



**RESEARCH ARTICLE**  
**TAXONOMIC CATALOG OF THE BRAZILIAN FAUNA**

## How many species of Mollusca are there in Brazil? A collective taxonomic effort to reveal this still unknown diversity

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**ABSTRACT.** The expression ‘you need to know to conserve’ is a well-known cliché among biologists. Documenting the richness of a group of organisms is the first step towards understanding biodiversity and preparing efficient conservation plans. In this context, many efforts have been made to quantify the number of species on Earth and estimate the number of species still unknown to science. A few countries have complete and integrated databases estimating the approximate number of species recorded for their territory, particularly in the Global South. In Brazil, a country of continental dimensions, revealing the richness of the second most diverse clade of invertebrates (=Mollusca) has been a goal of taxonomists. Recently, in an unprecedented, collective, and integrated effort among Brazilian malacologists, it was possible to estimate how many valid species of molluscs are there in Brazil. In this effort, more than 30 mollusc experts joined together to update the Taxonomic Catalogue of the Brazilian Fauna (TCBF), a governmental website that allows a quick and real-time updating of all Metazoan. So far, more than 5,000 updates have been made in TCBF, indicating the presence of 3,552 valid species of molluscs in Brazil, distributed among the main clades as follows: Caudofoveata (10 spp.), Sole-nogastres (6 spp.), Polyplacophora (35 spp.), Scaphopoda (43 spp.), Cephalopoda (92 spp.), Bivalvia (629 spp.) and Gastropoda (2,737 spp.). The present study, in addition to demonstrating for the first time the richness of Brazilian molluscs, also presents the state of the art of this important phylum of invertebrates highlighting its most representative and neglected groups.

**KEY WORDS.** Malacology, taxonomy, database, number of species, molluscan species, biodiversity, conservation.

## INTRODUCTION

Knowing the number of species, i.e., the richness on Earth is one of the most basic yet elusive questions in science (May 1988). Unfortunately, obtaining an accurate number is constrained by the fact that many species remain to be described and indirect attempts to estimate an answer to that question have been highly controversial (Mora et al. 2011). Even so, statistical modelling, extrapolation algorithms, and different other methodologies have been applied over the years to obtain this dreamy number (Erwin 1992, May 1992, Storks 1993, Hammond 1994). Currently, it is believed that there are about 8.7 million of eukaryotic species, of which

only ~1.2 million have been identified and described so far (Mora et al. 2011).

Little is known about the number of valid species for most countries in the Global South, especially in South America, home to five (Brazil, Colombia, Ecuador, Peru, Venezuela) of the 17 most biodiverse countries on the planet, with around 40% of the Earth’s biodiversity (UNEP-WCMC 2016). In Brazil, one of the top countries among them, estimates point to 133,000–211,340 eukaryotic species, representing 15–20% of the world total (Joly and Bicu-do 1998–1999, Lewinsohn and Prado 2002, 2005, SiBBR 2023). More than 70% of this important and very representative diversity is composed of invertebrates (96,660–128,840 spe-

cies.; probably underestimated), with the Phylum Mollusca being the second most diverse group (2,400–3,164 species) after Arthropoda (Lewinsohn and Prado 2005, Simone 2006, 2008, Rios 2009, Santos et al. 2009, Salvador 2019). While such estimates help researchers get a sense of the local molluscan diversity, only an actual number and identity of valid species can provide the basis for effective conservation plans. Until now, that list could only be obtained through outdated printed catalogues (e.g., Lange-de-Morretes 1949, Salgado and Coelho 2003, Simone 2006, Rios 2009) or gathered from the literature, where the information is scattered in many publications, some only in Portuguese (Migotto et al. 1993, Colley et al. 2012) and difficult to access (Simone 1999a, 1999b, 1999c).

To address this issue, more than 30 taxonomists specialised in molluscs gathered in 2022 to update the Taxonomic Catalogue of the Brazilian Fauna (Catálogo Taxonômico da Fauna do Brasil), a bilingual website that allows quick, real-time updates of species recorded for Brazil, creating the first and most up-to-date database on molluscs in South America. Herein, a list containing all valid species of Brazilian molluscs (from marine, freshwater and terrestrial environments, excluding fossils) is presented online (<http://fauna.jbrj.gov.br>), updating the national checklist of this diverse phylum and providing a basis for future censuses. In addition, we present a state of the art of knowledge of Mollusca in Brazil, highlighting its most representative and neglected groups and calling attention to areas that would benefit from future studies and to potential avenues for conservation and management.

## MATERIAL AND METHODS

### Taxonomic Catalogue of the Brazilian Fauna

All information, species/families' numbers, synonyms, and estimates provided by this paper was based on the TCBF-Mollusca database. Created in 2015 by more than 500 experts in many different groups of animals, the TCBF is an open access government website that allows experts on different animal groups to enter data about a given taxon in real time. Such data include information on taxonomic hierarchy (Phylum, Class, Order, etc.), synonyms, electronic data (species-ID, ITIS), typology (holotype, paratypes, etc.), life form and substrate, geographic distribution, main references, and more. Currently, this website is the main tool to update and insert new valid species of Metazoa from Brazil, which also has a public search function that can be accessed, in Portuguese or English, by anyone around the globe.

### Brazilian Zoology Group – Mollusca

The first list of valid species of Mollusca was inserted on the TCBF website in 2016 and since then, more than 5,000 updates have been performed, 85% in late 2022 (Sep-Dec), during the restructuring of TCBF coordination, the expansion of collaboration with Brazilian taxonomists, and the call-to-arms to produce the present publication. The TCBF Mollusca group has two coordinators (first and last authors of this paper) responsible for including new taxonomists on the platform and enabling their access to interest groups. So far, the group has 34 taxonomists (55% male, 44% female), based in 25 different Brazilian institutions and one in Norway. Our panel of experts comprises marine and non-marine scientists and professors, professional biologists, independent researchers, curators, collection managers, and graduate students, some with cross-disciplinary expertise in zoology, conservation, and oceanography (6% belonging to non-academic institutions).

### The Delphi technique

The Delphi technique is a method used for a group of individuals to collectively address a complex problem through a structured group communication process (Hasson et al. 2000). Usually applied in ecology and conservation papers, here we used the Delphi methodology to deal with a complex subject in zoology and taxonomy, the diversity of molluscs in Brazil. From September to December 2022, we brought together a core team of 34 participants specialising in a broad range of Brazilian malacofauna and each was invited to produce 1–3 issues on the state-of-the-art of Mollusca based on their interest groups. Each issue was described in paragraphs of 200–280 words (plus references) resulting in 46 issues in total. Due to distance and high costs for face-to-face meetings, these 34 people met a few times online for discussions. So, we used a modified Delphi-style voting process (Mukherjee et al. 2015), which has ensured that consideration and selection of issues remained repeatable, transparent, and inclusive. The coordination, therefore, scored the list of 46 issues from 1 (low) to 10 (high) based on the following criteria: (i) whether the issue is new (with 'new' issues scoring higher) or consistent with such an interest group, (ii) whether the issue is likely to be important and impactful over the next 10–20 years for taxonomic studies of molluscs in Brazil and, (iii) whether the issue specifically impacts on diversity, new technologies and/or conservation of Brazilian molluscs. Pertinent issues (scores between 8–10) were compiled by the coordinators and section leaders in a cohesive text to create each of the thematic sections (e.g., 'freshwater malacofauna') seen below in the Discussion.

## RESULTS AND DISCUSSION

Early estimates of the number of described molluscan species worldwide range from 34,000 to 120,000 (Storks 1993, Bouchet et al. 2002). The total diversity, including undescribed species, is often cited as 200,000 (Ponder et al. 2020), the vast majority of which are marine gastropods. Some databases and modern estimates point to a total of 76,000–84,600 described/valid species of recent Mollusca (Rosenberg 2014, WoRMS 2023). Based on the most recent estimates, over 50% of the molluscan diversity is unknown worldwide. The Recent Brazilian fauna has representatives of six living classes of Mollusca (i.e., all except Monoplacophora, see Table 1).

**Table 1. Summary of Brazilian Mollusca diversity based on the TCFB-Mollusca database and estimated unknown species.**

Taxon	Species	Synonyms	Valid species	Families	Genera	Estimated unknown species
Aplacophora	16		16			40–60
Caudofoveata	10	0		3	5	
Solenogastres	6	0		2	6	
Bivalvia	684		629			150–180
Archiheterodonta	13	1		2	8	
Anomalodesmata	61	3		11	25	
Imparidentia	320	29		35	150	
Palaeoheterodonta	87	3		2	18	
Protobranchia	58	4		11	27	
Pteriomorpha	145	15		19	77	
Gastropoda	2,811		2,737			300–450
Caenogastropoda	1,326	37		135	491	
Heterobranchia	1,158	28		103	353	
Neritimorpha	48	0		4	9	
Patellogastropoda	7	1		3	3	
Vetigastropoda	198	8		20	76	
Polyplacophora	35		35			40–50
Chitonida	33	0		5	9	
Lepidopleurida	2	0		2	2	
Scaphopoda	43		43			30–40
Dentaliida	18	0		3	9	
Gadiliida	25	0		3	11	
Cephalopoda	98		92			20–30
Decapodiformes	61	2		24	51	
Octopodiformes	35	4		14	24	
Monoplacophora	0	–	0	–	–	?
Neopilinida	0	–	–	–	–	–
<b>Total</b>	<b>3,687</b>	<b>135<sup>c</sup></b>	<b>3,552<sup>a</sup></b>	<b>401<sup>b</sup></b>	<b>1,354<sup>c</sup></b>	<b>580-810<sup>d</sup></b>

<sup>a</sup> (Valid species = total of species - synonyms). <sup>b</sup> Number of families recorded in Brazil for each higher taxonomic clade based on the TCFB-Mollusca database.

<sup>c</sup> Number of genera recorded in Brazil for each higher taxonomic clade based on the TCFB-Mollusca database. <sup>d</sup> Estimates based on personal opinion (i.e., field experience, information from checklists, lots of museum collections, etc.) of the experts in each taxon. <sup>e</sup> Synonym registration is still a work in progress on the TCFB platform, that is, it may still not reflect actual numbers.

In the entire Brazilian territory, including its marine Exclusive Economic Zone (EEZ), 3,552 valid molluscan species were found (distributed in 401 families), of which 2,523 are marine, 293 freshwater, and 734 terrestrial (BZG-Mollusca 2023) (Table 2). Figures 1 and 2 illustrates some representatives of the Brazilian fauna, showing the many shapes and colours of these molluscs.

**Table 2. Environmental summary of Recent molluscs from Brazil (= valid species), with total number of families per environment and estimated living species.**

Habitat	Recent (# species)	%	Families	Genera	Estimated species <sup>c</sup>
Marine <sup>a</sup>	2,525	71.08	337	1,181	
Freshwater	293	8.24	21	29	
Terrestrial	734	20.68	43	144	
<b>Total</b>	<b>3,552<sup>b</sup></b>	<b>100</b>	<b>401</b>	<b>1,354</b>	<b>4,132–4,362</b>

<sup>a</sup> Marine habitat includes species of mangrove and estuarine regions. <sup>b</sup> Total of valid species in TCFB-Mollusca database (excluding synonyms). The 3,552 species represent about 4,5% of all Mollusca diversity, based on average (= 80,300 spp.) between 76,000–84,600 valid species worldwide (Rosenberg 2014, WoRMS 2023). <sup>c</sup> Estimates based on personal opinion (i.e., field experience, information from checklists, lots of museum collections, etc.) of the experts in each taxon.

Brazil is a country of continental dimensions (8,516,000 km<sup>2</sup>) and, therefore, many areas are under-sampled or not sampled at all. Moreover, the country has suffered successive science budget slashes over the past seven years (Overbeck et al. 2018, Andrade 2019, Galvão-Castro et al. 2022), which discourages its youth from pursuing academic careers and consequently compromises the training of new taxonomists.

Clearly, a considerable portion of the fauna within the Brazilian territory remains to be described. This situation is true for almost all classes and subclasses of molluscs; being particularly problematic in the poorly studied Aplacophora, Polyplacophora and Scaphopoda (with relatively small absolute numbers). Of greatest conservation concern, however, are the number and proportion of undescribed land and freshwater molluscs, considering that they are the groups of invertebrates most threatened by extinction globally (Lydeard et al. 2004, Régnier et al. 2009 Miyahira et al. 2022). Likewise, marine species face their own set of threats. Molluscs can be affected by habitat destruction by anthropic actions (El-Gendy et al. 2021), overexploitation (Ng et al. 2016), pest species transported through agricultural and ornamental plants (Robinson 1999, Robinson and Slapcinsky 2005), ocean acidification (Parker et al. 2013, Shang et al. 2023), global warming (Gazeau et al. 2013), oil contamination, industrial waste, cleaning products disposal,





Figure 1. A small fraction of the diversity of shapes and colours of the Brazilian malacofauna: (A) *Gaza compta* Simone & Cunha, 2006, 19 mm long, marine gastropod, Margaritidae; (B) *Pomacea maculata* Perry, 1810, ~45 mm long, freshwater gastropod, Ampullariidae; (C) *Omalonyx convexus* (Heynemann, 1868), 2 cm long, terrestrial gastropod, Succineidae; (D) *Gadila pandionis* (Verrill & Smith, 1880), 11 mm long, scaphopod, Gadilidae; (E) *Eulima bifasciata* d'Orbigny, 1841, 8.1 mm long – marine gastropod, Eulimidae; (F) *Eucallista purpurata* (Lamarck, 1818), ~45 mm long, marine bivalve, Veneridae; (G) *Mactrella janeiroensis* (E.A. Smith, 1915), 27.7 mm long, marine bivalve, Mactridae; (H) *Octopus insularis* Leite & Haimovici, 2008, photo by C. Sampaio, ~80 mm long – cephalopod, Octopodidae; (I) *Megalobulimus oblongus* (Müller, 1774), ~118 mm long, terrestrial gastropod, Strophocheilidae; (J) *Biomphalaria glabrata* (Say, 1818), ~15 mm long, freshwater gastropod, Planorbidae; (K) *Cardiomya minerva* Lima, Oliveira & Absalão, 2020, 4.3 mm long, SEM image, marine bivalve, Cuspidariidae; (L) *Corbula patagonica* d'Orbigny, 1846, ~14 mm long, marine bivalve, Corbulidae; (M) *Scutopus variabilis* Passos, Corrêa & Miranda, 2021, ~12 mm long, aplacophoran, Caudofoveata; (N) *Chicoreus brevifrons* (Lamarck, 1822), ~40 mm long, marine gastropod, Muricidae.

microplastic pollution (Schaeffer-Novelli 1990, Migotto et al. 1993 Wang et al. 2021), trawling (Rogers et al. 2022), shell collecting (Zhang and Wu 2020, although that activity can

be harnessed for good such as in citizen science projects, e.g., Kerstes et al. 2019), pet trade (Ng et al. 2016), and/or introduction of exotic fauna (Carlton 1999). Against such

