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Diversity of Edwardsiidae sea anemones (Cnidaria: Anthozoa: Actiniaria) from Brazil, with the description of a new genus and species

Rafael Antônio Brandão[1], Luciana Câmara Gusmão[2] and Paula Braga Gomes[3]

[1]Programa de Pós-Graduação em Biologia Animal, Universidade Federal de Pernambuco, Av. Prof. Moraes Rego, 1235 – Cidade Universitária, Recife, Brazil; [2]Division of Invertebrate Zoology, American Museum of Natural History, Central Park West at 79th Street, 10024, New York, NY, USA and [3]Departamento de Biologia, Universidade Federal Rural de Pernambuco, Rua Dom Manoel de Medeiros, s/n, Dois Irmãos, Recife, Brazil

Original Article

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Author for correspondence:
Rafael Antônio Brandão,
E-mail: rabran19@gmail.com

Abstract

Edwardsiidae is one of the most speciose families within order Actiniaria with ~75 valid species of burrowing sea anemones. Five edwardsiids have been recorded in South Atlantic waters with only two species known for Brazil: *Nematostella vectensis* and *Edwardsia migottoi*. Such low diversity is probably the result of a historical small number of specialists in the region combined with difficulties in collecting and identifying these small burrowing animals. Although edwardsiids have been reported from Brazil since at least the 1960s, these reports did not include proper descriptions or specific identification, making comparison to other valid species impossible. Here we describe a new genus, *Isoscolanthus* gen. nov., and two new species: *Isoscolanthus iemanjae* sp. nov., *Isoscolanthus janainae* sp. nov. and we also describe *Scolanthus crypticus* sp. nov., the first species of the genus for Brazil. *Isoscolanthus* gen. nov. is easily distinguished from other edwardsiid genera by a combination of external (i.e. presence of periderm and nemathybomes in proximal end and 12 tentacles), microanatomical (i.e. four microcnemes) and cnidom features (i.e. pterotrichs in nemathybomes). In addition to the description of the new genus and species, we expand the range distribution of *Nematostella vectensis* and *Edwardsia migottoi* in the South-western Atlantic. The number of edwardsiids known from Brazil is raised from two to five species, substantially increasing the diversity of soft-bottom sea anemones for South Atlantic waters.

Introduction

Edwardsiidae is one of the most speciose families within order Actiniaria (Williams, 1981; Fautin *et al*., 2007; Daly & Ljubenkov, 2008; Fautin, 2013) including nine genera and ~75 species of burrowing sea anemones. Despite the broad distribution of its representatives, occurring from polar to tropical zones in all depths, including hypersaline environments (Daly *et al*., 2012) and Antarctic ice (Daly *et al*., 2013; Sanamyan *et al*., 2015), the number of edwardsiids recorded for the South Atlantic remains small and probably does not represent the true diversity of the group in the region. Only three species of Edwardsiidae have been recorded in South Atlantic waters: *Edwardsia sanctaehelenae* Carlgren, 1941 in Santa Helena island (Carlgren, 1941); *Nematostella vectensis* Stephenson, 1935, in the port area of Recife, in north-east Brazil (Silva *et al*., 2010); and *Edwardsia migottoi* Gusmão, Brandão & Daly, 2016 in south-east Brazil (Gusmão *et al*., 2016). Two other species, *Scolanthus intermedius* (McMurrich, 1893) and *Edwardsia inachi* Sanamyan, Sanamyan & Schories, 2015 occur in the Atlantic portion of the Southern Ocean, in the King George Island (Carlgren, 1927; Sanamyan *et al*., 2015).

The low number of species of Edwardsiidae in Brazil is possibly the result of a historical small number of sea anemone specialists in the region and anatomical characteristics of the group (i.e. small size and burrowing habits) that make them hard to collect and identify. In addition, the external morphology of edwardsiids resembles that of other animal phyla, such as Priapulida and Sipuncula, often leading to misidentifications by non-experts. Thus, most species of sea anemones recorded to Brazil correspond to large individuals inhabiting hard-bottom environments, such as coral reefs and intertidal pools in rocky shores (Corrêa, 1964; Dube, 1974; Pires *et al*., 1992; Gomes & Mayal, 1997; Zamponi *et al*., 1998), leaving the diversity of Actiniaria of soft-bottoms under-studied. Although the presence of edwardsiids in Brazil is known since at least 1967 (Tommasi, 1967), most reports have not included proper descriptions (e.g. Capitoli & Bemvenuti, 2004; Pagliosa, 2006; Pires-Vanin *et al*., 2013), preventing specific identification and comparison to other valid species (Gusmão *et al*., 2016). Hence, a detailed taxonomic study focusing on family Edwardsiidae is imperative to advance our understanding of the diversity of the group, and to inform future inventories and ecological studies of burrowing sea anemones in Brazil.

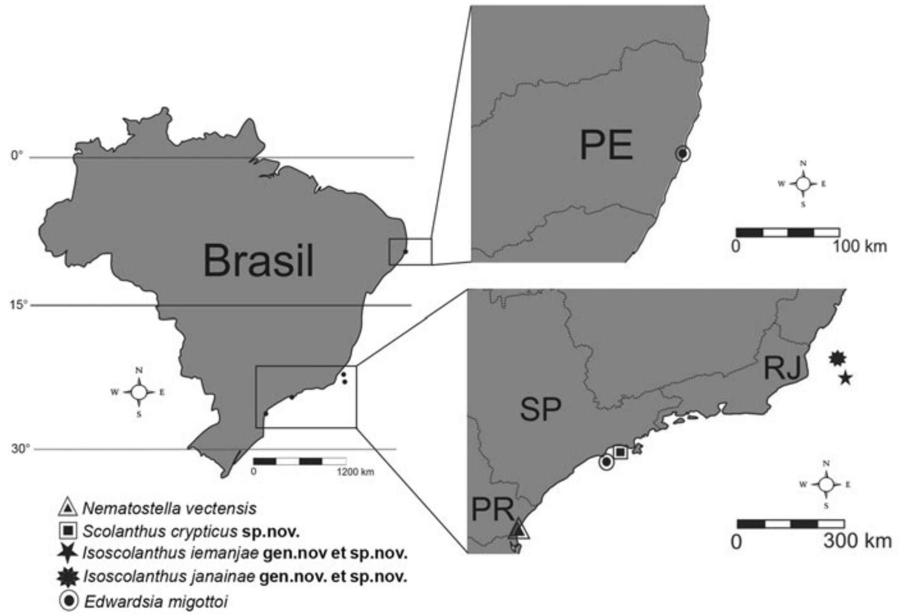

Fig. 1. Map showing the distribution of species of Edwardsiidae recorded from Brazil. Different symbols represent different species.

Materials and methods

Specimens examined

The descriptions of the taxa examined in the present study are based on unidentified specimens stored at the Marine Invertebrate Collections of the Museu Oceanográfico da Universidade Federal de Pernambuco (MOPE), the Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ) and Museu de Zoologia da Universidade de São Paulo (MZUSP).

Anatomical and microanatomical observations

We followed, whenever possible, the identification procedure proposed by Häussermann (2004). Formalin-fixed specimens were initially separated in morphotypes and examined whole, dissected and as serial sections. At least two whole individuals of each species examined were dehydrated and embedded in paraffin, cut in histological sections, 6–10 µm thick, and stained with hematoxylin-eosin (Humason, 1962). The cnidom of each species was determined from squash preparations of tentacles, column (and nemathybomes when present), actinopharynx and filaments. Cnidae capsules of at least two individuals per taxa were identified and 20 undischarged capsules of each type found were measured, whenever possible. Due to small size and small number of individuals, and because individuals are partially destroyed during cnidae sampling, we limited to three the number of individuals used for cnidom. For general cnidae terminology, we use a combination of classifications to better capture the underlying variation in cnidae morphology: the classification of Weill (1934) modified by Carlgren (1940) is combined with that of Schmidt (1969, 1972, 1974) thus we differentiate 'basitrichs' from '*b*-mastigophores' but also capture the underlying variation seen in 'rhabdoids'. In addition, we used England (1987) to differentiate nematocysts in the nemathybomes (i.e. pterotrichs from basitrichs). Photographs of each type of nematocyst were included to allow reliable comparison across terminologies and taxa (see Fautin, 1988). Higher classification of Actiniaria follows Rodríguez *et al.* (2014).

