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

Family Desmacellidae Ridley & Dendy, 1886

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Desmacellidae (Demospongiae, Poecilosclerida) are poecilosclerids lacking chelae, a feature shared with the closely related families Hamacanthidae and Merliidae. Desmacellidae are distinguished from these families by the lack of diancistra-like microscleres. Noticeable in this group is a preponderance of toxic or dermatitis-producing sponges. Six valid genera are included in the Desmacellidae, viz., *Biemna, Desmacella, Dragmatella, Microtylostylifer, Neofibularia* and *Sigmaxinella*. Nominal genera *Allantophora* and *Toxemna* are considered junior synonyms of *Biemna. Tylodesma, Tylosigma, Sigmotylotella* and *Sigmatoxella* are junior synonyms of *Desmacella. Hallmannia* is a junior synonym of *Microtylostylifer*. [*Fibularia*] is a senior synonym of *Neofibularia*, but is preoccupied. *Sigmaxia* is considered a junior synonym of *Sigmaxinella*.
Keywords: Porifera; Demospongiae; Poecilosclerida; Mycalina; Desmacellidae; *Biemna*; *Desmacella*; *Dragmatella*; *Microtylostylifer*; *Neofibularia*; *Sigmaxinella*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Desmacellina Ridley & Dendy, 1886: 336. Desmacellinae Ridley & Dendy, 1887: 58. Biemnidae Hentschel, 1923: 406. Sigmaxinellidae Lévi, 1955: 84.

Definition

Mycalina lacking chelae and diancistra-like microscleres. Microscleres include sigmas, microxeas, commata and raphides.

Diagnosis

Encrusting, massive, cup-shaped, fan-shaped and branching sponges. Megascleres are usually styles, occasionally oxeas or strongyles. Spicules are typically enclosed within plumose, reticulate, halichondroid-reticulate or compressed axial fibres. Microscleres are diverse, usually consisting of sigmas (one genus excepted), and often including microxeas of several sizes, raphides in trichodragmata or occurring singly, commata, some of which may be microspined or rugose. Species belonging to this family may occur in all oceans and at all depths.

Scope

Six genera out of fifteen nominal genera are considered valid, *Biemna, Desmacella, Dragmatella, Microtylostylifer, Neofibularia*, and *Sigmaxinella*.

Taxonomic remarks

A strong synapomorphy for Desmacellidae is lacking. There are no chelae, nor any diancistra-like microscleres. Toxiform microxeas and commata are common, but are shared with Merliidae. Hooper (1984b) revised some of the conflicting ideas existing in the literature regarding the concept of the Desmacellidae. Of special concern here is the hypothesis put forward by Hallmann (1917c) that *Desmacella* Schmidt, 1870 (and Desmacellidae) would be close to Axinellidae Carter, 1875b; while *Biemna* Gray, 1867a (and a separate family Biemnidae) would be closer to the Mycalidae according to a.o. Burton (1930c) and Lévi (1957). However, following the majority of authors (e.g., Van Soest, 1984b; Bergquist & Fromont, 1988; Hooper *et al*., 1991), we prefer to assign both *Biemna* and *Desmacella* to the Poecilosclerida and to the same family. Since Desmacellidae has priority over Biemnidae, the latter is designated a junior synonym. Desmacellids are lipochelous poecilosclerids which seemingly attained this condition through the loss of their ancestral chelae (following Van Soest, 1984b as Biemnidae). Other lipochelous poecilosclerid genera, in general, are confidently assigned to various families/suborders on the basis of possession of one or more synapomorphies shared with these groups (e.g., acanthostyles, or rosettes of microscleres, etc.). However, apart from the likely loss of chelae and presumably also the loss of sigmancistra-like microscleres, desmacellids do not share additional positive traits, so the monophyletic status of this group and its affinities with other families in the Mycalina, remain weakly established. Few reproductive data have been published on desmacellid genera to date. Brien (1973a: 304) records incubated larvae in *Tylodesma* (=*Desmacella*) *annexa*, inferring viviparity. Alternatively, *Neofibularia nolitangere* is an oviparous sponge with spectacular synchronous gamete release in reef populations (Reiswig, 1970a; Hoppe & Reichert, 1987). Although not an exclusive character for Desmacellidae, it is nevertheless striking that many species are the cause of severe dermatitis when touched.

Reviews

Hallmann (1917c), Burton (1930c), Hartman (1967), Hooper (1984b), Van Soest (1984b), Hooper & Wiedenmayer (1994), Hajdu (1995, 1999).

KEY TO GENERA

(1) Two widely divergent sizes of subtylostyles, the smaller may be considered microscleres ..... ***Microtylostylifer***
Subtylostyles may be present, but no distinct microsubtylostyles 2
(2) Fistular sponge with parchment-like surface enclosing a bladder-like body; styles and trichodragmas, no sigmas ..... ***Dragmatella***
Sigmas present 3
(3) Skeleton strongly compressed axially ..... ***Sigmaxinella***
No axial condensation; skeletons plumose, plumo-reticulate, reticulate or vaguely halichondrioid 4
(4) Megascleres tylostyles, occasionally styles; microscleres limited to sigmas and raphides ..... ***Desmacella***
Megascleres (subtylo-)styles, oxeas or strongyles; in addition to sigmas and raphides there are microxeas and often also commata; frequently producing dermatitis 5
(5) Ectosomal skeleton arranged brush-like; choanosomal skeletons mostly plumose or plumoreticulated ..... ***Biemna***
Ectosomal skeletons tangential, choanosomal skeletons neatly reticulated, spongin mostly abundant ..... ***Neofibularia***

BIEMNA GRAY, 1867

Synonymy

Biemna Gray, 1867a: 538. *Allantophora* Whitelegge, 1907: 505. *Toxemna* Hallmann, 1917c: 673. [*Toxemma*] de Laubenfels, 1936a: 124 (*lapsus*).

Type species

Desmacidon peachi Bowerbank, 1866: 349 (by original designation). This is generally considered a junior synonym of *Halichondria variantia* Bowerbank, 1861: 69.

