

Tardigrades Research in Brazil: an overview and updated checklist

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Abstract. Tardigrades are microscopic animals, commonly referred to as “water bears”, and comprise the phylum Tardigrada. They are found in diverse habitats in terrestrial, freshwater and marine environments worldwide. In this paper, it is presented a brief history of the study of tardigrades in Brazil and an updated species checklist of Brazilian tardigrades. Since the first report in 1913, the number of tardigrades records has increased, reflecting advances in the understanding the diversity of tardigrades in Brazil. A total of 100 species known from Brazil are listed, being 30 in marine and 70 in terrestrial and freshwater environments. The records are concentrated in Southeast (47.1%) and Northeast (41.3%) regions. Despite the advances, further research and sampling of new areas is still needed, besides reanalysis and confirmation of old records. Brazil, with its vast territory, extensive continental shelf and great diversity of biomes, has great potential to expand our knowledge of tardigrades fauna.

Key-Words. Eutardigrada; Heterotardigrada; Tardigrada; Exploration history.

Resumo. Tardígrados, também conhecidos como “ursos d’água”, são animais microscópicos que compõem o filo Tardigrada. São encontrados em diversos habitats de ambientes terrestres, de água doce e marinha. Uma breve história do estudo dos tardígrados no Brasil é apresentada, bem como a lista atualizada de espécies de tardígrados brasileiros. Desde o primeiro relato em 1913, o número de registros de tardígrados aumentou, refletindo os avanços no entendimento da diversidade brasileira de tardígrados. São listadas 100 espécies conhecidas para o Brasil, sendo 30 em ambientes marinhos e 70 em ambientes terrestres e de água doce. Os registros estão concentrados nas regiões Sudeste (47,1%) e Nordeste (41,3%). Apesar dos avanços, ainda são necessárias mais pesquisas e amostragens de novas áreas, além da reanálise e confirmação dos registros antigos. O Brasil, com seu vasto território, extensa plataforma continental e grande diversidade de biomas, tem um grande potencial para expandir nosso conhecimento sobre a fauna de tardígrados.

Palavras-Chave. Eutardigrada; Heterotardigrada; Tardigrada; História de exploração.

INTRODUCTION

Tardigrades are microscopic Ecdysozoans (Aguinaldo *et al.*, 1997), with 0.5 mm to 1.2 mm in length (excluding the last pair of legs), four pairs of locomotor appendages (lobopodous), generally ending with claws of varying numbers and shapes (Ramazzotti & Maucci, 1983). These animals are commonly referred to as “water bears” due to their bear-like appearance (legs with claws), and slow lumbering gait (Nelson *et al.*, 2015).

Since the first observation in 1773, 1,298 species of tardigrades (142 genera and 30 families) have been described, including two fossils species (Degma *et al.*, 2019). Two classes and four orders were accepted in the Tardigrada phylum. Eutardigrada constituted by Apochela and Parachela, and Heterotardigrada constituted by

Echiniscoidea and Arthrotardigrada (Jørgensen *et al.*, 2018). A third class, Mesotardigrada, was established by Rahm in 1937 based on the description of *Thermozodium esakii* Rahm, 1937 from a Japanese hot spring (Nelson *et al.*, 2015). However, the type material was lost, so Mesotardigrada is considered *nomen dubium* until new evidence is found (Grothman *et al.*, 2017). Recently, based on molecular data, Guil *et al.* (2019) proposed the creation of a new class, Apotardigrada, constituted by order Apochela, and consequently suppression of order Parachela and its superfamilies erected as orders (Fig. 1).

The tardigrades occupy a variety of habitats; they can be found in marine, freshwater, and terrestrial environments worldwide (Nelson, 2002). Heterotardigrada, with few exceptions, encompasses marine tardigrades that inhabit the inter-

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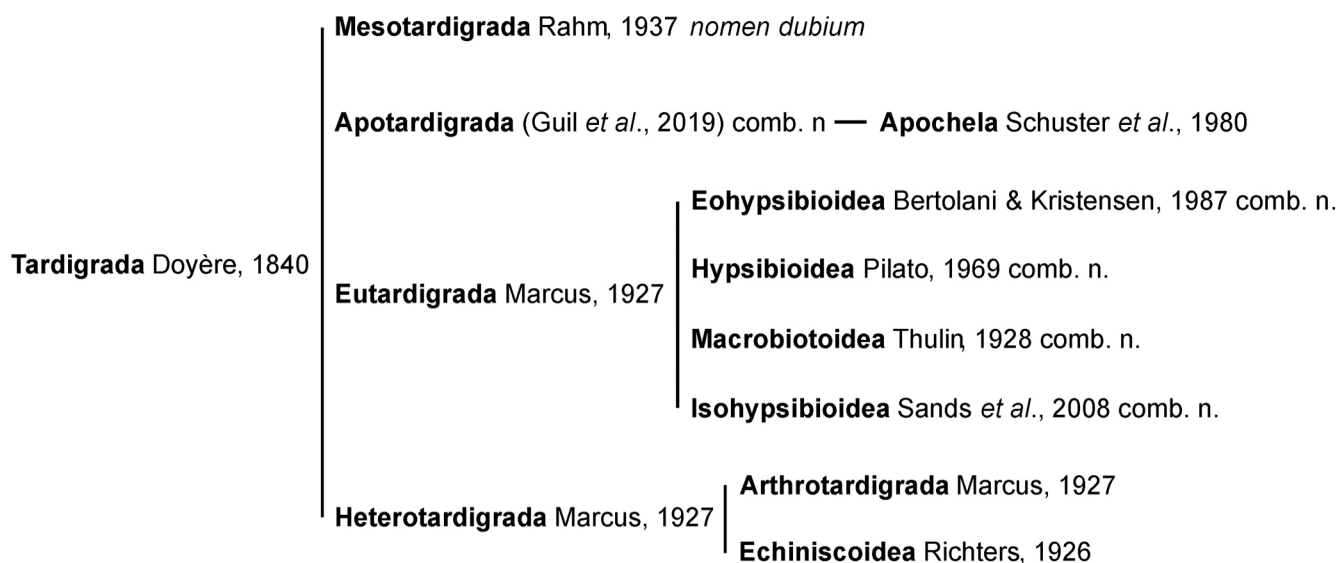


Figure 1. Systematics of Tardigrada according to proposal of Guil *et al.*, 2019.

tidal zone and shallow waters of the continental shelf as well as the deep-sea benthic sediments. On the other hand, Eutardigrada, and the new class Apotardigrada, mainly contain both terrestrial and freshwater species (Nelson *et al.*, 2015; Guil *et al.*, 2019).

