

New records of tardigrades from Colombia (Guatavita, Cundinamarca Department)

Jenny C. MELO¹, Eliana BELTRÁN-PARDO¹, Jaime Eduardo BERNAL¹, Łukasz KACZMAREK^{2,3,*}

¹Institute of Human Genetics, Pontifical Xavierian University, Bogota, Colombia

²Department of Animal Taxonomy and Ecology, Faculty of Biology, Adam Mickiewicz University in Poznań, Poznań, Poland

³Laboratory of Natural and Applied Invertebrate Ecology, Amazon State University, Puyo, Ecuador

Received: 12.05.2014 • Accepted: 13.08.2014 • Published Online: 04.05.2015 • Printed: 29.05.2015

Abstract. The water bears (Tardigrada) from Colombia are rather poorly known; thus, the aim of this research was to study the composition of tardigrade fauna inhabiting epiphytic and rock mosses in a high Andean forest in Guatavita. A 25-m² plot was delimited and 6 randomly chosen trees with epiphytic mosses were sampled. Twelve samples of epiphytic mosses and 6 of rock mosses were collected and examined. A total of 277 specimens and 6 eggs of 8 tardigrade taxa were found in these samples. All taxa are new records for Guatavita and 5—*Hypsibius dujardini* (Doyère, 1840); *Milnesium katarzynae* Kaczmarek et al., 2004; *Milnesium krzysztofi* Kaczmarek & Michalczyk, 2007; *Milnesium granulatum* Ramazzotti 1962; and *Paramacrobiotus danielae* (Pilato et al., 2001)—are also new for Colombia.

Key words: Andean forest, Eutardigrada, epiphytic mosses, Heterotardigrada, new records, rock mosses

1. Introduction

Tardigrades, commonly known as water bears, belong to the invertebrate superclade Ecdysozoa. These microscopic metazoans can be found in almost all aquatic and terrestrial ecosystems throughout the world (Ramazzotti and Maucci, 1983; Nelson, 2001). “Terrestrial” tardigrades usually inhabit the thin layer of water on cryptogam leaves or algae and the interstitial spaces between soil particles and leaf litter (Nelson and Marley, 2000; Nelson, 2002). At present, about 1200 tardigrade species have been described around the world (Guidetti and Bertolani, 2005; Degma and Guidetti, 2007; Degma et al., 2009–2014).

Interest in Colombian tardigrades is just developing, and as a consequence the tardigrade fauna in this region is still very poorly known. To date, only a few tardigrade papers have been published from this region, in which 30 tardigrade taxa have been reported: those of Richters (1911a, 1911b), Heinis (1914), Marcus (1936), Jerez and Narváez (2001), Jerez et al. (2002), and Degma et al. (2008).

In Colombia, about 50% of moss diversity is present in the high Andean forests (Armenteras et al., 2007; Rangel, 2008). Tardigrades prefer mountain habitats (e.g., Dastych, 1988). Therefore, a study on Tardigrada in these environments would substantially increase knowledge of the biodiversity of these organisms in the country as a whole. The aim of this research was to study the composition of tardigrade fauna in epiphytic

and rock mosses in a high Andean forest in Guatavita (Cundinamarca Department). In this paper, we report 8 tardigrade taxa (including 5 species new to Colombian fauna) found in Guatavita with some zoogeographical and taxonomical remarks and combine them with a complete list of all Colombian tardigrades.

2. Materials and methods

The study was conducted in a relic high Andean forest near Tominé Dam in Guatavita (Cundinamarca Department). All moss samples were collected from trees (12 samples) and rocks (6 samples) in a 25-m² research plot (04°56'N, 73°50'W; average altitude 2650 m a.s.l.). Samples were placed in paper bags until they were completely dry and were then stored at –20 °C. Detailed localities and geographical coordinates for all samples are presented in Table 1.

Tardigrades were extracted from the moss samples by a modified Baermann funnel filtration process (Whitehead and Hemming, 1965), a standard method for extracting active tardigrades (Convey and McInnes, 2005).

Tardigrades and their eggs were mounted on microscope slides in polyvinyl alcohol. Live specimens of *Hypsibius dujardini* (Doyère, 1840) and *Paramacrobiotus danielae* (Pilato, Binda, Napolitano & Moncada, 2001) were cultured on small petri dishes containing agar medium and a thin layer of filtered distilled water. Rotifers (isolated

* Correspondence: kaczmar@amu.edu.pl

Table 1. Locations of species found in the moss samples collected in Guatavita, Cundinamarca: *E. bigranulatus* (1), *H. dujardini* (2), *M. cf. hufelandi* (3), *M. cf. islandicus* (4), *Mil. katarzynae* (5), *Mil. krzysztofi* (6), *Mil. granulatum* (7), *P. danielae* (8).

