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Family Polymastiidae Gray, 1867

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Polymastiidae Gray (Demospongiae: Hadromerida) contains 14 genera and approximately 100 species. Species live in all oceans, but some genera are found predominantly in shallow waters at high latitude and in deep waters elsewhere. They are often globular, cushion shape or discoid. The genera of this family share a radiating choanoskeleton and a more or less complicated cortex, the outer layer being always a palisade of ectosomal spicules.

Keywords: Porifera; Demospongiae; Hadromerida; Polymastiidae; *Polymastia*; *Atergia*; *Acanthopolymastia*; *Proteleia*; *Pseudotrachya*; *Quasillina*; *Radiella*; *Ridleia*; *Sphaerotylus*; *Spinularia*; *Trachyteleia*; *Tentorium*; *Tylexocladus*; *Weberella.*

DIAGNOSIS & SCOPE

Synonymy

Polymastiidae Gray, 1867a: 527; Topsent, 1900: 131; Wilson, 1925: 347; Boury-Esnault, 1987: 29; Kelly-Borges & Bergquist, 1997: 400.

Definition

Hadromerida with a radiating choanoskeleton and a more or less complicated cortex, the outer layer being always a palisade of ectosomal spicules (tylostyles, or oxeas and/or exotyles). Megascleres are tylostyles, subtylostyles, strongyloxeas, styles or oxeas; microscleres may include centrotylote microxeas, acanthose microxeas, or raphides in trichodragmata.

Diagnosis

Hadromerida of massive, encrusting, globular, discate or pedunculate growth form. Surface slightly velvety or very hispid. The choanoskeleton is constituted by radial megasclere tracts. A complex specialised ectosomal skeleton is developed to a greater or lesser degree in different genera. It is composed of at least a palisade of tylostyles, or oxeas and/or exotyles (cladotylostyles, spherostyles, etc.). Spicules are two or three size categories of tylostyles, subtylostyles, strongyloxeas, styles or oxeas. Free spicules are always present in the choanosome which may be intermediary or ectosomal tylostyles as well as smooth centrotylote microxeas, acanthose microxeas, or raphides in trichodragmata. A fringe of long spicules is often present at the edge of the body at the contact with the substrata. When known, reproduction is oviparous, extrusion of oocytes and sperm occurs in the sea, and after cleavage of the egg a flattened blastula larvae is developed. Asexual reproduction by the production of stalked bead-like buds has been observed. Several genera are only found in very deep and or polar waters.

Scope

Twenty-six nominal genera have been included in the family at one time or another but only 14 are now considered to be valid. More than one hundred species have been published worldwide although many of them may be synonyms. The faunas of the Atlantic and deep polar regions are relatively well known, including northern New Zealand, the North Sea, and the Mediterranean in particular, but other faunas are relatively poorly known.

History and biology

The anatomy and cytology have been described only in some species of *Polymastia* (Boury-Esnault, 1974, 1976; Boury-Esnault *et al*., 1994a). The volume of choanocyte chambers is between 3400–7800 μm^3 which is within the range observed for other Hadromerida, and the choanocytes show a periflagellar sleeve as in many other hadromerids (Boury-Esnault *et al*., 1990). Different types of cells with inclusions are present which differ between species and can help to discriminate them. However, too few cytological studies have been conducted on Polymastiidae to use cytological characters at the family level of taxonomy. Reproduction is known only in the genus *Polymastia* (Fig. 1). They are oviparous and the eggs stay in a thick mucus, where the cleavage occurs, after leaving the parent body. The mature larva is a flattened blastula which is benthic and slithers along the substrata (Borojevic, 1967c). A case of asexual reproduction through budding of papillae has been also reported for *Polymastia arctica* (Merejkowsky, 1878). This phenomenon occurs quite frequently in this species and has been redescribed recently by Plotkin & Ereskovsky (1997).

Remarks

This family was erected by Gray, (1867a: 527) mostly for the genus *Polymastia* such that the definition given by Gray corresponds to the definition of *Polymastia*. Subsequently there has been a widespread consensus about the content of Polymastiidae such that since Wilson (1925: 347) generic composition has not changed very much, even if some authors like Dendy (1922b: 147) and de Laubenfels (1936a: 151) combined Suberitidae with Polymastiidae.

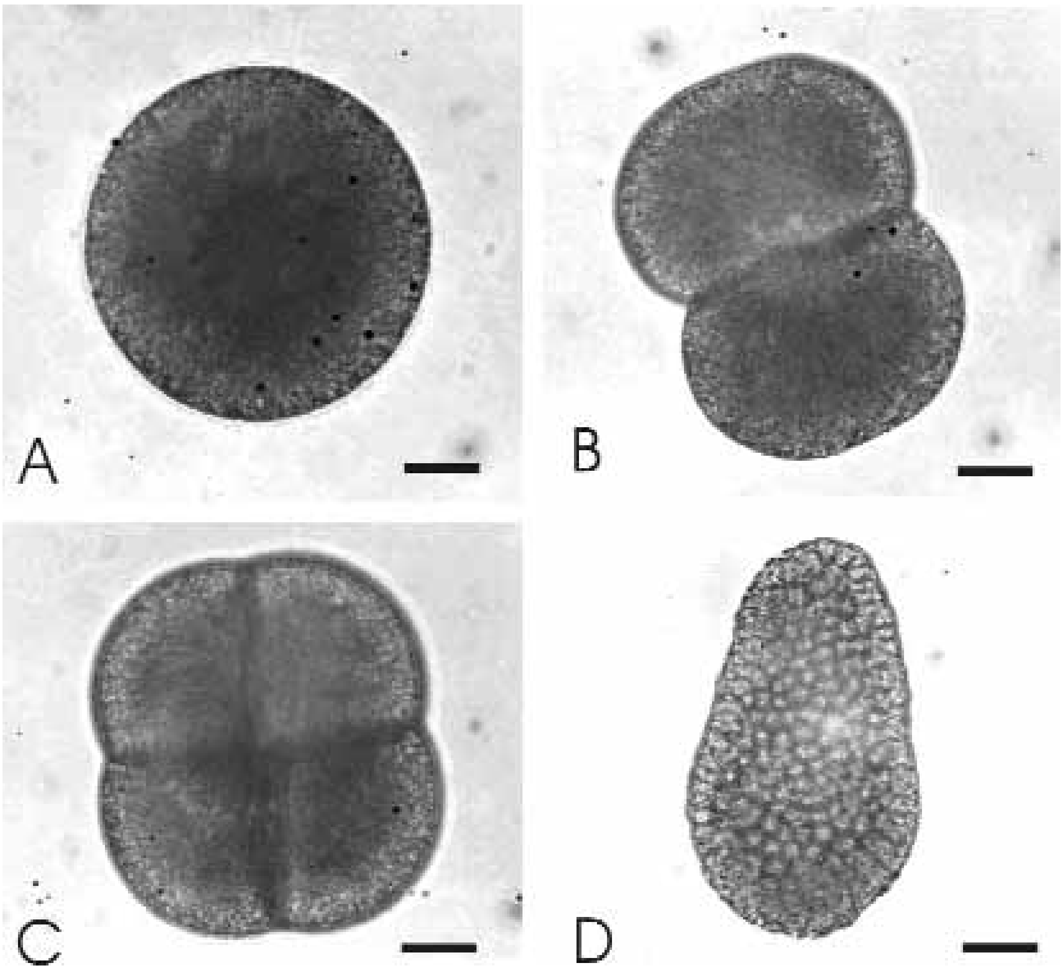

Fig. 1. *Polymastia robusta*, reproduction (R. Borojevic). A, egg (scale 25.3 μm). B, two blastomere embryo (scale 28.3 μm). C, four blastomere embryo (scale 26.4 μm). D, free larva (scale 30 μm).

KEY TO GENERA

(1) Polymastiidae with exotyles 2
Polymastiidae without exotyles 3
(2) Polymastiidae with grapnel-like spicules .... ***Proteleia***
Polymastiidae with spherotylostyles .... ***Sphaerotylus***
Polymastiidae with cladotylostyles .... ***Tylexocladus***
Polymastiidae with acanthose tylostyles .... ***Trachyteleia***
(3) Polymastiidae with the outer layer of the ectosomal skeleton constituted by a palisade of tylostyles 4
Polymastiidae with the outer layer of the ectosomal skeleton constituted by a palisade of oxeas .... ***Pseudotrachya***
(4) Free spicules of the choanoskeleton are smooth centrotylote oxeas, acanthose microxeas or raphides in trichodragmata 5
Free spicules of the choanoskeleton are ectosomal or intermediary tylostyles or subtylostyles 6
(5) Free spicules are smooth centrotylote microxeas .... ***Atergia***
Free spicules are acanthose microxeas .... ***Acanthopolymastia***
Free spicules are raphides in trichodragmata .... ***Spinularia***
(6) Polymastiidae with reduced choanoskeleton 7
Polymastiidae with developed choanoskeleton 8
(7) Choanoskeleton is reduced to bundles of free tylostyles .... ***Quasillina***
Choanoskeleton is reduced to a layer of tangential tylostyles in its outer part .... ***Ridleia***
(8) Choanoskeleton is radial 9
Choanoskeleton is reticulate .... ***Weberella***
(9) The ectosomal skeleton is constituted by a single layer of tylostyles perpendicular to the surface .... ***Tentorium***
The ectosomal skeleton is constituted by at least two layers 10
(10) The ectosomal skeleton from the upper part is different from the one of the lateral or lower part .... ***Radiella***
The ectosomal skeleton is identical on the whole surface .... ***Polymastia***

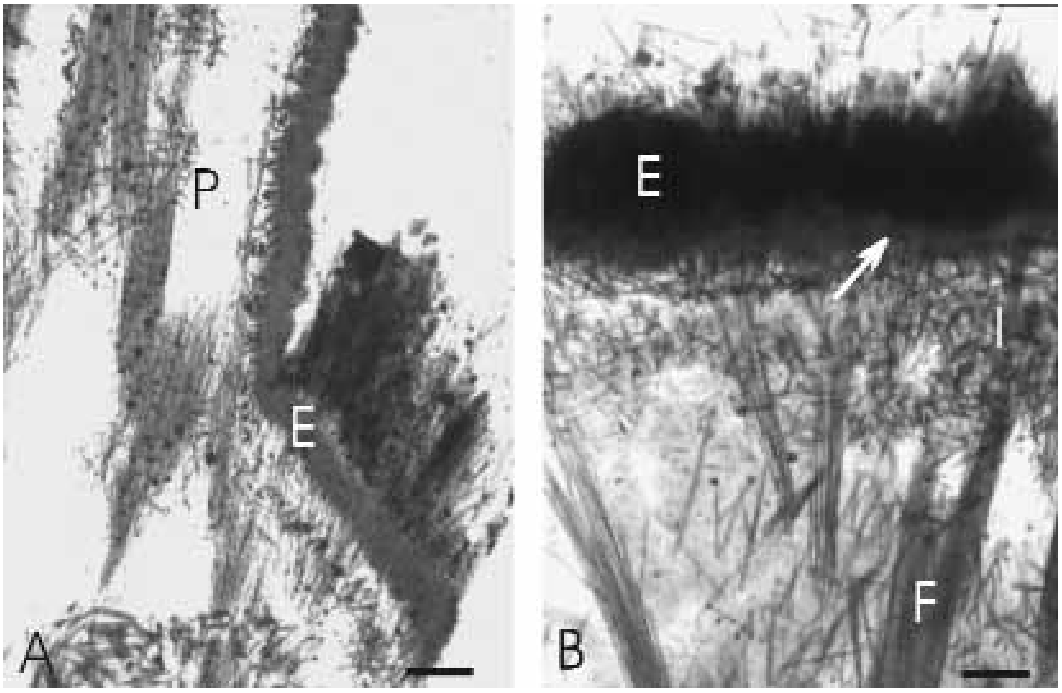

Fig. 2. *Polymastia.* A, thick longitudinal section through a papilla of a Swedish specimen of *Polymastia mamillaris* (abbreviations: P, papilla; E, ectosomal skeleton) (scale 340 μm). B, thick perpendicular section through the body of type specimen of *Polymastia mamillaris* (abbreviations: E, ectosomal skeleton; I, intermediary layer of the ectosomal skeleton; F, tracts of principal spicules; the arrow indicates the collagenous layer) (scale 340 μm).

POLYMASTIA BOWERBANK, 1864

Synonymy

Polymastia Bowerbank, 1864: 177. *Rinalda* Schmidt, 1870: 51; Morrow & Boury-Esnault, 2000: 329.*Pencillaria* Gray, 1867a: 527.

Type species

Spongia mamillaris Müller, 1806 (by monotypy).

Diagnosis

Thickly encrusting Polymastiidae, spherical or cushion-shaped, always with papillae. Skeleton composed of radial tracts of principal spicules between which free spicules are scattered. Ectosomal skeleton composed of at least two layers, the superficial one is a palisade of small tylostyles, the lower layer is made of intermediary spicules, tangential to the surface. The principal spicules can be tylostyles, subtylostyles, styles, and strongyloxeas, intermediary spicules are most often tylostyles, and ectosomal spicules are always tylostyles.

