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Aquatic tardigrades in Poland – a review

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Abstract: The diversity, distribution and ecology of aquatic Tardigrada in Poland remain poorly known. We reviewed the literature focused on tardigrades in Poland and recognized only 15 aquatic taxa which were reported from various freshwater and marine habitats. Among them, 12 are freshwater and three are marine taxa. *Hypsibius dujardini* is Poland's most widely-distributed hygrophilous species, but it represents rather a complex of cryptic species and their diagnosis requires integrative approaches. Most reports of aquatic tardigrades in Poland are accidental findings mostly from water bodies in Tatra Mountains or from lakes in Masurian Lake District. Some species were also reported from small ponds or wastewater treatment plants in other regions like Małopolska or Wielkopolska Provinces.

Key words: Europe, freshwater species, marine species, Tardigrada, water bears

Introduction

Poland is a central European country extended between latitudes 49° and 55°N, and longitudes 14° and 25°E. Entire country is located in a temperate warm transitional climatic zone. Air masses from both the Atlantic Ocean and the Eurasian landmass crosses in Poland. The continental impact increases gradually from the west to the east. However, the climate is also dependent upon local factors such as land cover and relief, vegetation cover and the presence of water bodies (Błażejczyk 2006). It has southern mountainous regions along with lowlands within the North European Plain. The natural landscape consists of three reliefs: the lowlands, the highlands and the mountains. The eastern part of Poland exhibits traits similar to eastern Europe, but the rest of it is connected to western Europe via climate, structure, and vegetation. The lowlands overrule where the average elevation of the entire country is ca. 170 m asl, and more than three-fourths of the land lies below 200 m asl. Ice age glaciers' actions form Poland relief which preceded over the northern part during Pleistocene Epoch. This huge and monotonous stretch of Polish lowlands comprises geologically recent deposits that lie over a vast structural basin. Nonetheless, the southern part of Poland is much older and has more exposed geological formations. The mountainous arc dominates the topography.

Various structural basins separate the mountain belt from the older structural mass. However, the northern part possesses swamps and dunes of the Baltic Sea coast (https://www.britannica.com/ place/Poland/Land). In Poland, there are ca. 7000 lakes with a surface area of more than 1 hectare and they cover around 1% of the country's total area (Choiński 2006). These lakes have quite uneven distribution and most of them are located in the northern and central parts of the country within the limit of the last glaciation, forming several well-distinguished lake districts. At the same time, there are few groups of lakes situated outside of the strip of postglacial deposits (Kolada et al. 2005). Moreover, millions of smaller, permanent and temporary, ponds and puddles are distributed more or less regularly thoughtout Poland. Additionally, in Poland, there are ca. 1100 rivers and streams, among which 28 longest rivers amount to a total length of 8984 km. All these aquatic habitats are potentially suitable for aquatic tardigrades.

Tardigrada, also known as water bears, is a phylum of micrometazoans with a size between 50 and 1200 µm. They inhabit various aquatic

(freshwater and marine) and terrestrial environments (Nelson et al. 2015). Water bears can be found in mosses, lichens, soil, sediments, on aquatic plants. Currently, tardigrades are included into two classes, four orders, 32 families, 153 genera, 1380 species and 30 subspecies (Guidetti and Bertolani 2005; Degma and Guidetti 2007; Degma et al. 2021). Marine ones reside in marine sediments and algae or are linked with larger invertebrates. Marine heterotardigrades have a maximum body length of ca. 200 μm and are generally smaller than limno-terrestrial tardigrades (Bartels et al. 2020). Marine eutardigrades are rare and only four species are known i.e., *Thulinius itoi* (Tsurusaki 1980), *Halobiotus arcturulius* (Crisp and Kristensen 1983), *Hab. crispae* (Kristensen 1982), and *Hab. stenostomus* (Richters, 1908) (Nelson et al. 2018). Freshwater habitats are generally lentic or lotic habitats where lotic includes flowing water like rivers, streams, cold and hot springs, and other permanent or intermittent bodies of water, and lentic are standing waters such as lakes, ponds, wetlands (including swamps and marshes), and temporary/ephemeral waterbodies, and in all of them, freshwater tardigrade species were reported (Nelson et al. 2018).

The ability of tardigrades to undergo cryptobiosis makes them quite unique in comparison to most of the other invertebrates (Keilin 1959). In an anhydrobiotic state, they are able to tolerate physical and chemical extremes (Rebecchi et al. 2007). Due to its extraordinary ability of tolerance of various extreme conditions it has also been named the "toughest animals on the Earth" (Copley 1999). However, Ramazzotti and Maucci (1983) verified that strictly freshwater and marine species are mostly desiccation intolerant, however with some exceptions (Jørgensen et al. 2015; Hygum et al. 2016; Kuzmic et al. 2018; Sørensen-Hygum et al. 2018; Kondo et al. 2019, 2020).

Up to now, only a few aquatic tardigrade species have been reported from Poland. The aim of this study is to review all the aquatic tardigrades found in the region, their diversity, and distribution.

