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Sponges (Demospongiae, Poecilosclerida) from New Deep-sea Frontiers in the Southwestern Atlantic: New Species, New Combinations and Taxonomic Remarks on *Echinostylinos*

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Echinostylinos comprises 11 species, among which a single, recently reported record for the South Atlantic. Here we propose two further new species from this ocean basin. *Echinostylinos iatapiuna* sp. nov. (2300–3200 m depth, São Paulo Ridge) and *Echinostylinos abyssalis* sp. nov. (4008 m depth, São Paulo Ridge). The latter pushes the genus' known distribution into the abyssal zone for the first time. The morphologic variation observed in the microscleres of *Echinostylinos* is briefly discussed, motivating our proposal to transfer *Echinostylinos glomeris* (Topsent, 1904, as *Esperiopsis*) to *Abyssocladia*, a stipitate or likely so, which compound with chelae of cleistochelae morphology to point to the latter genus as its best assignment. An identification key for *Echinostylinos* spp. is offered (now 13). In addition, a new species of *Chondrocladia* is described, namely *Chondrocladia* (*Chondrocladia*) *trisigmata* sp. nov. (3250–3270 m depth, south of the Vitória-Trindade seamounts' chain). Finally, some biogeographic considerations are made about abyssal sponge records in the South Atlantic.

Key words: Porifera, Shinkai, MD55, Abyssal fauna, Bathyal fauna, Manned submersible, South Atlantic, Carnivorous sponges

BACKGROUND

The southwestern Atlantic is characterized by prominent topographical features such as the Vitória-Trindade seamounts chain, the São Paulo Ridge and the Rio Grande Rise. The Vitória-Trindade seamounts chain is located offshore Brazil's eastern coast (off Espírito Santo state) and is characterized by a longitudinally oriented linear ridge, approximately 950 km long at the latitude of 20°30'S (Motoki et al. 2012). The Franco-Brazilian expedition "TAFF MD-55/Brazil 1987" sampled along these seamounts on board the R/V 'Marion Dufresne' in depths of 15 to 5100 meters (Tavares 1999), and most of the Porifera collection of this expedition had been untouched until recently (Tabachnick et al. 2009; Castello-Branco et al. 2016). The São Paulo Ridge is about 350 km long at the latitude of 28–29°S, and is located between the São Paulo Plateau, and the Vema Channel (off S and SE Brazil). It comprises a linear submarine chain with about 220 km extension, and bathymetric range between 2000 and 4400 m depth (Bassetto et al. 2000; Goto et al. 2017; Perez et al. 2020). In 2013, a Japanese-Brazilian scientific research expedition, 'Iata-Piuna', onboard the JAMSTEC R/V 'Yokosuka', along with the manned submersible 'Shinkai', sampled along the São Paulo

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Ridge and Rio Grande Rise, focused in the investigation of deep-sea ecosystems associated with geological and tectonic features in the area (Hajdu et al. 2017; Kitazato et al. 2017).

Echinostylinos Topsent, 1927 is a cold-water genus (55–2500 m), known from the North Atlantic, Northwest and South Pacific, with 11 species described this far. Included in the family Phellodermidae van Soest & Hajdu, 2002 with *Phelloderma* Ridley & Dendy, 1886, both genera are differentiated especially by the morphology of their isochelae. Affinities of phellodermids and cladorhizids (*Abyssocladia* Lévi, 1964 - Cladorhizidae Dendy, 1922, carnivorous sponges) are gradually becoming clearer. Originally proposed as pertaining to the Mycalidae Lundbeck, 1905 (Lévi, 1964), *Abyssocladia* has been placed amidst cladorhizids (*Asbestopluma* Topsent, 1901, *Chondrocladia* Thompson, 1873, *Cladorhiza* Sars, 1872) since its inception (Lévi 1964; Koltun 1970). Anyhow, van Soest and Hajdu (2002) considered *Abyssocladia* to be a likely junior synonym of *Phelloderma*, classified in their newly proposed Phellodermidae, that also included *Echinostylinos*. This decision was based on an interpretation of the chelae of these sponges to be of arcuate morphology, thus prompting recognition of their affinities to the abandoned suborder Myxillina (Morrow and Cardenas 2015). Subsequent work by Vacelet (2006) observed that sigmancistras were present in all seven species known until then, and some showed evidence of carnivory. This led him to transfer *Abyssocladia* to Cladorhizidae, despite a belief that the latter family might be polyphyletic. Molecular data generated by Vargas et al. (2012) verified the monophyly of Cladorhizidae, provided *Abyssocladia* was left in it. While Cladorhizidae includes 15 genera currently (de Voogd et al. 2022), Phellodermidae is left with *Echinostylinos* and *Phelloderma*, whose affinities have not yet been verified by any independent data source. Göcke et al. (2016) found additional evidence of "myxilline" affinity in their newly described *Phelloderma oxychaetoides* Göcke, Hajdu & Janussen, 2016, which possessed oxychaetes of similar morphology to those observed in irrefutable "myxillines" such as *Chaetodoryx* Topsent, 1927. It seems thus that *Phelloderma* and consequently Phellodermidae, are best classified away from the Cladorhizidae. For now, the "true" affinities of *Echinostylinos* remain an open question. As currently understood, *Echinostylinos* is recognizable by the possession of (strongylo) style megascleres and microscleres that include arcuate isochelae and, most of the times, sigmas. Notwithstanding, the first record for the South Atlantic was made only recently from 1100–1130 m depth at Campos Basin – *E. brasiliensis* Carvalho et al. 2016. This species bears tetradentate unguiferate isochelae as its only microscleres. With the above in mind, the main objectives of the present study were to describe two new South Atlantic species of *Echinostylinos* (including its first abyssal record) and one of *Chondrocladia*. In addition, two species formerly assigned to *Echinostylinos* are reassessed here, briefly redescribed, and transferred to *Abyssocladia*. An identification key for all known species of the former genus is proposed with updated comparative table, and a few considerations on its biogeography are advanced.

MATERIALS AND METHODS

The specimens studied are part of the Museu Nacional/UFRJ Porifera collection and they were part of two different expeditions. In the first of these, in 1987, MD-55 expedition with the R/V 'Marion Dufresne', specimens were dredged on the Vitoria-Trindade seamounts (SE Brazil). In the other, in 2013, the Iata-Piuna expedition with the 'Shinkai' manned submersible and "R/V "Yokosuka", specimens were collected by robotic arms on the São Paulo Ridge and Rio Grande Rise (SW Atlantic international waters; see Fig. 1). Specimens were studied following the standard procedures outlined in Hajdu et al. (2011). Morphometric data was obtained from 30 spicules, unless stated otherwise. Scanning electron microscopy pictures were taken on a JEOL JSM-6390LV Scanning Electron Microscope (SEM) of the Museu Nacional.

Additional comparative material of *Echinostylinos* species from other Porifera collections were analyzed (Muséum National d'Historie Naturalle). Abbreviations used: MNHN – Porifera collection, Muséum National d'Histoire Naturelle; MNRJ – Porifera Collection, Museu Nacional/UFRJ, Rio de Janeiro, Brazil.

RESULTS

TAXONOMY

Phylum Porifera Grant, 1836
Class Demospongiae Sollas, 1885
Subclass Heteroscleromorpha Cárdenas, Pérez & Boury-Esnault, 2012
Order Poecilosclerida Topsent, 1928
Family Phellodermidae van Soest & Hajdu, 2002
Genus *Echinostylinos* Topsent, 1927

Diagnosis: Anastomosing branches, erect bushes or semiglobular masses. Surface irregular or conulose. Skeleton of smaller ectosomal megascleres

(styles or subtylostyles) or assuming a partly erect and partly tangential position and larger choanosomal styles forming an axially condensed mass or a vague reticulation of tracts and single spicules. Microscleres arcuate chelae and sigmas (modified from van Soest and Hajdu 2002).

Remarks: Diagnosis adapted to included styles as the smaller ectosomal megascleres.

***Echinostylinos iatapiuna* sp. nov.**

(Fig. 2)

urn:lsid:zoobank.org:act:838127E5-28EA-4812-AC34-F123F61D9A61

Material examined: Holotype. MNRJ 17631, São Paulo ridge, Southwest Atlantic (Iata–Piúna Expedition, 'Shinkai' submersible, Dive 156–1, YK13-04, st.02, -28.4033 / -40.9816), coll. H. Kitazato, depth 2300–3300 m, 29.IV.2013.

Diagnosis: *Echinostylinos iatapiuna* sp. nov. is the only *Echinostylinos* with a single category of megascleres (styles) and one category each of sigmas and spatulate arcuate tridentate isochelae larger than 60 µm.

Description: Cushion-shaped, roundish and flattened like a cookie, 30 × 2.7 mm in area, 7 mm thick. Compressible, with irregular surface, color beige in ethanol (Fig. 2A).

