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Seven new species of sponges (Porifera) from deep-sea coral mounds at Campos Basin (SW Atlantic)

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Abstract

Deep-sea reefs and coral banks are increasingly known as highly biodiverse ecosystems where sponges constitute a significant proportion of builders and inhabitants. Albeit smaller in dimensions, Campos Basin coral mounds also harbor a rich associated fauna, whence only 16 species of sponges had been fully identified this far. Seven new species are described here, viz. *Geodia garoupa* sp. nov., *Vulcanella stylifera* sp. nov., *Trachyteleia australis* sp. nov., *Echinostylinos brasiliensis* sp. nov., *Xestospongia kapne* sp. nov., *Sympagella tabachnicki* sp. nov., and *Leucopsacus barracuda* sp. nov. Of the 24 species of sponges known from the area, only seven were found elsewhere too, thus suggesting a possible high endemism in Campos Basin. Nevertheless, the widespread occurrence of deep reef-framework building corals along a large sector of the Brazilian coast suggests these habitats and their associated fauna may be more widespread than currently appreciated. *Echinostylinos patriciae* nom. nov. is proposed for the New Zealand record of *E. reticulatus*.

Keywords: Demospongiae, Hexactinellida, New species, Deep-water, Slope, Brazil

Background

Knowledge of the deep sea sponges occurring off Brazil was gained over two important periods, firstly from the H.M.S. Challenger expedition of 1873–1876, and secondly, from a still ongoing effort, that started over 100 years after the first, when a series of, mostly improvised, research ships went off for the first dredgings planned under Project REVIZEE in 1997. This project organized several oceanographic expeditions until 2002, to be followed by Petrobras' own efforts through several environmental assessment projects, namely OCEANPROF, CAP-BC, ECOPROF and HABITATS. The latter have focused on Campos Basin, Brazil's main oil producing grounds, and were a response to the country's environmental authorities' request for good quality baseline data to support any future need for the evaluation of environmental impacts in Campos Basin. Similar efforts are expanding now to the north (e.g. Espírito Santo and Potiguar Basins) and south (Santos Basin). Preliminary results on the sponges present in these deep sea collections were published by Hajdu [27], Hajdu and Lopes [28], Hajdu et al. [30], Lavrado and Ignacio [42], Lopes and Hajdu [57, 58], Lopes et al. [59–61], Menshenina et al. [64], Muricy et al. [65, 66], Oliveira and Hajdu [68], Rodriguez and Muricy [78], Tabachnick et al. [90], Vieira et al. [107].

The present study reports seven new species collected in the deep waters of Campos Basin (off southeastern Brazil), including the first record of *Trachyteleia* [96], *Echinostylinos* [95], and *Leucopsacus* [35] for the South Atlantic Ocean.

Methods

Campos Basin covers more than 100,000 km^2 between the Vitória High (20.5°S) and the Cabo Frio High (24°S) on the Brazilian continental margin. Over 70 % of it lies in depths >200 m [13], and over 85 % of Brazilian crude oil and gas originates from this region. In 2003 PETROBRAS initiated a series of research projects for assessing environmental baseline data. The materials studied here were collected by box-corers, trawls and ROVs,

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between 744 and 1931 m depth, and are part of the outcome of three umbrella research projects coordinated by CENPES/PETROBRAS: Campos Basin Deep-sea Environmental Project (OCEANPROF), Campos Basin Deep-sea Coral Assessment Project (CAP BC), and Campos Basin Environmental Heterogeneity (HABITATS).

Specimens were identified through the preparation and analysis of dissociated spicules and thick-section mounts, which followed procedures described in [31] for Demospongiae, and [37], for Hexactinellida. The scanning electron microscopes (SEMs) used were a JEOL JSM-6460 LV and a ZEISS DSM-940A from CENPES/PETROBRAS, and a JEOL-6390 LV from Departamento de Invertebrados of Museu Nacional/UFRJ. The newly generated micrometric data for the calculation of means, unless stated otherwise, are derived from 25 spicules of each category for the hexactinellids, and 20 for demosponges, followed by an exhaustive search for maximum and minimum values of length and thickness. The descriptions generated were compared with a tabulation of micrometric, as well as geographic and bathymetric distribution data for all known species in the genera considered, except for *Geodia garoupa* sp. nov., compared only to species from the South Atlantic, the South Eastern Pacific and the Antarctic. Taxonomic authorities are listed in the comparative tables next to the species considered. Accordingly, they are not referred to in the text.

Following is a list of the abbreviations used and their meanings: CAP BC—Campos Basin Deep-sea Coral Assessment Project; CENPES—PETROBRAS' Research and Development Center, Rio de Janeiro, RJ, Brazil; HABITATS—Campos Basin Environmental Heterogeneity; MNRJ—Porifera Collection, Museu Nacional, UFRJ, Rio de Janeiro, RJ, Brazil; OCEANPROF—Campos Basin Deep-sea Environmental Project; PETROBRAS—Petróleo Brasileiro S.A., Brazil; UFRJ—Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil.

Results

SYSTEMATICS
Class DEMOSPONGIAE Sollas, 1885
Order TETRACTINELLIDA Marshall, 1876
Suborder ASTROPHORINA Sollas, 1887
Family GEODIIDAE Gray, 1867
Subfamily Geodiinae Sollas, 1888
Genus *Geodia* Lamarck, 1815
G. garoupa sp. nov.
(Fig. 1; Tables 1, 2)

Type material

Holotype: **OCEANPROF 1, BC-SUL**. MNRJ 7349, stn. 4 (Campos Basin, RJ, 22.366°S–39.893°W), 1130 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 07.ii.2003.

Paratypes: **OCEANPROF 1, BC-SUL**. MNRJ 7348, 7355, stn. 4 (Campos Basin, RJ, 22.366°S–39.893°W), 1130 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 07.ii.2003. **HABITATS 1.** MNRJ 14077, trawl 1 (Campos Basin, RJ, start 23.050°S–41.851°W, end 23.775°S–40.981°W), 1931 m depth; coll. R/V 'Gyre', demersal fisheries net, 03.iv.2008. MNRJ 14082, trawl 62 (Campos Basin, RJ), 1244.4 m depth; coll. R/V 'Gyre', demersal fisheries net, 29/iv/2008.

Diagnosis

Only *Geodia* in the Southwest Atlantic and Antarctica with two categories of oxeas, a single category of orthotriaenes tending to dichotriaenes (with or without bifurcated cladomes in different stages of development), plagiotriaenes, and sterrasters always larger than 100 µm.

Description

Habit irregularly massive, cushion-shaped, globular. The holotype (Fig. 1a) is the largest specimen, 7.4 cm in maximum diameter and 4.2 cm thick. Surface hispid, with spicules protruding 1–3 mm in some areas, and possibly removed from most of the surface by damage during trawling. Simple oscules with ~0.5 mm in diameter, pores scattered throughout the surface. Color alive is beige (MNRJ 14082). Consistency hard, but compressible.

Skeleton

Ectosomal skeleton, 1000–1750 µm thick, with small oxeas in the outer surface and a thin layer of small strongylasters, followed by a thick layer of sterrasters supported by the cladomes of the triaenes. The subectosomal region, underneath the cladomes, has large oval canals 308–1525 µm in diameter, with large oxyasters around. Choanosomal skeleton with dense, ascending, and multispicular tracts of oxeas and triaenes (Fig. 1b). Oxyasters and sterrasters are scattered in the skeleton.

Spicules (Table 1)

Oxeas I (Fig. 1c), large, similar to the small ones, tapering gradually, with 1014–3000 µm in length and 50–75 µm thick. Oxeas II (Fig. 1d), small, straight, occasionally curved, tapering abruptly, with 195–227 µm in length and 10–12 µm thick. Orthotriaene (Fig. 1e), with a large size range, small cladomes, with the tips bent down, usually modified to dichotriaenes, with vestigial deuterocladi, 150–300 × 50–100 µm; long, cylindrical rhabdomes, with tips gradually tapering, 1250–3275 µm in length and 50–275 µm thick. Plagiotriaenes (Fig. 1f), very rare and thin, almost always broken, and thus difficult to measure correctly. Anatriaenes (Fig. 1g), found only in the holotype (MNRJ 7349, n = 3), and two paratypes (MNRJ 14077, 14383; n = 1), also very rare and always

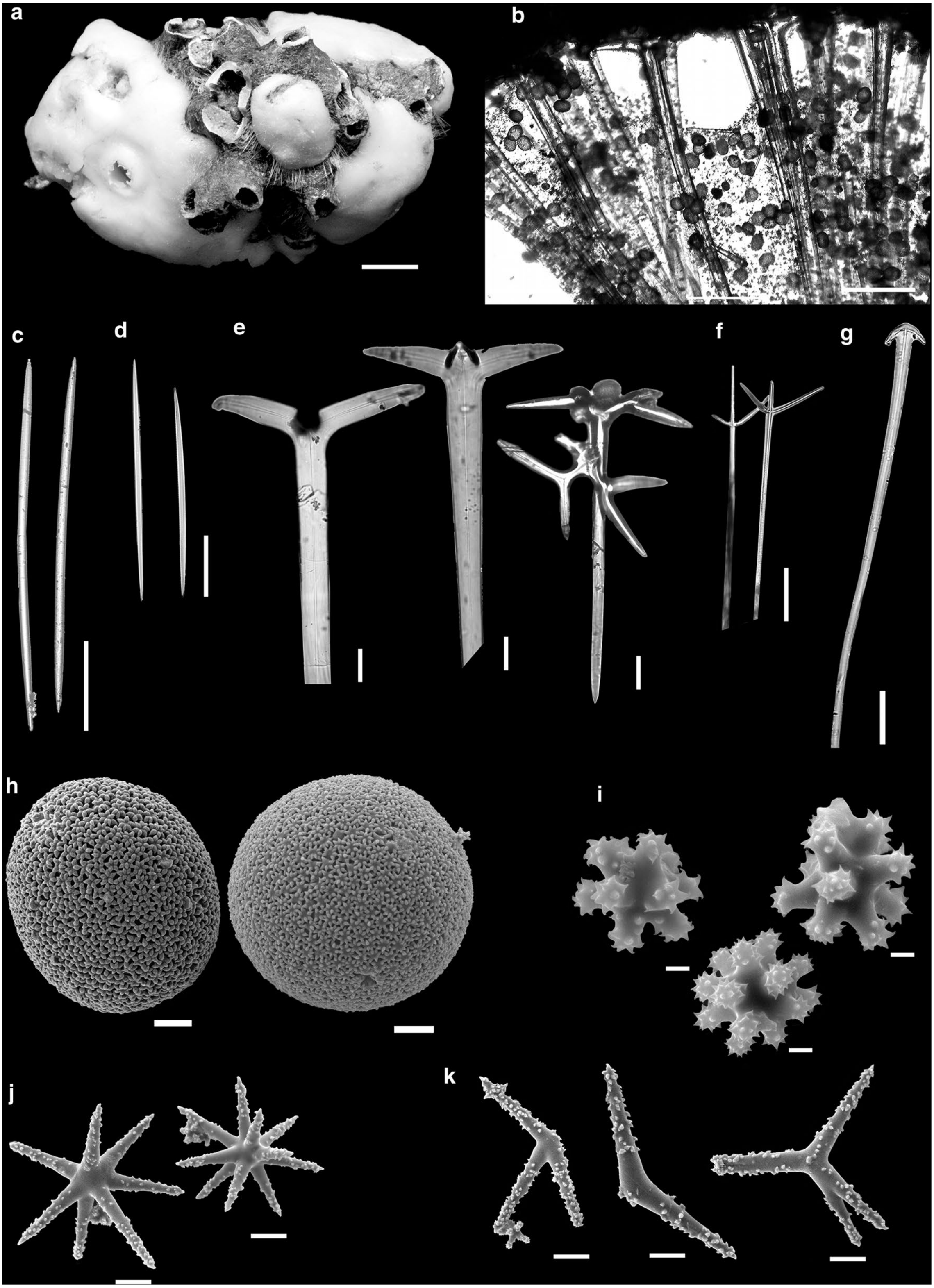


Fig. 1 *Geodia garoupa* sp. nov. **a** Holotype (MNRJ 7349). **b** Skeleton. **c** Oxeas I. **d** Oxeas II. **e** Ortho/Dichotriaenes. **f** Plagiotriaenes. **g** Anatriaene. **h**–**k** SEM of the spicules: **h** Sterrasters. **i** Strongylasters. **j** Oxyasters I. **k** Oxyasters II. *Scales* **a** = 10 mm; **b**, **c** = 500 µm; **d**–**g** = 100 µm; **h** = 20 µm; **i** = 2 µm; **j**, **k** = 10 µm

Table 1 Spicule measurements for *G. garoupa* sp. nov. Minimum — mean — maximum length/width, in µm

	MNRJ 7349 (holotype)	**MNRJ 7348 (paratype)**	**MNRJ 7355 (paratype)**	**MNRJ 14077 (paratype)**	**MNRJ 14082 (paratype)**
Oxeas	I. 1014–2100–2650/50–63–71 II. 201–210–222/10–11–12	I. 1265–2119–2500/50–63–71 II. 195–208–221/10–11–12	I. 1050–2419–3000/50–67–75 II. 220–225–227/10–11–12	I. 2889–3520.7–3918/34–42.2–48 II. 252–310.4–349/5–5.8–7	I. 1287–1790.4–2145/34–38.8–44 II. 262–474.3–718/10–12.2–14
Ortho/dichotriaene	r: 1250–1744–2878/99–120–140 c: 291–381.2–582/cl: 485–693.5–805	r: 1600–2670–3275/50–187–200 c: 281–392.8–543/cl: 504–684.8–873	r: 2789–2990–3100/52–176–275 c: 213–392.4–601 cl: 465–696.9–854	r: 2402–2885.7–3232/72–100.9–116 c: 301–483.5–669 cl: 698–848.7–970	r: 1725–1865–2125 (n = 5)/61–109.3–144 c: 291–379.2–436 (n = 11) cl: 630–759.8–912 (n = 9)
Plagiotriaene	r: n.r./7.5 (n = 1) c: 60 (n = 1) cl: 110 (n = 1)	r: > 3750/12–20 (n = 7) c: 75–130 (n = 7) cl: 90–270 (n = 7)	r: n.r./15 (n = 1) c: 130 (n = 1) cl: 150 (n = 1)	n.r.	r: n.r./12.5 (n = 1) c: 50 (n = 1)
Sterraster	123–130–137	130–139–144	133–140–144	108–116.4–123	126–136.5–155
Additional euasters	Ox I. 25–45.7–70 Ox II. 50–63.2–90 St. 6–8–10	Ox I. 15–40.5–65 Ox II. 30–48.0–90 St. 6–11–15	Ox I. 25–44.2–65 Ox II. 55–64.5–90 St. 6–9–15	Ox I. 20–31.9–50 Ox II. 25–42.5–75 (n = 4) St. 6–7.8–10	Ox I: 17–27.7–55 Ox II: 22–31.2–40 (n = 6) St. 6–8.8–12

r. rhabdome, *c.* clade, *cl.* cladome, *Ox.* oxyaster, *St.* strongylaster

broken; rhabdome 14.5–25 µm thick, cladi 29–50 µm, and cladome 68–85 µm. Sterrasters (Fig. 1h), spherical to oval, with rays finished by rosettes formed by 4–8 cylindrical actines, 123–144 µm in diameter. Strongylasters (Fig. 1i), small, with 6–12 short and thick rays, strongly spined mainly at the extremity, enlarged centrum, 6–15 µm in diameter. Oxyasters I (to sphaeroxyasters) (Fig. 1j), 8–14 slender and microspined rays, 15–70 µm in diameter. Oxyasters II (Fig. 1k), irregular, with rounded tips, 2–6 microspined rays, 22–90 µm in diameter, very rare, although more abundant in the holotype.

Habitat and distribution

The preserved specimen is attached to a fragment of the coral *Solenosmilia variabilis* Duncan, 1873. Provisionally endemic from the bathyal zone (1130–1931 m depth) at Campos Basin (SE Brazil).

Etymology

The name *garoupa*, the Brazilian term for the fish grouper, is used here as a noun in apposition to honor the research vessel, R.V. 'Astro Garoupa', on board which OCEANPROF's materials were collected, the holotype of the new species included.

