European Journal of Taxonomy 1030: 1–52
https://doi.org/10.5852/ejt.2025.1030.3135
europeanjournaloftaxonomy.eu
ISSN 2118-9773
2025 · Hulterström J. et al.

Received: 21 March 2025 • Accepted: 26 August 2025 • Published: 8 December 2025

Topic editor: Magalie Castelin • Section editor: Daniel Stec • Desk editor: Pepe Fernández

Monograph

urn:lsid:zoobank.org:pub:60D8486F-0A30-423A-832B-3B5BF58C20ED

Integrative taxonomy supports the description of two new species of Macrobiotidae (Tardigrada, Eutardigrada) from Kristianstads Vattenrike Biosphere Reserve in Sweden

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Abstract. Kristianstads Vattenrike Biosphere Reserve (KVBR) in the south of Sweden is a known hotspot for tardigrades, with almost a third of the country's tardigrades species reported from this location alone. Herein, the tardigrade diversity of the KVBR is further investigated. New records for the country are reported and two new species, *Macrobiotus vattenrikense* sp. nov. and *Paramacrobiotus marchelmoni* sp. nov., described using an integrative taxonomic approach. An updated multi-locus phylogeny to the family Macrobiotidae is provided with the inclusion of the newly described species.

Keywords. Biodiversity, *Macrobiotus*, morphology, *Paramacrobiotus*, phylogeny.

Hulterström J., Guidetti R., Jönsson K.I. & Atherton S. 2025. Integrative taxonomy supports the description of two new species of Macrobiotidae (Tardigrada, Eutardigrada) from Kristianstads Vattenrike Biosphere Reserve in Sweden. *European Journal of Taxonomy* 1030: 1–52. https://doi.org/10.5852/ejt.2025.1030.3135

Introduction

Tardigrada Doyère, 1840 is a phylum of small metazoans present within a broad range of substrates including: marine sediments from the littoral zone to abyssal depths (Bussau 1992), glacial cryoconite holes (Zawierucha *et al.* 2014), rock pools (Vecchi *et al.* 2022b; Troell & Jönsson 2023), limnic habitats, leaf-litter, soil, liverwort, lichen, and moss, from which they are most commonly studied (Nelson *et al.* 2018). The diversity and distributions of tardigrade fauna have been increasingly investigated over the last few decades, with the number of recognized species increasing significantly from ~530 species in 1983 (Ramazzotti & Maucci 1983) to more than 1500 species today (Degma & Guidetti 2024).

Nevertheless, modelled estimations conclude that the true diversity of the phylum is significantly higher (Bartels *et al.* 2016).

In total, 118 species of tardigrade (plus five additional species with incomplete or uncertain "cf." or "aff." designations) are known from Sweden (Guidetti *et al.* 2025, and references therein). Tardigrades have been recorded from almost every major Swedish province, including the Baltic Islands Öland and Gotland, with the vast majority reported from the provinces Uppland, Lappland, and, more recently, Skåne (Massa *et al.* 2021; Atherton *et al.* 2025; Guidetti *et al.* 2025). Located within the southernmost province of Skåne, Kristianstads Vattenrike Biosphere Reserve (KVBR) is a UNESCO designated area that incorporates urban environments and rural areas with natural habitats such as wetlands, forest, lakes, and rivers (Olsson *et al.* 2007). This ~1050 km^2 area is highly significant for tardigrade biodiversity since seven of the 28 (25%) Swedish type localities and 36 (30%) Swedish species are reported from KVBR (Massa *et al.* 2021; Atherton *et al.* 2025; Guidetti *et al.* 2025).

The limnoterrestrial eutardigrade family Macrobiotidae Thulin, 1928 consists of up to 15 genera. The most species-rich and widespread of these is *Macrobiotus* Schultze, 1834, whose exact composition and subsequent monophyly has recently been the subject of much discussion (Massa *et al.* 2021; Stec *et al.* 2021a; Vecchi *et al.* 2022c; Bertolani *et al.* 2023; Stec 2024; Vincenzi *et al.* 2024). While all modern phylogenetic analyses do consistently recover three lineages (denoted as clade "A", "B" and "C" by Stec *et al.* 2021a) for the taxon, no morphological definitions have been proposed that will either separate the three clades or encompass all the species morphologies.

A second genus of Macrobiotidae, *Paramacrobiotus* Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009, was erected based on integrative taxonomy and is distinguished by 1) the presence of three macroplacoids in the pharyngal bulb, 2) a microplacoid that, if present, is situated farther than its own length from the macroplacoid row and 3) possessing eggs with an areolated chorion. Two subgenera were proposed for the genus (Kaczmarek *et al.* 2017, amended by Marley *et al.* 2018), based on presence or absence of microplacoid, but were ultimately rejected after phylogenetic analyses determined they were non-monophyletic. They are instead currently accepted as the informal *richtersi* (with microplacoid) and *areolatus* (without microplacoid) morphogroups (Guidetti *et al.* 2019a; Stec *et al.* 2020c). *Paramacrobiotus* comprises 47 nominal species (Degma & Guidetti 2024), including two nomina dubia and two species which are based solely on genetic data without morphological distinction (Schill *et al.* 2010; Guidetti *et al.* 2019a; Stec *et al.* 2020c).

Herein, the tardigrade composition of two samples of moss collected from KVBR is documented, including some new records for the country. Two species, *Macrobiotus vattenrikense* sp. nov. and *Paramacrobiotus marchelmoni* sp. nov., are introduced for the first time based on a combination of morphological and molecular taxonomy. These descriptions form part of a larger ArtDatabanken sponsored biodiversity project that aims to catalog macrobiotid tardigrades within Sweden.

Material and methods

Substrate collection and animal extraction

Moss was collected from an open grassland pasture within KVBR in Skåne, Sweden (Sånnarna; 55°55′41.6″ N, 14°15′11.1″ E) on 21 March 2022 (Supp. file 1). The moss was growing on calcareous-rich sand with full sunlight exposure at an altitude of ~8 m above sea level. The sample was transported to the Swedish Museum of Natural History in Stockholm, where it was air dried and stored until extraction. During extraction, the dry sample was submersed in tap water for 0.5–3 h, then the contents were stirred vigorously and the top water poured through 250 µm and 40 µm mesh sieves. The sieves were back-washed with tap water into a petri-dish, and individual animals and eggs detected under a

Nikon SMZ 1500 stereo microscope. Water was poured back into the initial cup containing the substrate and the process repeated after ~24 h for an increased yield of individuals per sample.

Individual animals and eggs were transferred in water to a microscope glass slide under a cover slip and identified to the lowest possible taxonomic level with a Nikon Eclipse 80i compound microscope equipped with Differential Interference Contrast (DIC). Light micrographs were taken of each using a Canon EOS 5D Mark III digital camera. Animals and eggs were subsequently fixed on a permanent slide in Hoyer's fluid, prepared for Scanning Electron Microscopy (SEM), or saved in 95% ethanol for later DNA-analysis. Morphometric measurements were taken from fixed animals on slides under 100 × immersion oil objective using an ocular micrometer and from photographs of the same using GIMP ver. 2.10.36.

Critical point drying prior to SEM analysis was achieved by boiling the specimens in pure ethanol following the protocol in Guidetti *et al.* (2019b). Dry specimens were moved using an eyebrow hair mounted on a glass pipette onto double-sided carbon tape on a SEM stub. A thin layer of gold was applied using a sputter coater before viewing with FEI Quanta FEG 650 SEM at the Swedish Museum of Natural History, Stockholm.

All type material is stored in the Swedish Museum of Natural History in Stockholm, Sweden (SMNH) and in the Bertolani Collection of the University of Modena and Reggio Emilia, Italy (MUSN).

DNA extraction, amplification, and sequencing protocol

DNA from whole individual adults or eggs was extracted using a Qiagen DNeasy kit following the manufacturer's instructions. PCR amplification was performed using 0.2 ml PuReTaq Ready-to-go PCR Beads (GE Healthcare) with 5 pmol each forward and reverse primers and 3 µl DNA.

Four gene regions were selected for amplification: the ~650 bp "Folmer region" (Folmer *et al.* 1994) of the mitochondrial cytochrome oxidase subunit 1 (COI), the ~450 bp nuclear ribosomal internal transcribed spacer (ITS2), a ~900 bp fragment of the ribosomal large subunit (28S), and the full ~1800 bp ribosomal small subunit (18S), assembled from three overlapping fragments. For *Paramacrobiotus marchelmoni* sp. nov. the full 18S sequencing was unsuccessful, and a ~1300 bp fragment was amplified instead. Supp. file 2: sheet 1, lists all primer pairs and PCR protocols. PCR-product was examined on 1% agarose gel with gel-green and purified using ExoSAP-IT enzymes (Exonuclease and Shrimp Alkaline Phosphotase; GE Healthcare) and DNA sequencing was conducted by Macrogen Europe (Netherlands).

Sequences were assembled in Aliview ver. 1.28 (Larsson 2014) and checked for ambiguous base calls using FinchTV ver. 1.4.0 (Geospiza inc.). The mitochondrial COI gene was aligned as translated amino acids according to the standard invertebrate mitochondrial code to check for stop codons and pseudogenes.

Phylogenetic and species delimitation analyses

Newly generated sequences were combined with sequences of Macrobiotidae downloaded from GenBank as well as *Richtersius coronifer* (Richters, 1903) and *Diaforobiotus islandicus* (Richters, 1904), which were selected as outgroups. Appendix 1 lists the GenBank accession numbers for all sequences used in this study. Sequences were aligned in Aliview ver. 1.28 (Larsson 2014) using the incorporated MUSCLE algorithm (Edgar 2004) for multiple alignment. Concatenation of datasets from the genes COI, 18S, 28S, and ITS2 was done with Concatenator ver. 0.2.1 (Vences *et al.* 2022). The ITS2 dataset was cleaned of uninformative sites and ambiguously aligned blocks with Gblocks ver. 0.91.1 using the default settings and allowing for gap positions (Talavera & Castresana 2007).

Maximum likelihood (ML) phylogenetic analysis was conducted using the IQtree-web server (Trifinopoulos *et al.* 2016) with 1000 replicates of ultrafast bootstrap trees to test topological support. Modelfinder (Kalyaanamoorthy *et al.* 2017) incorporated in IQ-tree found the best fitting substitution model under the Bayesian Information Criterion for each dataset, and selected models are given in Supp. file 2: sheet 2.

Species inference was tested through multi-rate Poisson tree processes (mPTP) using default parameters under ML and Markov chain Monte Carlo (https://mptp.h-its.org; Kapli *et al.* 2017) using input trees generated from ML analyses of COI. Pairwise uncorrected genetic distances (p-distances) within and between species of *Macrobiotus* "clade B" and *Paramacrobiotus* were calculated in MEGA (Kumar *et al.* 2018) for the COI and the unfiltered ITS2 sequences, with each species defined following the results of the mPTP analysis.

Morphological and morphometric analysis

Animals and eggs fixed in Hoyer's fluid (Morek *et al.* 2016) were morphologically analysed and measured under 100 × oil immersion magnification. Morphometric measurements were processed in the Parachela ver. 1.8 template available from the Tardigrada Register, www.tardigrada.net/register (Michalczyk & Kaczmarek 2013). The measured data was supplemented with the *pt* index (Pilato 1981). Measurements of claws, eggs, and buccal apparatus were taken following Michalczyk & Kaczmarek (2017), and only if they were in the appropriate position. Claws were measured either in frontal or lateral view. Body length was measured excluding the hind legs, and the buccal tube from the posterior end of the oral cavity to the posterior end of the buccal tube within the pharynx. Inner and outer buccal tube width was measured at the stylet insertion point. The diameter of oval eggs was measured at the widest point. Egg processes were counted around the circumference with the widest margin of the egg in focus in accordance with Kaczmarek & Michalczyk (2017). Egg process height was measured in lateral view on the circumference. Figures were processed with GIMP ver. 2.10.36 (https://www.gimp.org/downloads/) and deep focus images were generated form a stack of 2–6 images using Helicon Focus ver. 8.2.2 (https://www.heliconsoft.com/software-downloads/).

Results

Faunistics

A total of eight morphospecies were isolated from the sample: *Hypsibius pallidus* Thulin, 1911; *Macrobiotus vattenrikense* sp. nov.; *Macrobiotus* aff. *nelsonae* Guidetti, 1998; *Milnesium tardigradum* Doyère, 1840; *Paramacrobiotus fairbanksi* Schill, Förster, Dandekar & Wolf, 2010; *Paramacrobiotus marchelmoni* sp. nov.; *Ursulinius lunulatus* (Iharos, 1966); and *Tenuibiotus* sp. The identification of *P. fairbanksi* was confirmed by DNA analyses (Figs 1, 3; Supp. files 3, 4, 5, 6) and represents a new record for Sweden. *Macrobiotus*. aff. *nelsonae* and *Tenuibiotus* sp. are likely new to science.

Paramacrobiotus marchelmoni sp. nov. and *P. fairbanksi* were initially distinguished from each other based on the shape of the microplacoid, which is comma-shaped in *P. fairbanksi* (Supp. file 7B) and heart-shaped with ventrolateral wings in *P. marchelmoni* (Fig. 9B). *Paramacrobiotus fairbanksi* has been meticulously studied numerous times from populations found over a wide geographic range: Antarctica (Kaczmarek *et al.* 2020b), Denmark (Gąsiorek *et al.* 2024), Finland (Vecchi *et al.* 2024b), Italy (Guidetti *et al.* 2019a), Poland (Stec *et al.* 2020c), Spain (Guil & Giribet 2012; Guidetti *et al.* 2019a), and USA (Alaska; Schill *et al.* 2010), and has never been reported with anything other than a comma-shaped microplacoid, supporting the character's validity as a way to distinguish between the two species. The species distinction was subsequently confirmed via differences in egg morphology (number of areolae surrounding each, widths of the processes bases and shape of the process apexes; see differential diagnosis for *P. marchelmoni* and compare Figs 9, 11 with Supp. file 7) and via molecular analysis (Fig. 3).

The specimens of *Macrobiotus* aff. *nelsonae* and *M. vattenrikense* sp. nov. were initially distinguished from each other based on the clearly smaller lunulae and large, elliptical pores of the former (Supp. file 8) compared to the larger lunulae and small, rounded cuticular pores of the latter (Figs 4–5). Their separation was subsequently confirmed by their different egg morphologies, with *M.* aff. *nelsonae* determined to be of the *nelsonae*-group based on the presence of oval areolae (Kaczmarek *et al.* 2023). Additionally, the eggs of *M.* aff. *nelsonae* had conical processes with a smooth and rounded cap on the apex that do not match the eggs of any described taxa in the *nelsonae*-group (Kaczmarek *et al.* 2023), which suggests the species is likely unknown to science. Unfortunately, all attempts to attain DNA sequences for the species were unsuccessful. The connection between the egg and the adult morphology of *M.* aff. *nelsonae* was facilitated by a hatchling.

Only a single adult specimen and no eggs were found for *Tenuibiotus* sp. The specimen matched the morphological characterization of *Tenuibiotus* Pilato & Lisi, 2011 as defined by Stec & Morek (2022): *tenuis*-type claws (Pilato & Lisi 2011), a non-porous cuticle, and a pharynx with rows of two macroplacoids – the first with a deep constriction – and single microplacoid (Supp. file 9). DNA sequences attained from the specimen grouped within the *Tenuibiotus* clade but were distinct from the available sequences of the other species of the genus (Fig. 1). This is the first record of the genus in Sweden.

Phylogenetic analyses

Results from individual gene and concatenated datasets were largely consistent with each other (Figs 1–3; Supp. files 3, 4, 5, 6) and with previous reports (Guidetti *et al.* 2009, 2019a; Stec *et al.* 2020d, 2021a; Kayastha *et al.* 2023b; Vincenzi *et al.* 2024). The COI and ITS2 gene trees (Supp. file 3, Supp. file 5) displayed lower support for deeper nodes, while the 18S and 28S gene trees (Supp. file 4, Supp. file 6) failed to separate several closely related species, but such results are unsurprising given the evolutionary rates of the loci (Klopfstein *et al.* 2017).

Figure 1 depicts the results of the family level analyses of the four gene concatenated dataset. *Sisubiotus* Stec, Vecchi, Calhim & Michalczyk, 2021, *Mesobiotus* Vecchi, Cesari, Bertolani, Jönsson, Rebecchi & Guidetti, 2016 and *Macrobiotus* + *Xerobiotus* Bertolani & Biserov, 1996 grouped together with moderate support. *Macrobiotus* formed three well-supported clades that correspond to clade "A", "B" and "C" of Stec *et al.* (2021a, 2022), Vecchi *et al.* (2022c), and Vincenzi *et al.* (2024), with *Xerobiotus* nested within *Macrobiotus* "clade B". *Macrobiotus vattenrikense* sp. nov. was recovered in "clade B" as sister to *Macrobiotus mileri* Stec, 2024.

Minibiotus Schuster, 1980 (in Schuster *et al.* 1980) comprised two paraphyletic lineages that grouped with a supported *Tenuibiotus* and *Paramacrobitous* clade. *Paramacrobiotus* was split into two evolutionary lineages corresponding to the *arelatus*-group and the *richtersi*-group + *P. lachowskae* Stec, Roszkowska, Kaczmarek & Michalczyk, 2018. *Paramacrobiotus marchelmoni* sp. nov. was recovered within the *richtersi*-group clade as sister to a clade consisting of *Paramacrobiotus gadabouti* Kayastha, Stec, Mioduchowska & Kaczmarek, 2023 (in Kayastha *et al.* 2023b) and an unidentified *Paramacrobiotus* sp. from New Zealand (*Paramacrobiotus* sp. "strain NZ.001"). The new species clustered as a single species with two sequences from GenBank: (I) "*Macrobiotus pallarii* tar407" collected from outside Madrid (Guil & Giribet 2012) and (II) *Paramacrobiotus* sp. "strain HU.012" collected in Budapest, Hungary (Stec *et al.* 2020c).

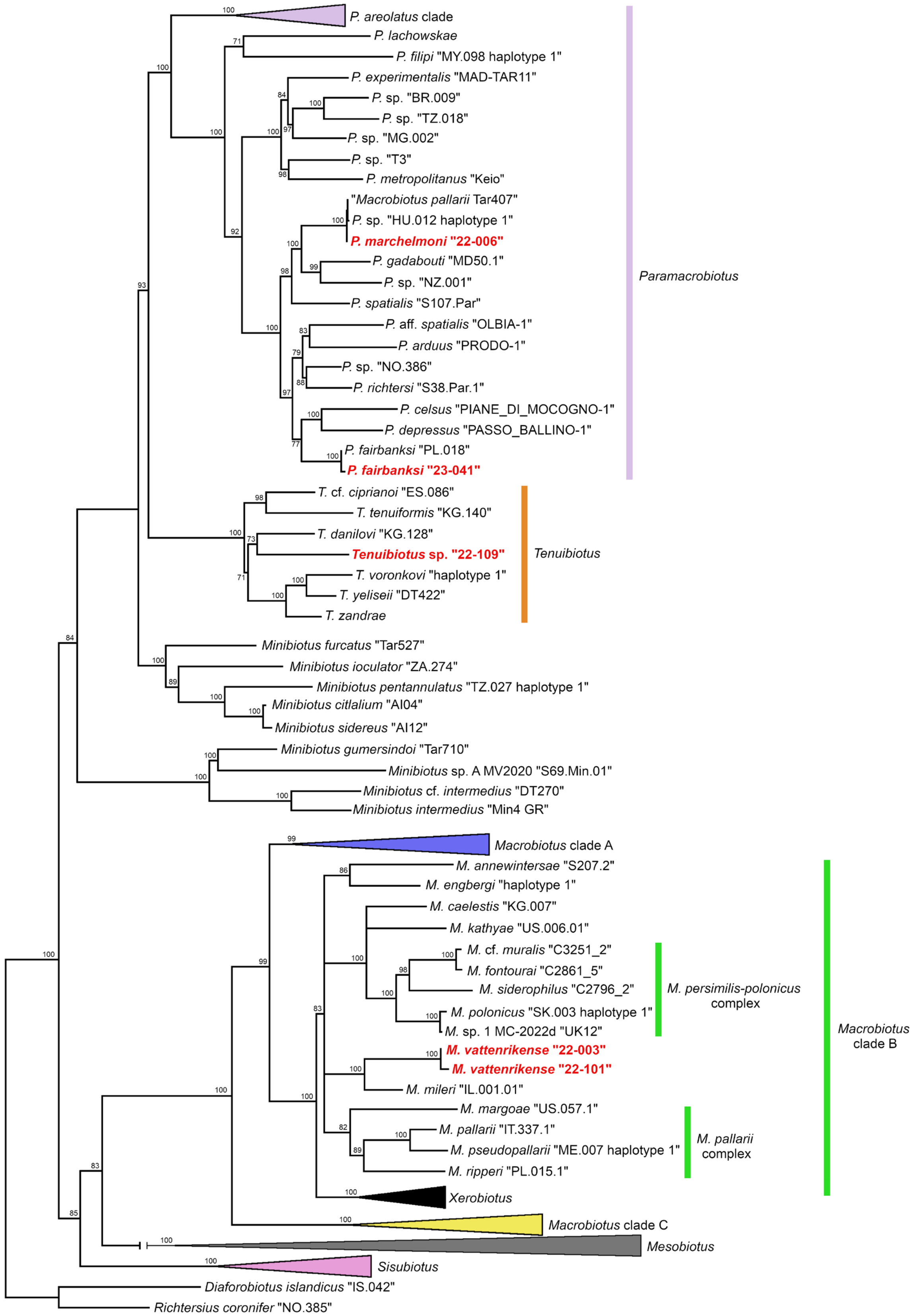

Fig. 1. Concatenated 18S, 28S, COI and ITS2 ML tree. Ultrafast bootstrap support is given at the nodes and species with newly generated genetic data are highlighted in red.