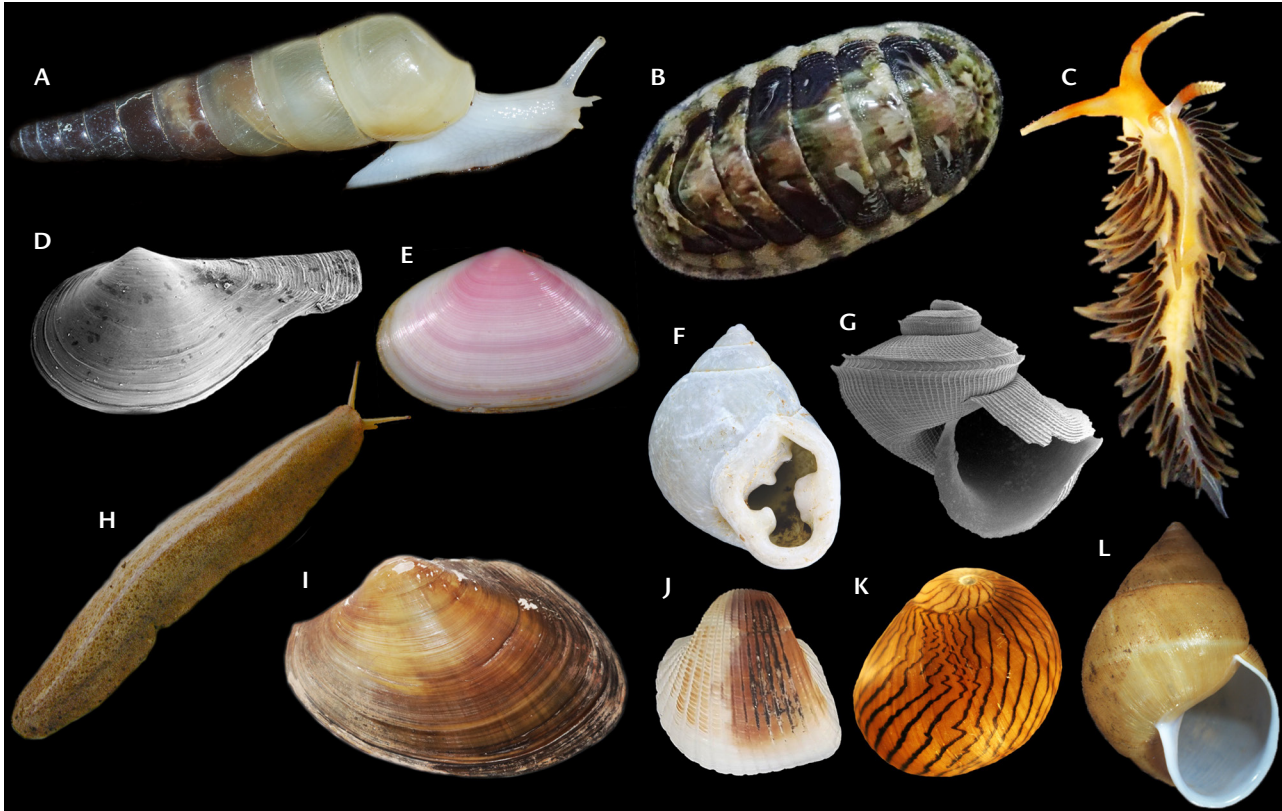


Figure 2. A small fraction of the diversity of shapes and colours of the Brazilian malacofauna: (A) *Obeliscus agassizi* Pilsbry, 1906, photo by L. Charles, ~4 cm long, terrestrial gastropod, Achatinidae; (B) *Ischnochiton striolatus* (Gray, 1828), 3 cm long, polyplacophoran, Ischnochitonidae; (C) *Phidiana lynceus* Bergh, 1867, 17 mm long, marine gastropod, Nudibranchia; (D) *Octoporia octopora* (Allen & Morgan, 1981, ~3 mm long, SEM image, marine bivalve, Cuspidariidae; (E) *Eurytellina punicea* (Born, 1778), ~70 mm long, marine bivalve, Tellinidae; (F) *Hyperaulax ramagei* (Smith, 1980), ~4.2 mm long, terrestrial gastropod, Odontostomidae; (G) *Anatoma campense* Pimenta & Geiger, 2015, ~3 mm long, SEM image; marine gastropod, Anatomidae; (H) *Phyllocaulis boraceiensis* Thomé, 1972, ~16 cm long, terrestrial gastropod, Veronicellidae; (I) *Anodontites trapesia* (Lamarck, 1819), 20 cm long, freshwater bivalve, Mycetopodidae; (J) *Anadara chemnitzii* (Philippi, 1851), ~5 cm long, marine bivalve, Arcidae; (K) *Neritina zebra* (Bruguère, 1792), 22 mm long, marine gastropod, Neritidae; (L) *Rhinus heterotrichus* (S. Moricand, 1836), ~2.2 cm long, terrestrial gastropod, Simpulopsidae.

overwhelming unfavourable odds, a significant number of species will likely become extinct before they have been formally described. The outlining of goals for the elaboration of conservation plans for Brazilian molluscs is thus a critical necessity.

Through the TCBF-Mollusca database, it was also possible to carry out a regional analysis of the diversity of molluscs and track the under-sampling in some Brazilian states. Furthermore, the number of taxonomists and university centres seem to be directly related to the number of species records per region. Of the 3,552 valid species of molluscs in Brazil, 12% are registered for the North region, 29%

Northeast, 4% Central-West, 38% Southeast, and 17% South. Among the taxonomists who make up the present work, 11% are based in the Northeast, 71% in the Southeast, and 14% in the South; North and Central-West have no representatives (Fig. 3). This distribution also coincides with the most universities (>80% of all higher education institutions) and the largest representation of Brazil's GDP (>85% in those three regions (Northeast, Southeast, South) (IBGE 2023).

Still, of the 401 families currently known in the Brazilian malacofauna, about 44% (176 families) of this diversity is contemplated in the specialties of our 34 taxonomists. This means that 225 families (56%) lack national specialists. It is

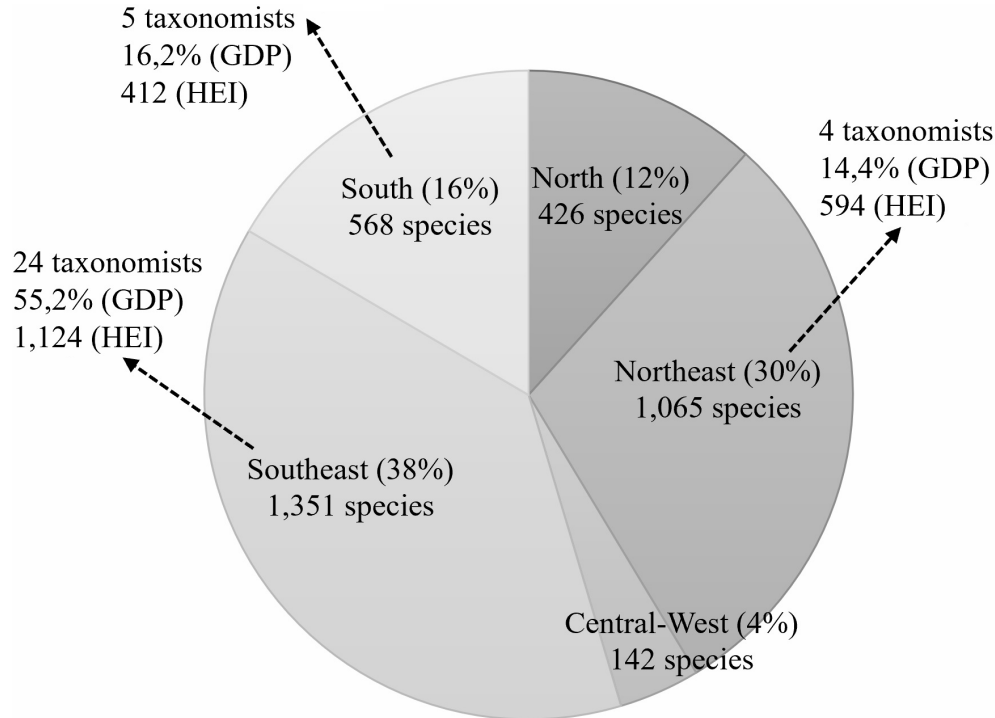


Figure 3. Distribution of 3,552 valid species of Mollusca and malacologists (=taxonomists) by region of Brazil and the possible correlation with socioeconomic indicators. Only the authors of this paper were counted (international authors excluded). (GDP) Gross Domestic Product, (HEI) Higher Education Institutions.

unquestionable that the number of taxonomists specialising in malacology in Brazil is greater than the authors of this paper. Currently, it is believed that there are around 80 such taxonomists in Brazil, circa 60% of which are members of Brazilian Society of Malacology (SBMa – Sociedade Brasileira de Malacologia, <http://sbmalacologia.com.br>), most with institutional affiliation; while the remaining 40% are mainly amateurs and shell collectors/traders, i.e., without a formal academic position (Machado and Simone 2022).

#### The diversity of molluscs in the Brazilian coast

The Brazilian continental margin extends for approximately 8,700 km, which makes it the 15<sup>th</sup> longest national coastline in the world (Nicolodi and Pettermann 2011). The entire coast lies adjacent to the Tropical and Subtropical Atlantic Ocean, with much of its seafloor within deep waters, presenting a very diverse suite of coastal environments that evolved during the Quaternary (Dominguez 2006, Gaurisas and Bernardino 2023). There are representatives of the Mollusca in most of these environments such as beaches, mangroves, estuaries, rocky shores, coral reefs, rhodolith

banks, among others. Also, it has species distributed from the intertidal zone, through to continental shelf (75–200 m) and slope (250–3,300 m), to the abyssal plains (3,500–4,485 m). Although supposedly well known, the features and nomenclature of undersea morphologic features of the Brazilian Continental Margin were only recently updated (Alberoni et al. 2020). Using a new Digital Terrain Model (DTM) it was possible to expand knowledge about the deeper areas of the Brazilian coast, for example, describing in detail the Ceará Gap (1,400–2,200 m), the Rio Grande do Norte Plateau (800–3,600 m), the Amazon Channel (1,500–4,550 m) and the Cruzeiro do Sul Rift (1,500–5,370 m) (Alberoni et al. 2020). This expansion of knowledge about new areas and depths in Brazil will likely have a direct impact on our understanding of the still unknown diversity of Mollusca.

Currently, the records based on the TCBF database point to a recently described species of Gastropoda, *Cordesia atlantica* Souza, Passos, Shimabukuro & Sumida, 2020, as the deepest record from the Brazilian coast (3,358 m). Table 3 shows the bathymetric ranges for all classes of Mollusca from Brazilian coast, highlighting the species with records in



**Table 3. Bathymetric range records for all clades of Mollusca on the Brazilian coast.**

Taxa*	Depth (m)	Species recorded at lower depths	Species recorded at greater depths	References
Aplacophora	30 – 1,358	<i>Falci-dens targatus</i>	<i>Claviderma virium</i> <sup>a</sup>	Corrêa et al. (2014, 2018)
Bivalvia	0 – 3,049	many (intertidal)	<i>Bentharca asperula</i> <sup>b</sup>	Passos and Birman (2009)
Gastropoda	0 – 3,358	many (intertidal)	<i>Cordesia atlantica</i> <sup>c</sup>	Souza et al. (2021a, 2021b)
Polyplacophora	0 – 408	most (rock shores)	<i>Hanleya brachyplax</i> <sup>d</sup>	Jardim and Simone (2010a, 2010b)
Scaphopoda	0 – 2,200	some (intertidal)	<i>Cadulus victori</i> <sup>e</sup>	Souza et al. (2020)
Cephalopoda	0 – 2,136	some (tide pools)	<i>Cirroteuthis muelleri</i> <sup>f</sup>	Haimovici et al. (2007)

\*Only species recorded within the limits of the Brazilian Territorial Sea, EEZ (Exclusive Economic Zone – from 12 to 200 nautical miles measured from the baseline) plus Continental Shelf extension (up to 350 nautical miles) were considered. <sup>a</sup>*C. virium* (360–1,358 m), known only from off Rio de Janeiro and Espírito Santo states, southeastern Brazilian coast from 19°36'27.21"S to 23°41'9.14"S and 039°10'14.62"W to 041°18'33.05"W, an endemic species. <sup>b</sup>*B. asperula* (1,680–3,049 m), off São Paulo and Rio de Janeiro States (24°12'S; 40°23'W). <sup>c</sup>Only known from South-west Atlantic deep-sea, in organic falls (whale bones and wood parcels) from 3,285–3,358 m (28°01'42.4"S, 43°31'46.8"W, off São Paulo State). In the same max. depth: *Rubyspira pescaprae* (1,491–3,358 m depth). <sup>d</sup>*H. brachyplax* (250–408 m), sta. 1126, off Cananéia, São Paulo State (25°44'S, 45°11'W), an endemic species. <sup>e</sup>*C. victori* (400–2,200 m), Camamu-Almada Basin, Bahia State (14°19'48"S, 38°32'39"W), an endemic species. <sup>f</sup>*C. muelleri* (1,292–2,136 m), Rio Real (Bahia) to Cabo de São Tomé (Rio de Janeiro) (11° to 22°S).

shallower and deepest waters, considering only the records within Brazilian Exclusive Economic Zone (EEZ) that comprises a total area of 3.6 million km<sup>2</sup>, ranking 11<sup>th</sup> in terms of size worldwide (De Leo et al. 2020).

Bathymetric information is essential for molluscan taxonomy, in some cases, as sometimes this information alone is enough to confirm or exclude the identification of some taxa. The TCBF platform still does not have the bathymetric information for public access, however, website improvements are being made to include it for all marine Brazilian molluscs.

It is also worth noting that due to the difficulty of determining deep-sea margins geographical boundaries, some species of molluscs known to be collected outside the limits of the EEZ, were considered as valid records for the Brazilian coast, although such taxa are marked with the acronym 'Off Brazil' on the TCBF-Mollusca website. This difficulty is justified because currently the geographical boundaries of the deep-sea are commonly structured by water masses, temperature, and productivity (Watling et al. 2013, Gauris and Bernardino 2023), information not always available in the literature.

Herein, the diversity of the marine mollusc fauna is presented prioritising the most neglected groups, that is, Aplacophora (16 spp.), Scaphopoda (43 spp.) and Polyplacophora (35 spp.), followed by the three most studied clades of the Brazilian coast, Cephalopoda (92 spp.), Bivalvia (513 spp.) and Gastropoda (1,837 spp.). Given the vast diversity of the latter two, only the 'state of the art' of their most representative groups will be addressed, highlighting the main taxonomic challenges for the next few years.