Material and methods

All the data were obtained from published papers i.e. (Marcus 1936; Dastych 1970, 1972, 1980, 1988; Mihelčič 1971; Hęciak 1976; Węglarska 1959, 1987a, 1987b, 1989; Węglarska and Korecka 1983; Hummon 1994; Kaczmarek and Michalczyk 2005; Kaczmarek et al. 2010a,b; Zawierucha 2011; Sobczyk et al. 2015; Zawierucha et al. 2015; Jakubowska-Krępska et al. 2019; Rost-Roszkowska et al. 2019; Janelt et al. 2020).

Actual species names are based on the actual checklist of Tardigrada species (Degma et al. 2021). Generic abbreviations follow Perry et al. 2019.

Specimens deposited at the Department of Animal Taxonomy and Ecology, Institute of Environmental Biology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61–614 Poznań, Poland, were photographed under an Olympus BX41 Phase Contrast light Microscope (PCM) associated with Olympus SC50 digital camera (Olympus Corporation, Shinjuku-ku, Japan).

All figures were assembled in Corel Photo-Paint 2017. For deep structures that could not be fully focused in a single photograph, a series of 2–10 images were taken every ca 0.5 μm and then assembled into a single deep-focus image manually in Corel Photo-Paint 2017.

The geographic coordinates and altitudes are provided using different font formats depending on the data origin:

– Original data, where provided, are in Roman and bold font.

– When original coordinates were not supplied, we have provided estimated data in italics. In order to estimate coordinates and/or altitude, we used Google Earth™ (ver. 7.3.2.5776) and the following rules:

– where a general locality, administrative unit, or specified location was provided (e.g., building, city, valley, province, mountain, or mountain range), the collection site was approximated to the center of the smallest viable unit (assisted by an additional data, e.g., altitude);

– for samples collected from or near a river/stream, the mid-point of the river/stream was chosen with consideration to additional data (e.g., altitude, region, or district).

Results and conclusions

Aquatic tardigrades in Poland were studied only occasionally and are very poorly known. Up to now, only 15 tardigrade taxa have been reported, including three marine and twelve freshwater species (Fig.1). Detailed information on the species, their localities, and distribution are presented in Table 1. In comparison almost 100 terrestrial tardigrade species have been reported from Poland (Kaczmarek 2008; Kaczmarek et al.

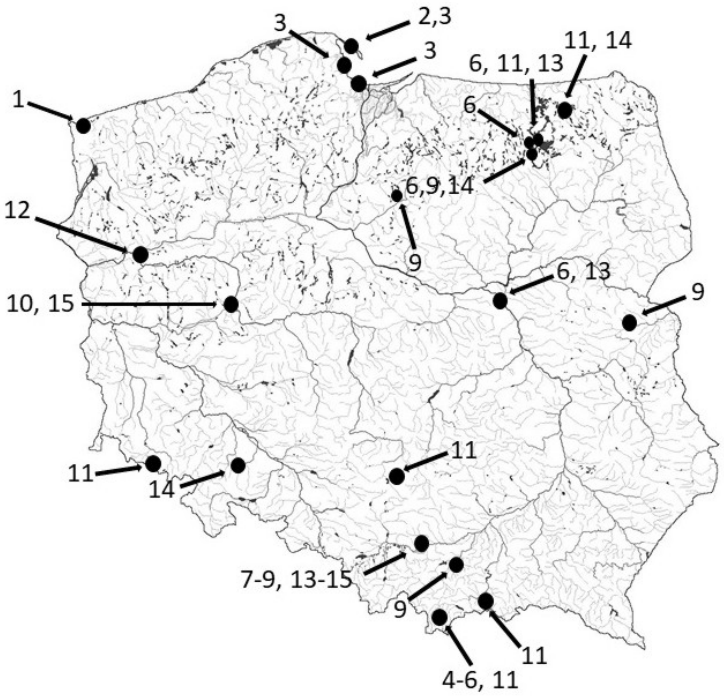
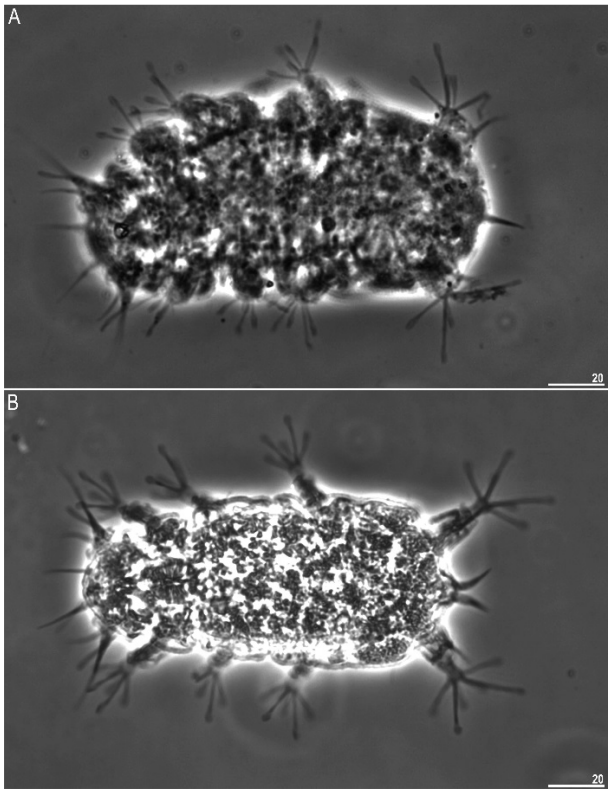


