



# Taxonomy and distribution of *Didiscus* and *Myrmekioderma* (Demospongiae: Axinellida) off the mouths of the two largest rivers in Brazil, with description of four new species

Joana Sandes<sup>1,2</sup> · Fernando Moraes<sup>1,2</sup> · Ulisses Pinheiro<sup>3</sup> · Guilherme Muricy<sup>1</sup>

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## Abstract

*Didiscus* Dendy, 1922 and *Myrmekioderma* Ehlers, 1870 are closely related genera of axinellid sponges, distinguished mainly by the presence of didiscorhabd microscleres in *Didiscus* and of trichodragmata in *Myrmekioderma*. Their family-level classification, however, is highly controversial, in part because their specific and morphological diversities are still poorly known. Here, we redescribed *Didiscus oxeatus* Hechtel, 1983 based on new specimens and revision of the holotype, described two new species of *Didiscus* and two new species of *Myrmekioderma* from off the Amazon and São Francisco river mouths in Northern and Northeastern Brazil. These two areas in the Tropical Atlantic (TA) are still understudied, especially when considering their high environmental and economic importance. We observed for the first time the presence of tylostyles in the holotype of *D. oxeatus*, as well as in the new specimens from Sergipe State. *Didiscus pseudoverdensis* sp. nov. has thick, strongly spined didiscorhabds with sharp ends; *Didiscus raraediscus* sp. nov. has small microspined oxeas; *Myrmekioderma guajajara* sp. nov. has microxeas and verrucose small oxeas; and *Myrmekioderma tenax* sp. nov. has both raphidiform and sinuous oxeas. The morphological diversities of both genera are expanded by the addition of new spicule types and ornamentations. Morphological data indicated that both *Didiscus* and *Myrmekioderma* should be classified in the family Heteroxyidae, in contrast to previous molecular studies, which suggest that they could belong at least in part to Raspailiidae. These two families and the genus *Myrmekioderma* are probably polyphyletic and need revision. The number of species of *Didiscus* and *Myrmekioderma* worldwide is raised to 11 and 13, respectively, of which five species of *Didiscus* and six of *Myrmekioderma* occur in the TA. Most species have narrow distributions, probably reflecting the low sampling effort. This study provides a more accurate picture of the biodiversity and distribution of *Didiscus* and *Myrmekioderma* in the TA and reinforces the importance of scientific explorations in understudied areas such as off the mouths of the Amazon and São Francisco rivers.

**Keywords** Porifera · Biodiversity · Heteroxyidae · Raspailiidae · Amazon River · São Francisco River

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✉ Joana Sandes  
jcf.sandes@gmail.com

<sup>1</sup> Museu Nacional, Departamento de Invertebrados, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, s/n, Rio de Janeiro, RJ 20940-040, Brazil

<sup>2</sup> Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Diretoria de Pesquisa, Rua Pacheco Leão, 915, Jardim Botânico, Rio de Janeiro, RJ 22460-030, Brazil

<sup>3</sup> Centro de Biociências, Departamento de Zoologia – Laboratório de Porifera – LABPOR, Universidade Federal de Pernambuco, Avenida Prof. Moraes Rêgo, 1235, Cidade Universitária, Recife, PE 50670-901, Brazil

## Introduction

The demosponge order Axinellida is a major group of Porifera, with over 470 species worldwide, representing approximately 8% of all species of the class (van Soest et al. 2020). The classification of the order, however, is highly controversial, and recent proposals based on molecular data have greatly changed previous morphology-based classifications (Hooper 2002a, b; Samaai and Kelly 2002; Cárdenas et al. 2012; Morrow and Cárdenas 2015; Morrow et al. 2019). In addition, the morphological and specific diversities of the order Axinellida are still poorly known, especially in regions such as the Tropical Southwestern Atlantic and North Brazil Shelf provinces (biogeographic classification *sensu* Spalding et al. 2007). The genera *Didiscus* Dendy, 1922 and

*Myrmekioderma* Ehlers, 1870 are examples of such problems of axinellid taxa.

The classification of *Didiscus* and *Myrmekioderma* is highly unstable. *Myrmekioderma* has been alternatively classified in families ‘Haploscleridae,’ Axinellidae, Jaspidae, Phorbasidae, Halichondriidae, Desmoxyidae, and Heteroxyidae, while *Didiscus* has been placed in families Latrunculiidae, Halichondriidae, Desmoxyidae, and Heteroxyidae (Hooper 2002a; Samaai and Kelly 2002; van Soest and Hooper 2005; Santos et al. 2016a).

Morphological characters suggest that *Didiscus* and *Myrmekioderma* are closely related and should belong to the same family (e.g., Hooper 2002a; Santos et al. 2016a). They share the same surface ornamentation, ectosomal architecture, choanosomal organization, and spicule composition, and are distinguished only by the presence of didiscorhabd microscleres in *Didiscus* and of trichodragmata and spined small oxeas in *Myrmekioderma* (Boury-Esnault and Rützler 1997; Hooper 2002a; van Soest and Hooper 2005). Phylogenetic studies based on morphological data suggest that *Didiscus* and *Myrmekioderma* are closely related and that the didiscorhabds of *Didiscus* could be derived from the spined small oxea of *Myrmekioderma* (van Soest et al. 1990).

This proximity is supported by phylogenetic analysis of 28S rRNA sequences that clustered the type species of *Myrmekioderma* [*M. granulatum* (Esper, 1829)] with *Didiscus* spp. in family Raspailiidae (Erpenbeck et al. 2005, 2007). In contrast, 18S rRNA and COX-1 sequences suggest that *Myrmekioderma* may be polyphyletic and more closely related to Axinellidae or Heteroxyidae than to *Didiscus*, which again clustered within the Raspailiidae (Erpenbeck et al. 2012; Redmond et al. 2013; Morrow et al. 2019). *Didiscus* is currently classified in the family Raspailiidae, whereas *Myrmekioderma* remains in Heteroxyidae waiting for further data (Morrow and Cárdenas 2015; Morrow et al. 2019; van Soest et al. 2020).

A good knowledge of the biodiversity, morphological variation, and species distribution is an essential pre-requisite to understand the phylogeny and biogeography of sponges. Although the genera *Didiscus* and *Myrmekioderma* are widely distributed in tropical and subtropical regions, their biodiversity is still poorly known and only nine species of *Didiscus* and 11 of *Myrmekioderma* have been described worldwide (Hooper 2002a; van Soest et al. 2020). In the Tropical Atlantic (TA) realm, only three species of *Didiscus* and four of *Myrmekioderma* were recorded: *D. gladius* Santos & Pinheiro, 2016 and *M. intrastrongyla* Sandes & Pinheiro, 2013 are endemic from the Brazilian coast; *D. oxeatus* Hechtel, 1983 and *M. rea* (de Laubenfels, 1934) occur both in Brazil (Muricy et al. 2011) and in the Caribbean (e.g., Pulitzer-Finali 1986); *Didiscus verdensis* Hiemstra & van Soest, 1991 is currently considered Amphi-Atlantic, also recorded off the mouth of the Amazon River (Moura et al.

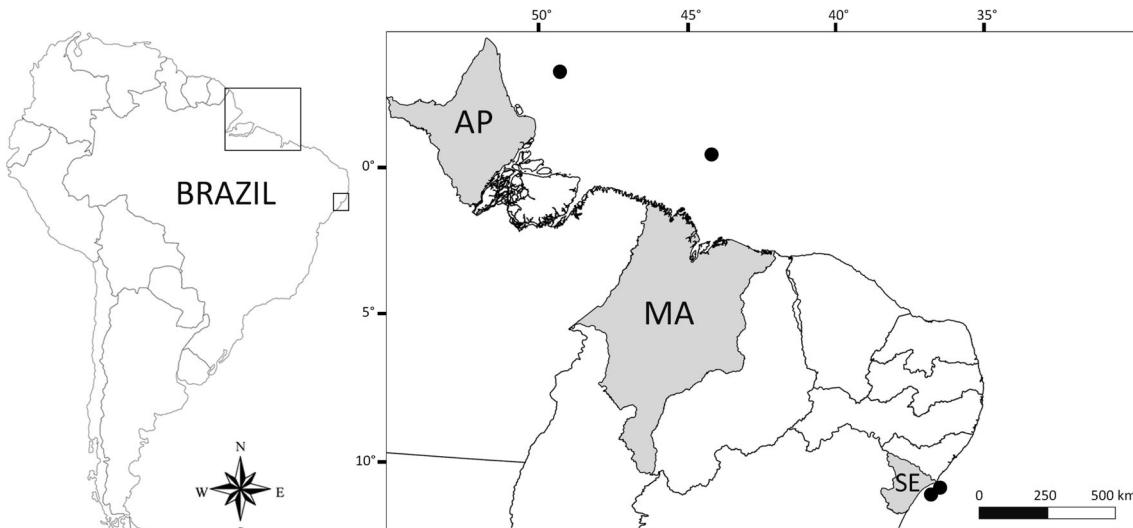
2016); and *M. gyroderma* (Alcolado, 1984) and *M. laminatum* Rützler, Piantoni, van Soest & Díaz, 2014 are Caribbean endemics.

Understudied areas, such as the deep-sea and off large river mouths, are potential sources of new species with relevant phylogenetic information. Traditionally, the presence of large rivers along the South America coastline (Orinoco, Amazon, Parnaíba and São Francisco) had been advocated as an effective barrier separating the Caribbean and Brazilian coral reef ecosystems, due to the formation of long stretches of mud bottoms and low salinity plumes (Ekman 1953; Briggs 1974; Hechtel 1976). Nevertheless, the study of benthic samples trawled off the Amazon River mouth showed the presence of a typical reef fish fauna associated with sponge bottoms, indicating the presence of a “sponge corridor” in mesophotic depths and high salinity waters under the river plume (Collette and Rützler 1977). Most sponge surveys in Brazil have been concentrated on hard bottoms and shallow-water ecosystems (e.g., Hechtel 1976, 1983; Muricy and Hajdu 2006; Hajdu et al. 2011; Moraes 2011), with fewer collections on soft bottoms and rhodolith beds (Sandes and Pinheiro 2013, 2014, 2016; Sandes et al. 2014, 2016; Santos et al. 2016b; Moura et al. 2016; Leal et al. 2017). Trawling and dredging surveys in the mesophotic carbonate reefs and rhodolith beds off the mouths of the Amazon and São Francisco rivers have recorded diverse sponge communities, including species of *Didiscus* and *Myrmekioderma* (Sandes and Pinheiro 2013; Moura et al. 2016; Sandes 2018). Most sponges from these two areas, however, remain undescribed, and many were identified only to genus level or above. Detailed taxonomic descriptions are needed to understand the diversity and distribution of marine sponges at these key biogeographic regions in the TA.

