POLISH POLAR RESEARCH
vol. 47 no. 1–2, pp. 35–45 DOI: 10.24425/ppr.2026.158403

# First record of the *Eremobiotus alicatai* (Binda, 1969) (Eutardigrada) from Svalbard Archipelago

Jędrzej WARGUŁA* and Łukasz KACZMAREK

*Department of Animal Taxonomy and Ecology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland*

***corresponding author:** *jedwar@amu.edu.pl*

**Received** 8 April 2026 **Accepted** 16 June 2026

**Abstract:** This is the first report of *Eremobiotus alicatai* (Binda, 1969) from Arctic soil mixed with leaf litter on West Spitsbergen (Svalbard Archipelago). Species identification was confirmed using an integrative approach combining detailed morphological examination with molecular analyses based on mitochondrial COI and nuclear markers ITS-2, 18S rRNA, and 28S rRNA. Newly obtained sequences were used to reconstruct a Templeton–Crandall–Sing haplotype network, enabling comparison with previously known populations of this species from Italy. Our results extend the known geographic range of *Ere. alicatai* and provide new data on its genetic diversity, contributing to a better understanding of the biogeography of soil tardigrades in the Arctic.

**Keywords:** Arctic, Spitsbergen, barcoding, haplotype network, soil, Tardigrada.

## Introduction

Tardigrades (waters bears) are microscopic invertebrates that inhabit nearly all environments on the Earth, ranging from equatorial rainforests to glacial surfaces in polar regions and highest mountain ranges (Nelson *et al.* 2018; Zawierucha *et al.* 2019; Topstad *et al.* 2020). In Arctic ecosystems, tardigrade diversity has been relatively well documented, with most studies focusing on their diversity in bryophytes, lichens, and freshwater habitats, including cryoconite holes (Zawierucha *et al.* 2013, 2017, 2021).

In total, 99 tardigrade taxa are currently known from Svalbard (Coulson *et al.* 2024). However, studies employing integrative taxonomy remain scarce and have mainly focused either on species new to science (six species) or on the redescriptions of previously described taxa (six species) (Gąsiorek *et al.* 2016, 2017, 2018; Zawierucha *et al.* 2016, 2018, 2020; Kaczmarek *et al.* 2018; Stec *et al.* 2019; Stec 2023). Consequently, only *ca.* 12% of all species reported from Svalbard have been sequenced using DNA barcoding methods. Only *Tenuibiotus voronkovi* (Tumanov 2007) was found to be associated with soil habitats (Zawierucha *et al.* 2016).

In recent years, there has been a growing number of research exploring the diversity of soil tardigrades in the Arctic (Czernekova *et al.* 2018; Devetter *et al.* 2021; Tůmova *et al.* 2024; Klimaszyk *et al.* 2026). However, these studies have primarily focused on their ecology, putting less emphasis on taxonomy. Nevertheless, all these studies have provided new insights into the occurrence of tardigrade genera previously not recorded in Arctic. Notably, a present study reports, for the first time, the presence of the *Eremobiotus alicatai* (Binda, 1969) on West Spitsbergen, a taxon which is quite common in European soil, but has never been reported in Arctic. Although, it should be mentioned that Klimaszyk *et al.* (2026) had reported specimen of undefined *Eremobiotus* species from Pyramiden (West Spitsbergen, Petunia Bay).

The genus *Eremobiotus* was established in 1992 by Biserov, who described the type species *Ere. ovezovae* Biserov, 1992 from Turkmenistan. Since then, only one additional species have been described in this genus: *Ere. ginevrae* Lisi, Binda and Pilato, 2016 from Italy. Members of this genus represents a frequent element of soil tardigrades (Hohberg 2006; Hohberg *et al.* 2011; Guil *et al.* 2015). The most often reported species, *Ere. alicatai*, is widely distributed in Europe (Binda 1969; Binda and Pilato 1972; Bertolani 1975, 1983; Dastych 1988; Zawierucha and Kaźmierski 2012; Camarda *et al.* 2024). Its distribution appears to be restricted to the continental Eurasia, with a single record from the northern Africa (McInnes,

1994) and western United States (Johansson *et al.* 2011). Most previous identifications of the *Ere. alicatai* populations were based solely on morphological analyses until a comprehensive redescription employing an integrative taxonomic framework was published by Camarda *et al.* in 2024. Since the release of genetic sequences from the type locality, no additional populations of this species have been reported elsewhere.

In this study, the identification of a new population of *Ere. alicatai* was confirmed through both morphological examination and molecular analyses, including mitochondrial COI and nuclear markers ITS-2, 18S rRNA, and 28S rRNA. The newly obtained sequences also enabled the reconstruction of a Templeton–Crandall–Sing (TCS) haplotype network, facilitating comparison with previously known European populations of *Ere. alicatai*.

## Materials and methods

### Sample processing

A soil sample with a large amount of *Dryas octopetala* leaf litter was collected at vicinity of Adam Mickiewicz University Polar Station "Petuniabukta" (78°41'08.29"N, 16°27'23.53"E) in Petunia Bay on West Spitsbergen (Svalbard) in August 2023 (Fig. 1). The sample was packed in a paper envelope, dried at the temperature of *ca.* 25°C and transported to the laboratory at the Faculty of Biology, Adam Mickiewicz University in Poznań (Poland).

Tardigrades were extracted from the sample and studied following the protocol by Stec *et al.* (2015). Six specimens belonging to Eutardigrada were extracted from the sample, out of which four were directly mounted in permanent microscope slides while the two were used for genetic analysis.

### Species identification

Specimens of the population which is the subject of this study perfectly fits the original description of *Ere. alicatai* (Binda 1969). However, to corroborate our identification, we compared the obtained genetic sequences with those published in the species redescription by Camarda *et al.* (2024).

### Microscopy and imaging

Specimens for morphological analyses were mounted on permanent microscope slides in Hoyer's medium and secured with cover slips. Slides were dried in a heater for two days at 60°C and sealed with transparent nail polish. Later, slides were analysed using an Olympus BX41 Phase Contrast Light Microscope (PCM) equipped with an Olympus SC50 digital camera (Olympus Corporation, Shinjuku-ku, Japan).

Photomicrographs were compiled using GIMP 2.10.36. For deep structures that could not be adequately shown in a single image, a series of 2–10 photomicrographs were taken at approximately 0.5 µm intervals. These images were then manually merged into a single deep-focus image using GIMP 2.10.36. Figure 1 was obtained from https://www.npolar. no/en/ and edited using https://www.canva.com. Figures 2–4 were assembled in *Corel Photo-Paint X6*, ver. 16.4.1.1281.


**Fig. 1.** Map showing Petunia Bay, located in the central part of Spitsbergen, with the localities where *Eremobiotus alicatai* and *Eremobiotus* sp. (Klimaszyk *et al.* 2026) were found indicated by blue dots. Map source: https://www.npolar.no/en/.

