



Taxonomy of *Melophlus* Thiele, 1899 and *Stellettinopsis* Carter, 1879, with description of two new species from Brazil (Demospongiae: Astrophorina)

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Abstract

In the present study, the demosponge genus *Melophlus* Thiele, 1899 is revised and the type specimens of all its species are re-examined. The diagnosis of the genus is amended, based on the presence in the type species, *M. sarasinorum* Thiele, 1899, of a well-developed ectosome of acanthomicrohabds and a dense feltwork of large oxeas, together with oxyasters and microxeas as microscleres; triaenes are absent. *Melophlus ruber* Lehnert & van Soest, 1998 and *Melophlus hajdui* Moraes, 2011 are here transferred to *Stellettinopsis* Carter, 1879 due to their superficial crust of large acanthomicrohabds, bouquets of oxeas in the ectosome, and rare triaenes previously overlooked. Additionally, we describe two new species of *Stellettinopsis* from Brazil and compare them to all valid species of the genus. *Stellettinopsis capixaba* sp. nov. is distinguished from its congeners especially by the presence of rare orthotriaenes with curved cladi and of three categories of spined euasters (oxyasters 1 and 2 and strongylasters); *Stellettinopsis baiana* sp. nov. is characterized mainly by the common orthodichotriaenes, spined oxyasters, and spined strongylasters. *Stellettinopsis* species have been often assigned to the genus *Melophlus* due to their similar spicule complement and rarity of triaenes. We suggest that skeletal architecture and the shape of microscleres are more useful than megascleres to separate genera with rare triaenes such as *Stellettinopsis* and *Stryphnus* from other astrophorids. Morphological data suggest that both *Stellettinopsis* and *Melophlus* should be re-allocated to the family Ancorinidae, but more comprehensive integrative studies are still needed to resolve the classification of Astrophorina.

Keywords Sponges · Porifera · Tetractinellida · Tropical Western Atlantic · Morphology

Introduction

The suborder Astrophorina Sollas, 1887 (subclass Heteroscleromorpha, order Tetractinellida) is highly diverse, with 1142 species widespread in all regions of the globe (van Soest et al. 2019a). Although the suborder has a high diversity of spicule types, which should facilitate the systematics of the group, its classification is still under debate (Cárdenas et al. 2011). In the *Systema Porifera*, five families were recognized within the order Astrophorida (Hooper and van Soest 2002), but recent molecular phylogenetic studies changed its status to suborder Astrophorina and expanded this number to 15 families (Cárdenas et al. 2012; Morrow and Cárdenas 2015). Regardless of the classificatory scheme adopted, some astrophorine families such as Ancorinidae Schmidt, 1870 and Geodiidae Gray, 1867 and many genera are still probably non-monophyletic. In addition, some genera traditionally classified in Ancorinidae on morphological grounds were transferred to Geodiidae based on

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molecular data, including independent small subunit 18S, 28S, and COI barcoding sequences: *Melophlus* Thiele, 1899, *Stellettinopsis* Carter, 1879 [in part], and *Penares* Gray, 1867 (Cárdenas et al. 2010, 2011; Redmond et al. 2013).

The genera *Melophlus* and *Stellettinopsis* share a superficial layer of acanthomicrohabds and the presence of choanosomal oxeas and euasters, but they differ mainly by a tangential layer of microhabds in three size categories (vs. one category in *Stellettinopsis*) and the absence of triaenes in *Melophlus* (vs. presence in *Stellettinopsis*) (Kelly and Sim-Smith 2012). However, triaenes can be very rare in some *Stellettinopsis* species, which can thus be misidentified as *Melophlus*. Details of skeletal arrangement have proven useful to distinguish between *Ancorina* Schmidt, 1862; *Ecionemia* Bowerbank, 1862; *Stryphnus* Sollas, 1886; and *Stellettinopsis* (Kelly and Sim-Smith 2012), but comparable data is still lacking for *Melophlus* and other ancorinid genera.

The genus *Melophlus* (family Geodiidae) currently has three valid species: *Melophlus sarasinorum* Thiele, 1899, type species of the genus, which is found all throughout the Western Pacific Ocean; *M. ruber* Lehnert & van Soest, 1998 from Jamaica; and *M. hajdui* Moraes, 2011 from NE Brazil (van Soest et al. 2019b). *Stellettinopsis* (Ancorinidae) contains seven species, generally distributed in warm temperate and tropical waters (Kelly and Sim-Smith 2012). Three of these species occur in the Tropical Western Atlantic Ocean (TWA): *Stellettinopsis euastrum* Schmidt, 1880 from Grenade; *S. fenimorea* de Laubenfels, 1934 from Puerto Rico; and *S. megastylifera* Wintermann-Kilian & Kilian, 1984, found in several Caribbean localities, from Bahamas to Panama (Cárdenas et al. 2009), Guyana (van Soest 2017), and in Northeastern Brazil (cf. van Soest 2017; = *Ecionemia* sp. sensu Hajdu et al. 2011). *Stellettinopsis euastrum*, however, has discoidal spicules similar to aspidasters and probably is a species of *Erylus* (P. Cárdenas, taxonomy note, van Soest et al. 2019c).

Molecular data are very informative for the systematics of the Astrophorina, although often giving results incongruent with morphological characters (Cárdenas et al. 2010, 2011; Redmond et al. 2013). Unfortunately, the DNA of the type specimens of most species of *Melophlus* and *Stellettinopsis* is difficult to be sequenced due to inadequate fixation (with formalin or 70% ethanol) or preservation (with 70% ethanol). In this contribution, we revise the morphology and taxonomy of the genus *Melophlus*, with emphasis on skeletal organization and spicule morphology in scanning electron microscopy (SEM). We redescribe the three currently accepted species of *Melophlus* and suggest the transfer of *M. hajdui* and *M. ruber* to *Stellettinopsis*. In addition, we describe two new species of *Stellettinopsis* from Brazil and discuss the delimitation of *Stellettinopsis* species, the differences between the genera *Stellettinopsis* and *Melophlus*, and their family-level classification, suggesting that both should be re-allocated to Ancorinidae.

Material and methods

A fragment of the holotype of *Melophlus sarasinorum* (type species of the genus) was lent by Institut für Systematische Zoologie from Museum für Naturkunde der Humboldt-Universität zu Berlin (ZMB-Por). A fragment of the holotype of *Melophlus ruber* was sent on loan by the Naturalis Biodiversity Center (ZMAPOR). The external morphology of these species was described based on the original and other descriptions available in the literature. The type material of *Melophlus hajdui* deposited in the Porifera collection of Museu Nacional—Universidade Federal do Rio de Janeiro (MNRJ) was re-examined. New specimens of *Melophlus hajdui* and the two new species were collected through SCUBA diving from 5 to 11 m depth and through trawling fishing nets between 27 and 52 m depth in the coast of Brazil and fixed in 70% ethanol. These specimens were deposited in the Porifera collections of Museu Nacional—Universidade Federal do Rio de Janeiro (MNRJ) and Universidade Federal de Sergipe (UFSPOR). The UFSPOR specimens were collected by the MARSEAL Project—Environmental Characterization of Sergipe and Alagoas Basin, coordinated by PETROBRAS/CENPES. Dissociated spicule mounts, SEM preparations, and skeletal sections were made using classical procedures for Demospongiae (Hajdu et al. 2011). Thick sections of the holotype of *Stellettinopsis capixaba* sp. nov. were cut with a low speed diamond saw (Extac Labcut 1010) using a diamond wafering blade on fragments embedded in epoxy resins. Measurements of each type of spicule were made from 30 spicules unless indicated otherwise and presented as minimum–mean–maximum for length/width or diameter.

Results

Systematics

Class Demospongiae Sollas, 1885

Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012

Order Tetractinellida Marshall, 1876

Suborder Astrophorina Sollas, 1887

Family Ancorinidae Schmidt, 1870

Definition. Encrusting, irregularly massive or clearly spherical Astrophorina, in some cases with long inhalant and/or exhalant tubes. The megascleres are triaenes with **short or** long rhabdome and oxeas. Microscleres are euasters (oxyasters, spherasters, **strongylasters**, **anthasters**, chasters, tylasters), sanidasters, **amphisandasters**, **sanidasterhabds**, and spiny or smooth microhabds (modified from Uriz 2002 and Kelly and Sim-Smith 2012; our amendments in boldface).

Genus *Melophlus* Thiele, 1899

Type species. *Melophlus sarasinorum* Thiele, 1899: 8.

Definition. Ancorinidae massive, with a well-developed ectosome (3–4 mm thick) composed of a superficial layer of acanthomicrohabds, below which is a dense feltwork of large oxeas, placed tangentially to the surface at the sponge periphery, but in disarray within the choanosome. Microscleres include acanthomicrohabds, oxyasters and microxeas. Trianaes are absent (modified from Uriz 2002; our amendments in boldface).

Remarks. We expanded the diagnosis of Uriz (2002) mainly to include details of the ectosomal skeleton organization (ectosome well developed, with a superficial layer of acanthomicrohabds and a thick internal layer with a dense feltwork of oxeas). These characters are essential to distinguish *Melophlus* from *Stelletinopsis*.

***Melophlus sarasinorum* Thiele, 1899**

(Figs. 1 and 2)

Melophlus sarasinorum (Thiele 1899: 8; Hajdu & van Soest 1992: 16; Pulitzer-Finali 1996: 103).

Jaspis bandae Brøndsted, 1934: 8.

Stelletinopsis isis de Laubenfels, 1954: 221.

Asteropus sarasinorum (Bergquist 1965: 187; van Soest 1989: 224).

Material examined. Holotype ZMB 2885, Kema, Sulawesi, Indonesia.

Diagnosis. *Melophlus* with a roughly ovoid shape, a large atrial cavity and rhizome-like prolongations on its base. Spicules are large oxeas, microspined microxeas, two categories of acanthomicrohabds and spined oxyasters.

Description (Fig. 1a–c). Roughly ovoid shape, with a large oscule on top of the sponge. At the base of the sponge, there are rhizome-like prolongations. The color in life is mustard, yellowish, or pinkish brown and, in ethanol, the internal color is beige with a light brown cortex, approximately 4 mm thick. The surface is rough and is covered with irregular papillae and numerous openings irregularly distributed between them. The consistency is hard, almost stony.

Skeleton (Fig. 1d). Ectosome with a thin external layer (250 μm thick) composed exclusively by scattered acanthomicrohabds I and II and a thick internal layer (2750 μm thick) with a dense feltwork of large oxeas, oxyasters, acanthomicrohabds I and II, and microspined microxeas. Choanosome with abundant oxyasters, acanthomicrohabds I, II and microspined microxeas; oxeas are irregularly scattered.

Fig. 1 *Melophlus sarasinorum* Thiele, 1899. **a–c** Specimens in situ in Guam, Micronesia (the specimen at the right side in c is diseased), photos Dr. Gustav Paulay; **d** cross-section showing the skeletal architecture: ectosome and choanosome (holotype—ZMB 2885). Scale bar: **d** = 690 μm

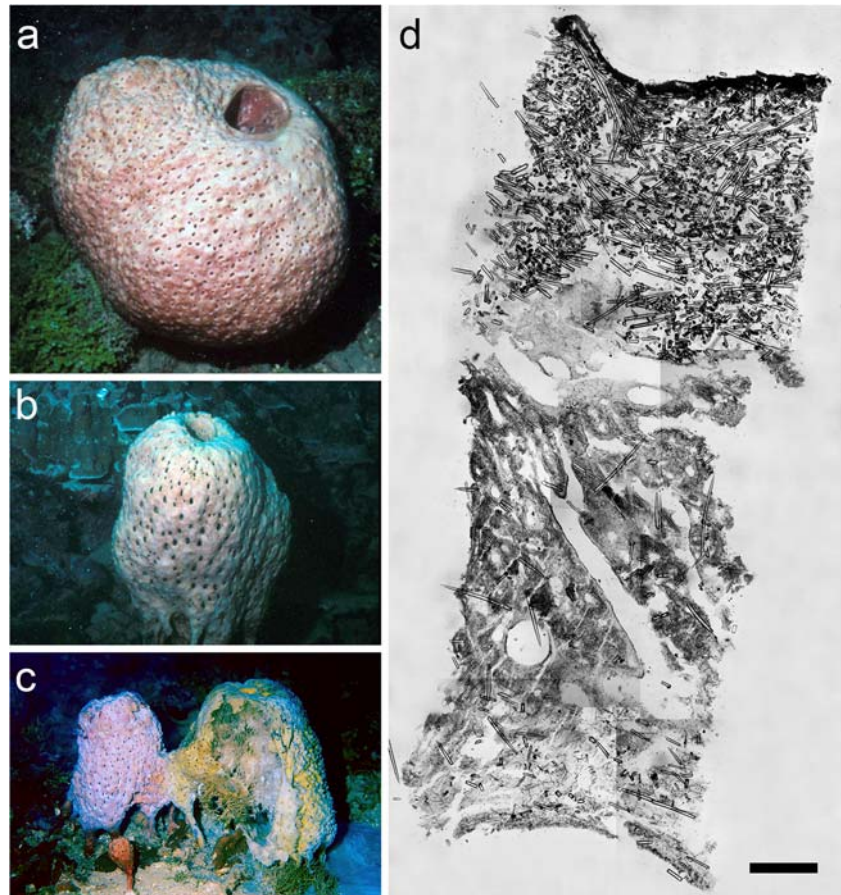
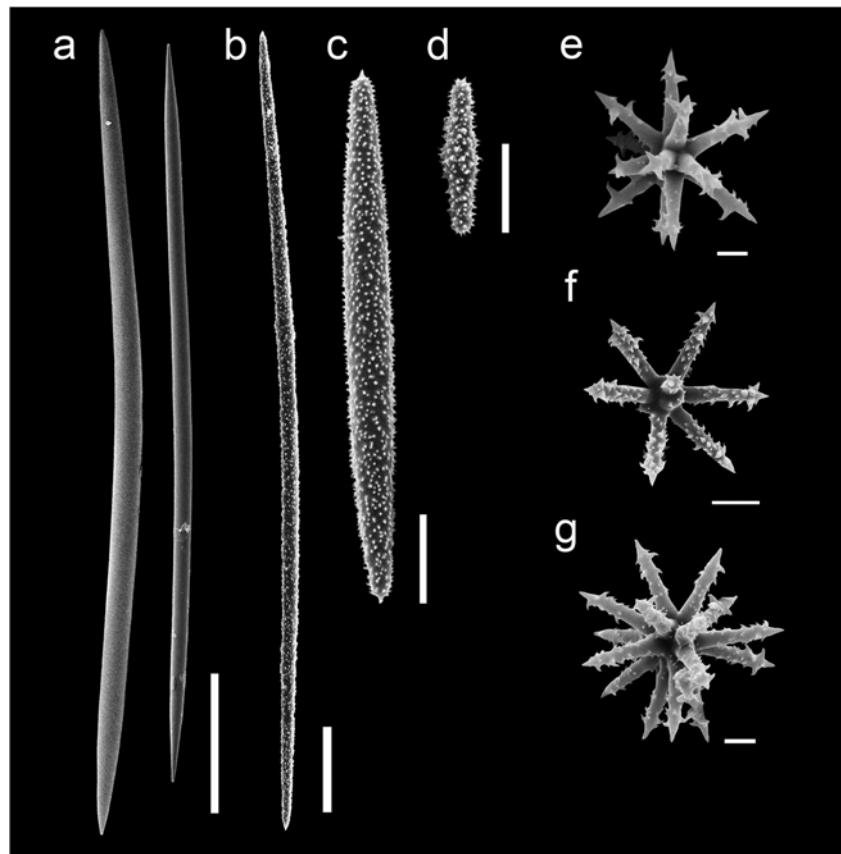


