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## A new species of *Diadumene* (Actiniaria: Diadumenidae) from the subtropical coast of Brazil

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### Abstract

*Diadumene paranaensis* n. sp., collected from the Yacht Club of Paranaguá (Paranaguá Bay, Paraná State, southern Brazil), is described as a new species of sea anemone, based on external and internal morphology, cnidome, and molecular data for 16S/CO3 mitochondrial DNA. This species is partially similar to *D. cincta* due to the presence of macrobasic p-amastigophores in the tentacles, but is distinguished by the cinclides arranged in longitudinal rows and microbasic p-amastigophores in the acontia.

**Key words:** Cnidaria, Anthozoa, taxonomy, sea anemone, cnidae, South Atlantic

### Introduction

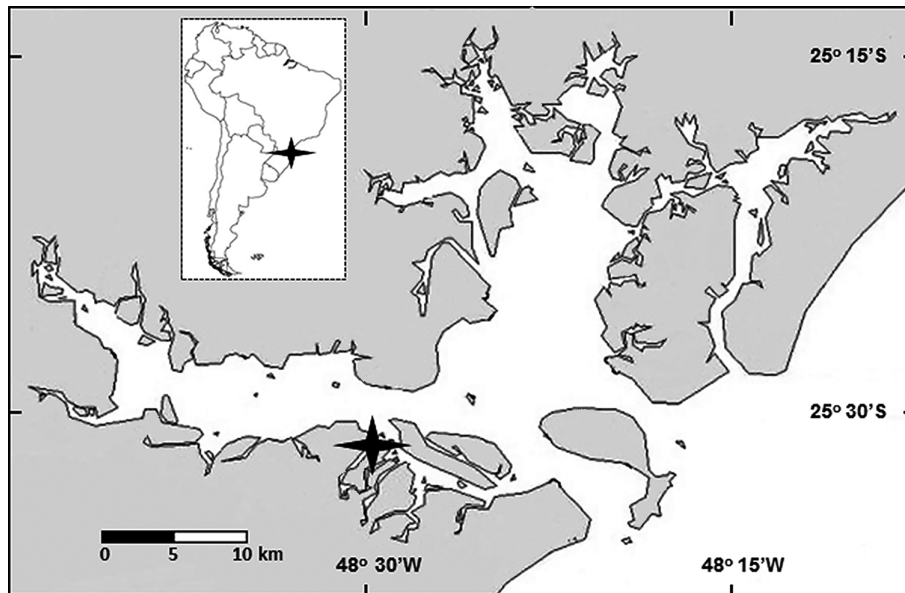
Sea anemones are among the most familiar invertebrates of rocky shores and sand beaches in some regions of the Brazilian coast (Corrêa 1964; Pires *et al.* 1992; Zamponi *et al.* 1998; Castro *et al.* 1999). There are records of 42 species in the country (Fautin 2013), but this number is a small fraction of the 1,100 known species in the world (Fautin 2013), especially in light of the extensive (8,000 km) coastline of Brazil. Most of the recorded species, such as *Bunodosoma caissarum* Corrêa in Belém, 1988 and *B. cangicum* Corrêa in Belém & Preslercravo, 1973, have large polyps and are quite conspicuous on rocky shores and in shallow waters (Belém & Preslercravo 1973; Belém 1988). Species with small polyps or that are found in cryptic environments (Corrêa 1973; Pires 1988; Pires *et al.* 1992; Excoffon *et al.* 1997; Silva *et al.* 2010) have been infrequently recorded, which may indicate that there are still many species to be recorded or described.

A species of the genus *Diadumene* Stephenson, 1920 has been recorded on the southwestern Atlantic coast of Brazil since 1977 (Belém & Monteiro 1977, as genus *Haliplanella* Hand, 1956). Some members of this genus form clusters of clonal polyps through asexual reproduction by longitudinal fission or pedal laceration (Chia 1976; Belém & Monteiro 1977; Shick 1991). Also, the genus has been recorded in various regions of the world and other areas of the southwestern Atlantic Ocean, as on the coast of Argentina (Excoffon *et al.* 2004, Molina *et al.* 2009). However, almost all of these records are of a single species, *Diadumene lineata* (Verrill, 1869) (= *Haliplanella lineata*), which is considered an introduced species in several parts of the world and often described as a ship fouling organism (Gollasch & Riemann-Zürneck 1996; Zabin *et al.* 2004).

Specimens of *Diadumene* have been found colonizing mussels, barnacles and artificial substrates in Paranaguá Bay. A population of *Diadumene*-like anemones was recorded by Correia & Loyola e Silva (1990) in the area but they did not attribute the specimens to a species. Here, we describe a species of *Diadumene* from Paranaguá Bay as *Diadumene paranaensis* n. sp. and compare it to the nine other known species of the genus.

