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# Limno-Terrestrial Tardigrada of Sub-Antarctic Islands—An Annotated Review

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**Abstract:** Research on the limno-terrestrial Tardigrada fauna of the Sub-Antarctic zone began almost 120 years ago. Here we present an overview of the literature data on the presence of tardigrades on sub-Antarctic islands, including the substrates on which they have been found. From 32 published sources, we found original data on the occurrence of 49 currently valid species on six sub-Antarctic islands/island groups. Of these, 9 species (18%) were originally described from this zone, another 13 species (26%) were described from Continental or Maritime Antarctica, almost half of these species (22 species—45%) were originally described from European localities, and the remaining 5 species (10%) were originally described from South America, Africa, or Australia. The validity of the records of individual species is discussed. We consider the presence of 29 species in the Sub-Antarctic to be doubtful. We ascertained a total of 90 combinations of species and islands or island groups. More than half (64%) of these will require confirmation in the future because we currently consider them doubtful. We can conclude that the tardigrade fauna of the sub-Antarctic islands is only very superficially known, and the occurrence of most species in this zone must be verified.

**Keywords:** limno-terrestrial Tardigrada; Sub-Antarctic; literature



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## 1. Introduction

Tardigrades are microscopic hydrophilic metazoans with a bilaterally symmetrical body and four pairs of legs that typically terminate in claws. The length of tardigrades is between 50 µm for the smallest juveniles to over 1200 µm for the largest adults of some species (e.g., [1,2]).

Tardigrades live in diverse marine, freshwater, and terrestrial habitats throughout the world, from oceanic depths to the tops of mountains [1].

Most of the known non-marine tardigrade species live on terrestrial substrates such as mosses, liverworts, cushion-shaped plants, lichens, and leaf litter. Some of these species also occur in freshwater habitats, while others are found exclusively therein [1,3].

The phylum Tardigrada is distributed all over the world. Although tardigrades represent organisms with passive dispersal that should not have distribution barriers, many limno-terrestrial species have a limited range of distribution [2].

Tardigrades reproduce only via eggs. Limno-terrestrial environments are most commonly colonized by populations of female eutardigrades and heterotardigrades using parthenogenesis as the means of reproduction [2].

Tardigrades can survive adverse periods in their environment by means of two types of dormancies: quiescence and diapause. Quiescence is represented by four forms of cryptobiosis: anhydrobiosis, cryobiosis, anoxybiosis, and osmobiosis [4]. Cryobiosis and anhydrobiosis are of particular importance for the survival of limno-terrestrial tardigrades in sub-Antarctic conditions.

Cryobiosis is induced by low temperatures and enables tardigrades to survive freezing and thawing. However, the rate of cooling must be slow, enabling frozen specimens to survive for several years. Cryobiotic ability is common in terrestrial species, but it is very rare, or even absent, in freshwater species [1,2].

Anhydrobiosis is induced by the loss of water from evaporation, which is why this ability is typical of terrestrial tardigrades. As the surrounding water evaporates, the entire body contracts, forming a barrel-shaped 'tun'. At the same time, the tardigrade loses more than 95% of its free and bound water and significantly reduces or suspends its metabolism. Adults and eggs can survive up to 20 years in the anhydrobiotic state. After the addition of water, the animal returns to an active state if the rate of desiccation was slow enough [2].

Encystment and resting eggs are involved in diapause. Encystment is known in some moss-dwelling, soil, and freshwater tardigrades. In nature, cysts can survive for months without completely exhausting their food reserves [2,4].

The number of known species of tardigrades in the world is currently close to 1500, and a few dozen new species are described every year (see [5]).

Antarctica is commonly divided into three main terrestrial biogeographic zones characterized by different climatic characteristics and different ecosystems: Continental Antarctica, Maritime Antarctic, and Sub-Antarctic (e.g., [6]).

Continental Antarctica consists of the mainland and adjacent islands with the exception of the west coast of the Antarctic Peninsula and the islands belonging to the Maritime Antarctic zone. The Continental zone is characterized by a harsh climate with an average monthly temperature not above freezing point and a total annual precipitation of approximately 10–15 cm. It lacks vascular plants, and sparse cryptogams are mainly represented by lichens (e.g., [7]).

The Maritime Antarctic zone comprises the western coast of the Antarctic Peninsula up to approximately 72° S and adjacent islands and more distant associated islands and archipelagos (South Shetland Islands, South Orkney Islands, South Sandwich Islands, and Bouvetøya). It has a cold, humid oceanic climate with mean monthly temperatures exceeding 0 °C for 1–4 months and an annual precipitation of 35–50 cm. Floristically, the area is home to two species of vascular plants and has a relatively rich and diverse flora of bryophytes and lichens (e.g., [7,8]).

The Sub-Antarctic zone consists of a ring of small isolated oceanic islands surrounding the continent at a relatively high latitude (ca. 46–54° S). The following six small island groups belong to the Sub-Antarctic (Figure 1):

1. South Georgia (British Overseas Territories, Atlantic Ocean);
2. Marion and Prince Edward Islands (Republic of South Africa, Indian Ocean);
3. Crozet Islands (French Southern and Antarctic Lands, Indian Ocean) (Îles Crozet, Terres australes et antarctiques françaises);
4. Kerguelen Islands (French Southern and Antarctic Lands, Indian Ocean) (Îles Kerguélen, Terres australes et antarctiques françaises);
5. Heard Island and McDonald Islands (Australia, Indian Ocean);
6. Macquarie Island (Australia, Pacific Ocean) (e.g., [7–9]).

The islands of this zone have cool oceanic temperate climates. For at least half the year, the mean monthly temperature is above the freezing point. The precipitation is higher than 90 cm per annum. The vegetation is tundra-like and is without arborescent vascular plants. It is composed mostly of woody herbs, forbs, pteridophytes, and cryptogams. Extensive grass heath, herb fields, and mires cover some lowland areas. Coastal regions consist of tussock grassland [7].

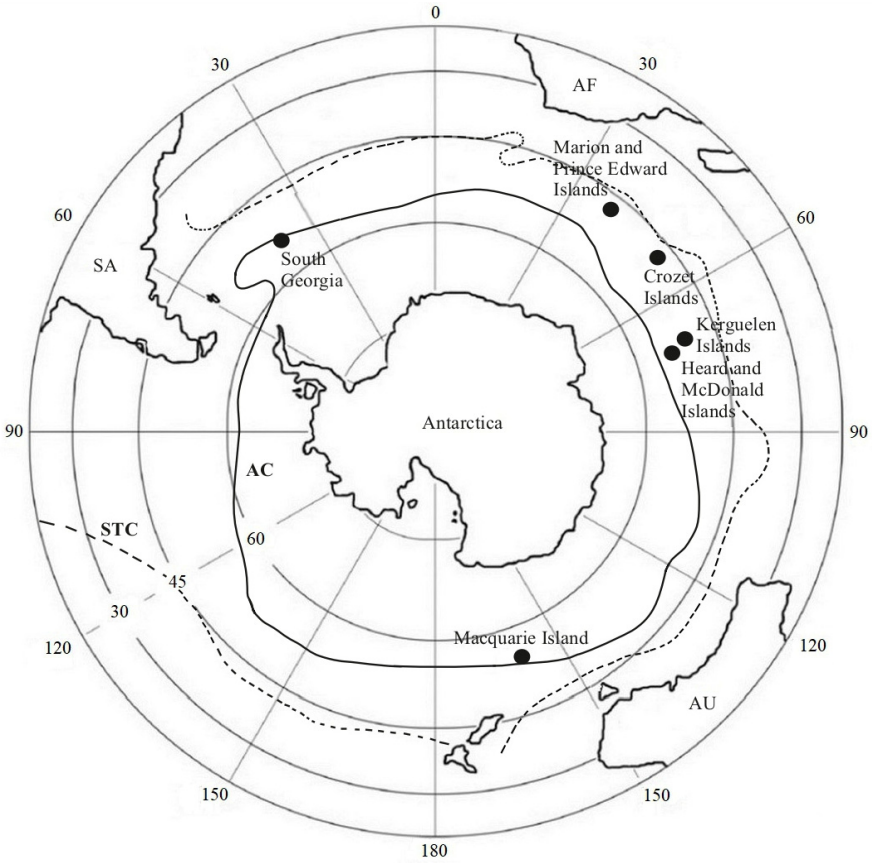


**Figure 1.** Location of sub-Antarctic islands/island groups and major circumpolar oceanic fronts (the locations of other small islands are not drawn, with the exception of the Falkland Islands). AF—Africa; AU—Australia; SA—South America; AC—Antarctic Convergence; STC—Subtropical Convergence (Map from Hofmeyr et al. [10], reproduced with permission from the first author and the publisher; South African Journal of Wildlife Research, published by Southern African Wildlife Management Association; map modified according to Leach et al. [11]).

A universally accepted geographic definition of the Sub-Antarctic does not exist, although it is commonly accepted as a meaningful term for this terrestrial biological zone. Based on ecoclimatic criteria (temperature and presence/absence of trees or woody shrubs), the Sub-Antarctic includes only those islands where trees or woody shrubs are absent. These islands represent a transition zone of continuous environmental conditions between the more extreme environments of the islands and archipelagos of Continental and Maritime Antarctica (Balleny, Peter I Øya, South Shetland, South Orkney, South Sandwich Islands, Bouvetøya) and the more temperate conditions of those cold temperate ocean islands and archipelagos with trees or woody shrubs, such as Islas Diego Ramírez, the Falkland Islands (Islas Malvinas), Tristan da Cunha, Gough Island, Amsterdam and Saint Paul Islands (Île Amsterdam and Île Saint-Paul), and the shelf islands of New Zealand—Campbell Island (Motu Ihupuku), Chatham Islands, Antipodes Islands, Auckland Islands, Bounty Islands, and Snares Islands (Tini Heke) (e.g., [12–15]). It should be mentioned that some authors also considered some of these cold temperate oceanic islands to be sub-Antarctic islands (see, e.g., Tierra del Fuego in [16], Campbell Island and Snares Islands in [17,18], New Zealand's shelf-island groups in [12,19], Falkland Islands and Gough Island in [19], and Saint Paul Island in [20,21]).