In the present study, we describe two new species of *Didiscus*, redescribe *Didiscus oxeatus*, and describe two new species of *Myrmekioderma*, all collected off the mouths of the Amazon and São Francisco rivers in Northern and Northeastern Brazil, respectively. We also uncover and discuss new data on the morphology, diversity and distribution of *Didiscus* and *Myrmekioderma*, which contribute for future taxonomic, systematic and biogeographic studies of these two poorly known and related axinellid genera.

## Material and methods

A total of 10 specimens were collected by dredge, bottom trawl and manned submersible off the mouths of the two largest rivers in Brazil: Amazon (North Region) and São Francisco (Northeast Region), in 2011 (February, June, and July), 2014 (September) and 2017 (July) (Fig. 1). Specimens were preserved in 70% ethanol and deposited in the Porifera Collections of the Universidade Federal de Sergipe



**Fig. 1** Sampling sites off the mouth of the Amazon and São Francisco rivers in Northern and Northeastern Brazil, respectively. AP, Amapá State; MA, Maranhão State; SE, Sergipe State

(UFSPOR) and Museu Nacional – Universidade Federal do Rio de Janeiro (MNRJ). The UFSPOR specimens were collected by MARSEAL Project – Environmental Characterization of Sergipe and Alagoas Basin, coordinated by PETROBRAS/CENPES, using RV Seward Johnson and RV Luke Thomas, while the MNRJ ones were sampled by Margem Equatorial Project (ANP/ PetroRio), using NHO Cruzeiro do Sul (Brazilian Navy) and RV Alucia (OceanX). Samples were photographed on board (fresh) or in the laboratory (fixed). Dissociated spicule slides and thick skeleton section mounts were made according to usual procedures for Demospongiae (e.g., Hajdu et al. 2011). Spicule measurements are presented in micrometers, based on 30 spicules and indicated as minimum–mean–maximum, length/width. Spicules were studied using Scanning Electron Microscopes (SEM) Jeol JSM-5600-LV at Instituto de Pesquisas Jardim Botânico do Rio de Janeiro (JBRJ) and JSM-6390 at Museu Nacional – Universidade Federal do Rio de Janeiro (MNRJ).

## Results

### Systematics

Class Demospongiae Sollas, 1885

Order Axinellida Lévi, 1953

? Family Heteroxyidae Dendy, 1905

**Diagnosis:** Encrusting, saccular, alveolar, massive or ramosse sponges often with hispid or conulose surfaces bearing smooth or spined microxea/ acanthomicrostrongyles microscleres, often centrangleate or strongly bent centrally, sometimes acanthose and rhabdose, usually found on the

ectosome, sometimes also with raphides occurring singly or in bundles (trichodragmata), or acanthose cladotoxa and birotules in one genus; megascleres monactinal (styles or tylostyles), diactinal (oxeas, strongyles) or both, may present modifications at the ends; choanosomal skeleton a confused arrangement of single spicules or widely spaced reticulate bundles of multispicular fibers, with little spongin, with poorly developed or no axial compression, and a relatively poorly differentiated extra-axial skeleton (disorganized-plumose); cortex absent in one genus (Santos et al. 2016a).

### Genus *Didiscus* Dendy, 1922

**Type species:** *Didiscus placospongoides* Dendy, 1922

**Diagnosis:** Heteroxyidae with massive-amorphous to lobate growth forms; spicules strewn in confusion and sporadically grouped in spongin-reinforced directionless tracts; ectosomal skeleton is a gradient from a perpendicular palisade to a tangential or paratangential arrangement of spicules with discorhab-like microscleres arranged perpendicular to the surface; surface with sculptured grooves and subdermal drainage canals (Hooper 2002a).

### *Didiscus oxeatus* Hechtel, 1983

(Figs. 2 and 3; Table 1)

**Synonyms:**

*Didiscus* sp., Hechtel (1976): 254

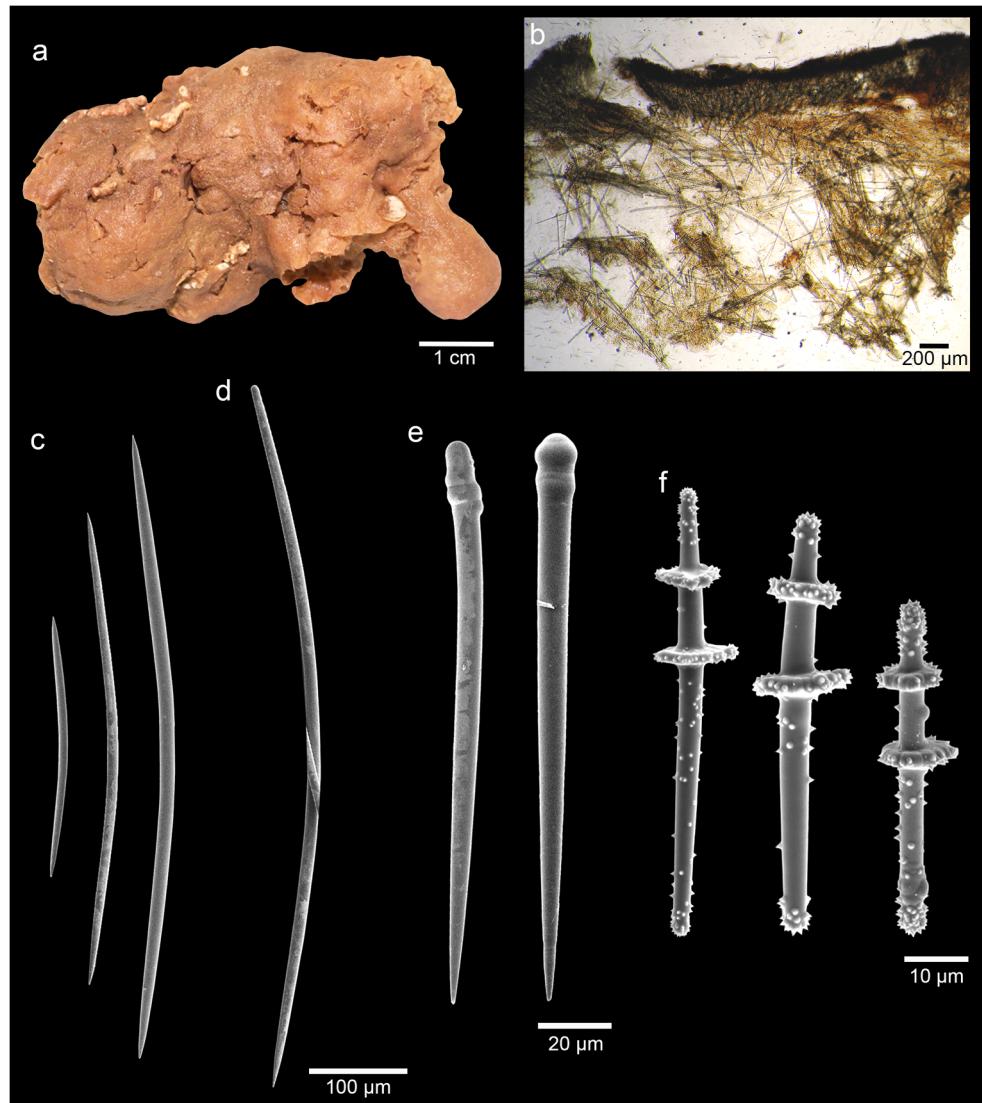
*Didiscus oxeata* Hechtel, 1983: 76; Kobluk and van Soest (1989): 1214; Hiemstra and van Soest (1991): 45; Díaz et al. (1993): 304; Lehnhert and van Soest (1998): 85; Lehnhert and van Soest (1999): 150; Alcolado (2002): 63; Moraes et al. (2006): 167; Muricy et al. (2008): 104; Vaske-Júnior (2010): 46; Moraes (2011): 154.

**Table 1** Comparative micrometric data of the spicules and overview of distribution of *Didiscus* species. All values in  $\mu\text{m}$ , expressed as follows: minimum–maximum or minimum–mean–maximum length/width. Names of provinces follow Spalding et al. (2007). *D.d.*, disc diameter of the didiscorhabds; *JT*, Java Transitional; *MS*, Mediterranean Sea; *NBS*, North Brazil Shelf; *TG*, Tristan Gough; *TNWA*, Tropical Northwestern Atlantic; *TSWA*, Tropical Southwestern Atlantic; *TSWP*, Tropical Southwestern Pacific; *WAT*, West African Transition; *WC*, Western Coral Triangle; *WIO*, Western Indian Ocean