Definition

Demacellidae with stylote or exceptionally oxeote megascleres arranged in plumoreticulate fashion; ectosomal skeleton consists of the brushed endings of choanosomal tracts; microscleres include sigmas, microxeas, commata and raphides.

Diagnosis

Massive, cup-shaped or tubular sponges, with uneven surface. Plumose or plumoreticulate choanosomal skeleton, with variable development of spongin fibres cored by (subtylo-)styles of a single size, occasionally replaced by oxeote spicules; ectosomal skeleton made up of brushes of megascleres making the surface often shaggy; microscleres include sigmas, raphides, microxeas, commata, microstrongyles and spheres. Most species cause a dermatitis-like reaction when in touch with bare skin. About 55 species occur in all oceans, in a large depth range.

Description of type species

Biemna variantia (Bowerbank, 1861) (Fig. 1A, C).

Synonymy. *Halichondria variantia* Bowerbank, 1861: 69 (see Burton, 1930c: 522 for full synonymy). *Desmacidon peachi* Bowerbank, 1866: 349; *Desmacella peachi* var. *stellifera* Fristedt, 1885: 29: pl. II fig. 10; *Desmacella peachi* var. *groenlandica* Fristedt, 1887: 441, pl. XXIV figs 38–45, pl. XXVIII fig. 14. *Desmacidon koreni* Schmidt, 1875: 117, pl. I fig. 7. *Gellius capilliferus* Levinsen, 1887: 357, pl. XXX figs 7–10. *Raphiodesma aculeatum* Topsent, 1888: 152. *Desmacella hamifera* Lundbeck, 1902: 93, pl. VII figs 4–6, pl. XVII fig. 1.

Material examined. Holotype: BMNH 1877.5.21.2112 – Unregistered slide of *Halichondria variantia*, labeled as '*Hymeniacidon variantia*, St Katherine's Rocks, Tenby, Mrs Brett. 1854'. Other material. Several specimens from Ireland and Norway, a.o. ZMA POR. 4288 – Sherkin Island, Ireland. The type material of *Desmacidon peachi* could not be found in a recent search of the BMNH collections (Ms C. Valentine, pers. comm.).

Description. Encrusting, becoming a thick cushion (e.g., 1–1.5 cm thick by 7 cm diameter; thickest at the centre and tapering to the edge). It can grow into cup-like or lamellate forms when mature. Colour beige, occasionally yellow. Surface uneven (Fig. 1C) with conulose projections, due to the ends of spicule fibres supporting the surface. Larger specimens may have a distinctly 'lumpy' or shaggy appearance due to development of surface projections. Several oscules, scattered across the upper surface of the sponge, seen as dark holes in surface. Inhalant pore areas are obvious between conulose projections when seen alive. Consistency very soft and friable. Skeleton plumose. Stout multispicular fibres (of styles), branching and anastomosing, ascend through the sponge and support the surface. Tissue is packed with abundant microscleres. Minimal amounts of spongin are present. Megascleres, styles, 360–(580)–700 μm, abruptly bent near the rounded end. Microscleres, sigmas of two size categories, ca. 50–70 μm and ca. 10–20 μm; microxeas and raphides, grading into each other, ca. 63–165 μm, gathered loosely into trichodragmata; commata, 10–20 μm, looking like small, halved sigmas. These microscleres are very numerous. Ecology and distribution. On vertical surfaces with moderately strong water movement, on underside of boulders; on mud, gravel, stones. Tolerant of brackish conditions. Arctic-boreal in distribution, south to ca. 40°N. Mostly recorded from deep water (down to 1608 m), although type locality (Tenby, S England) was intertidal. Recorded recently from Ireland, Wales, Scotland, Guernsey. If synonymy is correct then it occurs also off the coast of East Greenland, down to 250 m.

Remarks. In the present concept of the species high arctic specimens which tend to have styles up to 1500 μm long are tentatively included (various 'species' of Lundbeck, 1902 are thus considered synonyms). This species has had a chequered taxonomic history and a revision may decide that its name has been too severely compromised and has to be changed. A tropical representative of *Biemna* showing a full complement of spicules is *Biemna saucia* Hooper *et al*., 1991 (Fig. 1B).

The genus *Allantophora* Whitelegge, 1907: 505 (by monotypy, no material re-examined here) was erected for *Allantophora plicata* Whitelegge, 1907: 505, pl. XLV fig. 28 (holotype is AMS