Fig. 1. Localities of *Batillipes sp.* (1), *Batillipes mirus* (2), *Batillipes noerrevangi* (3), *Bertolanius weglarskae* (4), *Dactylobiotus ambiguous* (5), *Dactylobiotus dispar* (6), *Dactylobiotus parthenogeneticus* (7), *Diphascon higginsi* (8), *Grevenius granulifer* (9), *Grevenius pushkini* (10), *Hypsibius dujardini* (11), *Murrayon pullari* (12), *Pseudobiotus Megalonyx* (13), *Pseudobiotus kathmanae* (14) and *Thulinius ruffoi* (15) in Poland



← Fig. 2. A – *Batillipes mirus*, adult (PCM); B – *Batillipes noerrevangi*, adult (PCM). Scale bars in micrometres [μm]. Source : Zawierucha et al. (2015)

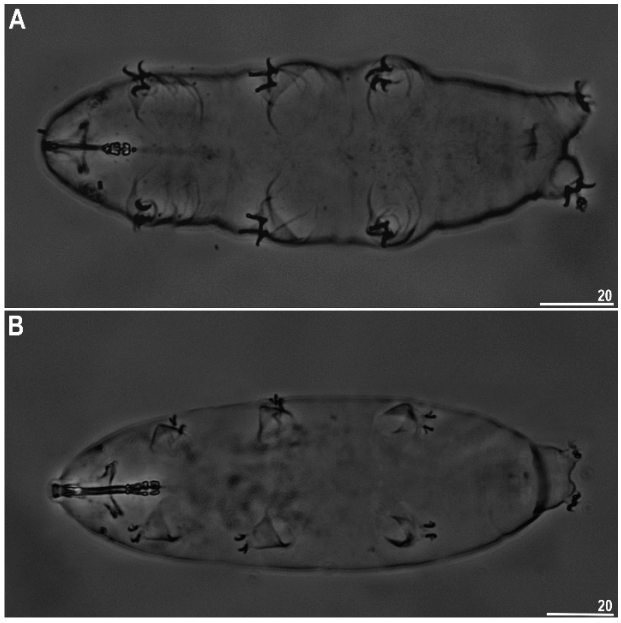


Fig. 3. A – *Hypsibius dujardini*, adult (PCM); B – *Murrayon pullari*, adult (PCM). Scale bars in micrometres [μm]

