

Family Myxillidae Dendy, 1922

Rob W.M. Van Soest

Zoological Museum, University of Amsterdam, P.O. Box 94766, 1090 GT Amsterdam, Netherlands. (soest@science.uva.nl)

Myxillidae Dendy (Poecilosclerida: Myxillina) is revised and narrowed down to a new concept including only those genera which combine the possession of anchorate chelae (or polydentate derivations) with diactinal ectosomal tornotes and choanosomal styles in a reticulate arrangement. Two genera deviating from this general concept are included here: i.e., *Hymenancora* with hymedesmioid skeleton, and *Psammochela* with only a single megasclere type, because of chelae similarities with other included genera. Other families with anchorate chelae are Desmacididae (oxeas as the only megascleres), Iotrochotidae (with birotulas) and Crambeidae (monactinal ectosomal tornotes and choanosomal styles). Thirty-three nominal genera answer to the new concept of Myxillidae and of these eight are considered valid: *Damiriopsis*, *Ectyonopsis*, *Hymenancora*, *Melonanchora*, *Myxilla*, *Plocamiancora*, *Psammochela*, *Stelodoryx*. In the large genus *Myxilla* four subgenera have been defined to alleviate classing the large numbers of species: *Myxilla* (*Myxilla*), *Myxilla* (*Burtonanchora*), *Myxilla* (*Ectyomyxilla*), and *Myxilla* (*Styloptilon*).

Keywords: Porifera; Demospongiae; Poecilosclerida; Myxillina; *Damiriopsis*; *Ectyonopsis*; *Hymenancora*; *Melonanchora*; *Myxilla* (*Myxilla*); *Myxilla* (*Burtonanchora*); *Myxilla* (*Ectyomyxilla*); *Myxilla* (*Styloptilon*); *Plocamiancora*; *Psammochela*; *Stelodoryx*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Myxilleae Dendy, 1922b: 85; Myxillidae Topsent, 1928c: 237.

Definition

Myxillina with anchorate or unguiferate chelae, choanosomal styles and diactinal ectosomal tornotes (oxeote and tylote).

Diagnosis

Encrusting, massive, lobate, fan-shaped or branching sponges. Specialised ectosomal skeleton composed of tornotes with smooth or apically spined bases, arranged as bouquets or lying paratangential or perpendicular to the surface. This is occasionally absent. Choanosomal skeleton composed of isotropic, anisotropic or plumoreticulate tracts of smooth or partially spined monactinal or diactinal choanosomal megascleres, sometimes echinated by small acanthose styles. Hymedesmioid arrangement occurs in thinly encrusting forms. Spongin development variable, usually consisting of light spongin cementing spicules together at their nodes, but sometimes with heavy fibres. Microscleres include one or more size and form categories of anchorate isochelae and/or derivatives (spatulate, unguiferous isochelae, sometimes anisochelate, occasionally polydentate), and one or two size categories of smooth sigmas.

Scope

Thirty three nominal genera are included in this family, of which eight are recognised here as valid: *Damiriopsis*, *Ectyonopsis*, *Hymenancora*, *Melonanchora*, *Myxilla*, *Plocamiancora*, *Psammochela*, *Stelodoryx*. One genus (*Myxilla*) has four recognized subgenera.

History and biology

Ridley & Dendy (1887) included sponges now considered members of Myxillidae into a larger subfamily Ectyoninae which was based on the possession of echinating acanthostyles (thus covering the present concepts of Myxillina + Microcionina). Hentschel, 1923 defined the family to include sponges with chelae, diactinal ectosomal megascleres and monactinal (often spined) choanosomal megascleres. He included hymedesmiids in the family, but kept Tedaniidae, Dendroricellidae, Coelosphaeridae and Crellidae as separate families. Topsent (1928c) employed a broad concept of Myxillidae including subfamilies Myxilliina, Tedaniinae and Phoriospongiinae, based on the possession of reticulate skeleton, diactinal ectosomal megascleres and monactinal choanosomal megascleres. A major difference of Topsent's subfamily Myxillinae with the presently employed contents of the family Myxillidae is the transfer of genera with arcuate chelae and a reticulate choanosomal skeleton to the family Coelosphaeridae, whereas Topsent restricted Coelosphaeridae to genera with hollow-bladder shape. De Laubenfels (1936a) also employed a large concept of Myxillidae, but included crellids and hymedesmiids in it. He subdivided this large group into two subfamilies, Myxillinae with smooth ectosomal megascleres, and Grayellinae with spined ectosomal megascleres. Within Myxillinae, he distinguished 'Myxillinae I' which more or less covered Topsent's Myxillinae, and 'Myxillinae II' which covered Topsent's Hymedesmiidae. Lévi (1973) followed Topsent's (1928c) classification, as did most other authors prior to Hajdu *et al.* (1994a). These authors restricted Myxillidae to genera possessing as chelae exclusively anchorate forms or derivatives thereof, in combination with diactinal tornotes. This was followed by Desqueyroux-Faúndez & Van Soest (1996). Here, Myxillidae is further restricted by exclusion from the family of genera *Desmacidon* and *Desmapsamma*, which go to a separate family Desmacididae based on the loss of choanosomal styles, and of genera possessing birotula microscleres, which go to a separate family Iotrochotidae. Myxillidae tend to be encrusting to massive sponges occurring on many different substrates, including rocks, mangrove roots, and sand. They may occur at considerable depths.

The majority of the species and genera have been reported from temperate and cold waters.

Taxonomic remarks

The concept of Myxillidae is here narrowed down further than any previous concept and clearly focused on the possession of anchorate or anchorate-derived chelae in combination with differentiated ectosomal and choanosomal megascleres. Reticulate skeletons (presumably by emphasis of skeletal zone I; see

chapter on suborder Myxillina) are common in this family, but in thinly encrusting or bladder-like sponges this may be obscured or absent, or replaced by an emphasis of zone II skeletons. The anchorate chelae may be tridentate, unguiferate or polydentate.

Previous reviews

Topsent (1928c), Hajdu *et al.* (1994a), Desqueyroux-Faúndez & Van Soest (1996).

KEY TO GENERA

- (1) Choanosomal skeleton includes smooth or spined strongyles 2
 Choanosomal skeleton consists of styles only 4
- (2) Strongyles large and thick; there are no zone II (cf. Fig. of Myxillina chapter) long styles 3
 Skeleton is plocamiid, i.e. there are long styles erect on a basal reticulation of strongyles *Plocamiancora*
- (3) Strongyles spined all over *Ectyonopsis*
 Strongyles smooth except the heads which may have light spination *Damiriopsis*
- (4) Microscleres include sphaerancorae *Melonanchora*
 No sphaerancorae 5
- (5) Chelae include polydentate chelae 6
 Chelae are spatulate or unguiferate with not more than 3 teeth *Myxilla*
- (6) Skeleton hymedesmioid *Hymenanchora*
 Skeleton reticulate 7
- (7) Tornotes present next to the choanosomal styles *Stelodoryx*
 No tornotes, a single megasclere type or no megascleres at all *Psammochela*

DAMIRIOPSIS BURTON, 1928

Synonymy

Damiriopsis Burton, 1928a: 124.

Type species

Damiriopsis brondstedti Burton, 1928a: 124 (by monotypy).

Definition

Myxillidae with choanosomal strongyles in an isotropic reticulation; no sigmas.

Diagnosis

Thickly encrusting. Surface rough. Ectosomal skeleton consisting of tylotes with spined apices. Choanosomal skeleton a close-meshed reticulation of thick strongyles rugose apices. Microscleres anchorate chelae. No sigmas, no echinating acanthostyles. One species.

Previous review

Burton (1928a).

Description of type species

Damiriopsis brondstedti Burton, 1928a (Figs 1, 4A).

Synonymy. *Damiriopsis brondstedti* Burton, 1928a: 124, pl. I figs 3–4, text-fig. 6.

Material examined. Holotype: BMNH 1926.10.1.20 (slide BMNH 1926.10.1.20a) – both labeled with unpublished species name ‘*dendyi*’.

Description. Small, irregularly massive, size 2 × 1 × 0.5 cm. Surface minutely hispid. Conspicuous subdermal cavities visible through a transparent surface membrane (Fig. 1A). Oscules 1.5 mm in diameter. Colour greyish-yellow (alcohol). Skeleton (Fig. 4A). Ectosomal skeleton consists of loose bouquets of tornotes, not forming a continuous skeleton. Choanosomal skeleton a rectangular, somewhat irregular reticulation of bundles of 2–4 strongyles thick. Spicules. Ectosomal tornotes are tylotes with spined apices (Figs 1B, 4A), 264–357 × 6–9 μm. Choanosomal spicules are thick strongyles with faintly rugose apices (Figs 1C, 2A), 625–1053 × 36–70 μm. Microscleres. Anchorate chelae in two distinct size categories (Figs 1D, 2A), 33–44 and 54–97 μm. Distribution and ecology. Known only from the Andaman Islands, from considerable depth, 234–522 m.

Remarks. Burton recorded the chelae as being anchorate as well as palmate. In light microscopy, the smaller chelae may superficially look like palmate, but under SEM they are clearly anchorate, similar to the larger category. This single species is related to the genera *Ectyonopsis* and *Stelotrochota* – here united under *Ectyonopsis* – because they share a choanosomal reticulation of thick strongyles. This is nevertheless retained as a separate genus because the choanosomal spicules are entirely spined.

ECTYONOPSIS CARTER, 1883

Synonymy

Ectyonopsis Carter, 1883b: 315. *Ectyonanchora* Lévi, 1963: 36. *Stelotrochota* Bakus, 1966b: 501.

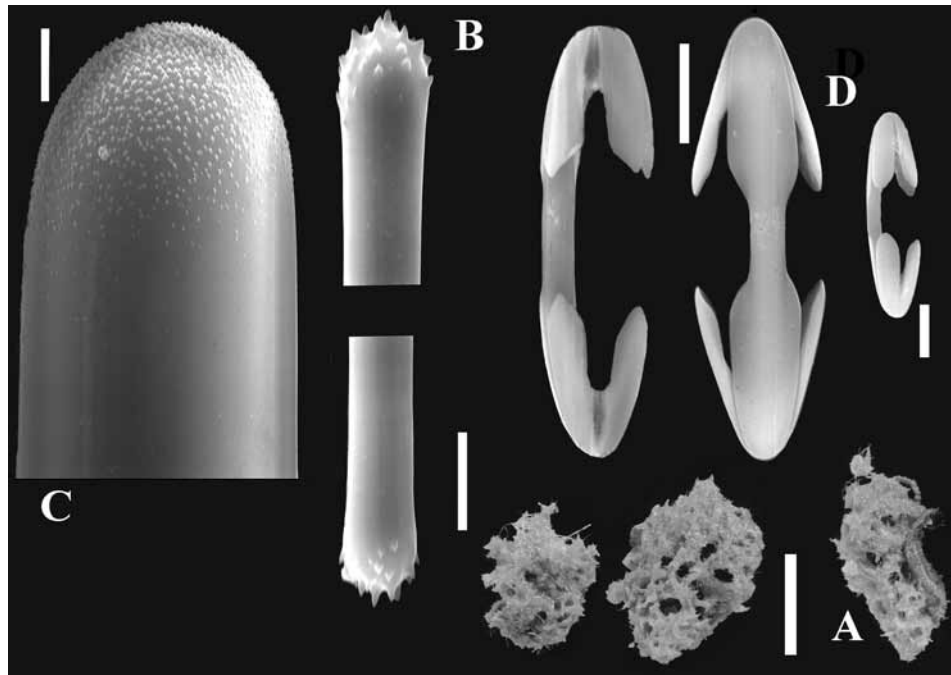


Fig. 1. *Damiriopsis brondstedii* Burton, 1928a. A, fragments of holotype (scale 1 cm). B–D, SEM photos of spicules of holotype (scale 10 µm).

Type species

Ectyonopsis ramosa Carter, 1883b: 315 (by monotypy).

Definition

Myxillidae with smooth tornotes with hastate/mucronate apices and an isotropic reticulation of thick acanthostrongyles, echinated by thick acanthostyles; microscleres are robust spatuliferous anchorate isochelae.

Diagnosis

Flabellate; ectosomal tornotes are entirely smooth with mucronate apices; choanosomal strongyles heavily spined all-over; echinating acanthostyles thick, heavily spined all-over; chelae spatulate anchorate. Four species.

Previous reviews

Lévi (1963), Desqueyroux-Faúndez & Van Soest (1996), both as *Ectyonancora*.

Description of the type species

Ectyonopsis ramosa (Carter, 1883b) (Fig. 2A–I).

Synonymy. *Ectyonopsis ramosa* Carter, 1883b: 315, pl. XIII fig. 5.

Material examined. Holotype (fragment): BMNH 1884.4.14.6 – labeled ‘From Type, South Australia’.

Description (partly from Carter, 1883b). A thick cluster of branches, up to 6 cm wide and 0.4 cm thick, rising from a hard contracted peduncular base. The sponge may form a clathrate blade by anastomosis. The remnants now representing the holotype

(Fig. 2A) consist of three thin-bladed fragments of which the largest is 2.5 × 1.5 × 0.4 mm. Consistency firm, colour brown in dry state. Surface finely grained, even. The ectosomal skeleton is represented by scattered tornotes. The skeleton (Fig. 2C–E) is an isodictyal-anisotropic reticulation of acanthostrongyles encased in spongin, echinated by similar but slightly longer acanthostyles (arrows in Fig. 2D). Spicules, acanthostrongyles (Fig. 2B, G) and acanthostyles (Fig. 2B, F), 177–270 × 20–24 µm, ectosomal tornotes (Fig. 2H), 165–188 × 4–6 µm, smooth with swollen, mucronate ends, more or less symmetrical. Anchorate isochelae (Fig. 2I) rather elongate-narrow, in a single size category, 21–30 µm. Distribution. South Australia, no further data.

