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TAXONOMIC CATALOG OF THE BRAZILIAN FAUNA

Expanding the taxonomic catalog of Brazilian meiofauna: diversity and distribution of the neglected phyla Tardigrada, Gastrotricha, and Kinorhyncha

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ABSTRACT. Meiofauna is a guild of microscopic organisms (delimited by the mesh width of two sieves, upper 500 µm and lower 44 µm) that inhabit the sediment grains and periphyton of aquatic environments (both freshwater and marine). Despite the fact that this definition is based on size, all the environments inhabited by these microorganisms present similar ecological challenges, which suggests that the meiofauna is a biologically and ecologically independent entity. Currently, meiofaunal organisms are represented in 23 of the 34 known metazoan phyla, including Tardigrada, Gastrotricha, and Kinorhyncha. The goal of this study was to compile information on the diversity and distribution of these phyla in Brazil. Based on the taxonomic contributions published until July 2023, a total of 97 Tardigrada species, 88 Gastrotricha species, and five Kinorhyncha species have been recorded. They are distributed throughout five biomes, eight hydrographic regions, 10 terrestrial biogeographic provinces, three marine biogeographical provinces, and 15 political states in Brazil. The species accumulation curve suggests that there are still many Tardigrada and Gastrotricha species to be discovered with increasing sampling effort, as the rate of discovery of new species is linearly increasing. Unfortunately, knowledge of the biodiversity of these meiofaunal groups is still limited due to sparse information on identity and distribution. We recommend future studies dealing with meiofauna taxa to prioritize redescribing endemic species based on integrative taxonomy and increase the number of the type series deposited in Zoological Museums (e.g., specimen photos). Furthermore, the training of researchers specialized in these taxa is a priority, as some of these phyla do not have any Brazilian specialists.

KEY WORDS. Biodiversity, endemic species, less-known taxon, Linnean shortfall, microinvertebrate, taxonomy.

INTRODUCTION

Meiofauna is a guild of microscopic organisms, i.e., a set of phylogenetically independent lineages that exploits the same ecological niche, formally delimited by the mesh width of two sieves, upper of 500 µm and lower of 44 µm (Giere 2009). Meiofaunal organisms are omnipresent in sediments and vegetation of marine and freshwater habitats, but can also be found in mosses, wet soils, and semi-aquatic agricultural ecosystems around the world (Higgins and Thiel 1988, Giere 2009, Fonseca et al. 2018).

Despite being a size-based definition, including exceptions such as larger vermiform organisms that can pass through the upper sieve due to their small diameter, despite being millimeters in length, the environments inhabited by these microinvertebrates present similar ecological challenges

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that allow considering the meiofauna as a biologically and ecologically independent entity (Higgins and Thiel 1988). These challenges are a major force in selecting traits that result in the "meiofaunal syndrome", that is, a series of morphological attributes, such as the reduction of body appendages, the elongation of the body to a worm-like shape, and the development of adhesive structures (Brenzinger et al. 2013).

Currently, the meiofaunal organisms are represented in 23 of the 34 known metazoan phyla, presenting diverse ecological interactions with distinct levels of trophic and energetic links with macrofauna and plankton communities (Giere 2009, Cerca et al. 2018). In an effort to compile information on the diversity and distribution of meiofauna in Brazil, several taxonomists with expertise in the meiofauna phyla Tardigrada, Gastrotricha, and Kinorhyncha have been continuously updating the Taxonomic Catalog of the Brazilian Fauna (in Portuguese: Catálogo Taxonômico da Fauna do Brasil – CTFB), an online catalog started in 2015.

Meiofaunal studies in Brazil had this early foundation in the 1930s with Dr. Eveline du Bois-Reymond Marcus and Dr. Ernest Gustav Gotthelf Marcus, as foreign researchers in Brazil fleeing from nazism in Germany; and posteriorly Brazilian researcher Dr. Veronica Fonseca-Genevois in the 1980s. The Marcus couple conducted a large number of studies in Brazil, mainly in the state of São Paulo, dealing with many distinct phyla (e.g., Tardigrada, Onychophora, Platyhelminthes, Oligochaeta, Bryozoa, Mollusca, and Nemertea) resulting in the publication of approximately 162 scientific papers (Mendes 1994). Notably, Ernest Marcus described the first marine tardigrade from the South Hemisphere, *Batillipes pennaki* Marcus, 1946.

Veronica Fonseca-Genevois embarked on her doctoral studies in France and, during this time, Dr. Renaud-Mornant (MNHN Paris, specialist in marine tardigrades) proposed a collaborative effort, starting a new era in meiofaunal research in Brazil (dos Santos et al. 2014). While Veronica Fonseca-Genevois primarily focused on marine nematodes, her contributions extended to various meiofauna taxa including Acari, Copepoda, Oligochaeta, and Tardigrada. In addition, she had a significant role in training over 200 students in meiobenthic studies (dos Santos et al. 2014). Nowadays, some research groups are actively studying meiofauna in Brazil, with the majority of these researchers directly and indirectly related to Fonseca-Genevois.

The aim of the present contribution was threefold: first, present a historical background of the taxonomic knowledge of some meiofaunal taxa found in Brazil; second, estimate a first scenario of species richness extrapolation of Tardigrada and Gastrotricha based on the actual taxonomic knowledge of these phyla compiled directly from The Taxonomic Catalog of the Brazilian Fauna; third, compile all available information on the Brazilian tardigrade, gastrotrich and kinorhynch species in a single resource and point out some future perspectives regarding these phyla.

MATERIAL AND METHODS

All data was gathered directly from the CTFB catalog, which has some of the authors of the present study responsible for feeding the taxonomic information in the database (ARS Garraffoni: Tardigrada, Gastrotricha, Kinorhyncha; E Santos and RC de Barros: Tardigrada). Geographic distribution data are organized in four datasets: i) biomes, as defined by the Brazilian Institute of Geography and Statistics (IBGE 2004); ii) hydrographic regions, as defined by the National Water Agency (ANA 2015); iii) political division in states plus the Federal District; iv) terrestrial and marine biogeographic regionalization, as defined, respectively, by Morrone et al. (2022) and Spalding et al. (2007). All maps were made using ArcGIS Desktop software and detailed in Adobe Photoshop CC software.

We use the hypothesis that a description rate curve can be extrapolated to a larger time frame, producing an estimate of the number of expected species based on the actual rate of species discovery, which was considered as the sampling effort. We accumulate the species found in Brazil by the year of the description of that species, treating the year as a sampling unit. The extrapolation of the cumulative curve of species in and within (Family level) each Phylum (Tardigrada and Gastrotricha) was based on the Chao2 estimator (Chao and Colwell 2017). We used the R package iNEXT (Hsieh et al. 2022) to estimate richness.

RESULTS

Below we present information about the taxonomy, classification, and phylogeny of these groups, as well as the historical background of the studies of these taxa in Brazil.

Tardigrada

Overview of Tardigrada

The phylum Tardigrada (from Latin, *tardus*, slow + *gradus*, step) comprises a group of hydrophilic micrometazoans, commonly known as tardigrades or "water bears". They were first described at the end of the 18th century by the German naturalist Johann August Ephraim Goeze (Goeze

1773) and named "il tardigrado" by Italian naturalist Lazzaro Spallanzani (Spallanzani 1776).

Tardigrades have a bilaterally symmetrical body, covered by a chitinous cuticle, and divided into a head and four trunk segments. Each segment of the trunk bears a pair of lobopods legs, usually ending in claws, digits, or digits ending in claws or suckers (Nelson et al. 2015, Schill 2019). In the last segment, the lobopods are turned backward. They have a complete digestive tract and a body cavity filled with coelomocytes, cells responsible for gas exchange, circulation, and nutrient storage. The nervous system consists of a simple brain and a ventral nerve chain with four bilobed ganglia. Tardigrades can be herbivores and feed on algae and/or plant cells; carnivores, feeding mainly on rotifers and nematodes, or even on other tardigrades; and omnivores feeding on mosses, invertebrates, and bacteria. They can be dioecious, parthenogenetic, or monoecious (Nelson et al. 2015, Schill 2019).

Tardigrades are found on all continents of the planet, inhabiting a wide range of terrestrial, freshwater, and marine habitats, from abyssal zones to the highest peaks (Ramazzotti and Maucci 1983, Kinchin 1994, Bertolani et al. 2009). The phylum is divided into two classes, Heterotardigrada Marcus, 1927 and Eutardigrada Marcus, 1927. The former class has both marine and limnoterrestrial/freshwater species and the latter contains mainly terrestrial and freshwater species but also few marine representatives. They are mainly found in substrates as sediments from beaches to deep-sea, but are also found associated with macroalgae (Santos et al. 2019a). Marine tardigrade dispersal occurs – as many meiofaunal groups – mainly by marine currents, although is limited by their low mobility and absence of larval stage (Boeckner et al. 2009, Santos et al. 2018). Limnoterrestrial tardigrades can survive in both freshwater and terrestrial environments. They are usually found in different types of substrates, such as mosses, lichens, algae, and soil, in addition to varied types of sediments in aquatic environments (Nelson 2002, Nelson et al. 2015). Active dispersal of terrestrial tardigrades is limited by body size, speed of movement, and the need for a constant film of water covering the body. Thus, dispersal occurs passively when eggs, cysts, and anhydrobiotic specimens are dispersed predominantly by wind. Other animals associated with terrestrial communities (e.g., birds) may also aid in the dispersal of terrestrial tardigrades (Nelson et al. 2015, Mogle et al. 2018).

They are probably the most famous cryptozoan due to their ability to survive in a wide spectrum of extreme environmental conditions, such as lack of water, temperature extremes, lack of food or oxygen, exposure to high levels of pollutants and ionizing radiation, or even the space vacuum (Ramazzotti and Maucci 1983, Kinchin 1994, Schill 2019).

Morphological and molecular studies have shown that Tardigrada is a monophyletic group within the molting animals belonging to the clade Ecdysozoa (Aguinaldo et al. 1997) and closely related to Panarthropoda, composed of Onychophora and Arthropoda (Nielsen et al. 1996, Giribet et al. 1996, Campbell et al. 2011, Dunn et al. 2014, Giribet and Edgecombe 2017, 2019).

Currently, 1,464 species of tardigrades have been described, including three fossil species, split into 159 genera and 33 families (Degma and Guidetti 2023). The description of new species is expected as new geographic regions are explored, possibly exceeding 2,000 (Bartels et al. 2016).

Historical background of Tardigrada studies in Brazil

In Brazil, they have been episodically explored, with the first records being made in 1910 (Murray 1913) and the early 1930s (Rahm 1931, 1932). We can distinguish at least two periods in which tardigrades were more intensely researched in Brazil.

The first period begins in the late 30s and lasts until the mid-50s. During this period, the German couple Ernest Gustav Gotthelf Marcus and Eveline du Bois-Reymond Marcus, then residing in Brazil, and the Brazilian researcher Dr. Rosina de Barros made dozens of new records, as well as the description of new species, many of them still valid today (de Barros 1938, 1939a, 1939b, 1942a, 1942b, 1943, Marcus 1937, 1946, du Bois-Reymond Marcus 1944, 1952). The first marine tardigrade from Brazil, *Batillipes pennaki* Marcus, 1946, was described at this time. After this period, other studies were sporadically published by Brazilian and foreign researchers (Iharos 1969, Höfling-Epiphanio 1972, Corrêa 1987, Renaud-Mornant 1980, 1984, 1989). Part of these studies were not executed in Brazilian universities, but biological samples were sent to European researchers who published those new species.