Fig. 2 *Melophlus sarasinorum* Thiele, 1899 (holotype—ZMB 2885). **a** Oxeas; **b** microspined microxea; **c** acanthomicrorhabd I; **d** acanthomicrorhabd II; **e–g** spined oxyasters. Scale bars: **a** = 200 μm ; **b** = 20 μm ; **c**, **d** = 10 μm ; **e** = 2 μm ; **f** = 5 μm ; **g** = 2 μm



Spicules of the holotype (Fig. 2). Megascleres: straight or slightly curved oxeas, with attenuated and quite slender tips, 999–1238–1433/16–34–51 μm . A few stylole modifications were observed (Fig. 2a). Microscleres: long, slender, microspined microxeas, with sharp tips, 54–159–212/3 μm (Fig. 2b). Acanthomicrorhabds in two size categories: (I) fusiform, with spined, acerate, or strongylote tips, 38.2–58.9–90.8/2.4–4.4–4.7 μm (Fig. 2c); (II) small, centrotylote, with rounded tips, 14.3–22.3–38.2/2.4–3.1–6.0 μm (Fig. 2d). Spined oxyasters with slender actines and spines often curved inwards, 7–13 rays, 9–14–19 μm in diameter (Fig. 2e–g).

Geographical distribution. Western Pacific: Indonesian Exclusive Economic Zone (van Soest 1989), Sulawesi Sea/Makassar Strait (Thiele 1899), Banda Sea (Brøndsted 1934), West Caroline Island (de Laubenfels 1954), Palau (Bergquist 1965), Bismarck Sea, Papua New Guinea (Pulitzer-Finali 1996).

Taxonomic remarks. This is the first redescription of the holotype of *Melophlus sarasinorum* since it was first described by Thiele, adding new data about its skeletal arrangement and spicule morphology in SEM. Some subsequent records of the species have strongylasters and a few also show tylasters (Thiele 1899; Brøndsted 1934; Bergquist 1965), both absent in the holotype. Such variations are probably intraspecific due to the broad distribution of this species, but may also indicate a case of cryptic speciation. The records of *Melophlus*

sarasinorum worldwide should be revised, but this is beyond the scope of this contribution.

The rhabdose microcleres of *Melophlus sarasinorum* were called “microxeas” by several authors (Thiele 1899; Brøndsted 1934; de Laubenfels 1954; Bergquist 1965), and “rough microrhabds” by others (Uriz 2002; Kelly and Sim-Smith 2012), illustrating the difficulty in distinguishing between microrhabds and microxeas. The term “microrhabd” generally refers to a straight, monaxonic microsclere, while a “microxea” is defined as a microsclere that is similar in shape to an oxea (Boury-Esnault and Rützler 1997). Therefore, both are straight monaxonic spicules and clearly synonymous by these definitions. In practice, they are usually distinguished by the more irregular shape of microrhabds, which are often stout, strongylote, or hastate, whereas microxeas are often longer, more slender, regular, and acerate. Thus, our redescription of *M. sarasinorum* includes two size categories of acanthomicrorhabds, which are distributed throughout the body (Fig. 2c, d), and a single category of microspined microxea that is restricted to the inner ectosome and choanosome (Fig. 2b).

Genus *Stellettinopsis* Carter, 1879

Type species. *Stellettinopsis corticata* Carter, 1879: 348.

Definition. Ancorinidae with massive, cushion-shaped, bulbous or thickly encrusting shape, with oxeas packed obliquely or paratangentially in the choanosome. The

ectosome is well developed and defined by bouquets of subdermal oxeas and triaenes, when present, emerging from the choanosome, in between which are large aquiferous canals. Euasters form a concentration below and throughout a crust of long microrhabds at the surface, and oxeas protrude through the surface, rendering it hispid and rough to the touch. Megascleres include medium-sized oxeas in 1 to 2 size categories with common stylote modifications, and relatively short triaenes of different types including dichotriaenes, plagiotriaenes, orthotriaenes, and rarely anatriaenes. Triaenes are frequently very rare **and sometimes absent**. Microscleres include relatively long strongylote or hastate acanthomicrorhabds that form a crust at the surface of the sponge, under which is a concentration of small tylasters, chiasters, oxyasters, **strongylasters**, **oxyspherasters** and rarely anthasters, in 1 to 2 size categories (modified from Kelly and Sim-Smith 2012; our amendments in boldface).

***Stellettinopsis hajdui* (Moraes, 2011), new combination**

(Figs. 3, 4, 5, and 6; Tables 1 and 2)

Melophlus hajdui Moraes, 2011: 77.

Type material (examined). *Melophlus hajdui* Moraes, 2011. Holotype MNRJ 2900, Salãozinho, Atol das Rocas, Rio Grande do Norte State, Brazil (3° 51' S 33° 40' W), depth 3 m, coll. F. Moraes, 04/xii/1999. Paratype MNRJ 7736, same locality of holotype, depth 2 m, coll. E. Hajdu, 26/x/2003.

Additional material examined. UFSPOR 361, off Piaçabuçu, Alagoas State, Brazil (10° 31' 10.56" S, 36° 6' 2.88" W), depth 52 m, leg. Petrobras, 03/vii/2011. UFSPOR 453, off Pirambu, Sergipe State, Brazil (10° 49' 26.4" S, 36° 36' 15.84" W), depth 27 m, leg. Petrobras 03/vii/2011. UFSPOR

299, UFSPOR 342, UFSPOR 345, UFSPOR 447, off Pirambu, Sergipe State, Brazil (10° 52' 21" S, 36° 32' 9.96" W), depth 47 m, leg. Petrobras, 03/vii/2011.

Comparative material (Table 1; Figs. 7 and 8). *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). MNRJ 15661, Isla Colón, Bocas del Toro, Panama (09° 21.10' N, 82° 15.57' W), colls. E. Hajdu and Sponge Course Team, 25/vii/2012. MNRJ 15876, Cayo Zapatilla, Bocas del Toro, Panama (9° 16' 12.68" N, 82° 03' 57.77" W), coll. G. Lôbo-Hajdu, 15/viii/2012. MNRJ 15893, Isla Escudo de Veragua, Bocas del Toro, Panama (09° 05' 51.86" N, 81° 34' 29.56" W), colls. C. Freeman and K. Matterson, 02/viii/2012 (Table 1).

Diagnosis. *Stellettinopsis* with skeleton composed of rare orthodichotriaenes and orthotriaenes, two categories of oxeas, oxeas I with stepped tips, long oxeote acanthomicrorhabds, and two categories of spined oxyasters.

Description (Fig. 3). Sponge globose, digitate, or elongate. After fixation, the type specimens are darker on their upper regions, with lateral regions beige. External color of other specimens varies from grayish-brown to pinkish beige (Fig. 3a, b), but the specimens from Sergipe and Alagoas states are dark brown to black (Fig. 3c, d). Internal color of all specimens is beige. Some specimens (UFSPOR 342, 361, and 447) are covered with calcareous algae and encrusted sediment (Fig. 3c). The surface varies from hispid to rugose, and in the type specimens, it is irregular with scattered mounds (up to 5 mm high). Oscules are circular to oval, measuring 1–10 mm in diameter. The holotype has many large exhalant canals converging to the oscule. The atrial cavity is 2.5 to 3.5 cm deep. The consistency is firm, varying from slightly compressible to incompressible.

Fig. 3 *Stellettinopsis hajdui* (Moraes, 2011) comb. nov. **a** Holotype (MNRJ 2900); **b** paratype (MNRJ 7736); **c** UFSPOR 361; **d** UFSPOR 345. Scale bars: **a–d** = 1 cm

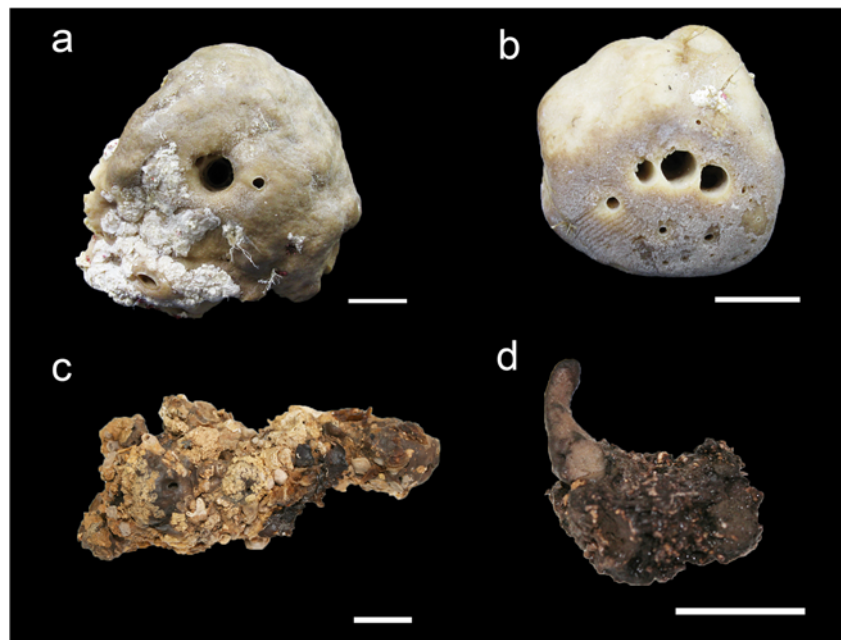
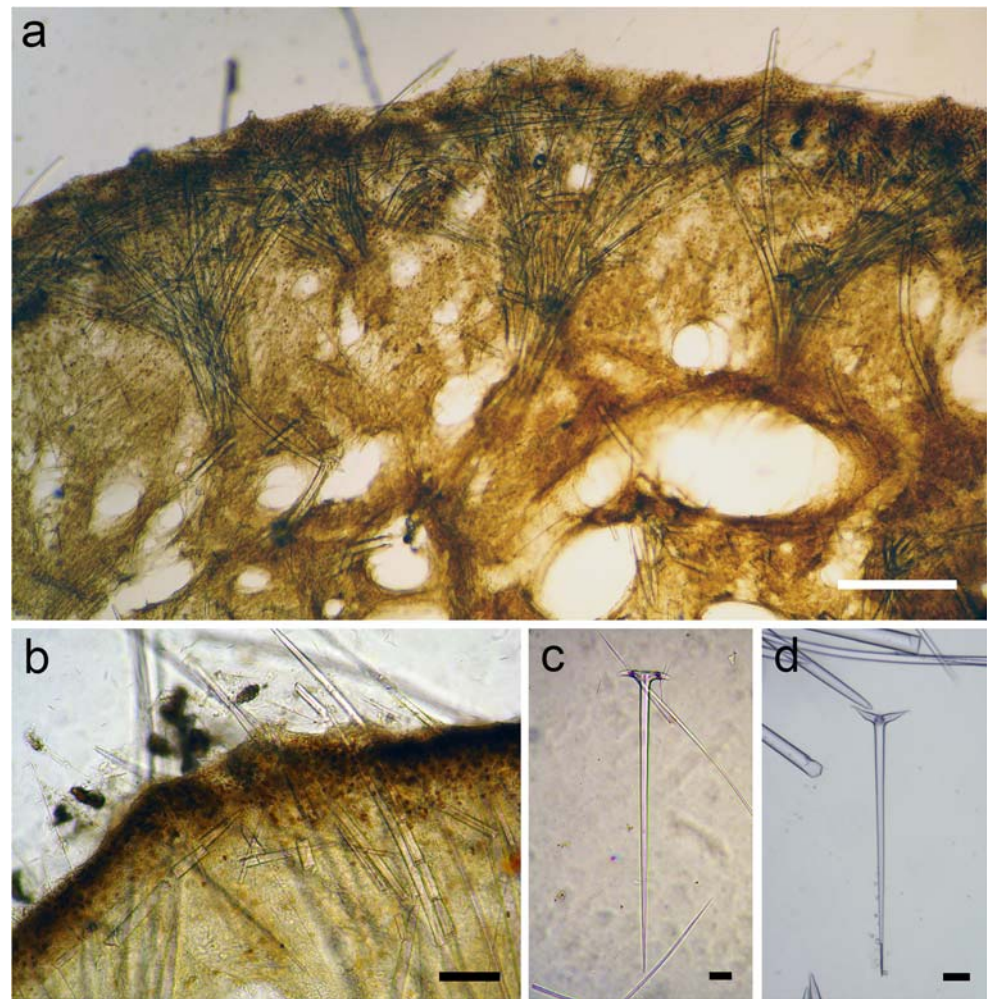


Fig. 4 *Stellettinopsis hajdui* (Moraes, 2011) comb. nov. **a** Cross-section showing the skeletal architecture of the ectosome and choanosome; **b** details of the ectosome showing the pigmented cells; **c** orthodichotriaene; **d** orthotriaene. Scale bars: **a** = 495 μm ; **b** = 125 μm ; **c** = 112 μm ; **d** = 112 μm



Skeleton (Fig. 4a, b). The ectosomal skeleton consists of a layer of oxyasters and acanthomicrohabds up to 200 μm thick, which is supported by bouquets of oxeas that emerge from the choanosome with canals between them. Some oxeas are arranged paratangentially to the surface, interconnecting the bouquets (Fig. 4a). Pigmented cells are abundant in the ectosome (Fig. 4b). The choanosomal skeleton consists of scattered acanthomicrohabds, oxyasters, and oxeas. Usually, the oxeas I form the tracts from which originate the ectosomal bouquets, whereas oxeas II are more abundant in the inner choanosome. The oxeas I also cross the ectosome, making the surface hispid.