## Material and methods

**Sampling.** Approximately 200 specimens were collected on five different dates between August 2009–2010, at the Yacht Club of Paranaguá in Paranaguá Bay ( $25^{\circ}30'53''\text{S}$ ,  $48^{\circ}29'58''\text{W}$ ) (Fig. 1). Clusters of mussels and barnacles with epizoid clonal sea anemones were removed from the concrete pilings of the wharf and transferred to aerated plastic containers. Anemones that were directly attached to the pilings were also collected by gently scraping them from the substratum. Photographs were taken *in vivo* and *in situ*. The specimens were transported to the laboratory, anesthetized with an 8%  $\text{MgCl}_2$  solution, preserved in 4% formaldehyde solution in seawater (FSW). Specimens used for molecular studies were directly preserved in 100% ethanol.



**FIGURE 1.** Map of Paranaguá Bay showing the study area (star). Inset map of South America indicates the location of Paraná state, southern Brazil.

**Morphological studies.** Whole, formalin-fixed specimens were examined externally. Some of these were prepared for histological sections and others were dissected for observation of internal structures. Histological sections ( $7\ \mu\text{m}$  thick) were made from 14 specimens collected on different dates. Slides were stained with haematoxylin/eosin and Mallory's triple stain (procedures modified from Pantin 1948). The distribution of the cnidae in different body parts was analyzed in eight specimens, using light microscopy (1000x magnification). Thirty non-discharged capsules of each type of cnida were chosen at random, measured, and photographed. Maximum, minimum, and mean values were calculated to determine the range of capsule sizes for each type of nematocyst. Cnida nomenclature is based on Östman (2000).

The morphology of the specimens was compared to the original descriptions of the nine valid species of *Diadumene* (according to Fautin 2013) and to additional references (Verrill 1898; Carlgren 1950; Parry 1952; Hand 1956; Manuel 1981) (Table 1). The recognition of the presence of catch-tentacles in some species is based on Stephenson (1935) and Williams (1975). The classification of Rodríguez *et al.* (2012) was followed. The material studied was deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP) in São Paulo, Brazil, and in the American Museum of Natural History (AMNH) in New York, USA. Other material examined included: *Diadumene cincta* (MNRJ 3326), *D. kameruniensis* (RMNH.COEL 19755, RMNH.COEL 32120), *D. leucolena* (RMNH.COEL 11472) and *D. lineata* (RMNH.COEL 23784).

**Procedures for molecular analysis.** Total DNA was obtained from samples of tentacles and columns. The kit for DNA extraction, PCR protocol to amplify the mitochondrial molecular markers (partial sequences of the ribosomal 16S gene -362 base pairs - and protein-coding CO3 gene - 381 base pairs), PCR product purification, BigDye® reaction and sequencing were based on the protocols outlined by Stampar *et al.* (2012, 2014). Sequences were assembled and edited (removing ambiguous base calls and primer sequences) using Geneious 5.4.4 (Drummond *et al.* 2011). New sequences were submitted to GenBank (Table 2). The sequences obtained were

compared to those [Daly et al. \(2008\)](#) and [Rodríguez et al. \(2012\)](#) generated for *D. cincta* and *D. luciae* (16S) and *D. cincta*, *D. lineata*, *D. leucolena* and *Diadumene* sp. (CO3), obtained from GenBank (Table 2). Molecular markers were aligned using MUSCLE with default parameters ([Edgar 2004](#)), and Kimura's two-parameter model of base substitution was used to calculate genetic distances using MEGA5 ([Tamura et al. 2011](#)).

**TABLE 1.** Morphological features of species of *Diadumene*, based on the following descriptions: *D. schilleriana* from Stoliczka (1869) and Annandale (1907, 1915); *D. neozelanica* from Carlgren (1924) and Parry (1952); *D. crocata* from Parry (1952); *D. kameruniensis* from Carlgren (1927); *D. cincta* from Stephenson (1925, 1935), Carlgren (1940) and Manuel (1981); *D. leucolena* from Hand (1956) and Carlgren (1950); *D. franciscana* from Hand (1956); *D. lighti* from Hand (1956); *D. lineata* from Verrill (1898), Hand (1956) and Manuel (1981). *Diadumene crocata* is not included in the table, as the description by Hutton (1880) does not include any of the listed characters.

	<i>D. schilleriana</i>	<i>D. neozelanica</i>	<i>D. kameruniensis</i>	<i>D. cincta</i>	<i>D. leucolena</i>	<i>D. franciscana</i>	<i>D. lighti</i>	<i>D. lineata</i>	<i>D. paranaensis</i>
<b>SCAPUS</b>									
<b>Cinclides</b>									
Scattered	X	X		X	X		X	X	
Longitudinal rows		X	X		X				X
Band near top of scapus						X			
Conspicuous			X	X	X			X	
Inconspicuous		X				X	X		X
Numerous		X		X	X				
Slightly elevated			X		X				
Endocoelic			X	X	X	X	X		X
Exocoelic					X		X		
<b>Aggregations of nematocysts</b>									
<b>PRESENCE OF CATCH-TENTACLES</b>		X	X	X	X				X
<b>CNIDOME</b>									
<b>Tentacles</b>									
Spirocysts				X	X	X	X	X	X
Atrich				X	X				X
Holotrich				X	X				X
Basitrich				X	X	X	X	X	X
Microbasic p-mastigophore				X		X	X	X	X
Microbasic p-amastigophore				X	X	X		X	
Macrobasic p-amastigophore				X			X		X
<b>Acontia</b>									
Basitrich				X	X	X	X	X	X
Microbasic p-mastigophore				X	X	X	X	X	X
Microbasic p-amastigophore								X	X

