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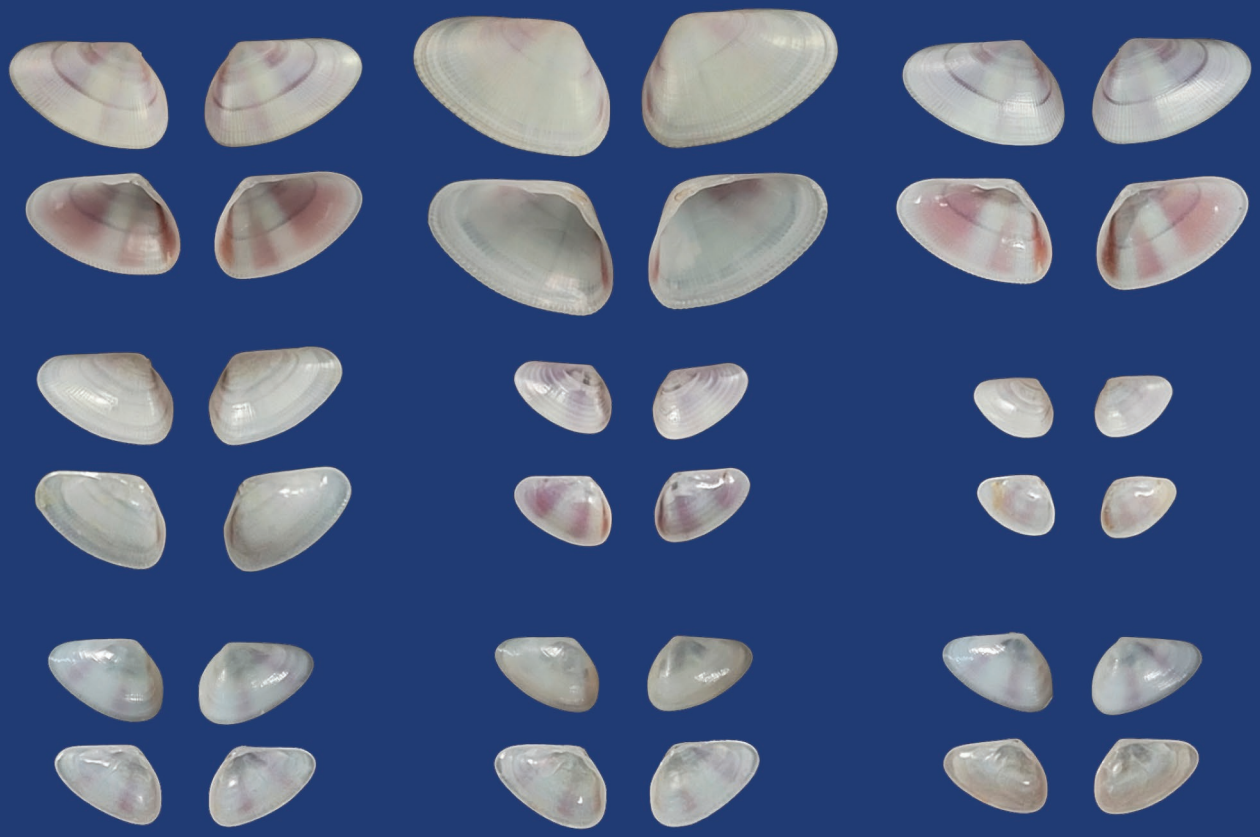

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Geometric morphometrics of donacids from Brazil reveals a new species, *Donax trapesialis* n. sp. from Northeastern coast

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ABSTRACT
The genus *Donax* Linnaeus, 1758 comprises 90 described bivalve species, five of which occur on the Brazilian coast. No taxonomic investigation has been conducted on the *Donax* species found along the Sergipe coast (Northeastern Brazil). In order to fill some of these gaps in the knowledge about Brazilian donacids, we employed conchological analysis and geometric morphometric approaches to compare the morphology of donacids in Sergipe with *D. gemmula* Morrison, 1971 from southeastern Brazil, species with which they closely resembled. Our conchological analysis revealed two morphotypes within the *Donax* genus. The first morphotype is readily identifiable as *D. gemmula*. The second morphotype exhibits significant morphological differences from all other *Donax* species. The results of the morphometric analysis statistically supported the findings of the conchological analysis. Therefore, our findings mark the second record of *D. gemmula* on northeastern Brazilian waters, supporting the hypothesis of a continuous distribution along the Brazilian coast. Additionally, we identified a new species, named *Donax trapesialis* n. sp., characterized by a consistently rounded posterior ridge, a trapezoidal shape with a wider anterior margin, a concave ventral margin, more ventrally positioned anterior and posterior extreme points, and often triradial purple zones. We provide a dichotomous key to all six Brazilian *Donax* species, including *D. trapesialis* n. sp.

KEY WORDS
NE Brazil,
Sergipe,
morphology,
bivalve,
new species.

RÉSUMÉ
La morphométrie géométrique des donacidés du Brésil révèle une nouvelle espèce, Donax trapesialis *n. sp., de la côte nord-est.*
Le genre *Donax* Linnaeus, 1758 comprend 90 espèces de bivalves décrites, dont cinq se trouvent sur la côte brésilienne. Aucune recherche taxonomique n'a été menée sur les espèces de *Donax* présentes le long de la côte de Sergipe (nord-est du Brésil). Afin de combler certaines lacunes dans la connaissance des donacidés brésiliens, nous avons utilisé des analyses conchologiques et des approches morphométriques géométriques pour comparer la morphologie des donacidés de Sergipe avec celle de *D. gemmula* Morrison, 1971 du sud-est du Brésil, espèce à laquelle ils ressemblent fortement. Notre analyse conchologique a révélé deux morphotypes au sein du genre *Donax*. Le premier morphotype est facilement identifiable comme *D. gemmula*. Le second morphotype présente des différences morphologiques significatives par rapport à toutes les autres espèces de *Donax*. Les résultats de l'analyse morphométrique ont statistiquement confirmé les conclusions de l'analyse conchologique. Nos observations attestent ainsi la deuxième mention de *D. gemmula* dans les eaux du nord-est du Brésil, soutenant l'hypothèse d'une distribution continue le long de la côte brésilienne. De plus, nous avons identifié une nouvelle espèce, nommée *Donax trapesialis* n. sp., caractérisée par une crête postérieure uniformément arrondie, une forme trapézoïdale avec un bord antérieur plus large, un bord ventral concave, des points extrêmes antérieurs et postérieurs positionnés plus ventralement et souvent des zones triradiales violettes. Une clé dichotomique est proposée pour les six espèces brésiliennes de *Donax*, y compris *D. trapesialis* n. sp.

MOTS CLÉS
NE Brésil,
Sergipe,
morphologie,
bivalve,
espèces nouvelles.

INTRODUCTION

Donax Linnaeus, 1758 is a genus of filter-feeding bivalves belonging to the Donacidae Fleming, 1828 family. These clams primarily inhabit tropical beaches, burrowing within the first few centimeters of intertidal zone sand (Morrison 1971). Also known as surf clams, many of its species exhibit tidal displacements, migrating seaward with the low tide and returning shoreward with the high tide (Ansell 1983; Moncada *et al.* 2022). Currently, about 90 species are described in *Donax* (Moncada *et al.* 2022), with five occurring on the Brazilian coast: *D. denticulatus* Linnaeus, 1758 from the states of Pará to Alagoas; *D. striatus* Linnaeus, 1767 from the states of Maranhão to Rio Grande do Norte; *D. vellicatus* Reeve, 1855 from the state of Rio Grande do Norte; and *D. hanleyanus* Philippi, 1847 and *D. gemmula* Morrison, 1971, from the states of Espírito Santo to Rio Grande do Sul (Rios 2009) (Fig. 1). Barroso *et al.* (2013) reported the discovery of *D. gemmula* in Ceará, northeastern Brazil. This finding led to two hypotheses: introduction via ship ballast water or a continuous distribution for *D. gemmula*, potentially ranging from Ceará to Rio Grande do Sul. While Morrison (1971) reported *D. vellicatus* from Rio Grande do Norte and possibly juveniles in Alagoas, no subsequent records of this species exist in Brazil (Barroso *et al.* 2013). This lack of records could be a result of its resemblance with *D. striatus* differing by being larger and less sharply ridged (Wade 1967; Domaneschi & Lopes 1989). As both species have been found living sympatrically (Morrison, 1971), *D. vellicatus* specimens may often be misidentified as *D. striatus*.

The Invertebrates Collection of the Federal University of Sergipe (Coleção de Invertebrados da Universidade Federal de Sergipe, CZUFS) houses thousands of donacid specimens sampled along the Sergipe coast during the 1990s. This study represents the first taxonomic investigation of *Donax* species in Sergipe, Brazil, employing both traditional morphological analysis and geometric morphometrics. Additionally, we provide a description of a new species based on shell morphology.

MATERIAL AND METHODS

In this study, we employed two distinct analytical approaches: conchological analysis, which is based on the traditional morphological characteristics of the shell, and morphometric analysis based on landmark and semilandmark geometric techniques.

