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Family Podospongiidae De Laubenfels, 1936

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Podospongiidae de Laubenfels (Demospongiae, Poecilosclerida) is resurrected to include taxa previously referred to Latrunculiidae Topsent based on the possession of spinose microrhabds (spinorhabds), as compared to acanthodiscorhabds, or 'chessman' spicules, in the latter. The family includes *Podospongia*, *Sigmosceptrella*, *Diacarnus* and *Negombata*, defined as having spinorhabds in one or two size classes disposed in a dense crust or scattered in a band within the ectosome. The family is included in Mycalina as *incertae sedis* based on an interpretation that the protorhabd of spinorhabds is sigmoid and potentially a sigmancistra derivative. The family also has clearly differentiated ectosomal and choanosomal skeletons; an extremely collagenous texture; where known, a viviparous reproductive strategy incubating large conspicuous bright yellow larvae; oxeas, strongyles, and variants of these megascleres; and a range of distinctive chemistries including norsesterterpene peroxides, to which cytotoxic latrunculins in *Negombata* are added, supporting postulated affinities with Mycalina and clearly differentiating them from Latrunculiidae. Species of Podospongiidae are more common in tropical and subtropical waters, occasionally also found in temperate and cold deep waters.
Keywords: Porifera; Demospongiae; Poecilosclerida; Podospongiidae; *Podospongia*; *Sigmosceptrella*; *Diacarnus*; *Negombata*.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Podospongiidae de Laubenfels, 1936a: 165.

Definition

Mycalina *incertae sedis* with a plumoreticulate radiating skeleton in which the primary fibres dominate and the secondary fibres are reduced or absent. The ectosomal skeleton can be very elaborate, forming dendritic umbelliform tracts that emanate from the apices of primary fibres. Megascleres are generally strongyloxeas but also include strongylote, tornote, stylote and oxeote modifications. Spinorhabd microscleres in two size categories form a crust or are scattered throughout the ectosome and choanosome.

Diagnosis

Thickly encrusting, digitate branching, massive tubular, vasiform to stipitate sponges with microscopically smooth conulose surface, and membranous oscules. Texture is tough, rubbery (almost cartilaginous in *Diacarnus*), compressible and fleshy to the touch. Colour in life is uniformly tan with surface pigmentation of maroon and oak brown *(Sigmosceptrella, Diacarnus)*, brilliant orange red (*Negombata*), or creamy to orange *(Podospongia)*. Structural megascleres include strongyloxeas (often vestigial in *Diacarnus*), robust curved anisostrongyles *(Negombata)* or more typically variants of styles, strongyles and oxeas *(Podospongia)*. Ectosomal skeleton with characteristic plumose 'starbursts' of spicule tracts, with fine, dendritic individual tracts arising from the ascending choanosomal fibres and expanding into tiny brushes in the ectosomal membrane (most elaborate and umbelliform in arrangement in *Diacarnus* and *Sigmosceptrella*). Choanosomal skeletal architecture dominated by huge thick hollow primary fibres interconnected by occasional short secondary fibres forming extremely elongate narrow meshes (in *Diacarnus* and *Sigmosceptrella*), or fibroreticulate, forming a tight-meshed square reticulation of anisostrongyles incorporated into clear fibres (in *Negombata*). Microscleres are spinorhabds, often in two size categories, with two whorls of spines arranged serially around the spicule, between a proximal and distal whorl of spines, one of which may be longer than the other. The protorhabd is sigmoid in *Sigmosceptrella, Negombata,* and *Podospongia*. Microscleres are typically arranged in a compact crust or are scattered throughout the ectosomal region, with smaller categories also present in the choanosome. Where known reproduction is viviparous, producing huge bright yellow-orange larvae throughout the year that are clearly visible to the unaided eye. *Diacarnus* and *Sigmosceptrella* are known to produce the biologically active compounds norsesterterpene peroxides, and *Negombata* produces latrunculins.

Scope

There are four valid genera, *Podospongia, Sigmosceptrella*, *Diacarnus*, and *Negombata*.

Distribution

Found throughout tropical to subtropical waters, occasionally in temperate to cold deep waters.

History and biology

Sigmosceptrella Dendy, 1922b, *Podospongia* du Bocage, 1869 and *Latrunculia* du Bocage, 1869 were initially included in a single family Latrunculiidae by Topsent (1922), defined as containing either spinose or discate microscleres and oxeote or stylote megascleres. Prior to the review of Kelly-Borges & Vacelet (1995) Latrunculiidae was considered to be monophyletic based on the common possession of these characteristic microscleres, even though these taxa represented at least three significantly different skeletal architectures and many other forms of microscleres. Kelly-Borges & Vacelet (1995) recognised the non-homologous nature of these various microscleres and illustrated the clear differences in the arrangements of their megasclere skeletons in each taxon, suggesting that their combined presence in a single family was

probably erroneous – although no alternative classification was proposed at that time.

This prior concept of Latrunculiidae has now been revised (Samaai & Kelly, this volume) to include only those taxa containing discate acanthose microrhabds (acanthodiscorhabds), that develop from a straight protorhabd, and are located in a tightly packed palisade in the ectosomal membrane. In Latrunculiidae megascleres are anisostyles arranged in a wispy reticulation and an ectosomal skeleton containing tangentially orientated megascleres. Latrunculiids also form thick encrusting masses and all have areolate porefields and raised oscular fistules. Based on the observation of larvae in *Latrunculia citharistae*, by Vacelet (1969), we conclude that the Latrunculiidae are viviparous. They also contain bioactive compounds, the discorhabdins and their derivatives, and pyroloquinoline alkaloids. These characters directly contrast with those of Podospongiidae, in particular the possession of a sigmoid protorhabd of the spinorhabds, indicative of potential affinities to Mycalina. Latrunculids also have a centre of diversity in the Southern Ocean, contrasting with the distribution of Podospongiidae found predominantly in tropical and subtropical waters.

