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Hypercalcified Extant Calcarea

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PART E, REVISED, VOLUME 4, CHAPTER 4C: HYPERCALCIFIED EXTANT CALCAREA

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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, 1828. 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, 2004), 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, 2004, 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]

Calcispongiae with a regular (equiangular and equiradiate) or exceptionally

Vacelet, Jean. 2012. Part E, Revised, Volume 4, Chapter 4C: Hypercalcified Extant Calcarea. Treatise Online 49:1–15, 9 fig.

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 basinucleate 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, 1910, 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 circlet of special triactines with long lateral actines. Basal skeleton reticulate, with meandroid structure, made up of fused, irregularly shaped, calcitic sclerodermites with vague clinogonal microstructure, generally without entrapped spicules. Aquiferous system leuconoid with basinucleated 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. 1*a–f.* **M. phanolepis,* Moorea, Central Pacific; *a*, view of specimen with living tissue (Vacelet, 1977); *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, new); see also Vacelet, Willenz, and Hartmann (2010, fig. 3,*1*) 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 sphinctozoans. 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

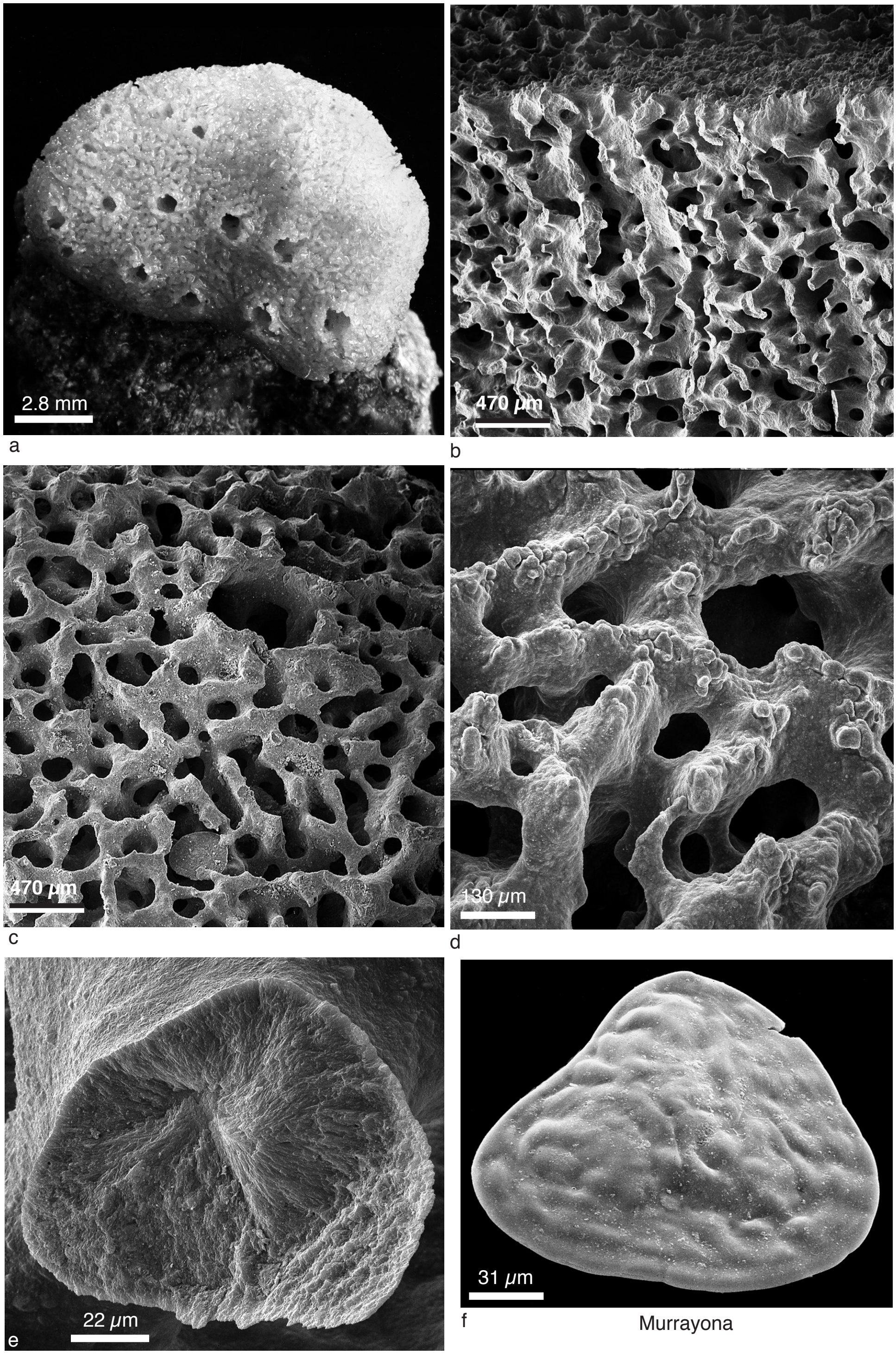

FIG. 1. Murrayonidae (p. 2).

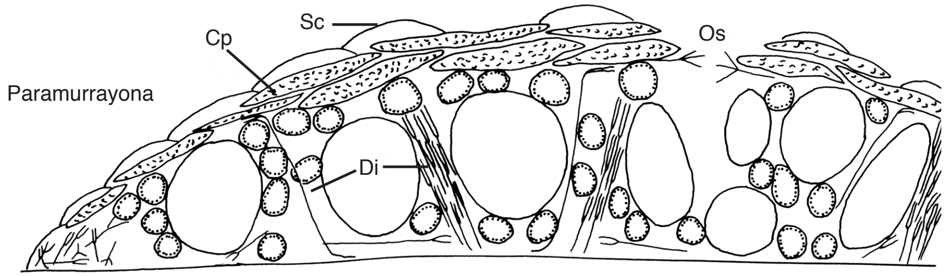

FIG. 2. Paramurrayonidae (p. 2–4).

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 calcitic plates, mostly rectangular, up to 1 mm in length and 50–100 µm thick. Choanosomal skeleton composed exclusively of diapason triactines, generally disposed in fascicles. Osculum 250 µm 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 basinucleated 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. 2. **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]

Calcispongiae 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 apinucleate, 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. 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 zygosis of irregularly curved or expanded ends. Linkage either a complex zygosis, 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. [The family includes five Recent genera, one of which (*Tulearinia*), is poorly