Results

Here we describe a new genus with two new species and a new species of the previously described genus *Scolanthus*. *Isoscolanthus* gen. nov. includes two new species: *Isoscolanthus iemanjae* sp. nov. and *Isoscolanthus janainae* sp. nov. *Scolanthus crypticus* sp. nov. is the first species of the genus recorded for the South-western Atlantic, expanding the range of the genus to the tropical South-western Atlantic. In addition, we expand the distribution of *Edwardsia migottoi*, previously known only from the South-east coast of Brazil (Gusmão *et al.*, 2016), to include the North-east coast of Brazil (Pernambuco state). The distribution of *Nematostella vectensis* Stephenson, 1935, recorded only from the north-east coast of Brazil (Silva *et al.*, 2010), is also expanded to include the south coast of Brazil (Paraná state) (see Figure 1).

SYSTEMATICS

Order ACTINIARIA Hertwig, 1882
Suborder ANENTHEMONAE Rodríguez & Daly in Rodríguez *et al.*, 2014
Superfamily EDWARDSIOIDEA Andres, 1881
Family EDWARDSIIDAE Andres, 1881

Diagnosis (adapted from Carlgren, 1949 with modifications from Daly & Ljubenkov, 2008; modifications in bold). **Anenthemonae** with elongate, vermiform body usually divisible into two or more regions: between long scapus provided with periderm and short capitulum may be short scapulus that lacks periderm and epidermal specializations. Proximal end rounded, without basilar muscles, may be differentiated into a physa. Single weak siphonoglyph. No sphincter muscle or acontia. Mesenteries divisible into macro- and microcnemes; always eight macrocnemes and at least four microcnemes. Macrocnemes comprise two pairs of directives and four lateral mesenteries, two on each side, whose retractors face sulcar (=ventral) directives. Retractors restricted, diffuse to strongly circumscript; parietal muscles always distinct.

Cnidom: Spirocysts, basitrichs, *b*-mastigophores, ***p*-mastigophores A**, pterotrichs, *t*-mastigophores.

Type species *Edwardsia beautempsii* de Quatrefages, 1842 designated by Carlgren (1949).

Remarks. We modified the familial diagnosis to reflect recent changes in higher-level classification of Actiniaria (i.e. Rodríguez *et al.*, 2012, 2014) and the combination of nematocyst terminology used in this study. These modifications have been made in all other diagnoses included in this study.

Isoscolanthus gen. nov.

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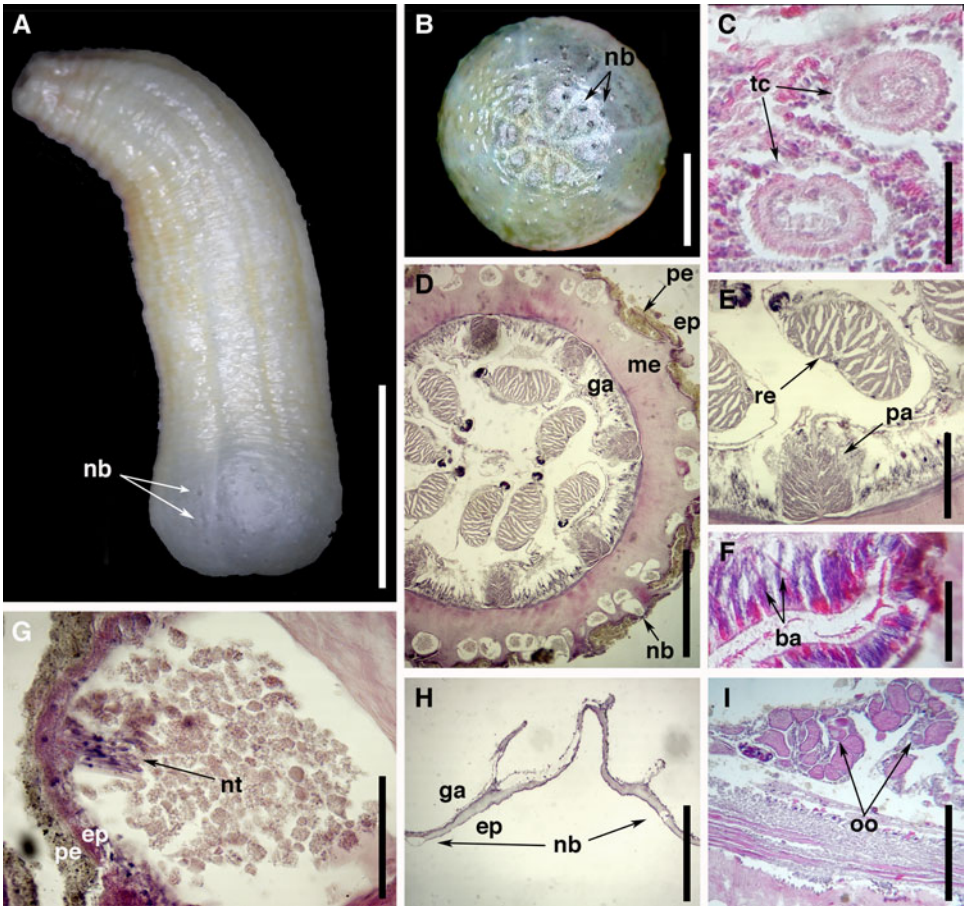

Fig. 2. External anatomy and microanatomy of *Isoscolanthus iemanjae* gen. et sp. nov.: (A) general view of a preserved specimen showing proximal rounded end with nemathybomes (arrows); (B) detail of proximal rounded end with several nemathybomes (arrows); (C) cross-section of two tentacles (arrows); (D) cross-section through mid-column showing several nemathybomes distributed in mesoglea of column and pairs of macrocnemes; (E) cross-section through mid-column showing a macrocneme with parietal and retractor muscle; (F) detail of actinopharynx showing large basitrichs (arrows); (G) detail of a nemathybome with pterotrichs (arrow); (H) detail of rounded proximal end with nemathybomes (arrows); (I) cross-section through mid-column showing gametogenic tissue of a macrocneme with oocytes (arrow). Abbreviations: ba, basitrich; ep, epidermis; ga, gastrodermis; me, mesoglea; nb, nemathybomes; nt, nematocysts; oo, oocytes; pa, parietal muscle; pe, periderm; re, retractor muscle; tc, tentacle. Scale bars: A, 20.0; B, 3.0; C, 0.17; D, 0.7; E, 0.4; F, 0.12; G, 0.04; H, 0.3; I, 0.2 mm.

Edwardsiidae with column divided in a distinct proximal end, scapus, scapulus and capitulum. Scapus and proximal end with periderm and scattered nemathybomes. Nemathybomes with pterotrichs. Eight macrocnemes span body length; four microcnemes present only in capitulum. Tentacles 12 in adults arranged in two cycles; all of same size or outer longer than inner ones. Retractor muscles well developed, circumscribed; parietal muscle well developed, symmetrical. Cnidom: spirocysts, basitrichs, pterotrichs and *p*-mastigophores A.

Type species. *Isoscolanthus iemanjae* sp. nov.

Etymology. The genus was named *Isoscolanthus* (from Greek *isos* 'equal' + *Scolanthus* 'a genus of sea anemones') due to its morphological similarity with *Scolanthus* Gosse, 1853. Gender: Masculine.