Sample code	Coordinates	Altitude (m a.s.l.)	Habitat	Species composition
M1A1GUA	04°56.231'N, 73°50.323'W	2635	Epiphytic	1, 2, 3, 4
M2A1GUA	04°56.237'N, 73°50.324'W	2635	Epiphytic	1, 3
M1A2GUA	04°56.251'N, 73°50.323'W	2655	Epiphytic	1, 2, 3
M2A2GUA	04°56.246'N, 73°50.311'W	2640	Epiphytic	1, 2, 3
M1A3GUA	04°56.245'N, 73°50.332'W	2660	Epiphytic	1, 2, 3, 5, 6
M2A3GUA	04°56.247'N, 73°50.331'W	2640	Epiphytic	1, 2, 3
M1A4GUA	04°56.243'N, 73°50.328'W	2640	Epiphytic	1, 2, 3
M2A4GUA	04°56.244'N, 73°50.330'W	2650	Epiphytic	1, 2, 3
M1A5GUA	04°56.246'N, 73°50.329'W	2640	Epiphytic	1
M2A5GUA	04°56.244'N, 73°50.333'W	2650	Epiphytic	2, 6, 7, 8
M1A6GUA	04°56.242'N, 73°50.334'W	2650	Epiphytic	2, 3, 7, 8
M2A6GUA	04°56.244'N, 73°50.335'W	2650	Epiphytic	2, 5, 6
M1R1GUA	04°56.246'N, 73°50.324'W	2650	Rock	2, 5, 8
M1R2GUA	04°56.245'N, 73°50.320'W	2655	Rock	-
M1R3GUA	04°56.244'N, 73°50.329'W	2640	Rock	1, 8
M1R4GUA	04°56.244'N, 73°50.332'W	2650	Rock	8
M1R5GUA	04°56.244'N, 73°50.333'W	2650	Rock	8
M1R6GUA	04°56.243'N, 73°50.335'W	2650	Rock	8

from the same mosses) or algae (*Scenedesmus acutus* and *Selenastrum capricornutum*, provided by Claudia Campos from the Microbiology Department, Pontifical Xavierian University) were used as a food source. The cultures allowed us to collect the adults and eggs for the identification of specimens from genera *Hypsibius* and *Paramacrobotus*.

The final species identification was made based on keys and original descriptions or redescrptions (Ramazzotti, 1962; Ramazzotti and Maucci, 1983; Dastych, 1988; Bertolani and Rebecchi, 1993; Pilato et al., 2001; Kaczmarek et al., 2004; Miller et al., 2005; Michalczyk and Kaczmarek, 2006; Kaczmarek and Michalczyk, 2007; Michalczyk et al., 2012a, 2012b).

3. Results

Tardigrades and/or their eggs were found in 94% of the samples (see Table 1). In total, 277 tardigrades and 6 eggs, representing 8 taxa, were extracted from 17 moss samples. Most of the specimens (247) representing 8 taxa were found in epiphytic mosses, and only 30 specimens of 4 taxa were present in rock mosses. *Echiniscus bigranulatus* Richters, 1907 dominated in epiphytic mosses with a value of 45.3% of all specimens found, while *P. danielae* represented 63.3% of the individuals found in moss samples from rocks. The data presented above are not sufficient to perform a statistical analysis to investigate associations between ecological parameters and diversity of tardigrades; however, they may be valuable for future studies, taking into consideration the scarcity of such studies performed in Colombia to date.

3.1. Taxonomic accounts

The species new for Colombia are indicated with an asterisk.

Phylum: **Tardigrada** Spallanzani, 1777

Class: **Heterotardigrada** Marcus, 1927

Family: **Echiniscidae** Thulin, 1928

Genus: *Echiniscus* C.A.S. Schultze, 1840

1. *Echiniscus bigranulatus* Richters, 1908

Material examined: 113 specimens in 10 samples (see Table 1).

Remarks: Collected specimens correspond perfectly to the redescription of this species (Michalczyk and Kaczmarek, 2006). In the present study, this species was found mostly in epiphytic mosses. According to Michalczyk and Kaczmarek (2006), *E. bigranulatus* sensu stricto is the nominal species for the complex of species and is known only from South and Central America (see also Table 2).

Class: **Eutardigrada** Richters, 1926

Order: **Parachela** Schuster, Nelson, Grigarick & Christenberry, 1980

Family: **Hypsibiidae** Pilato, 1969

Subfamily: **Hypsibiinae** Pilato, 1969

Genus: *Hypsibius* Ehrenberg, 1848

2. *Hypsibius dujardini* (Doyère, 1840)*

Material examined: Thirty-one mounted specimens and 5 cultured specimens, comprising several generations in 11 samples (see Table 1).

Remarks: The original description is unsatisfactory; therefore, the examined specimens were compared with the later descriptions (e.g., Ramazzotti and Maucci, 1983; Dastych, 1988; Miller et al., 2005). In the present study, this species was found mostly in the epiphytic mosses. It belongs to the cosmopolitan species complex with many older records that should be revised (Kinchin, 1994; McInnes, 1994; Guil et al., 2009; Kaczmarek and Michalczyk, 2009).