Table 1. Aquatic species and their localities in Poland

No	Species Name	Localities and citations	Substrate	Remarks
		Marine		
1	*Batillipes* sp. Pollock 1970	Międzyzdroje, (Wolin National Park), Poland, just east of the mouth of the Oder River in the Baltic Sea *53°56'N*, *14°27'E; 0 m b.s.l.* (Hummon 1994)	Littoral sands	Doubtful record (see Results and Discussion section for more details)
2	*Batillipes mirus* (Fig. 2A) Richters 1909	Puck Bay, sublittoral area near Gdynia *54°57'N*, *18°56'E*; depth 0.5 m The outer part – east of Jastarnia ***54°41'18.62"N***, *18°41'0.69"E*; depth 1.5 m (Zawierucha et al. 2015)	Non vegetated seabed	This is the third most commonly reported marine tardigrade, and it has been reported mainly from the northern hemisphere (Kaczmarek et al. 2015a)
3	*Batillipes noerrevangi* (Fig. 2B) Kristensen, 1978	Gdynia: ***54°29'58"N***, ***18°34'78"E***; depth 0.5 m Jastarnia: ***54°41'18.62"N***, ***18°41'0.69"E***; depth 1.5 m Jastarnia: ***54°41'24.36"N***, ***18°41'7.44"E***; depth 1.5 m Jastarnia: ***54°41'24.55"N***, ***18° 41'7.71"E***; depth 1.5 m Jastarnia: ***54°42'37"N***, ***18°54'07"E***; depth 1.5 m Ryw Mew: ***54°42'13.53"N***, ***18°32'26.69"E***; depth 3 m Ryw Mew: ***54°41'42,95"N***, ***18°31'54.85"E***; depth 3 m (Zawierucha et al. 2015)	Non vegetated seabed and vegetated seabed	Species known from intertidal localities with low water salinity (4-20‰) in the Baltic and North Sea (Kaczmarek et al. 2015a; Zawierucha et al. 2015).
		Freshwater		
4	*Bertolanius weglarskae* (Dastych, 1972)	Tatra Mts., Pyszniański brook: *49°14'N*, *19°51'E;* ***1100 m a.s.l.*** Sucha Woda brook: *49°16'N*, *20°01'E;* ***1350 m a.s.l.*** (Dastych 1972, 1988)	Mosses in brook	Species known from Holarctic localities, mostly Arctic and northern alpine environments (McInnes 1994).
5	*Dactylobiotus ambiguous* (Murray 1907a)	Tatra Mts., near Podskalnia Polanka, Sucha Woda brook: *49°17'N*, *20°03'E;* ***1020 m a.s.l.*** (Dastych 1988)	Mosses in brook	A Palaearctic or high latitude Holarctic species (McInnes 1994; Kaczmarek et al. 2015b).
6	*Dactylobiotus dispar* (Murray 1907b)	Mikołajskie Lake: *53°48'N*, *21°34'E; 100 m a.s.l.* Tałtowisko Lake: *53°53'N*, *21°34'E; 100 m a.s.l.* Bełdany Lake: *53°43'N*, *21°34'E; 100 m a.s.l.* Czos Lake: *53°52'N*, *21°19'E; 150 m a.s.l.* Warsaw: *52°23'N*, *21°01'E 100 m a.s.l.* Tatra Mts., Wielka Siklawa waterfall: *49°13'N*, *20°03'E;* ***1530 m a.s.l.***; Botanic Garden of the Jagiellonian University, pond: *50°04'N*, *19°57'E; 200 m a.s.l.* (Dastych 1980, 1988; Węglarska 1987a, 1989)	Freshwater sediments and floating leaves	Mostly Holarctic distribution (McInnes 1994), however, it can be a species complex (McInnes 1994; Kaczmarek et al. 2016)
7	*Dactylobiotus parthenogeneticus* (Bertolani 1982)	Botanic Garden of the Jagiellonian University, Kraków, Poland, pond: ***50°03'45"N***, ***19°57'27"E***; ***200 m a.s.l.***	Sediment samples	(Pogwizd and Stec 2020)
8	*Diphascon higginsi* (Binda 1971)	Botanical Garden, Kopernika 27, Kraków Poland, pond: ***50°03'44"N***, ***19°57'26"E***, ***205 m a.s.l.***	Rotting leaves in a pond	(Kosztyła et al. 2016)
9	*Grevenius granulifer* (Thulin 1928)	Biskupiec Pomorski: *53°48'N*, *19°38'E* Mikołajskie Lake: *53°48'N*, *21°34'E; 100 m a.s.l.* Białki: *52°13'N*, *22°29'E; 400 m a.s.l.* Kraków: *50°06'N*, *19°94'E; 200 m a.s.l.* Dobczyce: *49°90'N*, *20°08'E; 0 m a.s.l.* Botanic Garden of the Jagiellonian University, pond: *50°04'N*, *19°57'E; 200 m a.s.l.* (Węglarska 1959, 1987b; Węglarska and Korecka 1983; Dastych 1988)	Collected in peatbog, wet mosses from stumps or rotten branches in the ponds	Holarctic species (McInnes 1994), but this is probably a species complex.
10	*Grevenius pushkini* (Tumanov 2003)	near Brzeźno, temporary pond: ***52°29'25"N***, ***16°36'04"E***; *100 m a.s.l.* near Góra, temporary pond: ***52°29'02"N***, ***16°37'05"E***; *100 m a.s.l.* (Kaczmarek et al. 2010b) ***50°03044"N***, ***19°57026"E***, *205 m a.s.l.* Botanical Garden, Kopernika 27, Kraków Poland	Decaying plants floating in water, rotting leaves in a pond	Reported only from Poland and Russia (Tumanov 2003; Kaczmarek et al. 2010b, Kosztyła et al. 2016)
11	*Hypsibius dujardini* (Fig. 3A) (Doyère 1840)	Mikołajskie Lake: *53°48'N*, *21°34'E; 100 m a.s.l.*; Gołdapiwo Lake: *54°06'N*, *21°56'E; 100 m a.s.l.* ; Białki, pond *52°08'N*, *22°18'E; 150 m a.s.l.* Karkonoski National Park, Łomniczka Waterfall, *50°44'N*, *15°43'E;* ***980 m a.s.l.***, 1150m a.s.l.; Złoty Potok, spring: *50°41'N*, *19°24'E;* ***655 m a.s.l.***; Nature reserve "Wąwóz Homole", stream: *49°24'N*, *20°32'E;* ***500 m a.s.l.***; Many localities in Tatra Mountains streams, near Podskalnia Polanka, Sucha Woda brook: *49°17'N*, *20°03'E;* ***1020 m a.s.l.***, Wielka Siklawa waterfall: *49°13'N*, *20°03'E;* ***1530 m a.s.l.*** The Grabia River, near the road to Zielęcice, opposite the farm *51°57'N*, *19°07'E; 185 m a.s.l.* (Węglarska 1959; Dastych 1980, 1988; Zawierucha 2011)	Collected from wet stones or/and plants in the water or on the bank of rivers or lakes	It was reported in Poland not only in freshwater habitats. However, at present this species is considered as group of species and presence and distribution of this species in Poland need a verification. For more details see Results and Discussion section.