**TABLE 2.** Species and samples used for comparison of 16S mitochondrial DNA. Sequences downloaded from GenBank.

Species	16S	CO3	Reference
<i>Diadumene cincta</i>	EU190769.1	FJ489490	Daly <i>et al.</i> 2008; Rodríguez <i>et al.</i> 2012
<i>Diadumene lineata</i>	EU190774.1	FJ489506	Daly <i>et al.</i> 2008; Rodríguez <i>et al.</i> 2012
<i>Diadumene leucolena</i>	-	JF833006	Rodríguez <i>et al.</i> 2012
<i>Diadumene</i> sp.	-	JF833005	Rodríguez <i>et al.</i> 2012
<i>Diadumene paranaensis</i>	KT353112	KT353113	This study

## Results

### Class Anthozoa Ehrenberg, 1834

#### Subclass Hexacorallia Haeckel, 1866

#### Order Actiniaria Hertwig, 1882

#### Suborder Nynantheae Carlgren, 1899

#### Infraorder Thenaria Carlgren, 1899

#### Superfamily Metridioidea Carlgren, 1893

#### Family Diadumenidae Stephenson, 1920

#### Genus *Diadumene* Stephenson, 1920

#### *Diadumene paranaensis* n. sp.

(Figures 2–4)

**Type material.** *Holotype specimen:* MZUSP 1530, polyp without reproductive tissue, 6 mm height, 3 mm width, collected 25 October 2010, at the Yacht Club of Paranaguá, Paranaguá Bay, on mussel, depth of 1–2 m, salinity 26 psu, temperature 20° C. Preserved in 4% FSW.

*Paratype specimens:* MZUSP 1531, one specimen without reproductive tissue, same data as holotype. MZUSP 1532, six specimens without reproductive tissue, same data as holotype. MZUSP 1534, three specimens without reproductive tissue, collected 23 October 2009, preserved two days after collection in 4% FSW.

*Additional specimens:* MZUSP 1533, one specimen without reproductive tissue, collected 21 August 2009, preserved two days after collection in 4% FSW. MZUSP 1535, three specimens without reproductive tissue, collected 23 October 2009, preserved two days after collection in 100% ethanol. MZUSP 1536, three specimens without reproductive tissue, collected 22 February 2010, preserved two days after collection in 4% FSW. MZUSP 1537, six specimens without reproductive tissue, collected 23 August 2010, preserved two days after collection in 4% FSW. MZUSP 1909, transverse histological sections of specimen collected 23 October 2009. MZUSP 1910, longitudinal histological sections of specimen collected 23 October 2009. MZUSP 1911, transverse histological sections of specimen collected 22 February 2010. MZUSP 1912, longitudinal histological sections of specimen collected 22 February 2010. MZUSP 1913, transverse histological sections of specimen collected 24 May 2010. MZUSP 1914, longitudinal histological sections of specimen collected 24 May 2010. AMNH 6121, six specimens without reproductive tissue, collected 24 May 2010, preserved one week after collection in 4% FSW. AMNH 6122, seven specimens without reproductive tissue, collected 24 May 2010, preserved one week after collection in 4% FSW. AMNH 6123, eleven specimens without reproductive tissue, collected 21 August 2010, preserved three days after collection in 4% FSW. AMNH 6124, eleven specimens without reproductive tissue, collected 21 August

2010, preserved three days after collection in 4% FSW. AMNH 6125, longitudinal histological sections of specimen collected 22 February 2010. AMNH 6126, longitudinal histological sections of specimen collected 21 August 2010. AMNH 6127, transverse histological sections of specimen collected 24 May 2010. AMNH 6128, transverse histological sections of specimen collected 21 August 2010.

**TABLE 3.** Size and distribution of cnidae of *Diadumene paranaensis* n. sp. Measurements in micrometers ( $\mu\text{m}$ ), expressed as range of minimum and maximum values, mean size and standard deviation. L/W = mean ratio of length and width of the capsules measured; N = number of capsules measured; P = specimens that showed a particular type of cnida/specimens analyzed; F = frequency of each type of cnida (+++ = very common; ++ = common; + = not common).

