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Family Latrunculiidae Topsent, 1922

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Latrunculiidae Topsent (Demospongiae, Poecilosclerida *incertae sedis*) is revised substantially from prior concepts, recognizing two family taxa (Latrunculiidae and Podospongiidae) differentiated primarily by the morphology of microrhabd microscleres that reflect major ontogenetic differences in their formation. Latrunculiidae has discate acanthose microrhabd microscleres (acanthodiscorhabds or 'chessman' spicules), that form a dense perpendicular palisade in the outer ectosome, areolate porefields, and short fistular oscules on the sponge surface. Four genera are recognised as valid (*Latrunculia, Sceptrella, Strongylodesma* and *Tsitsikamma* gen. nov.), with suspected affinities to Poecilosclerida but no obvious close relatives within any of the suborders, and hence is allocated to Latrunculina subord. nov. *incertae sedis* in Poecilosclerida pending a more thorough phylogenetic analysis.

Keywords: Porifera; Demospongiae; Poecilosclerida; *incertae sedis*; Latrunculina; subord. nov.; Latrunculiidae; *Latrunculia*; *Sceptrella*; *Strongylodesma*; *Tsitsikamma* gen. nov.

DEFINITION, DIAGNOSIS, SCOPE

Synonymy

Latrunculiidae Topsent, 1922.

Definition

Wispy wide-meshed reticulate to reinforced reticulate choanosomal skeleton of anisostyles or strongyles, ectosomal skeleton compact tangential, microscleres are acanthodiscorhabds, or 'chessman' spicules, typically arranged vertically in a palisade on outside of ectosome.

Diagnosis

Massive encrusting, hemispherical, spherical or pedunculate sponges with areolate porefields and raised fistular oscules; surface smooth and velvety between fistules; texture leathery and barely compressible when in preservative, whole animal generally very dense with heavy uniform body mass. Colour in life typically brownish black with forest-green or blue tinges, liquorice brown, fawn, or forest green *(Latrunculia, Strongylodesma, Tsitsikamma)*, or pale beige to white *(Sceptrella)*. Structural megascleres are anisostyles or strongyles, rarely oxeas, these are frequently slightly irregular, sinuous, forming a compact tangential layer under the ectosome, and a wide-meshed reticulation in the choanosome. Microscleres are acanthodiscorhabds bearing apical and basal whorls of spines (apical whorl and manubrium) and several crenulate discs (subsidiary and median whorls) in between, typically arranged in a compact palisade of single perpendicular spicules, their bases buried in the ectosomal membrane. Based on the observation of larvae in *Latrunculia citharistae* by Vacelet (1969), we conclude that the Latrunculiidae are viviparous.

Latrunculia, Strongylodesma, and *Tsitsikamma* are known to contain biologically active discorhabdins and their derivatives. Bathymetric distribution is shallow sublittoral to bathybenthic. Biogeographic distribution is polar to warm temperate with centres of diversity and abundance in southern hemisphere temperate regions for *Latrunculia* and *Tsitsikamma*, southern and northern warm temperate to tropical regions for *Strongylodesma*, and northern hemisphere temperate regions for *Sceptrella*.

Scope

There are 12 nominal genera, four of which are considered to be valid Latrunculiidae, and include *Latrunculia, Sceptrella*, and *Strongylodesma*, the latter transferred from the poecilosclerid family Chondropsidae, and *Tsitsikamma* gen. nov. erected here (See Fig. 1). *Negombo* (with synonym *Oxylatrunculia*) is transferred to Desmoxyidae (Halichondrida), and *Sigmosceptrella, Diacarnus, Negombata, Podospongia* (with synonym *Alcyospongia*), are transferred to Podospongiidae (Poecilosclerida, with suspected affinities to Mycalina – see Kelly & Samaai, this volume). *Phlyctaenopora* Topsent and *Barbozia* Dendy, presently assigned to the poecilosclerid family Crellidae, are transferred *incertae sedis* to Mycalidae.

History and biology

Latrunculiidae was erected by Topsent (1922) to include genera with either spinose or discate microrhabds and anisostyle megascleres. Topsent initially included three genera in the family, *Sigmosceptrella* Dendy, 1922b, *Podospongia* du Bocage, 1869 and *Latrunculia* du Bocage, 1869. As for many other families within the Demospongiae Latrunculiidae was, and still is, the subject of considerable controversy. Until the review of Kelly-Borges & Vacelet (1995) it was considered to be monophyletic (Dendy, 1922b; Topsent, 1922, 1928c; Bergquist, 1968, 1978; Vacelet, 1969, Lévi, 1973; Wiedenmayer, 1977b; Boury-Esnault & van Beveren, 1984; Wiedenmayer, 1989; Hooper & Wiedenmayer, 1994; Hooper, 1986, 1997), and included *Didiscus* Dendy, 1922b in addition to the latter three genera. *Negombata* de Laubenfels, 1936a, *Diacarnus* Burton, 1934a, *Oxylatrunculia* Hoshino, 1981, *Sanidastra* Volkmer-Ribeiro & Watanabe, 1983, and *Alcyospongia* de Laubenfels, 1934, were subsequently added to the family, although the affinities between these genera were not always completely clear. *Sanidastra* is now clearly accepted as belonging to

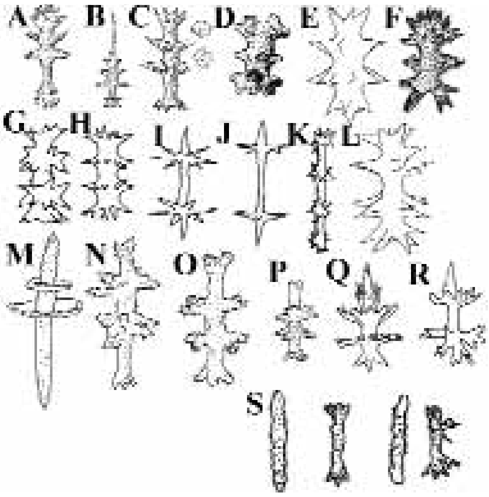


Fig. 1. Discorhabd microsclere morphologies used to define genera of Latrunculiidae, and discorhabd-like microscleres found in other groups of sponges as a comparison. A–B, *Latrunculia*, anisodiscorhabd and aciculodiscorhabd. C, *Sceptrella*, isoconicodiscorhabd ('sceptre'). D, *Tsitsikamma*, isochiadiscorhabd. E–F, *Sigmosceptrella*, spinorhabds. G–H, *Negombata*, spinorhabds. I–J, *Barbozia*, oxydiscorhabds. K–L, *Diacarnus*, spinorhabds. M, *Didiscus*, didiscorhabds. N, *Negombo*, sanidaster. O–P, *Oxylatrunculia*, sanidasters. Q–R, *Podospongia*, spinorhabds (podorhabds). S, *Sanidastra*, sanidasters.

the freshwater Spongillidae by Manconi & Pronzato (1996). Until the work of Kelly-Borges & Vacelet (1995) no distinction was made between discate and spined forms (i.e., with the prior assumption that these microrhabds were homologous), leading to considerable instability in the family.

Recent work on several genera within Latrunculiidae (Kelly-Borges & Vacelet, 1995; Van Soest, 1987; Van Soest *et al*., 1990) indicated that it might be polyphyletic, and these authors began the task of ascertaining the phylogenetic affinities of the various taxa. However, none of these studies could be construed as comprehensive revisions of the family, and thus such a revision was necessary and is presented here, although it remains incomplete given there are many new data awaiting publication (Samaai, unpublished data).