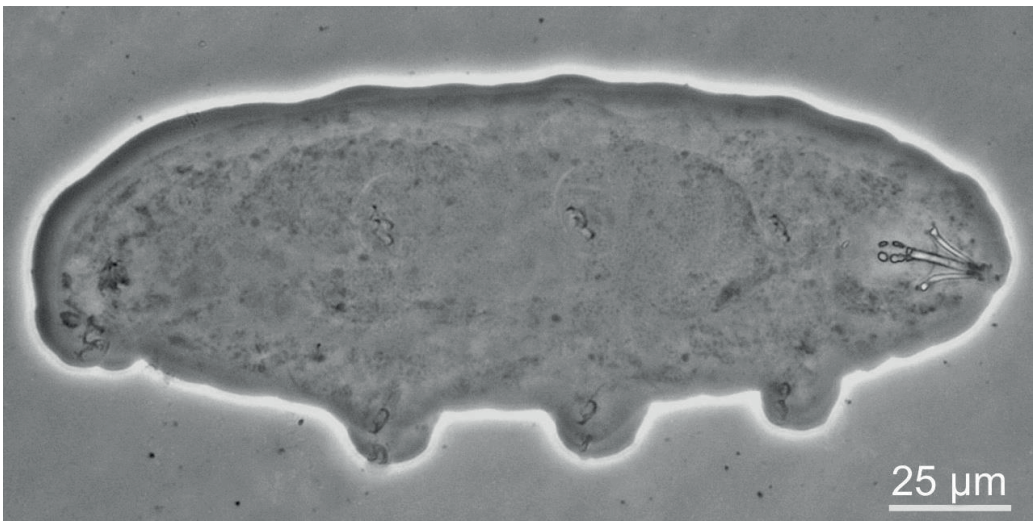


**Fig. 2**. *Eremobiotus alicatai* from West Spitsbergen: Habitus, dorso-ventral projection, PCM.

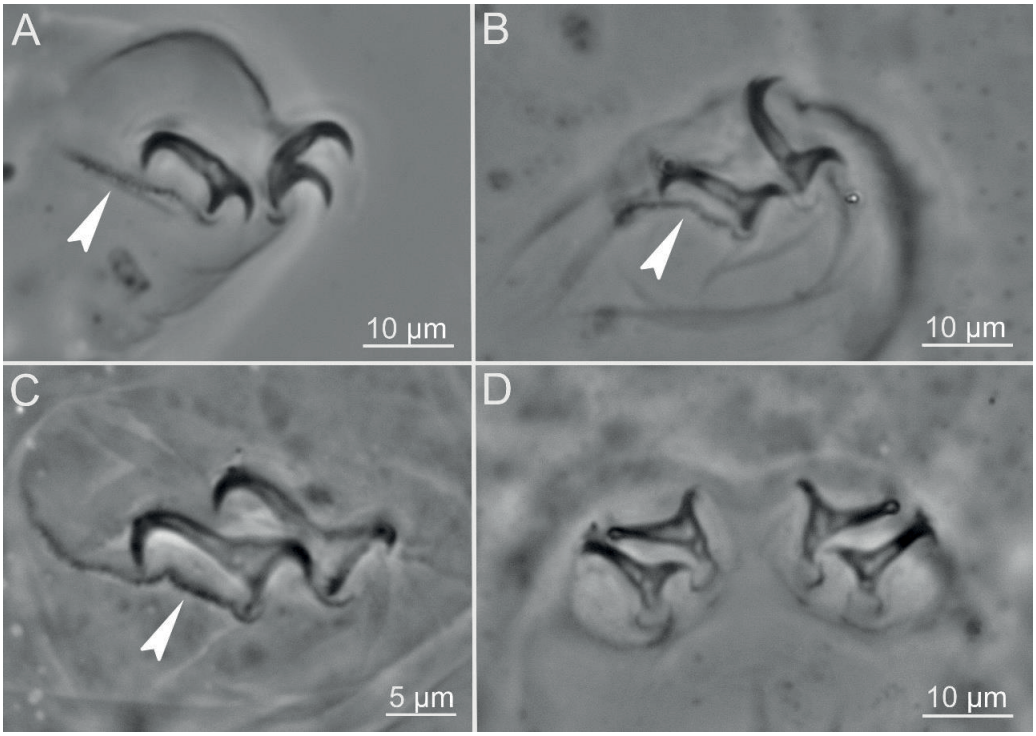


**Fig. 3.** *Eremobiotus alicatai* (West Spitsbergen population): **A** – claws I; **B** – claws II; **C** – claws III; **D** – claws IV. White arrowhead indicates cuticular bars on legs. All in PCM.

### Morphometrics and morphological nomenclature

All measurements are given in micrometres. Structures were measured only if they were not damaged and their orientation was suitable. Body length was measured from the anterior extremity to the end of the body, excluding hind legs. Measurements of the buccal tube length and the position of the stylet support insertion point were performed according to Pilato (1981). The *pt* index was calculated as the ratio of the length of a specific structure to the length of the buccal tube, expressed as a percentage Pilato (1981). Remaining measurements of the buccal tube were performed according to Kaczmarek and Michalczyk (2017). The claws measurements were performed according to Beasley *et al.* (2008) and Camarda *et al.* (2024).

Morphometric data were handled using modified "Parachela" ver. 1.8 template available from the Tardigrada Register (Michalczyk and Kaczmarek 2013). Raw morphometric data for specimens, examined in this study are given in Supplementary Materials (SM.01). Genus abbreviation method following Perry *et al.* (2019).

### Genotyping

The DNA was extracted from individual animals following a Chelex® 100 resin (Bio-Rad) extraction method by Casquet *et al.* (2012) with modifications described by Stec *et al.* (2015). To obtain the tardigrade exoskeleton, the remaining portion of the DNA extract containing Chelex®