In Brazil, however, tardigrades are still poorly known; there are about 80 taxa recorded in eight Brazilian states: Ceará, Pernambuco, Rio Grande do Norte, Minas Gerais, São Paulo, Rio de Janeiro, Rio Grande do Sul and Paraná (Gomes Júnior, 2015). The little information about the tardigrades fauna and their distribution in Brazilian regions are mainly a result of a scarcity of specialists and of taxonomic studies about the group. It is necessary to promote further studies and stimulate younger biologists to dedicate themselves to the study of the tardigrades in Brazil. To start this, it seems useful to remember the efforts made in the past and to know the current state-of-the-art, including the species already known. Thus, this paper presents a brief history of the study of tardigrades in Brazil and provides an updated species checklist of Brazilian tardigrades.

On tardigrades research In Brazil

The first work to report a tardigrade species in Brazil dates back to the early twentieth century, when the Scottish naturalist James Murray recorded the occurrence of *Macrobotus occidentalis* Murray, 1910; however, without specifying the Brazilian location (Murray, 1913). It was almost two decades after that new records of tardigrades were made. In 1931, the German zoologist Gilbert (Franz) Rahm reported the occurrence of the limnoterrestrial (non-marine) species *Echiniscus blumi* Richters, 1903, *Echiniscus testudo trifilis* (Doyère, 1840), *Macrobotus ambiguus* Murray, 1907, *Milnesium tardigradum trispinosum* Doyère, 1840, *Hypsibius alpinus* Murray, 1906 and *Hypsibius oberhauseri* Doyère, 1840 in bromeliad and mosses from São Paulo; *Echiniscus arc-tomys* Ehrenberg, 1853 in mosses from Rio de Janeiro;

Pseudechiniscus bispinosus Murray, 1907 in mosses from Pernambuco; *Macrobotus echinogenitus* Richters, 1903 and *Macrobotus hufelandi* Schultze, 1834 in mosses from Pernambuco and São Paulo; *Milnesium tardigradum* Doyère, 1840 in mosses from Pernambuco, Rio de Janeiro and São Paulo (Rahm, 1931). In the next year, Rahm added *Pseudechiniscus suillus papillata* Ehrenberg, 1853 (mosses from Rio de Janeiro) in the previous list and dated the record of *Milnesium tardigradum* in Pernambuco state from 1928 (Rahm, 1932).

The German naturalist couple Ernest Gustav Gotthelf Marcus and Eveline du Bois-Reymond Marcus were the first researchers to study tardigrades in a Brazilian institution. In 1936, Marcus and his wife left Berlin to live in São Paulo, as Ernest Marcus had accepted an invitation to head the Zoology Department at the University of São Paulo, from 1936 to 1963 (Corrêa, 1991; Edmunds, 1991; USP, 2019). Eveline and Ernest Marcus received Brazilian citizenships in 1940 and never again left the country (Corrêa, 1991). Together, Eveline and Ernest Marcus published over 280 papers on varied taxonomic groups (Sawaya, 1970; Corrêa, 1991), 27 of them on anatomy, histology, physiology, embryology, ecology, and systematics of tardigrades. Some articles published in São Paulo were written in Portuguese, as a way of honoring Brazil (Mendes, 1994); these included important works as "Sôbre a anabiose dos Tardigrados, com descrição duma nova especie" (Marcus, 1937), and "Sobre Tardígrados Brasileiros" (du Bois-Reymond Marcus, 1944). Eveline and Ernest Marcus described several new species of tardigrades, such as *Macrobotus sawayai* Marcus, 1937 (Marcus, 1937), *Batillipes pennaki* Marcus, 1946 (Marcus, 1946), and *Orzeliscus belopus* du Bois-Reymond Marcus, 1952 (du Bois-Reymond Marcus, 1952); they were the pioneers in the study of marine tardigrades on the Brazilian coast.

At the same time as Eveline and Ernest Marcus, Rosina de Barros was the first Brazilian researcher to dedicate herself to the study of tardigrades. Before joining geneticist Andre Dreyfus's team in 1943 (Formiga, 2010),

Barros had already published important works on the taxonomy of tardigrades, paying special attention to the state of São Paulo. Between 1938 and 1943, Barros released substantial papers (see Barros 1938, 1939a, b, 1942a, b, 1943), providing a profound basis for subsequent studies. The papers of Barros are the milestone in the Brazilian tardigradology. Barros described one genus, eight species, and four subspecies (Assunção, 1999b), including *Macrobotus evelinae* Barros, 1938 (Barros, 1938), *Macrobotus hibiscus* Barros, 1942 (Barros, 1942b), *Macrobotus primitivae* Barros, 1942 (Barros, 1942b), *Itaquascon umbellinae* Barros, 1939 (Barros, 1939a), and *Pseudobiotus juanita* Barros, 1939 (Barros, 1939b). The works of Ernest and Eveline Marcus, and Rosina de Barros represent the birth of Brazilian tardigradology.