Latrunculiidae was first established within the Order Poecilosclerida (Topsent, 1922, 1928c) but Bergquist (1968, 1978), Hartman (1982), and Wiedenmayer (1989) subsequently considered the family to have greater affinities with Hadromerida. This action was based on: the collagenous nature of the mesohyl (in some genera at least); the similarity of the areolate porefields to those in *Cliona*; similarity of the radial skeleton between *Tethya, Stylocordyla*, and *Podospongia*; presence of fistular oscules in *Polymastia*; presence of a microsclere crust in Spirastrellidae; and the similarity of sterol (Bergquist *et al*., 1980) and free amino acid patterns (Bergquist *et al*., 1969) with the hadromerids. Van Soest (1984b), on the other hand, stated that arguments are weak for placement in either Order, and included the family *incertae sedis* within the Porifera. As it is currently perceived, the family is heterogeneous, sharing features with both hadromerid sponges (Subclass Tetractinomorpha) and poecilosclerid sponges (Subclass Ceractinomorpha). Nevertheless, although there is indeed a suggested common ancestry to hadromerids the vast majority of characters are seen to be shared with poeciloscerids (Table 1). These include the type of megascleres, their arrangement within the sponge, the ontogenetic development of the microscleres, and their surface position (Carter, 1879b; Ridley & Dendy, 1887; Dendy, 1921; Topsent, 1922, 1928c; Bergquist, 1968, 1978; Lévi, 1973; Vacelet, 1969; Boury-Esnault, 1985; Hooper, 1986; Wiedenmayer, 1989; Kelly-Borges & Vacelet, 1995), all of which support the inclusion of Latrunculiidae within Poecilosclerida, but its relationships within the order remain *incertae sedis*.

REVISION OF LATRUNCULIIDAE

The major character that defines the genera *Latrunculia* and *Sceptrella* (Latrunculiidae) and *Podospongia, Negombata, Diacarnus* and *Sigmosceptrella* (Podospongiidae) is possession of acanthose microrhabds, traditionally used to unite them historically into a single family. Characters such as the form and disposition of

Table 1. Characters shared between Poecilosclerida and Hadromerida for the prior concept of family Latrunculiidae (Latrunculiidae + Podospongiidae).

Character	Poecilosclerida	Hadromerida
Microsclere disposition	ectosomal palisade, erect surface spicules	throughout ectosome + crust (armoured surface)
Microsclere morphology	Sigmoid protorhabd (Podospongiidae) Terminally spined strongyles	
Megasclere morphology	anisostyles, styles, polytylotes, terminally spined styles	polytylote features strongyloxeas erect palisade
Ectosomal architecture	tangential, plumoreticulate (dendritic), axial fibro-reticulation,	
Choanosomal architecture	reticulate, fibroreticulate	radial *(Podospongia)*
Gross morphology	massive encrusting, digitate branching	massive encrusting
Surface features	areolate porefields & fistulose oscules	areolate porefields & fistulose oscules
Colour	deep brown or green, bright colouration *(Zyzzya)*, bright red *(Negombata)*	red (Spirastrellidae)
Histology		highly collagenous *(Diacarnus)*
Bioactive chemistry	pyrroloquinoline alkaloids + norsesterterpene peroxides + latrunculins	sterol and free aminoacid patterns

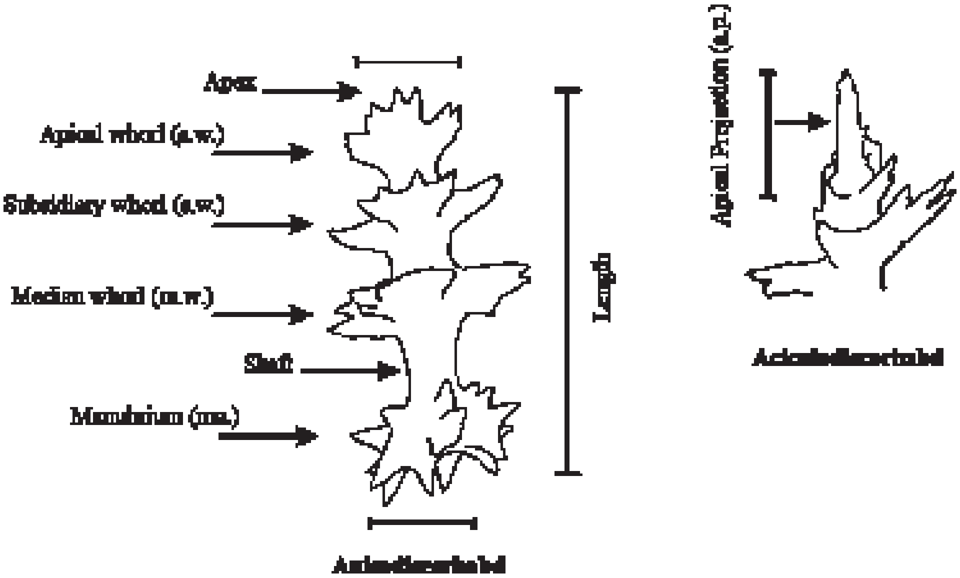


Fig. 2. Schematic representation of spicule terminology used to describe the discorhabd of *Latrunculia*.

these microscleres, the skeletal arrangement of the megascleres and the sponges' general morphology, have been used to distinguish genera from one another. However, Kelly-Borges & Vacelet (1995) demonstrated that acanthose microrhabds were non-homologous between certain groups of genera, correlated with clear differences in the arrangement of their megasclere skeletons within each taxon, leading them to the hypothesis that the prior concept of 'Latrunculiidae' was polyphyletic.

Microsclere ontogenetic development, morphology and disposition

Latrunculia. Species have anisodiscorhabds as microscleres (Figs 1–2). These have a straight shaft bearing four disc-like whorls of spines that are differentiated in size and shape. The apex of the spicule usually consists of a rosette or crown of spines and the base of the spicule, which is embedded in the ectosomal membrane, is called the manubrium (ma.). The shape of this part of the microsclere is typically bushy and spinose. Immediately beneath the apex of spines, is the apical whorl (a.w.), which has a uniform (non-partitioned) margin. Between the apical whorl and the manubrium are subsidiary (s.w.) and median whorls (m.w.) arranged more-or-less at equal distances along the shaft, although in some species these discs are closer to the apical end of the spicule. These central whorls are usually disc-shaped with crenulate margins, parallel with each other, and partitioned into several leaf-like flanges. Several species of *Latrunculia* also contain aciculodiscorhabds (Figs 1–2) which have an elongated apical spine.

Sceptrella. The microscleres are isoconicodiscorhabds or 'sceptres' (Figs 1, 5A–C) with a stout straight shaft bearing an apical whorl and manubrium that is not differentiated in size or form (prefix *conico-* means conical – see Boury-Esnault & Rützler, 1997, for terminology). The apical whorl differs from those in *Latrunculia s.s.* in that it is fused with the apex and consists of a rosette of crenulated spines. They also bear furcate or conical spines (subsidiary and median whorls) which are often acanthose and arranged at equal distances along the shaft.

Tsitsikamma gen. nov. These microscleres differ considerably from those in *Latrunculia* and *Sceptrella* as they are isochiadiscorhabds with a stout straight shaft, bearing three whorls of truncate tubercles (prefix *chia-* means trucate – see Bergquist & Kelly-Borges, 1991, for microsclere terminology), which are terminally acanthose (Figs 1, 6E–F). In these microscleres the subsidiary whorl is absent, the medium whorl is midway between manubrium and apical whorl.

Ontogenetic development of acanthomicrorhabds. Although the adult form of the microscleres in all of the above genera are superficially similar, it is their differences in developmental stages that gives a clear indication of their separate origins. Dendy (1921) referred to these developmental stages as reflecting their ontogenetic development, but it is equally tenable that these also reflect a transformational homology of character states. The anisodiscorhabds of *Latrunculia* follow a particular ontogenetic developmental pattern that starts with a straight protorhabd, as indicated by Dendy (1921, pl. 15 fig. 10a) (see Fig. 4G). In contrast, this developmental process, as suggested by Topsent (1922), clearly differs from the early ontogenetic stage of Podospongiidae (*Sigmosceptrella, Negombata*, and *Podospongia*) in that the protorhabd is sigmoid in the later species (see also Dendy. 1921; Wiedenmayer, 1989; Kelly-Borges & Vacelet, 1995). Although the protospinorhabds of *Diacarnus* are faintly reminiscent of the protoanisodiscorhabds of *Latrunculia* and *Sceptrella* (Fig. 5C), in that the protorhabd shaft is straight, the development of spines on the shaft in *Diacarnus* protospinorhabds is in complete contrast to the development of the discs in anisodiscorhabds. The protoisochiarhabd in *Tsitsikamma* gen. nov. (see Fig. 6G) is straight, and spines appear simultaneously on the distal curved ends of the shaft as in *Latrunculia* and *Sceptrella*. Although there are substantial differences in the ontogenetic development of microscleres between *Latrunculia, Sceptrella* and *Tsitsikamma*, the development of discs completely contrasts with the development of spines in spinorhabds of the Podospongiidae. The lack of microscleres in *Strongylodesma* is viewed here as a secondary loss during the evolution of the family; in all other characters there are remarkable similarities between *Strongylodesma, Latrunculia, Tsitsikamma* and *Sceptrella*.