REVISION OF PODOSPONGIIDAE

Prior concepts of Latrunculiidae included genera now allocated to Podospongiidae, based on the misinterpreted homology of microrhabd microscleres (discate versus spinose microrhabds, respectively), which are fundamentally different in their ontogenetic or developmental stages (see Latrunculiidae chapter). *Podospongia* (Topsent, 1928c; Boury-Esnault *et al*., 1994b; Lévi, 1993) *Diacarnus*, *Sigmosceptrella* and *Negombata* (Kelly-Borges & Vacelet, 1995) have tracts of strongyloxeas or variants of this form of megascleres, and spinorhabds in the ectosomal region. The spinorhabds are very similar across the group, with a tendency towards asymmetry in *Podospongia* and *Sigmosceptrella*. Unlike the latter three genera, which have an elaborate plumoreticulate skeleton, *Podospongia* has very simple tracts of spicules that radiate from a centrum in globular apex of the body (Fig. 1A). These tracts extend through the stalk to the base of the sponge where they attach the sponge to the surface in a root-like structure. Further comparisons between the families are provided in the chapter on Latrunculiidae (Samaai & Kelly, this volume).

Microsclere ontogenetic development, morphology and disposition

Microscleres of Podospongiidae are termed spinorhabds. These spicules dominate the ectosome in a compact crust, and are scattered in the choanosome. They are generally rod-shaped with four whorls of spines arranged serially along the spicule. Spinorhabds of *Negombata* range from very regular and whorled as in *Diacarnus*, to irregular and spiraster-like (Fig. 3A–B). In *Sigmosceptrella* the spinorhabds are more-or-less symmetrical, but the central whorls are separated by a much greater distance than they are from the apical and proximal whorls, giving the spicule a dumbbell shape (Fig. 3C–D). In addition, one of these end groups of whorls is often expanded, forming an asymmetry along the spicule. In *Diacarnus* the spicules are very regular with the four whorls separated equidistant along the shaft, with the two distal whorls forming a spinose crown (Fig. 3E–F). *Podospongia*, and one species of *Negombata* have spinorhabds and asymmetrical aciculospinorhabds, which have an elongated apical spine (Fig. 1B–C). Some species of *Podospongia* and one species of *Negombata* have aciculospinorhabds with elongated spines on both apical whorls. There are usually two size categories of spinorhabds. The protorhabd is sigmoid in *Sigmosceptrella, Negombata,* and *Podospongia*, and straight in *Diacarnus* (Fig. 3). These microscleres show no tendency to a vertical orientation as they do in some Latrunculiidae, except in the case of *Podospongia* in which the asymmetrical spinorhabds are vertically arranged in a palisade in the ectosome. The sigmoid tendency of the protorhabd is hypothesized as possible evidence for a close affinity to the Mycalina, as a potential sigmancistra derivative. Nevertheless, Podospongiidae remains *incertae sedis* within Mycalina, in particular, and Poecilosclerida in general, whereas the family taxon is clearly differentiated from Latrunculiidae (as revised here).

Megascleres & skeletal architecture

All Podospongiidae have strongyloxeas as megascleres, and *Negombata* and *Podospongia* have additional forms that include stout curved anisostrongyles in the former, and strongyloxeas with various stylote, tornote or oxeote modifications in latter. Anisostrongyles in *Negombata* are restricted to the fibrous network of the 'axial' region and they are embedded in spongin. The four podospongiid genera are characterised by the common possession of a fibroreticulate plumose skeleton, except in the case of *Podospongia*, which has tracts that radiate from a centrum into the globular mass and stalk. In *Diacarnus* huge spongin-reinforced fibres form elaborate dendritic umbelliform arrangements in the ectosome, while in *Sigmosceptrella*, these are less elaborate. In both these genera the primary fibres are huge and hollow with only minor secondary connections, whereas in *Negombata* the primary and secondary fibres are not readily distinguishable. *Podospongia* has a radiating stipitate morphology, and *Negombata* has an elaborate 'axial' fibroreticulation with 'extra-axial' radiating dendritic tracts that diverge from the fibroreticulation towards the ectosome.

Gross morphology

Sigmosceptrella and *Diacarnus* form digitate lobate rambling encrustations, large tubes and huge barrels in the case of *Diacarnus*. *Negombata* species are digitate or foliose. An as-yet undescribed species from Indonesia is pedunculate. *Podospongia* is stipitate and most species are tiny, being less than 60 mm in length, but mostly less than 10 mm. None of the genera have any special surface features, although *Podospongia* has an apical oscule that is fringed by a palisade of megascleres. These sponges are flexible, compressible and very elastic due to their rich collagenous mesohyl matrix. The texture is smooth and flesh-like as the sponge ectosome is also charged with abundant collagen.

Reproduction

In several species of *Sigmosceptrella, Diacarnus*, and *Negombata* reproduction is viviparous, with characteristically huge (2–3 mm diameter) bright yellow-orange larvae visible to the unaided eye produced throughout the year (Fig. 2D). No reproductive products have been observed in *Podospongia*.

Pigmentation

Podospongia, *Sigmosceptrella* and *Diacarnus* have a cream basal pigmentation and a mottled maroon or oak brown pigmentation in

the ectosomal membrane where they are exposed to light. *Negombata magnifica* and *N. corticata* are a brilliant orange red that is persistent in ethanol preservative for some time (Kelly-Borges & Vacelet, 1995). *Podospongia* spp are invariably described as cream or white in life.

Biochemistry

Sigmosceptrella and *Diacarnus* contain biologically active norsesterterpene peroxides (see Urban *et al*., 2000; Kelly-Borges & Vacelet, 1995). These include muqubilins recorded from a species of *Diacarnus* and specimens from the Red Sea identified as '*Prianos*'. This latter identification is highly suspect and it is likely that this material belongs to *Diacarnus*, for which species exist that have incomplete spicule complements, possessing only vestigial strongyloxeas similar to typical species of *Prianos* (containing only strongyles) (Urban *et al*., 2000). Cytotoxic latrunculins have been described from Red Sea species of *Negombata* (Gillor *et al*., 2000). The chemistry of *Podospongia* is unknown.