Remarks. The genus is here revived. It was never reported after its original description, which was incomplete, as Carter did not mention the anchorate isochelae.

The genus *Ectyonancora* Lévi, 1963 was erected for type species *Ectyonancora flabellata* Lévi, 1963: 36, pl. VIB fig. 40 (by subsequent designation; Desqueyroux-Faúndez & Van Soest, 1996: 47). The syntypes (MNHN LBIM DCL. 548 & 549 from South Africa, stat. FAL 330), were re-examined. These are erect, flabellate, lamellar sponges (Fig. 3A), 7.5 × 10 × 0.4 cm. Numerous small oscules of 0.5 mm diameter cover both sides. Brownish or ochre in alcohol. Skeleton (Fig. 4B). Loose tornotes and chelae are abundant in the detachable surface membrane. The choanosomal skeleton consists of thick spicule tracts enclosing isotropic meshes. Spicules. Ectosomal tornotes (Figs 3B, 4B), smooth with lanceolate apices, 145–180 × 7 µm. Choanosomal acanthostrongyles (Figs 3C, 4B), thick, heavily spined, 220–250 × 22–25 µm. Acanthostyles (Figs 3D, 4B), heavily spined (seem to be the same spicule type), 225–300 × 20–25 µm. Anchorate isochelae (Figs 3E, 4B) in two size classes, 27–32 and 40–57 µm. Distribution and ecology. Cape Town area, South Africa, on sandy rocky bottom with shells, 14–51 m. From this description it is clear that *Ectyonancora flabellata* is almost identical with *Ectyonopsis*

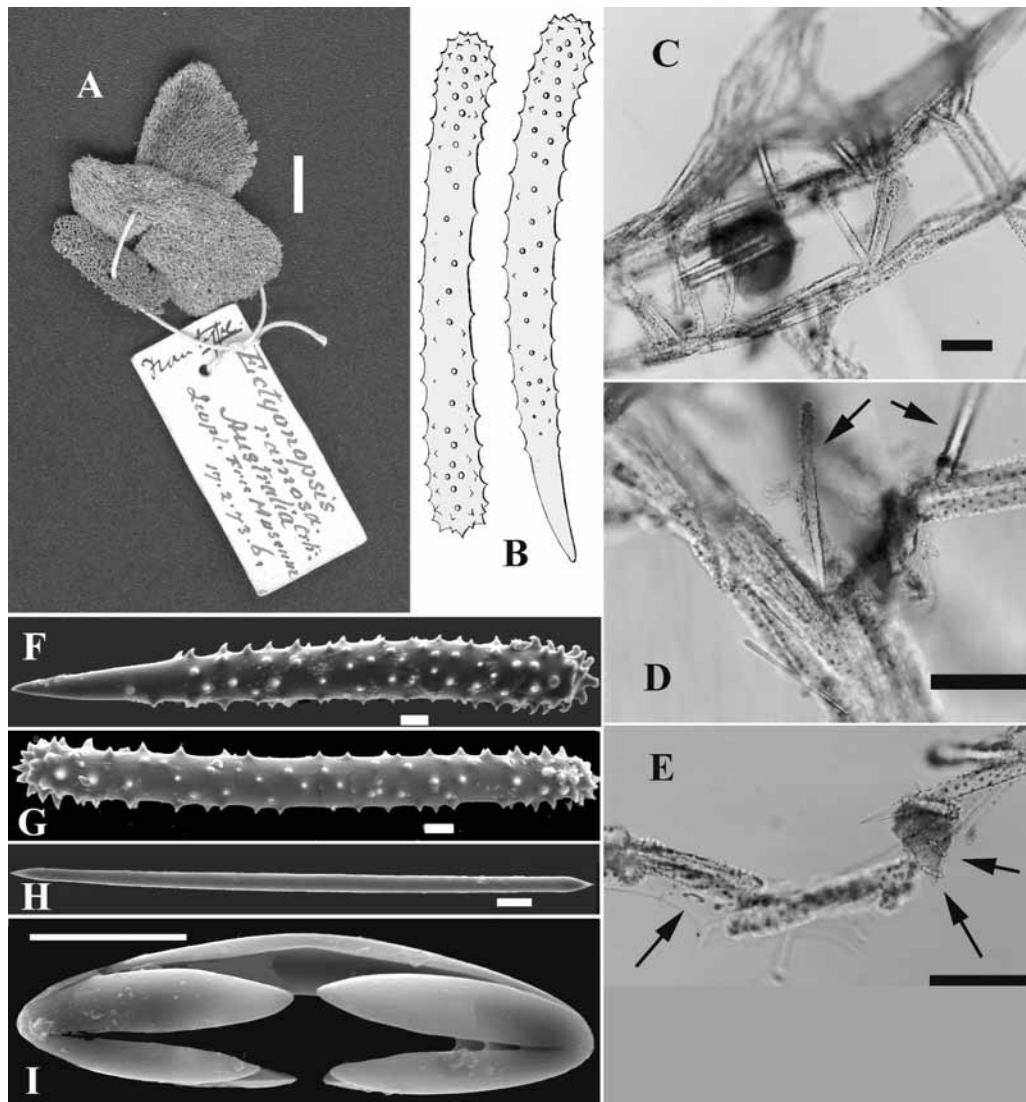


Fig. 2. *Ectyonopsis ramosa* Carter, 1883b. A, lectotype BMNH 1884.4.14.6 (scale 1 cm). B, drawing of megascleres reproduced from Carter's, 1883b: pl. XIII fig. 5 (sizes see text). C–E, microphotos of skeleton of lectotype (scale 100 μ m) (arrows in D indicate echinating acanthostyles, in E isochelae). F–I, SEM images of spicules of lectotype (scale 10 μ m).

ramosa, the only difference of substance being the presence of a second size category of isochelae. Several species have been described in this genus: *E. pluridentata* Lévi (1963), *E. panis* Boury-Esnault & van Beveren (1982) and *E. walvisensis* Uriz (1989), all from Southern Ocean localities. The latter is not an *Ectyonopsis* on account of its possession of long subectosomal styles. It conforms to *Plocamiancora* (cf. below).

The genus *Stelotrochota* Bakus, 1966b was erected (by monotypy) for *Stelotrochota hartmani* Bakus (1966b: 501, pl. 2b). A paratype (Fig. 3F) was examined, BMNH 1964.12.1.3, including slide 1964.12.1.3a, from San Juan Archipelago, Washington State, USA. This has ectosomal tylotes (Figs 3G, 4C), with one end globular and the other more elongate, both microspined on the head, 139–166 \times 7–9 μ m. Acanthostrongyles (Figs 3I, 4C), with swollen ends which are slightly unequal, entirely heavily spined, especially on the swollen ends, 185–211 \times 19–22 μ m. Chelae (Fig. 4C) robust, strongly curved, some are anchorate spatulate with well-developed alae, others are polydentate, likewise with 5 well-developed teeth,

some are unguiferate (Fig. 3H) with reduced short teeth, no clear size categories, 30–51 μ m. Skeleton (Fig. 4C). Ectosomal spicules loosely arranged, for the most part tangential; choanosomal skeleton somewhat irregular isotropic reticulation. This species is included in *Ectyonopsis* because of the overall close similarity in skeletal structure. The lack of echinating acanthostyles and the presence of spines on the tornote apices is judged to be of specific value, since these are common enough features of many individual myxillid species.

***HYMENANCORA* LUNDBECK, 1910**

Synonymy

Hymenancora Lundbeck, 1910. *Leptosiopsis* Topsent, 1927b: 13. *Hymesigmia* Topsent, 1927b: 14. *Leptosia sensu* Topsent, 1928c: 56 (not Topsent, 1892b: xxii). *Chiastostia* Topsent, 1928c:

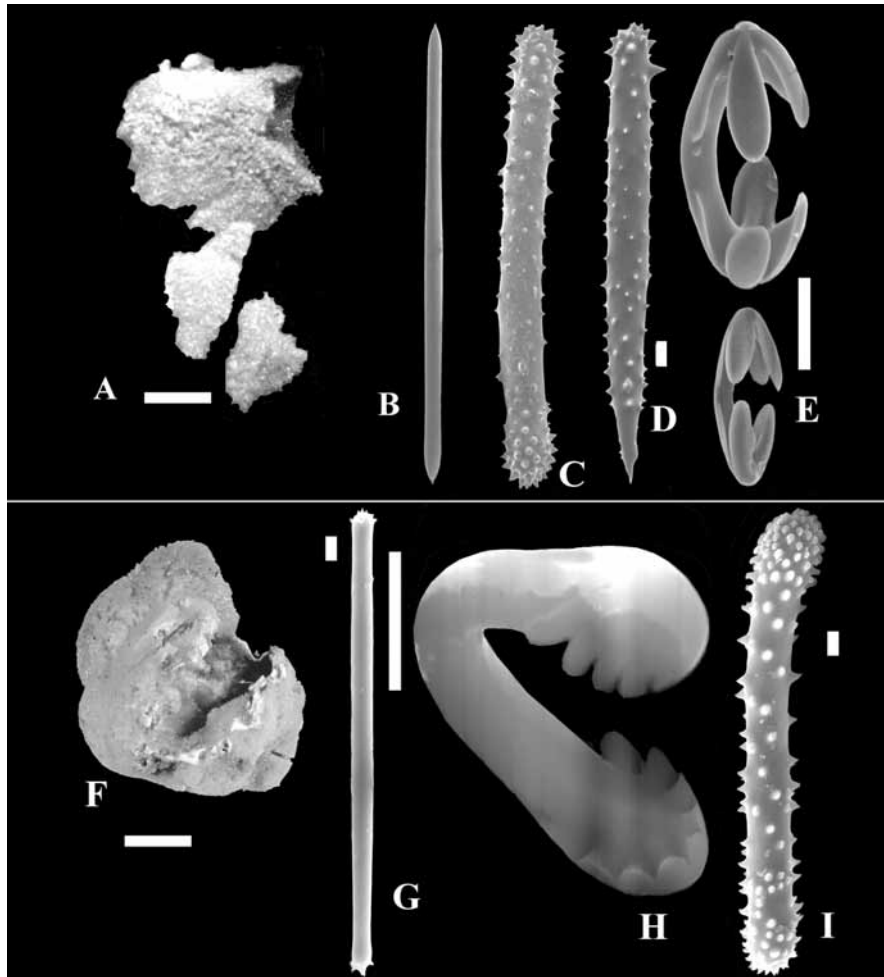


Fig. 3. A–E, *Ectyonopsis flabellata* (Lévi, 1963 as *Ectyonancora*). A, holotype (scale 1 cm). B–E, SEM photos made from spicules of the holotype (scale 10 μm). F–I, *Ectyonopsis hartmani* (Bakus, 1966b as *Stelotrochota*). F, habitus of paratype (scale 1 cm). G–I, SEM photos of spicules from paratype (scale 10 μm).

276. *Arndtanchora* de Laubenfels, 1936a: 110. *Jelissima* de Laubenfels, 1936a: 79. *Herceus* Koltun, 1959: 173.

Type species

Leptosia umbellifera Topsent, 1904b: 192 (by subsequent designation; de Laubenfels, 1936a: 87).

Definition

Myxillidae with hymedesmioid arrangement of acanthostyles; microscleres include polydentate anchorate chelae.

Diagnosis

Encrusting, with smooth or papillate surface; ectosomal skeleton with smooth ectosomal strongyles or styles, occasionally with polytylote tyles; choanosomal skeleton hymedesmioid with acanthostyles erect on the substrate, often in two functional categories, structural and echinating; microscleres are isochelae – occasionally anisochelae – often with polydentate alae, and sigmas, which are often absent. Approximately 20 species.

Previous reviews

Lundbeck (1910: 116), Desqueyroux-Faúndez & Van Soest (1996: 46).

Description of type species

Hymenancora umbellifera (Topsent, 1904b) (Fig. 5A).

Synonymy. *Leptosia umbellifera* Topsent, 1904b: 192, pl. XV fig. 4; *Hymenancora umbellifera*; Lundbeck, 1910: 116.

Material examined. Holotype: MOM (not seen). Schizotype: MNHN DT 1039 – ‘#40, Prince Albert 1895’.

Description (mostly from Topsent, 1904b). Smooth crust on *Siphonidium*, 0.5 mm in thickness. Colour white. Skeleton. Choanosomal skeleton hymedesmioid, with acanthostyles erect on the substrate, heads down; bundles of tornotes go to the surface, where they are arranged tangentially. Spicules. Ectosomal polytylote tornotes, somewhat anisotylole, smooth, $345 \times 4.5 \mu\text{m}$. Acanthostyles in a large size range, $130\text{--}450 \times 7\text{--}12 \mu\text{m}$. Chelae anchorate or unguiferate, polydentate, with on the average 5 teeth but may be up to 7–9 teeth, $26\text{--}30 \mu\text{m}$. Distribution and ecology. Azores, deep water.