Disposition within the skeleton. In *Latrunculia* the anisodiscorhabds are typically arranged in a single layer of perpendicular spicules forming a tightly packed palisade on the outside of the sponge, with the bases of the spicules buried in the ectosomal membrane. In *Sceptrella* and *Tsitsikamma* the arrangement is not as regular but the isodiscorhabds are also arranged in a single layer on the outside of the sponge. In contrast, the disposition of the microscleres in the Podospongiidae genera *Diacarnus, Sigmosceptrella, Podospongia*, and *Negombata* is quite different with the spinorhabds forming a thick crust within the ectosome and frequently throughout the distinct cortical region. These microscleres also show no tendency towards any vertical orientation.

Megascleres and skeletal architecture

Latrunculia, Tsitsikamma and *Sceptrella* have large often polytylote anisostyles, and *Strongylodesma* has strongyles as megascleres. Another so-far undescribed species of *Latrunculia* from the Sea of Okhotsk possesses terminally spined anisostyles (Samaai, unpublished). By comparison, Podospongiidae all have strongyloxeas, to which robust curved styles are added in *Negombata*, with the latter restricted to the choanosomal 'axial' fibroreticulation.

The general skeletal architecture that typifies Latrunculiidae is a large-meshed polygonal reticulation formed by wispy tracts of spicules with no spongin reinforcement. The ectosomal skeleton is a tangential layer of the same megascleres. This skeletal organisation is reminiscent of the genus *Phorbas* (Hymedesmiidae). Although the reticulation in *Sceptrella* is irregular and wispy, the structure at the base is slightly radial. The major differentiating characteristic of *Tsitsikamma* is the massive reinforcement of these meshes to form huge thick tracts that are visible with the unaided eye. The overall gross structure is honeycombed with convoluted layers, similar to poecilosclerid genera such as *Inflatella* and *Coelocarteria*. In contrast, Podospongiidae are characterised by the possession of a fibroreticulate plumose skeleton.

Gross morphology

Latrunculiidae present a range of growth forms extending from relatively thin encrustations to thick hemispherical masses. All taxa have areolate porefields and raised trumpet-like oscular fistules, and are velvety to the touch. The texture of *Latrunculia, Strongylodesma* and *Sceptrella* is very cakey, dense and compressible, and not very elastic. *Tsitsikamma* is extraordinarily tough and leathery due to the sponge's huge internal spicule tracts. Latrunculiidae are thus superficially similar to the genera *Zyzzya* (Acarnidae) and *Phorbas* (Hymedesmiidae). By comparison, growth forms of Podospongiidae are typically digitate and branching, flexible, compressible, very elastic due to rich collagen mesohyl, and lacking any special surface features.

Reproduction

Oocytes have been observed in southern hemisphere specimens of *Latrunculia, Strongylodesma*, and *Tsitsikamma* (Kelly unpubl. data), but Vacelet (1969) provides the only report of the presence of parenchymella larvae in *Latrunculia citharistae* Vacelet, indicating that the group are probably viviparous. No reproductive products have been observed in *Sceptrella*. Where known reproduction in Podospongiidae is viviparous (Ilan, 1995; Kelly-Borges & Vacelet, 1995).

Base pigmentation

Latrunculia, Strongylodesma, and *Tsitsikamma* have a characteristic base pigmentation of deep brownish black that is often and variously tinged with forest green and deep blue. These specimens exude a dark brownish or greenish black pigment; the ethanol preservative is always oily-looking and deeply pigmented. Preserved specimens always retain their dark pigmentation. Some species are a lighter oak brown throughout. As we have not seen *Sceptrella* in life their living colouration is uncertain, however, ethanol-preserved specimens are uniformly cream to tan. It is interesting to note that specimens of *Tsitsikamma* without discorhabdins are a lighter brown than their discorhabdin-containing siblings. Variation in pigmentation has been associated with increased levels of cytotoxicity in the genus *Latrunculia*, i.e., the most cytotoxic extracts of discorhabdins have been found from heavily pigmented green and brown sponges of *Latrunculia* (Perry *et al*., 1986; Perry *et al*., 1988b; Copp *et al*., 1994; Lill *et al*., 1995).

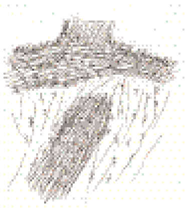
Biochemistry

Latrunculia spp. (Perry *et al*., 1986; Perry *et al*., 1988b; Kita *et al*., 1989; Copp *et al*., 1994; Lill *et al*., 1995; Yang & Baker, 1995; Beukes, 2000; Beukes *et al*., in press), and *Strongylodesma* spp. (Beukes, 2000; Beukes *et al*., in press) contain biologically active discorhabdins and their derivatives. A new pyrroloiminoquinone alkaloid tsitsikammamine, isolated from *Tsitsikamma* together with brominated discorhabdin derivatives, is structurally related to the makaluvamine compounds found in the poecilosclerid genus *Zyzzya* (Hooper *et al*., 1996; Beukes, 2000; Urban *et al*., 2000). Interestingly, *Tsitsikamma* gen. nov. also appears superficially to be morphologically intermediate between *Latrunculia* and *Zyzzya*, at least in terms of their general choanosomal skeletal arrangement (Table 2). The apparent relatedness of these compounds (discorhabdins, tsitsikammamines and makaluvamines) and isolation of derivatives (i.e., discorhabdins in *Zyzzya* spp., makaluvamines in *Latrunculia* sp. and 'hybrid' makaluvamines/discorhabdins in *Tsitsikamma*) is a promising target for future investigation. Determination of whether pyrroloquinoline alkaloids are a potential chemotaxonomic marker for these genera would also require investigation of the homology of their respective biosynthetic pathways.

A further group of compounds, the prianosins, were described from a Japanese sponge identified as *Prianos melanos* de Laubenfels, 1954, (Kobayashi *et al*., 1987; Cheng *et al*., 1988; Kobayashi *et al*., 1991; Van Soest *et al*., 1996a). These are in fact discorhabdins; prianosin A is identical to discorhabdin A and prianosin D to discorhabdin D (Perry *et al*., 1988a,b; Lill *et al*., 1995). Prianosin B and prianosin C are new pyrroloquinoline alkaloids (Van Soest *et al*., 1996a), similar to discorhabdins. It is likely, however, that this record of *P. melanos* is a misidentification for a *Strongylodesma*, since both taxa have depauperate morphological characteristics, including only strongyles as megascleres, lacking microscleres and dark brownish pigmentation (Urban *et al*., 2000).

Van Soest *et al*. (1996a) reported on the discovery of two groups of biogenetically unrelated alkaloids, cyclic guanidine alkaloids and pyrroloquinoline alkaloids called batzellins and isobatzellins, in sponges that had been assigned to *Batzella* (i.e., based

Table 2. Possible affinities between *Latrunculia* and *Tsitsikamma*, and *Zyzzya*

Character	*Latrunculia*	*Tsitsikamma* gen. nov.	*Zyzzya*
External morphology	massive encrusting, semispherical	massive encrusting, semispherical, pedunculate	thickly encrusting
Base pigmentation	brownish or greenish black	brownish or greenish black, pink	brownish black
Surface features	areolate porefields + fistular oscules	areolate porefields + fistular oscules	areolate porefields + fistular oscules
Skeletal architecture			
Ectosomal architecture	tangential megascleres + microsclere palisade	tangential megascleres + microsclere palisade	tangential megascleres

on their possession of a simple complement of strongyles in a wispy reticulation). The sponge with cyclic guanidine alkaloids, originally identified as *Batzella* (ZMA Por 8788), is now considered to be *Monanchora arbuscula* (Crambeidae), and the genus *Batzella*, like *Prianos*, is a dustbin taxon. Batzellin and iso-batzellin-containing sponges from Harbar Branch Oceanographic Institution, also identified as *Batzella* (HBOM 003:00050, HBOM 003:00051) are identical in all respects to *Strongylodesm*a, which also produces pyrroloquinoline alkaloids. These highly functionalised pyrroloquinoline alkaloids are very closely related to the discorhabdins of *Latrunculia* species and the makaluvamines of *Zyzzya*. These alkaloids thus become a strong consistent chemical marker for *Zyzzya, Latrunculia* and *Strongylodesma* (Urban *et al*., 2000).

