

# Current knowledge of the Tardigrada of Svalbard with the first records of water bears from Nordaustlandet (High Arctic)

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## Keywords

Checklist; Edgeøya; new species;  
Prins Karls Forland; soil fauna;  
Svalbard biodiversity.

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## Abstract

The first investigations of the tardigrades of Svalbard took place in the early 20th century and 30 papers on the subject have been published to date. In this article, we summarize available information on the distribution of tardigrades in this Arctic archipelago with remarks on the dubious species and records. Additionally, we examined 28 new moss, lichen and soil samples collected from the islands of Nordaustlandet, Edgeøya and Prins Karls Forland. These samples yielded 324 specimens, 15 exuvia and 132 free-laid eggs belonging to 16 limnoterrestrial species (Heterotardigrada and Eutardigrada). These include five first records of water bears from Nordaustlandet, eight new records for Edgeøya and four for Prince Karls Forland. The most dense population of tardigrades was found in a sample with 253 specimens/10 g of dry material and the least dense population in a sample with three specimens/10 g of dry material. The most frequently recorded species in samples collected in this study were *Testechiniscus spitsbergensis* Scourfield, 1897, *Macrobiotus harmsworthi* Murray, 1907, and *M. islandicus islandicus* Richters, 1904. This article also provides the first ever scanning electron microscope photomicrographs of *Tenuibiotus voronkovi* Tumanov, 2007.

To access the supplementary material for this article, please see Supplementary files under Article Tools online.

Tardigrada are a phylum of microscopic animals (typically 50–2100 µm in size) inhabiting a great majority of ecosystems throughout the world (Ramazzotti & Maucci 1983; Guil 2008). About 1170 species have been described worldwide (Guidetti & Bertolani 2005; Degma & Guidetti 2007; Degma et al. 2009–2013). Limnoterrestrial tardigrades are found mainly in mosses, lichens and soil habitats, whereas aquatic species live both in freshwater and marine environments. Tardigrades are recognized as possessing great environmental stress tolerance and are able to survive in extreme conditions on Earth and, through experimental exposure in low Earth orbit, to the space environment (Wełnicz et al. 2011; Guidetti et al. 2012). In addition to their typical microhabitats (e.g., mosses, lichens or soil), they are also able to dwell in cryoconite holes in alpine and polar glaciers (e.g., De Smet

& Van Rompu 1994; Grønhaug et al. 1999; Dastych 2004; Porazińska et al. 2004). It has also recently been shown that tardigrades inhabit detached moss balls ("glacier mice") that roll free on ice surfaces in the Arctic (Coulson & Midgley 2012). Despite the fact that studies of the tardigrades of the Svalbard islands were conducted by a number of researchers over a long period (e.g., Richard 1898; Richters 1903, 1904, 1911a, b; Murray 1907; Summerhayes & Elton 1923; Marcus 1936; De Smet et al. 1987, 1988; Van Rompu & De Smet 1988, 1991, 1994; Maucci 1996), only the tardigrade fauna of the largest island of the archipelago, Spitsbergen, is relatively well surveyed. In contrast, our knowledge of water bears of other islands of the Svalbard Archipelago is still very poor.

In this article, we list all the species found on every investigated island in the Svalbard Archipelago.

