Tardigrades of the Ivohibory forest (south-central Madagascar) with a description of a new Bryodelphax species

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Abstract
In this paper, samples of mosses and lichens collected from Ivohibory Forest (south-central Madagascar) were studied in search for tardigrades. In total, 39 tardigrade taxa were identified, 21 of which are new records for Madagascar. Moreover, one of these is a new species for science. Bryodelphax beniowskii sp. nov., described here based on morphological analysis. It is most similar to Bry. olszanowskii and Bry. parvuspolaris, but differs from them mainly by ventral plates arrangement and some other morphometric characters.

Keywords: Bryodelphax beniowskii sp. nov., heterotardigrada, Madagascar, Tardigrada, taxonomy

Introduction
Madagascar is the world’s fourth-largest Island located in the Indian Ocean around 400 km to the east of the eastern shores of Africa. It stretches between ~12° to ~28°S latitude, occupying in total ca. 590,000 km². Although originally a part of Gondwana, Madagascar Plate broke away from it together with Antarctic, Indian and Australian plates. Madagascar finally separated from the Seychelles and India ca. 66–90 million years ago, leading to its current form. Due to this unique history, the Island is sometimes called a microcontinent (de Wit 2003; Kusky et al. 2007).

Madagascar is characterised by a tropical climate with two climatic zones, each with its own distinct type of vegetation formations. The eastern side of the Island is covered in various evergreens, while its western part is mostly covered by deciduous flora. These zones are divided by a central mountain range, stretching along north-south axis of the Island (Du Puy & Moat 1996). Both zones are divided into several regions, each of which has distinctive climatic characteristics and a set of unique habitats.

Madagascar is characterised by high biological endemism, estimated at > 90% for terrestrial vertebrates and > 80% for vascular plants, and many of the taxa recorded on the Island are only found in one or very few localities (Goodman & Benstead 2003; Wilmé et al. 2006; Callmander et al. 2011). Currently, there are few taxa that are believed to be leftovers from the time when Madagascar was part of Gondwana, while most are assumed to be results of influx from Africa and Asia and subsequent speciation (Yoder & Nowak 2006; Warren et al. 2010; Buerki et al. 2013).

The study area, i.e. Ivohibory Forest is located in south-central Madagascar (approximately 22.598830S, 46.720841E, Ivohibe District, Fianarantsoa Province). It is predominantly covered by humid rainforest, situated on the eastern slopes of a hill
located on the dry side of the main mountain range. It is estimated to cover an area of 1,400 ha, with an elevation ranging between 900 and 1,500 m above sea level. The forest is surrounded by man-made savannah, as well as micropatches of dry forest (Wright & Houlihan 2017).

The phylum Tardigrada consists of ca. 1,400 species (Guidetti & Bertolani 2005; Degma & Guidetti 2007; Degma et al. 2021) that can be found in terrestrial, freshwater and marine environments around the world (Ramazzotti & Maucci 1983 and later translation by Beasley 1995; McInnes 1994; Nelson et al. 2015). Our knowledge on the diversity and distribution of terrestrial tardigrades in Madagascar is very poor. Up to this day, 23 species were reported from this Island, including 10 for which this is their type locality, i.e., *Cornechiniscus madagascariensis* Maucci, 1993, *Echiniscus succineus* Gąsiorek & Vončina, 2019, *Kristensenisius walteri* (Pilato & Lisi, 2003), *Macrobiotus madagassus* Maucci, 1993, *Macrobiotus porifini* Kuzdrowska, Mioduchowska, Gawlak, Bartylak, Kepel, Kepel & Kaczmarek, 2021, *Mesobiotus fiedleri* Kaczmarek, Bartylak, Stec, Kulpa, Kepel & Roszkowska, 2020a, *Milnesium matheusi* Kaczmarek, Grobys, Kulpa, Bartylak, Kmity, Kepel, Kepel & Roszkowska, 2019, *Mil. wrightae* Kaczmarek, Grobys, Kulpa, Bartylak, Kmity, Kepel, Kepel & Roszkowska, 2019, *Paramacrobiotus experimentalis* Kaczmarek, Mioduchowska, Poprawa & Roszkowska, 2020b, *Pseudochiniscus angelus alas* Roszkowska, Grobys, Bartylak & Kaczmarek, 2020 (Maucci 1993; Pilato & Lisi 2003; Bartylak et al. 2019; Gąsiorek & Vončina 2019; Gąsiorek et al. 2019a; Kaczmarek et al. 2019; Grobys et al. 2020, 2020a, 2020b; Roszkowska et al. 2020; Kuzdrowska et al. 2021).