continued of the Table 1

No	Species Name	Localities and citations	Substrate	Remarks
		Freshwater		
12	*Murrayon pullari* (Fig. 3B) (Murray 1907a)	Gorzów Wielkopolski: *52°44'N, 15°14'E; 0 m a.s.l.* (Marcus 1936)	No data	Holarctic species (McInnes 1994)
13	*Pseudobiotus megalonyx* (Thulin 1928)	Mikołajskie Lake: *53°48'N, 21°34'E; 100 m a.s.l.* Warsaw: *52°23'N, 21°01'E 100 m a.s.l.* Kraków: *50°06'N, 19°94'E; 200 m a.s.l.* (Węglarska 1959; Dastych 1988)	Sediments and aquatic vegetation	Palaearctic species (McInnes 1994), but with lot of taxonomic confusions (Kaczmarek et al. 2015b, 2017).
14	*Pseudobiotus kathmanae* (Nelson, Marley and Bertolani 1999)	Mikołajskie Lake: *53°48'N, 21°34'E; 100 m a.s.l.* Tałtowisko Lake: *53°53'N, 21°34'E; 100 m a.s.l.* Probarskie Lake: *53°49'N, 21°23'E; 150 m a.s.l.* Głęboczek Lake: *52°63'N, 15°85'E; 52 m a.s.l.* Kraków: *50°06'N, 19°94'E; 200 m a.s.l.* (Węglarska 1959; Mihelčič 1971; Dastych 1988)	Various freshwater samples	Reported from Poland as *Psb. augusti* (Murray 1907c), *Hypsibius augusti* or *Hypsibius* (*Isohypsibius*) *augusti*. The taxonomy of this species was confused with *Thu. augusti* (see Nelson et al. 1999; Bertolani et al. 1999). *Psb. kathmanae* has been reported from North America and Italy (Bertolani et al. 1999; Nelson et al. 1999), but other reports need to be verified.
15	*Thulinius ruffoi* (Fig. 4A-C) (Bertolani 1982)	Zelków, wastewater treatment plant (WTP): ***50°09'52"N***, ***19°48'26"E***; *350 m a.s.l.* Meteoryt Morasko Nature Reserve, small ponds: *52°29'N, 16°54'E; 100 m a.s.l.* Koziegłowy, wastewater treatment plant: ***52.4534°N***, ***16.9804°E***; *50 m a.s.l.*; A small pond in Okup Mały (Grabia Valley) *51°59'N, 19°06'E; 185 m a.s.l.* (Kaczmarek and Michalczyk 2005; Sobczyk et al. 2015; Jakubowska-Krępska et al. 2018; Rost-Roszkowska et al. 2019; Janelt et al. 2020; Zawierucha 2011)	Decaying leaves and waste water treatment plant sediments, the leafs of *Nymphaea alba*	Holarctic species (McInnes 1994; Kaczmarek et al. 2010a)

2010; Zawierucha et al. 2015; Gąsiorek et al. 2016; Nowak and Stec 2017, 2018; Stec et al. 2017; Gąsiorek and Degma 2018; Kaczmarek et al. 2018; Bryndová et al. 2020) and new for Poland and new for science terrestrial tardigrades are described regularly. This is clearly visible that aquatic tardigrades are much less studied and, as a result, underestimated.

Only three marine taxa were confirmed from the Polish part of the Baltic Sea, i.e., *Batillipes mirus* (Fig. 2A) Richters 1909, *Bat. noerrevangi* (Fig. 2B) Kristensen 1978 (Zawierucha et al. 2015) and *Batillipes* sp. The presence of the third taxon of the genus *Batillipes* was initially reported as *Bat. dicrocercus* Pollock 1970 reported by Hummon (1994) from the site close to Miedzyzdroje city, was questioned by Zawierucha et al. (2015). Two main reasons why the number of marine tardigrades reported in the Polish part of the Baltic Sea is low are *(i)* a small number of studies and *(ii)* low water salinity (Zawierucha et al. 2015). Baltic is a brackish ecosystem in some parts like Bothnia Bay water is almost pristine while near the straits of Denmark salinity is like in open Ocean. So, low Tardigrades biodiversity is due to a lack of studies rather than the low salinity, but further studies need to confirm this.

In freshwater habitats of Poland, only 12 eutardigrade species were reported. They were found in natural and wastewater treatment plant sediments, decaying plants, and wet mosses in streams, rivers, lakes, and ponds. However, most of them were reported a long time ago, and their identification is uncertain e.g., *Pseudobiotus megalonyx* (Thulin 1928) or *Psb. kathmanae* (Nelson et al. 1999). The other taxa like *Hypsibius dujardini* (Fig. 3A) (Doyére 1840) or Grevenius granulifer (Thulin 1928) are now considered species groups/complexes and nominal taxa in Poland need to be verified.

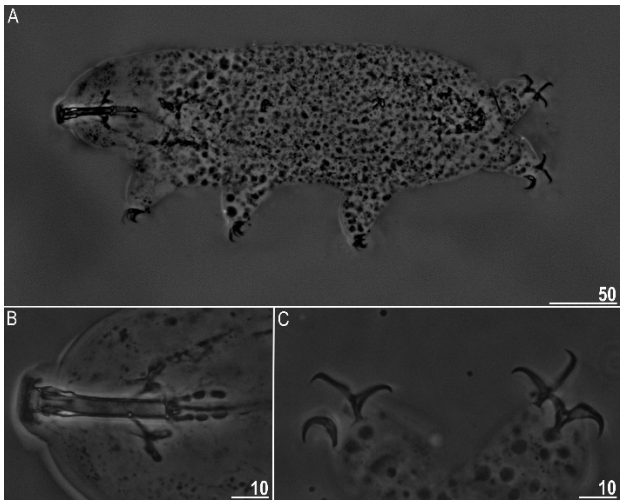


Fig. 4. A – *Thulinius ruffoi*, adult (PCM); B – buccal apparatus (PCM); C – claws IV (PCM). Scale bars in micrometres [μm]

Summarizing aquatic tardigrades in Poland are exceptionally poorly known in comparison to the

limno-terrestrial ones. Most of the reports are only accidental findings, and no systematic studies were conducted on aquatic tardigrades in Poland. Most of the species were reported from water bodies in Tatra Mountains or from lakes in Masurian Lake District. Some species are also reported from small ponds or wastewater treatment plants in different regions like Małopolska or Wielkopolska Province and Central Poland. Aquatic tardigrades from the rivers and streams are almost completely unknown in Poland. All these data show that more comprehensive studies are necessary to understand and describe the diversity of Polish freshwater and marine tardigrades.

