

RESEARCH ARTICLE

The exotic calcareous sponge *Heteropia glomerosa* (Calcarea: Heteropiidae) invading natural environments on the coast of São Paulo, Brazil

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ABSTRACT. Herein, we present morphological and genetic evidence of the presence of the exotic calcareous sponge *Heteropia glomerosa* (Bowerbank, 1873) on the northern coast of the state of São Paulo. We also report its occurrence on natural substrates in the region and a case of the sponge living in association with the cryptogenic ascidian *Phallusia nigra* Savigny, 1816—an ecological interaction never before mentioned in the literature. Previous records of *H. glomerosa* in Ilhabela and São Sebastião were restricted to artificial substrates, such as PVC panels. Furthermore, earlier studies along the Brazilian coast have indicated that its colonization occurs more frequently on artificial substrates, such as ropes, wood, plastic, concrete, and docks within marina and port areas. All the new records presented here are from beaches that have never been sampled before, including Ubatuba as a new locality. Additionally, this finding on natural substrates represents an advance in the knowledge of its distribution and serves as an alert to the potential expansion of this species to the southern coast of São Paulo. Further investigations into ecological aspects are necessary to understand the processes favoring geographical expansion and ecological interactions with native species. Therefore, it is essential to assess the ecological role of *H. glomerosa* in the environment by implementing long-term monitoring actions.

KEYWORDS. Alien species, marine invertebrates, natural substrate, southeastern ecoregion.

INTRODUCTION

Heteropia glomerosa (Bowerbank, 1873) is one of the three exotic calcareous sponges occurring on the Brazilian coast. The other two are *Paraleucilla magna* Klautau, Monteiro & Borojevic, 2004 and *Sycettusa hastifera* (Row, 1909) (Cavalcanti et al. 2020, Klautau et al. 2020, Ribeiro et al. 2021). Recent papers on the usage of *H. glomerosa* as a biological model for reproduction (Calazans and Lanna 2019), recruitment dynamics (Chagas et al. 2020), and integrative taxonomy (Klautau et al. 2020) produced biological information pointing to the invasive status of the species in Brazilian waters. However, so far, no environmental or economic impacts have been reported on the biological communities living nearby or in association with these three calcareous sponges.

Invasive species are those introduced intentionally or unintentionally by human activities to places outside their

natural distribution area, where they establish themselves, produce offspring, and disperse to new areas from the point of introduction. According to Decision VI/23 of the Conference of the Parties to the Convention on Biological Diversity, this definition does not require proof of current or potential negative impacts, as also emphasized by Decision V/8 (Richardson et al. 2000, Blackburn et al. 2011, Dechoum et al. 2024). Nevertheless, herein we are being conservative and adopting the status of “exotic/alien” for *H. glomerosa*, in agreement with what has been used in the literature on calcareous sponges given the difficulty of proving the exact point of introduction and due to uncertainty as to whether or not the species is undergoing geographic expansion. As of now, *H. glomerosa* is recognized as an exotic species in the Atlantic Ocean, with records along the Brazilian coast (Klautau et al. 2020). In other reported localities, including India (Dendy 1916), China (Liu 2008), Australia (Row and Hôzawa 1931), New Zealand (Kelly

et al. 2009), Indonesia (Van Soest and De Voogd 2015), and its type locality in South Africa (Bowerbank 1873), its status as native or alien remains uncertain.

Calazans and Lanna (2019) mentioned that *H. glomerosa* was very abundant in Todos os Santos Bay, Salvador, Bahia, and has been generally found as a large, conspicuous, and easily accessible species. They also revealed its opportunistic life-history strategy, characterized by early reproduction, producing abundant propagules and giving the species one of the greatest reproductive efforts among sponges. In addition, *H. glomerosa* showed continuous reproductive activity, a typical characteristic exhibited by the two other species of exotic calcareous sponges, *P. magna* and *S. hastifera*. The authors suggested that the rainy season is the best time for field efforts to prevent the expansion and establishment of the species.

Chagas et al. (2020), studying the recruitment dynamics of *H. glomerosa* in the same locality, found that the number of specimens on experimental plates was extremely low. Also, they did not notice seasonal patterns of recruitment, although the highest number of recruits occurred between February and April, mainly in the dry season. The authors hypothesized that the short period of immersion of the plates and the absence of a pre-established fouling community were the limiting factors for the species to establish itself.

Klautau et al. (2020) commented on the notorious abundance and wide distribution of *H. glomerosa* along the Brazilian coast since its first appearance, covering 2,900 km from 2005 to 2020. In addition, the authors found that *H. glomerosa* met seven of the 10 criteria proposed by Chapman and Carlton (1991) for recognizing an exotic species and hypothesized that biofouling was the main source of the sponge's introduction into the Western Atlantic. They also discussed the species' ability to colonize geographical areas with very distinct seawater temperatures, given that such environmental contrast is found between the northeast and southeast coasts of Brazil.

Among the three exotic calcareous sponges, *H. glomerosa* is the most widely dispersed, being present in the northeastern, eastern, and southeastern ecoregions of Brazil. This environmental tolerance, combined with a preference for artificial habitats, makes it the most successful exotic calcareous sponge to colonize such an extensive latitudinal gradient. In the southeastern ecoregions, records from the coast of Rio de Janeiro have been known for at least 20 years (Klautau et al. 2020), while the presence of the species further south, in São Paulo, was only confirmed in 2016 during a biofouling experiment (Oricchio et al. 2019).

