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Order Lithonida Vacelet, 1981, Recent

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Recent Lithonida (Calcarea, Calcaronea) contains two families of Calcaronea characterized by a hypercalcified skeleton, which is reinforced either by the linkage of tetractines or by the formation of a rigid basal mass of calcite. The living tissue has free calcareous spicules, most frequently including tuning-fork triactines, or diapasons. They appear as survivors of fossil 'pharetronids', a polyphyletic grouping of fossil calcareous sponges, and are presently restricted to submarine caves and to bathyal rocky environments. The fossil genera are not treated here.
Keywords: Porifera; Calcarea; Calcaronea; 'Pharetronids'; Minchinellidae; Petrobionidae; *Minchinella*; *Monoplectroninia*; *Petrobiona*; *Plectroninia*; *Petrostroma*; *Tulearinia*.

DEFINITION, SCOPE

Synonymy

Lithonida Vacelet, 1981: 314. Stereina de Laubenfels, 1955: 99 (pars).

Definition

Calcaronea with reinforced skeleton consisting either of linked or cemented basal actines of tetractines, or of a rigid basal mass of calcite. Diapason spicules generally present. Canal system leuconoid.

Scope

Lithonida contains two families with extant representatives, Minchinellidae Dendy & Row, 1913, with five Recent genera and several genera known only from the fossil record, and Petrobionidae Borojevic, 1979, which is monotypic.

History and biology

The order Lithonida was erected to include some sponges that were originally classified in the family Lithoninae Döderlein, 1892 (Vacelet, 1981). In the original definition the order included families Lelapiidae Dendy & Row, 1913 and Lepidoleuconidae Vacelet, 1967a, which have been subsequently transferred to Leucosolenida and Baerida respectively, and *Lelapiella* Vacelet, 1977a which has been transferred to Murrayonida Vacelet, 1981 (Borojevic *et al*., 1990). These sponges have a hypercalcified skeleton with high fossilization potential and hence are well represented in the fossil record. In Recent seas they survive in littoral caves and in bathyal environments.

Remarks

Fossil genera of Minchinellidae, which are in urgent need of a revision based on a thorough examination of their solid skeleton and in comparison with Recent specimens, are not treated in the chapter. Recent species appear as surviving forms of the 'pharetronids', a polyphyletic assemblage of fossil Calcarea (Vacelet, 1991).

KEY TO GENERA

(1) Skeleton including a solid mass of calcite ..... ***Petrobiona***
Skeleton without a solid mass of calcite 2
(2) Basal skeleton made of uncemented tri- and tetractines interlaced by their basal actines ..... ***Tulearinia***
Basal skeleton made of tetractines cemented in a rigid network 3
(3) Rigid network of tetractines embedded in a cement ..... ***Minchinella***
Rigid network of tetractines not embedded in a cement 4
(4) Basal skeleton made of a single category of tetractines ..... ***Monoplectroninia***
Basal skeleton made of two categories of tetractines 5
(5) Basal skeleton forming a thin basal layer (in Recent species) ..... ***Plectroninia***
Basal skeleton with ascending radial lines ..... ***Petrostroma***

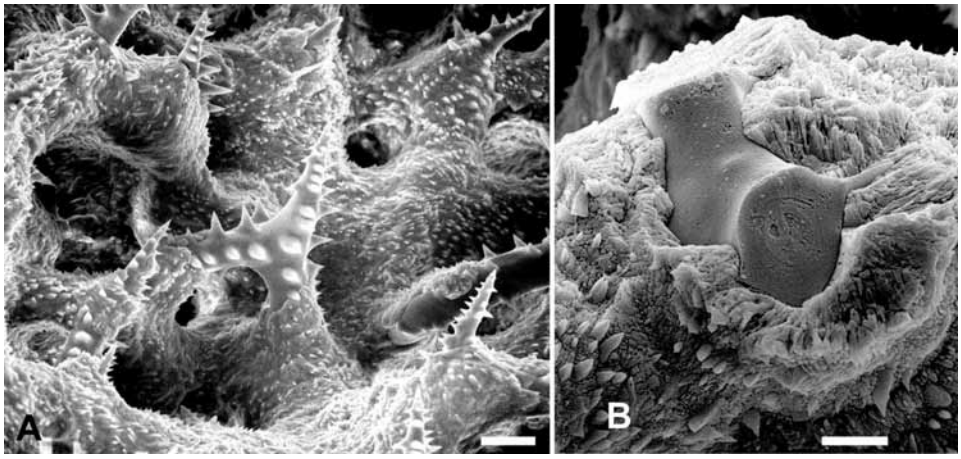

Fig. 1. *Minchinella lamellosa* Kirkpatrick, 1908d, holotype. A, SEM view of the basal skeleton of fused tetractines partially embedded in a calcareous cement (scale 25 μm) (from Vacelet, 1981). B, SEM view of a fracture in the basal skeleton (scale 15 μm) (from Vacelet, 1991).

