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Original Paper

Running Head: Suberitida from the unexplored Northeastern Brazil

Morphological description of six species of Suberitida (Porifera: Demospongiae) from the unexplored Northeastern Brazil, with emphasis on two new species

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Abstract

The Order Suberitida is defined as a group of marine sponges without an obvious cortex, a skeleton devoid of microscleres, and with a deletion of a small loop of 15 base pairs in the secondary structure of the 28S rDNA as a molecular synapomorphy. Suberitida comprises three families and 26 genera distributed worldwide, but mostly in temperate and polar waters. Twenty species were reported along the entire Brazilian coast, and although the Northeastern coast of Brazil seems to harbour a richest sponge fauna, our current knowledge is concentrated along the Southeastern Atlantic coast. A survey has been implemented along the northern coast of Brazil, and the collection allowed the identification of six species belonging to the Order Suberitida, two of them are considered new to science: *Suberites purpura* sp. nov., *Hymeniacidon upaonassu* sp. nov., and four, *Halichondria (Halichondria) marianae* Santos, Nascimento & Pinheiro, 2018, *Halichondria (H.) melanadocia* de Laubenfels, 1936, *Suberites aurantiacus* (Duchassaing & Michelotti, 1864), and *Terpios fugax* Duchassaing & Michelotti, 1864, being re-described. Taxonomic comparisons are made for Tropical Western Atlantic species and type species of the four genera. Finally, an identification key for the Western Atlantic *Suberites* species is provided.

Keywords: Marine sponges; intertidal; biodiversity; Halichondriidae, Suberitidae, Tropical Western Atlantic.

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INTRODUCTION

The order Suberitida has been recognized in 2015 by Morrow & Cárdenas after a major overturning of the Demospongiae classification. Some years before, Chombard and Boury-Esnault (1999) already created the suborder Suberitina, grouping the families Suberitidae and Halichondriidae, according to morphological and genetic traits. However, this taxonomic group did not appear in the *Systema Porifera* (Hooper & van Soest, 2002) due to several inconsistencies in systematics. In summary, the order is presently defined as a group of species without an obvious cortex and a skeleton devoid of microscleres. Megascleres are mostly styles, oxeas and/or tylostyles. The ectosome arrangement is tangential or paratangential. The skeleton of the choanosome is frequently confused, but a radial arrangement and/or ascending multispicular tracts can be found in several representatives (van Soest, 2002a,b; Erpenbeck & van Soest, 2002). The molecular synapomorphy that characterizes Suberitida is a deletion of a small loop of 15 base pairs in the secondary structure (D2) of the 28S rDNA when compared to other Heteroscleromorpha (Morrow & Cárdenas, 2015).

The order encompasses three families, 26 genera and 491 species distributed across the oceans. Along the Brazilian coast, only two families, nine genera, and, so far, 20 valid species were inventoried (Muricy *et al.*, 2011; van Soest *et al.*, 2019, Table 1). The Northeast region of Brazil seems to harbour the richest sponge fauna of Brazil; however, most of the studies were conducted along the Eastern littoral (Boury-Esnault, 1973; Muricy & Moraes, 1998; Hajdu *et al.*, 2011; Leonel *et al.*, 2011; Cedro *et al.*, 2013; Sandes & Pinheiro, 2013; Santos *et al.*, 2018) and around seamounts or oceanic islands (Salani *et al.*, 2006, Muricy *et al.*, 2008, Moraes 2011, Carvalho *et al.*, 2013), whereas the northern coast has received much less attention (Mothes *et al.*, 2004, Campos *et al.*, 2005).

In a recent study, van Soest (2017) has shown that the Caribbean Sea and the Brazilian coast share several representatives of the sponge fauna, the northern coast of Brazil thus appearing as a transitional area in the Tropical Western Atlantic (TWA) (Spalding *et al.*, 2007). Aiming at a better knowledge of the sponge fauna of this transitional region, surveys were realized at shallow waters length ways at the northern coast of Brazil. This work presents a focus on the order Suberitida with the description of six species from the intertidal zone, two considered new for science.

MATERIAL AND METHODS

Study area

The sampling was realized in the framework of the expeditions TAXPOMOL/2016 and Maranhão/2017 in the unexplored part of the northern coast of the Northeast region of Brazil, which is named Brazilian Semi-Arid Coast (Diniz & Oliveira, 2016). All samples were collected in the intertidal zone, on sandy beaches, with rocky tide pools, from the states of Maranhão and Ceará (Figure 1).

The Brazilian Semi-Arid Coast includes Maranhão, Piauí, Ceará and part of Rio Grande do Norte states, the shoreline being about 1065 km long. In this region, the climate average temperature is 25.8°C, the pluviometry is 262.3 ppm (Climate-data, accessed online, on 3rd April 2019), and it experiences the strongest winds of the Brazilian coast (Muehe, 1998). According to the oceanographic conditions, the region possesses the largest tidal range (8-12 m) along the Brazilian coast (Muehe, 1998). The sea water temperature average is always higher than 27°C, the chlorophyll a concentration varies from 0.2 to 4.3

mg.m⁻³, and the particulate organic carbon concentration (POC) is about 60 mg.m⁻³ at the sandy beaches of Ceará and Rio Grande do Norte, and an average of 397 mg.m⁻³ at the estuary of São Luís (Maranhão) (compiled data from Giovanni platform of NASA).

Sample collection and identification

Sponge samples were preserved in 92% ethanol and deposited in the Porifera Collection of the Museu Nacional (MN/UFRJ). Spicule and skeletal preparations followed classic protocols for Demospongiae species (Hajdu *et al.*, 2011). For each sponge individual, 50 spicules were measured in order to provide basic descriptors (minimal, mean, standard deviation, and maximal values) in comparative tables.

SYSTEMATICS

Phylum PORIFERA Grant, 1836

Class DEMOSPONGIAE Sollas, 1885

Subclass HETEROSCLEROMORPHA Cárdenas, Pérez and Boury-Esnault, 2012

Order SUBERITIDA Chombard & Boury-Esnault, 1999

Family SUBERITIDAE Schmidt, 1870

Genus *Suberites* Nardo, 1833

SYNONYMY. For synonymy see van Soest (2002b).

DEFINITION. Suberitidae harbouring tylostyles in two size categories, large at the choanosome, and small forming bouquets at the ectosome. The choanosomal skeleton is confused or alveolar with sub-radiate bundles of megascleres. Microscleres are not common, but spined centrotylote microstrongyles can be observed (van Soest, 2002b).

TYPE SPECIES. *Alcyonium domuncula* Olivi, 1792: 241 (by original designation).

Suberites purpura sp. nov.

(Figures 2, 3, 4, Table 2)

TYPE MATERIAL: HOLOTYPE. MNRJ 21343, Praia de Araçagi, São José de Ribamar, tidal pool (2°27'46.84"S 44°12'14.94"W), Maranhão State, Brazil, 0.5 m depth, coll. H. Fortunato, 5/XI/2017.

DIAGNOSIS. *Suberites purpura* sp. nov. is the only *Suberites* species from the Western Atlantic Ocean, purple in color, with a combination of tylostyles up to 1500 µm long and short and open bouquets in the ectosomal skeleton.

DESCRIPTION: External morphology (Figure 2A). Thickly encrusting to massive sponge, 10 x 5 cm size, and small oscules (<1 mm diameter). The surface is smooth but also microhispid and the consistency is firm, little compressible, and somehow cartilaginous. The color is purple outside, and orange at the basis and inside.

Skeleton (Figure 3A, B). The ectosomal skeleton is made of short and open bouquets (detail in Figure 3B) of small tylostyles. The choanosomal skeleton is confused with longer tylostyles forming rare branches. The skeleton is typically *Suberites*-like.

Spicules (Figure 4A, Table 2). Tylostyles with globose head in two divisible categories: small 208.5–790.2 / 4.8–21.6 μm , tyle width 5.3–18.1 μm , and large 860.7–1991.3 / 17.2–45.8 μm , tyle width 11.5–33.9 μm .

ECOLOGY. Only one specimen was found in a crevice of a tide pool, in a dark habitat.

DISTRIBUTION. Brazil: Northeastern Region: Maranhão State.

ETYMOLOGY. In Latin, the feminine noun, “purpura” = purple colored, refers to the external color of the species (Brown, 1956).