Tissue / Type of cnida	Range of length x width	Mean $\pm$ SD	L/W	N	P	F
<b>Tentacles</b>						
Spirocyst	10.28–17.85 x 2.65–4.72	14.54 $\pm$ 2.89 x 3.28 $\pm$ 1.01	4.52	50	2/8	+++
Atrich	25.8–34.2 x 7.2–11.4	31.02 $\pm$ 2.14 x 9.94 $\pm$ 1.09	3.22	30	1/8	++
Holotrich	21.6–27.6 x 4.8–7.2	25.34 $\pm$ 2.01 x 6.16 $\pm$ 0.76	4.28	40	2/8	++
Basitrich	7.2–21.2 x 1.2–3.6	14.03 $\pm$ 2.72 x 2.33 $\pm$ 0.44	6.21	80	8/8	+++
Microbasic p-amastigophore	19.8–26.4 x 3.6–6.0	22.75 $\pm$ 1.58 x 4.68 $\pm$ 0.58	4.94	60	8/8	+++
Macrobasic p-amastigophore	36.0–46.2 x 6.0–8.4	41.01 $\pm$ 2.46 x 7.29 $\pm$ 0.66	5.68	40	8/8	++
<b>Pharynx</b>						
Basitrich	16.8–21.28 x 1.2–3.7	19.67 $\pm$ 1.07 x 2.67 $\pm$ 0.71	8.04	30	5/5	+
Microbasic p-amastigophore	15–22.8 x 3–4.2	17.84 $\pm$ 1.65 x 3.64 $\pm$ 0.35	4.94	39	5/5	++
<b>Capitulum</b>						
Basitrich	9.6–13.5 x 1.2–2.4	10.85 $\pm$ 1.38 x 2.04 $\pm$ 0.53	5.63	26	5/5	+
Microbasic p-amastigophore	15.1–23.4 x 2.4–4.8	17.8 $\pm$ 2.04 x 3.60 $\pm$ 0.74	5.11	18	5/5	+
<b>Scapus</b>						
Basitrich	15.2–20.7 x 2.4–4.2	18.14 $\pm$ 1.22 x 3.04 $\pm$ 0.34	6.03	59	5/5	++
Microbasic p-amastigophore	9.9–15.6 x 3.0–4.8	12.78 $\pm$ 1.65 x 4.05 $\pm$ 0.53	3.23	14	5/5	+
<b>Filament</b>						
Basitrich	10.8–19.2 x 1.2–3.0	15.50 $\pm$ 2.19 x 1.86 $\pm$ 0.51	8.10	39	6/6	+++
Microbasic p-amastigophore	39.0–51.6 x 6.0–8.4	46.46 $\pm$ 1.28 x 7.07 $\pm$ 0.51	6.63	37	6/6	++
Microbasic p-amastigophore	7.2–12.9 x 2.8–4.8	11.20 $\pm$ 2.09 x 4.06 $\pm$ 0.78	2.81	62	6/6	++
Microbasic p-amastigophore	12.0–22.8 x 3.0–4.8	16.16 $\pm$ 2.33 x 3.77 $\pm$ 0.43	4.34	40	6/6	++
<b>Acontia</b>						
Basitrich	10.2–19.2 x 1.2–3.6	15.50 $\pm$ 2.01 x 1.96 $\pm$ 0.52	8.35	71	8/8	+++
Microbasic p-amastigophore	35.9–57.5 x 5.1–7.4	43.61 $\pm$ 4.17 x 6.07 $\pm$ 0.64	7.17	60	8/8	++
Microbasic p-mastigophore	41.1–57.0 x 5.4–8.4	46.59 $\pm$ 3.34 x 6.56 $\pm$ 0.78	7.31	85	8/8	+
Microbasic p-mastigophore	19.2–26.4 x 3.0–6.0	22.42 $\pm$ 2.71 x 4.42 $\pm$ 0.82	5.21	18	2/8	+

*Comparative material:* *Diadumene cincta* MNRJ 3326, 8 specimens, collected 21 November 1981, Ouwkerk, Province of Zeeland, The Netherlands, preserved in formaldehyde solution, leg. det. M.S.S. Lavayele. *Diadumene kameruniensis* RMNH.COEL 19755, 2 specimens, collection date unknown, Nigeria, Port Harcourt, preserved in formaldehyde solution. *Diadumene kameruniensis* RMNH.COEL 32120, data unknown, preserved in ethanol, det. Carlgren. *Diadumene leucolena* RMNH.COEL 11472, 3 specimens, collected 20 August 1973, Curaçao, Spaanse water, leg. det. J.C. den Hartog. *Diadumene lineata* RMNH.COEL 23784, 7 specimens, collected 13 October 1990, Veerse Meer, The Netherlands, preserved in formaldehyde solution, leg. M. Faase, det. J.C. den Hartog (1995).

**Type locality.** Yacht Club of Paranaguá, Paranaguá Bay, Paraná state, southern Brazil (25°30'53"S, 48°29'58"W).

**Etymology.** The specific name *paranaensis* refers to the state of Paraná, in Brazil, the type locality of the species.

**Diagnosis.** Clonal species of *Diadumene*; polyp with cinclides arranged in longitudinal rows, macrobasic p-amastigophores in the tentacles, and microbasic p-amastigophores in the acontia.



**FIGURE 2.** *Diadumene paranaensis* n. sp. *in vivo*. A: Expanded specimen, typical color of the species. B: Contracted specimens, showing color variation. C: Recently collected live specimen; arrow indicates ribbed lips. D: Column of a live specimen, highlighting the caputulum and scapus (indicated by dashed line); arrows indicate longitudinal rows of cinclides. E: Recently collected live specimen; arrow indicates catch tentacle. F: Living specimen kept in laboratory for one week with expanded catch tentacle. Scale: 5 mm.