Species inference with multi-rate Poisson tree processes (mPTP)

The mPTP analyses recovered 14 species in *Macrobiotus* "clade B" (Fig. 2) and 26 species in *Paramacrobiotus* (Fig. 3), with all nominal species as separate species. Additionally, *Macrobiotus fontourai* Bertolani, Cesari, Giovannini Rebecchi, Guidetti, Kaczmarek & Pilato, 2022 and *M.* cf. *muralis* Bertolani, Cesari, Giovannini Rebecchi, Guidetti, Kaczmarek & Pilato, 2022 were recovered as a single species, consistent with the ASAP-analysis in Bertolani *et al.* (2023). All specimens of *Macrobiotus vattenrikense* sp. nov. were delineated as single species, and all specimens of *Paramacrobiotus*

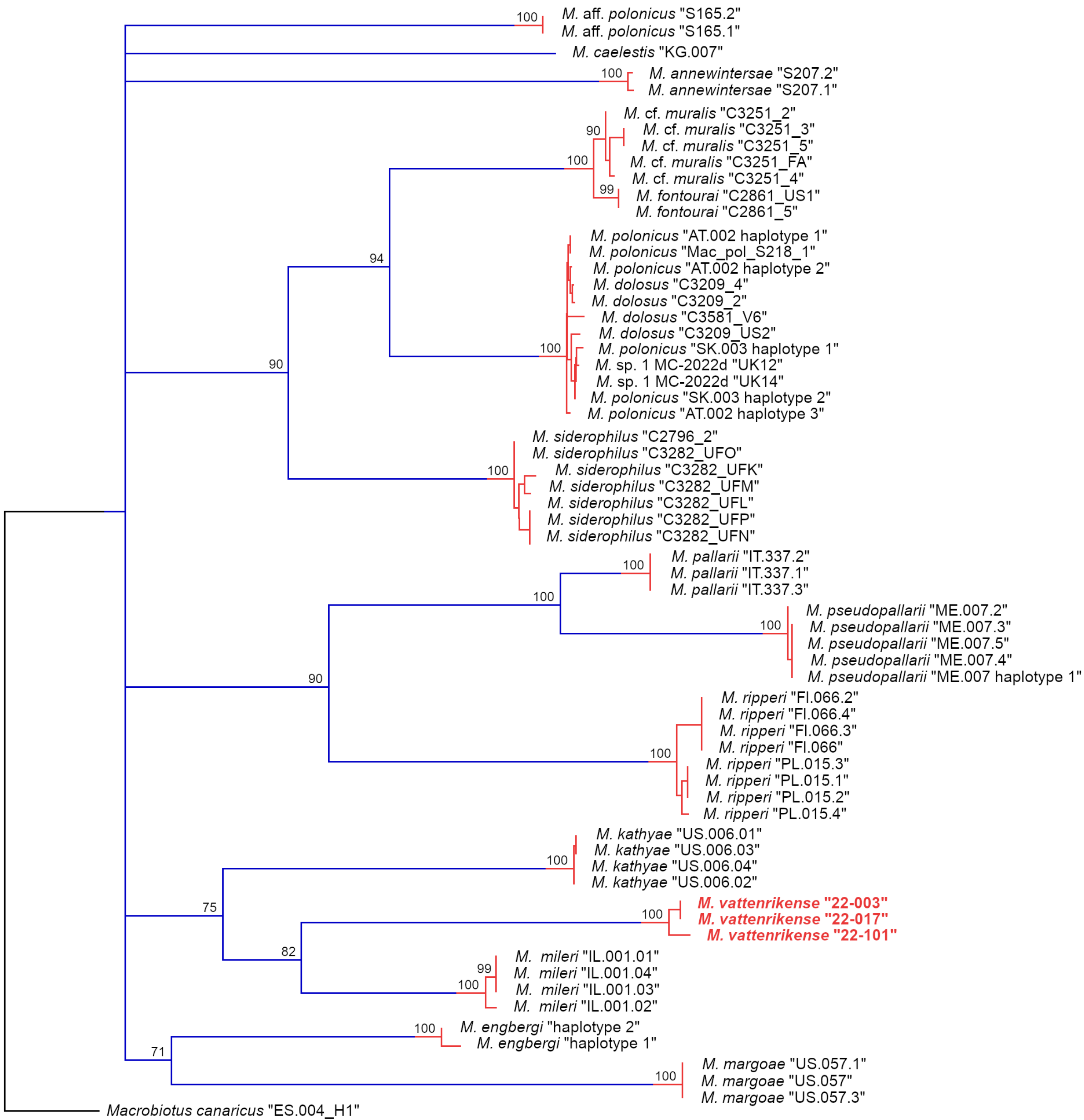

Fig. 2. Concatenated 18S and COI ML tree of *Macrobiotus* Schultze, 1834 "clade B" with results from the mPTP analysis. Ultrafast bootstrap support is given at the nodes, and specimens with newly generated genetic data are highlighted in red. Bars are colored consistent with the results of the mPTP analysis, where the transitions from blue to red represent speciation.

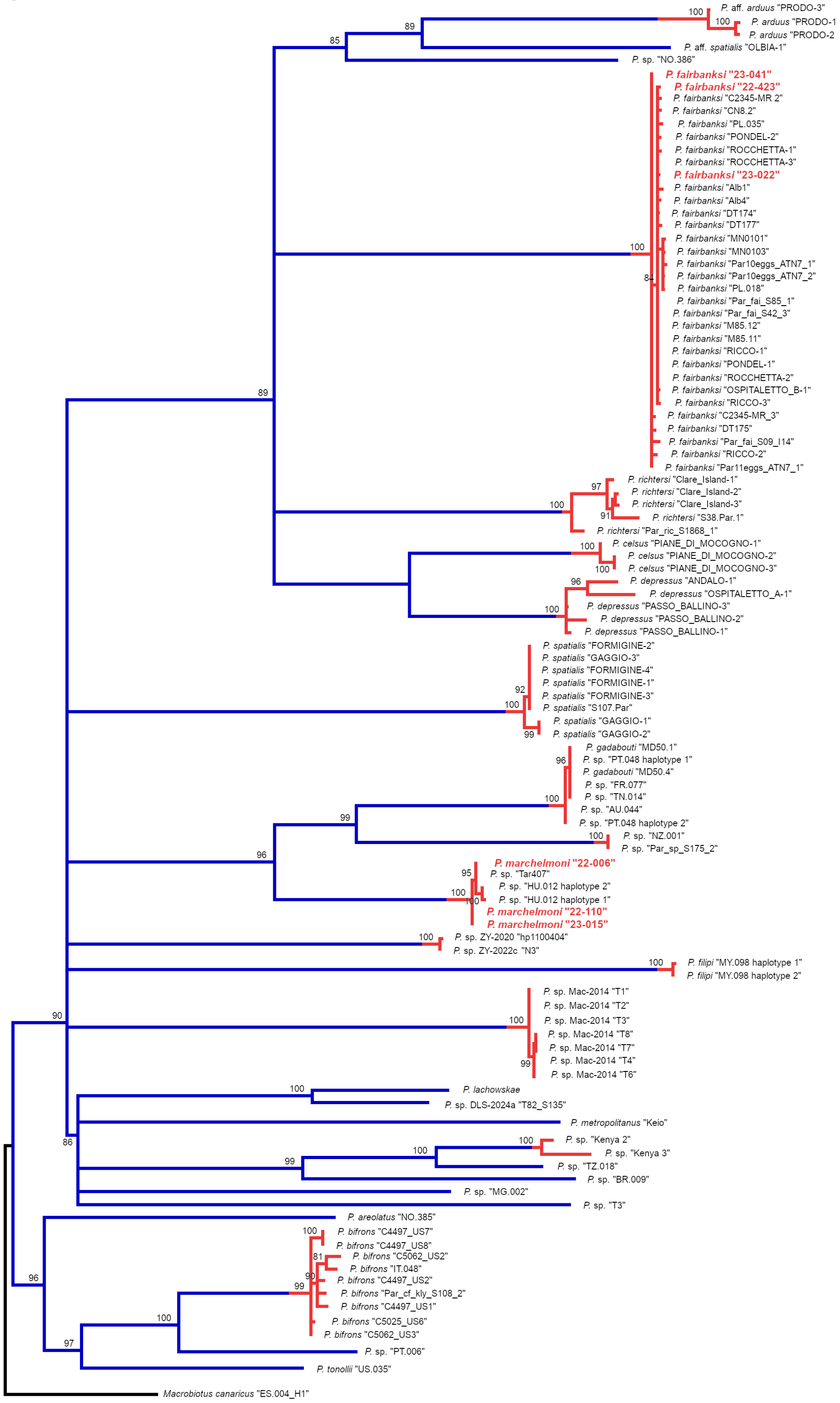

Fig. 3. Concatenated 18S and COI ML tree of *Paramacrobiotus* Guidetti, Schill, Bertolani, Dandekar & Wolf, 2009 with results from the mPTP analysis. Ultrafast bootstrap support is given at the nodes, and specimens with newly generated genetic data are highlighted in red. Bars are colored consistent with the results of the mPTP analysis, where the transitions from blue to red represent speciation.

marchelmoni sp. nov. + "*Macrobiotus pallarii* tar407" + *Paramacrobiotus* sp. "strain HU.012" were delineated as a single species.

Pairwise genetic distances within and between species of *Macrobiotus* "clade B" and *Paramacrobiotus* are given in Supp. file 2: sheets 3–6, with each species defined following the results of the mPTP analyses (Figs 2–3). For *Macrobiotus* "clade B", intraspecific distances were 0.0–4.2% for COI and 0.0–1.3% for ITS2 and interspecific distance were 14.0–24.9% for COI and 0.8–11.6% for ITS2. For *Paramacrobiotus*, intraspecific distance were 0.0–5.3% for COI and 0.0–1.6% for ITS2 and interspecific distance were 10.5–27.6% for COI and 1.4–32.7% for ITS2. For *P. fairbanksi*, specimens from Sweden differed from the specimens from other countries by 0.0–0.3% for COI and 0.0–0.9% for ITS2. Specimens of *P. marchelmoni* sp. nov. from Sweden differed from the specimen from Hungary ("HU.012") by 0.6–0.8% for COI and 0.9–1.5% for ITS2 and the specimen from Spain ("tar407") by 0.0–0.2% for COI (no ITS2 sequence is available for "tar407").

Taxonomy

Class Eutardigrada Richters, 1926
Order Parachela Schuster, Nelson, Grigarick & Christenberry, 1980
Family Macrobiotidae Thulin, 1928
Genus *Macrobiotus* Schultze, 1834

Macrobiotus vattenrikense sp. nov.
urn:lsid:zoobank.org:act:0F5EEA46-2A3D-4D72-B776-CB812C013993
Figs 4–8

Diagnosis

Macrobiotus with three bands of teeth in oral cavity armature (OCA): first and second of granules, and third of a transverse crest non-uniform in shape on the dorsal and ventral side, with a dorsal side with one elongated tooth and ventral side with two lateral and two medial teeth. Two macroplacoids, the first with a slight central constriction, the second with a pre-terminal constriction, and a comma-shaped microplacoid. Claws of similar size on all legs, with large, smooth lunulae on legs I–III and serrated on legs IV. Eggs of *hufelandi*-type with inverse goblet-shaped processes with indented process disks without granulation. Egg chorion with a wrinkled or granulated surface, appears solid in LM but with a ring of small pores around each process visible in SEM.

Etymology

The new species is named after the area of the type locality within Kristianstads Vattenrike Biosphere Reserve, in dedication to its high tardigrade biodiversity.

Material examined

A total of 16 animals and 7 eggs observed, including: 10 animals and 6 eggs mounted in Hoyer's fluid, 2 animals and 1 egg fixed for SEM, and 4 animals used for DNA extraction.

Type material

Holotype

SWEDEN • Skåne, Sånnarna; 55°55′41.6″ N, 14°15′11.1″ E; 8 m a.s.l.; 22 Mar. 2021; S. Atherton, R. Guidetti and K.I. Jönsson leg.; moss on calcareous-rich sand and rock; SMNH, slide SMNH-Type-10010.

Paratypes

SWEDEN • 9 specs, 5 eggs; same collection data as for holotype; GenBank nos: PX093653 to PX093655 (COI), PX093644 (ITS), PX093663, PX093664 (18S), PX093649, PX093650 (28S); SMNH, slides SMNH-Type-10011 to SMNH-Type-10015, SEM stub SMNH-Type-10016 • 2 specs, 2 eggs; same collection data as for holotype; MUSN, slides 24-081, 24-083.

Description

Morphometric measurements of animals and eggs are given in Tables 1 and 2, respectively (raw morphometric data in Supp. file 10).

Adult body length 335–530 µm, yellowish with black eyespots visible in live animals (Fig. 4A) and animals fixed in Hoyer's. Cuticle with small (up to 1 µm in diameter), round pores, visible with DIC (Fig. 4E) and clearly visible with SEM (Fig. 6C), scattered throughout the body cuticle. Very fine granulation clearly visible only with SEM distributed over the entire body, less dense on the ventral side (Fig. 6B–C). Medium granulation lateral and external to claws on legs I–III visible with DIC (Fig. 5B) and SEM (Fig. 6B). Legs IV with a patch of coarse granulation tapering centrally on the caudal segment and around the claws, clearly visible with DIC (Fig. 5D), and SEM (Fig. 6D). Pulvinus, gibbosities, and garter-like structures on the legs absent.

Rigid buccal tube of *Macrobiotus*-type (Pilato & Binda 2010) with ventral lamina, ten peribuccal lamellae and six sensory lobes. OCA of *hufelandi*-type (Kaczmarek & Michalczyk 2017) with an anterior band of teeth faintly visible as fine granules with DIC (Fig. 4C–D) and as small cones with SEM (Fig. 6A); a second band of larger granular teeth and a third row of posterior transverse ridges. Third row non-uniform; ventral side comprising two lateral teeth and a divided median tooth split into two (Fig. 4D, F), and dorsal side with a single, fused elongated tooth (Fig. 4C). Stylet furca typical of the genus and stylet support insertion point at 75–81% of the buccal tube. Bulbous muscular pharynx with three apophyses and three rows of two rodlike macroplacoids with the length series 1 > 2 and a microplacoid (Fig. 4B). First macroplacoid with slight central constriction. Second macroplacoid with deeper pre-terminal constriction. Comma-shaped microplacoid situated closer than its own length to the macroplacoid row.

Claws of *hufelandi*-type (Bertolani & Pilato 1988) of similar size on all legs. Large lunulae on all claws, and distinctly larger on legs IV (max. width on leg I–III 6–8 µm; leg IV 7–10 µm). Lunulae smooth on legs I–III and serrated on legs IV, visible with DIC (Fig. 5B–D), and SEM (Fig. 6B, D–E). Cuticular bars absent.

Gonochoristic. Males with sperm-filled testis and females with a spermatheca filled with bundles of sperm observed (Fig. 5A).

Ornamented eggs are spherical and laid freely, bare diameter 62.3–78.2 µm. Eggs of *hufelandi*-type (Kaczmarek & Michalczyk 2017; Figs 7A, 8A) with processes shaped as inverted goblets with strait or lightly sigmoidal trunks and terminal disks (Fig. 7A–C). Surface of the terminal disks smooth, concave with a deep hollow and cogwheel-shaped edges including 10–11 evenly spaced indentations (Figs 7D, 8). Process height 6.0–7.3 µm; base diameter 6.0–7.2 µm; terminal disk diameter 3.2–4.8 µm; and inter-process distance 2.9–4.2 µm. 23–25 processes on the egg circumference. The egg chorion is wrinkled and appears solid in DIC (Fig. 7E–F), but minute (< 0.25 µm in diameter) pores present around the bases of the processes are visible with SEM (Fig. 8B–C). Larger wrinkles surrounding the base of each process appear as a crown of thickenings in DIC (Fig. 7E–F).

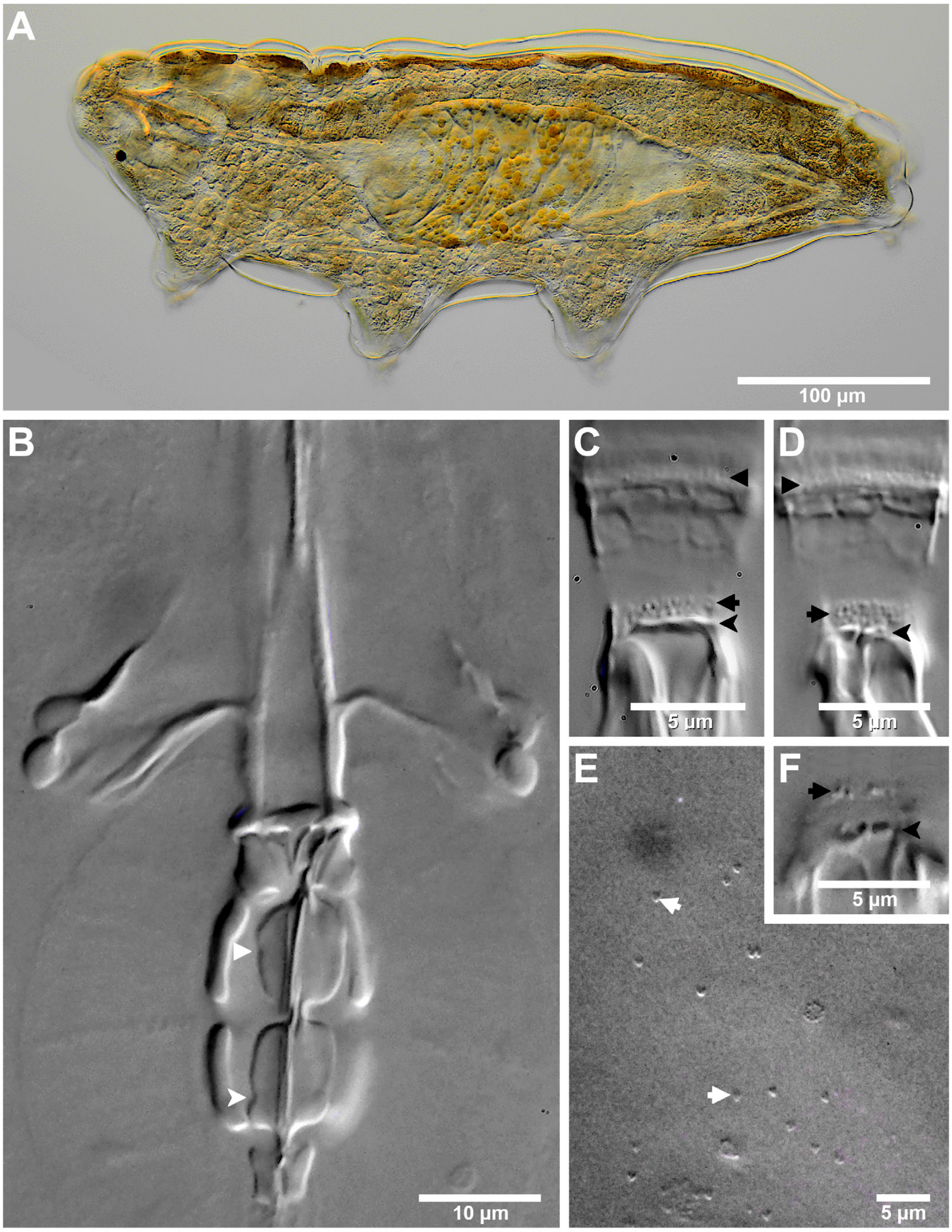

Fig. 4. *Macrobiotus vattenrikense* sp. nov. **A**. DIC photograph of paratype in water (SMNH, SMNH-Type-10013); whole body. **B**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10010); pharynx and placoids. **C**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10010); dorsal OCA. **D**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10010); ventral OCA. **E**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10010); body cuticle with small pores. **F**. DIC photograph of paratype in Hoyer's fluid (MUSN, 24-081); second and third rows of the ventral OCA. White arrowhead indicates slight constriction of the first macroplacoid; white indented arrowhead indicates constriction of the second macroplacoid; white full arrows indicate pores in the body cuticle; black arrowheads indicate first row of OCA; black full arrows indicate second row of OCA; black indented arrowheads indicate third row of OCA.

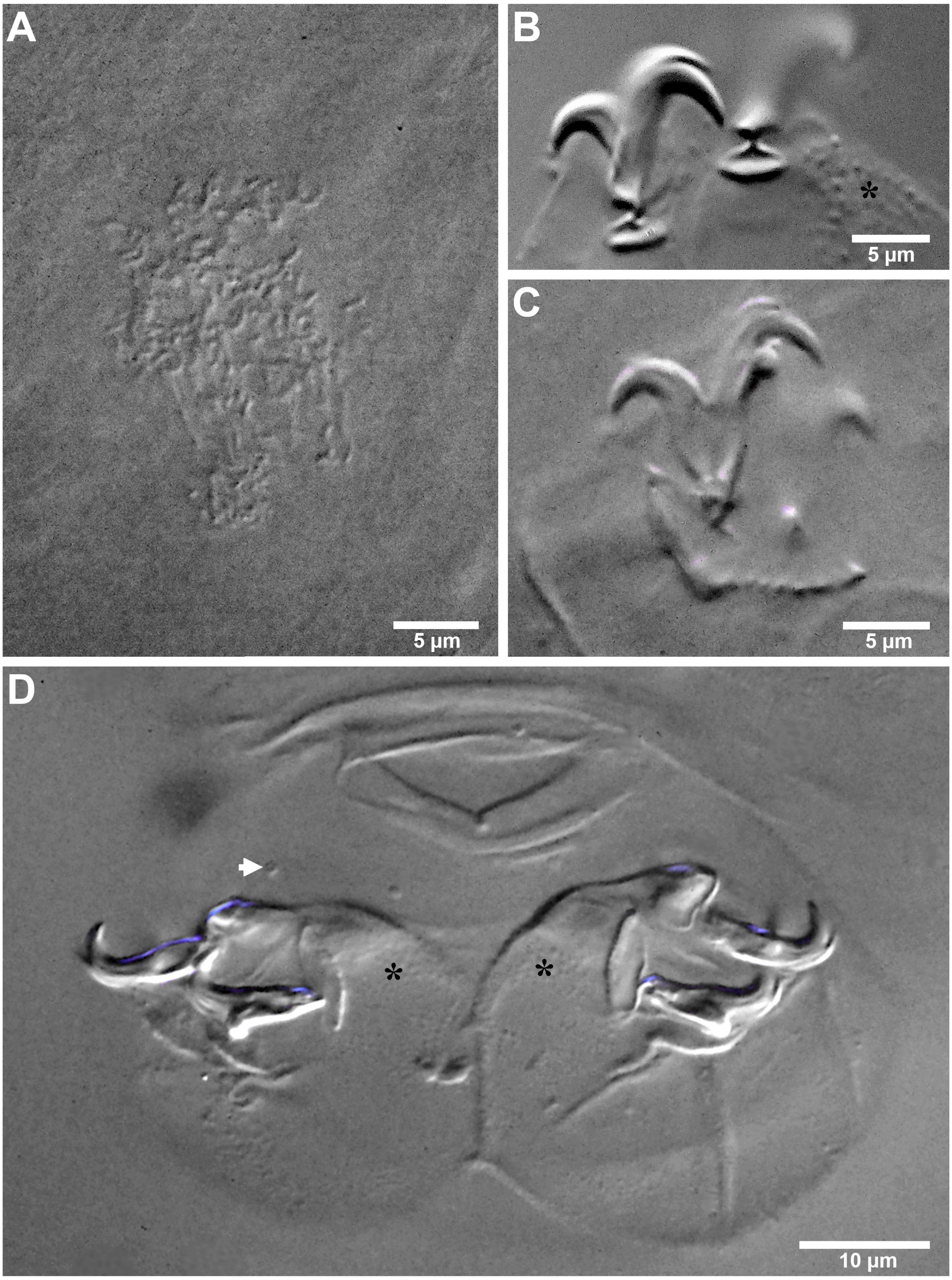

Fig. 5. *Macrobiotus vattenrikense* sp. nov. **A**. DIC photograph of paratype in Hoyer's fluid (SMNH, SMNH-Type-10011); spermatheca with sperm. **B**. DIC photograph of paratype in Hoyer's fluid (MUSN, 24-081); claws of leg I. **C**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10010); claws of leg IV. **D**. DIC photograph of paratype in Hoyer's fluid (MUSN, 24-081); legs IV. White full arrow indicates pores in the body cuticle; asterisks indicate leg granulation.