For the conchological analysis, 123 *Donax* sp. specimens from the shores of Atalaia, Robalo, and Mosqueiro beaches in Aracaju, Sergipe state, and housed in the CZUFS were included. Additionally, shells of 180 *D. gemmula*, 70 *D. striatus*, and 30 *D. hanleyanus* were included from the Collection of Malacology of Zoology Museum, University of São Paulo (Museu de Zoologia da Universidade de São Paulo, MZSP) and the Malacological Collection "Prof. Henry Ramos Matthews" Series B from the Federal University of Ceara (Coleção Malacológica "Prof. Henry Ramos Matthews" Série B da Universidade Federal do Ceará, CMPHRM-B). The analysis additionally incorporated shell images of 17 *D. vellicatus* from the Malacological Collection of the Academy of Natural Sciences of Drexel, Philadelphia (ANSP), the National Museum of Natural History, London (NMNH), and the Natural History Museum, New York (USNM). Shell morphology was assessed in reference to established bivalve literature, including Newell (1965), Morrison (1971), Ansell (1983), Rios (2009), and Barroso *et al.* (2013).

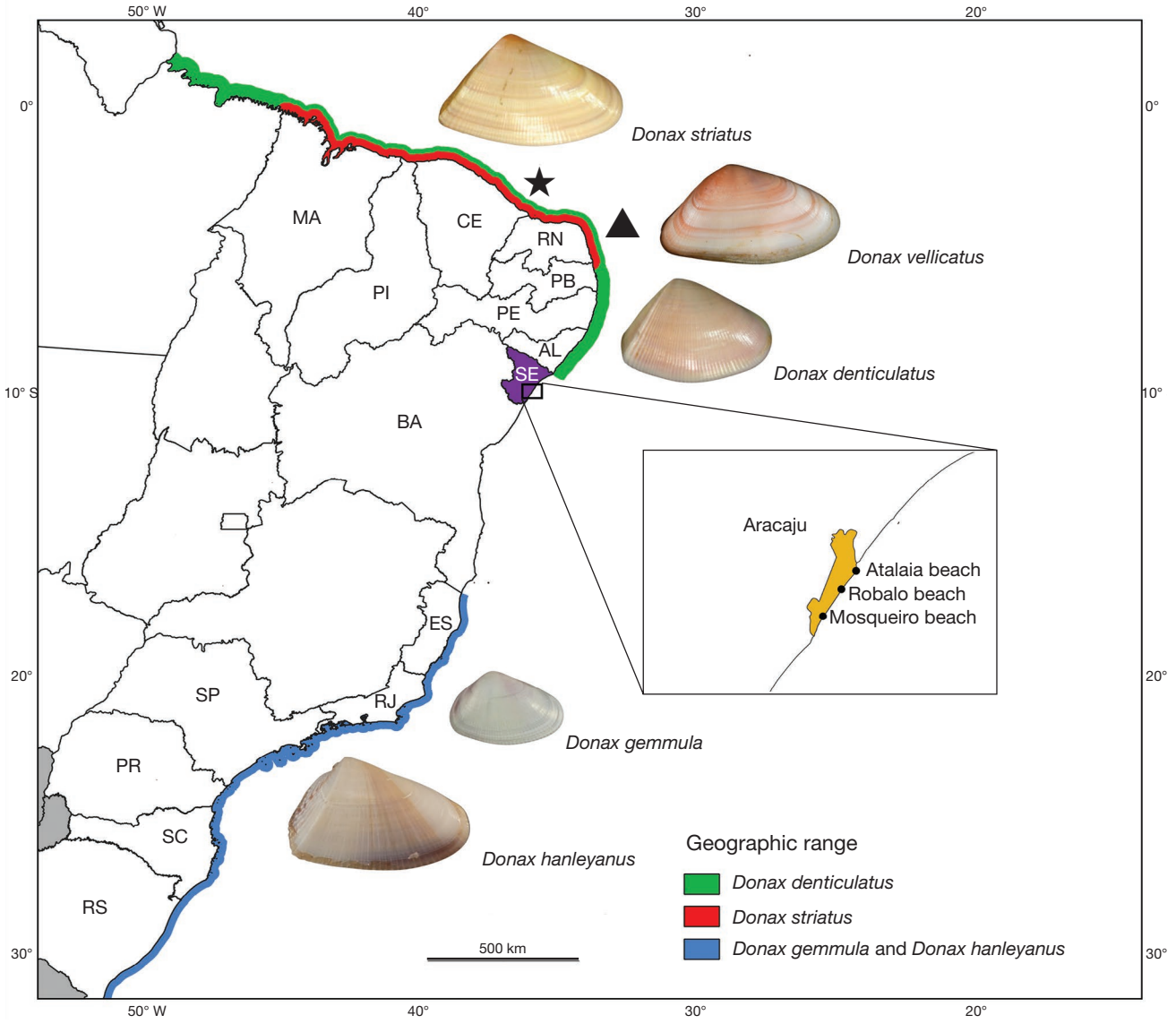

Fig. 1. — Geographic range of Brazilian species of *Donax* Linnaeus, 1758, adapted from Barroso *et al.* (2013): **black star** indicates record of *D. gemmula* Morrison, 1971 by Barroso *et al.* (2013) at the state of Ceará (CE); **black triangle** indicates record of *D. vellicatus* Reeve, 1855 by Morrison (1971) at the state of Rio Grande do Norte (**RN**); Sergipe state (**SE**) highlighted, displaying beaches where *Donax* sp. from this study were collected: Atalaia, Robalo and Mosqueiro. Shells from all specimens are displayed along the coast: *D. striatus* Linnaeus, 1967, NMR 19659; *D. vellicatus*, ANSP 300325; *D. denticulatus* Linnaeus, 1758, NMR 16966; *D. gemmula*, MZSP 026213; *D. hanleyanus* Philippi, 1847, MZSP 022091.

Morphometrical analysis included 88 specimens from the genus *Donax* collected in Aracaju, Sergipe state (northeastern region, NE) (Fig. 2) and 59 *D. gemmula* from Santos and São Sebastião, São Paulo state (southeastern region, SE) (Fig. 3). The samples were collected on exposed beaches, as detailed in Table 1. The analysis focused on specimens of *D. gemmula* from both SE and NE regions and *Donax* sp. due to the significant size and shape differences observed in these individuals compared to other Brazilian *Donax* species. Specimens location, reference numbers and measurements are detailed in Appendix 1.

Table 1. — Specimens used in morphometrical analysis.

State	Beach	Number of Individuals
Sergipe	Atalaia beach (AT)	30
	Robalo beach (RO)	29
	Mosqueiro beach (MO)	29
São Paulo	Canal 1 - Santos (SA)	30
	Barequeçaba - São Sebastião (SB)	29

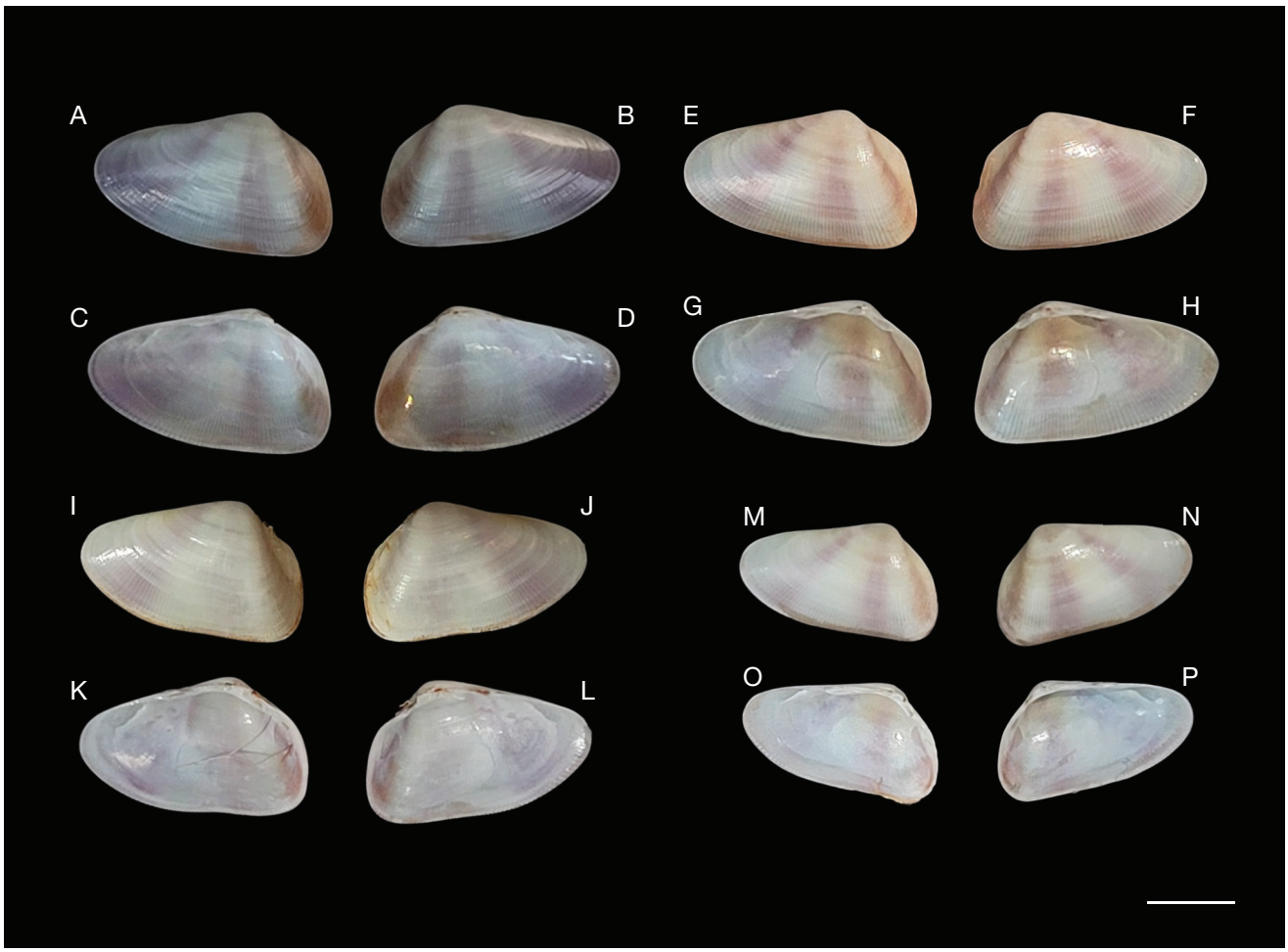

Fig. 2. — *Donax* sp. from Sergipe, Aracaju: **A-H**, Atalaia beach, CZUFS BIV - 00121; **I-P**, Robalo beach, CZUFS BIV - 00120. Scale bar: 5 mm.