### Description.

#### *External morphology* (Fig. 2)

Base: adherent, flat, usually circular in outline, but sometimes irregular; can be very elongated and irregular before longitudinal fission, to 4 times column width; color light orange or pale brown, lighter than column (Fig. 2A). Diameter of base of live specimen 0.1–1.5 mm; of preserved specimens, 0.1–1.3 mm.

Column: smooth, long, cylindrical when expanded; scapus and caputulum separated by collar that disappears in full extension; caputulum 1/4 to 1/3 as long as scapus. In contraction, caputulum retracts completely into scapus.

Column usually green or brownish in natural environment, but can be light orange, lighter aborally; after 1 wk in laboratory, light orange or pinkish (Fig. 2B and C). Cinclides in 4 to 6 longitudinal rows from collar to limbus, inconspicuous, not numerous, up to 6 per row (observed in 8 specimens) (Fig. 2D). Capitulum transparent to translucent, color lighter than scapus; actinopharynx visible through capitulum, mesenteric insertions visible as white lines. Diameter of column of live specimens 1–11 mm, of preserved specimens 1–10 mm; length of live specimens 5–20 mm, of preserved specimens 4–19 mm.

Oral disc: circular, wider than column when expanded, at least 1/2 of area without tentacles; mouth elongated; lips elevated and heavily ribbed (Fig. 2C). Oral disc brown to orange with white markings at base of tentacles; bright white markings seen on directive endocoels; region around lips usually darker; lips pale brown; after 1 wk in laboratory oral disc becomes light orange and the mesenteric insertions are visible. Diameter of oral disc of live specimens 0.1–1.0 mm, of preserved specimens 0.1–0.9 mm.

Tentacles: long (up to 0.8 cm), smooth, slender, tapered when extended, usually retractile, no apical pore; 48–80 arranged in 3–6 cycles; bifurcated tentacles occasionally present; coloration brown or green with white markings, becoming translucent to transparent after some time in laboratory. First and second cycles usually with 6 tentacles, other cycles are irregular; tentacles of inner cycles longer, tentacles of outer cycles poorly developed, small, and of varied lengths. Catch-tentacles may be present in first cycle, white, up to 1.5 cm long (Fig. 2E and F).

*Internal anatomy* (Fig. 3). Actinopharynx: ribbed and short, 1/3 to 1/2 of expanded column; same color or lighter than lips; tissue thick and ciliated (Fig. 3A). Two siphonoglyphs present, sometimes one (Fig. 3B).

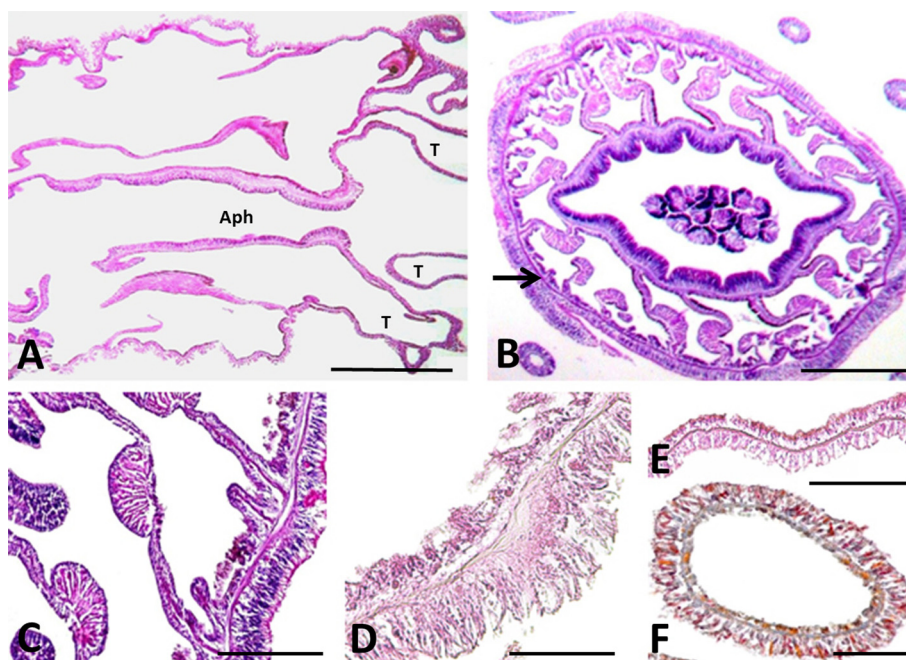
Mesenteries: in two or three cycles ( $6+6+12=24$  pairs); mesenteries of first cycle perfect (two pairs are directives). Third cycle may be present (Fig. 3B). Mesenteric filaments on mesenteries of first and second order.

Reproductive tissue: absent.

Acontia: well developed and numerous; on mesenteries of first and second cycles.

