

# HYPERCALCIFIED EXTANT CALCAREA: SYSTEMATIC DESCRIPTIONS

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## Class CALCAREA Bowerbank, 1864

[Calcarea BOWERBANK, 1864, p. 160] [=Calcispongia DE BLAINVILLE, 1830, p. 494]

Marine Porifera exhibiting mineral skeleton composed entirely of calcium carbonate. Skeleton represented by free diactine, triactine, tetractine spicules, that may be combined with a solid basal calcitic skeleton or basal spicules, either cemented together or completely embedded in an enveloping calcareous cement. Aquiferous system may be asconoid, syconoid, sylleibid, or leuconoid. Members of the Calcarea are viviparous, and their larvae are blastulae (diagnosis modified from MANUEL & others, 2002, p. 1103). [The calcitic sponges exhibit monocrySTALLINE calcareous spicules and have been grouped previously in either the Calcarea or the Calcispongia. The Calcispongia was a name proposed by DE BLAINVILLE (1830) for a genus, and then other early workers (e.g., JOHNSTON, 1842; HAECKEL, 1872) adopted it for wider use in recognizing the entire higher level subdivision of the group. Much later, MANUEL and others (2002, p. 1103), in their major *Systema Porifera* project overview of this higher level subdivision employing Calcispongia and Calcarea, recognized that, through the 20th century, the preferred usage of these two names was the Calcarea. Also, some doubt existed about the validity of the taxonomic name Calcispongia, and that it should continue to be used as a class-level taxon, given that DE BLAINVILLE (1830) and other 19th century workers had recognized the original genus as a synonym of *Grantia* FLEMING, 1828a. Nevertheless, MANUEL and others (2003, p. 311), and MANUEL (2006, p. 226) have recently proposed a two-fold subdivision of

the two group names: that Calcispongia be retained as the crown-based clade name, and Calcarea be employed for the stem-based clade. MANUEL's (2006, p. 226) suggestions are to reserve the name Calcispongia for the crown group, including the living calcareous sponge representatives and probably most, if not all, of their extinct relatives, and to employ the Calcarea for members of the stem group, which comprises not only all the representatives of the Calcispongia but also the exclusively Paleozoic Heteractinida HINDE, 1887 (Cambrian–Permian). These proposals have not yet been considered for general approval of sponge workers and to be ratified or formally abandoned. In the meantime, all calcareous sponges are described herein as being exclusively calcareans; they comprise a confirmed Mesozoic to Recent record, plus a doubtful earlier (Carboniferous–Permian) record, based on a few scattered, poorly documented occurrences (see FINKS & RIGBY, 2004d), and the possibly early Cambrian genus *Gravestockia* REITNER, 1992, which should be included in the class, because it has a “rigid skeleton of tetractine desmas” (FINKS & RIGBY, 2004d, p. 758). Class Calcarea is subdivided into two subclasses, Calcinea and Calcaronea, based on several independent characters. This subdivision has been recently confirmed by molecular characters (VOIGT, WÜLFING, & WÖRHEIDE, 2012).] ?Cambrian, ?Carboniferous, ?Permian, ?Jurassic, Cretaceous–Holocene.

## Subclass CALCINEA Bidder, 1898

[Calcinea BIDDER, 1898, p. 73]

Calcarea with a regular (equiangular and equiradial) or exceptionally parasagittal or sagittal triactines and/or a basal system of tetractines. In addition to the free spicules,

there may be a nonspicular basal calcareous skeleton. In terms of ontogeny, triactines are the first spicules to be secreted. Choanocytes are basinuclate with spherical nuclei. Basal body of flagellum is not adjacent to nucleus. *Calcinea incubate coeloblastula larvae* (MANUEL & others, 2002, p. 1109). *Holocene*.

## Order MURRAYONIDA

### Vacelet, 1981

[Murrayonida VACELET, 1981, p. 314]

*Calcinea* with reinforced skeleton consisting of a rigid network of calcite, of calcareous plates, or of spicule tracts generally composed of diapason triactines. Canal system leuconoid (VACELET & others, 2002a, p. 1153). [The order is comprised of three monotypic families, one of which, *Lelapiellidae* BOROJEVIC, BOURY-ESNAULT, & VACELET (1990), is not hypercalcified. There is no fossil record for this order.] *Holocene*.

## Family MURRAYONIDAE

### Dendy & Row, 1913

[Murrayonidae DENDY & ROW, 1913, p. 741]

Murrayonida in which the basal skeleton is composed of a rigid, calcareous, aspicular network. Cortex composed chiefly of overlapping calcareous scales in oscular zone, and of small triactines in pore zone. Choanosomal skeleton including free diapason triactines (VACELET & others, 2002a, p. 1153). *Holocene*.

*Murrayona* KIRKPATRICK, 1910b, p. 127 [*\*M. phanolepis*; M; holotype, NHM 1937.8.6.1]. Diagnosis as for family. Type species is globular, pyriform, or lamellate. Consistency hard, stony. Color white. Lamellate specimens with a distinct inhalant and exhalant surface, globular ones with special, generally equatorial, inhalant areas. Cortical skeleton of inhalant areas made up of a tangential reticulation of triactines. Exhalant surfaces covered by scales originating from equiangular triactines. Diapason triactines isolated under the scales, not building tracts. Osculum surrounded by cirlet of special triactines with long lateral actines. Basal skeleton reticulate, with meandroid structure, made up of fused, irregularly shaped, calcitic sclerodermites with vague clinogonal micro-

structure, generally without entrapped spicules. Aquiferous system leuconoid with basinuclate choanocytes. Embryo of blastula type (VACELET & others, 2002a). A single species, recorded from underwater caves and deep fore reef of Eastern Indian Ocean (Christmas Island) and Western and Central Pacific, 2–83 m depth. Meandroid structure of basal skeleton resembles stromatoporoid organization. Skeleton may be able to fossilize, but no fossil representative has yet been recognized (REITNER, 1992). *Holocene*: Eastern Indian Ocean, Western and Central Pacific. —FIG. 199a–f: *\*M. phanolepis*, Moorea, Central Pacific; a, view of specimen with living tissue (Vacelet, 1977a); b, SEM view of fracture of skeleton of another specimen near surface (top); c, SEM view of surface of skeleton on exhalant face, with trace of an osculum and a trapped superficial scale; d, SEM view of surface of skeleton on inhalant face; e, SEM view of microstructure on a fracture; f, calcareous scale (Vacelet, 2012); see also Fig. 3, I, herein, with diagrammatic section through a lamellar specimen of *M. phanolepis*, with inhalant face on left and inhalant one on right (Borojevic, Boury-Esnault, & Vacelet, 1990).

## Family PARAMURRAYONIDAE

### Vacelet, 1967

[Paramurrayonidae VACELET, 1967a, p. 49]

Murrayonida with choanosomal skeleton made up of fascicles of diapason triactines without any rigid structure. Cortical skeleton composed chiefly of superficial layer of overlapping calcareous scales and internal layer of free calcareous plates. [Paramurrayonidae differs from Murrayonidae mainly by the absence of a rigid aspicular skeleton, which is replaced by a cortical layer of calcareous plates. Such a cortical skeleton is slightly reminiscent of the external skeleton found in fossil and Recent siphonozoans. However, the plates are not fused but simply loosely joined by organic material, forming a nonfossilizable skeleton, and the body is not segmented (VACELET & others, 2002a, p. 1154).] *Holocene*.

*Paramurrayona* VACELET, 1967a, p. 49 [*\*P. corticata*; M; holotype, MNHN C1968-153]. Diagnosis as for family. Type species encrusting, roughly circular, 2–5 mm in diameter, 0.5 mm thick. Color brown, with a glistening, smooth surface. Surface covered with a layer of overlapping oval scales, 150–400 µm in maximum diameter, deriving from triactines. Underlying layer of



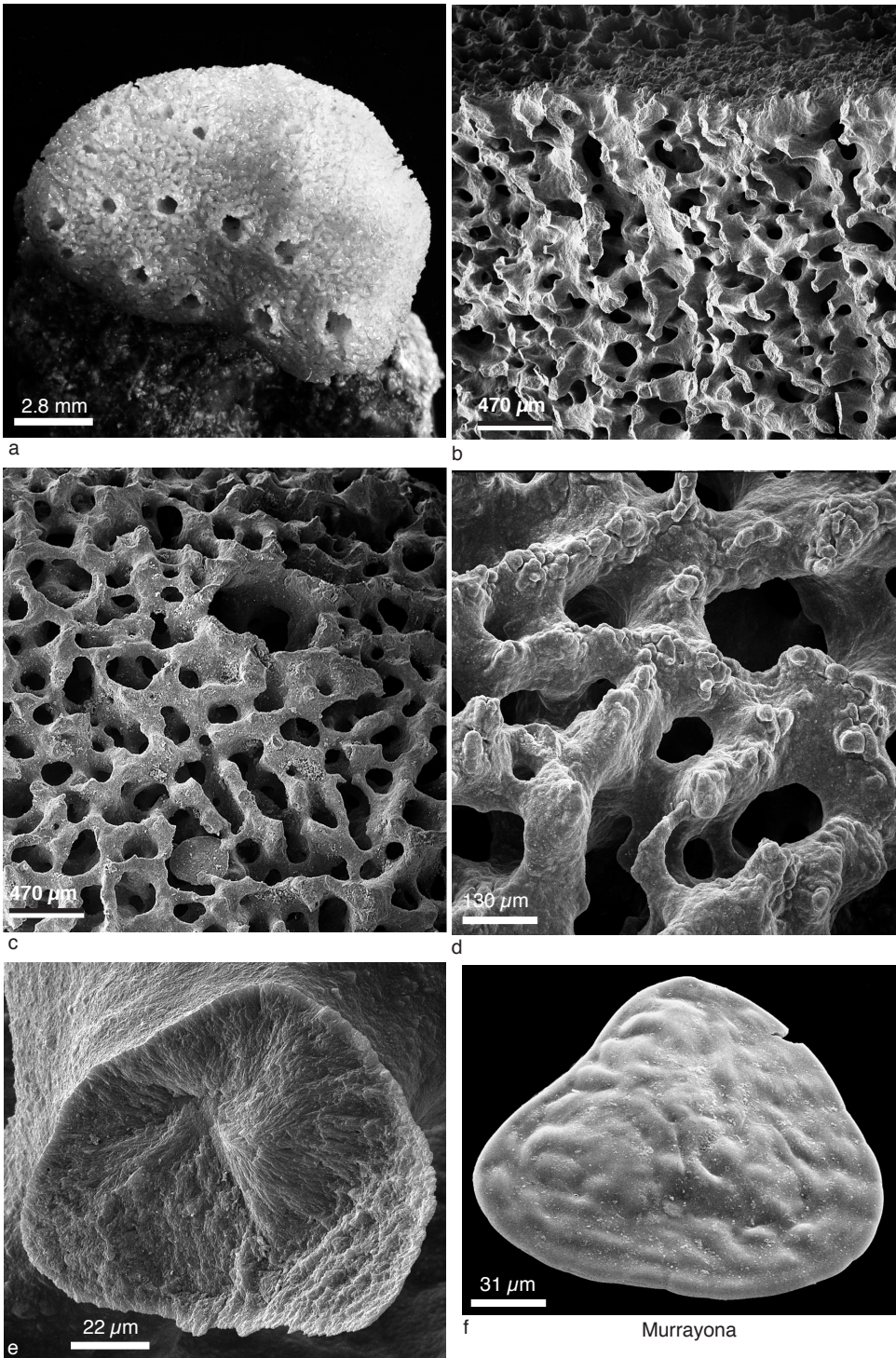


FIG. 199. Murrayonidae (p. 294).

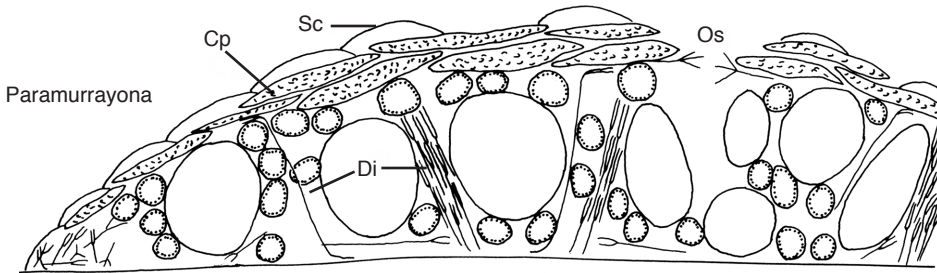


FIG. 200. Paramurrayonidae (p. 294–296).

calcitic plates, mostly rectangular, up to 1 mm in length and 50–100  $\mu\text{m}$  thick. Choanosomal skeleton composed exclusively of diapason triactines, generally disposed in fascicles. Osculum 250  $\mu\text{m}$  in diameter, approximately central in a zone devoid of scales and plates, surrounded by a circlet of special tetractines. Inhalant areas presumably located at periphery of sponge, where a few triactines, diapasons, and tetractines are localized. Aquiferous system leuconoid with basinuclated choanocytes. Embryo of blastula type. A single species, recorded from underwater caves and microcavities of coral reefs in Indian Ocean (Madagascar), Pacific Ocean (New Caledonia) and Caribbean (Jamaica) (VACELET & others, 2002a). *Holocene*: Indian Ocean, Western Pacific, and Caribbean. — FIG. 200. \**P. corticata*, diagrammatic section; *Di*, diapason triactines, single or in tracts; *Cp*, calcareous plates; *Os*, osculum; *Sc*, calcareous scales (Vacelet, 1967a).

### Subclass CALCARONEA Bidder, 1898

[Calcaronea BIDDER, 1898, p. 73]

**Calcareia** with diactines and/or sagittal triactines and tetractines, rarely also with regular spicules. In addition to free spicules, there may be a rigid basal skeleton, nonspicular or spicular (with spicules cemented together or completely embedded in an enveloping calcareous cement). In ontogeny, first spicules to be produced are diactines in settled larva. Choanocytes are apinuclate, and basal system of flagellum is adjacent to apical region of nucleus. Calcaronea incubate amphiblastula larvae (description modified from MANUEL & others, 2002, p. 1109). ?*Jurassic, Cretaceous–Holocene*.

### Order LITHONIDA Vacelet, 1981

[Lithonida VACELET, 1981, p. 315] [=Stereina DE LAUBENFELS, 1955, p. 99, *partim*]

Calcaronea with reinforced skeleton consisting of linked or cemented basal actines or tetractines. Diapason spicules generally present. Canal system leuconoid (description modified from VACELET & others, 2002b). [VACELET (1981, p. 315) proposed the order Lithonida to include the calcaronean families Petrobionidae and Lepidoleuconidae, based on the subfamily Lithoninae DÖDERLEIN, 1898. However, the Lepidoleuconidae was transferred to Baerida by BOROJEVIC, BOURY-ESNAULT, and VACELET (2000), and the Petrobionidae subsequently transferred also to the Baerida (MANUEL & others, 2003) and herein.] ?*Jurassic, Cretaceous–Holocene*.

