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## Annotated zoogeography of non-marine Tardigrada. Part I: Central America

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## Abstract

Dividing the world into nine regions, this first paper describes literature records of the limno-terrestrial tardigrades (Tardigrada) reported from Central America. Updating previously published species lists we have revised the taxonomy and provided additional habitat, geographic co-ordinates, and biogeographic comments. It is hoped this work will serve as a reference point and background for further zoogeographic studies.

**Key words:** biogeography, new records, species list, tardigrades, taxonomy

## Introduction

Whilst often referred to as one of the ‘minor’ or ‘lesser known’ phyla, the Tardigrada comprises a group of animals with an almost ubiquitous worldwide distribution. These micrometazoans average 500 µm as mature adults with a few larger taxa reaching over 2 mm and juveniles/larvae *ca.* 100 µm. Tardigrades are bilaterally symmetrical with five distinct ‘pseudosegments’: the head and four body segments, each bearing a pair of lobopod limbs most often terminated with claws. They are found in a variety of habitats from tropical rain forests to arid polar deserts, and from mountain tops to the abyssal ocean depths.

Initially identified in the 18<sup>th</sup> Century, tardigrades have been studied throughout the 20<sup>th</sup> Century, with modern interest focusing on the anabiotic adaptations of these mysterious animals (*e.g.* Welnicz *et al.* 2011). The early work was largely based on morphology with few physiological studies and latterly more discussion on evolutionary and systematic status. Recently, Marley *et al.* (2011) revised the higher subdivisions of the order Parachela and Pilato & Binda (2010) the families within this order. There has been additional ‘species complex’ revisions and new or revised taxonomic criteria, which is gradually including molecular data (*e.g.* Bertolani & Rebecchi 1993; Claxton 1998; Guidetti *et al.* 2000; Guidetti & Bertolani 2001; Jørgensen & Kristensen 2004; Guidetti *et al.* 2005; Jørgensen *et al.* 2010; Michalczyk *et al.* 2012a; 2012b). The monographs by Ramazzotti (1962a; 1972; 1974) with the final edition III (Ramazzotti and Maucci 1983) and its English translation (Beasley 1995) are still the main starting point for most taxonomic studies on tardigrades. A checklist of the currently known Tardigrada taxa (Guidetti & Bertolani 2005; Degma & Guidetti 2007) is regularly updated on the Internet (Degma *et al.* 2012). There is also a recently launched online tardigrade taxonomy data repository, the Tardigrada Register (Michalczyk & Kaczmarek 2013).

The first global biogeographic synthesis of non-marine tardigrades (McInnes 1994) provided limited species bio-distribution ranges within the confines of geopolitical borders, but remains the starting point for all subsequent studies on any aspect of taxonomy and biogeography. These baseline data have increased by over 70%, while distribution data can now be pinpointed to less than a degree of latitude and longitude. This literature and data explosion of the last two decades has prompted us to embark on an updated and enriched biogeography of the Tardigrada. The sheer quantity of data necessitates that this will be published as a series of nine papers, covering: Central America, South America, North America, Polar Regions, Europe, Africa, Asia, Australia, and Oceanic Islands. Each paper will be defined in detail with this, the first section, being the non-marine tardigrades of Central America (Figs 1–2).

anthropogenic or animal vectors, prevailing trade winds and ocean currents, especially the North Atlantic surface gyre flowing from Africa to the Americas. The transport of dust and aerosols from Africa to Central America (Prospero 1999; Trapp *et al.* 2010), as well as vegetation rafts borne on ocean currents (Renner 2004), may provide tardigrade dispersal opportunities. The alternative scenario is that we are observing species with inadequately sampled widespread distributions. The verification of introduced species requires good regional baseline data, where ‘new’ taxa could be attributed to transport enhanced dispersal. Unfortunately, the Central American tardigrade fauna cannot, as yet, support this type of analysis.

Tardigrades are small, potentially easily transported as eggs and tuns, and potentially ubiquitous. Even so, the current paradigm suggests that few species are cosmopolitan and most have more local distributions (*e.g.* Bertolani & Rebecchi 1993; Pilato & Binda 2001). This indeed corroborates the relatively high levels of apparent “endemism” in the data (Table 1). However, regionally focused surveys will always enhance local endemism (*e.g.* Cuba) and this is augmented by focusing on particular habitats which may not necessarily overlap with other adjacent regions. This suggests many currently ‘endemic’ species are indeed more widespread and that even small-scale surveys will yield significant numbers of new species.

To conclude we have catalogued 100 tardigrade taxa from over thirty papers covering only three countries of the Central American isthmus and nine Caribbean islands. While this accounts 85% of the total regional landmass area, this is actually less than a third of the Central American countries and islands. We suggest that there is significant potential to expand the regional tardigrade data where a significant portion (perhaps even the majority) of the fauna is endemic but remains undiscovered.