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References

Bartels P.J., Fontaneto D., Roszkowska M., Nelson D.R., Kaczmarek Ł., 2020, Latitudinal gradients in body size in marine tardigrades, Zool. J. Linn. Soc. 188(3):820–838.

Bertolani R., 1982, A new genus and five new species of Italian freshwater tardigrades, Boll. Mus. Civ. Stor. Nat. Verona. 114: 249–254.

Bertolani R., Marley N., Nelson D.R., 1999, Re-description of the genus *Thulinia* (Eutardigrada, Hypsibiidae) and of *Thulinia augusti* (Murray, 1907) comb. n., Zool. Anz. 238:139–145.

Błażejczyk K., 2006, Climate and bioclimate of Poland, [in:] Degórski M. (ed.) Natural and human environment of Poland. A geographical overview, IGiPZ PAN, Warsaw: 31–48.

Bryndová M., Stec D., Schill R.O., Michalczyk Ł., Devetter M., 2020, Dietary preferences and diet effects on life-history traits of tardigrades, Zool. J. Linn. Soc. 188(3): 865–877.

Choiński A., 2006, Katalog jezior Polski [The catalogue of Polish lakes], Wydaw. UAM, Poznań, 600 pp (in Polish).

Copley J., 1999, Indestructible, New Sci. 2209: 44–46.

Crisp M., Kristensen R.M., 1983, A new marine interstitial eutardigrade from east Greenland, with comments on habitat and biology, Vidensk, Meddel. Dansk Naturhist. Foren. 144: 99–114.

Dastych H., 1970, Materiały do znajomości niesporczaków (Tardigrada) Tatrzańskiego Parku Narodowego, Fragm. Faun. 16: 77–87.

Dastych H., 1972, *Isohypsibius weglarskae* sp. n. a new species of Tardigrada from Poland, Bull. Acad. Polon. Sc., Ser. Sc. Biol. 20: 271–274.

Dastych H., 1980, Niesporczaki (Tardigrada) Tatrzańskiego Parku Narodowego, Monogr. Fauny Pol. 9: 1–232.

Dastych H., 1988, The Tardigrada of Poland, Monogr. Fauny Pol. 16:1–255.

Degma P., Bertolani R., Guidetti R., 2021, Actual checklist of Tardigrada species (2009-2021, Ed. 40: 19-07-2021), 62 pp. Retrieved from https://iris.unimore.it/retrieve/handle/11380/1178608/358743/Actual%20checklist%20of%20Tardigrada%2040th%20Edition%2019-07-21.pdf

Degma P., Guidetti R., 2007, Notes to the current checklist of Tardigrada, Zootaxa 1579: 41–53.

Doyére P.L.N., 1840, Memoire sur les Tardigrades, Ann. Sci. Nat. Zool. Serie, 2(14):269–362.

Gąsiorek P., Stec D., Morek W., Zawierucha K., Kaczmarek Ł., Lachowska-Cierlik D., Michalczyk Ł., 2016, An integrative revision of Mesocrista Pilato, 1987 (Tardigrada: Eutardigrada: Hypsibiidae), J. Nat. Hist. 50: 2803–2828.

Gąsiorek P., Degma P., 2018, Three Echiniscidae species (Tardigrada: Heterotardigrada) new to the Polish fauna, with the description of a new gonochoristic *Bryodelphax* Thulin, 1928, Zootaxa 4410(1): 77–96.

Guidetti R., Bertolani R., 2005, Tardigrada. Tardigrade taxonomy: an updated check list of the taxa and a list of characters for their identification, Zootaxa 845:1–46.

Gyedu-Ababio T.K., Furstenberg J.P., Baird D., Vanreusel A., 1999, Nematodes as indicators of pollution: a case study from the Swartkops River system, South Africa, Hydrobiologia 397:155–169.

Hęciak S., 1976, Niesporczaki (Tardigrada) Gór Świętokrzyskich, Bad. Fizjogr. Pol. Zach. 29: 111–128.

Hummon W.D., 1994, Trans-and cis-Atlantic distributions of three marine heterotardigrades, Trans. Am. Microsc. Soc. 113(3):333–342.

Hygum T. L., Clausen L. K. B., Halberg K. A., Jørgensen A., Møbjerg N., 2016, Tun formation is not a prerequisite for desiccation tolerance in the marine tidal tardigrade *Echiniscoides sigismundi*, Zool. J. Linn. Soc. 178, 907–911.

Jakubowska-Krępska N., Gołdyn B., Krzemińska-Wowk P., Kaczmarek Ł., 2019, Tardigrades as potential bioindicators in biological wastewater treatment plants, Eur. J. Ecol. 4(2): 124–130.

Janelt K., Poprawa I., 2020, Analysis of encystment, excystment, and cyst structure in freshwater eutardigrade *Thulinius ruffoi* (Tardigrada, Isohypsibioidea: Doryphoribiidae), Divers 12(2): 62.

