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Family Hemiasterellidae Lendenfeld, 1889

John N.A. Hooper

Queensland Museum, P.O. Box 3300, South Brisbane, Qld, 4101, Australia. (JohnH@qm.qld.gov.au)

Hemiasterellidae Lendenfeld (Demospongiae, Hadromerida) contains 11 nominal genera, of which six are valid, and approximately 20 described species worldwide. Species live in all oceans, predominantly in shallow waters, are often dichotomously branching or flabellate, with hispid surface or conules and stiff texture. The family has a unique combination of euasters mainly at the surface, and monaxonic megascleres (styles and/or oxeas) with distinctly structured arrangement of axial and extra-axial skeletons. Genera are differentiated predominantly on the basis of whether megascleres are diactinal or monactinal, development of the axial and extra-axial skeletons, presence or absence of ectosomal specialisation, and euaster morphology.
Keywords: Porifera; Demospongiae; Hadromerida; Hemiasterellidae; *Adreus*; *Axos*; *Hemiasterella*; *Leptosastra*; *Paratimea*; *Stelligera*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Hemiasterellidae Lendenfeld, 1889b. Leptosastrinae Topsent, 1928c: 48, 56. [Astraxinellidae] Dendy, 1905 (*nomen nudum*).

Definition

Hadromerida with compressed axial plumose – plumoreticulate extra-axial skeleton composed of styles, oxeas or both, and smooth or partially microspined euasters.

Diagnosis

Encrusting, cup-shaped, arborescent or branching growth forms; megascleres are styles (in one genus acanthostyles), oxeas or both enclosed within axially compressed spongin fibres, or basally compressed in encrusting taxa, and plumose to plumoreticulate extra-axial branches, or sometimes without a definite axis; bouquets of smaller styles and/or oxeas sometimes protrude through surface; microscleres are euasters, smooth or partially microspined, often confined to an ectosomal crust.

Scope

Eleven genera have been included, or are potentially included in this family, although only six of these are now recognised, one (*Leptosastra*) monotypic, poorly known, and included here speculatively. Species are found in all seas but only about 25 species have so far been described.

History and biology

Hemiasterellidae was established for *Hemiasterella* Carter and *Epallax* Sollas (not Gray, cf. de Laubenfels, 1936a; Wiedenmayer, 1977b) with brief diagnosis "*Axinellidae with stellate microsclera*" (Lendenfeld, 1889b). Reid (1970) hypothesised that the common possession of asters in Axinellida (i.e., Hemiasterellidae), Astrophorida and Hadromerida formed a 'natural' taxon (Astrotetraxonida) having common ancestral stock. However, it is more likely that the concept of 'Axinellida' is polyphyletic and Hemiasterellidae belong to Hadromerida, with the implication that the characters compression of the axial skeleton and differentiated axial and extra-axial skeletons are homoplasious throughout the Demospongiae. Topsent (1928c) established Leptosastrinae for two of his own genera, *Leptosastra* Topsent, 1904b, and *Spirorhabdia* Topsent, 1918 (with type species *Spirastrella vidua* Schmidt, by monotypy), based on their common possession of ectosomal rhabds – smooth in the former and spined in the latter. The latter genus is now included in Crellidae whereas *Leptosastra*, and hence the subfamily name, belongs to Hemiasterellidae based on possession of euasters (but see below under Remarks for genus *Leptosastra*).

Differences with similar families

Hemiasterellids share their monactinal megascleres with the Hadromerida and for this reason they were formally transferred there by Voultsiadou-Koukoura & Van Soest (1991a). They differ from other hadromerids such as Polymastiidae and Spirastrellidae in having axially compressed choanosomal skeletons (sometimes loosely constructed or hymedesmoid, e.g., *Paratimea*, *Leptosastra*) and bouquets, tracts or single extra-axial spicules near the periphery, but they show similarities to *Aaptos* (Suberitidae) and *Tethya* (Tethyidae) in having predominantly style megascleres rather than tylostyles although some hemiasterellids retain long oxeas in the extra-axial skeleton. Hemiasterellidae can be further differentiated from Tethyidae in lacking an organic cortex and a substantially poorer diversity of euaster morphologies, and from *Jaspis* (Ancorinidae, Astrophorida), the latter having megascleres that are diactinal and confused in arrangement in the choanosomal skeleton, with a subectosomal tangential arrangement of megascleres supporting a crust of euasters. Voultsiadou-Koukoura & Van Soest (1991a) suggested further that similarities in euaster morphology between some *Jaspis* and some *Hemiasterella* may show in future that these genera are more closely related than presently acknowledged by their ordinal classification (see below).

Previous reviews

Hooper (1986), Voultsiadou-Koukoura & Van Soest (1991a).

KEY TO GENERA

(1) Axial skeleton poorly differentiated, plumo-reticulate skeleton ..... ***Hemiasterella***
Axial skeleton well developed, compressed reticulate 2
Axial skeleton lacking, but with a basal hymedesmioid skeleton 4
(2) Cortex poorly developed, with only a light crust of euasters (with smooth or spined rays, with oxeote, strongylote or tylote terminations) 3
Cortex well developed, with a thick crust of hexaradiate to cruciform euasters (anthasters) with thick heavily spined rays, confined mainly to the peripheral region ..... ***Axos***
(3) Microscleres euasters with thin strongylote or tylote rays, usually curved or sinuous, often branched, smooth or spined rays with small centrum ..... ***Adreus***
Microscleres short rayed oxyspheraster euasters with entirely smooth rays and thick centrum ..... ***Stelligera***
(4) Choanosomal megascleres tylostyles erect on substratum ..... ***Paratimea***
Choanosomal megascleres acanthostyles erect on substratum ..... ***Leptosastra***

ADREUS GRAY, 1867

Synonymy

Adreus Gray, 1867a: 545.

Type species

Dictyocylindrus fascicularis Bowerbank, 1866, 1874b (by monotypy).

Definition

Hemiasterellidae with strongly developed axial skeleton composed of long styles, poorly developed extra-axial skeleton composed of plumose brushes of smaller styles, and euasters with smooth or spined, thin strongylote or tylote sinuous rays which may be branched.

Diagnosis

Arborescent growth form; choanosomal skeleton with strongly compressed axis composed of long smooth tylostyles in bundles running longitudinally through branches, and poorly developed extra-axial skeleton composed of sparse plumose brushes of smaller smooth styles ascending to periphery; euasters with curved or sinuous, smooth or spined, strongylote or tylote rays often branched, mainly confined to the ectosomal region.

