



ANIMAL SCIENCE

New insights on the taxonomy of *Diadumene paranaensis* (Cnidaria: Actiniaria) associated with mangrove roots in the Brazilian semi-arid coast

YAGO A. DE MELO, MAYANE R. DE ARAÚJO, RAFAELA C. MAIA & PAULA B. GOMES

Abstract: A dense estuarine aggregation of *Diadumene paranaensis* Beneti, Stampar, Maronna, Morandini & Da Silveira, 2015 associated with *Rhizophora mangle* L. was found at the Arpoeiras Beach, mouth of Acaraú River, Ceará, Brazilian semi-arid coast. Here, we compare biological and taxonomical traits with the type material, collected from the portuary zone of Paranaguá Bay, and propose modifications in the diagnosis of the species, as well as of the family Diadumenidae and genus *Diadumene*, to align with the description of our specimens. In addition, we discuss its tolerance to high salinity and predict a much broader geographic range for this sea anemone in Brazil.

Key words: *Diadumene*, estuary, nematocyst, new occurrence, Northeast Brazil, sea anemone.

INTRODUCTION

Sea anemones are among the most well distributed anthozoans in the world (Daly et al. 2008, Rodríguez et al. 2014), successfully colonizing different types of substrates (e.g. rocky reefs, sand, mud or gravel bottoms) (Raghunathan et al. 2014, González-Muñoz et al. 2016), but also associated with living organisms such as scleractinian corals, sponges, crustaceans, mollusks, fishes, and even sea turtles, freshwater crocodiles and whale carcasses (Caine 1986, Frick et al. 2000, Randall & Fautin 2002, Patzner 2004, Mercier et al. 2011, González-Muñoz et al. 2012, Charruau & González-Muñoz 2016). Species belonging to the genus *Diadumene* Stephenson, 1920 are readily known for presenting high tolerance of abiotic stressors fluctuation (e.g., salinity, temperature, pH), being able to access practically all types of human-made structures (Gollasch & Riemann-Zürneck 1996, Podbielski et al. 2016, Glon et

al. 2020). Although less common, associations with mangrove and seagrass have also been registered for *Diadumene lineata* (Verrill, 1869) (Molina et al. 2009), *Diadumene leucolena* (Verrill, 1866) (Allee 1923, Olsen et al. 2013), and *Diadumene schilleriana* (Stoliczka, 1869) (Mitra & Pattanayak 2013, Mitra et al. 2019) in the USA, Argentina and India.

The ability to tolerate harsh environmental conditions exhibited by the genus *Diadumene* can be explained by a series of biological and ecological strategies displayed by many diadumenid species (Glon et al. 2020). Densely nematocyst-charged structures called acontia, and aggressive catch-tentacles for agonistic purposes, as well as being capable of different asexual propagation tactics, such as pedal laceration and longitudinal fission, may imply rapidly establishing populations under optimal conditions (Uchida 1932, Chia 1976, Minasian & Mariscal 1979, Ryan & Kubota 2016). In addition,

some individuals can be transported overseas by ships and minor vessels, increasing the distribution range of the species (Shick & Lamb 1977, Zabin et al. 2004, Glon et al. 2020).

From the 12 valid species within the genus, 4 can be found along the South American Atlantic coast: *Diadumene lineata*, *Diadumene paranaensis* Beneti, Stampar, Maronna, Morandini & Da Silveira, 2015, *Diadumene leucolena* and *Diadumene manezinha* Gusmão, Grajales & Rodríguez, 2018. *Diadumene paranaensis* was originally described from the portuary area of Paranaguá Bay, Brazil. Depth, salinity and water temperature were reported for the holotype, detached from a mussel, 1-2 meters deep, salinity of 26 psu at 20°C. Other individuals were found on mussels, oysters, and concrete pilings in a wharf sector. Despite the collection of numerous individuals, it has been hypothesized that it is a species not native to Brazil, since only individuals with no gametogenic tissue, most probably clones, were observed (Beneti et al. 2015, Glon et al. 2020). Later to its original description, *D. paranaensis* was shortly mentioned to occur in California, USA, on artificial structures (Glon et al. 2020)

Similarly, small anemones were observed in an estuarine zone, at Ceará State, Northeast Brazil, attached to mangrove roots. Here, we identify *D. paranaensis*, for the first time outside a direct portuary zone, as a more broad-ranged and salinity tolerant diadumenid than known, and discuss some taxonomic aspects related to morphological variation of fighting tentacles, and nematocyst terminology. Therefore, we suggest that since it appears to have a broader distribution, and because of its wide tolerance to changes in salinity, this species could be widely dispersed.

MATERIALS AND METHODS

Sampling

Individuals of *D. paranaensis* were collected on March, 2018, from an estuarine mangrove forest, at the Acaraú river mouth, Ceará state, Brazil (02°48'55" S, 40°12'14" W) (Figure 1). The sea anemones were found on clusters of mussels and oysters, or directly attached to *Rhizophora mangle* L. prop roots in the mesolitoral and infralitoral zones. Photographs *in situ* were taken to better capture the coloration and spatial distribution of specimens when alive. Specimens were then removed, transported to the Laboratório de Ecologia de Manguezais (ECOMANGUE/IFCE) and preserved in a saltwater solution of 10% formaldehyde.