REMARKS. The combination of tylostyles size ($>1500 \mu\text{m}$), the purple color, the short and open bouquets, and the geographic distribution make this species different from all other species from the TWA. The most similar species from the TWA is *S. aurantiacus* (Duchassaing & Michelotti, 1864); however, the spicule length of this species is never greater than 1000 μm . *Suberites caminatus* Ridley & Dendy, 1886, was described from Prince Edwards Islands in the Antarctic Indian Ocean, but the original description also included slightly variant material from off Rio de la Plata, in the Uruguay-Buenos Aires shelf; the name was also used by Boury-Esnault (1973) for material from Southeastern Brazil (see Ridley & Dendy 1886 in van Soest *et al.*, 2019). It has tylostyle sizes up to 600 μm , half of that of the new species. The disjunct distribution of this species calls for a comparative study to decide if the SW Atlantic material belongs to a different, yet unnamed species. The name *Suberites carnosus* (Johnston, 1842) was used by Ridley & Dendy (1886) and by Boury-Esnault (1973) for material respectively from Fernando de Noronha and Southeastern Brazil (see Johnston, 1842 in van Soest *et al.*, 2019). The former has spicules up to 560 μm , and the latter up to 430 μm and in a single size (see details in Table 2), unlike *S. purpura* sp. nov. Moreover, as *S. carnosus* from the Eastern Atlantic and the Mediterranean has a stalked plum-like shape and a large central osculum (Ackers *et al.*, 1992), and Boury-Esnault (1973) material is described as thinly encrusting, this record seems inaccurate. We suggest calling it *Suberites* aff. *carnosus* until a new taxonomic study is carried out. *Suberites purpura* sp. nov. also differs from the other species distributed in the Caribbean by its internal and external characteristics. *Suberites lobatus* (Wilson, 1902) has an encrusting growth form; *S. crispolobatus* van Soest, 2017 has a greyish brown color, with erect rounded branches, and dwells in rather deep water (50–85 m) habitats; and *S. distortus* Schmidt, 1870 presents a club-shaped yellow form. Unfortunately, the comparison with *Suberites heros* Schmidt, 1870, from the Eastern Caribbean, is difficult due the lack of anatomical data for the latter species. In fact, there are reasons to doubt if it is a valid species, as the author had mentioned that *S. heros* presents quite similar habit of the type species, *Suberites domuncula*, also in association with mollusks and possession of tylostyles with short and not pronounced tyles. Moreover, van Soest (2002b) informed that the lectotype conforms to *S. domuncula* due the presence of a hermit crab hole in the sponge and tylostyle in two categories. Thus, this species still need revision. Lastly, *S. purpura* sp. nov. differs from the Chesapeake Bay (United States) representative, *Suberites paradoxus* Wilson, 1931, because the last has a lamellar and buried habit with abundant sand grains incorporating the sponge tissue, and the tylostyles are slightly curved, with overlapping categories varying from 220 to 350 μm in length.

Suberites aurantiacus (Duchassaing & Michelotti, 1864)

(Figures 2, 3, 4, Table 2)

SYNONYMY: For synonymy see Rützler & Smith (1993).

TYPE LOCALITY: Caribbean Sea, Virgin Islands, St. Thomas.

MATERIAL EXAMINED. MNRJ 21405, MNRJ 21430 Araçagi beach, São José de Ribamar, tidal pool (2°27'46.84"S 44°12'14.94"W), Maranhão State, Brazil, coll. H. Fortunato, 5/XI/2017, MNRJ 21500, Meio beach, São José de Ribamar, tidal pool (2°28'19.11"S 44°13'8.73"W), Maranhão State, Brazil, coll. H. Fortunato, 5/XI/2017.

REDESCRIPTION: External morphology (Figure 2B, C, D). Sponges vary from encrusting to massive or subspherical habitat. The size of the examined individuals was approximately 12 x 8 cm (length x width). Their surface was velvety and rugose, with vesicles. Their consistency was firm and little compressible. Small oscula can be seen dispersed at the surface (1–5 mm in diameter). The color *in vivo* is mostly green externally (Figure 2B), but also bright orange and always yellow internally (Figure 2C, D).

Skeleton (Figure 3C, D). *Suberites*-like skeleton: small tylostyles forming generally wide (Figure 3C) or narrow (Figure 3D) bouquets in the ectosome, and a choanosomal skeleton confused, but with bundles in direction to the surface.

Spicules (Figure 4B, C). Tylostyles are a well formed with globose head without lobes, but with knobs in thinner spicules. Spicules are divided in two categories: small 140.0–386.4 μm / 2.4–12.2 μm , tyle width 3.1–12.2 μm , and large 376.2–830.0 μm / 4.9–20.7 μm , tyle width 5.2–18.3 μm .

ECOLOGY. The species has been observed on semi-exposed surfaces, mostly in shallow waters.

DISTRIBUTION. Tropical Western Atlantic: Gulf of Mexico, Caribbean Sea, and Brazilian Tropical and Temperate coasts.

REMARKS. *Suberites aurantiacus* is a widely distributed species in the TWA, showing a great polymorphism of growth form and color, especially when rocky-shore and mangrove individuals are compared. The specimens found along the northern coast of the Northeast region of Brazil are similar to others from the TWA by the presence of non-curved tylostyles in two size categories, varying from 140 to 800 μm , globose tyles, mostly green color externally and yellow internally, and the large ectosomal bouquets. An orange, subspherical morphotype, with ectosomal bouquets being narrower and with longer spicules, found living upside down in crevices of a tidal pool at Maranhão State (MNRJ 21500, Figures 2C and D, 3D and 4C), was assigned to of *S. aurantiacus* owing to the known variability and wide tolerance of this species. Molecular investigations may highlight how and why these polymorphisms occur and would also inform if this morphotype is really *S. aurantiacus*.

KEY TO THE GENUS *Suberites* FROM THE TROPICAL WESTERN ATLANTIC COMPARING TO THE TYPE SPECIES

- | | | |
|----|---|-------------------------|
| 1a | Two categories of tylostyles..... | 2 |
| 1b | One category of tylostyles..... | <i>S. aff. carnosus</i> |
| 2a | Colonization of gastropod shells..... | 3 |
| 2b | No colonization of gastropod shells..... | 4 |
| 3a | Slightly curved tylostyles producing subterminal (drop-shaped), annular swellings or well-formed tyles..... | <i>S. domuncula</i> |
| 3b | Slightly curved tylostyles possessing short and not pronounced tyles..... | <i>S. heros</i> |

4a	Shallow water habitat.....	5
4b	Mesophotic sponge (50–85 m) with erect rounded branches habit.....	<i>S. crispolobatus</i>
5a	(Sub)spherical, massive or encrusting growth form sponges.....	6
5b	Encrusting growth form.....	<i>S. lobatus</i>
5c	Club-shaped sponge with 2 mm oscula diameter.....	<i>S. distortus</i>
6a	Tylostyles length do not reach 1000 μm	7
6b	Tylostyles length exceed 1000 μm	8
7a	(Sub)spherical sponge with tylostyle length up to 600 μm	<i>S. caminatus</i>
7b	Thick encrusting to massive polychromatic sponge with tylostyle reaching 900 μm	<i>S. aurantiacus</i>
8	Thick encrusting to massive purple sponge with larger tylostyles exceeding 1500 μm length.....	<i>S. purpura</i> sp. nov.

Genus *Terpios* Duchassaing & Michelotti, 1864

SYNONYMY. For synonymy see van Soest (2002b).

DEFINITION. Thin encrusting Suberitidae. Spicules are exclusively tylostyles, with a lobate tyle. The colors of the species of this genus are commonly associated to those present in their symbiotic bacteria or cyanobacteria (Rützler & Smith, 1993).

TYPE SPECIES. *Terpios fugax* Duchassaing & Michelotti, 1864 (by subsequent designation; Topsent, 1900).

Terpios fugax Duchassaing & Michelotti, 1864

(Figure 5, Table 3)

SYNONYMY: see van Soest (2002b).

TYPE LOCALITY: U.S. Virgin Islands, St. Thomas.

TYPE MATERIAL: Lectotype BMNH 1928.11.12.11, designated by van Soest *et al.* (1983).

MATERIAL EXAMINED. MNRJ 18940, MNRJ 21696, Dois Coqueiros beach, Caucaia, tidal pool (3°41'17.19"S 38°36'35.25"W), Ceará State, Brazil, 0.5 m depth, coll. H. Fortunato, 11/IV/2016.

REDESCRIPTION: External morphology (Figure 5A). The sponge is thinly encrusting with small oscula (<1 mm) randomly distributed. The surface is uneven, microhispid, not detachable and without sub channels. The consistency is soft and fragile. The color is vivid dark blue *in vivo* and maintained after fixation in alcohol.

Skeleton. The ectosomal skeleton is not specialized, not detachable, but spicules can protrude the surface. The choanosome presents a low density of spicules, most directionless, but some arranged with the tyles facing the substratum and the acerate ends protruding the sponge surface.

Spicules (Figure 5B, Table 3). Tylostyles are smooth 131.0–259.4–324.4 μm / 2.2–4.3–6.2 μm (length / width). The tyles are generally flatten and/or round and multilobate with 3.7–9.4 μm of width.

ECOLOGY. The species has been observed on exposed and semi-exposed hard substrates in the subtidal zone.

DISTRIBUTION. Tropical Western Atlantic: Caribbean and Brazil (Northeast and Southeast Region).

REMARKS. The records from Ceará described here are similar to the type species. All three species of the genus distributed at the TWA are shared between the Caribbean and Brazil. Although *T. fugax* and *T. manglaris* are both encrusting and blue, the latter has exclusively flatten and quadrilobate tyles, while in the former there are both flatten and round tyles, and these are multilobate. *Terpios belindae* distinguishes itself by the red to orange color and a marked flatten tile.

Family Halichondriidae Gray, 1867

Genus *Hymeniacidon* Bowerbank, 1858

SYNONYMY. For synonymy see Erpenbeck & van Soest (2002).

DEFINITION. Halichondriidae that have an encrusting or massive and lobate growth form, and fistules covering the apical portion. Megascleres are exclusive small styles or stylotes (>500 μm). The ectosomal skeleton is tangential with intercrossing bundles made of a single type of megasclere. The choanosomal skeleton is mostly loose and confused, but it harbors some ascending vague bundles of megascleres (Erpenbeck & van Soest 2002).

TYPE SPECIES. *Hymeniacidon perlevis* (Montagu, 1814).