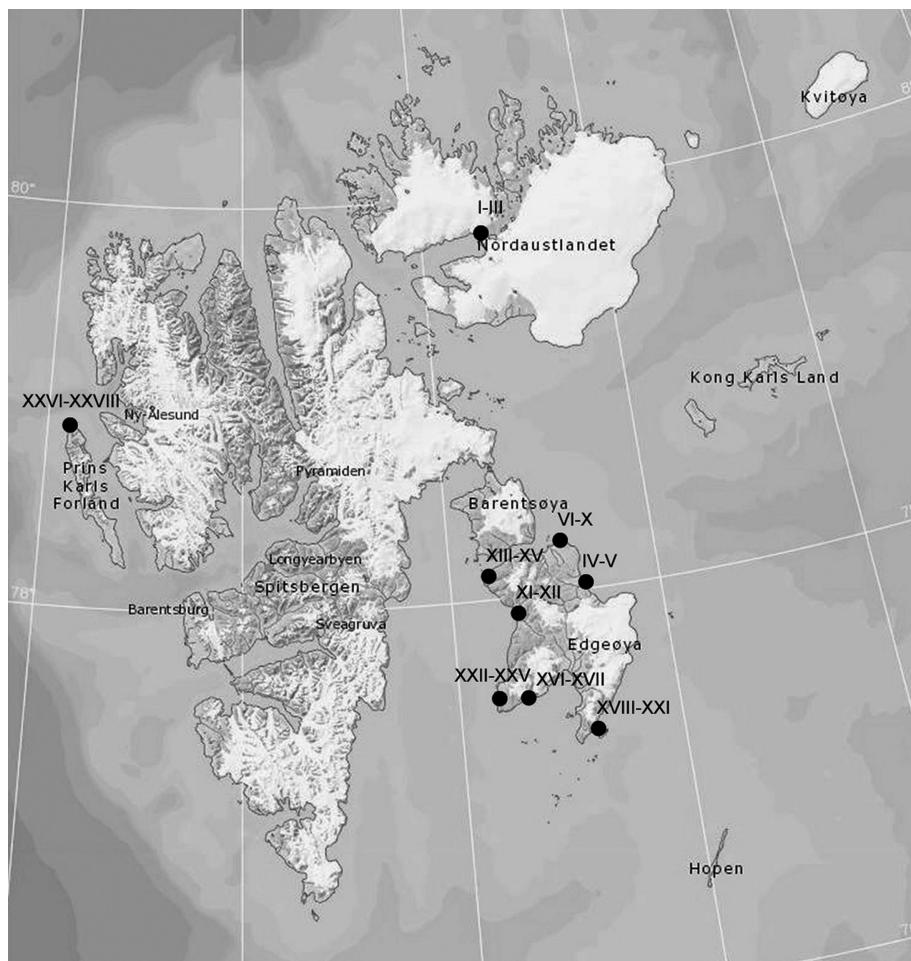
We exclude species mistakenly listed by Coulson & Refseth (2004) in a previous survey of the literature (e.g., *Isohypsibius fuscus* [Mihelčíč, 1971]). Moreover, we offer remarks on dubious species and records (e.g., *Acutuncus antarcticus* [Richters, 1904], *Hypsibius arcticus* [Murray, 1907]). Revision of the inventory of Svalbard is urgently required because of likely errors in the current inventories (Coulson 2013). Additionally, we also present new records of water bears from the islands of Edgeøya and Prins Karls Forland and the first records from Nordaustlandet.

## Materials and methods

In the summers of 2009 and 2010, 28 moss, lichen and soil samples were collected from the islands of Prins Karls Forland, Nordaustlandet and Edgeøya in Svalbard (Fig. 1). These were examined for the tardigrade fauna using standard methods (Ramazzotti & Maucci 1983; Dastych 1985). Twenty samples (71%) contained tardigrades (Table 1). All tardigrades collected were mounted on

microscope slides in Hoyer's medium. Species identification was based on the key to the world fauna of Tardigrada by Ramazzotti & Maucci (1983) as well as later descriptions and diagnostic keys (Dastych 1985, 1988; Bertolani & Rebecchi 1993; Miller et al. 2005; Kaczmarek & Michalczyk 2009; Kaczmarek et al. 2011; Kaczmarek, Zawierucha et al. 2012).

Only specimens determined to the species level are provided in the list of species from Prins Karls Forland, Edgeøya and Nordaustlandet. We decided to do so because records identified only to the generic level do not provide any additional information about the biodiversity range if other species of a genus have been already reported from a given area. In other words, it is not possible to designate a dubious record as a new record or another record of a species that has already been reported and identified to the species level. Doing so could lead to inaccurate estimates of biodiversity and confusion in faunistic checklists and biogeographic studies. In the list of species found during this study, the Roman numerals



**Fig. 1** Map of Svalbard with sampling sites (map from Norwegian Polar Institute).

**Table 1** List of samples investigated in this study, with data on the total number of specimens (S), the number of exuvia (E), the number of eggs (e) found and average density of specimens (calculated as the number of specimens per 10 g of dry sample).