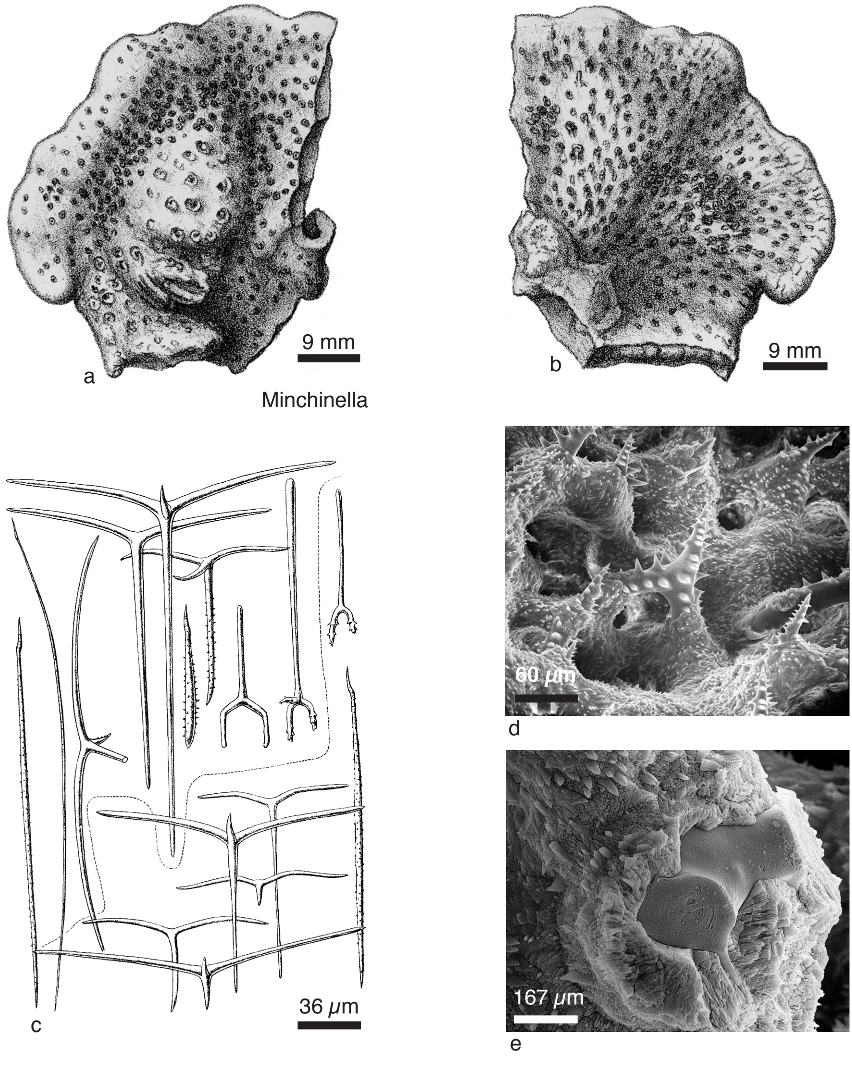

FIG. 3. Minchinellidae (p. 5–6).

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* BRYDONE, 1912; *Muellerithalamia* REITNER, 1987). 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, 2004, 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 µm 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 µm 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 µm. Sagittal triactines generally smooth, unpaired actine 104–156 by 5–9.5 µm, paired actines 49–87 µm. Diapason triactines not aligned in tracts, with smooth shaft, 133 µm long and prongs smooth or spinose, 25 µm long. Tetractines similar to triactines, with apical actine 17 µm 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. 3*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).

Monoplectroninia 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 *Plectroninia* 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 circlet 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. 4*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, new); *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 circlet 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 µm by 400 µm × 10 µm; diapasons aligned in tracts, 25–50 µm 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 *Plectroninia* and *Monoplectroninia*. *Petrostroma* may represent a growth form of sponges similar to Recent representatives of *Plectroninia*, 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. 5*a–e*. **P. 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