Description of type species

Adreus fascicularis (Bowerbank, 1866) (Fig. 1A–H).

Synonymy. *Dictyocylindrus fascicularis* Bowerbank, 1866: 110; 1874b: 45. *Adreus fascicularis*; Gray, 1867a: 545.

Material examined. Syntypes: BMNH 1910.1.38,39,43,44 (slides BMNH 1910.1.1.2461–2) – Vajon Bay, Guernsey.

Description. Thin, stiffly branched, arborescent growth form; axial skeleton strongly developed occupying majority of branch diameter, composed of bundles of long styles running longitudinally through branches; extra-axial skeleton more poorly developed with sparse plumose brushes of smaller styles, some vestigial or vermiform, ascending to ectosome but rarely protruding through surface; peripheral skeleton with light crust of euasters; fibres well developed and collagen abundant throughout mesohyl; megascleres styles of 2 sizes: larger axial styles long, thick, slightly curved at centre, evenly rounded smooth bases, tapering long points often telescoped (520–780 × 6–10 μm), smaller extra-axial styles ranging from straight to sinuous, with smooth rounded bases and sharp fusiform points (180–350 × 3–5 μm); euasters with thin strongylote or tylote rays, usually curved or sinuous, often branched, smooth or spined rays with small centrum (entire spicule 8–12 μm diameter).

Remarks. *Adreus* is arborescent with monactinal megascleres occurring in bundles, ascending towards the periphery and with apparent size differences between choanosomal and ectosomal megascleres (Topsent, 1928c). Euasters are not abundant, found mainly in the ectosomal region, but they are unusual in often having branching sinuous rays. Sexual reproduction with oviparous larvae has been reported by Brien (1973a). Voultsiadou-Koukoura & Van Soest (1991a) included only three species in the genus (*Dictyocylindrus fascicularis* Bowerbank, 1866 from the British Isles, *Vibulinus micraster* Burton, 1956 from W Africa and Mauritania, and *Timea stylifera* Arndt, 1927 from the Caribbean). The type species has usually been attributed by authors to the first volume of Bowerbank's monograph series (1864), whereas I could only find it mentioned in the second volume (1866) and figured in the third volume (1874b).

Distribution

East Atlantic, Caribbean.

AXOS GRAY, 1867

Synonymy

Axos Gray, 1867a. *Echinospongia* Gray, 1870a. Taxonomic decision for synonymy: de Laubenfels (1936a).

Type species

Axos cliftoni Gray, 1867a (by monotypy).

Definition

Hemiasterellidae with compressed axial skeleton and radial extra-axial skeleton composed of a single category of smooth styles; hexaradiate and cruciform euasters (anthasters) with thick heavily spined rays form a thick surface crust.

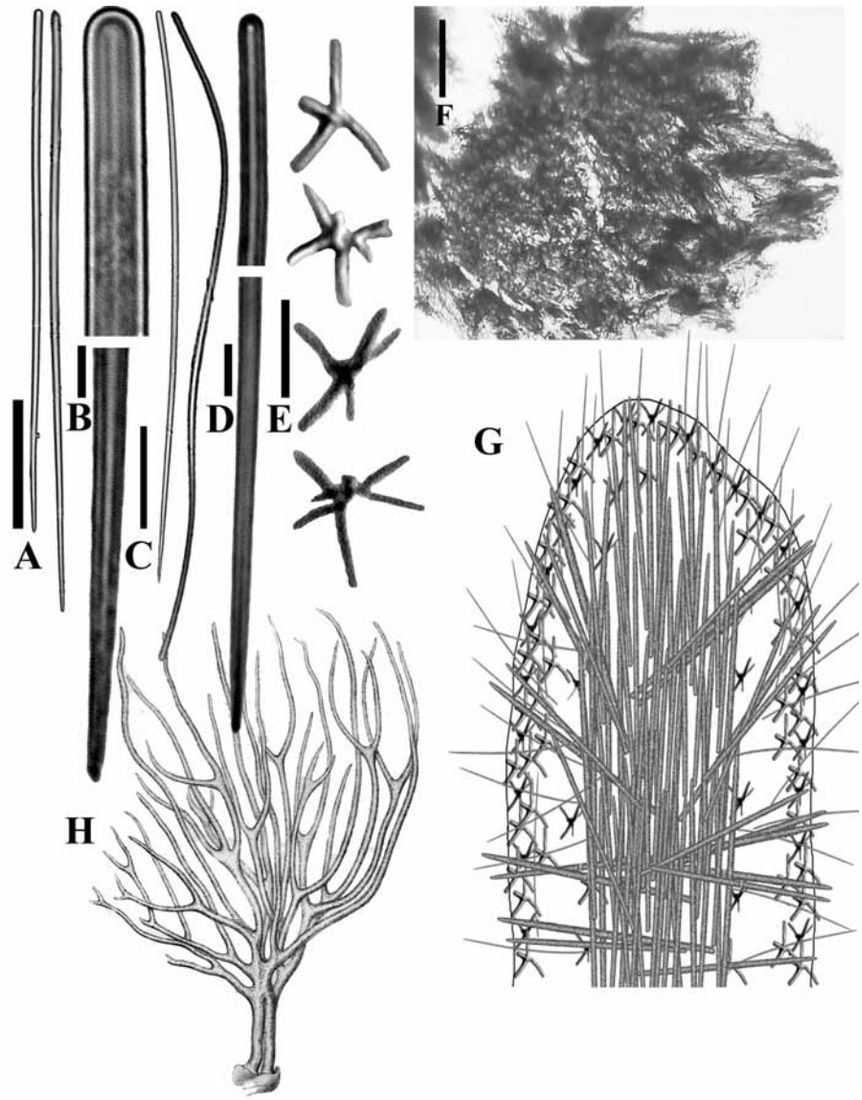

Fig. 1. *Adreus fascicularis* (Bowerbank) (syntypes). A, choanosomal styles (scale 150 μm). B, choanosomal style base and point (scale 10 μm). C, ectosomal styles (scale 50 μm). D, ectosomal style base and point (scale 10 μm). E, euasters (scale 10 μm). F, section through branch (scale 250 μm). G, reconstruction of idealised skeletal structure. H, specimen figured by Bowerbank, 1874b (from his plate 18, fig. 1).