Ecology, bathymetric and biogeographical distribution

Latrunculiidae are widespread, found predominantly in cold water with centres of diversity in the southern and northern hemispheres (Fig. 3). Species of *Latrunculia* are predominantly sublittoral and often a dominant organism in the benthic fauna. In all except Antarctica, the subantarctic and subtropical environments these sponges are found in relative abundance in exposed coastal environments attached to hard rocky substrate, often on vertical walls or rocky reef surfaces down to 30 m depth. In Antarctica *Latrunculia apicalis* is found under the sea-ice and grows on a sedimentary substrate of predominantly sponge spicules. Although the predominant centre of diversity for these genera appears to be in the southern hemisphere, the genus has an antiboreal distribution (Plate, Antarctica, subantarctic, South Africa, New Zealand, southwest Australia, Tasmania), extending into subtropical water (New Caledonia, Tonga, Southern Japan) and the western Boreal Pacific. There are only a few known species of *Sceptrella* and these appear to be uncommon in the environments in which they have been found. Species of *Sceptrella* are predominantly deepwater with a centre of diversity in the northern hemisphere, in the Atlantic Ocean. *Sceptrella* was first described off the coast of Florida but species have also been found off the Azores, the coast of Gibraltar, and the north coast of Norway down to a depth of 2460 m.

Strongylodesma was first described from an oceanic seamount in the southern Atlantic Ocean, and a shallow subtidal species has subsequently been found on southeast coast of South Africa. The genus is also known from New Caledonia (Vacelet & Kelly in Lévi, 1998) and Tonga (Kelly, unpublished). The seamount and the shallow subtidal South African species grow on hard rocky substrates, whereas the subtropical species grow attached to dead coral rubble in sandy lagoon environments (Vacelet & Kelly in Lévi, 1998). Species previously identified as *Batzella* from deepwater in the west central Atlantic region (Van Soest, 1996; Gunasekera *et al*., 1999) are now recognised as *Strongylodesma. Tsitsikamma* is only known from the unique, warm temperate region off the southeast coast of South Africa, where they are found in relative abundance in sheltered coastal rocky reefs down to 25 m depth.

Phylogenetic affinities

Latrunculia, Strongylodesma, Tsitsikamma and *Sceptrella* are unequivocally differentiated at a higher taxonomic level from Podospongiidae based on fundamental differences in having different development stages of their microrhabd microscleres.

The presumed homology of spicules and skeletal characters of Latrunculiidae (and Podospongiidae) have been diversely interpreted, resulting in the switching back and forth of the groups between the tetractinomorph Order Hadromerida and the ceractinomorph Order Poecilosclerida. However, whereas Podospongiidae has more obvious affinities with the Poecilosclerida Mycalidae (see Kelly & Samaai, this volume), those of Latrunculiidae remain more obscure, and hence remains *incertae sedis* within the Poecilosclerida subordinal classification.

Levels of speciation

Latrunculiidae, as revised here, is a small but well-defined family with four easily differentiated genera. *Latrunculia*, found predominantly in southern ocean waters, is characterised by abundant and what appears to have been rapid speciation. In New Zealand, as in the Polymastiidae (Kelly-Borges & Bergquist, 1997), species of *Latrunculia* are numerous and relatively difficult to differentiate and distinction is based upon genetic and small

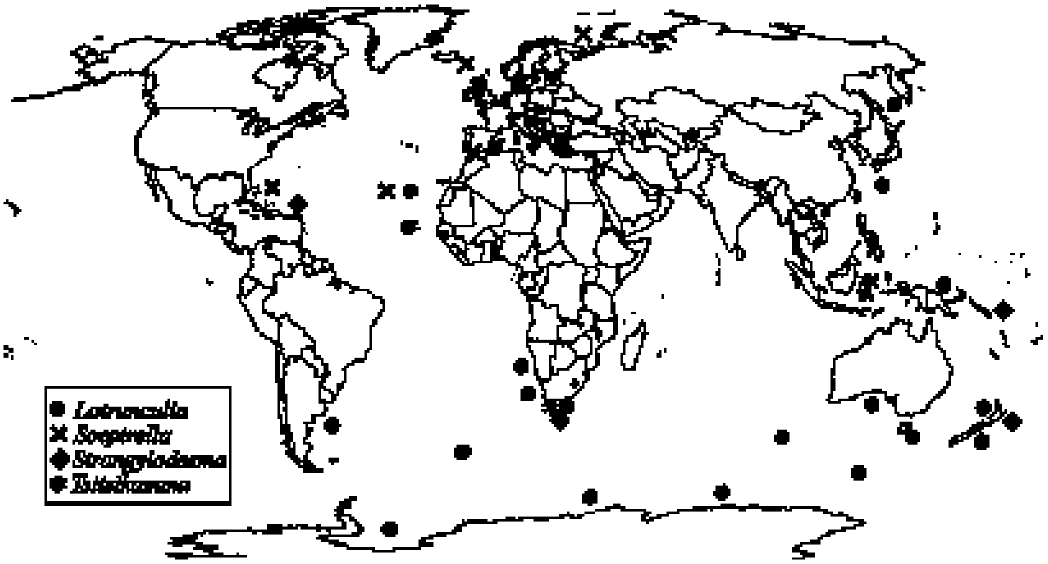


Fig. 3. Known distribution of Latrunculiidae. ●*Latrunculia*; ✖*Sceptrella*; ■ *Strongylodesma*; * *Tsitsikamma* gen. nov.

morphological and morphometric differences in spiculation (Alvarez *et al*., 2002). In South Africa however, species are discrete and easily differentiated. *Sceptrella* and *Strongylodesma* are characterised by having only a few discrete species that are geographically isolated. *Tsitsikamma* is known from two South African species.

Previous reviews

Carter (1879b); Ridley & Dendy (1887); Dendy (1921); Topsent (1922, 1928c); de Laubenfels (1934); Bergquist (1967, 1968, 1978); Hooper (1986); Wiedenmayer (1989); Kelly-Borges & Vacelet (1995); Urban *et al*. (2000); Alvarez *et al*. (2002).

KEY TO GENERA

(1) Megascleres anisostyles or styles, microscleres present 2
Megascleres strongyles, microscleres absent .... ***Strongylodesma***
(2) Microscleres anisodiscorhabds with spined apical whorl and manubrium, and disc-shaped median and subsidiary whorls ....***Latrunculia***
Microscleres are isoconicodiscorhabds with crenulated apical whorl, and conical or furcate whorls of spines ....***Sceptrella***
Microscleres are isochiadiscorhabds with cylindrical terminally acanthose truncate tubercles ....***Tsitsikamma***

LATRUNCULIA DU BOCAGE, 1869

Synonymy

Latrunculia du Bocage, 1869.

Type species

Latrunculia cratera du Bocage, 1869 (by monotypy).

Definition

Latrunculiidae with polygonal large-meshed reticulation formed by wispy tracts of anisostyles. Megascleres are typically smooth and sinuous, occasionally polytylote anisostyles to which terminally spined styles or diactinal spicules may be added. Microscleres are anisodiscorhabds. Aciculodiscorhabds, amphiaster-like microscleres, and acanthomicroxeas are present in one or other of two species. Microscleres are disposed in a palisade in the outer ectosome.