Studies on ecological interactions involving calcareous sponges are scarce. An investigation into the associated macrofauna was conducted on a small scale for *Paraleucilla magna* (Padua et al. 2013), but no such study exists for *H. glomerosa* or *S. hastifera*. Calazans and Lanna (2019) reported the removal of associated organisms (crustaceans, ascidians, algae, and others) during the cleaning of *H. glomerosa*, and Chagas et al. (2020) drew attention to several organisms colonizing the cables of the artificial plates; however, these authors did not mention evidence of direct interaction between these organisms and *H. glomerosa*.

Herein, we report the first record of *H. glomerosa* in São Paulo state on a natural substrate, comment on its association with a cryptogenic ascidian, and list important knowledge gaps to improve the understanding of its potential for geographical expansion.

MATERIAL AND METHODS

Sampling sites

Investigation of rocky shore areas for sponge sampling were conducted throughout 2023 in three municipalities along the coast of the state of São Paulo (Fig. 1), which are included in the Southeastern Brazil marine ecoregion (Spalding et al. 2007): Saco da Ribeira Bay (SRB) in Ubatuba (23°30'00.6"S; 45°07'05.6"W), Pedras Miudas Beach (PMB) (23°49'47.7"S; 45°23'23.4"W) in Ilhabela, and Toque-Toque Pequeno Beach (TTPB) (23°49'25.6"S; 45°32'02.2"W) in São Sebastião. All samplings were conducted at low tide, at depths of up to 0.5 m in rocky shore environments. Samples were fixed in 96% ethanol and later transferred to 100% ethanol.

At Saco da Ribeira Bay, in Ubatuba (Fig. 1A), the landscape consists of a bay with small boats and yachts in a highly polluted environment with suspended sediments (CETESB 2024). Two samplings were conducted in this area, one in April and the other in October 2023. At Pedras Miudas Beach, sampling occurred in September 2023. Pedras Miudas Beach (Fig. 1B) is a small beach facing the São Sebastião Channel—an area with constant traffic of large ships, close to Cabras Island, and used by swimmers and small boats. Finally, Toque-Toque Pequeno Beach, the most distant sampling site (Fig. 1C), yielded only one specimen. This beach is used for canoeing, artisanal fishing, and recreational swimming.

Morphological identification

The spicule composition of the specimens was analyzed under a microscope (Nikon), pictures were captured with a camera (Motic Image Plus 2.0), and measurements