Sample code	Island	Region	Latitude, longitude	Date	S, E, e	Sample type (dry weight)	Density
I	Nordaustlandet	Oxfordhalvøya	79°78'04"N 21°73'04"E	07/2009	S: 13 E: 22 e: 0	Moss, soil (1.93 g)	67
II	Nordaustlandet	Oxfordhalvøya	79°78'04"N 21°73'04"E	07/2009	S: 110 E: 1 e: 51	Moss, soil (10.09 g)	109
III	Nordaustlandet	Oxfordhalvøya	79°78'04"N 21°73'04"E	07/2009	S: 4 E: 0 e: 0	Moss, soil (1.97 g)	20
IV	Edgeøya	Blåbukta	78°03'27"N 22°52'53"E	07/2010	S: 8 E: 0 e: 1	Moss (2.26 g)	35
V	Edgeøya	Blåbukta	78°03'27"N 22°52'53"E	07/2010	S: 18 E: 1 e: 6	Moss (3.24 g)	56
VI	Edgeøya	Kapp Heuglin	78°15'02"N 22°50'40"E	07/2010	S: 3 E: 1 e: 1	Moss (1.24 g)	24
VII	Edgeøya	Kapp Heuglin	78°15'02"N 22°50'40"E	07/2010	S: 0 E: 0 e: 0	Moss, soil (15.12 g)	0
VIII	Edgeøya	Kapp Heuglin	78°14'46"N 22°48'21"E	07/2010	S: 0 E: 0 e: 0	Moss (1.99 g)	0
IX	Edgeøya	Kapp Heuglin	78°14'46"N 22°48'21"E	07/2010	S: 10 E: 0 e: 0	Moss (1.91 g)	52
X	Edgeøya	Kapp Heuglin	78°14'46"N 22°48'21"E	07/2010	S: 4 E: 0 e: 0	Moss (1.65 g)	24
XI	Edgeøya	Diskobukta	77°58'25"N 21°19'08"E	07/2009	S: 0 E: 0 e: 0	Moss, soil (3.92 g)	0
XII	Edgeøya	Diskobukta	77°58'25"N 21°19'08"E	07/2009	S: 3 E: 1 e: 0	Moss, soil (2.66 g)	11
XIII	Edgeøya	Kapp Lee	78°06'45"N 14°50'58"E	07/2009	S: 15 E: 1 e: 8	Moss (2.62 g)	57
XIV	Edgeøya	Kapp Lee	78°06'45"N 14°50'58"E	07/2009	S: 26 E: 0 e: 19	Moss (2.03 g)	128
XV	Edgeøya	Kapp Lee	78°06'45"N 14°50'58"E	07/2009	S: 2 E: 0 e: 0	Moss (3.20 g)	6
XVI	Edgeøya	Kraussbukta	77°50'09"N 20°85'30"E	07/2009	S: 1 E: 1 e: 0	Moss (3.62 g)	3
XVII	Edgeøya	Kraussbukta	77°50'09"N 20°85'30"E	07/2009	S: 0 E: 0 e: 0	Moss (1.57 g)	0
XVIII	Edgeøya	Negerdalen	77°17'42"E 22°53'37"E	07/2010	S: 0 E: 0 e: 0	Moss, soil (6.24 g)	0
XIX	Edgeøya	Negerdalen	77°17'42"E 22°53'37"E	07/2010	S: 6 E: 0 e: 6	Moss (3.45 g)	17

**Table 1** *Continued*

Sample code	Island	Region	Latitude, longitude	Date	S, E, e	Sample type (dry weight)	Density
XX	Edgeøya	Negerdalen	77°19'25"N 22°50'02"E	07/2010	S: 5 E: 0 e: 0	Moss (1.8 g)	28
XXI	Edgeøya	Negerdalen	77°19'25"N 22°50'02"E	07/2010	S: 0 E: 0 e: 0	Moss (4.46 g)	0
XXII	Edgeøya	Russebukta	77°32'22"N 20°50'53"E	07/2009	S: 0 E: 0 e: 0	Moss, soil (2.83 g)	0
XXIII	Edgeøya	Russebukta	77°32'22"N 20°50'53"E	07/2009	S: 44 E: 6 e: 2	Moss (1.74 g)	253
XXIV	Edgeøya	Russebukta	77°32'22"N 20°50'53"E	07/2009	S: 0 E: 0 e: 0	Moss (2.43 g)	0
XXV	Edgeøya	Russebukta	77°32'22"N 20°50'53"E	07/2009	S: 13 E: 2 e: 1	Moss (1.7 g)	76
XXVI	Prins Karls Forland	Fuglehuken	78°53'29"N 10°28'07"E	08/2010	S: 8 E: 0 e: 0	Moss (1.21 g)	66
XXVII	Prins Karls Forland	Fuglehuken	78°53'29"N 10°28'07"E	08/2010	S: 41 E: 1 e: 11	Moss (2.16 g)	190
XXVIII	Prins Karls Forland	Fuglehuken	78°53'29"N 10°28'07"E	08/2010	S: 3 E: 0 e: 4	Moss, lichen (2.28 g)	13