Samples collected from Manaus, in the Amazon region, in September 1966 contained *Paramacrobotus richtersi* (Murray, 1911) (Iharos, 1969). Höfling-Epiphanió (1972) registered *Batillipes mirus* Richters, 1909, and *Batillipes tubernatis* Pollock, 1971 on the São Paulo coast. Renaud-Mornant described one new species, *Tanarctus heterodactylus* Renaud-Mornant, 1980, and two new genera, *Chrysoarctus* Renaud-Mornant, 1984, and *Opydorscus* Renaud-Mornant, 1989, from the continental shelf of Brazil (Renaud-Mornant 1980, 1984, 1989). Two new species were described from the Iguazu falls (state of Paraná), *Isohypsibius sabellai* Pilato, Binda, Napolitano & Moncada, 2004 (Pilato *et al.*, 2004), and *Paramacrobotus centesimus* (Pilato, 2000) (Pilato, 2000). Other contributions were made from different laboratory techniques, including the collection and fixation of marine and freshwater tardigrades (Corrêa, 1987), laboratory culture methods of limnoterrestrial tardigrades (Pulschen & Meneghin, 2010) and protocols for processing tardigrades samples for scanning electron microscopy analysis (Gomes Júnior & Rocha, 2015).

Using morphological data, the biologist Cláudia Maria Leite Assunção was the first Brazilian researcher to explore the tardigrades phylogeny. In her PhD thesis, Assunção investigated the relationship between the subgroups Stygarctidae and Digitopoda, resulting in the establishment of Stygarctidae as a monophyletic taxon, and Digitopoda was branched into two clades (Assunção, 1994, 2001). The biologist Clélia Márcia Cavalcanti da Rocha maintains a research group on the systematics and ecology of tardigrades, working mainly with marine tardigrades of the northeastern coast of Brazil (Rocha, 2018). Recently, her group described the new species *Ligiarctus alatus* Gomes Júnior, Santos, da Rocha, Santos & Fontoura, 2018 (Gomes Júnior *et al.*, 2018), and three new *Batillipes* species from the Brazilian coast: *Batillipes dandarae* Santos, Rocha, Gomes Jr. & Fontoura, 2017; *Batillipes potiguarensis* Santos, Rocha, Gomes Jr. & Fontoura, 2017; and *Batillipes brasiliensis* Santos, Rocha, Gomes Jr. & Fontoura, 2017 (Santos *et al.*, 2017). Rocha also organized the first tardigrades scientific collection in Brazil (Rocha, 2018). Since 2017, the biologist André Rinaldo Senna Garraffoni has been developing a project that intends to redescribe all species with missing type material, whose type locality is in the state of São Paulo,

thus increasing the number of nuclear (18S and 28S) and mitochondrial (COI) gene sequences of the Brazilian tardigrades species deposited in Genbank (Garraffoni, 2019).

Until the late twentieth century, the tardigrades were sporadically studied in Brazil. However, despite of historical gaps, the future of tardigrades research in Brazil seems promising. The presence of researchers interested on tardigrades in the different regions of Brazil (Northeast, Southeast and South), the training of new researchers (e.g., Edivaldo Lima Gomes Júnior, Érika Santos, Mônica Marinho Verçosa, and Paola Visnardi Fassina), the increasing of Brazilian tardigrades records and the recent description of new species from Brazilian specimens, are pointing to new horizons. On the other hand, to strengthening the Brazilian tardigradology, it would be interesting the establishment of a cooperation network among Brazilian tardigrades researchers, in order to ensure the exchange of information and expertise.

On tardigrades diversity in Brazil

There are four relevant species surveys of tardigrades in Brazil: Assunção (1999a, b) listed six marine and 58 limnoterrestrial species for the state of São Paulo; Rocha *et al.* (2013) listed 27 marine species for the Brazilian coast; Gomes Júnior (2015) listed 80 tardigrades species, both marine and limnoterrestrial, and Rocha *et al.* (2016) updated the Brazilian limnoterrestrial checklist to 62 taxa. In the present update, the number of tardigrades records in marine environment increased to 30 (Table 1) and to 70 in terrestrial and freshwater environments (Table 2). There are fewer studies on freshwater and marine species compared to terrestrial species, and the major samples investigated were sediment (mud, sand and gravel) to marine, and mosses to limnoterrestrial tardigrades. Compared to Gomes Júnior's (2015) checklist, it was not found any record on tardigrade species in the state of Rio Grande do Sul. On the other hand, it was found one record in the state of Amazonas and new records in the state of Alagoas. The records are concentrated in Southeast (47.1%) and Northeast regions (41.3%) and reflect the historical construction of the Brazilian tardigradology and, consequently, the distribution of researchers (Fig. 2).

This sampling effort represents minimal due to the extensive continental dimension of Brazil. According to Kaczmarek *et al.* (2015a) over 65% of the Brazilian terrestrial area is undocumented. However, if we take into account the geographic extension of the country (8.511 million km²), the territorial sea (3.6 million km²), the richness of habitats and variety of Brazilian biomes, the percentage should be much higher, perhaps over 99%. In other words, the vast Brazilian territory virtually remains unexplored with respect to tardigrades.

While recognizing the advances in understanding biodiversity of Brazilian tardigrades in the last years, further research and sampling of new areas is still needed, particularly in those states not yet sampled. Old records,

Table 1. Marine tardigrades recorded in Brazilian coast.