Skeleton: Ectosome and choanosome undifferentiated. Spongin abundant. Megascleres in uni- to paucispicular, inter-crossing, loose ascending tracts, further obscured by megascleres strewn in confusion. Sigmas scattered everywhere, and isochelae mainly in the ectosome (Fig. 2B).

Spicules: Megascleres a single category of styles (Fig. 2C), smooth, straight to slightly curved, tapering gradually to acerate ends, 1100–1219–1350 × 20–24.8–28 µm. Microscleres isochelae and sigmas. Tridentate

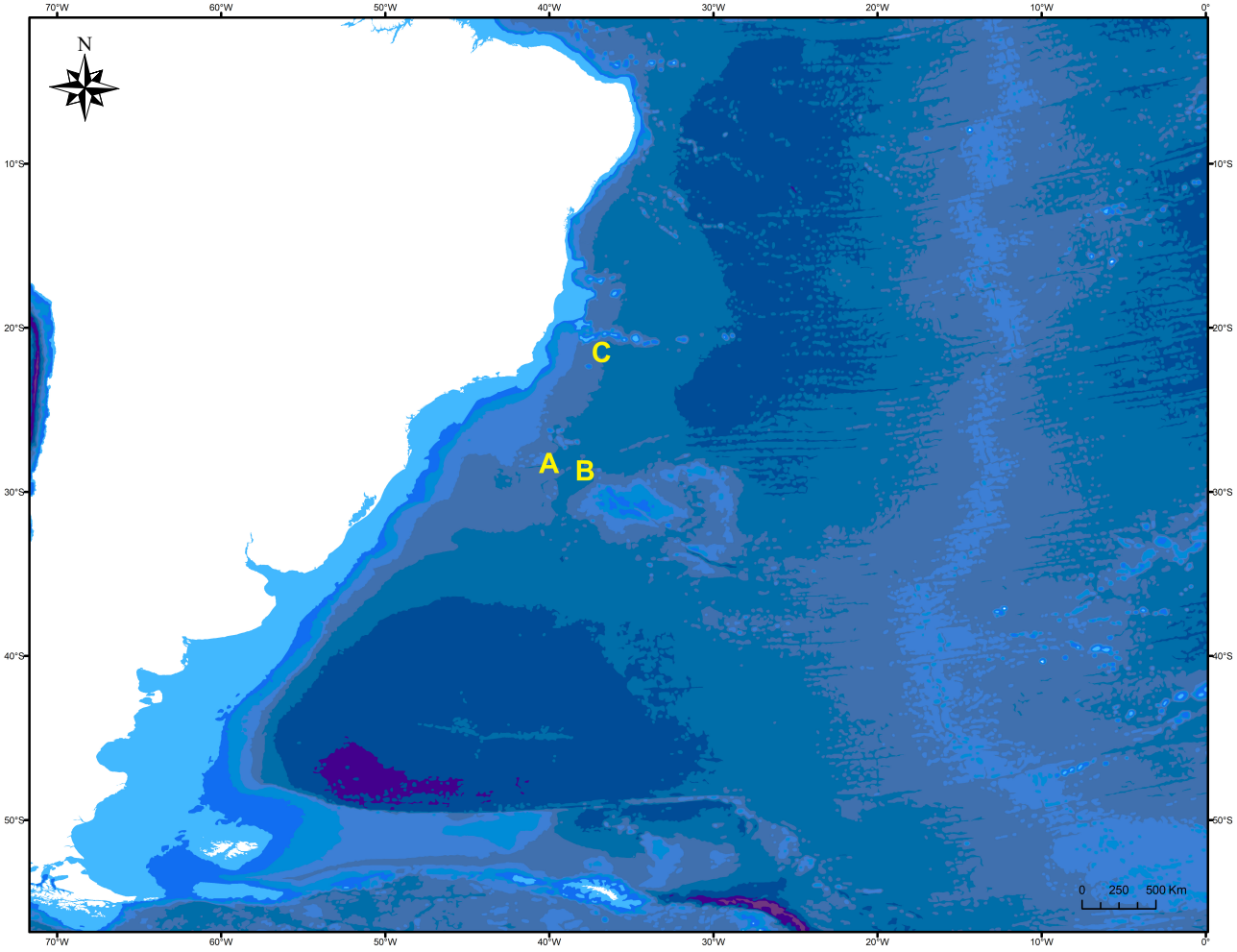


Fig. 1. Map of the sampled region in the Southwestern Atlantic: A) Sampling locality of *Echinostylinos iatapiuna* sp. nov.; B) Sampling locality of *Echinostylinos abyssalis* sp. nov.; and C) Sampling locality of *Chondrocladia* (*Chondrocladia*) *trisigmata* sp. nov.

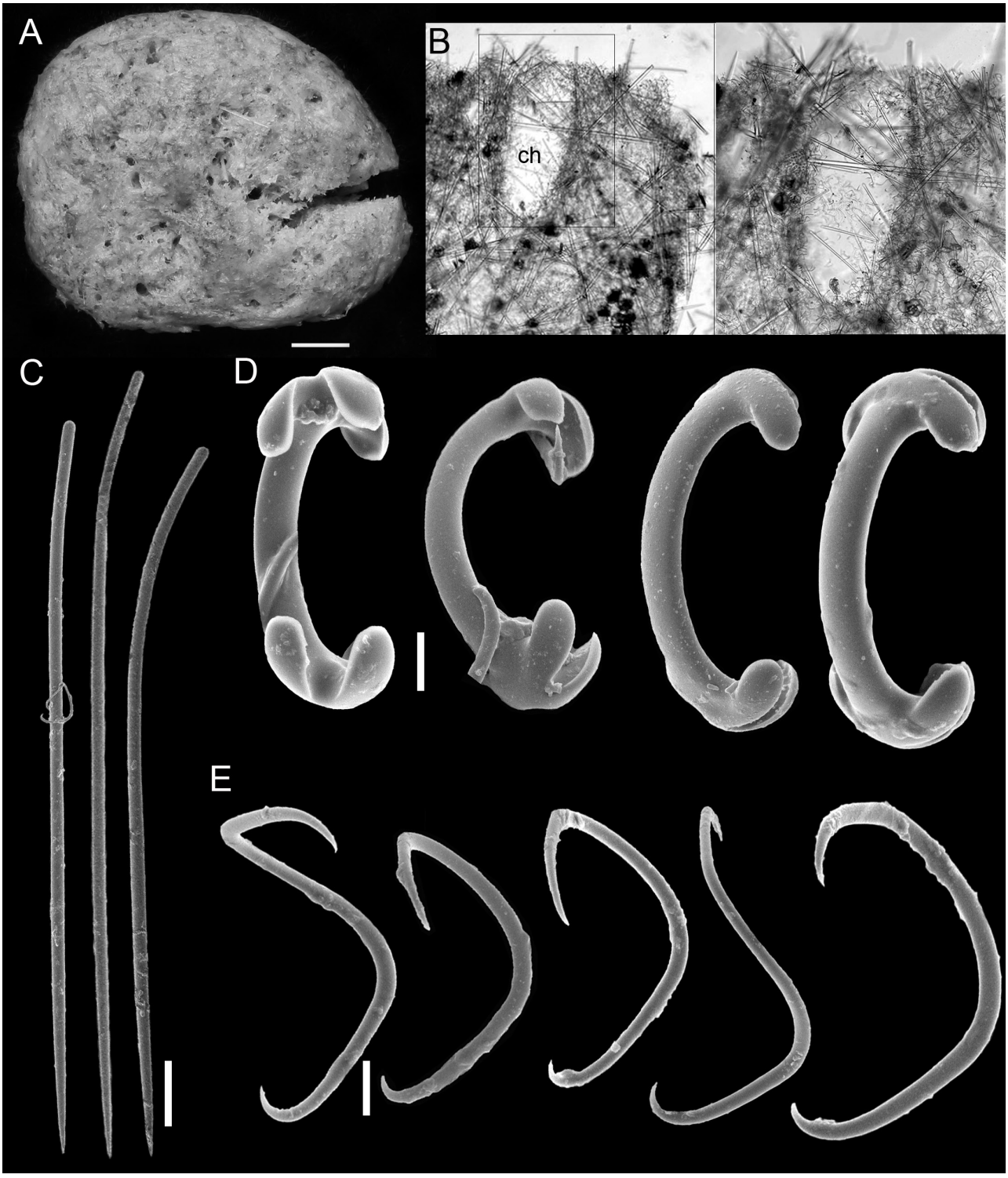


Fig. 2. Holotype of *Echinostylinos iatapiuna* sp. nov. (MNRJ 17631). A, preserved specimen; B, transversal section of skeleton; C, styles: D, isochelaes; E, sigmas. Scale bars: A = 5 mm; B–C = 100 μm; D–E = 10 μm.

isochelae (Fig. 2D), with short, feebly developed spatulate teeth, 68–73.5–88 µm. Sigmas, smooth (Fig. 2E), C or S–shaped, tapering gradually to both, asymmetrical apices, 60–71.1–88 µm.