Circulation in the Southern Ocean is dominated by the continuous eastward-flowing Antarctic Circumpolar Current, which has recently split into numerous circumpolar frontal systems [22]. The transition of warm, light subtropical water from lower latitudes to cold, dense Antarctic water in the south occurs in a step-like manner rather than as gradual

change across the breadth of the Southern Ocean. Oceanologists distinguish narrow bands (fronts) in which the surface temperature of the water changes rapidly. Between the fronts lie zones with relatively uniform water mass properties [23]. Inter-frontal zones have a steady flow and differ from each other in hydrochemical and hydrophysical characteristics [22]. Of the fronts, the most significant one is the Polar Front (Antarctic Convergence), dividing the Southern Ocean into two distinct regions: the sub-Antarctic region to the north and the Antarctic region to the south. The Polar Front has variable width characterized by steep gradients at sea-surface temperature; abrupt changes in phytoplankton abundance, zooplankton distribution, pelagic bird species, and weather conditions; and sometimes by a salinity maximum at the surface [24]. The sub-Antarctic and Antarctic regions of the Southern Ocean have different plankton and fish communities. Essentially, the terrestrial Sub-Antarctic zone is situated between the Antarctic and Subtropical Convergence (Figure 1) and consist of the islands in the southern Atlantic, Indian, and Pacific Oceans [25].

Tardigrada research on the sub-Antarctic islands began at the start of the 20th century. The first data were published by Richters [26] and were derived from a collection of moss samples that was received from the German South Polar Expedition. Later, Richters [20] published results from the material gathered during the Swedish South Polar Expedition. Both expeditions were directed at the Antarctic mainland, with a visit to the sub-Antarctic islands as part of their program [20,26]. In the early 20th century, Murray [27] also published results from the Sub-Antarctic zone, which were obtained during the British Antarctic Expedition 1907–1909. In addition to the Antarctic material gathered, other samples, mostly mosses, were collected from several distant countries, as this expedition practically circumnavigated the world [27].

Following a long hiatus, Marcus [28] and Ramazzotti [29] contributed to the knowledge of the sub-Antarctic tardigrade fauna, but since the 1970s, data on the distribution and taxonomy of sub-Antarctic limno-terrestrial Tardigrada have been increasing with every decade. Among these works, we mention here some of those that have contributed the largest number of original findings or descriptions of species from the Sub-Antarctic zone; namely [9,30–38].

Collected faunal data from the sub-Antarctic islands (among compilations from the entire world) can already be found in the monographs of Marcus (most recently in [39]), Ramazzotti (most recently in [40]), and, finally, in the monograph of McInnes [41], which was specifically devoted to the global geographical distribution of non-marine tardigrades. In it, the author lists 26 species from the Sub-Antarctic zone.

In view of the numerous nomenclature changes that have occurred since the previous publications [5], and with regard for the new knowledge about the zoogeography of limno-terrestrial tardigrades [42–46], we consider it useful to present this review on the distribution of limno-terrestrial Tardigrada on the islands of the Sub-Antarctic, in which we not only compile all available data on the fauna of non-marine tardigrades of the Sub-Antarctic from the oldest to the present but also express an opinion on the actual presence of each of the individual species reported from these islands.

## 2. Materials and Methods

We extracted data on the occurrence of specific Tardigrada species on specific islands/island groups of the Sub-Antarctic zone from the most complete possible spectrum of available potential sources dedicated to tardigrades of the Antarctic region, either exclusively or only marginally, from the oldest to the most current. Regarding monographs, we checked two (the first and the last) by Marcus [39,47], the final monograph by Ramazzotti and Maucci [40], as well as monographs devoted to the global distribution of limno-terrestrial tardigrades [41–46].

In our list of reported species from the Sub-Antarctic zone, we did not include taxa higher than species, species complexes, or pairs of species such as, e.g., the pair *Hypsibius* (*Diphascon*) *alpinus* + *H.* (*D.*) *pinguis* in [30] or *Macrobiotus hastatus*/*pullari* in [48].

When analyzing sources, we distinguished whether they contained primary data or data taken from another source (secondary data).

## 3. Results

Records of 49 limno-terrestrial Tardigrada species from 11 families and 25 genera in six sub-Antarctic islands/island groups (South Georgia, Marion Island from the Marion and Prince Edward Islands, Possession Island (Île de la Possession) from Crozet Islands, Kerguelen Islands, Heard Island from the Heard and McDonald Islands, and Macquarie Island) were found in 51 articles/monographs (32 contributed at least one original datum on the occurrence of a specific species on a specific island/island group, while the rest contained only secondary data).

In the following review of the records, data for each species are arranged as follows:

- Currently valid name of species with citation(s) of its description/definition;
- The name(s) under which the species was/were reported from the Sub-Antarctic, arranged in order of their appearance;
- The type locality of the species at the level of territorial units (state, island);
- The list of islands or island groups (if the name of the island was not published) from which the species was reported (references of original findings are in bold);
- Substrate(s) from which the species was extracted in the Sub-Antarctic (if given in the source(s));
- Remarks on the findings of the species in the Sub-Antarctic.

All of the species below are arranged in the list according to the current Checklist of Tardigrada Species [5]:

Phylum: Tardigrada Doyère, 1840 [49]
Class: Heterotardigrada Marcus, 1927 [50]
Order: Echiniscoidea Richters, 1926 [51]
Family: Oreellidae Ramazzotti, 1962 [52] (in [53])
*Oreella* Murray, 1910 [27]

1. ***Oreella mollis* Murray, 1910** [27]

*Oreella minor* Ramazzotti, 1964 [54]
*Oreella mollis* J. Murray, 1910 [8]
*Oreella mollis* Murray, 1910 [55]
***Terra typica*:** New South Wales (Australia) [27]
**Sub-Antarctic: South Georgia** [8], **[54]** and [55]
**Substratum:** moss [54]
**Remarks:** The species has been recorded from the Southern Hemisphere only [43]. The other records closest to South Georgia are from Argentina [56] and the Maritime Antarctic (e.g., [57]). *Oreella minor* was synonymized by Dastych et al. [58].

Family: Echiniscidae Thulin, 1928 [59]
*Barbaria* Michalczyk, Gąsiorek, Morek and Stec, 2019 [60]

2. ***Barbaria jenningsi* (Dastych, 1984)** [31]

*Echiniscus* cf. *jenningsi* Dastych, 1984 [9]
*Echiniscus jenningsi* Dastych [61]
*Echiniscus jenningsi* Dastych, 1984 [55,62]
***Terra typica*:** South Shetland Islands (Maritime Antarctic, Southern Ocean) [31]
**Sub-Antarctic: South Georgia [61]** and [62]; **Marion Island [55]**; **Macquarie Island [9]**
**Remarks**: The species have also been reported from other localities in the Maritime Antarctic zone (e.g., [8]), as well as from Continental Antarctica (e.g., [63,64]). According to Miller et al. [9], specimens from Macquarie Island differ from the original description, and this species complex requires revision.

*Echiniscus* C.A.S. Schultze, 1840 [65]

3. ***Echiniscus darienae* Miller, Horning and Dastych, 1995** [33]

*Echiniscus darienae* nov. sp. [33]
*Echiniscus darienae* Miller, Horning & Dastych, 1995 [9]
***Terra typica*:** Macquarie Island (Australia, Pacific Ocean) [33]
**Sub-Antarctic: Macquarie Island [9,33]**
**Substratum:** lichen (*Cladonia fimbriata* (L.) Fr.) [33]
**Remarks:** So far, the species has been reported from the type locality only.

4. ***Echiniscus kerguelensis* Richters, 1904** [26,66]

*Echiniscus kerguelensis* n. sp. [26,66]
*Pseudechiniscus kerguelensis* (Richt.) [47]
*Echiniscus* (*Echiniscus*) *kerguelensis* Richters [39]
*Echiniscus kerguelensis* Richters, 1904 [40,41]
***Terra typica*:** Kerguelen Islands (France, Indian Ocean) [26,66]
**Sub-Antarctic: Kerguelen Islands [26]**, [39–41,47] and **[66]**
**Substratum:** mosses [26,66]
**Remarks:** The species was regarded as a species dubia, according to Marcus [47]. It has been reported from almost all continents [41], including Continental Antarctica (e.g., [67]). However, due to its vague and insufficient description, its actual distribution outside the type locality is questionable. The species requires a redescription from the type locality so that the various records attributed to this species can be verified ([45]).

5. ***Echiniscus merokensis* Richters, 1904** [68]

*Echiniscus merokensis* Richters, 1904 [69]
***Terra typica*:** Norway (Europe) [68]
**Sub-Antarctic: Heard Island [69]**
**Remarks:** According to McInnes et al. [45], most of the records for the species (including the type locality) are Holarctic [41], which implies that the records from other regions require confirmation. Within the Antarctic region, it has also been reported from the Maritime Antarctic zone [70].

6. ***Echiniscus spiniger* Richters, 1904** [71]

*Echiniscus* cf. *spiniger* Richters, 1904 [9]
***Terra typica*:** Sweden (Europe) [71]
**Sub-Antarctic: Macquarie Island [9]**
**Remarks:** Miller et al. [9] found morphological differences between the studied individuals and the typical *Echiniscus spiniger,* including in the form of the cuticular sculpture. Thus, the presence of the species in Macquarie Island is not yet confirmed. The species is broadly distributed [41], with the closest record to the Sub-Antarctic zone reported from New Zealand [17]; however, at least some of those specimens do not belong to *E. spiniger* [72]. The species requires an integrative redescription based on a topotype population [46] so that its actual distribution can be clarified.