The second period marks the rebirth of Brazilian tardigradology and began at the end of the 90s. The seminal works are from the Brazilian researchers Dr. Claudia Maria Leite Assunção (Assunção 1999a, 1999b, 2001) and Dr. Clélia Márcia Cavalcanti da Rocha (da Rocha 1999, 2001), as well as the Italian Dr. Giovanni Pilato (Pilato 2000). Since 2010, the number of studies on tardigrades in Brazil by Brazilian researchers has increased and was followed by an increase in publications, with new species described, new occurrences, and approaches (da Rocha et al. 2013, 2016, de Barros 2020, Gomes Júnior and da Rocha 2015, Gomes Júnior et al. 2017, 2020, Guidetti et al. 2021, Santos et al. 2017, 2018, 2019b, Ugarte et al. 2023, Brotto-Guidetti et al. 2024). Currently, there are about one hundred reports of species occurring in the Brazilian biomes (de Barros 2020, Santos et al. 2023).

Gastrotricha

Overview of Gastrotricha

The phylum Gastrotricha (from Greek, *gaster*, stomach + *thrix*, hair) is composed of free-living acoelomate micrometazoans found in practically all aquatic environments worldwide, from freshwater psammon to periphyton or marine intertidal endobenthos to the deep sea (Balsamo et al. 2014, 2020, Garraffoni and Araújo 2020, Kånneby 2016). In these habitats, gastrotrichs can reach abundances that make them one of the top five most common taxa. Feasting on microbial biofilm and algae but also being prey to small active predators and macrofaunal sediment filters, they are an important component of the trophic web as a bridge between macro and microfauna (Hochberg 2000, Balsamo et al. 2020, Madji et al. 2020). The majority of gastrotrichs have a body length around 300 to 400 µm, but there are extremes from 60 µm (in some representatives of *Ichthydium*) to macroscopic worms reaching 3,500 µm (*Megadasys pacificus* Schmidt, 1974) (Balsamo et al. 2014, Kånneby 2016, Kieneke and Schmidt-Rhaesa 2015).

Currently, the taxa add up to 900 described species worldwide (Krizanova and Vd'ačný 2022) that are classically divided into the morphologically distinct orders Macrodasyida Remane, 1925 [Rao & Clausen, 1970], and Chaetonotida Remane, 1925 [Rao & Clausen, 1970] (Balsamo et al. 2014, 2020, Kånneby 2016). The former encompasses nine families and 38 genera of long, tape-shaped, worm-like animals bearing multiple adhesive tubes along the body length, with about 400 species of marine species and four exclusively freshwater species (e.g., Ruttner-Kolisko 1955, Kisielewski 1987, Garraffoni et al. 2010, 2019a, Todaro et al. 2012). The latter taxa, Chaetonotida, is composed of smaller tenpin-shaped animals distributed into seven families and 31 genera adding up to 500 species, characterized by the reduction of adhesive tube number to a single pair on the posterior region, or even a total loss of the structure in some lineages of periphytic animals (Garraffoni and Araújo 2020).

The diversity of body plans within the phylum is grouped by several synapomorphic characters. The set of locomotory cilia arranged through the ventral region, from the anterior head to the posterior end of the body is the most recognizable feature of the phylum, and where the name is derived (Hochberg and Litvaitis 2000, Kånneby 2016). Furthermore, the monophyly of the phylum is supported by the cuticle with two layers, frequently ornamented with a diversity of scales, spines, and plates, the motor and sensory cilia covered by epicuticle, adhesive tubes associated to a duo-glandular system that secrete adherent and releaser substances, the myoepithelial pharynx with triradiate lumen, and the intestinal tube partially enveloped by a set of duo-helicoidal muscle arrangements (Hochberg and Litvaitis 2000, Todaro et al. 2003, 2006, Petrov et al. 2007, Kieneke et al. 2008, Balsamo et al. 2014, 2020, Kieneke and Schmidt-Rhaesa 2015).

Since the discovery and description of the first gastrotrich in the late 18th century, its taxonomic position has been drifting between different branches of the Tree of Life. Müller (1773) grouped the first specimens in Infusorian, among small animals and protozoans, from where it was transferred to Rotataria by Ehrenberg (1830) until it was assigned the phylum rank Gastrotricha by Metschnikoff (1865). Even with the advent of phylogenetic techniques, its precise position in Bilateria presented inconsistencies between analyses based on morphological and molecular data (Winnepenninnckx et al. 1995, Wallace et al. 1996, Littlewood et al. 1998). It has even been considered close to rotifers (Hyman 1951), or part of Cycloneuralia (Sørensen et al. 2000); Neotrochozoa (Rieger 1976, Zrzavý et al. 1998); or even paraphyletic Platyzoa (Giribet et al. 2000, Garey 2002, Todaro et al. 2006).

Only recently, phylogenetic studies using molecular data (e.g., mitochondrial and nuclear markers, transcriptome) brought to light the monophyletic clade Rouphozoa composed of Gastrotricha and Platyhelminthes as a sister group to Lophotrochozoa (Struck et al. 2014, Egger et al. 2015, Laumer et al. 2015, Fromm et al. 2019). Despite that Giribet and Edgecombe (2019) proposed the duo-gland adhesive system as a possible synapomorphy for both taxa, Balsamo et al. (2020) questioned this hypothesis. Balsamo et al. (2020) pointed out that these features were recently studied in detail only in Platyhelminthes (Wunderer et al. 2019) and the studies of the gastrotrich duo-gland system are much older and highlighted that this system is probably not homologous in both taxa (Tyler and Rieger 1980, Ruppert 1991). Thus, a reanalysis of the duo-gland system in Gastrotricha, using modern morphological and molecular techniques is urgently needed.

Historical background of Gastrotricha studies in Brazil

The first records of Brazilian gastrotrichs date back to the early 1900s when three freshwater species were reported in Rio de Janeiro city (Murray 1913). Subsequently, new records of unpublished marine gastrotrichs were mentioned by du Bois-Reymond Marcus (1952) and Forneris (1985).

Even with these previous records, the field of Brazilian gastrotrichology can be considered truly inaugurated by the outstanding studies done by the Polish Dr. Jacek Kisielewski in the late 80s and early 90s. Kisielewski (1987) described two new genera and two new species of freshwater animals endemic to Brazil, including the enigmatic macrodasyid *Redudasys fornerise* Kisielewski, 1987. Afterward, he sampled various freshwater habitats across different Brazilian states, reporting 59 species, including 33 species previously known from Europe, and discovering 26 new species native to Brazil (Kisielewski 1991). This study significantly expanded our understanding of freshwater gastrotrichs in the world, particularly with the description of several new endemic species within Chaetonotidae and the extraordinarily rare semiplanktonic representatives of Dasydytidae Daday, 1905 and Neogosseidae Remane, 1927.

In the marine environment, only a decade later, we can consider that the first true taxonomical studies with gastrotrichs were done by Todaro and Rocha (2004, 2005) along the Northern coasts of the state of São Paulo. The authors described one new species, *Macrodasys fornerisae* Todaro & Rocha, 2004, and reported almost 50 other species, most of them undescribed species from both orders within Gastrotricha (Campos and Garraffoni 2019).

The taxonomical research with this taxon gained a new boost only after 2010, with the establishment of the first laboratory with national researchers and students interested in unraveling the diversity of Brazilian gastrotrichs. Thus, in the last decade, the description of new species and new records of freshwater (e.g., Garraffoni et al. 2017, 2019a, Minowa and Garraffoni 2020, 2021, Magpali et al. 2021) and marine (e.g., Todaro 2012, Campos et al. 2020, Araújo and Garraffoni 2021, Araújo et al. 2022) gastrotrichs have been constantly updated by Brazilian and international researchers leading to a constant improvement of the knowledge of the gastrotrichofauna in both environments along the Brazilian territory (Araújo et al. 2024).

Kinorhyncha

Overview of Kinorhyncha

The phylum Kinorhyncha (from Greek, *kinein*, to move + *rhynchos*, beak) is composed exclusively of marine and free-living metazoans with less than 1 mm in length, inhabiting sand or muddy sediments, from the intertidal zone to abyssal depths throughout the world (Neuhaus and Higgins 2002, Sørensen and Pardos 2008). Currently, the taxon contains 342 accepted species distributed in 31 genera and 10 families (Herranz et al. 2022, Neuhaus 2023).

The body of a kinorhynch can be divided into three regions: a) head: with a protrusible mouth cone surrounded by oral styles and an eversible introvert equipped with several circles of small scalids; b) neck: with small plates or placids, c) trunk: with eleven segments with spines or tubules bilaterally arranged (Higgins 1988, Sørensen and Pardos 2008).

The name Kinorhyncha and the first subdivision of the taxon were introduced by Dujardin (1851). For a long time, kinorhynch diversity was grouped into two major orders: Cyclorhagida and Homalorhagida. This classification was based on systematic hierarchies proposed by Zelinka (1896, 1907, 1928) and Higgins (1964) and recently modified and updated by Higgins (1990) and Adrianov and Malakhov (1996, 1999). However, this traditional classification has been revisited by new studies using molecular and morphological data, as distinct studies obtained the taxon Cyclorhagida as non-monophyletic (Dal Zotto et al. 2013, Yamasaki et al. 2013, Sørensen et al. 2015). Sørensen et al. (2015) established the first reconstruction based on morphology and molecular data and proposed a new systematization based on the phylogenetic analyses and assigned class rank to Cyclorhagida and Allomalorhagida, and consequently assigned order rank to the cyclorhagid groups (Echinorhagata, Kentrorhagata, and Xenosomata). This systematization was slightly modified by Herranz et al. (2022) due to new findings regarding the major clades within Kinorhyncha obtained as a result of the first phylogenomic analysis of the taxon including 21 species representing 15 genera: i) Cyclorhagida is composed of three subclades: Xenosomata, Kentrorhagata (now including the aberrant Zelinkaderes) and Echinorhagata, ii) Allomalorhagida is composed of two subclades: Pycnophyidae and Anomoirhaga (now accommodating the aberrant genera *Cateria* – previously nested within Cyclorhagida – and *Franciscideres* together with five additional genera).

For a long time, Kinorhyncha was considered a group of the Aschelminthes or Nemathelminthes; however, currently, they are grouped into Scalidophora, along with Priapulida and Loricifera, within the Ecdysozoa clade (Edgecombe et al. 2011, Nielsen 2012, Dunn et al. 2014).

Historical background of Kinorhyncha studies in Brazil

The taxonomy of the Brazilian kinorhynchs is incompletely known and only five species have been published so far (Gerlach 1956, Higgins 1968, Sørensen 2011, 2013, 2014, Dal Zotto et al. 2013, Neuhaus and Kegel 2015). Until 2013, only one aberrant species, *Cateria styx* Gerlach, 1956, belonging to Cateriidae Gerlach, 1956 was described from intertidal sands in a high-energy beach in Macaé (state of Rio de Janeiro). The taxonomic status of *Cateria* was discussed by Higgins (1968) based on new material collected at Toninhas beach in Ubatuba (state of São Paulo) and from Cavaleiros beach in Macaé, near the type location. In this same study, the author also designated a new lectotype and paralectotypes. Recently, Neuhaus and Kegel (2015) conducted a taxonomic restudy of type and non-type specimens belonging to *Cateria* and for the first time redescribed *C. styx* using light microscopy techniques.