Remarks

Polymastia was erected by Bowerbank in 1864. He designated *Halichondria mamillaris* 'Johnston, 1842' as the type species considering it to be 'the best type of *Polymastia*'. In fact '*mamillaris*' was not described by Johnston but by Müller (1806) under the name *Spongia mamillaris*. Johnston (1842) transferred '*mamillaris*' from *Spongia* to *Halichondria* and also synonymised *S. mamillaris* Müller, 1806 with *S. penicillus* Montagu, 1818. Bowerbank (1864) followed this view and seems to have ignored the description of Müller as there is no mention of this author in any text of Bowerbank (1864, 1866, 1872b) concerning *Polymastia mamillaris*. Vosmaer (1882a), followed by Levinsen (1887) and Fristedt (1887), considered both species to be distinct mainly because of the presence of very long spicules around the margin of specimens of '*penicillus*'. In fact, as stressed by Topsent (1900), they had confused this species with *Trichostemma hemisphaericum* Sars, 1872 while the description of '*penicillus*' by Montagu is clearly not a *Trichostemma*.

Distribution

About 50 species of *Polymastia* have been described in the literature. The Atlantic (Boury-Esnault, 1987; Boury-Esnault *et al*., 1994b; Morrow & Boury-Esnault, 2000) and New-Zealand regions (Kelly-Borges & Bergquist, 1997) are the best studied and each containing about 18 species. Several species such as *Polymastia mamillaris* have been cited worldwide but it has been demonstrated that this cosmopolitanism is based on weak taxonomy (Boury-Esnault *et al*., 1994a).

Description of type species

Polymastia mamillaris (Müller, 1806) (Fig. 2).

Synonymy. *Spongia mamillaris* Müller, 1806: 44; Bowerbank, 1864: 177; Morrow & Boury-Esnault, 2000: 329–330.

Material examined. Holotype: ZMUC '2.1.93' – Bohnslän, North-Atlantic, Swedish west coast, 58°15′N, 11°50′E. Other material. ZMUC – various material, Swedish west coast, coll. Ole Tendal, Björms Rev., 120–200 m, 11.07.1975; Ulvillarna, 150–225 m, 21.03.1977; East of Ramsô, 99–108 m, 16.05.1974; Säcken, 76 m, 13.05.1974; Säcken, 80–90 m, 16.10.1974.

Description. The type specimen is a fragment of a cushion-shaped, attached sponge approximately 35 × 18 × 7 mm thick. The upper surface is hispid. The surface of the sponge traps silt and the colour is only discernible on the papillae. The color is cream in alcohol. The specimen has 26 inhalant papillae and one exhalant. The mean length of the inhalant papillae is 8 × 2 mm in diameter. The exhalant papillae is 11 mm long and approximately 4 mm in diameter. The ectosomal skeleton (Fig. 2) is about 400 μm thick and composed of three layers: the upper layer is a dense palisade (~300 μm thick) of fusiform tylostyles, the middle layer is collagenous (~20 μm thick) and the lower layer is a tangential layer (~80 μm thick) made of intermediary spicules. Choanosomal tracts of principal spicules are 53–106 μm thick. These tracts are divided into two to three smaller ones below the ectosome. They cross the ectosome and echinate the surface by approximately 875 μm. Groups from two to five ectosomal spicules are scattered between the choanosomal tracts. They are particularly abundant below the tangential layer of intermediary spicules in a layer approximately 500 μm thick. The skeleton of the inhalant papillae consists of ascending multispicular megasclere tracts that run the length of the papillae. These are supported by a network of intermediary tylostyles arranged perpendicularly to the megasclere tracts. Towards the periphery there is a layer of tangentially arranged intermediary tylostyles and external to this a palisade composed of ectosomal tylostyles (Fig. 2A). Ectosomal tylostyles are fusiform, straight or slightly bent with a well marked head: 143–196 × 5.3–16 μm (mean 169 × 10.6 μm, $N > 50$). Intermediary styles or subtylostyles, straight 243–561 × 8–15.9 μm (mean 445 × 13.2 μm, $N > 50$). Principal spicules are straight, fusiform strongyloxeas, 742–1378 × 8–32 μm (mean 1052 × 24.5 μm $N > 50$).

Remarks. Specimens of *Polymastia* from the Swedish west coast collected between 76 and 225 m deep correspond to the form described by Müller. These show the following characters: ectosomal skeleton composed of three layers, groups from 2–5 ectosomal spicules scattered between the choanosomal tracts and particularly abundant below the tangential layer of the ectosome, shape of the ectosomal tylostyles (101–182 × 5.2–11.7, mean 148 × 8.4 μm, $N > 50$) and of the principal choanosomal spicules (strongyloxeas 461–1320 × 10.6–26.5, mean 853 × 20 μm, $N > 50$) (Morrow & Boury-Esnault, 2000).

Conversely, the holotype of *Polymastia mamillaris* does not correspond with what it is commonly called *P. mamillaris* in the Northeast Atlantic (Channel, North Sea, Irish Sea). The common NE Atlantic *Polymastia* has a two-layered cortex, free intermediary tylostyles in the choanosome and the shape of spicules is not fusiform (see Boury-Esnault, 1974, 1987). This species is actually *P. penicillus* Montagu, 1818 (Morrow & Boury-Esnault, 2000). Redescription of characters of *Spongia mamillaris* Müller, 1806 does not modify the definition of the genus *Polymastia* as it is presently understood and accepted (Boury-Esnault, 1987; Boury-Esnault *et al*., 1994a; Kelly-Borges & Bergquist, 1997). Consequently, the type species of *Polymastia* is *Spongia mamillaris* Müller, 1806, misidentified as *Halichondria mamillaris* 'Johnston, 1842' in the original designation by Bowerbank, 1864. The species is known only from the Swedish west coast between 75 and 225 m depth.

PROTELEIA DENDY & RIDLEY, 1886

Synonymy

Proteleia Dendy & Ridley, 1886: 152; Ridley & Dendy, 1887: 214; Lendenfeld, 1903: 29.

Type species

Proteleia sollasi Dendy & Ridley, 1886 (by monotypy).

Diagnosis

Disc-shaped Polymastiidae with aquiferous papillae. The ectosomal skeleton consists of a palisade of two layers of tylostyles which lie on a tangential layer of intermediary tylostyles. The ectosomal skeleton is echinated by grapnel-like spicules (exotyles). The choanosomal skeleton is composed of stout fibres of principal fusiform styles which end in a palisade. Between the fibres groups of grapnel-like spicules are visible. Besides the grapnel-like spicules three types of tylostyles and styles are present.

Remarks

Three valid species have been described in this genus: *Proteleia sollasi*, *P. borealis* Swartschewsky, 1906, and *P. burtoni* Koltun, 1964b: 28. *Tetilla truncata* Topsent, 1890b: 13 is here excluded as it was allocated erroneously to *Proteleia* by Lendenfeld, 1903: 29.

Distribution

The genus has a bi-polar distribution and wide bathymetric distribution from 18–3000 m.

Description of type species

Proteleia sollasi Dendy & Ridley, 1886 (Fig. 3).

Synonymy. *Proteleia sollasi* Dendy & Ridley, 1886: 152; Ridley & Dendy, 1887: 214.

Material examined. Holotype: BMNH-1887.5:2.62 – Simon's Bay, near Cape of Good Hope, South Atlantic, 18–37 m.

Description. The holotype is 63 mm long, 31 mm wide and about 13 mm in the thicker part. It is disc-shaped and had aquiferous papillae which can reach 8 mm long and 4 mm in diameter at the base. Colour in alcohol is yellowish-grey. Surface is minutely hispid and considerable amount of foreign matter is trapped in the palisade. The papillae are less hispid and are clean. The ectosomal skeleton is about 800–1000 μm thick and is composed of a complex palisade and a tangential layer of spicules. The palisade is composed of two layers: an outer layer of thin tylostyles disposed vertically about 150 μm thick. An inner layer of fusiform tylostyles (~350 μm thick) intermingled with the first one and also vertically arranged (Fig. 3A). Grapnel-like spicules are present in this palisade and project freely for a certain distance from the surface (Fig. 3B). The palisade lies on a tangential layer of fusiform tylostyles similar to those of the inner part of the palisade. The choanosomal skeleton is made of stout fibres of about 250 μm. These primary fibres expand into divergent brushes which penetrate right into the cortex (Fig. 3C). The skeleton of the papillae is similar to the one of the main body (Fig. 3D). However the ectosomal skeleton of the papilla is thinner and the exotyles are absent. In particular the tangential layer is not well separated from the inner

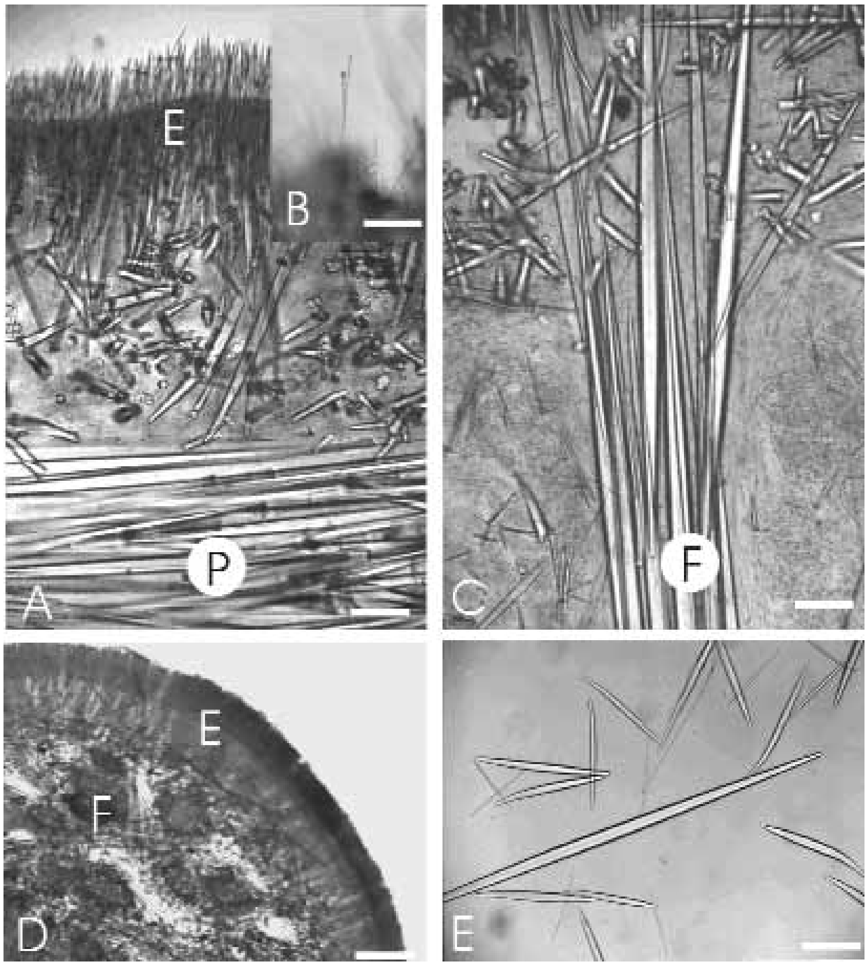

Fig. 3. *Proteleia*. A, micrograph of a slide of the ectosomal skeleton of *Proteleia sollasi* made by Dendy & Ridley (BMNH 87.5.2.62) (abbreviations: E, ectosomal skeleton; P, tangential layer of intermediary tylostyles) (scale 40 μm). B, details of grapnel-like spicules echinating the palisade (scale 80 μm). C, micrograph of a slide of the choanosomal skeleton of *Proteleia sollasi* made by Dendy & Ridley (BMNH 87.5.2.62) (abbreviation: F, tracts of principal spicules) (scale 40 μm). D, transverse section of a papilla through the specimen type (BMNH 87.5.2.62) (abbreviations: E, ectosomal skeleton; F, tracts of principal spicules) (scale 20 μm). E, ectosomal, intermediary and principal tylostyles (scale 60 μm).

layer of the palisade. Primary megascleres are fusiform styles sharply and gradually pointed: 530–1200 × 15–30 μm; intermediary megascleres are fusiform tylostyles which could be slightly curved: 190–222 × 11–19 μm; ectosomal tylostyles slender and slightly curved occurring in the outermost layer of the ectosomal skeleton: 131–175 × 4–5 μm; exotyles which are slender tylostyles with the point transformed in what has been called by Dendy & Ridley a grapnel and which is constituted by a small knob with three to four small teeth: 350–520 × 5–6 μm.

Remarks. This very beautiful sponge has not been observed since it was originally described by Dendy & Ridley (1886). The observation of slides from the type-specimen has shown that the skeleton has a very characteristic organisation without equivalent in the other genera. The type species is known only from the sublittoral near the Cape of Good Hope.

SPHAEROTYLUS TOPSENT, 1898

Synonymy

Sphaerotylus Topsent, 1898b: 244; *Radiella schoenus* Sollas, 1882a: 162 considered as *nomen nudum* by Kirkpatrick, 1908c: 18; Topsent, 1913a: 23 (under the name *Sphaerotylus schoenus*); Boury-Esnault & Van Beveren, 1982: 39; Lévi, 1993: 25; Uriz, 1988: 43.

Type species

Polymastia capitata Vosmaer, 1885a (by original designation).

Diagnosis

Polymastiidae with aquiferous papillae. Primary skeleton composed of tracts of principal spicules and an ectosomal skeleton made up of an inner tangential layer of intermediary tylostyles and an outer layer of small tylostyles reinforced by exotyles, called spherotylostyles by Topsent. The principal skeleton of papillae is constituted by longitudinal tracts of principal spicules and an ectosomal skeleton constituted by a palisade of small tylostyles only. The inner layer of tangential spicules and the exotyles are absent in the papillae.