Diagnosis

Encrusting to massive oval-shaped sponge with raised trumpet-like or mammiform oscular fistules and areolate porefields; surface velvety to the touch; texture is very cake-like, dense but compressible. Colour in life deep brownish-black or dark green, sometimes tinged with deep blue, in preservative specimens always retain their dark pigmentation. The choanosomal architecture consists of monactinal or rarely diactinal spicules arranged in an irregular, polygonal, large-meshed reticulation formed by wispy tracts of spicules, which lack spongin reinforcement. There is no distinction between primary and secondary tracts. The ectosomal skeleton is a tangential layer of choanosomal megascleres, being somewhat plumose at the base of the ectosome. Megascleres are typically smooth and sinuous, occasionally polytylote anisostyles to which terminally spined styles or diactinal spicules may be added. Microscleres are anisodiscorhabds. Aciculodiscorhabds, amphiaster-like microscleres, and acanthomicroxeas are present in one or other of two species. Microscleres are disposed in a palisade in the outer ectosome. Where known sponges are viviparous. *Latrunculia* spp. produce pyrroloquinoline alkaloids discorhabdins and their derivatives.

Previous reviews

Du Bocage (1869); Carter (1879b); Topsent (1922, 1928c); Ridley & Dendy (1887); Dendy (1921); de Laubenfels (1934); Burton (1934a); Hooper (1986); Wiedenmayer (1989); Kelly-Borges & Vacelet (1995); Urban *et al*. (2000); Alvarez *et al*. (2000b).

Description of type species

Latrunculia cratera du Bocage, 1869.

Synonymy. *Latrunculia cratera* du Bocage, 1869: 161, pl. 11 fig. 2.

Material examined. Holotype: Lost.

Description. Small thickly encrusting Latrunculiidae, with smooth, microscopically hispid surface. Surface usually with volcano-shaped or cylindrical oscules, together with mammiform to crater-shaped areolate porefields. Colour in life and in preservative unknown, (after du Bocage, 1869). The choanosomal skeleton consists of a large-meshed polygonal reticulation formed by wispy tracts of spicules with no spongin reinforcement. The ectosomal skeleton is a tangential layer of megascleres. The surface of the sponge has a distinct palisade of anisodiscorhabds (modified from du Bocage, no measurements given). Megascleres are smooth or polytylote anisostyles 160–190 × 6 μm. Microscleres are anisodiscorhabds 40 μm in length (after Burton, unpublished catalogue, BMNH).

Remarks. Du Bocage (1869) originally described *Latrunculia cratera* from Cape Verde in the Atlantic Ocean, distinguishing it from *Podospongia loveni* by the presence of a 'distinct dermis of thorny microscleres' forming a 'complete envelope around the sponge'. He named the species *Latrunculia cratera* but did not give a generic diagnosis nor any indication of its phylogenetic affinity. The original type material consisted of only one specimen (a holotype) and was deposited in the Museu Bocage, Lisbon, Portugal. Unfortunately, du Bocage's sponge collection was lost after the museum burnt down on in 1978. Alleged schizotypes of *Latrunculia cratera* have been reported in the Norman and Lervig collections in the BMNH, all of which have been examined and all transferred to other genera. No other record of *L. cratera* has been reported since its initial description by du Bocage, and with the destruction of the holotype the species is clearly *incertae sedis*. There is no provision under the ICZN to nominate a new type species for a genus once this is fixed (Anon., 1999, ICZN Articles 66–70). Consequently, the concept of *Latrunculia bocagei* Ridley & Dendy is used here to emend the genus diagnosis as a 'representative species' that exemplifies of *Latrunculia* given that the holotype of *L. cratera* is confirmed destroyed and the original description and diagnosis are completely inadequate to provide a firm concept for the genus.

Description of representative species

Latrunculia bocagei Ridley and Dendy, 1886 (Fig. 4).

Synonymy. *Latrunculia bocagei* Ridley and Dendy, 1886: 492; 1887: 238–239, pl. 44 fig. 1, pl. 45 fig. 8.

Material examined. Holotype: BMNH 1887.5.2.237. Holotype of variety: BMNH 1887.5.2.238 – Kerguelen.

Description. Massive, hemispherical sponge, 3 × 2.5 × 3.8 cm diameter (Fig. 4A). Surface smooth with volcano-shaped or cylindrical oscules, ~5 mm height, and mammiform areolate porefields. Ectosome thick and leathery not separable from underlying choanosome. Colour in life dark brown; in preservative pale yellow. The choanosomal skeleton is a very irregular polygonal-meshed reticulation formed by wispy tracts of smooth styles (Fig. 4B). These tracts range in width from 91–120 μm in thickness, forming meshes that are 200 μm wide. Towards the surface these spicules tend to be vertically arranged. The surface of the ectosome is aligned with an erect layer of single discorhabds (Fig. 4C). Beneath the discorhabds in the ectosome is a thick paratangential layer of densely interlocking megascleres, approximately 700 μm wide. Megascleres (Fig. 4D): anisostyles are smooth, centrally thickened, fusiform and faintly sinuous, 510 (455–547) × 16(16–18) μm diameter. Microscleres (Fig. 4E–G): anisodiscorhabds, the manubrium is an expanded spinose base armoured with two horizontally arranged whorls of spines followed by a smooth slender cylindrical shaft 20 μm long and 7 μm wide. Medium whorl is midway between manubrium and apical whorl, this is circular, flat and horizontally arranged, 30 μm in diameter, similar in diameter to the subsidiary and apical whorl, the subsidiary whorl is more or less perpendicular to the shaft. The spines of the apical whorl are slanted slightly upwards ending in a crown-like tuft of blunt terminally spined projections. The whorls are deeply notched along the rim and divided into four segments each segment possessing a denticulate margin or 7–8 spines, 66(57–71) μm in length.

Remarks. Although du Bocage (1869) failed to assign *Latrunculia* to a family or order, he described the sponge *L. cratera* in conjunction with *Podospongia loveni* du Bocage (1869). Carter (1879b) was the first to indicate affinity by placing *Latrunculia purpurea* in the Order Holorrhaphidota and *Latrunculia* (=*Negombata*) *corticata* in the Family Ectyonida (Order Echinonemata). His placement of the two species in different families was based on the differing structure of the 'flesh' spicules. Ridley & Dendy (1886, 1887) included *Latrunculia* with *Spirastrella* in Spirastrellidae on the basis that the discorhabds were thought to be related to spinispires forming an ectosomal crust as do the spirasters of *Spirastrella*. Various other authors (Kirkpatrick, 1900a, 1903b, 1908c; Stephens, 1915a; Hentschel, 1914; Dendy, 1921) followed Ridley & Dendy's (1887) classification for the placement of *Latrunculia* within Spirastrellidae, but Topsent (1922) placed the genus in the newly defined family Latrunculiidae together with *Podospongia* and *Sigmosceptrella*, thus separating the genus *Latrunculia* from Spirastrellidae. Various minor reorganisations in the taxonomic placement of *Latrunculia* were proposed, such as with the Family Choanitidae by de Laubenfels (1936a) and Bergquist (1961a), but Lévi (1973) adopted Topsent's (1922) system of classification in placing the genus with the Latrunculiidae in Poecilosclerida.

Twenty-seven species have been historically allocated to *Latrunculia*, giving the impression of a global distribution. According to redefined criteria for *Latrunculia* in this work, however, only eleven of the originally recognised species now conform to the strict definition of *Latrunculia*. The remainders are assigned to other genera, both within Latrunculiidae and elsewhere. An exhaustive inspection of world-wide museum material (Samaai, unpublished), has revealed the existence of a further nine previously undescribed species which are now also assigned to the genus. This brings the total number of species within *Latrunculia* to 20 (Samaai, unpublished).