indicate locality code, the first Arabic number indicates the number of specimens, the second Arabic number (in brackets) refers to exuvia and the third Arabic number (preceded by a plus sign) to eggs. Short zoogeographic comments for the recorded species from the Svalbard Archipelago are also provided.

To assess tardigrade population densities in our samples, we used the quotient of specimen number per 10 g of dry weight of the material (i.e., soil, moss or lichen). The samples and slides are deposited in the Department of Animal Taxonomy and Ecology at Adam Mickiewicz University in Poznań, Poland.

## Results

In this study, 16 Tardigrada species of two orders, Eutardigrada and Heterotardigrada, were found. New records for Nordaustlandet, Edgeøya and Prins Karls Forland are marked below with asterisks. The samples (Roman numbers) are described in Table 1.

The average density in samples containing tardigrades was 62 specimens per 10 g of dry material. A density greater than 100 specimens per 10 g was found only in four samples. The most dense population of tardigrades

was found in sample XXIII (253 specimens/10 g) and the least dense population in sample XVI (three specimens/10 g). In eight samples (29%), no tardigrades or their eggs were found.

In the Supplementary file, we list all tardigrade records from Svalbard known from the literature as well as from the present study: Spitsbergen, Prins Karls Forland, Bjørnøya, Barentsøya, Edgeøya, Hopen, Amsterdamøya, Svenskøya, Ryke Yseøyane, Kong Ludvigøyane and Nordaustlandet.

*Diphascon (Adropion) prorsirostre* Thulin, 1928\*. Samples II: 1, X: 4, XIII: 1. These are new records for Nordaustlandet and Edgeøya. The *Diphascon (Adropion) prorsirostre* complex is cosmopolitan (McInnes 1994); however, the majority of these records are old and need be confirmed.

*Diphascon (Diphascon) recamieri* Richters, 1911\*. Samples XIV: 1, XXVI: 5, XXVII: 2 (1), XXVIII: 1. These are new records for Prins Karls Forland and Edgeøya. This is a Holarctic species, recorded from sparse localities in Europe, Asia and North America (McInnes 1994).

*Echiniscus merokensis* Richters, 1904\*. Sample XXVIII: 1. This is a new record for Prins Karls Forland. The species is Palaearctic (McInnes 1994).

*Hypsibius dujardini* (Doyère, 1840). Samples IX: 8, XIV: 4. Species belongs to the cosmopolitan *convergens-dujardini* complex of species (McInnes 1994; Miller et al. 2005; Kaczmarek & Michalczyk 2009). Because the original description is inadequate and unsatisfactory, the examined specimens were compared with recent descriptions (e.g., Ramazzotti & Maucci 1983; Dastych 1988; Miller et al. 2005).

*Hypsibius convergens* (Urbanowicz, 1925)\*. Sample XXIII: 17 (1). This is a new record for Edgeøya. See remarks accompanying *H. dujardini*, above.

*Isohypsibius coulsoni* Kaczmarek et al. 2012\*. Sample XXVII: 14 (1). This is a new record for Prins Karls Forland, previously known only from Rotjesfjellet (Spitsbergen) (Kaczmarek, Zawierucha et al. 2012).

*Isohypsibius* cf. *marcellinoi* Binda & Pilato, 1971\*. Sample XII: 3 (1 with eggs). This is a new record for Edgeøya. Holoarctic (McInnes 1994). This species is very similar to *Isohypsibius dastychi* Pilato, Bertolani & Binda, 1982 but differs from it by the lack of sculpturing on the dorsal cuticle and by a different arrangement of dorsal teeth in the oral cavity. Our specimens clearly do not have sculptured cuticle, but oral cavities are not well preserved and do not allow the determination of teeth numbers. Although we are sure that our animals do not belong to *I. dastychi*, we are not able to confidently determine them to the species level.