### Family MINCHINELLIDAE Dendy & Row, 1913

[Minchinellidae DENDY & ROW, 1913, p. 739] [=Porosphaeridae DE LAUBENFELS, 1955, p. 99, *partim*; =Bactronellidae DE LAUBENFELS, 1955, p. 100, *partim*]

Basal skeleton consisting of a network of tetractines cemented or linked together by their basal actines, which are linked by zygois of irregularly curved or expanded ends. Linkage either a complex zygois, often reinforced by a calcareous cement of variable development that can completely embed whole network, or a simple entanglement. Microstructure of cement of orthogonal type. Superficial skeleton made of free spicules, mostly tangentially disposed in dermal membrane, generally including diapasons.

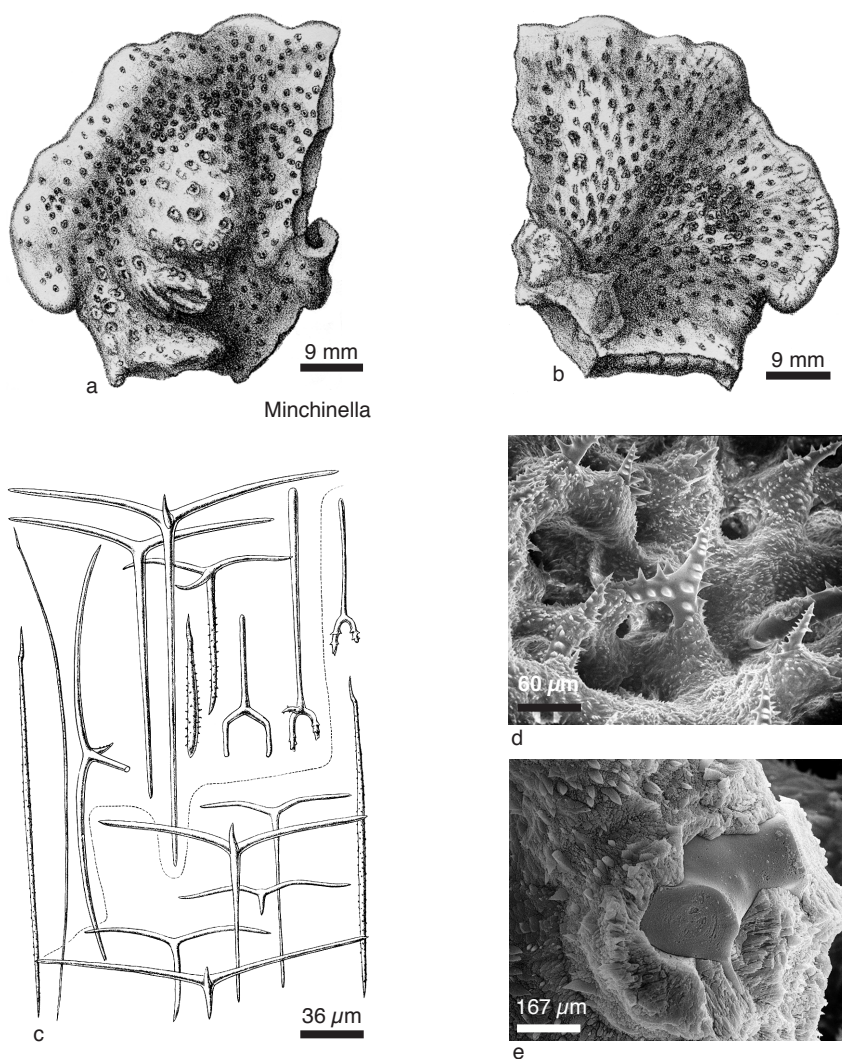


FIG. 201. Minchinellidae (p. 297–298).

[The family includes five Recent genera, one of which (*Tulearinia*), is poorly calcified and of uncertain affinity, and six fossil genera that range from Jurassic–Paleogene in age (*Porosphaera* STEINMANN, 1878; *Bactronella* HINDE, 1884; *Porosphaerella* WELTER, 1911; *Sagittularia* WELTER, 1911; *Retispinopora* BRYDENE, 1912; *Muellerithalamia* REITNER, 1987c). The diagnosis of the fossil and Recent genera are in need of revision, based on a careful reexamination of the type

material. A *Treatise* coverage of systematic descriptions of the fossil genera is presented elsewhere (see FINKS & RIGBY, 2004d, p. 754–756).] ?*Jurassic, Cretaceous–Holocene.*

*Minchinella* KIRKPATRICK, 1908, p. 504 [\**M. lamellosa*; OD; holotype, NHM 1900.10.22.1A]. Minchinellidae in which main skeleton consists of one category of tetractines linked together into rigid network by their basal actines and subsequently embedded in enveloping cement. Cortical skeleton composed of free spicules, diactines, triactines, diapasons, and tetractines. Type species erect

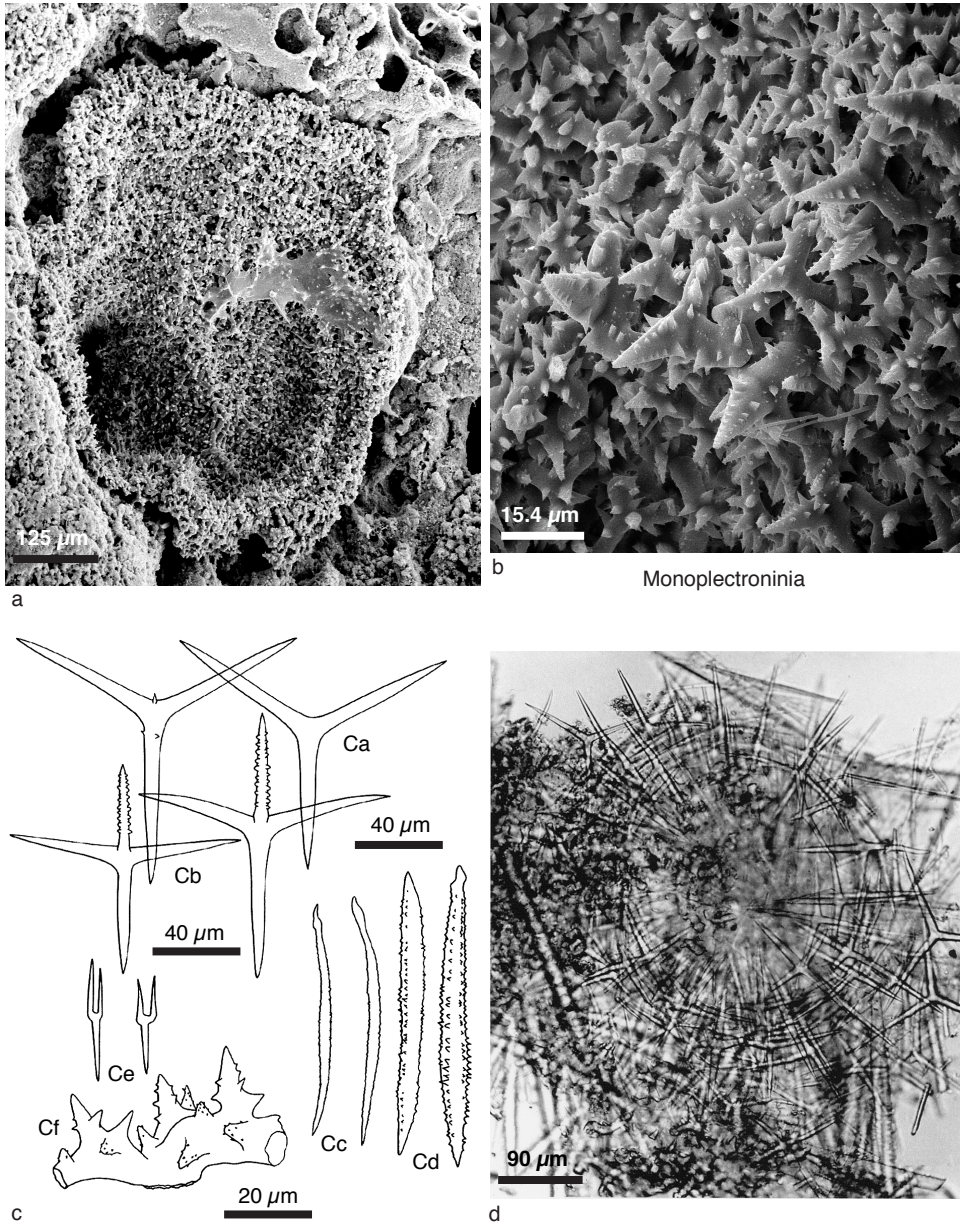


lamellar, with narrow base of attachment, 6.4 mm wide, 5.1 mm high, and 6.5 mm thick (holotype). Paratype smaller and ear shaped. Consistency hard, rigid. Poral face with pore chimneys, up to 3 mm in height and 1 mm in diameter, ending in drumlike membrane. Oscular face with cylindrical chimneys, 2 mm high, with a contracted end. Color in alcohol buff to brown, white at the rim. Choanocyte chambers 32.5  $\mu\text{m}$  in diameter, with choanocytes showing hourglass modification due to poor preservation. Skeleton of both surfaces composed of an ectosomal layer of spinose diactines. Skeleton of poral and oscular chimneys composed of outer coat of spinose diactines, with axis vertical or oblique to long axis of tube, several layers of triactines and tetractines with apical ray projecting into lumen of tube, and fringe of bristlelike diactines round poral orifice. At base of chimneys, triactines and tetractines with spinose rays become partially cemented together. Main skeleton a firm reticulation with ovoid or rectangular meshes, 140–190  $\mu\text{m}$  in total diameter, made of solid strands composed of spinose tetractines, with actines more or less completely embedded in calcitic cement of fibrillar, orthogonal microstructure. Apical ray is last to be embedded and, when free, pointing toward lumen. Diactines of several types, generally spinose, thicker on oscular face, 87–234 by 3.8–7.5  $\mu\text{m}$ . Sagittal triactines generally smooth, unpaired actine 104–156 by 5–9.5  $\mu\text{m}$ , paired actines 49–87  $\mu\text{m}$ . Diapason triactines not aligned in tracts, with smooth shaft, 133  $\mu\text{m}$  long and prongs smooth or spinose, 25  $\mu\text{m}$  long. Tetractines similar to triactines, with apical actine 17  $\mu\text{m}$  long. Cemented tetractines in a single size, with conical spines. Pacific Ocean (Vanuatu), 128 m depth. [A second species, *M. kirkpatricki* VACELET, 1981, from New Caledonia, differs mostly by nonlamellar shape and absence of aquiferous chimneys.] *Holocene*: southwestern Pacific Ocean.—FIG. 201*a–e*. \**M. lamellosa*, Api, New Hebrides, holotype; *a*, oscular surface; *b*, poral surface; *c*, spicules of poral and oscular surfaces (Kirkpatrick, 1908); *d*, SEM view of basal skeleton of partially embedded tetractines; *e*, SEM view of fracture in basal skeleton, showing a tetractine and cement (Vacelet, 1991).

**Monoplectronia** POULIQUEN & VACELET, 1970, p. 439 [\**M. hispida*; M; holotype, NHM 1970.4.24.1]. Minchinellidae in which main skeleton is composed of a basal layer made of one category of small tetractines linked together by their basal actines, while their apical actine remains free and points outward. Cortical skeleton made of free spicules, diactines, triactines, diapasons, and tetractines (VACELET & others, 2002b, p. 1187). Monotypic genus differs from Recent representatives of *Plectronia* in having basal skeleton devoid of large tetractines. Type species, small encrusting, 1.0–1.1 mm in diameter, 0.5 mm thick, white, with hispid surface. Cortical layer with layer of tangential smooth triactines and oblique spinose diactines. Osculum in cortical layer surrounded by cirlet of tangential tetractines with spinose apical actine

pointing toward lumen and smooth basal actines. Smooth diapasons dispersed in basal skeleton, not aligned in tracts. Main skeleton basal, made of a few layers of small spinose tetractines linked by basal actines, with apical actine remaining free and pointing outward. Choanocyte chambers irregularly tubular. Mediterranean (Marseille), dark submarine caves, 8–20 m depth (VACELET & others, 2002b). *Holocene*: Mediterranean.—FIG. 202*a–d*. \**M. hispida*, Cape Morgiou cave, Marseille, 15 m depth; *a*, SEM view of basal skeleton of fused tetractines; *b*, SEM view of basal skeleton with fused tetractines and a diapason (Vacelet, 2012); *c*, spicules: *Ca*, ectosomal triactines; *Cb*, perioscular tetractines; *Cc*, perioscular diactines; *Cd*, ectosomal diactines; *Ce*, diapason triactines; *Cf*, fused tetractines of basal skeleton; *d*, ectosome, with ectosomal spicules and tetractines forming a cirlet around osculum, and a fragment of basal skeleton (Pouliquen & Vacelet, 1970).

**Petrostroma** DÖDERLEIN, 1892, p. 145 [\**P. schulzei*; M; holotype, NHM 99.7.14.1] [not *Petrostroma* STEARN, 1991, p. 617, stromatoporoid; *Petridiostroma* STEARN, 1992, p. 531, *nom. nov. pro Petrostroma* STEARN, 1991]. Minchinellidae with large tetractines fused by their basal actines, forming radial lines that are linked by smaller tetractines, also fused by their basal actines. Cortical skeleton composed of free spicules, triactines, diapason, and tetractines. Type species a massive base from which arises several short, cylindrical branches, dichotomously divided at their ends, of stony consistency. Color whitish to yellowish. Cortical skeleton made of free triactines and tetractines and of bundles of diapasons. Main skeleton of inner part a firm reticulation of ascending and diverging strands made of fused tetractines, which are linked by secondary strands of smaller tetractines fused by their basal actines. Tetractines of main skeleton bearing some conical spines, with apical actines remaining most often free. Free spicules smooth tetractines and triactines in several layers (with a few spinose tetractines), with rays 100  $\mu\text{m}$  by 400  $\mu\text{m}$   $\times$  10  $\mu\text{m}$ ; diapasons aligned in tracts, 25–50  $\mu\text{m}$  in diameter (VACELET & others, 2002b, p. 1188). [The Recent representative has not been found again since its original description (DÖDERLEIN, 1892, 1898). Contrary to *Minchinella*, the tetractines linked by their basal actines are not subsequently embedded in a secondary cement. The mode of junction of the tetractines is rather similar to that in *Plectronia* and *Monoplectronia*. *Petrostroma* may represent a growth form of sponges similar to Recent representatives of *Plectronia*, which are thinly encrusting and thus do not develop such a complex system of ascending and radiating lines; in which case, the two genera could be synonyms. This question is pending examination of new material and a revision of the fossil genera of Jurassic–Miocene age being allocated to the family Minchinellidae (VACELET & others, 2002b).] *Cretaceous–Holocene*: France (Haute-Savoie), *Cretaceous*; Japan (Sagami Bay, 195–392 m depth), *Holocene*.—FIG. 203*a–e*. \**P.*



Monoplectroninia

FIG. 202. Minchinellidae (p. 298).