Ecology, bathymetric and biogeographical distribution

Podospongia is predominantly a deep-water sponge collected down to 600 m, typically found around 100 m or more. Species are known from New Caledonia, Natal coast of South Africa, north-eastern and central Atlantic Ocean. Three species of *Negombata* are known from the shallow tropical western Indian Ocean and southeast Asian waters, *Sigmosceptrella* overlaps this distribution and extends from the Western Indian Ocean to cool temperate southwest and eastern coasts of Australia. *Diacarnus* is common throughout southeast Asia and the central west Pacific, extending east to Fiji and south along the southwest, east and northeast coasts of Australia. Most species live in typical coral reef environments, on dead coral substrate, down to depths of about 50 m.

Phylogenetic affinities

The four genera included in Podospongiidae (*Podospongia, Diacarnus, Sigmosceptrella* and *Negombata*) form a cohesive group characterised by the possession of spinorhabds, as opposed to acanthodiscorhabds in Latrunculiidae (Kelly-Borges & Vacelet, 1995; Samaai & Kelly, this volume). This is considered to represent a fundamental difference in the ontogenetic development of these microscleres, and not merely a morphometic variation (see chapter on Latrunculiidae). In all genera except *Diacarnus* the protorhabd of the spinorhabd is sigmoid, or a derivative of a sigmoid shape. This ontogenetic development of microscleres, coupled with the predominance of a pseudoaxial plumoreticulate skeleton, strongyloxeas and anisostrongyles with various tornote, oxeote and stylote modifications and vivipary, indicate greater affinity with poecilosclerid sponges than with hadromerids (to which 'Latrunculiidae' of authors, i.e., Latrunculiidae + Podospongiidae, was previously assigned; see Samaai & Kelly, this volume). We consider that Podospongiidae has a greater affinity with the poecilosclerid suborder Mycalina than with Latrunculiidae, the latter assigned to its own suborder (Latrunculina subord. nov.) *incertae sedis* within Poecilosclerida. Closely related genera *Phlyctaenopora* Topsent and *Barbozia* Dendy were also previously included within Latrunculiidae, but are now assigned *incertae sedis* to the Mycalidae due to their possession of anisochelae. While Podospongiidae do not have chelae microscleres or any other type of microsclere that could be construed as directly (or obviously) linking them to the Mycalidae, their plumose, semi axial/extra-axial architecture of spongin-bound stylote or oxeote megascleres, and possession of a sigmoid protorhabd, suggest their affinities lie most clearly with the Mycalina (particularly with Cladhorizidae, Mycalidae).

This conclusion is supported by non-morphological evidence. Norsesterterpene peroxides have also been found in a species of *Mycale* (Capon & Macleod, 1987a) and the suggested poecilosclerid affinity of Podospongiidae is strengthened by molecular evidence. An 18S rDNA sequence of *Negombata corticata* was consistently contained within the clade containing two species of *Clathria* (Microcionidae, Poecilosclerida), rather than *Acanthochaetetes* (Spirastrellidae, Hadromerida) (Adams *et al*., 1999). Refer to further discussion in the chapter on Latrunculiidae.

KEY TO GENERA

(1) Choanosomal tracts radiating from a centrum, stipitate body ..... ***Podospongia***
Plumoreticulation 2
(2) Megascleres styles in addition to strongyloxeas ..... ***Negombata***
Megascleres strongyloxeas with various tornote, oxeote or stylote modifications 3
(3) Huge hollow primary fibres with umbelliform ectosomal skeleton, protorhabds of microscleres straight ..... ***Diacarnus***
Thick dense primary tracts with robust ectosomal tracts, surface crust of spinorhabds, protorhabds of microscleres sigmoid ..... ***Sigmosceptrella***

PODOSPONGIA DU BOCAGE, 1869

Synonymy

[*Lovenia*] du Bocage, 1868 (preocc.). *Podospongia* du Bocage, 1869: 160. *Alcyospongia* de Laubenfels, 1934: 18.

Type species

Podospongia loveni du Bocage, 1869: 160 (by monotypy).

Definition

Podospongiidae with tracts of oxeas with various strongylote, stylote, tornote and oxeote modifications radiating along the stalk and within the elliptical expansion above the stalk; spinorhabds and aciculospinorhabds are packed in a vertical arrangement in the ectosome and scattered throughout choanosome, protorhabds are sigmoid.