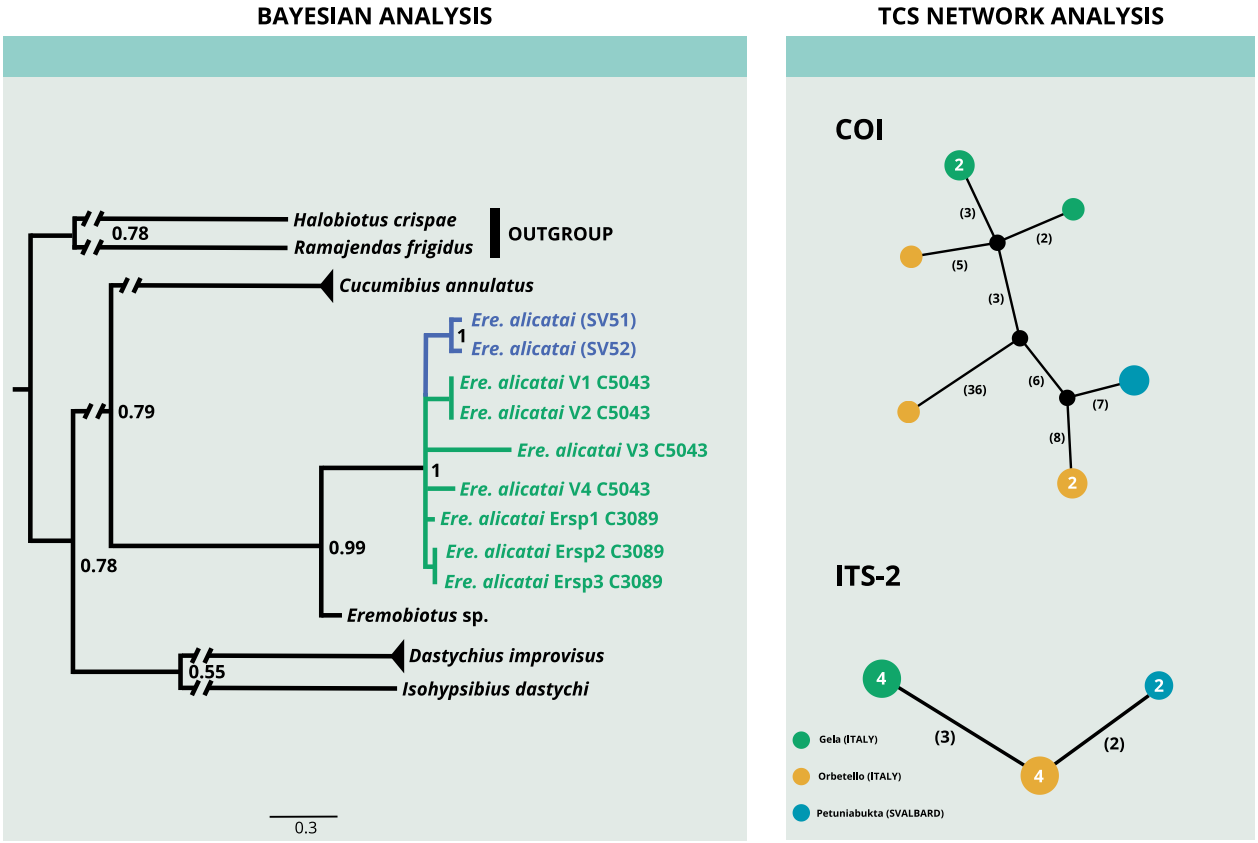


**Fig. 4**. Bayesian phylogenetic tree and haplotype network analyses of *Eremobiotus alicatai*. The left panel shows a Bayesian phylogenetic constructed sequences (18S rRNA+28S rRNA+ITS-2 + COI) of the genus *Eremobiotus*, *Dastychius* and *Cucumibius*. The newly identified population from West Spitsbergen (SV51 and SV52) is highlighted in blue. Populations from Italy are highlighted in green. Posterior probability (pp) values are shown at selected nodes. The right panel presents haplotype networks based on the COI (top) and ITS-2 (bottom) markers. Circle size is proportional to haplotype frequency, and colours denote geographic origin (Italy and Svalbard). Numbers on branches indicate mutational steps.

100 resin was diluted with dd$H_2O$ and transferred to a glass cube. The glass cube was examined under the stereomicroscope and when the exoskeleton was found, it was mounted in a permanent slide in Hoyer's medium.

A four DNA fragments differing in mutation rates (from the most to least conservative): the small ribosome subunit (18S rRNA, nDNA), the large ribosome subunit (28S rRNA, nDNA), the internal transcribed spacer (ITS-2, rDNA), and the cytochrome oxidase subunit I (COI, mtDNA). All fragments were amplified and sequenced according to the protocols described in Stec *et al.* (2015). Sequencing products were read with the ABI 3130xl sequencer at the Molecular Ecology Lab, Institute of Environmental Sciences of the Jagiellonian University, Kraków, Poland. Raw sequences were processed in BioEdit ver. 7.2.5 (Hall 1999) and the final sequenced were deposited in GenBank (https://www.ncbi.nlm.nih.gov/genbank).

## Phylogenetic analysis and genetic comparisons

Phylogenetic analysis and genetic comparisons were prepared based on the dataset used by Camarda *et al.* (2025) and newly obtained sequences. The list of all sequences used in the analysis is provided in Table 1. The DNA sequences from families Halobiotidae (Tumanov *et al.* 2024) and Ramajendidae (Tumanov 2022) were used as the outgroups. Sequence alignments were performed using the Q-INS-I method for all ribosomal markers (18S rRNA, 28S rRNA and ITS-2 rDNA) and mitochondrial marker (COI mtDNA) in MAFFT version 7. Alignments were then manually verified for non-conserved regions in BioEdit. After alignment, sequences were trimmed to lengths of 1049 bp (18S rRNA), 747 bp (28S rRNA), 424 bp (ITS-2 rDNA) and 560 bp (COI mtDNA) and subsequently concatenated with SequenceMatrix. Prior to partitioning, the concatenated alignment was divided into six blocks: three blocks for the ribosomal markers and three blocks for the different codon positions of the COI dataset. PartitionFinder using the Akaike Information Criterion (AIC), was employed and as the optimal partitioning scheme retained two predefined partitions with the best model GTR +I+G for all markers. Bayesian inference (BI) was performed on the concatenated dataset (18S rRNA+28S rRNA+ITS-2 rDNA + COI mtDNA) using MrBayes v3.263, with random starting trees. The analysis was run for 10 million generations, sampling every 1000 generations, and convergence was confirmed by an average stan-

**Table 1.** Complete list of species analyzed, with their GenBank accession numbers and source publications. Newly sequenced species highlighted in bold.

| Species | Accession numer for 18S rRNA | Accession numer for 28S rRNA | Accession numer for COI | Accession numer for ITS-2 | Source |
|---|---|---|---|---|---|
| *Cucumibius annulatus* 1–3 | PQ069998–70000 | PQ070026–28 | PQ067944–45 | PQ070051–53 | Tumanov *et al.* (2024) |
| *Dastychius improvisus* 1–5 | MK737028–31 | MK737035–39 | MK765502–05 | – | Mioduchowska *et al.* (2021) |
| *Eremobiotus alicatai* Ersp1–3 | HQ604951–53 | – | – | – | Bertolani *et al.* (2014) |
| *Eremobiotus alicatai* V1-4 | PQ386447–50 | – | PQ386466–69 | PQ428930–33 | Camarda *et al.* (2024) |
| ***Eremobiotus alicatai* SV51-52** | **PZ448006–07** | **PZ448009–10** | **PZ448012–13** | **PZ458958** | **This study** |
| *Eremobiotus* sp. | MK675928 | MK675917 | – | – | Gąsiorek *et al.* (2019a) |
| *Halobiotus crispae* | PQ070004 | PQ070031 | EF620413 | EF620421 | Møbjerg *et al.* 2007; Tumanov *et al.* (2024) |
| *Isohypsibius dastychi* | HQ604954 | – | | | Bertolani *et al.* (2014) |
| *Ramajendas frigidus* | MZ050453 | MZ050450 | MZ047789 | MZ050451 | Tumanov (2022) |

dard deviation of split frequencies below 0.01. Tracer v1.6 was used to ensure the Markov chains had reached stationarity and to determine the appropriate 'burn-in' period, which was the first 10% of generations. Effective Sample Size (ESS) values exceeded 200, and the consensus tree was obtained by summarizing the topologies after discarding the burn-in phase. The final tree was visualized using FigTree v1.4.3, available at http://tree.bio.ed.ac.uk/software/fig tree (accessed on 28 March 2026). The raw trees are included in Supplementary Materials (SM.02). To investigate the distribution of *Ere. alicatai*, haplotype networks were constructed for all available sequences of COI and ITS-2 markers of that species. Sequence alignments were performed using the AUTO setting for COI, ITS-2 markers in MAFFT version 7 (Katoh *et al.* 2002; Katoh and Toh 2008). After alignment, sequences were trimmed to lengths of 535 bp (COI) and 418 bp (ITS-2). Separate single-gene TCS haplotype networks (Clement *et al.* 2002) were generated in PopART ver.1.7 (Leigh and Bryant 2015).