Distribution and Ecology: Known only from its type locality, at bathyal depths (2300–3300 m) in the São Paulo ridge (SW Atlantic). The holotype was sampled associated to corals (*Solenosmilia* spp.).

Etymology: The specific epithet, *iatapiuna*, is proposed as a noun in apposition, and refers to the name of the oceanographic expedition in which this new species was collected.

Remarks: The species appearing closest to *Echinostylinos iatapiuna* sp. nov. is *E. schmidtii* (Arnesen, 1903; type locality Norway, 500 m depth), sharing the same spicule categories, viz. one category each of styles, isochelae and sigmas. However, the dimensions of these are considerably different so that no doubt rests that both are separate valid species. The type of *E. schmidtii* is apparently lost (cf. Carvalho et al. 2016), but the original description of isochelae around 40, and sigmas around 20 µm long, sets it confidently apart from the new species' 67–88 µm long isochelae, and 60–88 µm long sigmas. Additional species in *Echinostylinos* differ even further, both in terms of spicule categories present, as well as on morphometric aspects (see Table 2: a new version here of Table 8 in Carvalho et al. 2016). Comparison to the second new species proposed in the present study will be carried in the remarks to *E. abyssalis* sp. nov. (see below).

Echinostylinos abyssalis sp. nov.

(Fig. 3)

urn:lsid:zoobank.org:act:E21D5BEE-CA32-4F83-BBF9-B09979F8D0ED

Material examined: Holotype. MNRJ 17633, São Paulo Ridge, Southwest Atlantic (Iata–Piúna Expedition, Shinkai submersible, Dive 1333, -28.5133 / -41.6533), coll. H. Kitazato, depth 4008 m, 23.IV.2013.

Diagnosis: The only *Echinostylinos* with two categories of megascleres differentiated only by width, and microscleres, which are solely tridentate arcuate isochelae (tending to unguiferate morphology).

Description: Erect, perhaps semi-infundibuliform (half a funnel; but *in situ* image not very sharp, and collected specimens fragmented), fragile, largest fragment 75 mm long × 8 mm wide at the base, and 28 mm wide on apical region (Fig. 3B); smallest fragment 60 mm long × 4 mm wide at the base, and 29 mm wide on the apex. Compressible with irregular surface, color whitish *in situ*, beige in ethanol (Fig. 3A).

Skeleton: Ectosome with thinner megascleres (styles II) in ascending bundles. Choanosome with thicker megascleres (styles I) in ascending, loose, pauci- to multispicular tracts, sometimes forming ill-defined multispicular tracts. Microscleres abound all around (Fig. 3B).

Spicules: Megascleres are two categories of styles, both smooth and slightly curved, tapering gradually to acerate ends. Styles I, 572–781.8–854 × 17–19.7–24 µm (Fig. 3C); styles II, 446–497–582 × 7–10.6–12 µm (Fig. 3D). Microscleres, tridentate arcuate isochelae with pointy teeth, 29–32.5–36 µm (Fig. 3E).

Distribution and Ecology: Known only from its type locality, at an abyssal depth (4008 m) in the São Paulo ridge (SW Atlantic). Holotype founded growing on consolidated bottom.

Etymology: The specific epithet, *abyssalis*, is proposed as a noun in apposition, and refers to the type specimen's depth zone of occurrence, the abyssal zone.

Remarks: *Echinostylinos abyssalis* sp. nov. is distinguished among its congeners as the sole species bearing two categories of styles (differentiated by width), and a single category of microscleres, namely tridentate, somewhat unguiferate, arcuate isochelae. When compared to other *Echinostylinos* spp., *E. brasiliensis* (also from the SW Atlantic) appears the closest. However, *E. brasiliensis* presents only one category of megascleres and also of isochelae. With isochelae even smaller (22–28 µm) than those in the new species (29–36 µm). When compared to the other new species described above, *E. abyssalis* sp. nov. presents two categories of megascleres and only one of isochelae, while *E. iatapiuna* sp. nov. presents only one category of megascleres and isochelae plus sigmas. Regarding the isochelae shapes, *E. abyssalis* sp. nov. presents somewhat unguiferate alae, while in *E. iatapiuna* sp. nov. is spatulate. Additional species of *Echinostylinos* differ in terms of spicule categories present, and on morphometric aspects.

Family Cladorhizidae Dendy, 1922
Genus *Chondrocladia* Thomson, 1873

Diagnosis: Cladorhizidae with anchorate isochelae (Lee et al. 2012).

Subgenus *Chondrocladia* (*Chondrocladia*) Thomson, 1873

Diagnosis: *Chondrocladia* without a layer of special spicules (spear-like tylostyles or trochirhabds), lacking special rostriform (snoutlike) subtylostyles in filaments or terminal balls, and without planar vanes formed of evenly spaced upright branches (Lee et al. 2012).

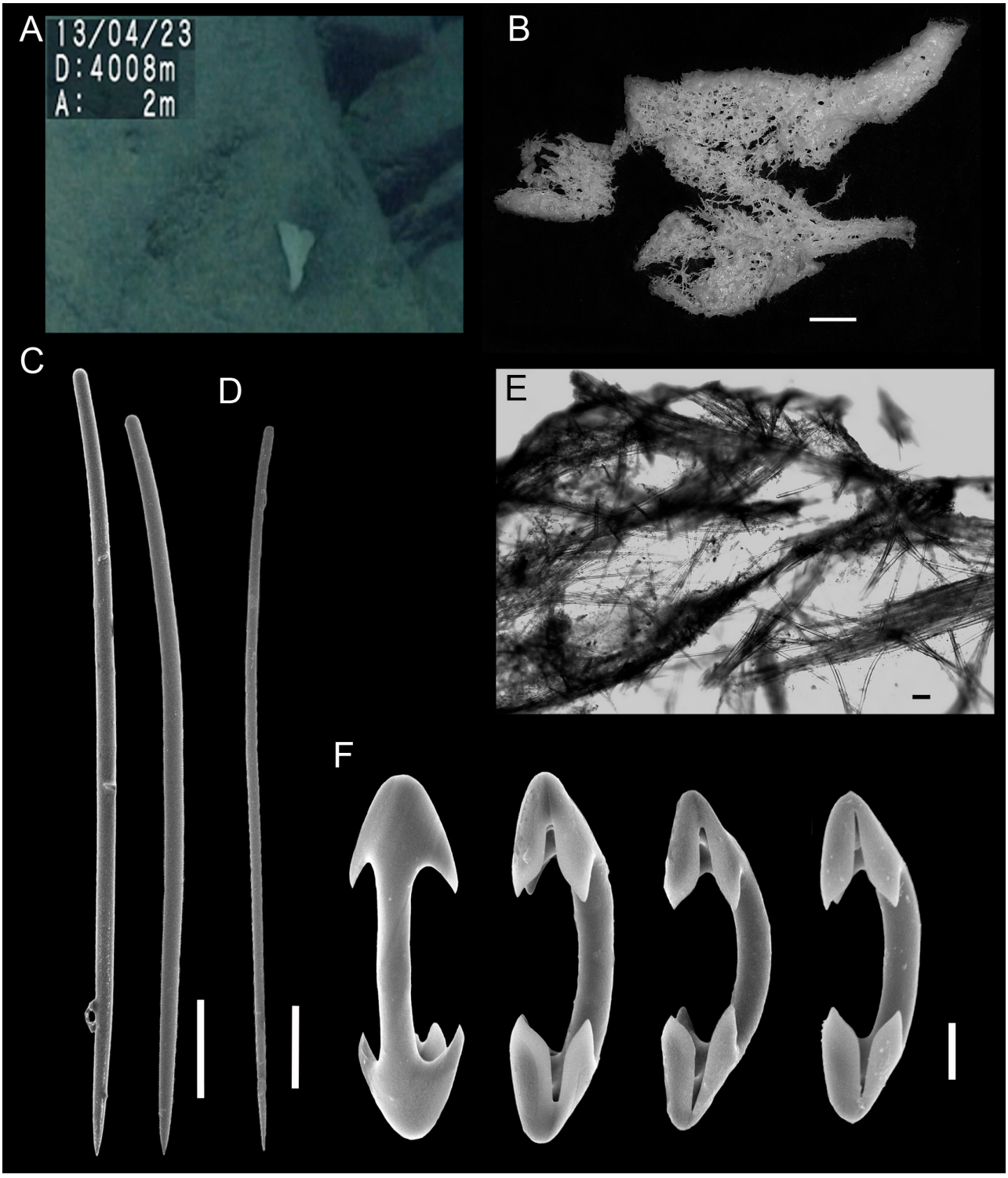


Fig. 3. Holotype of *Echinostylinos abyssalis* sp. nov. (MNRJ 17633). A, specimen *in situ*; B, specimen in ethanol; C, styles I; D, styles II; E, transversal section of skeleton; F, isochelae. Scale bars: B = 10 mm; C, D = 100 µm; E = 500 µm; F = 5 µm.