Prior to analysis, the right valve and soft tissues were removed from the specimens and discarded. The left valve was cleaned, dried, and their external view photographed using a Leica S8APO stereomicroscope equipped with a DMC2900 camera (Fig. 4). Eight fixed landmarks and 80 semilandmarks were selected and then were digitized in TpsDig2 v.2.32 (Rohlf *et al.* 2004). Generalized Procrustes Analysis (GPA) was performed in R v.4.2.1 (R Core Team 2022) using the geomorph package (Baken *et al.* 2021; Adams *et al.* 2022) to align the landmarks of all specimens. Additionally, a Kruskall-Wallis test and a Procrustes ANOVA was conducted in R to test the significance of variation along PC1 and PC2 between population pairs, and to test shape and size differences among the populations, respectively (Supplementary material 1, https://doi.org/10.6084/m9.figshare.27701988.v1).

We performed a Principal Component Analysis (PCA) using MorphoJ v.1.07a (Klingenberg 2011), to visualize potential shape differences among the various populations. Additionally, allometric patterns were evaluated using a multivariate regression between shape variables and centroid size. MorphoJ was also used to generate wireframes and transformation grids for visualizing shape variation.

We conducted a k-means clustering analysis in Google Colab using the first five Principal Components (PCs) to determine the number of morphotypes across all populations. K-means finds the number of groups (k) that best explains the data based on the inertia, the difference in variation for different values of k (Géron 2019).

Material for taxonomic comparisons

Donax gemmula

Brazil • 60 of 27.096 specimens; Praia do Mosqueiro, Aracaju; SE; CZUFS BIV 00122 • 45 specimens; Praia do Mosqueiro, Aracaju, SE; CZUFS BIV 00125 • 15 specimens; Banco dos Cajuais, CE; CMPHRM2683B • 30 of 50 specimens; Baraqueçaba, SP; MZSP 040943 • 30 of 70 specimens; Canal 1, SP; MZSP 26813.

Donax striatus

Brazil • 20 of 60 shells; Praia de Tibau, RN; CMPHRM2661B • 20 of 65 specimens; Porto do Mangue, RN; MZSP 096067 • 30 specimens; Ilha de Algodoal, PA; MZSP 147788.

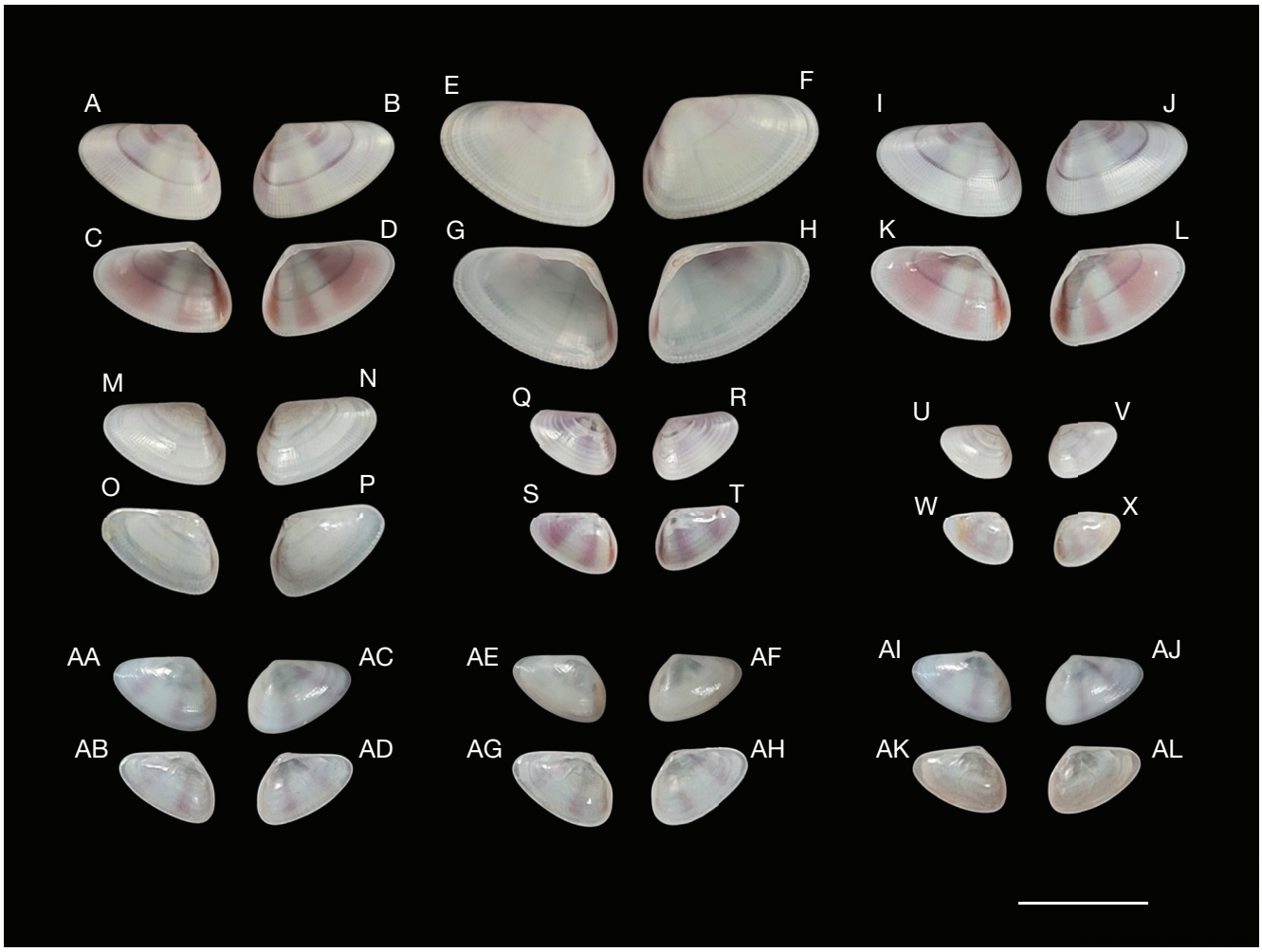

FIG. 3. — *Donax gemmula* Morrison, 1971: **A**-**X**, São Paulo state: **A**-**L**, Santos, MZSP 026213; **M**-**X**, São Sebastião, MZSP 040943; **AA**–**AL**, Sergipe state, Aracaju, Mosqueiro beach, CZUFS BIV - 00122. Scale bar: 5 mm.

Donax hanleyanus
Brazil • 10 specimens; Caravelas, BA; MZSP 008359 • 20 of 200 specimens; Ubatuba, SP; MZSP 022091.

Donax vellicatus
Brazil • 1 of 13 shells, Maceió, AL; ANSP 244133 • 4 of 200 shells; Areia Branca, RN; ANSP 300325 • syntype, 1 shell; locality unknown; NHMUK 1912.6.4.16 • 1 shell, RN; USNM 809529. **Columbia** • 1 shell; Santa Marta; USNM 444095 • 1 shell; USNM 444095. **Panama** • 1 shell, Colon; USNM 679611 • 1 shell; USNM 679611. **Vezenuela** • 1 shell, Miranda; USNM 680434 • 1 shell; USNM 707789. **Belize** • 1 shell; USNM 150331. **Honduras** • 1 shell; USNM 195090. **Guatemala** • 1 shell; USNM 271022. **Trindad and Tobago** • 1 shell; USNM 679313.

ABBREVIATIONS

Institutions

ANSP	Malacology Collection at the Academy of Natural Sciences of Philadelphia, Philadelphia;
CMPHRM-B	Coleção Malacológica Prof. Henry Ramos Matthews Série B;
CZUFS	Coleção Zoológica da Universidade Federal de Sergipe, Sergipe;
MZSP	Coleção do Museu de Zoologia da Universidade de São Paulo, São Paulo;
NHM	National History Museum, London;
NMR	Collection of Natural History Museum, Rotterdam;
ZUEC-BIV	Coleção de Bivalvia do Museu de Diversidade Biológica da UNICAMP, Campinas-São Paulo state.

Localities

AL	Alagoas state;
AT	Atalaia beach;
BA	Bahia state;
CE	Ceará state;
MO	Mosqueiro beach;
NE	Northeastern region of Brazil;
PA	Pará state;
RN	Rio Grande do Norte state;
RO	Robalo beach;
SA	Santos-São Paulo state;
SB	São Sebastião-São Paulo state;
SE	Southeastern region of Brazil;
SP	São Paulo state.