DNA sequences

Sequences for *M. vattenrikense* sp. nov. were attained for all four molecular markers and using four adult animals. ITS2 was represented by a single haplotype; 18S and 28S were represented by two haplotypes (uncorrected p-distance between haplotypes 0.06% and 0.11%, respectively), and COI was represented by three haplotypes (uncorrected p-distances between haplotypes 0.2–2.6%):

- 18S haplotype 1: specimen 22-003; 1769 bp; GenBank accession number PX093663;
- 18S haplotype 2: specimen 22-101; 1769 bp; GenBank accession number PX093664;
- 28S haplotype 1: specimens 22-003, 22-017; 921 bp; GenBank accession number PX093649;
- 28S haplotype 2: specimen 22-101; 921 bp, GenBank accession number PX093650;
- COI haplotype 1: specimen 22-017; 658 bp, GenBank accession number PX093653;

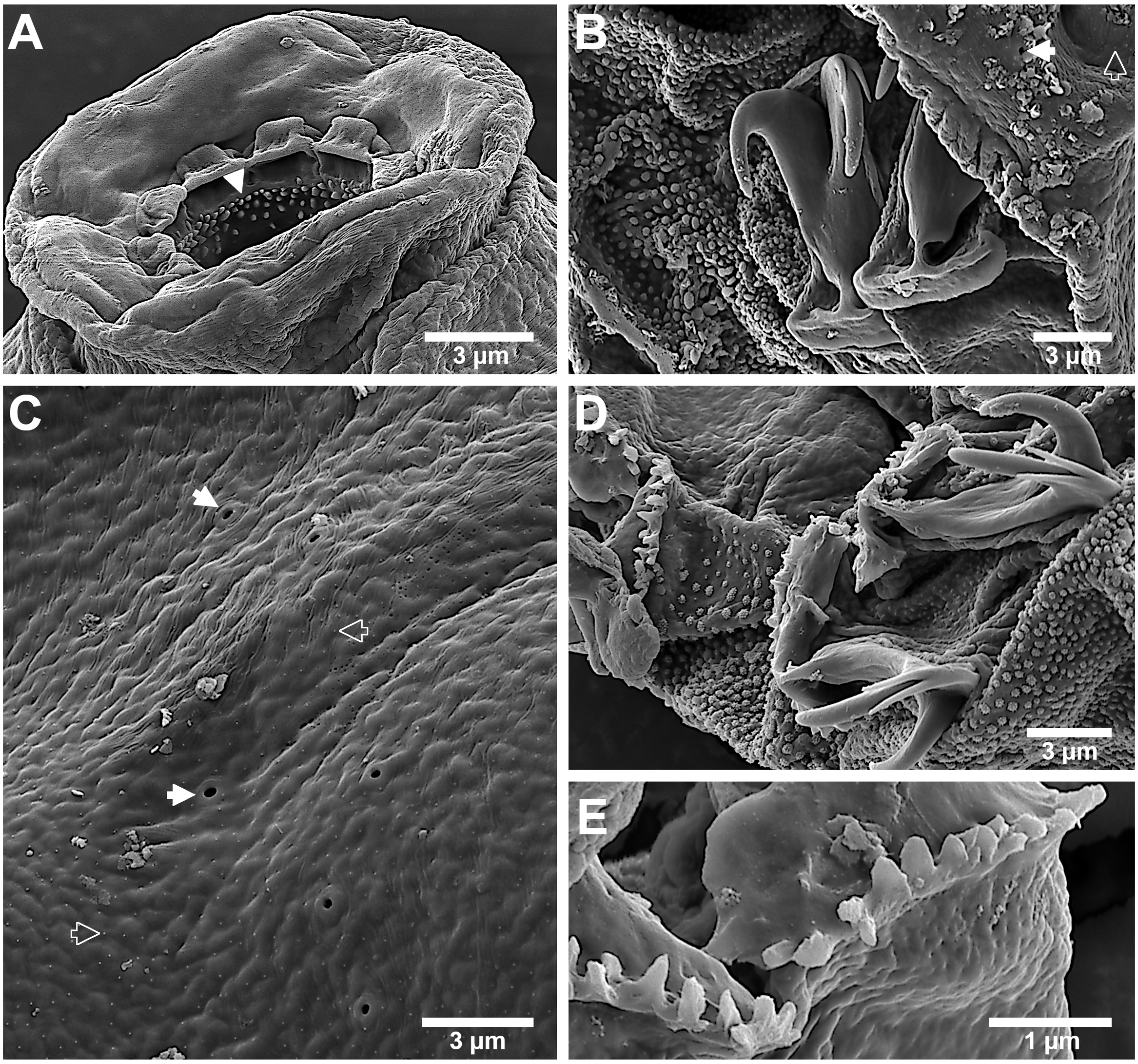

Fig. 6. *Macrobiotus vattenrikense* sp. nov., SEM photographs of paratype (SMNH, SMNH-Type-10016). **A**. Mouth opening. **B**. Claws of leg II. **C**. Details of the body cuticle. **D**. Leg IV. **E**. Serrated lunules of the claws of leg IV. White full arrows indicate pores in the body cuticle; empty full arrows indicate very fine granules on the body cuticle; white arrowhead indicates first row of OCA.

Table 1. Morphometric data for selected morphological characters of the new species, including the number of specimens measured (n), range of the absolute measurements (µm) and the range of the measurements relative to the buccal tube length (*pt*).

	***M. vattenrikenses* sp. nov.**			***P. marchelmoni* sp. nov.**		
	n	µm	*pt*	n	µm	*pt*
Body length	7	335–530	798–1233	16	238–710	528–1726
Bucco-pharyngeal apparatus						
-Buccal tube length	10	36.0–43.0	–	15	34.7–61.0	–
-Stylet support insertion	10	27.0–34.6	75.0–81.0	14	25.8–46.1	72.3–80.6
-Buccal tube external width	10	6.1–9.0	16.7–20.9	12	6.7–14.5	18.1–23.8
-Buccal tube internal width	10	4.1–5.3	10.1–13.9	12	3.6–11.4	9.6–18.8
-Ventral lamina length	8	22.0–26.1	58.1–61.1	13	22.5–38.0	53.2–75.2
Placoid lengths						
-Macroplacoid 1	10	8.4–10.6	21.4–27.8	13	5.3–11.5	13.0–20.0
-Macroplacoid 2	10	6.2–9.0	16.7–20.9	13	4.0–11.0	11.5–22.4
-Macroplacoid 3	–	–	–	13	7.5–17.9	18.3–29.4
-Microplacoid	9	3.1–5.0	8.6–11.6	14	2.5–5.0	6.7–10.0
-Macroplacoid row	10	14.3–22.0	37.1–52.8	13	19.5–46.0	52.1–75.7
-Placoid row	9	18.4–26.0	48.5–66.7	13	25.2–57.9	69.5–95.2
Claw I lengths						
-External primary	8	10.1–11.8	26.2–30.6	12	8.0–14.0	16.0–27.7
-External secondary	8	8.1–11.5	21.7–27.8	10	9.0–12.7	18.8–23.5
-Internal primary	7	9.0–11.9	24.9–30.6	11	10.0–13.6	18.9–27.5
-Internal secondary	6	7.0–10.0	19.4–27.8	9	8.0–12.5	17.3–23.1
Claw II/III lengths						
-External primary	8	9.7–12.0	23.3–33.3	12	11.0–15.0	21.4–32.6
-External secondary	7	7.7–11.0	18.6–30.6	12	9.0–14.0	18.0–27.5
-Internal primary	8	9.0–12.2	22.9–33.3	11	11.0–14.5	21.4–30.0
-Internal secondary	8	7.1–11.0	18.9–27.8	11	9.0–13.0	17.9–27.7
Claw IV lengths						
-Anterior primary	8	10.6–12.2	25.6–30.6	10	12.0–16.0	24.0–34.8
-Anterior secondary	6	7.3–9.4	18.4–21.9	10	10.0–13.0	20.0–28.3
-Posterior primary	10	9.9–12.2	23.8–33.3	11	12.0–16.0	23.2–32.6
-Posterior secondary	9	7.5–9.9	19.0–25.0	11	10.0–15.3	19.6–28.3

- COI haplotype 2: specimen 22-101; 658 bp;GenBank accession number PX093654;
- COI haplotype 3: specimens 22-003, 22-004-1; 658 bp; GenBank accession number PX093655;
- ITS2: specimens 22-003, 22-017, 22-101; 443 bp; GenBank accession number PX093644.

Morphological differential diagnosis

Macrobiotus vattenrikense sp. nov. has *hufelandi*-type OCA, serrated lunules on legs IV, and eggs with inverted goblet-shaped processes with terminal disks showing cogwheel-like indented margins and a deep central hollow, wrinkled chorions and very small pores surrounding the processes. Based on these characteristics, *M. vattenrikense* is most similar to five other species of *Macrobiotus* (note, the pores on

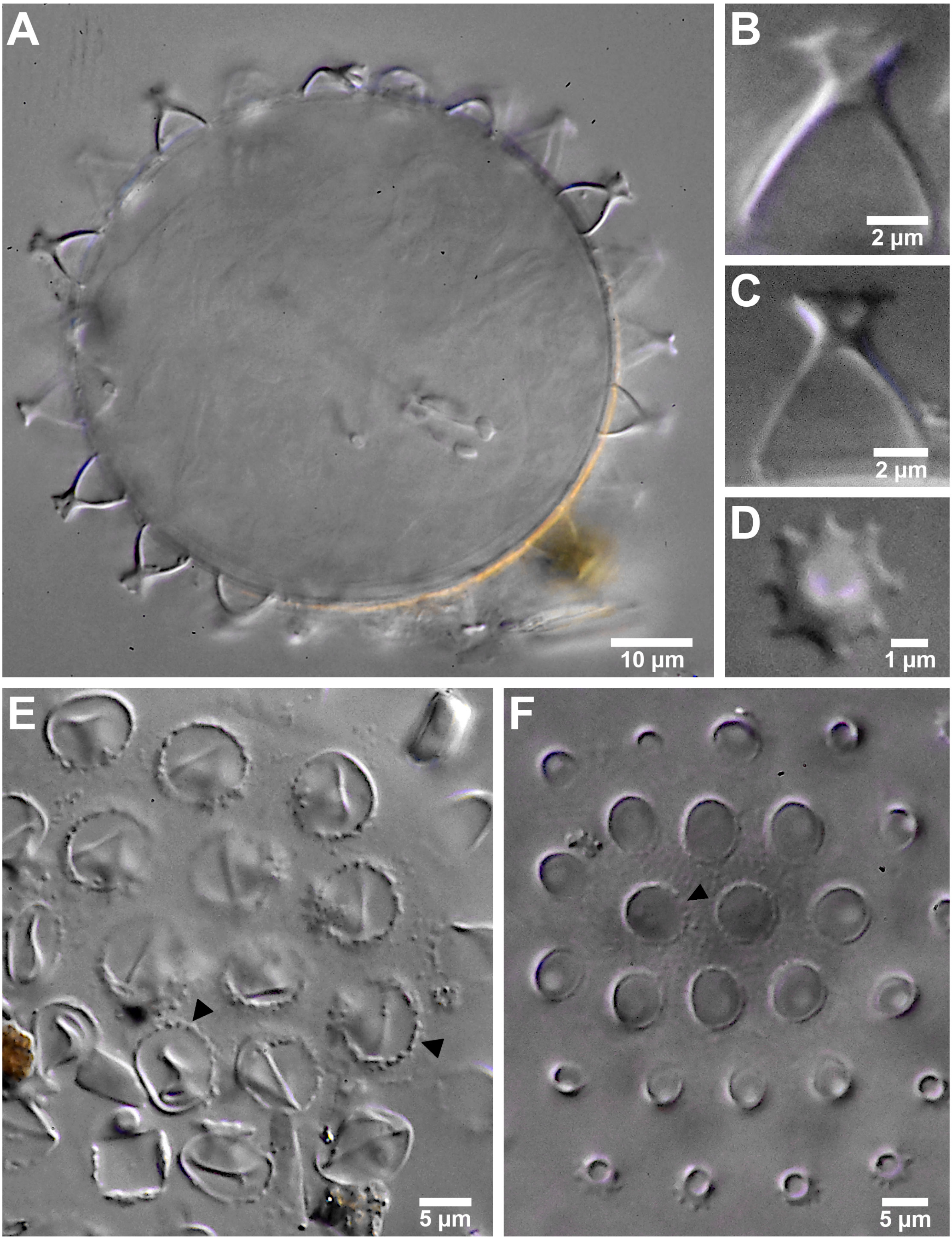

Fig. 7. *Macrobiotus vattenrikense* sp. nov., DIC photographs of egg in water (SMNH, 22-040) **A**. Whole egg. **B**–**C**. Examples of egg processes. **D**. Terminal disk of egg process. **E**–**F**. Base of processes and egg chorion. Black arrowheads indicate the crown of thickenings at the base of each process.

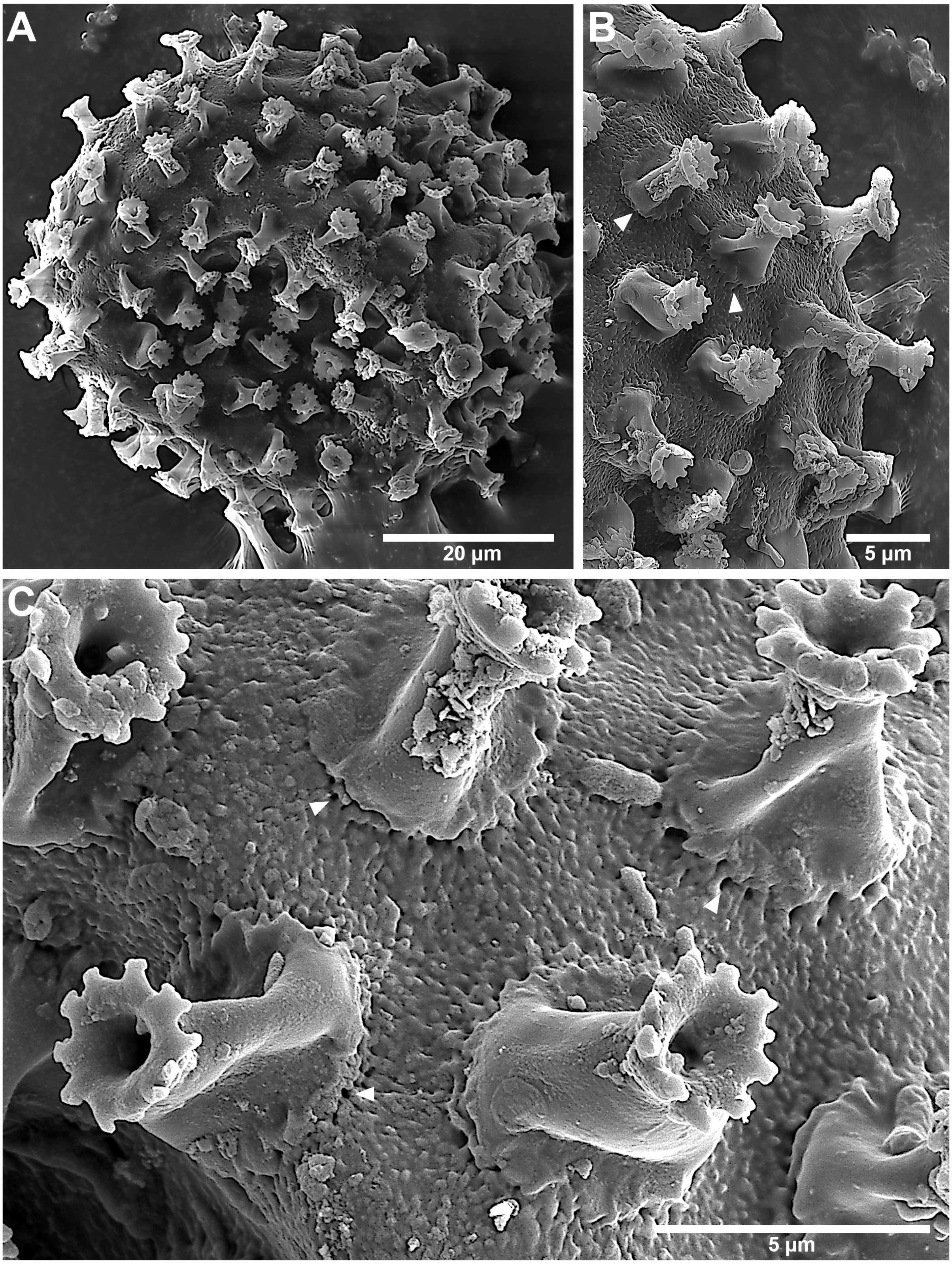

Fig. 8. *Macrobiotus vattenrikense* sp. nov., SEM photographs of egg (SMNH, SMNH-Type-10016). **A**. Whole egg. **B–C**. Egg processes and chorion. White arrowheads indicate examples of the very small pores that surround the base of each process.

Table 2. Morphometric data for the eggs of the new species, including the number of measurements for each character, the range of the measurements, the mean and standard deviation.

	M. vattenrikense sp. nov.			*P. marchelmoni* sp. nov.		
	n	Range (µm)	Mean ± SD (µm)	n	Range (µm)	Mean ± SD (µm)
Egg bare diameter	6	62.3–78.2	74.0 ± 6.2	13	67.0–92.4	77.2 ± 7.5
Egg full diameter	6	74.0–90.5	86.4 ± 6.4	13	92.5–115.0	102.2 ± 8.6
Process height	18	6.0–7.3	6.7 ± 0.4	40	10.0–16.5	13.0 ± 1.6
Process base width	18	6.0–7.2	6.8 ± 0.4	39	21.3–30.0	24.1 ± 2.4
Process width/height	18	0.86–1.17	1.01 ± 0.10	39	1.44–2.25	1.86 ± 0.23
Terminal disk width	18	3.2–4.8	4.0 ± 0.5	–	–	–
Interprocess distance	18	2.9–4.2	3.5 ± 0.4	30	4.0–10.0	5.8 ± 1.1
Processes on circumference	6	23–25	24.2 ± 1.0	14	10–12	11.1 ± 0.9

the egg may be easily overlooked with light microscopy/clearly visible only with SEM, and so species with similar egg morphologies that have not been observed with SEM are included):

Macrobiotus halophilus Fontoura, Rubal & Veiga, 2017 – the animals of *M. vattenrikense* sp. nov. differ from animals of *M. halophilus* in the wider buccal tube (external width *pt* 16.7–20.9 compared with *pt* 13.2–16.5 in *M. halophilus*); the lack of a deep constriction in the first macroplacoid; the paired ventromedial teeth and single fused dorsal tooth in the third band of the OCA (compared with an undivided ventromedial tooth and three distinct dorsal teeth in *M. halophilus*); the shorter claws (posterior claw IV *pt* 23.8–33.3 compared to 33.4–42.0 in *M. halophilus*); and the lack of male gibbosities. The eggs of *M. vattenrikense* are differentiated by the larger processes (height 6.0–7.3 µm compared to 3.9–5.9 µm in *M. halophilus*). In addition, the very small pores that are present surrounding the egg processes of *M. vattenrikense* have not been documented for *M. halophilus*, although eggs of the latter species have not been observed with SEM.

Macrobiotus marlenae Kaczmarek & Michalczyk, 2004 – the animals of *M. vattenrikense* sp. nov. differ from the animals of *M. marlenae* by the granulation present on all legs (compared to granulation only on legs IV in *M. marlenae*); the shallower constriction of the first macroplacoid; the subterminal constriction in the second macroplacoid; and the claws with larger lunules in *M. vattenrikense* The eggs of *M. vattenrikense* have more numerous (23–25 on the circumference compared to 16 in *M. marlenae*) processes that are shorter (6.0–7.3 µm compared to 8.4–8.8 µm in *M. marlenae*), more closely spaced (inter-process distance 2.9–4.2 µm compared with 4.5–6.5 µm in *M. marlenae*), and with much smaller terminal disks (diameter 3.2–4.8 µm compared to 9.5–11.4 µm in *M. marlenae*). In addition, the very small pores that are present surrounding the egg processes of *M. vattenrikense* have not been documented for *M. marlenae*, although eggs of the latter species have not been observed with SEM.

Macrobiotus ovovittatus Stec, 2024 – the animals of *M. vattenrikense* sp. nov. are smaller than animals of *M. ovovittatus* (335–530 µm compared to 570–879 µm in *M. ovovittatus*) and have a shorter first macroplacoids (*pt* 21.4–27.8 compared to *pt* 28.4–34.4 in *M. ovovittatus*) with shallower median incision. The new species is further distinguished by the paired ventromedial teeth and single fused dorsal tooth in the third band of OCA (compared with an undivided ventromedial tooth and three distinct dorsal teeth in *M. ovovittatus*), and the lack of cuticular bars below the claws of the first three pairs of legs (bars present in *M. ovovittatus*). The eggs of *M. vattenrikense* are smaller than those of *M. ovovittatus* (diameter without the processes 62.3–78.2 µm compared to 100.6–129.8 µm in *M. ovovittatus*) with fewer processes on the circumference (23–25 compared to 28–34 in *M. ovovittatus*), and smaller processes (height 6.0–7.3 µm compared to 9.5–13.5 µm in *M. ovovittatus*; diameter at the base 6.0–7.2 µm compared to 9.4–13.6 µm in *M. ovovittatus*) with smaller (diameter 3.2–4.8 µm compared to 6.1–8.7 µm in *M. ovovittatus*), solid terminal disks (covered by multiple light-refracting dots in *M. ovovittatus*).

Macrobiotus persimilis Binda & Pilato, 1972 (following the redescription of Bertolani *et al.* 2023) – the animals of *M. vattenrikense* sp. nov. differ from animals of *M. persimilis* in the lack of a deep constriction in the first macroplacoid; the shorter macroplacoids (first/second macroplacoid *pt* 21.4–27.8/16.7–20.9 compared to *pt* 32.0–33.8/22.8–24.2 in *M. persimilis*) and macroplacoid row (*pt* 37.1–52.8 compared to *pt* 54.7–57.2 in *M. persimilis*); the longer microplacoids (*pt* 8.6–11.6 compared to *pt* 7.7–8.0 in *M. persimilis*); the paired ventromedial teeth and single fused dorsal tooth in the third band of the OCA (compared with an undivided ventromedial tooth and three distinct dorsal teeth in *M. persimilis*); and the shorter claws (external claw III/IV *pt* 23.3–33.3/25.6–30.6 compared to 35.9–38.3/35.9–37.9 in *M. persimilis*). The eggs of *M. vattenrikense* are differentiated by the larger processes (height 6.0–7.3 µm compared to 3.7–5.3 µm in *M. persimilis*; diameter at the base 6.0–7.2 µm compared to 3.6–5.1 µm in *M. persimilis*). In addition, the very small pores that are present surrounding the egg processes of *M. vattenrikense* have not been documented for *M. persimilis*, although eggs of the latter species have not been observed with SEM.

Macrobiotus polonicus Pilato, Kaczmarek, Michalczyk & Lisi, 2003 – the animals of *M. vattenrikense* sp. nov. differ from the animals of *M. polonicus* by the presence of granulation lateral to the claws on legs I–III (absent in *M. polonicus*); the absence of lateral gibbosites on the hind legs (present in *M. polonicus*); the absence of sclerotized areas near the lunulae of legs I–III (present in *M. polonicus*). The eggs of *M. vattenrikense* differ by the smaller diameter of the process terminal disks (3.2–4.8 µm compared with 4.9–6.3 µm in *M. polonicus*) and by the minute pores surrounding each process (lack of egg pores for *M. polonicus* confirmed with SEM).

Macrobiotus trunovae Biserov, Pilato & Lisi, 2011 – the animals of *M. vattenrikense* sp. nov. differ from animals of *M. trunovae* by the paired ventromedial teeth and single fused dorsal tooth in the third band of the OCA (compared with an undivided ventromedial tooth and three distinct dorsal teeth in *M. trunovae*); the more anteriorly inserted stylet supports (*pt* 75.0–81.0 compared to 81.7–82.4 in *M. trunovae*); the smaller first macroplacoid (*pt* 21.4–27.8 compared to 28.3–31.4 in *M. trunovae*) with a much narrower constriction; and the similar sizes of the claws on all legs (compared to distinctly smaller claws on legs I–III than on legs IV in *M. trunovae*). The eggs of *M. vattenrikense* are smaller (diameter without processes 62.3–78.2 µm compared to 134.3 µm in *M. trunovae*) with fewer (23–25 on the egg circumference compared to 32 in *M. trunovae*) and smaller (length 6.0–7.3 µm compared to up to 10.9 µm in *M. trunovae*; diameter at the base 6.0–7.2 µm compared to 9.1–9.9 µm in *M. trunovae*) processes. In addition, the very small pores that are present surrounding the egg processes of *M. vattenrikense* have not been documented for *M. trunovae*, although eggs of the latter species have not been observed with SEM.

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

Paramacrobiotus marchelmoni sp. nov.
urn:lsid:zoobank.org:act:C91427F4-F50C-4A1F-A475-825777258AE5
Figs 9–11

Diagnosis

Paramacrobiotus without eyespots. Cuticle with fine dorsal granulation visible only in SEM, and medium-coarse granulation surrounding the claws of the legs I–IV visible with DIC and SEM. OCA with three bands of teeth: first composed of numerous small granules, second of a single row of vertical ridges, and third of three ventral and three dorsal transverse crests. Three rod-like macroplacoids and a distant microplacoid present. Claws of *hufelandi*-type with smooth lunulae. Freely laid eggs with sculptured areolae of *richtersi*-type; 10–12 reticulated processes around the circumference, conical with a mostly smooth apex.

Etymology

The species is proudly in dedication to Marc "Marchelmon" Hulterström, brother of the first author.

Material examined

A total of 38 animals and 24 eggs observed, including: 16 animals and 15 eggs mounted in Hoyer's fluid, 10 animals and 5 eggs fixed for SEM, and 11 animals and 4 eggs used for DNA analysis.

