown by serpulid worms. Depth range: 10–95 m in caves and deep fore reef. [REITNER (1992) reported a fossil species, *H. triassica*.] *Upper Triassic–Holocene*: Italy, *Upper Triassic*; Bahamas, Belize, Jamaica, *Holocene*.—FIG. 160a–l. \**H. miniana*, RBINSc-POR.098; *a*, seen *in situ* at depth of 25 m in reef cave on northern coast of Jamaica, scale bar, 2 cm (see also Fig. 1.6); *b*, surface of calcareous skeleton showing arborescent knoblike processes, scale, 2 mm; *c*, detail of arborescent process with aragonite crystals projected in all directions and protruding siliceous stylote spicules, scale bar, 200  $\mu\text{m}$ ; *d*, detail of siliceous spicule sticking out of aragonite skeleton, scale bar, 50  $\mu\text{m}$ ; *e–l*, curved styles (*e–i*, scale bar, 100  $\mu\text{m}$ ), varying greatly in length; detail of tips of styles with typically irregular shape (*j–k*; scale bar, 5  $\mu\text{m}$ ); and detail of an eroded spicule (*l*) as found entrapped in aragonite, scale bar, 5  $\mu\text{m}$  (West & others, 2013).—FIG. 161a–e. *H. triassica* REITNER, 1992, holotype, Carnian, Dolomites, northern Italy; *a*, basal skeleton nearly completely filled by synepitaxial cement, younger part showing partially open tubules (*l*), IPFUB/JR 1989,  $\times 6.5$ ; *b*, long monaxon tylostyles in basal skeleton,  $\times 80$ ; *c*, bundles of monocrystalline ferroan calcite spicule pseudomorphs, IPFUB/JR 1989,  $\times 177$ ; *d*, tangential section of slightly curved ferroan calcite spicule pseudomorph, IPFUB/JR 1989,  $\times 142$ ; *e*, monaxon tylostyle,  $\times 217$  (Reitner, 1992, pl. 31–32).

?*Spherolichiaetetes* GAUTRET & RAZGALLAH, 1987, p. 67 [\**S. spheroides*; OD; holotype CP196U3-23, paratype CP196U3-25, repository of both types unknown]. Growth form laminar to low domical; tubules irregular polygons in transverse section; in longitudinal section, tubules long, continuous, with tabulae; increase by intertubular budding or longitudinal fission; tubule walls aragonite spherules; megascleres and microscleres unknown. [This genus is placed questionably in the family Astroscleridae because, although it has typical spherulitic microstructure, spicules are unknown, and the skeletal construction appears to be somewhat different.]

*upper Permian (lower part)–upper Permian (upper part)*: Tunisia (Jebel Tébaga), *upper Permian (lower part)*; China, Greece, *upper Permian (upper part)*.—FIG. 162a–c. \**S. spheroides*, Tunisia; *a*, external morphology of basal skeleton of paratype, CP196U3-25,  $\times 1.9$ ; *b*, internal morphology of basal skeleton of specimen in view *a*,  $\times 1.9$ ; *c*, enlarged view of exterior of specimen in view *a* showing new tubule (*white X*) produced by intertubular budding,  $\times 102$  (Gautret & Razgallah, 1987, pl. 1, 4).—FIG. 163a–c. \**S. spheroides*, Tunisia; *a*, internal morphology of basal skeleton of holotype, CP196U3-23, showing continuous tubule walls and tabulae,  $\times 1.3$ ; *b*, spherulitic microstructure, symmetrical spherulite at end of tubule wall,  $\times 800$ ; *c*, asymmetrical spherulite near basal part of tubule,  $\times 800$  (Gautret & Razgallah, 1987, pl. 1, 4).

*Stromatospongia* HARTMAN, 1969, p. 2 [\**S. vermicola* HARTMAN, 1969, p. 3; OD; holotype YPM no. 6376]. Encrusting to massive Astroscleridae with verticillately spined styles, and basal skeleton associated with calcareous tubes of serpulid worms. Type species encrusting to massive, with an aragonitic basal skeleton always growing in association with tangled masses of serpulid worms. Surface of basal skeleton ornamented with processes 0.8 to 2 mm high. Living tissue forming a thin veneer in spaces between processes of basal skeleton. Color apricot to light salmon pink in life. Size up to 40 cm in diameter and 10 cm in height. Basal skeleton superficially marked by numerous upright, multibranched processes, 1.5–2 mm high, with the living tissue extending down into irregular spaces left between processes. Sclerodermites with aragonite crystals radiating in all directions from centers of calcification usually located around spicule heads (clinoagonal type with water-jet elements). Siliceous verticillately spined styles (acanthostyles), 75–519  $\mu\text{m}$  by 3.3–13  $\mu\text{m}$ , with a mean of 165–187  $\mu\text{m}$  by 6.2–8  $\mu\text{m}$ , with whorls of spines on shaft, more or less completely overgrown by aragonite. Eurypylous choanocyte chambers, 16–20  $\mu\text{m}$  in diameter. Association with serpulids appears obligatory. Depth range: 10–95 m under overhangs of deep fore reefs. Other Recent species include *S. norae* HARTMAN, 1969, and *S. micronesica* HARTMAN & GOREAU, 1976. *S. norae* occurs in the Caribbean, with or without association with serpulids. Basal mass of aragonite only reaches 4 cm in height. Surface processes of calcareous skeleton are lamellate in form, shorter and more closely spaced than in *S. vermicola*. Acanthostyles are similar in shape to those of *S. vermicola* but longer and thinner, 75–519  $\mu\text{m}$  by 2.7–9.1  $\mu\text{m}$ , with mean values of 195–215  $\mu\text{m}$  by 5.5–6.1  $\mu\text{m}$ . Spicules embedded in aragonite as the calcareous skeleton grows upward, and some of them become partially eroded. Color varies from cream to ecru beige.

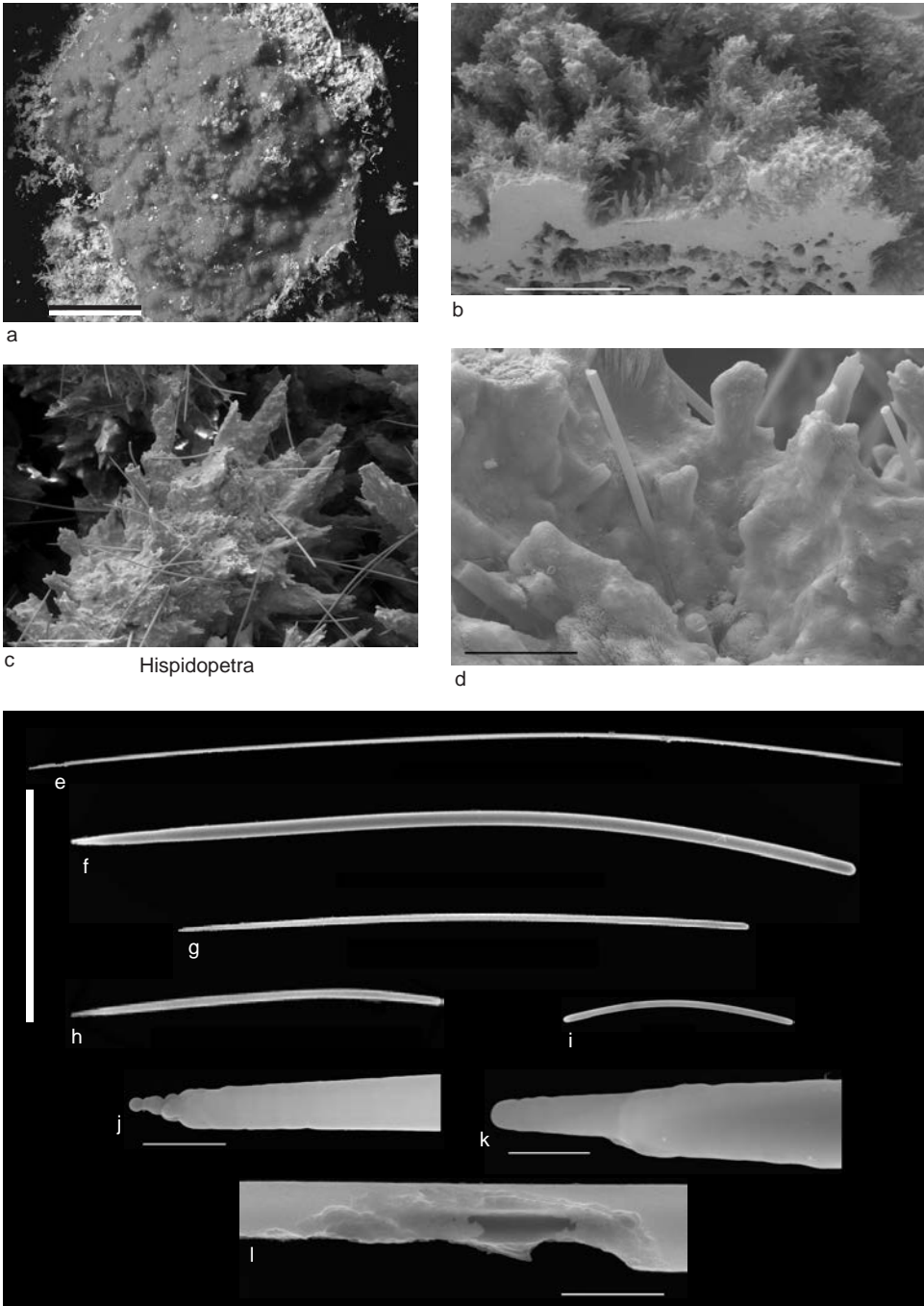
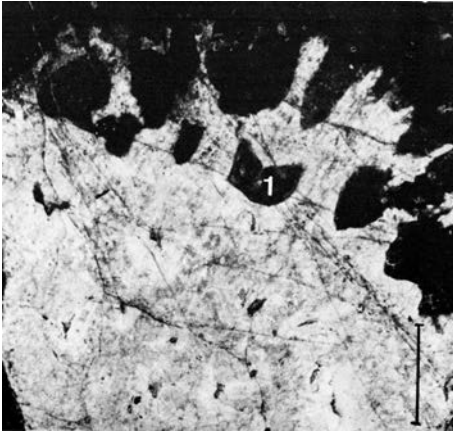
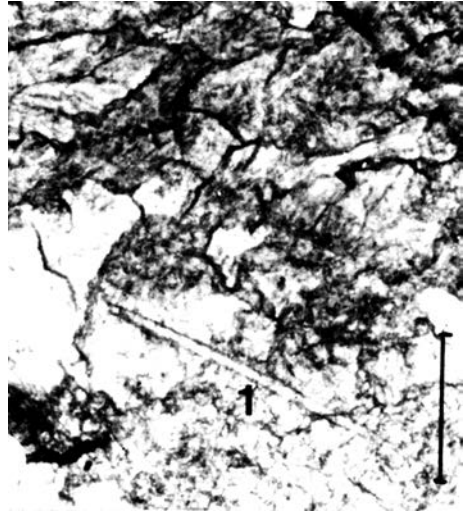


FIG. 160. Astroscleridae (p. 247–249).



a

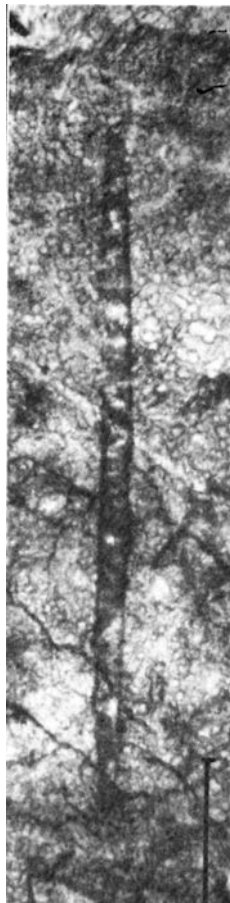


b



e

*Hispidopetra*



d



c

FIG. 161. *Astroscleridae* (p. 247–249).

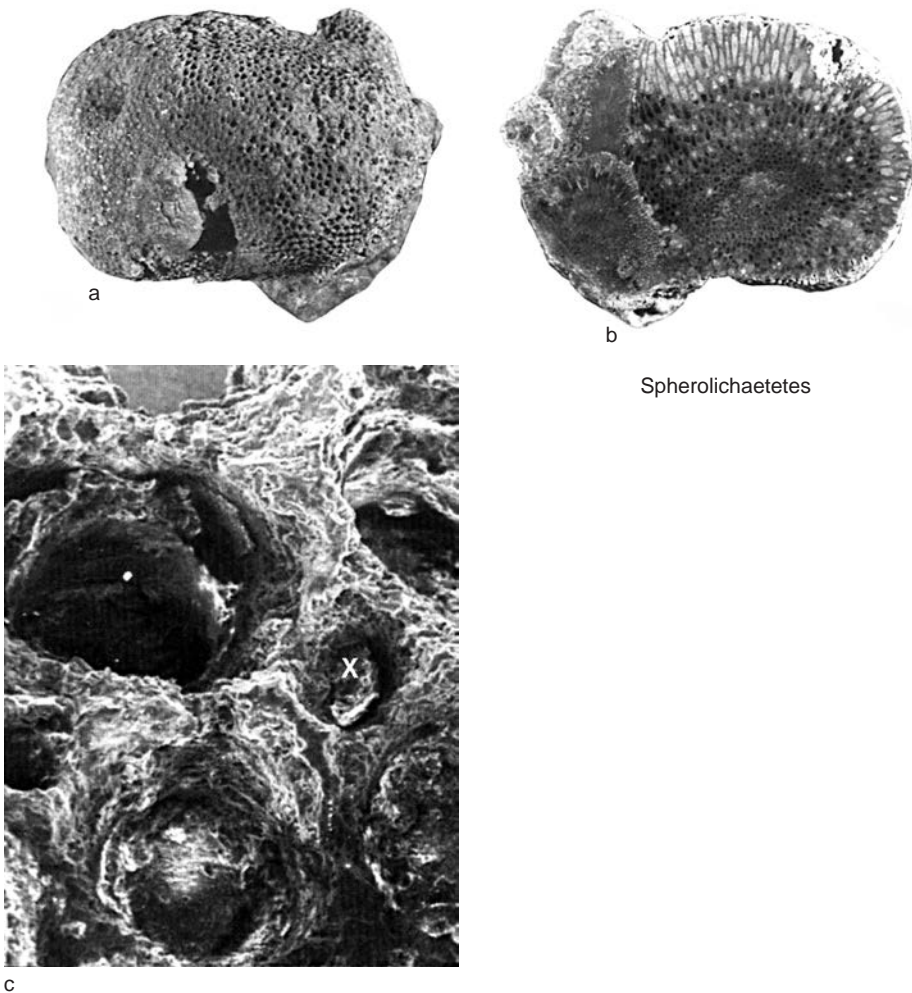


FIG. 162. Astrocleridae (p. 249).

Intercellular symbiotic bacteria abundant and highly diverse in shape; *S. micronesica* HARTMAN & GOREAU, 1976, occurs in the Pacific with a more variable form of surface processes of aragonite skeleton and smaller acanthostyles. Color varies from cream through yellowish cream to yellow-tan to ochre. [The genus is possibly synonymous with *Ceratoporella* (HARTMAN & GOREAU, 1972; WILLENZ & HARTMAN, 1989). Its superficial skeleton, however, is devoid of the regular tubules highly characteristic of *Ceratoporella*. Illustrations of the type species are poor, and *S. norae* better illustrates the characters of the genus.] *Holocene*: Bahamas, Jamaica, Pacific Ocean.—FIG. 164*a–j*. *S. norae*, RBINSc-

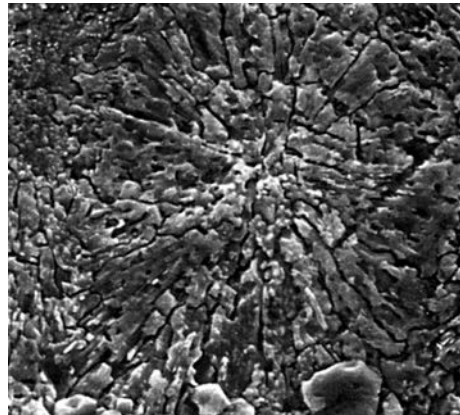
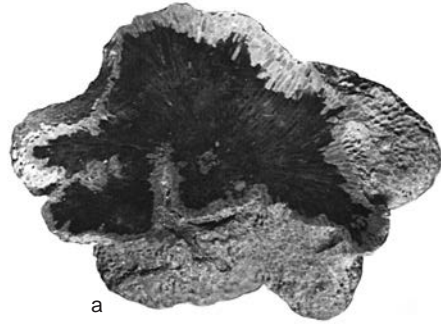
POR.096; *a*, seen *in situ*, at a depth of 25 m in a reef cave on northern coast of Jamaica, scale bar, 2 cm (see also Fig. 2.2); *b*, SEM view of skeleton with surface processes, scale bar, 1 mm (West & others, 2013); *c*, three-dimensional representation of living tissue and aragonite skeleton; *Ar*, aragonite skeleton; *C*, choanosome; *DM*, dermal membrane; *EC*, exhalant canal; *IS*, inhalant space or vestibule; *O*, osculum; *S*, spicule (Willenz & Hartman, 1989); *d–j*, acanthostyles of three different shapes (*d–f*, scale bar, 50  $\mu$ m); details of extremities of spicules (*g–h*, scale bars, 10  $\mu$ m), eroded spicule with detail (*i–j*, scale bars, 20  $\mu$ m, 5  $\mu$ m respectively (West & others, 2013).

Family MILLEPORELLIDAE  
Yabe & Sugiyama, 1935

RACHEL A. WOOD

[Milleporellidae YABE & SUGIYAMA, 1935, p. 152, 158] [=Millestrominidae GREGORY, 1898, p. 339; =Milleporididae YABE & SUGIYAMA, 1935, p. 158; =Milleporelloidae ALLOTTEAU, 1952, p. 392; =Millestromidae HUDSON, 1953, p. 885; =Parastromatoporidae HUDSON, 1959, p. 312]

Calcified agelasids with spicule framework of club-shaped styles in a plumose arrangement in vertical elements only. Microscleres absent. Primary calcareous skeleton dominated by radial elements of orthogonal or fascicular fibrous microstructure initiated at bases of spicules. Massive encrusting or dendroid gross morphology. Secondary calcareous skeleton, where present, growing epitaxially on primary. Traces of aquiferous system as astrorhizae and/or oscula. [The name family Millestrominidae GREGORY, 1898, never won general acceptance by later workers; indeed it has been largely ignored and probably should remain so, in accordance with Article 40.2, ICZN (1999, p. 46). The later-introduced family group name Milleporellidae YABE & SUGIYAMA, 1935, has, on the other hand, been adopted by most later workers either in the original, more restricted, or in a broader conception, of the family. WOOD (1987 p. 50) recommended this latter approach, merging members of both of YABE and SUGIYAMA'S (1935) families, the Milleporellidae and Milleporididae. These were formerly distinguished (see HUDSON, 1959) on differences in arrangements between their aquiferous systems, but WOOD (1987, p. 50) considered these differences to have no significance at the taxonomic level. Consequently, given the exclusion of GREGORY'S (1898) family name for the reasons stated above, WOOD (1987) concluded that the name Milleporellidae should take priority as the senior family group name; LECOMPTE, 1952a, p. 25; LECOMPTE, 1956, p. 138; GALLOWAY, 1957, p. 457. The inclusion of family Parastromatoporidae HUDSON, 1959, was proposed by WOOD (1987) due to finding of identical club-shaped styles in a plumose arrangement, and on the basis that astrosystems

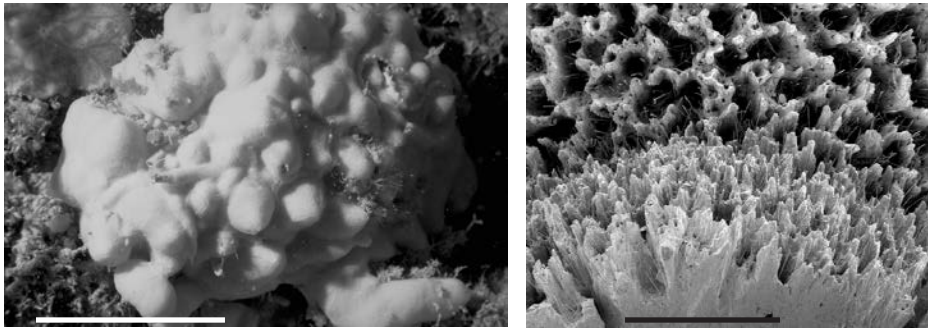


Spherolichaetetes

FIG. 163. Astroscleridae (p. 249).

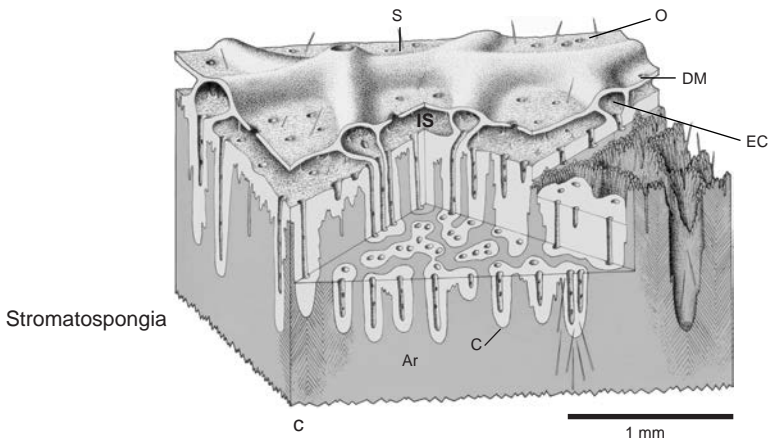
alone were insufficient diagnostic characteristics.] *Upper Triassic–Eocene*.

?*Milleporella* DENINGER, 1906, p. 67 [\**M. sardoa*; OD; =*M. ichnusae* DENINGER, 1906, p. 62] [=*Istriactis*



a

b



Stromatospongia

c

1 mm

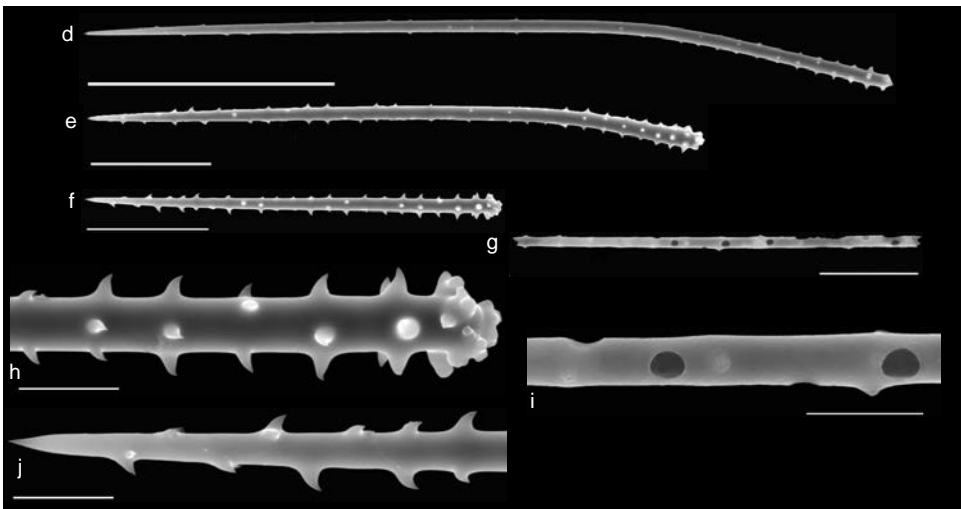


FIG. 164. Astroscleridae (p. 249–252).