Taxon	State	Substratum	Taxon	State	Substratum
<i>Actinarctus doryphorus doryphorus</i>	CE, RN	gravel, sand	<i>Halechiniscus perfectus</i>	PE, RN	sand
<i>Archechiniscus marci</i>	CE, RN	sand, mud	<i>Halechiniscus tuleari</i>	PE	gravel
<i>Angursa lingua</i>	CE, RN	sand, mud	<i>Ligiarctus alatus</i>	RN	sand
<i>Batillipes annulatus</i>	CE, PE	sand	<i>Mesostygarctus intermedius</i>	CE, PE, RN	sand, mud
<i>Batillipes brasiliensis</i>	AL	gravel, sand	<i>Neoarctus</i> sp.	CE, RN	mud
<i>Batillipes dandarae</i>	AL	sand	<i>Neostygarctus</i> sp.	CE, RN	mud
<i>Batillipes dicrocercus</i>	CE, PE	sand	<i>Opydorscus fonsecae</i>	CE, PE, RN	sand, mud
<i>Batillipes lesteri</i>	CE, PE, RN	sand	<i>Orzeliscus belopus</i>	AL, CE, PE, RN, SP	sand, mud
<i>Batillipes mirus</i>	SP	sand	<i>Parastygarctus sterreri</i>	CE, PE, RN	sand, mud
<i>Batillipes pennaki</i>	AL, CE, PE, RJ, SP	sand, mud, sea water	<i>Raiarctus aureolatus</i>	CE, RN	sand, mud
<i>Batillipes potiguarensis</i>	RJ, RN	gravel, sand	<i>Stygarctus bradyus</i>	PE	sand
<i>Chrysoarctus briandi</i>	CE, RJ, RN	sand, mud	<i>Tanarctus dendriticus</i>	CE, RN	mud
<i>Dipodarctus subterraneus</i>	PE	macroalgae (<i>Halimeda opuntia</i>)	<i>Tanarctus heterodactylus</i>	CE, PE, RJ, RN	gravel, sand, mud
<i>Echiniscoides sigismundi sigismundi</i>	SP	barnacles	<i>Tanarctus velatus</i>	CE, RN	sand, mud
<i>Florarctus hulingsi</i>	CE, RN	gravel, sand	<i>Wingstrandarctus intermedius</i>	CE, PE	macroalgae (<i>Halimeda opuntia</i>)

AL = Alagoas; CE = Ceará; PE = Pernambuco; RJ = Rio de Janeiro; RN = Rio Grande do Norte; SP = São Paulo.

Table 2. Limnoterrestrial tardigrades recorded in Brazil.

Species	State	Substratum	Species	State	Substratum
<i>Adropion scoticum scoticum</i>	SP	mosses, aquatic plants	<i>Macrobotus psephus</i>	SP	unknown
<i>Bryochœrus intermedius intermedius</i>	SP	mosses	<i>Macrobotus sawayai</i>	SP	mosses
<i>Bryodelphax alzirae</i>	SP	mosses, aquatic plants	<i>Mesobiotus coronatus</i>	SP	unknown
<i>Bryodelphax parvulus</i>	SP	mosses	<i>Mesobiotus furciger</i>	SP	unknown
<i>Dactylobiotus ambiguus</i>	SP	bromeliads	<i>Mesobiotus harmsworthi</i>	PE, PR, SP	mosses, aquatic plants
<i>Dianea papillifera</i>	SP	mosses, aquatic plants	<i>Mesobiotus orcadensis</i>	SP	unknown
<i>Diphascon alpinum</i>	SP	mosses	<i>Mesobiotus stellaris</i>	SP	unknown
<i>Diphascon pingue pingue</i>	SP	mosses, aquatic plants	<i>Milnesium tardigradum tardigradum</i>	PE, PR, RJ, SP	mosses, algae
<i>Doryphoribius evelinae</i>	MG, RJ, SP	mosses, aquatic plants	<i>Milnesium tardigradum trispinosa</i>	SP	mosses
<i>Doryphoribius flavus</i>	PE	mosses	<i>Minibiotus acontistus</i>	SP	unknown
<i>Echiniscus arctomys</i>	RJ	mosses, algae	<i>Minibiotus aculeatus</i>	PE	mosses
<i>Echiniscus blumi blumi</i>	SP	mosses	<i>Minibiotus intermedius</i>	PR, SP	mosses, aquatic plants
<i>Echiniscus crassispinosus crassispinosus</i>	PR, SP	mosses, aquatic plants	<i>Minibiotus julietae</i>	SP	unknown
<i>Echiniscus crassispinosus fasciatus</i>	PR, SP	mosses, aquatic plants	<i>Minibiotus marcusii</i>	SP	unknown
<i>Echiniscus dreyfusi</i>	SP	mosses	<i>Mopsechiniscus imberbis</i>	SP	unknown
<i>Echiniscus duboisi</i>	SP	mosses	<i>Mopsechiniscus schusteri</i>	Unknown	unknown
<i>Echiniscus evelinae</i>	PR, SP	mosses, aquatic plants	<i>Murrayon pullari</i>	SP	aquatic plants
<i>Echiniscus spiniger</i>	SP	mosses, aquatic plants	<i>Nebularmis phocae</i>	SP	mosses, aquatic plants
<i>Echiniscus tenuis</i>	SP	mosses, aquatic plants	<i>Paramacrobotus (Amicrobiotus) cf. areolatus</i>	PR	mosses
<i>Echiniscus testudo</i>	SP	mosses	<i>Paramacrobotus (Amicrobiotus) centesimus</i>	PR	mosses
<i>Fractonotus verrucosus</i>	SP	mosses, aquatic plants	<i>Paramacrobotus (Paramacrobotus) richtersi</i>	AM, PR, SP	leaf litter, mosses, aquatic plants, bromeliads
<i>Grevenius granulifer</i>	SP	unknown	<i>Pseudobiotus megalonyx</i>	SP	mosses, aquatic plants
<i>Grevenius myrops</i>	PR, SP	aquatic plants	<i>Pseudechiniscus bispinosus</i>	PE	mosses
<i>Hypsibius convergens</i>	SP	mosses, aquatic plants	<i>Pseudechiniscus facetialis</i>	Unknown	unknown
<i>Hypsibius microps</i>	SP	unknown	<i>Pseudechiniscus juanita</i>	SP	mosses
<i>Isahypsibius sabellai</i>	PR	mosses	<i>Pseudechiniscus novaezeelandiae novaezeelandiae</i>	PR, SP	mosses, aquatic plants
<i>Itaquascon umbellinae</i>	SP	mosses	<i>Pseudechiniscus novaezeelandiae aspinosa</i>	PE, PR, SP	unknown
<i>Macrobotus echinogenitus</i>	PE, SP	mosses	<i>Pseudechiniscus novaezeelandiae marinae</i>	SP	mosses, aquatic plants
<i>Macrobotus evelinae</i>	SP	mosses	<i>Pseudechiniscus suillus</i>	PR, RJ, SP	mosses, algae, aquatic plants
<i>Macrobotus furcatus</i>	SP	mosses, aquatic plants	<i>Ramazzottius oberhaeuseri</i>	RJ, SP	mosses, aquatic plants
<i>Macrobotus hibiscus</i>	SP	unknown	<i>Testechiniscus macronyx</i>	SP	mosses
<i>Macrobotus hufelandi</i>	PE, SP	mosses, aquatic plants	<i>Thulinus augusti</i>	SP	unknown
<i>Macrobotus occidentalis occidentalis</i>	PR	unknown	<i>Ursulinus nodosus</i>	SP	mosses, aquatic plants
<i>Macrobotus polyopus</i>	SP	unknown	<i>Viridiscus rufoviridis</i>	SP	mosses, aquatic plants
<i>Macrobotus primitivae</i>	PR, SP	mosses, aquatic plants	<i>Viridiscus viridis</i>	PR, SP	mosses, lichens