In the present paper, 122 samples collected in Ivohibory Forest area were studied and 39 tardigrade taxa are reported, seven of which are taxa not recorded outside of Madagascar. Furthermore, a new species for science of the genus *Bryodelphax* Thulin, 1928 is described based on morphological characters.

**Materials and methods**

**Samples and sample processing:** Samples of lichens and mosses were collected in the Ivohibory Forest in June 2017 (permits No 122/17/MEEF/SG/DGF/DSAP/SCB.Re and 150NEV06/MG17). Later they were packed in paper envelopes, dried at a temperature of ca. 30°C and sent to the laboratory at the Faculty of Biology, Adam Mickiewicz University in Poznań, Poland. There, tardigrades and their eggs were extracted from the samples and studied following the protocol of Dastych 1980b.

**Microscopy and imaging:** Adult specimens and eggs for light microscopy were mounted on microscope slides in Hoyer’s medium and secured with a coverslip and then examined under an Olympus BX41 phase contrast light microscope (PCM) with an Olympus SC50 digital camera (Olympus Corporation, Shinjuku-ku, Japan).

All figures were assembled in Inkscape 1.0.1. For deep structures that could not be fully focused on a single photograph, a series of 2–10 images were taken every ca. 0.5 μm and then manually assembled into a single deep-focus image in Adobe Photoshop 21.0.2.

**Morphometrics and morphological nomenclature:** Measurements of all morphological traits are given in micrometers [μm]. Structures were measured only if their orientation was suitable. Body length was measured from the anterior extremity to the end of the body, excluding the hind legs. The lengths of the claw branches were measured from the base of the claw to the top of the branch. The sp index is the ratio of the length of a given structure to the length of the scapular plate (scp) expressed as a percentage (Dastych 1999). It was later proposed as the psc index by Fontoura and Morais (2011). The ventral plate configuration in *Bryodelphax* species is given according to Kaczmarek et al. (2012). The genus abbreviations follow Perry et al. (2019).

Morphometric data were handled using the “Echiniscoidea” template available from the Tardigrada Register (Michalczyk & Kaczmarek 2013). Tardigrade taxonomy is according to Bertolani et al. (2014), Vecchi et al. (2016), Gąsiorek et al. (2019b, c; 2021c), Stec et al. (2020a, b, 2021).

**Comparative material:** For the identification and differentiation of the new species, we used the key by Gąsiorek et al. (2020). We also analysed and compared our new species with the type material of *Bry. aasae*Kristensen, Michalczyk & Kaczmarek, 2010, *Bry. asiaticus* Kaczmarek & Michalczyk, 2004, *Bry. brevidentatus* Kaczmarek, Michalczyk & Degma, 2005, *Bry. obszanoskii* Kaczmarek, Parnikoza, Gawlak, Esfeld, Peter, Kozieret ska & Roszkowska, 2018b and *Bry. parvuspolaris* Kaczmarek, Zawierucha, Smykla & Michalczyk, 2012.

Other species were identified based on original descriptions, redescriptions (Meyer 2016; Gąsiorek et al. 2018, 2019b) and keys by Ramazzotti and Maucci (1983), Biserov (1998), Claxton (1998), Kaczmarek et al. (2000), Fontoura and Pilato (2007), Michalczyk and Kaczmarek (2010), Morek et al. (2016), Kaczmarek and Michalczyk (2017),
Kaczmarek et al. (2017), Kaczmarek et al. (2020a), Tumanov (2020).

Results

In total, 1873 specimens and 314 eggs were found in 73 samples. They were identified as belonging to 39 different taxa (see Table I, Table II for more details).

**Taxonomic account of the new species**

**Phylum:** Tardigrada Doyère 1840  
**Class:** Heterotardigrada Marcus 1927  
**Order:** Echiniscoidea Richters 1926  
**Family:** Echiniscidae Thulin, 1928  
**Genus:** Bryodelphax Thulin, 1928

*Bryodelphax beniowskii* sp. nov. Bartyłak, Kayastha, Roszkowska & Kaczmarek  
(Table II, Figures 1–5)

Material examined

Five specimens: holotype (female) and four paratypes (all females) mounted on microscope slides in Hoyer’s medium.

**Description of the females (for measurements and statistics, see Table II):** Body yellow or light orange in living specimens (transparent after mounting on microscope slides in Hoyer’s medium) (Figure 1A, B). Eyes absent or not visible after mounting. Small and conical primary and secondary clavae. Cirri *interni* and *externi* with poorly developed cirrophores. Cirri *interni* always shorter than cirri *externi*. Only lateral cirri *A* present apart from head appendages. Cirri *A* of length typical for *Bryodelphax*, i.e., up to 25% of the total body length.