Diagnosis

Cylindrical branching and flabelliform growth forms with prominent surface conules; well developed compressed axial skeleton composed of styles; extra-axial skeleton composed of radial spicule tracts of the same styles perpendicular to the axis and protruding into surface conules; asters hexaradiate to cruciform with thick heavily spined rays (anthasters), confined mainly to the peripheral region forming a thick crust.

Description of type species

Axos cliftoni Gray, 1867a (Fig. 2A–G).

Synonymy. Unidentified sponge – Bowerbank, 1864: 260. *Axos cliftoni* Gray, 1867a: 546 (Not *Axos cliftoni*; Carter, 1879d: 284); *Dictyocylindrus dentatus* Bowerbank, 1873b: 321; *Echinospongia australis* Gray, 1870a: 272.

Material examined. Holotype: BMNH 1870.8.26.31 – NW Australia.

Description. Dichotomously branching, thickly cylindrical, whip-like, rubbery, flexible growth form with stipitate, rhizomous basal attachment, and prominent surface conules; ectosomal skeleton detachable with heavy cortex of euasters pierced at regular intervals by tracts of extra-axial styles forming light, continuous palisade; choanosomal axial skeleton massive, heavily compressed, irregular in cross-section (corresponding to distribution of surface conules), consisting of tight bundles of styles packed together running longitudinally through branches; extra-axial skeleton plumose, non-anastomosing, composed of styles radiating from axis to surface conules, with scattered euasters becoming more dense towards the periphery; megascleres consist of a single category of smooth fusiform styles (178–912 × 1.5–22 μm); microscleres hexaradiate or cruciform euasters with spined rays (anthasters) (8–37 μm).

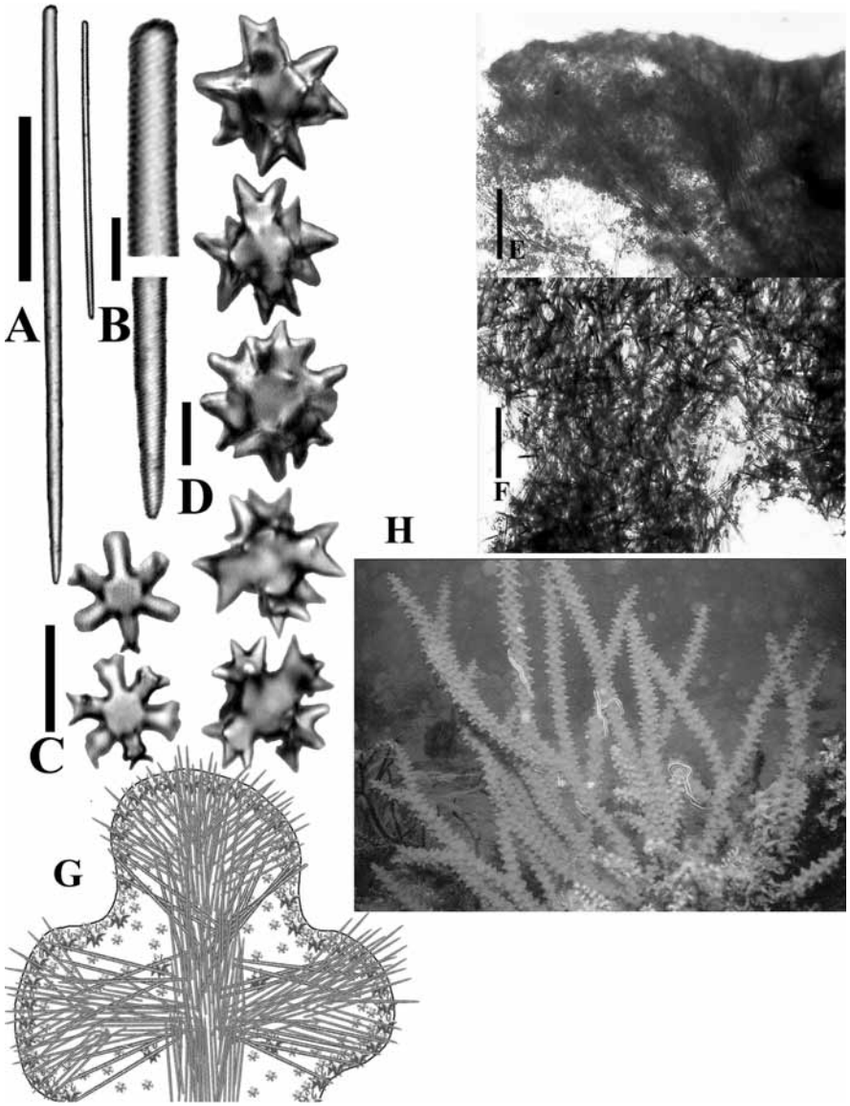

Fig. 2. *Axos cliftoni* Gray (holotype). A, styles (scale 100 μm). B. style base and point (scale 10 μm). C, smaller euasters (scale 10 μm). D, larger euasters (scale 10 μm). E, peripheral skeleton (scale 250 μm). F, axial skeleton (scale 250 μm). G, reconstruction of idealised skeletal structure. H, specimen of *A. flabelliformis in situ* (photo the author).

Remarks. *Axos* was established for *A. cliftoni*, named from a single spicule depicted by Bowerbank (1864). De Laubenfels (1936a) suggested that *Axos* and *Adreus* were closely related, with similar growth form and spiculation, with only euaster morphology (branching rays) and a greater proportion of styles than oxeas in *Axos* differentiating the two genera. This observation is erroneous, whereby *Axos* has only monactinal megascleres (styles) and euasters have spined (not branching) rays (in fact euasters of *Adreus* are characterised by possession of sinuous branching rays, not those of *Axos* as supposed by de Laubenfels, 1936a). Only two species of *Axos* are known, endemic to northern Australia. Burton (1934a) synonymised both species, presumably based on their nearly identical gross morphology, but Hooper (1986) showed that they differed substantially in their euaster morphology, both of which are classed as 'anthasters' as defined by Wiedenmayer (1994), for euasters with forked rays. De Laubenfels (1936a) also suggested that *Echinospongia* Gray (type species *E. australis* Gray, 1870a (by monotypy)) was synonymous with *Axos*, although the holotype is unknown and this cannot be corroborated.

Distribution

Endemic to northern Australia: WA, NT and Far N Qld.