Hymeniacidon upaonassu sp. nov.

(Figure 6, Table 4)

TYPE SPECIMENS: Holotype. MNRJ 21390, Panaquatira beach, São José de Ribamar, tidal pool (2°31'4.65"S 44°1'38.16"W), Maranhão State, Brazil.

Paratypes. MNRJ 21360, Panaquatira beach, São José de Ribamar, tidal pool (2°31'4.65"S 44°1'38.16"W), Maranhão State, Brazil, 0.5 m depth, coll. H. Fortunato, 5/XI/2017, MNRJ 21346, Araçagi beach, São José de Ribamar, tidal pool (2°27'46.84"S 44°12'14.94"W), Maranhão State, Brazil.

DIAGNOSIS. *Hymeniacidon upaonassu* sp. nov. has a yellow color and harbors conical fistules uniformly arranged covering the entire body without oscula at their apex.

DESCRIPTION: External morphology (Figure 6A). The sponge has a massive base and conical fistules covering the entire upper portion of the body. The holotype consists of a fragment of 13 x 9 x 3 cm (length x width x thickness). Its surface is rugose and rough, its consistency is friable and fleshy. No oscula can be seen. The color *in vivo* and after fixation is pale yellow.

Skeleton (Figure 6B). The ectosomal skeleton is not easily detachable from the choanosomal one, nor much defined. It tends to form a paratangential layer with intercrossing styles and subectosomal cavities. The choanosomal skeleton is confused, but multispicular tracts (30 μm thick) are present, and axial condensation of longitudinal tracts are observed in the fistules.

Spicules (Figure 6C, Table 4). Styles smooth, slightly curved, not divisible into two categories (128.5–220.3–495.9 μm / 1.9–5.6–10.9 μm).

ECOLOGY. The species is found in tide pools, covered by sand.

DISTRIBUTION. Brazil: Northeastern Region: Maranhão State.

ETYMOLOGY. “Upaon–Açu” is the historical indigenous name (Tupi–Guarani) of São Luís Island in Maranhão State, where all specimens here described were recorded.

REMARKS. *Hymeniacidon upaonassu* sp. nov. is the only species of the genus recorded in the Northeast region of Brazil. Indeed, the Brazilian record of *H. heliophila* (Wilson, 1911) is exclusive for the Southeast region, and *H. perlevis* (Montagu, 1814) is considered misidentified (Muricy *et al.*, 2011). The new species has the classical internal anatomy of the genus *Hymeniacidon* sharing many similarities with the above mentioned species. However, the whole body covered by fistules represents the main diagnostic trait of the new species. The absence of oscula in the apex of the fistules, and its yellow color also differ from the other species. The new Brazilian species also differs from the two Caribbean species, *H. caerulea* Pulitzer-Finali, 1986, which is blue in color, and *Hymeniacidon glabrata* Burton, 1954, which was found only by the species' author, and possesses styles exceeding 500 μm , that shapes more likely to stronglyloxeas. Moreover, both Caribbean species dwell in subtidal habitats.

Genus *Halichondria* Fleming, 1828

Subgenus *Halichondria* Fleming, 1828

SYNONYMY. For synonymy see Erpenbeck & van Soest (2002).

DEFINITION. *Halichondria* with smooth or digitate surface (Erpenbeck & van Soest 2002).

TYPE SPECIES. *Spongia panicea* Pallas, 1766: 388 (by original designation).

Halichondria (Halichondria) melanadocia de Laubenfels, 1936

(Figures 7–9)

SYNONYMY: For synonymy see Hajdu *et al.* (2011), Leonel *et al.* (2011), and Santos *et al.* (2018).

MATERIAL EXAMINED: MNRJ 21396, Panaquatira beach, São José de Ribamar, tidal pool (2°31'4.65"S 44°1'38.16"W), Maranhão State, Brazil, 0.5 m depth, coll. H. Fortunato, 5/XI/2017.

REDESCRIPTION WITH MODIFICATIONS: External morphology (Figure 7A). The observed specimen was moss green *in vivo*, and black in spirit. It had a thick encrusting to massive habit, forming a mat size of 12.0 x 10.0 cm (length x width). The surface was irregular but mostly rough, reticulated. The consistency was soft and compressible, easily torn, with several oscula on small projections (1.1 – 2.7 mm).

Skeleton (Figure 8A). The ectosomal skeleton is anisotropic, tangentially arranged with parallel spicules arrangement. The choanosomal skeleton is disorganized with randomly arranged spicules, although some multispicular tracings towards the ectosome are visible.

Spicules (Figure 9A). Oxeas are smooth, slightly curved, and in two distinct sizes: smaller 129.1–156.2–176.0 / 3.6–8.4–13.4 μm , larger 373.2–513.8–654.3 / 4.5–9.7–19.5 μm .

ECOLOGY. This is a shallow water species, found in rocky shores and sea grass bed from the tidal zone to ~20 m depth.

DISTRIBUTION. Tropical Western Atlantic: Caribbean and Brazil (Northeast Region).

REMARKS. The *Halichondria (H.) melanadocia* specimen described here is distinguished from the original description (Díaz *et al.*, 1993) by the presence of two categories of oxeas, reaching 600 μm and no odor after collection. On the other hand, the skeleton architecture, external habit and dark color in spirit are shared traits in comparison to the Caribbean specimens (Díaz *et al.*, 1993). *Halichondria (H.) melanadocia* was registered as *H. (H.) aff. melanadocia* for Brazil in two field guides, by Hajdu *et al.* (2011), for the state of Bahia, and by Leonel *et al.* (2011), for the state of Paraíba; while Santos *et al.*

(2018) defined that specimens of *H. (H.)* aff. *melanadocia* should be synonymized with *Halichondria (H.) marianae* Santos, Nascimento & Pinheiro, 2018. The specimen from this work differs from other congeners, including *H. (H.) marianae*, chiefly by the black color after fixation, and vulcaniform oscula. Moreover, *H. (H.) marianae* has oxeas exceeding 800 μm and more variation in color (see details below) than *H. (H.) melanadocia*. According to our data, specimens with spicules up to 600 μm must be named *H. (H.) melanadocia*, while those with oxeas exceeding 600 μm are *H. (H.) marianae*. Here the *Halichondria (H.) melanadocia* species is validated to the entire littoral of the Northeast region of Brazil.

Halichondria (Halichondria) marianae Santos, Nascimento & Pinheiro, 2018

(Figures 7–9, Table 5)

SYNONYMY: For synonymy see Santos *et al.* (2018).

TYPE LOCALITY: Brazil, Paraíba State, Carapibus beach, Conde City.

TYPE SPECIMENS: UFPEPOR 1861, Carapibus beach (7°17'57.66"S, 34°47'52.93"W), Conde City, Paraíba State, Brazil, 0.5–1 m depth, coll. G. G. Santos, 21/II/2015.

MATERIAL EXAMINED. MNRJ 21339, 21345, MNRJ 21363, Araçagi beach, São José de Ribamar, tidal pool (2°27'46.84"S 44°12'14.94"W), Maranhão State, Brazil, 0.5 m depth, coll. H. Fortunato, 5/XI/2017; MNRJ 21706, Dois Coqueiros beach, Caucaia, tidal pool (3°41'17.19"S 38°36'35.25"W), Ceará State, Brazil, 1 m depth, coll. H. Fortunato, 11/IV/2016.

REDESCRIPTION WITH MODIFICATIONS: External morphology (Figure 7B–C). Halichondriidae with an encrusting to massive growth form, with some erect lobes where the oscula are located, ranging from 1.1 to 2.7 mm in diameter. Surface is rough and rugose, detachable. Consistency is firm, fleshy, and compressible. Color *in vivo* is usually dark green but greyish and yellow are possible too and brown to greyish after fixation.

Skeleton (Figure 8B). The ectosomal skeleton is detachable with a regular reticulated tangential layer of intercrossing oxeas. The choanosomal skeleton is typically halichondroid with loose oxeas in confusion, but some ascending tracts can be seen. Few sponging fibers could be observed.

Spicules (Figure 9B–C). Oxeas are smooth, slightly curved, with two possible size categories: smaller 103.2–228.8–489.1 μm / 2.4–7.9–17.5 μm , larger 302.7–609.1–837.1 μm / 4.5–13.6–25.0 μm . An exception was found in MNRJ 21339, which possess twofold higher oxeas: smaller 244.5–411.3–925.7 μm / 4.8–12.4–26.8 μm , larger 1114.2–1286.6–1560.1 μm / 21.7–32.3–45.9 μm (length / width).

ECOLOGY. The species was found in tide pools, exposed to air at low tide. Association with algae was observed.

DISTRIBUTION. Tropical Western Atlantic: Brazil (Northeastern Region).

REMARKS. According to the new traits observed here, *Halichondria (H.) marianae* needs an improvement in its diagnosis. We suggest the combination of colors varying from moss green to yellow and smooth oxeas in two categories exceeding 800 μm as diagnostic traits. In this sense, the species significantly differs from all other species recorded in the Tropical Western Atlantic by the presence of oxeas larger than 1200 μm , especially *H. (H.) melanadocia*, the most similar congener. The other four Brazilian species are exclusive to the Western Temperate Southeastern Atlantic (see Carvalho & Hajdu, 2001) and do not share external or internal morphological traits.

