Systema Porifera: A Guide to the Classification of Sponges, Edited by John N.A. Hooper and Rob W.M. Van Soest

Family Hymedesmiidae Topsent, 1928

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Hymedesmiidae Topsent (Demospongiae, Poecilosclerida) is revised substantially to form a new concept within Myxillina for sponges with hymedesmioid or plumose skeletal arrangement in combination with the possession of arcuate chelae and smooth diactinal ectosomal megascleres. The formerly employed family Anchinoidae is here merged with a former concept of Hymedesmiidae, because no clear line can be drawn between the hymedesmioid and the anchinoid skeletal architecture. The family is close to Crellidae, sharing hymedesmioid and/or plumose skeletal arrangement and the possession of areolated porefields, but differs in lacking the surface specialization of tangentially arranged acanthoxeas and -styles. Ten genera and two subgenera, of 34 nominal genera, are considered valid. The species described as *Lissopocillon dendyi* Ferrer-Hernandez, 1916 is assigned to *Phorbas* and because the combination *Phorbas dendyi* is already occupied by *P. dendyi* (Topsent, 1913) a new name *Phorbas ferrerhernandezi* n. sp. is here proposed.
Keywords: Porifera; Demospongiae; Poecilosclerida; Myxillina; Hymedesmiidae; *Acanthancora*; *Hamigera*; *Hemimycale*; *Hymedesmia*; *Hymedesmia (Hymedesmia)*; *Hymedesmia (Stylopus)*; *Kirkpatrickia*; *Myxodoryx*; *Phorbas*; *Plocamionida*; *Pseudohalichondria*; *Spanioplon*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Hymedesmiidae Topsent, 1928c: 54. Anchinoidae Topsent, 1928c: 57. Phorbasidae de Laubenfels, 1936a: 62.

Definition

Myxillina with smooth ectosomal tornotes (basically diactinal, but may be anisotornotes or styles), a peripheral choanosomal plumose skeleton of bundles of smooth tornotes, a basal skeleton of acanthostyles, singly or in plumose bundles (may be absent), echinating acanthostyles (may be absent). Additional non-echinating acanthostyles or acanthoxeas may occasionally be present. Microscleres include arcuate chelas and sigmas, but may be absent.

Diagnosis

Encrusting, massive and branching sponges; surface with characteristic groups of pores (areoles) (shared with Crellidae). Megascleres smooth diactinal spicules (oxeote, tylote or strongylote, occasionally stylote tornotes), grouped together or scattered in the ectosome, but never forming a crust, lying perpendicular, tangential, or paratangential to the surface, and acanthostyles, which may typically occur in a larger size class, which is often partly smooth in the pointed half, and a smaller size, which is usually entirely spined. Diactinal spicules forming thinner or thicker plumose or plumo-reticulate tracts or columns in the choanosome, with only a thin coat of spongin, or without optically visible spongin. Columns usually consist of spicules identical to those in the ectosome, but sometimes these are replaced by acanthostyles. They may or may not be echinated by 1–2 sizes of acanthostyles. At the base of the sponge there is usually a spongin plate closely adhering the substrate and echinated by single acanthostyles or groups or bundles of acanthostyles. Microscleres may include arcuate isochelae and sigmas.

Scope

Thirty four nominal genera of which ten genera and two subgenera are considered valid. *Acanthancora, Hemimycale, Hamigera, Hymedesmia, Hymedesmia (Hymedesmia), Hymedesmia (Stylopus), Kirkpatrickia, Myxodoryx, Phorbas, Plocamionida, Pseudohalichondria, Spanioplon*.

History and biology

This family unites the former families Anchinoidae and Hymedesmiidae *sensu* Topsent, 1928c: 54 (excepting those genera with anchorate or palmate chelae, or with forceps), because no clear line can be drawn between the hymedesmioid and the anchinoid skeletal architecture. Hymedesmioid architecture grades into plumose architecture by strengthening and elongation of the subdermal tornote bundles. In fact the hymedesmioid architecture occurs in many, often unrelated, families (Raspailiidae, Microcionidae, Crambeidae, Crellidae), and thus using it to unite an arbitrary group of sponges with arcuate chelae appears not justified. It is proposed to abandon hymedesmioid architecture as a family character (it may dubiously be retained as a genus character).

Taxonomic remarks

Microscleres. These are the usual arcuate chelae and sigmas, either one or both of which may be absent. In some genera interesting modifications of the arcuate isochelae occur. Bipocilli-like microscleres were reported from a genus *Lissopocillon*, but these are merely malformed arcuate chelas and the genus is considered a junior synonym of *Phorbas*. Somewhat similar chelae were reported in a genus *Bipocillopsis*, but they are also obviously reduced chelae, and the genus is a junior synonym of *Hymedesmia*. True bipocilli are a synapomorphy for the genus *Iophon* (suborder Microcionina, family Acarnidae). Chiasto sigmas occur occasionally.

Genera excluded. A number of genera, which have traditionally been assigned to Hymedesmiidae based on their hymedesmioid

architecture, are here referred to other families on account of the characters of their microscleres. *Holorodesmia* Topsent, 1928c (type *Hymedesmia flaccida* Topsent, 1927b) is a *Clathria* (*Microciona*) (type slide examined in MNHN). *Hymedesanisochela* a Bakus, 1966b (type *H. rayae* Bakus, 1966b) is an Acarnidae, probably *Iophon* but it lacks bipocillae (paratype specimen examined in BMNH). *Quindesmia* de Laubenfels, 1936a (type *Hymedesmia inflata* Bowerbank, 1866) is a *Halicnemia*, as its type is a junior synonym of *H. patera*) (slide of type examined in BMNH). *Chiastosia* Topsent, 1928c (type *Myxilla pecqueryi* Topsent, 1892a) is a Myxillidae, genus *Hymenancora*. *Arndtanchora* de Laubenfels, 1936a (type *Leptosia sirventi* Topsent, 1927b) is a Myxillidae, genus *Hymenancora*. *Hymesigmia* Topsent, 1927b (type *H. japycina* Topsent, 1927b) is a Myxillidae, genus *Hymenancora*. *Lissomyxilla* Hanitsch, 1894a (type *Tethea spinosa* Bowerbank, 1874b) is a junior synonym of *Tethyspira* Topsent, 1890b (see de Laubenfels, 1936a), order Halichondrida, family Dictyonellidae. *Dendoricella* Lundbeck, 1905 (type *D. rhopalum* Lundbeck, 1905) is assigned to a separate family Dendoricellidae uniting plumose sponges with only oxeas and arcuate chelae. *Xytopsaga* Burton, 1932b (type *P. myxilloides* Burton, 1932b) is a junior synonym of genus *Fibulia*, family Dendoricellidae. *Fibulia* Carter, 1886c (type *F. carnosa* Carter, 1886c) goes to a separate family Dendoricellidae.

Sister family. The relationship with the family Crellidae is close, because of many shared features. The two families are kept apart because of the unique crellid ectosomal skeleton.

KEY TO GENERA

(1) Spicules exclusively smooth styles and strongyles, no microscleres or acanthose spicules ..... ***Hemimycale***
Microscleres and/or spined spicules present 2
(2) Microscleres are profusely ornamented chelae or derivates 3
Microscleres if present are smooth-shafted 4
(3) Skeleton structure hymedesmioid, i.e., with single acanthostyles erect on the substratum ..... ***Acanthancora***
Skeleton consistst of columns of tornotes without acanthostyles ..... ***Pseudohalichondria***
(4) All spicules smooth, spined spicules absent ..... ***Hamigera***
Lightly or more heavily spined spicules present 5
(5) Acanthostrongyles present forming a basal mass or reticulation ..... ***Plocamionida***
No acanthostrongyles or basal reticulation 6
(6) Skeleton hymedesmioid, i.e., with acanthostyles singly erect on the substratum ..... ***Hymedesmia***
Skeleton plumose or plumoreticulate, acanthostyles, if present, echinating the choanosomal tracts, incorporated in the skeletal columns or strewn in the interior, not singly erect on the substrate 7
(7) Accessory acanthose spicules (acanthostyles, acanthoxeas) present, strewn in the interior, not localized; choanosomal styles smooth or microspined ..... ***Spanioplon***
Acanthostyles localized in echinating position, or incorporated in the skeletal tracts 8
(8) Acanthostyles only in skeletal columns or tracts 9
Acanthostyles echinating the columns or tracts or strewn randomly 10
(9) A single category of acanthostyles ..... ***Phorbas***
Two distinct categories of acanthostyles ..... ***Myxodoryx***
(10) Acanthostyles in echinating position ..... ***Phorbas***
Acanthostyles in the columns and strewn in the interior, not echinating ..... ***Kirkpatrickia***

ACANTHANCORA TOPSENT, 1927

Synonymy

Acanthancora Topsent, 1927b: 12. *Hymenamphiastra* de Laubenfels, 1930: 27. *Ferrerhernandezia* de Laubenfels, 1936a: 87.

Type species

Leptosia schmidti Topsent, 1898b: 250 (by original designation).

Definition

Hymedesmiidae with modified spined-tuberculate chelae and hymedesmioid structure.

Diagnosis

Encrusting; ectosomal skeleton composed of smooth tornotes or anisotornotes, some with polytylote bases; choanosomal skeleton composed of acanthostyles erect on the substrate; microscleres are isochelae ornamented with smaller or larger spines, derived from arcuate isochelae; further microscleres may include chiastosigmas. Half a dozen species.

Previous reviews

Topsent, 1928c, Van Soest, 1984b.

Description of type species

Acanthancora schmidti (Topsent, 1898b) (Fig. 1A).

Synonymy. *Leptosia schmidti* Topsent, 1898b: 250, fig. 2b; Topsent, 1904b: 189, pl. XV fig. 9; *Acanthancora schmidti*; Topsent, 1927b: 12; Topsent, 1928c: 274.

Material examined. Holotype: MOM (not seen); MNHN DT961 – slide labeled 'PA 1897, 48' made from holotype.

Description (based on Topsent, 1898b, 1904b). Thinly encrusting, smooth, irregular. Colour white. Skeleton hymedesmioid, acanthostyles are arranged in bouquets with heads embedded in the spongin adhering the substrate. Tornotes are concentrated in the

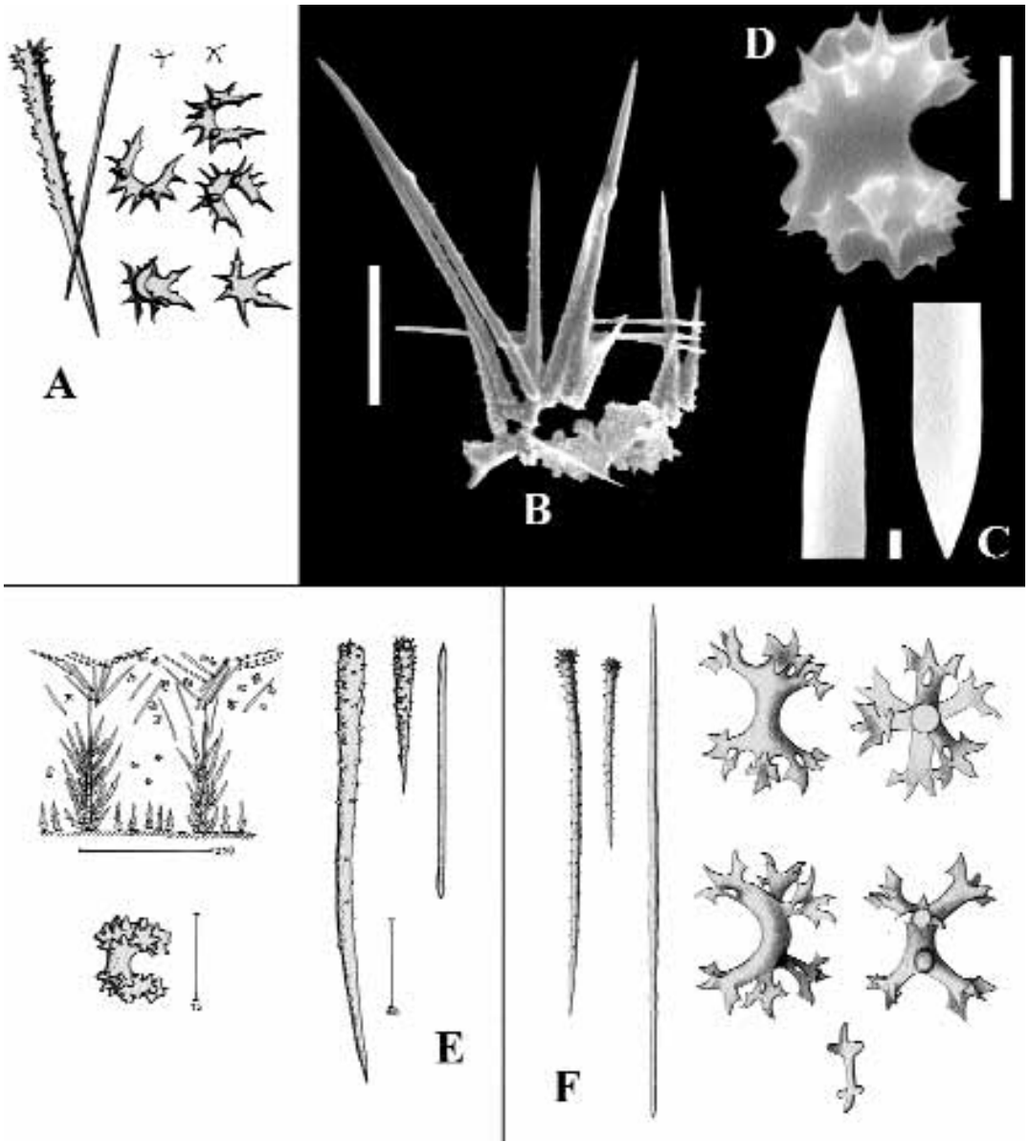

Fig. 1. *Acanthancora*. A, *Acanthancora schmidti* (Topsent, 1898b as *Leptosia*), drawing of spicules reproduced from Topsent (1904b, pl. XV fig. 9) (sizes see text). B–E, *Acanthancora cyanocrypta* (de Laubenfels, 1932 as *Hymenamphiastra*). B, SEM photo made from a paratype showing arrangement of the skeleton with groups of acanthostyles (scale 100 μm). C, details of apices of tornote (scale 1 μm). D, spined and deformed chela (scale 10 μm). E, drawing of skeleton and spicules made from a slide of a paratype. F, *Acanthancora aenigma* (Lundbeck, 1910 as *Hymedesmia*), type of *Ferrerhernandezia* de Laubenfels (1936a), drawing of spicules reproduced from Lundbeck (1910, pl. IX fig. 1) (sizes see text).

periphery, scattered singly among the numerous microscleres. Spicules, ectosomal tornotes, strongyle-like, inequiended, with a rounded and a mucronate end, 200–220 × 3 μm; choanosomal acanthostyles, of widely different sizes but not clearly differentiated in structural and echinating spicules, all entirely spined, 112–260 × 7–15 μm. Microscleres strongly deformed and spined, looking somewhat like diplasters, but presumably are derived from (arcuate) chelae, 12–14 μm. Chiastosigmas, 7–8 μm. Distribution and ecology. Azores; deep-water, 349 m.