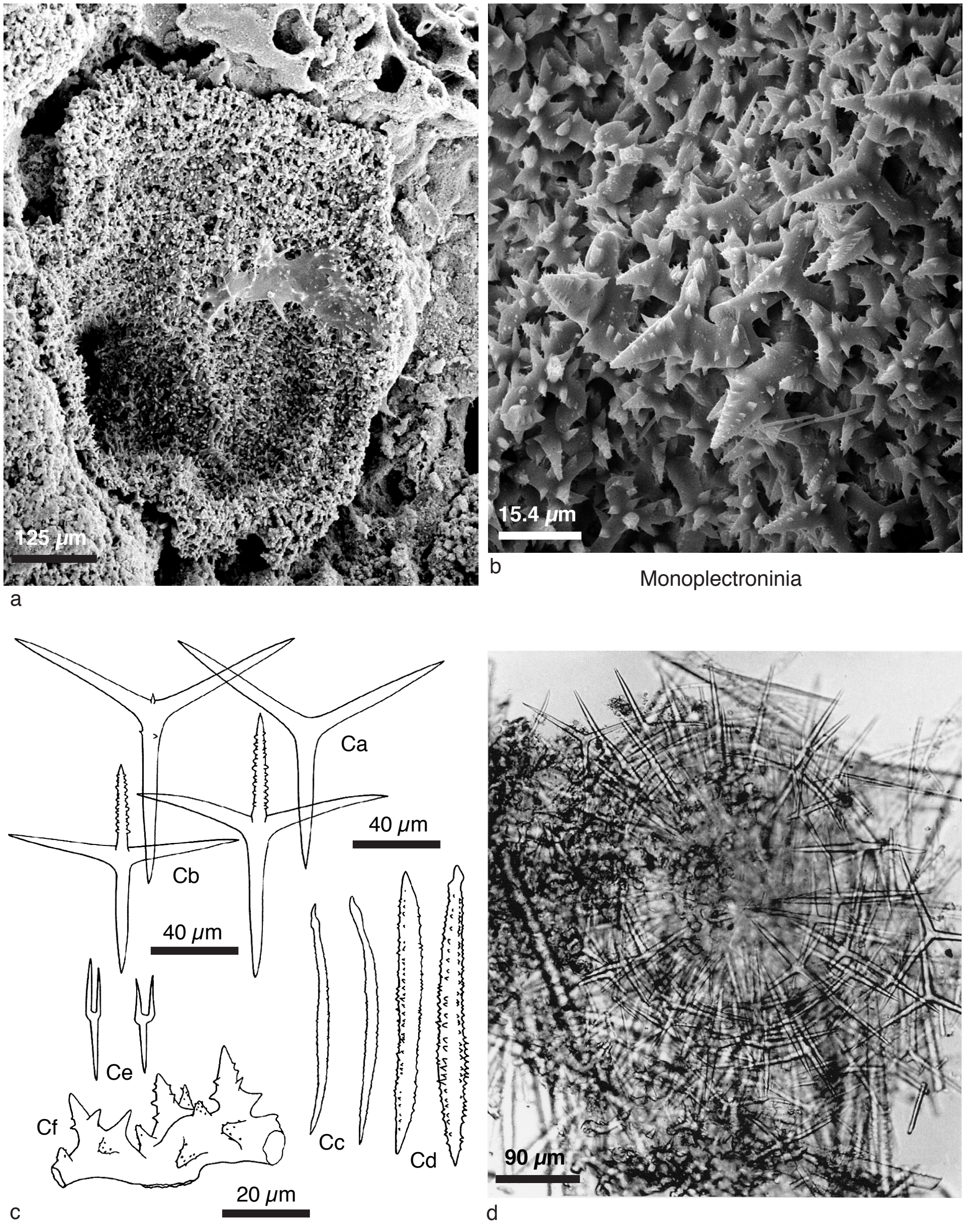

FIG. 4. Minchinellidae (p. 6).

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 zygosis in small tetractines, zygosis reinforced by cement layer in large tetractines. Cortical skeleton of free spicules tangentially arranged (VACELET & others, 2002b, 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