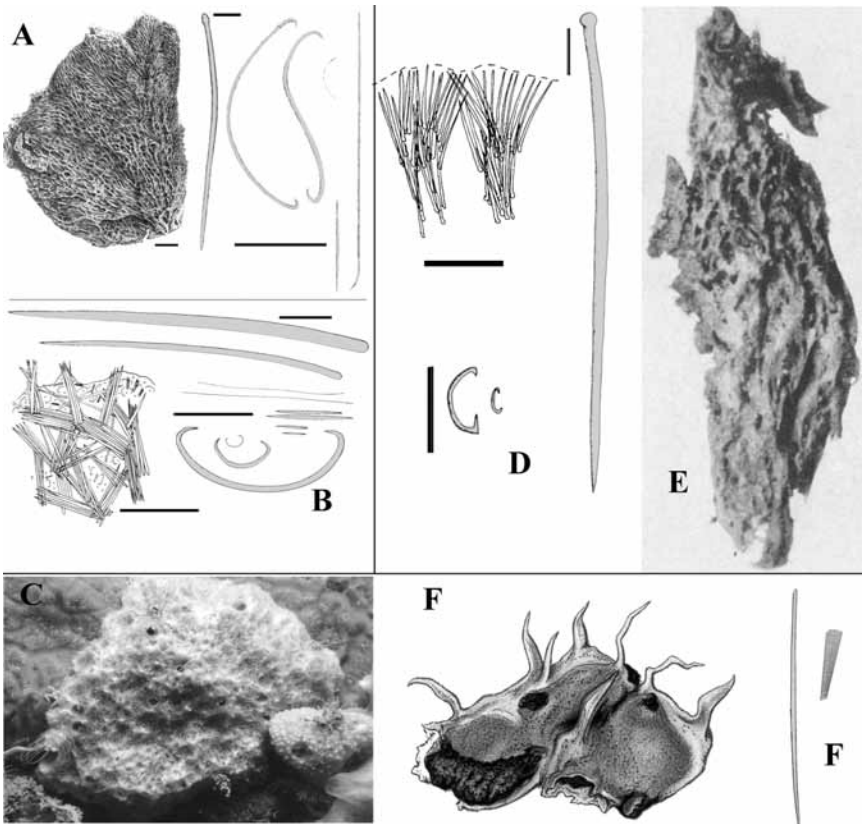

Fig. 1. A–B, *Biemna*. A, habit (scale 1 cm) and spicules (scales 50 μm) of *Desmacidon peachi* Bowerbank, 1866 (=*Biemna variantia*) (after Bowerbank, 1874, pl. LXIII figs 1–7). B, *Biemna saucia* Hooper *et al*., 1991, skeleton (scale 500 μm), megascleres (scale 50 μm) and spicules (scale 25 μm) (copied from Hooper *et al*., 1991, figs 1–9). C, Photo of live specimen of *Biemna variantia*, Ireland (courtesy B. Picton). D–E, *Desmacella*. D, skeleton (scale 500 μm) and spicules (scale 50 μm) of *Desmacella pumilio* Schmidt, 1870 (copied from Van Soest, 1984b: fig. 53). E, photo of specimen of *Desmacella pumilio* (copied from de Laubenfels, 1936a: pl. 22 fig. 1 (approx. life size). F–G, *Dragmatella*. F, habit of *Desmacella aberrans* Topsent, 1892a (copied from his pl. II fig. 7). G, spicules of the same (copied from his pl. IX, fig. 10).

G4345, cf. Hooper & Wiedenmayer, 1994: 157), on the basis of its possession of 'echinating' megascleres. Hallmann (1916b) was hesitant about the status of *Allantophora*, which was used both as a separate genus and as a subgenus of *Biemna*. Hooper (1984b), Hooper *et al*. (1991) and Hooper & Wiedenmayer (1994) considered *Allantophora* a subjective junior synonym of *Biemna* (*contra* Burton, 1930c), and this view is shared here, stressing the similar spicule complement of the type species of both. The genus *Toxemna* Hallmann, 1917c: 673 was erected (by original designation) for type species *Desmacella tubulata* Dendy, 1905: 155, pl. IX fig. 4 (type in BMNH) on the supposed occurrence of toxas in its type species. The spicules described by Dendy as toxas, organized in dragmata, are commata instead (Van Soest, 1984b). The relationships of *Biemna* to *Neofibularia* are discussed below.

DESMACELLA SCHMIDT, 1870

Synonymy

Desmacella Schmidt, 1870: 53. *Tylodesma* Thiele, 1903a: 944. *Sigmotylotella* Burton, 1932b: 295. *Sigmatoxella* de Laubenfels, 1936a: 121.

Type species

Desmacella pumilio Schmidt, 1870: 53 (by subsequent designation; Dendy, 1922b; invalid subsequent designation of *D. annexa*, by Topsent, 1925c: 704).

Definition

Desmacellidae with monactinal megascleres, arranged in plumose bundles; microscleres sigmas and raphides; the latter may be absent.

Diagnosis

Massive or thinly encrusting sponges with hispid surface. Reticulate, plumo-reticulate and vaguely halichondrioid choanosomal skeleton; poorly developed spongin fibres; megascleres tylostyles or styles of one or more sizes; microscleres sigmas and raphides. About 40 species distributed over all major areas of the oceans, predominantly in deeper waters.

Description of type species

Desmacella pumilio Schmidt, 1870 (Fig. 1D–E).

Synonymy. *Desmacella pumilio* Schmidt, 1870: 53, pl. V, fig. 14; de Laubenfels, 1936a: 114, pl. 22, fig. 1; Van Soest, 1984b: 136, pl. IX, fig. 2, text-fig. 53; *Desmacodes pumilio*; Vosmaer, 1880: 108; *Tylodesma pumilio*; Hallmann, 1916b: 519; Burton, 1930c: 525.

Material examined. Holotype: Unknown. Schizotype: BMNH 1870.5.3.27 – Slide of Schmidt's specimen, locality not mentioned, depth 592.5 m. ZMA 4761 – near Jamaica, 18°20′N 77°20′W, described in Van Soest, 1984b.

Description. The properties of the type species remain elusive, because the original description is minimal, and subsequent records of additional specimens show some discrepancies. Schmidt mentions there are two small, club-shaped, tubular sponges, with apical oscula, with tylostyles of varying sizes lying partly in fibres, and sigmas. It would also appear that there is no dermal skeleton and that the outermost spicules of the main skeleton project slightly at the surface. De Laubenfels' specimen (Fig. 1E) is 'amorphous', 8×3 cm, and there are groups of oscules, whereas Van Soest's specimen is a thin encrustation. Spicules (Fig. 1D), megascleres tylostyles, size given by de Laubenfels: 530–1400 × 9–17 μm, Van Soest gives 320–(480)–800 × 9–(11)–15 μm. Microscleres. Schmidt and de Laubenfels give a single size of sigmas, 38–78 μm and 30–40 μm respectively, whereas Van Soest records two sizes, larger sigmata, 45 μm, smaller sigmata, 15 μm. Apparently there are no raphides. This is a Caribbean deep-water species found between Cuba and Florida, and near Jamaica.