Remarks. The slide of the holotype examined contains large amounts of curved smooth oxeas, but these are obviously not proper. Also, the chiastosigmas mentioned by Topsent (1904b) are not found in the slide, which could mean that they may also not be proper. Topsent described a second Azoran deep-water species of *Acanthancora, A. clavatancora*, which seems quite close to *A. schmidti*, including the chiastosigmas. It is quite possible that the two belong to the same species. Burton (1959a) described *A. stylifera* from the Indian Ocean and Van Soest (1984b) *A. coralliophila* from the Caribbean. This genus is similar to *Hymedesmia*, differing in the peculiar microscleres, which are shared by non-hymedesmioid *Pseudohalichondria* (cf. below).

The genus *Hymenamphiastra* de Laubenfels, 1930 was erected for type species (monotypy) *H. cyanocrypta* de Laubenfels (1930: 27) (cf. also de Laubenfels, 1932: 87, fig. 51). A paratype, BMNH 1929.8.22.18, including two slides, was re-examined. The skeleton (Fig. 1B, E) of this blue thinly encrusting species has single large acanthostyles of 250–280 × 13 μm erect on the substrate surrounded and echinated by short acanthostyles of 75–90 × 10 μm

to form distinct tree-like bouquets. Ectosomal tornotes are thin and oxea-like with lanceolate apices (Fig. 1C,E), 160–170 × 3 μm. Microscleres are strongly deformed bluntly spined reduced chelae (Fig. 1D, E) of 10–15 μm. It conforms closely to *Acanthancora*.

The genus *Ferrerhernandezia* de Laubenfels, 1936a: 87 was erected for type species (by original designation) *Hymedesmia aenigma* Lundbeck (1910: 84, pl. IX fig. 1, here reproduced in Fig. 1F) (not examined). This is a thinly encrusting sponge with vertically placed acanthostyles, 130–340 × 14–21 μm, and bundles of ectosomal polytylote oxeote tornotes, 320–430 × 6–7 μm. Microscleres are 'asteroid' chelae, 28–35 μm. This combination of characters conforms closely to *Acanthancora*.

HAMIGERA GRAY, 1867

Synonymy

[*Cribrella*] Schmidt, 1862: 70 (preocc.). *Hamigera* Gray, 1867a. *Amoibodictya* Zahn *et al*., 1977: 105.

Type species

Cribrella hamigera Schmidt, 1862: 70 (by original designation).

Definition

Hymedesmiidae without acanthostyles; with strongyles or tylotes as tornotes; with coring and echinating smooth styles or subtylostyles; arcuate chelae.

Diagnosis

Encrusting to massive sponges; oscules slightly elevated, rounded, pores in characteristic and conspicuous areolate porefields; ectosomal diactinal spicules form fans around areolae; choanosomal skeleton composed of plumose tracts of smooth strongyles or strongylote tornotes, which may be mixed with smooth styles or subtylostyles, with echinating smooth styles or subtylostyles; microscleres are arcuate isochelae. Half a dozen species.

Previous review

Bergquist & Fromont, 1988: 73.

Description of type species

Hamigera hamigera (Schmidt, 1862) (Fig. 2A–E).

Synonymy. *Cribrella hamigera* Schmidt, 1862: 70, pl. VI fig. 13; Desqueyroux-Faúndez & Stone, 1992: 10, pl. XXIV fig. 138. *Amoibodictya forsteri* Zahn *et al*., 1977: 106, figs 1–6.

Material examined. Holotype: LMJG 15359 – Zara Canal. Schizotype: BMNH 1867.3.11.70 – slide of Schmidt #59, Adriatic.

Description. Encrusting to massive lobose (Fig. 2A–B), up to 2–3 cm thick, up to 10 cm in widest expansion. Smooth surface with conspicuous slightly elevated, oval areolae (Fig. 2B), with oscules on similar elevations. Consistency fleshy. Colour orange-red. Skeleton of the ectosome consists of strongyles or tylotes distributed tangentially and intercrossing, but they are arranged in parallel sheets in the wall of the areolae. The areolate surface contains mostly microscleres, strewn around the pores. Choanosomal skeleton consists of plumose bundles of strongyles echinated by smooth styles. Spicules (Fig. 2C–E), tornotes in the form of strongyles to tylotes (Fig. 2C), smooth with faintly swollen endings, 230–320 × 3–7 μm; styles to subtylostyles (Fig. 2D), often rather abruptly curved in the second half, 240–320 × 5–9 μm; arcuate isochelae (Fig. 2E), 15–22 μm. Distribution and ecology. Mediterranean; on rocks and under overhangs, down to 23 m.

Remarks. *Hamigera hamigera* was originally described in the genus [*Cribrella*] Schmidt, 1862 which was preoccupied by *Cribrella* Agassiz, 1835 (Echinodermata). The present species was fixed as the type species of [*Cribrella*] Schmidt, 1862 by Desqueyroux-Faúndez & Stone (1992). Subsequently, Gray (1867a) erected *Hamigera* with the same species, *C. hamigera* as the type. *Amoibodictya* Zahn *et al*. (1977: 105) is a synonym, because the type species (by monotypy) *A. forsteri* from the Adriatic is an obvious junior synonym of *Hamigera hamigera*.

This genus is distinguished from *Phorbas* and *Hymedesmia* by the absence of acanthostyles, instead of which smooth styles are found in echinating position. About half a dozen *Hamigera* species have been reported from Indo-Pacific and Australian-New Zealand waters.

HEMIMYCALE BURTON, 1934

Synonymy

Hemimycale Burton, 1934a: 556.

Type species

Desmacidon columella Bowerbank, 1874b: 243 (by original designation).

Definition

Hymedesmiidae without acanthostyles; without microscleres; megascleres strongyles and styles, not divisible into ectosomal or choanosomal spicules.

Diagnosis

Thickly encrusting to massive, with striking and characteristic areolated porefields; skeleton of plumose columns of mixed styles and slightly inequiended strongyles, which are probably derived from tornotes; the choanosomal columns fan out near the surface and strengthen the raised porefields; no microscleres. One definite valid species, but others may exist.

Previous review

Forster, 1955.

Remarks

Assignment of *Hemimycale* to this family is controversial, because of the uniform spiculation of smooth tornote-like spicules

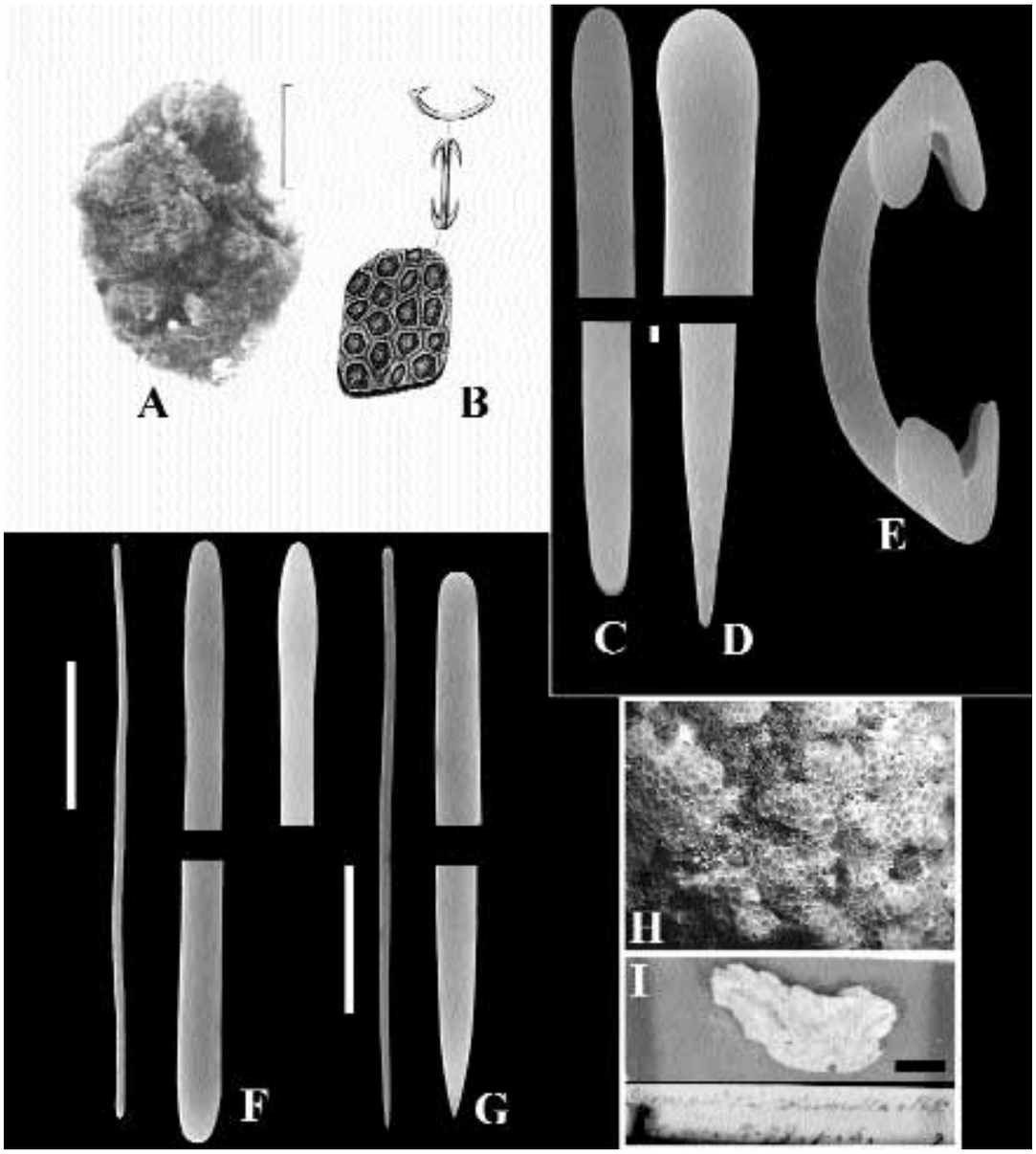

Fig. 2. A–E, *Hamigera hamigera* (Schmidt, 1862 as *Cribrella*). A, photo of holotype reproduced from Desqueyroux-Faúndez & Stone (1992, pl. XXIV fig. 138) (scale 1 cm). B, Schmidt's drawing of the type and microscleres (sizes see text). C–E, SEM photos of spicules made from the holotype (scale 1 μm). F–I, *Hemimycale columella* (Bowerbank, 1874b as *Desmacidon*). F–G, SEM photos of spicules made from the holotype (scale 100 μm). H, photo of live specimen made by Bernard Picton. I, photo of type specimen (scale 1 cm).

without clear differentiation and lack of microscleres. Several authors assigned it to the Halichondriidae, along with such genera as *Batzella* and *Ulosa*. The presence of stylote and strongylote derivatives of apparently the same spicule type would allow inclusion of this genus in the family Chondropsidae. However, the genus is here assigned to Hymedesmiidae corroborated by the conspicuous presence of surface areolae and skeletal architecture of strengthening of the elevated areolae by parallel arrangement of the spicules in the wall. These constitute compelling similarities with *Hamigera, Phorbas* and *Hymedesmia*. *Batzella* does not possess these traits, and moreover has spicules only in a single type, i.e., strongyles, which makes its assignment to Chondropsidae, away from *Hemimycale*, a logical and defendable action. *Ulosa* possesses exclusive styles. It has been misinterpreted for *Scopalina* (Halichondrida: Dictyonellidae) and is now assigned to Mycalina, family Esperiopsidae.

Description of type species

Hemimycale columella (Bowerbank, 1874b) (Fig. 2F–I).

Synonymy. *Desmacidon columella* Bowerbank, 1874b: 243, pl. LXXVIII figs 6–8; *Stylinos columella*; Topsent, 1892a: 136; *Stylotella columella*; Topsent, 1894b: 26; *Prianos columella*; de Laubenfels, 1932: 62 (also as *Prianos columellus* sic);

Hemimycale columella; Burton, 1934a: 556, fig. 10; Forster, 1955: 553, figs 1–3.

Material examined. Holotype BMNH 30.7.3.434, Exmouth, Bowerbank collection; four unregistered slides, BMNH 'Bk 818', Bowerbank collection.