## Results

### Taxonomic account

Class: Eutardigrada Richters, 1926.
Order: Parachela Schuster, Nelson, Grigarick and Christenberry, 1980.
Superfamily: Isohypsibioidea Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008
Family: Isohypsibiidae Sands, McInnes, Marley, Goodall-Copestake, Convey and Linse, 2008
Genus: *Eremobiotus* Biserov, 1992
Species: *Eremobiotus alicatai* (Binda, 1969)
(Figs. 2, 3A–D; Table 2)

### Material examined

Six animals. Specimens mounted on microscope slides in Hoyer's medium (four animals), processed for DNA sequencing (two animals), of which the exoskeleton was successfully recovered from only one specimen.

### Locality

78°41'08.29"N, 16°27'23.53"E; 71 m above sea level, West Spitsbergen, Svalbard, vicinity of the Adam Mickiewicz University Polar Station "Petuniabukta", Petunia Bay (Fig. 1), Arctic tundra, soil with *Dryas octopetala* leaf litter, coll. Łukasz Kaczmarek.

### Depositories

Four animals (slides: SV11/X, where the asterisk can be substituted by any of the following numbers: 1–3) and one exoskeleton after DNA extraction (slide: SV11/4) are deposited at the Department of Animal Taxonomy and Ecology, Faculty of Biology, Adam Mickiewicz University in Poznań, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland.

### Short diagnosis

The morphological characteristics and morphometric data fully corresponding to the original species description and later redescription (Binda 1969; Camarda *et al.* 2024)

**Table 2.** Measurements and *pt* values of selected morphological structures of individuals of *Eremobiotus alicatai* (West Spitsbergen population) mounted in Hoyer medium (N—number of specimens/structures measured; RANGE refers to the smallest and the largest structure among all measured specimens; SD—standard deviation, *pt*— ratio of the length of a given structure to the length of the buccal tube expressed as a percentage). The claws I–III were measured according to Beasley *et al.* (2008), the claws IV (*Eremobiotus*-type) were measured according to Camarda *et al.* (2024).

| CHARACTER | N | RANGE | | | | | | MEAN | | SD | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | µm | | | *pt* | | | µm | *pt* | µm | *Pt* |
| Body length | 4 | 180 | – | 408 | | – | | 263 | | 102 | |
| Buccal tube length | 5 | 20.9 | – | 31.3 | | | | 25.5 | – | 4.4 | – |
| Stylet support insertion point | 5 | 10.2 | – | 18.9 | *32.6* | – | *72.3* | 15.1 | *61.4* | 3.7 | *19.2* |
| Buccal tube external width | 5 | 2.4 | – | 3.8 | *10.7* | – | *12.3* | 2.9 | *11.3* | 0.7 | *0.7* |
| Buccal tube internal width | 5 | 1.3 | – | 2.5 | *6.1* | – | *7.9* | 1.7 | *6.7* | 0.5 | *0.8* |
| Placoid lengths | | | | | | | | | | | |
| Macroplacoid 1 | 5 | 3.2 | – | 5.5 | *14.0* | – | *17.4* | 4.0 | *15.5* | 1.0 | *1.4* |
| Macroplacoid 2 | 5 | 2.4 | – | 4.1 | *11.3* | – | *12.9* | 3.1 | *11.9* | 0.7 | *0.7* |
| Macroplacoid row | 5 | 6.3 | – | 10.9 | *30.1* | – | *34.9* | 8.2 | *31.8* | 2.0 | *2.1* |
| Claw I heights | | | | | | | | | | | |
| External base | 4 | 2.5 | – | 3.8 | *12.1* | – | *13.9* | 3.2 | *12.6* | 0.5 | *0.9* |
| External primary branch | 4 | 3.4 | – | 6.8 | *14.3* | – | *22.2* | 4.7 | *18.3* | 1.5 | *4.3* |
| External secondary branch | 4 | 2.4 | – | 4.4 | *11.2* | – | *14.1* | 3.3 | *12.9* | 0.9 | *1.5* |
| External base/primary branch (cct) | 4 | 54.6 | – | 97.6 | | – | | 72.6 | – | 21.1 | – |
| Internal base | 3 | 2.5 | – | 3.6 | *11.5* | – | *11.7* | 3.0 | *11.6* | 0.6 | *0.1* |
| Internal primary branch | 3 | 4.0 | – | 6.5 | *19.1* | – | *22.0* | 5.4 | *20.6* | 1.3 | *1.4* |
| Internal secondary branch | 3 | 2.8 | – | 4.1 | *13.0* | – | *13.5* | 3.4 | *13.2* | 0.6 | *0.3* |
| Internal base/primary branch (cct) | 0 | | ? | | | – | | ? | – | ? | – |
| Claw II heights | | | | | | | | | | | |
| External base | 3 | 2.5 | – | 3.9 | *11.4* | – | *14.8* | 3.0 | *12.7* | 0.7 | *1.8* |
| External primary branch | 3 | 3.6 | – | 5.5 | *15.3* | – | *22.1* | 4.6 | *19.5* | 0.9 | *3.6* |
| External secondary branch | 3 | 2.9 | – | 3.9 | *13.2* | – | *15.0* | 3.3 | *13.9* | 0.6 | *0.9* |
| External base/primary branch (cct) | 3 | 54.2 | – | 74.6 | | – | | 66.5 | – | 10.8 | – |
| Internal base | 4 | 2.5 | – | 4.4 | *10.3* | – | *14.1* | 3.1 | *12.2* | 0.9 | *1.6* |
| Internal primary branch | 4 | 2.8 | – | 8.1 | *11.6* | – | *25.9* | 5.3 | *20.7* | 2.2 | *6.7* |
| Internal secondary branch | 4 | 2.7 | – | 5.6 | *13.1* | – | *23.6* | 4.2 | *16.6* | 1.3 | *4.8* |

*Table 2 continued*

| CHARACTER | N | RANGE | | | | | | MEAN | | SD | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | µm | | | *pt* | | | µm | *pt* | µm | *Pt* |
| Internal base/primary branch (cct) | 4 | 46.2 | – | 107.6 | | – | | 65.2 | – | 28.5 | – |
| Claw III heights | | | | | | | | | | | |
| External base | 3 | 2.4 | – | 4.1 | *10.8* | – | *13.0* | 3.0 | *11.7* | 0.9 | *1.1* |
| External primary branch | 3 | 4.8 | – | 7.3 | *22.7* | – | *24.7* | 6.0 | *23.6* | 1.3 | *1.0* |
| External secondary branch | 3 | 2.8 | – | 4.2 | *11.8* | – | *14.2* | 3.3 | *13.1* | 0.8 | *1.2* |
| External base/primary branch (cct) | 3 | 44.0 | – | 55.5 | | – | | 49.8 | – | 5.8 | – |
| Internal base | 3 | 2.5 | – | 4.6 | *10.5* | – | *14.6* | 3.3 | *12.8* | 1.1 | *2.1* |
| Internal primary branch | 3 | 4.6 | – | 7.3 | *22.0* | – | *23.1* | 5.8 | *22.7* | 1.4 | *0.7* |
| Internal secondary branch | 3 | 2.5 | – | 5.1 | *10.8* | – | *16.3* | 3.4 | *13.0* | 1.5 | *2.9* |
| Internal base/primary branch (cct) | 3 | 45.5 | – | 62.9 | | – | | 56.6 | – | 9.6 | – |
| Claw IV heights | | | | | | | | | | | |
| Anterior branches distances | 4 | 6.6 | – | 13.4 | *31.0* | – | *42.7* | 9.2 | *35.5* | 3.0 | *5.4* |
| Anterior primary branch | 4 | 5.7 | – | 10.5 | *27.3* | – | *33.5* | 7.7 | *30.0* | 2.0 | *3.0* |
| Anterior secondary branch | 4 | 4.5 | – | 5.9 | *19.0* | – | *21.5* | 5.2 | *20.5* | 0.7 | *1.2* |
| Anterior base/primary branch (cct) | 4 | 98.4 | – | 132.8 | | – | | 118.6 | – | 15.3 | – |
| Posterior branches distances | 4 | 7.2 | – | 11.9 | *34.3* | – | *42.4* | 9.7 | *37.7* | 2.2 | *3.5* |
| Posterior primary branch | 4 | 5.7 | – | 9.3 | *25.8* | – | *29.6* | 7.0 | *27.3* | 1.6 | *1.6* |
| Posterior secondary branch | 4 | 3.3 | – | 5.2 | *15.2* | – | *19.7* | 4.4 | *17.1* | 0.8 | *2.0* |
| Posterior base/primary branch (cct) | 4 | 125.7 | – | 164.3 | | – | | 138.4 | – | 17.8 | – |