Chondrocladia (*Chondrocladia*) *trisigmata* sp. nov.

(Fig. 4)

urn:lsid:zoobank.org:act:ABEFBD2A-55AC-4051-B5FE-50E7FA873FFF

Material examined: Holotype. MNRJ 16000, continental rise to the south of the Vitória-Trindade seamounts' chain, off SE Brazil, Southwest Atlantic (R/V '*Marion Dufresne*' MD-55 Expedition, Stn. 8 CP17, -21.134 / -38.4349), collection method: dredge, 3250–3270 m depth, coll. N. Boury-Esnault, 11.V.1987.

Diagnosis: The only *Chondrocladia* (*Chondrocladia*) species with three categories of sigmas.

Description: Massive, rounded; smooth surface with scattered circular structures. No projections seen. Specimen in fragments (Fig. 4A), the biggest one 12 × 12 mm in area and 5 mm thick. Compressible consistence, rough and easy to tear. Color beige in ethanol.

Skeleton: Ectosomal skeleton with a layer of organic material, megascleres type II and microscleres arranged irregularly. Choanosomal skeleton with an irregular reticulation of megascleres just below the ectosome, and ascending tracts of styles I with microscleres randomly scattered in the body fragment analyzed.

Spicules: Megascleres are two size categories of styles. Styles I (Fig. 4C), smooth, fusiform, one end rounded and the other tapering gradually, conical or hastate; 1287–2126.9–3318 × 19–32.8–50 µm. Styles II (Fig. 4D), smooth, straight with one end rounded and the other hastate to conical; 378–1000.7–1232 × 14–18.6–22 µm. Microscleres are two categories of anchorate isochelae, and three categories of sigmas. Isochelae I (Fig. 4E), smooth, long shafted, tridentate with pointy alae, 65–82.2–98 µm long. Isochelae II (Fig. 4F), smooth tridentate with pointy alae, 37–42–50 µm long. Sigmas I (Fig. 4G), slender, tapering gradually to sharp ends, 77–90.5–96 µm long. Sigmas II (Fig. 4H), similar to sigmas I, but shorter, 22–28.2–36 µm long. Sigmas III (Fig. 4I), C-shaped, markedly fusiform, with central part bearing lateral fimbria-like expansions, 9.6–10.8–13 µm long.

Distribution and Ecology: Known only from its type locality, the continental rise to the south of the Vitória-Trindade seamounts chain region (SW Atlantic), at 3250–3270 m depth.

Etymology: The specific epithet, *trisigmata*, is used as a noun in apposition, and refers to the three categories of sigmas present in the new species, a distinguishing feature within its subgenus.

Remarks: Although these fragments, at first look, do not look like a carnivorous sponge, the specimen was dredged in 1984 on board of the R/V '*Marion Dufresne*', it is very common to receive damaged specimens or even only fragments. After careful analyzes of its peculiarities on the surface, plus skeleton and spicule set, we were convinced of its classification. *Chondrocladia* (*Chondrocladia*) presents 34 valid species distributed worldwide (Ekins et al. 2020; de Voogd et al. 2022). The new species differs from its congeners by the presence of three categories of sigmas (see comparative table including data from all species from every other subgenus, table 10 in Ekins et al. 2020). *Chodrocladia* (*C.*) *antarctica* Hentschel, 1914 and *C.* (*C.*) *concrescens* (Schmidt, 1880) (*sensu* Hestetun et al. 2016b) were originally reported with two categories each of styles, isochelae and sigmas, however, both species do not present a third category of sigmas (similar to the sigmoid isochelae of *Monanchora arbuscula*), an apomorphy of the new species. Further distinctness is apparent from a detailed analysis of spicules' shape and micrometries. Both formerly known species have sigmas that can reach considerably larger dimensions (143–165 µm, and 69–97 µm, respectively; cf. Göcke and Janussen 2013; Topsent 1920). In the case of *C.* (*C.*) *concrescens*, isochelae I can also be much larger (110–130 µm) and have six teeth, while isochelae II differ markedly in their bird-cage shape plus four to six teeth (Topsent 1920, fig. 3b; Hestetun et al. 2016b, fig. 7D).

New taxonomic combinations

In order to clarify some questions pointed in other studies related to *Echinostylinos* species (*e.g.*, see Carvalho et al. 2016; Vacelet and Kelly 2022), taxonomic revisions are needed and two new combinations are proposed below:

Genus *Echinostylinos* Topsent, 1927

Echinostylinos lingua new comb. (Koltun, 1970)

Mycalopsis lingua Koltun, 1970: 207; Fig. 21; Plate VIII, 3.

Type Material: Holotype, ZIRAS 16399, Zoological Institute of the Russian Academy of Sciences, Northwestern Pacific, Kurile-Kamchatka Trench area, off Shikotan Island (Station 5641, R/V "Vityaz"), 472–479 m depth (not studied here).

Diagnosis: Species characterized by the presence of only one category of megascleres (styles) 550–870 × 13–16 µm. Microscleres are palmate isochelae in two categories, and sigmas. Isochelae I with 44–55 µm and II with 18–32 µm. Sigmas, 77–148 µm (Koltun, 1970).

Remarks: Carvalho et al. (2016) considered the species *Esperiopsis lingua* (Koltun, 1970) as an

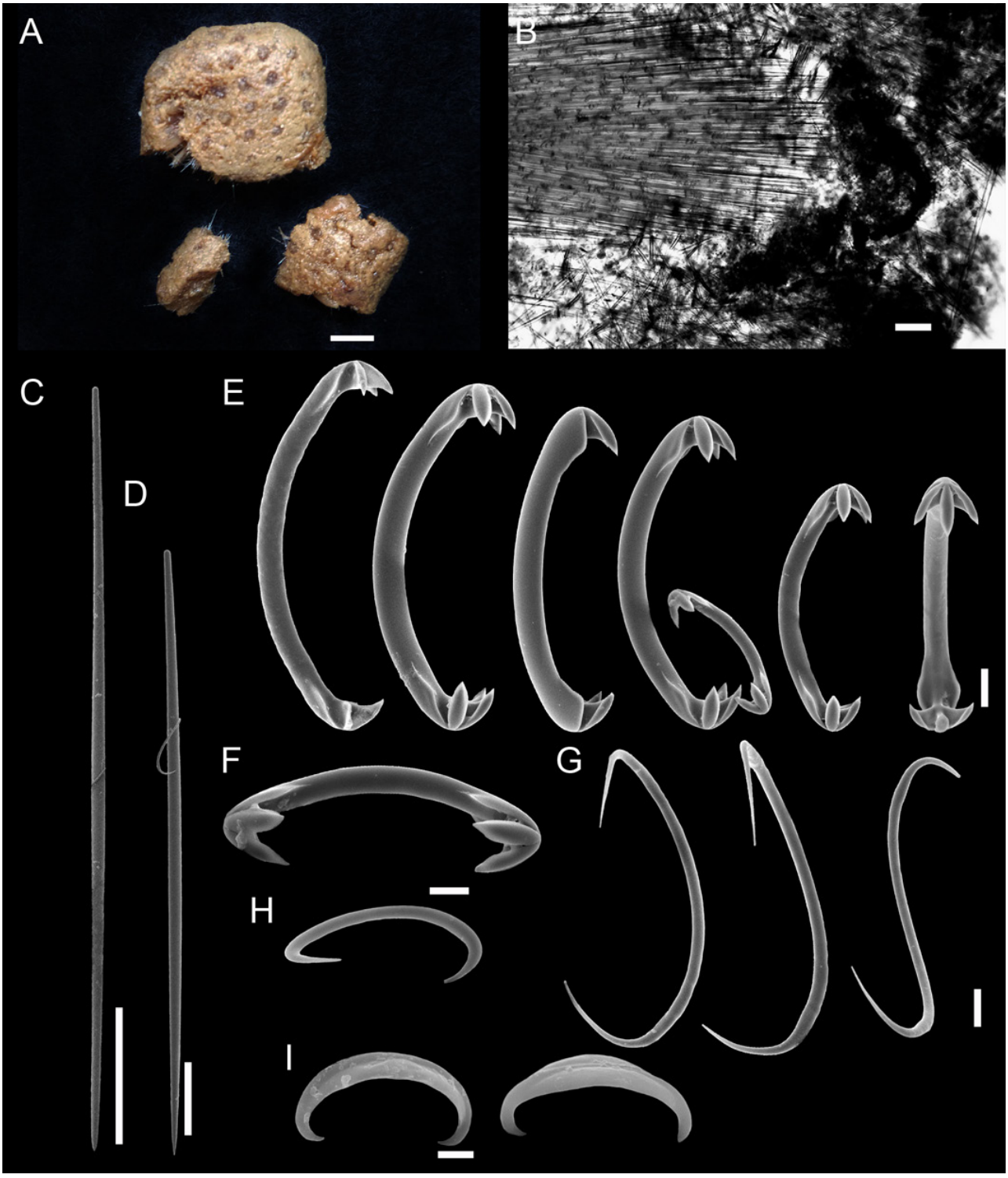


Fig. 4. Holotype of *Chondrocladia* (*Chondrocladia*) *trisigmata* sp. nov. (MNRJ 16000). A, preserved specimen (fragments); B, transversal section of skeleton; C, styles I: D, styles II; E, six isochelae I and one isochela II facing one of them; F, isochelae II; G, sigmas I; H, sigma II; I, sigmas III. Scale bars: A, H = 5 mm; B, D = 100 µm; C = 500 µm; E, G = 10 µm; F, I = 2 µm.