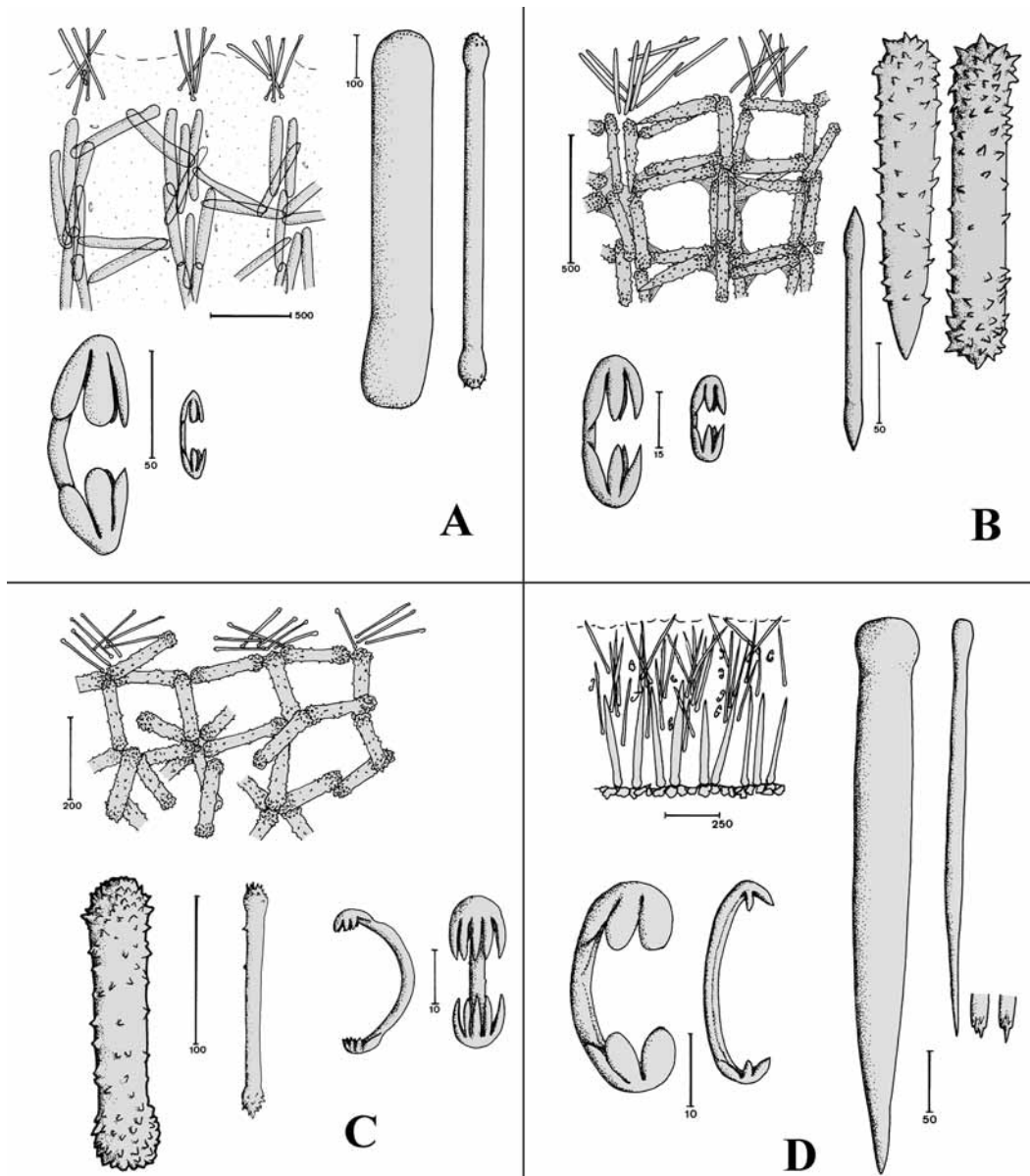


Fig. 4. A, *Damiriopsis bronstedii* Burton, 1928a, drawing of skeleton and spicules. B, *Ectyonopsis flabellata* (Lévi, 1963 as *Ectyonancora*), drawing of skeleton and spicules made from a slide of the holotype. C, *Ectyonopsis hartmani* (Bakus, 1966b as *Stelotrochota*), drawing of skeleton and spicules made from a slide of the BMNH paratype. D, *Hymenancora tenuissima* (Thiele, 1905 as *Hymedesmia*), drawing of skeleton and spicules (all four drawings made from slides of the respective type specimens).

Remarks. Most species of the genus are thinly encrusting deep-water species. The genus unites those former Hymedesmiidae that have anchorate, unguiferate or polydentate chelae. Because hymedesmioid architecture is a suspect character, it is possibly an artifactual group, which may need to be split up and distributed over other myxilline genera based on similarities of spicules. The type species designation by de Laubenfels could be challenged, since he can hardly be considered a ‘first reviser’ in the sense of the ICZN. His choice of Topsent’s species *Leptosia umbellifera* is rather random, and it might have been more logical to indicate one of Lundbeck’s extensively described species. Still, Lundbeck indeed named this species, as third in a list of literature records considered by him to be members of his new genus. Lundbeck assigned 13 species earlier described in the genus *Hymedesmia* to

this genus, but not all of these assignments have been followed by authors after Lundbeck. A 14th record is that of *Hymenancora lundbecki* Hentschel, 1912.

Topsent’s (1927b) genus *Leptosiopsis* was erected (by monotypy) for *L. inaequalis* (1927b: 13). Four type slides were examined, MNHN DT 1083. This is a thinly encrusting species from deep water (2165 m) off the Azores. The genus character is the peculiar polydentate anchorate anisochela, which resembles those of *Hymenancora* in their ‘normal’ half (Fig. 5C). The skeletal architecture is hymedesmioid with two size categories of acanthostyles, 217–245 × 20 μm, and 120–135 × 15 μm; ectosomal spicules are stylote, polytylote anisotornotes of 180–210 × 2 μm.

The genus *Hymesigmia* was erected by Topsent (1927b) for *H. japycina* Topsent (1927b: 14) (by monotypy). A type slide

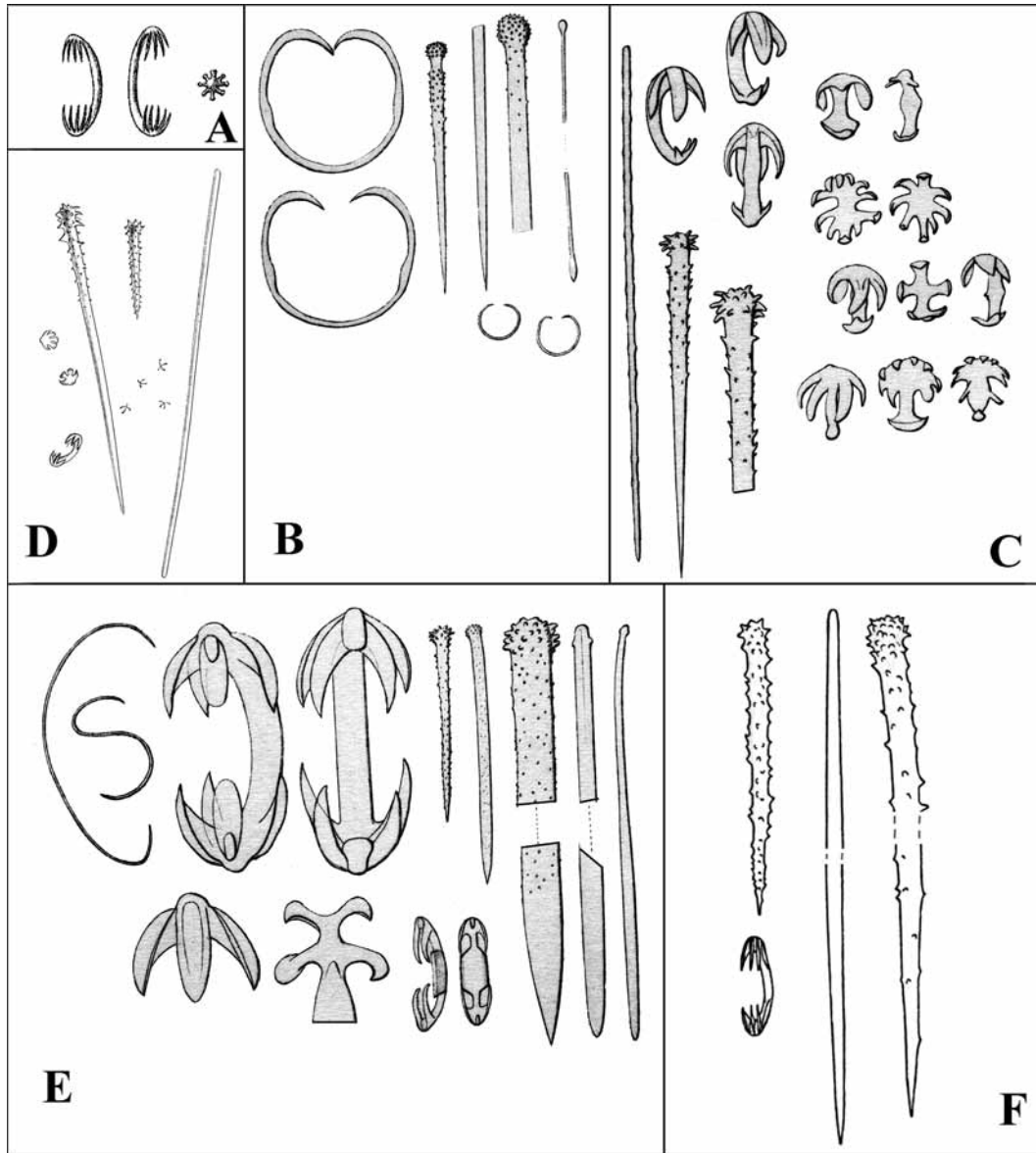


Fig. 5. *Hymenancora* species. A, *Hymenancora umbellifera* (Topsent, 1904b as *Leptosia*), drawing of chelae, reproduced from Topsent's plate XV fig. 4. B, *Hymenancora japycina* Topsent (1927b, as *Hymesigma*), drawing of spicules reproduced from Topsent's (1928c, plate IX fig. 26). C, *Hymenancora inaequalis* Topsent (1927b, as *Leptosiopsis*), drawing of spicules, reproduced from Topsent's (1928c, pl. IX figs 18–19). D, *Hymenancora pecqueryi* Topsent (1892a, as *Myxilla*), type of *Chiastostia* Topsent, 1928c, drawing of spicules reproduced from Topsent's plate IX fig. 16. E, *Hymenancora sirventi* Topsent (1927b as *Leptosia*), type of *Arndtanchora*, drawing of spicules reproduced from Topsent's (1928c) plate IX fig. 17. F, *Hymenancora orientalis* Koltun (1959, as *Herceus*), drawing of spicules reproduced from Koltun's fig. 134 (scales for all drawings see text).

MNHN DT 1085 was examined. This thinly encrusting hymedesmioid specimen was collected at the same deep-water station (2165 m) off the Azores as *Leptosiopsis inaequalis*. The slide preparations of both have many peculiarly incurved sigmas 70 μm high and 85 μm wide (Fig. 5B), which were described only for *H. japycina* by Topsent (they are the genus character for *Hymesigma*), but appear so common in the slide of *H. inaequalis* to be an unlikely contamination. The two specimens differ in the absence of the peculiar anchorate anisochelae in *H. japycina*, in the larger size of the acanthostyles (up to 660 μm) and also in the stylote nature of the ectosomal spicules (which may be up to 315 μm). It is possible they are closely related, and thus it is proposed to consider

Hymesigmia junior synonym of *Hymenancora* despite the absence of chelae in its type species.

Topsent (1928c) restricted the use of his genus *Leptosia* Topsent (1892b: xxii) to *Hymedesmia*-like species with anchorate chelae, thus making it implicitly a possible senior synonym of *Hymenancora*. However, since no anchorate-bearing species were assigned to *Leptosia* when originally erected, this appears to be illegal. Also, *Leptosia* is preoccupied by *Leptosia* Hübner, 1818 (Lepidoptera), see elsewhere in the chapter on Hymedesmiidae under *Hymedesmia* (*Stylopus*).

Topsent's (1928c: 276) genus *Chiastostia* was erected for type species (original designation) *Myxilla pecqueryi* Topsent, 1892a

(including var. *minima*). A type slide was examined (MNHN DT 940), as well as a slide of the var. *minima* (MNHN DT 1179). The genus was founded on the peculiar chiasmogonias (Fig. 5D), consisting of two normal sigmas apparently attached in their centre and thus forming spider-like spicules. Such spicules occur also in unrelated *Acanthancora clavata* Topsent (1927b), and *Guitarra* cf. *indica sensu* Van Soest (1988). With its hymedesmioid arrangement of strongylole tornotes, $470 \times 6 \mu\text{m}$, acanthostyles in two size classes of 420 and $120 \mu\text{m}$, and 5-teethed anchorate chelae, this deep water (1250–2460 m) species from the Azores conforms to the present genus; its peculiar choastogonias are considered a specific, but not a generic character.

De Laubenfels (1936a: 110) erected the genus *Arndtanchora* for type species *Leptosia sirventi* Topsent (1927b: 12) (by original designation). A type slide MNHN DT 1218 was examined. This is a deep water (2460 m) encrustation from the Azores. It has acanthostyles of two sizes, 840×33 and $160\text{--}210 \times 10 \mu\text{m}$, smooth ectosomal anisostyles of $230\text{--}385 \times 6.5 \mu\text{m}$, and two categories of chelae (Fig. 5E) one of which is the usual anchorate type of $50\text{--}60 \mu\text{m}$, with on average about 4 teeth, and the other is peculiar in being cleistochelate, approximately $20 \mu\text{m}$; it is here assumed that these are derived from anchorates. Thin sigmas occur in low numbers and may be foreign. A second species assigned to *Arndtanchora* is *Hymedesmia exigua* Kirkpatrick (1907a: 273); it is likewise a clear *Hymenancora* by its possession of anchorate chelae with 5 teeth (or 6, see Kirkpatrick, 1908c: pl. XXVI fig. 2c1).