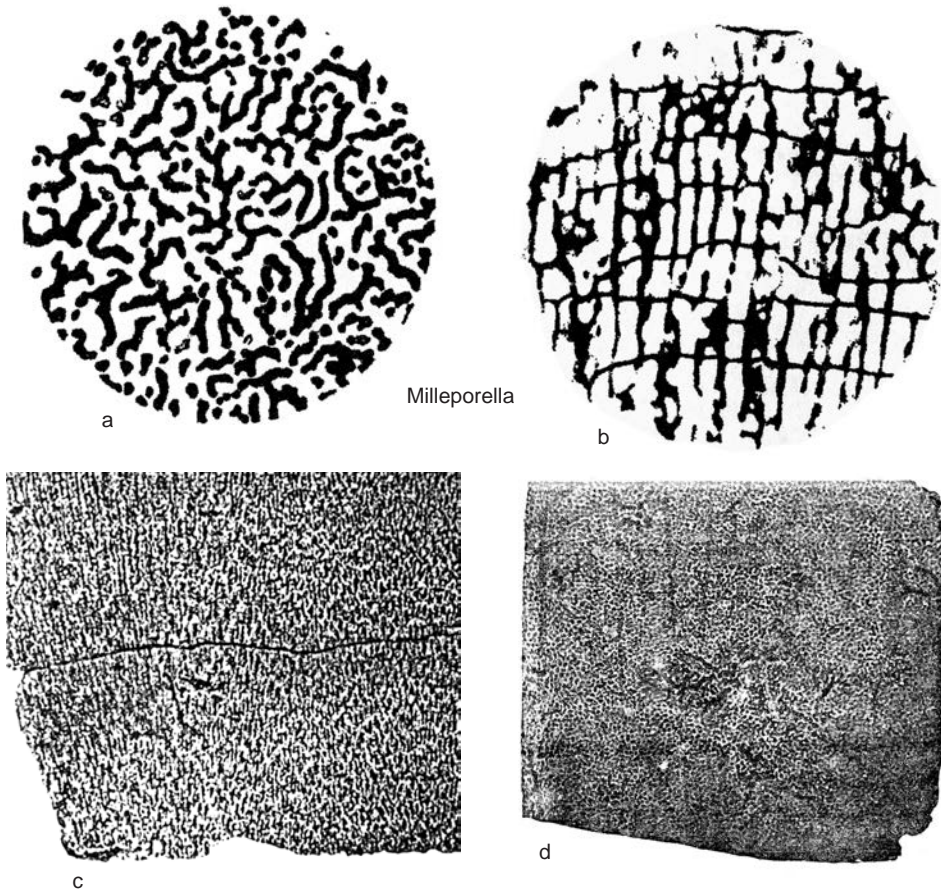


FIG. 165. Milleporellidae (p. 253–255).

MUNIER-CHALMAS, MS in coll. of DEHORNE, 1920, p. 99, *nom. nud.* (type, *M. adriatica* DEHORNE, 1920, p. 99, OD; = *Milleporella marticensis* DEHORNE, 1920, p. 100)]. No spicules noted to date. Presumed calcified agelasids with primary calcareous skeleton dominated by radial elements of fascicular fibrous microstructure. Massive encrusting or dendroid gross morphology. Secondary calcareous skeleton growing epitaxially on primary. Traces of aquiferous system as astrophorae and/or oscula. [DENINGER (1906) described *Milleporella* and *M. sardoa* as a new genus and new species, but only illustrated *M. ichnusae* n. g. n. sp. Likewise, DEHORNE (1920) did not illustrate *Istriactis sardoa* but illustrated *I. marticensis*. It is therefore assumed that *M. sardoa* is an invalid name and is replaced herein by *Milleporella ichnusae*. *M. ichnusae* DENINGER, 1906, and *M. marticensis* DEHORNE, 1920, are illustrated herein; type specimens thought to be lost. The genus name is listed

as questionable because so far no spicules have been found.] *Jurassic-Eocene*: Europe.—FIG. 165a–b.

\**M. ichnusae*, Upper Cretaceous, Sardinia; a, transverse section; b, longitudinal section, magnifications unknown, specimens thought to be lost (Deninger, 1906, pl. VII, 8a–b).—FIG. 165c–d. *M. marticensis* DEHORNE, 1920, upper Cretaceous, Hippurites beds of Martigues, Bouches-du-Rhône, France; c, transverse section,  $\times 3$ ; d, tangential section of same specimen as view c, showing stellar channels, similar to astrophorae,  $\times 2.7$  (Dehorne, 1920, pl. XVI, 1–2).

**Dehornella** Lecompte, 1952a, p. 16 [\**Stromatoporella hydractinoides* DEHORNE, 1920, p. 77; OD; holotype, Geological Laboratory, Sorbonne, pl. 6, 2, and thin sections a–c] [= *Astroporina* HUDSON, 1960, p. 196 (type, *A. stellifera* HUDSON, 1960, p. 197, OD, holotype, NHM, pl. 27, 1–2)]. Densely packed, plumose arrangement of club-shaped style spicules 110–135  $\mu\text{m}$  long, 13.5–17  $\mu\text{m}$  wide; continuous

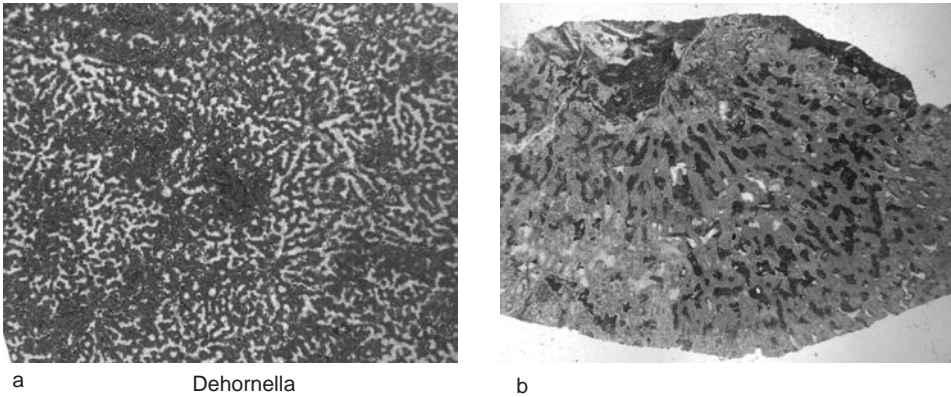


FIG. 166. Milleporellidae (p. 255–256).

fascicular fibrous vertical elements 100–300  $\mu\text{m}$  wide; subordinate pillar-lamellae; often with marked astrophorae, latilaminae, and tabulae; type material has been lost. Two other included species: *D. harrarensis* (WELLS, 1943, p. 50) exhibits an open reticulum, vertical elements generally 250–300  $\mu\text{m}$  wide, few tabulae, and styles that do not project, Oxfordian, Kurtcha, Harrar Province, Ethiopia, with wider distribution in upper Oxfordian–lower Aptian, Austria, France, Israel, Sinai, Ethiopia, Oman); *D. crustans* (HUDSON, 1960, p. 191), exhibits densely packed plumose styles that project, and vertical elements with anastomizing columns, abundant astrophorae, and aligned tabulae; lower Kimmeridgian, Makhtesh Hagadol, Israel, with wider distribution in Kimmeridgian, Israel, Dakkar, Somalia. *Upper Jurassic–Lower Cretaceous*: Portugal, Austria, France, Israel, Sinai, Lebanon, Egypt, Ethiopia, Somalia, Oman.—FIG. 166*a–b*. *D. harrarensis* (WELLS), light photomicrographs, lower Kimmeridgian, Wadi Bik, Ruus al Jebel, Oman; *a*, transverse section, NHM no. 4844c,  $\times 4$  (West & others, 2013); *b*, longitudinal section, NHM no. 4868a,  $\times 6$  (West & others, 2013).—FIG. 167, *1a–c*. *D. crustans* HUDSON, light photomicrographs, NHM no. 5170c, lower Kimmeridgian, Makhtesh Hagadol, Israel; *a*, longitudinal section,  $\times 4$  (West & others, 2013); *b*, longitudinal section,  $\times 20$  (West & others, 2013); *c*, longitudinal section of plumose spicule tract,  $\times 100$  (West & others, 2013).

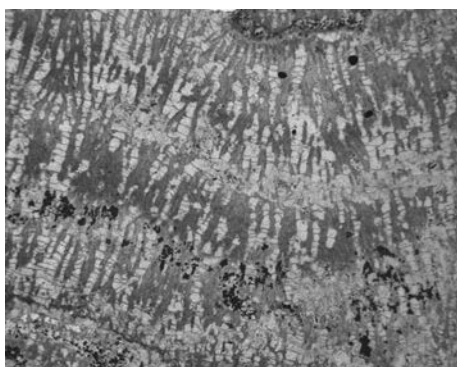
**Murania** KAZMIERCZAK, 1974, p. 341 [*\*M. lafeldi*; OD; holotype, ZPAL.Pf.1/1a–b]. Sheetlike, massive, or fasciculate calcareous skeleton of vertically arranged prismatic columns (pillars) that encase densely packed plumose arrays of club-shaped styles. [One other species, *M. reitneri*, is known from the Kimmeridgian, Austria, and the holotype is illustrated herein; *M. reitneri* only differs from the type species in one respect: having more slender columns, up to 0.32 mm diameter (mean of 0.32 mm), as compared with columns of the

type species, which are up to 0.5 mm in diameter (mean of 0.3 mm).] *Upper Triassic–Lower Cretaceous*: Austria, Kimmeridgian; Italy, *Upper Triassic*; Slovakia, Germany, Spain, Gulf of Mexico, *Lower Cretaceous*.—FIG. 167, *2a*. *\*M. lafeldi*, Z.Pal.Pf.1/1b, transverse section,  $\times 40$  (courtesy of Kazmierczak, 1974).—FIG. 167, *2b–c*. *M. reitneri* SCHLAGINTWEIT, light photomicrographs, holotype BSP 2003 X-5, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich, Kimmeridgian, Krahstein, Austria; *b*, transverse section,  $\times 8$ ; *c*, transverse section,  $\times 35$  (West & others, 2013).

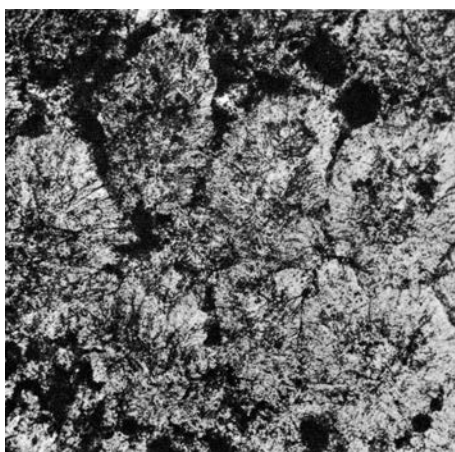
**Parastromatopora** YABE & SUGIYAMA, 1935, p. 183 [*\*Stromatopora japonica* YABE, 1903, p. 2; OD; holotype, University of Hokkaidu, UHR 00445] [= *Epistromatopora* YABE & SUGIYAMA, 1935, p. 183, obj.]. Milleporellidae with short styles 60  $\mu\text{m}$  in length, 18  $\mu\text{m}$  wide, with fascicular fibrous continuous columns, pillar-lamellae absent or subordinate, and numerous aligned tabulae. One other species, *P. libani* HUDSON, 1954c, p. 659, has columns forming tubules; no pillar-lamellae; canals converge toward central oscula and occurs in the upper Oxfordian–lower Kimmeridgian, Lebanon, Israel, and Yemen. [Type is not illustrated as spicules are not well preserved.] *Upper Jurassic (upper Oxfordian–lower Kimmeridgian)*: Japan, Lebanon, Israel, Yemen.—FIG. 168, *1a–b*. *P. libani* HUDSON, light photomicrographs, NHM no. 4789, lower Kimmeridgian, Toumatt, Lebanon, Israel; *a*, transverse section,  $\times 8$ ; *b*, transverse section,  $\times 8$  (West & others, 2013).

**Promillepora** DEHORNE, 1920, p. 97 [*\*P. pervinquieri*; M; = *Stromatopora douvillei* DEHORNE, 1920, p. 20, lectotype by LECOMPTE, 1952a, p. 23] [= *Amorphospongia* D'ORBIGNY, 1847, p. 178, *nom. nud.*]. Milleporellidae with short styles, maximum length 50  $\mu\text{m}$ , 12  $\mu\text{m}$  width in a loose plumose arrangement; fascicular fibrous microstructure; abundant, radially extensive tabulate oscula with no astrophorae. [*Stromatopora douvillei* DEHORNE,

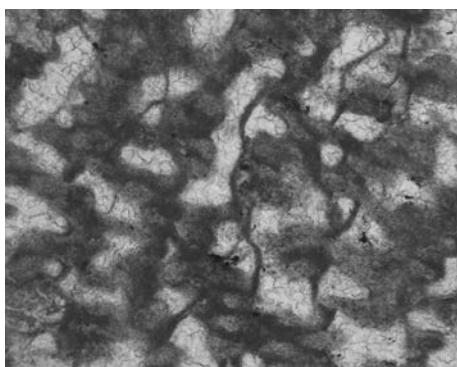




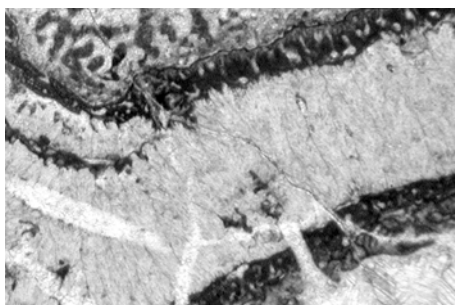
1a



2a



1b

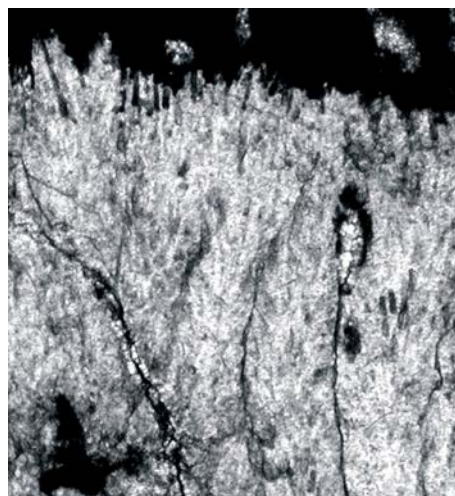


2b



1c

Dehornella



2c

Murania

FIG. 167. Milleporellidae (p. 255–256).

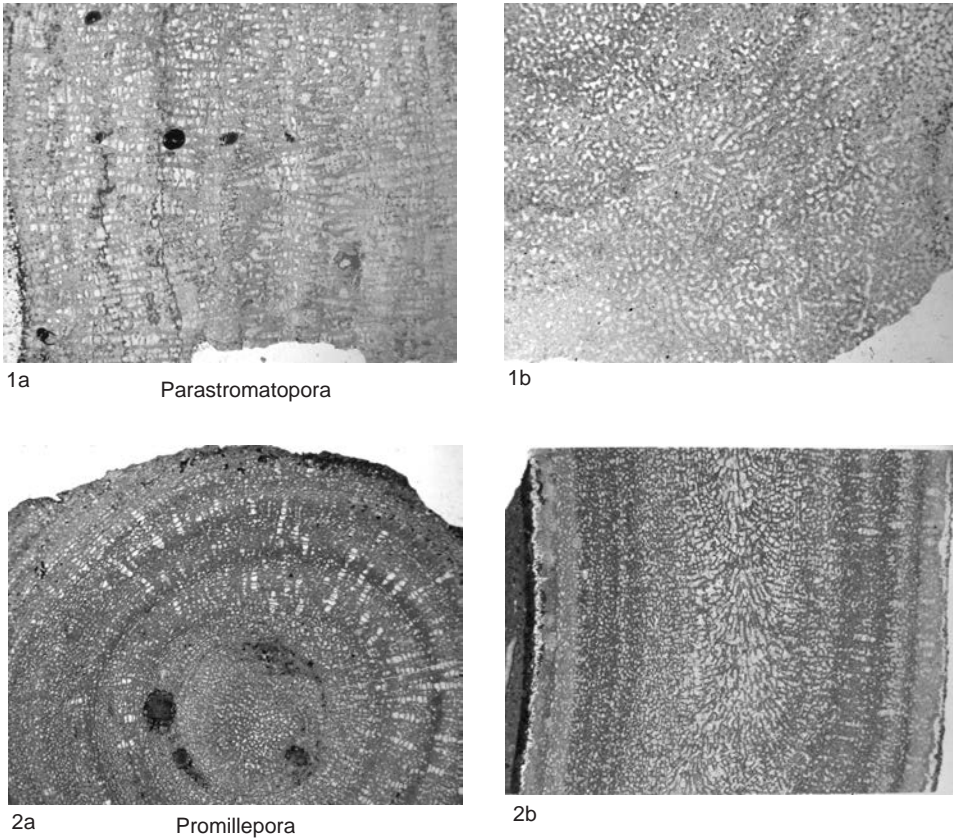


FIG. 168. Milleporellidae (p. 256–258).

1920, p. 20, has a common straight tabulate oscula, 140–300  $\mu\text{m}$  in diameter.] *Upper Jurassic* (upper Oxfordian–lower Kimmeridgian): Israel, Tunisia.—FIG. 168, 2a–b. \**P. pervinquieri*, light photomicrograph, lower Kimmeridgian, Makhtesh Hagadol, Israel; a, transverse section, NHM no. 4898A,  $\times 7$ ; b, transverse section, NHM no. 4901a,  $\times 7$  (West & others, 2013).

**Shuqraia** HUDSON, 1954a, p. 218 [\**Milleporidium zuffardi* WELLS, 1943, p. 51; OD; holotype AMNH 252900–259001]. Styles maximum of 80  $\mu\text{m}$  long, 7  $\mu\text{m}$  wide; regular columns forming tubules; orthogonal to fascicular fibrous skeleton. Type species with fibrous tabulae upon primary skeleton and loosely packed plumose styles; its distribution occurs in Israel, Ethiopia, Somalia, and Yemen; *S. hudsoni* (WOOD, 1987, p. 60–62) is another species with commonly stacked astrophorae, with distribution restricted to Yemen. *Upper Jurassic* (upper Oxfordian–lower Kimmeridgian): Yemen, Israel, Ethiopia, Somalia, Yemen, ?Japan.—FIG. 169, 1a–b. \**S. zuffardi* (WELLS), light photomicrograph, lower Kimmeridgian, Shuqra, southern Yemen; a, longitudinal section,

NHM no. 4485B,  $\times 6$ ; b, transverse section, NHM no. 4505,  $\times 15$  (West & others, 2013).—FIG. 169, 1c–d. *S. hudsoni* (WOOD), light photomicrograph, upper Oxfordian, Alam Abayadh, northern Yemen; c, tangential section, NHM no. 4570A,  $\times 7$ ; d, transverse section, NHM no. 4639a,  $\times 8$  (West & others, 2013).

**Steinerina** HUDSON, 1956b, p. 518, *nom. nov. pro Steineria* HUDSON, 1956a, p. 722, *non* MICOLETZKY, 1922, p. 119, nematode [\**Stromatopora romanica* DEHORNE, 1918, p. 221; OD; holotype, Geological Laboratory Sorbonne Specimen 27, HUDSON, 1956] [= *Romanactis* MUNIER-CHALMAS, *nom. nud.*, MS in coll. of DEHORNE, 1920, p. 88]. Milleporellidae with short pillars of fascicular fibrous microstructure up to 300  $\mu\text{m}$  in length; abundant tabular astrophorae up to 560  $\mu\text{m}$  in diameter; secondary epitaxial skeleton and common aligned tabulae. [One other species, *S. somaliensis* (= *Milleporidium somaliense* ZUFFARDI-COMERCI, 1931, p. 70), has an open reticulum with pillars up to 230  $\mu\text{m}$  in diameter and occurs in the upper Oxfordian–lower Kimmeridgian of Israel, Oman, and Somalia. Illustrations

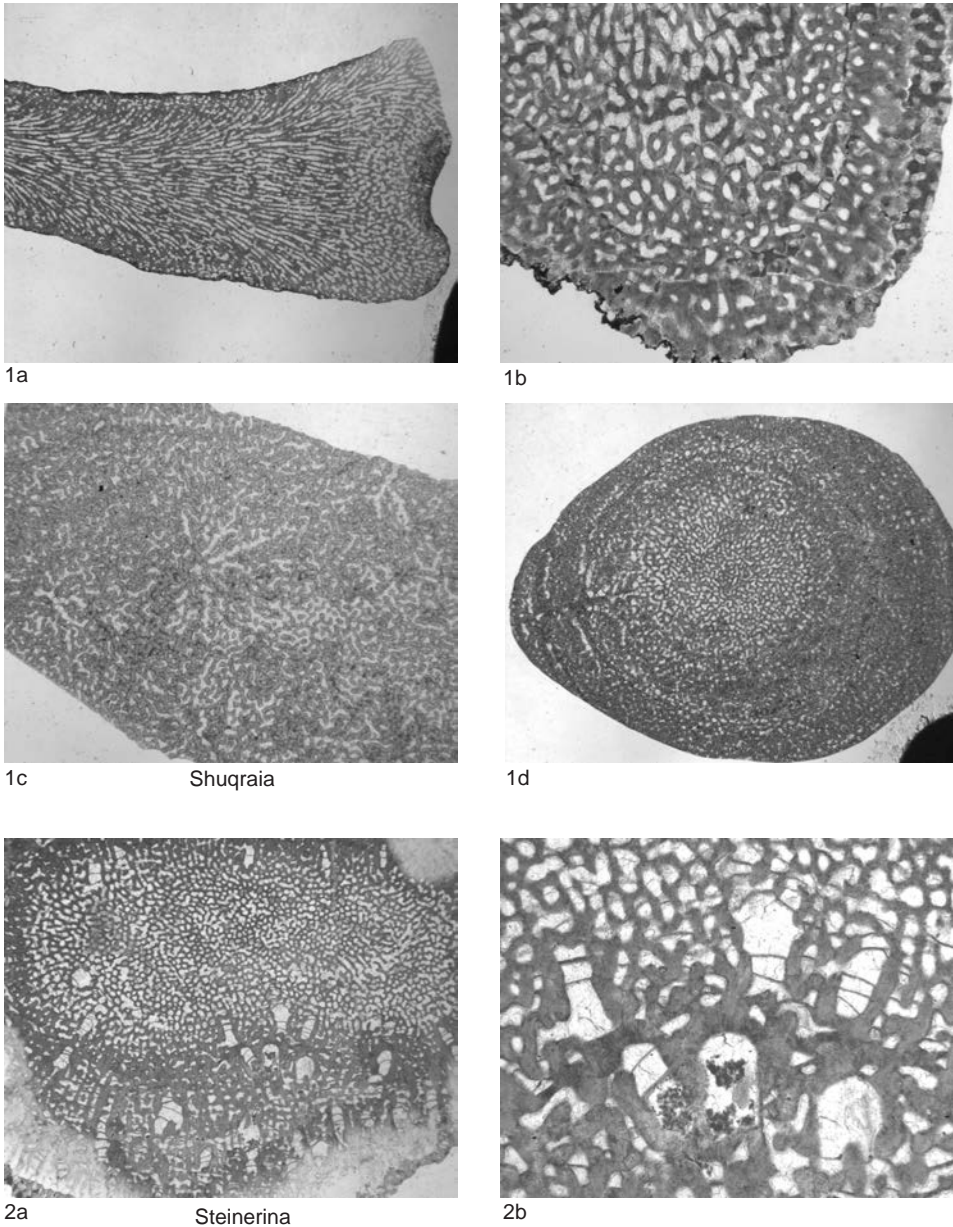


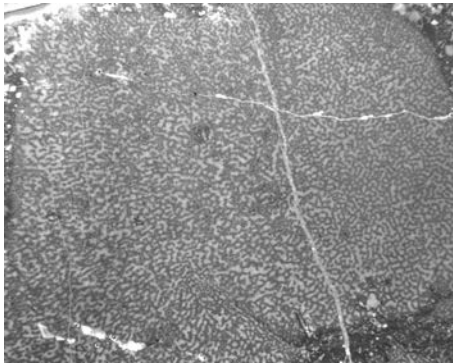
FIG. 169. Milleporellidae (p. 258–259).

of the type species are unavailable as the type material has been lost.] *Upper Jurassic (upper Oxfordian–lower Kimmeridgian)*: Romania, Israel, Oman, Somalia.—FIG. 169, 2a–b. *S. somaliensis* (ZUFFARDI-COMERCI, 1931), light photomicrograph, NHM no. 4973B, Wadi Bekr, Haushi, Oman; a, transverse section,  $\times 7$ ; b, transverse section,  $\times 35$  (West & others, 2013).