Spicules (Fig. 4c, d and Fig. 5) (average of all specimens; individual measurements in Table 1). Rare orthotriaenes and orthodichotriaenes were observed only in two of eight specimens, including the paratype but not the holotype; rhabdome: 470–537–600/15–20–30 μm , cladome: 91–112–160/7–12–17 μm ($N = 11$) (Fig. 4c, d). Rare small plagiotriaenes were observed in other three specimens; rhabdome: 230–243–257/4–6–10 μm , cladome: 15–17–20/2 μm . Oxeas I are thick (Fig. 5a), straight or slightly curved, with acerate, mucronate (Fig. 5a1) and stepped tips (Fig. 5a3),

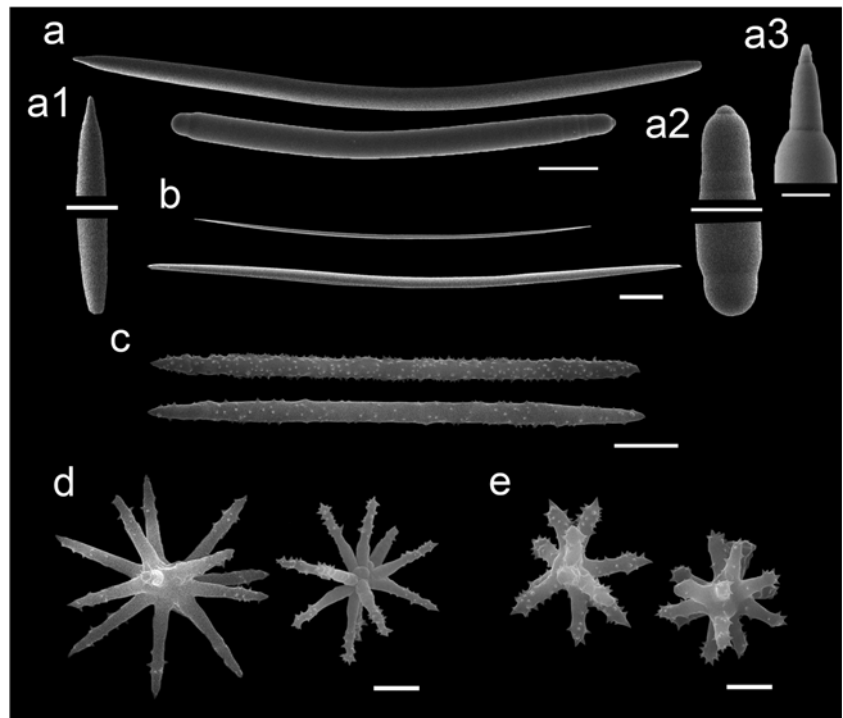
occasionally with stylote and strongylote modifications (Fig. 5a2): 610–841–1200/12–24–55 μm . Oxeas II are thin, slightly curved, with slender tips, 400–657–1110/2–7–16 μm (Fig. 5b). Acanthomicrohabds are straight or slightly curved with acerate ends, sometimes with reduced spines: 32–57–82/1–2.3–3.5 μm (Fig. 5c). Oxyasters are spined, variable in shape and ray thickness, with a considerable number of malformed or irregular spicules (Fig. 5d, e): oxyaster 1 are slender, spined only in the distal portion, 11 rays, 6–9–10 μm in diameter ($n = 18$) (Fig. 5d), and oxyaster 2 has short and stout actines, with irregular spines, 11–12 rays, 5–7–10 μm in diameter ($n = 21$) (Fig. 5e).

Ecology. This species occurs from 2 to 52 m depth, often associated to calcareous algae.

Geographical distribution (Fig. 6). Endemic from northeastern Brazil: Rocas Atoll (Rio Grande do Norte State), Alagoas, and Sergipe States (Moraes 2011; present study).

Taxonomic remarks. This species was originally allocated to the genus *Melophlus* by Moraes (2011), who reported the presence of oxeas, oxyasters, and acanthomicrohabds as the only spicule types. We observed, however, the presence of

Fig. 5 *Stellettinopsis hajdoui* (Moraes, 2011) comb. nov. (holotype—MNRJ 2900 and paratype—MNRJ 7736). **a** Variation of oxeas I; **a1–3** details of oxeas I tips; **b** oxeas II; **c** acanthomicrorhabs with acerate tips; **d** spined oxyaster 1; **e** spined oxyaster 2. Scale bars: **a** = 100 μm; **a1** = 20 μm; **a2**, **a3** = 50 μm; **b** = 100 μm; **c** = 5 μm; **d**, **e** = 2 μm



rare triaenes in the examined material, including the paratype. The specimens also have a crust of long acanthomicrorhabs

in a single size category at the surface supported by bouquets of oxeas with subcortical canals between them. All these

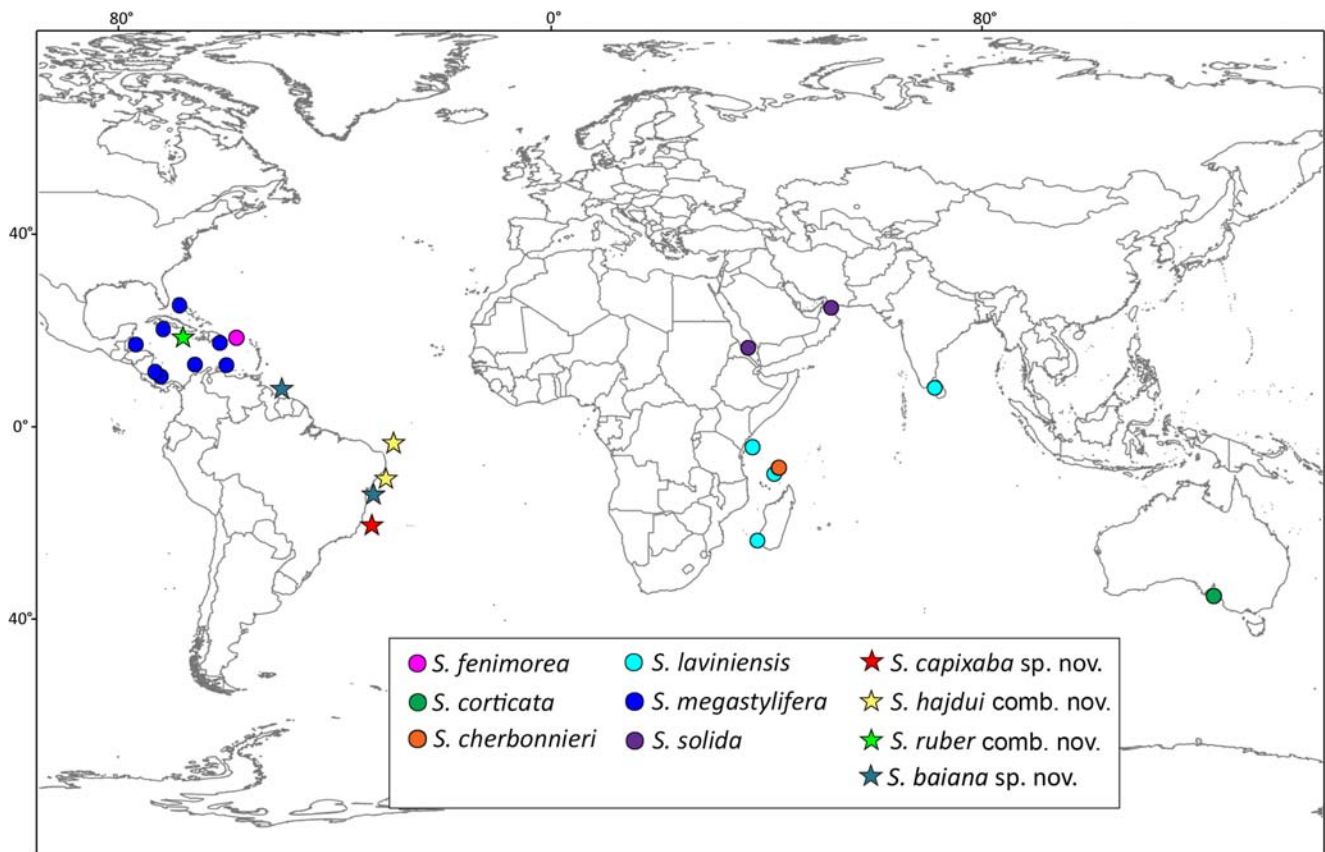


Fig. 6 World distribution of all *Stellettinopsis* species. Stars represent new records, and circles are records from the literature

Table 1 Spicule measurements of all specimens of *Stellettinopsis* studied here and of previous records of *S. megastylifera* and *S. baiana* sp. nov. (min–med–max length/width in micrometers)

Species/specimens examined	Locality	Oxeas	Triaxones	Microxeas	Acanthomicrotrahabds	Euaxters
<i>Stellettinopsis baiana</i> sp. nov.						
MNRJ 8339 (holotype)	NE Brazil (Bahia)	I: 1025–1226–1425/ 20–45–65 II: 770–978–1080/ 12–21–26 (n = 16)	Orthodichotriaxones: common R: 460–766–930/20–35–45 C: 80–180–230/7–23–28	190–246–422/1–2–5 (n = 12)	52–70–88/2–4–5	Strongylasters: 5–7–8 (n = 10) Oxyasters I: 7–9–12 (n = 3)
MNRJ 8420 (paratype)	NE Brazil (Bahia)	I: 1050–1239–1425/ 40–51–65 II: 990/25 (n = 1)	Orthodichotriaxones: common R: 680–744–800/25–38–60 C: 120–170–200/21–27–38 (n = 5)	207–232–253/2–3–4	50–64–80/4–5–6	Strongylasters: 5–6–7 (n = 6) Oxyasters I: 9–11–14 (n = 6)
Sensu Hajdu et al. 2011 (as <i>Ecionemita</i> sp.)	NE Brazil (Bahia)	I: 1190–1372/56–70	Orthodichotriaxones: common; Orthotriaxones: occasional R: 602–1050/42–56 C: 70–168/42–56	187–237/3.6 (cited as Oxeas II)	68–79/7.2–10.8	Oxyasters: 5.4–7.2
sensu van Soest 2017 (as <i>S. megastylifera</i>)	Guyana	I: 840–1161–1410/ 14–40.7–59 II: 426–603/4–7 (rare) Styles and strongyles: 882–960/43–54	Orthodichotriaxones: common R: 804–907–1058/ 30–41.7–51 C: 121–189–264 Plagiotriaxones: common ("shorter rhabdome and cladi") Protiraxones: rare R: 780/5 C: 30–66	–	66–78–99/4–5.3–7	Strongylasters: 5–6.6–8 Oxyasters: 11–13.4–17
<i>Stellettinopsis capixaba</i> sp. nov.						
MNRJ 7218 (holotype)	SE Brazil (Espírito Santo)	I: 900–1220–1425/ 15–31–50 II: 720–889–1000/5–8–10 (n = 3)	Orthotriaxones: very rare (exogenous?) R: >1113/20 C: 217/11 (n = 1)	175–237–353/1–2–5	32–50–64/1–3–5	Strongylasters: 8–8–8 (n = 2) Oxyasters I: 11–12–14 (n = 3) Oxyasters II: 6–7–8 (n = 8)
<i>Stellettinopsis hajdúi</i> comb. nov. (Morales, 2011)						
MNRJ 2900 (holotype)	NE Brazil (Rocas Atoll)	I: 675–936–1175/ 20–32–55 II: 420–868–1110/ 2–11–16	–	–	34–43–55/1–1.8–2	Oxyasters I: 9 (n = 1) Oxyasters II: 5–6–7 (n = 3)
MNRJ 7736 (paratype)	NE Brazil (Rocas Atoll)	I: 900–1019–1200/ 20–31–35 II: 530–827–1050/5–8–13	Orthotriaxones: rare R: 660/20 C: 25/17 (n = 1)	–	35–51–65/1–1.7–2	Oxyasters I: 8–8–8 (n = 2) Oxyasters II: 5–5–6 (n = 3)
UFSPOR 299	NE Brazil (Sergipe)	I: 610–772–880/15–21–28 II: 470–601–700/5–11–13	Plagiotriaxones: rare R: 242–249–257/4–7–10	–	37–58–75/2–2.2–3.5	Oxyasters I: 7–8–9 (n = 5)

Table 1 (continued)