Remarks

The South Atlantic, South Eastern Pacific and Antarctica harbour 27 species of *Geodia* (Table 2) according to [105], to which our proposed new species is compared here. Only six of these were reported to bear dichotriaenes, namely *australis*, *libera*, *magellani*, *perarmata*, *robusta*, and *stellata*. *Geodia australis* is the only of these with oxeas comparably long and thick, but differs from the new species by its possession of protriaenes, as well as very large sterrasters 266–352 µm in diameter. The remaining five species all have considerably larger oxeas than observed in the new species, with the exception of *libera*, which, instead, has much thinner oxeas. Several other distinctive traits permit further differentiation among these species, a notorious characteristic of species of *Geodia* and their unusually rich set of morphologic characters. However, one species stands out for its lack of sufficient comparative data to allow a clearcut diagnosis, namely *G. cf. reniformis* [92] (sensu [98]). No megasclere was associated to this species, thus demanding analysis of its microscleres. The reported two categories of oxyasters, one of spherasters and one of strongylasters (chiasters), differ substantially from the two oxyasters and one strongylaster found in the new species. In addition, while both categories of oxyasters in the new species customarily reach over 50–60 µm, in the Namibian species the smallest category is smaller than 30 µm.

Family VULCANELLIDAE Cárdenas, Xavier, Reveillaud, Schander & Rapp, 2011
Genus *Vulcanella* Sollas, 1886
Vulcanella stylifera sp. nov.
(Fig. 2; Tables 3, 4)

Type material

Holotype: **OCEANPROF 1, BC-SUL**. MNRJ 7343, stn. 4 (Campos Basin, RJ, start 22.407°S–39.921°W–end 22.366°S–39.893°W), 1128–1135 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 07.ii.2003.

Table 2 Comparative table of spicular micrometries for the species of *Geodia* of the South Atlantic Ocean, Magellan Region and Antarctic

	Oxeas Styles (S) Strongyles (Sg)	Triaenes	Sterrasters	Additional microscleres	Distribution/depth (m)
G. australis Silva & Mothes, 2000	I. 1403–3818/23–40 II. 180–418/3–7	Di = r: 1012–2246–3565/33–61–85; cl: 333–553.8–703 p: 161–192.1–238; d: 76–107.2–143 An = r: 1150–3450–6140/4.8–14.2–24 cl: 67–130.9–190; c: 48–110.6–181 Pr = r: 1334–3143.9–5865/4.6–10.4–23 cl: 86–154.2–276; c: 67–156.4–276 Pl (rare) = r: 828–1909/19–29; cl: 105–219/51–131	266–314.8–352/190–253.6–295	Sp: 20–26.3–32 Ox I. 35–43.2–52 Ox II. 16–23.7–32 So: 14–16.1–20 St: 4.6–7–9.2	Brazil/207–284
G. basilea Lévi, 1964	6000–9000/10	Or = r: 5200–5500/120–130 c: 700–900/100 An or Pr = r: 8000/30–35	135–140/105–110	Ox: 20–30 So: 14–16	South Africa/430
G. corticostylifera Hajdu, Muricy, Custodio, Russo and Peixinho, 1992	I. 335–2034/12–34 II. (S): 251–432/3.8–8.8	Or = r: 372–801–1116/11–17.2–25; c: 32.5–149–245	20–39.8–50	Ox I: 11–17.6–25 Ox II: 5–6.8–8	SE Brazil and Venezuela/3–82
G. cydonium (Jameson, 1811) sensu Hentschel [1929, as *G. mülleri* (Fleming, 1818)]	2000–4300 + rare styles	Or = r: 1600–4250; c: 240–470 An = r: 3300–6400; c: 31–170 Pr = r: 3000–5000 + assorted morphotypes	57–80	Ox: 20–51 Ox–Sp: 7–22 St: 16–36 St–Ty: 4–10	NE Atlantic, W Mediterranean, West Africa/20–400 (Burton, 1956, 1959)
G. dendyi Burton, 1926	1980/44	Or = r:1080/56; c: 240	140/120/100	Sp: 12–20 Ox: 32–44 (rays)	South Africa/91.5–549
G. gallica Von Lendenfeld, 1907	I. 2000–4500/30–180 II. (with central actines) 4000–6000/50–70 (S) 2300–3800/100–160 (rare)	Or, Pl^{a} = r: 3000–4500/60–130; cl: 300–770 An = r: 5000–9000/14–38; c: 40–80; cl: 80–115	68–125	Sp: 8–14 Ox: 10–20 Ox II: 58–68 mO: 90–140/3–5.5 mS: 60–78/4–5.5 mT: 34–77/4–6	South Africa/84
G. geodina (Schmidt, 1868) sensu Topsent (1938)	2200–2400/20–25	Or = r: 1250/16–18; c: 200–300	40–45	Ox I: 30 Ox II: 15–17	NE Atlantic, W Mediterranean, West Africa/32–95
sensu Sollas (1888, including the types)	2755/22	Or = r: 1420; c: 340	41	Ox: 56 Sp: 15	
sensu Lévi and Vacelet (1958)	2000/22–30	An = r: 1400; c: 35; cl: 60 Pl = r: >1000; c: 200	50	Ox I: 55 Ox II: 25 Sp: 14	
G. gibberosa Lamarck, 1815 sensu Silva, (2002, including schizo-holotype)	I. 250–3200/2.5–43 II. 100–437/2–8	Or = r: 290–3200/9–40; cl: 65–210; c: 21–304	29.5–108	So I:9.5–34.2 So II: 12.5–17.9 St: 2–12 Ox: 10–35.8	S and C Atlantic/0.5–72

Table 2 continued

	Oxeas Styles (S) Strongyles (Sg)	Triaenes	Sterrasters	Additional microscleres	Distribution/depth (m)
G. glariosa (Sollas, 1886) sensu Silva (2002, including sintype)	I. 503–1856/4.6–26 II. 218–522.5–4.8–28	Or = r: 1012–2856/23–52; cl: 143–646; c: 127–242 An = r: 1357–5319/6.9–21; cl: 34–117; c: 21–60 Pl = r: 483–2024/9–30; cl: 85–475; c: 48–230 Pr = r: 943–6086/6.9–23; cl: 114–351; c: 23–85	23–67	Ox: 9.2–26 Sp: 13–16 St: 6–10	Brazil/ <13–47.7
G. globosa (Baer, 1906)	I. 173–192/3 II. 183–722/7–18	Or = r: 703–1165/15–29; c: 62–246/14–15	37–62	Ox: 14–37 St: 3–4	South Africa
G. libera Stephens, 1915 sensu Lévi (1969)	2000–3000/20–27	Di = r: 2000–2500/50–65; p: 50–80; d: 35–110 An = r:/7; cl: 30–45 Pl = r: 400/7; c: 10 (probably small dicho)	60–70	Ox and So: 20–50 Chi: 8	South Africa/91.5
G. littoralis Stephens, 1915 sensu Lévi (1967)	I. 2000–3000/50–55 II. 225–325/4	Or = r: 1800–3000/30–45; c: 200–300 An = r: 3000–3500/10–15; cl: 90–95; c: 65–90 Pm = r: >3000/18–20; c: 35–120	75–85	Ox: 10–17 So: 13 Micraster: 0.5–4	South Africa/2
G. littoralis Stephens, 1915 sensu Samaai and Gibbons (2005)	2800–3280/70	Or = r: 3820–4200/72 An = r: 5000–5600/18 Pm = r: 6400/18	228–364/5	Ox I: 46–55 Ox II: 25–35 Ox III: 14 Micraster: 4–9	South Africa/ 2–25
G. magellani (Sollas, 1886) sensu Silva (2002, including the types)	2000–5710/45–65	Di = r: 3358–4950/58–119; p: 76–133; d: 142–323 An = r: 5730–8100/17–27; cl: 160–175; c: 110–130	92–135/69–106	Ox: 10–18 So: 18–24 St: 9.5–13	S Brazil, Magellan Region/81–450
G. megaster Burton, 1926	I. 4500/720 II. 120–450 (microxeas)	Or = r: 4140/72; c: 720/72 An = r: 24 (thick); c: 80 Pm = r: 24 (thick); c: 120	240/200/180	Sp: 4–8 St: 16–20 Ox: 40–60 (rays)	South Africa/91.5
G. ovifractus Burton, 1926	I. 6300/900 II. 280/4 (microxeas)	Or = r: 6300/144; c: 1980/126	670/520/520	Sp: 16–20 Ox: 16–20	South Africa/91.5
G. papyracea (Hechtel, 1965) sensu Silva (2002, including the types)	I. 580–1230.7/7.5–45 II. 60–223/2–12	An = r: 245–1030/2–9.6; cl: 12–60; c: 7–37 Pl = r: 280–1026/5–43; cl: 29–318; c: 11–172	28–94	Ox I: 14–48 Ox II: 12–37 St: 2.5–10	C Atlantic and Brazil/0–5

Table 2 continued

	Oxeas Styles (S) Strongyles (Sg)	Triaenes	Sterrasters	Additional microscleres	Distribution/depth (m)
G. perarmata Bowerbank, 1873 sensu Burton, 1926	I. 2000–6500/37–65 II. 2250–2800/5–8	Di = r: 2060–6800/64–170; cl: 400–600 An = I = r: 2400–11,500; c: 25–150 II = 2250–2800/slender than oxeas II Pr = r: 1100–3600; c: 25–140	75–130 108–185/100–135/100–126	Sp: 24–50 Ox: 13–50 St: 5–15	Indian Ocean/33–46
G. ramosa (Topsent, 1928)	2000/40	Or = r: 1500/55; c: 300–385 An =/10–15	80/60	Ox: 20–40 Sp: 12–16	Azores, Canary Isls., and W Africa/400
G. riograndensis Silva and Mothes, 2000	I. 2415–5721–8464/12–23 II. 1610–2082–2726/21–46 III. 247–487–741/5.7–11	Or = r: 1725–2819.8–3675/44–66.5–92 cl: 575–775.3–989; c: 253–365.4–437 An = r: 4501/9.5–12; c: 19–38 (rare) Pl (rare) = r: 1495–1886/28–39; cl: 460–506; c: 230–253 Pr (rare) = r: 3030–5282/9.5–19; cl: 95–204; c: 62–124 Pm (rare) = r: 2484–3404/9.5–19; c: 52–105 Am = r: 5937–7581/9.5–14.2; c: 19–38 Dn (rare) = r: 184/17; c: 157	57–98.1–124/48–89.9–114	Ox I: 64–86.4–117 Ox II: 14–20–30 St: 4.6–8.4–13	Brazil/200–300
G. robusta Lendenfeld, 1907	2600–6500/25–65 (and strongyles) Rare and smaller styles	Di = r: 4000–6800/120–170; p: 100–150; d: 140–300 An = r: 9000–11,500/10–53; c: 70–150; cl: 80–150 Pd = r: 7 (thickness); c: 100–130 Pm–Pmd = r:70–100/8–10; cl: 88–95	160–175(185)/135–155/110–120	Ox: 20 (rare) and 23–34 Ty: 4–12	South Africa/84
G. senegalensis Topsent, 1891 sensu Lévi (1952)	I. 950–1400/15 II. 180	Pl = r: 520–850/30; c: 100–150	60–80	Ox: 10–20 Sp: 5–6	Senegal
G. splendida Silva and Mothes, 2000	I. 2254–2681–3151/28–62 II. 228–432.7–684/5.7–19	Or = r: 3266–3689–4094/104–111.6–120 cl: 920–1165.7–1495; c: 437–589.8–759	95–148.2–171/86–119.7–152	Ox I: 78–100.1–131 Ox II: 12–17.9–23 St: 5.5–7.4–9.9	Brazil/201–520
Geodia sp. as *G.* cf. *reniformis* Thiele, 1898 sensu Uriz (1988)			135–153/100–110	Ox I: 30–70 Ox II: 18–26 Sp: 13/18 Chi: 5–8	Namibia/183

Table 2 continued

	Oxeas Styles (S) Strongyles (Sg)	Triaenes	Sterrasters	Additional microscleres	Distribution/depth (m)
G. stellata Lendenfeld, 1907	I. 11,000–13,000/35–50 II. 5000–7000/60–80 (95) III. 3000–4000/50 (S) 230–280/4–8	Di = r: 6000–7000/100–170; cl: 680–1000; p: 200–350; d: 200–350 An = I (upper part) = r: 11,000–14,000/18–45; c: 180–250; cl: 160–230 II (base) = 13,000–15,000/22–35; c: 100–140; cl: 130–180 III (rare) = r: 320/1.5 (5); c: 5; cl: 7 Pm (or promesodiaene) = r: 6000/15–30; c: 140–230; cl: 140–180	105–120/85–95/70–75	St I: 19–30 St II: 5–10 Sp: 16–21 Ox: 12–50 mO (rare): 110–135/4–5	South Africa/84
G. tylastra Boury-Esnault, 1973 sensu Silva (2002, including the types)	590–1020/9–19	Or = r: 530–966/6–18; cl: 140–430; c: 75–171	25–85	Ox: 11–27 Ty: 8–19	Brazil/23–94
G. vestigera (Dendy, 1924) sensu Koltun (1964)	I. 1900/20 II. 2000/120 III. 480/17	Or = 1400/25 (vestigial triaenes, represented by styles and abnormal forms)	140/120	Ox I: 64 Ox II: no measures St I: 24 St II: 12	Antarctic/19–252
G. vosmaeri (Sollas, 1886) sensu Silva (2002, inlcuding the types)	I. 636.5–1600/6.9–25 II. 55–370/1–11	Or = r: 500–2120/9.2–37; cl: 75–410	25–70	Ox: 11–30 So: 10–25 St: 4–9	C Atlantic and Brazil/0.2–640

Geodia sp. as *G.* cf. *reniformis* Thiele, 1898 sensu Uriz (1988)—probably the slides prepared by the author were part of a sieve area (according to the author)

Values are expressed in µm, as minimum − mean − maximum length/width value whenever available. n.r., not reported. Data are from original descriptions, unless stated otherwise

Or orthotriaene, *Di* dichotriaene, *An* anatriaene, *Pl* plagiotriaene, *Pr* protriaene, *Di* diaene, *Pm* promesotriaene, *Pd* prodiaene, *Pmd* promesodiaene, *Am* anamesotriaene, *r* rhabdome, *p* protocladi, *d* deuterocladi, *cl* cladome, *c* cladi, *mO* microxea, *mS* microstrongyle, *mT* microtylostyle, *Ox* oxyaster, *Sp* spheraster, *So* sphaeroxyaster, *St* strongylaster/sphaerostrongylaster, *Chi* chiaster, *Ty* tylaster, *Sp* sphaeroxyaster

[a] With modifications in mesoprodiaene, mesoplagiotriaene, mesodiaene, mesoplagiotriaene, and other malformed triaenes, with more than one cladome (Lendenfeld, 1907; Taf. XXXII)