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## References

- Arcidiacono, R. (1962) Contributo alla conoscenza dei Tardigradi dei Monti Nebrodi e descrizione di una nuova specie di *Itaquascon*. *Bollettino delle sedute dell'Accademia Gioenia di Scienze naturali Catania, Serie IV*, 3, 123–134.
- Bartels, P.J., Pilato, G., Lisi, O. & Nelson, D.R. (2009) *Macrobotus* (Eutardigrada, Macrobiotidae) from the Great Smoky Mountains National Park, Tennessee/North Carolina, USA (North America): two new species and six new records. *Zootaxa*, 2022, 45–57.
- Beasley, C.W. (1972) Some Tardigrades from Mexico. *The Southwestern Naturalist*, 17, 21–29. <http://dx.doi.org/10.2307/3669835>
- Beasley, C.W. (1981) Some Tardigrada from Puerto Rico. *The Texas Journal of Science*, 33(1), 9–12.
- Beasley, C.W. (1995) The phylum Tardigrada. Third Edition by G. Ramazzotti and W. Maucci, English Translation. *Published by the translator at McMurry University, Abilene, USA*, 1–1014.
- Beasley, C.W. & Pilato, G. (1987) Two new species of *Doryphoribius* (Eutardigrada, Hypsibiidae) from North America. *Animalia*, 14, 99–105.
- Beasley, C.W., Kaczmarek, Ł. & Michalczyk, Ł. (2008) *Doryphoribius mexicanus*, a new species of Tardigrada (Eutardigrada, Hypsibiidae) from Mexico (North America). *Proceedings of the Biological Society of Washington*, 121, 34–40. Available from <http://www.pbsw.org/doi/pdf/10.2988/07-30.1> (accessed 31 Dec. 2013).
- Bertolani, R. & Pilato, G. (1988) Struttura delle unghie nei Macrobiotidae e descrizione di *Murrayon* n. gen. (Eutardigrada). *Animalia*, 15, 17–24.
- Bertolani, R. & Rebecchi, Ł. (1993) A revision of the *Macrobotus hufelandi* group (Tardigrada, Macrobiotidae), with some observations on the taxonomic characters of eutardigrades. *Zoologica Scripta*, 22, 127–152.

<http://dx.doi.org/10.1111/j.1463-6409.1993.tb00347.x>

- Binda, M.G. & Pilato, G. (1972) Tardigradi muscicoli di Sicilia (IV Nota). *Bollettino dell'Accademia Gioenia di Scienze Naturali*, 11, 47–60.
- Binda, M.G. & Pilato, G. (1986) *Ramazottius*, nuova genere di eutardigrado (Hypsibiidae). *Animalia*, 13, 159–166.
- Biserov, V.I. (1998) Tardigrades of the Caucasus with a taxonomic analysis of the genus *Ramazottius* (Parachela: Hypsibiidae). *Zoologischer Anzeiger*, 236, 139–159.
- Claxton, S.K. (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.  
<http://dx.doi.org/10.3853/j.0067-1975.50.1998.1276>
- Da Cunha, A.X. & du Nascimento Ribeiro, F. (1962) A fauna de Tardígrados da Ilha da Madeira. *Memorias e estudos do Museu Zoológico da Universidade de Coimbra*, 279, 1–24.
- Da Cunha, A.X. & du Nascimento Ribeiro, F. (1964) Tardígrados de Angola. *Garcia de Orta, Lisboa*, 12, 397–406.
- Dastych, H. (1991) *Isohypsibius sattleri* (Richters 1902), a valid species (Tardigrada). *Senckenbergiana Biologica*, 71, 181–189.
- Dastych, H. (1992) *Paradiphascon manningi* gen. n. sp. n., a new water-bear from South Africa, with the erecting of a new subfamily Diphasconinae (Tardigrada). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 89, 125–139.
- Dastych, H. (1993) A new genus and four new species of semiterrestrial water-bears from South Africa (Tardigrada). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut*, 90, 175–186.
- Dastych, H. (1999) A new species of the genus *Mopsechiniscus* Du Bois-Reymond Marcus, 1944 (Tardigrada) from the Venezuelan Andes. *Acta Biologica Benrodis*, 10, 91–101.
- De Barros, R. (1939a) *Pseudechiniscus juanita* nova espécie de Tardigrado. *Boletim Biologico. Sao Paulo*, 4, 367–368.
- De Barros, R. (1939b) *Itaquascon umbellinae* gen. nov. spec. nov (Tardigrada, Macrobiotidae). *Zoologischer Anzeiger*, 128, 106–109.
- De Barros, R. (1942) Tardígrados de Estado de Sao Paulo, Brasil. II. Gênero *Macrobiotus*. *Revista Brasileira de Biologia*, 2, 373–386.
- Degma, P. & Guidetti, R. (2007) Notes to the current checklist of Tardigrada. *Zootaxa*, 1579, 41–53.
- Degma, P., Bertolani R. & Guidetti, R. (2012) Actual checklist of Tardigrada species (2009–2012, Ver. 21: 30-06-2012). (<http://www.tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf>)
- 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.
- Degma, P. & Pečalková, M. (2003) First records of Tardigrada in Slovakia from Stuzica National Nature Reserve (Bukovské vrchy Mts, NE Slovakia). *Biologia, Bratislava*, 58(2), 274 + 286.
- Doyère, P.L.N. (1840) Memoire sur les Tardigrades. *Annales des Sciences Naturelles, Zoologie, Paris, Series*, 2, 14, 269–362.
- Du Bois-Reymond Marcus, E. (1944) Sobre tardígrados Brasileiros. *Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo*, 1, 1–19.
- Du Bois-Reymond Marcus, E. (1960) Tardigrada from Curaçao, Bonaire and Los Testigos. *Studies on the Fauna of Curaçao and Other Caribbean Islands*, X, 45, 52–57.
- Ehrenberg, C.G. (1848) Fortgesetzte Beobachtungen über jetzt herrschende atmosphärische mikroskopische, etc. mit Nachtrag und Novarum Specierum Diagnosis. *Monatsberichte der Königlich Preussische Akademie des Wissenschaften zu Berlin*, 13, 370–381.
- Ehrenberg, C.G. (1853) Diagnoses novarum formarum. *Verhandlungen der Königlich Preussische Akademie der Wissenschaften zu Berlin*, 8, 526–533.
- Ehrenberg, C.G. (1859) Beitrag zur Bestimmung des stationären mikroskopischen Lebens in bis 20,000 Fuss Alpenhöhe. *Abhandlungen Königlich-Preussischen Akademie der Wissenschaften zu Berlin*, 429–456.
- Fontoura, P. & Morais, P. (2010) Assessment of traditional and geometric morphometrics for discriminating cryptic species of the *Pseudechiniscus suillus* complex (Tardigrada, Echiniscidae). *Journal of Zoological Systematics and Evolutionary Research*, 49 (Suppl. 1), 26–33.  
<http://dx.doi.org/10.1111/j.1439-0469.2010.00594.x>
- Fontoura, P. & Pilato, G. (2007) *Diphascon (Diphascon) faialense* sp. nov. a new species of Tardigrada (Eutardigrada, Hypsibiidae) from the Azores and a key to the species of the *D. pingue* group. *Zootaxa*, 1589, 47–55.
- Fontoura, P., Pilato, G. & Lisi, O. (2008) New records of eutardigrades (Tardigrada) from Faial and Pico Islands, the Azores, with the description of two new species. *Zootaxa*, 1778, 37–47.
- Fox, I. (1966) On the significance of tardigrades in the digestive tract of snails. *Proceedings of the First International Congress of Parasitology, Rome, Italy, 21–26 September, 1964*, 2, 1064.
- Fox, I. & Garcia-Moll, I. (1962) *Echiniscus molluscorum*, new tardigrade from the feces of the land snail, *Bulimulus exilis* (Gmelin) in Puerto Rico (Tardigrada: Scutechiniscidae). *Journal of Parasitology*, 48, 177–181.
- Guidetti, R. (1998) Two new species of Macrobiotidae (Tardigrada: Eutardigrada) from the United States of America, and some taxonomic considerations of the genus *Murrayon*. *Proceedings of the Biological Society of Washington*, 111, 663–673.
- Guidetti, R. & Bertolani, R. (2001) Phylogenetic relationships in the Macrobiotidae (Tardigrada: Eutardigrada: Parachela). *Zoologischer Anzeiger*, 240, 371–376.