*schulzei*, a, general view; b, ectosomal layer with ostia, triactines, and tetractines, and bundles of diapason; c, section through outer part of basal skeleton, with primary radial strands and secondary strands; d, small and large fused tetractines of basal skeleton; e, diapason triactine (Döderlein, 1898). **Plectroninia** HINDE, 1900, p. 51 [*P. halli*; OD; holotype, NMV P14357]. Minchinellidae with basal

skeleton made up of two types of fused tetractines, a layer composed of large tetractines and a layer of small tetractines. Tetractines fused by basal actines, with apical actine remaining free and pointing outward. Basal actines attached by simple zygois in small tetractines, zygois reinforced by cement layer in large tetractines. Cortical skeleton of free spicules tangentially arranged (VACELET & others, 2002b,



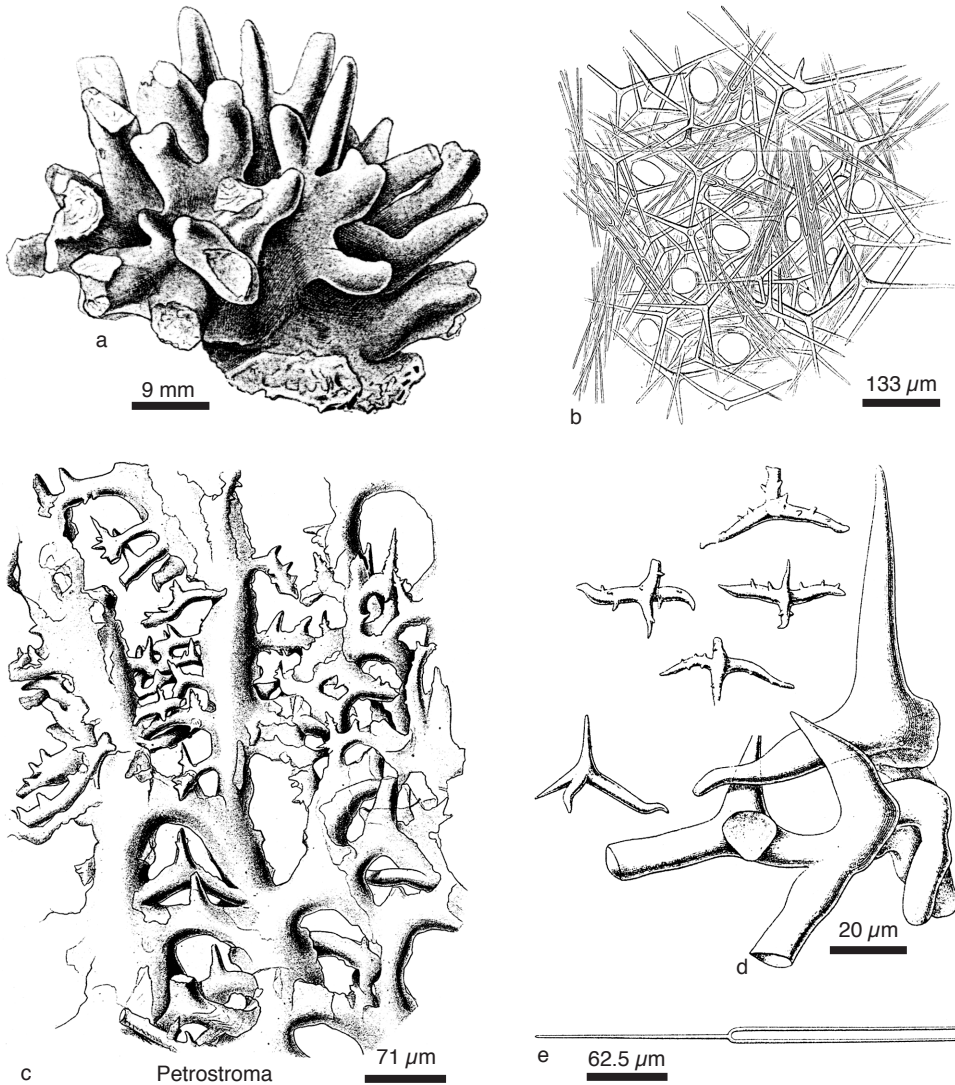
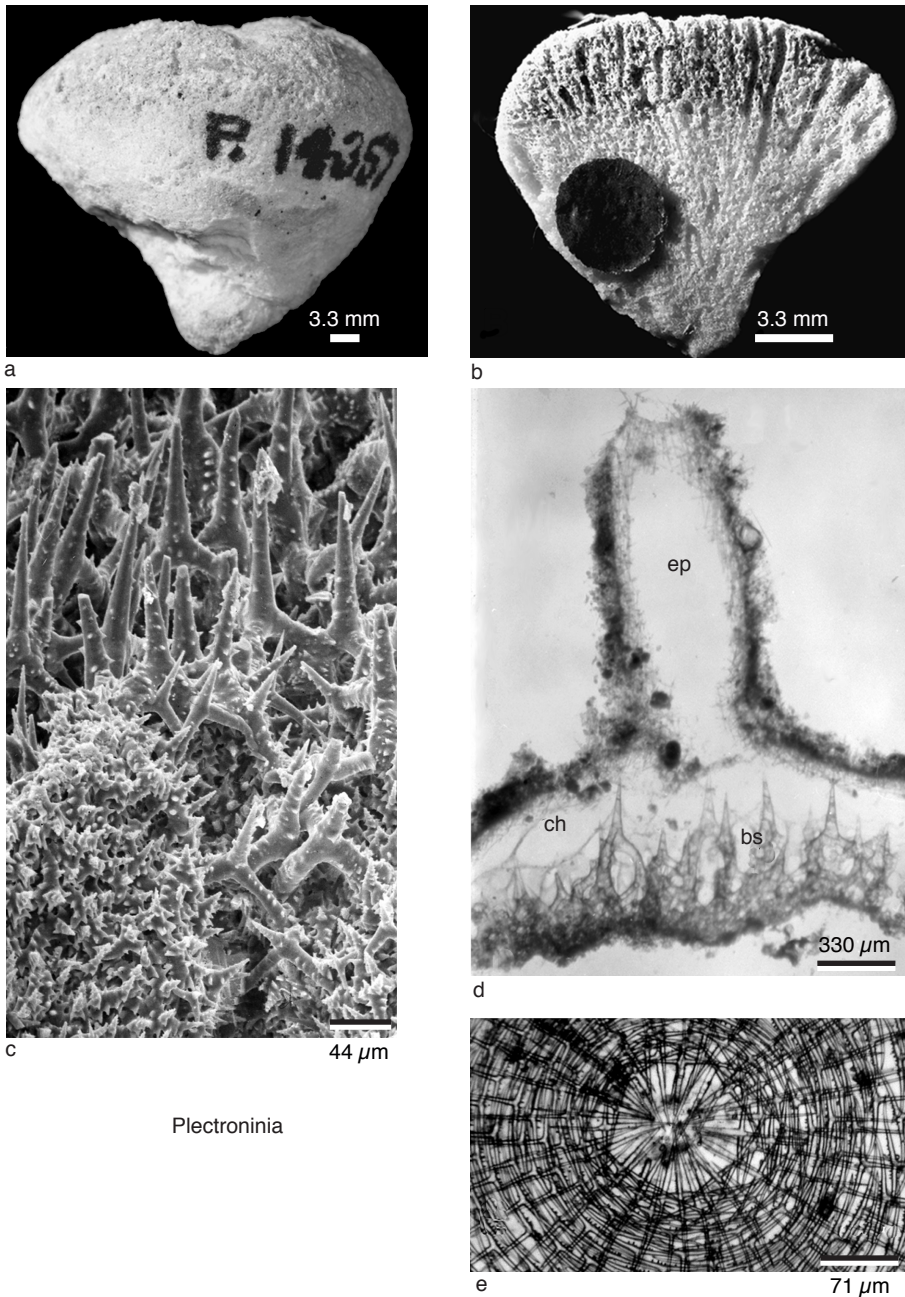


FIG. 203. Minchinellidae (p. 298–299).

p. 1188). Type species turbinate in shape, 16 mm high by 18 mm in greatest width. Sides covered by spicular dermal layer, partly preserved, interior skeleton firm, stony. Surface skeleton composed of free spicules tangentially disposed, with superficial layer of diactines, up to 610 μm by 10 μm, lying in parallel, overlying a layer made of diactines, triactines, and tetractines, including rare diaspans. Basal skeleton a multilayered reticulation made up of spinose tetractines, with basal actines unequal and irregularly curved, linked by expanded ends to basal actines of adjoining spicules, and with apical actine remaining free and pointed toward surface

of sponge. Tetractines simply attached by expanded ends to basal actines of adjoining tetractines in outer layers, the apposition being reinforced by thin calcitic cement in inner layers, where tetractines have different size. Traces of canals radiating from summit of sponge present, 200–500 μm in diameter (VACELET & others, 2002b). [Type species is from the lower part of the middle Miocene in the Fyansford Formation, north of Geelong, Victoria, Australia (PICKETT, 1983); and another undescribed fossil species is from the upper Miocene of south-eastern Spain (BARRIER & others, 1991). There are 13 Recent species, with a highly diverse dermal



*Plectroninia*

FIG. 204. Minchinellidae (p. 299–303).

skeleton of tangential spicules, in shallow water caves of the Indo-Pacific and Mediterranean, and in the bathyal zone, up to 1600 m depth with a large distribution. Recent species display an encrusting shape, and their allocation to the same genus as

the fossil *Plectroninia halli* is not certain. In both Recent and fossil taxa, the basal skeleton of fused tetractines is composed of two different layers of fused tetractines, but contrary to the fossil species, in which the layer of small tetractines is superficial,

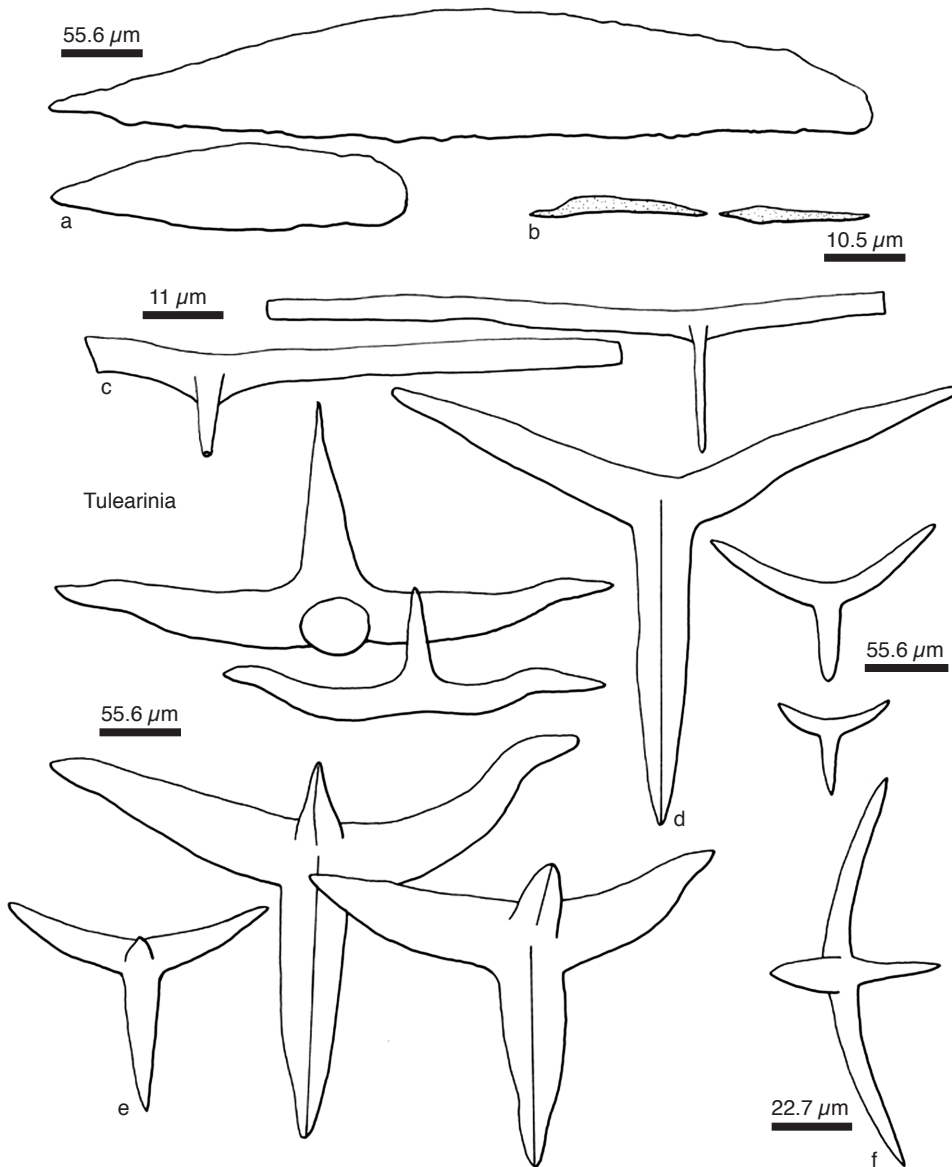


FIG. 205. Minchinellidae (p. 303).

this layer in Recent species is basal with regard to the layer of large tetractines. These Recent taxa could be classified alternatively in the genus *Bactronella* (Jurassic), as suggested by FINKS, HOLLOCHER, and THIES (2011). Another approach could be to describe them as comprising a new genus, but the introduction is dependent on a revision of the fossil genera in the Minchinellidae (VACELET & others, 2002b).] ?Jurassic, Cretaceous–Holocene: Germany, USA (North Carolina), Cretaceous;

Australia (Victoria), Spain, Miocene; Indopacific, Mediterranean, bathyal ocean, Holocene.—FIG. 204a–b. \**P. halli*; general view of holotype (Pickett, 1983, p. 106).—FIG. 204c. *P. neocaledoniense* VACELET, SEM view of basal skeleton made up of small and large fused tetractines, 25 m depth, New Caledonia (Vacelet & others, 2002b).—FIG. 204d. *P. bindei* KIRKPATRICK, section through Mediterranean specimen, Marseille, 5 m depth; *ep*, exhalant papillae; *ch*, choanosome; *bs*, basal skel-

eton (Pouliquen & Vacelet, 1970).—FIG. 204e. *P. vasseuri* VACELET, cortical skeleton of tangential triactines and osculum with a circllet of tetractines, Tuléar, Madagascar, 6 m depth (Vacelet, 1967b).

