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.

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 Thermoziadium 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-
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 *Macrobiotus 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), *Macrobiotus 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 arctomys* Ehrenberg, 1853 in mosses from Rio de Janeiro; *Pseudechiniscus bispinosus* Murray, 1907 in mosses from Pernambuco; *Macrobiotus echinogenitus* Richters, 1903 and *Macrobiotus 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 Tardigrados Brasileiros” (du Bois-Reymond Marcus, 1944). Eveline and Ernest Marcus described several new species of tardigrades, such as *Macrobiotus 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 André 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 subgroups (Assunção, 1999b), including Macrobiotus evelinae Barros, 1938 (Barros, 1938), Macrobiotus hibiscus Barros, 1942 (Barros, 1942b), Macrobiotus primitiae Barros, 1942 (Barros, 1942b), Itaquascon umbellinae Barros, 1939 (Barros, 1939a), and Pseudobiota 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 Paramacrobiotus richtersi (Murray, 1911) (Iharos, 1969), Höfling-Epiphonio (1972) registered Batillipes mirus Richters, 1909, and Batillipes tuberensis 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 Opydorpus Renaud-Mornant, 1989, from the continental shelf of Brazil (Renaud-Mornant 1980, 1984, 1989). Two new species were described from the Iguaçu falls (state of Paraná), Isohypsibisi sabellai Piloto, Binda, Napolitano & Moncada, 2004 (Piloto et al. , 2004), and Paramacrobiotus centesimus (Piloto, 2000) (Piloto, 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 (Pulsen & 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 Ligiaactrus 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 |
|-------|-------|------------|
| Actinactus doryphorus doryphorus | PR, SP | gravel, sand |
| Archechiniscus marci | CE, RN | sand, mud |
| Angara lingua | CE, RN | sand, mud |
| Batillipes annulatus | CE, PE | sand |
| Batillipes brasiliensis | AL | gravel, sand |
| Batillipes dandaranii | AL | sand |
| Batillipes dicrocerus | CE, PE | sand |
| Batillipes loresti | CE, PE, RN | sand |
| Batillipes minus | SP | sand |
| Batillipes pennesi | AL, CE, PE, RJ, SP | sand, mud, sea water |
| Batillipes potgiuemness | RJ, RN | gravel, sand |
| Chyoscoctus brianii | CE, RJ, RN | sand, mud |
| Dipodarctus subterraneus | PE | macroalgae (Halimeda opuntia) |
| Ethinoschops sigmoimundi sigmoimundi | SP | barnacles |
| Floractus fuliginis | CE, RN | gravel, sand |

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 |
|---------|-------|------------|
| Adriacon scoticum scoticum | SP | mosses, aquatic plants |
| Bryochoreus intermedius intermedius | SP | mosses |
| Bryodelphus atrior | SP | mosses, aquatic plants |
| Bryodelphus parvulus | SP | mosses |
| Dorychodrillus amphibius | SP | bremeliads |
| Diannes papillifera | SP | mosses, aquatic plants |
| Diaphascon alpinum | SP | mosses |
| Diaphascon pingue pisque | SP | mosses, aquatic plants |
| Doryphoribius flavus | MG, RJ, SP | mosses, aquatic plants |
| Echiniscus acronyx | RJ | mosses, algae |
| Echiniscus blami blami | SP | mosses |
| Echiniscus crenatuscrenatus crenatus | PR, SP | mosses, aquatic plants |
| Echiniscus crenatusfasciatus | PR, SP | mosses, aquatic plants |
| Echiniscus dreyfusii | SP | mosses |
| Echiniscus dhabisi | SP | mosses |
| Echiniscus exleneae | PR, SP | mosses, aquatic plants |
| Echiniscus spiniger | SP | mosses, aquatic plants |
| Echiniscus tenus | SP | mosses, aquatic plants |
| Echiniscus testudo | SP | mosses |
| Frongnotus verrucosus | SP | mosses, aquatic plants |
| Grevenius granulis | SP | unknown |
| Grevenius mymps | PR, SP | mosses, aquatic plants |
| Hypobiotus convergens | SP | mosses, aquatic plants |
| Hypobiotus microps | SP | unknown |
| Isohypobiotus sabelai | PR | mosses |
| Itaquosaic umbellinae | SP | mosses |
| Macrobiotus echninogaster | PE, SP | mosses |
| Macrobiotus echnius | SP | mosses |
| Macrobiotus ferruginis | SP | mosses, aquatic plants |
| Macrobiotus hibiscus | SP | unknown |
| Macrobiotus hufelandi | PE, SP | mosses, aquatic plants |
| Macrobiotus occidentalis occidentalis | PR | unknown |
| Macrobiotus polyopus | SP | unknown |
| Macrobiotus primitivae | PR, SP | mosses, aquatic plants |