AM = Amazonas; MG = Minas Gerais; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; SP = São Paulo.

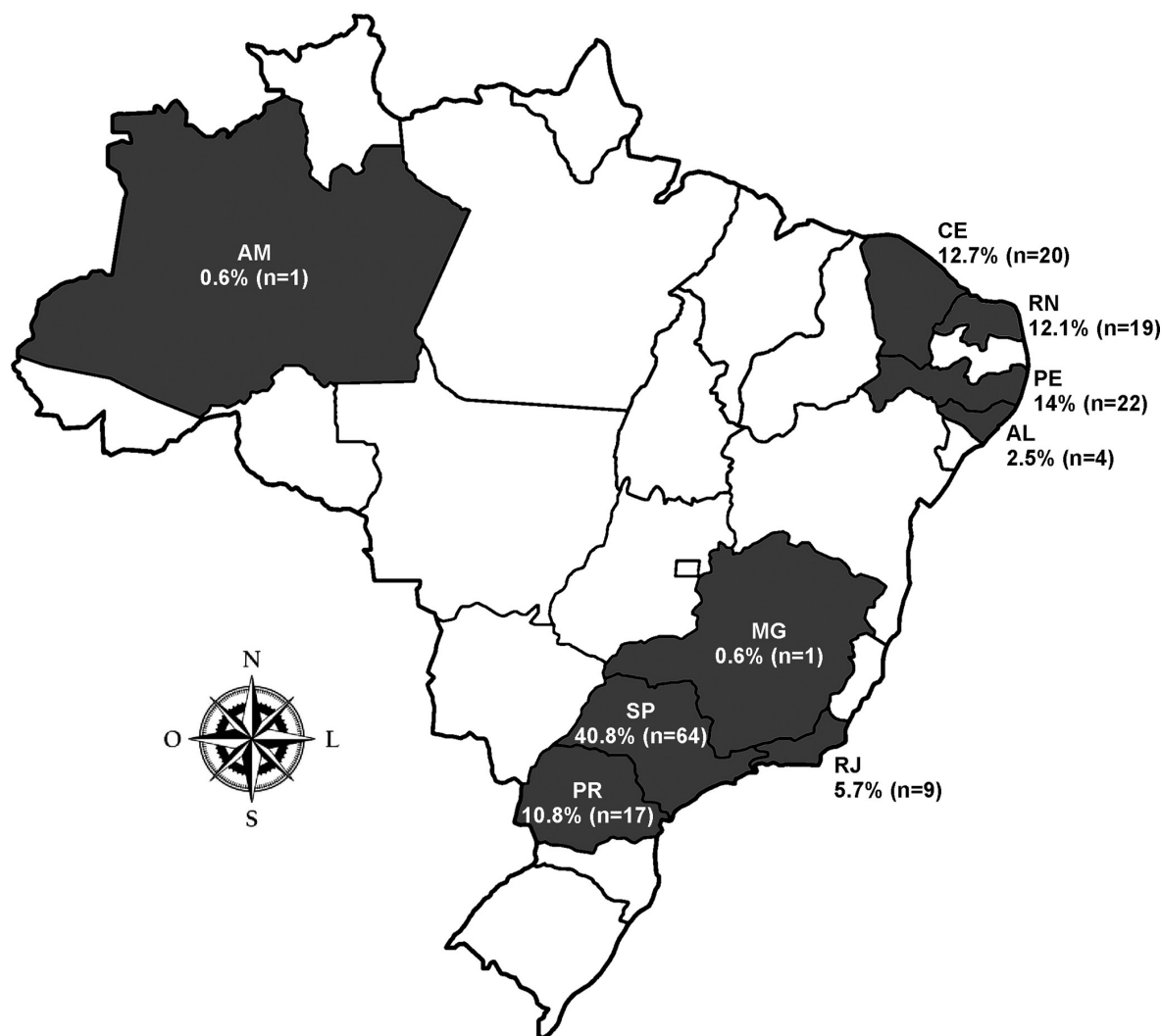


Figure 2. Brazilian records of tardigrades according the distribution frequency.

especially those that appeared only once, need to be confirmed with new specimens. Brazil, with its vast territory, extensive continental shelf and great diversity of biomes, has great potential to expand our knowledge of both marine and limnoterrestrial tardigrades fauna. Twenty-six tardigrade species (8 marine, 18 limnoterrestrial) have so far been originally described in Brazil, exhibiting this potentiality.

MATERIAL AND METHODS

Tardigrade species found in Brazil, according to the most recent classification (Degma *et al.*, 2019), are shown in the following checklist. References are reported within parentheses '()'. The species written in bold characters have Brazil as their type-locality. One species was invalidated, *Echiniscus fischeri* Richters, 1911 (Rocha *et al.*, 2016), and 24 species were reallocated (for details, see species checklist). According to Santos *et al.* (2018b), the specimens from Brazil were wrongly identified for the species *Batillipes tubernatis*, so the previous records from the Pernambuco coast (Rocha *et al.*, 2009) and São Paulo coast (Höfling-Epiphanyo, 1972) do not belong to this

species. For this reason, *Batillipes tubernatis* was left out of this Brazilian tardigrades checklist. On the other hand, although *Macrobotus sawayai* Marcus, 1937 has been omitted from modern taxonomic literature and requires redescription (Kaczmarek *et al.*, 2015a), it was kept on the checklist once its distribution is restricted to Brazil. Two new records from state of Paraná were included by the author: *Paramacrobotus (Amicrobotus) cf. areolatus* (Murray, 1907) sampled in mosses from Curitiba, and *Viridiscus viridis* (Murray, 1910) in lichens from Vila Velha state Park, Ponta Grossa (unpublished).