Echinostylinos species in their comparative table, although they did not formally propose the new combination, which is done here.

Genus *Abyssocladia* Lévi, 1964

Diagnosis: Cladorhizidae most often pedunculate, carrying a disk-shaped or flabelliform body with a radial architecture, in other cases pinnate or branching. Microscleres are a combination of abyssochelae, cleistochelae, arcuate chelae and/or sigmancistras, but not placochelae (Hestetun et al. 2016).

Abyssocladia glomeris new comb. (Topsent, 1904)

(Fig. 5)

Esperiopsis glomeris Topsent, 1904: 213, pl. XVII, fig. 3.
Camptisocale glomeris (Topsent, 1904). Topsent (1927: 7).

Material examined: Schizotype (slides presently re-examined). MNHN DT 1000, off Terceira, Azores, NE Atlantic (stn 866, S.A.S. Le Prince de Monaco; 38.8806 / -27.3847), 599 m depth, coll. S.A.S. Le Prince de Monaco, R/V 'Princesse Alice',02.VIII.1897.

Diagnosis: The only species of *Abyssocladia* with two categories of styles, 1400–1500 × 17–20 µm and 900–1000 × 7–8 µm, and only arcuate isochelae as microscleres (46–60 µm), often of abyssochelae morphology.

Brief Redescription (adapted from Topsent, 1904): The specimen is a whitish, elongated fragment, 20 mm long × 4 mm thick, without support; with soft consistency, smooth surface, and without distinct openings. The schizotype consists of a couple of slides with spicule dissociations and skeletal fragments.

Skeleton: Ectosome with tangential and compact bundles of styles II. Choanosome with styles I forming multispicular tracts. Microscleres abundant and randomly distributed (Fig. 5A; modified of Topsent 1904).

Spicules: Megascleres, styles in two categories. Styles I (Fig. 5A), smooth and straight sometimes slightly curved. Styles II (Fig. 5B), smooth and straight. According to Topsent (1904): styles I: 1400–1500 × 17–20 µm; styles II: 900–1000 × 7–8 µm. Microscleres, arcuate isochelae (Fig. 5C, D) with alae of both extremities ranging from totally separated to strongly interwoven as in abyssochelae: 46–60 µm (measures confirmed by the authors).

Distribution: Known only from its type locality, NE Atlantic, Azores, 599 m depth (Topsent, 1904).

Remarks: We propose the transfer of *Echinostylinos glomeris* (Topsent, 1904) to *Abyssocladia* Lévi, 1964 on account of its habit, skeleton and spicules, which appear more related to the latter genus, than to *Echinostylinos* or *Phelloderma*. The species originally described as *Esperiopsis glomeris* was transferred to *Echinostylinos* by van Soest and Hajdu (2002). Their rationale for the transfer actually supports our proposition, since they highlighted the skeletal similarity to *Echinostylinos*, but recognized the morphology of the isochelae in *glomeris* seemed to contradict this view, an observation they underestimated as likely of specific value only. Isochelae alone do not allow recognition of *Abyssocladia* spp. in many cases, but the typical branching shape and habit encourage us to transfer *Esperiopsis glomeris* to *Abyssocladia*.

On other *Echinostylinos*

During the process of review of the genus to describe the new species, considerations were taken regarding some known species of *Echinostylinos*:

Carvalho et al. (2016) discussed the possibility of a *E. shimushirensis* and *E. tubiformis* be synonymous. Here, we tabulated their morphological characteristics and habitat information based on their descriptions available (Fig. 6; Table 1).

Previous studies had discussed about spicule shape and classification of *Echinostylinos* species (Carvalho et al. 2016; Vacelet and Kelly 2022), we re-analyzed the type material of *Echinostylinos gorgonopsis*, here redescribed below:

Echinostylinos gorgonopsis Lévi, 1993

(Fig. 7)

Abyssocladia mucronata Vacelet, 2020: 269; Figs. 7–8.

Material examined: Holotype. *Echinostylinos gorgonopsis* Lévi, 1993 MNHN DCL 3612, New Caledonia, SW Pacific (BIOCAL 74; st. CP 45, 'l'ORSTOM' campaign; -23.1717 / 167.7163), 950–1000 m depth, coll. R/V 'Jean Charcot'.

Diagnosis: The only species of *Abyssocladia* with anisoxeas (525–650 × 4–5 µm) and tornotes (250–370 × 4–5 µm) as megascleres, and abyssochelae as its sole microscleres (30–50 µm).

Brief redescription (based on the holotype and Lévi (1993) description): Sponge, erect, arborescent, 14 cm long × 12 cm wide, with a short and cylindrical stalk (ca. 2 cm, broken). Most branches at the same plane, with 3–7 successive dichotomies. Irregular surface, rough to the touch, with small projections (lobes), giving the impression of a slight annealing, and with numerous circular openings at the apical branches. Sponge yellow to ocre in ethanol (modified from Lévi

1993; Fig. 6A).

Skeleton: Dense, with ascendant multispicular tracts of megascleres, and microscleres abundant especially on the surface.

Spicules (presently remeasured): Megascleres anisoxeas and tornotes (both as tornostyles in Lévi, 1993). Anisoxeas smooth, straight to slightly curved, with acerate and conical or mucronate ends; 440–513.9–620 × 15–16.8–18 µm. Tornotes smooth and straight, with acerate ends; 280–318.3–350 × 5–7.4–8 µm. Microscleres cleistochelae with 35–38.6–50 µm.

Distribution: Known from SW Pacific, New Caledonia, depth 950–1019 m (Lévi 1993; Vacelet 2020).

Remarks: Lévi chose to name *E. gorgonopsis* megascleres of tornostyles. However, after better detailed analysis through SEM images, we prefer to name the larger ones as anisoxeas, and the smaller ones, tornotes, according to the thesaurus of nomenclature for sponges (Boury-Esnault and Rützler 1997). The anisoxeas of *E. gorgonopsis* have acerate and conical or mucronate ends. The tornotes are straight and have acerate ends.

When we first analyzed the type, we had decided to propose the transfer of *Echinostylinos gorgonopsis* to *Abyssocladia* Lévi, 1964 on account of its habit, skeleton and spicules, which appear more related to the latter genus, than to *Echinostylinos* or *Phelloderma*. The arbuscular shape (gorgonian-like) of *E. gorgonopsis*, with a short stalk, its two categories of basally mucronated styles, and twisted cleistochelae (abyssochelae-like), concentrated at the surface of the