(Fig. 2–3). Body white, eyespots absent, with smooth cuticle and lacking of pores (Fig. 2). The buccal apparatus of the *Isohypsibius* type, with two macroplacoids in the pharynx without microplacoid or septulum (Fig. 2). Claws of legs I–III are of the modified *Isohypsibius* type with very wide angles between branches, small accessory points, internal claws possess characteristic indented cuticular bars (Fig. 3A–C). Claws IV are of the *Eremobiotus* type, with fused primary and secondary branches and asymmetrical accessory points and lunules bearing minute teeth (Fig. 3D).

## DNA sequences

A good quality sequences for all four of the before mentioned molecular markers from all four paragenophores were obtained. The 18S rRNA and 28S rRNA and COI mtDNA sequences were obtained from two individuals whereas the ITS-2 was obtained from one individual. All sequences within the markers are identical and represent a single haplotype: the 18S rRNA sequence (GenBank: PZ448006–07), 849–1007 bp long; the 28S rRNA sequence (GenBank: PZ448009–10), 658–685 bp long; the ITS-2 rDNA sequence, haplotype 1 (GenBank:

PZ458958), 436 bp long; and the COI mtDNA sequence, haplotype 1 (GenBank: PZ448012–13), 603-624 bp long.

### Haplotypes distribution

Haplotype network analyses based on the COI and ITS-2 markers revealed a clear geographic structuring of *Ere. alicatai* populations (Fig. 4). In the COI network, haplotypes from West Spitsbergen formed a distinct cluster separated from the Italian haplotypes by multiple mutational steps. The Italian samples were further subdivided into local haplotypes, with some central haplotypes showing higher frequencies, suggesting potential ancestral or more widespread variants. The West Spitsbergen haplotypes were fewer and closely related to each other, indicating lower diversity within this population. A similar pattern was observed in the ITS-2 network. Italian haplotypes (from Gela and Orbetello) formed a more diverse group, while the West Spitsbergen haplotypes constituted a separate, less diverse cluster. The number of mutational steps between geographic groups supports a clear genetic differentiation between Arctic and Mediterranean populations.

### Phylogenetic position

Bayesian inference analyses based on four molecular markers, 18S rRNA, 28S rRNA, ITS-2 rDNA and COI mtDNA, support the placement of the new population in genus *Eremobiotus* (Fig. 4). Sequences from the new population from Svalbard cluster together with sequences representing populations from Italy.

## Discussion

It is a first report of the *Ere. alicatai* in the Arctic which expand current knowledge of the species distribution and genetic diversity. Sequences generated in present study may serve as a valuable reference database for future studies on soil ecosystems functioning and assessing the impact of climate change on shifts in biological diversity (Pulleman *et al.* 2012; Filho *et al.* 2023; Delgado-Baquerizo *et al.* 2025).

Svalbard is considered as one of the better-studied regions in terms of tardigrade diversity, previous studies have focused mainly on mosses and lichens habitats, and cryoconite holes (Zawierucha *et al.* 2013, 2017, 2021). To date, investigations of soil-dwelling tardigrades have relied exclusively on traditional morphology-based approaches (Czernekova *et al.* 2018; Devetter *et al.* 2021; Tůmova *et al.* 2024; Klimaszyk *et al.* 2026), with exception of *Ten. voronkovi* (Zawierucha *et al.* 2016). Consequently, the database of genetic sequences for tardigrades inhabiting Svalbard soil remains extremely limited. Expanding this dataset is crucial both for biodiversity monitoring of Arctic soil and for resolving taxonomic uncertainties within the phylum. Among the taxa known from Svalbard soil are species representing species complexes or taxons require profound revisions, such as *Diphascon pingue* (Marcus, 1936), *Dip. nobilei* (Binda, 1969), and *Isohypsibius dastychi* Pilato, Bertolani and Binda, 1982, whose phylogenetic positions remain uncertain largely because of the lack of genetic data. Future studies employing an integrative taxonomic approach to soil tardigrades from Svalbard may substantially improve our understanding of both the ecology and phylogenetic relationships of this enigmatic group of animals.

The presence of *Ere. alicatai* in Svalbard could be explained by both accidental anthropogenic introduction, and gaps in the knowledge on soil tardigrades in general. Argument supporting introduction is the fact that for example soils in Pyramiden, where this taxon was found for the first time (Klimaszyk *et al.* 2026), where extensive lawn areas were historically established using soil imported from southern European Russia or Ukraine during the development of the settlement (Coulson *et al.* 2015). Such large-scale import of soil and organic material could have unintentionally introduced various microinvertebrates, including tardigrades, altogether with their propagules or dormant stages. This scenario is especially plausible given that *Ere. alicatai* is otherwise known exclusively from European localities, including Estonia, Italy, Poland and Russia (Binda 1969; Binda and Pilato 1972; Bertolani 1975, 1983; Dastych 1988; McInnes 1994; Zawierucha and Kaźmierski 2012; Lisi *et al.* 2016). Additional support for this interpretation comes from the habitat characteristics of the records. Both the population examined in this study and previously reported representatives of an undefined species of the genus *Eremobiotus* were found exclusively in areas strongly affected by human activity, including the industrial settlement of Pyramiden (Klimaszyk *et al.* 2026) and the vicinity of a research station. Notably, despite previous soil surveys conducted in other parts of Svalbard, representatives of the genus have not been recorded outside such anthropogenically influenced localities (Dastych, 1985; Czernekova *et al.* 2018; Devetter *et al.* 2021; Tůmova *et al.* 2024).

The capacity for long distance, human-mediated dispersal of tardigrades has been well documented (Gąsiorek *et al.* 2019b; Guil *et al.* 2022; Kayastha *et al.* 2023a, 2023b; Surmacz *et al.* 2025). Notably, the first records of *Eremobiotus* on Svalbard originate from this anthropogenically altered area, suggesting that the newly discovered population may have been introduced with imported substrate. In this context, previous studies documenting the presence of alien soil microinvertebrates, *e.g.* Acari and Collembola in the Petunia area, provide additional support for the hypothesis of anthropogenic introduction (Coulson 2015; Coulson *et al.* 2015). Moreover, apart from the geographical separation, populations also differed in the substrate from which they were collected, with the type population found in moss growing on sand, whereas our population was collected from soil mixed with leaf litter (Binda 1969; Camarda *et al.* 2024). However, because the exact source population from which the soil transported to Svalbard originated is unknown, no direct inference on the

geographic origin of this population can be made, especially given that genetic distance in tardigrades do not necessarily correlate with geographic distance as was shown in some previous studies (Jørgensen *et al.* 2007; Cesari *et al.* 2016; Morek *et al.* 2018). This suggests a certain degree of genetic divergence, although final conclusions are limited by the currently sparse sequence data available for *Ere. alicatai* across its range.