Morphological analysis

Specimens were observed externally for size, number and organization of structures such as tentacles and cinclides. Lately, they were dissected in order to analyze internal structures and fertility in the Laboratório de Ecologia e Conservação de Ecossistemas Marinhos (LECEM-UFRPE). Cross sections of the the column, 7 mm thick, were performed, embedded in parafin and stained with Hematoxylin/Eosin. For the cnidome, 30 capsules of each type of cnidae were photographed and measured from each relevant taxonomic structure with the aid of an optic microscope with 1000x magnification. These data were plotted in a size and frequency table, including the maximum, minimum length and width, as well as the mean and standard deviation values.

The study of Beneti et al. (2015) was consulted for taxonomic comparison. Diagnosis of *D. paranaensis* was reviewed based on Beneti et al. (2015) and Gusmão et al. (2018). Systematic classification follows Rodríguez et al. (2014). Nomenclature of the cnidae is discussed according Gusmão et al. (2018). Vouchers were

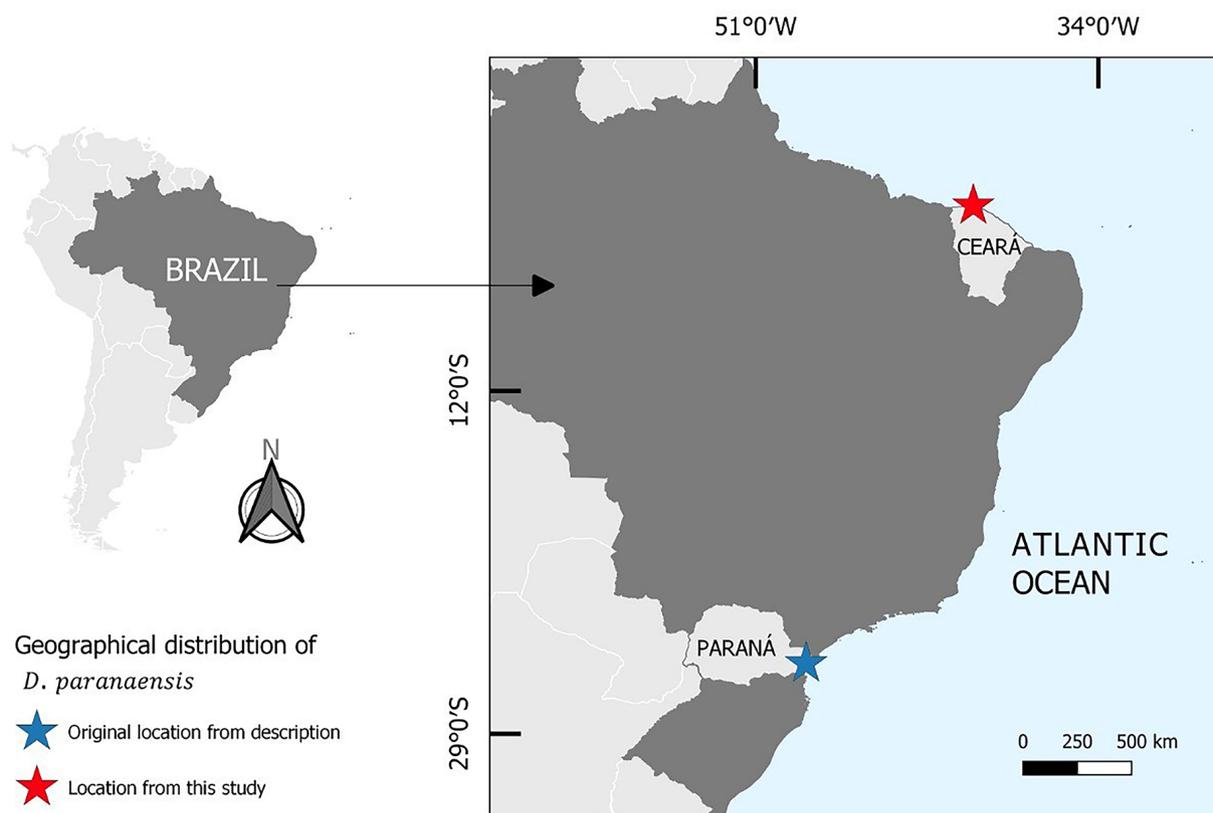


Figure 1. Geographical distribution of *D. paranaensis*, known from its type location, in Paraná state (blue star) and from the sampling location of this study (red star), in Ceará state, Brazil.

deposited in the Museu de Zoologia de São Paulo (MZUSP) and in the cnidarian collection of the Laboratório de Ecologia e Conservação de Ecossistemas Marinhos (LECEM-UFRPE).

RESULTS

Taxonomic identification

Superfamily Metridioidea Carlgren, 1893

Family Diadumenidae Stephenson, 1920

Diagnosis (modified from Gusmão, Grajales & Rodríguez, 2018; changes in bold):

Metridioidean with acontia with basitrichs and *p*-mastigophores B2a or basitrichs, *p*-mastigophores B1, and *p*-mastigophores B2a. No distinct marginal sphincter. **Tentacles of any cycle** may form fighting tentacles with holotrichs; these tentacles are ephemeral

and may be totally absent in some species or population of species that possess them.