Dorsal sculpture visible in PCM as black pillars and white pores. Distinctly thicker and darker margins of dorsal plates and internal margins of facets in plates present, as originally reported by Gąsiorek (2018). Pores large and easily detectable and distributed unevenly in scapular plate (6–16 pores/100 μm², x = 10, N = 15 (in total of 5 specimens, three different plate portions for each specimen were measured), Figure 2A) and in caudal (terminal) plate (0–17 pores/100 μm², x = 9, N = 15 (in total of 5 specimens, three different plate portions for each specimen were measured) Figure 2C). In other plates, pore density much lower (0–6 pores/100 μm², x = 3, N = 15 (in total of 5 specimens, three different plate portions for each specimen were measured)). In caudal plate pillars 0.3–0.8 μm in diameter and pseudopores 0.6–0.9 μm in diameter (Figure 2C). Paired and median plates divided horizontally by smooth stripes into anterior and posterior parts (Figures 1A, 2B). Median plates 1 and 2 divided by transverse stripes, median plate 3 undivided. Median plate 2 is the largest among all median plates. In addition, paired plates I and II are divided horizontally into two parts. Twelve poorly visible supplementary plates near median plates 1–3 (Figures 1A, 2B).

Ventral side with eight rows of faint greyish plates (formula VIII:2-2-4-2-4-2-4-1) (Figures 3, 4). First row with two plates situated at the level of head plate, i.e. in front of legs I, second row with two plates and third row with four plates situated between legs I and II, fourth row with two plates and fifth row with four plates situated between legs II and III, sixth row with two plates situated in line of legs III, seventh row with four plates situated in line with the gonopore and eighth row with one plate situated behind the gonopore. Three triangular genital plates (parts of rows seventh and eighth) surrounding the gonopore (two lateral, in line with the gonopore and the third one posterior to the gonopore (Figures 3, 5C). Pillars (0.3–0.5 μm) and pores (0.4–0.5 μm) on ventral plates visible under PCM.

Papilla-like structure on leg I hardly visible under PCM (Figure 5A), papillae on leg IV present (Figure 5C). External claws smooth, but internal ones with spurs facing downward and positioned close to the claw bases (Figure 5B). Female gonopore with the typical six-petal rosette (Figures 1B, 5C). Males, juveniles and eggs not found.

Remarks

Presence of pores on ventral plates (Figure 3) makes this species the first one in the genus *Bryodelphax* to have this distinct morphological characteristic.

**Type locality.** 46°43’14.1”E, 22°37’04.4”S, ca. 1198 m asl, Fianarantsoa Province, Ivohibory Forest, lichens on the tree trunk, 04.06.2017, coll. Marta Kepel and Andrzej Kepel.

**Type depositories.** Holotype (slide MAD98/3) and four paratypes (slides: MAD98/4, MAD98/5, MAD98/6 and MAD98/7) are deposited at the Department of Animal Taxonomy and Ecology,
Table I. Tardigrades found in the present study, in alphabetical order (* – species new for Madagascar; species new for science recorded in Iovihibory samples collected during the same expedition (described in current and previous papers) in bold).