FAMILY MINCHINELLIDAE DENDY & ROW, 1913

Synonymy

Minchinellidae Dendy & Row, 1913: 739. Porosphaeridae de Laubenfels, 1955: 99. Bactronellidae de Laubenfels, 1955: 100.

Definition

Lithonida in which the basal skeleton consists of a network of tetractines cemented or linked together in a variety of ways.

Diagnosis

The basal skeleton is made by the attachment or cementation of the basal actines of tetractines, which are linked by the zygosis of their irregularly curved or expanded ends. The linkage may be a complex zygosis, often reinforced by a calcareous cement of variable development which can completely embed the whole network, or may consist in a simple entanglement. The superficial skeleton consists of free spicules, mostly tangentially disposed in the dermal membrane, generally including diapasons.

Scope

Five Recent genera, one of which of rather uncertain affinity (*Tulearinia*) and approximately five fossil genera.

History and biology

Fossil sponges with a skeleton of fused tetractines were classified in the heterogeneous assemblage of Lithoninae Döderlein, 1892. Dendy & Row (1913) created Minchinellidae for Recent species of Calcarea with a fused skeleton, including fossil and Recent species of *Plectroninia* Hinde, 1900. Several fossil genera were included by de Laubenfels (1955) in the families Porosphaeridae and Bactronellidae, which are junior synonyms of Minchinellidae.

Remarks

The first stages of zygosis between the basal actines of the tetractines of the rigid skeleton resembles the zygosis of the 'lithistid' siliceous skeleton in the Demospongiae, although the junctions, and in some cases the whole skeleton, may be invested with a secondary calcareous cement. The relationship of extant representatives with fossil genera are presently unclear and are not treated in this chapter.

MINCHINELLA KIRKPATRICK, 1908

Synonymy

Minchinella Kirkpatrick, 1908d: 504.

Type species

Minchinella lamellosa Kirkpatrick, 1908d (by monotypy).

Diagnosis

Minchinellidae in which the main skeleton consists of one category of tetractines linked together into a rigid network by their basal actines and subsequently embedded in an enveloping cement. Cortical skeleton composed of free spicules, diactines, triactines, diapasons, and tetractines.

Description of type species

Minchinella lamellosa Kirkpatrick, 1908d (Fig. 1).

Synonymy. *Minchinella lamellosa* Kirkpatrick, 1908d: 504.

Material examined. Holotype: BMNH 1900.10.22.1A – Api, New Hebrides (Vanuatu), 110–1287 m depth. Paratype: BMNH 1900.10.22.1B – same locality.

Description. Erect lamellar growth form, with a 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 a drum-like membrane. Oscular face with cylindrical chimneys, 2 mm high, with a contracted end. Colour in alcohol buff to brown, white at the rim. Choanocytes chambers 32.5 μm in diameter, with choanocytes showing an hourglass modification due to poor preservation. Skeleton of both surfaces composed of an ectosomal layer of spinose diactines. Skeleton of the