Species/specimens examined	Locality	Oxeas	Trianaes	Microxeas	Acanthomicrohabdids	Euasters
UFSPOR 342	NE Brazil (Sergipe)	I: 650–844–950/15–24–29 II: 580–657–750/4–7–10	C: 15/2 ($n = 2$) Orthodichotrianaes: rare R: 470–537–600/15–20–30 C: 91–112–160/7–12–17 ($n = 10$)	–	48–66–80/1–2–2.5	Oxyasters II: 8 ($n = 1$) Oxyasters I: 6–7–10 ($n = 3$) Oxyasters II: 8–8–8 ($n = 3$)
UFSPOR 345	NE Brazil (Sergipe)	I: 690–864–990/17–24–29 II: 400–569–820/2–5–9	Plagiotrianaes: rare R: 230/4 C: 20/2 ($n = 1$)	–	32–63–80/1–2–2.5	Oxyasters I: 10 ($n = 1$) Oxyasters II: 7–7–8 ($n = 3$)
UFSPOR 361	NE Brazil (Alagoas)	I: 620–793–940/12–22–35 II: 520–579–700/3–6–8	–	–	37–62–82/1–2–3	Oxyasters I: 10–10–10 ($n = 2$) Oxyasters II: 5–5–6 ($n = 2$)
UFSPOR 447	NE Brazil (Sergipe)	I: 620–718–800/12–19–25 II: 500–588–650/5–8–10	–	–	45–59–70/1.5–2.2–2.3	Oxyasters I: 8–8–9 ($n = 4$) Oxyasters II: 8–9–9 ($n = 2$)
UFSPOR 453	NE Brazil (Sergipe)	I: 690–783–940/15–18–23 II: 410–568–680/2–3–5	Plagiotrianaes: rare R: 300/5 C: 15 ($n = 1$)	–	40–52–75/2–2.2–3	Oxyasters I: 7 ($n = 1$) Oxyasters II: 6–7–9 ($n = 3$)
<i>Stelletinopsis megastylifera</i> (Wintermann-Kilian & Kilian, 1984) MNRJ 15661	Panama	I: 950–1211–1425/ 30–41–50 II: 800–968–1125/ 15–21–25 ($n = 7$)	Plagiodichotrianaes: common R: 690–876–1000/30–42–60 C: 240–302–350/25–33–50 ($n = 18$) Plagiotrianaes I: common R: 690–876–1000/30–42–60 C: 240–302–350/25–33–50 Plagiotrianaes II: rare R: 540–620–700/30–30–30 C: 100–165–230/20–25–30 ($n = 2$) Plagiodichotrianaes: common R: 650–987–1175/25–44–60 C: 260–261–340/20–35–50 Plagiotrianaes I: common R: 650–987–1175/25–44–60 C: 260–261–340/20–35–50 Plagiotrianaes II: rare R: 390–529–960/15–21–40 C: 110–145–260/10–16–30 ($n = 13$)	180–211–263/2–3–5 ($n = 9$)	27–74–93/3–5–8 Strongylasters: 3–6–8 Oxyasters I: 10–14–23	
MNRJ 15876	Panama	I: 1225–1345–1450/ 45–52–60 II: 625–856–1050/ 10–17–20	–	155–196–250/1–3–4	75–87–108/5–6–8 Strongylasters: 5–6–8 Oxyasters I: 10–13–18	

Table 1 (continued)

Species/specimens examined	Locality	Oxeas	Trianaes	Microxeas	Acanthomicrohabds	Euasters
MNRJ 15893	Panama	I: 1125–1371–1575/ 50–58–65 II: 675–992–1175/ 20–27–35 (<i>n</i> = 9)	Plagiodychotrianaes: common R: 890–1011–1125/ 50–53–60 C: 240–355–420/ 30–41–50 (<i>n</i> = 8) Plagiotrianaes I: common R: 890–1011–1125/ 50–53–60 C: 240–355–420/ 30–41–50	180–214–258/2–4–5	65–89–108/4–5–8	Strongylasters: 2–5–8 Oxyasters I: 10–12–18
Sensu Wintermann-Kilian & Kilian, 1984 (as <i>Ecionemia</i>)	Colombia	I: 1180–1400/30–35 II: 730–900/10–15 Styles: 930–1100/35–45	Plagiotrianaes: common R: 250–410/11 C: 46 Plagiodychotrianaes: common R: 450–790/25	–	64–92/2–5	Strongylasters: 4–13
Sensu Pulitzer-Finali, 1986 (as <i>S. dominicana</i>)	Dominican Republic	760–1550/23–73	Orthotrianaes to plagiotrianaes or orthodichotrianaes: very rare R: 350–850/35–47 C: 20–150	–	55–84/2.5–4.5	Chiasters: 6–7.5 Oxyasters: 8.5–14.5
Sensu Cárdenas et al., 2009 (as <i>Ecionemia</i>)	Colombia, Panama, Bahamas, Dominican Republic	I: 1332–1524–1764/ 56–64.9–70 II: 520–815.2–1260/ 14–22.9–42	Plagiodychotrianaes: common R: 790–997.6–1222/ 50–64.7–80 C: 120–151.7–180 Anatrianaes: rare R: 228–278.3–334/1–1.3–2 C: 3–4–5 Protrianaes: rare R: 417/2.5–3.75–5.0 C: 27–32.5–38 (C)	182–215.4–317/ 2.5–4.0–5.0	59–98.6–138.3/4.5– 8.2–10.6	Strongylasters: 4–6.7–10 Oxyasters I: 9–13.1–19
<i>Stelletinopsis ruber</i> comb. nov. (Lehnert & van Soest, 1998)	Jamaica	I: 925–1179–1425/ 30–39–55 II: 675–837–1000/ 7–16–23	Orthotrianaes: very rare (exogenous?) R: >410/17 C: 71/17 (<i>n</i> = 1)	170–204–250/1–2–3	42–56–66/2–4–6	Strongylasters (some amphisanidaster-like): 8–9–10 (<i>n</i> = 6) Oxyasters I: 9–10–11 (<i>n</i> = 5)

N = 30 unless noted otherwise

R, rhabdome; *C*, cladome; –, not found

Table 2 Spicule measurements of all valid species of *Stellettinopsis* (min–med–max, min–max, or average length/width in micrometers)

Species of <i>Stellettinopsis</i>	Oxeas	Triaxenes	Microxeas	Acanthomicrothabds	Euasters
<i>S. baiana</i> sp. nov.	Oxea I: 1025–1233–1425/20–48–65 Oxea II: 770–978–1080/12–21–26	Orthodichotriaenes: common R: 460–755–930/20–37–60 C: 80–175–230/7–25–38	190–239–422/1–3–4	50–67–88/2–5–6	Strongylasters: 5–7–8 Oxyasters I: 7–10–14
<i>S. capixaba</i> sp. nov.	Oxea I: 900–1220–1425/15–31–50 Oxea II: 720–889–1000/5–8–10	Orthotriaenes with curved clads: extremely rare R: > 1113/20 C: 115/11	175–237–353/1–2–5	32–50–64/1–3–5	Strongylasters: 8–8–8 Oxyasters I: 6–8–12 Oxyasters II: 6–7–8
<i>S. cherbonnieri</i> Lévi, 1961	800–1000/25–60	–	–	45–130	Anthasters: 8–17 Spherasters: 8 Chiasters: 13
<i>S. corricata</i> Carter, 1879; sensu Carter, 1879; Sollas, 1888	1135/14	Orthotriaenes: rare 750	–	40/4	–
<i>S. fenimorea</i> (de Laubenfels, 1934)	> 1000/50	Dichotriaenes: rare 1100/45 Prodiaenes: rare 1100/45	–	60/1–3 (raphides?)	Tylasters
<i>S. hajdai</i> comb. nov. (Moraes, 2011); present study	Oxea I: 610–841–1200/12–24–55 Oxea II: 400–657–1110/2–7–16	Orthodichotriaenes: rare R: 470–537–600/15–20–30 C: 91–112–160/7–12–17	–	32–57–82/1–2.3–3.5	Oxyasters I: 6–9–10 Oxyasters II: 5–7–10
<i>S. laviniensis</i> (Dendy, 1905); sensu Kelly & Sim-Smith 2012	650–1300/12–55	Orthotriaenes: rare R: 660/20 C: 25/17 Plagiotriaenes: rare R: 230–243–257/4–6–10 C: 15–17–20/2	–	63–134/3–8	Chiasters: 6–8 Oxyasters I: 21
<i>S. megastylifera</i> (Wintermann-Kilian & Kilian, 1984) sensu Cárdenas et al., 2009, as <i>Ecionemia</i>	Oxea I: 1332–1524–1764/56–64.9–70 Oxea II: 520–815.2–1260/14–22.9–42	Plagiodichotriaenes: common R: 790–997.6–1222/50–64.7–80 C: 120–151.7–180	182–215.4–317/2.5–4.0–5.0	59–98.6–138.3/4.5–8.2–10.6	Strongylasters: 4–6.7–10 Oxyasters I: 9–13.1–19
<i>S. ruber</i> comb. nov. (Lehnert & van Soest, 1998)	Oxea I: 925–1179–1425/30–39–55 Oxea II: 675–837–1000/7–16–23	Anatriaenes: rare R: 228–278.3–334/1–1.3–2 C: 3–4–5 Protriaenes: rare R: 417/2.5–3.75–5.0 C: 27–32.5–38 (C)	170–204–250/1–2–3	42–56–66/2–4–6	Strongylasters: 8–9–10 Oxyasters I: 9–10–11
<i>S. solida</i> Lévi, 1965 sensu van Soest & Beglinger 2008	625–940/4–22	Orthotriaenes: very rare R: > 410/17 C: 71/17 Plagio- to orthotriaenes: common 306–720/56–180	–	63–96/1.5–3.0	Tylasters: 2–6 Oxyasters I: 9–10 Anthasters: rare 13

R, rhabdome; C, cladome

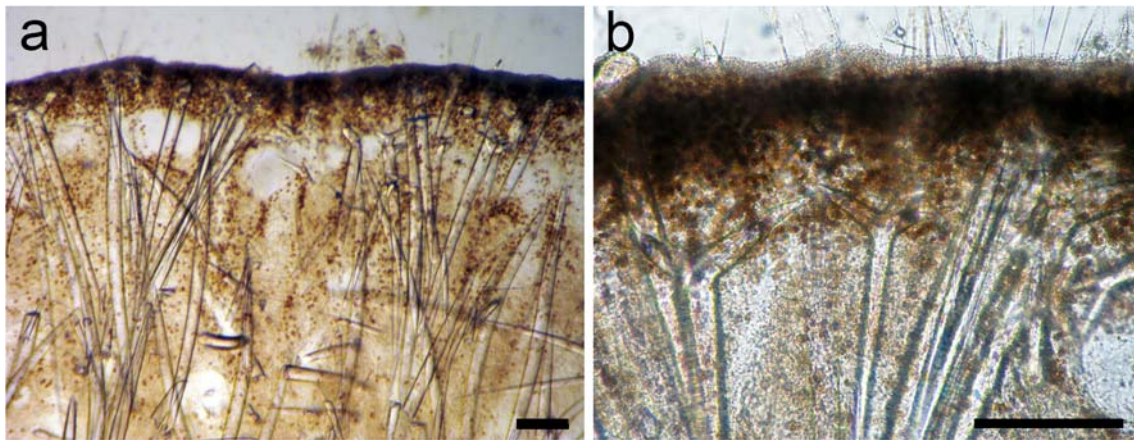


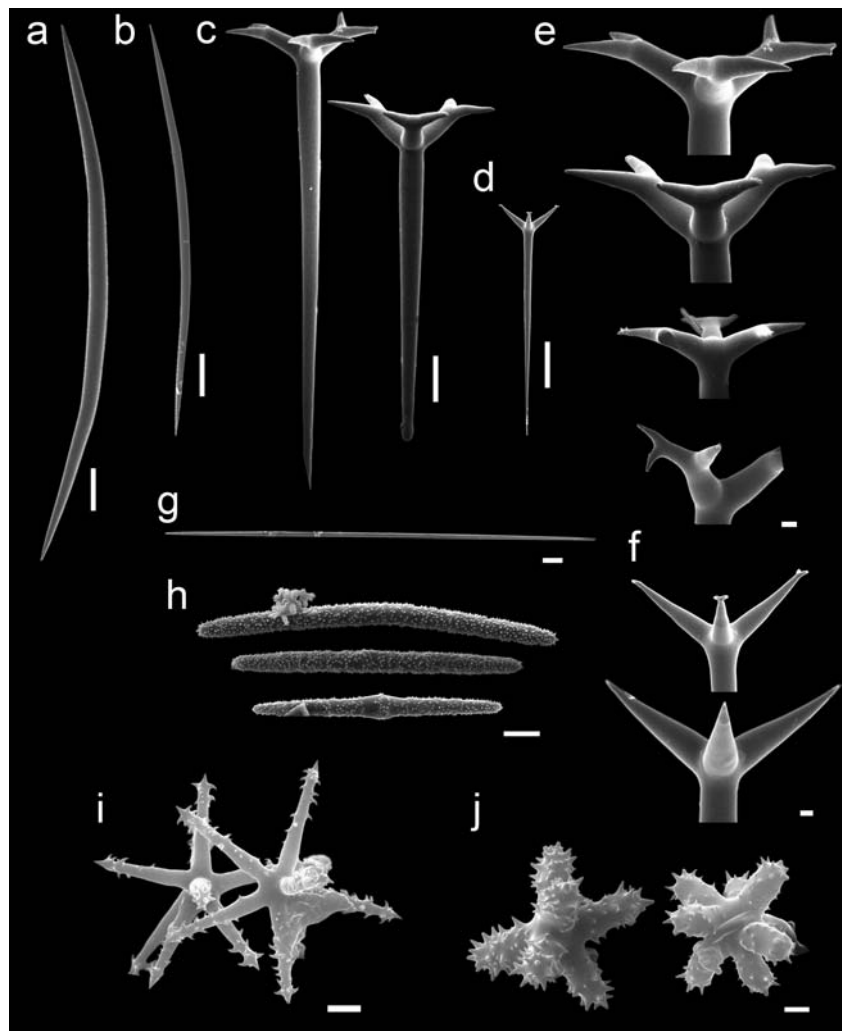
Fig. 7 *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). Images from MNRJ 15893. **a** Cross-section showing the skeletal architecture in ectosome and choanosome; **b** details of the cross-section showing the plagiodichotriaenes. Scale bars: **a** 175 μm ; **b** 200 μm

characteristics support the transfer of *Melophlus hajdui* to the genus *Stellettinopsis*.