| Taxon                                      | Sample number (number of specimens + number of eggs) | Remarks                                                                      |
|--------------------------------------------|------------------------------------------------------|------------------------------------------------------------------------------|
| 1. Bry. beniowskii sp. nov.*               | 98(5)                                                | Up to now known only from the type locality.                                |
| 2. Clc. (Dis.) polygonatus (Binda & Guglielmino, 1991) | 57(5)                                                | This species was only recorded from Tanzania and Madagascar (McInnes et al. 2017). |
| 3. Cremabiotus sp.*                        | 178(1)                                               | Final identification impossible due to presence of only single adult specimen and lack of eggs. |
| 4. Dip. zaniewi Kaczmarek & Michalczyk, 2004* | 53(1), 201(3), 238(1)                               | It is the first record of this species outside type locality in Republic of South Africa (Kaczmarek & Michalczyk 2004). |
| 5. Dor. amazzonicus Lisi, 2011*             | 10(1)                                                | Although we found only one specimen, it perfectly agrees with the original description (Lisi 2011). Until now, this species has been reported only from South America (Colombia, Ecuador – type locality) (Kaczmarek et al. 2015). |
| 6. Doryphoribius sp.                       | 11(1)                                                | Most likely a new species. However, due to the presence of only one specimen, its formal description is not possible. |
| 7. Ech. cavagnari Schuster & Grigarick, 1966* | 126(8), 179(1)                                       | The type locality of this species is Santa Cruz Island (Galapagos Islands, Ecuador). The species seems to have a tropical-subtropical distribution (Kaczmarek et al. 2014; Meyer 2016). |
| 8. Ech. manuelae da Cunha & do Nascimento Ribeiro, 1962* | 106(1)                                               | The species has a disjunct distribution (Kaczmarek et al. 2014, 2015) with reports from Madeira (type locality), Costa Rica, Argentina, Mexico and Uganda (Claps & Rossi 1988; Kaczmarek & Michalczyk 2010; Gasiorek & Kristensen 2018; Moreno-Talamantes et al. 2019). Furthermore, Gasiorek et al. (2021a) confirmed conspecificity of African and Neotropical populations. |
| 9. Ech. perarmatus Murray, 1907a*           | 76(2), 114(1)                                        | Pantropical species reported from Africa (Democratic Republic of Congo, South Africa), Indonesia, Hawaii, North and South America, and Mauritius (McInnes 1994; Kaczmarek et al. 2014; Kaczmarek et al. 2015; McInnes et al. 2017; Kiosya et al. 2021). |
| 10. Ech. testudo (Doyère, 1840)*           | 163(2), 241(4), 329(1)                               | Species widely distributed in the Arctic and Europe, with the type locality in France (McInnes 1994; Gasiorek et al. 2017b). However, reports from the other localities like Africa, South and North America or New Zealand suggest a cosmopolitanism of this taxon, probably associated with anthropogenic dispersal. (Gasiorek et al. 2019d, 2021a; Jorgensen et al. 2007; Kaczmarek et al. 2015, 2017). |
| 11. Ech. tritis Gasiorek & Kristensen, 2018 | 47(1), 127(16), 132(2), 139(346), 205(4)            | Species known only from Tanzania (Gasiorek & Kristensen 2018) and Madagascar (Bartylak et al. 2019). |

(Continued)
Table I. (Continued).

| Taxon                                      | Sample number (number of specimens + number of eggs) | Remarks                                                                 |
|--------------------------------------------|------------------------------------------------------|-------------------------------------------------------------------------|
| 12. *Hys. cf. convergens*                  | 152(1)                                               | *Hypsibius convergens* is a species complex (Kaczmarek & Michalczyk 2009) with global distribution (McInnes 1994) and nominal species-type locality in Lithuania. The nominal species still needs a modern redescription. |
| 13. *Hys. cf. scabropygus*                 | 18(1)                                                | *Hypsibius scabropygus* Cuénot, 1929 has the type locality in France and it is known mainly from European localities, but is recorded also from Africa, Asia and North America (McInnes 1994; McInnes et al. 2017). Some possible taxonomic confusion regarding this species was discussed by Zawierucha et al. (2014). In our study, only one damaged specimen was found, making the final identification impossible. |
| 14. *Hys. dujardini* (Doyère, 1840)*       | 6(1), 139(1), 152(1), 191(1), 199(8), 241(1), 329(1) | *Hypsibius. dujardini*, has been reported globally (e.g. McInnes 1994, Kaczmarek et al. 2014, 2015, McInnes et al. 2017). Morphological characteristics of our Madagascan specimens fit well with the recent redescription of this species (Gasiorek et al. 2018). |
| 15. *Kri. tessellatus* (Murray, 1910)*     | 10(6), 11(2), 12(4), 186(10 + 10)                    | Until now, species reported only from China (Hainan), Hawai, Japan (Mikurajima), Taiwan, Indonesia (Bali) and Australia (McInnes 1994; Dastych 1997; Li et al. 2008; Suzuki et al. 2018; Gasiorek et al. 2019b). |
| 16. *Mac. cf. drakensbergi*                | 245(1)                                               | Final identification was not possible due to the lack of eggs.          |
| 17. *Mac. hufelandi* group                 | 6(1), 10(8), 11(5), 16(1), 18(11), 19(2), 34(1), 47(7), 75(13), 85(14), 88(3), 98(2), 103(2), 106(8), 109(1), 110(16), 144(2), 163(1), 167(9), 168(27), 187(1), 193(1), 205(2), 211(1), 212(1), 238(53), 241(7), 319(1) | The accurate identification of the species was not possible due to lack of eggs, especially as two other species of the hufelandi group were found in the present study. |
| 18. *Mac. porifini* Kuzdrowska, Mioduchowska, Gawlak, Bartylok, Kepel, Kepel & Kaczmarek, 2021* | 96(115 + 15), 236(1 + 1), 76(4 + 1) | Recently described species of the hufelandi group known only from Madagascar (Kuzdrowska et al. 2021). |
| 19. *Mac. cf. sandrae*                     | 87(100 + 34)                                         | Species of the hufelandi group known only from Europe (type locality: Germany) (Bertolani & Rebecchi 1993; Kaczmarek & Michalczyk 2017), but morphologically extremely similar to *Mac. azzunae* Ben Marnissi, Cesari, Rebecchi & Bertolani, 2021 from Tunisia. |
| 20. *Meb. fiedleri* Kaczmarek, Bartylok, Stee, Kulpa, M. Kepel, A. Kepel & Roszkowska, 2020 | 145(25 + 33), 146(0 + 2), 152(7 + 3), 202(22 + 7) | Recently described species known only from Madagascar (Kaczmarek et al. 2020a). The accurate identification of the species was not possible due to lack of eggs which are crucial for correct identification of *Mesobiotus* species (Kaczmarek et al. 2018c, 2020a). However, it is highly probable that these specimens belong to *Meb. fiedleri*. |
| 21. *Mesobiotus* sp.                       | 11(1), 46(1), 106(3), 121(20), 124(2), 128(1), 144(1), 177(1), 236(2) | |