Description. Encrusting; several mm in thickness, lateral expansion up to 5 cm or more (Fig. 2I). Surface closely covered in numerous large rounded areolate porefields (Fig. 2H), which are conspicuous because they have elevated rims lighter coloured than the pore areas. Consistency soft, slippery. Colour bright red to pale orange or pink. No definite ectosomal skeleton, although scattered spicules occur tangentially in the skin; the walls of the areolae are supported by sheets of spicules. There is no differentiation in shape of the spicules into ectosomal and choanosomal spicules. Choanosomal skeleton consists of plumose bundles of spicules, branching and anastomosing infrequently. In many specimens a secondary skeleton of calcareous nodules is developed (see Vacelet *et al*., 1987); it is unclear whether this has taxonomic significance. Spicules. Probably only a single type, but their endings are either rounded at both ends, thus technically strongyles (Fig. 2F), or inequiended, occasionally one end mucronate, technically styles (Fig. 2G) or strongylostyles, 330–465 × 2–8 μm. Reproduction. Viviparous, April to October. Distribution and ecology. North East Atlantic, Mediterranean, Azores; on rocks, shallow water.

Remarks. So far this remains a monotypical genus, although Sarà (1960) and Sarà & Siribelli (1960) described two additional species from the Mediterranean, viz., *Hemimycale ambigua* and *H. brevicuspis*, both probable synonyms of *Crambe crambe* (see chapter on family Crambeidae). Vacelet *et al*. (1987: 260) recorded an unnamed species from the Red Sea. This assignment is challenged by Van Soest *et al*. (1996: 93), because its chemistry conforms to *Crambe* and *Monanchora*. A further record, although not corroborated by a description, is from Brazil (Muricy *et al*., 1991). The calcareous nodules described by Vacelet *et al*. (1987) were also recorded by Bowerbank in his plate LXXVIII as 'gemmules'.

HYMEDESMIA BOWERBANK, 1864

Synonymy

Hymedesmia Bowerbank, 1864: 190. *Sclerilla* Schmidt, 1868: 13. *Stegxella* Bowerbank, 1874b: xi. *Stegilla* Bowerbank, 1874b: xii. *Stylopus* Fristedt, 1885: 28. [*Leptosia*] Topsent, 1892b: xxii. *Tylosigma* Topsent, 1894a: 32. *Ectyodesmia* Topsent, 1928c: 55. *Ectyostylopus* Topsent, 1928c: 56. *Poecilochela* de Laubenfels, 1936a: 87. *Hymoxenia* Alander, 1938: 72.

Type species

Hymedesmia zetlandica Bowerbank, 1864 (by monotypy).

Definition

Hymedesmiidae with hymedesmioid skeleton.

Diagnosis

Persistently thinly encrusting; ectosomal skeleton composed of smooth ectosomal tornotes strewn at the surface and forming bundles in the choanosome; choanosomal basal skeleton hymedesmioid, composed of one or two sizes of acanthostyles standing singly erect on the substrate; microscleres are arcuate isochelae and/or sigmas. Many species.

Remarks

Hymedesmia is close to *Phorbas* in most spicular characters, but the two are separated by the hymedesmioid arrangement of the basal acanthostyles in *Hymedesmia* against the echinating and/or columnar arrangement of the acanthostyles in *Phorbas*. This distinction is problematical in individual species and may not be tenable eventually. In this family species with profusely ornamented spined chelae may show typical hymedesmioid (*Acanthancora schmidti, Hymedesmia crux*) or *Phorbas*-like arrangement (*Pseudohalichondria clavilobata*), indicating the low phylogenetic significance of these skeletal arrangements. In view of the large number of *Hymedesmia* and *Phorbas* species it is practical to maintain them as separate genera. In line with this decision it is also proposed to maintain two genera for Hymedesmiidae with spined chelae, i.e., *Acanthancora* for those with hymedesmioid structure, and *Pseudohalichondria* for those with a more *Phorbas*-like structure (cf. above and below). Because the number of *Hymedesmia* species is very large, it is proposed to employ two subgenera for convenience, *Hymedesmia s.s*. for species with microscleres (usually chelae, to which may be added sigmas), and *Stylopus* Fristedt, 1885 for species without microscleres. It is not likely that loss of chelae indicates close relationship, and the distinction is very likely to be artificial. *Dolichacantha* Hentschel, 1914 was erected for type species *D. macrodon* Hentschel (1914) from the Antarctic. The description of Hentschel (1914) records an extraordinary combination of spicules, including very long smooth tylotornotes acanthostyles of two distinct size classes, peculiar acanthostrongyles with numerous spined 'cladi', palmate isochelae and sigmas. Some of the spicules are said to be 'not numerous' (sigmas) and 'rare' (palmate isochelae). The shape and architecture is hymedesmioid, but there are long projections, and the acanthostyles are said to be mixed in with the tornotes. The peculiar acanthostrongyles are apparently arranged in bundles on the surface, making the sponge very hispid. It is difficult to decide which of the spicules are proper to the sponge, and thus the affinities of the sponge remained obscure. Koltun (1970) described a second species with the peculiar long acanthostrongyles with excessively long spines *D. shikotani* Koltun (1970). This apparently lacks the sigmas but the chelae are clearly pictured and stated to be palmate. Until further information is provided, it is assumed that sigmas are foreign, and that *Dolichacantha* is a deviating member of the microcionine family Acarnidae (see chapter on that family by Hooper).

Previous review

Lundbeck, 1910.

SUBGENUS *HYMEDESMIA* BOWERBANK, 1864

Synonymy

Sclerilla Schmidt, 1868: 13. *Stegxella* Bowerbank, 1874b: xi. *Stegilla* Bowerbank, 1874b: xii. *Tylosigma* Topsent, 1894a: 32.

Key to subgenera of *Hymedesmia*

(1) Chelae present ..... ***Hymedesmia***
No chelae ..... ***Stylopus***

Ectyodesmia Topsent, 1928c: 55. *Poecilochela* de Laubenfels, 1936a: 87. *Hymoxenia* Alander, 1938: 72.

Definition

Hymedesmia with chelae.

Description of type species

Hymedesmia (Hymedesmia) zetlandica Bowerbank, 1864 (Fig. 3A–F).

Synonymy. *Hymedesmia zetlandica* Bowerbank, 1864: 190; Bowerbank, 1874b: 73, pls XXIX figs 1–7; *Leptosia zetlandica* Topsent, 1894a: 31.

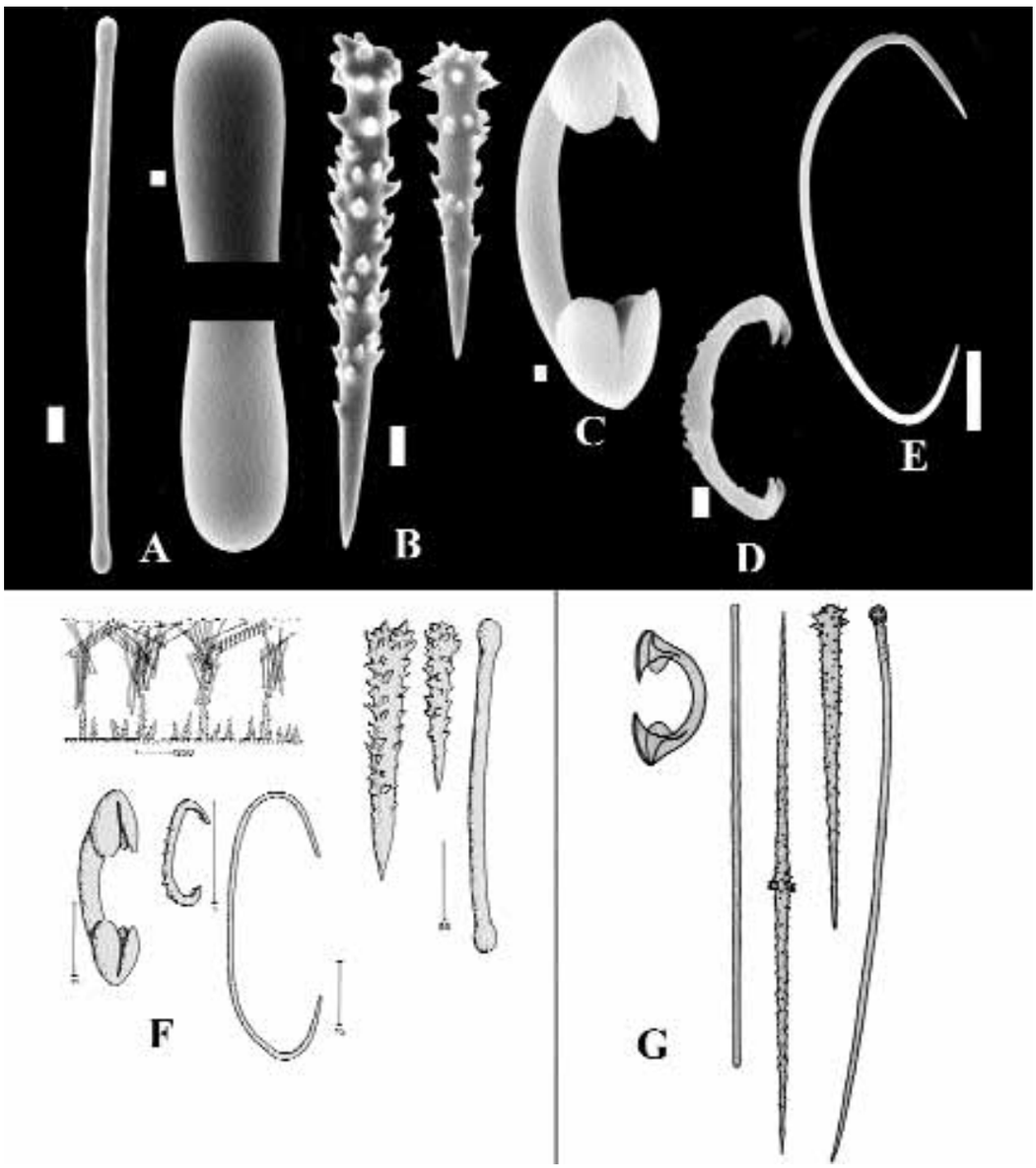

Fig. 3. *Hymedesmia*. A–F, *Hymedesmia (Hymedesmia) zetlandica* Bowerbank (1866). A–E, SEM photos of spicules made from the holotype (scale A left, B and E, 10 μm; A right, C, and D, 1 μm). F, drawing of skeleton and spicules made from a slide of the holotype. G, *Hymedesmia (Hymedesmia) inflata* (Alander, 1935 as *Hymoxenia*), reproduced from Alander (1935: fig. 1) (sizes see text).

Material examined. Holotype: BMNH unregistered – dry specimen and slide, Bk.467, Shetland.

Description. Thinly encrusting on pebbles. Lateral expansion up to 2 cm. Colour yellow or brownish yellow. Surface smooth, no oscules recorded. Skeleton (Fig. 3F) hymedesmioid, with single acanthostyles erect on the substrate, head embedded in a basal plate of spongin. Bundles of tornotes, 3–5 spicules in cross section, traverse the thin choanosome and fan out at the surface. Spicules (Fig. 3A–F), ectosomal and subectosomal symmetrical tylotes (Fig. 3A), 225–255 × 5–8 μm; acanthostyles (Fig. 3B), robust, with well-developed head, fully and heavily spined, in a wide size range of 80–150 × 10–20 μm, possibly divisible in two categories; arcuate isochelae of two distinct morphological types, larger normal shaped (Fig. 3C), 20–30 μm, smaller sigma-like reduced chelae (Fig. 3D), with only two sharp teeth, shaft undulate or bluntly spined, 10–15 μm; sigmas (Fig. 3E), wide and thin, in sigmodragmas, 40–70 μm. Distribution and ecology. Shetland, S and W coast of Ireland; from deeper water, 65 m and downward.

Remarks. The type of *Hymedesmia* is rather atypical for the large assemblage of species united traditionally under this genus name. Neither the second category of small reduced and spined chelae, nor the sigmas arranged in dragmata are found in any known *Hymedesmia*, while the possession of symmetrical tylote tornotes is quite infrequent. This combination is more reminiscent of *Lissodendoryx (Ectyodoryx)*, than of mainstream *Hymedesmia*. It needs to be kept in mind that the genus characters of *Hymedesmia* are obviously linked with the thin growth form, and this may prove to be an unreliable set of characters for determining phylogenetic relationships.

Topsent (1928c: 55) erected in a casual way a subgenus *Hymedesmia (Ectyodesmia)* for *Hymedesmia* in which the acanthostyles could be divided into larger main megascleres and smaller echinating acanthostyles. Since the type species of *Hymedesmia* has a smaller and a larger acanthostyle type, it would fall to Topsent's subgenus *Ectyodesmia*. However, the type species automatically belongs to the nominal subgenus, and this makes *Ectyodesmia* an objective synonym of *Hymedesmia (Hymedesmia)*.

The genus *Stegxella* Bowerbank, 1874b: xi was erected for type species (by original designatiom) *S. saccea* ascribed to Schmidt (1864), but no such combination is found in that publication. On the following page (p. xii) Bowerbank spelled the name as *Stegilla*, again not a name used in Schmidt's publication. Technically, *Stegilla* is a *nomen nudum*. De Laubenfels (1936a: 85) declared *Stegxella* to be a synonym of *Myxilla*. It is conceivable that both Bowerbank names are misspellings for *Sclerilla* Schmidt, 1868: 13, which de Laubenfels (1936a: 85) also declared to be a synonym of *Myxilla*, but of which the type species has not been fixed yet. This is here fixed as *Sclerilla filans* Schmidt (1868: 13), with lectotype specimen (dry) in MNHN, from Algiers. A Schmidt slide from Algiers, BMNH 1868.3.2.20, was examined, and Topsent (1938a) provided a redescription. Spicules include polytylote inequiended smooth tornotes, 150–175 × 3–4 μm, acanthostyles, 115–120 × 3 μm. The BMNH slide did not contain proper microscleres (a few broken sigmas), but Topsent recorded arcuate chelae, 21–24 μm and sigmas, 25–33 μm. This conforms to *Hymedesmia*, and it is proposed to consider *Stegxella* and *Stegilla* along with *Sclerilla* as synonyms of *Hymedesmia*.

