A revision of the genus Strongylodesma Lévi (Porifera: Demospongiae: Latrunculiidae) with descriptions of four new species

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The sponge genus Strongylodesma Lévi is reviewed and redefined, and now accommodates eight closely related species. The type species of Strongylodesma Lévi is redescribed and an additional two new species are described from the Indo-Pacific: S. novacaledoniae sp. nov. and S. tongaensis sp. nov. Several specimens previously identified as species of Batzella (Poecilosclerida: Chondropsidae) have been re-assigned to Strongylodesma, as the new species S. purpureus sp. nov. and S. nigra sp. nov. With the description here of new species from the Pacific Ocean and Caribbean Atlantic, the biogeographical distribution of Strongylodesma now appears to be generally tropical with a subtropical South African component, whereas previously it was only known from South Africa. Although species of Strongylodesma have not previously been recorded from the intermediate locations (Western Indian Ocean, South-east Asia, central west Pacific, and New Zealand), re-evaluation here will facilitate more readily the recognition of taxa in these intermediate regions, if they exist, in the future. The species are not widespread, except perhaps along the south-east coast of South Africa, and where they occur they are not abundant. Species occur over a wide depth range, from the intertidal in Tsitsikamma, South Africa, to 140 m in the Caribbean.

Keywords: Porifera, sponge, Demospongiae, Poecilosclerida, Latrunculiidae, Strongylodesma, taxonomy, new species, revision

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INTRODUCTION

The genus Strongylodesma Lévi was erected by Lévi (1969) for a deep-water sponge, S. areolata Lévi, 1969, found on the Vema Seamount in the southern Atlantic Ocean, off the west coast of South Africa. The affinity of this genus with Latrunculia has now been firmly established (Samaai & Kelly, 2002; Samaai et al., 2003, 2004; Antunes et al., 2005), yet in the past Strongylodesma was either unassigned (Lévi, 1969), incorrectly assigned (to Phoriospongiae in Lévi, 1998), or the species was incorrectly assigned for convenience to the poorly recognized genera Prianos and Batzella, both of which only possess strongyles. Recent revisions of these two genera have revealed that the type species of Prianos has the skeletal architecture of a cha-clinid sponge (delicate unispicular isotropic reticulation of strongyles) and is a synonym of Haliclona (Reniera) (de Weerdt, 2002), and the type species of Batzella has skeletal characteristics (plumose columns of strongyles) shared with other Chondropsidae (Van Soest, 2002).

It is interesting to note that in some specimens of strongyles with a ‘looped end’ or ‘shepherd’s crook’ malformation, had also become associated with the incorrect assignment of some specimens of Strongylodesma to Batzella. This association is most likely due to the fact that the first record of this unique malformation was described from a species of Batzella from Curacao (B. rosea Van Soest, 1984). The malformation is also seen in Caribbean and Pacific species of Strongylodesma, S. purpureus sp. nov. and S. nigra sp. nov, provisionally identified as Batzella by Van Soest (1996), and S. tongaensis sp. nov.

Thus, the accurate assignment of species with strongyles to Prianos, Batzella, or Strongylodesma, in the general taxonomic literature (e.g. de Laubenfels, 1954; Hoshino, 1981), and marine natural products literature (Sakemi et al., 1989; Sun et al., 1990; Van Soest et al., 1996; Gunasekera et al., 1999, 2003; see in Samaai & Kelly, 2002 and Samaai et al., 2004), and in general biodiversity inventory (M. Kelly & Lori J. Bell, CRRF, unpublished data), has proven difficult. The discovery of three new species of Strongylodesma from South Africa (Samaai et al., 2003, 2004) facilitated the clarification of a suite of diagnostic characters that now clearly define the genus Strongylodesma Lévi and confirm its monophyly. Strongylodesma has strongyles (smooth or terminally spined) arranged in a wispy polygonal reticulation within the choanosome, rather like that of Latrunculia, an ectosome composed of fibrillar collagen, green to brown coloration, hemispherical to encrusting morphology, an areolate aquiferous system with fungiform (mushroom-shaped) or concave porefields (Samaai & Kelly, 2002), and all known species contain pyrroloquinoline alkaloids (Van Soest et al., 1996;
Gunasekera et al., 2003; Antunes et al., 2004, 2005; Keyzers et al., 2004).

It was not until 2002 that *Strongylodesma* was reported from other locations than the type locality (Samaai & Kelly, 2002) despite comprehensive shallow and deep water collections emerging for the major world regions throughout this period. Samaai et al. (2004) described three new species from the warm temperate south-east and east coasts of South Africa, from intertidal pools and deeper water locations. The aim of this contribution is to evaluate the status of *Strongylodesma*, describe several new species from the Caribbean and Pacific regions, and correct several previous misidentifications. In doing so, we will clarify a framework for species recognition in the future.

**MATERIALS AND METHODS**

The taxonomic revision was carried out by reassessment of original and more recent descriptions, and examination of type material and additional specimens loaned from various institutions, as well as recently collected specimens (by SCUBA), by light and scanning electron microscopy (SEM) (see Samaai & Gibbons, 2005). Spicule dimensions are given as the mean length (range of length measurements) × mean width (range of width measurements) of 20 spicule measurements, unless otherwise stated. Abbreviations used in the text are as follows: MNHN (Muséum National d’Histoire Naturelle, Paris); HBOM (Harbour Branch Oceanographic Museum, Florida); BMNH (The Natural History Museum, London); NIWA (National Institute of Water and Atmospheric Research, Wellington); MKB (personal collection of Dr M. Kelly); T.S. (personal reference number of T. Samaai); OCDN—specimen sample numbers for United States National Cancer Institute shallow-water collection programme contracted to the Coral Reef Research Foundation (CRRF). A complete collection of all OCDN sponge specimens is at CRRF and with M.K. Additionally, an un-catalogued collection is located at the Smithsonian Institution (United States National Museum).

The outline maps (Africa, South Africa and the east coast coastline) were created with Coastline Extractor (http://www.ngdc.noaa.gov/mgg/shorelines/shorelines.html).