AM = Amazonas; MG = Minas Gerais; PE = Pernambuco; PR = Paraná; RJ = Rio de Janeiro; SP = São Paulo.
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-Epiphanio, 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 *Macrobiotus sawayai* Marcus, 1937 has been omitted from modern taxonomic literature and requires redescriptions (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: *Paramacrobiotus (Amicrobiotus) 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,
Class Eutardigrada Richters, 1926
Order Hypsibiidae Gul, Jørgensen & Kristensen, 2019
Family Hypsibiidae Pilato, 1969

**Adropion 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).

**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 Itaquasquetubia 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 Gul, Jørgensen & Kristensen, 2019**

**Family Doryphoribiidae Gašiorek, 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).

**Doryphorobius 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 Gašiorek 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 Gašiorek et al. (2019c).

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

**Thulinius 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 Gašiorek 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 Gašiorek 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.

**Ursulinius 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 Gašiorek et al. (2019c).

**Order Macrobiotoidea Gul, 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 Capivari, 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 *Minibiots* by Bertolani et al. (2014).
Macrobiotus 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.

Macrobiotus hufelandi Schultz, 1834 (Rahm, 1931, 1932; Marcus, 1939; Barros, 1942b; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Pulskens & Meneghin, 2010; Meyer, 2013; Kaczmarek et al., 2015a; Rocha et al., 2016).

Macrobiotus 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).

Macrobiotus polyopus Marcus, 1928 (Barros, 1942b; Ramazzotti & Maucci, 1983; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek et al., 2015a; Rocha et al., 2016).

Macrobiotus primitiae 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.

Macrobiotus 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). Found in Eldorado, state of São Paulo.

Macrobiotus 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 Itapetinga. Transferred from Macrobiotus by Vecchi et al. (2016).

Mesobiotus furciger (Murray, 1907) (Rocha et al., 2016). Transferred from Macrobiotus 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 Macrobiotus 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 Macrobiotus 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 Macrobiotus by Vecchi et al. (2016).

Minibiota 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 Macrobiotus by Guidetti et al. (2007).

Minibiota aculeatus (Murray, 1910) (Rocha et al., 2016).

Minibiota intermedius (Plate, 1888) (Barros, 1942b; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek et al., 2015a; Rocha et al., 2016).

Minibiota 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 Macrobiotus by Guidetti et al. (2007).

Minibiota marcus (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 Macrobiotus by Guidetti et al. (2007).

Paramacrobiotus (Amicrobiotus) cf. areolatus (Murray, 1907). Unpublished. Collected by the author in mosses from Curitiba, Paraná. Transferred from Macrobiotus by Guidetti et al. (2009).

Paramacrobiotus (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 Macrobiotus by Guidetti et al. (2009).

Paramacrobiotus (Paramacrobiotus) richtersi (Murray, 1911) (Marcus, 1939; Barros, 1942b; du Bois-Reymond Marcus, 1944; Iharos, 1969; Kaczmarek et al., 2015a). Transferred from Macrobiotus by Guidetti et al. (2019).

Family Murrayauidae 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 dandarae 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 Sol) 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-Epiphanio, 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 Ilhabela, state of São Paulo, in 3-5 depth, sand with rather much detritus.

**Batillipes potiguarenensis** 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).

**Para stygarctus 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 Styracolyidae 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).

**Bryo delphax 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.

Echiniscus arctomys Ehrenberg, 1853 (Rahm, 1931, 1932; Marcus, 1936, 1939; 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; Assunção, 1999b; 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 Murray, 1907 (Barros, 1942a; du Bois-Reymond Marcus, 1944; Assunção, 1999b; Meyer, 2013; Kaczmarek et al., 2015a).

Echiniscus crassispinosus crassispinosus (Murray, 1907) (Barros, 1942a; du Bois-Reymond Marcus, 1944; McInnes, 1994; Assunção, 1999b; Meyer, 2013; Kaczmarek et al., 2015a; Rocha et al., 2016).

Echiniscus dreyfusii Barros, 1942 (Barros, 1942a; Ramazzotti & Maucchi, 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 & Maucchi, 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 & Maucchi, 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 & Maucchi, 1983; McInnes, 1994; Rocha et al., 2016).

Mopsechiniscus schusteri Dastych, 1999 (du Bois-Reymond Marcus, 1944; Assunção, 1999b; Dastych, 2000; Meyer, 2013).

Mopsechiniscus schusteri Dastych, 1999 (du Bois-Reymond Marcus, 1944; Assunção, 1999b; Dastych, 2000; Meyer, 2013).

Mopsechiniscus schusteri Dastych, 1999 (du Bois-Reymond Marcus, 1944; Assunção, 1999b; Dastych, 2000; Meyer, 2013).
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