Remarks. The genus *Tylodesma* was erected by Thiele (1903a: 944) who believed that *Desmacella* was a synonym of *Hamacantha* Gray, 1867a, because the type species of the latter, *Hymedesmia johnsoni* Bowerbank, 1866, had been included by Schmidt (1870) in his list of species assigned to *Desmacella*. Dendy (1922b: 56) established the type species of *Desmacella*, as *D. pumilio*. Thiele's (1903a) view was in agreement with an earlier opinion expressed by Vosmaer (1887), and also based on the recognition that the remaining species assigned to *Desmacella* seemed to belong to a natural group. *Tylodesma* had its type species established by Hallmann (1916b: 518), as *Halichondria inornata* Bowerbank, 1866: 271, reluctantly, because the properties of Schmidt's (1870) *Desmacella* species did not appear to him sufficiently known. Bowerbank's species is represented by slides in BMNH made from the type, bearing the number 'Bk 654'. A recent search of the collections did not reveal any extant specimens (Ms C. Valentine, pers. comm.). This is a greyish white, massive, irregular species, occasionally with creeping branches. Thickness up to 7 cm. Surface irregular. Oscules few and rather large. Consistency fragile. Ectosomal skeleton a tangential layer of single megascleres or a reticulation of bundles, or a confused mass. Choanosomal skeleton multispicular bundles arranged in irregular reticulation. Megascleres tylostyles of great size variation, 190–1000 × 6–18 μm. Microscleres are sigmas, 20–45 μm, no raphides. Deep water, 100–270 m, recorded from Shetland, W coasts of Ireland, Norway, Portugal. Wiedenmayer (1977b) followed by many authors (e.g., Hooper, 1984b; Van Soest, 1984b; Bergquist & Fromont, 1988), argued that *Halichondria inornata* is very close to *Desmacella pumilio* in terms of spiculation, so that *Tylodesma* is better regarded as a junior synonym of *Desmacella*. This view is shared here.

The genus *Sigmotylotella* was erected on the fact that the bases of the tylostyles are often tuberculate. Its type species (by monotypy), *Sigmotylotella suberitoides* Burton, 1932b: 295, fig. 20 (holotype in BMNH 1928.2.15.400, labeled 'Discovery Exp. Stn. 6.'), possesses large, choanosomal tylostyles (1000 × 18 μm), with a curved shaft and well-developed spherical heads, arranged in a confused reticulation; and smaller ectosomal tylostyles (600 × 12 μm), similar in shape to the choanosomal ones, forming a dense palisade. Microscleres are sigmas, 28 μm. Hooper (1984b) already expressed doubts over the validity of this genus, arguing that tuberculate heads may be found in some *Desmacella* species, such as *D. grimaldii* (Topsent, 1892a) and *D. ithystela* Hooper, 1984b. What is left as a seemingly unique feature of *Sigmotylotella suberitoides* is its ectosomal palisade, which is not common in mycaline sponges. Ectosomal brushes, on the other hand, are very common, and these may be arranged in a dense side-by-side manner, which is often difficult to distinguish from a true palisade.

The genus *Sigmatoxella* de Laubenfels, 1936a: 121, with type species *Desmacella annexa* Schmidt, 1870: 53 (by original designation), was erected on account of the addition of toxiform raphides to an otherwise typical *Desmacella* set of spicules. We re-examined a slide of the type in the Natural History Museum, London, BMNH 1870.5.3.29; this appears to be the only extant type material (Desqueyroux-Faúndez & Stone, 1992). The species is described as massive or more thinly encrusting, occasionally forming erect masses, with irregular hispid surface. Size may exceed 5 cm. Size of oscules not recorded. Consistency fragile. Skeleton plumose, with ill-defined bundles and scattered single spicules generally directed towards the surface; no special ectosomal skeleton. Megascleres, tylostyles with prominent tyles, quite variable in size, 220–1050 × 2.5–14 μm. Microscleres, sigmas in two size classes: 25–42 and 11–15 μm; toxiform raphides, with a bend in the middle with a slight counter-bend on both sides: 50–115 × 0.5–2 μm. The species was originally described from 350 m deep off the coast of Florida, with a tantalizingly short description. The assignment of European specimens to Schmidt's species is tentative and conspecificity with specimens from the Indian Ocean likewise needs further corroboration. *Sigmatoxella* is considered a subjective junior synonym of *Desmacella*, in agreement with opinions expressed by Hooper (1984b), Van Soest (1984b) and Hooper *et al*. (1991).

DRAGMATELLA HALLMANN, 1917

Synonymy

Dragmatella Hallmann, 1917c: 640.

Type species

Desmacella aberrans Topsent, 1892a: 85 (by original designation).

Definition

Desmacellidae with fistular habit; spicules styles and trichodragmata.

Diagnosis

Encrusting sponges with hollow bladder-like habit, pointed fistules and parchment-like skin. Ectosomal skeleton a feltwork of tangentially arranged styles, choanosomal skeleton scanty bundles of styles. Microscleres exclusively long raphides arranged in sinuous

trichodragmata; no sigmata. The type species is from deep water in the North Atlantic; a second species from the South Pacific remains to be described.

Previous reviews

Hallmann, 1917c, Topsent, 1928c.

Description of type species

Dragmatella aberrans (Topsent, 1892a) (Fig. 1F–G).

Synonymy. *Desmacella aberrans* Topsent, 1892a: 85, pl. II fig. 7, pl. IX fig. 10; *Dragmatella aberrans*; Hallmann, 1917c: 640.

Material examined. Holotype: Presumably in MOM (not seen). Other material. MNHN DT1187 (slide) – labelled 'PA st. 475' (not from type).

Description (from Topsent, 1892a, 1928c). Small hollow sponge encrusting on stones or corals. No size quoted. Colour grey (preserved). Surface smooth, but provided with long thin, pointed fistules (Fig. 1F). Skeleton of the ectosome a tangential crust of intercrossing styles. Choanosomal skeleton consisting of thick spongin enforced bundles, mostly erect and occasionally branching; choanosome cavernous. Spicules (Fig. 1G) styles, somewhat curved, well-rounded, very slightly fusiform, and sharply pointed, 600–800 × 9–11.5 μm; raphides in very thick trichodragmas, 70–200 × 12–20 μm. Distribution. Azores, deep-water.