*Macrobiotus crenulatus* Richters, 1904. Samples XXVII: 7+7, XIV: 3, XV: 2, XVII: 1. This species is Holarctic (McInnes 1994).

*Macrobiotus harmsworthi harmsworthi* Murray, 1907. Samples XXVI: 2, XXVII: 9+4, XXVIII: 1+4, XIV: 3+3,

XXIII: 23 (5)+2, XXV: 14 (2)+1. This is the nominal taxon for a cosmopolitan species complex (McInnes 1994; Kaczmarek et al. 2011).

*Macrobiotus hufelandi* C.A.S. Schultze 1833\*. Samples VI: 0+1, XIV: 10+15. This is a new record for Edgeøya. The *M. hufelandi* group of species is cosmopolitan (McInnes 1994); however, the majority of older records need to be confirmed (Bertolani & Rebecchi 1993).

*Macrobiotus islandicus islandicus* Richters, 1904\*. Samples I: 0+4, II: 1+9, IV: 3+1, V: 2+1, XIX: 0+6. These are new records for Nordaustlandet and Edgeøya. Holarctic (McInnes 1994).

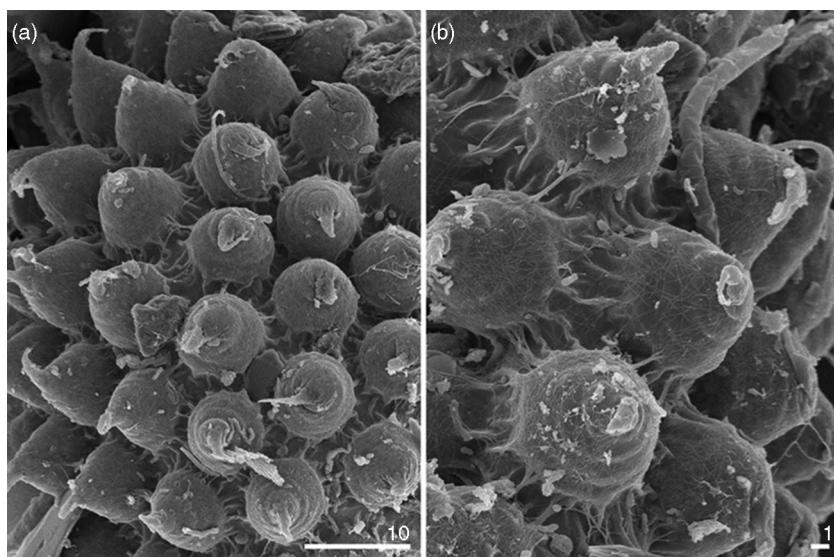
*Murrayon hibernicus* Murray, 1911\*. Sample IX: 1. This is a new record for Edgeøya. Holarctic, Indomalayan (McInnes 1994).

*Platirista angustata* Murray, 1905\*. Sample XXVI: 1. This is a new record for Prins Karls Forland. The species is Holarctic (McInnes 1994).

*Pseudechiniscus suillus* Ehrenberg, 1853\*. Samples II: 1, XX: 1. This is a new record for Nordaustlandet. The *P. suillus* group of species is cosmopolitan, but the distribution of the nominal species is unknown (McInnes 1994).

*Tenuibiotus voronkovi* Tumanov, 2007\*. Samples I: 4+18, II: 16+24, III: 10+7, V: 8 (1)+3, XIII: 10 (1)+8. Eggs of this species are presented in Fig. 2. These are new records for Nordaustlandet and Edgeøya. The species has been previously recorded only from Spitsbergen (Tumanov 2007).

*Testechiniscus spitsbergensis* Scourfield, 1897\*. Samples I: 8, II: 90, III: 4, IV: 3, V: 8, VI: 3. These are new records for



**Fig. 2** *Tenuibiotus voronkovi*: details of the eggshell, shown for the first time with scanning electron microscopy (scale bar in micrometres).