Remarks

Sphaerotylus was erected by Topsent (1898b) for the species *Polymastia capitata* Vosmaer, 1885a. However in 1913 Topsent

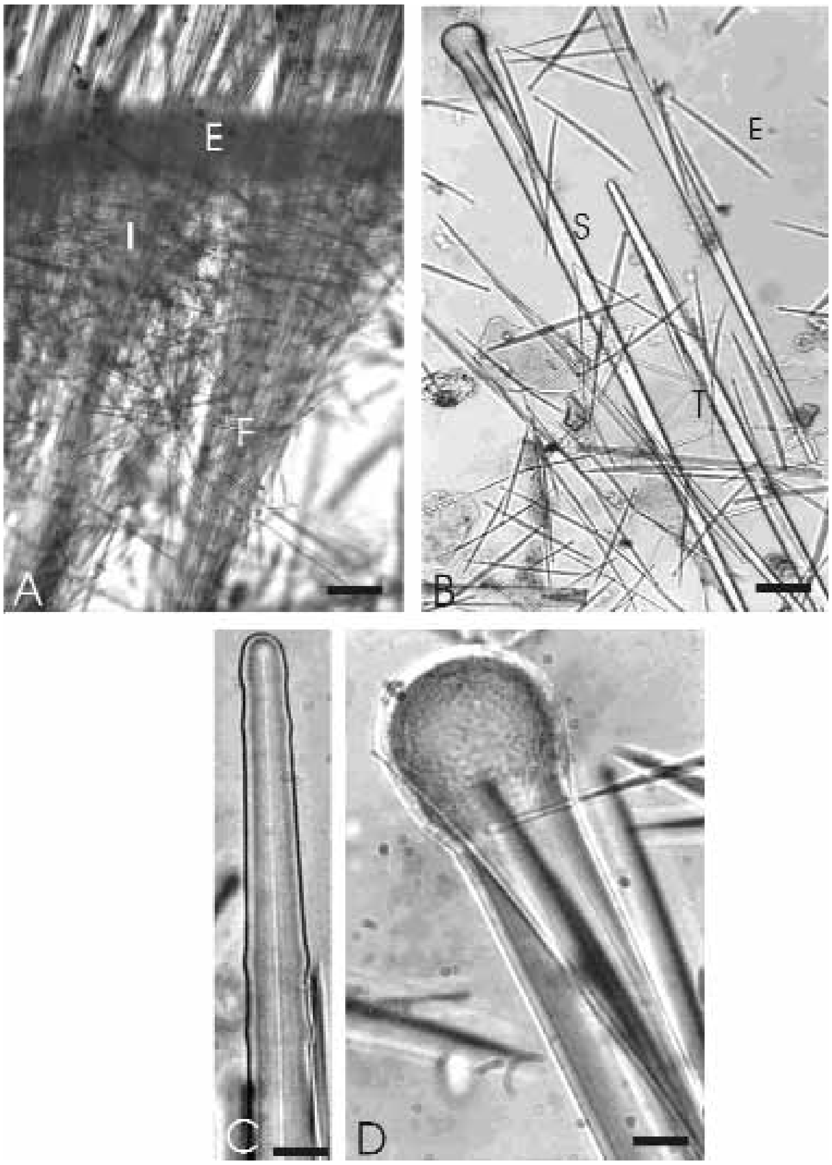

Fig. 4. *Sphaerotylus*. A, perpendicular section through the body of *Sphaerotylus capitatus* (abbreviations: E, ectosomal skeleton; I, tangential layer of intermediary tylostyles; F, tracts of principal spicules) (scale 40 µm). B, dissociated spicules of *Sphaerotylus capitatus*, portion of type (Norman collection BMNH 10.1.1.1199) (abbreviations: E, ectosomal tylostyles of the palisade; T, principal spicules, polytylote fusiform style; S, exotyles) (scale 30 µm). C, detail of the head of a principal style (scale 8 µm). D, detail of the head of an exotyle (scale 8 µm).

placed into synonymy the species *P. capitata* with *Radiella schoenus*, taking into account the description and the figure of Dendy & Ridley (1886: 156). Kirkpatrick (1908c: 18) considered that *R. schoenus*, which has no type specimen, type-locality or original description, should be declared a *nomen nudum*. About seven species or sub-species have been described. The type species *Sphaerotylus capitatus* has been reported from both Arctic and Antarctic regions. This discontinuous distribution seems to be an indication that we are faced with a new case of two sibling species (morphospecies), as already suggested by Lévi (1993).

Distribution

North Atlantic and Arctic region and sub-antarctic and Antarctic region, SW Pacific.

Description of type species

Sphaerotylus capitatus (Vosmaer, 1885a) (Fig. 4).

Synonymy. *Polymastia capitata* Vosmaer, 1885a: 16; Topsent, 1913a: 23; not Boury-Esnault & Van Beveren, 39; not Kirkpatrick, 1908c: 18; not Uriz, 1988: 43.

Material examined. Paralectotype: BMNH 10.1.1.672 – Willents Barentz Expedition 1880–1881, Barents Sea, 72°14′8N, 22°30′9E. Lectotype (not seen): RMNH 704. Paralectotype (not seen): ZMA 1841. Other material. MOM – stn 1052 (Topsent, 1913a, as *Sphaerotylus schoenus*).

Description. Globular specimen of about 2 cm in diameter and short papillae. The choanosomal skeleton is constituted by tracts of principal spicules of about 135 µm in diameter which do not go beyond the surface; between the tracts free intermediary spicules are found. The ectosomal skeleton is composed of an inner layer of tangential intermediary spicules about 400 μm thick, and a palisade of ectosomal spicules (400 μm thick) which is reinforced by a more or less dense layer of exotyles which can go 350 μm over the palisade. The skeleton of the papillae is constituted of longitudinal tracts of principal spicules between which free intermediary spicules are present. The ectosomal skeleton in the region of the papilla is composed only by a palisade of ectosomal spicules. Principal spicules (Fig. 4B, C) are slightly fusiform polytylote styles: 753–950 × 19–26 μm; intermediary spicules are tylostyles: 314–656 × 12–16 μm; ectosomal spicules are fusiform tylostyles with a well-marked head : 109–141 × 5.8–6.4; exotyles are spherotylostyles (Fig. 4B, D), these spicules being tylostyles the tip of which is transformed in a slightly spiny sphere: 650–950 × 18–32 μm, the thickest part of the shaft is close to the sphere.

Remarks. Specimens of *Sphaerotylus capitatus* described from the South Atlantic, sub-Antarctic or Antarctic region (Kirkpatrick, 1908c; Boury-Esnault & Van Beveren, 1982; Uriz, 1988) are very likely a new species. All the specimens identified as *Sphaerotylus capitatus* or *S. schoenus* from the sub-Antarctic or Antarctic regions have to be revised. The type species is known from the North Atlantic and Arctic Oceans.

TYLEXOCLADUS TOPSENT, 1898

Synonymy

Tylexocladus Topsent, 1898a: 102; 1898b: 242; 1904b: 122–123. Not *Atergia* Stephens, 1915a: 32; Topsent, 1928c: 151; Lévi, 1993: 23–24; Kelly-Borges & Bergquist, 1997: 393. Not Boury-Esnault *et al*., 1994b: 75.

Type species

Tylexocladus joubini Topsent, 1898a (by original designation).

Diagnosis

Massive spherical to hemispherical Polymastiidae without inhalant papillae. The surface is hispid. Oscule at the top of a small papilla. Choanosomal skeleton with robust primary tracts composed of tapering tylostyles linked by groups of one to three small tylostyles. Ectosomal skeleton consists of a palisade of small, robust tylostyles and cladotylostyles. Centrotylote microxeas scattered within the choanosome may be present.

Remarks

The genus was described by Topsent, 1898a,b for Polymastiidae with centrotylote microxeas and cladotylostyles. In 1915 Jane Stephens described *Atergia corticata* for a species which contained centrotylote microxeas, with long tylostyles mainly hispidating the periphery, thick spicules tracts and a palisade of robust tylostyles but without cladotylostyles. Topsent (1928c: 151) described new specimens of *T. joubini* two of which lacked cladotylostyles and had very long tylostyles. Consequently, he considered that these six specimens, collected from the same locality, all belonged to the same species and thus synonymised *Tylexocladus joubini* and *Atergia corticata*. This synonymy was accepted by most taxonomists with the exception of Dickinson (1945) who described *Atergia corona*, and Koltun (1964b) who described *Atergia acanthoxea* Koltun, 1964b. More recently Lévi (1993) described a new species of *Tylexocladus* from New Caledonia with cladotylostyles but without microxeas, and an *Atergia* species with acanthose microxeas and of course without cladotylostyles. After redescribing the type specimens of *T. joubini* and *A. corticata* Kelly-Borges & Bergquist (1997) considered that even if both genera were synonymous both species were distinct, and that *T. joubini* and *T. corticata* both occurred in the NE Atlantic. At the same time they described a new polymastiid genus *Acanthopolymastia* with acanthose microxeas similar to *Atergia acanthoxa*. Reconsidering all the species and the type-species described for *Tylexocladus, Atergia* and *Acanthopolymastia*, and to avoid confusion until a precise cladistic approach can be achieved, all three genera are retained here for the time being. There are three species of *Atergia* [*A. corticata* Stephens, 1915a, *A. corona* Dickinson, 1945 and *A. villosus* (Kelly-Borges & Bergquist, 1997 as *Tylexocladus*)], three species of *Acanthopolymastia* [*A. acanthoxa* (Koltun, 1964b), *A. pisiformis* Kelly-Borges & Bergquist, 1997 and *A. bathamae* Kelly-Borges & Bergquist, 1997] and two species of *Tylexocladus* [*Tylexocladus joubini* Topsent, 1898b and *Tylexocladus hispidus* Lévi, 1993].

Distribution

NE Atlantic, from 600–1360 m depth for *T. joubini*, and SW Pacific 150 m depth for *T. hispidus.*

Description of type species

Tylexocladus joubini Topsent, 1898b (Fig. 5).

Synonymy. *Tylexocladus joubini* Topsent, 1898b: 242; 1904b: 122–123; not *Atergia corticata* Stephens, 1915a: 32–33. Not Boury-Esnault *et al*, 1994b: 75–76.

Material examined. Holotype: MOM – Azores, 39°21′20″N, 33°26′8′W, depth 1360 m.

Description. The type specimen (Fig. 5A) resembles the illustration of Topsent (1904b, plate I, fig. 9). It is disc-shaped, attached to a branch of coral, about 2 cm in diameter and only 2 mm thick. It has a single oscule located on a top of a small papilla. The surface is finely hispid except on the oscular papilla which is smooth. The choanosomal skeleton is composed of primary tracts which stretch out from the base to the surface and consist of long tapering tylostyles. Between these tracts, groups of small and robust tylostyles are scattered and intermingled with abundant centrotylote microxeas. The ectosomal skeleton is formed by a dense palisade of small and robust tylostyles which is pierced at regular intervals by solitary, long and stout cladotylostyles (Fig. 5B). These spicules are set up below the palisade which they pierce and produce the hispid surface. Principal tylostyles: straight, with a well marked head and a very long and slender extremity; up to 1 mm long and 15 μm at the thickest. Ectosomal tylostyles: fusiform and slightly curved they have a globular head and a short extremity (175–300 × 10–12 μm). Cladotylostyles: these exotyles have a very characteristic denticulate distal extremity (Fig. 5C, D) where the axial canal of the spicule divided in several ramifications. The head is well-marked (550–650 × 20–25 μm). Centrotylote microxeas (50–120 × 3–5 μm) (Fig. 5C, D).