<i>Didiscus</i> species	Type locality	Distribution	Depth (m)	Choanosomal megascleres	Ectosomal megascleres		Didiscorhabds
<i>D. pseudoverdensis</i> sp. nov.	Ama pâ State, Brazil	NBS	90	Oxaea: 975–1230–1650/12–18–20	Oxaea: 210–328–430/6–8–10	70–79–88/2–4.5–5	D.d.1: 12–16–18 D.d.2: 7–11–13 (rare)
<i>D. raraediscus</i> sp. nov.	Sergipe State, Brazil	TSWA	47	Oxaea: 520–589–720/11–15–18	Oxaea: 152–197–235/3–6–9 (microspined)	32–58–75/1.2	D.d.1: 7–12–16 D.d.2: 3–5–8
<i>D. aceratus</i> (Ridley & Dendy, 1886) <i>sensu</i> Ridley & Dendy, 1887	Tristan Gough	TG WCT; TSWP	1–110	Strongyle: 850–1295/9–15	Strongyle: 275–450/7–10	25–54/2–6	D.d.1: 12 D.d.2: 8
<i>D. amisodiscus</i> Vacelet & Vasseur, 1971	Madagascar	WIO; JT	30–50	Style: 1200/10–15 (rare) Oxaea: 500–600/10	Oxaea: 200–350/7	45/4	D.d.1: 30 D.d.2: 10–15
<i>D. gladius</i> Santos & Pinheiro, 2016	Bahia State, Brazil	TSWA	25–50	Style: 510–695–890/0.9–1.4–2 Oxaea: 320–457–640/8–10–13	Oxaea: 148–185–231/4–6–7	67–74–81/3–4.5–6	D.d.1: 16 D.d.2: 9
<i>D. oreatus</i> Hechtel, 1983	Bahia State, Brazil	TNWA; TSWA	1–75	Oxaea: 570–1370/8–20*	Oxaea: 220–400/3–4.5	55–80/4–6	D.d.1: 15–20 D.d.2: 6–12
<i>D. placospongioides</i> Dendy, 1922	Cargados Carajos/Tromelin Islands	WIO	55	Oxaea: 1400/20 Tylostyle: 160/8	Oxaea: 400/11	90/5	D.d.1: 18 D.d.2: 12
<i>D. pseudodiscoidea</i> (Corriero, Scalera-Liaci & Pronzato, 1996)	San Domino Island, Italy	MS	0.5–2	Oxaea: 96–134–165/2–3.5–5 Microstrongyle: 12–27–40/3–6–7	—	96–134–165/ 2–3.5–5**	D.d.1: 9–11 D.d.2: 5–6
<i>D. spinoxectus</i> Corriero, Scalera-Liaci & Pronzato, 1997	Ustica Island, Italy	MS	1	Style to subtylostyle: 900–1120/9–13	Oxaea: 93–375/3–11	47–143/3–6	
<i>D. stylifer</i> Tsumamal, 1969	Israel	MS	0–7	Tylostyle: 140–260/10–12 Style: 660–1320/4–13 Tylostyle: 180–240/9–13	Oxaea: 120–310/4.5–11 Strongyle: 92–264/6.7–11 (rare)	40–86/2.2–5	D.d.1: 10–13 D.d.2: 6–9
<i>D. verdensis</i> Hiemstra & van Soest, 1991	Cape Verde Islands	WAT	6–15	Oxaea, style and strongyle: 430–1300/5–13	Oxaea and strongyle: 190–336/2–4 65–90/2–2.5	D.d.1: 12 D.d.2: 8	

\*, tylostyles may be present; \*\*, pseudodidiscorhabds

**Fig. 2** Morphological and anatomical characters of *Didiscus oxeatus* Hechtel, 1983. **a** Preserved specimen (UFSPOR 1070); **b** ectosome and choanosome in transverse section; **c** oxeas; **d** style; **e** tylostyles; **f** didiscorhabds



*Didiscus oxeatus*, Pulitzer-Finali (1986): 144; van Soest et al. (2020).

*Didiscus flavus* van Soest, 1984: 146 (*sensu* Hiemstra and van Soest 1991).

*Didiscus habanensis* Alcolado, 1984: 9 (*sensu* van Soest et al. 2020).

*Material examined.* UFSPOR 331, off Pirambu city, MARSEAL Project sta. #D3 (10°52' 21.00" S, 36°32' 9.96" W), 47 m depth, 3 July 2011; UFSPOR 1070, off Pirambu city, MARSEAL Project sta. #D2 (10°49' 19.56" S, 36°37' 3.36" W), 27 m depth, July 2011; both Sergipe State, NE Brazil, coll. Petrobras, leg. RV Seward Johnson.

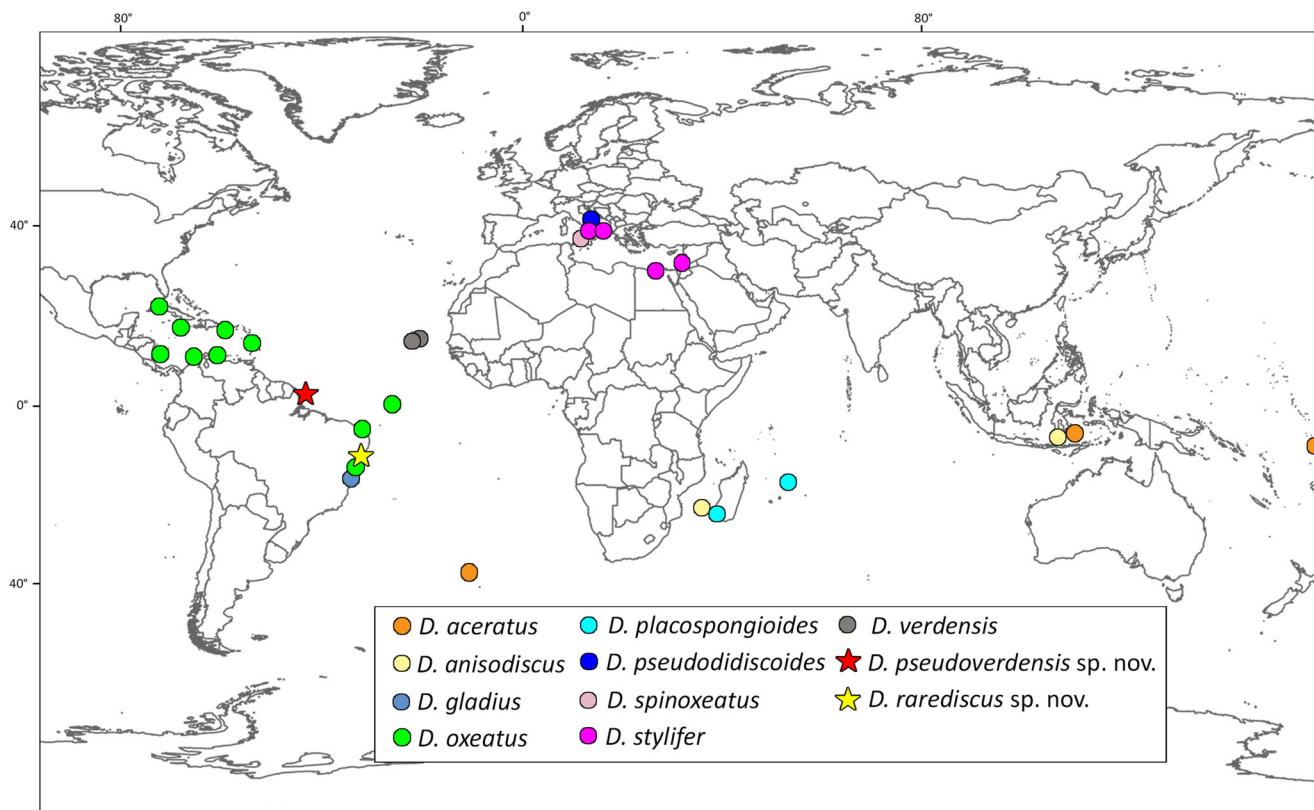
*Comparative material.* *Didiscus oxeata* Hechtel, 1983—MNRJ 14957 (fragment from holotype YPM 8968), Banco Santo Antonio, off Bahia, NE Brazil, 60 m depth, coll. J. Laborel, leg. RV Calypso, 9

February 1962. *Didiscus oxeata*, Muricy et al. 2008—UFPEPOR 303, 390, Bacia Potiguar, off Rio Grande do Norte State, NE Brazil, 64–75 m depth, coll. Petrobras, 22 May 2004. *Didiscus oxeata*, Moraes 2011—MNRJ 3580, 3582, 3601, São Pedro and São Paulo Archipelago, NE Brazil, 1.5–12 m depth, coll. Fernando Moraes, October 2000.

*Diagnosis.* *Didiscus* with large choanosomal oxeas, rare tylostyles and blunt-ended didiscorhabds.

*Description* (Fig. 2a). Massive to lobate shape, up to 6 cm length by 4 cm width and 2 cm high; surface smooth, but with some grooves; oscules not observed; consistency soft and compressible; color light brown in ethanol (Fig. 2a).

*Skeleton* (Fig. 2b). Ectosome is easily detachable (340–400 μm thick), composed by perpendicularly oriented didiscorhabds, together with bundles of transversal and



**Fig. 3** World distribution of all 11 *Didiscus* species. Stars represent new species and circles are records from the literature

tangential smaller oxeas. Choanosome composed by loose spicules (didiscorhabds and oxeas) and scattered multisicular tracts of larger oxeas oriented toward the surface, supporting the ectosome (Fig. 2b).

**Spicules** (Fig. 2c–f) (average of all specimens). Oxeas, tylostyles and didiscorhabds.

Oxeas (140–509–1390/2–11.8–20 µm): smooth, slightly curved, with hastate ends (Fig. 2c); modifications to styles are rare (Fig. 2d).

Tylostyles (101–174–257/5–7–10 µm): rare, smooth, straight and polytylote (Fig. 2e); more abundant in UFSPOR 331.

Didiscorhabds (52–65.5–80/2–4.6–8 µm): straight or slightly bent, heavily spined, specially towards the rounded ends; both the larger disc (10–14.5–18 µm in diameter) and the smaller one (7–12.4–15 µm in diameter) are flat, with irregular edges (Fig. 2f).