The genus *Jelissima* de Laubenfels (1936a: 79) was erected for type species (by original designation) *Hymedesmia tenuissima* Thiele (1905: 454, fig. 70). This was assigned to *Ectomyxilla* by Desqueyroux-Faúndez & Van Soest (1996: 41), but subsequent examination of 'co-type' (=paratype) material BMNH 1931.3.27.13 (with slide BMNH 1930.11.28.6, ex Berlin Museum collection) revealed that Lundbeck was right in assigning this to *Hymenancora*. It has an ectosomal skeleton consisting of brushes of tornotes, $200 \times 8 \mu\text{m}$, fanning out to form a tangential crust (Fig. 4D); choanosomal skeleton composed of single acanthostyles, possibly in two size categories, $100\text{--}290 \times 7\text{--}15 \mu\text{m}$, erect on the substratum. Microscleres anchorate isochelae, $10\text{--}30 \mu\text{m}$, of which the larger have 5 teeth, and sigmas, $45\text{--}48 \mu\text{m}$. The tornotes are peculiar in being oxeteotes with small spines scattered over the whole shaft, but no similarity to crellid arrangement exists.

Koltun's (1959) genus *Herceus* erected (by monotypy) for North Pacific *Herceus orientalis* Koltun (1959: 173, fig. 134, here reproduced as Fig. 5F) (holotype quoted to be in the Zoological Institute of the Academy SSSR), differs from the type species in having stylote tornotes, but is otherwise similar in skeleton. It has a hymedesmioid arrangement of acanthostyles of a wide size range, $176\text{--}416 \times 12\text{--}21 \mu\text{m}$. Tornotes, $290\text{--}416 \times 8\text{--}10 \mu\text{m}$, arranged in tufts or fibres. Chelae polydentate and unguiferate, $23\text{--}28 \mu\text{m}$. The species was collected at 28–63 m depth.

MELONANCHORA CARTER, 1874

Synonymy

Melonanchora Carter, 1874a: 212.

Type species

Melonanchora elliptica Carter, 1874a: 212 (by monotypy).

Definition

Myxillidae with smooth ectosomal tyloles. Microscleres include spherancoras.

Diagnosis

Fistular growth form, with paper-like thin ectosome composed of smooth ectosomal tyloles, smooth choanosomal styles, microscleres are spherancoras (also known as melonchelas) and anchorate chelae. Four species all from the Northern Hemisphere, concentrated in cold deep water.

Previous review

Desqueyroux-Faúndez & Van Soest (1996).

Description of type species

Melonanchora elliptica Carter, 1874a (Fig. 6).

Synonymy. *Melonanchora elliptica* Carter, 1874a: 212, pl. XIII figs 6–12, pl. XV fig. 35a–b; Vosmaer, 1885a: 31, pl. I fig. 14, pl. V figs 69–70.

Material examined. Holotype: BMNH 1882.7.28.54 – N Atlantic, 'Porcupine' Exped., 1869. Other material. ZMA POR. 1548-Arctic, Willem Barents Exped., stat. 4 (Vosmaer's material).

Description. Globular, surface corrugated, with projecting tubercles. Skin stiff, bladderlike. Size up to 10 cm diameter. Fragile, surface parchment-like. Colour grey. Skeleton. Ectosomal skeleton is a well-developed skin-like crust of tangential tyloles. Choanosomal skeleton ill-defined, vague tracts of styles. The interior is mostly a soft organic mass without spicule tracts. Spicules. Ectosomal tornotes (Fig. 6A) smooth, tylole or subtylole, with unequal ends, one being swollen, the other evenly rounded, $450\text{--}615 \times 13\text{--}15 \mu\text{m}$. Choanosomal smooth styles (Fig. 6B), $650\text{--}860 \times 13\text{--}15 \mu\text{m}$. Anchorate isochelae (Fig. 6D), relatively elongate and slim, with spatulate alae and well developed fimbriae, in two size categories, $24\text{--}44$ and $60 \mu\text{m}$. Spherancoras (melonchelas, Fig. 6C), $48\text{--}68 \mu\text{m}$. Distribution and ecology. Arctic, North Atlantic (including Caribbean?); deep water, 135 m.

Remarks. This is a distinct genus on account of its peculiar microscleres, which are derived from anchorate isochelae by fusion and proliferation of the alae (cf. Fig. 6C). Schmidt (1880b) reported this species also from the Caribbean, but that record needs to be confirmed, since Schmidt only compared the microscleres. A second North Atlantic species was described by Schmidt (1875), viz., *M. emphysema*. It has larger and thicker tornotes ($900 \times 25 \mu\text{m}$), and lacks styles. Koltun (1959, 1970) described two further species *M. kobjakovae* and *M. tetradentifera* from the North Pacific.

MYXILLA SCHMIDT, 1862

Synonymy

Myxilla Schmidt, 1862. *Dendoryx* Gray, 1867a: 535. *Emplocus* Gray, 1867a: 535. *Tereus* Gray, 1867a: 537. *Hastatus* Vosmaer, 1880: 136. *Ectomyxilla* Hentschel, 1914. *Crellomyxilla* Dendy, 1924: 364. *Burtonanchora* de Laubenfels, 1936a: 94. *Styloptilon* Cabioch, 1968b: 236.

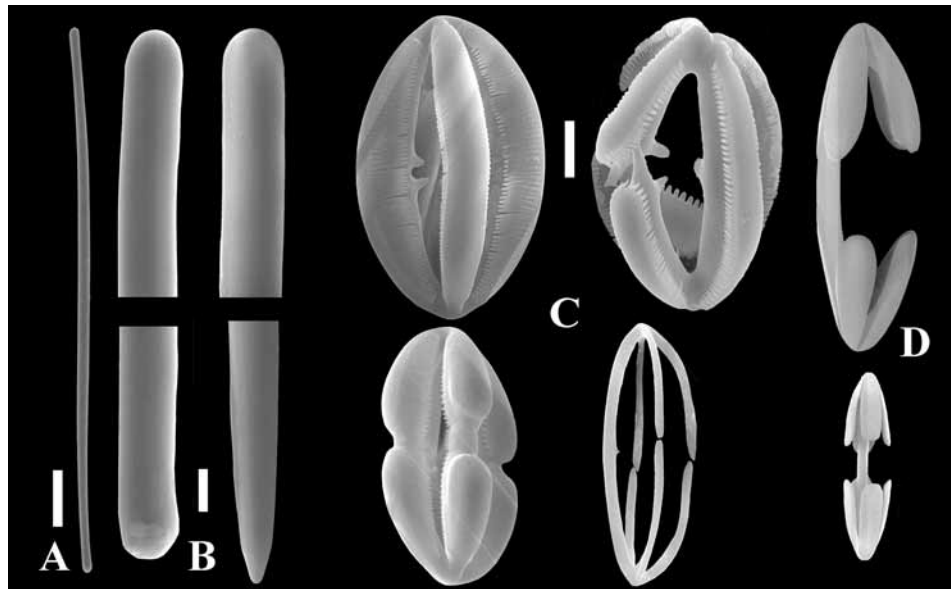


Fig. 6. *Melonanchora elliptica* Carter (1874a), SEM photos of spicules. A, tylole-strongyle (scale 100 μm). B, details of tylole-strongyle and style (scale 10 μm). C–D, microscleres (scale 10 μm). C, growth stages of spherancoras. D, two size categories of anchorate isochelae.

Type species

Halichondria rosacea Lieberkühn, 1859: 521 (by subsequent designation; de Laubenfels, 1936a: 85).

Definition

Myxillidae with ectosomal tylole tornotes with spined apices and a choanosomal reticulation of spined or smooth styles; microscleres include anchorate chelae with only 3 teeth.

Diagnosis

Encrusting, massive, stipitate or branching sponges. Surface irregular to conulose. The ectosomal tyloles have variable terminations: mucronate, frequently with 1 or few prominent spines, or exceptionally entirely smooth, forming both a tangential skeleton and vertical spicule brushes; choanosomal spicules stylote, usually styles with or without spined bases, forming a tight meshed isotropic reticulation or looser isodictyal skeleton; echinating acanthostyles often present but sometimes lost; microscleres are anchorate spatulate or unguiferate isochelae with 3 teeth, often of several sizes, and sigmas (the latter sometimes lost). About 85 species.

Previous review

Desqueyroux-Faúndez & Van Soest (1996).

Remarks

In accordance with proposals made by Desqueyroux-Faúndez & Van Soest (1996: 26) a wide definition of *Myxilla* is here employed. Three of the genera synonymized here with *Myxilla* were previously considered valid by various authors. They differ from *Myxilla s.s.* in characters presumed artificial: presence of a second, smaller category of acanthostyles (*Ectyomyxilla*) possession of smooth instead of spined styles (*Burtonanchora*), and plumose rather than reticulate arrangement of the skeleton (*Styloptilon*). Such characters, though hardly likely to be of phylogenetic significance, still may serve to separate groups among the large number of species answering to a wide definition of *Myxilla* employed here. These groups are used here as convenient subgenera. In contrast with Desqueyroux-Faúndez & Van Soest (1996) the genus *Stelodoryx* (with synonyms *Onychomyxilla* and *Pseudomyxilla*) is retained as valid, based on the possession of polydentate chelae (5 or more complete alae). The use of *Myxilla* is limited to species possessing chelae with only 3 complete alae.

Key to subgenera of *Myxilla*

- (1) Megascleres forming the main skeleton entirely smooth *Myxilla (Burtonanchora)*
 Megascleres of the main skeleton spined on the heads or entirely spined 2
- (2) Skeleton an isotropic reticulation 3
 Skeleton plumose *Myxilla (Styloptilon)*
- (3) A second smaller category of spined megascleres present *Myxilla (Ectyomyxilla)*
 Only a single category of spined megascleres *Myxilla (Myxilla)*

SUBGENUS *MYXILLA* SCHMIDT, 1862

Synonymy

Myxilla Schmidt, 1862. *Dendoryx* Gray, 1867a: 535. *Emplocus* Gray, 1867a: 535. *Tereus* Gray, 1867a: 537. *Hastatus* Vosmaer, 1880: 136.

Type species

Halichondria rosacea Lieberkühn, 1859: 521 (by subsequent designation; de Laubenfels, 1936a: 85).

Definition

Myxilla with isotropic skeleton made up of acanthostyles in a single size category.

Diagnosis

Predominantly massive to lobate sponges with punctate surface and often slimy when handled out of the water. Oscules usually prominent on apex of lobes or along ridges. Consistency firm but crumbly. Ectosomal megascleres usually short diactines, often with spined or mucronate endings. Choanosomal megascleres a single size category of short acanthostyles. Skeleton close-meshed isotropic, with 2 or more acanthostyles forming the sides. Microscleres abundant anchorate isochelae in one or more size categories and usually sigmas, often also in more than one size category. *Myxilla* (*Myxilla*) species have been reported from Northern Hemisphere and tropical waters, but appear rare or absent in Southern Oceans.

Remarks

The separation of *Myxilla* species with only a single acanthostyle category is probably artificial, because the skeletal structure of *Myxilla* species with a second category is often very similar. Still it allows easier identification among the many *Myxilla* species described. The distinction between arcuate and anchorate chelae was not made until Levinsen (1893b) and Lundbeck (1905, 1910) discussed the issue and pointed out the subtle but consistent differences between these chela types. Several *Myxilla* species described previous to Lundbeck, notably those of Ridley & Dendy (1887) possess arcuate chelae and need to be referred to coelosphaerid genera such as *Lissodendoryx* and *Ectydoryx*.

Description of type species

Myxilla (*Myxilla*) *rosacea* (Lieberkühn, 1859) (Figs 7, 8A).

Synonymy. *Halichondria rosacea* Lieberkühn, 1859: 521, pl. XI fig. 2; *Myxilla rosacea*; Schmidt, 1862: 71; Vosmaer, 1880: 123; Ackers *et al.*, 1992: 124, fig. 209. *Myxilla fasciculata*; Schmidt, 1862: 71 (not: Lieberkühn, 1869); Topsent, 1920a: 14. *Myxilla tridens* Schmidt, 1864: 36, pl. IV fig. 5.

Material examined. Neotype (designated herein): LMJG 15293 – Schmidt collection, Triest (cf. Desqueyroux-Faúndez & Stone, 1992: 14, fig. 141). Other material. ZMA POR. 00265 – Baie de Morlaix, NW France, 10 m.

Description (mostly from Ackers *et al.*, 1992). Cushions 0.5–1 cm thick (Fig. 7B), forming patches up to 15 cm across;

becoming branched – erect in deeper waters (Lieberkühn's type was described as finger-thick anastomosing branches). It may form upright growths around hydroid stems. Surface has a loose, porous appearance (Fig. 7B), similar to that of *M. incrustans*. Slightly hispid. The oscules are scattered across the animal, and have raised edges. Exhalant channels run up to the oscules; not apparent when preserved. Considerable quantities of slime are exuded. Consistency loose, somewhat crumbly, elastic. Colour yellow, or dirty rose-red, or brownish orange when alive. Skeleton (Fig. 8A). ectosomal tornotes are arranged in vertical brushes at the surface. The choanosomal skeleton is an isotropic paucispicular reticulation of acanthostyles, without echinating spicules. Microscleres are present throughout the sponge body. Spongin is scarce. Spicules (Figs 7A, 7C–H, 8A). surface tornotes bear three or four small spines at the ends (Figs 7C–D, 8A) and are 140–170 × 2–3 µm long (Lieberkühn: 170 µm). Megascleres of the choanosomal skeleton are acanthostyles whose spines are few but strong (Fig. 7E–F, 8A), and present throughout the length of the spicule, 140–200 × 3–6 µm (Lieberkühn pictured 2 acanthostyles of 170–200 × 5 µm). The microscleres are spatuliferous anchorate chelae (Figs 7G, 8A) of two sizes, 20–25 µm, and 12–15 µm, and small sigmata (Figs 7H, 8A), ca. 14–35 µm (Lieberkühn pictured 4 sigmas of 14–35 µm, see Fig. 7A). Distribution and ecology. Mediterranean, Atlantic coasts of France and Spain, British Isles, Faroes, Arctic; exposed sites, on rock, on shells, from the shore down to 300 m.