*Mopsechiniscus* du Bois-Reymond Marcus, 1944 [73]

7. ***Mopsechiniscus frenoti* Dastych, 1999** [34]

*Mopsechiniscus frenoti* sp. n. [34]
*M. frenoti* Dastych, 1999 [35]
*Mopsechiniscus frenoti* Dastych, 1999 [16]
***Terra typica*:** Crozet Islands (France, Indian Ocean) [34]
**Sub-Antarctic: Possession Island** [16], **[34]** and [35]
**Substratum:** moss [34]
**Remarks:** So far, the species has been recorded from the type locality only.

8. ***Mopsechiniscus imberbis* (Richters, 1908)** [20]

*Echiniscus imberbis* n. sp. [20]

*Pseudechiniscus imberbis* (Richt.) [47]
*Pseudechiniscus imberbis* (Richters) [39]
*Mopsechiniscus imberbis* (Richters, 1907) [8,16,40,41]
*Mopsechiniscus imberbis* (Richters, 1920) [32]
*M. imberbis* (Richters, 1908) [34]
*Mopsechiniscus imberbis* (Richters, 1908) [35,55]
*Mopsechiscus imberis* (Richters) [61]
***Terra typica*:** South Georgia (UK, Atlantic Ocean) [20]
**Sub-Antarctic: South Georgia** [8,16], **[20,32]**, [34], **[35]**, [39–41,47,55] and **[61]**
**Substratum:** mosses [32,35]
**Remarks:** The species was first mentioned in [74] but without a formal description, and therefore this first mention is a nomen nudum, according to Dastych [35], who provided a redescription. So far, the species has been reported from the type locality only. According to Kaczmarek et al. [43], although it was also reported from Argentina (e.g., [75]) and Venezuela [76], these reports actually represent *Mopsechiniscus granulosus* Mihelčič, 1967 [77] and *Mopsechiniscus schusteri* Dastych, 1999 [78], respectively.

*Pseudechiniscus* Thulin, 1911 [79]

9. ***Pseudechiniscus* (*Pseudechiniscus*) *suillus* (Ehrenberg, 1853)** [80]

*Echiniscus arctomys* Ehrenberg [26,66]
*Echiniscus arctomys* Ehrenbg. [20]
*Pseudechiniscus suillus* (Ehrenbg.) [47]
*Echiniscus* (*Echiniscus*) *arctomys* Ehrbg. [39]
*Pseudechiniscus suillus* (Ehrenberg, 1853) [9,21,41]
*Echiniscus arctomys* Ehrenberg, 1853 [41]
***Terra typica*:** Italy (Europe) [80]
**Sub-Antarctic: Marion Island [21]** and [41]; **Possession Island [26]** and [41,47]; **Kerguelen Islands** [20], **[26]** and [39,41,47,66]; **Macquarie Island [9]**
**Substratum:** mosses [26,66]
**Remarks:** In the past, it has been considered a cosmopolitan species [41]. From the nearest continents, the species has been reported from Continental Antarctica (e.g., [31]), from South Africa (e.g., [81]), and from New Zealand (e.g., [17]). Recently, the rich diversity of the *Pseudechiniscus suillus* species group was revealed, and the importance of the ventral pattern in the taxonomy of this species group was discovered [82–86]. Murray [27] wrote (p. 126) that "Prof. Richters informs me in a letter that all his records under the name *E. arctomys* should be *E. suillus*, Ehr.". Therefore, we included the reports of *E. arctomys* in [20,26,66] with *Pseudechiniscus suillus*, as well as those by Marcus [47], who reported *P. suillus* from the Kerguelen Islands and Possession Island on the basis of [26] (p. 238); that is, on the basis of the report on the occurrence of *E. arctomys*. The presence of the species in the Sub-Antarctic zone needs to be confirmed as it is very probable that another similar species or multiple other species was/were reported from the region. The recent *Pseudechiniscus suillus* redescription [83] enables this verification.

*Testechiniscus* Kristensen, 1987 [87]

10. ***Testechiniscus macronyx* (Richters, 1908)** [20]

*Echiniscus macronyx* n. sp. [20]
*Echiniscus macronyx* Richt. [47]
*Echiniscus* (*Echiniscus*) *macronyx* Richters [39]
*Echiniscus macronyx* Richters, 1907 [8,55,88]
*E. macronyx* Richters [61]
***Terra typica*:** South Georgia (UK, Atlantic Ocean) [20]
**Sub-Antarctic: South Georgia** [8], **[20]**, [39,47,55] and **[61,88]**
**Substratum:** moss (*Andreaea* Hedw.) [88]

**Remarks:** The species has been reported from the type locality only. It was also reported from Brazil, but this report is dubious [43]. According to Ottesen and Meier [32], the status of specimens attributed to *Echiniscus macronyx* by Richters [20] is unclear, but they probably represent an *Oreella* sp. According to Gąsiorek et al. [89], the species has a circum-Antarctic distribution and probably represents another genus.

Class: Eutardigrada Richters, 1926 [51]
Order: Apochela Schuster, Nelson, Grigarick and Christenberry, 1980 [90]
Family: Milnesiidae Ramazzotti, 1962 [53]
*Milnesium* Doyère, 1840 [49]

11. ***Milnesium antarcticum* Tumanov, 2006** [91]

*Milnesium antarcticum* Tumanov, 2006 [92]
***Terra typica*:** South Shetland Islands (Maritime Antarctic, Southern Ocean) [91]
**Sub-Antarctic: South Georgia [92]**
**Remarks:** So far, the species has been recorded from the type locality and the Sub-Antarctic only.

12. ***Milnesium tardigradum* Doyère, 1840** [49]

*Milnesium tardigradum* Doy. [20,66,93]
*Milnesium tardigradum*, Doyère [27]
*Milnesium tardigradum* Doy. [39,47]
*Milnesium tardigradum* Doyère, 1840 [8,9,32,94]
*Milnesium tardigradum* Doyére, 1840 [41]
*Milnesium tardigradum* Doyére [95]
*Milnesium* cfr. *tardigradum* [96]
*Milnesium* cf. *tardigradum* [55]
***Terra typica*:** France (Europe) [49]
**Sub-Antarctic**: **South Georgia** [8], **[20]** and [27,32,39,41,47,55,95]; **Marion Island [96]**; **Kerguelen Islands** [20,39,41,47], **[66]** and [93,94]; **Macquarie Island [9]**
**Substratum:** mosses [66,96], (*Racomitrium crispulum* (Hook. f. & Wilson) Wilson) [9]
**Remarks:** In the past, the species was considered cosmopolitan [41] until it was redescribed [97,98]. *Milnesium tardigradum* sensu stricto occurs mainly in the Palearctic with a few records from the Republic of South Africa, which have been interpreted as examples of anthropogenic dispersal [46,99]. Within the Antarctic region, it has been reported from Continental Antarctica (e.g., [8,67,94,100]), Maritime Antarctic (e.g., [20,31]), and Sub-Antarctic. All reports of *Milnesium tardigradum* before the redescription of the species are doubtful and need to be confirmed (see e.g., [43]), and this also applies to reports from all three Antarctic zones.

Order: Parachela Schuster, Nelson, Grigarick and Christenberry, 1980 [90]
Superfamily: Hypsibioidea Pilato, 1969 in Marley et al. 2011 [101,102]
Family: Calohypsibiidae Pilato, 1969 [101]
*Calohypsibius* Thulin, 1928 [59]

13. ***Calohypsibius ornatus* (Richters, 1900)** [103]

*Calohypsibius ornatus* [88]
*Calohypsibius* cfr. *ornatus* [96]
*Calohypsibius ornatus* (Richters, 1900) [9]
*Calohypsibius* cfr *ornatus* [8]
*Calohypsibius* cf. *ornatus* [55]
***Terra typica*:** Germany (Europe) [103]
**Sub-Antarctic: South Georgia** [8,55] and **[88]**; **Marion Island [96]**; **Macquarie Island [9]**
**Substratum:** moss [96], (*Orthotrichum* sp.) [88]
**Remarks:** The species is rare and has been reported mainly from the Palearctic and Nearctic regions, with a few reports from the Australian and Neotropical regions. It probably represents a species complex [41,43,46]. We believe that, due to the remoteness of the sub-

Antarctic localities from the type locality, the reports of the species from the Sub-Antarctic zone are doubtful and that it is necessary to validate them. However, a redescription of the species on the basis of new material from the type locality will first be necessary.

Family: Hypsibiidae Pilato, 1969 [101]
Subfamily: Diphasconinae Dastych, 1992 [104]
*Diphascon* Plate, 1888 [105]

14. ***Diphascon dastychi* Pilato and Binda, 1999** [106]

*Diphascon pingue* "variety B" [21]
*Diphascon (Diphascon) dastychi* sp. nov. [106]
*Diphascon pingue* ('Vaierty B') Marcus,1936 [55]
***Terra typica*:** Victoria Land (Antarctica) [106]
**Sub-Antarctic: South Georgia [21]** and [55,106]
**Remarks:** Pilato and Binda [106] concluded that the "variety B" of *Diphascon pingue* described by [31] should be considered a synonym of *D. dastychi*. Thus, the species is reported from Continental Antarctica and from the Sub-Antarctic zone, but this assumption [106] still requires confirmation.