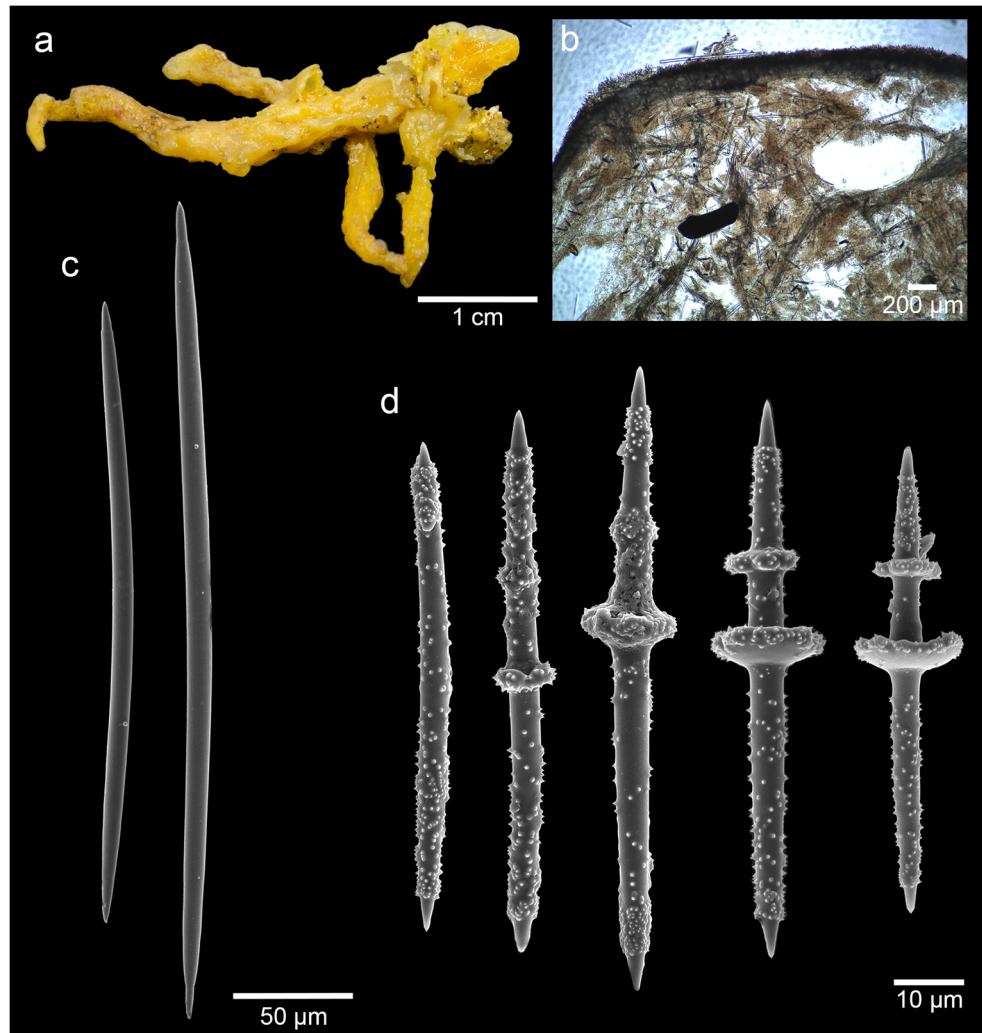
**Bathymetry and ecology.** The studied specimens were recorded at 27 and 47 m depth, on fine and coarse sand bottoms. The species' known depth range is 1–75 m.

**Geographical distribution** (Fig. 3; Table 1). Caribbean Sea: Bahamas, Cuba, Puerto Rico, Jamaica, Bonaire, Curaçao (Pulitzer-Finali 1986; Kobluk and van Soest 1989; Hiemstra and van Soest 1991; Díaz et al.

1993; Lehnert and van Soest 1998, 1999; Alcolado 1984, 2002) and Colombia (Zea et al. 2014). Brazil: Bahia State (Hechtel 1983), Rio Grande do Norte State (Muricy et al. 2008), São Pedro and São Paulo Archipelago (Moraes 2011) and Sergipe State (present study).

**Taxonomic remarks.** The large size range of oxeas and the shape of didiscorhabds with rounded ends are the main diagnostic characteristics of *Didiscus oxeatus*. This species was originally described from Bahia State, NE Brazil (Hechtel 1983), and was later recorded in Caribbean waters (e.g., Pulitzer-Finali 1986; Hiemstra and van Soest 1991; Zea et al. 2014). Subsequent sampling revealed additional records of *D. oxeatus* in Brazilian waters, including São Pedro and São Paulo Archipelago (Moraes et al. 2006; Moraes 2011), and Rio Grande do Norte State (Muricy et al. 2008). The studied specimens have rare tylostyles with polytylote modifications, similar to those of Curaçao populations (van Soest 1984, as *D. flavus*) and Cuba (Hiemstra and van Soest 1991; Alcolado 1984, as *D. habanensis*). Additionally, we described for the first time the presence of tylostyles in the holotype of *D. oxeatus*, as well as in the specimens from Rio Grande do Norte State (Hechtel

**Fig. 4** Morphological and anatomical characters of *Didiscus pseudoverdensis* sp. nov. **a** Fresh specimen on board (MNRJ 18731—holotype); **b** ectosome and choanosome in transverse section; **c** ectosomal and choanosomal oxeas, respectively; **d** didiscorhabds in several development stages



1983; Muricy et al. 2008). However, tylostyles were not reported in specimens from Jamaica (Díaz et al. 1993; Lehnert and van Soest 1999), Colombia (Zea et al. 2014) and São Pedro and São Paulo Archipelago (Moraes 2011), which should thus be carefully revised.

#### *Didiscus pseudoverdensis* sp. nov.

<http://zoobank.org/115DDD49-A8C0-4A73-BB56-08622AAADABA>

(Figs. 3 and 4; Table 1)

#### Synonyms:

*Didiscus verdensis*, Moura et al. (2016): 5; Table S2 [not Hiemstra and van Soest 1991: 41].

**Type material.** Holotype—MNRJ 18731, off Amazon River mouth, Amapá State, Northern Brazil ( $03^{\circ}35' 25.60''$  N,  $49^{\circ}07' 36.17''$  W), 90 m depth, coll. Fernando Moraes and Rodrigo Moura/ NHo Cruzeiro do Sul, 26 September 2014.

**Etymology.** The species name refers to its resemblance to *D. verdensis*, especially in external color and in the shape of the didiscorhabds.

**Diagnosis.** *Didiscus* with two size categories of smooth choanosomal and ectosomal oxeas and thick, strongly spined, sharp-ended didiscorhabds.

**Description** (Fig. 4a). Ramose shape, slightly branched, 3 cm high, with branches ranging from 3 to 10 mm in diameter; surface smooth, with grooves and slightly elevated ridges; oscules not observed; consistency firm, but compressible and elastic; color orange-yellow, becoming light beige in ethanol (Fig. 4a).

**Skeleton** (Fig. 4b). Ectosome easily detachable, 170  $\mu$ m thick, composed of perpendicular didiscorhabds, and erect, paratangential or tangential bundles of smaller oxeas. Choanosome formed by loose oxeas and didiscorhabds, but with some irregular tracts of larger oxeas oriented towards the ectosome; spongin moderately present (Fig. 4b).

*Spicules* (Fig. 4c–d). Oxeas in two size categories and didiscorhabds:

Oxea I (975–1230–1650/12–17.5–20 µm): choanosomal, smooth, straight or slightly curved, with hastate or mucronate ends (Fig. 4c);

Oxea II (210–327.5–430/6–7.9–10 µm): ectosomal, smooth and straight, with hastate or mucronate ends; some are slightly centrotylote, with rare tylote modifications (Fig. 4c);

Didiscorhabds (70–78.6–88/2–4.5–5 µm): straight or slightly bent, sharply pointed, and strongly spined, except the apices (when fully developed); larger disc (12–16–18 µm in diameter) slightly concave towards the smaller disc, which is almost flat (7–11–13 µm in diameter); both discs have irregular edges. Sometimes, these discs appear modified as simple rings or are absent (Fig. 4d).

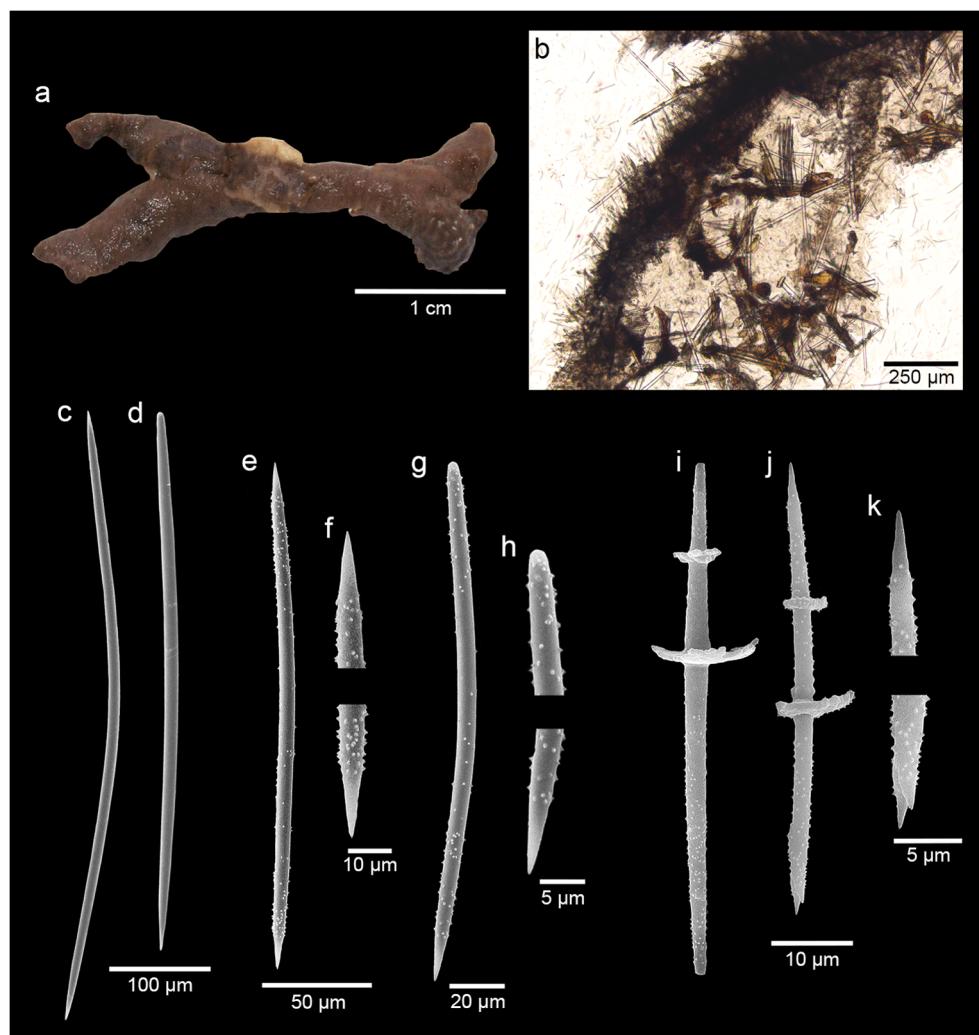
*Bathymetry and ecology.* The species was found at 90 m depth, on carbonate bottom (rhodolith beds). No associated organisms were recorded.