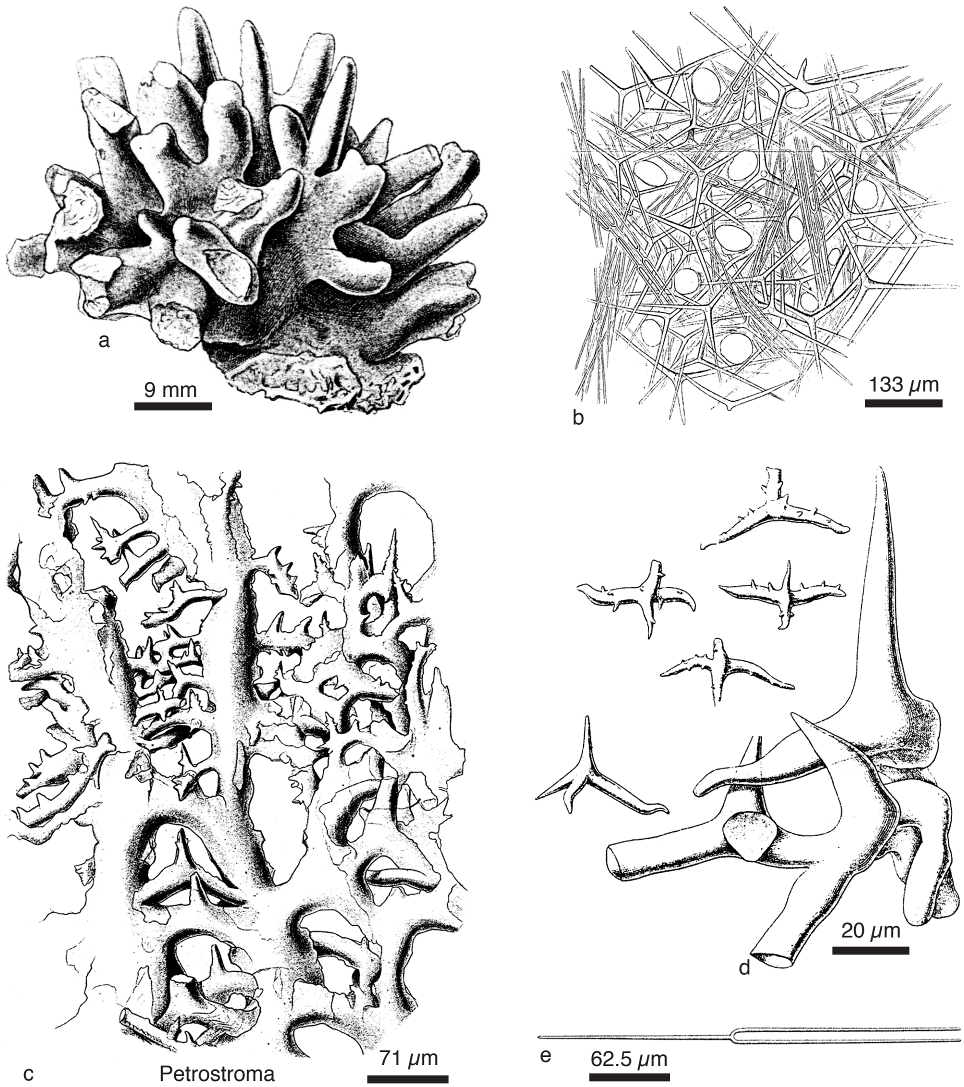

FIG. 5. Minchinellidae (p. 6–7).

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 diapasons. 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 southeastern Spain (BARRIER & others, 1991). There are 13 Recent species, with a highly diverse dermal 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