### The neglected fauna of Aplacophora

Aplacophora (Solenogastres + Caudofoveata) can be considered one of the least known clades among molluscs, even in the Brazilian coast. Considering the EEZ nine

species are catalogued (8 Caudofoveata + 1 Solenogastres) (e.g., Passos et al. 2019, 2021, 2022), apart from other seven species (2 Caudofoveata + 5 Solenogastres) described off Brazil (Scheltema 1985, Ivanov and Scheltema 2008, Cobo and Kocot 2020, 2021), both registered in TCBF platform. Usually inhabitants of deep waters (>200 m), worm-shaped, shell-less and small (< 20 mm), aplacophorans are generally unattractive when compared to other molluscs, a fact that perhaps explains the few specialists in Brazil (2 experts, the only ones in the Global South) and in the World (17 experts) (AplacBase 2023, M.S. Miranda pers. obs.). Recently, some of these experts got together to create the AplacBase (<https://aplabase.weebly.com/>), a website that provides general information about these much-neglected organisms.

Studies on the diversity of Aplacophora in Brazil are recent, due to the extensive sampling by offshore oil and gas industry in the last decade plus the establishment of the first consolidated research group in the Southeast of country (e.g., Corrêa et al. 2014, 2018, Miranda et al. 2020b). Considering the undescribed aplacophorans species worldwide, it is estimated that the number of species is ten times greater than the total currently known (~460 species) (Todt 2013, AplacBase 2023). For Brazilian waters, specifically, the efforts were initially focused in Caudofoveata (Fig. 1M) with some studies on their taxonomy (Passos et al. 2018, 2019, 2021, 2022), with 10 species recorded. Although underestimated it is possible to expect that the number of valid species of Caudofoveata doubles for the next 20 years in Brazil. In contrast, the Solenogastres are poorly studied in Brazil, making it difficult to estimate the possible number of species. Therefore, it is possible that the number of described species of Solenogastres (6 spp.) is at least one-tenth of their real diversity in Brazilian coast, or more than two times the estimated diversity of Caudofoveata (20 spp.), i.e., varying between 40–60 species.



Light microscopy, scanning and transmission electron microscopy (e.g., Corrêa et al. 2018), birefringence and confocal microscopy (e.g., Faller et al. 2012), as well as microtomography analysis and 3D reconstruction of histological sections (e.g., Metscher 2009. Señaris et al. 2014) are currently the main tools used to unravel the morphology and taxonomy of these weird marine molluscs.

### The understudied and enigmatic scaphopods

The Scaphopoda (=tusk shells) is one of the less species-rich molluscan classes with estimates of about 578 extant valid species (BZG-Mollusca 2023). They are exclusively marine, live as infaunal burrowers, and play an important role in marine benthos feeding primarily on foraminiferans, capturing their prey via feeding tentacles (known as captacula) (Bilyard 1974. Langer et al. 1995). Their predation has a significant impact on structuring local infaunal communities (Shimek 1990).

Usually under-studied, in the last eight years descriptions of new species of Scaphopoda were rare, i.e., only five extant species were described in the world, one of them from Brazilian waters (Souza et al. 2020). Currently, the Brazilian fauna have 43 species of scaphopods, which corresponds to approximately 7.5% of the total species known to science (BZG-Mollusca 2023). With only two specialists continuously studying scaphopods in Brazil, the group lacks taxonomists to advance the studies. However, in comparison to the global scenario there are many taxonomic revisions on this group in the last three decades in Brazil (Caetano et al. 2006, 2010). Despite that, the taxonomy of scaphopods is complex and in most cases the similar outline of shells makes identification difficult. In general, only empty shells are used for taxonomy, being rare papers detailing with the anatomy (Simone 2009a, Sigwart et al. 2017), and even rarer those that investigate the ultrastructure of spermatozoa (Hou and Maxwell 1991), a feature already known for its high phylogenetic signal. Methodologies and techniques such as morphometry and SEM (Scanning Electron Microscopy) are commonly used in the taxonomic works (Vilela et al. 2019, Souza and Caetano 2020). The challenge to perform an integrative approach with scaphopods from Brazil is to sample suitable specimens for molecular studies, since most materials available in collections are empty shells or specimens fixed in formalin.

In contrast with the dubious position of Scaphopoda among conchiferans, the phylogenetic backbone within the class is clearly divided into two major orders, Dentaliida and Gadilida, supported by molecular and anatomical data (Steiner 1998, Reynolds and Steiner 2008, Stöger et al.

2013, Wanninger and Wollesen 2019). Globally, Dentaliida comprises 296 extant valid species and Gadilida comprises 282 (BZG-Mollusca 2023). For Brazil, 18 species of Dentaliida were recorded and included in TCBF platform: 14 species within the genera *Antalis*, *Coccodentalium*, *Dentalium*, *Fisidentalium*, *Graptacme* and *Paradentalium*; two species of *Fustiaria* and two species of *Episiphon* (none of them are endemic). The Gadilida has 10 genera (*Bathoxiphus*, *Entalina*, *Heteroschismoides*, *Pertusiconcha*, *Cadulus*, *Compressidens*, *Gadila* (Fig. 1D), *Polyschides*, *Striocadulus*, *Annulipulsellum* and *Striopulsellum*) and 24 species recorded in TCBF (BZG-Mollusca 2023). Five species of Gadilida are endemic to the Brazilian coast, but it should be noted that many of them have only recently been described (2005–2020). In short, since the compilation of Souza et al. (2013), two taxa have been added to the Brazilian coast such as, *Cadulus victori* Souza, Caetano & Scarabino, 2020 and *Bathoxiphus ensiculus* Jeffreys, 1877.

Dentaliida comprises species with a conical foot and moderately large shells, usually characterized by a longitudinal sculpture, such as ribs or striae, and with the widest diameter at the anterior aperture, indeterminate maximum size and continuous growth (Reynolds and Steiner 2008). The study of Dentaliida in Brazil was initiated with the description of *Antalis circumcincta* (R.B. Watson, 1879) based on samples from the Challenger Expedition (1872–1876). Subsequent studies were developed with new records for the Brazilian waters, nomenclatural acts such as synonymy, new combinations, and others (Caetano et al. 2006), feeding behavior (Dantas et al. 2016) and interspecific relationships (Massud-Ribeiro and Caetano 2006). Unfortunately, Brazil does not currently have a consolidated research group for this clade, reducing the expectations of new taxa and/or new records for the next few years.

In the same way, most species of Gadilida have small shells lacking sculpture, bringing more difficulties in their taxonomy when compared to Dentaliida (Souza and Caetano 2020). The most recent novelties to the scaphopod fauna from Brazil were based on studies of Gadilida (Souza et al. 2020) and there is probably more hidden diversity in this group thinking in the challenge to assess intra- and interspecific variation. Ecological studies on Gadilida are lacking in Brazil.

### The cryptic diversity of Polyplacophora

Chitons (= Polyplacophora) are exclusively marine molluscs inhabiting a wide range of habitats from the intertidal zone (mostly in rocky shores) to the deep sea (Schwabe 2008, Avila-Poveda et al. 2021). The group generally displays

a conserved morphology with eight dorsal, usually overlapping shell plates, surrounded by a girdle that can bear ornamentations (Irisarri et al. 2020).

In the past two decades, for example, more than 200 species of chitons have been discovered and described globally (Alnashiri et al. 2023), i.e., about 16% of all known diversity. Currently, there are about 1,260 valid species of Polyplacophora worldwide (BZG-Mollusca 2023), of which 35 (in 11 genera) are recorded from Brazil, 16 of them being endemic (Jardim et al. 2022). Thus, the Brazilian fauna represents about 2.8% of all chiton fauna (BZG-Mollusca 2023).

The clade Polyplacophora consists of two monophyletic lineages, order Lepidopleurida and order Chitonida (Okusu et al. 2003), both with representatives in the Brazilian coast. The first has only two species recorded, *Hanleya brachplax* Jardim & Simone, 2010 and *Leptochiton darioi* (Righi, 1973), while Chitonida is the most representative, with 33 taxa in nine genera (BZG-Mollusca 2023) (Fig. 2B).

Studies on Polyplacophora in the Brazilian coast are scarce, especially considering the potential for describing new species and their high endemism rate (~45%). Some of these studies include faunal checklist (Migotto et al. 1993), ecological data (Barros et al. 2013) and/or morphological descriptions (Jardim and Simone 2010a, Jardim et al. 2017). Despite the different localities and approaches of these few articles, the lack of information about chitons in Brazil highlights the importance of studies focused on the group and the potential to reveal an understudied diversity. Nowadays, Brazil has few specialists publishing scientific results on the group, reducing expectations of new taxa descriptions for the coming years.

The chitons are considered taxonomically difficult (Sigwart et al. 2013) owing to their superficial resemblance in morphology within and between groups. In addition, novel morphological and anatomical characters plus molecular and population genetics data have revealed the cryptic diversity among chitons and the description of a huge number of new species (Alnashiri et al. 2023). The high rate of colour variation is also a taxonomic obstacle for this group, making it difficult to separate and consequently identify new species. Common among their populations, this feature seems to be an important population-level advantage, probably avoiding predators, including crabs and fish (Gonçalves-Rodrigues and Absalão 2005).

Although allometric variations and morphometric have been used to solve some taxonomic issues (Saad 1997, Avila-Poveda 2013, Ibáñez et al. 2018), mathematical models of diffraction patterns seem promising to describe shell patterning in some molluscs (Field and Golubitsky 2009),

but they have never been applied to the eight-shelled chiton armature (Sigwart 2018). In Brazil, specifically, none of these methods have yet been used in the taxonomy of Polyplacophora, which could partly explain the subtle advance in the knowledge of the group.

#### On the edge of discovery: the Cephalopoda clade

The first studies about cephalopods in Brazil started with the expeditions of European naturalists (d'Orbigny 1835, 1845, Gould 1852, Adam 1937). After the reviews of these samples, archived in European museums (Pickford 1955), only eight new species have been described so far (*Eledone massyae* Voss, 1964, *Doryteuthis surinamensis* Voss, 1974, *Vosseledone charrua* Palacio, 1978, *Eledone gaucha* Haimovici, 1988, *Graneledone yamada* Guerrero Kommritz, 2000, *Octopus insularis* Leite & Haimovici, 2008, *Lepidoctopus joaqui* Haimovici & Sales, 2019 and *Paroctopus cthulu* Leite, Lima, Lima & Haimovici, 2021) plus two redescribed. One of them, *O. insularis* (Fig. 1H) one of the most studied and abundant octopuses in the Atlantic and an important fishery's target was recently described by the two researchers more involved with the taxonomy of Cephalopoda in Brazil (Leite et al. 2008). Other experts also joined these two in the last decades, assisting in the morphological descriptions and elaborating checklists.

The first published faunal survey about cephalopods in Brazil reported 35 species, almost ten years later, this total was updated to 42 valid species (Haimovici 1985, Haimovici et al. 1994). Already in the next decade, the number of species doubled to 86, after an important taxonomic cooperation (Haimovici et al. 2009).

Nowadays, 92 valid species of Cephalopoda are reported for the Brazilian coast (31 species of Octopodiformes and 61 species of Decapodiformes), plus eight undescribed. These numbers represent ~12% of the world's cephalopod diversity, which is currently 775 species (Jereb and Roper 2005, Jereb et al. 2010, 2016). Brazilian diversity is probably underestimated since it has a vast coastline. In New Zealand, a country ~29 times smaller than Brazil in area, 100 cephalopod species are registered, 23 are undescribed, and about 10 species are still undiscovered (Spencer et al. 2009). In the Gulf of Mexico, 93 species of cephalopods are documented and 129 species in the Broad Caribbean (Judkins et al. 2016).

Around the world, the most studied cephalopods are benthic shallow water species of Octopodidae, which has ~300 species described (Norman 2016). The known diversity of this family in Brazil (13 spp.) corresponds to ~4.5% of the total species of the family worldwide.

The lack of knowledge about the Cephalopoda fauna is even greater for deep-sea, probably due to the difficulty of sampling and identification of living specimens (Ramirez-Llodra et al. 2010). In Brazil, specifically, most deep-water species studied have been collected as by-catch in commercial trawl fisheries (Perez et al. 2003). In that case, benthic octopuses could be under sampled and the use of subaquatic methodologies such as scuba diving enhances the chances of encountering cryptic species (Leite et al. 2008, 2021, O'Brien et al. 2021). The use of underwater remotely operated vehicles also helps access these animals, but at a high cost (Pratt et al. 2021). Other impediments to the advancement of studies on Cephalopoda in Brazil comes up against the constant decrease of specialists, added to the small number of specimens deposited in Brazilian collections, making difficult comparisons between species and description of new taxa.

Currently, the most representative collections of Cephalopoda in Brazil are at Universidade Federal do Rio Grande (Laboratório de Recursos Pesqueiros Demersais e Cefalópodes, Instituto de Oceanografia) (680 lots) and at the Museu de Zoologia da Universidade de São Paulo (MZUSP) (1,113 lots). Others, of smaller size, are in private collections at university laboratories, not formally registered. Unfortunately, one of the most important collections of cephalopods in Brazil, archived in Museu Nacional do Rio de Janeiro (222 museum lots), was almost entirely lost (199 lots) during a tragic fire in 2018 (A.D. Pimenta pers. obs.).

Therefore, considering the unexplored deep-sea areas in Brazil, the undescribed species, and the advances in the new underwater methodologies, it is expected that more species could be added to the TCBF platform in the next few years.

### Marine bivalves: novelties and taxonomic challenges

The bivalves represent the second most species-rich clade of Mollusca, after gastropods. For the marine environment, bivalves and cephalopods are one of the main sources of animal protein and play a key role in fisheries and aquaculture (Bieler et al. 2013, Wijsman et al. 2019). Compared to other molluscs, bivalves have probably the highest economic and ecological importance not only as food but also based on their benthic biomass (Bouchet et al. 2002, Giribet 2008).

In Brazil, currently, 516 species of marine bivalves are registered, representing about 15% of the entire national diversity of Mollusca (BZG-Mollusca 2023). Globally, the Brazilian bivalve fauna represent ~3.1% of the 16,702

valid species of Recent marine bivalves described to date (BZG-Mollusca 2023).

Herein, we highlight the state of the art and conservation aspects of the most taxonomically problematic groups of Brazilian bivalves, such as the subclass Anomalodesmata (58 spp.), the superfamilies Arcoidea (27 spp.), Limopsoidea (7 spp.), Ostreoidea (10 spp.) and Mactroidea (12 spp.) plus the families Veneridae (41 spp.), Tellinidae (49 spp.) and Corbulidae (13 spp.).