Genus *Diadumene* Stephenson, 1920

Diagnosis (modified from Gusmão, Grajales & Rodríguez, 2018; changes in bold):

Diadumenidae with well-developed pedal disc. Column smooth, divisible into scapus and capitulum separated by a collar. Scapus with cinclides scattered or arranged in longitudinal rows; sometimes on top of raised projections. No distinct marginal sphincter. Margin of capitulum tentaculate. Tentacles long, smooth, numerous, retractile, regularly arranged except if asexual reproduction is present. **Tentacles of any cycle** may form fighting tentacles, typically thicker than feeding tentacles and containing holotrichs among other nematocysts; these may be absent in some species or individuals of

species that possess them. Outer tentacles may have *p*-mastigophores B2b. Six pairs of perfect mesenteries, two siphonoglyphs, and two pairs of directives usually present; their number may vary due to asexual reproduction. Mesenteries more numerous distally than proximally. Retractors diffuse, more or less restricted. Parietobasilar and basilar musculatures weak. Perfect mesenteries and stronger imperfect ones fertile. Acontia with basitrichs and *p*-mastigophores B2a or basitrichs, *p*-mastigophores B1, and *p*-mastigophores B2a. Cnidom: spirocysts, basitrichs, *p*-mastigophores A, *p*-mastigophores B1, *p*-mastigophores B2a, *p*-mastigophores B2b, and holotrichs.

Diadumene paranaensis Beneti, Stampar, Maronna, Morandini & Da Silveira, 2015

Material examined

Ceará, Brazil. Arpoeiras Beach, mangrove roots in estuary, Acaraú River, 2°48'55"S, 40°12'14"W, collected by Mayane R. de Araújo and Rafaela C. Maia, July, 2017 (0 m), salinity 34-37, water temperature 27.4 - 27.8°C, 127 specimens. MZUSP 8732 (100 specimens). LC 141 (27 specimens). Material for comparison: MZUSP 1530. MZUSP 1531, MZUSP 1534 (from original publication).

Diagnosis. (modified from Beneti et al. 2015; changes in bold, additions in italics):

Clonal species of *Diadumene*; *Tentacles of any cycle may form fighting tentacles*; Polyp with cinclides arranged in longitudinal rows, *outer tentacles may have p-mastigophores B2b*; **acontia with basitrichs and *p*-mastigophores B2a.**

Description

External morphology

Body cylindrical, globose, sometimes elongated or rather flattened (Fig. 2a-f). Column 2 to 9 mm in height, 2 to 11 mm in diameter, quite inflated,

translucent in some individuals (Fig. 2a). Clear division between scapus and scapulus, delicate fosse (Fig. 2c). Capitulum thin, short. Scapus of a rough appearance in preserved specimens with contracted column (Fig. 2b-d). Inconspicuous cinclides, more easily noticed when the column is inflated. Cinclides not on top of elevations or projections, forming longitudinal rows of up to 5 or 6 cinclides in each row (Fig. 2a). Oral disc slightly contracted or fully exposed with broad mouth and thick lips, sometimes elevated in a conical projection. Lips with twelve folds, some of them with smaller wrinkles. Number and tentacular organization quite variable. Between 28 and 70 short, conical tentacles, some of which swollen at base, lacking an apical pore. Tentacles irregularly arranged in 4 to 6 cycles, those of the innermost cycles larger and more developed. Fighting tentacles observed in any cycle, larger and thicker than the feeding ones, may have autotomized tips (Fig. 2b). Wide distended base, sometimes with folds, but never exceeding the diameter of the column.

Internal anatomy

Cinclides endocoelic, associated with the first two cycles of mesenteries. Wide and deep actinopharynx, with many folds, reaches approximately 1/3 of the length of the column. Two siphonoglyphs, each attached to a pair of directive mesenteries (Fig. 2h). Longitudinal musculature of the tentacles ectodermal. Marginal sphincter absent. Mesenteries arranged in 3-4 irregular cycles (6+6+12+n), more mesenteries distally than proximally. Number of mesenteries varies due to asexual reproduction. First cycle of mesenteries, including directives, perfect, second and third cycles imperfect. Some pairs from the last two cycles with unevenly developed mesenteries. First and second cycles with filaments and acontia, third cycle without these structures. Gametogenic tissue absent.