<http://dx.doi.org/10.1078/0044-5231-00044>

- 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. & Pilato, G. (2003) Revision of the genus *Pseudodiphascon* (Tardigrada, Macrobiotidae) with the erection of three new genera. *Journal of Natural History*, 37, 1679–1690.
- Guidetti, R., Rebecchi, L. & Bertolani, R. (2000) Cuticule structure and systematics of Macrobiotidae (Tardigrada: Eutardigrada). *Acta Zoologica*, 81, 27–36.
- Guidetti, R., Gandolfi, A., Rossi, V. & Bertolani, R. (2005) Phylogenetic analysis of Macrobiotidae (Eutardigrada, Parachela): a combined morphological and molecular approach. *Zoologica Scripta*, 34, 235–244.  
<http://dx.doi.org/10.1111/j.1463-6409.2005.00193.x>
- Guidetti, R., Schill, R.O., Bertolani, R., Dandekar, T. & Wolf, M. (2009) New molecular data for tardigrade phylogeny, with the erection of *Paramacrobiotus* gen. n. *Journal of Zoological Systematics and Evolutionary Research*, 47, 315–321.  
<http://dx.doi.org/10.1111/j.1439-0469.2009.00526.x>
- Heinis, F. (1911) Beitrag zur Kenntnis der zentralamerikanischen Moosfauna. *Revue Suisse de Zoologie*, 19, 253–266.
- Herrera-Vasquez, J. (2003) Diversidad y densidad de tardigrados (Tardigrada) en cuatro zonas de vida de Costa Rica. *Brenesia*, 59/60, 77–82.
- Herrera-Vasquez, J.H. & Vargas, M.V. (2003) Tardigrades (Tardigrada) from the western part of the central valley, Costa Rica with some ecological annotations. *Brenesia*, 59/60, 69–76.
- Iharos, G. (1963) The zoological results of Gy. Topal's collectings in South Argentina, 3. Tardigrada. *Annales Historico-Naturales Musei Nationalis Hungarici*, 55, 293–299.
- Iharos, G. (1966) Neue Tardigraden–Arten aus Ungarn. *Acta Zoologica Academiae Scientiarum Hungaricae*, 12, 111–122.
- Iharos, G. (1982) Tardigradologische Notizen. I. *Miscellanea Zoologica Hungarica*, 1, 85–90.
- Jørgensen, A. & Kristensen, R. M. (2004) Molecular phylogeny of Tardigrada - investigation of the monophyly of Heterotardigrada. *Molecular Phylogenetics and Evolution*, 32, 666–670. <http://dx.doi.org/10.1016/j.ympev.2004.04.017>
- Jørgensen, A., Møbjerg, N. and Kristensen, R. M., (2010) Phylogeny and evolution of the Echiniscoidea (Echiniscoidea, Tardigrada) - an investigation of congruence between molecules and morphology. *Journal of Zoological Systematics and Evolutionary Research*, 49 (Suppl. 1), 6–16.  
<http://dx.doi.org/10.1111/j.1439-0469.2010.00592.x>
- Kaczmarek, Ł. (2003) New records of and key to Tardigrada from Costa Rica. *Zootaxa*, 177, 1–4.
- Kaczmarek, Ł. & Michalczyk, Ł. (2002a) *Echiniscus barbarae*, a new species of tardigrade from Cuba Island (Tardigrada: Heterotardigrada, Echiniscoidea, 'arctomys group'). *Zootaxa*, 53, 1–4.
- Kaczmarek, Ł. & Michalczyk, Ł. (2002b) *Calohypsibius schusteri* Nelson et. McGlothlin, 1996 and *Macrobiotus crenulatus* Richters, 1904 – new species of water bears (Tardigrada) for fauna of Poland (in Polish). *Przeгляд Zoologiczny*, 46(1–2), 67–69.
- Kaczmarek, Ł. & Michalczyk, Ł. (2004a) First record of the genus *Doryphoribius* Pilato, 1969 from Costa Rica (Central America) and description of a new species *Doryphoribius quadrituberculatus* (Tardigrada: Hypsibiidae). *Genus*, 15, 447–453.
- Kaczmarek, Ł. & Michalczyk, Ł. (2004b) New records of Tardigrada from Cyprus with a description of the new species *Macrobiotus marlenae* (hufelandi group) (Eutardigrada: Macrobiotidae). *Genus*, 15, 141–152.
- Kaczmarek, Ł. & Michalczyk, Ł. (2007) A new species of Tardigrada (Eutardigrada: Milnesiidae): *Milnesium krzysztofi* from Costa Rica (Central America). *New Zealand Journal of Zoology*, 34, 297–302.  
<http://dx.doi.org/10.1080/03014220709510088>