Jørgensen A., Møbjerg N., 2015, Notes on the cryptobiotic capability of the marine arthrotardigrades Styraconyx haploceros (Halechiniscidae) and *Batil-*

lipes pennaki (Batillipedidae) from the tidal zone in Roscoff, France, Mar. Biol. Res. 11: 214–217.

Kaczmarek Ł., 2008, Niesporczaki: Tardigrada (Water bears: Tardigrada), [in:] Bogdanowicz W., Chudzicka E., Pilipuk I., Skibińska E. (eds), Fauna Polski. Vol. 3: Charakterystyka i wykaz gatunków (The fauna of Poland. Vol. 3: Characteristics and list of species), MIIZ PAN, Warszawa: 543–548.

Kaczmarek Ł., Bertolani R., Nędzyńska-Stygar M., 2010a, *Thulinius saltursus* comb. nov.: a new systematic position for *Isohypsibius saltursus* Schuster, Toftner & Grigarick, 1978 (Eutardigrada: Hypsibiidae) and a key for the genus *Thulinius*, Zootaxa 2483: 58–64.

Kaczmarek Ł., Gołdyn B., Czyż M., Michalczyk Ł., 2010b, First records of *Isohypsibius pushkini* Tumanov, 2003 (Tardigrada, Eutardigrada, Hypsibiidae) from Poland, Biol. Lett. 47(2): 81–85.

Kaczmarek Ł., Michalczyk Ł., 2005, *Thulinius ruffoi* Bertolani, 1981– rodzaj i gatunek niesporczaka (Tardigrada) nowy dla fauny Polski, Prz. Zool. 1(49): 57–59.

Kaczmarek Ł., Bartels P.J., Roszkowska M., Nelson D.R., 2015a, The Zoogeography of Marine Tardigrada, Zootaxa 4037(1): 1–189.

Kaczmarek Ł., Michalczyk Ł., McInnes S.J., 2015b, Annotated zoogeography of non-marine Tardigrada. Part II: South America, Zootaxa 3923(1): 1–107.

Kaczmarek Ł., Michalczyk Ł., McInnes S.J., 2016, Annotated zoogeography of non-marine Tardigrada. Part III: North America and Greenland, Zootaxa 4203(1): 1–249.

Kaczmarek Ł., Kosicki J.Z., Roszkowska M., 2018, Tardigrada of Bory Tucholskie National Park, Zaborski Landscape Park, and their surroundings (Pomerania Province, Poland), Turk. J Zool. 42: 6–17.

Keilin D., 1959, The Leeuwenhoek Lecture – The problem of anabiosis or latent life: history and current concept, Proc. Royal Soc. B 150(939): 149–191.

Kolada A., Soszka H., Cydzik D., Gołub M., 2005, Abiotic typology of Polish lakes. Limnologica 35(3): 145–150.

Kondo K., Mori M., Tomita M., Arakawa K., 2019, AMPK activity is required for the induction of anhydrobiosis in a tardigrade *Hypsibius exemplaris*, and its potential up-regulator is PP2A, Genes Cells. 24(12): 768–780.

Kondo K., Mori M., Tomita M., Arakawa K., 2020, Pretreatment with D942, a furancarboxylic acid derivative, increases desiccation tolerance in an anhydrobiotic tardigrade *Hypsibius exemplaris*, FEBS Open Bio 10(9): 1774–1781.

Kosztyła P., Stec D., Morek W., Gąsiorek P., Zawierucha K., Michno K., Ufir K., Małek D., Hlebowicz K., Laska A., Dudziak M., 2016, Experimental taxonomy confirms the environmental stability of morphometric traits in a taxonomically challenging group of microinvertebrates, Zool. J. Linn. Soc. 178(4):765–775.

Kristensen R.M., 1978, Notes on marine Heterotardigrades. 1. Description of two new *Batillipes* species, using the electron microscope, Zool. Anz. 200:1–17.

Kristensen R.M., 1982, New aberrant eutardigrades from homothermic springs on Disko Island, West Greenland, Proc. of the Third International Symposium on Tardigrada, East Tennessee State University Press, Johnson City: 203–220.

Kuzmic M., Richaud M., Cuq P., Frelon S., Galas, S., 2018, Carbonylation accumulation of the *Hypsibius exemplaris* anhydrobiote reveals age-associated marks, PloS One 13(12): e0208617.

Marcus E., 1936, Tardigrada, Tierreich 66: 1–340.

McInnes S.J., 1994, Zoogeographic distribution of terrestrial/freshwater tardigrades from current literature, J. Nat. Hist. 28: 257–352.

McInnes S.J., Michalczyk Ł., Kaczmarek Ł., 2017, Annotated zoogeography of non-marine Tardigrada. Part IV: Africa, Zootaxa 4284(1): 1–74.

Mihelčič F., 1971, Süsswassertardigraden aus Nordeuropa, Insect Syst. Evol. 2(3):205–214.

Murray J., 1907a, XXIV – Scottish Tardigrada, collected by the Lake Survey. Trans. R. Soc. Edinburgh 45:641–666.

Murray J., 1907b, The encystment of Macrobiotus, The Zoologist 11: 4–11.

Murray J., 1907c, Scottish Tardigrada collected by the Lake Survey, Trans. R. Soc. Edinburgh 45: 641–668.