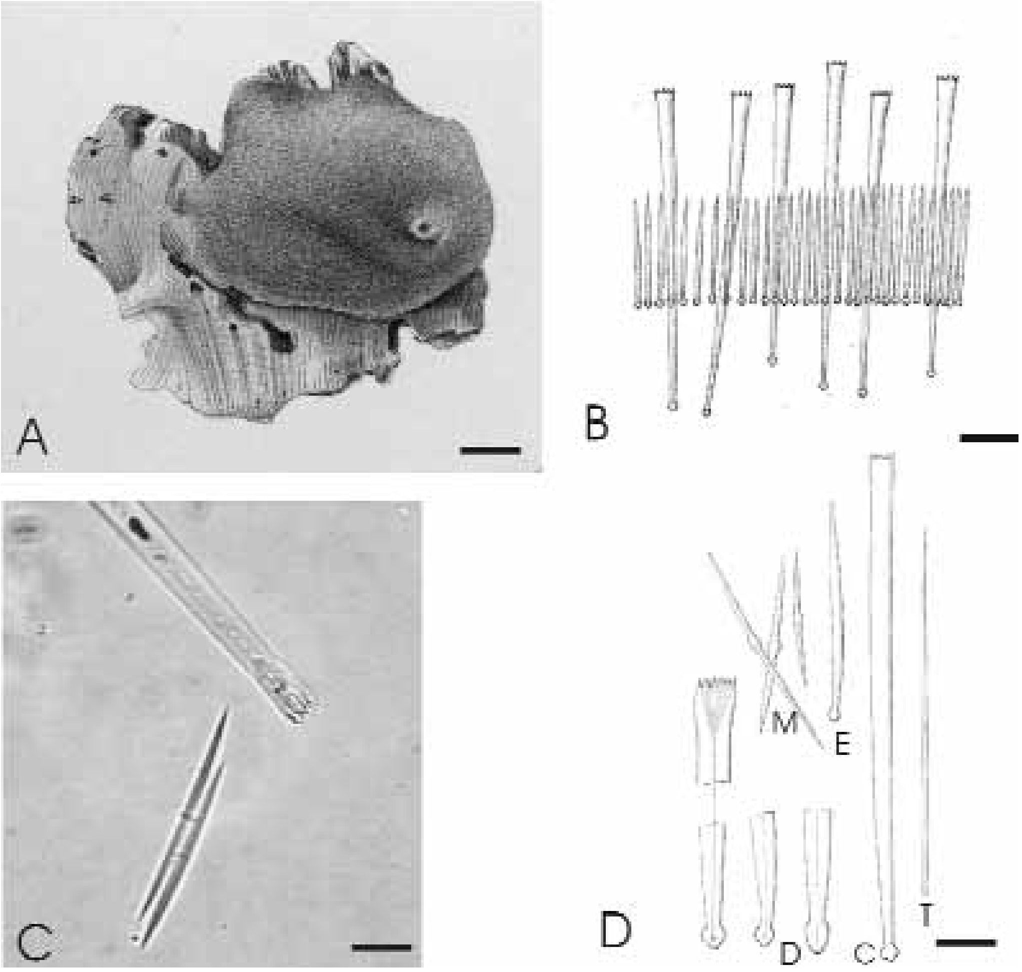

Fig. 5. *Tylexocladus*. A, type specimen of *Tylexocladus joubini* (from Topsent 1904b, pl. I, fig. 9) (scale 26 mm). B, schema of the palisade composed by small and robust tylostyles which is pierced at regular intervals by cladotylostyles (from Topsent, 1904b, pl. XII, fig. 10) (scale 115 μm). C, detail of the denticulate extremity of a cladotylostyle and two centrotylote microxeas (scale 29 μm). D, spicules (from Topsent 1904b, pl. XII, fig. 11) (abbreviations: M, centrotylote microxeas; E, ectosomal tylostyles; C, cladotylostyles; T, principal tylostyles; D, details of the extremities of the cladotylostyles and the head of the principal tylostyles) (scales T, 183 μm; C, E, 60 μm; D, M, 32 μm).

Remarks. In other specimens described by Topsent (1928c: 152) dimensions of cladotylostyles may reach 1700 × 35 μm. *Tylexocladus joubini* was found only by the 1896 and 1905 Prince Albert I de Monaco expeditions to the N Atlantic, West of the Azores Islands from 650–1360 m depth, in areas between 39°21′–39°26′N to 31°05′–31°22′W.

ATERGIA STEPHENS, 1915

Synonymy

Atergia Stephens, 1915a: 32–33; Topsent, 1928c: 152 (as *Tylexocladus joubini* for two specimens from station 2210); Dickinson, 1945: 36; Lévi, 1993: 26; Boury-Esnault *et al*., 1994b: 75 (as *Tylexocladus joubini*); Kelly-Borges & Bergquist, 1997: 396 (as *Tylexocladus corticata*).

Type species

Atergia corticata Stephens, 1915a (by original designation).

Diagnosis

Spherical to hemispherical Polymastiidae without inhalant papillae. Choanosomal skeleton composed by radial tracts of principal tylostyles which fan out very slightly beneath the cortex which they pierce. A hispid fringe is often visible around the margin. The ectosomal skeleton is composed of a palisade of small tylostyles. Scattered in the choanosome are small tylostyles and centrotylote microxeas.

Remarks

Refer to discussion for *Tylexocladus*. Three species are allocated here to *Atergia: A. corticata, A. villosus* (Kelly-Borges & Bergquist, 1997), and *A. corona* Dickinson, 1945, but not *A. purpurea* Laubenfels, 1954: 204.

Distribution

NE Atlantic, from the West of Ireland to the Gibraltar strait; 500–1200 m depth, Pacific Chatham islands and St James Bank off Cape San Lucas (22°50′30″N, 110°15′W (150 m depth).

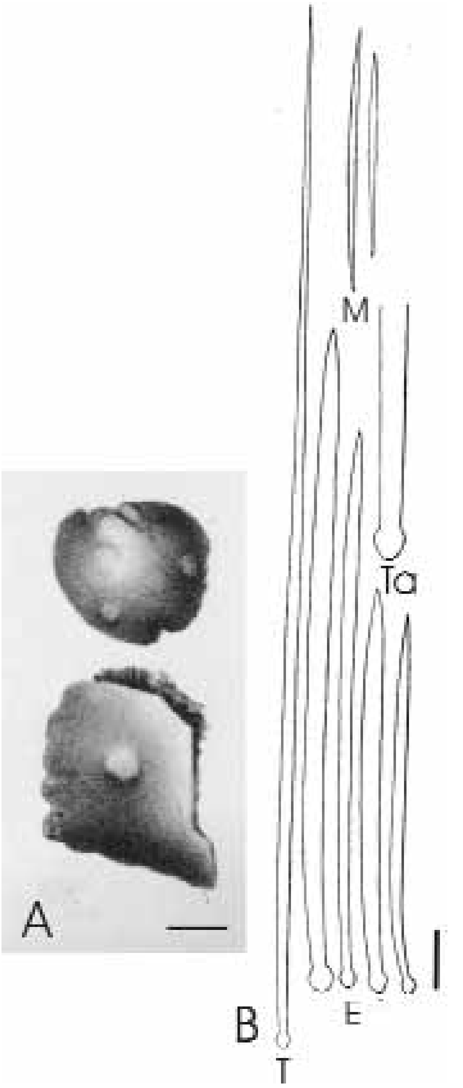

Fig. 6. *Atergia*. A, type specimen of *Atergia corticata* (from Stephens, 1945, pl. III, figs 2–3) (scale 4.5 mm). B, spicules (from Stephens, 1915a, pl. V, fig. 4) (abbreviations: T, principal tylostyles; E, ectosomal tylostyles; Ta, detail of the head of a principal tylostyles; M, centrotylote microxeas) (scales T, 80 μm; E, Ta, 34 μm; M, 18 μm).

Description of type-species

Atergia corticata Stephens, 1915a (Fig. 6).

Synonymy. *Atergia corticata* Stephens, 1915a: 32–33.

Material examined. Holotype: BMNH 1953.11.11.12 – 54°17′N, 11°33′W, 700 m depth. Other material. Gibraltar strait, 35°56′N, 5°35′E, 534–604 m depth (Boury-Esnault *et al*., 1994b).

Description. Disc-shaped specimen, 15 mm in diameter and 5 mm in thickness in the centre (Fig. 6A). The surface is hispid particularly at the periphery. The choanosomal skeleton is composed of strongly radiating tracts, which emanate from the base of the sponge and end beyond the surface. Centrotylote microxeas and small tylostyles criss-cross the primary tracts. The ectosomal skeleton is a very dense palisade of small tylostyles. The principal tylostyles often pierce the surface making it very hispid. Principal tylostyles are straight with a well marked head and a very long, slender extremity (780–1350 × 12–18 μm). Ectosomal tylostyles are slightly curved and have a fusiform shaft, with a well-marked head and a short extremity (175–340 × 12 μm). Hispidating tylostyles may reach more than two millimetres in length, with very long and thin extremities, but are quite similar in shape to the principal tylostyles. Microxeas with a slight swelling at the centre of the spicule (45–100 × 3 μm) (Fig. 6B).

Remarks. The hispidating spicules vary in abundance and length between different specimens, mostly however because they are usually broken. This kind of spicule is very frequent in species living in mud bottoms and their abundance may be linked to environmental conditions. The type species is distributed in the NE Atlantic, from the West of Ireland to the Gibraltar Strait and around the Azores Islands; 500–1200 m depth.

ACANTHOPOLYMASTIA KELLY-BORGES & BERGQUIST, 1997

Synonymy

Acanthopolymastia Kelly-Borges & Bergquist, 1997.

Type species

Atergia acanthoxa Koltun, 1964b (by original designation).

Diagnosis

Polymastiidae with a cushion-shaped or discoid shape and a single low oscular papilla. The edge of the sponge body is very hispid whereas the other part of the surface is only minutely hispid. The choanoskeleton is composed by tracts of tylostyles or subtylostyles which project well beyond the surface at the edge. The ectosomal skeleton is composed of a palisade of small tylostyles. Acanthose microxeas are very abundant both in the ectosome and choanosome.

Remarks

This genus was erected by Kelly-Borges & Bergquist (1997) for the species previously placed in *Atergia* but having acanthose microxeas densely packed in the choanosome and the ectosome. Three species are included in this genus: *A. acanthoxa* (Koltun, 1964b), *A. pisiformis* Kelly-Borges & Bergquist, 1997 (described as *Atergia acanthoxa* by Lévi, 1993), and *A. bathamae* Kelly-Borges & Bergquist, 1997.

Distribution

This genus is so far known only from the Southwest Pacific, from deeper waters 500–3300 m depth.

Description of type species

Acanthopolymastia acanthoxa (Koltun, 1964b) (Fig. 7).

Synonymy. *Atergia acanthoxa* Koltun, 1964b: 27. Not *Atergia acanthoxa* Lévi, 1993: 26; *Acanthopolymastia acanthoxa* Kelly-Borges & Bergquist, 1997: 396.

Material examined. Holotype (fragment, courtesy of Vladimir Koltun): SME-Po57 – Antarctica, Ross Sea, 68°00′S, 160°07′W.

Description. Body-cushion shaped, about 4 cm diameter and 1 cm thick (Fig. 7A). A very long fringe is present at the edge. The choanoskeleton is formed by radial tracts of principal spicules

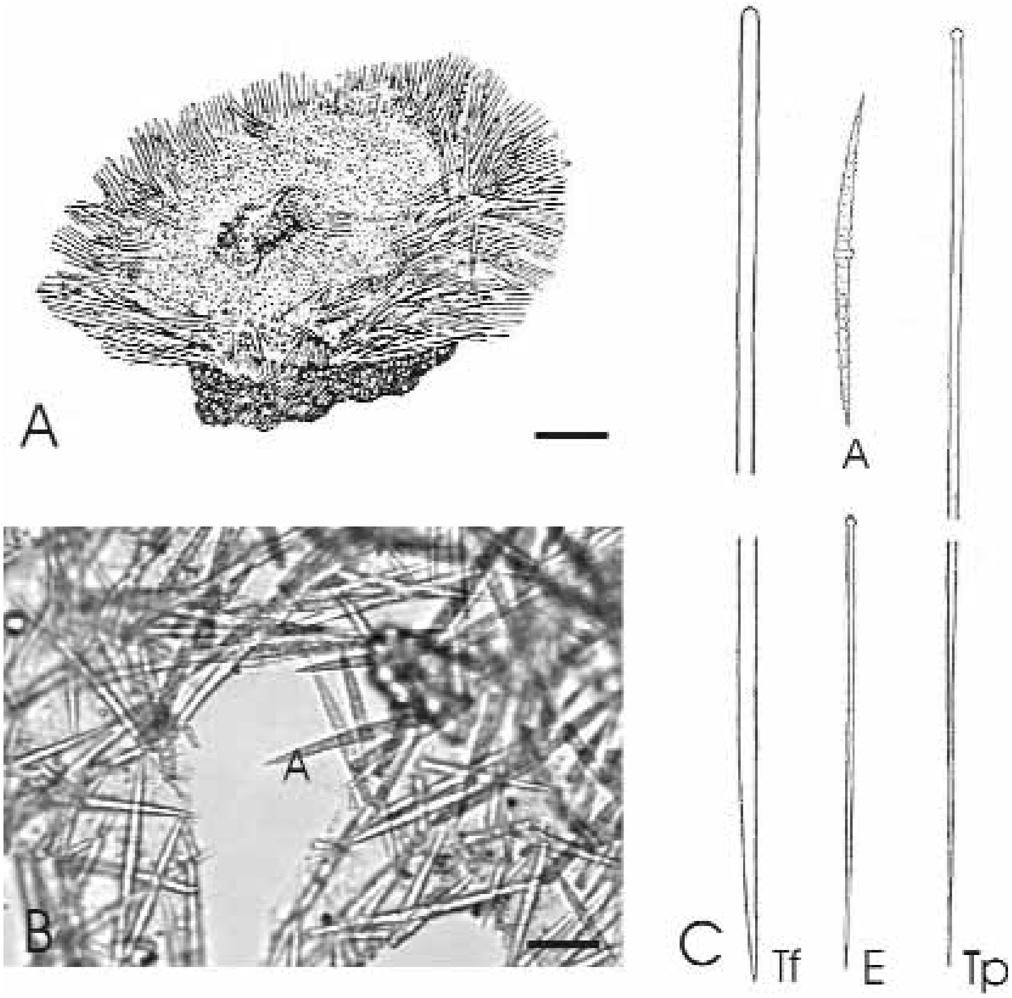

Fig. 7. *Acanthopolymastia*. A, type specimen of *Acanthopolymastia acanthoxa* (from Koltun, 1964b, as *Atergia*, fig. 3). Note: in the center the oscular papilla and at the periphery the fringe of long spicules (scale 7.5 mm). B, part of the ectosomal skeleton where the dense layer of acanthoxeas is clearly visible (abbreviation: A, acanthoxea) (scale 30 μm). C, spicules from the type specimen (from Koltun, 1964b, fig. 3) (abbreviations: Tf, spicules of the fringe; E, ectosomal tylostyles; A, acanthoxea; Tp, principal tylostyles) (scales Tf, E, Tp, 77 μm; A, 22 μm).

between which there is numerous acanthoxeas. The ectosomal skeleton, 500–600 μm thick, is composed of a dense layer of irregularly distributed acanthoxeas (Fig. 7B) and an outer palisade of ectosomal spicules. Principal tylostyles or subtylostyles 1650–2350 × 16–21 μm; styles or subtylostyles of the fringe up to 7 mm long and 14–34 μm wide; ectosomal tylostyles 460–630 × 8–10 μm; acanthose centrotylote microxeas 98–185 × 5–8 μm (Fig. 7C).