Remarks. Topsent (1892a) originally considered this species to be a *Desmacella*. Hallman, 1917c assigned the new genus to his concept of the family Axinellidae near to *Biemna*, which was included in Axinellidae by him. Later, Topsent (1928c: 224) believed this was a reduced coelosphaerid, on account of the fistular habit with parchment-like skin. Both views have merit, although neither proposal is well-founded. The combination of styles and trichodragmata is not conclusive, but the fistular habit is also certainly polyphyletic. By assigning *Dragmatella* to Desmacellidae, we assume implicitly that sigmata have become lost. The second, undescribed species from the SE Pacific is very similar in spicule sizes and form.

MICROTYLOSTYLIFER DENDY, 1924

Synonymy

Microtylostylifer Dendy, 1924: 381. *Hallmannia* Burton, 1930c: 519.

Type species

Microtylostylifer anomalus Dendy, 1924 : 382 (by monotypy).

Definition

Desmacellidae with a small category of (subtylo-)styles concentrated at the surface; microscleres are microstyles, microxeas or raphides, uncommon sigmas.

Diagnosis

Massive but small sponges with smooth surface. Ectosomal skeleton tangential, consisting of bundles of small subtylostyles, arranged rosette-like. Main skeleton plumoreticulate, consisting of large subtylostyles (mycalostyles). Microscleres very common in the type species, consisting of microstyles/raphides occurring singly or arranged in trichodragmas. Sigmas are definitely present but uncommon. Two species known, one from New Zealand, the other from Indonesia.

Description of type species

Microtylostylifer anomalus Dendy, 1924 (Fig. 2A–G).

Synonymy. *Microtylostylifer anomalus* Dendy, 1924: 382, pl. XV figs 46–49.

Material examined. Holotype: BMNH 1923.10.1.162 (wet), 1923.10.1.162a (slides) – Three Kings Islands, New Zealand, 180 m depth.

Description (modified from Dendy, 1924 and re-examination of the holotype). Small, massive sponge (fragment) of 1.5 cm diameter. Consistency crumbly but harsh. No apparent oscules. Colour in alcohol light yellowish grey. Ectosomal skeleton (Fig. 2D) easily detachable, transparent, consisting of a reticulation of bundles of megascleres and single spicules, with large numbers of microsubtylostyles scattered in between. Choanosomal skeleton (Fig. 2E) an irregular reticulation of bundles of mycalostyles and single spicules, with scattered but dense single microsubtylostyles. Megascleres mycalostyles to styles, constricted below the rounded end (Fig. 2A, F), sharply pointed at the other end, up to 750 × 27 μm. Microsubtylostyles (Fig. 2B–C), of the same shape but much smaller, and definitely classified as microscleres, uniformly 64 × 1.6 μm. Sigmas (Fig. 2G) of several sizes are present throughout the skeleton but are not common, and it is assumed that they are native to the sponge.

Remarks. Dendy (1924) assigned the genus to Suberitidae and compared it to Polymastiidae. However, there seems to be little in common with that group. Assignment of this genus to Desmacellidae is based on the shape of the megascleres, which are clearly mycalostyles, and the reticulate choanosomal skeleton with tangential ectosomal skeleton, which is shared with some *Biemna* and *Neofibularia*. The peculiar microsubtylostyles in such large quan-tities is a unique marker and the genus is considered valid with confidence.

The genus *Hallmannia* Burton, 1930c: 519 was erected for type species *Biemna aruensis* Hentschel, 1912: 352, pl. XV fig. 9, pl. XIX fig. 22 (by original designation) from Indonesia (not: [*Hallmannia*] Burton, 1931: 352, a junior homonym for type species [*Hallmannia*] *spirophora* Burton, 1931 = *Rhabderemia spirophora*). The holotype, SMF 958 was re-examined. This sponge is similar to *Microtylostylifer anomalus* in having a (plumo)reticulate choanosomal skeleton (see Fig. 3A), and a complement of large subtylostyles (Fig. 3D), 400–720 × 12–15 μm, and very much smaller subtylostyles (Fig. 3B–C, E–F), 88–136 μm (up to 3 μm in thickness), many of which are arranged in tight bundles (Fig. 3C). The latter are curved and were considered as homologous to commata by Hentschel, but this is highly debatable. As with *M. anomalus*, we observed uncommon sigmas (Fig. 3G). Hallman (1916b: 501) considered this species to be a polymastiid, which in turn induced Burton (1930c) to erect a separate genus *Hallmannia* for it. However, Hentschel's assignment to Desmacellidae appears correct, although the homology of the small subtylostyles to commata seems far-fetched. *Hallmannia aruensis* conforms in all major details to *Microtylostylifer* and accordingly it is a junior synonym.