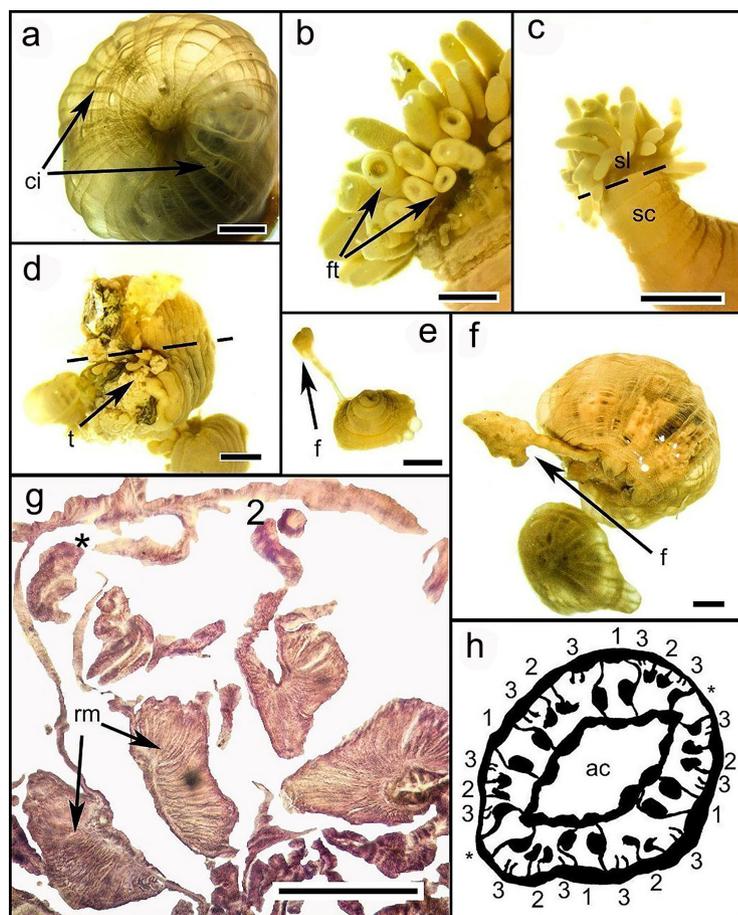


Figure 2. *Diadumene paranaensis* collected from Ceará state, Brazil. Aspects of the column and asexual reproduction strategies: a, inflated column evidencing rows of cinclides (arrows); b, upper lateral view of column showing fighting tentacles from the third and fourth cycles, lacking its tips (arrows); c, small specimen with distended column. Clear division of scapulus and scapus, separated by a delicate fosse (dashed line); d, regeneration process of the pedal disc. Note the small rock fragments on each side of the damaged column (dashed line), with tentacles withdrawn from the oral disc (arrow), escaping from the base aperture; e, f, pedal laceration process, forming new individuals through small fragments (arrows); Mesenterial arrangement: g, Cross section through midcolumn, showing a directive pair (asterisk), with well-developed retractor muscle processes (arrows), and a regular pair of mesenteries from the second cycle; h, Scheme of the general mesenterial organization in *D. paranaensis*, illustrating directive mesenteries (asterisks), as well as all three cycles of mesenteries. Legend: ci, cinclides; ft, fighting tentacles; f, fragment; rm, retractor muscle; ac, actinopharynx. Scale bar: a - f, 10 mm; g, 0.5 mm.

Retractor muscle strong, diffuse to restricted, weakly developed in the third cycle (Fig. 2g). Weak parietobasilar musculature in all mesenteries. Acontia up to 10 mm long, abundant.

Cnidom

Spirocysts, holotrichs, basitrichs, microbasic *p*-mastigophores B1, microbasic *p*-mastigophores B2a and microbasic *p*-mastigophores B2b (Table I).

Geographic distribution

Diadumene paranaensis was originally described from the portuary zone of Paranaguá Bay, Paraná, Brazil (Beneti et al. 2015) and, mentioned to occur at Santa Barbara Channel and San Francisco Bay, California, USA (Glon et al. 2020). This last study briefly mentions its occurrence based on

the identification of a *Diadumene* sp. collected earlier (Carlton, unpublished data) and used in some phylogenetic studies (Rodríguez et al. 2012, 2014). Although not providing further details over the variation and morphology differences between Atlantic and Pacific populations, the authors recognize the californian individuals of *D. paranaensis* as being recent established and, as in Paraná, probably not native to that location. Even though we decided not to include the californian populations in our distribution map (Fig. 1), we recognize this Pacific distribution of the species and emphasize the importance of better describing new populations of *D. paranaensis* for comparison and species statement purposes.

Table I. Comparison of size and distribution of cnidae of *D. paranaensis* from this study and from original description (Beneti et al. 2015). M, mean; SD, standard deviation; N, number of capsules measured; F, frequency: +++ very common, ++ common, + not common/rare. * The smaller category of *p*-mastigophore found in the scapus of the original description was not observed, which we do not consider problematic due to the rarity of this cnidae. **We present the larger *p*-mastigophores and the *p*-amastigophores of the acontia in the original description as a single category, due to recent taxonomic argumentation (see Discussion).