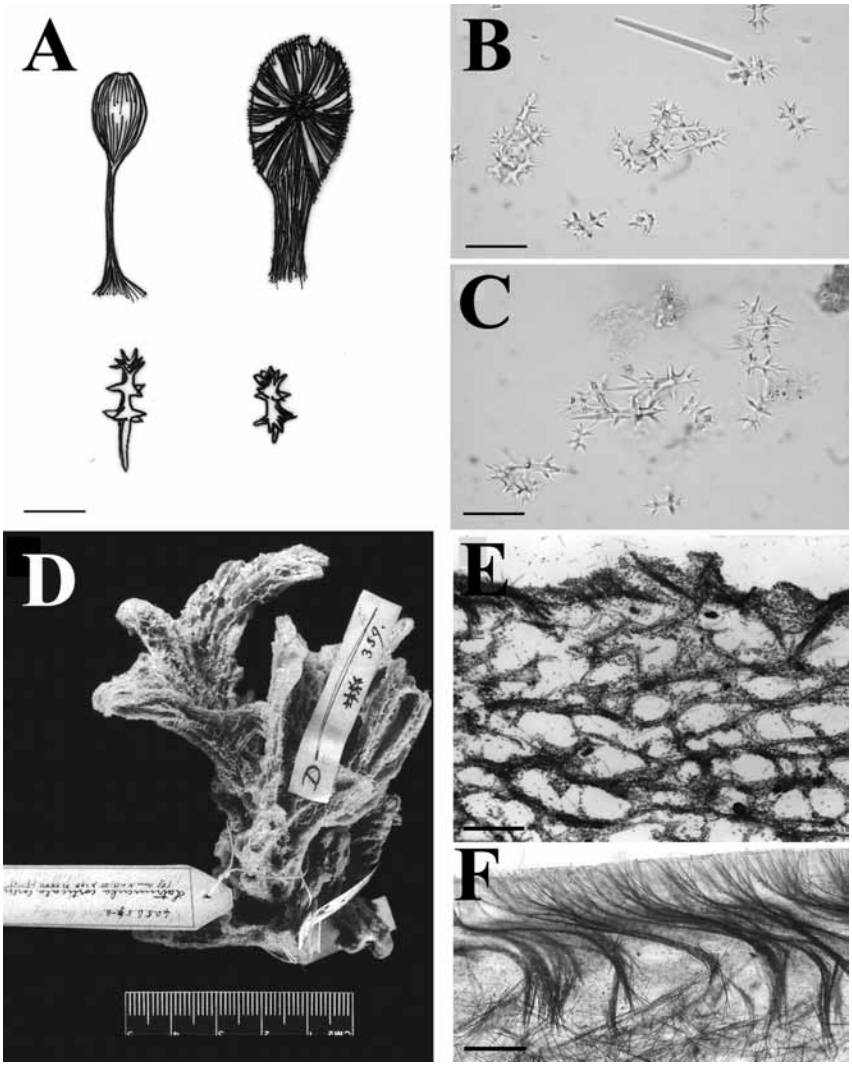

Fig. 1. *Podospongia* (A–C) and *Negombata* (D–F). A–B, *Podospongia loveni* Bocage (redrawn from du Bocage, 1869, pl. 10, fig. 1). A, whole sponge (upper left) and vertical section showing radiating tracts of megascleres that emerge to form a solid stalk, and crypt-like apical oscule (upper right) (scale 10 mm). Aciculospinorhabd (lower left) and spinorhabd (lower right) microscleres that form a crust in the ectosome and scattered throughout the choanosome (scale 30 μm). B, (paratype MNHN LBIM.DT 1115) aciculospinorhabds and spinorhabds (scale 40 μm). C, *Alcyospongia india* de Laubenfels, 1934 (holotype USNM 22365), aciculospinorhabds with prominent apical spine (scale 40 μm). D–E, *Negombata corticata* (Carter) (holotype BMNH 1840.6.56–58; after Kelly-Borges & Vacelet, 1995). D, holotype (scale 50 mm). E, ectosomal and choanosomal skeleton (scale 600 μm). F, *Negombata magnifica* (Keller) (schizotype BMNH 1908.9.24.118, after Kelly-Borges & Vacelet, 1995), ectosomal and choanosomal skeleton (scale 60 μm).

Diagnosis

Predominantly stipitate with an elliptical head, usually less than 6 cm in total length, typically less than 20 mm long, apical oscule often with a fringe of megascleres, possibly rarely thinly encrusting. Megascleres are modified oxeas radiating from a centrum in uniform tracts extending into the stalk where they extend to root-like processes for attachment. Microscleres are smooth straight spinorhabds of a variety of forms including asymmetrical and symmetrical forms, and aciculospinorhabds; reproduction and biochemistry unknown; colour in life uniformly cream to white.

Previous reviews

Topsent (1922, 1928c); de Laubenfels (1936a); Boury-Esnault *et al*. (1994b).

Description of type species

Podospongia loveni du Bocage, 1869 (Fig. 1A–B).

Synonymy. [*Lovenia*] *borealis* du Bocage, 1868: 37 [*nomeno blitum*]. *Podospongia loveni* du Bocage, 1869: 160.

Material examined. Holotype: Lost.

Description (modified from du Bocage, 1869). Sponge composed of a curved vertical stem and an elliptical head, strongly attached to the substratum by a large base not divided into root-like processes (Fig. 1A). There is a single apical oscule. The surface of the elliptical portion has numerous depressions and is uneven and bristling with the emergent tips of the megasclere tracts. The ectosomal region is distinctive with a layer of spinorhabd microscleres that are aligned vertically in the ectosome. The skeleton consists of radiating tracts of megascleres (which appear from the illustrations to be a mixture of oxeas, strongyles and strongyloxeas, 400–500 μm

long) which extend into the axis of the sponge (Fig. 1A). Microscleres are scattered in the choanosome as well (Fig. 1A).

Remarks. *Podospongia* was erected by du Bocage (1869) to replace the genus [*Lovenia*], which he had earlier erected for *Lovenia borealis* du Bocage (du Bocage, 1868). The genus name was preoccupied by *Lovenia* Desor, 1847, an echinoderm. Theoretically the species name *P. borealis* has priority over the name *P. loveni.* However, the former has not been used after 1899 and therefore prevailing usage is maintained (ICZN Art. 23.9; Anon., 1999).' The holotype has since been confirmed destroyed.

It is not necessary to emend the genus diagnosis as the original description and subsequent descriptions of *Podospongia loveni* (Topsent, 1928c; Boury-Esnault *et al*., 1994b) and other species (Lévi, 1993; Kirkpatrick, 1903) are adequate to provide a firm concept of the species, and consequently also of the genus. A slide of spicules of a paratype specimen of *Podospongia loveni*, from Portugal, supplied by Professor Claude Lévi, conforms closely to du Bocage's original description (Fig. 1B). The genus is characterised by its stipitate gross morphology, with unusual modified oxeote spicules radiating in tracts from a centrum in the centre of the globular head. Spicule tracts are aligned longitudinally within the stalk or peduncle. In some species, the base of the peduncle forms fine rhizoid-like structures for attachment to the substrate. Aciculospinorhabds form a crust within the ectosome.

De Laubenfels (1934) considered *Alcyospongia* (type species *A. india* de Laubenfels, 1934: 18) to belong to Latrunculiidae because of its apparent relationship to the genus *Podospongia*. This West Indies specimen (USNM 22365) was differentiated from *Podospongia* by its possession of 'straight streptasters', and the fact that the centrum from which the tracts radiated was at the base of the globular mass, rather than at its centre, as in *Podospongia*. In all other characters, the sponge is similar to species of *Podospongia*. Examination of the type specimen revealed that the centrum was depressed in the globular region, but we consider that it could easily be the result of dehydration as an artifact of preservation. A new spicule preparation revealed that the 'straight streptasters' were foreign, and very similar to those that would occur in astrophorid families, and that the sponge had asymmetrical spinorhabds as in other species of *Podospongia* (Fig. 1C). Sigmoid protorhabds were also present in the new spicule preparation. De Laubenfels (1934) regarded the new genus assignment as doubtful, considering that the position of point of radiation of the tracts may not be that important phylogenetically. Given that the streptasters are foreign inclusions or may have been from another sponge at the time of collection, we concur with de Laubenfels' doubts and hereby formally relegate *Alcyospongia* into synonymy with *Podospongia*.