Nordaustlandet and Edgeøya. The species is Holarctic (McInnes 1994).

## Discussion

Tardigrade surveys carried out in Svalbard have been fragmentary and the numbers of species known from different islands of the archipelago are proportional to the number of papers concerning these islands. Because the majority of studies have been performed on the largest island—Spitsbergen—this island has also the longest tardigrade species list: 80 (excluding dubious records; see Supplementary file), with 95% of all species known from the entire archipelago. Second, in terms of species diversity, is Prins Karls Forland 23 (27%), followed by Hopen with 22 (26%), Bjørnøya with 20 (24%) species and Edgeøya with 20 (24%) species. Fifteen (18%) species are known from Barentsøya, nine (11%) from Amsterdamsøya, five (6%) from Nordaustlandet and five (6%) from Kong Ludvigøya, one (1%) from Svenskøya and one species (1%) from Ryke Yseøyane (all figures exclude dubious records; see Supplementary file).

The total number of valid water bear species known from Svalbard is 85. However, given the poor sampling coverage, it is very likely that the real number of species inhabiting the islands is far greater. For example, the tardigrade fauna of the archipelago's second largest island, Nordaustlandet, has not been assayed until this study, in which we found five species in only three samples. Moreover, among tardigrades only two marine species (*Halobiotus arcturulus* Crisp & Kristensen, 1983 and *H. crispae* Kristensen, 1982) have been recorded so far (Smykla et al. 2011) and they are probably a small fraction of the real biodiversity of this area. It should also be borne in mind that many older records date from the time when species complexes, such as the *Macrobiotus harmsworthi* group, were considered single cosmopolitan species and, since the archipelago is isolated from the mainland Europe by about 700 km and from Greenland by about 450 km of sea a careful examination of the Svalbardian tardigrade fauna would probably reveal more endemic species instead the five already described (*Bryodelphax parvuspolaris* Kaczmarek, Zawierucha et al. 2012, *Isohypsibus ceciliae* Pilato & Binda, 1987, *I. coulsoni* Kaczmarek Zawierucha et al. 2012, *I. karenae* Zawierucha 2013; and *Tenuibiotus voronkovi* [Tumanov, 2007]).

The most frequently recorded species in samples collected in this study were *Testechiniscus spitsbergensis* and *M. harmsworthi* (each found in six samples), and *M. islandicus* (recorded in five samples). All of these species were also abundant in previous faunistic

surveys conducted on Spitsbergen. Dastych (1985) reported *T. spitsbergensis* and *M. islandicus*. *islandicus* whereas Kaczmarek, Zawierucha et al. (2012) reported *Diphascon (Diphascon) recamieri*, *T. spitsbergensis*, *M. islandicus* and *M. harmsworthi* as species that occurred most frequently in their analysed samples. Thus, both earlier studies and that reported here show the dominance of these species, with *T. spitsbergensis* clearly the most prevalent.

## Acknowledgements

The authors thank Professor Willem De Smet and Sandra McInnes for help with a paper by Richters (1911b). They express sincere thanks to Professor Giovani Pilato for his valuable comments on *I. marcellinoi* and to Professor R. M. Kristensen for valuable comments on *H. arcticus*. They are also grateful to Paulo Fontoura and another (anonymous) reviewer for their valuable comments that improved the manuscript. This work was supported by the Polish Ministry of Science and Higher Education via the "Diamond Grant" (Diamentowy Grant) programme, grant no. DI 2011 035241, to K. Z.