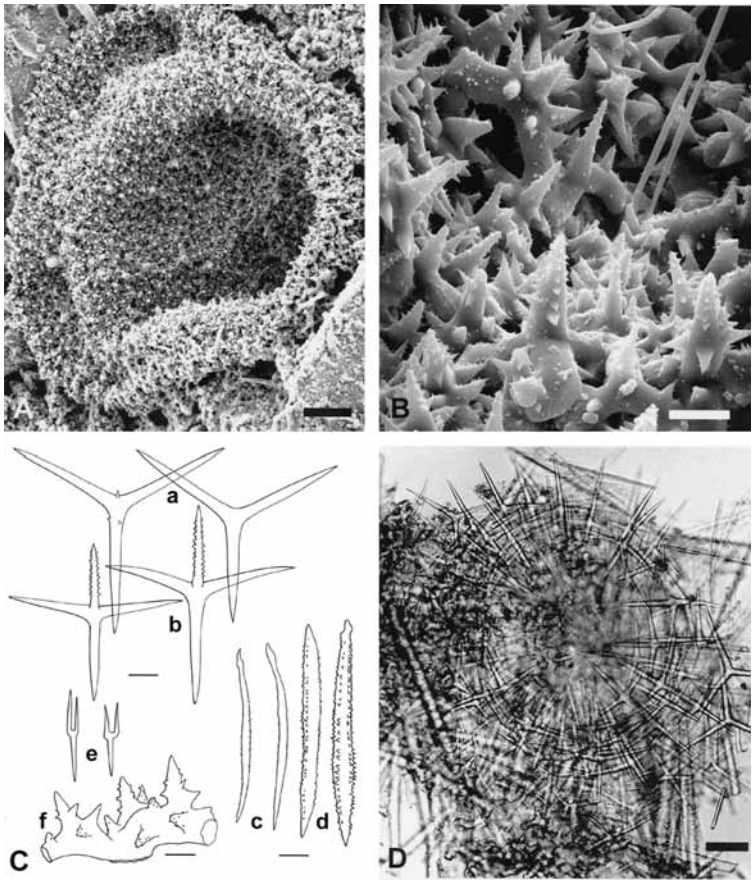

Fig. 2. *Monoplectroninia hispida* Pouliquen & Vacelet, 1970. A, SEM view of the basal skeleton of fused tetractines (scale 100 μm). B, SEM view of the basal skeleton with fused tetractines and a diapason (scale 15 μm). C, spicules; a, ectosomal triactines; b, perioscular tetractines; c, perioscular diactines; d, ectosomal diactines; e, diapason triactines; f, fused tetractines of the basal skeleton (scales a–e, 20 μm; f, 10 μm). D, ectosome, with ectosomal spicules and tetractines forming a circlet around the osculum, and a fragment of the basal skeleton (scale 50 μm) (C–D, from Pouliquen & Vacelet, 1970).

poral and oscular chimneys composed of an outer coat of spinose diactines with the axis vertical or oblique to the long axis of the tube, several layers of triactines and tetractines with the apical ray projecting into the lumen of the tube, and a fringe of bristle-like diactines round the poral orifice. At the base of the 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 a calcitic cement of fibrillar microstructure (Fig. 1). Apical ray the last to be embedded and, when free, pointing towards the lumen. Diactines of several types, generally spinose, thicker on the oscular face, 87–234/3.8–7.5 μm. Sagittal triactines generally smooth, unpaired actine 104–156/5–9.5 μm, paired actines 49–87 μm. Diapason triactines not aligned in tracts, with a smooth shaft, 133 μm long and prongs smooth or spinose, 25 μm long. Tetractines similar to triactines, with an apical actine 17 μm long. Cemented tetractines in a single size, with conical spines.

Remarks. A second species, *M. kirkpatricki* Vacelet, 1981 from New Caledonia, differs mostly by the non-lamellar shape and the absence of aquiferous chimneys.

Distribution

Pacific Ocean (Vanuatu and New Caledonia).

MONOPLECTRONINIA POULIQUEN & VACELET, 1970

Synonymy

Monoplectroninia Pouliquen & Vacelet, 1970: 439.

Type species

Monoplectroninia hispida Pouliquen & Vacelet, 1970 (by monotypy).

Diagnosis

Minchinellidae in which the 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 outwards. Cortical skeleton made of free spicules, diactines, triactines, diapasons and tetractines.

Description of type species

Monoplectroninia Pouliquen & Vacelet, 1970 (Fig. 2).

Synonymy. *Monoplectroninia hispida* Pouliquen & Vacelet, 1970: 439.

Material examined. Holotype: BMNH 1970.4.24.1 – Marseille, Mediterranean, in dark submarine caves, 8–20 m depth.

Other material. 17 specimens from Mediterranean caves (Marseille).

Description. Small encrusting growth form, 1.0–1.1 mm in diameter, 0.5 mm thick, white, with a hispid surface. Cortical layer with a layer of tangential smooth triactines and oblique spinose diactines. Osculum in the cortical layer surrounded by a circlet of tangential tetractines with a spinose apical actine pointing towards the lumen and smooth basal actines. Smooth diapasons dispersed in the basal skeleton, not aligned in tracts. Main skeleton basal, made of a few layers of small spinose tetractines linked by their basal actines, with the apical actine remaining free and pointing outwards. Choanocyte chambers irregularly tubular.

Remarks. The genus is monotypic. It differs from Recent representatives of *Plectroninia* by possession of a basal skeleton which includes only a reticulation formed by the smaller tetractines, the larger tetractines being absent.

Distribution

Mediterranean.

PLECTRONINIA HINDE, 1900

Synonymy

Plectroninia Hinde, 1900: 51.

Type species

Plectroninia halli Hinde, 1900 (by monotypy).