*Geographical distribution* (Fig. 3; Table 1). Provisionally endemic from off the Amazon River mouth, Amapá State, Northern Brazil.

*Taxonomic remarks.* This specimen was firstly identified off the Amazon River mouth as *Didiscus verdensis* by Moura et al. (2016) due to their similarity in the shape of didiscorhabds and external color. However, *D. verdensis* has thinly encrusting shape, styles and strongyles (Hiemstra and van Soest 1991) that are absent in the studied specimen, which now received a new name: *Didiscus pseudoverdensis* sp. nov. In addition, the oxeas and didiscorhabds of *D. verdensis* are thinner than the ones in the new species (Table 1).

*Didiscus pseudoverdensis* sp. nov. differs from all other species of the genus by the presence of two size categories of smooth ectosomal and choanosomal oxeas and thick, strongly and entirely spined, sharp ended didiscorhabds. The other two known species of *Didiscus* in the TA are clearly distinguished from the new species by the rounded ends of didiscorhabds, grooved surface and orange tinges in *D. oxeatus*, while

**Fig. 5** Morphological and anatomical characters of *Didiscus raraediscus* sp. nov. **a** Preserved specimen (UFSPOR 463—holotype); **b** ectosome and choanosome in transverse section; **c** choanosomal oxea; **d** style modification of choanosomal oxea; **e**–**f**, ectosomal oxea; **g**–**h**, style modification of ectosomal oxea; **i**–**k**, didiscorhabds



*D. gladius* has styles, smaller and thinner oxeas, and rugose or finely spined didiscorhabds. *Didiscus placospongioides* shares with *Didiscus pseudoverdensis* sp. nov. similar size categories of oxeas and sharp-ended, spined didiscorhabds. However, this Indian Ocean species has a massively encrusting shape and surface with polygonal pattern, similar to *Placospongia* species (Hiemstra and van Soest 1991) (Table 1).

#### *Didiscus raraediscus* sp. nov.

<http://zoobank.org/EF3D8753-01CA-4E42-ACA3-BB54FC000ECE>

(Figs. 3 and 5; Table 1)

**Type material.** Holotype—UFSPOR 463, off Pirambu city, MARSEAL Project sta. #D3 ( $10^{\circ} 52' 21.00''$  S,  $36^{\circ} 32' 9.96''$  W), Sergipe State, NE Brazil, 47 m depth, coll. Petrobras, leg. RV Seward Johnson, 3 July 2011.

**Etymology.** The species name refers to the rarity of didiscorhabds in the studied material.

**Diagnosis.** *Didiscus raraediscus* sp. nov. has digitate shape, smooth choanosomal oxeas, microspined ectosomal oxeas and rare, thin and microspined didiscorhabds with sharp ends.

**Description** (Fig. 5a). Digitate shape, with 2.5 cm high by 3 mm wide; surface smooth, but rough to the touch; oscules not observed; consistency soft; color light brown in ethanol (Fig. 5a).

**Skeleton** (Fig. 5b). Ectosome is easily detachable, 220  $\mu\text{m}$  thick, formed by a palisade of didiscorhabds and smaller microspined oxeas. Choanosome is disorganized, composed mainly by large and smooth oxeas, but some loose microspined oxeas and didiscorhabds are also present (Fig. 5b).

**Spicules** (Fig. 5c–k). Two categories of oxeas and didiscorhabds:

Oxea I (520–589–720/11–14.7–18  $\mu\text{m}$ ): choanosomal, large, smooth, slightly curved, with hastate ends (Fig. 5c); modifications to styles are rare (Fig. 5d).

Oxea II (152–197–235/4–6–9  $\mu\text{m}$ ): ectosomal, microspined, small and slightly curved, with hastate ends (Fig. 5e–f); few modifications to styles (Fig. 5g–h); the spines are concentrated on the ends, but few are smooth and thin.

Didiscorhabds (32–58–75/1.2  $\mu\text{m}$ ): rare, asymmetrical, slightly curved, sharply pointed, microspined, with malformed discs showing irregular edges: larger disc (7–12–16  $\mu\text{m}$  in diameter) is concave towards the flat smaller one (3–5–8  $\mu\text{m}$  in diameter) (Fig. 5i–k).

**Bathymetry and ecology.** The species occurs at 47 m depth, on sandy bottoms. No associated organisms were recorded.

**Geographical distribution** (Fig. 3; Table 1). Provisionally endemic from off São Francisco River mouth, Sergipe State, Northeastern Brazil.

**Taxonomic remarks.** *Didiscus raraediscus* sp. nov. differs from all other species of the genus by the presence of microspined oxeas, in addition to the rarity of didiscorhabds. *Didiscus raraediscus* sp. nov. and *D. spinoxeatus* Corriero, Scalera-Liaci & Pronzato, 1997 are the only species of the genus

that have small microspined oxeas. However, in *D. spinoxeatus* the microspined oxeas are considered didiscorhabd variations and compose the ectosomal skeleton together with smooth ectosomal oxeas. In contrast, *Didiscus raraediscus* sp. nov. has only microspined ectosomal oxeas; smooth ectosomal oxeas are absent. In addition, *D. spinoxeatus* has styles, subtylostyles and tylostyles in the choanosome (Corriero et al. 1997), all absent in the new species. Among TA species, *D. gladius* resembles *Didiscus raraediscus* sp. nov. in their didiscorhabds with sharp points and finely spined shaft, but is distinguished from the new species by the presence of centrotylote oxeas and styles. The ectosomal oxeas of *D. gladius* have a granular spination that is subtler than in the spined oxea of *Didiscus raraediscus* sp. nov. *Didiscus verdensis*, from Cape Verde Islands, also has didiscorhabds similar to *Didiscus raraediscus* sp. nov., but it differs by the thinly encrusting shape and the presence of smooth ectosomal oxeas, styles and strongyles (Table 1).

#### *Myrmekioderma Ehlers, 1870*

**Type species:** *Alcyonium granulatum* Esper, 1829

**Diagnosis:** Massive or encrusting growth forms. Surface hispid, with characteristic excavating meandering, sinuous or straight canals and grooves sometimes forming polygonal tuberculate plates. Choanosomal skeleton collagenous, with compressed central portion composed of a confused halichondroid mass of larger choanosomal megascleres ranging from acanthoxeas and oxeas, strongyles or less frequently styles, forming irregular, ascending, multispicular tracts bound together with sparse collagen (spongin fibers present in some species, but not all). Subectosomal skeleton composed of ascending tracts of the same spicules running radially or obliquely to surface, with larger choanosomal megascleres protruding, and frequently cavernous towards the periphery. Ectosomal skeleton without specialized spiculation, although smaller (acanth-)oxeas protrude from subectosomal region, forming a dense ‘peel’ of closely adjacent brushes perpendicular or paratangential. Megascleres consist of two distinct categories of oxeas, strongyles, or more rarely styles, sometimes sinuous and centrally flexed, either entirely smooth or with even spination; the larger choanosomal spicules more variable in their terminations than the smaller ectosomal ones, which are typically oxeas or acanthoxeas. Microscleres raphides in trichodragmata, in one or more categories, the larger usually sinuous or curved (Hooper 2002a).

#### *Myrmekioderma guajajara* sp. nov.

<http://zoobank.org/884B6191-13DE-43FC-A875-A8F7A94AB852>

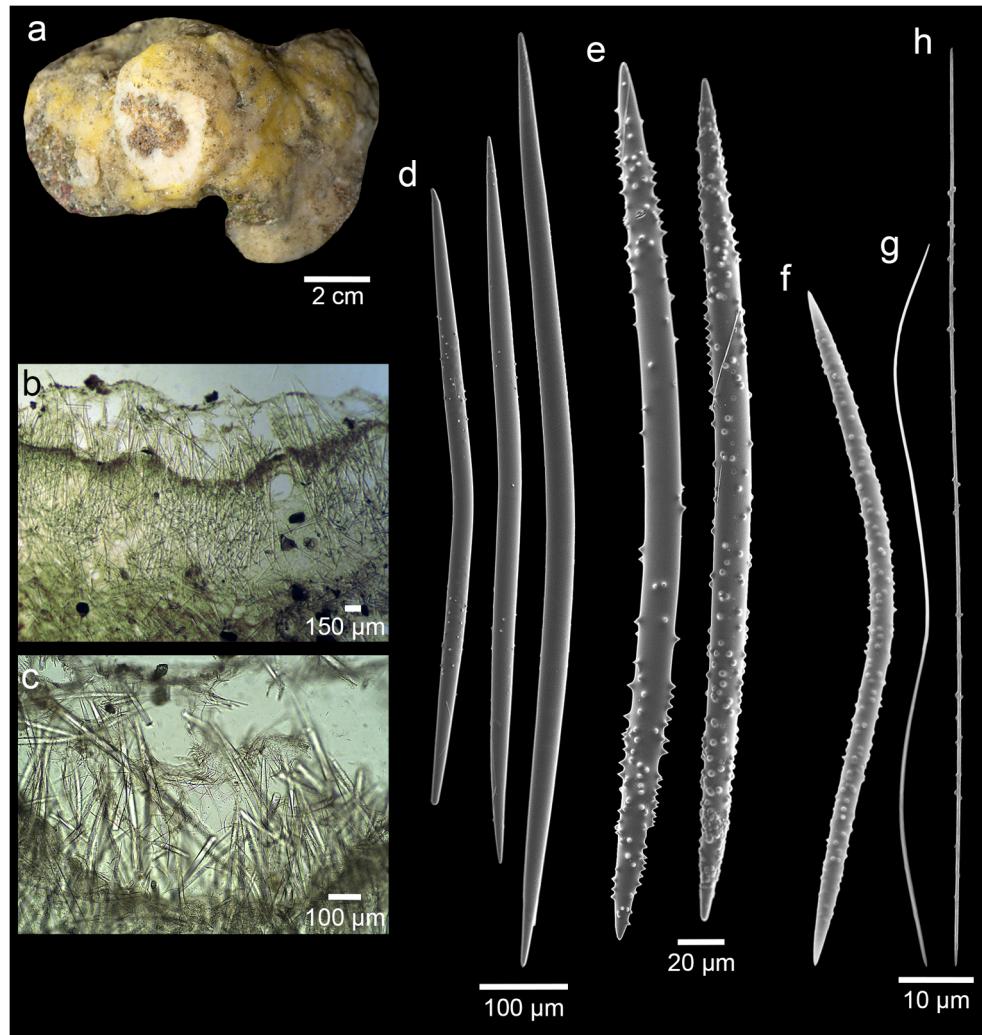
(Figs. 6 and 7; Table 2)

**Type material.** Holotype—MNRJ 21285, off Amazon River mouth, Maranhão State, NE Brazil ( $0^{\circ} 27' 11.16''$  S,  $43^{\circ} 58' 59.99''$  W), 180 m depth, coll. Rodrigo Moura and Fernando Moraes, leg. RV Alucia, 15 July 2017.