15. ***Diphascon langhovdense* (Sudzuki, 1964)** [94]

*Diphascon (Diphascon) chilenense langhovdense* (Sudzuki, 1964) [9]
***Terra typica*:** Queen Maud Land (Antarctica) [94]
**Sub-Antarctic: Macquarie Island [9]**
**Substratum:** lichens (*Cladonia coniocraea* (Flörke) Spreng., *Pseudocyphellaria glabra* (Hook. f. & Taylor) C.W. Dodge) [published as *Pseudocyphellaria delisea*, which is now a synonym], moss (*Racomitrium crispulum*) [9]
**Remarks:** In addition to the type locality, the species has also been reported from other Antarctic regions—Continental Antarctica (see e.g., [107]) and Maritime Antarctic (see e.g., [31]), as well as from Tasmania [108] and New Zealand [109].

16. ***Diphascon mirabilis* Dastych, 1984** [31]

*Diphascon mirabile* Dastych, 1984 [32]
*Diphascon* (*Diphascon*) *mirabilis* Dastych, 1984 [41]
*Diphascon* (*Diphascon*) *mirabilis*; Dastych (1984) [8]
*Diphascon mirabilis* Dastych, 1984 [55]
***Terra typica*:** South Shetland Islands (Maritime Antarctic, Southern Ocean) [31]
**Sub-Antarctic: South Georgia** [8], **[32]** and [41,55]
**Substratum:** mosses [32]
**Remarks:** Apart from the Atlantic part of the Sub-Antarctic zone, it has been reported from two archipelagos of the Maritime Antarctic (e.g., [8,31]).

17. ***Diphascon pingue* (Marcus, 1936)** [39]

*Diphascon pingue* (Marcus, 1936) [32]
*Diphascon* (*Diphascon*) *pingue* (Marcus, 1936) [8,41]
*Diphascon pingue* [88]
*Diphascon* (*Diphascon*) cf. *pingue* Marcus, 1936 [9]
*Diphascon* sp. (*pingue* type) [110]
*Diphascon* (*Diphascon*) cf. *pingue* [62]
***Terra typica*:** Germany, Switzerland (Europe) [39]
**Sub-Antarctic: South Georgia** [8,9], **[32]**, [41,62], **[88]** and [110]; **Macquarie Island [9]**
**Substratum:** mosses [32], (*Andreaea* Hedw.) [88], (*Ditrichum punctulatum* Mitt.) [9]
**Remarks:** It is the nominal species for the *Diphascon pingue* group, which is a complex of morphologically very similar species (see e.g., [106]). The species was considered cosmopolitan in the past [41,45,46] but is probably restricted to the Holarctic [44]. In the Antarctic region, it has been reported from Continental Antarctica (e.g., [111]), Maritime Antarctic (e.g., [112]), and also from the Sub-Antarctic. Several new species from the *pingue*

group were subsequently described from the Antarctic region [106], and therefore the occurrence of *Diphascon pingue* sensu stricto in this region must be verified (see also [9], according to which all reports of *Diphascon pingue* from Antarctica should be revisited). Since Jennings [30] reported a pair of *Diphascon alpinum* Murray, 1906 [113] and *D. pingue* (and not a specific species) from South Georgia, we do not include his report in the above list of species records.

18. ***Diphascon polare* Pilato and Binda, 1999** [106]

*Diphascon pinguis* (Marcus, 1936) variety "A" [31]
*Diphascon (Diphascon) polare* sp. nov. [106]
*Diphascon pingue* ('Vaierty A') Marcus, 1936 [55]
***Terra typica*:** Victoria Land (Antarctica) [106]
**Sub-Antarctic: South Georgia [31]** and [55,106]
**Substratum:** mosses [31]
**Remarks:** Pilato and Binda [106] determined that the "variety A" of *D. pingue* described by Dastych [31] should be considered a synonym *D. polare*. Thus, the species has been recorded from Continental Antarctica and possibly also from the Sub-Antarctic, but the assumption of the latter [106] must be verified.

19. ***Diphascon puniceum* (Jennings, 1976)** [57]

*Diphascon* (*Adropion*) *puniceum* Jennings, 1976 [9]
***Terra typica*:** South Orkney Islands (Maritime Antarctic, Southern Ocean) [57]
**Sub-Antarctic: Macquarie Island [9]**
**Remarks:** In addition to the type locality, it has also been reported from other localities of the Maritime Antarctic (see e.g., [31]), as well as from Continental Antarctica (e.g., [114], although this record is questionable according to [115]), and also from Australia [116].

Subfamily: Hypsibiinae Pilato, 1969 [101]
*Hypsibius* Ehrenberg, 1848 [117]

20. ***Hypsibius convergens* (Urbanowicz, 1925)** [118]

*Macrobiotus tetradactylus* Greeff [26]
*Hypsibius* (*Hypsibius*) *convergens* (Urbanowicz) [39]
*Hypsibius (H.) convergens* (Urb.) [119]
*Hypsibius (H.) convergens* Urbanowicz, 1925 [29]
*Hypsibius convergens* (Urbanowicz, 1925) [32,40,41,55]
*Hypsibius* cfr *convergens* [8]
***Terra typica*:** Denmark, Germany, Latvia (Europe; originally Pologne-nord-est, Côte de Riga, Mecklembourg, Ile de Bornholm et Scandinavie méridionale) [118]
**Sub-Antarctic: South Georgia** [8], **[32]** and [41,55]; **Possession Island [26]** and [39,41]; **Kerguelen Islands [26,29]** and [39–41,119]; **Heard Island [26]** and [39,41]
**Substratum:** interstitial environment (probably in a stream sediment) in a sea bay at the mouth of a stream [29], mosses [26,32], mud in a pond bottom [32]
**Remarks:** In the past, it was considered a cosmopolitan species [41]. Within the Antarctic region, it has been reported from Continental Antarctica (e.g., [119]) and the Sub-Antarctic. Ramazzotti [29] expressed uncertainty about the identification of this species from the Kerguelen Islands but finally favored *H. convergens* because this species was already known from these islands (see [39]). Marcus [39] noted the presence of the species on sub-Antarctic islands based on the finding by Richters [26] of *Macrobiotus tetradactylus* Greeff [120], which Marcus considered at that time to be a synonym of *Hypsibius convergens*. Similarly, other authors who listed the species from Possession Island [41], from the Kerguelen Islands [40,41,119], and from Heard Island [41] obviously started from [39]. Convey and McInnes [8] reported the species from South Georgia, apparently on the basis of the original report in [32], but obviously had doubts about the identity of the species (without any explanation) as they called it *Hypsibius* cfr *convergens* (sic). Therefore, Velasco-Castrillón et al. [55] wrote in Supplementary material that the report of *Hypsibius convergens* from

South Georgia in [8] is probably a misidentification. Thus, the only finding of the species in South Georgia (see [32]) is questionable. So, it is clearly necessary to confirm the presence of *H. convergens* in the Sub-Antarctic. Today, we know that *Hypsibius convergens* is the nominal species of a species complex with an unknown geographic distribution. It is most likely either a Palearctic or Holarctic species [45]. Its integrative redescription based on a population from the type locality is needed [46] in order to verify the presence of the species in the Sub-Antarctic zone. Ramazzotti [29] did not state a substratum from which *H. convergens* was collected—we completed the probable substratum in the paragraph.

21. ***Hypsibius dujardini* (Doyère, 1840)** [49]

*Hypsibius* (*Hypsibius*) *dujardini* (Doy.) [39]
*Hypsibius dujardini* (Doyère, 1840) [9,31,32,55]
*Hypsibius dujardini* (Doyére, 1840) [41]
*Hypsibius* cf. *dujardini* (Doyére) [95]
*Hypsibius* cfr *dujardini* [8]
*Hypsibius dujardin* (Doyere) [48]
*Hypsibius* cfr. *dujardini* [110]
*Hypsibius* cf. *dujardini* [62,121]
***Terra typica*:** France (Europe) [49]
**Sub-Antarctic: South Georgia** [8], **[31,32]** and [41,55,62,95,110,121]; **Crozet Islands** [39]; **Macquarie Island [9,48]**
**Substratum:** mosses [31,32]
**Remarks:** *Hypsibius dujardini* is the nominal species of a complex of similar species with an apparently global distribution (although it has not yet been recorded from the Australian continent) [41,46]. Its recent integrative redescription [122] makes it possible to verify its identity outside the neotype locality (Paris), which is currently its only confirmed distribution. It is likely that *Hypsibius dujardini* sensu stricto is a Palearctic or Holarctic species [45]. Within the Antarctic region, so far, it has been reported from the Maritime Antarctic (e.g., [123]) and from the Sub-Antarctic. All these previous findings are doubtful and must be verified.

22. ***Hypsibius murrayi* (Richters, 1907)** [66]

*Macrobiotus Murrayi* n. spec. [66]
*Macrobiotus murrayi* [20]
*M. murrayi* [27]
*Hypsibius murrayi* (Richt.) [47]
*Hypsibius* sp. [9]
*Hypsibius heardensis* sp. nov. [121]
*Hypsibius heardensis* Miller, McInnes & Bergstrom, 2005 [38]
*Hypsibius murrayi* (Richters, 1907) [38]
***Terra typica*:** Crozet Islands (France, Indian Ocean) [66]
**Sub-Antarctic: South Georgia [20]**, [27] and **[38]**—*H. murrayi*; **Possession Island** [38]—*H. murrayi*, [47] and **[66]**; **Kerguelen Islands [38]**—*H. murrayi*; Main Island, Guillou Island, Mayes Island, Verte Island; **Heard Island** [38]—*H. heardensis*, *H. murrayi* and **[121]**; **Macquarie Island [9]**, [38]—*H. murrayi* and [121]
**Substratum:** mosses [38,66], (*Sanionia uncinata* (Hedw.) Loeske) [121]
**Remarks:** Apart from sub-Antarctic islands, the species has been reported from the Antarctic Peninsula (e.g., [20]). Miller et al. [121] re-examined the *Hypsibius* sp. reported by [9] from Macquarie Island and confirmed it as *H. heardensis*. According to Dastych [38], *H. heardensis* should be considered a junior synonym of *H. murrayi*.