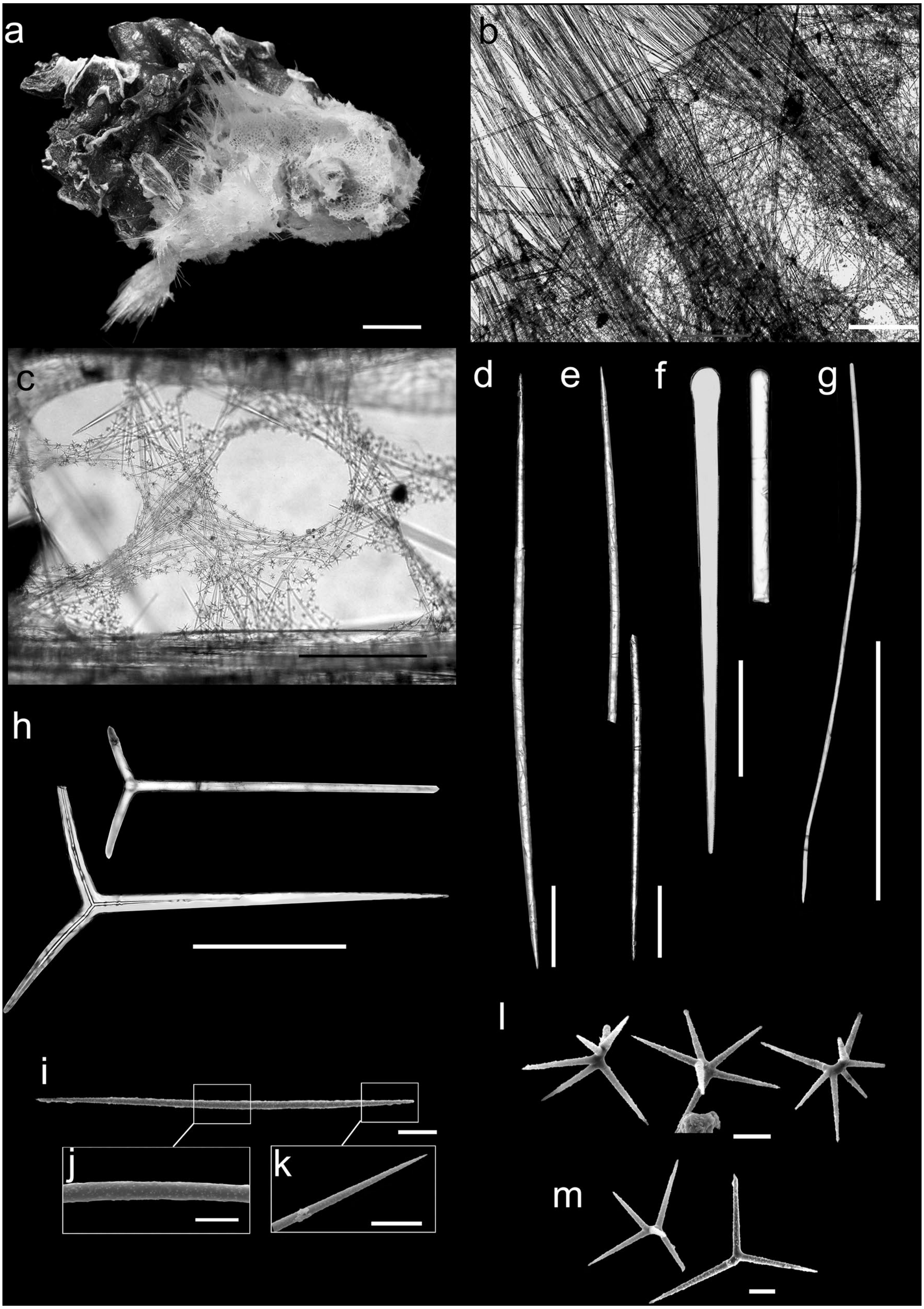


Fig. 2 *Vulcanella stylifera* sp. nov. **a** Holotype (MNRJ 7343). **b** Ectosomal skeleton. **c** Choanosomal skeleton showing the detail of the openings of the aquiferous system. **d** Oxea I. **e** Oxea II. **f** Exotyle. **g** Style. **h** Triaenes. **i**–**m** SEM of the spicules: **i** Microxea. **j** Detail of the middle of the microxea. **k** Detail of the extremity of the microxea. **l** Spirasters. **m** Metasters. *Scales* **a** = 1 mm; **b**, **c** = 500 μm; **d**–**h** = 500 μm; **i** = 20 μm; **j**–**m** = 10 μm

Table 3 Spicule measurements of *V. stylifera* sp. nov. minimum — mean — maximum length/width, in μm

	MNRJ 7343 (holotype)	MNRJ 7344 (paratype)	MNRJ 7345 (paratype)	MNRJ 7988 (paratype)	MNRJ 7997 (paratype)
Choanosomal oxeas	3375–3897–4540/40–44–46	3167–3345–4646/38–40–43	3175–3798–4600/38–45–50	3178–3900–4534/39–41–44	3283–3600–4000/38–39–40
Echinating oxeas	5770–7000–11,496/23–30–38	5750–8960–12,000/24–32–38	5762–8890–12,000/29–38	7003–8834–9833/20–28–38	6915–9318–11,090/20–27–30
Exotyles	2403–3125–3780/66–69–75	2499–3050–3910/69–72–75	2250–3400–4000/60–69–75	1950–3765–4000/63–69–75 (115)	(1350) 2400–3345–3967/(40) 66–70–75
Styles	1850–2095–2525 (n = 5)/10–15–27.5 (n = 6)	1050–1575 (n = 2)/7.5–12–15 (n = 5)	1250–1325 (n = 2)/5–8.6–10 (n = 7)	n.f./17.5–20 (n = 2)	n.f./15 (n = 1)
Orthotriaenes	r: 875–1329–1725/50–65–75 c: 529–801–1120/44–46–48	r: 895–1001–1725/51–60–70 c: 525–634–700/43–48–49	r: 875–1232–1725/50–56–75 c: 525–890–1200/40–47–50	r: 899–999–1421/54–63–70 c: 535–687–1140/48–50–33	r: 875–1254–1725/50–68–75 c: 525–888–1200/40–48–55
Annulated microxeas	130–350–446/1.9–2.1–2.5	231–333–400/1.9–2–2.5	192–233–380/1.9–2.2–2.5	176–295–369/2–2.3–2.5	176–345–400/1.8–2–2.5
Spirasters	28–34–40	32–34–38	30–38–40	32–34–39	34–47–40
Metasters	43–45–48	43–46–47	45–46–47	44–45–48	43–45–47

r rhabdome, *c* cladome, *n.f.* not found

Paratypes: **OCEANPROF 1, BC-SUL.** MNRJ 7344, 7345, stn. 4 (Campos Basin, RJ, start 22.407°S–39.921°W–end 22.366°S–39.893°W), 1128–1135 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 07.ii.2003. MNRJ 7997; stn. 4-2 (Campos Basin, RJ, start 22.407°S–39.926°W–end 22.357°S–39.893°W), 1100 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 29.viii.2003. **OCEANPROF 2, BC-NORTE**. MNRJ 7988, stn. 16 (Campos Basin, RJ, start 22.272°S–39.889°W–end 22.219°S–39.870°W), 1059 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 22.viii.2003.

Diagnosis

Vulcanella with large exotyles (1350–4000 μm long) and styles. Furthermore, no other species in the genus has a combination of oxeas always larger than 2000 μm, triaenes bearing rhabdomes frequently larger than 1000 μm, annulated microxeas frequently over 300 μm long, metasters >40 μm in diameter, and spirasters >30 μm in diameter.

Description

Encrusting or cushion-shaped (Fig. 2a), 66 × 44 × 42 mm (holotype; largest diameter × smaller diameter × thickness) — 21 × 11 × 3 mm (paratype, 7997). Surface hirsute, with a neat sieve-like tangential layer ornamented by large surrounding bundles of megascleres, mainly around the oscules (2–3 mm in diameter), which are irregularly distributed along the surface. Pores were not observed. Consistency is compressible and the specimen is easily broken apart. Colour in ethanol is dark beige to light brown.

Skeleton

Ectosome (Fig. 2b) with bases of triaenes and exotyles, together with dense and almost erect tracts of large oxeas perpendicular to the surface, and piercing it up to 1 cm. It is possible to see some smaller megascleres between these tracts, some of them undoubtedly foreign. Choanosome (Fig. 2c) with a dense, radial architecture of multispicular tracts of oxeas and styles, as well as spirasters and metasters scattered throughout. Annulated oxeas tend to be concentrated around the openings of the aquiferous system, with regular diameter (300–500 μm) and uniform distribution.

Spicules (Table 3)

Oxeas I (Fig. 2d), robust, slightly curved, with extremities abruptly tapered, occasionally strongyloid, 3167–4646 μm long and 38–50 μm thick. Oxeas II (Fig. 2e), echinating, slender, with extremities abruptly tapered, occasionally strongyloid, 5750–12,000 μm long and 20–38 μm thick. Exotyles (Fig. 2f), occasionally strongyloid, robust, straight or slightly curved on the median region, 1350–4000 μm long and 60–75 μm thick. Styles (Fig. 2g), rare, slender, tapering gradually, and slightly curved or flexuous, 1050–2525 μm long and 5–27.5 μm thick. Orthotriaenes (Fig. 2h), robust, ranging to plagiotriaenes; terminations usually thin, only occasionally strongyloid; rhabdomes, 875–1725 μm long and 50–75 μm thick; cladomes, 525–1200 μm long and 40–50 μm thick. Annulated microxeas (Fig. 2i–k), straight or slightly curved, tapering gradually, rings clearly visible at the central region, occasionally centrotylote, 130–446 μm long and 1.8–2.5 μm thick. Spirasters

Table 4 Comparative table of spicular micrometries, distribution and depth for the species of *Vulcanella*

	Oxeas (or derivates)	Triaenes	Calthrops	Microxeas	Mt, metaster Sp, spiraster St, streptaster Pl, plesiaster	Distribution/depth (m)
V. aberrans (Maldonado and Uriz, 1996)	I. 1500–3115/23–70 II. 3500–6000/9–20	Or–Pl[a] = r: 565–1125/9–15; c: 150–350/7–15		I: 150–315/3–7 II: 65–140/2–2.5	Mt: 18–25 Sp: 6–21	W Mediterranean/70–120
Vulcanella cf. aberrans sensu Cárdenas and Rapp (2012)	I. Up to 5000/3–6.3–14 II. 1921–2789–3473/21–43.6–70	Or = r: 152–892–1315/23–37.6–62 c: 183–392.9–566 (n = 15) Di = r: 152–892–1315/23–37.6–62 c: 70–99–129 + 72–135.0–194 (n = 12)		I: 317–397.8–520/5–6–8 II. 181–239.2–245/3–3.2–4 III. 67–116.2–166/2	Mt: 14–25.0–39 St[b]: 14–25.0–39	Norway/320
V. acanthoxea (Tanita and Hoshino, 1989)	I. 1550–5000/33–120 II. >5000/5 III. 300–440/10–23 (achantoxeas)		550–990/70–110 (r = 150)	95–190/2–6	Mt: <25 Sp: <20	Japan/300
V. bifacialis (Wilson, 1925)	I. 2500–4500/60–90 II. 1500–12,000/10–20	r: 250–350/50–70 cl: 500–1110/50–80		250/4	Mt: 24 Sp: 16–20 St: 16–40 Pl I: 25 Pl II: 32	Philippines/n.r.
V. cribrifera (Sollas 1888)	I. 3035/67 II. >7500/32 Strongyles: 357/28	Or = r: 1000/40 cl: 250/32	286–636/39.5–80	110	Mt: 11.8 (rays) Sp: 16–20	Cape Verde/186–238
V. cribriporosa (Lebwohl, 1914)	I. 1900–3300/40–67 II. Up to 5000/7–10	Pl = r: 480–760/35–50/ cl: 150–340 Or = r: 180–540/22–55/cl: 210–590/22–55	Chelotrops: r: 250–690/38–85/ cl: cl: 240–690/38–85	100–190/4–6	Mt: 21–38 Sp: 16–20	Japan/n.r.
V. doederleini (Thiele, 1898)	I. 1750–2500/65 II. 4000/15	Present	300–450/65	I. 270/12 II. 70–90	Sp	Japan/n.r.
V. gracilis (Sollas 1888)	I. 3800/100 II. 5600/15		830/64	350/11.5	Mt: 12 (rays) Sp: 15	Cape Verde/186–238
V. horrida (Schmidt, 1870) sensu Maldonado (2002)	I. >3000/35 II. >5000/142		400–1100/40–100	I: 200–500/8–13 II: 100–180/3–4.5	Sp: 12–18	N Atlantic, Florida and Azores/60–2500
V. netheides (Lebwohl, 1914)	I. 750–3500/18–150 II (tylostyles). 550–2550/35–170 III (strongyles, subtylotes). 2000–2600/100 IV. 4000–7000/12–13	Pl: r: 590–795/30–52; cl: 90–220 Or[c]: r: generally 40–140/40–115; cl: 240–840/30–110		60–405/2.5–18	Mt: 19–34 Sp: 14–23	Japan/n.r.
V. orthotriaena (Lévi and Lévi, 1983)	2400–3600/12–80	Or–Di (almost calthrops) = r: 900–1200/45–50; cl: 500–700/40–50 (rare dichotriaenes of the same dimensions)		270–400/5–8	St: 15–20(rays)/45 Sp: no measures	New Caledonia/360–365
V. osculanigera (Dickinson, 1945)	I. 2100/75 II. 800/2 III. 375/10		410/95		Asters: 15	Mexico/13

Table 4 continued

	Oxeas (or derivates)	Triaenes	Calthrops	Microxeas	Mt, metaster Sp, spiraster St, streptaster Pl, plesiaster	Distribution/depth (m)
V. porosa (Lebwohl, 1914)	I. 800–3800/30–125 II. 12,000/16	Or = cl: 300–850 Pl = r: 500–1100/30–50; cl: 90–260/70–75		100–405/3–14	Mt: 11–22	Japan/n.r.
V. theneides (Burton, 1959)	I. 6000–8000/40–56	Or = r = c: 480–800/32–50			St: 22–50	Indic Oc./878
V. tricornis (Wilson, 1904)	I. 2500–5000/85–135 II. up to 25,000 III. 3000–5000/12		1000/700	I: 400–500/8–16 II: 120	Mt: 20 Sp I: 20 Sp II: 24–26	Central Atlantic/99

Values are expressed in µm, as minimum — mean — maximum length/width value whenever available. Data are from original descriptions, unless stated otherwise

n.r. not reported, *Pl* plagiotriaene, *Or* orthotriaene, *Di* dicotriaene, *r* rhabdome, *cl* clade, *c* cladome

[a] Also pseudocalthrops, which seems to be malformations

[b] All intermediates exist between spirasters, metasters, and plesiasters

[c] Seems to be calthrops

(Fig. 2l), 6–8 rays, with two or more twists, 28–40 µm in largest diameter. Metasters (Fig. 2m), 4–6 rays, 43–48 µm in largest diameter.

Habitat and distribution

Provisionally endemic from the bathyal zone of Campos Basin (SE Brazil), 1059–1130 m depth, where the species appears to be moderately common, occurring associated with *S. variabilis*.

Etymology

The specific epithet *stylifera* is derived from the species possession of styles.

Remarks

The exotyles seen in the new species might be triaenes with reduced cladomes, as apparent from their slightly conical shape, similar to rhabdomes in general. However, due to the lack of intermediate forms that might support the hypothesis of suppression of the cladomes, we prefer to believe these spicules to be truly monaxonic. In addition, it is not possible to see any bi/trifurcation at the basal extremity of the axial filament, which could indicate the spicule's poliaxonic character.

Vulcanella has recently been allocated in Vulcanellidae [12] based on molecular data. These authors also raised subgenus *Annulastrella* [62] to full generic status, and transferred it to Theneidae. Triaenes have been secondarily lost in this genus. As a consequence, there no longer is an undisputed subgeneric classification for *Vulcanella*.

Fourteen species of *Vulcanella* are known worldwide (Table 4): *Vulcanella aberrans*, *V. acanthoxea*, *V. bifacialis*, *V. cribrifera*, *V. cribriporosa*, *V. doederleini*, *V. gracilis*, *V. horrida*, *V. netheides*, *V. orthotriaena*, *V. osculanigera*, *V. porosa*, *V. theneides* and *V. tricornis*. None of these possess a category of styles, but malformed triaenes may be common (e.g. [62]). Nevertheless, to the best of our knowledge, the clearly recognizable category seen in the new species has not been reported previously in the literature, and appears to us a convincing support for recognition of the new species. Rather than relying onthis single diagnostic character, a thorough comparison was made where every known species was contrasted to the newly proposed one, and every spicule category considered.

The echinating oxeas in the new species can frequently be 10,000 µm long, but they will never be as large as those in *Vulcanella tricornis*, which attains 25,000 µm. On the other hand, several species reach only up to 5000–6000 µm, and can be confidently distinguished on the basis of this character alone. These species are *V. aberrans, V. cribriporosa, V. doederleini, V. gracilis, V. orthotriaena* and *V. osculanigera*. Smaller rhabdomes in the triaenes also distinguish a series of species: *V. aberrans, V. bifacialis, V. cribrifera, V. cribriporosa, V. netheides, V. orthotriaena, V. porosa* and *V. theneides*. Microxeas that are consistently smaller than those of the new species occur in *V. acanthoxea, V. cribrifera, V. cribriporosa* and *V. doederleini* (with, in addition, a second category of much smaller microxeas). Metasters and/or spirasters can also be consistently smaller, as is the case of those in *V. aberrans, V. acanthoxea, V. bifacialis, V. cribrifera, V. cribriporosa, V. gracilis, V. horrida, V. netheides, V. porosa* and *V. tricornis*. It is obvious from the above remarks that the new species has spicules which frequently reach quite larger dimensions when contrasted to the same categories in other *Vulcanella* spp. Some species possess calthrops, a spicule category absent from the new species. This character adds further support for the distinction of *V.*

acanthoxea, V. cribrifera, V. cribriporosa, V. doederleini, V. gracilis, V. horrida, V. osculanigera and *V. tricornis*.