Remarks. *Isoscolanthus* gen. nov. is differentiated from other edwardsiids based on external morphology and cnidom. The presence of nemathybomes in members of *Isoscolanthus* gen. nov. differentiates the genus from species of *Nematostella*, *Drillactis* Verrill, 1922, *Edwardsiella* Andres, 1883, *Paraedwardsia* Carlgren in Nordgaard, 1905, and *Synhalcampella* Carlgren, 1921, all of which lack this columnar specialization. All remaining genera within Edwardsiidae (i.e. *Scolanthus*, *Edwardsia*, *Edwardsianthus* England, 1987 and *Halcampogeton* Carlgren, 1937) present nemathybomes on the column as well. The presence of periderm and nemathybomes on proximal end differentiates *Isoscolanthus* gen. nov. from *Edwardsia*, *Edwardsianthus* and *Halcampogeton*. *Isoscolanthus* gen. nov. is differentiated from *Scolanthus* by the number of microcnemes (four in *Isoscolanthus* gen. nov.; at least eight in *Scolanthus*) and, consequently, by the number of tentacles (12 in *Isoscolanthus* gen. nov.; 16 or more in *Scolanthus*). The type of nematocyst in nemathybomes further differentiates *Isoscolanthus* gen. nov. from *Scolanthus* (pterotrichs in *Isoscolanthus* gen. nov; basitrichs in *Scolanthus*).

Despite the presence of a distinct proximal end in *Isoscolanthus* gen. nov., the epidermis of the region is not thickened and well differentiated from the scapus as seen in species with true physa *sensu* Carlgren & Stephenson (1928) (e.g. *Edwardsia* and *Nematostella* Stephenson, 1935). Instead, the proximal end of *Isoscolanthus* gen. nov. has a narrower mesoglea compared to the scapus and, in some specimens, a slight constriction separating scapus from proximal end; this may also be observed in species of *Scolanthus* (e.g. *S. callimorphus*: Schmidt, 1979).

Isoscolanthus iemanjae sp. nov.
(Figures 2–3, Table 1)

TYPE MATERIAL (6 specimens)

Holotype: MZUSP 2723, 1 adult specimen, 902 m depth, Bacia de Campos (22°42′S 40°10′W), Rio de Janeiro, Brazil, sample date unknown.

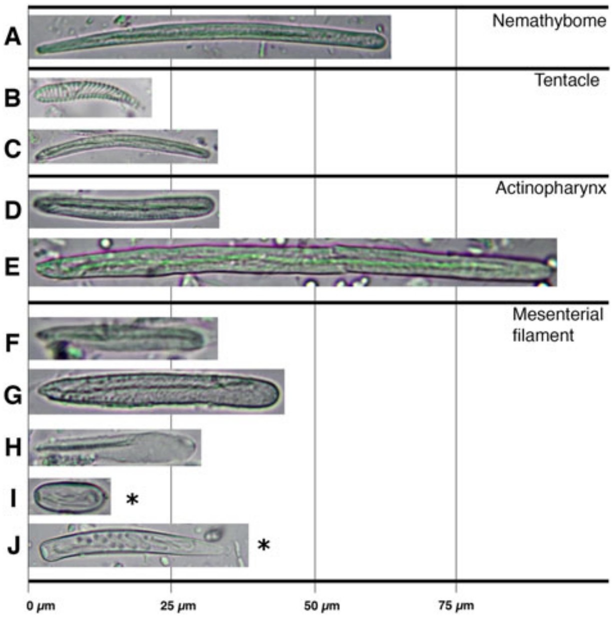

Fig. 3. Cnidom of *Isoscolanthus iemanjae* sp. nov.: (A) pterotrich; (B) spirocyst; (C) basitrich; (D) basitrich I; (E) basitrich II; (F) basitrich I; (G) basitrich II; (H) *p*-mastigophore A; (I) holotrich I; (J) holotrich II. *Nematocysts present possibly due to contamination.

Paratypes: MZUSP 2713, 1 adult specimen, 212 m depth, Bacia de Campos (22°41′S 40°37′ W), Rio de Janeiro, Brazil, sample date unknown. MZUSP 2715, 1 adult specimen, 212 m depth, Bacia de Campos (22°41′S 40°37′ W), Rio de Janeiro, Brazil, sample date unknown. MZUSP 2717, 1 adult specimen, 902 m depth, Bacia de Campos (21°08′S 40°10′W), Rio de Janeiro, Brazil, sample date unknown; MZUSP 2718, 1 adult specimen, 902 m depth, Bacia de Campos (21°08′S 40°10′W), Rio de Janeiro, Brazil, sample date unknown. MZUSP 2724, 1 adult specimen, 902 m depth, Bacia de Campos (21°08′ S 40°10′W), Rio de Janeiro, Brazil, sample date unknown.

DIAGNOSIS

Isoscolanthus with column mesoglea thicker distally than proximally. Retractor muscle without pennon. Parietal muscle strong, well developed and ~ two-thirds the size of retractor muscle. Actinopharynx with a very long category of basitrichs (50.7–100.1 × 3.6–5.1 μm).

DESCRIPTION

External anatomy. Proximal end rounded, externally differentiated from rest of column but not true physa (Figure 2A); no central pore present. Column robust, length 15–20 mm and diameter 6–9 mm; wider proximally than distally; divided in four regions: well delimited proximal end, scapus, scapulus and capitulum. All examined specimens with distal portion of column retracted, including part of scapus, scapulus and capitulum. Periderm fine-grained, tightly adherent, covering whole column from distal scapus to proximal end (Figure 2A, B). Nemathybomes single, conspicuous, scattered on column from distal scapus to proximal end; sparser on scapus (Figure 2A), but more aggregated on proximal end (Figure 2A, B). Tentacles small, always 12 in adults, arranged in two cycles, presumably all of same size (Figure 2C).

Internal anatomy and microanatomy. Mesenterial arrangement typical for Edwardsiidae: eight macrocnemes span length of body (Figure 2D), four microcnemes only in capitulum at base of tentacles. Retractor muscle of macrocnemes relatively weak, circumscribed (Figure 2D), without proximal pennon (Figure 2E).

Table 1. Size ranges of the cnidae of *Isoscolanthus iemanjae* gen. nov. et sp. nov.

Categories	Range of length and width of capsules (μm)	$\bar{X} \pm$ SD	S	N	Categories	Range of length and width of capsules (μm)	$\bar{X} \pm$ SD	S	N
Nemathybome									
Pterotrich (A)	32.6–71.5 × 2.8–4.0	63.7 ± 7.3 × 3.3 ± 0.3	86	4/4					
Tentacles									
Spirocyst (B)	09.9–23.4 × 2.2–4.1	17.0 ± 3.5 × 3.3 ± 0.5	76	3/3					
Basitrich (C)	15.2–69.0 × 2.5–4.2	32.3 ± 14.2 × 3.3 ± 0.4	67	3/3					
Actinopharynx									
Basitrich I (D)	22.9–42.1 × 2.8–5.5	36.2 ± 4.1 × 4.7 ± 0.5	71	3/3					
Basitrich II (E)	50.7–100.1 × 3.6–5.1	90.1 ± 11.1 × 4.4 ± 0.3	50	2/3					
Filament									
Basitrich I (F)	24.6–35.0 × 3.4–4.9	30.5 ± 2.5 × 4.1 ± 0.4	84	4/4	Basitrich II (G)	29.0–45.5 × 4.1–6.4	40.9 ± 3.6 × 5.4 ± 0.5	82	4/4
p-mastigophore A (H)	25.8–34.0 × 5.2–8.2	30.6 ± 1.9 × 6.5 ± 1.0	88	4/4	Holotrich I (I)*	11.2–12.7 × 4.8–7.6	12.2 ± 0.6 × 5.8 ± 1.1	10	1/4
Holotrich II (J)[a]	30.7–45.8 × 4.7–7.0	37.4 ± 5.5 × 5.9 ± 0.8	7	1/4					

$\bar{X}$, mean; SD, standard deviation; S, proportion of specimens in which each cnidae was found; N, Total number of capsules measured.
[a]Cnidae present probably due to contamination (see species remarks).