Nevertheless, the currently known distribution of *Ere. alicatai* may still be strongly underestimated due to the limited sampling of tardigrade fauna, in soil and leaf litter, across many regions of Europe, including Scandinavian countries. Therefore, a broader natural distribution of this species, potentially extending into the High Arctic, cannot be excluded, and the occurrence of *Ere. alicatai* on Svalbard may also represent a naturally established population rather than an exclusively anthropogenic introduction. At the same time, the genetic differences observed in the analysed markers (COI and ITS-2) indicate that the newly discovered population is not identical to those known from Italy. Similar patterns have already been documented in tardigrades, where genetically highly similar or identical populations were recorded from Svalbard and geographically distant regions of the world despite substantial geographic separation (Zawierucha *et al.* 2023). Therefore, future studies should focus on generating comparable molecular data from populations in other parts of Europe to better understand the species phylogeography and dispersal patterns.

## Conclusion

This is first record of *Ere. alicatai* in Arctic, confirmed through an integrative taxonomic approach combining morphological and molecular evidence. Our finding expands the known distribution and genetic data available for this species while also highlighting the still limited knowledge of soil and leaf litter tardigrade diversity in Svalbard. These results demonstrate also the importance of further integrative studies on soil-dwelling tardigrades in the High Arctic, which may substantially improve current knowledge of their diversity, ecology, and biogeographic patterns.

## Acknowledgements

The research underlying this article was funded by an AMU IDUB grant (No 083/06/POB1/0001): “Tardigrades in the vicinity of the Adam Mickiewicz University Polar Station (Petuniabuka) and potential changes in their diversity in response to anthropopression”. This research has been partially conducted in the framework of the activities of BARg (the Biodiversity and Astrobiology Research group). We sincerely thank the reviewers for their thorough evaluation of the manuscript and for their valuable comments and suggestions, which helped to improve its quality.

## References

Beasley C.W., Kaczmarek Ł and 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, doi: 10.2988/07-30.1.

Bertolani R. 1975. Cytology and systematics in Tardigrada. *Memorie dell'Istituto Italiano di Idrobiologia* 32: 17–35.

Bertolani R. 1983. Tardigradi muscicoli delle dune costiere italiane, con descrizione di una nuova specie. *Atti Della Società Toscana Di Scienze Naturali Memorie*, Serie B, 90: 139–148.

Bertolani R., Guidetti R., Marchioro T., Altiero T., Rebecchi L. and Cesari M. 2014. Phylogeny of Eutardigrada: New molecular data and their morphological support lead to the identification of new evolutionary lineages. *Molecular Phylogenetics and Evolution* 76: 110–126, doi: 10.1016/j.ympev.2014.03.006.

Binda M.G. 1969. New data on the tardigrades of Sicily, with the description of two new species (in Italian). *Bollettino delle Sedute dell'Accademia Gioenia di Szienze Naturali in Catania*, S. IV, 9: 623–633.

Binda M.G. and Pilato G. 1972. Moss-dwelling tardigrades of Sicily (IV Note) (in Italian). *Bollettino Delle Sedute Dell'accademia Gioenia Di Scienze Naturali Di Catania* Serie 4: 47–60.

Biserov V.I. 1992. A new genus and three new species of tardigrades (Tardigrada: Eutardigrada) from the USSR. *Bollettino di Zoologia* 59: 95–103, doi: 10.1080/11250009209386654.

Camarda D., Frigieri F., Guidetti R., Cesari M. and Lisi O. 2024. Lights on tardigrade biodiversity: integrative redescription of *Eremobiotus alicatai* (Eutardigrada, Isohypsibiidae) with new insights on its morphology, phylogeny, and biogeography. *Organisms Diversity & Evolution* 25: 55–80, doi: 10.1007/s13127-024-00657-8.

Camarda D., Lisi O., Stec D. and Vecchi M. 2025. Description of a new genus and species of Isohypsibioidea (Tardigrada), together with its mitochondrial genome sequence. *Arthropod Systematics & Phylogeny* 83: 427–445, doi: 10.3897/asp.83.e150460.

Casquet J., Thebaud C. and Gillespie R.G. 2012. Chelex without boiling, a rapid and easy technique to obtain stable amplifiable DNA from small amounts of ethanol-stored spiders. *Molecular Ecology Resources* 12: 136–141, doi: 10.1111/j.1755-0998.2011.03073.x.

Cesari M., Vecchi M., Palmer A., Bertolani R., Pilato G., Rebecchi L. and Guidetti R. 2016. What if the claws are reduced? Morphological and molecular phylogenetic relationships of the genus *Haplomacrobiotus* May, 1948 (Eutardigrada, Parachela). *Zoological Journal of the Linnean Society* 178: 819–827, doi: 10.111/zoj.12424.

Clement M., Snel, Q., Walker P., Posada D. and Crandall K. 2002. TCS: Estimating gene genealogies. *Parallel and Distributed Processing Symposium, International Proceedings* 2: 184.

Coulson S.J. 2015. The alien terrestrial invertebrate fauna of the High Arctic archipelago of Svalbard: potential implications for the native flora and fauna. *Polar Research* 34: 27364, doi: 10.3402/polar.v34.27364.

Coulson S.J., Fjellberg A., Melekhina E.N., Taskaeva A., Lebedeva N., Belkina O., Seniczak S., Seniczak A. and Gwiazdowicz D. 2015. Microarthropod communities of industrially disturbed or imported soils in the High Arctic; the abandoned coal mining town of Pyramiden, Svalbard. *Biodiversity and Conservation* 24: 1671–1690, doi: 10.1007/s10531-015-0885-9.

Coulson S.J., Bartlett J., Bostrom S., Brittain J.E., Christoffersen K.S., Convey P., de Smet W., Dozsa-Farkas K., Ekrem T.,

Fjellberg A., Fureder L., Gillespie M.A.K., Gustafsson D., Gwiazdowicz D., Kaczmarek Ł., Kolicka M., Laniecki R., Moerman T. Seniczak, Simon J.C., Stur E., Søli G.E.E., Wieczorek K., Zawierucha K. and Zmudczynska-Skarbek, K. 2024. On the terrestrial and freshwater invertebrate diversity of the high Arctic archipelago of Svalbard: A revised species inventory and synopsis of the community composition. *Arctic Science* 10: 799–814, doi:10.1139/as-2024-0017.

Czernekova M., Jönsson K.I., Hajer J. and Devetter M. 2018. Evaluation of extraction methods for quantitative analysis of tardigrade populations in soil and leaf litter. *Pedobiologia* 79: 1–5, doi: 10.1016/j.pedobi.2018.06.005.

Dastych H. 1985. West Spitsbergen Tardigrada. *Acta Zoologica Cracoviensia* 28: 169–214.