23. ***Hypsibius pallidus* Thulin, 1911** [79]

*Hypsibius pallidus* Thulin, 1911 [8,9,31,32,41,55]
***Terra typica*:** Sweden (Europe) [79]
**Sub-Antarctic: South Georgia** [8], **[31]** and [32,41,55]; **Macquarie Island [9]**

**Substratum:** mosses [31]
**Remarks:** *Hypsibius pallidus* is a predominantly European species, but with a Holarctic distribution, and exceptionally, it has also been reported from the Southern Hemisphere [41,43,45]. Within the Antarctic region, it has only been reported from the Sub-Antarctic. It belongs to the *Hypsibius convergens–dujardini* species complex and can easily be confused with other species of the complex. According to Kaczmarek et al. [43], the presence of the species in South America is doubtful. Therefore, we are of the opinion that the presence of the species on the sub-Antarctic islands needs to be verified.

Subfamily: Itaquasconinae Bartoš (in Rudescu, 1964) [124]
*Adropion* Pilato, 1987 [125]

24. ***Adropion gordonense* (Pilato, Claxton and Horning, 1991)** [116]

*Diphascon* (*Adropion*) *gordonense* Pilato, Claxton & Horning, 1991 [9]
***Terra typica*:** New South Wales (Australia) [116]
**Sub-Antarctic: Macquarie Island [9]**
**Remarks:** The species was recorded from the type locality and Macquarie Island only [9,116].

25. ***Adropion greveni* (Dastych, 1984)** [31]

*Hypsibius* (*D.*) *scoticus* [30]
*Diphascon greveni* sp. nov. [31]
*Diphascon scoticum* (Murray, 1905) [32]
*Diphascon* (*Adropion*) *greveni* Dastych, 1984 [9,54,62]
*Adropion greveni* (Dastych, 1984) [70]
***Terra typica*:** South Shetland Islands (Maritime Antarctic, Southern Ocean) [31]
**Sub-Antarctic: South Georgia** [9], **[30]** and [31,32,54,62,70]; **Macquarie Island [9]**
**Remarks:** The species was reported only from southern Argentina [126], Maritime Antarctic (e.g., [70]), and Sub-Antarctic. According to Dastych [31], *A. greveni* was recorded as *Hypsibius* (*Diphascon*) *scoticus* Mur. by Jennings [30] from South Georgia and several other localities. Ottesen and Meier [32] reported *Diphascon scoticum* from South Georgia only on the basis of Jennings [30], so their report also referred to the finding of *A. greveni*.

26. ***Adropion scoticum* (Murray, 1905)** [127]

*Diphascon crozetense* n. sp. [66]
*Diphascon scoticum*, Murray [27]
*Hypsibius scoticus* (J. Murr.) [47]
*Hypsibius* (*Diphascon*) *scoticus* (John Murr.) [39]
*Diphascon* (*Adropion*) *scoticum* J. Murray, 1905 [41]
***Terra typica*:** Scotland (UK, Europe) [127]
**Sub-Antarctic: Possession Island** [27,39,41,47] and **[66]**
**Substratum:** moss [66]
**Remarks:** The species has previously been considered cosmopolitan [41]. Insufficient morphological description of the species has led to the reporting of various similar species from around the world under the same name. An integrated description of the nominal species of this complex is needed [46] to be able to verify whether specimens, primarily from non-European locations, belong to *Adropion scoticum* sensu stricto. Therefore, we also consider reports of this species from the Antarctic region to be doubtful and that these may potentially represent new species. *Diphascon crozetense* is a synonym of *A. scoticum*, according to Murray [27].

*Guidettion* Gąsiorek and Michalczyk, 2020 [128]

27. ***Guidettion prorsirostre* (Thulin, 1928)** [59]

*Diphascon* (*Adropion*) *prosirostre* Thulin, 1928 [9]
***Terra typica*:** Sweden, Germany, Scotland (UK) (Europe) [59]
**Sub-Antarctic: Macquarie Island [9]**

**Remarks:** This species has been reported mainly from the Holarctic region [41]. It requires a modern revision based on new material from the type locality. Species records from the Southern Hemisphere (Chile, New Zealand, Sub-Antarctic) are doubtful and require re-examination (see [46]).

Subfamily: Pilatobiinae Bertolani, Guidetti, Marchioro, Altiero, Rebecchi and Cesari, 2014 [129]
*Pilatobius* Bertolani, Guidetti, Marchioro, Altiero, Rebecchi and Cesari, 2014 [129]

28. ***Pilatobius rugosus* (Bartoš, 1935)** [130]

*Diphascon* (*Diphascon*) cf. *rugosum* (Bartoš, 1935) [9]
***Terra typica*:** Slovakia (Europe) [130]
**Sub-Antarctic: Macquarie Island [9]**
**Remarks:** Due to the fact that *Pilatobius rugosus* was originally described from Europe and probably has a Holarctic distribution (see [41,44]), and also because individuals from Macquarie Island did not correspond to the original description of the species [9], it is most likely that these records represent a different species. The presence of *Pilatobius rugosus* in the Sub-Antarctic zone must therefore be verified.

*Incerta subfamilia* [129]
*Acutuncus* Pilato and Binda, 1997 [131]

29. ***Acutuncus antarcticus* (Richters, 1904)** [26,66]

*Hypsibius* (*H.*) *antarcticus* [30]
*Hypsibius arcticus* (Murray, 1907) [31]
*Hypsibius antarcticus* Richters, 1904 [32]
*Hypsibius arcticus* Murray, 1910 [32]
*Hypsibius antarcticus* (Richters, 1904) [41,132]
*Hypsibius arcticus* (J. Murray, 1907) [41]
*Hypsibius antarcticus*? [133]
*Acutuncus antarcticus* (Richters, 1904) [8,9,55,121,123,134]
*Acutuncus antarcticus* Richters [135]
*Acutuncus antarcticus* [92,110,136]
***Terra typica*:** Kaiser Wilhelm II Land (Antarctica) [26,66]
**Sub-Antarctic: South Georgia** [8], **[30]**, **[31]**—eggs only, [32,41]—*H. antarcticus*, *H. arcticus*, [55], **[92]** and [110,123,132,134,136]; **Heard Island** [121], **[133]** and [134–136]; **Macquarie Island [9]** and [134,136]
**Substratum:** filamentous green algae in a freshwater pool [121,133], mosses [31]
**Remarks:** In the past, in addition to the Antarctic region, it was also reported from Europe, Greenland, and sporadically from South America [41,43]. According to Dastych [132], all records of *Hypsibius arcticus* (Murray, 1907) [137] in Antarctica must be considered to be *Hypsibius antarcticus* (Richters). The species can be considered pan-Antarctic, as it is distributed in the Continental, Maritime, and Sub-Antarctic zones. However, a population from Dronning Maud Land showed a sufficient genetic distance from other genetically studied populations for it to be considered a potentially new species [134] (see also [138]). Therefore, we suggest that the populations on the sub-Antarctic islands should be genetically tested to confirm that they do not belong to another yet unknown similar species. That pending, we can tentatively consider them as populations of *A. antarcticus*.

Family: Ramazzottiidae Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008 [92]
*Hebesuncus* Pilato, 1987 [125]

30. ***Hebesuncus mollispinus* Pilato, McInnes and Lisi, 2012** [139]

*Hebesuncus mollispinus* sp. nov. [139]
*Hebesuncus mollispinus* Pilato, McInnes & Lisi, 2012 [55]
***Terra typica*:** Charcot Island (Maritime Antarctic, Southern Ocean) [139]
**Sub-Antarctic: South Georgia** [55] and **[139]**
**Substratum:** moss (*Andreaea* Hedw.) [139]

**Remarks:** So far, the species has been recorded only from the Maritime Antarctic and Sub-Antarctic [139].

31. ***Hebesuncus schusteri* (Dastych, 1984)** [31]

*Hebesuncus* cf. *schusteri* Dastych, 1984 [9]
*Hebesuncus schusteri* (Dastych 1984) [139]
***Terra typica*:** Enderby Land (Antarctica) [31]
**Sub-Antarctic: Macquarie Island [9]** and [139]
**Remarks:** So far, the species has been reported only from the Antarctic region: Continental Antarctica (e.g., [140]—as *Hebesuncus* cf. *schusteri*), Maritime Antarctic (e.g., [31]), and Sub-Antarctic. Miller et al. [9] reported the species as *Hebesuncus* cf. *schusteri* due to the absence of eggs, so the presence of the species in the Sub-Antarctic zone requires confirmation.

*Ramazzottius* Binda and Pilato, 1986 [141]

32. ***Ramazzottius oberhaeuseri* (Doyère, 1840)** [49]

*Macrobiotus Oberhäuseri* Doyère [26]
*Macrobiotus Oberhäuseri* Doy. [66]
*Hypsibius oberhaeuseri* (Doy.) [47]
*Hypsibius oberhaeuseri* (Doyère, 1840) [31]
*Ramazzottius oberhaeuseri* (Doyère, 1840) [32]
*Ramazzottius oberhaeuseri* (Doyére, 1840) [41]
*Ramazzottius* cfr *oberhaeuseri* [8]
*Ramazzottius oberhäuseri* (Doyère, 1840) [55]
***Terra typica*:** France and Germany (Europe) [46]
**Sub-Antarctic: South Georgia** [8], **[31]** and [32,41,55]; **Kerguelen Islands [26]**, [41,47] and **[66]**; **Heard Island [66]**
**Substratum:** mosses [26,31,66]
**Remarks:** *Ramazzottius oberhaeuseri* was previously considered a single cosmopolitan species [41]. However, a complex of similar species exists, some of which have already been described, and the geographic distribution of the nominal species has to be revised in the future [142]. The species was recently redescribed [143], and so far, the only confirmed report is its neotype location in Paris. However, this integrative redescription now allows for the verification of other records of the species [46]. Within the Antarctic region, besides the Sub-Antarctic, it has been reported from Continental Antarctica (e.g., [119]), and also from the Maritime Antarctic (e.g., [74]). Richters [66] listed the species only from the Kerguelen Islands on p. 295, while the table on p. 265 mentioned it only from Heard Island. It is possible that one of these two data is a mistake.