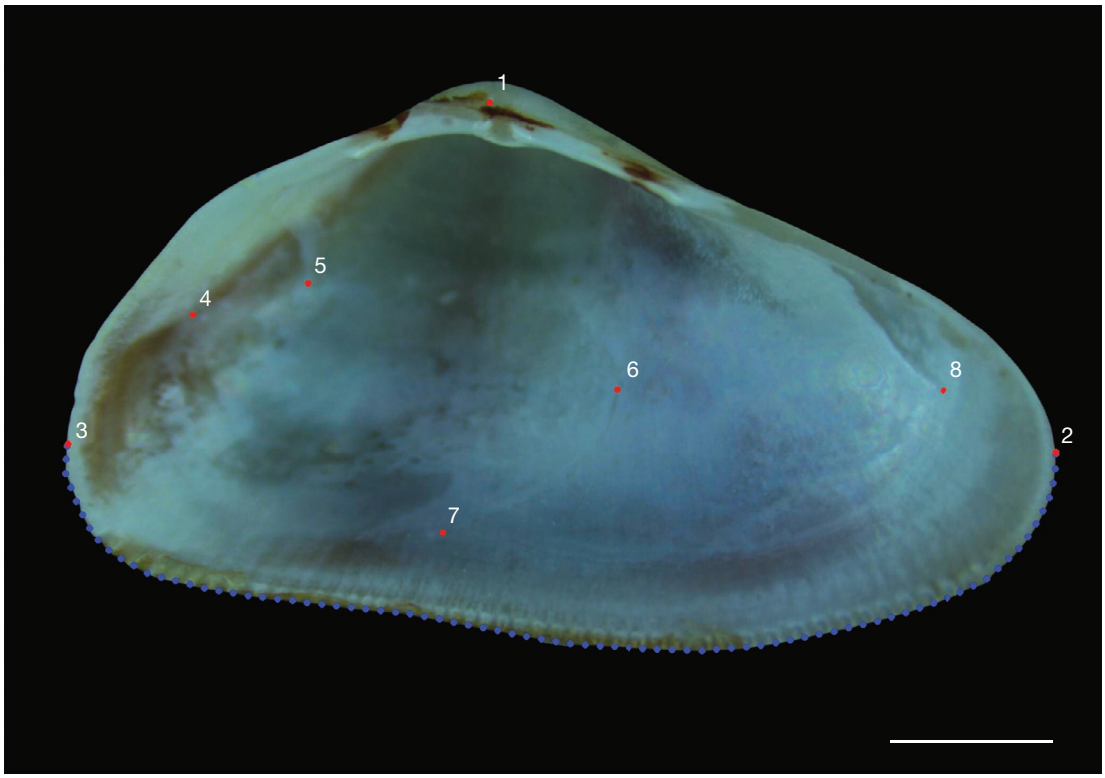

Fig. 4. — Internal surface of the left valve of a *Donax* Linnaeus, 1758 new species. The eight landmarks used in the morphometric analysis are represented by dots: **1**, umbo; **2**, most anterior point; **3**, most posterior point; **4**, most ventral point of the posterior adductor muscle scar; **5**, intersection of the pallial sinus and the posterior adductor muscle scar; **6**, most anterior point of the pallial sinus; **7**, Intersection of the pallial sinus and the pallial line; **8**, intersection of the pallial line and the anterior adductor muscle scar. 80 semilandmarks distributed evenly along the ventral margin. Scale bar: 2 mm.

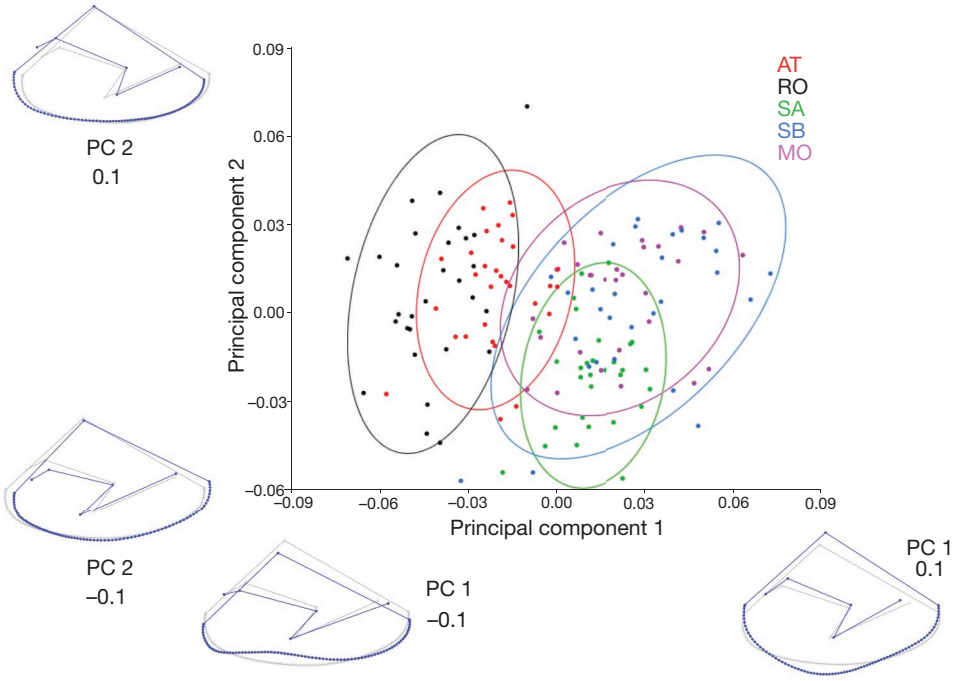

Fig. 5. — Principal Component Analysis (**PCA**) between the populations in this study (**AT**, Atalaia; **RO**, Robalo; **SA**, Santos; **SB**, São Sebastião; **MO**, Mosqueiro). Confidence ellipses indicate areas on which 90% of the individuals of each group are located. At the extreme points of both the first and second principal components axes are wireframes that represent the shape of individuals approximately at those points in each axis (scale factors of -0,1 and 0,1) in **dark blue**, in comparison to the mean configuration, in **gray**.

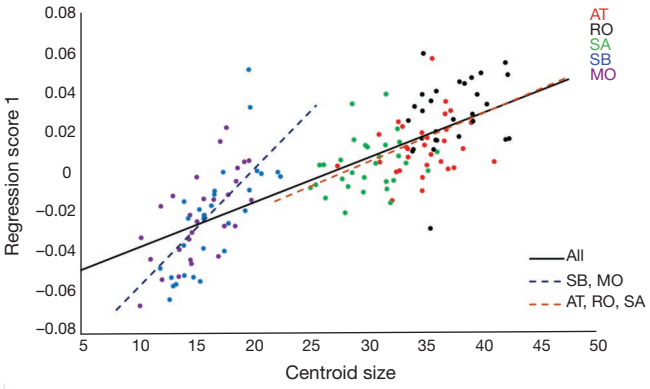

FIG. 6. — Linear regression between shape, represented by the Regression Score 1, a multivariate value derived from the Procrustes coordinates, and size, represented by the Centroid Size between the populations (**AT**, Atalaia; **RO**, Robalo; **SA**, Santos; **SB**, São Sebastião; **MO**, Mosqueiro). Regression line for the whole model is shown as a **solid black line**; regression lines for the major groups ("AT + RO + SA" and "SB + MO") are represented by **orange** and **blue dashed lines**, respectively.

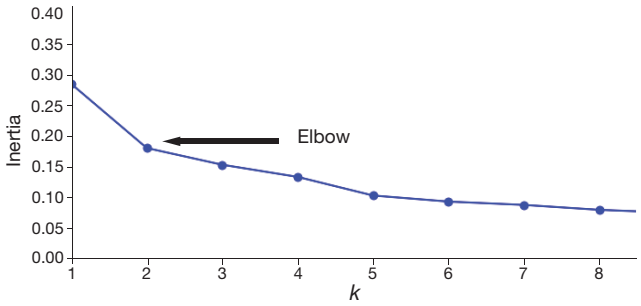

FIG. 7. — K-means made from the first five PCs of the PCA. Inertia indicates changes of the variation in the data, and k indicates the number of groups. The sharp curve, elbow, shows the k on which there is a sudden change of inertia, which suggests the k that best explains the data.

TABLE 2. — Analysis of Variance (ANOVA) of the shape (Procrustes coordinates) and size (centroid size) between populations. Abbreviations: **Df**, degrees of freedom; **MS**, mean of SS; **SS**, sum of squared distances.

	Df	SS	MS	R^2	F	p-value
Shape						
Species	1	0.099	0.099	0.028	4	< 0.005
Residuals	145	0.340	0.002	0.971	–	–
Total	146	0.350	–	–	–	–
Size	–	–	–	–	–	–
Species	1	3.4×10^{-6}	3.4×10^{-6}	0.046	6	< 0.01
Residuals	145	7.1×10^{-6}	4.9×10^{-7}	0.954	–	–
Total	146	7.4×10^{-6}	–	–	–	–

TABLE 3. — Number of individuals of each population assigned to the groups generated by the k-means analysis for k = 2 and k = 3.

Site	k = 2 (a)	k = 2 (b)	k = 3 (a)	k = 3 (b)	k = 3 (c)
Atalaia Beach (AT)	26	4	24	3	3
Robalo Beach (RO)	29	0	29	0	0
Mosqueiro Beach (MO)	3	26	1	20	8
Santos (SA)	1	29	0	3	27
São Sebastião (SB)	1	28	0	21	8

RESULTS

We identified two populations with distinct conchological characteristics along the Northeastern Brazilian Coast (NE).