The genus *Microstylifer* Vacelet, 1969 (Vacelet, 1969: 179) was originally described as having styles of three sizes with

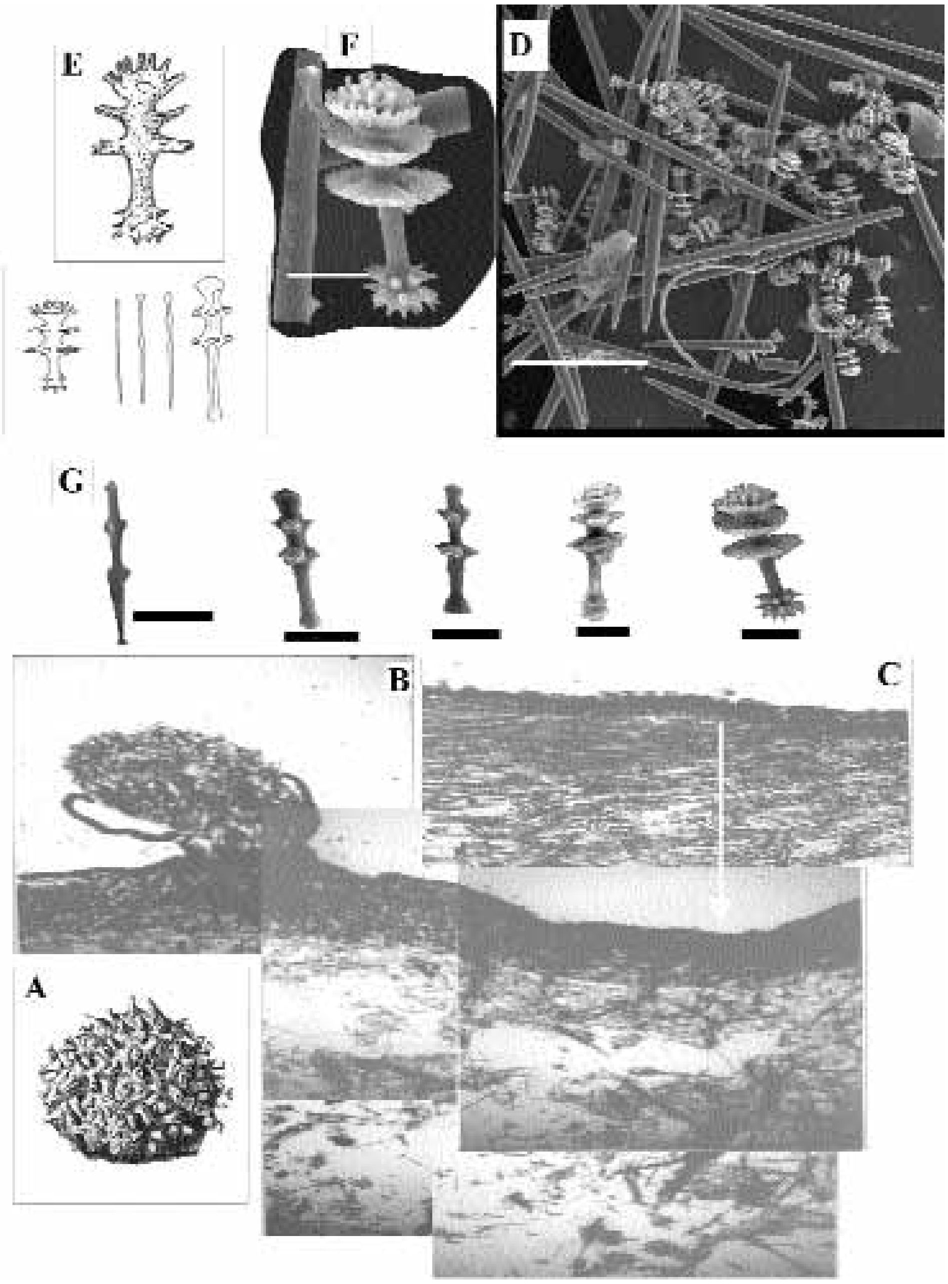


Fig. 4. A–G, *Latrunculia bocagei* du Bocage (1869). A, holotype (after Ridley and Dendy, 1887: pl. 44 fig. 1). B–C, photomicrograph of skeletal architecture made from a slide of the holotype. E, drawing of discorhabds made from a slide of the holotype. D, F–G, SEM photos of spicule made from the holotype (scales D, 150 μm; F, 20 μm). G, developmental stages of discorhabds (scale 20 μm).

microspined heads, the smallest microstyles forming a palisade in the ectosome and present in the fascicles of the megascleres. Vacelet (1969) considered the genus to be an axinellid, but had reservations about this assignation. Re-examination of a microscope slide of the holotype of the type species, *Microstylifer rugosus* Vacelet (MNHN DJV10) (by monotypy), courtesy of Rob Van Soest, revealed that the megascleres had constricted necks, frequently malformed heads, and they were occasionally polytylote. The distal ends were frequently blunt. The spicule slide contained only a few spicules, including foreign sigmas and several latrunculid discorhabds, indicating a potential affinity with Latrunculiidae. One species of *Latrunculia* is also known to possess microspined styles, but nevertheless, it is very unlikely that discorhabds would have been overlooked by Vacelet (1969) when initially describing this species because if they were definitely present they would have been visible in the ectodermal palisade. Moreover, the species was described as hispid with projecting styles, whereas no Latrunculiidae are hispid as they have a tangential ectosomal megasclere skeleton. The only evidence for affinity of *Microstylifer* with Latrunculiidae, apart from the discorhabds in the slide, is the 'vague tracts of megascleres' in the choanosome and the oblique layer of megascleres at the ectosome. However, above the oblique layer there is a palisade of microstyles. If discorhabds were native to this species they would be in this layer, and no Latrunculiidae in our knowledge has microstyles. Until fresh material is examined, or a histological section of the holotype can be examined, this species

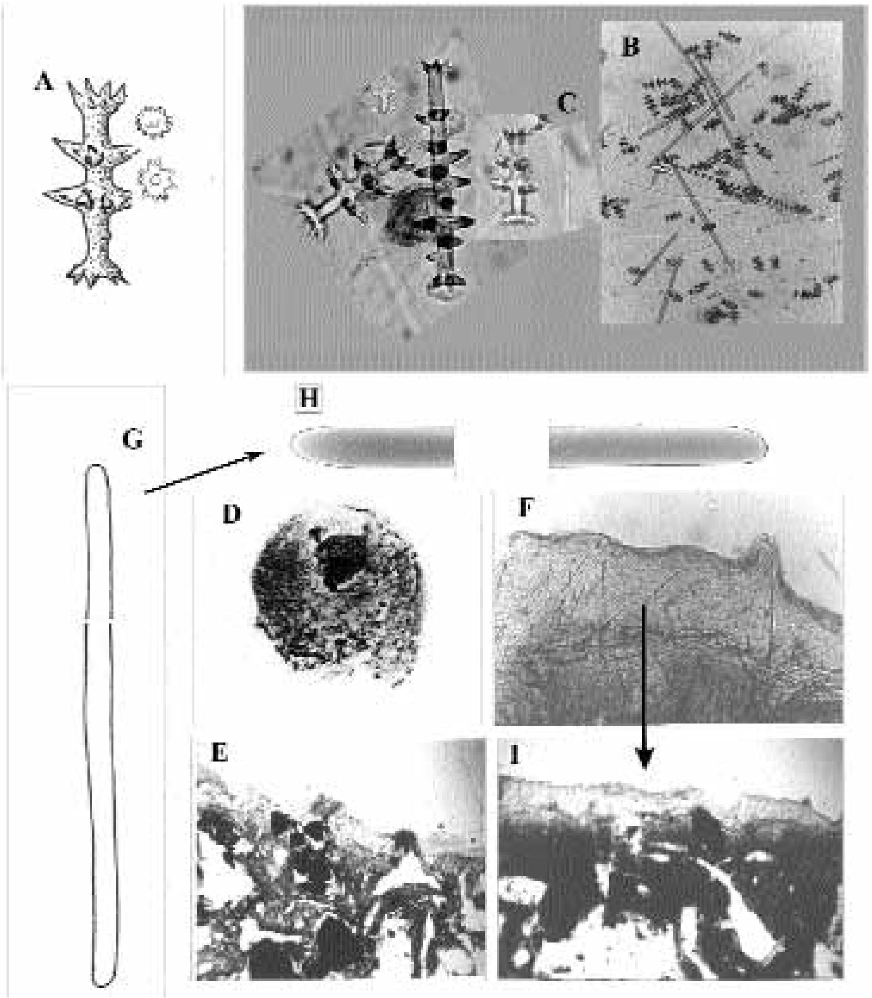


Fig. 5. A–C, *Sceptrella regalis* Schmidt, 1870. A, drawing of discorhabd made from a slide of the holotype. B–C, photomicrograph of microscleres made from a slide of the holotype. B, mature sceptres. C, developing isoconicodiscorhabd. D–G, *Strongylodesma areolata* Lévi (1969). D, holotype (diameter 25 × 13 × 30 mm) (after Lévi, 1969: 956, pl. 2 fig. 5). E–F, photomicrograph of skeletal architecture made from a slide of the holotype. G–H, drawing and SEM photo of strongyle from the holotype.

is a very questionable Latrunculiidae, and presently Poecilosclerida *incertae sedis*.