Remarks. This species is known only from the Antarctic coast, Ross Sea, from considerable depth (3200–3400 m).

QUASILLINA NORMAN, 1869

Synonymy

Quasillina Norman, 1869b: 329. Vosmaer, 1885a: 20; Ridley & Dendy, 1887: 226; Dendy, 1888: 520; Topsent, 1898a: 102; Topsent, 1900: 157; Boury-Esnault *et al*., 1994b: 70. ? *Bursalina* Schmidt, 1875: 116. Also Bowerbank, 1862a: 71.

Type species

Euplectella brevis Bowerbank, 1862a (by original designation).

Diagnosis

Polymastiidae with a short peduncle and an ovoid body, with a single apical oscule at the summit. From the inside to the outside the ectosomal skeleton is composed of ascending primary tracts, a tangential layer of spicules perpendicular to the primary tracts and an external layer made of tufts of small styles perpendicular to the surface. The choanoskeleton is reduced to consist only of dispersed bundles of small styles. Megascleres are styles, subtylostyles, strongyloxeas or tylostyles of two or three sizes.

Remarks

Four species are included in the genus: *Q. brevis, Q. richardi* Topsent, 1913a and *Q. intermedia* Boury-Esnault, Pansini & Uriz, 1994b, *Q. translucida* Desqueyroux-Faundez & Van Soest, 1997. *Quasillina quiza* described by de Laubenfels (1954: 211) from the central West Pacific is certainly not a Polymastiidae. The most important character of this genus is the fact that the tracts of principal megascleres are localized within the inner part of the ectosome and do not constitute the choanosomal skeleton as in the other Polymastiidae. The choanoskeleton is reduced to bundles of small

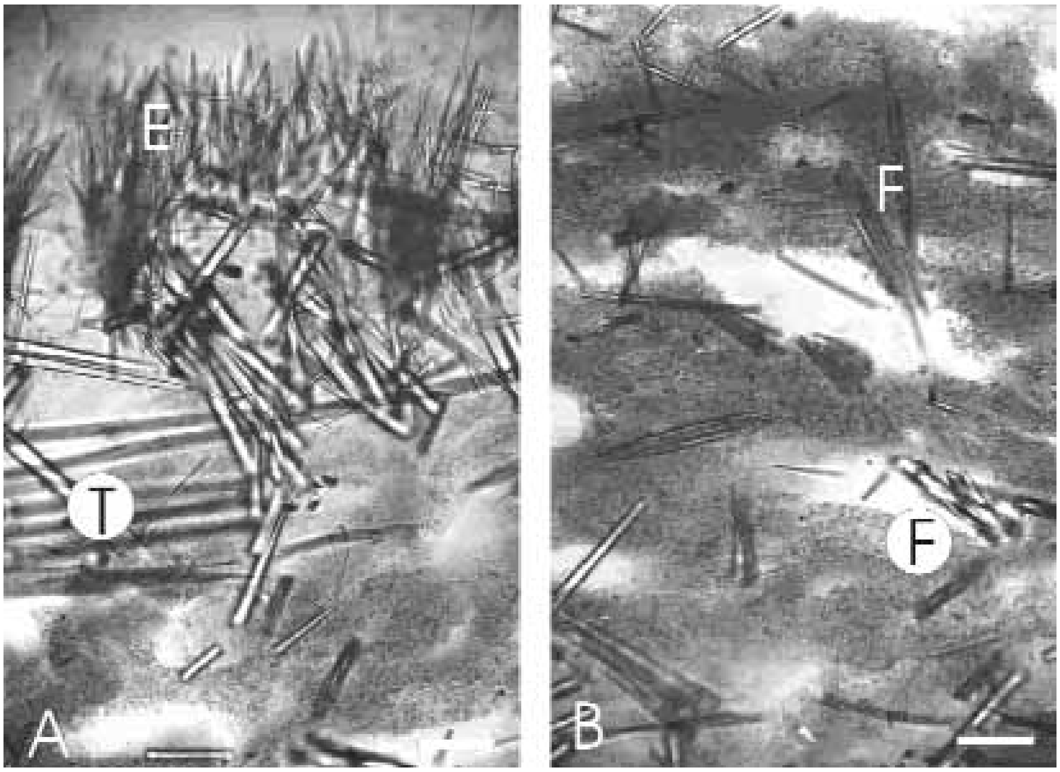

Fig. 8. *Quasillina*. A, histological section of the ectosome of *Quasillina brevis* from the 'Challenger' collection (abbreviations: E, ectosomal skeleton, see tufts of small styles; T, tangential layer of principal styles) (scale 50 µm). B, histological section of the choanosome of *Quasillina brevis* from the 'Challenger' collection (abbreviation: F, small styles in free bundles) (scale 50 µm).

styles which correspond to the free spicules often found between the principal tracts in most of the polymastid genera.

Distribution

This genus is known predominantly from the Northern hemisphere, from the Arctic, NE Atlantic and Mediterranean seas. The bathymetric distribution varies between 15–700 m depth with the most littoral stations located in the Arctic.

Description of type species

Euplectella brevis (Bowerbank, 1862a) (Fig. 8).

Synonymy. *Euplectella brevis* Bowerbank, 1862a: 71. *Polymastia brevis*; Bowerbank, 1866: 64; Bowerbank & Norman, 1882: 16 & 31; Lendenfeld, 1897a: 222; *Quasillina brevis*; Norman, 1869b: 329; Vosmaer, 1885a: 20; Vosmaer, 1887: 330; Ridley & Dendy, 1887: 226; Dendy, 1888: 520; Hanitsch, 1894a: 175 & 203; Topsent, 1900: 158–164; Lundbeck, 1909: 452; Brøndsted, 1914: 522; Stephens, 1915a: 30; Rezvoj, 1928; 81; Hentschel, 1929: 869; Brøndsted, 1933: 14; Burton, 1959b: 13; Koltun, 1964b: 150; 1966: 89; Boury-Esnault *et al*., 1994b: 71.

Material examined. Holotype: BMNH 10.1.5 & 6 – North Atlantic, Shetland. Other material. MOM – stn 247 (Topsent, 1904b: 132); BALGIM collection (Boury-Esnault *et al*., 1994b: 71).

Description. Whitish pedunculate sponge with an ovoid body about 2–3 cm high and 5–10 mm in diameter. The oscule is located at the upper part of the sponge. The surface is velvety. The ectosome is tough whereas the choanosome is fleshy. The choanoskeleton is composed only of small styles in free bundles of 5 to 12 (Fig. 8B). The ectosomal skeleton is composed from inside to outside by a layer of primary tracts which are closely related to a second layer of tangential spicules, exactly perpendicular to the tracts, and superficially by tufts of small styles perpendicular to the surface (Fig. 8A) and between which the ostia open. Principal styles are fusiform and resemble strongyloxeas: 600–990 × 10–26 µm; small ectosomal styles: 135–210 × 2.6–5.3 µm.

Reproduction. Spermatogenesis was observed in Arctic material in June (Vosmaer, 1885a).

Remarks. This species was perfectly described by Topsent (1900: 158). Its seems to be relatively abundant in all the NE Atlantic and Mediterranean, with one record from the tropical E Pacific.

RIDLEIA DENDY, 1888

Synonymy

Ridleia Dendy, 1888: 515; Topsent, 1898a: 102; Boury-Esnault *et al*., 1994b: 72–73. Not *Ridleia dendiia* Laubenfels, 1934: 10–11. Not *Ridleia peleia* Laubenfels, 1954: 207. Not *Ridleia sensu* de Laubenfels, 1936a: 151.

Type species

Ridleia oviformis Dendy, 1888 (by monotypy).

Diagnosis

Pedunculate egg-shaped sponge with an oscular papilla. Skeleton mainly confined to the ectosome. From outside to inside

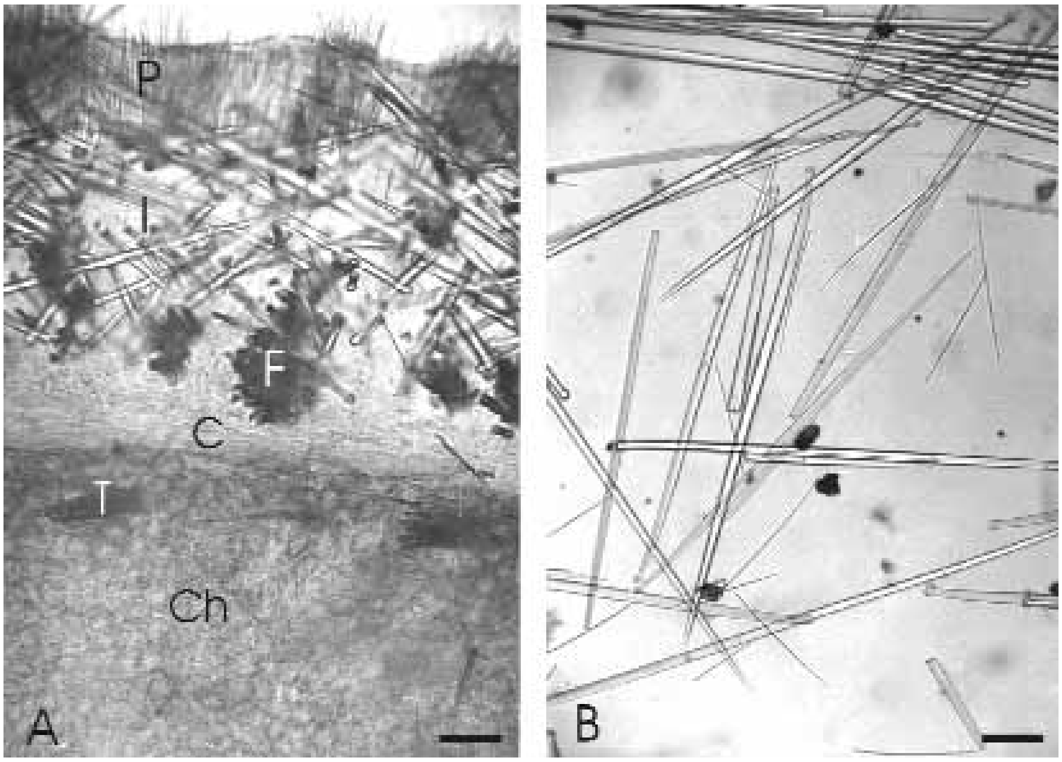

Fig. 9. *Ridleia*. A, histological slide from the Dendy collection of *Ridleia oviformis* (abbreviations: P, palisade of the ectosomal skeleton; I, tangential layer of intermediary spicules; F, tracts of principal spicules; C, collagenous layer at the limit between ectosome and choanosome; T, tangential layer of ectosomal tylostyles in the outermost region of the choanosome; Ch, choanosome) (scale 32 μm). B, different kinds of tylostyles present in *Ridleia oviformis* (scale 36 μm).

there is a palisade of ectosomal tylostyles, a layer of intermediary tylostyles and longitudinal tracts of principal tylostyles which lie on a collagenous layer. In the outermost region of the choanosome there is a tangential layer of ectosomal tylostyles. The spicules are tylostyles in three size categories. Choanocyte chambers are diplodal.

Remarks

In addition to the type species two other species were allocated to *Ridleia* by de Laubenfels (1936a): *Ridleia dendiia* Laubenfels, 1934 and *Ridleia peleia* Laubenfels, 1954. These species do not belong to Polymastiidae, indeed if they belong to Hadromerida at all, the skeleton being confused and without a spicule palisade. De Laubenfels (1936a) referred them to *Ridleia* based on the shape of their spicules but did not take into account the organization of the skeleton.

Distribution

Northeast Atlantic, from 60°0′ to 35°54′1″N and 5°13′ to 31°21′20″W, from 150–950 m depth.

Description of type species

Ridleia oviformis Dendy, 1888 (Fig. 9).

Synonymy. *Ridleia oviformis* Dendy, 1888: 515; Topsent, 1904b: 124; 1928c: 150–151; Boury-Esnault *et al.*, 1994b: 72–73.

Material examined. Holotype: BMNH 83.12.13.69 – NE Atlantic, NW of Scotland, 60°0′N, 5°13′W, 571 m depth. Other material. From the ibero-moroccan Gulf, 35°54′1″N, 6°14′5 W, 150 m depth (Boury-Esnault *et al.*, 1994b: 72–73); MOM – Prince Albert I de Monaco expedition, station 2214, West of Florès, 39°16′10″N, 31°21′20″W (identified by Topsent, 1928c: 150–151).