The genus was already registered for the South Atlantic [30], although this is the first full species description for a *Vulcanella* from this area.

Order POLYMASTIIDA Morrow & Cárdenas, 2015
Family POLYMASTIIDAE Gray, 1867
Genus *Trachyteleia* Topsent, 1928
Trachyteleia australis sp. nov.
(Fig. 3; Tables 5, 6)

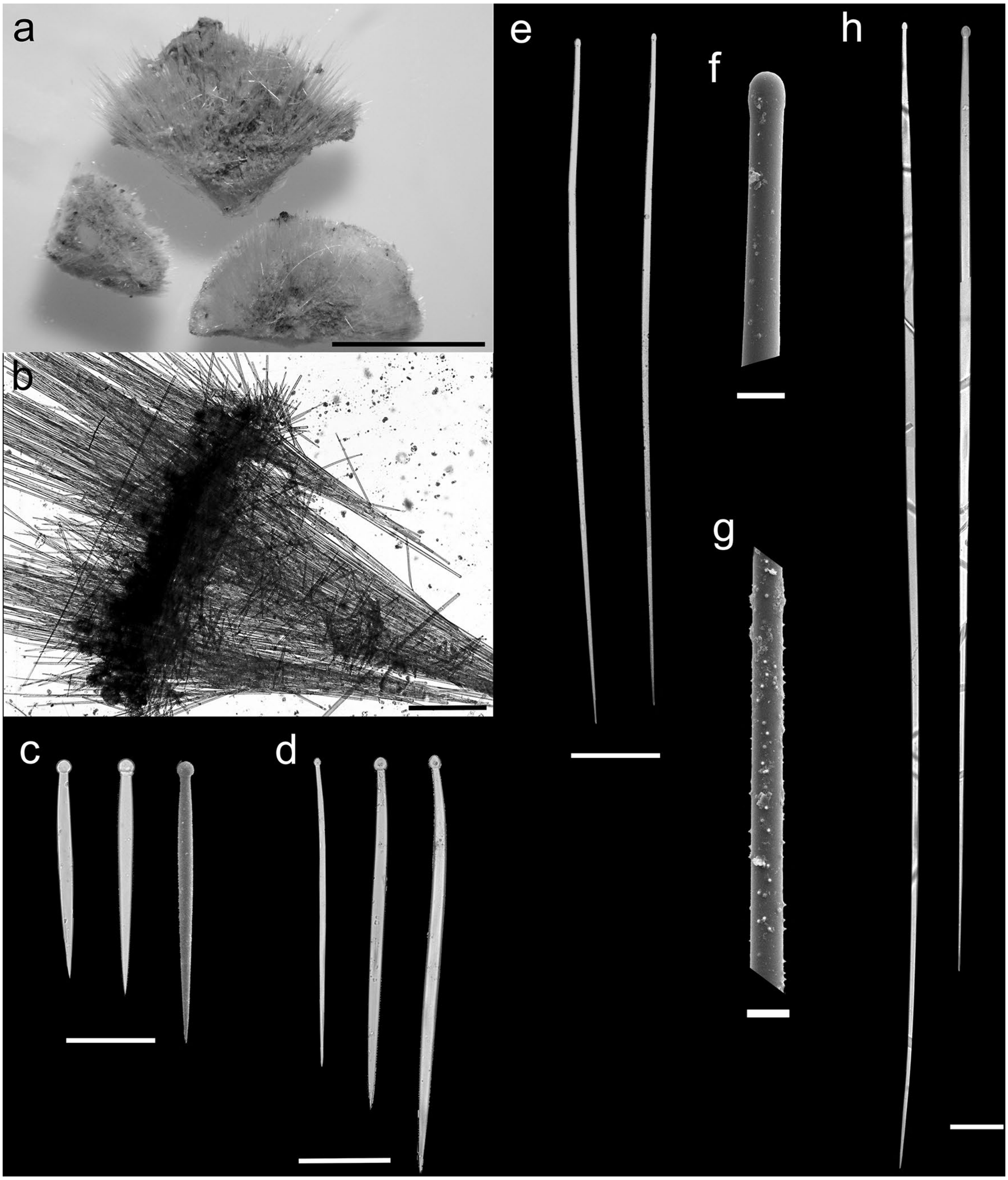


Fig. 3 *Trachyteleia australis* sp. nov. **a** Holotype (MNRJ 7359). **b** Choanosomal skeleton. **c** Tylostyles I. **d** Tylostyles II. **e** Exotyles. **f**, **g** SEM of the spicules: **f** base of the exotyle; **g** detail of the spines of exotyle. **h** Subtylostyles. *Scales* **a** = 5 mm; **b** = 500 µm; **c**–**e**, **h** = 100 µm; **f**, **g** = 10 µm

Table 5 Spicule measurements of *Trachyteleia australis* sp. nov. minimum – mean – maximum length/width, in µm

	MNRJ 7359 (holotype)	MNRJ 7358 (paratype)	MNRJ 8014 (paratype)
Ectosomal tylostyles	213–271–495/15–19.1–22	155–297–504/9–17.9–21	155–198–252/12–13–14.4
Choanosomal tylostyles	281–405–534/8–13.3–22	271–481–747/6–12.2–22	165–415–737/6–10.8–14.4
Exotyles	611–974 to >1484/8–10.7–12	640–871–1193/7–8.5–11	650–1040–1329/7–10.4–17
Choanosomal subtylostyles	659–1480–>3392/11–15.9–29	786–1868–>2037/9–16.3–29	776–1839–3841/8–15.4–31

Table 6 Comparative table of spicule micrometries, distribution and depth for the species of *Trachyteleia*

	Ectosomal/small tylostyles	Tylostyles	Exotyles	Distribution/depth (m)
T. hispida sensu de Laubenfels (1949)	90–180/2–4	900–1800/27	2600/20	NE Atlantic/14–388
T. stephensi Topsent, 1928	175–275/4–5	490–560/12	590–735/10–18	N Atlantic, N Mediterranean/1740
sensu Boury-Esnault (2002)	170–275/5	Principal 490–570/11	Intermediate 310–395/8	590–735/23
T. australis sp. nov.	155–504/9–22	271–747/6–22	611–2377/7–29	Campos Basin, Brazil/1100–1630

Values are expressed in µm. Data are from original descriptions, unless stated otherwise

Type material

Holotype: **OCEANPROF 1, BC-NORTE**. MNRJ 7359, stn. 18 (Campos Basin, RJ, start 22.270°S–39.791°W–end 22.221°S–39.789°W), 1622–1628 m depth, coll. R/V 'Astro Garoupa', demersal fisheries net, 12.ii.2003.

Paratypes: **OCEANPROF 1, BC-NORTE**. MNRJ 7358, stn. 18 (Campos Basin, RJ, start 22.270°S–39.791°W–end 22.221°S–39.789°W), 1622–1628 m depth, coll. R/V 'Astro Garoupa', demersal fisheries net, 12.ii.2003. **OCEANPROF 2, BC-SUL**. MNRJ 8014, stn. 2-1 (Campos Basin, RJ, start 22.512°S–40.016°W–end 22.479°S–39.977°W), 1107–1141 m depth, coll. R/V 'Astro Garoupa', demersal fisheries net, 27.viii.2003.

Diagnosis

Trachyteleia with ectosomal tylostyles up to 500 µm long and 22 µm thick.

Description

Massive fragments with 1 × 1 cm. Surface hispid with echinating spicules (Fig. 3a). Consistency hard, only slightly compressible. Color alive is beige to yellow, and light to dark-beige after fixation with ethanol.

Skeleton

Ectosomal skeleton a dense layer of tylostyles, traversed by echinating choanosomal subtylostyles and exotyles. Choanosomal skeleton radial, with dense, multispicular ascending tracts of choanosomal tylostyles, exotyles and subtylostyles (Fig. 3b).

Spicules (Table 5)

Tylostyles I (Fig. 3c), ectosomal, smooth, straight, markedly fusiform, robust, with well developed tyle, 155–504 µm long and 9–22 µm thick. Tylostyles II (Fig. 3d), choanosomal, smooth, slightly curved at the base, slightly fusiform, relatively slender, 271–747 µm long and 6–22 µm thick. Exotyles (Fig. 3e–g), choanosomal, rough, or microspined in the central region, 611–1484 µm long and 7–17 µm thick. Choanosomal subtylostyles (Fig. 3h), large and smooth, 659–3841 µm long and 8–31 µm thick.

Habitat and distribution

Provisionally endemic from the bathyal zone of Campos Basin (SE Brazil), at 1107–1628 m depth.

Etymology

The specific epithet, *australis*, is the Latin word for "from the South", which highlights the fact that this is the first record of *Trachyteleia* for the Southern Hemisphere.

Remarks

Only two species were previously known in *Trachyteleia*, *T. hispida* and *T. stephensi*, recognized by the presence of distally microspined exotyles [8] similar to those found in the Brazilian specimens.

Nevertheless, several differences separate the new species from the other two previously known. The ectosomal tylostyles I in *T. australis* sp. nov. are larger than those in *T. hispida* (up to 180 µm) and in *T. stephensi* (up to 275 µm). Intermediate and principal tylostyles are not always well separated in *T. hispida* and *T. stephensi* sensu [96], as well as in the new species. In *T. australis* sp. nov. they are larger than the intermediate/principal tylostyles of *T. stephensi*, and smaller than the same category in *T. hispida* (Table 6). Exotyles are much smaller in *T. stephensi* than in the new species (up to 735 and 2377 µm, respectively). While in *T. hispida* they can be about 2600 µm long, similar to the larger ones in *T. australis* sp. nov.

This is the first record of the genus for the South Atlantic, and the whole Southern Hemisphere.

Order Poecilosclerida Topsent, 1928
Family Phellodermidae van Soest & Hajdu, 2002
Genus *Echinostylinos* Topsent, 1927
Echinostylinos brasiliensis sp. nov.
(Fig. 4; Tables 7, 8)

Type material

Holotype: **OCEANPROF 1, BC-SUL**, MNRJ 7328, stn. 4 (Campos Basin, RJ, start 22.407°S–39.921°W–end 22.366°S–39.893°W), 1130 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 07.ii.2003.

Paratype: **OCEANPROF 2, BC-SUL**, MNRJ 8001c, MNRJ 8003c, stn. 4-2 (Campos Basin, RJ, start 22.407°S–39.926°W–end 22.357°S–39.893°W), 1100 m depth; coll. R/V 'Astro Garoupa', demersal fisheries net, 29.viii.2003.

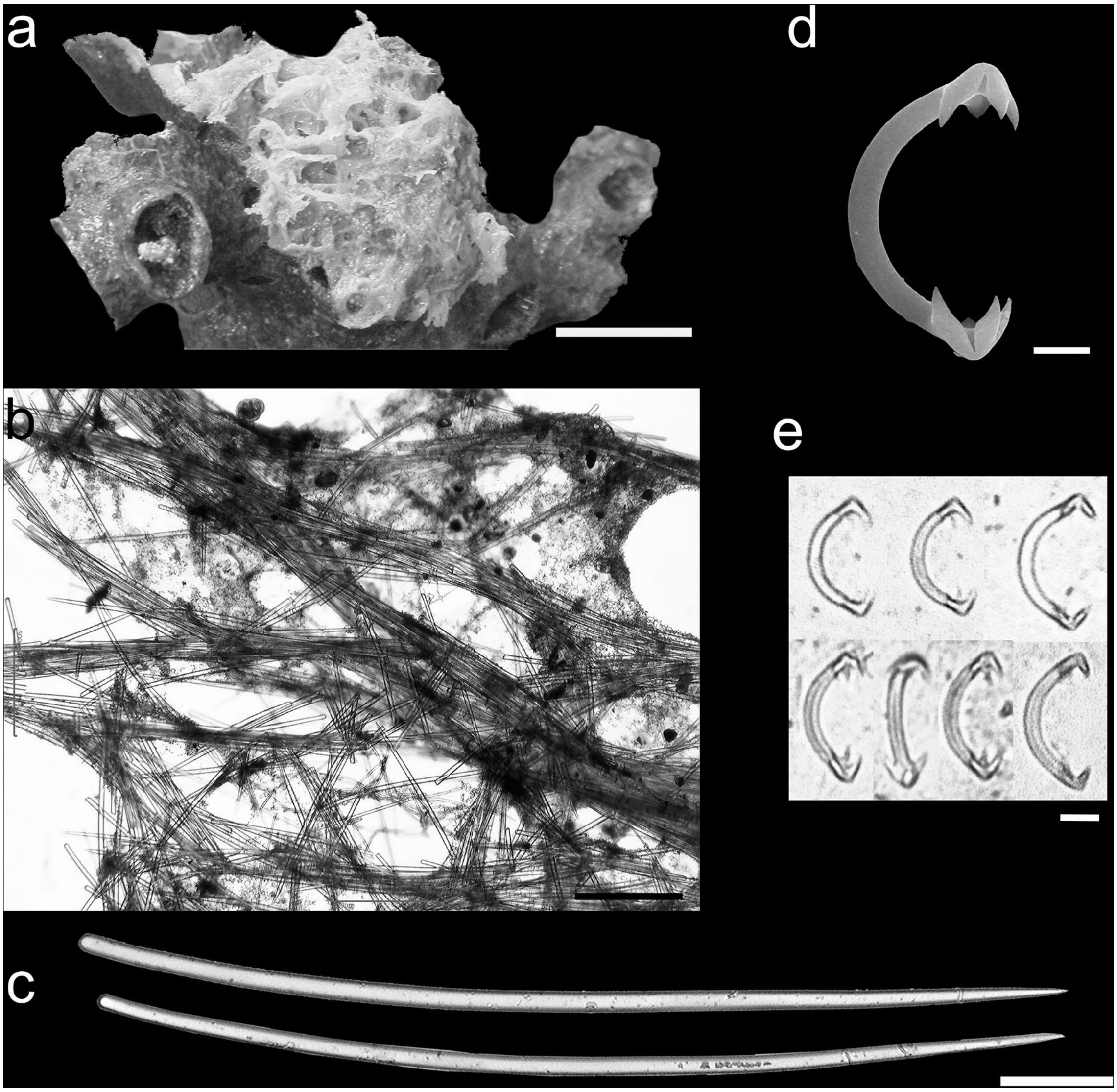


Fig. 4 *Echinostylinos brasiliensis* sp. nov. **a** Holotype (MNRJ 8003c). **b** Skeleton. **c** Styles. **d** SEM of the isochelae. **e** Isochelae. *Scales* **a** = 10 mm, **b** = 500 μm, **c** = 100 μm, **d** = 5 μm, **e** = 10 μm

Table 7 Spicule micrometries for *E. brasiliensis* sp. nov. minimum — mean — maximum length/width, in µm

	MNRJ 7328 (holotype)	MNRJ 8001c (paratype)	MNRJ 8003c (paratype)
Styles	778–883–1020/18–19–20	831–947–1067/17.5–19.5–22.5	776–876–1048/18–20–22
Arcuate isochelae	25–27–29	22–25–30	22–24–26

Table 8 Comparative table of spicule micrometries, distribution and depth for the species of *Echinostylinos*

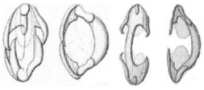
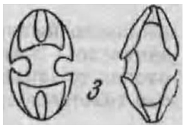
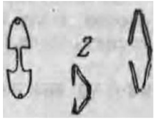
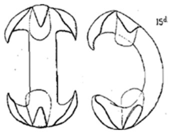
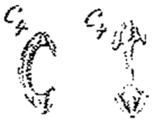
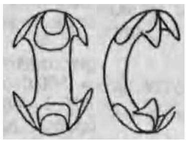
	Styles	Arcuate isochelae (or as noted otherwise)	Sigmas	Distribution/depth (m)
E. brasiliensis sp. nov.	I: 776–1048/18–22	22–30 		Campos Basin, Brazil/1100–1130
E. glomeris (Topsent, 1904)	I: 900–1000/7–8 II: 1400–1500/17–20	60 		Azores/599
E. gorgonopsis Lévi, 1993	I: 250–370/4–5	30–50 		New Caledonia/950–1000
("arbusculaire" = *Abyssocladia*?)	II: 525–650/16–17			
E. hirsutus Koltun, 1970	I: 400–540/5–10 II: 660–1650/45–54 III: ?	18–27 	I: 16–22	NW Pacific/1440–1540
E. lingua (Koltun, 1970) (as *Esperiopsis* in WPD)	550–870/13–16	I: 44–55 (possibly arcuate) II: 18–32 (possibly palmate)  	I: 77–148	NW Pacific/472–479
E. mycaloides Koltun, 1970	I: 495–610/8 II: 825–935/18–24 III: 200–325 × 5	71–94 		NW Pacific/ 2165–2265

Table 8 continued

	Styles	Arcuate isochelae (or as noted otherwise)	Sigmas	Distribution/depth (m)
E. patriciae nom.nov. (=*E. reticulatus* sensu Bergquist and Fromont, 1988)	I: 387–530/8–13 II: 202–300/3–6	28–40 	I: 22–36 II: 15–18	New Zealand/55–110
E. reticulatus Topsent, 1927	I: 500–560/26–30 II: 245–280/3	27–43/5–9 	I: 22 II: 15	Azores/919
E. schmidti (Arnesen, 1903)	1200	40 	20	Norway/500
E. shimushirensis Koltun, 1970	I: 275–358/5–8 II: 1320–1590/29–37	32–54 	I: 27–48 II: 16–22	NW Pacific/445
E. stylophora (Lévi and Lévi, 1983)	I. 300–320 II. 700–800/30–40	I. 38–40 × 25 (arcuate) II. 20 (arcuate) 	30–60	New Caledonia/510–525
E. tubiformis (Lévi, 1993)	I. 1300–1400/30 II. 300–370/5	35–48 × 30 (arcuate) 	I. 30/2 II. 15–19/1	New Caledonia/965

Values are expressed in μm, length/width value. Data are from original descriptions, unless stated otherwise

Diagnosis

The only species of *Echinostylinos* with a single category of megascleres, and markedly curved unguiferate isochelae 22–30 μm long.