**Tulearinia** VACELET, 1977a, p. 354 [\**T. styliifera*; M; holotype, MNHN J.V.-76-1]. Minchinellidae in which basal skeleton consists of tetractines with basal actines interwoven but not cemented, and with underlying layers of triactines linked in same way (VACELET & others, 2002b, p. 1190). Type species small, encrusting, 3 mm in maximum diameter, 0.7–0.8 mm thick. Color white, surface hispid, with osculum 0.4 mm in diameter, lined by thin triactines and a few tetractines. Surface skeleton composed of an outer layer of thick tangential or oblique diactines, and a layer of tangential triactines, overlying choanosome zone. Choanocyte chambers 55–75  $\mu$ m in diameter, surrounded by microdiactines; canals lined by special tetractines, choanocytes apinucleate. Under choanosome, basal skeleton made of several layers of tetractines interwoven by basal actines, with apical actine pointing toward surface, and basal layer of interwoven triactines. Indian Ocean (Madagascar, La Réunion), New Caledonia, in submarine caves of the front reef, 3–37 m depth (VACELET & others, 2002b). [This genus is monotypic and assigned with some reservation to the family Minchinellidae. Diapasons are absent; the basal skeleton is not solidly linked, and the spicules are only slightly entangled together through their crooked ends, without the true zygotis that characterizes Minchinellidae. This mode of union may be seen either as a transitional stage to the minchinellid structure or as a convergent mode of skeletal reinforcement in the high energy habitat of the tunnels of front reefs. The affinity of the genus thus remains rather uncertain.] *Holocene*: Indian Ocean and southwestern Pacific.—FIG. 205a–f. \**T. styliifera*, spicules of holotype; *a*, diactines from outer layer; *b*, microdiactines; *c*, perioscular triactines; *d*, triactines; *e*, tetractines from basal network; *f*, tetractine from canals (Vacelet, 1977a).

### Order BAERIDA Borojevic, Boury-Esnault, & Vacelet, 2000

[Baerida BOROJEVIC, BOURY-ESNAULT, & VACELET, 2000, p. 249]

Leuconoid Calcaronea with skeleton either composed exclusively of microdiactines, or in which microdiactines constitute exclusively or predominantly a specific sector of skeleton, such as choanoskeleton or atrial skeleton. Large or giant spicules are frequently present in cortical skeleton, from which they may partially or fully invade choanoderm. In sponges with reinforced cortex, inhalant pores may be restricted to sievelike ostia-bearing region.

Dagger-shaped, small tetractines (pugioles) are frequently sole skeleton of exhalant aquiferous system. An aspicular calcareous skeleton may be present (diagnosis modified from BOROJEVIC & others, 2002). [The order contains four families, two of which, Baeriidae and Trichogypsidae, are not hypercalcified, and are not treated here.] *Pleistocene–Holocene*.

### Family PETROBIONIDAE Borojevic, 1979

[Petrobionidae BOROJEVIC, 1979, p. 529]

Baerida of thickly encrusting or subspherical growth form. Basal skeleton composed of a solid mass of calcite consisting of elongated sclerodermites that form a series of crests between which lies living tissue, with survival structures made of reserve cells filling small canaliculi of the skeleton. Aquiferous system leuconoid. Free spicules triactines, tuning-fork triactines (diapasons), pugiole tetractines, and microdiactines. Spicules randomly trapped within the massive skeleton do not dissolve (description modified from VACELET & others, 2002b, p. 1191). [The monogeneric family Petrobionidae was classified in the order Lithonida in *Systema Porifera* (VACELET & others, 2002b). A recent reevaluation of morphological and molecular characters suggests a classification in the order Baerida (MANUEL & others, 2003). No counterpart of the skeleton microstructure older than 30,000 years is known in the fossil record.] *Pleistocene–Holocene*.

**Petrobiona** VACELET & LÉVI, 1958, p. 318 [\**P. massiliana*; M; holotype, MNHN C. 1968.814]. Diagnosis as for family. Type species massive, subspherical or multilobate with a dead stalk in calm environments, encrusting in high energy environments. Maximum size of living head 1.0–1.2 cm in diameter, with stalk 2 cm long, up to 6 cm in diameter when encrusting. Texture stony. Color pure white. Surface smooth. Oscules apical in subspherical or multilobate specimens, 0.6–0.8 mm in diameter. Living tissue located at surface and between crests of basal skeleton, with choanosome 600  $\mu$ m thick, anchored in basal skeleton by tracts of reserve cells filling canaliculi 50–90  $\mu$ m in diameter. Aquiferous system leuconoid, choanocyte chambers 50–80  $\mu$ m in diameter. Spicules: sagittal triactines (actines



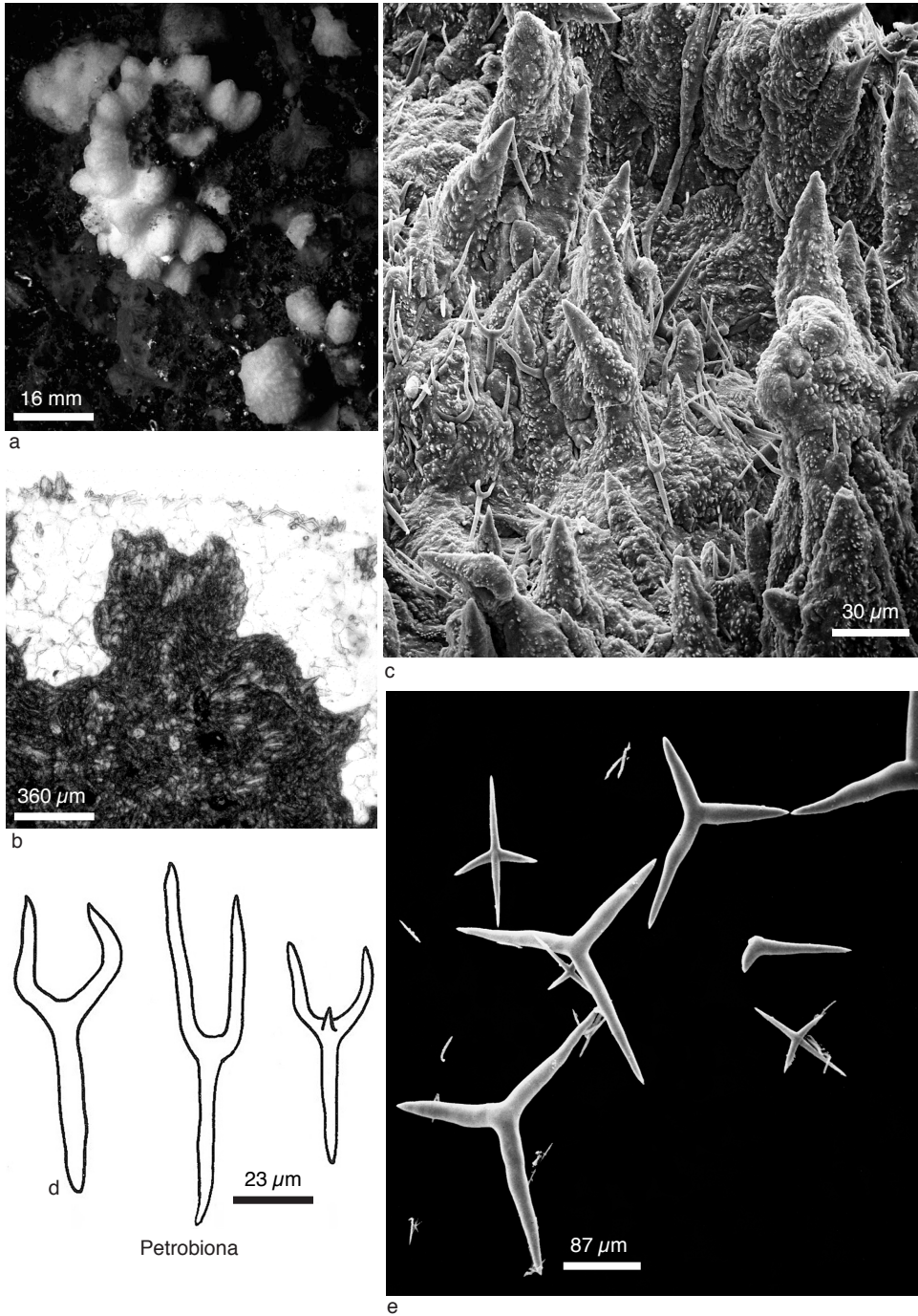


FIG. 206. Petrobionidae (p. 303–305).



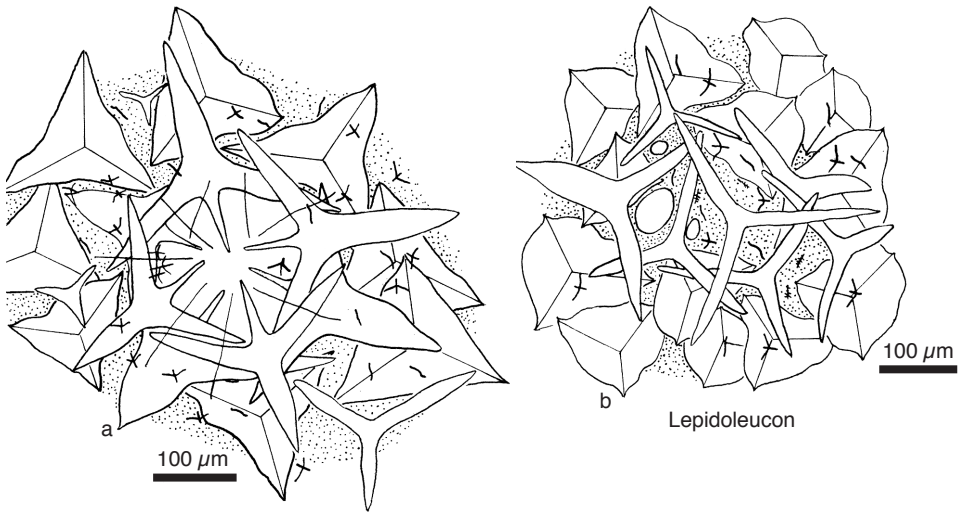


FIG. 207. Lepidoleuconidae (p. 305–306).

25–200 µm by 6–40 µm), tuning-fork (diapason) triactines (basal actine 30–70 µm by 5–8.5 µm; lateral actines 20–50 µm by 4–7 µm), pugiole tetractines in two categories (lateral actines 40–130 µm by 22–28 µm and 16–40 µm by 5.5–8.5 µm, axial actines 8–100 µm by 10–28 µm and 30–70 µm by 5.5–8.5 µm), rugose microdiactines 30–60 µm by 2–3 µm. Basal calcareous skeleton in calcite, solid, with crests and depressions on surface, built up of elongate, irregular sclerodermites, with radial orientation of crystals from longitudinal axis, 80–150 µm in maximum size. Some spicules entrapped in basal skeleton, randomly arranged and showing no sign of dissolution. Reproduction by amphiblastula larva, with unusually complex nourishment process of oocyte and embryo. A single species in Mediterranean: eastern basin (Adriatic, Ionian Sea, Crete, Malta, Tunisia), western part of the western basin (not recorded west of the Rhone delta and Algeria). Common near entrance of dark caves, more rarely on undersurface of stones, 0.5–25 m depth. Fossil skeletons recorded from a cave on Crete that emerged 1500 years ago (VACELET, 1980b) and from Pleistocene cliffs of southern Italy dating back 30,000 years (VACELET, 1991). *Pleistocene–Holocene*: Mediterranean caves.—FIG. 206a–e. \**P. massiliana*; a, several specimens *in situ* in Marseille cave, 10 m (Vacelet, 2012); b, section through apical zone, showing massive skeleton, choanocyte chambers, and surface spicules (Vacelet, 2012); c, SEM view of skeleton surface with tuning-fork spicules partially entrapped (Vacelet, 1991); d, tuning-fork triactines (Vacelet, 1964); e, calcareous spicules, triactines, pugioles, and microdiactines (Vacelet, 2012). See also Fig.

3,5c, herein, calcitic sclerodermite of the so-called flake-spherulitic or fibro-radial type in *Petrobiona massiliana* (GAUTRET, 1986); and diagrammatic vertical section through three living hypercalcified sponges possessing masses of storage cells in Fig. 3,5a–c, herein).

**Family LEPIDOLEUCONIDAE**  
**Vacelet, 1967**

[Lepidoleuconidae VACELET, 1967a, p. 54]

Baerida with leuconoid organization and irregular outer layer of scales derived from triactines. Choanoskeleton exclusively composed of scattered microdiactines. Ostia localized in a special area where triactines are not transformed into scales. Osculum with a circlet of modified tetractines. [The calcareous superficial scales derived from triactines are reminiscent of the scales of Murrayonidae and Paramurrayonidae in subclass Calcinea. The organization of the skeleton, however, is similar to that of other Baerida.] *Holocene*.

**Lepidoleucon** VACELET, 1967a, p. 54 [\**L. inflatum*; M; holotype, MNHN C1968-149]. Diagnosis as for family. Type species tiny, hemispherical, 0.4–1 mm in diameter, covered by several superficial layers of triangular or rounded scales, 160 µm

in maximum diameter, deriving from triactines. Osculum single, central, with a cirlet made by inflated lateral actines of special tetractines, whose apical actine is directed toward center of aperture. Ostia localized in lateral area, devoid of scales and bearing large triactines. Color yellowish or brownish. Choanoskeleton exclusively composed of microdiactines. Aquiferous system leuconoid, with apinucleated choanocytes. Amphiblastula larvae

(BOROJEVIC & others, 2002, p. 1199). *Holocene*: Indian Ocean (Madagascar), Western and Central Pacific (New Caledonia, Tuamotu Islands), in underwater caves and tunnels of the fore-reef zone, 3–30 m depth.—FIG. 207*a–b*. \**L. inflatum*; *a*, surface view of osculum, with tetractines, triactines, scales, microdiactines, and microtetractines; *b*, surface view of inhalant area, with triactines, scales, microdiactines, and microtetractines (Vacelet, 1967a).