Diagnosis

Minchinellidae with a 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 their basal actines, with the apical actine remaining free and pointing outwards. Basal actines attached by simple zygosis in small tetractines, zygosis reinforced by a cement layer in large tetractines. Cortical skeleton of free spicules tangentially arranged.

Previous reviews

Pickett, 1983; Vacelet, 1981.

Description of type species

Plectroninia halli Hinde, 1900 (Fig. 3).

Synonymy. *Plectroninia halli* Hinde, 1900: 51; Pickett, 1983: 106.

Material examined. Holotype (not seen): NMV P14357 (not seen).

Description (from Hinde, 1900; Pickett, 1983). Turbinate in shape, 16 mm high by 18 mm in greatest width. Sides covered by a spicular dermal layer, partly preserved, interior skeleton firm, stony. Surface skeleton composed of free spicules tangentially disposed, with a superficial layer of diactines, up to 610/10 μm, lying in parallel, overlying a layer made of diactines, triactines and tetractines, including rare diapasons. Basal skeleton a multiple-layered reticulation made up of spinose tetractines, with the basal actines unequal and irregularly curved, linked by their expanded ends to the basal actines of the adjoining spicules, and with the apical actine remaining free and pointed towards to the surface of the sponge. Tetractines simply attached by their expanded ends to the basal actines of adjoining tetractines in the outer layers, the apposition being reinforced by a thin calcitic cement in the inner layers, where the tetractines have a different size. Traces of canals radiating from the summit of the sponge present, 200–500 μm in diameter.

Remarks. The genus was originally described for a fossil from the Eocene strata from Australia (Victoria), but subsequently revised to the Early and Middle Miocene strata (Pickett, 1983). Twelve Recent species, with an encrusting shape quite different to that of *P. halli*, have been allocated to *Plectroninia*, following Kirkpatrick (1900a) who considered for *P. hindei* that his specimens were juvenile with an incomplete growth. The Recent species are in fact fully grown specimens, 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 is basal in regard to the layer of large tetractines in Recent species. These Recent taxa possibly belong to a new genus, but its erection is pending a revision of fossil genera of Minchinellidae, such as *Bactronella* Hinde, 1900; *Porosphaera* Steinmann, 1878; *Porosphaerella* Welter, 1910; *Sagitullaria* Welter, 1910; *Tretocalia* Hinde, 1900. The dermal skeleton, made of tangential spicules, shows a high diversity in the 12 known Recent species (Vacelet, 1981).

Distribution

Early and Middle Miocene of Australia. Recent species cosmopolitan, in shallow water caves and bathyal zone up to 1600 m depth.

PETROSTROMA DÖDERLEIN, 1892

Synonymy

Petrostroma Döderlein, 1892.

Type species

Petrostroma schulzei Döderlein, 1892 (by monotypy).

Diagnosis

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.

Description of type species

Petrostroma schulzei Döderlein, 1892 (Fig. 4).

Synonymy. *Petrostroma schulzei* Döderlein, 1892: 143; Döderlein, 1898: 15.

Material examined. Holotype (not seen): BMNH. Other material. A small dry fragment from Döderlein in the BMNH.