	Categories	Length x width (µm)	M± SD	N	F	Length x width (µm)	M± SD	
	<i>D. paranaensis</i> (this study)				<i>D. paranaensis</i> (Beneti et al. 2015)			
COLUMN*	(A) Basitrichs I	14.23–19.45 x 2.33–3.43	17.09±1.32 x 2.83±0.32	30	+	9.6–13.5 x 1.2–2.4	10.85±1.38 x 2.04±0.53	
	(B) Basitrich II	21.21–25.93 x 5.21–8.17	23.6±1.27 x 6.68±0.93	30	++	15.2–20.7 x 2.4–4.2	18.14±1.22 x 3.04±0.34	
	(C) <i>p</i> - mastigophores B2a	18.05–26.8 x 3.2–4.41	21.31±2.37 x 3.67±0.41	30	+	9.9–15.6 x 3.0–4.8	12.78±1.65 x 4.05±0.53	
TENTACLES	(D) Spirocysts	21.15–31.31 x 4.03–6.61	26.69±3.2 x 5.31±0.73	30	+++	10.28–17.85 x 2.65–4.72	14.54±2.89 x 3.28±1.01	
	(E) Holotrichs I	21.76–24.62 x 5.01–5.55	22.78±0.93 x 5.26±0.19	10	+	25.8–34.2 x 7.2–11.4	31.02±2.14 x 9.94±1.09	
	(F) Holotrichs II	38.23–50.91 x 12.33–16.14	44.28±4.45 x 14.27±1.19	30	+++	21.6–27.6 x 4.8–7.2	25.34±2.01 x 6.16±0.76	
	(G) Basitrichs	15.96–23.78 x 2.45–3.04	19.53±2.34 x 2.84±0.16	30	++	7.2–21.2 x 1.2–3.6	14.03±2.72 x 2.33±0.44	
	(H) <i>p</i> - mastigophores B2a	30.67–40.6 x 5.28–8.1	35.75±2.85 x 6.64±0.82	30	+++	19.8–26.4 x 3.6–6.0	22.75±1.58 x 4.68±0.58	
	(I) <i>p</i> - mastigophores B2b	50.34–54.21 x 9.78–10.43	52.51±1.62 x 10.12±0.23	10	+	36.0–46.2 x 6.0–8.4	41.01±2.46 x 7.29±0.66	
ACTINOPHARYNX	(J) Basitrichs	21.56–30.25 x 3.35–4.6	26.51±2.31 x 3.96±0.5	30	+++	16.8–21.28 x 1.2–3.7	19.67±1.07 x 2.67±0.71	
	(K) <i>p</i> - mastigophores B2a	18.05–26.8 x 3.2–4.41	21.31±2.37 x 3.67±0.41	30	++	15–22.8 x 3–4.2	17.84±1.65 x 3.64±0.35	
FILAMENT	(L) Basitrichs	11.9–16.98 x 1.65–2.45	13.66±1.19 x 2.21±0.21	30	++	10.8–19.2 x 1.2–3.0	15.50±2.19 x 1.86±0.51	
	(M) <i>p</i> - mastigophores B1	12.04–15.88 x 5.2–7.77	13.99 ± 1.16 x 6.74±0.62	30	++	12.0–22.8 x 3.0–4.8	16.16±2.33 x 3.77±0.43	
	(N) <i>p</i> - mastigophores B2a I	22.54–26.99 x 4.3–5.26	25.31±1.17 x 4.67±0.37	30	++	7.2–12.9 x 2.8–4.8	11.20±2.09 x 4.06±0.78	
	(O) <i>p</i> - mastigophores B2a II	38.45–49.08 x 6.01–7.53	44.4±3.49 x 6.52±0.46	30	++	39.0–51.6 x 6.0–8.4	46.46±1.28 x 7.07±0.51	
ACONTIA**	(P) Basitrichs	17.0–20.64 x 2.28–3.22	19.02±0.99 x 2.76±0.32	30	+++	10.2–19.2 x 1.2–3.6	15.50±2.01 x 1.96±0.52	
	(Q) (N) <i>p</i> - mastigophores B2a I	20.56–25.97 x 4.4–5.98	22.93±2.0 x 5.07±0.56	10	+	19.2–26.4 x 3.0–6.0	22.42±2.71 x 4.42±0.82	
	(R) (N) <i>p</i> - mastigophores B2a II	48.66–58.65 x 12.7–14.69	54.34±3.49 x 13.82±0.74	30	+++	35.9–57.5 x 5.1–7.4 41.1–57.0 x 5.4–8.4	43.61±4.17 x 6.07±0.64 46.59±3.34 x 6.56±0.78	

Biological information

Individuals associated with oysters and mussels, in mangrove prop roots. Several individuals had inflated column, giving buoyancy to the polyp (Fig. 2a, f). The inflation is present at any height of the column (along the entire length, just at the pedal disc, or the distal portion). Some individuals show asexual reproduction by pedal laceration (Fig. 2e, f).

Taxonomic remarks

In order to update the taxonomic status of the group, we propose brief modifications in the diagnoses of both family Diadumenidae, genus *Diadumene* and *D. paranaensis*, to include the morphological variation of the individuals analyzed in our study. The description of *D. paranaensis*, for the Bay of Paranaguá (Beneti et al. 2015) is quite complete, taking into consideration coloration, external morphology, histology and cnidom. However, these authors adopted the study of Östman et al. (2010) to present the set of cnidae displayed in their specimens. A more suitable nomenclature that, in our opinion, more adequately contemplates the diversity of nematocysts found in *Diadumene*, is the one proposed by Gusmão et al. (2018), adapted from Sanamyan et al. (2012). In our study, we use this nomenclature aiming to standardize and facilitate the comparison of other diadumenid species described so far, as well as of future new records. The diagnosis proposed herein contemplates the development of fighting tentacles in practically any of the tentacle cycles, and a different nomenclature for the microbasic *p*-amastigophores, revised as *p*-mastigophores B2a. Indeed, some of our specimens showed fighting tentacles in the last tentacle cycles, a feature not covered by the diagnosis of the *Diadumene* genus and family Diadumenidae. The ephemeral and enigmatic nature of these structures (Hand 1956, Williams

1975, Purcell 1977, Purcell & Kitting 1982, Watson & Mariscal 1983) supports our observations and evidences a morphological plasticity displayed in *D. paranaensis* populations that may result from distinct environmental conditions and the unique dynamics of each population settlement processes.

DISCUSSION

Diadumene paranaensis is believed to be a non-native species in both Brazilian and Californian locations due to the clonal structure of those populations (Beneti et al. 2015, Glon et al. 2020). Although not directly stated from a maritime traffic area, our observations of *D. paranaensis* in Arpoeiras Beach evidences a more extreme tolerance to high salinity ranges for the species than what was described from Paranaguá Bay. Significant salinity levels were indicated for species such as *D. cincta* (34.29‰), *D. lineata* (34-35‰) and *D. franciscana* (39‰) (Scatolini & Zedler 1996, Podbielski et al. 2016, Escribano-Álvarez & López-González 2018, Schutter et al. 2019). Likewise, as for associations with estuarine plants, Molina et al. (2009) registered the presence of *D. lineata* in association with *Spartina alterniflora* roots on salt marshes of Bahía Blanca, Argentina, where salinity values reach up to 38‰. Considering the documented salinity regimes of Paranaguá Bay, (12-34‰) and Arpoeiras Beach (5.73 – 41.55‰) (Lana et al. 2001, Santos & Maia 2021), is presumable that *D. paranaensis* follows the examples of other *Diadumene* species, and should be stated as a noticeable osmoconformer.