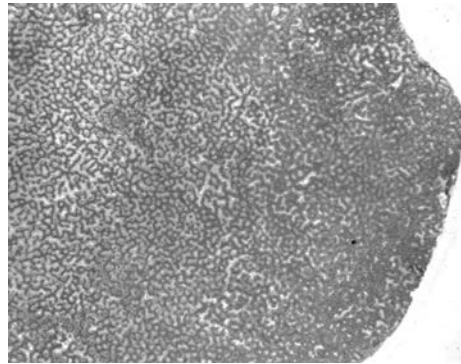
**Family ACTINOSTROMARIIDAE**  
**Hudson, 1955**

[Actinostromariidae HUDSON, 1955c, p. 238] [=Stromatorhizidae HUDSON, 1957, p. 5]

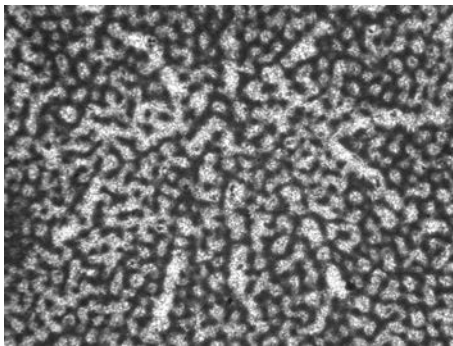
Calcareous skeleton with an open reticulate arrangement of pillars and pillar-lamellae



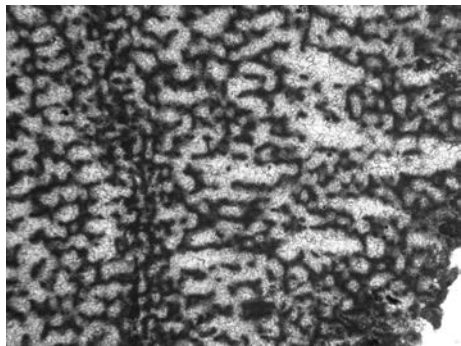
1a Actinostromaria



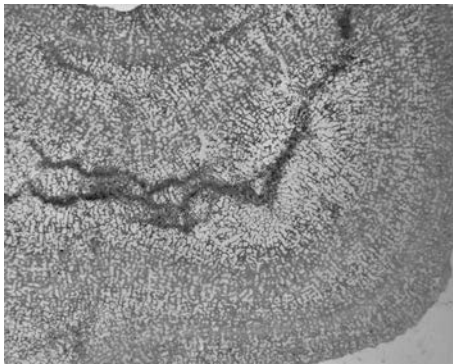
1b



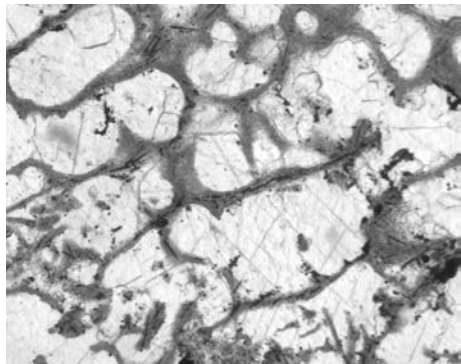
2a Actostroma



2b



3a Actinostromarianina



3b

FIG. 170. Actinostromariidae and Actinostromarianinidae (p. 260–261).

composed of a spicule framework of styles and possible triaxines, and an enclosing fibrous orthogonal microstructure; possible triaxines placed at pillar-lamellae junctions (description adapted from WOOD, 1987, p. 70). *Upper Jurassic–Upper Cretaceous*.

**Actinostromaria** MUNIER-CHALMAS in TORNQVIST, 1901, p. 1116 (HAUG, 1909, pl. 97, no text, *nom. nud.*) [*\*A. stellata* DEHORNE, 1915, p. 733; SD DEHORNE, 1915, p. 733; according to DEHORNE (1915, p. 733), MUNIER-CHALMAS neither described nor illustrated *A. stellata*, and thus a holotype was not originally designated, and now type material has been lost]. Open reticulate

arrangement of pillars and pillar-lamellae with fibrous orthogonal microstructure with a spicule framework of styles and possible triaxines. *Upper Jurassic–Upper Cretaceous*: France, Slovakia, Japan.—FIG. 170, 1a–b. *A. sp.*, light photomicrograph, upper Oxfordian, Trnovski Gost, Slovenia; *a*, longitudinal section, NHM no. H 5491,  $\times 8$ ; *b*, transverse section, NHM no. H 5492,  $\times 8$  (West & others, 2013).

**Actostroma** HUDSON, 1958, p. 91 [*\*A. damesini* HUDSON, 1958, p. 92; OD; holotype, NHM 4890; =*Actostroma nasri* HUDSON, 1958, p. 95; =*Actostroma kubni* HUDSON, 1958, p. 96]. Primary calcareous skeleton encloses spicule framework of intramural styles and possible triaxines; skeletal elements orthogonal to fascicular fibrous. Abundant astrorhizal canals and oscula, sometimes tabulate styles and possible triaxines; skeletal elements dominantly pillars and pillar-lamellae, forming partially open to closed tubule-like mesh; tabulae only seen in astrorhizal canals; latilaminae and mamelons commonly present; nodular, encrusting, or dendroid external morphology. *Upper Jurassic (lower Kimmeridgian)*: Israel, ?China.—FIG. 170, 2a–b. *\*A. damesini*, light photomicrograph, Israel; *a*, transverse section, NHM no. 4891a,  $\times 15$ ; *b*, longitudinal section, NHM no. 4892a,  $\times 15$  (West & others, 2013).

### Family ACTINOSTROMARIANINIDAE Wood, 1987

[Actinostromarianinidae WOOD, 1987, p. 74]

Calcareous skeleton with long thin styles or tylostyles in a radial arrangement and an irregular or orthogonal fibrous microstructure. *Upper Jurassic (upper Oxfordian–upper Kimmeridgian)*.

**Actinostromarianina** Lecompte, 1952a, p. 9 [*\*Stromatopora milleporoides var. romanica* DEHORNE, 1920, p. 87; OD; there is no indication of a designated holotype in DEHORNE (1920, p. 86–88); apparently the type material is lost]. Thin styles or tylostyles (180  $\mu\text{m}$  length by 8  $\mu\text{m}$  width) arranged in loose, radial manner, with densely packed central axis; primary calcareous skeleton of irregular or fascicular fibrous microstructure; secondary calcareous skeleton may or may not be present; granular, aligned tabulae; nodular or dendroid morphology; astrorhizae weakly developed or indistinguishable. *A. lecompti* HUDSON, 1955c, p. 230 (MILAN, 1969, p. 179) has a secondary calcareous skeleton in form of orthogonal rim, sometimes forming latilaminae. Primary calcareous skeleton of irregular microstructure. Another species, *A. praesalevensis* (ZUFFARDI-COMERCI, 1931, p. 49) (YABE & SUGIYAMA, 1935; HUDSON, 1955c, p. 230) has a nodular morphology and primary calcareous skeleton of fascicular fibrous microstructure forming pillars 70–250  $\mu\text{m}$  and pillar-lamellae (50–70  $\mu\text{m}$  diam-

eter). Aligned tabulae between 15–30  $\mu\text{m}$  thick. No discernible astrorhizal systems in form of orthogonal rim, sometimes forming latilaminae. *Upper Jurassic (upper Oxfordian–upper Kimmeridgian)*: France, Romania, Ethiopia, Yemen, Iraq.—FIG. 170, 3a–b. *A. lecompti* HUDSON, light photomicrograph, NHM no. 4608a, upper Kimmeridgian, Alam Abayadh, northern Yemen; *a*, transverse section,  $\times 5$ ; *b*, transverse section,  $\times 30$  (West & others, 2013).

### Family UNCERTAIN

RONALD R. WEST and RACHEL A. WOOD

**Blastoporella** CUIF & EZZOUBAIR, 1991, p. 264 [*\*Blastochaetetes karachensis* CUIF & FISCHER, 1974, p. 11; OD; *Blastoporella karachensis* CUIF & FISCHER, 1974, p. 11–12 is designated as the “standard species” (currently in J.-P. Cuif collections of the Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris; it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN) for *Blastoporella*, in CUIF and EZZOUBAIR, 1991, p. 264, but neither a holotype nor paratypes were designated. The earlier (original) description of *Blastochaetetes karachensis* (CUIF & FISCHER, 1974, p. 11–12, pl. III, 2–3), however, did refer to these unnumbered images as the holotype, and illustrated (pl. III, 4–5) two other unnumbered specimens as well (see Fig. 172c)]. Growth form domical, fungiform to conical with astrorhizae; tubules irregularly shaped (alveolar) in transverse section with connecting pores; irregular tubule shape due to connecting pores clearly visible in longitudinal section; tubules increase by longitudinal fission, rarely by intertubular budding; penicillate, water-jet (fascicular fibrous) aragonitic microstructure; megaccleres and microscleres unknown (description modified from CUIF & FISCHER, 1974; CUIF & EZZOUBAIR, 1991). *Triassic (Carnian–Norian)*: northern Italy (Dolomites), *Carnian*; Turkey (Alakir Çay), *Norian*.—FIG. 171a–d. *\*B. karachensis* (CUIF & FISCHER), Carnian, Triassic, northern Italy; *a*, toptype, upper exterior surface of fungiform basal skeleton with astrorhizae,  $\times 1.5$ ; *b*, toptype, longitudinal section of astrorhizae,  $\times 10$ ; *c*, toptype, transverse section of astrorhizae,  $\times 14$  (Cuif & others, 1973, pl. 1); *d*, holotype, transverse section showing connections (pores) between tubules,  $\times 17$  (Cuif & Fischer, 1974, pl. III, 5).—FIG. 172a–e. *\*B. karachensis* (CUIF & FISCHER), Carnian, Triassic, northern Italy; *a*, toptype, transverse section of tubules showing connection (pore) between two tubules (*black X*) in lower left,  $\times 28$  (Cuif & Ezzoubair, 1991, pl. 2); *b*, holotype, longitudinal section showing connections between tubules,  $\times 15$  (Cuif & Fischer, 1974, pl. III, 3); *c*, longitudinal section of another specimen showing connections between tubules,  $\times 22.5$  (Cuif & Fischer, 1974, pl. III, 5); *d*, toptype, longitudinal section of tubules showing connection (pore) between tubules (*white X*),  $\times 52$ ; *e*, toptype,

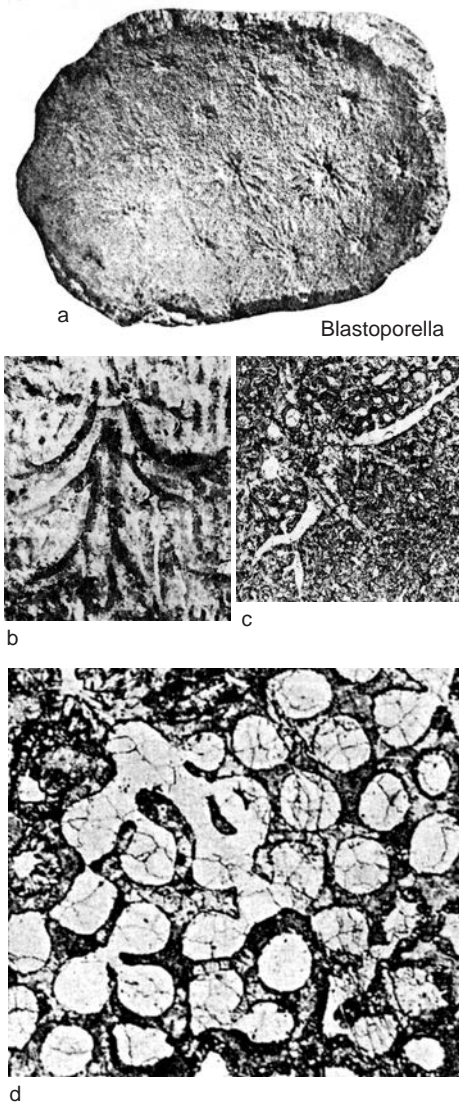


FIG. 171. Uncertain (p. 261–262).

tangential section showing penicillate, water-jet (fascicular fibrous) microstructure of tubule walls,  $\times 400$  (Cuif & Ezzoubair, 1991, pl. 2).

**Kemeria** CUIF & EZZOUBAIR, 1991, p. 264 [*\*K. pachytheca*; OD; unnumbered holotype, from near Kemer village; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN)]. Growth form, irregular,

nodular, composed of jointed tubules; tubule walls alveolar, characterized by superimposed layers of bundles of penicillate fibers in transverse and longitudinal section, some with small pores; penicillate, water-jet (fascicular fibrous possible aragonite) microstructure; some tubules filled by secondary fascicular crystals; megascleres and microscleres unknown (description based on CUIF & EZZOUBAIR, 1991). [It is uncertain whether all the views are from parts of the holotype, or some include parts of other type specimens, or represent different, undesignated specimens.] *Triassic (Carnian–Norian)*: northern Italy (Dolomite Alps), *Carnian*; Turkey (Alakir Çay), *Norian*.—FIG. 173a–b. *\*K. pachytheca*; a, transverse section of tubules with walls composed of numerous penicillate units, each unit going to extinction in transmitted polarized light,  $\times 12.5$ ; b, enlargement of part of view a showing details of penicillate microstructure of tubule walls,  $\times 100$  (Cuif & Ezzoubair, 1991, pl. 2).—FIG. 174a–d. *\*K. pachytheca*; a, SEM of penicillate water-jet (fascicular fibrous) microstructure of tubule walls,  $\times 93$ ; b, enlargement of view a of penicillate water-jet (fascicular fibrous) microstructure of tubule walls,  $\times 217$ ; c, slightly oblique longitudinal section showing an opening (pore, white X) between two tubules, note penicillate microstructure,  $\times 26$ ; d, secondary fascicular crystals filling tubules, inferred to be continuous,  $\times 156$  (Cuif & Ezzoubair, 1991, pl. 2).

**Keriocoelia** CUIF, 1974, p. 149 [*\*K. conica*; OD; CUIF (1974) did not designate a holotype nor paratypes; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN)]. DIECI and others (1977) studied 12 topotype specimens (including IPUM 19091, 19092, 19093) and 9 unnumbered specimens, all of which are in the Zardini Collections, IPUM]. Growth form low domical, fungiform with well-developed basal layer; tubules irregular polygons in plan view increasing distally by addition of small spherulites that produce a notched appearance; compact mass produced by secondary penicillate filling of tubules; tubule walls spherulitic aragonite; styliform megascleres and microscleres unknown (DIECI & others, 1977). [See also *Keriocoelia* in FINKS & RIGBY (2004d, p. 598).] *Triassic (Carnian)*: Italy.—FIG. 175a–f. *\*K. conica*, Cassian Formation, northern Italy; a, lateral view of basal skeleton of topotype, IPUM 19091, note fungiform growth form and basal layer,  $\times 3.6$ ; b, upper surface of basal skeleton of topotype, IPUM 19091,  $\times 3.9$  (Dieci & others, 1977, pl. 1); c, irregular upper (distal) surface of tubules due to continuous addition of small spherules,  $\times 13.6$ ; d, transverse section showing spherulitic microstructure of tubule walls and partial to complete filling of tubules with penicillate aragonite,  $\times 30$ ; e, detailed drawing

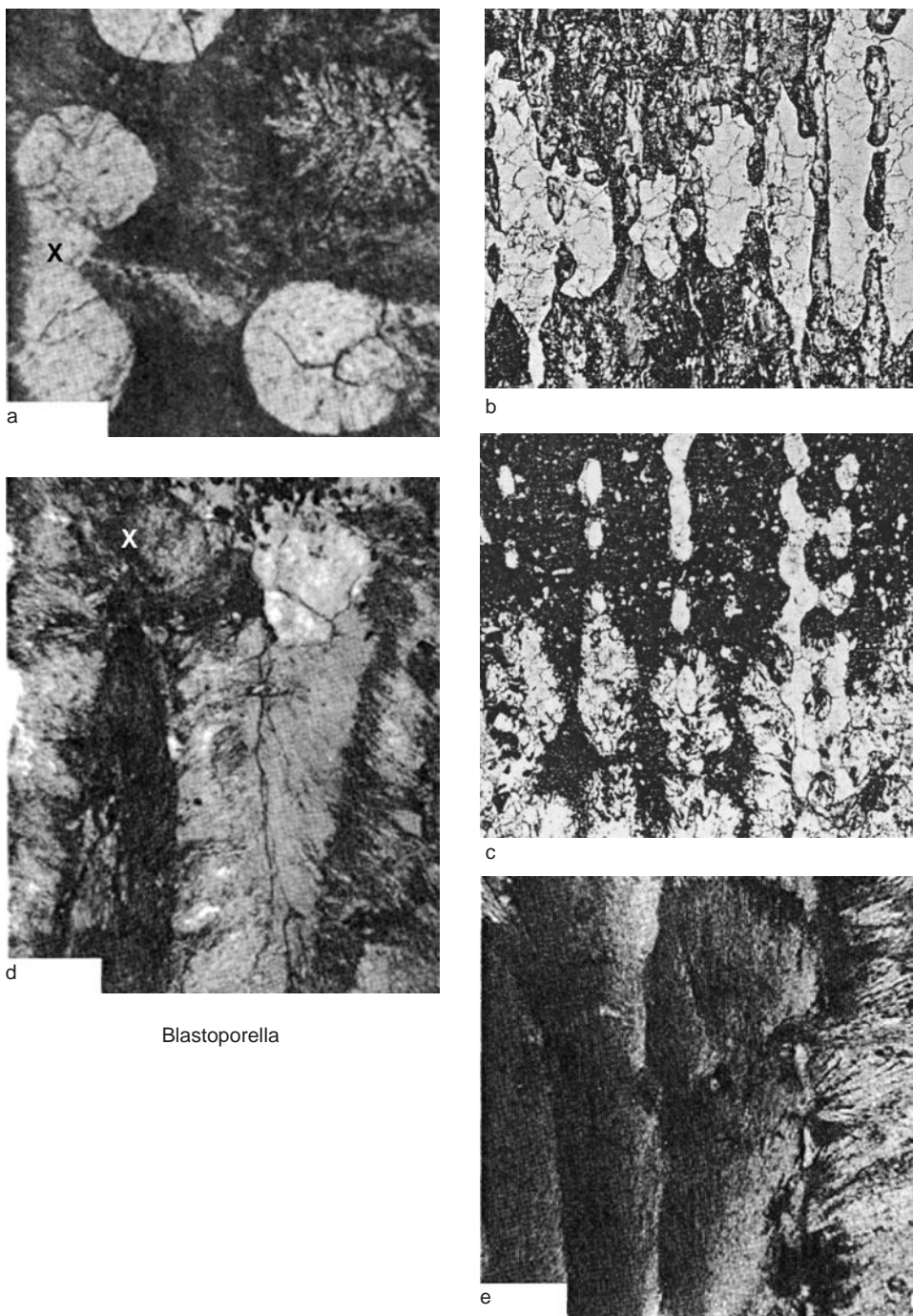
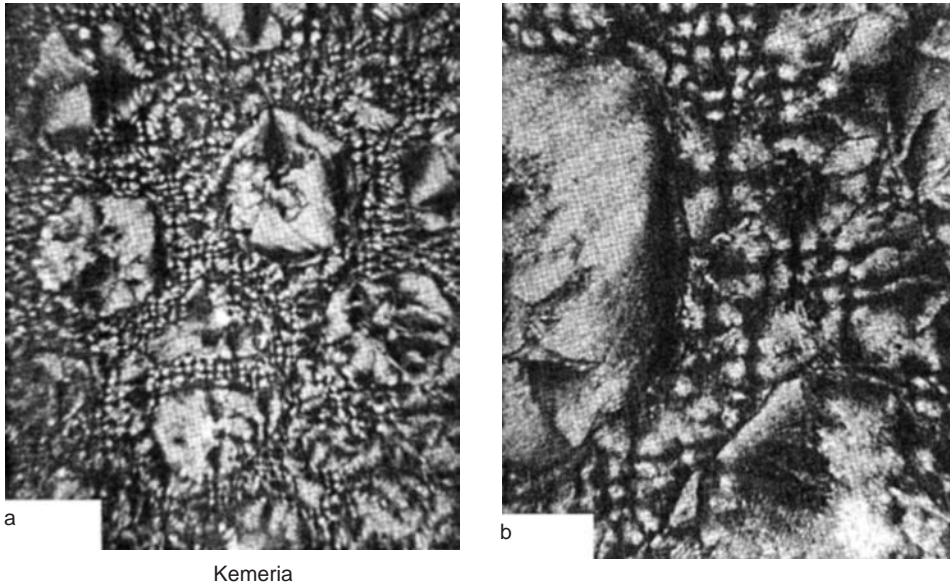


FIG. 172. Uncertain (p. 261–262).



Kemeria

FIG. 173. Uncertain (p. 262).

of transverse section, tubule walls composed of perfectly centered spherules; subsequently, tubules filled with fascicular rods of aragonite,  $\times 85$  (Cuif, 1974, p. 150, pl. 31); *f*: thin section, topotype, IPUM 19093, showing stylifom megascleres,  $\times 700$  (Dieci & others, 1977, pl. 3).