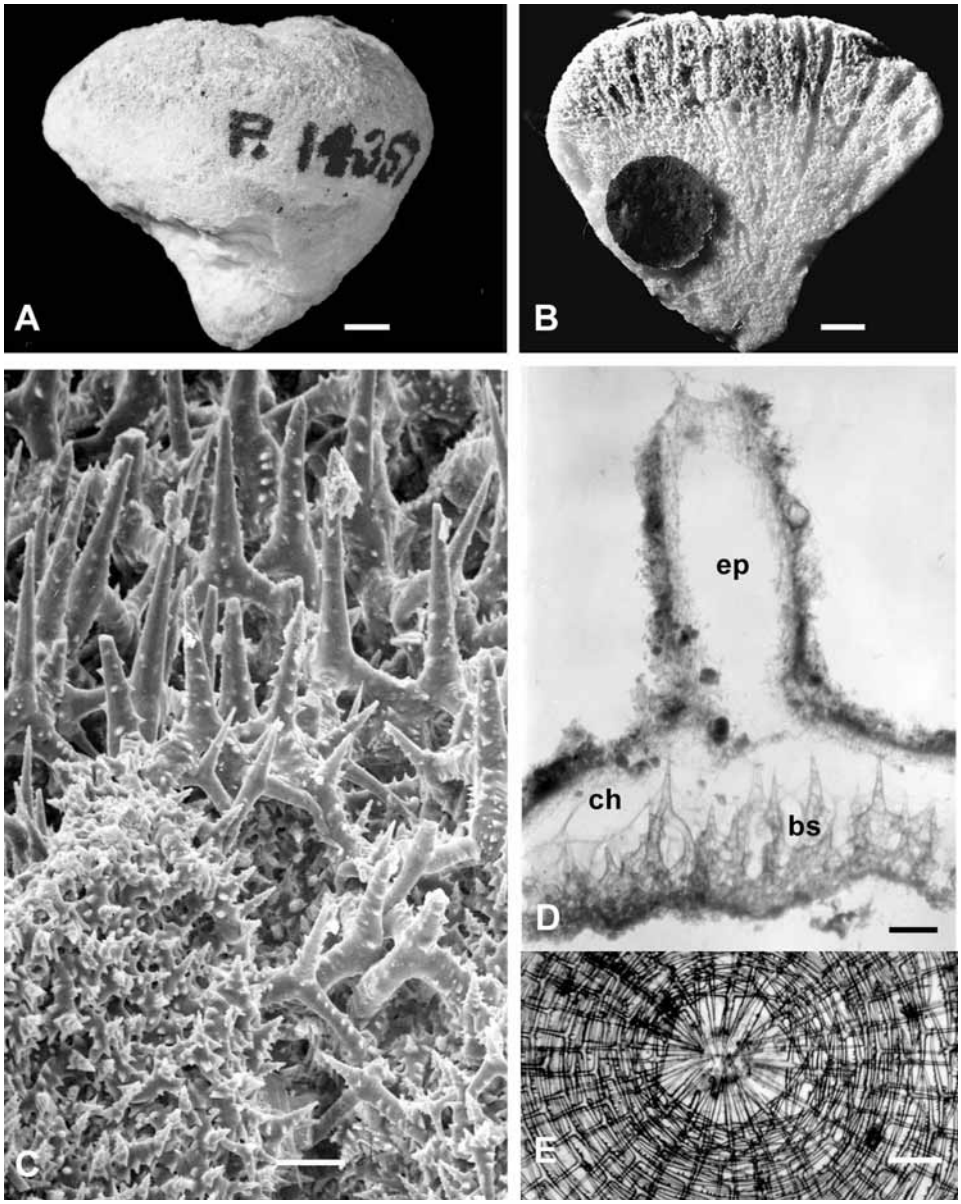

Fig. 3. *Plectroninia* Hinde, 1900. A–B, *Plectroninia halli* Hinde, 1900 general view of the holotype (scale 2 mm) (from Pickett, 1983). C, *P. neocaledoniense* Vacelet, 1981, SEM view of the basal skeleton made up of small and large fused tetractines (scale 40 μm). D, *P. hindei* Kirkpatrick, 1900b, section through a Mediterranean specimen (abbreviations: ep, exhalant papillae; ch, choanosome; bs, basal skeleton) (scale 200 μm) (from Pouliquen & Vacelet, 1970). E, *P. vasseuri* Vacelet, 1967b, cortical skeleton of tangential triactines and osculum with a circlet of tetractines (scale 50 μm).

Description (mostly from Döderlein, 1898). Massive base from which arises several short, cylindrical branches, dichotomously divided at their ends, of stony consistency. Colour whitish to yellowish. Cortical skeleton made of free triactines and tetractines, and of bundles of diapasons. Main skeleton of the 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 the main skeleton bearing some conical spines, with the apical actines remaining most often free. Free spicules smooth tetractines and triactines in several layers (with a few spinose tetractines), with rays 100–400/10 μm; diapasons aligned in tracts, 25–50 μm in diameter.

Remarks. This genus has not been found again since Döderlein's original description. 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 an the examination of new material and a revision of the fossil genera allocated to the family Minchinellidae.

Distribution

Japan (Sagami Bay), 195–392 m depth.