HEMIASTERELLA CARTER, 1879

Synonymy

Hemiasterella Carter, 1879d. *Epallax* Sollas, 1888. *Kalastrella* Kirkpatrick, 1903b. *Tylaspis* Lévi & Lévi, 1983b. Taxonomic decision for synonymy: Voultsiadou-Koukoura & Van Soest (1991a) and present work.

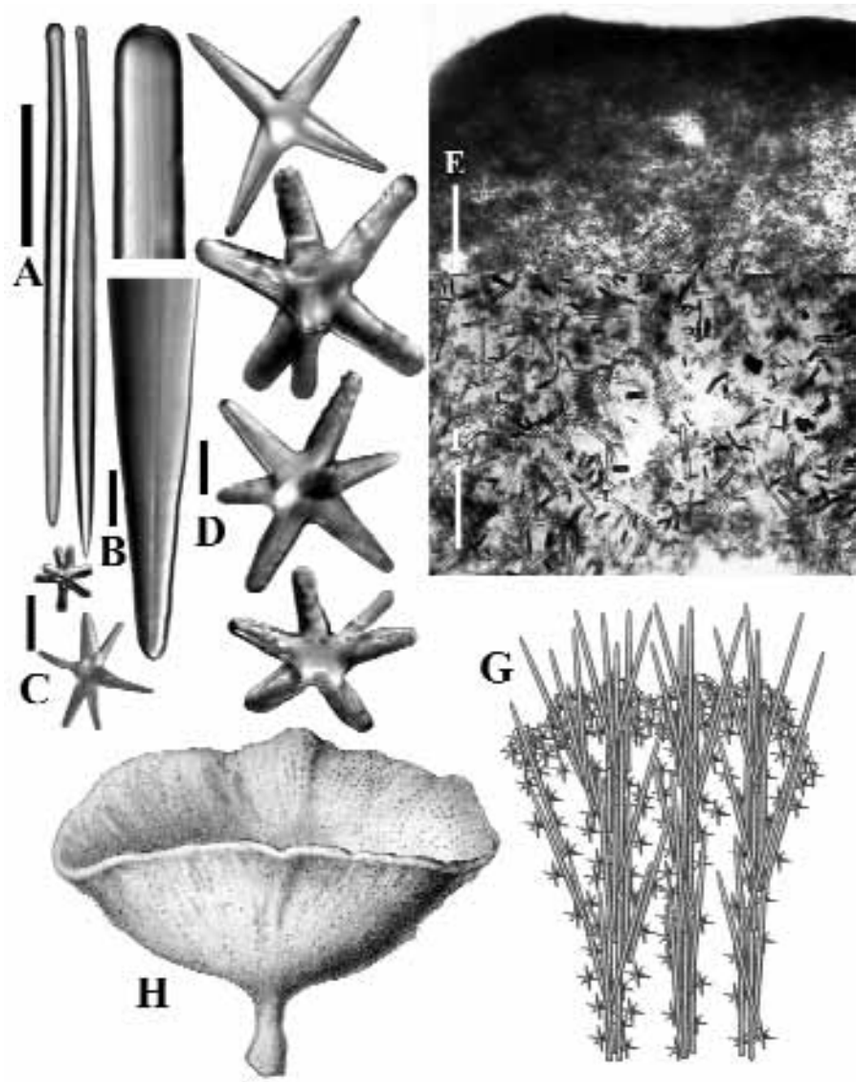

Fig. 3. *Hemiasterella typus* Carter (holotype). A, styles (scale 250 μm). B, style base and point (scale 10 μm). C, small euasters (scale 10 μm). D, large euasters (scale 10 μm). E, peripheral skeleton (scale 250). F, axial skeleton (scale 250 μm). G, reconstruction of idealised skeletal structure. H, *Hemiasterella (Epallax) callocyathus* Sollas, 1888 (from his plate 10, fig. 1).

Type species

Hemiasterella typus Carter, 1879d (by original designation).

Definition

Hemiasterellidae with vasiform, cup-shaped or massive growth forms lacking axial condensation, with plumo-reticulate choanosomal skeleton; euaster with thick acanthose strongylote rays, sometimes calthrops-like.

Diagnosis

Exclusively vasiform, plate-like, flattened branching or massive growth forms; choanosomal and peripheral skeletons are loosely arranged more-or-less plumo-reticulate, without apparent axial compression or differentiation between axial and extra-axial regions, composed of styles and/or oxeas without functional arrangement to any particular part of skeleton; ectosomal euasters typically with thick, acanthose, strongylote rays, sometimes calthrops-like (rays reduced to 2–4, curved, asymmetrical or branching rays), predominant in peripheral region but not forming a surface crust.

Description of type species

Hemiasterella typus Carter, 1879d (Fig. 3A–G).

Synonymy. *Hemiasterella typus* Carter, 1879d: 146.

Material examined. Holotype: BMNH unknown. Other Material. BMNH 1936.3.4.406, slide BMNH 1936.3.4.406a – 'John Murray' Expedition.

Description. Thinly flabellate, convoluted margins, short stalk, firm texture; ectosomal skeleton with thick cortex composed of euasters, not detachable, with few thick styles protruding a short

distance through surface; extra-axial skeleton not well developed with few radial megascleres embedded near periphery or forming sparse radial tracts ascending from axis; extra-axial region packed with euasters; axial region loosely reticulate, slightly compressed tracts of megascleres without obvious fibre component; megascleres long, thick, straight or slightly curved, fusiform styles, sometimes subtylostyles, usually with rounded bases and sharp points, sometimes points slightly telescoped (550–1450 × 22–35 μm); microscleres euasters of more than one variety, most commonly with thick, acanthose, strongylote, terminally microspined rays (25–60 μm diameter), smaller euasters with terminal subtylote swellings usually microspined (12–20 μm diameter), and less commonly oxyasters with small centrum and pointed, smooth rays (8–20 μm diameter).

Remarks. *Hemiasterella typus* has exclusively stylote megascleres, whereas the genus currently contains a diverse group of species in which megascleres include monactinal, diactinal spicules, or a combination of both. The architecture is commonly more-or-less plumo-reticulate, and growth form is exclusively vasiform or cup-shaped (Topsent, 1919; Dendy, 1922b). Species, like the type species with monactinal megascleres, have apparent affinities with *Axos* and *Timea* (Timeidae, Hadromerida), whereas other species with only oxeas (e.g., *H. affinis* Carter, 1879d), or both oxeas and styles (e.g., *H. complicata* Topsent, 1919) show superficial similarities to *Jaspis* (Coppatiidae, Astrophorida). For this reason the higher taxonomic placement of *Hemiasterella*, and hence Hemiasterellidae, is still equivocal (e.g., Bergquist, 1968; Wiedenmayer, 1977b; Hooper, 1986; Voultsiadou-Koukoura & Van Soest, 1991a).