**Leiospongia** D'ORBIGNY, 1849b, p. 548 [*Achilleum verrucosum* MÜNSTER, 1841, p. 26; SD ENGESER & TAYLOR, 1989, p. 40] [= *Leiofungia* de FROMENTEL, 1860b, p. 49, obj.; = *Hartmanina* DIECI, RUSSO, & RUSSO, 1974b, p. 141, obj.]. Growth form domical to small columnar, some fungiform; basal layer well developed with growth ridges; tubules polygon in plan view with irregularly spaced tabulae; tubules increase by longitudinal fission or intertubular budding; walls and tabulae composed of spherulitic aragonite. [Spicules and/or spicule pseudomorphs are unknown from the type species, *L. verrucosum*, but acanthostyle or fusiform megascleres are known, arranged parallel to growth direction in *Leiospongia* sp.; microscleres unknown (ENGESER & TAYLOR, 1989, fig. 3F; DIECI, RUSSO, & RUSSO, 1974b); see also *Hartmanina* FINKS & RIGBY, 2004d, p. 595. For more on the taxonomic history of this genus and assigned species, see ENGESER and TAYLOR (1989, p. 40–43) and DIECI, RUSSO, and RUSSO (1974b).] *Triassic (Carnian)*: northern Italy.—

FIG. 176*a–b*. \**L. verrucosum* (MÜNSTER), lectotype, AS VII 383 in collections at SSPHG, Cassian Formation; *a*, lateral view of basal skeleton of lectotype,  $\times 2$ ; *b*, spherulitic microstructure of basal skeleton,  $\times 950$  (Dieci, Russo, & Russo, 1974b, pl. 51–52).—FIG. 176*c–d*. *L. alpina* (KLIPSTEIN, 1845 in 1843–1845), holotype, S10462, NHM, Cassian Formation; *c*, lateral view,  $\times 4.4$ ; *d*, basal view showing basal layer,  $\times 4.4$  (Engeser & Taylor, 1989, p. 41).—FIG. 177*a–c*. *L.* sp., figured as *Calamopora* (?) *gnemidium* by KLIPSTEIN (1845 in 1843–1845, pl. 19, 15*b*), S10464 NHM, Cassian Formation; *a*, lateral view of specimen,  $\times 4.9$ ; *b*, SEM photograph of upper surface showing tubule shapes,  $\times 38$ ; *c*, tylostyle megasclere in tubule wall,  $\times 475$  (Engeser & Taylor, 1989, p. 44).

**Sclero-coelia** CUIF, 1974, p. 147 [*S. hispida*; OD; CUIF (1974) did not designate a holotype, nor paratypes; currently the specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN). DIECI and others (1977) studied one topotype specimen in the Zardini Collections, IPUM no. 19097]. Growth form laminar, compact, thick; delicate, arborescent



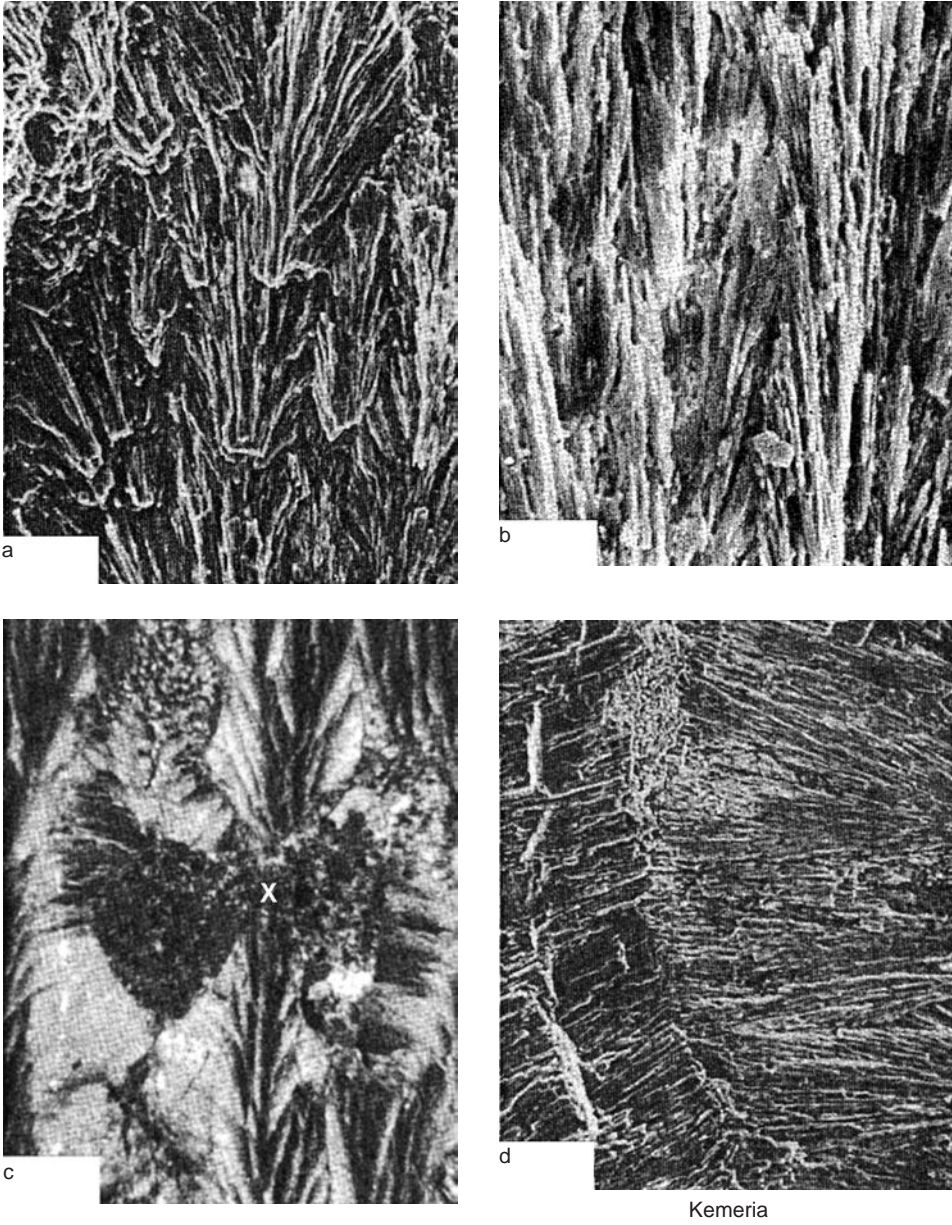
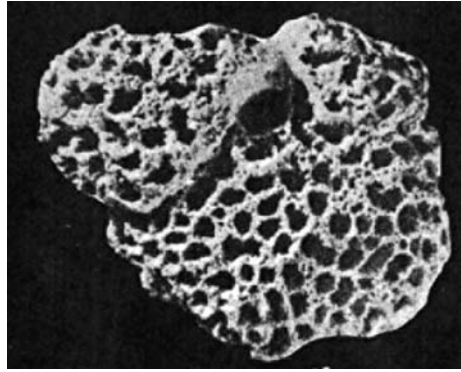


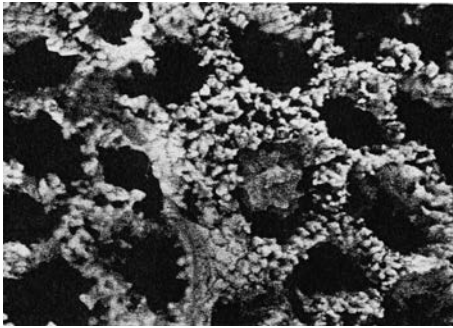
FIG. 174. Uncertain (p. 262).



a

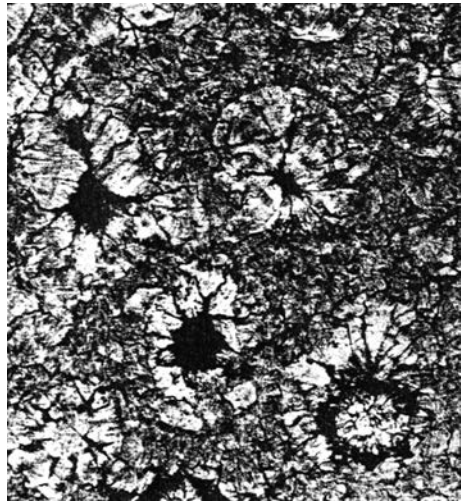


b

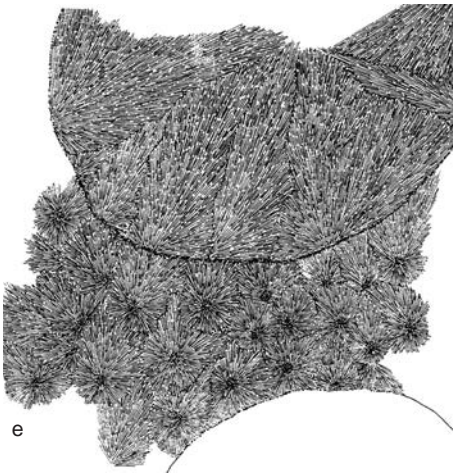


c

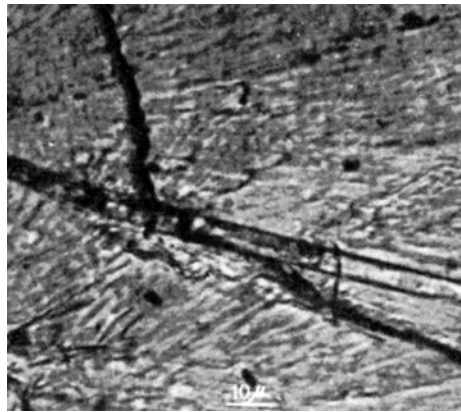
Keriocoelia



d



e



f

FIG. 175. Uncertain (p. 262–264).

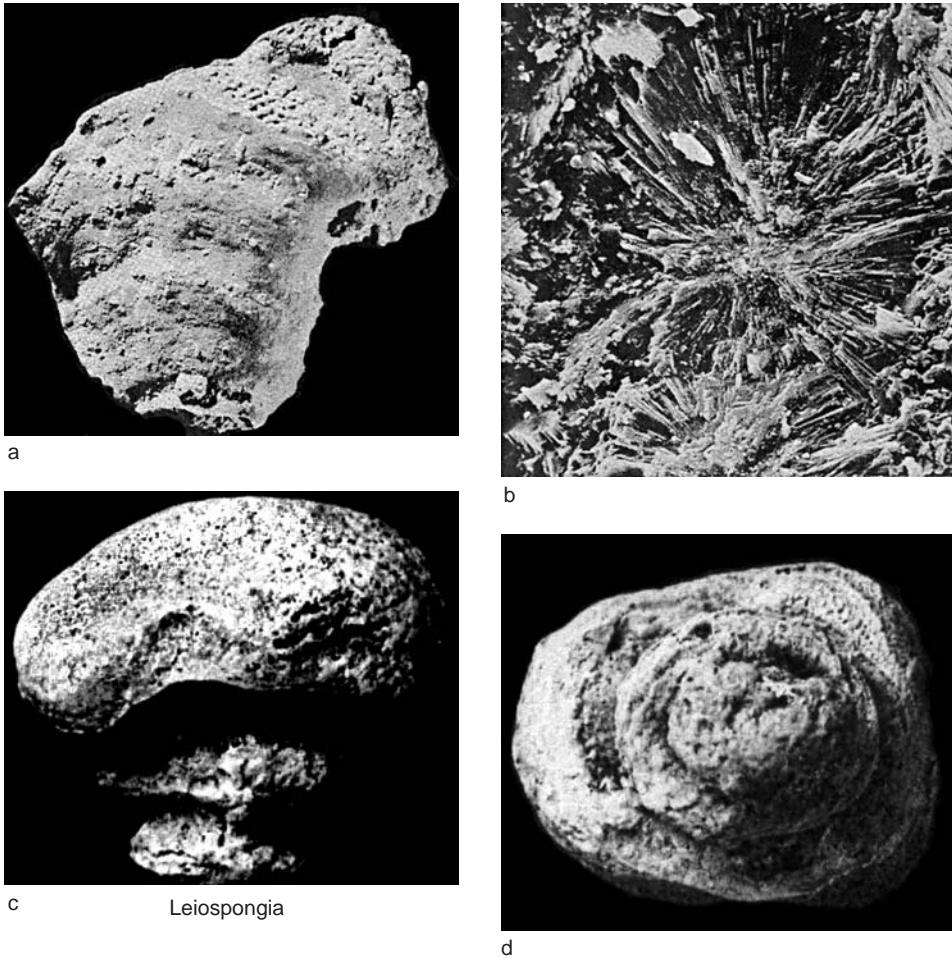
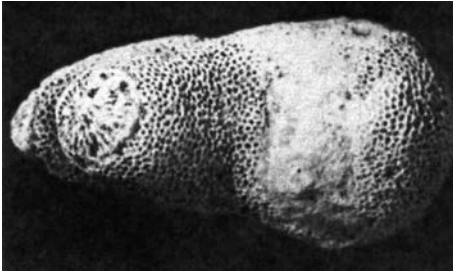


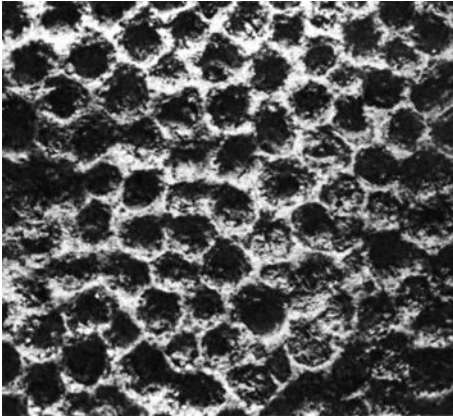
FIG. 176. Uncertain (p. 262–264).

calcareous processes on growing surface resulting in felted appearance; aragonitic penicillate, water-jet (fascicular fibrous) secondary microstructure filling tubules is continuous with primary aragonitic spherulitic microstructure of tubule walls; acanthostyle megascleres 45 to 77  $\mu\text{m}$  long, numerous; microscleres unknown (description modified from CUIF, 1974; DIECI & others, 1977; see also FINKS & RIGBY, 2004d, p. 600–601). *Triassic (Carnian)*: Italy.—FIG. 178a–d. \**S. hispida*, Cassian Formation, northern Italy; a, morphology of upper surface,  $\times 3$ ; b, detail of upper surface of vertical (tubule) walls,  $\times 44$ ; c, penicillate, water-jet (fascicular fibrous) secondary microstructure of topotype IPUM 19097,  $\times 450$  (Dieci & others, 1977, pl. 2);

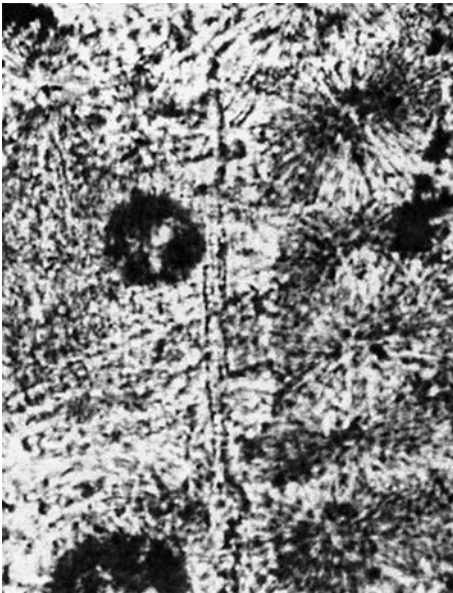
d, transverse section in transmitted polarized light of primary spherulitic microstructure that forms tubule walls,  $\times 115$  (Cuif, 1974, p. 148, pl. 30).—FIG. 179a–d. \**S. hispida*, Cassian Formation, northern Italy; a, detailed drawing of transverse section of spherules that form vertical processes (possible tubule walls), compare with view d,  $\times 60$  (Cuif, 1974, p. 148, fig. 4); b, pseudomorph acanthostyle megasclere in topotype IPUM 19097, oriented diagonally relative to crystalline fibers of basal skeleton,  $\times 2000$ ; c, pseudomorph acanthostyle megasclere in topotype, IPUM 19097, embedded in crystalline fibers of basal skeleton,  $\times 2000$  (Dieci & others, 1977, pl. 2, 1b, 1a); d, mold of part of an acanthostyle megasclere (fragment of spicule is visible



a



b



c

Leiospongia

FIG. 177. Uncertain (p. 264).

on left side of illustration) in topotype IPUM 19097,  $\times 2000$  (adapted from Dieci & others, 1977, pl. 2, 1c).

**Sobralispongia** SCHMID & WERNER, 2005, p. 655 [*S. densespiculata*; OD; holotype CSGP 4217]. Encrusting calcified agelasid with spicule framework of club-shaped styles and subtylostyles with plumose arrangement in vertical elements only; asterlike microscleres; primary calcareous skeleton dominated by radial elements of orthogonal or fascicular fibrous or irregular microstructure; meandroid surface features. *Upper Jurassic (lower Kimmeridgian)*: Portugal.—FIG. 180a–c. *\*S. densespiculata*, Sobral del Monte Agraco; a, longitudinal section, CSGP 4217,  $\times 6$ ; b, oblique section, light photomicrograph, holotype CSGP 4217,  $\times 9$ ; c, longitudinal section, light photomicrograph, specimen BSP 2003 IV 4d,  $\times 26$  (Schmid & Werner, 2005).

## Order HAPLOSCLERIDA Topsent, 1928

[*nom. correct.* DE LAUBENFELS, 1955, p. 37, *pro* Haplosclerina TOPSENT, 1928, p. 66] [=Nepheliospongia BERGQUIST, 1980, p. 4]

JEAN VACELET, PHILIPPE WILLENZ,  
and WILLARD D. HARTMAN

Demospongiae in which the main skeleton is partially or entirely composed of isodictyal, anisotropic, or isotropic, occasionally alveolate reticulation of spongin fibers and/or spicules, with uni- to multispicular tracts of diactinal spicules forming triangular, rectangular, or polygonal meshes. Megascleres are exclusively oxeote or strongylote, bonded together with collagenous spongin or closed within spongin fibers; microscleres, if present, may include sigmas and/or smooth toxas (both frequently centrangulate), microxeas or microstrongyles, and in one group amphidiscs (VAN SOEST & HOOPER, 2002b, p. 831); FINKS and RIGBY (2004a, p. 53) attributed the order Haplosclerida to TOPSENT, 1898, as follows: “*nom. correct.* DE LAUBENFELS, 1955, p. 37, *pro* Haplosclerina TOPSENT, 1898, p. 93;” however, Haplosclerina is not mentioned on p. 93 of TOPSENT, 1898; FINKS and RIGBY (2004a) also followed DE LAUBENFELS (1955, p. 37). *Carboniferous (Pennsylvanian)–Holocene.*

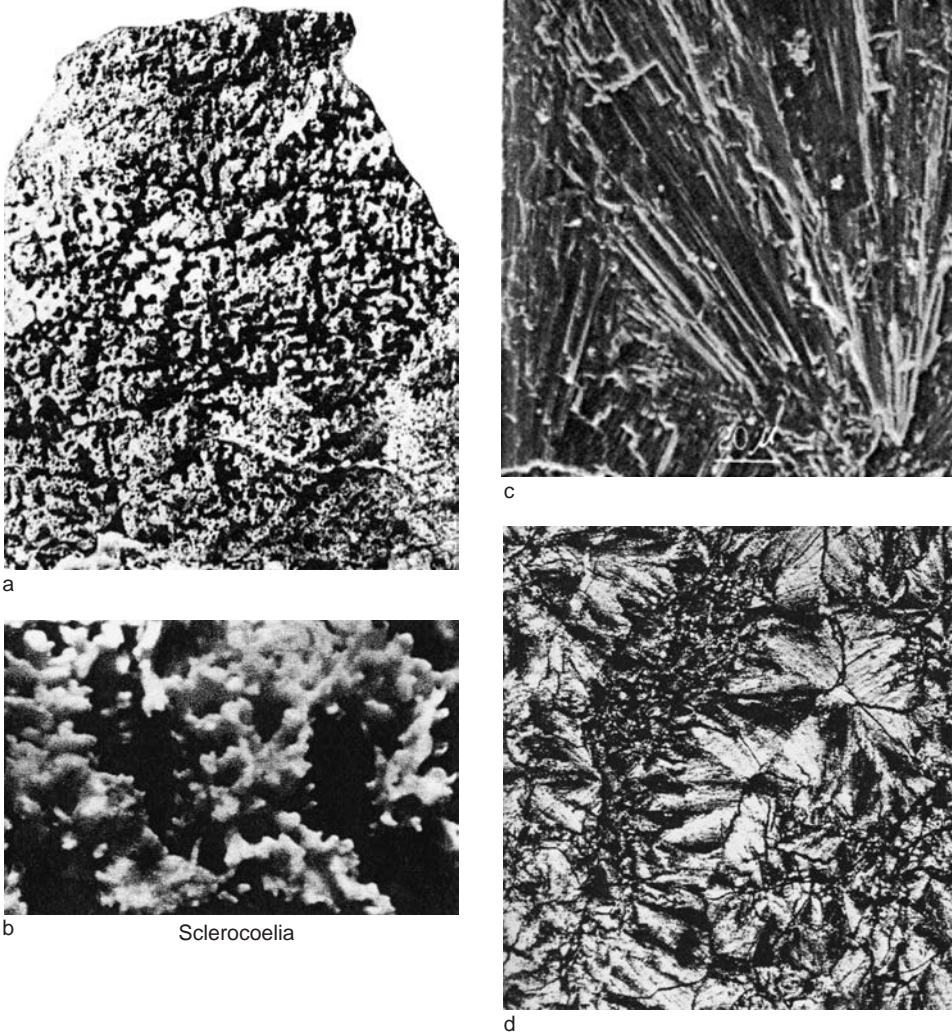


FIG. 178. Uncertain (p. 264–268).

**Family CALCIFIBROSPONGIIDAE**  
**Hartman, 1979**

[Calcifibrospongiidae HARTMAN, 1979, p. 473]

Semiglobular or flattened aragonitic masses covered by a thin veneer of organic tissue. Surface with evenly scattered, depressed oscules. Siliceous skeleton composed of a reticulation of thin strongyles. No ectosomal specialization.

Aragonitic basal skeleton consists of a meshwork of tubes, pillars, and lamellae that intergrade peripherally with spicular skeleton. Canal system penetrates aragonitic meshwork to a varying degree, depending on episodes of growth (VAN SOEST, 2002b, p. 918). *Holocene*.