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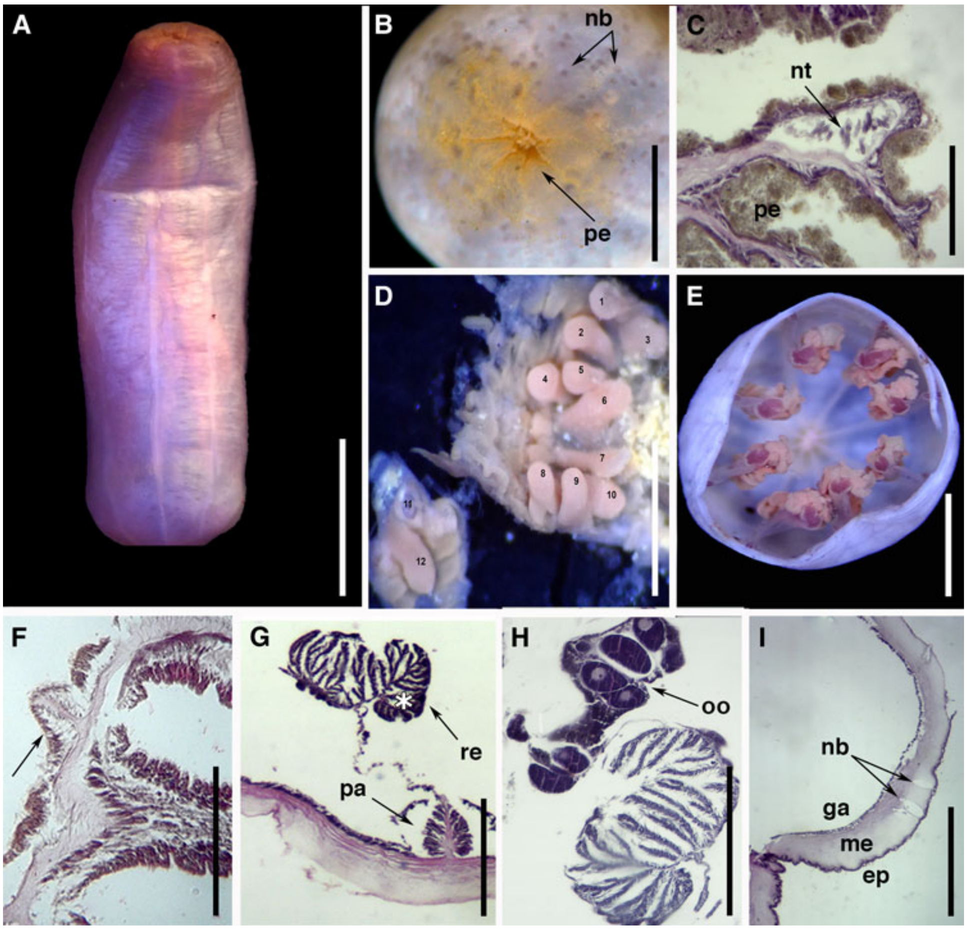

Fig. 4. External anatomy and microanatomy of *Isoscolanthus janainae* sp. nov.: (A) Lateral view of a preserved specimen; (B) detail of proximal rounded end with sparse periderm and several nemathybomes (arrows); (C) detail of a nemathybome with nematocysts; note the periderm; (D) detail of distal column showing the 12 tentacles; (E) cross-section through mid-column showing eight macrocnemes; (F) cross-section through capitulum showing a microcneme at the base of tentacles (arrow); (G) detail of a macrocneme showing parietal and retractor muscle with a pennon (asterisk); (H) detail of retractor with large pennon and gametogenic tissue with oocytes; (I) longitudinal section through column showing nemathybomes in mesoglea (arrows). Abbreviations: ep, epidermis; ga, gastrodermis; me, mesoglea; nb, nemathybomes; nt, nematocysts; oo, oocytes; pa, parietal muscle; pe, periderm; re, retractor muscle. Scale bars: A, 10.0; B, 3.0; C, D, 0.1; E, 3.0; F, 0.6; G, 0.25; H, 0.20; I, 0.5 mm.

Retractor with few muscle processes (15 in average) variable in height, with low degree of ramification, more branched closer to body wall (Figure 2E). Parietal muscle large, almost same size as retractor, well developed, symmetrical, ovoid, with 12–14 processes, most branched closer to body wall; central lamella of equal thickness, forming peduncle of 0.01 mm (Figure 2E). Actinopharynx thick, with long basitrichs present (Figure 2F). Mesoglea thicker distally at actinopharynx level (0.3 mm) than at gastrovascular cavity level (0.06 mm). Nemathybomes conspicuous, sunken into mesoglea, most below epidermis but some protruding into it; filled with grain-like particles and pterotrichs (Figure 2G). Nemathybomes on proximal end generally smaller than those in scapus (Figure 2H). Gametogenic tissue occurs right below actinopharynx where filaments are very reduced. Gonochoric; all examined specimens with oocytes (Figure 2I).

Cnidom. Spirocysts, basitrichs, pterotrichs and *p*-mastigophores A. See Figure 3 and Table 1 for size and distribution.

Distribution. The species is known from three collection sites in the type locality of Bacia de Campos, off the coast of the state of Rio de Janeiro, Brazil, between 202–902 m depth.

Etymology. Species named after the water deity Yemoja from the Yoruba religion. In Brazil, Iemanjá (as it is written in Portuguese) is known as 'The Queen of the Ocean' and worshipped by followers of Candomblé and Umbanda.

Remarks. We did not include the holotrichs found in filaments of *I. iemanjae* sp. nov. in the cnidom of the genus (or the species) as these nematocysts were found in only one specimen. We believe it is a case of contamination by feeding similar to the one described for *E. migottoi* (see Gusmão *et al*., 2016).

Isoscolanthus janainae sp. nov.
(Figures 4 and 5, Table 2)

TYPE MATERIAL (11 specimens)

Holotype: MNRJ 8688, 1 adult specimen, 295–300 m depth, offshore Rio de Janeiro (21°31′S 40°08′W), Rio de Janeiro, Brazil (St. 56 CB96), coll. 1987 by TAAF.

Paratypes: MZUSP 2729, 10 specimens, sampled at same site and point of the holotype. Additional material: MZUSP 7937, 105 specimens, Rio de Janeiro (21°31′S 40°08′W), Brazil, coll. 31/v/1987 by TAAF.

DIAGNOSIS

Isoscolanthus with retractor muscle with pennon. Parietal muscle at least one-third the size of retractor muscle. Small category of basitrichs in actinopharynx (26.7–46.2 × 3.0–4.9 μm).

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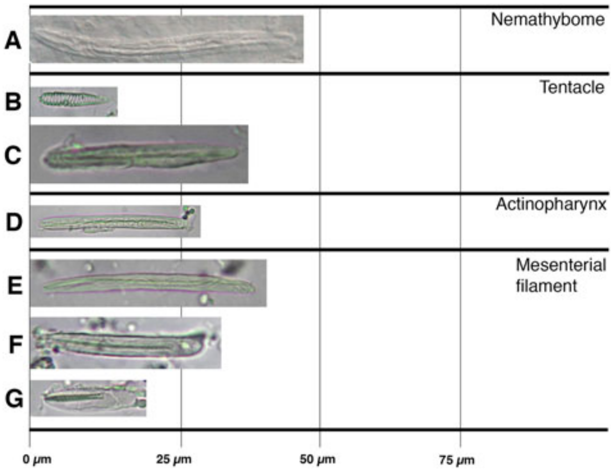

Fig. 5. Cnidom of *Isoscolanthus janainae* sp. nov.: (A) pterotrich; (B) spirocyst; (C) basitrich; (D) basitrich; (E) basitrich I (F) basitrich II; (G) *p*-mastigophore A.