DISCUSSION

The description of two new species of Suberitida from intertidal marine habitats of Maranhão State emphasizes that the sponge biodiversity of the Brazilian northern coast is underestimated. This research also shows that many new species of sponges are waiting to be discovered in easily accessible habitats, and with low financial and logistic cost.

Although the order Suberitida is accepted, it remains a matter of debate because of the non-monophyly in some families, and genera and because the main diagnostic traits are overlapping or absent in some groups (Morrow & Cárdenas, 2015). However, some traits could be highlighted in the two new species described here. For the genus *Suberites*, the tylostyles distinction in two size categories (Rützler & Smith, 1993), and the type of ectosomal bouquet are important diagnostic traits, which must be added in the diagnosis of the genus, instead of colors, which may vary hugely (e.g. *Suberites aurantiacus*, see Collin *et al.*, 2005, Muricy & Hajdu, 2006, Hajdu *et al.*, 2011). The genus *Hymeniacidon* does not vary much concerning internal characteristics (Díaz *et al.*, 1993, Erpenbeck & van Soest, 2002); however, the external features, such as color and type of the fistules, seem to be diagnostic traits at the species level. In this sense, morphological traits must be applied carefully as one characteristic may be useful for one group but not for another.

Suberites purpura sp. nov. and *S. aurantiacus* from Maranhão State were found at the intertidal zone, sometimes totally outside the water. These records contrast with the literature that indicates *Suberites* as a genus commonly found in subtidal cold waters (van Soest, 2002b). The color variability is not a peculiarity of *S. aurantiacus*, since such a polymorphism is also known in *Suberites diversicolor* Becking & Lim, 2009 from the Indian Ocean. Four species of *Suberites* are now recorded along the Brazilian coast, one restricted to the Northeast coast (*S. purpura*), two widely distributed (*S. aurantiacus* and *S. carnosus*), and *S. caminatus* being the only one exclusive of temperate waters (Boury-Esnault, 1973). *Suberites aurantiacus* from Brazil, Caribbean and Gulf of Mexico coast and *S. caminatus* from South and North Atlantic, may include more than one genetic lineage, but phylogeographic studies are needed to solve the question. For now, we recommend using *Suberites* aff. *carnosus* until the completion of taxonomic studies of this species comparing all populations distributed in the Atlantic Ocean (Brazil, Açores, Northwest Africa and Northeast Atlantic Ocean) and the Mediterranean Sea with the type material of the Irish coast.

Terpios fugax is common along the Caribbean and Brazilian coasts, and very easily recognizable thanks to its bright blue color and thinly encrusting growth form. Rützler & Smith (1993) indicated that the tyle form was the major trait for the genus, even to distinguish the two blue sympatric species of the Caribbean Sea (*T. fugax* and *T. manglaris*). Another blue *Terpios* is *T. gelatinosus* (Bowerbank, 1866), which was recognised as a junior synonym of *T. fugax* for the Mediterranean Sea. However, the low spicular density (van Soest, 2002b), the elongated lobate tylostyle heads, and the loss of color after fixation distinguish both species (HFMF personal observations). Therefore, sponges recorded outside TWA (see Topsent, 1934, Thomas, 1985) call for an urgent revision.

Hymeniacidon upaonassu sp. nov. is the first species of this genus described for the Northeast region of Brazil. It has the same pale yellow color of the type species *Hymeniacidon perlevis* from

Europe. Other specimens recorded from the cold waters of China and Argentina coasts possess the same color and morphology (Gastaldi *et al.*, 2018). In turn, the orange *H. heliophila* originally from Florida, is widespread in the Caribbean Sea, and is also recorded for the Southeast region of Brazil (Muricy *et al.*, 2011). These three species have similar morphologies, except for the type of the fistules. The new species differs from the other two distributed in the Caribbean, *H. glabrata* and *H. caerulea*. Both have spicules larger than 500 μm , not common to *Hymeniacion* species. Moreover, the former is subtidal and *H. caerulea* is blue, differing from *H. upaonassu*, which seems to be exclusively intertidal and pale yellow.

Halichondria (*Halichondria*) *melanadocia* and *H. (H.) marianae* are the only species of the genus recorded to the Northeast of Brazil. Both share many morphological traits but differ in the size of spicules and main color. Although these characteristics can be considered plastic, the genus has few diagnostic traits (Alvarez & Hooper, 2011), therefore, the taxonomy of the group needs an urgent revision, including additional tools, such as ecology, genetic, reproduction and metabolomics. This need is corroborated by phylogenetic reconstructions with both 18S and 28S nuclear markers, which indicate a paraphyly for the genus (Redmond *et al.*, 2013; Thacker *et al.*, 2013; Gastaldi *et al.*, 2018).

In this survey, we were able to identify new species of Suberitida according to morphological traits. We observed that not all traits are diagnostic for all genera, for example, color in *Suberites* and spicules size in *Hymeniacion* are unsatisfactory to describe species. However, these features work quite well the other way around. Considering this, we suggest spongiologists to meticulously examine the ectosomal bouquets, and whether the tylostyles are divided into different size categories for all *Suberites* representatives. *Hymeniacion* external features, mainly fistule form, must be carefully described in order to differentiate species. Finally, *Terpios* should be further evaluated according to the tyle form and the color after fixation in ethanol, which are crucial features to decipher differences between species.

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1 TABLES

2

3 TABLES

4 **Table 1.** State of the art on the occurrence of Order Suberitida in Brazil. All Brazilian records can be seen
5 in Muricy *et al.* (2011).

Family	Genus	Species
Suberitidae Schmidt, 1870	<i>Aptos</i> Gray, 1867	<i>A. glutinans</i> Moraes, 2011
		<i>A. hajdui</i> Carvalho, da Silva & Pinheiro, 2013
	<i>Suberites</i> Nardo, 1833	<i>A. potiguarensis</i> Carvalho, da Silva & Pinheiro, 2013
		<i>A. bergmanni</i> de Laubenfels, 1950
		<i>S. aurantiacus</i> (Duchassaing & Michelotti, 1864)
		<i>S. caminatus</i> Ridley & Dendy, 1886
	<i>Terpios</i> Duchassaing & Michelotti, 1864	<i>S. carnosus</i> (Johnston, 1842)
		<i>T. belindae</i> Rützler & Smith, 1993
		<i>T. fugax</i> Duchassaing & Michelotti, 1864
		<i>T. manglaris</i> Rützler & Smith, 1993
Halichondriidae Gray, 1867	<i>Amorphinopsis</i> Carter, 1887	<i>A. atlantica</i> Carvalho, Hajdu, Mothes & van Soest, 2004
		<i>Ciocalapata</i> de Laubenfels, 1936
	<i>Ciocalypta</i> Bowerbank, 1862	<i>C. minuspiculifera</i> Lage, Carvalho & Menegola, 2013
		<i>C. alba</i> Carvalho, Carraro, Lerner & Hajdu, 2003
	<i>Halichondria</i> Fleming, 1828	<i>H. (H.) cebimarensis</i> Carvalho & Hajdu, 2001
		<i>H. (H.) marianae</i> Santos, Nascimento & Pinheiro, 2018
		<i>H. (H.) migottea</i> Carvalho & Hajdu, 2001
		<i>H. (H.) sulfurea</i> Carvalho & Hajdu, 2001
	<i>Hymeniacidon</i> Bowerbank, 1858	<i>H. (H.) tenebrica</i> Carvalho & Hajdu, 2001
		<i>H. heliophila</i> (Wilson, 1911)
<i>Topsentia</i> Berg, 1899	<i>T. ophiraphidites</i> (de Laubenfels, 1934)	

Table 2. Comparison of the tylostyles and tyles, growth forms and color of all *Suberites* species from the Tropical Western Atlantic and the type species *Suberites domuncula* Olivi, 1792. Spicules values are in micrometres (μm) and presented as minimal–mean (standard deviation)–maximal length / width. N = 50.