Family: **Macrobiotidae** Thulin, 1928

Genus: *Macrobiotus* C.A.S. Schultze, 1834

3. *Macrobiotus cf. hufelandi*

Material examined: Sixty-one specimens in 9 samples (see Table 1).

Remarks: *Macrobiotus hufelandi* C.A.S. Schultze, 1834, sensu stricto is a nominal species for a cosmopolitan group of species (McInnes, 1994). Species from this group require a very careful taxonomic analysis, including the examination of egg morphology. Additionally, many new species have been described in this group in the past few years (e.g., Bertolani et al., 2011; Biserov et al., 2011; Pilato et al., 2012; Guidetti et al., 2013; see also Bertolani and Rebecchi, 1993 for the diagnostic key to the group). Unfortunately, we did not find eggs in our material; thus, correct identification to the species level was not possible. In the present study, this species was found only in the epiphytic mosses. *Macrobiotus hufelandi* has been reported from a few localities in Colombia, but most of them require confirmation based on modern literature (see Table 2).

4. *Macrobiotus cf. islandicus*

Material examined: One specimen in 1 sample (see Table 1).

Remarks: *Macrobiotus islandicus* Richters, 1904, sensu stricto should probably be considered as a nominal species for a cosmopolitan group of species (McInnes, 1994; see also Table 2). Due to the absence of eggs in the examined material, correct identification to species level was not possible. Only 1 specimen was found in epiphytic moss.

Genus: *Paramacrobiotus* Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009

5. *Paramacrobiotus danielae* (Pilato et al., 2001)*

Material examined in this study: Forty-nine specimens in 7 samples (see Table 1) and 6 eggs from the culture.

Remarks: Collected specimens and eggs correspond perfectly to the original description (Pilato et al., 2001). Previously, the species was known only from Ecuador and Peru (see Table 2). Species were collected mostly from rock mosses.

Order: **Apochela** Schuster, Nelson, Grigarick & Christenberry, 1980

Family: **Milnesiidae** Ramazzotti, 1962

Genus: *Milnesium* Doyère, 1840

6. *Milnesium granulatum* Ramazzotti, 1962*

Material examined: Five specimens in 2 samples (see Table 1).

Remarks: Our specimens correspond perfectly with the original description and later redescription (Ramazzotti, 1962; Michalczyk, et al., 2012a, 2012b). This species was found only in 2 epiphytic mosses. It was previously reported from only a few disjunct localities in South America and Europe (see also Table 2).

Table 2. An alphabetical list of Colombian tardigrade species with their localities and taxonomical and/or zoogeographical remarks (departments where the tardigrades were reported: A- Antioquia, B- Arauca, C- Bogota, D- Cauca, E- Cundinamarca, F- Santander, G- Tolima, H- Valle del Cauca, ?- undefined). Source codes mean the following references: 1- Degma et al. (2008), 2- Heinis (1914), 3- Jerez and Narváez (2001), 4- Marcus (1936), 5- Richters (1911a), 6- Richters (1911b), 7- present study.