- Kaczmarek, Ł. & Michalczyk, Ł. (2009a) Redescription of *Hypsibius microps* Thulin, 1928 and *H. pallidus* Thulin, 1911 (Eutardigrada: Hypsibiidae) based on the type material from the Thulin collection. *Zootaxa*, 2275, 60–68.
- Kaczmarek, Ł. & Michalczyk, Ł. (2009b) Two new species of Macrobiotidae, *Macrobiotus szepteykii* (harmsworthi group) and *Macrobiotus kazmierskii* (hufelandi group) from Argentina. *Acta zoologica cracoviensia*, 52B(1–2), 87–99.  
[http://dx.doi.org/10.3409/azc.52b\\_1-2.87-99](http://dx.doi.org/10.3409/azc.52b_1-2.87-99)
- Kaczmarek, Ł. & Michalczyk, Ł. (2010) The genus *Echiniscus* Schultze, 1840 (Tardigrada) in Costa Rican (Central America) rain forests with descriptions of two new species. *Tropical Zoology*, 23(1), 91–106.
- Kaczmarek, Ł., Diduszko, D. & Michalczyk, Ł. (2011a) New records of Mexican Tardigrada. *Revista Mexicana de Biodiversidad*, 82(4), 1324–1327.
- Kaczmarek, Ł., Michalczyk, Ł. & Beasley, C.W. (2004) *Milnesium katarzynae* sp. nov., a new species of eutardigrade (Milnesiidae) from China. *Zootaxa*, 743, 1–5.
- Kaczmarek, Ł., Michalczyk, Ł. & Degma, P. (2007) Description of a new tardigrade, *Macrobiotus barbarae* (Eutardigrada: Macrobiotidae) from the Dominican Republic. *Annales Zoologici (Warszawa)*, 57(3), 363–369.
- Kaczmarek, Ł., Michalczyk, Ł. & Guidetti, R. (2006) Description of the new species *Calcarobiotus (C.) longinoi* sp. nov. (Eutardigrada, Macrobiotidae) from Costa Rica with the diagnostic key to the genus *Calcarobiotus*. *Italian Journal of Zoology*, 73, 247–253.  
<http://dx.doi.org/10.1080/11250000600831642>
- Kaczmarek, Ł., Gołdyn, B., Prokop, Z.M. & Michalczyk, Ł. (2011b) 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.
- Kathman, R.D. (1990) Eutardigrada from Vancouver Island, British Columbia, Canada, including a description of *Platicrista cheleusis* n.sp., *Canadian Journal of Zoology*, 68(9), 1880–1895.  
<http://dx.doi.org/10.1139/z90-268>
- Kendall-Fite, K. & Nelson, D.R. (1996) Two new species of tardigrades from Short Mountain, Tennessee, U.S.A. *Zoological Journal of the Linnean Society*, 116, 205–214.  
<http://dx.doi.org/10.1111/j.1096-3642.1996.tb02344.x>
- Lisi, O. (2011) Remarks on *Doryphoribius flavus* (Iharos, 1966), and description of three new species (Tardigrada, Hypsibiidae). *Zootaxa*, 2834, 17–32.
- Marcus, E. (1927) Zur Anatomie und Ökologie mariner Tardigraden. *Zoologische Jahrbuecher Systematik*, 53, 487–558.
- Marcus, E. (1928) Spinnentiere oder Arachnoidea. IV Bärtierchen (Tardigrada). *Tierwelt Deutschlands und der angrenzenden Meeresteile*. Verlag von Gustav Fischer, Jena, 12, 1–230.  
<http://dx.doi.org/10.1007/bf02340364>
- Marcus, E. (1936) Tardigrada. *Das Tierreich*, 66, 1–340.
- Marley, N.J., McInnes, S.J. & Sands, C.J. (2011) Phylum Tardigrada: A re-evaluation of the Parachela. *Zootaxa*, 2819, 51–64.
- Maucci, W. (1954) Tardigradi nuovi della fauna Italiana. *Atti della Societa Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 93, 576–585.
- Maucci, W. & Ramazzotti, G. (1981). *Cornechiniscus* gen. nov.: Nuova posizione sistematica per i cosiddetti « *Pseudechiniscus* gruppo *cornutus* », con descrizione di una nuova specie (Tardigrada, Echiniscidae). *Memorie dell'Istituto Italiano di Idrobiologia « Dottore Marco de Marchi », Pallanza*, 39, 147–151.
- May, R.M. (1948) Nouveau genre et espèce de Tardigrade du Mexique: *Haplomacrobotus Hermosillensis*. *Bulletin de la Société Zoologique de France*, 73, 95–97.
- McInnes, S.J. (1994) Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History*, 28, 257–352.  
<http://dx.doi.org/10.1080/00222939400770131>
- Mehlen, R.H. (1969a) Tardigrada: taxonomy and distribution in Costa Rica. *Transactions of the American Microscopical Society*, 88, 498–505.  
<http://dx.doi.org/10.2307/3224244>
- Mehlen, R.H. (1969b) New Tardigrada from Texas. *The American Midland Naturalist*, 81, 395–404.  