With about 800 species, the clade Anomalodesmata Dall, 1889 is known to harbour the rarest and most specialised species of marine bivalves and includes a major clade of carnivorous taxa (Figs 1K, 2D), as well as the enigmatic watering pot shells (Morton and Machado 2019, 2021). In Brazil, 58 valid species of anomalodesmatan are currently known, representing ~7.3% of worldwide Anomalodesmata's fauna. Among the 22 families known of Anomalodesmata (Machado and Passos 2022), 11 are recorded on the Brazilian coast (BZG-Mollusca 2023). In the last 15 years, there has been a considerable advance in the knowledge of the group in Brazil with important taxonomic revisions (e.g., Oliveira and Absalão 2009, Absalão and Oliveira 2011, Pimenta and Oliveira 2013), faunal surveys (e.g., Tallarico et al. 2014, Barroso et al. 2016), descriptions of new species (e.g., Simone and Cunha 2008, Machado and Passos 2015, de Lima et al. 2020), functional morphology studies (e.g., Morton et al. 2016a, 2016b, 2019), including anatomical descriptions via X-ray microtomography (Machado et al. 2019), sperm ultrastructure (e.g., Campos et al. 2020) and the production of the first video of a living carnivorous bivalve (Machado et al. 2017). There are currently two research groups in Brazil working with Anomalodesmata, with good perspectives for new taxa descriptions in the next 10 years. It is also worth noting that the most species of Anomalodesmata are usually rare, with small dimensions (<10 mm long), generally inhabiting deeper waters, and with a distribution in a patch pattern, factors that would alone strongly suggest the inclusion of many of their members in the Red List (IUCN). Currently, no species of Anomalodesmata is in the Brazilian Red List.

Among the Pteriomorphia bivalves, the superfamily Arcoidea is considered one of the most diverse groups with a total of 27 species, after Mytiloidea and Pectinoidea (29 spp.) (BZG-Mollusca 2023). Brazilian arcoids are exclusively marine, most occurring only in shallow waters (<200 m depth), except by a few species of arcids that have wider bathymetric distributions or live in deep waters – e.g., *Bentharca asperula* (Dall, 1881). Arcidae, one of the largest families of bivalves in Brazil (19 spp.), presents abundant populations with their shells



being frequent in the drift line of Brazilian beaches – e.g., *Anadara chemnitzii* (R.A. Philippi, 1851) (Fig. 2J). While most arcids and noetiids live attached by byssal threads, glycymeridids are infaunal and occur in the subtidal zone. Brazilian arcoids have received little attention in recent years, except for Prado and Nascimento (1994) and Passos and Birman (2009), who furnished data on the geographical distribution of *Bentharca asperula*; Simone and Chichvarkhin (2004), who investigated the morphology of *Barbatia candida* (Helbling, 1779) and *Fugleria tenera* (Adams, 1845); Simone (2009b) that described *Acar transmar* Simone, 2009 and Francisco et al. (2012), who described four new species, one of them in a new genus (*Paranadara*). Amaral et al. (2006) and the catalogues of Rios (2009) have general information on the Brazilian arcoids. Testud (1967) and Coelho and Campos (1975) are important contributions on the taxonomy of arcids, and Penna-Neme (1978) on glycymeridids; Testud (1967) also approached the noetiids. Oliver and Allen (1980) reviewed the deep-sea species of Arcoidea from the Atlantic, with records from Brazil.

Regarding the Limopsoidea, also an exclusively marine group of bivalves, both the families Limopsidae and Phyllobryidae are present in Brazilian waters, with four and three species, respectively. Limopsoids live attached to the substratum by byssus threads, occurring from shallow to deep waters. *Limopsis janeiroensis* Smith, 1915 is recorded from Brazil since 1915. The deep-sea species *Limopsis aurita* (Brocchi, 1814) and *L. minuta* (Philippi, 1836) were reviewed by Oliver and Allen (1980), and Esteves (1984) described as new *L. davinae*. Among phyllobryids, *Cosa brasiliensis* is known from Klappenbach (1966), while *Cosa caribaea* Abbot, 1958 and *Cratis antillensis* (Dall, 1881) are recorded by Rios (2009). Amaral et al. (2006) also furnished data on both families, specially for specimens collected in the São Paulo coast.

The superfamily Ostreoidea includes marine and brackish water species adapted to the sessile epifaunal communities attached to hard substrates. Both tolerance and resistance to environmental variations allowed the Ostreoidea to colonize different marine habitats, from coastal regions with clear waters and high salinity levels, to estuarine environments with turbid waters and variable salinity levels (Quayle 1981). The clade comprises 80 species with a wide-spread distribution (Huber 2010). The Ostreidae, the most diverse family of Ostreoidea, includes species of economic importance, and well known for their high intraspecific variation, which makes identification problematic (Amaral and Simone 2014). For Brazil, specifically, representatives of three genera are known: *Crassostrea* characterized by having a flat right valve and a wider, more convex left valve

that is adhered to the substrate; *Ostrea*, small to large shells, sub circular to slightly elongated dorsoventrally, right valve plicate, with blue, red, or purple radial spots; left valve is more inflated and with well-defined plications, and marginal denticles (chomata) (Amaral and Simone 2014); and *Dendostrea* characterized by species small to medium size, sub circular, irregular to elongate, with small spines along their length. All of these three genera have representatives in the Brazilian coast: *Ostrea* (3 spp.), *Crassostrea* (4 spp.) and *Dendostrea* (2 spp.) (BZG-Mollusca 2023).

The second family of Ostreoidea, Gryphaeidae, also recorded in Brazilian waters, has medium to large shells, usually oval, with marginal plicae, and internal vesicular structures in the shell, presence of chomata and lobed auricle, with the rectum passing through the ventricle (Harry 1985). The valves are coloured with red, blue or purple spots; internally they have a dark purple colour, and the edges of the valves are normally black.

The Mactroidea is represented along the Brazilian coast by twelve species grouped into three families, Anatinellidae that bears the genera *Anatina* and *Raeta*, Mactridae, with *Mulinia*, *Mactrotoma*, *Mactrellona*, *Trinitasia*, *Mactra* and *Mactrella* (Fig. 1G), and Mesodesmatidae, with only one species, *Amarilladesma mactroides* (Reeve, 1854). The taxonomy of Mactridae and Anatinellidae species was revised by Signorelli and Scarabino (2010) and Signorelli and Pastorino (2012), who highlighted the importance of analysing the type-material to solve taxonomic issues and misidentifications of their species. Mactridae species are characterized by the inverted V-shaped cardinal tooth in the left valve that is formed by two single teeth; in the right valve, the cardinal teeth are not fused, and the anterior and posterior lateral teeth have, in general, only on cusp (Signorelli 2021). Anatinellidae species have thin, fragile shells, a slight posterior shell gape, a narrow non articulating pseudocardinal-like lamellae near the hinge in each valve, with or without sinus (Signorelli and Carter 2016).

Among the 75 families of marine bivalves from Brazil, Veneridae (41 spp.) and Tellinidae (49 spp.) are the most diverse, while Corbulidae (13 spp.) is one of the most taxonomically challenging.

Members of the Veneridae are primarily shallow-water, filter-feeding clams found in marine or estuarine environments (Mikkelsen and Bieler 2008) (Fig. 1F). They are characterized by their oval to suborbicular and subtrigonal shell shapes, thick walls, well-developed lunule, escutcheon sometimes present and well-marked, and smooth, thin periostracum (Coan et al. 2000). The pallial sinus can vary

in size and shape, external sculpture can range from smooth to strongly sculptured with lamellae, nodules, and/or spines. The ventral margin may be smooth, grooved, or crenulated, and the umbo can be anteriorized or subcentral (Mikkelsen and Bieler 2008). The hinge has three cardinal teeth, which may be bifid or simple. In the right valve, there are middle, anterior, and posterior cardinal teeth (1, 3a, and 3b, respectively), while the left valve has the anterior, middle, and posterior cardinal teeth (2a, 2b, and 4b, respectively) (Harte 1998). There are also anterior lateral teeth, and rarely a posterior lateral one.

On the Brazilian coast, Veneridae is represented by 28 genera. The genera *Pitar* and *Tivela* have the highest number of species, five each. In Brazil, we have few specialists in Veneridae, one of the families with the highest number of species among bivalves. This makes the correct survey of species and work in malacological collections particularly slow.

The Tellinidae comprises about 60–70% of all tellinoid richness (Morton et al. 1998), with more than 90 genera allocated in two subfamilies – Tellininae and Macominae. It is not an easy task to distinguish a morphological characteristic exclusive to all species in this group due to a very different shell morphology possessing a well-developed pallial sinus – the largest among the tellinoids (Marques et al. 2022). This feature is strongly associated with internal anatomy and its specialisation in a deep infaunal habit.

The tellinid fauna, in Brazil, presents 49 species and seems to share several species that occur in the Caribbean, but with less diversity (Mikkelsen and Bieler 2008, Turgeon et al. 2009). On the other hand, *Tellina iheringi* Dall, 1900 is an example of exclusive occurrences ranging from southeastern Brazil to Argentina coast (Boss 1966a, 1966b). Of these occurrences, about 20 species are well known from the Brazilian coast – much due to occurrences closer to the coast, such as *Eurytellina punicea* (Born, 1778) (Fig. 2E), *Angulus gibber* (Ihering, 1907) or *Scissula sandix* (Boss, 1968) (Rios 2009). Some of these are well known from estuarine or near-estuarine environments, such as *Austromacoma constricta* (Bruguère, 1792) and *Eurytellina lineata* (Turton, 1819) (Arruda and Amaral 2003). In contrast, the rarest species occur further from the coast or offshore, related to occasional technical collections with specialised vessels – as in the case of *Ameritella diantha* (Boss, 1964) or *Eurytellina vespuciana* (d’Orbigny, 1853) (Tenório 1984). Only *Tellina brasiliiana* Spengler, 1798 is endemic to Brazil (Rios 1994). From the advance of Brazilian taxonomic studies, we had the addition of two species endemic to the southeast coast: *Austromacoma biota* (Arruda & Domaneschi, 2005) and

*Eurytellina angrensis* Marques & Simone, 2014 (Arruda and Domaneschi 2005, Marques and Simone 2014).

In coastal environments of Brazil, species of Corbulidae, included in the Order Myida, figure among the most abundant molluscs (Denadai and Amaral 1999, Arruda et al. 2004). In a recent review, Arruda (2020) identified 12 marine species based on shell characteristics, grouped into five genera: *Corbula*, *Caryocorbula*, *Juliacorbula*, *Tenuicorbula* and *Varicorbula*. Arruda (2020) also observed that the species have overall conservative characteristics, producing difficulties in species identification, being common for collections to present several misidentified lots. These similarities may be related to the allometric characteristics exhibited between species, which have been well demonstrated for *Caryocorbula* (Anderson and Roopnarine 2005). Despite the similarities exhibited between the shells of different species, they exhibit great variability within the species during shell growth. This variability is partly due to accretion processes that make non-thickened individuals quite different from those having undergone shell thickening process. The different thickening processes that occur in Corbulidae have been described by Goodwin et al. (2008). Thickening of the valve alters the general shape of the shell, the characteristics of the hinge beyond the width and height of the valve, producing an individual with very different general characteristics (Arruda 2020). The specific shell accretion and growth processes demonstrated by Corbulidae should therefore be considered when studying the diversity of the family.

Of the species that occur in Brazil, three show great morphological variability throughout their distribution: *Caryocorbula swiftiana* (C.B. Adams, 1852), *Corbula patagonica* d’Orbigny, 1846 (Fig. 1L), and *Juliacorbula aequivallis* (Philippi, 1836), and these forms should be analysed in more detail. In addition, six of the 12 species found in Brazil also show a high degree of similarity with species from the eastern Pacific Ocean, and the similarity between these species still needs to be investigated.

Many challenges still exist for the advancement of studies on marine bivalves in Brazil, especially for groups of deep waters (>200 m) that depend on constant financial support to fund expeditions along the EEZ. Different from the most neglected groups (e.g., Aplacophora, Polyplacophora) there are many consolidated research groups in Brazil working and producing results of the highest quality on marine bivalves. On average, five new species of marine bivalves are described per year in Brazil, indicating a periodicity of new taxa described and the potential for expansion of knowledge about the group in Brazil.

## Marine gastropods, where the Mollusca reached its largest diversity

Marine gastropods are a heterogeneous assembly of taxa, and it is the higher diverse one, comprising practically half of the molluscan diversity (Rosenberg 2014). All main gastropod groups have a marine origin and occur in sea as a whole or have at least a small branch in it. This is the case, for example, of the heterobranch superorder Eupulmonata, a huge gastropod branch almost exclusively non-marine, but possessing the Order Ellobiida, which mostly contains marine lineages (Harzhauser et al. 2023). In Brazil, the 1,837 valid species of marine gastropods are distributed among five subclasses, Patellogastropoda (7 spp.), Vetigastropoda (198 spp.), both exclusively marine; Neritimorpha (11 spp.), Caenogastropoda (1,203 spp.), both predominantly marine; and Heterobranchia (418 spp.), being about half marine (BZG-Mollusca 2023). Representatives of the subclass Neomphaliones have not yet been recorded in Brazilian waters.

The marine environment usually includes the estuary, which in Brazil has several species of gastropod, both in low salinity regions, and in regions close to its opening to the sea, usually including different assemblies. Gastropods also live in all marine environments, mainly those benthic like rocky areas and unconsolidated substrates; in all depths, from supratidal to hadal levels, having obviously higher diversity in shallower habitats (Laheng et al. 2023). Several gastropods also are free from benthos, occurring in the water column both, like plankton (e.g., Euthecosomata pteropods), and active swimming (e.g., Gymnosomata pteropods); while other are floating, like janthinids and glaucids (Churchill et al. 2011, 2014).

Related to mode of life, marine gastropods have all of them, except flying capacity. There are herbivores, carnivores, omnivores, microphages, predators, foragers, filter-feedings, ecto- and endoparasites, etc. There are groups sessile, semi-sessile, diggers, resistant to waves, interstitial, fossorial, epiphytes, among others (Simone 2011).

Marine gastropods also have commercial importance. Some larger ones are consumed as food all along the Brazilian coast (e.g., Boffi 1979). Their shells are widely used in handicrafts for ornaments and jewellery (e.g., Alves et al. 2006), and even for shell collections.

In this huge wide range of issues, it is impossible to perform a complete report on marine gastropods in exiguous brochures. Thus, this report is not complete to all taxa that occur in Brazilian coast, but so to the groups that possess specialists in the country. They are organized below in a rather phylogenetic order, mainly considering the classification proposed by

BZG-Mollusca (2023) plus Simone (2011) for some specific cases of internal organisation. This last has a classification purely based on morphology, a scenario not totally considered in the former. Therefore, the order is Vetigastropoda, Neritimorpha, Caenogastropoda and Heterobranchia.

The diverse gastropod group Vetigastropoda has approximately 4.000 living marine species occurring all over the globe, at all seas and depths (Cunha et al. 2022). Vetigastropods include abalones, turban snails, top snails, keyhole limpets, slit shells, and small slit shells dating from the Cambrian/Ordovician boundary (Uribe et al. 2016). The group contains morphological synapomorphies of an epipodium with epipodial sense organs with sensory structures known as bursicles (Geiger et al. 2008). Currently, the systematics of vetigastropods is composed of 37 families arranged in eight superfamilies: Lepetelloidea; Lepetodriolea; Scisurelloidea; Fissurelloidea; Haliotiodea; Trochoidea; Pleurotomarioidea; Seguenzioidea (Cunha et al. 2022). Among these, only Lepetodriolea (hydrothermal vent limpets) does not occur in Brazil.