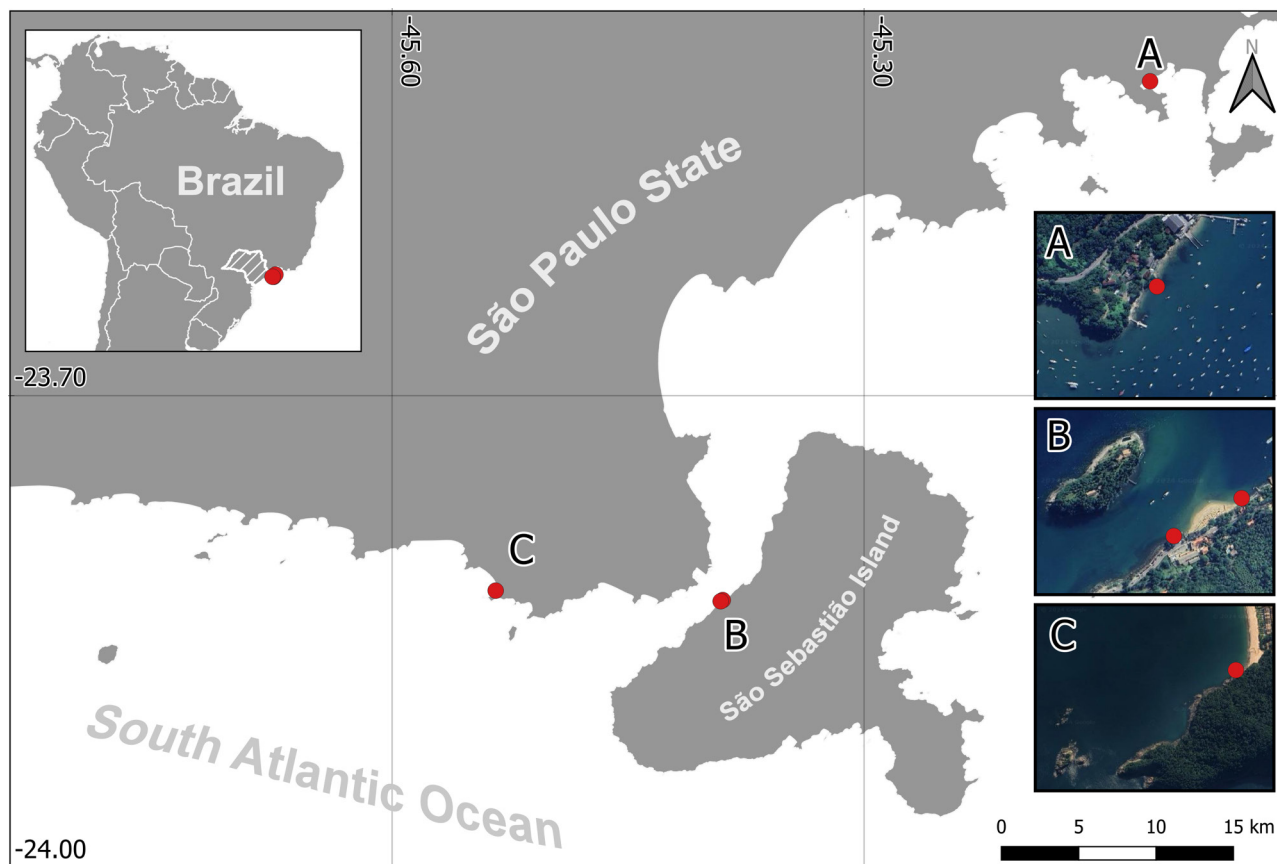


Figure 1. Map illustrating the study area located on the northern coastline of São Paulo State. (A) Saco da Ribeira Bay; (B) Pedras Miudas Beach; (C) Toque-Toque Pequeno Beach.

were performed using ImageJ v1.54g. Only one specimen from each site was measured. The results are presented in tabular form, including the minimum (min), mean, standard deviation (SD), and maximum (max) values, along with the number of spicules analyzed (N). Identification followed standard protocols (Klautau and Valentine 2003) with a subsequent modification: the substitution of Canada balsam for Entellan (Merck) as the mounting medium for spicule slides (Cavalcanti et al. 2014).

Genetic identification

Two specimens, one from Pedras Miudas Beach (PPM12) and another from Toque-Toque Pequeno Beach (TTP39), were analyzed. DNA was extracted using an Easy-pure Genomic DNA Kit (TransGen Biotech). The C-region of the Large Subunit (LSU) rRNA was amplified by polymerase chain reaction (PCR) with the primers: fwd 5'-GAAAAG-CACTTTGAAAAGAGA-3' (Voigt and Wörheide 2016) and rv

5'-TCCGTGTTTCAAGACGGG-3' (Chombard et al. 1998). PCR mixes contained 1× buffer (*Taq* DNA Polymerase 5U, Ludwig), 0.2 mM dNTP, 2.5 mM $MgCl_2$, 0.33 mM of each primer, one unit of *Taq* DNA polymerase (Ludwig), and 100–150 ng of DNA in a final volume of 25 μ L. Amplification followed a first cycle of 4 min at 94 °C, 1 min at 50 °C, and 1 min at 72 °C; 35 cycles of 1 min at 92 °C, 1 min at 50 °C, and 1 min at 72 °C; and a final cycle of 6 min at 72 °C. PCR products were purified using a DNA Extraction and Purification Kit (NovaBiotecnologia).

Sequences were trimmed and edited using Geneious v. 11.1.5. BLAST searches were performed to confirm the identity of the sequences (<http://www.ncbi.nlm.nih.gov/blast/>). Sequences from GenBank were combined with newly generated ones (Table 1) to construct a phylogenetic tree. DNA alignments were performed using the online MAFFT v. 7 platform (Katoh et al. 2019) with the Q-INS-i strategy (Katoh and Toh 2008) and default parameters.

Table 1. Species, ecoregions, vouchers, and GenBank accessions used in phylogenetic analyses.

Species	Marine Ecoregion	Voucher Number	GenBank Accession
<i>Anamixilla torresi</i>	Halmahera	RMNH 6572	MF686072
<i>Grantessa tumida</i>	Southern Caribbean	UFRJPOR 6701	MF472616
<i>Grantessa woerheidei</i>	Southern Red Sea	RMNH 9586	MF872773
<i>Heteropia glomerosa</i>	Southeastern Brazil	TTP39*	PX549218
<i>Heteropia glomerosa</i>	Southeastern Brazil	PPM12*	PX549217
<i>Heteropia glomerosa</i>	Eastern Brazil	UFRJPOR 6151	MN402721
<i>Heteropia glomerosa</i>	Eastern Brazil	UFRJPOR 6191	MN402722
<i>Heteropia glomerosa</i>	Eastern Brazil	UFRJPOR 7608	MN402723
<i>Heteropia glomerosa</i>	Eastern Brazil	UFRJPOR 7609	MN402724
<i>Heteropia minor</i>	Sulawesi Sea/Makassar Strait	RMNHPPOR 1872	MF686070
<i>Heteropia minor</i>	Banda Sea	RMNHPPOR 3603	MF686068
<i>Heteropiidae</i> sp.	St. Helena and Ascension Islands	RMNHPPOR-SA86	MH385248
<i>Sycettusa hastifera</i>	Northern and Central Red Sea	ZMA 13443	MF872778
<i>Sycettusa hirsutissima</i>	Northern and Central Red Sea	RMNH 9588	MF872776
<i>Sycettusa simplex</i>	Maldives	RMNH 10154	MF872779
<i>Sycettusa zanzibarisi</i>	Seychelles	ZMA 11568	MF872783
<i>Uteopsis argentea</i>	Sulawesi Sea/Makassar Strait	RMNHPPOR 1871	MF686074
<i>Uteopsis argentea</i>	Sunda Shelf/Java Sea	RMNHPPOR 2598	MF686075
<i>Uteopsis argentea</i>	Northeast Sulawesi	RMNHPPOR 6593	MF686076

*New sequences.