*Calcifibrospongia* HARTMAN, 1979, p. 468 [*C. actinostromarioides*; M; holotype YPM no. 9114]. Description as for family. Type species mushroom

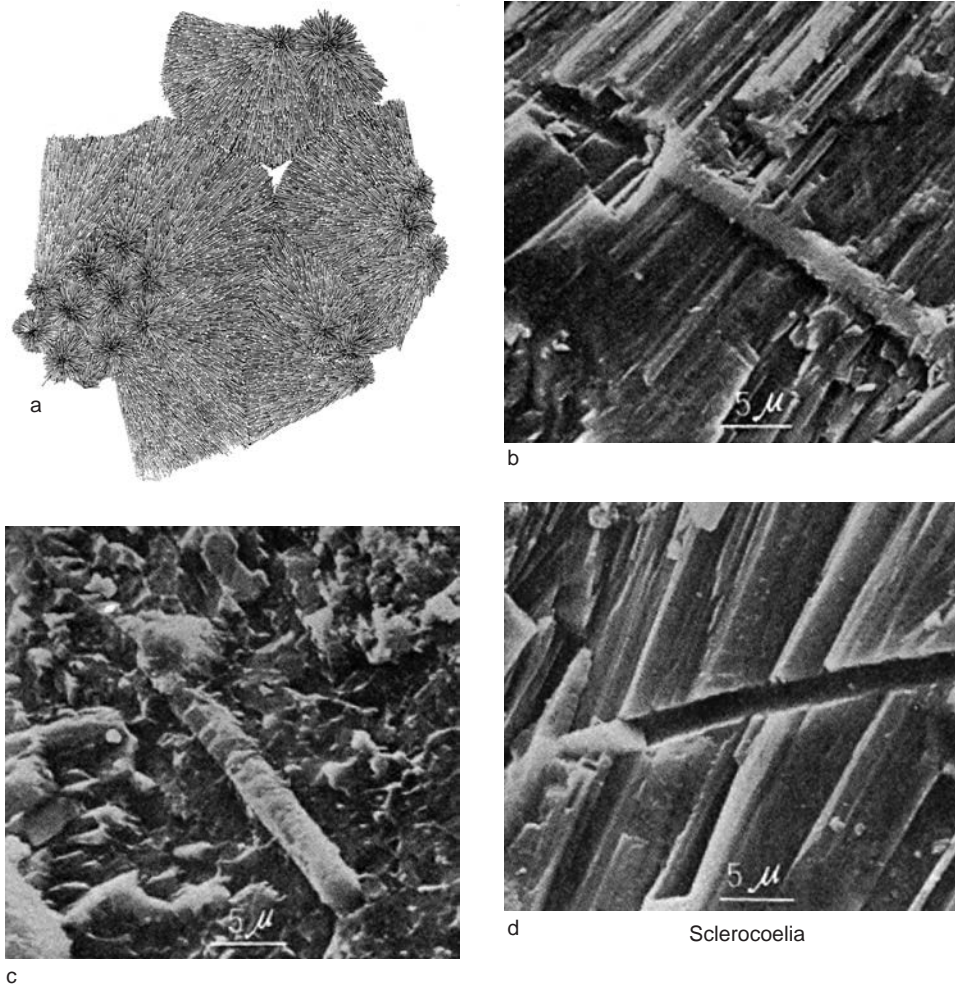


FIG. 179. Uncertain (p. 264–268).

shaped (smaller specimens), dome shaped to flattened with a broad base of attachment. Size up to 30 cm by 30 cm by 10 cm. Surface smooth when alive, provided with many evenly distributed, rounded, slightly depressed oscules, with a faint trace of astrorhizae. Color brownish tan or tannish orange alive. Soft parts—apart from the pinacoderm—entirely incorporated in basal calcareous skeleton. Calcareous skeleton is laid down

within the organic fibers that surround the tracts of siliceous spicules. Microstructure of aragonite is organized as acicular crystalline units with spherulitic or sclerodermite-like patterns. The inhalant canals lead into system of cavities of calcareous skeleton, and likewise exhalant canals run through calcareous mass over a considerable distance to end in vestibules immediately underneath pinacoderm. Ectosomal region is supported for a small distance by free

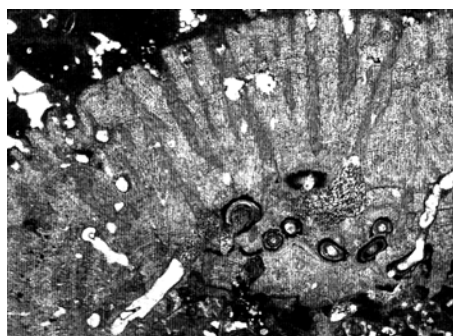
siliceous spicules arranged in a uni- or paucispicular isodictyal reticulation. In subectosomal region, spicule tracts, which are aligned in collagenous matrix, become focal points for calcification, and further down into sponge, spicules become entirely enclosed in calcium carbonate. Siliceous skeletal meshes and calcareous cavities match closely in size, smaller meshes varying from 55–175  $\mu\text{m}$  in diameter, many larger ones represented by various canals and tubes. Choanocyte chambers, about 20  $\mu\text{m}$  in diameter, and mesohyl tissues are found to a variable depth within calcareous basal mass and are rich in symbiotic prokaryotes. In larger specimens, a layer of 1.5–3 cm thick is alive, underneath which there are dead layers of similar thickness marking intervals of death and regeneration. Spicules are thin, gently curved strongyles, 130–210  $\mu\text{m}$  by 3–6  $\mu\text{m}$ . Both ends often produce numerous concentric additions. Epizoic zoanths grow on surface of some specimens, with polyps regularly spaced and isolated from sponge within an armored cyst laid down by sponge and reinforced with strongyles. Occurs in shaded, deep reef habitats (HARTMAN, 1979; WILLENZ & HARTMAN, 1994; VAN SOEST, 2002b). *Holocene*: Carribean (Bahamas).—FIG. 181*a-i*. \**C. actinostromarioides*, RBINSc-POR.061; *a*, underwater photograph of specimen about 30 cm by 60 cm, under an overhang at depth of 30 m on forereef wall south of Jamaica Bay, southern tip of Acklins Island, Bahamas, scale, 15 cm (see also Fig. 1.3); *b*, part of calcareous skeleton with large exhalant canal in center, and smaller exhalant canals entering main one laterally, scale bar, 2 mm; *c*, enlargement of surface of skeleton, with small round holes that are inhalant canals, scale, 500  $\mu\text{m}$ ; *d*, detail of aragonitic skeleton with protruding siliceous spicules, scale, 100  $\mu\text{m}$ ; *e*, pattern of siliceous spicules in exopinacoderm, scale, 200  $\mu\text{m}$ ; *f-i*, siliceous spicules with thin, slightly curved strongyle (*f*, scale, 50  $\mu\text{m}$ ); ends of strongyles with numerous concentric additions (*g-b*, scale, 5  $\mu\text{m}$ ); *i*, eroded strongyle as found enclosed in calcareous skeleton, showing a general surface pitting, scale, 2  $\mu\text{m}$  (West & others, 2013).

**Family EUZKADIELLIDAE**  
**Reitner, 1987**

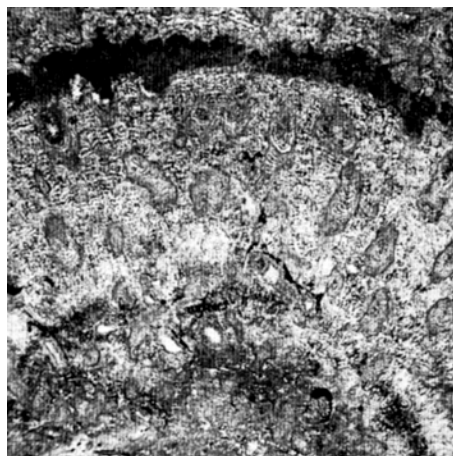
[Euzkadiellidae REITNER, 1987a, p. 204]

RACHEL A. WOOD and RONALD WEST

Calcified haplosclerids with a reticulate spicular skeleton and a spherulitic calcareous skeleton. *Lower Cretaceous*.

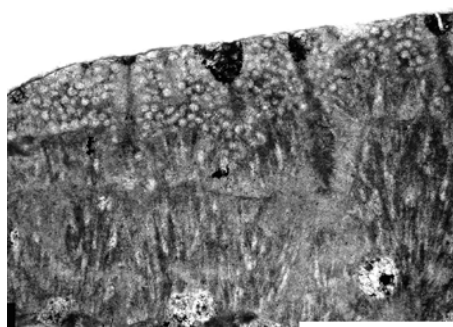


a



b

Sobralispongia



c

FIG. 180. Uncertain (p. 268).

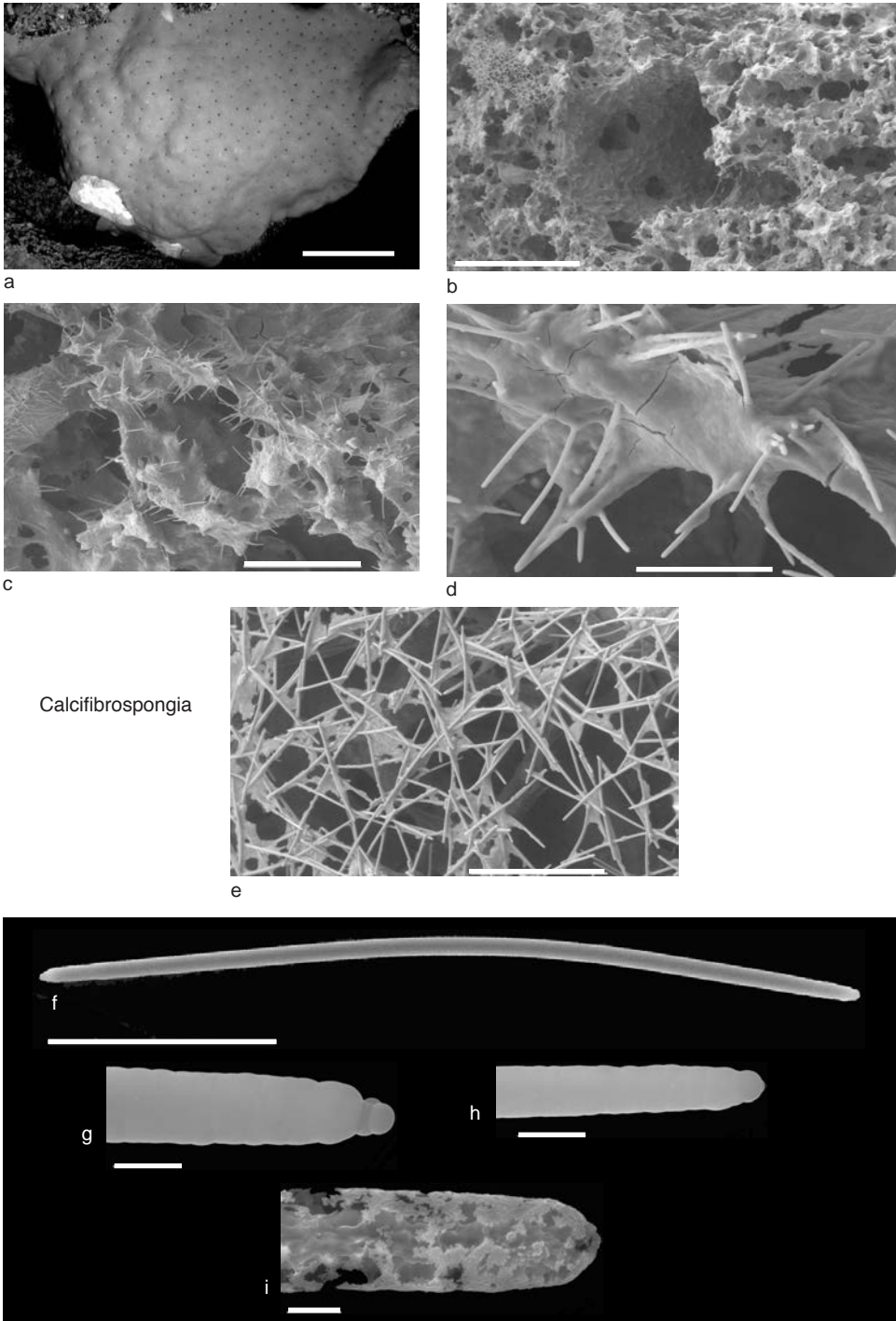


FIG. 181. Calcifibrospongiidae (p. 269–271).



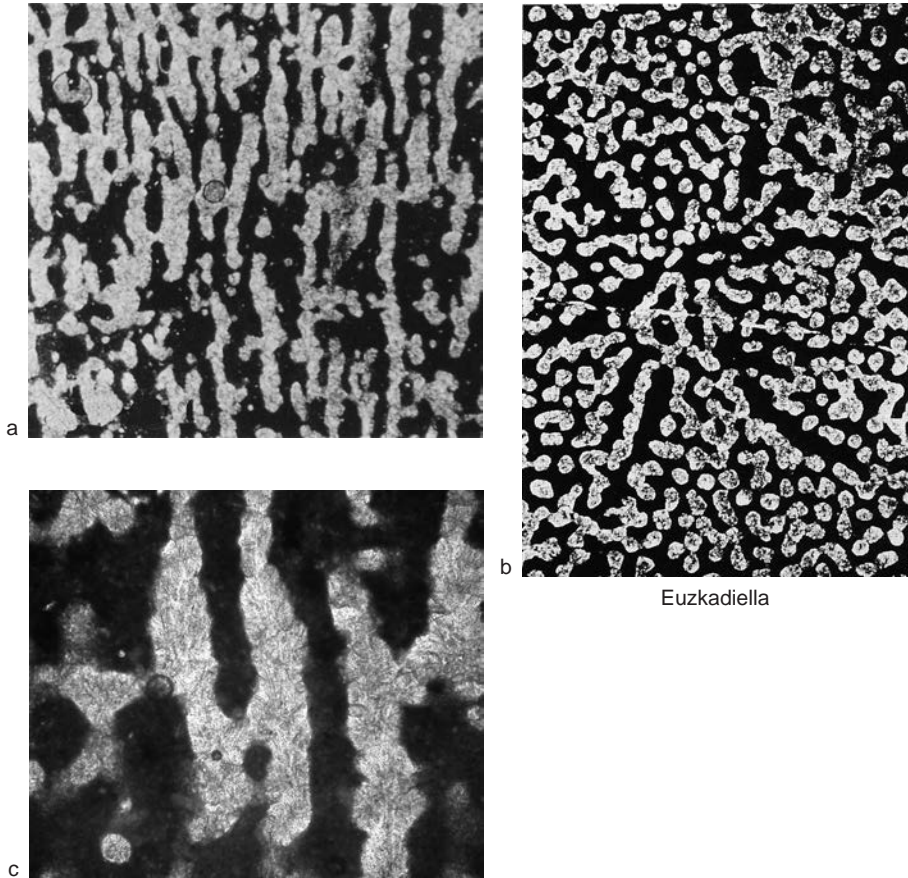


FIG. 182. Euzkadiellidae (p. 273).

**Euzkadiella** REITNER, 1987a, p. 204 [*\*E. erenoensis*; OD; holotype NHM H 5478a]. Plumose skeleton of large subtylostyles and oxes, as well as transversely arranged smaller strongyle spicules that form a reticulate pattern and astrorhizae; spherulitic calcareous skeleton. *Lower Cretaceous*: Spain.—FIG. 182a–c. *\*E. erenoensis*, light photomicrograph, NHM H 5478a, Ereño, Guipuzco Province; a, longitudinal section,  $\times 4$  (Reitner, 1987a, p. 207, fig. 3c); b, longitudinal section,  $\times 25$  (West & others, 2013); c, transverse section,  $\times 3$  (Reitner, 1987a, p. 207, fig. 3c).

#### Family NEWELLIDAE

Wood, Reitner, & West, 1989

[Newellidae WOOD, REITNER, & WEST, 1989, p. 86]

Calcified haplosclerids with a regular isodactyl arrangement of megascleres, with a secondary aragonitic skeleton. *Carboniferous* (*Middle Pennsylvanian*).

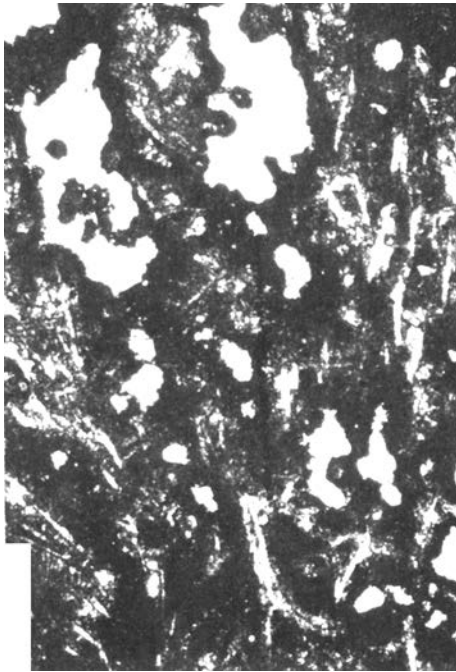
**Spongonewellia** ÖZDIKIMEN, 2009, p. 212, *nom. nov. pro Newellia* WOOD, REITNER, & WEST, 1989, p. 86, *non* ANDRÉ, 1962, arachnid [*\*Parallelopora mira* NEWELL, 1935, p. 341; OD; holotype, University of Kansas, KUMIP 58231]. Radial plumose styles, subtylostyles, and strongyles and transverse strongyles forming lateral connections. *Carboniferous* (*Middle Pennsylvanian*): USA (Kansas).—FIG. 183a–c. *\*S. mira* (NEWELL), longitudinal section, KUMIP 58231, Anderson County; a, light photomicrograph,  $\times 10$ ; b, SEM,  $\times 186$ ; c, SEM,  $\times 500$  (Wood, Reitner, & West, 1989, p. 88–89).

#### Order DICTYOCERATIDA Minchin, 1900

[*nom. correct.* BERGQUIST, 1978, p. 176, *pro* Dictyoceratina MINCHIN, 1900, p. 153]

JEAN VACELET

Demospongiae that have a spongin fiber skeleton constructed in an anastomosing



a



c

Spongonewellia



b

FIG. 183. Newellidae (p. 273).

plan. Choanocyte chambers are either diplodal or eurypylous. Larvae are incubated parenchymellae with a posterior ring or cap of long cilia. Also, chambered hypercalcified sponges (so-called Sphinctozoa) of the siphonate type that are devoid of fiber and

spicule skeleton, with aragonitic, porate external wall, may occur within the order. [Four families of the Dictyoceratida exhibit nonmineralized, nonspicular, horny (that is, keratose) members, including the well-known bath sponges (adapted from COOK &

BERGQUIST, 2002, p. 1021), with only one of these families (the family Dysideidae GRAY, 1867) being represented as having a fossil record: three of its listed genera range from the Jurassic to Holocene (see FINKS & RIGBY, 2004a, p. 44). Previously this order was defined as lacking a mineralized or spicule skeleton. However, the additional family added here, Vaceletiidae REITNER & ENGESER (1985, p. 163), is comprised of chambered hypercalcified sponges of siphonate type, having an aragonitic, porate external wall and lacking a fiber or spiculate skeleton. This family is referred to on the basis of the analyses of rDNA sequences, proving that its eponymous, monophyletic genus *Vaceletia* is a keratose demosponge (WÖRHEIDE, 2008, p. 433).] ?*Cretaceous, Eocene–Holocene.*

**Family VACELETIIDAE**  
**Reitner & Engeser, 1985**

[Vaceletiidae REITNER & ENGESER, 1985, p. 163]

Chambered Dictyoceratida with a calcified skeleton of the sphinctozoan siphonate type, with atrium of almost constant diameter and a special atrium wall. No secondary canal system in atrium wall. Spicule and fiber skeleton totally lacking. Chambers low, containing numerous vertical pillars. Exopores simple. Exowall, interwall, and endowall with the same pattern of perforation (description adapted from REITNER & ENGESER, 1985, and amended to accommodate this family as a keratose sponge; see WÖRHEIDE, 2008). ?*Cretaceous, Eocene–Holocene.*

Family Vaceletiidae was first recognized, based both in living and fossil forms as type genus *Vaceletia* PICKETT, 1982, and fossil (Eocene) genus, *Marinduqueia* YABE & SUGIYAMA, 1939, in the original conception of REITNER and ENGESER (1985, p. 163), as a member of the order Verticillitida TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977 (only included in part in the family Verticillitidae STEINMANN, 1882). However, other authors have treated the family Vaceletiidae as a junior synonym of family Verticillitidae STEINMANN, 1882, within the order Verticillitida TERMIER &

TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977 (see SENOWBARI-DARYAN, 1990, p. 48; and SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a, p. 1521), and subfamily Verticillitinae STEINMANN, 1882, of family Verticillitidae (see FINKS & RIGBY, 2004d, p. 712, and SENOWBARI-DARYAN & RIGBY, 2011, p. 70). Nine genera have been maintained in the subfamily, including the type genus *Verticillites* DEFRANCE, 1829, the living and fossil *Vaceletia*, and fossil *Marinduqueia* (see FINKS & RIGBY, 2004d, p. 712, and SENOWBARI-DARYAN & RIGBY, 2011, p. 70).

It should be noted that both orders Verticillitida TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977 (see SENOWBARI-DARYAN & GARCÍA-BELLIDO, 2002a, p. 1521, table 1) and Vaceletida RIGBY, 2004a (p. 4), 2004c (p. 691) that include family Verticillitidae STEINMANN, 1882, were validly constituted, though their overall family compositions are rather different. The order Vaceletida FINKS & RIGBY, 2004d, was given a broader conception, incorporating many more families and exhibiting more widely ranging stratigraphic records (e.g., Cambrian and Permian). The relationships of a number of these families, especially those containing Cambrian taxa, need to be further assessed. The order Verticillitida, with its narrower scope, should retain priority of usage.

The status of Vaceletiidae (following REITNER & ENGESER, 1985, p. 163) remains uncertain: whether it should be reinstated as an independent family and be transferred only with type genus *Vaceletia* and possibly *Marinduqueia* to the order Dictyoceratida; or whether the morphologically closely related genera (*Vaceletia* plus eight fossil genera) belonging to the subfamily Verticillitinae should all be transferred to the Dictyoceratida (see compilation of FINKS & RIGBY, 2004d, p. 712–719, and list in SENOWBARI-DARYAN & RIGBY, 2011, p. 70). Possibly future comparative work on the fossil taxa may help resolve the taxonomic relationships, for example, by intensive studies of the microstructures within their skeletons. However, for the

present, it seems best to transfer only the type genus *Vaceletia* (and possibly *Marinduqueia*) of the family Vaceletiidae to the order Dictyoceratida, and leave all the other genera still considered to be fossil sphinctozoans as verticillitid and verticillitid members of the order Verticillitida TERMIER & TERMIER in H. TERMIER, G. TERMIER, & VACHARD, 1977, as followed by FINKS and RIGBY (2004d) and SENOWBARI-DARYAN and RIGBY (2011).