More than 30 years after Higgins' study, Sørensen (2011) published the first report of *Echinoderes* from Brazil from material collected at São Francisco Beach in São Sebastião and Martim de Sá Beach in Caraguatatuba (state of São Paulo). All specimens collected in São Francisco were juveniles, but the single specimen collected in Martim de Sá was an unidentified species. In 2013, Dal Zotto and co-authors described another aberrant kinorhynch, from Ilhabela and São Sebastião (state of São Paulo) and Guaratuba (state of Paraná), with morphological characters unknown for the entire taxon, called *Franciscideres kalenesos* Dal Zotto, Di Domenico, Garraffoni & Sørensen, 2013. However, due to uncertainties and conflicting findings between morphological and molecular data, the authors preferred to classify *Franciscideres* as incertae sedis. After, Sørensen et al. (2015) designated the new family Franciscideridae to accommodate *Franciscideres* and an undescribed new genus based on a phylogenetic relationship obtained by molecular and morphological (with the presence of a neck region with a segment-like ring as an apomorphic feature) data.

Sørensen (2014) described three new species, *Echinoderes ajax*, *E. marthae*, and *E. astridae* from the Araçá Bay in São Sebastião (state of São Paulo) as part of the project "Biodiversity Inventory of Meiofauna at Araçá Bay". It is important to point out that the study done by Sørensen (2014) was only the second contribution to the systematics of *Echinoderes* (the richest genus in Kinorhyncha) from the entire Atlantic South American coastline.

Quantitative results

A total of 190 species of the three taxa mentioned in the present study were recorded for Brazil until June 2023 (Tardigrada: 97 species; Gastrotricha: 88 species; Kinorhyncha: 5 species) (Fig. 1), from which 66 (35%) are endemic to the country (Tardigrada: 20 species; Gastrotricha: 41 species; Kinorhyncha: 5 species). Interesting to note that all Kinorhyncha species described from Brazil are endemic and respectively, 21% and 46% of Tardigrada and Gastrotricha species are endemic to this country. The average rate of description by year in each phylum is extremely low if we consider the period from the first Brazilian species described

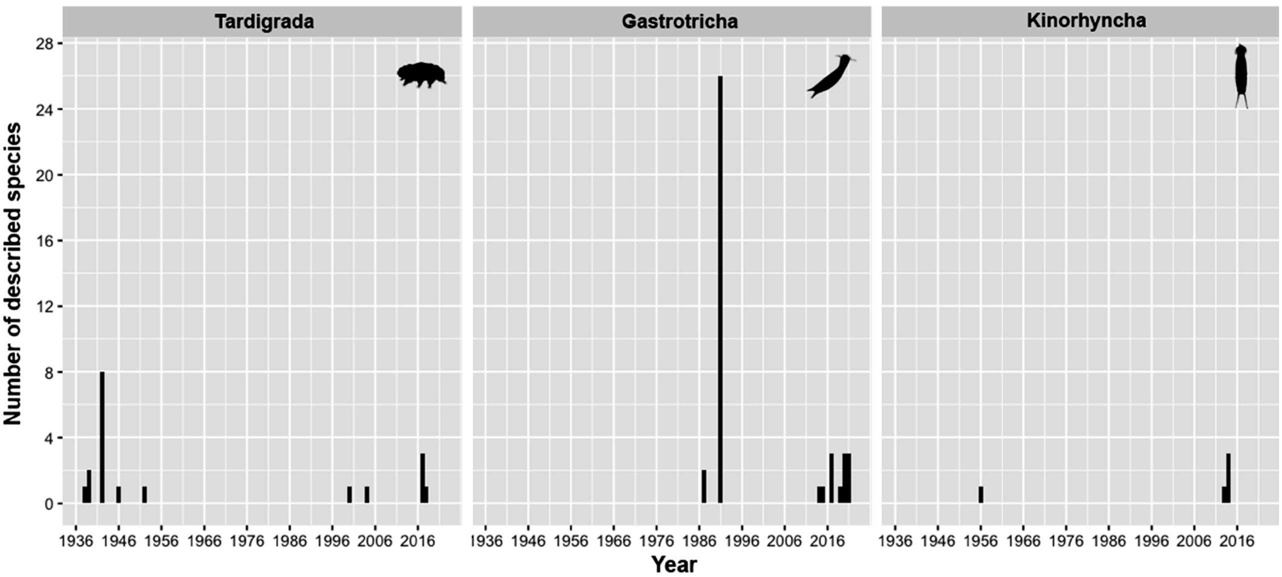

Figure 1. Number of Tardigrada, Kinorhyncha and Gastrotricha species described or reported to Brazil by year (from 1936 to July 2023).

within each phylum until now (Tardigrada: 0,23 species/year; Gastrotricha: 1,13 species/year; Kinorhyncha: 0,07 species/year) (Fig. 1).

Atlantic Forest is the biome with the highest number of known species reaching 88 species (Tardigrada: 45; Gastrotricha: 43), followed by 21 from Cerrado (Tardigrada: 5; Gastrotricha: 16), 11 from Amazon Forest (Tardigrada: 2; Gastrotricha: 9), 4 from Caatinga (Tardigrada: 4) and 4 from Pantanal (Gastrotricha: 4) (Figs 2C, 3C). Atlantic Forest also presents the highest proportion of endemic species, with 71 endemic species (Tardigrada: 40; Gastrotricha: 31), whereas Cerrado has 8 endemic species (Tardigrada: 4; Gastrotricha: 4).

Concerning the hydrographic regions, the Paraná Hydrographic Region has 102 species recorded (Tardigrada: 45; Gastrotricha: 57) and showed the highest number of species, followed by the Southeast Atlantic Hydrographic Region with 47 (Tardigrada: 15; Gastrotricha: 32) (Figs 2D, 3D). São Paulo and Rio de Janeiro (Southeastern Region) are the states with more species records, respectively with 121 (Tardigrada: 50; Gastrotricha: 71) and 22 (Tardigrada: 10; Gastrotricha: 12), whereas Pernambuco and Rio Grande do Norte (Northeastern Region) have 21 Tardigrada species in each state (Figs 2A, 3A).

Regarding the biogeographic regionalization, terrestrial meiofaunal species were more frequently sampled in the Atlantic province (146, Tardigrada: 90; Gastrotricha: 56), followed by Paraná Forest province (51, Tardigrada: 22; Gastrotricha: 29) and Cerrado province (20, Tardigrada: 5; Gastrotricha: 15) (Figs 2B, 3B), whereas marine meiofaunal

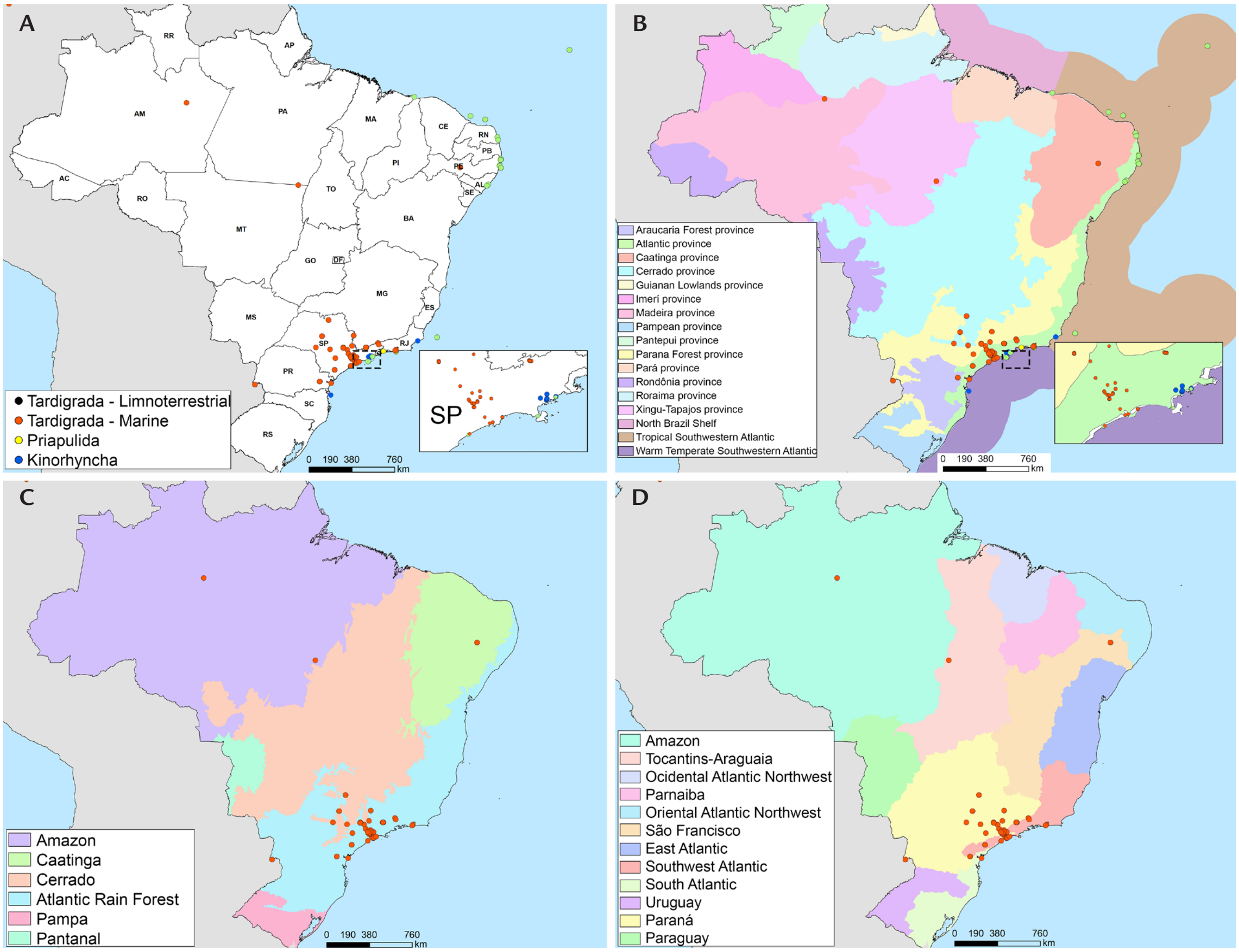

Figure 2. Map of Brazil in South America showing sampling sites of Tardigrada, Kinorhyncha and Priapulida: (A) the 26 states plus the Federal District; (B) the terrestrial and marine bioregionalization; (C) the six continental biomes following IBGE (2004); (D) the twelve hydrographic regions in the country following ANA (2015).