No.	Species/subspecies	Source	Departments	Remarks
1	<i>Acutuncus antarcticus</i> (Richters, 1904) sensu lato	2	A	Heinis (1914) describes “eggs with blunt thorn-like projections surrounded by a hyaline skin” similar to those described for <i>Acutuncus antarcticus</i> . This Colombian record may require confirmation.
2	<i>Adropion scoticum</i> (Murray, 1905) sensu lato	2	C	Cosmopolitan (McInnes, 1994); however, the majority of records need to be verified.
3	<i>Calohypsibius ornatus</i> (Richters, 1900)	2	C	Cosmopolitan species (McInnes, 1994) with high intraspecific variability (Bartoš, 1940, Ramazzotti and Maucci, 1983), or rather a species complex (Michalczyk and Kaczmarek, 2005).
4	<i>C. verrucosus</i> (Richters, 1900)	3	F	Species with disjunct distribution, known from Europe, Asia, and South America (McInnes, 1994).
5	<i>Diphascon chilense</i> Plate, 1888	2, 5	A, C, G	Cosmopolitan (McInnes, 1994), but the revision of the geographic distribution of the species is probably needed.
6	<i>Echiniscus bigranulatus</i> Richters, 1908	2, 7	E	This species belongs to the <i>bigranulatus</i> group of species with a Neotropical and Antarctic distribution, and it can easily be mistaken for other members of the group (see Michalczyk and Kaczmarek, 2006, 2007). All records prior to 2006 require reexamination to confirm species identification.
7	<i>E. blumi</i> Richters, 1903	2	A	Cosmopolitan (McInnes, 1994).
8	<i>E. quadrispinosus</i> Richters, 1902 sensu lato	2	A, C	There is considerable morphological variation in the global records of <i>E. quadrispinosus</i> , which suggests a species complex. Most of the records of this species are from the Holarctic (McInnes, 1994). In this situation, their presence in Colombia should be verified.
9	<i>E. spiniger</i> Richters, 1904	2	E	Species with rather disjunct distribution (McInnes, 1994).
10	<i>E. testudo</i> (Doyère, 1840)	2, 4	A, D, H	Specimens from Colombia were cited by Heinis (1914) as <i>Echinscus</i> spec. and later attributed by Marcus (1936) to <i>E. testudo</i> . Holarctic taxon (McInnes, 1994; Jørgensen et al., 2007). The Colombian record seems doubtful.
11	<i>E. wendti</i> Richters, 1903 sensu lato	5, 6	G	This species from the <i>arctomys</i> group of species is largely Holarctic in distribution and with single reports from other zoogeographical regions (McInnes, 1994).
12	<i>Hypsibius arcticus</i> (Murray, 1907) sensu lato	3	F	Dastych (1991) suggested that the status of <i>H. arcticus</i> should be verified due to insufficient morphological information.
13	<i>H. dujardini</i> (Doyère, 1838)*	7	E	This species belongs to the <i>convergens-dujardini</i> complex of species, which is cosmopolitan (McInnes, 1994; Miller et al., 2005; Kaczmarek and Michalczyk, 2009).
14	<i>H. fuhrmanni</i> Heinis, 1914	2	A	The original description (Heinis, 1914) was not sufficient to enable Marcus (1936) to attribute the species positively to genus <i>Hypsibius</i> , and the correct taxonomic position of this species is unclear. Currently endemic to Colombia.
15	<i>I. prosostomus</i> Thulin, 1928	3	F	Cosmopolitan (McInnes, 1994), but needing a redescription.
16	<i>Macrobiotus echinogenitus</i> Richters, 1903 sensu lato	2	A, C, ?	Cosmopolitan (McInnes, 1994), but for more details see Maucci (1986) and Binda (1988). The presence of this species in Colombia needs to be confirmed.

Table 2. (Continued).

No.	Species/subspecies	Source	Departments	Remarks
17	<i>M. harmsworthi</i> Murray, 1907 sensu lato	2, 3, 5	C, F, G, H	The nominal species for a cosmopolitan species complex (McInnes, 1994), so with an unknown geographic range (see also Kaczmarek et al., 2011).
18	<i>M. hufelandi</i> C.A.S. Schultze, 1834 sensu lato	2, 3, 5, 7	A, C, E, F, G, ?	The nominal species for a cosmopolitan species complex (McInnes, 1994), so with an unknown geographic range.
19	<i>M. islandicus</i> Richters, 1904 sensu lato	3, 7	E, F	<i>Macrobotus islandicus</i> sensu stricto has mostly Holarctic distribution (McInnes, 1994). All non-Holarctic records have to be confirmed.
20	<i>M. occidentalis</i> Murray, 1910 sensu lato	3	F	Mostly Holarctic distribution with a few records from other regions (McInnes, 1994).
21	<i>M. rubens</i> Murray, 1907	2	G	It has a very disjunct distribution (McInnes, 1994). However, given the locus typicus is in the Himalayas, report from Colombia needs a confirmation.
22	<i>Milnesium granulatum</i> (Ramazzotti, 1962)*	7	E	Species with disjunct distribution, recorded from Chile, Italy, Romania, and USA (Ramazzotti, 1962; Bartels et al., 2014; Ciobanu et al. 2014).
23	<i>Milnesium katarzynae</i> Kaczmarek et al., 2004*	7	E	Species with pantropical distribution, known only from China and Costa Rica (Kaczmarek et al., 2004, 2014a). This is the third record of this species.
24	<i>M. krzysztofi</i> Kaczmarek and Michalczyk, 2007*	7	E	Species with Neotropical distribution, known only from Costa Rica and Peru (Kaczmarek et al., 2014a, 2014b). It is the third record of this species.
25	<i>M. tardigradum</i> Doyère, 1840 sensu lato	2, 3	A, C, D, F	Probably Palearctic or Holarctic distribution. All records of <i>M. tardigradum</i> prior to its redescription (Michalczyk et al., 2012a, 2012b) should be verified. Additionally, Meyer (2013) stated: "The vast majority of records of <i>M. tardigradum</i> in earlier papers on the Americas should now be reassigned to <i>Milnesium tardigradum</i> sensu lato, either because the provided description differs significantly from <i>M. tardigradum</i> sensu stricto or because insufficient description is provided to make a determination."
26	<i>Minibiotus intermedius</i> (Plate, 1888)	2, 3	A, C, E, F, ?	<i>Minibiotus intermedius</i> used to be considered as cosmopolitan, but according to more modern taxonomy it is a species complex (Claxton, 1998).
27	<i>Murrayon pullari</i> (Murray, 1907)	2	H	Holarctic, with few non-Holarctic localities (McInnes, 1994).
28	<i>Paramacrobotus areolatus</i> (Murray, 1907) sensu lato	3	F	The nominal species for a cosmopolitan (McInnes, 1994) <i>P. areolatus-richtersi</i> species group, so with an unknown geographic range (see also remarks in Kaczmarek et al., 2014a).
29	<i>P. danielae</i> (Pilato et al., 2001)*	7	E	Species with Neotropical distribution, known only from Ecuador and Peru (Pilato et al., 2001, 2002, 2003, 2004). This is the third record of this species.
30	<i>P. derkai</i> (Degma, Michalczyk & Kaczmarek, 2008)	1	B	Species currently endemic to Colombia (Degma et al., 2008).
31	<i>P. richtersi</i> (Murray, 1911) sensu lato	3	F	The nominal species for a cosmopolitan (McInnes, 1994) <i>P. areolatus-richtersi</i> species group, so with an unknown geographic range (see also remarks in Kaczmarek et al., 2014a).