Remarks. The type is presumably lost and Schmidt's material from Triest (Fig. 11B) is topotypical, thus it is proposed to adopt this as neotype. In Lieberkühn's original description there is no mention of chelae, nor are they figured (cf. Fig. 7A) and the description of the skeleton is also atypical: "Die Nadelzüge bestehen aus vielen nebeneinanderliegenden Nadeln von zweierlei Form ...". Schmidt (1862) at first just repeated this description but later (Schmidt, 1868: 27) acknowledged his oversight and reported the occurrence of 'Doppelhaken' in the Triest specimens of *M. rosacea*. Superficially, *M. rosacea* can be very similar to *M. incrustans*, but it does not seem to form the raised, oscule-bearing ridges of the latter species. Examination of the tornote ends at high power is necessary to confirm identification. Typical members of this subgenus next to the type species are *M. incrustans* (Johnston, 1842), *M. fimbriata* (Bowerbank, 1882), and *M. mexicensis* (Dickinson, 1945), but a comprehensive enumeration is beyond the scope of the present revision.

The genus *Dendoryx* Gray (1867a: 535) was erected for type species (by original designation) *Halichondria incrustans sensu* Bowerbank, 1866: 249 (= *H. incrustans* Johnston, 1842). The type specimen of this species could not be found in the BMNH collection, accordingly it is proposed to designate the figured specimen in Bowerbank (1874b, pl. XLIV fig. 7), BMNH 1930.7.3.271, Hastings, Bk 2013, as neotype. For a description of this species one is referred to Ackers *et al.* (1992) and Van Soest *et al.* (1999).

The genus *Emplocus* Gray (1867a: 535) was erected (by original designation) for type species *Myxilla tridens* Schmidt (1864: 36) which has been synonymized with *M. rosacea* by Vosmaer (1880: 123) and Burton (1930c: 533), thus making *Emplocus* an objective junior synonym. Examination of a specimen of Schmidt, LMJG 15291, and a slide of Schmidt from the Adriatic, BMNH 1868.3.11.98, confirmed the previous conclusions (cf. Fig. 7C–H).

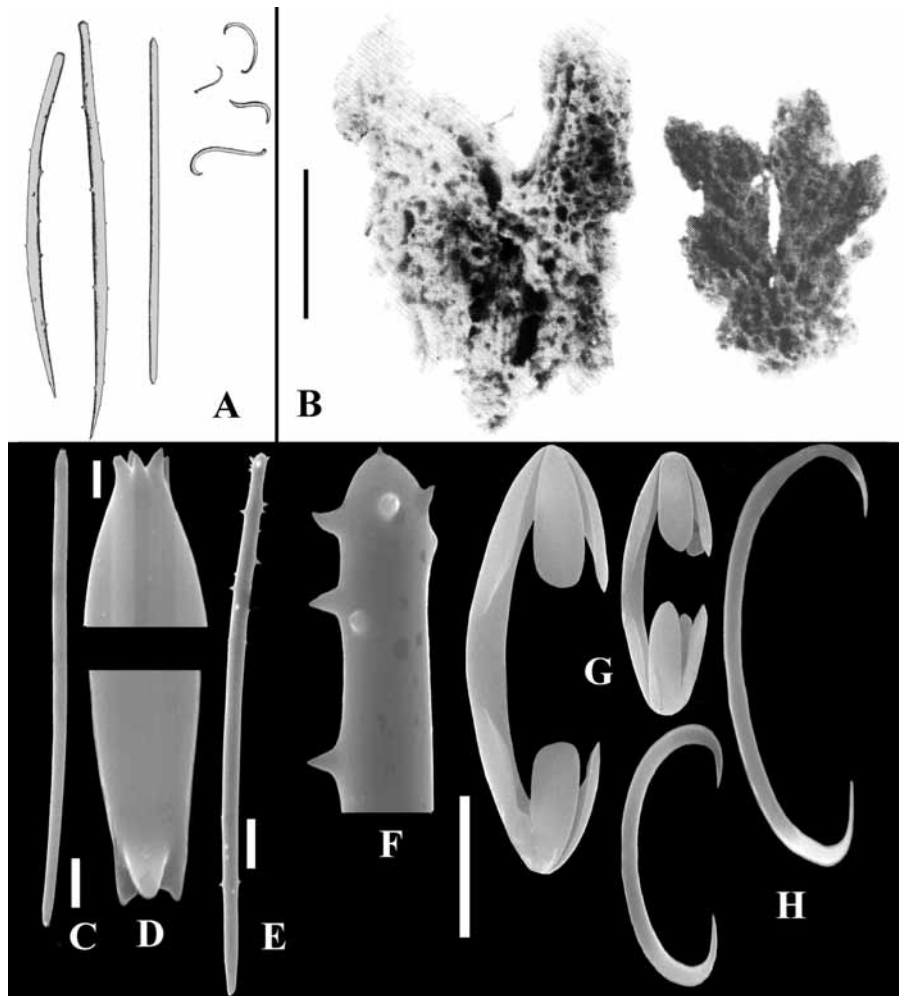


Fig. 7. *Myxilla rosacea* (Lieberkühn, 1859 as *Halichondria*), type of *Myxilla*. A, drawing of spicules reproduced from Lieberkühn's pl. XI fig. 2 (size see text). B, Schmidt's (1862) fragments of the Venice specimen of *Myxilla rosacea*, proposed as neotype material, reproduced from Desqueyroux-Faúndez & Stone's (1992, fig. 141) (scale 1 cm). C–H, SEM photos of spicules made of one of Schmidt's type specimens of *Myxilla tridens*, LMJG 15291 (considered a junior synonym of *M. rosacea*) (scales 10 μ m, except D, 1 μ m).

The genus *Tereus* Gray (1867a: 537) was erected (by original designation) for type species *Isodictya fimbriata* (Bowerbank, 1866: 337), a species quite similar to *M. rosacea*, differing only in life appearance (more orangy, no slime) and in details of tornote apices; sigmas tend to be rare. The dry type from Shetland and three unregistered slides, BMNH #Bk 759, were examined and found to conform to descriptions in, for example Ackers *et al.*, 1992 and Van Soest *et al.*, 1999; sigmas were not found in the type slide.

The genus *Hastatus* Vosmaer (1880: 136) was erected (by original designation) for *Isodictya lurida* Bowerbank (1866: 336), a synonym of *Myxilla fimbriata* (Bowerbank, 1866), which makes this genus an objective synonym of *Tereus* Gray (1867a), which in its turn is doubtlessly a synonym of *Myxilla* (*Myxilla*). Slides of the type, BMNH unregistered, Bk 758, of unknown origin, bearing the indication 'Type' and of a second specimen, here assigned paralectotype #Bk 757, from the coast of Devon. They conform to *Myxilla fimbriata*, and likewise do not contain sigmas.

The genus *Stegxella* Bowerbank (1874b) was synonymized with *Myxilla* by de Laubenfels (1936a: 85), but it is here reassigned as a synonym of *Hymedesmia* (*q.v.*).

SUBGENUS *BURTONANCHORA* DE LAUBENFELS, 1936

Synonymy

Burtonanchora de Laubenfels, 1936a: 94.

Type species

Myxilla crucifera Wilson, 1925: 430 (by original designation).

Definition

Myxilla with choanosomal styles smooth, never spined.

Diagnosis

Flabelliform or massive sponges. Skeleton a reticulation of smooth styles. Ectosomal skeleton bundles of tornotes fanning out to form a tangential skeleton at the surface. Microscleres tridentate anchorate isochelae and sigmas. Species answering to the definition of *Burtonanchora* have been reported from tropical as well as polar areas, and also in deep water.

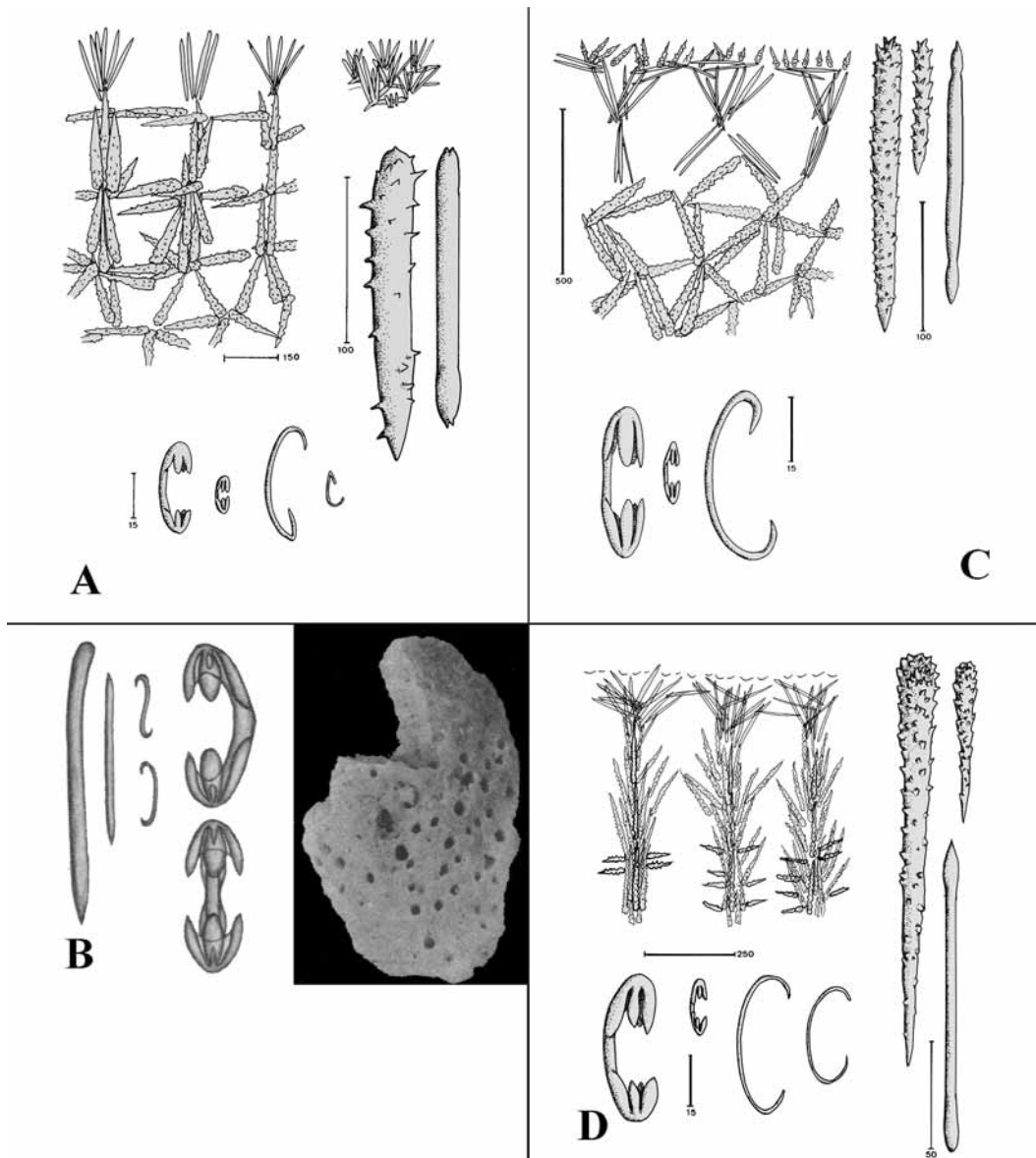


Fig. 8. A, *Myxilla (Myxilla) rosacea* (Lieberkühn, 1859), drawing of skeleton and spicules made from a representative specimen in the ZMA collection (ZMA POR. 00265). B, *Myxilla (Burtonanchora) crucifera* Wilson (1925), habitus and spicules, reproduced from Wilson's pls 42 fig. 5 and 49 figs 3–4 (size see text). C, *Myxilla (Ectyomyxilla) kerguelensis* (Hentschel, 1914), drawing of skeleton and spicules made from the type of *Crellomyxilla intermedia* Dendy (1924), considered a junior synonym. D, *Myxilla (Styloptilon) ancoratum* (Cabiocch, 1968b), drawing of skeleton and spicules made from a slide of the holotype.

Remarks

The smooth styles may seem a clear distinction from the spined styles found in most *Myxilla* species. However, some species are known to have only a few spines or very faint spination, making this distinction dubious.

Description of type species

Myxilla (Burtonanchora) crucifera Wilson, 1925 (Fig. 8B).

Synonymy. *Myxilla crucifera* Wilson, 1925: 430, pl. 42 fig. 5, pl. 49 figs 3–4; *Burtonanchora crucifera*; de Laubenfels, 1936a: 94.

Material examined. None. Holotype: USNM 21359–'Albatross' Philippine Expedition, stat. D5168 (not examined).

Description. (from Wilson, 1925). Flabelliform (Fig. 8B), about 4 × 5 × 0.8 cm. The convex surface bears regularly distributed oscules of 1–2 mm in diameter. The concave surface is irregular and bears closely set pores. Firm consistency. Light brown (alcohol). Skeleton. ectosomal tornotes form brushes at the surface which fan out to form a tangential layer. The main skeleton is isotropic in the interior but may become somewhat anisotropic at the periphery. Meshes are enclosed by 2–6 spicules. Spicules (Fig. 8B). Tornotes oxeote, smooth straight, 165–200 × 6–7 μm; styles, short, fat, entirely smooth, 270–300 × 18–21 μm; anchorate isochelae in two size categories, 40 and 10 μm; sigmas in two size categories, 50–70 and 10 μm. Distribution. Philippines.