**Vaceletia** PICKETT, 1982, p. 241, *nom. nov. pro Neocoelia* VACELET, 1977b, p. 509, *non* MCKELLAR, 1966 [*Neocoelia crypta* VACELET, 1977b, p. 509; OD; holotype, MNHN DJV39]. Cylindrical, solitary or irregularly branching, with chambered skeleton of siphonate type composed of an irregular arrangement of aragonite crystals. Spicules and spongin fibers absent. Inhalant openings in outer wall of porate type, with simple exopores provided with spines extending toward center of aperture. Exowall, interwall, and endowall with same pattern of perforation. Exhalant canal siphonate, sometimes with longitudinal dividing wall. Regular, pillar-like filling structures in chambers. Earlier chambers filled in by calcareous deposit, which also partly or wholly covers surface of basal part of skeleton. [The type species is cylindrical, with irregular swellings and constrictions marking successive chambers, solitary or irregularly branching. Living part 5–9 mm high and 3 mm in diameter. Dead bases of the same diameter, with a variable development, often covered by a thin epitheca and filled in with a secondary deposit. Color of living tissue grey in life, and in alcohol, skeleton white. Skeleton of living part made of series of thin-walled, crescent-shaped chambers, 0.6 mm high near center, traversed by cylindrical central canal (siphon or atrium), 0.7–0.9 mm in diameter, with proper wall. Dome-shaped walls of chamber supported by regular pillars, 40–50  $\mu$ m in diameter, perpendicular to wall and regularly spaced. Walls from chamber and atrium all 50  $\mu$ m thick, bearing apertures regularly arranged, 100  $\mu$ m in diameter, with variable number of short radial spines. Spicules and spongin fibers absent, both in skeleton and in living tissue. Living tissue located inside chambers, except thin pinacoderm lying on surface of outer wall and bearing ostia. Osculum apical, 0.5–0.8 mm in diameter. Ostia 25–50  $\mu$ m in diameter, unique in center of each aperture of outer chamber wall. Choanocyte chambers aphodal, 40–45  $\mu$ m in diameter, with short aphodus. Tissue containing a high density of morphologically diverse intercellular bacteria. Microstructure of skeleton microgranular, consisting of a feltwork of aragonite crystals organized into nodules with noncalcified center (GAUTRET, 1985). Skeleton secreted as an organic template that is subsequently mineralized (VACELET, 1979b; REITNER & WÖRHEIDE, 2002). Reproduction viviparous, by incubated parenchymella. Large distribution throughout Indo-West Pacific area, in semi-closed cavities of coral reef-front caves and bathyal environments, 10–530 m depth.

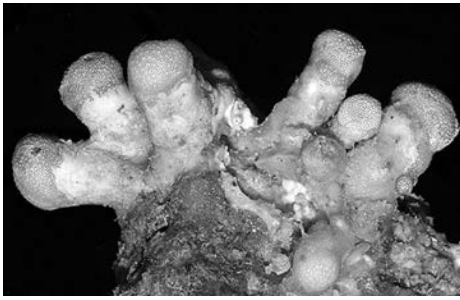
Only a single Recent species, the type *V. crypta*, has been described. However, in bathyal environments and in some reef caves, this sponge may have a branching, colonial mode of growth, enabling it to build large aggregates up to 30 cm in diameter and probably more (VACELET & others, 1992; WÖRHEIDE & REITNER, 1996), thus retaining the building capabilities of its fossil counterparts. The skeleton is more heavily calcified, with thicker pillars and chamber walls, with a longitudinal wall dividing the central canal. These variations, as well as others presently undescribed, may either be specific, meaning that there are several species of living sphinctozoans, or may indicate a large morphological plasticity, which could have implications for interpretation of fossil species. The fossil record includes two species, *V. progenitor* PICKETT, 1982, and *V. faxensis* (RAVN, 1899), respectively, from the Eocene of Australia and Denmark (CLAUSEN, 1982; PICKETT, 1982), and a doubtful species from the Campanian of Spain (REITNER, 1992). In the absence of spicules and a fibrous skeleton, the affinities of *Vaceletia* in terms of other extant orders of Demospongiae remain uncertain. However, recent results of molecular taxonomy indicate an affinity with keratose sponges of the order Dictyoceratida (LAVROV, WANG, & KELLY, 2008; WÖRHEIDE, 2008), while some spiculate fossil representatives of order Verticillitida suggest an uncertain affinity with Haplosclerida (REITNER & WÖRHEIDE, 2002). The genus *Vaceletia* is here classified in family Vaceletiidae, as suggested by WÖRHEIDE (2008). The family is here classified in Dictyoceratida, with a tentative redefinition of the order. At this time it cannot be determined whether other fossil members of the former Verticillitida are possibly comparable to keratose sponges or distinct from this group.] ?*Cretaceous, Eocene–Holocene*: Spain, ?*Cretaceous*; Western Australia, *Eocene*; tropical Indo-West Pacific, *Holocene*.—FIG. 184a–f. \**V. crypta* (VACELET); a, view of specimens from cavities of front coral reef, New Caledonia, 15 m water depth,  $\times 1.6$  (West & others, 2013); b, fragment of an aggregate built by colonial, bathyal form, Norfolk Ridge, 250 m,  $\times 0.6$  (West & others, 2013); c, SEM view of vertical section of skeleton, with dead bases bored by a *Thoosa* sp., New Caledonia, 25 m,  $\times 12.5$  (West & others, 2013); d, SEM view of surface of skeleton, partially covered by epitheca, Norfolk Ridge, 250 m,  $\times 127$  (West & others, 2013); e, section through skeleton and living tissue, Great Barrier Reef, 10 m,  $\times 80$  (West & others, 2013); f, section through skeleton and living tissue of growing specimen, showing skeleton, with template of new chamber (top) and living tissue,  $\times 60$  (Vacelet, 1979b).

## Order UNCERTAIN Family BURGUNDIIDAE Dehorne, 1920

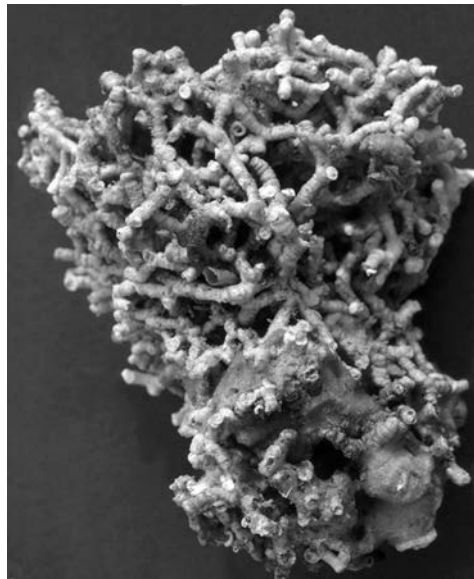
RACHEL A. WOOD

[*nom. correct.* HUDSON, 1954b, p. 48, *pro* Burgundides DEHORNE, 1920, p. 69]

Possible aspiculate calcified demosponges with a fibrous microstructure and concentric

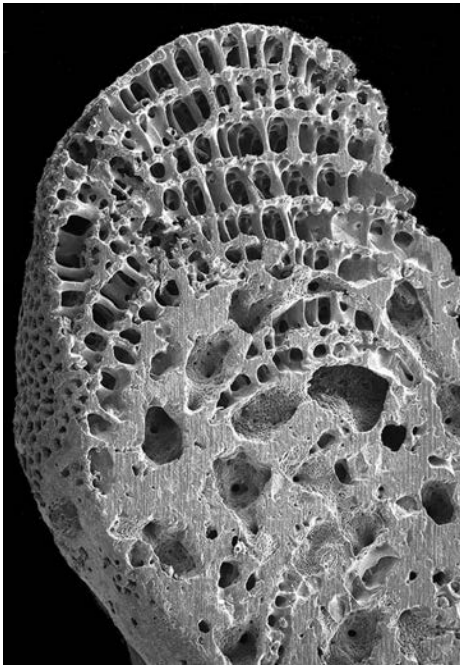


a

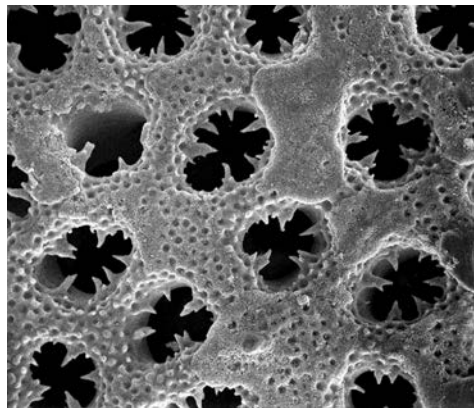


b

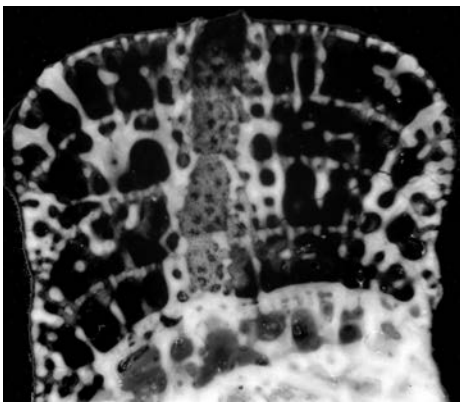
Vaceletia



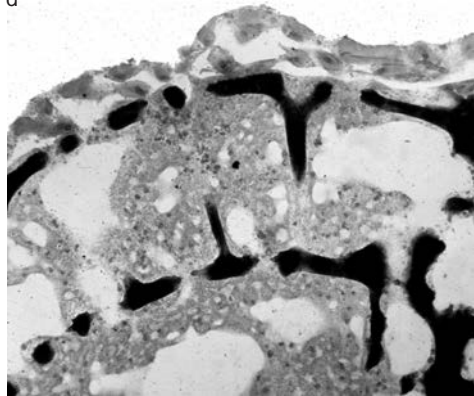
c



d



e



f

FIG. 184. Vaceletiidae (p. 276).

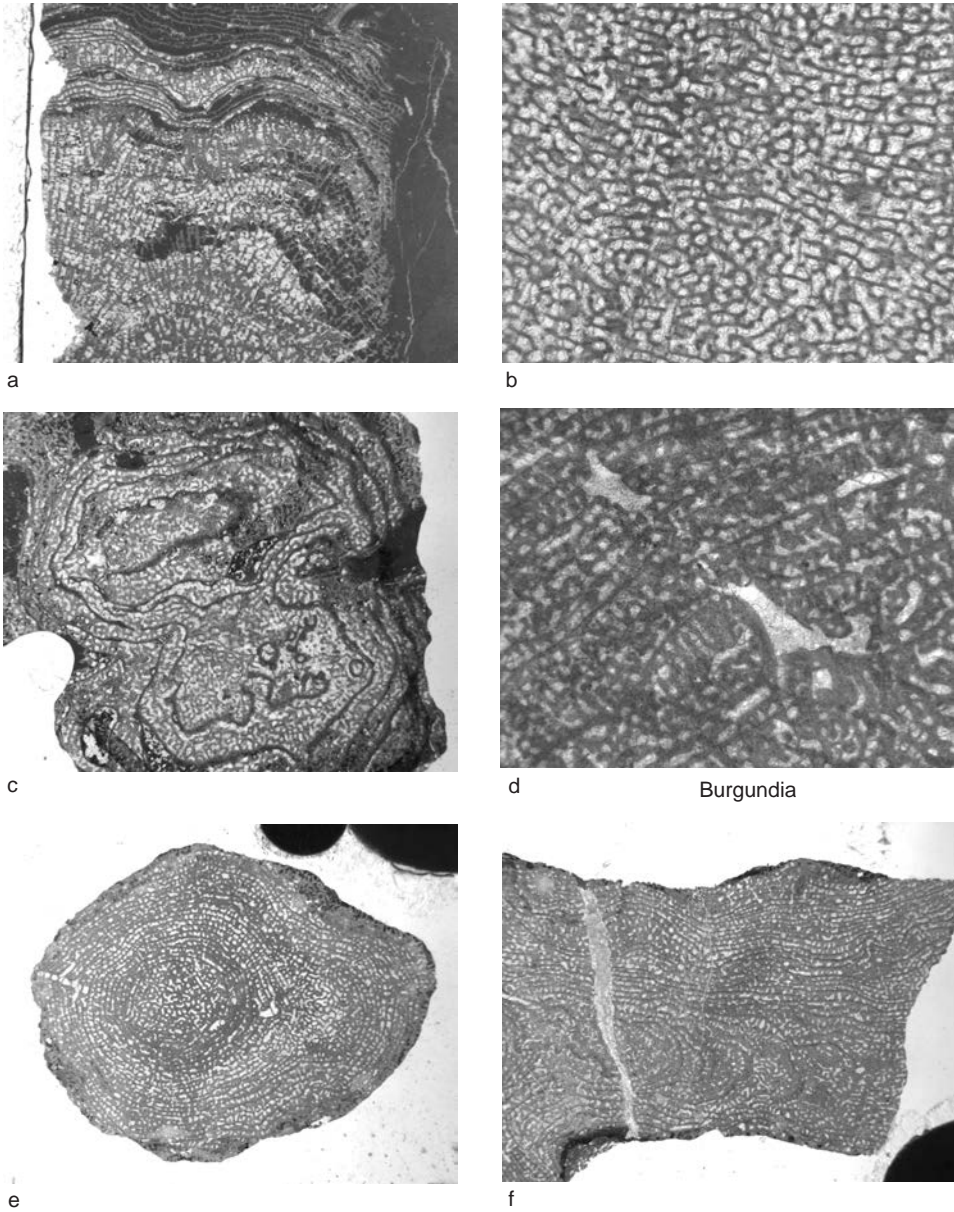


FIG. 185. Burgundiidae (p. 278–281).

perforated laminae. Aquiferous system may or may not bear tabulate oscula and astrophorae. *Upper Jurassic–Lower Cretaceous.*

**Burgundia** DEHORNE, 1916, p. 430 [*B. trinorchii* DEHORNE, 1916, p. 431; OD; holotype, Geological Laboratory Sorbonne, fig. 1, collection of Munier-Chalmas; = *Circoporella semiclastrata* HAYASAKA, 1917, p. 58; = *Plassenia alpine* YABE & SUGIYAMA,

1931a, p. 113; = *Burgundia semiclastrata* HAYASAKA, 1917, p. 56; STEINER, 1932, p. 184; = *Burgundia* cf. *semiclastrata* HAYASAKA, 1917, p. 56; KELLAWAY & SMITH, 1938, pl. 21, 5; = *Circoporella semiclastrata* HAYASAKA, 1917, p. 56; YABE & SUGIYAMA, 1941a, p. 39; = *Burgundia barremensis* YAVORSKY, 1957, p. 27; ? = *Burgundia alpina* YABE & SUGIYAMA, 1931a, p. 113; FENNINGER & HOTZL, 1965, p. 39] [? = *Stromatoporidaum* VINASSA DE REGNY, 1915,

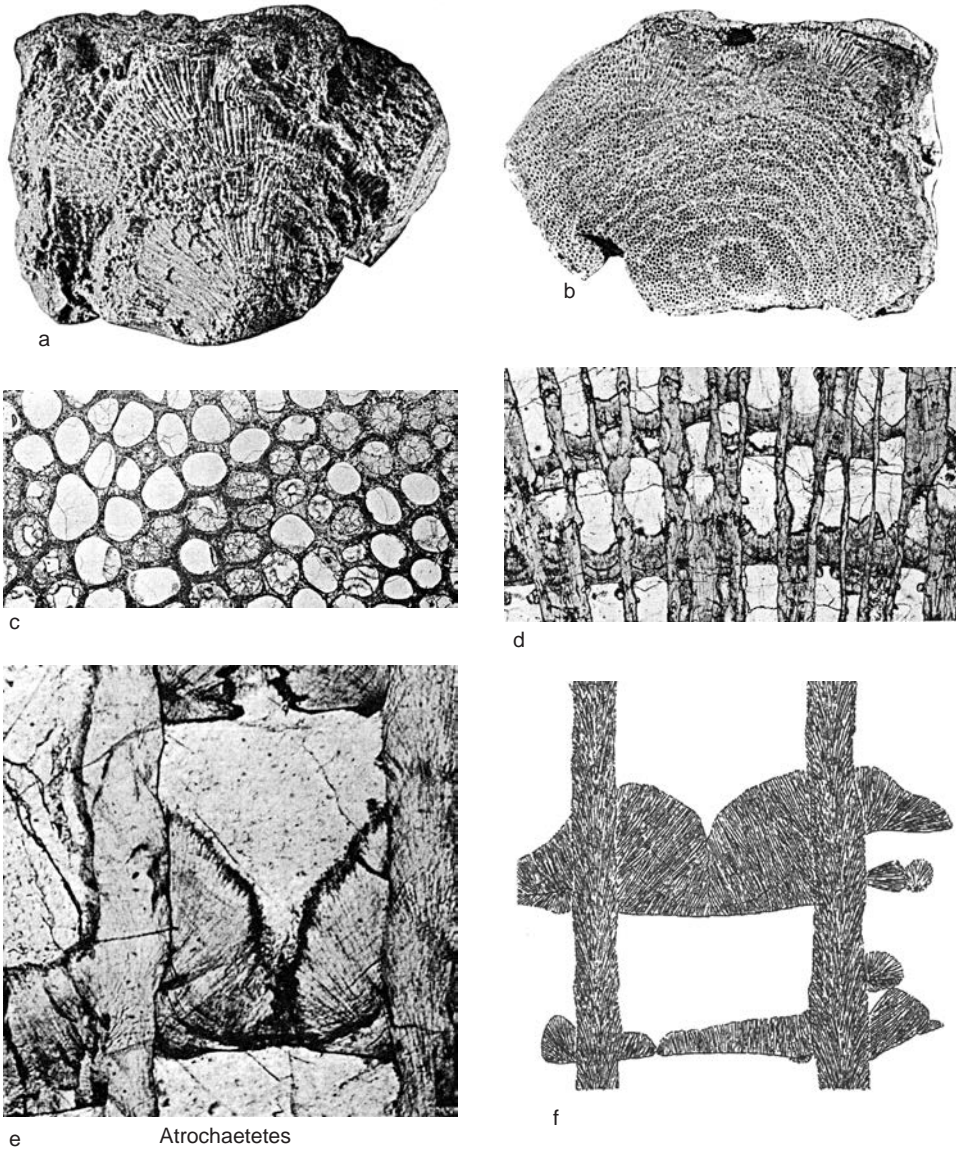
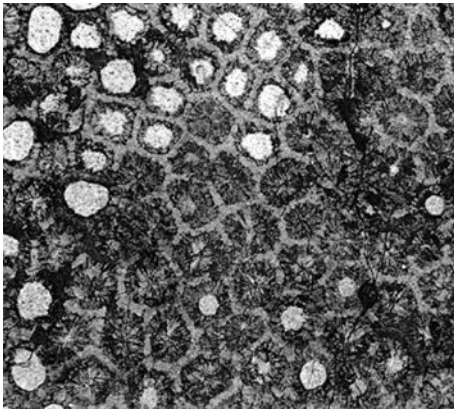


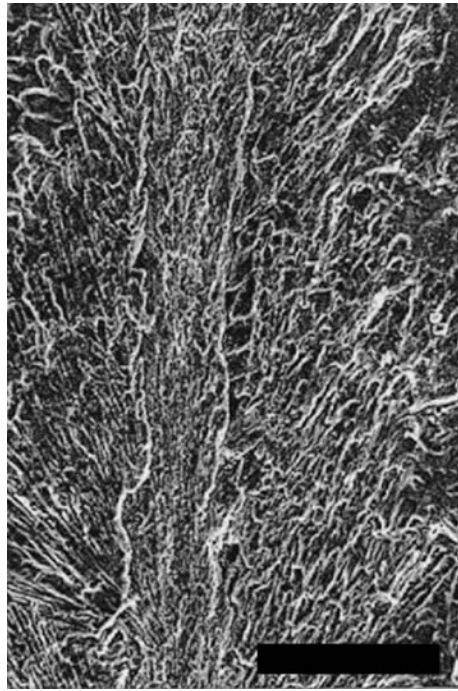
FIG. 186. Uncertain (p. 281–283).

p. 108 (type, *S. globosum*, OD); =*Circoporella* HAYASAKA, 1917, p. 57 (type, *C. semiclatharata*, OD); =*Plassenia* YABE & SUGIYAMA, 1931a, p. 113 (type, *P. alpina*, OD); =*Bekhmeia* HUDSON, 1954b, p. 48 (type, *B. wetzeli* HUDSON, 1954b, p. 49, OD)]. Burgundiid with ability to produce tabulae. Microstructure ranging from orthogonal to fascicular fibrous. Massive, nodular or dendroid gross morphology. Aquiferous units may possess tabulate oscula and/or astrophorizae (see WOOD,

1987). Type species is massive or nodular with vertical elements of 40–70  $\mu\text{m}$  diameter; holotype from Portlandian, Upper Jurassic, Saone et Loire, Vers, France; type species distributed through upper Oxfordian–Hauterivian, France, Spain, Russia, and Japan. Another species, *B. ramosa* PFENDER, 1937, p. 133, has a coarse reticulum or normally short-branched vertical elements (pillars) of 50–90  $\mu\text{m}$  diameter but no axial reticulum; synonyms are as follows: =*Burgundia ramosa* PFENDER, 1937,



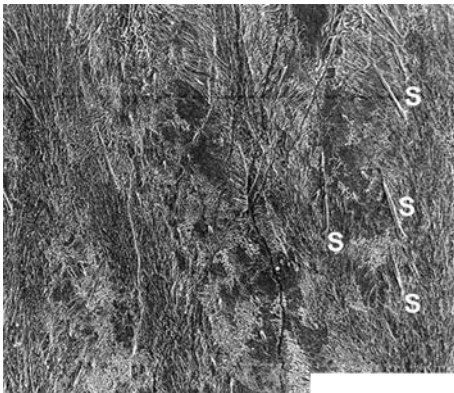
a



d



b



c

*Atrochaetetes*



e

FIG. 187. Uncertain (p. 281–283).



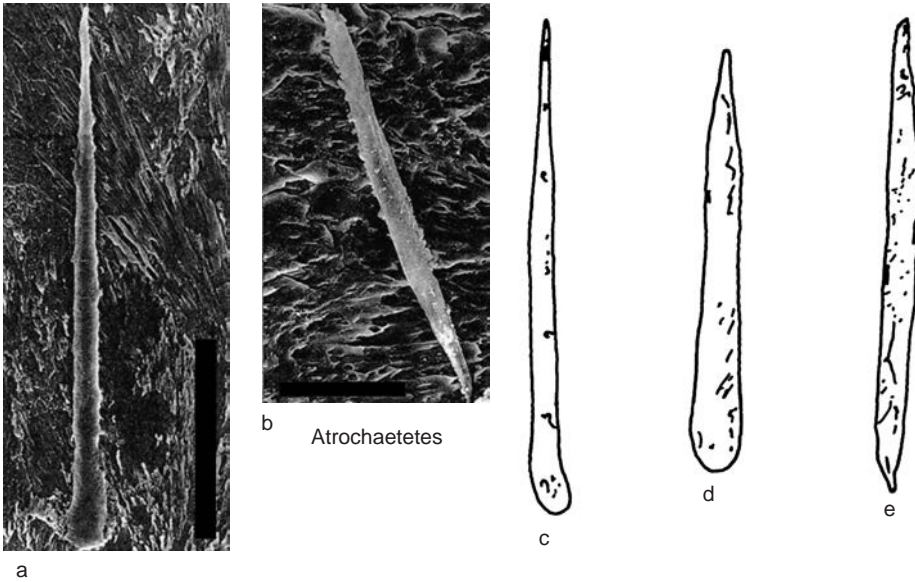


FIG. 188. Uncertain (p. 281–283).

p. 133; =*Burgundia campanae* PFENDER, 1937, p. 135; =*Burgundia steinerae* HUDSON, 1955c, p. 228; FENNINGER, FLÜGEL, & HÖTZL, 1963, p. 235; =*Burgundia steinerae* HUDSON, 1955c, p. 228; FENNINGER & HÖTZL, 1965, p. 40; =*Burgundia mammelonata* FENNINGER & HÖTZL, 1965, p. 40; =*Burgundia semiclastrata* (HAYASAKA, 1917, p. 57); TURNŠEK & MASSE, 1973, p. 237; =*Burgundia massiliensis* TURNŠEK & MASSE, 1973, p. 237; =*Burgundia steinerae* HUDSON, 1955c, p. 228; DONG & WANG, 1983, p. 417; this species extends from upper Oxfordian–Hauterivian, France, Spain, Syria, Iraq, and China. A third species, *B. wetzeli* (HUDSON, 1954b, p. 49), is a nodular or dendroid *Burgundia* with an axial nonlaminar reticulum formed of tubules, and an outer laminate reticulum with simple unbranched pillars limited to one interlaminar space; and stacked astrophorals systems with tabulate oscula; synonyms are as follows: =*Bekmeia wetzeli* HUDSON, 1954b, p. 49; =*Burgundia wetzeli* HUDSON, 1954b, p. 48; =*Burgundia wetzeli* TURNŠEK & MASSE, 1973, p. 223; it occurs in the Hauterivian, France, Spain, and Iraq. *Upper Jurassic–Lower Cretaceous*: France, Spain, Syria, Iraq, Yemen, China, Russia, Japan.—FIG. 185a–b. \**B. trinorchii*, light photomicrograph, Portlandian, Villereouse, France; a, longitudinal section, NHM no. 4044,  $\times 15$ ; b, transverse section, NHM no. 3594,  $\times 20$  (West & others, 2013).—FIG. 185c–d. *B. ramosa* PFENDER, light photomicro-

graph, upper Oxfordian, Wadi Leeben, Sharwain Range, Qishn, Yemen; c, transverse section, NHM no. H 4615 a,  $\times 15$ ; d, upper Hauterivian, Cretaceous, La Mounine, Marseille, France; longitudinal section, NHM no. H 5486,  $\times 30$  (West & others, 2013).—FIG. 185e–f. *B. wetzeli* (HUDSON), light photomicrograph, Hauterivian, Bekhme Gorge, Iraq; e, transverse section, NHM no. 4428 b, part of holotype,  $\times 3$ ; f, longitudinal section, NHM no. 4431,  $\times 3$  (West & others, 2013).