DESCRIPTION

External anatomy. Proximal end rounded, differentiated from rest of column but not true physa (Figure 4A); no central pore present. Column delicate, length 8–20 mm and diameter 3–7 mm, divided in four regions: well delimited proximal end, scapus, scapulus and very short capitulum. Periderm thin, not adherent, deciduous, covering whole column from distal scapus to proximal end (Figure 4B, C); most specimens did not have periderm on scapus or proximal end. Nemathybomes single (Figure 4C), inconspicuous, scattered on column from distal scapus to proximal end; larger on scapus (Figure 4C) than in proximal end (Figure 4B). Nemathybomes arranged in longitudinal rows between insertions of macrocnemes (Figure 4A). Tentacles 12 in adults, arranged in two cycles with outer ones presumably longer than inner ones (Figure 4D).

Internal anatomy and microanatomy. Mesenterial arrangement typical for Edwardsiidae: eight macrocnemes span length of body (Figure 4E), four microcnemes only in capitulum at base of tentacles (Figure 4F). Retractor muscle of macrocnemes strong, circumscribed, with easily recognizable pennon (Figure 4G, H). Retractor with relatively numerous processes (14–20) and few ramifications, more branched at the pennon (Figure 4G, H). Parietal muscle small, symmetrical, ovoid, with 16–19 lateral processes relatively unbranched; central lamella forming peduncle 0.015 mm wide closer to body wall (Figure 4G). Mesoglea thicker distally at the actinopharynx level (0.27 mm) than at gastrovascular cavity level (0.06–0.13 mm). Nematthybomes single, inconspicuous, sunken into mesoglea, most below epidermis (Figure 4I) but some protruding into it (Figure 4C); with only pterotrichs. Proximal end with small invagination but no terminal pore (Figure 4I). Gonochoric; all examined specimens with oocytes (Figure 4H).

Cnidom. Spirocysts, basitrichs, pterotrichs and *p*-mastigophores A. See Figure 5 and Table 2 for size and distribution.

Distribution. The species is known from a single collection site in the type locality (21°31′S 40°08′W), off the coast of the state of Rio de Janeiro, Brazil, between 295–300 m depth.

Etymology. Species also named after water deity Yemoja from the Yoruba religion which receives different names in Brazil, one of which is Janaína.

Table 2. Size ranges of the cnidae of *Isoscolanthus janainae* gen. nov. et sp. nov.

Categories	Range of length and width of capsules (µm)	$\bar{X} \pm$ SD	S	N	Categories	Range of length and width of capsules (µm)	$\bar{X} \pm$ SD	S	N
Nemathybome									
Pterotrich (A)	40.0–47.0 × 3.2–4.0	44.2 ± 2.3 × 3.7 ± 0.3	45	4/4					
Tentacles									
Spirocyst (B)	12.7–26.0 × 2.2–4.7	19.3 ± 3.3 × 3.9 ± 0.6	91	4/4					
Basitrich (C)	26.7–46.2 × 3.0–4.9	37.9 ± 5.3 × 3.5 ± 0.4	88	4/4					
Actinopharynx									
Basitrich(D)	16.3–43.3 × 2.6–4.5	27.2 ± 8.8 × 3.5 ± 0.6	87	4/4					
Filament									
Basitrich I (F)	23.4–51.6 × 3.0–4.1	43.0 ± 7.5 × 3.6 ± 0.3	20	1/4	Basitrich II (G)	27.1–37.0 × 3.9–5.1	31.7 ± 2.5 × 4.6 ± 0.3	83	4/4
p-mastigophore A (H)	19.6–25.0 × 4.3–6.0	22.5 ± 1.2 × 5.4 ± 0.4	81	4/4					

$\bar{X}$, mean; SD, standard deviation; S, proportion of specimens in which each cnidae was found; N, Total number of capsules measured.

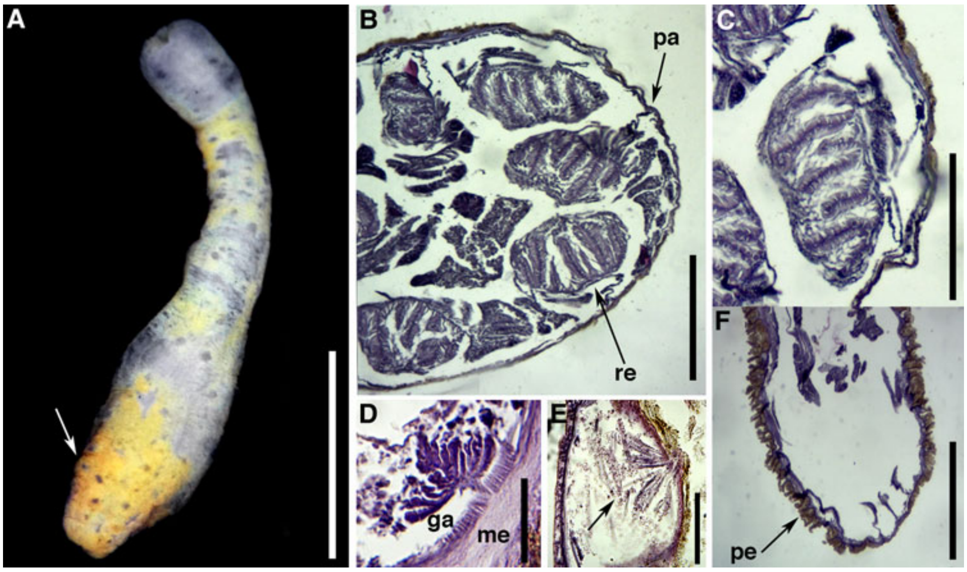

Fig. 6. External anatomy and microanatomy of *Scolanthus crypticus* sp. nov.: (A) general view of a preserved specimen showing proximal rounded end with periderm and nemathybomes (arrow); (B) cross-section through mid-column showing pairs of macrocnemes; (C) detail of a macrocneme showing poorly developed retractor muscle; (D) detail of small parietal muscle; (E) detail of a nemathybome with nematocysts; (F) longitudinal section through proximal end showing periderm. Abbreviations: ga, gastrodermis; me, mesoglea; pa, parietal muscle; pe, periderm; re, retractor. Scale bars: A, 5; B, 0.4; C, 0.15; D, 0.06; E, 0.05; F, 0.5 mm.

Remarks. Due to the poor preservation state of the material, only a few specimens exhibited preserved nemathybomes and these exhibited a reduced number of undischarged nematocysts.

Despite the uniformity in external and internal anatomy and cnidom seen in members of *Isoscolanthus* gen. nov., the two species of the genus can be differentiated by microanatomical features and cnidae: mesenteries have retractors much larger and with a pennon and parietal muscles larger and more branched in *Isocolanthus iemanjae* sp. nov. than in *Isoscolanthus janainae* sp. nov.; although pterotrichs in the nemathybomes partially overlap in their lower range, *I. iemanjae* sp. nov. has much longer pterotrichs (32.6–71.5 × 2.8–4.0 µm) compared with *I. janainae* sp. nov. (40.0–47.0 × 3.2–4.0 µm). Likewise, nematocyst sizes are generally larger in other tissues of *I. iemanjae* sp. nov. than in *I. janainae* sp. nov. (e.g. basitrichs in tentacles, *p*-mastigophores A in filaments), with a category of basitrichs in *I. iemanjae* sp. nov. not found in *I janainae* sp. nov. Although both species co-occur in Bacia de Campos, Rio de Janeiro, *I. iemanjae* sp. nov. has a broader bathymetric range (212–902 m) only overlapping in shallower depths with *I. janainae* sp. nov. (i.e. 295–300 m).