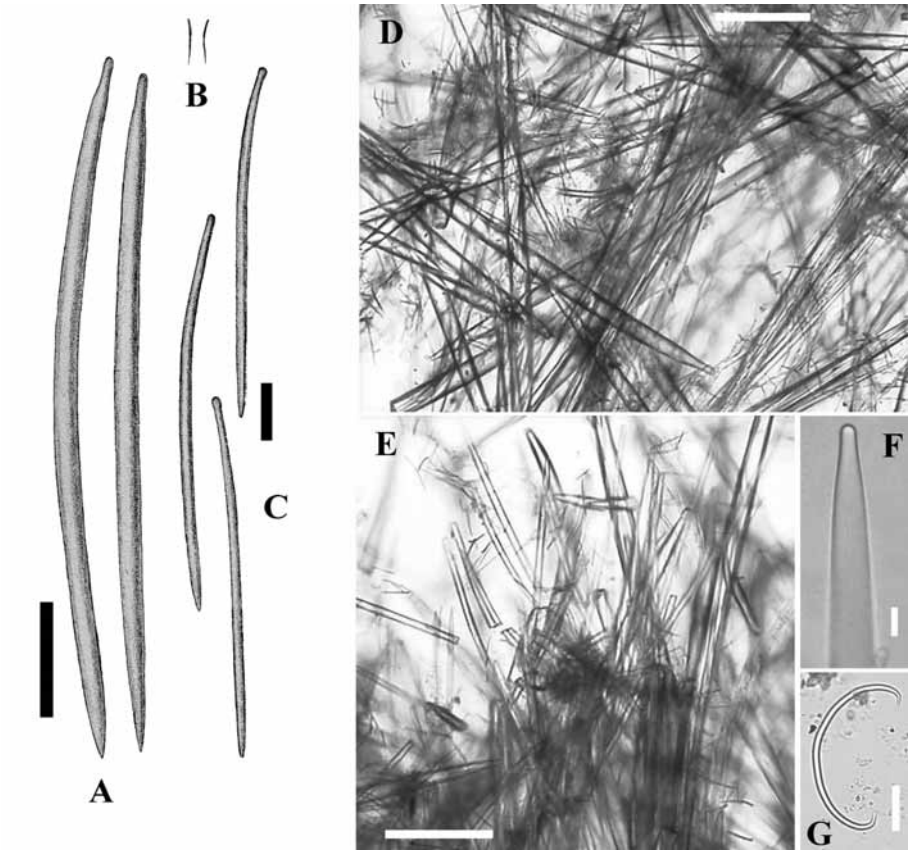

Fig. 2. A–G, *Microtylostylifer anomalus* Dendy, 1924. A–C, drawings of spicules reproduced from Dendy's Pl. V figs 46–49. A, large subtylostyles (scale: 100 μm). B, small subtylostyles (scale see A). C, the same enlarged (scale: 10 μm). D–G, photographs of sections and spicules made by J.N.A. Hooper. D, ectosomal skeleton (scale: 100 μm). E, perpendicular section (scale: 100 μm). F, detail of head of subtylostyle (scale: 10 μm). G, sigma (scale: 10 μm).

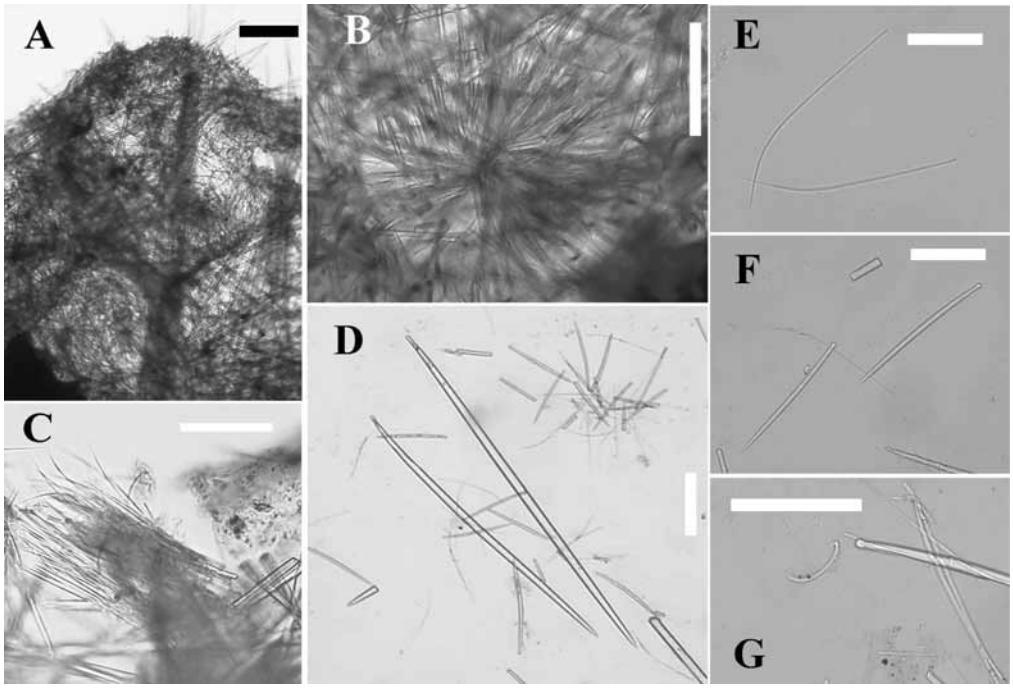

Fig. 3. A–G, *Microtylostylifer aruensis* (Hentschel, 1912 as *Biemna*), type of *Hallmannia* Burton, 1930c, photos made by J.N.A. Hooper. A, cross section showing reticulate choanosomal skeleton (scale: 500 μm). B, surface 'bouquets' of microsubtylostyles (scale: 100 μm). C, bundles of microsubtylostyles (scale: 50 μm). D, large subtylostyles (scale: 100 μm). E–F, microsubtylostyles (scale: 50 μm). G, sigma (scale: 50 μm).