Epallax and *Kalastrella* are clearly synonyms of *Hemiasterella. Epallax* (type species *E. callocyathus* Sollas, 1888 (by monotypy) schizotypes BMNH 1894.11.16.480–3) (Fig. 3H) is vasiform, has diactinal megascleres occassionally modified to quasi-monactinal styles or tylostyles, and an architecture consisting of longitudinal bundles of megascleres in a more-or-less radial plumose arrangement. The type species has, in addition to simple oxyasters common to other hemiasterellids, branching calthrops-like asters for which Sollas (1888) inferred parallels with the genus *Thenea* Gray (Theneidae, Astrophorida). *Kalastrella* (type species *K. vasiformis* Kirkpatrick, 1903b (by monotypy) schizotype BMNH 1902.11.16.6) is vasiform, has both monactinal and diactinal/quasi-diactinal megascleres, and microspined rays on euasters. Skeletal architecture is more-or-less compressed with interconnected lacunae which bear extra-axial small bundles of oxeas and styles projecting at right angles to the ectosome (Kirkpatrick, 1903b), and it too was merged with *Hemiasterella* by Topsent (1919) and Dendy (1921), most closely related to *H. complicata* Topsent.

Tylaspis (type species *Tylaspis topsenti* Lévi & Lévi, 1983b (by original designation), holotype MNHNDCL2920 (not seen)), is less confidently included into synonymy with *Hemiasterella* given that it has an amorphous massive growth form (unlike the well-defined vasiform, plate-like or branching growth forms of most of the described species), and on this basis there may be some justification for recognising it as a distinct genus. However, it shares with these 'typical' *Hemiasterella* species the lack of any axial condensation of the choanosomal skeleton, unlike other hemiasterellids, and moreover *Hemiasterella* species do commonly demonstrate intraspecific variability in growth forms. Lévi & Lévi (1983b) suggested *T. topsenti* had closest affinities to *Jaspis*-like taxa (now in Ancorinidae) and Topsent's (1928c) concept of *Halicnemia*, now dispersed amongst the hemiasterellids including *Stelligera* (see chapter on Desmoxyidae), but *Tylaspis* appears to be most closely related to *Hemiasterella* to which it is here assigned.

De Laubenfels (1936a) included several species of *Hemiasterella* in the Coppatiidae (Astrophorida), although Wiedenmayer (1977b) suggested that skeletal architecture is quite different between these groups. Nevertheless, there are several species of *Jaspis* without obvious radial architecture and with modified oxeote megascleres (strongyles, strongyloxeas and quasi-monactinal spicules) which may indeed belong to the Hemiasterellidae (e.g., *Coppatias carteri* (Ridley, 1884a)) (Hooper, 1986).

Voultsiadou-Koukoura & Van Soest (1991a) included 10 species in the genus (*H. typus* Carter, 1879d from Australia, *H. affinis* Carter, 1879d from unknown locality, *H. callocyathus* (Sollas, 1888) from Northern Australia and PNG, *H. vasiformis* (Kirkpatrick, 1903b) from SE Africa, *H. complicata* Topsent, 1919 from Madagascar and Indonesia, *H. intermedia* Dendy, 1922b from W. Indian Ocean and Indonesia, *H. elongata* Topsent, 1928c from Morocco and Cape Verde Is, *H. digitata* Burton, 1929a from Antarctica, *H. strongylophora* Lévi, 1956c from Madagascar, and *H. aristoteliana* Voultsiadou-Koukoura & Van Soest (1991a) from the Aegean Sea). The inclusion of *Tylaspis topsenti* Lévi & Lévi, 1983b, from deeper waters off New Caledonia into synonymy with *Hemiasterella* brings the total number of described species to 11.

Distribution

Indian and West Pacific Ocean, Antarctica, E Atlantic, E Mediterranean.

PARATIMEA HALLMANN, 1917

Synonymy

Paratimea Hallmann, 1917c. *Halistella* Sarà, 1958.

Type species

Bubaris constellata Topsent, 1893c (by original designation).

Definition

Hemiasterellidae lacking an axially compressed skeleton, having instead a (sub-)hymedesmioid choanosomal skeleton with long tylostyles erect on the substratum, and bundles of smaller centrotylote tornotes or oxeas in both the peripheral and choanosomal skeletons; microscleres are smaller thick-centred euasters and larger short-rayed oxyspherasters.

Diagnosis

Hemiasterellidae with thickly encrusting growth form and essentially hymedesmioid skeleton arrangement composed of erect choanosomal tylostyles and paratangential tracts of centrotylote ectosomal tornotes, the latter also scattered throughout the skeleton in dragmata. Microscleres are oxyasters without a prominent centrum and oxyaster euasters with slightly swollen centrum.

Description of type species

Paratimea constellata (Topsent, 1893c) (Fig. 4A–H).

Synonymy. *Bubaris constellata* Topsent, 1893c: 33; *Paratimea constellata*; Hallmann, 1917c: 675.