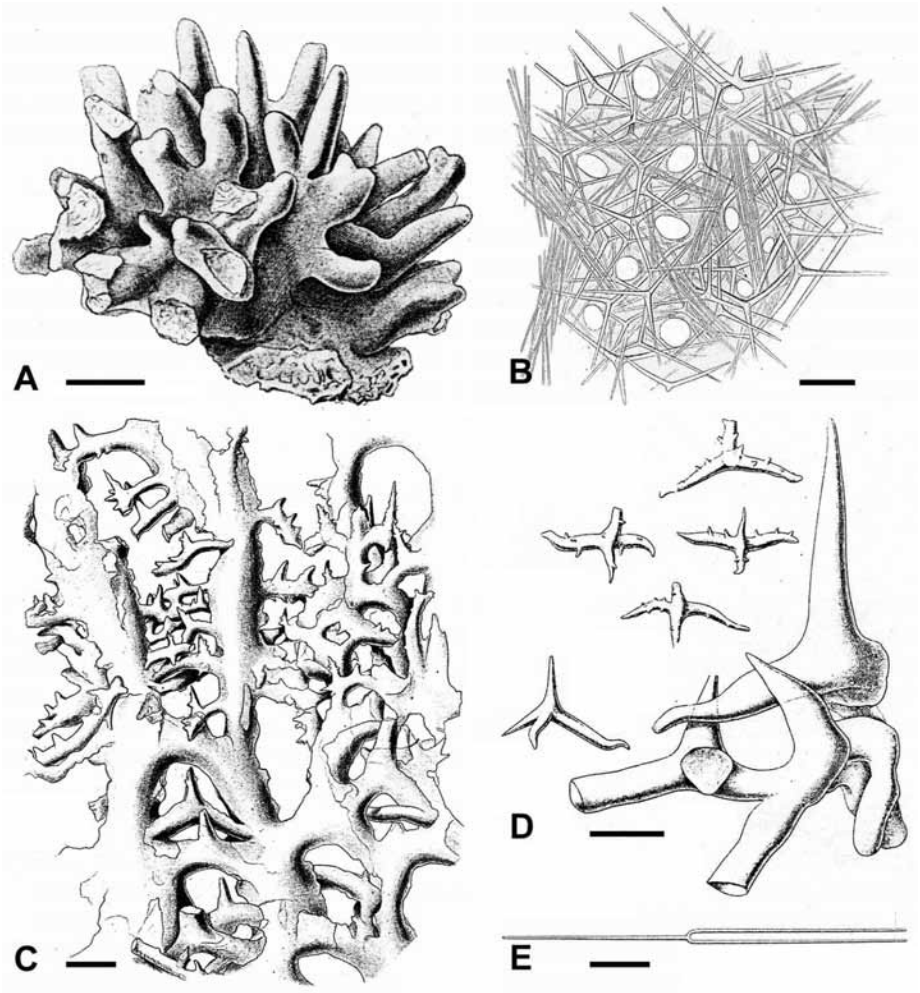

Fig. 4. *Petrostroma schulzei* Döderlein, 1892. A, general view (scale 10 mm). B, ectosomal layer with ostia, triactines and tetractines, and bundles of diapason (scale 100 μm). C, section through the outer part of the basal skeleton, with primary radial strands and secondary strands (scale 50 μm). D, small and large fused tetractines of the basal skeleton (scale 20 μm). E, diapason triactine (scale 50 μm) (from Döderlein, 1898).

TULEARINIA VACELET, 1977

Synonymy

Tulearinia Vacelet, 1977a.

Type species

Tulearinia stylifera Vacelet, 1977a (by monotypy).

Diagnosis

Minchinellidae in which the basal skeleton consists of tetractines with the basal actines interwoven but not cemented, and with underlying layers of triactines linked in the same way.

Description of type species

Tulearinia stylifera Vacelet, 1977a (Fig. 5).

Synonymy. *Tulearinia stylifera* Vacelet, 1977a: 354; Vacelet, 1981: 346.

Material examined. Holotype: MNHN J.V-76-1 – Madagascar. Other material. Several specimens from Madagascar, La Réunion and New Caledonia.

Description. Small encrusting growth form, 3 mm in maximum diameter, 0.7–0.8 mm thick. Colour white, surface hispid, with an 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 the choanosome zone. Choanocyte chambers 55–75 μm in diameter, surrounded by microdiactines; canals lined by special tetractines, choanocytes apinucleate. Under the choanosome, basal skeleton made of several layers of tetractines interwoven by their basal actines, with the apical actine pointing towards the surface, and of a basal layer of interwoven triactines.

Remarks. 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 which characterizes Minchinellidae. This mode of union may be seen either as a transitional stage to the minchinellid