### Family UNCERTAIN

RONALD R. WEST

*Atrochaetetes* CUIF & FISCHER, 1974, p. 7 [\**A. tamnifer* CUIF & FISCHER, 1974, p. 8, fig. 2; pl. I, 1; pl. II, 1–3; pl. IV, 4–5; OD; specimen is illustrated as holotype (unnumbered), and although not specified, it is assumed that specimen(s) are in the J.-P. Cuif Collection, Laboratoire de Pétrologie sédimentaire et Paléontologie, Université Paris XI, Orsay, Paris (it is expected that this material will later be transferred to the Institut de Paléontologie, MNHN)]. Growth form domical to conical; tubules irregular polygons in transverse section; tubules continuous, subparallel in longitudinal section; tubulae subhorizontal, commonly thickened by fan-shaped deposit extending into tubules at junction of tabulae and tubule walls; penicillate aragonitic microstructure; tubules

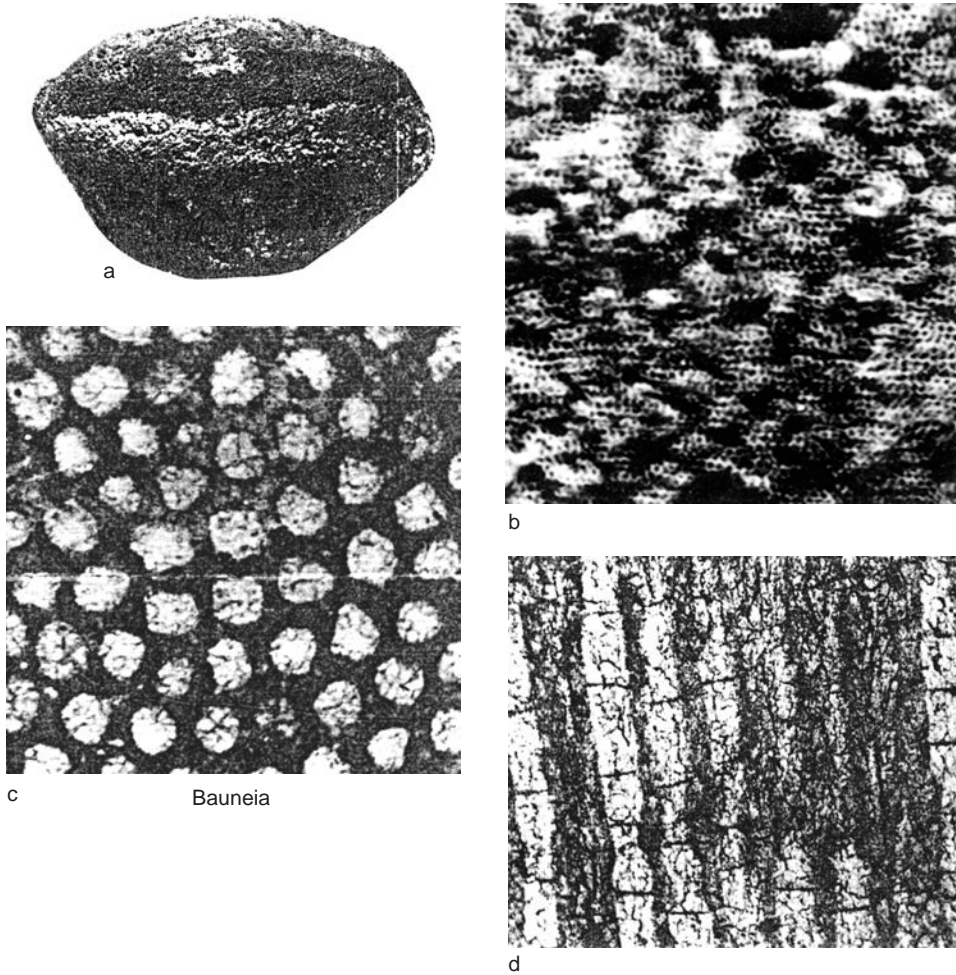


FIG. 189. Uncertain (p. 283–284).

increase commonly by intertubular budding, rarely longitudinal fission. Spicules and/or spicule pseudomorphs unknown from type species, but spicule pseudomorphs and additional information on the microstructure from three specimens of *A. alakirensis* CUIF & FISCHER (1974, p. 9–10) from the same stratigraphic and geographic locality as *A. tamnifer* are reported by CREMER (1995). *A. alakirensis*: growth form domical to conical with distinct growth bands associated with quasi-tabulae where tufts of crystal fibers (secondary wall) merge; true tabulae unknown; tubules polygonal to circular in transverse section of variable size; tubules long, subparallel in longitudinal section; aragonite inferred original mineralogy; primary tubule wall microstructure penicillate, water-jet (fascicular fibrous); secondary wall tufts of crystal fibers attached to primary tubule walls; tubules

increase by intertubular budding and longitudinal fission; calcite monaxon tylostyle megasclere pseudomorphs in secondary wall, some attached to primary tubule wall, extending (pointed ends) into tubules; three types of monaxon tylostyle megascleres (2.4–15  $\mu\text{m}$  wide and 53–292  $\mu\text{m}$  long): short, thick (53–97  $\mu\text{m}$  long), long, slender (110–292  $\mu\text{m}$ ), and rare oxes (58–80  $\mu\text{m}$  long); microscleres unknown (CREMER, 1995, p. 166–170). *Upper Triassic (Carnian)–Upper Jurassic, ?Lower Cretaceous*: Turkey (Anatolia Region), *Carnian–Norian*; northwestern Turkey, *Upper Jurassic, ?Lower Cretaceous*.—FIG. 186a–f. \**A. tamnifer*, Carnian, Triassic, Turkey, all images are from unnumbered holotype in the J. P. Cuiif collection; *a*, lateral view of basal skeleton,  $\times 0.8$ ; *b*, polished surface of basal skeleton,  $\times 0.85$ ; *c*, transverse section,  $\times 9$ ; *d*, longitudinal section,  $\times 7.5$ ; *e*, longitudinal section

showing microstructure and fan-shaped deposits at junction of tabulae and tubule walls,  $\times 52$ ; *f*, detailed drawing of microstructure of tubule walls and fibroradial deposits associated with some tabulae, compare with view *e*,  $\times 55$  (Cuif & Fischer, 1974, pl. I, fig. 1–2, *d, e*; pl. II, fig. 1, *c*; pl. IV, fig. 4–5, *a, b*; ).—FIG. 187*a–e*. *A. alakirensis* CUIF & FISCHER, Carnian–Norian, Anatalya Region, Turkey, Paleontological Institute, University of Erlangen–Nurnberg (IPE); *a*, transverse section of generally polygonal tubules, secondary walls (darker color) increase thickness of tubule walls, specimen 19F40,  $\times 21$ ; *b*, primary (light colored) and secondary (darker colored) tubule walls in longitudinal section, specimen 19F40,  $\times 17.6$ ; *c*, longitudinal section showing penicillate, water-jet (fascicular fibrous) microstructure and megascleres in secondary walls (*white S*), specimen 19F40,  $\times 80$ ; *d*, longitudinal section of primary (center) and secondary (both sides) tubule walls, specimen 19F40,  $\times 317$ ; *e*, longitudinal section of calcification centers of two areas in secondary tubule wall (tufts of crystal fibers), specimen 19F43,  $\times 800$  (Cremer, 1995, p. 168, pl. 25).—FIG. 188*a–e*. *A. alakirensis* CUIF & FISCHER, Carnian–Norian, Anatalya Region, Turkey, Paleontological Institute, University of Erlangen–Nurnberg (IPE); *a*, typical tylostyle megasclere with knoblike rounded end, specimen 19F40,  $\times 567$ ; *b*, less common are oxea megasclere, pointed at both ends, specimen 19F43,  $\times 900$ ; *c–e*, diagrammatic sketches of three types of megascleres observed in this species, *c*,  $\times 500$ , *d*,  $\times 750$ , *e*,  $\times 1000$  (Cremer, 1995, p. 168, pl. 25).

**Bauneia** PETERHANS, 1927, p. 389 [*Monotrypa multitalulata* DENINGER, 1906, p. 63; M; Deninger Collection, University of Freiburg, Germany; = *Chaetetes capri* ANGELIS D'OSSAT, 1905, p. 12, *vide* FISCHER, 1970, p. 176, Royal Geological Museums (Rome or Naples)] [?= *Pseudomonotrypa* RESHETKIN, 1926, p. 7, for two or more species from the Crimean Jurassic; see also YAVORSKY, 1947, p. 22; FISCHER (1970, p. 174) stated that no type species had been chosen, *vide* HILL, 1981, p. 519]. Growth form globular, nodular; tubules on upper surface felted, irregular polygons in transverse section; tubules long, subparallel in longitudinal section, divided by thin, irregularly spaced, subhorizontal tabulae; tubules increase by intertubular budding and longitudinal fission; penicillate, water-jet (fascicular fibrous) microstructure. [Spicules and/or spicule pseudomorphs are unknown in the type species, but CREMER (1995, p. 172–173) provided the following information on the spicules and the inferred aragonitic microstructure of a single specimen identified as ?*Bauneia* sp.: tubules sub-polygonal to elliptical in transverse section; tubules increase by intertubular budding; microstructure of primary and secondary tubule walls penicillate, water-jet (fascicular fibrous) with secondary wall commonly filling tubules; calcite monaxon tylostyle megasclere pseudomorphs (82–140  $\mu\text{m}$  long, 7–11  $\mu\text{m}$  wide) without preferred arrangement in primary and secondary wall, most attached

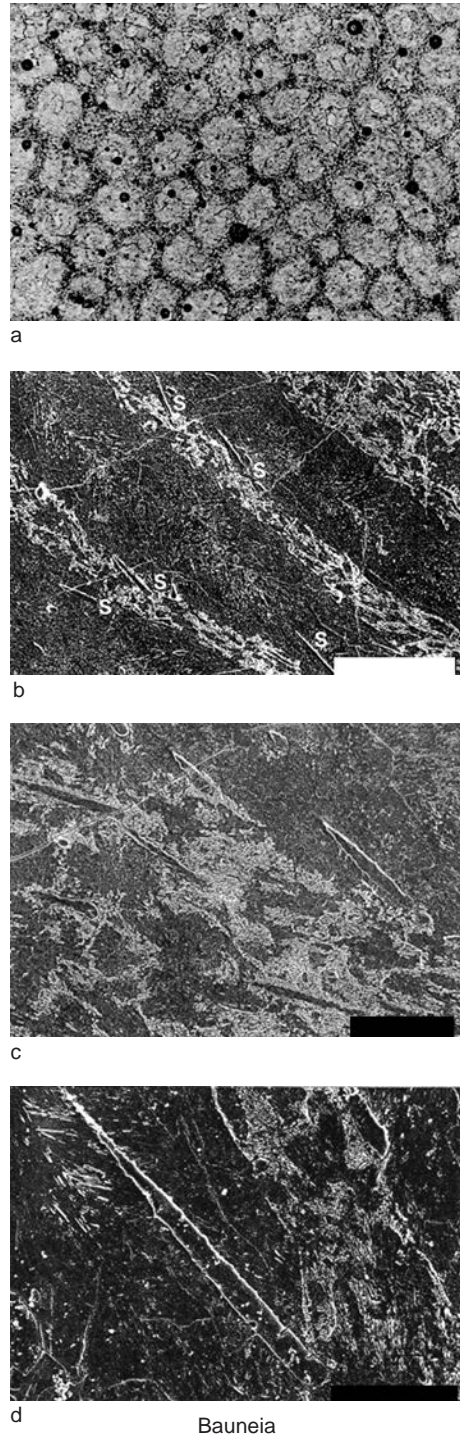


FIG. 190. Uncertain (p. 283–284).

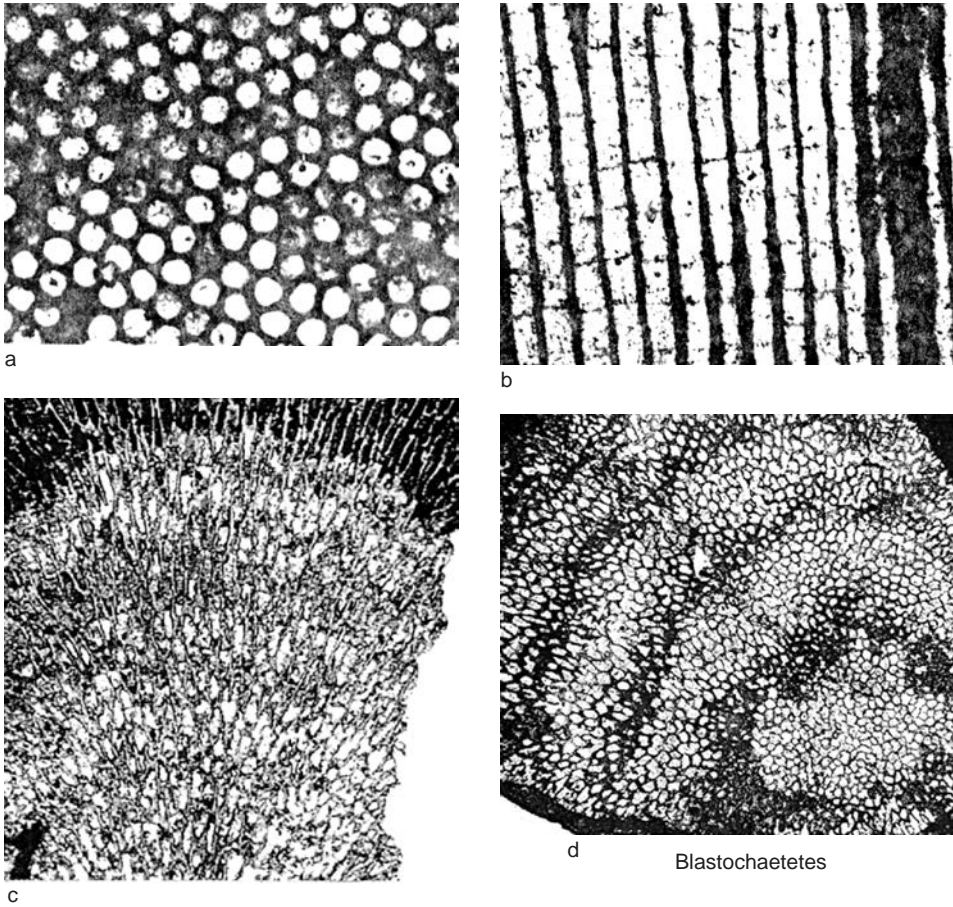
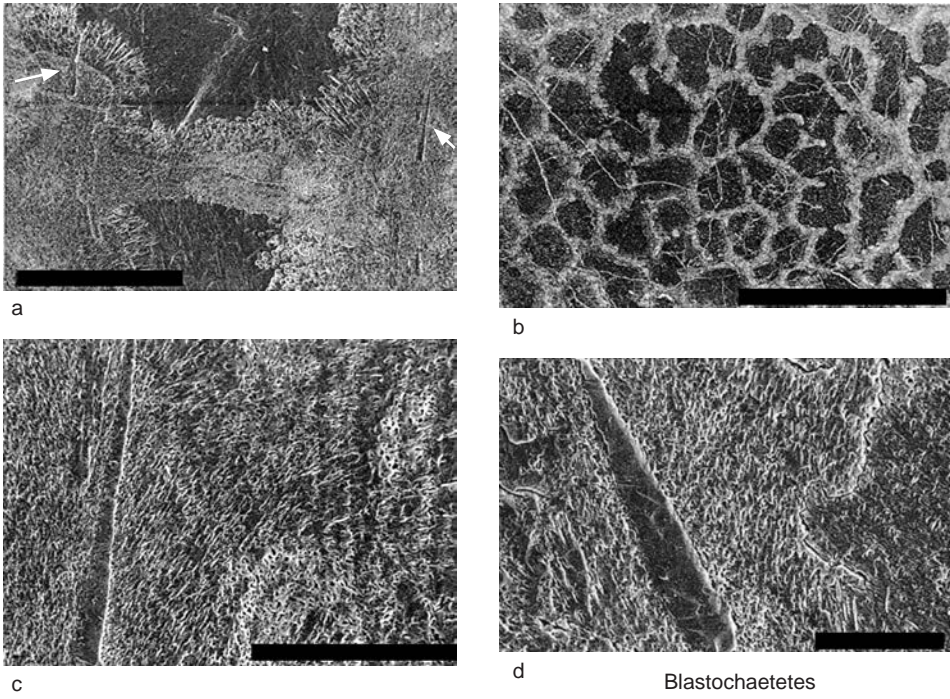


FIG. 191. Uncertain (p. 284–287).

via rounded end to, or in, primary wall; microscleres unknown.] *Triassic (Norian)–Upper Jurassic (Tithonian)*: Turkey (Anatolya), Oman, Tajikistan, *Norian*; Italy, Portugal, Czech Republic, *Oxfordian, Tithonian*.—FIG. 189*a–d*. \**B. multitabulata* (DENINGER), Tithonian, Italy; *a*, lateral view of basal skeleton,  $\times 0.8$ ; *b*, detail of external surface,  $\times 4$ ; *c*, transverse section,  $\times 29$ ; *d*, longitudinal section,  $\times 25$  (Peterhans, 1927, pl. X–XI).—FIG. 190*a–d*. ?*B.* sp. *Norian*, Turkey, Deninger Collection, University of Freiburg, Germany and the Royal Geological Museums (Rome or Naples);

*a*, transverse section showing subpolygonal to elliptical tubules, 19E9/2c,  $\times 19.5$ ; *b*, longitudinal section showing spicular basal skeleton (white S, spicules), 19E9/2c,  $\times 70$ ; *c*, enlargement of part of view *b* showing tylostyle megascleres attached in primary wall (mottled area) of tubules,  $\times 167$ ; *d*, tylostyle megasclere in secondary wall of tubule with rounded end in primary wall of tubule, 19E9/2c,  $\times 300$  (Cremer, 1995, pl. 27).  
**Blastochaetetes** DIETRICH, 1919, p. 210 [\**Chaetetes capilliformis* MICHELIN, 1844 in 1840–1847, p. 112; OD]. Growth form domical to columnar

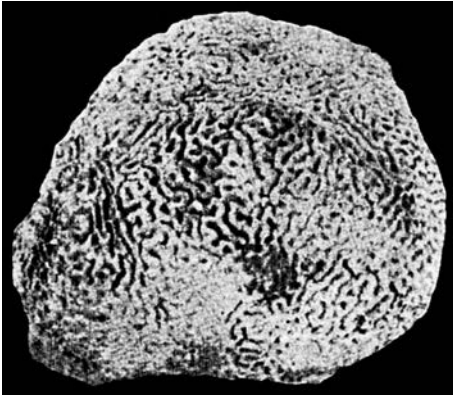


e

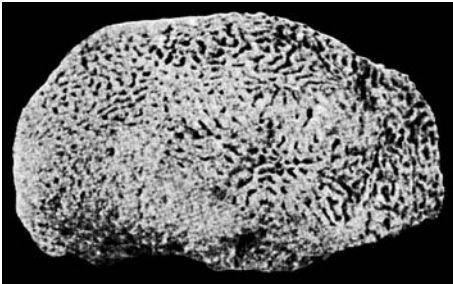


f

FIG. 192. Uncertain (p. 284–287).



a



b



c

Meandripetra

(possible branching); tubules polygonal in transverse section, filled with drusy calcite; pseudosepta present; tubules long, diameter varies, imperforate; tabulae thin, horizontal or slightly tilted, irregularly placed; tubules increase by intertubular budding, rarely by longitudinal fission; aragonite or Mg calcite inferred original mineralogy. [DIETRICH (1919) based his genus on specimens from the Oxfordian of Chatel-Censoir, Yonne, France, that he referred to MICHELIN's species; DIETRICH's types were interpreted by FISCHER (1970) as a new species of *Bauneia*, and if DIETRICH's description of his specimens is taken as his designation of them as types, then *Blastochaetetes* would become a senior synonym of *Bauneia* PETERHANS, 1927. However, FISCHER recognized *Chaetetes capilliformis* MICHELIN, 1844 in 1840–1847, p. 112 (in Michelin Collection of the NMNH, Paris, Oxfordian, Jurassic, Saint Mihiel, Meuse, France) as the type specimen; *vide* HILL, 1981, p. 519. Whereas neither microstructure and spicules nor spicule pseudomorphs have been recognized in the type species, another species exhibits some of these details. BIZZARINI and BRAGA (1978, p. 44–46) first described *Blastochaetetes dolomitica* from the Carnian Dolomite Alps of Italy (holotype MIGUP no. 26064; paratypes MIGUP nos. 28=6065–66), and CREMER (1995, p. 170–172) provided a more complete diagnosis and description of *B. dolomitica*, based on specimens from the Norian of Turkey, in the Cremer collection in the Paleontological Institute, University of Erlangen-Nürnberg, IPE); growth form domical to conical, growth bands distinct; in transverse section, tubules irregular polygons, vary in size and shape with pseudosepta; tubule walls with knoblike thickenings in longitudinal section; tabulae frequent, plain to concave, often with thickened margins, irregularly spaced; tubules increase by intertubular budding and longitudinal fission; primary wall layer penicillate, water-jet (fascicular fibrous) microstructure; secondary wall layer thin, epitaxial fibrous calcite; calcite pseudomorph tylostyle megascleres (49–109  $\mu\text{m}$  long) long, slender, and short, club shaped in both primary and secondary wall layers, lacking preferred orientation; microscleres unknown (description adapted from CREMER, 1995, p. 170–172).] *Triassic (Carnian)*–*Upper Cretaceous*: Italy, Turkey, *Carnian*–*Norian*; France, Italy, Spain, *Jurassic (Tithonian)*–*Upper Cretaceous*.—FIG. 191a–b. \**B. capilliformis* (MICHELIN), Tithonian, France, unnumbered specimens; a, transverse section of basal skeleton,  $\times 20$ ; b, longitudinal section of basal skeleton,  $\times 20$  (Peterhans, 1929b, pl. VI).—FIG. 191c–d. *B. dolomitica* BIZZARINI & BRAGA, *Norian*, Tilki Deligi Tepe and B., Alankoyu, Turkey; c, longitudinal section of basal skeleton, specimen TTR/1a,  $\times 3.8$ ; d, transverse section of basal skeleton, specimen TTM12,  $\times 2.6$  (Cremer,

FIG. 193. Uncertain (p. 287–289).