The genus *Poecilochela* de Laubenfels, 1936a: 87 was erected for type species (by original designation) the Antarctic *Myxilla decepta* Kirkpatrick (1907a: 278, not illustrated here). The holotype and slides BMNH 1908.2.5.160(b+f) were examined. This material is scanty, thinly encrusting on a branching bryozoan. Megascleres are single acanthostyles, erect on the substrate, larger ones, 423–517 × 14–20 μm surrounded by a circle of smaller acanthostyles, 172–205 × 9–12 μm. Ectosomal strongyles, inequiended, one end mucronate, 234–288 × 3–4.5 μm. Microscleres consist of a majority of normal arcuate isochelae, 19–23 μm, and reduced unguiferate and malformed ('bipocillae') presumed derivates thereof, 8–15 μm. These do not constitute enough evidence for separate generic status of this single species.

The genus *Hymoxenia* Alander, 1938 was erected for Norwegian type species (by monotypy) *H. inflata* Alander (1938. 72, fig. 1, here reproduced as Fig. 3G), type stated to be in the Gothenburg Museum. This is an encrusting species conforming entirely to *Hymedesmia*, including single acanthostyles erect on the substrate, in two size classes, 650–1400 × 20–25 μm and 150–200 × 8–10 μm, ectosomal tylotes, 320–385 × 3–5 μm, and arcuate chelae, 50–60 μm, but having in addition an accessory spicule type of centrotylote acanthoxeas. These spicules, 290–400 × 8–10 μm, are very probably merely 'double' versions of the small acanthostyles, and accordingly the genus is considered a junior synonym.

The genus *Tylosigma* Topsent, 1894a: 32 was erected for type species (by original designation) *Hymedesmia campechiana* Topsent (1889: 30, fig. 8C) from the Caribbean coast of Mexico. A slide of the type, MNHN DT1844, was examined. The species is an atypical *Hymedesmia* by lacking proper chelae and diactinal tornotes. The microscleres are large sigmas arranged in dragmas and small sigmas, which are possibly reduced chelae, not unlike those of *H. zetlandica*. The smaller tylostyles may be considered as tornotes. In view of the similarities with *H. zetlandica* it is proposed to consider *Tylosigma* a junior synonym of *Hymedesmia (Hymedesmia)*.

SUBGENUS *STYLOPUS* FRISTEDT, 1885

Synonymy

Stylopus Fristedt, 1885: 28. [*Leptosia*] Topsent, 1892b: xxii (preocc.). *Ectyostylopus* Topsent, 1928c: 56.

Type species

Stylopus coriaceus Fristedt, 1885: 28 (by monotypy).

Definition

Hymedesmia without microscleres.

Description of type species

Hymedesmia (Stylopus) coriacea (Fristedt, 1885) (Fig. 4A–B).

Synonymy. *Hymeniacidon dujardini* Bowerbank, 1866: 244. Not *Halisarca dujardini* Johnston, 1842. *Leptosia dujardini*; Topsent, 1894b. 8. *Hymedesmia broendstedi* Burton, 1930b: 497. *Stylopus coriaceus* Fristedt, 1885: 28, pl. II, fig. 8. *Hymedesmia coriacea*; Van Soest, 1987b: 20.

Material examined. Syntype: BMNH 1927.2.22.3 – Bohuslan, Sweden, coll. S. Lovén.

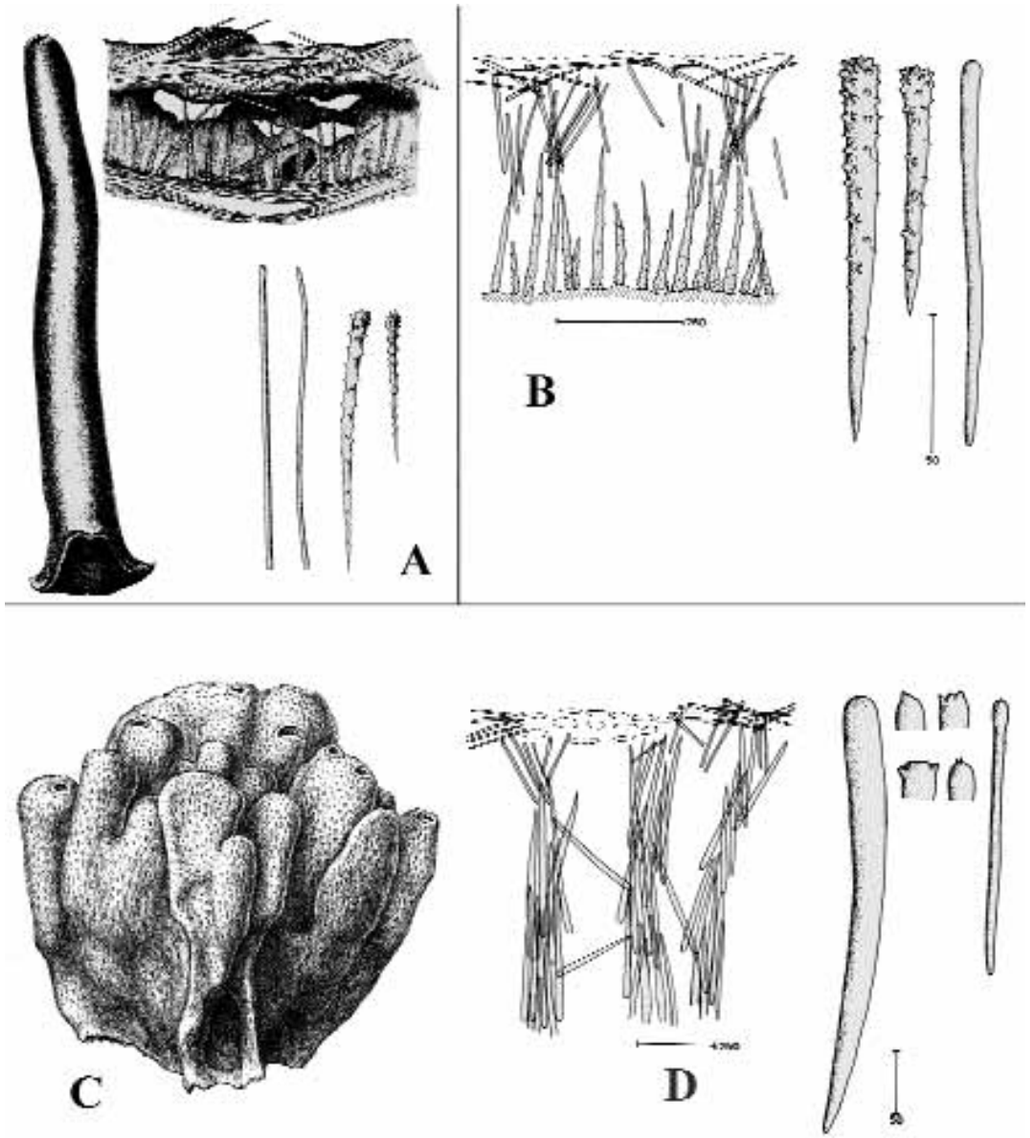

Fig. 4. A–B, *Hymedesmia (Stylopus) coriacea* (Fristedt, 1885). A, drawing of shape, skeleton and spicules of the type material, reproduced from Fristedt (1885, pl. II fig. 8) (sizes see text). B, drawing of skeleton and spicules made from a slide of one of the syntypes. C–D, *Kirkpatrickia variolosa* (Kirkpatrick, 1907a as *Tedania*). C, drawing of the holotype (reproduced from Kirkpatrick's pl. XXI fig. 1; size see text). D, drawing of skeleton and spicules made from a slide of the holotype.

Description. Thinly encrusting on other organisms (barnacles, brachiopods, tubeworms (see type of Fristedt, reproduced here as Fig. 4A), algae, corals). Surface smooth, mucous. Consistency firm. Skeleton (Fig. 4A–B) of the ectosome consists of brushes of tornotes fanning out to form tangential single spicules; choanosomal skeleton consists of single acanthostyles erect on the subtstrate, from which arise ill-defined bundles of tornotes. Spicules (Fig. 4A–B), strongylote or anisotylote tornotes about 200 × 2.5 μm (range given by Van Soest, 1987b: 140–280 × 2–4 μm). Acanthostyles in a wide size range, probably divisible in two categories, 120–180 × 5–8 μm (range given by Van Soest, 1987b: 56–312 × 1.7–8 μm). Distribution and ecology. Sweden (Fristedt), E Atlantic S to Mediterranean and W Africa, on stones, shells and corals, shallow-water down to 100 m.

Remarks. The reason for preferring the name *coriacea* Fristedt, 1885 over *dujardini sensu* Bowerbank, 1866, is that the latter was ascribed to Johnston, 1842. Bowerbank misinterpreted *Halisarca dujardini* Johnston, 1842 for the present species, so the name *dujardini* cannot be used for it.

The genus [*Leptosia*] Topsent, 1892b: xxii was originally erected for a group of three species consisting of *Hymedesmia zetlandica, Hymeniacidon dujardini* Bowerbank, 1866 (not *Halisarca dujardini* Johnston, 1842), and *Leptosia exilis* Topsent, 1892b (=*Forcepia luciensis* Topsent, 1890b). De Laubenfels (1936a: 88), for unexplained reasons, designated *H. dujardini* as type species, whereas Topsent himself (e.g., 1892a, 1904b, 1928c) expressly mentioned chelae in his definitions of [*Leptosia*]. In 1928, Topsent, when confronted with the fact that *Hymedesmia* was a valid genus covering more-or-less his concept of [*Leptosia*], restricted the use of it to species with anchorate chelae (a concept here covered by the genus *Hymenancora*), but this is impossible because the original series of sponges did not contain species with anchorate chelae.

Despite its unfortunate choice, de Laubenfels' type species designation appears valid, and accordingly *Hymeniacidon dujardini sensu* Bowerbank is the type species. Bowerbank's specimen BMNH 1910.1.1.124 and five unregistered slides, Bk 536, 537 and 539, from Strangford Lough, N Ireland, were examined. By its possession of 2 sizes of acanthostyles and strongylote tornotes, this is confirmed to be a clear junior synonym of *Hymedesmia (Stylopus) coriacea* (cf. also Van Soest, 1987b). Since [*Leptosia*] Topsent, 1892b was already preoccupied by *Leptosia* Hübner, 1818 (Lepidoptera), *Stylopus* remains the valid subgenus name.

Topsent, 1928c: 56 erected a subgenus *Stylopus (Ectyostylopus*) for *Stylopus* with two categories of acanthostyles. The type species is *Hymedesmia dermatus* Lundbeck, 1910 (monotypy). This distinction is considered superfluous and *Ectyostylopus* is considered a junior synonym of *Hymedesmia (Stylopus)*.

KIRKPATRICKIA TOPSENT, 1912

Synonymy

Kirkpatrickia Topsent, 1912: 3.

Type species

Tedania variolosa Kirkpatrick, 1907a: 279 (by original designation).

Definition

Hymedesmiidae with strongylote tornotes and smooth or spined styles in plumose but anastomosing bundles; no microscleres.

Diagnosis

Flabellate or digitate; pores grouped in sieve-plates (areolae). Ectosomal skeleton composed of ectosomal strongylote tornotes or strongyles in tangential tracts and whispy brushes on the surface (the latter around pores). Choanosomal skeleton composed of loosely agglomerated primary and secondary fibres cored by choanosomal styles, curving out towards the surface in the peripheral skeleton. Megascleres choanosomal styles with smooth or spined bases microscleres are absent. Three or four species.

Previous review

Koltun, 1964b.

Description of type species

Kirkpatrickia variolosa (Kirkpatrick, 1907a) (Fig. 4C–D).

Synonymy. *Tedania variolosa* Kirkpatrick, 1907a: 279; Kirkpatrick, 1908c: 32, pl. XXI fig.1, pl. XXV fig. 1; *Kirkpatrickia variolosa*; Topsent, 1912: 3.

Material examined. Holotype: BMNH 1908.2.5.162. Paratype: BMNH 1908.2.5.164 – from Winter Quarters, Antarctica. Paratype: BMNH 1908.2.5.163 (not examined).

Description. Thickly flabellate or digitate fronds, up to 18 cm high, 13 cm wide, ending in sphinctrate oscules (Fig. 4C). Surface covered with slightly raised areolate porefields. Consistency soft and fleshy. Colour orange-red, pale brown in alcohol. Skeleton (Fig. 4D) of the ectosome consists of spicules arranged in bouquets, fanning out and becoming tangentially arranged at the surface. Walls of the areolae strengthened by vertical palissades. Choanosomal skeleton plumoreticulate, with longitudinal spicule tracts connected irregularly by thinnner spicule tracts. Spicules (Fig. 4D), ectosomal tornotes, strongylote, up to 260×6.5 μm. Choanosomal styles smooth, with occasional spines, about 400×13 μm. Distribution and ecology. Antarctic and Subantarctic Islands; shallow-water.

Remarks. The genus has been associated with Tedaniidae, but it lacks onychaetes, and the possession of areolated porefields is a strong indication it is related to *Phorbas* and *Hymedesmia*. It differs from these genera in the absence of microscleres and the plumoreticulate architecture. It is also close to *Myxodoryx* but this genus possesses echinating acanthostyles. Three other species have been assigned to *Kirkpatrickia*, viz., *Tedania coulmani* Kirkpatrick (1907a), *K. spiculophila* Burton & Rao (1932), and *K. borealis* Koltun (1970). They differ from the type in having properly spined styles and in the shape of the tornotes.

MYXODORYX BURTON, 1929

Synonymy

Myxodoryx Burton, 1929a: 438.

Type species

Lissomyxilla hanitschi Kirkpatrick, 1907a: 275 (by original designation).

Definition

Hymedesmiidae with strongylote tornotes and lightly (spined) styles in plumose but anastomosing bundles; with a separate (smaller) category of non-echinating acanthostyles with spines only on the lower (pointed) half; no microscleres.