**RESULTS**

**List of species described**

Class DEMOSPONGIAE Sollas, 1885
Order POECILOSCLERIDA Topsent, 1928
Suborder LATRUNCULINA Kelly & Samaai, 2002
Family LATRUNCULIIDAE Topsent, 1922

**Genus Strongylodesma** Lévi, 1969


**SYNONYMY**

*Strongylodesma areolata* Lévi, 1969; pl. 2, figure 4c;
Samaai & Kelly, 2002: 717, figure 5.

**DIAGNOSIS**

Massive hemispherical, pedunculate, or thinly encrusting sponges, with areolate porefields and raised fistular oscules; texture in life soft, slightly elastic, compressible, leathery in preservative. Colour in life typically liquorice brown, dark green, olive, brown or khaki, often tinged with forest-green or blue, or rarely pale beige to white. Structural megascleres are styles or anisostrongyles, rarely oxeas, these are frequently slightly irregular, sinuous, forming a compact tangential layer under the ectosome, and a wide-meshed reticulation in the choanosomal that, in some genera, is bounded by broad dense ascending (*Cyclacanthia* Samaai, Govender & Kelly), or chamber-forming tracts (*Tsitsikamma* Samaai & Kelly). Microscleres are typically acanthose anisolodicorhabds, or ‘chessman’ spicules, or isosinodicorhabds (*Cyclacanthia* Samaai, Govender & Kelly), bearing various apical and basal whorls (manubrium) of discrete spines that merge to various degrees to form crenulate discs; the subsidiary and median whorls (in the upper half and midway along the shaft, respectively) are variously present, and form crenulate to spinose discs. Microscleres are typically arranged in a compact or irregular palisade of spicules orientated perpendicular to the ectosome, their bases buried in the ectosomal membrane. Viviparous. Shallow sublittoral to abyssal, polar to warm temperate (modified from Samaai & Kelly, 2002).

**Genus Strongylodesma** Lévi 1969

**TYPE SPECIES**


**SYSTEMATICS**

Family LATRUNCULIIDAE Topsent, 1922

**RESULTS**

List of species described

Class DEMOSPONGIAE Sollas, 1885
Order POECILOSCLERIDA Topsent, 1928
Suborder LATRUNCULINA Kelly & Samaai, 2002
Family LATRUNCULIIDAE Topsent, 1922

**Genus Strongylodesma** Lévi, 1969

*Strongylodesma areolata* Lévi, 1969

**DIAGNOSIS**

Spherical or hemispherical Latrunculidae with elevated volcano-shaped or cylindrical oscules and fungiform or concave elliptical areolate porefields. Colour in life, brown to reddish brown. Choanosomal architecture consists of megascleres arranged in an irregular, large-meshed reticulation formed by wispy tracts of spicules, which lack spongine reinforcement. The ectosomal skeleton consists of a band of paratangential strongyles, the thickness of which differs considerably between species. The subectosomal skeleton is frequently a clear band of collagenous mesohyl, but may be unrecognizable as a distinct region in some species. Megascleres support the raised surface structures and may protrude beyond the surface. Megascleres are smooth, or terminally spined strongyles in one size category, some of which have a ‘looped end’ or ‘shepherd’s crook’ malformation. *Strongylodesma* spp. contain pyrroloquinoline alkaloids such as batzellins, isobatzellins, discorhabdins and their derivatives (modified from Samaai & Kelly, 2002).

Previous reviews. Samaai (2002); Samaai & Kelly (2002); Samaai et al. (2003, 2004); Antunes et al. (2004, 2005)
**Strongylodesma areolata** Lévi, 1969
(Figures 1A, 2A, 2B, 4; Table 1).

**TYPE SPECIES**
*Strongylodesma areolata* Lévi, 1969: 959, pl. 2, figure 4c.

*Strongylodesma areolata* Lévi, 1969: 959, pl. 2, figure 4c; Samaai & Kelly, 2002: 717, figure 5.

**MATERIAL**

**DIAGNOSIS (MODIFIED FROM LÉVI, 1969)**
Massive encrusting Latrunculiidae (Figure 1A), with smooth surface. Surface usually with membraneous fungiform oscules, together with flat circular or elliptical areolate porefields. Colour in life reddish-brown, beige in preservative. The texture of the sponge is firm and compressible.

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**Fig. 1.** Gross morphology of *Strongylodesma* spp: (A) *Strongylodesma areolata* Lévi, 1969 (reproduced from Lévi, 1969); (B) *Strongylodesma algoaensis* Samaai & Kelly, 2003 (reproduced from Samaai et al., 2003); (C) *Strongylodesma tsetskammaensis* Samaai & Kelly, 2003 (reproduced from Samaai et al., 2003); (D) *Strongylodesma aliwaliensis* Samaai, 2004 (reproduced from Samaai et al., 2003, 2004); (E) *Strongylodesma purpureus* sp. nov. (picture from HBOI); (F) *Strongylodesma nigra* sp. nov. (picture from HBOI); (G) *Strongylodesma tongaensis* sp. nov. (picture from M. Kelly).
Megascleres are faintly terminally microspined strongyles, 299 (282–319) μm, N = 20 (Figure 2A). The choanosomal architecture consists of an irregular polygonal-meshed reticulation of wispy tracts of faintly microspined strongyles (Figure 2B). 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 mesohyal 227–270 μm thick, the base of which is lined with a thin band of paratangential strongyles (20 μm deep). Strongyles protrude beyond the surface in a haphazard manner. The sponge (whose habitat and depth is unknown), has only been recorded from the Vema Seamounts in the South Atlantic (Figure 4).

**Geographical Distribution**

Vema Seamount (South Atlantic) (Figure 4). The Vema Seamount is located at the following location; latitude 31º 37.20’ S, longitude 8º 20.40’ E.

**Chemistry**

Unknown.