Type material

Holotype

SWEDEN • Skåne, Sånnarna; 55°55′41.6″ N, 14°15′11.1″ E; 8 m a.s.l.; 22 Mar. 2021; S. Atherton, R. Guidetti and K.I. Jönsson leg.; moss on calcareous-rich sand and rock; SMNH, slide SMNH-Type-10017.

Paratypes

SWEDEN · 23 specs, 15 eggs; same collection data as for holotype; SMNH, slides SMNH-Type-10018 to SMNH-Type-10029, SEM stub SMNH-Type-10030 • 3 specs, 5 eggs; same collection data as for holotype; GenBank nos: PX093656 to PX093658 (COI), PX093645, PX093646 (ITS), PX093665 (18S), PX093651 (28S); MUSN, slides 22-030, 22-037 and 22-103.

Description

Morphometric measurements and statistics given in Tables 1 and 2 (raw morphometric data is given in Supp. file 11).

Paramacrobiotus with body length 238–710 µm (Fig. 9A). Eyespots absent. Cuticle transparent in live animals and after fixation in Hoyer's fluid. Dorsal body cuticle with even and very fine granulation, visible only with SEM (Fig. 10A–B). A patch of larger granulation lateral to the claws on legs I–III and coarse granulation fully surrounding the claws on legs IV visible with DIC and SEM (Figs 9F, 10B–D). Cuticular pores, gibbosities, and papillae absent.

Mouth antero-ventral; ten peribuccal lamellae present. Buccal apparatus with a rigid tube of *Macrobiotus*-type (Pilato & Binda 2010) with ventral lamina. OCA comprising three bands of teeth (Fig. 9C–D). First band a field of small granular teeth situated closely behind the peribuccal lamellae. Second band one row of vertical ridges, uniform in shape on both ventral and dorsal side. Third band situated close to the second, with three ventral and three dorsal teeth, with the lateral teeth wider (larger along the left/right axis) and shorter (smaller along the anterior/posterior axis) than the median tooth for each side. Ventral teeth thinner (smaller along the left/right axis) than dorsal teeth (Fig. 9C). Latero-dorsal teeth triangular, narrowing away from the median tooth (Fig. 9D). No additional granular teeth observed between the second and third band of OCA. Globular pharyngeal bulb with triangular pharyngeal apophyses, three rod-shaped macroplacoids with length sequence $2<1<3$, and a microplacoid (Fig. 9B). First macroplacoid drop-like. Second macroplacoid oval. Third macroplacoid with a subterminal constriction, ending in posterior bulbs. Microplacoid heart-shaped, with antero-lateral wings, and situated distant from the third macroplacoid, further than its length.

Double-claws of *hufelandi*-type (Bertolani & Pilato 1988). Main claw branches with evident accessory points. Smooth lunulae on all claws (Figs 9E, 10B–D). Paired muscle attachments below claw present. Cuticular bars absent.

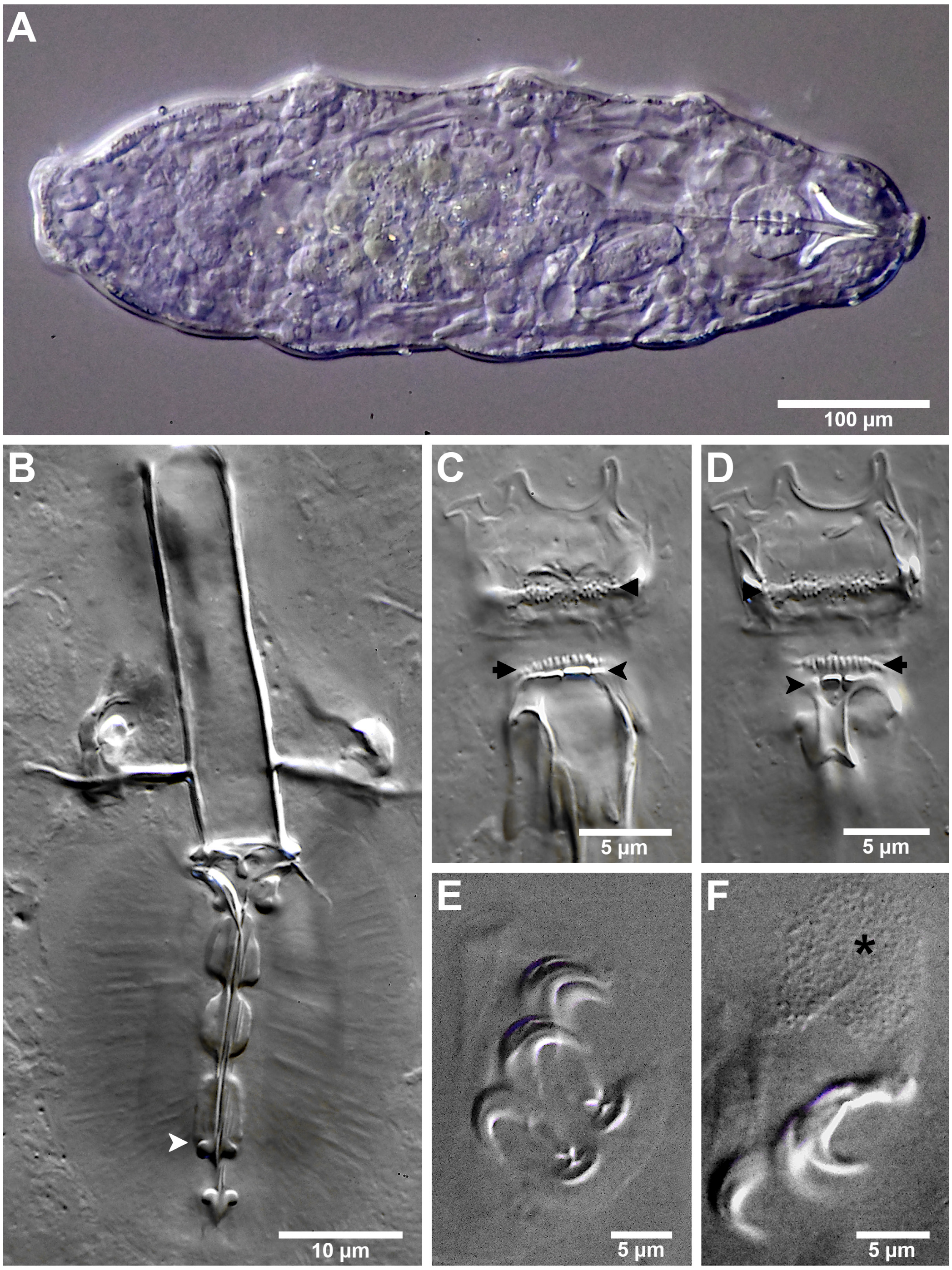

Fig. 9. *Paramacrobiotus marchelmoni* sp. nov. **A**. DIC photograph of paratype in water (SMNH, SMNH-Type-10018); whole body. **B**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10017); pharynx and placoids. **C**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10017); dorsal OCA. **D**. DIC photograph of holotype in Hoyer's fluid (SMNH, SMNH-Type-10017); ventral OCA. **E**. DIC photograph of paratype in Hoyer's fluid (MUSN, 22-103); claws of leg I. **F**. DIC photograph of paratype in water (SMNH, SMNH-Type-10019); claws of leg IV. White indented arrowhead indicates constriction of the third macroplacoid; black arrowhead indicates first row of OCA; black full arrows indicate second row of OCA; black indented arrowheads indicate third row of OCA; asterisk indicates leg granulation.

Gonochoristic. Males with sperm filled testis observed, as well as females with eggs.

Ornamented eggs laid freely, *richtersi*-type (Kaczmarek *et al.* 2017; Fig. 11A–B), diameter without processes 67.0–92.4 µm. Processes conical, short (10–16.5 µm) and wide (21.3–30.0 µm), with a smooth rounded apex (Fig. 11A–E). 10–12 processes on the circumference (Fig. 11B). Processes smooth in SEM (Fig. 11A) but labyrinthine layer visible in DIC as a reticular pattern of small, evenly distributed meshes (Fig. 11C). Processes surrounded by a single ring of 12 areolae (Fig. 11A, G). Areolae with sculpturing comprising dot-like indentations, faintly visible fixed in Hoyer's with DIC and clearly visible with SEM (Fig. 11F).

DNA sequences

Sequences for *P. marchelmoni* sp. nov. were attained for all four molecular markers using 11 animals and four eggs. 18S and 28S were represented by one haplotype; ITS2 was represented by two haplotypes (uncorrected p-distances between haplotypes 0.81%), and COI was represented by three haplotypes (uncorrected p-distances between haplotypes 0.16–0.31%):

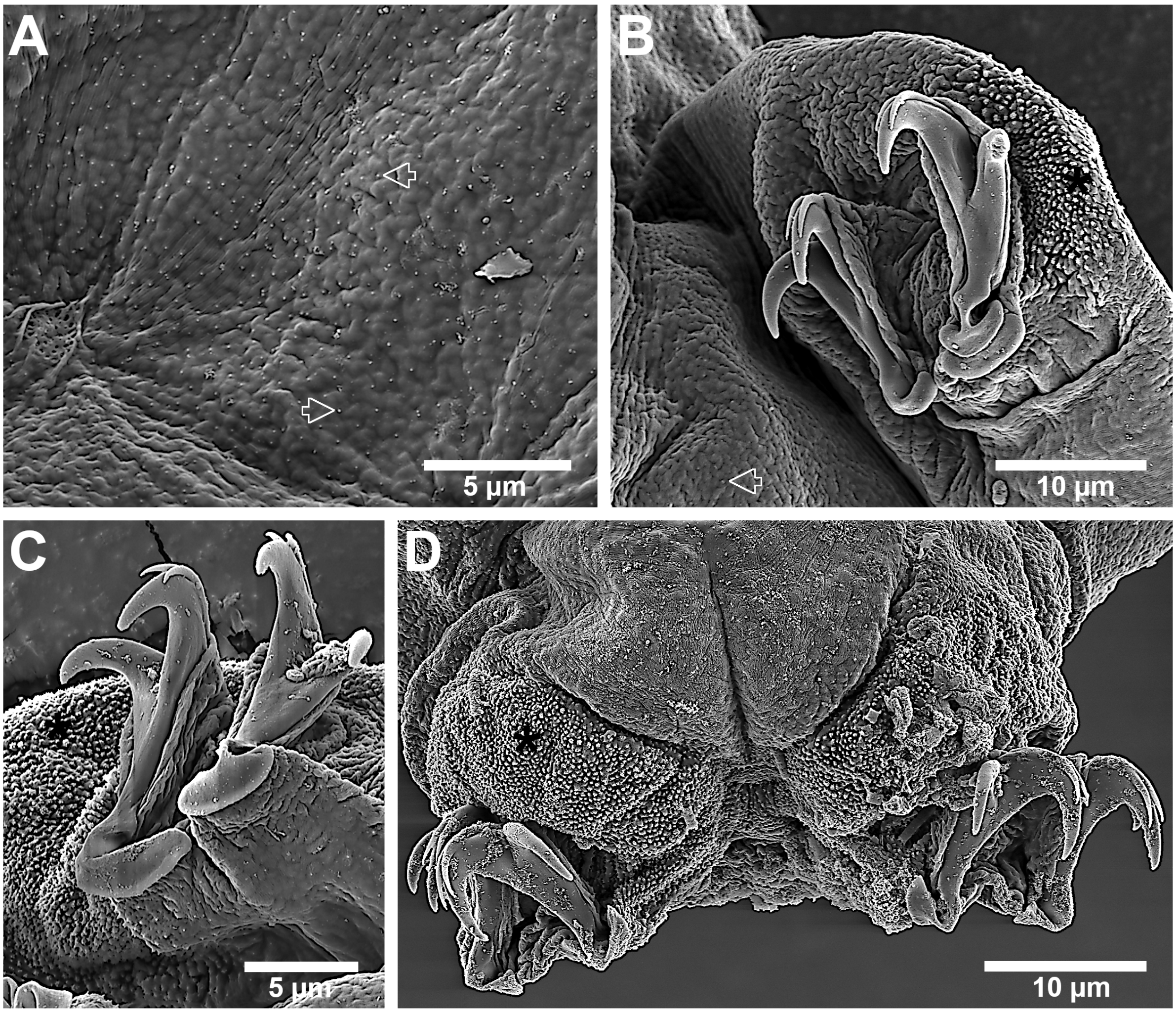

Fig. 10. *Paramacrobiotus marchelmoni* sp. nov., SEM photographs of paratype (SMNH, SMNH-Type-10030). **A**. Details of the body cuticle. **B**. Leg I. **C**. Claws of leg III. **D**. Legs IV. Empty full arrows indicate very fine granules on body cuticle; asterisks indicate leg granulation.

– 18S: specimens 22-004, 22-006, 22-007, 22-019, 22-034, 22-110, 22-113; 1302 bp, GenBank accession number PX093665;
– 28S: specimens 22-004, 22-019, 22-029, 22-110, 23-015; 921 bp, GenBank accession number PX093651;

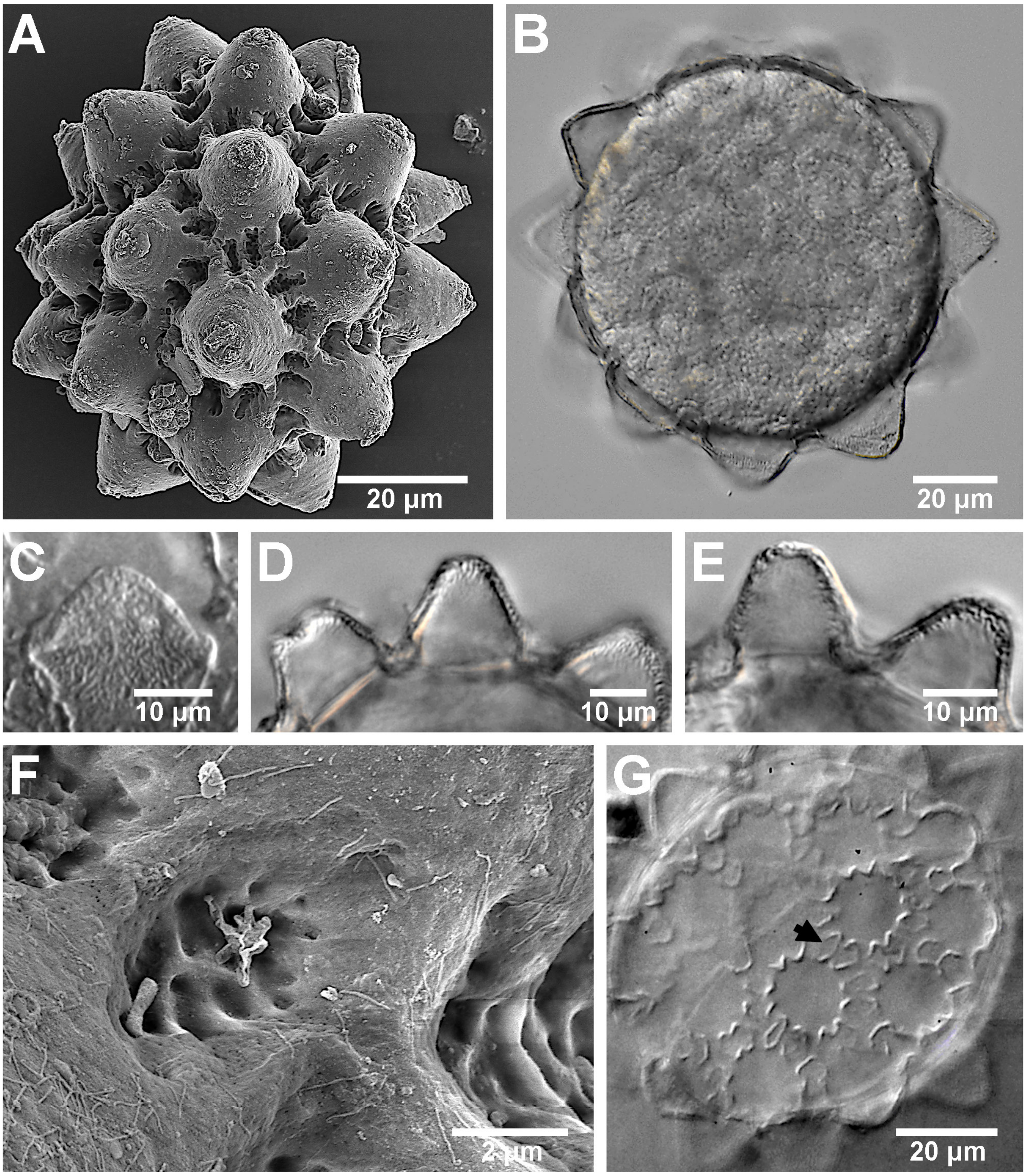

Fig. 11. *Paramacrobiotus marchelmoni* sp. nov. eggs. **A**. SEM photograph (SMNH, SMNH-Type-10030); whole egg. **B**. DIC photograph in water (SMNH, SMNH-Type-10024); whole egg. **C–E**. DIC photographs in water (SMNH, SMNH-Type-10024); examples of egg processes. **F**. SEM photograph (SMNH, SMNH-Type-10030); details of the areolae. **G**. DIC photograph in water (SMNH, SMNH-Type-10028); base of the egg processes. Black full arrow indicates areolae surrounding each egg process.

- COI haplotype 1: specimens 22-004, 22-006, 22-007, 22-019, 22-026, 22-029, 22-034, 22-102, 22-108; 636 bp, GenBank accession number PX093656;
- COI haplotype 2: specimens 22-106, 22-110, 22-113, 23-041; 636 bp, GenBank accession number PX093657;
- COI haplotype 3: specimen 23-015, 636 bp, GenBank accession number PX093658;
- ITS2 haplotype 1: specimens 22-029, 22-102; 370 bp; GenBank accession number PX093645;
- ITS2 haplotype 2: specimens 22-004, 22-006, 22-007, 22-019, 22-034, 22-110, 22-113; 370 bp, GenBank accession number PX093646.

Morphological differential diagnosis

Based on the presence of a microplacoid, *P. marchelmoni* sp. nov. is a member of the *richtersi* morphogroup (Kaczmarek *et al.* 2017). Species of this morphogroup may be difficult or sometimes impossible to distinguish morphologically, with distinguishing features frequently limited to a few differences in egg shell morphologies or reproductive biology (Guidetti *et al.* 2019a). Indeed, *P. marchelmoni* is very similar to ten species of this group by the following criteria: *richtersi*-type of egg, with areolae with sculpturing (Kaczmarek *et al.* 2017), and egg processes with a blunt apex without a cap-like structure. However, *P. marchelmoni* can be differentiated from each by the following:

Paramacrobiotus arduus Guidetti, Cesari, Bertolani, Altiero & Rebecchi, 2019 – the animals of *P. marchelmoni* sp. nov. lack cuticular bars below the claws of the first three pairs of legs. The eggs of the new species are larger (diameter without processes 67.0–92.4 µm compared to 55.3–62.3 µm in *P. arduus*), with processes that are surrounded by more areolae (12 compared with 5 "double" areolae in *P. arduus*) and that are much wider at the base (diameter 21.3–30.0 µm compared to 10.4–16.3 µm in *P. arduus*) with a more rounded and less narrow apex than those of *P. arduus.*

Paramacrobiotus celsus Guidetti, Cesari, Bertolani, Altiero & Rebecchi, 2019 – the animals of *P. marchelmoni* sp. nov. lack cuticular bars below the claws of the first three pairs of legs, and the microplacoid has a different shape (heart-shaped with antero-lateral wings compared to drop-shaped in *P. celsus*). Additionally, the eggs of *P. marchelmoni* have processes with wider bases (diameter 21.3–30.0 µm compared to 14.3–18.2 µm in *P. celsus*).

Paramacrobiotus depressus Guidetti, Cesari, Bertolani, Altiero & Rebecchi, 2019 – the animals of *P. marchelmoni* sp. nov. have much more evident granulation on all legs compared with *P. depressus* and lack cuticular bars below the claws of the first three pairs of legs. The microplacoid has a different shape (heart-shaped with antero-lateral wings compared to comma-shaped in *P. depressus*). The eggs are larger in *P. marchelmoni* (diameter without processes 67.0–92.4 µm compared to 56.2–66.2 µm in *P. depressus*) with much wider (21.3–30.0 µm compared to 12.4–15.2 µm in *P. depressus*) egg processes.

Paramacrobiotus fairbanksi (following the redescription of Guidetti *et al.* 2019a) – animals of *P. marchelmoni* sp. nov. differ from animals of *P. fairbanksi* in the heart-shaped microplacoid (compared to a comma-shape microplacoid in *P. fairbanksi*), and the new species is gonochoristic (males are presumed absent for *P. fairbanski*). The eggs of *P. marchelmoni* have more areolae surrounding each process (12 compared with 5–6 "double" areolae in *P. fairbanksi*) and processes with wider bases (21.3–30.0 µm compared to 10.9–20.8 µm in *P. fairbanksi*) and smoother, more rounded apexes.

Paramacrobiotus gerlachae (Pilato, Binda & Lisi, 2004) – the animals of *P. marchelmoni* sp. nov. differ from the animals of *P. gerlachae* by the absence of cuticular bars near the lunules of legs I–III (present in *P. gerlachae*); by the cuticular granulation on legs I–III (absent in *P. gerlachae*); and by the more distinct granulation on leg IV (granulation very faint in *P. gerlachae*). The egg processes are wider in *P. marchelmoni* (base diameters 21.3–30 µm compared with 16.8–18.7 µm in *P. gerlachae*).

Paramacrobiotus halei (Bartels, Pilato, Lisi & Nelson, 2009) – animals of *P. marchelmoni* sp. nov. differ from animals of *P. halei* by the absence of the cuticular tubercles (present in *P. halei*); the narrower buccal tube (*pt* 18.1–23.8 compared with *pt* 26.5–28.6 in *P. halei*); and the longer internal claw II (*pt* 21.4–30.0 compared with *pt* 20.4–21.1 in *P. halei*). The eggs of *P. marchelmoni* are smaller (full diameter 92.5–115.0 µm compared with 117.0–121.0 µm in *P. halei*) with processes with smoother, more rounded apexes.

Paramacrobiotus pius Lisi, Binda & Pilato, 2016 – animals of *P. marchelmoni* sp. nov. differ from animals of *P. pius* in the lack of cuticular bars below the claws on the first three pair of legs (present in *P. pius*), the longer third macroplacoid (*pt* 18.3–29.4 compared to 14.2–14.6 in *P. pius*) and the longer macroplacoid/placoid rows (*pt* 52.1–75.7/69.5–95.2 compared to *pt* 41.4–43.1/53.0–56.2 in *P. pius*). The eggs of *P. marchelmoni* have processes with smooth apices (compared to apices with short spines in *P. pius*) and are surrounded by more numerous areolae (12 compared to 5 "double" areolae in *P. pius*).

Paramacrobiotus richtersi (Murray, 1911) (following the redescription of Guidetti *et al.* 2019a) – the animals of *P. marchelmoni* sp. nov. differ from the animals of *P. richtersi* in the undivided medioventral crest in the third band of the OCA and the lack of cuticular bars below the claws of the first three pairs of legs (bars present in *P. richtersi*). The eggs of *P. marchelmoni* differ in the processes, which are shorter (10.0–16.5 µm compared to 17.1–22.1 µm in *P. richtersi*) and wider (diameter 21.3–30.0 µm compared to 17.1–21.2 µm in *P. richtersi*) and thus have a stouter appearance than those of *P. richtersi*.

Paramacrobiotus sklodowskae (Michalczyk, Kaczmarek & Węglarska, 2006) – the animals of *P. marchelmoni* sp. nov. differ from the animals of *P. sklodowskae* by the absence of eyespots (present in *P. sklodowskae*); by the more anteriorly inserted stylet support (*pt* 72.3–80.6 compared with *pt* 81.8–85.2 in *P. sklodowskae*); and by the larger third macroplacoid (*pt* 18.3–29.4 compared to *pt* 16.7–18.0 in *P. sklodowskae*). The eggs are differentiated by the process surfaces, which are always smooth in *P. marchelmoni* (ring folds present in *P. sklodowskae*).