Further analysis of our specimens revealed that fighting tentacles can be found in any cycle, rather than being restricted to the first cycle, as previously believed. Interestingly, fighting tentacles are observed in the inner cycles of metridioid anemones, rarely the

third one (Gusmão et al. 2018), but only in the outer cycles of actinoidean anemones that possess them (Sanamyan et al. 2013). Therefore, *D. paranaensis* is the first registered acontiate sea anemone displaying this tentacle configuration. The missing tips, which suggest agonistic autotomization (Williams 1975, Purcell 1977), and the presence of holotrichs in some tentacles from the first to the last cycles in the specimens from Arpoeiras Beach, suggest that this is a more plastic biological attribute, which may play a crucial role in intra and interspecific interactions in the aggregation of individuals and population dynamics.

The updated diagnoses presented in this study (see Taxonomic remarks) relies on the matter of standardizing *Diadumene* species descriptions. The interpretation of nematocysts, in particular, is quite variable, with different systems of nomenclature from being adopted from work to work, making comparison at the population/species level quite difficult. Some of the most discussed nematocysts are, undoubtedly, the holotrichs and microbasic *p*-mastigophores. As discussed by Gusmão et al. (2018), microbasic *p*-amastigophores are now recognized as microbasic *p*-mastigophores B2a, macrobasic *p*-mastigophores, stated as *p*-mastigophores B2b, and atrichs also possess small spines and are considered to be holotrichs. In our analysis, relying on new observations, we modify the nomenclature of the cnidae used in the original description of *D. paranaensis*, since it adopts the terms amastigophores and atrichs. Our findings that, in fact, just one type of *p*-mastigophore is found in the acontia, but in two distinct size classes, uniting the *p*-amastigophores (35.9–57.5 µm long x 5.1–7.4 µm wide) and the larger *p*-mastigophores (41.1–57.0 µm long by 5.4–8.4 µm wide) from the original description of *D. paranaensis*, was confirmed by the analysis of the type material. We also

reinforce the convenience of a comprehensive review in the study of nematocysts in order to standardize and clarify the real taxonomic and systematic values of this character in *Diadumene*.

Brazil represents the largest coast among South American countries, includes the second largest mangrove area of the planet, and Paranaguá is considered as a main port in South America, with its coast also surrounded by mangroves (Neves et al. 2007, Mauro & Serejo 2015, Moschetto et al. 2021). Such traits denote a significance in proportioning suitable environmental conditions for *Diadumene* populations to settle down. Two new species and one new record were described for the 2010's (Beneti et al. 2015, Gusmão et al. 2018), consequently, the genus appears to be subsampled and must occupy a broader geographic range in the country, with presumable new registers in the future. Based in our findings, we add that the more than 4000 km distance between Paranaguá Bay and Arpoeiras Beach populations of *D. paranaensis* may reveal a high dispersal potential, following other diadumenid species examples, whose drivers are yet to be properly inferred in forthcoming studies.

REFERENCES

- ALLEE WC. 1923. Studies in marine ecology. I. The distribution of common littoral invertebrates of the Woods Hole region. *Biol Bull* 44: 167-191.
- BENETI JS, STAMPAR SN, MARONNA MM, MORANDINI AC & DA SILVEIRA FL. 2015. A new species of *Diadumene* (Actiniaria: Diadumenidae) from the subtropical coast of Brazil. *Zootaxa* 4021 (1): 56-168.
- CAINE EA. 1986. Carapace epibionts of nesting loggerhead sea turtles: Atlantic coast of USA. *J Exp Mar Biol Ecol* 95 (1): 15-26.
- CARLGREN O. 1893. Studien über nordische Actinien. *Kungliga Svenska Vetenskapsakademiens Handlingar* 25: 1-148.