**Remarks**

In the early 1960s, a collection of material from the Vema Seamount was sent to the Muséum National d'Histoire Naturelle, Paris, amongst which were several unidentified sponge species. In 1969, Lévi described and published the sponge collection, amongst which was a description of the first species of *Strongylodesma*. There are no verifiable records of *S. areolata* subsequent to its original description. *Strongylodesma areolata* was well described by Lévi (1969), who clearly differentiated it from *Prianos*, *Hymeniacidon* and *Strongylacidon* based on the skeletal architecture and strongyle megascleres. Species of *Strongylodesma* have strongyles as megascleres with a distinctive paratangential ectosomal layer, the thickness of this layer differing considerably between species, most of which have very thick layers.
In *Strongylodesma* the ectosomal strongyles tend to be arranged peripherally perpendicular to the surface; this arrangement is assumed to be homologous to that of the erect layer of anisodiscorhabds of *Latrunculia* (Samaai & Kelly, 2002; Samaai et al., 2003, 2004).

*Strongylodesma areolata* differs from *S. algoaensis*, *S. tsitsikammaensis* and *S. aliwaliensis* by the smaller size of the megascleres (299 (282–319) × 6 (5–7) μm in the holotype MNHN VEM 131-DC1.1425), and in the possession of terminally spined strongyles (as opposed to smooth strongyles in the South African species) (see Table 1). The subectosomal skeleton of *S. areolata* is a clear band of collagenous mesohyl 227–270 μm thick, the base of which is a thin layer of paratangential strongyles (20 μm deep) (see Samaai, 2002; Samaai & Kelly, 2002). This clear region is absent in South African *Strongylodesma*. The areolate porefields of *S. areolata* are flat and circular while those in the South African species are fungiform.

*Strongylodesma algoaensis* Samaai & Kelly, 2003 (Figures 1B, 2C, 2D, 4; Table 1)  
*Strongylodesma algoaensis* Samaai et al., 2003: 16, figures 3D, 5E, 6D.

**MATERIAL**  
Holotype: BMNH 1996.7.3.3: Algoa Bay, Port Elizabeth, South Africa, 33° 50’ S 25° 45’ E, collected by P. Coetzee, University of Port Elizabeth, 15 April 1994, 15 m.
Paratype: SAM H-4964: Algoa Bay, Port Elizabeth, South Africa, 33° 50’S 25° 45’E, collected by Dr P. Coetzee, University of Port Elizabeth, 15 April 1994, 15 m.

**DIAGNOSIS (MODIFIED FROM SAMAII ET AL., 2003)**  
Massive spherical to hemispherical sponge (Figure 1B), with numerous large vase-shaped membranous oscules, and fungiform areolate porefields. Sand particles are present in the sponge surface. Colour in life, oak brown, in preservative, dark chocolate brown. The texture of the sponge is soft, compressible and fleshy. Megascleres are smooth anisostrongyles with a distinctive axial canal, 328 (307–355) × 9 (7.2–9.6) μm (Figure 2C). The choanosomal skeleton consists of an irregular polygonal-meshed reticulation of wispy tracts of anisostrongyles approximately 95–100 μm thick (Figure 2D). Towards the surface the tracts are perpendicular to the surface of the sponge, diverging just beneath the ectosome into fine plumose brushes 120–150 μm thick. The subectosome is a loose feltwork of paratangential anisostrongyles approximately 120–200 μm deep, above which these spicules become erect or oblique and pierce the surface. Anisostrongyles form a compact palisade around the opening of the papillae. The sponge was found in a moderately rugged rocky bottom habitat, with patches of sand between these rocks, together with coral and other sponges, at a depth of 15 m.

**GEOGRAPHICAL DISTRIBUTION**  
South Africa, Port Elizabeth (Figure 4).

**CHEMISTRY**  
Contain biologically-active pyrroloquinoline alkaloids, discorhabdins A, D & H and 3-dihydridiscorhabdins (Antunes et al., 2004).

**REMARKS (EMENDED FROM SAMAII ET AL., 2003)**  
*Strongylodesma algoaensis* differs from the genus holotype of the type species S. areolata Lévi by the larger size of the megascleres (328 (307–355) × 9 (7.2–9.6) μm (Table 1)), and in the possession of smooth strongyles (as opposed to faintly terminally spined strongyles in the holotype). This species is known so far only from the description of Samaai et al. (2003) and is one of three species described from South Africa. It is closest to *S. tsitsikammaensis* (Samaai et al., 2003), from which it differs in habitat, the latter found in intertidal rock pools and gullies and the former restricted to deeper waters on rocky platforms. The two species differ in coloration, *S. algoaensis* is brown while *S. tsitsikammaensis* is greenish brown. The oscules of *S. algoaensis* have no internal divisions as in *S. tsitsikammaensis*. The two species have quite different textures; *S. algoaensis* is fleshy and compressible while *S. tsitsikammaensis* is much firmer. This is reflected in the structure of the subectosomal region in both species; that of *S. algoaensis* is a loose feltwork of megascleres 120–200 μm deep, whereas in the former species the subectosome is densely packed and 320 μm deep.

*Strongylodesma tsitsikammaensis* Samaai & Kelly, 2003 (Figures 1C, 2E, F, 4; Table 1)  
*Strongylodesma tsitsikammaensis* Samaai et al., 2003: 18, figures 3E, 5F, 6E.

**MATERIAL**  
Holotype: BMNH 1996.7.3.5: Rheeders Bay, Tsitsikamma, South Africa, 34° 10’S 23° 54’ E, 1.5 m, collected by Dr P. Coetzee, University of Port Elizabeth, Dr M. Davis-Coleman, Rhodes University, 27 June 1996.
Paratype: SAM H-4965: Rheeders Bay, Tsitsikamma, South Africa, 34° 10’S 23° 54’E, collected by Dr P. Coetzee, University of Port Elizabeth, Dr M. Davis-Coleman, Rhodes University 15 July 1996, 1.5 m; SAM H-4966: Rheeders Bay, Tsitsikamma, South Africa, 34° 10’S 23° 54’E, collected by Dr P. Coetzee, University of Port Elizabeth, Dr M. Davis-Coleman, Rhodes University 20 September 1996, 15 m; SAM H-4967: Algoa Bay, Port Elizabeth, South Africa, 33° 50’S 25° 45’ E, collected by Dr P. Coetzee, University of Port Elizabeth, 15 October 1998, 1.5 m; SAM H-4970: Rheeders bay, Tsitsikamma, South Africa, 34° 10’S 23° 54’E, intertidal rock pools, depth 2 m, collected by M. Davis-Coleman, Rhodes University, 5 April 1999.