Diagnosis

Massive growth form; ectosomal skeleton composed of smooth tylotes with mucronate bases forming tangential and oblique tracts at the surface; choanosomal skeleton confused reticulate, with branching fibres cored by smooth choanosomal styles and echinated by acanthostyles with verticillate spination; microscleres are absent. A single species.

Description of type species

Myxodoryx hanitschi (Kirkpatrick, 1907a) (Fig. 5A–C).

Synonymy. *Lissomyxilla hanitschi* Kirkpatrick, 1907a: 275; Kirkpatrick, 1908c: 26, pl. XXII fig. 7, pl. XXVI fig. 4; *Myxodoryx hanitschi*; Burton, 1929a: 438.

Material examined. 'Cotype': BMNH 1908.2.5.132 (including 2 slides BMNH 1908.2.5.132 c+e) – 'Discovery' collection, Antarctic. The type material consists of three specimens, two of which are from the same location, Coulman Island, the other, smaller specimen is from Barrier. The latter specimen is here chosen as the lectotype, because it has a complete ectosome.

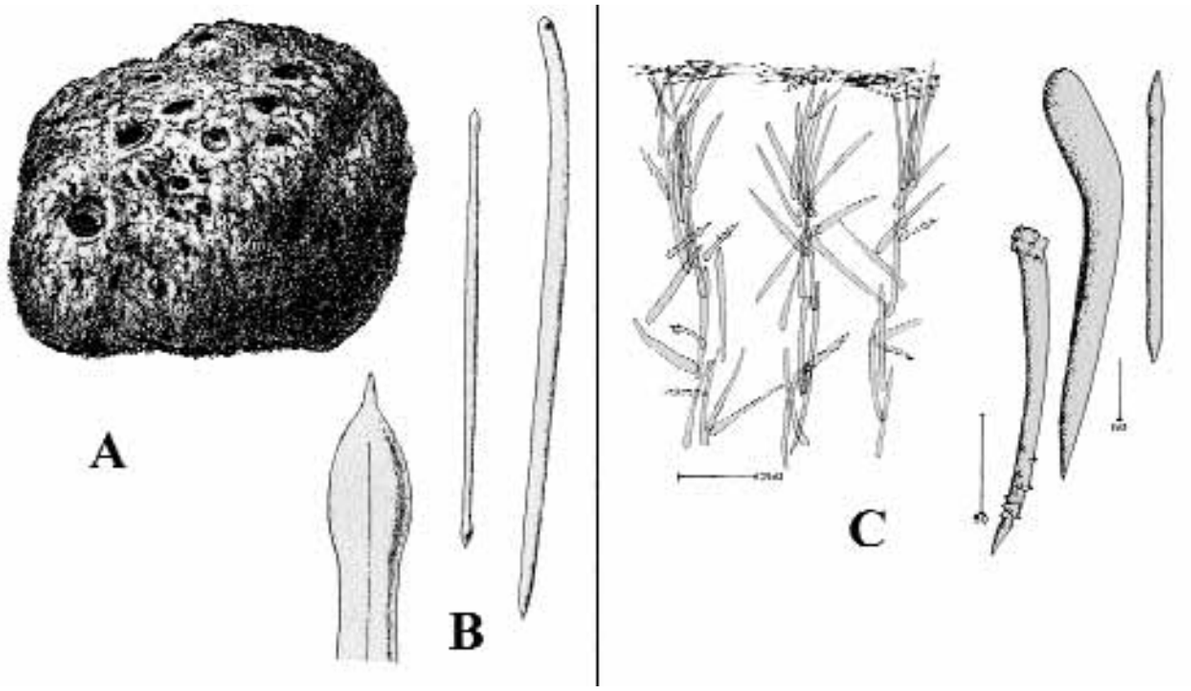

Fig. 5. *Myxodoryx hanitschi* (Kirkpatrick, 1907a as *Lissomyxilla*). A, drawing of habit reproduced from Kirkpatrick (1908c, pl. XXII fig. 7) (sizes see text). B, drawing of spicules reproduced from Kirkpatrick (1908c, pl. XXVI fig. 4) (sizes see text). C, drawing of skeleton and spicules made from a slide of the holotype.

Description. Lobate sponges (Fig. 5A), with transparent dermal membrane roofing over extensive subdermal openings. Surface areolae are not conspicuously developed. Colour whitish grey. Skeleton (Fig. 5C) of the periphery consists of brushes of ectosomal spicules fanning out at the surface and becoming tangentially arranged. Choanosomal skeleton plumose, confused, with longitudinal tracts echinated by acanthostyles. Spicules (Fig. 5B–C), ectosomal tornotes tylote-like with pointed mucronate endings, 280–(317.4)–350 × 6–(7.6)–10 μm. Styles smooth, curved near the blunt end, sharp-pointed, 385–(449.2)–503 × 15–(19.3) – 22 μm. Echinating acanthostyles, with long spines at the head and near the pointed end, but virtually smooth inbetween, 210–(260.3)–288 × 12–(13.6)–18 μm. Distribution and ecology. Antarctic; deep-water.

Remarks. The species was originally assigned to *Lissomyxilla* Hanitsch, 1894a, which is a junior synonym of *Tethyspira* Topsent, 1890b (Halichondrida: Dictyonellidae). So far the genus remains monotypical, and also somewhat isolated from other Hymedesmiidae. No closely related genera are apparent.

PHORBAS DUCHASSAING & MICHELOTTI, 1864

Synonymy

Phorbas Duchassaing & Michelotti, 1864: 92. *Anchinoe* Gray, 1867a: 535. [*Pronax*] Gray, 1867a: 536. *Suberotelites* Schmidt, 1868: 12. *Plumohalichondria* Carter, 1876: 236. *Clathrissa* Lendenfeld, 1888: 217. *Stylostichon* Topsent, 1892a: 111. *Lissopocillon* Ferrer-Hernandez, 1916. 32. *Grayax* de Laubenfels, 1936a: 63. *Merriamium* de Laubenfels, 1936a: 83. *Pronaxella* Burton, 1931d: 168. *Bipocillopsis* Koltun, 1964b: 79. *Podotuberculum* Bakus, 1966b: 505.

Type species

Phorbas amaranthus Duchassaing & Michelotti, 1864 (by subsequent designation; de Laubenfels, 1936a: 63).

Definition

Hymedesmiidae with plumose tracts of tornotes and/or acanthostyles, echinated by acanthostyles (but these may be absent); microscleres normal-shaped chelae and sigmas, which may be absent.

Diagnosis

Thickly encrusting, massive or ramose sponges. Pores grouped in sieve-plates (areolae); ectosomal skeleton with a crust of isochelae and diactinal spicules which form fans disposed at right angles and tangential to the surface; heavily spined acanthostyles core plumose or plumo-reticulate choanosomal tracts, or these may be replaced by smooth diactinal tornotes; echinating acanthostyles also heavily spined; microscleres are arcuate isochelae and sigmas, both of which may be absent. About 70 species.

Taxonomic remarks

Voultsiadou-Koukoura & Van Soest (1991b) demonstrated that the alleged distinction between *Phorbas, Anchinoe* and *Stylostichon* (viz., skeletal columns consisting of tornotes only or of acanthostyles only) intergrades in the various species assignable to these genera. Consequently, it was proposed to merge these genera and this is followed here. Perhaps a subdivision of the now enlarged genus *Phorbas* is possible based on the possession of a

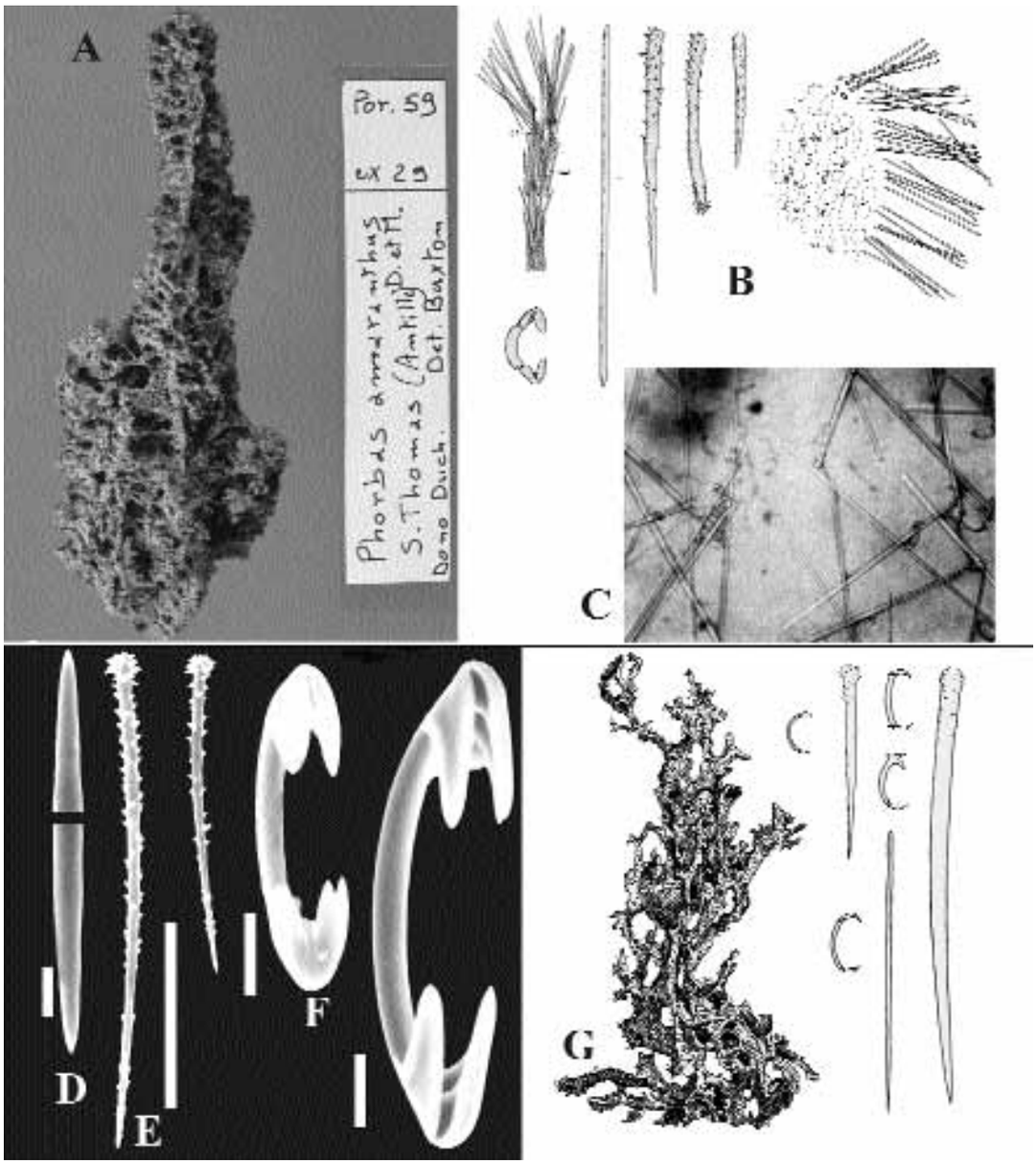

Fig. 6. *Phorbas*. A–B, *Phorbas amaranthus* Duchassaing & Michelotti (1864). A, habit of holotype (photo K. Rützler). B, drawing of skeleton and spicules reproduced from Van Soest (1984b, text-fig. 34). C, microphoto of spicules reproduced from de Laubenfels (1936a, pl. 11 fig. 1 as *Merriamium tortuganensis*). D–F, *Phorbas perarmatus* (Bowerbank, 1866 as *Hymeniacidon*), type of *Anchinoe* Gray, 1867a, SEM photos of spicules made from the type (scale 10 μm; except D, 100 μm). G, *Phorbas nexus* (Koltun, 1964b as *Bipocillopsis*), drawing of habit and spicules reproduced from Koltun's fig. 19 (sizes see text).

single acanthostyle size category (*Phorbas s.s.*) or two size categories, a larger acanthostyle coring the choanosomal bundles, a smaller echinating the columns (*Suberotelites*). This is best postponed until the species content of *Phorbas s.l.* is properly revised. The genus *Acanthodoryx* Lévi, 1951, on paper at least, appears to be close to *Phorbas*. However, the type species *A. fibrosa* Lévi 1951 lacks the surface areolae, and the skeleton is plumoreticulate rather than plumose; echinating acanthostyles are lacking. For these reasons, *Acanthodoryx* is assigned to the family Coelosphaeridae, and considered a subgenus of *Lissodendoryx* (see chapter Coelosphaeridae).

Description of type species

Phorbas amaranthus Duchassaing & Michelotti, 1864 (Fig. 6A–C).

Synonymy. *Phorbas amaranthus* Duchassaing & Michelotti, 1864. 92, pl. XXI fig. 1; Van Soest, 1984b: 86, pl. VI fig. 7, text-fig. 34. *Merriamium tortugasense* de Laubenfels, 1936a: 83, pl. 11, fig. 1.

Material examined. Mus. Torino POR. 59 – St. Thomas (cf. Fig. 5A). Other material. Many additional specimens from various Caribbean localities.

Description. Encrusting, several mm in thickness, with distinctive areolate surface patterns. Consistency soft, easily damaged. Gives off a red exudate when squeezed. Skeleton (Fig. 6B) of the ectosome a tangential arrangement of loose tornotes; walls of areolae strengthened by parallelly arranged tornotes; microscleres surround the pores. Choanosomal skeleton of thick (ca. 100 μm in diameter) columns of tornotes mixed with increasing numbers of acanthostyles towards the base; columns lightly echinated by acanthostyles. Spicules (Fig. 6B), robust smooth oxeote tornotes, straight with hastately pointed apices, 235–266 × 3.5–5.5 μm. Large acanthostyles with occasional strongylote modifications, 129–182 × 5–8 μm. Shorter echinating acanthostyles, 91–112 × 4.5–7.5 μm. Robust arcuate isochelae with short alae, 20–24 μm. Distribution and ecology. Caribbean; encrusting the base of corals in the reef environment, 6–33 m.