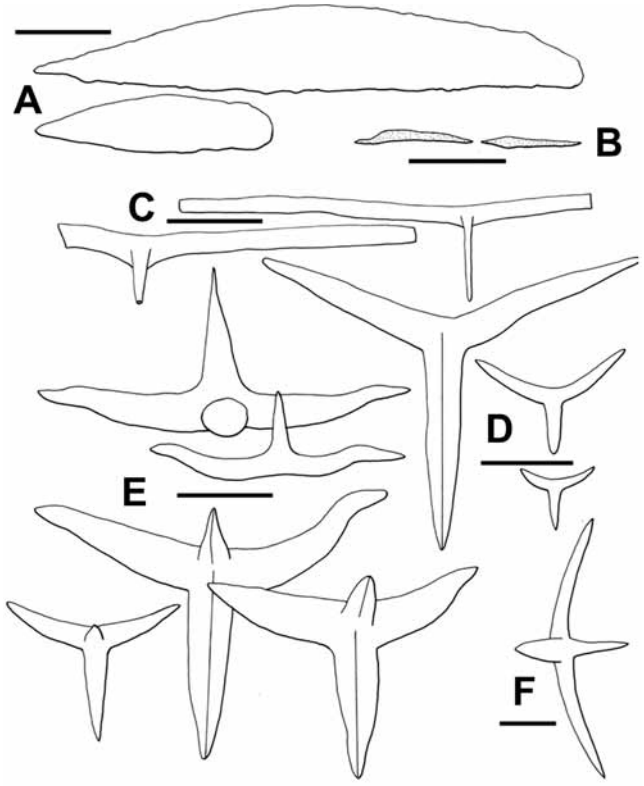

Fig. 5. *Tulearinia stylifera* Vacelet, 1977a, spicules of holotype. A, diactines from the outer layer (scale 100 μm). B, microdiactines (scale 20 μm). C, perioscular triactines (scale 20 μm). D, triactines (scale 100 μm). E, tetractines from the basal network (scale 100 μm). F, tetractine from canals (scale 25 μm) (from Vacelet, 1977a).

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.

Distribution

Indian Ocean (Madagascar, La Réunion), New Caledonia, in submarine caves of the front reef, 3–37 m depth.

FAMILY PETROBIONIDAE BOROJEVIC, 1979

Synonymy

Petrobionidae Borojevic, 1979: 529.

Diagnosis

Lithonida 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 the 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.

Scope

Monotypic, with a single species.

History and biology

The genus was first described in the family Murrayonidae, which also possesses a calcitic basal skeleton (Vacelet & Lévi, 1958). *Murrayona*, however, has clear affinities with the subclass Calcinea and the two genera were subsequently classified in two different subclasses of Calcarea (Borojevic, 1979). *Petrobiona* is the only member of the Calcarea that is provided with survival structures ('pseudogemmules') enclosed within the calcareous skeleton (Vacelet, 1964, 1990). The histology, cytology, reproduction and mode of secretion of the basal skeleton have been thoroughly studied. The single known species lives in Mediterranean submarine caves and is known from both living specimens and fossil remains from Pleistocene strata in the Mediterranean.

Remarks

The presence of pugiole tetractines and the general organization of the living tissue could indicate affinities with the Baeriidae. Although *Petrobiona* has features of fossil 'Pharetronids' such as a basal skeleton and tuning-fork spicules, the microstructure of its basal skeleton has not been recognized in sponges from the fossil record older than Pleistocene (Cuif *et al*., 1979).

PETROBIONA VACELET & LÉVI, 1958

Synonymy

Petrobiona Vacelet & Lévi, 1958.

Type species

Petrobiona massiliana Vacelet & Lévi, 1958 (by monotypy).

Diagnosis

As for family.

Previous review

Vacelet, 1964.

Description of type species

Petrobiona massiliana Vacelet & Lévi, 1958 (Fig. 6).

Synonymy. *Petrobiona massiliana* Vacelet & Lévi, 1958: 318. *Petrobiona incrustans* Sarà, 1963a.

Material examined. Holotype: MNHN C. 1968. 814 – Mediterranean. Other material. Numerous specimens from the Mediterranean.

Description. Massive, subspherical or multilobate growth form with a dead stalk in calm environments, encrusting in high energy environments. Maximum size of the living 'head' 1.0–1.2 cm in diameter with a stalk 2 cm long, up to 6 cm in diameter when encrusting. Texture stony. Colour pure white. Surface smooth. Oscules apical in subspherical or multilobate specimens, 0.6–0.8 mm