Remarks. Several other species were assigned to *Burtonanchora* by de Laubenfels (1936a): *Myxilla lacunosa* Lambe (1892: 70), *M. hastata* Ridley & Dendy (1886: 472),

M. magna Topsent (1916: 168), *M. pedunculata* Lundbeck (1905: 148), *M. pistillaris* Topsent (1916: 169), *M. spongiosa* Ridley & Dendy (1886: 471) and *Amphilectus osculosus* Topsent (1893c). Lévi (1960a, 1963, 1965) added *Burtonanchora myxilloides* (West Africa), *B. sigmatifera* (South Africa) and *B. gracilis* (Red Sea). Desqueyroux-Faúndez & Van Soest (1996: 34) added a further species, *Myxilla (Burtonanchora) asymmetrica* to this group, but reassigned (p. 31) *M. spongiosa* to the subgenus *Myxilla (Myxilla)* (as junior synonym of *Myxilla (Myxilla) mollis* Ridley & Dendy (1886: 471) on account of the slight spination of the styles.

SUBGENUS *ECTYOMYXILLA* DENDY, 1924

Synonymy

Ectyomyxilla Hentschel, 1914: 103 (not Lundbeck, 1909: 445 = *nomen nudum*). *Crellomyxilla* Dendy, 1924: 364.

Type species

Ectyomyxilla kerguelensis Hentschel, 1914: 103 (by original designation).

Definition

Myxilla with a smaller category of spined styles in addition to the main (acantho-)styles.

Diagnosis

Encrusting, massive, flabellate or branching sponges with irregular surface. Skeleton isotropic paucispicular, which may become loosely anisotropic in some species. Megasccleres include two size categories of acanthostyles, one of which may form a surface palisade or is echinating the nodes of the skeletal meshes. Tornotes smooth or lightly spined on the apices. Microsccleres anchorate isochelae and sigmas. Many *Myxilla (Ectyomyxilla)* have been described from cold or deep water.

Remarks

Contrary to what Desqueyroux-Faúndez & Van Soest (1996: 27) maintained, the name *Ectyomyxilla* is a *nomen nudum*, because Lundbeck (1909: 445) did not mention any species when erecting this genus. The subsequent use of the name by Hentschel (1914: 103) does not satisfy Article 12.2.5 of the ICZN (Anonymous, 1999) as type species designation. However, the name may still be used in the sense of Hentschel (1914), and it takes his authorship. Thus, its type species is *Ectyomyxilla kerguelensis* Hentschel, 1914 by monotypy. This group unites the *Myxilla*-like species with a second smaller category of entirely spined styles. In the type species (cf. below) the smaller spined styles occur as an ectosomal palisade. In other species considered to belong to the subgenus *Ectyomyxilla*, these spicules may occur in the usual echinating position at the nodes of the choanosomal reticulation.

Previous reviews

Lundbeck (1909), Hentschel (1914), Dendy (1924), Desqueyroux-Faúndez & Van Soest (1996), Maldonado & Young (1998a).

Description of type species

Myxilla (Ectyomyxilla) kerguelensis (Hentschel, 1914) (Figs 8C, 9).

Synonymy. *Ectyomyxilla kerguelensis* Hentschel, 1914: 103, pl. IV fig. 10, pl. VII fig. 10. *Crellomyxilla intermedia* Dendy, 1924: 364, pl. XV figs 16–21.

Material examined. No type material of Hentschel was reexamined. Holotype of *Crellomyxilla intermedia* Dendy: BMNH 1923.10.1.145 – ‘Terra Nova’ Exped. stat. 90, Three Kings islands, New Zealand, 180 m (this is considered a junior synonym).

Description. Elongated, subcylindrical; branches of 7 cm diameter, 11.5 cm high. Surface uneven, granular. Dendy’s fragments (Fig. 9A) are black in alcohol, but apparently this was induced by osmic acid; other smaller fragments are white in alcohol; Hentschel’s material (Fig. 9G) was greyish brown. Skeleton. Ectosomal skeleton (Fig. 8C) consists of two layers: an outer layer of single acanthostyles perpendicular to the surface, points outwards, carried by partly tangentially arranged bouquets of tornotes. Choanosomal skeleton (Fig. 8C) isotropic, with triangular meshes in the peripheral skeleton, becoming quadrangular deeper in the choanosome; meshes made up of 1–4 spicules. Hentschel records rare echinating acanthostyles. Spicules. Ectosomal acanthostyles (Figs 8C, 9C, J), short and thick, entirely spined, 56–100 × 5–12 μm; ectosomal tornotes (Figs 8C, 9D, H) with swollen mucronate apices, 152–210 × 5–7 μm; choanosomal styles (Figs 8C, 9B, I), entirely acanthose, with thick spines, 176–225 × 14–17 μm). Microsccleres. anchorate chelae (Figs 8C, 9E, K) in two size categories, 28 and 16 μm (Hentschel’s material: only a single category, 12.5–19 μm); sigmas (Figs 8C, 9F, L), 17–36 μm. Distribution and ecology. Kerguelen, New Zealand; deeper water.

Remarks. *Crellomyxilla intermedia* Dendy, 1924 shares most characters, including the smaller acanthostyles concentrated in the ectosome, with *Myxilla (Ectyomyxilla) kerguelensis* and is generally considered synonymous (compare Fig. 8A–F with 8G–L). A further species sharing this character is *M. (E.) chilensis* (Thiele, 1905: 443, figs 22, 62). Species answering to the definition of *Myxilla*, but possessing echinating acanthostyles next to choanosomal styles are: *M. arenaria* Dendy (1905: 169), *M. (Ectyomyxilla) dracula* Desqueyroux-Faúndez & Van Soest (1996: 37), *Ectyomyxilla hentscheli* Burton (1929a: 438), *M. mariana* Ridley & Dendy (1886: 472), *M. massa* Ridley & Dendy (1886: 473), *M. mariana tylacantha* Hentschel (1914), *E. methanophila* Maldonado & Young (1998a: 798), *M. nobilis patagonica* Ridley & Dendy (1886: 473), *Myxilla parasitica* Lambe (1893: 31), and *E. ramosa* Bergquist & Fromont (1988: 87).

The genus *Jelissima* de Laubenfels, 1936a (type species *Hymedesmia tenuissima* Thiele, 1905) was assigned to *Ectyomyxilla* by Desqueyroux-Faúndez & Van Soest (1996), but subsequent examination of ‘co-type’ material revealed that it answers to the definition of *Hymenancora* (cf. above).

SUBGENUS *STYLOPTILON* CABIOCH, 1968

Synonymy

Styloptilon Cabioch, 1968b: 236.

Type species

Styloptilon ancoratum Cabioch, 1968b: 236 (by monotypy).

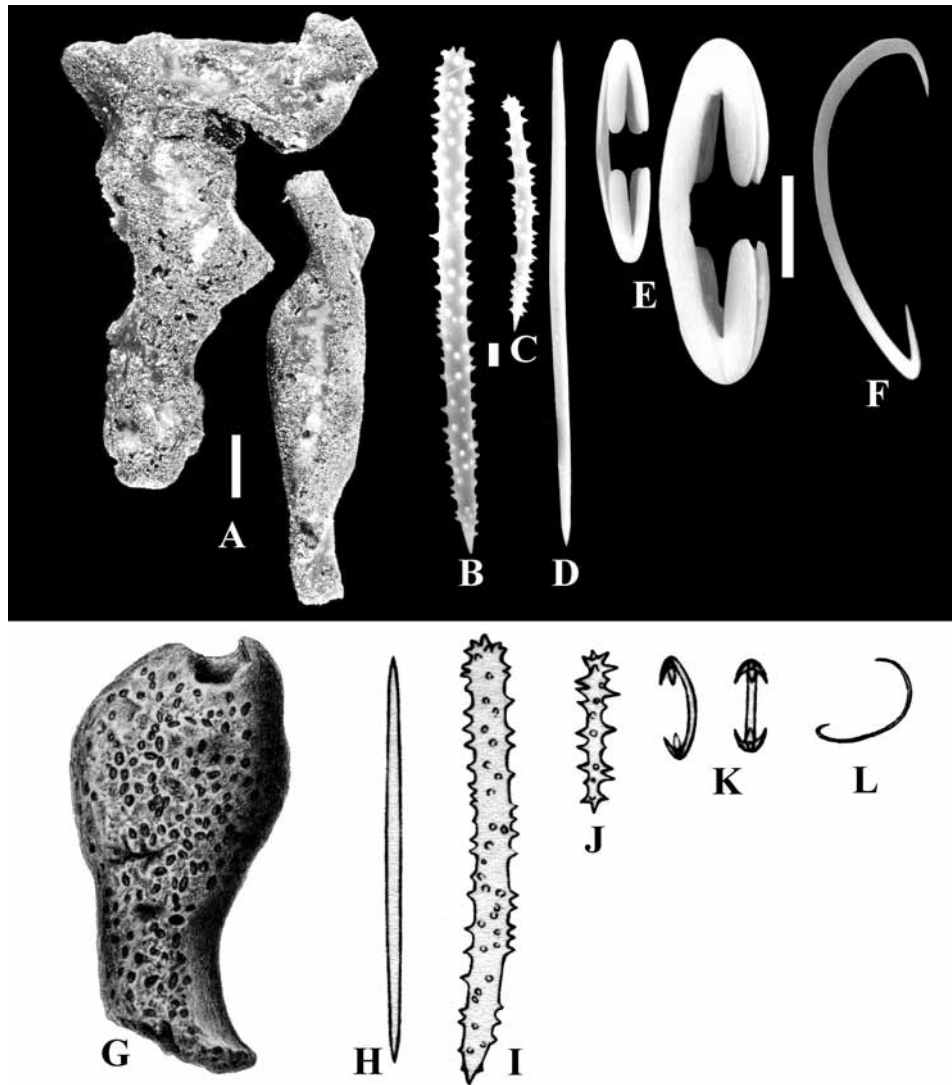


Fig. 9. *Myxilla* (*Ectyomyxilla*) *kerguelensis* (Hentschel, 1914 as *Ectyomyxilla*). A, two type fragments of *Crelomyxilla intermedia* Dendy (1924), considered a junior synonym (scale 1 cm). B–F, SEM photos of spicules made from the type material of *Crelomyxilla intermedia* (scales 10 μm). G–L, Hentschel's drawings of habit and spicules reproduced from his pls. IV fig. 10 and pl. VII fig. 10 (sizes see text).

Definition

Myxilla with plumose skeleton.

Diagnosis

Encrusting; with a plumose skeleton of bundles of larger acanthostyles echinated by similar acanthostyles. Tornotes anisoxeote. Microscleres anchorate chelae and sigmas. So far only a single species has been assigned to this subgenus and its status as a separate group is thus uncertain. Still, its plumose skeletal architecture prevents its inclusion in *Myxilla* (*Myxilla*).

Description of type species

Myxilla (*Styloptilon*) *ancoratum* (Cabioc, 1968b) (Fig. 8D).

Synonymy. *Styloptilon ancoratum* Cabioc, 1968b: 236, fig. 10B; Solórzano & Urgorri, 1993: 64.

Material examined. Holotype: specimen from the Roscoff area, incorporated in the collections of the Station Biologique de Roscoff.

Description (partly after Cabioc, 1968b). Thinly encrusting, about 1 mm in thickness, agglutinating shell debris. The surface is finely hispid. Colour yellowish white in alcohol. Skeleton (Fig. 8D). the dermal membrane is charged with microscleres and carried by bouquets of tornotes, which also form short tangential bundles. The bouquets of tornotes are in turn erected on the peripheral ends of the choanosomal spicule tracts, which consist of acanthostyles. The skeletal columns are thick and form a plumoreticulate skeleton, in which the longitudinal elements dominate. Spicules (Fig. 8D). Tornotes smooth with pointed, but unequal ends, one being slightly swollen; they may be somewhat polytylote or have an irregular outline, 140–200 \times 2.5–5 μm ; acanthostyles are entirely spined and perhaps divisible in two size categories, 100–135 \times 5–8 μm and 190–280 \times 5–10 μm , but they do not constitute two functional categories (main and echinating). Microscleres spatulate anchorate isochelae in two size categories, 35–48 μm and 11–15 μm ; sigmas in a single variable size category, 32–50 μm . Distribution and ecology. Atlantic coasts of France and Spain; on pebbles down to 85 m.

Remarks. The species remains ill-known. Its characters are in between those of *Phorbis* (plumose columns, pointed tornotes, two sizes of acanthostyles) and *Myxilla* (anchorate chelae).