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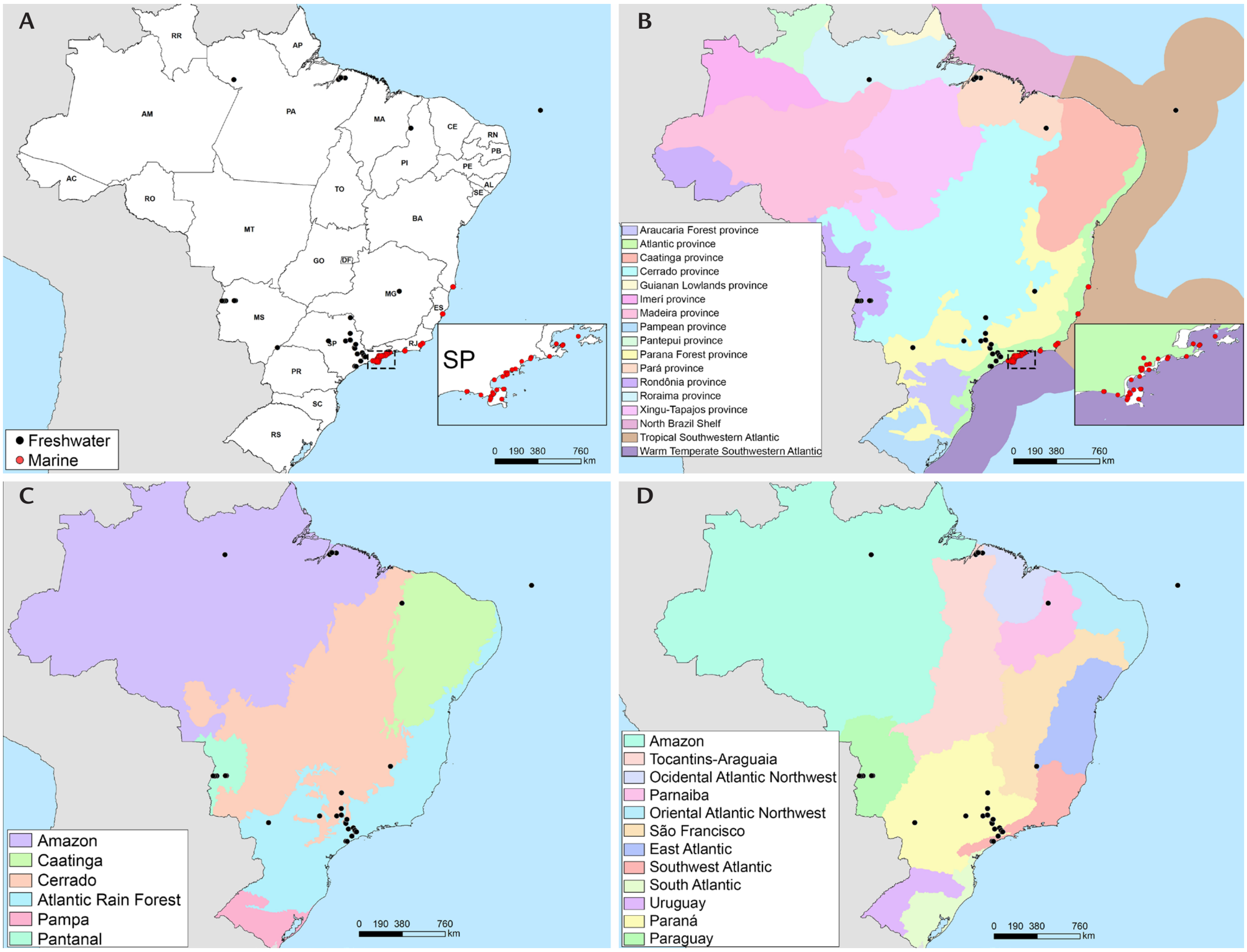

Figure 3. Map of Brazil in South America showing sampling sites of Gastrotricha: (A) the 26 states plus the Federal District; (B) the terrestrial and marine bioregionalization; (C) the six continental biomes following IBGE (2004); (D) the twelve hydrographic regions in the country following ANA (2015).

species were more often sampled in the Tropical Southwestern Atlantic province (33, Tardigrada: 29; Gastrotricha: 3; Kinorhyncha 1) followed by Warm Temperate Southwestern Atlantic province (37, Tardigrada: 6; Gastrotricha: 27; Kinorhyncha 4) (Figs 2B, 3B).

The temporal accumulation curve of species of Tardigrada and Gastrotricha shows a linear pattern of increase, not indicating an asymptotic trajectory (Fig. 4A, 4B), which means that the rate of discovery of new species is linearly increasing. For Tardigrada, considering a constant rate of discovery of new species, an average of 194 species would be expected, ranging between 164 and 225 species. This scenario does not change when predicting expected richness based on Family rank. Half of the tardigrade families do not allow any extrapolation due to the low richness (Fig. 4A) and for those we did estimate richness (Hypsibiidae, Halechiniscidae, Macrobiotidae, and Echiniscidae, Fig. 5A) the pattern of temporal accumulation still holds, with a linear increase in species discovery. In Gastrotricha, the pattern is the same as in Tardigrada, a linear increase in species discovery with time leading to an extrapolated number of 167 species, ranging between 133 and 202 species, assuming the same rate of discovery we found till now (Fig. 4B). Estimating the richness of each Gastrotricha family shows a scenario of only four families (out of 10) with sufficient sampling to predict richness (Fig. 5B). Overall, we expect that the number of species of both phyla will double. However, there is a clear uncertainty in each estimation.

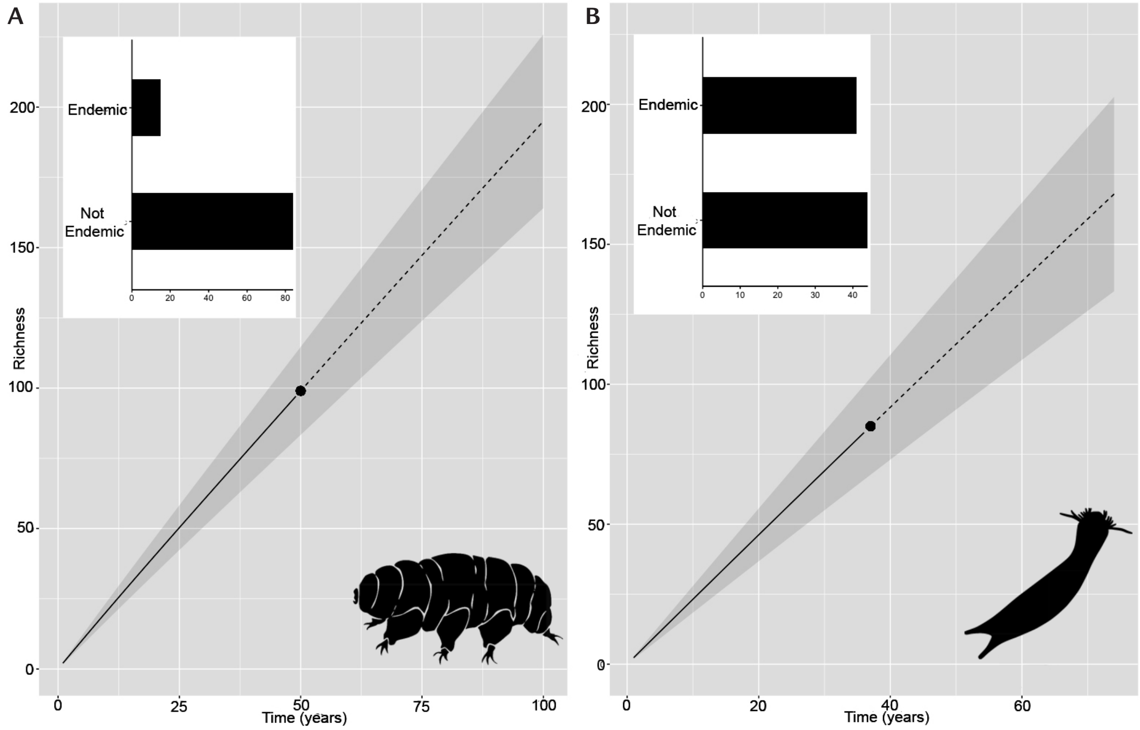

Figure 4. Temporal accumulation curve of species of (A) Tardigrada and (B) Gastrotricha and the number of endemic and not endemic species in Brazil. Solid lines depict the interpolated curves, representing the rate of species description over time, while dashed lines extend these curves to show extrapolated rates. The gray areas surrounding the curves signify the 95% upper and lower bound confidence intervals for the estimated species description rates. Actual counts of described species are denoted by dots.

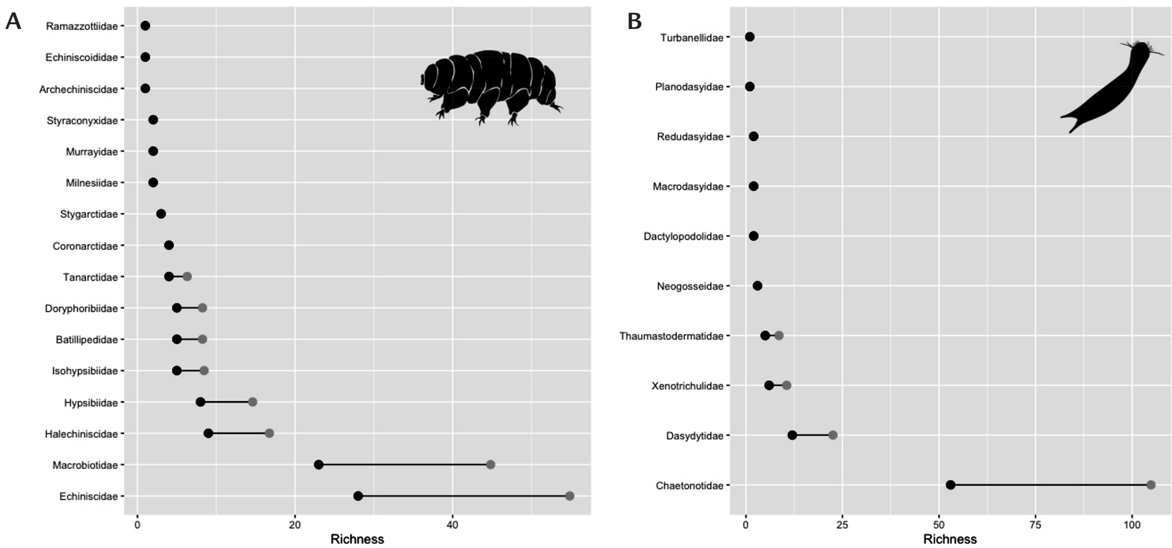

Figure 5. Species richness estimation within (A) Tardigrada and (B) Gastrotricha families in Brazil. Dark dots represent the actual number of described species and gray dots the extrapolated number of species for families with a number of described species that allows extrapolation.

DISCUSSION

Even though the description of the diversity of meiofaunal taxa has been improved by new techniques and sampling protocols (Fonseca et al. 2018) and they represent an important component of biodiversity in various ecosystems, these taxa are often underestimated due to challenges posed by their extremely small size and the fragility of their bodies (Curini-Galletti et al. 2012, Garraffoni and Freitas 2017, Garraffoni et al. 2019b). It can be confidently stated that a significant portion of the research dealing with taxonomic, diversity, and distribution patterns regarding these marine, freshwater, and terrestrial organisms found in Brazil is still in its early stages. This worrisome panorama can be related to the modus operandi to study and identify these fragile organisms with tiny bodies (Garraffoni et al. 2019b); the time-consuming activity and resources required to train a taxonomist, and the low number of Brazilian experts dedicated to the study of these taxa (see below). Thus, Brazilian meiofaunal taxa exemplify well the groups that are globally under pressure and have shortfalls in accessing biodiversity knowledge, two of which (among a total of seven) are known as the Linnean and Wallacean shortfalls (Hortal et al. 2015).

The discrepancy between the number of described species and the number of existing species is referred to as the Linnean deficit (Hortal et al. 2015). This deficiency can be particularly severe in meiofauna (Fonseca et al. 2018), as the number of studies aiming to discover new species is markedly lower compared to research on macrofauna (Fenchel and Finlay 2004). The Wallacean deficit is related to the lack of information regarding the geographic distribution of species and low sampling effort due to geographical and accessibility constraints (Hortal et al. 2015). It is worth noting that both deficiencies lead to a specific problem in meiofauna, known as the "paradox of meiofauna" (Giere 2009). The scarcity of taxonomic knowledge on the species level results in imprecise species delimitation and misidentification, leading these species to exhibit artificially ubiquitous distributions, which is paradoxical for small benthic meiofaunal organisms with limited dispersal capability, short life cycle, and no pelagic larval phase (Fenchel and Finlay 2004, Fonseca et al. 2018).