Description

The holotype and largest specimen is encrusting an area 2.3 × 1.7 cm, with short, irregular, anastomosing branches (Fig. 4a). Its surface is slightly hispid, and no special ornamentation, pores, or oscules have been observed. Consistency is compressible and color in ethanol beige.

Skeleton

Choanosomal skeleton organized, with tracts of styles, occasionally reticulated, or some styles crossing the tracts (Fig. 4b). Spongin can be present in several points, and isochelae are abundant all over the sponge.

Spicules (Table 7)

Megascleres (Fig. 4c)—styles varying little in dimensions, smooth, slightly curved, tapering gradually to sharp ends, 776–1067 μm long and 17.5–22.5 μm thick. Microscleres (Fig. 4d, e)—unguiferate isochelae with a markedly curved shaft in profile view, and four sharp alae on each extremity, 22–30 μm.

Habitat and distribution

Provisionally endemic from the bathyal zone of Campos Basin (SE Brazil), at 1100–1130 m depth.

Etymology

The specific epithet, *brasiliensis*, relates to its type locality, off south-eastern Brazil, and for this being the sole known species of the genus reported from the Brazilian coast.

Remarks

Ten species have been allocated in *Echinostylinos*, nine of which remain accepted as valid: *E. glomeris*, *E. gorgonopsis*, *E. hirsutus*, *E. mycaloides*, *E. reticulatus*, *E. schmidtii*, *E. shimushirensis*, *E. stylophora* and *E. tubiformis*. *Echinostylinos unguiferus* has been transferred to *Monanchora* on account of the anchorate nature of its isochelae (referred to as unguiferate by Esteves [25], Van Soest [102]). On the basis of the remarks offered by Van Soest and Hajdu [104] on the unlikelihood of the conspecificity of New Zealand and Azorean records of *E. reticulatus*, we decided to propose a new name for the former record, namely *E. patriciae* nom.nov. (honouring Dame Patricia Bergquist, first author of the record—holotype NIWA 105240, paratpe NIWA 105473). This is done not just because of the distant localities of occurrence and remarkably distinct bathymetry of both, but also to highlight some morphological divergence such as the much thicker megascleres and smaller sigmas in the type specimen of *E. reticulatus*.

Table 8 summarizes the morphological data and known distribution of every species, and was used for a detailed comparison with the new species. The genus was formerly known from the North Atlantic, NW and Center-South Pacific, from a depth range of 55–2500 m. The new species described is the first record of *Echinostylinos* for the entire South Atlantic, and is clearly distinguished from the remaining species in having only a single category of megascleres, as well as unguiferate isochelae, shorter than 30 μm.

The styles of *E. brasiliensis* sp. nov. are smaller than those of *E. glomeris*, *E. hirsutus*, *E. shimushirensis*, and *E. tubiformis*; larger than those of *E. gorgonopsis*, *E. reticulatus*, *E. patriciae* nom.nov., *E. schmidti*, and *E. stylophora*; and similar to those of *E. mycaloides*.

Further, the new species from Campos Basin has isochelae that are smaller than those of *E. glomeris*, *E. gorgonopsis*, *E. mycaloides*, *E. patriciae* nom.nov., *E. reticulatus*, *E. shimushirensis*, *E. schmidtii*, *E. stylophora*, and *E. tubiformis*; and similar to those of *E. hirsutus*, although this species has two categories of megascleres. Considering the shape of the isochelae, *E. mycaloides* is the species coming closer to *E. brasiliensis* sp. nov., as both share the unguiferate, strongly arched pattern in their isochelae. The former species has, nevertheless, isochelae 3× as large as those in the new one. Other species have notoriously distinct isochelae morphologies, frequently much stouter, with spatulate alae. An exception is *E. hirsutus*, of dubious affinities, with much reduced isochelae of unclear morphology. This species should be reexamined under SEM for a sounder assignment to *Echinostylinos*.

Echinostylinos schmidtii has been only poorly illustrated by Arnesen [2] and needs to be redescribed. Unfortunately the whereabouts of its type material could not be traced in Bergen or Oslo and it appears to be lost (H.T. Rapp, pers. comm. on 2014 09 26). In principle it has a single category of styles, which would bring it close to the new species, but the large sigmas and the seemingly typical arcuate spatulate isochelae would set Arnesen's species far from the Brazilian material described above.

Echinostylinos shimushirensis and *E. tubiformis* might be synonymous, as both share a similar spicule set, with quite comparable spicule dimensions (Table 8). Both species were also recorded from the same depth zone, but given their far apart occurrence (7600 km away), and slightly divergent habit and isochelae morphology, we prefer to hold their formal synonimization until the type materials of both have been reexamined.

Order HAPLOSCLERIDA Topsent, 1928
Family PETROSIIDAE van Soest, 1980
Genus *Xestospongia* de Laubenfels, 1932
Xestospongia kapne sp. nov.
(Fig. 5; Table 9)

Type material

Holotype: **CAP BC**, MNRJ 13541, Caratinga Oil Field 9.5″, bank 3 (Campos Basin, RJ, 22.623°S–40.264°W), 923 m depth, coll. R/V 'Toisa Conqueror', ROV, 12/iii/2006.

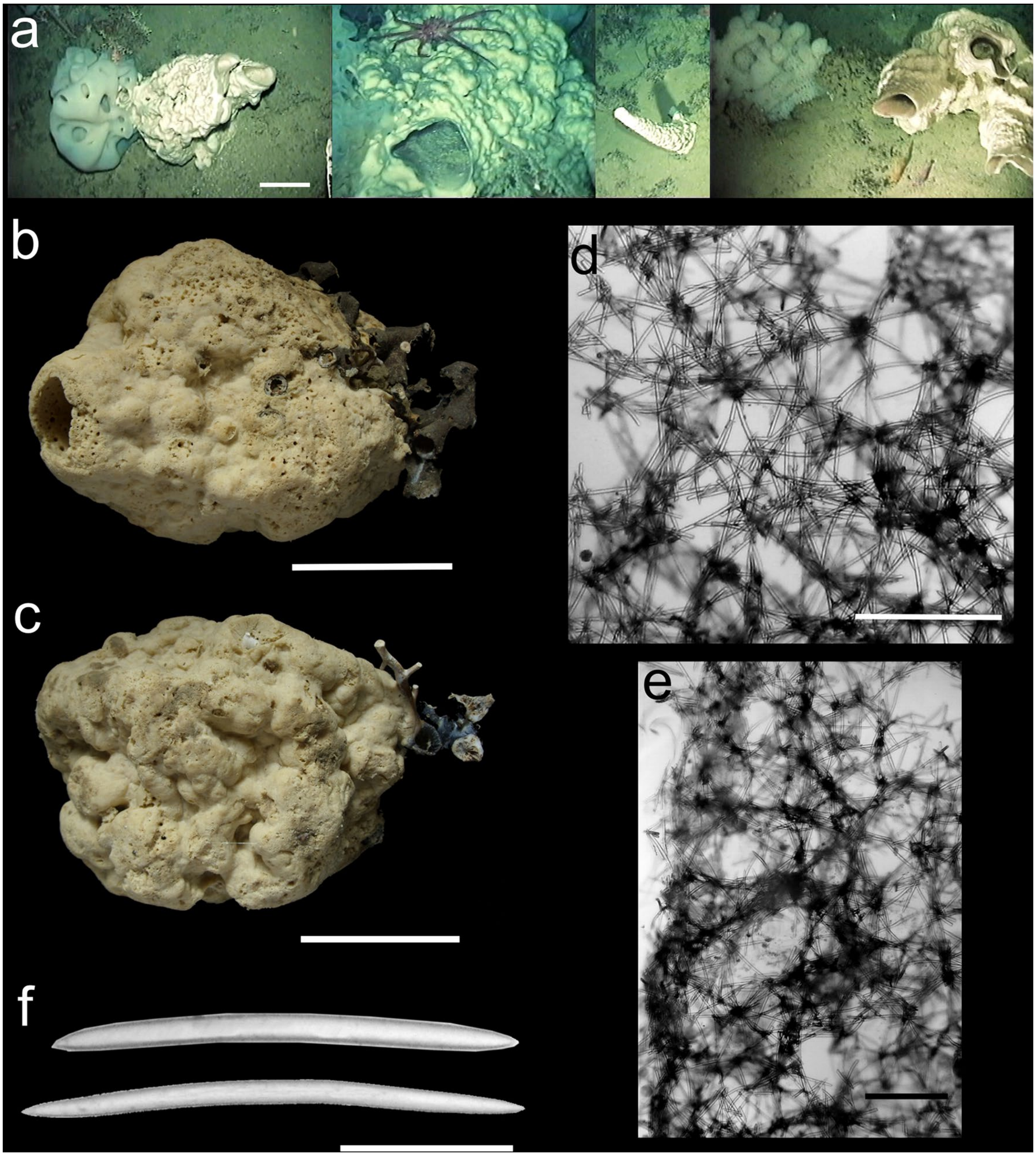


Fig. 5 *Xestospongia kapne* sp. nov. **a** Several specimens in situ. **b**, **c** Holotype preserved in ethanol. **d** Ectosomal skeleton. **e** Choanosomal skeleton. **f** Oxeas. *Scales* **a**–**c** = 10 cm; **d**, **e** = 500 µm; **f** = 100 µm

Comparative material *Petrosia friabilis* Topsent, 1892 (holotype, MOM 04 0159)

Diagnosis

Xestospongia with oxeas ranging from 200 to 300 µm in length, barrel- or chimney-shaped, found at deep waters (877–1053 m).

Description

Massive, robust, barrel- or chimney-shaped, with an irregular contour and a large apical pseudo-oscule (Fig. 5a–c). The surface has lobular projections and shallow depressions or gaps, and rough texture. Several specimens were recognized from video footage, where it was nicknamed “cannon-sponge”. Some of these form

Table 9 Comparative table of spicule micrometries, distribution and depth data for the species of *Xestospongia* de Laubenfels, 1932

	Spicules	Distribution/depth (m)
X. arenosa van Soest and de Weerdt, 2001	Ox: 342–514/7–14	Caribbean/14–41
X. bergquistia Fromont, 1991	Ox: I. 218–386/8.4–16 (variable in shape)/II. 269–336 × 2–8.4	NE Australia/6–15
X. bocatorensis Díaz, Thacker, Rützler and Piantoni, 2007	Ox: 230–320 Si: 10–26	Caribbean/6–12
X. caminata Pulitzer-Finali, 1986	Ox-St: 200–280/5–14	Caribbean/5–25
X. clavata Pulitzer-Finali, 1993	Ox: 300–335/25–30	W Indian Ocean/130
X. coralloides (Dendy, 1924)	Ox: 250/16	New Zealand/ca. 1823
X. delaubenfelsi Riveros, 1951	Ox: 220/11	Chile/55
X. deweerdtae Lehnert and van Soest, 1999	Sg: 272–346/16–32	Caribbean/10–80
X. diprosopia (de Laubenfels, 1930)	Ox: 400/30	California/500
X. dubia (Ristau, 1978)	Ox: 140–180/10–16	California/0–7
X. edapha (de Laubenfels, 1930) sensu de Laubenfels (1932)	Ox: 260–270/13–15 Si: 100/30	California/n.r.
X. emphasis (de Laubenfels, 1954)	Ox: 185–205/9–10 Si: 17–18	Micronesia/< 2
X. friabilis (Topsent, 1892) (holotype remeasured)	Ox: 210 Ox: 116–165–204/2–4.7–7	Azores/130–927
X. grayi (Hechtel, 1983)	Sg: 201–334–433/3.5–6.9–10	Brazil/probably shallow
X. hispida (Ridley and Dendy, 1886)	Ox: 370/21	Kerguelen/46
sensu Uriz (1988)	Ox: 290–325/13–21	Namibia/7–239
X. informis Pulitzer-Finali, 1993	Ox: 345–390/16–23	W Indian Ocean/70
X. madidus (de Laubenfels, 1954)	Sg: 225/8 Ox: 300/1–4	Micronesia/3
X. mammillata Pulitzer-Finali, 1982	Ox: 160–330/1.5–14	NE Australia/n.r.
X. menzeli (Little, 1963)	Ox, Sg, St I: 75–106–178/3–4–5 II: 89–94–98/1–1.3–2 (immature or microxeas)	Gulf of Mexico/1.5
X. muta (Schmidt, 1870)	Ox–Sg: 173–461	Tropical W Atlantic/2–94
sensu Van Soest (1980)	Ox, Sg: 303–380–435/11–18.8–23	Caribbean/4–92
X. novaezealandiae Bergquist and Warne, 1980	Ox: 240–314/10–18	New Zealand/20–40
X. papuensis Pulitzer-Finali, 1996	Sg: 195–245/13–14	Papua New Guinea/15
X. plana (Topsent, 1892)	Ox: 235–250/9	W Mediterranean/n.r.
X. portoricensis van Soest, 1980	Sg: 377–409–429/15–17.4–19	Caribbean/10–90
X. rampa (de Laubenfels, 1934)	Sg: 330–380/12–13 Ox: 100–300 × 2–3 (microrhabds)	Caribbean/60–220
X. ridleyi (Keller, 1891)	Ox, Sg: 300–400/10	Red Sea/33
X. testudinaria (Lamarck, 1815) sensu Vacelet and Vasseur (1965)	Ox, Sg: 230–280/6–13	Indo Pacific/n.r.
sensu Lévi (1961)	Ox, Sg: 175–475/10–12	W Indian Ocean/40
X. testudinaria var. fistulophora (Wilson, 1925)	Ox: 400–440/22	Philippines/n.r.
X. tuberosa Pulitzer-Finali, 1993	Ox: 130–270/7–13	W Indian Ocean/48
X. vansoesti Bakus and Nishiyama, 2000	Ox: 152–300/2–16	Philippines/10
X. variabilis (Ridley, 1884)	Ox: 400/19	Australia/13–22
X. variabilis (Topsent, 1892)[a]	Ox: 530/33	Azores/454–736
X. variabilis var. crassa (Wilson, 1904)	Ox: 510/32 (rarely St)	Galapagos/96
X. viridenigra (Vacelet, Vasseur and Lévi, 1976)	Sg, Ox: 230–280/6–11	W Indian Ocean/2–3
X. wiedenmayeri van Soest, 1980	Ox, Sg: 230–349–428/11.5–15.3–18	Caribbean/intertidal—1.5

Values are expressed in µm, as minimum — mean — maximum length/width value whenever available. Data are from original descriptions, unless stated otherwise

n.r. not reported, *Ox* oxeas, *St* styles, *Sg* strongyles, *Si* sigmas

[a] *Xestospongia variabilis* (Topsent, 1892, as *Petrosia v.*) is a junior homonym of *X. variabilis* (Ridley, 1884, as *Halichondria v.*) and should be renamed, which we refrain from doing here as we did not examine biological materials of either

clusters of up to three chimneys, and the largest specimens recorded were presumably nearly 50 cm tall.