CONCHOLOGY

The northeastern population of Mosqueiro beach presented diagnostic characteristics consistent with *D. gemmula*: small and subglobose shells (mean width 4.66 mm, height 3.13 mm), a rounded posterior ridge, evenly spaced crenulations along the ventral margin, and a whitish glossy coloration with faint triradial purplish zones that are more prominent on the internal surface (Morrison 1971; Passos & Domaneschi 2004; Rios 2009). The remaining populations from the NE region could not be assigned to any known Brazilian *Donax* species and thus we recognized them as belonging to a new species, presenting a larger size, a shorter height-length ratio, and a slightly concave ventral margin as differential characters. This classification is discussed further below.

MORPHOMETRY

The morphometric analysis results support the findings from the conchological analysis. Principal Component Analysis (PCA) revealed a high degree of similarity between the *D. gemmula* specimens from Aracaju (NE) and both *D. gemmula* populations from São Paulo (SE). The remaining *Donax* sp. populations from the northeast (NE) exhibited moderate overlap amongst themselves, and minimal to moderate overlap with the other populations, respectively (Fig. 5).

The Principal Component 1 (PC1) explains 44.15% of the variation and is associated with the curve of the ventral margin, the umbo, the intersections between the pallial sinus/line and the adductor muscle scars, and both the most anterior and most posterior points. Specimens of *Donax* sp. from Atalaia and Robalo beaches showed no significant differences between each other, and both differed from the remainder populations (p-value Dunn test < 0.001, Appendix 2). They presented a concave ventral margin, with a more ventral-posterior umbo, intersections between pallial line/sinus further from the center of the shell and extreme points located more ventrally in relation to the muscle scars and umbo. Overall, they presented a wider shape, more dorsal-ventrally truncated and slightly more inequilateral, with a more elongated anterior side in relation to the *D. gemmula* populations.

The Principal Component 2 (PC2) explains 24.77% of the variation and is associated with the shape of the pallial sinus and the length of the pallial line. The differences in variance among the population pairs along this PC were mostly non-significant, with the exception of the population of Santos (SE), which differed from all others by presenting a sharper pallial sinus and a larger pallial line (p-value Dunn test < 0.001). The remaining PC's account for 31.17% of the variation.

The multivariate regression between the Procrustes coordinates and the centroid size showed that the shape is not independent of the size (p-value < 0.0001). Approximately 6.9% of the shape variation can be explained by size differences (Fig. 6). *D. gemmula* specimens from the Mosqueiro

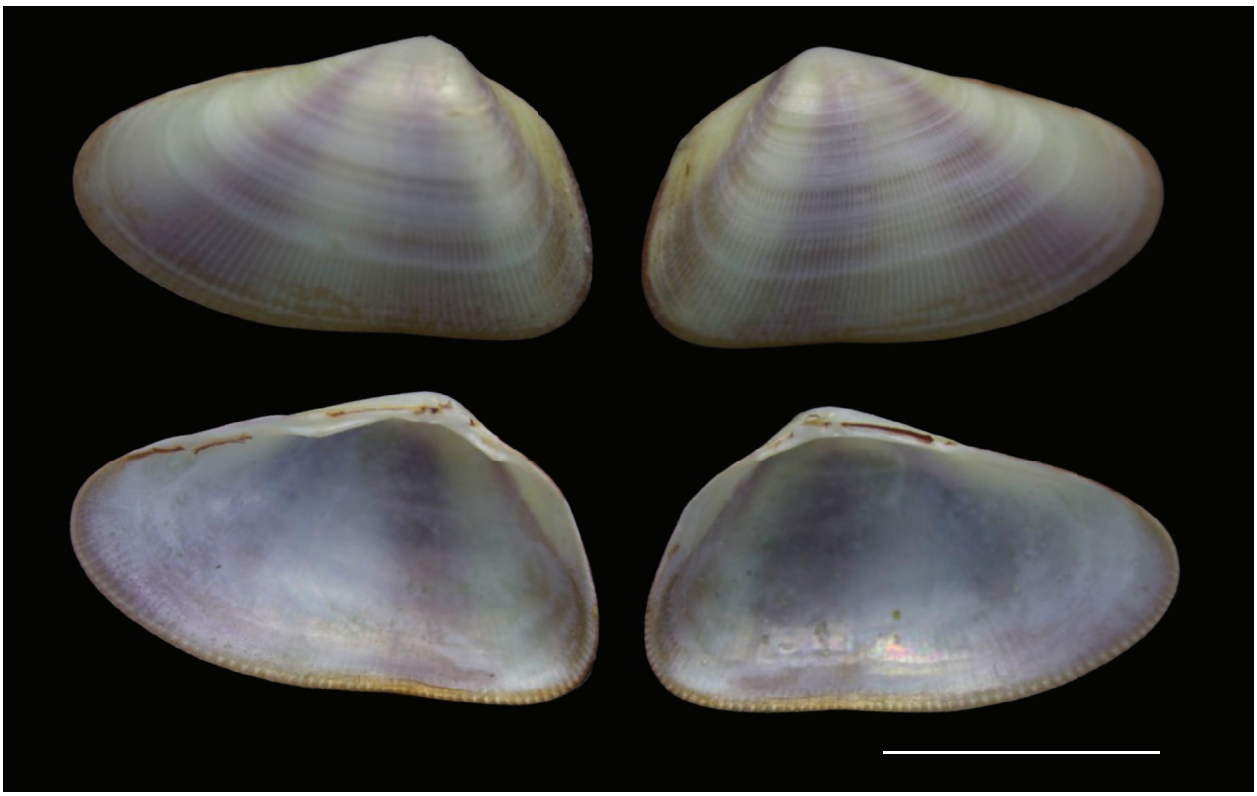

FIG. 8. — *Donax trapesialis* n. sp. holotype, CZUFS BIV-00123, Sergipe, Aracaju - Robalo beach. Scale bar: 5 mm.

beach (NE) and São Sebastião (SE) populations were the smallest and formed a distinct size group separate from all other populations. Interestingly, the *D. gemmula* from Santos (SE) exhibited an intermediate size. Conversely, *Donax* sp. specimens were the largest in size. The Procrustes ANOVA showed that species groups (either *D. gemmula* or *Donax* sp.) were a significant factor in determining both shape and size (p-value < 0.01 and 0.005 respectively) and explained 2.85% of shape and 4.59% of size in the populations (Table 2).

K-means suggested that two morphotypes best explain the data (Fig. 7). However, k = 2 resulted in a relatively low silhouette score (0.294) (Supplementary material 1, https://doi.org/10.6084/m9.figshare.27701988.v1). This grouping correlated to the *Donax* sp. from Robalo and Atalaia beaches (NE) and the *Donax gemmula* from Mosqueiro beach (NE), Santos and São Sebastião (SE) described by the PCA analysis (Table 3). When considering k = 3, the *Donax* sp. remained mostly grouped together, while the *Donax gemmula* populations were divided into two groups, one containing most of the specimens from Santos and the other most of the specimens from São Sebastião and Mosqueiro.

TAXONOMY

According to our morphometric and conchological analyses of specimens of *Donax* from Sergipe, we identified the presence of *D. gemmula* populations and recognized a new species that is formally described below.

Family DONACIDAE Fleming, 1828
Genus *Donax* Linnaeus, 1758

Donax trapesialis n. sp.
(Figs 8; 9)

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TYPE MATERIAL. — **Holotype**. **Brazil** • 1 specimen; Sergipe, Aracaju, Robalo beach; 11°01'47"S, 37°04'39"W; depth 0.5 m; II.1996; Carmen Guimarães leg.; intertidal sand; CZUFS BIV-00123.
Paratypes. **Brazil** • 50 specimens; same data as for holotype; CZUFS BIV-00124, CMPHRM 7519B, MZSP167895, MNRJ 37065, ZUEC-BIV 8626.

ETYMOLOGY. — This species is named after its trapezoid shape, a result of the more ventrally positioned anterior and posterior extreme points of the shell.

OTHER MATERIAL EXAMINED. — **Brazil** • 60 of 15.664 specimens; same data as for holotype; CZUFS BIV 00120 • 60 of 12.865 specimens; Sergipe, Aracaju, Atalaia beach; 10°58'43"S, 37°2'11"W; CZUFS BIV 00121 • 60 of 27.066 specimens; Sergipe, Aracaju, Mosqueiro beach; 11°06'19"S, 37°07'45"W; CZUFS BIV 00122.

TYPE LOCALITY. — Brazil, Robalo beach, Aracaju, Sergipe state (11°01'47.4"S, 37°04'39.0"W).

DIAGNOSIS. — This species differs from all other Brazilian species of *Donax* by the following combination of characteristics: evenly rounded posterior ridge, height/length ratio of 1/2 to 3/5, trapezoid shape with anterior and posterior extreme points close to the ventral margin, and concave or flat ventral margin.