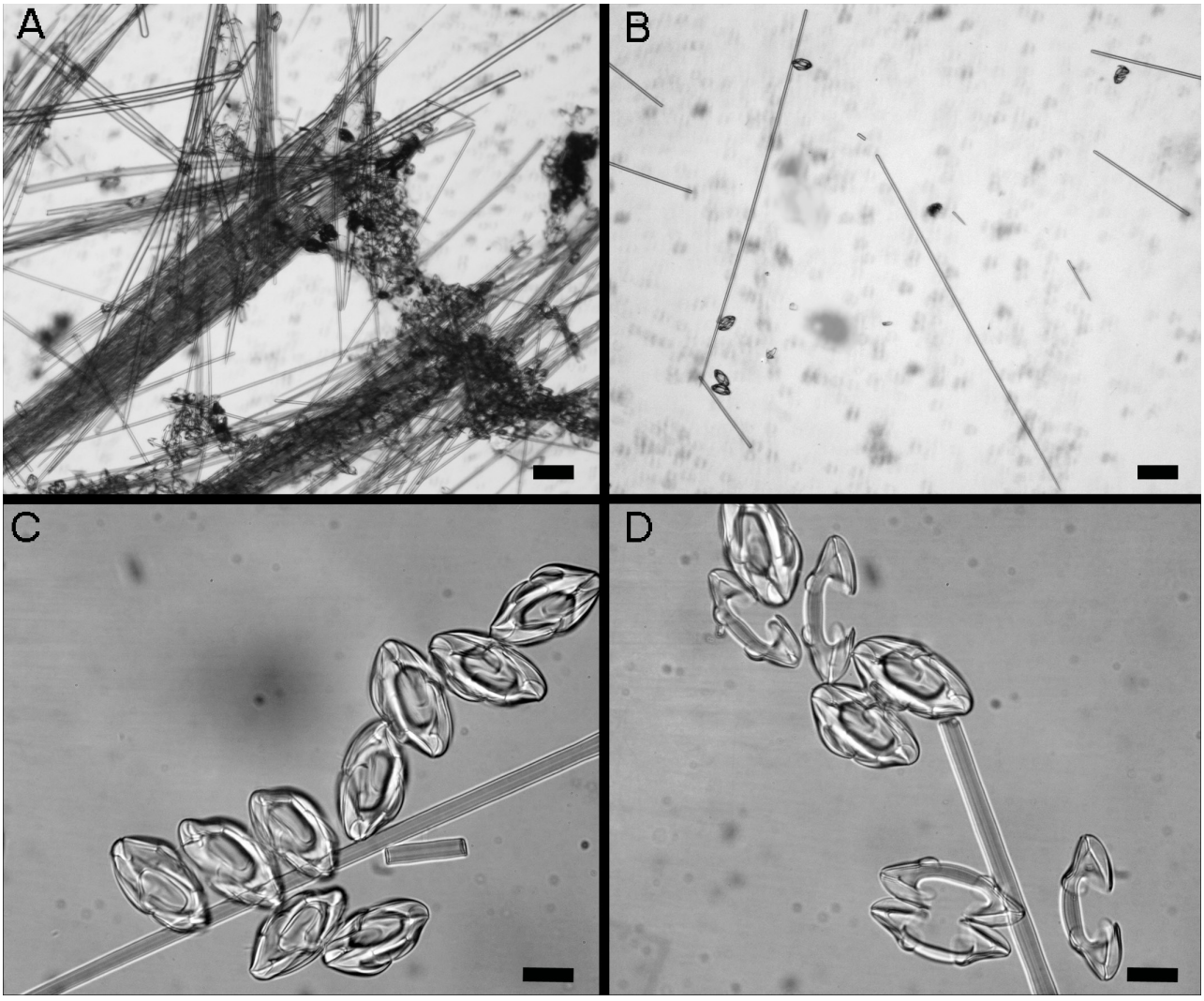


Fig. 5. *Abyssocladia glomeris* new comb. (Topsent, 1904), holotype slides (MNHN DT 1000). A, skeleton section fragment showing styles I and II and isochelae along tracts; B, styles II; C, D, isochelae. Scale bars: A, B = 100 µm; C, D = 20 µm.

sponge (Fig. 6) are easily correlated to the habit of a typical carnivorous sponge, such as *Abyssocladia* spp. (*sensu* Vacelet 2006). However, after discovered of new samples with redescriptions of the former, plus a synomymization of an *Abyssocladia* species from the same region (*Abyssocladia mucronata* Vacelet, 2020) in *Echinostylinos* (Vacelet & Kelly, 2022), we have decided to keep this species as valid. The authors (Vacelet and Kelly 2022) highlighted the similarities of both species, equating the lobes with openings observed on video records with the channels reported by Lévi (1993), choosing to synonymize both species. Evolution is made of several reversions and convergences, and there are cases reported in the literature, of channels in *Chondrocladia* (although none has ever been recorded in an *Abyssocladia*). With the evidence of possible channels suggesting a filter feeding habit we prefer to keep *E. gorgonopsis* as *Echinostylinos* (including Vacelet's synonymized species). In a future study, this and other hypotheses about *Echinostylinos* and *Abyssocladia* can be tested by DNA sequencing.

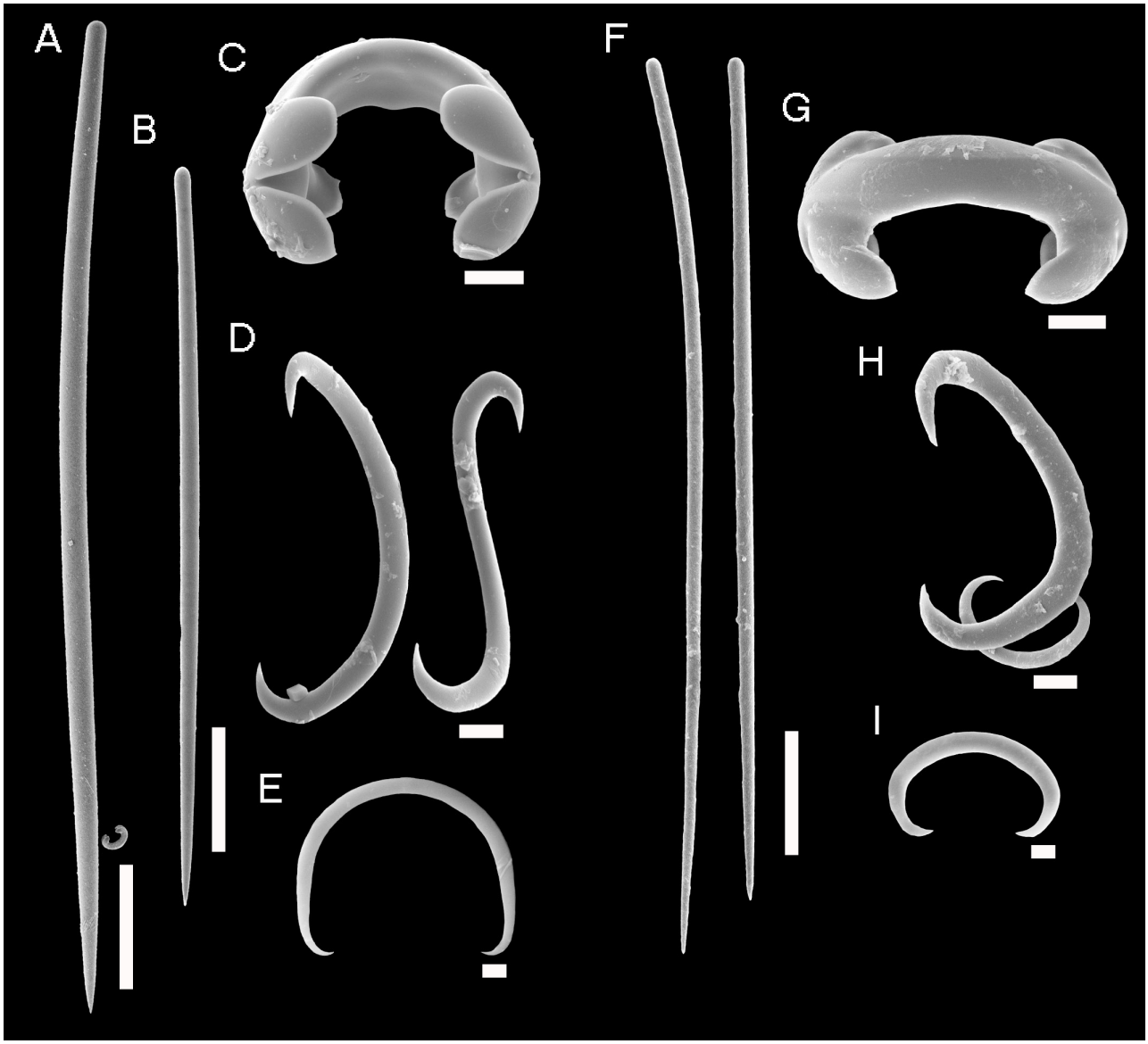


Fig. 6. *Echinostylinos shimushirensis* Koltun, 1970 vs. *Echinostylinos tubiformis* (Lévi, 1993) spicular set. A–D, *E. shimushirensis* (holotype, ZIRAS 10693; reanalyzed here): A, Styles I; B, styles II; C, isochelae; D, sigma I; E, sigma II. F–J, *Echinostylinos tubiformis* (holotype, MNHN DCL 3611, reanalyzed here): F, Styles II; G, isochelae from the back side; H, sigma I; I, sigma II. Scale bars: A = 200 μm, B, F = 50 μm; C, G = 10 μm; D, H = 5 μm; E, I = 2 μm.