Remarks. A common genus with cosmopolitan distribution. *Anchinoe* Gray, 1867a: 535 was erected for type species (by monotypy) *Hymeniacidon perarmatus* Bowerbank, 1866 from Shetland. The holotype, BMNH 1910.1.1.144 was re-examined. This is a thin crust on a stone. Surface provided with conspicuous areolate porefields. The skeleton consists of an ectosomal tangential skeleton of intercrossing tornotes of 445–510 × 4–9 μm, with the walls of the areolae supported by parallel bands of tornotes. Ectosomal skeleton is carried by choanosomal plumose bundles of tornotes (Fig. 6D) with a low number of long acanthostyles (Fig. 6E), 283–305 × 4–8 μm, mixed in. The bundles of 60–100 μm in diameter are profusely echinated by short acanthostyles (Fig. 6E), 142–165 × 4–7 μm. Arcuate chelae (Fig. 6F) in two size categories, 62–92 and 28–44 μm. This sponge conforms closely to the type species of *Phorbas*.

The genus *Bipocillopsis* Koltun, 1964b: 79 was erected for type species (by monotypy) the Antarctic *B. nexus* Koltun (1964b: 80, fig. 19, here reproduced in Fig. 6G). No material was examined (stated to be housed in the Zoological Institute of the Russian Academy of Sciences). This is a mass of branches with irregular surface provided with porefields (clearly pictured by Koltun, but not mentioned in his description). Tornotes are stylote, 370–480 × 5–7 μm, and form anastomosing bundles, echinated by acanthostyles, spined lightly, 520–720 × 15–25 μm. Chelae, 16–20 μm, are peculiar, but likely to originate from arcuate chelae in view of their resemblance to the reduced chelae of *Fibulia*. The drawing and the description of Koltun do not entirely match, and it is possible that there is a second smaller category of acanthostyles pictured in his fig. 19 (here reproduced), but not mentioned in the text. If the choanosomal tracts are indeed made up of stylotornotes, as is apparently what Koltun describes, then the peculiar reduced chelae are the only difference with *Phorbas*, and accordingly the genus is considered a junior synonym.

The genus *Clathrissa* Lendenfeld, 1888 was erected for type species *C. arbuscula* Lendenfeld, (1888: 217, pl. V fig. 2) (by subsequent designation; Hallmann, 1912: 146). The following type and other material was examined, BMNH 1886.12.12.22 (labeled 'Herkunft Port Jackson 1140'), slide BMNH 1954.2.10.73 and slide 1954.2.12.52 (both Dendy collection). All that material is identical and concerns a mass of papillar projections, possibly constituting fused branches, size 10 cm high, 8 cm in diameter (Fig. 7A). The skeleton consists of plumose bundles of oxeote tornotes (Fig. 7B), 192–230 × 3–5 μm, echinated by acanthostyles (Fig. 6C), 100–126 × 3–8 μm, towards the interior grading into bundles of long acanthostyles 180–207 × 7–9 μm. Chelae are the usual arcuate type (Fig. 7D), 20–30 μm. This conforms closely to the type of *Phorbas*, and accordingly *Clathrissa* is considered a junior synonym.

The genus *Lissopocillon* Ferrer-Hernandez, 1916 was erected for type species (by monotypy) *L.dendyi* Ferrer-Hernandez, 1916: 32, fig. 10 (here reproduced as Fig. 7E), a lobate-mammillate sponge of 15 × 12 × ?cm. Surface provided with areolated pore fields and oscules of the same size. Colour probably reddish. Skeleton of diactinal oxeote tornotes, 300–320 × 6–8 μm, arranged in the ectosome and in the choanosomal tracts, in the bundles partly replaced by large acanthostyles, averaging 256 × 12–14 μm. The bundles are echinated by shorter acanthostyles, averaging 128 × 6–12 μm. Chelae in two size categories, normal arcuate isochelae, about 26 μm, and smaller malformed chelae, up to 20 μm. The latter were called 'pocillos' by Ferrer-Hernandez and constitute the generic character. Such malformed chelae are not unusual in Myxillina and may not even be a species character, let alone a genus character. In most features *L. dendyi* conforms to *Phorbas lieberkuehni* Burton (1930c: 532, as *Hymedesmia*), a replacement name for *Halichondria fasciculata sensu* Lieberkühn, 1859: 522. The consequence of reassignment of *Lissopocillon dendyi* to *Phorbas* is that it will have to be given a new name, since the combination *Phorbas dendyi* is already reserved for the species originally described as *Stylostichon dendyi* Topsent, 1913. It is here proposed to rename *Lissopocillon dendyi* as *Phorbas ferrerhernandezi* n.sp., although it may turn out to be a junior synonym of *Phorbas lieberkuehni* Burton when type material is re-examined.

The genus *Merriamium* de Laubenfels, 1936a was erected for type species (by monotypy) *Merriamium tortuganensis* de Laubenfels (1936a: 83, pl. 11 fig. 1, here reproduced as Fig. 6C). The type specimen, USNM 22418 from Florida, was reexamined. It has surface areolae and a skeleton consisting of bundles of oxeote tornotes gradually converted to bundles of acanthostyles; microscleres are in a single size category of arcuate chelae. This is an obvious junior synonym of *Phorbas amaranthus* (see also Van Soest, 1984b: 88), making *Merriamium* an objective synonym of *Phorbas* as both share the same type species. De Laubenfels' (1939) monograph of *Merriamium* contains a mixture of *Hymedesmia, Phorbas* and *Lissodendoryx (Ectyodoryx)* species.

The genus *Plumohalichondria* Carter, 1876 was erected for type speces (by monotypy) *Plumohalichondria microcionides* Carter (1876: 236, pl. XII fig. 11 pl. XV fig. 30). The type specimen, BMNH 1882.7.28.47, labelled 'Porcupine coll. stat. 51, 440 fms, between Scotland and Faroe Islands' was re-examined (cf. Fig. 7F). It is a lobe with irregular mammillated surface and firm consistency. Skeleton (Fig. 7G) consisting of plumose bundles of sharply pointed oxeote tornotes, 430–630 × 10–13 μm, towards the interior replaced by long club-shaped acanthostyles, spined profusely on the head but virtually smooth along the shaft, 695–1140 × 20–28 μm. The bundles are echinated by short acanthostyles, spined all-over, 235–300 × 12–14 μm. Chelae (Fig. 7G) are arcuate, and occur in a large size range, probably divisible in two categories, 65–125 and 42–63 μm. The species is only remarkable for the large size of acanthostyles and chelae.

The genus *Podotuberculum* Bakus, 1966b was erected for type species (by monotypy) *P. hoffmanni* Bakus (1966b: 505, fig. 23, here reproduced as Fig. 8A). A paratype, BMNH 1964.12.1.4, from San Juan Island, W coast of North America, was re-examined. This is encrusting and its surface bears 'tubercles', i.e., areolae. Spicule sizes and shape conform closely to those of *Myxilla versicolor californiana* de Laubenfels (1932:81), with strongylote tornotes of about 250 × 4–8 μm, styles with spined heads, about

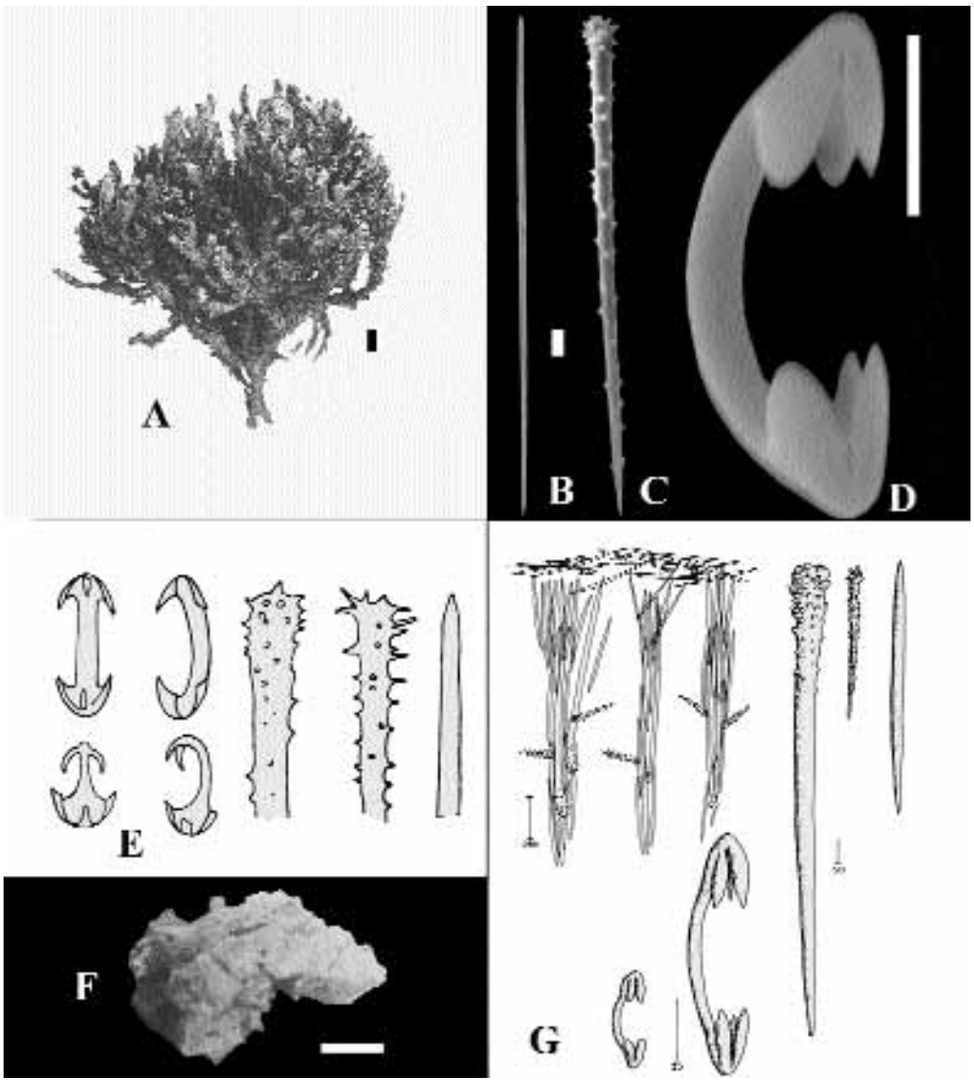

Fig. 7. *Phorbas* species. A–D, *Phorbas arbuscula* (Lendenfeld, 1888 as *Clathrissa*). A, habit of holotype reproduced from Lendenfeld's pl. V fig. 2 (sizes see text). B–D, SEM photos of spicules made from the type (scale 10 μm). E, *Phorbas ferrerhernandezi* n.sp., replacement name for *Phorbas dendyi* (Ferrer-Hernandez, 1916 as *Lissopocillon*), drawing of spicules reproduced from Ferrer-Hernandez's fig. 10 (sizes see text). F–G, *Phorbas microcionides* (Carter, 1876 as *Plumohalichondria*). F, fragment of type specimen (scale 1 cm). G, drawing of skeleton and spicules made from a slide of the type.

250 × 12 μm, some of which take up an echinating position while other are mixed with the tornotes coring the choanosomal bundles. No microscleres. On paper this species comes close to *Kirkpatrickia*, but in that genus the choanosomal tracts are connected by secondary tracts, and no echinatig spicules are found. It conforms to *Phorbas*.

The genus [*Pronax*] Gray, 1867a: 536 was erected for type species (by monotypy) *Hymeniacidon plumosa* Bowerbank, 1866: 195 (=*Spongia plumosa* Montagu, 1818). The specimen here proposed as lectotype, BMNH 1930.7.3.484 (certainly Johnston's specimen, possibly Montagu's specimen) and slides of Montagu's specimen consisting of 5 unregistered slides, three of which are labeled 'Spongia plumosa Mont, portions from various parts of type with Dr Grant. Devon Coast. Bk 944, Bk945', and two are labeled 'Spongia plumosa Mont. (Microciona plumosa Bk) Montagu's Type Spec. Hab.?', were examined. The cuts and spicules conform to Bowerbank's description. It is a massively encrusting orange sponge, with a tuberculate surface, but the areolae are very small and indistinct. Ectosomal skeleton a tangential mass of intercrossing oxeote tornotes (Fig. 8C), 140–165 × 3–6 μm. Choanosomal skeleton (Fig. 8B) is a system of plumose bundles of acanthostyles (Fig. 8D), 160–200 × 8–12 μm, anastomosing at sharp angles, and profusely echinated by shorter acanthostyles (Fig. 8D), 70–100 × 4–7 μm. Spongin well-developed. Arcuate isochelae (Fig. 8E) of 15–20 μm. The bundles of acanthostyles contain a core of oxeas in their peripheral parts, thus testifying of the artificiality of distinguishing a separate genus for *Phorbas*-like species with a predominance of acanthostyles in the choanosomal tracts. The name [*Pronax*] is preoccupied by *Pronax* Gray, 1867a: 526 (Clionaidae).