RESULTS

Phylum Tardigrada Doyère, 1840

Class Apotardigrada Guil, Jørgensen & Kristensen, 2019

Order Apochela Schuster, Nelson, Grigarick & Christenberry, 1980

Family Milnesiidae Ramazzotti, 1962

Milnesium tardigradum tardigradum Doyère, 1840 (Rahm, 1931, 1932; Marcus, 1936, 1939; Barros, 1943; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção,

1999b; Pulschen & Meneghin, 2010; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Milnesium tardigradum trispinosa Rahm, 1931 (Rahm, 1931, 1932; Marcus, 1939; Ramazzotti & Maucci, 1983; McInnes, 1994; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). *nomen dubium* according to Morek *et al.* (2016); not valid according to Suzuki (2016).

Class Eutardigrada Richters, 1926

Order Hypsibioidea Guil, Jørgensen & Kristensen, 2019

Family Hypsibiidae Pilato, 1969

Adropion scoticum scoticum (Murray, 1905) (Barros, 1943; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Subgenus *Adropion* of the genus *Diphascon* raised to genus level by Bertolani *et al.* (2014).

Diphascon alpinum Murray, 1906 (Rahm, 1931, 1932; Marcus, 1936, 1939; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Diphascon pingue pingue (Marcus, 1936) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Hypsibius convergens (Urbanowicz, 1925) (Barros, 1943; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Hypsibius microps Thulin, 1928 (Barros, 1943; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Itaquascon umbellinae Barros, 1939 (Barros, 1939a; Ramazzotti & Maucci, 1983; Kaczmarek *et al.*, 2015a). Found in mosses, in Itaquaquecetuba and sampled by Berta and Ruth Lange de Morretes.

Family Ramazzottiidae Sands, McInnes, Marley, Goodall-Copestake, Convey & Linse, 2008

Ramazzottius oberhaeuseri (Doyère, 1840) (Rahm, 1931, 1932; Marcus, 1936; Barros, 1943; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Order Isohypsibioidea Guil, Jørgensen & Kristensen, 2019

Family Doryphoribiidae Gąsiorek, Stec, Morek & Michalczyk, 2019

Doryphoribius evelinae (Marcus, 1928) (Marcus, 1936, 1939; Barros, 1943; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Doryphoribius flavus (Iharos, 1966) (Rocha *et al.*, 2016).

Grevenius granulifer (Thulin, 1928) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes,

1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Isohypsibius* by Gąsiorek *et al.* (2019c).

***Grevenius myrops* (du Bois-Reymond Marcus, 1944)** (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in the state of São Paulo, in aquariums of the Department of Zoology – USP, and in a stream in Santo Amaro; and in the state of Paraná, Curitiba, among aquatic plants. Transferred from *Isohypsibius* by Gąsiorek *et al.* (2019c).

Pseudobiotus megalonyx (Thulin, 1928) (du Bois-Reymond Marcus, 1944; Kaczmarek *et al.*, 2015a).

Thulinus augusti (Murray, 1907) (du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Rocha *et al.*, 2016). Transferred from *Isohypsibius* by Bertolani (2003).

Family Isohypsibiidae Sands, McInnes, Marley, Goodall-Copestake, Convey & Linse, 2008

Dianea papillifera (Murray, 1905) (Barros, 1943; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Isohypsibius* by Gąsiorek *et al.* (2019c).

Fractonotus verrucosus (Richters, 1900) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Calohypsibius* by Gąsiorek *et al.* (2019a).

***Isohypsibius sabellai* Pilato, Binda, Napolitano & Moncada, 2004** (Pilato *et al.*, 2004; Meyer, 2013; Kaczmarek *et al.*, 2015a). Found in Iguazu falls, state of Paraná, in a moss sample.

Ursulinus nodosus (Murray, 1907) (Marcus, 1936, 1939; Barros, 1943; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Isohypsibius* by Gąsiorek *et al.* (2019c).

Order Macrobiotioidea Guil, Jørgensen & Kristensen, 2019

Family Macrobiotidae Thulin, 1928

Macrobiotus echinogenitus Richters, 1903 (Rahm, 1931, 1932; Marcus, 1936, 1939; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

***Macrobiotus evelinae* Barros, 1938** (Barros, 1938; Marcus, 1939; Ramazzotti & Maucci, 1983; McInnes, 1994; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Capivarí, Campos de Jordão, in mosses on trees collected by Juanita Fortlage.

Macrobiotus furcatus Ehrenberg, 1859 (Barros, 1942b; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Re-transferred from *Minibiotus* by Bertolani *et al.* (2014).