Paramacrobiotus spatialis Guidetti, Cesari, Bertolani, Altiero & Rebecchi, 2019 – the animals of *P. marchelmoni* sp. nov. possess an undivided medioventral crest in the third band of the OCA (subdivided into three round teeth in *P. spatialis*). The eggs of *P. marchelmoni* have wider processes (21.3–30.0 µm compared to 15.2–20.4 µm in *P. spatialis*) with smooth apices (compared to apices with tubercles as in *P. spatialis*).

Discussion

Macrobiotus

Macrobiotus vattenrikense sp. nov. was recovered as sister to *M. mileri*, and together formed a clade (= *Macrobiotus* "clade B") with *M. annewintersae* Vecchi & Stec, 2021, *M. engbergi* Stec, Tumanov & Kristensen, 2020, *M. caelestis* Coughlan, Michalczyk & Stec, 2019, 5 species of the *persimilis-polonicus* complex (Bertolani *et al.* 2023), 4 species of the *pallarii* complex (Stec *et al.* 2021b) and species of *Xerobiotus*. *Macrobiotus vattenrikense* and *M. mileri* share similar morphologies of the egg chorion: very small pores surrounding the egg processes are visible with SEM, but the egg chorion may appear solid under light microscopy. Very small pores ("micropores"; Coughlan *et al.* 2019) were also described occasionally (although not always) occurring between the processes on the egg chorion of *M. caelestis*. All other species of the clade lack all pores, including pores visible only with SEM, while species with pores that are clearly visible with both light microscopy and SEM are recovered only in *Macrobiotus* "clade A". Further, disk morphology is quite variable within the clade, with elongated arms in *M. annewintersae*, wide and flat disks in *M. caelestis*, reduced disks in *M. mileri*, serrated/indented disks in *M. engbergi* and indented disks in *M. vattenrikense* and the other species of the *persimilis-polonicus* complex.

Seven species of *Macrobiotus* have now been reported from Sweden: *M. echinogenitus* Richters, 1903; *M. hufelandi* C.A.S. Schultze, 1834, although the records of this species before its redescription by Bertolani & Rebecchi (1993) have to be confirmed; *M. macrocalix* Bertolani & Rebecchi, 1993; *M. persimilis* Binda & Pilato, 1972; *M. polonicus* Pilato, Kaczmarek, Michalczyk & Lisi, 2003; *M. trunovae* Biserov, Pilato & Lisi, 2011; and *M. vattenrikense* sp. nov. (Richters 1904; Carlzon 1909; Thulin 1911; Durante Pasa & Maucci 1979; Sohlenius *et al.* 1997; Jönsson 2003, 2007; Massa *et al.* 2021; Guidetti *et al.* 2025). Two additional species designated nomen inquirendum (Stec *et al.* 2021a), *M. brevipes* Mihelčič, 1971 and *M. longipes* Mihelčič, 1971, and five with partial or uncertain identifications: *M.* aff. *nelsonae, M*. aff. *polonicus, M.* aff. *wandae*, *M*. cf. *polonicus*, and *M.* cf. *terminalis*, have also been documented for the country (Mihelčič 1971; Jönsson 2007; Massa *et al.* 2021; Vecchi & Stec 2021).

Paramacrobiotus

Paramacrobiotus marchelmoni sp. nov. was described and *P. fairbanksi* reported from Sweden for the first time. Although the distribution of *P. marchelmoni* is confirmed only by molecular data, it is of interest that while most species of *Paramacrobiotus* have restricted geographical ranges, with many endemic to only a single type location (Guidetti *et al.* 2019a; Kayastha *et al.* 2023c; Gąsiorek 2024), both species reported here have larger distributions with relatively low intraspecific haplotype diversity even between distant populations (e.g., up to 0.8% for *P. marchelmoni* and 0.7% for *P. fairbanksi* for COI; Supp. file 2: sheet 5). Populations of *P. marchelmoni* occur in Sweden, Spain ("Tar407", originally misidentified as *Macrobiotus pallarii*; Stec *et al.* 2021b) and Hungary (*Paramacrobiotus* sp. "HU.012"; Stec *et al.* 2020c), while the presence of *P. fairbanksi* has been confirmed in Antarctica (Kaczmarek *et al.* 2020b), Denmark (Gąsiorek *et al.* 2024), Finland (Vecchi *et al.* 2024b), Italy (Guidetti *et al.* 2019a), Poland (Stec *et al.* 2020c), Spain (Guil & Giribet 2012; Guidetti *et al.* 2019a), USA (Alaska; Schill *et al.* 2010) and now Sweden.

Reproductive mode has been hypothesized to be one important indicator of biogeographic range for tardigrades (Guidetti *et al.* 2016, 2019a; Gąsiorek 2024). Asexually reproducing species are generally predicted to have wider distributions than sexual species since they are better able to colonize new areas easily without being subjected to bottleneck effects or outbreeding depression (Artois *et al.* 2012; Tilquin & Kokko 2016). Following this reasoning, it is not so surprising that asexually reproducing species such as *P. fairbanksi* and *P. gadabouti* are known from multiple zoogeographic realms (Guidetti *et al.* 2019a; Stec *et al.* 2020c; Kayastha *et al.* 2023b; this study) while other bisexual species of the genus are locally restricted (Guidetti *et al.* 2019a; Gąsiorek 2024). Nevertheless, *P. marchelmoni* sp. nov. is bisexual and has a range that extends at least across Europe. Similar examples exist for other tardigrades, e.g., in *Macrobiotus* with the bisexual species *Macrobiotus vladimiri* Bertolani, Biserov, Rebecchi & Cesari, 2011 and *M. macrocalix* being found within a broad range of localities within Europe (Cesari *et al.* 2009; Stec *et al.* 2021a). In addition to reproductive mode, anhydrobiotic ability has also been theorized to have a significant impact on distribution range as being able to stay anhydrobiotic longer with a high survival rate will increase the potential to disperse over a larger area (Gasiorek 2024).

Stec *et al.* (2020c) hypothesized that the wide distribution patterns of *P. fairbanksi* as well as other tardigrade species known from more than one zoogeographic realm were due to human-mediated dispersion, since their records come from highly populated and touristic locations. Though it is extremely difficult to quantify exactly how the dispersal of *P. fairbanksi* or any species of tardigrade is influenced by anthropogenic factors, neither the KVBR nor especially Antarctica would likely qualify as highly populated (in 2023, the density of Kristianstad Municipality, for instance, was 69 persons/km^2 [Statistiska Centralbyrån, Sweden] compared to, e.g., 387 persons/km^2 in Fairbanks, Alaska [United States Census Bureau, USA]). The explanation for the current correlation between populated, touristy areas and records of *P. fairbanksi* is perhaps better attributed to geographical sampling bias. It is a well-documented phenomenon that more easily accessible areas have higher amounts of known biodiversity (e.g., Fontaneto *et al.* 2012; Barbosa *et al.* 2013; Yang *et al.* 2014; Hortal *et al.* 2015; Meyer *et al.* 2015; Garraffoni *et al.* 2021) since collectors are far more likely to stay within relatively short distances of inhabited areas and research facilities. Especially for smaller-sized organisms (Hortal *et al.* 2015), the numbers and nationalities of taxonomists and the locations of the research stations where they have historically worked are far more significant predictors of a species' known spatial distribution than actual environmental or biological drivers (Fontaneto *et al.* 2012). Following this effect, the current observed distribution pattern of *P. fairbanksi* likely reflects the distribution of the researchers more than the real distribution of the species itself, and additional sampling efforts, especially in more distant or difficult to access areas, will be necessary to understand the true geographical range of the species.

In total, six species of *Paramacrobiotus* have now been reported from Sweden: *P. richtersi* (Mihelčič 1971; Durante Pasa & Maucci 1979; Guidetti *et al.* 2025), *P. areolatus* (Murray, 1907) (Guidetti *et al.* 2025), *P. peteri* (Pilato, Claxton & Binda, 1989) (Massa *et al.* 2021), *P. pius* (Massa *et al.* 2021), *P. fairbanksi* and *P. marchelmoni* sp. nov. However, all reports of *P. richtersi* from across Sweden were prior to its re-description with molecular analysis (Guidetti *et al.* 2019a) and during a time in which the species was believed to be cosmopolitan. The presence of *P. fairbanksi* and the very similar morphologies of the two species (in addition to molecular differences, *P. fairbanksi* is distinguished only by the presence of triploidy and apomictic parthenogenesis; Guidetti *et al.* 2019a), suggests that previous reports of *P. richtersi* may represent instances of misidentified *P. fairbanski*. Alternately, the confirmed occurrences of *P. richtersi* in Jyväskylä and Turku, Finland (Vecchi *et al.* 2022c, 2024b) in addition to its type locality on Clare Island, Ireland (Guidetti *et al.* 2019a) prevents the previous reports from being wholly dismissed since the geographic range of *P. richtersi* likely does extend over Sweden. More research is needed to clarify the situation.

Conclusion

With the description of two new species from southern Sweden and the new record of *P. fairbanksi*, the total number of known species of Tardigrada and Macrobiotidae in the country increases to 121 and 28 respectively, of which 39 (32%) and 18 (64%), respectively, occur specifically in the KVBR, further cementing the locale as a tardigrade hotspot. The additional records of *M*. aff. *nelsonae* and *Tenuibiotus* sp. emphasize that hidden tardigrade diversity remains and our efforts to reveal the true biodiversity of the area must continue.

Acknowledgements

We would like to thank Bodil Cronholm and the staff of the DNA laboratory at NRM for their help with DNA amplification and sequencing. We also thank Sabine Stöhr and Andreas Karlsson for their help with the SEM.

Author contributions

SA conceived and administered the project. SA, RG and KIJ conducted the fieldwork. All authors extracted animals, identified species, and collected morphological data. SA and JH performed DNA extractions, amplification and sequencing and analyzed the data. JH prepared the figures and drafted the manuscript. All authors reviewed and edited the manuscript.

Conflict of interests

The authors declare no conflict of interests.

Funding

This research was supported by a grant from the Swedish Taxonomy Initiative (SLU.dha.2021.4.3-124) to SA. This research was also partially funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for tender No. 3138 of 16 December 2021, rectified by Decree n. 3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU. Project Code [CN_00000033], Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP E93C22001090001, Project title "National Biodiversity Future Center – NBFC" to RG.

Data availability

The data underlying this article are available in the GenBank Nucleotide Database at https://www.ncbi.nlm.nih.gov/genbank/, and can be accessed with accession numbers listed in Appendix 1. Type materials were deposited at the Swedish Museum of Natural History in Stockholm, Sweden (SMNH) or at the Bertolani Collection of University of Modena and Reggio Emilia, Italy (MUSN).

References

Artois T., Fontaneto D., Hummon W.D., McInnes S.J., Todaro M.A., Sørsensen M.V & Zullini A. 2012. Ubiquity of microscopic animals? Evidence from the morphological approach in species identification. *In*: Fontaneto D. (ed.) *Biogeography of Microscopic Organisms: Is Everything Small Everywhere*: 245–249. Cambridge University Press, Cambridge.

Atherton S., Hulterström J., Guidetti R. & Jönsson K.I. 2025. Three new species of *Mesobiotus* (Eutardigrada: Macrobiotidae) from Sweden with an updated phylogeny of the genus. *Scientific Reports* 15: 4535. https://doi.org/10.1038/s41598-025-88063-8

Barbosa A.M., Pautasso M. & Figeuiredo D. 2013. Species-people correlations and the need to account for survey effort in biodiversity analyses. *Diversity and Distributions* 19: 1188–1197. https://doi.org/10.1111/ddi.12106

Bartels P.J., Apodaca J.J., Mora C. & Nelson D.R. 2016. A global biodiversity estimate of a poorly known taxon: Phylum Tardigrada. *Zoological Journal of the Linnean Society* 178: 730–736. https://doi.org/10.1111/zoj.12441

Basu S., Babu R., Siddique A. & Purushothaman J. 2023. Integrative description of *Paramacrobiotus bengalensis* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae), a new limno-terrestrial tardigrade species from the state of West Bengal, India. *European Journal of Taxonomy* 890: 23–48. https://doi.org/10.5852/ejt.2023.890.2249

Bertolani R. & Pilato G. 1988. Struttura delle unghie nei Macrobiotidae e descrizione di *Murrayon* n. gen. (Eutardigrada). *Animalia* 15: 17–24.

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. https://doi.org/10.1111/j.1463-6409.1993.tb00347.x

Bertolani R., Rebecchi L., Giovannini I. & Cesari M. 2011. DNA barcoding and integrative taxonomy of *Macrobiotus hufelandi* CAS Schultze 1834, the first tardigrade species to be described, and some related species. *Zootaxa* 2997: 19–36. https://doi.org/10.11646/zootaxa.2997.1.2

Bertolani R., Guidetti R., Marchioro T., Altiero T., Rebecchi L. & 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. https://doi.org/10.1016/j.ympev.2014.03.006

Bertolani R., Cesari M., Giovannini I., Rebecchi L., Guidetti R., Kaczmarek Ł. & Pilato G. 2023. The *Macrobiotus persimilis-polonicus* complex (Eutardigrada, Macrobiotidae), another example of problematic species identification, with the description of four new species. *Organisms Diversity & Evolution* 23: 329–368. https://doi.org/10.1007/s13127-022-00599-z

Brandoli S., Cesari M., Massa E., Vecchi M., Rebecchi L. & Guidetti R. 2024. Diverse eggs, diverse species? Production of two egg morphotypes in *Paramacrobiotus bifrons*, a new eutardigrade species within the *areolatus* group. *The European Zoological Journal* 91: 274–297. https://doi.org/10.1080/24750263.2024.2317465

Bussau C. 1992. New deep-sea Tardigrada (Arthrotardigrada, Halechiniscidae) from manganese nodule area of the eastern South Pacific. *Zoologica Scripta* 21: 79–91. https://doi.org/10.1111/j.1463-6409.1992.tb00311.x

Caicedo M., Arquez M., Castro L. R. & Quiroga S. 2017. Códigos de barras genéticos en una especie de *Paramacrobiotus* (Tardigrada: Parachela) en Santa Marta, Colombia. *Intropica: Revista del Instituto de Investigaciones Tropicales* 12 (1): 15–22.

Carlzon C. 1909. Schwedische Tardigraden. *Zoologischer Anzeiger* 34: 137–142.

Cesari M., Bertolani R., Rebecchi L. & Guidetti R. 2009. DNA barcoding in Tardigrada: the first case study on *Macrobiotus macrocalix* Bertolani & Rebecchi 1993 (Eutardigrada, Macrobiotidae). *Molecular Ecology Resources* 9: 699–706. https://doi.org/10.1111/j.1755-0998.2009.02538.x

Cesari M., Giovannini I., Bertolani R. & Rebecchi L. 2011. An example of problems associated with DNA barcoding in tardigrades: a novel method for obtaining voucher specimens. *Zootaxa* 3104 (1): 42–51. https://doi.org/10.11646/zootaxa.3104.1.3

Cesari M., Giovannini I., Altiero T., Guidetti R., Cornette R., Kikawada T. & Rebecchi L. 2022. Resistance to extreme stresses by a newly discovered Japanese tardigrade species, *Macrobiotus kyoukenus* (Eutardigrada, Macrobiotidae). *Insects* 13 (7): 634. https://doi.org/10.3390/insects13070634

Coughlan K. & Stec D. 2019. Two new species of the *Macrobiotus hufelandi* complex (Tardigrada: Eutardigrada: Macrobiotidae) from Australia and India, with notes on their phylogenetic position. *European Journal of Taxonomy* 573: 1–38. https://doi.org/10.5852/ejt.2019.537

Coughlan K., Michalczyk Ł. & Stec D. 2019. *Macrobiotus caelestis* sp. nov., a new tardigrade species (Macrobiotidae: *hufelandi* group) from the Tien Shan mountains (Kyrgyzstan*). Annales Zoologici* 69: 499–513. https://doi.org/10.3161/00034541ANZ2019.69.3.002

Degma P. & Guidetti R. 2024. Actual checklist of Tardigrada species. https://doi.org/10.25431/11380_1178608. [accessed 9 Jan. 2025].

Durante Pasa M.V. & Maucci W. 1979. Tardigradi muscicoli della Grecia. *Zeszyty Naukowe Uniwersytetu Jagiellońskiego, Prace Zoologiczne* 5: 19–45.

Edgar R.C. 2004. MUSCLE: Multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797. https://doi.org/10.1093/nar/gkh340

Erdmann W., Kosicki J.Z., Kayastha P., Mioduchowska M. & Kaczmarek Ł. 2024. An integrative description of *Mesobiotus mandalori* sp. nov. (Eutardigrada, Macrobiotoidea) from Poland. *The European Zoological Journal* 91 (1): 378–394. https://doi.org/10.1080/24750263.2024.2341884

Folmer O., Black M., Hoeh W., Lutz R. & Vrijenhoek R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3: 294–299.

Fontaneto D., Barbosa A.M., Segers H. & Pautasso M. 2012. The 'rotiferologist' effect and other global correlates of species richness in monogonont rotifers. *Ecography* 35: 174–182. https://doi.org/10.1111/j.1600-0587.2011.06850.x

Garraffoni A., Sørensen M.V., Worsaae K., Di Domenico M., Sales L.P., Santos J. & Lourenco A. 2021. Geographical sampling bias on the assessment of endemism areas for marine meiobenthic fauna. *Cladistics* 37 (5): 571–585. https://doi.org/10.1111/cla.12453

Gąsiorek P. 2024. Catch me if you can or how paradigms of tardigrade biogeography evolved from cosmopolitism to 'localism'. *Zoological Journal of the Linnean Society* 202: zlad191. https://doi.org/10.1093/zoolinnean/zlad191

Gąsiorek P., Sørensen M.V., Lillemark M.R., Leerhøi & Tøttrup A.P. 2024. Massive citizen science sampling and integrated taxonomic approach unravel Danish cryptogam-dwelling tardigrade fauna. *Frontiers in Zoology* 21: 27. https://doi.org/10.1186/s12983-024-00547-x

Guidetti R., Gandolfi A., Rossi V. & Bertolani R. 2005. Phylogenetic analysis of Macrobiotidae (Eutardigrada, Parachela): A combined morphological and molecular approach. *Zoologica Scripta* 34 (3): 235–244. https://doi.org/10.1111/j.1463-6409.2005.00193.x

Guidetti R., Schill R.O., Bertolani R., Dandekar T. & Wolf M. 2009. New molecular data for tardigrade phylogeny, with the erection of *Paramacrobiotus* gen. nov. *Journal of Zoological Systematics and Evolutionary Research* 47: 315–321. https://doi.org/10.1111/j.1439-0469.2009.00526.x

Guidetti R., Peluffo J.R., Rocha A.M., Cesari M. & Peluffo M.C.M. 2013. The morphological and molecular analyses of a new South American urban tardigrade offer new insights on the biological meaning of the *Macrobiotus hufelandi* group of species (Tardigrada: Macrobiotidae). *Journal of Natural History* 47 (37–38): 2409–2426. https://doi.org/10.1080/00222933.2013.800610

Guidetti R., Rebecchi L., Bertolani R., Jönsson K.I., Kristensen R.M. & Cesari M. 2016. Morphological and molecular analyses on *Richtersius* (Eutardigrada) diversity reveal its new systematic position and lead to the establishment of a new genus and a new family within Macrobiotoidea. *Zoological Journal of the Linnean Society* 178: 834–845. https://doi.org/10.1111/zoj.12428

Guidetti R., Cesari M,. Bertolani R., Altiero T. & Rebecchi L. 2019a. High diversity in species, reproductive modes and distribution within the *Paramacrobiotus richtersi* complex (Eutardigrada, Macrobiotidae). *Zoological Letters* 5: 1–28. https://doi.org/10.1186/s40851-018-0113-z

Guidetti R., Massa E., Bertolani R., Rebecchi L. & Cesari M. 2019b. Increasing knowledge of Antarctic biodiversity: New endemic taxa of tardigrades (Eutardigrada; Ramazzottiidae) and their evolutionary relationships. *Systematics and Biodiversity* 17: 573–593. https://doi.org/10.1080/14772000.2019.1649737

Guidetti R., Jönsson K.I. & Kristensen R.M. Checklist of Swedish tardigrades. 2015-2025, Ver. 2: 00-00-2025. Available from http://www.hkr.se/swedishtardigrades [accessed 28 Feb. 2025].

Guil N. & Giribet G. 2012. A comprehensive molecular phylogeny of tardigrades — adding genes and taxa to a poorly resolved phylum-level phylogeny. *Cladistics* 28: 21–49. https://doi.org/10.111/j.1096-0031.2011.00364.x

Hortal J., de Bello F., Diniz-Filho J.A.F., Lewinsohn T.W., Lobo J.M. & Ladle R.J. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 46: 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

Itang L.A., Stec D., Mapalo M.A., Mirano-Bascos D. & Michalczyk Ł. 2020. An integrative description of *Mesobiotus dilimanensis*, a new tardigrade species from the Philippines (Eutardigrada: Macrobiotidae: *furciger* group). *Raffles Bulletin of Zoology* 68: 19–31. https://doi.org/10.26107/RBZ-2020-0003

Jönsson K.I. 2003. Population density and species composition of moss-living tardigrades in a boreo-nemoral forest. *Ecography* 26: 355–364. https://doi.org/10.1034/j.1600-0587.2003.03458.x

Jönsson K.I. 2007. Long-term experimental manipulation of moisture conditions and its impact on moss-living tardigrades. *Journal of Limnology* 66: 119–125. https://doi.org/10.4081/jlimnol.2007.s1.119

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

Kaczmarek Ł., Gawlak M., Bartels P.J., Nelson D.R. & Roszkowska M. 2017. Revision of the genus *Paramacrobiotus* Guidetti *et al.* 2009 with the description of a new species re-descriptions and a key. *Annales Zoologica* 67: 627–656. https://doi.org/10.3161/00034541ANZ2017.67.4.001

Kaczmarek Ł., Zawierucha K., Buda J., Stec D., Gawlak M., Michalczyk Ł. & 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 (10): e0204756. https://doi.org/10.1371/journal.pone.0204756

Kaczmarek Ł., Bartylak T., Stec D., Kulpa A., Kepel M., Kepel A. & Roszkowska M. 2020a. Revisiting the genus *Mesobiotus* Vecchi *et al.*, 2016 (Eutardigrada, Macrobiotidae) – remarks, updated dichotomous key and an integrative description of new species from Madagascar. *Zoologischer Anzeiger* 287: 121–146. https://doi.org/10.1016/j.jcz.2020.05.003

Kaczmarek Ł., Mioduchowska M., Kačarević U., Kubska K., Parnikoza I., Gołdyn B. & Roszkowska M. 2020b. New records of Antarctic Tardigrada with comments on interpopulation variability of the *Paramacrobiotus fairbanksi* Schill, Förster, Dandekar and Wolf, 2010. *Diversity* 12 (3): 108. https://doi.org/10.3390/d12030108

Kaczmarek Ł., Roszkowska M., Poprawa I., Janelt K., Kmita H., Gawlak M., Fialkowska E. & Mioduchowska M. 2020c. Integrative description of bisexual *Paramacrobiotus experimentalis* sp. nov. (Macrobiotidae) from republic of Madagascar (Africa) with microbiome analysis. *Molecular Phylogenetics and Evolution* 145: 106730. https://doi.org/10.1016/j.ympev.2019.106730

Kaczmarek Ł., Kayastha P., Roszkowska M., Gawlak M. & Mioduchowska M. 2022. Integrative redescription of the *Minibiotus intermedius* (Plate, 1888)—The type species of the genus *Minibiotus* RO Schuster, 1980. *Diversity* 14 (5): 356. https://doi.org/10.3390/d14050356

Kaczmarek Ł., Rutkowski T., Zacharyasiewicz M., Surmacki A., Osiejuk T.S. & Kayastha P. 2023. New species of Macrobiotidae (Eutardigrada) from Cameroon (Africa), characteristics of *Macrobiotus* morpho-groups and a key to the *Nelsonae* group. *Annales Zoologici* 73: 1–15. https://doi.org/10.3161/00034541ANZ2023.73.1.001

Kalyaanamoorthy S., Minh B., Wong T., von Haeseler A. & Jermiin L.S. 2017. ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods* 14: 587–589. https://doi.org/10.1038/nmeth.4285

Kapli P., Lutteropp S., Zhang J., Kobert K., Pavlidis P., Stamatakis A. & Flouri T. 2017. Multi-rate Poisson tree processes for single-locus species delimitation under maximum likelihood and Markov chain Monte Carlo. *Bioinformatics* 33: 1630–1638. https://doi.org/10.1093/bioinformatics/btx025

Kayastha P., Roszkowska M., Mioduchowska M., Gawlak M. & Kaczmarek, Ł. 2021. Integrative descriptions of two new tardigrade species along with the new record of *Mesobiotus skorackii* Kaczmarek *et al.*, 2018 from Canada. *Diversity* 13 (8): 394. https://doi.org/10.3390/d13080394

Kayastha P., Mioduchowska M., Gawlak M., Sługocki Ł., Araújo R., Silva J.G. & Kaczmarek Ł. 2023a. Integrative description of *Macrobiotus kosmali* sp. nov. (*hufelandi* group) from the Island of Madeira (Portugal). *The European Zoological Journal* 90 (1): 126–138. https://doi.org/10.1080/24750263.2022.2163312

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

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

Kiosya Y., Pogwizd J., Matsko Y., Vecchi M. & Stec D. 2021. Phylogenetic position of two *Macrobiotus* species with a revisional note on *Macrobiotus sottilei* Pilato, Kiosya, Lisi & Sabella, 2012 (Tardigrada: Eutardigrada: Macrobiotidae). *Zootaxa* 4933 (1): 113–135. https://doi.org/10.11646/zootaxa.4933.1.5

Klopfstein S., Massingham T. & Goldman N. 2017. More on the best evolutionary rate for phylogenetic analysis. *Systematic Biology* 66: 769–785. https://doi.org/10.1093/sysbio/syx051

Kumar S., Stecher G., Li M., Knyaz C. & Tamura K. 2018. MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35 (6): 1547–1549. https://doi.org/10.1093/molbev/msy096

Larsson A. 2014. AliView: A fast and lightweight alignment viewer and editor for large data sets. *Bioinformatics* 30 (22): 3276–3278. https://doi.org/10.1093/bioinformatics/btu531

López-Sandoval D., Montiel-Parra G. & Pérez T.M. 2025. New records of tardigrades from Mexico with the description of *Paramacrobiotus puma* sp. nov. (Eutardigrada: Macrobiotidae). *Revista Mexicana de Biodiversidad* 96: e965488. https://doi.org/10.22201/ib.20078706e.2025.96.5488

Mapalo M.A., Stec D., Mirano-Bascos D. & Michalczyk Ł. 2016. *Mesobiotus philippinicus* sp. nov., the first limnoterrestrial tardigrade from the Philippines. *Zootaxa* 4126 (3): 411–426. https://doi.org/10.11646/zootaxa.4126.3.6

Mapalo M.A., Stec D., Mirano-Bascos D. & Michalczyk Ł. 2017. An integrative description of a limnoterrestrial tardigrade from the Philippines, *Mesobiotus insanis*, new species (Eutardigrada: Macrobiotidae: harmsworthi group). *Raffles Bulletin of Zoology* 65: 440–454.