<http://dx.doi.org/10.2307/2423979>
- Meyer, H.A. (2011) Tardigrada of Grand Cayman, West Indies, with descriptions of two new species of eutardigrade, *Doryphoribius tessellatus* (Hypsibiidae) and *Macrobotus caymanensis* (Macrobotidae). *Zootaxa*, 2812, 28–40.
- Meyer, H.A. (2012) A new water bear, *Minibiotus julianae*, from the Caribbean Island of Dominica (Tardigrada: Eutardigrada: Parachela: Macrobotidae). *Proceedings of the Biological Society of Washington*, 125(1), 54–60.
- Meyer, H.A. & Hinton, J.G. (2012) Tardigrades (Phylum Tardigrada) of the Island of Barbados in the West Indies, with the Description of *Milnesium barbadosense* sp. n. (Eutardigrada: Milnesiidae). *Caribbean Journal of Science*, 46(2–3): 194–202.
- Michalczyk, Ł. & Kaczmarek, Ł. (2005) The first record of the genus *Calohypsibius* Thulin, 1928 (Eutardigrada: Calohypsibiidae) from Chile (South America) with a description of a new species *Calohypsibius maliki*. *New Zealand Journal of Zoology*, 32, 287–292.  
<http://dx.doi.org/10.1080/03014223.2005.9518420>
- Michalczyk, Ł. & Kaczmarek, Ł. (2006a) 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. (2006b) *Macrobotus huziori*, a new species of Tardigrada (Eutardigrada: Macrobotidae) from Costa Rica (Central America). *Zootaxa*, 1169, 47–59.
- Michalczyk, Ł. & Kaczmarek, Ł. (2006c) A new species *Macrobotus magdalenae* (Tardigrada: Eutardigrada: Macrobotidae, *richtersi* group) from Costa Rican rain forest (Central America). *New Zealand Journal of Zoology*, 33, 189–196.  
<http://dx.doi.org/10.1080/03014223.2006.9518444>
- 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. & Kaczmarek, Ł. (2010) Description of *Doryphoribius dawkinsi*, a new species of Tardigrada (Eutardigrada: Hypsibiidae) from the Costa Rican highlands, with the key to the genus *Doryphoribius*. *Zootaxa*, 2393, 46–58.
- Michalczyk, Ł. & Kaczmarek, Ł. (2013) Tardigrada Register: a comprehensive online data repository for tardigrade taxonomy. *Journal of Limnology*, 72(S1), 175–181.  
<http://dx.doi.org/10.4081/jlimnol.2013.s1.e22>
- Michalczyk, Ł. Kaczmarek, Ł. & Weglarska, B. (2006) *Macrobotus sklodowskiae* sp. nov. (Tardigrada: Eutardigrada: Macrobotidae, *richtersi* group) from Cyprus. *Zootaxa*, 1371, 45–46.
- Michalczyk, Ł., Wehnicz, 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., Wehnicz, 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, W.R. & Mehlen, R.H. (2007) Tardigrades of North America: re-description of *Echiniscus tamus* Mehlen, 1969 (Tardigrada: Heterotardigrada: Echiniscoidae: Echiniscidae). *Proceedings of the Biological Society of Washington*, 120(2), 184–188.
- Miller, W.R., McInnes, S.J. & Bergström, D.M. (2005) Tardigrades of the Australian Antarctic: *Hypsibius heardensis* (Eutardigrada: Hypsibiidae: *dujardini* group) a new species from sub-Antarctic Heard Island. *Zootaxa*, 1022: 57–64.
- Murray, J. (1905) The Tardigrada of the Forth Valley. *Annales of Scottish Natural History*, 55, 160–164.
- Murray, J. (1907a) Some South African Tardigrada. *Journal of the Royal Microscopical Society*, 5, 515–524.  
<http://dx.doi.org/10.1111/j.1365-2818.1907.tb01665.x>
- Murray, J. (1907b) Scottish Tardigrada collected by the Lake Survey. *Transactions of the Royal Society of Edinburgh*, 45, 641–668.  
<http://dx.doi.org/10.1017/s0080456800011777>
- Murray, J. (1907c) Arctic Tardigrada, collected by William S. Bruce. *Transactions of the Royal Society of Edinburgh*, 45, 669–681.  
<http://dx.doi.org/10.1017/s0080456800011789>
- Murray, J. (1907d) VI.—Some Tardigrada from the Sikkim Himalaya, *Journal of the Royal Microscopical Society*, 3, 269–273.  
Available from: <http://www.biodiversitylibrary.org/page/5445866#page/345/mode/lup> (accessed 31 Dec.2013)