Retractors: well developed, diffuse, on mesenteries of first and second cycles (Fig. 3C).

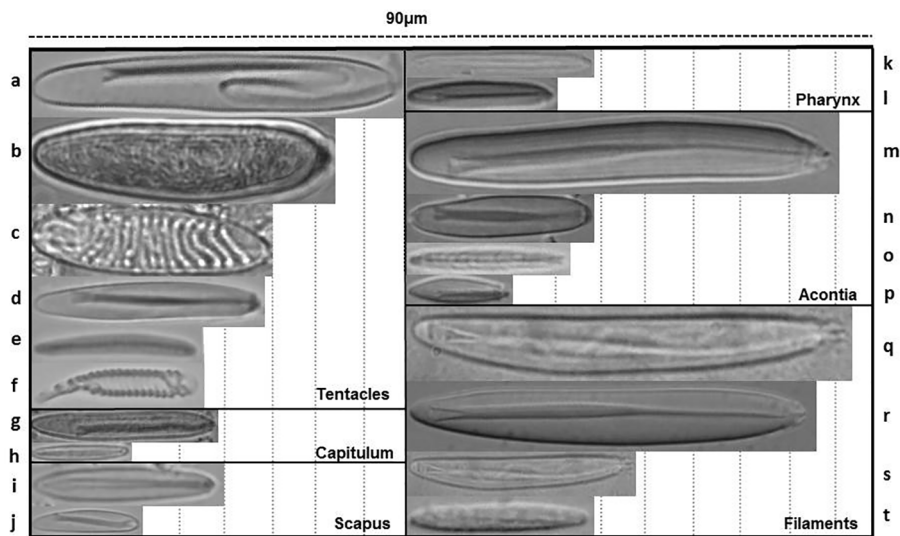
Muscles: parietobasilar (Fig. 3C) and basilar muscles (Fig. 3D) weakly developed. Marginal sphincter absent (Fig. 3E); no ectodermal musculature in tentacles (Fig. 3F).



**FIGURE 3.** Histological sections of *Diadumene paranaensis* n. sp. A: Longitudinal section (oral region to the right). Scale: 2 mm. B: Transverse section of the actinopharynx region; specimen with two cycles of imperfect mesenteries; arrow indicates imperfect mesenteries of the third cycle. Scale: 2 mm. C: Transverse section of the actinopharynx region; detail of the retractor and parietobasilar muscles. Scale: 0.3 mm. D: Basilar muscle in a longitudinal section. Scale: 0.2 mm. E: Detail of sphincter in a longitudinal section. Scale: 0.2 mm. F: Transverse section of a tentacle. Scale: 0.05 mm. Aph – actinopharynx; T – tentacles.

Cnidae: spirocysts, basitrichs, microbasic amastigophores, microbasic p-mastigophores, microbasic p-amastigophores, macrobasic p-amastigophores. Atrichs and holotrichs present in catch-tentacles (for measurements see Table 3) (Fig. 4).

*Molecular data.* The comparison of the partial 16S mitochondrial rDNA sequence of the species from Paranaguá Bay with the two existing sequences of members of the genus showed that the Brazilian species is more similar to *D. cincta* than to *D. lineata*. The K2P distance of the species from Paranaguá Bay is 0.02 from *D. lineata* and 0.003 from *D. cincta*. The topology of the alignment was directly assessed (Sinniger *et al.* 2008), and the following pattern was observed: the sequence of *D. cincta* in comparison with *D. paranaensis n. sp.* has 356 congruencies and only 1 transition; the sequence of *D. lineata* in comparison with *D. paranaensis n. sp.* has 349 congruencies, 3 transitions and 4 transversions; and the sequence of *D. lineata* in comparison with *D. cincta* has 351 congruencies, 3 transitions and 3 transversions. The CO3 mitochondrial rDNA sequence from *Diadumene paranaensis n. sp.* was compared to four different specimens from the same genus, obtained from GenBank. In this case, the nucleotide variation (K2P distance) was much higher, with 0.069 from *D. leucolea*, 0.051 from *D. lineata*, 0.051 from *D. cincta* and 0.018 from *Diadumene sp.* (an unidentified species from Rodríguez *et al.* 2012)(Table 4).



**FIGURE 4.** Representative undischarged cnidae of *Diadumene paranaensis n. sp.* from each region of the body. Dashed line along upper edge is the scale. Letters on left and right sides refer to the different types of cnidae, as follows: a = Macrobasic p-amastigophore; b = Atrich; c = Holotrich; d, g, j, k, m, n, o, r = Microbasic p-amastigophore; e, h, i, l, p, t = Basitrich; f = Spirocyst; q, s = Microbasic p-mastigophore. Difference between atrichs and holotrichs is based on England (1991).

**TABLE 4.** K2P distances between *Diadumene* species sampled for this study, considering molecular markers CO3 and 16S. The upper part of the table refers to CO3 and the lower part to 16S; distances considering *D. paranaensis* in bold; - indicates there is no data for the comparison.