Species	Site	Tylostyle (smaller)	Tylostyle (larger)	Tyle width (smaller; larger)	Tyle form	Growth form	Color
<i>S. domuncula</i> ¹	Adriatic Sea	100–350 / 4–8	250–480 / 5–8		Slightly subterminal, but mostly well-formed. Rare annular swellings in the neck	Massive	Bright orange
<i>S. caminatus</i> ²	SW Brazil	240–600 / 3–12			Rounded head	Subspherical	Brownish in alcohol
<i>S. aff. carnosus</i> ³	SW Brazil	230–430 / 6–12			Cylindrical, cotton swab shape; subtylostyle similarity	Thinly encrusting	Ochre in alcohol
<i>S. crispolobatus</i> ⁴	Guiana	186– 266 –396 / 3– 5.9 –10	456– 724 –858 / 9– 11.4 –14		Rounded head, with small tuberculate prominence	Ramose	Beige in alcohol
<i>S. distortus</i> ⁵	Antilles	n.r.				Club shaped	Yellowish
<i>S. heros</i> ⁵	Antilles	n.r.				<i>S. domuncula</i> -like	
<i>S. lobatus</i> ⁶	Puerto Rico	200–300 / 3–4	650–850 / 10–15			Spherical	Greyish brown
<i>S. paradoxus</i> ⁷	Virginia, USA	220–300 / 7	280–350 / 8			Lamellar	Greenish
<i>S. aurantiacus</i> ^{8,9}	Panama	130–750 / 2.5–19			Rounded head with apex prominence	Encrusting to massive	Bright orange, green
<i>S. aurantiacus</i> ¹⁰	NE Brazil	140–395–680 / 1–3–6			Rounded head with apex prominence	Encrusting to massive	Green and yellow
<i>S. aurantiacus</i> ¹¹	SW Brazil	115–940			Rounded head with apex prominence	Encrusting to massive	Widely variable; always yellow inside
<i>S. aurantiacus</i> ¹² MNRJ 21405	NE Brazil	140.0– 184.7 (45.2)–291.7 / 2.4– 5.5 (1.4)–8.3	376.2– 591.1 (133.7)–791.7 / 4.9– 10.0 (3.3)–16.1	3.1– 6.3 (1.5)–8.6; 5.2– 9.9 (2.0)–13.6	Rounded head with apex prominence	Encrusting to massive	Green and yellow
<i>S. aurantiacus</i> ¹² MNRJ 21430	NE Brazil	165.8– 238.3 (65.1)–386.4 / 4.3– 7.3 (2.1)–12.2	428.8– 501.5 (145.5)–830.9 / 7.5– 11.1 (3.6)–20.7	3.8– 7.8 (2.0)–12.2; 7.6– 10.2 (3.9)–18.3	Rounded head with apex prominence	Encrusting to massive	Green and yellow
<i>S. aurantiacus</i> ¹² MNRJ 21500	NE Brazil	151.9– 242.9 (66.0)–401.0 / 3.4– 6.9 (2.6)–13.8	437.2– 566.9 (76.4)–635.0 / 5.6– 12.1 (5.0)–20.7	3.0– 6.7 (2.0)–11.6; 5.3– 7.8 (2.4)–11.8	Rounded head with apex prominence	Subspherical	Bright orange and yellow
<i>S. purpura</i> ¹² MNRJ 21343	NE Brazil	208.5– 432.1 (149.9)–790.2 / 4.8– 11.4 (4.2)–21.6	860.7– 1322.3 (322.2)–1991.3 / 17.2– 27.7 (7.7)–45.8	5.3– 13.3 (3.1)–18.1; 11.5– 23.1 (6.1)–33.9	Rounded head	Encrusting to massive	Purple and orange

¹van Soest (2002b), ²Ridley & Dendy (1886), ³Boury-Esnault (1973), ⁴van Soest (2017), ⁵Schmidt (1870), ⁶Wilson (1902), ⁷Wilson (1931), ⁸Rützler & Smith (1993),

⁹Duchassaing & Michelotti (1864), ¹⁰Moraes (2011), ¹¹Muricy & Hajdu (2006), ¹²Present study.

Table 3. Comparative tylostyles dimensions and head shape, locality and color of *Terpios* spp. from the Tropical Western Atlantic. Values are expressed in micrometres (µm) as minimum–mean (standard deviation)–maximum length / width. N = 100.

Sample	Site	Tylostyle	Tyle size (width)	Tyle form	Color
<i>T. belindae</i> ¹	Caribbean	140–430 / 3–9	5–12.5	Robust, flatten; bi, quadri or multilobate	Red to brown
<i>T. manglaris</i> ¹	Caribbean	140–460 / 2.5–7	4.5–10	Flatten; quadrilobate	Cooper blue
<i>T. fugax</i> ¹	Caribbean	150–460 / 2.5–5	5–8	Wrinkled, round or flatten; uni to multilobate	Vivid blue, cooper green
<i>T. fugax</i> ² (MNRJ 18940)	NE Brazil	131.0– <u>241.8</u> (55.6)–322.1 / 2.2– <u>3.8</u> (1.0)–6.2	3.7– <u>6.5</u> (1.5)–9.4	Flatten and round; uni to multilobate	Dark blue
<i>T. fugax</i> ² (MNRJ 21696)	NE Brazil	148.6– <u>277.1</u> (45.7)–327.4 / 3.0– <u>4.8</u> (0.8)–6.2	4.8– <u>6.7</u> (0.8)–8.3	Flatten and round; uni to multilobate	Dark blue

Comparative data in ¹Rützler & Smith (1993). ²Present study.

Table 4. Comparison of the main traits of all *Hymeniacidon* species from the Tropical Western Atlantic, with addition of Rio de Janeiro State, Southeast (SE) of Brazil and the type species *Hymeniacidon perlevis* (Montagu, 1814) data. Values are in micrometres (μm), as minimal–mean (standard deviation)–maximal length / width. N = 50.

Specimens	Site	Styles (μm)	Color	Habitat
<i>H. perlevis</i> ¹	NE Atlantic	152–475 / 3–12	Orange–Yellow	Intertidal and shallow subtidal
<i>H. caerulea</i> ²	Caribbean	420–530 / 7–12	Blue	On coral rubble and mangrove
<i>H. glabrata</i> ²	Caribbean	240–800 / 4–24	Pale greyish–yellow	Subtidal
<i>H. heliophila</i> ³	Caribbean	130–450 / 3–10	Orange	Shallow waters (mangrove roots or rocky shore)
<i>H. heliophila</i> ⁴	SE Brazil	130–330 / 1–7	Orange	Intertidal to 15 m
<i>H. upaonassu</i> ⁵ MNRJ 21390	NE Brazil	143.9– <u>222.3</u> (95.7)–488.2 / 1.9– <u>5.8</u> (1.7)–10.3	Yellow	Tide pool
<i>H. upaonassu</i> ⁵ MNRJ 21346	NE Brazil	163.9– <u>291.5</u> (89.5)–495.9 / 2.7– <u>6.0</u> (2.0)–10.9	Yellow	Tide pool
<i>H. upaonassu</i> ⁵ MNRJ 21360	NE Brazil	128.5– <u>233.9</u> (89.1)–454.8 / 2.4– <u>5.0</u> (1.8)–9.7	Yellow	Tide pool

¹Erpenbeck & van Soest (2002), ²Burton (1954), ³Díaz *et al.* (1993), ⁴Muricy & Hajdu (2006), ⁵Present study.

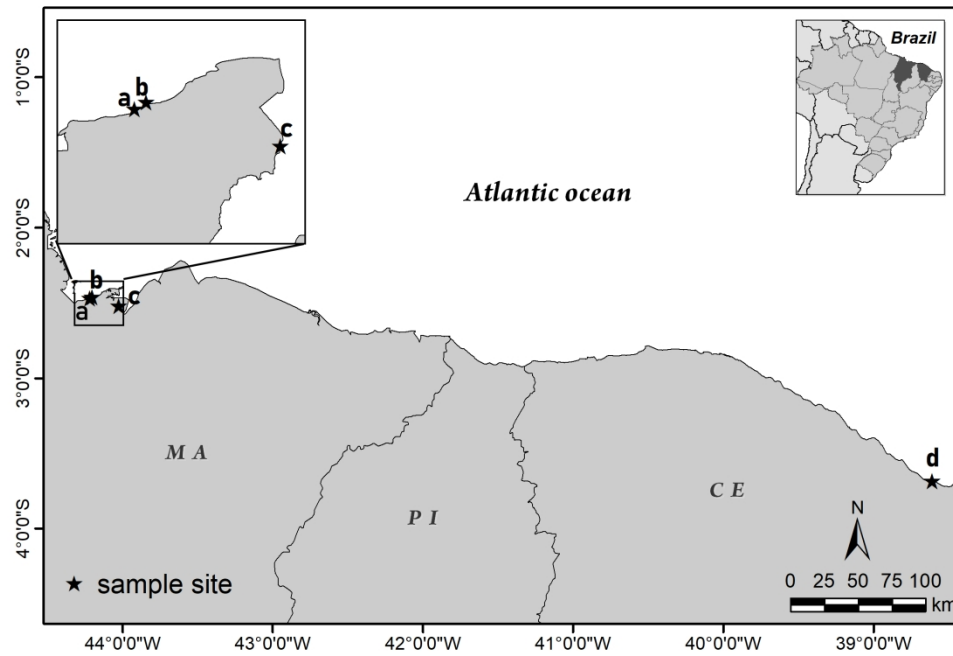


Fig. 1. Part of the Brazilian Semi-Arid Coast at the northern region of the Brazilian coast, with the location of sampling sites. The highlight in the right corner shows the position of the states on the map of Brazil. The small letters indicate the sites where sponge species were collected: a) Araçagi beach, b) Meio beach, c) Panaquatira beach, depicted enlarged at the highlight in the left corner; and d) Dois Coqueiros beach. MA = Maranhão state, PI = Piauí state, CE = Ceará state.

210x148mm (299 x 299 DPI)

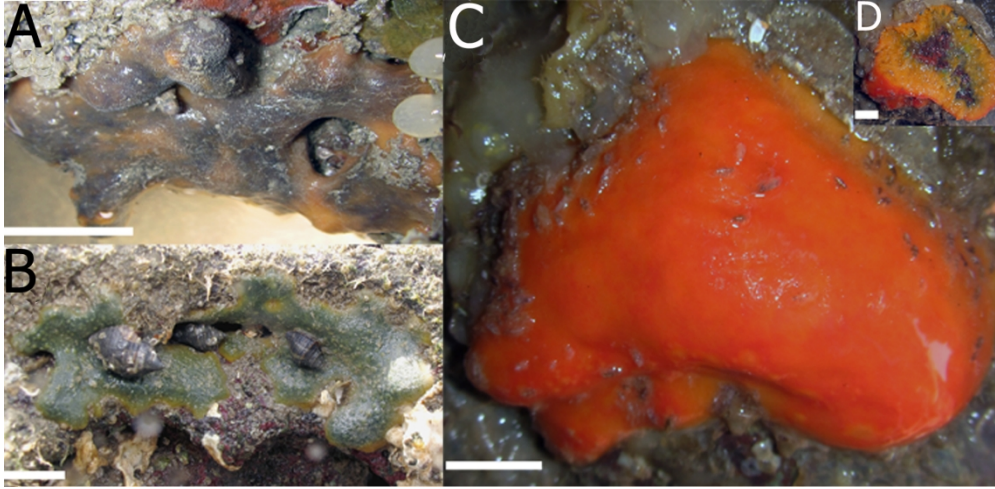


Fig. 2. In situ images presenting the external morphology of *Suberites* specimens: A: *Suberites purpura* sp. nov. (MNRJ 21343); B, C, D: *Suberites aurantiacus* (Duchassaing & Michelotti, 1864) (B – MNRJ 21430, C, D – MNRJ 21500). Scale: A, D = 1 cm; B, C = 2 cm.