- Murray, J. (1910) Tardigrada. British Antarctic Expedition 1907 – 1909. *Reports on the Scientific Investigations, Vol. 1 Biology (Part V)*, 83–187.
- Murray, J., (1911) Arctiscoida. *Proceedings of the Royal Irish Academy*, 31: 1–16.
- Nelson, D. R. & McGlothlin, K.L. (1996) A new species of *Calohypsibius* (Phylum Tardigrada, Eutardigrada) from Roan Mountain, Tennessee–North Carolina, U.S.A. *Zoological Journal of the Linnean Society*, 116, 167–174.  
<http://dx.doi.org/10.1111/j.1096-3642.1996.tb02341.x>
- Péterfi, F. (1956) Contribuzioni la Cunoasterea Tardigradelor din R. P. R. *Studii si Cercetari de Biologie*, 7, 149–155.
- Petersen, B. (1951) The tardigrade fauna of Greenland. A faunistic study with some few ecological remarks. *Meddelelser om Grønland, København*, 150(5), 5–94.
- Pilato, G. (1969) Schema per una nuova sistemazione delle famiglie e dei generi degli Eutardigrada. *Bollettino delle sedute dell'Accademia Gioenia di Scienze naturali in Catania, serie IV*, 10, 181–193.
- Pilato, G. (1971) Su una nuova specie di *Doryphoribius* (Eutardigrada, Hypsibiidae) e considerazioni sulla posizione filogenetica del genere. *Bollettino di Zoologia*, 38, 145–149.  
<http://dx.doi.org/10.1080/11250007109436964>
- Pilato, G. (1987) Revision of the genus *Diphascon* Plate, 1889, with remarks on the subfamily Itaquasconinae (Eutardigrada, Hypsibiidae). In *Biology of Tardigrades, R. Bertolani (ed), Selected Symposia and Monographs U.Z.I., 1, Mucchi, Modena*, 337–357.
- Pilato, G. (1997) *Astatumen*, a new genus of the Eutardigrada (Hypsibiidae, Itaquasconinae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, 12 (156), 205–208.
- Pilato, G. (2006) Remarks on the *Macrobotus polyopus* group, with the description of two new species (Eutardigrada, Macrobiotidae). *Zootaxa*, 1298, 37–47.
- Pilato, G. & Binda, M.G. (1998) A comparison of *Diphascon* (*D.*) *alpinum* Murray, 1906, *D.* (*D.*) *chilenense* Plate, 1889 and *D.* (*D.*) *pingue* Marcus, 1936 (Tardigrada), and description of a new species. *Zoologischer Anzeiger*, 236, 181–185.
- Pilato, G. & Binda, M.G. (1999) Three new species of *Diphascon* of the *pingue* group (Eutardigrada, Hypsibiidae) from Antarctica. *Polar Biology*, 21, 335–342.  
<http://dx.doi.org/10.1007/s003000050370>
- Pilato, G. & Binda, M.G. (2001) Biogeography and Limno-terrestrial Tardigrades: Are They Truly Incompatible Binomials? *Zoologischer Anzeiger*, 240, 511–516.  
<http://dx.doi.org/10.1078/0044-5231-00061>
- Pilato, G. & Binda, M.G. (2010) Definition of families, subfamilies, genera and subgenera of the Eutardigrada, and keys to their identification. *Zootaxa*, 2404, 1–54.
- Pilato, G. & Kaczmarek, Ł. (2007) *Macrobotus alvaroi*, a new species of eutardigrade (Tardigrada, Macrobiotidae) of the *polyopus* group from Costa Rica (Central America). *Zootaxa*, 1479, 1–7.
- Pilato, G. & Lisi, O. (2006) Notes on some tardigrades from southern Mexico with description of three new species. *Zootaxa*, 1236, 53–68.
- Pilato, G. & Pennisi, G. (1976) Prime notizie sui tardigradi di Cirenaica. *Animalia*, 3, 243–258.
- Pilato, G. & Sperlinga, G. (1975) Tardigradi muscicoli di Sardegna. *Animalia*, 2, 79–90.
- Pilato, G., Binda, M.G. & Lisi, O. (2004) Notes on tardigrades of the Seychelles with the description of three new species. *Italian Journal of Zoology*, 71, 171–178.  
<http://dx.doi.org/10.1080/11250000409356569>
- Pilato, G., Binda, M.G. & Lisi, O. (2006) Eutardigrada from New Zealand, with descriptions of two new species. *New Zealand Journal of Zoology*, 33, 49–63.  
<http://dx.doi.org/10.1080/03014223.2006.9518430>
- Pilato, G., Fontoura, P. & Lisi, O. (2007) Remarks on the *Echiniscus viridis* group, with the description of a new species