	<i>D. paranaensis</i>	<i>D. cincta</i>	<i>D. lineata</i>	<i>D. leucolea</i>	<i>Diadumene sp</i>
<i>D. paranaensis</i>		<b>0.051</b>	<b>0.051</b>	<b>0.069</b>	<b>0.018</b>
<i>D. cincta</i>	<b>0.003</b>		0.065	0.065	0.037
<i>D. lineata</i>	<b>0.020</b>	0.017		0.052	0.051
<i>D. leucolea</i>	-	-	-		0.060
<i>Diadumene sp</i>	-	-	-	-	

## Discussion

The absence of reproductive tissue from all anemones collected suggests that the specimens of this new species were all clone mates. We collected specimens from different points in the Yacht Club, on varied substrates and across all seasons. Islands and piers surrounding the location were also searched, but no other sea anemone of the genus was found. Despite its possible clonal condition, *Diadumene paranaensis n. sp.* has a unique combination of features that is not observed in other species of the genus (Table 1).



**Morphological data.** The genus *Diadumene* was proposed by Stephenson (1920) to accommodate the species described by Stolickza (1869) (originally *Sagartia schilleriana*). Members of this genus possess, among other characteristics, the following distinguishing features: smooth column divisible into scapus and capitulum, separated by collar, the lack of a marginal sphincter, and the presence of basitrichs and microbasic p-mastigophores in the acontia (Stephenson, 1920; Fautin *et al.* 2008). Because *Diadumene lineata* is considered to be a member of the genus (Williams 1980), its diagnosis must also include the presence of microbasic amastigophores in the acontia.

**TABLE 5.** Size and distribution of cnidae of *Diadumene cincta* (MNRJ 3326). Measurements in micrometers ( $\mu\text{m}$ ), expressed as range of minimum and maximum values, mean size in parentheses. L/W = mean ratio of length and width of the capsules measured; N = number of capsules measured; P = number of specimens examined for this type of cnida; F = frequency of each type of cnida (+ + + = very common; + + = common).

Tissue / Type of cnida	Range of length x width	Mean $\pm$ SD	L/W	N	P	F
<b>Tentacle</b>						
Spirocyst	13.17–16.97 x 2.43–3.72	14.67 $\pm$ 2.02 x 3.31 $\pm$ 0.73	4.53	5	2	+ + +
Basitrich	ruptured				2	+ + +
Microbasic p-amastigophore	24.99–27.37 x 3.94–4.35	26.29 $\pm$ 1.89 x 4.13 $\pm$ 0.98	6.39	4	2	+ + +
Macrobasic p-amastigophore	45.12–51.35 x 7.92–9.46	48.40 $\pm$ 2.32 x 8.92 $\pm$ 1.01	5.44	5	2	+ +
<b>Acontia</b>						
Basitrich	11.53–17.62 x 0.76–2.76	15.28 $\pm$ 1.75 x 1.84 $\pm$ 0.99	8.77	30	1	+ + +
Microbasic p-mastigophore	45.91–58.48 x 5.76–7.43	50.16 $\pm$ 2.76 x 6.49 $\pm$ 1.21	7.78	30	1	+ +

The recognition of *Diadumene paranaensis* n. sp. was based on external and internal morphology, muscle elements, and cnidae composition (Table 1). The other nine presently recognized species of *Diadumene* are very similar in shape, and some problems were found while comparing the species' descriptions. Some of them were based exclusively on preserved specimens (*D. kameruniensis* and *D. neozelanica*) (Carlgren 1924; 1927), which prevented an accurate description of some features in detail. Moreover, some species' color patterns were not considered since they vary among populations and even within populations (*e.g.* *D. lineata* and *D. leucolena*) (Hand 1956). Specimens of *D. paranaensis* n. sp. maintained in the laboratory were fed with *Artemia* nauplii, which probably explains the polyps' light orange or pinkish coloration after a few days. However, it is important to acknowledge that some polyps were already light orange or pink when collected.

The absence of information about internal anatomy in the description of *D. crocata* (Parry 1952) prevented it from being completely included in the comparison with other species. Last, the irregularity in the anatomy of polyps (number of tentacles, mesenteries, etc.) due to asexual reproduction or to differences in size or age is not uncommon (Hyman 1940) and has been mentioned by some authors for species of *Diadumene* (*e.g.* Dunn 1982).

The characters of the material from RMNH.COEL were consistent with their descriptions, although it was not possible to observe the delicate cinclides in the preserved specimens. Only in preserved specimens of *D. kameruniensis* were we able to identify cinclides in longitudinal rows. Based on the available published descriptions, as well as on the comparison of the museum specimen (MNRJ 3326), *D. cincta* and *Diadumene paranaensis* n. sp. have similar morphologies. However, a key morphological character that distinguishes them is the arrangement of the cinclides on the scapus, since those of *Diadumene paranaensis* n. sp. are arranged in longitudinal rows, while the cinclides of *D. cincta* are scattered (Stephenson 1925, 1935; Manuel 1981). According to the literature, *D. leucolena*, *D. kameruniensis*, and *D. neozelanica* are the only other species of this genus with cinclides in longitudinal rows (Parry 1952; Hand 1956).