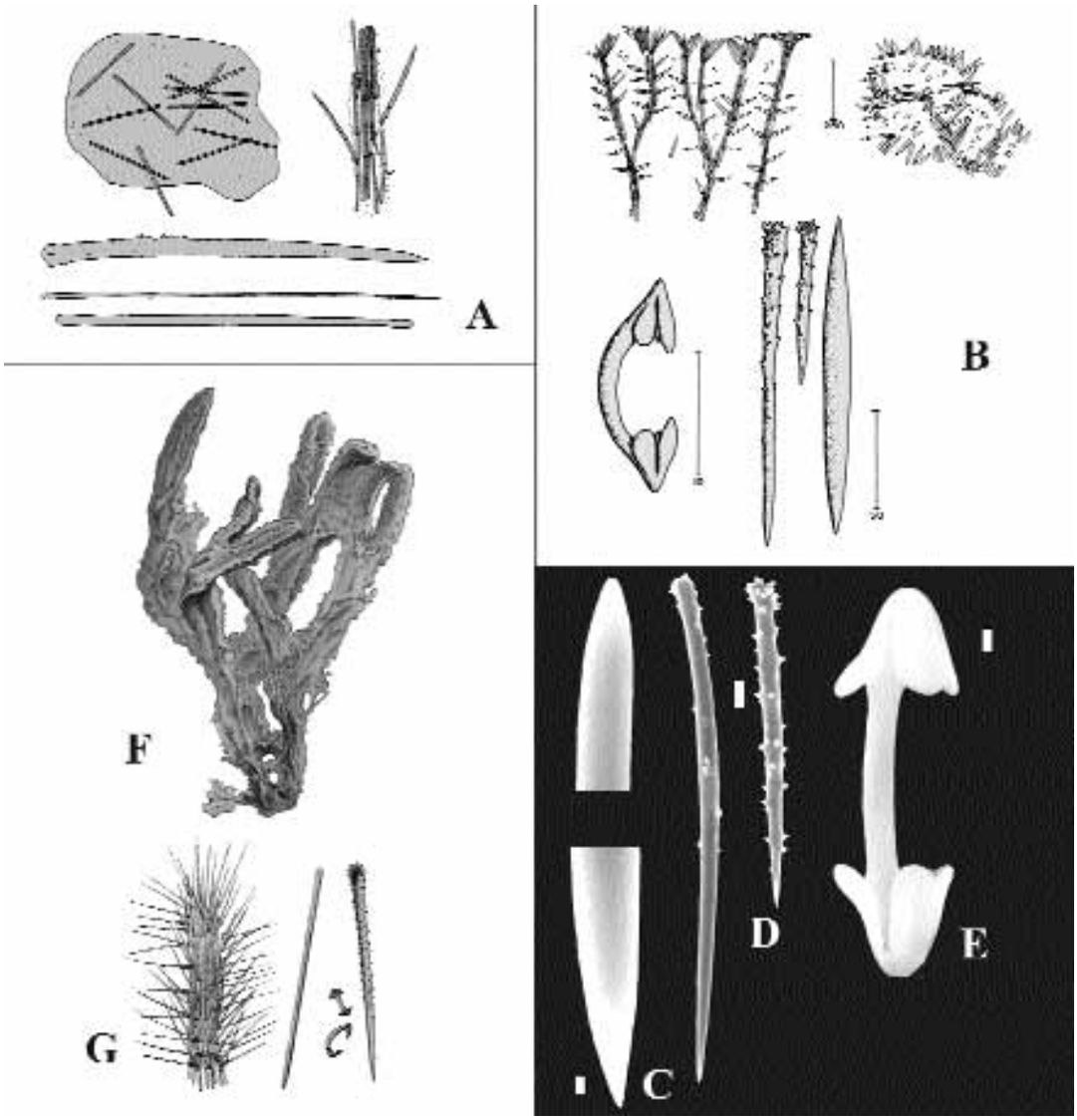

Fig. 8. *Phorbas* species. A, *Phorbas hoffmanni* (Bakus, 1966b as *Podotuberculum*), drawing of skeleton and spicules reproduced from Bakus' text-fig. 23 (sizes see text). B–E, *Phorbas plumosus* (Montagu, 1818 as *Spongia*), type of *Pronax* Gray (1867a) and *Pronaxella* Burton (1931d). B, drawing of skeleton and spicules made from a slide of the type. C–E, SEM photos of spicules made from the type (scale 1 μm; except D, 10 μm). F–G, *Phorbas dendyi* (Topsent, 1892a as *Stylostichon*). F, drawing of holotype reproduced from Topsent (1892a. pl. II fig.6) (size see text). G, drawing of skeleton and spicules reproduced from Topsent (1892a. pl. XI figs 9–10) (sizes see text).

The genus *Pronaxella* Burton, 1931d: 168 was erected as a replacement name with the same species *Spongia plumosa* Montagu (1818) as type (by original designation). Since *Pronax plumosus* is now assigned to *Phorbas, Pronaxella* likewise becomes a junior synonym. De Laubenfels (1936a: 63) was apparently unaware of Burton's proposed replacement name, and he proposed *Grayax* as a second replacement name, likewise a junior synonym of *Phorbas*.

The genus *Stylostichon* Topsent, 1892a: 111 was erected for type species (by subsequent designation; Lundbeck, 1909) *S. dendyi* Topsent (1892a: 112, pl. II fig. 6, pl. XI figs 9–10, here reproduced as Fig. 8F–G) (see Voultsiadou-Koukoura & Van Soest (1991b) for a justification of assuming *S. dendyi* as the type). *Stylostichon dendyi* is a lobate to arborescent sponge (Fig. 8F) of soft consistency. Topsent maintains the skeletal columns are entirely filled with acanthostyles, but Norwegian specimens in ZMA similar to the Azoran type specimen demonstrate the presence of mixtures of acanthostyles and tornotes in peripheral parts of the skeletal columns. Columns profusely echinated by acanthostyles (Fig. 8G) of the same size range as those in the columns. Spiculation. Strongylote tornotes (Fig. 8G), 210–300 × 4–8 μm. Acanthostyles (Fig. 8G), about 180–350 × 10–18 μm. Arcuate isochelae (Fig. 8G), about 15–56 μm.

The genus *Suberotelites* Schmidt, 1868 was erected for type species *S. mercator* Schmidt (1868: 12, pl. II fig. 15) (by monotypy). A fragment of Schmidt's type was re-examined in MNHN. The species was also redescribed by Topsent (1938a: 12), and Pulitzer-Finali (1983: 565 as *Anchinoe*, fig. 65, here reproduced

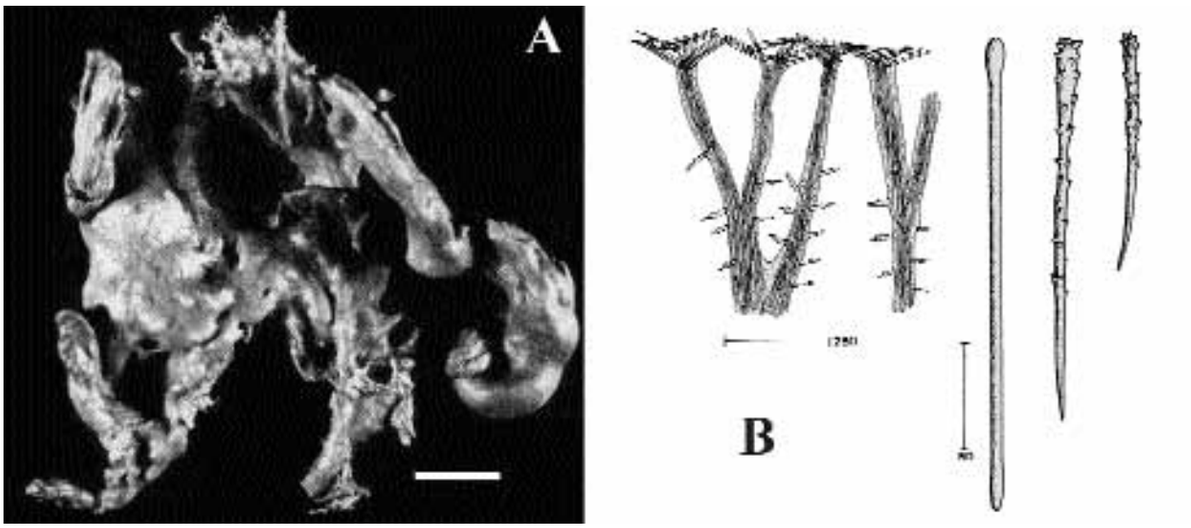

Fig. 9. *Phorbas mercator* (Schmidt, 1868 as *Suberotelites*). A, photo of habit, reproduced from Pulitzer-Finali (1983 fig. 65) (size see text). B, drawing of skeleton and spicules made from a fragment of the holotype.

as Fig. 9A). The sponge is a greyish crust, with some digitate projections of 1.5 cm long. The skeleton (Fig. 9B) consists of polyspicular bundles of 50–100 μm diameter with a coating of spongin, anastomosing irregularly but frequently. The bundles are predominantly cored by anistrongylote tornotes (Fig. 9B), 200–250 × 2–4 μm, but occasionally acanthostyles (Fig. 9B), 190–205 × 7.5–8 μm are mixed in. The bundles are echinated sparingly by shorter acanthostyles (Fig. 9B), 80–160 × 4.5–6 μm. No microscleres. The lack of chelae is considered a species character and accordingly *Suberotelites* is a junior synonym of *Phorbas*.

PLOCAMIONIDA TOPSENT, 1927

Synonymy

Plocamionida Topsent, 1927b: 16. *Hymendectyon* Bakus, 1966b: 476.

Type species

Microciona ambigua Bowerbank, 1866: 136 (by subsequent designation; de Laubenfels, 1936a: 77).

Definition

Hymedesmiidae with plocamiid basal skeleton. Megascleres mucronate tornotes, long acanthostyles, and basal acanthostrongyles. Microscleres arcuate chelae.

Diagnosis

Encrusting. Ectosomal skeleton contains paratangential brushes of tornotes. Choanosomal skeleton with hymedesmioid architecture, with long smooth styles erect on the substrate, singly or in bundles, and protruding through the surface. Long acanthostyles and short acanthostrongyles forming a reticulate basal skeleton, and also short echinating acanthostyles erect on the substrate and clustered around the bases of the long spicules; microscleres are arcuate isochelae. Three or four species.

Previous review

Topsent, 1928c.

Description of type species

Plocamionida ambigua (Bowerbank, 1866) (Fig. 10A–F).

Synonymy. *Microciona ambigua* Bowerbank, 1866: 136; Bowerbank, 1874b: 65, pl. XXXV, figs 1–9; *Hastatus ambiguus*. Fristedt, 1885: 31, pl. II, fig. 1; *Plocamia ambigua*; Topsent, 1894b: 8; *Plocamionida ambigua*; Topsent, 1927b: 16; Topsent, 1928c: 303.

Material examined. Lectotype (designation herein): BMNH 1910.1.1.65 (dry) – Shetland, encrusting shell. Paralectotype: BMNH 1930.7.3.227 – Shetland, encrusting *Lima* shell, both Norman collection; two unregistered slides, Bk 435.

Description. Thin sheets, up to ca. 20 cm across (the lectotype specimen is now a little piece of shell, 2.5 × 1.5 × 0.5 cm with a crust on it). Surface even, hispid; reported as tuberculate in Mediterranean specimens. Oscules numerous and small. Consistency soft, but difficult to determine because very thin. Colour pale red, orange, yellow or ochre. Grey-brown in alcohol, light brown dried. Skeleton (Fig. 10F) a basal layer of acanthostrongyles lying tangentially to the substratum or forming an irregular thin basal reticulation ('plocamiid' skeleton) with short, entirely spined acanthostyles oriented more-or-less at right angles to the substratum with their heads towards the base. Larger acanthostyles and much larger almost smooth styles project from this basal layer, the latter protruding through the ectosomal region. There is a surface layer of tornotes arranged as bouquets or somewhat tangentially. Chelae are scattered sparsely in a layer near the surface. Spicules (Fig. 10A–G), straight, very slender tornotes (Fig. 10A), in the type 235–(252.7)–274 × 2.5–3 μm, ca. 200–420 μm in length over the range of the species. They may have short and simple mucrons at their ends. The principal spicules of the main skeleton are large styles (Fig. 10B), lightly acanthose at the

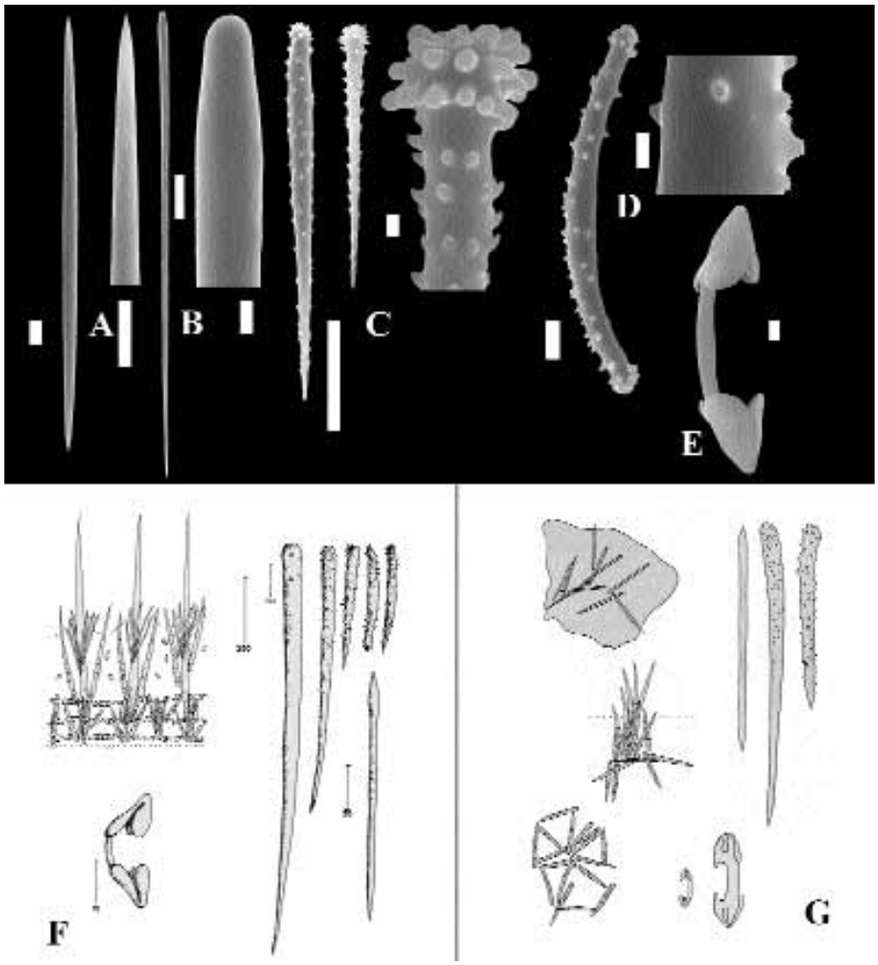

Fig. 10. *Plocamionida*. A–F, *Plocamionida ambigua* (Bowerbank, 1866 as *Microciona*). A–E, SEM photos of spicules made from the lectotype (scales A left and right, B right, D left, 10 μm; scale B left, C left, 100 μm; scale C right, D right, E, 1 μm). F, drawing of skeleton and spicules made from a slide of the lectotype. G, *Plocamionida lyoni* (Bakus, 1966b as *Hymendectyon*), drawing of skeleton and spicules reproduced from Bakus' text-fig. 16 (sizes see text).

head but otherwise smooth, measuring 500–960 × 6–14 μm in the type, up to 2000 × 28 μm in other specimens. Auxiliary spicules are smaller, entirely spined acanthostyles (Fig. 10C), in two distinct categories, the larger surrounding the heads of the main styles, 311–(353.0)–432 × 7–(8.2)–9 μm in the type, the smaller echinating the nodes of the basal skeleton, 149–(190.4)–235 × 5–(5.8)–7 μm in the type; overall acanthostyle sizes over the range of the species about 155–450 μm. Acanthostrongyles (Fig. 10D) entirely spined, curved, with often unequally swollen ends, may be distorted and variable; spines have a crown of smaller spines, 98–(102.8)–110 × 3.5–(4.2)–5 μm; 70–180 μm in other specimens. Microscleres arcuate chelae (Fig. 10E) with curved shafts, 20–(23.0)–26 μm in the type, 19–37 μm in other specimens. Distribution and ecology. NE Atlantic, Mediterranean; on bivalve shells, stones, bedrock and saddle oysters, 40–360 m.