Superfamily: Isohypsibioidea Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008 [92]
Family: Doryphoribiidae Gąsiorek, Stec, Morek and Michalczyk, 2019 [144]
*Grevenius* Gąsiorek, Stec, Morek and Michalczyk, 2019 [144]

33. ***Grevenius asper* (Murray, 1906)** [145]

*Macrobiotus tetradactylus* Greeff [26]
*Macrobiotus tetradactyloides* n. sp. [66]
*Macrobiotus asper* Murray [20]
*M. asper* [27]
*Hypsibius asper* (J. Murr.) [47]
*Hypsibius tetradactyloides* (Richt.) [47]
*Hypsibius tetradactylus* (Greeff) [47]
*Hypsibius* (*Isohypsibius*) *asper* (John Murr.) [39]
*Hypsibius* (*Isohypsibius*) *tetradactyloides* (Richters) [39]
*Hypsibius* (*Isohypsibius*) *asper* (J. Murray) [28]
*Hypsibius* (*Isohypsibius*) *asper* [30]
*Isohypsibius asper* (J. Murray, 1906) [40,41,54]

*Isohypsibius tetradactyloides* (Richters, 1907) [37,40,41,121]
*Isohypsibius asper* (Murray, 1906) [32,37]
*Isohypsibius asper*; Murray (1906) [8]
*Isohypsibius asper* Murray, 1906 [55]
***Terra typica*:** South Orkney Islands (Maritime Antarctic, Southern Ocean) [145]
**Sub-Antarctic: South Georgia** [8], **[20]**, [27], **[30]**, [32], [37,40,41]—*I. asper*, [39,47]—*H. asper* and [54,55]; **Possession Island [26]**, **[37]**—*I. asper*, *I. tetradactyloides*, [39]—*H. tetradactyloides*, [40,41]—*I. tetradactyloides*, [47]—*H. tetradactyloides*, *H. tetradactylus* and **[66]**; **Kerguelen Islands [26,28]**, **[37]**—*I. asper, I. tetradactyloides*, [41]—*I. asper*, *I. tetradactyloides* and [47]—*H. tetradactylus*; **Heard Island [26]**, [37,40,41]—*I. tetradactyloides*, [39]—*H. tetradactyloides*, [47]—*H. tetradactyloides*, *H. tetradactylus*, **[66]** and [121]
**Substratum:** algae [28], mosses [26,66]
**Remarks:** According to McInnes [41], *I. asper* occurs in Europe, the Maritime Antarctic (see also, e.g., [114]), and Sub-Antarctic, while *I. tetradactyloides*, apart from Europe, has also been sporadically recorded in Asia, Africa, North America, South America, and the Sub-Antarctic. According to Dastych [37], the finding of *Macrobiotus tetradactylus* Greeff [120] in Kerguelen by Richters [26] refers instead to *I. tetradactyloides*, and it is a junior synonym of *Isohypsibius asper*. Since, in addition, *Macrobiotus tetradactyloides* [66] was described from the Sub-Antarctic zone (from the Possession and Heard Islands), the occurrence of *Grevenius asper* on the sub-Antarctic islands does not raise fundamental doubts. Marcus [28] reported *Hypsibius* (*Isohypsibius*) *asper* from "Géorgie du Sud (île Paulet)". However, we have not been able to verify a location named in this way in relation to South Georgia. The interpretation of the location is complicated by the presence of a Paulet Island off the northern coast of the Antarctic Peninsula. Therefore, we did not include the citation [28] in the list for South Georgia.

Family: Isohypsibiidae Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008 [92]
*Dianea* Gąsiorek, Stec, Morek and Michalczyk, 2019 [144]

34. ***Dianea papillifera* (Murray, 1905)** [146]

*Isohypsibius papillifer* (J. Murray, 1905) [8,54]
*Isohypsibius papillifer* [136]
*Isohypsibius papillifer* Murray, 1905 [55]
***Terra typica*:** Scotland (UK, Europe) [146]
**Sub-Antarctic: South Georgia** [8], **[54]** and [55,136]
**Remarks:** The species has been sporadically reported from all continents, suggesting a species complex [41,43]. Because of the insufficient original description in [146], further study of the type material or an integrative redescription using a topotype population is needed to clarify the actual distribution of the species. Given that the species was described from Europe, its report from South Georgia seems doubtful and has to be verified.

35. ***Dianea sattleri* (Richters, 1902)** [147]

*Macrobiotus Sattleri* Richters [26,66]
*Hypsibius sattleri* (Richt.) [47]
*Hypsibius* (*Isohypsibius*) *sattleri* (Richters) [39]
*Isohypsibius sattleri* Richters, 1902 [41]
*Isohypsibius* cf. *sattleri* (Richters, 1902) [9]
***Terra typica*:** Germany, Switzerland (Europe) [147]
**Sub-Antarctic: Possession Island [26]**, [39,41,47] and **[66]**; **Kerguelen Islands [26]**, [39,41,47] and **[66]**; **Macquarie Island [9]**
**Substratum:** mosses [26,66]
**Remarks:** Past species records have suggested a cosmopolitan distribution of the species [41]. It was morphologically redescribed by Dastych [148] using the original Richters slide. Within the Antarctic region, it has been reported from the Maritime Antarctic (e.g., [57]) and Sub-Antarctic. The literature-based, supposedly cosmopolitan distribution [41] requires taxonomic re-evaluation of all the specimens attributed to *I. sattleri* [45]. In view of

the fact that the species was described from Europe, we consider all its records from the Sub-Antarctic zone to be doubtful, and it will be necessary to confirm them. The species needs an integrative redescription based on a topotype population [46] so that its actual distribution can be clarified.

*Isohypsibius* Thulin, 1928 [59]

36. ***Isohypsibius prosostomus* Thulin, 1928** [59,79]

*Isohypsibius prosostomus* Thulin, 1928 [8,31,32,41,55]
***Terra typica*:** Sweden (Europe) [79]
**Sub-Antarctic: South Georgia** [8], **[31]** and [32,41,55]
**Substratum:** mosses [31]
**Remarks:** Thulin [79] described the "Swedish form" of *Hypsibius tetradactylus* (Greeff) and later renamed it *Isohypsibius prosostomus* in [59]. The species has a largely Palearctic or Holarctic distribution, with just some records from other regions. So far, it has not been reported from Continental or Maritime Antarctica [41]. It probably comprises a species complex. The original description of *I. prosostomus* lacks important details, and a re-evaluation of the type material is required to clarify the subsequent conflicting descriptions [45]. For example, according to Ramazzotti and Maucci [40], *I. prosostomus* has cuticular bars on legs I–III, although these were not mentioned in the original species description [59]. The identity of specimens from South Georgia that have been attributed to this species needs to be verified.

*Ursulinius* Gąsiorek, Stec, Morek and Michalczyk, 2019 [144]

37. ***Ursulinius nodosus* (Murray, 1907)** [81]

*Macrobiotus nodosus*, Murray [27]
*Isohypsibius nodosus* (J. Murray, 1907) [40,41]
*Macrobiotus nodosus* Murray, 1907 [9,33]
***Terra typica*:** Republic of South Africa (Africa) [81]
**Sub-Antarctic: Macquarie Island** [9], **[27]** and [33,40,41]
**Remarks:** The species has been reported from a limited number of localities from each continent, with the exception of Australia and Antarctica [41], which indicates a possible species complex [45]. It was considered a nomen dubium by Dastych [149]. The species identity of the specimens from Macquarie Island must be verified.

Family: Ramajendidae Tumanov, 2022 [150]
*Ramajendas* Pilato and Binda, 1990 [151]

38. ***Ramajendas heatwolei* Miller, Horning and Dastych, 1995** [33]

*Ramajendas heatwolei* nov. sp. [33]
*Ramajendas heatwolei* Miller, Horning & Dastych, 1995 [9]
*Ramajendas heatwolei* Miller and others, 1995 [123]
***Terra typica*:** Macquarie Island (Australia, Pacific Ocean) [33]
**Sub-Antarctic: Macquarie Island [9,33]** and [123]
**Substratum:** plant (*Colobanthus muscoides* Hook. f.) [33]
**Remarks:** The species is currently known from the type locality only.

39. ***Ramajendas renaudi* (Ramazzotti, 1972)** [29]

*Hypsibius* (*Isohypsibius*) *renaudi* sp. nov. [29]
*Hypsibius* (*Isohypsibius*) *renaudi* Ramazzotti, 1972 [57]
*Isohypsibius renaudi* (Ramazzotti, 1972) [40]
*Hypsibius renaudi* Ramazzotti, 1972 [31]
*Ramajendas renaudi* (Ramazzotti, 1972) [9,33,41,123]
***Terra typica*:** Kerguelen Islands (France, Indian Ocean) [29]
**Sub-Antarctic: Kerguelen Islands** [9], **[29]** and [31,33,40,41,57,123]
**Substratum:** sand in slightly brackish water [29]

**Remarks:** In addition to the type locality, it has also been reported from the Maritime Antarctic zone (e.g., [152]). Pilato and Binda [151], as well as Miller et al. [33], however, consider some reports of the species from this area to represent *R. frigidus*. This interpretation still requires verification.