Genus Scolanthus Gosse, 1853

Diagnosis. (Adapted from Daly & Ljubenkov, 2008 and Manuel, 1981*a*, 1981*b*; additions in italics) Edwardsiidae with body divisible into scapus and scapulus. Proximal region of body rounded, provided with nemathybomes *and periderm*; nemathybomes scattered or forming several longitudinal rows on scapus. *Nemathybomes with basitrichs.* At least eight microcnemes. Tentacles *at least* 16 in adults, arranged octamerously; inner ones shorter than outer ones. Retractor muscles relatively large, well developed, diffuse to circumscript; parietal muscles distinct, symmetrical, well-developed. Cnidom: spirocysts, basitrichs, *b*-mastigophores and *p-mastigophores A*.

Type species. *Scolanthus callimorphus* Gosse, 1853 by monotypy

Remarks. We have included in the diagnosis of *Scolanthus* the presence of periderm in the proximal end as this character can help differentiate species of this genus from other edwardsiid genera. Although we acknowledge most *Scolanthus* species have imperfectly known cnidom (Daly & Ljubenkov, 2008) and the distinction between basitrichs and pterotrichs can be difficult without observation of discharged capsules (Daly & Ljubenkov, 2008), all species of *Scolanthus* described have nemathybomes with basitrichs. This includes the recently described species *Scolanthus triangulus* Daly & Ljubenkov, 2008 and *Scolanthus scamiti* Daly & Ljubenkov, 2008, which undoubtedly have basitrichs in the nemathybomes (e.g. Daly & Ljubenkov, 2008). This information is included in the diagnosis pending a revision of the genus.

Scolanthus crypticus sp. nov.
(Figures 6 and 7, Table 3)

TYPE MATERIAL (41 specimens)

Holotype: MNRJ 8687, 1 Adult specimen, 40 m depth offshore São Sebastião (23°50′S 45°10′W), São Paulo, Brazil. coll. 19/iv/1986.

Paratypes: MNRJ 8686, 10 adult specimens, sampled with the type; MOPE 0873, 6 adult specimens, 35 m depth, offshore Ubatuba (23°39′S 44°53′W), São Paulo, Brazil, coll. 20/iv/1986. MOPE 0874, 6 adult specimens, 47 m depth, offshore Ubatuba (23°38′S 44°49′W), São Paulo, Brazil, coll. 22/i/1986. MOPE 0875, adult 4 specimens, 35 m depth, offshore Ubatuba (23°40′S 44°59′W), São Paulo, Brazil, coll. 20/iv/1986. MNRJ 8684, 7 adult specimens, 45 m depth offshore Ubatuba (23°44′S 45° 00′W), São Paulo, Brazil, coll. 20/i/1986. MNRJ 8685, 8 adult specimens, 40 m depth, offshore Ubatuba (23° 34′S 44°48′ W) São Paulo, Brazil, coll. 22/i/1986.

DIAGNOSIS

Scolanthus with inconspicuous nemathybomes arranged in longitudinal rows between macrocnemes; thick periderm present. Tentacles with long basitrichs (26.9–56.5 × 2.5–4.2 µm). Nemathybome nematocysts shorter than 60 µm (24.3–56.3 × 3.9–5.5 µm). Length of whole animal in contraction to 15 mm, diameter 2.0–4.0 mm.

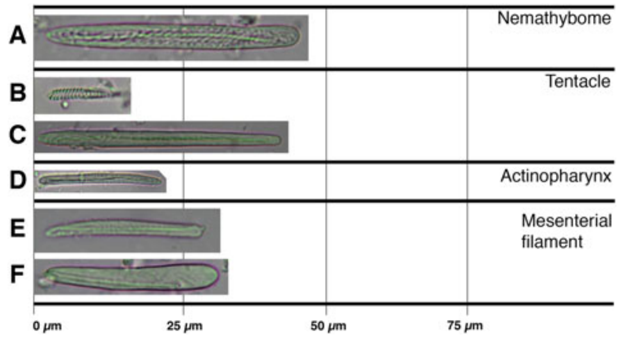

Fig. 7. Cnidom of *Scolanthus crypticus* sp. nov.: (A) basitrich; (B) spirocyst; (C) basitrich; (D) basitrich; (E) basitrich; (F) basitrich.

DESCRIPTION

External anatomy. Most specimens examined with proximal end damaged. Proximal end rounded, not differentiated in true physa (Figure 6A). Column delicate, slender, length 10.0–15.0 mm and diameter 2.0–4.0 mm, divided in two regions: scapus and scapulus. Periderm thick, adherent, orange, composed of fine mud grains, covering scapus (Figure 6A). Nemathybomes single, inconspicuous, in longitudinal rows between insertions of macrocnemes from distal scapus to proximal scapus (Figure 6A). Tentacles up to 16 in adults; presumably arranged in two cycles.

Internal anatomy and microanatomy. Eight macrocnemes span length of body, eight microcnemes only in scapulus at the base of tentacles. Retractor muscle of macrocnemes poorly developed, circumscribed, without proximal pennon (Figure 6B, C). Retractor muscle with 5–7 processes of similar height and low degree of ramification (Figure 6C). Parietal muscle small, poorly developed, asymmetrical, triangular; central lamella forming peduncle no more than 0.003 mm wide (Figure 6B, D). Mesoglea of column thicker distally (0.03 mm) than proximally (0.006 mm). Nemathybomes relatively small, inconspicuous, sunken into mesoglea, distributed in longitudinal rows between macrocneme insertions (Figure 6E), most protruding into epidermis (Figure 6E). Proximal region of body with thick periderm, nemathybomes and mesogleal projections (Figure 6F). All examined individuals sterile.

Cnidom. Spirocysts and basitrichs. See Figure 7 and Table 3 for size and distribution.

Distribution and natural history. This species is known from its type locality (23°50′S 45°10′W) and five collection sites off the coast of São Paulo between São Sebastião and Ubatuba, Brazil, between 35–47 m depth.

Etymology. The species was always found among specimens of *E. migottoi* and at first glance they looked very alike. Therefore it was named 'crypticus', the latin term for 'cryptic'.

Remarks. Species within *Scolanthus* are differentiated mainly by geographic distribution, nemathybome arrangement and cnidom. *Scolanthus crypticus* sp. nov. is the first species of the genus recorded for the South-western Atlantic Ocean, the other species being from the North Atlantic Ocean (*S. callimorphus* Gosse, 1853; *Scolanthus ingolfi* (Carlgren, 1921); *Scolanthus curacaoensis* (Pax, 1924); *Scolanthus nidarosiensis* (Carlgren, 1942)), Atlantic portion of the Southern Ocean (*S. intermedius*), and Pacific Ocean (*Scolanthus ignotus* (Carlgren, 1922), *Scolanthus armatus* (Carlgren, 1931), *S. triangulus*, *S. scamiti*). In addition, *Scolanthus crypticus* sp. nov. belongs to a group of species within

Table 3. Size ranges of the cnidae of *Scolanthus crypticus* sp. nov.

Categories	Range of length and width of capsules (μm)	$\bar{X} \pm$ SD	S	N	Categories	Range of length and width of capsules (μm)	$\bar{X} \pm$ SD	S	N
Nemathybome									
Basitrich (A)	24.3–56.3 × 3.9–5.5	47.6 ± 6.8 × 4.9 ± 0.4	70	3/3					
Tentacles									
Spirocyst (B)	11.9–19.3 × 2.0–3.3	14.7 ± 1.9 × 2.7 ± 0.4	61	3/3					
Basitrich (C)	26.9–56.5 × 2.5–4.2	44.3 ± 9.1 × 3.4 ± 0.4	62	3/3					
Actinopharynx									
Basitrich (F)	24.6–29.1 × 2.1–2.9	23.8 ± 2.2 × 2.5 ± 0.2	64	2/3					
Filament									
Basitrich I (H)	24.7–34.4 × 2.1–3.3	29.0 ± 2.0 × 2.7 ± 0.3	62	3/3	Basitrich II (I)	30.5–35.6 × 3.9–6.0	33.4 ± 1.6 × 5.0 ± 0.5	70	3/3

$\bar{X}$, mean; SD, standard deviation; S, proportion of specimens in which each cnidae was found; N, Total number of capsules measured.