- (Tardigrada, Echiniscidae). *Journal Limnology (Suppl. 1)*, 66, 33–39.  
<http://dx.doi.org/10.4081/jlimnol.2007.s1.33>
- Pilato, G., Binda, M.G., Napolitano, A. & Moncada, E. (2000) The specific value of *Macrobiotus coronatus* De Barros 1942, and description of two new species of the *harmsworthi* group (Eutardigrada). *Bollettino delle sedute della Accademia Gioenia di Scienze Naturali in Catania*, 33: 103–120.
- Pilato, G., Binda, M.G., Napolitano, A. & Moncada, E. (2001) Notes on South American tardigrades with the description of two new species: *Pseudechiniscus spinerectus* and *Macrobiotus danielae*. *Tropical Zoology*, 14, 223–231.  
<http://dx.doi.org/10.1080/03946975.2001.10531154>
- Pilato, G., Kaczmarek, Ł., Michalczyk, L. & Lisi, O. (2003) *Macrobiotus polonicus*, a new species of Tardigrada from Poland (Eutardigrada: Macrobiotidae, "hufelandi group"). *Zootaxa*, 258, 1–8.
- Plate, L. (1889) Beiträge zur Naturgeschichte der Tardigraden. *Zoologische Jahrbücher. Abteilung für Anatomie und Ontogenie der Tiere*; Band 39, Heft 2, 1916. Available from: <http://www.biodiversitylibrary.org/page/11176489#page/495/mode/1up> (accessed 31 Dec. 2013)
- Prospero, J.M. (1999) Long-term measurements of the transport of African mineral dust to the southeastern United States: Implications for regional air quality. *Journal of Geophysical Research*, 104(D13), 15, 917–15, 927.  
<http://dx.doi.org/10.1029/1999jd900072>
- Ramazzotti, G. (1943) Nuova varietà del Tardigrado *Pseudechiniscus cornutus*. *Rivista di Scienze Naturali 'Natura'*, 34, 89–90.
- Ramazzotti, G. (1957) Due Nuove specie di Tardigradi extra-europei. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 96, 188–191.
- Ramazzotti, G. (1959) Il gruppo dell'*Echiniscus viridis* con la nuova specie *E. perviridis* e *Macrobiotus pustulatus*, altra nuova specie (Tardigrada). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale in Milano*, 98, 303–309.
- Ramazzotti, G. (1962a) Il Phylum Tardigrada. *Memorie dell'Istituto Italiano di Idrobiologia, Pallanza*, 14, 1–595.
- Ramazzotti, G. (1962b) Tardigradi del Cile, con descrizione di quattro nuove specie e di una nuova varietà. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 101, 275–287.
- Ramazzotti, G. (1964) Tardigradi del Cile II, con descrizione di due nuove specie e note sulla scultura degli Echiniscidae. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 103, 89–100.
- Ramazzotti, G. (1972) Il phylum Tardigrada (seconda edizione aggiornata). *Memorie dell'Istituto Italiano di Idrobiologia, Pallanza*, 28, 1–732.
- Ramazzotti, G. (1974) Supplemento a Il phylum Tardigrada (Seconda Edizione, 1972). *Memoire dell'Istituto Italiano di Idrobiologia*, 31, 69–179.
- Ramazzotti, G. & Maucci, W. (1983) Il Phylum Tardigrada (III edizione riveduta e aggiornata). *Memorie dell'Istituto Italiano di Idrobiologia*, 41, 1–1012.
- Richters, F. (1902) Beiträge zur Kenntnis der fauna der Umgebung von Frankfurt a. M. *Bericht über die Senckenbergische Naturforschende Gessellschaft in Frankfurt am Main*, 1–21.
- Richters, F. (1904a) Vorläufiger Bericht über die Antarktische Moosfauna. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 236–239.
- Richters, F. (1904b) Arktische Tardigraden. *Fauna Arctica*, 3, 495–508.
- Richters, F. (1907) Antarktische Tardigraden. *Zoologischer Anzeiger*, 31, 915–916.
- Richters, F. (1908a) Moosbewohner. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition (1901–1903)*, Bd V Liefg 2, 1–16.  
<http://dx.doi.org/10.5962/bhl.title.6756>
- Richters, F. (1908b) Beitrag zur Kenntnis der Moosfauna Australiens und der Inseln des Pazifischen Ozeans. *Zoologische Jahrbücher abteilung für Systematik Ökologie und Geographie der Tiere*, 26, 196–213.
- Richters, F. (1908c) Moosfauna-Studien. *Bericht über die Senckenbergische Naturforschende Gessellschaft in Frankfurt am Main*, 14–30.
- Richters, F. (1909) Tardigraden unter 77°S Br. *Zoologischer Anzeiger*, 34, 604–606.
- Richters, F. (1926) Tardigrada. In: "Handbuch der Zoologie Vol. 3". Kükenthal, W. & Krumbach, T. (Eds.), *Walter de Gruyter & Co. Berlin and Leipzig*, 58–61.
- Riggin, G.T. (1962) Tardigrada of Southwest Virginia: with the addition of a new marine tardigrade species from Florida. *Virginia Agricultural Experiment Station Technical Bulletin*, 152, 1–145.
- Riggin, G.T. (1963) Tardigrades from Costa Rica. *The Proceedings of the Louisiana Academy of Sciences*, 26, 15–17.
- Rudescu, L. (1964) Tardigrada. *Fauna Republicii Populare Romine*, 4(7), 1–401.
- Schultze, C.A.S. (1834) *Macrobiotus Hufelandii* animal e crustaceorum classe novum, reviviscendi post diuturnam asphixiam et aridiatem potens, etc. 8, 1 tab. C. Curths, Berlin.
- Schultze, C.A.S. (1840) *Echiniscus Bellermanni*; animal crustaceum. *Berolini, Apud G. Reimer*, 1–8.
- Schuster, R.O. (1971) Tardigrada from the Barranca del Cobre, Sinaloa and Chihuahua, Mexico. *Proceedings of the Biological Society of Washington*, 84, 213–224.
- Schuster, R.O. & Grigarick, A.A. (1966) Tardigrada from the Galápagos and Cocos Islands. *Proceedings of the California Academy of Sciences*, 34, 315–328.
- Schuster, R.O. & Toftner, E.C. (1982) Dominican Republic Tardigrada. *Proceedings of Third International Symposium on the*