Marley N.J., Gawlak M., Bartels P.J., Nelson D.R., Roszkowska M., Stec D. & Degma P. 2018. A clarification for the subgenera of *Paramacrobiotus* Guidetti, Schill, Bertolani, Dandekar and Wolf, 2009, with respect to the International Code of Zoological Nomenclature. *Zootaxa* 4407 (1): 130–134. https://doi.org/10.11646/zootaxa.4407.1.9

Marnissi J.B., Cesari M., Rebecchi L. & Bertolani R. 2021. Integrative description of a new Tunisian tardigrade species, *Macrobiotus azzunae* sp. nov. (Eutardigrada, Macrobiotidae, *hufelandi* group). *European Journal of Taxonomy* 758: 122–146. https://doi.org/10.5852/ejt.2021.758.1429

Massa E. & Vecchi M. 2024. Description of *Macrobiotus kathyae* sp. nov. (Parachela: Macrobiotidae) and first records of tardigrades from Indiana (USA). *Zootaxa* 5471 (3): 301–317. https://doi.org/10.11646/zootaxa.5471.3.1

Massa E., Guidetti R., Cesari M., Rebecchi L. & Jönsson K.I. 2021. Tardigrades of Kristianstads Vattenrike Biosphere Reserve with description of four new species from Sweden. *Scientific Reports* 11: 4861. https://doi.org/10.1038/s41598-021-83627-w

Meyer C., Kreft H., Guralnick R. & Jetz W. 2015. Global priorities for an effective information basis of biodiversity distributions. *Nature Communications* 6: 8221. https://doi.org/10.1038/ncomms9221

Michalczyk Ł. & Kaczmarek Ł. 2013. The Tardigrada Register: A comprehensive online data repository for tardigrade taxonomy. *Journal of Limnology* 72: 175–181. https://doi.org/10.4081/jlimnol.2013.s1.e22

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

Mihelčič F. 1971. Susswassertardigraden aus Nordeuropa. *Entomologica Scandinavica* 2: 205–214. https://doi.org/10.1163/187631271X00211

Morek W., Stec D., Gasiorek P., Schill R.O., Kaczmarek L. & Michalczyk L. 2016. An experimental test of eutardigrade preparation methods for light microscopy. *Zoological Society of the Linnean Society* 178: 785–793. https://doi.org/10.1111/zoj.12457

Nelson D.R., Bartels P.J. & Guil N. 2018. Tardigrade ecology. *In*: Schill R. (ed.) *Water Bears: The Biology of Tardigrades*: 163–210. Zoological Monographs vol 2. Springer, Cham. https://doi.org/10.1007/978-3-319-95702-9_7

Nelson D.R., Fletcher R.A., Guidetti R., Roszkowska M., Grobys D. & Kaczmarek Ł. 2020. Two new species of Tardigrada from moss cushions (*Grimmia* sp.) in a xerothermic habitat in northeast Tennessee (USA, North America), with the first identification of males in the genus *Viridiscus*. *Biodiversity and Conservation* 8: e10251. https://doi.org/10.7717/peerj.10251

Nowak B. & Stec D. 2018. An integrative description of *Macrobiotus hannae* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Poland. *Turkish Journal of Zoology* 42 (3): 269–286. https://doi.org/10.3906/zoo-1712-31

Olsson P., Folke C., Galaz V., Hahn T. & Schultz L. 2007. Enhancing the fit through adaptive co-management: Creating and maintaining bridging functions for matching scales in the Kristianstads Vattenrike Biosphere Reserve Sweden. *Ecology and Society* 12: 1–17. https://doi.org/10.5751/ES-01976-120128

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

Pilato G. & Binda M.G. 2010. Definition of families, subfamilies, genera and subgenera of the Eutardigrada and keys to their identification. *Zootaxa* 2404: 1–54. https://doi.org/10.11646/zootaxa.2404.1.1

Pilato G. & Lisi O. 2011. *Tenuibiotus*, a new genus of Macrobiotidae (Eutardigrada). *Zootaxa* 2761: 34–40. https://doi.org/10.11646/zootaxa.2761.1.2

Polishchuk A., Kayastha P., Kiosya, Y., Mioduchowska M., Gawlak M. & Kaczmarek Ł. 2024. Integrative redescription of the *Xerobiotus euxinus* Pilato, Kiosya, Lisi, Inshina & Biserov, 2011 (Tardigrada: Eutardigrada: Macrobiotidae) population from Ukraine. *The European Zoological Journal* 91 (2): 1120–1133. https://doi.org/10.1080/24750263.2024.2405223

Ramazzotti G. & Maucci W. 1983. Il Phylum Tardigrada. *Memorie dell'Istituto Italiano di Idrobiologia, Pallanza* 41: 1–1012.

Richters F. 1904. Beitrag zur Verbreitung der Tardigraden im südlichen Skandinavien und an der Mecklenburgischen Küste. *Zoologischer Anzeiger* 28: 347–352.

Roszkowska M., Ostrowska M., Stec D., Janko K. & Kaczmarek Ł. 2017. *Macrobiotus polypiformis* sp. nov., a new tardigrade (Macrobiotidae; *hufelandi* group) from the Ecuadorian Pacific coast, with remarks on the claw abnormalities in eutardigrades. *European Journal of Taxonomy* 327: 1–19. https://doi.org/10.5852/ejt.2017.327

Roszkowska M., Stec D., Gawlak M. & Kaczmarek Ł. 2018. An integrative description of a new tardigrade species *Mesobiotus romani* sp. nov. (Macrobiotidae: *harmsworthi* group) from the Ecuadorian Pacific coast. *Zootaxa* 4450 (5): 550–564. https://doi.org/10.11646/zootaxa.4450.5.2

Schill R.O., Förster F., Dandekar T. & Wolf M. 2010. Using compensatory base change analysis of internal transcribed spacer 2 secondary structures to identify three new species in *Paramacrobiotus* (Tardigrada). *Organism Diversity and Evolution* 10: 287–296. https://doi.org/10.1007/s13127-010-0025-z

Schuster R.O., Nelson D.R., Grigarick A.A. & Christenberry D. 1980. Systematic criteria of the Eutardigrada. *Transactions of the American Microscopical Society* 99: 284–303. https://doi.org/10.2307/3226004

Short K.A., Sands, C.J., McInnes S.J., Pisani D., Stevens M.I. & Convey P. 2022. An ancient, Antarctic-specific species complex: large divergences between multiple Antarctic lineages of the tardigrade genus *Mesobiotus*. *Molecular Phylogenetics and Evolution* 170: 107429. https://doi.org/10.1016/j.ympev.2022.107429

Sohlenius B., Boström S. & Ekebom A. 1997. Metazoan microfauna in an ombrotrophic mire at Abisko, northern Sweden*. European Journal of Soil Biology* 33: 31–39.

Statistiska Centralbyrån Sverige. Folkmängden efter region civilstånd ålder och kön. År 1968–2023. Available from https://www.statistikdatabasen.scb.se [accessed 9 Jan. 2025].

Stec D. 2019. *Mesobiotus datanlanicus* sp. nov., a new tardigrade species (Macrobiotidae: *Mesobiotus harmsworthi* group) from Lâm Đồng Province in Vietnam. *Zootaxa* 4679 (1): 164–180. https://doi.org/10.11646/zootaxa.4679.1.10

Stec D. 2021. Integrative descriptions of two new *Mesobiotus* species (Tardigrada, Eutardigrada, Macrobiotidae) from Vietnam. *Diversity* 13 (11): 605. https://doi.org/10.3390/d13110605

Stec D. 2022a. An integrative description of two new *Mesobiotus* species (Tardigrada: Eutardigrada: Macrobiotidae) with updated genus phylogeny. *Zoological Studies* 61: e85. https://doi.org/10.6620/ZS.2022.61-85

Stec D. 2022b. *Macrobiotus rebecchii* sp. nov.: A new limno-terrestrial and hermaphroditic tardigrade from Kyrgyzstan. *Animals* 12 (21): 2906. https://doi.org/10.3390/ani12212906

Stec D. 2024. Integrative taxonomy supports two new species of *Macrobiotus* (Tardigrada: Eutardigrada: Macrobiotidae) allowing further discussion on the genus phylogeny. *European Journal of Taxonomy* 930: 79–123. https://doi.org/10.5852/ejt.2024.930.2481

Stec D. & Kristensen R.M. 2017. An integrative description of *Mesobiotus ethiopicus* sp. nov. (Tardigrada: Eutardigrada: Parachela: Macrobiotidae: *harmsworthi* group) from the Northern Afrotropic region. *Turkish Journal of Zoology* 41 (5): 800–811. https://doi.org/10.3906/zoo-1701-47

Stec D. & Morek W. 2022. Reaching the monophyly: Re-evaluation of the enigmatic species *Tenuibiotus hyperonyx* (Maucci, 1983) and the genus *Tenuibiotus* (Eutardigrada). *Animals* 12: 404. https://doi.org/10.3390/ani12030404

Stec D., Smolak R., Kaczmarek Ł. & Michalczyk Ł. 2015. An integrative description of *Macrobiotus paulinae* sp. nov. (Tardigrada: Eutardigrada: Macrobiotidae: *hufelandi* group) from Kenya. *Zootaxa* 4052 (5): 501–526. https://doi.org/10.11646/zootaxa.4052.5.1

Stec D., Morek W., Gąsiorek P., Blagden B. & Michalczyk Ł. 2017. Description of *Macrobiotus scoticus* sp. nov. (Tardigrada: Macrobiotidae: *hufelandi* group) from Scotland by means of integrative taxonomy. *Annales Zoologici* 67 (2):181–197. https://doi.org/10.3161/00034541ANZ2017.67.2.001

Stec D., Arakawa K. & Michalczyk Ł. 2018a. An integrative description of *Macrobiotus shonaicus* sp. nov. (Tardigrada: Macrobiotidae) from Japan with notes on its phylogenetic position within the *hufelandi* group. *PLoS ONE* 13 (2): e0192210. https://doi.org/10.1371/journal.pone.0192210

Stec D., Kristensen R.M. & Michalczyk Ł. 2018b. Integrative taxonomy identifies *Macrobiotus papei*, a new tardigrade species of the *Macrobiotus hufelandi* complex (Eutardigrada: Macrobiotidae) from the Udzungwa Mountains National Park (Tanzania). *Zootaxa* 4446 (2): 273–291. https://doi.org/10.11646/zootaxa.4446.2.7

Stec D., Krzywański Ł. & Michalczyk Ł. 2018c. Integrative description of *Macrobiotus canaricus* sp. nov. with notes on *M. recens* (Eutardigrada: Macrobiotidae). *European Journal of Taxonomy* 452: 1–36. https://doi.org/10.5852/ejt.2018.452

Stec D., Roszkowska M., Kaczmarek L. & Michalczyk L. 2018d. An integrative description of a population of *Mesobiotus radiatus* (Pilato, Binda & Catanzaro, 1991) from Kenya. *Turkish Journal of Zoology* 42 (5): 523–540. https://doi.org/10.3906/zoo-1802-43

Stec D., Roszkowska M., Kaczmarek Ł. & Michalczyk Ł. 2018e. *Paramacrobiotus lachowskae*, a new species of Tardigrada from Colombia (Eutardigrada: Parachela: Macrobiotidae). *New Zealand Journal of Zoology* 45: 43–60. https://doi.org/10.1080/03014223.2017.1354896

Stec D., Dudziak M. & Michalczyk Ł. 2020a. Integrative descriptions of two new Macrobiotidae species (Tardigrada: Eutardigrada: Macrobiotoidea) from French Guiana and Malaysian Borneo. *Zoological Studies* 59: e23. https://doi.org/10.6620/ZS.2020.59-23

Stec D., Kristensen R.M. & Michalczyk Ł. 2020b. An integrative description of *Minibiotus ioculator* sp. nov. from the Republic of South Africa with notes on *Minibiotus pentannulatus* Londoño *et al.*, 2017 (Tardigrada: Macrobiotidae). *Zoologischer Anzeiger* 286: 117–134. https://doi.org/10.1016/j.jcz.2020.03.007

Stec D., Krzywański Ł., Zawierucha K. & Michalczyk Ł. 2020c. Untangling systematics of the *Paramacrobiotus areolatus* species complex by an integrative redescription of the nominal species for the group, with multilocus phylogeny and species delineation in the genus *Paramacrobiotus*. *Zoological Journal of the Linnean Society* 188: 694–716. https://doi.org/10.1093/zoolinnean/zlz163

Stec D., Tumanov D.T. & Kristensen R.M. 2020d. Integrative taxonomy identifies two new tardigrade species (Eutardigrada: Macrobiotidae) from Greenland. *European Journal of Taxonomy* 614: 1–40. https://doi.org/10.5852/ejt.2020.614

Stec D., Vecchi M., Calhim S. & Michalczyk Ł. 2021a. New multilocus phylogeny reorganises the family Macrobiotidae (Eutardigrada) and unveils complex morphological evolution of the *Macrobiotus hufelandi* group. *Molecular Phylogenetics and Evolution* 160: 106987. https://doi.org/10.1016/j.ympev.2020.106987

Stec D., Vecchi M., Dudziak M., Bartels P.J., Calhim S. & Michalczyk Ł. 2021b. Integrative taxonomy resolves species identities within the *Macrobiotus pallarii* complex (Eutardigrada: Macrobiotidae). *Zoological Letters* 7: 9. https://doi.org/10.1186/s40851-021-00176-w

Stec D., Vončina K., Kristensen R.M. & Michalczyk Ł. 2022. The *Macrobiotus ariekammensis* species complex provides evidence for parallel evolution of claw elongation in macrobiotid tardigrades. *Zoological Journal of the Linnean Society* 195: 1067–1099. https://doi.org/10.1093/zoolinnean/zlab101

Sugiura K., Matsumoto M. & Kunieda T. 2022. Description of a model tardigrade *Paramacrobiotus metropolitanus* sp. nov. (Eutardigrada) from Japan with a summary of its life history, reproduction and genomics. *Zootaxa* 5134 (1): 92–112. https://doi.org/10.11646/zootaxa.5134.1.4

Talavera G. & Castresana J. 2007. Improvement of phylogenies after removing divergent and ambiguously aligned blocks from protein sequence alignments. *Systematic Biology* 56: 564–577. https://doi.org/10.1080/10635150701472164

Thulin G. 1911. Beiträge zur Kenntnis der Tardigradenfauna Schwedens. *Arkiv för Zoologi Universität Lund* 7: 1–60. https://doi.org/10.5962/bhl.part.1270

Tilquin A. & Kokko H. 2016. What does the geography of parthenogenesis teach us about sex? *Philosophical Transactions of the Royal Society B: Biological Sciences* 371: 20150538. https://doi.org/10.1098/rstb.2015.0538

Trifinopoulos J., Nguyen L.T., von Haeseler A. & Minh B.Q. 2016. W-IQ-TREE: A fast online phylogenetic tool for maximum likelihood analysis. *Nucleic Acids Research* 44: W232–W235. https://doi.org/10.1093/nar/gkw256

Troell S. & Jönsson K.I. 2023. Occurrence of tardigrades and morphometric and chemical conditions in rock pools by the Baltic Sea. *Scientific Reports* 13: 19776. https://doi.org/10.1038/s41598-023-46697-6

Tsvetkova A.Y. & Tumanov D.V. 2024. *Tenuibiotus yeliseii* sp. nov., a new species of Macrobiotidae (Tardigrada: Eutardigrada) from Svalbard, Norway, with discussion of taxonomic criteria within the genus and its phylogeny. *Zoosystematica Rossica* 33 (1): 28–47. https://doi.org/10.31610/zsr/2024.33.1.28

Tumanov D.V. 2020. Integrative description of *Mesobiotus anastasiae* sp. nov. (Eutardigrada, Macrobiotoidea) and first record of *Lobohalacarus* (Chelicerata, Trombidiformes) from the Republic of South Africa. *European Journal of Taxonomy* 726: 102–131. https://doi.org/10.5852/ejt.2020.726.1179

Tumanov D.V., Androsova E.D., Avdeeva G.S. & Leontev A.A. 2022. First faunistic investigation of semiterrestrial tardigrade fauna of North-West Russia using the method of DNA barcoding. *Invertebrate Zoology* 19 (4): 452–474. https://doi.org/10.15298/invertzool.19.4.08

Tumanov D.V., Androsova E.D., Gavrilenko M.D. & Kalimullin A.A. 2024. Integrative description of two new species of the genus *Mesobiotus* (Eutardigrada, Macrobiotoidea) from Russia, with an updated phylogeny of the genus. *European Journal of Taxonomy* 947: 20–52. https://doi.org/10.5852/ejt.2024.947.2619

United States Census Bureau. Profile of Fairbanks City Alaska year 2023. Available from https://www.data.census.gov [accessed 9 Jan. 2025].

Vecchi M. & Stec D. 2021. Integrative descriptions of two new *Macrobiotus* species (Tardigrada, Eutardigrada, Macrobiotidae) from Mississippi (USA) and Crete (Greece). *Zoosystematics and Evolution* 97: 281–306. https://doi.org/10.3897/zse.97.65280

Vecchi M., Cesari M,. Bertolani R., Jönsson K.I., Rebecchi L. & Guidetti R. 2016. Integrative systematic studies on tardigrades from Antarctica identify new genera and new species within Macrobiotoidea and Echiniscoidea. *Invertebrate Systematics* 30: 303–322. https://doi.org/10.1071/IS15033

Vecchi M., Choong H. & Calhim S. 2022a. *Sisubiotus hakaiensis* sp. nov. (Tardigrada, Macrobiotidae), a new tardigrade species from Calvert Island (British Columbia, Canada). *European Journal of Taxonomy* 823: 64–81. https://doi.org/10.5852/ejt.2022.823.1815

Vecchi M., Ferrari C., Stec D. & Calhim S. 2022b. Desiccation risk favours prevalence and diversity of tardigrade communities and influences their trophic structure in alpine ephemeral rock pools. *Hydrobiologia* 849 (9): 1995–2007. https://doi.org/10.1007/s10750-022-04820-0

Vecchi M., Stec D., Vuori T., Ryndov S., Chartrain C. & Calhim S. 2022c. *Macrobiotus naginae* sp. nov. a new xerophilous tardigrade species from Rokua Sand Dunes (Finland). *Zoological Studies* 61: 22. https://doi.org/10.6620/ZS.2022.61-22

Vecchi M., McDaniel J.L., Chartrain J., Vuori T., Walsh E.J. & Calhim S. 2023. Morphology, phylogenetic position, and mating behaviour of a new *Mesobiotus* (Tardigrada) species from a rock pool in the Socorro Box Canyon (New Mexico, USA). *The European Zoological Journal* 90 (2): 708–725. https://doi.org/10.1080/24750263.2023.2263033

Vecchi M., Dykyy I., Khoyetskyy P., Vuori T., Calhim S. & Trokhymets V. 2024a. The tardigrade *Mesobiotus aradasi* (Binda, Pilato & Lisi, 2005) is widely distributed along the Antarctic Peninsula. *Polar Biology* 47 (3): 227–238. https://doi.org/10.1007/s00300-023-03222-9

Vecchi M., Stec D., Rebecchi L., Michalczyk Ł. & Calhim S. 2024b. Ecology explains anhydrobiotic performance across tardigrades, but the shared evolutionary history matters more. *Journal of Animal Ecology* 93 (3): 307–318. https://doi.org/10.1111/1365-2656.14031

Vences M., Patmanidis S., Kharchev V. & Renner S.S. 2022. Concatenator, a user-friendly program to concatenate DNA sequences, implementing graphical user interfaces for MAFFT and FastTree. *Bioinformatics Advances* 2: vbac050. https://doi.org/10.1093/bioadv/vbac050

Vincenzi J., Cesari M., Kaczmarek Ł., Roszkowska M., Mioduchowska M., Rebecchi L., Kiosya Y. & Guidetti R. 2024. The xerophilic genera *Xerobiotus* and *Pseudohexapodibius* (Macrobiotidae; Tardigrada): Biodiversity, biogeography and phylogeny. *Zoological Journal of the Linnean Society* 200: 111–141. https://doi.org/10.1093/zoolinnean/zlad129

Yang W., Ma K. & Kreft H. 2014. Geographical sampling bias in a large distributional database and its effects on species richness-environment models. *Journal of Biogeography* 40: 1415–1426. https://doi.org/10.1111/jbi.12108

Zawierucha K., Kolicka M., Takeuchi N. & Kaczmarek Ł. 2014. What animals can live in cryoconite holes? A faunal review. *Journal of Zoology* 295: 159–169. https://doi.org/10.1111/jzo.12195

Zawierucha K., Kolicka M. & Kaczmarek Ł. 2016. Re-description of the Arctic tardigrade *Tenuibiotus voronkovi* Tumanov, 2007 (Eutardigrada; Macrobiotidea), with the first molecular data for the genus. *Zootaxa* 4196 (4): 498–510. https://doi.org/10.11646/zootaxa.4196.4.2

Printed versions of all papers are deposited in the libraries of three of the institutes that are members of the *EJT* consortium: Muséum national d'Histoire naturelle, Paris, France; Royal Museum for Central Africa, Tervuren, Belgium; Royal Belgian Institute of Natural Sciences, Brussels, Belgium. The other members of the consortium are: Meise Botanic Garden, Meise, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark; Naturalis Biodiversity Center, Leiden, the Netherlands; Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; Leibniz Institute for the Analysis of Biodiversity Change, Bonn – Hamburg, Germany; National Museum of the Czech Republic, Prague, Czech Republic; The Steinhardt Museum of Natural History, Tel Aviv, Israël.