Access to the deep sea has increased our knowledge of the diversity of Vetigastropoda in Brazil over the past few decades (e.g., Simone and Cunha 2006, Cavallari et al. 2019), although there are still few specialists in Vetigastropoda systematics in Brazil. This shortage of specialists is a limiting factor in assessing the real diversity of this deep-water group.

The largest taxon within Vetigastropoda is the Superfamily Trochoidea. Trochoideans are morphologically diverse, ranging in size from just a few millimetres to large commercially treated iconic shells (Williams et al. 2008). The three most diverse families of turban and top snails are Calliostomatidae, Trochidae, and Turbinidae. Although they have received considerable attention in the past few years, their inner relationships are still in progress. Trochoidea includes 12 families (Cunha et al. 2022), in which 91 species distributed in Areneidae, Calliostomatidae, Liotiidae, Margaritidae, Phasianellidae, Skeneidae, Solariellidae, Trochidae and Turbinidae families occur in the Brazilian waters. Areneidae was described in 2012 including two genera: *Arene* H. & A. Adams, 1854 with 37 species and *Cynisca* Kilburn, 1970 with seven African species. *Arene* occurs in the Atlantic-Pacific Oceans with 11 species in Brazil (BZG-Mollusca 2023).

Calliostomatidae is a diverse family, with ~250 species of medium size, diagnosed by a protoconch with a honeycomb sculptured pattern and a long, delicate, and serrated rachidian (Williams et al. 2010). However, differentiation in protoconch and radulae are observed among the four subfamilies within calliostomatid: the most diverse Calliostomatinae, Fautricinae,



Margarellinae, Thysanodontinae and Xeniostomatinae (Williams et al. 2010, McLean 2012). Calliostomatids are important carnivores, eating sessile invertebrates such as cnidarians and sponges. *Calliostoma* Swainson, 1840, for example, comprises about 70 species in the Western Atlantic, some of which are distributed in subgenera. In Brazil, specifically, about 23 valid species are registered (Cavallari et al. 2019), being *Calliostoma depictum* Dall, 1927 frequently associated with black urchin *Echinometra lucunter* (Linnaeus, 1758).

Margaritidae includes 16 species in the Atlantic coast of South America, distributed in three genera: *Margarites* Gray, 1847, *Gaza* Watson, 1879, and *Callogaza* Dall, 1881 (Simone and Birman 2006, Simone and Cunha 2006), both recorded from Brazil (BZG-Mollusca 2023). Shell characters of margaritids are inconclusive for group diagnostics (Williams 2012). The radula has a large oval/base of rachidian and lateral teeth, and a later marginal plate is usually present. However, the degree of development as an articulatory structure is variable (Hickman and McLean 1990, Simone and Cunha 2006). In all, six species of Margaritidae have been recorded in Brazil to date (Cavallari et al. 2019), all of them from the deep sea (100–900 m) (Simone and Birman 2006).

Since the classical systematic revision of Trochoidea proposed by Hickman and McLean (1990), studies focusing on the systematics of Trochoidea and Vetigastropoda have greatly changed the taxon composition and arrangement of subfamilies of Trochidae (Williams et al. 2008). Currently, composed of 10 subfamilies, Trochidae is a diverse family, particularly in the tropical Indo-West Pacific. Trochoid-shaped shells might be one of the reasons why species of trochids are common in the intertidal zone, as they reduce predation by shell-crushing predators (Williams 2012). In Brazil, there are two species of *Snaptocochlea* Pilsbry, 1890 (Fossarininae) and one species of *Halistylus* Dall, 1890 (Hastylinae) (BZG-Mollusca 2023), both genera with small to minute shells and a thin or absent nacreous layer (Hickman and McLean 1990). Turbinidae (=turban shells), in turn, have four subfamilies. No morphological diagnoses are recognized for the Turbinidae in recent systematic classifications (e.g., Cunha et al. 2022), although characters such as a calcareous operculum (secondarily lost in Tegulinae), rachidian without interaction along the row, and lateral teeth with the lateral edge of the apical cusp serrate were found in a morphological phylogeny for Tegulinae (Dornellas et al. 2020). There are 12 valid species inhabiting Brazilian waters, two of which are *Agathistoma viridulum* (Gmelin, 1791) and *Lithopoma tectum* ([Lightfoot], 1786), very abundant in the intertidal zone with a wide range of distribution.

Another important marine gastropod subdivision is Neritimorpha possessing only the family Neritidae. It is represented on the Brazilian coast by the genera *Nerita*, *Neritina*, *Neritopsis*, *Smaragdia* and *Vitta*, with 10 valid species (BZG-Mollusca 2023). Several species of this group can be found forming aggregates in estuarine roots and trees, constituting usually dense and extended populations (Matthews-Cascon et al. 1990), consequently invading freshwater environments through the estuaries (Govindan and Natarajan 1972). The main morphological characters of Neritidae include a globose shell with few whorls, short spire (Hyman 1967a), lack of columella, calcareous operculum and a rhipidoglossate radula (Martins et al. 2002). The members of this family can be highly variable, showing a great variety of colours and patterns (Tan and Clements 2008).

Caenogastropoda is the largest Mollusca subdivision, including about half of the Gastropoda diversity (Simone 2011). An important character, of the several ones, is the diaphragmatic septum, a structure that divides anatomically the head-foot from visceral mass (Simone 2021). This structure permitted, among several evolutive implications, the gigantism and the development of the proboscis, although many branches of Caenogastropoda are composed of microgastropods.

In the past two decades, faunistic surveys in several regions of the world recognized micromolluscs among the richest families (e.g., Sasaki 2008, Middelfart et al. 2016). According to Middelfart et al. (2020), micromolluscs are those species whose adult specimens have dimensions less than 10 mm but for alternative definition, of up to 5 mm, see Sasaki (2008). They represent important components of the malacofauna in most of the marine environments being abundant and valuable for the analysis of species composition. They can colonise and explore environments usually inaccessible for macromolluscs or even particular lifestyles such as micropredation or parasitism (Ponder 1969). Micromolluscs include the great majority of undescribed molluscan taxa (Geiger et al. 2007), and even well-studied areas still harbour a significant percentage of undescribed species (Geiger 2018). These minute molluscs evolved in many different lineages of Mollusca, in marine and terrestrial environments, but their larger diversity is present in the marine Gastropoda.

Based on the results of an extensive survey of marine malacofauna in New Caledonia, Albano et al. (2011) introduced the term 'Big five' to the top-five Molluscan families in terms of species richness: Cerithiopsidae, Triphoridae, Eulimidae, Pyramidellidae and 'Turridae s.l.' this last one is

now dismembered in several families after recent molecular approaches. These families are predominantly composed of microgastropods and many of its members tend to present specific lifestyles/feeding habits of parasitism or micropredation, in many cases with species-specific relation (Albano et al. 2011).

Middelfart et al. (2016) highlighted that in Australia, for example, of the 10 most diverse families of marine molluscs, only three are strictly macroscopic while the others are essentially microgastropods (e.g., Rissoidae, Triphoridae, Eulimidae, and Cerithiopsidae).

In Brazil, microgastropods represent around 45% of the total number of species recorded (BZG-Mollusca 2023). While some families traditionally recognized by their large shells include some few species that are micromolluscs (e.g., Naticidae, Epitoniidae, Muricidae), around 1/3 of the 195 families of marine gastropods from Brazil are exclusively or mainly composed of micromolluscs (BZG-Mollusca 2023).

Among the top-10 richest families of marine gastropods in Brazil, three are mainly composed of micromolluscs (Pyramidellidae – the top-one, which actually is heterobranchian, Eulimidae and Triphoridae). Other very representative families of marine microgastropods are Caecidae, Chilodontidae, Barleeidae, Tornidae, Rissoidae, Seguenziidae, Cerithiopsidae, Solariellidae and Anatomidae.

The taxonomic study of micromolluscs was, to some extent, neglected in Brazil until the end of last century, being limited to sporadic description of species, or its inclusion in inventories and checklists. Thus, the precise composition of many families remained underestimated for a long period and presented confusion due to dubious records of species. In many instances, such records were based on a somewhat vague comparison with Caribbean/North American samples, hiding the potential endemism in Brazilian malacofauna and hindering a well knowledge of geographic distribution patterns. In some cases, the first record of a genus was presented without a complete determination of the species, especially in deep-sea surveys (e.g., Absalão 2010).

The neglect in micromolluscs studies was attributed by Middelfart et al. (2016) to the difficulty in collecting, demanding specific equipment and adequate mesh size; to the laborious work to sort; and to the expensive methods for study and illustration (e.g., SEM). Besides that, micromolluscs have a bad reputation of presenting taxonomic difficulties (Bouchet et al. 2002).

In the 1990s, a series of Governmental actions aimed to map the marine biodiversity in Brazil (e.g., REVIZEE) rendered a robust and large-scale sample of micromolluscs, in both continental shelf and slope, that were the main source

for a series of taxonomic revisions and description of species (e.g., Absalão et al. 2005, Pimenta et al. 2009). Pyramidellidae is, therefore, a good example of how these expeditions help to increase the number of new species of microgastropods in Brazil. From 2000, a series of taxonomic works (e.g., Pimenta et al. 2011) increased the number of known species of Pyramidellidae from 35 to 101. Although this is the richest family of marine gastropods from Brazil and in the world, the number of 101 species can be still considered outdated, considering the species from deep sea that remain unknown; actually, unpublished data estimates that it will enlarge in at least 50% (A.D. Pimenta unpublished data).

Another example of knowledge increasing about richness as a consequence of taxonomic studies is Triphoroidea. Until the catalogue of Rios (2009), only nine species of Triphoridae were recorded from Brazil; recent studies (e.g., Fernandes and Pimenta 2020) increase that number to 52, with estimates of at least 70 species in Brazil. In the same way, unpublished data indicate that the number of species in Cerithiopsidae will rise from 12 to ~40 species (A.D. Pimenta, unpublished data).

Eulimidae, which was also included in the 'Big Five' by Albano et al. (2011), are known as parasites of the five extant classes of echinoderms, a specialist lifestyle with several morphological adaptations to this habit (Warén 1983, Takano and Kano 2014). Taxonomic revisions of eulimids were conducted mainly in the Indo-Pacific and Northeast Atlantic. Currently, this family comprises about 100 genera and 960 species (considering only living groups) (BZG-Mollusca 2023). In Brazil, TCBF platform records 24 genera, most with a worldwide distribution. Currently 59 valid species are registered in Brazil (~6% of the global richness of Eulimidae) (BZG-Mollusca 2023), although still have at least more 30 species to be recorded or described in the country (L.S. Souza and A.D. Pimenta, unpublished data). These numbers also confirm Eulimidae in the ranking of the 'Big Five' gastropod families of Brazil. However, most species are known only from empty shells, a common scenario of several microgastropods, which hinders the knowledge of the systematics and life history (e.g., parasite-host relationship) of this group.

A proper scenario of micromolluscs richness in Brazil is still far from satisfactory. Many families lack a complete revision, several new records of genera, especially in deep-sea, should be confirmed, and new techniques, involving DNA, are required to solve the taxonomy of cryptic species with large geographic distribution. Besides that, knowledge of biology aspects, especially in the feeding habits and reproduction mode are still absent for the great majority of the

species. Thus, the premise of Sasaki (2008) that discovering and describing micromolluscan faunas is an unlimited frontier anywhere in the world and that their study is essential in the malacology of the 21<sup>st</sup> century is also valid for knowledge of Brazilian marine malacofauna.

Changing the subject to the families that usually have macrosnails (but not all), the Naticidae is represented on the Brazilian coast by 11 genera and 29 valid species (BZG-Mollusca 2023). Members of this family have a globular shell with a low spire, expanded body whorl, with a wide opening, and foot with an extensive propodium (Hyman 1967b); plus, a wide horny operculum, weakly pigmented eyes and a taenioglossate radula (Strong 2003).

The Naticidae are a cosmopolitan family that lives from the intertidal zone to several thousand metres depth. The naticids are predators, commonly feeding on bivalves but also other gastropods, in enveloping their prey with their foot and drilling a hole into the shells to reach the soft parts with their proboscis (Huelsken et al. 2008).

Muricidae is among the most diverse and taxonomically complex neogastropod families, comprising about 1,600 exclusively marine species distributed throughout the globe (Barco et al. 2010). The family stands out for its species richness and a wide diversity of shell shapes and ornamentation. While it includes highly specialised taxa (i.e., ectoparasites), its representatives are mostly generalist predators (Taylor et al. 1980). Their main anatomical characteristic is the presence of an accessory boring organ (ABO) used in predatory activity and shared by most taxa of this family (Harasewych 1998). The classification of muricids was traditionally based on conchological and radular features, and divergences in the interpretation of these morphological characters pose many taxonomic challenges (Barco et al. 2010). Recent phylogenetic studies based on molecular data sought to clarify the classification of the group (e.g., Claremont et al. 2013). However, the classification of muricids is still under debate, especially at the subfamily level. In Brazil, the Muricidae are represented by 10 of the 12 subfamilies recognized in the latest classification proposed by Bouchet et al. (2017). However, the number of muricid species in the country (82 valid species) does not seem to reflect the real family's diversity. This problem may be related to the reduced number of specialists in Brazil and the taxonomic challenges imposed by the high intraspecific conchological variability of the group. Some works have already revealed that even widely known, widespread species in Brazil may represent species complexes (e.g., De Biasi et al. 2016, Simone 2017), suggesting that the local muricid biodiversity is potentially underestimated.

Another important marine gastropod subdivision, usually with subclass status, is Heterobranchia, including most of the marine slugs, but also some shelled taxa.

The heterobranch family Architectonicidae, a shelled taxon, includes 12 extant genera and ca. 150 species widely distributed in shallow to deep tropical/subtropical waters worldwide. These shelled gastropods have a long planktonic larval stage, which explains their generally extensive ranges. They develop into specialised benthic carnivores that feed mainly on cnidarians, such as corals and anemones, and exhibit associated anatomical (e.g., radular) modifications (Bieler 1993, Bieler and Petit 2005). Architectonicids are mainly characterized by their broadly conical/discoid heterostrophic shell with a wide umbilicus and horny operculum bearing spirally arranged lamellae. The number of known architectonicid representatives recorded in Brazil remained for decades at eight to nine species depending on taxonomic changes, and none of them was considered endemic (Rios 1985, 1994, 2009, Rosenberg et al. 2009). However, this number was expanded in 2011 onward, with studies based on projects and expeditions such as REVIZEE Nordeste and Marion Dufresne MD55, focused on deep-sea environments (Tenório et al. 2011, Cavallari et al. 2013, 2014). Currently, the family encompasses nine genera and 17 species in Brazil, five of which are considered endemic to date. Future discoveries regarding architectonicids in Brazilian waters are likely to reside in the deep sea, and the fact that some of the areas not yet studied are in oil extraction sites (e.g., the Pre-Salt layer) is of particular concern (Cavallari et al. 2014). Regrettably, there are no expert groups focused on or actively working with architectonicids in Brazil now.