In addition to the low number of known species, there are a limited number of experts specialized in the identification of these animals, which is reflected in the scarcity of biogeographic, ecological, and diversity studies. Furthermore, there is a lack of suitable type (series) material, limited descriptions, and few photographic or illustrative records (Garraffoni and Freitas 2017, Garraffoni et al. 2019b). This issue affects a considerable portion of these taxa, leading to confusion in identifications and 'false' occurrence records, thereby hindering biogeographic, phylogenetic, and diversity studies and raising questions about the accuracy of this information, compromising future research efforts (Cerca et al. 2018, Garraffoni et al. 2021, Magpali et al. 2021).

As pointed out by Garraffoni et al. (2021), the available information on global meiofaunal diversity has a strong bias in favor of the Northern Hemisphere compared to the Southern Hemisphere. Tardigrades, gastrotrichs, and kinorhynchs were first described in Europe during the 18th and 19th centuries, but in Brazil, new species were only discovered in the 20th and 21st centuries. Marcus (1937) described the first Brazilian freshwater/limnoterrestrial tardigrade and successively brought to light a marine species – that came to be the first description for the Southern Hemisphere (Marcus 1946). Kisielewski (1987) contributed with the first freshwater gastrotrichs followed by marine species of Todaro and Rocha (2004). Kinorhyncha had its first description by Gerlach (1956). If we consider the first Brazilian researchers that participated in the description of new species of these taxa, the numbers are even worse: first on freshwater Tardigrada was done by de Barros (1938), and marine one by Santos et al. (2017); freshwater Gastrotricha by Garraffoni and Melchior (2015); Kinorhyncha by Dal Zotto et al. (2013).

Interesting to note that the sampling bias can also be observed on a regional scale, as most of the meiofauna sampling sites in Brazil are concentrated in the state of São Paulo. This unequal distribution of the sampling effort is directly related to human and financial factors. São Paulo houses the first meiofaunal studies done in Brazil in the early XX century (see Introduction and Historical background of Tardigrada, Kinorhyncha and Gastrotricha studies in Brazil) and also has the financial support provided by FAPESP (São Paulo Research Foundation) through the Biota Program, which contributed to provide structural and logistical support that leverages the advancement of our knowledge about the fauna and plant biodiversity in this state (Joly et al. 2010, Percequillo et al. 2022).

There are several methods, with different degrees of complexity to estimate richness, ranging from expert opinion to extrapolation from samples and rates of species description (May 1988, Costello and Wilson 2011, Mora et al. 2011, Bartels et al. 2016). Nevertheless, regardless of the chosen method, it is still quite impossible to ascertain how many species there are of most zoological groups (Mora et al. 2011, Caley et al. 2014) mainly because research and funding in systematics/taxonomy lag behind the number of species to be discovered.

Our analysis showed that the cumulative richness, observed and extrapolated, of Tardigrada and Gastrotricha, are unsaturated, that is, did not reach an asymptote. Furthermore, the analysis among families within each Phylum showed an asymmetry in richness showing some taxa are sampled less frequently which could be just the evolutionary result of macroevolution between lineages and/or a sampling effect. Thus, we are aware that the explanatory power of our results from the species cumulative curve of both taxa is weaker than we would expect. This happened because there is a true hidden taxonomic diversity yet to be described due to inventory incompleteness, and, unfortunately, a pattern similar is observed for marine tardigrades and gastrotrichs (Costello and Wilson 2011, Bartels et al. 2016).

Currently, there are few groups of researchers in Brazil dedicated to studying the meiofaunal groups analyzed in the present contribution, such as Clélia Rocha, who focuses on marine tardigrades, at the "Universidade Federal Rural de Pernambuco"; André Rinaldo Senna Garraffoni, who focuses on limnoterrestrial tardigrades, freshwater and marine Gastrotricha, and Kinorhyncha at "Universidade Estadual de Campinas" and Maikon Di Domenico, who focuses on Kinorhyncha, at "Universidade Federal do Paraná". Thus, the training of new researchers in the taxonomy/systematics of these meiofaunal groups and the consolidation of these research groups is crucial to continue their legacy. Nevertheless, despite the difficulties mentioned and discussed above regarding the study of these meiofaunal groups, some actions have been taken to change their current state of knowledge.

In the last years, Brazilian meiofaunal researchers have been trying to increase the students' engagement and interest in meiofaunal taxa by organizing regular symposiums, such as the V International Scalidophora Workshop (2019), I Brazilian Symposium of Meiofauna (2020), II Brazilian Symposium of Meiofauna (2021) and I Brazilian Symposium of Tardigrada (2022). These kinds of events are great opportunities for senior researchers to share their knowledge in many fields with younger researchers. Furthermore, increasing the number of undergraduate lectures that aim to teach how to collect, sort, and identify these tiny animals, can also help to make them more visible and attractive to undergraduate and graduate students (Guidetti et al. 2021).

In conclusion, given the sporadic nature in which the gastrotrichs, tardigrades, and kinorhynchs fauna have been studied in Brazil, several shortfalls still need to be addressed, mainly Linnaean, Wallacean, and Darwinian shortfalls. Some goals are considered priorities for Brazilian meiofauna researchers, such as: a) a review of species that have Brazil as the type-site and indication of neotypes, since the original specimen has not been preserved or has been lost; b) an expansion of sample areas, since a significant part of the Brazilian territory remains unexplored; and c) training of new specialists in this taxon, especially in taxonomy and ecology.

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LITERATURE CITED

Adrianov AV, Malakhov VV (1996) The phylogeny and classification of the class Kinorhyncha. Zoosystematica Rossica 4: 23–44.

Adrianov AV, Malakhov VV (1999) Cephalorhyncha of the World Ocean. KMK Scientific Press, Moscow, 328 pp.

Aguinaldo AM, Turbeville JM, Linford LS, Rivera MC, Garey JR, Raff R, Lake JA (1997) Evidence for a clade of nematodes, arthropods, and other molting animals. Nature 387: 489–493. https://doi.org/10.1038/387489a0

ANA (2015) Conjuntura dos Recursos Hídricos no Brasil: regiões hidrográficas brasileiras. Agência Nacional de Águas, Brasília, 163 pp. Available online at http://www.ana.gov.br

Araújo TQ, Garraffoni ARS (2021) Description of a New Scaled Species of *Ptychostomella* (Gastrotricha: Macrodasyida) from the Brazilian coast and a cladistics analysis of the genus. Taxonomy 1(4): 278–289. https://doi.org/10.3390/taxonomy1040022

Araújo TQ, Wieloch AH, Hochberg R, Garraffoni ARS (2022) Description of *Xenotrichula tropicalis* sp. nov. (Gastrotricha: Chaetonotida) and new records of Xenotrichulidae species from Brazil and USA. Annales Zoologici 72(2): 167–185. https://doi.org/10.3161/00034541ANZ2022.72.2.001

Araújo TQ, Minowa AK, Garraffoni ARS (2024) Trends on Gastrotricha research: a bibliometric analysis. Biologia. https://doi.org/10.1007/s11756-024-01686-6

Assunção CML (1999a) Tardigrada. In: Joly CA, Bicudo CEM (Eds) Biodiversidade do Estado de São Paulo: síntese do conhecimento ao final do século XX – Invertebrados Marinhos. Fundação de Amparo à Pesquisa do Estado de São Paulo, São Paulo, 185–189.

Assunção CML (1999b) Tardigrada. In: Ismael D, Valenti WC, Matsumura TT (Eds) Biodiversidade do Estado de São Paulo: síntese do conhecimento ao final do século XX – Invertebrados de água doce. Fundação de Amparo à Pesquisa do Estado de São Paulo, São Paulo, 61–64.

Assunção CML (2001) Análise filogenética em Macrocephala (Tardigrada, Archeotardigrada). PhD Thesis, Universidade de São Paulo, São Paulo, 87 pp. https://doi.org/10.11606/T.41.2002.tde-16052014-170610

Balsamo M, Grilli P, Guidi L, d'Hondt JL (2014) Gastrotricha: biology, ecology and systematics. Families Dasydytidae, Dichaeturidae, Neogosseidae, Proichthydiidae. Backhuys Publishers, Kerkwerve, 187 pp.

Balsamo M, Artois T, Smith III JP, Todaro MA, Guidi L, Leander BS, Van Steenkiste NW (2020) The curious and neglected soft-bodied meiofauna: Rouphozoa (Gastrotricha and Platyhelminthes). Hydrobiologia 847(12): 2613–2644. https://doi.org/10.1007/s10750-020-04287-x

Bartels PJ, Apodaca JJ, Mora C, Nelson DR (2016) A global biodiversity estimate of a poorly known taxon: phylum Tardigrada. Zoological Journal of the Linnean Society 178: 730–736. https://doi.org/10.1111/zoj.12441

Bertolani R, Altiero T, Nelson D (2009) Tardigrada (Water Bears). Encyclopedia of Inland Waters 2: 443–455. https://doi.org/10.1016/B978-012370626-3.00188-5

Boeckner MJ, Sharma J, Proctor HC (2009) Revisiting the meiofauna paradox: dispersal and colonization of nematodes and other meiofaunal organisms in low-and high-energy environments. Hydrobiologia 624: 91–106. https://doi.org/10.1007/s10750-008-9669-5

Brenzinger B, Haszprunar G, Schrödl M (2013) At the limits of a successful body plan-3D microanatomy, histology and evolution of Helminthope (Mollusca: Heterobranchia: Rhodopemorpha), the most worm-like gastropod. Frontiers in Zoology 10: 1–27. https://doi.org/10.1186/1742-9994-10-37

Brotto-Guidetti E, Morek W, Garraffoni ARS (2024) Morphological and molecular evidence for a new species of the genus Milnesium Doyère, 1840 (Tardigrada: Apochela) from South America. Zoologischer Anzeiger 309: 55–65. https://doi.org/10.1016/j.jcz.2024.01.004

Caley MJ, Fisher R, Mengersen K (2014) Global species richness estimates have not converged. TREE 29: 187–188. https://doi.org/10.1016/j.tree.2014.02.002

Campbell LI, Rota-Stabellia O, Edgecombeb GD, Marchioroc T, Longhorna SJ, Telfordd MJ, et al. (2011) MicroRNAs and phylogenomics resolve the relationships of Tardigrada and suggest that velvet worms are the sister group of Arthropoda. Proceedings of National Academy of Science 108(38): 15920–15924. https://doi.org/10.1073/pnas.1105499108

Campos A, Todaro MA, Garraffoni ARS (2020) A new species of *Paraturbanella* Remane, 1927 (Gastrotricha, Macrodasyida) from the Brazilian coast, and the molecular phylogeny of Turbanellidae Remane, 1926. Diversity 12: 42. https://doi.org/10.3390/d12020042

Campos A, Garraffoni ARS (2019) A synopsis of knowledge, zoogeography and an online interactive map of Brazilian marine gastrotrichs. PeerJ 7: e7898. https://doi.org/10.7717/peerj.7898

Cerca J, Purschke G, Struck TH (2018) Marine connectivity dynamics: clarifying cosmopolitan distributions of marine interstitial invertebrates and the meiofauna paradox. Marine Biology 165: 1–21. https://doi.org/10.1007/s00227-018-3383-2

Chao A, Colwell RK (2017) Thirty years of progeny from Chao's inequality: estimating and comparing richness with incidence data and incomplete sampling (invited article). Statistics and Operation Research Transactions 41: 3–54. https://doi.org/10.2436/20.8080.02.49

Corrêa DC (1987) Tardigrada. In: Sociedade Brasileira de Zoologia (Ed.) Manual de técnicas para preparações zoológicas. Sociedade Brasileira de Zoologia, Campinas, 1–6.