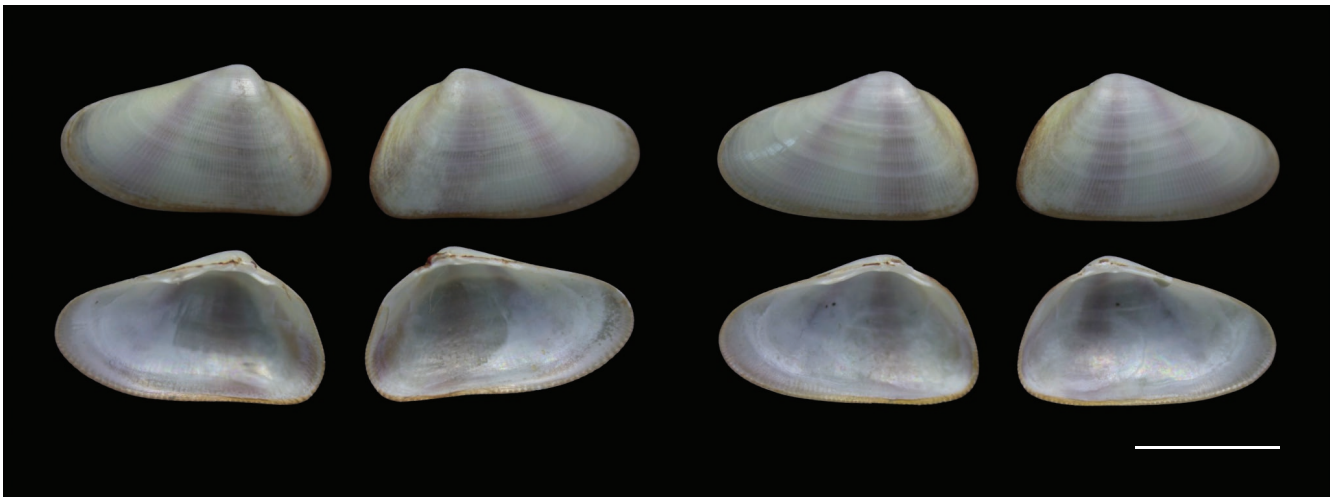

FIG. 9. — *Donax trapesialis* n. sp. paratypes, CZUFS BIV-00124, Sergipe, Aracaju - Robalo beach. Scale bar: 5 mm.

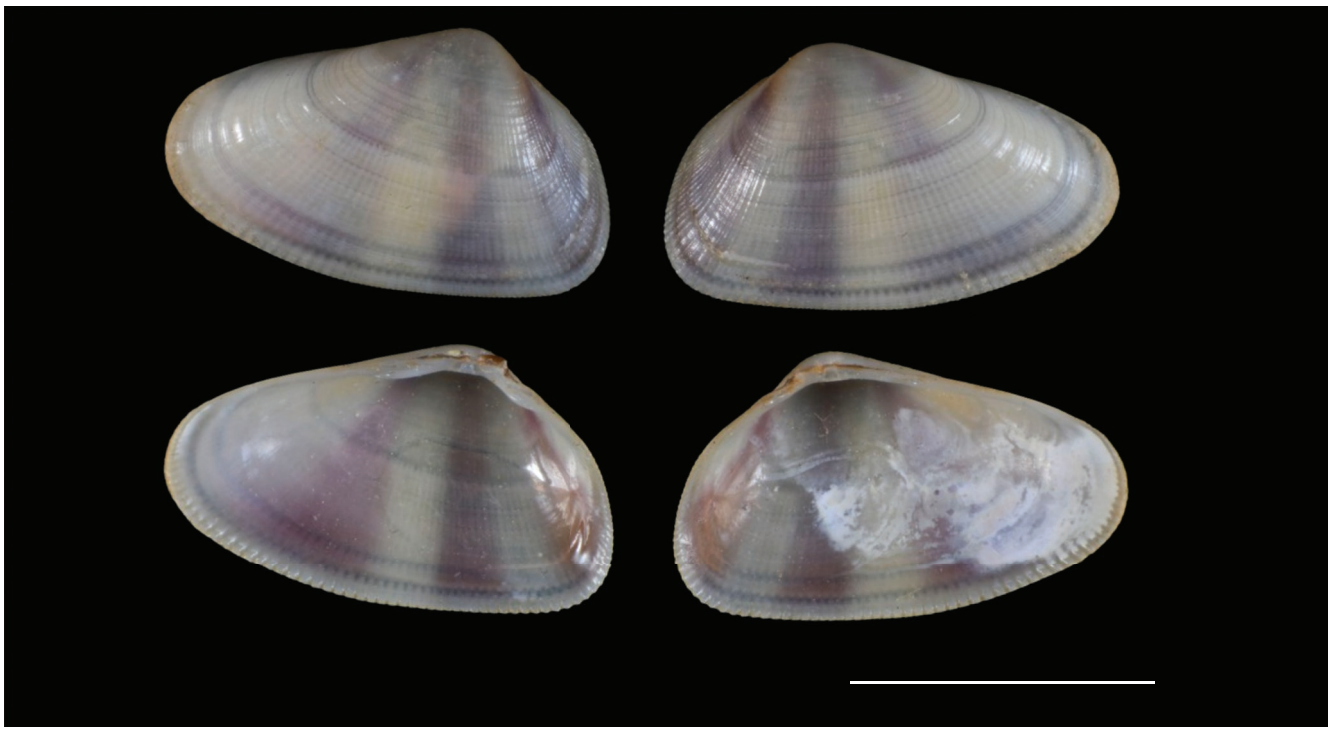

FIG. 10. — *Donax trapesialis* n. sp., ANSP 244133. Maceió, Ponta Verde, identified by Morrison (1971) as possible young specimens of *D. vellicatus* Reeve, 1855. Scale bar: 5 mm.

DESCRIPTION

Characteristic "donaciform", wedge shape of the genus, laterally compressed with a truncated posterior side and elongated anterior side (Morton 2016). Shell minute for the genus (8.5 mm width × 4.5 mm height, holotype), whitish or light grayish, often with triradial purple zones. Valve somewhat trapezoid due to the more ventrally positioned anterior and posterior extreme points. Posterior and anterior external surfaces of the shell ornated by radial incised lines and divided by an evenly rounded posterior ridge. Ventral margin flat or concave around its middle, with thinner and more numerous crenulations at the central region of the shell, larger and less numerous at the anterior and posterior sides, disappearing near the anterior end. Prominent umbones. Narrow hinge plate, with lateral teeth near the umbones, thicker in the left valve than in the right valve. Symmetrical posterior and anterior cardinal teeth in the right valve, uneven in the left valve. Large pallial sinus, exceeding half the height of the shell chamber and more than half the length between both adductor muscle scars.

DICHOTOMOUS KEY TO BRAZILIAN *DONAX* LINNAEUS, 1758, ADAPTED FROM LIMA & MARQUES (PERS. COMM.)

1. Nodular posterior surface ..... *Donax hanleyanus* Philippi, 1847
— Non-nodular posterior surface 2

2. Evenly rounded posterior ridge 3
— Carinate posterior ridge with an angle 4

3. Concave or flat ventral margin, trapezoid shape ..... *Donax trapesialis* n. sp.
— Convex ventral margin, subglobose shape ..... *Donax gemmula* Morrison, 1971

4. Visible growth lines, punctuated ..... *Donax denticulatus* Linnaeus, 1758
— Imperceptible growth lines 5

5. Strongly triangular, sharp posterior ridge ..... *Donax striatus* Linnaeus, 1767
— Moderately triangular, wide, unevenly rounded posterior ridges, two posterior slope surfaces easily distinguishable ..... *Donax vellicatus* Reeve, 1855

Thin, deciduous periostracum, visible only near the ventral margin of the shells. Soft parts could not be studied due to poor fixation and preservation.

REMARKS

Despite the sympatric occurrence with *D. gemmula* along the Sergipe coast, this species exhibits several key morphological differences. Notably, it is larger overall and wider relative to its height (height/width ratio of 1/2 to 3/5 for *D. trapesialis* n. sp. and > 2/3 for *D. gemmula*). Additionally, *D. trapesialis* n. sp. possesses a more elongated anterior side, due to a more posterior position of the umbo, a flatter or more concave ventral margin (compared to the convex margin of *D. gemmula*), and a more ventrally positioned anterior and posterior extreme points of the shell. Overall, its shape is more trapezoidal and less subglobose. In contrast to *D. striatus*, *D. hanleyanus*, and *D. denticulatus*, this species exhibits an evenly rounded posterior ridge. These latter species possess a distinctive sharp posterior ridge with a carina running from the dorsal to the ventral margin. This carinate feature is even present in juveniles of *D. hanleyanus* and *D. striatus*, highlighting a consistent difference (Morrison 1971; Barroso *et al.* 2013). Morrison (1971) previously suggested that specimens from a lot deposited in the ANSP collection, obtained from Alagoas should be juveniles of *D. vellicatus* (ANSP 244133, Fig. 10). However, the consistent absence of adult *D. vellicatus* specimens among the extensive collection of *D. trapesialis* n. sp. housed in the Invertebrates Collection (CZUFS BIV 00120, 15.519 specimens; CZUFS BIV 00121, 12.835 specimens) makes this hypothesis unlikely. This lack of adult *D. vellicatus* specimens further strengthens the case for recognizing *D. trapesialis* n. sp. as a distinct species.

DISCUSSION

The discovery of *D. gemmula* at this new northeastern Brazilian site strengthens the hypothesis proposed by Barroso *et al.* (2013) regarding a continuous geographic distribution of this species along the Brazilian coast. Conchological and morphometric analyses revealed clear distinctions between *D. gemmula* and *D. trapesialis* n. sp. Population analysis using k-means clustering reinforced this finding, separating the two species into distinct morphotypes (groups). This clustering pattern aligns with the results of the shape-size linear regression, where the smaller *D. gemmula* specimens form a separate group from the other populations.

The study revealed an allometric relation between shape and size in the specimens, meaning size explains only 6.9% of the shape variation. This suggests that other factors likely play a more significant role in shaping morphology. Alternatively, the observed differences could be due to phenotypic plasticity within *D. gemmula*, as seen in other *Donax* species. For example, Ocaña & Fernández (2011) found that *D. striatus* and *D. denticulatus* specimens collected from different Cuban beaches exhibited variations in the allometric relationships of height, length, and width.