Dastych H. 1988. The Tardigrada of Poland. *Monografie Fauny Polski* 16: 1–255.

Delgado-Baquerizo M., Eldridge D.J., Liu Y.R., Liu Z.W., Coleine C. and Trivedi P. 2025. Soil biodiversity and function under global change. *PLoS Biology* 23: e3003093, doi: 10.1371/journal.pbio.3003093.

Devetter M., Háněl L., Raschmanová N., Tůmová M. and Schlaghamersky J. 2021. Terrestrial invertebrates along a gradient of deglaciation in Svalbard: Long-term development of soil fauna communities. *Geoderma* 383: 114720, doi: 10.1016/j.geoderma.2020.114720.

Filho W., Nagy G., Setti A., Sharifi A., Donkor F., Batista K. and Djekic I. 2023. Handling the impacts of climate change on soil biodiversity. *Science of The Total Environment* 869: 161671, doi: 10.1016/j.scitotenv.2023.161671.

Gąsiorek P., Stec D., Morek W., Zawierucha K., Kaczmarek Ł., Lachowska-Cierlik D. and Michalczyk Ł. 2016. An integrative revision of *Mesocrista* Pilato, 1987 (Tardigrada: Eutardigrada: Hypsibiidae). *Journal of Natural History* 50: 2803–2828, doi: 10.1080/00222933.2016.1234654.

Gąsiorek P., Zawierucha K., Stec D. and Michalczyk Ł. 2017. Integrative redescription of a common Arctic water bear *Pilatobiotus recamieri* (Richters, 1911). *Polar Biology* 40: 2239–2252, doi: 10.1007/s00300-017-2137-9.

Gąsiorek P., Stec D., Zawierucha K., Kristensen R.M. and Michalczyk Ł. 2018. Revision of *Testechiniscus* Kristensen, 1987 (Heterotardigrada: Echiniscidae) refutes the polar-temperate distribution of the genus. *Zootaxa*, 4472: 261–297, doi: 10.11646/zootaxa.4472.2.3.

Gąsiorek P., Stec D., Morek W. and Michalczyk Ł. 2019a. Deceptive conservatism of claws: distinct phyletic lineages concealed within Isohypsibioidea (Eutardigrada) revealed by molecular and morphological evidence. *Contributions in Zoology* 88: 78–132, doi: 10.1163/18759866-20191350.

Gąsiorek P., Vončina K. and Michalczyk Ł. 2019b. *Echiniscus testudo* (Doyère, 1840) in New Zealand: anthropogenic dispersal or evidence for the 'Everything is Everywhere' hypothesis? *New Zealand Journal of Zoology* 46: 174–181, doi: 10.1080/03014223.2018.1503607.

Guil N., Rodrigo E. and Marchordon A. 2015. Soil tardigrade biodiversity with the description of a new eutardigrade genus and its phylogenetic position. *Systematics and Biodiversity* 13: 234–256, doi: 10.1080/14772000.2014.986554.

Guil N., Guidetti R., Cesari M., Marchioro T., Rebecchi L. and Machordom A. 2022. Molecular phylogenetics, speciation, and long distance dispersal in tardigrade evolution: A case study of the genus *Milnesium*. *Molecular Phylogenetics and Evolution* 169: 107401, doi: 10.1016/j.ympev.2022.107401.

Hall T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symptoms*, Ser 41: 95–98.

Hohberg K. 2006. Tardigrade species composition in young soils and some aspects on life history of *Macrobiotus richtersi* J. Murray, 1911. *Pedobiologia* 50: 267–274, doi: 10.1016/j.pedobi.2006.02.004.

Hohberg K., Russell D.J. and Elmer M. 2011. Mass occurrence of algal-feeding tardigrade *Apodibius confusus*, in the young soils of a post-mining site. *Journal of Zoological Systematics and Evolutionary Research* 49: 62–65, doi: 10.1111/j.1439-0469.2010.00600.x.

Johansson C., Calloway S., Miller W.R. and Linder E.T. 2011. Are urban and rural tardigrade (Tardigrada) communities distinct and determined by pH: A case study from Fresno County California. *The Pan-Pacific Entomologist* 87: 86–97, doi: 10.3956/2010-27.1.

Jørgensen A., Møbjerg N., Kristensen R.M. 2007. A molecular study of the tardigrade *Echiniscus testudo* (Echiniscidae) reveals low DNA sequence diversity over a large geographic area. Proceedings of the Tenth International Symposium on Tardigrada. *Journal of Limnology* 66: 77–83, doi: 10.4081/jlimnol.2007.s1.77.

Kaczmarek Ł and Michalczyk Ł. 2017. The *Macrobiotus hufelandi* (Tardigrada) group revisited. *Zootaxa* 4363: 101–123, doi: 10.11646/zootaxa.4363.1.4.

Kaczmarek Ł., Zawierucha K., Buda J., Stec D., Gawlak M., Michalczyk Ł. and Roszkowska M. 2018. An integrative redescription of the nominal taxon for the *Mesobiotus harmsworthi* group (Tardigrada: Macrobiotidae) leads to descriptions of two new *Mesobiotus* species from Arctic. *PLOS|ONE* 13: 1–43, doi: 71/journal.pone.0204756.

Kayastha P., Stec D., Sługocki Ł. Gawlak M., Mioduchowska M., Kaczmarek Ł. 2023a Integrative taxonomy reveals new, widely distributed tardigrade species of the genus *Paramacrobiotus* (Eutardigrada: Macrobiotidae). *Scientific Report* 13: 2196. doi: 10.1038/s41598-023-28714-w.

Kayastha P., Szydło W., Mioduchowska M. and Kaczmarek Ł. 2023b. Morphological and genetic variability in cosmopolitan tardigrade species—*Paramacrobiotus fairbanksi* Schill, Förster, Dandekar & Wolf, 2010. *Scientific Reports* 13: 17672, doi: 10.1038/s41598-023-42653-6.

Katoh K. and Toh H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9: 286–298, doi: 10.1093/bib/bbn013.

Katoh K., Misawa K., Kuma K. and Miyata T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–66.

Klimaszyk P., Magowski W., Kaczmarek Ł., Woszczyk M., Niedzielski P., Łaniecki R., Warguła J. and Gołdyn B. 2026. Soil chemical and biological responses to a sparse, early-stage black-legged kittiwake (*Rissa tridactyla*) colony in the Arctic mining settlement Pyramiden (Svalbard). *Scientific Reports* 16: 11648, doi: 10.1038/s41598-026-42627-4.

Leigh J.W. and Bryant D. 2015. PopART: Full-feature soft-ware for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116, doi: 10.1111/2041-210X.12410.

Lisi O., Binda M.G. and Pilato G. 2016. *Eremobiotus ginevrae* sp. nov. and *Paramacrobiotus pius* sp. nov., two new species of Eutardigrada. *Zootaxa* 4103: 344–360, doi: 10.11646/zootaxa.4103.4.3.

McInnes S.J. 1994. Zoogeographic distribution of terrestrial /freshwater tardigrades from current literature. *Journal of Natural History*, 28: 257–352, doi: 10.1080/00222939400770131.

Michalczyk Ł. and Kaczmarek Ł. 2013. The Tardigrada Register: a comprehensive online data repository for tardigrade taxonomy. *Journal of Limnology* 72(s1): 175–181, doi: 0.4081/jlimnol.2013.s1.e22.