Stellettinopsis hajdui comb. nov. differs from the other species of the genus in the possession of oxeas with mucronate,

stepped tips, acanthomicrohabds slightly spined with acerate tips, rare orthodichotriaenes, plagiotriaenes and orthotriaenes, two categories of oxyasters, and absence of strongylasters. *Stellettinopsis hajdui* comb. nov. and *S. megastylifera* have

Fig. 8 *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). Spicules of MNRJ 15661, 15876 and 15893 (SEM). **a** Oxea I; **b** oxea II; **c** plagiodichotriaenes; **d** plagiotriaene; **e** details of the plagiodichotriaenes cladomes; **f** details of the plagiotriaene cladome; **g** microoxea; **h** stronglyloid acanthomicrohabds; **i** oxyasters; **j** strongylasters. Scale bars: **a–d** = 100 μm ; **e** = 20 μm ; **f–h** = 10 μm ; **i** = 2 μm ; **j** = 1 μm



similar spicules, but they differ consistently in details of spicule shape. *Stellettinopsis megastylifera* always has abundant plagiodichotriaenes with longer and thicker rhabdome (790–1222/50–80 μm) than in *S. hajdui* comb. nov., which has very rare, short orthodichotriaenes (470–600/15–30 μm). *Stellettinopsis megastylifera* also differs by its thicker oxeas I with acerate tips (56–70 vs. 12–55 μm in *S. hajdui* comb. nov.), presence of microxeas, more stronglyloid and thicker acanthomicrohabds (4.5–10.6 μm in width vs. 1.0–3.5 μm in *S. hajdui* comb. nov.), larger oxyasters (9–19 vs. 6–10 μm) and presence of strongylasters, which are absent in *S. hajdui* comb. nov. (Tables 1 and 2; Fig. 8). *Stellettinopsis femimorea* from the Caribbean differs from *S. hajdui* comb. nov. by its longer oxeas (> 1000 μm) and tylasters as the only euaster microscleres (Table 2).

Although we identified six additional specimens from Sergipe and Alagoas states as *S. hajdui* comb. nov., they show some morphological differences to the types that suggest that they could belong to a different species. The type specimens from Rocas Atoll are whitish, globose (Fig. 3a, b) and have rare orthotriaenes (found only in the paratype) and thicker oxeas I (675–1200 long by 20–55 μm wide). In contrast, the additional specimens are brown, digitate or elongate (Fig. 3c, d), with rare orthodichotriaenes and plagiotriaenes, and thinner oxeas I (610–990 long by 12–35 μm wide). We decided to identify both populations as *S. hajdui* comb. nov. based on their high similarity in most other morphological characters, especially the size and shape of oxyasters and acanthomicrohabds. Additionally, it is possible that all specimens have orthodichotriaenes, orthotriaenes, and

plagiotriaenes, but they were overlooked due to their extreme rarity. This possible species complex should be further investigated through detailed morphological analysis coupled with molecular methods and larger sample sizes.

***Stellettinopsis ruber* (Lehnert & van Soest, 1998), new combination**

(Figs. 6, 9, and 10; Tables 1 and 2)

Melophlus ruber Lehnert & van Soest, 1998: 74; Berube et al. 2012: 33.

Material examined. Holotype ZMAPOR 12741, Jamaica, Discovery Bay, Blue Hole near Columbus Park (18° 28' 0.1" N, 77° 24' 0" W), 15 m depth, 20/i/1993.

Comparative material (Table 1; Figs. 7 & 8). *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). MNRJ 15661, Isla Colón, Bocas del Toro, Panama (09° 21.10' N, 82° 15.57' W), colls. E. Hajdu and Sponge Course Team, 25/vii/2012. MNRJ 15876, Cayo Zapatilla, Bocas del Toro, Panama (9° 16' 12.68" N, 82° 03' 57.77" W), coll. G. Lôbo-Hajdu, 15/viii/2012. MNRJ 15893, Isla Escudo de Veragua, Bocas del Toro, Panama (09° 05' 51.86" N, 81° 34' 29.56" W), colls. C. Freeman and K. Matterson, 02/viii/2012.

Diagnosis. Vase-shaped *Stellettinopsis* with two categories of oxeas, rare orthotriaenes, smooth microxeas, strongylote acanthomicrohabds, spined oxyasters, spined strongylasters, and amphisaniaster-like strongylasters.

Description (Fig. 9a). Vase-shaped sponge with an expanded wavy margin in maturity. The surface is conulose and rough to the touch. The consistency is elastic, compressible, but difficult to tear. Color dark red in vivo, becoming dark

Fig. 9 *Stellettinopsis ruber* (Lehnert & van Soest, 1998) comb. nov. **a** Holotype (ZMAPOR 12741) in situ in Discovery Bay, Jamaica, photo H. Lehnert (from van Soest et al. 2019b); **b** cross-section showing the skeletal architecture of ectosome and choanosome (holotype–ZMAPOR 12741); **c** broken orthotriaene. Scale bars: **b** = 200 μm ; **c** = 100 μm

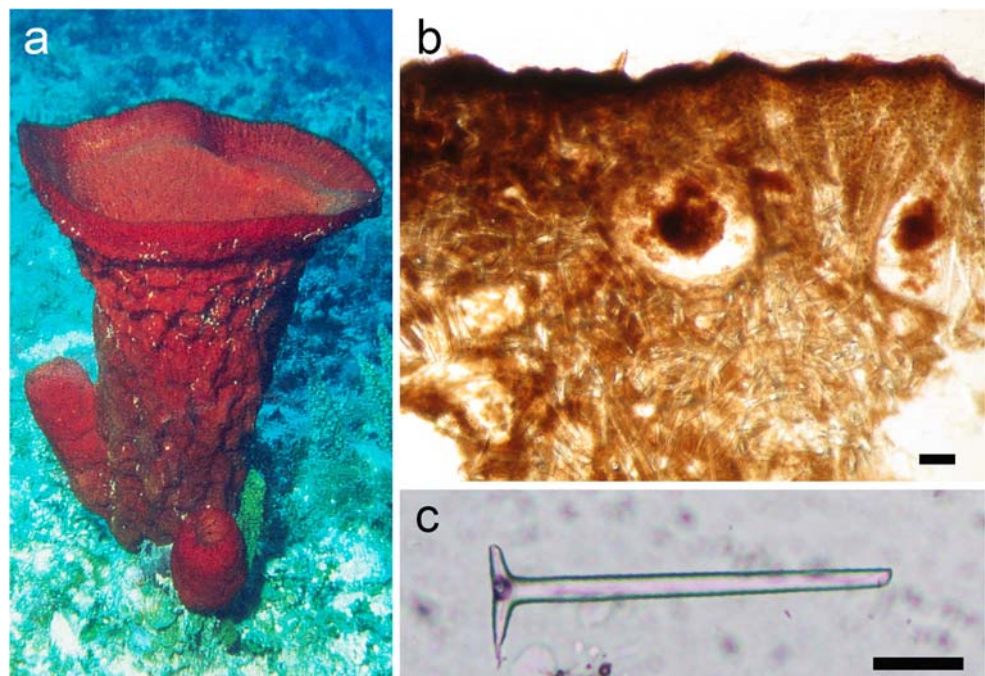
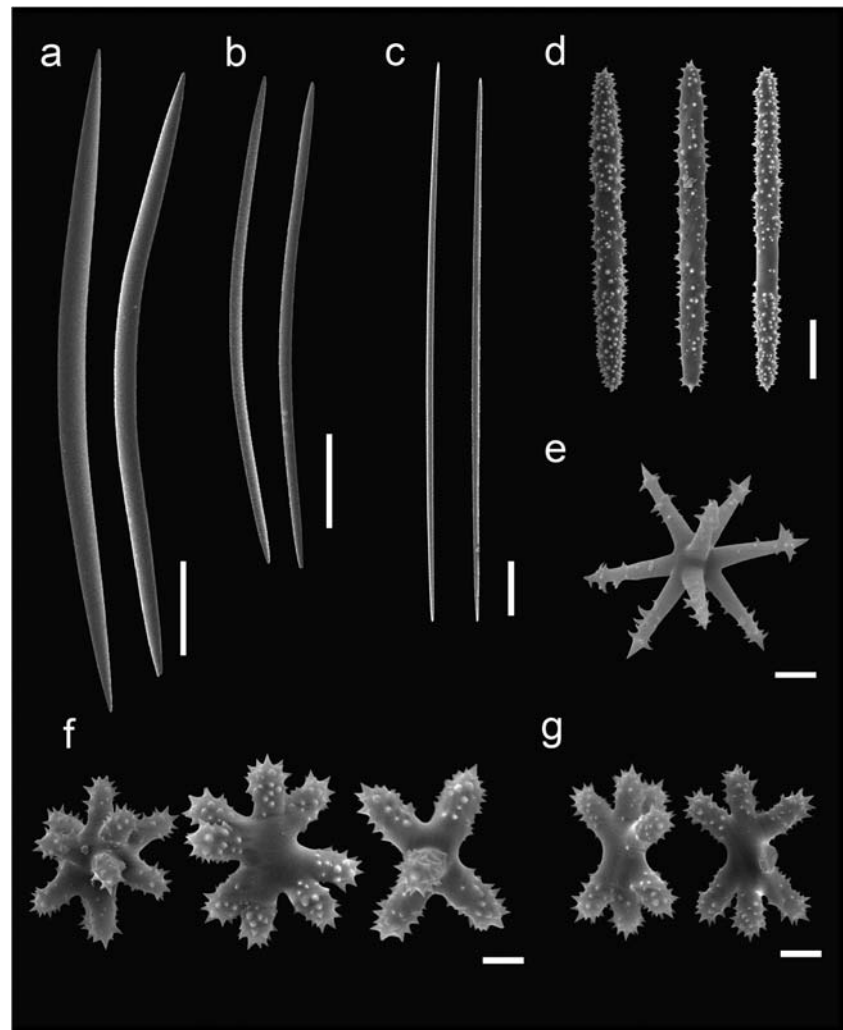


Fig. 10 *Stellettinopsis ruber* (Lehnert & van Soest, 1998) comb. nov. (holotype—ZMAPOR 12741). **a** Oxeas I; **b** oxeas II; **c** microxeas; **d** stronglyloid acanthomicrohabds; **e** oxyaster; **f** strongylasters; **g** amphisnidasters-like strongylasters. Scale bars: **a, b** = 200 μm ; **c** = 20 μm ; **d** = 10 μm ; **e–g** = 2 μm



reddish brown externally and light reddish brown internally in ethanol (from Lehnert and van Soest 1998).

Skeleton (Fig. 9b). Ectosomal skeleton made of a cortical layer of acanthomicrohabds, strongylasters, and oxyasters, up to 100 μm thick, which is supported by narrow bouquets of oxeas that emerge from the choanosome with canals between them. The choanosomal skeleton is a mass of scattered oxeas together with scattered microxeas, acanthomicrohabds, and euasters. Abundant pigmented cells were observed in both ectosome and choanosome.

Spicules of the holotype (Fig. 9c; Fig. 10). Orthotriaenes are very rare (only one was observed): rhabdome long and straight (>410 μm length and 17 μm width); clads short and straight, 71/17 μm (Fig. 9c). Oxeas I thick, straight or slightly curved, with sharp tips, 925–1179–1425/30–39–55 μm (Fig. 10a). Oxeas II are thin, slightly curved, with sharp tips, 675–837–1000/7–16–23 μm (Fig. 10b). Microxeas are thin, straight, smooth, 170–204–250/1–2–3 μm (Fig. 10c). Acanthomicrohabds are stout, with strongylote ends, 42–56–66/2–4–6 μm (Fig. 10d). Oxyasters are slender, spined

only in the distal portion, 8–10 rays, 9–10–11 μm in diameter ($n = 5$) (Fig. 10e). Strongylasters are spined (Fig. 10f), variable in shape to amphisnidaster-like strongylasters (Fig. 10g), 6–9 rays, 8–9–10 μm in diameter ($n = 6$).

Ecology. This species was found at 15 m depth in a shallow reef habitat (Lehnert and van Soest 1998). It was reported as the most common component of hawksbill sea turtle diet in the Caribbean region of Honduras (Berube et al. 2012).

Geographical distribution (Fig. 6). Caribbean Sea (Jamaica, Honduras) (Lehnert and van Soest 1998; Berube et al. 2012).

Taxonomic remarks. *Stellettinopsis ruber* comb. nov. was originally described as *Meloplus* by Lehnert and van Soest (1998). Our reexamination of the holotype showed the presence of rare orthotriaenes, but as only one spicule was found, it is uncertain if it is proper or an artifact. However, other characteristics such as a surface layer of acanthomicrohabds in a single category and ectosomal bouquets of oxeas also suggest that the species is more closely allied with *Stellettinopsis* than with *Meloplus* (Uriz 2002; Kelly and Sim-Smith 2012). We add to the original description of

S. ruber comb. nov. the presence of three size classes of oxeas (called here “oxeas I,” “oxeas II,” and “microxeas”) and the amphisanidaster-like variation in strongylaster shape.

Stellettinopsis ruber comb. nov. differs from the other species of the genus by the combination of vaseform shape together with smooth microxeas, strongylote acanthomicrohabds, spined oxyasters, strongylasters, and especially by its amphisanidaster-like strongylasters. Amphisanidasters are usually found in species of *Stryphnus*, which differs from *Stellettinopsis* by the presence of two layers of triaenes, ectosome with sanidasters and amphisanidasters and by the absence of acanthomicrohabds and ectosomal bouquets of oxeas (Kelly and Sim-Smith 2012).

When compared to its congeners from the TWA, *S. ruber* comb. nov. is more similar to *S. megastylifera*, which shares the presence of smooth microxeas, strongylote acanthomicrohabds, oxyasters, and strongylasters. However, the two species are easily distinguished by the vase-shaped form and dark red color of *S. ruber* versus the massive lobate shape and light brown color of *S. megastylifera* and by the abundance, shape, and size of the plagiodichotriaenes of *S. megastylifera* (Tables 1 and 2; Fig. 8). The presence of

dichotriaenes, prodiaenes, and tylasters in *S. fenimorea* and the occurrence of two categories of oxyasters and acerate acanthomicrohabds in *S. hajdui* comb. nov. distinguish these species from *S. ruber* comb. nov. (Tables 1 and 2).