**Table 2** Comparative micrometric data of the spicules and overview of distribution of *Myrmekioderma* species. All values in  $\mu\text{m}$ , expressed as follows: minimum–maximum or minimum–mean–maximum length/width. Names of provinces follow Spalding et al. (2007). CJOI, Central Indian Ocean Islands; ECT, Eastern Coral Triangle; EIP, Eastern Indo-Pacific; L, Lusitanian; MS, Mediterranean Sea; NBS, North Brazil Shelf; RSGA, Red Sea and Gulf of Aden; SA, Somalia/Arabian; TNWA, Tropical Northwestern Atlantic; TSWA, Tropical Southwestern Atlantic; WIO, Western Indian Ocean; WSIS, West and South Indian Shelf; WTSWA, Warm Temperate Southwestern Atlantic

<i>Myrmekioderma</i> species	Type locality	Distribution	Depth (m)	Choanosomal megascleres	Ectosomal megascleres	Raphides or Trichodragmata
<i>M. guajigana</i> sp. nov.	Maranhão State, Brazil	NBS	180	Oxea: 575–857–1100/15–23–30 Style: 650–845–950/10–13–20 (n=5)	Oxea: 175–417–650/8–16–30 Microxea: 64–87–117/1–2,1–3 (n=7)	19–70–130
<i>M. tenax</i> sp. nov.	Amapá and Sergipe States, Brazil	NBS; TSWA	47–90	Oxea I: 520–701–1020/6–19–35 Oxea II: 180–230–420/1–3–5	Oxea: 180–302–560/5–7–13	25–79–124
<i>M. denayi</i> (Burton, 1959)	Western Arabian Sea	WIO; SA	38–113	Oxea I: 900/48 Oxea II: 450/24	Oxea: 170/10	I: 320/8 II: 35–70/14
<i>M. granulatum</i> (Esper, 1829) <i>sensu</i> Hooper (2002a)	Unknown	CJOI; WIO; WSIS	2–42	Oxea, strongyle and style: 495–950/8–22	Oxea: 305–708/3–12	110–155/10–15
<i>M. giroderma</i> (Alcolado, 1984)	Cuba	TNW A	20	Oxea: 180–1000/1–31 $\mu\text{m}$	Oxea: 240–400/7–11	—
<i>M. indemaresi</i> Stjå, Maldonado, Farias & Rueda, 2019	Gulf of Cadiz	L	380–455	Oxea: 200–1020/3–30	Oxea: up to 520/15	35–212/1.2–1.4
<i>M. intrastrongyla</i> Sandes & Pinheiro, 2013	Sergipe State, Brazil	TSWA	20–30	Strongyle: 300–550–792/6–11–20	Oxea: 156–308–413/3–7–11 $\mu\text{m}$	I: 38–69–110 II: 12–19–29
<i>M. laminatum</i> Rützler, Piantoni, van Soest & Diaz, 2014	Belize	TNWA	20	Oxea, style, strongyloxea: 304–897–1050/5–13–16	Oxea, style, strongyle: 289–365–440/7–12–16	7–130/0.1–0.5
<i>M. niveum</i> (Row, 1911)	Red Sea	RSGA	6	Oxea: 350–430/6–10	—	—
<i>M. pacificum</i> Pulitzer-Finali, 1996	Papua New Guinea, Bismarck Sea	ECT	6	Oxea: 650–850/27–45 (tyloite and strongly lute modifications)	Oxea: 280–470/7–16	100–130
<i>M. rea</i> (de Laubenfels, 1934) <i>sensu</i> Diaz et al. (1993)	Puerto Rico	TNWA; NBS; WTSWA	37–73	Oxea, strongyloxea and style: 260–600–800/5–11–20	Oxea: 170–300–500/5–8–15	13–26/3–10
<i>M. spelaicum</i> (Pulitzer-Finali, 1983)	Tremiti Islands, Adriatic Sea	MS	2–12	Oxea: 460–740/14–21	140–280/4.5–12	Up to 300
<i>M. tuberculatum</i> (Keller, 1891)	Eritrea, Red Sea	RSGA	—	Oxea: 500/7.5 Strongyles (rare)	—	—

**Fig. 6** Morphological and anatomical characters of *Myrmekioderma guajajara* sp. nov. **a** Fresh specimen on board (MNRJ 21285—holotype); **b** ectosome and choanosome in transverse section; **c** detail of ectosome; **d** choanosomal oxeas; **e** ectosomal oxeas; **f** microxea; **g** sinuous raphide; **h** straight raphide



**Etymology.** The species name is given in honor to the first inhabitants of Maranhão State, the native Brazilian tribe “Guajajara.”

**Diagnosis.** *Myrmekioderma guajajara* sp. nov. has smooth or spined choanosomal oxeas, heavily spined or verrucose ectosomal oxeas, rare styles, smooth or microspined sinuous ectosomal microxeas and raphides.

**Description** (Fig. 6a). Thick encrusting sponge, 1 cm thick. The surface is velvety to the touch, with slightly elevated lobes and foreign debris. The consistency is hard and incompressible. The color is cream with some yellow spots, becoming light beige to gray in ethanol (Fig. 6a).

**Skeleton** (Fig. 6b–c). Ectosomal skeleton well developed, 600 μm wide. It is formed by a layer of tangential microxeas at the surface, together with loose bundles of perpendicular oxeas, mostly of the smaller and spined type (Oxea II); microxeas are also located strewn in confusion between the ectosomal oxeas (Fig. 6b–c). The choanosomal skeleton is dense, composed mainly by scattered oxeas I and II (Fig. 6b).

**Spicules** (Fig. 6d–h). Two categories of oxeas, rare styles, microxeas and raphides.

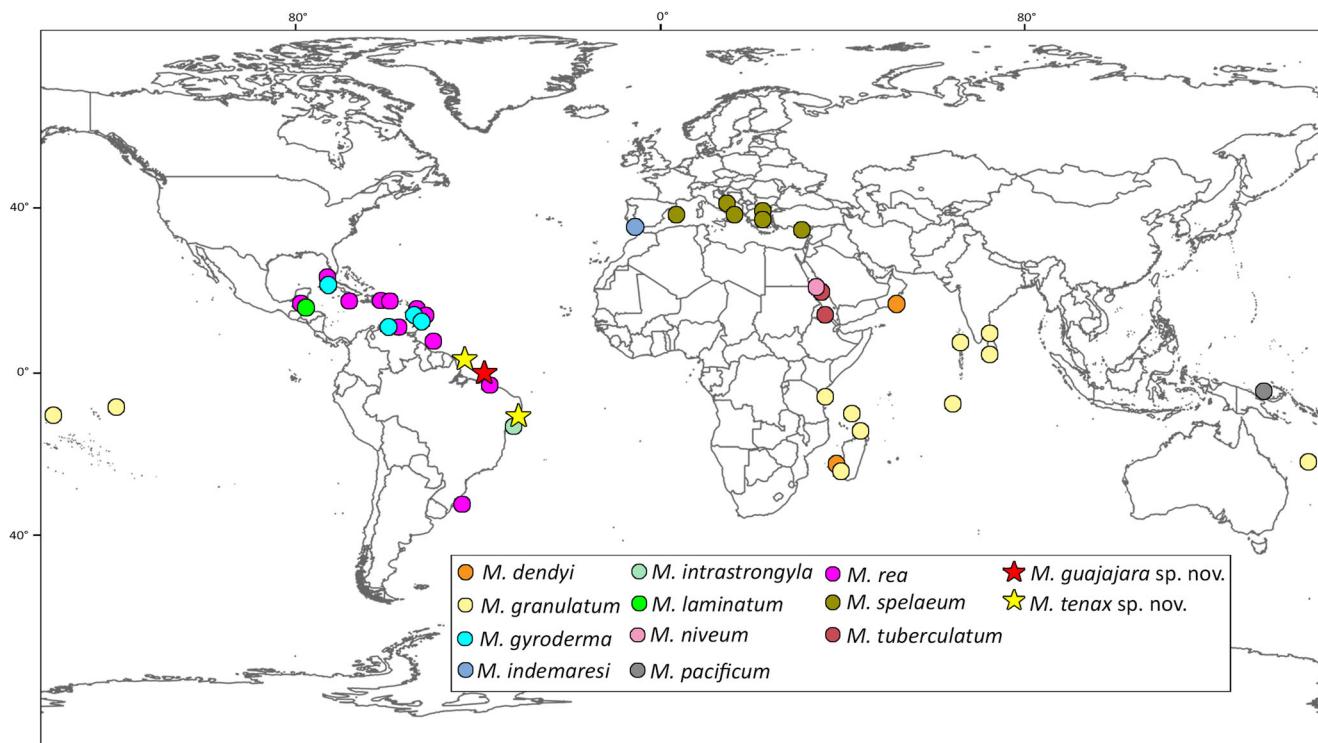
Oxeas I (575–857.5–1100/15–23.5–30 μm): choanosomal, smooth or slightly spined, with spines generally located near the ends; hastate, mucronate and blunt ends are common (Fig. 6d).