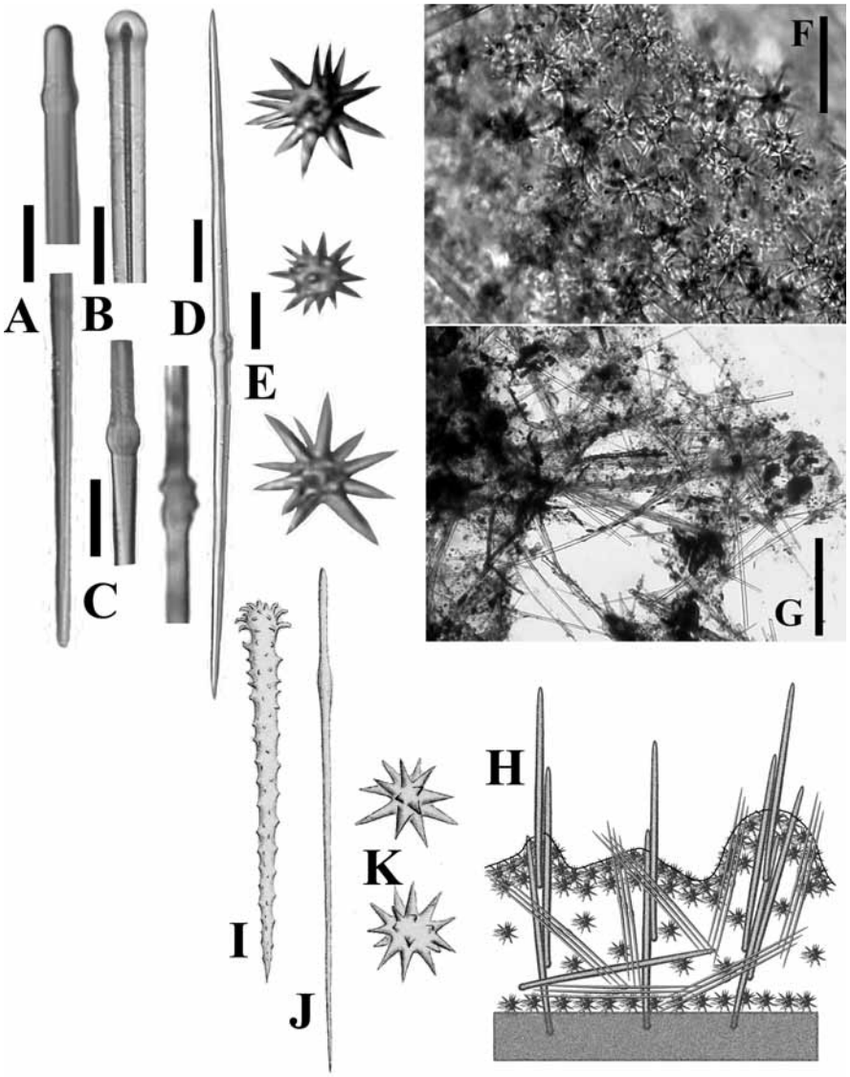

Fig. 4. A–H, *Paratimea constellata* (Topsent) (Mauritania specimen). A, tylostyle base and point (scale 50 μm). B, tylostyle base (scale 50 μm). C, centrotylote tornote centra (scale 50 μm). D, centrotylote tornote (scale 100 μm). E, oxyaster euasters (scale 10 μm). F, ectosomal crust of oxyasters (scale 40 μm). G, peripheral skeleton (scale 250 μm). H, reconstruction of idealised skeletal structure. I–K, *Leptosastra constellata* Topsent (reproduced from Topsent, 1904b, pl. 15, fig. 15). I, choanosomal acanthostyle. J, ectosomal 'rhabd'. K, oxyspheraster euasters (for sizes refer to the text).

Material examined. Holotype: MOM (not seen). Other material. ZMA POR7348 – Maio I., Cape Verde Is., coll. R.W.M. Van Soest, 40 m depth, dredge, 27.viii.86. ZMA POR15292 – Mauritania, dredge.

Description. Thinly encrusting, conulose and highly hispid surface; ectosomal skeleton with long choanosomal tylostyles protruding more than 1 mm through the surface, often in bundles, occasionally singly, and long tornotes in bundles perpendicular, paratangential or occasionally tangential to the surface; choanosomal skeleton with erect, paratangential or tangential bundles of centrotylote tornotes scattered throughout the skeleton forming irregular criss-crossing tracts; single or sparse bundles of tylostyles are erect or paratangential to the substrate, forming an essentially hymedesmioid skeleton (although this is difficult to observe in either available material or published descriptions); the mesohyl is abundantly invested with collagen throughout; asters are scattered throughout the skeleton although most dense in both peripheral and basal parts of the skeleton. Megascleres consist of choanosomal tylostyles, very long and relatively robust, with swollen terminal or subtylote basal swellings ('trilobate' heads according to Topsent), and long tapering sharp points (greater than 1 mm–3.5 mm × 12–18 μm); tornotes with centrotylote swellings, variable in morphology (i.e., multiple tylotes), straight or slightly bent at centre, occasionally sinuous and in curved dragmata within the skeleton, with more-or-less symmetrical, sharply-pointed ends (750–1100 × 6–11 μm). Microscleres are oxyasters without a prominent centrum (18–25 μm diameter), and oxyaster euasters with slightly swollen centrum (14–19 μm diameter), both with numerous sharply pointed rays.

Remarks. The original description of *B. constellata* was only very brief and lacked illustrations, whereas Topsent (1897b: 245) redescribed this material in more detail and also provided (rudimentary) spicule drawings. He again mentioned the species based on new material (Topsent, 1928c: 181), but added little to the original description, whereas the present material (based on collections of R.W.M. Van Soest from two disparate localities: Cape Verde Islands and Mauritania), represents the first record of the

species from outside the Mediterranean, and subsequent to Topsent's original records. This present material shows some variability from the holotype having slightly larger asters with a more prominent centrum (Mauritania specimen), and a reduced number of megascleres (Cape Verde Islands specimen). Nevertheless, megasclere morphology is consistent between all populations, and it is considered here that populations are conspecific. The redescription above, and the reconstruction of skeletal architecture (Fig. 4H) is based on both this new material and Topsent's (1897b) extensive redescription of the holotype given that the ZMA material lacks some detail due to its thinly encrusting nature.

Paratimea differs from most other hemiasterellids in lacking an axially compressed skeleton, having instead a subhymedesmioid basal skeleton (with predominantly paratangential spicule tracts, and only few true erect spicules on the substrate), and in this respect is most similar to, and potentially congeneric with, *Leptosastra* (coincidentally with the same type species name although both clearly different taxa). The two genera are retained separately for the time being given substantially different geometries of their respective choanosomal megascleres: tylostyles versus acanthostyles (see *Leptosastra*).

Hallmann (1917c) suggested that *P. constellata* was similar to *Halicnemia* in possessing tylostyles and centrotylote diactinal spicules forming the ectosomal skeleton, and were it not for the presence of these ectosomal spicules he would have assigned the taxon to *Timea* (Timeidae). He tentatively included it in the Spirastrellidae. Hooper (1986) suggested that it might be an encrusting form of *Stelligera*, as judged from its relatively poor published description, given that their respective type species were superficially similar in aster morphology, whereas Voultsiadou-Koukoura & Van Soest (1991a) indicated that it may be a valid taxon. These latter authors assigned five species to the genus: *Bubaris constellata* Topsent (from the Mediterranean (plus the two new locality records noted here)), *P. galaxea* de Laubenfels (1936a) (from Florida), *Halicnemia duplex* (Topsent, 1927b) (from Morocco), *P. pierantonii* Sarà, 1958 and *P. oxeata* Pulitzer-Finali, 1977 (both from Naples). To this list should be added *Halistella pierantonii* Sarà, 1958, the type species of the genus *Halistella*, which is clearly also a *Paratimea*.