Distribution

Podospongia is generally found in deeper water down to 600 m, from the Natal coast of South Africa, New Caledonia and the central and north Atlantic. *Latrunculia normani* Stephens is also most probably a species of *Podospongia* but it is thinly encrusting, the only character that does not conform to the diagnosis of the genus.

NEGOMBATA DE LAUBENFELS, 1936

Synonymy

Negombata de Laubenfels, 1936a: 159.

Type species

Latrunculia corticata Carter, 1879b: 298 (by original designation).

Definition

Podospongiidae with a small square-meshed reticulation of strongyloxeas and robust styles bound into clear spongin, dendritic plumose tracts arise from this 'axial' fibroreticulation in an 'extra-axial' region, microscleres are irregular spinorhabds, these are packed in the outer ectosome and are abundant throughout the choanosome, protorhabds pseudo-sigmoid (recurved).

Diagnosis

Erect, foliose, pedunculate, digitate, branching. Compressible, with an extremely smooth surface through which large pores are clearly visible. Megasclere skeleton consists of uniform, elongate, to square-meshed reticulation of clear spongin cored fairly irregularly with thick, slightly curved oxea with strongylote ends, and a clear hollow axial canal. Ectosome with thin fusiform wavy oxeas in tracts that fan within a thick collagenous ectosome, ultimately forming surface brushes. Microscleres, irregular spinorhabds in two sizes, largest very irregular, thick, without a distinct shaft, smaller, with a distinct straight or curved shaft with spines of uneven length arranged roughly in two central whorls and two terminal bunches, terminally commonly double. Immature microscleres, straight rods in which one or more spines from apices are strongly recurved, disposed predominantly on the extreme external surface of the ectosome, but can also be very dense within the choanosome (modified from Kelly-Borges & Vacelet, 1995).

Previous reviews

De Laubenfels (1936a); Hooper (1986); Kelly-Borges & Vacelet (1995).

Description of type species

Negombata corticata (Carter, 1879b) (Fig. 1D–E).

Synonymy. *Latrunculia corticata* Carter, 1879b: 298. *Latrunculia tarentina* Pulitzer-Finali, 1983: 513.

Material examined. Holotype: BMNH 1840.5.6.56–58.

Description (modified from Kelly-Borges & Vacelet, 1995). Sponge (in the dried state) is erect and composed of short, curved, flanged, narrow fans of different lengths with a restricted base of attachment (Fig. 1D). Surface texture of dry sponge is fibrous and roughened; Carter (1879b) described the fresh sponge as 'chondroid' and 'smooth' with pores 20 μm diameter and 74 μm apart. Colour yellowish white in dry sponge. The choanosomal skeleton consists of a central axis of rectangular meshes formed by spongin fibres, 300–600 μm diameter, not clearly differentiated into primary and secondary tracts (Fig. 1E). Megascleres are not arranged uniformly within fibres, but rather, are scattered singly or in groups, and oblique or occasionally perpendicular to the fibre axis. An ectosomal skeleton of wavy oxeas is present, but this has collapsed in the holotype, rendering the arrangement difficult to determine. The holotype of *Negombata magnifica* (Keller) shows this feature more clearly (Fig. 1F). Microscleres are densely packed on the sponge surface and also in the choanosome, almost obscuring

fibres (Kelly-Borges & Vacelet, 1995). Megascleres are oxeas, being thick, straight or slightly curved with rounded strongylote ends, 346(317–384) × 10–12 μm, and thin with ends fusiform, 422(394–451) × 2.4–6 μm. Microscleres are spinorhabds of 2 size classes, having slightly curved or spiraled spines of uneven lengths, 26–35 μm in length (Fig. 3A–B).

Remarks. *Negombata* is clearly differentiated from *Latrunculia* (Latrunculiidae) by its regular axial fibrous reticulation, a dendritic-plumose extra-axial skeleton, and irregular spinorhabds (Kelly-Borges & Vacelet, 1995). *Negombata* also differs from *Diacarnus*, *Sigmosceptrella* and *Podospongia* in having two forms of strongyloxea megascleres, one of which is robust, curved, anisostrongyle which is always embedded in the spongin of the axis. In *N. kenyensis* these spicules have stylote modifications to one end rendering their appearance style-like. Microscleres of *Negombata* are spinorhabds and are densely packed in the sponge ectosome, but they are irregular and the spines are spiraled rather than serially arranged as in the other three genera. A particular characteristic of this genus is the faintly translucent glass-smooth surface, noted by Keller (1889), when he described *N. magnifica*.

Distribution

Negombata has a similar distribution to *Sigmosceptrella* (see below), although species do not extend into the West Central Pacific or into Australia. *Negombata* is represented so far by four species, three of which have a brilliant orange-red colouration and a digitate or leafy gross morphology: *Negombata magnifica* and *N. corticata* from the Red Sea; *Negombata kenyensis* Pulitzer-Finali from Zanzibar; and a new pedunculate species still undescribed from Indonesia, with a cream-orange colouration.

DIACARNUS BURTON, 1934

Synonymy

Diacarnus Burton, 1934: 549.

Type species

Axos spinipoculum Carter, 1879b: 286 (by original designation).

Definition

Podospongiidae with strongyloxeas arranged in huge hollow spongin-bound primary fibres, connected by sparse thin secondary fibres, umbelliform dendritic arrangements of thin tracts emerge from the apex of each primary fibre. Microscleres are regular spinorhabds with whorls of spines arranged equidistant along the shaft of the spicule, forming a crust at the surface of the sponge or in a mid-ectosomal band, and are scattered throughout the choanosome, protorhabds straight.