From the marine slugs or semislugs, an important branch is the Sacoglossa, a clade with status from order to superorder (BZG-Mollusca 2023). Currently ~300 species of Sacoglossa are known, a group of highly specialised herbivorous sea slugs (Jensen 1996). Commonly called 'sap-sucking' slugs, sacoglossans have a feeding apparatus adapted to pierce the cell wall of algae and then suck out its cytoplasm (Jensen 1997). Furthermore, some lineages can retain live and functional chloroplasts in their digestive gland, which is a rare physiological adaptation in the animal kingdom known as kleptoplasty (Christa et al. 2014). Although intriguing, sacoglossans are difficult to find in the field due to their small size (>30 mm in length), cryptic lifestyle, and low population densities (Jensen 1997). The highest diversity of Sacoglossa is reported in tropical waters of the Pacific and the Caribbean Sea (Jensen 2007). In Brazil, specifically, 29 species have been reported up to now, some of which were



from original descriptions (e.g., Marcus 1955, Marcus and Marcus 1963), while others were documented in faunistic inventories (e.g., Padula et al. 2012, Galvão-Filho et al. 2015, Delgado et al. 2022). Unfortunately, some species were only reported in their original descriptions, or synonymized based on limited data (Marcus 1956). The low number of sacoglossans reported in Brazil may be related to the limited sampling efforts conducted in the region, which were almost exclusively related to the work of the Marcus between the 1950s and 1980s (Jensen 2007).

From the so-called true marine slugs (e.g., Simone 2018) are the nudibranchs, technically Nudipleura, a clade with status from order to superorder (BZG-Mollusca 2023). There are 126 valid species of nudipleurans recognized from Brazil, of which 126 species are Nudibranchia and 10 species are Pleurobranchida (BZG-Mollusca 2023). The data analysis shows that most of the sampling efforts/papers in Nudipleura were concentrated in Rio de Janeiro, São Paulo and Alagoas states (e.g., Padula et al. 2012, Alvim and Pimenta 2013). The other sampled states represent sparse and occasional records. Moreover, some states were never sampled, such as Piauí, Paraíba, Sergipe and Paraná. It is clear that Nudipleura presents the Linnean and the Wallacean shortfalls, which are fundamental impediments to the establishment of initiatives for biodiversity conservation (Cardoso et al. 2011). The challenges for new studies are (i), to know the real biodiversity of Brazil, through studies in states that are little or no sampled, and the entire Brazilian coast with regard to the deep sea; (ii), improve the descriptions of the known species, since most of them were described based on few preserved specimens with superficial descriptions and (iii), the use of integrative species delimitation approach to elucidate cryptic species.

Alvim and Pimenta (2013) recognized 13 species of Discodorididae from Brazil, whereas in the TCBF platform are listed 15 valid species. The discrepancy is related to *Thordisa lurca* (Ev. & Er. Marcus, 1967) and *Thordisa ladislavii* (Ihering, 1886). *Thordisa lurca*, originally described for Colombia, was recorded from Brazil by Valdés et al. (2006) without specifying the exact location in Brazil or state in which collection this specimen was deposited (Alvim and Pimenta 2013), making it difficult to assess the validity of this record. *T. ladislavii*, originally described for Santa Catarina, has superficial descriptions, which does not allow checking its validity. Both were considered here, as no taxonomic action was taken regarding them. Like Nudipleura, the most sampled states and consequently with the highest number of occurrences are Rio de Janeiro, Alagoas and São Paulo. In contrast, some

states have no record at all, such as Piauí, Ceará, Paraíba, Sergipe, Espírito Santo, Paraná and Rio Grande do Sul. There is an urgent need for studies along the entire Brazilian coast in order to have a real idea of biodiversity; this is the only way to be able to solve taxonomic problems like *T. ladislavii*. Discodorididae presents one of the only registered deep sea species of Nudipleura for Brazil, *Taringa iemanja* Alvim & Pimenta, 2013. This occurrence shows great potential for new species for this environment.

As for Pleurobranchida, TCBF recognizes ten valid species for Brazil (BZG-Mollusca 2023). This order consists of two families: Pleurobranchaeidae and Pleurobranchidae. The first one presents two valid species, reported from Sergipe, Bahia, Rio de Janeiro, São Paulo and Rio Grande do Sul. The great challenges for the study of Pleurobranchaeidae are (i), species burrow in soft bottoms, needing specific sample collection for this habitat and (ii), most species are brownish and quite similar externally, which requires an integrative taxonomy to clarify the large number of synonyms per species. Pleurobranchidae, in turn, presents eight valid species in Brazil (BZG-Mollusca 2023). Among the valid species, *Berthella stellata* (Risso, 1826) has an uncertain record for the Brazilian coast (Ghanimi et al. 2020), which makes a study based on molecular species delimitation tools essential. Pleurobranchidae presents greater sampling on the coast, but some states remain unrecorded, such as Piauí, Ceará, Paraíba, Sergipe, Paraná and Rio Grande do Sul.

The future challenges of the studies on the marine gastropods lie in poorly explored areas, like north Brazilian coast and deep sea, regions in which lots of new taxa have been recently discovered. However, even in shallower environments novelties constantly appear, not only as unexpected surprises, but also studying species with wide geographic distribution, e.g., from North Carolina (USA) to South Brazil. About half of the studied species that supposedly have that condition reveal actually a set of similar-shelled taxa with more restricted distribution. Thus, several novelties come from supposedly known species. Therefore, an important task has been to refine the taxonomy of the Brazilian local fauna, which in part is regarded as an impoverished derivative from the Caribbean one up to São Paulo-Santa Catarina level. This Caribbean faunistic connection, however, frequently does not resist a more detailed taxonomic study.

#### The freshwater malacofauna

Although usually not diverse and colourful as their marine relatives, freshwater molluscs are important for ecosystem functioning, economic, cultural, and public health

issues (Vaughn 2018, Strong et al. 2008, Miyahira et al. 2022). Moreover, several groups are threatened by habitat modification and the introduction of invasive species and thus, the decline of freshwater mollusc populations worldwide is notorious (e.g., Lydeard et al. 2004, Strong et al. 2008, Cowie et al. 2017a, Miyahira et al. 2022). With a total of 293 valid species, the freshwater mollusc fauna in Brazil represents about 8.3% of all current known diversity. Usually with a lack of taxonomic studies, the group as a whole has its diversity underestimated. Currently, it is believed that only half of the freshwater gastropod and bivalve species have been properly described in the Brazilian territory and that, therefore, their real diversity would be double the current one (i.e., 586 spp.) (Simone 1999b).

Most of freshwater mollusc research is based in two main axes: invasive species – e.g., *Limnoperna fortunei* (Dunker, 1857), *Corbicula* spp., and *Melanoides tuberculata* (Müller, 1774) and public health (mainly Planorbidae and especially *Biomphalaria* spp.). Simone (2006) stated that 95% of the references in his book about non-marine molluscs was related to Planorbidae. Therefore, there is a long way to go in the study of most, if not all, freshwater groups in Brazil. Herein, freshwater bivalves (116 spp.) and gastropods (177 spp.) will be presented separately, highlighting their most representative groups (Table 4).

### Freshwater bivalves

Among the most representative groups of freshwater bivalves in Brazil are, (i) Unionida (84 spp.), (ii) Sphaeriidae (17 spp.) and (iii) Cyrenidae (7 spp.) (Table 4). These three clades represent the main radiations of the bivalve's intro freshwaters in Brazil. There are also other species included in typical marine families, but with some freshwater representatives like *Anticorbula fluviatilis* Adams, 1860 (Corbulidae) and the invasive *L. fortunei* (Mytilidae).

Unionida is the largest exclusive group of freshwater Bivalvia. In Brazil, there are only two families: Mycetopodidae and Hyriidae. This group is composed of large freshwater mussels (reaching up to ~25 cm) or naiads and presents a unique life cycle that includes a parasitic stage in vertebrates, usually fishes (Wächtler et al. 2001). According to the TCBF database, Hyriidae has 52 species in eight genera, and Mycetopodidae 32 species in 10 genera. Hyriidae diversity is concentrated at Amazonas basin, whereas Mycetopodidae diversity is at Río de La Plata basin (Pereira et al. 2014). However, there are some under sampled areas and several species lack taxonomic revision, a strong indication of underrated diversity (Cuezzo et al. 2020, Miyahira et al. 2022). Never-

**Table 4. Diversity of freshwater molluscs in the Brazilian territory.**

Class	Order/subclass	Families	Genera	Valid species	
Bivalvia	Unionida	Hyriidae	8	52	
		Mycetopodidae	10	32	
	Venerida	Cyrenidae	2 <sup>a</sup>	7	
		Sphaeriida	Sphaeriidae	4	17
	Myiida	Corbulidae	1	1 <sup>b</sup>	
		Dreissenidae	2 <sup>c</sup>	5	
			Erodonidae	1	1
			Mytilida	Mytilidae	1
	Gastropoda	Caenogastropoda	Thiaridae	2	32 <sup>e</sup>
			Ampullariidae	5	49
Tateidae			1	12	
Cochliopidae			3	15	
Tomichiidae			1	7	
Hygrophila		Chiliniidae	1	9	
		Lymnaeidae	3	7	
		Physidae	3	3 <sup>f</sup>	
		Planorbidae	12	41	
		Bulinidae	2	2	
Total			62	293 <sup>g</sup>	

<sup>a</sup> It includes the invasive genera *Corbicula* (3 spp.) and native *Cyanocyclus* (4 spp.). <sup>b</sup> It includes the species *Anticorbula fluviatilis* from the Amazonian region. <sup>c</sup> It includes *Rheodreissena* (typically freshwater) and the invasive genus *Mytilopsis* (brackish water, tolerating low salinities). <sup>d</sup> It is represented by the invasive species, *Limnoperna fortunei*. <sup>e</sup> It is represented by the invasive species, *Melanoides tuberculata*. <sup>f</sup> It is represented by the invasive species, *Physa acuta* Draparnaud, 1805. <sup>g</sup> Total number of valid species of Brazilian freshwater molluscs (18 families), based on the TCBF-Mollusca database.

theless, these freshwater mussels also depend on preserved habitats and are severely threatened by habitat modification and the introduction of invasive species (Miyahira et al. 2022, 2023). A good taxonomical and ecological understanding of these species is essential for conservation efforts. Miyahira et al. (2019) revalidated and redescribed *Rhipidodonta garbei* (Ihering, 1910) that was previously considered synonymous, restricting its distribution, and raising different conservation strategies.

By contrast, Sphaeriidae is a family of minute freshwater clams (less than 1 cm). In TCBF there are 17 species in four genera: *Eupera*, *Pisidium*, *Sphaerium* and *Musculium*. *Pisidium* is the most diverse genus with nine species, whereas *Sphaerium* and *Musculium* has only one species recorded in Brazil. However, these numbers are certainly outdated. Other South American species of Sphaeriidae were revised by Cristián Ituarte (Argentina), but a comprehensive revision of Brazilian species is still lacking (Cuezzo et al. 2020). The small dimensions of these clams always hindered the studies with this group, despite being relatively common in inventories. There are some ecological and population dynamics studies

of *Pisidium* (Anflor-de-Oliveira and Mansur 2001, Mansur et al. 2001) and a revision of some species of *Eupera* (Mansur and Meier-Brook 2000) dealing with Brazilian species.

Finally, Cyrenidae is better known as the invasive species of *Corbicula*. Three species of this genus, *C. fluminea* (Müller, 1774), *C. largillierti* (Philippi, 1844) and *C. fluminalis* (Müller, 1774), were introduced in Brazil and are now widespread (Cuezzo et al. 2020). In TCBF, the native cyrenids are represented by four species of *Cyanocyclus*, as also a brackish water species of *Polymesoda*. However, this group lacks taxonomical studies, and this diversity is probably underestimated. A recent revision of Uruguayan species of *Cyanocyclus* that included some Brazilian species, recovered as valid some taxa previously considered synonymous, such as *Cyanocyclus guahybensis* Marshall, 1927 (Cuezzo et al. 2020). In addition to the focus on invasive species in this group, it is also necessary to dedicate efforts to native species of Cyrenidae. This group is also important in conservational aspects as some studies showed population declines related to habitat modification and the introduction of invasive species (Clavijo and Carranza 2018).

### Freshwater gastropods

The freshwater gastropods in Brazil belong to two distinct lineages, the Caenogastropoda and the Hygrophila, both of which also include introduced species (see below). Among the Caenogastropoda, the Ampullariidae are the most expressive group. Members of this family are popularly known as ‘apple snails’ due to their (for the most part) large globose shells (reaching up to 17 cm). Out of the four currently recognized genera in Brazil, the most speciose is *Pomacea* Perry, 1810 (Fig. 1B), with circa 30 species (Berthold 1991, Cowie and Thiengo 2003, Simone 2006, Cowie and Héros 2012, Cowie et al. 2015, 2017b). Traditional morphological taxonomy of ampullariids is confounded by shell variability and by most species remaining poorly studied, though recent studies combining DNA sequences with sound morphological data have begun to clarify it (Hayes et al. 2012, 2015, Barbosa et al. 2022). Ampullariids have both a gill and a lung, which allows them to breathe in and out of the water, and their most striking feature is perhaps the egg masses. The eggs of *Pomacea* spp. are generally coloured (e.g., pink, green, red) with a calcareous shell, and typically laid as a cluster on emergent vegetation above the water line (eggs of other genera are weakly coloured, white or translucent, laid in a gelatinous matrix below the water – Thiengo et al. 2011, Hayes et al. 2015). Two species of note are *Pomacea maculata* Perry, 1810 and *P. lineata* (Spix in Wagner, 1827),

which are intermediate hosts of *Angiostrongylus cantonensis* (Chen, 1935), the nematode that causes the zoonosis eosinophilic meningitis.

Still within the Caenogastropoda, another taxon of interest is Tomichiidae, which has only recently received enough support to be recognized as a distinct family. This was achieved through a molecular phylogenetic study of its members, focusing on the Brazilian *Idiopyrgus* (Salvador et al. 2022a). Tomichiidae is a relict Gondwanan family containing three genera, one in each continent (South America, southern Africa and Australia) (Salvador et al. 2022a).

Finally, representatives of the caenogastropod family Tateidae seem to be widespread in the country, including in cave environments. While some troglophile and troglotic species have already been described, the number of still undescribed species in caves is expected to be high (Salvador et al. 2022b).

The Hygrophila belong to the Heterobranchia and are closely related to the Eupulmonata (see next session on terrestrial gastropods). This clade contains freshwater gastropods that lack an operculum and are simultaneous hermaphrodites, sometimes capable of self-fertilisation (Cuezzo et al. 2020, Saadi et al. 2020). In Brazil, the two superfamilies Chilinoidea (restricted to the southern region of the country) and Lymnaeoidea (widely distributed through the country) are divided into five families with 62 species (Table 4). The families of Lymnaeoidea with most studies in Brazil are Planorbidae (Fig. 1J) and Lymnaeidae, as both include intermediate hosts of *Schistosoma mansoni* Sambon, 1907 and *Fasciola hepatica* Linnaeus, 1758, being thus important for public health (Neves et al. 2022). Finally, Hygrophila species are among the most endangered animals worldwide (Lydeard and Cummings 2019) and further studies on the lesser-known species are particularly urgent.