SCEPTRELLA SCHMIDT, 1870

Synonymy

Sceptrella Schmidt, 1870: 58.

Type species

Sceptrella regalis Schmidt, 1870 (by monotypy).

Definition

Latrunculiidae with anisostyles arranged in wispy irregular polygonal meshes, ectosomal skeleton consists of a tangential layer of anisostyles, with an erect palisade of microscleres, microscleres are isoconicodiscorhabds ('sceptres') with furcate whorls of spines, on a straight axial rod.

Diagnosis

Encrusting sponges with mammiform papillae and areolate porefields; surface even, non-hispid. Colour in life and in preservative rose-tan to grey. Microscleres are isoconicodiscorhabds with furcate whorls of spines, on a straight axial rod, megascleres are smooth styles or anisostyles. Choanosomal architecture consists of anisostyles arranged in wispy irregular polygonal meshes, ectosomal skeleton consists of a tangential layer of anisostyles, with an erect palisade of microscleres.

Previous review

None.

Description of type species

Sceptrella regalis Schmidt, 1870 (Fig. 5).

Synonymy. *Sceptrella regalis*, Schmidt, 1870: 58, pl. 5 fig. 24; *Latrunculia regalis*; Van Soest, 1984b: 149; Wiedenmayer, 1994: 73.

Material examined. Holotype (fragment): BMNH 1870.5.3.22 (spicule slide) – Florida, 262 fathoms.

Description (after Schmidt, 1870). Sponge encrusting, bearing oscular processes, surface even, non-hispid. Colour in life unknown; in preservative grey, texture unknown. The choanosomal architecture consists of anisostyles arranged in wispy irregular polygonal meshes, the base of the choanosome is somewhat radial. The ectosomal skeleton consists of a tangential layer of anisostyles with isoconicodiscorhabds scattered in the choanosome and form a palisade at the surface. The megascleres are smooth centrally thickened fusiform anisostyles 410 × 11 μm (Fig. 5B). Microscleres are isoconicodiscorhabds, or 'sceptres' (Fig. 5A, C). These spicules have a stout shaft, the manubrium is surrounded by a ring of obliquely directed spines, and at equal distances along the shaft are two whorls of projecting similar spines, which are armed with secondary spines. The apical whorl is oblique and arranged in a crown-like structure. There are three size categories: 50 μm; 70 μm; 127 μm in length.

Remarks. Schmidt (1870) presumed that the type species of *Sceptrella, S. regalis*, collected off the Florida coast, was closely related to *Latrunculia* as it had anisostyles and a similar skeletal architecture, although he recognised that the microsclere was spinose and bore little resemblance to the lobed discorhabd microscleres characteristic of *Latrunculia*. When Schmidt (1875) described *Sceptrella triloba* from Norway he synonymised *Sceptrella* with *Latrunculia* on the basis of identical skeletal and spicule morphology. Thiele (1905) and Burton (unpublished catalogue in the BMNH), transferred the species *Sceptrella triloba* to *Latrunculia*.

However, Carter (1879b: 358–359, pl. 29 figs 14–15) clearly illustrated the difference between the microscleres of *Sceptrella* and *Latrunculia*, stating that 'the spines may be microspined as in *Sceptrella regalis* Schmidt, or the groups on the shaft may be transformed into circular plates with serrated margins, as in *Latrunculia cratera*'. Examination of the spicule slide of holotype *Sceptrella regalis* reveals that although the microscleres of this genus arise from a straight protorhabd as in *Latrunculia*, the post development of spicules differs. The whorls of spinose projections develop simultaneously in *Sceptrella* in contrast to the asynchronised development of the different whorls in *Latrunculia*, and the spines develop directly from the shaft and are smooth or entirely microspined. *Sceptrella* is upheld here as a valid genus of Latrunculiidae.

Several specimens identified as *Latrunculia* have been transferred to *Sceptrella*. Presently we recognise six valid species of *Sceptrella*, including *S. regalis* Schmidt, *S. triloba* Schmidt, *S. biannulata* Topsent, *S. insignis* Topsent, and *S. insignis* var. *regularis*. At least one more species of *Sceptrella* is known from Icelandic waters, but remains unnamed (Samaai, unpublished).

STRONGYLODESMA LÉVI, 1969

Synonymy

Strongylodesma Lévi, 1969: 959.

Type species

Strongylodesma areolata Lévi, 1969 (by monotypy).

Definition

Latrunculiidae with wispy polygonal reticulation of strongyles with no distinction between primary and secondary tracts. The ectosomal skeleton consists of a clear thick band of collagenous mesohyl, the base of which has a thin band of paratangential strongyles. Megascleres are smooth or terminally spined strongyles in one size category.

Diagnosis

Massive spherical or hemispherical sponges with elevated volcano-shaped or cylindrical oscules and fungiform or concave elliptical areolate porefields. Colour brown to reddish brown. The choanosomal skeleton consists of a wispy polygonal reticulation of tracts of strongyles with no distinction between primary and secondary tracts. The ectosomal skeleton consists of a clear thick band of collagenous mesohyl, the base of which has a thin band of paratangential strongyles. The thickness of this paratangential layer differs considerably between species. Most species have a very thick layer. Strongyles support the raised surface structures and protrude beyond the surface. Megascleres are smooth, or terminally spined strongyles in one size category. Microscleres absent. *Strongylodesma* spp. contain pyrroloquinoline alkaloids such as batzellins, isobatzellins, discorhabdins and their derivatives.

Previous review

None.

Description of type species

Strongylodesma areolata Lévi, 1968 (Fig. 5).

Synonymy. *Strongylodesma areolata* Lévi, 1969: 959, pl. 2 fig. 4c.

Material examined. Holotype: MNHN LBIM DCL 1425 – Vema Seamount.

Description. Sponge massive encrusting, 25 × 13 × 30 mm in diameter (Fig. 5D); surface smooth with flat circular or elliptical areolate porefields which are 0.5–3.5 mm in diameter. Oscules are raised and membranous. Colour in life reddish-brown, beige in preservative. Texture firm and compressible. Choanosomal architecture consists of an irregular polygonal-meshed reticulation of wispy tracts of faintly microspined strongyles (Fig. 5E). These tracts range in width from 9–100 μm in thickness, forming meshes that are 120 μm wide. The ectosomal skeleton consists of a clear thick band of collagenous mesohyl 227–270 μm thick, the base of which is a thin band of paratangential strongyles (20 μm deep) (Fig. 5F). Strongyles protrude beyond the surface (Fig. 5F) in a haphazard manner. Megascleres are faintly terminally microspined strongyles, 299(282–319) × 6(5–7) μm in length (Fig. 5G–H). Microscleres absent.

Remarks. The holotype of *Strongylodesma areolata* was first described by Lévi (1968) from the Vema Seamount in the south Atlantic Ocean, and included in Spirastrellidae. Conversely, an unnamed species of *Strongylodesma* described by Battershill (in Lévi 1998) was placed in Phoriospongiidae (=Chondropsidae) (Poecilosclerida) on the basis that some other taxa of phoriospongiids also possessed areolate porefields, and no doubt also because many have strongyles as their primary megascleres (although these are usually coupled with chelae microscleres, e.g., *Strongylacidon* etc.). If other characters are taken into account, however, including skeletal architecture, base pigmentation, and biochemistry, the majority are shared with *Latrunculia*. Species of *Strongylodesma* differ primarily from those of *Latrunculia* and *Sceptrella* in that they lack microscleres and that the megascleres are strongyles.