Skeleton

Ectosomal skeleton with a loose reticulation formed by the tangential arrangement of spicules composing the terminal tufts of ascending choanosomal spiculo-fibers (Fig. 5d). Ectosomal meshes are seen here and there, with 140–250 μm in diameter. Choanosomal architecture with a reticulation that is clearly visible only in some areas, overlaid by abundant oxeas in confusion (Fig. 5e). Meshes are only seldom observed, being 200–400 μm in diameter. The distinction between primary ascending fibers and interconnecting secondaries is unclear.

Spicules

Oxeas (Fig. 5f)—Relatively robust, usually slightly curved, tapering gradually, with 204–<u>265.1</u>–301 μm in length and 11–<u>12.6</u>–14 μm thick. Derived and rare forms have more accentuated curvatures, and sometimes styloid or subtylostyloid ends.

Habitat and distribution

Provisionally endemic from the bathyal zone of Campos Basin (SE Brazil), at 877–1053 m depth.

Etymology

The specific epithet relates to the chimney-like habit of the species (*kapne* = Greek for chimney), and is used here as a noun in apposition.

Remarks

The genus *Xestospongia* is found from the intertidal to 1800 m depth. It has ca. 35 species known worldwide, 12 of which occurring in the Atlantic Ocean [105]. Only *X. grayi* and *X. muta* were known from Brazil until now, both from warm and shallow waters of the Northeastern coast, and they differ from the new species due to the presence of strongyles as megascleres [32, 67]. Likewise, another 13 species also possess strongyles in their spicule set (see Table 9), thus differing from the new species. The possession of sigmas sets *X. bocatorensis*, *X. edapha*, and *X. emphasis*, apart from *X. kapne* sp. nov.

Only seven species of *Xestospongia* were known to occur deeper than 100 m (Table 9): *X. clavata*, *X. coralloides*, *X. diprosopia*, *X. friabilis*, *X. hispida*, sensu [98], *X. rampa*, and *X. variabilis*, sensu [93]. All of them possess oxeas as megascleres, except for *X. rampa*, which has strongyles and can be easily differentiated from the new species through this character. *X. clavata*, *X. diprosopia*, and *X. variabilis*, sensu [93] have oxeas that are always larger than 300 μm long and 30 μm thick, being thus also considerably distinct from the new species. Despite the possession of oxeas smaller than 300 μm in length, *X. coralloides*, *X. friabilis* and *X. hispida*, sensu [98] are quite distinct from the new species too. The oxeas in *X. friabilis* can be much smaller than those in *X. kapne* sp. nov., with a minimum length of 116 μm (holotype remeasured; Table 9), in contrast to a minimum of 204 μm in the new species. *X. hispida*, sensu [98], from Namibia, has oxeas whose minimum length is much longer than observed in the smallest oxeas of the new species (290 × 204 μm, respectively). The habit of *X. coralloides* and *X. hispida* is also a distinctive character, being flat-lammelate and lobate, respectively, with no tubular structures topped by large pseudoscules.

Some *Xestospongia* spp. approach the new species in having only oxeas and in a similar size range (Table 9): *X. bergquistia*, *X. delaubenfelsi*, *X. mammillata*, *X. novaezelandiae*, *X. plana*, *X. tuberosa*, and *X. vansoesti* [4]. In addition to most of these species being shallow water dwellers (down to 55 m depth), further slight differences appear when contrasting them to *X. kapne* sp. nov. *X. bergquistia* was described as an erect, cup-shaped sponge, thus reminiscent of the barrel-shaped new species. Nevertheless, the former species possibly has two categories of oxeas, one of them much thinner (2–8 μm thick), and the other with occasional styloid ends, which coupled to its very far distribution and shallow-water habit, renders the hypothesis of co-especificity with the new species highly unlikely. Very thin oxeas are also found in *X. mammillata* and *X. vansoesti* (1.5 and 2 μm thick, the smallest ones, respectively), although no suggestion has been made of these being anything but young forms. *Xestospongia delaubenfelsi* and *X. plana* have a flattened habit too, which is considerably distinct from the barrel-shape of the new species. Besides, they are known only from very far, biogeographically unrelated localities (Chile and the Mediterranean, respectively), and in none of them oxeas reach 300 μm in length. *Xestospongia novaezelandiae* (from New Zealand) is erect massive and irregular, and *X. tuberosa* (from the Western Indian Oc.) is lobate, thus also differentiating in shape from the new species.

Class HEXACTINELLIDA Schmidt, 1870
Subclass HEXASTEROPHORA Schulze, 1886
Order LYSSACINOSIDA Zittel, 1877
Family ROSSELLIDAE Schulze, 1885
Genus *Sympagella* Schmidt, 1870
Sympagella tabachnicki sp. nov.
(Figs. 6, 7; Tables 10, 11)

Type material

Holotype: **CAP BC** Rota Gas, MNRJ 13365, trecho 1, Espadarte Field (Campos Basin, RJ, 22.757°S–40.433°W), 945 m depth, coll. R/V 'Toisa Conqueror', ROV, 22/iii/2005.

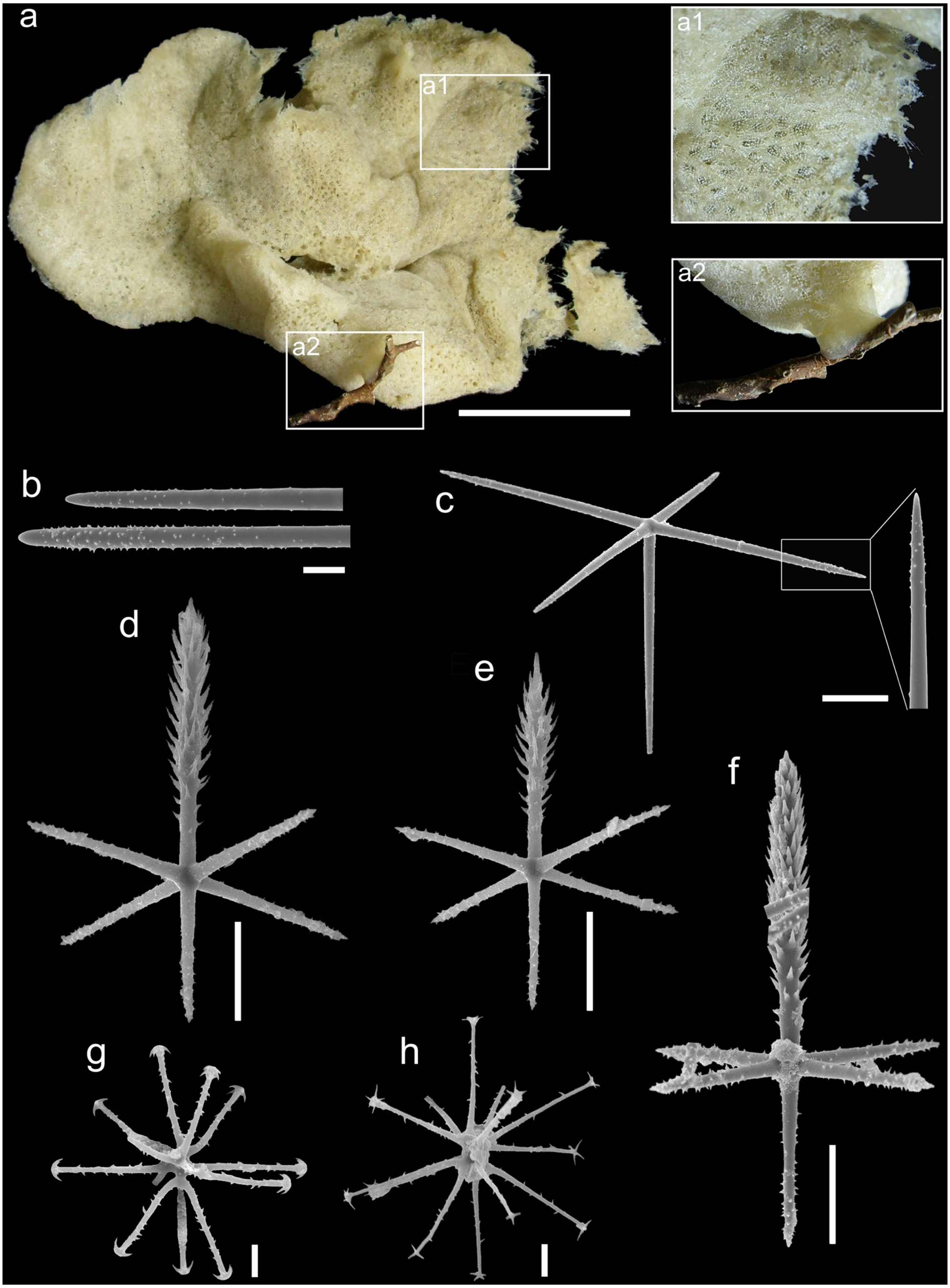


Fig. 6 *Sympagella tabachnicki* sp. nov. **a** Holotype (MNRJ 13365), **a1** detail of the dermal surface and **a2** base. **b**–**h** SEM of the spicules: **b** ends of the choanosomal diactins, **c** hypoatrial pentactin, **d** dermal pinular, **e**, **f** atrial pinular hexactins, **g** discohexaster, and **h** onychexaster. Holotype: **d**, **e**. Paratype: **b**, **c**, **f**–**h** (MNRJ 7315A). *Scales*: **a** = 50 mm; **b** = 20 μm; **c** = 100 μm; **d**–**f** = 50 μm; **g**, **h** = 10 μm

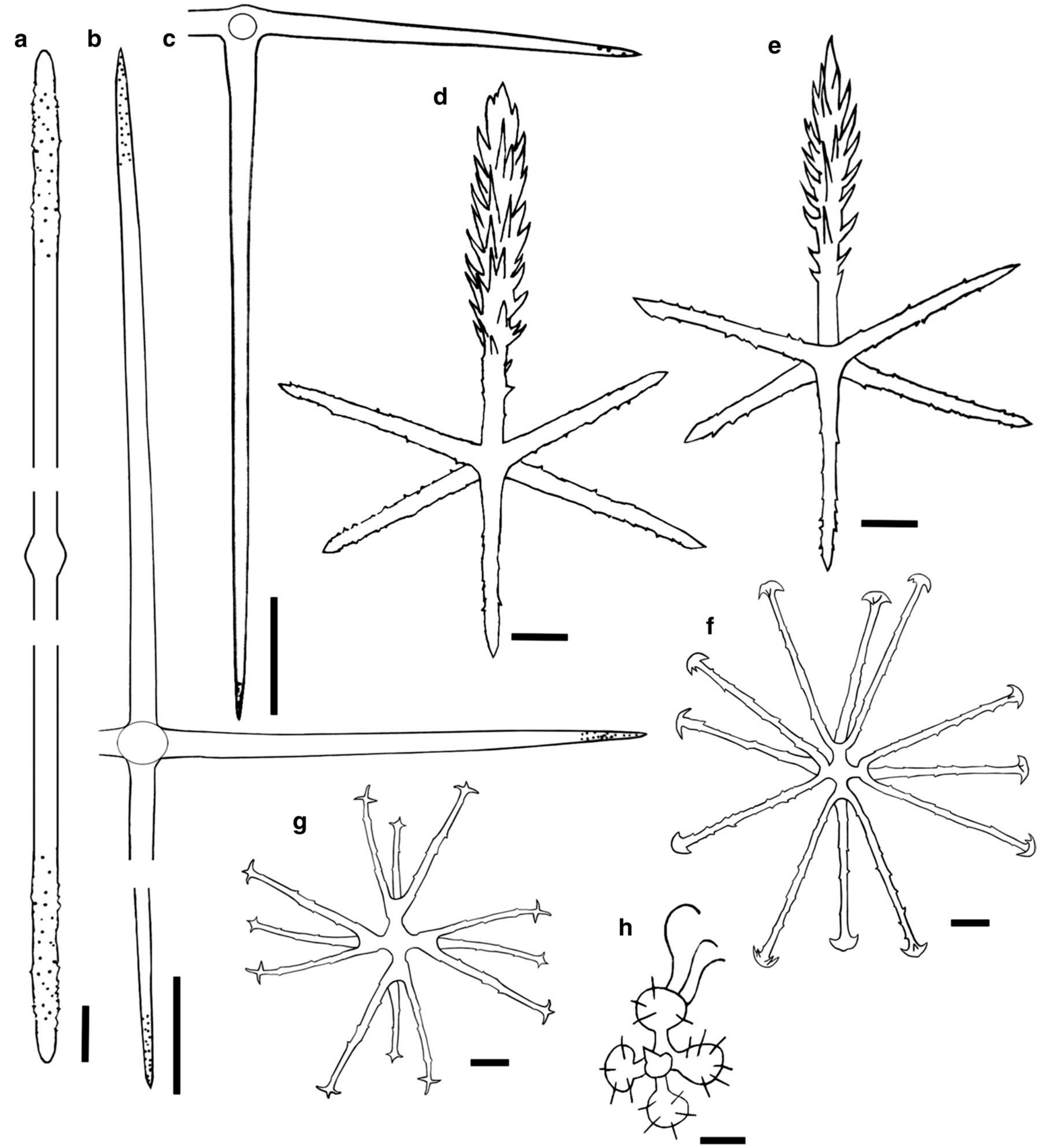


Fig. 7 *Sympagella tabachnicki* sp. nov. Spicules. **a** Choanosomal diactin, **b** choanosomal hexactin, **c** hypoatrial pentactin, **d** dermal pinular hexactin, **e** atrial pinular hexactin, **f** discohexaster, **g** onychexaster, and **h** strobiloplumicome. Holotype: **a**, **c**–**g**. Paratypes: **b** (MNRJ 13362) and **h** (MNRJ 7315A). *Scales* **a**, **d**, **e** = 20 μm; **b**, **c** = 100 μm; **f**, **g** = 10 μm; **h** = 5 μm

Paratypes: **OCEANPROF 1, BC-SUL**, MNRJ 7315A, 7316, stn 4 (Campos Basin, RJ, 22.366°S–39.893°W), 1128–1135 m depth, coll. R/V 'Astro Garoupa', demersal fisheries net, 07/ii/2003. **CAP BC Duto Gas**, MNRJ 13362, trecho 1, Espadarte Field (Campos Basin, RJ, 22.757°S–40.433°W), 945 m deep, coll. R/V 'Toisa Conqueror', ROV, 22/iii/2005.

Comparative material: *Sympagella nux* Schmidt, 1870—USNM 7588 (holotype, one dissociated spicule slide).