(Continued)
Table I. (Continued).

| Taxon | Sample number (number of specimens + number of eggs) | Remarks |
|-------|------------------------------------------------------|---------|
| 22. *Mil. argentinum* Roszkowska, Ostrowska & Kaczmarek, 2015* | 110(6), 127(10), 193(7), 210(1), 110(5) | Our specimens fit well with the original description (Roszkowska et al. 2015). It is the first report of this species outside of the type locality in Argentina. |
| 23. *Mil. cf. beatae* | 127(1) | Species reported from Argentina and USA (Roszkowska et al. 2015; Tibbs et al. 2016). In our study, only one damaged specimen was found, making the final identification impossible, despite the specimen fitting the description of the species (Roszkowska et al. 2015). |
| 24. *Mil. cf. dornensis* | 127(1) | Species reported from Romania (type locality) and Poland (Ciobanu et al. 2015; Kaczmarek et al. 2018a). *Mil. cf. dornensis* was reported also from Tunisia (Gąsiorek et al. 2017a). Despite fitting the original description (Ciobanu et al. 2015), accurate identification of the species was not possible due to presence of a single specimen. |
| 25. *Mil. matheusi* Kaczmarek, Grobys, Kulpa, Bartylak, Kmita, M. Kepel, A. Kepel & Roszkowska, 2019 | 86(4), 88(18), 132(22 + 3), 136(23), 139(19), 193(4 + 9), 212(2) | Recently described species known only from Madagascar (Kaczmarek et al. 2019). |
| 26. *Mil. wrightae* Kaczmarek, Grobys, Kulpa, Bartylak, Kmita, M. Kepel, A. Kepel & Roszkowska, 2019 | 2(3), 76(2), 87(10), 109(29), 96(2), | Recently described species known only from Madagascar (Kaczmarek et al. 2019). |
| 27. *Min. africanaus* Binda & Pilato, 1995* | 87(37), 114(1), 174(1), 193(15) | This species was reported from the Democratic Republic of Congo and Tanzania (Mcinnes et al. 2017). |
| 28. *Min. cf. intermedius* | 10(5), 11(2), 34(4), 47(1), 98(4), 106(12), 109(6), 167(1), 187(3), 210(1), 217(9), 236(5) | Final identification was not possible due to the lack of eggs. Originally described from Chile (Plate 1889), *Min. intermedius* was considered cosmopolitan (e.g. McInnes 1994) and it was later shown to be a species complex (Claxton 1998). Recently, several findings of this species have been reported from Africa (Mcinnes et al. 2017), however, it was suggested that they should be re-examined and possibly belong to a different species. |
| 29. *Min. pseudostellarus* Roszkowska, Stec, Ciobanu & Kaczmarek, 2016* | 47(5), 76(1), 86(6), 110(11), 126(1), 127(1), 136(4), 137(5), 193(1), 211(1), 238(9) | Our specimens perfectly agree with original description (Roszkowska et al. 2016). It is reported for the first time outside of its type locality in Argentina. |
| 30. *Mam. cf. hastatus* | 148(5 + 9), 151(5 + 4) | Type locality in Scotland. This relatively rare species has a large Palearctic distribution (Mcinnes et al. 2017). Although our specimens agree with original description (Murray 1907b; Ramazzotti & Maucci 1983 with English translation by Beasley 1995), we reason that this species needs redescription due to incomplete diagnosis. |
| 31. *Neb. cirinoi* (Binda & Pilato, 1993) | 76(2), 85(1), 114(1), 163(1), 195(9), 233(2) | Species with wide distribution in African (Tanzania, Madagascar and Democratic Republic of Congo), as well as Asian (Malay Archipelago) tropics (Mcinnes et al. 2017; Gąsiorek et al. 2021b). |
Table I. (Continued).