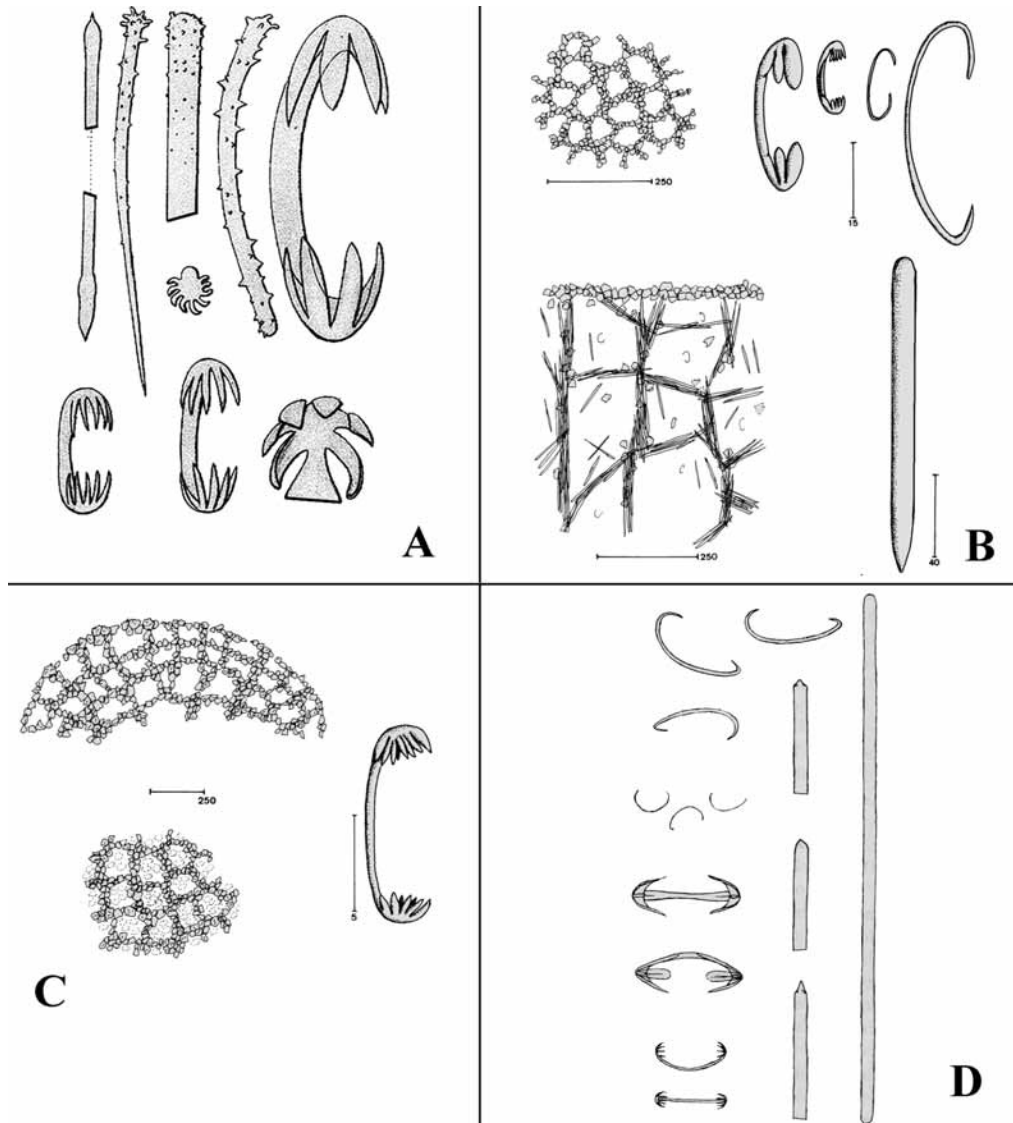


Fig. 10. A, *Plocamiancora denticulata* Topsent (1927b), drawing of spicules reproduced from Topsent (1928c, pl. X fig. 17) (sizes see text). B, *Psammochela elegans* Dendy (1916a) drawing of skeleton and spicules made from the slide of the holotype. C, *Psammochela chaliniformis* (Carter, 1885b as *Dysidea*), type of *Psammodyx* Burton (1934a), drawing of skeleton and polydentate chelae made from a slide of the holotype. D, *Psammochela psammodes* (Hentschel, 1911 as *Desmacidon*), type of *Anomomyxilla* Burton (1934a), drawing of spicules reproduced from Hentschel (1911, fig. 19) (sizes see text).

PLOCAMIANCORA TOPSENT, 1927

Synonymy

Plocamiancora Topsent, 1927b: 17. *Plocamissa* Burton, 1935c: 401.

Type species

Plocamiancora denticulata Topsent, 1927b: 17 (by original designation).

Definition

Myxillidae with plocamiid skeletal structure.

Diagnosis

Encrusting; smooth ectosomal tornotes; choanosomal skeleton plocamiid with an isotropic basal reticulation of single acanthostrogyles echinated by long microspined styles in ascending plumose axial columns; short acanthostyles echinating skeletal tracts; microscleres are unguiferate or polydentate anchorate isochelae. Three species.

Previous review

Topsent (1928c).

Description of type species

Plocamiancora denticulata Topsent, 1927b (Fig. 10A).

Synonymy

Plocamiancora denticulata Topsent, 1927b: 17; Topsent, 1928c: 307, pl. X fig. 17. ? *Plocamiancora arndti* Alander, 1942: 54, pl. 12 fig. 16.

Material examined. Lectotype (slide): MNHN DT. 1164 – labeled ‘St. 1420, 1902’. Paralectotypes (2 slides): MNHN DT. 1081 – labeled ‘St. 1116, 1901’.

Description (from Topsent, 1928c). Extended crusts, all on stony or gorgonian corals, with hispid surface. Colour greyish (in alcohol). Skeleton plocamiid, i.e., with a basal isotropic reticulation of acanthostrongyles, singly or in bundles of two or three, upon which single long acanthostyles are erected, at their base echinated by groups of smaller acanthostyles. Spicules (Fig. 10A). Smooth oxecote anisotornotes with mucronate endings, 308–350 × 4–5 μm; long acanthostyles, somewhat curved at the base, spined only on the blunt end, 600–850 × 20–30 μm; smaller echinating acanthostyles, entirely spined, 224–490 × 10–12 μm; acanthostrongyles, strongly curved, spined predominantly at both ends, lighter inbetween, 140–160 × 10 μm; large unguiferate-spatulate chelae with 3–5 teeth, 73–85 μm; smaller unguiferate-polydentate chelae with 5–9 teeth, 38–52 μm. Distribution and ecology. Azores; deep water, 1740–2460 m.

Remarks. This genus in many aspects represents the model Myxillina, as it contains all three skeletal zones found in the various genera and families of this group, and resembles certain Microcionina genera such as *Antho* and *Lithoplocamia*. *Plocamiancora arndti* Alander (1942) is probably a synonym of *P. denticulata*, but was distinguished on the lack of polydentate (5-toothed) chelae. This is subject to variation. Uriz (1987) reported *P. denticulata* from 260 m off the coast of SW Africa, but later (1989) assigned this to a new species of *Ectyonancora*, *E. walvisensis* Uriz (1989: 73). However, this is not an *Ectyonopsis* (senior synonym of *Ectyonancora*) because of its possession of long styles erect on the isotropic reticulation of acanthostrongyles. It conforms to the present definition of *Plocamiancora*, and accordingly is renamed *Plocamiancora walvisensis*. Solórzano *et al.* (1991: 182, fig. 4) recorded a *Plocamiancora* spec. from the N coast of Spain. This clearly conforms to *Rotuloplocamia octoradiata* Lévi (1952) (see chapter on family Iotrochotidae).

The type species (original designation) of *Plocamissa* Burton (1935c: 401), i.e., *Plocamia igzo* de Laubenfels, 1932: 102 (type USNM 22058 from California re-examined), in spite of de Laubenfels' inadequate description, conforms in all important respects to *Plocamiancora denticulata* except for the smaller size of the polydentate chelae. The ectosomal skeleton contains strongly developed bouquets of anisotornotes many of which have one mucronate and one microspined rounded end (Fig. 11A). Because some of them are smooth (Fig. 11A right) they were not distinguished by de Laubenfels from the choanosomal styles. The structural styles (Fig. 11B) are united in bundles and have spined heads, size 350 × 35 μm; these are echinated at the base by rare, thin acanthostyles (Fig. 11C) of approximately 190 × 11 μm; the basal/central isotropic reticulation is made up of dumbbell-shaped acanthostrongyles (Fig. 11D) of 130 × 13 μm. The chelae are small polydentate anchorates (Fig. 11E) of 14 μm.

PSAMMOCHELA DENDY, 1916**Synonymy**

Psammochela Dendy, 1916a: 126. *Psammodyryx* Burton, 1934a: 556. *Anomomyxilla* Burton, 1934a: 555.

Type species

Psammochela elegans Dendy, 1916a: 126 (by monotypy).

Definition

Myxillidae with a single megasclere category consisting of smooth styles or strongyles. The skeleton consists of a reticulation of megascleres and sand grains. Microscleres include anchorate chelae, and/or small polydentates; sigmas may be present.

Diagnosis

Massively encrusting. Ectosomal skeleton with a fine-meshed reticulation of small sand grains; choanosomal skeleton irregularly reticulate, composed of thin fibres with poor spongin, cored with sand and styles, and numerous sand particles and spicules dispersed within the mesohyl; megascleres are styles; microscleres are anchorate and polydentate isochelae and sigmas.

Remarks

The three species united here under *Psammochela* share the presence of sand columns replacing the choanosomal skeleton, and anchorate chelae or derived forms. In other respects they show considerable differences: *P. elegans* has styles as megascleres, *P. psammodes* has strongyles, and *P. chaliniformis* lacks megascleres entirely. Their close relationship is uncertain.

Previous reviews

Dendy (1916a), Burton (1934a), Wiedenmayer (1989: 67).

Description of type species

Psammochela elegans Dendy, 1916a (Figs 10B, 11F–J).

Synonymy. *Psammochela elegans* Dendy, 1916a: 126, pl. I fig. 6, pl. III fig. 22.

Material examined. Lectotype: BMNH 1920.12.9.36. Paralectotype: BMNH 1920.12.9.37 – 2 unregistered slides CN XVIII.3.

Description. Irregular lamellar or digitate sponges (Fig. 11F), often forming long slender processes, up to 9 cm long 0.3–1 cm in diameter. Surface irregularly rugose or finely conulose, but smooth in between. Oscules small and scattered. No colour recorded. Skeleton (Fig. 10B). Ectosomal skeleton consists of a tight-meshed reticulation of fine sand grains, meshed 50–80 μm in diameter, with few megascleres and microscleres. Choanosomal skeleton an isotropical to irregular reticulation of spicule tracts mixed with sand grains. Meshes 100–200 μm, tracts with up to 5 spicules in cross section. Spicules (Figs 10B, 11G–J). No ectosomal megascleres; choanosomal styles (Fig. 11G), smooth straight, relatively robust, rather uniformly about 160 × 5–7 μm; chelae in two categories, one commonplace tridentate anchorate chelae (Fig. 11I) of 24–25 μm (these are not abundant and may possibly be foreign), and abundant small polydentate chelae (Fig. 11H) of about 12 μm, with 9 or more alae; sigmas (Fig. 11J) in two size categories, 50 μm and 12 μm (Dendy gives 33 μm and a much smaller category). Distribution and ecology. India, Indonesia; rocky bottom, 5–7 m.

Remarks. The type species is one of the sand sponges which so frequently demonstrate reduced skeleton and spicule complement.

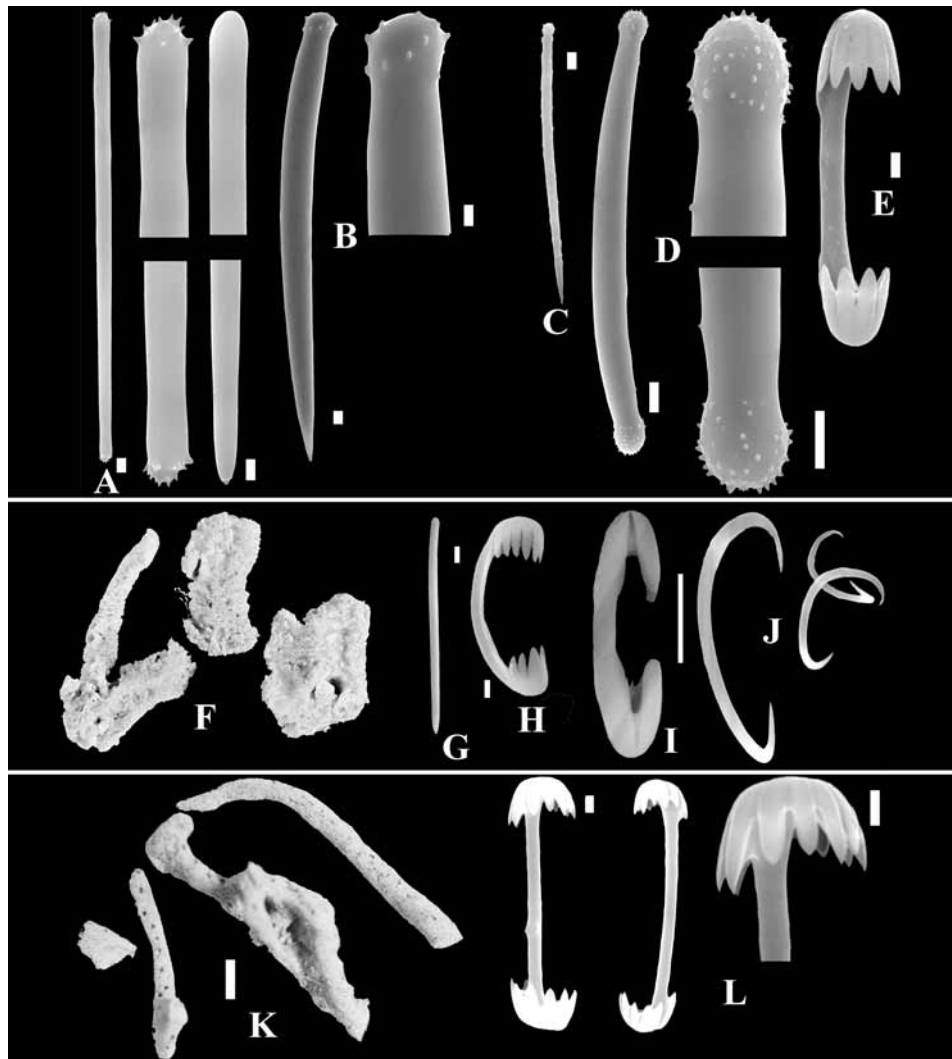


Fig. 11. A–E, *Plocamiancora igzo* (de Laubenfels, 1932 as *Plocamia*), type of *Plocamissa* Burton (1935c), SEM photos of spicules made from the type (scales 10 μ m; except E, 1 μ m). F–J, *Psammochela elegans* Dendy (1916a). F, fragments of the holotype (scale 1 cm). G–J, SEM photos of spicules made from the type (scales 10 μ m; except H, 1 μ m). K–L, *Psammochela chaliniformis* (Carter, 1885b as *Dysidea*), type of *Psammodyryx* Burton (1934a). K, fragments of holotype (scale 1 cm). L, SEM photos of polydentate chelae (scale 1 μ m).