The use of k-means and other multivariate analyses as taxonomic tools is relatively recent and has yielded compelling results, serving both as a proxy for biodiversity (Seifert *et al.* 2014) and in decision-making regarding new taxa (Kuo *et al.* 2017). However, it is crucial to recognize that these tools serve as adjuncts in the paradigm of integrative taxonomy, where final taxonomic decisions rely on consensus from all available data sources – morphometric, anatomical, morphological, and molecular. K-means applied to geometric morphometrics performs optimally when the groups analyzed exhibit strong biological correlations, as seen in 'compact cloud clusters' (Peng & Guiqiong 2011). Other forms of multivariate analysis have demonstrated coherence comparable to molecular results (e.g., Gu *et al.* 2022). This multi-tool analytical framework is critical for minimizing errors in assessing malacological biodiversity (Padial *et al.* 2010), whether stemming from species inflation (alpha errors = splitter hypothesis) or underestimation of local biodiversity (beta errors). Therefore, the data presented here, supported by consensus from morphometric and traditional conchological characters, strongly suggest that *D. trapesialis* n. sp. represents a new species on the Brazilian coast. These findings open avenues for further exploration of bivalve diversities along the South American coast. We

advocate for future standardized surveys employing diverse taxonomic tools to achieve a comprehensive understanding of marine biodiversity.

Lima & Marques (pers. comm.) developed a dichotomous key for *Donax* species from the Caribbean to South America, that we adapted to better distinguish the Brazilian *Donax* species, including *Donax trapesialis* n. sp. and *D. vellicatus*, as seen above.

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APPENDICES

Appendix 1. — Specimens used in morphometric analysis and allometry. Abbreviations: **SE**, Sergipe; **SP**, São Paulo and see Material and methods.

Collection number	Ref number	Species	Locality	Height (mm)	Lenght (mm)
CZUFS BIV 00120	RO01	*Donax trapesialis* n. sp.	Aracaju-SE	6.480	10.140
CZUFS BIV 00120	RO02	*Donax trapesialis* n. sp.	Aracaju-SE	6.510	10.730
CZUFS BIV 00120	RO03	*Donax trapesialis* n. sp.	Aracaju-SE	6.670	11.790
CZUFS BIV 00120	RO04	*Donax trapesialis* n. sp.	Aracaju-SE	6.070	11.120
CZUFS BIV 00120	RO05	*Donax trapesialis* n. sp.	Aracaju-SE	7.050	10.700
CZUFS BIV 00120	RO06	*Donax trapesialis* n. sp.	Aracaju-SE	7.100	12.040
CZUFS BIV 00120	RO07	*Donax trapesialis* n. sp.	Aracaju-SE	6.122	10.948
CZUFS BIV 00120	RO08	*Donax trapesialis* n. sp.	Aracaju-SE	6.513	11.813
CZUFS BIV 00120	RO09	*Donax trapesialis* n. sp.	Aracaju-SE	6.118	10.605
CZUFS BIV 00120	RO10	*Donax trapesialis* n. sp.	Aracaju-SE	7.200	12.207
CZUFS BIV 00120	RO11	*Donax trapesialis* n. sp.	Aracaju-SE	7.485	12.583
CZUFS BIV 00120	RO12	*Donax trapesialis* n. sp.	Aracaju-SE	6.123	10.569
CZUFS BIV 00120	RO13	*Donax trapesialis* n. sp.	Aracaju-SE	6.042	10.598
CZUFS BIV 00120	RO14	*Donax trapesialis* n. sp.	Aracaju-SE	7.346	12.695
CZUFS BIV 00120	RO15	*Donax trapesialis* n. sp.	Aracaju-SE	6.898	11.816
CZUFS BIV 00120	RO16	*Donax trapesialis* n. sp.	Aracaju-SE	6.898	11.833
CZUFS BIV 00120	RO17	*Donax trapesialis* n. sp.	Aracaju-SE	6.616	10.736
CZUFS BIV 00120	RO18	*Donax trapesialis* n. sp.	Aracaju-SE	6.981	11.864
CZUFS BIV 00120	RO19	*Donax trapesialis* n. sp.	Aracaju-SE	6.635	10.806
CZUFS BIV 00120	RO20	*Donax trapesialis* n. sp.	Aracaju-SE	6.343	10.271
CZUFS BIV 00120	RO21	*Donax trapesialis* n. sp.	Aracaju-SE	6.768	11.443
CZUFS BIV 00120	RO22	*Donax trapesialis* n. sp.	Aracaju-SE	6.519	11.383
CZUFS BIV 00120	RO23	*Donax trapesialis* n. sp.	Aracaju-SE	7.145	12.745
CZUFS BIV 00120	RO24	*Donax trapesialis* n. sp.	Aracaju-SE	6.719	11.474
CZUFS BIV 00120	RO25	*Donax trapesialis* n. sp.	Aracaju-SE	6.055	10.774
CZUFS BIV 00120	RO26	*Donax trapesialis* n. sp.	Aracaju-SE	6.099	10.370
CZUFS BIV 00120	RO27	*Donax trapesialis* n. sp.	Aracaju-SE	6.617	11.177
CZUFS BIV 00120	RO28	*Donax trapesialis* n. sp.	Aracaju-SE	6.886	10.836
CZUFS BIV 00120	RO29	*Donax trapesialis* n. sp.	Aracaju-SE	6.365	10.486
CZUFS BIV 00120	RO30	*Donax trapesialis* n. sp.	Aracaju-SE	7.434	12.587
CZUFS BIV 00121	AT01	*Donax trapesialis* n. sp.	Aracaju-SE	5.558	9.390
CZUFS BIV 00121	AT02	*Donax trapesialis* n. sp.	Aracaju-SE	7.185	10.986
CZUFS BIV 00121	AT03	*Donax trapesialis* n. sp.	Aracaju-SE	6.381	10.444
CZUFS BIV 00121	AT04	*Donax trapesialis* n. sp.	Aracaju-SE	6.457	10.354
CZUFS BIV 00121	AT05	*Donax trapesialis* n. sp.	Aracaju-SE	6.227	9.529
CZUFS BIV 00121	AT06	*Donax trapesialis* n. sp.	Aracaju-SE	6.651	11.126
CZUFS BIV 00121	AT07	*Donax trapesialis* n. sp.	Aracaju-SE	6.171	9.953
CZUFS BIV 00121	AT08	*Donax trapesialis* n. sp.	Aracaju-SE	6.211	10.444
CZUFS BIV 00121	AT09	*Donax trapesialis* n. sp.	Aracaju-SE	6.248	9.594
CZUFS BIV 00121	AT10	*Donax trapesialis* n. sp.	Aracaju-SE	6.133	9.740
CZUFS BIV 00121	AT11	*Donax trapesialis* n. sp.	Aracaju-SE	6.534	10.041
CZUFS BIV 00121	AT12	*Donax trapesialis* n. sp.	Aracaju-SE	6.112	10.460
CZUFS BIV 00121	AT13	*Donax trapesialis* n. sp.	Aracaju-SE	6.133	9.971
CZUFS BIV 00121	AT14	*Donax trapesialis* n. sp.	Aracaju-SE	6.534	11.439
CZUFS BIV 00121	AT15	*Donax trapesialis* n. sp.	Aracaju-SE	6.410	10.730
CZUFS BIV 00121	AT16	*Donax trapesialis* n. sp.	Aracaju-SE	6.596	11.060
CZUFS BIV 00121	AT17	*Donax trapesialis* n. sp.	Aracaju-SE	4.808	8.340
CZUFS BIV 00121	AT18	*Donax trapesialis* n. sp.	Aracaju-SE	6.093	10.048
CZUFS BIV 00121	AT19	*Donax trapesialis* n. sp.	Aracaju-SE	7.137	11.604
CZUFS BIV 00121	AT20	*Donax trapesialis* n. sp.	Aracaju-SE	6.336	11.001
CZUFS BIV 00121	AT21	*Donax trapesialis* n. sp.	Aracaju-SE	5.646	9.253
CZUFS BIV 00121	AT22	*Donax trapesialis* n. sp.	Aracaju-SE	6.485	11.141
CZUFS BIV 00121	AT23	*Donax trapesialis* n. sp.	Aracaju-SE	6.072	10.436
CZUFS BIV 00121	AT24	*Donax trapesialis* n. sp.	Aracaju-SE	6.401	11.032
CZUFS BIV 00121	AT25	*Donax trapesialis* n. sp.	Aracaju-SE	6.012	9.757
CZUFS BIV 00121	AT26	*Donax trapesialis* n. sp.	Aracaju-SE	6.469	10.345
CZUFS BIV 00121	AT27	*Donax trapesialis* n. sp.	Aracaju-SE	6.421	10.788
CZUFS BIV 00121	AT28	*Donax trapesialis* n. sp.	Aracaju-SE	6.577	10.973
CZUFS BIV 00121	AT29	*Donax trapesialis* n. sp.	Aracaju-SE	6.301	10.758
CZUFS BIV 00121	AT30	*Donax trapesialis* n. sp.	Aracaju-SE	7.531	12.063
CZUFS BIV 00122	MO01	*Donax gemmula*	Aracaju-SE	2.854	4.143
CZUFS BIV 00122	MO02	*Donax gemmula*	Aracaju-SE	3.116	4.362
CZUFS BIV 00122	MO03	*Donax gemmula*	Aracaju-SE	2.931	4.375
CZUFS BIV 00122	MO04	*Donax gemmula*	Aracaju-SE	3.319	5.386
CZUFS BIV 00122	MO05	*Donax gemmula*	Aracaju-SE	3.606	5.809
CZUFS BIV 00122	MO06	*Donax gemmula*	Aracaju-SE	2.695	3.713

Appendix 1. — Continuation.