**DIAGNOSIS (MODIFIED FROM SAMAII ET AL., 2003)**  
Massive semispherical sponge (Figure 1C), with numerous randomly scattered cylindrical or volcano-shaped, thin-lipped oscules, having internal dividing membranes. The areolate porefields are smooth and fungiform. Sand particles sometimes present on the surface of the sponge. Colour in life greenish-brown, interior brown; in preservative dark leather brown. The texture of the sponge is resilient, but slightly compressible. Megascleres are smooth anisostrongyles, 348 (307–403) μm thick (Figure 2E). The choanosomal skeleton consists of a dense, meandering, irregular reticulation of wispy tracts of megascleres approximately 80–100 μm thick (Figure 2F).
# Table 1. Review of Strongylodesma species worldwide, including new material examined.

<table>
<thead>
<tr>
<th>Genus/species</th>
<th>Authority</th>
<th>Reference number</th>
<th>Previous designation</th>
<th>By whom designated</th>
<th>Locality</th>
<th>Spicule dimensions</th>
<th>Gross morphology</th>
<th>Colour in life</th>
<th>Strongyle type</th>
<th>Chemistry</th>
</tr>
</thead>
<tbody>
<tr>
<td>Strongylodesma algoaensis</td>
<td>Samaai &amp; Kelly, 2003</td>
<td>BMNH 1996.7.3.3</td>
<td>Samaai &amp; Kelly</td>
<td>Algoa Bay, South Africa</td>
<td>328 (307–355) × 9 (7.2–9.6) µm</td>
<td>Massive spherical</td>
<td>Oak brown</td>
<td>Smooth</td>
<td>Discorhabdins A, D &amp; H; 3-dihydrodiscorhabdins</td>
<td>Unknown</td>
</tr>
<tr>
<td>Strongylodesma tsitsikammaensis</td>
<td>Samaai &amp; Kelly, 2003</td>
<td>BMNH 1996.7.3.5</td>
<td>Samaai &amp; Kelly</td>
<td>Tsitsikamma, South Africa</td>
<td>348 (307–403) × 7.32 7 (7.2–9.6) µm</td>
<td>Masssive semispherical</td>
<td>Greenish brown</td>
<td>Smooth</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
<tr>
<td>S. purpureus</td>
<td>sp. nov.</td>
<td>HBOM 003:00922</td>
<td>Batzella sp.</td>
<td>Van Soest et al., 1996</td>
<td>276.5 (250–290) × 4.8 (4.8) µm</td>
<td>Encrusting</td>
<td>Purple brown</td>
<td>Smooth (malformed)</td>
<td>Discorhabdins S, T &amp; U</td>
<td>Unknown</td>
</tr>
<tr>
<td>Strongylodesma nigra</td>
<td>sp. nov.</td>
<td>HBOM 003:00983</td>
<td>Batzella sp.</td>
<td>Gunasekera</td>
<td>Bahamas (Caribbean)</td>
<td>331.5 (350–317) × 2.4 (2.4) µm</td>
<td>Encrusting</td>
<td>Black</td>
<td>Micropinned</td>
<td>Batzellins A &amp; C; Isobatzellins A–D</td>
</tr>
<tr>
<td>Strongylodesma novacaledoniae</td>
<td>sp. nov.</td>
<td>HBOM 003:00501</td>
<td>Batzella sp.</td>
<td>Van Soest et al., 1996</td>
<td>Bahamas (Caribbean)</td>
<td>310.5 (260–350) × 4.8 (2.4) µm</td>
<td>Encrusting</td>
<td>Brown</td>
<td>Smooth</td>
<td>Unknown</td>
</tr>
<tr>
<td>Strongylodesma tongaensis</td>
<td>sp. nov.</td>
<td>OCDN 5532-W</td>
<td>Strongylodesma sp.</td>
<td>Tonga</td>
<td>294.5 (260–330) × 2.4 (2.4) µm</td>
<td>Encrusting</td>
<td>Dark green</td>
<td>Smooth</td>
<td>Unknown</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
In the deeper choanosome the tracts are ill-defined but diverge towards the surface where they become more robust and plumose, tracts now 200–250 μm wide. Interstitial megascleres are common. The subectosome is a dense paratangential feltwork of anisostrongyles approximately 320 μm deep; these protrude beyond the surface in a haphazard manner. The sponge is found in intertidal rock pools and sand-filled gullies, associated with bryozoa, algae, hard coral and other sponges, at a depth of between 1.5–2.0 m. In deeper waters off Algoa Bay the sponge is found on moderately rugged rocky bottom, with patches of sand between rocks, together with coral and other sponge at a depth of 15 m.

**GEOGRAPHICAL DISTRIBUTION**
South Africa (Tsitsikamma and Port Elizabeth) (Figure 4).

**CHEMISTRY**
Unknown.

**REMARKS**
*Strongylodesma tsitsikammaensis* is very similar to species of *Latrunculia* in the field, with areolate porefields and typical greenish-brown coloration. This species differs from others in its firm but compressible texture, habitat, thin-lipped volcano shaped oscules with internal membranes and fairly large smooth anisostyles (see Table 1). It is superficially very similar to *S. algoaensis* in being semispherical and having a brownish external coloration when alive, with numerous areolate porefields.

*Strongylodesma aliwaliensis* Samaai, 2004
(Figures 1D, 2G, 2H, 4; Table 1)

*Strongylodesma aliwaliensis* Samaai et al., 2004: 1–11, figures 2A, B, C; 3A, B, C, D.