Tree construction was performed in IQ-TREE v. 2.4.0 (Minh et al. 2020), applying the best-fit substitution model for the C-LSU dataset (TIM+F+I+G4), as determined by the Bayesian Information Criterion (BIC). Branch support was calculated using ultrafast bootstraps (Minh et al. 2013, Hoang et al. 2018) with 100,000 replicates. Final trees were rendered in FigTree v. 1.4.0 and stylized in Adobe Photoshop. The uncorrected p-distance was calculated in MEGA X (Kumar et al. 2018) to estimate intraspecific and interspecific variability.

RESULTS

A total of 23 specimens were collected on small rocks covered by algae and other encrusting invertebrates in sciaphilous habitats (shaded environments characterized by low light availability) along the low intertidal zone: 13 specimens at Saco da Ribeira Bay (SRB), nine specimens at Pedras Miudas Beach (PMB), and one specimen at Toque-Toque Pequeno Beach (TTPB). At Pedras Miudas, one individual was found at the base of *Phallusia nigra*, a cryptogenic ascidian (Fig. 2B).

Morphological evidence

The external shape of the sponge *Heteropia glomerosa* is highly variable in the number, diameter, and height of the tubes that are connected at the base (Fig. 2B). It resembles a bunch of bananas (Fig. 2A). The shape of each tube can also

vary between cylindrical or pyriform, and straight or curved (Fig. 2B). The ornamentation of the oscula can also present certain variation, with the crown being well-developed, scarce, or even absent. These variations can be seen within the same individual or among individuals. The color in some individuals is white, but in others it could be light beige or beige, mainly because of the accumulation of thin sediment and micro-incrustation on its external surface. The external wall of the body has an appearance of armor because of the presence of large diactines disposed longitudinally side-by-side, forming a rigid reinforcement (Fig. 2C). The thickness of the wall is relatively thin, slightly wider than 100 μ m (Fig. 2D, E); in contrast, the species is composed of several types of spicules (Fig. 3). The specimens from which the spicules were prepared have seven distinct categories (Fig. 3), and measurements are shown in Table 2.

Genetic evidence

The two specimens analyzed were identified as *H. glomerosa* based on morphological evidence. The phylogenetic reconstruction using the molecular marker C-LSU grouped all sequences of *H. glomerosa* retrieved from GenBank with our two specimens in the same clade (Fig. 4). Additionally, the calculation of p-distance values shows an intraspecific variation of 0%–1%, which corroborates our morphological findings, confirming the specific status of these two specimens