Supplementary files

Supp. file 1. Photograph of the location where the samples were taken. https://doi.org/10.5852/ejt.2025.1030.3135.13969

Supp. file 2. Molecular account. https://doi.org/10.5852/ejt.2025.1030.3135.13971

Sheet 1. Primers and PCR protocols used in this study.
Sheet 2. Models selected for each gene and dataset in the ML analyses.
Sheet 3. Pairwise genetic distances of COI sequences within and between species of *Macrobiotus*, as defined by mPTP analyses. n/a is listed when only a single sequence was analyzed.
Sheet 4. Pairwise genetic distances of ITS2 sequences within and between species of *Macrobiotus*, as defined by mPTP analyses. n/a is listed when only a single sequence was analyzed.
Sheet 5. Pairwise genetic distances of COI sequences within and between species of *Paramacrobiotus*, as defined by mPTP analyses. n/a is listed when only a single sequence was analyzed.

Sheet 6. Pairwise genetic distances of ITS2 sequences within and between species of *Paramacrobiotus*, as defined by mPTP analyses. n/a is listed when only a single sequence was analyzed.

Supp. file 3. COI gene tree of Macrobiotidae Thulin, 1928.
https://doi.org/10.5852/ejt.2025.1030.3135.13973

Supp. file 4. 18S gene tree of Macrobiotidae Thulin, 1928.
https://doi.org/10.5852/ejt.2025.1030.3135.13975

Supp. file 5. ITS2 gene tree of Macrobiotidae Thulin, 1928.
https://doi.org/10.5852/ejt.2025.1030.3135.13977

Supp. file 6. 28S gene tree of Macrobiotidae Thulin, 1928.
https://doi.org/10.5852/ejt.2025.1030.3135.13979

Supp. file 7. *Paramacrobiotus fairbanksi* Schill, Förster, Dandekar & Wolf, 2010 collected from Sweden. **A**. DIC photograph of whole body. **B**. DIC photograph of placoids. **C**. DIC photograph of base of the egg processes. **D**. SEM photograph of egg processes and areolae. **E–G**. DIC photographs of egg processes. Black full arrow indicates examples of the "double" areolae that surround each egg process.
https://doi.org/10.5852/ejt.2025.1030.3135.13981

Supp. file 8. *Macrobiotus* aff. *nelsonae* Guidetti, 1998. **A**. DIC photograph of specimen in water (SMNH, 22-036); whole body. **B**. DIC photograph of specimen in water (SMNH, 22-036); macroplacoids. **C**. DIC photograph of specimen in water (SMNH, 24-085); juvenile hatching from egg. **D–E**. DIC photograph of specimen in water (SMNH, 24-085); examples of egg processes. **F**. DIC photograph of specimen preserved in Hoyer's medium (SMNH, 24-079); claws of leg III. **G**. DIC photograph of specimen preserved in Hoyer's medium (SMNH, 24-079); legs IV; white arrow indicates pores on cuticle, asterisks indicate large granulation. **H**. DIC photograph of specimen in water (SMNH, 24-085); egg chorion; black arrows indicate oval areolae surrounding processes. https://doi.org/10.5852/ejt.2025.1030.3135.13983

Supp. file 9. *Tenuibiotus* sp., DIC photographs of specimen in water (SMNH, 22-109). **A**. Whole body. **B**. Pharynx and macroplacoids, white arrowhead indicates deep constriction of the first macroplacoid. **C**. Claws of leg I. **D**. Claws of leg IV. https://doi.org/10.5852/ejt.2025.1030.3135.13985

Supp. file 10. Raw morphometric measurements for specimens of *Macrobiotus vattenrikense* sp. nov.
https://doi.org/10.5852/ejt.2025.1030.3135.13987

Supp. file 11. Raw morphometric measurements for specimens of *Paramacrobiotus marchelmoni* sp. nov.
https://doi.org/10.5852/ejt.2025.1030.3135.13989

Appendix 1 (continued on next 14 pages). GenBank Accession numbers for COI, 18S, ITS, and 28S sequences of all specimens analysed in this study. New sequences are highlighted in red.

Taxon	Specimen	COI	18S	ITS	28S	Taxon name in GenBank	Notes	Reference in GenBank
Diaforobiotus islandicus	IS.042	MT808072	MT812470	MT812597	MT812461	*Diaforobiotus islandicus*		Stec *et al.* 2020d
Macrobiotus aff. *polonicus*	S165.1	MW593929	MW588026	MW588021	MW588032	*Macrobiotus* aff. *polonicus* S165		Vecchi & Stec 2021
Macrobiotus aff. *polonicus*	S165.2	MW593930	MW588027	MW588020	MW588033	*Macrobiotus* aff. *polonicus* S165		Vecchi & Stec 2021
Macrobiotus almadai	ZYL123	MW990245	MW995180			*Macrobiotus almadai*		Wang *et al.* (unpubl.)
Macrobiotus annewintersae	S207.1	MW593927	MW588025	MW588019	MW588030	*Macrobiotus annewintersae*		Vecchi & Stec 2021
Macrobiotus annewintersae	S207.2	MW593928	MW588024	MW588018	MW588031	*Macrobiotus annewintersae*		Vecchi & Stec 2021
Macrobiotus ariekammensis ariekammensis	NO.393.01	MZ460999	MZ463668	MZ463657	MZ463674	*Macrobiotus ariekammensis ariekammensis*		Stec *et al.* 2022
Macrobiotus ariekammensis groenlandicus	GL.018.04	MZ461006	MZ463664	MZ463654	MZ463679	*Macrobiotus ariekammensis groenlandicus*		Stec *et al.* 2022
Macrobiotus azzunae	C4218_T5	MW698698				*Macrobiotus* sp. 1 MC-2021	temporary taxon name has not been updated in GenBank at time of writing	Marnissi *et al.* 2021
Macrobiotus azzunae	C4218_V4	MW698697	MW695447	MW695454	MW695450	*Macrobiotus* sp. 1 MC-2021	temporary taxon name has not been updated in GenBank at time of writing	Marnissi *et al.* 2021
Macrobiotus basiatus	USA/NEL/1	MT502116	MT498094	MT505165	MT488397	*Macrobiotus* sp. 1 DG-2020	temporary taxon name has not been updated in GenBank at time of writing	Nelson *et al.* 2020
Macrobiotus birendrai	CN8.101	MW656266	MW680641	MW680418	MW680644	*Macrobiotus birendrai*		Kayastha *et al.* 2021
Macrobiotus caelestis	KG.007	MK737922	MK737073	MK737072	MK737071	*Macrobiotus caelestis*		Coughlan *et al.* 2019
Macrobiotus canaricus	ES.004_H1	MH057765	MH063925	MH063928	MH063934	*Macrobiotus canaricus*		Stec *et al.* 2018c
Macrobiotus canaricus	ES.004_H2	MH057766				*Macrobiotus canaricus*		Stec *et al.* 2018c
Macrobiotus cf. *hufelandi*	C2959a	HQ876590		OP596303		*Macrobiotus* cf. *hufelandi* 1 MC-2011		Bertolani *et al.* 2011
Macrobiotus cf. *muralis*	C3251_2	OP561785	OP596299			*Macrobiotus* cf. *muralis*		Bertolani *et al.* 2023
Macrobiotus cf. *muralis*	C3251_3	OP561786	OP596300			*Macrobiotus* cf. *muralis*		Bertolani *et al.* 2023

Appendix 1 (continued).

Macrobiotus cf. *muralis*	C3251_4	OP561788				*Macrobiotus* cf. *muralis*		Bertolani *et al.* 2023
Macrobiotus cf. *muralis*	C3251_5	OP561789				*Macrobiotus* cf. *muralis*		Bertolani *et al.* 2023
Macrobiotus cf. *muralis*	C3251_FA	OP561787	OP596301			*Macrobiotus* cf. *muralis*		Bertolani *et al.* 2023
Macrobiotus cf. *nelsonae*	1		HQ604965			*Macrobiotus*		Bertolani *et al.* 2014
Macrobiotus cf. *recens*	ES.006 haplotype 1	MH057768	MH063927	MH063932	MH063936	*Macrobiotus* cf. *recens* DS-2018		Stec *et al.* 2018c
Macrobiotus cf. *sapiens*	S12.Mac.1	OK662997	OK663226	OK663215	OK663237	*Macrobiotus* cf. *sapiens*		Vecchi *et al.* 2022c
Macrobiotus cf. *shonaicus*	MM1-2018	LC431582		LC431591		*Macrobiotus* cf. *shonaicus*		Matsumoto & Sugiura (unpubl.)
Macrobiotus crustulus	GF.271	MT260371	MT261912	MT261907	MT261903	*Macrobiotus crustulus*		Stec *et al.* 2020a
Macrobiotus dolosus	C3209_2	OP561772	OP596290			*Macrobiotus dolosus*		Bertolani *et al.* 2023
Macrobiotus dolosus	C3209_4	OP561774				*Macrobiotus dolosus*		Bertolani *et al.* 2023
Macrobiotus dolosus	C3209_US2	OP561773				*Macrobiotus dolosus*		Bertolani *et al.* 2023
Macrobiotus dolosus	C3581_V6	OP561775	OP596292			*Macrobiotus dolosus*		Bertolani *et al.* 2023
Macrobiotus engbergi	haplotype 1	MN444824	MN443039	MN443036	MN443034	*Macrobiotus engbergi*		Vecchi *et al.* 2024b
Macrobiotus engbergi	haplotype 2	MN444825		MN443037		*Macrobiotus engbergi*		Vecchi *et al.* 2024b
Macrobiotus fontourai	C2861_5	OP561783	OP596295			*Macrobiotus fontourai*		Bertolani *et al.* 2023
Macrobiotus fontourai	C2861_US1	OP561784	OP596296			*Macrobiotus fontourai*		Bertolani *et al.* 2023
Macrobiotus glebkai	UA.003	MW246134	MW247177	MW247180	MW247176	*Macrobiotus glebkai*		Kiosya *et al.* 2021
Macrobiotus hannae	PL.010	MH057764	MH063922	MH063923	MH063924	*Macrobiotus hannae*		Nowak & Stec 2018
Macrobiotus hufelandi	C2953a	HQ876585	OP596302			*Macrobiotus hufelandi*		Bertolani *et al.* 2023
Macrobiotus hufelandi	S605.Mac.1	OK662992	OK663221	OK663210	OK663232	*Macrobiotus hufelandi*		Bertolani *et al.* 2023
Macrobiotus joannae	1		HQ604974			*Macrobiotus joannae*		Bertolani *et al.* 2014
Macrobiotus kamilae	IN.030 haplotype 1	MK737920	MK737070	MK737067	MK737064	*Macrobiotus kamilae*		Coughlan & Stec 2019
Macrobiotus kathyae	US.006.01	PP386934	PP391285	PP391289	PP391287	*Macrobiotus* sp. MV2024	temporary taxon name has not been updated in GenBank at time of writing	Massa & Vecchi 2024

Appendix 1 (continued).

Macrobiotus kathyae	US.006.02	PP386935	PP391286	PP391290	PP391288	*Macrobiotus* sp. MV2024	temporary taxon name has not been updated in GenBank at time of writing	Massa & Vecchi 2024
Macrobiotus kathyae	US.006.03	PP386932				*Macrobiotus* sp. MV2024	temporary taxon name has not been updated in GenBank at time of writing	Massa & Vecchi 2024
Macrobiotus kathyae	US.006.04	PP386933				*Macrobiotus* sp. MV2024	temporary taxon name has not been updated in GenBank at time of writing	Massa & Vecchi 2024
Macrobiotus kirghizicus	KG.062.01	MZ461002	MZ463666	MZ463659	MZ463672	*Macrobiotus kirghizicus*		Stec *et al.* 2022
Macrobiotus kosmali	M8.1	OP141639	OP142472	OP153786	OP143765	*Macrobiotus kosmali*		Kayastha *et al.* 2023a
Macrobiotus kristenseni	C3291_A02_V2	KC193573	KC193577			*Macrobiotus kristenseni*		Guidetti *et al.* 2013
Macrobiotus kyoukenus	C4313_US3	ON809462	ON818314	ON818301	ON818309	*Macrobiotus kyoukenus*		Cesari *et al.* 2022
Macrobiotus macrocalix	PL.110	MH057767	MH063926	MH063931	MH063935	*Macrobiotus macrocalix*		Stec *et al.* 2018c
Macrobiotus margoae	US.057	MN888315	MN888368	MN888340	MN888354	*Macrobiotus margoae*		Vecchi & Stec 2021
Macrobiotus margoae	US.057.1	MT807927	MT809072	MT809098	MT809084	*Macrobiotus margoae*		Stec *et al.* 2021b
Macrobiotus margoae	US.057.3	MT807928		MT809099		*Macrobiotus margoae*		Stec *et al.* 2021b
Macrobiotus mileri	IL.001.01	OR544397	OR543312	OR543316	OR543320	*Macrobiotus mileri*		Stec 2024
Macrobiotus mileri	IL.001.02	OR544398	OR543313	OR543317	OR543321	*Macrobiotus mileri*		Stec 2024
Macrobiotus mileri	IL.001.03	OR544399				*Macrobiotus mileri*		Stec 2024
Macrobiotus mileri	IL.001.04	OR544400				*Macrobiotus mileri*		Stec 2024
Macrobiotus noongaris	AU.031	MK737919	MK737069	MK737066	MK737063	*Macrobiotus noongaris*		Coughlan & Stec 2019
Macrobiotus ovovittatus	GL.001.01	OR544395	OR543311	OR543314	OR543318	*Macrobiotus ovovittatus*		Stec 2024
Macrobiotus pallarii	IT.337.1	MT807924	MT809069	MT809094	MT809081	*Macrobiotus pallarii*		Stec *et al.* 2021b
Macrobiotus pallarii	IT.337.2	MT807925	MT809070	MT809095	MT809082	*Macrobiotus pallarii*		Stec *et al.* 2021b
Macrobiotus pallarii	IT.337.3	MT807926	MT809071	MT809096	MT809083	*Macrobiotus pallarii*		Stec *et al.* 2021b
Macrobiotus papei	TZ.027	MH057763	MH063881	MH063921	MH063880	*Macrobiotus papei*		Stec *et al.* 2018b
Macrobiotus paulinae		KT951668	KT935502	KT935500		*Macrobiotus paulinae*		Stec *et al.* 2015

Appendix 1 (continued).

Macrobiotus polonicus	AT.002 haplotype 1	MN888317	MN888369	MN888337	MN888355	*Macrobiotus polonicus*	Vecchi & Stec 2021
Macrobiotus polonicus	AT.002 haplotype 2	MN888318		MN888338		*Macrobiotus polonicus*	Vecchi & Stec 2021
Macrobiotus polonicus	AT.002 haplotype 3	MN888319				*Macrobiotus polonicus*	Vecchi & Stec 2021
Macrobiotus polonicus	SK.003 haplotype 1	MN888320	MN888370	MN888334	MN888356	*Macrobiotus polonicus*	Vecchi & Stec 2021
Macrobiotus polonicus	SK.003 haplotype 2	MN888321		MN888333		*Macrobiotus polonicus*	Vecchi & Stec 2021
Macrobiotus polonicus	Mac_pol_S218_1	OQ968326				*Macrobiotus polonicus*	Vecchi *et al.* 2024b
Macrobiotus polypiformis	haplotype 1	KX810011	KX810008	KX810010	KX810009	*Macrobiotus polypiformis*	Roszkowska *et al.* 2017
Macrobiotus pseudopallarii	ME.007 haplotype 1	MN888316	MN888365	MN888336	MN888351	*Macrobiotus pseudopallarii*	Vecchi & Stec 2021
Macrobiotus pseudopallarii	ME.007.2	MT807920	MT809066		MT809078	*Macrobiotus pseudopallarii*	Stec *et al.* 2021b
Macrobiotus pseudopallarii	ME.007.3	MT807921	MT809067	MT809091	MT809079	*Macrobiotus pseudopallarii*	Stec *et al.* 2021b
Macrobiotus pseudopallarii	ME.007.4	MT807922	MT809068	MT809092	MT809080	*Macrobiotus pseudopallarii*	Stec *et al.* 2021b
Macrobiotus pseudopallarii	ME.007.5	MT807923		MT809093		*Macrobiotus pseudopallarii*	Stec *et al.* 2021b
Macrobiotus rebecchii	KG.001.01	OP477442	OP479887			*Macrobiotus rebecchii*	Stec 2022b
Macrobiotus ripperi	FI.066	MN888312	MN888366	MN888343	MN888352	*Macrobiotus ripperi*	Vecchi & Stec 2021
Macrobiotus ripperi	FI.066.2	MT807933	MT809076	MT809103	MT809089	*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	FI.066.3	MT807934		MT809104		*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	FI.066.4	MT807935		MT809105		*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	PL.015.1	MT807929	MT809074	MT809100	MT809086	*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	PL.015.2	MT807930		MT809101	MT809087	*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	PL.015.3	MT807931				*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus ripperi	PL.015.4	MT807932		MT809102		*Macrobiotus ripperi*	Stec *et al.* 2021b
Macrobiotus rybaki	GR.011.1	MW593931	MW588029	MW588022	MW588034	*Macrobiotus rybaki*	Vecchi & Stec 2021
Macrobiotus sandrae	C2945e	HQ876577				*Macrobiotus sandrae*	Bertolani *et al.* 2011
Macrobiotus sandrae	S859.Mac.1	OK662994	OK663223	OK663212	OK663234	*Macrobiotus sandrae*	Vecchi *et al.* 2022c
Macrobiotus sapiens			DQ839601	GQ403680		*Macrobiotus sapiens*	Schill *et al.* 2010
Macrobiotus scoticus		KY797267	KY797265	KY797268	KY797266	*Macrobiotus scoticus*	Stec *et al.* 2017

Appendix 1 (continued).

Macrobiotus scoticus	DK.056.1	OK662989	OK663217	OK663206	OK663228	*Macrobiotus scoticus*		Vecchi *et al.* 2022c
Macrobiotus shonaicus	haplotype 1	MG757136	MG757132	MG757134	MG757133	*Macrobiotus shonaicus*		Stec *et al.* 2018a
Macrobiotus siderophilus	C2796_2	OP561776	OP596293			*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFK	OP561777				*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFL	OP561778				*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFM	OP561779				*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFN	OP561780	OP596294			*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFO	OP561781				*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus siderophilus	C3282_UFP	OP561782				*Macrobiotus siderophilus*		Bertolani *et al.* 2023
Macrobiotus sottilei	PL.352	MW246133	MW247178	MW247179	MW247175	*Macrobiotus sottilei*		Kiosya *et al.* 2021
Macrobiotus sp.	DI02	OP684780		OP696675		*Macrobiotus* sp.		Amezcua-Martinez *et al.* (unpubl.)
Macrobiotus sp. 1 MC-2022d	UK12	OQ525891	OQ525899	OQ548104	OQ525904	*Macrobiotus* sp. 1 MC-2022d		Mioduchowsk *et al.* (unpubl.)
Macrobiotus sp. 1 MC-2022d	UK14	OQ525890	OQ525897		OQ525905	*Macrobiotus* sp. 1 MC-2022d		Mioduchowsk *et al.* (unpubl.)
Macrobiotus sp. 1 YW-2020	BN140005	MT863704	MT872214			*Macrobiotus* sp. 1 YW-2020		Wang (unpubl.)
Macrobiotus sp. 1 ZY-2020	HP1110201	MW187003	MW183923			*Macrobiotus* sp. 1 ZY-2020		Yuan *et al.* (unpubl.)
Macrobiotus sp. n. MM-2020	MAD967	MT246661	MT241900		MT241898	*Macrobiotus* sp. n. MM-2020		Kuzdrowska *et al.* (unpubl.)
Macrobiotus terminalis	C2868_N02	JN673959	OP596308			*Macrobiotus terminalis*		Cesari *et al.* 2011
Macrobiotus vattenrikense sp. nov	22-003	PX093655	PX093663	PX093644	PX093649		COI haplotype 3; 18S haplotype 1; ITS haplotype 1; 28S haplotype 1	this study
Macrobiotus vattenrikense sp. nov	22-004-1	PX093655					COI haplotype 3	this study
Macrobiotus vattenrikense sp. nov	22-017	PX093653		PX093644	PX093649		COI haplotype 1; ITS haplotype 1; 28S haplotype 1	this study

Appendix 1 (continued).

Macrobiotus vattenrikense sp. nov	22-101	PX093654	PX093664	PX093644	PX093650		COI haplotype 2; 18S haplotype 2; ITS haplotype 1; 28S haplotype 2	this study
Macrobiotus vladimiri	FI.068	MN888327	MN888375	MN888347	MN888360	*Macrobiotus vladimiri*		Vecchi & Stec 2021
Mesobiotus aradasi	KPRI-MF-1	MW727934	MW751962			*Mesobiotus* cf. *furciger*	see Vecchi *et al.* 2024a	Short *et al.* 2022
Mesobiotus aradasi	S1982.Meb.1	OQ928737	OQ933000	OQ940183	OQ932999	*Mesobiotus aradasi*		Vecchi *et al.* 2024a
Mesobiotus bockebodicus	22-044	PQ365775	PQ367888		PQ367894	*Mesobiotus* sp. 1 SA-2024a	temporary taxon name has not been updated in GenBank at time of writing	Atherton *et al.* 2025
Mesobiotus cf. barabanovi	KG.002	MN313170	MN310392	MN310390	MN310388	*Mesobiotus* cf. *barabanovi*		Kaczmarek *et al.* 2020a
Mesobiotus cf. *furciger*	AF01-MF-2	MW727944	MW751946			*Mesobiotus* cf. *furciger*		Short *et al.* 2022
Mesobiotus datanlanicus	VN.026	MK578905	MK584659	MK584657	MK584658	*Mesobiotus datanlanicus*		Stec 2019
Mesobiotus diegoi	ZA.001.02	OP143857	OP142526	OP142514	OP142520	*Mesobiotus diegoi*		Stec 2022a
Mesobiotus dilimanensis	PH.006	MN257047	MN257048	MN257050	MN257049	*Mesobiotus dilimanensis*		Itang *et al.* 2020
Mesobiotus efa	Lembolovo.DT262	OR803035	OR804457	OR805169	OR805135	*Mesobiotus* sp. 1 DVT-2023b	temporary taxon name has not been updated in GenBank at time of writing	Tumanov *et al.* 2024
Mesobiotus emiliae	22-046	PQ365768	PQ367886		PQ367892	*Mesobiotus emiliae*		Atherton *et al.* 2025
Mesobiotus ethiopicus	ET.004	MF678794	MF678793	MN122776	MF678792	*Mesobiotus ethiopicus*		Stec & Kristensen 2017
Mesobiotus fiedleri	MG.001	MH676056	MH681585	MH681724	MH681693	*Mesobiotus fiedleri*		Kaczmarek *et al.* 2020a
Mesobiotus furciger	Macro_06_313	MW727960	MW751939			*Mesobiotus furciger*		Short *et al.* 2022
Mesobiotus harmsworthi	haplotype 1	MH195150	MH197146	MH197154	MH197264	*Mesobiotus harmsworthi*		Kaczmarek *et al.* 2018
Mesobiotus hilariae	Novolazarevskaya_C_1	KT226108	KT226071			*Mesobiotus hilariae*		Vecchi *et al.* 2016
Mesobiotus huecoensis	S2027.4	OQ756247	OQ756248			*Mesobiotus huecoensis*		Vecchi *et al.* 2023
Mesobiotus imperialis	VN.061.01	OL311514	OL257855		OL257867	*Mesobiotus imperialis*		Stec 2021
Mesobiotus insanis		MF441491	MF441488	MF441490	MF441489	*Mesobiotus insanis*		Mapalo *et al.* 2017
Mesobiotus maklowiczi	ZA.002.01	OP143855	OP142525		OP142518	*Mesobiotus maklowiczi*		Stec 2022a

Appendix 1 (continued).