Table 2. (Continued).

No.	Species/subspecies	Source	Departments	Remarks
32	<i>Pseudechiniscus novaezeelandiae</i> (Richters, 1908) sensu lato	2, 3, 5	A, F, G	This taxon appears to have a wide distribution (McInnes, 1994), which suggests a species complex that requires further study.
33	<i>P. suillus</i> (Ehrenberg, 1853) sensu lato	2, 5	A, E, F, G,	The nominal species for a cosmopolitan species complex (McInnes, 1994; Fontoura and Morais, 2011), so with an unknown geographic range (see also remarks in Kaczmarek et al., 2014a).
34	<i>Ramazottius oberhaeuseri</i> (Doyère, 1840) sensu lato	2	A, D, G	The nominal species for a cosmopolitan (McInnes, 1994) species complex, but the majority of older records need to be confirmed (see also Pilato et al., 2013 and remarks in Kaczmarek et al., 2014a).
35	<i>Richtersius coronifer</i> (Richters, 1903)	2	D	The species is known mainly from localities in the Holarctic (McInnes, 1994). In this situation, the Colombian record requires confirmation.

7. *Milnesium katarzynae* Kaczmarek, Michalczyk & Beasley, 2004*

Material examined: Ten specimens in 3 samples (see Table 1).

Remarks: Our specimens correspond perfectly to the original description (Kaczmarek et al., 2004). This species was found in both epiphytic and rock mosses. Previously reported only from a few tropical localities (see also Table 2).

8. *Milnesium krzysztofi* Kaczmarek & Michalczyk, 2007*

Material examined: 7 specimens in 3 samples (see Table 1).

Remarks: Our specimens correspond perfectly to the original description (Kaczmarek and Michalczyk, 2007). This species was found only in 2 epiphytic mosses. Previously reported only from 2 Neotropical localities (see also Table 2).

4. Discussion

As pointed out in Section 1, tardigrades of Colombia are poorly known and only a few papers, mostly faunistic, on this region have been published. The first studies of Colombian tardigrades, conducted by Richters (1911a, 1911b), reported 6 taxa from Antioquia, Bogota, Tolima, Santander, Valle del Cauca, and Cundinamarca departments (Table 2). In 1914, Heinis reported 21 taxa (including 1 new for science and 15 new records) from different regions of Colombia. Later papers on Colombian tardigrades were published very sporadically, and until now only 30 taxa have been reported from this country (see Table 2). Additionally, at present, many taxa known from Colombia belong to species complexes, and their presence in Colombia is doubtful and needs confirmation

(e.g., the nominal species *Milnesium tardigradum* Doyère, 1840; *Macrobotus hufelandi*; *M. harmsworthi* Murray, 1907; *Paramacrobotus areolatus* (Murray, 1907); and *Pseudechiniscus suillus* (Ehrenberg, 1853)). In conclusion, 35 tardigrade species (including the 8 taxa reported in this study) are known from 8 Colombian departments, whereas the tardigrade fauna of the other 25 Colombian departments is completely unknown. In contrast, more species have been reported from smaller or much smaller but better studied countries/areas, e.g., for Turkey ca. 50 species, Costa Rica ca. 60, Svalbard ca. 90, Sicily and neighboring islands 98, Poland ca. 100, Slovakia ca. 100, Hungary ca. 120, and Romania ca. 140 (see Degma, 2006; Kaczmarek et al. 2010a, 2010b; Kaczmarek et al., 2012; Vargha, 2012; Zawierucha et al., 2013; Ciobanu et al., 2014; Coulson et al., 2014; Lisi et al., 2014). Knowledge on the tardigrade fauna of Colombia also looks very poor in comparison with knowledge of tardigrade fauna of Central and South America (100 species known from Central America, 220 from South America, and 251 from the entire Neotropical region) (Meyer, 2013; Kaczmarek et al., 2014b). However, it is also important to point out that knowledge of tardigrades from Neotropical regions, which have the highest biodiversity in the world, is very poor in general (e.g., from Belize, El Salvador, Guatemala, Honduras, Panama, and many small island countries of Central America, 0 species are known; Cuba 1; Curaçao 1; Dominica 3; Saint Lucia 4; Barbados 5; Cayman Islands 6; Paraguay 7; Surinam 1; Nicaragua 5; Puerto Rico 9; Dominican Republic 16; Ecuador ca. 20; Venezuela ca. 20; Uruguay ca. 25; Peru 28; Bolivia ca 35; Mexico 42; Brazil ca. 60; Chile ca. 60; Argentina ca. 110) (see: Meyer, 2013; Kaczmarek et al., 2014a, 2014b). To conclude, Colombia and other Neotropical regions include a number of