| Taxon                                                | Sample number (number of specimens + number of eggs) | Remarks                                                                 |
|------------------------------------------------------|------------------------------------------------------|------------------------------------------------------------------------|
| 32. *Pam. experimentalis* Kaczmarek, Mioduchowska, Poprawa & Roszkowska, 2020 | 11 (111 + 100), 86 (2 + 1), 198 (11 + 11)            | Recently described species known only from Madagascar (Kaczmarek et al. 2020b). |
| 33. *Pam. richtersi* group                          | 10(18), 34(3), 45(2), 110(1), 114(2), 163(1), 177(8), 179(1), 193(3), 238(5), 319(10) | Accurate identification of these specimens were not possible due to the lack of eggs, especially as two other species of the *richtersi* group were found in the present study (*Pam. savai* and *Pam. experimentalis*). |
| 34. *Pam. savai* (Binda & Pilato, 2001)*            | 11(6 + 1), 168(65 + 3), 205 (4 + 1), 217 (22 + 46), 224 (63 + 20) 34 (1), 87 (70) | Until now, recorded only from type locality in Sri Lanka (Binda & Pilato 2001). Recently described species known only from Madagascar (Roszkowska et al. 2020). |
| 35. *Pse. (Meridioniscus) angelusalas* Roszkowska, Grobys, Bartyłak & Kaczmarek, 2020 | 168(1), 195(2)                                           | Low number of specimens made exact identification impossible. This species has a limited distribution in the Republic of South Africa and Tanzania (McInnes et al. 2017). |
| 36. Pseudochiniscus (Meridioniscus) sp.             | 10(1), 88(1), 106(1)                                      | Adult specimens morphologically similar to *Ramazzottius oberhaeuser* (Doyère, 1840). However, the final identification of the species was not possible due to the lack of eggs. Despite fitting the description of the species (Iharos 1969), accurate identification of the species was not possible due to presence of a single specimen. |
| 37. *Ram. szeptyczy* (Dastych, 1980b)*              | 109(1), 139(2), 191(1), 241(1), 326(1)                   |                                                                                  |
| 38. *Ramazzottius* sp.                              | 34(1)                                                  |                                                                                  |

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Etymology. *Bryodelphax beniowskii* was chosen to commemorate Mateusz Maurycy Michał Franciszek Serafin August Beniowski (in Hungarian: Benyovszky, in Slovak: Benövský), a military officer, adventurer and writer, national hero in Poland, Hungary and Slovakia. In the 18th century, he organised two expeditions to Madagascar, where he was killed and buried.

Differential diagnosis

Within the *weglarskae* group (distinguished due to presence of ventral plates), only *Bry. olszanowskii* Kaczmarek, Parnikoza, Gawlak, Esefeld, Peter, Kozeretska & Roszkowska, 2018b and *Bry. parvuspolaris* Kaczmarek, Zawierucha, Smykla & Michalczyn, 2012 have eight plate rows (Gasiorek et al. 2020) which is why only these two are considered for differential diagnosis. Adult females of *Bry. beniowskii* sp. nov. differ from:

1. *Bry. olszanowskii*, reported only from the type locality in Antarctic (Kaczmarek et al. 2018ab) by: different ventral plate formula (VIII:2-2-4-2-4-2-4-1 in the new species *vs.* VIII:4-1-1-2-2-2-2-2-2 in *Bry. olszanowskii*), presence of papilla-like structure on leg I and absence of dentate collar on legs IV.

2. *Bry. parvuspolaris* known from the type locality in Spitsbergen (Kaczmarek et al. 2012) by: different ventral plate formula (VIII:2-2-4-2-4-2-4-1 in the new species *vs.* VIII:1-1-2-2-2-2-2-2-1 in *Bry. parvuspolaris*), higher *sp* of cirrus internus (33.4–40.1 in the new species *vs.* 22.4–26.3 in *Bry. parvuspolaris*), higher cirrus *intext* length ratio (63%–75% in the new species *vs.* 43%–53% in *Bry. parvuspolaris*), presence of papilla-like structure on leg I, presence of papilla on legs IV and absence of dentate collar on legs IV.

Discussion

In recent years, the number of known tardigrade taxa from Madagascar almost doubled from 13 in
2003 to 23 at the time of the current study (Maucci 1993; Pilato & Lisi 2003; Bartylak et al. 2019; Kaczmarek et al. 2019; Gašiorek & Vončina 2019; Gašiorek et al. 2019a; Grobys et al. 2020; Kaczmarek et al. 2020a; 2020b; Roszkowska et al. 2020; Kuzdrowska et al. 2021). In this study we present further 21 taxa (including one new for science) reported from Madagascar. However, the taxonomic status and distribution of some of newly reported species need to be clarified.