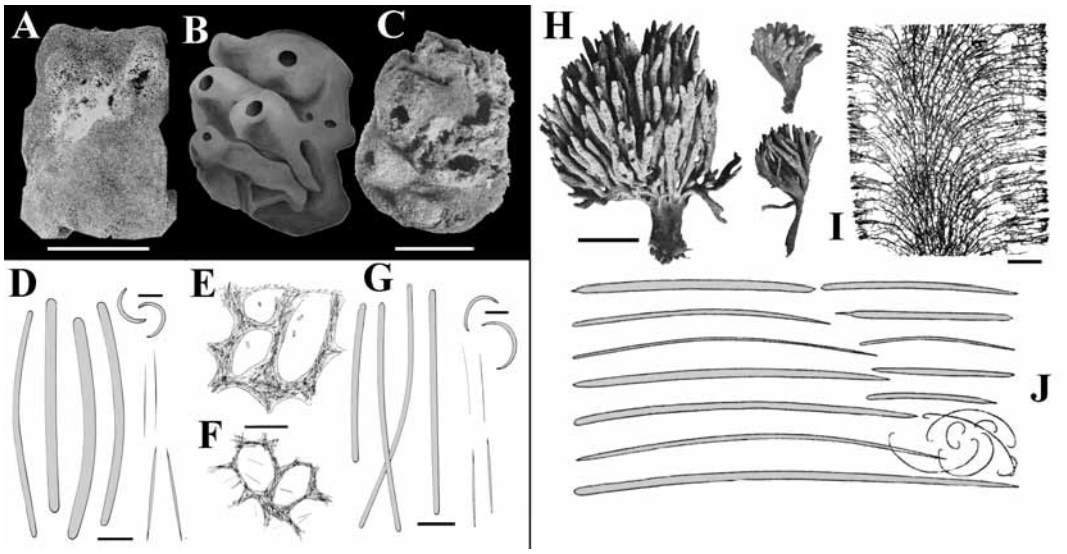

Fig. 4. A–G, *Neofibularia* Hechtel, 1965. A, photo of holotype of *Fibularia massa* Carter, 1882a (scale 5 cm) (copied from Hartman, 1967: pl. I, fig. 2). B, drawing of *Amphimedon nolitangere* Duchassaing & Michelotti, 1864 (copied from their plate XV, fig. 3). C, photo of type specimen of the latter, Museum Torino nr. 42 (scale 5 cm) (copied from Hartman, 1967: pl. I, fig. 1). D, drawing of spicules of holotype of *Fibularia massa* (scales: megascleres, 50 μm; microscleres, 10 μm) (copied from Hartman, 1967: fig. 2). E–F, drawings of cross section of choanosomal skeleton and tangential view of surface of a Curaçao specimen of *Neofibularia nolitangere* (scale 500 μm) (copied from Van Soest, 1984b: fig. 55). G, drawing of spicules of holotype of *Amphimedon nolitangere* (scales: megascleres, 50 μm; microscleres, 10 μm) (copied from Hartman, 1967: fig. 1). H–J, *Sigmaxinella* (for scales see text). H, habits of *S. australiana* Dendy, 1897 (copied from Hallmann, 1916b, pl. XXXIII, figs 1–3). I, cross section of a branch of the same (copied from Hallmann, 1916b, p. XXXIV, fig. 1). J, drawing of spicules of the same (copied from Hallmann, 1916b, text-fig. 12).

NEOFIBULARIA HECHTEL, 1965

Synonymy

Neofibularia Hechtel, 1965: 23; [*Fibularia*] Carter, 1882a: 282 (preocc. by *Fibularia* Lamarck, 1816, Echinodermata).

Type species

Fibularia massa Carter, 1882a: 282 (by subsequent designation; de Laubenfels, 1936a: 54). This is generally considered a junior synonym of *Amphimedon nolitangere* Duchassaing & Michelotti, 1864: 82.

Definition

Desmacellidae with diactinal megascleres, exceptionally stylote, and reticulate choanosomal skeleton; microscleres include sigmas, raphides, microxeas and commata.

Diagnosis

Massive or tubular sponges with irregular surface. All species are toxic sponges causing severe dermatitis. Irregular isodictyal choanosomal skeleton. Megascleres diactinal (strongyles, oxeas) or sometimes styles; microscleres sigmas, raphides, microxeas and commata. Four species have been described from tropical Atlantic and West Pacific locations.

Previous review

Hartman, 1967.

Description of type species

Neofibularia nolitangere (Duchassaing & Michelotti, 1864) (Fig. 4A–G).

Synonymy. *Amphimedon nolitangere* Duchassaing & Michelotti, 1864: 82, pl. XV, fig. 3; *Fibulia nolitangere*; de Laubenfels, 1936a: 51; *Neofibularia nolitangere*; Hartman, 1967: 7, fig. 1, pl. I, fig. 1. *Fibularia massa* Carter, 1882a: 282; *Gellius massa*; Arndt, 1927: 151, pl. II fig. 5; *Neofibularia massa*; Hechtel, 1965: 23.

Material examined. Holotype: Mus. Torino 42 – St. Thomas (photo in Hartman, 1967: pl. I, fig. 1, here reproduced in Fig. 4C). There are fragments (schizolectotypes) in MNHN (D.NBE 1062) and BMNH (1928.11.12.34). The holotype of *Fibularia massa* (photo in Hartman, 1967: pl. I fig. 2, here reproduced in Fig. 4A), from Long Cay, Bahamas, is kept in the City of Liverpool Museums, according to Hartman (1967), under nr. CLM108. An additional Liverpool Museum reg. nr. is LIVCM:ZI 69 (Mr Ian Wallace, pers. comm.). A slide of the type is kept in BMNH (1939.3.24.47) (Ms C. Valentine, pers. comm.).

Description. Massive to cake-shaped in smaller specimens, developing an apical depression and growing out into groups of wide-vented tubes (Fig. 4A–C). Colour dark red or brown. Surface optically smooth, hispid to the touch, occasionally shaggy. Size up to 30 cm high and wide. The ectosomal skeleton (Fig. 4F) may be traversed at regular intervals by vertical choanosomal spongin fibres cored by strongyles, which may project beyond the sponge surface giving it a hispid appearance. Alternatively, a regular reticulate pattern of flattened spongin fibres may occur at the surface. Where this reticulation meets the terminations of the vertical choanosomal fibres, a few spicules may protrude through the ectosome, but in these cases the sponge surface is rather smooth. Both

types of surface may occur in a single specimen. The choanosomal skeleton (Fig. 4E) consists of an irregular reticulation of flattened spongin fibres cored by strongyles. Most strongyles are disposed in rows parallel to the fibres, but some occur diagonally, piercing the fibres in all directions. Microscleres occur throughout the sponge. All types may be found at the surface, but sigmas are more abundant. Regularly arranged groups of microxeas do not occur near the surface. All types of microscleres may be found associated with the surface of the spongin fibres. Oscules may open individually at the surface, at times at the summit of an upright lobe of the sponge, or they may open into wide cloacas. Spicules (Fig. 4D,G). Sizes based on measurements of holotype of *Fibularia massa* provided by Hartman (1967: 25): strongyles, often gently curved, seldom straight, a few sinuous, 226–(316)–348 × 6.1–(7.2)–9.2 μm. Microscleres, sigmas, with roughened ends, 18–(20)–22 μm × 1.4–1.6 μm; microxeas, faintly roughened, occurring singly or in dragmas, 104–(112)–124 × 1.8–(2.0)–2.2 μm thick; raphides, occurring singly or in loosely arranged goups, 82–(95)–110 × 0.8–1.0 μm; commata, 7 × 0.8 μm. Distribution and ecology. This is a widespread species in Caribbean reefs.