***Stellettinopsis baiana* sp. nov.**

<http://zoobank.org/51737369-00F1-43C0-A148-68BC6830C92C>

(Figs. 6, 11, and 12; Tables 1 and 2)

Synonyms: *Ecionemia* sp., Hajdu et al. 2011: 71.

Stellettinopsis megastylifera, van Soest 2017: 78 (*non*: *Ecionemia megastylifera* Wintermann-Kilian and Kilian 1984, Cárdenas et al. 2009).

Type material. Holotype MNRJ 8339, Canal de Madre de Deus, Baía de Todos os Santos, Salvador, Bahia State, Brazil (12° 45' 21.09" S, 38° 37' 17.08" W), depth 5 to 12.5 m, colls. E. Hajdu, C. Santos and E. Esteves, 07/vi/2004. Paratype MNRJ 8420, same locality of holotype, depth 5 to 12.5 m, colls. E. Hajdu and C. Santos, 07/vi/2004.

Comparative material (Table 1; Figs. 7 and 8). *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). MNRJ 15661, Isla Colón, Bocas del Toro, Panama

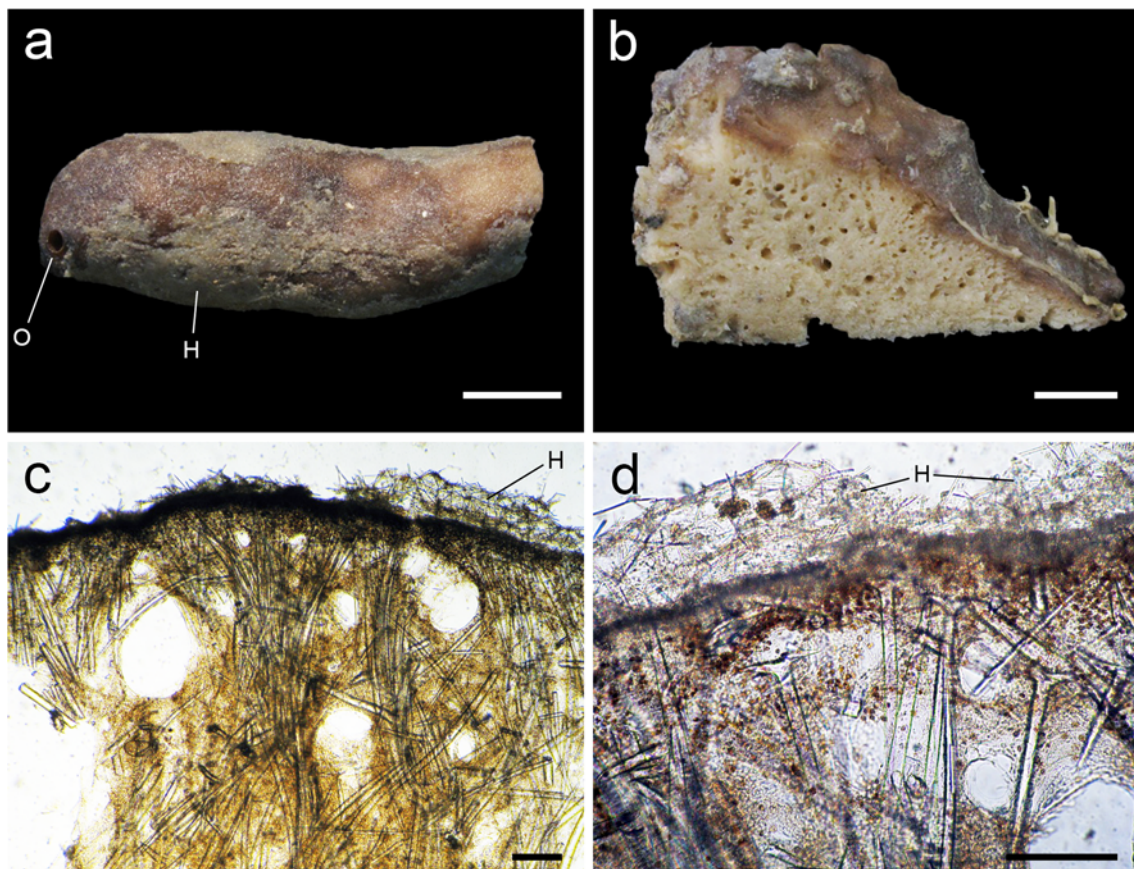
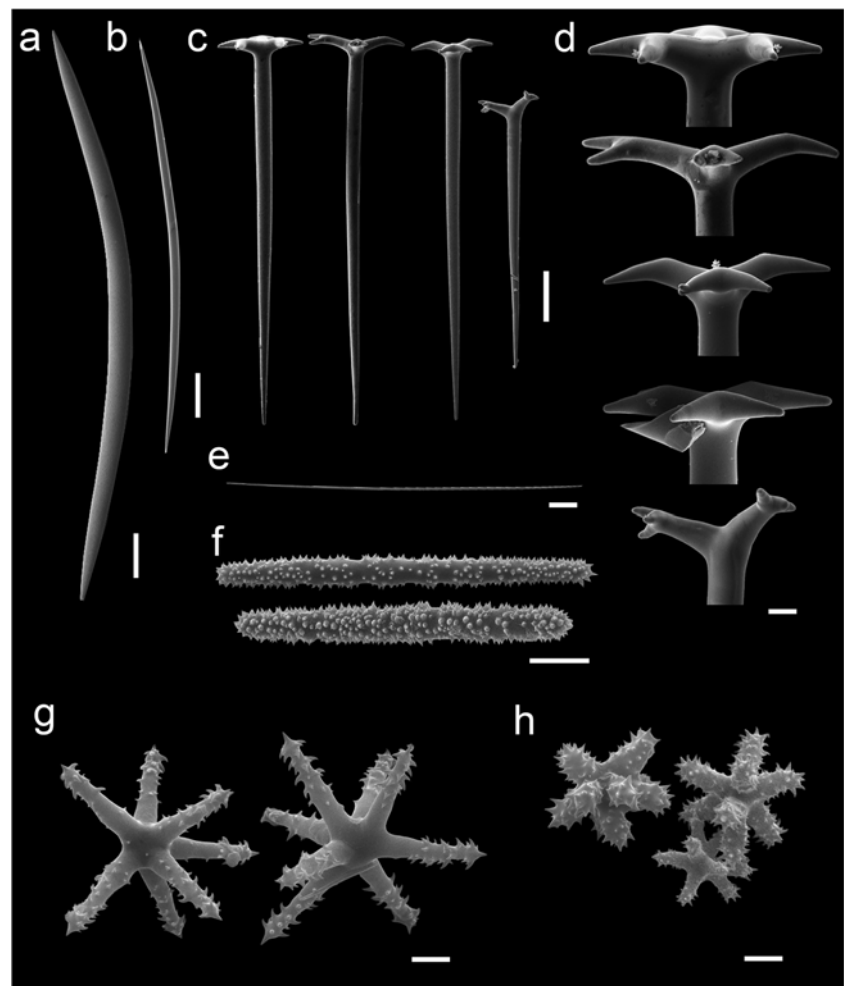


Fig. 11 *Stellettinopsis baiana* sp. nov. **a** Holotype (MNRJ 8339); **b** paratype (MNRJ 8420); **c** cross-section showing the skeletal architecture in ectosome and choanosome; **d** details of the cross-

section showing the orthodichotriaenes. O, oscule; H, epibiont sponge *Haliclona* sp. Scale bars: **a**, **b** = 1 cm; **c**, **d** = 250 μ m

Fig. 12 *Stellettinopsis baiana* sp. nov. **a** Oxea I; **b** oxea II; **c** orthodichotriaenes; **d** details of the orthodichotriaenes cladomes; **e** microxea; **f** stronglyloid acanthomicrohabds; **g** oxyasters; **h** Strongylasters. Scale bars: **a–c** = 100 μ m; **d** = 20 μ m; **e, f** = 10 μ m; **g, h** = 2 μ m



(09° 21.10' N, 82° 15.57' W), colls. E. Hajdu and Sponge Course Team, 25/vii/2012. MNRJ 15876, Cayo Zapatilla, Bocas del Toro, Panama (9° 16' 12.68" N, 82° 03' 57.77" W), colls. G. Lôbo-Hajdu, 15/viii/2012. MNRJ 15893, Isla Escudo de Veragua, Bocas del Toro, Panama (09° 05' 51.86" N, 81° 34' 29.56" W), colls. C. Freeman and K. Matterson, 02/viii/2012.

Etymology. The species name is a noun in apposition referring to women born in Bahia State, popularly known in Brazil as “baianas,” here dedicated to our colleague from Bahia Anaíra Lage for her remarkable contribution to sponge taxonomy.

Diagnosis. *Stellettinopsis* with orthodichotriaenes relatively common, two categories of oxeas, smooth microxeas, acanthomicrohabds with rounded tips, and spined oxyasters and strongylasters.

Description (Fig. 11a, b). Shape massive to irregularly lobate or cylindrical, 3–4 cm in diameter and up to 15 cm in length. The paratype has scattered rounded protuberances up to 3 mm high (Fig. 11b). The color in vivo is dark grayish-brown externally and beige internally. After fixation in ethanol, the external color of the holotype is dark brown (Fig. 11a),

and the paratype is dark brown on the top of lobes and light brown in between the lobes (Fig. 11b); the internal color of both specimens is beige. The surface is usually covered with encrusted sediments and associated organisms. The surface varies from hispid to rugose. Oscules are circular, surrounded by a darker-colored raised rim (Fig. 11a), 2–4 mm in diameter (observed only in the holotype). The consistency is hard and incompressible.

Skeleton (Fig. 11c, d). The ectosomal skeleton is composed of a layer of oxyasters, strongylasters, and acanthomicrohabds, up to 125 μ m thick, which is supported by bouquets of oxeas and orthodichotriaenes that emerge from the choanosome, with large canals between them (Fig. 11c, d). Microxeas are usually found piercing the surface. Pigmented cells are abundant in the ectosome (Fig. 11d). The choanosomal skeleton is made of scattered oxeas together with randomly dispersed oxyasters, strongylasters, and acanthomicrohabds (Fig. 11c).

Spicules (Fig. 12; average of all specimens; individual measurements in Table 1). Oxeas I stout, straight or slightly curved, with acerate, mucronate and blunt tips, with rare stylote modifications, 1025–1233–1425/20–48–65 μ m (Fig. 12a). Oxeas II are thin, straight, or slightly curved, with

fusiform tips, 770–978–1080/12–21–26 μm (Fig. 12b). Orthodichotriaenes have thick rhabdome, with strongylote and, rarely, oxeote ends, 460–755–930/20–37–60 μm . The cladomes are orthotriaenes-like, short, with rounded ends, but, occasionally, they can have a secondary ramification with rounded projections, 80–175–230/7–25–38 μm (Fig. 12c, d). One spicule that could be classified as a “plagiotrichodiaene” was found but was considered a malformation (Fig. 12c, d). Microxeas are slender, smooth, and straight, 190–239–422/1–3–4 μm (Fig. 12e). Acanthomicrohabds are stout, heavily spined, with strongylote ends, 50–67–88/2–5–6 μm (Fig. 12f). Oxyasters have 7–8 slender rays, 7–10–14 μm in diameter ($n=9$), with spines often curved inwards (Fig. 12g). Strongylasters are spined, with 8 rays, 5–7–8 μm in diameter ($n=16$) (Fig. 12h).

Ecology. The specimens were collected at 5–12.5 m depth, in Todos os Santos Bay, an environment with high sediment load, associated to cnidarians and sponges of the genus *Haliclona* Grant, 1841 (Fig. 11a–d).

Geographical distribution (Fig. 6). Bahia State, NE Brazil (present study), and Guyana Shelf (van Soest 2017 as *Stellettinopsis megastylifera*).

Taxonomic remarks. *Stellettinopsis baiana* sp. nov. was previously described from NE Brazil as *Ecionemia* sp. by Hajdu et al. (2011), and later synonymized with *Stellettinopsis megastylifera* by van Soest (2017). We revised the two specimens described by Hajdu et al. (2011) and found that both have a superficial crust of long acanthomicrohabds and bouquets of oxeas separated by subectosomal openings that support the allocation of this species in *Stellettinopsis*, as suggested by van Soest (2017). We also observed, however, that the specimens described by Hajdu et al. (2011) from Bahia and van Soest (2017) from Guyana have very similar spicules and are distinguishable from *S. megastylifera* sensu stricto and all other congeners by details in spicule shape that support their redescription here as a new species.

The main differences between *S. baiana* sp. nov. and *S. megastylifera* are the shape and abundance of the dichotriaenes. The three specimens of *S. megastylifera* from Panama revised here have abundant long, stout plagiodichotriaenes, in agreement with previous descriptions of the species (Fig. 8a, b; Wintermann-Kilian and Kilian 1984; Pulitzer-Finali 1996; Cárdenas et al. 2009). In contrast, in *S. baiana* sp. nov., the triaenes are orthodichotriaenes and are less common, shorter, and thinner than in *S. megastylifera* (Fig. 12c, d; Hajdu et al. 2011; van Soest 2017). *Stellettinopsis megastylifera* further differs from the new species by its longer and thicker acanthomicrohabds (69–138.3/4.5–9.0 vs. 50–88/2–6 μm in *S. baiana* sp. nov.; Tables 1 and 2; Fig. 8).

Stellettinopsis hajdui comb. nov. differs from *S. baiana* sp. nov. by the shape of its oxeas, which often have stepped and mucronate ends, the rarity of orthodichotriaenes, and the absence of strongylasters. *Stellettinopsis ruber* comb. nov. is vasiform and has amphisaniaster-like strongylasters and

Stellettinopsis fenimorea differs from *S. baiana* especially by the rarity of dichotriaenes and protriaenes, the presence of tylasters, and the absence of oxyasters and strongylasters (Table 2). The new species differs from all its congeners by the combination of orthodichotriaenes, two categories of oxeas, smooth microxeas, strongyloid acanthomicrohabds, oxyasters, and strongylasters.