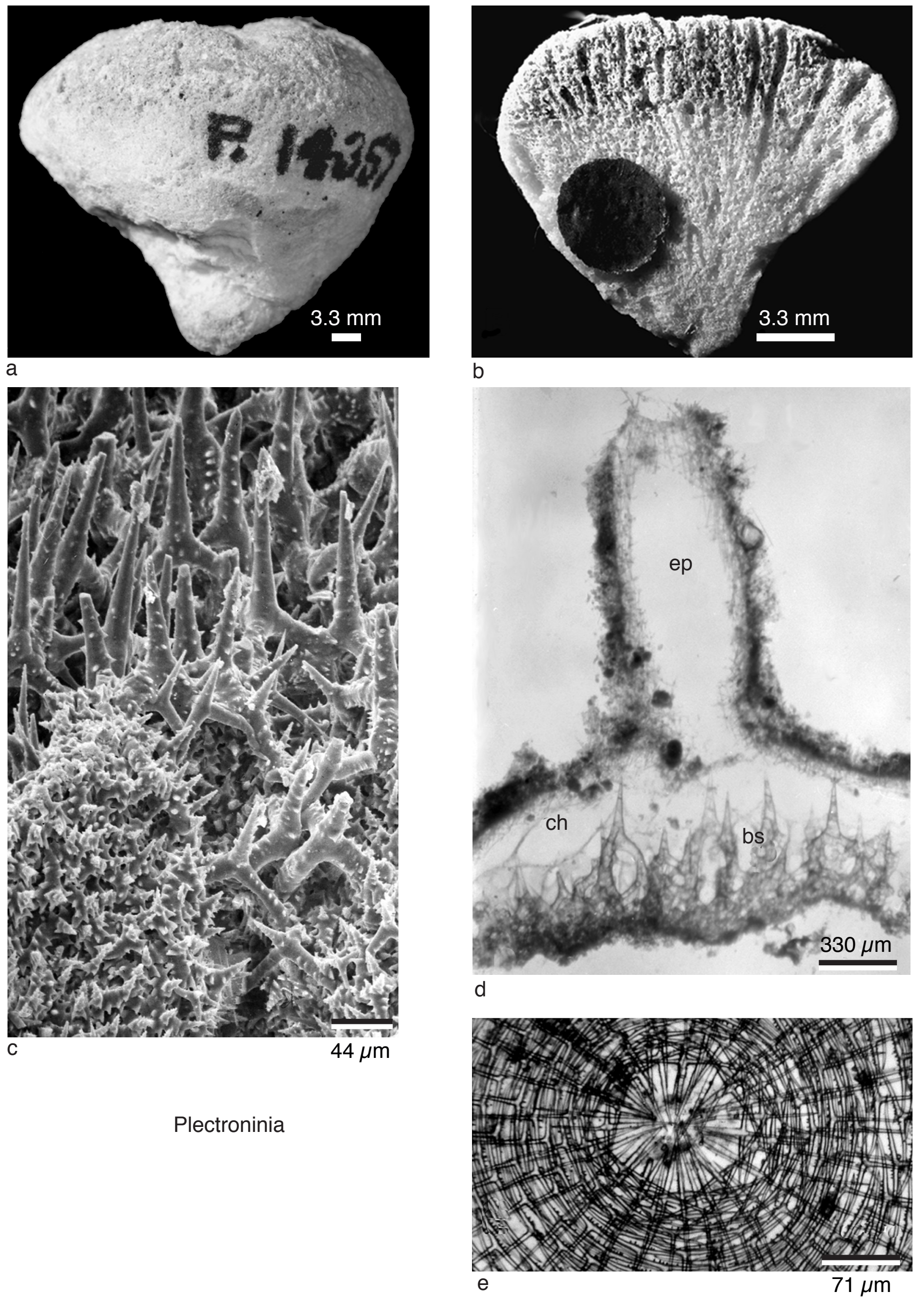

FIG. 6. Minchinellidae (p. 7–10).

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, 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,