Diagnosis

Sympagella without prostalia lateralia, composed by diactins and hexactins as single choanosomal spicules;

Table 10 Spicule micrometries for *S. tabachnicki* sp. nov

	MNRJ 13365 (holotype)	MNRJ 7315A (paratype)	MNRJ 7316 (paratype)	MNRJ 13362 (paratype)
Diactin L	2864 ± 1108 (1075–4725)	3048 ± 1282 (1300–6200)	2664 ± 1061 (1075–5175)	2936 ± 1133 (1050–5150)
W	$13.0 \pm 5.0_{10}$ (8–25)	$15.5 \pm 5.6_{10}$ (10–28)	$12.3 \pm 4.8_{10}$ (8–23)	$12.5 \pm 3.1_{10}$ (8–18)
Choanosomal hexactin				
Ray L	215_1	$552 \pm 125.3_{10}$ (380–800)	420_1	554_1
W	9_1	$22.5 \pm 3.5_{10}$ (15–25)	$26.7 \pm 5.8_3$ (20–30)	10_1
Hypodermal pentactin				
Tangential ray L	428 ± 67.5 (325–550)	$419 \pm 56.1_{18}$ (320–510)	$368 \pm 98.0_{10}$ (230–520)	324 ± 62.4 (210–480)
W	$18.3 \pm 1.2_{10}$ (18–20)	$23.5 \pm 3.4_{10}$ (20–30)	$21.0 \pm 3.9_{10}$ (15–25)	$15.5 \pm 1.6_{10}$ (13–18)
Proximal ray L	$814 \pm 164.2_4$ (725–1060)	$760 \pm 293.5_5$ (425–1125)	$1425–1475_2$	335_1
W	$19.4 \pm 3.8_4$ (18–25)	$22.5 \pm 3.8_8$ (15–25)	$15–20_2$	$13–15_2$
Hypoatrial pentactin				
Tangential ray L	348 ± 88.4 (235–735)	$454 \pm 53.4_9$ (390–540)	$517 \pm 104.3_{15}$ (310–720)	437 ± 76.4 (270–590)
W	$15.3 \pm 2.2_{10}$ (10–18)	$22.8 \pm 2.6_9$ (18–25)	$24.0 \pm 3.2_{10}$ (20–30)	$22.3 \pm 1.4_{10}$ (20–25)
Proximal ray L	$520 \pm 67.3_3$ (465–595)	750_1	$875–2025_2$	920_1
W	$14.2 \pm 1.4_3$ (13–15)	$25.6 \pm 2.7_9$ (23–30)	$23.6 \pm 2.4_7$ (20–25)	$25–30_2$
Dermal pinular hexactin				
Pinular ray L	136 ± 22.7 (95–185)	144 ± 42.8 (90–280)	152 ± 25.8 (90–200)	131 ± 20.9 (85–185)
W	$24.3 \pm 3.1_{10}$ (20–28)	$28.0 \pm 4.2_{10}$ (23–38)	$24.8 \pm 2.8_{10}$ (20–30)	$23.0 \pm 3.1_{10}$ (18–28)
Tangential ray L	112 ± 14.6 (80–135)	107 ± 26.5 (70–175)	106 ± 14.1 (80–135)	100 ± 10.5 (75–120)
W	$10.0 \pm 1.2_{10}$ (8–13)	$10.0 \pm 1.3_{10}$ (8–9)	$8.8 \pm 1.3_{10}$ (8–10)	$8.8 \pm 1.3_{10}$ (8–10)
Proximal ray L	84.6 ± 8.7 (70–100)	82.3 ± 13.8 (63–113)	84.7 ± 10.5 (63–115)	79.0 ± 7.8 (60–95)
W	$9.0 \pm 1.3_{10}$ (8–10)	$9.0 \pm 1.3_{10}$ (8–10)	$9.5 \pm 1.6_{10}$ (8–13)	$9.5 \pm 1.1_{10}$ (8–10)
Atrial pinular hexactin				
Pinular ray L	138 ± 16.8 (100–170)	143 ± 17.3 (108–178)	145 ± 27.6 (90–185)	131 ± 17.6 (100–170)
W	$21.3 \pm 3.4_{10}$ (15–25)	$27.5 \pm 4.4_{10}$ (20–33)	$26.6 \pm 3.1_{10}$ (23–33)	$26.5 \pm 2.1_{10}$ (23–30)
Tangential ray L	99 ± 11.9 (65–125)	104 ± 10.8 (85–128)	114 ± 34.5 (83–265)	91 ± 10.6 (75–110)
W	$7.8 \pm 0.8_{10}$ (8–10)	$10.5 \pm 1.1_{10}$ (10–13)	$11.0 \pm 2.4_{10}$ (8–15)	$10.0 \pm 2.9_{10}$ (8–18)
Proximal ray L	79.4 ± 7.3 (70–100)	89.1 ± 12.3 (70–123)	88.5 ± 10.0 (68–110)	$77.0 \pm 7.8_{25}$ (65–95)
W	8_{10}	$9.0 \pm 1.3_{10}$ (8–10)	$11.0 \pm 2.7_{10}$ (8–18)	$9.5 \pm 1.1_{10}$ (8–10)
Microscleres				
Strobiloplumicome d	38_1	33_1	–	$23.8 \pm 4.3_4$ (20–30)
1^{ary} rosette d	15_2	$20.8 \pm 2.9_{10}$ (18–25)	20_1	$15.4 \pm 1.0_6$ (15–18)
Discohexaster d	98.2 ± 13.1 (55–120)	84.7 ± 9.6 (60–103)	82.1 ± 9.1 (65–100)	87.8 ± 11.6 (55–100)
Onychexaster d	$78.2 \pm 7.5_{18}$ (63–90)	77.9 ± 9.8 (58–98)	69.2 ± 6.9 (55–83)	76.3 ± 8.9 (55–98)
Primary rosette d	$12.8 \pm 2.2_{10}$ (10–15)	$13.3 \pm 2.4_{10}$ (10–18)	13_1	$12.3 \pm 1.8_{10}$ (10–15)

All measurements are in µm: mean $\pm$ SD_n (range if not 25)

L length, *W* width, *d* diameter

dermal and atrial pinular hexactins with columnar-shaped pinular rays; hypodermal and hypoatrial pentactins present; strobiloplumicomes, discohexasters and onychexasters as microscleres.

Description

Basiphytose sponge with saccular body, thin walls (ca. 1 mm), attached to solid substrate by a base (Fig. 6a). Holotype is 115 long × 154 wide × 16 mm thick. Paratypes are composed of fragments.

Skeleton

Choanosomal skeleton composed of diactins and rare hexactins. Hypodermalia and hypoatrialia are pentactins. Dermalia and atrialia are pinular hexactins. Basalia are hexactins fused to each other by synapticules.

Spicules (Table 10)

Choanosomal diactins are smooth and curved, with conical and microspined ends (Figs. 6b, 7a). Choanosomal hexactins have slightly curved rays with microspined

Table 11 Comparative morphological and distributional data for the species of *Sympagella* Schmidt, 1870

Species	Body form	Choanosomal spicules	Hypodermalia /hypoatrialia	Dermalia/atrialia	Microscleres	Locality/depth
S. tabachnicki sp. nov. (compiled from holotype and paratypes)	Saccular	D. 1075–6200/8–25 H. 380–800/9–25 (rare)	P_{HD}. tan. 210–550/15–30 pro. 425–1475/13–25 P_{HA}. tan. 235–735/10–30 pro. 465–2025/13–30	H_{DP}. pin. 85–280/18–38 tan. 70–175/8–13 pro. 63–115/8–13 H_{AP}. pin. 90–185/15–33 tan. 65–265/8–18 pro. 65–123/8–18	sp. 20–38/15–25 dh. 55–120 on. 55–98	SW Atlantic (Campos Basin, RJ)/945–1135 m
S. anomala Ijima, 1903 (orig. descr.)	Saccular or funnel-like	D. up to 2000/35 H. 700/15 (Exceptionally, tauactins and stauractins)	P. tan. 600/34 (can be absent)	H_{DP}. tan. 75–100	sp. 34–64 dh. 42 on. 68–100	Japan/430–572 m
sensu Lévi and Lévi (1989)		D. I. 6000/70–80 D. II. 2000–3000/15–25	P. tan. 300–800/15–25	H_{DP}. pin. 80–85/20 pro. 55–60 H_{AP}. pin. 110/10 pro. 70	sp. 25–45 dh/on. 45 ox. 60–100	Philippines/1650–1660 m
S. cantharellus (Lendenfeld, 1915) (orig. descr.)	Mushroom-like	D. 2200–9100/5–80 H. 160–2200 (Both can be spined)	P. tan 250–770/16–47 pro. 150–1370/15 (can be absent)	H_{DP}. 100–385 H_{AP}. 100–270	sp. 47–69 on. 39–130 ox. 90–133	Central–NO Pacific/4063 m
S. clavipinula Tabachnick and Lévi, 2004 (orig. descr.)	Funnel-like	D. 760–2580/9–30 H. 80–250/9–15 (And rare pentactins and stauractins)	P. tan. 340–1000/23–46 pro. 680–840/23–46	h_{dp}. pin. 182–258/19–122 tan. 53–91/7–23 pro. 76–106/7–23 h_{ap}. pin. 213–410/19–38 tan. 76–129/8–9 pro. 91–144/8–9	sp. 22–50 dh. 72–104/7–18 on, ox. 58–86/9–18	New Caledonia/680–780 m
S. cooki Tabachnick and Menshenina (2013) (orig. descr.)	Funnel-like	D. I: 1200–10,000/40–320 D. II: 1400–6800/6–15	P. tan. 500–700 pro. 1300–1400/20–30 H. 160–680/6–50	h_{dp}. pin. 67–130 tan. 63–89 pro. 37–81/5–7 h_{ap}. pin. 78–141 tan. 52–174 prox. 52–147/5–7) p_p. rare	sp. 25–47/11–14 on, hh. 107–141/6–15 oc. 104–148	N Mid–Atlantic Ridge/2620–2676 m
S. ecomari Tabachnick and Menshenina (2013) (orig. descr.)	Unknown (fragments)	D. 2400–3900/15	P. tan. 280–500 pro. 1140–610/20 H_{HD}. ray directed outside body 200; other rays 400–300 H_{HA}. ray directed inside the body 700–600/20 (Rare hexactins)	h_{dp}. pin. 93–267/7 tan. 78–148/4–5 pro. 59–122/4–5 h_{ap}. 70–196/7 tan. 67–111/4–5 pro. 37–85/4–5 p_p. rare	sp. 29–58/7–18 dh. 54–80/7–16 dc. rare	N Mid-Atlantic Ridge/2428–2623 m
S. gracilis (Schulze, 1903) (orig. descr.)	Funnel-like	D. 3000–5000/60–100 H. up to 1500	P. 400	h_{dp}. pin. 100–150/20–30 tan. 60 prox. 80 h_{ap}. pin. 160–260/40	sp. 40–50 on/ox. 80–100	Indonesia (Timor)/421 m

Table 11 continued

Species	Body form	Choanosomal spicules	Hypodermalia /hypoatrialia	Dermalia/atrialia	Microscleres	Locality/depth
S. johnstoni (Schulze, 1886) sensu Janussen et al. (2004)	Funnel-like (with prostalia lateralia)	D. 1800–10,000/10–500 H. large	P. present H. large	h_{dp}. pin. 60–173 tan. 66–133 pro. 15–184 h_{ap}. pin. 77–184 tan. 61–122 pro. 56–128	sp. 34–67/13–27 dh, on. 63–97/8–21 dc. 113–147	Antarctic and Subantarctic Islands/567–1543 m
S. multihexastera Tabachnick, Janussen and Menschenina, 2008 (orig. descr.)	Lamella-like (fragments)	D. 1500–2900/10–130 H. 150–370/10–26	P. tan. 250–870/14–26 pro. 300–1000/14–26	$H_{dp.}$ pin. 66–143 tan. 41–77 pro. 41–77/2–3 $H_{Ap.}$ pin. 92–204 an. 41–71; pro. 51–82	sp. 29–63/13–25 dh. 101–105/8–17 on. 63/8 ox, oc, hh. 76–113/8–17	NW Australia, 405 m
S. nux Schmidt, 1870 sensu Tabachnick (2002)	Saccular or funnel-like	D. 335–2128/4–12 H. 100–600/8–16	P. tan. 180–850/8–16 pro. 270–912/8–16 (Rare stauractins)	p_{dp}. pin. 50–137/6–12; tan. 23–122 h_{ap}. pin. 76–836/4–11; tan. 41–500; pro. 38–304	sp. 18–58/7–22 dh. 32–100/5–11 th. 29–32/7–11 ox, oc, md. present	W Mediterranean, Cape Verde Islands, Caribbean and SE Atlantic, 27–1476 m

Values are in µm

D diactins, *dh* discohexasters, *dc* discohexactins, *H* hexactins, H_{AP} atrial pinular hexactins, H_{DP} dermal pinular hexactins, H_{HA} hypoatrial hexactins, H_{HD} hypodermal hexactins, *hh* hemioxyhexasters, H_P pinular hexactins, *md* microdiasters, *oc* oxyhexactins, *on* onychexasters, *ox* oxihexasters, *P* pentactins, P_{DP} dermal pinular pentactins, P_{HA} hypoatrial pentactins, P_{HD} hypodermal pentactin, *pin* pinular ray, P_P pinular pentactins, *pro* proximal ray, *sp* strobiloplumicomes, *tan* tangential ray, *th* tylohexasters or tylohexactins ends (at least in the distal and proximal rays), which gradually taper (Fig. 7a). Hypodermalia and hypoatrialia are smooth pentactins with microspined and pointed ends (Figs. 6c, 7c). Dermalia and atrialia are hexactins with variably developed pinular rays bearing short spines; tangential and proximal rays are microspined, with conical or pointed ends (Figs. 6d–f, 7d, e). Microscleres are strobiloplumicomes, discohexasters and onychexasteres. Typical strobiloplumicomes are always found broken (Fig. 7h). Discohexasters (Figs. 6g, 7f) are spherical with toothed discs, with short primary rays and three long, spined, secondary rays. Onychexasters (Figs. 6h, 7g) have short primary rays and three long, microspined, secondary rays. In addition, a series of rare microscleres was observed, but judged to be of external origin: oxyhexasters (68–113 µm, n = 17), discohexactins (75–115, n = 4), onychexactins (58–60 µm, n = 2) and oxyhexactins (55–145 µm, n = 12) were found in the paratypes; and rare hemioxyhexasters (95–130 µm, n = 3), in the holotype and paratypes as well.

Habitat and distribution

This species is known only from its type locality in the SW Atlantic (Espadarte Field, Campos Basin, SE Brazil), 945–1135 m.

Etymology

The proposed name, *tabachnicki*, is in honour of Dr. Konstantin Tabachnick (Institute of Oceanology, Russian Academy of Science), who already described over 120 hexactinellid taxa from all around the world, including the Campos Basin area.

Remarks

The genus presently contains nine recognized species distributed in the Atlantic and Pacific Oceans, and Antarctica, between 27 and 4063 m depth (Table 11): *S. anomala* from NO Pacific, *S. cantharellus* from Central-NO Pacific, *S. clavipinula* from New Caledonia, *S. cooki* and *S. ecomari* from the Northern Mid-Atlantic Ridge, *S. gracilis* from Indonesia, *S. johnstoni* from Antarctica and Subantarctic Islands, *S. multihexastera* from NW Australia, and *S. nux* from the Mediterranean, Cape Verde Islands, the Caribbean, and SE Atlantic.

The Japanese *S. anomala* has been recently re-examined by [37], who have emphasized the pinular rays of its hexactins to be lanceolate in shape (thickest in the middle, fusiform). From Ijima's original description [36] it is apparent that only dermalia are lanceolate. Pinular hexactins of the Brazilian species have columnar-shaped pinular rays. Furthermore, Ijima's species was found to bear diactins as large as 2000 µm only, in great contrast to the 6000 µm reached by a few spicules in the new species. Exceptionally, *S. anomala* may bear choanosomal tauactins and stauractins, and its hypodermal/hypoatrial pentactins can be absent, which further distinguish the Japanese and Brazilian species.

Lèvi and Lèvi [53] described a rather deviating specimen of *S. anomala* from the Philippines, albeit judging it to be decidedly conspecific to the type. This specimen has a much larger and stouter category of choanosomal diactins (up to 6000/70–80 µm), as well as oxyhexasters. These authors did not mention the presence of choanosomal hexactins, tauactins and stauractins. We find the cospecificity hypothesis to be very unlikely, but the clarification of this issue is beyond the scope of the present contribution. Instead, we must figure how the Philippines' material differs from the new species presently described. This is obvious in the shape of the dermal pinules, which are lanceolated in the Philippines' sponge, the extremely stout choanosomal diactins (up to 70/80 µm), and the oxyhexasters, which are lacking in the new species.