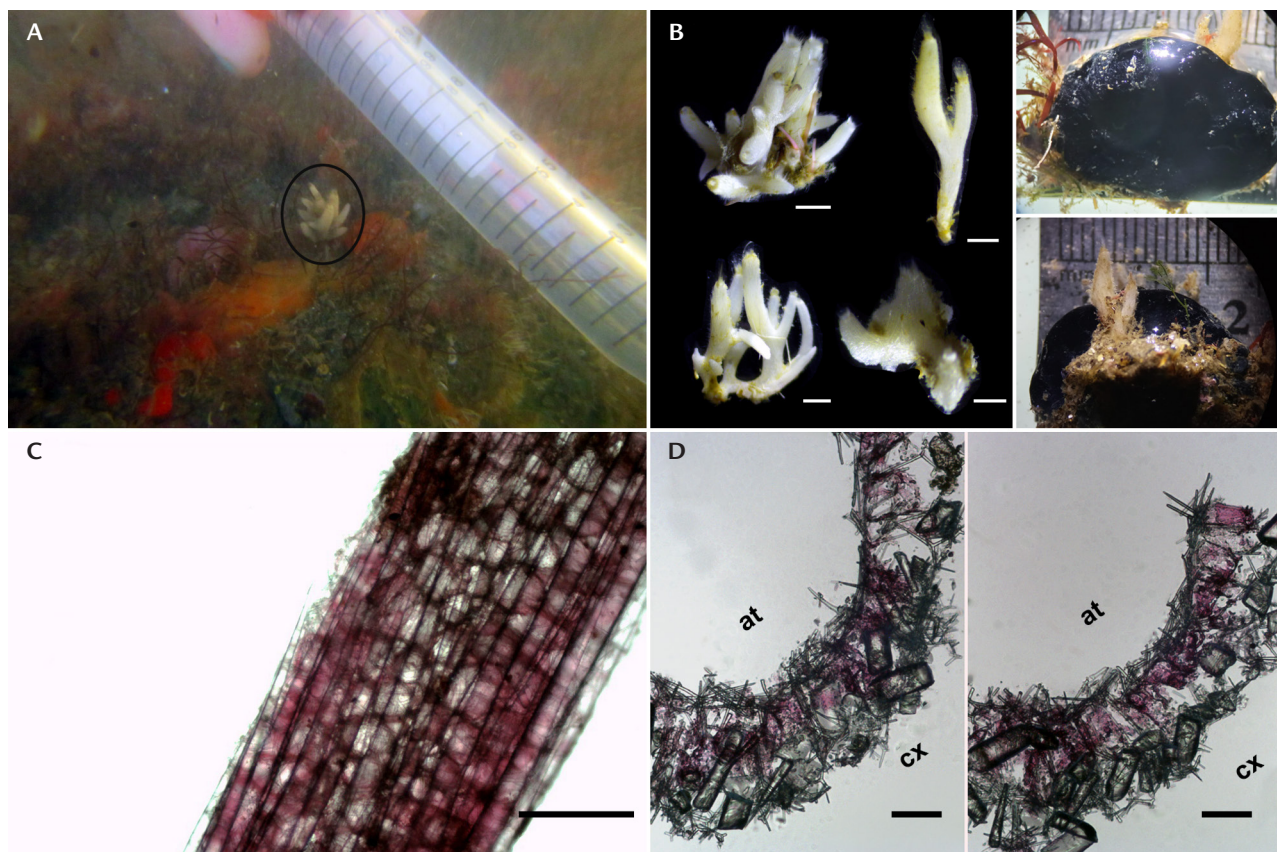


Figure 2. Morphological aspects of *Heteropia glomerosa* (SRB07). (A) Specimen in vivo, highlighted within the black circle, observed on a rocky shore at Saco da Ribeira Bay. (B) Specimens of *H. glomerosa* preserved in ethanol (SRB01, PPM06, PPM14, TTP39), inset shows the sponge associated with the black ascidian *Phallusia nigra*. Scale bars: 2 mm. (C) Longitudinal section showing the organization of the cortical diactines of the sponge. Scale bar: 100 μ m. (D) Cross-section showing the skeleton organization of the sponge (PPM04), cx = cortex and at = atrium. Scale bar: 100 μ m.

as *H. glomerosa*. Therefore, this constitutes genetic evidence that is in line with morphological data, allowing us to extrapolate the species determination to the other 21 specimens.

DISCUSSION

Monitoring and controlling invasive species are key strategies for assessing the environmental impacts associated with their presence. For calcareous sponges, however, monitoring is challenging due to their small size and laborious taxonomy. *Heteropia glomerosa* is one of the few species found along the Brazilian coast with external morphological traits that allow for preliminary identification in the field. Still, detailed morphological analyses and, when possible, molecular approaches remain the most reliable methods for accurate identification. The sampled

specimens showed a spicule composition consistent with what has been documented for the species. Likewise, in general, the dimensions of the seven categories of spicules are within the expected range for the species, with a few exceptions. The measurements of the specimens from Brazil (Ceará, Bahia, Arraial do Cabo) are the closest to the data presented here, but lower than those of the holotype. Some differences were observed in the sizes of the diactines and in the apical ray of tetractines. The values of the diactines from our specimens were higher than the values for the specimen from Ceará. Also, the dimensions of the apical ray of the tetractines of our specimens (16.8 μ m) were closest to those from the species *Uteopsis argentea* (Poléjaeff, 1883) (18.4 μ m). Therefore, spicule size is another characteristic evaluated in this study that supports our identification. All the characteristics and their variations commented here are

Table 2. Spicules measurements of the specimens of *Heteropia glomerosa* for the respective localities: Saco da Ribeira Bay, Pedras Miudas Beach and Toque-Toque Pequeno Beach.