- Tardigrada*. East University Press, Johnson City, Tennessee 37614-0002, USA, 221–236.
- Schuster, R.O., Nelson D.R., Grigarick A.A. & Christenberry D. (1980) Systematic criteria of the Eutardigrada. *Transactions of the American Microscopical Society*, 99, 284–303.  
<http://dx.doi.org/10.2307/3226004>
- Séméria, Y. (1985) Deux nouvelles formes de Tardigrades du Nicaragua: *Echiniscus maesi* n. sp. (Heterotardigrada, Echiniscoidea, Echiniscidae) et *Macrobiotus islandicus nicaraguensis* n. ssp. (Eutardigrada, Macrobiotidae). *Comptes rendus de l'Académie des Sciences Série 3*, 300(1), 9–11.
- Spallanzani, L. (1777) Osservazioni e sperienze intorno ai vermicelli spermatici dell'uomo e degli animali. *Opuscoli di Fisica Animale e Vegetabile. Opuscola II*. Modena. 277pp.
- Thulin, G. (1911) Beiträge zur Kenntnis der Tardigradenfauna Schwedens. *Arkiv för Zoologi*, 7(16), 1–60.
- Thulin, G. (1928) Über die Phylogenie und das System der Tardigraden. *Hereditas*, 11, 207–266.  
<http://dx.doi.org/10.1111/j.1601-5223.1928.tb02488.x>
- Trapp, J.M., Millero, F.J. & Prospero J.M. (2010) Trends in the solubility of iron in dust-dominated aerosols in the equatorial Atlantic trade winds: Importance of iron speciation and sources. *Geochemistry Geophysics Geosystems*, 11, Q03014, 22.  
<http://dx.doi.org/10.1029/2009gc002651>
- Urbanowicz, C. (1925) Sur la variabilité de *Macrobiotus oberhaeuseri*. *Bulletin biologique de la France et de la Belgique (Paris)*, 59, 124–142.
- Welnicz, W., Grohme, M.A., Kaczmarek, Ł., Schill, R.O. & Frohme, M. (2011) Anhydrobiosis in tardigrades - the last decade. *Journal of Insect Physiology*, 57(5), 577–583.  
<http://dx.doi.org/10.1016/j.jinsphys.2011.03.019>
- Węglarska, B. (1973) Tardigrada in High Tatra localities bare of snow with a description of *Itaquascon pawlowskii* sp. n. *Věstník Československé Společnosti Zoologické*, 37, 150–154.