176x86mm (299 x 299 DPI)

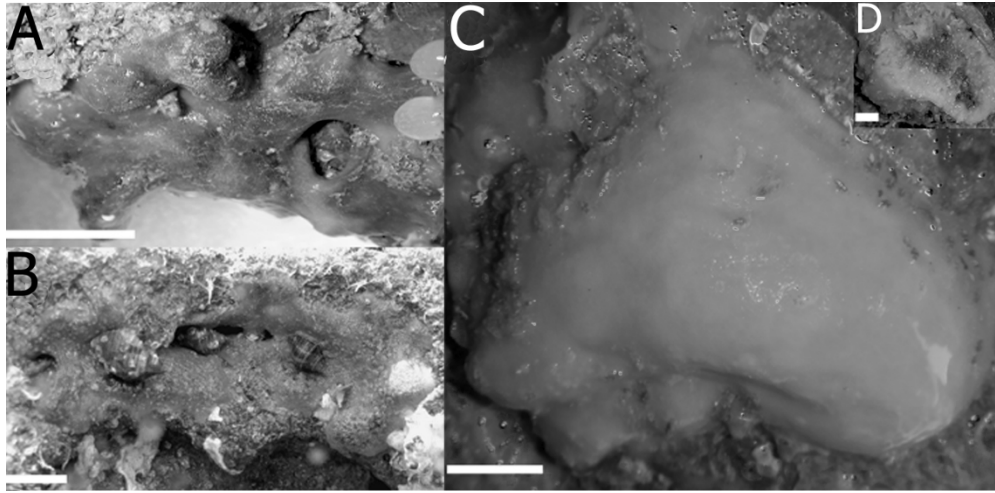


Fig. 2. In situ images presenting the external morphology of Suberites specimens: A: *Suberites purpura* sp. nov. (MNRJ 21343); B, C, D: *Suberites aurantiacus* (Duchassaing & Michelotti, 1864) (B – MNRJ 21430, C, D – MNRJ 21500). Scale: A, D = 1 cm; B, C = 2 cm.

176x85mm (300 x 300 DPI)

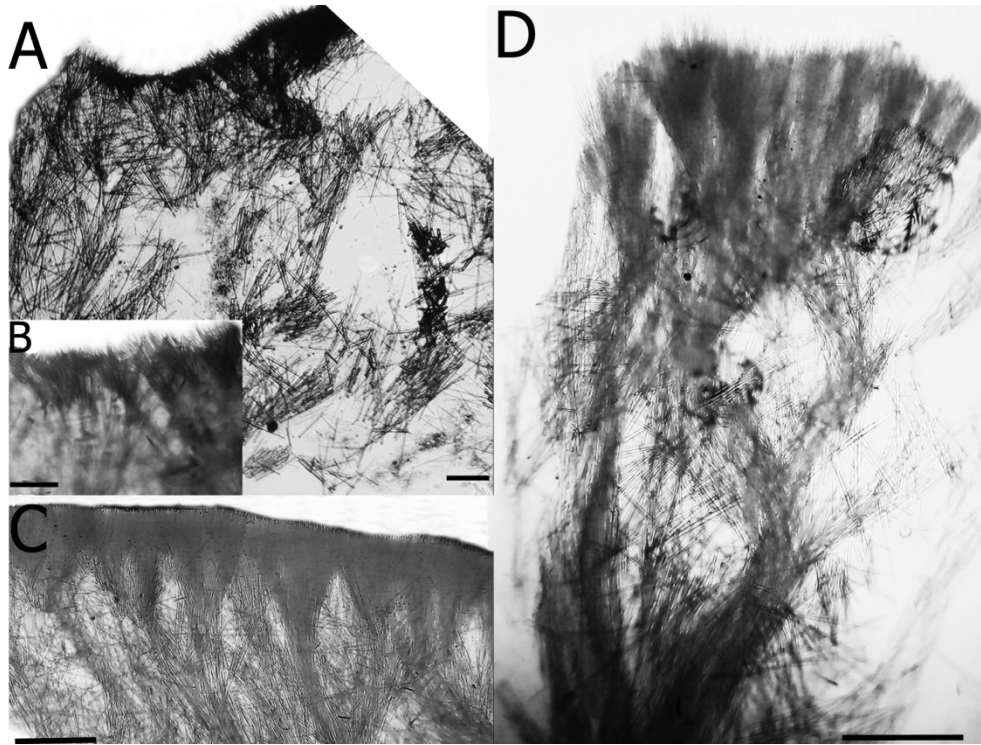


Fig. 3. Optical microscopy images presenting the skeleton architecture of *Suberites* specimens. *Suberites purpura* sp. nov. (MNRJ 21343), A: ectosomal skeleton with short bouquets of small tylostyles and confused choanosomal skeleton with longer tylostyles forming rare branches, B: detail of short bouquets; *Suberites aurantiacus* (Duchassaing & Michelotti, 1864), C: 'Suberites-like skeleton' - small tylostyles forming wide bouquets in the ectosome (MNRJ 21405), D: Orange morphotype of *Suberites aurantiacus*, confused choanosomal skeleton, with bundles in direction to the surface (MNRJ 21500). Scale: A, C, D = 200 μ m; B = 100 μ m.

164x121mm (300 x 300 DPI)

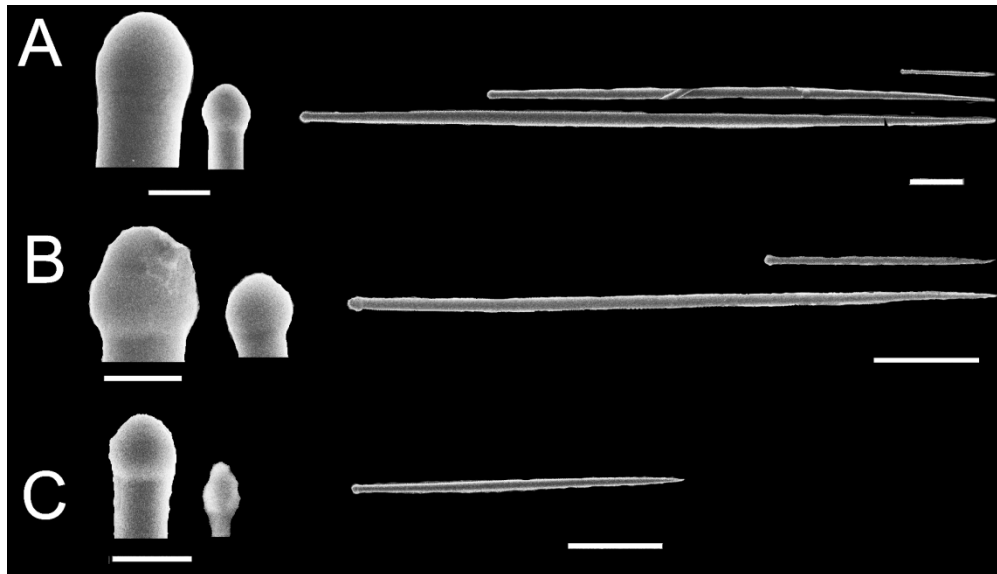


Fig. 4. Tylostyle size and fusiform form of *Suberites* species. A: *Suberites purpura* sp. nov.; B, C: *Suberites aurantiacus* (Duchassaing & Michelotti, 1864). Scale: tylostyles = 100 µm; tyles = 10 µm. The orange morphotype of *Suberites aurantiacus* is represented in C.