Seven species of *Strongylodesma* are now recognised, including three species from South Africa, a new species from New Caledonia (Vacelet & Kelly in Lévi, 1998), and one from Tonga (Kelly, unpublished). A further two Caribbean species are now recognised amongst the Harbor Branch Oceanographic Institution collections (HBOM 003:00922) and (HBOM 003:00050, HBOM 003:00051).

TSITSIKAMMA GEN. NOV.

Type species

Tsitsikamma favus gen. nov., sp. nov.

Definition

Latrunculiidae with elliptical honeycomb-like chambers (*sensu stricto*), or a single sac-like chamber (*sensu lato*), chamber walls being very thick tracts of style megascleres. Microscleres are isochiarhabds.

Diagnosis

Massive encrusting, hemispherical or pedunculate sponges with a smooth undulating surface, covered with large robust cylindrical or volcano-shaped oscules and raised cauliform areolate porefields. Colour in life is dark liver brown to dark turquoise, or pinkish brown. The texture is extraordinarily tough and leathery. Megascleres are styles, microscleres are isochiarhabds. Elliptical honeycomb-like chambers, or a single sac-like chamber surrounding a soft mesohyl with wispy tracts characterise the genus. The walls of the chambers or sac are extremely thick, up to 1500 μm, and visible with the unaided eye. The chambered holotype is incompressible. Microscleres are present in an irregular palisade on the surface ectosome and lining the internal tracts. Chemistry includes pyrroloquinoline alkaloids (tsitsikammamines), and the discorhabdin derivatives 14-Bromo-3-dihydrodiscorhabdin C and 14-Bromodiscorhabdin C.

Etymology

Tsitsikamma means 'clear water' in Khoi language, and the genus has been named for the type locality, a unique area of south-east Africa.

Previous reviews

Pertaining only to the chemistry literature: Urban *et al.* (2000), Beukes (2000), Beukes *et al.* (in press).

Geographic distribution

Rheeders Bay, Tsitsikamma National Park, East Coast, South Africa; Algoa Bay, Port Elizabeth, East Coast, South Africa.

Description of type species

Tsitsikamma favus gen. nov., sp. nov. (Fig. 6).

Material examined. Holotype: BMNH1997.7.3.2 – Rheeders Bay, Tsitsikamma National Park, 34°10′S, 23°54′E, South Africa, depth 22 m, coll. P. Coetzee, 1995. Paratypes: BMNH – several specimens from Rheeders Bay, Knoll reef Tsitsikamma National Park, and Algoa bay, Port Elizabeth, South Africa. Habitat. Depth range 18–22 m on rocky substrate, associated with soft and hard coral and other invertebrates.

Description. Sponge is massive, ovo-spherical, sometimes thickly encrusting, 1–8 cm high and 10–15 cm wide (Fig. 6A). Texture is hard and only slightly compressible, resilient and leathery; surface smooth and crowded with large single to multichambered cylindrical lance-shaped oscules, 1–4 mm wide, 8 mm high and many pedunculate cauliform areolate porefields, 3 mm wide, 5–6 mm high, with no membrane; colour in life is dark brown or liver brown and between the cauliform structures dark turquoise, in alcohol, ectosome dark turquoise, choanosome dark brown. The choanosome is divided into honeycomb-like chambers and convoluted layers by very thick reinforced tracts of anisostyles, these tracts range in width from 1000–1700 μm thick, forming meshes that are elliptical in shape and 5800 μm wide. These tracts are lined with microscleres, suggesting that they may represent an early ectosermal surface, and that the sponge grows in size and volume by putting on new chambers, as in many species of *Petrosia* and *Coelocarteria*. Within and between the chambers and convoluted layers the skeleton consists of an ill-formed, irregular reticulation of small anisostyles, these tracts range in width from 100–150 μm (Fig. 6B). Microscleres are isochiadiscorhabds and these are abundant throughout the choanosome. The ectosome is composed of a thick dense feltwork of tangential and paratangential anisostyles approximately 900 μm wide. This layer is present in the fistulae with anisostyles disposed in a compact regular vertical to oblique arrangement supporting the cauliform areolate structures. A single layer of erect isochiadiscorhabds (48 μm wide) lines the surface of the ectosome (Fig. 6C). Megascleres in two categories of anisostyles, (1) slightly curved and thickened centrally, 621(537–700) × 14(14) μm, n = 20; (2) thinner slightly curved centrally: 530(480–566) × 9.6(9.6)μm (Fig. 6D). Microscleres are isochiadiscorhabds with three whorls of cylindrical, conical tubercles, the apex of each tubercular projection is acanthose: 48(41–60) × 9(7.2–9.6)μm (Fig. 6E–G). Reproduction: oocytes present in specimens but no further indication of reproductive mode yet corroborated.

Etymology. *favus* = honeycomb (L.).

Remarks. The huge spicule tracts that compartmentalise the body of *Tsitsikamma favus* are remarkable and clearly differentiate it from *Latrunculia, Strongylodesma* and *Sceptrella*, and other related demosponges. The characters that link the genera are the base pigmentation, chemistry, the surface palisade of microscleres and the soft skeletal parts. A second penduncular sac-like species is known from Algoa Bay, Port Elizabeth, South Africa.

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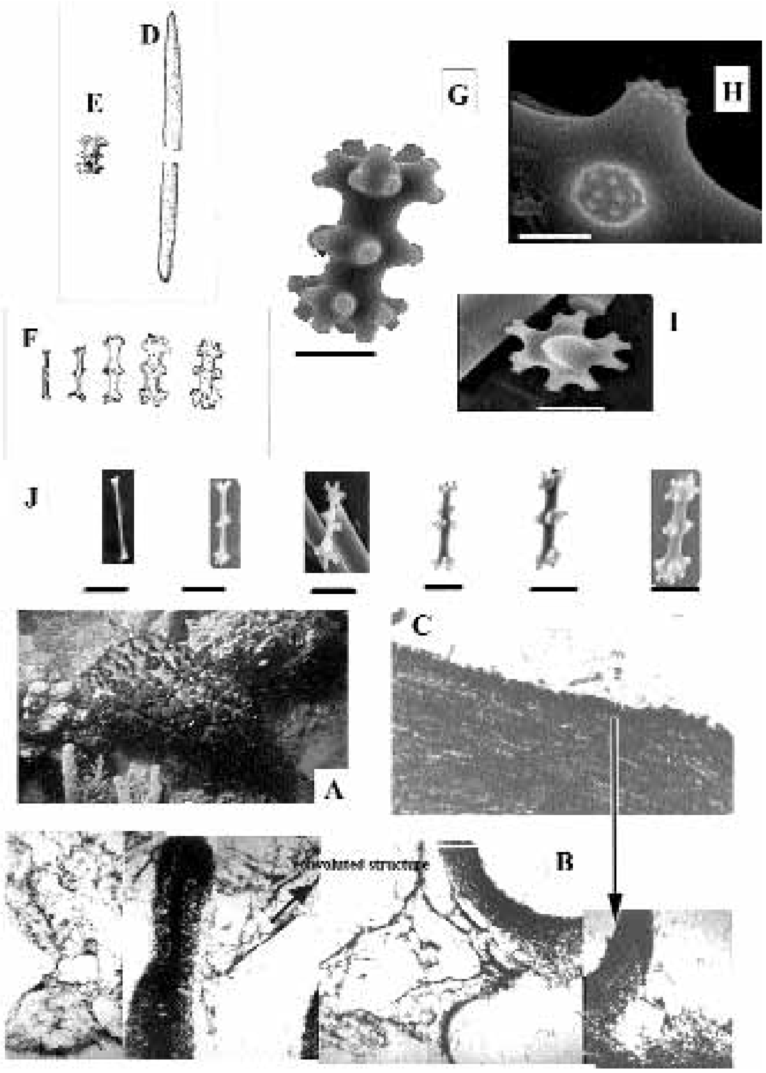

Fig. 6. A–G, *Tsitsikamma favus* gen. nov. sp. nov. A, holotype. B–C, photomicrograph of skeletal architecture made from a slide of holotype. D–F, megasclere and microsclere drawing made from the holotype slide. G–I, SEM photos of isochiasdiscorhabd and terminations (scales G, 20 µm; H, 3.8 µm; I, 10 µm). J, developmental stages of isochiadiscorhabds (scale 20 µm).

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