## References

- Bertolani R. & Rebecchi L. 1993. A revision of the *Macrobiotus hufelandi* group (Tardigrada, Macrobiotidae), with some observations on the taxonomic characters of eutardigrades. *Zoologica Scripta* 22, 127–152.
- Coulson S.J. 2013. The terrestrial invertebrate fauna of the Svalbard Archipelago in a changing world; history of research and challenges. *Canadian Entomologist* 145, 131–146.
- Coulson S.J. & Midgley N.G. 2012. The role of glacier mice in the invertebrate colonisation of glacial surfaces: the moss balls of the Falljökull, Iceland. *Polar Biology* 35, 1651–1658.
- Coulson S.J. & Refseth D. 2004. The terrestrial and freshwater invertebrate fauna of Svalbard (and Jan Mayen). In P. Prestrud et al. (eds.): *A catalogue of the terrestrial and marine animals of Svalbard*. Skrifter 201. Pp. 57–122. Tromsø: Norwegian Polar Institute.
- Dastych H. 1985. West Spitsbergen Tardigrada. *Acta Zoologica Cracoviensia* 28, 169–214.
- Dastych H. 1988. *The Tardigrada of Poland. Monografie Fauny Polski* 16. Warsaw: PWN.
- Dastych H. 2004. *Hypsibus thaleri* sp. nov., a new species of a glacier-dwelling tardigrade from the Himalayas, Nepal (Tardigrada). *Mitteilungen Hamburgisches Zoologisches Museum* 101, 169–183.
- Degma P., Bertolani R. & Guidetti R. 2009–2013. *Actual checklist of Tardigrada species*. Version 22. Accessed on the internet at <http://www.tardigrada.modena.unimo.it/miscellanea/Actual%20checklist%20of%20Tardigrada.pdf> on 1 March 2013

- Degma P. & Guidetti R. 2007. Notes to the current checklist of Tardigrada. *Zootaxa* 1579, 41–53.
- De Smet W.H. & Van Rompu E.A. 1994. Rotifera and Tardigrada from some cryoconite holes on a Spitsbergen (Svalbard) glacier. *Belgian Journal of Zoology* 124, 27–37.
- De Smet W.H., Van Rompu E.A. & Beyens L. 1987. Rotifera, Gastrotricha en Tardigrada uit Shetland, Faroeën en Spitsbergen. (Rotifera, Gastrotricha and Tardigrada from Shetland, Faroe and Spitsbergen islands.) *Natuurwetensch Tijdschrift* 69, 81–102.
- De Smet W.H., Van Rompu E.A. & Beyens L. 1988. Contribution to the rotifers and aquatic Tardigrada of Edgeøya (Svalbard). *Fauna Norvegica Series A* 9, 19–30.
- Grøngaard A., Pugh P. & McInnes S. 1999. Tardigrades and other cryoconite biota, on Greenland Ice Sheet. In H. Greven (ed.): *Proceedings of the Seventh International Symposium on the Tardigrada, August 1997, Düsseldorf, Germany*. *Zoologischer Anzeiger* 238, 211–214.
- 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., Rizzo A.M., Altiero T. & Rebecchi L. 2012. What can we learn from the toughest animals of the Earth? Water bears (tardigrades) as multicellular model organisms in order to perform scientific preparations for lunar exploration. *Planetary and Space Science* 74, 97–102.
- Guil N. 2008. New records and within-species variability of Iberian tardigrades (Tardigrada), with comments on the species from the *Echiniscus-blumi-canadensis* series. *Zootaxa* 1757, 1–30.
- Kaczmarek L., Goldyn B., Prokop Z.M. & 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 L. & Michalczyk Ł. 2009. 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 L., Zawierucha K., Smykla J. & Michalczyk Ł. 2012. Tardigrada of the Revdalen (Spitsbergen) with the descriptions of two new species: *Bryodelphax parvuspolaris* (Heterotardigrada) and *Isohypsibius coulsoni* (Eutardigrada). *Polar Biology* 35, 1013–1026.
- Klekowski R.Z. & Opaliński K.W. 1989. Oxygen consumption in Tardigrada from Spitsbergen. *Polar Biology* 9, 299–303.
- Marcus E. 1936. *Tardigrada. Das Tierreich* 66. Berlin: de Gruyter.
- Maucci W. 1996. Tardigrada of the Arctic tundra with description of two new species. *Zoological Journal of the Linnean Society* 116, 185–204.