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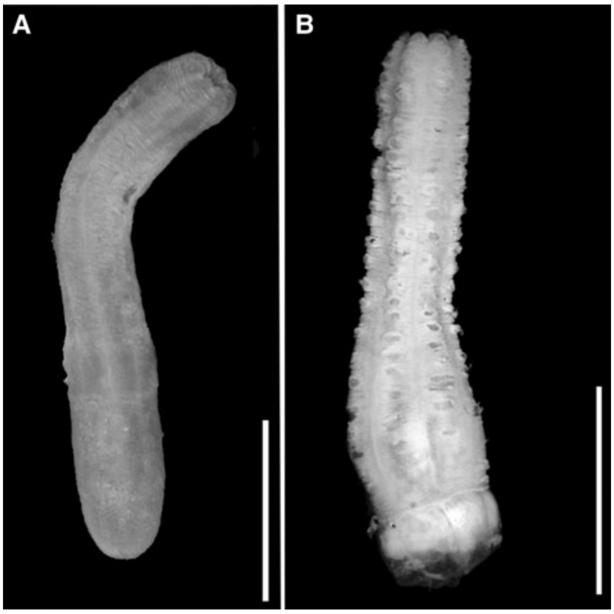

Fig. 8. External anatomy and microanatomy of *Nematostella vectensis* Stephenson, 1935 and *Edwardsia migottoi* Gusmão, Brandão & Daly, 2016 (A) general view of a preserved specimen of *Nematostella vectensis*; note the column without any specialization; (B) general view of a preserved specimen of *Edwardsia migottoi* showing longitudinal rows of nemathybomes with periderm and physa without periderm. Scale bars: A, 2.0; B, 10 mm.

Scolanthus lacking *p*-mastigophores A (together with the type species *S. callimorphus*, *S. armatus*, *S. ingolfi*, *S. ignotus* and *S. triangulus*). Of those species, only *S. crypticus* sp. nov. and *S. callimorphus* have nemathybomes arranged in longitudinal rows, all other species have them scattered on scapus and proximal end. These two species can be further differentiated based on the non-overlapping size range of basitrichs in nemathybomes (24.28–56.33 × 3.93–5.54 µm in *S. crypticus* sp. nov.; 62.4–87.0 × 3.0–4.8 µm in *S. callimorphus*), and geographic distribution (*S. crypticus* sp. nov. in South-western Atlantic; *S. callimorphus* in North-east Atlantic). Regarding microanatomical traits, *S. crypticus* sp. nov. resembles *S. triangulus* as both have weak retractors with few muscle processes. However, these two species can be differentiated by length of basitrichs in nemathybomes (50–60 µm in *S. crypticus* sp. nov.; 63–89 µm in *S. triangulus*), non-overlapping geographic distribution (*S. crypticus* sp. nov. in Atlantic; *S. triangulus* in Pacific) and disjunct bathymetry (*S. crypticus* sp. nov. collected up to 47 m; *S. triangulus* collected from 85 m to 271 m).

All individuals of *S. crypticus* sp. nov. were collected together with specimens of *E. migottoi* indicating a pattern of sympatry commonly found between species of *Edwardsia* and *Scolanthus* (see Daly & Ljubenkov, 2008).

Genus Nematostella Stephenson, 1935

Diagnosis. See Stephenson (1935)

Type species. *Nematostella vectensis* Stephenson, 1935 by original designation.

Nematostella vectensis Stephenson, 1935
(Figure 8A)

Nematostella vectensis: Stephenson, 1935; Pax, 1936; Carlgren, 1945; Hand, 1957; Sanders, Mangelsdorf & Hampson, 1965; Williams, 1973; Manuel, 1981a, 1981b; Hand & Uhlinger, 1994; Williams, 2003; Silva *et al.*, 2010.

Nematostella pelucida: Crowell, 1946; Carlgren, 1949.

DIAGNOSIS
See Williams (1975)

Examined material (19 individuals)

MOPE 0876, 6 individuals, 0–2 m, depth, Baía de Guaratuba (25°52′S 48°42′W), Paraná, Brazil, coll. iii/2012; MOPE 0877, 7 individuals, 0–2 m depth, Baía de Guaratuba (25°51′S 48°38′W), Paraná, Brazil, coll. x/2012; MOPE 0878, 6 individuals, 0–2 m depth, Baía de Guaratuba (25°51′S 48°38′W), Paraná, Brazil, col-l.xi/2012.

Distribution. *Nematostella vectensis* was originally described from England, off the coast of Isle of Wight (Stephenson, 1935), with its current distribution now including other localities around the English coast (Reitzel *et al.*, 2008), the east and west coasts of the USA (Reitzel *et al.*, 2008) and the north-east of Brazil (Silva *et al.*, 2010). Here we extend the distribution of the species in Brazil to include the state of Paraná in the south coast of Brazil, between 0–2 m depth.

Remarks. All specimens examined were stained with Rose Bengal by the collector (Gisele Morais, Federal University of Paraná) which hindered detailed examination of external anatomical characters. Additionally, given the small size of individuals we could not examine the cnidae from actinopharynx with the precision necessary to avoid contamination. Microanatomical and cnidae features of the specimens examined, however, closely agree with those given by Williams (1975). Here we recorded the occurrence of *N. vectensis* for the state of Paraná in the south coast of Brazil in a harbour environment similar to the one described by Silva *et al.* (2010) for the Port of Recife more than 3000 km away. Because it is not possible to confirm the presence of the species in Paraná before the study of Silva *et al.* (2010), we cannot establish whether *N. vectensis* is spreading along the Brazilian coast.

Genus *Edwardsia* de Quatrefages, 1842

Diagnosis. See Daly & Ljubenkov (2008)

Type species. *Edwardsia beautempsii* de Quatrefages, 1842 by subsequent designation (Carlgren, 1949).

Edwardsia migottoi Gusmão, Brandão & Daly, 2016
(Figure 8B)

DIAGNOSIS
Very small individuals, length 1.7–6.3 mm; scapus covered by deciduous ferruginous periderm; eight longitudinal rows of tubercles with nemathybomes with two types of nematocysts: *t*-mastigophores (42.9–75.8 × 2.4–4.2 µm) and pterotrichs (59.8–119.1 × 3.9–7.1 µm).

Examined material. (32 individuals) MOPE 0867, 10 adult specimens, 44 m depth, offshore Ubatuba (23°34′S 44°48′W), São Paulo, Brazil, coll. 22/i/1986; MOPE 0868 , 4 adult specimens, 20 m depth, offshore Ubatuba (23°43′S 45°13′W), São Paulo, Brazil, coll. 21/i/1986; MOPE 0869, 6 specimens, 47 m depth, offshore Ubatuba (23°47′S 45°49′W), São Paulo, Brazil, coll. 22/i/1986; MOPE 0870, 6 specimens, 46 m depth, offshore Ubatuba (23°45′S 45°00′W), São Paulo, Brazil, coll. 26/x/1985; MOPE 08671, 1 specimen, 40 m depth, offshore Ubatuba (23°50′S 45° 10′W), São Paulo, Brazil, coll. 27/x/1985; MOPE 0879, 5 specimens, 1 m depth, offshore Cabo de Santo Agostinho (8°25′S 34° 57′W), Pernambuco, Brazil, coll. 14/xii/2015.

Distribution. *Edwardsia migottoi* is previously known only from its type locality in Praia do Araçá, São Sebastião (São Paulo). Here we extended the distribution of the species to include Ubatuba which is also located in the state of São Paulo, ~80 km from the type locality. In addition, the species has been collected in Cabo de Santo Agostinho in the state of Pernambuco, extending the distribution of the species to include the north-eastern coast of Brazil.