**MATERIAL**
Holotype: SAM H-5083 (cross reference TS 970): Umkomaas, Aliwal Shoal, east coast of South Africa, 3° 26′ 20″S 32°
02°558'E, collected by Toufiek Samaai and Vic Peddemors, 4 September 2003, at a depth of 18 m.

Paratype: SAF 94-23: Umkomaas, Aliwal Shoal, east coast of South Africa, 30°26'02"S 32°02'558'E, collected by Greg Hooper, 21 June 1994, at a depth of 18 m. TS VG 1: Umkomaas, Aliwal Shoal (Raggie Cave and Anvil Rock), east coast of South Africa, 30°26'02"S 32°02'558'E, collected by Toufiek Samaai, 1 May 2004, at a depth of 15 m.

**DIAGNOSIS** (modified from Samaai et al., 2004)
Massive, hemispherical sponge (Figure 1D), sometimes thickly encrusting with an ectsosomal layer not easily separable from the underlying choanosomal tissue, approximately 1 mm thick. The surface of the sponge is smooth with numerous, randomly scattered cylindrical or volcano-shaped oscules, with no internal canal divisions, and smooth mushroom-like areolate porefields. Sand particles and other epifauna (hydroids and red algae) present on the surface and within the choanosomal tissue of the sponge. Colour in life dark olive green; in preservative dark oily brown/black. The texture of the sponge is soft and compressible. Megascleres are smooth strongyles, with one end narrower than the other. 428 (235–590) × 7 (4–9) μm, N = 20 (Figure 2G). The choanosome is divided into ‘honey-comb like’ chambers and convoluted layers by very thick reinforced tracts of strongyles, these tracts range in width 100–294 μm thick (paratype 200–490 μm thick) (Figure 2H). These convoluted layers are a dense paratangential feltwork of strongyles, similar to that found in the ectsosome, suggesting that these convoluted layers may represent an early ectsosomal surface. Within and between the ‘honey-comb like’ chambers and convoluted layers the choanosome is much softer, containing the skeleton that consists of an ill-formed, irregular reticulation of strongyles, these tracts range in width from 50–100 μm, with no distinction between the primary and secondary tracts. Towards the centre of the choanosome the tracts are more confused and ill-defined, and towards the surface they become more robust and vertically arranged and radiate to form plumose tracts 200 μm wide. Scattered throughout the choanosome, between the tracts, are a few interstitial megascleres in the same category as the main spicules. The ectsosome is composed of a dense irregular interlocking paratangential feltwork of strongyles approximately 200–350 μm deep. Below this interlocking paratangential layer a clear band of collagenous mesohyl is present. Strongyles do not protrude beyond the surface. The sponge is found on the shallow reef platform of Aliwal shoal, at a depth of 18 m and on the vertical surfaces on the outside of a cave and boulder at a depth of 15 m. This species is very rare and is found in areas where there is current flow.

**GEOGRAPHICAL DISTRIBUTION**
South Africa (Umkomaas) (Figure 4).

**CHEMISTRY**
Preliminary chemical analysis (Keyzers et al., 2004) of sponge extracts has confirmed the presence of several pyrroloiminoquinone products, for example makaluvamine I.

**REMARKS** (taken from Samaai et al., 2004)
A variety of specimens were seen in the field, but they were all allopatric in their distribution at the type locality. Specimens of *S. aliwaliensis* are found on the same habitat type as described for *S. algoaensis* (both are restricted to deeper waters on rocky platforms), but differs from it in that the former is found in subtropical waters on the east coast and the latter in the warm temperate waters on the south-east coast of Algoa Bay (South Africa). *Strongylodesma tsitsikammaensis* on the other hand is restricted to the intertidal rock pools and gullies in the Tsitsikamma National Park region. *Strongylodesma aliwaliensis* also differ from the two known South African species in coloration; *S. tsitsikammaensis* is greenish brown while *S. algoaensis* is brown, whereas the new species is a dark olive green colour. *Strongylodesma aliwaliensis* also differs from *S. tsitsikammaensis* and *S. algoaensis* in having much larger megascleres ((S. tsitsikammaensis 348 (307–403) × 7.32 (7.2–9.6) μm; S. algoaensis 328 (307–355) × 9 (7.2–9.6) μm)), and in that the strongyles taper off or become narrow on one side, a character not previously recorded in the strongyles of *Strongylodesma*.

The ectsosome also differ in the structure of the paratangential layer between the three South African species; in *S. algoaensis* the ectsosome is composed of a loose feltwork.
of paratangential strongyles; in S. tsitsikammandoichn and S. algoaensis the ectosome is dense and interlocking differing only in the presence of a clear subectosomal mesohyl layer in S. algoaensis. Strongylodesma alivaliensis is very similar to species of Latruncula in the field, with areolate porefields, a soft, inflated, compressible texture, and a typical dark pigmentation. It is only at the histological level that the genus and this species are distinguishable, by a lack of microscleres.

**Strongylodesma purpureus** Samaai & Kelly sp. nov.  (Figures 1E, 3A, 3B, 4; Table 1)

Van Soest et al., 1996: 95, figure 3; Batzella sp. Gunasekera et al., 1999: 174; Gunasekera et al., 2003: 1616.

**MATERIAL**


**DESCRIPTION**

Thickly encrusting sponge following contours of substrata (Figure 1E), up to 2.5 cm high and 3.5 cm wide. Texture soft, compressible, fleshy. Surface smooth, with numerous scattered cylindrical membranous oscules, 5 mm × 10 mm wide and high, and fungiform areolate porefields 1 mm high and 8 mm wide. Sand particles are present especially within the choanosome of the sponge. Colour in life purple brown; in preservative brown. Ectosome very thin and membranous, and readily separable from underlying choanosome.

**SPICULES**

Megascleres. Acanthostrongyles: Isodiametric with equally shaped apices but spicules are curved in centre, making it bow shaped. A few malformed ‘shepherd’s crook’ strongyles occur. Under SEM strongyles show a strong apical microspination, 276.5 (250–290) μm × 4.8 (4.8) μm, N = 20 (Figure 3A).