Description. The holotype has an egg-shaped body, 15 mm high and 7 mm wide, ending in an oscular papilla and fixed by a small peduncle to pebbles. The colour in spirit is pale yellow and the consistency is cork-like. The skeleton is almost entirely confined to the ectosome. From outside to inside, a palisade of thin ectosomal tylostyles lies on a tangential layer of intermediary tylostyles. In the inner part of the ectosome, longitudinal tracts of principal tylostyles followed by a collagenous layer which indicate the limit between ectosome and choanosome. In the outer-most region of choanosome a layer of tangential ectosomal tylostyles is present, representing the only remnant of the choanosomal skeleton (Fig. 9A). Principal tylostyles are straight tylostyles with a well-marked head: 400–900 μm × 12 μm. Intermediary tylostyles are slightly fusiform, with a well-marked head: 250–350 × 7 μm. Ectosomal tylostyles are very slender, frequently curved and they taper gradually to the apex: 130–200 × 2 μm (Fig. 9B).

Reproduction. Small oocytes were observed in the histological slides of the Dendy collection.

Remarks. Although this species has been collected only on four occasions Dendy's (1888) description was so accurate that it makes it perfectly recognisable. It shares with all Polymastiidae longitudinal tracts of megascleres and palisade of ectosomal tylostyles but the skeleton is almost exclusively confined to the ectosomal region. The type species has been recorded from various sites in the NE Atlantic – Northwest of Scotland (60°0′N, 5°13′W, 571 m depth), close to the Azores (Banc Princesse Alice, 37°57′N, 29°14′45″W, 200 m depth, W of Florès, 39°16′10″N, 31°21′20″W, 650–914 m depth), and more recently from the ibero-morrocan Gulf (35°54′1″N, 6°14′5W, 150 m depth).

RADIELLA SCHMIDT, 1870

Synonymy

[*Trichostemma*] Sars, 1869: 250 (*nomen nudum*). *Radiella* Schmidt, 1870: 48; Schmidt, 1880b: 77; de Laubenfels, 1936a: 150. *Trichostemma* Sars, 1872: 62–63; Ridley & Dendy, 1887: 216; Topsent, 1898a: 101; Dendy, 1922b:151; Wilson, 1925: 347; Boury-Esnault *et al*., 1994b: 73.

Type species

Radiella sol Schmidt, 1870 (by subsequent designation).

Diagnosis

Circular lenticular or hemispherical Polymastiidae. The skeleton of the lower face of the sponge is composed of an envelope of principal subtylostyles or styles covered by a thin palisade of ectosomal tylostyles. The upper face is composed of one or two layers of tylostyles. The choanosomal skeleton is composed of diverging tracts emanating from a central nucleus at the base of the sponge and by groups of fusiform tylostyles. The inhalant and exhalant apertures are grouped on papillae.

Remarks

The status of the genus *Radiella* has been controversial. Schmidt (1870: 48) described briefly a new genus *Radiella* without designation of a type species or a type specimen. He allocated two species to this genus: *R. spinularia* (Bowerbank, 1866) and his new species from the Gulf of Mexico *R. sol. Tethea spinularia* Bowerbank, 1866 is in fact the type species of the genus *Spinularia* Gray, 1867a, which was considered to be valid by Stephens (1915a). Previously Sars, 1869 alluded to a new genus and species, *Trichostemma hemisphaericum*, in a species list detailing little more than only geographical information (Lofoten islands, Arctic-Atlantic area, between 200–300 m depth). The species and genus were only later carefully described by Sars in 1872. Thus, Schmidt (1880b: 77) claimed that *Trichostemma hemisphaericum* described by Sars in 1872 was synonym of *Radiella sol*, described in 1870. Since this time both genera have been used equally by authors, or following Ridley & Dendy (1887) who used *Trichostemma* in preference because it was well described, or following the 'ruling' of Schmidt (1880b) and the rules of zoological nomenclature. A specimen identified by Schmidt as *Radiella sol* was discovered in the USNM Washington, although it does not correspond to the illustration of Schmidt (1870, plate 4, fig. 6). Nevertheless, *Trichostemma* is considered here to be a synonym of *Radiella* following Article 12 of the International Code of Zoological Nomenclature (Anon., 2000).

Five species are presently considered to belong to this genus: *Radiella sol* Schmidt, 1870, *R. hemisphaericum* (Sars, 1872), *R. sarsi* (Ridley & Dendy, 1886), *R. irregularis* (Ridley & Dendy, 1886) and *R. straticularis* (Wilson, 1925). Two other species have been assigned to this genus but are reallocated to *Polymastia: Trichostemma grimaldi* Topsent, 1913a (by Topsent, 1927c: 257) and *Radiella tissieri* Vacelet, 1961b (by Uriz & Rosell, 1990: 378).

Distribution

Three species have been described from the Atlantic: *R. sol* Schmidt, 1870 (West central Atlantic), *R. hemisphaericum* (Sars, 1872) (Arctic and North Atlantic), *R. sarsi* (Ridley & Dendy, 1886) (NE Atlantic and Mediterranean sea), and two species from the Pacific ocean *R. irregularis* (Ridley & Dendy, 1886) and *R. straticularis* (Wilson, 1925). All belong to the deep water fauna.

Description of type species

Radiella sol Schmidt, 1870 (Fig. 10).

Synonymy. *Radiella sol* Schmidt, 1870: 48; Sars, 1872: 62–63; Topsent, 1913a: 20–21; Ridley and Dendy, 1886: 216; Lundbeck, 1909: 451–452; *Polymastia hemisphaericum*; Vosmaer, 1885a; Koltun, 1964a: 149; Koltun, 1966: 78.

Material examined. ? Holotype: USNM 990 – 17°28′N, 77°30′W, 1116 m depth, 'Blake' expedition 1878–1879 (identified by Schmidt). Other material. *Trichostemma hemisphaericum*: MOM – Prince Albert I de Monaco expedition to the Atlantic, stn 1052; Norwegian coast 65°41′N, 9°30′E, 440 m; stn 960 between Norway and Bear Island, 72°37′N, 20°00′E, 394 m depth. Comparative material. MOM – misidentified as *T. hemisphaericum* Topsent, 1892a, stn. 161 46°4′40″N, 49°2′33″W, 1267 m depth.

Description. The holotype is hemispherical, 2 cm in diameter, 7 mm thick (Fig. 10A). On the upper side 15 papillae about 1 mm high were observed. The edge of the body is covered by a very long fringe. The surface is velvety. The ectosomal skeleton of the upper face is about 1500 μm thick, composed of a palisade of ectosomal tylostyles (~850 μm thick) and a paratangential layer of criss-crossed fusiform tylostyles (~650 μm thick) (Fig. 10B). The choanosomal skeleton is composed of diverging tracts of principal tylostyles (250–340 μm in diameter) emanating from a central nucleus at the base of the sponge, and by numerous rosettes of fusiform tylostyles. The skeleton of the lower face of the sponge is composed of an envelope of principal subtylostyles covered by a thin palisade of ectosomal tylostyles (Fig. 10C). Ectosomal tylostyles straight or slightly curved with a well marked head 290–390 × 11 μm; intermediary fusiform tylostyles 460–620 × 26 μm; principal subtylostyles straight and with an acerate extremity: 795–2290 × 11–32 μm and subtylostyles of the fringe which are >5 mm long and about 50 μm thick.

Remarks. Presently it is impossible to ascertain if this specimen from the West central Atlantic is a synonym of '*hemisphaericum*' from the Arctic and North Atlantic. A detailed revision of specimens from the Arctic with other specimens from West central Atlantic is necessary before making such a decision. The type species is known from the West central Pacific, from deep waters.

WEBERELLA VOSMAER, 1885

Synonymy

Weberella Vosmaer 1885a: 16; Topsent, 1928c: 149; Vacelet, 1960a: 261; Uriz, 1975: 429–442; Boury-Esnault *et al*., 1994b: 76.

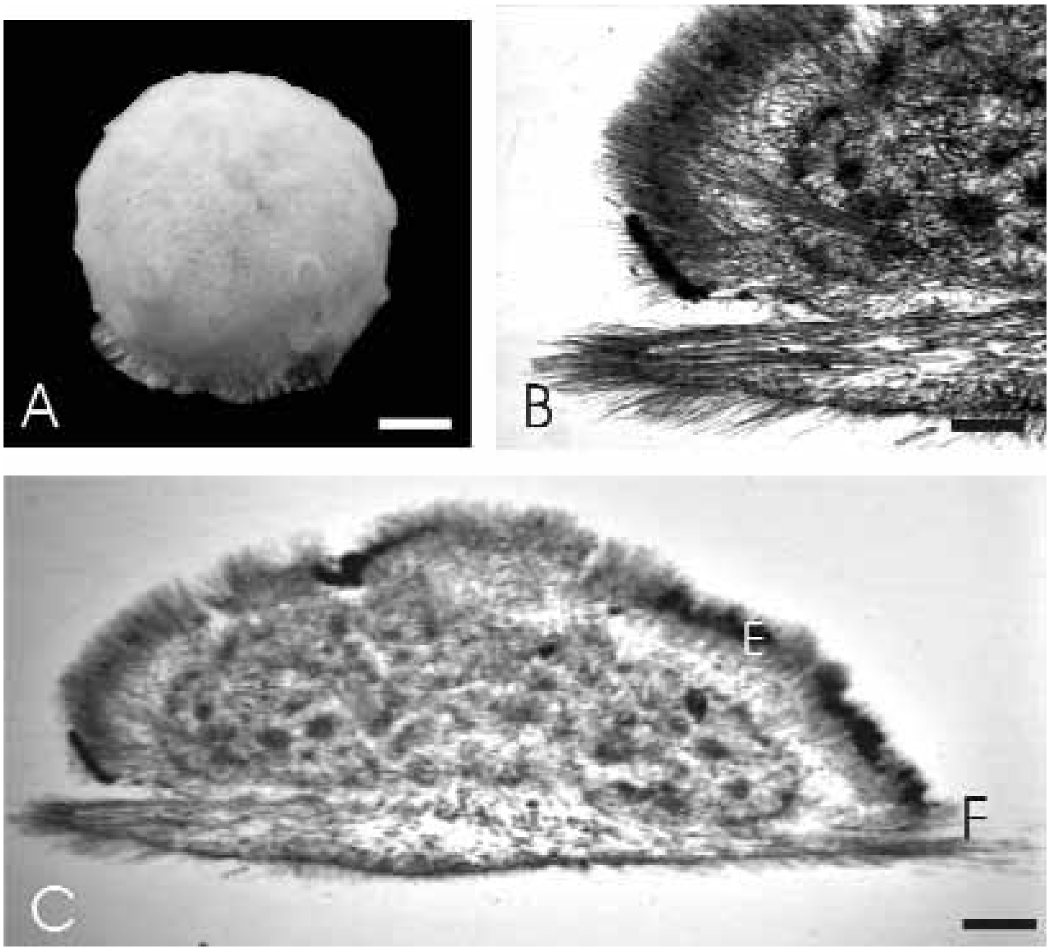

Fig. 10. *Radiella*. A, type specimen of *Radiella sol* (from USNM 990) (scale 4 mm). B, detail of the ectosomal basal skeleton through a thick section of *Radiella sol* (scale 170 μm). C, transverse section of a specimen of *Radiella sol* (abbreviations: E, ectosomal skeleton; F, fringe) (scale 1 mm).

Type species

Alcyonium bursa Müller, 1806 (by original designation).

Diagnosis

Polymastiidae with small aquiferous papillae, reticulate choanosomal skeleton, and an ectosomal skeleton composed of a palisade of tylostyles which lie on a paratangential layer of criss-crossed tylostyles. Only two category of tylostyles present.

Remarks

Two species have been described for this genus: *Weberella bursa* (Müller, 1806) from the NE Atlantic and *W. verrucosa* Vacelet, 1960a from Mediterranean Sea and the Gibraltar strait. In the literature there is a confusion between *Suberites bursa* Schmidt, 1862: 68 which has been allocated to *Polymastia* by Lendenfeld (1897a: 117) and the species of Müller (1806) which has also been allocated to the genus *Polymastia* by Koltun (1964a: 149).

Distribution

NE Atlantic and Mediterranean seas.

Description of type species

Weberella bursa (Müller, 1806) (Fig. 11).

Synonymy. *Alcyonium bursa* Müller 1806: 43; *Weberella bursa* Vosmaer, 1885a: 16; Topsent, 1928c: 149; Uriz, 1975: 430; Boury-Esnault *et al*., 1994b: 76. *Polymastia bursa* Koltun, 1964a: 149; Koltun, 1966: 76. Not *Suberites bursa* Schmidt 1862: 68. Not *Polymastia bursa* Lendenfeld, 1897a: 117.

Material examined. Holotype: Unknown – Arctic Ocean, 72°36′N, 24°57′E, depth 250 m. Other material. BMNH 63.71.29.87 – from Koltun Collection registered in Leningrad Museum under the number 7827; BALGIM collection – stn DR-42 (Boury-Esnault *et al*., 1994b); MOM, stn 1463 (Topsent, 1928c).