Spicule	Actine	Length (μm)				Width (μm)			
		Min	Mean	SD	Max	Min	Mean	SD	Max
SRB 01									
Cortical diactine		303	1095.8	489	2251.5	9.4	44.9	17.2	74.1
Cortical triactine	Paired	51.3	89.6	25.4	138.7	5.9	6.9	0.9	9.1
	Unpaired	43.4	68.7	12.8	91.1	4.9	6.7	1.0	8.4
Pseudosagittal	Paired 1	39.3	104.0	23.9	135.9	4.5	6.6	0.9	9.3
Triactine	Paired 2	35.6	78.3	20.2	110.2	5.3	7.1	1.1	10.3
	Unpaired	20.1	61.9	30.1	149.6	4.5	7.1	1.0	8.2
Subatrial Triactine	Paired	58.9	90.6	18.5	134.1	4.4	6.3	1.0	8.5
	Unpaired	86.4	165.6	43.0	265.9	5.6	7.4	1.1	9.9
Atrial Triactine	Paired	44.2	82.2	15.8	112.9	4.5	6.5	0.9	8.4
	Unpaired	56.6	94.5	27.2	185.3	5.1	7.0	0.9	8.0
Atrial Tetractine	Paired	63.9	113.7	22.8	152.2	5.4	17.9	1.4	10.9
	Unpaired	81.7	157.6	49.2	299.8	5.6	7.5	1.2	10.1
	Apical	8.1	17.9	10.1	50.1	3.5	5.4	0.8	6.6
PMB 06									
Cortical diactine		512.6	1301.4	574.9	2875.5	24.5	59.5	12.6	77.1
Cortical triactine	Paired	53.9	121.2	29.8	159.1	4.7	8.9	1.7	11.9
	Unpaired	45.5	77.0	17.6	107.6	5.7	8.0	1.7	11.9
Pseudosagittal	Paired 1	92.3	135.1	23.3	198.6	6.2	10	1.4	11.2
Triactine	Paired 2	55.4	97.6	19.1	147.9	5.7	9.4	1.6	12.1
	Unpaired	19.5	72.9	18	103.7	5.9	9.3	1.5	11.9
Subatrial Triactine	Paired	64.1	105.8	32.2	180	4.4	7.6	1.5	10.8
	Unpaired	118.5	188.3	60.5	376.1	3.8	7.6	2.2	13.2
Atrial Triactine	Paired	47.5	81.7	16.4	118	5.1	6.6	0.8	8.3
	Unpaired	76.9	100.7	16.2	136.1	4.9	6.3	0.8	8.2
Atrial Tetractine	Paired	83.9	132	23.7	176.9	5.8	9.1	1.3	11.6
	Unpaired	138.2	197.1	58.4	304.5	7.0	7.8	0.9	10.7
	Apical	13.1	28.2	16.0	73.5	5.2	6.4	0.9	8.6
TTPB 39									
Cortical diactine		405.8	789.1	267	1666.1	19.2	39.7	9.2	51.5
Cortical triactine	Paired	59.9	94.6	17.4	123.1	4.0	6.6	1.0	8.2
	Unpaired	23.0	74.0	22.4	116.3	5.0	6.1	0.9	9.3
Pseudosagittal	Paired 1	54.5	112.5	23.5	144	4.7	7.1	1.1	8.7
Triactine	Paired 2	52.1	82.5	14.6	118.5	4.4	6.9	1.4	9.9
	Unpaired	32.2	70.7	16.9	98.5	3.9	7.7	1.4	9.2
Subatrial Triactine	Paired	58.6	94.5	15	118.9	4.9	6.2	0.6	7.3
	Unpaired	102.6	152.9	31.3	219.8	4.9	6.5	1.1	10.1
Atrial Triactine	Paired	67.3	90.0	14.9	128	5.5	6.7	1.0	9.3
	Unpaired	73.8	125.9	22.9	149.7	4.7	6.3	0.8	8.3
Atrial Tetractine	Paired	73.8	125.9	22.9	149.7	4.7	6.3	0.8	8.3
	Unpaired	67.2	159.8	51.2	239	4.8	6.4	0.9	8.7
	Apical	9.5	16.8	6.7	35.8	3.8	4.7	0.6	5.9

compatible with what was described in Klautau et al. (2020) for the Brazilian specimens.

Among the records along the Brazilian coast, *H. glomerosa* has been repeatedly reported growing on artificial substrates in ports, recreational marinas, and mollusk farms

(Calazans and Lanna 2019, Chagas et al. 2020, Klautau et al. 2020). Although there are no records of the species on ship hulls, these structures are among the main vectors suspected of transporting and spreading exotic calcareous sponges, facilitating their colonization in new areas (Ribeiro et al. 2022).