Oxeas II (175–417.5–650/8–16.1–30 μm): ectosomal, straight or slightly curved, and strongly spined, especially towards the ends; some have warts instead of spines, scattered throughout the whole spicule, but generally grouped at the ends (Fig. 6e); modifications to acanthostyles and acanthostyngles are rare.

Styles (650–845–950/10–13–20 μm): rare, smooth, and sinuous; some are polytylote.

Microxeas (64–86.6–117/1.5–2.1–3 μm): small and thin, slightly curved, curved in the middle or sinuous, microspined or smooth (Fig. 6f).

Raphides (19–70.3–130 μm) sinuous or straight (Fig. 6g–h).



**Fig. 7** World distribution of all 13 *Myrmekioderma* species. Stars represent new species and circles are records from the literature

Trichodragmata not found.

**Bathymetry and ecology.** The species was found at 180 m depth, on hard carbonate bottom. No organisms were recorded as epibionts.

**Geographical distribution** (Fig. 7; Table 2). Provisionally endemic from the region under influence of the Amazon River mouth, at the upper slope of Maranhão State, Northeastern Brazil.

**Taxonomic remarks.** *Myrmekioderma guajajara* sp. nov. differs from the other 11 species of the genus by the presence of verrucose ectosomal oxeas, together with microspined and sinuous microxeas. *Myrmekioderma guajajara* sp. nov. is clearly distinct from all its congeners in the TA: *M. gyroderma* has larger choanosomal oxeas and smaller microspined ectosomal oxeas; *M. intrastrongyla* has choanosomal strongyles and two categories of trichodragmata; and both *M. laminatum* and

*M. rea* have oxeas with styloid and strongyloid modifications. Additionally, none of these species have sinuous microxeas and verrucose ectosomal oxeas as the new species do (Table 2).

#### *Myrmekioderma tenax* sp. nov.

<http://zoobank.org/B7A05DCC-94C9-4C8F-9198-05E4589FB298>

(Figs. 7 and 8; Tables 2 and 3)

#### Synonyms:

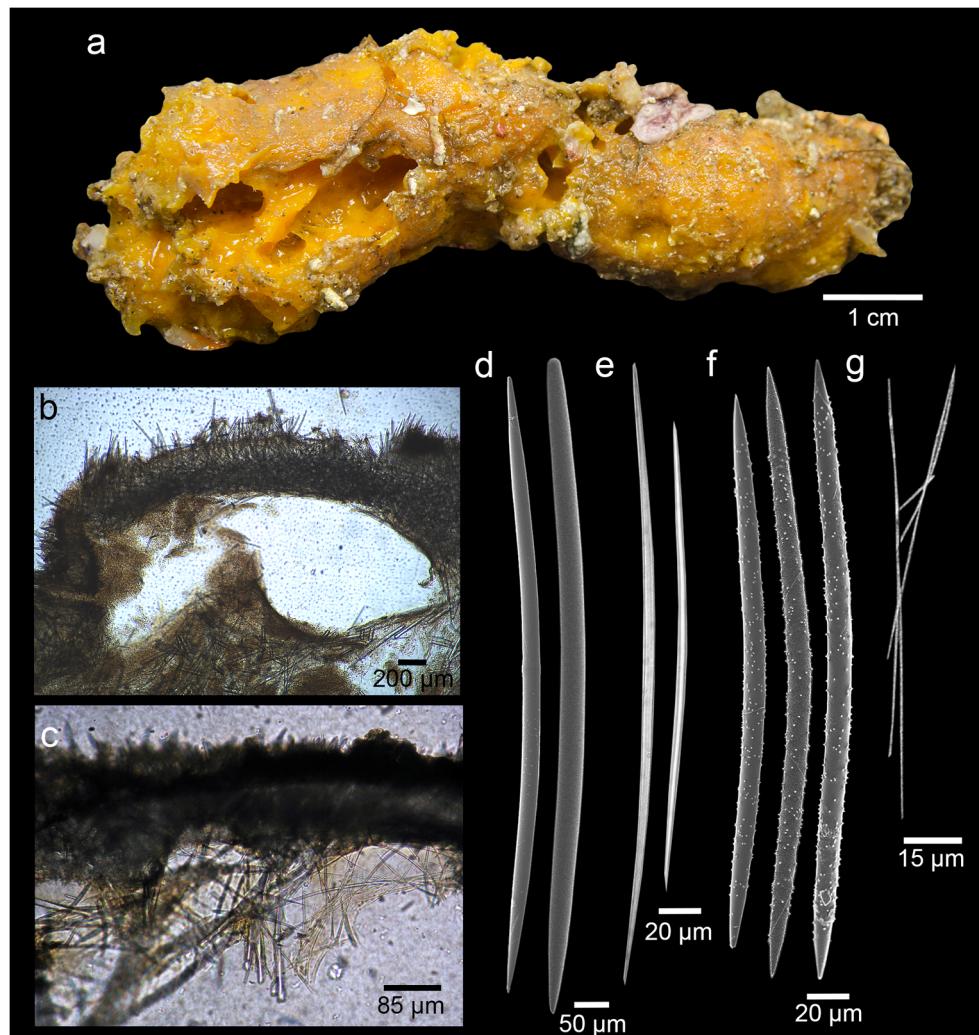
*Myrmekioderma* sp., Moura et al. (2016): Table S2.

**Type material.** Holotype—MNRJ 18743, off Amazon River mouth, Amapá State, N Brazil ( $03^{\circ} 35' 25.60''$  N,  $49^{\circ} 07' 36.167''$  W), 90 m depth, coll. Fernando Moraes and Rodrigo Moura/ NHo Cruzeiro do Sul, 26 September 2014. Paratypes—UFSPOR 834, Brejo Grande city, MARSEAL Project #CZ03 sta. ( $10^{\circ} 35' 21.48''$  S,  $36^{\circ}$

**Table 3** Spicule measurements of all specimens of *Myrmekioderma tenax* sp. nov. herein studied. All values in  $\mu\text{m}$ , expressed as follows: minimum–maximum or minimum–mean–maximum length/width

Specimens examined	Choanosomal oxea I	Choanosomal oxea II	Ectosomal oxea (microspined)	Trichodragmata
MNRJ 18743 (Holotype)	600–882.5–1020/6–28–35	180–256.5–340/1–3.2–5	250–361–560/7–10.3–13	99–112.4–124
UFSPOR 352 (Paratype)	520–582.7–670/9–13.5–17	—	197–223.2–245/5–6.0–7	25–29.6–35
UFSPOR 666 (Paratype)	530–628.3–700/12–17–20	180–201.3–233/1–2.5–4	180–321.3–270/5–5.7–8	12–73–120
UFSPOR 668 (Paratype)	530–620.5–700/7–12.5–18	190–252.5–420/2–2.6–4	145–244.5–390/6–7.4–10	30–39.2–50 (n=3)
UFSPOR 834 (Paratype)	550–620–690/11–14.8–20	182–209.5–335/1–2.6–4	200–231–260/5–6.1–8	17–40–83 (n=4)

**Fig. 8** Morphological and anatomical characters of *Myrmekioderma tenax* sp. nov. **a** Fresh specimen on board (MNRJ 18743—holotype); **b** ectosome and choanosome in transverse section; **c** detail of ectosome; **d** choanosomal oxeas, including the styloid variation; **e** raphidiform oxeas; **f** ectosomal oxeas; **g** raphide



19° 33.24" W), Sergipe State, NE Brazil, 54 m depth, coll. Petrobras, leg. RV Luke Thomas, February 2011; UFSPOR 666, 668, off Pirambu city, MARSEAL Project #D3 sta. (10° 52' 21.00" S, 36° 32' 9.96" W), Sergipe State, NE Brazil, 47 m depth, 29 June 2011; UFSPOR 352, off Pirambu city, MARSEAL Project #D3 sta. (10° 52' 21.00" S, 36° 32' 9.96" W), Sergipe State, NE Brazil, 47 m depth, 03 July 2011.

**Etymology.** The species name refers to the remarkably sticky mucous released by the sponge after collection. From Latin *tenax* = sticky.

**Diagnosis.** *Myrmekioderma tenax* sp. nov. has smooth choanosomal oxeas, microspined ectosomal oxeas, raphidiform oxeas, raphides, and trichodragmata. It produces a sticky mucus.

**Description** (Fig. 8a). Massive or ramoso shape, 6 cm length by 2 cm width (holotype), with branches ranging from 1 to 10 mm in diameter in ramoso specimens; surface velvety to the touch, with slightly elevated ridges and grooves; consistency soft and compressible, releasing a very sticky mucus;

osculles not observed; color reddish orange, becoming yellowish beige to dark brown in ethanol (Fig. 8a).

**Skeleton** (Fig. 8b–c). Ectosome easily detachable (150–500 μm thick), formed by a layer of microspined oxeas (Oxea III) in a perpendicular, paratangential or tangential arrangement. Choanosomal skeleton plumo-reticulate, with tracts and meshes poorly defined. Pauci- to multispicular tracts of oxeas support the ectosome, ending in bouquets protruding at the surface. Oxeas II usually arranged around oxeas I in the subectosomal tracts (Fig. 8b–c).

**Spicules** (Fig. 8d–g) (average of all specimens; individual measurements in Table 3). Oxeas in three categories, raphides, and trichodragmata.

Oxeas I (520–701.2–1020/6–19.5–35 μm): choanosomal, large, smooth, and slightly curved, with hastate ends; modifications to styles are common (Fig. 8d).

Oxeas II (180–230–420/1–2.7–5 μm): subectosomal, raphidiform, smooth, slightly curved in the middle portion, or sinuous (Fig. 8e).

Oxeas III (180–301.8–560/5–7.3–13 µm): ectosomal, small, slightly curved, and microspined, with spines heavily scattered along the spicule or slightly concentrated on the ends (Fig. 8f).

Raphides and trichodragmata (25–79.0–124 µm) (Fig. 8g).

**Bathymetry and ecology.** The specimens were sampled from 47 to 90 m depth, on carbonate bottoms (rhodolith beds). Macroalgae, bryozoans, and ascidians were recorded as epibionts.

**Geographical distribution** (Fig. 7; Table 2). Amapá and Sergipe States, N and NE Brazil, off the mouths of Amazon and São Francisco rivers, respectively.