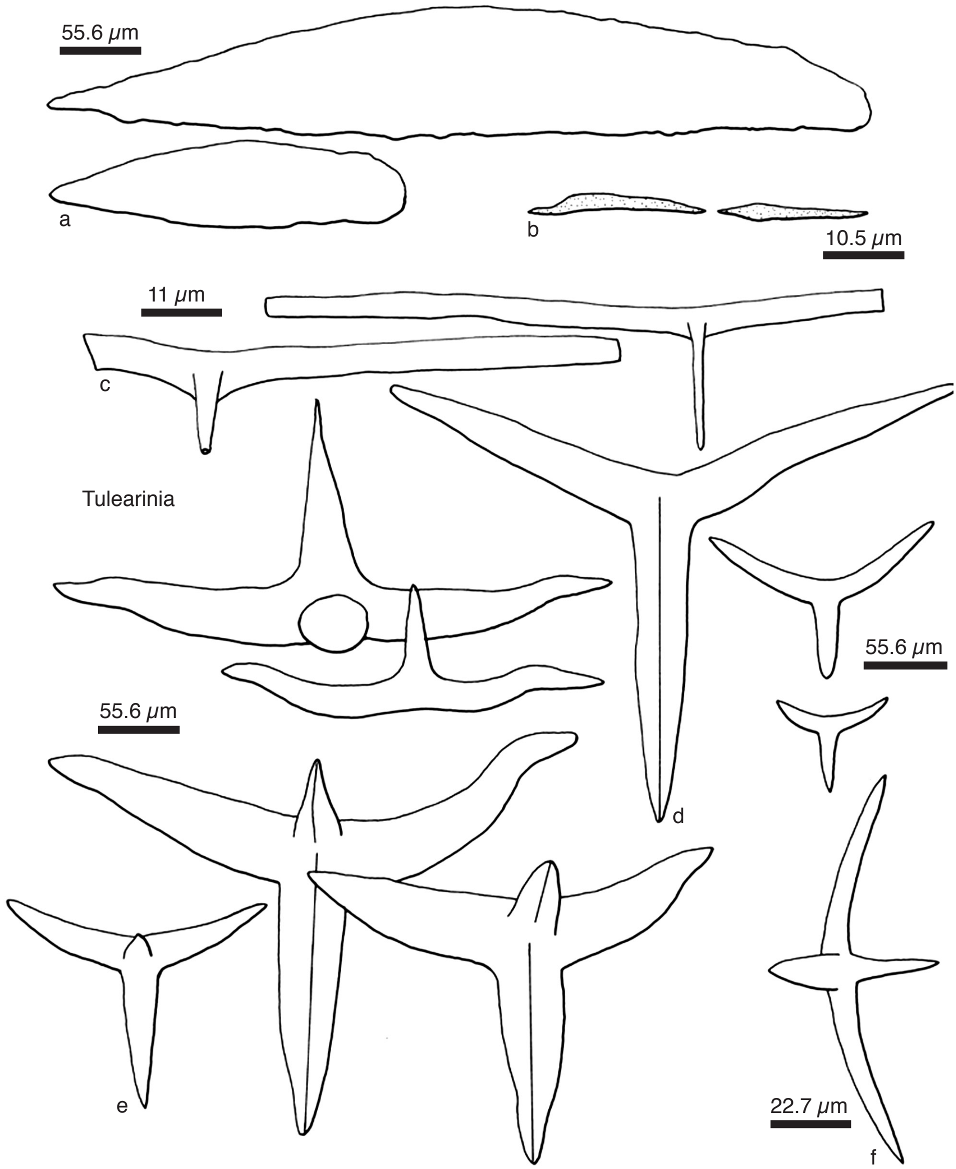

FIG. 7. Minchinellidae (p. 11).

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. 6*a–b*. **P. halli;* general view of holotype (Pickett, 1983, p. 106).——FIG. 6*c*. *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. 6*d*. *P. hindei* KIRKPATRICK, section through Mediterranean specimen, Marseille, 5 m depth; *ep,* exhalant papillae; *ch,* choanosome; *bs,* basal skeleton (Pouliquen & Vacelet, 1970).——FIG. 6*e*. *P. vasseuri* VACELET, cortical skeleton of tangential triactines and osculum with a circlet of tetractines, Tuléar, Madagascar, 6 m depth (Vacelet, 1967b).

Tulearinia Vacelet, 1977, p. 354 [**T. stylifera*; 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 µm 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 zygosis 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. 7*a–f*. **T. stylifera*, 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, 1977).

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 µm thick, anchored in basal skeleton by tracts of reserve cells filling canaliculi 50–90 µm in diameter. Aquiferous system leuconoid, choanocyte chambers 50–80 µm in diameter. Spicules: sagittal triactines (actines 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