Mesobiotus mandalori	2.18.1.2	OP825090	OP829143	OP829058	OP829056	*Mesobiotus* sp. m MM-2022	temporary taxon name has not been updated in GenBank at time of writing	Erdmann *et al.* 2024
Mesobiotus mandalori	22-053	PQ365769	PQ367887		PQ367893	*Mesobiotus* sp. m MM-2022	temporary taxon name has not been updated in GenBank at time of writing	Atherton *et al.* 2025
Mesobiotus marmoreus	VN.055.01	OL311516	OL257856	OL257861	OL257868	*Mesobiotus marmoreus*		Stec 2022a
Mesobiotus occultatus	DT97	OR803042	OR794157	OR805249	OR794158	*Mesobiotus occultatus*		Tumanov *et al.* 2024
Mesobiotus peterseni	GL.002.01	OP143859	OP142528	OP142516	OP142522	*Mesobiotus peterseni*		Stec 2022a
Mesobiotus philippinicus		KX129796	KX129793	KX129795	KX129794	*Mesobiotus philippinicus*		Mapalo *et al.* 2016
Mesobiotus radiatus	KE.008	MH195147	MH197153	MH197267	MH197152	*Mesobiotus radiatus*		Stec *et al.* 2018d
Mesobiotus romani	EC.002	MH195149	MH197158	MH197150	MH197151	*Mesobiotus romani*		Roszkowska *et al.* 2018
Mesobiotus skanensis	22-153	PQ365777	PQ367889		PQ367895	*Mesobiotus* sp. 2 SA-2024a	temporary taxon name has not been updated in GenBank at time of writing	Atherton *et al.* 2025
Mesobiotus skorackii	CN8	MW656257	MW680643		MW680636	*Mesobiotus skorackii*		Kayastha *et al.* 2021
Mesobiotus sp.	BI02	OP684777		OP696672		*Mesobiotus* sp.		Amezcua-Martinez *et al.* (unpubl.)
Mesobiotus sp.	NO.234	MH195153	MH197148	MH197156	MH197265	*Mesobiotus furciger* group sp.		Kaczmarek *et al.* 2018
Mesobiotus sp.	RU.017	MH195154	MH197149	MH197157	MH197266	*Mesobiotus harmsworthi* group sp.		Kaczmarek *et al.* 2018
Mesobiotus sp. 1	DVT-2020	MT904513	MT903468	MT903470	MT903612	*Mesobiotus* sp. 1		Tumanov 2020
Mesobiotus sp. Fl	Mes_sp_S16_3	OQ968323	OQ974689	OQ974696	OQ974704	*Mesobiotus* sp. Fl		Vecchi *et al.* 2024b
Mesobiotus sp. VN	Mes_sp_ VN036_04	OQ968314	OQ974691			*Mesobiotus* sp. VN		Vecchi *et al.* 2024b
Mesobiotus vulpinus	DT553	OR803040	OR804461	OR805172	OR805140	*Mesobiotus* sp. 2 DVT-2023b	temporary taxon name has not been updated in GenBank at time of writing	Tumanov *et al.* 2024
Mesobiotus zelmae	22-239	PQ365781	PQ367891		PQ367896	*Mesobiotus* sp. 3 SA-2024a	temporary taxon name has not been updated in GenBank at time of writing	Atherton *et al.* 2025
Mesobiotus cf. *intermedius*	DT270	OP013287	OP035718	OP035707	OP035798	*Minibiotus* cf. *intermedius*		Tumanov *et al.* 2022

Appendix 1 (continued).

Minibiotus citlalium	AI04	OP684765		OP696660		*Minibiotus citlalium*		Amezcua-Martinez *et al.* (unpubl.)
Minibiotus furcatus	Tar527	FJ435802	FJ435746		FJ435760	*Minibiotus furcatus*		Guil & Giribet 2012
Minibiotus gumersindoi	Tar710	FJ435803	FJ435748		FJ435761	*Minibiotus gumersindoi*		Guil & Giribet 2012
Minibiotus intermedius	Min4 GR	ON005160	ON005189		ON005195	*Minibiotus intermedius*		Kaczmarek *et al.* 2022
Minibiotus ioculator	ZA.274	MT023412	MT023998	MT024000	MT024041	*Minibiotus ioculator*		Stec *et al.* 2020b
Minibiotus pentannulatus	TZ.027 haplotype 1	MT023413	MT023999	MT024001	MT024042	*Minibiotus pentannulatus*		Stec *et al.* 2020b
Minibiotus sidereus	AI12	OP684770		OP696665		*Minibiotus sidereus*		Amezcua-Martinez *et al.* (unpubl.)
Minibiotus sp. A MV2020	S69.Min.01	MW306859	OK663227	OK663216	OK663238	*Minibiotus* sp. A MV2020		Vecchi *et al.* 2022b
Paramacrobiotus marchelmoni sp. nov.	22-004	PX093656	PX093665	PX093646	PX093651		COI haplotype 1; 18S haplotype 1; ITS haplotype 2; 28S haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-006	PX093656	PX093665	PX093646			COI haplotype 1; 18S haplotype 1; ITS haplotype 2	this study
Paramacrobiotus marchelmoni sp. nov.	22-007	PX093656		PX093646			COI haplotype 1; ITS haplotype 2	this study
Paramacrobiotus marchelmoni sp. nov.	22-019	PX093656	PX093665	PX093646	PX093651		COI haplotype 1; 18S haplotype 1; ITS haplotype 2; 28S haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-026	PX093656					COI haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-029	PX093656		PX093645	PX093651		COI haplotype 1; 18S haplotype 1; 28S haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-034	PX093656	PX093665	PX093646			COI haplotype 1; 18S haplotype 1; ITS haplotype 2	this study
Paramacrobiotus marchelmoni sp. nov.	22-102	PX093656		PX093645			COI haplotype 1; ITS haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-106	PX093657					COI haplotype 2	this study

Appendix 1 (continued).

Paramacrobiotus marchelmoni sp. nov.	22-108	PX093656					COI haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-110	PX093657	PX093665	PX093646	PX093651		COI haplotype 2; 18S haplotype 1; ITS haplotype 2; 28S haplotype 1	this study
Paramacrobiotus marchelmoni sp. nov.	22-113	PX093657	PX093665	PX093646			COI haplotype 2; 18S haplotype 1; ITS haplotype 2	this study
Paramacrobiotus marchelmoni sp. nov.	23-015	PX093658					COI haplotype 3	this study
Paramacrobiotus marchelmoni sp. nov.	23-041	PX093657					COI haplotype 2	this study
Paramacrobiotus aff. *arduus*	PRODO-3	MK041022				*Paramacrobiotus* aff. *arduus*		Guidetti *et al.* 2019a
Paramacrobiotus aff. *spatialis*	OLBIA-1	MK041002	MK041026			*Paramacrobiotus* aff. *spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus arduus	PRODO-1	MK041020	MK041032			*Paramacrobiotus arduus*		Guidetti *et al.* 2019a
Paramacrobiotus arduus	PRODO-2	MK041021				*Paramacrobiotus arduus*		Guidetti *et al.* 2019a
Paramacrobiotus areolatus	NO.385	MH675998	MH664931	MH666080	MH664948	*Paramacrobiotus areolatus*		Stec *et al.* 2020c
Paramacrobiotus bifrons	C4497_US1	PP236542		PP240910		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	C4497_US2	PP236543		PP240911		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	C4497_US7	PP236544		PP240912		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	C4497_US8	PP236545		PP240913		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	C5025_US6	PP236551		PP240918		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	C5062_US2	PP236553		PP240919		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024

Appendix 1 (continued).

Paramacrobiotus bifrons	C5062_US3	PP236554		PP240920		*Paramacrobiotus* sp. 1 MC-2024a	temporary taxon name has not been updated in GenBank at time of writing	Brandoli *et al.* 2024
Paramacrobiotus bifrons	IT.048	MH676007	MH664937	MH666085	MH664955	*Paramacrobiotus* sp.	see Brandoli *et al.* 2024	Stec *et al.* 2020c
Paramacrobiotus bifrons	Par_cf_kly_ S108_2	OQ968322		OQ974697		*Paramacrobiotus* cf. klymenki	see Brandoli *et al.* 2024	Vecchi *et al.* 2024b
Paramacrobiotus celsus	PIANE_DI_ MOCOGNO-1	MK041017	MK041031			*Paramacrobiotus celsus*		Guidetti *et al.* 2019a
Paramacrobiotus celsus	PIANE_DI_ MOCOGNO-2	MK041018				*Paramacrobiotus celsus*		Guidetti *et al.* 2019a
Paramacrobiotus celsus	PIANE_DI_ MOCOGNO-3	MK041019				*Paramacrobiotus celsus*		Guidetti *et al.* 2019a
Paramacrobiotus danielae	GY26001		MZ081363	MZ081364		*Paramacrobiotus danielae*		Wang *et al.* (unpubl.)
Paramacrobiotus depressus	ANDALO-1	MK041015				*Paramacrobiotus depressus*		Guidetti *et al.* 2019a
Paramacrobiotus depressus	OSPITALETTO_ A-1	MK041016				*Paramacrobiotus depressus*		Guidetti *et al.* 2019a
Paramacrobiotus depressus	PASSO_ BALLINO-1	MK041012	MK041030			*Paramacrobiotus depressus*		Guidetti *et al.* 2019a
Paramacrobiotus depressus	PASSO_ BALLINO-2	MK041013				*Paramacrobiotus depressus*		Guidetti *et al.* 2019a
Paramacrobiotus depressus	PASSO_ BALLINO-3	MK041014				*Paramacrobiotus depressus*		Guidetti *et al.* 2019a
Paramacrobiotus experimentalis	MAD-TAR11	MN097837		MN073464	MN073465	*Paramacrobiotus experimentalis*		Kaczmarek *et al.* 2020c
Paramacrobiotus fairbanksi	22-423	PX093660	PX093666			*Paramacrobiotus fairbanksi*		this study
Paramacrobiotus fairbanksi	23-022	PX093661				*Paramacrobiotus fairbanksi*		this study
Paramacrobiotus fairbanksi	23-041	PX093659	PX093666	PX093647	PX093648	*Paramacrobiotus fairbanksi*		this study
Paramacrobiotus fairbanksi	Alb1	ON911918				*Paramacrobiotus fairbanksi*		Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	Alb4	ON911917				*Paramacrobiotus fairbanksi*		Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	C2345-MR_2	AY598778				*Macrobiotus richtersi*		Guidetti *et al.* 2005
Paramacrobiotus fairbanksi	C2345-MR_3	AY598779				*Macrobiotus richtersi*		Guidetti *et al.* 2005

Appendix 1 (continued).

Paramacrobiotus fairbanksi	CN8.2	ON911919	ON872387		ON872382	*Paramacrobiotus fairbanksi*	Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	DT174	OP013289		OP035709		*Paramacrobiotus fairbanksi*	Tumanov *et al.* 2022
Paramacrobiotus fairbanksi	DT175	OP013290		OP035710		*Paramacrobiotus fairbanksi*	Tumanov *et al.* 2022
Paramacrobiotus fairbanksi	DT176			OP035711		*Paramacrobiotus fairbanksi*	Tumanov *et al.* 2022
Paramacrobiotus fairbanksi	DT177	OP013291		OP035712		*Paramacrobiotus fairbanksi*	Tumanov *et al.* 2022
Paramacrobiotus fairbanksi	DT181			OP035713		*Paramacrobiotus fairbanksi*	Tumanov *et al.* 2022
Paramacrobiotus fairbanksi	M85.11	ON911920				*Paramacrobiotus fairbanksi*	Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	M85.12	ON911921			ON872383	*Paramacrobiotus fairbanksi*	Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	MN0101	ON911923	ON872389		ON872384	*Paramacrobiotus fairbanksi*	Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	MN0103	ON911922			ON872385	*Paramacrobiotus fairbanksi*	Mioduchowsk *et al.* (unpubl.)
Paramacrobiotus fairbanksi	OSPITALETTO_B-1	MK041011				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	Par_fai_S09_I14	OQ968319				*Paramacrobiotus fairbanksi*	Vecchi *et al.* 2024b
Paramacrobiotus fairbanksi	Par_fai_S42_3	OQ968318				*Paramacrobiotus fairbanksi*	Vecchi *et al.* 2024b
Paramacrobiotus fairbanksi	Par_fai_S85_1	OQ968320				*Paramacrobiotus fairbanksi*	Vecchi *et al.* 2024b
Paramacrobiotus fairbanksi	Par10eggs_ATN7_1	MN964281	MN960302		MN960306	*Paramacrobiotus fairbanksi*	Kaczmarek *et al.* 2020b
Paramacrobiotus fairbanksi	Par10eggs_ATN7_2	MN964282	MN960303		MN960307	*Paramacrobiotus fairbanksi*	Kaczmarek *et al.* 2020b
Paramacrobiotus fairbanksi	Par11eggs_ATN7_1	MN961616	MN960304			*Paramacrobiotus fairbanksi*	Kaczmarek *et al.* 2020b
Paramacrobiotus fairbanksi	PL.018	MH676011	MH664941	MH666090	MH664950	*Paramacrobiotus fairbanksi*	Stec *et al.* 2020c
Paramacrobiotus fairbanksi	PL.035	MH676012	MH664942	MH666091	MH664959	*Paramacrobiotus fairbanksi*	Stec *et al.* 2020c
Paramacrobiotus fairbanksi	PONDEL-1	MK041009	MK041029			*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	PONDEL-2	MK041010				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	RICCO-1	MK041003				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a

Appendix 1 (continued).

Paramacrobiotus fairbanksi	RICCO-2	MK041004				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	RICCO-3	MK041005	MK041027			*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	ROCCHETTA-1	MK041006				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	ROCCHETTA-2	MK041007	MK041028			*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus fairbanksi	ROCCHETTA-3	MK041008				*Paramacrobiotus fairbanksi*	Guidetti *et al.* 2019a
Paramacrobiotus filipi	MY.098 haplotype 1	MT260372	MT261913		MT261904	*Paramacrobiotus filipi*	Stec *et al.* 2020a
Paramacrobiotus filipi	MY.098 haplotype 2	MT260373				*Paramacrobiotus filipi*	Stec *et al.* 2020a
Paramacrobiotus gadabouti	MD50.1	OP394113	OP394210			*Paramacrobiotus gadabouti*	Kayastha *et al.* 2023b
Paramacrobiotus gadabouti	MD50.4	OP394114	OP394212			*Paramacrobiotus gadabouti*	Kayastha *et al.* 2023b
Paramacrobiotus lachowskae		MF568534	MF568532	MF568535	MF568533	*Paramacrobiotus lachowskae*	Stec *et al.* 2018e
Paramacrobiotus metropolitanus	Keio	LC649796		LC649794	LC649797	*Paramacrobiotus metropolitanus*	Sugiura *et al.* 2022
Paramacrobiotus richtersi	CLARE_ ISLAND-1	MK040992	MK041023			*Paramacrobiotus richtersi*	Guidetti *et al.* 2019a
Paramacrobiotus richtersi	CLARE_ ISLAND-2	MK040993				*Paramacrobiotus richtersi*	Guidetti *et al.* 2019a
Paramacrobiotus richtersi	CLARE_ ISLAND-3	MK040994				*Paramacrobiotus richtersi*	Guidetti *et al.* 2019a
Paramacrobiotus richtersi	Par_ric_S1868_1	OQ968324				*Paramacrobiotus richtersi*	Vecchi *et al.* 2024b
Paramacrobiotus richtersi	S38.Par.1	OK662995	OK663224	OK663213	OK663235	*Paramacrobiotus richtersi*	Vecchi *et al.* 2022c
Paramacrobiotus sp.	AU.044	MH675999	MH664932	MH666081	MH664949	*Paramacrobiotus* sp.	Stec *et al.* 2020c
Paramacrobiotus sp.	BR.009	MH676000	MH664934	MH666082	MH664952	*Paramacrobiotus* sp.	Stec *et al.* 2020c
Paramacrobiotus sp.	FR.077	MH676003	MH664935	MH666083	MH664953	*Paramacrobiotus* sp.	Stec *et al.* 2020c
Paramacrobiotus sp.	Group 3		EU038081	GQ403678		*Paramacrobiotus richtersi* group	Guidetti *et al.* 2009
Paramacrobiotus sp.	HU.012 haplotype 1	MH676005	MH664936	MH666084	MH664954	*Paramacrobiotus* sp.	Stec *et al.* 2020c
Paramacrobiotus sp.	HU.012 haplotype 2	MH676006				*Paramacrobiotus* sp.	Stec *et al.* 2020c
Paramacrobiotus sp.	Kenya 2	EU244598				*Paramacrobiotus* sp. ‘*richtersi*’ group	Schill *et al.* 2010

Appendix 1 (continued).

Paramacrobiotus sp.	Kenya 3	EU244599				*Paramacrobiotus* sp. '*richtersi*' group		Schill *et al.* 2010
Paramacrobiotus sp.	MG.002	MH676008	MH664938	MH666086	MH664956	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	NO.386	MH676009	MH664939	MH666088	MH664957	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	NZ.001	MH676010	MH664940	MH666089	MH664958	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	Par_sp_S175_2	OQ968321				*Paramacrobiotus* sp.		Vecchi *et al.* 2024b
Paramacrobiotus sp.	PT.006	MH676013	MH664943	MH666092	MH664960	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	PT.048 haplotype 1	MH676014	MH664944	MH666093	MH664961	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	PT.048 haplotype 2	MH676015				*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	T3	OP531839	ON923868			*Paramacrobiotus* sp.		Basu *et al.* 2023
Paramacrobiotus sp.	Tar407	FJ435807	FJ435741		FJ435756	*Macrobiotus pallarii*	see Discussion	Guil & Giribet 2012
Paramacrobiotus sp.	TN.014	MH676016	MH664945	MH666094	MH664962	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp.	TZ.018	MH676017	MH664933	MH666095	MH664951	*Paramacrobiotus* sp.		Stec *et al.* 2020c
Paramacrobiotus sp. DLS-2024a	T82_S135	PP414782	PP416751	PP416753	PP416752	*Paramacrobiotus* sp. DLS-2024a		López-Sandoval *et al.* 2025
Paramacrobiotus sp. MAC-2014	T1	KF788251				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T2	KF788252				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T3	KF788253				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T4	KF788254				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T6	KF788255				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T7	KF788256				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. MAC-2014	T8	KF788257				*Paramacrobiotus richtersi* group sp. 1 MAC-2014		Caicedo *et al.* 2017
Paramacrobiotus sp. ZY-2020	hp1100404	MT731035	MT723894			*Paramacrobiotus* sp. ZY-2020		Yuan *et al.* (unpubl.)
Paramacrobiotus sp. ZY-2022c	N3	OP870172			ON819001	*Paramacrobiotus* sp. ZY-2022c		Yuan *et al.* (unpubl.)

Appendix 1 (continued).

Paramacrobiotus spatialis	FORMIGINE-1	MK040995	MK041024			*Paramacrobiotus spatialis*		Guidetti *et al.* 2009
Paramacrobiotus spatialis	FORMIGINE-2	MK040996				*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	FORMIGINE-3	MK040997				*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	FORMIGINE-4	MK040998				*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	GAGGIO-1	MK040999				*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	GAGGIO-2	MK041000				*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	GAGGIO-3	MK041001	MK041025			*Paramacrobiotus spatialis*		Guidetti *et al.* 2019a
Paramacrobiotus spatialis	S107.Par	OK662996	OK663225	OK663214	OK663236	*Paramacrobiotus spatialis*		Vecchi *et al.* 2022c
Paramacrobiotus tonollii	US.035	MH676018	MH664946	MH666096	MH664963	*Paramacrobiotus tonollii*		Stec *et al.* 2020c
Richtersius coronifer	NO.385	MH676053	MH681760	MH681763	MH681757	*Richtersius coronifer*		Stec *et al.* 2020c
Sisubiotus hakaiensis	Sis.hak.S1911	OM523181	OM523054	OM523057	OM523059	*Sisubiotus hakaiensis*		Vecchi *et al.* 2022a
Sisubiotus spectabilis	FI.067	MN888322	MN888371	MN888331	MN888357	*Sisubiotus spectabilis*		Stec *et al.* 2021a
Tenuibiotus cf. ciprianoi	ES.086	MN888328	MN888376	MN888348	MN888361	*Tenuibiotus* cf. *ciprianoi*		Stec *et al.* 2021a
Tenuibiotus danilovi	KG.128	MN888329	MN888377	MN888349	MN888362	*Tenuibiotus danilovi*		Stec *et al.* 2021a
Tenuibiotus sp.	22-109	PX093662	PX093667		PX093652	*Tenuibiotus* sp.		this study
Tenuibiotus tenuiformis	KG.140	MN888330	MN888378	MN888350	MN888363	*Tenuibiotus tenuiformis*		Stec *et al.* 2021a
Tenuibiotus voronkovi	haplotype 1	KX810042	KX810045	KX810046	KX810049	*Tenuibiotus voronkovi*		Zawierucha *et al.* 2016
Tenuibiotus yeliseii	DT422	OR145334	OR142418	OR142424	OR142426	*Tenuibiotus* sp. 1 DVT-2023a	temporary taxon name has not been updated in GenBank at time of writing	Tsvetkova & Tumanov 2024
Tenuibiotus zandrae		MN444827	MN443040	MN443038	MN443035	*Tenuibiotus zandrae*		Stec *et al.* 2020c
Xerobiotus arenosum	C4411_V4	OR397039	OR398024		OR398050	*Xerobiotus arenosum*		Vincenzi *et al.* 2024
Xerobiotus cf. *reductus*	PL3177_1	OR397050	OR398033		OR398056	*Xerobiotus* cf. *reductus*		Vincenzi *et al.* 2024
Xerobiotus euxinus	check 1.4	PP469626	PP439986	PP470593	PP440001	*Macrobiotus euxinus*	see Vincenzi *et al.* 2024	Polishchuk *et al.* 2024
Xerobiotus euxinus	C3834_V4	OR397005	OR398005		OR398119	*Macrobiotus euxinus*	see Vincenzi *et al.* 2024	Vincenzi *et al.* 2024
Xerobiotus gretae	C4341 G	MW581665	MW588434	MW588431	MW588438	*Macrobiotus gretae*	see Vincenzi *et al.* 2024	Massa *et al.* 2021
Xerobiotus litus	C4383_2	OR397000	OR398002		OR398118	*Xerobiotus litus*		Vincenzi *et al.* 2024

Appendix 1 (continued).

Xerobiotus naginae	S226.Mac.1	OK662990	OK663219		OK663230	*Marobiotus naginae*	see Vincenzi *et al.* 2024	Vecchi *et al.* 2022c
Xerobiotus pseudohufelandi	C2358-XP1	AY598776	HQ604989			*Xerobiotus pseudohufelandi*		Guidetti *et al.* 2005
Xerobiotus reductus	PL_3176_1	OR397048	OR398028		OR398130	*Xerobiotus reductus*		Vincenzi *et al.* 2024
Xerobiotus sp.	PL.360	MN888325	MN888373	MN888345	MN888358	*Xerobiotus* sp.		Vecchi & Stec 2021
Xerobiotus sp.	ZA.373	MN888326	MN888374	MN888346	MN888359	*Xerobiotus* sp.		Vecchi & Stec 2021
Xerobiotus sp. 1 MC-2023a	C3306_V1	OR397025	OR398020		OR398123	*Xerobiotus* sp. 1 MC-2023a		Vincenzi *et al.* 2024