Remarks. A further N Atlantic species of *Plocamionida* is *P. microcionides* (Carter, 1876, as *Hymeraphia*). The genus *Hymendectyon* Bakus, 1966b was erected for type species (by monotypy) *Hymedectyon lyoni* Bakus (1966b: 476, pl. IIa, text-fig. 16, here reproduced as Fig. 10G) (no material examined). According to Bakus, this is a 'persimmon'-coloured encrustation dredged up near the San Juan Archipelago, W coast of North America. Skeleton consists of a dense plocamiid skeleton of small acanthostyles, spined all over, 100–128 × 7–9 μm, upon which longer acanthostyles, with spined only in the upper half, 160–345 × 12–16 μm, are arranged in an erect outwardly projecting position. Their heads are surrounded by a bouquet of smaller acanthostyles. Ectosomal spicules are smooth oxeote tornotes, 133–153 × 4 μm. Chelae are arcuate, 25–35 μm. Although several discrepancies with *P. ambigua* are apparent (small size of the acanthostyles, absence of acanthostrongyles), the plocamiid skeleton in combination with the full spicule complement, make this species a likely member of *Plocamionida*, and accordingly *Hymendectyon* is considered a junior synonym.

PSEUDOHALICHONDRIA CARTER, 1886

Synonymy

Pseudohalichondria Carter, 1886c: 454.

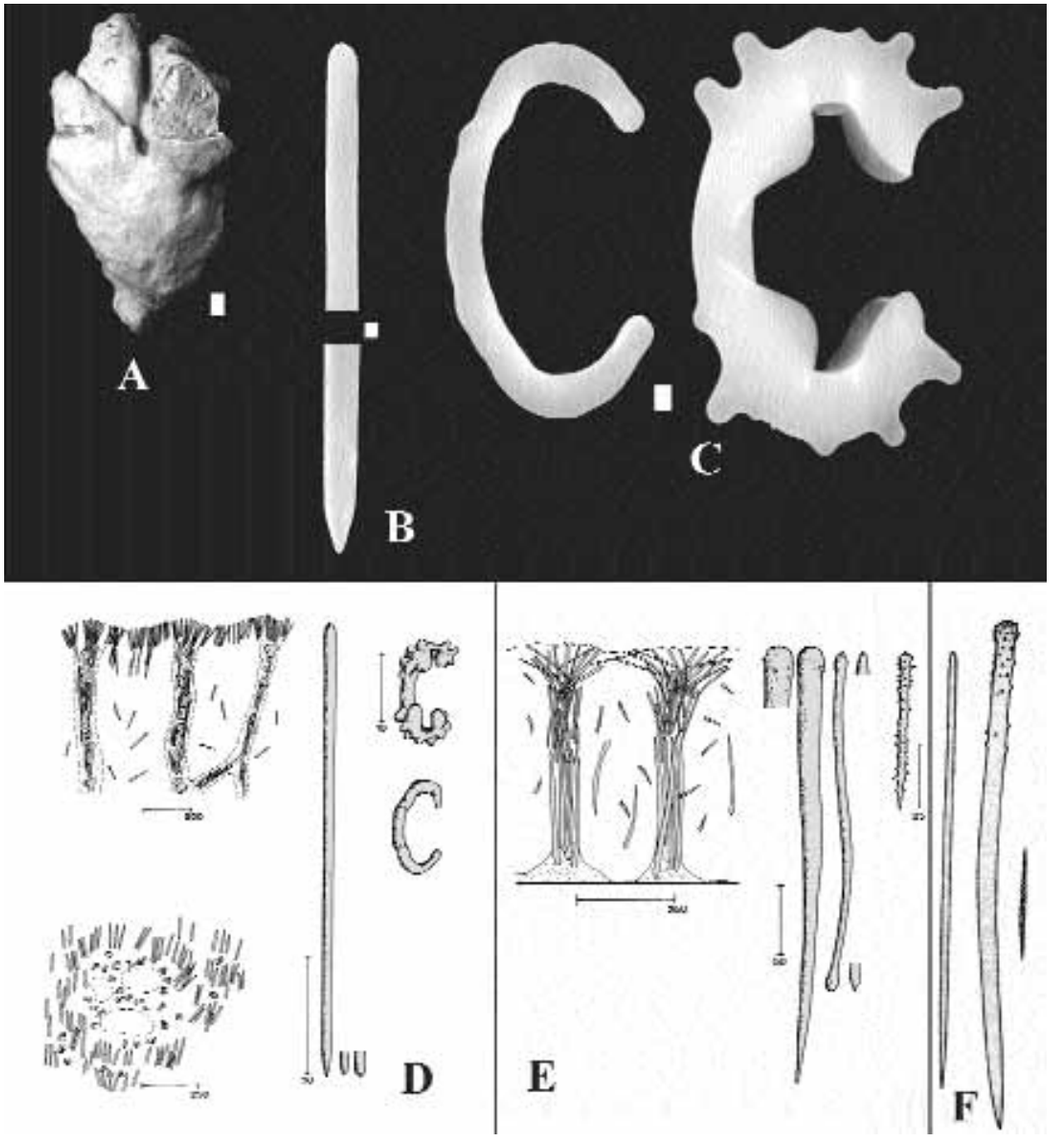

Fig. 11. A–D, *Pseudohalichondria clavilobata* Carter, 1886c. A, habit of holotype (scale 1 cm). B–C, SEM photos of spicules made from the holotype (scale 1 μm). D, drawing of skeleton and spicules made from a slide of the holotype. E, *Spanioplon armaturum* (Bowerbank, 1866 as *Hymeniacidon*), drawing of skeleton and spicules made from a slide of the holotype. F, *Spanioplon werthi* (Hentschel, 1914 as *Acanthoxa*) drawing of spicules reproduced from Hentschel's pl. VII fig. 4 (sizes see text).

Type species

Pseudohalichondria clavilobata Carter, 1886c: 454 (by monotypy).

Definition

Hymedesmiidae with plumose columns of smooth tornotes, without acanthostyles, with modified spined chelae.

Diagnosis

Massive, flabellate; ectosomal skeleton with subtylostyles; choanosomal skeleton composed of thick fibres cored with sand and subtylostyles; microscleres are spined arcuate isochelae.

Previous reviews

Carter, 1886c; de Laubenfels, 1936a.

Description of type species

Pseudohalichondria clavilobata Carter, 1886c (Fig. 11A–D).

Synonymy. *Pseudohalichondria clavilobata* Carter, 1886c: 454, pl. X figs 6–9.

Material examined. Holotype: BMNH 1886.12.15.81 (including 2 slides) – Port Philip Heads.

Description. Massive-lobose (Fig. 10A), substipitate, size $15 \times 10 \times 10$ cm. Surface smooth with very slightly raised small pore-areas. Compressible, but compact consistency, fleshy. Colour yellowish-white in alcohol. Skeleton (Fig. 11D) of the ectosome

a single-spicule palisade of megascleres strengthening the porefields and ranging individually slightly above the surface. Microscleres evenly distributed around the ostia. Choanosomal skeleton feebly developed consisting of single widely spaced spongin fibres with a core of megascleres and sand grains, 50–300 μm thick depending of the amount of sand, running straight from the interior to the surface. Few interconnecting fibres of about the same thickness. Distance between the fibres may be >1000 μm or more. Spicules, smooth styles (Fig. 11B), interpreted as tornotes, found singly at the surface and filling the fibres, 200–250 × 1.5–4 μm. Sigmoid, strongly warty-undulating microscleres (Fig. 11C) assumed to be derived from arcuate chelae, 12–18 μm. Distribution. South Australia.

Remarks

This genus shares the peculiar chela-modification with *Acanthancora* but is otherwise radically different in structure, possessing elaborate shape and lacking acanthostyles. Even the chelae, though both technically 'spined', are morphologically distinct. A second species, *P. fibrosa* was described by Whitelegge (1901) from the same geographic area; its skeleton is a bit tighter-meshed, but the main difference with *P. clavilobata* is the growth form which is distinctly arborescent.

SPANIOPLON TOPSENT, 1890

Synonymy

Spanioplon Topsent, 1890b: 31. *Acanthoxa* Hentschel, 1914: 96.

Type species

Hymeniacidon armatura Bowerbank, 1866: 183 (by original designation).

Definition

Hymedesmiidae with non-echinating accessory acanthostyles or acanthoxeas. No chelae.

Diagnosis

Encrusting. Ectosomal skeleton composed of smooth anisotornotes, smooth or microspined choanosomal styles, small acanthostyles or acanthoxeas dispersed (possibly homologues of echinating spicules or true microscleres), chelae absent. Three species.

Previous review

Van Soest, 1987b.

Description of type species

Spanioplon armaturum (Bowerbank, 1866) (Fig. 11E).

Synonymy. *Hymeniacidon armatura* Bowerbank, 1866: 183; Bowerbank, 1874b: 88, pl. XXXIV figs 12–15; *Spanioplon armaturum*; Topsent, 1890b: 31. *Hymedesmia stephensi* Burton, 1930b: 494.

Material examined. Holotype: BMNH 1930.7.3.125 – Strangford Lough, thin crust on *Pecten* shell. Schizotypes (slides): BMNH unregistered-labeled '*Hymeniacidon armaturum* Strangford Lough, Dr Dickie, #Bk. 509 (R1835 and R1836)'.

Description. Thinly encrusting, up to 1 cm thick and 9 cm in lateral expansion. Surface smooth with obvious exhalant canals, which may become grooves when the sponge is taken out of the water. In places the surface is conulose. Few oscules, and no obvious areolate porefields. Consistency soft. Colour greyish yellow. Skeleton (Fig. 11E) consists of lumose bundles of styles rising up from a basal plate of spongin. They integrade towards the periphery with bundles of tornotes which fan out when reaching the surface, forming a tangential skeleton. Loose styles and many acanthostyles are scattered singly in the choanosome. The acanthostyles are not echinating and are simulating microscleres. Spicules (Fig. 11E), tornotes, irregularly bent or curved, inequiended, ends tylote or mucronate, 186–(221.3)–242 × 2.5–(3.85)–5 μm. Styles, in majority smooth and with a faint tyle, occasionally with a spined head, 258–(269.7)–282 × 5–(7.65)–10 μm. Acanthostyles thin, straight, long-spined except in the middle part, 42–(50.6)–61 × 2–(2.95)-3.5 μm. Distribution and ecology. European coasts from Norway to the Mediterranean, on bivalve shells and stones, down to 50 m.

Remarks. A second species, *S. fertile* Topsent (1892a: 117, pl. XI fig. 11) differs in spicule sizes and in possessing centrotylote oxeas as tornotes, which is unusual in Myxillina. The genus name was also used for species with chelae. *S. cheliferum* Hentschel (1912: 368; type specimen SMF 1571 re-examined), which is assigned to *Clathria* (cf. also Hooper, 1996a), and *S. osculosum* (Topsent, 1892b: xxiii, as *Amphilectus*), which conforms to *Phorbas*. De Laubenfels (1936a) considered *Spanioplon* to be a junior synonym of *Stylopus*, but this has echinating acanthostyles different from the arrangement in *S. armaturum*.

The genus *Acanthoxa* Hentschel, 1914 was erected for type species (by monotypy) the Antarctic *A. werthi* Hentschel (1914: 96, pl. VII fig. 4, here reproduced as Fig. 11F), a massive species of 3 × 2 × 2 cm. It has ectosomal stylote tornotes, 312–360 × 7–8 μm, carried by plumose tracts of acanthostyles, 456–504 × 11–15 μm, apparently becoming arranged in a network near the substrate. The accessory spicules are acanthoxeas, 120–144 × 2.5 μm, scattered in the choanosome. The species shares the absence of echinating/basal acanthostyles, accessory acanthose spicules, and the absence of microscleres with *Spanioplon*. Boury-Esnault & Van Beveren (1982: 100, pl. XVII fig. 65, text-fig. 29) proposed to synonymize *Acanthoxa* with *Spanioplon* and this is here endorsed.