Remarks. Edwardsia migottoi is the only species of the genus known from Brazil. The specimens examined here closely agree with the description of Gusmão *et al.* (2016). Unlike Gusmão *et al.* (2016), however, we did not find holotrichs in the filament and did not observe a terminal pore in the physa. This small discrepancy does not compromise our identification as the presence of holotrichs in the filament of *E. migottoi* is hypothesized by Gusmão *et al.* (2016) to result from contamination by feeding. In addition, the presence of a terminal pore can be difficult to observe in histological sections and is not considered a highly informative character for the systematics of the group.

Discussion

The importance of some traits to the circumscription of Isoscolanthus *gen. nov.*

Among other characters, mesentery and tentacle arrangement have often been used to distinguish species and genera within Actiniaria (Stephenson, 1921; Carlgren, 1949). In edwardsiids, the overall number of microcnemes and their location, which is directly related to number of tentacles, has been regarded as a character of generic importance. *Edwardsianthus*, for example, was erected by England (1987) to include species of *Edwardsia* with six pairs of microcnemes in the second cycle resulting in 20 tentacles as opposed to microcnemes developing in lateral and ventral exocoels resulting in the 12–36 tentacles seen in most species of *Edwardsia.* The phylogenetic analyses of Daly (2002) recovered *Edwardsianthus* as a distinct group more closely related to members of *Scolanthus* than *Edwardsia*, corroborating England's (1987) hypothesis that mesentery development and resulting microcneme arrangement may be a trait of systematic and taxonomic value. Both species of *Isoscolanthus* gen. nov. have four microcnemes and 12 tentacles which is a combination present in only seven species of *Edwardsia* (e.g. Daly *et al.*, 2012) and no species of *Scolanthus* (England, 1987). Based on our finds, we agree with previous authors that different modes of mesentery and tentacle development may be an important feature for the taxonomy and systematics of Edwardsiidae.

Isoscolanthus gen. nov. is the second genus of Edwardsiidae to have pterotrichs in its cnidom. Although England (1987) was the first to define pterotrichs, this nematocyst had been previously noted in nemathybomes of *Edwardsia tuberculata* by Düben & Koren (1847) and later in *Edwardsia hantuensis* by England (1987). Based on drawings by Manuel (1977), England (1987) also inferred the presence of pterotrichs in *Edwardsia timida* de Quatrefages, 1842 and *Edwardsia beautempsi* de Quatrefages, 1842. An undischarged pterotrich capsule incorporates features of nematocysts without shaft (i.e. haplonemes) and those with a shaft (i.e. mastigophores) (England, 1987). Pterotrichs have been identified as *b*-mastigophores by Carlgren (1940) and Manuel (1977) but unlike *b*-mastigophores which have a homogeneous shaft, pterotrichs have a shaft divided in four regions: a basal part folded with few large pointed spines arranged spirally followed by a heavily armed region with thick close-set spines not arranged spirally, similar to the feathers of an arrow, and a distal-most region armed with small spirally arranged spines (England, 1987). Pterotrichs were, until now, exclusive to some members of *Edwardsia*, usually co-occurring with *t*-mastigophores in nemathybomes of certain species (e.g. *Edwardsia beautempsi*, *Edwardsia californica*) (see England, 1987 and Daly & Ljubenkov, 2008). In members of *Isoscolanthus* gen. nov., however, only pterotrichs are found in nemathybomes. Although the distinction between pterotrichs and *b*-mastigophores or basitrichs *sensu* Weill (1934) modified by Carlgren (1940) is not always straightforward based on undischarged capsules, the folded region in the proximal part of the capsule and its shape (i.e. thinner becoming broader distally) can help differentiate these nematocysts. We cannot comment on morphological differences between pterotrichs found in *Edwardsia* or *Isoscolanthus* gen. nov. as we did not observe discharged capsules, however the undischarged capsules are very similar.

The status of Scolanthus *and the importance of cnidae in its circumscription*

Scolanthus has a convoluted taxonomic history. Being first considered a synonymy of *Edwardsia* (Gosse, 1860), it was later resurrected by Manuel (1981a, 1981b), who also synonymized *Isoedwardsia* Carlgren, 1921 and *Alfredus* Schmidt, 1979 under *Scolanthus* based on the presence of nemathybomes on the proximal end and absence of *p*-mastigophores A in their cnidom. The uncertainty regarding the presence of *p*-mastigophores A in *Scolanthus* has made its circumscription difficult, leading Manuel (1981*a*, 1981*b*) to doubt membership of *S. nidarosiensis* and *S. curacaoensis* (former species of *Isoedwardsia* which have *p*-mastigophores A) within *Scolanthus*. Given that presence or absence of a type of nematocyst has been regarded as of generic importance (England, 1987), Manuel's hesitation is understandable. The phylogenetic analyses by Daly (2002) recovered two species of *Scolanthus* without *p*-mastigophores A (*S. armatus* and *S. callimorphus*) in a monophyletic clade sister to a species of *Edwardsia* without *p*-mastigophores A (*E. intermedia*). Thus, Daly (2002) proposed to broaden the circumscription of *Scolanthus* to include *E. intermedia* (currently *S. intermedius*) and all other species with nemathybomes on proximal end whether or not they have *p*-mastigophores A. We agree with the circumscription of *Scolanthus* given by Daly & Ljubenkov (2008) pending a revision of all species in the genus.

The presence of *b*-mastigophores in species of *Scolanthus* remains controversial. The only species which undoubtedly has *b*-mastigophores in addition to basitrichs in its cnidom is *S. nidarosiensis* (Carlgren, 1942). Given that basitrichs can exhibit dense spines on the proximal tubule that may look like a rigid thickened shaft and, thus, be easily mistaken for a shaft of *b*-mastigophores (Cutress, 1955; Reft, 2012), the absence of *b*-mastigophores in other *Scolanthus* could be explained by difficulties involved in distinguishing undischarged capsules of these nematocysts. Similarly, *b*-mastigophores may exhibit a very gradual change between shaft and terminal tubule, even as small as 0.1 µm, or the gradual change can be completely absent (Östman, 1987, 2000; Cutress, 1955), in which case no clear distinction exists between basitrichs and *b*-mastigophores. The nematocyst seen in the filaments of *S. crypticus* sp. nov. (Figure 7F) exemplifies this predicament. Although we identify these nematocysts as basitrichs, the shape of the capsule and size and morphology of the proximal tubule resembles aphyllonemes of Reft (2012) which are only known from filaments of family Actiniidae Rafinesque, 1815. The size of undischarged capsules of aphyllonemes (32.8–36.6 × 2.5–3.6 µm; see Reft, 2012) coincides with the nematocysts in filaments of *S. crypticus* sp. nov., except the latter were generally wider (30.5–35.6 × 3.9–6.0 µm). This is the first time aphyllonemes are hypothesized to occur in superfamily Edwardsioidea, but nematocysts seen in filaments of *I. iemanjae* sp. nov. (Figure 3G), *Edwardsia juliae* and *Edwardsia olguini* (Figures 5O and 7M respectively: see Daly & Ljubenkov, 2008) and actinopharynx of *S. triangulus* are also possibly aphyllonemes (see Figure 11H: Daly & Ljubenkov, 2008).

Alternatively, the use of different nematocyst nomenclatures might explain the presence of *b*-mastigophores in the diagnosis of *Scolanthus* in studies that use Schmidt's (1969, 1972, 1974) nomenclature which does not distinguish basitrichs from *b*-mastigophores (e.g. Manuel, 1981a, 1981b; Daly, 2002; Daly & Ljubenkov, 2008). Given that all nominal species of *Scolanthus* have imperfectly known cnidom (England, 1987) and no pictures or drawings of the nematocysts are included in descriptions, we left *b*-mastigophores in the diagnosis of the genus as presented by Daly & Ljubenkov (2008), pending a proper revision of all species of the genus, including the type *S. callimorphus*.

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