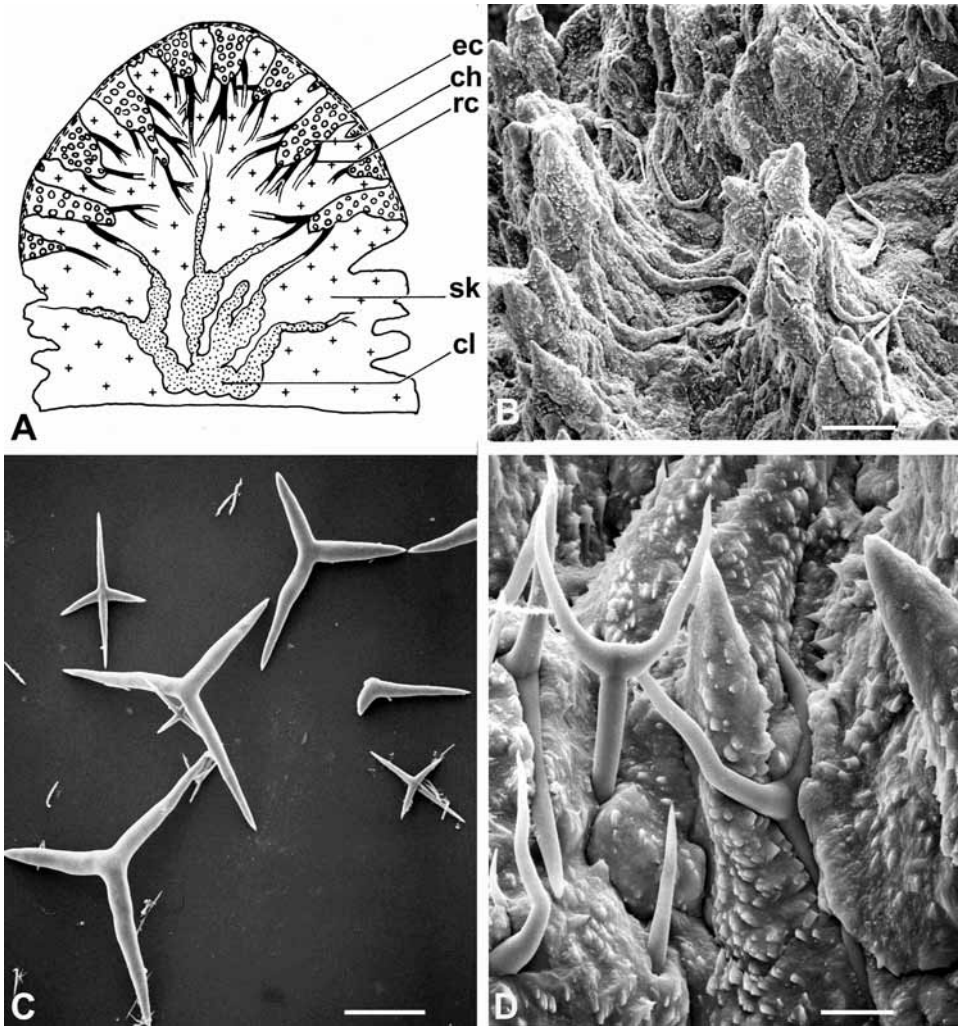

Fig. 6. *Petrobiona massiliana* Vacelet & Lévi, 1958. A, diagram of skeletal organization (ec, ectosome and superficial skeleton; ch, choanosome; rc, accumulation of reserve cells in canaliculi; sk, massive calcareous skeleton; cl, excavating clionid sponge) (from Vacelet, 1964). B, surface view of the calcareous skeleton (scale 100 μm) (from Vacelet, 1991). C, calcareous spicules, triactines, pugiole tetractines and microdiactines (scale 100 μm). D, surface view of the calcareous skeleton with diapason triactines entrapped in the basal skeleton (scale 20 μm).

in diameter. Living tissue located at the surface and between the crests of the basal skeleton, with a choanosome 600 μm thick anchored in the 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 × 6–40 μm), tuning-fork (diapason) triactines (basal actine 30–70 × 5–8.5 μm; lateral actines 20–50 × 4–7 μm), pugiole tetractines in two categories (lateral actines 40–130 × 22–28 μm and 16–40 × 5.5–8.5 μm, axial actines 8–100 × 10–28 μm and 30–70 × 5.5–8.5 μm), rugose microdiactines 30–60 × 2–3 μm. Basal calcareous skeleton in calcite, solid, with crests and depressions on the surface, built up of elongate, irregular sclerodermites, with a radial orientation of the crystals from a longitudinal axis, 80–150 μm in maximum size. Some spicules entrapped in the basal skeleton, randomly arranged and showing no sign of dissolution. Reproduction by amphiblastula larva, with an unusually complex nourishment process of oocyte and embryo.

Distribution and ecology. 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 the entrance of dark caves, more rarely on the under surface of stones, 0.5–25 m depth. Subfossil skeletons recorded from a cave on Crete that emerged 1500 years ago (Vacelet, 1980b) and fossil skeletons recorded from Pleistocene cliffs of south Italy dating back to 30,000 years (Vacelet, 1991).

Remarks. The type species has not been recorded from the westernmost part of the Western Mediterranean. However, its presence in the Mediterranean seems to be very ancient.

Distribution

As for type species.