Diagnosis (modified from Kelly-Borges & Vacelet, 1995)

Massive, barrel-shaped, tubular or lobate-digitate sponges. Surface with single or multiple conules or blunt broad tubercles or mounds, microscopically smooth, slippery and rubbery. Ostia radiate in stellate formation in shallow rounded depressions, oscules apical with low fleshy raised collars. Texture extremely tough, almost cartilaginous, fleshy, elastic. Colour in life cream base with pale purple-pink, and mottled with deep reddish brown and yellow brown. Skeletal arrangement plumoreticulate with huge thick hollow fibres optically visible, connected sparsely by thin secondary fibres. Ectosome dense, highly collagenous, distinct from the underlying choanosome, with layers of collencytes and collagen fibrils parallel to the surface. Megascleres are strongyloxeas, with a faint subterminal swelling at the proximal end, with the distal end oxeote or more typically strongylote. Microscleres are two size categories of spinorhabds. Sponges incubate huge bright orange-yellow larvae.

Previous reviews

Carter (1879b); Hooper (1986); Ilan (1995); Kelly-Borges & Vacelet (1995).

Description of type species

Diacarnus spinipoculum (Carter) (Fig. 2A–C).

Synonymy. *Axos spinipoculum* Carter, 1879b: 286; *Diacarnus spinipoculum*; Burton, 1934: 549; *Latrunculia spinipoculum*; Hooper, 1986: 181. *Latrunculia hallmanni* Wiedenmayer, 1989: 41.

Material examined. Holotype: BMNH 1846.10.14.174.

Description (modified from Kelly-Borges & Vacelet, 1995). Large spherical to oval barrel-shaped sponge with a deep central atrium, oscules, scattered on interior walls of atrium (Fig. 2A). Surface heavily tuberculate to mammillate, rubbery and microscopically smooth to touch. Colour in life, mahogany brown, mottled with pale pinkish red, rim of apical atrium and atrium walls cream-white. Cream in ethanol. The choanosomal skeleton consists of large primary fibres, 500–900 μm diameter, which radiate towards the surface, connected by rare short secondary fibres, 250–300 μm diameter, or anastomosing with adjacent primary fibres in the deeper choanosome (Fig. 2B). Primary fibre tip divides into an umbel of numerous slender dendritic spicule tracts, 38–70 μm, where the primary fibres passes through ectosome-choanosome boundary. Dendritic spicule tracts occasionally branch below surface and diverge and ramify within ectosome, where they form slightly fanned brushes (see Fig. 2C). Ectosomal skeleton, 1200–1500 μm deep, extremely dense with parallel collagen fibrils, easily distinguished from underlying choanosome which is dense and soft. A plumose ectosomal skeleton of wavy oxeas is present, but this has collapsed in the holotype, rendering the arrangement difficult to determine. Larger microscleres are scattered predominantly around edges of exhalant canals in choanosome, around ectosomal lacunae, and just below lower boundary of ectosome where smaller thinner spinorhabds are also found. Megascleres are strongyloxeas with slight subterminal swellings, 57(53–65) × 2(1–5)μm. Microscleres are spinorhabds of 2 size classes, 46–57 μm in length (Fig. 3E–F).

Remarks. In a revision of *Axos* Gray (Hemiasterellidae, Hadromerida) Hooper (1986) transferred *Axos spinipoculum* to *Latrunculia* in recognition of the superficial similarity of the general skeletal and spicule features to those of *Latrunculia sensu lato*. Kelly-Borges & Vacelet (1995) progressed this idea further by reassigning this species to a revised concept of Burton's *Diacarnus*. They also noted that the skeletal arrangements, microsclere morphology and arrangement, colouration and texture differed from all known species of *Latrunculia*, and that *Diacarnus*