Description. Globular or ovoid sponge (Fig. 11A) with a firm consistency and a finely hispid surface. The largest specimens described are about 10 cm in diameter. Small oscular papillae (1–5 mm high) are located on the upper part. The choanoskeleton is composed of ascending primary tracts of tylostyles of about 50 μm in diameter, which are intersected by secondary tracts. This reticulation is easily visible at the periphery. Within the mesh of this net free groups of ectosomal tylostyles are present. The ectosomal skeleton (~350 μm thick) is composed of an outer palisade of small tylostyles (~250 μm thick) (Fig. 11B) which lie on an inner paratangential layer of criss-crossed tylostyles (~90 μm thick). The skeleton of the

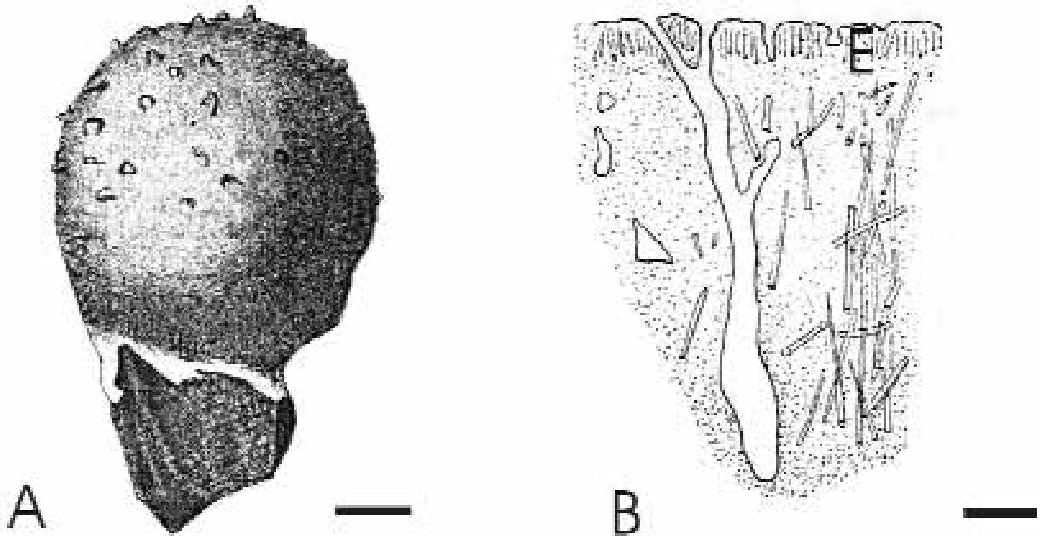

Fig. 11. *Weberella*. A, type specimen of *Weberella bursa* (from Vosmaer, 1885a, pl. I, fig. 12) (scale 1 cm). B, schematic drawing of the organization of the skeleton of *Weberella bursa* (from Vosmaer, 1885a, pl. 17, fig. 6) (abbreviation: E, ectosomal skeleton) (scale 500 μm).

papillae is similar. Principal tylostyles are slightly fusiform with an ovoid often mucronated head: 340–650 × 6–12 μm; ectosomal tylostyles are slightly curved with a well-rounded head: 90–160 × 3–6 μm.

Remarks. This species is easily recognised although rarely collected, found in the NE Atlantic from the Arctic to the ibero-moroccan Gulf; from 130–960 m depth.

TENTORIUM VOSMAER, 1887

Synonymy

[*Thecophora*] Schmidt 1870: 50 (preocc.; Vosmaer, 1885a: 18). *Tentorium* Vosmaer, 1887: 329; Ridley & Dendy, 1887: 221; Topsent, 1917: 36; Topsent, 1928c: 151; Boury-Esnault & Van Beveren, 1982: 37.

Type species

Thecophora semisuberites Schmidt, 1870 (by original designation).

Diagnosis

Polymastiidae with columnar or globular growth form protected by a dense cylindrical sheath of longitudinally placed spicules which form a solid imperforate layer. The ectosomal skeleton contains bundles of smaller spicules arranged in a palisade and is limited to the upper surface of the cylinder. Ostia are present on the upper surface. The oscule at the top of a small papilla is on centre of the upper surface. Megascleres are subtylostyles and tylostyles.

Remarks

Thecophora Schmidt was preoccupied by a species of Diptera, Insecta (*Thecophora* Rondani, 1845), and hence the creation of a new name by Vosmaer (1887). Although the type specimen of the genus is clearly recognizable given the precise description of Vosmaer (1885a: 18–19) the allocation of other species, such as *papillatus* (Kirkpatrick, 1907a) by Topsent (1917: 36) or *caminatus* (Ridley & Dendy, 1887) by Koltun (1976: 168) require a very careful revision of all specimens before any decision could be made as to their correct allocation to this genus. For the present we consider there are two species in this genus: the type species and *Tentorium papillatum*. The type species has been reported from both the Arctic and Antarctic regions, although this discontiguous distribution may indicate the possibility that there are two sibling species hiding under this name.

Distribution

NW Atlantic, South Atlantic, Arctic and Antarctic regions.

Description of type species

Tentorium semisuberites (Schmidt, 1870) (Fig. 12).

Synonymy. *Thecophora semisuberites* Schmidt 1870: 50; Vosmaer, 1885a: 18; Brøndsted, 1914: 522–523; Ferrer-Hernandez, 1914b: 19; Stephens, 1915a: 29–30; Hentschel, 1929: 868–869; Koltun, 1959: 163; 1964a: 148. Not *T. semisuberites* Boury-Esnault & Van Beveren, 1982: 37 and all material from the South Atlantic and Antarctic.

Material examined. Holotype: ZMUC – Ubekendl, Arctic Ocean "det. Schmidt".

Description. The body is cylindrical with a semi-spherical upper part and has about 1–3 cm high and 0.5–1.5 cm in diameter (Fig. 12A). The surface of the cylinder is smooth whereas the upper part is rough. There are 1–3 oscules located at the summit of small papillae. Ostia are located on the upper part of the sponge. The principal skeleton is composed of tracts of tylostyles oriented according to the axis of the cylinder (Fig. 12B). The ectosomal skeleton is composed of a palisade of ectosomal fusiform tylostyles on the upper surface and by a tangential layer of intermediary fusiform tylostyles on the side of the cylinder. Principal tylostyles or subtylostyles with a tapering tip: 950–2400 × 13–24 μm;

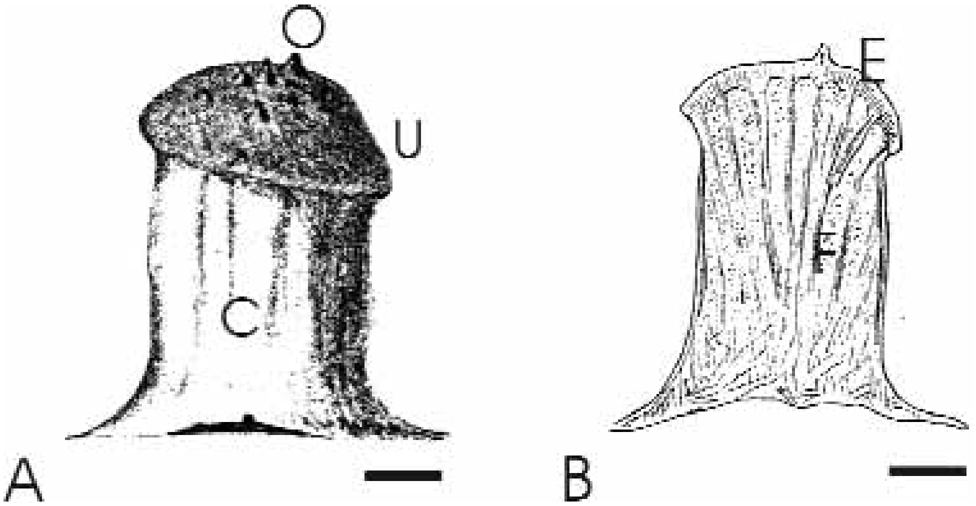

Fig. 12. *Tentorium*. A, type specimen of *Tentorium semisuberites* (from Vosmaer, 1885a, pl. I, fig. 23) (abbreviations: O, oscule; U, upper part of the sponge; C, cylindrical body) (scale 0.6 cm). B, schematic drawing of a longitudinal section through the body of a specimen of *Tentorium semisuberites* (from Vosmaer, 1885a, p. 19, fig. 9) (abbreviations: E, ectosomal skeleton; F, tracts of principal spicules) (scale 0.5 cm).

intermediary fusiform tylostyles: 800–1150 × 20–33 μm; ectosomal fusiform tylostyles: 270–670 × 13–20 μm.

Remarks. The southern specimens from South Atlantic (Inaccessible Island close to Tristan da Cunha, Ridley & Dendy, 1887) and from Kerguelen (Boury-Esnault & Van Beveren, 1982) probably represent a new species of *Tentorium* as they are not conspecific with the type species. The type species is found in the Artic and North Atlantic, from Greenland to the Azores, relatively deep water except in high latitudes where it may be collected in the littoral zone.

SPINULARIA GRAY 1867

Synonymy

Spinularia Gray 1867a: 524. *Rhaphidorus* Topsent, 1898b: 244; 1904b: 120; Stephens, 1915a: 31; Topsent, 1928c: 150; Lévi, 1993: 25.

Type species

Tethea spinularia Bowerbank, 1866 (by original designation).

Diagnosis

Small, more or less discoid Polymastiidae. Surface minutely hispid except at the edge where there is a strong hispidation present. Choanosomal skeleton composed of primary tracts of tylostyles between which trichodragmata are found. Ectosomal skeleton is composed of a palisade of ectosomal tylostyles. There are no true aquiferous papilla and the oscule is located at the upper part of the sponge and is slightly raised above the general surface.

Remarks

This genus has a relatively complicated story which was eventually solved by Stephens (1915a). A second species of this genus was recently found in the bathyal zone of New Caledonia (Lévi, 1993).

Distribution

NE Atlantic and SW Pacific in the bathyo-abyssal zone (650–4000 m deep). In the Northern part of the Atlantic (Norway, Greenland and Sweden coasts) it can be collected as shallow as 50–250 m deep.

Description of type species

Spinularia spinularia (Bowerbank, 1866) (Fig. 13).

Synonymy. *Tethea spinularia* Bowerbank, 1866: 94. *Spinularia tetheoides* Gray, 1867a: 524. *Radiella spinularia* Schmidt, 1870: 48. *Polymastia spinularia* Hanitsch, 1894a: 202. *Rhaphidorus setosus* Topsent, 1898b: 245; Alander, 1942: 76.

Material examined. Holotype: BMNH: 10.1.1.1183 – Norman collection (slides), Shetland. Other material. MOM – stns 683 and 3293 (Topsent, 1904b, 1928c). Not BMNH 10.1.1.594A (Norman collection) [=*Atergia corticata*].

Description. (Morphology based on MOM material, skeleton based on BMNH slides) Small discoid sponge with a diameter of about 12 mm and a thickness of 3–4 mm. Specimens are often fixed to pebbles or shells (Fig. 13A). The surface is especially hispid towards the edge of the sponge where the spicules project a considerable distance. No aquiferous papillae are present and the oscule is slightly raised above the surface. Choanosomal skeleton is composed of tracts of tylostyles between which raphides in trichodragmata are present. The ectosomal skeleton is composed of a simple palisade of ectosomal tylostyles (Fig. 13B). Principal tylostyles are slightly fusiform, with an acerate tip and an ovoid head: 900–1450 × 18–22 μm; echinating tylostyles of the edge can reach up to 2000–2500 μm; ectosomal tylostyles are straight, fusiform and with a well-marked head: 180–310 × 10–13 μm; raphides in trichodragmata (Fig. 13C): 70–120 μm.

Remarks. All descriptions of this species are congruent although the length of trichodragmata is the most variable element and can reach 260 μm in some Azorean and Irish specimens (Topsent, 1928c; Stephens, 1915a). The type species is known only from the NE Atlantic.