- CHARRUAU P & GONZÁLEZ-MUÑOZ R. 2016. Epibiont sea anemones inhabiting the American crocodile *Crocodylus acutus*. *Mar Biodivers* 46(1): 11-12.
- CHIA F. 1976. Sea anemone reproduction: patterns and adaptive radiations. In: *Coelenterate ecology and behavior*, Plenum Press, New York, p. 261-270.
- DALY M, CHAUDHURI A, GUSMÃO L & RODRÍGUEZ E. 2008. Phylogenetic relationships among sea anemones (Cnidaria: Anthozoa: Actiniaria). *Mol Phylogenet Evol* 48 (1): 292-301.
- ESCRIBANO-ÁLVAREZ P & LÓPEZ-GONZÁLEZ PJ. 2018. Facing the arrival of newcomers: an intertidal sea anemone approach (Hexacorallia, Actiniaria). *Biol Invasions* 20(10): 2945-2962.
- FRICK MG, WILLIAMS KL, VELJACIC D, PIERRARD L, JACKSON JÁ & KNIGHT SE. 2000. Newly documented epibiont species from nesting loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. *MTN* 88: 3-5.
- GLON H, DALY M, CARLTON JT, FLENNIKEN MM & CURRIMJEE Z. 2020. Mediators of invasions in the sea: life history strategies and dispersal vectors facilitating global sea anemone introductions. *Biol Invasions* 2(11): 3195-3222.
- GOLLASCH S & RIEMANN-ZÜRNECK K. 1996. Transoceanic dispersal of benthic macrofauna: *Haliplanella luciae* (Verrill, 1898) (Anthozoa, Actiniaria) found on a ship's hull in a shipyard dock in Hamburg Harbour, Germany. *Helgoländer Meeresun* 50(2): 253-258.
- GONZÁLEZ-MUÑOZ R, SIMÕES N, SANCHEZ-RODRIGUEZ J, RODRIGUEZ E & SEGURA-PUERTAS L. 2012. First inventory of sea anemones (Cnidaria: Actiniaria) of the Mexican Caribbean. *Zootaxa* 3556(1): 1-38.
- GONZÁLEZ-MUÑOZ R ET AL. 2016. Sea anemones (Cnidaria: Actiniaria, Corallimorpharia, Ceriantharia, Zoanthidea) from marine shallow-water environments in Venezuela: new records and an updated inventory. *Mar Biodivers Rec* 9(1): 1-35.
- GUSMÃO LC, GRAJALES A & RODRÍGUEZ E. 2018. Sea anemones through X-rays: visualization of two species of *Diadumene* (Cnidaria, Actiniaria) using micro-CT. *Am Mus Novit* 2018(3907): 1-47.
- HAND C. 1956. The sea anemones of central California Part III. The acontiarian anemones. *Wasmann J Biol* 13: 189-251.
- LANA PC, MARONE E, LOPES RM & MACHADO EC. 2001. The Subtropical Estuarine Complex of Paranaguá Bay, Brazil. In: SEELIGER U & KJERFVEB (Eds) *Coastal Marine Ecosystems of Latin America*. *Ecol Stud* 144: 131-145.
- MAURO FDM & SEREJO CS. 2015. The family Caprellidae (Amphipoda: Caprelloidea: Caprellidae) from Campos Basin, Southwestern Atlantic, with a key of species occurring in Brazil. *Zootaxa* 4006(1): 103-127.
- MERCIER A, SCHOFIELD M & HAMEL J. 2011. Evidence of dietary feedback in a facultative association between deep-sea gastropods and sea anemones. *J Exp Mar Biol Ecol* 396(2): 207-215.
- MINASIAN JR LL & MARISCAL RN. 1979. Characteristics and regulation of fission activity in clonal cultures of the cosmopolitan sea anemone, *Haliplanella luciae* (Verrill). *Biol Bull* 157(3): 478-493.
- MITRA S & PATTANAYAK JG. 2013. Diversity and Distribution of Sea-Anemones (Cnidaria: Actiniaria) in the Estuaries and Mangroves of Odisha, India. *Rec Zool Surv India* 113(3): 113-118.
- MITRA S, SHAW S & MISHRA SS. 2019. Animal diversity in the mangrove forest at Bichitrapur of Balasore district, Odisha, India-A case study. *Rec Zool Surv India* 119(1): 9-17.
- MOLINA L, VALIÑAS MS, PRATOLONGO PD, ELIAS R & PERILLO GME. 2009. First record of the sea anemone *Diadumene lineata* (Verrill 1871) associated to *Spartina alterniflora* roots and stems, in marshes at the Bahía Blanca estuary, Argentina. *Biol Invasions* 11(2): 409-416.
- MOSCHETTO FA, RIBEIRO RB & DE FREITAS DM. 2021. Urban expansion, regeneration and socioenvironmental vulnerability in a mangrove ecosystem at the southeast coastal of São Paulo, Brazil. *Ocean Coast Manage* 200: 105418.
- NEVES CS, ROCHA RM, PITOMBO FB & ROPER JJ. 2007. Use of artificial substrata by introduced and cryptogenic marine species in Paranaguá Bay, southern Brazil. *Biofouling* 23(5): 319-330.
- OLSEN YS, FOX SE, HOFMAN L & VALIELA I. 2013. Benthic community composition and faunal stable isotopic signatures differ across small spatial scales in a temperate estuary. *Mar Environ Res* 86: 12-20.
- ÖSTMAN C, KULTIMA JR & ROAT C. 2010. Tentacle cnidae of the sea anemone *Metridium senile* (Linnaeus, 1761) (Cnidaria: Anthozoa). *Scientia Marina* 74(3): 511-521.
- PATZNER RA. 2004. Associations with sea anemones in the Mediterranean Sea: a review. *Ophelia* 58(1): 1-11.
- PODBIELSKI I, BOCK C, LENZ M & MELZNER F. 2016. Using the critical salinity (S crit) concept to predict invasion potential of the anemone *Diadumene lineata* in the Baltic Sea. *Mar Biol* 163(11): 1-15.