**Cnidome.** Many species of sea anemones with acontia have been defined using the cnidome as a distinguishing character, and indeed we chose to do so here, focusing on the types of nematocysts found in each species rather than on cnidae sizes. Although we acknowledge that some authors have suggested that this is not always particularly informative (Fautin 1988; Acuña *et al.* 2003; Francis 2004), the simplicity of the *Diadumene* polyp makes it important to use all information we can to compare it to other species. The cnidae of most regions of

the polyps of *D. cincta* (MNRJ 3326) were poorly preserved, but it was possible to identify and measure a sufficient number of the non-discharged cnidae of the tentacles. In contrast, the nematocysts on the acontia were well preserved and could be measured (Table 5). The nematocysts of *Diadumene paranaensis* **n. sp.** were generally similar in type and size to those of the Dutch specimens of *D. cincta*, but *D. cincta* has no microbasic p-amastigophores in the acontia. Cnidae from the tentacles and acontia of all RMNH.COEL specimens were identified but not measured, and the types of nematocysts were consistent with the species descriptions.

The cnidome of *Diadumene paranaensis* **n. sp.** has features in common with those of *D. cincta*, *D. lighti*, and *D. lineata*. The first two of these species share macrobasic p-amastigophores in the tentacles (Carlgrén 1940; Hand 1956). We did not examine deposited material or molecular sequences of *D. lighti*, which prevented us from making further comparisons concerning this species. The feature shared with *D. lineata* is the presence of microbasic p-amastigophores in the acontia, in addition to basitrichs and microbasic p-mastigophores (Hand 1956), which are common to all the species of *Diadumene* (Rodríguez *et al.* 2009). However, in *Diadumene paranaensis* **n. sp.**, two size classes of microbasic p-mastigophore were recognized, whereas *D. lineata* has only one size of this type of cnida (Hand 1956). Hence, our species has no exclusive character, but rather a group of features that are not seen in combination in any other species of the genus *Diadumene*.

The presence of catch-tentacles relates *Diadumene paranaensis* **n. sp.** to *D. cincta*, *D. leucolena*, *D. lineata*, *D. kameruniensis*, *D. neozelancia* and *D. schilleriana*; however, this character should not be considered diagnostic, due to its ephemerality (Hand 1956). Atrichs and holotrichs were not observed in most of the specimens from Paranaguá Bay, although many of them have tentacles with a blunt appearance, which is assumed to be the primordium of a catch-tentacle (Hand 1956).

**Molecular data.** The definition of a sea anemone species based exclusively on morphological features can be a difficult task, especially among the anemones possessing acontia (Rodríguez *et al.* 2012), so supporting molecular information can be extremely valuable (Gusmão & Daly 2010; Gomes *et al.* 2011). The information obtained on the 16S and, especially, CO3 sequences demonstrated that *Diadumene paranaensis* **n. sp.** present an important molecular variability from the previously described species of the genus. On the other hand, it is already widely known that the genetic distance for mitochondrial markers between species of the same genus within Anthozoa is a doubtful taxonomic tool (Shearer *et al.* 2002; Dohna & Kochzius 2015), except for Ceriantharia, which is claimed to be a separate evolutionary clade from Hexacorallia and Octocorallia (Stampar *et al.* 2014). Sinniger *et al.* (2008) suggested that it is possible to use the alignment to compare species or groups of species. However, molecular data have not been sufficient to define the species, and the absence of nuclear gene information and associated markers in particular continues to be a major obstacle (Dohna & Kochzius 2015). A more exploratory analysis is required in this family as a whole, taking into account nuclear genomic data to understand how molecular diversity should be properly related to species delimitation in this group, and especially in the Hexacorallia clade (Stampar *et al.* 2014).

**Biological and biogeographic considerations.** Recent surveys and experiments were carried out in the Yacht Club of Paranaguá, and although several introduced species were recorded, *D. cincta* and *D. lineata* were not found (Cangussu *et al.* 2010). We cannot affirm that the specimens recorded by Correia & Loyola e Silva (1990) are of *Diadumene paranaensis* **n. sp.**, as we have not found the material collected at the time. The abundance of anemones currently observed may be explained by the population's ability to maintain a high rate of asexual reproduction in spite of the adverse abiotic factors found in the estuary. Additionally, some laboratory studies have shown that the species tolerates variations in several abiotic factors, including temperature, salinity and desiccation (pers. observ.). This may indicate that these anemones are a potentially invasive species.

Most species of the genus *Diadumene* have a limited known distribution (Fautin 2013), although *D. lineata* is widely distributed and is considered to be highly invasive, as well as being the only species of the genus that has been reported previously in Brazil (Belém & Monteiro 1977; Zamponi *et al.* 1998; Farrapeira *et al.* 2007). In this study, we determined that *Diadumene paranaensis* **n. sp.** is highly similar to *D. cincta*. This latter species has apparently never been found on the Brazilian coast, and its range of distribution is limited to the northeastern Atlantic Ocean and to European seas (Fautin 2013).

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