***Stellettinopsis capixaba* sp. nov**

<http://zoobank.org/4668CF17-22CD-4510-87C9-3A6897AE37D0>

(Figs. 6, 13, and 14; Tables 1 and 2)

Melophlus sp., Muricy et al. 2006: 9.

Type material. Holotype MNRJ 7218, REVIZEE Programme, Score Central V, station #33R, Vitória-Trindade Seamount Chain, Espírito Santo State, Brazil (20° 34' 59.28" S, 38° 04' 31.32" W), depth 55 m, coll. R/V Astro Garoupa, 19/vii/2001.

Comparative material (Table 1; Figs. 7 and 8). *Stellettinopsis megastylifera* (Wintermann-Kilian & Kilian, 1984). MNRJ 15661, Isla Colón, Bocas del Toro, Panama (09° 21.10' N, 82° 15.57' W), colls. E. Hajdu and Sponge Course Team, 25/vii/2012. MNRJ 15876, Cayo Zapatilla, Bocas del Toro, Panama (9° 16' 12.68" N, 82° 03' 57.77" W), colls. G. Lôbo-Hajdu, 15/viii/2012. MNRJ 15893, Isla

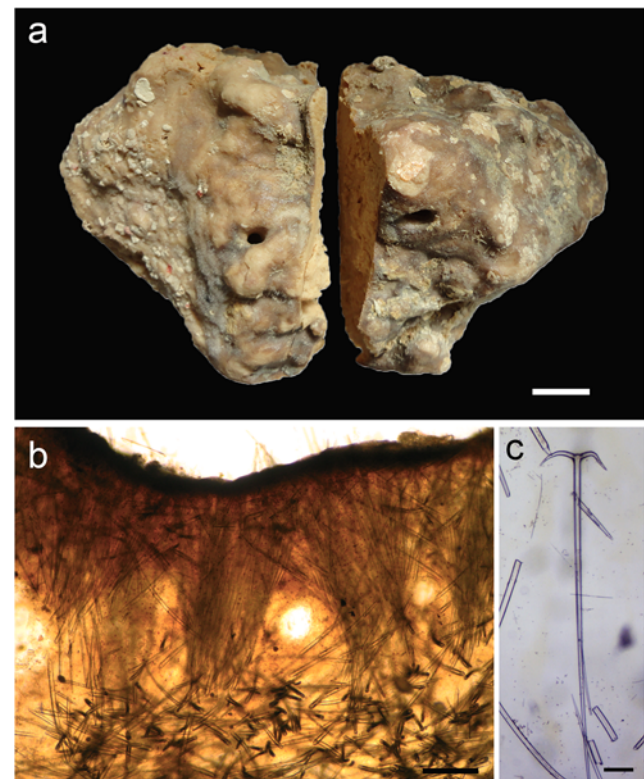
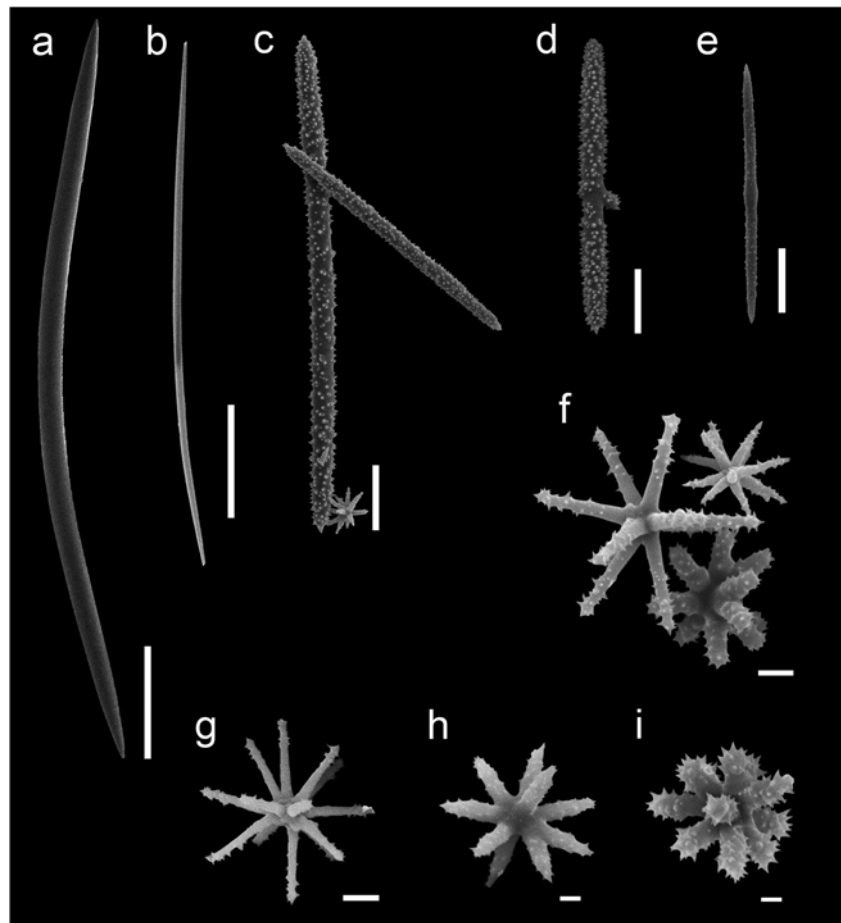


Fig. 13 *Stellettinopsis capixaba* sp. nov. **a** Holotype (MNRJ 7218); **b** cross-section showing the skeletal architecture in ectosome and choanosome; **c** curved orthotriaene. Scale bars: **a** = 2 cm; **b** = 200 μm ; **c** = 100 μm

Fig. 14 *Stellettinopsis capixaba* sp. nov. **a** Oxea I; **b** oxea II; **c** acanthomicrohabds with acerate tips and spined oxyaster 2; **d** stronglyloid acanthomicrohabd; **e** centrotylote acanthomicrohabd; **f** spined oxyaster 1, spined oxyaster 2 and spined strongylaster; **g** spined oxyaster 1; **h** spined oxyaster 2; **i** spined strongylaster. Scale bars: **a** = 200 μ m; **b–d** = 10 μ m; **e, f** = 1 μ m; **g, h** = 2 μ m



Escudo de Veragua, Bocas del Toro, Panama (09° 05' 51.86" N, 81° 34' 29.56" W), colls. C. Freeman and K. Matterson, 02/viii/2012.

Etymology. The species name is a noun in apposition referring to the people born in Espirito Santo State, popularly known in Brazil as “capixabas.”

Diagnosis. *Stellettinopsis* with skeleton composed of a unique combination of rare orthotriaenes with curved clads, two categories of oxeas, smooth microxeas, acanthomicrohabds with rounded or acerate tips, and three categories of euasters: spined oxyasters 1 and 2 and spined strongylasters.

Description (Fig. 13a). Shape massive irregular, up to 11.5 × 7.0 × 9.0 cm (length × width × height). The color in ethanol is brown externally and dark beige internally. The surface is strongly hispid, with scattered rounded protuberances. Only two oscula were observed, both circular to oval, with 3 and 7 mm in diameter. Atrial cavity measures 4.5 cm depth. The consistency is hard and incompressible, stony.

Skeleton (Fig. 13b). The ectosome has a surface layer up to 300 μ m thick with oxyasters, strongylasters, and acanthomicrohabds. This layer is supported by bouquets of oxeas that emerge from the choanosome, with canals and abundant pigmented cells between them. The microxeas are present in the subectosomal region, perpendicular to the

surface, usually piercing the ectosome. The choanosomal skeleton is made of scattered oxeas together with randomly dispersed oxyasters, strongylasters, and acanthomicrohabds.

Spicules of the holotype (Fig. 13c; Fig. 14). Orthotriaenes with curved cladi, extremely rare (only one was observed): rhabdome long and slightly curved (> 1113 μ m length and 20 μ m length and width); cladome short and curved (217 μ m length), clads 115/11 μ m (Fig. 13c). Oxeas I are thick, straight, or slightly curved, with hastate tips and rare stylote modifications, 900–1220–1425/15–31–50 μ m (Fig. 14a). Oxeas II are thin, straight, or slightly curved, with fusiform tips, 720–889–1000/5–8–10 μ m ($n = 3$) (Fig. 14b). Microxeas are thin, straight, smooth, 175–237–353/1–2–5 μ m. Acanthomicrohabds are stout, with acerate or rounded tips (Fig. 14c, d), sometimes centrotylote (Fig. 14e), 32–50–64/1–3–5 μ m. Two categories of oxyasters: oxyaster 1 long, slender, and spined only in the distal portion, 11–12–14 μ m in diameter ($n = 3$) (Fig. 14f, g); oxyaster 2 short, stout, with irregular spines and acerate tips, 6–7–8 μ m in diameter ($n = 8$) (Fig. 14f, h). Strongylasters are short, stout, and spined, 8 μ m in diameter ($n = 2$) (Fig. 14f, i).

Ecology. The specimen was collected at 55 m depth, associated to rhodoliths.

Geographical distribution (Fig. 6). Endemic from the Vitória-Trindade Seamounts Chain, Espírito Santo State, SE Brazil.

Taxonomic remarks. This species was assigned to *Stellettinopsis* based on the presence of a superficial layer of acanthomicrohabds and euasters, a disorganized choanosome, and bouquets of oxeads in the ectosome. The orthotriaenes are extremely rare and only one spicule was found, so it is uncertain if it is proper of the sponge or exogenous. *Stellettinopsis capixaba* sp. nov. differs from the other species of the genus by the combination of oxeads, stout acanthomicrohabds with rounded or acerate tips, very rare orthotriaenes with curved cladi, oxyasters in two categories, and strongylasters. The new species is distinguishable from its congeners in the TWA by details in the shape of the spicules. *Stellettinopsis hajdui* comb. nov. differs from *S. capixaba* sp. nov. by the shape of oxea I with stepped and mucronate ends, the presence of rare orthodichotriaenes, and by the absence of microxeads and strongylasters. *Stellettinopsis megastylifera* differs by having abundant plagiodichotriaenes, larger and thicker acanthomicrohabds (cf. Cárdenas et al. 2009: 59–98.6–138.3/4.5–8.2–10.6 μm vs. 32–50–64/1–2.7–5), and one category of oxyasters (vs. two in *S. capixaba* sp. nov.) (Tables 1 and 2; Fig. 8); *Stellettinopsis ruber* comb. nov. has orthotriaenes, one category of oxyaster, and a vase-shaped form; *S. baiana* sp. nov. has common orthodichotriaenes and one category of oxyasters (Tables 1 and 2) and *S. fenimorea* has dichotriaenes, prodiaenes, and only tylasters as euasterose microscleres (Table 2).

Discussion

Species delimitation in *Stellettinopsis*

The genus *Stellettinopsis* is relatively homogeneous and most of its 10 species are similar in external morphology, skeletal arrangement, and spicule complement. The morphological distinction between species is often subtle and must be interpreted with caution, due to the high intraspecific variation of many characters.

External morphology is of little usefulness for species delimitation. Most species of *Stellettinopsis* are massive, irregular, or globular, with brownish, yellowish, or grayish colors, hispid surface, and firm consistency. The main exceptions are *S. ruber* comb. nov., with a distinctive vasiform shape and bright red color, and *S. laviniensis* and *S. fenimorea* with digitiform projections (Dendy 1905; Lévi 1961). The skeletal architecture is useful to distinguish *Stellettinopsis* from other Ancorinid genera, but not to differentiate between species of *Stellettinopsis*. All species of the genus have a disorganized choanosomal skeleton, ectosomal brushes of oxeads and, when

present, of triaenes, and a cortex of microhabds and euasters (Tables 2 and 3).

Our results indicate that spicule geometry is more informative for species delimitation than skeletal architecture or external morphology, but some spicules may be more informative than others. All species of *Stellettinopsis* have oxeads, but their shape varies in different species. For instance, the oxeads of *S. megastylifera* are stout and fusiform, while those of *S. capixaba* sp. nov. are slender and hastate, and those of *S. hajdui* comb. nov. have stepped endings and are often stronglyloid. However, these differences are often too subtle and the intraspecific variation is so high that they can seldom be used for species delimitation in *Stellettinopsis*. The same problem applies to microxeads and acanthomicrohabds, although the size of the acanthomicrohabds helps to distinguish between the genera *Stellettinopsis* and *Ecionemia* (Table 3).

Triaenes are absent in *S. cherbonnieri* and are extremely rare in many species such as *S. corticata*, *S. capixaba* sp. nov., *S. hajdui* comb. nov., and *S. ruber* comb. nov. (Lévi 1961; Kelly and Sim-Smith 2012; present study). However, they are common in *S. megastylifera*, *S. laviniensis*, *S. solida*, and *S. baiana* sp. nov., and triaene morphology can be useful for distinction of these species of *Stellettinopsis*. Dichotriaenes were found in five species: *S. baiana* sp. nov., *S. megastylifera*, *S. laviniensis*, *S. hajdui* comb. nov., and *S. fenimorea*. However, their shape varies: *S. megastylifera* and *S. laviniensis* have plagiodichotriaenes, while *S. baiana* sp. nov. and *S. hajdui* comb. nov. have orthodichotriaenes (Lévi 1961; Cárdenas et al. 2009; present study). *Stellettinopsis laviniensis* also has distinctive anatriaenes with hair-like rhabdomes, and *S. fenimorea* has rare but exclusive prodiaenes (de Laubenfels 1934). These spicules are quite distinct from each other and their shape appears to be consistent within species, but they must be interpreted cautiously due to the low abundance in some species. For example, the orthotriaenes with curved cladi of *S. capixaba* sp. nov. are exclusive of this species, but due to their extreme rarity, it is uncertain if they are produced by the sponge or artifacts. Plagio-, pro-, and anatriaenes are often very rare and can be easily overlooked; therefore, the presence/absence of any triaene category is not reliable for species distinction in *Stellettinopsis* (Table 2).