Mioduchowska M., Kačarević U., Miamin V., Giginiak Y., Parnikoza I., Roszkowska M. and Kaczmarek Ł. 2021. Redescription of Antarctic eutardigrade *Dastychius improvisus* (Dastych, 1984) and some remarks on phylogenetic relationships within Isohypsibioidea. *The European Zoological Journal* 88: 117–131, doi: 10.1080/24750263.2020.1854877.

Møbjerg N., Jørgensen A., Eibye-Jacobsen J., Halberg K. A., Persson D. and Kristensen R. M. 2007. New records on cyclomorphosis in the marine eutardigrade *Halobiotus crispae* (Eutardigrada: Hypsibiidae). *Journal of Limnology* 66: 132–140.

Nelson D.R., Bartels P.J. and Guil N. 2018. Tardigrade ecology. *In:* Schil, R.O. (ed.) *Water Bears: The Biology of Tardigrades*. Springer, Cham: 163–210, doi: 10.1007/978-3-319-95702-9_7.

Perry E., Miller W.R. and Kaczmarek Ł. 2019. Recommended abbreviations for the names of genera of the phylum Tardigrada. *Zootaxa* 4608: 145–154, doi: 10.11646/zootaxa.4608.1.8.

Pilato G. 1981. Analisi di nuovi caratteri nello studio degli Eutardigrada. *Animalia* 8: 51–57.

Pulleman M., Creamer R., Hamer U., Helder J., Pelosi C., Pérès G. and Rutgers M. 2012. Soil biodiversity, biological indicators and soil ecosystem services—an overview of European approaches. *Current Opinion in Environmental Sustainability* 4: 529–538, doi: 10.1016/j.cosust.2012.10.009.

Stec D., Smolak R., Kaczmarek Ł. and Michalczyk Ł. 2015. An integrative description of *Macrobiotus paulinae* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Kenya. *Zootaxa* 4052: 501–526, doi: 10.11646/zootaxa.4052.5.1.

Stec D., Krzywański Ł., Zawierucha K. and Michalczyk Ł. 2019. Untangling systematics of the *Paramacrobiotus areolatus* species complex by integrative redescription of the nominal species for the group, with multilocus phylogeny and species delineation within the genus *Paramacrobiotus*. *Zoological Journal of the Linnean Society* 188: 694–716. doi: 10.1093/zoolinnean/ziz.163.

Stec D. 2023. Integrative taxonomy helps to revise systematics and questions the purported cosmopolitan nature of the type species within the genus *Diaforobiotus* (Eutardigrada: Richtersiusidae). *Organisms Diversity and Evolution* 23: 309–328, doi: 10-1007/s13127-022-00592-6.

Surmacz B., Budzik K., Matsko Y. and Stec D. 2025. Human impact on microinvertebrate diversity and distributions: questioning the resilience of tardigrades. *Global Ecology and Biogeography* 34: 12, doi: 10.1111/geb.70167.

Topstad L., Guidetti R., Majaneva M. and Ekrem T. 2020. Multimarker DNA metabarcoding reflects tardigrade diversity in different habitats. *Genome* 64: 217–231, doi: 10.1139/gen-2019-0218.

Tumanov D.V. 2022. End of a mystery: Integrative approach reveals the phylogenetic position of an enigmatic Antarctic tardigrade genus *Ramajendas* (Tardigrada, Eutardigrada). *Zoologica Scripta* 51: 217–231, doi: 10.1111/zsc.12521.

Tumanov D.V., Shunatova N. and Fedyuk K. 2024. Integrative description of *Grevenius annulatus* (Eutardigrada, Isohypsibioidea) from North-West Russia with new data on the species cuticular structure leads to the institution of a new genus. *Zoologica Scripta* 54: 232–252, doi: 10.1111/zsc.12703.

Tůmová M., Jílková V., Macek P. and Devetter M. 2024. Tardigrade distribution in soils of high Arctic habitats. *Ecology and Evolution* 14: e11386, doi: 10.1002/ece3.11386.

Zawierucha K. and Kaźmierski A. 2012. The first records of tardigrades (Tardigrada, Eutardigrada) from Estonia. *Zoology and Ecology* 22: 111–113.

Zawierucha K., Coulson S.J., Michalczyk Ł. and Kaczmarek Ł. 2013. Current knowledge of the Tardigrada of Svalbard with the first records of water bears from Nordaustlandet (High Arctic). *Polar Research* 32: 20886, doi: 10.3402/polar.v.32i0.20886.

Zawierucha K., Kolicka M. and Kaczmarek Ł. 2016. Re-description of the Arctic tardigrade *Tenuibiotus voronkovi* (Tumanov, 2007) Eutardigrada: Macrobiotidae, with the first molecular data for the genus. *Zootaxa* 4196: 498–510. doi: 10.11646/zootaxa.4196.4.2

Zawierucha K., Węgrzyn M., Ostrowska M. and Wietrzyk P. 2017. Tardigrada in Svalbard lichens: diversity, densities and habitat heterogeneity. *Polar Biology* 40: 1385–1392, doi: 10.1007/s00300-016-2061-2.

Zawierucha K., Stec D., Lachowska-Cierlik D., Takeuchi N., Li Z. and Michalczyk Ł. 2018. High mitochondrial diversity in a new water bear species (Tardigrada: Eutardigrada) from mountain glaciers in central Asia, with the erection of a new genus *Cryoconicus*. *Annales Zoologici* (Warszawa) 68: 179–201, doi: 10.3161/00034541ANZ2018.68.1.007.

Zawierucha K., Buda J., Azzoni R.S., Niśkiewicz M., Franzetti A. and Ambrosi R. 2019. Water bears dominated cryoconite hole ecosystems: densities, habitat preferences and physiological adaptations of Tardigrada on an alpine glacier. *Aquatic Ecology* 53: 543–56, doi: 10.1007/s10452-019-09707-2

Zawierucha K., Buda J., Novotna Jaromerska T., Janko K., and Gąsiorek P. 2020. Integrative approach reveals new species of water bears (*Pilatobius*, *Grevenius*, and *Acutuncus*) from Arctic cryoconite holes, with the discovery of hidden lineages of *Hypsibius*. *Zoologischer Anzeiger* 289: 141–165, doi: 10.1016/j.jcz.2020.09.004.

Zawierucha K., Porazinska D.L., Ficetola G.F., Ambrosini R., Baccolo G., , Buda, J., Ceballos J.L., Devetter, M., Dial R., Franzetti A., Fuglewicz U., Gielly L., Łokas E., Janko K., Novotna Jaromerska T., Kościński A., Kozłowska A., Ono W., Parnikoza I., Pittino F., Poniecka E., Sommers P., Schmidt S.K., Shain D., Sikorska S., Uetake J., Takeuchi N. 2021. A hole in the nematosphere: tardigrades and rotifers dominate the cryoconite hole environment, whereas nematodes are missing. *Journal of Zoology* 313: 18–36, doi: 10.1111/jzo.12832.

Zawierucha K., Kašparová E.Š., McInnes S., Buda J., Ambrosini R., Devetter M., Ficetola G.F., Franzetti A., Takeuchi N., Horna P., Novotná Jaroměřská T., Ono M., Šabacká M. and Janko K. 2023. Cryophilic Tardigrada have disjunct and bipolar distribution and establish long-term stable, low-density demes. *Polar Biology* 46: 1011–1027, doi: 10.1007/s00300-023-03170-4.