# A LIST OF UPPER PALEOZOIC–MESOZOIC STROMATOPOROID-LIKE GENERA; AND EXCLUDED TAXA

COLIN W. STEARN and CARL W. STOCK

For over a century, certain upper Paleozoic to Mesozoic fossils of marine sessile benthic organisms with calcareous skeletons, many containing astrophorizae, were included with the Ordovician–Devonian Stromatoporoidea, and many of these were included in the same families as the earlier Paleozoic genera (e.g., KÜHN, 1939b; LECOMPTE, 1956). The biological affinities of many of these upper Paleozoic and Mesozoic genera are still in doubt. Like the Stromatoporoidea, they have been assigned to a variety of invertebrate groups such as the hydrozoans, sponges, bryozoans, and foraminiferans. The hydrozoan affinity was strongly supported (e.g., LECOMPTE, 1956) by the similarities of some Jurassic–Cretaceous forms to Recent Hydrozoa (see *Morphologic Affinities of the Paleozoic Stromatoporoidea to Other Fossil and Recent Groups*, p. 543–549). Only relatively recently have some genera among the Mesozoic forms been found to contain spicules or spicule pseudomorphs (e.g., G. TERMIER, H. TERMIER, & RAMALHO, 1985; H. TERMIER, G. TERMIER, & RAMALHO, 1985; WOOD, 1987) that demonstrate a relationship with the demosponges. Some of the nonspicular forms contain astrophorizae, diagnostic of the Porifera, that confirm they are sponges, but not all genera contain astrophorizae.

In the 19th century, before thin sections became a standard method of research, many genera of calcareous crusts were established with inadequate diagnoses and illustrations. Some of these have been determined to be inorganic tufas, stromatolites formed by cyanobacteria, poorly preserved corals and sponges, or calcareous algae. Most are impossible to identify consistently, cannot be traced through type specimens, and have been noted in the literature only in the original description. KÜHN (1939b, p.

60–62) gave an extensive list of these useless genera, which is not repeated here. A few of the genera that have received some comment in the literature are listed below; for others, the reader is referred to KÜHN's (1939b) list and FINKS and RIGBY (2004d).

Upper Paleozoic–Mesozoic stromatoporooid-like fossils are more difficult to study than their Ordovician–Devonian analogs. This difference is due to the limited number of paleontologists studying the late Paleozoic–Mesozoic forms. As STOCK (2001) noted, for the period 1926–2000, there were 734 publications on Ordovician–Devonian stromatoporooids, but only 230 on Carboniferous–Cretaceous forms. Whereas 6 paleontologists (R. G. S. Hudson; A. Schnorf-Steiner; G. Termier; H. Termier; D. Turnšek; R. Wood) produced more than 10 publications on Jurassic–Cretaceous stromatoporooid-like taxa from 1926 to 2000, 14 paleontologists did the same for the Ordovician–Devonian stromatoporooids (O. V. Bogoyavlenskaya; D.-Y. Dong; E. Flügel; S. Kershaw; V. G. Khromykh; A. I. Lessovaya; B. Mistiaen; H. Nestor; V. N. Riabinin; J. St. Jean; C. W. Stearn; C. W. Stock; B. D. Webby; V. I. Yavorsky). A large number of publications are representative of a major research commitment by the author to a particular taxon. Clearly, this relatively large number of specialists, in many cases interacting with each other on a regular basis, led to a more coherent understanding of the earlier stromatoporooids than was possible for later stromatoporooid-like forms.

The above-noted uncertainties with regard to the taxonomic position of many of the upper Paleozoic–Mesozoic, nonspicular, stromatoporooid-like taxa, the lack of a coherent, consistent classification system for this taxon, and the additional lack of anyone currently specializing in the study of the nonspicular

stromatoporoid-like forms has discouraged the authors from presenting here a systematic paleontology of the group. In this alphabetical list of stromatoporoid-like genera, the geologic systems from which type species were collected are indicated. Excluded taxa (either not stromatoporoid-like poriferans or not Porifera) are listed on p. 310.

- Actinostromina** GERMOVŠEK, 1954, p. 351 [*A. oppidana*; OD]. *Upper Jurassic*: Slovenia.
- Adriatella** MILAN, 1969, p. 180 [*A. poljaki* MILAN, 1969, p. 181; OD]. *Upper Jurassic*.
- Aksaeoporella** BOJKO, 1979, p. 57 [*A. arta* BOJKO, 1979, p. 58; OD]. [BOJKO (1979) placed this genus in the stromatoporoids, but it also resembles chaetetids and hydrozoans.] *Upper Triassic*: Tadjikistan (Pamirs).
- Aphralysia** GARWOOD, 1914, p. 268 [*A. carbonaria* GARWOOD, 1914, p. 269; OD]. [Several authors (e.g., PIA, 1937) have considered the genus to be a stromatoporoid, but GALLOWAY (1957) returned it to the algae.] *Carboniferous (Missippian)*: England (Westmoreland).
- Astrostylopsis** GERMOVŠEK, 1954, p. 361 [*A. slovenica*; OD] [= *Trupetostromaria* GERMOVŠEK, 1954, p. 365 (type, *T. circoporea*, OD)]. *Upper Jurassic*: Slovenia.
- Atelostroma** DONG & WANG, 1983, p. 417 [*A. jurasicum* DONG & WANG, 1983, p. 418; OD]. *Upper Jurassic*: China (Xizang).
- Axiotubullina** DONG & WANG, 1983, p. 419 [*A. columna*; OD]. *Upper Jurassic*: China (Xizang).
- Baastadiostroma** BROOD, 1972, p. 404 [*B. typicum*; OD]. *Upper Cretaceous*: Sweden.
- Burgundostromaria** TURNŠEK, 1970, p. 199 [*B. zlatibornensis* TURNŠEK, 1970, p. 200; OD]. *Upper Cretaceous*: Serbia.
- Cassianostroma** FLÜGEL, 1960, p. 51 [*C. kupperi* FLÜGEL, 1960, p. 51–52; OD]. *Triassic*: Italy.
- Ceraostroma** KÜHN, 1926, p. 413 [*C. steinmanni*; OD]. *Jurassic*: Austria.
- Circopora** WAAGEN & WENTZEL, 1887, p. 957 [*C. foveolata* WAAGEN & WENTZEL, 1887, p. 958–960; OD]. *Permian, ?Triassic*: Pakistan, Austria, Russia, Indonesia.
- Coenostella** TURNŠEK, 1966, p. 355 [*C. thomasi* TURNŠEK, 1966, p. 356; OD]. *Upper Jurassic*: Slovenia.
- Convexistroma** BOJKO, 1984b, p. 62 [*C. irregularis*; OD]. *Lower Jurassic*: Tadjikistan (Pamirs).
- Crimestroma** YAVORSKY, 1947, p. 16 [*C. borissiaki*; OD]. *Upper Jurassic*: Ukraine (Crimea).
- Cylicopsis** LE MAÎTRE, 1935, p. 43 [*\*Stromatomorpha (Cylicopsis) atlantis* LE MAÎTRE, 1935, p. 43; OD]. *Lower Jurassic*: Morocco.
- Dehornaeporella** TERMIER in G. TERMIER, H. TERMIER, & RAMALHO, 1985, p. 204 [*\*Stromatopora choffati* DEHORNE, 1917a, p. 118; OD]. [G. TERMIER, H. TERMIER, & RAMALHO (1985) noted the presence of monaxon spicules (styles) in the type species.] *Upper Jurassic*: Egypt (Sinai), Israel, Oman, Portugal, Slovenia.
- Dongqiastroma** DONG & WANG, 1983, p. 415 [*\*D. lamellatum*; OD]. *Upper Jurassic*: China (Xizang).
- Dongqiastromaria** DONG & WANG, 1983, p. 417 [*\*D. grossa*; OD]. *Upper Jurassic*: China (Xizang).
- Desmopora** YAVORSKY, 1947, p. 17 [*\*D. listrigonorum*; OD]. *Upper Jurassic*: Ukraine (Crimea).
- Disparistromaria** SCHNORF, 1960b, p. 439 [*\*D. tenuissima* SCHNORF, 1960b, p. 440; OD]. *Cretaceous*: Switzerland.
- Ellipsactinia** STEINMANN, 1878, p. 116 [*\*E. ellipsoidea* STEINMANN, 1878, p. 117; OD]. *Upper Jurassic*: Austria.
- Emscheria** SCHNORF-STEINER, 1958, p. 461 [*\*E. netherensis* SCHNORF-STEINER, 1958, p. 462; OD]. *Upper Cretaceous*: France.
- Gurumdistroma** BOJKO, 1984b, p. 65 [*\*G. astrorhizoides*; OD]. *Lower Jurassic*: Tadjikistan (Pamirs).
- Hudsonella** TURNŠEK, 1966, p. 361 [*\*H. otlicensis* TURNŠEK, 1966, p. 362; OD]. *Upper Jurassic*: Slovenia.
- Incrustospongia** MOLINEUX, 1994, p. 980 [*\*I. meandrica* MOLINEUX, 1994, p. 980–981; OD]. [FINKS & RIGBY (2004c) placed this laminated encrusting form in Demospongiae, order and family Uncertain.] *Carboniferous (Pennsylvanian)*: USA (Texas).
- Jillua** KRUMBECK, 1913, p. 134 [*\*J. tubifera*; OD]. [Comments in FLÜGEL & SY (1959); see also YABE & SUGIYAMA (1935) and KÜHN (1939b), who based the genus on surface features only.] *Upper Triassic*: Indonesia.
- Komia** KORDE, 1951, p. 181 [*\*K. abundans*; OD] [= *Ungdarella* MASLOV, 1956, p. 73 (type, *U. americana*; OD), *non* KORDE, 1951, *non* TOOMEY & JOHNSON, 1968, p. 577]. [Although originally described as an alga and confirmed as such by STOCK & others (1992), WILSON, WAINES, & COOGAN (1963) placed these fossils in the Stromatoporoidea.] *Carboniferous (Pennsylvanian)*: Japan, Russia (Urals), USA (southwestern states).
- Lamellata** FLÜGEL & SY, 1959, p. 60 [*\*L. wahneri* FLÜGEL & SY, 1959, p. 61; OD]. [The genus was compared with *Ellipsactinia*, *Nigriporella*, and *Sphaeractinia* by FLÜGEL & SY (1959). KONISHI (1959) wrote that the genus is a synonym of *Tubiphytes* MASLOV.] *Upper Triassic*: Austria, Greece (Corfu).
- Lithopora** TORNQUIST, 1900, p. 128 [*\*L. koeneni*; OD]. *Triassic*: Italy.
- Milleporidium** STEINMANN, 1903, p. 2 [*\*H. remesi*; OD]. *Upper Jurassic*: Austria.
- Millestroma** GREGORY, 1898, p. 340 [*\*M. nicholsoni* GREGORY, 1898, p. 341; OD]. [The genus is composed of bundles of fine tubes that suggest affinity to the bryozoans (DEHORNE, 1920); however, GREGORY (1898) placed it in the hydrozoans.] *Upper Cretaceous*: Egypt.
- Myrioporina** KÜHN, 1939b, p. 34 [*\*Myriopora verbeeki* VOLZ, 1904, p. 187; OD]. [HUDSON (1956a) considered that *Myriopora* of REUSS (1846) was a *lapsus calami* for *Myriopora* DE BLAINVILLE (1830) and that *Myriopora* VOLZ, 1904, was a homonym