Superfamily: Macrobiotoidea Thulin, 1928 (in Marley et al. 2011) [59,102]
Family: Macrobiotidae Thulin, 1928 [59]
*Macrobiotus* C.A.S. Schultze, 1834 [153]

40. ***Macrobiotus denticulus* Dastych, 2002** [36]

*Macrobiotus denticulus* sp. nov. [36]
***Terra typica*:** Kerguelen Islands (France, Indian Ocean) [36]
**Sub-Antarctic: Kerguelen Islands [36]**
**Substratum:** moss [36]
**Remarks:** According to Dastych [36], some of the individuals of *M. hufelandi* reported from Kerguelen by Richters [66] belong to the species *M. denticulus*. The species is currently only known from the type locality.

41. ***Macrobiotus echinogenitus* Richters, 1903** [68,154]

*Macrobiotus echinogenitus* Richters [26,66]
*Macrobiotus echinogenitus* Richters, 1903 [41]
***Terra typica*:** Spitsbergen (Norway, Arctic Ocean) [154]
**Sub-Antarctic: Possession Island** [41] and **[66]**; **Kerguelen Islands [26]**, [41] and **[66]**
**Substratum:** mosses [26,66]
**Remarks:** It is the nominal species of a cosmopolitan species group requiring taxonomic redescription to clarify its distribution [45,46]. Within the Antarctic region, it has been reported from the Maritime Antarctic (e.g., [145]) and Sub-Antarctic zones. All these findings are doubtful and will need to be verified after a redescription of the species.

42. ***Macrobiotus hufelandi* C.A.S. Schultze, 1834** [153]

*Macrobiotus Hufelandi* Schultze [26]
*Macrobiotus Hufelandi* C. Schultze [66]
*Macrobiotus hufelandi* C. A S. Schultze [20]
*Macrobiotus hufelandii* C. A. S. Schultze [47]
*Macrobiotus hufelandi* Schultze, 1833 [31,41]
*Macrobiotus* cf. *hufelandi* Schultze, 1833 [21]
*Macrobiotus hufelandi* Schultze, 1843 [32]
*Macrobiotus* cfr *hufelandi* [8]
*Macrobiotus* cf. *hufelandi* [55]
***Terra typica*:** Germany (Europe) [153]
**Sub-Antarctic: South Georgia** [8,21], **[31,32]** and [41,55]; **Possession Island [26]** and [41,47]; **Kerguelen Islands** [20,21,41,47] and **[66]**
**Substratum:** lichens [32], mosses [26,31,66]
**Remarks:** The species has long been considered cosmopolitan [41]. It is currently the nominal species for the *Macrobiotus hufelandi* group, a group of several dozen morphologically similar species (see e.g., [155]). Within the Antarctic region, it has been reported from Continental Antarctica (e.g., [156]), from the Maritime Antarctic (e.g., [21]), and from the Sub-Antarctic. All original reports of the species (and this also applies to the Antarctic region) that preceded the revision of the species [157,158] must be considered doubtful and need to be verified. Richters [66] noticed that not all the individuals of this species from Kerguelen Islands are the same—he especially noted differences in the processes of the eggs, and this, in our opinion, indicates that at least two species of the genus *Macrobiotus* were in his material. In his paper describing *Macrobiotus denticulus*, Dastych [36] wrote that, based on Richters' photomicrograph (Plate 20, Figure 4) in [66], the egg shown does not belong to that species nor to *M. hufelandi* but to another supposedly new species of the *hufelandi* group, and that this additional new species was also found in Dastych's Kerguelen Islands

material, though less frequently, and it was more similar to *M. hufelandi* (as re-defined by Bertolani and Rebecchi [157]) than to *M. denticulus*.

*Mesobiotus* Vecchi, Cesari, Bertolani, Jönsson, Rebecchi and Guidetti, 2016 [64]

43. ***Mesobiotus furciger* (Murray, 1907)** [145,159]

*Macrobiotus furcatus* Murray [20]
*Macrobiotus furciger*, Murray [27]
*Macrobiotus furciger* J. Murr. [47]
*Macrobiotus furciger* John. Murr. [39]
*Macrobiotus furciger* [30,110]
*Macrobiotus furciger* Murray, 1907 [31]
*Macrobiotus furciger* Murray, 1906 [32,160]
*Macrobiotus furciger* J. Murray, 1906 [41]
*Macrobiotus* sp. (? *M. furciger* J. Murray) [95]
*Macrobiotus* cf. *furciger* Murray, 1907 [9]
*Macrobiotus furciger*; Murray (1906) [8]
*M. furciger* [136]
Macrobiotus cf. furciger [62]
***Terra typica*:** South Orkney Islands (Maritime Antarctic, Southern Ocean) [145]
**Sub-Antarctic: South Georgia** [8], **[20]**, [27], **[30–32]** and [39,41,47,62,95,110,160]; **Marion Island [136]**; **Macquarie Island [9]**
**Substratum:** mosses [31,32], mud from a pond bottom, soil [32]
**Remarks:** Murray [145] first described the species under the name *Macrobiotus furcatus*. He later described it again and renamed it *Macrobiotus furciger* [159]. Therefore, *M. furcatus* Murray (non-Ehrenberg) is a synonym of *M. furciger* [47]. Binda et al. [160] redescribed *M. furciger* sensu stricto on the basis of material from South Georgia, which is outside the locus typicus of the species. According to Short et al. [161], it is unlikely that the redescribed South Georgia specimens represent *Mesobiotus furciger* sensu stricto because the redescription was not based on a topotype population, and the authors found substantial genetic differences between different geographic regions. The species is in need of an integrative redescription based on a topotype population [46]. Due to doubts about the identity of *M. furciger* specimens from South Georgia [62,95], as well as in Macquarie Island [9], we consider it necessary to verify the occurrence of this species in the Sub-Antarctic.

44. ***Mesobiotus harmsworthi* (Murray, 1907)** [137]

*Macrobiotus harmsworthi* Murray [162]
*Macrobiotus harmsworthi* J. Murr. [47]
*Macrobiotus harmsworthi* John Murr. [39]
*Macrobiotus harmsworthi* J. Murray, 1907 [41]
*Macrobiotus* cf. *harmsworthi* Murray, 1907 [9]
***Terra typica*:** Franz Joseph′s Land (Russia, Arctic Ocean), Svalbard (Norway, Arctic Ocean) [137]
**Sub-Antarctic: Kerguelen Islands** [39,41,47] and **[162]**; **Macquarie Island [9]**
**Substratum:** moss (*Racomitrium crispulum*) [9]
**Remarks:** *Mesobiotus harmsworthi* sensu stricto was recently redescribed using integrative taxonomy by Kaczmarek et al. [163] as being from the neotype locality in Svalbard, and this is its only currently confirmed locality. It is a nominal species for a morphogroup of very similar species with a cosmopolitan distribution, and its redescription allows the verification of records for this species outside the neotype locality ([46]; see Kaczmarek et al. [164] for diagnostic key). Within the Antarctic region, it has been reported from Continental Antarctica (e.g., [115]), from the Maritime Antarctic (e.g., [165]), and also from the Sub-Antarctic. According to Miller et al. [9], their specimens belong to the *harmsworthi* group but, without embryonate eggs, it is not possible to identify the animals to the species level. They further stated that there may be several species in their collections; one may be new, but they must remain unspecified until material with both adult animals and eggs can

be examined. All the sub-Antarctic taxa attributed to *Mesobiotus harmsworthi* are doubtful and need to be verified.

45. ***Mesobiotus liviae* (Ramazzotti, 1962)** [166]

*Macrobiotus* cfr. *liviae* Ramazzotti, 1962 [31]
*Macrobiotus liviae* Ramazzotti, 1962 [32,41]
*Macrobiotus* cf. *liviae* Dastych, 1984 [41]
*Macrobiotus* cfr *livia* [8]
*Macrobiotus* cf. *liviae* [55]
***Terra typica*:** Chile (South America) [166]
**Sub-Antarctic: South Georgia** [8], **[31,32]** and [41,55]
**Substratum:** lichens, mud from a pond bottom [32], mosses [31,32]
**Remarks:** So far, the species has only been reported from Chile, the Dominican Republic, the U.S.A., and New Zealand [41,44], and from the Antarctic region, only from the South Orkney Islands [167] and South Georgia. The occurrence of the species in the Antarctic region must be verified due to previous uncertainty in its identification (see [31,167]).

*Minibiotus* R.O. Schuster, 1980 [90]

46. ***Minibiotus asteris* Claxton, 1998** [168]

*Minibiotus asteris* Claxton, 1998 [9]
***Terra typica*:** Tasmania (Australia, Pacific Ocean) [168]
**Sub-Antarctic: Macquarie Island [9]**
**Remarks:** Currently, the species is known only from southern Australia, southern New Zealand [46], and the sub-Antarctic Macquarie Island.

47. ***Minibiotus intermedius* (Plate, 1888)** [105]

*Macrobiotus intermedius* Plate [26,39,47,66]
*Minibiotus intermedius* (Plate, 1888) [41]
***Terra typica*:** Chile (South America) and Germany (Europe) [105]; neotype from Germany [169]
**Sub-Antarctic: Possession Island [26]**, [39,41,47] and **[66]**
**Substratum:** mosses [26,66]
**Remarks:** First considered a cosmopolitan species [41] due to an insufficient original description [105], which was based on individuals from two continents, after the revision of the genus *Minibiotus* [168], the species was recognized as representing a complex of species. Within the Antarctic region, the species has only been reported from the Sub-Antarctic zone. We consider all reports of the species prior the morphological revision of the genus *Minibiotus* [168], and thus also before the integrative redescription of *Minibiotus intermedius* [169], doubtful and in need of further study.