*Bryodelphax benioskii* sp. nov. is the second species of the genus *Bryodelphax* reported from Madagascar, but it should be mentioned that *Bry. parvulus* Thulin, 1928 was reported from the Island long time ago (Maucci 1993). Taking into consideration that the type locality of *Bry. parvulus* is in Lapland (Thulin 1928) and since that time many new species of this genus were described (Degma et al. 2021), its presence in Madagascar needs confirmation.

Three species found in present study were previously known only from Africa, i.e., *Diphascon zaniewi* Kaczmarek & Michalczyk, 2004, *Minibiotus africus* Binda & Pilato, 1995 and *Ramazzottius szeptycki* (Dastych, 1980a). These species should be temporarily considered as species restricted to Africa.

Furthermore, three species, i.e., *Mil. argentinum* Roszkowska, Ostrowska & Kaczmarek, 2015, *Min. pseudostellatus* Roszkowska, Stec, Ciobanu & Kaczmarek, 2016 and *Doryphoribus amazzonicus* Lisi, 2011 were up to now reported only from South America and their presence in Madagascar might suggest a long distance, anthropogenic dispersal. A similar distribution was recently presented for *Minibiotus pentannulus* Londoño, Daza, Lisi & Quiroga, 2017 which was described from South America and later reported in South Africa by Stec et al. 2020a). Similarly, *Pam. savaii* (Binda & Pilato, 2001) reported here were recorded from distant locality in Sri Lanka. Considering these discoveries, these species can be potentially considered long-distance migrants.

| CHARACTER | RANGE | MEAN | SD | Holotype |
|-----------|-------|------|----|---------|
| Body length | N | µm | sp | µm | sp | µm | sp | µm | sp |
| Scapular plate length | 5 | 122 | 605 | 731 | 129 | 681 | 5 | 59 | 131 | 731 |
| Head appendages lengths | 5 | 17.9 | 20.7 | 19.1 | 1.3 | 17.9 | - | - | - | - |
| Cirrus internus | 6.1 | 33.4 | 40.1 | 7.5 | 38.3 | 1.0 | 3.3 | ? | ? |
| Cephalic papilla | 2.7 | 14.8 | 21.5 | 3.4 | 18.0 | 0.5 | 2.9 | 2.7 | 14.8 |
| Cirrus externus | 6.6 | 36.9 | 63.2 | 9.8 | 51.0 | 2.3 | 10.1 | 6.6 | 36.9 |
| Clava | 2.9 | 15.6 | 24.1 | 3.7 | 19.5 | 0.6 | 3.8 | 4.1 | 23.2 |
| Cirrus A | 27.6 | 142.6 | 179.0 | 29.7 | 155.8 | 1.8 | 14.3 | 32.0 | 179.0 |
| Cirrus A/Body length ratio | 20% | 24% | - | 23% | - | 2% | - | 24% | - |
| Cirrus intern/extern length ratio | 63% | 75% | - | 71% | - | 5% | - | ? | - |
| Papilla on leg IV length | 2 | 1.9 | 10.8 | 12.1 | 2.1 | 11.5 | 0.2 | 0.9 | 1.9 | 10.8 |
| Claw 1 lengths | Branch | 5 | 5.4 | 6.6 | 28.3 | 35.7 | 5.9 | 31.2 | 5.0 | 2.9 | 5.4 | 30.3 |
| | Spur | 1.1 | 1.4 | 6.3 | 7.0 | 1.3 | 6.6 | 0.2 | 0.3 | ? | ? |
| | Spur/branch length ratio | 19% | 24% | - | 21% | - | 3% | - | ? | - |
| Claw 2 lengths | Branch | 5 | 4.9 | 6.3 | 26.9 | 31.0 | 5.5 | 28.6 | 0.5 | 1.7 | 5.3 | 29.5 |
| | Spur | 1.1 | 1.3 | 5.6 | 6.4 | 1.2 | 6.0 | 0.1 | 0.3 | 1.1 | 5.9 |
| | Spur/branch length ratio | 18% | 23% | - | 21% | - | 3% | - | 0 | - |
| Claw 3 lengths | Branch | 5 | 4.8 | 5.7 | 24.3 | 29.0 | 5.2 | 27.1 | 0.3 | 1.8 | 5.2 | 29.0 |
| | Spur | 1.0 | 1.2 | 5.1 | 6.0 | 1.1 | 5.7 | 0.1 | 0.4 | 1.0 | 5.7 |
| | Spur/branch length ratio | 20% | 23% | - | 21% | - | 1% | - | 0 | - |
| Claw 4 lengths | Branch | 5 | 5.8 | 6.5 | 30.5 | 32.5 | 6.0 | 31.6 | 0.3 | 0.8 | 5.8 | 32.5 |
| | Spur | 1.1 | 1.2 | 6.2 | 6.8 | 1.3 | 6.5 | 0.1 | 0.3 | 1.1 | 6.2 |
| | Spur/branch length ratio | 19% | 21% | - | 20% | - | 1% | - | 0 | - |
Figure 1. *Bryodelphax beniowskii* sp. nov.: A—dorsal projection of the entire animal, arrows indicate divisions of paired and median plates into anterior and posterior parts, arrowheads indicate supplementary plates near median plates (holotype), B—ventral projection of the entire animal, asterisk indicates gonopore (holotype). Scale bars in [μm]. All PCM.