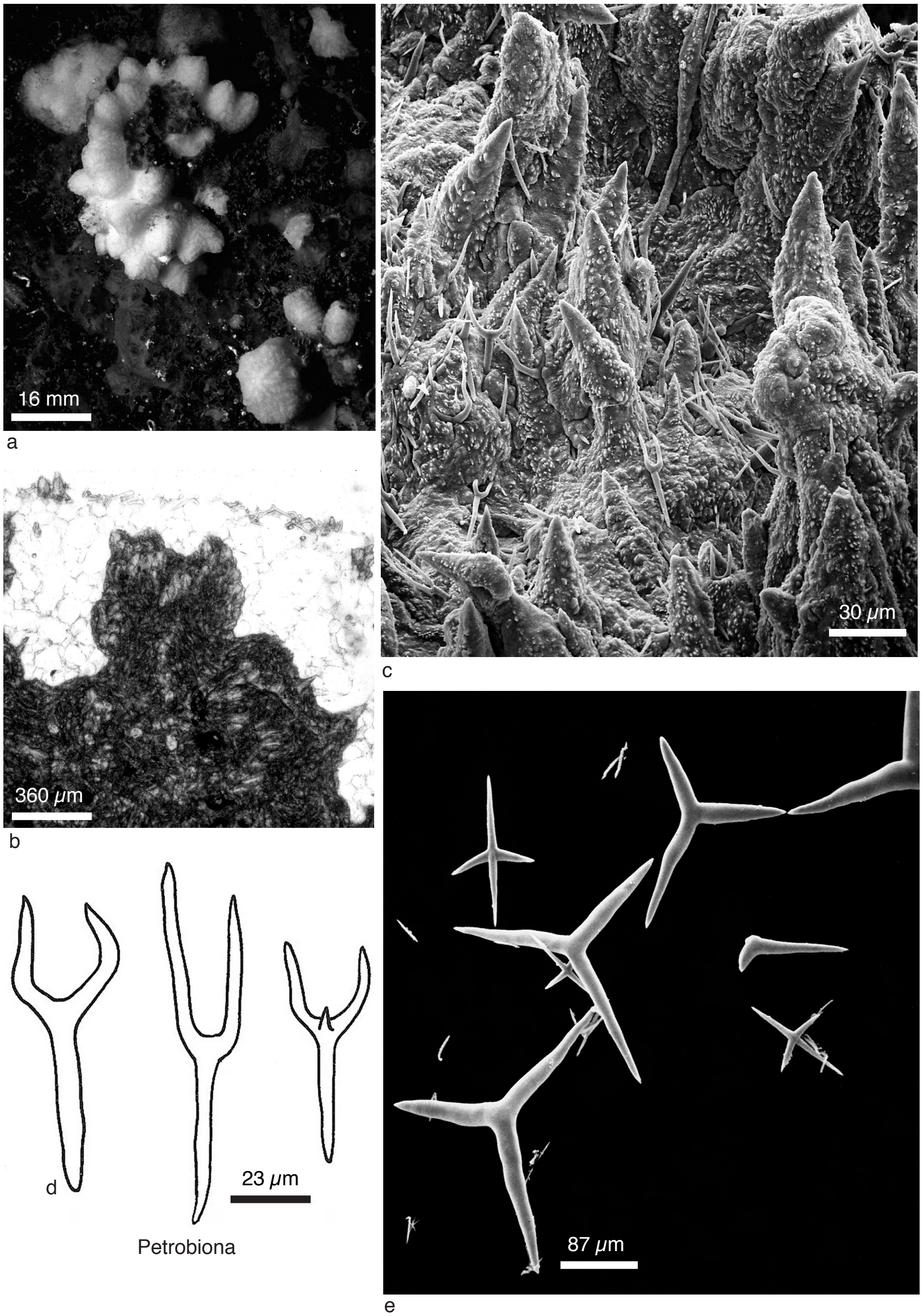

FIG. 8. Petrobionidae (p. 11–13).

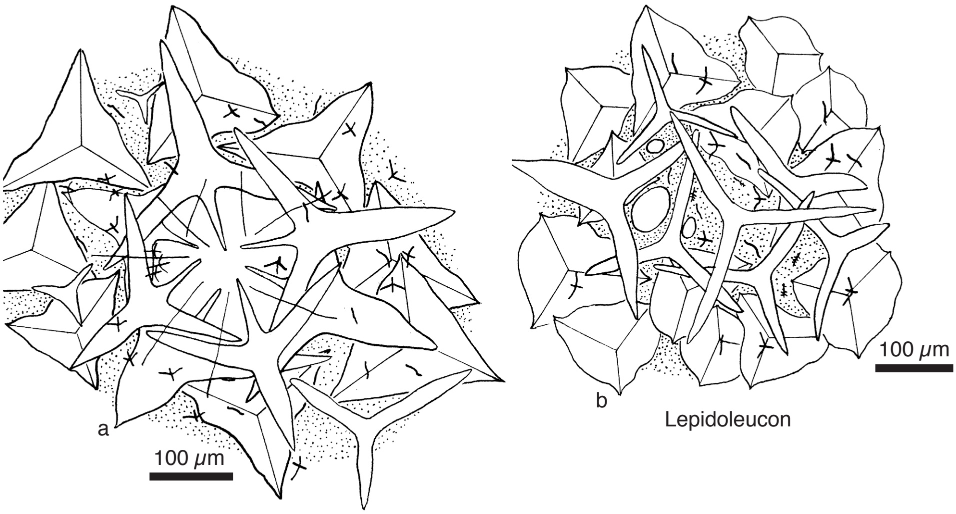

FIG. 9. Lepidoleuconidae (p. 13–14).

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, 1980) and from Pleistocene cliffs of southern Italy dating back to 30,000 years (VACELET, 1991). *Pleistocene–Holocene*: Mediterranean caves.——FIG. 8*a–e*. **P. massiliana*; *a,* several specimens *in situ* in Marseille cave, 10 m (Vacelet, new); *b*, section through apical zone, showing massive skeleton, choanocyte chambers, and surface spicules (Vacelet, new); *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, new). See also VACELET, WILLENZ, and HARTMANN (2010, fig. 3,*5c*), 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 VACELET, WILLENZ, and HARTMANN (2010, fig. 3,*5a–c*).

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 circlet 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. 9*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).

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