species-rich and important tropical biogeographic zones in which the tardigrade fauna is currently poorly explored.

Acknowledgments

The authors would like to thank the 4 anonymous reviewers for their valuable comments to the manuscript. This research was supported by the Human Genetics

Institute, Pontificia Universidad Javeriana, Colombia. This work was also partially funded by the Prometeo Project of the Secretariat for Higher Education, Science, Technology, and Innovation of the Republic of Ecuador. Studies were partially conducted in the framework of the activities of BARg (Biodiversity and Astrobiology Research group).

References

- Armenteras D, Cadena VC, Moreno RP (2007). Evaluación del estado de los bosques de niebla y de la meta 2010 en Colombia. Bogotá, Colombia: Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, pp. 1–76 (in Spanish).
- Bartels PJ, Nelson DR, Kaczmarek Ł, Michalczyk Ł (2014). The genus *Milnesium* (Tardigrada: Eutardigrada: Milnesiidae) in the Great Smoky Mountains National Park (North Carolina and Tennessee, USA), with the description of *Milnesium bohleberi* sp. nov. *Zootaxa* 3826: 356–368.
- Bartoš E (1940). Über die Variation der art *Hypsibius ornatus* Richt. (Tardigrada). *Zool Jahrb Syst* 73: 369–384 (in German).
- Bertolani R, Biserov V, Rebecchi L, Cesari M (2011). Taxonomy and biogeography of tardigrades using an integrated approach: new results on species of the *Macrobiotus hufelandi* group. *Invertebr Zool* 8: 23–36.
- Bertolani R, Rebecchi L (1993). A revision of the *Macrobiotus hufelandi* group (Tardigrada, Macrobiotidae), with some observations on the taxonomic characters of eutardigrades. *Zool Scr* 22: 127–152.
- Binda MG (1988). Redescrizione di *Macrobiotus echinogenitus* Richters, 1904 e sul valore di buona specie di *Macrobiotus crenulatus* Richters, 1904 (Eutardigrada). *Animalia* 15: 201–210 (in Italian).
- Biserov V, Pilato G, Lisi O (2011). *Macrobiotus trunovae* sp.n., a new species of tardigrade from Russia. *Invertebr Zool* 8: 57–62.
- Ciobanu DA, Moglan I, Zawierucha K, Kaczmarek Ł (2014). New records of terrestrial tardigrades (Tardigrada) from Ceahlău National Park with zoogeographical and taxonomical remarks on Romanian water bears. *North-West J Zool* (in press).
- Claxton SK (1998). A revision of the genus *Minibiotus* (Tardigrada: Macrobiotidae) with descriptions of eleven new species from Australia. *Records of the Australian Museum* 50: 125–160.
- Convey P, McInnes SJ (2005). Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. *Ecology* 86: 519–527.
- Coulson SJ, Convey P, Aakra K, Aarvik L, Ávila-Jiménez ML, Babenko A, Biersma EM, Boström S, Brittain JE, Carlsson AM et al. (2014). The terrestrial and freshwater invertebrate biodiversity of the archipelagos of the Barents Sea; Svalbard, Franz Josef Land and Novaya Zemlya. *Soil Biol Biochem* 68: 440–470.
- Dastych H (1988). The Tardigrada of Poland. *Monograf Faun Pol* 16: 1–255.
- Dastych H (1991). Redescription of *Hypsibius antarcticus* (Richters, 1904), with some notes on *Hypsibius arcticus* (Murray, 1907) (Tardigrada). *Mitt Hamb Zool Mus Inst* 88: 141–159.
- Degma P (2006). First records of two Heterotardigrada (Tardigrada) species in Slovakia. *Biologia (Bratislava)* 61: 501–502.
- Degma P, Bertolani R, Guidetti R (2009–2014). Actual checklist of Tardigrada species. 2009–2014, Ver. 26: 10-07-2014. Available online at <http://www.tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf>.
- Degma P, Guidetti R (2007). Notes to the current checklist of Tardigrada. *Zootaxa* 1579: 41–53.
- Degma P, Michalczyk Ł, Kaczmarek Ł (2008). *Macrobiotus derkai*, a new species of Tardigrada (Eutardigrada, Macrobiotidae, *huziori* group) from the Colombian Andes (South America). *Zootaxa* 1731: 1–23.
- Fontoura P, Morais P (2011). Assessment of traditional and geometric morphometrics for discriminating cryptic species of the *Pseudechiniscus suillus* complex (Tardigrada, Echiniscidae). *J Zool Syst Evol Res* 49: 26–33.
- Guidetti R, Bertolani R (2005). Tardigrade taxonomy: an updated check list of the taxa and a list of characters for their identification. *Zootaxa* 845: 1–46.
- Guidetti R, Peluffo JR, Rocha AM, Cesari M, Moly de Peluffo MC (2013). The morphological and molecular analyses of a new South American urban tardigrade offer new insights on the biological meaning of the *Macrobiotus hufelandi* group of species (Tardigrada: Macrobiotidae). *J Nat Hist* 47: 2409–2426.
- Guil N, Sánchez-Moreno S, Machordom A (2009). Local biodiversity patterns in micrometazoans: are tardigrades everywhere? *Syst Biodivers* 7: 259–268.
- Heinis F (1914). Die Moosfauna Columbiens. In: *Voyage d'exploration scientifique en Colombie*. Mem Soc Neuchateloise Sci Nat 5: 675–730 (in German).
- Jerez J, Narváez E (2001). Tardígrados (Animalia: Tardigrada) de la Reserva El Diviso-Santander, Colombia. *Biota Colomb* 2: 145–151 (in Spanish).
- Jerez J, Narváez E, Restrepo R (2002). Tardígrados en musgos de la Reserva el Diviso (Santander, Colombia). *Rev Col Entomol* 28: 199–206 (in Spanish).
- Jørgensen A, Møbjerg N, Kristensen, RM (2007). A molecular study of the tardigrade *Echiniscus testudo* (Echiniscidae) reveals low DNA sequence diversity over a large geographic area. *J Limnol* 66: 77–83.