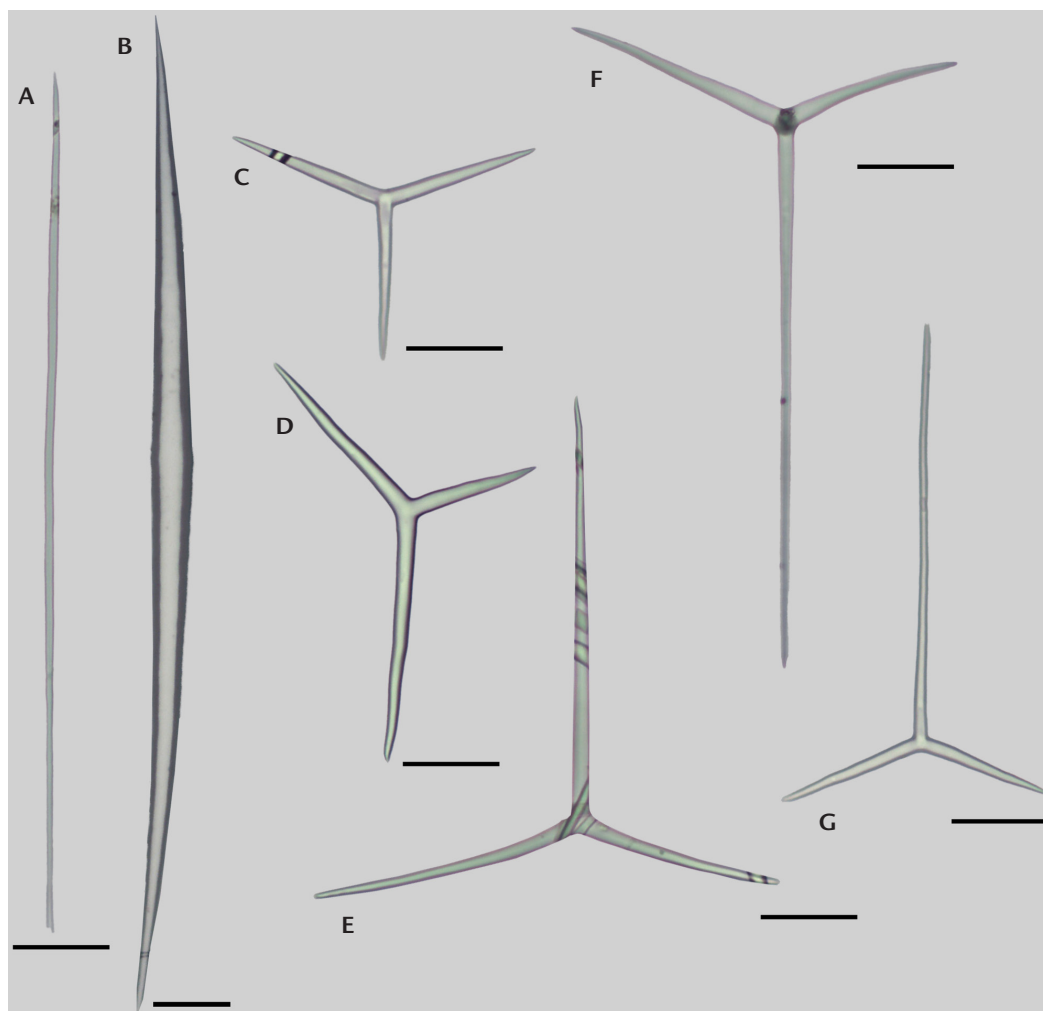


Figure 3. Spicules of *Heteropia glomerosa* (PPM06). (A) Cortical trichoxea; (B) Cortical diactine; (C) Cortical triactine; (D) Subcortical pseudosagittal triactine; (E) Subatrial triactine; (F) Atrial tetractine; (G) Atrial triactine. Scale bars: A, C-G = 50 µm; B = 100 µm.

Currently, there is no evidence that the exotic species *H. glomerosa* constitutes a real or potential threat to the environment, economy, or biological communities. This animal exhibits remarkable growth, reproduction, and colonization in artificial environments, but little is known about how these traits are affecting the species' ability to invade and spread. Therefore, close observation and the recording of new localities are essential to understanding the extent of its distribution. Research in population genetics may reveal whether the presence of this species in Brazil is the result of a single event or multiple events and identify the sites of initial colonization, as demonstrated by the study conducted on the species *P. magna* (Cavalcanti et al. 2020).

Our observations on natural substrates are an important record for future investigations; as *H. glomerosa* was observed interacting with a local cryptogenic species, it may also play an ecological role for the native fauna.

The environments where the specimens were found exhibit distinct characteristics. At Saco da Ribeira Bay, individuals occurred either on boulders surrounded by a benthic community or on smooth rock surfaces. At Pedras Miudas Beach, the specimens were encountered on a beach with numerous fragmented rocks of varying sizes. The rocks were covered by red algal mats hosting a community of marine organisms inhabiting the substrate. In this area, the specimens were nestled among the algae and attached to