- McInnes S.J. 1994. Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature. *Journal of Natural History* 28, 257–352.
- Mihelčič F. 1971. Süßwasser tardigraden aus Nordeuropa. (Freshwater Tardigrada from northern Europe.) *Entomologica Scandinavica* 2, 205–214.
- 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. 1907. Arctic Tardigrada, collected by Wm. S. Bruce. *Transactions of the Royal Society of Edinburgh* 45, 669–681.
- Pilato G., Bertolani R. & Binda M.G. 1982. Studio degli *Isohypsibius* del gruppo *elegans* (Eutardigrada, Hypsibiidae) con descrizione di due nuove specie. (Studies on the *Isohypsibius elegans* group [Eutardigrada, Hypsibiidae] with description of two new species.) *Animalia* 9, 185–198.
- Porazińska D.L., Fountain A.G., Nylen T.H., Tranter M., Virginia R.A. & Wall D.H. 2004. The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arctic, Antarctic and Alpine Research* 36, 84–91.
- Ramazzotti G. & Maucci W. 1983. *Il phylum Tardigrada: III edizione riveduta e aggiornata. (II phylum tardigrade: third edition revised and updated.) Memorie dell' Istituto Italiano di Idrobiologia* 41. Verbania: Institute of Hydrobiology.
- Richard J. 1898. Sur la faune des eaux douces explorées en 1898 pendant la campagne du yacht *Prince-Alice* (Lofoten, Spitsberg, Iles Beeren, Hope, de Barents, et Færøer). (On the freshwater fauna explored in 1898 during the campaign yacht *Prince Alice* [Lofoten, Spitsbergen, islands of Beeren, Hope, Barents and the Faroe Islands].) *Memoires Société Zoologique de France* 11, 326–338.
- Richters F. 1903. Nordische Tardigraden. (Nordic Tardigrada.) *Zoologischer Anzeiger* 27, 168–172.
- Richters F. 1904. Arktische Tardigraden. (Arctic Tardigrada.) *Fauna Arctica* 3, 494–508.
- Richters F. 1911a. Duc d'Orléans, campagne arctique de 1907. *Faune des mousses. Tardigrades. (The Duke of Orléans, Arctic campaign of 1907. Fauna of the mosses. Tardigrada.)* Bruxelles: Charles Bulens.
- Richters F. 1911b. Moosfauna, Tardigrada. (Moss fauna.) In A. Koenig (ed.): *Avifauna Spitzbergensis. (Avifauna of Spitsbergen.)* Pp. 283–286. Bonn: Druck von W. Büxenstein.
- Scourfield D.J. 1897. Contributions to the non-marine fauna of Spitsbergen. Part I. Preliminary notes, and reports on the Rhizopoda, Tardigrada, Entomostraca, &c. *Proceedings of the Zoological Society of London* 65, 784–792.
- Smykla J., Kaczmarek L., Huzarska K. & Michalczyk Ł. 2011. The first record of a rare marine tardigrade, *Halobiotus crispa* Kristensen, 1982 (Eutardigrada: Hypsibiidae), from the Svalbard Archipelago. *Polar Biology* 34, 1243–1247.
- Summerhayes V.S. & Elton C.S. 1923. Contribution to the ecology of Spitsbergen and Bear Island. *Journal of Ecology* 11, 214–286.
- Tumanov D.V. 2007. Three new species of *Macrobiotus* (Eutardigrada, Macrobiotidae, *tenuis*-group) from Tien Shan (Kirghizia) and Spitsbergen. *Journal of Limnology* 66, 40–48.
- Van Rompu E.A. & De Smet W.H. 1988. Some aquatic Tardigrada from Bjørnøya (Svalbard). *Fauna Norvegica Series A* 9, 31–36.

- Van Rompu E.A. & De Smet W.H. 1991. Contribution to the freshwater Tardigrada from Barentsøya, Svalbard ( $78^{\circ}30'N$ ). *Fauna Norvegica Series A* 12, 29–39.
- Van Rompu E.A. & De Smet W.H. 1994. Freshwater tardigrades from Hopen, Svalbard ( $76^{\circ}31'N$ ). *Fauna Norvegica Series A* 17, 1–9.
- Węglarska B. 1965. Die Tardigraden (Tardigrada) Spitzbergens. (The tardigrades [Tardigrada] on Spitsbergen.) *Acta Zoologica Cracoviensis* 11, 43–51.
- Wełnicz W., Grohme M.A., Kaczmarek Ł., Schill R.O. & Frohme M. 2011. Anhydrobiosis in tardigrades—the last decade. *Journal of Insect Physiology* 57, 577–583.
- Zawierucha K. 2013. Tardigrada from Arctic tundra (Spitsbergen) with a description of *Isohypsibus karenae* sp. n. (Isohypsibiidae). *Polish Polar Research* 34, 351–364.