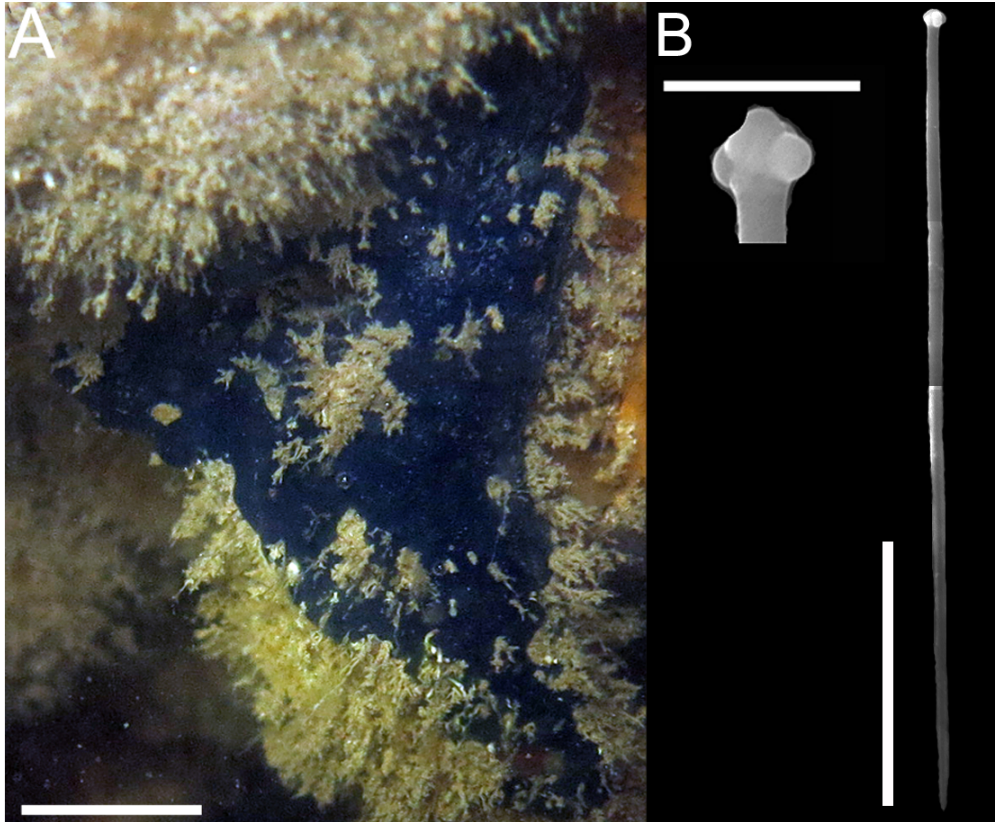


Fig. 5. *Terpios fugax* Duchassaing & Michelotti, 1864. A: Specimen in a tide pool, at Ceará state. B: The tylostyle of *T. fugax* with detail for flattened and round multilobate tylostyle. Scale: tylostyle 50 μm , tyle 10 μm .

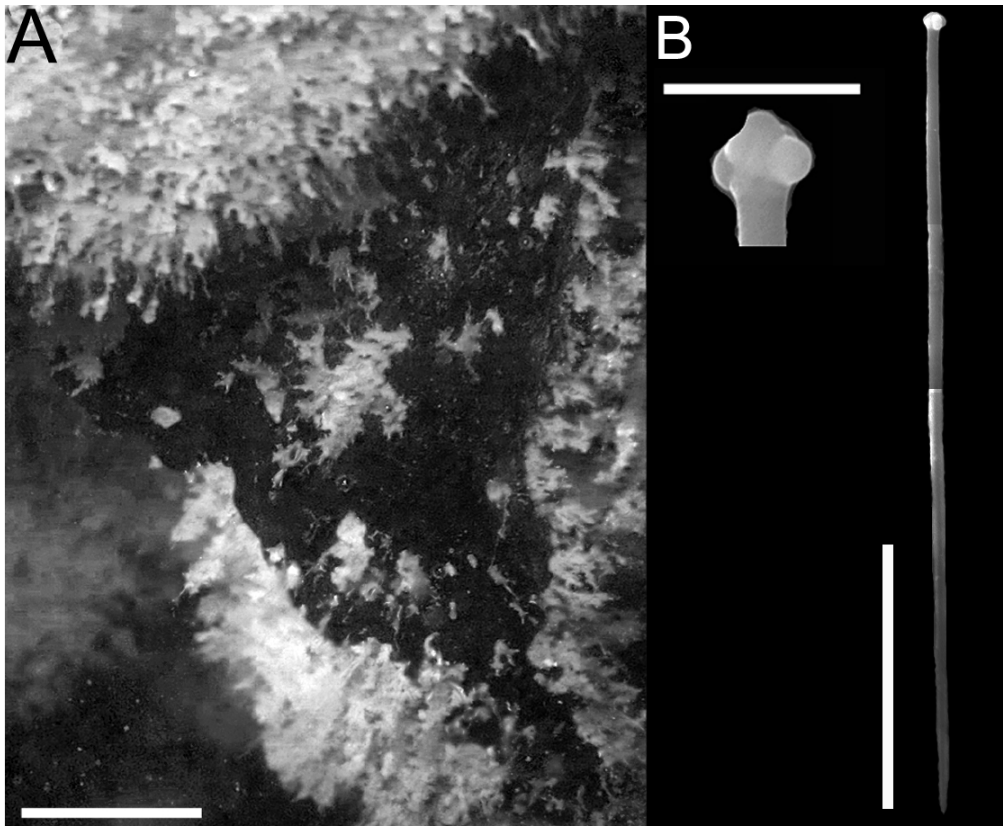


Fig. 5. *Terpios fugax* Duchassaing & Michelotti, 1864. A: Specimen in a tide pool, at Ceará state. B: The tylostyle of *T. fugax* with detail for flattened and round multilobate tylostyle. Scale: tylostyle 50 μm , tyle 10 μm .

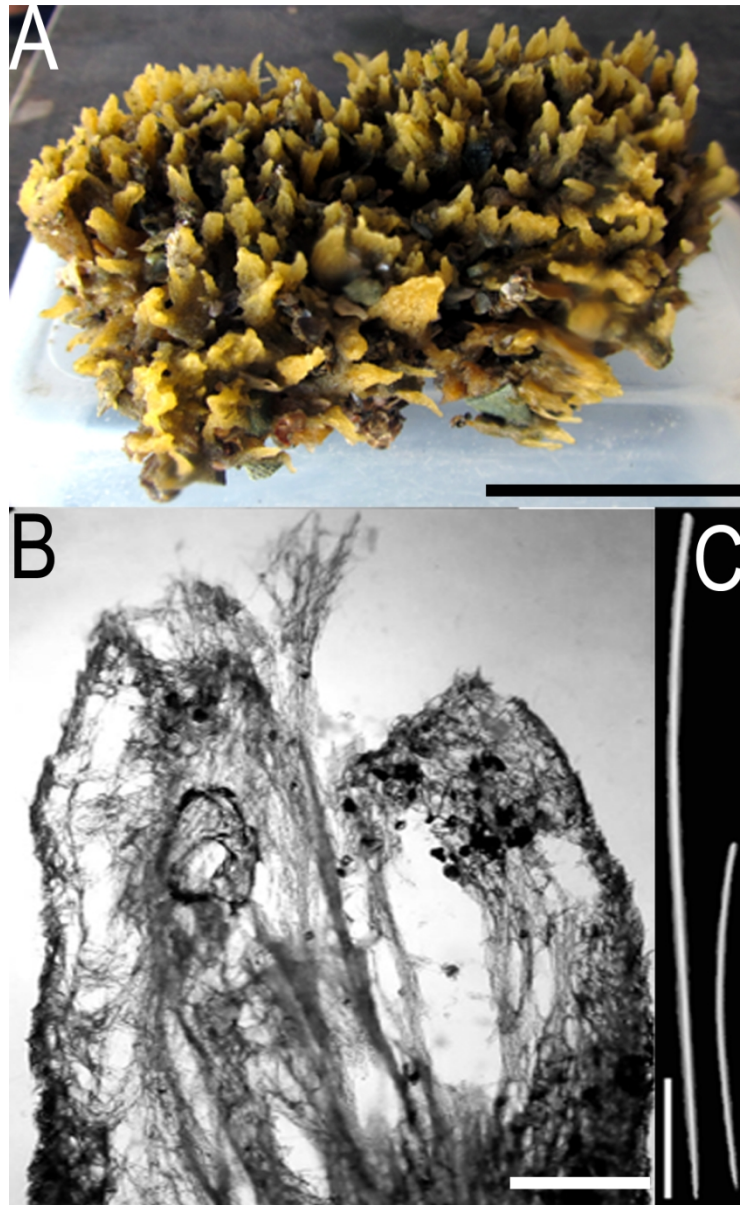


Fig. 6. External and internal anatomy of *Hymeniacion upaonassu* sp. nov. A) External traits of the new species, scale: 5 cm, B) Architecture of the skeleton, scale: 500 μ m, C) styles, scale: 50 μ m.