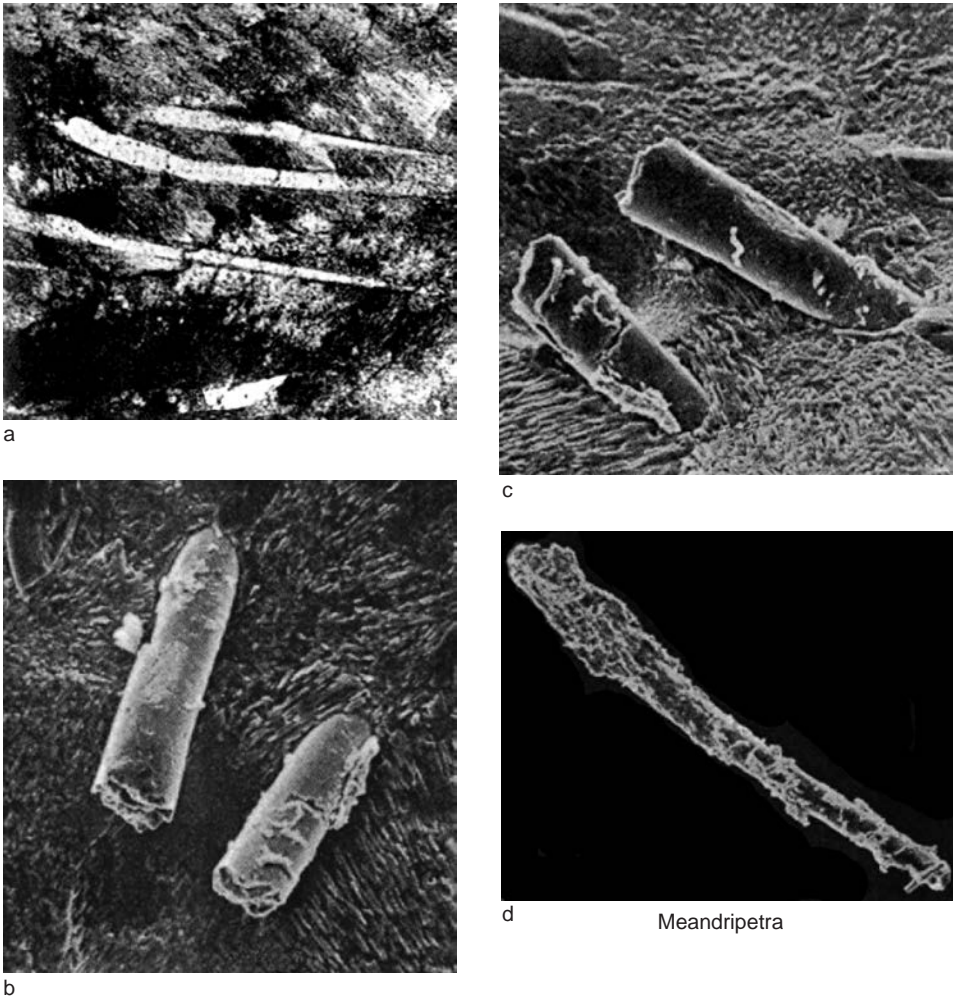


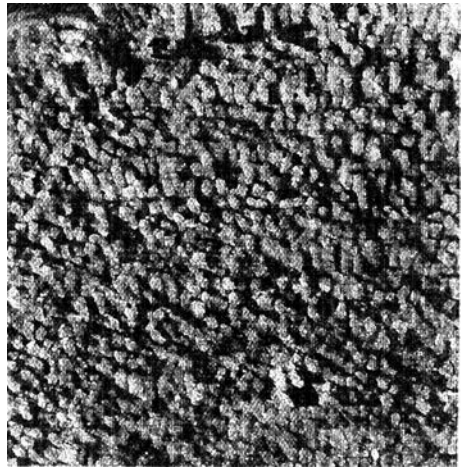
FIG. 194. Uncertain (p. 287–289).

1995, p. 170, pl. 26).—FIG. 192a–f. *B. dolomiticus* BIZZARINI & BRAGA, Norian, Tilkideligi Tepe and B., Alankoyu, Turkey; *a*, tabula between tubule walls, *white arrows* indicate tylostyle megascleres embedded in primary wall of specimen TTR/1a,  $\times 130$ ; *b*, irregular tubule shape and pseudosepta in transverse section of specimen TTH12,  $\times 16.5$ ; *c*, penicillate, water-jet (fascicular fibrous) microstructure of primary tubule walls, with embedded slender, tylostyle megasclere,  $\times 400$ ; *d*, unnumbered specimen with short clublike tylostyle megasclere,  $\times 900$ ; *e*–*f*, diagrammatic sketches of tylostyle megascleres from an unnumbered specimen,  $\times 750$ ,  $\times 675$  (Cremer, 1995, p. 170, pl. 26).

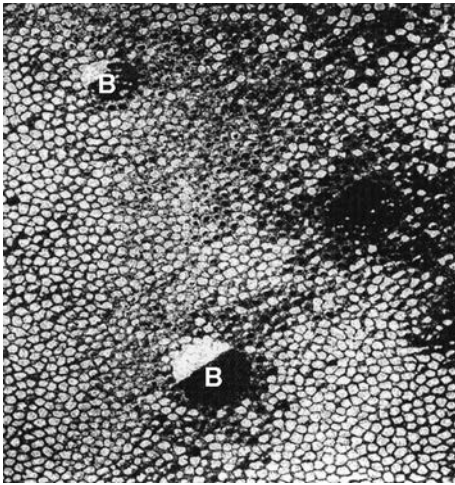
**Meandripetra** DIECI & others, 1977, p. 232 [*\*M. zardini*; OD; holotype 19094, paratype 19095; Zardini Collection, IPUM]. Growth domical to fungiform; tubules meandroid on upper surface; short, lamellate distal processes; in longitudinal section, tubules filled with secondary calcite deposits, except distal 2–3 mm; tubules increase by longitudinal fission; aragonitic penicillate, water-jet (fascicular fibrous) microstructure; straight to slightly curved tylostyle megascleres occur as pseudomorphs, some of pyrite, and molds; microscleres unknown. *Triassic (Carnian)*: Italy.—FIG. 193a–c. *\*M. zardini*, Cassian Formation, Alpe di Specie, near Cortina d'Ampezzo, northern



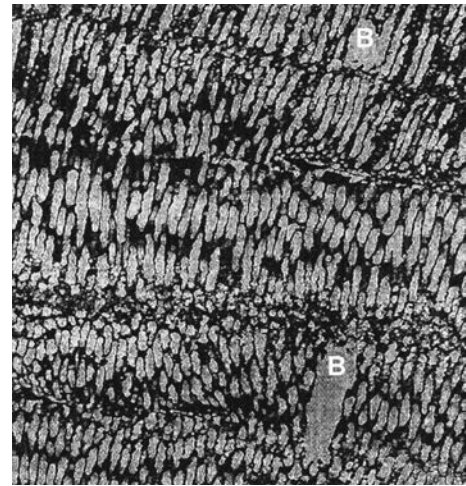
a



b

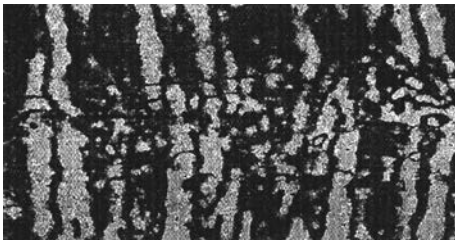


c



d

Ptychochaetetes (Ptychochaetetes)



e

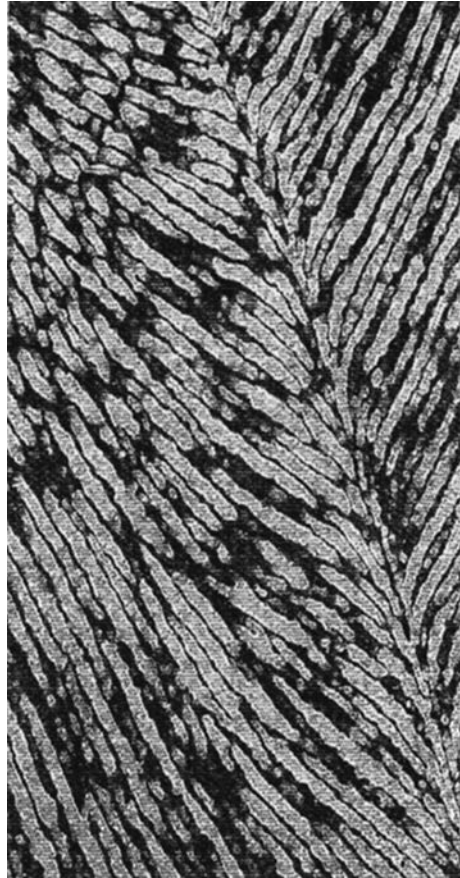
FIG. 195. Uncertain (p. 289–291).



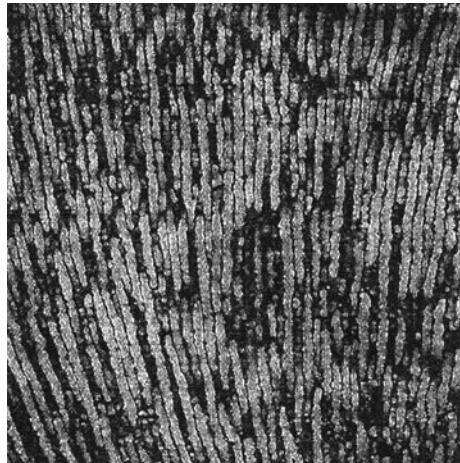
Italy; *a*, holotype, upper surface of basal skeleton, IPUM 19094,  $\times 2.5$ ; *b*, holotype, lateral view of basal skeleton, IPUM 19094,  $\times 2.5$ ; *c*, paratype, upper surface of basal skeleton, IPUM 19095,  $\times 1.9$  (Dieci & others, 1977, pl. 1–3).—FIG. 194*a–d*. \**M. zardini*, Cassian Formation, Alpe di Specie, near Cortina d'Ampezzo, northern Italy; *a*, paratype, straight to slightly curved tylostyle megascleres in thin section, IPUM 19095,  $\times 110$ ; *b*, paratype, pyritic pseudomorphs of tylostyle megascleres in penicillate, water-jet (fascicular fibrous) microstructure of tubule walls, IPUM 19095,  $\times 500$ ; *c*, paratype, pyritic pseudomorphs of tylostyle megascleres in tubule walls, IPUM 19095,  $\times 500$ ; *d*, paratype, isolated pyritized pseudomorph of slightly curved, encrusted tylostyle megasclere, IPUM 19095,  $\times 170$  (Dieci & others, 1977, pl. 1–3).

**Ptychochaetetes** KOEHLIN, 1947, p. 4 [\**P. ramosus* KOEHLIN, 1947, p. 4–6, pl. 1, 1–2, pl. 2, 1–4; OD]. Growth form laminar to low domical with distinct interruption partings; tubules of compacted granular calcite; tubules rounded polygons in transverse section with large openings, inferred borings, partially filled with calcite; pseudosepta present; tubules elongate, slightly curved in longitudinal section; tabulae thin, more or less at same level in adjacent tubules; tubule walls with and without pores, composed of radial fibers; tubules increase by longitudinal fission and intertubular budding. [Spicules and/or spicule pseudomorphs are not known from the type species, *P. ramosus*, but TERMIER and TERMIER (1976) documented pyrite pseudomorphs of monaxon tylostyle megascleres, the primary and secondary tubule walls, and the thin tabulae in a Kimmeridgian specimen of *Ptychochaetetes* sp. from Spain. CREMER (1995) also documented the microstructure and calcite pseudomorphs of tylostyle monaxon megascleres in a Triassic specimen of *Ptychochaetetes* sp. from Turkey: long, slender to club-shaped tylostyles (77–192  $\mu\text{m}$  long, 7–11  $\mu\text{m}$  wide) usually in secondary wall, but may be in, or attached to, the primary wall; microscleres unknown; and microstructure of both walls penicillate, water-jet (fascicular fibrous), inferred to be aragonite; quasi-tabulae formed by thickened secondary walls at level of tabulae. *Triassic (Norian)–Miocene (Burdigalian)*: Turkey (Tilkideli Tepe), Tajikistan, *Norian*; Austria, Portugal, Switzerland, Spain, *Jurassic (Kimmeridgian)*; France (l'Ain), *Miocene (Burdigalian)*.

**Ptychochaetetes (Ptychochaetetes)**. Description as for genus. *Triassic (Norian)–Jurassic (Kimmeridgian)*: Turkey (Tilkideli Tepe), Tajikistan, *Norian*; Austria, Portugal, Switzerland, Spain, *Kimmeridgian*.—FIG. 195*a–e*. \**P. (P.) ramosus*, type specimens in Naturhistorisches Museum, Basel, *Kimmeridgian*, Switzerland; *a*, holotype, general laminar growth form, NMB A 390,  $\times 1.5$  (note: vertical lines are not part of the specimen); *b*, holotype, corroded granular calcite tubules on upper surface, NMB A 390,  $\times 7.3$ ; *c*, tangential section, nearly transverse,



a



b

Ptychochaetetes (Ptychochaetetes)

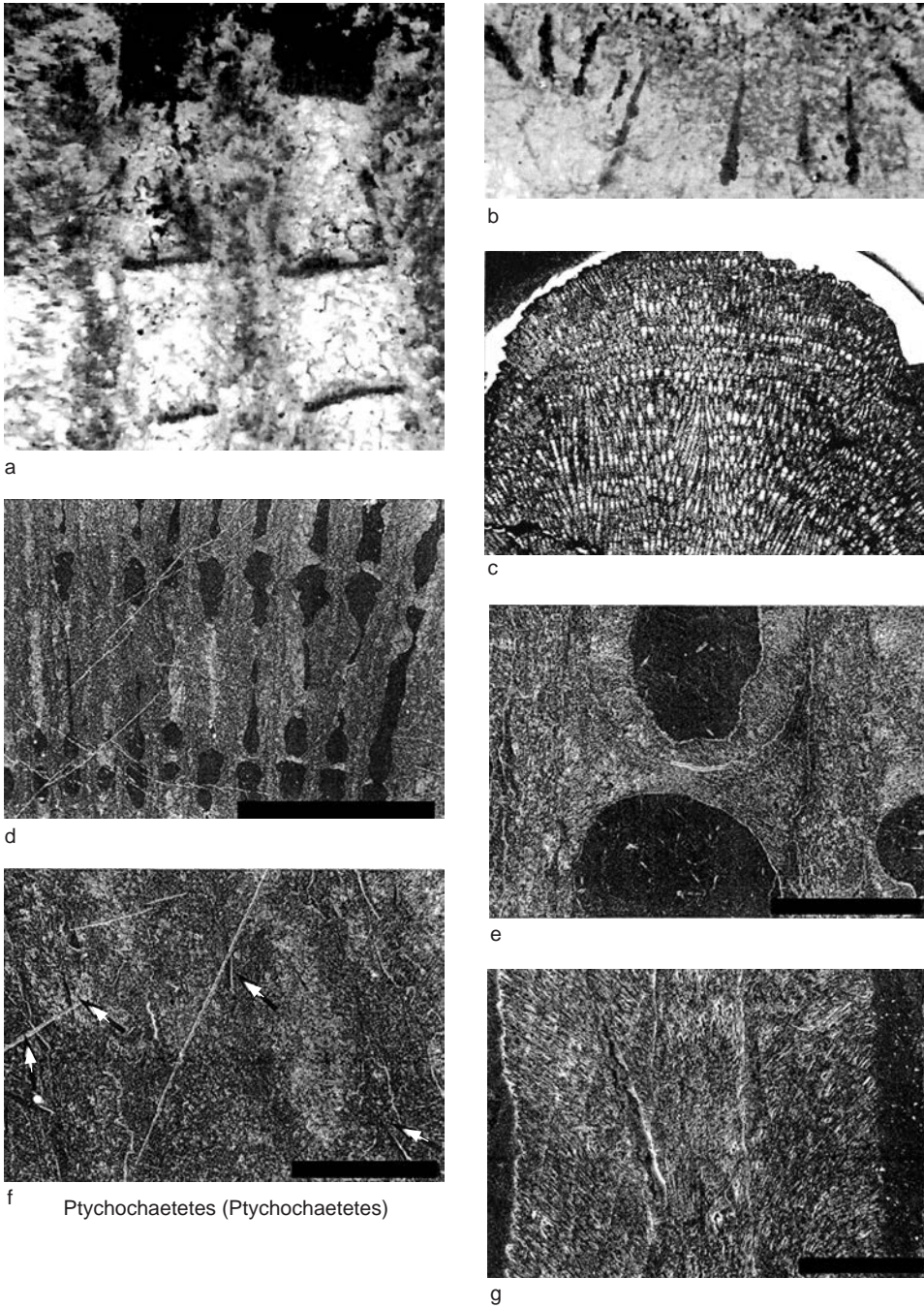


FIG. 197. Uncertain (p. 289–291).

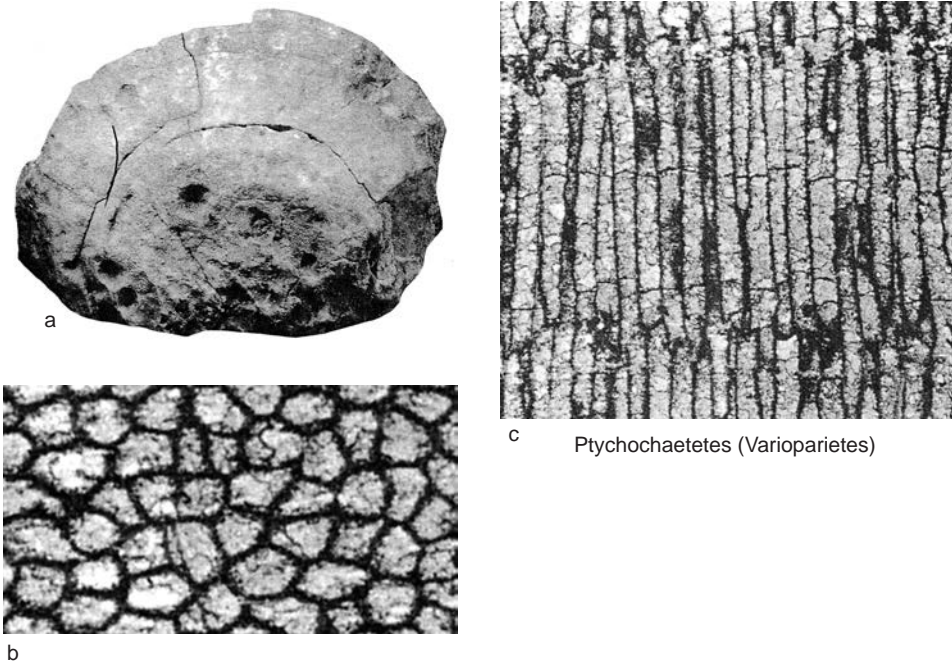


FIG. 198. Uncertain (p. 289–291).

showing cross sectional shape of tubules; note large holes partially filled (geopetal) with calcite (*white B*), possibly borings,  $\times 7.5$ ; *d*, second nondesignated type specimen (invalidly named a type species) in a slightly oblique section shows tubules and what appear to be growth interruptions and possible borings (*white B*),  $\times 6.4$ ; *e*, enlargement of longitudinal section of another type specimen (invalidly named as type species) showing irregularities in tubules at apparent growth interruptions,  $\times 42$  (Koechlin, 1947, pl. 1–2).—FIG. 196*a–b*. \**P. (P.) ramosus*, other type specimens in Naturhistorisches Museum, Basel, Kimmeridgian, Switzerland; *a*, longitudinal section showing apparent branching of tubules as result of oblique contact during growth,  $\times 7.5$ ; *b*, longitudinal section of elongate, curved tubules,  $\times 7.9$  (Koechlin, 1947, pl. 1–2).—FIG. 197*a–b*. *P. (P.)* sp. TERMIER & TERMIER, Kimmeridgian, Jabaloyes, Spain; *a*, enlargement of specimen in longitudinal section,  $\times 79$ ; *b*, iron oxide pseudomorphs of monaxon tylostyle megascleres near upper surface of another specimen,  $\times 179$  (Termier & Termier, 1976, pl. 1).—FIG. 197*c–g*. *P. (P.)* sp. CREMER, Norian, Tilkidigli Tepe, Turkey; *c*, longitudinal section of domical form, TTR20 specimen in Cremer collection in Erlangen, Germany (IPE),  $\times 1.9$ ; *d*, longitudinal section of tubules with tabulae at same level in adjacent tubules, TTR20,  $\times 16$ ; *e*, longitudinal section of primary tubule walls

and secondary basal skeleton, TTR20,  $\times 120$ ; *f*, tylostyle megascleres (*white arrows*) embedded in both primary tubule walls and secondary basal skeleton, TTR20,  $\times 105$ ; *g*, tylostyle megasclere attached to penicillate, water-jet (fascicular fibrous, clinogonal) primary wall of tubule; note the microstructure of primary wall and secondary basal skeleton are the same, TTR20,  $\times 300$  (Cremer, 1995, pl. 26–27).

*Ptychochaetetes (Varioparietes)* BODERGAT, 1975, p. 293 [\**P. (V.) resurgens*; OD; Department of Earth Sciences, Claude-Bernard University, Lyon, France, collection no. 5 090 26 192 02]. Growth form domical; tubules in transverse section irregular polygons with pseudosepta; tubules long, subparallel with thin tabulae at more or less the same level in adjacent tubules. *Miocene (Burdigalian)*: France (l'Ain).—FIG. 198*a–c*. \**P. (V.) resurgens*; *a*, lower surface of basal skeleton, holotype, no. FSL 171 000,  $\times 0.4$ ; *b–c*, paratype, no. FSL 171 007; *b*, transverse section,  $\times 67$ ; *c*, longitudinal section,  $\times 30$  (Bodergat, 1975, pl. 27–28).

## ACKNOWLEDGMENTS

RONALD R. WEST

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