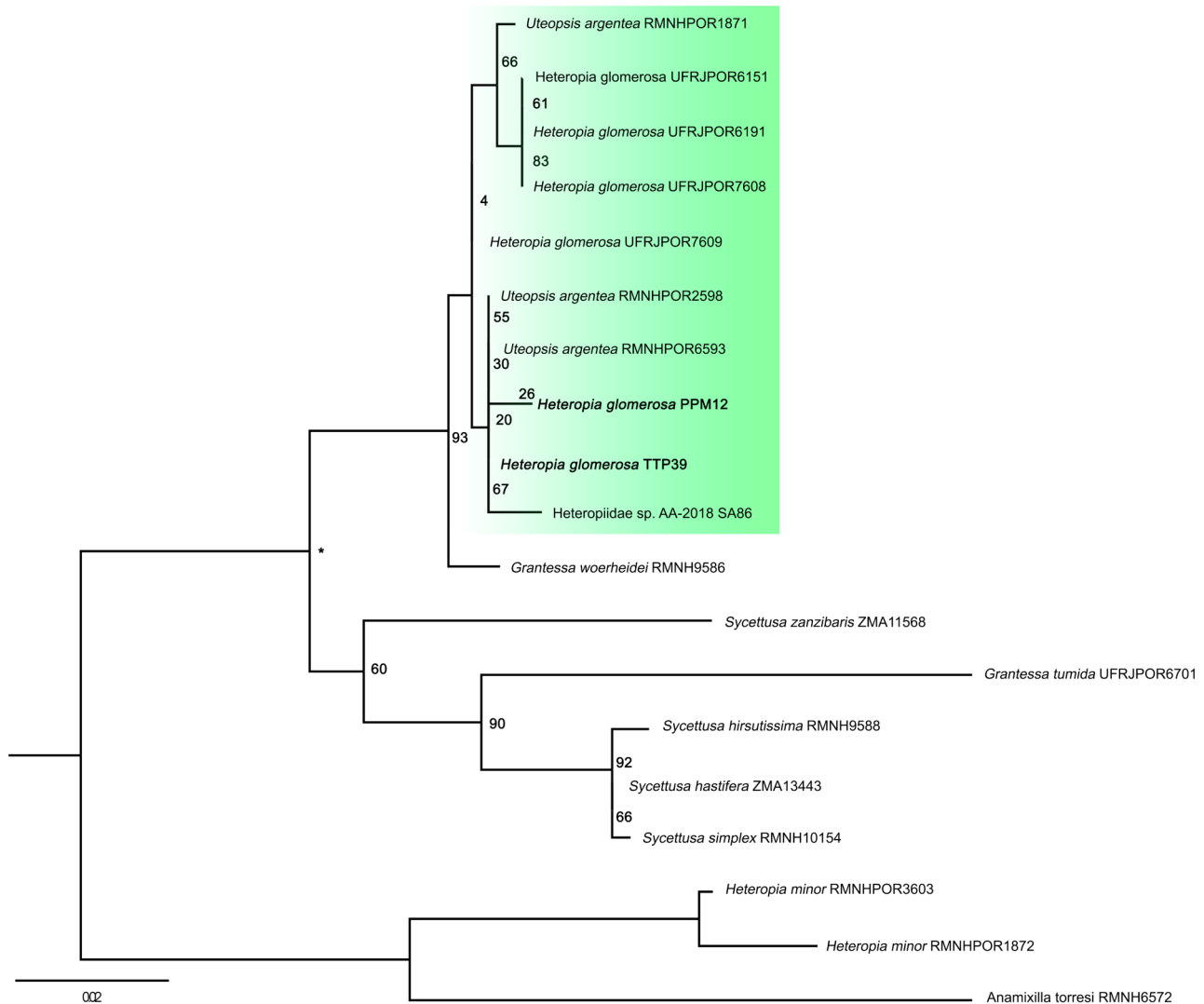


Figure 4. Maximum likelihood phylogenetic tree constructed with the C-LSU sequences of Heteropiidae and Jenkinidae. Bootstrap values are given on the branches. New sequences are in bold. Bootstraps = 100% are presented with an asterisk (*).

the rock surface. At Toque-Toque Pequeno Beach, a single specimen was found on a rocky substrate. This was the only site where the presence of *H. glomerosa* was less abundant than other groups of calcareous sponges. The rocks at this location were less densely occupied than at the other sites, and the *H. glomerosa* specimen from this area was the smallest collected.

Individual specimens were easily distinguished across all sites, as they did not form a colonial cluster but rather showed isolated and scattered growth on the substrate. The substrate was either communal, shared with other sponges, algae, bryozoans, and cnidarians, or consisted of bare rock.

All individuals were collected in dark crevices or underneath rocks, a common trait of many calcareous sponges, which tend to be photosensitive and attach preferentially to shaded locations.

Despite our record of the association between *H. glomerosa* and *P. nigra*, what catches our attention is that the black solitary ascidian is also under suspicion of being an exotic species in the Atlantic Ocean. *Phallusia nigra* was first described for the Red Sea, then recorded for the Indian, Pacific, Atlantic, and Mediterranean Oceans (WoRMS, OBIS, and GBIF). On the Brazilian coast, it has been recorded from Ceará, Alagoas, Bahia, Espírito Santo, Rio de Janeiro,

and São Paulo (SiBBr, Rocha et al. 2012) and classified as a cryptogenic species. Evidence from population genetics has pointed to a possible evolutionary origin of *P. nigra* in the Western Atlantic (Vandepas et al. 2015), and populations over 8,000 km along the western Atlantic have been shown to be a single evolutionary lineage, with high gene flow, high level of heterozygosity, and wide dispersal capacity, supposedly by anthropogenic vectors (Nóbrega et al. 2004). According to the GBIF database, the species has its northernmost distribution in Bermuda and its southern limit in São Paulo, Brazil.

We reinforce the necessity to continue filling important knowledge gaps about *H. glomerosa* by investigating, for instance, population genetics, phylogeography, larval behavior and preferences, niche modeling, ecological interactions, and chemical compounds for a better understanding of its biological requirements and its potential for spreading as an exotic invasive species. This set of studies could provide relevant information for drawing up action plans in the event of negative impacts. Although we have been conservative and adopted the term “exotic” and “non-invasive”, the findings of this article point to the species’ ability to colonize natural substrates, albeit in low abundance and with sparse distribution among individuals.

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Submitted: July 1, 2025

Accepted: November 17, 2025

Editorial responsibility: Rosana M. da Rocha

Author Contributions

RB: Conceptualization, Data Curation, Visualization, Validation, Writing – original draft, Writing – review & editing. SNS: Funding Acquisition, Resources, Writing – review & editing, Supervision. FA: Conceptualization, Methodology, Validation, Writing – review & editing, Supervision.

Competing Interests

The authors have declared that no competing interests exist.

Data Availability Statement

Datasets generated or analyzed in this study are available from the corresponding author on reasonable request.

Funding

This work was partly supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 2022/16193-1), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, 304267/2022-8) to SNS.

Ethical Statement

This study did not involve live vertebrate animals and therefore did not require approval by an ethics committee. Field

activities were conducted under collection permits issued by SISBIO (permit no. 90938).

AI Statement

No artificial intelligence tools were used in the preparation of this manuscript.

How to cite this article

Bazzo R, Stampar SN, Azevedo F (2026) The exotic calcareous sponge *Heteropia glomerosa* (Calcarea: Heteropiidae)

invading natural environments on the coast of São Paulo, Brazil. *Zoologia* 43: e25030. <https://doi.org/10.1590/S1984-4689.v43.e25030>

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