The new species differs from *S. cantharellus* by the possession of choanosomal diactins considerably smaller and thinner (1075–6200/8–25 vs. 2200–9100/5–80 µm), which can be spined in the Pacific species. Additionally, *S. cantharellus* has a mushroom-like body form and oxyhexasters, whereas the new species has a saccular body form and no oxy-tipped microscleres. The hypodermal/hypoatrial pentactins can be absent in *S. cantharellus.*

Important distinguishing features for the new species in comparison to *S. clavipinula* are the presence of hypodermal/hypoatrial pentactins with smaller tangential rays (210–550/15–30 in the former vs. 340–1000/23–46 µm in the latter) and absence of oxyhexasters (in the former). Additionally, *S. clavipinula* has dermal pinular hexactins with spherical, club-shaped pinular rays (artichoke-like). Rare choanosomal stauractins were found in the New Caledonian species, whereas we failed to find a single spicule in the four S. Atlantic specimens described here.

Sympagella tabachnicki sp. nov. differs from N Atlantic *Sympagella* species by the absence of hypodermal/hypoatrial hexactins and the presence of onychexasters. The only species in the genus with diactins as the sole choanosomal megasclere are *S. anomala*, *S. cooki* and *S. ecomari*, which sets them apart from the new species who has choanosomal hexactins in addition. Furthermore, *S. cooki* possesses oxy-tipped microscleres (oxyhexasters, hemioxyhexasters and oxyhexactins), absent in the S. Atlantic species. Also, rare pinular pentactins are found in both species from N. Atlantic, but not in the new species.

The new species can be differentiated from *S. gracilis* by the latter's much thicker choanosomal diactins

(60–100 µm), dermal pinular hexactins with relatively smaller pinular rays (100–150/20–30 µm), possession of oxyhexasters, and lack of discohexasters.

Sympagella johnstoni is the only species in the genus with prostalia lateralia and conules in the body wall. The new species further differs from *S. johnstoni* by the latter's much larger choanosomal diactins (1800–10,000 µm) and possession of hypodermal/hypoatrial hexactins and discohexactins. Janussen et al. [37] reported diactins in *S. johnstoni* to be up to 500 µm thick, but this is a likely mistake, as the figure provided by these authors illustrates a 50 µm thick diactin, much more in accordance to values observed in other species of *Sympagella*, albeit still much thicker than the new species.

The new species differs from *S. multihexastera* by the latter's much smaller and thicker choanosomal diactins (1500–2900/10–130 µm), choanosomal hexactins with smaller rays (150–370 µm), dermal and atrial pinular hexactins with relatively smaller tangential and proximal rays (dermal: 41–77 µm; atrial: 41–71, 51–82 µm) and possession of oxyoidal microscleres (oxyhexasters, hemioxyhexasters and oxyhexactins).

Sympagella tabachnicki sp. nov. differs from *S. nux* by the latter's presence of dermal pinular pentactins (instead of hexactins), tylohexasters, oxyhexasters, oxyhexactins and microdiasters, and absence of onychexasters. In addition, *S. nux* has much larger and thinner atrial pinular hexactins (76–836/4–11 µm), and rare hypodermal/hypoatrial stauractins.

The Japanese *S. anomala* and *S. johnstoni* can be considered closer to new species by the presence of choanosomal diactins and hexactins, hypodermal/hypoatrial pentactins, pinular hexactins and only disco and onychotipped microscleres. However, the new species described here is distinguished from all species of *Sympagella* by one or more characters quoted above.

Family LEUCOPSACIDAE Ijima, 1903
Genus *Leucopsacus* Ijima, 1898
Leucopsacus barracuda sp. nov.
(Fig. 8; Tables 12, 13)

Type material

Holotype: **CAP BC** Barracuda, MNRJ 13368, area 40 line 37 (Campos Basin, RJ, 22.522°S–40.246°W), 744 m deep, coll. R/V 'Toisa Conqueror', ROV, 17/iii/2006.

Paratype: **CAP BC** Caratinga Oil Field 9.5', MNRJ 13369, bank 3 (Campos Basin, RJ, 22.623°S–40.264°W), 923 m deep, coll. R/V 'Toisa Conqueror', ROV, 12/iii/2006.

Diagnosis

Leucopsacus with diactins and hexactins as choanosomal spicules, dermal pentactins and small discohexasters (up to 80 µm) as microscleres, in addition to anchorate discohexactins and rare hemidiscohexasters.

Description

Basiphytose sponge with ovoid body, thin walls (ca. 2 mm), attached to solid substrate (coral) by a base (Fig. 8a). Holotype is 8 mm long × 7 mm wide, with a short peduncle about 1 mm in length, and osculum 3 mm in diameter. Paratype is composed by a fragment, 7 mm long × 10 mm wide × 1 mm thick.

Skeleton

Choanosomal skeleton composed by hexactins and diactins. Dermalia are pentactins and basalia are hexactines fused to each other by synapticules.

Spicules (Table 12)

Choanosomal hexactins are smooth, with straight or curved rays and pointed ends (Fig. 8b). Choanosomal diactins are smooth and curved, with a central knob and microspined pointy ends (Fig. 8c–e). Dermalia are smooth pentactins with conical and microspined ends (Fig. 8f). Microscleres are anchorate discohexactins and discohexasters. One hemidiscohexaster was found in the holotype and it was considered proper. Anchorate discohexactins have long and microspined rays with toothed discs (Fig. 8g). Discohexasters (Fig. 8h) have short primary rays and four long, microspined secondary rays.

Habitat and distribution

This species is known only from its type locality in the SW Atlantic (Barracuda Field, Campos Basin, SE Brazil), 744–923 m. Holotype was collected epibiontic on dead *Enallopsammia rostrata* (Pourtalès, 1878).

Etimology

The proposed name, *barracuda*, is a noun in apposition, derived from the species' type locality, Barracuda Oil Field (Campos Basin, SW Atlantic).

Remarks

The genus presently contains four recognized species distributed in the Atlantic and Pacific Oceans, between 214 and 1378 m depth (Table 13): *L. distantus* from New Caledonia, *L. ingolfi* from Boreal Atlantic, *L. orthodocus* from Japan, and *L. scoliodocus* from Japan and

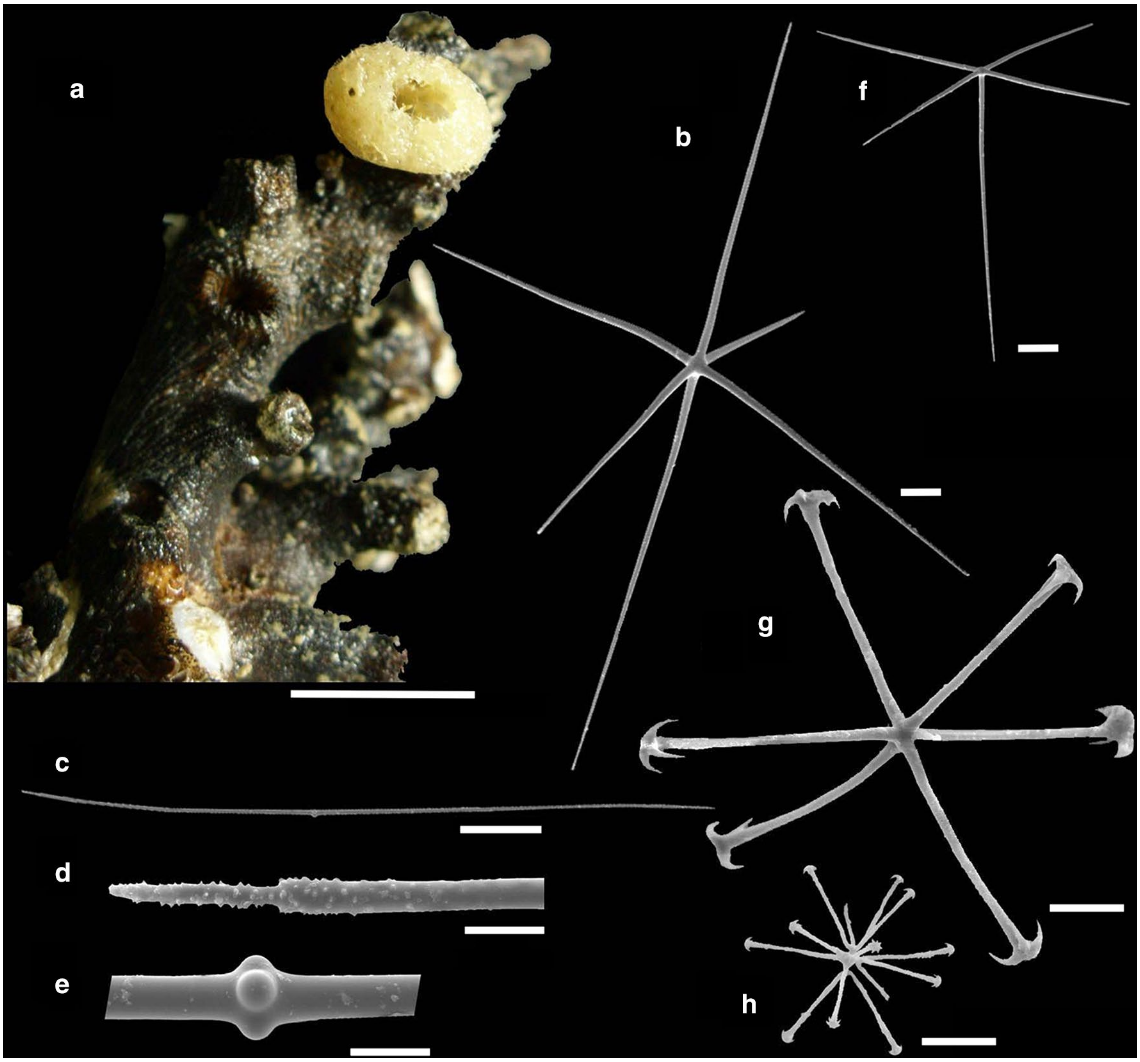


Fig. 8 *Leucopsacus barracuda* sp. nov. **a** Holotype (MNRJ 13368). **b**–**h** SEM of the spicules: **b** choanosomal hexactin, **c** choanosomal diactin, **d** end of the choanosomal diactin, **e** central knob of the choanosomal diactin, **f** dermal pentactin, **g** anchorate discohexactin, and **h** discohexaster. Holotype: **b**–**g**. Paratype: **h** (MNRJ 13369). *Scales* **a** = 10 mm; **b**, **f** = 100 μm; **c** = 200 μm; **d**, **e**, **g**, **h** = 20 μm

Cape Verde Island. *Leucopsacus ingolfi* is closest to the new species by the presence of choanosomal diactins and absence of atrial hexactins. However, the new species differs from N Atlantic species by the presence of larger choanosomal hexactins (380–1334 vs. 300 μm), dermal pentactins (tangencial rays 287–677 and proximal rays 493–1047 vs. tangencial rays 180 and proximal rays 400 μm) and anchorate discohexactins (95–165 vs. 70 μm) and, much smaller discohexasters (38–78 vs. 440 μm).

Discussion

Deep sea sponge grounds are considered Vulnerable Marine Ecosystems (VME; [34]). This is so because (1) they are important as shelter and nursery for juvenile life-stages, (2) are fragile (low recovery prognosis), (3) usually harbor long-lived and slow-growing dominant species, (4) and can increase habitat heterogeneity (ecological processes dependent on the highly structured system). Despite the fact that, given data available now, there seems to be no deep-sea sponge reefs nor ostur

Table 12 Spicule measurements of *L. barracuda* sp. nov

	MNRJ 13368 (holotype)	MNRJ 13369 (paratype)
Choanosomal hexactin L	$1051.7 \pm 189.7_{4}$ (923–1334)	$614.4 \pm 138.9_{25}$ (380–872)
W	$16.9 \pm 3.2_{4}$ (13–20)	$8.8 \pm 1.8_{10}$ (8–13)
Choanosomal diactin L	$2859.4 \pm 757.9_{8}$ (1500–3950)	$2332.1 \pm 435.6_{7}$ (1675–2775)
W	$10.3 \pm 1.6_{8}$ (8–13)	$6.8 \pm 1.9_{7}$ (5–10)
Dermal pentactin		
Tangential ray L	$570.6 \pm 69.9_{13}$ (410–677)	$324.2 \pm 32.9_{5}$ (287–369)
W	$15.8 \pm 1.7_{10}$ (13–18)	$9.4 \pm 2.4_{4}$ (8–13)
Proximal ray L	$1015.7 \pm 27.2_{3}$ (995–1047)	$493–790_{2}$
W	$15.8 \pm 1.4_{3}$ (15–18)	10_{2}
Microscleres		
Anchorate discohexaster d	$139.1 \pm 15.2_{16}$ (115–165)	95_{1}
Discohexaster d	$53.8 \pm 8.4_{25}$ (38–78)	$59.7 \pm 7.6_{25}$ (43–70)
Hemidiscohexaster d	100_{1}	Not found

(*Geodia* banks) in the Campos Basin area, there occur nevertheless important sponge aggregations associated to the deep-sea coral mounds [56, 58, 61], and these are obviously fragile and vulnerable.

For some time, notable deep-sea coral mounds were known to occur at Campos Basin. Viana et al. [106] reported these to extend for hundreds of meters in length and tens in width, reaching up to 15 m in height, and spreading over at least 40 km. Similar structures were later reported from the perimeter of seabed pockmarks at Santos Basin (700 m depth) by Sumida et al. [84], who interpreted their finding as supporting evidence for the widespread occurrence of coral banks off SE Brazil. In both cases, it is the highly oxygenated and vigorously flowing Antarctic Intermediate Waters, as well as likely seepage of light hydrocarbons that seem to render possible the occurrence of these complex communities. The uniqueness along the Brazilian coast of these SE Brazilian deep sea habitats is unlikely. This is so in view of the occurrence of isolated records of azooxanthelate reef-building corals off most of the Brazilian coast [14, 39, 69], and of similar prevailing environmental conditions along a vast stretch of the NE South-American slope (Brazil's SE and NE slope) [15, 17, 56]. Lopes et al. [59] drew attention to the fact that Brazil was not equipped for state-of-the-art academic studies of deep sea habitats then, due to lack of appropriate oceanographic vessels. This scenario has been changing lately, so that great expectations exist on forthcoming findings of deep-sea coral and sponge banks on the Brazilian continental slope.

Table 13 Comparative morphological and distributional data for the species of *Leucopsacus* Ijima, 1898

Species	Choanosomal spicules	Dermal pentactins	Atrial hexactins	Anchorate discohexactins	Discohexasters	Other microscleres	Locality/depth (m)
L. barracuda sp. nov. (compiled from holotype and paratype)	H. 380–1334/8–20 D. 1500–3950/5–13	tan. 287–677/8–18 pro. 493–1047/10–18		95–165	38–78	hd. 100 (rare)	SW Atlantic (Campos Basin, RJ)/744–923
L. distantus Tabachnick and Lévi, 2004 (orig. descr.)	H. 1000–5500/4–91 (also pentactins and stauractins)	tan. 1100–1800/38 pro. 4100–4200		262–245	I. 47–58 II. 532–912		New Caledonia/680–700
L. ingolfi Burton, 1928 (orig. descr.)	H. 300 (media) D. present	tan.180 pro. 400		70	440 (media)		Boreal Atlantic/1317–1376
L. orthodocus Ijima, 1898 sensu Tabachnick (2002)	H. rays up to 500 D. 1500 (rare)	tan. 270 pro. 2 × tan	280 (at least)	110–168	50–88	hd. present	Japan/214–429
L. scoliodocus Ijima, 1903 (orig. descr.)	H. rays up to 4000 D. present	tan. 500–800 pro. 2 × tan	260–340	100–180	46–70	s. 38–50	Japan/572
L. scoliodocus *var. retroscissus* Topsent, 1904 (orig. descr.)	H. rays up to 2000 D. rare	tan. 400–500/25–30		105	40–60	hd. present s. 50	Cape Verde Islands/598–1378

Values are in µm

D diactins, *H* hexactins, *hd* hemidiscohexasters, *s.* sigmatocomes, *pro* proximal ray, *tan* tangential ray

Authors' contributions
MSC concluded descriptions and plates of Demospongiae, drafted species' remarks and article discussion. DAL identified and described the Hexactinellida. BC drafted species descriptions and plates for the Demospongiae, aside *Xestospongia*. EH took part in identification of all species, in rounding up descriptions, remarks, tables, plates and the discussion. All authors read and approved the final manuscript.

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