Identification key for the species of *Echinostylinos*

1. Unguiferate isochelae 2
- Spatulate isochelae 7
- Abyssochelae-like isochelae ..... *E. gorgonopsis* Lévi, 1993
2. Isochelae tridentate 3
- Isochelae tetradentate ..... *E. brasiliensis* Carvalho, Lopes, Cosme & Hajdu, 2016
3. Only one category of megascleres ..... *E. schmidtii* (Arnesen, 1903)
- Two categories of megascleres 4
- Two categories of megascleres ..... *E. mycaloides* Koltun, 1970
4. Sigmas present 5
- Sigmas absent ..... *E. abyssalis* sp. nov.
5. More than one category of chelae and sigmas 6
- Only one category of chelae and sigmas ..... *E. hirsutus* Koltun, 1970
6. Only one category of chelae and two of sigmas ..... *E. patriciae* Carvalho, Lopes, Cosme & Hajdu, 2016
- Two categories of chelae and only one of sigmas ..... *E. stylophora* (Lévi & Lévi, 1983)
7. A single category of megascleres 8
- More than a single category of megascleres 9
8. Only one category of chelae and sigmas ..... *E. iatapiuna* sp. nov.
- Two categories of chelae and only one of sigmas ..... *E. lingua* (Koltun, 1970)
9. (Largest megascleres up to 600 µm, occurrence in the Atlantic Ocean ..... *E. reticulatus* Topsent, 1927
- Largest megascleres >1000 µm, occurrence in the Pacific Ocean 10
10. Body massive narrowed basally with low conules; smaller category of sigmas u-shaped (flagellate condition) ..... *E. shimushirensis* Koltun, 1970
- Erect sponge gradually widening away from the base; smaller category of sigmas c-shaped ..... *E. tubiformis* (Lévi, 1993)

DISCUSSION

Taxonomic considerations regarding *Echinostylinos*

Contrasting data tabulated by Carvalho et al. (2016; modified here in Table 2) and our new data, it

Table 1. Comparative description of *E. shimushirensis* and *E. tubiformis*. Measurements all in µm (micrometers)

	External Morphology	Skeleton	Styles	Isochelae	Sigmas	Distribution/ depth (m)
E. shimushirensis Koltun (1970) - original description	Massive body, narrowed basally, surface densely strewn with low conuli. The flat upper part of the body is often marked with broad irregular depressions and also bears openings up to 3 mm in diameter, which may be open or closed by the dermal membrane. Color yellowish–beige	Main skeleton fibrous, composed of thick, slightly curved styles. Longitudinal section of the sponge clearly shows central vertical tracts giving rise at an acute angle to lateral branches that gradually bend toward the surface, and end in radial fibers whose distal parts resemble conuli	I: 1320 – 1590 × 29 – 37 II: 275 – 358 × 5 – 8	32–54	I: 27–48 II: 16–22	NW Pacific / 472–479
present study (holotype, ZIRAS 10693)			I: 1430 – 1637.8 – 2031 × 36–39.2–46 II: 291–328.2 – 388 × 7	34 – 45.8 – 53	I: 36–40.3–48 II: 17–18.3–22	
E. tubiformis (Lévi, 1993) -original description	Sponge erect and measuring 200 mm high and 12 mm by 5 mm in diameter at the top; It gradually widens from the base of fixation. There is an axial cavity over a large part of the height; It opens at the top of the sponge, in the middle of a membrane in a 1–2 mm oscule, slightly set back from the end of the wall	Skeleton with ascending fibers of styles, which branch and form the envelope of the axial cavity. From this envelope, transverse radial styles, sometimes slightly reticulate, and palissadic bouquets of small styles start. Microsclers are abundant	I: 1300 – 1400 × 30 II: 300 – 370 × 5	35–48 × 30 (arcuate)	I: 30 × 2 II: 15–19 × 1	New Caledonia / 430–965
present study (holotype, MNHN DCL 3611)			I: 572–827.1 – -960 × 29– 35.7 –41 II: 262–291.3 – 359 × 5– 6.6 –10	48 – 55.2 – 60 (arcuate)	I: 26–31.9–41 II: 12–14.7–17	

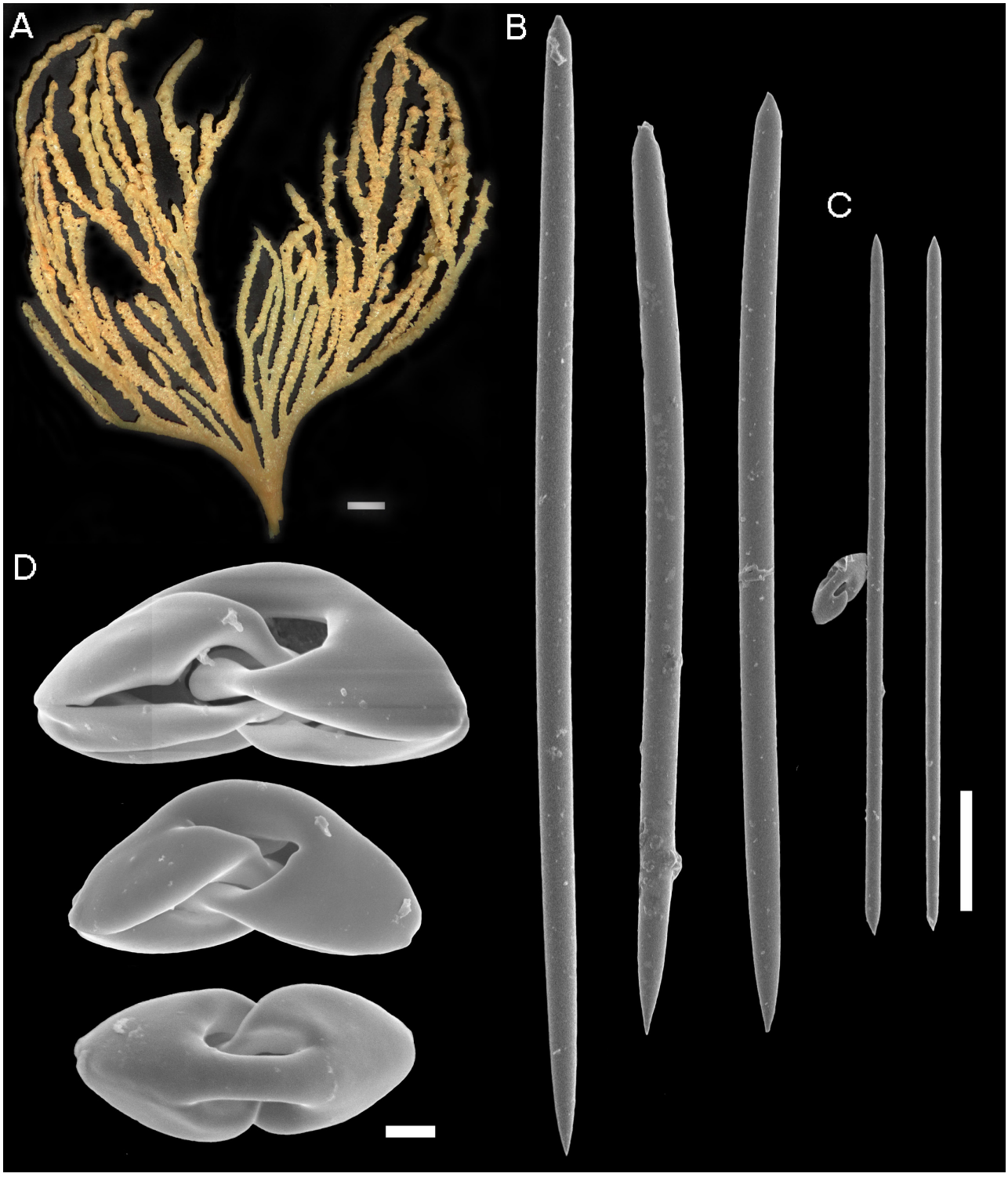


Fig. 7. *Echinostylinos gorgonopsis* Lévi, 1993, holotype. (MNHN DCL 3612). A) specimen; B) mucronated styles I; C) mucronated styles II; D) cleistochelae. Scale bars: A = 1 cm; B–C = 50 µm; D = 5 µm.