**SKELETON**

Choanosomal architecture consists of an irregular polygonal-skeleton with a dense and interlocking differing only in the presence of a clear subectosomal mesohyl layer in S. algoaensis. Strongylodesma alivaliensis is very similar to species of Latruncula in the field, with areolate porefields, a soft, inflated, compressible texture, and a typical dark pigmentation. It is only at the histological level that the genus and this species are distinguishable, by a lack of microscleres.

**SUBSTRATE, DEPTH RANGE AND ECOLOGY**

Found on rubble rocky slope, with patches of sand between rocks, at a depth of 133 m. Sponges are quite abundant in this region. The sponge incorporates sediment (Halimeda plates) into its skeleton.

**GEOGRAPHICAL DISTRIBUTION**

Caribbean (Figure 4).

**ETYMOLOGY**

Named for the purple coloration of this species, purpureus (L.).

**CHEMISTRY**

Gunasekera et al. (1999) reported discorhabdin P from sample HBOI 24-VIII-94-3-001, whilst Gunasekera et al. (2003) reported pyrroloiminoquinone alkaloids (discorhabdins S, T, and U) from sample HBOI 22-X-00-1-002.

**REMARKS**

Van Soest (1996) provisionally identified several specimens of *S. purpureus* sp. nov. as *Batzella* sp. (Poeiclosclerida: Chondropsidae), noting the presence of curious malformed ‘shepherd’s crook’ strongyles seen in *Batzella rosea* from Curacao (Van Soest 1984). Thus, many sponges with ‘shepherd’s crook’ strongyles were assigned to *Batzella* in the marine natural products literature in particular (Pomponi in Van Soest, 1989; Sun et al., 1990; Gunasekera et al., 1999, 2003), despite their uncharacteristically dark coloration and areolate surface structures. A recent revision of the status of *Batzella* confirms that it has the skeletal characteristics (plumose columns of strongyles) of other Chondropsidae (Van Soest, 2002) and thus is clearly separate from *Strongylodesma* as recognized here.

The discovery of pyrroloiminoquinone alkaloids and discorhabdins in the type material of *S. purpureus* sp. nov. (Gunasekera et al., 1999, 2003) raises the possibility that these Caribbean specimens are more closely related to *Strongylodesma*, despite the presence of malformed strongyles. Coupled with the oily dark purple-brown coloration, thickly encrusting morphology, and areolate surface structures, the chemistry identified from this species strongly links these specimens with species of *Strongylodesma*, which are known to contain discorhabdins and their derivatives (Samaai & Kelly, 2002; Samaai et al., 2003, 2004; Antunes et al., 2004; Keyzers et al., 2004), and the Latrunculidae in general (Samaai & Kelly, 2002; Antunes et al., 2005).

**Strongylodesma nigra** Samaai & Kelly sp. nov.  (Figures 1F, 3C, 3D, 4; Table 1)

*Batzella* sp. Sakemi et al., 1989: Sun et al., 1990: 4964; Van Soest et al., 1996: 95, figure 3.

**MATERIAL**

Holotype: HBOM 003:00051 ((sample ID-14-XI-87-3-001 (cross reference Ts 38a)), Bahamas, Great Bahama Bank, west end, 26° 41’67”N 79° 06’60”W, depth 125 m, collected by E. Armstrong, 12 August 1990.

Paratype: HBOM 003:00050 ((sample ID-3-VI-84-3-001 (cross reference Ts 35)), Bahamas, Great Bahama Bank, between Lucaya and Freetown, 26° 32’3’S 78° 30’09”W, depth 118 m, collected by E. Armstrong, 1 August 1990.
DESCRIPTION
Small, amorphous sponge (Figure 1F). Available voucher fragments are about 1 cm in thickness. Surface smooth, with no apparent oscules or areolate porefields visible. Texture compressible, but firm. Colour in life black; in preservative tan. Ectosome very thin, and readily separable from underlying choanosome.

SPICULES
Megascleres. Microspined strongyles: Isodiametric with equally shaped apices. A few malformed shepherd’s crook’ strongyles occur. Under SEM strongyles show a faint apical microspination, 331.5 (270–350) μm × 2.4 (2.4) μm, N = 20 (Figure 3C).

SKELETON
Choanosomal architecture consists of an irregular vague polygonal-meshed reticulation of wispy tracts of faintly microspined strongyles (Figure 3D). These tracts range in width from 50–60 μm in thickness, forming very ill-formed meshes. Towards the surface the tracts are perpendicular, diverging just beneath ectosome into fine plumose brushes, 100 μm thick. The ectosome is composed of a thin feltwork of tangential to paratangential lying strongyles approximately 70 μm deep. In some places this layer may be 400 μm deep, or, spicule orientations may be confused and sparse creating a band of colagenous mesohyal 50–100 μm thick. The surface is pierced by a sparse disorganized layer of erect or oblique strongyles.

SUBSTRATE, DEPTH RANGE AND ECOLOGY
The holotype was found on a rocky wall at a depth of 125 m and specimen HBOM 003:00051a was found on a rocky slope, with patches of sand between rocks, at a depth of 118 m. Depth range 118–125 m.

GEOGRAPHICAL DISTRIBUTION
Caribbean (Figure 4).

ETYMOLOGY
Named for the black coloration of the sponge, nigra (L.)

CHEMISTRY
According to Sakemi et al. (1989), Sun et al. (1990) and Van Soest et al. (1996), this sponge contains pyrroloquinoline alkaloids (batzellins A–C (20–22) and isobatzellins A–D (23–26)).