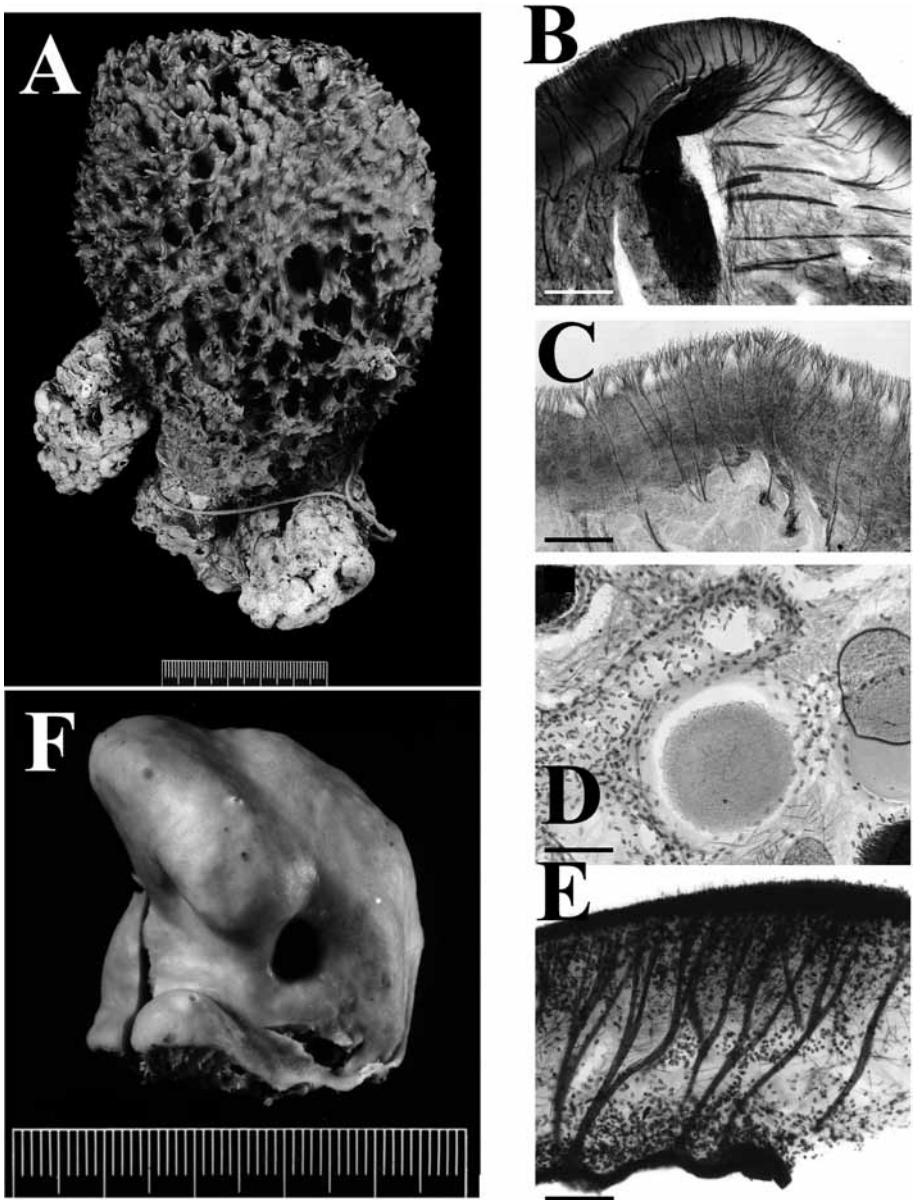

Fig. 2. *Diacarnus* (A–D) and *Sigmosceptrella* (E–F). A–B, *Diacarnus spinipoculum* (Carter) (holotype BMNH 1846.10.14.174, after Kelly-Borges & Vacelet, 1995). A, holotype (scale 50 mm). B, ectosomal and upper choanosomal skeleton (scale 130 μm). C, *Diacarnus bellae* Kelly-Borges & Vacelet (holotype BMNH 1994.5.22.11, after Kelly-Borges & Vacelet, 1995), ectosomal and upper choanosomal skeleton (scale 150 μm). D, *Diacarnus megaspinorhabdosa* Kelly-Borges & Vacelet (specimen QMG305013, after Kelly-Borges & Vacelet, 1995), incubated larva (scale 2 mm). E, *Sigmosceptrella quadrilobata* Dendy (holotype BMNH 1925.11.1.1641), skeletal arrangement (scale 60 μm). F, *Sigmosceptrella fibrosa* Dendy (holotype BMNH 1925.11.1.717) (scale 50 mm).

spinipoculum possibly represented a family separate from Latrunculiidae. Species of *Diacarnus* are particularly common across the Indo-Pacific and it is surprising that the genus had not been differentiated from typical latrunculiids prior to the review of Kelly-Borges & Vacelet (1995). These sponges are very characteristic as they produce huge yolk-like yellow-orange larvae which are 2–3 mm in diameter, these appear to be present year round (Fig. 2D) (see Ilan, 1995). *Diacarnus* have an extremely collagenous texture and feel and look somewhat like uncooked chicken in life, complete with sinew-like cartilagenous fibres. Most species of *Diacarnus* were assigned to *Latrunculia* prior to the review of Kelly-Borges & Vacelet (1995). *Diacarnus* differs from other members of Podospongiidae in that it has numerous species that are difficult to differentiate, unlike *Sigmosceptrella* and *Negombata* that are represented by discrete, easily recognisable species – a phenomenon that has been noted for Western Indian Ocean Porifera in general (Kelly-Borges & Valentine, 1995). This is in complete contrast to the poriferan fauna of Southeast Asia, Australasia, Micronesia, and the West Central Pacific where, apart from the presence of the same very discrete, easily recognisable species, many genera have numerous sibling species which are difficult to differentiate based solely on skeletal features. This is particularly evident for genera of Chalinidae, Niphatidae, Petrosiidae, Callyspongiidae, Halichondriidae, Microcionidae and others.

The genus *Sceptrintus* Topsent, 1898b (Topsent, 1898b: 239; 1904b: 117, pl. 1, fig. 11, pl. 12, fig 4) from the Azores was originally

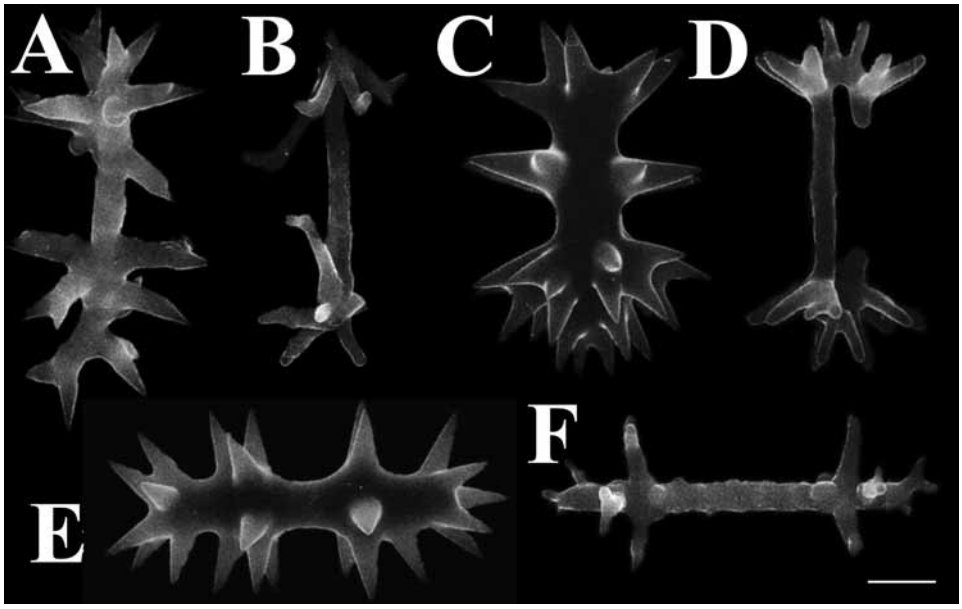

Fig. 3. Spinorhabds and immature protorhabds of *Negombata*, *Sigmosceptrella* and *Diacarnus*. A, *Negombata magnifica* (Keller), mature spinorhabd. B, *Negombata magnifica* (Keller), semi-sigmoid protorhabd. C, *Sigmosceptrella quadrilobata* Dendy, mature spinorhabd. D, *Sigmosceptrella quadrilobata* Dendy, sigmoid protorhabd. E, *Diacarnus ardoukobae* Kelly-Borges & Vacelet, mature spinorhabd. F, *Diacarnus ardoukobae* Kelly-Borges & Vacelet, mature spinorhabd (scale 8 μm).