The abundance of microscleres seems to be more constant within species of *Stellettinopsis* than that of triaenes, and the morphology of the euasters in SEM is particularly useful for species distinction. Most species of *Stellettinopsis* have two or three categories of euasters, with species-specific combinations of different spicule morphologies (Tables 1 and 2).

Oxyasters are present in at least six species, and two distinct morphologies can be recognized. Oxyaster I is the most common type; it has slender, cylindrical actines with spines often curved inwards and with a spike at the tips (Figs. 5d, 8e, 10e, 12g, and 14f, g). Oxyaster type II has short, stout, conical actines, with small irregular spines and acerate tips (Figs. 5e

Table 3 Comparison between genera *Ecionemia*, *Stellettinopsis* and *Melophlus*. Modified from Kelly and Sim-Smith (2012)

Characters	<i>Ecionemia</i>	<i>Stellettinopsis</i>	<i>Melophlus</i>
Ectosome			
Thickness	Thin (~ 100 µm)	Thick (~ 3 mm)	Thick (~ 3 mm)
Pigmented cells	+	+	–
Aquiferous canals (cavernous)	+	+	–
Crust of acanthomicrohabds	+	+	+
Tangential feltwork of oxeas	–	–	+
Bouquets of oxeas and triaenes	–	+	–
Choanosome			
Architecture	Strictly radial	Disorganized	Disorganized
Megascleres			
Oxeas size categories	3	2	1
Triaenes types	Dicho-/ortho-/plagio-/ana-	Dicho-/ortho-/plagio-/ana-	–
Triaenes abundance	Common	Often rare to absent	–
Microscleres			
Euasters I	Chiasters, tylasters, oxyasters, spherotylasters, spherochiasters	Chiasters, tylasters, oxyasters, spherasters	Spined oxyasters
Euasters II	–	Oxyasters, strongylasters, anthasters	–
Acanthomicrohabds	5–17 µm (max. 52 in 1 sp.), rounded ends	32–138 µm, strongylote or acerate	14–90 µm, 2 categories, stout
Microxeas	–	Smooth	Microspined

+, present; –, absent

and 14f, g); it was found only in *S. hajdii* comb. nov. and *S. capixaba* sp. nov.

Strongylasters accompany the oxyasters in *S. megastylifera*, *S. ruber* comb. nov., *S. baiana* sp. nov., and *S. capixaba* sp. nov., but in *S. ruber* comb. nov. they often show characteristic amphisanidaster-like modifications (Figs. 8e, f, 10f, g, 12h, and 14f, i). Tylasters are only found in *S. fenimorea* and *S. solida*, and *S. cherbonnieri* has anthasters and spherasters (Table 2). Chiasters were reported in *S. corticata* and *S. laviniensis*, but they were not studied through SEM. SEM is essential for the detailed analysis of microscle morphology and must be used for the identification of species of *Stellettinopsis*.

The spicules of *S. cherbonnieri*, *S. laviniensis*, and *S. corticata* (type species of the genus) were illustrated only by *camera lucida* drawings, with poor resolution of microscle morphology (Sollas 1888; Dendy 1905; Lévi 1961). There are no illustrations available of other two poorly known species, *S. euastrum* and *S. fenimorea* (Schmidt 1880; de Laubenfels 1934). It has been suggested that *S. euastrum* could belong to *Erylus* due to the presence of aspidasters (Schmidt 1880; P. Cárdenas, taxonomy note, van Soest et al. 2019c). We agree with this suggestion based on Schmidt's (1868, 1880) descriptions and drawings and we do not consider it a valid species of *Stellettinopsis*, but the type specimen should be revised and its spicules re-examined under SEM before a formal transfer to *Erylus* can be done confidently. *Stellettinopsis cherbonnieri*, *S. laviniensis*, *S. corticata*, and *S. fenimorea* also need detailed

description of euasters and microhabds morphology in SEM to ascertain their taxonomic status.

Nomenclatural problems also hamper the taxonomy of *Melophlus* and *Stellettinopsis*. The rhabdose microcleres of *Melophlus sarasinorum* have been called either “microxeas” or “rough microhabds” by different authors (e.g., Thiele 1899; Brøndsted 1934; de Laubenfels 1954; Bergquist 1965; Uriz 2002; Kelly and Sim-Smith 2012). Here, we distinguish the microhabds by their more irregular, often stout, strongylote or hastate shape, whereas microxeas are longer, slender, and more often acerate. Spines are secondary in this classification: there are species with smooth microhabds and spiny microxeas, although they are rarer than the acanthomicrohabds and smooth microxeas. The microhabds of *Stellettinopsis* species have been called “lumpy raphides,” “acanthomicroxeas,” “spined microxeas,” “spiny microhabds,” and “acanthomicrohabds” by different authors (de Laubenfels 1934; Lévi 1961, 1965; Uriz 2002; Cárdenas et al. 2009; Kelly and Sim-Smith 2012). We used here the term “acanthomicrohabds” because it implies in the presence of dense, small spines making a rugose surface of the spicule rather than long, well-separated spines (Kelly and Sim-Smith 2012).

The euasters of *S. solida* have been described as chiasters/strongylasters by Lévi (1965) and as tylasters, oxyasters, and anthasters by van Soest and Beglinger (2008). Similarly, the asters of *S. laviniensis* were reported as chiasters/oxyasters by Dendy (1905) and Kelly and Sim-Smith (2012) and called

strongylasters by Lévi (1961). The standardization of spicule nomenclature based on SEM analysis is essential for the taxonomy of *Stellettinopsis*, which would also benefit from an integrative taxonomic approach including molecular data. There are few DNA sequences of *Stellettinopsis* species available in GenBank, but these can be useful for species delimitation in the genus as well as for phylogenetic analysis (Cárdenas et al. 2009, 2011; Redmond et al. 2013).

Morphological distinction between astrophorine genera: the case of *Melophlus*, *Stellettinopsis*, and *Ecionemia*

Historically, spicule shape and size have been the main morphological characters used to differentiate astrophorine genera, especially in the family Ancorinidae (reviewed by Uriz 2002). Earlier authors placed more emphasis on the presence or absence of cortex (e.g., Sollas 1888; Topsent 1894), but the skeletal arrangement has been later considered as adaptive and of little use for taxonomy (Hajdu and van Soest 1992). Many authors thus emphasized the importance of triaenes and microscleres geometry and ornamentation over the skeletal architecture (e.g., Bergquist 1965; Hajdu and van Soest 1992; Uriz 2002). The presence of triaenes, microrhabds, and sanidasters was used to distinguish *Melophlus* from *Stellettinopsis*, and between *Asteropus*, *Stryphnus*, and *Ancorina* (e.g., Hajdu and van Soest 1992; Uriz 2002; Carvalho 2008). However, triaenes can be very rare in species of *Stellettinopsis* and *Stryphnus* (Kelly and Sim-Smith 2012; present study). These rare spicules have been easily overlooked by taxonomists in the past, leading to misidentifications and adding noise to classifications by confounding rarity of spicule types with absence or “secondary losses.”

Our revision showed that the genera *Stellettinopsis* and *Melophlus* have often been confounded in the southwestern Atlantic due to the extreme rarity of triaenes in some species of *Stellettinopsis* (Kelly and Sim-Smith 2012). It was only after exhaustive searching that we were able to determine their certain presence in *Melophlus ruber* and *Melophlus hajdui*, suggesting their transfer to *Stellettinopsis*. This change is also supported by the ectosomal bouquets of oxeas presented by both species, typical of *Stellettinopsis*, and by their long acanthomicrorhabds (Kelly and Sim-Smith 2012).

Equally exhaustive searches were required to convince us of the true absence of triaenes in *Melophlus sarasinorum*. Eventual generic assignment was confirmed, however, by differences in their skeletal arrangement, especially the presence of ectosomal bouquets of oxeas in *Stellettinopsis* versus a dense feltwork of large oxeas in the ectosome of *Melophlus* (Table 3). Thus, using skeletal architectural differences negates the need for using the presence or absence of triaenes as a key character.

In agreement with previous morphological studies, we found that microsclere shape is also useful for distinction between Ancorinid genera (Uriz 2002; Kelly and Sim-Smith 2012). We have shown that *Melophlus* has two categories of acanthomicrorhabds and one of microspined microxeas, whereas species of *Stellettinopsis* have only one category of long acanthomicrorhabds and sometimes microxeas (Kelly and Sim-Smith 2012; Table 3). Our data support the view of Kelly and Sim-Smith (2012) that these genera are better recognized by the skeletal organization and microsclere geometry and ornamentation than on the potentially misleading presence versus absence of triaenes, microrhabds, or sanidasters. This applies not only to the genera *Melophlus*, *Stellettinopsis*, and *Ecionemia*, but also to many other genera of the suborder Astrophorina, especially the ancorinids like *Stryphnus* and *Ancorina*.

The combination of microsclere geometry and skeletal organization supports the distinction and validity of *Melophlus*, *Ecionemia*, and *Stellettinopsis* (Table 3). *Ecionemia* shares with *Melophlus* the presence of microrhabds at the surface, but it has a radial choanosomal skeleton (Kelly and Sim-Smith 2012). *Stellettinopsis* and *Ecionemia* are very similar and have been considered synonyms (Uriz 2002). However, *Ecionemia* can be distinguished from *Stellettinopsis* by a strictly radial choanosomal skeleton (vs. paratangential to oblique), and short acanthomicrorhabds (vs. long in *Stellettinopsis*; Table 3; Kelly and Sim-Smith 2012; present study).

Our transfer of two species of *Melophlus* to *Stellettinopsis* makes *Melophlus* a monotypical genus restricted to Indo-Pacific waters and clearly distinct from all other ancorinid (and geodiid) genera by its ectosomal feltwork of oxeas, two categories of acanthomicrorhabds, and microspined microxeas. The genus *Stellettinopsis* now has 10 species (excluding *S. euastrum*), of which seven occur in the Tropical Western Atlantic (Fig. 6, Table 2). All of them possess common to rare triaenes, oxeas, euasters, long acanthomicrorhabds, and ectosomal bouquets of oxeas.

Higher classification of *Melophlus* and *Stellettinopsis*

Traditional morphological studies usually place *Melophlus*, *Ecionemia*, and *Stellettinopsis* in the family Ancorinidae, based on skeletal arrangement and the shared presence of spiny microrhabds and euasters (Hajdu and van Soest 1992; Uriz 2002; Kelly and Sim-Smith 2012). However, molecular studies based on three independent markers, one mitochondrial (COI) and two nuclear (18S and 28S rRNA), support the placement of *Melophlus* and *Ecionemia/Stellettinopsis* (in part) in the family Geodiidae (Cárdenas et al. 2011; Redmond et al. 2013). This classification implies in the assumption of extensive homoplasies and secondary losses in many morphological characters, especially the aspidasters and sterrasters which are synapomorphic for the two subfamilies of Geodiidae, Geodiinae and Erylinae. The inclusion of *Melophlus* in Geodiidae also makes the family more

heterogeneous, reflecting its likely non-monophyly (Chombard et al. 1998; Cárdenas et al. 2011). Although this transfer had relatively good bootstrap and some additional biochemical support, it was based on a single undescribed and unidentified specimen of *Melophlus* sp., which was neither a type specimen nor belongs to the type species of the genus, *M. sarasinorum* (Cárdenas et al., 2011). We consider that this specimen is probably not a good representative of the genus, to the point of formally basing its transfer to another family. That does not negate, however, the hypothesis that *Melophlus* could be an *Erylus* that lost its aspidasters, which should be further investigated before it can be incorporated in the classification.

Some species of *Ecionemia* have also been shown to group with Geodiidae based on COI, 28S and 18S rRNA sequences, and were thus included in the Geodiinae^P PhyloCode clade (Cárdenas et al. 2011): *Ecionemia megastylifera*, *E. alata*, and *E. robusta* (Cárdenas et al. 2011; Redmond et al. 2013). However, other species such as *E. acervus* (type species of *Ecionemia*), *E. demera*, and *E. walkeri*, with small sanidaster-like microrhabds, are considered closer to the Ancorinidae^P (Cárdenas et al. 2011). The Geodiinae^P clade also includes species of *Jaspis* and *Stelletta*, and *Ecionemia robusta* clusters first with three species of *Stelletta* rather than with *Geodia* (Cárdenas et al. 2011). Posterior taxonomic changes such as the resurrection of *Stellettinopsis* and the transfer of *E. robusta* to *Ancorina* make the interpretation of these molecular phylogenetic trees less straightforward, and most authors currently classify *Ecionemia* and *Stellettinopsis* in the family Ancorinidae (Uriz 2002; Cárdenas et al. 2011; Kelly and Sim-Smith 2012; van Soest et al. 2019a). The skeletal arrangement and spicule composition of the species described here support the placement of *Melophlus* and *Stellettinopsis* in Ancorinidae, contrary to molecular data but in agreement with previous morphological revisions (Uriz 2002; Kelly and Sim-Smith 2012).

The phylogeny of the suborder Astrophorina is still highly controversial and the families Ancorinidae and Geodiidae as currently understood are probably polyphyletic, based on either genetic or morphological evidence. We suggest that *Melophlus*, *Ecionemia*, and *Stellettinopsis* should be kept in the family Ancorinidae, but this classification is questionable due to the incongruences between molecular and morphological characters and to the high level of morphological homoplasy found in the suborder (Cárdenas et al. 2011; Redmond et al. 2013). Future studies should integrate detailed morphological observations and a larger number of genetic markers in phylogenetic analyses based on type specimens and type species whenever possible, to achieve a more stable and natural classification of the Astrophorina.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval No animal testing was performed during this study.

Sampling and field studies All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgments when applicable.

Data availability Data sharing is not applicable to this article as no datasets were generated or analyzed during the current study.

Author contribution statement JS and UP conceived and designed research. JS and JL conducted experiments. JS and GM analyzed data. JS wrote the manuscript. All authors read and approved the manuscript.

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