While most Hygrophila are ‘traditional’ snails, there are also limpets that are part of this clade. These animals are well represented in Brazil, representing almost one quarter of the total species of Hygrophila (Santos 2003). There are 17 species of freshwater limpets in the country, divided between Bulinidae (*Burnupia* Walker, 1912) and seven genera belonging to the Ancylinae within Planorbidae (Table 4). Given their simple shell morphology and small size, when integrative morphological and molecular studies are conducted, there is a tendency to increase the number of known species.

### The diversity of terrestrial gastropods in Brazil

Even though terrestrial gastropods are usually considered a single group, there are different and phylogenetic



ically unrelated lineages of gastropods that independently colonised land (Vermeij and Watson-Zink 2022). In Brazil, there are three such lineages, the Helicinoidea (belonging to the Neritimorpha), the Cyclophoroidea (belonging to the Caenogastropoda), and the Eupulmonata (belonging to Heterobranchia) (Table 5). The first two superfamilies are typically referred to as ‘operculate snails’ because they have an operculum to close the shell’s aperture like their marine relatives. The Eupulmonata, in turn, lack the operculum, which was lost in the evolutionary history of the lineage they stem from (Barker 2001). Eupulmonata also include a few minor marine lineages but are mostly made up of terrestrial snails and slugs belonging to groups known as Systellommatophora and Stylommatophora. For a review of the history of the study of land snails in Brazil, see Salvador (2019).

Both the Helicinoidea (37 spp.) and Cyclophoroidea (22 spp.) are not particularly diverse in Brazil, especially when compared to other tropical areas worldwide where they are more speciose (Salvador 2019). Nevertheless, the current taxonomy of the helicinoidea is poorly resolved and this group might still prove to be more diverse in Brazil than initially thought.

In Brazil, terrestrial Systellommatophora are represented by Veronicellidae (leatherleaf slugs), a widespread tropical and subtropical family that is particularly speciose in Brazil (Simone 2006). In fact, Veronicellidae is the only family of native slugs in the country (Thomé and Gomes 2011). They are easily distinguishable from other slugs (all belonging to the Stylommatophora; see below) in several aspects, such as the mantle covering the entire dorsal region, absence of respiratory pore, presence of contractile superior tentacles and bifurcated inferior tentacles, besides many internal anatomical peculiarities (Thomé et al. 2006, Thomé and Gomes 2011). Despite the large number of specific names proposed in the past for this family in Brazil, many are synonyms or have precarious descriptions and/or lost type materials (Thomé 1993, Thomé and Gomes 2011). Currently, circa 24 species are recognized in the country classified in nine genera, the most well-known being *Phyllocaulis* Colosi, 1922 (Fig. 2H) from the Atlantic Forest (Thomé 1976, Gomes et al. 2010). Morphoanatomical features of these slugs have been proven largely insufficient for proper identification and delimitation of species in some genera and molecular data is slowly being brought into fore to better understand this group (e.g., Gomes et al. 2010, 2013). The leatherleaf slugs are important as agricultural pests and intermediate hosts of nematodes that cause parasitoses in humans and

**Table 5. Diversity of land snails in Brazilian territory.**

Order/Superorder	Families	Genera	Valid species
Neritimorpha	Helicinidae	2	36
	Proserpinidae	1	1
Caenogastropoda	Neocyclotidae	1	2
	Diplommatinidae	2	6
	Megalomastomidae	3	13
	Veronicellidae	9	24
	Gastrocoptidae	1	7
Eupulmonata	Strobilopsidae	1	1
	Bulimulidae	19	158
	Simpulopsidae	3	33
	Orthalicidae	3	20
	Amphibulimidae	2	8
	Megaspiridae	2	8
	Odontostomidae	15	94
	Ferussaciidae	2	3
	Achatinidae	13	41
	Spiraxidae	2	2
	Streptaxidae	6	53
	Strophocheilidae	8	88
	Scolodontidae	9	40
	Charopidae	5	15
	Succineidae	4	10
	Gastrododontidae	2	3
	Urocoptidae	1	3
	Euconulidae	2	4
	Solaropsidae	1	27
	Labyrinthidae	1	2
	Epiphragmophoridae	1	2
	Agriolimacidae	1	2
	Ariophantidae	1	1
	Clausiliidae	1	1
Cystopeltidae	2	9	
Discidae	1	1	
Helicarionidae	1	1	
Helicidae	2	2	
Helicodiscidae	1	1	
Limacidae	3	3	
Milacidae	1	1	
Oxychilidae	1	1	
Philomycidae	1	1	
Thysanophoridae	1	1	
Valloniidae	1	1	
Vertiginidae	3	3	
<b>Total</b>		<b>144</b>	<b>734<sup>a</sup></b>

<sup>a</sup> Total number of valid species of Brazilian land snails (43 families), based on the TCBF-Mollusca database.

animals (Thomé 1993, Ramos et al. 2021, Thiengo et al. 2022). *Sarasinula linguaeformis* (C. Semper, 1885) is the most widespread species in Brazil, being common in urban areas and having several reports of association to nematodes that cause parasitoses and to agricultural losses (Ohlweiler et al. 2010, Thiengo et al. 2022).

Stylommatophora represent most of the diversity of terrestrial gastropods in Brazil (all introduced and non-native terrestrial species belong to this group as well). Among stylommatophorans, the Orthalicoidea tree snails are the most diverse group, making up more than 40% of the described native species in Brazil (321 species). This Gondwanan superfamily is likewise diverse throughout South America (e.g., Breure and Mogollón-Avila 2016, Breure and Araujo 2017), but that high proportion in Brazil might be inflated due to their large and typically colourful shells making them more prone to collecting and describing (Salvador 2019). Even so, many orthalicoid species are known only from their original descriptions or have scarce additional data, particularly ecological (e.g., Breure 1979). Some of the families within this group, like Odontostomidae, Megaspiridae and Simpulopsidae (Fig. 2F, L) have a history of conflicting classification and complex taxonomy and are in need of revision.

Taxa with minute and/or dull shells (e.g., Punctoidea, Pupilloidea, Scolodontidae) are typically undersampled and less studied in Brazil, and thus, potentially hide the largest portion of yet-undescribed species (Salvador et al. 2018a).

Furthermore, a higher diversity is expected in taxa such as Strophocheilidae (particularly Megalobuliminae), Subulininae, and Streptaxidae, that sometimes have large shells, but for which morphological features do not always allow good species definition. Consequently, some species complexes are thought to occur in these groups. Further molecular and ecological data, complementary to morpho-anatomical data, can help to solve this. Among these taxa, of particular interest is the Strophocheilidae, the only South American family (with a few occurrences in the Antilles as possible introductions) outside the Orthalicoidea (Fig. 2F).

Strophocheilidae is made up of comparatively large animals with bulky shells and because of that, they have been studied by many researchers throughout the last century, including their biology and ecology (e.g., Bequaert 1948, Lange-de-Morretes 1952, Leme 1973, Miranda et al. 2015, 2020a, Simone 2022a). Currently, circa 90 species (living or Holocene sub-fossils) are recognized in the Brazilian territory, representing a bit over 10% of the country's native terrestrial molluscs (Salvador 2019, Fontenelle et al. 2021, Fontenelle and Salvador 2023). However, they still present a taxonomic challenge; their homogenous and at times confusing conchological and anatomical features, as well as a lack of molecular data, has led to species being constantly described, revised, and synonymised (e.g., Salvador et al. 2018b, Fontenelle et al. 2019, 2021). Notably, the status of

synonymized subgenera within the most speciose genus in the family, *Megalobulimus* Miller, 1878 (circa 60 species occur in Brazil, of which some are the biggest land snails in the country) (Fig. 1I), needs revision. The areas where Strophocheilidae are most speciose are the Andean Amazon and eastern and southern Brazil (Bequaert 1948, Ramírez et al. 2012); however, it is currently unknown whether this is an actual natural phenomenon or simply the result of a lack of sampling in other regions of Brazil. Moreover, there is also a taxonomic bias in the studies on this family, since the majority of publications focus on *Megalobulimus*, whereas the other genera are less known in comparison (Simone 2016, 2022a). Finally, the Strophocheilidae are also important from an archaeological perspective, as they (particularly the megasnails, *Megalobulimus* spp.) are a prominent component of Brazilian shell mounds (e.g., Fontenelle et al. 2019, Gernet et al. 2022, Fontenelle and Salvador 2023).

The pantropical Subulininae (formerly classified as Subulinidae, but now a part of Achatinidae, Fig. 2A) is also an interesting case. There is scarce information on fundamental biological attributes of this clade, including anatomy, life history, and distribution of most species (D'Ávila 2022). The group's classification is still largely dependent on conchological features and only a select subset of species has anatomical or molecular data (Schileyko 1999, D'Ávila et al. 2020). While that is not uncommon in Gastropoda, this is particularly problematic in the Subulininae, considering that they present usually simple shells, which are not only uninformative for taxonomy but also supposedly highly variable within each species. As such, the presence of cryptic species is conceivable and the accomplishment of an all-embracing inventory of subulinines occurring in Brazil is dependent on new advances in the taxonomy of this group. Several Subulininae species from around the world have been introduced to places outside their native range (including to Brazil) and notably, the exact place of origin of some species are still uncertain (Simone 2006, Silva et al. 2019, Darrigran et al. 2020).

A similar situation can be found in the cosmopolitan family Succineidae, whose members possess thin unornamented shells with few useful characters for taxonomy. Even so, their classification is still based to a large extent on shell morphology (Lanzieri 1966), which is also valid for the 12 species found in Brazil, although anatomical studies have helped to solve some long-standing taxonomic issues (e.g., Arruda and Thomé 2008a, 2008b). Of the three genera present in Brazil, *Omalonyx* d'Orbigny, 1837 is of particular note, as their reduced unguiform shell prevents the withdrawal

of the animal's soft body, consisting in one of the few cases of limacization in snail families in Brazil (the other being in Orthalicoidea – Simone 2006).

Several new species (and genera) of terrestrial gastropods (belonging to all three major lineages mentioned above) have been described in the past decade-and-a-half (Birckolz et al. 2016, Salvador 2019), so it is to be expected that many more are yet to come. Notably, in the past decade, there has been increasing interest in the land snail fauna inhabiting caves, with several new troglomorphic and potentially troglomorphic species have been described (Salvador et al. 2022b, 2023b). Considering that Brazil has over 20,000 caves (CECAV 2020) and that these secluded environments are 'favourable' to speciation (Weigand 2014), it is expected that more cave-dwelling snails will be found and described in the future (Salvador et al. 2022b).

Recent surveys in urban areas are also starting to reveal an aspect of the Brazilian fauna that has been historically largely ignored. For instance, the study of Alexandre et al. (2017) in Rio de Janeiro identified species whose records were the first for the entire state, while Martins and Simone (2014) described a new species from a small city park in São Paulo, the most populous city in the Americas. This is in line with a renewed global interest in the topic, as urban areas are set to grow in the coming decades, increasing the potential for rapid evolution within their boundaries (Schilthuizen 2018).

Finally, through a combination of new collection and sampling efforts (e.g., Salvador et al. 2018a, 2022a) and investigation of 'old' natural history collections (e.g., Silva et al. 2019, Salvador et al. 2023a), species occurring in neighbouring countries but previously unknown from Brazil have been consistently added to the national checklist. Notably, that included the very first reports of families Vertiginidae, Thysanophoridae and Urocoptidae (Salvador et al. 2018a, 2021, Simone 2022b). This is probably the situation of other species that occurs in other countries' territories along the Brazilian border.

### Non-native species in Brazil

Alongside environmental change, one of the major anthropic impacts worldwide is the introduction of non-native species. Introduced species can have a wide array of effects on local environments: they can have no significant impact whatsoever, being restricted to anthropically modified environments, to becoming invasive and affecting crops, infrastructure, human and livestock health, and threaten native species (Barker 2002, Nakano and Strayer 2014, Lu

et al. 2018, Darrigran et al. 2020). Globalisation of trade has meant new and more introductions more recently, and climate change will likely add up to the trend (Rosa et al. 2022b, Teles et al. 2022, Hausdorf 2023).

Throughout the past centuries, several species have been introduced in Brazil and became naturalised (Simone 2006, Darrigran et al. 2020, Miyahira et al. 2020, Rosa et al. 2022a, Pedro et al. 2023). While the effects of most non-native molluscs in Brazil remain understudied, a few species are known to be problematic. Among the marine molluscs, examples of harmful species include the predatory veined rapa whelk *Rapana venosa* (Valenciennes, 1846), as well as various clams and mussels that compete for space with native species and physically alter the environment (Darrigran et al. 2020); the latter include the scissor date mussel *Leiosolenus aristatus* (Dillwyn, 1817) which bores into calcareous substrates, including the shells of other molluscs (Simone and Gonçalves 2006).

In freshwater, some species are of particular interest to public health, as they can be intermediate hosts of native and/or introduced parasites (Darrigran et al. 2020, Carranza et al. 2023). Some freshwater bivalves, notably the golden mussel *Limnoperna fortunei*, can cause impacts to the environment, to native species, and to infrastructure (Carranza et al. 2023). The red-rimmed melania snail *Melanoides tuberculata* was shown to displace native species of freshwater snails and can raise public health issues (Carranza et al. 2023).

Many of the introduced terrestrial gastropods have little to no impact reported, as they tend to be largely restricted to habitats that are already heavily modified by humans (e.g., Rosa et al. 2022b), though some are also being found in natural environments (e.g., *Deroceras laeve* (Müller, 1774) and *Meghimatium pictum* (Stoliczka, 1873); J.O. Arruda pers. obs.). Other problematic species include slugs that can become serious agricultural pests (Darrigran et al. 2020) and the giant African snail *Achatina fulica* Bowdich, 1822, which has increased its distribution in South America whereas native populations of giant native snails *Megalobulimus* spp. are decreasing (Teles et al. 2022). Furthermore, several species of land snails and slugs can be intermediate hosts of nematode parasites such as *Angiostrongylus* spp. that can infect humans and animals (Darrigran et al. 2020).

The latest two exotic terrestrial species to be found in Brazil were the Japanese jumping snail *Ovachlamys fulgens* (Gude, 1900) and the horntail snail *Macrochlamys indica* Godwin-Austen, 1883 (Agudo-Padrón and Luz 2017, Teixeira et al. 2017), which make up interesting cases of new introductions because their rapid spread in Brazil could be

monitored thanks to the community science platform iNaturalist (<https://www.inaturalist.org/>) (Rosa et al. 2022a, 2022b).