Remarks. The distinction of *Neofibularia* from *Biemna* is subtle (e.g., Hooper, 1996b). Hooper & Lévi (1993a) and Hooper (1996b) suggested that species of *Neofibularia* and *Biemna* share the dermatitis-production, and may be considered closely related also for that reason. Currently, both genera are distinguished essentially by their skeletal arrangement. *Neofibularia*, known from only a few species, has a rather uniform skeletal architecture; while *Biemna*, on the contrary, is quite diverse in that respect, ranging from halichondrioid-reticulate to hymedesmioid, with sub-renieroid reticulate and plumose examples (Hooper, 1996b). The distinction of monactinal vs. diactinal megascleres appears to transgress the respective genus boundaries, with both genera showing species with either of those megascleres.

SIGMAXINELLA DENDY, 1897

Synonymy

Sigmaxinella Dendy, 1897: 240. *Sigmaxia* Hallmann, 1916b.

Type species

Sigmaxinella australiana Dendy, 1897: 240 (by subsequent designation; Hallmann, 1916b: 535).

Definition

Desmacellidae with axially compressed reticulate skeleton and extra-axially plumose skeleton; spicules styles, sigmas and microxeas.

Diagnosis

Arborescent or stipitate growth form. Cylindrical branches, rarely fused to form a flabellate sponge, with optically smooth surface. Condensed axial skeleton, plumose or plumo-reticulate to plumose extra-axial skeleton, well-developed spongin fibres; plumose, erect ectosomal skeleton; megascleres coring styles or anisostyles of a single size; microscleres are sigmas and microxeas. About a dozen species have been described from South Australia, S New Zealand and a few Indian Ocean locations.

Previous reviews

Hallmann, 1916b, Hooper, 1984b.

Description of type species

Sigmaxinella australiana Dendy, 1897 (Fig. 4H–I).

Synonymy. *Sigmaxinella australiana* Dendy, 1897: 240; Hallmann, 1916b: 535, pl. XXXIII figs 1–3, pl. XXXIV fig. 1, text-fig. 12.

Material examined. BMNH 1902.10.18.408–409 (slides). Holotype and paratypes: NMV G2292 – *fide* Hooper (1984b: 32).

Description (adapted from Dendy, 1897 and Hooper, 1984b). Erect, stipitate, ramose, bushy sponge. Branches cylindrical-compressed, dichotomously branching in two planes. Size up to 18 cm high, branches 3–8 mm in diameter. Oscules are shallow stelliform depressions, 1–2 mm in diameter, arranged in rows along the branches. Colour brownish red to rufous orange. Surface minutely hispid, generally smooth. Choanosomal skeleton an axially condensed reticulation of spicule tracts enclosed in visible spongin; extra-axial skeleton plumose ending in peripheral spicule brushes; no special ectosomal skeleton. Mesh size 100–250 μm, spicule tracts 40–100 μm in the axial region, with a core of 4–5 spicules in cross section. Connecting fibers may be devoid of spicules. Megascleres styles, and some strongylote modifications, 120–450 × 2–17 μm. Microscleres sigmas in two size categories, 25–45 μm and 9–16 μm; microxeas singly or in trichodragmas, 20–45 μm. Distribution. South Australia.

Remarks. The importance of the axial condensation of the skeletal architecture has been intensely debated lately (e.g., Hooper, 1984b; Bergquist & Fromont, 1988; Hooper *et al*., 1991; Van Soest, 1991). In spite of the currently widespread (although not unanimous) acceptance of the artificiality of taxa such as the Axinellida, the discussion has not settled down, but merely changed its level of universality. The axial compression of the choanosomal skeleton is now seen as either a likely synapomorphy for several genera, or a species-specific marker (e.g., *Esperiopsis desmophora* Hooper & Lévi, 1989; *Mycale quadripartita* Boury-Esnault, 1973). The recognition of *Sigmaxinella* depends on the synapomorphic value of the axial compression of the skeleton in sponges which otherwise are similar to *Biemna*. The possession of commata and microxeas in the latter may be regarded as further discriminating features.

The genus *Sigmaxia* Hallmann (1916b: 535, pl. XXXIII fig. 5, pl. XXXVI figs 2–3) was erected for type species *Axinella flabellata* Carter, 1885d: 361 (by original designation), types BMNH 1886.12.15.471 (dry, here designated paralectotype), 1886.12.15.473 (wet, here designated lectotype). Dendy (1897: 241) assigned this species to *Sigmaxinella*, but Hallmann decided the skeleton was less clearly axially condensed and thus could not fit into *Sigmaxinella.* Moreover, *S. flabellata* has trichodragmata as a further character distinguishing it from *S. australiana*. Hooper (1984b: 6) maintained *Sigmaxia* as distinct from *Sigmaxinella*, but subsequently acknowledged that they are probably synonyms (Hooper & Wiedenmayer, 1994: 154). As pointed out above, recent discussions (e.g., Van Soest, 1991) resulted in a lower emphasis of axially condensed skeletons as a character for genus or family distinction due to the obvious adaptive value of a reinforced axis in branching sponges. Raphides in trichodragmata are widespread

in desmacellids and obviously not of generic value. The properties of *Axinella flabellata* largely overlap with *Sigmaxinella* and it is proposed to consider *Sigmaxia* a junior synonym.

ACKNOWLEDGEMENTS

Clare Valentine (BMNH) is thanked most sincerely for the provision of type specimens and/or other specimens on loan. Mr Ian Wallace (CLM) provided information on the type specimens of *Fibularia massa*. John N.A. Hooper provided illustrations of *Microtylostylifer*. EH is further thankful to CAPES, CNPq, FAPERJ and FAPESP, from Brazil, and the organizers of the International Conference on Sponge Science (Otsu, Japan) for financial support to attend the '*Systema Porifera*' Workshops and to construct the means for writing this revision.