REMARKS
Strongylodesma novacealedoniae sp. nov. was originally described by Van Soest et al. (1996) as a species of Batzella (Poecilosclerida: Chondropsiidae), yet as for S. purpureus sp. nov., the chemical, morphological and coloration characteristics suggest strong affinity with Latrunculiidae in general and Strongylodesma in particular. Strongylodesma nigra sp. nov. differ from S. purpureus sp. nov. by the smaller size of the megascleres (Table 1) that are also faintly apical microspined. The two species differ in coloration, S. nigra sp. nov. is black while S. purpureus sp. nov is purple brown. The two species have quite different textures; S. purpureus sp. nov. is fleshy and compressible while S. nigra sp. nov. is much firmer.
**REMARKS**

*Strongylodesma novacaledoniae* sp. nov. was first identified by Hooper & Battershill in Lévi (1998: 121) but was never fully described. It is highly characteristic in life with the almost spherical morphology and beautiful light chocolate brown coloration in life. *Strongylodesma novacaledoniae* sp. nov. differs from *S. areolata* Lévi in several ways; it has much longer and slimmer strongyles, it differs in the thickness and structure of the euctosomal paratangential layer, and the megascleres are smooth compared to being slightly spined.

*Strongylodesma tongaensis* Samaai & Kelly sp. nov. (Figures 1G, 3G, 3H, 4; Table 1)

**MATERIAL**

Holotype: BMNH2008.5.2.3. Tonga, Tongatapu, outer reef north of Atata Island, north side, Pacific Ocean, 21° 02'03"S 175° 16'32"W, 24 m, collected by Patrick L. Colin, CRRF, 19 November 1997 (OCDN 5532-W).

Paratype: BMNH 2003.4.10.1: Toachel Mid (K-B Channel), Koror side, Republic of Palau, 07° 21.64’N 134° 30.17’E, depth 10 m, collected by Patrick L. Colin, CRRF on 7 April 1998 (OCDN 5532-W).

**DESCRIPTION**

Thin encrusting sponge conforming to substrate (Figure 1G). Surface rugose, with oscula 5–8 mm in diameter, with elevated rims and slightly raised areolate porefields up to 8 mm high. Texture compressible, dense and breaks easily. Colour in life dark green; in preservative dark brown. The sponge exudation makes the alcohol green. Ectosome very thin and not readily separable from underlying choanosome.

**SPICULES**

Megascleres. Strongyles: Isodiametric with equally shaped apices, with a few having either bulge or uniform apices. A few malformed, shepherd-staff or crooked strongyles occur, approximately 800 μm wide. The surface is pierced by a sparse disorganized layer of erect or oblique strongyles.

**SKELETON**

The choanosomal skeleton is a firm, dense, well developed, irregular polygonal reticulation of chambers divided by very thick reinforced tracts of strongyles, 100–200 μm in thickness, with meshes that are 800 μm wide (Figure 3H).

Within and between these layers of thick strongyles the choanosome is much softer, containing the skeleton that consists of an ill-formed, irregular reticulation of strongyles, with no distinction between the primary and secondary tracts. Towards the centre of the choanosome the tracts are more confused and ill-defined, and towards the surface these spicules tend to be vertically arranged, 150 μm thick and not diverging into plumose brushes. Scattered throughout the choanosome, between the tracts, are numerous strongyles. Strongyles also encircle the choanosomal chambers. Beneath the euctosome, in the subectosome, is a thick paratangential–tangential layer of densely interlocking megascleres, approximately 400 μm wide. The surface is pierced by a sparse disorganized layer of erect or oblique strongyles.

**SUBSTRATE, DEPTH RANGE AND ECOLOGY**

Found on an overhang in reef habitat with a gentle slope to sand and coral rubble, 24 m.

**GEOGRAPHICAL DISTRIBUTION**

Kingdom of Tonga, Republic of Belau (Palau), Federated States of Micronesia (Figure 4).

**ETYMOLOGY**

Named for the type locality.

**CHEMISTRY**

Unknown.

**REMARKS**

*Strongylodesma tongaensis* sp. nov. is the second record of the genus from the Pacific Ocean. Geographically, its nearest neighbour is *S. novacaledoniae* sp. nov. from New Caledonia. *Strongylodesma tongaensis* sp. nov. differ markedly from *S. novacaledoniae* sp. nov., in having thinner malformed ‘shepherd’s crook’ strongyles, and in having a thick paratangential to tangential subectosomal layer of densely interlocking megascleres, approximately 400 μm wide. *Strongylodesma tongaensis* sp. nov. is thinly encrusting whereas *S. novacaledoniae* sp. nov. is almost spherical.

**DISCUSSION**

Species of *Strongylodesma* are now relatively easily recognizable amongst sponge species with strongyles as the only megasclere (*Batzella* and *Prianos*), and which lack microscleres or other inclusions. The strongyles in *Strongylodesma* are arranged in a tangential layer under the euctosome, and form a wide-meshed polygonal reticulation in the choanosome. Species are generally massive, with raised areolate porefields that are either raised and fungiform, or concave. They lack any form of microsclere, and in particular, they lack the anisodiscorhabds that separate them from species of *Latrunculia*, to which they are very closely related and from which they are impossible to differentiate in the field. *Prianos* has the skeletal architecture of a chalinid sponge (delicate unisipicular isotropic reticulation of strongyles) and is a synonym of *Haliclona* (Reniera) (de Weerdt, 2002), and the type species of *Batzella* has skeletal characteristics (plumose columns of strongyles) shared with other Chondropsidae (Van Soest, 2002).

In terms of their secondary metabolite chemistry, species of *Strongylodesma* contain biologically active discorhabdins and their derivatives (Samaai & Kelly, 2002; Antunes et al., 2005) that possess the characteristic pyrroloiminoquinone substructure. These compounds are now routinely isolated from species in the latrunculiid genera *Latrunculia*, *Tsitsikamma* and *Strongylodesma*, but have also been identified from various specimens incorrectly identified as *Negombata*, *Batzella*, *Prianos*, *Damiria*, *Histodermella* and *Zyzzya*. A recent taxonomic revision of the genus *Latrunculia* (Samaai et al., 2006) concluded that only 27 of the 36 species were valid, and a plethora of biologically active compounds were associated with the genus (and family). In this revision, a ‘*Latrunculia*’ that produced the macrocytic lactone latrunculin A, was reassigned to *Negombata* (family Podospongidae), while sesterterpene peroxide producing ‘*Latrunculia*’ specimens were reassigned to *Diacarnus* or *Simpsonetrella*, also in the family Podospongidae (Kelly, 2000; Samaai, 2002; Kelly & Samaai, 2002; Samaai & Kelly, 2002; Antunes et al.,
2005; Samaai et al., 2006). A sponge identified as Prianos melanos de Laubenfels, 1954, from Okinawa, Japan, is also more correctly identified with Strongylocentrotus (see Kelly, 2000; Samaai & Kelly, 2002; Antunes et al., 2005). The prianosins described in this species (Kobayashi et al., 1987, 1991; Cheng et al., 1988; Van Soest et al., 1996) are synonymous with discorhabdins (Perry et al., 1988a, b; Lill et al., 1995; Van Soest et al., 1996), and the sponge had dark brownish pigmentation and strongyles as the only spicules.