- of *Myriopora* REUSS and *Myriopora* DE BLAINVILLE and hence was not available, and to resolve the nomenclatural problem, he recognized KÜHN's genus *Myrioporina* as valid to replace the names that DE BLAINVILLE, REUSS, and VOLZ had used for this taxon.] *Jurassic*: Indonesia (Sumatra).
- Palaeoaplysina** KROTOW, 1888, p. 549 [\**P. laminaeformis*; OD; neotype P209-3 (TCHUVASCHOV, 1973)] [= *Mezenia* STUCKENBERG, 1895, p. 130 (type, *M. rozeni*, OD); FLÜGEL, 1961b; = *Uralotimania* RIABININ, 1915, p. 23 (type, *U. reticulata*, OD)]. [This is a common reef-forming fossil organism of the lower Permian and Carboniferous rocks of western and arctic North America and Russia. It has a unique cellular microstructure and a complex system of internal canals parallel to the base in the lower part, bending upward to the upper surface. The genus has generally been assigned to either the hydrozoans or sponges and suggestions that it is an alga are rejected by recent researchers. Recent papers on this common fossil include: DAVIES (1971); DAVIES & NASSICHUK (1973, 1986); WATKINS & WILSON (1989).] *Carboniferous (Pennsylvanian)–lower Permian*: Canada (arctic islands, Yukon), Russia (Urals, Russian platform), USA (California, Idaho).
- Palacomillepora** GABILLY & LAFUSTE, 1957, p. 355 [\**P. liassica*; OD]. *Lower Jurassic*: France.
- Paradehornella** BOİKO, 1989, p. 56 [\**P. astriferum*; OD]. *Middle Jurassic*: Tadjikistan (Pamirs).
- Paramilleporella** FENNINGER in FENNINGER & HÖTZL, 1965, p. 20 [\**P. gracilis*; OD]. *Upper Jurassic*: Austria.
- Paratubuliella** DONG & WANG, 1983, p. 423 [\**P. pertabulata*; OD]. *Upper Jurassic*: China (Xizang).
- Parksia** LECOMPTE, 1952a, p. 24 [\**Stromatopora douvillei* DEHORNE, 1918, p. 220; OD]. *Upper Jurassic*: Tunisia.
- Paronaria** TERMIER & TERMIER, 1984, p. 236 [\**Parkeria provali* PARONA in PARONA, CREMA, & PREVER, 1909, p. 161; OD]. *Cretaceous*: Italy.
- Periomipora** H. TERMIER, G. TERMIER, & RAMALHO, 1985, p. 980 [\**P. elegantissima*; OD]. [H. TERMIER, G. TERMIER, & RAMALHO (1985) noted the presence of monaxon spicules in the type species.] *Upper Jurassic*: Portugal.
- Reticullina** TURNŠEK, 1966, p. 364 [\**R. rectangularis* TURNŠEK, 1966, p. 365; OD]. *Upper Jurassic*: Slovenia.
- Rhizoporiidum** PARONA in PARONA, CREMA, & PREVER, 1909, p. 158 [\**R. irregulare*; OD]. *Cretaceous*: Italy.
- Sarawakia** HASHIMOTO, 1973, p. 210 [\**S. ellipsactinoides* HASHIMOTO, 1973, p. 211; OD]. *Upper Jurassic*: Malaysia (Sarawak).
- Saresiastroma** BOİKO, 1989, p. 57 [\**S. conceptum* BOİKO, 1989, p. 58; OD]. *Middle Jurassic*: Tadjikistan (Pamirs).
- Sarmentofascis** G. TERMIER, H. TERMIER, & VACHARD, 1977, p. 146 [\**Cladocoropsis cretacia* TURNŠEK, 1968, p. 357; OD]. *Lower Cretaceous*: Montenegro.
- Scaniostroma** BROOD, 1972, p. 396 [\**S. gracilis*; OD]. Resembles the spongiomorphs (see discussion of this group, p. 311). *Upper Cretaceous*: Sweden.
- Sedekiastroma** BOİKO, 1984b, p. 60 [\**S. liassica* BOİKO, 1984b, p. 61; OD]. *Lower Jurassic*: Tadjikistan (Pamirs).
- Shamovella** RAUSER-CHERNOUSOVA, 1950, p. 17 [\**S. obscura* MASLOV, 1956, p. 82; SD RIDING, 1993; see discussions regarding the validity of *Shamovella* versus *Tubiphytes*: RIDING & GUO (1992); RIDING (1993); RIDING & BARKHAM (1999)] [= *Tubiphytes* MASLOV, 1956, p. 82 (type, *T. obscurus*; OD); = *Nigriporella* RIGBY, 1958, p. 584 (type, *N. magna*, OD, lost); Permian, Texas, USA]. [RIDING & GUO (1992) discussed the possible affinity of this widespread fossil as a cyanobacterium, hydrozoan, rhodophyte, poriferan, or foraminiferan and concluded that it is most likely a sponge.] *Carboniferous–Cretaceous (mainly Permian)*.
- Siphostroma** STEINER, 1932, p. 79 [\**S. arzieri* STEINER, 1932, p. 99; OD]. [Discussed by YABE & SUGIYAMA (1935), KÜHN (1939b), and LECOMPTE (1952a).] *Cretaceous*: Switzerland.
- Sphaeractinia** STEINMANN, 1878, p. 115 [\**S. diceratina*; OD]. *Upper Jurassic*: Austria.
- Sporadoporiidum** GERMOVŠEK, 1954, p. 370 [\**S. rakoveci*; OD]. *Upper Jurassic*: Slovenia.
- Steinerella** LECOMPTE, 1952a, p. 26 [\**Stromatopora mecosola* STEINER, 1932, p. 103; OD]. *Lower Cretaceous*: Switzerland.
- Stromatoporellata** BAKALOW, 1910, p. 5 [\**S. mammillaris*; OD]. [Described on the basis of surface characteristics only. Holotype not available (see FLÜGEL & SY, 1959).] *Upper Triassic*: Bulgaria.
- Stromatoporellina** KÜHN, 1927, p. 550 [\**Stromatoporella haugi* DEHORNE, 1917b, p. 70; OD] [= *Astro-rhizopora* SCHNORF-STEINER, 1958, p. 454 (type, *Stromatoporella haugi* DEHORNE, 1917b, p. 70, OD)]. *Upper Cretaceous*: France.
- Stromatoporina** KÜHN, 1927, p. 550 [\**Stromatopora tornquisti* DENINGER, 1906, p. 66; OD]. *Triassic*: Italy (Sardinia).
- Stromatorhiza** BAKALOW, 1906, p. 13 [\**Thamnaraea? granulosa* KOPY, 1888, p. unknown; OD]. [HUDSON (1955a) gave the most complete discussion and suggested synonymy with *Cyllicopsis* LE MAITRE, *Astrotylopsis* GERMOVŠEK, and *Trupetostromaria* GERMOVŠEK.] *Jurassic*: Switzerland.
- Stromatostroma** BAKALOW, 1910, p. 4 [\**S. triassicum*; OD]. *Triassic*: Bulgaria.
- Tauripora** YAVORSKY, 1947, p. 16 [\**T. astroites* YAVORSKY, 1947, p. 16–17; OD]. *Permian*: Crimea.
- Tosastroma** YABE & SUGIYAMA, 1935, p. 158 [\**T. tokunagai* YABE & SUGIYAMA, 1935, p. 185; OD]. *Upper Jurassic*: Japan.
- Tubuliella** TURNŠEK, 1966, p. 357 [\**T. fluegeli*; OD]. *Upper Jurassic*: Slovenia.
- Tubulopareites** SCHNORF, 1960a, p. 430 [\**T. constans* SCHNORF, 1960a, p. 432; OD]. *Upper Cretaceous*: France.
- Xizangstromatopora** DONG, 1981, p. 118 [\**X. densata* DONG, 1981, p. 119; OD]. *Upper Jurassic*: China (Xizang).
- Yezoactinia** HASHIMOTO, 1960, p. 95 [\**Y. shotombestuensis* HASHIMOTO, 1960, p. 96; OD]. *Upper Jurassic*: Japan.



## EXCLUDED TAXA

- Aprutinopora** PARONA in PARONA, CREMA, & PREVER, 1909, p. 150 [*\*A. osimoi* PARONA in PARONA, CREMA, & PREVER, 1909, p. 151; OD]. [Questionably a bryozoan (KÜHN, 1939b).] *Cretaceous*: Italy.
- Cerkesia** MOISEEV, 1944, p. 24 [*\*C. robinsoni* MOISEEV, 1944, p. 25; OD] [= *Cercessia* FLÜGEL, 1961b, p. 74, *lapsus calami*]. [MOISEEV (1944) suggested relationships with the actinostromatids, siphonostromatids, and burgundiids, but his illustrations suggest this may be a bryozoan. Used by only MOISEEV.] *Upper Triassic*: Georgia and Russia (Caucasus).
- Cycloporidium** PARONA in PARONA, CREMA, & PREVER, 1909, p. 157 [*\*C. tuberiforme*; OD]. ["Description and illustration very unclear" (KÜHN, 1939b, p. 58).] *Cretaceous*: Italy.
- Elephantaria** OPPENHEIM, 1930, p. 1 [*\*E. lindstroemi* OPPENHEIM, 1930, p. 2; OD]. [Possibly a scleractinian coral.] *Cretaceous*: Austria.
- Lichuanopora** FAN, RIGBY, & ZHANG, 1991, p. 66 [*\*L. bancaoensis*; OD]. [Skeleton consists of open, longitudinal tubes with walls penetrated by pores. Possibly a hydrozoan.] *upper Permian*: China (Hubei).
- Likinia** IVANOVA & ILKHOVSKY in ILKHOVSKY, 1973, p. 11 [*\*L. nikitini*; OD]. [May be a hydrozoan.] *Carboniferous*: Russia (Oka River).
- Lophiostroma** NICHOLSON, 1891a, p. 160 [*\*Labechia? schmidtii* NICHOLSON, 1886a, p. 16; OD]. [SUGIYAMA (1939) used this lower Paleozoic genus for calcareous crusts, identifying them as belonging to the genus *Lophiostroma*. Also, MORI (1980, p. 238–239) recorded *Lophiostroma ozawai* YABE & SUGIYAMA, 1931a, as a brachiopod shell. A brief discussion of the need to exclude these "calcareous crusts" from a relationship with the type species of *Lophiostroma* (?*Labechia*) *schmidtii* (NICHOLSON, 1891a), is also included in the systematic descriptions of the Labechiida, p. 749.] *Carboniferous–Permian*: Japan.
- Megastroma** MONTANARO-GALLITELLI, 1954, p. 79 [*\*M. lecomptei*; OD]. [FLÜGEL & FLÜGEL-KÄHLER (1968) suggested this may be an inorganic structure.] *Permian*: Italy (Sicily).
- Neostroma** TORNIQUIST, 1901, p. 1117 [*\*N. sumatraense*; OD]. [FLÜGEL (1961b) synonymized this genus with the scleractinian coral *Actinacis* D'ORBIGNY.] *Cretaceous*: Indonesia (Sumatra).
- Parkeria** CARPENTER in CARPENTER & BRADY, 1870, p. 724 [*\*P. sphaerica* CARTER, 1877, p. 61; OD] [= *Millarella* CARTER, 1888, p. 178 (type, *M. cantabrigiensis*, OD)]. [A hydrozoan cnidarian (TERMIER & TERMIER, 1984).] *Cretaceous*: England, India.
- Porosphaera** STEINMANN, 1878, p. 120 [*\*Millepora globularis* PHILLIPS, 1829, p. 155; OD]. [In Calcareo (FINKS & RIGBY, 2004d, p. 756).] *Upper Cretaceous*: Czech Republic, England, France, Germany.
- Rhizostromella** PARONA in PARONA, CREMA, & PREVER, 1909, p. 160 [*\*R. apennina*; OD]. ["Description and illustration worthless" (KÜHN, 1939b, p. 62).] *Cretaceous*: Italy.
- Sphaerostromella** YABE & SUGIYAMA, 1931a, p. 123 [*\*S. shikokuensis*; OD]. [The skeleton is spherical with zooids like a bryozoan. It has been considered to be a bryozoan (KÜHN, 1939b), hydrozoan (FLÜGEL, 1961b), or not a stromatoporoid (FLÜGEL & FLÜGEL-KÄHLER, 1968).] *Carboniferous*: Japan.
- Stromactinia** VINASSA DE REGNY, 1911, p. 19 [*\*S. triassica* VINASSA DE REGNY, 1911, p. 20; OD]. [STEINER (1932) related this genus to *Ellipsactinia*. FLÜGEL (1961b, p. 71) placed it in the alga *Sphaerocodium*.] *Upper Triassic*: Hungary (Lake Balaton).
- Stromaporidium** VINASSA DE REGNY, 1915, p. 108 [*\*S. globosum*; OD]. [The genus has been placed in the Hydrozoa (VINASSA DE REGNY, 1915), algae (PARONA, 1928; SUGIYAMA, 1939), or *incerta sedis* (FLÜGEL & SY, 1959).] *Upper Triassic*: Indonesia.
- Thalaminia** STEINMANN, 1878, p. 112 [*\*Ceriopora crispa* GOLDFUSS, 1826, p. 38; OD]. [According to FLÜGEL (1961b, p. 71), this is a nonstromatoporoid sponge, but FINKS, REID, and RIGBY (2004) did not include it with the Porifera.] *Upper Jurassic–Lower Cretaceous*: France.

# SYSTEMATIC DESCRIPTIONS OF THE CLASS AND ORDER UNCERTAIN: FAMILY DISJECTOPORIDAE

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The reef facies of the Permian and Late Triassic in the Tethyan faunal realm contains encrusting and domical carbonate fossils of organisms composed of rods that form a framework. These fossils are now composed of calcite but may originally have been aragonite, as many show recrystallization microfabrics. Their systematic position has been controversial, and they have commonly been placed in the Hydrozoa (KÜHN, 1939b; LECOMPTE, 1956; FLÜGEL & SY, 1959) and also referred to as late Paleozoic stromatoporoids. Like the stromatoporoids, their framework skeleton is commonly traversed by tabulated longitudinal and tangential canals or tubes. These have suggested an affinity to the Cnidaria and particularly to the Hydrozoa, but similar tubes are found in several groups of hypercalcified sponges. Now that the Paleozoic stromatoporoids are recognized as having structures closely resembling living hypercalcified sponges, the disjectoporids are here tentatively placed in the Porifera, but their affinity with the major groups of this phylum is obscured by their total lack of preserved spicules.

The spongiomorphs, Middle Triassic to Upper Cretaceous carbonate fossils, are composed of a framework of largely longitudinal rods that resembles that of the disjectoporids. They have been linked to the disjectoporids and also considered to have been hydrozoans (e.g., FLÜGEL & SY, 1959). However, recent work by GAUTRET and associates (GAUTRET, EZZOUBAIR, & CUIF, 1992; GAUTRET, DAUPHIN, & CUIF, 1994) has shown that the spongiomorphs are cnidarians related to the scleractinian superfamily

Poriticae GRAY, 1842. They are therefore not considered further in this volume devoted to the hypercalcified sponges.

## Class and Order UNCERTAIN (?DEMOSPONGIAE or ?CALCAREA)

### Family DISJECTOPORIDAE Tornquist, 1901

[Disjectoporidae TORNQVIST, 1901, p. 1121; LECOMPTE, 1956, p. 138; KÜHN, 1939b, p. 48; FLÜGEL & SY, 1959, p. 14] [=Coenostromidae WAAGEN & WENTZEL, 1887, p. 925, *partim*; =Coenostromatidae WENTZEL, 1889, p. 18; *non* Coenostromatidae WAAGEN & WENTZEL; STEARN & others, 1999]

Laminar, incrusting, and irregular carbonate skeletons composed of a three-dimensional meshwork of longitudinal and tangential rods (trabeculae), thickened and fused where they intersect, enclosing rounded interspaces, forming an irregular grid in longitudinal sections. Skeletal framework traversed by long, tabulated tubes (canals) and irregular, poorly defined, tangential canal systems. *Permian–Triassic*.

*Disjectopora* WAAGEN & WENTZEL, 1887, p. 947  
[\**D. milleporaeformis* WAAGEN & WENTZEL, 1887, p. 948; OD]. Laminar, encrusting to domical skeleton composed of longitudinal (or radial) and tangential (or concentric) rods, intersecting and thickening at subspherical nodes to form irregular, three-dimensional grid. Interspace voids rounded, subspherical, irregularly superposed, aligned tangentially in longitudinal section, giving skeleton concentric banding. Tangential rods may appear to unite into tangential sheets, or laminae, perforated by rounded pores approximately the diameter of nodes where rods thicken at intersections. Vaguely defined, locally tabulated, longitudinal, cylindrical voids approximately twice the diameter of interspaces widely scattered in skeleton. In tangential section, rods cut as circles between