Table 2. Updated comparative table of *Echinostylinos* species (modified from Carvalho et al. 2016). n.r. = not reported. Some of the figures included here are from the original descriptions: in Arnesen (1903), Bergquist and Fromont (1988), Koltun (1970), Lévi (1993), Lévi and Lévi (1983), and Topsent (1927)

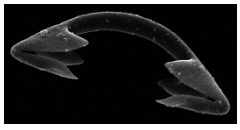
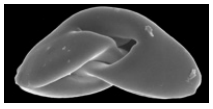
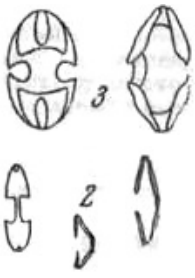
	Styles	Isochelae	Sigmas	Distribution/depth (m)
E. iatapiuna n. sp.	1100–1350 × 20–27.5	66–88 3 alae – spatulate 	60–88	São Paulo ridge, Southwest Atlantic / 2300–3300
E. abyssalis n. sp.	I: 572–582 × 16.8–24 II: 446–582 × 7–12	29–36 3 alae – unguiferate 	absent	São Paulo Rigde, Southwest Atlantic / 4008
E. brasiliensis Carvalho et al. 2016 (orig. descr.)	I: 776–1048 × 18–22	22–29 4 alae – unguiferate 	absent	Campos Basin, Brazil / 1100–1130
E. gorgonopsis Lévi, 1994	A: 525–650 × 4–5 T: 250–370 × 4–5	30–50 	absent	New Caledonia / 950–1019
E. hirsutus Koltun, 1970 (orig. descr.)	I: 400–540 × 5–10 II: 660–1650 × 45–54 III: ?	18–27 n.r. – unguiferate 	I: 16–22	Sea of Okhotsk, NW Pacific / 1440–1540
sensu Stone et al. (2011)	I: 1320 × 25 II: 350 × 9	27–30 n.r. – unguiferate	40	Alaska – Central Aleutian Islands / 665–711
E. lingua n. comb. (Koltun, 1970) (orig. descr.)	550–870 × 13–16	I: 44–55 (possibly arcuate) II: 18–32 (possibly palmate) 3 alae – spatulate 	I: 77–148	NW Pacific / 472–479

Table 2. (Continued)

	Styles	Isochelae	Sigmas	Distribution/depth (m)
E. mycaloides Koltun, 1970 (orig. descr.)	I: 495–610 × 8 II: 825–935 × 18–24 III: 200–325 × 5	71–94 3 alae – unguiferate 	absent	NW Pacific / 2165–2265
E. patriciae (Bergquist & Fromont, 1988) (orig. descr., as *E. reticulatus*)	I: 387–530 × 8–13 II: 202–300 × 3–6	28–40 3 alae – spatulate 	I: 22–36 II: 15–18	New Zealand / 55–110
E. reticulatus Topsent, 1927 (orig. descr.)	I: 500–560 × 26–30 II: 245–280 × 3	27–43 × 5–9 3 alae – spatulate 	I: 22 II: 15	Azores / 919–927
E. schmidti (Arnesen, 1903) (orig. descr.)	1200	40 3 alae – spatulate 	20	Norway / 500
E. shimushirensis Koltun, 1970 (orig. descr.). See Table 1 above)	I: 275–358 × 5–8 II: 1320–1590 × 29–37	32–54 3 alae – spatulate 	I: 27–48 II: 16–22	NW Pacific / 445
E. stylophora (Lévi & Lévi, 1983) (orig. descr.)	I: 300–320 II: 700–800 × 30–40	I: 38–40 × 25 (arcuate) II: 20 (arcuate) 3 alae – unguiferate 	30–60	New Caledonia / 510–525
E. tubiformis (Lévi, 1993) (orig. descr.). See Table 1 above)	I: 1300–1400 × 30 II. 300–370 × 5	35–48 × 30 (arcuate) 3 alae – spatulate 	I: 30 × 2 II: 15–19 × 1	New Caledonia / 430–965 m

is impressive how much the morphology of the chela varies among species attributed to *Echinostylinos*, even after the above genus transfers argued for. Two obvious groups appear recognizable. Species with markedly curved, slender, unguiferate chelae with quite small heads include *E. brasiliensis* and *E. mycaloides*. Species with markedly curved, stout, seemingly spatulate chelae with small, compressed heads, include *E. lingua* new comb., *E. reticulatus* (type species), *E. shimushirensis*, *E. stylophora* and *E. tubiformis*. Standard tridentate spatuliferous chelae might suggest evolutionary proximity between *E. iatapiuna* sp. nov. and *E. patriciae*, but the chelae of the later need a more detailed study of their micromorphology under SEM before further inference of its affinities can be built. *Echinostylinos hirsutus* (reduced sigmoid-chelae), and *E. abyssalis* sp. nov. (tridentate arcuate chelae with pointy alae) do not seem to belong in any obvious similarity cluster of isochelae morphology in this genus. The chelae of *E. schmidti* are too roughly drawn to allow any inference of affinities, and its type specimen appears to be lost, thus preventing any further conclusions (H.T. Rapp, *in litt.*; cf. Carvalho et al. 2016).

The possibility that *E. shimushirensis* and *E. tubiformis* might be synonymous was already commented by Carvalho et al. (2016). We prefer to keep both separate and valid on account of a series of characters, reinforced by their known occurrences 7600 km apart from each other. The habits and the morphology of the sigmas as well, differ between both species (Fig. 6; Table 1). *Echinostylinos shimushirensis* (holotype, ZIRAS 10693) has a massive body, narrowed basally, with low conules abundantly spread at the surface; and a smaller category of u-shaped sigmas approaching the flagellate condition. *Echinostylinos tubiformis* (holotype, MNHN DCL 3611), on the other hand, is an erect sponge, gradually widening away from the base, and its sigmas are morphologically different from *E. shimushirensis*' smaller category, which is c-shaped.

Biogeographic considerations

Only one *Echinostylinos* had been recorded from the South Atlantic until now, *E. brasiliensis* Carvalho, Lopes, Cosme & Hajdu, 2016. This number has raised to three after the proposition of two new species in the present study. The new species described above include samples with depth records between 2000 and 4008 meters deep in the Southwestern Atlantic. Most species of *Echinostylinos* were recorded from the bathyal zone, with the exception of *E. patriciae*, that is from the mesophotic (55–110 m) and *E. abyssalis* sp. nov., from the abyssal (4008 m). Surprisingly, species richness is a little higher in the Atlantic (seven spp) than the Pacific (five spp). No species has been recorded from the Indian Ocean yet. Latitudinally, there are two Boreal and ten Temperate species. Among the later, three are Subtropical. In terms of bathymetry, the Pacific holds the shallowest record (55 m, *E. patriciae*), while the Atlantic holds the deepest (4008 m, *E. abyssalis* sp. nov.). The deepest Pacific record is that of *E. mycaloides* (2265 m). The shallowest Atlantic record is that of *E. schmidti* (500 m).

The new records proposed here contemplate the South Atlantic lower bathyal province (Watling et al. 2013), *Chondrocladia* (*C*) *trisigmata* sp. nov. and *E. iatapiuna* sp. nov.; and the Brazilian abyssal province, *E. abyssalis* sp. nov. The entire South Atlantic comprises only seven records to depths deeper than 4000 m. Among those, two are glass-sponges (*Euplectella sanctipauli* Castello-Branco, Collins & Hajdu, 2020 and *Holascus stellatus* Schulze, 1887) and five are demosponges (*Cladorhiza inversa* Ridley & Dendy, 1886, *Chondrocladia* (*C.*) *levii* Cristobo, Urgorri & Rios, 2005, *Chondrocladia* (*C.*) *nicolae* Cristobo, Urgorri & Rios, 2005, *Chondrocladia* (*C.*) *vaceleti* Cristobo, Urgorri & Rios, 2005, and *E. abyssalis* n. sp.). Concerning the last group, four of them were sampled in only one expedition in the Southeastern Atlantic (all belong in Cladorhizidae). This reflects how premature it is to advance any reasonable estimate of sponge diversity in South Atlantic's bathyal and abyssal zones. Records are simply too sparse to allow any meaningful inference of species accumulation curves.

CONCLUSIONS

The present study adds two new species to *Echinostylinos*, transfers a species of *Esperiopsis* into this latter genus, but also proposes the transfer of one species formerly classified in *Echinostylinos*, to *Abyssocladia*, thus increasing the number of known species in *Echinostylinos* from 11 to 13 valid species and from 38 to 39 species in *Abyssocladia*. Additionally, a new species of *Chondroncladia (Chondrocladia*) is described here, increasing the number of known species in the subgenus from 34 to 35.

The genus *Echinostylinos* was formerly known from a depth range of 55–2500 m (Carvalho et al. 2016), but both new species described here came from deeper zones, with *E. abyssalis* sp. nov. pushing the genus' known deepest record into the abyssal, at 4008 m depth. As highlighted above, the genus demands an integrative taxonomic revision in order to verify its monophyly, which is challenged among other aspects,

by the marked disparity of isochelae morphologies seen in its species.

Furthermore, given the finding of the new species reported above, their relative aggregation in the SW Atlantic, and the incompleteness of the inventory of South Atlantic's deep-sea biota as a whole, it is to be expected that new species will come up with continued exploratory investigations in this area. The recent finding of an hexactinellid sponge garden in the Rio Grande rise (Hajdu et al. 2017) is a strong support for this claim. If an entire habitat can hide shallower than 1000 m depth, tiny little creatures deeper than 3000–4000 m can surely do it much better.

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Authors' contributions: CCB performed the species description, discussion and draft the manuscript. EH drafted the manuscript and reviewed descriptions. Both authors read and approved the final manuscript.

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Ethics approval consent to participate: Not applicable.

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