- Kaczmarek Ł, Cytan J, Zawierucha K, Diduszko D, Michalczyk Ł (2014a). Tardigrades from Peru (South America), with descriptions of three new species of Parachela Zootaxa 3790: 357–379.
- Kaczmarek Ł, Gołdyn B, Czyż M, Michalczyk Ł (2010a). The first records of *Isohypsibius pushkini* Tumanov, 2003 (Eutardigrada, Hypsibiidae) from Poland. Biol Lett 47: 81–85.
- Kaczmarek Ł, Gołdyn B, Prokop ZM, Michalczyk Ł (2011). New records of Tardigrada from Bulgaria with the description of *Macrobiotus binieki* sp. nov. (Eutardigrada: Macrobiotidae) and a key to the species of the *harmsworthi* group. Zootaxa 2781: 29–39.
- Kaczmarek Ł, Gołdyn B, Wełnicz W, Michalczyk Ł (2010b). Ecological factors determining Tardigrada distribution in Costa Rica. J Zool Syst Evol Res 49: 78–83.
- Kaczmarek Ł, Jakubowska N, Michalczyk Ł (2012). Current knowledge on Turkish tardigrades with a description of *Milnesium beasleyi* sp. nov. (Eutardigrada: Apochela: Milnesiidae, the *granulatum* group). Zootaxa 3589: 49–64.
- Kaczmarek Ł, Michalczyk Ł (2007). A new species of Tardigrada (Eutardigrada: Milnesiidae): *Milnesium krzysztofi* from Costa Rica (Central America). New Zeal J Zool 34: 297–302.
- Kaczmarek Ł, Michalczyk Ł (2009). Redescription of *Hypsibius microps* Thulin, 1928 and *H. pallidus* Thulin, 1911 (Eutardigrada: Hypsibiidae) based on the type material from Thulin collection. Zootaxa 2275: 60–68.
- Kaczmarek Ł, Michalczyk Ł, Beasley CW (2004). *Milnesium katarzynae* sp. nov., a new species of eutardigrade (Milnesiidae) from China. Zootaxa 743: 1–5.
- Kaczmarek Ł, Michalczyk Ł, McInnes SJ (2014b). Annotated zoogeography of non-marine Tardigrada. Part I: Central America. Zootaxa 3763: 1–62.
- Kinchin IM (1994). The Biology of Tardigrades. London, UK: Portland Press Ltd, pp. 1–186.
- Lisi O, Sabella G, Pilato P (2014). *Mixibius parvus* sp. nov. and *Diphascion (Diphascion) ziliense* sp. nov., two new species of Eutardigrada from Sicily. Zootaxa 3802: 459–468.
- Marcus E (1936). Tardigrada. Das Tierreich 66: 1–340.
- Maucci W (1986). Tardigrada. Fauna d'Italia, Bologna, Calderini 24: 1–388.
- McInnes SJ (1994). Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. J Nat Hist 28: 257–352.
- Meyer HA (2013). Terrestrial and freshwater Tardigrada of the Americas. Zootaxa 3747: 1–71.
- Michalczyk Ł, Kaczmarek Ł (2005). The first record of the genus *Calohypsibius* Thulin, 1928 (Eutardigrada: Calohypsibiidae) from Chile (South America) with description of a new species *Calohypsibius maliki*. New Zeal J Zool 32: 287–292.
- Michalczyk Ł, Kaczmarek Ł (2006). Revision of the *Echiniscus bigranulatus* group with a description of a new species *Echiniscus madonnae* (Tardigrada: Heterotardigrada: Echiniscidae) from South America. Zootaxa 1154: 1–26.
- Michalczyk Ł, Kaczmarek Ł (2007). *Echiniscus ganczareki*, a new species of Tardigrada (Heterotardigrada: Echiniscidae, *bigranulatus* group) from Costa Rica. Zootaxa 1471: 15–25.
- Michalczyk Ł, Wełnicz W, Frohme M, Kaczmarek Ł (2012a). Redescriptions of three *Milnesium* Doyère, 1840 taxa (Tardigrada: Eutardigrada: Milnesiidae), including the nominal species for the genus. Zootaxa 3154: 1–20.