- Macrobotus hibiscus** Barros, 1942 (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Casa Branca, countryside of São Paulo.
- Macrobotus hufelandi** Schultze, 1834 (Rahm, 1931, 1932; Marcus, 1939; Barros, 1942b; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Pulschen & Meneghin, 2010; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Macrobotus occidentalis occidentalis** Murray, 1910 (Murray, 1913; Marcus, 1936, 1939; du Bois-Reymond Marcus, 1944; McInnes, 1994; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Macrobotus polyopus** Marcus, 1928 (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Macrobotus primitivae** Barros, 1942 (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Eldorado, state of São Paulo.
- Macrobotus psephus** du Bois-Reymond Marcus, 1944 (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Macrobotus sawayai** Marcus, 1937 (Marcus, 1937; Assunção, 1999b; Kaczmarek *et al.*, 2015a). Found in Pacaembu, state of São Paulo, in mosses on trees.
- Mesobiotus coronatus** (Barros, 1942) (Barros, 1942b; McInnes, 1994; Assunção, 1999b; Pilato *et al.*, 2004; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in the city of Itapetininga. Transferred from *Macrobotus* by Vecchi *et al.* (2016).
- Mesobiotus furciger** (Murray, 1907) (Rocha *et al.*, 2016). Transferred from *Macrobotus* by Vecchi *et al.* (2016).
- Mesobiotus harmsworthi** (Murray, 1907) (Marcus, 1939; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Macrobotus* by Vecchi *et al.* (2016).
- Mesobiotus orcadensis** (Murray, 1907) (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Macrobotus* by Vecchi *et al.* (2016).
- Mesobiotus stellaris** (du Bois-Reymond Marcus, 1944) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Campos do Jordão, state of São Paulo. Transferred from *Macrobotus* by Vecchi *et al.* (2016).
- Minibiotus acontistus** (Barros, 1942) (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a). Found in the city of Serra Negra. Transferred from *Macrobotus* by Guidetti *et al.* (2007).
- Minibiotus aculeatus** (Murray, 1910) (Rocha *et al.*, 2016).
- Minibiotus intermedius** (Plate, 1888) (Barros, 1942b; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Minibiotus julietae** (Barros, 1942) (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Juqueri and Osasco cities, state of São Paulo. Transferred from *Macrobotus* by Guidetti *et al.* (2007).
- Minibiotus marcusii** (Barros, 1942) (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found near Santo Amaro, state of São Paulo. Transferred from *Macrobotus* by Guidetti *et al.* (2007).
- Paramacrobotus (Amicrobiotus) cf. areolatus** (Murray, 1907). Unpublished. Collected by the author in mosses from Curitiba, Paraná. Transferred from *Macrobotus* by Guidetti *et al.* (2009).
- Paramacrobotus (Amicrobiotus) centesimus** (Pilato, 2000) (Pilato, 2000; Meyer, 2013; Kaczmarek *et al.*, 2015a). Found in Iguazu falls, state of Paraná, in a moss sample. Transferred from *Macrobotus* by Guidetti *et al.* (2009).
- Paramacrobotus (Paramacrobotus) richtersi** (Murray, 1911) (Marcus, 1939; Barros, 1942b; du Bois-Reymond Marcus, 1944; Iharos, 1969; Kaczmarek *et al.*, 2015a). Transferred from *Macrobotus* by Guidetti *et al.* (2019).
- Family Murrayidae Guidetti, Rebecchi & Bertolani, 2000**
- Dactylobiotus ambiguus** (Murray, 1907) (Rahm, 1931, 1932; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Murrayon pullari** (Murray, 1907) (du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Class Heterotardigrada Marcus, 1927**
Order Arthrotardigrada Marcus, 1927
Family Archechiniscidae Binda, 1978
- Archechiniscus marci** Schulz, 1953 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).
- Family Batillipedidae Ramazzotti, 1962**
- Batillipes annulatus** Zio, 1962 (Rocha *et al.*, 2009, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).
- Batillipes brasiliensis** Santos, Rocha, Gomes Jr. & Fontoura, 2017 (Santos *et al.*, 2017). Found in shallow sublittoral medium to coarse, gravels and quartz sands, in low energy (Sossego Beach) and estuarine beaches (Forte Orange Beach and Gunga Beach), and in reef pools of high energy beaches (Amor Beach).
- Batillipes dandaræ** Santos, Rocha, Gomes Jr. & Fontoura, 2017 (Santos *et al.*, 2017). Mainly found in shallow sublittoral fine to medium calcareous and

quartz sands in low energy and estuarine beaches as Gunga Beach and Forte Orange Beach and occasionally in high energy beaches (Ponta do Sal) and in reef pools as in Patacho Beach.

Batillipes dicrocercus Pollock, 1970 (Rocha *et al.*, 2009, 2013; Miller & Perry, 2016).

Batillipes lesteri Kristensen & Mackness, 2000 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Batillipes mirus Richters, 1909 (Höfling-Epiphany, 1972; Assunção, 1999a; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Batillipes pennaki Marcus, 1946 (Marcus, 1946; Ramazzotti & Maucci, 1983; Assunção, 1999a; Victor-Castro *et al.*, 1999; Rocha *et al.*, 2000, 2004, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016; Santos *et al.*, 2017). Found in sand and sea water from Ipanema Beach, state of Rio de Janeiro. Collected by Tanea Kristina S. Björnberg in 1946.

Batillipes potiguarensis Santos, Rocha, Gomes Jr. & Fontoura, 2017 (Santos *et al.*, 2017; Santos *et al.*, 2018a). Found in shallow sublittoral medium to coarse gravels and quartz sands, in reef pools of high energy beaches (Amor Beach) and low energy beaches (Francês Beach).

Family Halechiniscidae Thulin, 1928

Chrysoarctus briandi Renaud-Mornant, 1984 (Renaud-Mornant, 1984; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Dipodarctus subterraneus (Renaud-Debyser, 1959) (Rocha *et al.*, 2009, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Florarctus hulingsi Renaud-Mornant, 1976 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Halechiniscus perfectus Schulz, 1955 (Moura *et al.*, 2009; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Halechiniscus tuleari Renaud-Mornant, 1979 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Ligiarctus alatus Gomes Júnior, Santos, da Rocha, Santos & Fontoura, 2018 (Gomes Júnior *et al.*, 2018). Found in Potiguar Basin, state of Rio Grande do Norte, at 150 m below the sea level in bioclastic and litoclastic sand.

Opydorscus fonsecae Renaud-Mornant, 1989 (Renaud-Mornant, 1989; Assunção, 1999a; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016). Found in continental shelf of Fortaleza, state of Ceará, depth 40 m, in fine sediments, sandy-muddy.