Zyzyzza versus Latrunculidae

Makaluvic acids, damirones and makaluvamines are consistently, but not exclusively, reported from specimens in the genus Zyzyzza (Poecilosclerida: Acarnidae, formerly Iophonidae) (see Fu et al., 1996; Kelly, 2000).

A sponge originally identified from Palau as Damiria sp. (Poecilosclerida: Acarnidae) (Sterle & Faulkner, 1991), and a specimen originally identified from Indonesia as Histoderma sp. (Poecilosclerida: Coelosphaeridae) (Carney et al., 1993), both yielded damirones, makaluvamines and discorhabdins. They were reassigned to Zyzyzza fuliginosa by Van Soest et al. (1996) (Poecilosclerida: Acarnidae) on the basis of their shared chemistry and morphological characteristics. Interestingly, makaluvic acids, damirones and makaluvamines, and discorhabdins (common to the Latrunculidae) have now also been isolated from a South African latrunculid species Cyclacanthia bellea Samaai & Kelly, 2004. The discovery of a new pyrroloiminoquinone alkaloid (tsitsikamamine) that is biosynthetically intermediate to the makaluvamines of Zyzyzza (Kelly, 2000; Samaai & Kelly, 2002; Antunes et al., 2005) and the discorhabdins of the Latrunculidae, has also been isolated from Tsitsikamma favus Samaai & Kelly, 2002.

Makaluvic acids, damirones, and makaluvamines, common to species of Zyzyzza (Poecilosclerida: Acarnidae), and discorhabdins, common to species of Latrunculidae, Strongylocentrotus, and Tsitsikamma (Poecilosclerida: Latrunculidae), have been found in some species of Zyzyzza and Cyclacanthia (Poecilosclerida: Latrunculidae), indicating affinity between these genera. The discovery of tsitsikamamine, biosynthetically intermediate to makaluvamines and discorhabdins, also isolated from Tsitsikamma favus, adds support for this affinity (Perry et al., 1988a, b; Kelly, 2000; Samaai & Kelly, 2002) and confirms that the pyrroloquilonine alkaloids are a strong consistent chemotaxonomic marker for these genera (see also Kelly, 2000; Samaai & Kelly, 2002; Antunes et al., 2005). The majority of known species of Zyzyzza and Latrunculidae also share an intensely dark brownish-black base coloration to which may be overlaid an oily purplish, greenish, and blueish sheen. Zyzyzza and latrunculid genera share a similar general skeletal structure of tracts of diactinal megascleres that form polygonal cells ranging from wispy to firm honey-comb-like structures (see Samaai & Kelly, 2002), and some species of Latrunculidae and Strongylocentrotus have an acanthose terminus on the megascleres (Zyzyzza has acanthose strongyles and tylostyles with acanthose termini). The genera also share specialized areolate quiferous structures.

The combination of these chemical and morphological characters across various Latrunculidae genera and Zyzyzza in Acarnidae suggest that the genus Zyzyzza might, at the very least, be reassigned to suborder Latrunculina, and at best, to within family Latrunculidae. However, Zyzyzza has palmate isochelae, not found in any latrunculid genus, and fully acanthose strongyles, indicating that a careful comparison of Zyzyzza to other Acarnidae is warranted before any further action is taken.

In summary, at present eight species of Strongylocentrotus are known to exist worldwide, four of which have been described from South Africa and the South Atlantic. Even though a rich and diverse sponge fauna exists within the south-west Atlantic, Indian Ocean, Mediterranean, New Zealand and Australia (evidence from the extensive literature and inventory on sponges) (e.g. Lévi, 1964; Bergquist, 1965, 1968; Bergquist & Fromont, 1988; Kelly-Borges & Bergquist, 1988; Hooper & Lévi, 1993; Pulitzer-Finali, 1993; Van Soest, 1994; Hooper & Wiedenmayer, 1994; Colin & Arneson, 1995; Kelly-Borges & Valentine, 1995; Kelly, 1997; Hooper et al., 2000), the genus has never been recorded from these localities. Strongylocentrotus has a low degree of diversity and disparity amongst its few characters, but differences may be recognized in the size-range variation and shape distinction of the strongyles, external coloration, habitat, gross morphology and the conspicuously distinct variations in the choanosomal skeleton.

The most speciose and diverse regions for Strongylocentrotus from a biogeographical perspective is the surrounding waters of South Africa (Samaai et al., 2003, 2004). The occurrence of the genus in the Caribbean, the south-west Pacific and the south-east Atlantic and its possible absence in the south-west Atlantic, the eastern Pacific, and the surrounding waters of Australia and New Zealand represent a widely disjunct distribution of the genus across the centre of the Pacific and Atlantic Oceans. The discovery of the new species S. purpureus sp. nov. and S. nigra sp. nov. in the Caribbean extends the distribution of this genus further north within the Atlantic Ocean and it is also a first record of this genus for this region. An explanation for the known distribution of Strongylocentrotus is difficult and future efforts are required to search for additional outlying species and populations to precisely define the distribution limits of the general distribution of the genus. The observation that the genus appears to be absent from most of the subtropical/warm temperate south-west Atlantic favours the scenario that the Caribbean or New Caledonian species are basal lineages in the Strongylocentrotus clade, with South African species probably being more derived as a consequence of a later divergence.

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