*Echiniscus cavagnarii* Schuster & Grigarick, 1966 and *Kri. tessellatus* (Murray, 1910) are known from tropical or subtropical regions and should be considered as likely pantropical species. Moreover, it should also be mentioned that *Kri. walteri* (Pilato & Lisi, 2003) recorded from Madagascar is very similar to *Kri. tessellatus*.

*Echiniscus manuelae* da Cunha & do Nascimento Ribeiro, 1962 has a disjunct Afrotropical-Neotropical distribution (Gasiorek et al. 2021a). The next member of the genus *Echiniscus*, i.e., *Ech. testudo* (Doyère, 1840) is considered as species with wide distribution. Reports of this species from localities in Africa, South and North America or New Zealand may suggest a cosmopolitan distribution of this taxon, probably associated with anthropogenic dispersal (Jørgensen et al. 2007; Gasiorek et al. 2019d).

Specimens of *Hys. dujardini* found in the present study fit recent redescription of this species (Gasiorek et al. 2018). Its distribution is now very unclear. This species was considered cosmopolitan in the past (McInnes 1994), but almost all records of this taxon need a confirmation based on modern taxonomy.

Two taxa were identified as *Mur. cf. hastatus* and *Hys. cf. convergens*. These species have a very unclear taxonomic position and a redescription of both taxa, from the type localities, is necessary. Both species were described from Europe (Murray 1907a; Urbanowicz 1925) and it is highly probable that Madagascan specimens should be considered as different species, however this confirmation will only be possible after

Figure 2. *Bryodelphax beniowskii* sp. nov.: A—pores on scapular plate (holotype); B—pores on paired and median plates, arrow indicates division of paired plate into anterior and posterior parts, arrowheads indicate supplementary plates near median plates (holotype) C—pores on terminal plate (holotype). Scale bars in [μm]. All PCM.

Figure 3. *Bryodelphax beniowskii* sp. nov.: ventral plates. Roman numerals indicate the rows in which the ventral plates are arranged, arrows indicate patches of granulation around gonopore (holotype). Scale bars in [μm]. PCM.
Another taxon *Macrobiotus cf. sandrae* is extremely similar to *Mac. azzunae* Ben Marnissi, Cesari, Rebecchi & Bertolani, 2021 from Tunisia and without molecular studies unambiguous identification is problematic (Ben Marnissi et al. 2021).

The other taxa i.e., *Ursulinius cf. cameruni*, *Hys. cf. scabropygus*, *Crenubiotus* sp., *Macrobiotus cf. drakensbergi*, *Mil. cf. beatae*, *Mil. cf. dornensis* and *Min. cf. intermedius* reported as new for Madagascar fauna were identified based on small number of specimens and for some of them eggs (which are crucial for correct identification) were missing. Presence of *Urs. cameruni* (Iharos, 1969) and *Mac. drakensbergi* Dastych, 1993 on Madagascar is highly probable as both species were described from Africa (Mcinnes et al. 2017).

We also identified many specimens only to the genus level or to the group of species i.e. *Ramazzottius* sp., *Doryphoribius* sp., *Mac. hufelandi* group, *Mesobiotus* sp., *Pam. richtersi* group and *Pseudechiniscus* (*Meridioniscus*) sp. Correct identification of these individuals was not possible due to lack of eggs or small number of specimens. It should also be stated that some of the specimens of *Mac. hufelandi* group, *Mesobiotus* sp. or *Pam. richtersi* group may belong to species reported from Madagascar in previous studies or in the present study, however, without eggs, it is not possible to say so with certainty.

In summary, tardigrade fauna of Madagascar is very poorly known but seems to be very rich because even in a very small area studied in the present research, many new species for science were found (Kaczmerek et al. 2019; Bartylak et al. 2019; Roszkowska et al. 2020; Kaczmerek et al. 2020a, b; Kuzdrowska et al. 2021, as well as the present study), altogether with many species new for Madagascar.
Disclosure statement

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