**Taxonomic remarks.** *Myrmekioderma tenax* sp. nov. differs from the other species of the genus by the presence of three categories of oxeas, being one ectosomal and two choanosomal, and trichodragmata (Table 2). The sinuous and raphidiform oxeas arranged around the choanosomal spicule tracts of *Myrmekioderma tenax* sp. nov. are here reported for the first time to the genus. The species most similar to *Myrmekioderma tenax* sp. nov. in the TA is *M. gyroderma* from Cuba, Colombia, and the Bahamas, which shares similar choanosomal oxeas that are large, smooth and thick, and smaller microspined oxeas (Alcolado 1984). However, *M. gyroderma* has meandering surface grooves, two categories of oxeas (smooth and microspined), and lacks trichodragmata. Many authors reported the variability of the acanthose condition of the smaller oxeas and the presence of trichodragmata in *M. gyroderma* (Díaz et al. 1993; van Soest and Stentoft 1988). Additionally, Díaz et al. (1993) raised the possibility that trichodragmata are rare in the type material examined by Alcolado (1984) and could have been overlooked. In any case, the presence of raphidiform oxeas and the smooth surface (without grooves) are here considered as sufficient evidence to propose a new species. However, we reinforce the need to review the *M. gyroderma* records, specially the type material, to check for the presence of rare trichodragmata.

## Discussion

### Morphology and classification of *Didiscus* and *Myrmekioderma*

The description of four new species in this study increases the diversity of *Didiscus* from nine to 11 species and of *Myrmekioderma* from 11 to 13 species. In addition, the diversity of anatomical traits of both genera is expanded by the addition of new spicule types and ornamentations: tylostyles previously overlooked in the holotype of *Didiscus oxeatus*, small microspined oxeas in *Didiscus raraediscus* sp. nov., microspined microxeas and verrucose smaller oxeas in *Myrmekioderma guajajara* sp. nov., and sinuous raphidiform oxeas in *Myrmekioderma tenax* sp. nov.

*Didiscus raraediscus* sp. nov. is the first species of the genus with small microspined oxeas and rare didiscorhabds. Usually, the didiscorhabds of *Didiscus* exhibit variations including rudimentary or absent discs, similar to microspined oxeas of *Myrmekioderma*, although much smaller (van Soest et al. 1990). The small microspined oxeas of *Didiscus raraediscus* sp. nov. are identical to the small oxeas of *Myrmekioderma* spp., with tapering points and rugose spination, but they are larger than the didiscorhabds of *D. raraediscus* sp. nov. This justifies the interpretation of didiscorhabds and microspined oxeas as being distinct spicule categories. The microspined oxeas of *D. raraediscus* sp. nov. seems to be another evidence of the close affinities between *Didiscus* and *Myrmekioderma*.

The presence of tylostyles with polytylote modifications is rather common in *Didiscus*, being reported in *D. aceratus* (Ridley & Dendy, 1886), *D. oxeatus*, *D. placospongoides*, *D. spinoxeatus*, and *D. stylifer* Tsuranamal, 1969. In the first diagnosis of *Didiscus*, Dendy (1922) pointed out to the presence of echinating tylostyles in *D. placospongoides*, suggesting a possibly ectyonine origin.

The sinuous microspined microxeas of *Myrmekioderma guajajara* sp. nov. are reported here for the first time in the genus. These microscleres closely resemble the crescent-shaped acanthoxeas of *Desmoxya* Hallmann, 1917, which are also abundant in the surface as in *M. guajajara* sp. nov. However, *Desmoxya* has only one category of smooth megascleres, lacks a specialized ectosomal skeleton (van Soest and Hooper 2005) and has recently been classified in the order Poecilosclerida (Morrow et al. 2019).

The sinuous raphidiform oxeas arranged around the megascleres in the subectosomal tracts of *Myrmekioderma tenax* sp. nov. resemble the sinuous raphides of *Epipolasis* de Laubenfels, 1936. The genus *Epipolasis* (Halichondriidae Gray, 1867) has two categories of oxeas, raphides, and trichodragmata and is distinguished from *Myrmekioderma* only by the lack of acanthose megascleres (Erpenbeck and van Soest 2002). Due to the variability of the acanthose condition of the small oxeas in *Myrmekioderma* species, some authors considered that the genus *Epipolasis* is not valid and assigned *Epipolasis* species to *Myrmekioderma* (van Soest et al. 1990; Díaz et al. 1991, 1993). We suggest that all *Myrmekioderma* species without acanthose megascleres should be revised, including *M. dendyi* (Burton, 1959), *M. indemaresi* Sitjà, Maldonado, Farias & Rueda, 2019, *M. niveum* (Row, 1911), *M. pacificum* Pulitzer-Finali, 1996, and *M. spelaeum* (Pulitzer-Finali, 1983). The relationship between *Myrmekioderma* and *Epipolasis* is a further problem in the systematics of *Myrmekioderma*.

Phylogenetic studies with different molecular markers support alternative classifications of *Didiscus* and *Myrmekioderma*. Analyses of 28S rRNA barcoding sequences clustered

*Myrmekioderma granulatum* (the type species of *Myrmekioderma*) with *Didiscus* spp. in Raspailiidae (Erpenbeck et al. 2005, 2007). In contrast, cox-1 mtDNA sequences placed *Myrmekioderma* spp. within the Axinellidae or Heteroxyidae (Erpenbeck et al. 2012; Morrow et al. 2019). Sequences of 18S rRNA indicated that *Myrmekioderma* may be polyphyletic, with *M. granulatum* in Raspailiidae and *M. rea* in Axinellidae (Redmond et al. 2013). The most recent classification based on molecular data retains *Myrmekioderma* in Heteroxyidae (in part) and transferred *Didiscus* to Raspailiidae (Morrow et al. 2019; van Soest et al. 2020). However, more data is needed to resolve the incongruences between phylogenetic hypotheses based on different molecular markers.

In contrast, morphological data clearly support the placement of both *Didiscus* and *Myrmekioderma* in the family Heteroxyidae instead of Raspailiidae. The two genera have a disorganized choanosomal skeleton typical of Heteroxyidae, without the ectosomal bouquets of smaller megascleres, the axial condensation in the choanosome and the echinating acanthostyles typical of Raspailiidae (Hooper 2002a, 2002b; Santos et al. 2016a). We tentatively adhered here to this classification because our study was restricted to morphological data and due to the conflicting results of molecular analyses.

The currently available evidence suggests that *Didiscus* is monophyletic and defined by the presence of exclusive didiscorhabds, which is a good morphological synapomorphy. In contrast, the genus *Myrmekioderma* and the two families Heteroxyidae and Raspailiidae are probably polyphyletic, based on either morphological or molecular evidence (Hooper 2002a, 2002b; Erpenbeck et al. 2005, 2007, 2012; Redmond et al. 2013; Santos et al. 2016a; Morrow et al. 2019). Extensive revisions of these taxons, integrating morphological and multi-marker molecular approaches, are still required to achieve a more stable classification.

## Distribution of *Didiscus* and *Myrmekioderma* in the Tropical Atlantic

Our results raised the diversity of *Didiscus* and *Myrmekioderma* in the TA to 11 species, of which eight occur in the Brazilian Exclusive Economic Zone. The TA harbors the highest diversity of both genera in the world, with five of the 11 species of *Didiscus* (45.4%) and six of the 13 *Myrmekioderma* (46.1%; Figs. 3 and 7).

*Myrmekioderma rea* has the widest distribution among these species, occurring in the Tropical Northwestern Atlantic, North Brazil Shelf, and Warm Temperate Southwestern Atlantic provinces (Muricy et al. 2011; van Soest et al. 2020). However, this apparently wide distribution may be due to misidentifications, specially the records from Brazilian waters, resulting from high morphological variation in descriptions of *Myrmekioderma rea* (Rosa-Barbosa 1995; Mothes et al. 2004; Sandes and Pinheiro 2013). *Didiscus oxeatus* has a wide but disjunct distribution,

occurring in the Tropical Northwestern and Southwestern Atlantic provinces, but lacking in the North Brazil Shelf (Muricy et al. 2011; van Soest et al. 2020). In contrast, most species of both genera in the TA have restricted distributions, and *Myrmekioderma tenax* sp. nov. is the only species occurring in both the North Brazil Shelf and in the Tropical Southwestern Atlantic provinces. *Myrmekioderma gyroderma* and *M. laminatum* are endemic from the Caribbean, and the other six species are endemic from Brazilian waters: *Myrmekioderma guajajara* sp. nov. is restricted to the North Brazil Shelf province; *Didiscus gladius*, *D. raraediscus* sp. nov., *D. pseudoverdensis* sp. nov. and *M. intrastrongyla* occur only in the Tropical Southwestern Atlantic province. *Myrmekioderma laminatum*, *M. guajajara* sp. nov., *Didiscus gladius*, *D. raraediscus* sp. nov. and *D. pseudoverdensis* sp. nov. are known by only one or two specimens from a single locality each, being considered provisionally endemic. Our results demonstrate that these restricted distribution patterns probably reflect the low number of collections, especially in the mesophotic carbonate reefs and rhodolith beds off the mouths of Amazon and São Francisco rivers.

Most species of *Didiscus* and *Myrmekioderma* from Brazilian waters were collected in mesophotic environments, from 47 to 180 m depth. The apparently restricted off coast and deep-water distributions of these both genera may contribute to their low species diversity estimation in Brazilian waters until now. Therefore, with the increasing of sampling efforts in still understudied regions, such as the areas under influence of the mouths of the Amazon and São Francisco rivers, the discovery of new species and the (re) analysis of previously known species of *Didiscus* and *Myrmekioderma*, including more specimens of the ones described in the present work, will contribute to a better understanding of the taxonomy, systematics, biodiversity and distribution of these genera in the Tropical Atlantic Ocean.

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## Compliance with ethical standards

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

**Ethical approval** No animal testing was performed during this study.

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

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

**Author contribution** JS and FM conceived and designed research. FM collected the material. JS processed samples. JS, FM, UP and GM analyzed data. JS, FM and GM wrote the manuscript. All authors revised and approved the manuscript.

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