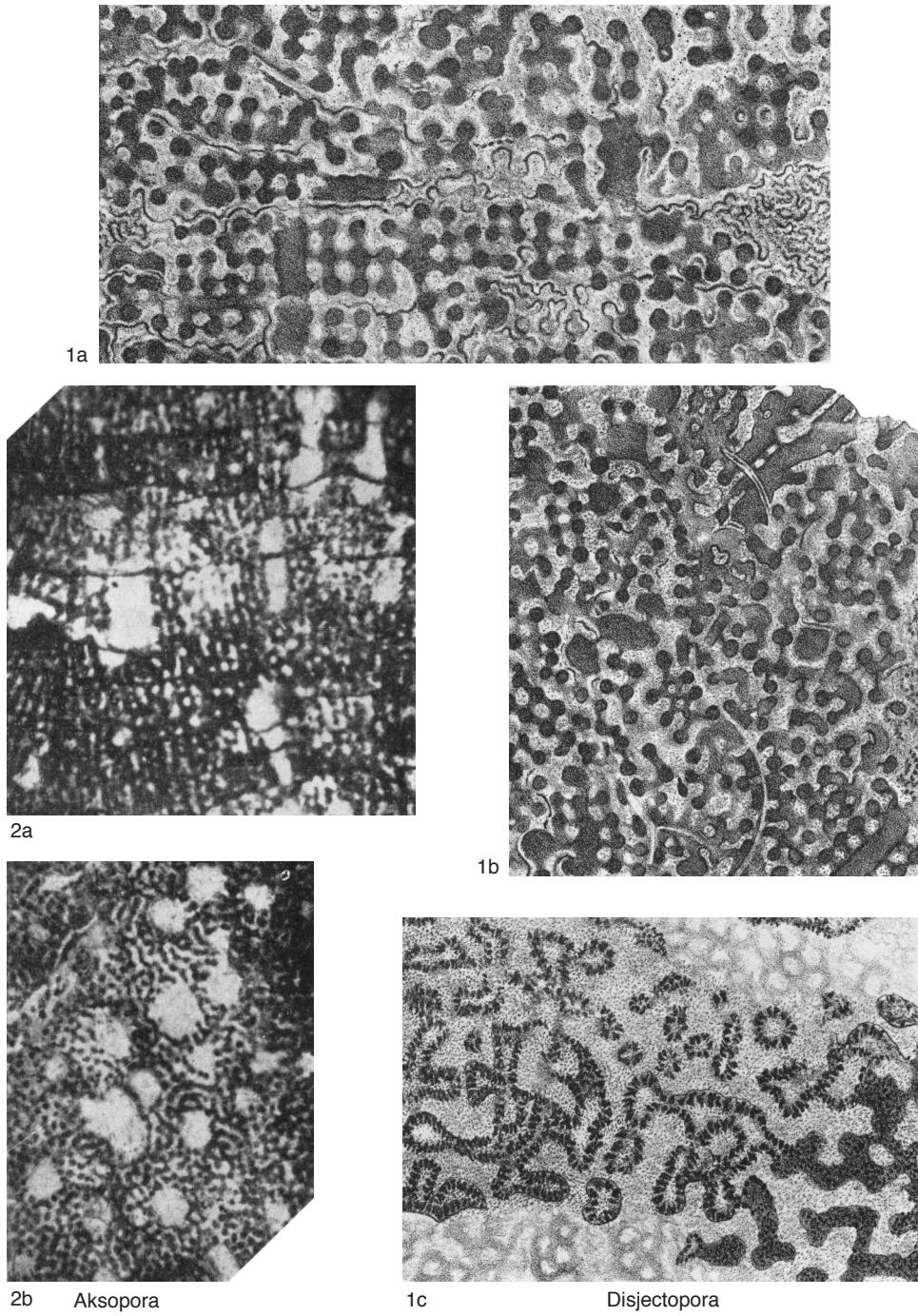


FIG. 208. Disjectoporidae (p. 311–313).



nets of tangential rods and joined into irregular masses perforated by round pores where section cuts nets. Poorly defined, tangential canal systems may be evident. *upper Permian—Upper Triassic, ?Upper Jurassic*: Pakistan, South China, Japan, Italy, Indonesia, ?Canada (eastern continental shelf).—FIG. 208, 1a–c. \**D. milleporaeformis*, Salt Range, Pakistan; *a*, longitudinal section,  $\times 50$ ; *b*, tangential section,  $\times 50$ ; *c*, part of longitudinal section (*a*) in altered state,  $\times 100$  (Waagen & Wentzel, 1887).

**Aksopora** BOIKO, 1970b, p. 50 [497] [\**A. tenuitrabeculata*; OD] [= *Aksupora* BOIKO, 1979, p. 55 (type, *A. tenuitrabeculata* BOIKO, 1979, p. 56, *lapsus calami*)]. Skeleton domical, composed of longitudinal rods, regularly joined by tangential rods to form porous, tangential laminae that produce latilamination. Network of rods traversed by long, wide, tabulated, longitudinal canals without walls, passing through several latilaminae. In tangential section, rods joined into network with round interspaces. Astorhizae inconspicuous. Similar to *Pamirporora* but with longer longitudinal canals. *Upper Triassic*: Pamir Mountains, Tadjikistan.—FIG. 208, 2a–b. \**A. tenuitrabeculata*, holotype, IGD1492, Norian–Rhaetian; *a*, longitudinal section through axis of skeleton showing longitudinal canal system,  $\times 6$ ; *b*, tangential section,  $\times 6$  (Boiko, 1970b).

**Arduorhiza** WENTZEL, 1889, p. 1–24 [\**Carterina pyramidata* WAAGEN & WENTZEL, 1887, p. 945–947; OD] [= *Carterina* WAAGEN & WENTZEL, 1887, p. 944, obj., *non* BRADY, 1884, a foraminiferan; = *Carta* STECHOW, 1921, p. 253, obj; = *Carterinula* STRAND, 1928a, p. ?1–8 (see LECOMPTE, 1956, p. 138; STOCK & others, 1992, p. 10; no type species designated, according to STOCK & others, 1992)]. Skeleton conical with apex down, formed of highly irregular meshwork of rods without prominent or extensive longitudinal or tangential elements, enclosing subspherical interspaces, traversed by wide, prominent, longitudinal canals without walls, and similar tangential, serpentine, and radial canals prominent in tangential section. Tabulae rare. Type shows some canals divided radially by thin, so-called pseudosepta with swollen tips; canals may be an overgrown, parasitic, or commensal organism (Fig. 209c). *upper Permian*: Pakistan (Salt Range), Slovenia.—FIG. 209a–c. \**A. pyramidata*, Salt Range; *a*, tangential section showing canal systems and subspherical interspaces (matrix is dark),  $\times 50$ ; *b*, longitudinal section (matrix is dark),  $\times 50$ ; *c*, fractured surface showing minute canals with so-called pseudosepta (matrix is white),  $\times 30$  (Waagen & Wentzel, 1887).

**Balatonia** VINASSA DE REGNY, 1908, p. 13–14 [\**B. koechi* VINASSA DE REGNY, 1908, p. 14–17; OD]. Domical to upwardly expanding carbonate skeletons, a few centimeters across, with interior zones of open, irregular structure and peripheral zones dominated by closely set, longitudinal rods. In interior zone, rods, about 50 micrometers wide, irreg-

ular in cross section, join to form open network with vermiform interspaces generally radiating outward from axial growth center. In peripheral zones, rods, mostly longitudinal, anastomosing, joined at intervals by swelling that may be aligned locally tangentially but not sufficiently to produce concentric laminae or marked latilamination. In tangential section of peripheral zones, rods of irregular cross section enclose vermiform and labyrinthine interspaces. Large (up to 0.2 mm diameter), round, longitudinal, sparsely tabulated canals present in the peripheral zones of some specimens or species. *middle Permian, Upper Triassic*: ?South China, Austria, Hungary.—FIG. 210, 1a–c. \**B. koechi*, Lake Balaton, Hungary; *a*, longitudinal section of peripheral zone,  $\times 5$ ; *b*, tangential section of interior zone,  $\times 5$ ; *c*, longitudinal section,  $\times 7$  (Vinassa de Regny, 1911).

**Cancellistroma** WU, 1991, p. 98 [\**C. ramosa*; OD] [= *Concentristroma* WU, 1991, p. 99 (type, *C. eucalla*, OD); = *Tubulistroma* WU, 1991, p. 100 (type, *T. irregularis*, OD); = *Fungistroma* WU, 1991, p. 101 (type, *F. daemonia*, OD)]. Skeleton ramose, highly irregular or encrusting, composed of longitudinal and tangential rods, swollen at their intersections, forming a grid in which one or the other is more prominent. Skeleton traversed by longitudinal tubes or canals wider than interspaces between rods, in some species of several different sizes. Tangential canal systems present in some species. *middle Permian*: China (Guangxi).—FIG. 211, 1. \**C. ramosa*, holotype, longitudinal section, No. XB36-4-5, Maoku Formation, Xiangbo,  $\times 2$  (Wu, 1991).

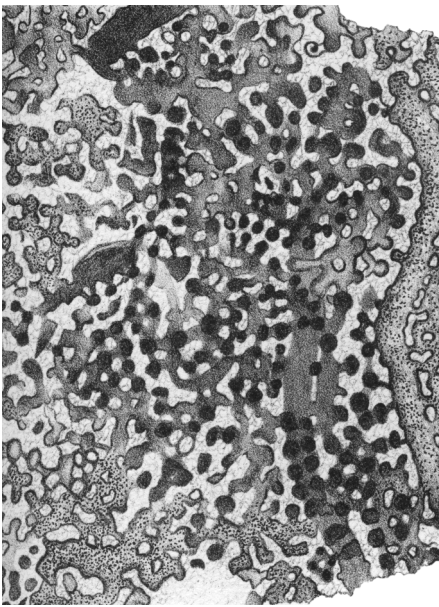
**Irregulatozora** WAAGEN & WENTZEL, 1887, p. 951 [\**I. undulata* WAAGEN & WENTZEL, 1887, p. 952; OD]. Laminar to encrusting skeleton of highly irregular longitudinal and tangential rods, thickened to nodes at their intersections, enclosing rounded voids in both longitudinal and vertical sections, forming an irregular meshwork penetrated by longitudinal and tangential canals. Longitudinal canals short, without walls, subcircular in cross section, with widely scattered tabulae. Tangential canals irregular, short, vermiform openings in meshwork, without evident pattern. Similar to *Disjectopora* but more irregular. *upper Permian, ?Upper Triassic*: Pakistan, ?Indonesia.—FIG. 211, 2a–b. \**I. undulata*, Salt Range, Pakistan; *a*, tangential section,  $\times 5$ ; *b*, longitudinal section, dark areas are interspaces or canals,  $\times 38$  (Waagen & Wentzel, 1887).

**Pamirporora** BOIKO, 1970b, p. 49 [492] [\**P. concentrica*; OD]. Skeleton domical, irregular to columnar, composed of distinct axial and peripheral zones. In axial zone, rods merge into continuous network to enclose longitudinal cylindrical canals. In peripheral zone, rods (about 50 micrometers across) largely separate but joined at intervals to form dense laminae. Tabulated, longitudinal canals (about 0.3 mm in diameter) common in

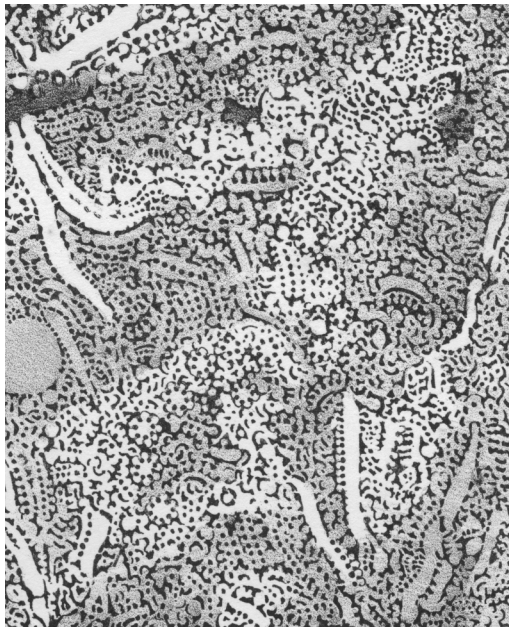


a

Arduorhiza



b



c

FIG. 209. Disjectoporidae (p. 313).

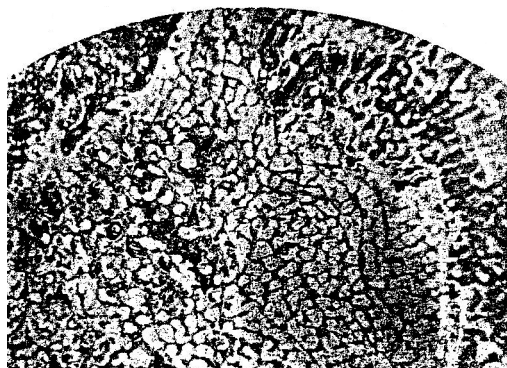




1a

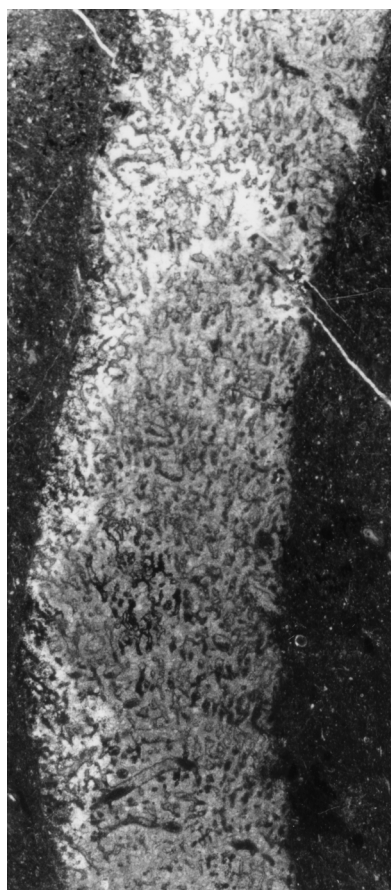


1b



1c

Balatonia



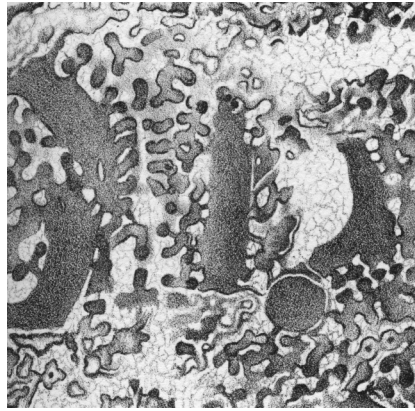
2

Pseudopalaeoaplysina

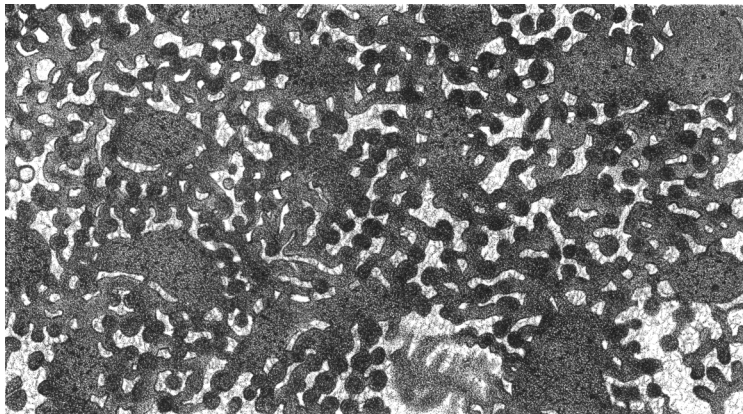
FIG. 210. Disjectoporidae (p. 313–319).