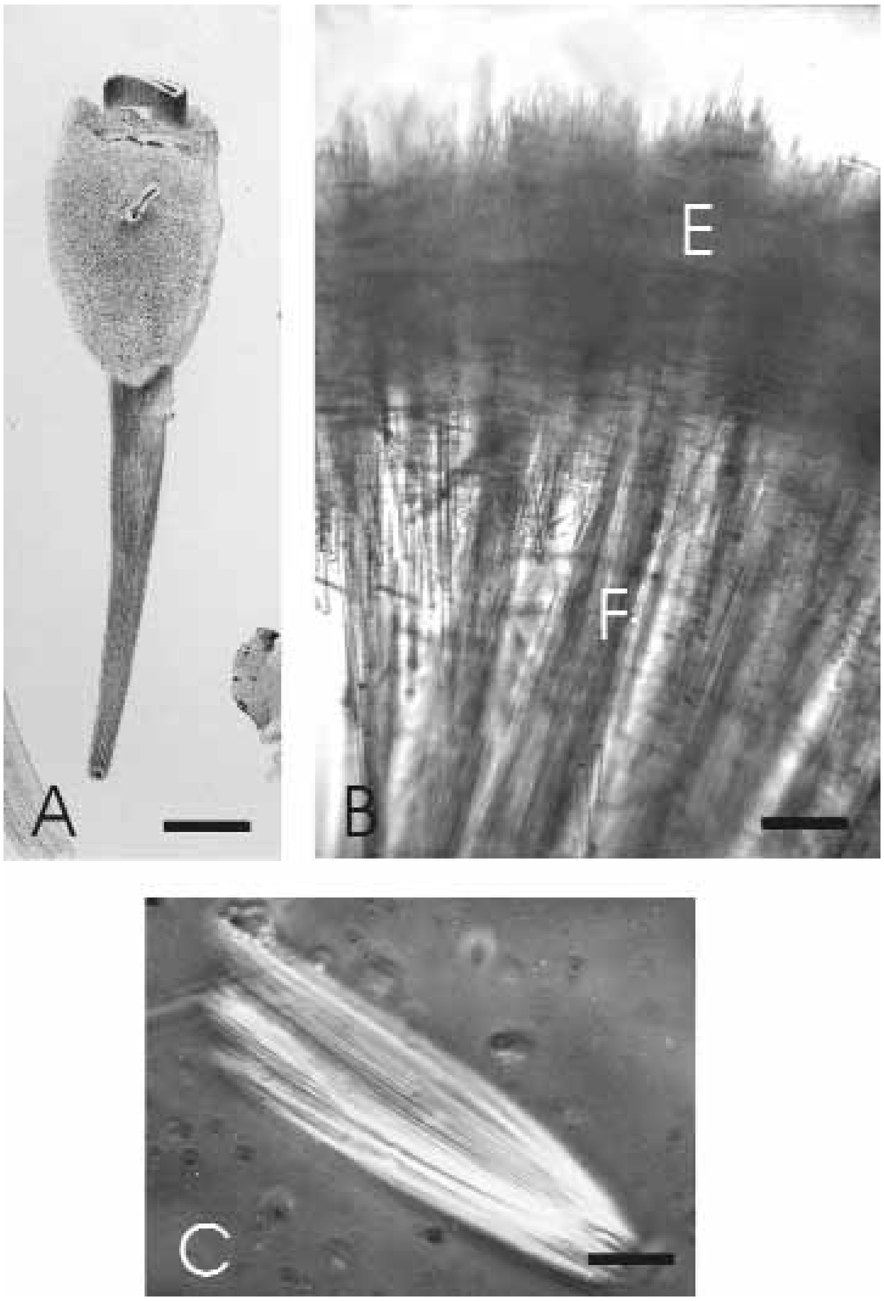

Fig. 13. *Spinularia*. A, specimen of *Spinularia spinularia* (from Topsent, 1904b, as *Rhaphidorus setosus*, pl. I, fig. 6) (scale 1 cm). B, thick section through the body of *Spinularia spinularia*, slide from the Norman collection (BMNH 10.1.1.1183) (abbreviations: E, ectosomal skeleton; F, tracts of the principal spicules) (scale 100 µm). C, detail of raphides in trichodragmata (scale 14 µm).

PSEUDOTRACHYA HALLMANN, 1914

Synonymy

Pseudotrachya Hallmann, 1914: 286; Vacelet, 1969: 178; Boury-Esnault *et al.*, 1994b: 69. *Anomolissa* (partim) de Laubenfels, 1934: 17; Van Soest & Stentoft, 1988: 79 (for *A. amaza*).

Type species

Trachya hystrix Topsent, 1892a (by monotypy).

Diagnosis

Polymastiidae with radial skeleton of subtylostyles or styles which project through the surface rendering it very hispid. Ectosomal skeleton composed of a palisade of small oxeas. Small oxeas of the same type are scattered in the choanosome.

Remarks

Pseudotrachya was erected by Hallmann (1914) for *Solasella hystrix* (Topsent, 1892a) and has been previously assigned to the

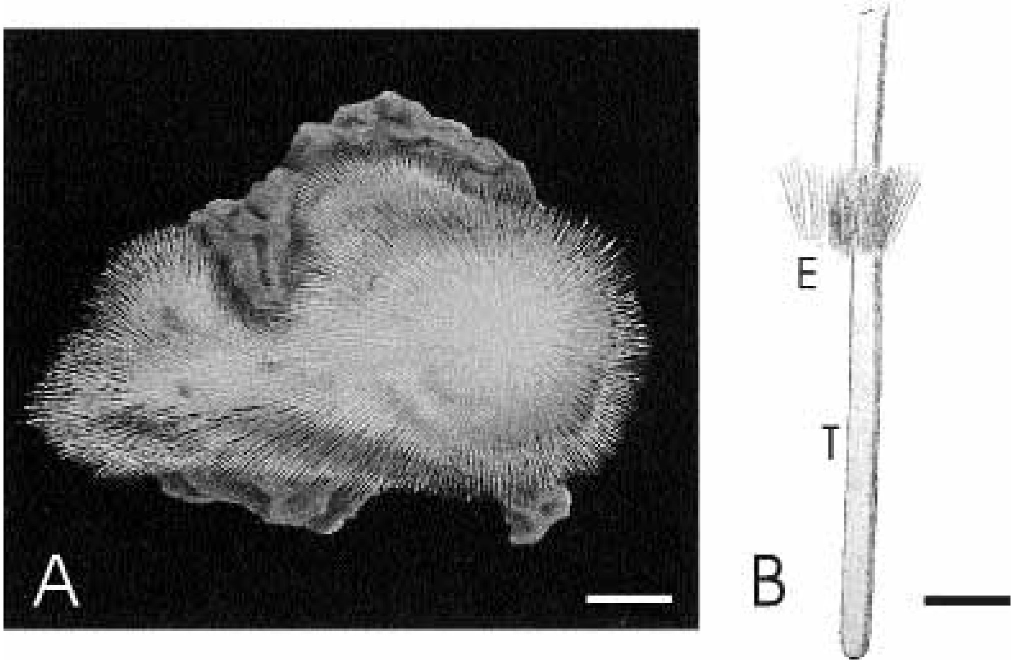

Fig. 14. *Pseudotrachya*. A, type specimen of *Pseudotrachya hystrix* (from Topsent, 1892a, as *Trachya hystrix*, pl. I, fig. 10) (scale 0.6 cm). B, schema of a style (T) echinating the palisade of oxeas (E) (from Topsent, 1892a, pl. XI, fig. 13) (scale 180 μm).

Axinellidae, by Topsent (1904b, 1928c) and Hallmann (1914), but always with some doubt. It was recently considered to be a hadromerid by Van Soest & Stentoft (1988) and included in Tethyidae, but again with some doubt. However, Topsent (1904b) stated it was not a Tethyidae and Boury-Esnault *et al*. (1994b) suggested its closest affinities were with Polymastiidae.

Distribution

Atlantic ocean (from the Western Mediterranean to the Puerto Rican Deep in the east, and to South Africa in the south), 100–954 m depth although specimens have been recorded from 25 m depth in obscure caves on the Provence coast (Western Mediterranean basin).

Description of type species

Pseudotrachya hystrix (Topsent, 1892a) (Fig. 14).

Synonymy. *Trachya hystrix* Topsent, 1892a: 75. *Solasella hystrix* Topsent, 1898a: 111; Kirkpatrick, 1903b: 247; Topsent, 1904b: 142. *Pseudotrachya hystrix* Topsent, 1928c: 180; Vacelet 1969: 178; Van Soest & Stentoft, 1988: 79; Boury-Esnault *et al*., 1994b: 70. *Pseudotrachya oxystyla* Sarà, 1959b: 3–6. *Anomolissa amaza* de Laubenfels, 1934: 17. ? *Suberitechinus* de Laubenfels, 1949a: 21.

Material examined. Holotype: MNHN-DT. 896 – 'L'Hirondelle' expedition, 1888, stn. 234, Azores, between Pico and São Jorge islands, 38°30′35″N, 28°16′20″W. Other material. Mediterranean, stn 153 and 135 from the BALGIM expedition (personal collection) (Boury-Esnault *et al.*, 1994b). *Anomolissa amaza*: UNSM.22348 (de Laubenfels, 1934: 17).

Description. The holotype is attached to pebbles, with a cushion shape and a maximum length of 4 cm and 2 cm width (Fig. 14A). The colour in alcohol is whitish outside and pale yellow inside. The surface is echinated by very long spicules. The skeleton is composed of an ectosomal palisade of small oxeas (Fig. 14B) and choanosomal radial tracts of megascleres which protrude through the palisade. Ectosomal oxeas are also dispersed within the tracts of choanosomal megascleres. Oxeas are slightly fusiform with acerate extremities (185–253 × 6 μm) and tylostyles or subtylostyles which can reach 7 mm length in the holotype. In other material these tylostyles were shorter reaching only about 2000–4000 × 44 μm. In some Mediterranean specimens the megascleres can vary from styles to oxeas (Sarà, 1959b: 3–6; Vacelet, 1969: 178).

Remarks. *Pseudotrachya* is presently considered to be monospecific. However, the type species has a very wide alleged distribution, from Mediterranean to the Caribbean and to South Africa, and it is highly suspected that it comprises two or more cryptic sibling species. In fact we can hypothesise that these discontiguous populations comprise at least three or four species: *P. hystrix* from Azores and perhaps also extending into the Mediterranean; a Caribbean species which could be called *P. amaza* as already suggested by Lehnert & Van Soest (1999), and a South African species as yet unnamed. To date, however, there has been no formal revision of this species complex and the conspecificity between these regional populations remains speculative.

TRACHYTELEIA TOPSENT, 1928

Synonymy

Trachyteleia Topsent 1928c: 152. ? *Suberitechinus* de Laubenfels, 1949a: 21.

Type species

Trachyteleia stephensi Topsent, 1928c (by monotypy).

Diagnosis

Polymastiidae without papillae, with radiating tracts of tylostyles and tracts of small tylostyles in between. The ectosomal skeleton is composed by a palisade of small tylostyles. The surface is echinated by distally acanthose tylostyles which are considerably thicker than the primary spicules.

Remarks

The type species has never been collected since the Prince Albert I de Moncao expedition in 1911. Unfortunately the entire specimen was used by Topsent for his spicule preparation although in this preparation the different types of spicules are very clear in addition to some non-dissociated parts of the skeleton.

Distribution

NE Atlantic, Azores.

Description of type species

Trachyteleia stephensi Topsent, 1928c (Fig. 15).

Synonymy. *Trachyteleia stephensi* Topsent, 1928c, 152–154, pl. 6, fig.11.

Material examined. Holotype (slide only): MNHN DT 1285 – 38°01′N, 25°21′W, Azores, 1740 m depth.

Description. The holotype consists of a very small hispid crust and was grey in alcohol (now destroyed and only extant as a spicule preparation). There are neither visible papillae nor visible apertures. The choanosomal skeleton is composed of radial polyspicular tracts between which intermediary tylostyles are scattered; the ectosomal skeleton is composed of a tangential layer of intermediary tylostyles on which lies a palisade (300 μm thick) of ectosomal tylostyles reinforced by exotyles which hispidate the surface. Principal tylostyles are straight with a mucronate head and with a very thin and acerate extremity: 490–570 × 11 μm; the intermediary tylostyles are straight or slightly curved with the same general shape that the principals: 310–395 × 8 μm; the ectosomal tylostyles are slightly curved: 170–275 × 5 μm. The exotyles are straight, the axial canal is well visible and can be seen to pass through the central cavity of the head; the sharp extremity of the exotyle is rough and has a length of about 80 μm: 590–735 × 23 μm.

Remarks. It is with some hesitation that we decide to retain this monospecific genus. However, the type preparation and the description of Topsent are excellent, and we prefer to keep it separate from other Polymastiidae until new data become available. *Suberitechinus* de Laubenfels, 1949a (type species *Tethea hispida* Bowerbank, 1864b, from off Portland, Maine, NW Atlantic) is currently uncertain in its allocation. From its published description and recommendations of Hentschel (1929: 924), it appears to have affinities to Polymastiidae rather than Suberitidae, possibly related to *Trachyteleia*, being strongly hispid, with a cortex, three sizes of tylostyles and apparently lacks papillae. This allocation requires verification through checking type material in the National Museum of Canada, Ottawa, if it still exists.

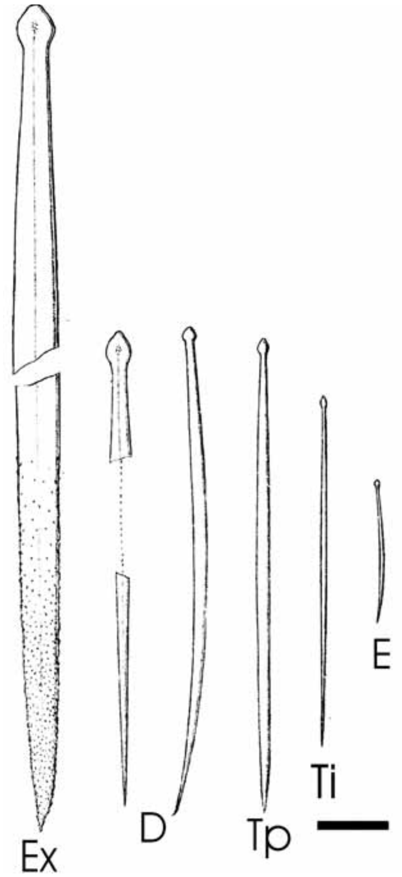

Fig. 15. *Trachyteleia*. Spicule types present in *Trachyteleia stephensi* (from Topsent, 1928c, pl. VI, fig. 11) (abbreviations: Ex, exotyle; Tp, principal tylostyle; Ti, intermediary tylostyle; E, ectosomal tylostyle; D, details of ectosomal tylostyle and principal tylostyle) (scales E, Tp, Ti, 100 μm; D, Ex, 25 μm).

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