Burton (1934a) synonymized it with *Phoriospongia fibrosa* Ridley (1884a), but justification for this is thin, since this species has oxeas as megascleres and these are quoted as much thicker than the styles of Dendy's type; furthermore *fibrosa* has tridentate, rather than polydentate chelae. Burton's (1934a) record of *P. fibrosa* is dubious because he could not find any microscleres. Several other species have been assigned to this genus: *Psammochela rigida* (Bowerbank, 1875b: 289, as *Halichondria*) from Singapore is close to *P. elegans* and a possible senior synonym; however, there is apparently no sand reticulation at the surface, which is a distinct difference. *P. recife* and *P. tyloa* Boury-Esnault (1973: 283) have tylotes as megascleres and arcuate isochelae. They do not conform to *Psammochela* and are very likely coelosphaerids, probably members of the subgenus *Anomodoryx* of the genus *Lissodendoryx*.

The genus *Anomomyxilla* Burton (1934a: 555) was erected (by original designation) for type species *Desmacidon psammodes* Hentschel (1911: 322, fig. 19), type specimen not examined. This has an ectosomal skeleton composed of strongyles (Fig. 10D), 136–166 \times 2–3 μ m, of the same form as found in the choanosome,

forming loose dermal brushes supporting a close-meshed tangential skeleton of sand and foreign spicules (sandy crust); choanosomal skeleton consists of an irregular network of fibres incorporating sand and foreign spicules, and with plumose tracts of strongyles; microscleres are rare spatulate anchorate isochelae, 15–17 μ m, and unguiferous isochelae, 9–10 μ m, and sigmas in two size categories, 25–32 and 10–12 μ m.

The genus *Psammodyryx* Burton, 1934a: 556 was erected (by original designation) for type species *Dysidea chaliniformis* Carter (1885b: 217) from South Australia, collected from a depth of 35 m. Syntypes BMNH 1886.12.15.341 (with slide) and 343 were re-examined. Since these represent two distinct species, a lectotype is here chosen: BMNH 1886.12.15.341 (see remarks below). Originally the type specimen (Fig. 11K) was a compressed bunch of solid cylindrical stalks rising from a common stem; size about 30 \times 12 \times 2.5 cm. Branches small and 0.3–2 cm in diameter. Only a few fragments have survived. Oscules in rows on the branches. Consistency fragile (dry). Colour reddish brown. Skeleton (Fig. 10C) composed of a neat isodictyal reticulation of sand grains without proper megascleres. Ectosomal skeleton a reticulation of

rounded meshes of ca. 100 µm in diameter. The only spicules present are polydentate unguiferate isochelae (Figs 10C, 11L) of 10–12 µm. There is confusion among the BMNH specimens labeled 'Dysidea chaliniformis', due to the fact that two distinctly different species have received identical or similar labeling. Burton (1934a) omitted to check the type specimens when he indicated this species as the type of his new genus *Psammodyx*. BMNH 1886.12.15.341 conforms to the genus definition of Burton ('reduced Myxillae (?) with skeleton composed of a reticulation of horny fibres filled with sand and foreign spicules; microscleres isochelae unguiferae') and accordingly this is here chosen as the lectotype. The labels with this specimen in Miss S.M. Stone's handwriting say: '?Chalinopsilla arborea var. micropora Lendenfeld, 1889, p. 149, South coast of Australia J.B. Wilson Coll.', and an older label, possibly in Carter's handwriting says "Dysidia chaliniformis fragment of main mass which is net (1790) Australia" (information provided by Clare Valentine). The fragment of the type redescribed by Dendy (1896) was also taken from this specimen. Confusion with Dendy's *Chondropsis chaliniformis* (attributed to Lendenfeld, 1889a, because this author described specimens with strongyles and sigmas not conforming to *Dysidea chaliniformis*) may well have occurred among the various curators of the BMNH collection. The other presumed type specimen, BMNH 1886.12.15.343, though labeled as the holotype (in Miss S.M. Stone's handwriting), and later reassigned to *Psammochela* by Burton, appears to belong to *Echinoclathria*, probably *E. subhispida* (Carter). It has proper styles and lacks chelae. Possibly as a result of this long-time confusion, Burton (1934a) also recorded Great Barrier Reef material as *Chondropsis chaliniformis* (Carter), while quoting *Dysidea chaliniformis* Carter, 1885b as a synonym, without referring to his action of a few pages further, viz., naming this same *Dysidea chaliniformis* Carter, 1885b as type of his new genus *Psammodyx*. Burton (1934a) also included *Desmacidon arenosa* Whitelegge (1906: 478) from South East Australia in *Psammodyx*. On paper this sounds very similar to *P. chaliniformis*, and this was also realized by Whitelegge. Differences he noted were a massive shape (7 × 4.5 × 3 cm), less clearly developed spongin fibres and a larger size of the chelae (15 µm).

STELODORYX TOPSENT, 1904

Synonymy

Stelodoryx Topsent, 1904b: 174. *Onychomyxilla* Topsent, 1927b: 12. *Pseudomyxilla* Koltun, 1955b: 14.

Type species

Stelodoryx procera Topsent, 1904b: 174 (by monotypy).

Definition

Myxillidae with reticulate skeleton and a full complement of megascleres; microscleres include polydentate anchorate isochelae.

Diagnosis

Stalked, lobate, massive or encrusting sponges. Resembling *Myxilla* in most respects, including ectosomal tornotes and reticulate

choanosomal skeleton. The choanosomal megascleres are smooth or spined styles, and a second category of smaller echinating acanthostyles may be present. Microscleres include polydentate (5 or more alae) anchorate or unguiferate isochelae and sigmas. Occasionally tridentate anchorate chelae may be also present. About 10 species. Most representatives of this genus originate from deep water or from boreal or Antarctic waters.

Remarks

The name of the genus suggests stalked growth form such as found in the type species as a genus character, but growth form is not likely to constitute a valid generic character. Other growth forms are also included and accordingly the genera *Onychomyxilla* and *Pseudomyxilla* are here synonymized with *Stelodoryx*.

Previous review

Burton (1932).

Description of type species

Stelodoryx procera Topsent, 1904b (Fig. 12A).

Synonymy

Stelodoryx procera Topsent, 1904b: 174, pl. III fig. 5, pl. XIV fig. 17, pl. XVIII fig. 2.

Material examined. Holotype (slides): MNHN DT. 990 – labeled 'PA 1895 53'. Slides of topotypical specimens: MNHN DT. 989 – labeled 'PA st. 1349'. DT. 991 – labeled 'PA 1897, 53'.

Description. A stalked species (Fig. 12A), 2–6 cm high; main body flattened, softly spongy, with grooved irregular surface. Colour pale brown. Skeleton. Ectosomal skeleton of brushes of tornotes; the main body has a typical *Myxilla*-like isotropic reticulation of 1–3 spicules per side; the stalk has a plumoreticulate arrangement of long styles forming thick longitudinal bundles connected here and there by short cross-bundles. Spicules. Ectosomal anisotornotes, with a thicker more heavily spined end, and a thinner more lightly spined end, 235–300 × 5 µm; choanosomal styles of the main body, entirely smooth, blunt-ending, 350–650 × 12 µm; styles of the stalk, entirely smooth, pointed, 990–1300 × 20–23 µm. Microscleres. Anchorate, 5-teethed chelae in two morphologically distinct forms, with spatulate, long teeth 35–55 µm (possibly in two size categories), and thin, elongate chelae with short spiky teeth (50–55 µm). Distribution and ecology. Azores; deep water, on rocks or on stalks of gorgonians, 350–1200 m.

Remarks. The type species differs from other species described in this genus by its possession of clearly localized choanosomal megasclere categories, probably correlated with the stalked shape. However, if more than one species would exist with that differentiation, a separate (sub)genus may need to be recognized for stalked species.

Koltun (1955b) erected the genus *Pseudomyxilla* for *P. vitjazi* Koltun (1955b: 14, by monotypy) emphasizing the reduced unguiferate teeth of the isochelae. However, *S. procera* possesses chelae with reduced teeth next to spatulate chelae. The difference with *Pseudomyxilla* thus becomes void. *P. vitjazi* (Fig. 12C) has tornotes with microspined apices of 190–290 × 4–7 µm, choanosomal acanthostyles entirely spined, 435–520 × 20–29 µm, and polydentate

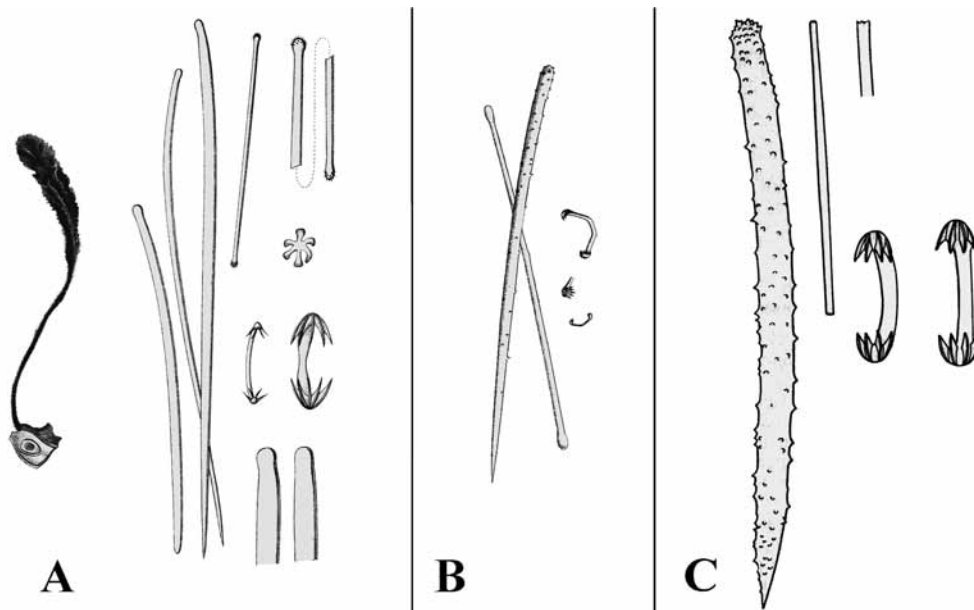


Fig. 12. A, *Stelodoryx procera* Topsent (1904b), drawings of habit and spicules reproduced from Topsent (1904b, pl. III fig. 5, pl. XIV fig. 17, pl. XVIII fig. 2). B, *Stelodoryx pectinata* Topsent (1892a as *Dendoryx*), type of *Onychomyxilla* Topsent (1927b), drawing of spicules reproduced from Topsent (1892a, pl. X fig. 6). C, *Stelodoryx vittazi* (Koltun, 1955b as *Pseudomyxilla*), drawing of spicules reproduced from Koltun (1959, fig. 78) (all sizes see text).

unguiferate isochelae of 26–40 μm . It is a deep water species (115–820 m) from the NE Pacific.

The genus *Onychomyxilla* Topsent (1927b: 12) was erected (by original designation) for type species *Dendoryx pectinata* Topsent (1892a: 100, pl. X fig. 6). A MNHN slide (DT. 995) of the holotype was examined, labeled 'No. 78. Camp. Hironnelle, 1888, 125', from the Azores area, 861–2460 m. Its skeleton is basically a paucispicular reticulation of acanthostyles, with echinating acanthostyles at the nodes. Ectosomal skeleton of bundles of tyloles, which are smooth, with well-developed tyloles, 415–500 \times 4–5 μm ; choanosomal acanthostyles (Fig. 24B), curved, mostly smooth with few big spines near the blunt end and a few small spines near the pointed end, 448–504 \times 13–16 μm ; smaller echinating acanthostyles, similarly spined, 224–266 \times 8 μm . Microscleres are polydentate isochelae (Fig. 12B), sometimes slightly anisochelate, with numerous short sharp teeth, in two size categories, 36–60 μm and 18–22 μm . This species could be regarded as a deviating

Hymetrochota (cf. chapter on family Iotrochotidae) which has failed to develop its birotulas. Its characters are apparently stable since several specimens were obtained from different localities off the Azores. The species is allocated to *Stelodoryx* because true birotulas are absent.

Several *Stelodoryx* and *Pseudomyxilla* species have been described from various parts of the world, most of them from cold or deep water: *S. chlorophylla* Lévi (1993: 49), *S. cribrigera* (Ridley & Dendy, 1887: 472, as *Myxilla*), *S. flabellata* Koltun (1959: 119) *S. lissostyla* (Koltun, 1959: 124, as *Pseudomyxilla*), *S. multidentata* (Boury-Esnault & van Beveren, 1982: 93, as *Pseudomyxilla*), *S. phyllomorpha* Lévi (1993: 51), *S. pluridentata* (Lundbeck, 1905: 151, as *Myxilla*), and *S. toporoki* Koltun (1958: 57). Koltun considered *Chondrocladia alascensis* Lambe (1894: 119) a member of *Stelodoryx*, but this conforms clearly to *Monanchora*. However, his own specimen recorded as *Stelodoryx alascensis* appears to be a true *Stelodoryx*.