1  
Cancellistroma



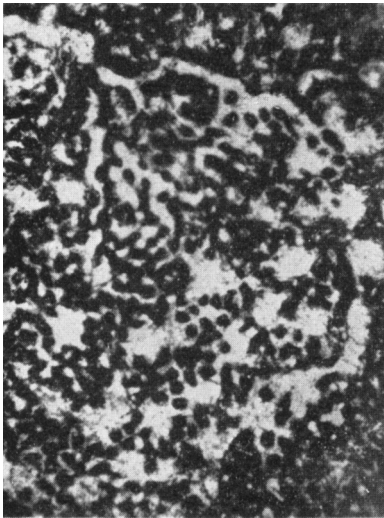
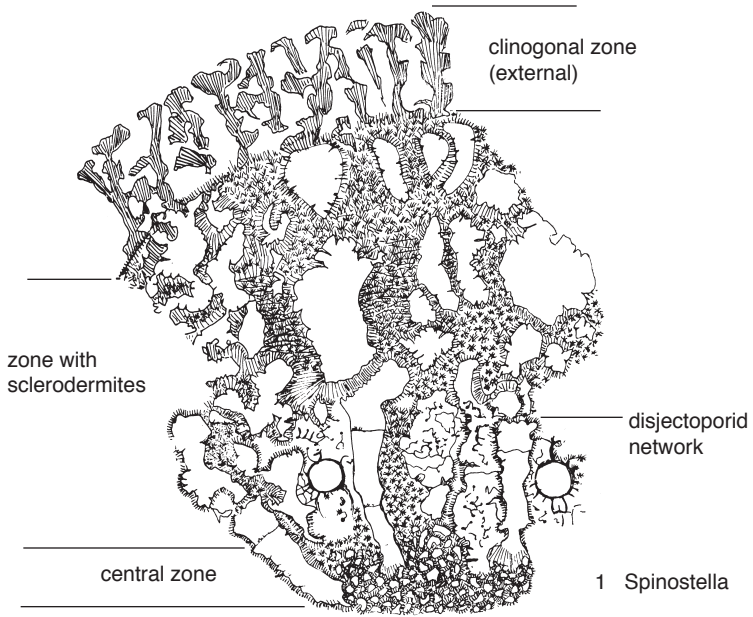
2a  
Irregulatopora



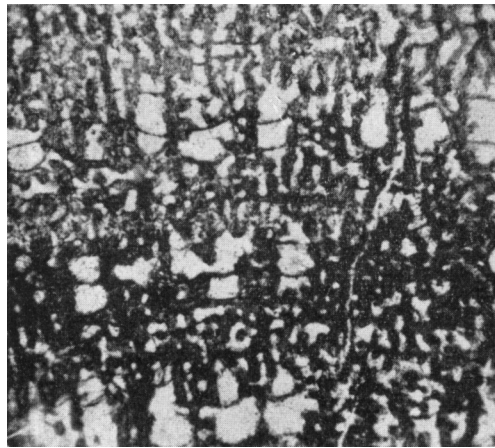
2b

FIG. 211. Disjectoporidae (p. 313).





2a



2b

Pamiropora

FIG. 212. Disjectoporidae (p. 313–320).

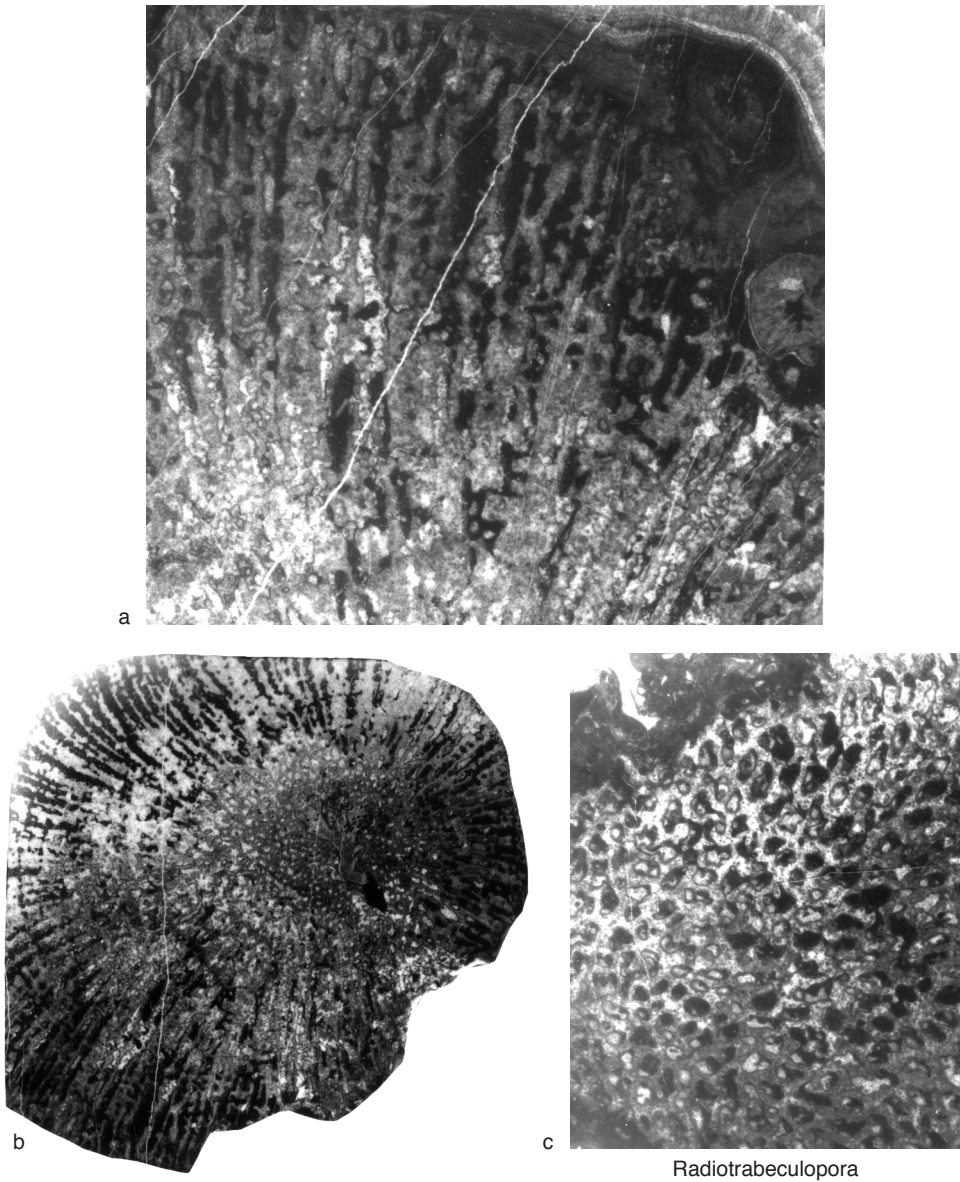


FIG. 213. Disjectoporidae (p. 319–320).

peripheral zone, in concentric zones separated by zones without canals, resulting in prominent latilamination. In tangential section, smaller canals in form of astrophorae common. *Upper Triassic*: Tadjikistan (Pamir Mountains).—FIG. 212, 2a–b. \**P. concentrica*; a, longitudinal section, peripheral zone,  $\times 16$ ; b, tangential section showing astrophorae and cut rods, IGD 1500, Norian–Rhaetian, south-eastern Pamirs,  $\times 16$  (Boiko, 1970b).

*Pseudopalaeoaplysina* FAN, RIGBY, & ZHANG, 1991, p. 66 [*\*P. sinensis*; OD]. Skeleton thin plate (about 0.5 mm), apparently attached at one edge, with smooth lateral sides, composed of rods fanning outward and upward from axial plane. Rods dividing outward, discontinuous in longitudinal section, circular in cross section, or more commonly united irregularly laterally to enclose longitudinal interspaces of circular, labyrinthine, and serpentine cross sections.

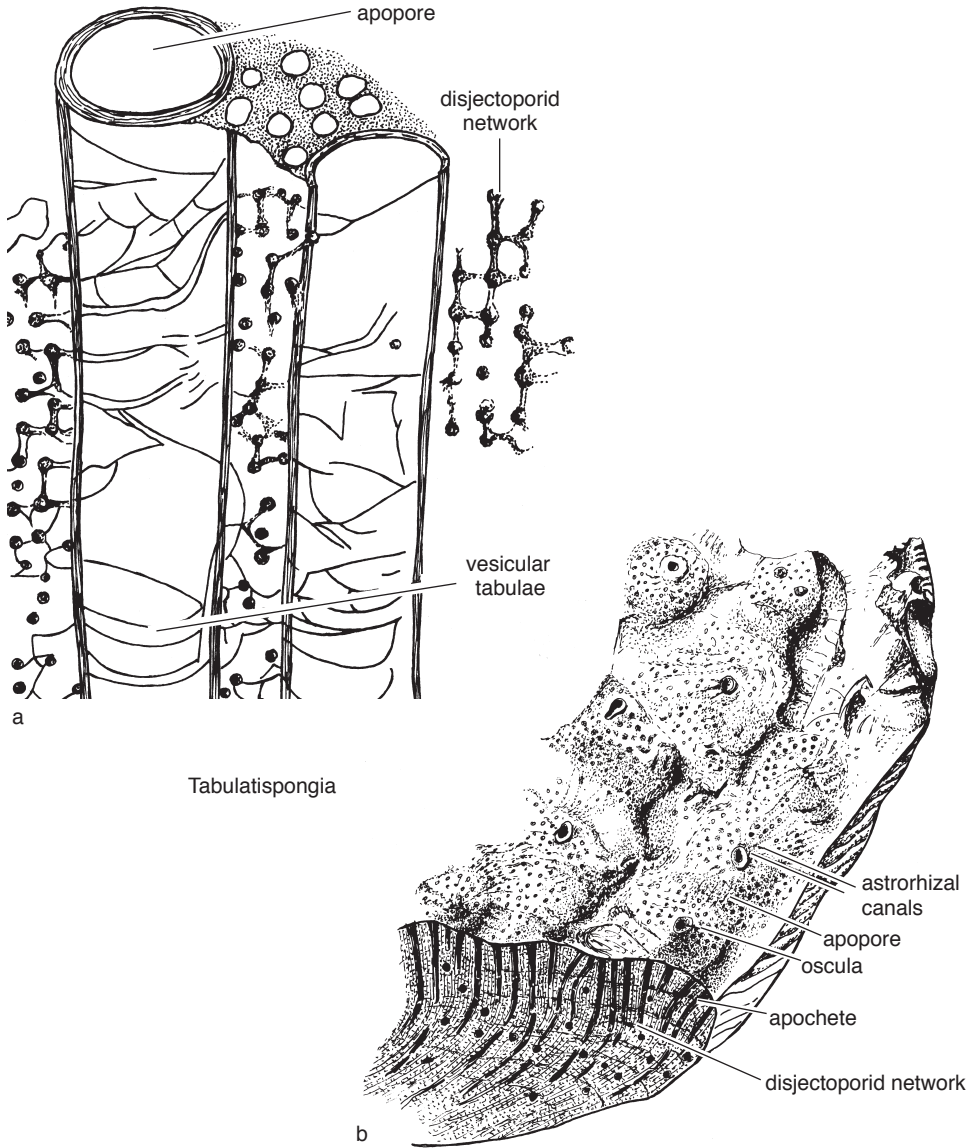


FIG. 214. Disjectoporidae (p. 320).

Interspaces, where circular in section, may resemble longitudinal canals but not crossed by dissepiments or tabulae and completely infiltrated by sedimentary matrix. Tangential structures inconspicuous. *middle Permian*: China (Guangxi).—FIG. 210,2. \**P. sinensis*, holotype, IG0094, Maoku Formation, Xiangbo, longitudinal section,  $\times 2$  (Stearn, 2010a). **Radiotrabeulopora** FAN, RIGBY, & ZHANG, 1991, p. 56 [\**R. xiangboensis*; OD] [= *Tubulispongia* WU,

1991, p. 35 (type, *T. concentrica*, OD); = *Flabellisclera* WU, 1991, p. 36 (type, *F. discreta*, OD); = *Gigantosclera* WU, 1991, p. 38 (type, *G. deformis*, OD); = *Gracilitubulus* WU, 1991, p. 39 (type, *G. perforatus*, OD); = *Fungispongia* WU, 1991, p. 39 (type, *F. circularis*, OD) (see FINKS & RIGBY, 2004d, p. 624)]. Skeleton irregular, encrusting to columnar, composed of central and peripheral zones. Peripheral zones composed of longitudinal



rods, merging and dividing but generally parallel, interrupted by numerous small pores, united by short bridges (nodellike swellings) that are not aligned to form persistent tangential structures, in type species breaking up into nodes (i.e., beaded). Interspaces longitudinally elongated, approximately width of rods (about 0.5 mm). In axial zones, rods merge to enclose subcylindrical interspaces, producing a continuous network structure traversed by astrorhizal canals in some species. *lower Permian–upper Permian*: USA (California), South China (Guangxi, Yunnan), Tunisia. — FIG. 213a–c. \**R. xiangboensis*, Maoku Formation, Xiangbo, China; *a*, holotype, longitudinal section in peripheral zone showing rods joined by short bridges, IG 5154,  $\times 5$ ; *b*, section of whole holotype showing peripheral and axial zones, IG 5154,  $\times 2$ ; *c*, tangential section of axial zone, paratype, IG 5155,  $\times 4$  (Stearn, 2010a).

**Spinostella** TERMIER & TERMIER, 1980, p. 4 [\**S. praecursor*; OD; no number or repository given]. Skeleton cylindrical; composed of three zones: an axial zone of chaetetid-like, honeycomb structure; an intermediate zone of irregular, spherulitic, structural elements traversed by wide, open canals lined with small spines, and rarer tabulated canals; an outer zone of irregular but dominantly radial struc-

tural elements of fasciculate microstructure, and a surface showing canals of astrorhizal form. [This is not a typical disjectoporiid and does not have the framework of rods of this group; however, it was placed by TERMIER & TERMIER (1980) in the family Disjectoporidae. The holotype, as they noted, shows many features of the Ceratoporellidae.] *upper Permian*: Tunisia (Djebel Tebaga). — FIG. 212, *1*. \**S. praecursor*, drawn from holotype; section of segment of cylindrical skeleton from axial to peripheral zones,  $\times 57.5$  (Termier & Termier, 1980).

**Tabulatispongia** TERMIER & TERMIER, 1977a, p. 30 [\**T. stromatoporoides*; OD]. Skeleton tabular, encrusting, composed of an open, rectilinear, three-dimensional grid of finely fibrous, longitudinal and tangential rods that expand into nodes where they fuse. Longitudinal canals with distinct walls and irregular, numerous tabulae, traverse skeleton, leading to pores on surface at crests of mamelons and centers of tangential astrorhizal canal systems. *upper Permian*: Tunisia (Djebel Tebaga). — FIG. 214a–b. \**T. stromatoporoides*, ?drawn from holotype; *a*, longitudinal section, diagrammatic, approximately  $\times 25$ ; *b*, longitudinal section and surface diagram, approximately  $\times 1$  (Termier & Termier, 1977b).