Costello MJ, Wilson SP (2011) Predicting the number of known and unknown species in European seas using rates of description. Global Ecology and Biogeography 20: 319–330. https://doi.org/10.1111/j.1466-8238.2010.00603.x

Curini-Galletti M, Artois T, Delogu V, De Smet WH, Fontaneto D, Jondelius U, et al. (2012) Patterns of diversity in soft-bodied meiofauna: dispersal ability and body size matter. Plos One 7(3): e33801. https://doi.org/10.1371/journal.pone.0033801

da Rocha CMC, Castro FJV, Fonsêca-Genevois V (1999) Efeito da granulometria e da topografia sobre a distribuição de *Batillipes pennaki* (Marcus, 1946) em zona tropical típica – restinga do Paiva, Pernambuco, Brasil. Trabalhos Oceanográficos da Universidade Federal de Pernambuco 27(2): 89–102. https://doi.org/10.5914/tropocean.v27i2.2820

da Rocha CMC, Fonsêca-Genevois V, Castro FJV (2001) Distribuição espaço-temporal de *Batillipes pennaki* Marcus, 1946 (Tardigrada, Heterotardigrada) na margem Sul da ilha de Itamaracá (Pernambuco, Brasil). Trabalhos

Oceanográficos da Universidade Federal de Pernambuco 28(1): 35–46. https://doi.org/10.5914/tropocean.v28i1.2714

da Rocha CMC, Gomes Júnior EL, Santos ECL (2016) Brazilian limnoterrestrial tardigrades (Bilateria, Tardigrada): new occurrences and species checklist updates. Revista Nordestina de Zoologia 10: 21–31.

da Rocha CMC, Santos ECL, Gomes Júniorr EL, Moura JR, Silva LGS, Barbosa DF (2013) New records of marine tardigrades from Brazil. Journal of Limnology 72(S1): 102–107. https://doi.org/10.4081/jlimnol.2013.s1.e12

dal Zotto M, Di Domenico M, Garraffoni ARS, Sørensen MV (2013) *Franciscideres* gen. nov. – a new, highly aberrant kinorhynch genus from Brazil, with an analysis of its phylogenetic position. Systematics and Biodiversity 11: 303–321. https://doi.org/10.1080/14772000.2013.819045

de Barros R (1938) *Macrobiotus evelinae*, uma nova espécie de tardígrados. Boletim Biológico (Nova Série) 3: 52–54.

de Barros R (1939a) *Itaquascon umbellinae* gen. nov. sp. nov. (Tardigrada, Macrobiotidae). Zoologischer Anzeiger 128: 106–109.

de Barros R (1939b) *Pseudobiotus juanitae* nova espécie de tardígrado. Boletim Biológico (Nova Série) 4: 367–368.

de Barros R (1942a) Tardígrados do estado de São Paulo, Brasil. I. Introdução. Gêneros "*Echiniscus*" e "*Pseudechiniscus*". Revista Brasileira de Biologia 2: 257–269.

de Barros R (1942b) Tardígrados do estado de São Paulo, Brasil. II. Gênero *Macrobiotus*. Revista Brasileira de Biologia 2: 373–386.

de Barros R (1943) Tardígrados do estado de São Paulo, Brasil. III. Gêneros *Hypsibius*, *Itaquascon* e *Milnesium*. Revista Brasileira de Biologia 3: 1–10.

de Barros RC (2020) Tardigrades Research in Brazil: an overview and updated checklist. Arquivos de Zoologia 51(1): 1–11. https://doi.org/10.11606/2176-7793/2020.51.01

Degma P, Guidetti R (2023) Actual checklist of Tardigrada species. Available online at: https://iris.unimore.it/handle/11380/1178608 [Acessed: 28/07/2023]

dos Santos GAP, Moens T, Valdes Y, Larrazabal MEL (2014) Verônica da Fonsêca-Genevois and the rise of meiofauna studies in Brazil. Life and contribution of a pioneer, in memoriam. Marine Biodiversity 44(3): 229–236. https://doi.org/10.1007/s12526-014-0251-2

du Bois-Reymond Marcus E (1944) Sobre Tardígrados Brasileiros. Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 13: 1–28.

du Bois-Reymond Marcus E (1952) On South American Malacopoda. Boletins da Faculdade de Philosophia, Sciencias e Letras, Universidade de São Paulo, Zoologia 17: 189–209. https://doi.org/10.11606/issn.2526-4877.bsffclzoologia.1952.125190

Dujardin F (1851) Sur un petit animal marin, l'Echinodère, formant un type intermédiaire entre les Crustacés et les Vers. Annales des Sciences Naturelles 15: 158–173.

Dunn CW, Giribet G, Edgecombe GD, Hejnol A (2014) Animal phylogeny and its evolutionary implications. Annual Review of Ecology, Evolution, and Systematics 45: 371–395. https://doi.org/10.1146/annurev-ecolsys-120213-091627

Edgecombe GD, Giribet G, Dunn CW, Hejnol A, Kristensen RM, Neves RC, Rouse GW, Worsaae K, Sørensen MV (2011) Higher-level metazoan relationships: recent progress and remaining questions. Organisms Diversity & Evolution 11: 151–172. https://doi.org/10.1007/s13127-011-0044-4

Egger B, Lapraz F, Tomiczek B, Müller S, Dessimoz C, Girstmair J, et al. (2015) A transcriptomic-phylogenomic analysis of the evolutionary relationships of flatworms. Current Biology 25(10): 1347–1353. https://doi.org/10.1016/j.cub.2015.03.034

Ehrenberg CG (1830) Organisation, Systematik und geographisches Verhältniss der Infusionsthierchen. Königlichen akademie der wissenschaften, Berlin, 108 pp. https://doi.org/10.5962/bhl.title.2077

Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. Bioscience 54(8): 777–784. https://doi.org/10.1641/0006-3568(2004)054[0777:TUOSSP]2.0.CO;2

Fonseca G, Fontaneto D, Di Domenico M (2018) Addressing biodiversity shortfalls in meiofauna. Journal of Experimental Marine Biology and Ecology 502: 26–38. https://doi.org/10.1016/j.jembe.2017.05.007

Forneris L (1985) Gastrotricha. In: Sociedade Brasileira de Zoologia (Ed.) Manual de técnicas para preparações zoológicas. Sociedade Brasileira de Zoologia, Campinas, 11.1–11.14.

Fromm B, Tosar JP, Aguilera F, Friedländer MR, Bachmann L, Hejnol A (2019) Evolutionary implications of the microRNA-and piRNA complement of *Lepidodermella squamata* (Gastrotricha). Non-coding RNA 5(1): 19. https://doi.org/10.3390/ncrna5010019

Garey JR (2002) The lesser-known protostome taxa: an introduction and a tribute to Robert P. Higgins. Integrative and Comparative Biology 42(3): 611–618. https://doi.org/10.1093/icb/42.3.611

Garraffoni ARS, Araujo TQ, Lourenço AP, Balsamo M (2010) New data on freshwater psammic Gastrotricha from Brazil. Zookeys (60): 1. https://doi.org/10.3897/zookeys.60.495

Garraffoni ARS, Melchior MP (2015) New species and new records of freshwater *Heterolepidoderma* (Gastrotricha: Chaetonotidae) from Brazil with an identification key to the genus. Zootaxa 4057(4): 551–568. https://doi.org/10.11646/zootaxa.4057.4.5

Garraffoni ARS, Araújo TQ, Lourenço AP, Guidi L, Balsamo M (2017) A new genus and new species of freshwater Chaetonotidae (Gastrotricha: Chaetonotida) from Brazil with phylogenetic position inferred from nuclear and mitochondrial DNA sequences. Systematics and Biodiversity 15(1): 49–62. https://doi.org/10.1080/14772000.2016.1214189

Garraffoni ARS, Araújo TQ, Lourenço AP, Guidi L, Balsamo M (2019a) Integrative taxonomy of a new *Redudasys* species (Gastrotricha: Macrodasyida) sheds light on the invasion of fresh water habitats by macrodasyids. Scientific Reports 9(1): 2067. https://doi.org/10.1038/s41598-018-38033-0

Garraffoni ARS, Kieneke A, Kolicka M, Corgosinho PH, Prado J, Nihei SS, Freitas AV (2019b) ICZN Declaration 45: a remedy for the nomenclatural and typification dilemma regarding soft-bodied meiofaunal organisms? Marine Biodiversity 49: 2199–2207. https://doi.org/10.1007/s12526-019-00983-7

Garraffoni ARS, Freitas AVL (2017) Photos belong in the taxonomic Code. Science 355(6327): 805–805. https://doi.org/10.1126/science.aam7686

Garraffoni ARS, Araújo TQ (2020) Keys to Neotropical and Antarctic Fauna. In: Damborenea C, Rogers DC, Thorp JH (Eds) Phylum Gastrotricha. Academic Press, London, 125–143. https://doi.org/10.1016/B978-0-12-804225-0.00007-1

Garraffoni ARS, Sørensen MV, Worsaae K, Di Domenico M, Sales LP, Santos J, Lourenço A (2021) Geographical sampling bias on the assessment of endemism areas for marine meiobenthic fauna. Cladistics 37(5): 571–585. https://doi.org/10.1111/cla.12453

Gerlach SA (1956) Über einen aberrantenVertreter der Kinorhynchen aus dem Küstengrundwasser. Kieler Meeresforsch 12: 120–124.

Giere O (2009) Meiobenthology: the microscopic motile fauna of aquatic sediments. Springer-Verlag Heidelberg, Berlin, 2nd ed., 527 pp.

Giribet G, Carranza S, Baguñà J, Riutort M, Ribera C (1996) First molecular evidence for the existence of a Tardigrada + Arthropoda clade. Molecular Biology and Evolution 13: 76–84. https://doi.org/10.1093/oxfordjournals.molbev.a025573

Giribet G, Distel DL, Polz M, Sterrer W, Wheeler WC (2000) Triploblastic relationships with emphasis on the acoelomates and the position of Gnathostomulida, Cycliophora, Plathelminthes, and Chaetognatha: a combined approach of 18S rDNA sequences and morphology. Systematic Biology 49(3): 539–562. https://doi.org/10.1080/10635159950127385

Giribet G, Edgecombe GD (2017) Current understanding of Ecdysozoa and its internal phylogenetic relationships. Integrative and Comparative Biology 57: 455–466. https://doi.org/10.1093/icb/icx072

Giribet G, Edgecombe GD (2019) The phylogeny and evolutionary history of arthropods. Current Biology 29(12): R592–R602. https://doi.org/10.1016/j.cub.2019.04.057

Goeze JAE (1773) 2. Beobachtung: Über den kleinen Wasserbären. In: Bonnet HK (Ed.) Abhandlungen aus der Insectologie, 355–367.

Gomes Júnior EL, da Rocha CMC (2015) Microscopia eletrônica de varredura com tardígrados (Filo Tardigrada): sugestão de protocolos adaptados às peculiaridades do grupo. Revista Nordestina de Zoologia 9(2): 16–32.