- Michalczyk Ł, Wełnicz W, Frohme M, Kaczmarek Ł (2012b). Corrigenda of Zootaxa, 3154: 1–20. Redescriptions of three *Milnesium* Doyère, 1840 taxa (Tardigrada: Eutardigrada: Milnesiidae), including the nominal species for the genus. Zootaxa 3393: 66–68.
- Miller WR, McInnes SJ, Bergstrøm DM (2005). Tardigrades of the Australian Antarctic: *Hypsibius heardensis* (Eutardigrada: Hypsibiidae: *dujardini* group) a new species from sub-Antarctic Heard Island. Zootaxa 1022: 57–64.
- Nelson DR (2001). Tardigrada. In: Thorp J, Covich A, editors. Ecology and Classification of North American Freshwater Invertebrates. 2nd ed. San Diego, CA, USA: Academic Press, pp. 527–550.
- Nelson DR (2002). Current status of the Tardigrada: evolution and ecology. Integrative and Comp Biol 42: 652–659.
- Nelson DR, Marley NJ (2000). The biology and ecology of lotic Tardigrada. Freshwater Biol 44: 93–108.
- Pilato G, Binda MG, Lisi O (2003). Remarks on some species of tardigrades from South America with description of *Minibiotus sidereus* n. sp. Zootaxa 195: 1–8.
- Pilato G, Binda MG, Napolitano A, Moncada E (2001). Notes on South American tardigrades with the description of two new species: *Pseudechiniscus spinirectus* and *Macrobiotus danielae*. Trop Zool 14: 223–231.
- Pilato G, Binda MG, Napolitano A, Moncada E (2002). Tardigrades from Ecuador with the description of two new species: *Mixibius ornatus* spec. nov. and *Diphascion (Adropion) onorei* spec. nov. Stud Neotrop Fauna E 37: 175–179.
- Pilato G, Binda MG, Napolitano A, Moncada E (2004). Remarks on some species of tardigrades from South America with description of two new species. J Nat Hist 38: 1081–1086.
- Pilato G, D'Urso V, Lisi O (2013). *Ramazzottius thulini* (Pilato, 1970) *bona species* and description of *Ramazzottius libycus* sp. nov. (Eutardigrada, Ramazzottidae). Zootaxa 3681: 270–280.
- Pilato G, Kiosya Y, Lisi O, Sabella G (2012). New records of Eutardigrada from Belarus with the description of three new species. Zootaxa 3179: 39–60.
- Ramazzotti G (1962). Tardigradi del Cile, con descrizione di quattro nuove specie e di una varietà. Atti Soc Ital Sc Nat 101: 275–287 (in Italian).
- Ramazzotti G, Maucci W (1983). Il Phylum Tardigrada. Mem Ist Ital Idrobiol 41: 1–1012 (in Italian).
- Rangel CO (2008). Colombia diversidad biótica VI: Riqueza y diversidad de los musgos y líquenes en Colombia. Bogota, Columbia: CINDEC Universidad Nacional de Colombia (in Spanish).

- Richters F (1911a). Südamerikanische Tardigraden. Zool Anz 38: 273–277 (in German).
- Richters F (1911b). Faune des mousses. Tardigrades. Duc d'Orleans. Campagne arctique de 1907. Impr Sci C Buelens, Bruxelles: 1–20 (in French).
- Vargha B (2012). Localities of the Hungarian water bears (Tardigrada). e-A Nat Pann 4: 103–142.
- Whitehead AG, Hemming JR (1965). A comparison of some quantitative methods of extracting small vermiform nematodes from soil. Ann Appl Biol 55: 25–38.
- Zawierucha K, Coulson J, Michalczyk Ł, Kaczmarek Ł (2013). Current knowledge on the Tardigrada of Svalbard with the first records of water bears from Nordaustlandet (High Arctic). Polar Res 32: 20886.