Orzeliscus belopus du Bois Raymond-Marcus, 1952 (du Bois-Reymond Marcus, 1952; Ramazzotti & Maucci, 1983; Assunção, 1999a; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016; Santos *et al.*, 2017). Found in the coast of Island of São Sebastião, near Ilhabela, state of São Paulo, in 3-5 depth, sand with rather much detritus.

Wingstrandarctus intermedius (Renaud-Mornant, 1967) (Rocha *et al.*, 2009, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Family Neoarctidae (Grimaldi de Zio, D'Addabbo Gallo & Morone De Lucia, 1992)

Neoarctus sp. (Rocha *et al.*, 2013; Miller & Perry, 2016).

Family Neostygarctidae de Zio Grimaldi, D'Addabbo Gallo & De Lucia Morone, 1987

Neostygarctus sp. (Rocha *et al.*, 2013; Miller & Perry, 2016).

Family Stygarctidae Schulz, 1951

Mesostygarctus intermedius (Renaud-Mornant, 1979) (Rocha *et al.*, 2009, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016). Transferred from *Pseudostygarctus* by Hansen *et al.* (2012).

Parastygarctus sterreri Renaud-Mornant, 1970 (Moura *et al.*, 2009; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Stygarctus bradypus Schulz, 1951 (Rocha *et al.*, 2009, 2013; Verçosa *et al.*, 2009; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Family Styraconyxidae Kristensen & Renaud-Mornant, 1983

Angursa lingua Bussau, 1992 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Raiarctus aureolatus Renaud-Mornant, 1981 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b).

Family Tanarctidae Renaud-Mornant, 1980

Actinarctus doryphorus doryphorus Schulz, 1935 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Tanarctus dendriticus Renaud-Mornant, 1980 (Renaud-Mornant, 1980; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Tanarctus heterodactylus Renaud-Mornant, 1980 (Renaud-Mornant, 1980; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Tanarctus velatus McKirdy, Schmidt & McGinty-Bayly, 1976 (Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

Order Echiniscoidea Richters, 1926

Family Echiniscidae Thulin, 1928

Bryochoerus intermedius intermedius Murray, 1910 (Barros, 1942a; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).

Bryodelphax alzirae (du Bois-Reymond Marcus, 1944) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci,

- 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in the littoral zone of Bertioga, state of São Paulo.
- Bryodelphax parvulus* Thulin, 1928 (Barros, 1942a; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus arctomys* Ehrenberg, 1853 (Rahm, 1931, 1932; Marcus, 1936, 1939; McInnes, 1994; Meyer, 2013; Kaczmarek *et al.*, 2015a). *Nomen inquirendum* according to Gąsiorek *et al.* (2019b).
- Echiniscus blumi blumi* Richters, 1903 (Rahm, 1931, 1932; Marcus, 1936, 1939; Barros, 1942a; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus crassispinosus crassispinosus* Murray, 1907 (Barros, 1942a; du Bois-Reymond Marcus, 1944; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a).
- Echiniscus crassispinosus fasciatus* Marcus, 1928 (Barros, 1942a; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus dreyfusi* Barros, 1942 (Barros, 1942a; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in São Vicente, state of São Paulo.
- Echiniscus duboisi* Richters, 1902 (Barros, 1942a; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus evelinae* Barros, 1942 (Barros, 1942a; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Barretos, state of São Paulo.
- Echiniscus spiniger* Richters, 1904 (Barros, 1942a; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus tenuis* Marcus, 1928 (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Echiniscus testudo* (Doyère, 1840) (Rahm, 1931, 1932; Marcus, 1936, 1939; Barros, 1942a; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Mopsechiniscus imberbis* (Richters, 1907) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Rocha *et al.*, 2016).
- Mopsechiniscus schusteri* Dastych, 1999 (du Bois-Reymond Marcus, 1944; Assunção, 1999b; Dastych, 2000; Meyer, 2013).
- Nebularmis phocae* (du Bois-Reymond Marcus, 1944) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Campos do Jordão, state of São Paulo, nearly 1.900 m. Transferred from *Echiniscus* by Gąsiorek *et al.* (2019b).
- Pseudechiniscus bispinosus* (Murray, 1907) (Rahm, 1931, 1932; Marcus, 1936, 1939; Ramazzotti & Maucci, 1983; McInnes, 1994; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Pseudechiniscus facettalis* Petersen, 1951 (McInnes, 1994; Meyer, 2013).
- Pseudechiniscus juanita* Barros, 1939 (Barros, 1939b, 1942a; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Campos do Jordão, state of São Paulo, collected by Juanita Fortlage.
- Pseudechiniscus novaezeelandiae novaezeelandiae* (Richters, 1908) (Barros, 1942a; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a).
- Pseudechiniscus novaezeelandiae aspinosa* Iharos, 1963 (Rocha *et al.*, 2016).
- Pseudechiniscus novaezeelandiae marinae* Bartoš, 1934 (Marcus, 1939; Ramazzotti & Maucci, 1983; McInnes, 1994; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Pseudechiniscus suillus* (Ehrenberg, 1853) (Rahm, 1931, 1932; Marcus, 1936, 1939; Barros, 1942a; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Testechiniscus macronyx* (Richters, 1907) (Barros, 1942a; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016).
- Viridiscus rufoviridis* (du Bois-Reymond Marcus, 1944) (du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Found in Campos do Jordão, state of São Paulo, in mosses on trees. Transferred from *Echiniscus* by Gąsiorek *et al.* (2019b).
- Viridiscus viridis* (Murray, 1910) (Marcus, 1936, 1939; Barros, 1942a; du Bois-Reymond Marcus, 1944; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek *et al.*, 2015a; Rocha *et al.*, 2016). Transferred from *Echiniscus* by Gąsiorek *et al.* (2019b).

Family Echiniscoididae Kristensen & Hallas, 1980

- Echiniscoides sigismundi sigismundi* (M. Schultze, 1865) (du Bois-Reymond Marcus, 1952; Assunção, 1999a; Rocha *et al.*, 2013; Kaczmarek *et al.*, 2015b; Miller & Perry, 2016).

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