Gomes Júnior EL, Santos É, da Rocha CMC, Santos PJP, Fontoura P (2017) A new species of *Ligiarctus* (Tardigrada, Arthrotardigrada) from the Brazilian continental shelf, Southwestern Atlantic Ocean. Marine Biodiversity 48(1): 5–12. https://doi.org/10.1007/s12526-017-0709-0

Gomes Júnior EL, Santos É, da Rocha CMC, Santos PJP, Fontoura P (2020) The Deep-Sea Genus *Coronarctus* (Tardigrada, Arthrotardigrada) in Brazil, South-Western Atlantic Ocean, with the Description of Three New Species. Diversity 12(2): 63. https://doi.org/10.3390/d12020063

Guidetti EB, Campos A, Batistão AR, Silva AT, Bilatto CG, Salgado KA, Araújo TQ, Garraffoni ARS (2021) Gastrotrichs and tardigrades in a remnant of Atlantic Forest (Serra do Japi, SP, Brazil). Biota Neotropica 21(2): e20201165. https://doi.org/10.1590/1676-0611-bn-2020-1165

Herranz M, Stiller J, Worsaae K, Sørensen MV (2022) Phylogenomic analyses of mud dragons (Kinorhyncha). Molecular Phylogenetics and Evolution 168: 1–10. https://doi.org/10.1016/j.ympev.2021.107375

Higgins RP (1964) Three new kinorhynchs from the North Carolina coast. Bulletin of Marine Science of the Gulf and Caribbean 14: 479–493.

Higgins RP (1968) Taxonomy and postembryonic development of the Cryptorhagae, a new suborder for the mesopsammic kinorhynch genus *Cateria*. Transactions of the American Microscopical Society 87: 21–39. https://doi.org/10.2307/3224334

Higgins RP (1988) Kinorhyncha. In: Higgins RP, Thiel H (Eds) Introduction to the Study of Meiofauna. Smithsonian Institution Press, Washington DC, 328–331.

Higgins RP (1990) Zelinkaderidae, a new family of cyclorhagid Kinorhyncha. Smithsonian Contributions to Zoology 500: 1–26. https://doi.org/10.5479/si.00810282.500

Higgins RP, Thiel H (1988) Introduction to the Study of Meiofauna. Smithsonian Institution Press, London, 488 pp.

Hochberg R, Litvaitis MK (2000) Phylogeny of Gastrotricha: a morphology-based framework of gastrotrich relationships. The Biological Bulletin 198(2): 299–305. https://doi.org/10.2307/1542532

Höfling-Epiphanio E (1972) Ocorrência de *Batillipes mirus* Richters, 1909 e *B. tubernatis* Pollock, 1971 (Tardigrada) no litoral brasileiro. Ciência & Cultura 24: 358–359.

Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ (2015) Seven Shortfalls that Beset Large-Scale Knowledge of Biodiversity. Annual Review of Ecology, Evolution, and Systematics 46(1): 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Hsieh TC, Ma KH, Chao A (2022) iNEXT: iNterpolation and EXTrapolation for species diversity. R package, v. 3.0.0.

Hyman LH (1951) The Invertebrates: Acanthocephala, Aschelminthes and Entoprocta: The Pseudocoelomate Bilateria. Mcgraw-Hill Book Company, New York, Toronto, London, 550 pp.

IBGE (2004) Mapa de Biomas e de Vegetação do Brasil. Instituto Brasileiro de Geografia e Estatística. Available online at: http://www.ibge.gov.br/

Iharos G (1969) The Scientific Results of the Hungarian Soil Zoological Expeditions to South America. Öpuscula Zoologica Budapest 9(2): 279–289.

Joly CA, Rodrigues RR, Metzger JP, Haddad CF, Verdade LM, Oliveira MC, Bolzani VS (2010) Biodiversity conservation research, training, and policy in São Paulo. Science 328: 1358–1359.

Kånneby T (2016) Phylum Gastrotricha. In: Thorp JH, Covich AP (Ed.) Freshwater Invertebrates. Elsevier, 115–130. https://doi.org/10.1016/B978-0-12-385028-7.00007-X

Kinchin IM (1994) The Biology of Tardigrades. Portland Press, London, 186 pp.

Kieneke A, Riemann O, Ahlrichs WH (2008) Novel implications for the basal internal relationships of Gastrotricha revealed by an analysis of morphological characters. Zoologica Scripta 37: 429–460. https://doi.org/10.1111/j.1463-6409.2008.00334.x

Kieneke A, Schmidt-Rhaesa A (2015) Gastrotricha. In: Schmidt-Rhaesa A (Ed.) Handbook of Zoology. Gastrotricha and Gnathifera. De Gruyter, Berlin, Boston, 134 pp. https://doi.org/10.1515/9783110274271.1

Kisielewski J (1987) Two new interesting genera of Gastrotricha (Macrodasyida and Chaetonotida) from the Brazilian freshwater psammon. Hydrobiologia 153(1): 23–30. https://doi.org/10.1007/BF00005502

Kisielewski J (1991) Inland-water Gastrotricha from Brazil. In: Bierzyńska B, Czechowski W, Głogowski S, Kierych E, Pokryszko B, Riedel A, Slipiński AS (Eds) Annales Zoologici. Instytut Zoologii Polskiej Akademii Nauk, Warszawa, 1–168.

Križanová FR, Vd'ačný P (2022) A huge undescribed diversity of the subgenus *Hystricochaetonotus* (Gastrotricha, Chaetonotidae, *Chaetonotus*) in Central Europe. European Journal of taxonomy 840: 1–93. https://doi.org/10.5852/ejt.2022.840.1941

Laumer CE, Bekkouche N, Kerbl A, Goetz F, Neves RC, Sørensen MV, et al. (2015) Spiralian phylogeny informs the evolution of microscopic lineages. Current Biology 25(15): 2000–2006. https://doi.org/10.1016/j.cub.2015.06.068

Littlewood DTJ, Telford MJ, Clough KA, Rohde K (1998) Gnathostomulida: an enigmatic metazoan phylum from both morphological and molecular perspectives. Molecular Phylogenetics and Evolution 9(1): 72–79. https://doi.org/10.1006/mpev.1997.0448

Magpali L, Machado DR, Araújo TQ, Garraffoni ARS (2021) Long distance dispersal and pseudo-cryptic species in Gastrotricha: first description of a new species (Chaetonotida, Chaetonotidae, Polymerurus) from an oceanic island with volcanic rocks. European Journal of Taxonomy 746: 62–93. https://doi.org/10.5852/ejt.2021.746.1319

Majdi N, Schmid-Araya JM, Traunspurger W (2020) Preface: Patterns and processes of meiofauna in freshwater ecosystems. Hydrobiologia 847: 2587–2595. https://doi.org/10.1007/s10750-020-04301-2

Marcus E (1927) Zur Anatomie und Ökologie mariner Tardigraden. Zoologische Jahrbücher. Abteilung für Systematik 53: 487–558.

Marcus E (1937) Sôbre a anabiose dos Tardigrados, com descrição de uma nova espécie. Boletim Biologico 3(5): 7–13.

Marcus E (1946) *Batillipes pennaki*, a new marine tardigrade from the North and South American Atlantic coast. Comunicaciones Zoologicas del Museo de Historia Natural de Montevideo 33(2): 1–3.

May RM (1988) How many species are there on earth? Science 241: 1441–1449. https://doi.org/10.1126/science.241.4872.1441

Mendes EG (1994) Ernest Marcus. Estudos Avançados 8: 209–213.

Metschnikoff E (1865) Über einige wenig bekannte niedere Thierformen. Zeitschrift für wissenschaftliche Zoologie 15: 450–463.

Minowa AK, Garraffoni ARS (2020) Assessing biodiversity shortfalls of freshwater meiofauna from the Atlantic Forest: New species, distribution patterns and the first total-evidence phylogeny of semiplanktonic Gastrotricha. Molecular Phylogenetics and Evolution 152: 106926. https://doi.org/10.1016/j.ympev.2020.106926

Minowa AK, Garraffoni ARS (2021) Seek and you shall find: new species of the rare genus *Ornamentula* (Gastrotricha: Chaetonotida) and first record outside of type-locality. Zoologia 38: e56781. https://doi.org/10.3897/zoologia.38.e56781

Mogle MJ, Kimball SA, Miller WR, McKown RD (2018) Evidence of avian-mediated long distance dispersal in American tardigrades. PeerJ 6: e5035. https://doi.org/10.7717/peerj.5035

Mora C, Tittensor DP, Adl S, Simpson AGB, Worm B (2011) How many species are there on Earth and in the ocean? Plos Biology 9: e1001127. https://doi.org/10.1371/journal.pbio.1001127

Morrone JJ, Escalante T, Rodríguez-Tapia G, Carmona A, Arana M, Mercado-Gómez JD (2022) Biogeographic Regionalization of the Neotropical Region: New Map and Shapefile. Anais da Academia Brasileira de Ciência 94(1): e20211167. https://doi.org/10.1590/0001-3765202220211167

Müller OF (1773) Vermivm terrestrium et fluviatilium: seu animalium infusoriorum, helminthicorum et testaceorum, non marinorum, succincta historia. Havniae et Lipsiae, apud Heineck et Faber, 1–214. https://doi.org/10.5962/bhl.title.46299

Murray J (1913) Notes on the natural history of Bolivia and Peru: including a report on the Rhizopoda by G.H. Wailes. Edinburgh Oceanographic Laboratory, Edinburgh, 45 pp.

Nelson DR (2002) Current status of the Tardigrada: evolution and ecology. Integrative and Comparative Biology 42: 652–659. https://doi.org/10.1093/icb/42.3.652

Nelson DR, Guidetti R, Rebecchi L (2015) Phylum Tardigrada. In: Thorp JH, Covich AP (Eds) Freshwater Invertebrates. Elsevier, 347–380. https://doi.org/10.1016/B978-0-12-385026-3.00017-6

Neuhaus B (2023) World Kinorhyncha Database. Available online at: https://www.marinespecies.org/kinorhyncha [Acessed: 29/06/2023] https://doi.org/10.14284/457

Neuhaus B, Kegel A (2015) Redescription of *Cateria gerlachi* (Kinorhyncha, Cyclorhagida) from Sri Lanka and of *C. styx* from Brazil, with notes on *C. gerlachi* from India and *C. styx* from Chile, and the ground pattern of the genus. Zootaxa 3965(1): 1–77. https://doi.org/10.11646/zootaxa.3965.1.1

Neuhaus B, Higgins RP (2002) Ultrastructure, biology and phylogenetic relationships of Kinorhyncha. Integrative and Comparative Biology 42: 619–632. https://doi.org/10.1093/icb/42.3.619

Nielsen C (2012) Animal Evolution: Interrelationships of the Living Phyla. Oxford University Press, Oxford, 3rd ed., 464 pp. https://doi.org/10.1093/acprof:oso/9780199606023.001.0001

Nielsen C, Scharff N, Eibye-Jacobsen D (1996) Cladistic analyses of the animal kingdom. Biological Journal of the Linnean Society 57: 385–410. https://doi.org/10.1111/j.1095-8312.1996.tb01857.x

Percequillo AR, Barbosa MFC, Bockmann FA, Bogoni JA, Esguícero ALH, Lamas C, Moraes GJ, Pinto-da-Rocha R, Silveira LF (2022) Natural history museums and zoological collections of São Paulo State. Biota Neotropica 22(spe): e20221426. https://doi.org/10.1590/1676-0611-BN-2022-1426

Petrov NB, Pegova AN, Manylov OG, Vladychenskaya NS, Mugue NS, Aleshin VV (2007) Molecular phylogeny of Gastrotricha on the basis of a comparison of the 18S rRNA genes: rejection of the hypothesis of a relationship between Gastrotricha and Nematoda. Molecular Biology 41: 445–452. https://doi.org/10.1134/S0026893307030107

Pilato G (2000) *Macrobiotus centesimus*, new species of Eutardigrade from the South America. Bollettino dell'Accademia Gioenia di Scienze Naturali di Catania 33: 97–101.