- PURCELL JE. 1977. Aggressive function and induced development of catch tentacles in the sea anemone *Metridium senile* (Coelenterata, Actiniaria). *Biol Bull* 153(2): 355-368.
- PURCELL JE & KITTING CL. 1982. Intraspecific aggression and population distributions of the sea anemone *Metridium senile*. *Biol Bull* 162(3): 45-359.
- RAGHUNATHAN C, RAGHURAMAN R, CHOUDHURY S & VENKATARAMAN K. 2014. Diversity and distribution of sea anemones in India with special reference to Andaman and Nicobar Islands. *Rec Zool Surv India* 114(2): 269-294.
- RANDALL J & FAUTIN D. 2002. Fishes other than anemonefishes that associate with sea anemones. *Coral Reefs* 21(2): 188-190.
- RODRÍGUEZ E, BARBEITOS M, DALY M, GUSMÃO LC & HÄUSSERMANN V. 2012. Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). *Cladistics* 28(4): 375-392.
- RODRÍGUEZ E, BARBEITOS MS, BRUGLER MR, CROWLEY LM, GRAJALES A, GUSMÃO L, HÄUSSERMANN V, REFT A & DALY M. 2014. Hidden among sea anemones: the first comprehensive phylogenetic reconstruction of the order Actiniaria (Cnidaria, Anthozoa, Hexacorallia) reveals a novel group of hexacorals. *PLoS ONE* 9(5): e96998.
- RYAN WH & KUBOTA S. 2016. Morphotype distribution of the sea anemone *Diadumene lineata* in Tanabe Bay, Wakayama: a comparison with Uchida (1936) after 80 years. *P Seto Mar Biol Lab* 44: 1-6.
- SANAMYAN NP, SANAMYAN KE & MCDANIEL N. 2013. Two new shallow water sea anemones of the family Actiniidae (Cnidaria: Anthozoa: Actiniaria) from British Columbia (NE Pacific). *Invertebr Zool* 10: 199-216.
- SANAMYAN NP, SANAMYAN KE & TABACHNICK KR. 2012. The first species of Actiniaria, *Spongiactis japonica* gen. n., sp. n. (Cnidaria: Anthozoa) an obligate symbiont of a glass sponge. *Invertebr Zool* 9(2): 127-141.
- SANTOS MRD & MAIA RC. 2021. Obras de Urbanização e os Impactos Ambientais sobre a Macrofauna Bentônica: Estudo de Caso em uma Praia do Litoral Cearense. *J Integr Coast Zone Manag* 21(3): 135-145.
- SCATOLINI SR & ZEDLER JB. 1996. Epibenthic invertebrates of natural and constructed marshes of San Diego Bay. *Wetlands* 16(1): 24-37.
- SCHUTTER M, DORENBOSCH M, DRIESSEN FMF, LENGKEEK W, BOS OG & COOLEN JWP. 2019. Oil and gas platforms as artificial substrates for epibenthic North Sea fauna: Effects of location and depth. *J Sea Res* 153: 101782.
- SHICK JM & LAMB AN. 1977. Asexual reproduction and genetic population structure in the colonizing sea anemone *Haliplanella luciae*. *Biol Bull* 153(3): 604-617.
- STEPHENSON TA. 1920. On the classification of Actiniaria. Part I. — Forms with acontia and forms with a mesogloal sphincter. *Q J Microsc Sci* 64: 425-574.
- STOLICZKA F. 1869. On the anatomy of *Sagartia schilleriana* and *Membranipora bengalensis*, a new coral and a bryozoon living in brackish water at Port Canning. *J Asiat Soc Beng* 38: 28-63.
- UCHIDA T. 1932. Occurrence in Japan of *Diadumene luciae*, a remarkable actinian of rapid dispersal. *J Fac Sci, Hokkaido Univ, S VI* 2: 69-82.
- VERRILL AE. 1866. On the polyps and echinoderms of New England, with descriptions of new species. *Proc Boston Soc Nat Hist* 10: 333-357.
- VERRILL AE. 1869. Review of the corals and polyps of the west coast of America. *Trans Conn Acad Arts Sci* 1: 377-558.
- WATSON GM & MARISCAL RN. 1983. The development of a sea anemone tentacle specialized for aggression: morphogenesis and regression of the catch tentacle of *Haliplanella luciae* (Cnidaria, Anthozoa). *Biol Bull* 164(3): 506-517.
- WILLIAMS RBA. 1975. Redescription of the brackish-water sea anemone *Nematostella vectensis* Stephenson, with an appraisal of congeneric species. *J Nat Hist* 9(1): 1-64.
- ZABIN CJ, CARLTON JT & GODWIN LS. 2004. First report of the Asian sea anemone *Diadumene lineata* from the Hawaiian Islands. *Bishop Mus Occas Pap* 79: 54-58.

How to cite

DE MELO YA, DE ARAÚJO MR, MAIA RC & GOMES PB. 2024. New insights on the taxonomy of *Diadumene paranaensis* (Cnidaria: Actiniaria) associated with mangrove roots in the Brazilian semi-arid coast. *An Acad Bras Cienc* 96: e20230101. DOI 10.1590/0001-3765202420230101.

*Manuscript received on February 4, 2024;
accepted for publication on April 7, 2024*

YAGO A. DE MELO¹

<https://orcid.org/0000-0003-3462-8165>

MAYANE R. DE ARAÚJO²

<https://orcid.org/0000-0002-8508-085X>

RAFAELA C. MAIA²

<https://orcid.org/0000-0001-5871-4610>

PAULA B. GOMES¹

<https://orcid.org/0000-0002-1555-1484>

¹Universidade Federal Rural de Pernambuco, Departamento de Biologia, Grupo de Pesquisa em Antozoários, Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, 52171-900 Recife, PE, Brazil

²Instituto Federal de Educação, Ciência e Tecnologia do Ceará, Laboratório de Ecologia de Manguezais, Avenida Desembargador Armando de Sales Louzada, s/n, Monsenhor Edson, 62580-000 Acaraú, CE, Brazil

Correspondence to: **Yago Araújo de Melo**

E-mail: yagomelo809@gmail.com

Author contribution

MAYANE ROCHA DE ARAÚJO and RAFAELA CAMARGO MAIA: collected the specimens and analyzed the document. YAGO ARAÚJO DE MELO: analyzed the specimens and wrote the content of the document. PAULA BRAGA GOMES: wrote and analyzed the document.