assigned to the Spirastrellidae, but is transferred here to Podospongiidae with some reservation. The type species, *Sceptrintus richardi* Topsent (by monotypy), has styles that are lightly spined, being occasionally verticillate, and spinorhabd-like microscleres of 2 sizes. One of the microscleres is huge, being as large, or larger than the megascleres. The choanosome is dominated by discasters of all sizes scattered abundantly without orientation between loose tracts of styles. There are no visible fibres, rendering the texture of the sponge firm but friable. At the surface of the sponge discasters and styles appear to be tangential and paratangential, the styles being grouped into small bundles that do not project through the surface. Discasters are smaller at the surface. The sponge is massive and very smooth with no visible oscules or papillae, reminding Topsent of the genus *Latrunculia*. The colouration appears to be mottled yellow. The proposed tentative affinity of *Sceptrintus* with Podospongiidae is based upon the similarity of the microscleres and their protorhabds, with the spinorhabd form of *Diacarnus* in particular. The surface morphology and colouration seem to be similar as well. However, the styles are quite different as they are lightly spined and the microscleres are enormous compared to those of *Diacarnus* species. The skeletal details are also quite different from *Diacarnus*, *Sigmosceptrella* and *Negombata*. A more definite assignment may be arrived at through examination of fresh material.

Distribution

Diacarnus contains numerous species, some of which are reasonably easy to differentiate in the field based on their gross morphology. However, for most species, a combination of the gross morphology, architecture of the ectosomal region, morphology of microscleres and their disposition within the ectosome, provide the clearest indication of species (Kelly-Borges & Vacelet, 1995). Species diversity is highest in Papua New Guinea and the Philippines, with different species recorded from the southwest Pacific (New Caledonia) to the Great Barrier Reef, and Micronesia.

***SIGMOSCEPTRELLA* DENDY, 1922**

Synonymy

Sigmosceptrella Dendy, 1922b: 136.

Type species

Spirastrella fibrosa Dendy, 1897: 254 (by original designation).

Definition

Podospongiidae with well-defined plumose tracts of strongyloxeas, no secondary fibres are apparent, radiating and diverging from a spongin base, in one case in the form of a candelabra. Microscleres are asymmetrical spinorhabds with sigmoid protorhabds, forming a thick crust at the surface of the sponge and densely scattered within the choanosome.

Diagnosis

Thickly encrusting, lobate, semi-digitate sponge with a smooth to faintly conulose surface. The choanosomal skeleton consists of large diverging dendritic or plumose tracts that are not joined by secondary fibres, diverging to form brushes in the ectosome. Megascleres are strongyloxeas. The ectosome is packed with abundant spinorhabds which are characteristically dumbbell shaped and often asymmetrical.

Previous reviews

Dendy (1921); Dendy (1922b); Kelly-Borges & Vacelet (1995).

Description of type species

Spirastrella fibrosa Dendy, 1897: 254 (Fig. 2F).

Synonymy. *Spirastrella fibrosa* Dendy, 1897: 254. *Latrunculia conulosa* Hallmann, 1912: 126.

Material examined. Holotype: BMNH 1925.11.1.717.

Description. Sponge forms a thick lobate mass, with a conulose surface, the texture is rubbery (Fig. 2F). The choanosomal skeleton is composed of strongyloxeas which form dense well-defined fibres which spring from the base of the sponge, diverging to form brushes, or candelabra, below the ectosome. The ectosome is well-defined as it is packed with spinorhabds and dense with collagen. The ectosome is not detachable.

Remarks. *Sigmosceptrella* was first introduced by Dendy (1921), in a description of characteristic spicules but without mention or a description of the type species (and thus a *nomen nudum*), and so the genus was not formally described until Dendy (1922b). In describing *Sigmosceptrella quadrilobata* Dendy, 1922b, from Mauritius, Dendy stated that he considered his '*Spirastrella*' *fibrosa* Dendy, 1897, from Port Phillip Heads, Australia, was the true holotype of *Sigmosceptrella*. Figure 2E illustrates the skeletal organisation of the holotype of *Sigmosceptrella quadrilobata*, an encrusting species. The skeletal arrangement of the type species, *Sigmosceptrella fibrosa*, is very similar but branching of the primary fibre occurs more towards the apex of the fibre, giving the appearance of an unruly candelabra. Examination of the type species *Sigmosceptrella fibrosa* and *S. quadrilobata* reveals characteristics that clearly differentiate *Sigmosceptrella* from *Diacarnus* and *Negombata*. The largest microscleres of *Sigmosceptrella* are very similar to those of *Diacarnus* and *Negombata*, but the spicules are dumbbell-shaped and one end of the spinorhabd is enlarged and thus asymmetrical (Fig. 3 C–D). These microscleres are also packed densely in the ectosome and rather than occurring in a scattered band within the ectosome (like *Diacarnus* and *Negombata*).

Sigmosceptrella clearly fits within the revised concept of Podospongiidae, and is probably most closely related to *Diacarnus* in that it has plumose tracts of megascleres that diverge to form dendritic fibres in the ectosome and brushes at the surface. While the choanosomal tracts are less elaborate than those in *Diacarnus* spp., and the spinorhabds are dumbbell-shaped and occasionally aciculate, the general pattern of architecture is very similar within the family as a whole. The protorhabds are also sigmoid.

Distribution

Sigmosceptrella are less diverse and have more discrete species distributions than *Diacarnus*, widely dispersed in cool temperate waters of New South Wales and western Australia *(S. fibrosa)* and the Western Indian Ocean *(S. quadrilobata)*.

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