Rahm G (1931) Tardigrada of the South of America (esp. Chile). Revista Chilena de História Natural 35: 118–141.

Rahm G (1932) Freilebende Nematoden, Rotatorien und Tardigraden aus Südamerika (besonders aus Chile). C. Tardigrada. Zoologischer Anzeiger 98: 113–128.

Ramazzotti G, Maucci W (1983) Il Phylum Tardigrada. Memorie dell'Istituto Italiano di Idrobiologia, Pallanza 41: 1–1012.

Rao GC, Clausen C (1970) *Planodasys marginalis* gen. et sp. nov. and Planodasyidae fam. nov. (Gastrotricha Macrodasyoidea). Sarsia 42: 73–82. https://doi.org/10.1080/00364827.1970.10411164

Remane A (1925) Organisation und systematische Stellung der aberranten Gastrotrichen. Verhandlungen der deutschen zoologischen Gesellschaft 30: 121–128.

Remane A (1927) Neue Gastrotricha Macrodasyoidea. Zoologische Jahrbuecher Abteilung fuer Systematik Oekologie und Geographie der Tiere 54: 203–242.

Renaud-Mornant J (1980) Description de trois espèces nouvelles du genre *Tanarctus* Renaud-Debyser, 1959 et création de la sous-famille des tanarctinae, subfam. nov. (Tardigrada, Heterotardigrada). Bulletin du Muséum National d'Histoire Naturelle 4: 129–141. https://doi.org/10.5962/p.283868

Renaud-Mornant J (1984) Halechiniscidae (Heterotardigrada) de la campagne Benthedi, canal du Mozambique. Bulletin du Muséum National d'Histoire Naturelle 6: 67–88. https://doi.org/10.5962/p.285940

Renaud-Mornant J (1989) *Opydorscus*, un nouveau genre d'Orzeliscinae et as signification phylogénique (Tardigrada, Arthrotardigrada). Bulletin du Muséum National d'Histoire Naturelle 11(4): 763–771. https://doi.org/10.5962/p.288268

Rieger RM (1976) Monociliated epidermal cells in Gastrotricha: Significance for concepts of early metazoan evolution. Journal of Zoological Systematics and Evolutionary Research 14: 198–226. https://doi.org/10.1111/j.1439-0469.1976.tb00937.x

Ruppert EE (1991) Gastrotricha. In: Harrison FW, Ruppert EE (Eds) Microscopic Anatomy of Invertebrates Aschelminthes. Wiley-Liss, New York, vol. 4, 41–109.

Ruttner-Kolisko A (1955) *Rheomorpha neiswestnovae* und *Marinellina flagellata*, zwei phylogenetisch interessante Wurmtypen aus dem Süsswasserpsammon. Österreichische Zoologische Zeitschrift 6: 55–69.

Santos É, da Rocha CMC, Gomes Júnior EL, Fontoura P (2017) Three new *Batillipes* species (Arthrotardigrada: Batillipedidae) from the Brazilian coast. Zootaxa 4243(3): 483–502. https://doi.org/10.11646/zootaxa.4243.3.4

Santos É, Gomes Júnior EL, da Rocha CMC, Bartels PJ, Fontoura P (2018) A closer look at *Batillipes dicrocercus* and new records of *Batillipes potiguarensis* (Tardigrada: Arthrotardigrada) from the Brazilian coast with comments on intra- and interspecific variability. Iheringia, Série Zoologia 108: e2018041. https://doi.org/10.1590/1678-4766e2018041

Santos É, Rubal M, Veiga P, Bartels PJ, da Rocha CM, Fontoura P (2019a) On the distribution of *Batillipes tubernatis* Pollock, 1971 (Arthrotardigrada: Batillipedidae) in the Atlantic Basin. Marine Biodiversity 49(2): 621–631. https://doi.org/10.1007/s12526-017-0834-9

Santos É, Veiga P, Rubal M, Bartels PJ, da Rocha CMC, Fontoura P (2019b) *Batillipes pennaki* Marcus, 1946 (Tardigrada: Arthrotardigrada): deciphering a species complex. Zootaxa 4648 (3): 549–567. https://doi.org/10.11646/zootaxa.4648.3.9

Santos É, Gomes Júnior EL, Barros RC (2023) Tardigrada in Catálogo Taxonômico da Fauna do Brasil. PNUD, available online at: http://fauna.jbrj.gov.br/fauna/faunadobrasil/21 [Acessed: 28/07/2023]

Schill RO (2019) Water Bears: The Biology of Tardigrades. Springer International Publishing, 419 pp. https://doi.org/10.1007/978-3-319-95702-9

Schmidt P (1974) Interstitielle Fauna von Galapagos. IV. Gastrotricha. Mikrofauna Meeresbodens 26: 1–76.

Sørensen MV (2011) Kinorhyncha. In: Amaral ACZ, Nallin SAH (Eds) Biodiversidade e ecossistemas bentônicos marinhos do litoral norte do Estado de São Paulo. Instituto de Biologia, São Paulo, 106–110.

Sørensen MV (2013) Phylum Kinorhyncha. In: Zhang ZQ (Ed.) Animal biodiversity: an outline of higher-level classification and survey of taxonomic richness. Zootaxa 3703: 63–66. https://doi.org/10.11646/zootaxa.3703.1.13

Sørensen MV (2014) First account of echinoderid kinorhynchs from Brazil, with the description of three new species. Marine Biodiversity 44: 251–274. https://doi.org/10.1007/s12526-013-0181-4

Sørensen MV, Pardos F (2008) Kinorhynch systematics and biology – an introduction to the study of kinorhynchs, inclusive identification keys to the genera. Meiofauna Marina 16: 21–73.

Sørensen MV, Funch P, Willerslev E, Hansen AJ, Olesen J (2000) On the phylogeny of the Metazoa in the light of Cycliophora and Micrognathozoa. Zoologischer Anzeiger 239: 297–318.

Sørensen MV, Dal Zotto M, Rho HS, Herranz M, Sanchez N, Pardos F, Yamasaki H (2015) Phylogeny of Kinorhyncha, based on morphology and two molecular loci. Plos One 10: e0133440. https://doi.org/10.1371/journal.pone.0133440

Spallanzani L (1776) Il tardígrado, le anguilline delle tegole e quelle del grano rachitico. Opuscoli di Fisica Animale e Vegetabile 1(4): 524–556.

Spalding MD, Fox HE, Allen GR, Davidson N, Ferdaña ZA, Finlayson MAX, et al. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57(7): 573–583. https://doi.org/10.1641/B570707

Struck TH, Wey-Fabrizius AR, Golombek A, Hering L, Weigert A, Bleidorn C, et al. (2014) Platyzoan Paraphyly based on phylogenomic data supports a noncoelomate ancestry of Spiralia. Molecular Biology and Evolution 31(7): 1833–1849. https://doi.org/10.1093/molbev/msu143

Todaro MA (2012) A new marine gastrotrich from the State of São Paulo (Brazil), with a key to species of *Pseudos-*

tomella (Gastrotricha, Thaumastodermatidae). ZooKeys 223: 39–51. https://doi.org/10.3897/zookeys.223.3975

Todaro MA, Littlewood DTJ, Balsamo M, Herniou EA, Cassanelli S, Manicardi G, et al. (2003) The interrelationships of the Gastrotricha using nuclear small rRNA subunit sequence data, with an interpretation based on morphology. Zoologischer Anzeiger-A Journal of Comparative Zoology 242(2): 145–156. https://doi.org/10.1078/0044-5231-00093

Todaro MA, Rocha CE (2004) Diversity and distribution of marine Gastrotricha along the northern beaches of the State of São Paulo (Brazil), with description of a new species of *Macrodasys* (Macrodasyida, Macrodasyidae). Journal of Natural History 38: 1605–1634. https://doi.org/10.1080/0022293031000156169

Todaro MA, Rocha CE (2005) Further data on marine gastrotrichs from the State of São Paulo and the first records from the State of Rio de Janeiro (Brazil). Meiofauna Marina 14: 27–31.

Todaro MA, Telford MJ, Lockyer AE, Littlewood DTJ (2006) Interrelationships of the Gastrotricha and their place among the Metazoa inferred from 18S rRNA genes. Zoologica Scripta 35(3): 251–259. https://doi.org/10.1111/j.1463-6409.2006.00228.x

Todaro MA, Dal Zotto M, Jondelius U, Hochberg R, Hummon WD, Kånneby T, Rocha CE (2012) Gastrotricha: a marine sister for a freshwater puzzle. Plos One 7(2): e31740. https://doi.org/10.1371/journal.pone.0031740

Tyler S, Rieger GE (1980) Adhesive organs of the gastrotricha: I. Duo-gland organs. Zoomorphologie 95(1): 1–15.

Ugarte PDS, Suzuki LP, Cruvinel LG, Garraffoni ARS (2023) Georeferenced database and interactive online map of limnoterrestrial and freshwater Tardigrada from Central and South America. Biota Neotropica 23: e20231498. https://doi.org/10.1590/1676-0611-BN-2023-1498

von Daday E (1905) Süsswasser-Mikrofauna Paraguays. Untersuchungen über die Süsswasser Mikrofauna Paraguays. In: Chun C (Ed.) Zoologica. Vol. 44, 1–349.

Wallace RL, Ricci C, Melone G (1996) A cladistic analysis of pseudocoelomate (aschelminth) morphology. Invertebrate Biology 115(2): 104–112. https://doi.org/10.2307/3227041

Winnepenninckx B, Backelijau T, Mackey LY, Brooks JM, De Wachter R, Kumar S, Garey J (1995) 18S rRNA data indicate that aschelminthes are polyphyletic in origin and consist of at least three distinct clades. Molecular Biology and Evolution 12(6): 1132–1137. https://doi.org/10.1093/oxfordjournals.molbev.a040287

Wunderer J, Lengerer B, Pjeta R, Bertemes P, Kremser L, Lindner H, et al. (2019) A mechanism for temporary bioadhesion. Proceedings of the National Academy of Sciences 116(10): 4297–4306. https://doi.org/10.1073/pnas.1814230116

Yamasaki H, Hiruta SF, Kajihara H (2013) Molecular phylogeny of kinorhynchs. Molecular Phylogenetics and Evolution 67: 303–310. https://doi.org/10.1016/j.ympev.2013.02.016

Zelinka C (1896) Demonstration von Tafeln der Echinoderes- Monographie. Verhandlungen der deutschen Zoologischen Gesellschaft 6: 197–199.

Zelinka C (1907) Zur Kenntnis der Echinoderen. Zoologischer Anzeiger 32: 130–136.

Zelinka C (1928) Monographie der Echinodera. Wilhelm Engelmann, Leipzig, 369 pp.

Zrzavý J, Mihulka S, Kepka P, Bezděk A, Tietz D (1998) Phylogeny of the Metazoa based on morphological and 18S ribosomal DNA evidence. Cladistics 14(3): 249–285. https://doi.org/10.1111/j.1096-0031.1998.tb00338.x

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