The higher taxonomic placement of *Paratimea* has been in question for some time. Hallmann (1917c) proposed to combine the aster-bearing axinellids, including *Halicnemia* Bowerbank, *Laonoenia* Hallmann and *Paratimea* Hallmann (all possessing choanosomal tylostyles and ectosomal centrotylote oxeas) within the Desmoxyidae (which are otherwise defined by their acanthose microxeote ectosomal spicules). Topsent (1928c) rejected this system, as well as Hallmann's genera (including *Paratimea*), retaining these taxa within a single genus (*Halicnemia*). However, in the strict sense *Halicnemia* (viz., *H. patera* Bowerbank, *H. gallica* (Topsent) and *H. geniculata* Sarà) has tylostyles, ectosomal oxeas (often polytylote), and acanthose microxeas (Bowerbank, 1864, 1866; Topsent, 1897b; Descatoire, 1966), and clearly belongs with the Desmoxyidae (Lévi, 1973), closely related to *Higginsia*. By comparison, *Halicnemia sensu* Hallmann is polyphyletic, with one group belonging to the Astrophorida, and a second group (viz., *Paratimea* s.s., and including *H. duplex* Topsent, *H. constellata* (Topsent), and *Paratimea galaxea* de Laubenfels) having euasters, centrotylote oxeas and choanosomal tylotes, belonging to the Hemiasterellidae.

Distribution

Mediterranean, NE and central E Atlantic, Caribbean.

LEPTOSASTRA TOPSENT, 1904

Synonymy

Leptosastra Topsent, 1904b: 194; 1928c: 56; de Laubenfels, 1936a: 111.

Type species

Leptosastra constellata Topsent, 1904b (by monotypy).

Definition

Hemiasterellidae lacking an axially compressed skeleton, having instead a hymedesmioid choanosomal skeleton composed of erect acanthostyles, with smooth, very thin subtylote or centrotylote monactinal (or diactinal) 'rhabds' (tornotes), and an ectosomal cortex of oxyspheraster euasters.

Diagnosis

Very thinly encrusting plaque; ectosomal skeleton with a dense crust of spheraster euasters and reinforced with sparse bundles of very thin monactinal (or occasionally diactinal) 'rhabds' (tornotes) below this crust; choanosomal skeleton hymedesmioid with acanthostyles embedded in basal spongin and erect on the substratum.

Description of type species

Leptosastra constellata Topsent, 1904b (Fig. 4I-K).

Synonymy. *Leptosastra constellata* Topsent, 1904b: 194–195, pl. 15, fig. 15; Stephens, 1921: 63.

Material examined. None – Azores.

Description (from Topsent, 1904b). Thinly encrusting forming an extensive plaque, colour white, smooth surface; choanosomal skeleton composed of acanthostyles erect on (echinating) the substratum, with their bases embedded in basal spongin and points supporting the ectosomal skeleton; subectosomal and ectosomal regions reinforced with tornotes (described as 'rhabds'); ectosome with a thick crust of euasters confined entirely to the outer surface, through which sparse bundles of tornotes occasionally protrude. Choanosomal acanthostyles heavily and evenly spined, in a single size class, with straight shaft, swollen tyle and sharply pointed (80–100 × 7 μm). Ectosomal and subectosomal 'rhabds' occur in restricted numbers, embedded in small groups in the mass of euasters, having a straight smooth shaft, asymmetrical ends (defined as either monactinal or diactinal, although only the former are figured by Topsent), and a subtylote swelling closer to the basal end than to the point of the spicule, occasionally polytylote (135 × 2 μm). Euasters are spherasters with numerous conical, pointed actines and a thick centrum (20–23 μm diameter).

Remarks. *Leptosastra* is monotypic. Despite having type species with identical names *Leptosastra* and *Paratimea* are clearly not identical, differing substantially in the geometry of their principal (choanosomal) structural megascleres – acanthostyles and tylostyles, respectively. Whether these differences can sustain these genera separately remains uncertain, but re-examination of the holotype of the former is essential to such a decision (presumably located in the MOM, but not confirmed). Nevertheless, the current decision to not amalgamate both genera is supported by the nature (and possibly origin) of the subectosomal/ ectosomal megascleres, which are defined as 'rhabds' and tornotes, respectively. Both can be potentially defined