130x211mm (300 x 300 DPI)

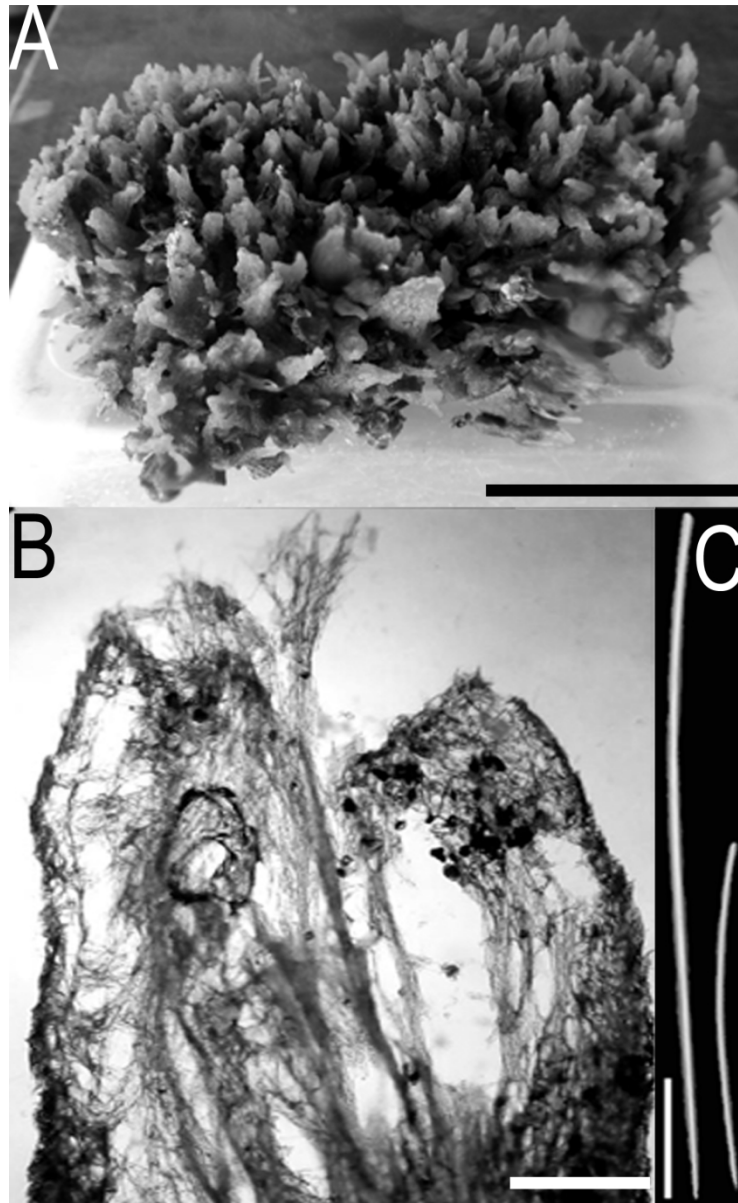


Fig. 6. External and internal anatomy of *Hymeniacion upaonassu* sp. nov. A) External traits of the new species, scale: 5 cm, B) Architecture of the skeleton, scale: 500 μ m, C) styles, scale: 50 μ m.

130x211mm (300 x 300 DPI)

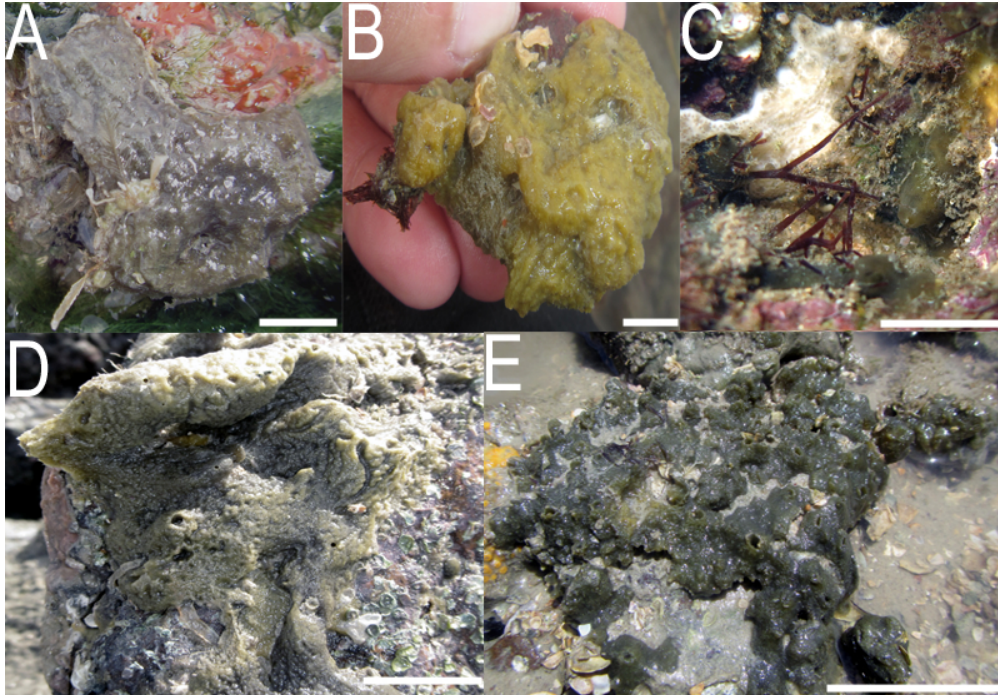


Fig. 7. External anatomy variations of Halichondria (Halichondria). A–D: Halichondria (H.) marianae Santos, Nascimento & Pinheiro, 2018; E: Halichondria (H.) melanadocia de Laubenfels, 1936. Scale: A–C = 1 cm, D–E = 2 cm. Morphotype of H. (H.) marianae with oxeas exceeding 1500 μm is represented in A.

67x46mm (300 x 300 DPI)

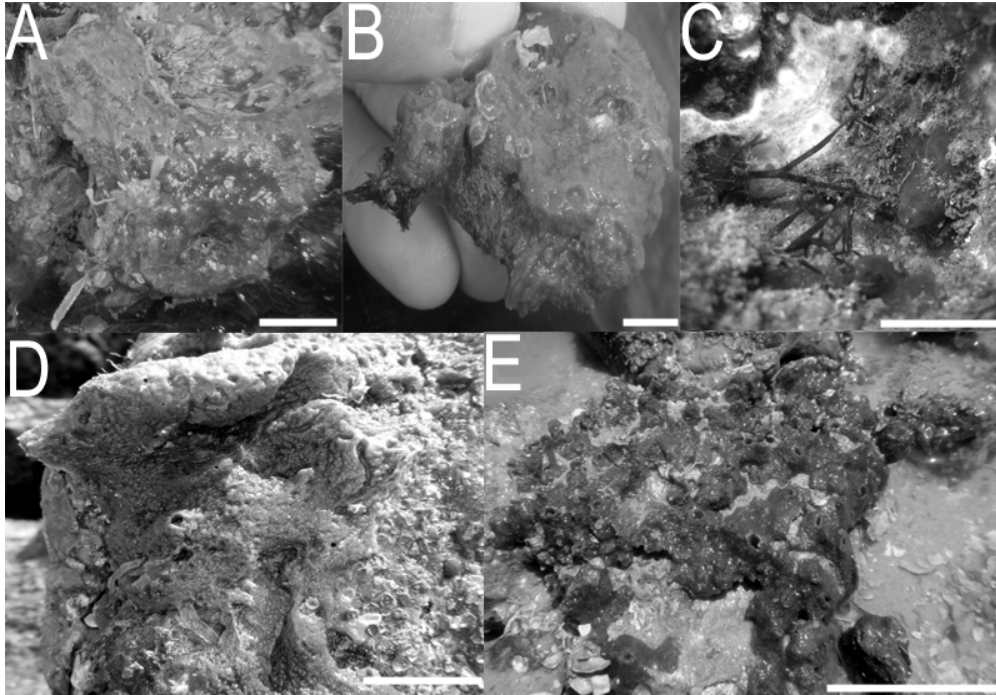


Fig. 7. External anatomy variations of Halichondria (Halichondria). A–D: Halichondria (H.) marianae Santos, Nascimento & Pinheiro, 2018; E: Halichondria (H.) melanadocia de Laubenfels, 1936. Scale: A–C = 1 cm, D–E = 2 cm. Morphotype of H. (H.) marianae with oxeas exceeding 1500 μm is represented in A.

67x46mm (300 x 300 DPI)

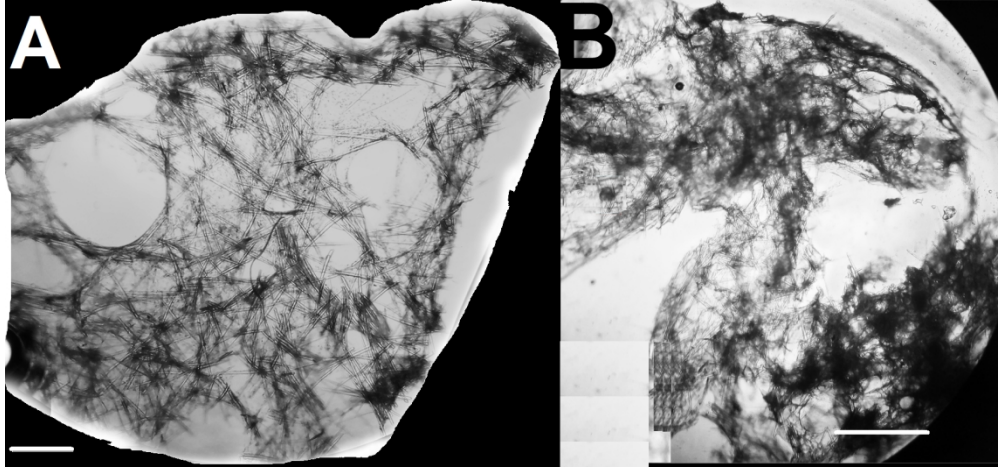


Fig. 8. Skeleton architecture of Halichondria (Halichondria). A: Halichondria (H.) melanadocia de Laubenfels, 1936; B: Halichondria (H.) marianae Santos, Nascimento & Pinheiro, 2018. (A) and H. marianae (B). Scale: 100 μ m.

153x71mm (300 x 300 DPI)



Fig. 9. Smooth oxeas Halichondria (Halichondria). A: Halichondria (H.) melanadocia de Laubenfels, 1936; B–C: Halichondria (H.) marianae Santos, Nascimento & Pinheiro, 2018. Scale = 100 μ m. The morphotype of H. (H.) marianae with oxeas exceeding 1500 μ m is represented in B.

72x107mm (300 x 300 DPI)