Family: Murrayidae Guidetti, Rebecchi and Bertolani, 2000 [170]
*Dactylobiotus* R.O. Schuster, 1980 [90]

48. ***Dactylobiotus ambiguus* (Murray, 1907)** [171]

*Macrobiotus ambiguus* J. Murray [28]
*Pseudobiotus augusti* [172]
*Dactylobiotus ambiguus* (J. Murray, 1907) [41,54]
*Dactylobiotus* cf. *ambiguus* (Murray, 1907) [9]
*Dactylobiotus* cfr *ambiguus* [8]
*Dactylobiotus* cfr. *ambiguus* [110]
*Dactylobiotus ambiguus* (Murray, 1907) [55]
***Terra typica*:** Shetland Islands (UK, Atlantic Ocean), Spitsbergen (Norway, Arctic Ocean) [171]
**Sub-Antarctic: South Georgia** [8], **[54]** and [55,110]; **Marion Island [28]** and [41]; **Possession Island [28]** and [41]; **Heard Island [9]**; **Macquarie Island [9,172]**
**Remarks:** This species has a largely Palearctic or high-latitude Holarctic distribution, with limited reports from other regions [41]. Within the Antarctic region, the species

has been reported not only from the Sub-Antarctic, but also from the Maritime Antarctic zone (e.g., [173]). In light of the description of *Dactylobiotus caldarellai* Pilato and Binda, 1994 [174] from Tierra del Fuego and *D. ovimutans* Kihm, Kim, McInnes, Zawierucha, Rho, Kang and Park, 2020 [175] from South Shetland Islands (Maritime Antarctic), all records of *D. ambiguus* from the Southern Hemisphere should be revisited [9]. Similarly, according to McInnes and Convey [110], the Antarctic form of *Dactylobiotus ambiguus* is possibly synonymous with *D. caldarellai*. Watson [176] (according to Miller et al. [33]), Miller et al. [9], and Selkirk et al. [172] reported the occurrence of *Thulinius augusti* (Murray, 1907) [171] from Macquarie Island. Later analysis of some of the original samples and original microscopic slides [9] determined that the material did not represent *Thulinius augusti* but rather *Dactylobiotus* cf. *ambiguus*. Miller et al. [9] stated that *D. ambiguus* had been found in South Georgia and cited Ottesen and Meier [32], but we omit this information here because Ottesen and Meier [32] reported *D. dispar* and not *D. ambiguus* from South Georgia.

49. ***Dactylobiotus dispar* (Murray, 1907)** [177]

*Dactylobiotus dispar* (Murray, 1907) [32]
*Dactylobiotus dispar* (J. Murray, 1907) [41]
***Terra typica*:** United Kingdom (Europe), Spitsbergen (Norway, Arctic Ocean), Franz Joseph′s Land (Russia, Arctic Ocean) [177]
**Sub-Antarctic: South Georgia [32]** and [41]
**Substratum:** moss, mud from a pond bottom [32]
**Remarks:** While the species has been reported from every continent, its distribution is predominantly Palearctic [41]. Within the Antarctic region, it has only been reported in the Sub-Antarctic zone. Given that the species was originally described from the Palearctic region, and the report of the species from South Georgia was not supported with eggs (at least, the authors did not mention them), we consider it necessary that the presence of *D. dispar* in South Georgia be confirmed.

## 4. Discussion

In addition to the forty-nine currently valid species listed, the following taxa were also reported from the Sub-Antarctic but were not included in the above list:

- *Echiniscus muscicola* Plate, 1888 [105]: Reported from Kerguelen Islands by Richters [66]. The taxonomical status of the species is now considered unclear. It is considered a species inquirenda in [39,47]. It is currently invalid, and due to the insufficient description of the species based on immature specimens [137], it is not possible to identify it with any currently valid species.
- *Macrobiotus krynauwi* Dastych and Harris, 1995 [178]: Reported from South Georgia by Velasco-Castrillón et al. [55] (Supplementary Material, Table S1) based on data in Dastych [31] and Convey and McInnes [8]. However, we did not find a mention of this species in Dastych [31]. Convey and McInnes [8] do list *Macrobiotus krynauwi*, but only in Continental Antarctica. Therefore, we consider the report of the species from South Georgia in Velasco-Castrillón et al. [55] a mistake.
- *Macrobiotus Vanhöffeni* Richters, 1904: Richters [26] described it from Possession Island. The taxonomical status of the species is now considered unclear. It is considered a species dubia in [39,47]. We cannot identify this now invalid species with any of the valid ones because of the insufficient description.

From the list, we also omitted reports of tardigrades from cold temperate oceanic islands (see Introduction), which the recording authors considered to be sub-Antarctic: Île Saint-Paul [20,21], Snares Islands [17], and Campbell Island [17,18].

## 5. Conclusions

Of the 49 species reported from the Sub-Antarctic zone, 9 species (18%) were originally described directly from the Sub-Antarctic, 8 species (16%) were described from the Maritime

Antarctic, and 5 species (10%) from Continental Antarctica. Almost half of the species (twenty-two species—45%) were originally described from European localities, three species (6%) were described from southern parts of Australia, one species (2%) from South Africa, and one species (2%) from South America.

Of these 49 recorded species, we consider the records of 29 species (59%) to be doubtful, and new or re-evaluated material is necessary to verify their status in this zone (see also Table 1).

**Table 1.** Tardigrada species reported from islands of the Sub-Antarctic (islands/island groups and species in alphabetical order).

| Island/Island Group | Species | References |
| --- | --- | --- |
| Heard Island | ***Acutuncus antarcticus***, *Dactylobiotus ambiguus*, *Echiniscus merokensis*, ***Grevenius asper***, *Hypsibius convergens*, ***H. murrayi***, *Ramazzottius oberhaeuseri* | [9,26,37–41,47,66,69,121,133–136] |
| Kerguelen Islands | *Dianea sattleri*, ***Echiniscus kerguelensis***, ***Grevenius asper***, *Hypsibius convergens*, ***H. murrayi***, ***Macrobiotus denticulus***, *M. echinogenitus*, *M. hufelandi*, *Mesobiotus harmsworthi*, *Milnesium tardigradum*, *Pseudechiniscus suillus*, ***Ramajendas renaudi***, *Ramazzottius oberhaeuseri* | [9,20,21,26,28,29,31,33,36–41,47,57,66,93,94,119,123,162] |
| Macquarie Island | ***Acutuncus antarcticus***, ***Adropion gordonense***, ***A. greveni***, *Barbaria jenningsi*, *Calohypsibius ornatus*, *Dactylobiotus ambiguus*, *Dianea sattleri*, ***Diphascon langhovdense***, *D. pingue*, ***D. puniceum***, ***Echiniscus darienae***, *E. spiniger*, *Guidettion prorsirostre*, *Hebesuncus schusteri*, *Hypsibius dujardini*, ***H. murrayi***, *H. pallidus*, *Mesobiotus furciger*, *M. harmsworthi*, *Milnesium tardigradum*, ***Minibiotus asteris***, *Pilatobius rugosus*, *Pseudechiniscus suillus*, ***Ramajendas heatwolei***, *Ursulinius nodosus* | [9,27,33,38,40,41,48,121,123,134,136,139,172] |
| Marion Island | ***Barbaria jenningsi***, *Calohypsibius ornatus*, *Dactylobiotus ambiguus*, *Mesobiotus furciger*, *Milnesium tardigradum*, *Pseudechiniscus suillus* | [21,28,41,55,96,136] |
| Possession Island | *Adropion scoticum*, *Dactylobiotus ambiguus*, *Dianea sattleri*, ***Grevenius asper***, *Hypsibius convergens*, *H. dujardini*, ***H. murrayi***, *Macrobiotus echinogenitus*, *M. hufelandi*, *Minibiotus intermedius*, ***Mopsechiniscus frenoti***, *Pseudechiniscus suillus* | [16,26–28,34,35,37–41,47,66] |
| South Georgia | ***Acutuncus antarcticus***, ***Adropion greveni***, ***Barbaria jenningsi***, *Calohypsibius ornatus*, *Dactylobiotus ambiguus*, *D. dispar*, *Dianea papillifera*, *Diphascon dastychi*, ***D. mirabilis***, *D. pingue*, *D. polare*, ***Grevenius asper***, ***Hebesuncus mollispinus***, *Hypsibius convergens*, *H. dujardini*, ***H. murrayi***, *H. pallidus*, *Isohypsibius prosostomus*, *Macrobiotus hufelandi*, *Mesobiotus furciger*, *M. liviae*, ***Milnesium antarcticum***, *M. tardigradum*, ***Mopsechiniscus imberbis***, ***Oreella mollis***, *Ramazzottius oberhaeuseri*, ***Testechiniscus macronyx*** | [8,9,16,20,21,27,30–32,34,35,37–41,47,54,55,61,62,70,88,92,95,106,110,121,123,132,134,136,139,160] |

bold = species whose occurrence on the island is considered probable; bold and underlined = species whose occurence on the island is certain as the island is its type locality.

We ascertained a total of 90 combinations of species and islands/island groups (see also Table 1), of which 40 were not listed either in the review by McInnes [41], mainly because these records were published after 1994, or in the review by Velasco-Castrillón [55], who included in the list of taxa in Table S1 in Supplementary Material only records from a single sub-Antarctic island (South Georgia). Of the 90 species occurrences on specific islands/island groups, 58 (64%) require confirmation as we currently consider them doubtful (see also Table 1).

As can be seen from the above, the fauna of the sub-Antarctic islands is only very superficially known, and the occurrence of most species in this zone must be verified. Furthermore, with a sufficiently detailed survey, the presence of several hitherto unknown species of tardigrades will certainly be found on these islands.

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