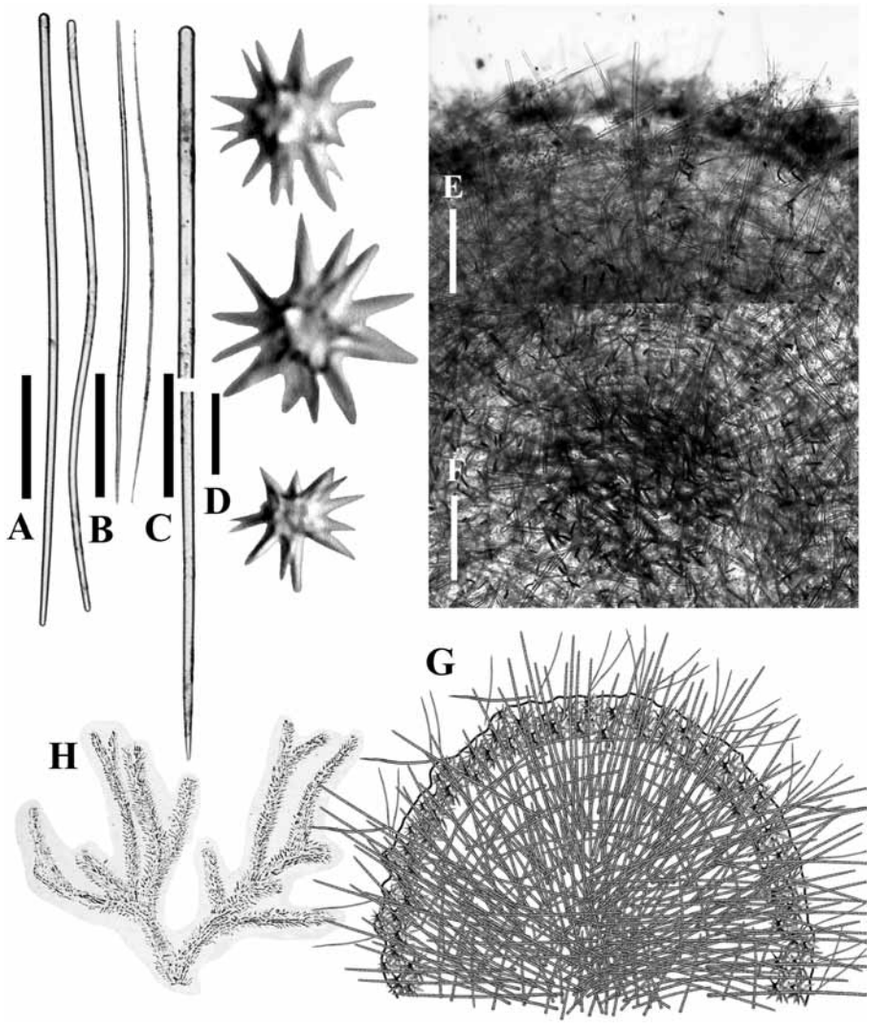

Fig. 5. A–G, *Stelligera stuposa* (Montagu) (schizotype). A, choanosomal styles (scale 150 μm). B, ectosomal styles (scale 150 μm). C, extra-axial styles (scale 150 μm). D, euasters (scale 10 μm). E, peripheral skeleton (scale 250 μm). F, axial skeleton (scale 250 μm). G, reconstruction of idealised skeletal structure. H, *Spongia stuposa* Montagu, 1818 (from his plate 3, fig. 1).

as tornotes, whereas those of *Leptosastra* are significantly thinner and shorter than those of *Paratimea* that they may indeed be microscleres, and hence warranting description as 'rhabds' by Topsent (1904b). The type species of *Leptosastra* was initially allocated close to the hymedesmiids, such as *Leptosia*, based on its possession of a hymedesmioid skeleton composed of acanthostyles, with geometry resembling echinating acanthostyles found in many poecilosclerid families. However, Topsent (1940b) reported that the species had euasters forming a distinct, thick cortex. If this is true then it negates any such phylogenetic interpretation, with the genus more appropriately allocated to the present concept of Hemiasterellidae. It is possible, but not yet proven, that *L. constellata* belongs to Hymedesmiidae, with its reported euasters potentially representing modified acanthostyles (as suggested by Dendy, 1922b) or chelae (with potential affinities to *Spirorhabdia* or *Acanthancora*). Correct allocation of this genus requires re-examination of the presently elusive holotype.'

Distribution

Known only from the North Atlantic.

STELLIGERA GRAY, 1867

Synonymy

Stelligera Gray, 1867a. *Vibulinus* Gray, 1867a. Taxonomic decision for synonymy: Voultsiadou-Koukoura & Van Soest (1991a).

Type species

Raspailia stelligera Schmidt, 1862 (by original designation) (junior synonym of *Spongia stuposa* Montagu, 1818; Voultsiadou-Koukoura & Van Soest, 1991a).

Definition

Hemiasterellidae with several distinct structural regions: a slightly compressed axial skeleton of longer styles and oxeas; a reticulate extra-axial skeleton of smaller styles and/or oxeas; longer extra-axial styles radiating from the axis to periphery; and

an ectosomal skeleton of small styles surrounding the longer projecting extra-axial styles; microscleres are short-rayed oxyspheraster euasters with a thick centrum and forming a thin ectosomal crust.

Diagnosis

Thinly branching growth form and prominently hispid surface; choanosomal skeleton composed of long styles and oxeas forming a slightly compressed axis; extra-axial skeleton with radial and reticulate components, the former composed of long projecting styles perpendicular to axis, the latter consisting of shorter styles/oxeas forming an irregular reticulation; ectosomal skeleton composed of brushes of small styles surrounding protruding extra-axial styles (analogous to the Raspailiidae ectosomal condition), and also with a thin ectosomal crust of thick-centred, short-rayed oxyspheraster euasters.

Description of type species

Stelligera stuposa (montagu, 1818) (Fig. 5A–H).

Synonymy. *Raspailia stelligera* Schmidt, 1862: 60; *Spongia stuposa* Montagu, 1818: 79.

Material examined. Holotype: SM not seen, schizotype MNHN DCL1239L – Quarnero, Adriatic. Other material. Schizotypes of *S. stuposa*: BMNH 1910.1.1.2463–5 – British Isles.

Description. Thinly cylindrical, dichotomously branching growth form with prominently hispid surface; ectosomal skeleton with thin crust of euasters, through which protrude long extra-axial styles surrounded by bouquets of thin ectosomal styles tangential to the surface; megascleres protrude up to 400 μm from surface, producing hispid surface; choanosomal skeleton with slightly compressed axis composed of thinner styles and oxeas, and with extra-axial skeleton divided into two components, one composed of shorter axial styles/oxeas forming irregular reticulation throughout mesohyl, the other composed of longer extra-axial styles radiating from axis to periphery; megascleres are long, thick, straight or slightly curved styles of the extra-axial skeleton, with rounded or slightly telescoped points and evenly rounded bases (1200–2850×15–25 μm), shorter, thick styles, stongylote styles, or sometimes oxeas, slightly curved, with rounded bases and strongylote or fusiform points (550–950 × 8–13 μm), ectosomal megascleres are short, thin styles or anisoxeas, curved, often sinuous, occasionally rhaphidiform (380–720 × 3–8 μm); microscleres short-rayed oxyspheraster euasters with entirely smooth rays and thick centrum (8–22 μm).

Remarks. *Stelligera* is arborescent to lobodigitate, occasionally slightly flabelliform, and has both oxeas and styles (or tylostyles) as megascleres and smooth euasters as microscleres. Re-examination of type material supports the proposal by Voultsiadou-Koukoura & Van Soest (1991a) that *S. stelligera* and *S. stuposa* are synonyms (possibly together with *S. rigida* (Montagu, 1818) from the British Isles and *S. nux* Lendenfeld, 1897a from the Mediterranean, although these types have not yet been redescribed), making *Vibulinus* (with type species *Spongia stuposa* Montagu, 1818 (by monotypy) schizotypes BMNH 1910.1.1.2463–4) an objective synonym of *Stelligera*. This leaves only two valid species in the genus (the type species from the British Isles, Mediterranean and Adriatic, and *S. columnata* Lévi, 1959 from W Africa).

Distribution

East Atlantic, Mediterranean.