Collection number	Ref number	Species	Locality	Height (mm)	Lenght (mm)
CZUFS BIV 00122	MO07	*Donax gemmula*	Aracaju-SE	3.337	5.486
CZUFS BIV 00122	MO08	*Donax gemmula*	Aracaju-SE	3.345	5.184
CZUFS BIV 00122	MO09	*Donax gemmula*	Aracaju-SE	3.441	5.210
CZUFS BIV 00122	MO10	*Donax gemmula*	Aracaju-SE	3.172	4.417
CZUFS BIV 00122	MO11	*Donax gemmula*	Aracaju-SE	2.934	4.061
CZUFS BIV 00122	MO12	*Donax gemmula*	Aracaju-SE	3.772	5.950
CZUFS BIV 00122	MO13	*Donax gemmula*	Aracaju-SE	3.027	4.592
CZUFS BIV 00122	MO14	*Donax gemmula*	Aracaju-SE	2.324	3.177
CZUFS BIV 00122	MO15	*Donax gemmula*	Aracaju-SE	3.393	4.948
CZUFS BIV 00122	MO16	*Donax gemmula*	Aracaju-SE	3.111	4.751
CZUFS BIV 00122	MO17	*Donax gemmula*	Aracaju-SE	3.495	5.659
CZUFS BIV 00122	MO18	*Donax gemmula*	Aracaju-SE	3.830	5.985
CZUFS BIV 00122	MO19	*Donax gemmula*	Aracaju-SE	3.702	5.573
CZUFS BIV 00122	MO20	*Donax gemmula*	Aracaju-SE	3.093	4.312
CZUFS BIV 00122	MO21	*Donax gemmula*	Aracaju-SE	3.567	5.747
CZUFS BIV 00122	MO22	*Donax gemmula*	Aracaju-SE	3.201	4.712
CZUFS BIV 00122	MO23	*Donax gemmula*	Aracaju-SE	2.906	4.626
CZUFS BIV 00122	MO24	*Donax gemmula*	Aracaju-SE	2.529	3.337
CZUFS BIV 00122	MO25	*Donax gemmula*	Aracaju-SE	3.084	4.372
CZUFS BIV 00122	MO26	*Donax gemmula*	Aracaju-SE	3.564	5.073
CZUFS BIV 00122	MO27	*Donax gemmula*	Aracaju-SE	2.572	4.008
CZUFS BIV 00122	MO28	*Donax gemmula*	Aracaju-SE	2.941	4.033
CZUFS BIV 00122	MO29	*Donax gemmula*	Aracaju-SE	2.590	3.588
CZUFS BIV 00122	MO30	*Donax gemmula*	Aracaju-SE	2.305	3.132
MZSP 26813	SA01	*Donax gemmula*	Santos-SP	5.277	8.537
MZSP 26813	SA02	*Donax gemmula*	Santos-SP	6.622	9.938
MZSP 26813	SA03	*Donax gemmula*	Santos-SP	6.130	9.588
MZSP 26813	SA04	*Donax gemmula*	Santos-SP	6.003	8.819
MZSP 26813	SA05	*Donax gemmula*	Santos-SP	7.212	9.340
MZSP 26813	SA06	*Donax gemmula*	Santos-SP	5.984	9.244
MZSP 26813	SA07	*Donax gemmula*	Santos-SP	7.506	10.765
MZSP 26813	SA08	*Donax gemmula*	Santos-SP	5.589	8.632
MZSP 26813	SA09	*Donax gemmula*	Santos-SP	5.582	8.374
MZSP 26813	SA10	*Donax gemmula*	Santos-SP	6.206	9.806
MZSP 26813	SA11	*Donax gemmula*	Santos-SP	5.772	9.034
MZSP 26813	SA12	*Donax gemmula*	Santos-SP	5.482	8.480
MZSP 26813	SA13	*Donax gemmula*	Santos-SP	6.533	9.567
MZSP 26813	SA14	*Donax gemmula*	Santos-SP	6.174	9.458
MZSP 26813	SA15	*Donax gemmula*	Santos-SP	5.170	7.958
MZSP 26813	SA16	*Donax gemmula*	Santos-SP	6.767	10.523
MZSP 26813	SA17	*Donax gemmula*	Santos-SP	5.248	7.542
MZSP 26813	SA18	*Donax gemmula*	Santos-SP	6.313	9.542
MZSP 26813	SA19	*Donax gemmula*	Santos-SP	5.573	8.983
MZSP 26813	SA20	*Donax gemmula*	Santos-SP	6.118	9.586
MZSP 26813	SA21	*Donax gemmula*	Santos-SP	6.079	8.801
MZSP 26813	SA22	*Donax gemmula*	Santos-SP	6.691	9.710
MZSP 26813	SA23	*Donax gemmula*	Santos-SP	5.036	7.615
MZSP 26813	SA24	*Donax gemmula*	Santos-SP	6.361	9.703
MZSP 26813	SA25	*Donax gemmula*	Santos-SP	5.009	7.763
MZSP 26813	SA26	*Donax gemmula*	Santos-SP	6.433	9.538
MZSP 26813	SA27	*Donax gemmula*	Santos-SP	5.375	8.189
MZSP 26813	SA28	*Donax gemmula*	Santos-SP	5.452	8.302
MZSP 26813	SA29	*Donax gemmula*	Santos-SP	5.102	8.529
MZSP 26813	SA30	*Donax gemmula*	Santos-SP	5.044	7.861
MZSP 040943	SB01	*Donax gemmula*	São Sebastião-SP	3.174	4.686
MZSP 040943	SB02	*Donax gemmula*	São Sebastião-SP	3.976	6.042
MZSP 040943	SB03	*Donax gemmula*	São Sebastião-SP	4.243	6.734
MZSP 040943	SB04	*Donax gemmula*	São Sebastião-SP	3.394	5.277
MZSP 040943	SB05	*Donax gemmula*	São Sebastião-SP	3.285	4.993
MZSP 040943	SB06	*Donax gemmula*	São Sebastião-SP	3.122	4.484
MZSP 040943	SB07	*Donax gemmula*	São Sebastião-SP	3.725	5.847
MZSP 040943	SB08	*Donax gemmula*	São Sebastião-SP	2.859	4.044
MZSP 040943	SB09	*Donax gemmula*	São Sebastião-SP	4.124	6.284
MZSP 040943	SB10	*Donax gemmula*	São Sebastião-SP	3.338	4.880
MZSP 040943	SB11	*Donax gemmula*	São Sebastião-SP	2.819	3.874
MZSP 040943	SB12	*Donax gemmula*	São Sebastião-SP	3.347	5.007
MZSP 040943	SB13	*Donax gemmula*	São Sebastião-SP	4.336	6.756
MZSP 040943	SB14	*Donax gemmula*	São Sebastião-SP	3.900	5.874
MZSP 040943	SB15	*Donax gemmula*	São Sebastião-SP	3.617	6.062
MZSP 040943	SB16	*Donax gemmula*	São Sebastião-SP	3.261	4.615

Appendix 1. — Continuation.

Collection number	Ref number	Species	Locality	Height (mm)	Lenght (mm)
MZSP 040943	SB17	*Donax gemmula*	São Sebastião-SP	3.620	5.221
MZSP 040943	SB18	*Donax gemmula*	São Sebastião-SP	3.263	4.730
MZSP 040943	SB19	*Donax gemmula*	São Sebastião-SP	3.264	4.753
MZSP 040943	SB20	*Donax gemmula*	São Sebastião-SP	2.888	4.217
MZSP 040943	SB21	*Donax gemmula*	São Sebastião-SP	3.168	4.779
MZSP 040943	SB22	*Donax gemmula*	São Sebastião-SP	3.055	4.293
MZSP 040943	SB23	*Donax gemmula*	São Sebastião-SP	3.834	6.200
MZSP 040943	SB24	*Donax gemmula*	São Sebastião-SP	2.796	4.329
MZSP 040943	SB25	*Donax gemmula*	São Sebastião-SP	3.592	5.376
MZSP 040943	SB26	*Donax gemmula*	São Sebastião-SP	2.826	3.993
MZSP 040943	SB27	*Donax gemmula*	São Sebastião-SP	2.713	3.851
MZSP 040943	SB28	*Donax gemmula*	São Sebastião-SP	2.514	3.681
MZSP 040943	SB29	*Donax gemmula*	São Sebastião-SP	2.816	4.242

Appendix 2. — Dunn test's p-values for the distance between populations. Kruskal-Wallis indicates overall p-value for the distance among all populations. Abbreviations: see Material and methods.

Comparison	p-value (PC1)	p-value (PC2)
Kruskal-Wallis	<0.001	<0.001
AT - RO	0.030	0.725
AT - MO	<0.001	0.634
AT - SB	<0.001	0.474
AT - SA	<0.001	<0.001
RO - MO	<0.001	0.900
RO - SB	<0.001	0.716
RO - SA	<0.001	<0.001
MO - SA	0.270	<0.001
MO - SB	0.536	0.811
SA - SB	0.085	<0.001

Supplementary material 1. — Photographs of 147 Brazilian *Donax* specimens from the states of Sergipe and São Paulo. Abbreviations: **AT**, Atalaia beach; **RO**, Robalo beach; **MO**, Mosqueiro beach; **SA**, Santos-SP; **SB**, São Sebastião-SP. Raw data with landmarks for allignment in R as well as for analyses in MorphoJ are also provided, including scripts and complimentary files. https://doi.org/10.6084/m9.figshare.27701988.v1