Nelson D.R., Bartels P.J., Guil N., 2018, Tardigrade ecology, [in:] Schill R.O. (ed.), Water Bears: The Biology of Tardigrades, Springer, Cham: 163–210.

Nelson D. R., Guidetti R., Rebecchi L., 2015, Phylum tardigrada, [in:] Thorp J.H., Rogers D.C. (eds), Ecology and general biology. Thorp and Covich's freshwater invertebrates, Elsevier, Amsterdam: 347–380.

Nelson D.R., Marley N.J., Bertolani R., 1999, Re-description of the genus *Pseudobiotus* (Eutardigrada, Hypsibiidae) and of the new type species *Pseudobiotus kathmanae* sp. n., Zool. Anz. 238:311–317.

Nowak B., Stec D., 2017, The first record of *Macrobiotus vladimiri* Bertolani, Biserov, Rebecchi and Cesari, 2011 (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Poland, Turk. J Zool. 41: 558–567.

Nowak B., Stec D., 2018, An integrative description of *Macrobiotus hannae* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Poland, Turk. J Zool. 42: 269–286.

Perry E., Miller W.R., Kaczmarek Ł., 2019, Recommended abbreviations for the names of genera of the phylum Tardigrada, Zootaxa 4608: 145–154.

Pollock L.W., 1970, *Batillipes dicrocercus* n. sp., *Stygarctus granulatus* n. sp. and other Tardigrada from Woods Hole, Massachussetts, USA, Trans. Amer. Micr. Soc. 89:38–52.

Ramazzotti G., Maucci W., 1983, II Phylum Tardigrada, Mem. Ist. Ital. Idrobiol. 41:1–1012.

Rebecchi L., Altiero T., Guidetti R., 2007, Anhydrobiosis: the extreme limit of desiccation tolerance, Invertebr. Surviv. J. 4(2): 65–81.

Richters F., 1909, Tardigraden-Studien, Ber. Senckenb. Nat. Ges. 40: 28–45.

Rost-Roszkowska M., Janelt K., Poprawa I., 2019, Fine structure of the midgut epithelium of *Thulinius ruffoi* (Tardigrada, Eutardigrada, Parachela) in relation

to oogenesis and simplex stage, Arthropod Struct. Dev. 49: 128–136.

Sobczyk M., Michno K., Kosztyła P., Stec D., Michalczyk Ł., 2015, Tolerance to ammonia of *Thulinius ruffoi* (Bertolani, 1981), a tardigrade isolated from a sewage treatment plant, Bull. Environ. Contam. Toxicol. 5(6):721–727.

Sørensen-Hygum T.L., Stuart R.M., Jørgensen A., Møbjerg N., 2018, Modelling extreme desiccation tolerance in a marine tardigrade, Sci Rep. 8: 11495.

Stec D., Zawierucha K., Michalczyk Ł., 2017 An integrative description of *Ramazzottius subanomalus* (Biserov, 1985) (Tardigrada) from Poland, Zootaxa 4300(3): 403–420.

Thulin G., 1928, Über die Phylogenie und das System der Tardigraden, Hereditas 11(2-3): 207–266.

Tsurusaki, N., 1980, A new species of marine interstitial Tardigrada of the genus *Hypsibius* from Hokkaido Northern Japan, Annot. Zool. Japon. 53: 280–284.

Tumanov D., 2003, Four new *Isohypsibius* species from Russian fresh waters (Tardigrada, Hypsibiidae), Bull. Inst. R. Sci. Nat. Belg. Biol. 73:183–189.

Vicente, F., 2010. Micro-invertebrates conservation: forgotten biodiversity, Biodivers. Conserv. 19: 3629–3634.

Węglarska B., 1959, Die Tardigraden (Tardigrada) Polens. I. Tardigraden der Woiwodschaft Kraków, Acta Zool. Cracov. 4: 699–745.

Węglarska B., 1987a, Morphology and ultrastructure of the excretory system in *Dactylobiotus dispar* (Murray) (Eutardigrada), [in:] Bertolani R. (ed.), Biology of Tardigrades. Vol. 1. Mucchi, Modena: 25–33.

Węglarska B., 1987b, Studies on the excretory system of *Isohypsibius granulifer* Thulin (Eutardigrada, [in:] Bertolani R. (ed.), Biology of Tardigrades. Vol. 1. Mucchi, Modena: 15–24.

Węglarska B., 1989, Ultrastructure of tardigrade *Dactylobiotus dispar* (Murray 1907) cuticle, Acta. Biol. Crac. 31:57–62.

Węglarska B., Korecka T., 1983, Tardigrada from Dobczyce area (Poland), Zesz. Nauk. UJ 29: 83–92.

Zawierucha K., 2011, Water bears (Tardigrada) of Okup Mały (Grabia Valley, Central Poland), Bad. Fizjogr. Ser. C 52: 47–52.

Zawierucha K., Grzelak K., Kotwicki L., Kaczmarek Ł., Kristensen R.M., 2015, First observation of the marine tardigrades *Batillipes mirus* and *Batillipes noerrevangi* (Arthrotardigrada, Batillipedidae) from a strongly brackish part of the Polish Baltic Sea coast, Mar. Biol. Res. 11(8): 859–868.