### Past and present: a summary of the history and species numbers

Many researchers, Brazilian or otherwise, helped build the foundations of the country's malacology (Simone 2003, Colley et al. 2012), including Wagner (1827), d'Orbigny (1840), Watson (1886), Dall (1889, 1927), Ihering (1897), Pilsbry (1888), Maury (1937 – first president of SBMa), Haas (1938), Lange-de-Morretes (1949 – the first catalogue of Brazilian molluscs), Marcus (1956) and Marcus and Marcus (1963), and Klappenbach (1965). In 1969, the SBMa was founded in Juiz de Fora, Minas Gerais, bringing together the main names of national malacology, and since then it has been central in organising the national conference, the Encontro Brasileiro de Malacologia (EBRAM), and in facilitating collaboration between malacologists in Brazil. Membership reached its peak between 1969–1989 when the SBMa still brought together academics and shell collectors. Currently, the SBMa has 139 associates and has shown stability in new applications, with seven to 10 new members per year, mostly undergraduate and graduate students.

As mentioned above, there have been past catalogues of the Brazilian molluscan fauna – or parts of it (e.g., Lange-de-Morretes 1949, Salgado and Coelho 2003, Simone 2006, Rios 2009), but there have been few attempts to estimate the total diversity of these animals in the country – that is, including still undiscovered species. Virtually, the only works to propose richness estimations were those of Simone (1999a, 1999b, 1999c; respectively, for marine molluscs, freshwater gastropods, and terrestrial gastropods, in general) and Avelar (1999 – for freshwater bivalves). Those authors made their estimates based on their understanding of the then-known fauna and their perceptions of gaps in the knowledge. Together, they suggested that only 1/3 of the terrestrial mollusc species and 1/2 of the marine and limnic species were then known. At the time, around 2,580 valid species of Mollusca were recorded for Brazil, i.e., about 72% of the diversity recorded in the present paper (3,552 spp.). Table 6 compiles data from the last two decades establishing some comparisons with 90s.

As seen in Table 6, over the last 24 years around 970 valid species were added to the Brazilian malacofauna (i.e., ~40 species per year). The highlights are the Aplacophora and Cephalopoda, whose totals quadrupled and doubled, respectively. Overall, the marine species are halfway towards the estimate made by Simone (1999c), however, the same is not true for terrestrial and freshwater species. The total

**Table 6.** Total number of valid species of molluscs recorded for Brazil in the last two decades per each class and environment (marine, freshwater, terrestrial).

Groups/Environments	Number of species			Addition (%)
	90's	2023	Added	
Aplacophora	4	16	12	400%
Bivalvia	515	629	114	22.13%
Gastropoda	1,963	2,737	774	39.42%
Polyplacophora	25	35	10	40%
Scaphopoda	30	43	13	43.33%
Cephalopoda	45	92	47	104.44%
Monoplacophora	0	0	–	–
Marine	1,604	2,525	921	57.4%
Freshwater	308	293	-15	-4.8%
Terrestrial	670	723	53	7.9%
<b>Total</b>	<b>2,582<sup>a</sup></b>	<b>3,552<sup>b</sup></b>	<b>970<sup>c</sup></b>	

<sup>a</sup> Number of valid species of Mollusca per class and environments recorded for Brazil in 1999 (Simone 1999a, 1999b, 1999c; Avelar 1999). <sup>b</sup> Number of valid species in 2023 based on TCFB-Mollusca database (excluding synonyms). <sup>c</sup> Number of valid species added to the Brazilian malacofauna in 24 years (1999 to 2023).

number of freshwater molluscs actually decreased in the past 24 years. Several new species have been described during that period (Birckolz et al. 2016, Mansur et al. 2019), so the decrease can be due to overcounting in 1999 (more likely) and/or absence of some valid species in the TCFB, due to a lack of specialists in many freshwater groups. Regardless, the estimates of the total doubling in number (Avelar 1999, Simone 1999b) currently seem improbable. The terrestrial gastropods are likewise very far from Simone's (1999a) estimate that the number would triplicate, despite the increase in work in the past decades (Birckolz et al. 2016, Salvador 2019). Thus, while it is recognized that there is still much undiscovered diversity among land snails and slugs (see discussion above), the original estimate is probably the most unrealistic. Table 1 offers new estimates based on the experience of the present authors in their taxa of expertise.

Regardless of any estimates, Brazilian malacology has moved forward in these two and a half decades due to the effort and dedication of its taxonomists. Even so, many other factors may influence the future of new malacological discoveries in Brazil, such as (i) expansion of the sampling effort in under-sampled areas of Continental Brazil (especially in the North and Central-West regions), (ii) new expeditions on the Brazilian coast, (iii) development of new techniques for deep sea studies, (iv) access (=cost) and availability of equipment and technologies that are already widely used in other countries (e.g., micro-CT scanners, ROVs – Remotely Operated Vehicles, Satellite Oceanography, genetic barcoding), among others.



### A brief comparison between intercontinental molluscan faunas

Brazilian ecosystems are famous for their high biodiversity; Brazil is one of the most biodiverse countries on the planet for most animal taxa (Lewinsohn et al. 2005). However, as seen in Table 7, this richness is not necessarily apparent in the malacofauna. There are a number of issues that come into play in explaining that disconnect.

Despite being relatively speciose, the Brazilian malacofauna has, in some cases, only a fraction of the biodiversity seen elsewhere (Table 7), especially considering its continental dimensions and the fact that it is a predominantly tropical country. Notably, some places several times smaller than Brazil in territory (e.g., Mexico, Indonesia, New Zealand) have an equivalent or greater number of molluscan species (Table 7). This relative low number of valid species in Brazil can be observed in all environments: marine, freshwater, and terrestrial.

For land and freshwater environments, for example, this can be largely explained by the small number of studies relative to such a large territory and such richness of biomes and ecosystems. That is exacerbated in some regions of the country, notably the Amazon, due to a combination of factors such as history, accessibility, resources, and funding (Salvador 2019). As previously mentioned, when the coverage of studies is increased and the geographical and taxonomic biases are dealt with, it is expected that many unknown species will be described, thus increasing the total seen in Table 7.

Another explanation that has been brought to fore is the hypothesis of low soil pH, in which the more acidic soils in large parts of the country would result in a lower diversity of molluscs, in particular of land snails (L.R.L. Simone pers.

obs.). That hypothesis, however, remains untested in Brazilian territory. Although results obtained in the northwest Iberian Peninsula have even shown a preference of some species of terrestrial gastropods for acidic soils (Ondina et al. 2004).

The comparatively low number of marine species is perhaps more complex to explain, as the study of marine molluscs has historically received more attention in the country. The Atlantic is geologically the youngest Ocean, and while this has been used in the past to explain its lower diversity when compared to the Indo-Pacific, that idea does not hold up. It has been shown that the higher diversity on the Pacific coast of South America is explained by the coastal length and that, when corrected for that variable, biodiversity on both 'sides' are equivalent (Miloslavich et al. 2011). Nevertheless, there are additional factors that might come into play, such as: high influence of freshwater contribution, with high sediment influx and turbidity that can affect the number of species; direction of marine currents that carry nutrients away from Brazil; taxonomic inflation in other regions' faunas. In any event, those are hypotheses, and certainly more studies are needed to determine if and how the above-mentioned factors explain the patterns of the Brazilian fauna.

Finally, it is also worth mentioning the museums that house the malacological collections, which can provide elements to solve taxonomic issues. Currently in Brazil, after the partial destruction, by the fire of September 2018, of one of the richest and oldest malacological collections of the country (~43,600 lots before the fire/8,300 lots now) (A.D. Pimenta pers. obs.), hosted by the Museu Nacional, in Rio de Janeiro (MNRJ), ten collections deserve to be highlighted by their expressive number of archived molluscs, such as: (i)

Table 7. A brief comparison between some intercontinental molluscan faunas.

Categories	South America		North America		Oceania Asia	
	Brazil	Argentina <sup>a</sup>	Mexico <sup>c</sup>	Australia <sup>d</sup>	New Zealand <sup>e</sup>	Indonesia
Families	401	227	~400	455	338	?
Genera	1,354	447	~1,900	2,653	275	?
Valid species <sup>f</sup>	3,552	1,043	6,113	10,143	4,588	?
Estimated species	~4,250 <sup>a</sup>	~1,905	~7,613	~15,000	~4,700	~15,000 <sup>f</sup>

<sup>a</sup> Total of valid species (excluding synonyms). <sup>b</sup> Average of estimates (i.e., 4,132–4,362 spp.) based on our experts' opinion. <sup>c</sup> Numbers based on Bigatti and Signorelli (2018, 862 spp. – marine molluscs), Pereira et al. (2014, 60 spp. – freshwater bivalves), Rumi et al. (2006, 2008, 101 spp. – freshwater gastropods) and Virgillito and Miquel (2014 20 spp. – exotic land snails). The estimated species number was based mainly on marine species data, considering that probably only 50 per cent of the marine invertebrate's diversity of the Argentine Sea was mentioned in the literature so far. <sup>d</sup> Numbers of marine species included species from Mexican Pacific coast, Gulf of Mexico and Caribbean (Castillo-Rodríguez 2014, 4,643 spp. – marine molluscs); Czaja et al. (2020, 195 spp. (13 families + 61 genera) – freshwater gastropods + 97 spp. – freshwater bivalves) and Naranjo-García and Fahy (2010, 1,178 spp. (42 families + 69 genera) – land snails). <sup>e</sup> Australian Faunal Directory, available on <https://biodiversity.org.au/afd/taxa/MOLLUSCA/statistics>. <sup>f</sup> Based on Spencer et al. (2009) plus the Museum of New Zealand <https://collections.tepapa.govt.nz/topic/965>. <sup>g</sup> Estimate based on Kartika and Mu (2014) and LIPI (The Indonesian Institute of Science). No database or papers were found to fill the numbers of families, genera and valid species.

Museu de Zoologia at Universidade de São Paulo (MZUSP) (~165,000 lots, contemplating species of all environments and regions of Brazil) (L.R.L. Simone pers. obs.), (ii) Museu Oceanográfico 'Prof. Eliézer de C. Rios' (MORG), Universidade Federal do Rio Grande (~54,000 lots, most of dry collection from all Brazilian regions) (P. Spotorno-Oliveira. pers. obs.), (iii) Museu de Ciências Naturais do Rio Grande do Sul (MCNZ) (~42,000 lots, mainly freshwater fauna from North, Southeast and South regions) (J.O. Arruda pers. obs.), (iv) Coleção Malacológica do Instituto de Biologia, Universidade Federal do Rio de Janeiro (IBUFRJ) (~24,000 lots, mainly deep marine fauna from Southeast region) (C.D.C. Oliveira pers. obs.), (v) Museu de Diversidade Biológica (MDBio), Universidade Estadual de Campinas (16,890 lots, mainly marine fauna from Southeast and South regions) (M. Borges pers. obs.), (vi) Museu de Malacologia Prof. Maury Pinto de Oliveira (MMPMPO), Universidade Federal de Juiz de Fora (~15,000 lots, mainly marine fauna from Northeast, Southeast and South regions) (S. D'Ávila. pers. obs.), (vii) Coleção de Malacologia Médica (CMM), Fiocruz Minas (~14,000 lots of freshwater molluscs of medical and veterinary importance) (see <http://cmm.fiocruz.br/>), (viii) Coleção de Moluscos do Instituto Oswaldo Cruz (CMIOC), Fiocruz Rio de Janeiro (15,000 lots of non-marine molluscs from all regions of Brazil) (S.S. Thiengo. pers. obs.), (ix) Coleção de Moluscos da Universidade do Estado do Rio de Janeiro (Col.Mol.UERJ), Rio de Janeiro (~14,000 lots of freshwater molluscs from all Brazilian regions and terrestrial snails from Atlantic Rainforest) (S.B dos Santos. pers. obs.), and (x) Coleção Malacológica Prof. Henry Ramos Matthews (CMPHRM), Universidade Federal do Ceará (12,601 lots, mainly marine fauna of the North and Northeast regions) (H. Matthews-Cascon. pers. obs.). Many other relevant collections of molluscs are scattered throughout many institutions of Brazil, but with less representativeness (<10,000 lots), e.g., Coleção Malacológica do LEBIO/CEM/UFPR at Universidade Federal do Paraná (~9,000 lots, mainly marine fauna of Paraná State) (C.E. Belz pers. obs.), Coleção de Moluscos do Museu de História Natural Capão da Imbuia (MHNCIMo) (6,093 lots, mainly marine fauna of Paraná State) (Moura-Cordeiro et al. 2021), Museu de Ciências Naturais (MUCIN) at Universidade Federal do Rio Grande do Sul (~3,000 lots, mainly freshwater molluscs of Rio Grande do Sul State), among others.

Therefore, in a quick comparison with other countries, the Museo Argentino de Ciencias Naturales (MACN), for example, have about 17,000 lots of molluscs (<https://www.macnconicet.gob.ar/investigacion/>); the Museum of New Zealand Te Papa Tongarewa has around 340,000 lots (R.B.

Salvador pers. obs.), while the Australian Museum Malacology collection has ~910,500 lots (<https://australian.museum/>), almost three times more lots than all the main malacological collections in Brazil combined.

With scarce resources, efforts to digitise malacological collections (especially type specimens) are also rare in Brazil, which makes it difficult for Brazilian and foreign researchers to access the vast wealth of its collections and, consequently, preventing recognition of the importance of these collections worldwide.

Over the course of their history, Brazilian science museums have seen good times and bad in the realms of preservation, funding, and public policy. However, in the last seven years particularly, withdrawal of many public policies had a fast, deep impact in the form of programme discontinuity, a lack of conservation and preservation, the interruption of research and other studies, absence of new hires of collections curators, with buildings and collections being handed over to others and/or completely abandoned (Massarani and Rocha 2021). For this reason, it is essential and urgent to maintain policies that bring stability and continuous resources to Brazilian museums.

## FINAL REMARKS

For the first time a collective effort among malacologists has brought to light the species number of Brazilian molluscs, cataloguing 3,552 valid species throughout all the national territory (including the EEZ) and providing a complete list of these species (available through the open access platform <http://fauna.jbrj.gov.br>). This fresh number represents about 4.5% of all known mollusc species worldwide (i.e., 76,000–84,600). Marine species are the most diverse corresponding to 71.08% (2,525 spp.) of all Brazilian mollusc fauna, followed by terrestrial gastropods (20.68%) and freshwater species (8.24%), both distributed among 401 families and 1,354 genera. Except for Monoplacophora, Brazil has representatives of all other six classes of Mollusca such as, Aplacophora (16 spp.), Polyplacophora (35 spp.), Scaphopoda (43 spp.), Cephalopoda (92 spp.), Bivalvia (629 spp.) and Gastropoda (2,737 spp.). Although it is considered one of the most biodiverse countries in the world, the discontinuity of investments in science continues to be the main limiting factor for expanding knowledge of the mollusc fauna in Brazil, preventing the training of taxonomists, as well as the exploration of new sampling areas (e.g., the Amazon, caverns, deep sea) and new methods (e.g., environmental barcoding).

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#### Author Contributions

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